

Interactive report

Tracking the time-course of attentional involvement in spatial working memory: an event-related potential investigation

Amishi P. Jha*

Department of Psychology and Center for Cognitive Neuroscience, University of Pennsylvania, 3815 Walnut St., Philadelphia, PA 19104, USA

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Abstract

Spatial working memory is a cognitive brain mechanism that enables the temporary maintenance and manipulation of spatial information. Recent neuroimaging and behavioral studies have led to the proposal that directed spatial attention is the mechanism by which location information is maintained in spatial working memory. Yet it is unclear whether attentional involvement is required throughout the period of active maintenance or is only invoked during discrete task-phases such as mnemonic encoding. In the current study, we aimed to track the time-course of attentional involvement during spatial working memory by recording event-related brain potentials (ERPs) from healthy volunteers. In Experiment 1, subjects performed a delayed-recognition task. Each trial began with the presentation of a brief stimulus (S1) that indicated the relevant location that subjects were to maintain in working memory. A 4.8–5.3 sec delay interval followed during which a single task-irrelevant probe was presented. The delay interval concluded with a test item (S2) to which subjects made a response indicating whether the S2-location was the same as the S1-memory location. To determine if attention was differentially engaged during discrete phases of the trial, task-irrelevant probes were presented early (400–800 msec following S1-offset) or late (2600–3000 msec following S1-offset) during the delay interval. Sensory-evoked ERPs (P1 and N1) elicited by these irrelevant probes showed attention-like modulations with greater amplitude responses for probes occurring at the S1-memory locations in comparison to probes presented at other locations. This pattern was obtained for both early- and late-delay probes. Probe-evoked activity during delayed-recognition trials was similar to activity observed when spatial attention was explicitly focused on a location in visual space (Experiment 2). These results are consistent with a model of spatial working memory in which perceptual level selective attention is utilized throughout the entire period of active maintenance to keep relevant spatial information in mind.

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1. Introduction

Working memory and selective attention are cognitive constructs central to the dynamic interplay between perception, thought and action. Yet, only recently have the details of their relationship been explored [3,10,13–15]. One class of models has suggested that selective visual attention, defined as the set of processes by which relevant information is given higher priority in perceptual, decision, and response operations [37], is ideally suited to facilitate control over the contents of working memory [3,10]. These

control operations are thought to be subserved by the coordinated effort of specialized subregions within frontal and parietal cortex that have been reported in attention tasks (e.g. Refs. [11,18,19,23,33]) and working memory tasks (e.g. Refs. [7,9,12,21,20]).

To directly assess the degree of overlap in brain regions active during voluntary orienting of spatial attention and spatial working memory, Corbetta et al. [10] manipulated the duration of the interval between an attention directing cue and a subsequent attentional target in a recent fMRI study. They demonstrated that frontal and parietal regions activated during the initial allocation of spatial attention shortly after cue presentation, continued to be active when the cue-target interval was lengthened to 7 sec. They

*Tel.: +1-215-573-0210; fax: +1-215-898-1982.

E-mail address: apjha@psych.upenn.edu (A.P. Jha).

concluded that the circuit that is active during spatial attentional orienting is identical to the circuit activated during working memory maintenance operations at longer delays. Labar et al. [24] also reported a high degree of correspondence in frontal-parietal activity during working memory and attention when there was minimal overlap in task features.

Models of attention [35] and working memory [32] propose that these frontal-parietal control operations have their modulatory effects downstream within posterior perceptual regions. In an elegant series of studies, Awh and co-workers [2–6] tested a specific hypothesis regarding perceptual level effects relating spatial working memory and spatial attention. They proposed that the online maintenance (rehearsal) of information in spatial working memory necessitates directed allocation of spatial selective attention to memory locations. This attentional allocation was predicted to bias extrastriate activity in favor of memory locations. Such biasing within extrastriate cortex has been observed during attention tasks in the form of tonic effects [8,22,25] as well as stimulus-evoked enhancements for stimuli appearing in attended versus unattended locations (e.g. Refs. [27,30]).

To test their prediction, Awh and co-workers conducted delayed-recognition experiments during fMRI [2] and ERP [6] recording. Subjects were to remember spatial locations, presented during the memory array (S1), over the course of a delay interval until a test item (S2) was presented. A continuous series of task-irrelevant probes with random onset asynchronies were presented during the delay. Activity was averaged over all delay-spanning probes. Consistent with their hypothesis, fMRI activity within extrastriate cortex as well as scalp-recorded P1 and N1 ERP components were greater in amplitude for probes appearing at memory versus non-memory locations.

