

Neural Mechanisms of Global and Local Processing: A Combined PET and ERP Study

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Abstract

■ The neural mechanisms of hierarchical stimulus processing were investigated using a combined event-related potentials (ERPs) and positron emission tomography (PET) approach. Healthy subjects were tested under two conditions that involved selective or divided attention between local and global levels of hierarchical letter stimuli in order to determine whether and where hemispheric differences might exist in the processing of local versus global information. When attention was divided between global and local levels, the N2 component of the ERPs (260- to 360-msec latency) elicited by the target stimuli showed asymmetries in amplitude over the two hemispheres. The N2 to local targets was larger over the left hemisphere, but the N2 to global targets tended to be slightly larger over the right hemisphere. However, the shorter-latency, sensory-evoked P1 component (90- to 150-msec latency) was not different for global versus local targets under conditions of divided attention. In contrast, during selective attention to either global or local targets, asymmetries in the N2 component were not observed. But under selective attention condi-

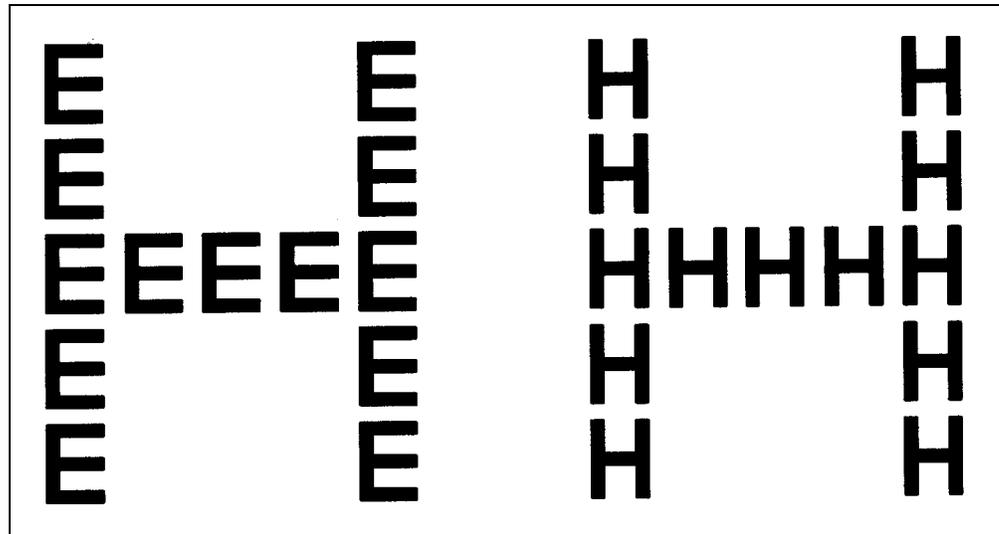
tions, the sensory-evoked P1 components in the extrastriate cortex were enlarged for global versus local attention. Increased regional cerebral blood flow in the posterior fusiform gyrus bilaterally was observed in the PET data during selective attention to either global or local targets, but neither these nor the P1 component showed any tendency toward hemispheric difference for global versus local attention. Neither were there any activations observed in the parietal lobe during selective attention to global versus local targets. Together these data indicate that early sensory inputs are not modulated to gate global versus local information differentially into the two hemispheres. Rather, later stages of processing that may be asymmetrically organized in the left and right hemispheres operate in parallel to process global and local aspects of complex stimuli (i.e., the N2 effect of the ERPs). This pattern of results supports models proposing that spatial frequency analysis is only asymmetric at higher stages of perceptual processing and not at the earliest stages of visual cortical analysis. ■

INTRODUCTION

Visual perception involves the analysis of the hierarchical structure of features, objects, and scenes. For example, the perception of a flock of migrating geese includes analyses at the global level to perceive their v-shaped formation and at the local level to note the individual objects in the scene, the birds themselves, or the individual features of each bird—that is, their bodies, heads, wings, and so on. Thus, natural visual processing involves the analysis of global and local form within hierarchically organized visual stimuli. The complexity of hierarchically organized stimuli presents the visual system with the difficult computational problem of how to parse objects and represent them without losing either global or local information.

There has been a long debate about the mechanisms that underlie global and local perception in vision. The global precedence theory (Navon, 1977) suggests that a single computational resource processes hierarchical stimuli in a sequential order from the global to the local level. These studies used experimentally constructed hierarchical stimuli such as the letter shown in Figure 1. The large (global) letter H is composed of an arrangement of small (local) letters, each of which is a distinct letter itself. The findings from such studies were that global patterns were identified faster than local patterns (global reaction time advantage) and that global patterns influenced the relative speed of responding to local patterns but not vice versa (global-to-local interference). From these findings it was initially concluded that global information is analyzed before local information and,

Figure 1. Examples of the stimuli used in this study. Left, the letter H is formed at the global level by the letters E at the local level. The global and local letters could either be different (left of figure) or the same. In the study, only one hierarchical letter was presented on each trial. A fixation spot (not shown) was present in the center of the display, and a frame surrounded the locations at which the letters would be flashed. Both the letters and frame were actually presented white on a black background.



hence, that a single processing resource was sufficient to explain perception of hierarchical stimuli.

Subsequent studies, however, have shown that the reaction time (*RT*) advantage and the direction of interference do not necessarily covary. Lamb and Robertson (1988) conducted a divided-attention experiment in which subjects had to attend simultaneously to both levels of a hierarchical letter like that in Figure 1. They found that variations in the visual angle subtended by the stimulus pattern influenced the relative speed of responding to global versus local targets, but had no effect on the direction of interference. At larger visual angles, local targets were identified faster than global targets, but global distracters interfered with the responding to local targets. Local distracters, however, had no effect on responses to global targets. Based on this dissociation between a local *RT* advantage and a global direction of interference, Lamb and Robertson proposed that separate computational resources were involved in global and local analysis.

This conceptualization has received support from studies in neurological patients with focal cortical lesions. Robertson, Lamb, and Knight (1988) investigated neurological patients with left and right temporal and parietal cortex lesions. Using global-local target detection tasks, they found that attentional control was normal in patients with lesions centered in the superior temporal gyrus but was disrupted in patients with lesions in the inferior parietal lobe. In contrast, automatic perceptual encoding was impaired in patients with lesions in the superior temporal gyrus and temporal parietal junction but was not affected by lesions in the parietal lobe. In addition, perceptual impairment showed an asymmetric hemispheric distribution, being more severe for local targets in patients with left hemisphere lesions and for global targets in patients with right hemisphere lesions. The authors concluded that a single mechanism could

not mediate global-local analysis but that both attentional and perceptual mechanisms in separate brain systems were involved.

Event-related brain potential (ERP) recordings have provided further evidence for a distributed organization of global and local processing (Heinze & Münte, 1993; Heinze, Münte, Johannes, & Mangun, 1994c). ERPs are scalp-recorded voltage fluctuations that reflect neural activity that is time-locked to stimulus (or response) events. In the previous ERP studies it was found that global and local processing during divided attention between global and local levels was associated with a negative polarity ERP component (N2) over posterior scalp areas. The N2 effects for global and local target processing had similar onset latencies but only partially overlapping time courses for global and local targets. Interestingly, these effects were distributed asymmetrically over the scalp at temporal and occipital scalp regions—the N2 component was greater in amplitude for local than for global targets over the left but not over the right hemisphere. Because the N2 component was the shortest-latency electrophysiological sign of target discrimination in this task, it was concluded that global and local pattern analysis is performed in parallel by lateralized perceptual systems.

