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Editorial

What is the parietal lobe contribution to human memory?

Among the benefits to have emerged with the advent of functional neuroimaging has been the possibility of detecting regions of the brain that are engaged during cognitive processing, but whose involvement had previously remained relatively unappreciated by researchers who had to rely solely on evidence from lesion studies. For example, many years of neuropsychological investigation concentrated on the medial temporal lobe as being the most critical area for memory function, on the basis of the severe memory impairments reported in patients like HM (Scoville & Milner, 1957). The importance of the roles played by other brain regions, such as prefrontal cortex, in the encoding and retrieval of mnemonic information was, with a few exceptions (e.g., Janowsky, Shimamura, & Squire, 1989), underemphasized until the publication of innovative neuroimaging studies in the 1990s. Taking prefrontal cortex as an example, these studies highlighted that ventrolateral and dorsolateral frontal regions are involved in the elaboration and organization of to-be-remembered material during encoding, as well as the maintenance and monitoring of recovered information during retrieval (see Fletcher & Henson, 2001; Simons & Spiers, 2003, for reviews). With the development of more sophisticated methods of localizing structural brain lesions anatomically, neuropsychological studies motivated by the functional imaging data have subsequently provided valuable converging evidence about the necessity of these prefrontal regions for accurate memory (e.g., Alexander, Stuss, & Fansabedian, 2003; Duarte, Ranganath, & Knight, 2005).

Another brain region whose apparently key role in memory has only been revealed by functional neuroimaging is lateral parietal cortex. As noted in recent reviews (e.g., Rugg, Otten, & Henson, 2002; Wagner, Shannon, Kahn, & Buckner, 2005), several studies in the mid-1990s reported greater activity in lateral and medial parietal cortex during blocks of memory trials than during other conditions. With the development of event-related methods to distinguish activity associated with different intermixed trial-types, activation in parietal regions was observed in a number of studies that compared correctly recognized previously encountered “old” items with correctly rejected non-presented “new” items, suggesting a role in operations contributing to successful retrieval (e.g., Konishi, Wheeler, Donaldson, & Buckner, 2000). A further common finding has been greater activation in parietal cortex when recognition is accompanied by retrieval of details concerning the context in which old items were previously encountered (using either remember/know or source memory tests), suggesting that the region may be particularly important for conscious recollection (e.g., Henson, Rugg, Shallice, Josephs, & Dolan, 1999). Indeed, as has been noted previously (Simons et al., 2008), neuroimaging studies of recollection that reported whole-brain results have more frequently observed activity in lateral parietal cortex than in other brain areas that are generally considered more important for memory, such as frontal, midline diencephalic, and medial temporal lobe regions.

On the basis of the neuroimaging findings, a number of suggestions have been made as to the functional contribution that lateral parietal cortex might make to memory. For instance, in their comprehensive review, Wagner et al. (2005) considered three possible hypotheses. The first of these was the *attention to internal representations hypothesis*, which proposed that parietal cortex may direct attention towards particular aspects of internally generated mnemonic representations. The second, the *mnemonic accumulator hypothesis*, postulates that activity in parietal regions may reflect a memory strength signal that can be used to guide behavioral responses in relation to a decision criterion. The third possible hypothesis proposed was the *output buffer hypothesis*, according to which parietal cortex acts as a temporary storage buffer in which information retrieved from long-term memory can be maintained in a form accessible to decision-making processes. As noted by Wagner et al., the extant neuroimaging data appear to be partly, but not completely, explained by each of the three proposed hypotheses. For example, the attention to internal representations hypothesis cannot easily account for the retrieval success effects that have often been observed. The mnemonic accumulator hypothesis assumes a unitary memory strength signal (consistent with some views; Wixted, 2007), rather than the alternative theoretical perspective of independent familiarity and recollection processes that has informed the design (and interpretation of the data) of most neuroimaging studies to date. However, it is conceivable that familiarity and recollection depend on independent non-lateral parietal processes, but that these two kinds of memory share a common lateral parietal mechanism that generates a memory strength signal. Finally, the output buffer hypothesis cannot readily explain observations of parietal activity that correlates with the subjective perception that an item had been encountered previously, irrespective of its true status (Wheeler & Buckner, 2003).

