We used positron emission tomography (PET) to investigate the neural correlates of selective attention in humans. We examined the effects of attending to one side of space versus another (spatial selection) and to one sensory modality versus another (intermodal selection) during bilateral, bimodal stimulation of vision and touch. Attention toward one side resulted in greater activity in several contralateral areas. In somatosensory cortex, these spatial attentional modulations were found only when touch was relevant. In the intraparietal sulcus, spatial attentional effects were multimodal, independent of the modality attended. In occipital areas, spatial modulations were also found during both visual and tactile attention, indicating that tactile attention can affect activity in visual cortex; but occipital areas also showed more activity overall during visual attention. This suggests that while spatial attention can exert multimodal influences on visual areas, these still maintain their specificity for the visual modality. Additionally, irrespective of the attended side, attending to vision activated posterior parietal and superior premotor cortices, while attending to touch activated the parietal operculi. We conclude that attentional selection operates at multiple levels, with attention to locations and attention to modalities showing distinct effects. These jointly contribute to boost processing of stimuli at the attended location in the relevant modality.

Introduction

In an environment that provides us with many competing sensory inputs, an important goal for the brain is to filter out irrelevant information and select the appropriate stimuli to guide behaviour. Endogenous attention allows us voluntarily to select subsets of the sensory input and enhance the perception of just these attended stimuli (Desimone and Duncan, 1995; Pashler 1998). In recent years, the use of neuroimaging techniques has begun to reveal the physiological basis of selective attention in humans (Corbetta et al., 1991; Heinze et al., 1994; Tzourio et al., 1997; Kastner et al., 1999; Hopfinger et al., 2000; Driver and Frackowiak, 2001). In a typical imaging experiment on selective attention (Heinze et al., 1994), subjects are presented with several stimuli simultaneously and are required to attend some of these (targets), while ignoring the others (distractors). Brain activity is measured while subjects attend to one subset of items compared with activity when attention is focused on a different set of stimuli during the same stimulation. Such studies have shown that selective attention modulates activity in brain areas that represent the attended stimuli, including sensory areas. Most of the previous studies of this type employed targets and distractors in the same sensory modality, with selective attention thus operating intramodally. Intramodal selection can be based on many different attributes of the sensory input, such as colour or motion-direction during visual stimulation (Corbetta et al., 1991) and roughness or duration during tactile stimulation (Burton et al., 1999). In studies of spatial selective attention, the position of the stimuli is the critical stimulus attribute for selection, distinguishing targets and distractors. Heinze et al. (Heinze et al., 1994) provide a prototypical example for the visual modality. Subjects were presented bilaterally with visual symbols in the left and right hemifields. In different blocks, covert attention was sustained to one side or the other to perform a perceptual discrimination on stimuli just at the attended location. Brain activity was directly compared for covert attention to one side versus the other side, revealing increased blood flow in occipital areas contralateral to the attended side. This demonstrates modulation of activity in sensory cortical regions that respond to stimulation at the attended location. Similar results have since been obtained within audition, or within touch. For example, Tzourio et al. (Tzourio et al., 1997) used binaural presentations in a purely auditory study. Comparison of brain activity during attention to sounds at the left versus right ear revealed modulations in contralateral auditory cortex [see also (Alho et al., 1999)]. We recently demonstrated analogous modulation by tactile selective attention within the somatosensory system (Macaluso et al., 2000). In different blocks subjects attended either the left or the right hand during bilateral tactile stimulation. When activity in these two conditions was compared, we found increased blood flow in the contralateral postcentral gyrus. Overall, these results suggest that when two stimuli in the same modality are presented simultaneously in opposite hemifields, intramodal selective attention to one side results in modulation of contralateral sensory-specific areas.

Fewer functional imaging studies have investigated the neural correlate of intermodal selective attention, whereby one sensory modality versus another is selected. Here the critical question concerns the effect of attending to one modality or another during multimodal stimulation. An early pioneering study (Roland, 1982) used trimodal stimulation, presenting visual, tactile and auditory stimuli simultaneously. Subjects were asked to attend just one modality to perform a discrimination task within it. Blood flow was monitored using $^{133}$Xe-injection and a low resolution positron emission tomography (PET) camera. The results provided the first demonstration that selective attention can modulate activity in brain regions that process stimuli in a particular modality. Similarly, Frith and Friston demonstrated modulation of visual cortex when attention was directed toward the visual stream versus to sounds, during bimodal audio-visual stimulation (Frith and Friston, 1996), although this study did not find any corresponding modulation of auditory areas for attention to the sound. The latter effects were successfully detected in a more recent study (Kawashima et al., 1999), which also used simultaneous audio-visual stimulation [see Eimer and Schröger (Eimer and Schröger, 1998) for related effects of intermodal selective attention using ERP methods]. In the present study we combined both intermodal and intramodal attentional selection within a single experimental...
paradigm, during PET scanning. Our subjects received bilateral and bimodal visuo-tactile stimulation. In different blocks, they attended one particular side and one particular modality. This approach allowed us to ask several new questions. First, the contralateral modulations previously observed in unimodal experiments concerning spatial attention (Heinze et al., 1994; Hopfnger et al., 2000), might affect activity in similar or different sensory-specific areas to the intermodal modulations observed for selective attention to one modality versus another during multimodal stimulation (Kawashima et al., 1999; Downar et al., 2000), but any such overlap has never been tested directly within a single imaging study. A design which contains both spatial selection and modality selection within the same experiment could reveal any overlap or differences between the two types of attentional effects.

Second, in a recent PET experiment (Macaluso et al., 2000), we demonstrated that effects of spatial attention for vision and for touch have both unimodal and multimodal components. Unimodal spatial effects were found in modality-specific areas (e.g. superior occipital gyrus for vision and postcentral gyrus for touch), while multimodal spatial effects were located in the intraparietal sulcus (a polysensory association region). A potentially interesting finding was that the same study also showed that sustaining tactile attention toward one hemifield resulted in modulation of contralateral visual areas. This provided some initial evidence that endogenous spatial attention may be allocated on a multimodal basis (Driver and Spence, 1998; Eimer and Schröger, 1998), affecting both multimodal and unimodal brain areas. But this raises the question of how visual areas can maintain selectivity for visual input at the attended location. The combined engagement of intramodal and intermodal selective attention within a single study, as in the present design, could reveal the mechanisms underlying this.

