

Neural mechanisms of global/local processing of bilateral visual inputs: an ERP study

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Accepted 13 February 2005

Available online 29 March 2005

Abstract

Objective: Examine the neural mechanisms of global/local processing of multiple hierarchical stimuli.

Methods: Event-related brain potentials (ERPs) were recorded from adults who selectively attended to the global or local level of two compound letters that were simultaneously presented in the left and right visual fields, respectively. The compound stimuli were either broadband in spatial frequency (SF) spectrum or contrast balanced to remove low SFs. Subjects were asked to detect the presence of a global or local target that might appear in either the left or the right visual field in separate blocks of trials.

Results: Attention to the local level of broadband stimuli elicited a positivity over lateral occipital sites at 80–120 ms (P1) with larger amplitude than those in the global attention condition. However, global attention produced an enhanced positivity at 240–320 ms (P2) over lateral occipital sites relative to local attention. Both the P1 and P2 waves in the global condition were of larger amplitudes over the left than right hemispheres. Contrast balancing eliminated the P1 and P2 effects and modulated the hemispheric asymmetry of the long-latency occipital positivity.

Conclusions: The results provide ERP evidence for modulations of neural activities in the visual cortex by global/local attention to concurrently presented multiple compound letters. Moreover, the modulation of brain activities by global/local attention depends upon the presence of low SFs in the compound stimuli.

Significance: The ERP results of this study contribute to the understanding of neural mechanisms of the processing of simultaneously-presented multiple compound stimuli.

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Keywords: Bilateral visual input; Compound stimulus; Contrast balancing; ERPs; Global/local attention; Spatial frequency

1. Introduction

Perception of hierarchical visual scenes requires coordinated processing of information at both global and local levels of compound stimuli. However, processing of global and local aspects of hierarchically organized stimuli may be different in terms of both time courses and neural substrates. Navon (1977) first found that reaction times (RTs) to the identification of a global structure (e.g. the large letter

in Fig. 1a) are shorter than those to the identification of its local elements (e.g. the small letters in Fig. 1a). Moreover, the global shape interferes with response speed to the local items when global and local information is conflicting but not vice versa. It has been hypothesized that global features are perceived earlier and/or faster than local features. The neural mechanisms underlying global/local perception have been investigated extensively using event related brain potentials (ERPs). For example, in a divided attention task, researchers recorded ERPs from subjects who were required to identify targets that appeared at the global or local level of compound stimuli in the same block of trials (Han et al., 2000; Heinze and Münte, 1993). They found an occipito-temporal negativity peaking between 200 and 300 ms

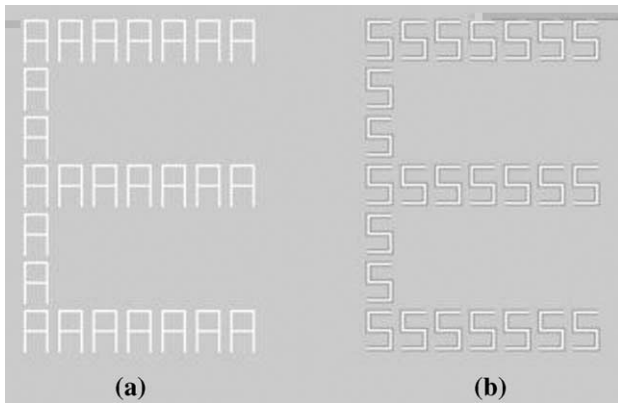


Fig. 1. Illustrations of the compound stimuli used in the current study. (a) A broadband stimulus is composed of a global 'E' made up of local 'A'; (b) a contrast balanced (CB) stimulus is composed of a global 'E' made up of local 'S'.

(the posterior N2) that showed larger amplitudes to local than to global targets. Similar modulation of the posterior N2 by global/local attention was observed in a selective attention task in which subjects identified global or local targets in separate blocks of trials (Han and Chen, 1996; Han et al., 1997, 1999). The enhancement of the posterior N2 in the local relative to global conditions was eliminated when selection of an individual local element was eased by making one local figure pop out from the global structure (Han and He, 2003; Han et al., 2001). Han and Chen (1996), Han et al. (1997, 1999, 2000)) showed further that an early lateral occipital positivity between 80 and 120 ms (P1) was enlarged in the local than global attention conditions, suggesting that selective attention to the global or local aspect of compound stimuli involves a mechanism of amplitude modulation of neural activities in the visual cortex as early as 80 ms after stimulus onset.

