

The Role of Spatial Selective Attention in Working Memory for Locations: Evidence from Event-Related Potentials

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Abstract

■ We investigated the hypothesis that the covert focusing of spatial attention mediates the on-line maintenance of location information in spatial working memory. During the delay period of a spatial working-memory task, behaviorally irrelevant probe stimuli were flashed at both memorized and nonmemorized locations. Multichannel recordings of event-related potentials (ERPs) were used to assess visual processing of the probes at the different locations. Consistent with the

hypothesis of attention-based rehearsal, early ERP components were enlarged in response to probes that appeared at memorized locations. These visual modulations were similar in latency and topography to those observed after explicit manipulations of spatial selective attention in a parallel experimental condition that employed an identical stimulus display. ■

INTRODUCTION

The neural substrates of spatial working memory have been investigated extensively both in nonhuman primates (for reviews, see Fuster, 1995; Ungerleider, 1995; Goldman-Rakic, 1987) and in humans (reviewed in Awh & Jonides, 1998). These studies have implicated an interactive frontal-parietal network of cortical areas that mediates the on-line storage of location information. These data have supported functional dissociations among different types of working memory (e.g., between spatial and object working memory—Courtney, Ungerleider, Keil, & Haxby, 1996; Smith et al., 1995; Wilson, O'Scalaidhe, & Goldman-Rakic, 1993; and between spatial and verbal working memory—Smith, Jonides, & Koeppe, 1996), but less progress has been made in understanding *how* this frontal-parietal system accomplishes the goal of maintaining location information on-line.

A hypothesis was suggested on the basis of findings of considerable overlap between the frontal and parietal brain regions that participate in spatial working memory on the one hand, and spatial selective attention on the other (Awh, Smith, & Jonides, 1995; Awh & Jonides, 1998). In addition, human neuroimaging studies have shown activations in posterior extrastriate visual areas in association with spatial working memory (e.g., Awh et al., 1999; Courtney et al., 1996; Owen, Evans, &

Petrides, 1996; Smith et al., 1995; Jonides et al., 1993) that are comparable to those observed during spatial selective attention (e.g., Gratton, 1997; Mangun, Hopfinger, Kussmaul, Fletcher, & Heinze, 1997; Woldorff et al., 1997; Heinze et al., 1994; Petersen, Corbetta, Miezin, & Shulman, 1994). Thus, it has been proposed that the active maintenance of location-specific representations may be mediated by focal shifts of spatial selective attention to the memorized locations (Awh et al., 1995; Awh, Jonides, & Reuter-Lorenz, 1998; Smyth & Scholey, 1994).

Two lines of behavioral evidence support the hypothesis of attention-based rehearsal. First, it has been observed that when subjects are holding a location in working memory, the visual processing of stimuli appearing in that location is facilitated relative to stimuli appearing in nonmemorized locations (Awh et al., 1995, 1998). This fulfills a clear prediction of the attention-based rehearsal hypothesis that follows from the well-documented effects of spatial selective cueing on reaction time and target detection (e.g., Anllo-Vento, 1995; Luck et al., 1994; Posner, 1980). In addition, several studies have demonstrated that if subjects are hindered in their ability to attend the memorized locations, memory accuracy is impaired (Awh et al., 1998; Smyth & Scholey, 1994; Smyth, 1996). These interference studies make the important point that

not only does the locus of spatial attention correspond with the memorized locations, but also that attention makes a functional contribution to the maintenance of location information.

Although neuroimaging studies have provided evidence that common cortical areas are active during spatial attention and spatial working-memory operations, these measurements of cerebral blood flow patterns do not indicate whether or not the timing of the stimulus selection processes within these cortical areas is equivalent in the two situations. Event-related brain potential (ERP) recordings have shown that stimulus selection during spatial attention occurs at an early level of processing and involves an amplitude modulation of sensory-evoked brain activity in extrastriate visual cortex beginning at around 80 msec after stimulus onset (e.g., Hillyard & Anllo-Vento, 1998; Anllo-Vento & Hillyard, 1996; Harter & Anllo-Vento, 1991; Eason, Harter, & White, 1969). In particular, stimuli at attended locations elicit enhanced positive (P1, latency 80–130 msec) and negative (N1, latency 150–200 msec) ERP components in relation to stimuli at unattended locations. These observations have led to the idea that spatial attention operates as a gain control mechanism that modulates the amplitude of sensory signals in the extrastriate visual pathways (Hillyard & Munte, 1984; Hillyard & Anllo-Vento, 1998; Hillyard, Vogel, & Luck, 1998). Accordingly, if these same spatial attention mechanisms participate in maintaining information in spatial working memory, we would expect to find that stimuli presented at locations being held in memory would elicit ERPs with similar spatio-temporal patterns of amplitude enhancement as those observed in attention experiments.

