Research report

Dynamics of the spatial scale of visual attention revealed by brain event-related potentials

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Abstract

The temporal dynamics of the spatial scaling of attention during visual search were examined by recording event-related potentials (ERPs). A total of 16 young participants performed a search task in which the search array was preceded by valid cues that varied in size and hence in precision of target localization. The effects of cue size on short-latency (P1 and N1) ERP components, and the time course of these effects with variation in cue-target stimulus onset asynchrony (SOA), were examined. Reaction time (RT) to discriminate a target was prolonged as cue size increased. The amplitudes of the posterior P1 and N1 components of the ERP evoked by the search array were affected in opposite ways by the size of the precue: P1 amplitude increased whereas N1 amplitude decreased as cue size increased, particularly following the shortest SOA. The results show that when top-down information about the region to be searched is less precise (larger cues), RT is slowed and the neural generators of P1 become more active, reflecting the additional computations required in changing the spatial scale of attention to the appropriate element size to facilitate target discrimination. In contrast, the decrease in N1 amplitude with cue size may reflect a broadening of the spatial gradient of attention. The results provide electrophysiological evidence that changes in the spatial scale of attention modulate neural activity in early visual cortical areas and activate at least two temporally overlapping component processes during visual search.   © 2001 Elsevier Science B.V. All rights reserved.

1. Introduction

When a spatial cue directs a person's attention to a region of the visual field, a stimulus presented there is detected and discriminated faster and more accurately than when the same stimulus is presented elsewhere [18,45]. Processing of a target stimulus is also facilitated by the *precision* of cues to target location. Compared to a large, imprecise cue, a small, precise cue speeds reaction time (RT) to a target in both detection [1] and visual search tasks [12,13].

The effects of cue size have been extensively examined in the context of visual search. In the typical study, participants are required to identify a target presented in an array of objects such as letters [12,13]. The search array is preceded by a cue that varies in size over trials. When a range of cues from small to large is provided within a block of trials, target RT shows continuous modulation with such trial-to-trial changes in cue size. Target RT increases monotonically with cue size, pointing to a mechanism of dynamic adjustment of the spatial scale of attention [12,13]. The slope of the RT-cue size function reflects the efficiency and dynamic range of the attention scaling mechanism. For example, compared to normal controls, demented individuals show markedly reduced slope, indicative of a highly constricted and relatively inflexible spatial scale of attention [43,44].

The neural mechanisms underlying the spatial scaling of attention have not been investigated to date. To do so, we used event-related potentials (ERPs) because their high temporal resolution is well suited to uncovering the

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dynamics of the spatial scaling of attention during visual search. Several ERP studies of cued spatial attention in vision have been reported following a pioneering report by Eason [10], but, unlike the present study, cue size was not varied in these studies [20,32,33,35,36,40,46]. In the typical study, spatial attention is directed by a cue to either the left or right visual field and targets always appear in the same location and in isolation within either visual field. A prominent finding from these previous studies is that spatial cueing modulates the amplitudes of target-evoked ERP components recorded from scalp sites over lateral occipital cortex when the target appears at the cued location. Validly cued targets evoke larger P1 (80–120 ms) and N1 (160–200 ms) ERP components over posterior scalp areas in both detection [10,19,34] and discrimination tasks [20,26,32].

Extensive analyses of the P1 component indicate that spatial cueing enhances target-related cortical activity in extrastriate visual processing areas approximately 50–100 ms following stimulus onset [4,32]. Functional brain imaging studies have suggested that a fronto-parietal network of cortical areas may act as the source for this extrastriate modulation which is involved whenever spatial attention is shifted [6,8]. In addition, there is also evidence that other brain regions, including the superior frontal, posterior parietal, temporo-parietal and temporo-occipital cortices are involved in visuospatial attention [7,23,24].

Greenwood et al. [13] proposed that cue-driven attentional shifting and attentional scaling represent two inter-related aspects of the covert attention system. If so, then the P1 and N1 ERP components should also be modulated by manipulations of the spatial scale of attention, namely by changes in cue size. Previous studies have only examined the effect of cue-directed shifts of spatial attention on these ERP components, without examining changes in the spatial scale of attention.

The effect of cue-driven attention shifting on target RT varies with the cue-target interval or stimulus onset asynchrony (SOA) [45]. RT to a validly cued target typically declines with SOA until an optimal point of facilitation is reached and then increases as the SOA is increased beyond that point. Recent work has indicated a time course to effects of location cues on the P1 ERP component as well. Hopfinger and Mangun [22] found that while the P1 to a target was larger for a cued than for an uncued location at a short SOA, P1 was larger at the *uncued* location at a longer SOA. The reduction in P1 amplitude at long SOAs could not be attributed to a simple neuronal refractory effect between cue and target. In the present study we also examined the influence of SOA on attentional scaling. Previous behavioral studies have shown that the cue size effect on RT develops over time, with maximal facilitation at an SOA of about 500 ms [13].

The present experiment examined the effects of cue size driven changes in attentional scaling on short-latency (P1 and N1) ERP components and the time course of these

effects with variation in cue-target SOA. Cues of variable size were followed by a search array containing a specified target. Luck and co-workers [26–30] have also reported several ERP studies in which spatial attention effects were assessed. However, our study differed from this work not only in the use of variable size cues, but also in the task conditions. Luck et al. [30] varied the search task because they were interested in assessing the attentional demands of feature and conjunction search [47]. They presented a probe stimulus following the onset of the search array and recorded ERPs to the probe in both search conditions. In contrast, we kept the search task constant and varied the size of the precue and the SOA. We recorded ERPs separately both to the precue and to the search array. This allowed an assessment of the neural effects of attentional scaling and the time course of these effects.