The modulation of neural activities associated with the processing of compound stimuli can be different in hemispheric lateralization between global and local attention conditions. ERPs to compound stimuli presented at central fixation induced a larger occipito-temporal negativity (Heinze and Münte, 1993; Heinze et al., 1994; Schatz and Erlandson, 2003) or target-specific difference waves (Han et al., 2000; Proverbio et al., 1998) over the right hemisphere in the global condition but over the left hemisphere in the local condition. Similarly, positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) studies observed increased regional cerebral blood flow or hemodynamic responses in the right lateral occipital cortex when attending to the global structure of compound stimuli but in the left occipital cortex when attending to the composing local elements (Fink et al., 1996; Han et al., 2002; Martinez et al., 1997, but see Heinze et al., 1998; Sasaki et al., 2001). Together with the findings that left hemisphere lesions slow local responses or result in deficits of memory of local features whereas right hemisphere lesions delay global responses or damage

the memory of global features (Delis et al., 1986; Lamb et al., 1989; 1990; Robertson et al., 1988), the neuroimaging results are consistent with a proposal that global and local perception is mediated by separate subsystems in the right and left hemispheres, respectively. In addition, the modulation of early neural activities by global/local attention and related hemispheric lateralization are influenced by stimulus retinal locations. For instance, when compound letters were presented in the left (LVF) or right (RVF) visual field, global/local attention failed to modulate the P1 component (Han et al., 2003). In addition, there were no evident asymmetric activities in the visual cortex associated with global or local processing when compound stimuli were displayed unilaterally (Han et al., 1999, 2000, 2003). Similar results were also found in a recent fMRI study (Han et al., 2002).

Most of the previous studies recorded neural activities related to the processing of one compound stimulus presented either at the fixation or unilaterally. However, the visual system is often confronted with multiple compound stimuli in the visual environment. The neural mechanisms differentiating global and local perception of simultaneously presented multiple compound stimuli have been poorly understood. Evans et al. (2000) recorded ERPs to bilateral hierarchical figures and found that the P1 was enhanced over the right hemisphere in the global relative to the local condition but a reverse pattern over the left hemisphere. Nevertheless, these effects were observed under the circumstance that compound stimuli required to be identified always appeared in one hemifield in one block of trials. Therefore only one compound stimulus in a designated hemifield was task relevant even though two compound stimuli were displayed simultaneously. In a recent fMRI study, Han et al. (2004) asked subjects to detect infrequent global or local targets presented in a display composed of two compound letters that were simultaneously presented in the LVF and RVF, respectively. They found that, while behavioural responses were more accurate and faster to global than to local targets, attention to the global level of bilateral visual inputs induced stronger activations in the left and right temporal cortex relative to attention to the local level. However, attention to the local level generated stronger activations in bilateral superior parietal cortex compared with attention to the global level. These results provide neuroimaging evidence for the functional dissociation of global/local processing of bilateral visual inputs in the brain.

The current study further address the issue of neural mechanisms of global/local processing of bilateral visual inputs by recording high-density ERPs elicited by two compound letters presented simultaneously in the LVF and RVF, respectively. While subjects were asked to detect a designated target that might appear either in the LVF or in the RVF, ERPs were recorded in the condition when subjects attended to the global or local aspects of the compound stimuli. To compensate for the low temporal

resolution of fMRI signals in our previous work (Han et al., 2004), the current ERP study investigated how global/local attention modulates the neural activities underlying early sensory-perceptual processing that takes place in several hundreds milliseconds after stimulus onset. It is of particular interests if modulations of the visual activities by global/local attention are different between conditions when the visual system receives central or unilateral input and bilateral inputs.

In addition, this study examined whether the differential global/local processing of bilateral visual inputs depends upon low spatial frequencies (SFs) in compound stimuli. Previous research has shown evidence that processing of low and high SF information contributes to the global and local perception, respectively (Shulman and Wilson, 1987; Shulman et al., 1986). ERP studies (Han et al., 2003) also showed that the domination of global features at the early stage of the processing of compound stimuli was weakened when low SFs were removed by contrast balancing, a technique that eliminates all long-distance space-averaged luminance differences and thus produces stimuli without low SFs (Lamb and Yund, 1993; 1996). Similar to our previous research (Han et al., 2002, 2003), the current experiment employed two sets of compound stimuli, one containing broadband of SF spectrum and one from which low SFs were removed by contrast balancing. ERPs to the broadband and contrast balanced (CB) compound letters were compared to explore the role of low SFs in the perception of global and local features of bilateral visual inputs.

2. Methods

2.1. Participants

Sixteen undergraduate students (12 male, 4 female; 19–24 years of age) from Peking University participated in the experiment as paid volunteers. All participants were right-handed, had normal or corrected-to-normal vision, and gave informed consent according to the guidelines of Department of Psychology, Peking University.

2.2. Stimuli

The stimuli were global letters made up of local letters in a 7×7 matrix, as illustrated in Fig. 1. Three capital letters (A, E, and S) were used to produce compound letters, resulting in 6 combinations (i.e. global/local: A/E, A/S, E/A, E/S, S/A, S/E). All letters served as target and nontarget stimuli in separate blocks of trials. In each block of trials a designated target appeared only at the global or local level of one of the two compound letters that were presented simultaneously in the LVF and RVF, respectively. For example, if global letter A was defined as a target, in the target present condition, stimuli A/E or A/S could appear

randomly in the LVF or the RVF accompanied by distractors (e.g. E/A, E/S, S/A, or S/E) in the contralateral hemifield. In the target absent condition, two distractors appeared simultaneously in the LVF and RVF, respectively. In the global attention condition, the global letters in the LVF and RVF were different on all trials. Similarly, the local letters in the LVF and RVF were different on all trials in the local attention condition. At a viewing distance of 120 cm, global letters were 2.1° wide and 3.0° high and local letters were 0.22° wide and 0.35° high.