The present study tests this prediction by making a direct comparison of the ERP modulations observed during two separate conditions that used an identical stimulus display but required subjects to perform tasks of spatial attention and spatial working memory, respectively. In the memory condition (illustrated in Figure 1), subjects were required to remember three locations in either the right or the left visual field during an 8.7-sec delay interval. While subjects held these locations in memory, a series of unilateral visual probes (checkerboards) were flashed in random order either to the same visual field as the memorized locations, or to the opposite hemifield. The subjects made no behavioral responses to the probes, and visual ERPs to the probes at memorized and nonmemorized locations were recorded. At the end of the delay period, a single memory target was presented, and subjects indicated whether or not its location was the same as any of the three they were holding in memory. In the attention condition, the same subjects performed an explicit spatial attention task. The stimulus display was the same as the one used during memory trials, except for the near-threshold flashes (targets) that appeared interspersed amongst the behaviorally irrelevant visual

probes. Subjects were instructed to pay attention to the visual field indicated by the cues,¹ and to press a button whenever they detected a near-threshold target in that visual field. Thus, a direct comparison was made between the effects of spatial rehearsal and spatial selective attention on the ERPs elicited by identical visual probes.

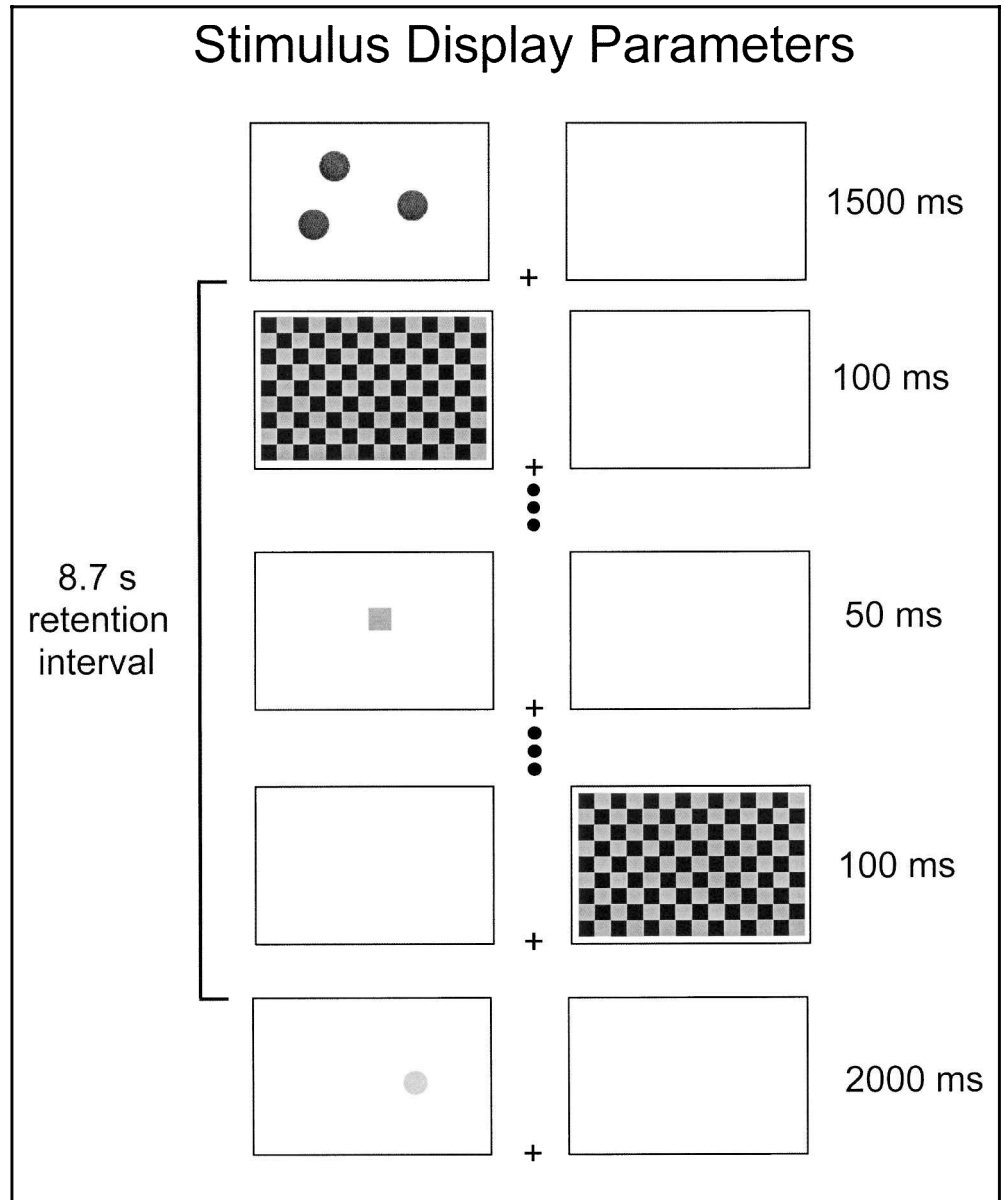
RESULTS AND DISCUSSION

Figures 2 and 3 display the grand average ERP waveforms elicited by the visual probes that appeared during the retention interval of the spatial memory task, and during the target-detection period of the attention task. Three major ERP components were evident in all conditions: a P1 deflection peaking at around 125 msec after probe onset that was largest at posterior temporal and occipital electrodes sites; a posterior N1 peak with a latency of around 190 msec and an amplitude maximum at parietal scalp-sites; and an anterior N1 that peaked at around 150 msec after probe onset and was maximal over frontal and central areas. As Figures 2 and 3 illustrate, the probes that were superimposed