2. Methods

2.1. Subjects

Sixteen students (12 male and five female) ranging in age from 22 to 32 years (mean 28.3) from The Catholic University of America and University of Maryland participated as paid volunteers. All subjects were healthy, right-handed, and had corrected visual acuity of 20/40 on a Rosenbaum Pocket Vision Screener.

2.2. ERP recording

The electroencephalogram (EEG) was recorded using an electrode cap with 14 tin scalp electrodes placed at midline sites Fz, Cz, Pz, Oz, and lateral sites at C3, C4, P3, P4, T5, T6, O1, O2, OL, and OR, with the reference on the right mastoid. The OL and OR sites were located half way between O1 and T5 and between O2 and T6, respectively. The vertical electrooculogram (EOG) was recorded with electrodes placed above and below the right eye. All inter-electrode impedances were maintained below 5 kΩ. The EEG and EOG were amplified using a 0.1–100 Hz bandpass and continuously sampled at 250 Hz/channel for off-line analysis. ERPs were averaged over a 1000-ms epoch including a 200-ms prestimulus baseline. Trials with EOG artifacts (mean EOG voltage exceeding ±65 μV) and those contaminated with artifacts due to amplifier clipping, bursts of electromyographic (EMG) activity, or peak-to-peak deflection exceeding ±65 μV were excluded from averaging.

2.3. Stimuli

A location-cued visual search task based on one developed by Greenwood et al. [13] was used. A search array was preceded by a precue that indicated the subsequent

target location. Cues varied in size and hence in their spatial precision. The SOA between the precue and target was varied randomly over the following three ranges of intervals: (1) short (230–350 ms), (2) medium (500–650 ms), and (3) long (800–950 ms). Each trial began with a 5×5 grid of lines (43.6° wide×30.5° tall) presented for 300 ms, after which the location precue was shown. As shown in Fig. 1, the precue was a rectangle superimposed on this grid. There were three cue sizes: (1) small (1×1 grid, 8.7×6.1°), (2) medium (2×2 grid, 17.4×12.2°), and (3) large (3×3 grid, 26.2×18.3°). Following one of the three SOAs, the cue was turned off and the search array was presented with the target appearing within the area indicated by the precue. The target was a vertically oriented crescent curving either to the left or the right and surrounded by ten horizontally oriented crescents defined as distractors (see Fig. 1). The ten distractors were always present in the search array on every trial and for each precue size. For the small precue size, only a single target appeared within the cued area. However, in order to reduce the potential confound of spatial uncertainty and within-cued area distractor interference, the number and location of distractors was randomly varied for the medium and large cue sizes, so that the large cued area did not necessarily contain more distractors than the medium size precue. Fig. 1 shows an example trial where both the medium and large cues contained two distractors. The target stimulus always appeared within the cued area so that all trials were valid, with the exception of 10% catch trials on which no target was presented.

2.4. Procedures

Following presentation of the 5×5 grid for 300 ms, the location precue appeared for one of the three SOAs before the search array containing the target and distractors was presented for 1500 ms (Fig. 1). Either the target alone or the target with several distractors (for medium and large size precues) was presented inside the cued area depending on the size of the cue. The task was to decide whether the crescent's horns were pointing to the right or to the left. The subject was instructed to press the left button with his/her left thumb if the horns of the crescent pointed to the left and to press the right button with the right thumb if the horns pointed right. Subjects were asked to respond as quickly and as accurately as possible.

2.5. ERP data analysis and statistics

The adjacent response (Adjar) filter method [50] was employed in order to remove the possibility that changes in the early ERP components evoked by the search array might be caused by overlapping neural activity evoked by the precue. The averaged epoch for ERPs was 1000 ms including a 200-ms pre-stimulus baseline. EEG epochs evoked by each precue size and SOA conditions were averaged separately (nine ERPs each for the precue and for the target for each combination of cue size and SOA). The actual number of individual trials per ERP waveform ranged from 43 to 59 (mean 52).