Stimuli were presented on a grey (116 cd/m^2) background. Each local letter of broadband stimuli was made up of lines that were brighter (204 cd/m^2) than background (see Fig. 1). The CB stimuli were identical to the broadband stimuli except that the lines composing each local letter were surrounded by lines that were darker (73 cd/m^2) than the background. The change in luminance from background was approximately twice as great for bright lines as for dark lines (see Fig. 1). Since dark lines occupied twice as much area as bright ones, the space-averaged luminance of the CB stimuli equaled that of the background. The arrangement of the luminance levels of the brighter and darker areas comprising the local letters and the grey background removed spectral power below 3 cycles/degree from the CB stimuli (see Lamb et al., 1999 for the result of spectral power analysis).

2.3. Procedure

A fixation cross was continuously visible in the center of a computer monitor. Two compound letters were simultaneously displayed to the left and right of fixation, respectively. The distance between the fixation and inner edge of each compound stimulus was 1.6° . The stimulus displays were presented for 200 ms, and the interstimulus intervals (ISI) were randomized between 300 and 500 ms.

Subjects were asked to remain fixated on the fixation cross. A selective attention paradigm was used. Each block of trials began with a large or a small letter made up of solid black lines. The large or small letter was as large as the global or local letters of the compound stimuli and served as a cue to indicate target level (global or local) and target shape (A, E, or S). The cue remained on the screen until the subject initiated the block by pressing a button on a joystick with the right thumb. Broadband and CB stimuli were presented in separate sessions. For each set of stimuli, after 30 trials for practice, 3 blocks of 240 trials were presented for global and local tasks, respectively. There were 20% targets in each block of trials. Subjects were asked to respond to the global or local target letter by pressing a button with the right thumb. Half of the subjects were presented with broadband stimuli first whereas the others with CB stimuli first. The sequence of global and local tasks was counterbalanced across subjects. Instructions emphasized both response speed and accuracy.

2.4. ERP data recording and analysis

The electroencephalogram (EEG) was recorded from 120 scalp electrodes, which were labeled with number from 1 to 120 (Fig. 2). Electrodes 59–71 were arranged along the midline of the skull. Other electrodes were located approximately symmetrically at the left and right sides of the skull. The position of each electrode was measured from each individual subject with a probe for sensing the 3D position of the probe tip with respect to a magnetic field source in the head support. The mean scalp location of each electrode site was estimated by averaging each electrode location across all subjects and was used for calculating voltage topographies. The skin resistance of each electrode was made less than 5 k Ω . An electrode at the right mastoid was used as reference. Eye blinks and vertical eye movement were monitored with electrodes located below the right eye. The horizontal eye movement was recorded from electrodes placed 1.5 cm lateral to the left and right external canthi. The EEG was amplified (band pass 0.1–70 Hz) and digitized at a sampling rate of 250 Hz. The ERPs in each stimulus condition were averaged separately off-line with averaging epochs beginning 200 ms before stimulus onset and continuing for 1000 ms. Trials contaminated by eye blinks, eye movements, or muscle potentials exceeding $\pm 50 \mu\text{v}$ at any electrode were excluded from the average.

Mean voltage of ERPs were obtained (a) at 20-ms intervals starting at 60 ms after stimulus onset and continuing until 200 ms post-stimulus and (b) at 40-ms

intervals from 200 to 800 ms poststimulus. Because ERP peak latencies to CB stimuli were significantly delayed relative to broadband stimuli, we also measured peak amplitudes and latencies to examine the effect of contrast balancing. Peak latencies were measured relative to stimulus onset. Table 1 shows time windows of the measurements of ERP peak amplitudes and latencies. Statistical analysis were conducted at each pairs of electrodes selected from frontal (32–87, 34–89), parietal (37–92, 38–93), occipito-temporal (18–118, 19–99, 41–96, 42–97, 43–98, 44–72, 45–73, 6–120) regions. Because preliminary analyses showed that most of the effects were evident over the posterior areas, more electrodes were selected from the occipito-temporal than other areas for the analysis.