on those locations to-be-memorized or to-be-attended (i.e., cued locations) elicited larger amplitudes for all three components than did the probes that appeared at uncued locations [$F(1, 11) = 44.6, p < .05$; $F(1, 11) = 13.1, p < .05$; $F(1, 11) = 10.1, p < .05$ for the main effect of cue on P1, posterior N1 and anterior N1 components, respectively]. These cueing effects were very similar in amplitude in the memory and attention tasks, and no component showed a significant interaction of cue and task.

Consistent with previous electrophysiological studies of spatial selective attention (Anllo-Vento & Hillyard, 1996; Clark & Hillyard, 1996; Mangun, 1995), the modulations of the P1 component were greatest over the electrodes contralateral to the visual field of probe presentation [$F(1, 11) = 5.3, p < .05$; for the interaction of cue, visual field, and hemisphere]. The P1 effect differed between the memory and attention conditions in one respect; the modulations observed contralateral to left-visual-field stimuli in the attention condition were larger than in the memory condition [$F(1, 11) = 6.2, p < .05$; for the interaction of cue, visual field, hemisphere, and task].²

The visual ERP modulations observed in the memory and attention tasks were similar in scalp topography as well as in time course. These components are best visualized in terms of difference waves formed by subtracting the ERPs to the probes on the uncued side from the ERPs to the same stimuli when that side was cued (i.e., memorized or attended). Figures 4 and 5 show isovoltage contour maps of the difference waves corresponding to the P1, anterior N1, and posterior N1 components. For probes in both visual fields, the modulations of the P1 component were focused at occipito-temporal electrode sites contralateral to the probes, and

Figure 1. Schematic of the trial events in the memory and attention trials. The initial cues (circles) designated the locations to be remembered in the memory condition, and the side to be attended in the attention condition. Circles in red (cross-hatched) indicated the relevant side in both conditions. Probes (large checkerboards) occurred at random in left and right visual fields. Targets (small squares) appeared *only* during the spatial attention condition. Otherwise, all aspects of the stimulus displays were identical across conditions.