One issue that remains unanswered from previous work is whether the engagement of selective attention during working memory is required throughout the entire delay interval, when maintenance operations are presumably ongoing. For example, if attention is most critical during mnemonic encoding, as has recently been suggested in studies of long-term memory [1], P1 and N1 enhancements would be expected to be greater for probes appearing shortly after the S1-memory cue is presented compared to probes presented later in the delay interval.

The aim of the current studies was to replicate and extend previous findings by tracking the time-course of perceptual-level attentional involvement in spatial working memory. ERPs were recorded to task-irrelevant probes presented during discrete time bins during the delay interval of a spatial delayed-recognition task. The extrastriate-generated [16] P1 and occipito-temporal N1 components were examined for early (400–800 msec following S1 offset) and late (2600–3000 msec) delay probes to address two specific questions. Firstly, are neural responses modulated during the delay interval in a manner similar to

that obtained when attention is explicitly directed to a location in space? Secondly, if so, is the magnitude of attention-like neural activity comparable for early and late delay probes?

2. Experiment 1

2.1. Materials and methods

2.1.1. Participants

Ten females and nine males (ages 18–34) participated in one 5-hour session. Four of these participants were eliminated because they did not comply with instructions to maintain gaze at fixation. All participants were right-handed with normal or corrected-to-normal vision. All participants provided written consent and received cash compensation.

2.1.2. Stimuli and design

Subjects viewed an NEC 4FG computer monitor from a distance of 75 cm. They were instructed to maintain fixation on a small central cross throughout the trial and their fixation was verified with both electro-oculographic (EOG) and infrared video monitoring methods. Each trial of the delayed-recognition task consisted of a memory item (S1) presented for 300 msec, a delay-interval of 4800–5300 msec, and a single test stimulus (S2) presented for 300 msec that terminated the delay-interval. The inter-trial interval was 1–1.5 s. S1 was a $1.53^\circ \times 1.53^\circ$ diamond that appeared in one of six possible primary locations on 90% of trials. S2 was a 2.29° diameter circle that appeared equiprobably at any of these positions regardless of the S1 location on that trial. These locations were roughly lateral, medial, and central within each hemifield. On the remaining 10% of the trials, stimuli occurred at one of six secondary positions which were in close proximity to the six primary locations. Although analyses were restricted to trials during which stimuli appeared at the primary locations, the purpose of having these secondary locations was to discourage subjects from adopting a behavioral strategy of verbally encoding and maintaining positional information (Fig. 1).

Subjects were instructed to remember the location of S1 and maintain that location in-mind throughout the delay interval. They made a choice-button response with the index finger of their left or right hand to indicate whether S2 did or did not match the S1 location. Subjects were encouraged to respond as quickly and accurately as possible.

During the delay-interval, a single task-irrelevant probe stimulus ($1^\circ \times 1^\circ$ square) appeared for 31 msec. Subjects were instructed to ignore the probe and were informed that this stimulus was irrelevant to the memory task. The probe occurred in the S1-location on half of the trials (memory congruent condition), and at one of the other five possible