Thus, to date, although some experimental findings are compatible with the assumption of a single processing resource, more recent data suggest the involvement of multiple processing resources in global-local perception. In particular, both perceptual and attentional mechanisms may contribute to the analysis of hierarchical stimuli, and these may involve both spatial attention and feature-based or categorical attention (e.g., Robertson, Egly, Lamb, & Kerth, 1993). However, the neuroanatomical substrates of these processes are not completely understood. This is because, despite the important information obtained from studies in neurological patients,

such data have provided us with only one view of the neural substrates of global-local processing. Similarly, the ERP data provide evidence for multiple neural systems being involved but provide very little information as to the anatomical locus of ERP differences for global and local processing. It is important to try to provide additional anatomical information regarding the brain systems involved in global-local analysis in order to test existing theories of a hemispheric asymmetry and to identify the participating brain areas with an anatomical resolution higher than is available through lesion analysis or ERPs alone.

The present study aims to further investigate the neural basis of hierarchical pattern analysis by using both high temporal (ERP) and high spatial resolution (positron emission tomography, PET) measures of the neural processes involved in global and local stimulus analysis. We investigated global and local processing during two conditions. The first was a selective-attention condition to either global or local levels—in separate sessions, ERP and PET measures were obtained for the same observers performing the selective-attention task. For this selective-attention task, subjects were instructed to attend selectively to target letters either at the global or local level for each block of trials. The second condition included divided-attention between global and local levels—only ERPs were collected during this condition. In the divided-attention task, subjects had to respond to target letters both at the global and local levels within the same block of trials. These effects were compared to neutral (passive) viewing conditions during which the subjects merely viewed the stimuli while maintaining fixation of their eyes centrally.

RESULTS

Behavioral Results

Mean RTs for correct trials in the task conditions are summarized in Figure 2, and presented in Table 1 together with hit rates. In the selective-attention task, mean RTs for global and local targets (when letters were the same at global and local levels) were not significantly different (409.2 msec versus 408.2 msec). This equivalence of RT for selective attention to global and local target processing indicates that overall behavioral arousal was roughly equated between conditions, thereby reducing the possibility that any differences in physiological measures between conditions might result from effects of task difficulty or other nonspecific factors. However, the degree of interference produced by distracters at global and local levels differed significantly for RT. Distracters at the local level were found to interfere more with detection of global targets (31.4 msec slowing) than did distracters at the global level with detection of local targets (10.1 msec slowing); this difference was reliable as shown by a significant target level

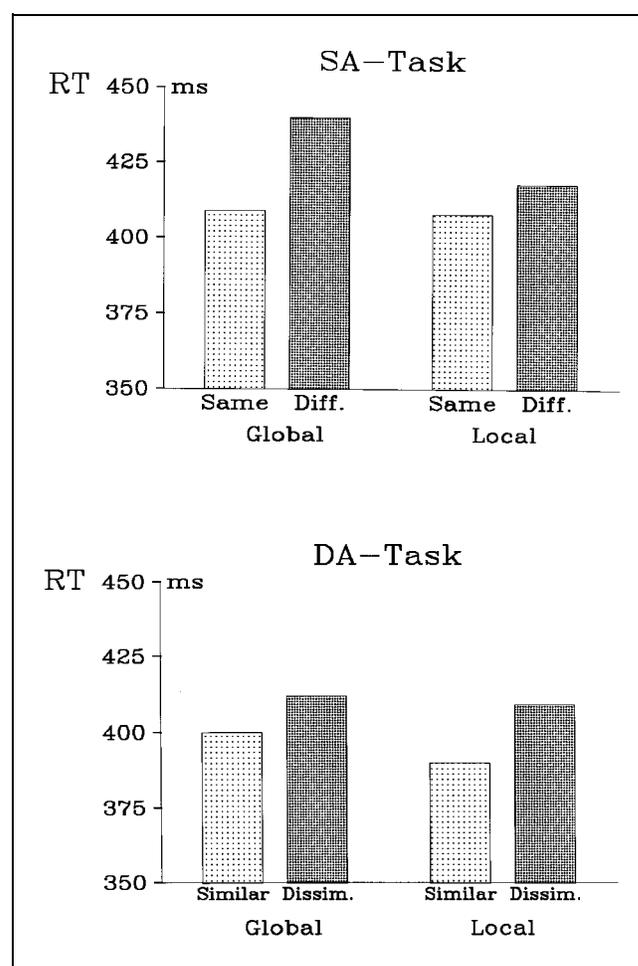


Figure 2. Mean reaction times to target letters in the selective-attention (SA) task (top) and divided-attention (DA) task (bottom). In the SA task, letters at the global and local levels could be the same or different. In the DA task, letters at the global and local levels could be similar in form (letters S and E) or dissimilar in form (letters H and A) and could appear at either the global or local level.

by similarity interaction ($F(1, 9) = 10.5, p < 0.01$). The hit rates showed a similar pattern, but these effects did not reach significance.

In the divided-attention task, mean RTs to global and local targets in trials with similar global and local letters were not significantly different (399.9 versus 389.9 msec). Significant interference effects occurred in both directions: Both global and local targets were identified faster with similar than with dissimilar distracters at the other level (main effect of interference: $F(1, 9) = 18.4, p < 0.002$). The magnitude of this interference effect, however, was about the same for global and local targets (no significant target level by interference interaction).

Physiological Results

Selective Attention Task

The PET activations for the global versus neutral condition and local versus neutral condition are shown in

Table 1. Mean reaction times (milliseconds) and hit rates (percentage correct) and standard deviations. Scores are given for cases when letters at global and local levels were the same (selective-attention task), or similar or dissimilar (divided-attention task).

Reaction Time	Global		Local	
	Mean	sd	Mean	sd
Selective-attention task				
Same	409.2	31.1	408.2	33.9
Different	440.6	32.9	418.3	39.6
Collapsed	424.7	30.7	413.2	36.5
Divided-attention task				
Similar	399.9	38.7	389.9	31.0
Dissimilar	412.1	34.1	409.1	34.2
Collapsed	406.0	36.2	399.4	32.2

Hit Rate	Global		Local	
	Mean	sd	Mean	sd
Selective-attention task				
Same	91.4	5.6	92.5	7.2
Different	89.4	7.8	92.1	9.0
Collapsed	90.4	6.6	92.3	8.0
Divided-attention task				
Similar	86.1	2.9	90.7	1.9
Dissimilar	85.1	3.7	90.2	2.4
Collapsed	85.6	3.2	90.5	1.8

Figure 3—the stereotactic coordinates of these activations are presented in Table 2. In the attend-global condition, activation in posterior brain areas were confined to the left inferior occipital gyrus and left and right fusiform gyri; additional activations were observed in the left motor cortex, thalamus, and anterior cingulate gyrus. Similar results were obtained in the attend-local condition; however, in this condition the activation in the right fusiform gyrus failed to reach significance. To determine whether this effect indicated a significant difference between the two attention conditions in the right fusiform gyrus, the average activation was calculated over all voxels inside a spherical region of interest (diameter, 10 mm) placed at the center of each of the activations. These values were obtained for all subjects and compared for attend-local versus attend-global conditions using *t* statistics. No significant difference was found between the right fusiform gyrus responses in the attend-global versus attend-local condition. The activations for globally directed versus locally directed attention can be viewed in Figure 3 by comparing the left and right columns at the appropriate sagittal section.

