

Crossmodal Spatial Influences of Touch on Extrastriate Visual Areas Take Current Gaze Direction into Account

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Summary

Recent results indicate that crossmodal interactions can affect activity in cortical regions traditionally regarded as “unimodal.” Previously we found that combing touch on one hand with visual stimulation in the anatomically corresponding hemifield could boost responses in contralateral visual cortex. Here we manipulated which visual hemifield corresponded to the location of the stimulated hand, by changing gaze direction such that right-hand touch could now arise in either the left or right visual field. Crossmodal effects on visual cortex switched from one hemisphere to the other, depending on gaze direction, regardless of whether the hand was seen. This indicates that crossmodal influences of touch upon visual cortex depend on spatial alignment for the multimodal stimuli, with gaze posture taken into account.

Introduction

Much research on sensory processing in humans is concerned with a single sensory modality at a time. However, there is increasing interest in the issue of crossmodal interactions and their neural basis (e.g., Stein and Meredith, 1993; Kawashima et al., 1995; Sathian et al., 1997; Driver and Spence, 1998a; Calvert et al., 1999; Downar et al., 2000; Macaluso et al., 2000a). Behavioral studies demonstrate that stimuli in different sensory modalities can interact to affect perception (e.g., Driver and Spence, 1998b; Bertelson et al., 2000; McDonald et al., 2000; Shams et al., 2000; Spence et al., 2000). Several brain regions have been proposed as possible candidates for such crossmodal interactions. These include superior temporal sulcus (e.g., Calvert et al., 2000; Downar et al., 2000), inferior parietal lobule (Graziano and Gross, 1995; Macaluso et al., 2000b), intraparietal sulcus (Bremmer et al., 2001a; Macaluso et al., 2000a), premotor regions (Bremmer et al., 2001a), and superior colliculus (Stein and Meredith, 1993). Such regions are *multimodal* brain areas, containing neurons that respond to stimulation in more than one sensory modality (e.g., Leinonen et al., 1980; Bruce et al., 1981; Meredith and Stein, 1996; Duhamel et al., 1998; Andersen et al., 1997). Crossmodal effects might reflect interactions within such multimodal structures, where inputs from

different sensory modalities converge (Colby and Goldberg, 1999; Massaro, 1999).

Some evidence now suggests, however, that feed-forward convergence to multimodal structures may not tell the whole story, indicating that crossmodal interactions may also affect activity in brain areas traditionally considered as *unimodal* (e.g., Sathian et al., 1997; Driver and Spence, 1998a; Calvert et al., 1999; Eimer and Driver, 2000; Macaluso et al., 2000b; McDonald et al., 2000). Although some of these results might be explained by use of visual imagery during nonvisual tasks (see Sathian et al., 1997), other evidence concerning spatially specific crossmodal links now suggests that visuo-tactile interactions can affect activity within unimodal visual areas in a stimulus-driven (exogenous) manner (Macaluso et al., 2000b; Kennett et al., 2001; see also McDonald et al., 2000).

Such findings of spatially specific crossmodal influences on unimodal brain areas raise an important new issue concerning their spatial nature. While relatively early visual areas represent locations in terms of *retinal* locations, tactile stimulation is initially represented in *somatotopic* coordinates. When the eyes move or arm posture changes (as continuously occurs in daily life), the spatial alignment of such representations will change relative to each other. In our previous study (Macaluso et al., 2000b), the spatial relation of visual and tactile stimuli was fixed. Stimulation of the right hand always occurred in the right visual field, while any stimulation of the left hand always occurred in the left visual field. It is therefore possible that the observed effect of multimodal spatial congruency (Macaluso et al., 2000b) simply depends on bimodal stimulation of the same hemisphere. Such an interpretation would fit theories based on interhemispheric competition (Kinsbourne, 1970). This account would imply that, irrespective of the relative position of the visual and tactile stimuli in external space, stimulation of the *right* hand should always boost activity related to visual stimuli presented in the *right* visual field (because both modalities should activate the same hemisphere). Conversely, stimulation of the left hand should always boost visual responses to left visual field stimulation. A different prediction arises if crossmodal spatial interactions depend instead upon the spatial alignment of visual and tactile stimuli (e.g., in external space, or relative to the head or body). If so, a right-hand tactile stimulation should be able to boost visual responses for either the right or left visual field, depending on the current position of that hand with respect to the retina (see Driver and Spence, 1998a; Spence et al., 2000). Signals regarding current posture may be taken into account to update the “mapping” between spatial representations for different sensory modalities that initially use different coordinate systems (i.e., retinocentric for vision versus somatotopic for touch).