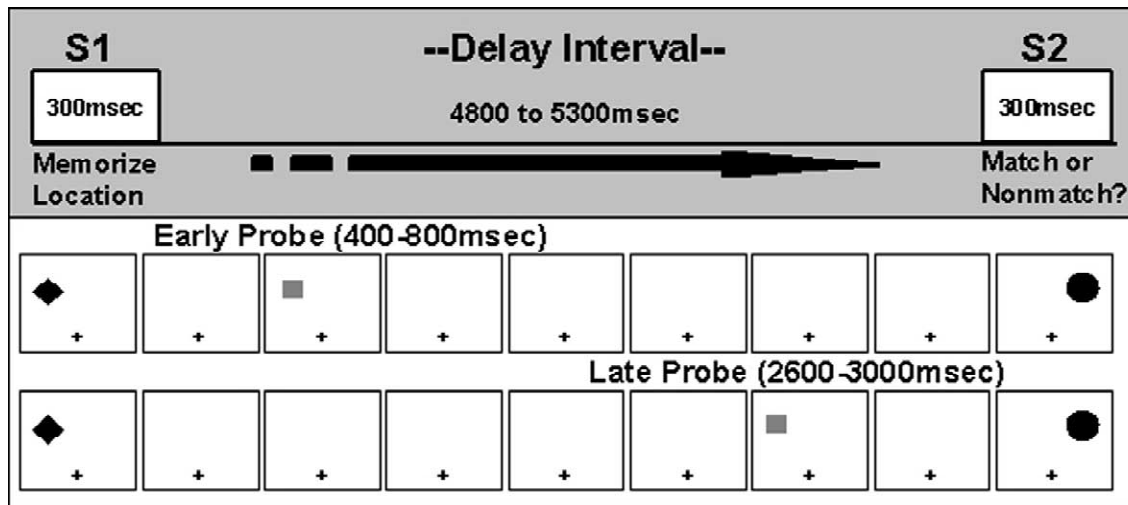


Fig. 1. Temporal sequence of events in spatial working memory task. Subjects performed a delayed-recognition task during which each trial began with the presentation of an S1 memory cue for 300 msec, followed by a delay interval of 4800–5300 msec, and ending with the presentation of an S2 test item for 300 msec. During the delay interval, a task-irrelevant probe appeared for 31 msec at either the S1 location or another location. These probes appeared early during the delay interval (400–800 msec following S1 offset) or late (2600–3000 msec following S1 offset). All stimuli appeared at one of 12 stimulus locations which were difficult to verbally recode.

primary positions on the other half (memory noncongruent condition). The probe stimulus was presented 400–800 msec (early delay-interval probe) after S1-offset on half of the trials and 2600–3000 msec (late delay-interval probe) after S1-offset on the other half of trials. Subjects were not informed of these probabilities nor were they aware of them as revealed by post-experiment questionnaires.

2.1.3. Data acquisition

Scalp potentials were recorded using 64 tin electrodes distributed over the scalp and referenced to the right mastoid. All electroencephalographic (EEG) activity as well as eye movement recordings were amplified with a bandpass of 0.01–100 Hz, and digitized at 256 Hz. Vertical eye movements and blinks were recorded with an electrode located below the left eye which was referenced to the right mastoid. Horizontal eye movements were recorded using a bipolar montage of electrodes on the outer canthus of each eye that were referenced to one another. Off-line, artifact rejection analysis was carried out to remove all trials with detectable eye-movements or amplifier blocking. For each subject, EOGs time-locked to S1-onset were averaged separately for right and left hemifield stimuli to determine if subjects had been making systematic eye-movements to the S1 locations. Any subjects showing even small systematic laterally occurring residual eye-movements (after artifact rejection), as well as subjects that showed any other deviations from fixation, were removed from further analysis (four out of 19 subjects). For the 15 remaining subjects, no more than 10% of trials in the relevant conditions were rejected due to eye movements, blinks, or amplifier blocking in the channels of interest. Thus, the ERP response patterns derived from the remain-

ing subjects were reliably free of eye movement contamination. It is therefore unlikely that eye movements are responsible for the pattern of ERP responses observed in these subjects.

For each subject, EEG was averaged over an epoch beginning 2000 msec prior and 4000 msec following relevant stimuli. The resulting ERPs were algebraically re-referenced to the mastoid contralateral to the recording site. Thus, electrodes on the left half of the scalp were re-referenced to the right mastoid, and electrodes on the right were referenced to the left mastoid, whereas electrodes in the central band were re-referenced to the average of the right and left mastoid electrode sites.

2.1.4. Data analysis

ERPs were analyzed for only those trials on which performance was correct. Since our primary aim was to determine if posterior-perceptual processing was modulated in an attention-like manner during spatial working memory, our analyses were restricted to posterior electrode sites which have been shown to produce maximal activity during the P1 and N1 time-ranges in studies of spatial attention (e.g. Ref. [28]). These are: lateral-occipital sites (OL, OR) and temporal-occipital sites (T5, T6). For each electrode pair, repeated measures analysis of variance tests (ANOVA) were performed for time windows corresponding to the P1 and N1 components. In each ANOVA, mean amplitude measurements were analyzed with the following factors: spatial congruency between probe and S1 (congruent versus noncongruent with memory location), probe latency following S1 (early: 400–800 msec versus late: 2600–3000 msec), electrode site (contralateral versus

ipsilateral), probe hemifield (left versus right), and probe location within the visual field (lateral, medial, central).