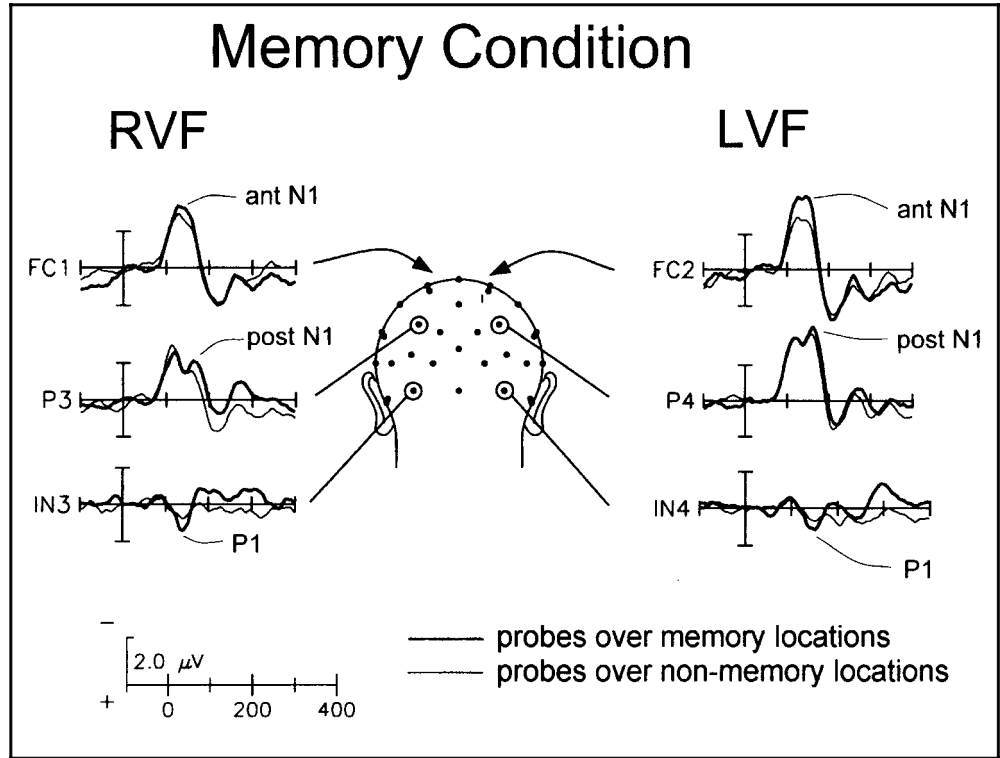


the distributions were similar for the memory and attention tasks. The anterior N1 effects were more broadly distributed over frontal/central electrode sites in response to the right-field probes. The left-field probes elicited a similar response in the memory condition, but were concentrated over more posterior sites in the attention condition. The modulations of the posterior N1 component were largest over central/parietal electrode sites, with the distributions extending to more lateral sites for right-field stimuli than for left-field stimuli. In both the memory and attention conditions, the posterior N1 modulations were larger in the right visual field.

A repeated-measures ANOVA of the normalized-differences wave amplitudes tested the apparent similarities in component topography in the two tasks. The interaction of task, hemisphere, and electrode site failed to

reach significance for the anterior N1 or posterior N1 [$F(17, 187) < 1.6$ in both cases], but this interaction was significant for the P1 component [$F(17, 187) = 4.5, p < .05$]. This interaction for the P1 component reflects the larger visual modulations contralateral to the visual probes in the attention condition than in the memory condition. Visual inspection of the component topographies suggests that this interaction was driven mainly by the left-visual-field responses, and this interpretation is supported by a significant interaction of task, hemisphere, electrode site, and visual field for the P1 component [$F(17, 187) = 4.1, p < .05$]. Finally, the interaction of task and electrode was significant only for the anterior N1 component [$F(17, 187) = 4.0, p < .05$], reflecting a more anterior scalp distribution of this effect in the memory condition than in the attention condition.

Figure 2. ERP waveforms elicited by behaviorally irrelevant probes superimposed upon memorized and nonmemorized locations. ERPs shown are from three representative scalp sites over the hemisphere contralateral to the probes appearing in the right visual field (RVF) and left visual field (LVF).



In summary, similar amplitude enhancements were elicited by the same irrelevant visual probes whether they had to be remembered or to be attended, supporting the idea that spatial rehearsal involves selective spatial orienting towards locations held in working memory. The ERP signature of these visual modulations was very similar in amplitude and latency across the two

conditions, but some differences were observed in the component topography of these tasks. The anterior N1 component was localized over more anterior electrode sites in the memory condition than in the attention condition, and the P1 component had a stronger contralateral focus for left visual field probes in the attention condition than in the memory condition. Although the

Figure 3. ERP waveforms elicited by behaviorally irrelevant probes appearing over attended (cued side) and unattended (uncued side) locations (in the spatial attention condition).

