



# Spatial attention and crossmodal interactions between vision and touch

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## Abstract

In the present paper, we review several functional imaging studies investigating crossmodal interactions between vision and touch relating to spatial attention. We asked how the spatial unity of a multimodal event in the external world might be represented in the brain, where signals from different modalities are initially processed in distinct brain regions. The results highlight several links between visual and tactile spatial representations. First, we found that activity in the anterior part of the intraparietal sulcus was influenced by stimulus position independently of the modality of the stimulation. This is consistent with crossmodal interactions via sensory convergence from early modality-specific spatial maps to higher-order multimodal regions. Second, we found that stimulation in, or attention to, one modality could affect activity in areas dedicated to a different modality, in a spatially-specific manner. These spatial crossmodal effects in unimodal regions demonstrate congruous activity in anatomically distant brain areas that represent similar external locations, implicating a distributed network of spatial representations in crossmodal integration. Finally, the results suggest that the temporo–parietal junction may be involved in aspects of controlling spatial attention, for both vision and touch. A multimodal attentional system may influence activity in distinct brain areas representing common regions of space for different modalities, thus suggesting a link between spatial attention and crossmodal integration. © 2001 Elsevier Science Ltd. All rights reserved.

*Keywords:* Space; Multimodal; Integration; fMRI; PET; Humans

## 1. Introduction

Daily life provides continuous stimulation of our sensory systems. In many cases, a single event in the external world produces multimodal signals, as when a visible object moves to touch you. Such multimodal signals are perceived via different sensory receptors (e.g. retina and skin), and are initially processed in different cortical regions (e.g. visual and somatosensory cortices, in this example). In order to produce an appropriate behavioural response to the external event, the brain needs to relate information from different senses and represent the unity of the external event. These integrative processes may rely on multiple cues, such as the content of the multimodal signals (e.g. are the signals associated to the same object?), the temporal synchrony of the input and/or its spatial coherence. In this article,

we will consider mechanisms that depend on the spatial location of the external event, using vision and touch. In other words, how does the brain represent the fact that two sensory inputs (e.g. a touch on the finger and a flash of light nearby) originate from the same external location, and what are the consequences of this spatial coherence?

According to a modular and hierarchical view of the functional organisation of the brain, it might be expected that the spatial location of any input will at first be represented in modality-specific areas, and only subsequently transmitted to higher-order multimodal areas. This would suggest a feed-forward mechanism for spatial coding, where integration is achieved by convergence from ‘lower level’ unimodal maps, to ‘higher level’ multimodal spatial representations [3,28]. However, while intuitive, such a model might not fully resolve the issue of crossmodal integration. For instance, the presence of multiple unimodal and multimodal spatial maps may raise the problem of how coherent patterns of activations can be achieved be-

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tween all these multiple representations, only deferring any solution to the integration issue.

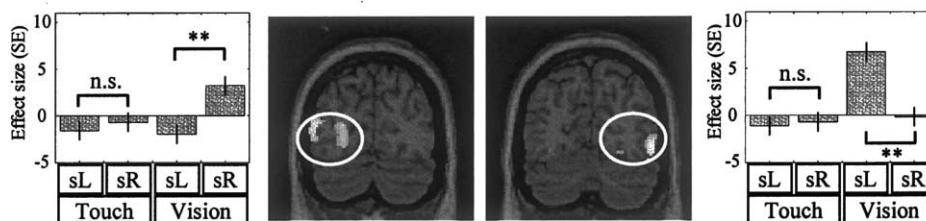
In this paper, we will first present the results of a functional imaging study aimed at mapping unimodal versus multimodal spatial representations for vision and touch in the human brain, in a purely stimulus-driven paradigm. We will then review several imaging studies of crossmodal attention, which highlight the substantial influence of spatial attention upon both unimodal and multimodal brain areas. Overall, the evidence presented here confirms the existence of both unimodal and multimodal spatial representations in the human brain. However, the results also suggest that crossmodal integration does not exclusively arise at the level where input from unimodal areas converges on multimodal areas. Specifically, it appears that crossmodal spatial attention can also affect processing in unimodal brain regions, even those which respond to a currently task-irrelevant modality (see also Eimer in this volume, for

logically similar effects revealed by event-related brain potentials). This implies that spatial information may be automatically shared across multiple representations, in a spatially coherent manner, which can produce multimodal influences upon unimodal brain areas. We propose that a multimodal attentional control system may mediate these crossmodal effects upon unimodal areas.

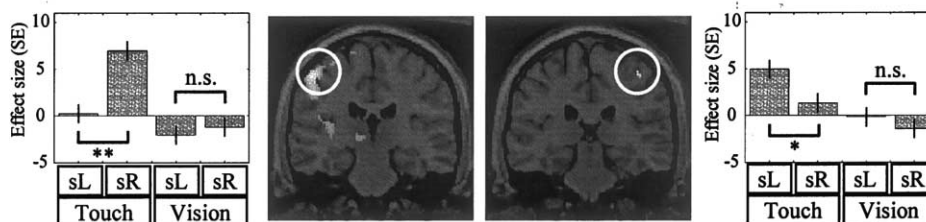
## 2. Mapping visual and tactile spatial representations

When studying spatial coding in the brain, perhaps the simplest experimental approach is to present stimuli in different locations and to determine which brain areas show differential responses depending on the position of the stimulus. This methodology can be extended to address crossmodal spatial issues, with a critical distinction now arising between those areas that

### A. VISION: Lateral and inferior occipital lobe



### B. TOUCH: Postcentral gyrus



### C. BIMODAL: Anterior intraparietal sulcus

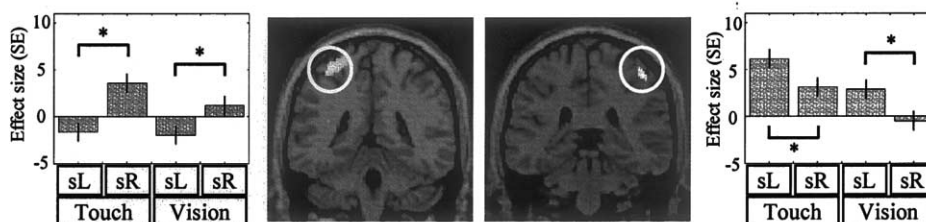


Fig. 1. Areas responding to contralateral peripheral stimulation. (A) Occipital areas showed contralateral responses only during visual stimulation. (B) The postcentral gyrus activated only during contralateral tactile stimulation. (C) The anterior part of the intraparietal sulcus showed differential responses depending on the location of the stimulus, independently of the modality of the stimulation (vision or touch). Effect sizes are expressed in standard error (S.E.) units (as also for Figs. 2, 3 and 5). sL/sR refers to the side stimulated (left or right). (\*\* for  $P$ -uncorrected  $< 0.001$ ; \* for  $P < 0.05$ ; n.s. for  $P > 0.1$ ). Statistical threshold for the anatomical sections displayed:  $P$ -uncorrected = 0.001, except for the cluster in the left postcentral gyrus:  $P = 0.01$ ).