Finally, our design included baselines conditions that should allow us to highlight any brain areas engaged during selective attention to peripheral stimuli, independently of which side was attended and which sensory modality was attended. Any such areas would provide possible candidates for controlling spatial attention across sensory modalities, providing a possible source for any multimodal spatial attentional modulations.

**Methods and Materials**

**Subjects**

Nine volunteers participated in this study. All were right-handed males (mean age 27 years, range 24–38). None had a psychiatric or neurological history. After explanation of the experimental procedures, subjects gave informed written consent. The work was approved by the Joint Ethics Committee of The Institute of Neurology and The National Hospital for Neurology and Neurosurgery.

**Paradigm**

Subjects were tested in a 2 × 2 factorial blocked design, during bimodal (visuo-tactile) stimulation that was bilateral for both modalities, with both sides and both modalities being stimulated at the same time. One factor was the covertly attended side: left or right. The second factor was the attended modality: vision or touch. There were also two baseline conditions. In both baseline conditions, subjects performed a central detection task that controlled for the response requirements of those conditions involving peripheral attention to one or the other side. During one ‘stimulation’ baseline, the subjects also received the (now unattended) bilateral–bimodal peripheral stimulation; in the other, no peripheral stimulation was delivered. The six conditions will be referred to as follows: attend vision–left (VL), vision–right (VR), touch–left (TL), touch–right (TR), central task with unattended peripheral stimulation (US) and central task with no peripheral stimulation (NS). All six conditions were replicated twice, with the order counterbalanced within and across subjects.

**Stimuli**

While lying in the scanner, the subject held onto a plastic handle with each hand, 25° to the left or right of the midline. Inside each handle there was a solenoid (12 V) which could deliver tactile stimulation to the thumb. Directly visible to the subject, an LED (10 mm in diameter) was attached just in front of each thumb. This setup allowed presentation of visual and tactile stimulation at closely similar locations on each side. The thumbs were restrained on the fixed plastic handle with Velcro to ensure contact with the tactile stimulator throughout. A central fixation point was displayed on a computer screen.

In the four main experimental conditions (TL, TR, VL, VR) and also the US blocks, the stimulation was always bimodal and bilateral: flashing red lights on both sides together with 30 Hz vibrations on both thumbs. Each block of stimulation comprised a 2 min sequence of events. Single pulses (150 ms on) or double pulses (150 ms on, 150 ms off, 150 ms on) were presented on each side and in each modality. The sequences were random with a 3:1 ratio of single to double pulses. There was one event in each modality and each side every second. The random order of single and double pulses was independent in the two hemispheres and two modalities. Double pulses on the attended side, in the attended modality only, served as targets for overt responses (see below).

A grey cross in the centre of the computer screen was used as a fixation point. During all conditions, at unpredictable intervals this fixation cross became brighter for 50 ms. These constituted the targets for the baseline (US and NS) conditions. The occurrence of these brightness increments was independent of the timing of the stimuli delivered in the periphery, but matched the frequency of the double pulses in each of the peripheral streams (i.e. occurring 30 times during each 2 min block). This ensured that the same number of overt responses was produced at the same rate during all the conditions of attention to one side and also during the two baseline tasks.

**Task**

During the four conditions of covert attention to peripheral stimulation on one side, the task was analogous irrespective of attended side or modality. As instructed before each scan, subjects sustained covert attention to the stimuli in only one hemifield and only one modality, to detect double pulses in that stream, while ignoring all distractor events (e.g. single and also double pulses in both modalities) presented in the other hemifield, or on the same side but in the unattended modality. When a target double pulse occurred at the attended location and in the attended modality only, the subjects had to respond by quickly saying ‘bip’. Single pulses in the attended hemifield and attended modality did not require any response. During the conditions of peripheral attention to one or other side, the occasional brightening of the fixation point was to be ignored.

During the two baseline conditions, subjects were asked to concentrate only on the fixation point and to detect changes in its brightness level. Again, the response was verbal: quickly saying ‘bip’ whenever the central brightening occurred. This control task was introduced to eliminate any trivial activations related to the production of overt vocal responses when we tested for common activations in all four conditions of peripheral covert attention.

**Monitoring Adherence to the Central Fixation Instruction**

Eye position was recorded with a CCD camera placed below the computer screen, in front of the subject. An infrared LED was directed towards the eye to ensure a good image, while leaving the subject in darkness. Inspection of the video recordings indicated that subjects did not systematically saccade towards the targets on one or the other side (these were located at 25° of eccentricity) and that they were following the instruction to maintain central fixation. This non-automated technique did not allow us to quantify eye position, but it ensured a good qualitative assessment, permitting easy identification of leftward and rightward saccades that subjects were asked to make at the beginning and at the end of each 2 min scanning block. Future studies could use computerized eye-monitoring procedures to provide quantitative analysis of eye position.
While overt visual orienting (i.e. deviations in the direction of gaze) was monitored by the video throughout each scanning block, one should also consider whether overt tactile orienting (by hand movement) could have arisen, to modify the intensity of the tactile stimulation, depending on the instructions of attending one side and one modality. We sought to avoid this by restraining the subject’s thumbs to the stimulation apparatus throughout with Velcro. In addition, the PET results indicate that the critical modulations for tactile attention were in somatosensory areas and not in motor areas (see Results). However, future studies should consider monitoring muscle activity during tactile attention using electromyography (EMG), or by placing pressure sensors between the stimulated site and the stimulating device.

