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Discussion forum

# What is the parietal lobe contribution to long-term memory?

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Until relatively recently, the lateral parietal lobe (PL) was not considered an important region for long-term memory, typically associated instead with functions such as visuospatial attention and visually-guided reaching. Scientific interest in a possible link with episodic memory was fuelled by the realisation of an intriguing discrepancy between functional imaging studies of episodic memory retrieval, which showed consistent PL activation, and the seemingly unaffected memory performance in patients with PL lesions. Shallice and Cooper dedicated a section in their book *The Organisation of Mind* to this newly emerged topic, reflecting how it has rapidly become an established research focus in the cognitive neurosciences.

Research into the role of PL regions in memory has grown following Wagner et al.'s (2005) review of the functional neuroimaging literature, which highlighted how PL responses, in particular on the left, are closely linked with episodic retrieval success. A number of studies have reported greater PL activation during recollection of contextual details than during familiarity-based recognition, both when items are separated based on participants' introspective ratings (Henson et al., 1999), and when participants are asked to orient towards contextual details as opposed to item familiarity during retrieval (Dobbins et al., 2002). This retrieval success effect may relate to subjective aspects of recollection, as it has been observed for stimuli that participants subjectively consider to have been previously encountered but that are actually novel in the experimental context, a phenomenon known as "perceived oldness" (Wheeler and Buckner, 2003).

Meta-analyses have confirmed the prevalence of parietal activity in the functional magnetic resonance imaging (fMRI) literature, with one analysis by Simons et al. (2008) identifying that PL regions may be more consistently activated during recollection (in around 90% of studies examined) than "core" episodic memory regions such as the medial temporal lobes (MTL; around 40% of studies). Another meta-analysis by Skinner and Fernandes (2007) reported a comparable high proportion of lateral PL activity during "recollectively-based" versus familiarity-based response conditions (83%), though their analysis also identified a similarly high frequency of MTL activity. Different inclusion criteria were used in the two meta-analyses, with Simons et al.'s (2008) analysis including studies involving several different operationalisations of recollection, but only those that reported unbiased whole-brain results, whereas Skinner and Fernandes (2007) did not include studies that used source memory tasks, and included studies that restricted analysis to a priori regions of interest, likely to have led to greater sensitivity to MTL activations. Despite these minor inconsistencies, both analyses converge in demonstrating strikingly common PL activation during recollection across studies.

Considering the extensive parietal activity exhibited by healthy participants during memory retrieval, one might expect prominent memory impairments in parietal patients, contradicting the classic view that their difficulties lie instead with abilities like visuospatial attention. However, neuropsychological evidence for such memory impairments is sparse. Shallice and Cooper describe an experiment by Simons et al. (2008), who compared performance on a difficult source memory task in PL patients and controls, where the patients' parietal lesions overlapped closely with regions activated in healthy subjects performing the same task. Despite this overlap, patient performance on the recollection task was unimpaired. Other neuropsychological studies, involving autobiographical memory tasks in bilateral PL patients (Berryhill et al., 2007) or Remember/Know responses in unilateral PL patients (Davidson et al., 2008), have replicated the finding that parietal patients are not amnesic, but suggest that performance on memory tasks may not be entirely normal either: patients produce reduced numbers of

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'remember' responses and a lack of richness, vividness and specificity of freely recalled autobiographical events.

Such findings suggest that lateral PL lesions may be associated with reductions in the conscious experience of recollection. While "objective" memory performance, such as accuracy on tests of recognition or source memory, exhibits no obvious decline, "subjective" memory, the personal experience of one's own episodic memory, may be impaired. This prediction was recently addressed by Simons et al. (2010), who tested both unilateral and bilateral PL patients on source memory tasks that incorporated measures of both objective recollection (source accuracy) and subjective recollection (trial-by-trial recollection confidence). Both unilateral and bilateral PL patients exhibited unimpaired accuracy on the source tasks, but the bilateral patients in particular were significantly reduced in their rated subjective recollection confidence, indicating that their personal experience of memory may be diminished. As well as explaining the neuropsychological findings, the subjective recollection hypothesis has recently been directly supported by fMRI findings that lateral PL activity tracks subjective confidence whereas MTL activity is associated with objective accuracy (Qin et al., 2011; see also Slotnick, 2010). However, what is currently lacking is characterisation of the information processing operations performed by PL regions that appear to be captured better by "subjective" measures like confidence and vividness than "objective" measures like recognition or source accuracy. One possibility is that lateral PL, as part of a functional network that includes the MTL (Vincent et al., 2008), may be involved in recombining multisensory feature representations, which are themselves distributed around the brain, enabling us to experience the rich and vivid detail that characterises remembering. The challenge now is to develop tasks that are capable of going beyond subjective ratings, objectively measuring the parietal contribution to remembering, which must after all be adaptive for behaviour at some level. A number of candidate tasks exist, and we are currently evaluating their sensitivity to PL dysfunction.

In sum, previous evidence suggests a role for the lateral PLs in subjective aspects of episodic memory retrieval, but raises many questions about the nature of this involvement including, for example, how it relates to other cognitive functions such as attention (Cabeza et al., 2008). As Shallice and Cooper argue, for a conclusive interpretation of the data from neuroimaging findings, parallel neuropsychological findings are required. However, patient studies rarely involve lesions that are specific to a single region, and functional reorganisation cannot be ruled out. The regions activated in neuroimaging studies are often distributed over several centimetres of parietal cortex, with a number of functionally distinct sub-regions likely to exist (e.g., Nelson et al., 2010). To address these issues, transcranial magnetic stimulation (TMS) may have potential for exploring the causal relationship between specific PL regions and memory. It is possible using TMS to investigate the effect on memory of temporary PL dysfunction with a spatial resolution of a few millimetres, important for determining possible functional distinctions within the relatively specific PL sub-regions that have been proposed. It may be with such methods that future advances in this fascinating research area will be made.

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