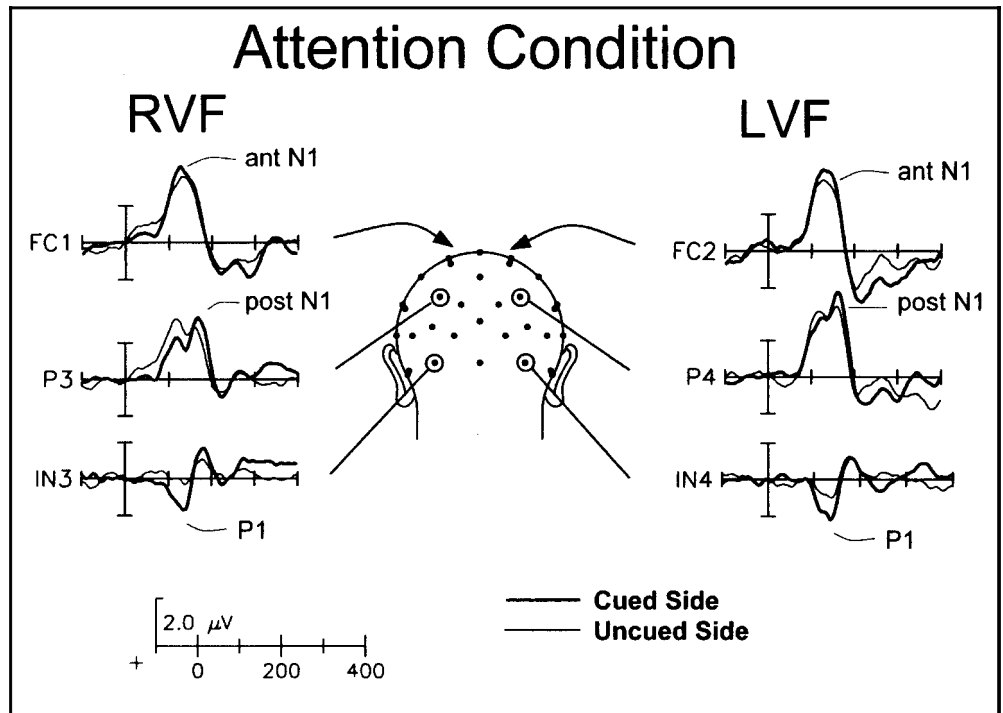
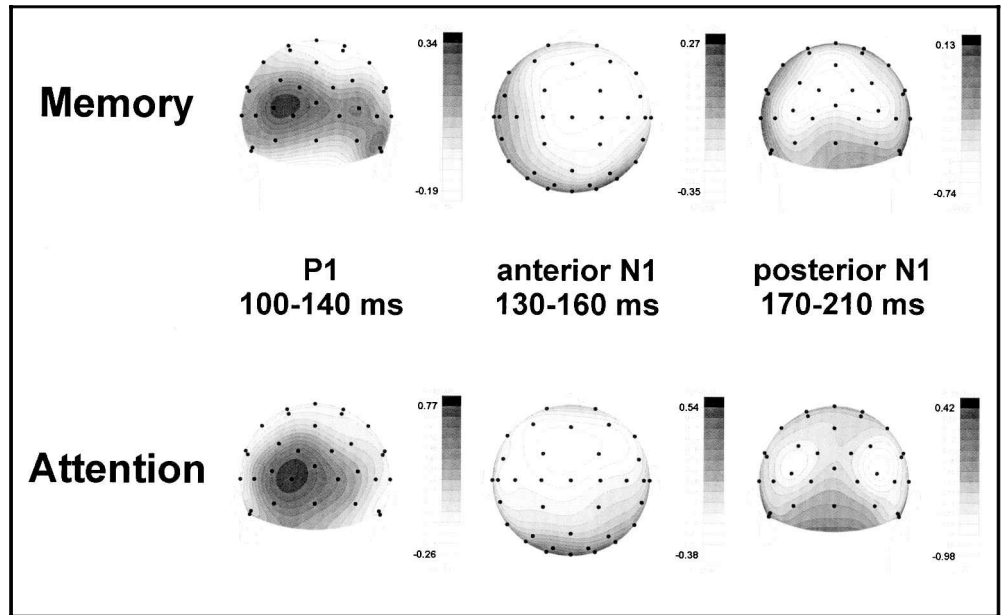


Figure 4. Isovoltage contour maps of the P1 (100–140 msec), anterior N1 (140–160 msec) and posterior N1 (160–190 msec) to right visual field stimuli.

