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Multimodal mechanisms of attention related to rates of spatial shifting in vision and touch

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Abstract Covert attention can be directed spatially in several different sensory modalities (e.g. vision and touch). Recent psychological experiments indicate the existence of crossmodal links in spatial attention, but their neural basis in humans remains underspecified. We used positron emission tomography (PET) to assess the role of stimulus modality in the activity of brain regions involved in different rates of spatial attention shifting. A 2×2 factorial design manipulated the rate (high versus low) of spatial attention shifts between left and right hemifields, plus the sensory modality (vision versus touch) of stimulation. Two brain regions showed activations related to attentional shift-rate, independent of the stimulated modality: these were the right frontopolar gyrus, and the right posterior superior temporal sulcus (STS). The anterior area showed higher blood flow with the high rate of shifts in spatial attention, while the posterior area showed higher flow during the low rate conditions, where attention was sustained for longer on one side. No area showed a significant rate effect in one modality without an effect in the second modality. These results demonstrate multimodal roles for the activated brain regions in relation to the rate of spatial attention shifting, plus right-hemisphere dominance for this. They also suggest that anterior and posterior regions of the spatial-attention network play different roles in attention shifting.

Keywords Attention · Space · Multimodal · Vision · Touch

Introduction

Attention can be covertly directed to specific locations in space, resulting in enhanced perception at the attended location (e.g. James 1890; Posner 1980). Although the majority of work on this topic has concerned vision, psychological experiments have now revealed similar effects of spatial attention within hearing (e.g. Spence and Driver 1997) and touch (e.g. Whang et al. 1991). Moreover, recent psychological studies have begun to uncover crossmodal links in spatial attention, such that attending to a particular location in one modality leads to a similar distribution of attention in other modalities (e.g. see Driver and Spence 1998, for review).

There have been many recent functional imaging studies of spatial attention, primarily in vision. These can be separated into those concerned with the control mechanisms responsible for shifting attention (e.g. Corbetta et al. 1993, 2000; Nobre et al. 1997), versus those concerned with assessing the effect of attending to a particular location on brain responses to incoming sensory stimuli (e.g. Heinze et al. 1994; Hopfinger et al. 2000). The latter have demonstrated modulation of modality-specific brain areas, at relatively early stages of sensory processing (e.g. Tzourio et al. 1997; Mangun et al. 1998; Macaluso et al. 2000). In contrast, studies on control mechanisms have highlighted activation of higher-order frontal, parietal and temporal areas. Most of these studies have only examined the visual modality (e.g. Gitelman et al. 1999; Rosen et al. 1999; Corbetta et al. 2000). The present experiment was designed to examine processes relating to the rate of covert spatial attention shifting, in both vision and touch. The aim was to test whether the same neural control structures may be involved for these two modalities.

In a classic study of shifts in spatial attention for vision, Corbetta et al. (1993) used PET to measure blood flow as normal subjects underwent several different attentional conditions. The critical comparison concerned conditions where subjects were asked to shift covert attention successively through five predictable positions in

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one particular hemifield (during peripheral stimulation for a manual target-detection task), versus sustaining their covert attention at central fixation to detect targets there instead (with any peripheral flashes now becoming task-irrelevant). The results showed that superior parietal and superior frontal regions were activated in the shifting task as compared with the sustained task. Some predominance for right-hemisphere regions was suggested, as these were activated when shifting attention within either peripheral hemifield. This agreed with the right-hemisphere dominance for spatial attention found in clinical studies of attentional biases after unilateral brain injury, in patients with spatial neglect (e.g. Weintraub and Mesulam 1987; Bisiach and Vallar 1988).

Similar results have since been obtained in other imaging experiments on spatial shifts of visual attention, which used tasks similar to the psychological cueing studies instigated by Posner (1980). In such tasks, a spatial cue precedes the visual target, to direct covert attention to a particular location. Nobre et al. (1997) compared such a visual spatial-cueing task with a rest baseline, and showed activation of a distributed network of superior fronto-parietal areas. More recently, Gitelman et al. (1999) employed a more subtle control condition (a central detection task, while irrelevant stimuli flashed in the periphery) and found activation of similar regions. Additionally this study also showed activation of the superior/posterior temporal lobe plus anterior insula, during the attention shifting visual task. Although the use of a central detection task removed any confound due to differences in the sensory stimulation or motor responses, the control task never required peripheral discrimination. Using event-related fMRI, Corbetta and colleagues (Corbetta et al. 2000) were able to control for this aspect of the spatial cueing task. Their results showed that when attention had to be shifted from the cued location to the opposite hemifield, where an "invalid" target was presented, activity increased in the right temporo-parietal junction.

