

Neural mechanisms involved in the processing of global and local aspects of hierarchically organized visual stimuli

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Summary

We investigated the functional anatomy involved in sustaining or switching visual attention between different perceptual levels, using functional imaging measures of neural activity. Two experiments were carried out using hierarchically organized letters (i.e. large letters made out of small letters). In a divided-attention task, subjects were required to switch attention between local and global levels. The number of successive stimuli for which subjects had to sustain attention to either the global or local level co-varied significantly with temporal–parietal activations bilaterally. Other activations were also observed in the right orbitofrontal cortex, the right dorsolateral prefrontal cortex, and the right middle temporal gyrus. The number of switches between levels co-varied significantly with activations in the left supplementary motor area and the left medial parietal cortex. In the directed-attention task, subjects were required to attend to either the

global or local level of the stimuli throughout all trials; attention to the global aspect resulted in significant activation of the right lingual gyrus while attention to the local aspect significantly activated the left inferior occipital cortex. We suggest that left hemisphere activations with increasing numbers of switches between perceptual levels reflect increased demands on an executive attentional system, while sustained attention to either level activates a predominantly right hemispheric network involving temporal–parietal and dorsolateral prefrontal regions. Overall, the results provide evidence for relative hemispheric specialization for global and local processing in accordance with previous neuropsychological studies. In addition, the findings demonstrate that early visual processing mechanisms in the prestriate cortex are influenced by an attentional system in temporal–parietal areas.

Keywords: global/local processing; visual attention; prestriate cortex; temporal–parietal cortex; PET

Abbreviations: ANCOVA = analysis of covariance; BA = Brodmann area; LG = large stimuli, globally directed attention; LL = large stimuli, locally directed attention; rCBF = regional cerebral blood flow; SG = small stimuli, globally directed attention; SL = small stimuli, locally directed attention; SPM = statistical parametric mapping

Introduction

The right hemisphere is dominant for many visuospatial functions, although recent neuropsychological experiments suggest that the pattern of hemispheric asymmetry is more complex than a simple dichotomy: each hemisphere is dominant for processing different types of visual information (Hellige, 1993; Posner, 1995).

That the bicycle has wheels, which in turn have spokes,

exemplifies the fact that our visual world is intrinsically organized in an ‘hierarchical’ fashion. In the above example, the spokes are local relative to the global wheel, but the wheel is also local relative to the global bicycle. Psychological studies using stimuli with larger figures (global forms) made of smaller figures (local components) show global precedence (Navon, 1977); the global aspect of a complex visual stimulus

is perceived more quickly than its local aspects (global advantage) and global processing interferes with local processing (global interference). However, global advantage and global interference can be turned into local advantage and local interference by experimental manipulations of, for example, visual angle, number of local elements, retinal locus and shape (Lamb and Robertson, 1988; Hughes *et al.*, 1990). Furthermore, the subject's attentional set can influence global and local processing (Kinchla *et al.*, 1983), suggesting that perceptual (exogenous) and controlled attentional (endogenous) mechanisms interact during the processing of hierarchically organized stimuli (Martin, 1979; Hoffman, 1980; Sergent, 1982; Kinchla *et al.*, 1983; Lamb and Robertson, 1988; Hughes *et al.*, 1990; Robertson and Lamb, 1991).

Classical Gestalt psychology and neuropsychological studies in patients with temporal–parietal lesions suggest a right hemisphere bias for global processing (i.e. perception of and attention to the whole) and a left hemisphere bias for local processing [i.e. perception of and attention to the focal aspects of a complex visual scene (Robertson *et al.*, 1988; Robertson and Lamb, 1991; Hellige, 1993)]. However, such hemispheric asymmetries are relative rather than absolute (Polster and Rapsak, 1994). The precise mechanisms underlying global/local processing and their relationship to hemispheric asymmetries remain poorly understood.

In this study, we investigate the functional anatomy of directed and divided visual attention to global and local aspects of hierarchically structured figures. We used PET in normal human subjects, to index neural activity and determine significant changes in relative regional cerebral blood flow (rCBF) (Raichle, 1987) across conditions. The aim of the study was to investigate the neural mechanisms involved in the processing of global and local aspects of hierarchically organized visual stimuli. Such stimuli are ideal to study the influence of attention on sensory processes, as no change in visual input is required across conditions. The sole requirement is for subjects to follow the instruction to attend to either the global or local level of the stimulus (directed attention) or to attend to a predefined target occurring at either level (divided attention). Based on the results from patients with lesions we predicted that the modulatory source of visual attention would be temporal–parietal (Robertson and Delis, 1986; Robertson *et al.*, 1988; Robertson and Lamb, 1991). How this region influences sensory processing of local or global levels is more difficult to predict. Previous functional imaging (Corbetta *et al.*, 1991; Heinze *et al.*, 1994) and animal studies (Moran and Desimone, 1985; Spitzer *et al.*, 1988; Motter, 1993) raise the possibility that the locus of interaction between attention and visual processes resides early in the visual processing stream. Furthermore, neuropsychological studies suggest right hemisphere dominance during global processing and left dominance during local processing.

A preliminary report on some of the data presented has been published elsewhere (Fink *et al.*, 1996).

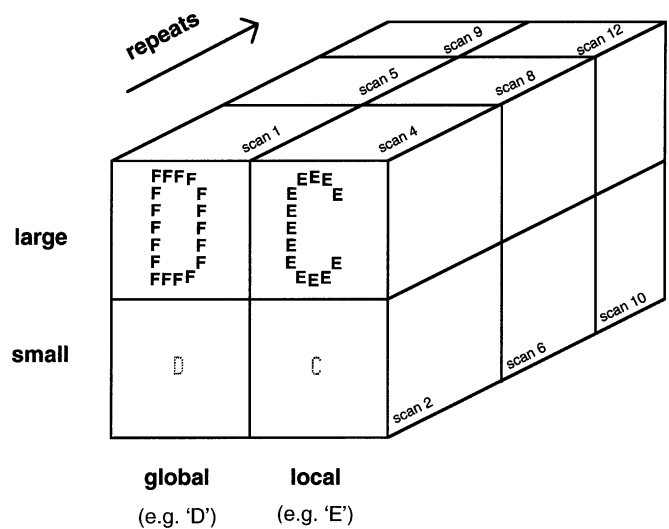


Fig. 1 Study design of Experiment 1 (directed-attention task). The D and C represent the global level and the F and E represent the local level of the stimuli. All figures used were non-congruent for the global and local level. During the task subjects were required to attend to either the global or the local level and to name the appropriate letter (e.g. her 'F' and 'E' during the local processing task and 'D' and 'C' during the global processing task). To study the effects of stimulus size on global and local processing, both large and small figures were used.