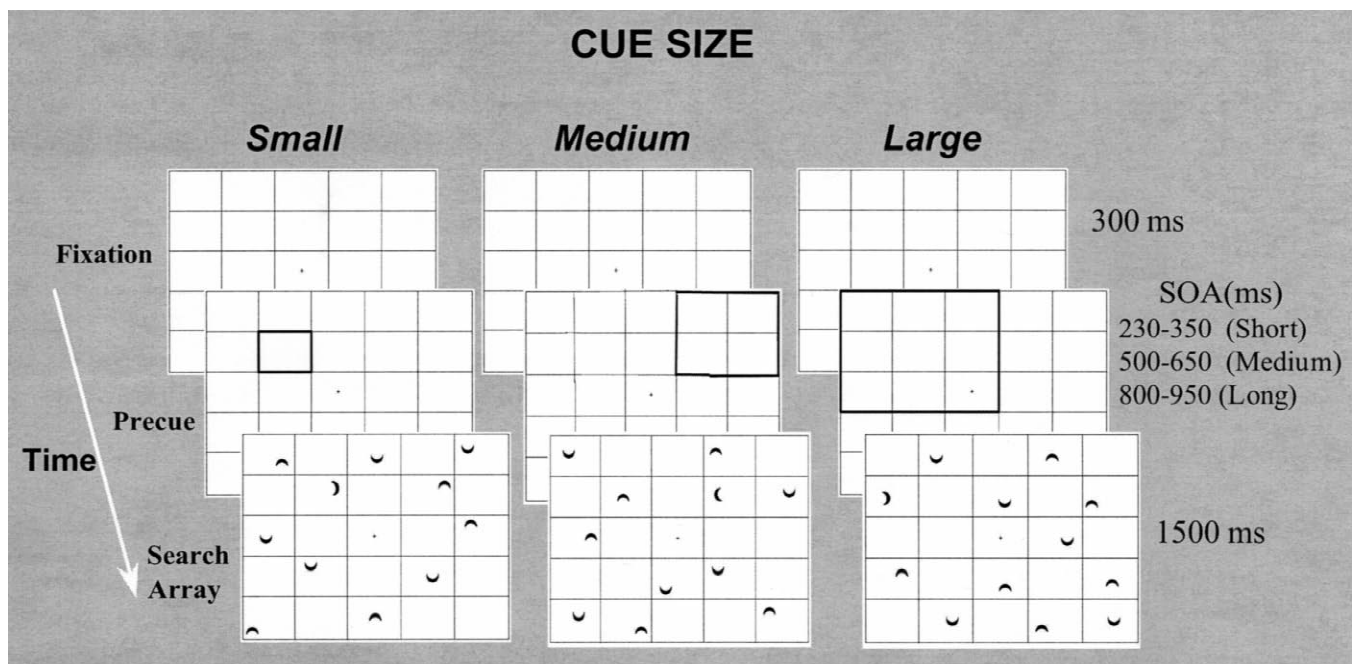Previous work suggests that attention modulates the P1

Fig. 1. Example of stimuli showing the fixation grid, precue, and search array. The target is the vertically oriented crescent, presented among ten horizontally oriented distractor crescents.

recorded from posterior sites (OL, OR, T5, T6) [19,22]. Hence P1 was analyzed from posterior sites only in the 50–150-ms time window. The visual N1 component may have separable anterior and posterior subcomponents [32,49]. Hence the anterosuperior N1 (at Fz, Cz, C3 and C4 sites) and inferoposterior N1 (at T5, T6, Oz, OL, OR, O1 and O2) were analyzed separately in 75–125 and 140–180 ms time windows, respectively. Peak amplitudes were determined by calculating the value from baseline to the respective peak. Results were expressed as mean±standard error (S.E.).

The latencies and amplitudes of ERP components were analyzed using three-way repeated measures analyses of variance (ANOVAs). The ANOVA factors were precue size (three levels: small, medium, large), SOA (three levels: short, medium, long), and electrode site (four sites for anterosuperior N1 and seven sites for inferoposterior P1 and N1). The p values of all main and interaction effects were corrected using the Greenhouse–Geisser method for repeated-measures effects. In comparing the scalp distributions of different components, the data were first

normalized to control for distribution×electrode interactions resulting simply from differences in component amplitude [38].

3. Results

3.1. Behavioral performance

Mean accuracy proportions and median RTs were calculated for each participant for each condition. As shown in Fig. 2A, the mean accuracy rate, error rate and failure to respond were 94.9, 1.4, and 3.7%, respectively. Thus accuracy was very high across all conditions. Nevertheless, accuracy decreased as precue size increased ($F_{2,15} = 20.90$, $P < 0.0001$). Failure to respond increased as precue size increased ($F_{2,15} = 19.79$, $P < 0.0001$).

