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Hemispheric specialization for global and local processing: the effect of stimulus category

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SUMMARY

Neuropsychological evidence indicates that the global aspect of complex visual scenes is preferentially processed by the right hemisphere, and local aspects are preferentially processed by the left hemisphere. Using letter-based hierarchical stimuli (Navon figures), we recently demonstrated, in a directed-attention task, lateralized neural activity (assessed by positron emission tomography) in the left prestriate cortex during local processing, and in the right prestriate cortex during global processing. Furthermore, temporal-parietal cortex was critically activated bilaterally in a divided-attention task that involved varying the number of target switches between local and global levels of letter-based hierarchical stimuli. Little is known about whether such stimulus categories influence such hemispheric lateralization. We now present data on brain activity, derived from positron emission tomography, in normal subjects scanned during either local or global processing of object-based hierarchical stimuli. We again observe attentional modulation of neural activity in prestriate cortex. There is now greater right-sided activation for local processing and greater left-sided activation for global processing, which is the opposite of that seen with letter-based stimuli. The results suggest that the relative differential hemispheric activations in the prestriate areas during global and local processing are modified by stimulus category.

1. INTRODUCTION

Perceptual analysis of our visual world involves selective attention to its global and local features (Navon 1977). Differential hemispheric dominance for the perception of global (right hemisphere) or local (left hemisphere) aspects of complex visual scenes is suggested by neuropsychological studies both in normal subjects and in patients with cerebral lesions (Robertson *et al.* 1988; Hellige 1993; Boles & Karner 1996). Using positron emission tomography (PET) to measure changes in neural activity, we recently demonstrated that directing attention to the global aspect of hierarchically organized letters (i.e. large letters made of small letters; Navon 1977) leads to differential neuronal activation in the right prestriate cortex, and directing attention to local aspects leads to differential activation in the left inferior occipital cortex (Fink *et al.* 1996). Furthermore, this study showed that neural activity in the temporal-parietal cortex covaried with the duration of sustained attention to either level. These findings suggested that the temporal-parietal cortex exerts attentional control over the perceptual

processes involved in global and local processing that take place in the prestriate cortex (Fink *et al.* 1996). The former conclusion is consistent with reports of impaired global and local processing in patients with lesions of the temporal-parietal cortex (Robertson *et al.* 1988).

Despite over 20 years of neuropsychological and neurophysiological investigations, little is known concerning which factors determine hemispheric specialization for global and local processing (Hellige 1993). The prime source of evidence has involved letter-based hierarchically organized stimuli (Kinchla *et al.* 1983; Robertson *et al.* 1988), and it is hence unclear whether stimulus category influences such hemispheric asymmetries (Brown & Kosslyn 1995). In this study we investigate whether stimulus type influences the global/local asymmetries demonstrated in early visual processing areas (Fink *et al.* 1996). We measured brain activity, indexed by relative changes in regional cerebral blood flow (rCBF), while subjects performed a task that required either global or local processing of 'hierarchically' organized object-based visual stimuli (i.e. large objects made of small objects). Across conditions, the stimulus characteristics were invariant, but subjects were required to attend to and name either the global or the local aspect of the presented stimulus.

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2. MATERIAL AND METHODS

(a) Subjects

Ten normal healthy male volunteers (aged 19–35 years) were recruited. All were right-handed and had no history, past or current, of neurological or psychiatric illness. Informed written consent was obtained. Permission to administer radioactivity was given by the Administration of Radioactive Substances Advisory Committee of the Department of Health, UK. The study was approved by the Ethics Committee of the National Hospital for Neurology and Neurosurgery (London, UK).

(b) Paradigm design

An example of the figures used as stimuli during the globally and locally directed attention tasks is shown in figure 1.

The anchor (made of small cups) and the cup (made of small anchors) constitute the global level; the small anchors and cups constitute the local level. All figures were non-congruent for global and local levels. The black figures were presented on a white background during the 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 objects (cup, anchor, crescent moon, rectangle, ring, triangle, parallelo-