2.2. Results

2.2.1. Behavioral results

To determine if the task-irrelevant probes interfered with performance during the delayed-recognition task, an ANOVA was conducted on response times (RT) and accuracy scores (percent correct) with the following factors: probe congruency (congruent versus noncongruent) and probe latency (early versus late). Neither response times nor accuracy was significantly influenced by probe congruency ($P > 0.3$) or probe timing ($P > 0.1$). Overall, subjects were very accurate and fast in performing the memory task (88% correct, mean RT=643 msec).

2.2.2. Electrophysiological results

2.2.2.1. P1 component. A focal positive-going voltage deflection was observed 78–117 msec following probe onset with an occipito-temporal distribution (see Fig. 2A). This was identified as the P1 component. As predicted by the attentional maintenance hypothesis, there was a main effect of probe congruency with greater amplitude responses for congruent versus noncongruent probes at electrode sites OL/OR ($F(1,14)=8.74$; $P < 0.01$) and T5/T6 ($F(1,14)=6.59$; $P < 0.02$). Importantly, this congruency effect in P1 amplitude was present for early and late probes (see Fig. 2C and E). The magnitude of the congruency effect (defined as the difference in amplitude during congruent and noncongruent trials) did not differ as a function of probe latency as revealed by a non-significant congruency \times latency interaction ($P > 0.1$). The overall amplitude values were greater at contralateral electrode sites. P1 amplitudes did not significantly differ as a function of probe hemifield or location within the hemifield.

2.2.2.2. N1 component. An occipito-temporal negative-going voltage deflection observed 125–191 msec following the probe was identified as the N1-component (see Fig. 2B). Similar to the P1-component, the N1 was significantly amplitude modulated as a function of probe congruency with greater amplitude responses for congruent versus noncongruent probes. A main effect of memory congruency was observed at both electrode pairs tested: OL/OR ($F(1,14)=9.48$; $P < 0.008$) and T5/T6 ($F(1,14)=7.75$; $P < 0.014$). There was no significant congruency by latency interaction at any electrode site for this component (see Fig. 2D and F). Thus, both early and late probes were significantly amplitude modulated as a function of probe congruency. The overall amplitude values were greater at ipsilateral electrode sites. N1 amplitudes did not signifi-

cantly differ as a function of probe hemifield or location within the hemifield.

Thus, the P1 and N1 congruency effects observed during early- and late-delay probes are consistent with the hypothesis that attention is directed toward memory locations throughout the trial in the service of ongoing maintenance in working memory. To be clear, even though the probes occurred at the S1-memory location on 50% of trials, the probes themselves could not have caused the P1 and N1 enhancements described above. This is because P1 and N1 modulations index the amount of attentional biasing within extrastriate cortex that is present *before* the stimulus appears [31]. This is thought to occur using a gain control mechanism [17]. Any reorienting initiated due to the appearance of the 31 msec probe would be observed subsequent to the probe-evoked activity itself, perhaps during S2-evoked activity. We were concerned about the possibility that subjects may have voluntarily or automatically reoriented attention to the probe location after the probe appearance. However, the behavioral data reveal that neither probe location nor latency significantly influenced behavioral performance at S2.

3. Experiment 2

The goal of Experiment 2 was to confirm that attentional modulations are observed for task-irrelevant stimuli presented during perceptual-based attention tasks as opposed to mnemonic tasks. Previous studies have manipulated delay length during delay-recognition tasks [21] and attentional orienting tasks [10] to assess the degree of overlap between brain regions involved in working memory and attention. Although the strength of such delay-manipulations is that stimulus properties can be held constant across attention and working memory requirements, it is likely that mnemonic and selective attentional orienting remain conflated due to task requirements. In Experiment 2, stimulus constancy across experiments was sacrificed in the service of ensuring that attention and working memory were unconfounded. This was done by using a spatial attentional orienting task (e.g. Ref. [34]) whose key feature was that S2 responses were directed by S1-location and not based on mnemonic requirements of maintaining S1's location in working memory.

3.1. Materials and methods

3.1.1. Participants

Eight females and seven males (ages 19–23) participated in one 5-hour session. Four of these participants were eliminated because they did not comply with instructions to maintain gaze at fixation. All participants were right-handed with normal or corrected to normal vision. All participants provided written consent and received cash compensation.