In the present study, we used event-related fMRI to investigate the effect of current gaze posture on visuo-tactile crossmodal spatial influences upon visual cortex. We delivered multimodal visuo-tactile stimulation either

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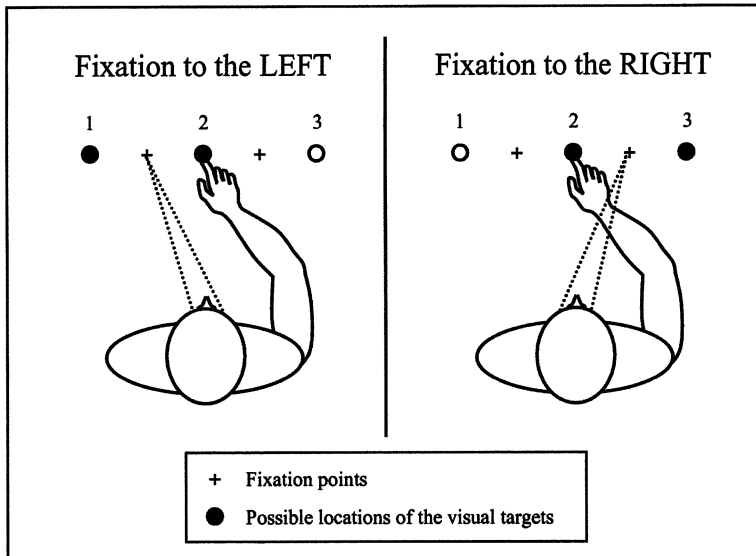


Figure 1. Schematic Depiction of Stimulus Positions and Gaze Directions Relative to the Subject's Head/Body

While lying in the scanner, subjects kept the right hand aligned with the head/body midline (at position 2). Fixation was maintained either to the left (as shown in the left panel of the figure) or to the right (right panel) of this central position. During leftward fixation, visual targets could be presented at either position 1 or position 2, while during rightward fixation, visual targets could be presented either at position 2 or position 3. Any task-irrelevant tactile stimulation was always delivered at position 2, to the right hand only. Thus spatially congruent multimodal stimulations arose in the right retinal hemifield during leftward fixation, but in the left retinal hemifield during rightward fixation. The right hand was visible for the first experiment, but completely occluded for the second experiment.

at the same or at different external locations, while manipulating gaze direction. Given our previous results (Macaluso et al., 2000b), we expected spatially specific crossmodal modulations in visual cortex (lingual/fusiform gyri). We predicted (given Macaluso et al., 2000b) that bimodal stimulation at the same external location would produce an increased visual response, while bimodal stimulation at different locations should not. To assess visual responses, we compared activity during visual stimulation of the contralateral versus ipsilateral visual fields. Note that because of this, all our reported crossmodal effects are spatially specific and cannot be due to nonspecific effects of merely adding any second stimulus in touch, or of changing gaze direction per se.

Our manipulation of gaze direction entailed that, on some trials, spatially congruent multimodal stimulations would occur in one visual field, while on other trials, multimodal spatial congruence would occur in the opposite visual field, despite that the possible tactile stimulation to just the right hand remained unchanged. Figure 1 illustrates this. When the subject fixated to the left, multimodal correspondence in external space occurred when the tactile stimulation at the centrally located right hand was delivered concurrently with a visual target in the *right* visual field (i.e., both stimuli in position 2: see Figure 1). If touch to the centrally located right hand was combined with a target in the *left* visual field, the multimodal stimulation occurred at different external locations when fixating left (i.e., position 1 for vision and position 2 for touch). The critical point is that the reverse was true when the subject fixated to the right. Now multimodal correspondence in external space was only obtained when the same touch was presented together with a visual target in the *left* rather than right visual field (i.e., both stimuli in position 2: see Figure 1). It is important to note that this simple manipulation of gaze direction will have dramatic consequences for neural representation of the stimuli in the brain. During left fixation, visual and tactile stimuli in a spatially congruent external location (i.e., at position 2) will initially be processed in the *same* hemisphere (i.e., the left hemi-

sphere); but during right fixation, the spatially congruent bimodal stimulation (still at position 2) will now be processed in *opposite* hemispheres for the two modalities (still left hemisphere for touch, but now right hemisphere for vision).