Material and methods

Subjects

Sixteen healthy male volunteers (aged 19–32 years) took part in the study. All were right-handed and had no history, past or current, of neurological or psychiatric illness. Informed written consent was obtained from all subjects prior to participation. The study involved administration of 4.5 mSv effective dose equivalent of radioactivity per subject. Permission to administer radioactivity was obtained from the ARSAC (Administration of Radioactive Substances Advisory Committee of the Department of Health of the UK). The study was approved by the local ethics committee of the National Hospital for Neurology and Neurosurgery (London, UK).

Paradigm design

Figure 1 shows examples of the figures used as stimuli during the globally and locally directed attention tasks and the design of Experiment 1, the directed attention task. In the upper left box the D constitutes the global level and the F the local level. All figures used were non-congruent for the global and local levels. The figures were presented in black on a white background during the PET rCBF measurements. A stimulus appeared every 1.5 s and remained for 300 ms, in the centre of a 14 inch video display unit at a viewing distance of 40 cm. Twelve different letters (P, S, H, K, T, E, F, L, V, C, D, N) were used to create the figures which appeared in a quasi-random sequence that did not permit the same letter to appear on the local and global levels on

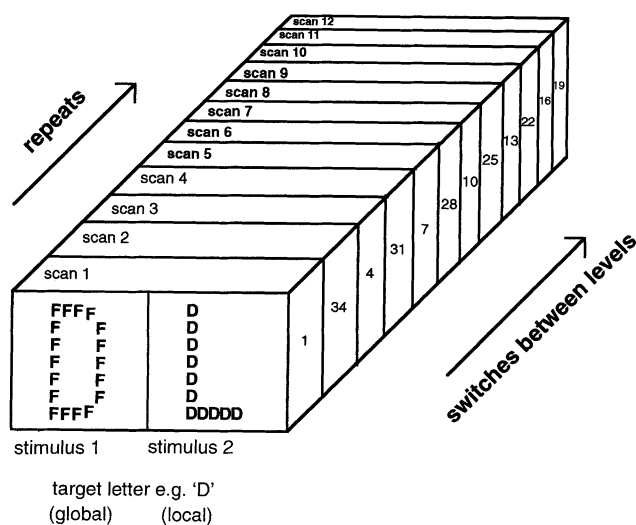


Fig. 2 Study design of Experiment 2 (divided attention task). During the divided attention task, a preselected target letter appeared at either the global or the local level (in this example a 'D'). Subjects were required to name the level at which the target letter appeared (e.g. in this case for stimulus 1 'global' and for stimulus 2 'local'). The number of switches between levels (global and local) was parametrically varied (counterbalanced across subjects) between one and 34 per minute across scans.

successive trials (Tipper *et al.*, 1994). In order to study possible effects of stimulus size, both large figures (170×72 mm, made up of letters 21×13 mm, and subtending overall visual angles of 24° and 10°) and small figures (30×14 mm, made of letters 3.5×2.5 mm, visual angle 4° and 2°) were used.

In this experiment (Experiment 1, directed attention task), 10 normal-sighted male right-handed volunteers were studied. They were instructed to attend and name either the global or local attribute of the stimulus (a letter). Each sequence of stimulus presentations began 10 s prior to PET scanning. The experiment involved 12 sequential relative rCBF measurements per subject; the four testing conditions were presented in a fully factorial design: globally directed attention, large stimuli (LG); locally directed attention, large stimuli (LL); globally directed attention, small stimuli (SG); and locally directed attention, small stimuli (SL). Globally and locally directed attention tasks and large and small stimulus sequences were alternated.

Figure 2 shows examples of the figures used and the design of Experiment 2 (divided attention task). In this experiment, six normal-sighted male right-handed volunteers were studied. The same stimuli (large letters only; P, S, H, K, T, E, F, L, V, C, D, N), presentation rate, and number of measurements were used. This time, however, a preselected target letter appeared at either the global or the local level. Subjects were required to name at which of the two levels the target letter had appeared ('global' or 'local'). The number of switches between levels (global or local) was varied on successive trials from one to 34 per minute (40 stimuli per minute were given). The number of times that a given target

letter occurred at the local or the global level was kept roughly equal across the rCBF measurements. Again, a quasi random sequence prevented the same stimulus from occurring on successive trials.

PET-scanning

Relative regional cerebral blood flow (rCBF) was measured by recording the regional distribution of cerebral radioactivity following the intravenous injection of ^{15}O -labelled water [^{15}O is a positron emitter with a half-life of 2.1 min (Mazziotta *et al.*, 1985; Fox and Mintun, 1989)]. The PET measurements were carried out using a Siemens/CPS ECAT EXACT HR+ (model 962) PET scanner (CTI Inc., Knoxville, Tenn., USA) with a total axial field of view of 155 mm covering the whole brain. Data were acquired in three-dimensional mode (Townsend *et al.*, 1991) with inter-detector collimating septa removed and a 'Neuro-Insert' installed to limit the acceptance of events originating from out-of-field-of-view activity (from the whole body).

For each measurement of relative rCBF, 9 mCi of H_2^{15}O were given i.v. as a slow bolus over 20 s (Silbersweig *et al.*, 1993). Twelve consecutive PET scans were collected, each beginning with a 30-s background scan before the delivery of the slow bolus. Emission data were thereafter collected sequentially over 90 s after tracer arrival in the brain and corrected for background. This process was repeated for each emission scan with 10 min between scans to allow for adequate decay of radioactivity. All emission scan data were corrected for the effects of radiation attenuation (e.g. by the skull) by means of a transmission scan taken prior to the first relative rCBF measurement. The corrected data were reconstructed into 63 transverse planes (separation 2.4 mm) and into 128×128 pixels (size 2.1×2.1 mm) by three-dimensional filtered back projection using a Hann filter of cutoff frequency 0.5 cycles per pixel and applying a scatter correction. The resolution of the images was 6 mm (at full width half maximum).

MRI

In a separate session, an MRI image of each subject's brain was obtained (i) to exclude the possibility of morphological/pathological abnormalities and (ii) for stereotactic normalization into the standard anatomical space (*see below*). This was performed with a 2 Tesla system (VISION, Siemens AG, Germany) using a three-dimensional T_1 -weighted imaging technique producing 54 transaxial slices (1×1×3 mm) which gave high grey to white matter contrast.