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The consistency with which neuroimaging studies of memory have observed activity in lateral parietal cortex has been a surprise to many neuropsychology researchers because it contradicts the prevailing view from clinical studies that these regions of the parietal lobe do not play a necessary role in memory function. This is in contrast to medial parietal regions, damage to which is well known to result in amnesia (Cavanna & Trimble, 2006; Valenstein et al., 1987). Instead, studies of patients with lateral parietal lobe damage have almost universally focused on the difficulties such patients tend to experience with visual and spatial attention, or with visually guided action (e.g., Mesulam, 1999; Milner & Goodale, 1995). Although memory impairments in patients with lateral parietal lobe lesions are not routinely reported, the neuroimaging results raise the possibility that these patients may nonetheless have subtle memory deficits that are not picked up using standard neuropsychological tests, but which may nonetheless impact on the patients' functioning. This issue recently began to be addressed by a study that used neuroimaging and neuropsychological approaches to determine whether the same regions of the parietal lobe that are activated during recollection are indeed necessary for accurate remembering to occur (Simons et al., 2008). Using a source memory task similar to those employed in many previous neuroimaging studies, the authors confirmed that significant activity was observed in lateral parietal cortex when healthy volunteers correctly recollected the context in which items were previously encountered. Patients with unilateral parietal lobe lesions that overlapped closely with the regions activated in the healthy volunteers were, however, not significantly impaired when undertaking the same source memory task. These data, along with others demonstrating that patients with bilateral parietal lesions are not apparently amnesic (although they may produce diminished detail in spontaneous autobiographical recollections; Berryhill, Phuong, Picasso, Cabeza, & Olson, 2007), further constrain possible accounts of the parietal lobe contribution to memory.

The recent patient results provide a challenge to researchers seeking to understand the role played by parietal cortex in human memory. On the one hand, the abundant evidence from neuroimaging studies suggests that parietal regions support processes that tend to be extensively engaged during memory performance. On the other hand, the neuropsychological data suggest that these processes, whatever they may be, might not be so critical to performance that circumscribed parietal lobe lesions produce the severe kinds of debilitating memory failures that are characteristic of amnesia. The goal of devising a theoretical explanation that takes account of both neuroimaging and neuropsychology data has been the motivation for a number of the papers contained in this Special Section. Contributed by leading researchers in the field of human memory, the papers provide an overview of the current state of the art in parietal lobe memory research, combining theoretical appraisals with reports of novel empirical findings from converging methods including neuroimaging, electrophysiology, and neuropsychology.

The first paper in the Special Section, by Davidson and colleagues, extends the neuropsychological studies of long-term memory performance following lateral parietal lesions mentioned above. Consistent with the findings of Simons et al. (2008), patients with focal unilateral parietal lobe damage performed normally at recall and source recollection of previously presented word-definition pairings, although they were impaired when asked to make remember/know judgments about their subjective experience of remembering the pairings. Davidson et al. also tested retrieval of remote autobiographical memories in their patients, observing normal levels of "remember" judgments in this retrograde domain, but reduced levels of detail in the patients' autobiographical narratives, consistent with the results of Berryhill et al. (2007). Further assessment of one of the patients suggested that she had reduced confidence in her memory, and that her subjective experience of her memories was that they lacked richness or vividness. It may be that the impaired *subjective experience of memory* reported by this patient explains the discrepancy observed in Davidson et al.'s data between reduced "remember" judgments (based primarily on subjective recollection) and preserved source memory (a more objective means of assessing recollection; Perfect, Mayes, Downes, & Van Eijk, 1996).

Further investigation of the effects of lateral parietal lesions on memory are provided in the papers by Haramati and colleagues, and by Berryhill and Olson. Haramati et al. examined performance of patients with extensive left or right unilateral parietal lobe damage on recognition memory for visually presented words and objects and for auditorily presented environmental sounds. Patients with left parietal lobe lesions performed normally on all the recognition memory tasks, whereas patients with right-sided damage exhibited impairments in recognition of objects and sounds that further analysis linked to extra-parietal damage. On the basis of these results, the authors concluded that parietal lobe damage does not impair recognition memory and that, of the three possible accounts proposed by Wagner et al. (2005), the *output buffer hypothesis*, linking parietal cortex with working memory processes, may fit the available data best. Consistent with this view, the papers in this issue by Berryhill and Olson provide persuasive evidence that parietal lobe damage results in working memory impairments. In their first paper, Berryhill and Olson demonstrate that patients with unilateral right parietal lobe lesions were significantly impaired on visual working memory tasks involving short-term retention of spatial location and stimulus identity for colors, shapes, and common objects. Berryhill and Olson's second paper extends this work to patients with bilateral parietal lobe damage, reporting significant deficits in short-term recognition of the order in which stimuli had been presented. Strikingly, Berryhill and Olson found the recognition deficits more severe than cued recall deficits, contrary to what is sometimes reported in hippocampal amnesia (e.g., Mayes, Holdstock, Isaac, Hunkin, & Roberts, 2002) and some evidence that these deficits may have affected long-term as well as working memory. If replicable, this detailed pattern of findings presents a challenge to current accounts of lateral parietal memory functions.

