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Neuropsychologia 46 (2008) 665–678

NEUROPSYCHOLOGIA

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# Maintaining structured information: An investigation into functions of parietal and lateral prefrontal cortices

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Received 23 March 2007; received in revised form 19 September 2007; accepted 20 September 2007
Available online 6 October 2007

**Abstract**

Working memory – including simple maintenance of information as well as manipulation of maintained information – has been long associated with lateral prefrontal cortex (PFC). More recently, evidence has pointed to an important role for posterior parietal cortex (PPC) in supporting working-memory processes as well. While explanations have emerged as to the nature of parietal involvement in working-memory maintenance, the apparent involvement of this region in working-memory manipulation has not been fully accounted for. We have hypothesized that parietal cortex, through its representation of spatial information, in conjunction with dorsolateral PFC, supports organization of information (manipulation) and the maintenance of information in an organized state. Through computational modeling, we have demonstrated how this might be achieved. Presently, we consider a pair of fMRI experiments that were designed to test our hypothesis. Both experiments involved simple working-memory delay tasks with contrasts between maintenance of information in organized and unorganized states, as well as contrasts between high and low working-memory load conditions. Two different kinds of organization, associative (grouping) and relational, were employed in the two studies. Across both studies, superior parietal cortex (BA 7) demonstrated a significant increase in activity associated with maintenance of information in an organized state, over and above any increases associated with increased working-memory load. During the delay period, dorsolateral PFC (BA 9) exhibited similar increases for both organization and load; however, this region was particularly engaged by organization demand during the initial cue period. Functional connectivity analysis indicates interaction between dorsolateral prefrontal cortex (DLPFC) and superior parietal cortex, especially when organization is required.


*Keywords:* Working memory; Cognitive control; Organization; fMRI; BA 7; SPL; Spatial relational representations; Chunking

## 1. Introduction

Central to the performance of complex cognition is the ability to hold information in mind in a manner, and for a length of time, such that it can be used in some computation or cognitive operation. The mechanism that supports this *working-memory* capacity has been long associated with lateral prefrontal cortex (latPFC). Early evidence for this link has come from primate lesion studies (Butters & Pandya, 1969; Jacobsen, 1936) and from single-unit recording (Fuster & Alexander, 1971; Goldman-Rakic, Funahashi, et al., 1991). More recently, especially with the advent of neuroimaging, evidence has accumulated that in addition to latPFC, a second brain region, posterior parietal cortex (PPC), also plays an important role in working memory; however, the nature of PPC involvement in working memory has been subject to considerable debate (for review, see Wager & Smith, 2003).

One hypothesis is that PPC is involved in working memory for certain domains of information, especially spatial information. This idea is supported by the fact that PPC, including both the superior parietal lobe (SPL, BA 7) and the inferior parietal lobe (IPL, BA 40), is frequently activated during spatial working-memory storage tasks (Courtney, Ungerleider, et al., 1996; Wager & Smith, 2003). In fact, these parietal regions are involved in a wide range of spatial tasks—not just in working memory (see, e.g. Andersen, 1995; Kesner, Farnsworth, et al., 1991). However, it has also been shown that IPL activation is strongly

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doi:10.1016/j.neuropsychologia.2007.09.015

associated with phonological working-memory tasks (Jonides, Schumacher, et al., 1998; Wager & Smith, 2003), suggesting that this region may be important for phonological storage as well.

The hypothesis about domain-specificity of PPC in working memory has its analogue with respect to latPFC: it has been proposed that dorsolateral prefrontal cortex (DLPFC) mainly subserves working memory for spatial information, while ventrolateral prefrontal cortex (VLPFC) mainly subserves working memory for object information (Wilson, Scalaidhe, et al., 1993). Anatomical evidence lends credence to this view, insofar as VLPFC is relatively well connected to inferotemporal cortex, a region thought to be the locus of object representation, while DLPFC is better connected to PPC and its representations of spatial information (Petrides & Pandya, 1984). However, this domain-specific view has been contradicted by the demonstration of VLPFC involvement both in the maintenance of spatial information and in the maintenance of non-spatial information (Owen, Stern, et al., 1998).

