

available at www.sciencedirect.comwww.elsevier.com/locate/brainres**BRAIN
RESEARCH****Research Report****Modality-specific control processes in verbal versus spatial working memory**Scott Watter^{a,*}, Jennifer J. Heisz^a, James W. Karle^a, Judith M. Shedden^a, Ivan Kiss^{a,b}^aDepartment of Psychology, Neuroscience and Behaviour, McMaster University, Ontario, Canada^bLakeridge Health Corporation, Ontario, Canada

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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.

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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

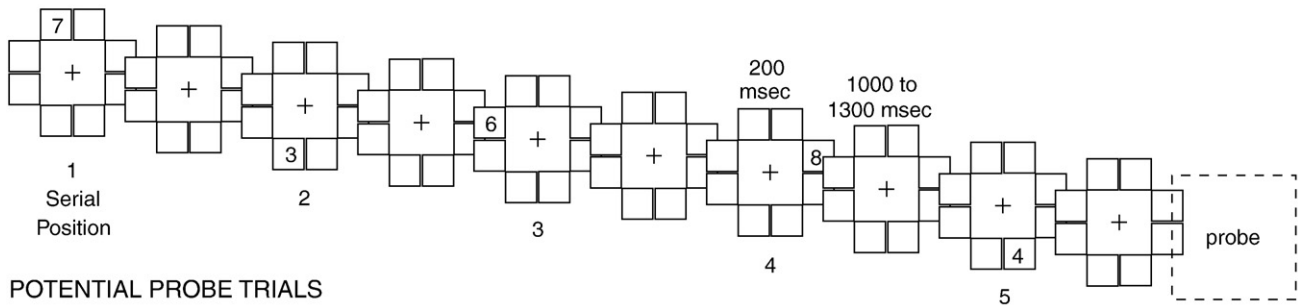
activity for subsequently presented items. In contrast, when participants were asked to remember the last two or three items, parietal and left prefrontal amplitudes increased progressively over the course of five sequential digits.

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

EXAMPLE STIMULUS SEQUENCE



POTENTIAL PROBE TRIALS

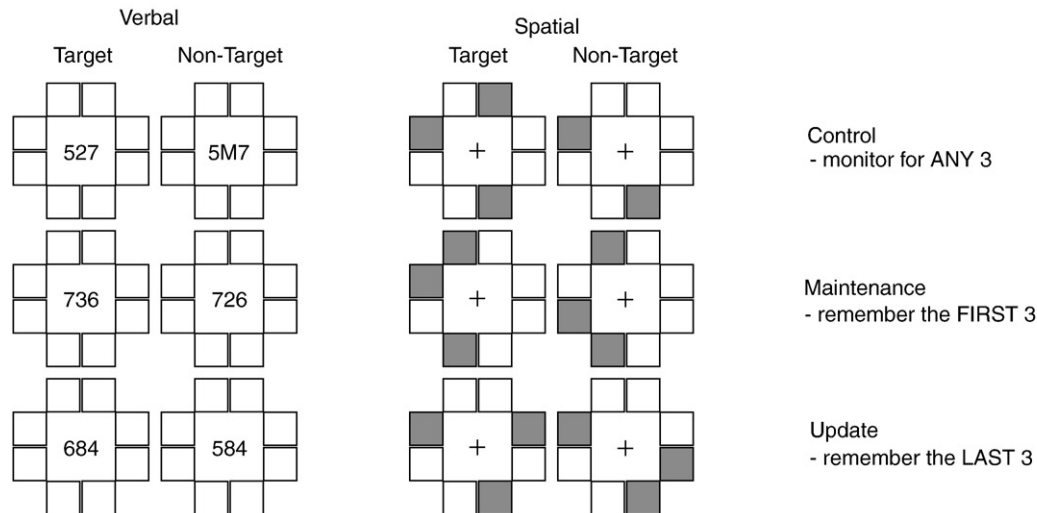


Fig. 1 – Example stimulus sequence and probe trials for verbal versus spatial WM conditions in control, maintenance and update tasks. Sequences of 3 to 8 randomly selected digits were presented in one of eight regular positions around a central fixation point, with no repetition of digit identity or spatial location within any sequence of three stimuli. Participants responded only to a probe display presented at the end of a variable-length stimulus sequence. Participants remembered digit identities in the verbal WM condition, and spatial location of digits in the spatial WM condition.

generally, differences in verbal and visuospatial WM control processes could be reflected in different task-general and modality-specific substrates of control, as might be expected from the existing literature concerning localization of WM function to areas of prefrontal cortex and elsewhere (e.g., Collette et al., 2007; Gruber and Von Cramon, 2003). Alternatively or additionally, differences in control of verbal versus visuospatial WM might also be qualitative, in the sense that different types of control operations might be observed for different modalities, possibly depending on the nature of these representations—for example, verbal information is inherently serial in nature and may have to be processed as such; in contrast, the ability to represent multiple items of visuospatial information configurally may allow for qualitatively different kinds of control in visuospatial WM.

2. Results

2.1. Overt behaviour

Participants' overall mean reaction times and mean error rates are presented in Fig. 2. Mean error rates were comparable across verbal (14.6%) and spatial (14.4%) working memory

tasks, and across target (14.2%) and nontarget (14.9%) trials, F values < 0.1 . Error rate was highest for the updating task (23.7%), compared to maintenance (12.0%) and control tasks (7.9%), with a significant main effect of task type, $F(2,34) = 21.12$, $p < 0.001$. No other main effects or interactions were observed for error data.

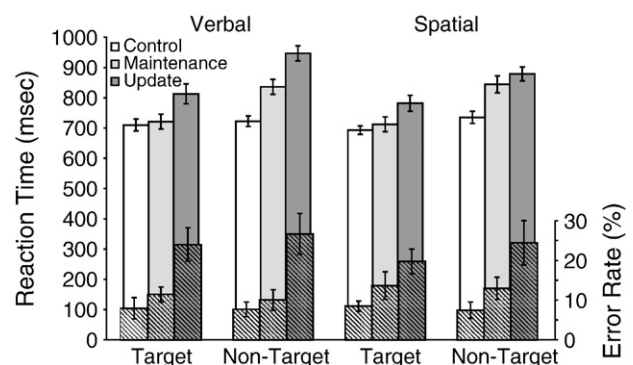


Fig. 2 – Mean reaction times (left axis) and error rates (right axis) for probe trials. Data are divided by WM modality (verbal and spatial), probe type (target, nontarget), and task type (control, maintenance, and update). Error bars represent standard errors of the mean.

Participants' mean reaction times were fastest for the control task (714 msec), followed by maintenance (778 msec) and updating tasks (854 msec), with a significant main effect of task type, $F(2,34)=36.05$, $p<0.001$. While performance on control and maintenance trials was comparable between verbal and spatial tasks, verbal working memory performance was slower than spatial performance for updating trials, supported by an interaction of task type and working memory

type, $F(2,34)=4.83$, $p<0.05$. Reaction time was also influenced by probe type; on target trials, the maintenance task was relatively fast, approaching performance of the control task, but on nontarget trials, this was relatively slower, with updating tasks slower again in all conditions. These findings were supported by a significant interaction of probe type and task type, $F(2,34)=20.04$, $p<0.001$, modifying a main effect of probe type, $F(1,17)=41.60$, $p<0.001$.