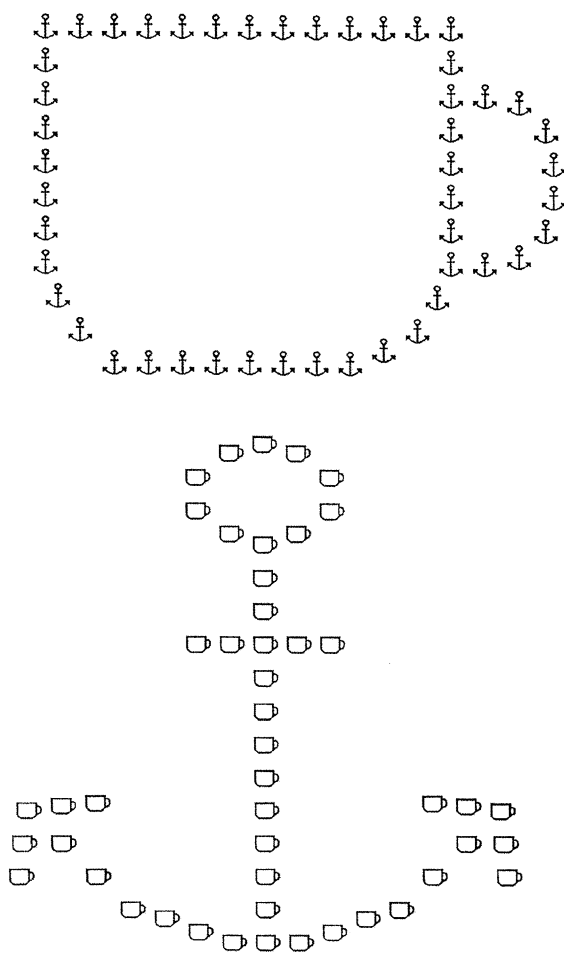


Figure 1. Example of figures used as stimuli during the global and local tasks. The anchor (made of small cups) and the cup (made of small anchors) constitute the global level, with the small cups and anchors being the local level. All figures were non-congruent for global and local levels.

gram, star, square, suitcase, arrow, diamond) were used to create the figures that appeared in a quasi-random sequence which prevented the same figure appearing at the local and global levels on successive trials (Tipper *et al.* 1994). Stimulus size was 110 mm × 110 mm, made of small objects (6 mm × 6 mm), and subtending visual angles of approximately 16° and 1°, respectively.

During the study, subjects were instructed to attend to either the global or local level and to name the appropriate attribute. Each sequence of stimulus presentations commenced 10 s prior to PET scanning. A total of 12 relative rCBF measurements was taken per subject; the two conditions relevant to the specific question addressed by the study involved eight of these 12 measurements, which were presented in a counter-balanced design.

(c) 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 & Mintun 1989). The PET measurements were carried out using a Siemens/CPS ECAT EXACT HR+ (model 962) PET scanner (CTI Inc., Knoxville, TN, 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.

For each measurement of relative rCBF, 9 mCi of H_2^{15}O (effective dose equivalent of 0.4 mSV) were given intravenously as a slow bolus over 20 s (Silbersweig *et al.* 1993). Data collection started 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. Emission scan data were corrected for the effects of radiation absorption by the skull (by means of a transmission scan taken prior to the first rCBF measurement). Following attenuation correction, the data were reconstructed to 63 transverse planes (separation 2.4 mm) and into 128 × 128 pixels (size 2.1 mm) by three-dimension-filtered back projection using a Hanning filter of cut-off frequency 0.4 cycles per pixel, and applying a scatter correction. The resolution of the resulting images was 6 mm (at full width half maximum, FWHM).

(d) Magnetic resonance imaging

In separate sessions, a magnetic resonance (MR) image of each subject's brain was obtained (a) to exclude subjects with any morphological/pathological abnormalities and (b) for stereotactic normalization into the standard anatomical space (see below). The MR images were obtained with a 2 Tesla system (VISION, Siemens AG, Germany) using a three-dimensional T_1 weighted imaging technique producing 108 transaxial slices ($1 \times 1 \times 1.5 \text{ mm}^3$).

(e) Image processing

All calculations and image manipulations were performed on a SPARC workstation (SUN Computers). PROMATLAB software (MATHWORKS Inc., USA) was used to calculate and display images. Statistical parametric mapping software (SPM95; Wellcome Department of Cognitive Neurology, London, UK) was used for image realignment, image

Table 1. Relative increases in brain activity associated with global and local processing during a selective attention task with object-based hierarchically organized visual stimuli

region	side	coordinates			Z-score
		<i>x</i>	<i>y</i>	<i>z</i>	
<i>a</i> globally directed attention					
cuneus/calcarine sulcus* (BA 17/18)	L	-4	-88	8	4.2
lingual gyrus (BA 18)	L	-10	-76	-12	4.1
<i>b</i> locally directed attention					
inferior occipital cortex	R	24	-98	-12	4.6

Coordinates (in standard stereotactic space; Talairach & Tournoux 1988) refer to maximally activated foci as indicated by the highest Z-score within an area of activation associated with globally and locally directed attention. *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 is given in parentheses (Talairach & Tournoux 1988). R = right, L = left.

Level of significance: $p < 0.05$ corrected for multiple non-independent comparisons.

* No significant difference between the two hemispheres (direct comparison with homologous region).

normalization, smoothing and to create statistical maps of significant relative rCBF changes (Friston *et al.* 1995*a, b*).

(f) Realignment, transformation and smoothing of PET images

Using SPM95 software (Friston *et al.* 1995*a*) all PET scans were realigned to the first emission scan to correct for head movement. A mean relative rCBF image was created. Each individual's MR and PET mean image were then co-registered and subsequently transformed into a standard stereotactic anatomical space (Talairach & Tournoux 1988; Friston *et al.* 1995*a*). The same image transformation was thereafter applied to all PET scans of the respective individual. The PET images were then filtered using a low-pass Gaussian filter (16 mm filter size, effective image resolution of $16 \times 18 \times 20 \text{ mm}^3$ at FWHM) to reduce the variance due to individual anatomical variability and to improve signal-to-noise ratio (Friston *et al.* 1995*a*). The resulting pixel size in stereotactic space was $2 \times 2 \text{ mm}^2$ with an interplane distance of 4 mm. Data were thereafter expressed in terms of standard stereotactic coordinates in the *x*-, *y*- and *z*-axes (as defined in table 1).

