The influence of stimulus location on the brain activation pattern in detection and orientation discrimination
A PET study of visual attention


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Summary
This PET study concerns changes in regional cerebral blood flow (rCBF) associated with orientation discrimination tasks and with simple detection of the stimulus. The difference in rCBF between discrimination and detection represents the discrimination, or 'task', component of the response. We have examined how such differences are influenced by the position of the visual stimulus and also how they change when a peripheral distractor is added to a relevant central stimulus. We first determined the regions in which the task produced the main effect regardless of stimulus position or distraction with an additional stimulus. In these selected regions, we determined the interactions between task and stimulus position and the interactions between task and stimulus addition. Five regions were more active during orientation discrimination than during stimulus detection: the inferior occipital cortex, the right putamen, the superior parietal lobe, the anterior cingulate cortex and the left lower and the right upper premotor area. Stimulus addition interacted with task only in the lower premotor area. Interactions between the task and stimulus position occurred in the occipital and parietal cortex and in the putamen. When a central stimulus was presented instead of a peripheral one the difference between orientation discrimination and stimulus detection was significantly larger in the inferior occipital lobe and in the right putamen. Conversely, the difference between orientation discrimination and stimulus detection in the superior parietal lobe was significantly larger when a peripheral stimulus was presented instead of a central one.

Keywords: superior parietal lobe; inferior occipital lobe; orientation discrimination; visual attention; PET scan

Abbreviations: BA = Brodmann area; DETC = detection of a central stimulus; DETCP = detection performed with central and peripheral stimuli presented together; DETP = detection of a peripheral stimulus; EOG: electro-oculography; FWHM = full width half maximum; IDC = identifying the orientation of a central stimulus; IDC P = identifying the orientation of a peripheral stimulus; rCBF = regional cerebral blood flow

Introduction
Two previous PET studies demonstrated that two distinct types of attention, selective attention to stimulus features and visuospatial attention, activate dissociable brain circuits (Corbetta et al., 1991, 1993). Visuospatial attention involves the superior parietal lobe as well as superior frontal areas (Corbetta et al., 1993). Conversely, when subjects attend to the attributes of stimuli randomly distributed over the visual field, inferior and lateral occipital areas are activated rather than parietal or frontal regions (Corbetta et al., 1991). The aim of the current study was to assess the effects of combining feature-specific attention with peripheral attention. Subjects had to attend to the orientation of a grating or simply to
detect its appearance as quickly as possible. The main experimental manipulation consisted of changing the object's location. Peripheral allocation of attention is required in both detection and discrimination tasks when the stimulus is at 5° eccentricity but not when it is at the centre of the visual field, whereas only the orientation discrimination task requires selective attention for orientation. We tested two alternative hypotheses: first, when peripheral attention and attention to stimulus orientation are needed simultaneously, two distinct circuits may be activated in an additive way and we should find main task or position effects but no interaction between them. Secondly the circuit involved in orientation discrimination may change with changing stimulus locations and the network involved in peripheral attention may depend on the requirements for feature selection. According to that hypothesis knowledge of the regional activations arising during separate execution of these two functions might not allow one to deduce to what degree these regions will be activated during simultaneous execution of these functions. Specific regions would then show interaction effects between task and stimulus position in addition to main effects of task or position. We tested these two hypotheses by first locating the regions concerned with orientation discrimination regardless of stimulus position. Subsequently, we determined in which of these regions the rCBF responses depended on interactions between the task and stimulus position. We examined the interaction effects in only a limited set of voxels preselected on the basis of a prior orthogonal subtraction because this allowed us to restrict the number of multiple comparisons.

The peripheral attention required by our discrimination task differed conceptually from the attention studied in the spatial cueing paradigm of Corbetta et al. (1993) in that the latter can be considered as purely spatial selective attention or, in other words, attention towards ‘empty space’. In contrast, our task required directing attention towards an object whose location was manipulated. Selective attention is possible not only at the level of features or locations but also at the level of objects (Duncan, 1984; Vecera and Farah, 1994; Egly et al., 1994). The current study allowed us to assess how the functional neuroanatomy of attention to an object’s features is modulated by the object’s location.

A second variable which could interact with the type of task is the addition of a behaviourally irrelevant peripheral distractor to the central stimulus. A portion of neurons in areas VI, V2 and V4 respond differently to different grating orientations in the presence of competing stimuli compared with their response when the grating is presented in isolation (Motter, 1993). We examined the interaction between the type of task and stimulus addition following the same statistical approach as that applied to the interaction between the type of task and stimulus position.

All stimuli used in the present study consisted of gratings. Apart from position these simple stimuli differed in only one way, i.e. orientation. With appropriately controlled presentation of these stimuli, subjects can use only this single cue to make the discrimination. The use of simple stimuli and simple tasks has clear advantages in several fields of brain research (Orban et al., 1990; Vogels and Orban, 1994) including PET activation studies (Dupont et al., 1993). Complex visual stimuli may elicit cognitive processes beyond the explicit requirements of the task performed, complicating the interpretation of regional cerebral blood flow (rCBF) changes (Sergent, 1994). The simple stimuli we used in this study should reduce the occurrence of these inadvertent automatic processes.