Median RT increased significantly with cue size ($F_{2,15} = 76.70$, $P < 0.0001$), and SOA ($F_{2,15} = 5.21$, $P < 0.05$). The mean RTs were 579.9, 675.6, 821.1 ms for the small, medium and large cue sizes, respectively. As shown in Fig.
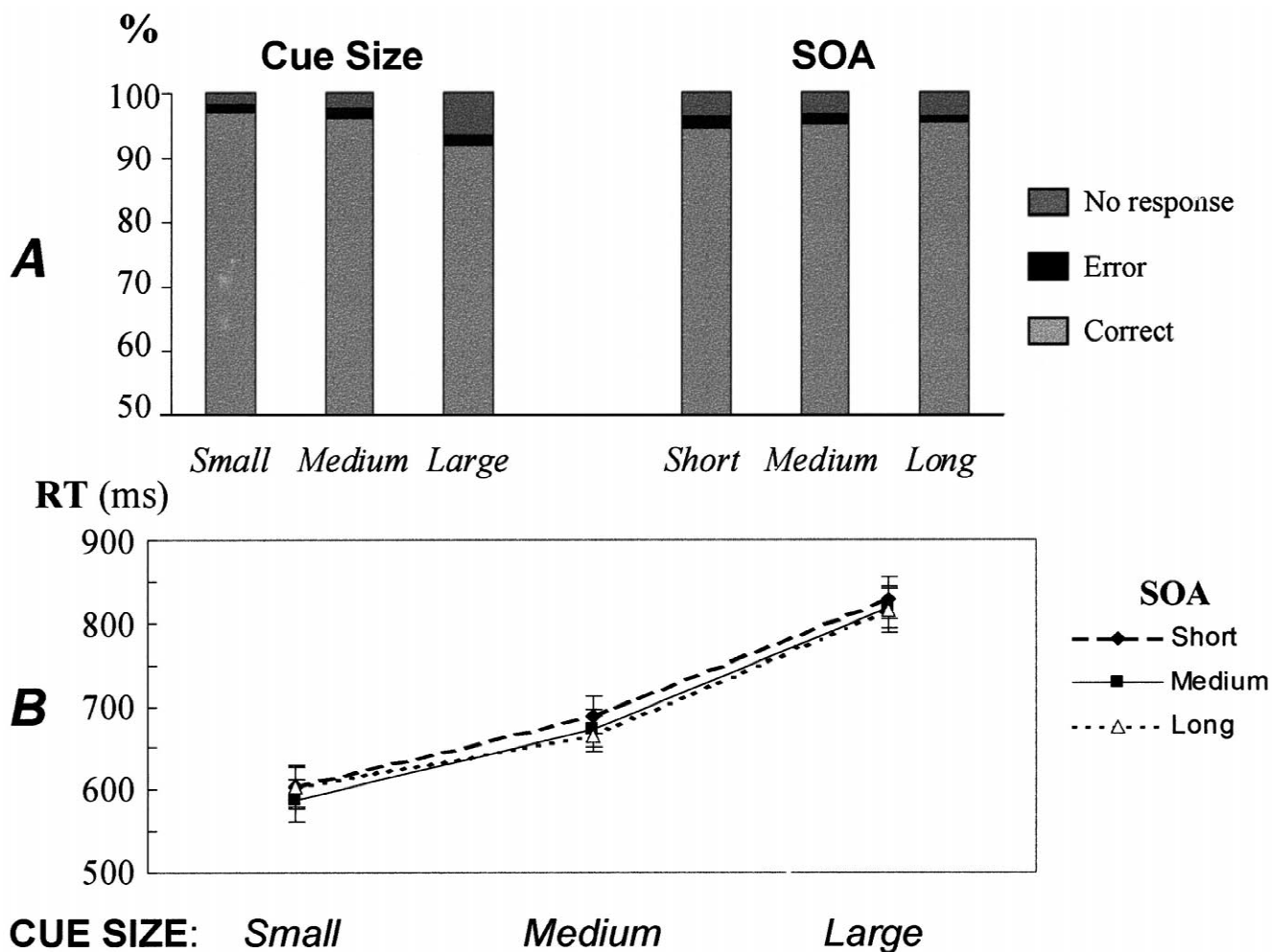