(g) Statistical analysis

Following stereotactic normalization, the data were assessed on a pixel-by-pixel basis using SPM95 (Friston *et al.* 1995*b*). Task-related differences in global CBF, within and between subjects, were removed by treating global activity as the covariate (Friston *et al.* 1995*b*). 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 $100 \text{ ml}^{-1} \text{ min}^{-1}$) and an associated adjusted error variance (Friston *et al.* 1995*b*). This allowed planned comparisons of mean blood flow distributions across conditions. For each pixel, across all subjects and all scans, the mean relative rCBF values were calculated separately for the main effects. Comparisons of the two main effect means were made using the *t*-statistic, thereafter transformed into normally distributed Z-statistics. The resulting set of z-values constituted a statistical parametric map (SPM{z}-map) (Friston *et al.* 1995*b*). The level of significance was set to $p < 0.05$, corrected for multiple non-independent comparisons.

For the analysis of hemisphere \times condition effects, all PET images were flipped (in the *x*-axis). Flipped and unflipped images were then compared for every voxel. This gave all the condition-specific observations for the ipsilateral and contralateral hemisphere. An SPM with *t*-statistics was calculated in the usual way, testing explicitly for a condition \times hemisphere interaction at all voxels. We predicted activation in the areas implicated by the main effects and therefore no correction for multiple comparisons was needed. Accordingly the SPM was thresholded at a $p < 0.05$, uncorrected. The study \times condition interaction was identified by using an SPM that tested directly for a study \times condition interaction. This interaction compared the findings of the present study with the findings obtained in our previous study using an identical methodology in all respects except that the hierarchical stimuli were letter-based (Fink *et al.* 1996). The latter comparisons did not require correction because the regions of interest had been identified on the basis of the main effects.

For individual studies, PET data were analysed in an identical way to the group data. Because only four repeated measures were available per condition for each subject, the SPM was thresholded at a $p < 0.01$, uncorrected. The analysis of data from each individual was restricted to 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 in the absence of anatomical 'blurring', which is a feature of the group analysis.

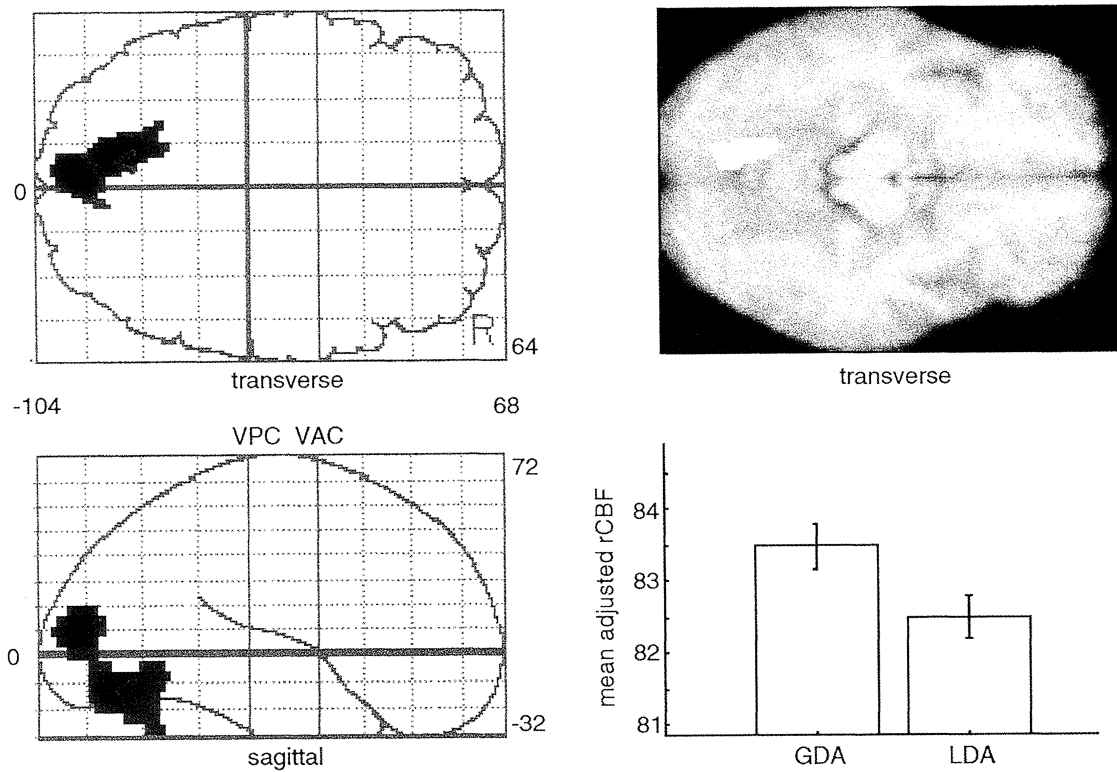
(h) Localization of activations

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

3. RESULTS

The patterns of differential relative activations seen in our previous study were replicated (Fink *et al.* 1996):