The ERPs recorded in the selective-attention task showed that attended global targets elicited a slightly

larger temporal-occipital P1 component (90- to 150-msec latency) than attended local targets—the P1 was also larger in both task conditions versus neutral (Figure 4). The overall difference in P1 for global versus local conditions was small but statistically reliable ($F(1, 9) = 5.96$, $p < 0.04$). The later N2 component (260- to 360-msec latency) was not significantly different in amplitude for global versus local targets, although there was a nonsignificant trend over medial occipital sites (O1, O2, IN3, and IN4) for it to be larger to local targets (see Figure 4). The N2 was, however, significantly larger over the left than right hemisphere for both global and local targets ($p < 0.001$) during the selective-attention task.

The relationship between PET and electrophysiological measures was investigated using inverse dipole modeling. Previously we reported that the P1 attention effect for spatial selective attention, and attentional activations in the region of the posterior fusiform gyrus were related. This conclusion was based upon modeling (Heinze et al., 1994b) and covariations of PET and ERP effects with task variables (Mangun, Hopfinger, Kussmaul, Fletcher, & Heinze, 1997). Here we wanted assess the extent to which this relationship held for the P1 in the present study and whether or not the N2 component

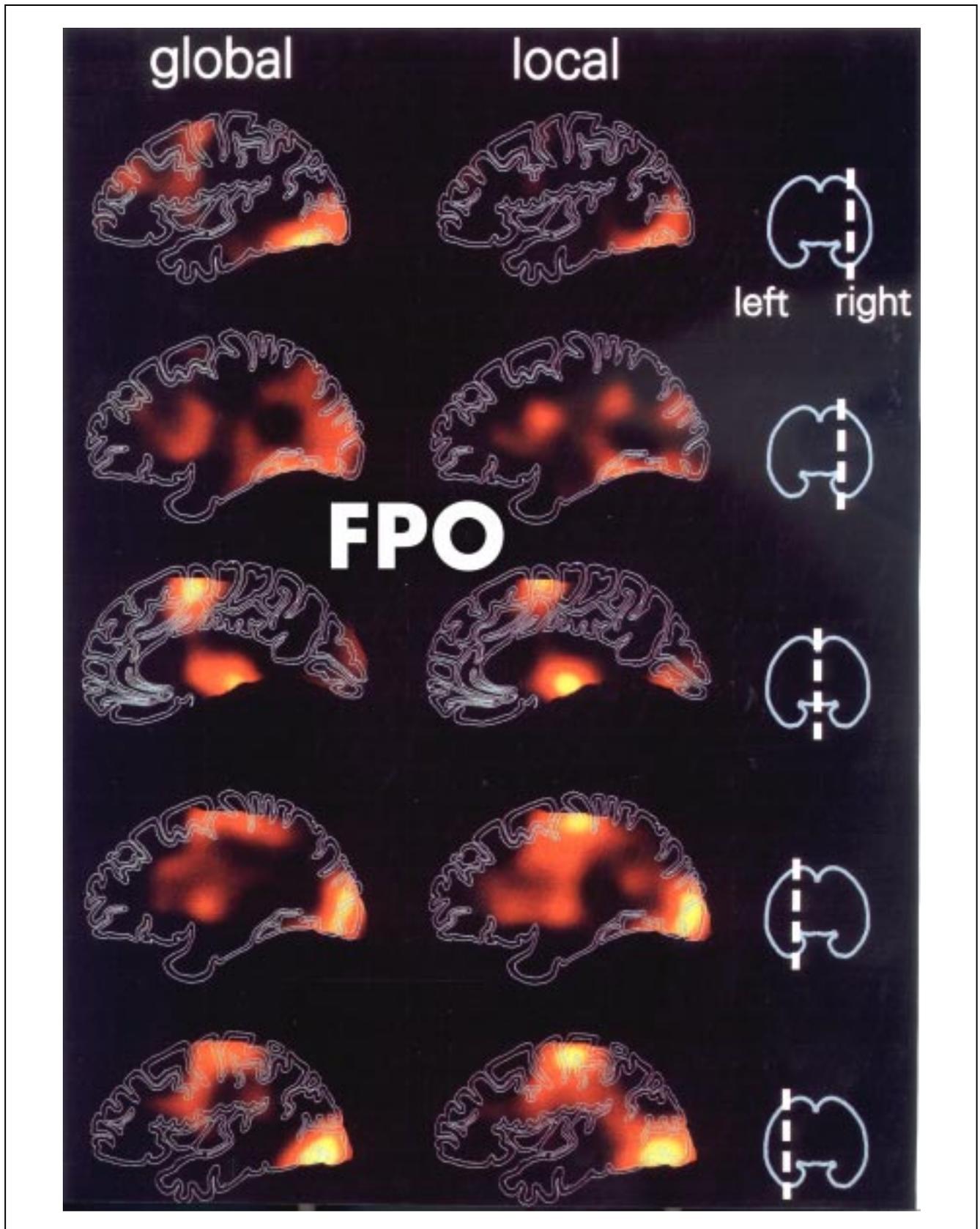


Figure 3. PET activations across the 10 subjects in the selective attention task. The images were obtained by subtracting the images in the neutral (passive) viewing condition from those in the attend global condition (left column images) or the attend local condition (right column). The planes of the sagittal sections are shown diagrammatically at right. The full-scale PET radiation subtraction images are overlaid onto the corresponding outline slice from the Talairach atlas (Talairach & Tournoux, 1988). See text for details.

Table 2. Talairach Coordinates, *t* Values, and Anatomical Labels for PET Activations

	<i>Talairach coordinates</i>			<i>Gyrus</i>	<i>Brodmann</i>
	<i>tval</i>	<i>x</i>	<i>y</i>		
<i>ATTEND Global—Neutral</i>					
Upper left	4.65	27	-88	2	G.occipit.inf 18
Left	5.38	37	-73	-10	G.fusiform/Gom 18/19
Right	4.79	-42	-67	-11	G.fusiform/Gom 18/19
Thalamus	4.16	-1	-25	-4	Nucleus ruber
Motor-cortex	4.13	34	-26	47	G.precentr. 4
Gyrus cinguli	5.4	4	-3	49	GC/G.front.med. 24/6
Frontobasal	-4.05	3	41	-8	G.front.med. 10
Parietal	-5.38	3	-55	29	Precuneus/GC 7/31
<i>ATTEND Local—Neutral</i>					
Left	4.68	28	-88	0	G.occipit.inf 18
Left	4.84	37	-73	-10	G.fusiform/Gom 18/19
Right	3.66	-42	-68	-11	G.fusiform/Gom 18/19
Thalamus	5.33	2	-19	-4	Nucleus ruber
Motor-cortex	4.69	34	-24	47	G.precentr. 4
Gyrus cinguli	4.1	1	-4	53	GC/G.front.med. 24/6
Frontobasal					
Parietal	-4.34	2	-57	33	Precuneus/GC 7/31
<i>ATTEND Global + Local—Neutral</i>					
Left	4.64	27	-88	1	G.occipit.inf 18
Left	5.08	37	-73	-10	G.fusiform/Gom 18/19
Right	4.18	-42	-67	-11	G.fusiform/Gom 18/19
Thalamus	4.56	-1	-21	-4	Nucleus ruber
Motor-cortex	4.40	34	-24	47	G.precentr. 4
Gyrus cinguli	4.68	3	-3	51	GC/G.front.med. 24/6
Frontobasal					
Parietal	-4.83	3	-56	30	Precuneus/GC 7/31

might also be generated in or near this region of extrastriate cortex. Because the differences in activity for global versus local attention were very small (ERP) or even nonsignificant (PET), the modeling was performed using data collapsed over global and local attention conditions [i.e., (Attend global - neutral) + (Attend local - neutral)]. This improved the signal-to-noise ratios of the data that were modeled (Figure 5, top row).

