

Hemispheric Asymmetry in Global/Local Processing: Effects of Stimulus Position and Spatial Frequency

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We examined the neural mechanisms of functional asymmetry between hemispheres in the processing of global and local information of hierarchical stimuli by measuring hemodynamic responses with functional magnetic resonance imaging (fMRI). In a selective attention task, subjects responded to targets at the global or local level of compound letters that were (1) broadband in spatial-frequency spectrum and presented at fixation; (2) broadband and presented randomly to the left or the right of fixation; or (3) contrast balanced (CB) to remove low spatial frequencies (SFs) and presented at fixation. Central broadband stimuli induced stronger activation in the right middle occipital cortex under global relative to local attention conditions but in the left inferior occipital cortex, stronger activation was induced under local relative to global attention conditions. The asymmetry over the occipital cortex was weakened by unilateral presentation and by contrast balancing. The results indicate that the lateralization of global and local processing is modulated by the position and SF spectrum of the compound stimuli. The global attention also produced stronger activation over the medial occipital cortex relative to the local attention under all the stimulus conditions. The nature of these effects is discussed. © 2002 Elsevier Science (USA)

Key Words: compound stimulus; contrast balancing; fMRI; global/local processing; hemispheric asymmetry; spatial frequency; occipital cortex.

INTRODUCTION

Visual perception of complex scenes requires the coordinated processing of images on both global and local levels. During global processing local elements are grouped into perceptual wholes, whereas during local

processing scene elements are analyzed as individual objects. Global and local processing has been widely studied using compound letters similar to that shown in Fig. 1a, where the global letter is made up of many smaller letters on a local level (Navon, 1977).

Neuropsychological studies indicate that separate

et al., 1989, 1990; Robertson *et al.*, 1988). These results suggest that the right and left hemispheres are specialized for global and local processing, respectively.

Behavioral studies of the lateralization of global/local processing in normal subjects have shown small and inconsistent asymmetries when stimuli are presented unilaterally in the left or right visual fields. Some researchers have found faster reaction times (RTs) to global targets presented in the left visual field (LVF) than in the right visual field (RVF) and a reverse pattern for local responses (Sergent, 1982; Kimchi and Merhav, 1991). Other researchers, however, failed to find such asymmetry (Boles and Karner, 1996; Martin, 1979; Polich and Aguilar, 1990), or have shown that the apparent asymmetries may result from differences in criterion rather than detection (Han *et al.*, 2002b).

Event-related potential (ERP) studies have shown conflicting results as well. Evans *et al.* (2000) found that an early positive component between 80 and 120 ms after sensory stimulation was enhanced over the left hemisphere in the local relative to the global condition and over the right hemisphere in the global relative to the local condition. Such a pattern of hemispheric asymmetry in global/local processing was also observed in a late occipito-temporal negativity (Heinze *et al.*, 1994) and global and local target-specific differ-

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ence waves (Han *et al.*, 2000; Proverbio *et al.*, 1998). However, other ERP studies did not find such a pattern of hemispheric asymmetry in global/local processing (Han *et al.*, 1997, 1999a, 2002b).

The results of brain imaging studies are also conflicting. For example, positron emission tomography (PET) studies found that attention to global letters enhanced activation over the right lingual gyrus whereas locally directed attention enhanced activation over the left inferior occipital cortex (Fink *et al.*, 1996, 1997). In a task to identify the orientation of compound gratings, Fink *et al.* (1999) further showed that global attention increased occipital activity in the right hemisphere only when relatively high spatial frequency (SF) stimuli were used and local attention increased occipital activity in the left hemisphere only when relatively low SF stimuli were used. Because the global shapes appeared more prominent than the local shapes for the high SF stimuli whereas the reverse was true for the low SF stimuli, Fink *et al.* argued that the asymmetric occipital activities associated with global and local processing were modulated by perceptual salience of global and local shapes. A functional magnetic resonance imaging (fMRI) study found similar hemispheric asymmetry in global/local processing over the occipitotemporal cortical junctions (Martinez *et al.*, 1997). However, other PET (Heinze *et al.*, 1998) and fMRI (Sasaki *et al.*, 2001) studies failed to replicate hemispheric asymmetry over the occipital cortices possibly because perceptual salience of the global shapes was impaired by composing global letters with few local letters (Heinze *et al.*, 1998) or nontypical Navon-type compound stimuli were used (Sasaki *et al.*, 2001).