globally directed attention



locally directed attention

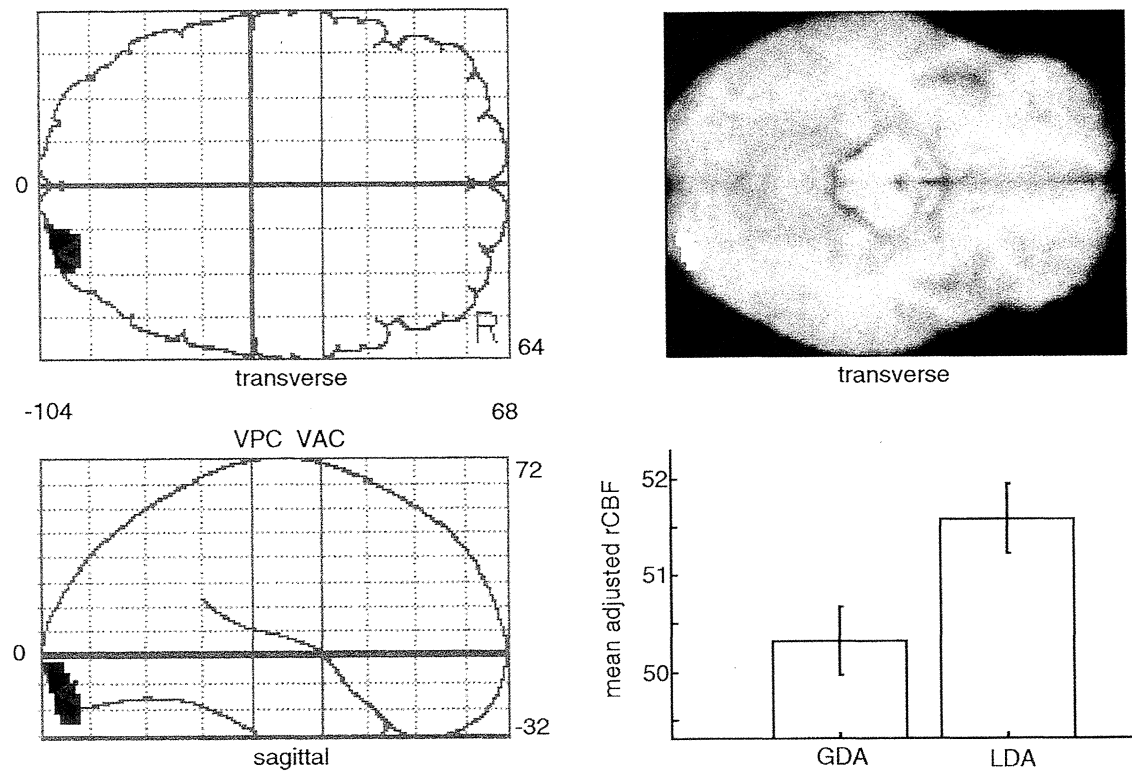


Figure 2. Relative regional cerebral blood flow (rCBF) increases (for the group of ten subjects) associated with globally and locally directed attention. Areas of significant relative rCBF increases ($p < 0.05$, corrected for multiple non-independent comparisons) are shown as through-projections onto representations of standard stereotactic space (Talairach & Tournoux 1988). The sagittal images view the brain from the side, the transverse images view the brain from the top. To show the functional anatomy of the activation and its relationship to underlying anatomy, the