Acquisition of rCBF Data

PET scans were performed with a CTI Exact HR+ (CTI Inc., Knoxville, USA) 32-slice scanner, with retracted collimating septa covering a field of view of 15.5 cm. Subjects received an intravenous bolus of $^{15}$O infused over 20 s, followed by a 20 s saline flush. There were 12 successive administrations of $^{15}$O, each separated by 8 min. Images were reconstructed with a Hanning filter of 0.5 cycles/pixel, full width at half maximum (FWHM) 6.5 mm. Data were acquired in a 90 s scan frame after injection of $^{15}$O. Each condition (i.e. stimulation and task) began 20–30 s before image acquisition and continued for 2 min. Total counts per voxel during the build-up phase of radioactivity served as an estimate of rCBF (Mazziotta et al., 1985; Fox and Mintun, 1989).

Analysis of the rCBF Data

To facilitate intersubject pooling, the rCBF data were realigned, spatially (stereotactically) normalized and smoothed. The scans of each subject were realigned using the first as reference. The six parameters (three translations and three rotations) of this rigid body transformation were estimated using a least-squares approach (Friston et al., 1995). Normalization parameters to the Montreal Neurological Institute (MNI) standard space (Collins et al., 1994) were estimated using the mean of the PET images. As a final pre-processing step, the images were smoothed using an isotropic Gaussian kernel (FWHM of 16 mm).

The data were analysed using Statistical Parametric Mapping (SPM99, www.fil.ion.ucl.ac.uk). The effects of condition, subject and global flow effects were estimated according to the general linear model using the SPM software (SPM). The SPM(t) values were transformed to the unit normal distribution, SPM(Z).

Our design sought to investigate several types of selective processing in relation to endogenous attention: the effects of spatial attention to one hemifield versus another (with separation of unimodal spatial effects, found only when attending one modality, versus multimodal spatial modulations, found regardless of the attended modality); the effects of intermodal attention to one modality versus another (irrespective of the attended side); and the overall effect of peripheral attention to one or other side versus attending to the central fixation point (independently of the side or modality attended). We used a set of criteria to isolate specific patterns of activation corresponding to these effects of interest. The multiple criteria all consisted of a main comparison (used to assign Z-values and to locate the activation peaks), plus a set of additional constraints that ensured that any activated area conformed to the specific pattern of activity required. Note that our use of multiple criteria can only make our analyses more conservative. A small volume correction procedure was used (Worsley et al., 1996) to determine statistical significance and to assign corrected P-values to the voxels we report. This procedure corrects for the number of voxels tested within a prespecified volume, rather than for all the voxels in the imaged volume (i.e. the whole brain in our case). For the present experiment, spheres 16 mm in radius (the same size as the spatial smoothing kernel) were used to define volumes of interest. These were centred according to previous results (Macaluso and Frith, 2000; Macaluso et al., 2000), which provide data sets that are independent of the present study. Any activation outside these predicted regions is reported only if it survived correction for multiple comparisons when considering the whole brain as the search volume.

Spatial Selective Attention

Spatial attentional modulations can be divided into unimodal spatial effects (modulation depending on the attended side, but only when one specific modality was attended), versus multimodal spatial effects (areas showing effects of attended side independently of the attended modality). In order to separate these specific patterns of activation we employed criteria previously introduced (Macaluso et al., 2000). Unimodal effects were detected by testing for a simple effect of attended side during attention to one modality [for vision, (VL) > (VR) or (VR) > (VL); for touch, (TL) > (TR) or (TR) > (TL), initial threshold set at $P_{uncorrected} = 0.001$], with all voxels passing this first criterion also required to show an interaction between attended side and attended modality (at $P_{uncorrected} = 0.05$). Multimodal effects were detected by testing for a main effect of attended side [(VL + TL) > (VR + TR); or (VR + TR) > (VL + TL), initial threshold set at $P_{uncorrected} = 0.001$], with the additional constraint that voxels passing this criterion also had to show a simple effect of attended side within both modalities (for attend left: (VL) > (VR) and (TL) > (TR); or for attend right: (VR) > (VL) and (TR) > (TL), at $P_{uncorrected} = 0.05$). These multiple criteria were applied voxel-by-voxel, resulting in SPM maps that included the whole brain, with a Z-value and an uncorrected $P$ value associated to each voxel. As described above, corrected $P$ values were subsequently assigned using spheres centred at the maxima of the spatial attentional effects we previously reported (Macaluso et al., 2000), or in symmetric regions for the opposite hemisphere. Hence, our predictions about the expected location of any given effect were used to reduce the search volume from the total number of voxels in the whole brain, to the few thousand voxels contained in our 16 mm radius spheres (Worsley et al., 1996). These spherical search volumes were in the superior occipital gyrus, occipito-temporal junction, intraparietal sulcus and superior postcentral gyrus.

Intermodal Selective Attention

The effect of attending to one modality versus the other modality was highlighted using the main effect of attention to vision versus attention to touch, or vice versa, pooling across conditions of spatial attention to the left and right side [for attending vision, (VL + VR) > (TL + TR); for attending touch, (TL + TR) > (VL + VR), initial threshold set at $P < 0.001$]. Additionally, we constrained this analysis to areas that also showed a modulation during peripheral attention in either vision or touch, as compared with the baseline of unattended peripheral stimulation [for attending vision, (VL + VR) > 2*(US); for attending touch, (TL + TR) > 2*(US), at $P < 0.05$]. This latter criterion ensured that any reported area was indeed boosted when peripheral stimulations in one modality were attended. Just as for the spatial attentional effects, small volume correction was then used to assign corrected $P$ values. For the main effect of attended modality, the search volumes were centred according to the main effects of sensory stimulation reported in our previous visuo-tactile study, where only one modality was stimulated bilaterally at a time (Macaluso et al., 2000). These fell in the superior occipital gyrus, occipito-temporal junction and superior parietal gyrus for vision, and the superior postcentral gyrus and parietal operculum for touch.