Table 1  
Contralateral responses to visual and tactile stimulation

	Left hemisphere		Right hemisphere	
	Co-ordinates	Z-value	Co-ordinates	Z-value
<i>Vision</i>				
Lateral occipital lobe	-48 -76 12	4.6	54 -70 -6	5.5
<i>Touch</i>				
Post-central gyrus	-50 -24 54	5.3	44 -28 56	2.8
<i>Multimodal</i>				
Anterior intraparietal sulcus	-28 -34 64	4.9	46 -34 58	3.7

Anatomical location and statistical scores for the areas showing differential responses depending on the side stimulated. Co-ordinates and Z-scores refer to the peak activation for the contrast comparing stimulation of one side versus stimulation of the opposite side. For the unimodal effect this was the simple effect of side within the corresponding modality. For the multimodal effects, this was the main effect of side across both modalities. All activations were contralateral to the stimulated side.

show spatially-specific responses only for stimuli delivered to one modality (unimodal spatial representations), and areas that show particular spatial effects independently of the modality stimulated (multimodal spatial

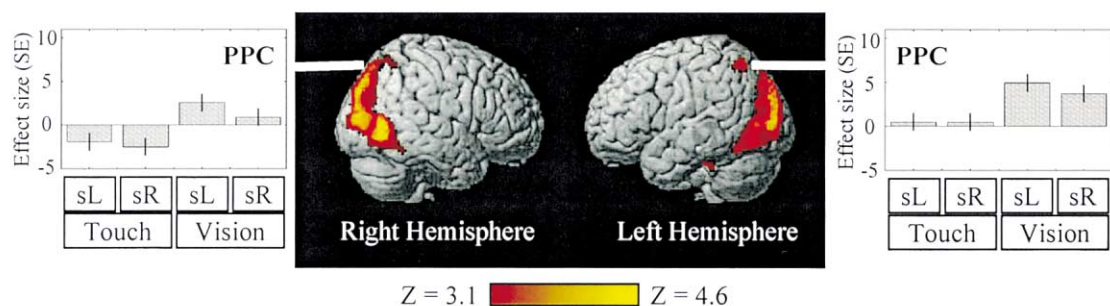
representations). Finding any multimodal spatially-specific responses would demonstrate that the brain can extract spatial information from very different input (i.e. from different sensory modalities), to segregate space as a specific supramodal dimension of the sensory input.

In the next section, we will present the results of an earlier unpublished fMRI experiment, where eight subjects received either visual stimulation (via one or the other of two LEDs attached to either thumb) or tactile stimulation (air-puffs to either thumb), in either the left or the right hemifield during blocked fMRI scanning. The aim of the study was to test for common ‘multimodal’ spatial effects across modalities (i.e. differential activity depending on the hemifield stimulated, but independent of the modality), and also for unimodal spatial effects (i.e. effect of stimulated side only for stimulation in one modality).

### 2.1. Unimodal spatial effects

Unimodal spatial effects were identified by comparing left versus right or right versus left stimulation within one modality (at  $P < 0.001$  uncorrected), adding the constraint that no such spatial effect should be present during stimulation of the other modality ( $P > 0.1$ ). For vision, this revealed activation of contralateral occipital areas as would be expected (see Fig. 1A and Table 1). Left occipital areas activated during right

#### A. VISION minus Touch



#### B. TOUCH minus Vision

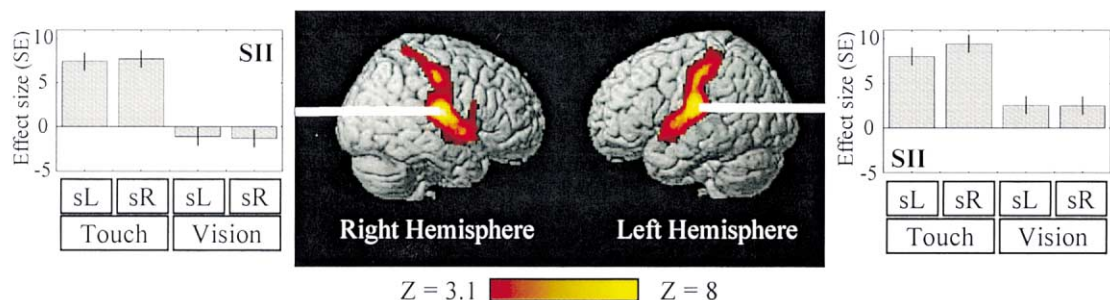


Fig. 2. Areas that showed differential responses depending on the modality stimulated. (A) Vision versus touch. (B) Touch versus vision. These comprised areas with contralateral responses (see Fig. 1.), plus several new areas. The new areas were the posterior parietal cortex (PPC) for vision and the parietal operculum (SII, secondary somatosensory area) for touch. Signal plots (in S.E. units) in these areas demonstrate responses to both contralateral and ipsilateral stimulation. (sL/sR again refers to the side stimulated).