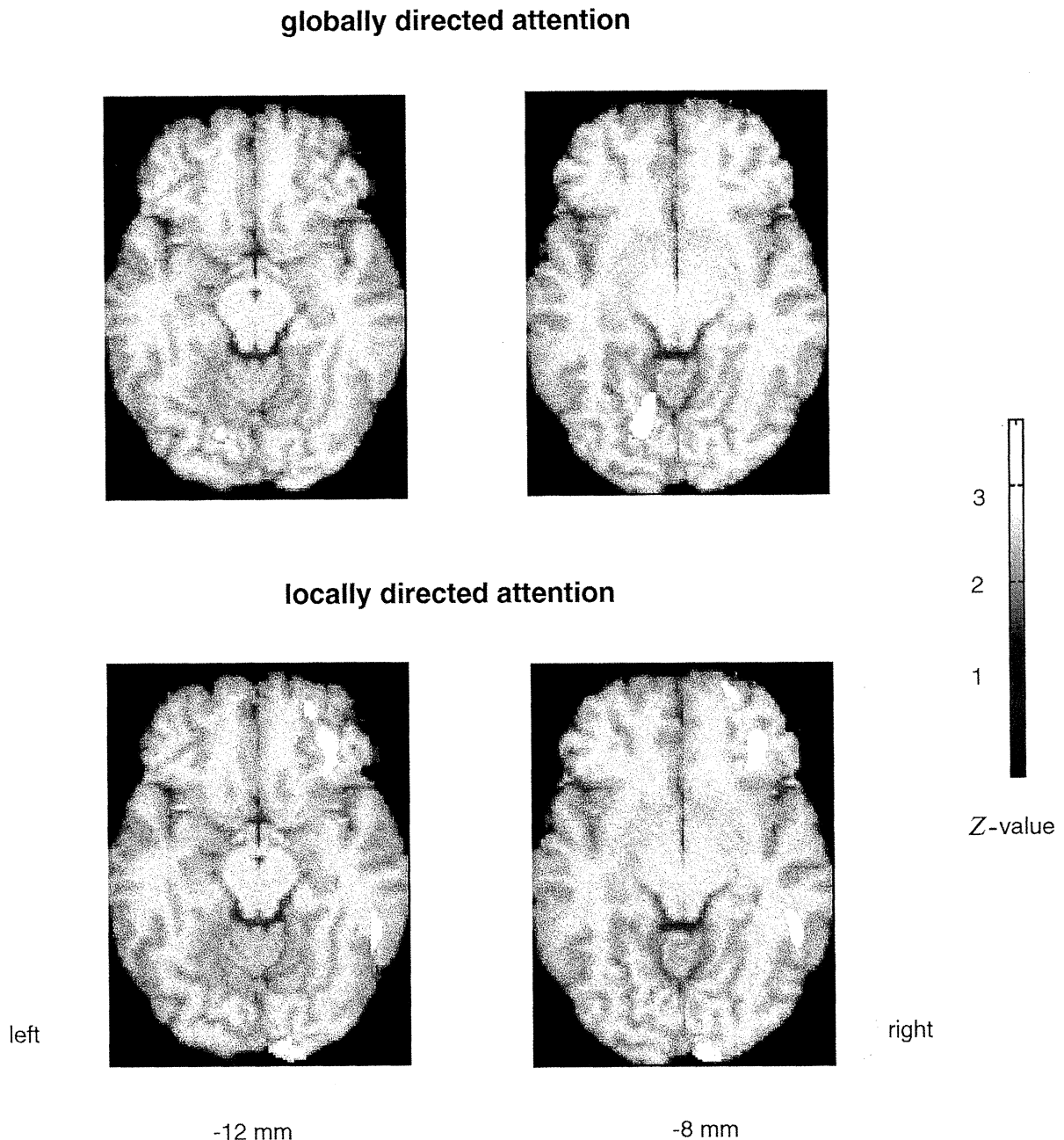


Figure 3. Relative regional cerebral blood flow (rCBF) increases (for subject L.B.) associated with globally and locally directed attention after coregistration and superimposition of MR and PET SPM $\{z\}$ -maps. To detail the functional anatomy of the activations and their relationship to underlying anatomy, areas of significant relative rCBF increases ($p < 0.01$, uncorrected) are shown superimposed on transverse MR sections (distance below the intercommissural AC-PC line) in mm. There is left-hemispheric neuronal activation centred on the lingual gyrus during globally directed attention and right-hemispheric neuronal activation centred on the inferior occipital cortex during locally directed attention. The colour bar indicates the z-statistics achieved (z-value). Other activations were observed, but are not reported as single subject analysis was restricted to those areas in the striate and prestriate cortex that were observed in the group analysis (see §2).

transverse SPM $\{z\}$ -maps were superimposed on the group mean MR image, that had been spatially normalized into the same anatomical space (Talairach & Tournoux 1988). The red arrows indicate the local maximum within an area of activation. There is left-hemispheric neuronal activation centred on the lingual gyrus and the calcarine sulcus during globally directed attention and right-hemispheric neuronal activation centred on the inferior occipital cortex during locally directed attention. The exact coordinates of the local maxima within the areas of activation and their z-statistics are given in table 1a and 1b. In addition, adjusted mean rCBF (arbitrarily adjusted to a mean of 50 ml 100 ml $^{-1}$ min $^{-1}$; see §2) and standard error of the adjusted means per condition are displayed for the respective pixels of maximally significant relative rCBF change within areas of activation in the left lingual gyrus (globally directed attention) and the right inferior occipital cortex (locally directed attention). R = right, GDA = globally directed attention, LDA = locally directed attention, VPC = vertical plane through the posterior commissure, VAC = vertical plane through the anterior commissure; numbers at axes refer to coordinates of stereotactic space (Talairach & Tournoux 1988).

visual attention directed to the global aspect differentially activated the lingual gyrus, and attention to the local aspect differentially activated the inferior occipital cortex ($p < 0.05$, corrected for multiple non-independent comparisons; figure 2, table 1).

There was a crucial difference with our study of letter-based stimuli (Fink *et al.* 1996). In the current experiment, attending to the global aspect of objects showed relatively greater activity in the left lingual gyrus, and attending to the local aspect showed relatively greater activity in the right inferior occipital cortex.