Fig. 2. (A) Top: Mean accuracy, error, and no response rates for the three size cues (left) and three SOA conditions (right). (B) Bottom: Reaction time (RT) as a function of cue size for each SOA.
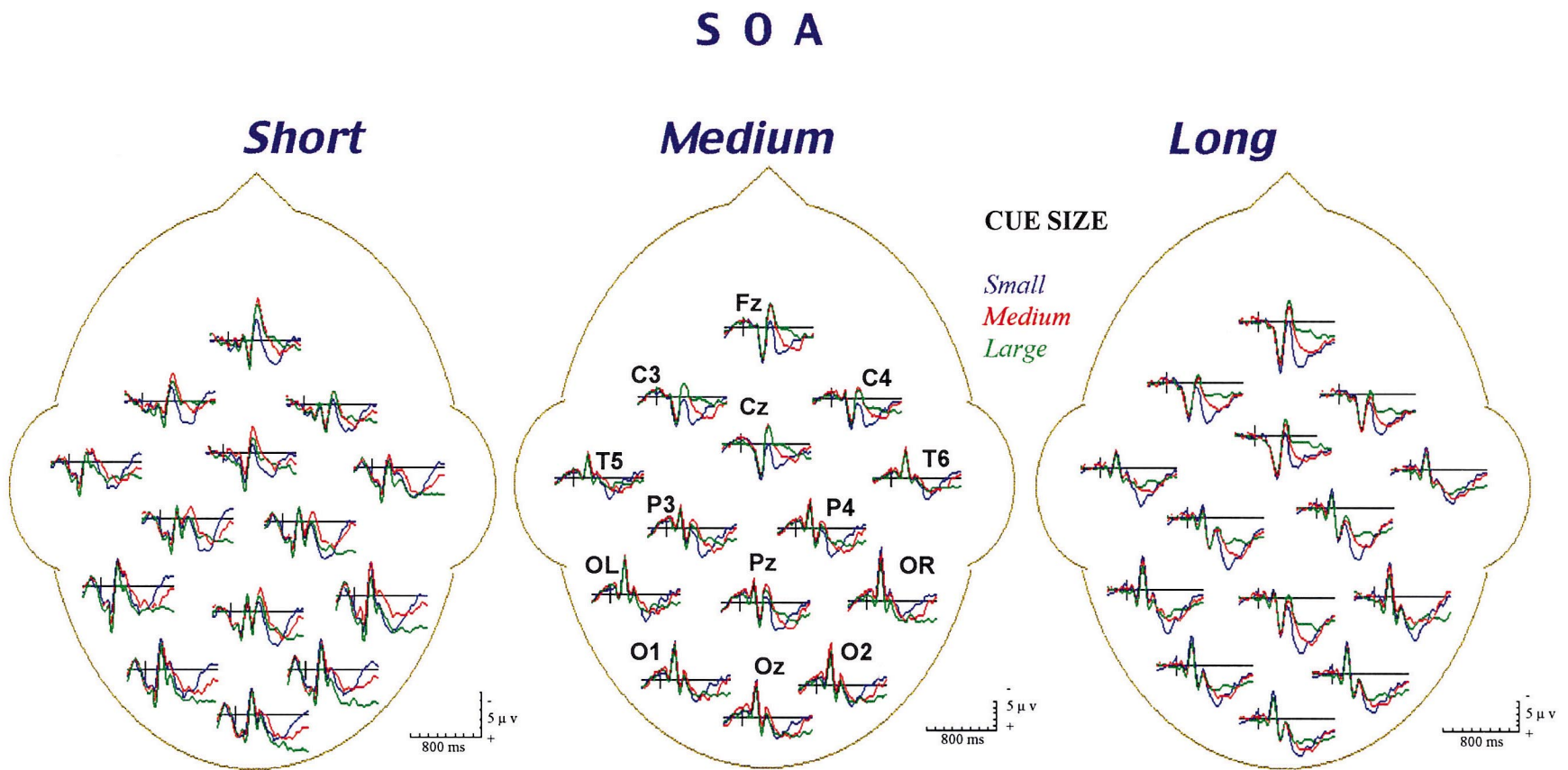
Fig. 3. Grand-average (*n*=16) ERP waveforms evoked by the search array for the small (blue line), medium (red line) and large precue sizes (green line) in short (left, SOA 230–350 ms), medium (middle, 500–650 ms) and long (right, 850–900 ms) SOA conditions.
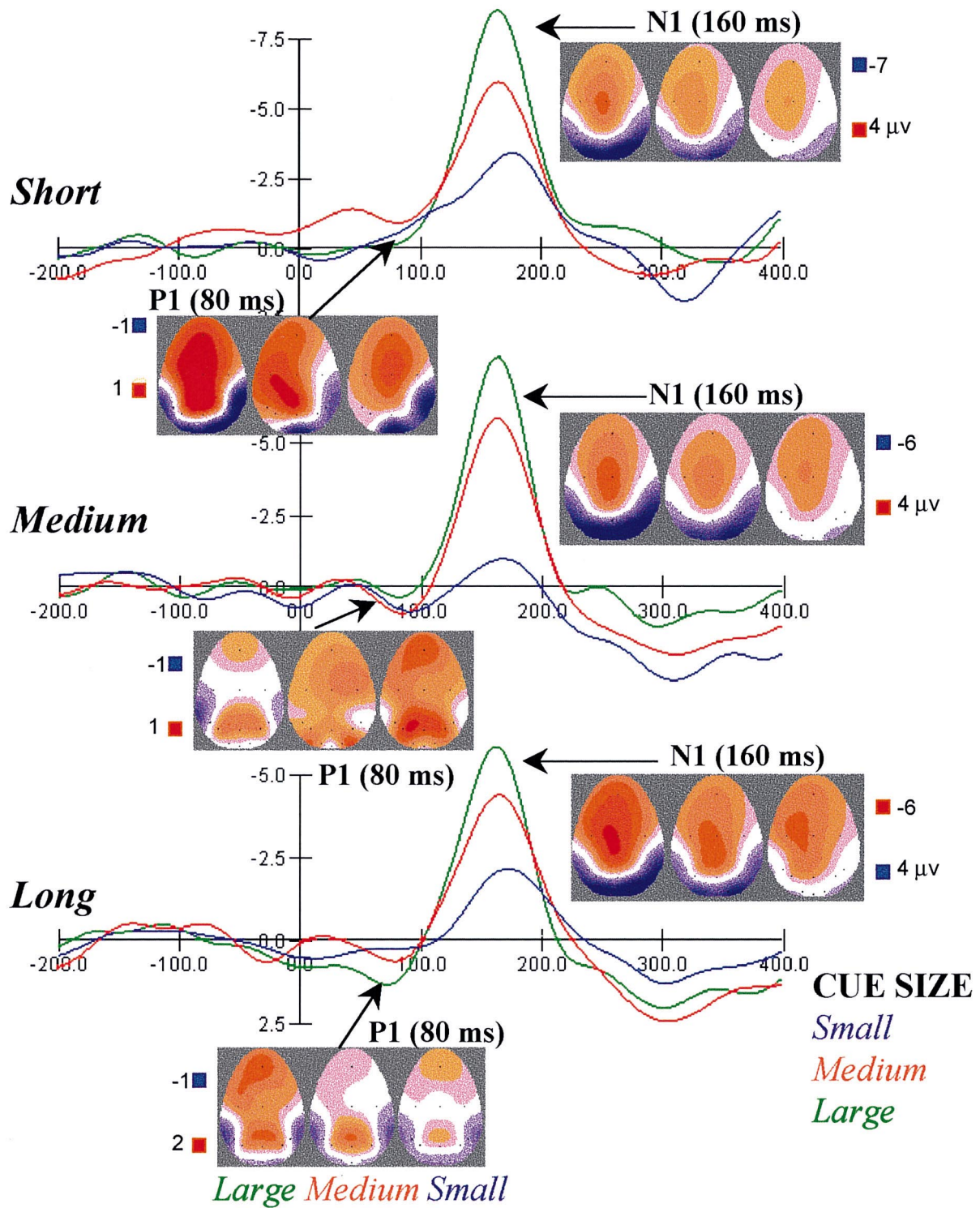
Fig. 4. Enlarged ERP waveforms at the OR electrode site and topographies of P1 and N1 ERP components elicited by the cue for each cue size and SOA condition.
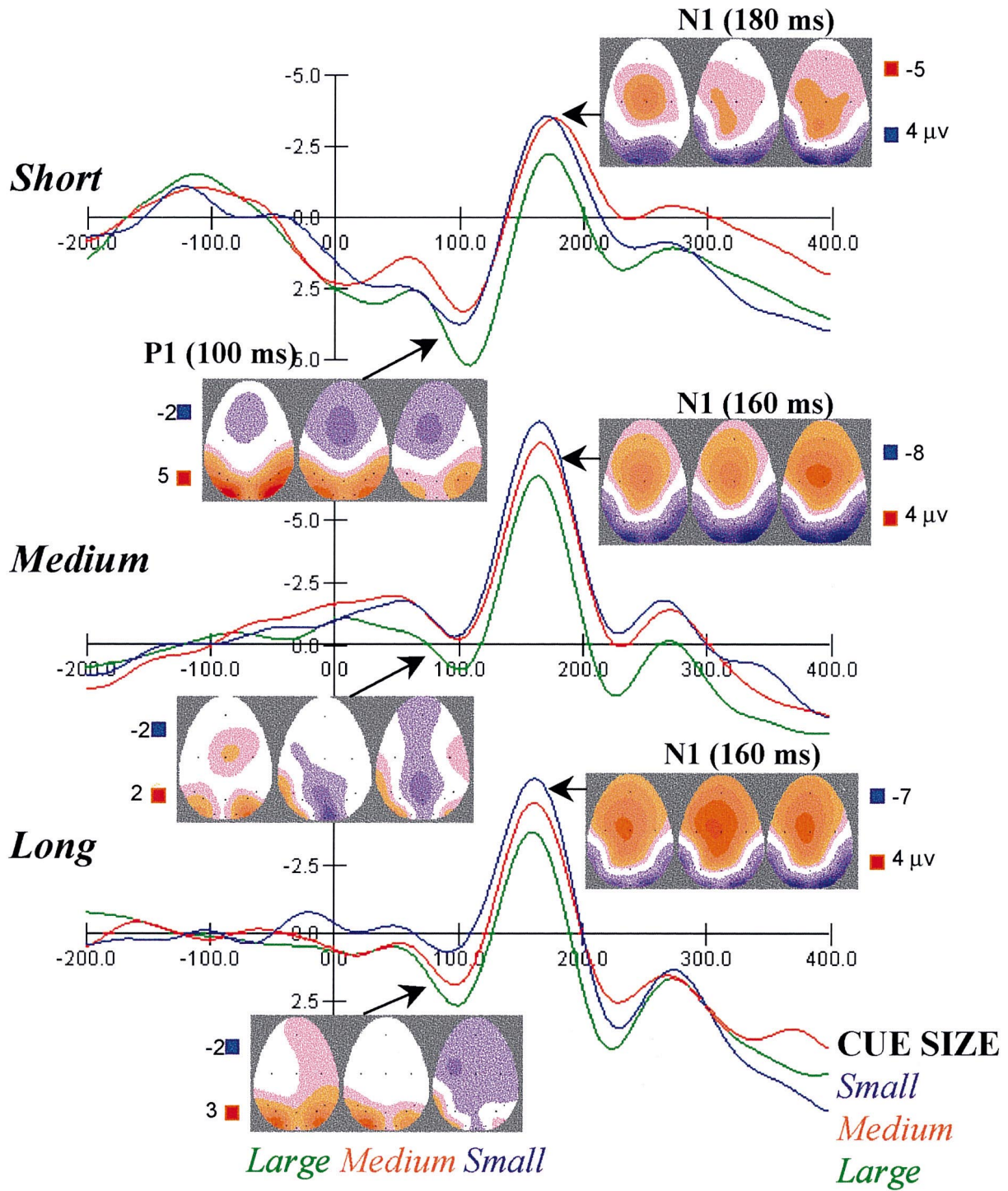
Fig. 5. Enlarged ERP waveforms at the OR electrode site and topographies of P1 and N1 ERP components elicited by the search array for each cue size and SOA condition.