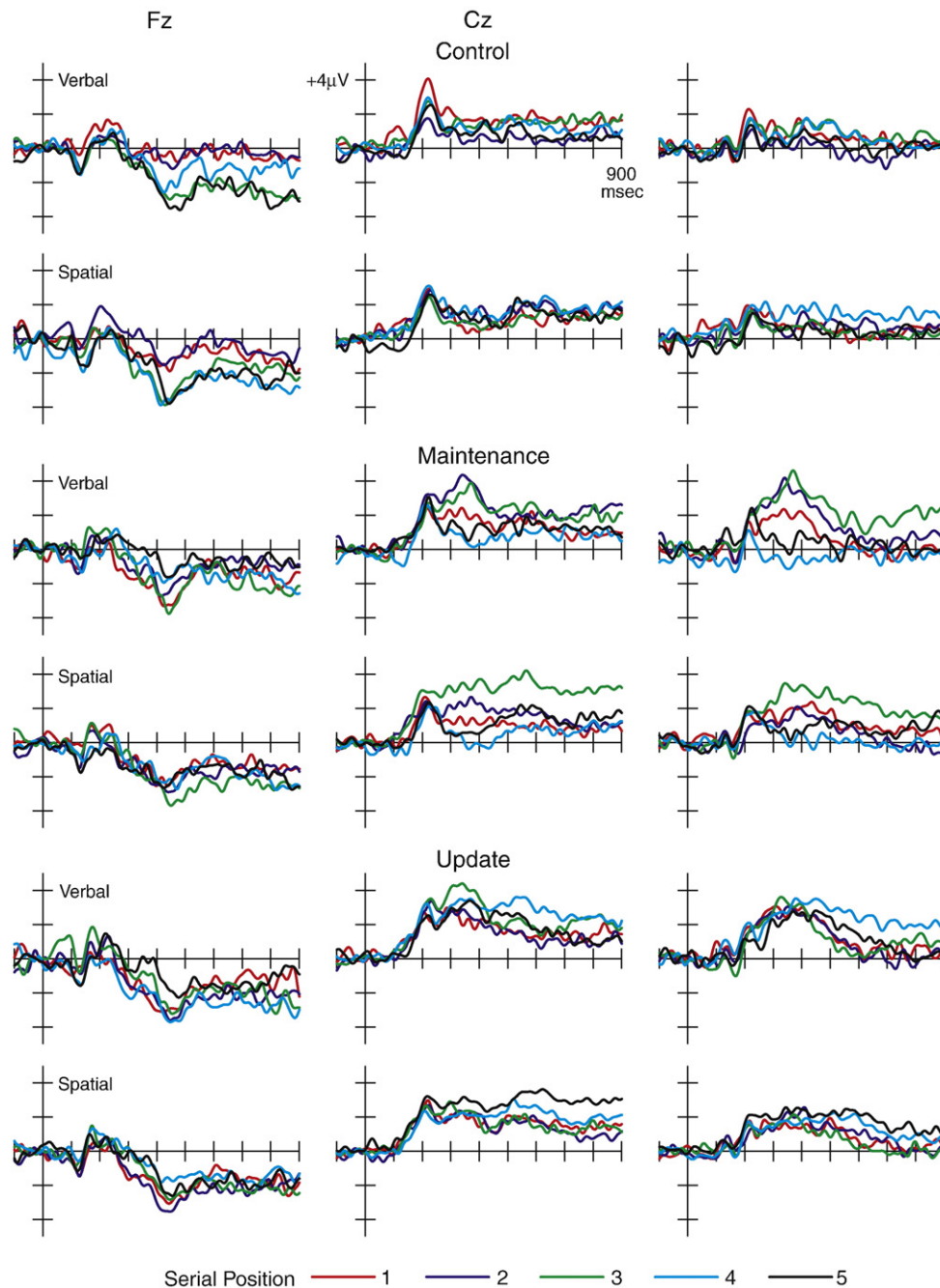


Fig. 3 – Grand average stimulus-locked ERP waveforms at electrode Fz, Cz, and Pz for memory item (nonprobe) trials. Data are divided by task type (control, maintenance, and update), WM modality (verbal and spatial), and serial position (1–5). Mean amplitude data were assessed over a central parietal region of interest to characterize effects on a P300-like component (300- to 450-msec epoch) and a positive slow wave (450- to 900-msec epoch). Corresponding average mean amplitude data from the centroparietal region of interest for these analysis epochs are presented graphically in Fig. 4.

2.2. ERPs over parietal regions

Fig. 3 shows grand mean ERP waveforms at Fz, Cz, and Pz electrodes for stimuli presented in serial positions 1 to 5 (not responses to targets), for verbal and spatial modalities, and control, maintenance, and updating tasks. Visual inspection of grand mean waveforms identified a distinct P300-like waveform with a peak at approximately 350 msec over centroparietal areas in maintenance and updating conditions, with subsequent positive slow wave activity persisting to the end of our measurement epoch for some conditions. From these observations, we defined two time windows for analysis of centroparietal mean amplitude data—300 to 450 msec and 450 to 900 msec.

2.2.1. The 300- to 450-msec window

The Cz and Pz waveforms shown in Fig. 3 are representative of the general pattern of data observed over our centroparietal region of interest. The left side of Fig. 4 shows condition averages for the mean amplitude data for our centroparietal region of interest. A substantial P300-like component was observed in maintenance and updating tasks but was absent

in the control task, supported by a main effect of task type, $F(2,34)=16.15$, $\epsilon=0.80$, $p<0.001$. Within maintenance and updating conditions, this component was larger for verbal than spatial modalities, supported by a main effect of WM modality, $F(1,17)=4.98$, $p<0.05$, and the interaction of WM modality and task type, $F(2,34)=3.40$, $\epsilon=0.97$, $p<0.05$. The magnitude of this component also varied over serial position, $F(4,68)=14.55$, $\epsilon=0.66$, $p<0.01$. In the maintenance task, amplitudes were observed to grow progressively larger from serial position 1 to 3, with position 4 and 5 amplitudes close to baseline levels. In contrast, the amplitude of this P300-like component was substantial for all serial positions in the updating task. This pattern of data was supported by the interaction of task type and serial position, $F(8,136)=10.50$, $\epsilon=0.62$, $p<0.001$.

To better characterize these apparent effects of task type on mean amplitudes, we assessed control, maintenance and updating tasks separately via repeated-measures ANOVAs with factors of working memory modality (verbal and spatial) and serial position (1, 2, 3, 4, and 5). In the control task, no effects or interactions of WM modality or serial position were observed, F values <1.7 , with no suggestion of linear or quadratic trends over serial positions, F values <1.1 .