During fMRI scanning, our subjects were required to detect any visual onset while ignoring the task-irrelevant, unseen tactile stimulations delivered to the right hand. Gaze was maintained for eight successive trials either to the left or to the right (see Figure 1 and Experimental Procedures). Note that the possible external locations of the visual targets were shifted along with the current direction of gaze (see Figure 1), so that the visual targets were presented *at the same possible retinal locations*, irrespective of gaze direction. However, the change of gaze altered the retinal location of any spatially congruent multimodal stimulation (from one visual hemifield to the other). We predicted that this change in retino-centric location for the critical spatially congruent multimodal stimulation (despite the constant somatotopic location of any tactile stimulation on the right hand) should result in a shift of the anatomical locus of the crossmodal effects upon visual cortex, from one hemisphere to the other. This would demonstrate that postural information (here the current direction of gaze) is taken into account in determining crossmodal spatial interactions.

In a second experiment, we repeated the same manipulations, but now occluded the stimulated right hand from sight completely. This should reveal whether any crossmodal effect of spatially congruent touch on visual areas (and/or any modulation of this by current gaze direction) is dependent on seeing the current visual location of the stimulated hand.

Results

fMRI Analysis

Our analyses sought first to localize brain areas whose response to visual targets was determined by which retinal hemifield these fell in (i.e., differential activation

depending on visual stimulation in the left versus right visual field, or vice versa), with activation expected in contralateral occipital visual areas. Following Macaluso et al. (2000b), within these areas we then investigated any effect of multimodal spatial correspondence during bimodal trials (i.e., when touch was delivered concurrently at the same external location as the visual target, versus bimodal stimulation in different external locations). In addition, we now tested for any effect of eye position (leftward versus rightward gaze) upon these multimodal spatial effects upon visual responses.

Effects of Visual Stimulation in Different Visual Fields, and of Right-Hand Tactile Stimulation

The effect of the retinal hemifield of visual stimulation was revealed by comparing brain responses to lateralized visual targets in one visual field versus another, pooling across the two different fixation locations, and irrespective of the presence or absence of touch. For the right-visual-field minus left-visual-field comparison, this meant comparing targets presented at position 2 versus position 1 during left fixation (see Figure 1), and position 3 versus position 2 for right fixation. Thus, these comparisons should reveal activation of brain areas that represent the left or right side of visual space in terms of *retinal* visual field.

The results of these analyses are shown in Figures 2A and 2B for the first experiment (with hand visible; see also Table 1) and 2D and 2E for the second experiment (with hand occluded; see also Table 2). As expected, the right- minus left-visual-field comparison activated superior and lateral occipital gyri, extending into ventral occipital areas to include lingual and fusiform gyri, all contralateral to the stimulated visual hemifield (see ventral view at center of Figures 2A and 2D). The same comparison also revealed activation of contralateral left posterior parietal lobule and left intraparietal sulcus (see lateral view of the left hemisphere in Figures 2A and 2D). The reverse comparison (visual target in left- minus right-visual-field) showed a similar pattern, but now with all activation clusters in the right hemisphere. Peak activations were detected in superior, lateral, and ventral occipital areas (see Figures 2B and 2E and Tables 1 and 2). In neither of the two experiments did this comparison activate the right posterior parietal lobule or intraparietal sulcus (which might have been active during both left and right visual field stimulation). Contralateral primary visual cortex was activated only in the second experiment, for stimulation of right visual field (see Table 2). This lack of consistent V1 activation may be due to the low-contrast peripheral stimulation used, and/or to the continuous visual stimulation provided by the illuminated background in the scanner environment. This outcome is consistent with our previous results (Macaluso et al., 2000b), using similar experimental visual stimuli. A different type of visual stimulus might be required to study crossmodal interactions in primary visual cortex.