2B, RT at the short (230–350 ms) SOA was higher than that at the medium (500–650 ms) and long (800–950 ms) SOAs.

3.2. P1 Component

3.2.1. Cue-evoked P1

The only significant effect for the amplitude of the P1 (mean peak latency 98.1 ms) evoked by the cue was electrode site. P1 was largest over left temporal and occipital scalp, $F_{6,90}=4.97$, $P<0.0005$ (OL, 1.26; T5, 1.04 μV). No other effects on posterior P1 amplitude were significant. Cue size significantly affected P1 latency ($F_{2,30}=7.70$, $P<0.005$), such that latency to the small cue (106.7 ms) was significantly longer than that to the medium (95.4 ms) and large size cues (92.2 ms). P1 latency also varied with electrode site, $F_{6,90}=2.390$, $P<0.05$, with the shortest latency seen over the occipital area (95.3 ms for Oz, O1, O2).

3.2.2. Search array-evoked P1

Grand-average ERPs to the search array for each cue size and SOA are shown in Fig. 3. The P1 evoked by the array (101.6 ms) was largest over lateral occipital scalp, $F_{6,90}=8.58$, $P<0.0001$ (OL, 2.69; OR, 2.56 μV). P1 amplitude was affected by changes in cue size as early as 70–80 ms after target onset, suggesting primary visual processing was modulated by cue-driven scaling of spatial attention. P1 amplitude increased with cue size, $F_{2,30}=8.96$, $P<0.001$ (1.68, 2.00, and 2.53 μV for the small, medium, and large cues, respectively). P1 amplitude was largest following the short SOA (3.71 μV) relative to both the medium (0.66 μV) and long SOAs (1.83 μV), $F_{2,30}=35.59$, $P<0.0001$.