Overall Effect of Peripheral Attention

To highlight the overall effect of attending covertly to peripheral stimuli on either side versus attending at central fixation, we compared the four conditions of peripheral attention (i.e. attend left or right in vision or touch) versus the central task (i.e. attend both sides), and tested for a main effect of peripheral attention [(VL + VR + TL + TR) > 4*(US), initial threshold set at $P < 0.001$]. Additionally, we checked that every single condition of peripheral attention activated above baseline [(VL > US) and (VR > US) and (TL > US) and (TR > US), all at $P < 0.05$]. Corrected levels of significance were established according to search volumes centred in line with our previous results (Macaluso and Frith, 2000), where sustained peripheral visual attention had been compared with a central fixation baseline. These volumes fell in the intraparietal sulcus, medial frontal gyrus, inferior and superior premotor cortex, superior temporal sulcus and cerebellum.
Results

Behavioural Performance
In the four conditions of peripheral attention to one side, the percentages of correct discriminations (i.e. correct vocal responses to double pulses) were: 87% for VL, 82% for VR, 74% for TL and 78% for TR. Means (SEM) of the reaction times were 508 (38) ms for VL, 509 (36) ms for VR, 530 (35) ms for TL and 526 (31) ms for TR. A two-way ANOVA on the reaction times found no significant effect of attended side ($P > 0.85$) and no interaction between side and attended modality ($P > 0.66$). Nevertheless, a weak effect of attended modality was present ($P < 0.03$), with vision yielding somewhat faster performance than touch overall. Reaction times for the central detection task at fixation were 537 (33) ms (93% correct detection) for the condition with peripheral stimulation (US) and 552 (32) ms (91% correct detection) for the baseline without peripheral stimulation (NS).

PET Data
Our design allowed us to ask three main questions. First, comparing attention to the left versus right hemisphere, and vice versa, should reveal any modulatory effects of selective spatial attention. Assessing this for both modalities should allow us to separate unimodal versus multimodal effects of this kind. Second, direct comparison of all conditions of peripheral visual attention versus tactile attention (and vice versa) should reveal the neural correlate of intermodal selection of one sensory modality versus another during bimodal stimulation, which we can then compare with the neural substrate of any spatial-attention effects. Finally, subtraction of the central task employed during baseline from all conditions of peripheral attention should highlight any brain regions involved in sustaining spatial attention to peripheral stimulation on either side, independently of attended modality and hemisphere.

Spatial Selective Attention
Spatial attentional modulations were investigated by directly comparing attention to one side versus attention to the opposite side during the same bimodal stimulation. Importantly, the use of two modalities within the same experiment allowed us to differentiate between areas that were modulated only when attention was directed toward one location in one specific modality (unimodal spatial effects), versus areas activated for attention to one side versus the other independently of the modality attended (multimodal spatial effects).

Unimodal Spatial Effects for Vision Only. One single region showed increased rCBF for attention to the contralateral hemisphere only when vision was attended. This was the left superior occipital gyrus (see Fig. 1A and Table 1), which showed high activity when visual attention was sustained toward the contralateral right hemisphere (Fig. 1A, rCBF plot on the left). The reverse comparison, visual attention to left side versus visual attention to the right side (along with the additional constraints, see Methods) did not reveal any significant unimodal effect in the right hemisphere (where only multimodal effects were detected, see below). This apparent asymmetry (and others below) will be discussed later.

Unimodal Effects for Touch Only. Analogously for touch, only one region showed significant unimodal spatial attentional modulation. Comparing tactile attention to the right side versus the left side showed increased blood flow in the left postcentral gyrus (see Fig. 1B and Table 1), contralateral to the attended side. The reverse comparison, left versus right, did not show any significant effect of spatial attention. As the rCBF plot shows (Fig. 1B, on the right) all conditions involving peripheral tactile stimulation activated the right postcentral gyrus. While this region did show most activity during contralateral tactile attention to the left side (third bar from the left), this effect did not survive our criteria for significance (a sub-threshold peak was found at $x, y, z = 48, -30, 58; Z = 2.2$).

Together with the coronal section, Figure 1B also shows a sagittal section through the dorsal part of the left hemisphere. Here, the location of the most anterior part of the activation, for tactile attention to the right side, can be seen in relation to the central sulcus (indicated as ‘CS’ in this figure). The activation was entirely posterior to the central sulcus (i.e. in somatosensory cortex), without any voxel in the pre-central (motor) cortex. This fits our interpretation that this change in blood flow is related to modulation of the sensory input rather than any change in motor behaviour (see also Methods).

Multimodal Spatial Effects for both Vision and Touch. Several areas showed a main effect of attending one hemisphere versus the other, independently of the attended modality (see Table 1). These were all contralateral to the attended side. The anterior part of the left intraparietal sulcus was activated for attention to the right hemisphere (Fig. 2A). The rCBF plot (left side of Fig. 2A) shows that the differential effect of attending right minus attending left was present during both visual attention (VR > VL) and also tactile attention (TR > TL), revealing the multimodal nature of the responses in this area. Analogously to the unimodal effects described above, the reverse comparison (i.e. attend left minus right) did not reveal any modulation of the right intraparietal sulcus that satisfied our criteria for significance (maximum at $x, y, z = 42, -46, 64; Z = 2.5$), which was similarly active during all conditions of peripheral stimulation.

Two additional areas showed multimodal spatial effects (i.e. during both visual and tactile attention to one side or the other) that were symmetrical. These were the occipito-temporal junction and the superior occipital gyrus (adjacent to the cluster showing unimodal spatial effects in vision only, cf. Figs 1A and 2B). The rCBF plots in Figures 2B and 2C show that the modulatory effects of sustaining attention to one side versus the other side in these areas were independent of the attended modality. It is interesting to note that these areas are traditionally considered purely visual areas, but here they displayed spatial attentional modulation also when touch was attended on one side versus the other. Related results were obtained in a previous experiment (Macaluso et al., 2000), which differed in presenting bilateral stimulation within only one modality at a time, rather than in both modalities concurrently. Here we show that even if task-irrelevant visual distractors are presented concurrently with tactile stimuli at the location that was attended in touch, visual areas representing the same side are still boosted. Unlike all the other spatial attentional modulations described above, for these two areas (i.e. superior and middle occipital gyri) we found symmetrical spatial effects in the two hemispheres. That is, signal increases were detected in the left hemisphere for attention to the right side, while in the right hemisphere signal increases occurred during attention to the left side (see Fig. 2B,C).