Figure 2 also shows activations related to presentation of the task-irrelevant *tactile* stimulation (Figure 2C with hand visible, and 2F with hand occluded). As expected, tactile stimulation of the right index finger activated contralateral left superior post-central gyrus, the primary somatosensory representation of the right hand (Coghill et al., 1994; Francis et al., 2000). In addition,

activation was detected in the parietal operculum, possibly corresponding to the secondary somatosensory area (Burton et al., 1993). This activation was confined to the left hemisphere in the first experiment (hand visible, Figure 3C). In the second experiment, some weaker activation was found also in the right hemisphere, with the cluster extending to the superior temporal gyrus and superior temporal sulcus (hand occluded, Figure 3F).

Effect of Spatial Alignment for Bimodal Stimulation

Our main aim was to investigate the effect of presenting an irrelevant tactile stimulus either spatially congruent with the concurrent visual target in external space, or in a different external location to it. Thus for each experiment, we compared trials when touch was presented at the same external location as the visual target, versus trials when visual and tactile stimulations were presented on opposite external sides, *given the current fixation*. Note that touch was delivered to the right hand located in the right visual field during left fixation, but to the same right hand (at the same external location) in the left visual field when gaze was directed rightwards. Hence, the critical effect of external spatial correspondence (on trials with multimodal stimulation only) occurred for right-visual-field stimulation during leftward fixation, but for left-visual-field stimulation during rightward fixation. Because multimodal correspondence in external space always occurred in position 2 (see Figure 1), we used exclusive masking (as implemented in SPM99; www.fil.ion.ucl.ac.uk) to ensure that the critical multimodal effects could *not* be accounted for simply by presentation of a visual target alone in position 2. Hence, any voxel showing an interaction between side of the visual targets and direction of gaze in trials when touch was absent was removed from the critical analysis (threshold for exclusion was p -uncorrected = 0.05).

This analysis revealed significant activation of the lingual gyri, extending into posterior fusiform gyri. Figure 3 shows the activation clusters superimposed on a coronal section of the structural MNI template, for the two experiments. The plotted bars for each hemisphere indicate the size of the effect of *contralateral-minus-ipsilateral visual targets* (expressed in standard error units), according to current gaze direction and the presence or absence of touch. This effect is simply the difference between activation for contralateral-minus-ipsilateral visual targets (i.e., right-visual-field minus left-visual-field targets, for the left hemisphere; and left-visual-field minus right-visual-field targets, for the right hemisphere). It is therefore a spatially specific visual response. The critical effect of congruency in external space for multimodal stimulation is highlighted within each graph by the difference between the two rightmost bars (blue arrows in Figures 3A–3D). To further confirm that the activations were not simply due to the change of gaze direction per se, for each activated cluster we also tested for the main effect of gaze direction during stimulation of the contralateral visual hemifield only, and the interaction between gaze direction and presence of touch for this.

Experiment 1: Hand Visible (Table 3). For the *left lingual/fusiform* gyrus, the effect of visual targets in the contralateral right visual field (minus left visual field) was particularly strong (z value = 3.6; p -corrected = 0.055)