3.3. N1 Component

3.3.1. Cue-evoked N1

The only significant effect for the amplitude of the anterosuperior N1 (142.3 ms) was for electrode site, $F_{3,45}=8.20$, $P<0.0005$. The largest N1 was at right center scalp (C4, 1.29 μV). The anterosuperior N1 latency was later for the small cue (153.8 ms) than for the medium (139.4 ms) and large cues (133.6 ms), $F_{2,30}=5.44$, $P<0.01$.

The amplitude of the inferoposterior N1 increased as cue size increased, regardless of SOA (Fig. 4), perhaps simply as a consequence of the physical size of the evoking stimulus (-2.55, -4.44, -6.68 μV for the small, medium, and large cues, respectively, $F_{2,30}=63.20$, $P<0.0001$). There was also a significant main effect of site, $F_{6,90}=11.30$, $P<0.0001$: N1 amplitude was greatest at the right occipital site (O2, -5.79; OL, -5.73 μV). There were no significant effects for inferoposterior N1 latency elicited by cues.

3.3.2. Search array-evoked N1

The only significant effect for the anterosuperior N1 amplitude was for electrode site, $F_{3,45}=5.84$, $P<0.005$. The largest N1 was over the frontal area (Fz, 1.36 μV).

As Fig. 5 shows, the amplitude of the inferoposterior N1 decreased as cue size increased, regardless of SOA (5.34, 4.76, 4.48 μV for the small, medium, and large cues, respectively, $F_{2,30}=4.57$, $P<0.05$). As with the anterosuperior N1, the inferoposterior N1 showed a significant main effect of site, $F_{6,90}=10.07$, $P<0.0001$. N1 amplitude was greatest at the right occipital site (OL, -5.94; O2, -5.53 μV). In contrast to the results for P1, the array-evoked inferoposterior N1 was largest for the medium SOA (6.55 μV) compared to the long (4.92 μV) and the short SOAs (3.10 μV), $F_{2,30}=33.69$, $P<0.0001$. There was also a significant interaction between site and SOA ($F_{12,180}=2.38$, $P<0.01$), reflecting a larger SOA effect over occipital scalp. With respect to latency, the inferoposterior N1 latency was longer for the medium cue (169.0 ms) than for the large (165.8 ms) and small cues (165.4 ms), $F_{2,30}=6.39$, $P<0.005$. Finally, N1 latency also decreased with increased cue-array SOA (175.8, 163.5, 160.9 ms, respectively), $F_{2,30}=30.93$, $P<0.0001$.

4. Discussion

The results of the present study provide electrophysiological evidence that changes in the spatial scale of attention, as induced by trial-by-trial changes in the size of valid location cues, modulates neural activity in early visual cortical areas. Previous attention shifting studies have shown that valid spatial cueing of a broad region of the visual field affects the P1 and N1 components of the ERP to target stimuli presented in that field, in comparison to invalid or neutral cues [10,19,20,32,34,35]. In the present study cue validity was held constant at 100% (excepting 10% catch trials) and the size of the cued regions was systematically varied. The results showed that cue size variation influences the same ERP components as does cue validity, but the effects of attentional scaling differ from those of attention shifting. We have previously shown that location cues varying in size affect the efficiency with which targets can be identified among distractors in a complex visual field, with target RT increasing with cue size [12]. The present ERP findings suggest that such attentional scaling influences the way visual input at the cued location is processed very early in the processing stream.

Consistent with our previous work [12,13], search RT was progressively slowed by increases in precue size from small to medium to large. The amplitude of the P1 component of the ERP to the search array also increased with cue size, even at the shortest SOA employed. Thus, when top down information about the region to be

searched was less precise, RT was slowed and the neural generators of P1 became more active. The increase in activity may reflect the additional computations required in changing the spatial scale of attention to the appropriate element size to facilitate target discrimination. This requirement would be greatest for the large cue and least for the small cue, reflected in an increase in P1 amplitude with cue size. This effect was not seen in the ERP evoked by the cue itself but only in the ERP evoked by the search array. This suggests that the consequences of cuing develop over time. We have observed that in a visual search task, RT benefits of location cuing are poorly developed at 100 or 200 ms after cue onset [11,12]. On that basis, little effect of cue size would be expected on precue-evoked ERP components in that latency range.

The lateral occipital P1 represents the earliest stage of visual processing to be modulated by cued spatial attention [19,35]. The region over which P1 amplitude is maximal overlies prestriate visual cortex [3,20,22]. Single cell recording studies in monkeys indicate those prestriate areas of the occipital, temporal and parietal lobes, not striate cortex itself, are the source of neural modulation of spatial attention [5,9]. A combined fMRI and ERP study found striate cortex modulation of spatial attention with fMRI, but not with ERPs, interpreted as arising from feedback from extrastriate to striate cortex [37]. The present results for the array-evoked P1 therefore suggest that visual processing is modulated by spatial scaling of attention very early in the processing stream, as early as 70–80 ms, and probably in prestriate visual cortex [20,32]. Furthermore, the finding that P1 amplitude increased with cue size at a short SOA, is consistent with the Hopfinger and Mangun [22] report of increased amplitude of P1 evoked by a target occurring at the cued location when the SOA was less than 234 ms. In that study the valid cue was fairly closely matched in size to the size of the target. The present results also indicate that activity of the generators of P1 is modulated by the precision of the information about the region where the target is expected. Thus while previous work shows that P1 amplitude is modulated by top-down information about the *location* of the target, this study shows that P1 amplitude reflects as well as the *precision* of that information. Additionally, reduced precision of information about target location is associated with *increased* neural activity, reflecting the heightened need to scale the attentional focus at target onset when precues are imprecise.