### Methods

#### Subjects

Ten subjects aged 19–24 years participated. They were strictly right-handed, drug-free, had no neurological or psychiatric history, and had a normal brain MRI. The total radiation for each subject was <10 mSv. They gave their written informed consent in accordance with the Declaration of Helsinki. The experimental procedures were approved by the Ethical Committee of the Medical School, Katholieke Universiteit Leuven.

#### Stimulus characteristics

Stimuli were displayed on a PTC1426 screen (width, 13.6°; height, 9.70°) controlled by an ATARI TT microcomputer. The monitor was mounted above the scanner bed at an angle of 52° relative to the horizontal at a viewing distance of 114 cm.

The fixation point had a diameter of 0.17°. The central stimulus (Fig. 1A) was a square-wave grating with a spatial frequency of 2 cycles per degree and a mean luminance of 38 cd m\(^{-2}\) presented in a circular 2° diameter window. To prevent the use of cues other than orientation, the grating’s phase was randomly shifted. To avoid the appearance of jagged oblique edges, the grating was presented on a 50% noise background. The peripheral stimulus (Fig. 1B) had a diameter of 4° and was located on the horizontal meridian with its centre at 5° to the left of the fixation point. In a third stimulus condition, the central and the peripheral stimulus were shown simultaneously (Fig. 1C).

Due to limitations in size of the monitor which could be mounted above the scanner bed, the central stimulus and the fixation point had to be placed 3° to the right of the screen centre. Thus, in all experimental conditions, the subjects directed their gaze 3° to the right (at the fixation point or at the centre of the central stimulus). The gaze direction remained constant during the entire image acquisition time and was identical for all six experimental conditions. The peripheral stimulus was on the subjects’ left in terms of retinotopic and craniotopic coordinates.

#### Task characteristics

The subjects held a push button in each hand. In the orientation identification tasks they had to press the right
button with their right hand within 400 ms in response to a vertical grating and the left button with their left hand when the orientation of the grating was oblique. The first task was to identify the orientation of a central grating presented alone (IDC). The orientation was randomly set at vertical or oblique. In the second orientation identification task only the peripheral grating was shown (IDP). In the third identification task the central and the peripheral grating were presented simultaneously (IDCP) and the subjects responded to the orientation of the central grating. In IDCP, the orientations of central and peripheral stimuli were randomized independently. In 50% of the trials, the orientation cue provided by the peripheral grating was opposite to that of the central grating. The exposure time for all three identification tasks was 300 ms and the interstimulus interval was 550 ms. The fixation spot was shown during the interstimulus interval and it was turned off during central stimulus presentation.

The three detection tasks comprised one with the central stimulus alone (DETC), one with the peripheral stimulus only (DETP) and one with both central and peripheral stimuli, presented together (DETCP); subjects had to press both buttons within 200 ms of stimulus presentation. The stimulus was presented for 300 ms in these detection tasks with an interstimulus interval of 550±200 ms; the jitter in the interstimulus interval was introduced to reduce stimulus predictability.

In both identification and detection tasks, binaural auditory feedback was provided through earphones, with a low-pitched sound for a wrong response and a high-pitched sound for a correct one. One hundred trials were administered for each task. The performance score was calculated as the number of correct responses within the response window over the total number of trials.

The differences between conditions for sensory, cognitive and higher motor processes are listed in Table 1. Response selection during the identification tasks consisted of selecting the left or right hand depending on an external cue, while the detection task required a stereotypical bimanual response paced by the external cue. The DETCP task did not involve orienting to the central grating or attentional filtering because both the central and the peripheral distractor appeared at the same moment and therefore yielded converging information.

### Recording of eye movements

Horizontal eye movements were monitored with contact electrodes placed on the outer ocular canthi and a reference electrode placed between the eyes. To ensure detection of gaze shifts at the onset and the end of the task, subjects were required to read aloud a digit appearing at the fixation point just before and just after the task. Electro-oculographical (EOG) recordings were stored on disk. The EOG was

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**Table 1 Processes involved in the different task conditions**

<table>
<thead>
<tr>
<th></th>
<th>IDC</th>
<th>IDP</th>
<th>IDCP</th>
<th>DETC</th>
<th>DETP</th>
<th>DETCP</th>
</tr>
</thead>
<tbody>
<tr>
<td>Central visual stimulation</td>
<td>+</td>
<td>−</td>
<td>+</td>
<td>+</td>
<td>−</td>
<td>+</td>
</tr>
<tr>
<td>Peripheral visual stimulation</td>
<td>−</td>
<td>+</td>
<td>+</td>
<td>−</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Feature identification</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>−</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>Response selection</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>−</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>Attention directed centrally</td>
<td>+</td>
<td>−</td>
<td>+</td>
<td>+</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>Attention directed peripherally</td>
<td>−</td>
<td>+</td>
<td>−</td>
<td>−</td>
<td>+</td>
<td>−</td>
</tr>
<tr>
<td>Ignoring a peripheral distractor</td>
<td>−</td>
<td>−</td>
<td>+</td>
<td>−</td>
<td>−</td>
<td>−</td>
</tr>
</tbody>
</table>

IDC = identifying the orientation of a central stimulus; IDP = identifying the orientation of a peripheral stimulus; IDCP = identifying the orientation of a central stimulus in the presence of a peripheral distractor; DETC = detection of a central stimulus; DETP = detection of a peripheral stimulus; DETCP = detection performed with central and peripheral stimuli presented together.
calibrated using the fixation point and horizontal visually guided saccades of 2° and 4° amplitude.

