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Where in the brain does visual attention select the forest and the trees?

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THE perceptual world is organized hierarchically: the forest consists of trees, which in turn have leaves. Visual attention can emphasize the overall picture (global form) or the focal details of a scene (local components)¹. Neuropsychological studies have indicated that the left hemisphere is biased towards local and the right towards global processing. The underlying attentional and perceptual mechanisms are maximally impaired by unilateral lesions to the temporal and parietal cortex^{2,3}. We measured brain activity of normal subjects during two experiments using ‘hierarchically’ organized figures. In a directed attention task, early visual processing (prestriate) areas were activated: attention to the global aspect of the figures activated the right lingual gyrus whereas locally directed attention activated the left inferior occipital cortex. In a subsequent divided attention task, the number of target switches from local to global (and vice versa) covaried with temporal–parietal activation. The findings provide direct evidence for hemispheric specialization in global and local perception; furthermore, they indicate that temporal–parietal areas exert attentional control over the neural transformations occurring in prestriate cortex.

We measured brain activity, indexed by regional cerebral blood flow (rCBF), in two separate experiments using ‘hierarchically’ organized visual stimuli (Fig. 1). In the first experiment, subjects were asked to attend to and name either the global or the local aspect of the figures in separate blocks of trials. As psychophysical differences in global and local processing may be confounded by differences in stimulus size⁴, we controlled for size effects by

presenting both large and small hierarchical figures in a factorial experimental design. In the second experiment, a preselected target letter appeared at either the global or the local level and the subjects were required to say at which of the two levels the target had appeared. The number of times that the target switched from the global to the local level (or vice versa) on successive trials varied parametrically across the experiment.

In the first experiment, as predicted, marked differences in neuronal activation associated with figure size were observed in the striate (primary visual) cortex: large stimuli were associated with extensive striate activation and small stimuli with more restricted posterior (foveal) striate activations ($P < 0.05$, using statistical parametric mapping and corrected for multiple non-independent comparisons). In addition, when subjects attended to the global aspect of figures, significant increases in relative rCBF were seen in the right lingual gyrus (Brodmann area 18; $P < 0.05$, corrected; Table 1, Fig. 2). When subjects attended to the local attribute, there was a significant relative rCBF increase in the left inferior occipital cortex (BA 18; $P < 0.05$, corrected, Table 1, Fig. 2). A direct comparison of rCBF changes between the two hemispheres indicated that these lateralized effects were statistically significant ($P < 0.01$). A significant interaction between figure size and the activation due to local processing was observed in the left inferior occipital cortex (BA 18, Fig. 2) alone, where the difference

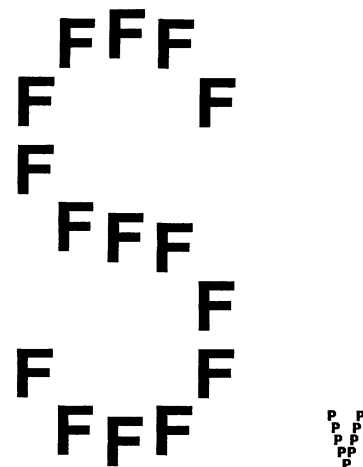


FIG. 1 Example of figures used as stimuli during the global and local processing experiments. The S and the V represent the global level and the F and the P the local level. All figures used were non-congruent for the global and local level. During the rCBF measurements, the figures were shown every 1.5 s for 300 ms in the centre of a 14 inch video display unit at a viewing distance of 40 cm. In the first experiment, 12 different letters were used to create the figures. These were presented in a quasi-random sequence that prevented the same letter appearing at the local or global level on successive trials¹⁶. To study stimulus size effects on global and local processing, both large figures (170 × 72 mm, made of letters 21 × 13 mm, visual angle subtended 24° and 10°) and small figures (30 × 14 mm, made of letters 3.5 × 2.5 mm, visual angle 4° and 2°) were used. Subjects were instructed to attend to either the global or the local level and to name the appropriate letter. rCBF measurements were performed during the following four conditions: global directed attention, large stimuli; local directed attention, large stimuli; global directed attention, small stimuli; local directed attention, small stimuli. Subjects lay with eyes open in a quiet, darkened room. Twelve rCBF measurements were performed per subject (three repeats per condition); globally and locally directed attention tasks were alternated. During the second experiment (divided attention), the same stimuli, (large letters only), presentation rate and number of measurements were used, however, this time a preselected target letter appeared at either the global or the local level. The number of switches between perceptual levels was varied on successive trials from 1 to 34 per min. The number of times that a given target letter occurred at the global or the local level was kept roughly equal across the rCBF measurements. A quasi-random sequence prevented the same stimulus from occurring on successive trials.