RTs and hits were subjected to repeated measures analyses of variance (ANOVAs) with Level of Attention (global or local), Hemifield (targets appeared in the LVF or RVF), Frequency Content (broadband vs. CB stimuli) as independent variables. The ERP n8(t) T abl. 4(for)achn-366.5(to)

Table 2
Mean RTs (ms) and hit rates (%) (standard deviation) in each stimulus condition

	Global attention		Local attention	
	LVF	RVF	LVF	RVF
RTs				
Broadband	461 (42)	446 (44)	509 (39)	499 (39)
CB	545 (50)	530 (44)	508 (40)	502 (35)
Hit				
Broadband	97 (3.9)	98 (2.3)	60 (17.9)	58.7 (18.2)
CB	86.8 (9.5)	83.8 (12.5)	55.4 (16.7)	58.3 (15.1)

targets did not differ between broadband and CB stimuli ($F(1,15)=0.018, P>0.1$). There was a global RT advantage for broadband stimuli ($F(1,15)=22.71, P<0.001$) whereas a local RT advantage for CB stimuli ($F(1,15)=8.16, P<0.05$). Neither the main effect of Hemifield nor its interactions with other factors were significant ($P>0.05$).

Subjects hit more broadband than CB targets ($F(1,15)=17.45, P<0.001$) and more global than local targets ($F(1,15)=87.48, P<0.001$). As there was a reliable interaction of Frequency Content \times Level of Attention ($F(1,15)=6.71, P=0.02$), post-hoc analyses were conducted and revealed higher accuracies to broadband relative

to CB targets in the global condition ($F(1,15)=19.50, P<0.001$) but no difference between broadband and CB targets in the local condition ($F(1,15)=1.07, P>0.1$). False alarms were low (broadband: 2.9%, CB: 3.1%) and were not influenced by contrast balancing and level of attention ($P>0.2$).

3.2. Electrophysiological data

Grand-averaged ERPs across 16 subjects were computed separately for each stimulus condition and are illustrated in Figs. 3 and 4. Broadband nontarget stimuli evoked a positive deflection between 80 and 150 ms (P1) followed by a negative component between 160 and 220 ms (N1) over the lateral occipital sites (see Fig. 3). Broadband nontarget stimuli also elicited a positive wave between 240 and 320 ms (P2) over posterior occipital areas. ERPs to CB nontarget stimuli were also characterized with P1 (130–180 ms) and N1 (200–300 ms). However, no prominent P2 was observed in ERPs to CB stimuli. Instead, there was negative deflection between 300 and 420 ms (N360) over the posterior electrodes. Both broadband and CB targets produced long-latency negativities between 330 and 400 ms over the posterior sites (posterior N2) and between 260

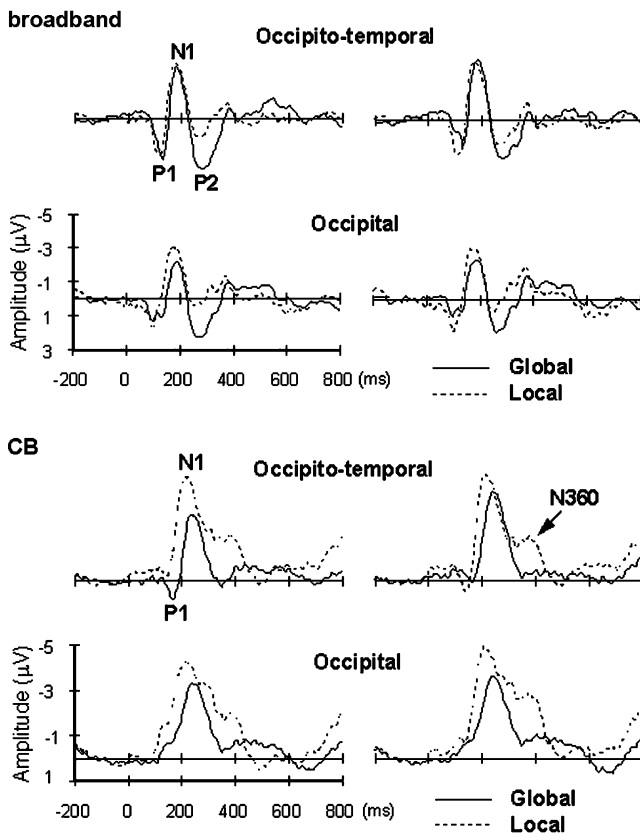


Fig. 3. ERPs to broadband and CB nontarget stimuli in the global and local conditions at occipital and occipito-temporal electrodes. These were characterized with the posterior P1, N1 and P2.