The current experiment further addressed the issue of hemispheric lateralization in global/local processing using fMRI. The first objective was to verify the hemispheric asymmetry in global/local processing, as observed in the previous PET and fMRI studies using compound letters presented in the center of the visual field. The experiment was designed to identify the relative difference between the patterns of activation associated with global and local processing. We were particularly interested in whether the left occipital cortex showed stronger activation under local rather than global conditions and the right occipital cortex showed stronger activation under global rather than local conditions.²

The second objective was to determine how the asymmetry is affected by stimulus position. Previous studies that showed hemispheric asymmetry in global/local processing usually displayed compound stimuli in the center of the visual field (Fink *et al.*, 1996; Han *et al.*, 2000; Heinze *et al.*, 1994; Martinez *et al.*, 1997) or in the two visual fields simultaneously (Evans *et al.*, 2000), whereas those failed to replicate such asymmetry presented compound stimuli unilaterally in the LVF or RVF (Han *et al.*, 1999a, 2002a). Han *et al.* (2002a) suggested that central presentation allows the two hemispheres equal access to stimulus information and leads to competition between the two hemispheres for processing the information. The competition during a global task results in stronger activation in the right than in the left hemisphere with a converse pattern observed in local tasks. When compound stimuli are presented unilaterally, however, the conditions conducive to competition are eliminated and the hemispheric asymmetry in global/local processing may be attenuated. Since there has been no research to study the effect of stimulus position on laterality associated with global/local processing systematically, the current work examined this hypothesis by recording hemodynamic responses associated with global and local processing of compound stimuli presented in the center of the visual field or randomly in the LVF or RVF. If the

son, 1987), has led to the development of a model of hemispheric lateralization in global/local processing based on SF filtering (Ivry and Robertson, 1998), which assumes that the right hemisphere operates as a low-pass filter and carries on global processing based on low SFs, and the left hemisphere operates as a high-pass filter and accomplishes local processing based on high SFs. The evidence supporting this model comes from patient studies that suggest right hemisphere dominance in global processing and left hemisphere dominance in local processing (Lamb *et al.*, 1989, 1990; Robertson *et al.*, 1988) and normal subjects studies that suggest that the left and right hemispheres are biased toward efficient use of higher and lower SF information, respectively (Christman *et al.*, 1997; Kitterle *et al.*, 1991). According to Ivry and Robertson's (1998) model, when the compound stimuli include only a limited range of high SFs, differentiation between global and local information cannot be based on low and high SFs and thus other features must be used. Under this condition, the hemispheric asymmetry associated with low and high SF processing during hierarchical analysis should be weakened or eliminated. We tested this hypothesis by comparing hemodynamic responses related to global/local processing of compound stimuli that were either broadband in SF spectrum or contrast balanced (CB) to eliminate low SFs³ that is critical for global processing. Although contrast balancing may also reduce medial SFs that may partially contribute to local processing there has been evidence that contrast balancing produced larger effects on global rather than local processing (Lamb and Yund, 1993, 1996).

MATERIALS AND METHODS

Subjects

Ten normal healthy adults (6 men, 4 women; aged between 19 and 43 years) participated in this study as paid volunteers. All had normal or corrected-to-normal vision. All participants were right-handed, without neurological disorders, and gave informed consent according to the guidelines of the Veterans Administration and the University of California, Davis.

³ If Ivry and Robertson's hypothesis (i.e., the hemispheric asymmetry in global/local processing of compound stimuli is based on low- and high-pass filtering operated in the right and left hemispheres, respectively) is correct, it may be predicted that the hemispheric asymmetry in global/local processing should be weakened if perception of compound stimuli is only conducted based on high SFs. Thus it is sufficient to test Ivry and Robertson's model by using high-pass compound stimuli. Low-pass filtering (i.e., blurring local elements of compound stimuli) impairs local perception seriously and makes the difficulty of global and local perception incompatible, and thus was not used in the current study.