Dipole modeling of the intracranial sources of this component was performed using the BESA method (e.g., Scherg, 1992) but following the logic we have employed

previously of using the functional imaging data to constrain the electrical modeling (for a theoretical review see Mangun, Hopfinger, & Heinze, 1998). Briefly, a three-shelled spherical head model was used and was coregistered with the PET activity using the common Talairach stereotactic space. Point dipoles were placed into the loci of PET activations, which in this case included three dipoles—one dipole in the left motor cortex and two others in the left and right extrastriate cortex in the fusiform gyrus activations (see Table 2, bottom: Global + Local minus Neutral). However, there were no con-

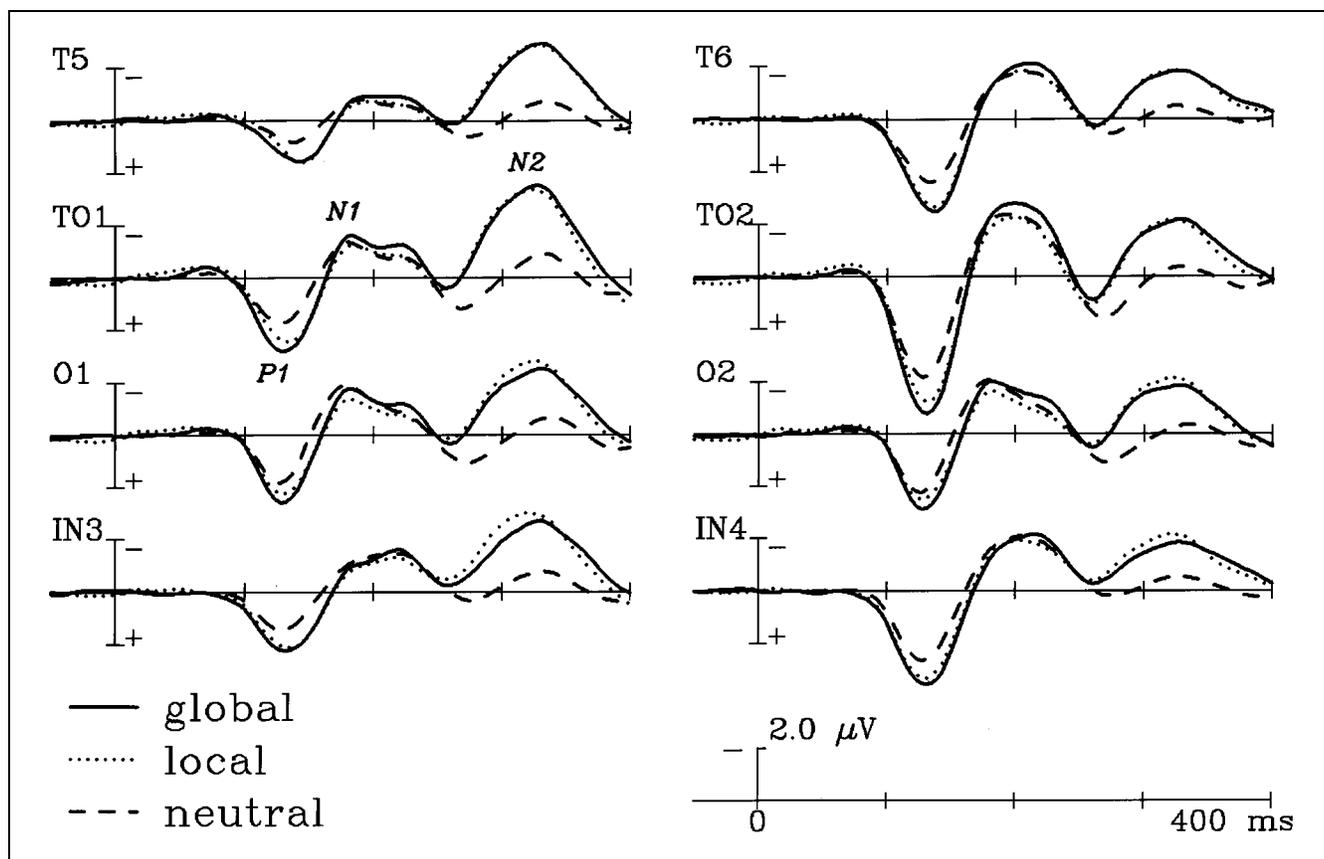


Figure 4. Grand average ERPs across the 10 subjects in the selective attention task. The ERPs (plotted negative polarity upward) are shown for left and right posterior temporal (T5, T6), lateral occipital (TO1, TO2), occipital (O1, O2), and inferior occipital (IN3, IN4) scalp sites. Stimulus onset is at the vertical calibration bar, and tick marks indicate 100-msec intervals. The P1 and N2 components are labeled at the TO1 sites but can be observed at all these posterior sites.

straints placed upon these dipoles; that is, their locations, orientations, and magnitudes were permitted to vary. The BESA method uses an iterative minimization procedure to arrive at a model in which the residual difference (i.e., percentage of residual variance) between model and recorded data is smallest. The dipoles yielded the optimal model with one dipole in the left motor cortex and the other two dipoles located near the PET activations in the extrastriate cortex (slightly more medial for both hemispheres and also more anterior for the left hemisphere). This model had a residual variance of 1.55% (Figure 5, middle and bottom rows). The addition of a fourth “test” dipole did not significantly reduce the residual variance (less than 0.5%), whereas removing one dipole to yield a two-dipole model resulted in an unreasonably high residual variance (~25%). This latter exercise was used to determine the optimality of the three-dipole model being employed.

Dipole modeling of the left lateralized N2 component using the same three-dipole model did not yield a reasonable solution (e.g., one dipole was placed in extracerebral structures). A two-dipole solution yielded a residual variance of ~5% with one dipole placed in the left motor cortex and the other in the left temporal lobe, far from any significant PET activations (Figure 6). Thus,

overall there was not a good correspondence between PET activations and the N2 component, but there was a close relationship between the activations in the extrastriate cortex and the electrical activity in the P1 latency range.

Divided-Attention Task

In the divided-attention condition where only ERPs were recorded (Figure 7), the pattern of effects differed from those in the selective-attention condition. The N2 amplitude was higher for local than for global targets at the left temporal-occipital scalp sites but was about the same or slightly higher for global than for local targets at the corresponding right scalp sites (significant target level \times hemisphere interaction: $F(1, 9) = 5.96, p < 0.04$). This effect was strongest at the temporal sites (target level \times hemisphere \times electrode position interaction: $p < 0.004$). The early P1 component, on the other hand, was not different for global versus local targets under conditions of divided attention.