between local and global processing was augmented by increasing figure size. The absence of differential rCBF increases in lateral temporal–parietal areas, during either local or global tasks, led us to conjecture that this was because subjects were not required to switch attention between the two levels (blocked presentation).

FIG. 2 Relative rCBF increases (for the ten subjects) associated with globally $((A + C) - (B + D))$ and locally $((B + D) - (A + C))$ 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 space¹⁵. Sagittal, side view; transverse, view from above. Transverse SPM{z} maps were superimposed upon the group mean magnetic resonance (MR) image, that had been spatially normalized into the same anatomical space¹⁵. Red arrows indicate the local maximum within the area of activation. There is right-hemispheric neuronal activation centred on the lingual gyrus during globally directed attention and left-hemispheric neuronal 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 space¹⁵. The exact coordinates of the local maxima and their Z statistics are given in Table 1. Adjusted means rCBF (to a mean of $50 \text{ ml dl}^{-1} \text{ min}^{-1}$) \pm s.e.m. for each condition are displayed for the local maxima. LG, large stimulus with global attention; LL, large with local attention; SG, small with global; SL small with local. There is a dependency on stimulus size of the adjusted blood flow response in early visual processing in both areas. A significant interaction of stimulus size on the rCBF response during local processing was observed in the left inferior occipital cortex, but no such interaction was seen in the right lingual gyrus. METHODS. In experiment 1, 10 normal-sighted male right-handed volunteers were studied using a position emission tomography (PET) scanner (Siemens) in 3D mode with a 15-cm axial field of view. Relative rCBF was measured from the distribution of radioactivity after slow bolus intravenous injection of H_2^{15}O (9 mCi per scan, each lasting 90 s)¹⁷. Attenuation-corrected data were reconstructed into 63 image planes with a resulting resolution of 6 mm at full-width-half-maximum. For each subject, structural images were obtained with a 2 T Magnetom VISION (Siemens). Statistical parametric mapping (SPM95) software was used for image realignment, transformation into standard stereotactic space, smoothing and statistical analysis^{18,19}. All measurements per condition were averaged across subjects. State-dependent differences in global flow were varied out using ANCOVA. Main effects and interactions were assessed with contrasts of the adjusted task means using the *t*-statistic subsequently transformed into the normally distributed Z statistic. The resulting set of Z values constituted a statistical parametric map (SPM{z}) which was then thresholded at $P < 0.05$ (corrected for multiple comparisons). The hemisphere \times condition interaction was identified by using SPM. This did not require correction because these regions were identified on the basis of the (independent) main effects.

We addressed this hypothesis in a second experiment, in which we determined the rCBF changes that correlated with the number of attentional target switches between perceptual levels. Only activations relevant to the specific hypothesis concerning the temporal–parietal cortex and prefrontal areas are reported.