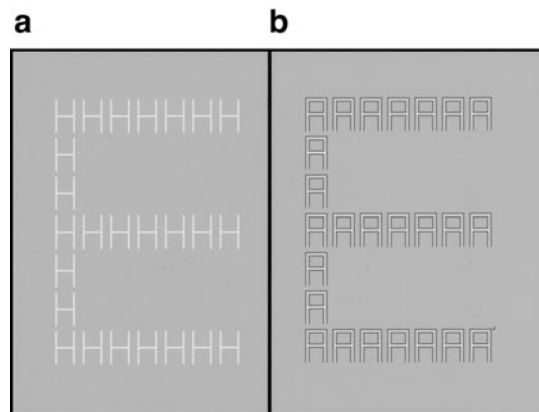


FIG. 1. Illustrations of the compound stimuli used in the current study. (a) A broadband compound letter (i.e., a global E is made up of local Hs, which were composed of white lines on a gray background); (b) A CB compound letter (i.e., a global E is made up of local As, the white lines of which are surrounded by lines that were darker than the background).

Stimuli

Stimuli were presented with a PC running Presentation software (www.neurobehavioralsystems.com) through a Sharp LCD projector onto a rear-projection screen located at the subject's feet. The screen was viewed with an angled mirror positioned on the head coil. The stimuli were global letters made up of local letters in a 7×7 matrix, as illustrated in Fig. 1. Letters "H" and "S" served as targets while letters "A" and "E" served as distractors. Stimulus patterns either contained one target at the global level (i.e., global/local letters were H/A, S/A, H/E, or S/E) or the local level (i.e., global/local letters were A/H, E/H, A/S, or E/S), or contained no targets (i.e., A/E or E/A), resulting in 10 stimulus figures. From a viewing distance of 277 cm, global letters were 4.2° wide and 6.1° high. Local letters were 0.45° wide and 0.70° high.

Compound stimuli were presented on a gray (16.4 cd/m^2) background. Each local letter of the broadband stimuli was composed of lines that were brighter (29.3 cd/m^2) than the background. The CB stimuli were identical to the broadband stimuli except that the bright lines composing each local letter were surrounded by lines that were darker (10.1 cd/m^2) than the background. The change in luminance from background was approximately twice as great for bright lines as for dark lines. Because dark lines occupied twice as much area as bright ones, the space-averaged luminance of the CB stimuli equaled that of the background. This arrangement of the luminance levels removed virtually all detectable spectral power below 3 cycles/degree from the CB stimuli (see Lamb *et al.*, 1999, for the results of spectral power analysis). All lines (both bright and dark) were approximately 0.02° thick.

There were three stimulus conditions in the current experiment: (1) central broadband stimuli, (2) unilat-

eral broadband stimuli, (3) central CB stimuli. A fixation cross of $0.30 \times 0.45^\circ$ was continuously visible in the center of the screen under all the stimulus conditions. Subjects were instructed to maintain fixation at all times on the fixation cross.⁴ Under the central broadband and CB stimulus condition, the compound stimuli were displayed in the center of the visual field. The center of compound letters was 0.83° above the fixation so that compound stimuli and the fixation cross did not overlap. The compound stimuli were randomly displayed to the left or the right of the fixation in the unilateral broadband stimulus condition.⁵ The fixation and the inner edge of the compound stimulus were 1.7° apart. The stimulus displays were presented for 200 ms. Stimulus intervals were randomized between 500 and 1000 ms.

Experimental Design

Two scans of 308 s were obtained under each stimulus condition and were averaged together.⁶ Each scan

⁴ We did not measure subjects' eye movements when subjects were in the scanner because of limitation of recording technique. However, the effects of eye movements on global/local processing were evaluated by the results of our ERP study (Han *et al.*, 2002b), which used the same experimental design (unilateral presentation) as that in the current fMRI study and recorded subjects' vertical and horizontal eye movements with electrodes below the left eye and lateral to the left and right external canthi. The electrophysiological results showed that eye movements were small (less than $2 \mu\text{V}$) and the patterns of eye movements under the global and local conditions were very similar. The results suggest that differential eye movements under the global/local conditions contributed trivially to the modulation of hemispheric asymmetry in global/local processing under the condition of the current experiment.