Training session
Prior to the scanning session, subjects underwent two 1.5 h training sessions, during which they were trained on the identification as well as the detection tasks. During this training the vertical–oblique orientation difference was set for each subject individually and for each of the identification tasks. Starting with large orientation differences and long response windows, these task parameters were decreased in a stepwise manner dependent on the subject's performance. At the end of the training they performed all six experimental tasks at a level of ≥75% correct with, on average, an orientation difference of 6.4° (SD = 1.3) for the central stimulus and 18° (SD = 1.9) for the peripheral stimulus, with the response window set at 400 ms during discrimination and 200 ms during detection. The orientation differences for the central stimulus were larger in this study than those used in a previous study (Dupont et al., 1993), mainly to compensate for the shorter response times (400 ms instead of 600 ms).

Data acquisition
The brain was scanned in 2D mode with a PET scanner of the type ECAT931-08-12 (CTI, Knoxville, Tenn., USA) (voxel size was x = 1.878 mm, y = 1.878 mm, z = 6.75 mm; transaxial spatial resolution 8.5 mm full width half maximal (FWHM); axial spatial resolution 6.75 mm FWHM; axial field of view, 10.5 cm) (Spinks et al., 1988).

Preparatory phase
Contact electrodes were placed and earphones installed. The subject's head was immobilized with a thermally molded headholder and positioned parallel to the infero-orbitomeatal line using laser alignment beams. A rectilinear scan was taken for positioning. The subject then familiarized himself with the particular task conditions by performing each task once.

Image acquisition
A transmission scan with a germanium–gallium source was taken to correct for attenuation. The task order was pseudorandomized using a Latin square design. Each subject was scanned once in six different conditions. For each condition, 50 mCi 15O2-labelled H2O was injected over a period of 12 s and the task was started at the same instant as the injection. The acquisition began as soon as the intracranial radioactivity count rate rose sharply, i.e. 29±2 s after the onset of the task. The first 40 s of image acquisition were used for further analysis. An interval of at least 15 min separated two successive injections. The attenuation corrected data were reconstructed as 15 planes using filtered back projection with a Hanning filter of cut-off frequency 0.5 cycles per pixel. The brain tissue radiation count rate was used as a measure of rCBF.

Data analysis
Calculations and image manipulation were carried out on Sun SPARC computers (Sun Microsystems, Mountain View, Calif., USA) using ANALYZE image display software (BRU, Mayo Foundation, Rochester, Minn., USA). For statistical analysis, Statistical Parametric Mapping (MRC Cyclotron Unit, London, UK) version SPM95 was used.

Individual data
Images of all six conditions were available for each of the 10 subjects. The scans from each subject were realigned using the first image as a reference. They were stereotactically transformed to a standard template in the Talairach space. The procedure involved a 12 parameter affine (linear) and a quadratic (nonlinear) 3D transformation, followed by a 2D piece-wise nonlinear matching that allows for normalization at a finer anatomical scale (Friston et al., 1995a). Images were smoothed with a Gaussian filter of 20×20×12 mm³.

Group analysis
Data were analysed using a randomized block design with global brain activity as covariate of no interest fixed at 50ml dl⁻¹ min⁻¹ (Friston et al., 1995b). The final image resolution (FWHM) was x = 19.1 mm, y = 23.0 mm, z = 17.4 mm. The upper level of the search volume was anteriorly at z = 52 mm and posteriorly z = 48 mm. The lower level of the search volume was at z = 24 mm.

Main effect of task and interaction effect.
Four comparisons were made to address our principal question: in which of the areas/voxels showing a main effect of task does an interaction occur between task and stimulus position or between task and stimulus addition? In this context, if two contrasts are orthogonal, the probability used to reject the null hypothesis in a combined set of two contrasts is approximately equal to the product of the P values obtained in each of the contrasts (Fletcher et al., 1995). We selected the voxels showing both a main task effect (Z > 3.90; uncorrected P < 0.00005) and an interaction effect (Z > 1.66; uncorrected P < 0.05). The voxels surviving these two criteria have an overall significance of an uncorrected P < 0.000005, corresponding to a Z score of 4.65. These P values are not corrected for multiple non-independent comparisons because the correction procedure requires a Gaussian distribution of the Z map (Friston et al., 1995b) and the conjunction map does not fulfill that requirement.
Voxels with a main effect of task, i.e. the brain areas concerned with orientation discrimination, were defined by subtracting the sum of the responses to all three detection tasks from the sum of those to all three discrimination tasks \([\text{IDC}+\text{IDCP}+\text{IDP}-(\text{DETC}+\text{DETCP}+\text{DETP})]\). Subsequently, we determined in the resulting local maxima the interaction effect between task and stimulus position. The difference between discrimination and detection performed with a central stimulus was compared with the difference between discrimination and detection performed with a peripheral stimulus. Our analysis focused on rCBF increases so the comparison was performed in both directions \([\text{IDC}-(\text{DETC}+\text{DETCP}+\text{DETP})\text{ and (IDP}-(\text{DETP}) (\text{IDC}-(\text{DETC})]\). In order to determine the interaction effect between task and the presence of a peripheral distractor, the difference between discrimination and detection performed using a central stimulus was subtracted from the difference between discrimination and detection performed using a central plus a peripheral stimulus \([\text{IDCP}-(\text{DETCP})-(\text{IDC}-(\text{DETC})]\).