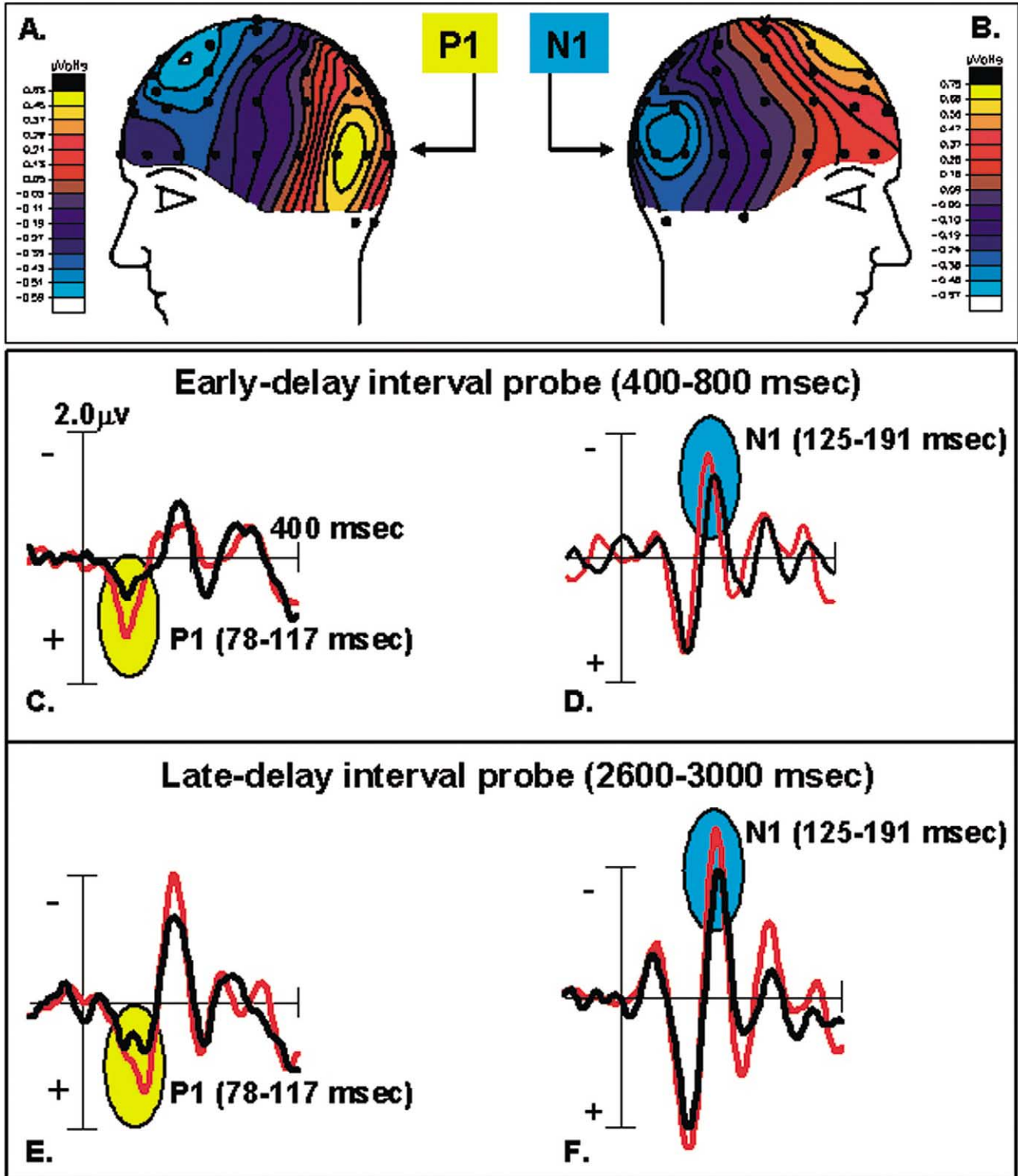


Fig. 2. ERP results for the task-irrelevant probes during spatial working memory. (A) Scalp topographic voltage maps for the difference in amplitude for congruent minus noncongruent early delay probes (400–800 msec following S1-offset) in the P1 time-range (78–117 msec following probe onset). (B) Scalp topographic voltage maps for the difference in amplitude for congruent minus noncongruent early delay probes in the N1 time-range (125–191 msec following probe onset). (C and D) Waveform responses for probes during the P1 time-range at contralateral occipital electrodes and during the N1 time-range at ipsilateral occipital electrodes for probes presented 400–800 msec following S1-offset. (D and F) Waveform responses for probes during the P1 time-range at contralateral occipital electrodes and during the N1 time-range at ipsilateral occipital electrodes for probes presented 2600–3000 msec following S1-offset. The effects were collapsed for right and left stimuli at lateral, medial, and central probe locations within each hemifield. Red waveform=congruent; black waveform=noncongruent.