Image processing

All calculations and image manipulations were performed on a SPARC workstation (SUN Computers). ANALYZE and PROMATLAB software (Mathworks Inc., USA) were used to calculate and display images. Statistical parametric mapping

Table 1 Relative increases in brain activity during a directed attention task using complex hierarchically organized visual stimuli

Region	Side	x,	y,	z	Z-score
(A) Global versus local: (LG + SG) – (LL + SL) Lingual gyrus (BA 18)	R	16,	–74,	0	5.0
(B) Local versus global: (LL + SL) – (LG + SG) Inferior occipital gyrus (BA 18)	L	–22,	–96,	–8	5.3
(C) Large versus small: (LG + LL) – (SG + SL) Primary visual cortex (BA 17)	L	–2,	–86,	–4	13.4
	R	16,	–84,	12	8.6
(D) Small versus large: (SG + SL) – (LG + LL) Inferior occipital/usiform gyrus (BA 17/18)	L	–26,	–96,	–12	4.1
	R	28,	–96,	–8	4.3

Coordinates are in standard stereotactic space (Talairach and Tournoux, 1988) and refer to maximally activated foci as indicated by the highest Z-score within an area of activation associated with globally and locally directed attention, or large and small stimuli; *x* is the distance in millimetres to the right (+) or left (–) of the midsagittal (interhemispheric) line; *y* is the distance anterior (+) or posterior (–) to the vertical plane through the anterior commissure; and *z* is the distance above (+) or below (–) the intercommissural line. For each anatomical location, an estimate of the Brodmann (BA) area is given in parentheses, which is based on the stereotactic atlas of Talairach and Tournoux (1988) and the group mean MRI. R = right; L = left; LG = large stimuli, globally directed attention; LL = large stimuli, locally directed attention; SG = small stimuli, globally directed attention; SL = small stimuli, locally directed attention.

(SPM) software (SPM95; Wellcome Department of Cognitive Neurology, London, UK) was used for image realignment, image normalization, smoothing and to create statistical maps of significant relative rCBF changes (Friston *et al.*, 1995a, b).

Realignment, transformation and smoothing of PET images

All PET scans were realigned to the first emission scan, using SPM95 software (Friston *et al.*, 1995a) to correct for head movement. A mean relative rCBF image was created for each subject and edited to remove counts representing blood flow to the skull or scalp. Each individual's MR image and PET mean image (serving as a template for the individual PET images) were then transformed into a standard stereotactic anatomical space (Friston *et al.*, 1995a; Talairach and Tournoux, 1988) using linear proportions and a non-linear sampling algorithm. The PET images were thereafter filtered using a low-pass Gaussian filter (resulting in an image resolution of 12 mm) to reduce the variance due to individual anatomical variability and to improve signal-to-noise ratio (Friston *et al.*, 1995a). The resulting pixel size in stereotactic space was 2×2 mm with an interplane distance of 4 mm. Data were thereafter expressed in terms of standard (*x*, *y*, *z*) stereotactic coordinates (as defined in Table 1).

Statistical analysis

Following stereotactic normalization, statistical analysis was performed. For Experiment 1 (directed attention task), the main effects of test conditions (globally versus locally directed attention; large versus small stimuli) and their interaction were estimated on a pixel-by-pixel basis using SPM95 (Friston *et al.*, 1995b). Task related differences in global

CBF, within and between subjects, were removed by treating global activity as the covariate (Friston *et al.*, 1995b). This removed systematic state-dependent differences in global blood flow associated with the different conditions which can obscure task related regional alterations in activity. For each pixel in stereotactic space the ANCOVA generated a condition-specific adjusted mean rCBF value (arbitrarily adjusted to 50 ml/100 ml/min) and an associated adjusted error variance (Friston *et al.*, 1995b). This allowed the planned comparisons of the mean blood flow distributions across all sets of conditions. The mean relative rCBF values were calculated separately for each of the main effects, for each pixel, and across all subjects and all scans. Comparisons of the means were made using the *t*-statistic and thereafter transformed into normally distributed Z-statistics. The resulting set of Z-values constituted a statistical parametric (SPM_{*t(z)*}) map (Friston *et al.*, 1995b). For the contrasts of interest, significance was set at *P* < 0.05, corrected for multiple non-independent comparisons. The data were analysed for the two main effects (globally versus locally directed attention; large versus small stimuli) and their interaction. These comparisons were intended to identify those cortical areas concerned with the properties in question (i.e. locally and globally directed attention, large and small visual stimuli) and to assess whether stimulus size modulates the effects of globally and locally directed attention.

For Experiment 2 (divided attention task), the same data analysis was performed. SPM95 was then used to assess (i) significant co-variation of relative rCBF with the number of target switches (from either the local to the global level or vice-versa) and (ii) significant covariation of relative rCBF with the number of successive stimuli for which the subjects had to sustain attention to either the global or the local level. The resulting SPM_{*t(z)*} map was thresholded at *P* < 0.01

(uncorrected) as the experiment was specifically concerned with the temporal–parietal areas. These areas were predicted *a priori* on the basis of previous neuropsychological studies (Robertson *et al.*, 1988; Robertson and Lamb, 1991). Other activations were observed but are reported at a level of $P < 0.001$ (uncorrected) only.

To assess hemispheric asymmetries in rCBF responses, hemisphere \times condition interactions were identified using SPM95. This did not require correction because these regions were identified on the basis of the (independent) main effects.

Single-subject data analysis

For individual subjects, PET data were analysed in an identical way to the group data. The SPM maps were thresholded at $P < 0.01$, uncorrected. The analysis of data from each individual was restricted to the areas showing significant activations in the group analysis. Since PET data had been co-registered to the same individual's MR scan, precise anatomical localization of relative rCBF changes was possible.

Localization of activations

The stereotactic coordinates of the pixels of local maxima of significant changes in relative rCBF were determined within areas of significant relative rCBF change associated with the different tasks. The anatomical localization of these local maxima was assessed by reference to the standard stereotactic atlas of Talairach and Tournoux (1988). Additional validation of this method of localization was obtained after superimposition of the SPM_{z} maps on the group mean MRI image calculated after each individual's MRI image had been stereotactically transformed into the same standard stereotactic space (Friston *et al.*, 1995a).