In contrast to the effects of spatial scaling of attention on P1, N1 amplitude decreased with cue size. The decrease in N1 with cue size may reflect the consequences of a broader attentional focus induced by the larger cues. Many previous studies of visual–spatial selective attention have indicated that the visual N1 is larger for attended-location stimuli than for unattended-location stimuli [19,20,26, 32,34]. Moreover, studies of divided attention to multiple auditory [17,21,41], visual [10,39,48], and audio-visual

channels [2,15,31,42] have shown that N1 amplitude decreases as the number of stimulus channels attended to increases. These findings were interpreted as indicating that N1 amplitude reflects a gradient of attention allocation. The gradient would be sharply peaked (and N1 amplitude would be high) when only one channel was attended to, but would be more spread out (and N1 amplitude would be low) when attention was divided between multiple channels. The interpretation of N1 amplitude as reflecting the gradient of spatial attention is also supported by more recent studies in which N1 was recorded to stimuli presented at differing distances from an attended location [22,29,30,33,35]. This view would predict that as the spatial gradient of attention is broadened by increasing cue size, N1 amplitude would be reduced. This was precisely the result obtained in the present study. The largest effect was obtained for the N1 (peak around 160 ms) recorded over the right occipital scalp sites (OL and O2). Alternatively, Vogel and Luck [49] have recently argued that N1 reflects a discrimination process operating within the focus of attention. If so, then N1 might be larger under conditions when such discrimination is rapid, as when the cue size is small and the demands of scaling minimal. When the cue is large, discrimination is slowed and the generators of the N1 perhaps delayed or asynchronous, smearing the N1 and apparently reducing its amplitude.

The effects of precue size on target RT and on P1 and N1 amplitudes are unlikely to be due to increased distractor interference. The total number of distractors was fixed on each trial and the number and location of distractors in the cued area was randomly varied so that there was no systematic difference between the medium and large size precues. It could be argued that since the small precued area contained only a single target without any distractors, that distractor interference was less. However, this explanation is ruled out because we obtained cue size effects across the medium and large cues as well, which were matched for degree of distractor interference within the cued area.

The dissociation of cue size effects on P1 and N1 noted in the present study using 100% valid cues has also been obtained in the more traditional cue-validity studies in which valid and invalid cues are compared. The P1 attention effect is measurable even in the absence of N1 attention effects, when subjects are required to attend to the left or right hemifield of a visual display while fixating a central point [27]. In a visual spatial attention task [14], stimuli were presented at the vertical and horizontal meridian. The P1/N1 enhancement typically found on the horizontal dimension was not observed on the vertical dimension. Very recently, Handy and Mangun [16] recorded ERPs to low- and high-perceptual load targets in their experiment 1. The P1 amplitude was slightly larger for the cued target than for the uncued target, but the N1 was smaller for the cued target than for uncued target. In

their experiment 2, the target duration was reduced and a mask presented at the target location following target offset. As a result, the N1 was larger for the cued target than for the uncued target. These results show that P1 and N1 effects can be dissociated depending on perceptual load. In the present experiment, several distractors were presented with the target, increasing perceptual load. Thus, the results are broadly consistent with those of Handy and Mangun [16].

Previous work on visual search has shown that varying the demands of search can differentially affect visual ERP components. With regard to easy, feature search, P1 was not altered under popout relative to target absent conditions. Popout affected only later components, with the posterior N2 enlarged by a target popout item compared to a non-target popout item [28]. Conjunction search, on the other hand, viewed as more demanding than feature search by virtue of requiring additional processing [47], did enhance not only P1 but also both anterior and posterior N1 components when evoked by a probe at the location of the conjunction target [25]. This finding was interpreted as indicating that sensory processing was altered within a spatial region during visual search.

One difficulty with using ERPs to investigate visual search is that the target is, by definition, embedded in the search array. This necessitates either measuring the ERP to the entire array [28] or using a method such as that used by Luck et al. [25] in which a probe was presented at the location of the conjunction target 250 ms after its appearance. Both solutions have drawbacks. Because we were not interested in the ERP to the target per se, but rather in the electrophysiological consequences of dynamically scaling the attentional focus, the present study measured the ERP to the entire search array while manipulating attentional scaling using a precue. Our results suggest that neuronal cell populations participating in search have their activity modulated by top-down information about the size of the area to be searched. Furthermore, the generators of P1 and the inferoposterior N1 are differentially affected by top-down influences arising as a consequence of precue precision. Consistent with the discussion above, these results suggest several, possibly simultaneous, processes important in cued search. One, reflected in P1, may be an active process involved in changing the spatial scale of attention in response to processing demands. A second process, reflected in inferoposterior N1, may reflect the gradient of attention [35], or demands of discrimination within that gradient [49]. In any case, the present results suggest that the neural generators of both P1 and the posterior N1 are on the path of discrimination, reflecting processes important for visual search. The neuronal cell populations generating P1 and N1 appear to be in the primary visual processing stream. Although the populations appear to mediate different aspects of search, activity of both is modulated by prior, top-down information about the size of the region to be searched.

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