**Main effect of stimulus position or stimulus addition**

The \(P\) values obtained by the subsequent single subtractions are corrected for multiple non-independent comparisons (Friston et al., 1995b). With that procedure, a corrected \(P < 0.1\) means one false positive activation over 10 subtractions. This risk of an error means an acceptable compromise between specificity and sensitivity, especially when the regions activated are of \textit{a priori} interest. In the fifth and the sixth subtraction, the main effect of stimulus position at a corrected \(P < 0.1\) (\(Z > 3.90\)) was determined comparing the sum of the two tasks performed with only a central stimulus and the sum of the two tasks performed with only a peripheral stimulus \([\text{IDC}-(\text{DETC}+\text{DETCP}+\text{DETP})\text{ and (IDP}-(\text{DETP}) (\text{IDC}-(\text{DETC})]\). In the seventh subtraction, the main effect of stimulus addition at a corrected \(P < 0.1\) (\(Z > 3.90\)) was determined by subtracting the sum of the two tasks performed with a central stimulus from the sum of the two tasks performed with a central plus a peripheral stimulus \([\text{IDCP}-(\text{DETCP})-(\text{IDC}-(\text{DETC})]\).

**Additional subtractions**

Three additional subtractions were made to allow a statistical description of the functional profiles of the voxels selected in the subtractions mentioned above. These were between discrimination and detection performed with the central stimulus only, with the peripheral stimulus only and with the central plus peripheral stimulus, respectively.

**Results**

**Psychophysics**

The mean performance during scanning is shown in Table 2. A repeated-measures one-way ANOVA comparison between the performance scores in the six different conditions was not significant at a level \(P < 0.05\) \([F(4,36) = 1.57]\).

Horizontal saccades of \(\geq 2^\circ\) lay within the limits of detectability of the EOG for all subjects. Two bidirectional saccades were found in the IDCP condition of one subject. Another unidirectional EOG deflection was observed in the IDP of one subject, but no deflection was found at the end

**Table 3 Main effect of task**

<table>
<thead>
<tr>
<th>(x)</th>
<th>(y)</th>
<th>(z)</th>
<th>Difference in rCBF (ml dl(^{-1}) min(^{-1}))</th>
<th>(Z)</th>
</tr>
</thead>
<tbody>
<tr>
<td>R. lingual/fusiform gyrus border</td>
<td>30</td>
<td>-70</td>
<td>-4</td>
<td>2.08</td>
</tr>
<tr>
<td>R. fusiform gyrus</td>
<td>38</td>
<td>-70</td>
<td>-16</td>
<td>2.86</td>
</tr>
<tr>
<td>L. fusiform gyrus</td>
<td>-28</td>
<td>-76</td>
<td>-16</td>
<td>1.53</td>
</tr>
<tr>
<td>R. putamen</td>
<td>24</td>
<td>10</td>
<td>8</td>
<td>1.65</td>
</tr>
<tr>
<td>Medial superior parietal lobule</td>
<td>-2</td>
<td>-62</td>
<td>48</td>
<td>1.72</td>
</tr>
<tr>
<td>Anterior cingulate</td>
<td>-8</td>
<td>0</td>
<td>48</td>
<td>2.86</td>
</tr>
<tr>
<td>R. upper area 6</td>
<td>18</td>
<td>0</td>
<td>48</td>
<td>2.48</td>
</tr>
<tr>
<td>L. lower area 6</td>
<td>-50</td>
<td>-2</td>
<td>32</td>
<td>1.55</td>
</tr>
</tbody>
</table>

The second to fourth columns show the Talairach coordinates of the local maxima (in millimetres); \(x \neq 0\) at the midline (+/- = right/ left-sided); \(y = 0\) at the anterior commissure (+/- = anterior/posterior); \(z = 0\) at the AC-PC level (+/- = superior/inferior). The third column contains the mean rCBF difference, calculated as the difference between the sum of the three discrimination tasks and the sum of the three detection tasks divided by three; the fourth column contains the standard error of the difference; the fifth column contains the \(Z\) (significance) score. L. = left; R. = right.
Fig. 2 Maps of Z values showing the effect of task, i.e., showing the significance of positive differences in rCBF after subtracting the sum of the detection data from the sum of the identification data. The Z map is projected upon the mean MRI image. The subject's MRI image was first co-registered with the mean of his realigned PET images. The subject's mean PET image was then stereotactically transformed together with the subject's co-registered MRI. Finally, the mean of 10 normalized MRI was calculated. The colour code corresponds to the statistical significance: yellow for $Z > 3.10$; black for $Z > 3.90$ and white for $Z > 5.00$.

of the oculomotor trace, when the digit was read. All other traces were virtually identical to the fixation trace of the calibration. Thus, all 10 subjects had maintained fixation well.