Results

Directed attention task effects

In Table 1, A and B summarize the regions displaying increases in relative regional cerebral blood flow (rCBF) associated with each of the directed attention tasks. Figure 3A provides a pictorial representation in the form of SPM_{z} maps of the areas with increase of relative rCBF during each of the directed attention tasks. For the globally directed attention tasks (LG + SG – LL – SL) the only significant increase in relative rCBF was observed in the right lingual gyrus [$P < 0.05$, corrected for multiple comparisons; Brodmann area (BA) 18; Table 1 (A) and Fig. 3A]. Relative rCBF increases in the respective homologous contralateral region did not reach significance. Increases in relative rCBF during the locally directed task (LL + SL – LG – SG) were observed in the left inferior occipital cortex [$P < 0.05$, corrected; BA 18; Table 1 (B) and Fig. 3A] only. Again, rCBF increases in the respective homologous contralateral

regions did not reach significance. A direct comparison of rCBF changes between the two hemispheres indicated that both lateralization effects were statistically significant ($P < 0.01$). No differential relative rCBF increases were observed, during either globally or locally directed-attention tasks, in lateral temporal–parietal areas.

Stimulus size effects

In Table 1, C and D summarize the principal areas associated with increases in relative rCBF concerned with the difference between large and small visual stimuli (irrespective of the direction of attention). Figure 3B provides a pictorial representation in the form of SPM_{z} maps of the areas with relative rCBF increases. As predicted, the presentation of large stimuli (LG + LL – SG – SL) led to extensive significant relative rCBF increases in the striate cortex ($P < 0.05$, corrected; BA 17) bilaterally [Table 1 (C) and Fig. 3B], extending into the prestriate cortex and temporal–occipital areas bilaterally ($P < 0.05$, corrected).

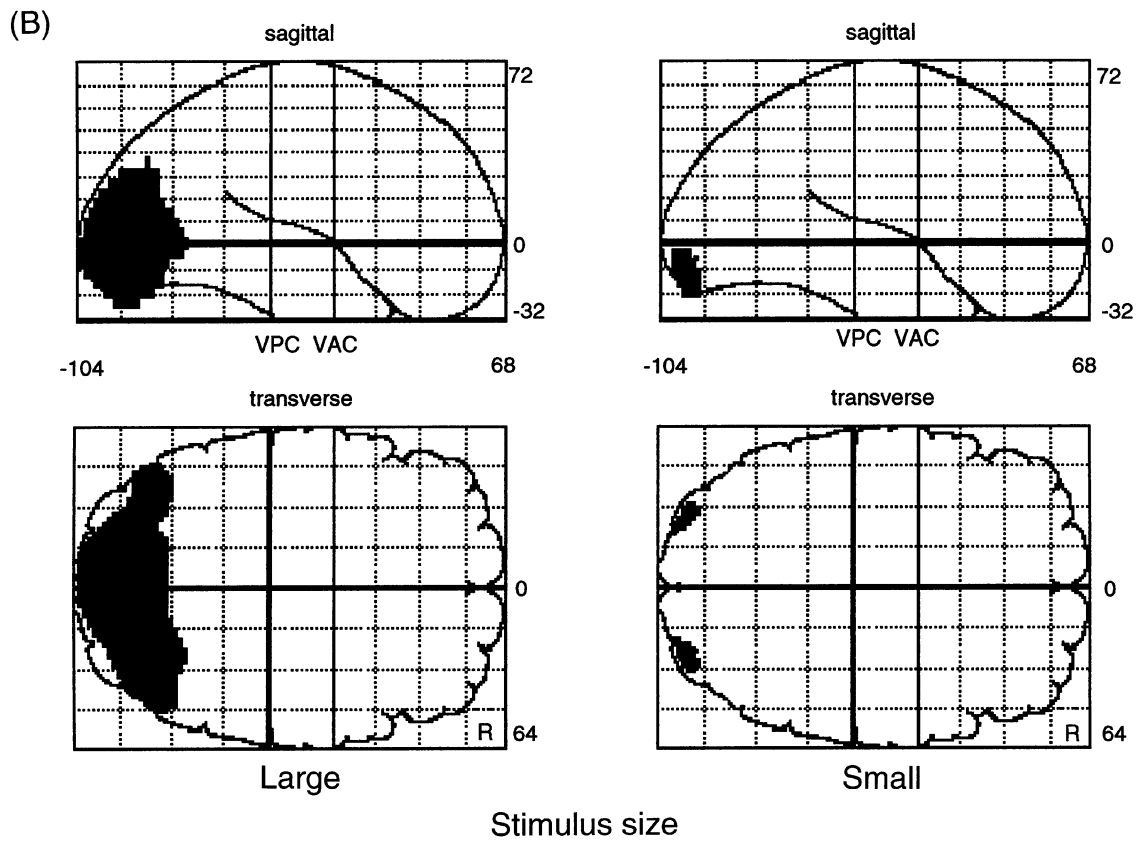
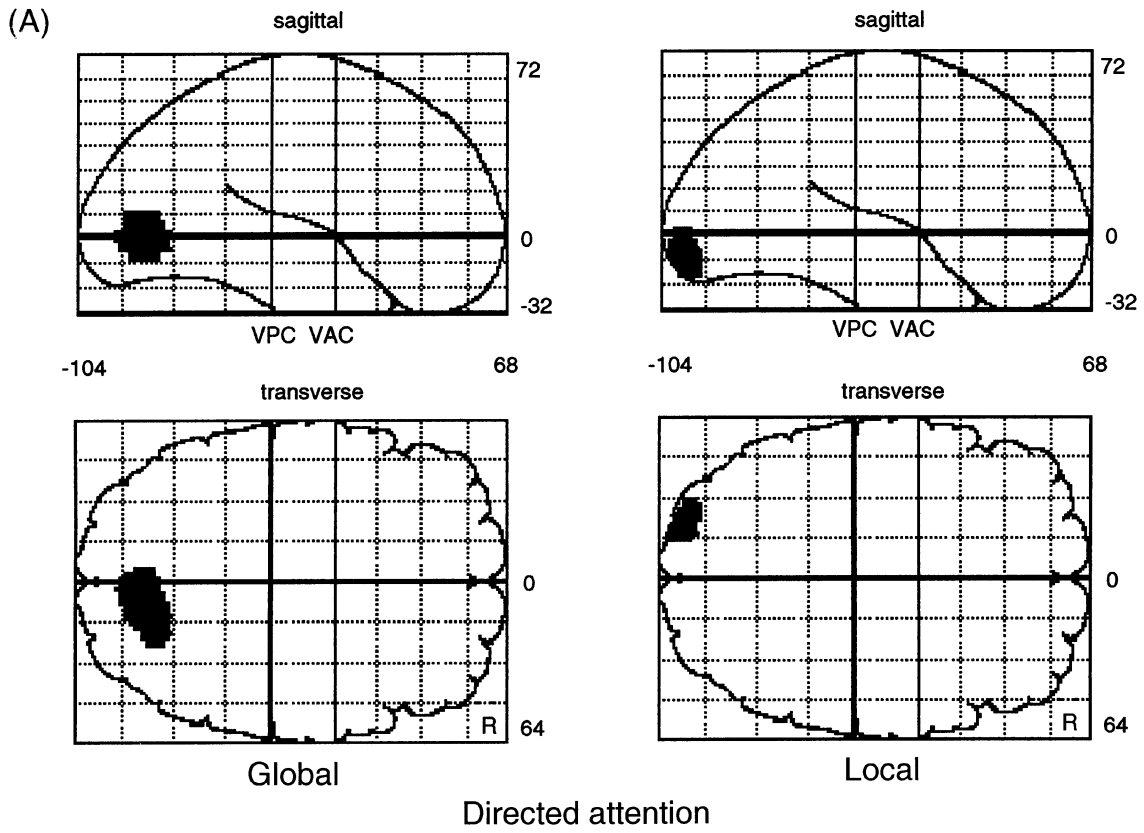
Relative increases in rCBF associated with the small visual stimuli (SG + SL – LG – LL) were observed in a restricted lateral posterior (foveal) part of the occipital cortex [$P < 0.05$, corrected; BA 17/18; Table 1 (D) and Fig. 3B] bilaterally.