Activation of such temporo-parietal regions during shifts of visuospatial attention may be relevant to the multimodal issue, concerning attentional mechanisms that operate across different sensory modalities (Driver and Spence 1998). Physiological evidence from animals indicates that both the inferior parietal lobule (Graziano and Gross 1995) and subdivisions of the superior temporal sulcus contain multimodal, visual-tactile representations (Bruce et al. 1981; Hikosaka et al. 1988). Additionally, a particular role for the superior temporal sulcus in multimodal aspects of spatial attention might also be anticipated on the basis of a recent functional imaging study. Downar et al. (2000) presented subjects with trimodal stimulation (i.e. concurrent visual, auditory and tactile stimulation). For each modality, two types of stimuli could be delivered; for example, in the visual modality, the stimulus was either a red or a blue abstract shape. During scanning, the stimulation within each of the three concurrent modalities could independently switch from one type to the other type, causing a transient change within that sensory modality. Transients oc-

curing in one specific modality caused increased brain activity in corresponding unimodal brain areas. By contrast, the superior temporal sulcus was activated independently of the modality of the change, demonstrating the multimodal nature of this region.

In the present study, we sought to identify brain areas involved in shifts of spatial attention for both vision and touch, while avoiding any comparison of discriminations made in the periphery with those made centrally. In order to do this, we manipulated whether the rate of spatial attentional shifting was high or low, by means of a predictable spatial sequence of target stimuli in one modality or the other. Successive stimuli within a block either alternated hemifields (high shift-rate), or changed hemifield only after five trials (so that in this low shift-rate condition, spatial attention was sustained on one side prior to the switch, and then on the other side). The stimulation was either all visual within a block, or all tactile. We tested for commonalities versus differences in the effect of attentional shift-rate on the activated brain regions across these two sensory modalities.

Although our design overcomes possible confounds that may arise when conditions of attention shifting are compared with low-level baselines or central tasks, note that it can only reveal multimodal mechanisms of spatial attention for brain areas which are sensitive to changes in the rate of attention shifting.

Materials and methods

Subjects

Eight volunteers participated in this study (mean age 26 years, range 21–34). All were right-handed males. None had 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

We tested the subjects in a 2×2 factorial design. One factor was the modality of stimulation: vision or touch. The second orthogonal factor was the rate of shifts in spatial attention between left and right hemifields: high rate or low rate. Attentional shifts were enforced by changing the side of sensory stimulation (see Fig. 1). In the high-rate conditions, stimuli changed side every trial (every 1.5 s); during the low rate, shifts occurred every five stimuli (once every 7.5 s). The four conditions yielded by the 2×2 design were each blocked, and replicated three times in each subject (with the exception of one subject, who for technical reasons performed only the visual conditions, four times each, and one subject who was scanned four times in the touch condition with high shift-rate). We will refer to the four conditions as: [HV], for high-rate vision; [LV], [HT] and [LT]. The order of these conditions was counter-balanced within and across subjects.

Stimuli

Subjects lay in the scanner with their arms bent at about 70 degrees, and their hands visible. In the lower part of the visual field,

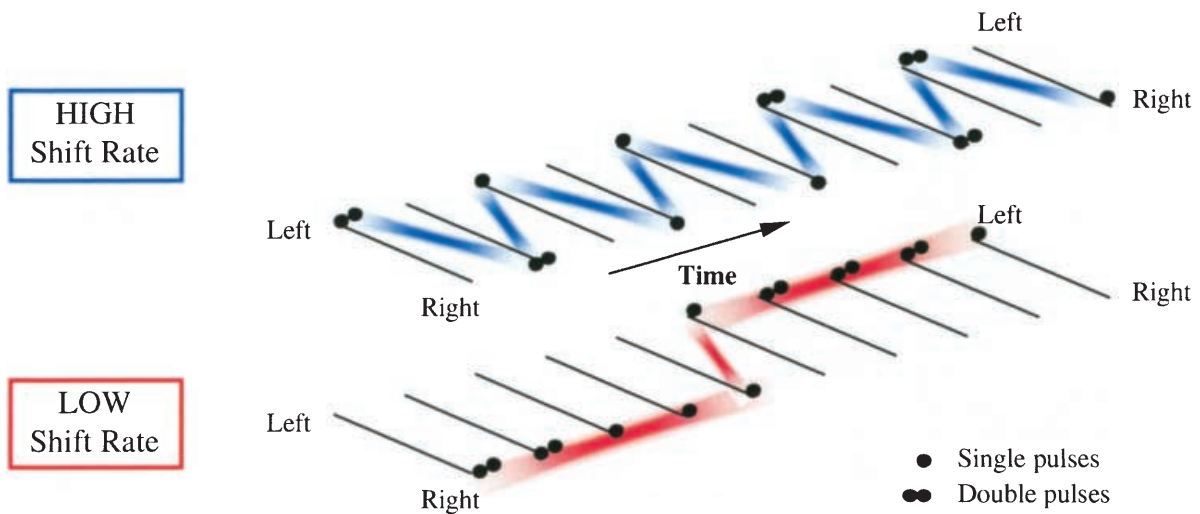


Fig. 1 Schematic representation of the task. Subject had to maintain central fixation during the scanning period. Each stimulus was unilateral; predictable changes in the stimulated hemifield determined the rate of attentional shifts (high shift rate shown above, low shift rate below). Stimulation was either visual or somatosensory. Both visual and tactile blocks consisted of a random sequence of single and double pulses. The task of the subject was to respond after each stimulus, by saying either “one” or “two”, depending on whether a single or double pulse was given