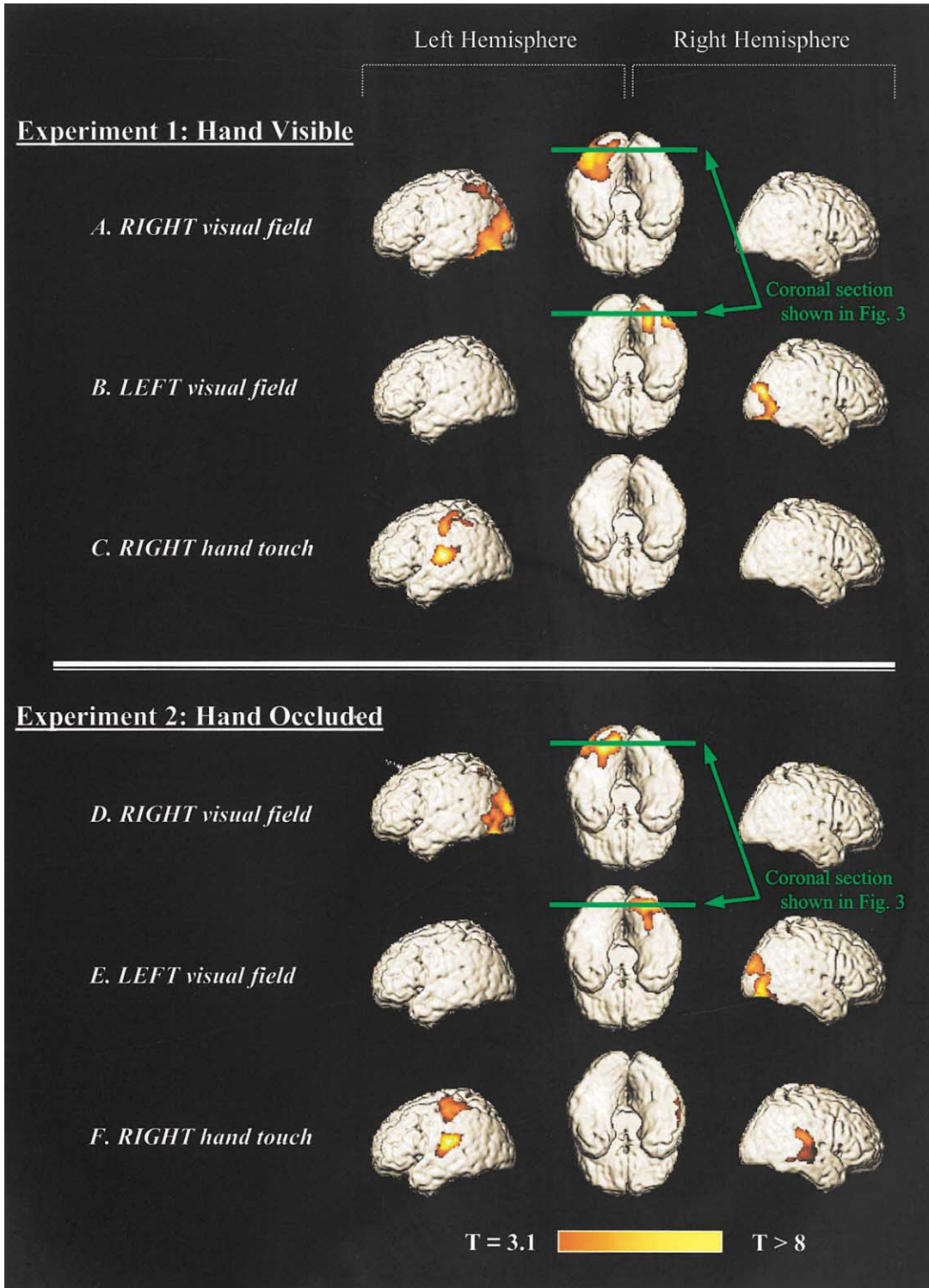


Figure 2. Main Effects of Lateralized Stimulation

Lateralized sensory stimulation produced activation in contralateral sensory-specific areas. (A)–(C): first experiment (right hand visible); (D)–(F): second experiment (right hand occluded). (A and D) Brain activations for targets in the (retinal) right minus left visual field are rendered on the surface of the MNI brain template; cerebellum removed to allow direct view of the ventral occipital surface. (B and E) Left-visual-field targets minus right-visual-field targets. (C and F) Main effect of tactile right-hand stimulation, showing activation of contralateral primary somatosensory areas in the left hemisphere, plus additional higher order somatosensory areas (parietal operculum). Green lines indicate location of coronal section shown in Figure 3, demonstrating here that the lingual/fusiform region shown there responded to stimulation of the contralateral *retinal* visual field.