The next paper in the Special Section, by Vilberg and Rugg, provides an informative meta-analysis of findings from the neuroimaging literature relating to the retrieval of information from long-term memory. The results of this analysis support previous suggestions that there may be a functional distinction between superior and inferior regions of lateral parietal cortex. Vilberg and Rugg propose that superior parietal cortex activity may depend on the task-relevance of stimuli rather than reflecting a role in memory specifically, because, for example, the same region is activated during detection of ‘oddball’ stimuli in a sequence of distracters and, during a recognition memory task, activity is sensitive to the proportion of old and new items. Vilberg and Rugg’s meta-analysis links inferior parietal cortex directly with a role in the successful recollection of the context in which stimuli were previously encountered, on the basis of observations, for instance, that inferior parietal regions are sensitive to the amount of information recollected, but are insensitive to the old/new ratio of test items, and because activity associated with old items is observed irrespective of whether participants are instructed to respond to old or new items, or both. Similar to the accounts by Haramati et al. and Berryhill and Olson noted above, Vilberg and Rugg interpret their data as favoring a variant of the output buffer hypothesis, proposing that inferior parietal cortex forms part of a cortical network supporting a multi-modal *episodic buffer* (Baddeley, 2000). According to Baddeley’s conception, the episodic buffer acts as an interface between long-term memory and the central executive, storing retrieved information temporarily in an integrated, multi-modal form accessible to decision-making processes. Such an interpretation might account for the apparent insensitivity of inferior parietal activity, observed in Vilberg and Rugg’s meta-analysis, to whether recollected stimuli were verbal (e.g., words) or non-verbal (e.g., objects) (although this has rarely been tested directly; see Simons et al., 2008).

A prediction of the episodic buffer account is examined by Ally and colleagues in their paper in the Special Section. The authors obtained event-related potentials (ERPs) during a recognition memory task in which test stimuli (pictures of common objects) were presented either in the same viewpoint as during the prior study phase, or in rotated or non-canonical viewpoints. Demands on an episodic buffer would be expected to increase along with the amount of mental imagery transformation required to match the perceived test object with those represented in long-term memory. However, Ally et al. observed that the duration of the parietal ERP signal associated with successful recognition memory was longer in the same viewpoint condition than in the other conditions, conflicting with the episodic buffer hypothesis of parietal function. ERP data was also acquired from a patient with unilateral parietal lobe damage who performed normally on the same recognition memory task, showing reduced parietal activity but enhanced activity over frontal electrodes relative to controls. Data from one patient must be treated with caution, but this latter finding might suggest that intact recognition and recollection after parietal lesions may be observed because patients recruit frontally mediated compensatory mechanisms to support their accurate memory performance. Ally et al. cite anecdotal evidence that patients with parietal lesions sometimes report a lack of vividness and low confidence in their memories. Echoing the suggestion made by Davidson et al. (this issue), Ally and colleagues propose that the parietal activity observed in their ERP data, and that typically seen in neuroimaging experiments, may reflect the *subjective experience of recollection*. Such an explanation, they argue, might account both for the available neuroimaging data and for the findings that parietal patients produce impoverished spontaneous autobiographical recollections but are typically unimpaired on more objective recollection tasks.