their hands rested on two vertical wooden supports (250 mm wide), each hand in its respective hemifield at 25 degrees to the left or right of the midline. A computer screen was located centrally. On each peripheral wooden support we attached a small structure accommodating a red LED (10 mm in diameter) and a solenoid (12 V). The index finger of each hand was restrained so that the subject could not avoid tactile stimulation when delivered to that finger by the solenoid (30 Hz vibrations). Each LED was placed 1 cm in front of the index finger on that side; thus, any visual stimulation appeared at a very similar location to the tactile stimulation on the same side. Each block comprised a 2-min sequence of unimodal stimulation (either visual or tactile). Independently of the modality stimulated, the sequence always consisted of successive unilateral trials (on either the left or the right side), with an intertrial interval of 1500 ms. At both rates of attention switching, half of the stimuli were delivered to the right side and half to the left, so that over the 2 min of a block an equal number of stimuli was presented in the two hemifields (hence, bilateral activation of sensory cortices could be expected). A random half of the trials were single pulses (lasting 200 ms), the other half were double pulses (130 ms on, 40 ms off, 130 ms on for vision; or 135 ms on, 30 ms off, 135 ms on, for touch).

Task

Prior to the beginning of the scanning experiment, subjects were familiarised with the task for 10 min, and were made aware of the two rates at which the stimuli could switch between hemifields (high versus low rate). Before each scan, subjects were informed about the shifting-rate that would follow. During the scanning period, a small white cross was displayed on the central computer screen, and the subject had to maintain central fixation (which was monitored; see below). The task was to attend covertly to any peripheral stimulation, in order to discriminate single versus double pulses. Subjects had to give a verbal response after each stimulus: either “one” or “two”.

Monitoring of eye position

Eye position was monitored with a CCD camera placed a few centimetres above the left eye. An infrared LED was directed towards the eye to ensure a good image, while leaving the subject in darkness. This ensured a good qualitative assessment of eye-position, but did not permit formal analysis of eye-position traces. Nevertheless, it allowed us to check that subjects were not systematically saccading towards the targets, but were following the instruction to maintain central fixation.

Structural MRI

Before or after the PET scanning session, each subject underwent a structural MRI scan. Images were acquired using a VISION scanner operating at 2 Tesla (Siemens, Erlangen, Germany). The T1 MPRAGE sequence (TE=4 ms, TR=9.5 s, TI=600 ms) gave a resolution of $1 \times 1 \times 1.5$ mm.

Acquisition of rCBF data during PET scanning

Scans were performed on 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 $H_2^{15}O$ infused over 20 s followed by a 20-s saline flush. There were 12 successive administrations of $H_2^{15}O$, each separated by 8 min. Images were reconstructed with a Hanning filter of 0.5 to a full width at half maximum (FWHM) of 6.5 mm. Data were acquired in a 90 s scan frame after injection of 8–10 mCi of $H_2^{15}O$. Each block began 20–30 s before image acquisition. Total counts per voxel during the build-up phase of radioactivity served as an estimate of the 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) normalised 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). The structural MRI of each subject was co-registered to the mean PET image of the same subject. The coregistered structural images were transformed into the Montreal Neurological Institute (MNI) standard space (Collins et al. 1994). This procedure involves 12 linear and quadratic three-dimensional transformations. Residual variance was corrected using a set of smooth basis functions (Friston et al. 1995). Normalisation param-

eters were then applied to 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 (SPM97d; www.fil.ion.ucl.ac.uk). The effects of condition, subject, reaction time, repetition and global flow effects were estimated according to the general linear model at each and every voxel (93 residual degrees of freedom). A blocked one-way ANCOVA with global activity, effect of repetition and reaction times as covariates of no interest was used. Reaction times and repetition effects were included in the analysis to account for any performance differences observed between conditions. To test hypotheses about regionally specific condition effects, the estimated effects were compared using linear compounds (contrasts). The resulting set of voxel values for each contrast constitute a statistical parametric map of the t -statistic $SPM\{t\}$. The $SPM\{t\}$ were transformed to the unit normal distribution $SPM\{Z\}$. We report multimodal rate effects when, at a given voxel, we could demonstrate a main effect of rate at $P < 0.001$, together with simple effects within both modalities at $P < 0.05$. Adding the latter constraint was a precaution to ensure that any effects reported as “multimodal” did not merely reflect a very strong simple effect of rate within just one modality, dominating the absence of such an effect within the other modality. Note that adding these constraints can only make our analyses more conservative, as they require further tests to be passed.