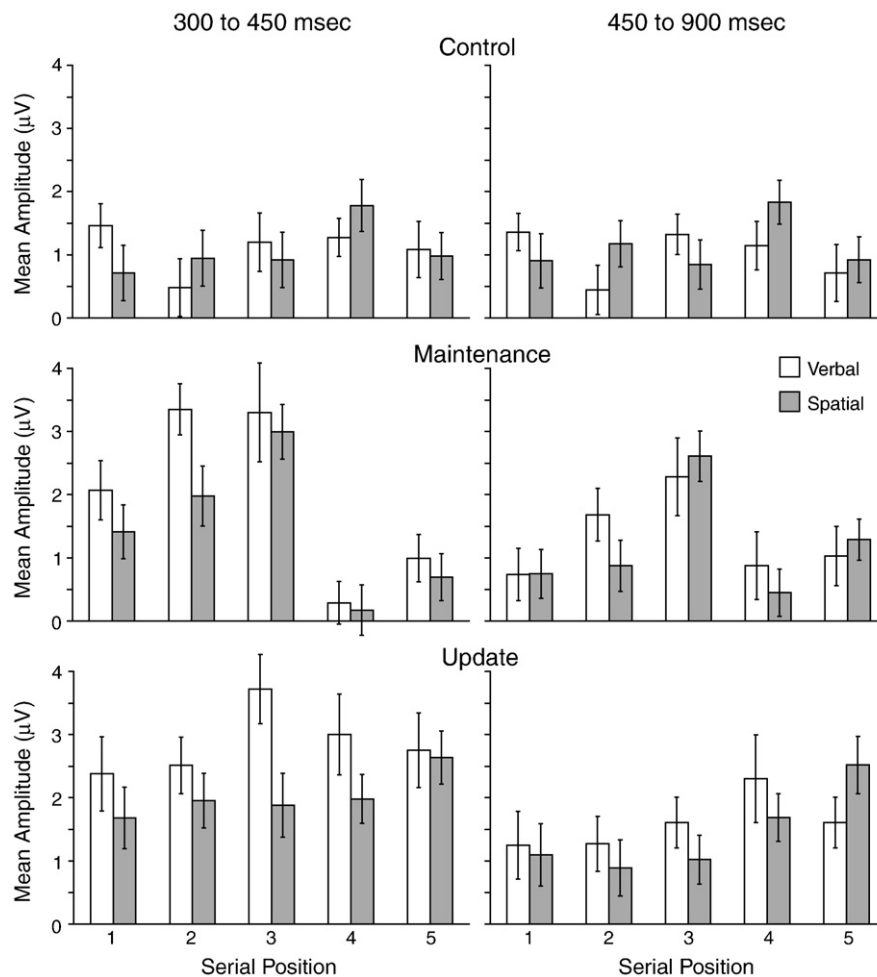


Fig. 4 – Average mean amplitudes from the centroparietal region of interest for 300- to 450-msec and 450- to 900-msec analysis epochs. Data are divided by task type (control, maintenance, and update), WM modality (verbal and spatial), and serial position (1–5). Error bars represent standard errors of the mean.

In the *maintenance* task, amplitude differences were observed across serial position. For both WM modalities, mean amplitude appeared to increase from serial position 1 to be maximal at serial position 3, with serial positions 4 and 5 at or near baseline. This was supported by a significant main effect of serial position, $F(4,68)=18.05$, $\varepsilon=0.70$, $p<0.001$, with no interaction between serial position and WM modality, $F(4,68)=0.95$, $p=ns$. This pattern of data was further supported by significant linear and quadratic trends for serial position, $F(1,17)=18.65$, $p<0.001$ and $F(1,17)=17.76$, $p<0.01$, respectively, with no such trends for the interaction of serial position and WM modality, $F(1,17)=1.84$, $p=ns$ and $F(1,17)=0.01$, $p=ns$, respectively. Finally, mean amplitudes appeared to be generally larger for verbal than spatial modalities, although this main effect was marginal, $F(1,17)=3.64$, $p=0.074$.

In the *updating* task, mean amplitudes were generally larger in verbal compared to spatial WM modalities, $F(1,17)=9.82$, $p<0.01$, with no main effect of serial position, $F(4,68)=1.51$, $\varepsilon=0.78$, $p=ns$, and no interaction of WM modality and serial position, $F(4,68)=1.51$, $\varepsilon=0.63$, $p=ns$. These data supported the general observation of substantial P300-like components at all serial positions. Within these data, amplitudes in the verbal WM modality appeared maximal at the third serial position, compared to a progressive increase over serial positions 1 to 5 in the spatial WM modality. A significant linear trend of serial position, $F(1,17)=5.26$, $p<0.05$, and a marginal quadratic trend for the interaction of serial position and WM modality, $F(1,17)=4.23$, $p=0.055$, reflected these observations.

2.2.2. The 450- to 900-msec window

The Cz and Pz waveforms shown in Fig. 3 are again representative of the general pattern of data observed over our centroparietal region of interest for this later analysis window. The right panel of Fig. 4 shows condition averages for mean amplitude measures in this analysis window. Separate analysis of this later time window was conducted to potentially help to dissociate earlier P300-related processing from subsequent working memory-related slow wave activity over centroparietal areas, following Kiss et al. (2007). In contrast to the earlier analysis window, no overall amplitude differences were observed between verbal and spatial modalities, $F(1,17)=0.07$, $p=ns$. Where positive slow wave amplitudes were consistently low across serial positions in the control task, substantial positive slow wave activity was seen most prominently for serial position 3 in the maintenance task, and to generally increase across serial positions 1 to 5 in the updating task. These observations were supported by a significant main effect of serial position, $F(4,68)=3.37$, $\varepsilon=0.79$, $p<0.05$, and a marginal main effect of task type, $F(2,34)=3.06$, $\varepsilon=0.76$, $p=0.077$, modified by the interaction of task type and serial position, $F(8,136)=5.15$, $\varepsilon=0.71$, $p<0.001$.

To better investigate the influence of task type on these later slow wave mean amplitudes, additional repeated-measures ANOVAs with factors of working memory modality (verbal and spatial) and serial position (1, 2, 3, 4, and 5) were again performed to separately assess control, maintenance, and updating task performance. In the control task, no main effects were observed for WM modality or serial position, F values <1.7 , although a marginal interaction of WM modality and serial position was observed, $F(4,68)=2.45$, $\varepsilon=0.84$, $p=0.067$. This interaction did not appear to reflect a systematic pattern of variability across serial

positions for either verbal or spatial WM modalities, with no linear or quadratic trends observed for either the interaction of WM modality and serial position or the related main effects, F values <1.2 .

In the *maintenance* task, a sustained slow wave positivity was observed for serial position 3 in both spatial and verbal WM modalities, with other serial positions having smaller and more similar amplitudes. This observation was supported by a main effect of serial position, $F(4,68)=8.37$, $\varepsilon=0.82$, $p<0.001$, with a significant quadratic trend for serial position, $F(1,17)=10.92$, $p<0.01$, and no linear trend, $F(1,17)=0.07$, $p=ns$. There was no main effect of WM modality, $F(1,17)=0.15$, $p=ns$, and no interaction of WM modality and serial position, $F(4,68)=1.03$, $\varepsilon=0.86$, $p=ns$.

In the *updating* task, mean slow wave amplitudes appeared to increase progressively over serial position in general, similarly for verbal versus spatial modalities. These observations were supported by a main effect of serial position, $F(4,68)=3.17$, $\varepsilon=0.88$, $p<0.05$, with a significant linear trend, $F(1,17)=11.07$, $p<0.01$, and no quadratic trend, $F(1,17)=0.52$, $p=ns$. There was no main effect of WM modality, $F(1,17)=0.62$, $p=ns$, and no interaction of WM modality with serial position, $F(4,68)=1.56$, $\varepsilon=0.77$, $p=ns$.

