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Research Report

Modality-specific control processes in verbal versus spatial working memory

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ABSTRACT

Over the past decade, neuroimaging and electrophysiological studies of working memory (WM) have made progress in distinguishing the neural substrates of central executive (CE) functions from substrates of temporary storage subsystems. However, the degree to which CE-related processes and their substrates may be further fractionated is less clear. The present study measured event-related potentials (ERPs) in a running memory paradigm, to study modality-specific CE-related processes in verbal and spatial WM. Participants were asked to remember either verbal (digit identity) or spatial (digit location) information for the first or last three items in a variable length sequence of spatially distributed digit stimuli. Modality-specific WM demand-sensitive ERP amplitude effects were selectively observed over left prefrontal areas under verbal WM performance and over right prefrontal areas under spatial WM performance. In addition, distinct patterns of item-by-item sensitivity under high-CE-demand conditions suggested qualitatively different processing strategies for verbal versus spatial tasks. These results suggest that both modality-specific and task-general CE-related processes are likely operational in many WM situations and that careful dissociative methods will be needed to properly further fractionate and characterize these component CE-related processes and their neurological substrates.

1. Introduction

For over 30 years now, the construct of working memory (WM) (Baddeley, 2000; Baddeley and Hitch, 1974) has been highly influential in framing research on cognitive control and short-term memory. The working memory model describes an explicit separation between mechanisms of temporary storage, including verbal/auditory and visuospatial subsystems, and a supervisory "central executive" (CE) system that controls and coordinates the use and manipulation of information within these subordinate stores (Baddeley, 2000). As research into these interacting systems has progressed into neuroimaging and electrophysiological realms, it has become increasingly important to distinguish the activity of CE-related control processes themselves from the temporary storage/representational activity that these CE processes modulate (Corbetta and Shulman, 2002). For example, a substantial review by Cabeza and Nyberg (2000) showed that original functional neuroimaging data reported as selectively underlying verbal WM processes across a range of studies implicated substantial proportions of frontal and parietal cortices bilaterally, plus cingulate and cerebellar regions—it seems likely that subsets of these identified

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substrates are responsible for component processes within a larger WM framework.

A number of studies over the last decade have made progress in distinguishing the neural signatures of CE-related processes from those of verbal and visuospatial WM storage activity (e.g., Collette et al., 2007; Gruber and Von Cramon, 2003; Marklund et al., 2007; Narayan et al., 2005; Raye et al., 2007). While data from these and other studies have generally supported the overall picture of dorsolateral prefrontal cortex (DLPFC) and superior parietal cortex involvement in CE-related processes summarized by D'Esposito et al. (1988) and Smith and Jonides (1999), a clear picture of the fractionation of CE processes in DLPFC and related cortical substrates has been harder to establish. For example, in a review of imaging studies of CE-related processes in WM, Collette and Van der Linden (2002) reported that while tasks requiring updating of WM contents mainly showed left DLPFC lateralization for verbal materials and right DLPFC lateralization for spatial materials, a considerable degree of bilateral prefrontal cortical involvement was also often present, along with other systematic involvement of superior parietal and other cortical sites. As Collette et al. (2007) noted more recently, studying CE processes is difficult due to the complex, interactive, and often compound nature of the processes themselves—effective isolation of CE processes for study is often spoiled by contamination from other executive and nonexecutive processes that cannot be effectively experimentally constrained.

Several recent studies have been successful in distinguishing component processes in WM through methods focusing on stimulus encoding and representation. Kiss et al. (2007) used a variant of a running memory procedure to investigate item-by-item load-sensitivity under a range of maintenance and updating demands in verbal WM. Kiss et al. demonstrated selective parietal and left prefrontal sensitivity to item-specific demands on encoding and CE-related updating processes in verbal WM, using a running memory procedure that required a response to a probe stimulus only at the end of a randomly varying sequence of stimulus trials. This general procedure allowed Kiss et al. (2007) to observe ERP correlates of encoding and manipulating information in WM, independent of decision or response processes. Their procedure asked participants to either monitor for any set of two probe letters within a series of single digits (the control task), to remember the first two digits in a series for later comparison with a probe display (the maintenance task), or to remember the last two digits in a series for a subsequent probe comparison, requiring updating of WM contents throughout a stimulus series (the updating task). Kiss et al. (2007) crossed these varying task demands with varying WM load (two- versus three-digit memory demands), all within-subjects, and used the pattern of ERP effects over serial positions of to-be-remembered stimulus presentations to identify and characterize WM-relevant brain responses with respect to parametrically varying trial conditions.

Kiss et al. (2007) observed a progressive increase in parietal and left prefrontal ERP amplitude responses over the first and second presented digits when participants were asked to remember the first two digits in a sequence, and over the first, second, and third presented digits when participants were asked to remember the first three items, with relatively little activity for subsequently presented items. In contrast, when participants were asked to remember the last two or three items, parietal and left prefrontal amplitudes increased progressively over the course of five sequential digits.

Our present study sought to examine the extent to which control of stimulus encoding and CE-related updating processes in visuospatial WM were consistent with the systematic effects in verbal WM described by Kiss et al. (2007). McCollough et al. (2007) have recently demonstrated posterior parietal/parieto-occipital ERP activity consistent with the actual representation of a visual stimulus in WM. Our study aimed to examine the higher-order complement to the more basic representational WM activity of the study of McCollough et al. (2007) and to directly compare and contrast visuospatial WM control activity to like processes in verbal WM. In basic conceptions of WM (Baddeley, 2000; Baddeley and Hitch, 1974), slave representational systems for visuospatial and verbal information are, by definition, modal (but cf., the Episodic Buffer formulation in Baddeley, 2000), and CE processes, by definition, are amodal and, until recently, considered as unitary. There has been increasing work in fractionating the CE (e.g., Miyake, et al., 2000), with a number of distinct general functions including updating, inhibition, and shifting now generally recognized. A related consideration is whether component CE processes may be recruited or implemented differently depending on the task at hand or the modality of information to be processed (Collette and Van der Linden, 2002), or even whether some control processes one would typically consider as "executive" in nature may themselves be modality-specific. Our present study sought to explicitly examine the contribution of task-general WM-related CE processes to verbal versus visuospatial WM representations, versus effects suggesting the presence of modality-specific CE processes.

Using the same *control*, *maintenance*, and *updating* task instructions as Kiss et al. (2007), we asked participants to remember sets of three items in separate sessions of verbal and spatial WM tasks. To equate verbal and spatial versions of our WM tasks as much as possible, our memory stimuli were of identical form across all tasks and modalities, with single digits presented at one of eight regular positions around a central fixation point (see Fig. 1). For verbal tasks, participants were instructed to remember the identity of the presented digit; for spatial tasks, participants were instructed to remember the spatial position of the presented digit. Probe tasks following a variable length stimulus sequence presented only verbal (centrally presented digits) or spatial information (coloured stimulus positions), respectively. This design allowed the observation of ERP measures reflecting encoding- and representation-related processes (including associated control processes) for a sequence of stimuli, before decision or response requirements for a later probe task.

In all of this, our focus was to examine how varying CE-related demands on visuospatial WM were reflected in ERP data in comparison to verbal WM performance. As our primary focus, we sought to replicate the selective left-lateralized frontal sensitivity to sequential verbal WM-relevant stimuli under high CE demand, demonstrated by Kiss et al. (2007); as a complement to this, our study examined right frontal ERP responses for selective sensitivity to sequential visuospatial WM-relevant stimuli under the same high CE demands. More