Results

Behavioural performance

Performance was accurate in all conditions and in all subjects. A two-way within-subject ANOVA compared reaction times in the four conditions (excluding the subject who performed only for one modality). This analysis (see Table 1) found no overall effect of shift-rate [$F(1,6)=0.33$, NS], a main effect of stimulated modality [$F(1,6)=16.0$, $P < 0.01$, with faster responses to vision], but no interaction [$F(1,6)=0.20$, NS]. Within the low-shift rate conditions, we also compared reaction times to the first stimulus after the shift, versus reaction times to the four subsequent stimuli combined (note that all of these were presented in the same hemifield, since in the low-rate condition the stimulus side switched every five trials). This analysis again showed an effect of modality [$F(1,6)=12.5$, $P < 0.02$, with faster responses to visual stimuli], but in addition demonstrated an effect of attention shifting [$F(1,6)=36.1$, $P < 0.01$], with slower reactions on the trial where the target suddenly switched trials, as compared with reactions when the target was at the same location for four successive trials (see Table 1). This effect did not interact with modality [$F(1,6)=4.3$, NS].

The effect of the modality of the task, with touch slower than vision, might be due to differences in stimulus characteristics across modalities. For this reason, reaction times were modelled as confound effects in the rCBF data analysis. The finding that sustaining attention on one side for extended periods (five successive trials) caused slow responses to a target suddenly presented in the opposite hemifield was expected. This is likely to represent the cost of disengaging attention from a position that has been relevant for several successive trials (e.g. Posner 1980; Spence et al. 2000).

Table 1 Reaction times. Mean reaction times (in milliseconds) for the four experimental conditions. In brackets are the SEM. Single and double pulses are pooled. Times refer to the beginning of the stimulation. Italic numbers refer to reaction times for stimuli occurring at different points in the low-rate sequence. *Sustained* mean reaction times to the four stimuli when subjects maintained attention to one hemifield. *First stimulus* reaction times to the first stimulus after the shift in the low rate conditions

		Vision	Touch
High rate		885 (39)	942 (28)
Low rate	Mean	885 (36)	954 (23)
	<i>Sustained</i>	878 (36)	945 (22)
	<i>First stimulus</i>	900 (39)	990 (27)

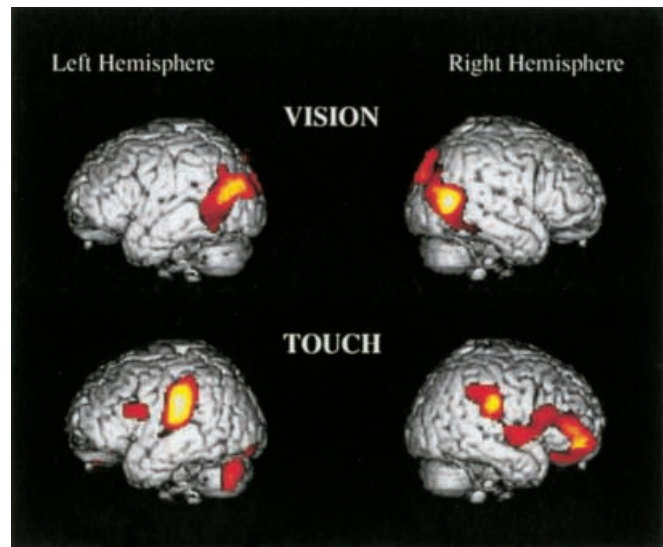


Fig. 2 Areas sensitive to the modality of stimulation rendered on a 3D image of the MNI brain. Visual regions are defined as areas that showed a higher mean rCBF during the visual task than the somatosensory task. The reverse comparison defines tactile areas

PET activations related to the sensory modality of the shifting task

Visual activations

Comparing scans acquired while subjects performed the shifting task with visual stimuli, versus the somatosensory scans (i.e. $[HV+LV] > [HT+LT]$), identified areas associated with the visual task. Since the PET signal was integrated over 90 s, our unilateral stimulations on either side (which changed hemifield every 1.5 s or 7.5 s), caused bilateral stimulation of visual cortex over the scanning period. As expected, this produced bilateral activation of the occipital lobe. The clusters extended from the middle occipital gyrus dorsally to the superior occipital lobe (Fig. 2 top, and Table 2). Previous studies demonstrated that activity in these areas can be affected by spatial attention (Mangun et al. 1998). However, the design of the present experiment did not allow us to distinguish activity related to the sensory stimulation, from

modulations of the sensory response associated with attention (see Kastner et al. 1999). No activation was detected in primary visual cortex, possibly because of the low-contrast and peripheral stimulation we used in a constantly illuminated environment. The cuneus also showed significant activation, with the maxima in the left hemisphere, but clearly involving both hemispheres. Additionally, a significant main effect of vision over touch was also found in the left hippocampus. Interestingly, this hippocampal modality effect was dependent on the rate of attentional shift (leading to an interaction between rate and modality), as discussed later.