A different interpretation of the data is offered by Cabeza in his paper in the Special Section. Cabeza considers the episodic buffer account proposed by Vilberg and Rugg, but notes previous neuroimaging evidence associating an integrative, multi-modal working memory system akin to the episodic buffer with right prefrontal cortex and linking parietal cortex with material-specific working memory systems (Prabhakaran, Narayanan, Zhao, & Gabrieli, 2000). Instead, Cabeza proposes a *dual attentional processes hypothesis* to explain the episodic memory data, drawing on previous theories of attention (e.g., Corbetta & Shulman, 2002) to suggest that dorsal parietal cortex supports top-down attentional processes guided by retrieval goals, whereas ventral parietal cortex subserves bottom-up attentional processes captured by retrieval output. Note that the anatomical labels “dorsal” and “ventral” used by Cabeza correspond more-or-less to the “superior” and “inferior” parietal regions identified by Vilberg and Rugg. Cabeza argues that the dual attentional hypothesis can accommodate more of the previous neuroimaging findings than the other proposed accounts. For example, Cabeza cites observations of greater activity in dorsal parietal cortex for correct recognition responses accompanied by low rather than high confidence, consistent with a role in the goal-directed top-down attentional processes likely to increase as a function of retrieval effort. By contrast, ventral parietal cortex showed the opposite pattern, consistent in Cabeza’s view with stronger capture of bottom-up attention by relevant stimuli when memory performance is high. As well as accounting for other findings in the neuroimaging literature, Cabeza argues that the reduced levels of detail in spontaneous (but not cued) autobiographical recollections observed in patients with parietal lesions are consistent with the dual attentional hypothesis. According to this interpretation, the patients’ reduced spontaneous detail might be attributed to a deficit in the capture of bottom-up attention by mnemonic representations, whereas the patients’ ability to access memory details when asked specific questions about them might, in Cabeza’s view, suggest that top-down attentional processes are intact.

Support for the idea that superior and inferior parietal cortex might subserve top-down and bottom-up attentional control of memory, respectively, comes from the final paper in the Special Section, by Ciaramelli et al. These authors review a large number of studies from the previous neuroimaging literature and identify that activation in superior parietal cortex is consistently observed when the allocation of top-down resources to memory retrieval might be considered to be maximal, such as when correct recognition responses are accompanied by low confidence, when responses are associated with familiarity rather than recollection, and for recognition of high rather than low frequency words. Conversely, Ciaramelli et al. argue that activity in inferior parietal cortex tends to be observed when the bottom-up attentional capture by retrieved information is maximal, such as when memories are retrieved with high confidence, when responses are associated with vivid recollection, and when deep encoding conditions are used to promote high memory strength. On the basis of these findings, Ciaramelli et al. propose a two process *attention to memory hypothesis*, similar to Cabeza's account in this issue, according to which superior parietal cortex participates, as part of a prefrontal network, in strategic pre-retrieval operations and post-retrieval monitoring processes, whereas inferior parietal cortex subserves more automatic, mnemonic detection processes. Ciaramelli et al. argue that their hypothesis can account for the findings of all the neuroimaging experiments they reviewed, as well as the data from patients with parietal lobe lesions on tests of objective and subjective recollection, and thus provides a fuller explanation than the competing proposals.

This Special Section offers examples of the rapidly growing body of research seeking to understand the nature of the parietal lobe contribution to memory. As is evidenced from this brief overview, the precise role played by lateral parietal cortex in memory function is still up for grabs, but it seems certain that the hypothesis that eventually gains the most support (whether it is one described here or one still to be conceived) must be capable of explaining the data from neuroimaging *and* neuropsychology. Identifying this hypothesis will not be easy, for several reasons. First, predicting effects of lateral parietal lesions will be tricky if functional re-organization can occur, as Ally et al.'s preliminary findings suggest (perhaps effects of transcranial magnetic stimulation will be less subject to functional re-organization). Second, lateral parietal lesions are rarely, if ever, selective so use of large numbers of patients with sophisticated imaging and measurement procedures will be needed to discriminate between hypotheses proposing different inferior/superior functional differences. Third, the extent to which current hypotheses are incompatible with each other needs clarification. Even if the different hypotheses make clearly distinct predictions, the possibility that there is more than one kind of lateral parietal function (for example, different kinds of mnemonically directed attention as well as kinds of working memory) will need to be taken into account. However, it is clear from the work in this Special Section that rapid progress is being made in addressing these issues. A research topic that was largely undiscovered a few years ago has become a major focus for cognitive neuroscience investigators in laboratories around the world. One of the attractions of the topic may be that it provides an illustration of how cognitive neuroscience has matured from a field that might in the past have been fascinated by one experimental method or another, to a scientific discipline that recognizes that a full understanding of how cognitive operations are organized in the brain requires convergence across all available experimental techniques.