Table 2  
Bilateral responses to visual and tactile stimulation

	Hemisphere	Co-ordinates	Z-value
<i>Vision</i>			
Occipito–parietal junction	L	–26 –62 58	4.6
	R	20 –80 46	4.5
<i>Touch</i>			
Parietal operculum	L	–60 –16 10	6.6
	R	58 –14 16	>8
<i>Multimodal</i>			
Intraparietal sulcus	L	–40 –50 56	5.5
	R	38 –34 44	5.9
Superior premotor cortex	L	–32 –2 58	7.1
	R	56 –6 38	7.5
Superior temporal sulcus	L	–54 –44 10	5.6
	R	60 –24 2	>8

Areas showing responses to both contralateral and ipsilateral stimulation. Modality specific effects were detected by direct comparison of stimulation in one modality versus the other modality. Multimodal effects were highlighted comparing all four types of stimulation (left or right, in vision or touch) versus a baseline without any peripheral stimulation. All comparisons activated symmetrical clusters in the two hemispheres.

stimulation and right occipital areas activated for left stimulation. Several peaks were found, including lingual, fusiform and lateral occipital gyri. For touch, we found that right tactile stimulation caused contralateral signal increase in the left post-central gyrus (see Fig. 1B, left side of the figure), with the activation extending anteriorly into the central sulcus and left motor cortex. The reverse

comparison, left versus right, showed weak activation of the right post-central gyrus ( $P < 0.003$ , see Table 1). Overall, the results were in agreement with earlier imaging studies within vision [10] and touch [2], which had found that at the initial unimodal stages of stimulus processing in the cortex, brain responses are mainly contralateral to the location of the stimuli.

## 2.2. Bimodal spatial effects across both vision and touch

Common spatial effects for both vision and touch were identified by testing for a main effect of side of the stimulation when pooled across modality ( $P < 0.001$ ), in the presence of simple effects of side within each modality ( $P < 0.05$ ). The latter constraint was included to insure that both vision and touch contributed to any multimodal effect; note that adding it can only make our criteria for the main effect of side more conservative. This revealed contralateral activation in the intraparietal sulcus. The peaks were found in the anterior part of the intraparietal sulcus, at the junction with the post-central sulcus (see Fig. 1C), just posteriorly to the unimodal tactile clusters (compare with Fig. 1B). This finding of multimodal visuo–tactile responses in the intraparietal sulcus supports earlier observations in non-human primates [3,18], that found bimodal visuo–tactile neurones in several intraparietal regions and adjacent areas (e.g. areas VIP and 7b).

## 2.3. Non-spatial effects

Within the same design, we also tested for main effects

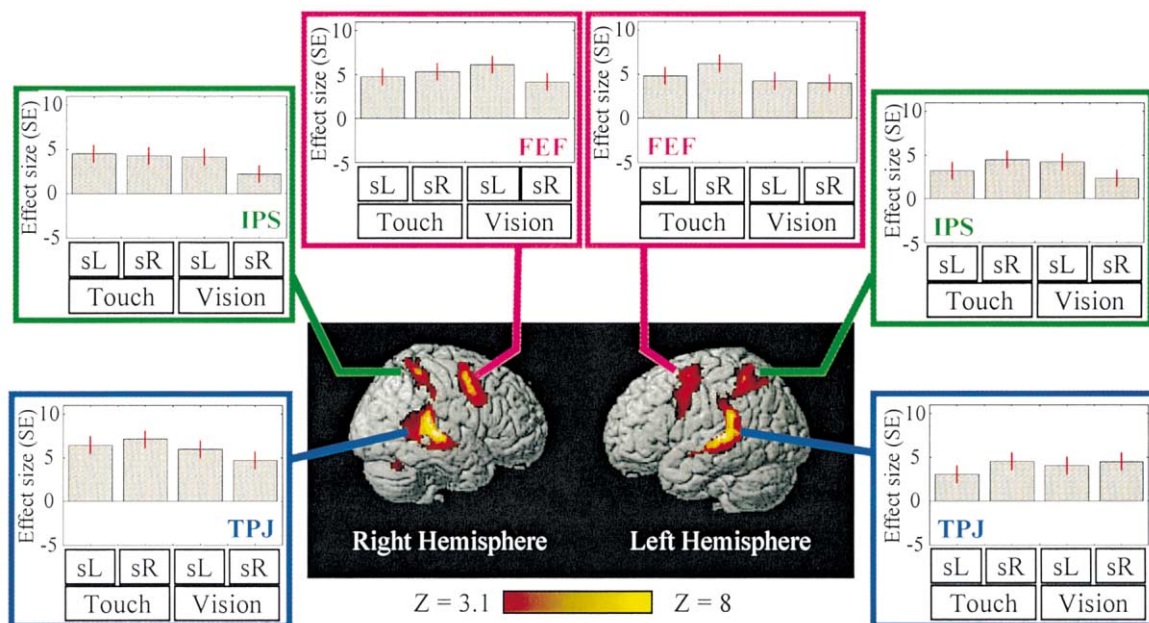


Fig. 3. Brain regions responding to all four types of stimulation (left and right, in vision and touch). Interestingly, these bimodal visuo–tactile activations overlapped with areas earlier associated with control of visuo–spatial attention. (FEF, frontal eye field; IPS, intraparietal sulcus; TPJ, temporo–parietal junction).

of the modality of the stimulation, irrespective of the stimulus position. As expected, this comparison revealed activation of visual or somatosensory cortices (Fig. 2A and B, respectively). These included all areas showing modality-specific spatial effects (i.e. inferior and lateral occipital gyri for vision and superior post-central gyrus for touch). This confirms the intuitive prediction that modality-specific spatial effects should be found within areas responding to stimulation of one specific modality. The same comparison also revealed activation of several other regions, which did not show any effect of stimulated side (see Table 2). For vision, these activations were found in the occipito–parietal junction and superior parietal gyrus, while tactile stimulation caused activation of the parietal operculum and insulae. These areas responded to both contralateral and ipsilateral stimulation (see plots in Fig. 2A and B). This is in agreement with the earlier studies showing that as processing proceeds from early to later areas within the hierarchical organisation of both the visual and somatosensory systems, there is a transition from mainly contralateral to increasingly bilateral responses [2,37].

Between each block of unimodal and unilateral stimulation (i.e. left or right, in vision or touch), imaging data were also acquired during central fixation, with no peripheral stimulation. This baseline allowed us to test for any brain areas responding to all four types of stimulation (i.e. left and right, in vision and touch). Although this comparison has to be taken cautiously (as white noise was played to the subject throughout the stimulation blocks only, to mask any noise associated with the tactile events), activation was found in several potentially interesting areas: the intraparietal sulcus, the frontal eye field and the temporo–parietal junction (see Fig. 3 and Table 2). These areas have been previously associated with spatial attention in unimodal visual studies [7,20,31], but here activated during both visual and tactile stimulation on either side. These results raise the possibility that these areas might be involved in exogenous orienting to peripheral tactile, as well as peripheral visual stimuli. Indeed, these activations are very similar to those found in an earlier study, which linked them to multimodal attention shifts [11].