An alternative theory holds that VLPFC supports basic maintenance, or online storage, of information in any domain, while DLPFC supports higher level control processes variously referred to as updating, monitoring, or manipulation (D'Esposito, Postle, et al., 1999; Petrides, 1995). This process-specific theory was motivated by evidence that mid-DLPFC lesions in monkeys selectively impair performance on self-ordered pointing tasks (Petrides, 1995), and also by neuroimaging data showing increased DLPFC activity when subjects were asked to alphabetize a set of letters during the delay period of a working-memory task (D'Esposito et al., 1999). It has been shown that rearranging items according to preference similarly engages DLPFC (Wagner, Maril, et al., 2001), as does reversing the order of a set of items (Crone, Wendelken, et al., 2006; Sakai & Passingham, 2003).

A number of brain imaging studies have failed to show a sharp division of maintenance and manipulation processes onto VLPFC and DLPFC, respectively (Veltman, Rombouts, et al., 2003). This is perhaps not surprising, given that manipulation of items in working memory relies on their maintenance, and given the strong interconnection between VLPFC and DLPFC. And several recent studies provide additional forms of evidence for a specific role for DLPFC in manipulation processes. One study showed that increased DLPFC activity associated with manipulation is predictive of subsequent long-term memory (Blumenfeld & Ranganath, 2006). In a developmental fMRI study, children, who make disproportionately more errors than adults on trials requiring manipulation (item order reversal) relative to maintenance, exhibited an adult-like activation profile for VLPFC but failed to recruit right DLPFC during the period when manipulation was required (Crone et al., 2006). Finally, transcranial magnetic stimulation of DLPFC has been shown to specifically disrupt manipulation (Postle, Ferrarelli, et al., 2006).

Regardless of the success of the process-specific theory in explaining activity within latPFC, the theory fails to address one major relevant finding: a recent meta-analysis of working memory indicates that PPC (in particular, SPL), bilaterally, is strongly associated with the updating, order, and manipulation processes that have been linked to DLPFC (Wager & Smith, 2003). In fact, based on evidence from the meta-analysis, the association of SPL with these high-level working-memory processes may be stronger than that of DLPFC.

### *1.1. Hypothesis—PPC, latPFC, and organization in working memory*

What, then, is the role of PPC in working memory, and specifically of SPL in high-level working-memory processes such as manipulation? If PPC serves as a storehouse of specific kinds of information, such as spatial and phonological representations, then it is likely that this region does play a role in their maintenance, and much evidence suggests that this is indeed the case (Jonides et al., 1998; Wager & Smith, 2003). However, a role in basic maintenance does not account for the data implicating superior parietal cortex involvement in working-memory manipulation. To account for this involvement, and in consideration of evidence that this region is also involved in representation of spatial information, we propose that SPL supports working-memory manipulation – or more generally, working memory involving organized content – by virtue of its rich representation of space and spatial relationships. Specifically, we propose that while the primary role of SPL is spatial processing, in the presence or absence of working-memory demand, it is the spatial relational representations stored in SPL that are the substrate for organization of items in working memory. For example, in a task that requires one to arrange or rearrange a set of items according to some rule (e.g. alphabetize letters, arrange pictures by size or preference), spatial relational representations in SPL (e.g. concepts like *above* or *between*) provide the structure or organizational framework into which the items are placed and maintained.

Manipulation can be said to occur whenever changes are made to organizational structure; this would happen whenever a new organization is created (e.g. arranging a set of abstract pictures) or when item placement is altered (e.g. reversing words in a list). Manipulation should strongly recruit SPL. Maintenance of arbitrary structure or organization over a set of items, though not an example of manipulation, should also involve SPL; thus, neurons involved in spatial relational representations in SPL would exhibit sustained activity to support maintenance of organizational structure.

It should be noted that our hypothesis is similar to another proposal, that numerical or magnitude representations in SPL support maintenance of order information, which was put forward to explain SPL activation in a serial order working-memory task (Marshuetz, Reuter-Lorenz, et al., 2006; Marshuetz, Smith, et al., 2000). Our hypothesis can be considered a generalization of this idea, insofar as numerical representations are probably related to spatial representations and serial order is one type of organization.

Other previous studies are also relevant to the current investigation. The finding that left parietal cortex is engaged during in the transformation of letter strings in an abstract symbol-manipulation task (Anderson, Qin, et al., 2004) is highly relevant, as the transformation of letter strings can be seen as an example of organization or manipulation in working memory.