⁵ In our ERP study (Han, 2002b), the LVF and RVF stimuli were intermixed in the same blocks of trials. Such a unilateral-presentation condition was designed to eliminate the effect of eye movements. The current fMRI study used the same experimental design (unilateral presentation condition) as that in our ERP study so that we were able to compare the results from both studies. Such a design of the fMRI experiment made us unable to examine Hemisphere \times Visual Field interaction without using event-related analysis. However, this is not essential to the current work because what we were really interested in is the interaction of Attention (global vs local) \times Hemisphere (left vs right), which is useful for demonstrating hemispheric asymmetry in global/local processing (Fink *et al.*, 1996, 1997). Because of limitation of tools for data analysis, we did not do event-related analysis of the fMRI data under the unilateral-presentation condition. However, the results of the block design did not affect the accuracy of localizing activation associated with global and local processing as the results of central broadband stimuli of the current work coincided very well with the results of previous work (Fink *et al.*, 1996, 1997). Most important, such a block design does not affect the conclusion we made here.

⁶ We performed retinotopic mapping using grating-like stimuli to identify the boundaries between V1 and V2 in the current experiment. However, for unknown reasons, we failed to obtain clear results from most of the subjects. This made it difficult to localize the effects of global/local attention in V1 and V2 based on retinotopy. Thus we had to use coordinates in Talairach space to refer to the Brodmann areas that showed differential activation between global and local processing.

consisted of 11 epochs of 25 trials (28 s for each epoch), alternating between global and local attention conditions. The first epoch of each scan was excluded from statistical analysis to obtain a similar baseline for all the following epochs of trials. There were 10% target stimuli in each scan. At the beginning of each epoch, a large or a small letter made up of solid black lines was presented for 1000 ms to inform subjects of target shape (H or S) and target level (global vs local). The sizes of global and local cues were the same as those of global and local letters of the compound stimuli. Subjects pressed a hand-held fiber-optic response button to indicate detection of the designated global or local target. The order of stimulus conditions was counterbalanced across subjects. Subjects were given 6 to 10 epochs of trials for practice prior to brain imaging.

Image Acquisition

Brain imaging was performed using a Marconi 1.5-T scanner and a three-axis local gradient head coil. Twenty axial slices of functional images that covered the whole cerebral cortex were acquired using echoplanar imaging ($128 \times 128 \times 20$ matrix with $1.87 \times 1.87 \times 5$ -mm spatial resolution, TR = 2000 ms, TE = 40 ms, FOV = 240 mm, flip angle = 90°). Anatomical images were obtained with a standard 3D T1-weighted sequence (resulting in a $256 \times 212 \times 256$ matrix with $0.938 \times 1.13 \times 0.938$ -mm spatial resolution, TR = 15 ms, TE = 4.47 ms, flip angle = 35°). Subjects' heads were immobilized during the scanning sessions using pieces of foam.

Analysis of Imaging Data

SPM99 (Wellcome Department of Cognitive Neurology, London, UK) implemented in MATLAB (Math Works, Natick, MA) was used for imaging data processing and analysis. For each subject, functional images were realigned to the first scan to correct the head movement between scans. The structural image was coregistered with the mean image produced during the process of realignment. All images were normalized to a $2 \times 2 \times 2$ -mm³ Montreal Neurological Institute (MNI) template in Talairach space (Talairach and Tournoux, 1988) using bilinear interpolation. Functional images were spatially smoothed using a Gaussian filter with a full-width at half-maximum (FWHM) parameter set to 5 mm. Data were modeled using a boxcar function. Contrasts were used to compare the effect of attention (global vs local) for each stimulus condition. Regions preferentially engaged by global processing were defined as areas more activated by the global attention than by the local attention. Regions preferentially engaged by local processing were defined as areas more activated by the local attention than by the global attention. Statistical effects of attentional conditions for each type of stimulus were first assessed

in individual subjects. Random effect analyses were then conducted across the group of 10 subjects based on statistical parameter maps from each individual subject to allow population inference. Areas of significant activation were identified at the cluster level for values exceeding an uncorrected P value of 0.001 for each individual subject and an uncorrected P value of 0.01 for the group analysis. Clusters of voxels smaller than 30 voxels were not displayed.