3.1.2. Stimuli and design

Similar to Experiment 1, the trial sequence was: S1 presentation (300 msec), followed by an S1–S2 interval (1200–2000 msec) and ending with S2 presentation (300 msec). Unlike Experiment 1 which required active maintenance of location information over the delay, the time-period between S1 and S2 in Experiment 2 was an ‘attention-interval’ during which spatial attention was to be voluntarily directed to the relevant location indicated by S1. S1 equiprobably appeared in one of two locations which were the left-most and right-most positions from Experiment 1 (8.03° lateral to fixation). Both locations were demarcated by box outlines that were part of the standing background on the screen throughout the experiment (see Fig. 3). This was done to minimize working memory load for relevant locations. The subjects’ task was to direct attention to the S1-location throughout the trial and wait for S2 to appear there. When S2 appeared at the S1 location, subjects were to determine if it was a short or long bar. Thus, the judgment at S2 was orthogonal to the match/or nonmatch status of S2’s location relative to S1. The relative size of S2 was titrated across subjects and across runs to ensure that subject performance was above chance (>60% correct) but not too high so as to make directed allocation of attention to the relevant position perfunctory. When S2 appeared in the unattended hemifield, subjects were instructed not to respond. On half of the trials, task-irrelevant probes that were congruent or noncongruent with the direction of attention were presented during the S1–S2 interval for 31 msec. The probes were presented 400–800 msec after S1. On the remaining trials during which no probes were presented, the S1–S2 interval was 400–1200 msec (25% of total trials) or 1200–2000 msec (25% of total trials). These no-probe trials were included to encourage subjects to begin attending immediately after S1-onset and discourage subjects from adopting a strategy of orienting to the S1 position only after a probe appeared.

3.1.3. Data analysis

Separate ANOVAs were conducted for waveforms time-locked to probe onset for each electrode pair (OL, OR and T5, T6). In each ANOVA, mean amplitude measurements were analyzed with the following factors: probe congruency (congruent versus noncongruent with attention location), probe hemifield (left versus right), and electrode site (contralateral versus ipsilateral).

3.2. Results

3.2.1. Behavioral results

Note that in this experiment behavioral responses were to be made to valid targets only. Overall, subjects achieved above chance performance and were fast in performing the attention task (63% correct, and mean RT=810 msec). To determine if probe congruency with the attention location influenced performance, an ANOVA was conducted with a single factor: probe congruency (congruent versus noncongruent with the location of attention). Neither speed nor accuracy was significantly influenced by congruency of the task-irrelevant probe stimulus ($P>0.53$).

3.2.2. Electrophysiological results

3.2.2.1. P1 component. Similar to the results in Experiment 1, a focal occipito-temporal positive-going voltage deflection was observed 78–117 msec following probe onset for the P1 component (see Fig. 4A). As predicted by previous studies of spatial attention (e.g. Ref. [27]), there was a main effect of probe congruency with greater amplitude responses for probes that appeared at attended versus unattended locations (congruent greater than noncongruent) at electrode sites OL/OR ($F(1,10)=8.56$; $P<0.01$) and T5/T6 ($F(1,10)=11.01$; $P<0.003$). The overall amplitude values were greater at contralateral electrode