Interactions

A significant interaction between figure size and the activations due to global and local processing was observed in the left inferior occipital cortex (BA 18) only during the locally directed-attention task. This interaction was an augmentation of activation by increased figure size during local processing. No such interaction was seen in the right lingual gyrus during the globally directed task.

Divided attention task effects

Variation in the number of target switches between levels (global and local) significantly co-varied, as predicted, with temporal–parietal (but not with prestriate) activation. These areas were predicted *a priori* on the basis of previous studies of patients with lesions to those areas and their consequent deficits in global and local processing (Robertson *et al.*, 1988; Robertson and Lamb, 1991). The number of successive stimuli for which subjects had to sustain their attention to either the local or the global level (because the target continued to be located at the same level) was significantly correlated with relative rCBF increases in the temporal–parietal cortex on the right ($x = 32$ mm, $y = -72$ mm, $z = 32$ mm; Z-score = 3.5, $P < 0.001$; BA 39/19; Fig. 4) and the posterior part of the superior temporal gyrus on the left ($x = -48$ mm, $y = -54$ mm, $z = 16$ mm; Z-score = 2.9, $P < 0.01$; BA 22/39; Fig. 4). Further activations were observed at a significance level of $P < 0.001$ (uncorrected) in the right temporal cortex, the right orbital–frontal cortex and the right dorsal–lateral prefrontal cortex (Fig. 5; Table



2). A correlation of rCBF with an increasing number of target switches from the global to the local level (or vice-versa) was observed ($P < 0.001$, uncorrected) in the left supplementary motor area (BA 6, Fig. 5, Table 2) and the left medial parietal cortex (BA 7, Fig. 5, Table 2).

Single subject analysis

Data analysis for each subject of Experiment 1 revealed that eight of the 10 subjects showed patterns of activation consistent with the group result (i.e. lateralization and localization of activations in prestriate and striate areas). Data analysis for each subject of Experiment 2 revealed that five of the six subjects showed patterns of activation consistent with the group result.

Discussion

This study provides direct evidence of relative hemispheric specialization for global and local processing of hierarchical visual stimuli (large letters made of small letters); globally directed attention primarily involves the right hemisphere and locally directed attention primarily involves the left hemisphere. These hemispheric differences arise in early stages of visual processing in the prestriate visual cortex despite the fact that the stimuli were invariant across conditions (i.e. there were no differences in spatial frequency between the two conditions, although the global condition directed attention to low frequencies while the local condition directed attention to high frequencies). These observations, together with the correlation between rCBF in the temporal–parietal cortex and the number of successive stimuli for which subjects had to sustain their attention to either level, fit the following model. Attentional processes are controlled by temporal–parietal areas, and this attentional control modulates the sensory neural responses in the prestriate cortex during global and local processing.

Though it is widely accepted that attention can affect early stages of sensory processing, little is known about the neural mechanisms underlying the interaction of attention, perception and sensory input. Corbetta *et al.* (1991) used PET to measure cerebral blood flow changes during selective (i.e. directed) and divided-attention tasks when subjects had to discriminate changes in shape, colour and speed. With

changing stimuli, significant activations ($Z > 1.96$) were observed in many areas. During the selective attention task, activations were observed in prestriate areas and, in addition, in the globus pallidus, caudate nucleus, lateral orbitofrontal cortex, posterior thalamus/colliculus and insular-premotor regions. The divided-attention task yielded additional activations in the anterior cingulate and the dorsolateral prefrontal cortex. These findings suggest that attentional systems are separate from the actual ‘signal-processing’ areas that are modulated by attention. Similar results have been obtained in macaques; attention modulates the response of space-selective cells in prestriate and striate areas (Moran and Desimone, 1985; Spitzer *et al.*, 1988; Motter, 1993). As stimulus characteristics (across conditions) changed throughout these experiments, the question remains as to whether and where selective visual attention interacts with signal processing, and/or whether such changes could simply be due to intrinsic selectivity within sensory systems (Desimone and Duncan, 1995).

Study design

In studying the functional anatomy of global and local processing (i.e. of directed (Experiment 1) and divided (Experiment 2) visual attention to global and local aspects of a complex visual scene), we used stimuli that have been well evaluated in neuropsychological and psychophysical studies; i.e. Navon figures (Navon, 1977). Much is known about the sensory (exogenous) processes and volitional (endogenous) attentional processes involved in global and local processing of such stimuli (Rafal and Robertson, 1995). Since psychophysical differences in global and local processing may be confounded by differences in stimulus size (Hellige, 1993) we used both large and small stimuli, in a factorial design (Experiment 1), to control for possible interactions of stimulus size and selective visual attention. This design limited Experiment 1 to a non-parametric ‘blocked’ presentation. That is, within each rCBF measurement subjects were directed either globally or locally and did not need to ‘switch’ attention between levels. Hence the activations in Experiment 1 do not reflect central attentional mechanisms, but rather the signal-processing consequences of an activated attentional system. Experiment 2, in which we varied the number of switches between levels