2.3. ERPs over frontal regions

Fig. 5 shows grand mean ERP waveforms for left and right frontal regions of interest, for stimuli presented in serial positions 1 to 5 (not responses to targets), for verbal and spatial modalities. Frontal regions of interest involved arrays of six electrodes per hemisphere centered over F3 and F4 positions, approximating the corresponding scalp position of underlying dorsolateral prefrontal cortex (Herwig et al., 2003). Visual inspection of grand mean waveforms identified a bilaterally distributed broad negative component beginning at approximately 300 msec to 350 msec and peaking at approximately 450 msec, followed by an extended negative slow wave with a variable positive drift for the remainder of the measurement epoch. To better investigate the extended frontal negative slow wave activity, we assessed mean amplitudes over a 600-msec to 900-msec time window to isolate this activity from the observed earlier component.

2.3.1. The 600- to 900-msec window

This analysis window defined a bilateral prefrontal negative slow wave, with variable positive drift, isolated from the observed broad negative peak observed within a 350-msec to 550-msec window, shown in Fig. 5. Fig. 6 shows condition averages for mean amplitude data for left and right regions of interest for this analysis window. Systematic amplitude effects were observed on this late slow wave component. Amplitudes were generally more negative for maintenance and updating tasks compared to control, $F(2,34)=6.69$, $\varepsilon=0.78$, $p<0.01$. A main effect of hemisphere was also observed, $F(1,17)=9.06$, $p<0.01$, with generally more negative amplitudes over the left area of interest compared to the right. In addition, a main effect of serial position, $F(4,68)=2.96$, $\varepsilon=0.84$, $p<0.05$, and the marginal interaction of serial position and WM modality, $F(4,68)=2.46$, $\varepsilon=0.79$, $p=0.070$, supported the observation of apparently distinct patterns of serial position effects across WM modalities and tasks.

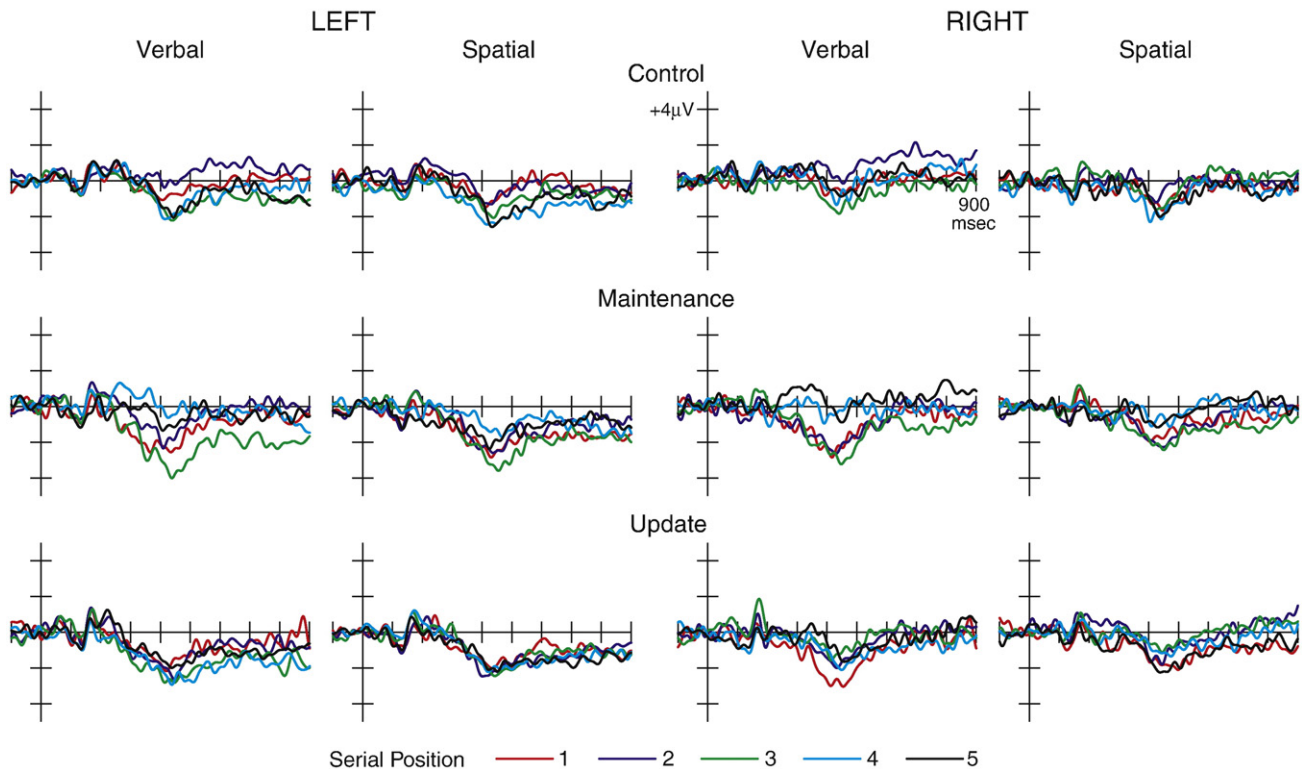


Fig. 5 – Grand average stimulus-locked ERP waveforms for left and right frontal regions of interest for memory item (nonprobe) trials. Data are divided by task type (control, maintenance, and update), WM modality (verbal and spatial), and serial position (1–5). Mean amplitude data were assessed over these regions of interest to characterize effects on a late negative slow wave (600- to 900-msec epoch). Corresponding average mean amplitude data from the left and right frontal regions of interest for this analysis epoch are presented graphically in Fig. 6.

To better characterize these effects, we examined control, maintenance, and updating tasks separately. For control and maintenance tasks, we conducted separate repeated-measures ANOVAs with factors of hemisphere (left and right), working memory modality (verbal and spatial), and serial position (1, 2, 3, 4, and 5). For the updating task, we had particular a priori predictions of selective sensitivity to serial position effects over left frontal areas for verbal WM and right frontal areas for spatial WM, based on prior findings of selective left frontal sensitivity under verbal WM demands from Kiss et al. (2007). To this end, for the updating task, we conducted targeted trend analyses on sequential serial position data, separately for verbal and spatial WM modalities over left and right frontal regions of interest, to directly examine these predictions.

In the *control* task, amplitudes were generally more negative over left versus right frontal regions, $F(1,17)=7.41$, $p<0.05$, and for spatial versus verbal modalities, $F(1,17)=5.62$, $p<0.05$. An effect of serial position was also observed, $F(4,68)=3.04$, $\epsilon=0.81$, $p<0.05$, with a significant interaction of WM modality and serial position, $F(4,68)=3.52$, $\epsilon=0.89$, $p<0.05$. These effects appeared to be substantially driven by a considerable positive shift of amplitudes in serial position 2 for the verbal modality. No other effects or interactions were observed, F values <1.6 .

In the *maintenance* task, slow wave amplitudes were observed to be maximally negative at serial position 3, for both verbal and spatial modalities, and over both left and right frontal regions of interest, supported by a main effect of serial position, $F(4,68)=$

2.88, $\epsilon=0.70$, $p<0.05$, and no interactions of serial position with any other variables, F values <1 . A main effect of hemisphere supported the observation of more negative slow wave amplitudes over our left versus right frontal region of interest, $F(1,17)=4.70$, $p<0.05$. Spatial and verbal amplitude effects appeared to be quite similar over our right region of interest; over the left region of interest, mean amplitudes appeared generally more negative for the spatial WM modality, although the interaction of hemisphere and WM modality was only marginal, $F(1,17)=3.06$, $p=0.099$.