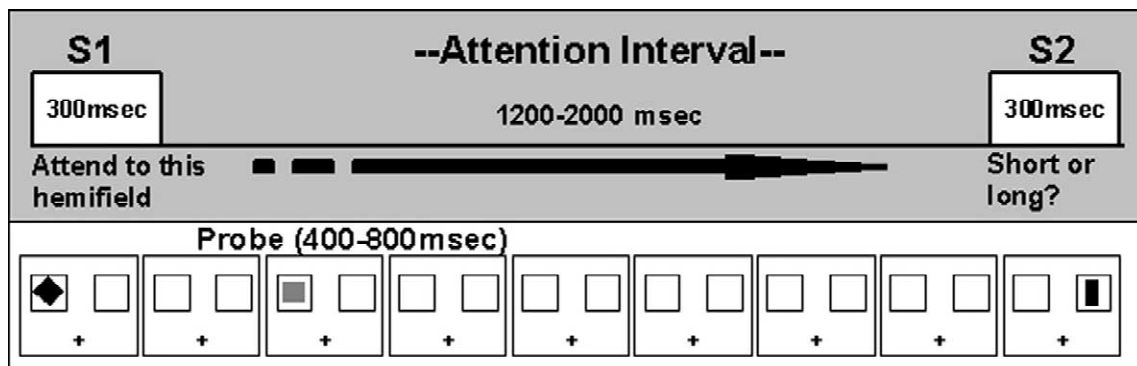


Fig. 3. Temporal sequence of events in spatial attention task. Subjects performed an attention-orienting task during which each trial began with the presentation of an S1 for 300 msec which directed subjects to attend to one of two locations demarcated by box outlines that were part of the standing background. S1 offset was followed by an attention interval during which attention was to be sustained at the S1-location. During half of the trials, a task irrelevant probe stimulus appeared in the attended or unattended hemifield for 31 msec during this interval. Each trial ended with the presentation of an S2 discrimination stimulus for 300 msec. The subjects were to determine if the S2 stimulus was a short or long bar.