The scalp distribution of the N2 effect (global minus local targets) for divided- and selective-attention conditions is shown in Figure 8 as scalp current density (SCD) maps. SCD is proportional to the transcranial current

Figure 5. Relationship between ERP and PET measures of visual processing. Modeling was performed using data collapsed over global and local attention conditions versus neutral viewing in order to investigate relationship between P1 and N2 (see Figure 6) components of ERP and activations observed in the occipital cortex in PET. The scalp voltage topography for the P1 sensory-evoked response is shown from a posterior view at top left and from a lateral view at bottom left. The corresponding PET activations are shown at top right in coronal section and at the middle and bottom right in sagittal sections. The subtracted radiation images are shown overlaid onto the corresponding slice from the Talairach atlas. The orientations and locations for the three best-fit dipole (two in ventral occipital lobe) and one in left motor cortex are shown overlaid onto the PET images in the sagittal slices.

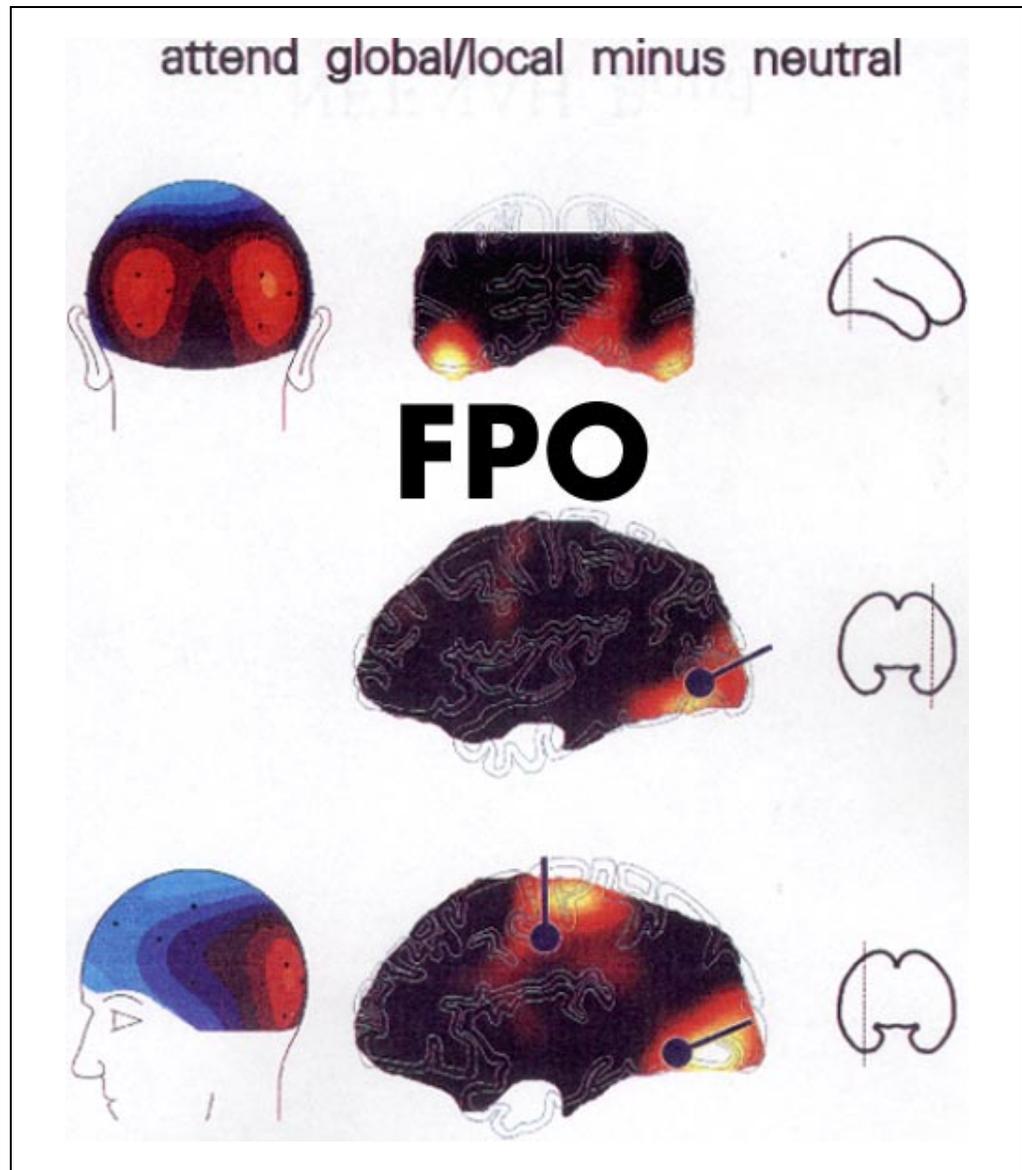
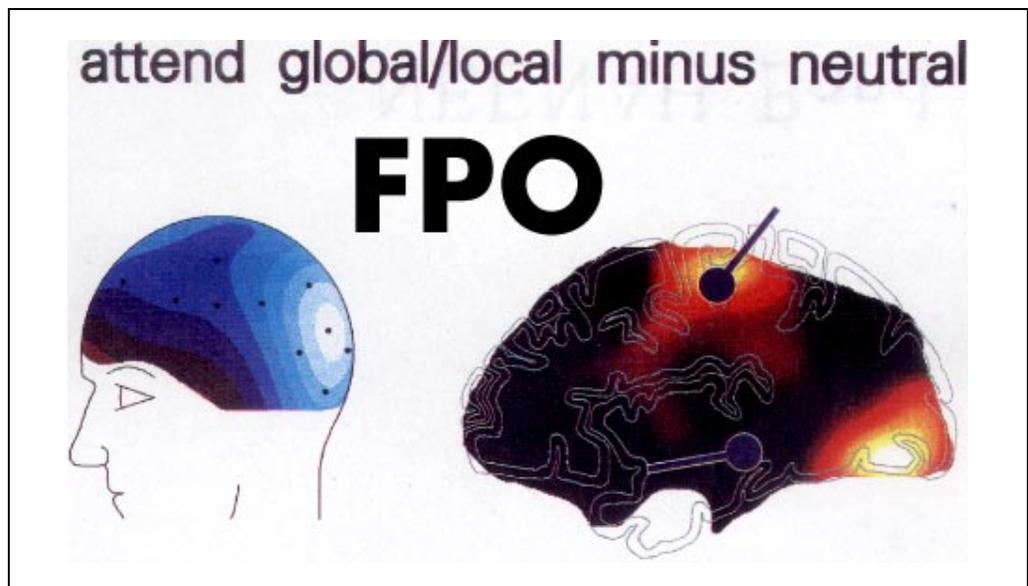


Figure 6. Relationship between N2 component of ERP and PET images. No good correspondence could be found between the N2 component (shown as scalp topography at left) and PET activations. See text for details.



flowing into and out of the scalp at every point and is most sensitive to local current sources. The SCD analysis of the global minus local target ERPs was calculated in the 250- to 350-msec time range, which corresponded to the N2 component. As can be seen in Figure 8, the global-local difference for the divided-attention task was associated with a clearly lateralized electrocortical pattern consisting of a source-sink configuration over the left hemisphere, whereas during selective-attention, no hemispheric differences were present in this (or any other) time range.

DISCUSSION

The goal of the present study was to investigate the mechanisms by which the brain analyzes hierarchical visual stimuli, wherein information is present at both the global and local levels. Hierarchical letter stimuli were used, and attention was either selectively directed to targets at either the global or local levels or divided between global and local levels. Physiological correlates of global and local analysis were obtained using both ERPs and PET. Together with reaction time measures of global and local processing and interference between the two levels, these physiological measures provided information about the time course and functional anatomy of component processes involved in the analysis of hierarchical stimuli.