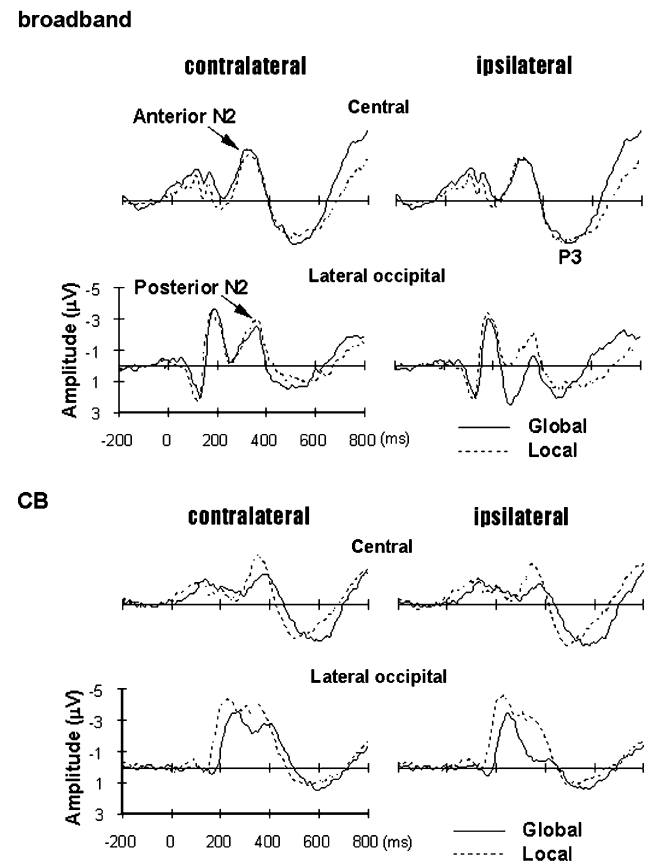


Fig. 4. ERPs to broadband and CB target stimuli in the global and local conditions at central and lateral occipital electrodes. These were characterized with the posterior and anterior N2 and the P3.

and 400 ms over the central areas (anterior N2) and a positivity between 400 and 700 ms (P3) over the central-parietal sites (see Fig. 4). As can be seen in Fig. 3, the P1 and N1 peak latencies to CB stimuli were significantly delayed relative to those to broadband stimuli ($F(1,15)=480.1$, and 834.1 , $P<0.001$). Moreover the P1 peak amplitude was reduced ($F(1,15)=14.08$, $P<0.002$) whereas the N1 peak amplitude was enlarged ($F(1,15)=11.3$, $P<0.005$) by contrast balancing.

3.2.1. Broadband stimuli

Voltage topographies showed that the P1 component had maximum amplitudes over bilateral lateral occipital areas (Fig. 5). The P1 to nontarget stimuli recorded at lateral occipital sites showed shorter peak latencies in the local than global conditions ($F(1,15)=5.20$, $P<0.04$). ANOVAs conducted on the mean amplitudes of ERPs to nontargets revealed a significant main effect of Level of Attention between 80 and 120 ms at lateral occipital electrodes ($F(1,15)=5.62$, $P<0.03$) due to the fact that the P1 was of larger amplitudes in the local than global attention conditions. Moreover, there was a reliable interaction of Level of Attention \times Hemisphere at 100–120 ms ($F(1,15)=4.92$, $P<0.04$), suggesting that the P1 enlargement in the local relative to global conditions was more salient over the right relative to left hemispheres. Post-hoc analysis confirmed that this interaction arose from the fact that the P1 amplitude was larger over the left than right hemispheres in the global condition ($F(1,15)=15.46$, $P<0.002$) whereas the P1 amplitude did not differ between the left-side and right-side electrodes in the local condition ($F<1$).

The N1 amplitudes did not differ between global and local attention conditions ($P>0.5$). ERPs to nontargets

were also characterized by the enlarged P2 wave in lateral occipital cortex in the global relative to local conditions, resulting in a significant main effect of Level of Attention between 240 and 320 ms ($F(1,15)=11.4$, $P<0.005$). There was also a reliable interaction of Level of Attention \times Hemisphere ($F(1,15)=5.90$, $P<0.03$), suggesting that the modulation of the P2 component by global/local attention was stronger at electrodes over the left than right hemispheres. Post-hoc analysis showed that the interaction was due to the fact that the P2 was of larger amplitude over the left than right hemispheres in the global condition ($F(1,15)=6.19$, $P<0.03$) whereas the P2 amplitude did not differ between electrodes over the left and right hemispheres in the local condition ($F(1,15)=2.06$, $P>0.1$). Similar to P1, the P2 wave also had maximum amplitudes over bilateral occipital areas (see Fig. 5).

Both global and local targets elicited larger amplitudes of the posterior N2 at occipito-temporal electrodes contralateral than ipsilateral to the hemifield where targets appeared, resulting in significant interactions of Hemifield \times Hemisphere ($F(1,15)=23.2$, $P<0.001$). The posterior N2 was of larger amplitude to local relative to global targets ($F(1,15)=6.09$, $P<0.03$). ANOVAs of the anterior N2 amplitudes showed a reliable interaction of Level of Attention \times Hemifield \times Hemisphere ($F(1,15)=7.58$, $P<0.02$). Post-hoc analyses confirmed that global targets generated larger amplitudes of the anterior N2 at contralateral than ipsilateral electrodes ($F(1,15)=39.6$, $P<0.001$), whereas no such laterality effect was observed for the anterior N2 to local targets ($F(1,15)=1.19$, $P>0.3$). The P3 amplitudes and latencies did not differ between the global and local conditions ($P>0.5$).