In the *updating* task, different patterns of negative slow wave amplitudes were observed over serial positions for left versus right hemispheres with verbal versus spatial WM modalities. Initial trend analyses examining all factors in the updating task revealed a significant quadratic trend for the interaction of hemisphere and serial position, $F(1,17)=6.50$, $p<0.05$, and a significant quadratic trend for the interaction of WM modality with serial position, $F(1,17)=8.07$, $p<0.05$, with no linear or quadratic trend for the main effect of serial position, F values <1.3 . Amplitudes were also generally observed to be more negative in the left versus right region of interest, $F(1,17)=12.53$, $p<0.01$.

Subsequent directed trend analysis of serial position data in left versus right frontal regions of interest with verbal versus spatial WM modalities revealed a distinctive pattern of selective left-verbal and right-spatial sensitivity to sequential CE-related stimulus demands. Over the left frontal region of interest for the verbal WM modality, slow wave amplitudes were relatively

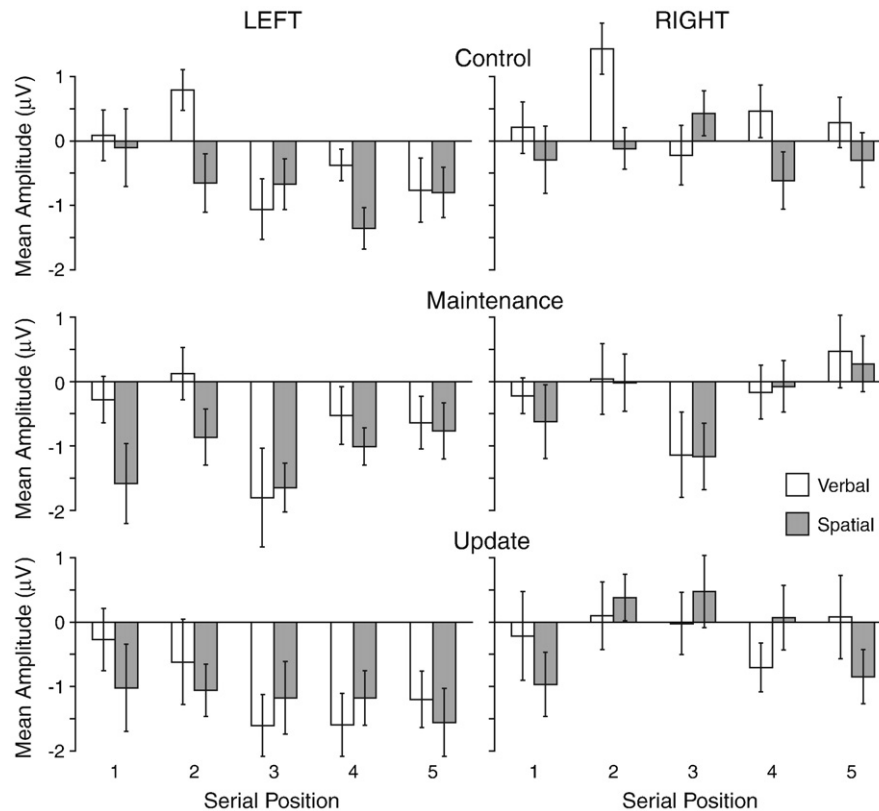


Fig. 6 – Average mean amplitudes from the left and right frontal regions of interest for the 600- to 900-msec analysis epoch. Data are divided by task type (control, maintenance, and update), WM modality (verbal and spatial), and serial position (1–5). Error bars represent standard errors of the mean.

small at serial position 1 and became increasingly negative as serial position progressed, supported by a significant linear trend, $F(1,17)=5.06$, $p<0.05$, and no significant quadratic trend, $F(1,17)=2.61$, $p=0.12$. In contrast, amplitudes for the spatial WM modality over the left frontal region of interest did not appear to be sensitive to serial position, reflected by no evidence of linear or quadratic trends across serial positions, F values <0.7 .

Over the right frontal region of interest, slow wave amplitudes for the spatial WM modality appeared to be selectively sensitive to serial position, although with a different pattern of effects to verbal WM over left frontal areas. For the spatial WM modality, amplitudes appeared to be relatively large and negative beginning at serial position 1, to subsequently decrease for serial positions 2 and 3, and to then become increasingly negative again over positions 4 and 5. This pattern of serial position data for spatial WM was supported by a strong quadratic trend, $F(1,17)=10.33$, $p<0.01$, with no linear trend, $F<0.1$. In contrast, amplitudes for the verbal WM modality over the right frontal region of interest did not appear to be sensitive to serial position, reflected by no evidence of linear or quadratic trends across serial positions, F values <0.2 .

3. Discussion

Our study employed a running memory task adapted from Kiss et al. (2007) that allowed us to obtain relatively pure

measures of stimulus-related encoding and manipulation of information in WM, independent from decision- or response-related processes. Participants were asked to remember different aspects of the same visually presented displays under either verbal (remember digit identities) or spatial instructions (remember locations). All participants completed all combinations of control, maintenance and updating tasks across both verbal and spatial sessions, for a completely within-subjects design.

3.1. Overt behaviour

Participants' manual responses to probe trials were assessed to ensure that they were adequately performing our WM tasks. Overall reaction time and error rate performance was consistent with expectations of increasing difficulty through control, maintenance, and updating tasks, with no evidence of a speed-accuracy trade-off, and were consistent with the patterns of behavioural data from Kiss et al. (2007). Performance appeared equivalent between verbal and spatial conditions for control and maintenance tasks, suggesting that our verbal and spatial tasks were relatively well matched with respect to extracting and encoding relevant information from our combined numerical-spatial stimuli. Responses were relatively slower for verbal versus spatial WM in the updating condition. This could suggest that earlier but now irrelevant items in a verbal WM updating sequence imparted greater proactive

interference than spatial positions, perhaps due to the more practiced or semanticized and thus durable nature of number representations compared to our experiment-specific spatial stimuli.

3.2. ERPs

ERP amplitudes were assessed from a central parietal region of interest to characterize P300-like and positive slow wave effects and from bilateral frontal regions of interest centered over dorsolateral prefrontal cortex to best characterize a late negative slow wave effect. Several interesting patterns of data were observed for maintenance and updating tasks. Central and parietal waveform data presented in Figs. 3 and 4, and bilateral prefrontal waveform data presented in Figs. 5 and 6 illustrate systematic serial position effects modulated by memory task type and WM modality.

3.2.1. Verbal WM

Findings in our verbal WM tasks closely replicated the pattern of effects previously reported by Kiss et al. (2007) in an equivalent set of verbal WM tasks. In our verbal maintenance task (remember the first three digits), our participants demonstrated a progressive increase in P300 and parietal slow wave amplitude over serial positions 1 to 3, with notable sustained slow wave activity in position 3, and negligible or baseline activity for positions 4 and 5. These data fit well with expectations of processes involved with representing new information in working memory. The distinct prolonged slow positive wave for position 3 stimuli may reflect processes involved with recoding and representation activity of a complete three-item memory set, when participants were aware that they did not need to remember any subsequently presented stimulus information. In the verbal updating task (remember the last three digits), continued enhanced parietal amplitude effects over serial positions 4 and 5 are consistent with continuing WM encoding demands over all serial positions.