In each task (selective and divided attention), the reaction times to global versus local target letters were similar. In the selective-attention task, interference was stronger from the local to the global level. This pattern is in line with that demonstrated previously in cuing studies (e.g., Robertson, Egly, Lamb, & Kerth, 1993), and supports a spatial attention mechanism. Such a mechanism could be similar to the zoom lens model of Eriksen and Yeh (1985), where during global attention the size of the attentional spotlight is widened thereby encompassing both the global and local elements of the stimulus. During local attention, the spotlight is zoomed down to the size of local stimulus elements, thereby gating the information at the global level. However, in the divided-attention task, interference effects occurred with about the same magnitude in both directions. This pattern supports the idea that global and local analyses can occur in parallel when attention is divided (e.g., Lamb & Robertson, 1989; Heinze & Münte, 1993). As argued by Lamb and Robertson, the symmetrical effects of target detection speed and interlevel interference suggest that partially separate mechanisms may be mediating these effects. These mechanisms may involve separate categorical attention processes for global and local stimuli over the same region of visual space, perhaps based upon the spatial frequency differences between global and local stimuli (Hughes, Fendrich, & Reuter-Lorenz, 1990; Robertson, Lamb, & Zaidel, 1993; Shulman & Wilson, 1987). Such mechanisms may be asymmetrically dis-

tributed in the two hemispheres (Robertson et al., 1988; Robertson et al., 1993). What neural correlates exist for these different attentional systems in the intact brain?

The earliest sign of differential processing of global versus local targets was found in the selective-attention task. There was an amplitude modulation of the posterior P1 component starting at about 100-msec latency—the P1 was larger when attention was directed globally than when it was directed locally. No differences were observed in the N2 component for selective attention to global versus local targets. Thus, during selective attention, the P1 component was primarily correlated with differences in global versus local analysis.

The fact that the P1 amplitude changed in the selective-attention condition supports the view that spatial attention can be involved in mediating perceptual analysis during selective global and local processing (e.g., Robertson, Egly, Lamb, & Kerth, 1993). This can be concluded because a large number of ERP studies have shown that modulation of the P1 amplitude in a visual selective-attention task reflects selection on the basis of spatial location (see Mangun, 1995, for a review), whereas changes of subsequent components (selection negativities) indicate selection based on other features such as color, shape, or orientation (Harter & Aine, 1984). Importantly for the interpretation of the present data, the amplitude of the P1 component has been shown to vary as a function of the size of the attended spatial region (Heinze et al., 1994a), as well as the amount of resources allocated to this area (Mangun & Hillyard, 1990). Therefore, the P1 amplitude difference between attended global and local targets might reflect differential allocation of spatial attention to the area encompassing the size of the global or local letter. That is, if during the global task the subjects distributed their attentional “spotlight” more broadly so as to encompass the entire spatial extent of the stimulus array, more facilitation of the total stimulus would ensue and the P1 would be larger. In contrast, if during the local task they reduced the size of their attentional spotlight to focus upon a small region of the array in order to discriminate the local targets, the P1 elicited by the entire display would be reduced as attention inhibited the surrounding portions of the array that were outside the attentional focus.

In previous reports we have related the P1 component of the ERP to activity in the fusiform gyrus during spatial selective attention (Heinze et al., 1994b; Mangun et al., 1997). In the present study, PET was used to investigate whether a similar neural mechanism might be involved in the effects of selective global and local attention on information processing. PET activations in the left and right fusiform gyrus were obtained in comparisons of either locally or globally directed attention with passive viewing of the stimuli. These activations (collapsed across global and local conditions) were

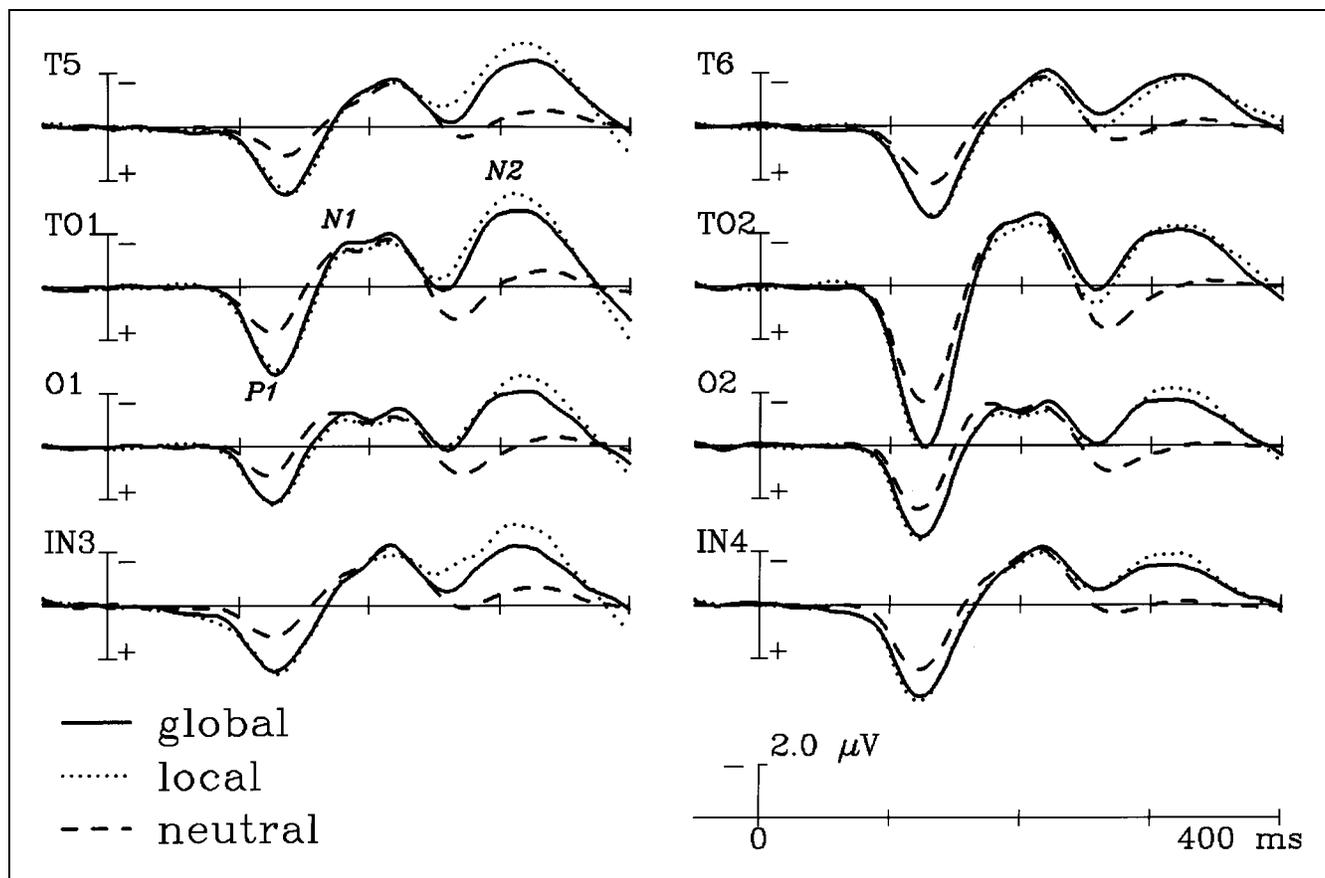


Figure 7. Grand average ERPs across the 10 subjects in the divided-attention condition. Differences in the N2 elicited by target stimuli can be seen over the left hemisphere (left column) and right hemisphere (right column). In particular, the N2 to local targets (dotted line) was greater in amplitude than the N2 to global targets (solid line) over the left hemisphere (T5 and T01 sites in particular), but over the right hemisphere, the N2 to global and local targets are more similar in amplitude.

related to the P1 component of the ERP via dipole modeling. Models of the P1 component derived from unconstrained inverse fitting of three dipoles to the grand-average ERPs indicated that dipoles near the PET activations provided the best explanation of the scalp-recorded data. Together with our previous work (Heinze et al., 1994b; Mangun et al., 1997), these data suggest that the P1 effects reflect neural processes in extrastriate cortex.