To further confirm the lateralization effect of global/local attention over the occipital cortex, the mean normalized signal values of a cubic region of interest (ROI, illustrated in Fig. 2) with volume of 3.1 cm^3

For unilateral broadband stimuli, global attention generated stronger activation over the medial occipital cortex (BA 19) relative to the local attention condition,

central broadband and CB stimuli, an ANOVA was conducted on the mean values of the ROI over the occipital cortex with factors being Stimulus Set (broadband vs CB), Level of Attention, and Hemisphere. There was a significant interaction of Stimulus Set \times Level of Attention \times Hemisphere ($F(1,9) = 5.53, P < 0.04$), indicating that the pattern of hemispheric asymmetry over the occipital cortex associated with global/local processing was different between central broadband and CB stimuli.

DISCUSSION

The present study used a target detection task to examine hemispheric asymmetry in global and local processing of compound stimuli. The same procedure and motor response were used for all the three conditions so that the difference in both behavioral and hemodynamic responses between the conditions reflects the effects of stimulus position and SF contents of stimuli. Response accuracies were high, indicating that subjects were successful in attending to the global and local levels of compound letters. Similar to Pomerantz (1983), we found that moving broadband stimuli from the fovea to the periphery slowed RTs particularly under the local condition. In contrast, removing low SFs from compound stimuli by contrast balancing slowed RTs particularly under the global condition and resulted in a local RT advantage, consistent with previous reports (Lamb and Yund, 1993, 1996).

There has been debate regarding whether activities of the left and right occipital cortices are differentially modulated by attention to the global or local level of compound stimuli (Fink *et al.*, 2000; Mangun *et al.*, 2000). In a task of selectively naming the global or local letters that were presented in the center of the visual field, Fink *et al.*, (1996) found that the regional cerebral blood flow (rCBF) was increased over the left inferior occipital cortex and the right lingual gyrus by locally and globally directed attention, respectively. However, Heinze *et al.* (1998) failed to replicate these results in a similar selective attention task. We showed here that, when broadband compound letters were presented in the center of the visual field, locally directed attention was associated with stronger activation over the left inferior occipital cortex in an area close to that of Fink *et al.* (1996). The focus of the right lateral occipital activation in the global attention condition is more lateral and anterior compared to the results of Fink *et al.* (1996), but is consistent with the fMRI results of Martinez *et al.* (1997). The lateralized modulations of occipital activities by global/local attention revealed by our fMRI results is in agreement with the ERP studies (Evans *et al.*, 2000; Han *et al.*, 2000), which found that occipito-temporal activities show larger amplitudes over the right hemisphere when attending to the global shape and larger amplitudes over the left hemisphere

when attending to the local shape. Taken together, these results support the proposition that global and local properties of compound stimuli are differentially represented in the two hemispheres at an early stage of visual processing.