References

Alexander, M. P., Stuss, D. T., & Fansabedian, N. (2003). California Verbal Learning Test: Performance by patients with focal frontal and non-frontal lesions. *Brain*, *126*, 1493–1503.

Baddeley, A. D. (2000). The episodic buffer: A new component of working memory? *Trends in Cognitive Sciences*, *4*, 417–423.

Berryhill, M. E., Phuong, L., Picasso, L., Cabeza, R., & Olson, I. R. (2007). Parietal lobe and episodic memory: Bilateral damage causes impaired free recall of autobiographical memory. *Journal of Neuroscience*, *27*, 14415–14423.

Cavanna, A. E., & Trimble, M. R. (2006). The precuneus: A review of its functional anatomy and behavioural correlates. *Brain*, *129*, 564–583.

Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, *3*, 201–215.

Duarte, A., Ranganath, C., & Knight, R. T. (2005). Effects of unilateral prefrontal lesions on familiarity, recollection, and source memory. *Journal of Neuroscience*, *25*, 8333–8337.

Fletcher, P. C., & Henson, R. N. A. (2001). Frontal lobes and human memory: Insights from functional neuroimaging. *Brain*, *124*, 849–881.

Henson, R. N. A., Rugg, M. D., Shallice, T., Josephs, O., & Dolan, R. J. (1999). Recollection and familiarity in recognition memory: An event-related functional magnetic resonance imaging study. *Journal of Neuroscience*, *19*, 3962–3972.

Janowsky, J. S., Shimamura, A. P., & Squire, L. R. (1989). Source memory impairment in patients with frontal lobe lesions. *Neuropsychologia*, *27*, 1043–1056.

Konishi, S., Wheeler, M. E., Donaldson, D. I., & Buckner, R. L. (2000). Neural correlates of episodic retrieval success. *NeuroImage*, *12*, 276–286.

Mayes, A. R., Holdstock, J. S., Isaac, C. L., Hunkin, N. M., & Roberts, N. (2002). Relative sparing of item recognition memory in a patient with adult-onset damage limited to the hippocampus. *Hippocampus*, *12*, 325–340.

Mesulam, M. M. (1999). Spatial attention and neglect: Parietal, frontal and cingulate contributions to the mental representation and attentional targeting of salient extrapersonal events. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences*, *354*, 1325–1346.

Milner, A. D., & Goodale, M. A. (1995). *The visual brain in action*. Oxford: OUP.

Perfect, T. J., Mayes, A. R., Downes, J. J., & Van Eijk, R. (1996). Does context discriminate recollection from familiarity in recognition memory? *Quarterly Journal of Experimental Psychology*, *49A*, 797–813.

Prabhakaran, V., Narayanan, K., Zhao, Z., & Gabrieli, J. D. E. (2000). Integration of diverse information in working memory within the frontal lobe. *Nature Neuroscience*, *3*, 85–90.

Rugg, M. D., Otten, L. J., & Henson, R. N. A. (2002). The neural basis of episodic memory: Evidence from functional neuroimaging. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences*, *357*, 1097–1110.

Scoville, W. B., & Milner, B. (1957). Loss of recent memory after bilateral hippocampal lesions. *Journal of Neurology Neurosurgery and Psychiatry*, *20*, 11–21.

Simons, J. S., Peers, P. V., Hwang, D. Y., Ally, B. A., Fletcher, P. C., & Budson, A. E. (2008). Is the parietal lobe necessary for recollection in humans? *Neuropsychologia*, *46*, 1185–1191.

Simons, J. S., & Spiers, H. J. (2003). Prefrontal and medial temporal lobe interactions in long-term memory. *Nature Reviews Neuroscience*, *4*, 637–648.

Valenstein, E., Bowers, D., Verfaellie, M., Heilman, K. M., Day, A., & Watson, R. T. (1987). Retrosplenial amnesia. *Brain*, *110*, 1631–1646.

Wagner, A. D., Shannon, B. J., Kahn, I., & Buckner, R. L. (2005). Parietal lobe contributions to episodic memory retrieval. *Trends in Cognitive Sciences*, *9*, 445–453.

Wheeler, M. E., & Buckner, R. L. (2003). Functional dissociation among components of remembering: Control, perceived oldness, and content. *Journal of Neuroscience*, *23*, 3869–3880.

Wixted, J. T. (2007). Dual-process theory and signal-detection theory of recognition memory. *Psychological Review*, *114*, 152–176.

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