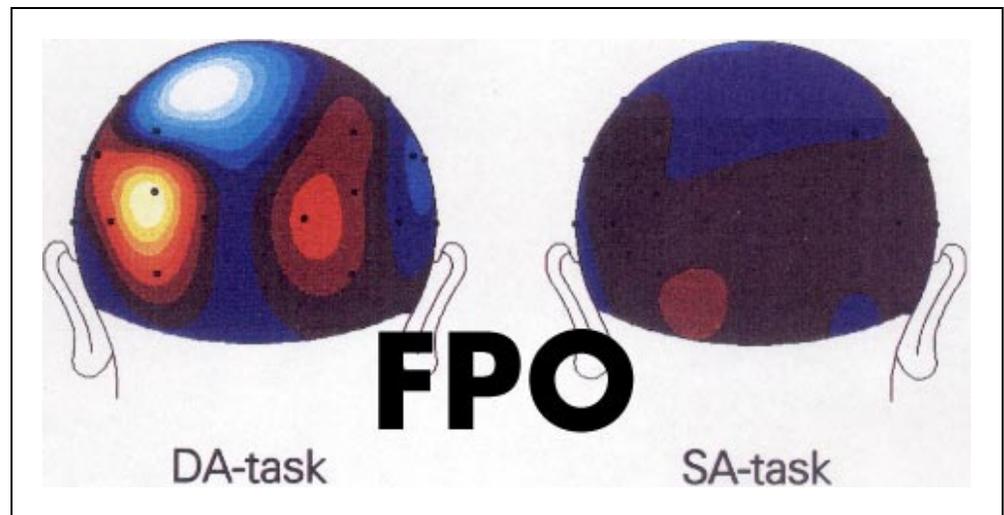
Hemispheric asymmetries were evident in the fusiform activity as decreases in right fusiform activity during locally directed attention, but these effects were not found to be significant in direct statistical analysis. Thus, neither the P1 component of the ERPs nor the PET activations in extrastriate cortex provide evidence for significant hemispheric asymmetries for global versus local attention. This suggests that gating of visual inputs asymmetrically to the two hemispheres during globally versus locally directed attention is not a major contributor to hemispheric differences in global versus local processing (c.f., Fink et al., 1996; Fink et al., 1997). The PET data also showed no evidence of modulations in the lateral parietal cortex, which might have been expected

given the evidence that lesions of parietal-temporal junction biases global versus local processing in neurological patients (Robertson et al., 1988). This negative finding in PET was also reflected in the N2 component of the ERPs recorded over lateral temporal-parietal cortex, which showed no hemispheric asymmetry for globally versus locally directed selective attention and is consistent with recent PET data (Fink et al., 1996).

In contrast to the absence of hemispheric effects in the selective-attention condition, significant hemispheric asymmetries were obtained in the N2 component of the ERPs to global versus local targets in the divided-attention condition. The N2 to global targets was larger over the right hemisphere, but to local targets the N2 was larger over the left hemisphere. This ERP pattern is consistent with evidence from neurological lesion analysis (Robertson et al., 1988), and our prior ERP results (Heinze & Münte, 1993; Heinze et al., 1994c). Such an effect most likely reflects a higher stage of perceptual analysis that may be asymmetrically active during conditions of divided attention between global and local stimulus levels.

Overall, the results of this study provide further evi-

Figure 8. Scalp current density SCD maps of the N2 effect (difference between global and local N2 components) in the divided-attention (DA) task (left) and selective-attention (SA) task (right). Hemispheric differences were most pronounced when attention was divided between local and global levels of the hierarchical stimuli.



dence against the assumption that a single resource processes global and local patterns in a sequential order. Rather, the temporal and spatial patterns of ERP activity suggest that at least partially different mechanisms are involved (see also Heinze & Münte, 1993; Heinze et al., 1994c). This conclusion is in line with that of Robertson and colleagues who have proposed this distinction based on neuropsychological studies (e.g., Robertson et al., 1988; Robertson, Egly, Lamb, & Kerth, 1993).

Hemispheric asymmetries for global versus local processing were observed in the present data, when attention was divided between global and local levels (ERP data) but not during selective attention to one level or the other (ERP and PET data). One interpretation for these results is that global-local processing involves hemispheric asymmetries that are based on a *relative* size or spatial frequency representation for the stimuli (e.g., Rafal & Robertson, 1995). As a result, during the divided-attention conditions, the complete range of sizes or spatial frequencies is computed, and two hemispheres distribute processing in order to maximize processing efficiency, leading to the observed asymmetries. In contrast, during selective attention to either local or global levels, a readjustment of hemispheric processing via relative spatial frequencies minimizes overall hemispheric differences between each condition. The foregoing model could explain the modest hemispheric differences for global versus local processing observed in the present study as measured by both ERPs and PET during selective attention to different levels within the hierarchical display.

The significant hemispheric asymmetries for global versus local processing in the N2 component of the ERPs is strong evidence in favor of the idea that when both global and local targets are relevant, as is often the case in everyday vision, the processing in the two hemispheres is not equivalent. The right hemisphere appears to be more involved in analysis of global targets, whereas

the left hemisphere is more involved in local target analysis. The mechanisms of this effect remain unclear. Recently Fink and colleagues (1996) suggested that hemispheric asymmetries in global versus local processing are derived from descending influences of temporal-parietal regions onto early extrastriate visual analysis. The idea is that the asymmetries are manifest within the visual cortex but reflect descending influences from the temporal-parietal cortex. Although plausible, and consistent with their data, the Fink et al. model does not provide a good explanation of the present results. Their model predicts global-local asymmetries of the early visual cortical activity during both divided and selective attention to level. We found no such asymmetries in the P1 component of the ERP, and the corresponding PET data provided little evidence to support this idea. However, we did find a significant hemispheric asymmetry in the longer-latency N2 component, which scalp current density mapping and dipole analysis indicated was probably not generated in the extrastriate cortex. Although this latter conclusion cannot be strongly stated, the latency of the N2 relative to the P1 (which we know is generated in the extrastriate cortex) indicates that hemispheric asymmetries in global-local processing occur much later in visual analysis than do the processes typically associated with “early” extrastriate visual analysis. Thus, we are not compelled to accept the model of Fink and colleagues. Rather, it appears that hemispheric asymmetries in global versus local processing reflect higher-order aspects of visual analysis and not merely a gating of early processes (see Ivry & Robertson, 1998), as is the case for mechanisms such as spatial selective attention (e.g., Mangun, 1995).