More interestingly, we found that the lateralized extrastriate activation associated with global/local processing was attenuated by unilateral presentation. These results are in agreement with the hypothesis that lateralization in global/local processing depends, to a certain degree, upon stimulus position in the visual field (Han Yund *et al.*, 2002b). A possible account for these effects is that both hemispheres are capable of processing stimuli on either global or local levels, with the right hemisphere being superior in analyzing global patterns and the left hemisphere superior in analyzing local patterns. When stimulus information arrives in the two hemispheres simultaneously, the two hemispheres compete for processing the information at the proper level. Consequently, globally directed attention results in stronger activation in the right than in the left hemisphere and locally directed attention leads to a reverse pattern, as reflected in the asymmetric occipital activation induced by the central broadband stimuli. When compound stimuli are presented unilaterally, however, stimulus information is initially projected to the contralateral occipital cortex and then must be transmitted to the ipsilateral hemisphere through corpus callosum if it is to be further processed there. This interhemispheric transmission may cause information loss and/or a time delay before the ipsilateral occipital cortex can participate in global or local processing, and thus weaken the competition between the two hemispheres and eliminate the early lateralized occipital activation. This proposal is consistent with the current fMRI findings and is also in accord with the ERP findings that activities over the occipito-temporal areas show hemispheric asymmetry in global/local processing when compound letters are presented in the center of the visual field (Han *et al.*, 2000; Heinze *et al.*, 1994) whereas no such asymmetry is observed under the condition of unilateral presentation (Han *et al.*, 1999a; Han *et al.*, 2002b).

Unlike the central broadband stimuli, the unilateral broadband stimuli produced activation over the right temporal-parietal junction in the global attention condition, suggesting that the right hemisphere dominates the left at the level of high order processing of the global shape of unilateral compound letters. The focus of the temporal-parietal activation is consistent with the findings of the patient study (Robertson *et al.*, 1988), which showed that lesions of the right temporal-parietal junction selectively slow the responses to the global structure of compound letters. Fink *et al.* (1996, 1997) found asymmetric occipital activation associated with global and local processing when attention did not switch between global and local levels in the same

block of trials and asymmetric temporal-parietal activation when attention had to switch between global and local levels. Fink *et al.* suggest that temporal-parietal regions may exert attentional control over global and local processing. If this is correct, it may be proposed that the findings of the lesion studies (Lamb *et al.*, 1989, 1990; Robertson *et al.*, 1988) may principally refl

Heinze *et al.*) may weaken local element grouping (Han, 1999b; Han and Humphreys, 1999, 2002), and thus reduce the enhanced activity over the right occipital cortex associated with global attention. Similarly, when subjects were asked to discriminate X vs + compound shapes that were displayed in the center of the visual field (Sasaki *et al.*, 2001), subjects could use only a few local figures around fixation to perform the global task. Indeed, the location of any single local shape (other than the one at fixation) provides sufficient information to identify the global shape. This might diminish the difference in SF used in the global and local tasks, and thus weakens the asymmetric occipital activities based on SF filtering or on a grouping process.

Our current experiment also found stronger activation over the medial occipital cortex in the global relative to local attention conditions for the central broadband stimuli, which is similar to Sasaki *et al.*'s (2001) results. We showed further that this occipital activity associated with global processing was evident irrespective of retinal position and SF content of the compound stimuli. Because the medial occipital activation was observed when both global and local shapes were displayed in the peripheral visual field, it may not simply reflect enhanced peripheral representation of the stimulus displays in the global than in the local task. A possible explanation is that the enlargement of an attentional window in the global relative to the local task (Robertson *et al.*, 1993) may enhance the neuronal responses associated with the processing of the stimuli inside the attentional spotlight. This top-down attentional modulation is not affected by where compound stimuli are presented and whether low SFs are available in the stimuli. Alternatively, it is possible that the medial occipital activation may reflect the process of perceptual grouping that is required for the perception of global shape (Han, 1999b; Han and Humphreys, 1999). The latter hypothesis is consistent with our recent ERP study which found that grouping of local elements produced enhanced activation over the medial occipital cortex between 100 and 120 ms after sensory stimulation (Han *et al.*, 2001b, 2002a).

CONCLUSIONS

The present study provided fMRI evidence that the left and right extrastriate cortices are differentially activated by attention to the global or the local aspects of compound letters that were displayed in the center of the visual field. In addition, we showed that this asymmetry was eliminated by unilateral stimulus presentation, consistent with a model of lateralization of global/local processing based on competition between the two hemispheres. The asymmetric occipital activation associated with global and local processing was also diminished by removing low SFs from the stimuli, suggesting a role of SF filtering in that cortical area

during the processing of compound letters. Mechanisms other than SF filtering (such as local element grouping) may also contribute to the lateralized occipital activity related to global processing.

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