Table 1. Effect of Sensory Stimulation in Experiment 1 (*Hand Visible*)

Anatomical Area	Hemisphere	Coordinates	z values	p values
RIGHT Visual Field Stimulation				
Lingual/fusiform gyrus	Left	-28 -74 -16	>8	<0.001
Superior occipital gyrus	Left	-24 -92 18	6.3	<0.001
Middle occipital gyrus	Left	-52 -74 4	5.6	<0.001
Superior parietal gyrus	Left	-28 -64 58	4.2	<0.001
LEFT Visual Field Stimulation				
Lingual/fusiform gyrus	Right	26 -72 -10	5.2	<0.001
Superior occipital gyrus	Right	36 -78 18	4.4	<0.001
Middle occipital gyrus	Right	50 -70 -2	3.8	<0.001
Tactile Stimulation of the RIGHT Hand				
Superior post-central gyrus	Left	-48 -20 48	5.0	0.004
Parietal operculum	Left	-52 -20 10	5.9	<0.001

Anatomical areas, Talairach coordinates, z values, and corrected p values for the regions showing a main effect of sensory stimulation in first experiment (hand visible). For vision, we compared visual targets in the right versus left retinal hemifield (and vice versa), pooling across leftward or rightward fixation, and presence or absence of touch. For tactile stimulation, we compared all trials with tactile stimulation versus all trials without. P values are corrected for multiple comparisons. Coordinates in millimeters: x, distance to right (+) or left (-) of the midsagittal plane; y, distance anterior (+) or posterior (-) to vertical plane through anterior commissure; z, distance above (+) or below (-) intercommissural (AC-PC) line.

when touch on the right hand was presented at the same location as these visual targets in external space: that is, during *leftward* fixation (see red bar third from left, in plot for the left hemisphere in Figure 3A). During rightward fixation, the same touch was now presented at a visual location ipsilateral to this hemisphere (i.e., in the left visual field), which reduced the effect of contralateral right visual targets (fourth bar from left, in plot for the left hemisphere in Figure 3A). Thus, vision and touch at the same external location boosted responses to contralateral visual targets, while touch at the opposite location in external space did not. This cannot be explained simply by the external location of the visual target itself (i.e., at position 2; see Figure 1) during leftward fixation because the direction of gaze did *not* significantly affect the size of the visual responses when touch was not present (see first and second bars from left in Figure 3A; p -uncorrected > 0.05). If only stimulation of the right visual field is considered (rather than the right- minus left-visual-field difference), some main effect of gaze direction was found (see Table 3), but critically there was also an interaction between direction

of gaze and presence of touch (z value = 2.8; p -corrected = 0.040). Thus, although the response for right-visual-field targets was somewhat higher during leftward fixation, this effect was significantly larger in the presence of touch, further underlining the crossmodal nature of the critical effect.

An analogous pattern of activation was found for the lingual/fusiform region in the *right hemisphere*, with the increased effect for contralateral-minus-ipsilateral visual targets during spatially congruent tactile stimulation now being specific to *rightward* rather than leftward fixation (z value = 4.0; p -corrected = 0.005). When fixating right, multimodal stimulation that was spatially congruent in external space arose in the left visual hemifield, contralateral to this hemisphere (although note that the right-hand touch itself was now ipsilateral to this hemisphere, in somatotopic terms). The amplification of the effect during multimodal spatial alignment can be appreciated by comparing the third and fourth bars from the left in the plot of Figure 3B (see blue arrow). Again this effect was not observed when touch was absent (see first and second bars from the left in Figure 3B;

Table 2. Effect of Sensory Stimulation in Experiment 2 (*Hand Occluded*)

Anatomical Area	Hemisphere	Coordinates	z values	p values
RIGHT Visual Field Stimulation				
Lingual/fusiform gyrus	Left	-22 -76 -8	>8	<0.001
Superior occipital gyrus	Left	-20 -98 16	7.3	<0.001
Middle occipital gyrus	Left	-40 -88 4	5.3	<0.001
Calcarine fissure	Left	-8 -90 0	6.6	<0.001
Superior parietal gyrus	Left	-14 -62 60	3.9	0.122
LEFT Visual Field Stimulation				
Lingual/fusiform gyrus	Right	30 -78 -10	6.2	<0.001
Middle occipital gyrus	Right	40 -82 0	4.9	<0.001
Superior occipital gyrus	Right	20 -92 20	5.2	0.002
Tactile Stimulation of the RIGHT Hand				
Superior post-central gyrus	Left	-46 -18 60	5.7	<0.001
Parietal operculum	Left	-48 -22 20	7.0	<0.001
	Right	56 -28 20	4.3	0.001

Anatomical areas, Talairach coordinates, z values, and corrected p values of regions showing a main effect of sensory stimulation in the second experiment (hand covered). Occlusion of the hand did not substantially affect the event-related responses to sensory stimulation (compare with Table 1, and see also Figure 2). P values are corrected for multiple comparisons.

