Interactions between spatial attention and global/local feature selection: an ERP study

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Received 31 May 2000; accepted 14 June 2000

The present study examined the interaction between spatial attention and global/local feature processing of visual hierarchical stimuli. Event-related brain potentials (ERPs) were recorded from subjects who detected global or local targets at attended locations while ignoring those at unattended locations. Spatial attention produced enhanced occipital P1 and N1 waves in both global and local conditions. Selection of local features enhanced posterior P1, N1 and N2 waves relative to selection of global features. However, the modulations of the P1 and N2 by global/local feature selection were stronger when spatial attention was directed to the left than the right visual fields. The results suggest neurophysiological bases for interactions between spatial attention and hierarchical analysis at multiple stages of visual processing. NeuroReport 11:2753–2758 © 2000 Lippincott Williams & Wilkins.

Key words: Event-related potentials; Hierarchical stimulus; Spatial attention

INTRODUCTION

Visual attention can be directed to specific locations in the visual field. Studies employing event-related brain potentials (ERPs) have shown that spatial attention enhances the amplitudes of the short-latency sensory components (P1 and N1) of the ERPs elicited by stimuli at attended locations [1], which possibly reflects processing modulations in prestriate visual cortex [2,3]. In contrast, visual attention to other stimulus features, such as color, motion or spatial frequency produces a longer-latency, broad selection negativity (SN) that begins 70–100 ms after the P1 effect and has a more anterior distribution [4,5]. Moreover, there appears to be a hierarchical relationship between spatial attention and the selection of other stimulus features: ERP indices of selection of color or motion are prominent only at spatially attended locations [5].

Visual attention can also be directed to different levels of a visual scene. For example, subjects may selectively attend to either the global or local level of compound letters like those shown in Fig. 1. Navon found that responses to global targets were faster than responses to local targets, and global distractors interfered with local target processing but not vice versa [6]. He argued for a global precedence effect, suggesting that visual pattern processing proceeds from global to local levels.

Recent electrophysiological studies have found that selection of global/local features of hierarchical stimuli modulates ERPs. For example, Heinze et al. recorded ERPs to targets that could appear at the global or local level of compound letters with equal probability (a divided attention paradigm) [7,8]. They found that a posterior N2 was larger to local than to global targets. Han et al. observed similar larger N2 amplitudes to local targets in a selective attention paradigm where subjects discriminated global or local stimuli in separate blocks of trials [9–11]. In addition, they found that the short-latency P1 component was reliably enhanced in local compared to global attention conditions. The modulations of the P1 and N2 by global/local feature selection were observed with either compound letters or compound shapes [9,10] presented in the center or the periphery of the visual field [9,11] in both selective and divided attention tasks [10,12].

Although there is a hierarchical relationship between spatial attention and the selection of non-spatial stimulus features (such as color and motion), the relationship between spatial attention and global/local feature selection remains undefined. In previous studies, hierarchical stimuli were presented either in the center of the visual field [7–10,12] or eccentrically but with equal allocation of spatial attention in the two hemifields [11]. In the current experiment we examined if global/local feature selection depends on the prior allocation of spatial attention and when spatial attention starts to interact with global/local feature processing. Compound letters were presented randomly in the left visual field (LVF) and the right visual field (RVF). Subjects attended to stimuli in the LVF or the RVF and responded to either the global or local level targets in the attended hemifield.
MATERIALS AND METHODS

Subjects: Fifteen graduate students (10 females) ranging in age from 20 to 26 years participated in this experiment as paid volunteers. The subjects were neurologically normal and had normal or corrected-to-normal vision. Informed consent was obtained after the situation was explained.

Stimuli: White compound letters on a black background were presented on a computer-controlled video monitor 57 cm from the participant’s eyes. A fixation cross, subtending 0.3 × 0.2° of visual angle, was continuously visible in the center of the monitor. The stimuli were flashed in either the LVF or the RVF in random order. Each stimulus consisted of a global letter (H or E) made up of local letters (H or E) in 7 × 7 matrix, as shown in Fig. 1. The global and local letters subtended an angle of 3.3 × 5.6° and 0.4 × 0.6°, respectively. The distance between the fixation cross and the center of each compound stimulus was 2.9°. Stimulus duration was 200 ms. Interstimulus intervals were randomized between 600 and 1000 ms.