In summary, this simple mapping experiment with stimuli in different positions and different modalities highlights several points. First, it identified areas showing differential responses depending on stimulus location. Unimodal spatial effects were found in occipital areas for vision and in post-central regions for touch, presumably reflecting the separation of the afferent input from the left and right hemifield early in the cortical sensory pathways. On the more important crossmodal issue, it was interesting to find multimodal, yet spatially-specific, responses in the anterior intraparietal sulcus. This suggests that some intraparietal areas may encode spatial information from different sources (e.g. different sensory

modalities) to form higher-level multimodal spatial representations [1,4,26]. Another result of the present study was the identification of multimodal areas, whose responses were not affected by the different stimulus positions used (i.e. activation for both contralateral and ipsilateral stimulation). These were localised elsewhere in the intraparietal sulcus, and in the frontal eye field plus temporo–parietal junction. Interestingly, these areas have been earlier associated with control of covert spatial orienting in purely visual studies [7,20,31].

Overall, these results are consistent with the spatial location of an external stimulus first being represented cortically in modality-specific maps. At a later stage along the processing pathways, the different inputs appear to converge, probably leading to the formation of multimodal spatial representations. Here, signals originating from the same external spatial location could in principle interact, to reconstruct the coherence of a single multimodal external event (arising from a unique location), thus achieving a form of crossmodal integration based upon stimulus location.

These results thus accord with one simple mechanism for crossmodal integration; namely feed-forward convergence from unimodal to multimodal brain areas [15,28,36]. They may also provide a potential neuronal substrate for some of the crossmodal links reported in behavioural studies of spatial attention [13,34]. Such studies have found that when visual attention is voluntarily directed to one location, judgement of tactile stimuli presented at the same location is also improved, and vice-versa. Our finding of contralateral multimodal visuo–tactile representations in the anterior intraparietal sulcus could in principle account for such behavioural cross-modal effects, if spatial attention modulates processing in such multimodal regions, as well as in unimodal areas [19,21].

In the next section, we will describe several imaging studies investigating the effect of voluntarily attending to a particular location in either vision or touch. These studies demonstrate attentional modulation of both modality-specific and also multimodal contralateral representations. Interestingly, these studies also showed that when one modality is attended at one particular place, sensory-specific maps representing the same location but in a different modality are also affected (see Eimer, this volume, for related findings using event-related brain potentials). When attention is directed to one location, multimodal and also unimodal spatial maps seem to be coherently tuned to the attended location, somewhat independently of the modality attended or stimulated.

### 3. Selection of currently relevant spatial locations: multimodal and unimodal effects

Many of the earlier imaging studies on spatial selective attention have considered only a single modality at a time.

A study by Heinze and colleagues [19] provides a typical example for vision (see also [39], plus Hopfinger et al., this volume). While fixating the centre of the screen, subjects were shown two streams of rapidly presented pairs of symbols. Pairs of stimuli were simultaneously flashed on the left and on the right of the central fixation point. The task was to attend either leftwards or rightwards, pressing a button when the two symbols in the pair on the attended side were identical. This study showed that when attention was maintained to the left hemifield, neural activity increased in the right fusiform gyrus, and vice-versa, suggesting that visual selective attention can affect brain activity at a relatively early (modality-specific) level of stimulus processing (see also Downing et al.; Hopfinger et al.; Kastner and Ungerleider; plus Nobre, all in this volume). Similar results have been obtained in other unimodal studies that examined either auditory [38] or tactile attention, indicating that modulation of contralateral unimodal brain regions is a prevalent mechanism for spatial attentional selection.

However, these earlier studies on selective spatial attention used only one sensory modality within each experiment. The use of different modalities within the same experiment could in principle reveal any multimodal mechanisms of selective spatial attention, as described in behavioural studies [13,29,34]. This should allow us some insight into how a system comprising multiple unimodal and multimodal spatial representations engages in spatial attentional selection.

We have used functional imaging to examine a basic spatial selective-attention paradigm, again with stimuli presented simultaneously in the two hemifields, but now with either visual or tactile stimulation within the same PET experiment [26]. In different scanning blocks, subjects attended the left or the right hemifield during either visual or tactile bilateral stimulation. Any visual stimulation was delivered near to the possible tactile stimulation on the hands, thus requiring sustained attention to similar spatial positions on one side or the other, but in different modalities. The comparison of attention to one hemifield versus attention to the opposite hemifield revealed increased activity in contralateral brain areas. The critical new question was whether the modality of the bilateral stimulation would affect the pattern of contralateral modulations. We found that ‘unimodal’ areas (i.e. in the occipital lobe for vision and the post-central gyrus for touch) showed contralateral attentional modulation primarily during bilateral stimulation of the corresponding modality, while multimodal areas (i.e. the anterior intraparietal sulcus) showed contralateral attentional effects independently of the modality stimulated. The unimodal results replicated the basic finding earlier observed within just vision (see [19]) and also showed corresponding spatial attentional modulation for touch within somatosensory cortex. The multimodal attentional modulation of the intraparietal sulcus provides a possible

neuronal substrate for the crossmodal effects described in behavioural studies of crossmodal links in endogenous spatial attention [34]. It may also provide an anatomical locus related to the ERP findings on crossmodal endogenous attention as documented by Eimer and colleagues (see Eimer, this volume).

Thus far, these endogenous attentional effects observed during bilateral stimulation in our PET study [26] can be related to the stimulus-driven findings of the fMRI experiment presented above. The PET study showed that endogenous attention can affect activity in multiple spatial representations, with a segregation between unimodal and multimodal effects. The unimodal and multimodal areas observed closely matched the findings of the fMRI experiment, which had used only unilateral, unimodal stimulation rather than bilateral and bimodal stimulation, and which had no requirement for endogenous attentional selection. The PET study [26] thus suggests that the unimodal and multimodal areas revealed by spatially-specific stimulation can also be modulated by endogenous spatial attention, during bilateral stimulation.