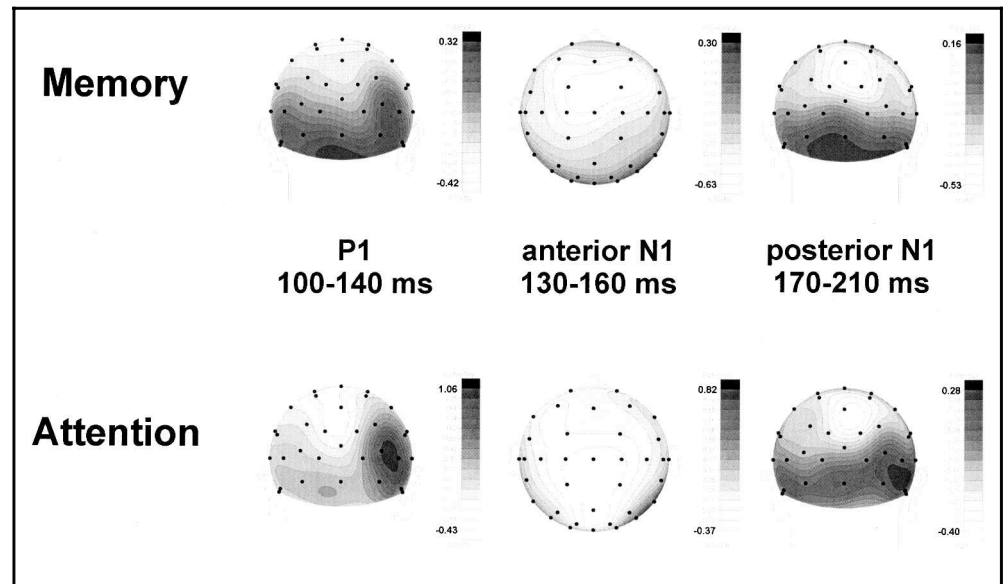


stimulus displays were virtually identical in the two tasks (except for the presence of dim target stimuli in the attention condition), it is difficult to rule out differences in subjects' orienting strategies during these tasks. While the visual modulations observed in both tasks suggest selective spatial orienting, there may have been differences in the way spatial attention was distributed in the memory and attention conditions. In the attention condition, subjects were responsible for detecting targets anywhere within the entire area inside the rectangle on the cued side. In the memory condition, however, our hypothesis would suggest that subjects were attending to three specific locations within the visual field during a single trial. These putative differences in orienting strategy may account for some of the differences we ob-

served in the scalp topography of the visual modulations across tasks.

These data extend previous evidence regarding the neural mechanisms of spatial rehearsal in working memory. While neuroimaging studies have shown that similar cortical regions are recruited during spatial working memory and spatial attention, the current studies show that spatial rehearsal produces an enhancement of the early P1 (110–140 msec) and N1 (140–160 msec) components of the ERP to stimuli at memorized locations. Moreover, the timing and scalp topography of these visual ERP modulations were similar to those that were observed after explicit manipulations of spatial selective attention. These ERP similarities provide strong support for a common mechanism of facilitated early processing

Figure 5. Same as Figure 4 for left visual field stimuli.



in the visual pathways during both spatial rehearsal and spatial attention.

The P1 modulations observed in this study had a ventral-lateral scalp distribution in both the memory and attention conditions. Previous source analyses of such P1 distributions have suggested that these effects originate in ventral-lateral extrastriate cortex (Martinez et al., 1999; Clark & Hillyard, 1996; Heinze et al., 1994). These localization data are in line with fMRI data that show activation of similar early visual areas during spatial rehearsal (Awh et al., 1999). This anatomical correspondence suggests that the rehearsal-related modulations that have been observed in extrastriate visual cortex reflect the early facilitation of visual processing for locations maintained in memory.