Procedure: Subjects were verbally instructed to attend to one hemifield prior to each block of 100 trials and to press a key with the right thumb to the designated global or local target (H or E) in the attended hemifield. Forty practice trials were presented prior to testing. A total of 800 trials in eight blocks were presented in global and local conditions, respectively. Accordingly, there were four blocks of trials for each type of target (global H, global E, local H, local E). In two blocks of trials, subjects responded to targets appearing in the LVF. In the other two blocks, subjects responded to targets appearing in the RVF. Target letters occurred randomly in 20% of the trials in both visual fields, but subjects responded only to attended visual field targets. The presentation sequence of different types of targets was counterbalanced across subjects.

ERP recording and data analysis: The electroencephalogram (EEG) was recorded from standard electrode locations F3, F4, C3, C4, P3, P4, O1, O2, T5, T6. Two additional electrodes: TO1 (located 50% of the distance between O1 and the midpoint between P3 and T5) and TO2 (located 50% of the distance between O2 and the midpoint between P4 and T6) were also used. All electrodes were referred to an average mastoid reference. The EEG was band pass filtered (0.1–40 Hz) and digitized at a sampling rate of 256 samples/s. Eye blinks were monitored with an electrode located below the right eye. The horizontal electro-oculogram (EOG) was recorded from electrodes placed about 1.5 cm lateral to the left and right external canthi. Trials containing eye blinks, eye movements deflections exceeding ±80 μV at any electrode, and trials with incorrect behavioral responses were excluded from the ERP averages. The baseline for ERP measurements was the mean voltage of a 200 ms prestimulus interval.

Fig. 1. Hierarchical stimuli and experimental design of the present study. Subjects responded to either global or local targets in the specified hemifield. A portion of the sequence attend-global (H)-right is shown.
ERP components were defined as positive or negative deflections between the following time windows over parietal/occipital/temporal electrodes: P1 (80–140 ms), N1 (130–190 ms), P2 (200–280 ms), N2 (250–350 ms) and P3 (320–600 ms). Behavioral data were analyzed with ANOVA with factors being hemifield (stimuli were presented in the LVF or the RVF), global/local feature selection (attend to the global or local levels of the hierarchical stimuli), and consistency (global and local letters were consistent or inconsistent). The ANOVAs of ERP mean peak amplitudes and peak latencies were computed with hemifield, spatial attention (attended or unattended), global/local feature selection, consistency, and hemisphere (electrodes on the left or right hemisphere) as factors.

RESULTS

Performance: A global precedence effect was obtained: reaction times (RTs) to global targets were faster than those to local targets (F(1,14) = 30.78, p < 0.001; Table 1). RTs were also faster when the global and local letters were consistent than when they were inconsistent (F(1,14) = 8.25, p < 0.02). This was due to an interference effect on RTs in local but not global conditions, which produced a significant interaction between global/local feature selection and consistency (F(1,14) = 30.49, p < 0.001). RTs were also faster to RVF than LVF targets (F(1,14) = 11.90, p < 0.004). However, no interactions involving hemifield reached significance. Accuracy measures were consistent with the RT effects but showed less sensitivity to global/local differences. False alarm rates were 0.49% and 0.05% for local and global conditions, respectively. Subjects responded correctly to 95.7% of global targets and 98.0% of local targets, with no significant effects of hemifield, global/local feature selection, attendance (attended or unattended), global/local feature selection, consistency, and hemisphere (electrodes on the left or right hemisphere) as factors.

ERPs: The grand average ERPs recorded at occipitotemporal sites in response to non-target global and local stimuli are shown in Fig. 2. The measures of ERP amplitudes of each component are presented in Table 2. The effect of global/local consistency and its interaction with other factors were not significant for any component, and are therefore not reported below.

There was a significant effect of spatial attention on the P1 (F(1,14) = 8.96, p < 0.01). Stimuli at attended locations evoked larger P1s than those at unattended locations. The effects of spatial attention were more pronounced for stimuli presented in the LVF than in the RVF (F(1,14) = 5.36, p < 0.04).