Effects at prefrontal sites for verbal WM tasks showed complementary patterns of results with respect to parietal sensitivities to task-specific WM demands, with laterality differences in the extent of these correspondences under high CE-related demand. For the maintenance task, a maximal negative amplitude response was observed at serial position 3 in both left and right frontal regions of interest. With higher-demand CE-related requirements in the updating task, sensitivity to progressive verbal WM demands over serial stimulus positions was observed selectively over the left frontal region of interest. These data are consistent with previous findings of a left prefrontal-parietal network for CE-related control processes in verbal WM, replicating Kiss et al. (2007) and consistent with other recent studies of verbal WM control processes (e.g., Collette et al., 2007; Gruber and Von Cramon, 2003).

While our verbal WM findings replicated the selective left frontal sensitivity to serial position ERP effects from Kiss et al. (2007), we note that some of our effects were less pronounced or somewhat compressed compared to these prior findings. We suggest that these differences may be due to differences in stimulus presentation between the two studies. In contrast to

our presentation of stimuli randomly at one of eight positions, Kiss et al. (2007) presented single digits in the same position in the center of the screen on every trial. This consistent and predictable presentation would likely lead to more consistent and less time-variable processing of stimuli, with less temporal jitter of subsequent ERP components and resultant cleaner, larger components.

3.2.2. Spatial WM

In our spatial WM conditions, data from our maintenance task followed the pattern of effects seen in our verbal maintenance task. P300 components were notably smaller and less distinct for spatial tasks, possibly reflecting a more variable time course for the establishment of a coherent WM representation for relatively novel spatial position stimuli compared with well-learned digit identities. Despite this difference, similar progressive amplitude effects for serial positions 1 to 3 were observed in the maintenance task for P300, with similar extended slow positive wave activity for position 3, with position 4 and 5 amplitudes at or near baseline throughout. Likewise, at both left and right frontal sites, late slow wave activity was maximally negative at position 3. Taken together, these data suggest that participants were approaching the encoding of verbal and spatial information in our maintenance tasks in a similarly progressive way, incorporating new stimulus information into their current WM set in an increasingly effortful manner as serial position increased, with the sustained activity following the third (and final to-be-remembered) stimulus likely reflecting additional recoding and representation processes in WM.

In contrast to the similarity of ERP effects in spatial and verbal WM maintenance tasks, participants' ERP data revealed a markedly different but distinct pattern of effects in the spatial updating task, again demonstrating modality-specific frontal laterality differences under high-demand CE-related conditions. Right frontal sites were observed to be selectively sensitive to sequential stimulus presentations with higher-demand CE-related requirements for visuospatial information in the updating task. In addition, the pattern of this lateralized serial position sensitivity appeared to be qualitatively different to the pattern of left frontal sensitivity for verbal updating: right frontal sites with the spatial updating task showed a maximal positive effect at serial position 1, which decreased to a minimum effect at position 3, and then increased again to position 5.

We suggest that these data may reflect the neurological instantiation of a distinct task-wide strategic approach to encoding and updating an ongoing set of spatial positions in the absence of knowing how long the memory sequence will be. Considering the specific and progressive demands that our observed frontal negative slow wave displayed sensitivity to in our other conditions—i.e., selective enhancement of this frontal late negative slow wave for critical position 3 stimuli in verbal and spatial maintenance tasks bilaterally, and selectively over left frontal sites with increasing serial positions with verbal WM demands—it would appear that participants were doing a substantial amount of WM-specific work in response to the first stimulus of a series in the spatial updating task, well beyond that apparently required to sufficiently encode and represent this first stimulus in other

situations. The relatively smaller amounts of work that stimuli 2 and 3 were seen to require suggests that participants may have been deliberately and effortfully establishing a more complex spatial representation on presentation of the first stimulus in our spatial updating task, into which spatial positions from stimuli 2 and 3 could be easily integrated. The increased negativity in right frontal negative slow wave amplitudes at serial positions 4 and 5 would reflect the first and subsequent times that participants needed to substantially modify their coherent three-item spatial WM representation under this performance strategy.

Patterns of P300 amplitudes over serial positions for spatial updating suggested a less prominent attentional response to stimuli in the third sequential position, compared to verbal updating; in contrast, P300 responses to spatial and verbal maintenance tasks were both quite prominent. These P300 data are consistent with our suggested account of qualitatively distinct spatial updating performance: enhancement of frontal slow wave negativity for the serial position 1 stimulus likely represents CE-related activity other than enhanced processing and representation of the stimulus 1 item itself, given comparable P300 activity to subsequent spatial stimuli and position 1 verbal updating stimuli; relatively smaller P300 responses to the serial position 3 stimulus for spatial updating compared to verbal updating would reflect easier representation and integration of stimulus 3 into a coherent WM set, as a result of earlier additional CE-related work following the first stimulus to establish a spatial WM representation into which subsequent stimuli could be more easily integrated.

The observation of this distinct pattern of data in the spatial updating task suggests that participants have flexible control over complex strategic approaches to task performance, and that participants can (unsurprisingly) approach individual tasks in the way that seems most appropriate, with regard to trading off effort for adequate performance. Participants could likely have employed this same position 1 spatial preparation strategy for the maintenance task, but apparently chose not to. We suggest that in the maintenance task, participants quickly learn that they can adequately maintain the first three items by spending time after the third item is presented to represent and recode their to-be-remembered items and that this is considerably less effortful than the up-front preparation they are forced into in the spatial updating task. The verbal updating task, in contrast, does not allow for this kind of configural benefit to encoding, and to the extent it may (in a temporal sense, perhaps), is likely already well learned as part of normal verbal development.

Unfortunately, we did not collect formal debriefing information from participants regarding their strategies for task performance across our various conditions. The informal feedback we did gather from participants regarding their task strategies suggested that most adopted a visualization strategy for the visuospatial conditions and that they reported having to concentrate and try hard particularly in the spatial updating condition due to stimulus positions being difficult to remember. While not conclusive, these comments reflect a performance style that would be consistent with our first-item spatial preparation interpretation for our spatial updating data. We also note that while our presentation of stimulus items was the same between verbal and spatial conditions,

our end-of-trial probe tasks were not—with verbal probes of three digits presented centrally as a three-digit number (in order of presentation sequence), and spatial probes of three rectangles presented as a single three-item spatial display, the digit sequences maintained some additional sequential information that the spatial items did not. It might be suggested that differences in this sequence information made one modality easier than the other or that the probes themselves could have affected participants' strategies and our differences between modalities. We suggest that this is unlikely, primarily from our own data—participants' spatial maintenance performance showed the same pattern of data suggestive of progressively increasing CE activity as in verbal maintenance and updating conditions, suggesting that differences in the probe displays themselves were not the primary cause of our differential modality effects.

These observations complete a distinct dissociation of prefrontal lateralization of sensitivity to modality-specific WM demand effects for verbal versus spatial information, with left prefrontal serial order sensitivity to verbal WM control process demands, and right prefrontal serial order sensitivity to spatial WM control process demands. In addition to these data showing lateralization of modality-specific sensitivities to CE-related demands, we also observed evidence of more task-general CE-related effects over prefrontal sites. While our left frontal region of interest demonstrated increased negativity to overall task difficulty for spatial WM tasks, we did not observe particular sensitivity to serial order effects in left prefrontal areas for spatial updating, nor in right prefrontal areas for verbal updating. We suggest that these left frontal effects in spatial maintenance and updating may reflect more task-general control processes, and not modulation of modality-specific WM control.

