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

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 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.*, an.asedJT9661 gsJT9661292Le077 TJT5 eral broadband stimuli, (3) central CB stimuli. A fixation cross of $0.30 \times 0.45°$ was continuously visible in the center of the screen under all the stimulus condiin 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^2 (a square of 56 voxels through 7 slices of normalized images) were subjected to a two-way ANOVA with Level of Attention (global vs local) and Hemisphere (left vs right) as independent variables. The size of the ROI was decided based on the cluster size of group analysis and projected back to individual subjects. The ROI was centered at the occipital maximum of the SPM(*t*)-mat from group analysis and was measured in both hemispheres (the Talairach coordinates of the center of ROI were about *x*, *y*, *z* □ □52, □64, □10 under the global condition, and *x*, *y*, *z* □ □30, □92, □8 under the local condition).

RESULTS

RTs, hits, and false alarms are shown in Table 1. They were subjected to ANOVAs with Frequency Content (broadband vs CB stimuli), Level of Attention (global vs local), and Visual Field (central vs unilateral) as independent variables. Responses to central broadband stimuli were faster than those to central CB (*F*(1,9) □ 48.8, *P* □ 0.001) and unilateral broadband stimuli (*F*(1,9) □ 7.18, *P* □ 0.03). RTs to central broadband stimuli did not differ between global and local attention cos,attention con7TJ-8.25iTJ-8.25iTJ-8.28.25iT

TABLE 2

Brain Areas Activated during Global and Local Tasks Under Each Stimulus Condition in the Group Analysis

Condition/region	Voxels, No.	BA	*X*	*Y*	*Z*	*Z* value
Central broadband						
Global attention						
Right middle occipital gyrus	213	19,37	52	−64	−10	3.83
Medial occipital gyrus	61	18	12	−96	22	3.58
Parieto-occipital sulcus	121	19	−10	−74	30	3.44
Local attention						
Left inferior occipital gyrus	52	18	−30	−92	−8	3.45
Unilateral broadband						
Global attention						
Cuneus and precuneus	281	19	2	−84	30	3.58
Right temporal-parietal junction	137	39	56	−66	20	3.74
Central contrast balanced						
Global attention						
Right middle occipital gyrus	79	19,37	54	−64	−10	3.50
Medial occipital gyrus	88	18	−8	−98	14	3.72
Local attention						
Precuneus	162	7	4	−64	42	3.57
Left inferior occipital gyrus	36	18	−26	−94	−6	3.55
Right inferior occipital gyrus	34	18	22	−96	−4	3.45
Left superior temporal gyrus	312	22,42	−42	−12	8	4.84
Left postcentral gyrus	191	1,2	−40	−26	60	4.53
Right temporal-parietal junction	99	39	50	−52	22	3.99

Note. Uncorrected $P < 0.01$ for all clusters listed in the table; Voxels, No., number of voxels in a cluster.

For unilateral broadband stimuli, global attention generated stronger activation over the medial occipital cortex (BA 19) relative to the local attention condition, as shown in Fig. 4. Unlike central broadband stimuli, there was no evident lateralized activation over the occipital cortex associated with global or local attention. However, globally directed attention produced stronger activation over the right temporal-parietal junction relative to locally directed attention. Because no significant activation was observed under the local attention condition, Fig. 4 shows only the results under the global attention condition.

For central CB stimuli, stronger activation was also observed over the medial occipital areas (BA 18) under the global relative to the local attention condition (Fig. 5). Global attention also activated the right middle occipital areas (BA 19, 37). Local attention activated bilateral inferior occipital gyrus (BA 18), left superior temporal gyrus (BA 22, 42), left postcentral gyrus (BA 1, 2), and the right parieto-temporal junction (BA 39). However, the interaction between Level of Attention and Hemisphere was not significant in the ROI analysis of the occipital activation ($F(1,9) = 2.13$, $P > 0.1$). To further confirm the difference in the occipital asymmetry associated with global/local processing between

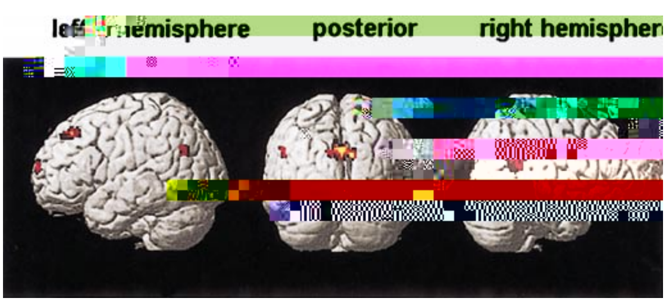

FIG. 4. Brain areas activated by attention to the global level of unilateral broadband stimuli. The results of the group analysis from 10 subjects were rendered on a 3-D structural image of the MNI template provided by SPM99. Threshold for activation of all clusters was $P < 0.01$ (uncorrected).

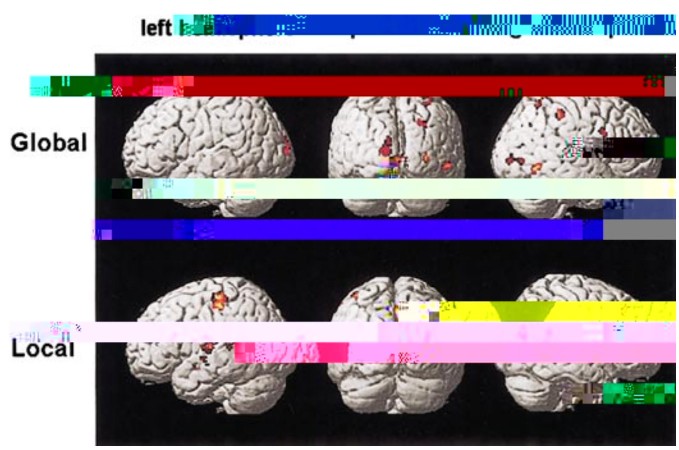

FIG. 5. Brain areas activated by attention to the global or local level of central CB stimuli. The results of the group analysis from 10 subjects were rendered on a 3-D structural image of the MNI template provided by SPM99. Threshold for activation of all clusters was $P < 0.01$ (uncorrected).

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 □ Level of Attention □ 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

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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