Global/local feature selection also modulated the amplitude of the P1: it was larger in local than global conditions between 100 and 120 ms (F(1,14) = 4.57, p < 0.05). The effect of global/local selection was different between the stimuli at attended and unattended locations, producing a significant interaction between spatial attention and global/local feature selection (F(1,14) = 4.59, p < 0.05). Furthermore, the reliable triple interaction of spatial attention × global/local feature × hemifield indicated that the effect of the global/local feature selection was stronger when spatial attention was directed to the LVF than to the RVF (F(1,14) = 4.70, p < 0.05). Post-hoc comparisons showed that the P1 was larger in local relative to global conditions when spatial attention was directed to the LVF (p < 0.03) whereas the P1 amplitudes did not differ between the two conditions when spatial attention was directed to the RVF (p > 0.2).

The occipito-temporal N1 was larger over the right than over the left hemisphere (F(1,14) = 10.11, p < 0.01), and over the hemisphere contralateral to the stimulated hemifields (F(1,14) = 47.25, p < 0.001). Stimuli at attended locations elicited enhanced N1 amplitudes in comparison with those at unattended locations (F(1,14) = 5.71, p < 0.03). As with the P1, the effect of spatial attention was larger for the stimuli presented in the LVF than the RVF (F(1,14) = 6.20, p < 0.03). The N1 amplitudes were relatively enhanced in local relative to global conditions (F(1,14) = 7.29, p < 0.02).
However, modulations of the N1 by global/local feature selection did not differ between spatially attended and unattended locations ($F(1,14) = 1.17, p > 0.2$). Global/local feature selection also delayed the N1 peak latencies in local (161 ms) relative to global conditions (156 ms; $F(1,14) = 26.54, p < 0.02$).

The P2 amplitudes were larger at electrodes contralateral to the stimulated hemifields than at ipsilateral sites ($F(1,14) = 8.04, p < 0.02$). Unlike the P1 and N1, the P2 was larger in global than local conditions ($F(1,14) = 5.92, p < 0.03$). The larger P2 amplitude in global relative to local conditions was stronger over the right hemisphere than over the left hemisphere ($F(1,14) = 5.47, p < 0.04$).

The N2 amplitude was larger in local than global conditions ($F(1,14) = 4.96, p < 0.04$). The larger N2 amplitude in local relative to global conditions was different between the stimuli presented at spatially attended and unattended locations, resulting in a significant interaction between spatial attention and global/local feature selection ($F(1,14) = 4.27, p < 0.05$). As the triple interaction of spatial attention $\times$ global/local $\times$ feature hemifield was also significant ($F(1,14) = 6.73, p < 0.02$), post-hoc comparisons were conducted and showed that spatial attention to the LVF increased the N2 enhancement in local relative to global conditions ($p < 0.04$) whereas spatial attention to the RVF reduced the N2 enhancement ($p < 0.03$). The differential effects of spatial attention on the N2 enhancement in local relative to global conditions are illustrated in Fig. 3.

P3 peak latencies to target stimuli showed a reliable interaction between hemifield and global/local feature selection ($F(1,14) = 6.56, p < 0.02$), due to the fact that P3 peak latencies were shorter in global than local conditions (398 vs 428 ms) for targets in the LVF whereas no significant differences were seen for targets in the RVF (global: 402 ms, local: 404 ms).

**DISCUSSION**

The high accuracy and low false alarm rates indicate that the subjects were able to focus their attention on the appropriate level of hierarchical stimuli presented in the
attended hemifield. The RTs showed a global precedence effect, which was similar for targets presented in the LVF and the RVF.

The effects of spatial attention on ERPs replicated the findings of previous work [1]. The amplitudes of the P1 and N1 were enhanced to stimuli in spatially attended locations. This effect was stronger for stimuli presented in the LVF than in the RVF, possibly reflecting a right hemisphere dominance in directing spatial attention [13–15].

Global/local feature selection produced effects on both early and late ERP components. Both P1 and N1 components were enlarged when attention was directed to local relative to global levels of the compound letters. The P1 effect corroborates the findings of previous studies in which hierarchical stimuli were presented in the center of the visual field or were presented peripherally with spatial attention equally allocated to the two hemifields [9–11]. Since the present study showed that the P1 was modulated by both spatial attention and global/local feature selection and previous work has localized the spatial attention-modulated P1 to early prestriate cortical regions [2,3], it is possible that the P1 effect associated with global/local processing in the current experiment also reflects the modulation of processing in prestriate visual cortices. This is consistent with brain imaging study which showed metabolic activation of prestriate occipital cortex associated with local and global tasks [16]. Note that the P1 could be larger in global relative local conditions when the global precedence effect was absent in RTs [8]. The contrast between these studies suggest that the initial differential sensory-perceptual processing contributes to the global precedence effect observed in behavioural data.