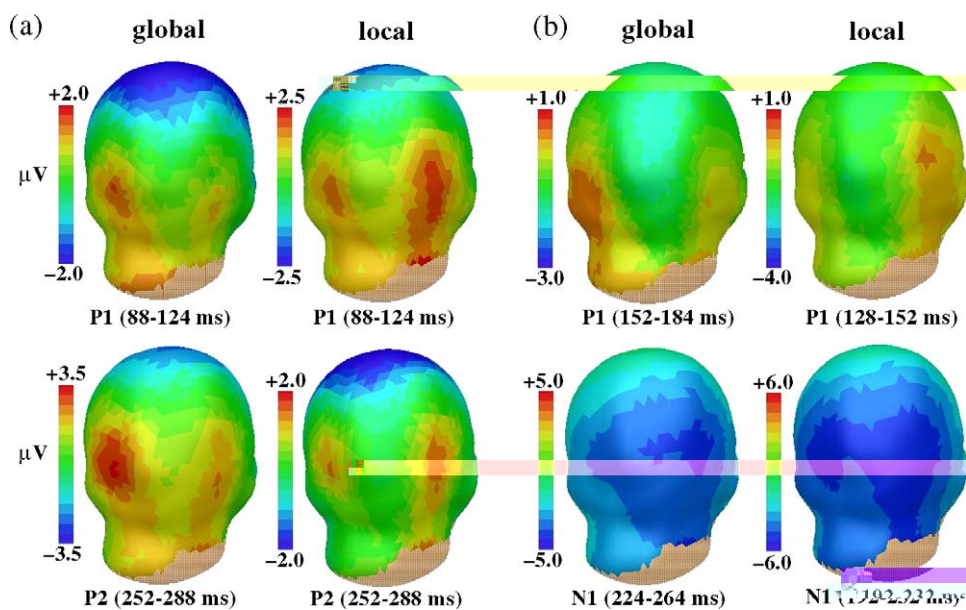


Fig. 5. Voltage topographies of grand average ERPs to (a) broadband nontargets and (b) CB nontargets in the global and local conditions, respectively. The P1 and P2 to broadband stimuli and the P1 and N1 to CB stimuli showed maximum amplitudes over bilateral occipital areas.

3.2.2. CB stimuli

ANOVAs showed a main effect of Level of Attention on P1 and N1 latencies to CB nontargets at lateral occipital electrodes ($F(1,15)=7.38$, and 7.42 , $P<0.02$). This is because the P1 and N1 peaked earlier in the local than global conditions. The main effect of Level of Attention did not reach significance on the P1 amplitudes ($P>0.25$). However, there was a reliable interaction of Level of Attention \times Hemisphere ($F(1,15)=5.09$, $P<0.04$) due to the fact that the P1 peak amplitudes was larger in the global than local conditions over the left hemisphere whereas there was a reverse pattern over the right hemisphere. Post-hoc analysis confirmed that the P1 amplitude was larger at electrode over the left than right hemispheres in the global condition ($F(1,15)=5.10$, $P<0.037$) whereas the P1 amplitude in the local condition did not differ between the electrodes over the two hemispheres ($F<1$). Similar to the P1 elicited by broadband stimuli, the P1 to CB nontarget stimuli had maximum amplitudes over the lateral occipital areas (see Fig. 5).

The N1 mean amplitudes at 200–320 ms were larger in the local than global conditions at occipital areas ($F(1,15)=7.59$, $P<0.02$). Moreover, this effect was stronger over the left than right hemisphere ($F(1,15)=6.49$, $P<0.02$). This asymmetric modulation resulted from the fact that the N1 was of larger amplitude over the right than left hemispheres in the global condition ($F(1,15)=7.63$, $P<0.01$) whereas no such difference was found in the local condition ($F<1$). The long-latency negativity elicited by CB nontarget stimuli (N360) was also of larger amplitudes in the local than global conditions at 320–400 ms ($F(1,15)=18.6$, $P<0.001$). However, the enhancement of the N360 did not differ between electrodes over the left and right hemispheres ($P>0.5$).

Similar to broadband targets, CB local targets also elicited larger long-latency negativity between 280 and 420 ms (the posterior N2) at occipito-temporal electrodes relative to CB global targets ($F(1,15)=11.5$, $P<0.005$). Both global and local CB targets also elicited larger amplitudes of the anterior and posterior N2 components at contralateral than ipsilateral electrodes to the hemifield where target was presented, resulting in a significant interaction of Hemifield \times Hemisphere ($F(1,15)=27.0$ and 36.1 , $P<0.001$, respectively). However, this effect on the posterior N2 was more pronounced in the global than local conditions, resulting in a reliable interaction of Level of Attention \times Hemifield \times Hemisphere ($F(1,15)=17.3$, $P<0.002$). The P3 component peaked earlier in the local relative to global attention conditions ($F(1,15)=14.1$, $P<0.002$).