Intermodal Attention to one Sensory Modality versus Another
Our design also allowed us to investigate the effect of intermodal attention to one sensory modality versus another during the
bimodal stimulation. We tested for the main effect of attention to vision minus attention to touch and vice versa, pooling conditions of attention to the left and right side.

**Attention to Vision.** The main effect of attention to vision versus touch revealed activation in several areas (Table 2). These comprised the superior occipital gyrus and occipito-temporal junction, where the preceding analyses reported above had found modulations depending on the spatially attended side. This shows for the first time that the very same regions can be

<table>
<thead>
<tr>
<th>Table 1</th>
<th>Coordinates and statistics for the areas showing either unimodal or multimodal spatial effects of attended side. All activations were contralateral to the attended side.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Attend right</td>
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<tr>
<td>Unimodal</td>
<td>Coordinates</td>
</tr>
<tr>
<td>Vision: superior occipital gyrus</td>
<td>–24</td>
</tr>
<tr>
<td>Touch: superior postcentral gyrus</td>
<td>–42</td>
</tr>
<tr>
<td>Multimodal</td>
<td>Coordinates</td>
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<td>Intraparietal sulcus</td>
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<tr>
<td>Superior occipital gyrus</td>
<td>–22</td>
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<tr>
<td>Occipito-temporal junction</td>
<td>–50</td>
</tr>
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</table>

The coordinates refer to the maximum that was found within a spherical region of interest centred according to the activations previously reported (Macaluso et al., 2000). P-values are corrected for the extent of these spherical search volumes (16 mm radius).
modulated by both intramodal (spatial) and intermodal (one modality versus another) selective attention. Moreover, the finding of a main effect of visual attention over tactile attention for these areas substantiates the suggestion made above that the multimodal spatial modulations we reported earlier can indeed affect visual areas.

In addition to these areas, attention to vision activated the right posterior parietal lobe. This region has been previously associated with the control of visuo-spatial attention (Corbetta et al., 1993; Nobre et al., 1997; Wojciulik and Kanwisher, 1999). In our task, this parietal region did not show any effect of attended side (see plots in Fig. 3A, left panel), indicating a functional segregation between occipital areas modulated by spatial attention to one side versus the other, and the posterior parietal activation. The latter might conceivably reflect a modality-specific control structure for visual attention in particular. Figure 3A also shows

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Figure 2. Multimodal effects of spatial selective attention that were independent of the sensory modality that was attended. (A) Activation in the anterior part of the left intraparietal sulcus. The histogram for the left intraparietal sulcus (left side of A, with gray bars) shows that the effect of attended side was present both when vision was relevant (bar 2 versus bar 1) and also when touch was relevant (bar 4 versus bar 3). The symmetrical region in the right hemisphere did not show any significant effect of attended side (see histogram on the right side of A, with white bars). (B, C) Contralateral attentional modulation in occipital cortex. Note that, while in the intraparietal sulcus there was no main effect of the attended modality, in occipital cortex the multimodal effect of spatial attention was found in the presence of a main effect of vision over touch. Consequently, in visual areas maximal activity was detected for attention to contralateral, visual stimulation (*P < 0.05).
activation of the superior right premotor cortex ($x, y, z = 30, -4, 50; Z\text{-score} = 3.8; \text{corrected } P\text{-value } = 0.437$). This activation was not predicted on the basis of the search volumes of interest from our previous work (Macaluso et al., 2000) and did not pass our conservative statistical thresholds, so we report it only as a trend. However, many previous studies of visual attention have shown activation in similar superior premotor regions (Corbetta et al., 1993; Nobre et al., 1997; Hopfinger et al., 2000), often with concomitant activation of superior parietal areas, as here. The present finding of a main effect of vision over touch here suggests that this superior fronto-parietal network might be preferentially engaged during visual rather than tactile attention.

Attention to Touch. The reverse comparison, tactile attention to either side versus visual attention to either side, activated postcentral regions. The activation peaks were in the inferior part of the postcentral gyrus (see Fig. 3B and Table 2), with the clusters extending into the parietal operculum (secondary somatosensory cortex, SII). The test for an overall effect of attending touch versus vision in the superior postcentral gyrus (where the unimodal tactile spatial attentional modulations were found) showed significant results (Table 2). However, close inspection of the anatomical location of the clusters indicated that only in the right hemisphere was a peak activation present around the primary somatosensory representation of the hand, in the superior postcentral gyrus. In the left hemisphere the voxels surviving our statistical tests were part of the large cluster centred in the inferior postcentral gyrus. The rCBF plots of the left superior postcentral gyrus show that activity decreased for tactile attention to the ipsilateral hand (cf. TL and US in Fig. 1B, left plot). Similar deactivations in postcentral regions during tactile attention have been previously reported (Drevets et al., 1995). By contrast, in the right superior postcentral gyrus (Fig. 1B, right plot) activity during both contralateral (TL) and ipsilateral (TR) attention was higher than baseline (US).

### Table 2

Areas showing a main effect of attended modality

<table>
<thead>
<tr>
<th>Attend</th>
<th>Anatomical area</th>
<th>Coordinates</th>
<th>Z-values</th>
<th>Corrected P-values</th>
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</thead>
<tbody>
<tr>
<td>Vision</td>
<td>Occipito-temporal junction</td>
<td>-44 -74 8</td>
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<td></td>
<td></td>
<td>-42 -72 6</td>
<td>4.9</td>
<td>0.000</td>
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<tr>
<td></td>
<td>Superior occipital gyrus</td>
<td>26 -72 38</td>
<td>4.8</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td>Right superior parietal gyrus</td>
<td>-20 -62 30</td>
<td>4.3</td>
<td>0.001</td>
</tr>
<tr>
<td>Touch</td>
<td>Parietal operculum</td>
<td>26 -64 50</td>
<td>4.2</td>
<td>0.002</td>
</tr>
<tr>
<td></td>
<td>Superior postcentral gyrus</td>
<td>54 -32 44</td>
<td>4.2</td>
<td>0.002</td>
</tr>
</tbody>
</table>

The coordinates refer to the maximum that was found within a spherical region of interest centred according to the activations previously reported (Macaluso et al., 2000). P-values are corrected for the extent of these spherical search volumes (16 mm radius).