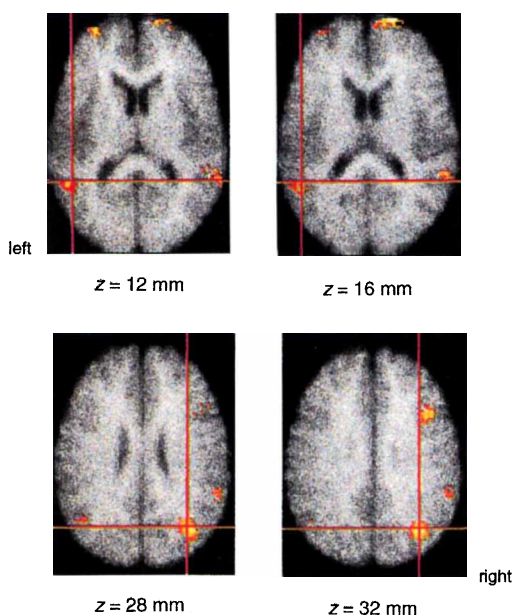
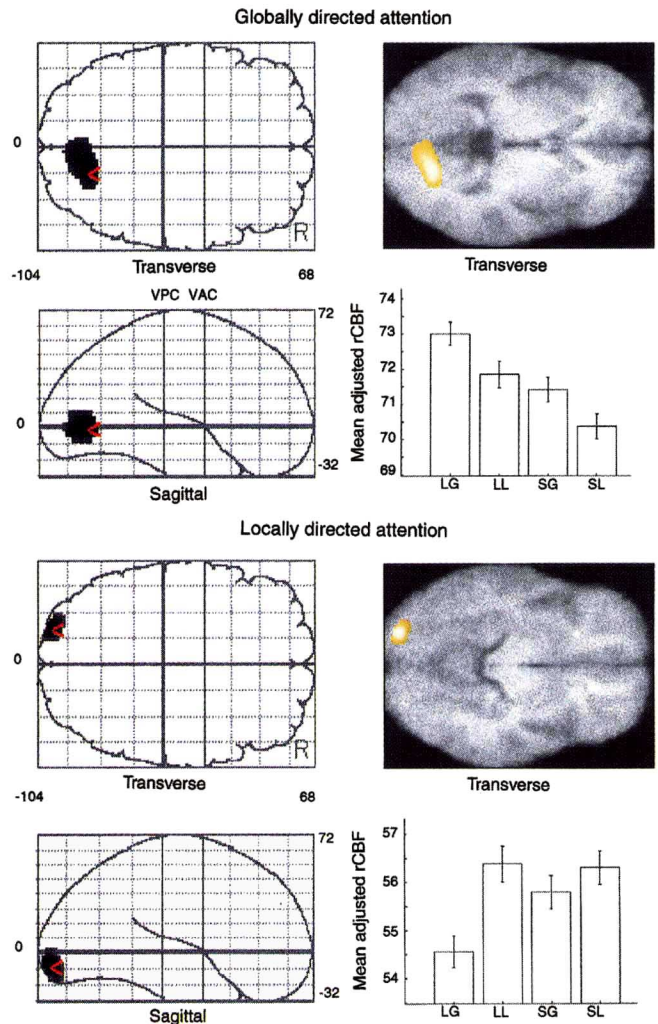


FIG. 3 Relative rCBF increases (for the 6 subjects) seen in experiment 2. Areas of significant relative rCBF increase ($P < 0.01$) are shown superimposed upon transverse sections of the group mean MR-image that had been spatially normalized into the same anatomical space¹⁵. The red cross-hair indicates the local maxima within the areas of activation in the posterior part of the left superior temporal gyrus (upper row) and in the temporal–parietal–occipital junction (lower row). z, distance above the intercommissural (AC–PC) line in mm. The exact coordinates of the local maxima and their z statistics are given in Table 1.

METHODS. Six normal-sighted male right-handed volunteers were studied using identical equipment, data acquisition and processing, as in experiment 1 (Fig. 2). SPM95 (ref. 19) was used to assess significant covariation of relative rCBF with the number of target switches from either the global to the local level (or vice versa). The resulting SPM{z} was thresholded at $P < 0.01$ (uncorrected) as the experiment was specifically concerned with the temporal–parietal areas. Other activations are not reported.

Variation in the number of target switches significantly co-varied, as predicted, with temporal-parietal (but not with prestriate) activation. The number of successive stimuli for which subjects had to sustain attention to either the global or the local level was significantly correlated with blood-flow increases in the temporal-parietal cortex on the right ($P < 0.001$, Fig. 3, Table 1) and on the left ($P < 0.01$, Fig. 3, Table 1).