Somatosensory activations

The reverse comparison ($[HT+LT]>[HV+LV]$) highlighted areas activated more during the tactile task than the visual task (Fig. 2 bottom, and Table 2). This revealed bilateral activation of the postcentral gyrus extending into the parietal operculum (secondary somatosensory cortex), and to the insula in the right hemisphere. These are all regions traditionally associated with processing of somatosensory stimuli (Kaas 1983; Burton et al. 1993).

Table 2 Main effect of modality. Anatomic areas, co-ordinates and Z-values of voxels showing maximal sensitivity to the different sensory stimuli. High rate and low rate scans acquired in one modality were compared with all the conditions in the other modality. Anatomic areas were determined by superimposing PET activations on the structural MR image of the MNI standard brain

	Anatomic area	Co-ordinates	Z-values
Vision	Middle occipital gyrus	46, -60, 10	6.9
		-40, -62, 10	6.0
	Cuneus	14, -76, 32	4.7
		-4, 78, 28	6.0
	Left hippocampus	-24, -16, -14	3.9
Touch	Inferior post-central gyrus	60, -22, 26	5.3
		-54, -26, 26	6.4
	Inferior frontal gyrus	56, 18, 12	4.1
		-56, 16, 20	4.4
	Right insula	46, -4, -2	5.7
	Right lateral orbital gyrus	42, 46, 4	4.7
	Left cerebellum	-40, -78, -28	4.4
	Right medial orbital gyrus	18, 44, -24	4.3
	Pons	6, -22, -32	4.0

Table 3 Effects of attention shifting in both vision and touch. Regions showing an effect of the rate of attentional shifts. We found two regions that showed modality independent responses: the right frontopolar gyrus (high rate>low rate) and the posterior part of the

Rate	Anatomic area	Main effect across modalities		Simple main effect within each modality		
		Co-ordinates	Z-values	Modality	Co-ordinates	Z-values
High	Right fronto-polar gyrus	28, 64, -6	3.8	Vision	30, 64, -6	2.4
				Touch	24, 64, -6	3.3
Low	Right superior temporal sulcus	54, -40, 2	4.0	Vision	60, -38, 6	3.1
				Touch	52, -42, 2	3.6

Additionally, several areas were activated in inferior frontal cortex, somewhat lateralised to the right hemisphere. In a previous experiment that used exactly the same stimulation apparatus, again comparing tactile and visual stimulations (Macaluso et al. 2000), we observed very similar foci of activation in post-central areas but activation of frontal areas was not observed. This suggests that activation of the latter regions might reflect some difference in performing the shifting tasks in touch and vision rather than merely the sensory stimulation per se.

Multimodal (modality-independent) effects of attentional shifting rate

Any multimodal effects of shifting rate were determined by testing for a main effect of rate across modalities in the presence of simple main effects within each modality (i.e. not only passing $[HV+HT]>[LV+LV]$, but also $HV>LV$, and also $HT>TV$; see earlier section on the analysis of rCBF data). This analysis revealed one multimodal area showing higher rCBF for the high-shift conditions than for the low-shift conditions, and one area showing the reverse pattern.

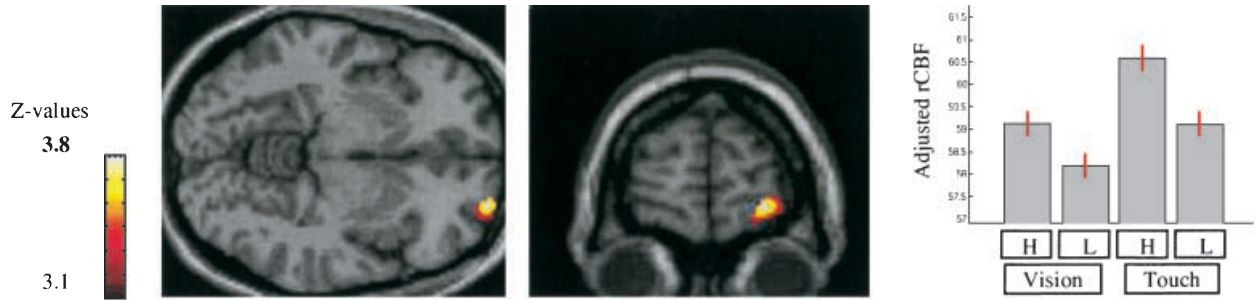
High rate minus low rate of spatial attention shifting

The contrast testing for areas with higher activity during the high shift-rate condition (irrespective of the modality used to induce these attentional shifts) revealed a single cluster in the right frontopolar gyrus (see Table 3, Fig. 3A.1). Every voxel within this cluster survived our criteria of not only showing a main effect of rate across modality, but also a corresponding simple effect of rate within each modality considered alone. The plot of the maximum shows that the blood flow was higher, for both modalities, during the high shifting rate than during the low rate. Additionally, it can be seen that, at the plotted voxel, a main effect of touch over vision was also present when pooling across rates (see section above on main effect of the modality of the task). Hence, the lowest activity was measured during the low shift rate in vision.