However, the attentional PET experiment with bilateral stimulation differed in finding some multimodal effects in ‘unimodal’ brain areas. Specifically, the superior occipital gyrus and the occipito-temporal junction showed a strong main effect of modality stimulated (more active for visual than for tactile stimulation), but spatial attentional modulations were still detected during the tactile, as well as the visual task. This suggests that when tactile attention was directed to one hemifield, visual areas representing the corresponding location were also modulated. Effectively, this means that activity in visual cortex was modulated according to the required direction for tactile attention, implying related patterns of activation for anatomically distant unimodal areas (i.e. post-central gyrus and extrastriate occipital areas). The localisation of some crossmodal attentional effects in occipital cortex is in agreement with the proposal that crossmodal effects can influence relatively early ‘unimodal’ levels of perceptual analysis (see reference [29] and also Eimer, this volume, for similar arguments).

It might be argued that these crossmodal effects of the attended side in visual areas during a tactile task arose merely because the subjects chose to direct visual attention towards the location of the attended tactile stimulation. Thus, the parallel modulation of unimodal visual and tactile representations might not be an inherent characteristic of the composite system of multiple spatial representations, but merely an option that subjects can choose to exercise. This possibility can be difficult to exclude (although see the ERP evidence in Eimer, this volume; plus behavioural evidence [12,34,35] suggesting that subjects find it difficult to attend separate locations in different modalities, even when the task explicitly requires this). We addressed the issue in a second PET experiment [24]. We now pre-

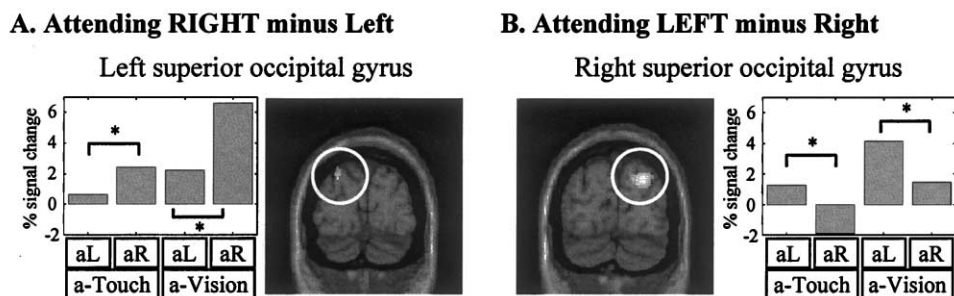


Fig. 4. Crossmodal attentional effects in visual areas during attention to tactile stimuli on one or the other side. Subjects were presented with concurrent bimodal and bilateral stimulation. During each block they attended to one side (aL or aR) and one modality (a-Vision or a-Touch; see [24]). The occipital cortex showed increased blood flow during attention to the contralateral hemifield. Critically, these spatially-specific attentional modulations in visual cortex were observed also when only touch was attended as task relevant (compare the two leftmost bars within each plot). Activity is expressed in percent signal change compared with unattended bilateral-bimodal stimulation during a task performed on the central fixation cross. (Statistical threshold for the anatomical sections,  $P = 0.001$ ).

sented subjects with a bilateral and bimodal visuo–tactile stimulation (again with vision and touch presented at the same external locations on each side). According to the instructions given before the scanning block, subjects directed attention to one hemifield and only one modality (e.g. attend touch-left). Subjects were asked to perform a perceptual discrimination within one modality, while receiving distractor stimuli in the other modality, at the same location (in addition to the distractors in the opposite hemifield for both modalities). The distractors at the attended location could disagree with the response required to the targets. In this case, the best strategy would seem to be to direct only tactile attention to the relevant location, as required for the somatosensory task. In fact, our imaging results showed that despite the concurrent presence of visual distractors during the tactile task, several occipital areas continued to show contralateral attentional modulation depending on which side was task-relevant for touch (see Fig. 4). The superior occipital lobe and the occipito–temporal junction showed a higher signal when vision rather than touch was attended (i.e. a main effect of attended modality, consistent with these areas playing a visual role), but nevertheless spatial effects were still observed here independently of the modality that was attended. This means that during both attention to

vision and attention to touch on one side, occipital regions showed higher blood flow for attention to the contralateral hemifield compared with attention to the ipsilateral hemifield. These results suggest that the mechanisms involved in co-ordinating activity across multiple spatial representations cannot be easily overcome even when the task is designed to discourage them, for instance by presenting distractors in one modality at the target location for the other modality (see also Eimer, this volume; plus related behavioural evidence from [12,33–35]).

Further evidence for crossmodal influences on unimodal brain areas in the context of spatial attention comes from a recent event-related fMRI study [27]. Unlike the earlier two PET experiments [24,26], which had investigated crossmodal links during voluntary endogenous attention, here we addressed crossmodal links during exogenous (stimulus-driven) attention. Subjects received either left or right visual stimulation (near to one or other hand) and on half of the trials a simultaneous tactile stimulation was also delivered to one hand. We found that when the tactile stimulation was presented at the same location as the visual stimulus, activity in contralateral visual areas in response to the visual stimulation was significantly amplified (see Fig. 5). It is important to note

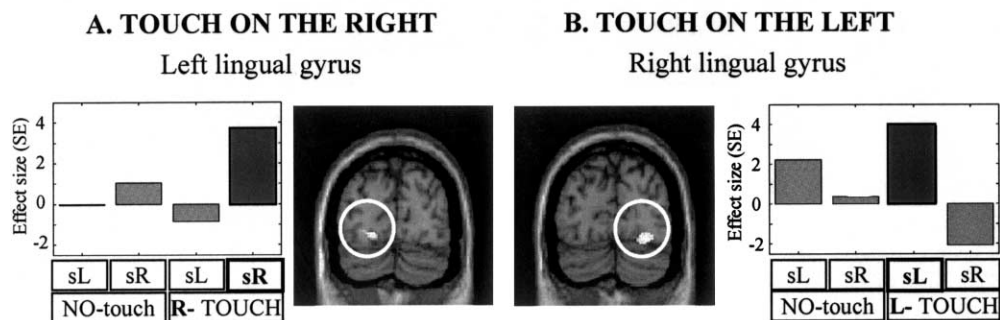


Fig. 5. Modulation of contralateral visual responses by spatially congruent tactile stimulation [27]. Subjects received either left (sL) or right (sR) visual stimulation. On half of the trials, touch was simultaneously delivered either to the right or to the left hand (Fig. 5A and B, respectively). Which hand could be stimulated differed between subject groups. These irrelevant tactile stimulations modulated visual responses in contralateral occipital areas, with higher responses when the tactile stimulation was present together with a spatially congruent visual event on the same side. (Statistical threshold for the anatomical sections,  $P = 0.05$ ).

that the sole task of the subjects was to detect the visual onsets, and that any tactile stimulation did not predict the location of these visual targets. Therefore, there could be no advantage in voluntarily using the tactile stimulus to direct visual attention. These fMRI results suggest that peripheral tactile stimulation can affect visual responses within occipital areas in a spatially-specific exogenous manner, in a similar way as tactile endogenous attention can also lead to spatially-specific modulation of contralateral visual areas.