Main effect of task and interaction effects

$$(IDC+IDCP+IDP)-(DETC+DETCP+DETP)$$

The main effect of the task was determined by subtracting the sum of the detection tasks from the sum of the discrimination tasks. A significant main effect was observed in six regions, listed in Table 3 and displayed in Fig. 2. In the right inferior occipital lobe, two activation peaks can be distinguished: one lies at the border between the lingual and the fusiform gyrus ($30,-70,-4$) and the other more laterally in the right ($38,-70,-16$) fusiform gyrus. The left fusiform gyrus ($-28,-76,-16$) is also activated. Subcortical activation occurred in the right putamen ($24,20,8$). A superior parietal activation site contained a medial local maximum ($-2,-62,48$; $Z = 3.98$) flanked by two minor activation peaks in the right ($22,-58,48$; $Z = 3.25$) and left superior parietal lobule ($-24,-58,48$; $Z = 3.76$). A frontal activation site consisted of the premotor cingulate area ($-8,0,48$) and the right upper Brodmann area 6 ($18,0,48$). A second frontal activation was localized in the left lower Brodmann area 6 ($-50,-2,32$).

$$(IDC-DETC)-(IDP-DETP)$$

These and other interaction effects are listed in Table 4. The rCBF differences between orientation identification and detection at the border between right lingual and fusiform gyrus, in the left fusiform gyrus and in the right putamen were larger when the tasks were performed with a central instead of a peripheral stimulus. The graphs are shown in Fig. 3A–C.

$$(IDP-DETP)-(IDC-DETC)$$

When tasks were performed with a peripheral instead of a central stimulus, the rCBF difference was larger only in the superior parietal lobule. This region, as mentioned above, consisted of a medial local maximum and two additional local maxima on the right and the left. An interaction effect was observed in the medial superior parietal lobule and also in the right superior parietal lobule but not in the left

[Image of Fig. 2 showing Z maps]
Table 4 Interaction effects

<table>
<thead>
<tr>
<th>(IDC–DETC)–(IDP–DETP)</th>
<th>x</th>
<th>y</th>
<th>z</th>
<th>Difference in rCBF</th>
</tr>
</thead>
<tbody>
<tr>
<td>R lingual/fusiform gyrus border</td>
<td>30</td>
<td>-70</td>
<td>-4</td>
<td>1.71</td>
</tr>
<tr>
<td>L. fusiform gyrus</td>
<td>-28</td>
<td>-76</td>
<td>-16</td>
<td>1.37</td>
</tr>
<tr>
<td>R putamen</td>
<td>24</td>
<td>10</td>
<td>8</td>
<td>2.15</td>
</tr>
<tr>
<td>Medial superior parietal lobule</td>
<td>-2</td>
<td>-62</td>
<td>48</td>
<td>-1.52</td>
</tr>
<tr>
<td>R superior parietal lobule</td>
<td>22</td>
<td>-58</td>
<td>48</td>
<td>-1.44</td>
</tr>
<tr>
<td>(IDC–DETCP)–(IDC–DETC)</td>
<td>-50</td>
<td>-2</td>
<td>32</td>
<td>1.05</td>
</tr>
</tbody>
</table>

The top part of the table shows the effect of changing the stimulus position (peripheral to central) on the task-related rCBF. The last row shows the effect of adding a peripheral distractor on the (central) task-related rCBF. See Tables 1 and 3 for abbreviations and details.

The graphs of the medial and the right parietal local maximum are shown in Fig. 4A and B.

(IDC–DETCP)–(IDC–DETC)
Only in the lower Brodmann area 6 (BA6) was the task-dependent rCBF increase (Table 4) during orientation identification larger when a peripheral stimulus was added to the central stimulus than when the central stimulus was presented in isolation. This is shown in Fig. 5.

Main effects of stimulus position or addition

(IDC+DETC)–(IDP+DETP)
Presentation of a central grating results in extensive bilateral occipital activation comprising the occipital pole, the lingual gyr and the inferior and middle occipital gyri. The activation peaks are listed in Table 5 and include the calcarine sulcus (−12,−100,−8) and bilaterally the lingual gyr (−24,−84,16 and 24,−92,−16). The left fusiform gyrus region mentioned above (−28,−76,−16) was significantly more active (Z = 6.69) during central than during peripheral stimulation but no significant main effect was observed in the aforementioned right fusiform peak (Z = 2.57), probably because the subtracted peripheral conditions with a grating in the left visual hemifield weakly activated the right but not the left extrastriate cortex. Neither was there any main effect of stimulus position at the aforementioned border between right lingual and fusiform gyr (Z = −0.09).

(IDP+DETP)–(IDC+DETC)
As shown in Fig. 6, a 4° diameter grating at 5° eccentricity in the left visual hemifield results in right-sided medial occipital activation near the crossing of the calcarine and the parietooccipital sulcus (16,−60,8). A significant rCBF increase is also observed in the left postcentral gyrus (−58,−14,24). A subthreshold activation was revealed in...
Fig. 4 Visualization of the interaction effect in the areas in which response to peripheral orientation discrimination is larger than would be expected from the response to peripheral stimulation or to orientation discrimination or from the mere addition of both responses. The interaction is visualized by the difference in slope between the lines. The code is identical to that in Fig. 3. In the left superior parietal lobe, the rCBF difference between IDP and DETP did not reach statistical significance (P > 0.01; Z = 2.98). No main effect of stimulus position was observed in the superior parietal lobe (P > 0.01) and neither was there any significant difference between IDC and DETC (P > 0.05), between IDCP and DETCP (P > 0.01) or between IDCP and IDC (P > 0.05).

primary visual cortex at 8,—86,0 (Z = 3.04), 14 mm anterior and at the opposite side of the striate peak caused by central stimulation. Due to smoothing, right-sided activation with peripheral stimulation probably partially overlaps with the right-sided activation due to central stimulation. This overlap cancels out in the comparisons between IDC + DETC and IDP + DETP and this explains the shift of the striate activation peak revealed by (IDC + DETC) — (IDP + DETP) towards the left side.