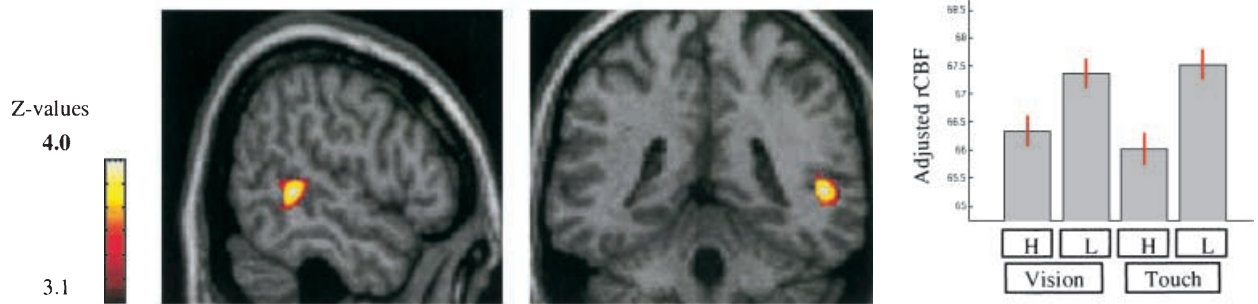
right superior temporal sulcus (low rate>high rate). For these two regions, we report co-ordinates and Z-scores of the maxima of the main effect across modalities and of the maxima of the two simple main effects within the cluster

A. Commonalities between vision and touch

1.- HIGH rate versus low rate: *Right Fronto-polar Gyrus*



2.- LOW rate versus high rate: *Right Superior Temporal Sulcus*



B. Interaction between shift rate and modality: *Left Hippocampus*

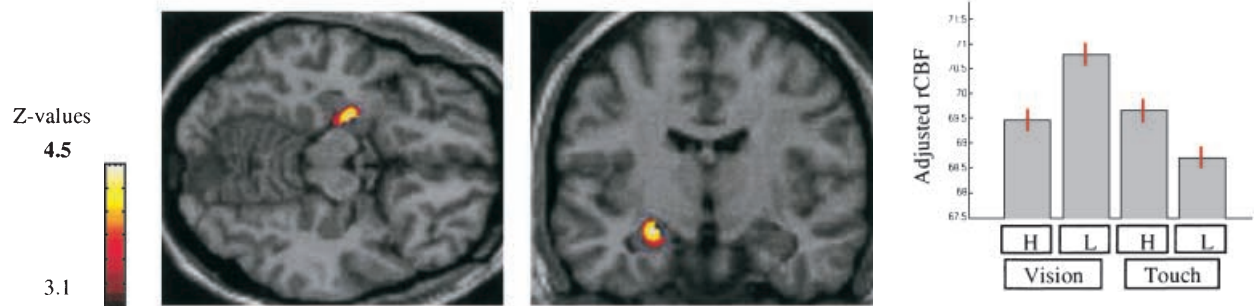


Fig. 3 **A** Anatomy and rCBF plots (mean adjusted to 50 ml/dl per min for the whole brain, \pm SEM) for the two areas showing sensitivity to the rate of spatial attentional shifts independently of the sensory modality stimulated. PET activations of the contrasts high rate versus low rate (3A.1), or low rate versus high rate (3A.2), were superimposed on the structural magnetic resonance image of the MNI brain. Sections are taken through the maxima. The rCBF plots of the maxima show that the differential response depending on the rate of attention shifting was independent of the modality stimulated. **B** Anatomical localisation of the activation in the left hippocampus, with rCBF plot. (H high shift rate; L low shift rate)

Low rate versus high rate of spatial attention shifting

The reverse contrasts tested for higher rCBF with a low rate of shifts in spatial attention. We again required not only a main effect of shift rate across the two modalities, but also the presence of corresponding simple effects of rate within each modality. This revealed a single area activated more strongly for low shift-rates in both modalities, within the posterior part of the right superior temporal sulcus (see Table 3). Fig. 3A.2 shows the anatomical localisation of the cluster. Again, the rCBF plot for the maximum shows that the rate effect was independent of

the modality stimulated. In the superior temporal sulcus there was no effect of the modality of stimulation, when pooling across rates.

Modality-specific effects of attentional shifting rate

Contrasts testing for an interaction between stimulated modality and rate of spatial attention shifts ([LV+HT]>[HV+LT]) revealed an unexpected but highly reliable activation of the left hippocampus ($x, y, z = -24, -10, -14$; $Z\text{-score} = 4.5$). Activity was high for the low shift-rate in vision, but low for the low shift-rate in touch (see rCBF plot in Fig. 3B). The reverse interaction ([HV+LT]>[LV+HT]) revealed no significant activations.