The present results converge with previous evidence to support a model of attention-based rehearsal in which an interactive frontal and parietal network mediates the allocation of spatial attention to locations that are held in working memory. We propose that this spatial focusing of attention results in location-specific changes in early visual processing, which allows the prolonged activation of spatially specific representations in working memory. Further work is needed to determine the extent of overlap between the brain systems that mediate spatial working memory and spatial selective attention. One possibility is that spatial selective attention comprises a subset of a larger network that mediates the maintenance of spatial information in working memory (e.g., Awh & Jonides, 1998). If so, the delineation of these nonoverlapping components will be a key goal for advancing our understanding of spatial working memory.

METHODS

Subjects

Twelve volunteers (nine males, three females, age range 19–30 years) were paid to participate in this experiment. Nine subjects were right-handed and three (males) were left-handed. Two additional subjects were eliminated because of failure to maintain fixation during the experimental trials. All subjects had normal or corrected-to-normal vision.

Tasks and Stimuli

The stimuli were presented on a computer-controlled video monitor placed 75 cm from the subject. The central fixation cross was visible throughout each block of trials and was flanked by two rectangular boxes outlined in white (see Figure 1). Each box was approximately 9° wide and 6° tall, and was situated in the upper visual field with its lower edge along the horizontal

meridian. The inner edge of each box was 3° lateral to the fixation point. Memory locations were selected at random from within a central 8.5° × 5.5° zone of the outline boxes.

Memory Condition

At the beginning of each trial, three cues (red dots, each 0.8° in diameter) marked the locations to be memorized within one of the boxes. Subjects were instructed to remember the locations of the red dots. Beginning 1,500 msec after the offset of the cues, a sequence of 16 unilateral visual probes was presented. Probe durations were 100 msec and the interstimulus interval varied pseudo-randomly between 300 and 500 msec, with the constraint that all probe presentations were completed by 7.2 sec after cue offset. The probes were rectangles, filled with a gray and black checkerboard pattern that filled the entire region inside a single outline box. The checkerboard pattern had a luminance of 0.4 cd/m², with a check-size of 0.5°. Eight probes appeared within each box during each trial, and the order of the right and left probe presentations varied randomly. At 8.7 sec after the offset of the cues, a single green dot (memory probe) with a diameter of 0.8° appeared within the box in the cued side box. The green dot matched the location of one of the three cued positions on 50% of the trials.

Subjects held one response key in each hand (corresponding to “yes” and “no”) and indicated whether the memory probe occupied the same position as any of the three that they were holding in memory. Subjects were instructed to give priority to accuracy over speed. Each subject received 32 trials of practice before the experimental session began. Trial-by-trial feedback was provided during practice, so that subjects could optimize memory performance. After practicing and for the rest of the experiment subjects were informed of their overall accuracy at the end of each block (32 trials per block). The mean accuracy of memory judgments during the experimental blocks was 63%.

Attention Condition

The stimulus display for the attention trials was identical to that of the memory trials, except that target stimuli were also presented during the interval when probe stimuli occurred. Subjects were instructed to direct attention towards the box where the red dots appeared, and to press a button (held in the dominant hand) each time they detected a target within the attended box. The targets were small, dim gray squares (0.9° on each side) with a luminance of 0.04 cd/m². The duration of each target was 50 msec. The timing of the target presentations was randomly determined, with the constraint that no target appeared within 100 msec of another target or a visual probe. Targets could appear anywhere within the

outline boxes, and their positions were randomly determined for each trial. During each trial, between zero and three targets were presented independently within each box; all event configurations were equiprobable.

Subjects received 32 trials of practice on the attention task before the experimental blocks began. They were informed of hits, false alarms, and misses as they occurred during practice. Responses occurring between 200–1500 msec after target onset were considered hits. During the experimental blocks, subjects were informed of their overall performance after each block. During experimental blocks, subjects detected an average of 81% of targets with an average of 4.0 false alarms per block.

Four memory and four attention blocks were administered during separate halves of the experimental session, which lasted about 2.5 hr. Task order was counterbalanced across subjects.

Recording and Analysis

The EEG was recorded from 42 scalp sites using non-polarizable electrodes mounted in an elastic cap using a modified 10–20 system montage. The standard sites were FP1, FP2, Fz, F3, F4, FC1, FC2, FC5, FC6, F7, F8, Cz, C1, C2, C3, C4, C5, C6, CP1, CP2, Pz, P3, P4, O1, O2, T3, T4, T5, T6, and left mastoid, with the right mastoid serving as reference. Additional intermediate sites were Ipz, Inz, IN3, IN4, IN5, IN6, PO1, PO2, TO1, TO2, CT5, and CT6 (see Clark, Fan, & Hillyard, 1995; Clark & Hillyard, 1996). An electrode placed below the left eye was used to monitor eye blinks and vertical eye movements. A bipolar pair of electrodes placed just lateral to the right and left external canthi were used to monitor horizontal eye movements. The EEG from each site was digitized at 250 Hz and amplified with a bandpass of 0.01–80 Hz.