(IDC + DETCP) — (IDC + DETC)
The addition of a peripheral grating to a central grating leads to right-sided medial occipital activation, comprising the medial part of the right lingual gyrus, the calcarine and the cuneus. One of the local maxima lies in primary visual cortex (10,—90,0; 5.71), near the subthreshold activation revealed by (IDP + DETP) — (IDC + DETC) (8,—86,0). A second local maximum lies in the cuneus (—6,—90,12; 5.11).

Discussion
We have examined the rCBF activation pattern when peripheral attention and selective attention for an object’s features are needed simultaneously. We first determined the brain regions involved in orientation discrimination by subtracting the sum of the responses during detection tasks from the sum of those during orientation discrimination tasks. Significant activation occurred in the inferior occipital cortex, the right putamen, the superior parietal lobule, the premotor cingulate and the right and left lateral premotor cortex. We subsequently determined in which of these regions task and stimulus position interact. Such an interaction was observed in three regions: only in the superior parietal lobe was the task-dependent rCBF increase larger for tasks performed with a peripheral stimulus than when identical tasks were performed with a central stimulus. Conversely, in the left and right inferior occipital cortex and in the right putamen, the task-modulation was larger when the tasks were performed with a central instead of a peripheral stimulus. Finally, in lower BA6, the task-dependent rCBF modulation increased when a peripheral distractor was added to the central stimulus.

Changes in rCBF associated with different stimulus locations are not a consequence of differences in task difficulty or acquired skills (Raichle et al., 1994) since in our study the difficulty between tasks was matched for each individual and subjects were trained on all tasks beforehand. Due to the shorter response window in detection and the jitter used in the interstimulus interval, the performance was equal in the detection and the orientation identification tasks. Thus, the rCBF difference between these tasks was not due to non specific differences in arousal level either.
Table 5  *Main effect of stimulus position*

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<thead>
<tr>
<th></th>
<th>x, y, z</th>
<th>Differences in rCBF</th>
<th></th>
<th>Differences in rCBF</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>(IDC+DETC)-(IDP+DETP)</td>
<td></td>
<td>(IDP+DETP)-(IDC+DETC)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mean</td>
<td>SE</td>
<td>Z</td>
</tr>
<tr>
<td>Calcarine sulcus</td>
<td>-12,-100,-8</td>
<td>3.65</td>
<td>0.43</td>
<td>7.44</td>
</tr>
<tr>
<td>R. lingual gyrus</td>
<td>24,-84,-16</td>
<td>2.55</td>
<td>0.45</td>
<td>7.50</td>
</tr>
<tr>
<td>L. lingual gyrus</td>
<td>-24,-92,-16</td>
<td>4.92</td>
<td>0.55</td>
<td>5.39</td>
</tr>
<tr>
<td>R. calcarine/parieto-occipital crossing</td>
<td>16,-60.8</td>
<td>NS</td>
<td></td>
<td></td>
</tr>
<tr>
<td>L. postcentral gyrus</td>
<td>-58,-14.24</td>
<td>NS</td>
<td>1.50</td>
<td>4.40</td>
</tr>
</tbody>
</table>

This table shows the increases in the rCBF response when the stimulus position is changed regardless of task, i.e. pooling the detection and discrimination data. The left hand side shows responses which were larger with a central stimulus and on the right the peripheral stimulus was more effective. See Tables 1 and 3 for abbreviations and details. NS = not significant.

**The neural circuitry for stimulus detection and orientation identification in peripheral vision**

The parietal cortex was the only area where rCBF during orientation discrimination performed with a peripheral stimulus differed significantly from that during detection. The medial activation peak had the strongest task effect and the right-sided peak had the strongest interaction effect. This right-sided peak (22,-58,48) is very close to the right superior parietal focus (21,-61,50) reported by Corbetta *et al.* (1993) and is located near the superior bank of the intraparietal sulcus. As between-subject anatomical variability is high for this sulcus, the superior bank of the intraparietal sulcus may...
well have contributed to the signal in our group analysis. The graphs of Fig. 4A and B allow us to determine how the interaction effect in this area arose. First, parietal rCBF was not significantly increased when detection with a central stimulus was subtracted from orientation discrimination with a central stimulus. The absence of parietal activation confirms previous results from PET studies dealing with central orientation identification (Dupont et al., 1993) and with selective attention for shape, colour and speed (Corbetta et al., 1991). Furthermore, the absence of significant parietal activation in IDC–DETC also implies that the parietal activation is not due to the necessity of selecting a motor response (Deiber et al., 1991). If that were the case, a main effect of the task in the absence of an interaction between task and stimulus position would be expected, as we observed in the anterior cingulate and right upper premotor cortex in agreement with earlier studies (Dupont et al., 1993).

Neither can orienting of attention towards a peripheral stimulus fully explain the superior parietal functional profile. In DETP, attention is oriented towards the peripheral stimulus and nevertheless, superior parietal rCBF is even lower than in DETC (Fig. 4A and B). This decrease during detection contributes to both the main task effect and the interaction effect. Although it remains to be established which parietal subarea in monkeys corresponds to which parietal subdivision in humans, the rCBF decrease during detection of a peripheral stimulus is analogous to single neuron recording results in monkey area 7a; the neuronal activity in area 7a for validly cued locations is lower than for invalidly cued locations (Robinson et al., 1995). This mechanism may favour detection of new events. The single neuron results and the superior parietal rCBF profile in this study are in agreement with the theory of Posner et al. (1987) that the parietal lobule is not involved in simple reaction time tasks when a stimulus remains on a fixed peripheral location.