3.3. General discussion

The present study is informative with respect to the fractionation of modality-specific and task-general CE-related processes in prefrontal and related cortical substrates of WM abilities. Our design appears to be primarily useful in revealing CE-related processes, as opposed to substrates of representation of verbal or visuospatial WM contents. Firstly, in theoretical terms, even the easier of our two memory tasks (maintenance—remember the first three items) requires the integration of several distinct stimuli over time into a single WM set for later evaluation; our updating task (remember the last three items) requires this activity and likely additional processes as well. We suggest that ERP correlates (1) sensitive only to relevant stimulus information, (2) with selective prolonged activity following anticipated final-item stimuli, and (3) with the same areas and patterns showing increased activity with updating demands, most likely reflect control processes directing the effortful encoding, representation, and recoding of WM contents, and not the representation of this information itself. These ERP components likely do not reflect the rehearsal or maintenance of information in WM per se, as this activity does not persist over the course of a trial until a response is made (identified most clearly in the maintenance condition, where no new stimuli are required to be encoded following item 3). Our findings are particularly contrastive and complementary with recent data from

McCollough et al. (2007), who demonstrate load-sensitive, contralateral delay-period activity in posterior parietal cortex for laterally presented visuospatial target sets, suggestive of the direct neural signal of the temporary representation of this stimulus information itself.

The selective sensitivity for serial position effects at our left prefrontal area of interest for CE-demanding verbal updating, and right prefrontal area of interest for CE-demanding spatial updating, is suggestive of a substantial bilateral dissociation in prefrontal cortex for modality-specific WM control processes. In addition to these lateralized modality-specific substrates, we observed evidence of additional left hemisphere prefrontal sensitivity to overall task difficulty for spatial tasks, with generally more negative prefrontal slow wave activity across all serial positions for maintenance and updating tasks. These amplitude effects at left frontal sites without sensitivity to item-by-item differences in modality-specific visuospatial WM demands may represent more task-general CE-related processes. In addressing the fractionation of WM processes within prefrontal cortex, we demonstrate that typically lateralized modality-specific CE-related processes and more task-general CE-related processes all appear to exist within prefrontal cortex and that even within a single WM task one should expect to observe contributions from a number of these different processes. Considered together with our corresponding item-sensitive parietal effects, our data support the notion of separable verbal (left) and visuospatial (right) prefrontal substrates embodying modality-specific control processes in WM, which may recruit additional task-general substrates depending on task and performance requirements.

As an interesting final note, our study also appears to demonstrate a direct neurophysiological observation of differential strategy use across WM modalities in our high-demand updating condition. In comparison to the increasingly effortful engagement with progressive stimulus items in our verbal WM updating task, participants appeared to engage in a substantially greater degree of work in response to the first stimulus item in the spatial updating task, with subsequent second and third items requiring relatively little work to successfully integrate into their WM set. This qualitative difference in CE-related control between modalities is not a modality-specific difference per se, but reflects a distinction in the recruitment and application of CE processes relative to the particular qualities and affordances of modality-specific information—we suggest in this case, the ability to represent multiple pieces of visuospatial information in a single configural representation. Such modality-specific affordances for different kinds of WM demands would seem to be straightforward to observe given distinct enough tasks and might be adapted to be a useful approach for investigating strategic or group differences in spatial or other kinds of WM processing.

4. Experimental procedures

4.1. Participants

Eighteen individuals (15 females; mean age 22 years, range 18–34 years) from McMaster University's student population took

part in this study in exchange for course credit or as uncompensated volunteers. All participants reported normal or corrected-to-normal vision. Our recruitment notice requested right-handed participants only, although two participants reported being left-handed on debriefing; our findings did not change if we excluded these participants from analysis, and so we include their data here. Four additional participants were excluded on the basis of technical difficulties and incomplete participation, and an additional six participants were excluded due to excessively noisy ERP data. Informed written consent was obtained from each participant before the experiment.

4.2. Apparatus and stimuli

Stimulus presentation and response registration and recording were conducted with Presentation software (Version 10.3, Neurobehavioral Systems, <http://www.neurobs.com>), running on a Pentium 4 PC under a Windows XP operating system. Stimuli were presented using a 17-inch colour CRT monitor, running at a frame rate of 75 Hz and a resolution of 1024 × 768 pixels. A chin rest was used to maintain a constant viewing distance of approximately 80 cm. The experiment was conducted in a quiet, dimly lit room.

Stimuli were white digits (0–9), presented in 58-point Helvetica font on a black background, each subtending a vertical visual angle of approximately 1.5°. These stimuli were presented one at a time, at one of eight constant positions spaced evenly around the center of the screen. Eight dark grey square boxes indicated these potential stimulus positions and remained on screen throughout the experiment. These boxes were approximately 2° of visual angle square, placed approximately 2° of visual angle away from the centre of the screen. A fixation point was marked by a dark grey cross in the center of the screen. Examples of these displays are shown in the top panel of Fig. 1. On each trial, a variable sequence of single digits was displayed one at a time in order, followed by a probe display to which participants made a response. Probe displays consisted of either a centrally presented string of either three digits or two digits and a letter (A, B, D, F, H, K, M, N, P, R, T, V, or X) or a set of three or two spatial positions indicated by colouring in a subset of the ever-present stimulus placeholder boxes. Examples of these probe displays are presented in the bottom panel of Fig. 1. Stimuli were presented for 200 msec, with a randomly varying interstimulus interval (onset-to-onset) of 1200 to 1500 msec.

4.3. Procedure

The experiment consisted of two sessions both lasting approximately 30 minutes, with a short break in between. A verbal working memory session required participants to focus on the identity of presented digit stimuli, with spatial position being irrelevant, and a spatial working memory session required participants to focus on the spatial locations of digit stimuli, with identity irrelevant. Session order was counter-balanced between participants. Within each session, participants performed three different types of task—control, maintenance, and updating—presented in short blocks. Six blocks of each task type were presented in mixed and

counterbalanced order for each of the two different working memory sessions. Each of these blocks contained five trials. A trial consisted of a series of single-digit stimuli presented one at a time in order, followed by a probe display, illustrated in the top panel of Fig. 1. Digit stimuli sequences were three to eight items long, determined pseudorandomly, with three-, four-, and five-item runs each occurring with 25% probability, and six-, seven-, and eight-item runs each occurring with 8.33% probability. Within a single trial, stimulus sequences were constrained so that the digit identity and spatial position of a stimulus in run position n were different from both the identity and position of stimuli occurring in run positions $n-1$ and $n-2$. Probe displays were targets or nontargets (defined below), randomly determined but constrained to occur as two of one type and three of the other within a five-trial block.