Our findings indicate that globally directed attention involves the right hemisphere, and locally directed attention the left hemisphere, confirming the indications of previous studies^{2,5}. A striking feature of our findings is that the hemispheric processing differences are apparent in the early stages of visual processing in pre-striate cortex, even though the visual stimuli were invariant across conditions. Our observations thus extend previous reports on selective attention⁶⁻⁸ in that they demonstrate a 'top-down' modulation of the processing of identical input in early visual areas. The areas activated differentially in the lingual gyrus (global processing) and the inferior occipital cortex (local processing) encroach onto the cuneus but do not include the striate cortex (area V1). According to human anatomical and imaging evidence, the focus in the left inferior occipital cortex falls between V1/V2 and V2/V3 boundaries, whereas the focus in the right lingual gyrus falls anterior to the V2/V3 boundaries⁹⁻¹¹. In the second experiment, 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) during the divided attention task is of particular interest: it is predicted by the locus of lesions in patients with impaired global and local processing abilities^{2,5}. Temporal-parietal regions seem to exert attentional control over global and local processing.

Our observations imply that neuronal activity in early visual areas does not only represent the sensory attributes of a retinal image^{8,12}. The independent effects of stimulus size and global processing on the neuronal activation in the right lingual gyrus contrasts with the interaction of stimulus size and local processing in the left inferior occipital cortex. It is evident that the activations are not solely determined by stimulus size (or correlated differences in spatial frequencies), which was controlled across conditions. One explanation for the observed interaction is that for small hierarchical stimuli, even the global form has a strong local aspect by virtue of retinal size. The differential activations observed may thus reflect attentional modulation of the respective retinotopic fields within V2 and V3 during global and local processing. For any specific complex visual stimulus, global processing necessarily involves a larger peripheral visual field and local processing involves the central visual field.

Reports of impaired global processing in patients with right

TABLE 1 Brain activity associated with global and local processing during attentional tasks

Region	Side	Coordinates			Z-score
		x	y	z	
Experiment 1 (A + C) – (B + D): globally directed attention					
Lingual gyrus (BA 18)	R	16	-74	0	5.0
Experiment 1 (B + D) – (A + C): locally directed attention					
Inferior occipital gyrus (BA 18)	L	-22	-96	-8	5.3
Experiment 2: divided attention					
Temporal-parietal-occipital junction (BA 39/19)	R	32	-72	32	3.5
Superior temporal gyrus (BA 22/39)	L	-48	-54	16	2.9

In experiment 1, coordinates (in standard stereotactic space¹⁵) refer to maximally activated foci as indicated by the highest Z-score within an area of activation associated with globally or locally directed attention. In experiment 2, coordinates refer to maximally activated foci associated with the number of successive stimuli to which subjects had to sustain attention to either global or local levels during a divided attention task (for details see Fig. 1). x, distance (mm) to right (+) or left (-) of the midsagittal line; y, distance anterior (+) or posterior (-) to vertical plane through the anterior commissure; z, distance above (+) or below (-) the intercommissural (AC-PC) line. For each anatomical location, an estimate of the Brodmann area (BA) is given in parentheses¹⁵. R, right; L, left. Coordinates of the border of V1/V2 are -10, -98, -4, and of V2/V3 are -20, 78, -4 (ref. 10).

temporal-parietal lesions (but without visual-field deficits) and impaired local processing with similar left temporal-parietal lesions support the concept of hemispheric asymmetry and suggest that the temporal-parietal regions are critical for local and global processing^{2,5}. However, the interpretation of lesion studies is limited by compensatory mechanisms and both local and global processing can be preserved after large unilateral brain lesions¹³. The absence of a differential temporal-parietal activation during the global and local tasks in our first experiment with normal subjects is most probably a result of presenting stimuli in blocks. In situations where the subject does not know in advance the level at which the relevant stimulus will occur, the temporal-parietal cortices may mediate the voluntary distribution and/or maintenance of selective attention^{4,14}.

In our second experiment, we confirmed this prediction by demonstrating temporal-parietal activations in a divided attention task. We show that the modulatory influence of temporal-parietal activity during global and local processing has its predominant effect in pre-striate cortex, at an early stage of visual processing. Damage to temporal-parietal cortex can accordingly impair either global or local processing because of the attentional control that these areas exert over the computations performed in pre-striate cortex. □

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