Overall these findings highlight two complementary mechanisms for crossmodal interactions, based on stimulus location and/or the direction of spatial attention. First, we found that the anterior part of the intraparietal sulcus contains bimodal contralateral representations of space, for both vision and touch. These probably reflect convergent feed-forward projections from unimodal visual and tactile cortical maps to produce multimodal contralateral representations [1,4]. In the anterior intraparietal sulcus, spatial information is apparently segregated from other attributes of the input (e.g. sensory modality). We found that the multimodal spatial representations in these areas can be modulated by voluntarily directing covert attention to different locations. As would be expected for truly multimodal brain areas, we found modulations here due to spatial attention independently of the modality that was stimulated [26] or attended [24].

Secondly, spatial information appears to be shared across anatomically distant ‘unimodal’ spatial (contralateral) representations. In particular, tactile stimulation and/or tactile attention were found to influence activity in visual areas under several circumstances. We demonstrated modulations of contralateral visual occipital areas both when tactile attention was voluntarily directed to one hemifield (endogenous attention [24,26]) and also when unpredictable tactile stimulation was used to capture attention (exogenous attention [27]). This suggests that some mechanism can convey spatial information associated with touch to visual areas, in a spatially-specific manner. Such a mechanism might play an important role in maintaining spatial coherence in a system of multiple representations, and might be viewed as a form of crossmodal integration by coordination of distributed spatial representations, rather than crossmodal integration by feed-forward convergence alone [15].

#### **4. Possible control mechanisms for spatial attention across vision and touch**

What allows tactile information (or tactile attention) to affect processing in ‘unimodal’ visual areas in a spatially-specific manner? When addressing this question it might be useful to consider also the possible mechanisms involved in spatial modulation of visual

areas during purely unimodal visual tasks (see also Hopfinger et al.; Kastner and Ungerleider; Dowing et al.; Nobre et al.; Rees and Lavie, all in this volume). Although no direct causality has yet been established, one reasonable hypothesis is that higher-order areas in parietal and frontal lobes may act as sources of the modulatory signals that influence more posterior sensory areas [6,8,9,20,21]. The identification of such control structures, and the assignment of specific functions to each of them, is still a debated topic, often with different tasks or comparisons leading to somewhat different results. For instance, Kastner and colleagues [21] showed that superior parietal (and frontal) areas are active when attention is voluntarily directed toward peripheral locations in anticipation of stimulation there (see also Kastner and Ungerleider, this volume), suggesting that these regions may act as sources of the modulatory signal, which affect activity in earlier visual areas (see also [6]). On the other hand, Hopfinger and colleagues [20] using a selective attention paradigm (i.e. with targets and distractors presented simultaneously) proposed that one additional likely source of these control processes was to be found in more inferior regions of the parietal lobule.

In relation to the present issue of crossmodal interactions it is worth underlining that, given the hierarchical organisation of the visual system, attentional control of posterior sensory areas even in unimodal visual studies may presumably rely on back-projections, whether or not such control originates from posterior parietal [6], inferior parietal [20] and/or frontal areas [9]. This raises the possibility that tactile influences upon visual areas might analogously arise because touch can affect processing in the same higher-order areas that act as sources for the modulations observed during purely visual tasks. Possible preliminary support for this might conceivably be gleaned from the earlier unpublished fMRI stimulation experiment that was presented at the beginning of this paper. There we showed that intraparietal, frontal and temporo-parietal areas can indeed respond to both visual and tactile stimulation. However, this still does not directly address the critical question about possible involvement of these areas in a supramodal attentional control system, which may allow tactile information, or tactile attention, to influence visual responses.

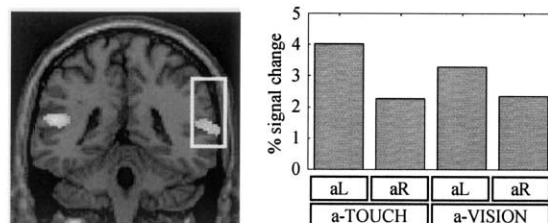
In several imaging experiments we have used comparisons similar to those earlier employed in purely visual studies, to determine the role of such areas during both visual and tactile spatial attention. For instance, we have compared sustained selective peripheral attention to one or other side, versus central attention, to investigate possible mechanisms for endogenous control of covert spatial attention in both visual and tactile tasks. We have also used attention-shifting paradigms to study stimulus-driven (exogenous) spatial

attention for both visual and tactile targets (analogously to earlier purely visual studies [6]).

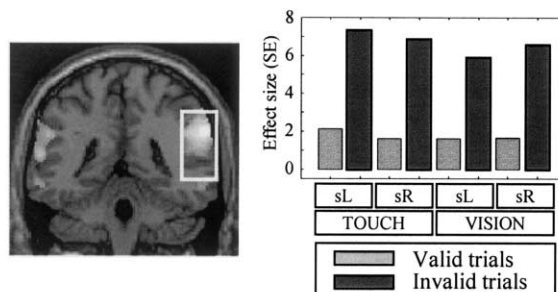
The effect of covert endogenous attention to peripheral locations in vision and touch could be highlighted in one of the PET studies described above [24], which presented concurrent bimodal and bilateral stimulation. The design included a control condition that allowed us to compare each of the peripheral attention conditions (i.e. attend vision or touch in the left or right hemifield) against a central task (detection of brief luminance changes at the fixation point). Importantly, the bilateral peripheral visuo–tactile stimulation was still presented during the latter control condition, excluding any possible confounds due to the sensory stimulation alone. This comparison revealed bilateral activation of the superior temporal sulcus (in the superior/posterior part of the temporal lobe) and the frontal eye field, two regions earlier associated with visuo–spatial attention [5,23,30], but found here for both visual and tactile covert attention to peripheral stimuli. In Fig. 6A, activity in the right superior temporal sulcus during the four conditions of peripheral attention to one side is plotted in terms of percent signal change with respect to the central attention condition. All conditions of covert attention to one or other side resulted in increased blood flow, here independently of the side or modality attended. These results suggest that these regions may be involved in voluntary maintenance of peripheral covert attention to one or other side in both vision and touch.