As the present findings suggest a hemispheric reversal of our previous results, we assessed their significance. First, we compared rCBF changes between the two hemispheres, testing for the significance of lateralization within the current study. The differences between hemispheres were significant (inferior occipital cortex: $p = 0.001$, z -value = 3.1; lingual gyrus: $p = 0.002$, z -value = 2.9). Second, we performed a *post hoc* analysis to explore the issue of content-related hemispheric reversal. We directly compared rCBF changes observed using object-based stimuli with those found using the identical experimental set-up, but with letter-based stimuli (large letters made of small letters). This analysis tests the significance of the reversal in relative hemispheric specializations between the two studies. The reversal in relative hemispheric specializations was significant (inferior occipital cortex: $p = 0.001$, z -value = 3.2; lingual gyrus: $p = 0.01$, z -value = 2.4).

In seven subjects, the individual pattern of activations was congruent to the group one. The remaining three subjects failed to show any significant striate or prestriate activation. Figure 3 shows images of one subject demonstrating rCBF increases in the left lingual gyrus during globally directed attention and in the right inferior occipital cortex during locally directed attention.

4. DISCUSSION

Relative hemispheric specialization for global and local processing is known to depend on the specific experimental setting, particularly the individual's 'attentional' set. This suggests the involvement and interaction of both 'bottom-up' (exogenous) and 'top-down' (endogenous) processes (Kinchla & Wolfe 1979; Robertson & Lamb 1991; Boles & Karner 1996). That relative stimulus size and relative spatial frequency influence behavioural and physiological findings during global and local processing (Sergent 1982; Hellige 1993) shows that 'bottom-up' (stimulus-driven) processes account, in part, for the observed hemispheric specialization. Studies of patients with temporal-parietal lesions (but without visual field defects) demonstrate increased reaction time for identifying global letters and poor delayed copying for global aspects of letters and of drawings of objects after right inferior parietal lesions; local aspects are similarly impaired after left posterior superior temporal gyrus lesions (Robertson *et al.* 1988; Robertson & Lamb 1991). These findings support the notion of 'top-down' modulation during global and local processing. They

also suggest that content-specificity for global and local processing is not obtained at the temporal-parietal level: in the delayed copying task, equivalent effects were obtained with both letters and objects after unilateral temporal-parietal damage.

The areas activated in the present study lie in the lingual gyrus, encroaching into the calcarine sulcus during global processing, and in the inferior occipital cortex during local processing. These activations involve similar anatomical regions to those identified in our study using letter-based stimuli (Fink *et al.* 1996), though the pattern of differential relative activations is now reversed across hemispheres. The local maximum within the area of activation associated with local processing falls towards the outer border of lower V3. The area activated during global processing comprises the left lingual gyrus (area V1/V2 and possibly V3) and encroaches into the left calcarine sulcus (at the boundary of V1 and V2) (Serenio *et al.* 1995; Shipp *et al.* 1995). It must be stressed that the differences between global and local processing are relative not absolute hemispheric differences. The respective homologous areas in the contralateral hemispheres also showed increases in relative rCBF associated with the respective tasks. However, such increases were not significant while the differential relative rCBF increases between hemispheres were statistically significant. The anatomically distinct areas of activation within the early visual processing system may 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 (Fink *et al.* 1996).

Three methodological issues require discussion before our results can be interpreted. The first concerns the spatial resolution of the method, the second concerns the reliability of the data, and the third issue concerns eye movements. It might be thought that the precision with which the local maxima are reported is not in keeping with the spatial resolution of the PET images (6 mm at full width half maximum, 16–20 mm after image smoothing). However, it is essential to distinguish between the spatial resolution of the image within a scan (6 mm), and the ability to distinguish between local maxima that come from different scans. It has been demonstrated that peaks from different scans can be distinguished if they are separated by only 2–3 mm (Fox *et al.* 1987; Shipp *et al.* 1995; Fink *et al.* 1997).

The issue of localization of the different areas is not the same as the issue of reliability of our data. In analysing the differences between globally and locally directed attention we used a criterion of $p < 0.05$, corrected for multiple non-independent comparisons. This strict criterion, which may produce false negatives, was adhered to as we were determined to avoid false positives. By contrast, the tests for laterality of asymmetries observed in the lingual gyrus and the inferior occipital cortex concerned specific voxels rather than the whole image space. Therefore, no correction for multiple comparisons was needed. This also applies

to the test between the two studies, which used identical equipment, image processing and data analysis, but different stimuli.

The third issue concerns why the experiment was conducted in free vision rather than with fixation. To include a fixation point would have produced a third hierarchical level. As a result, a further local level competing with the local level of the Navon figure would have been introduced and would potentially have interacted with the processing we wished to investigate.

What factors, then, explain the differential activation of early visual processing areas during global and local tasks? The classical view of 'Gestalt' psychology holds that the right hemisphere is primarily concerned with the perception of wholes, and the left hemisphere is concerned with constituent (local) elements (Bradshaw & Nettleton 1981). That the right hemisphere may be biased toward low spatial frequencies and the left hemisphere toward high spatial frequencies suggests that spatial frequency might account for hemispheric differences in global and local processing (Hellige 1993). The observed activations, in both this and our previous study (Fink *et al.* 1996), are not easily explained by differences in spatial frequency, because stimulus characteristics were constant across conditions. If spatial frequency was the sole determinant of hemispheric specialization in these studies, no 'flipping' of differential neural activations during the directed attention tasks would be expected to occur with a change in stimulus category (from letters to objects). Our finding of a reversal of hemispheric asymmetry in early visual cortex dependent on stimulus category questions the generalization that all relevant areas of the right hemisphere are concerned with the perception of 'wholes' across all categories of stimuli.