Discussion

The present study investigated neural areas sensitive to the rate of covert shifts of spatial attention. The aim was to determine if such structures would be engaged only during covert orienting to stimuli in one specific modality (vision or touch), or if they would operate independently of the sensory modality used. In order to avoid any confounds due to comparing a central task with a peripheral covert orienting task, we instead manipulated the rate of attention shifting between the two hemifields. This meant that the multimodal issue could only be studied for areas displaying some sensitivity to our shift-rate manipulation. It is possible that other components of the spatial attention network (e.g. intraparietal areas, frontal eye-field and subcortical structures) might also show multimodal properties, in a different paradigm that does not rely on the rate of attention shifts in particular.

Rate effect independent of the modality stimulated

Our experiment highlighted two regions that showed an effect of the shift-rate of spatial attention, independent of the sensory modality employed. These were the right frontopolar gyrus and the superior temporal sulcus. Finding these areas supports the hypothesis that parts of the network for reallocating spatial attention operate supramodally. Previous behavioural studies have demonstrated substantial links between vision and touch in tasks concerned with attention shifting. For example, Spence et al. (1998) showed that cueing one side of the space with a visual stimulus resulted in enhanced tactile discrimination at the same location. Analogously, tactile spatial cues can be effective in improving visual judgements. Our finding of brain areas involved in spatial attention-shifting, irrespectively of the stimulated modality, may help to understand such crossmodal behavioural effects. Our data demonstrate the existence of multimodal spatial representation related to covert attention, in the right frontopolar gyrus and STS.

Superior temporal sulcus

Our low-rate shifting conditions preferentially activated the right superior temporal sulcus. The multimodal nature of this structure has been previously demonstrated using single cell recordings in non-human primates (Bruce et al. 1981; Hikosaka et al. 1988), and more recently using fMRI in humans (Downar et al. 2000). As already described in the Introduction, Downar and colleagues found activation of the STS during sensory transients, independently of the modality of the transient. In relation to our results, it is interesting to note that in Downar et al.'s experiment the stimulation of the three modalities occurred in different external locations (i.e. on the leg for touch, straight ahead for vision and over headphones for audition). Hence, each transient may have caused a reorienting of spatial attention.

Direct evidence for an involvement of the STS in spatial orienting has been suggested on the basis of both monkey and human lesion data. Luh et al. (1986) showed that lesions to the superior temporal sulcus can cause neglect in monkeys. Lavadas et al. (1998) reported crossmodal spatial deficits in humans. Patients were presented with concomitant stimulation in the two hemifields, which could be in different modalities. On the left (contralesional) side, the stimulus was always tactile, while on the right side the stimulus could be visual. The results showed that a right visual stimulus could impair the patient's ability to detect a left tactile target. Although many different brain regions were damaged in this group of patients, the temporo-parietal junction was one of the regions more frequently affected.

Within visual attentional research, some apparent discrepancies existed in the past between patient data and imaging experiments. While deficits of spatial attention were often associated with lesion of the temporo-parietal junction (Vallar and Perani 1986; Friedrich et al. 1998), several past imaging experiments had implicated the superior parietal lobule as a centre for control of visuo-spatial attention (e.g. Petersen et al. 1994; Nobre et al. 1997). However, more recent imaging findings have highlighted the particular importance of the temporo-parietal junction in visuo-spatial covert orienting (see Gitelman et al. 1999; Kim et al. 1999; Corbetta et al. 2000; Hopfinger et al. 2000). In the present experiment, the lack of activation of superior parietal areas may relate to the fact that all our conditions involved target discrimination at peripheral locations (see Vandenberghe et al. 1996). Direct comparison between shift rates may not reveal any activation of these areas, since all our conditions required peripheral attention (unlike Corbetta et al. 1993 and many subsequent studies), so that such areas may have been equally active in all our conditions. As a consequence of this, we were unable to determine to what extent superior parietal areas, which are known to be involved in spatial attention, operate supramodally.

Further evidence for an involvement of posterior temporo-parietal regions in spatial attention comes from event-related potentials (ERPs) in scalp recordings. In a

variation on Posner's (1980) visual cueing studies of spatial attention, Yamaguchi et al. (1994) measured event related potentials in the period between cue and target onset. They observed negative potential shifts over right temporo-parietal regions between 500 and 800 after cue onset. The authors suggested that this might reflect activity related to maintenance of attention towards the expected location. In the present experiment, the posterior multimodal activation was associated with the low shift rate. During these conditions, attention was maintained to one hemifield for several successive trials before a shift; hence the observed activation of the STS is likely to reflect a region concerned with committing spatial attention to a particular peripheral location. Critically, here we show that this does not depend on the sensory modality stimulated, demonstrating multimodal mechanisms of spatial covert attention.