Fig. 3 (A) Relative rCBF increases (for the 10 subjects) associated with globally and locally directed attention (Experiment 1). Areas of significant relative rCBF increases ($P < 0.05$, corrected for multiple non-independent comparisons) are shown as through-projections onto representations of standard stereotactic space (Friston *et al.*, 1995a; Talairach and Tournoux, 1988). Sagittal, side view; transverse, view from above. There is right-hemispheric activation centred on the lingual gyrus during globally directed attention and left-hemispheric activation centred on the inferior occipital cortex during locally directed attention. R = right; VAC = vertical plane through the anterior commissure; VPC = vertical plane through the posterior commissure; numbers at axes refer to coordinates of stereotactic space (Friston *et al.*, 1995a). The exact coordinates of the local maxima and their Z-statistic are given in Table 1 (A and B). (B) Relative rCBF increases (for the 10 subjects) associated with large and small visual stimuli (Experiment 1). Areas of significant relative rCBF increases ($P < 0.05$, corrected for multiple non-independent comparisons) are displayed in the same format as A. There is extensive bilateral activation centred on the primary visual cortex and extending into the posterior inferior temporal–occipital cortex during analysis of the large stimuli and restricted posterior (foveal) activation centred on the inferior occipital cortex during analysis of the small stimuli. The exact coordinates of the local maxima and their Z-statistic are given in Table 1 (C and D).

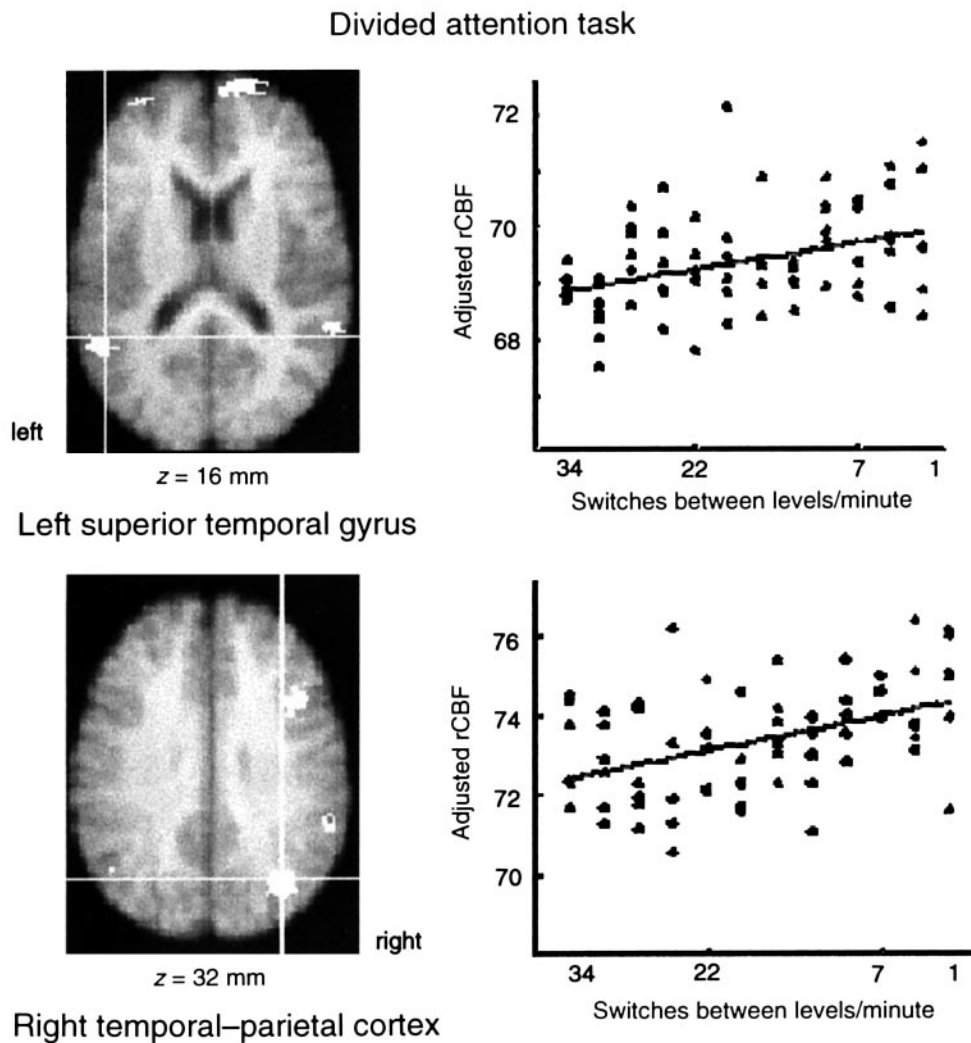


Fig. 4 Relative rCBF increases (for the six subjects) seen with globally/locally divided attention (Experiment 2). Areas of significant relative rCBF increases ($P < 0.01$) correlated with the number of successive stimuli for which subjects had to sustain attention to either the global or the local level are shown superimposed upon transverse sections of the group mean MRI that had been spatially normalized into the same anatomical space (Friston *et al.*, 1995a; Talairach and Tournoux, 1988). The white cross-hairs indicate the local maxima within the areas of activation in the posterior part of the left superior temporal gyrus (*above*) and in the right temporal-parietal-occipital junction (*below*). z is the distance above the intercommissural (AC-PC) line in mm. The exact coordinates of the local maxima and their Z -statistic are given in the results section. In addition, adjusted rCBF values are plotted against the decreasing number of switches between levels (i.e. the increasing number of successive stimuli for which the subjects had to sustain attention to either the global or local level). A simple linear regression line between adjusted rCBF and the number of switches is superimposed.

(global and local) parametrically, is, in contrast, predicated on the progressive engagement of central attentional mechanisms. We reasoned that the number of switches between levels should co-vary with the central mechanisms that mediate attentional switches ('costs of switching'). The design likewise allowed us to determine rCBF changes correlated with sustaining attention to either level and hence reveal the central mechanisms that maintain attention to global or local levels of hierarchical stimuli ('costs of sustaining attention').