Putative alternative explanations for differential hemispheric activations in prestriate areas involve differences in eye movements between the two conditions. For example, analysis of the global stimulus could require more eye movements than the analysis of a constituent element. Likewise, differential activations in prestriate areas V2 and V3 might reflect differential eccentricity of gaze: letter-based tasks may provoke the initial deviation of eyes to the right, whereas object-based tasks may direct gaze to the left (Kinsbourne 1972). Kinsbourne's finding would not, however, explain why in our experiments, it is the more difficult (local) task that provokes greater left hemisphere prestriate activations for letters, but greater right hemisphere activations for objects. Indeed, the opposite would be predicted if the harder task resulted in a more pronounced deviation of gaze in the directions that Kinsbourne (1972) reported for verbal and non-verbal tasks. There is ample evidence from animal studies of oculomotor input into early visual areas (Trotter *et al.* 1996), but none, to our knowledge, that would help explain our current findings or those of Fink *et al.* (1996). In principle, differences in oculomotor behaviour (number and direction of saccades or slow drifts in gaze) in the different conditions might, of course, interact (or interfere) with our results. But we know of no well-motivated hypothesis that could

predict the interaction between stimulus type (letter or object) and level of representation (local or global).

We accordingly propose the following two-component model. First, the contrasting hemispheric activations in prestriate areas during global and local processing represent a 'top-down' (endogenous) effect of stimulus level. This attentional modulation of neural activity in early stages of visual processing takes place in the absence of a change in stimulus characteristics between the local and the global tasks (but dependent in our experiment on task instructions). Second, the current results, when compared with those in our previous study (Fink *et al.* 1996), suggest that the neural consequences in early visual cortex of attentional modulation underpinning hemispheric specialization for global and local processing are strongly influenced by stimulus category.

The hypothesis of category dependence is at variance with the assumption (derived from studies of unilateral lesions of temporal-parietal cortex) that the neural instantiation of local and global processing is content-neutral (Robertson & Lamb 1991; Halligan & Marshall 1994). Our findings suggest rather that local processing (the most demanding aspect of hierarchical stimuli) is undertaken by the hemisphere specialized for the stimulus category that is presented. Thus, when incongruent hierarchical letter stimuli are presented, local letters are processed by the left (language) hemisphere. When hierarchical object stimuli are presented, the right hemisphere (specialized for object recognition; McCarthy & Warrington 1990) processes the local objects. In a neutral context, the attentional system is by default set to global (Hellige 1993). We propose that hierarchically organized stimuli automatically engage local processing in the hemisphere specialized for the content of the task, and the other hemisphere remains in relatively global mode. Upon instruction to attend to either the global or the local level, 'top-down' processes enhance the level required (local or global) by the task demands of the experiment. This division of labour might reflect the fact that, all else being equal, local stimuli impose greater perceptual demands on the recognition system. Accordingly, it would make biological sense to assign difficult perceptual processing to the hemisphere specialized for the material to be processed.

Finally, we note that all the evidence from human lesions and direct cortical stimulations indicates that prestriate areas in the immediate vicinity of area 17 only process information from the contralateral visual hemifield (Zeki 1993). Thus a lateralized category-dependent effect on areas involved in the early stages of visual processing of global or local aspects of hierarchically organized stimuli (kept constant across conditions) reinforces previous reports that neuronal activity in early visual areas does not represent only the sensory attributes of retinal images, but also top-down influences of selective attention (Moran & Desimone 1985; Motter 1993; Heinze *et al.* 1994; Fink *et al.* 1996).