Further evidence for a supramodal role of superior/posterior temporal and inferior parietal (i.e. temporo–parietal junction, TPJ) regions in spatial attention comes from studies of spatial attention-shifting in vision and touch. Such shifting paradigms have been mainly used within just the visual modality in imaging studies to date. Results in such visual studies consistently show activation of frontal, parietal and posterior/superior temporal structures [6,7,17,31]. For instance, Corbetta et al. [6] used event-related fMRI during a classic endogenous spatial cueing paradigm, similar to that popularised by Posner [32]. On a trial-by-trial basis a central symbolic cue indicated the most likely location for a subsequent visual target. In the majority of the trials (valid trials), the target was indeed presented at the cued location. However, on a minority of trials (invalid trials), the visual target was presented in the hemifield opposite to the one indicated by the central cue. According to Posner [32], such invalid trials should trigger an additional shift of attention from the cued location, to the actual target location. Hence, comparison of invalid minus valid trials during brain imaging should highlight brain areas involved in the reorienting of spatial attention. Importantly, this direct comparison of invalid versus valid trials is matched for several task components, such as trivial sensory-motor factors plus

### A. PERIPHERAL SUSTAINED ATTENTION



### B. ATTENTION SHIFTING



### C. CHANGES IN EFFECTIVE CONNECTIVITY

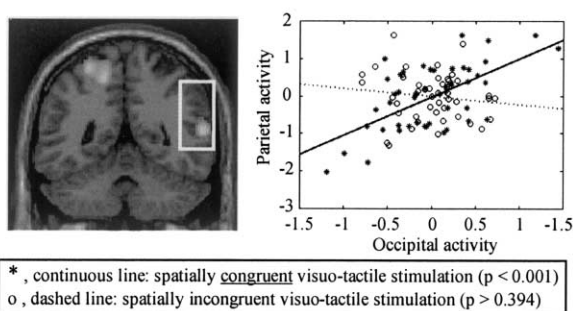


Fig. 6. Activation of the right temporo–parietal junction in several tasks engaging visual and tactile spatial attention. (A) Visual or tactile peripheral attention (sustained to one side or the other during bilateral stimulation) compared with central detection [24]. All four conditions of covert peripheral attention (attending left or right in vision or touch) induced signal increase compared with the central task (baseline activity during central detection is set to zero in this plot, see also Fig. 4). (B) Invalid trials activated the temporo–parietal junction during a spatial cueing paradigm [25]. This activation was observed independently of the modality or the side (sL/sR) of the targets. Effect sizes are expressed in standard error units. (C) Increased coupling between parietal and visual areas during spatially congruent visuo–tactile stimulation versus spatially incongruent stimulation [27] (example for a single subject). The plot indicates a positive correlation between temporo–parietal and occipital areas specifically when touch was found to affect processing in visual cortex (see also Fig. 5); that is, during bimodal stimulation at a common external location. (Statistical threshold for the anatomical sections displayed, (A)  $P = 0.01$ ; (B and C)  $P = 0.001$ ).

subtler processes like the requirement to discriminate peripheral targets.

Recently, we used a modified version of this classic endogenous spatial cueing paradigm during event-re-

lated fMRI. We added the critical new factor that targets could now be either visual or tactile [25]. On a trial-by-trial basis, an auditory cue symbolically instructed the subjects to direct attention to one hemifield. Subsequently, a target appeared either at the cued location (80% of the trials) or in the opposite hemifield (20%). Consistent with recent results within the visual modality (e.g. Corbetta et al. [6]), we found that on invalid trials with target presented at the unattended location, brain activity increased in the temporo–parietal junction (and also inferior premotor cortex). Critically, this signal increase was independent of the modality of the target (see plots in Fig. 6B), indicating that a common neural system operated when attention-shifts were required during this task, for both visual and tactile targets. Similar observations were recently reported by Downar and colleagues [11], who also found activation of the temporo–parietal junction in a task engaging attentional control functions for vision and touch (plus audition in their study).

Finally, we have been able to demonstrate some link between activation of multimodal structures in temporo–parietal regions, and spatially-specific exogenous effects of tactile stimulation upon unimodal visual areas, using analyses of effective connectivity [16]. This method of analysis assesses any differential coupling between activity in different brain regions, depending on the condition during which activity is measured. We performed such an analysis on event-related fMRI data from subjects performing the simple detection of visual onsets in the left or right hemifield, either with or without simultaneous tactile stimulation at the same location [27]. As earlier described, when touch was stimulated at the same external location as a visual event, this resulted in amplification of activity in contralateral visual occipital areas (i.e. the lingual gyrus). Our analysis of connectivity tested if any brain region showed a significant change in coupling with the lingual gyrus (see Fig. 5), specific to the condition of spatially-congruent bimodal stimulation. Such a change in coupling was indeed found for the inferior parietal lobule (i.e. dorsal part of the temporo–parietal junction). This coupling increased during bimodal spatially-congruent stimulation (i.e. precisely when amplification of visual responses by touch was observed), as compared with bimodal stimulation when vision and touch were stimulated in opposite hemifields (i.e. when no amplification occurred). Fig. 6C shows illustrative results for one subject. The coronal section is taken through the maximum in the inferior parietal lobule for the coupling-related activation in this subject. The signal of this region is plotted against the signal in the vi-

sual occipital area contralateral to the touch (i.e. lingual gyrus). Activity in the two regions correlated during trials with spatially-congruent bimodal stimulation (continuous line), but did not when the visual and tactile stimuli were presented in opposite hemifields (dashed line). These results are consistent with our hypothesis that stimuli in one modality (i.e. touch) may affect activity in anatomically distant, unimodal areas that are responsible for processing stimuli in a different modality (vision), but at the same location, via higher-order multimodal areas (i.e. regions of the temporo–parietal junction here).