However, in contrast to prevailing views, superior parietal rCBF increased drastically when subjects performed a different task with the peripheral stimulus: it was significantly higher during orientation discrimination than during detection ($P < 0.001$). This interaction between stimulus position and task has not been previously described using functional anatomical techniques: Corbetta et al. (1993) investigated only detection, fixation and passive viewing, while in another PET study of visuospatial attention, visual form identification was compared with passive viewing (Heinze et al., 1994). Neither do we know of any similar effect described in single-neuron studies. Such studies demonstrated the influence of stimulus location (Motter and Mountcastle, 1981), stimulus relevance (Bushnell et al., 1981) and cueing (Robinson et al., 1995) in posterior parietal neurons but, to our knowledge, no report has suggested that superior parietal neuronal activity depends on the type of task performed with a peripheral, behaviourally relevant stimulus.

How do our findings relate to other neuroimaging studies on peripheral attention? As mentioned earlier, a nearly identical parietal region is activated when subjects have to detect sensorially cued peripheral targets appearing across changing locations (Corbetta et al., 1993). The two studies taken together indicate that the functional anatomy of purely spatial selective attention overlaps with that for attention to features of peripheral objects.

To what extent do our findings agree with previous PET investigations concerning attention to features of peripheral objects? When subjects perform a visual search task for single features no parietal activation occurs. However, a search task for a conjunction of features, strongly activates the parietal lobule (Corbetta et al., 1995). The attentional template (Desimone and Duncan, 1995; Duncan, 1996) used during visual search for single features is mainly based on feature-selection. Therefore, the absence of parietal activation can be explained by the absence of any location-based selection. However, searching for a conjunction of features using only feature selection is highly inefficient. In this sense, the conjunction data are reconcilable with our results: both indicate that pure feature-selection as such does not involve parietal cortex, whereas an additional need for attentive selection of either locations or of peripherally located objects does. Other paradigms studied with PET and closer to ours examined rCBF differences during shape discrimination of peripheral objects. In support of our findings, Woldorff et al. (1995) used a go/no-go task where targets were defined by their shape; they reported parietal activation during the active task when compared with passive viewing of identical stimuli. In contrast, Heinze et al. (1994) did not find any parietal activation in a similar paradigm where targets were defined as two identical false font shapes within either the left or the right visual hemifield. According to Posner et al. (1987), the parietal cortex is mainly involved in shifting attention and particularly disengaging attention. One could deduce from that theory and from the discrepancy between the studies mentioned that the experimental tasks differ in their need for attentional shifting. Attention may be directed towards the fixation point during the blank interval between successive stimuli and shift covertly to the peripheral stimulus as soon as it appears. These shifts may be more frequent in peripheral discrimination than in detection, e.g. because feature selection requires more focused attention than detection does. So why would this lead to parietal activation in our study and not in that of Heinze et al. (1994)? In our own study, the interval between successive trials was fixed at 550 ms. However, in the study of Heinze et al. (1994) it was randomized and ranged between 250 and 550 ms which may have favoured allocation of attention to an ‘empty space’. So, the interaction between task and object location in our study might be a special case of attentional shifting. Alternatively, the stimulus duration in the study of Heinze et al. (1994) was 100 ms compared with 300 ms in our own and, in that study, subjects had to compare between shapes. If the superior parietal lobule is involved in feature selection concerning objects on one fixed peripheral location (Vandenberge et al., 1995) maintained attention may be more pronounced with longer stimulus duration. Parietal involvement in the later stages of
maintained attention has been demonstrated electrophysiologically (Yamaguchi et al., 1994). Furthermore, in addition to different time-courses of stimulus presentation, the requirements for feature selection may have been higher during our study as the orientation differences were adapted prior to the experiment in order to be close to the perceptual threshold for each individual. Only further research will allow us to distinguish between these possibilities.

The neural circuitry for stimulus detection and orientation identification in central vision

Blood flow in three inferior occipital areas increases during selective attention for stimulus orientation: the right lingual/ fusiform gyrus, the right fusiform gyrus and the left fusiform gyrus. One of these areas (30, -70, -4) has almost identical coordinates as the possible homologue of V4 defined by Zeki et al. (1991) (26, -68, -8); they subtracted the results of passive viewing of an isochromatic display from those during passive viewing of a coloured display. The fusiform gyrus peaks (38, -70, -16 and -28, -76, -16) are near the active regions observed by Heinze et al. (1994) (27, -77, -14 and -28, -73, -14) when comparing attention for shape with passive viewing. The task-effect predominantly occurred in the right hemisphere in agreement with our earlier studies on central orientation discrimination (Dupont et al., 1993). The task-dependent effects in occipital cortex are stronger than in our earlier orientation discrimination study (Dupont et al., 1993) and this may have been due to higher task demands caused by the shorter response windows and shorter stimulus presentation times in the current study (for similar effects in language experiments see Price et al., 1994).