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REFERENCES

- Boles, D. B. & Karner, T. A. 1996 Hemispheric differences in global versus local processing: still unclear. *Brain and Cognition* **30**, 232–243.
- Bradshaw, J. C. & Nettleton, N. C. 1981 The nature of hemisphere specialization in man. *Behav. Brain Sci.* **4**, 51–91.
- Brown, H. D. & Kosslyn, S. M. 1995 Hemispheric differences in visual object processing: structural versus allocation theories. In *Brain asymmetry* (ed. R. J. Davidson & K. Hugdahl), pp. 77–97. Cambridge, MA: MIT Press.
- Fink, G. R., Halligan, P. W., Marshall, J. C., Frith, C. D., Frackowiak, R. S. J. & Dolan, R. J. 1996 Where in the brain does visual attention select the forest and the trees? *Nature, Lond.* **382**, 626–628.
- Fink, G. R., Frackowiak, R. S. J., Pietrzyk, U. & Passingham, R. E. 1997 Multiple non-primary motor areas in the human cortex. *J. Neurophysiol.* **77**, 2164–2174.
- Fox, P. T., Miezin, F. M., Allman, J. M., van Essen, D. C. & Raichle, M. E. 1987 Retinotopic organization of human visual cortex mapped with positron emission tomography. *J. Neurosci.* **7**, 913–922.
- Fox, P. T. & Mintun, M. A. 1989 Non-invasive functional brain mapping by change distribution analysis of average PET images of H₂¹⁵O tissue activity. *J. Nucl. Med.* **30**, 141–149.
- Friston, K. J., Ashburner, J., Frith, C. D., Poline, J.-B., Heather, J. D. & Frackowiak, R. S. J. 1995a Spatial registration and normalization of images. *Human Brain Mapping* **2**, 1–25.
- Friston, K. J., Holmes, A. P., Worsley, K. J., Poline, J.-B., Frith, C. D. & Frackowiak, R. S. J. 1995b Statistical parametric maps in functional imaging: a general linear approach. *Human Brain Mapping* **2**, 189–210.
- Halligan, P. W. & Marshall, J. C. 1994 Toward a principled explanation of unilateral neglect. *Cog. Neuropsychol.* **11**, 167–206.
- Heinze, H. J., Mangun, G. R., Burchert, W. *et al.* 1994 Combined spatial and temporal imaging of brain activity during visual selective attention in humans. *Nature, Lond.* **372**, 543–546.
- Hellige, J. B. 1993 *Hemispheric asymmetry: what's right and what's left*. Cambridge, MA: Harvard University Press.
- Kinchla, R. A. & Wolfe, J. 1979 The order of visual processing: 'top down', 'bottom up' or 'middle out'. *Percept. Psychophys.* **25**, 225–231.
- Kinchla, R. A., Solis-Macias, V. & Hoffman, J. 1983 Attending to different levels of structure in a visual image. *Percept. Psychophys.* **33**, 1–10.
- Kinsbourne, M. 1972 Eye and head turning indicates cerebral lateralization. *Science, Wash.* **176**, 539–541.
- Mazziotta, J. C., Huang, S. C., Phelps, M. E., Carson, R. E., MacDonald, N. S. & Mahoney, K. 1985 A non-invasive positron computed tomography technique using oxygen-15 labelled water for the evaluation of a neurobehavioral task battery. *J. Cereb. Blood Flow Metab.* **5**, 70–78.
- McCarthy, R. A. & Warrington, E. K. 1990 *Cognitive neuropsychology: a clinical introduction*. San Diego: Academic Press.
- Moran, J. & Desimone, R. 1985 Selective attention gates visual processing in the extrastriate cortex. *Science, Wash.* **229**, 782–784.
- Motter, B. C. 1993 Focal attention produces spatially selective processing in visual cortical areas V1, V2, and V4 in the presence of competing stimuli. *J. Neurophysiol.* **70**, 909–919.
- Navon, D. 1977 Forest before trees: the precedence of global features in visual perception. *Cog. Psychol.* **9**, 353–383.
- Robertson, L. C., Lamb, M. R. & Knight, R. T. 1988 Effects of lesions of temporal-parietal junction on perceptual and attentional processing in humans. *J. Neurosci.* **8**, 3757–3769.
- Robertson, L. C. & Lamb, M. R. 1991 Neuropsychological contributions to theories of part/whole organization. *Cog. Psychol.* **23**, 299–330.
- Sereno, M. I., Dale, A. M., Reppas, J. B. *et al.* 1995 Borders of multiple visual areas in humans revealed by functional magnetic resonance imaging. *Science, Wash.* **268**, 889–893.
- Sergent, J. 1982 About face: left-hemisphere involvement in processing of physiognomies. *J. Exp. Psychol. Human Perception Performance* **8**, 253–272.
- Shipp, S., Watson, J. D. G., Frackowiak, R. S. J. & Zeki, S. 1995 Retinotopic maps in human prestriate visual cortex: the demarcation of areas V2 and V3. *Neuroimage* **2**, 125–132.
- Silbersweig, D. A., Stern, E., Frith, C. D. *et al.* 1993 Detection of thirty-second cognitive activations in single subjects with positron emission tomography: a new low-dose H₂¹⁵O regional cerebral blood flow three-dimensional imaging technique. *J. Cereb. Blood Flow Metab.* **13**, 617–629.
- Talairach, J. & Tournoux, P. 1988 *Coplanar stereotaxic atlas of the human brain*. Stuttgart: Thieme.
- Tipper, S. P., Weaver, B. & Houghton, G. 1994 Behavioural goals determine inhibitory mechanisms of selective attention. *Q. J. Exp. Psychol.* **47** A, 809–840.
- Townsend, D. W., Geissbiller, A., Defrise, M., Hoffman, E. J., Spinks, T. J., Bailey, D. L., Gilardi, M.-C. & Jones, T. 1991 Fully three-dimensional reconstruction for a PET camera with retractable septa. *IEEE Trans. Med. Imag.* **10**, 505–512.
- Trotter, Y., Celebrini, S., Stricanne, B., Thorpe, S. & Imbert, M. 1996 Neural processing of stereopsis as a function of viewing distance in primate visual cortical area V1. *J. Neurophysiol.* **76**, 2872–2885.
- Zeki, S. 1993 *A vision of the brain*. Oxford: Blackwell Scientific Publications.

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