Frontopolar gyrus

For both modalities, the conditions of high-shift rate activated the right frontopolar gyrus, suggesting that this region is multimodal and sensitive to spatial factors. We attribute this activation to the high demand on executive processes in the high-rate condition, where spatial attention had to be shifted to the opposite side every 1.5 s. On the basis of clinical lesion studies, prefrontal structures have long been associated with executive processes and attention shifting, and patients with large frontal lesions show characteristic slowness and perseveration when such shifts are required (e.g. Luria 1966; Shallice 1988). Moreover, recent studies of frontal patients have shown that damage to right inferior frontal areas can cause contralesional spatial neglect (Husain et al. 1996), consistent with a role in spatial attention in particular. Finally, both degenerative studies (Jones and Powell 1970) and anterograde plus retrograde labelling experiments in monkeys (Selzer and Pandya 1989) demonstrate direct and reciprocal connections between multimodal areas in the superior temporal sulcus and the anterior part of the inferior frontal lobe. This speaks in favour of our hypothesis that the two areas showing multimodal activations in the present experiment play complementary roles in the control of spatial attention within both vision and touch.

We found no activations in superior frontal cortex, unlike previous imaging studies on purely visual attention. This may relate to the lack of differential activation for the superior parietal lobe, which may have been equally active in all our conditions. Activations of superior frontal areas are frequently reported together with superior parietal activations (Corbetta et al. 1993; Nobre et al. 1997). This probably reflects the high connectivity between these two brain regions (Goldman-Rakic 1988; Morecraft et al. 1993). A superior fronto-parietal network has been associated with spatial sensory-motor transformations (Andersen et al. 1985; Colby 1998). Signals proceed from early visual areas, where the encoding

is retinotopic, to higher areas integrating proprioceptive information with current motor intentions, in more abstract spatial co-ordinates. It is possible that in our study this pathway was not particularly active because of the non-spatial nature of the motor output required by our task (i.e. verbal responses).

Differential responses to shifting rate depending on the modality stimulated

Considering our design, we might expect that some brain areas would have proved sensitive to the rate of attentional shift only when one particular modality was stimulated. Any such area would be a candidate for a modality-specific component of spatial attentional control. But no such area was found, further substantiating our conclusion that covert spatial orienting is a multimodal process (see also Driver and Spence 1998). The only effect we found that depended on modality was in the left hippocampus, where we showed an opposite effect of attention shifting rate depending on the modality stimulated. Here, rCBF increased with increased shift rate in touch, but decreased with increased shift rate in vision. This unexpected result can be interpreted in two different ways. The left hippocampus could be directly involved in the attentional shift and reverse its role depending on the modality of the stimulation. Alternatively, the observed interaction might result from a rate-dependent sensitivity to the modality of stimulation. The blood flow plot is consistent with the latter hypothesis. The two high-rate conditions had similar mean adjusted rCBF, while the two low-rate conditions demonstrated a striking effect of stimulated modality. This pattern fits with the left hippocampus showing a modality effect (favouring vision) only during the low-rate condition, without any effect of sensory modality during high-rate stimulation. Subjects may have locked onto a particular "allocentric" location only during the low-rate visual conditions, as tactile stimuli may always be coded egocentrically instead. The hippocampus has long been associated with allocentric spatial representation (O'Keefe and Speakman 1987; Maguire et al. 1998). On the other hand, it could be premature to rule out the possibility that the hippocampus may play a role in spatial covert orienting. Activations of the hippocampus in experiments addressing spatial attention have been found before (Corbetta et al. 1993), and further experiments are needed to address its role in this.

Conclusions

The present experiment investigated the neural correlates of different rates of spatial attention shifting, in vision and touch. The aim was to assess if any common brain systems are involved in spatial attention shifting for both visual and tactile stimulation. Varying the rate of attentional shifts between the two hemifields, in vision and touch, has the methodological advantage that irrelevant

task components (such as sensory input, motor requirements, and the need to make peripheral sensory discriminations) were all closely matched across the different rate conditions. We found that activity in the posterior part of the right superior temporal sulcus and in the frontopolar gyrus was sensitive to the rate of spatial attention shifting. Critically, in both these regions, the changes in rCBF were independent of the modality of stimulation.

The superior temporal sulcus was preferentially activated during the low rate conditions. We suggest that this activation relates to the fact that spatial attention was sustained on one side for several trials, before an abrupt shift. In the fronto-polar region, blood flow increased with increased shifting rate. This activation probably reflects the executive functions associated with voluntary control of the frequent shifts during the high rate conditions. We conclude that, in the right hemisphere, these posterior and anterior associative areas play different roles in spatial covert orienting, but that both operate multimodally. These regions are likely to be part of the network that allocates spatial attentional resources across sensory modalities, providing a possible physiological basis for the crossmodal links in spatial attention recently observed in behavioural experiments (Driver and Spence 1998).

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