The ERP and PET evidence from the selective-attention condition do, however, indicate that spatial attention mechanisms may be employed during selective attention to level. Such a mechanism could operate to filter irrelevant information from global distracters onto

local targets by narrowing the size of the attentional spotlight when attending to the local level. This mechanism, however, does not appear to be asymmetrical between the two hemispheres.

METHODS

Subjects

Ten right-handed student volunteers (three females, seven males) were paid for participation in the study. They ranged in age from 22 to 28. All subjects had normal or corrected-to-normal vision and normal neurological status.

Stimuli

Stimuli were large capital letters made up of small capital letters. Global letters were constructed from local letters in a 5×5 matrix (see Figure 1). Global letters subtended 2.5° vertically at a viewing distance of 70 cm. Local letters were 0.34° in height. Both global and local letters were 1.5 times as tall as they were wide. Stimulus durations were 100 msec.

In the selective-attention task (ERP and PET), subjects were instructed to respond only to letters at the global or local level for each block of trials. The eight (global/local) stimuli were: H/H, H/E, S/A, S/S, A/A, A/S, E/H, E/E. Stimuli were white on a dark background and presented in the center of a color computer monitor. During each run, a white frame continuously demarcated the region in which the stimulus would be flashed, and a dot in the center of the screen served as a fixation point for the eyes.

In the divided-attention task (ERP only), both global and local letters were relevant on every trial. Therefore, stimuli containing the same letter at the global and local level would be ambiguous and were not used in this task. In order to measure interference effects between global and local patterns, similarity between target and distracter letters was varied. As in Lamb and Robertson (1989), the letters S, E, H, and A were selected—the letters S and E are similar to each other in form and dissimilar from the letters H and A. Similarly, H and A are similar to each other and dissimilar to S and E. Therefore, interference was measured as the interaction between similar and dissimilar target and distracter letters. There were eight hierarchical stimuli in all: H/A (global H and local A), H/E, S/A, S/E, A/H, A/S, E/H, and E/S.

Procedure

In the selective-attention task, all the eight possible hierarchical letter stimuli were presented in each run. Only one letter was a target in a run and which letter was target was varied across runs. The interstimulus intervals varied between 300 and 600 msec (rectangular distribu-

tion). Before each run, subjects were told to attend to the global or local level of the stimuli and to indicate after each letter whether a target letter was present at the attended level by pressing a button with the right index finger. Stimuli were presented in a pseudorandom order with at least one nontarget stimulus after a target stimulus. Both accuracy and speed of response were emphasized to the subjects.

In the divided-attention condition, the same number of total stimuli and runs were presented as in the selective-attention condition, but the stimulus onset asynchrony (SOA) varied randomly between 800 and 1200 ms (rectangular distribution) in order to match overall task difficulty with the selective-attention condition. As in the selective-attention condition, the target letter was varied across runs. Stimuli were presented in random order with a target letter in 50% of the stimuli (25% at the global level, 25% at the local level). The subjects' task was to indicate after each letter stimulus whether the designated target letter was present at *either* the global or local level by pressing a button with the right index finger. Again, both accuracy and speed of response were emphasized to the subjects.

ERP Recording and Analysis

For the ERP sessions, 40 runs of 80 trials each were presented for the selective-attention conditions, and the same for the divided attention condition. In addition to the selective- and divided-attention runs, for each condition the subjects also viewed 20 runs of "neutral" trials in which they performed neither task but merely maintained fixation. They were given 16 practice runs in each condition in which each letter served as target four times.

ERPs were recorded from the scalp by using tin electrodes mounted in an electrode cap (Electro-Cap International, Inc.) and located at standard sites covering the scalp. These included the International 10–20 System sites F3, F4, Fz, C3, C4, Cz, P3, P4, P7, P8, T3, T4, T5, T6, O1, O2, and Oz. Additional sites were also used that were located and named with respect to standard sites: FC5, C5, CT5, TO1, and IN3 over the left hemisphere and their mirror-image positions over the right hemisphere (see Heinze et al., 1994c, for description). All scalp electrodes were referenced to the right mastoid during recording but were subsequently algebraically rereferenced to the average of the left and right mastoids by subtracting one-half the voltage from the left mastoid channel from all the scalp channels. Eye blinks were monitored with an electrode beneath the right eye, and lateral eye movements were measured as the voltage between electrodes at the left and right outer canthi (horizontal electrooculogram—EOG). Possible changes in pupil size between different conditions (attend global, attend local) were monitored using a video monitoring device and quantified by measurements made directly from these record-

ings—no pupillary changes were found between conditions.

The EEG was amplified with a filter bandpass of 0.01 to 64 Hz, digitized at a rate of 250 samples per second and averaged off-line. Automatic artifact-rejection was employed off-line to reject eye blinks, eye movements, and excessive muscle activity or movement artifacts. Mean amplitude and latency was calculated for the following ERP components: P1 (100- to 150-msec time range), N1 (180 to 230 msec), N2 (270 to 370 msec), and P3 (400 to 700 msec).

All ERP and behavioral measures were analyzed using repeated measures analyses of variance (ANOVA). RTs and hit rates for detecting targets were analyzed using two factors: *target level* (target global versus target local) and *interference* [target/distracter similar (divided-attention task) or identical (selective-attention task) versus dissimilar]. ERP effects were analyzed with three factors: *target level* (target global versus target local), *interference* (target/distracter similar or identical versus dissimilar), and *hemisphere of recording* (left versus right). Separate ANOVAs were used for frontal (F3, F4, Fz, FC5, and FC6), central (C3, C4, C5, C6, Cz, CT5, and CT6), parietal (P3, P4, and Pz), temporal (T3 and T4), and temporal-occipital (T5, T6, O1, O2, Oz, TO1, and TO2) scalp sites with *electrode position* as an additional factor in each ANOVA when more than two electrodes were included in the analysis. For example, for the posterior scalp analysis, the *hemisphere of recording* factor compared left hemisphere sites (T5, TO1, and O1) to right hemisphere sites (T6, TO2, and O2), whereas the *electrode position* factor compared posterior temporal (T5 and T6), temporal-occipital (TO1 and TO2), and occipital (O1 and O2) sites.

PET Scanning and Analysis

PET activity was measured in the selective attention condition using a SIEMENS ECAT 951/31 scanner. The same 10 subjects performed six blocks (attend global, attend local, neutral viewing; each condition repeated twice). Each block began with a 40-sec period in which subjects fixated the center point, and the stimuli began. Subjects were then instructed to begin attending to the appropriate level (for the attend global and local conditions) and performing the task. Twenty seconds later, a bolus of 10 ml saline with 50 mCi of 15-O-labeled water (half-life 123 sec) was injected via intravenous catheter in the right arm. Data were acquired over the period from 20 to 60 sec after injection.

For data analysis, the PET scans were reoriented and then rescaled into stereotactic coordinates using a modification of the procedure of Friston et al. (1989)—head position was evaluated using 68-Ge scalp markers (see Heinze et al., 1994b). After global normalization, the two scans per attention condition (global, local, and neutral) were averaged together for each subject and

then filtered (Hanning 18 mm FWHM). Difference images (attend global or local minus neutral) were calculated and then averaged over the 10 subjects. Because tissue radiation counts are roughly linear with cerebral blood flow over the interval that data was acquired (Fox et al., 1989), the effects were considered to reflect regional cerebral blood flow. Statistical analysis used a modified *t* statistic (Worsley et al., 1992) to assess significant blood flow changes in the difference images.

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