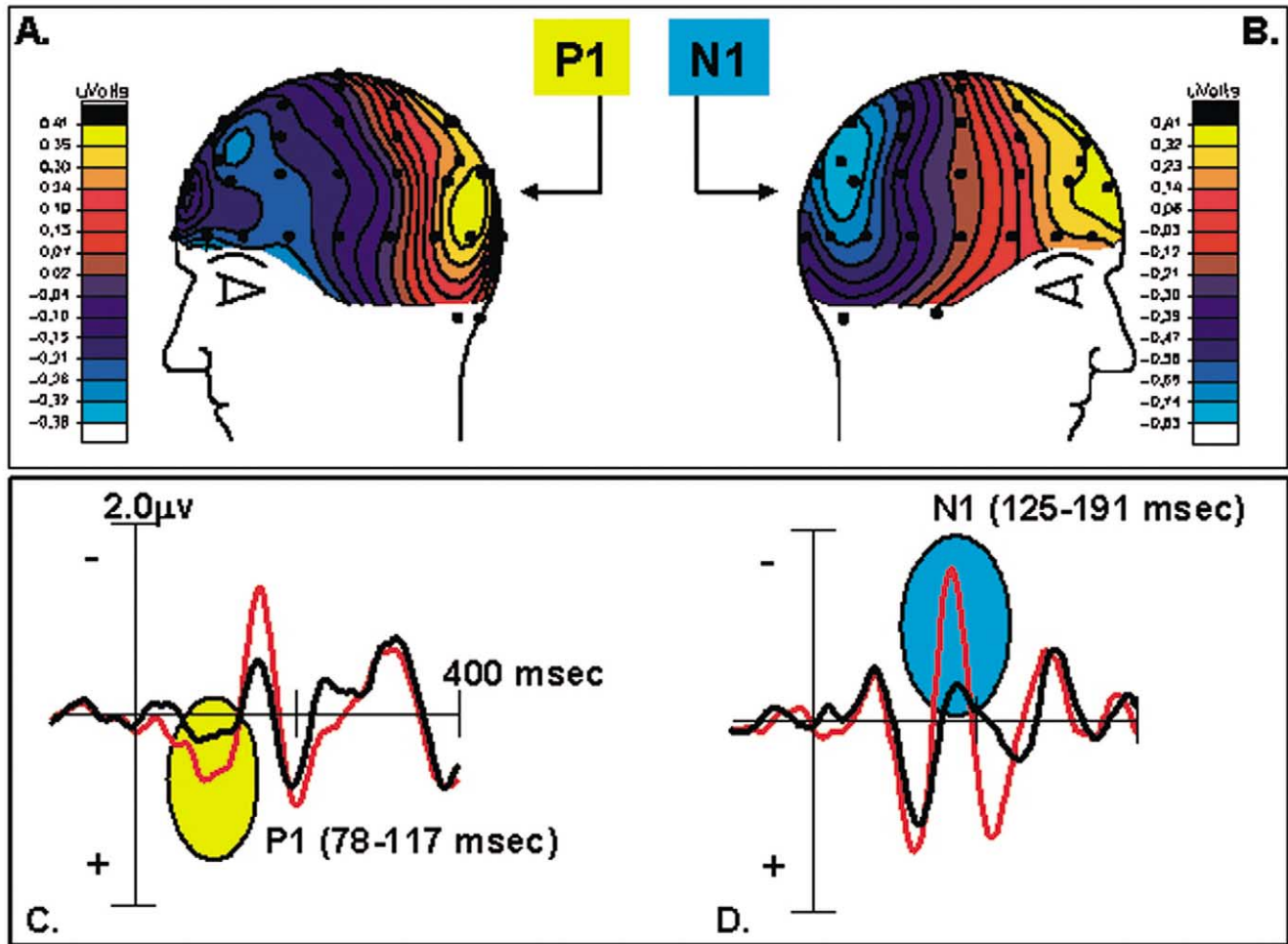


Fig. 4. ERP results for task-irrelevant probes during spatial attention task. (A) Scalp topographic voltage maps for the difference in amplitude for congruent minus noncongruent attention probes in the P1 time-range (78–117 msec following probe onset). (B) Scalp topographic voltage maps for the difference in amplitude for congruent minus noncongruent probes in the N1 time-range (125–191 msec following probe onset). (C and D) Waveform responses for probes during the P1 time-range at contralateral occipital electrodes and during the N1 time-range at ipsilateral occipital electrodes for probes presented 400–800 msec following S1-offset. Red waveform=congruent; black waveform=noncongruent.

sites (see Fig. 4C). P1 amplitudes did not significantly differ as a function of probe hemifield.

3.2.2.2. N1 component. Similar to the P1 effects, the N1 component had a focal posterior distribution (see Fig. 4B) and was significantly amplitude modulated as a function of probe congruency. A main effect of congruency was observed at both electrode sites OL/OR ($F(1,10)=15.12$; $P<0.003$), and T5/T6 ($F(1,10)=19.9$; $P<0.001$). The overall amplitude values were greater at ipsilateral electrode sites (see Fig. 4D). N1 amplitudes did not significantly differ as a function of probe hemifield.

4. Discussion

In the current set of studies, the time-course of attentional involvement in working memory was investigated. Task-irrelevant probes were presented early and late during

the delay interval of a spatial working memory delayed-recognition task (Experiment 1). We reasoned that if continued allocation of spatial attention is required for ongoing maintenance, the magnitude of attention-like enhancements in the P1 and N1 ERP components should be comparable for early and late delay probes. ERPs were analyzed for probes that occurred at the memory location (congruent) and probes occurring elsewhere (noncongruent). Both P1 and N1 components had larger amplitude responses for congruent versus noncongruent probes. Importantly, the magnitude of the congruency effect was comparable for early and late delay probes. The timing and amplitude of probe-evoked activity during Experiment 1 was comparable to probe activity during a spatial selective attention task (Experiment 2).

In addition to the amplitude modulations in the P1 and N1 time-ranges, the scalp distributions of these components were investigated. There was a high degree of correspondence between the topographic voltage distribu-

tion for the P1 component across Experiments 1 and 2. The strongest activation occurred at the contralateral occipital electrode sites in both studies.

Although the N1 component had a maximal peak at ipsilateral occipital electrode sites in both Experiments 1 and 2, the correspondence was not as strong for the scalp distribution of this component across the two experiments. The magnitude of the N1 effect was larger and the scalp distribution was broader during the spatial attention task relative to the spatial working memory task. Since the N1 component is believed to reflect the engagement of feature-based attentional processing [26], it is possible that the attentional discrimination task utilized in Experiment 2 required a greater engagement of this process relative to the spatial working memory task.

Nonetheless, the P1 and N1 components both resulted in significant amplitude modulations in occipital electrode sites for both early- and late-delay probes. Previous spatial attention studies that have combined ERP recordings with neuroimaging methods have demonstrated that the generator site for the P1 component is in extrastriate cortex [28,29]. Thus, the current results are consistent with a model of working memory in which extrastriate activity is biased in favor of processing stimuli occurring at relevant working memory locations throughout the period of active working memory maintenance.

It is important to keep in mind that the high degree of similarity between responses to probes presented during the spatial working memory task and the spatial attention task suggests that perhaps the same cognitive mechanism is being performed during both of these tasks. Namely, spatial attention may be actively engaged during the retention interval of a spatial working memory task to keep information active. Alternatively, it is possible that attention-like responses during spatial working memory were observed only because subjects adopted an attentional orienting strategy to complete the delayed-recognition task. If spatial attention was only a preferred strategy and is not an integral part of spatial working memory maintenance, memory performance should not be affected if subjects are prevented from attending during the delay interval. However, recent behavioral studies [5,36] suggest that when subjects are prevented from attending during working memory, their performance suffers. Thus, it is unlikely that spatial attentional involvement is simply a preferred strategy for maintaining information in working memory. Rather, spatial attention appears to be a vital part of working memory maintenance.

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