Overall Effect of Attending Covertly to Peripheral Locations

To highlight the overall effect of peripheral covert attention to

A. VISION: Right posterior parietal and superior premotor cortex

B. TOUCH: Post-central gyri and parietal operculi

Figure 3. Main effects of intermodal attention to one modality versus the other. (A) Activation of right superior fronto-parietal areas during visual attention (although only the posterior region survived correction for multiple comparisons). These areas were activated during attention to vision, irrespective of the attended side. The histogram on the left shows activity in the right posterior parietal cortex, while that on the right shows activity in the right superior premotor cortex (where the main effect of vision over touch is reported as a trend, with activity in the five conditions displayed with white bars). (B) The main effect of tactile attention activated the inferior postcentral gyr and parietal operculum. Again, which side was attended did not affect activity in these areas.
either side, we compared the four conditions of peripheral attention (i.e. attend left or right in vision or touch) minus the central detection task with peripheral stimulation (US). In this comparison, the sensory stimulation and the requirements for overt responses were identical, thus removing trivial effects from any resulting activations.

We found that all conditions of peripheral attention activated the superior temporal sulcus and the superior premotor cortex, bilaterally (see Table 3). The latter activations were found in the fundus of the precentral sulci, at the intersection with the superior frontal sulci, possibly in correspondence with the human frontal eye-field (Petit et al., 1997). The same comparison also revealed activation of the medial wall of the superior frontal gyrus. This region may correspond to the supplementary motor area (Fink et al., 1997). The cerebellum was also activated. Superior temporal and superior frontal activations are displayed in Figure 4. The rCBF plots show that, independently of attended modality and side, these regions were activated above baseline (US). The premotor activation overlapped with the sub-threshold activation observed in the direct comparison of visual versus tactile attention. This suggests that this area operates prevalently during peripheral covert visual attention, but can be recruited to some extent during peripheral covert tactile attention.

Overall, comparison of the conditions of peripheral covert attention versus central attention indicates that a common system of brain areas (particularly the superior temporal sulci and superior premotor cortices) might be responsible for maintaining peripheral covert attention to either side, independently of the sensory modality or the hemifield which is attended.

### Discussion

We used PET to investigate the neural basis of selective attention to locations and to sensory modalities in humans. Subjects received bilateral, bimodal visuo-tactile stimulation, and in different blocks attended either the left or right side, in either vision or touch. We tested for unimodal versus multimodal effects of spatial selection (i.e. effects of attended side that were either unique to one modality, or common to vision and touch) and orthogonally for activations related to the selection of one modality versus the other during the bimodal stimulation (i.e. intermodal selection). We found both unimodal and multimodal spatial affects. Moreover, we could separate areas that showed modulation by both spatial and intermodal selection, versus areas activated during selection of one sensory modality that

### Table 3

Areas activated during peripheral attention to either side compared with stimulation baseline (US)

<table>
<thead>
<tr>
<th>Anatomical area</th>
<th>Coordinates</th>
<th>Z-values</th>
<th>Corrected P-values</th>
</tr>
</thead>
<tbody>
<tr>
<td>Superior temporal sulcus</td>
<td>68 -40 10</td>
<td>3.6</td>
<td>0.018</td>
</tr>
<tr>
<td></td>
<td>-50 -36 16</td>
<td>4.3</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>-38 0 42</td>
<td>4.3</td>
<td>0.002</td>
</tr>
<tr>
<td>Premotor cortex</td>
<td>52 0 46</td>
<td>3.6</td>
<td>0.016</td>
</tr>
<tr>
<td></td>
<td>-38 0 42</td>
<td>4.3</td>
<td>0.002</td>
</tr>
<tr>
<td>Medial frontal gyrus</td>
<td>4 10 46</td>
<td>4.3</td>
<td>0.001</td>
</tr>
<tr>
<td>Cerebellum</td>
<td>18 -44 -44</td>
<td>3.8</td>
<td>0.009</td>
</tr>
<tr>
<td></td>
<td>-28 -58 -58</td>
<td>3.4</td>
<td>0.029</td>
</tr>
</tbody>
</table>

The coordinates refer to the maximum that was found within a spherical region of interest centred according to the activations previously reported (Macaluso and Frith, 2000). P-values are corrected for these search volumes (16 mm radius).

### Figure 4

Areas activated by all conditions of peripheral attention to either side. (A) Bilateral activation of the posterior part of the superior temporal sulcus. (B) Bilateral activation of the superior premotor cortex, with corresponding signal plots. In the same coronal section, the activation of the medial frontal gyrus is also visible.
were not also modulated by spatial attention, or vice versa. Finally, comparison of all conditions of peripheral attention to either side versus a central task with equivalent stimulation revealed activation of multimodal areas that might conceivably be involved in controlling covert spatial attention, independently of the side and modality attended. It is important to note that for the critical conditions, the sensory stimulation and the number of overt responses remained unchanged. Hence, all the differential patterns of activation between the conditions found here have to be interpreted in relation to purely endogenous attentional factors that accorded with the pre-scanning instructions (i.e. attend-left in vision, or in touch, etc.).

**Attentional Selection of the Relevant Peripheral Location**

Unlike previous studies on selective spatial attention with bilateral stimulations (Heinze et al., 1994; Tzourio et al., 1997; Macaluso et al., 2000), the present experiment used concurrent bimodal stimulation, thus allowing us to distinguish unimodal versus multimodal effects of selective spatial attention, solely as a function of which modality was task-relevant. Unimodal effects were found in contralateral occipital cortex when vision was relevant and in contralateral somatosensory cortex when touch was relevant, supporting previous suggestions that selective spatial attention can modulate brain activity at a relatively early stage of sensory-specific stimulus processing (Heinze et al., 1994). For the visual modality, we found spatial attentional modulations in the superior occipital gyrus, with no significant modulation of ventral visual areas, unlike earlier workers (Heinze et al., 1994; Vandenberghe et al., 1997), and no effect in primary visual cortex, again unlike previous findings (Brechtzynski and DeYoe, 1999; Somers et al., 1999). The lack of attentional effects in these areas probably relates to the peripheral and low-contrast stimulation employed here, in agreement with previous results when a similar stimulation protocol was used (Macaluso et al., 2000).