For the *maintenance* task, participants were instructed to remember the first three items presented in a sequence (digit identities in the verbal session, spatial locations of presented digit stimuli in the spatial session), and then when the probe display appeared at the end of the random-length sequence, respond as to whether the probe information matched the stimulus information for those first three items. The bottom panel of Fig. 1 shows examples of the probe displays. For the verbal session, probe displays consisted of the initial three stimulus digits presented in order at fixation (temporarily obscuring the fixation cross) as target (match) probes, or this same display with one of the three digits changed ± 1 , both randomly determined, as nontarget (nonmatch) probes. For the spatial session, probe displays consisted of the initial three spatial positions, indicated by colouring the relevant three placeholder boxes dark grey as target probes, or this same display with one of the three spatial positions changed to an adjacent open position, randomly determined, as nontarget probes.

The *updating* task was similar to the maintenance task, except with participants instead instructed to remember the last three items presented in a sequence. Probe items were constructed as for the maintenance task, using information from the last three presented items in the random-length sequence. For the *control* task, participants were not asked to remember any information from the single digit sequences. Instead, participants were asked to monitor for either a set of three letters in the verbal session, or a set of three positions in the spatial task (i.e., the probe displays), shown at the end of the same kinds of random-length single-digit stimulus sequences as in the other tasks. For the verbal task, probe display targets were three randomly selected digits (constrained so that each of the three digits were different), with nontargets composed in the same manner, with one of these digits replaced with a letter, both randomly determined. For the spatial task, probe display targets were three randomly selected spatial positions coloured grey, with nontargets composed of only two coloured spatial positions.

Participants completed one short block of each trial type (control, maintenance, updating) as practice, before beginning each of the two sessions (verbal and spatial). Participants received written instructions on screen before each block, informing them of the task type (control, maintenance, or

updating), and instructing them to “Look for ANY 3 [digits/positions],” “Remember the FIRST three [digits/positions],” or “Remember the LAST 3 [digits/positions],” respectively. Participants responded with their right index and middle fingers on the “1” and “2” keypad keys on a standard computer keyboard to indicate match or nonmatch responses to probe displays. Response mapping was counterbalanced across participants. Instructions emphasized both speed and accuracy of performance in all tasks.

4.4. Event-related potential recording

The ActiveTwo Biosemi electrode system (BioSemi, Amsterdam, the Netherlands) was used to record continuous electroencephalographic (EEG) activity from 128 Ag/AgCl scalp electrodes. Additional six electrodes were used: four to record horizontal and vertical eye movements, located just lateral to the outer canthi and just below each eye; and two additional electrodes—common mode sense (CMS) active electrode and driven right leg (DRL) passive electrode—which substitute for the ground electrodes used by traditional systems (see documentation available from the BioSemi company for more information, <http://www.biosemi.com/fac/cms&drl.htm>). The BioSemi system has no conventional reference electrode, with monopolar signals from each active electrode stored digitally, and rereferencing done via software after initial data acquisition. In the present study, the continuous EEG signal was acquired with an open pass-band from DC to 150 Hz and digitized at 512 Hz. The signal was band-pass-filtered offline at 0.1 to 30 Hz and rereferenced to a common average reference.

ERP data manipulation, waveform averaging, and analysis were conducted with EEProbe software (ANT, <http://www.ant-software.nl>). EEG and EOG artifacts were removed using a $\pm 35 \mu\text{V}$ deviation over 200-msec intervals on all electrodes. EEG data for all trials were manually inspected offline. Trials with large eye-blink voltage deviations were excluded from analysis; remaining trials with eye blink contamination were corrected by a subtraction of VEOG propagation factors via a regression algorithm on EOG components, based on per-participant eye-blink prototype characterizations and propagation factors constructed from a minimum of 50 blink examples per participant, again with EEProbe software. Blink-corrected trials comprised 10.5% of each participant's data set on average, with 8.2% blink-corrected trials in the overall data set. ERP epochs for analysis were defined by a total 1000-msec recorded EEG epoch, with a 100-msec prestimulus baseline and 900-msec interval following stimulus onset. Trials where participants responded incorrectly to probe displays were excluded from analysis. ERP waveforms were averaged separately for each electrode for each serial position, task type (control, maintenance, and updating), and working memory condition (verbal and spatial).

4.5. Data analysis

Mean reaction times for correct trials and mean error proportions were calculated for probe trials for each subject for all combinations of task type (control, maintenance, and updating),

working memory type (verbal and spatial), and probe type (target and nontarget), collapsing over trials with different stimulus run lengths. Mean reaction time and error rate data were analysed separately via repeated-measures analysis of variance (ANOVA), with the above three factors as within-subjects variables.

While our behavioural analyses focused on overt responses to probe displays, our ERP analyses focused on stimulus-locked activity related to individual stimuli presented in the digit sequences prior to the response-demanding probe displays. Our analyses were confined to the first five temporal sequence positions, owing to the decreasing number of trials per condition in later run positions. Importantly, participants were not required to make any response directly to these single-digit stimuli. Our main ERP analyses focussed on two general regions of interest, following methods and findings from Kiss et al. (2007), and consistent with maximal amplitude effects observed from initial visual inspection of grand mean waveforms: a central parietal region of interest, comprising electrodes at approximate Cz and Pz positions, plus additional sets of two electrodes approximately 2 cm to the right and left of these positions (six electrodes total); and bilateral frontal regions of interest comprised of 2 × 3 electrode arrays centered on F3 and F4 electrode positions, respectively. The left frontal region of interest was composed of pairs of electrodes positioned at 1 cm anterior and posterior to F3, more medially at F1 and the midpoint of F1–AF1, and more laterally 1 cm posterior to F5 (F5') and 1 cm anterior and slightly lateral of FC3 (FC3'); the right frontal region of interest was symmetrically matched to these locations.

These three regions were chosen to capture potential hemispheric differences in frontal control processes across verbal and visuospatial tasks and to observe associated frontal-parietal activity. Although previous work has revealed lateralized posterior parietal activity when the task required participants to remember items presented in left versus right visual hemifields (McCollough et al., 2007), our primary focuses in parietal areas were to characterize the patterns of P300-like and late centrally maximal parietal slow wave activity previously described by Kiss et al. (2007) and to examine the potential differences in serial position ERP effects between verbal and spatial WM demands. Initial visual inspection of parietal grand mean waveform data suggested a centrally maximal set of parietal effects, with some extension to either side of the midline. Given their similarity to data from Kiss et al. (2007) and our focus on the particular item-specific patterns of sequential activity within these centrally maximal effects, we elected to focus on a midline-centered area of interest to maximize our ability to detect relevant ERP effects and not to additionally investigate parietal laterality effects.

At the central parietal region of interest, we identified two distinct epochs for analysis: a 300- to 450-msec epoch capturing a distinct P300-like component, peaking at approximately 350 msec, and a 450- to 900-msec epoch capturing extended slow wave activity, distinct from P300-like activity in the earlier analysis epoch. Mean amplitude data were assessed separately for these two epochs via three-way repeated-measures ANOVA with Greenhouse–Geisser correction, with factors of working memory type (verbal and spatial),

task type (control, maintenance, and updating), and run position (1, 2, 3, 4, and 5). At frontal regions of interest, we identified a 600- to 900-msec epoch capturing late negative slow wave activity, separate from an earlier broad bilateral negative component peaking at approximately 450 msec. Our bilateral frontal analyses were focused on late negative slow wave activity, with mean amplitude data assessed via four-way ANOVA with Greenhouse–Geisser correction, with factors of hemisphere (left and right), plus those used for the central parietal analyses described above.

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