4. Discussion

The present study investigated the neural mechanisms underlying global/local processing of two compound letters

displayed simultaneously in the LVF and RVF, respectively. The compound stimuli were either broadband in SF spectrum or contrast balanced to remove low SFs. We found that, while RTs to broadband compound stimuli showed a global precedence effect, an early ERP component (P1) at 80–120 ms with maximum amplitudes in the occipito-temporal areas was enlarged in the local relative to global attention conditions. This P1 effect accords with the results of previous ERP studies that used central presentations (Han and Chen, 1996; Han et al., 1997; 2000). Because the P1 component elicited by visual stimuli has generators in the extrastriate cortex (Clark and Hillyard, 1996), the current ERP results, together with the previous neuroimaging studies (Fink et al., 1996; Han et al., 2002; Lux et al., 2004), support the proposition that attention to the global and local levels of compound stimuli modulates neural activities in the extrastriate cortex as early as 80 ms after stimulus onset. Moreover, this early global/local attention effect holds under both conditions when the visual system is confronted with a single compound stimulus and with multiple compound stimuli.

The prior ERP study has shown that the modulation of the P1 component by global/local attention was eliminated when a single compound letters is presented randomly in the LVF or RVF (Han et al., 2003). It may be argued that the difference in the P1 effect between the prior experiments using central and unilateral presentations might reflect per se the difference in global/local processing between foveal and peripheral vision. Nevertheless, the P1 effect observed here suggests that this may not be true given that the compound stimuli were displayed peripherally and bilaterally.

low SFs play a critical role in the global precedence effect observed for the broadband stimuli and that CB stimuli are indeed transmitted through high SF channels, which are characterized by long temporal integration times (Breitmeyer, 1975; Breitmeyer and Ganz, 1977). Similar to the previous study (Han et al., 2003), contrast balancing also reduced the P1 amplitude, which possibly arose from the difference in luminance between the broadband and CB stimuli. Furthermore, our current ERP data showed that the P1 enhancement in the local relative to global conditions observed for the broadband stimuli was eliminated when low SFs were taken away from the compound stimuli. Thus a broadband SF spectrum is necessary for the P1 enlargement in association with local attention in the current experiment. Given these facts, it may be proposed that the increased P1 related to the local processing of broadband stimuli reflects an initial high-SF based selection process in local perception when low SFs are available in stimulus displays. This initial high-SF based selection takes place because low SF information that mediates global perception is transmitted faster than high SF information (Breitmeyer, 1975; Breitmeyer and Ganz, 1977) and competes with local perception even when subjects are asked to selectively attend the local aspect of compound stimuli. When low SFs are removed by contrast balancing, the domination of global features at the early stage of the processing of compound stimuli was weakened (Han et al., 2003) and thus the initial high-SF based filtering is not necessary for local perception. Consequently, the P1 effect disappeared for the CB stimuli.

We also found that a long-latency positivity at 240–320 ms (P2) over the posterior bilateral occipital regions was enlarged when subjects attended to the global relative to the local levels of broadband compound stimuli. This P2 effect was evident under the condition of bilateral presentation but not of unilateral presentation (Han et al., 2003). In addition, the current work showed that the P2 was evident for broadband stimuli and disappeared when low SFs were eliminated by contrast balancing. Therefore the P2 component in the current experiment possibly indexed a low-SF based processing of multiple simultaneously presented compound stimuli that was particularly salient in the global attention condition. The P1 and P2 effects together provide ERP evidence for the dissociation of global/local processing of bilateral visual inputs in time, incorporating with the prior fMRI study (Han et al., 2004) that showed dissociation of global/local processing of bilateral visual inputs in different brain areas. Nevertheless, the voltage topographies did not show a clear separation of the neural sources that generated the P1 and P2 components. Therefore, although the local and global processing of multiple broadband compound stimuli was indexed by enhanced P1 and P2 components, respectively, it is unclear whether the P1 and P2 effects had distinct neural substrates underlying local and global processing of multiple compound stimuli such as those shown in the fMRI study (Han et al., 2004).

The ERP results also revealed a different pattern of the modulation of the N1 component between broadband and CB stimuli. The N1 amplitudes did not differ between global and local conditions for the broadband stimuli. Nevertheless, contrast balancing resulted in enhancement of the N1 in local relative to global conditions. Han et al. (2003) suggested that the increased N1 in the local condition may reflect a space-based orienting of attention to a specific local item in a global structure. In the current experiment, this space-based selection process may not be necessary when local perception of broadband stimuli could be conducted by the high-SF based selection. When low SFs were removed from the compound stimuli, both global and local information had to be transmitted by the high SF channels. Thus local perception could not be distinguished from global perception simply by the high-SF based selection process. Under this circumstance, space-based orienting of attention was required for local processing and thus resulted in enhanced N1 in the local relative to global conditions. Local processing of the CB compound letters also generated a long-latency negative component (N360) over the occipito-temporal area, which possibly reflects a process of evaluation and recognition of local shapes under the condition when local processing could not be conducted based on high-SFs.