ERPs were averaged off-line using a computer program that extracted overlapping epochs of the EEG beginning 500 msec before the visual probes and continuing for 1000 msec poststimulus. Artifact rejection was performed off-line before averaging to remove epochs containing blinks, eye movements, muscle activity, or amplifier blocking. An additional procedure was also used to ensure the absence of systematic changes in fixation that might contaminate the spatial attention effects. EOGs were averaged separately for different experimental conditions over the temporal window of an entire trial (10-sec windows); these measurements allowed us to search for any slow drifts in fixation that might have been correlated with the locus of the cues. These averages did not reveal any systematic eye movements or drifts towards the cued locations.

ERPs to probes were averaged separately according to visual field (cued or uncued), condition (memory or attention), the side of the memory or attention cue (cued or uncued), visual field where probes were

Table 1. Measurement Windows and Electrode Sites Used to Analyze the Major ERP Components

<i>Parameter</i>	<i>P1</i>	<i>Anterior N1</i>	<i>Posterior N1</i>
Measurement window (msec)	110–140	140–160	160–190
Electrode sites	O1, O2, IN3, IN4, IN5, IN6, TO1, TO2, T5, T6	F3, F4, FC1, FC2, C1, C2, C3, C4, CP1, CP2	O1, O2, IN3, IN4, IN5, IN6, TO1, TO2, T5, T6, P3, P4, PO1, PO2

presented (left or right) and electrode locations. The amplitude of each component was quantified as the mean voltage within a specified latency window, relative to a 100-msec prestimulus baseline (latency windows and electrode sites measured are specified in Table 1). For each of the principal ERP components (P1, anterior N1, and posterior N1), a repeated measures ANOVA was carried out using four factors: cued side (whether the visual probes appeared were presented in the same side as the locations that were cued to be memorized or attended, or on the opposite side), task (memory or attention), visual field (left or right), and hemisphere (left or right contralateral or ipsilateral—i.e., the side of the electrode relative to that of the evoking stimulus).

In order to evaluate the similarities in scalp distribution of the ERP modulations in the two tasks, ANOVAs were carried out on the topographies of the cued minus uncued difference waves for the P1, anterior N1, and posterior N1 components. For these analyses, components were normalized according to McCarthy and Wood (1985). These repeated measures ANOVAs included factors of task (memory vs. attention), visual field (right vs. left), hemisphere (right vs. left), and electrode site (using all sites specified in Table 1, plus F7/8, Fp1/2, and T3/4).

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Notes

1. From here on, we designate as “cues” the initial displays consisting of three red dots that signaled the beginning of a trial. In the memory condition, these stimuli marked the three locations to be memorized, while in the attention condition, they indicated the visual field to be attended.
2. These analyses revealed a few other minor interactions. Both the posterior N1 and anterior N1 components were larger over contralateral electrode sites [$F(1,11) = 7.0, p < .05$; $F(1,11) = 8.7, p < .05$; for the interaction of visual field and

hemisphere on the posterior N1 and anterior N1 components]. In addition, the posterior N1 component showed a significant interaction of task and visual field. The posterior N1 evoked by right visual field probes was smaller in the memory task than in the attention task [$F(1,11) = 6.9, p < .05$]. Finally, in both the memory and attention conditions, the posterior N1 modulations were larger in the right visual field than in the left, for a significant interaction of cue and visual field [$F(1,11) = 11.2, p < 0.05$]. These interactions were peripheral to the main cueing effects of interest and will not be considered further.

3. This analysis also revealed significant interactions of hemisphere and site during the latency of the posterior N1 and the anterior N1 components. In this case, however, the interactions appeared to reflect idiosyncratic site-specific differences between hemispheres. Because the primary focus of these analyses was to identify task-related interactions (i.e., significant differences in the topography of attention effects across the memory and attention tasks), we will not attempt to interpret these interactions further.

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