Some of our spatial-attention results also showed a degree of hemispheric asymmetry with most of the spatial attentional effects found in the left hemisphere for attention to the right side, without significant symmetric activation in the right hemisphere for attention to the left side (although trends in the expected direction were generally present). This pattern was also found previously (Macaluso et al., 2000). Moreover, a subsequent study (Macaluso and Frith, 2000) found that this may relate to some left-hemisphere dominance for the present single/double pulse discrimination task.

The test for any multimodal modulations by spatial attention was of particular interest (i.e. effects of attended side regardless of the currently relevant modality). In a previous study (Macaluso et al., 2000) we reported initial evidence that multimodal spatial attentional effects may be found not only in high association areas (e.g. the intraparietal sulcus), but also in ‘unimodal’ occipital visual areas (e.g. superior occipital gyrus). In the present experiment we replicate both these findings and provide further observations concerning the cross-modal effects in unimodal visual areas. In contrast to the previous study, here we presented visual distractors near to the position that was attended in touch, when only touch was relevant. The finding of cross-modal modulations in occipital areas during tactile attention in this situation thus indicates that selective spatial attention can boost activity in brain areas that are processing distractors.

This appears to challenge the common assumption that selective attention amplifies activity only in areas processing task-relevant stimuli or features (Corbetta et al., 1991), while suppressing activity related to any distractors (Drevets et al., 1995; Macaluso et al., 2000). However, our results are in agreement with recent behavioural data on cross-modal links in spatial attention showing that visual distractors presented during a tactile task produce stronger interference effects when near to the current focus of tactile attention (Spence et al., 2000a). Here, we provide a possible physiological basis for this cross-modal influence, whereby spatial selective attention can automatically affect both multimodal and unimodal representations of the contralateral hemifield. Visual distractors presented at the tactually attended location can thus also receive enhanced processing, which could explain the cross-modal interference effects documented behaviourally (Spence et al., 2000a).

Several different hypotheses can be put forward to explain the observed modulation in visual areas during peripheral tactile attention. One might suggest that visual attention was automatically captured by the sudden onset of peripheral visual stimuli, even during the tactile task. This exogenous effect might have boosted activity in contralateral visual cortex. However, note that in the present study the distractors were always delivered concurrently on both sides of space, so any increase in attention capture by task-irrelevant visual events on the same side as the task-relevant tactile events would have to depend on cross-modal spatial links. Moreover, in a previous study we showed that spatially specific attentional modulation in occipital visual areas can be observed during tactile spatial attention even in absence of any peripheral visual distractors (Macaluso et al., 2000).

Another possible account for the observed cross-modal effects might relate to the potential willingness of the subjects to direct visual attention, as well as tactile attention, to the instructed location during the tactile task. However, several lines of evidence already suggest that cross-modal links in spatial attention are not simply a voluntary strategy on the part of the subject. For instance, behavioural experiments have shown that subjects find it difficult to attend separate locations in different modalities, when the task explicitly requires this (Spence and Driver, 1996; Spence et al., 2000a,b). Similarly, ERP studies have demonstrated that early spatially specific sensory components (e.g. N1 for vision) can be subject to cross-modal influences (e.g. when a different modality is attended) and that these influences are not merely strategic, being eliminated when separate locations must be attended in the two modalities, thus demonstrating that cross-modal links prevent such separation (Eimer, 1999). Taken together, the present results and previous findings indicate that the allocation of spatial attentional resources to one location in different modalities might not be a matter of choice, but rather might reflect a fundamental mechanism of cross-modal integration.

Our finding of spatially specific attentional modulations in visual cortex during the tactile task raises the new question of how subjects are able to select the correct tactile target for response, rather than the visual distractor presented at the same location. If tactile selective attention to one side boosts activity related to both tactile and visual stimuli at the attended location, some additional mechanism is needed to select just the relevant tactile targets for further processing and to determine overt responses. The results of the present experiment suggest two possible mechanisms for this. First, occipital visual areas that showed a multimodal effect of spatial attention also showed an effect of intermodal attention, with lower rCBF when touch was attended rather than vision. Second, additional brain regions (i.e. parietal operculum for touch and posterior parietal cortex for vision) were selectively activated when one particular modality had to be selected.
Attentional Selection of the Relevant Sensory Modality

Although behavioural measurements indicated that the visual task was performed somewhat faster and with higher accuracy, the direct comparison between attention to one modality versus the other did not reveal any activation in cingulate or other subdivisions of the frontal cortex that have previously been associated with task difficulty (Barch et al., 1997). Instead, these comparisons predominantly showed activation of sensory-specific areas. During attention to the visual modality (versus touch), rCBF increases were detected in the superior and lateral occipital gyri, where spatial selective attention was also found to have modulatory influences. The modulation of these areas by intermodal attention is in agreement with previous reports when visual attention was either voluntarily directed (Roland, 1982; Frith and Friston, 1996; Kawashima et al., 1999) or automatically attracted by sudden stimulus changes (Downar et al., 2000) during multimodal stimulation. In the context of the present design, the overlap between spatial and intermodal effects is particularly relevant. We have discussed above our finding that activity in contralateral occipital areas increased during tactile attention, which might enhance the processing of visual distractors in the actually attended location. However, the overlap of this multimodal modulation by spatial attention with the orthogonal effects of intermodal attention effectively means that in these visual areas activity was at its maximum when visual attention was directed toward the contralateral hemisphere. Hence, despite the presence of multimodal effects of spatial attention, modulations by intermodal selective attention were still able to ensure specificity of vision over touch in these visual areas.