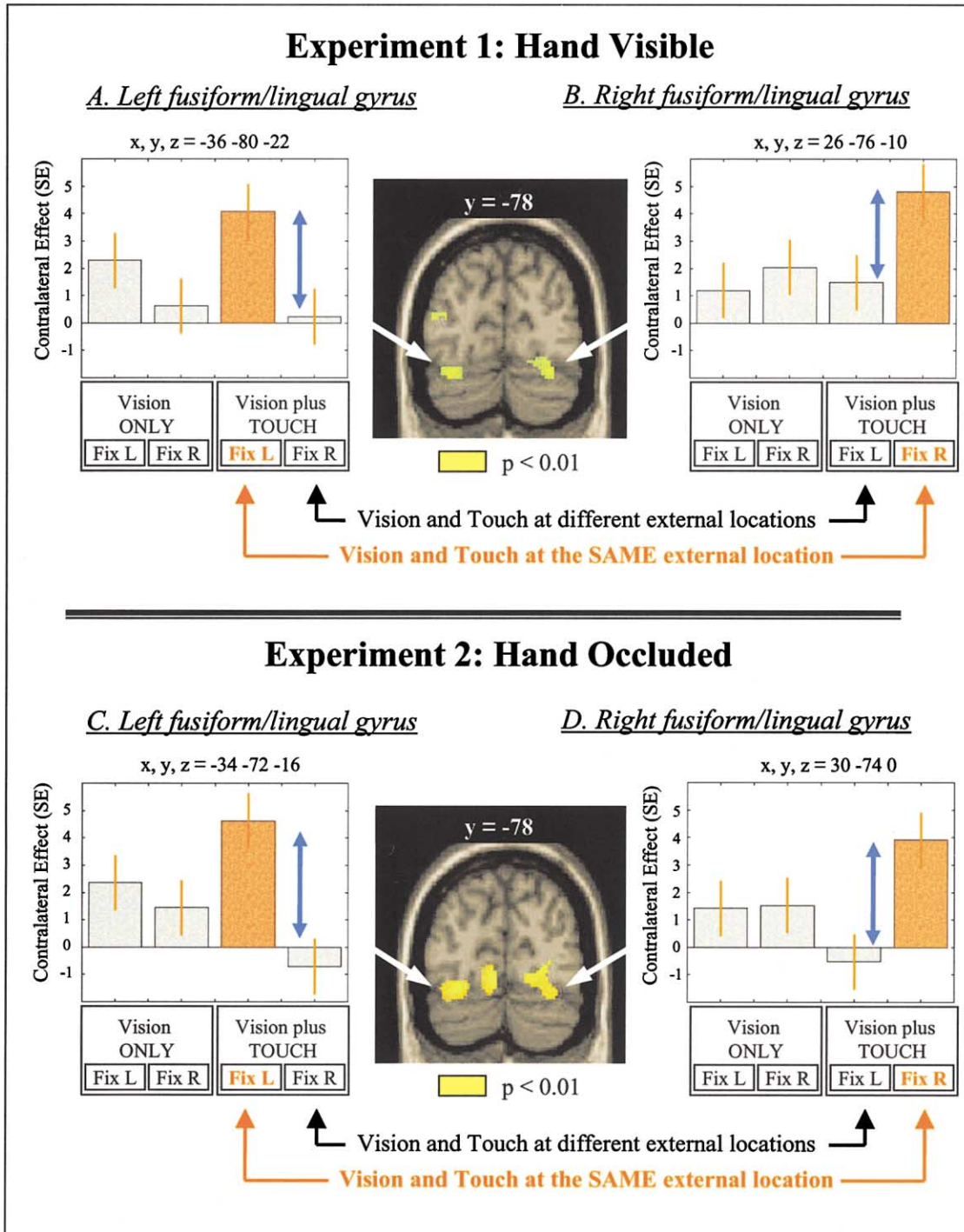


Figure 3. Effect of Multimodal Congruency in External Space

Anatomical location and signal plots (in standard error units) for areas showing a significant effect of spatial congruence for multimodal stimulation (i.e., at same versus different external locations). (A)–(B): first experiment (right hand visible); (C)–(D): second experiment (right hand occluded). Plots show effect of contralateral-minus-ipsilateral visual targets (i.e., activity for stimulation in the retinal visual field contralateral minus ipsilateral to the cluster), according to direction of gaze and presence or absence of touch. For left hemisphere (Figures 3A and 3C), plot shows activity for right- minus left-visual-field stimulation, while for right hemisphere (Figures 3B and 3D), effects are calculated for left- minus right-visual-field stimulation. For both hemispheres, positive values thus indicate larger responses for visual targets presented in the contralateral retinal visual field. Critical crossmodal effects are highlighted by differences between the third and fourth bar from the left (bars 3 and 4), within each graph (see blue arrows). In left hemisphere (Figures 3A and 3C), responses specific to contralateral visual targets combined with tactile stimulation on the right hand are significantly larger during left fixation (bar 3) than during right fixation (bar 4); see blue arrow. During such left fixation, both visual and tactile stimulation were presented in the contralateral visual hemifield (i.e., in spatial correspondence; see Figure 1); during right fixation, tactile stimulation was ipsilateral to this hemisphere (i.e., vision and touch in different external

Table 3. Crossmodal Influences and Modulation by Gaze Direction

Anatomical Area	Statistical Test	Co-ordinates	z	p values
Experiment 1: Hand Visible				
Left lingual/fusiform	a. Spatial correspondence in multimodal trials	-32 -74 -22	3.6	0.055
	b. Gaze direction × Touch	-36 -80 -22	2.8	0.040
	c. Main effect of gaze direction: Left > Right	-24 -76 -20	3.9	0.001
Right lingual/fusiform	a. Spatial correspondence in multimodal trials	32 -80 -22	4.0	0.005
	b. Gaze direction × Touch	26 -76 -10	2.7	0.050
	c. Main effect of gaze direction: Right > Left	22 -74 -10	2.7	0.047