Regional activations

The areas activated differentially during the directed visual attention tasks, the right lingual gyrus (during global processing) and the left inferior occipital cortex (during local processing), both encroach onto the cuneus. According to human anatomical and imaging evidence, the focus in the left inferior occipital cortex lies within V2 while the focus in the right lingual gyrus falls near the V2/V3 boundary (Clarke, 1994; Sereno *et al.*, 1995; Shipp *et al.*, 1995). The right lingual gyrus activation is close to activations previously

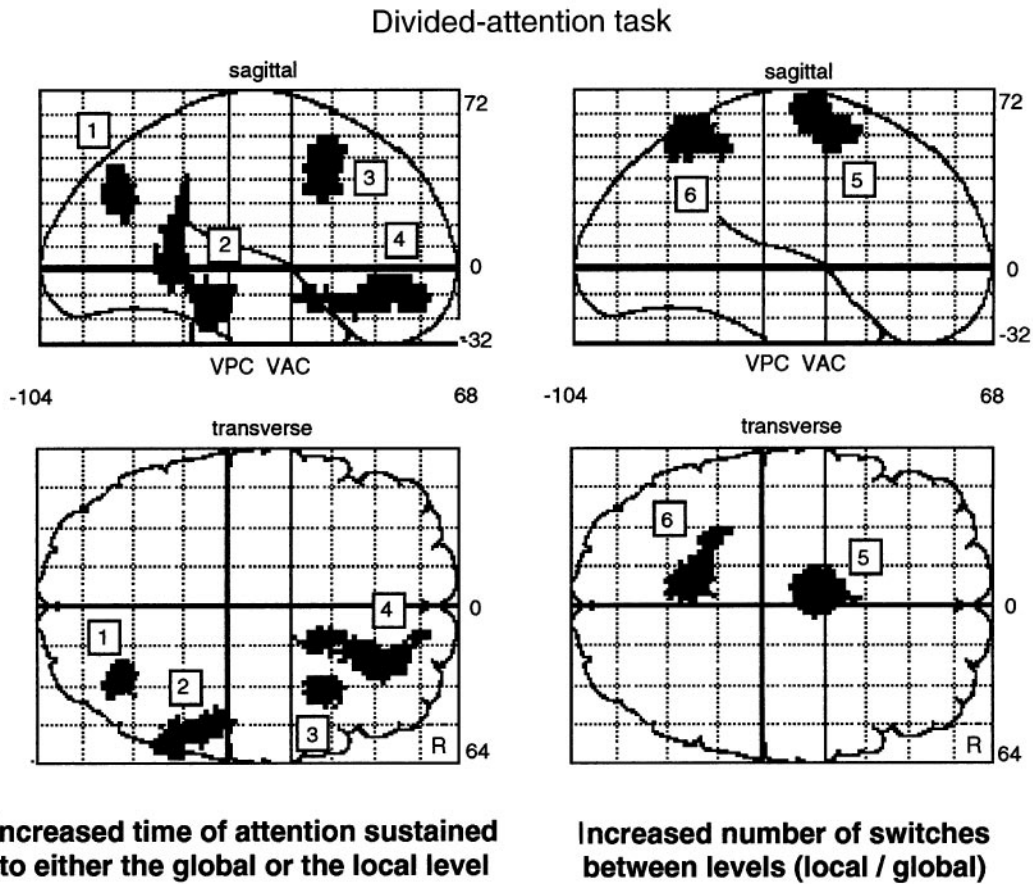


Fig. 5 Relative rCBF increases (for the six subjects) associated with an increasing time of attention sustained to one or the other level (left of figure) and relative rCBF increases associated with an increasing number of switches from the global to the local level (or vice-versa, right of figure). Areas of significant relative rCBF increases ($P < 0.001$, uncorrected) are displayed in the same format as described in Fig. 3. There is a positive correlation of rCBF with an increasing number of successive stimuli for which subjects had to sustain attention to either global or local level in the right temporal–parietal–occipital junction (1), the right temporal cortex (2), the right dorsolateral prefrontal cortex (3) and the right orbitofrontal cortex (4). A positive correlation of rCBF with increasing number of switches between levels is seen in the left supplementary motor area (5) and the left medial parietal cortex (6). R = right; VAC = vertical plane through the anterior commissure; VPC = vertical plane through the posterior commissure; numbers at axes refer to coordinates of stereotactic space (Friston *et al.*, 1995a). The exact coordinates of the local maxima and their Z-statistic are given in Table 2.

Table 2 Relative increases in brain activity during a divided attention task using complex hierarchically organized visual stimuli

Region	Side	x,	y,	z	Z-score
(A) Correlation of rCBF with sustaining attention to either global or local level					
Orbital–frontal cortex (BA 10/32)	R	24,	32,	–8	3.8
Temporal–parietal–occipital junction (BA 39/19)	R	32,	–72,	32	3.5
Dorsal–lateral prefrontal cortex (BA 8)	R	34,	10,	44	3.5
Medial temporal gyrus (BA 21/37)	R	54,	–50,	0	3.5
(B) Correlation of rCBF with increasing number of switches between levels					
Supplementary motor area (BA 6)	L	–4,	–4,	60	4.5
Medial parietal cortex (BA 7)	L	–8,	–54,	–56	3.6

Coordinates are in standard stereotactic space (Talairach and Tournoux, 1988) and refer to maximally activated foci as indicated by the highest Z-score within an area of activation associated with (A) an increasing number of successive stimuli for which the subjects had to sustain attention to either the global or local level, and (B) an increasing number of target switches between global and local. See legend of Table 1 for details. The level of significance was set at $P < 0.001$ (uncorrected).

reported to be associated with changes in shape (Corbetta *et al.*, 1991). The differential activations within V2 and V3 may reflect attentional modulation of the respective retinotopic fields within V2 and V3 during local and global processing. For any hierarchical stimulus, global processing necessarily involves a larger peripheral visual field and local processing usually involves the central visual field. As stimuli were invariant across conditions, and the only experimental change involved instructions, these findings strongly support the hypothesis that neural activity in early visual areas does not solely represent the physical attributes of a retinal image (Moran and Desimone, 1985; Corbetta *et al.*, 1990; Motter, 1993). In contrast to Corbetta *et al.* (1991), we did not observe any activation outside occipital areas during the directed (selective) attention task. Two factors may be responsible: (i) we adopted a higher statistical threshold, and/or (ii) there were major differences in the conditions used as references for the statistical comparison (Corbetta *et al.*, 1991).

Marked differences in neural activations associated with figure size were observed in the striate (primary visual) cortex; large stimuli were associated with extensive striate activation and small stimuli with restricted posterior (foveal) activations. Such a topographic [anterior (large) and posterior (small)] representation within the primary visual cortex follows from the spatial organization of early visual areas (Zeki, 1993). Furthermore, our findings parallel a recent report on neural correlates of mental images of varied size (Kosslyn *et al.*, 1995).