Modulations of longer-latency ERP components were also associated with global/local feature selection in the current study. The P2 was larger in global than local conditions while the N2 was enhanced in local relative to global conditions. These are in agreement with previous studies [7,10,11]. The results indicate that global/local feature selection modulates brain activities at multiple levels of visual information processing, from early sensory processing to late target perception.

More important, the present study provided electrophysiological evidence for the interaction between spatial attention and global/local feature selection. The earliest sign of this interaction was observed in the P1 component. There was a P1 enlargement related to local feature selection when spatial attention was directed to the LVF, whereas the P1 did not differ between global and local conditions when spatial attention was directed to the RVF. Similarly, the modulation of the N2 by global/local feature selection was also contingent upon the direction of spatial attention. Spatial attention to the LVF enlarged the enhancement of the N2 in local relative to global conditions, while spatial attention to the RVF reduced the N2 enhancement. This interaction was true even when the hierarchical stimuli were located in the unattended hemifield.

This asymmetric pattern of interaction between spatial attention and global/local feature selection possibly resulted from the asymmetric role played by the two hemic-
spheres in global and local feature processing. Patient studies have shown that perceptual impairment is more severe for global targets in patients with right hemisphere lesions and for local targets in patients with left hemisphere lesions [17,18], which suggests that the right hemisphere dominates global processing whereas the left hemisphere dominates local processing. Because low- and high-frequency stimuli are discriminated faster when presented respectively in the LVF and the RVF [19], it has been proposed that the hemispheric dominance in global/local processing may reflect an asymmetrical representation of spatial frequency information in the two hemispheres [20]. The right hemisphere is more efficient in processing high frequencies which underlie global feature analysis whereas the left hemisphere is good at processing high frequencies which underlie local feature analysis. Based on this hypothesis it may be argued that the interaction between spatial attention and global/local feature selection could reflect the asymmetric representation of spatial frequency information in the two hemispheres. As each hemisphere dominates directing attention to the contralateral hemifield [21,22], spatial attention to the LVF may lead to stronger activation of the right hemisphere and thus enhances the processing of low-frequency information while producing cost in processing high-frequency information. This benefits the representation of global features and produces costs in representing local features. As a result, more neural resources are required for selection and representation of local features, as indexed by the enlargement of the P1 and N2 waves in the local condition. In contrast, spatial attention to the RVF may enhance the processing of high-frequency information relative to low-frequency information. Therefore, local processing is facilitated and requires less neural resources (indexed by decreased P1 and N2 amplitudes). It seems that spatial attention modulates global/local feature processing by changing relative background activities of the two hemispheres. As the P1 reflects early sensory processing and the N2 reflects global/local target perception [7], our data suggest that spatial attention modulates global/local feature processing at multiple levels of processing.

The present ERP data indicate that the relationship between global/local feature selection and spatial attention is fundamentally different from the relationship between spatial attention and selections of other stimulus features. For example, color and motion selections indexed by the long-latency SN do not depend on directions of spatial attention [4]. The pattern of the interaction between spatial attention and global/local feature selection observed here suggests that selection of global/local features of hierarchical stimuli is mediated, at least partially, by mechanisms distinct from those underlying selections of other stimulus features (such as color and motion).

Finally, our data showed that selection of global/local feature influenced peak latencies of both early sensory and late endogenous components; i.e. N1 and P3 latencies were shorter in global than local conditions. These results suggest that the global precedence effect observed in the behavioral performance begins with automatic, short-latency sensory mechanisms (indexed by N1) and continues to be reflected in the time required for evaluation of targets (indexed by P3) [23].

CONCLUSION

Our data suggest that directions of spatial attention modulate global/local feature selection. Directing attention to the LVF result in stronger activation of the posterior cortex in local relative to global feature selections. However, directing attention to the RVF reduces the differential involvement of neural resources in global/local feature processing.

REFERENCES


Acknowledgements: This work was supported by a grant from the National Foundation of Sciences, P. R. China and by National Institutes of Mental Health (MH-41544), National Institute of Neurological Disease and Stroke (NS - 32893), and the VA Research Service, USA. We thank Lynn Robertson and Janelle Weaver for helpful comments.