The rCBF increase during selective attention for orientation is in line with physiological studies of the ventral pathway in monkeys. Where fine discrimination of stimulus orientation is required, the neuronal responses in V4 are enhanced (Spitzer et al., 1988). Conversely, neuronal activity in inferotemporal cortex is attenuated when detection is compared with a feature identification task (Richmond and Sato, 1987). Analogous to these studies, the rCBF increase in the subtraction between identification and detection may reflect rCBF increase (enhancement) during feature identification or rCBF decrease (attenuation) during detection. The interaction effect may indicate that neurons with a foveal receptive field are more susceptible to attentional modulations than neuronal populations with extrafoveal receptive fields or that these neurons are more susceptible to attenuation during the detection.

Equally relevant is the absence of any interaction between task and stimulus position in the right fusiform gyrus. This suggests that it is involved in orientation discrimination of both central and peripheral stimuli.

No modulation was observed in occipital sites when a distractor was added. This can be interpreted in the framework of the competitive integration model (Desimone and Duncan, 1995; Duncan, 1996): the ventral visual system is biased towards objects in the centre of the visual field as there are many more neurons with central than with peripheral visual receptive fields. This central predominance in occipital cortex is also obvious in Fig. 6. As bottom-up biases already lend the central stimulus a strong competitive bias, top-down attentional modulation may be unnecessary for favouring the central stimulus; this could explain both the absence of any effect of a distractor in the ventral occipital cortex and the very weak effect of it in the superior parietal lobule (Fig. 4B). Similarly, the absence of an interaction between stimulus position and task in the right fusiform gyrus may be due to top-down attentional control counteracting these bottom-up biases.

Extra-visual areas with an interaction effect between stimulus position/addition and task

Blood flow in the right putamen was increased during orientation discrimination with respect to detection only when tasks were performed with a central stimulus but not with a peripheral stimulus. Its activation during central orientation discrimination compared with detection is in agreement with earlier studies (Dupont et al., 1993). Visually responsive neurons (Caan et al., 1984) and projections from area TE (Saint-Cyr et al., 1990) have been demonstrated in the monkey's putamen. We can only speculate on the origin of the interaction effect.

Equally unexpected is the profile of activation in lower BA6: the difference between discrimination and detection is larger in the presence of a peripheral distractor. In the monkey the lower BA6 contains visually responsive neurons and a representation of external space (Gentilucci et al., 1988). Moreover, when a visual cue in one of the four visual field quadrants indicates to which of the quadrants to attend (mnemonic attentional cue), and is then followed by an identical type of visual cue indicating in which direction to move (intentional cue), a larger portion of ventral premotor neurons are activated after the mnemonic attentional cue than after the intentional cue. The dorsal premotor cortex shows the converse relationship (Boussaoud and Wise, 1993). This supports the evidence obtained from monkey studies (Rizzolatti et al., 1983) and from this human brain mapping study that lower premotor cortex has a role in covert attention. The neurophysiological and PET result also suggest that this involvement in covert attention may be more pronounced when there is competition for attention between locations or objects.

Hypothetical anatomical model

We did not statistically model modifications of connectional strengths between areas as a function of changes in stimulus position (McIntosh et al., 1994). Two rules may none the less allow us to pose a hypothetical anatomical model...
The difference between discrimination and detection is greater with central stimulation while the occipital areas, the difference between discrimination and detection is identical for both locations. The activation site at the crossing of the calcarine and the parieto-occipital sulcus which was more pronounced for peripheral as opposed to central stimulation may serve as a relay station between striate and superior parietal cortex, analogous to the parieto-occipital area in monkeys which has a relatively large representation of the peripheral field (Galletti et al., 1991; Distler et al., 1993) and one of the major relay stations between monkey striate and superior parietal cortex (Andersen et al., 1990). The superior parietal contribution to feature identification of peripheral stimuli could lie in the processing of specific features of peripheral objects as such, but very little neurophysiological support exists for such a hypothesis; orientation processing is probably mainly performed in the ventral occipital cortex even when objects are located in the periphery. A good candidate is the right fusiform gyrus which has a weak position effect (central greater than peripheral) and which is the only occipital area with a main task effect and no interaction effect. So what does the parietal cortex contribute to selective attention for features of peripheral objects? According to one hypothesis, which is partially based on single-neuron studies (Motter, 1993), the superior parietal cortex has a weak position effect (central greater than peripheral) and which is the only occipital area with a main task effect and no interaction effect. So what does the parietal cortex contribute to selective attention for features of peripheral objects? According to one hypothesis, which is partially based on single-neuron studies (Motter, 1993), the superior parietal lobule contributes to selective attention for features of peripheral objects as such, but very little neurophysiological support exists for such a hypothesis; orientation processing is probably mainly performed in the ventral occipital cortex even when objects are located in the periphery.

**Conclusion**

In this study, we examined what happens when two functions, visuospatial attention and attention to perceptual attributes, are summoned up at the same time. Our results are in accordance with the model of an interactive brain (Farah, 1994) in which the circuits are not simply activated in an additive way. Instead, the components of the circuitry for orientation discrimination are recruited differently according to the position of the stimulus. In ventral occipital areas and putamen, rCBF differences between discrimination and detection are higher when central stimuli are used. In contrast, superior parietal rCBF differences after subtracting detection from discrimination are higher when peripheral stimuli are used. This implies that the superior parietal role in orienting of attention depends on the specific task performed with the peripheral stimulus.
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