Interestingly, the current experiment observed asymmetric neural activities in the visual cortex related to global/local processing of bilateral visual inputs. The amplitudes of the P1 and P2 components to broadband nontargets were larger at electrodes over the left than right hemispheres in the global condition. In the local condition, however, no evident asymmetric activities were observed¹. The asymmetric P1 and P2 components suggest that the hemispheric asymmetry for global processing may take place even when the visual system is confronted with multiple compound stimuli at the same time. Thus lateralization for the processing of global/local properties of compound stimuli can be generalized to the condition when multiple compound stimuli are displayed simultaneously. Furthermore, as the compound letters were displayed in the peripheral visual field, the lateralized P1 and P2 in the global condition indicate that the lateralized global processing is not specific for compound stimuli

¹ As one of the reviewer suggested that low hits might be the reason for the missing hemispherical difference for local stimuli in the ERP results, we reanalyzed the ERP results in terms of subjects' hits. One way to do this was to average the ERP data separately for the subjects whose hits were higher than 70% and lower than 70%. It turned out that the ERP data did not show hemispherical difference for local stimuli even for the subjects with hits higher than 70%. However, as there were only three subjects whose hits were higher than 70%, we reanalyzed the ERP data in another way. We organized the subjects into two groups. The ERP data of half of the subjects with high hits were averaged together and the ERP data of half of the subjects with low hits were averaged together. It turned out that neither the grand ERPs from the two groups of subjects showed hemispherical difference in the local attention condition, suggesting that there was no correlation between hits and hemispheric asymmetry in the local condition.

presented at fixation. However, the pattern of lateralization of global processing of bilateral visual inputs is different from that observed in the studies using central presentations where stronger activities were observed over the right hemisphere in the global attention condition (Fink et al., 1996, 1999; Han et al., 2002; Heinze and Münte, 1993). The pattern of asymmetric neural activities underlying global processing of multiple compound stimuli observed here is not surprising given that left hemisphere dominance of global processing has been observed other neuroimaging studies. For example, it is found that attention to the global aspects of object-based compound stimuli induced greater left-sided activation in the left occipital cortex (Fink et al., 1997). This is different from the results of the studies using compound letters (Fink et al., 1996, 1999; Han et al., 2002; Heinze and Münte, 1993) and suggests that stimulus category may modify the relative differential hemispheric activations in the visual cortex during global and local processing (Fink et al., 1997). We showed here that the number of compound letters also influences the hemispheric specialization for global and local processing. The hemispheric asymmetry in global/local processing might be essentially different between the central and bilateral presentation conditions. When compound stimuli are presented at fixation, both the left and right hemispheres are involved in the representation of a single compound figure. The two hemispheres compete for the processing of different levels of a single compound stimulus. In the bilateral presentation condition, however, each hemisphere is engaged in the representation of a distinct compound figure in the contralateral hemifield. Under this circumstance the two hemispheres competed

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asymmetric behavioral performances may be dissociated from asymmetric neural activities underlying global/local perception and reflect a shift of response criterion (Han et al., 2003). Given the above analysis, it is not surprising that some behavioral studies using unilateral presentation found faster global responses to the LVF stimuli relative to the RVF stimuli but a reverse pattern for local RTs (Hübner, 1997; 1998; Sergent, 1982) whereas other researchers failed to replicate these results (Boles and Karner, 1996; Martin, 1979; Polich and Aguilar, 1990). The inconsistent behavioral results may arise from the difference in response criterion shift rather than differential neural mechanisms underpinning global/local perception.

5. Conclusion

We reported ERP evidences that attention to the global and local levels of two simultaneously presented compound letters modulates neural activities in the visual cortex as early as 80 ms after stimulus onset. Local attention induced a larger P1 whereas global attention generated a larger P2 over the lateral occipital sites. Together with our prior fMRI studies (Han et al., 2004), our results provide evidence for the dissociation of global and local processing of bilateral visual inputs in both time courses and brain structures. Moreover, the P1 and P2 waves were of larger amplitudes over the left than right hemispheres in the global condition, suggesting left-hemisphere dominance in global perception of bilateral visual inputs, which is different from that of central presentation of a single compound letter. Contrast balancing abolished the P2 asymmetry and produced a larger N1 over the right than left hemispheres in the global attention condition. We suggest that the interactions between the two hemispheres induced by bilateral visual inputs may contribute to the unbalanced engagement of the left and right hemispheres in global/local processing, which may be essentially different from that in the central or unilateral presentation conditions. In addition, since the asymmetric neural activities related to global and local processing were influenced by contrast balancing, we suggest that low SF filtering contributes to the hemispheric asymmetries in global/local perception at certain stages of the processing of compound stimuli.

Acknowledgements

This work was supported by National Natural Science Foundation of China (Project 30225026 and 30328016), the Ministry of Science and Technology of China (Project 2002CCA01000), and Learning and Cognition Lab, Capital Normal University. We thank Li Yao for help in data collection. Yi Jiang's current address: Department of Psychology, University of Minnesota, 75 East River Road, Minneapolis, MN 55455, USA.

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