In the second experiment (divided attention task), the activation of non-homologous regions in the right temporal–parietal–occipital junction (BA 39/19) and in the left posterior aspect of the superior temporal gyrus (BA 22/39) is of particular interest. The finding is predicted by the locus of lesions in patients with impaired global and local processing abilities (Robertson *et al.*, 1988; Robertson and Lamb, 1991). Other areas showing a positive correlation of rCBF with sustained attention to either the global or local level were the right orbital–frontal cortex, the right dorsal–lateral prefrontal cortex and the right lateral posterior temporal cortex. In contrast, the areas showing a correlation with an increasing number of target switches from one processing level to the other (supplementary motor area and medial parietal cortex) were both in the left hemisphere.

The former result is consistent with previous studies reporting an association between selective visual attention or sustained attention and right hemisphere processes, in particular with right frontal areas (Heilman and Van Den Abell, 1980; Hellige, 1993; Pardo *et al.*, 1991; Deutsch *et al.*, 1987; Wilkins *et al.*, 1987; Whitehead, 1991; Posner, 1995; Rueckert and Grafman, 1996). Regarding the left hemispheric activations with an increasing number of switches between levels, we know no investigations (physiological or pathological) of the brain areas involved in switching between global and local levels of visual processing. Activation of frontal regions of the left hemisphere may reflect the operation

of a supervisory attentional system (Shallice and Burgess, 1996) with activation of the supplementary motor area indexing the growing attentional demands on the subject when responding to the increased alternations of stimulus target levels by consciously shifting attention between levels. This may be the functional equivalent of the prior level interference reported in reaction time studies (Rafal and Robertson, 1995). The activation of a medial parietal area in the left hemisphere is in keeping with the anatomical connections of this area to the supplementary motor area and suggests feedback processes from executive to secondary somatosensory areas (Murray and Coulter, 1981). The observed medial parietal cortex activation is close to the superior parietal cortex activation described in another task involving shifts of spatial attention (Corbetta *et al.*, 1995). This suggests that shifts of location and of scale share, in part, a common anatomy.

Clinical implications

When visual stimuli with both global and local aspects are presented to patients for delayed copying, subjects with left hemisphere lesions are more impaired in local processing, while subjects with right hemisphere lesions are more impaired on the global aspect (Robertson and Lamb, 1991). Increased reaction times for global processing in patients with right temporal–parietal lesions (but without visual field deficits) and similar increases for local processing with left temporal–parietal lesions also imply hemispheric asymmetry for global and local processing (Robertson and Lamb, 1991). An account of the symptoms of left visual-spatial neglect in terms of impaired global processing is given in Halligan and Marshall (1994). An important caveat, however, is that even following extensive unilateral brain damage, some patients can still perform both global and local processing tasks. Presumably their unaffected hemisphere is primarily responsible, although the impaired hemisphere may also contribute to its preferential mode of processing (Polster and Rapcsak, 1994). Hemispheric asymmetries in global and local processing are thus relative, not absolute, and any interpretation of lesion studies is further limited by compensatory mechanisms ('plasticity'). Nevertheless, lesion studies and our functional imaging findings provide complementary evidence for the importance of temporal–parietal cortex in the attentional control of global and local processing.

Interaction between stimulus size and local and global processing

The independent effects of stimulus size and global processing on the neural activation in the right lingual gyrus contrast with the interaction of stimulus size and local processing in the left inferior occipital cortex. These latter activations cannot be explained by stimulus size alone, which was

controlled. The most parsimonious explanation for the interaction is that for small hierarchical stimuli even the global form has a strong local aspect by virtue of retinal size. Accommodation, vergence and pupil size may be modulated by instructions to attend to local or global levels of the stimuli, and by stimulus size. However, there is no reason to suspect that such effects, *per se*, will result in lateralized neural activation in prestriate or temporal-parietal cortex.

Spatial frequency

Shulman *et al.* (1986) established a link between local/global processing and spatial frequency in letter Navon figures. Differences in tuning to low- and high-spatial frequencies may be responsible for hemispheric specificity in global and local processing (Hughes *et al.*, 1996). Global precedence may depend on the low spatial frequency component of complex visual stimuli (Davis, 1981; Badcock *et al.*, 1990). As the visual stimuli used in the present study were identical for both global and local conditions, our results are unlikely to reflect spatial frequency aspects of the stimuli in any direct fashion, although the two conditions do indeed direct attention to two different spatial frequency domains. The processing of large versus small stimuli leads to bilateral and symmetrical activation, which is further evidence that spatial frequency plays, at most, a minor role in the hemispheric asymmetries observed in our study. Nonetheless, attentional mechanisms can modulate the processing of spatial frequencies associated with the two levels (Hellige, 1993; Luck and Hillyard, 1994). In the context of results from event-related potential studies (Heinze and Münte, 1993) our findings suggest that attentional filtering occurs in the occipital cortex under the control of feedback from higher cortical regions. This downstream attentional filtering may take place after a preliminary feature-based analysis of the stimulus (Lamb *et al.*, 1990) that is intrinsically sensitive to low- and high-frequency aspects of the inspected scene. It is interesting to note that a similar hemispheric asymmetry has been found in the auditory domain. The right hemisphere seems to be faster and more accurate in pitch discrimination for low frequency sounds, while the left hemisphere performs better with high frequency sounds (Ivry and Leiby, 1993).

Visual attention

The differential activation of prestriate areas during local and global processing reflects the locus of interaction of attention and early visual processing. When subjects do not know in advance the level at which the relevant stimulus will occur, the temporal-parietal cortices mediate the voluntary distribution and/or maintenance of selective attention. Other areas may also be involved in visual attention and global/local processing, and it would be possible to image the commonalities of global and local processing by introducing a reference state. We chose not to include such a reference

here because it would have decreased the statistical power of the experiments. The current findings directly demonstrate both the source of 'top-down' attentional modulation and its effects. Our results suggest that volitional (endogenous) attentional processes can influence visual processing at early sensory levels.

Conclusions

The present study provides the first direct evidence of relative hemispheric specialization and attentional modulation of early activity in prestriate cortex during global and local processing. The results also suggest a modification to current accounts of the contribution of temporal-parietal cortex to global and local processing. This region may mediate and sustain the distribution of attention to local or global aspects of a complex visual scene. That voluntary attention can be directed from one area (e.g. temporal-parietal cortex) while the consequences of such attention are elaborated in another (e.g. prestriate) is not an unreasonable example of biological engineering.

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