A second potentially important mechanism for selecting target stimuli in the appropriate modality relates to the activation of additional brain areas. For vision, these were the right posterior parietal cortex and the right superior premotor cortex (although the latter did not pass our strict statistical thresholds); while attention to touch resulted in activation of the parietal operculum. Fronto-parietal and opercular regions have previously been associated, respectively, with visual attention (Corbetta et al., 1993; Wojciulik and Kanwisher, 1999; Kawashima et al., 1999; Hopfinger et al., 2000) and tactile attention (Mima et al., 1998; Burton et al., 1999). Here, we describe a distinction between attentional effects in these higher-order visual and somatosensory areas versus attentional effects in relatively early areas (i.e. occipital areas for vision and superior postcentral gyrus for touch). While the latter showed an effect of spatial attention and were also affected by intermodal attention, the former showed only an overall effect of intermodal attention. This distinction may relate to the type of representations that can be found at the two levels of the hierarchy. In relatively early visual and somatosensory cortices, responses are mainly contralateral, whereas posterior parietal areas (Mott and Mountcastle, 1981) and parietal operculum (Fox et al., 1987; Simoes and Hari, 1999) can respond to both ipsilateral and contralateral stimulation. Thus, while spatial selection of one side versus the other appears to affect only these areas that have predominantly contralateral spatial representations, intermodal selection was found to act at several levels. These included the recruitment of additional brain regions (e.g. posterior parietal lobule for vision and parietal operculum for touch), where spatial representations are not strongly lateralized to the contralateral side of space.

Several previous studies on visuo-spatial attention have suggested that a critical difference between lower-level sensory areas (e.g. posterior occipital areas) and higher-order areas (e.g. in the parietal and frontal lobe) might translate to top-down mechanisms of spatial covert orientation. According to this view, parietal areas might act as sources of the attentional control signals, to bias activity in earlier visual areas in occipital cortex depending on the attended side (Kastner et al., 1999; Corbetta et al., 2000; Hopfinger et al., 2000). Hence, only occipital areas, the site of the attentional modulations, might display differential activity according to the attended side, while parietal areas might be equally active for both leftward and rightward attention. The present results of a main effect of vision over touch in posterior parietal cortex (with no difference for attention to the left or right hemisphere) suggest that such control processes might be modality-specific, with the parietal areas selectively controlling activity in occipital areas during attention to vision. Analogously, high-order somatosensory areas in the parietal operculum might act as tactile-specific control areas, biasing activity in postcentral areas.

The present design used blocked data acquisition, with brain activity collapsed into a single PET image across many consecutive trials and the intervals between them. Therefore, we could not assess whether the observed rCBF changes reflected a modulation of the brain responses to each incoming sensory input or, instead, to the preparatory state that proceeded each trial, i.e. baseline shifts (Kastner et al., 1999). Indeed, both these processes might have influenced our results. Future studies might investigate this important issue by using different imaging techniques (such as functional magnetic resonance). Higher temporal resolution should allow separation of preparatory brain activity from activity evoked by the sensory stimulation, providing further insight into the mechanisms underlying covert spatial orienting in different sensory modalities [see Kastner et al. and Hopfinger et al. for similar studies within vision (Kastner et al., 1999; Hopfinger et al., 2000)] and to the influences of cross-modal links on both preparatory and stimulus-related activity.

Maintenance of Covert Spatial Attention to Peripheral Locations

The inclusion of a baseline condition of central attention, with the bilateral visuo-tactile peripheral stimulation now unattended (US), allowed us to highlight brain areas activated during all conditions of covert peripheral attention. Activations were found in the superior temporal sulcus and frontal eye-field. Some previous evidence indicates that the superior temporal sulcus might play an important role in cross-modal attention. Single-unit recording in monkeys has shown that neurons in FST (floor of the posterior STS) have visual and tactile receptive fields (Bruce et al., 1981). Experimentally induced lesions of this area in monkeys (Luh et al., 1986; Watson et al., 1994) and damage of similar regions in humans (Vallar and Perani, 1986; Friedrich et al., 1998) have been associated with spatial attentional deficits, such as unilateral neglect. More recently, studies (Downar et al., 2000) have demonstrated the multimodal role of the STS in an exogenous attention paradigm. In their experiment, subjects were presented with concurrent visual and tactile (plus auditory) stimulation. Transient changes of stimulus identity in one of the three stimulations activated unimodal areas of the corresponding sensory modality. Interestingly, supramodal activations (i.e. areas that responded to changes independently of the modality in which the change occurred) were found in the superior temporal sulcus. In our very different study of purely endogenous attention, activation of the STS was analogously found multimodally during attention to peripheral locations in both vision and touch. This is in agreement with
previous activation of the STS during sustained peripheral selective attention in purely visual tasks (Macaluso and Frith, 2000) and purely tactile tasks (Macaluso et al., 2000). Unlike our previous experiments, sensory stimulation and overt responses were here matched between the conditions of peripheral attention and the baseline condition (US), strengthening previous suggestions that the STS may play a multimodal role in sustaining spatial attention to peripheral locations.

Conclusions
We used a paradigm that combined spatial selective attention and intermodal selective attention during PET scanning to investigate mechanisms of selection for locations and for sensory modalities in the human brain. Attention to one hemifield resulted in activation of contralateral regions, both in multisensory areas (i.e. intraparietal sulcus) and unimodal structures (visual and somatosensory cortices). Interestingly, contralateral visual areas were modulated during tactile spatial attention also, suggesting that spatial attention is allocated on a multimodal basis to effect even relatively early stages of stimulus processing; see previously published work (Eimer and Schröger, 1998; Driver and Spence, 1998) for related ERP and behavioural evidence. Selection of the correct sensory modality at the attended location appears to have at least two neuronal correlates. First, we found that intermodal attention to vision (versus touch) modulated the same occipital areas that were affected multimodally by spatial attention. This overlap between spatial and intermodal effects at a common neuronal locus may constitute one means of promoting processing specifically of stimuli at the attended location, in the attended modality. Second, the posterior parietal lobe and parietal operculum were selectively activated for attention to vision or to touch, respectively, possibly providing an additional substrate for selection of the relevant sensory input during multimodal stimulation. Finally, the superior temporal sulcus (and superior premotor cortices) were associated with the maintenance of peripheral attention, irrespective of the modality or side attended, implicating these regions in attentional control for both vision and touch.

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