## 5. Conclusions

In this paper, we have discussed results from several imaging studies (including earlier unpublished data) which investigated the neural mechanisms of crossmodal interactions between vision and touch, in the context of spatial attention. We asked how the spatial unity of a single multimodal event in the external world might be represented in the brain, given that multiple spatial maps coexist, and that these are anatomically distant for separate sensory modalities. In the first section of this article we presented some new data, which allowed us to classify brain regions according to whether stimulus position and/or modality of the stimulation affects their activity. We found that stimulus position can affect brain activity both in a modality-specific manner for some brain regions, and in a multimodal manner for other regions. Modality-specific spatial effects were found relatively early in the cortical sensory processing pathways, while bimodal visuo–tactile responses were localised in higher association areas (i.e. the anterior part of the intraparietal sulcus). This may be consistent with crossmodal spatial integration occurring through converging feed-forward sensory pathways, which has become a standard model for crossmodal integration [14,28,36]. However, when we examined spatial attentional effects, we found that unimodal and multimodal brain regions showed related patterns of activation (e.g. signal increase during attention to contralateral locations), indicating possible interplay between the different spatial representations. Thus, tactile stimulation and/or attention to tactile stimuli on one side can affect activity within unimodal visual areas (extrastriate occipital areas), in addition to somatosensory (post-central gyrus) and multimodal (intraparietal sulcus) regions. These results highlight multiple but congruently active representations of space, arguing for an integrative mechanism based upon mutual influences rather than purely feed-forward convergence.

In the final part of paper, we presented evidence that may provide some initial indications about the control mechanisms enabling the coordination of spatially-specific activities within such distributed system. In particular, we highlighted regions in the temporo-parietal junction that respond to both visual and tactile stimulation, but did not show any specificity depending on the side stimulated (with the stimulus positions used here). These areas have earlier been associated with control of visuo-spatial attention [6], and were shown here to also be involved in tactile attention. It is possible that these may act as sources of the attentional signals that affect visuo-spatial contralateral representations in the occipital lobe, during purely visual tasks. Here we showed that these areas are also affected by tactile attention, suggesting that a common attentional control system might be responsible for the integration of unimodal and multimodal spatial representations.

One simple model would be that signals from unimodal regions contralateral to a stimulus (e.g. extrastriate occipital cortex for vision and post-central gyrus for touch) feed forward to multimodal control areas that receive afferent projections from both modalities and both hemifields (e.g. temporo-parietal junction). In these control regions, signals from different modalities and locations can interact. At this stage, additional signals specifying current posture (e.g. eye and limb position) might also have an influence [1]. Similarly, voluntary attention may also act at this high level to generate anticipatory spatial biases (e.g. in accordance with instructions concerning which hemifield and/or modality has to be attended). The output of such high-level areas could produce modulatory signals that might then influence appropriate unimodal spatial representations, where spatial attentional modulations are generally observed, via back-projections. However, because the control structures operate at a multimodal level, the results of the computations occurring at this control (source) level would also be transferred to unimodal areas (sites) for other modalities, leading to the observed coherence between anatomically distant spatial representations (see also Eimer, this volume for related arguments concerning event-related potentials).

Future work could directly test some predictions related to the propositions outlined above. In all the experiments reviewed here, the position of the eyes and the limbs was kept constant, with the left visual field and left hand placed in the left hemifield relative to the head and body (and vice-versa on the right). Given that spatial codes in early sensory regions are expressed in receptor-centred coordinates (retinotopic for vision and body-centred for touch), it will be im-

portant to understand the frame(s) of reference in which crossmodal effects arise in unimodal areas [34]. Specifically, any finding of crossmodal effects that ‘re-map’ in unimodal areas across changes in posture (see [34]) could support the hypothesis that the sources of these modulations are located in areas that re-map space according to the current relative position of the receptors (e.g. in temporo-parietal and frontal areas). Another element of the proposal outlined here concerns the possible role of spatial attention in the coordination of unimodal and multimodal spatial representations. Such a link between attentional control and coherent activity in anatomically distant brain areas would predict that any interference at the level of the attentional control might disrupt spatial coherence between the distant spatial representations. This might be tested by presenting subjects with a primary crossmodal spatial attention task (to fully engage the control attentional system), while also measuring stimulus-driven brain activity related to secondary task-irrelevant bimodal stimulations. It might be anticipated that any crossmodal influences on unimodal areas induced by the irrelevant bimodal stimulation (e.g. when spatially congruent versus incongruent irrelevant stimuli) might be suppressed during high attentional load in the primary multimodal task (see [22]; plus Rees and Lavie, this volume). The effects of spatially congruent versus incongruent bimodal stimulation could also be tested in patients with intact sensory-specific areas, but lesioned higher association areas (e.g. temporo-parietal junction). According to the proposals highlighted above, it may be expected that the spatial relation of two stimuli in different modalities would not affect activity in the intact unimodal regions, when the critical association areas are lesioned. Alternatively, transcranial magnetic stimulation (TMS) could be used to transiently disrupt processes in such high-order attentional areas in normal subjects. This should also result in attenuation of crossmodal influences upon unimodal brain areas. TMS might also help to reconstruct the suggested temporal sequence for stimulus-driven effects of feed-forward activations, engagement of multimodal control structures and then feed-back effects from these areas to unimodal areas.

In conclusion, the experiments presented here suggest at least two mechanisms for crossmodal spatial interactions between vision and touch. First, as commonly suggested (e.g. [3,28]) convergent feed-forward projections from unimodal to multimodal representations may allow stimuli in different modalities to interact in a spatially-specific manner in higher associative areas. Second, and more surprisingly, we found that directing attention towards one side of space for one modality can result in modulation of

both unimodal and multimodal contralateral representations, including unimodal areas which respond to a different modality. We suggest that a common multimodal attentional control system may mediate spatially-specific crossmodal effects on unimodal areas, via back-projections. Taken together, these results suggest links between spatial attention and crossmodal integration for vision and touch.

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