Experiment 2: Hand Occluded				
Left lingual/fusiform	a. Spatial correspondence in multimodal trials	-34 -76 -16	4.2	0.006
	b. Gaze direction × Touch	-34 -72 -16	2.7	0.034
	c. Main effect of gaze direction: Left > Right	-24 -78 -18	2.4	0.069
Right lingual/fusiform	a. Spatial correspondence in multimodal trials	22 -88 14	4.3	0.002
	b. Gaze direction × Touch	30 -74 0	2.9	0.038
	c. Main effect of gaze direction: Right > Left	-	-	n.s.

Crossmodal influences and gaze-dependent effects in the lingual/fusiform region as observed in the two experiments. For each cluster we report the maximum for: (a) modulation of responses to contralateral-minus-ipsilateral visual targets by spatial correspondence (i.e. interaction between gaze direction and stimulated visual field, during multimodal stimulation only); (b) interaction between gaze direction and presence of touch during stimulation of just the contralateral visual field (showing a stronger effect of gaze direction in presence of touch); (c) main effect of gaze direction during stimulation of the contralateral visual field only. P values are corrected for multiple comparisons. (n.s.: p-uncorrected > 0.05).

p-uncorrected > 0.05). When considering left-visual-field stimulation only, there was some main effect of gaze direction (see Table 3), but again this was significantly modulated by the presence of touch (z value = 2.7; p-corrected = 0.050).

Experiment 2: Hand Occluded (Table 3). The spatially specific crossmodal effects, and their modulation by gaze direction, were replicated for the second experiment with the hand occluded. In the *left hemisphere* (see Figure 3C), maximal effects for contralateral-minus-ipsilateral visual targets were observed when combined with right-hand touch during leftward fixation (i.e., for spatially coincident multimodal stimulation in the contralateral right visual field; z value = 4.2; p-corrected = 0.006). Rightward fixation resulted in minimal activity for contralateral-minus-ipsilateral visual targets with concurrent touch (note that during rightward fixation, the right hand was located in the left visual field, ipsilateral to this hemisphere). When considering only right-visual-field stimulation (rather than the right-minus-left difference), there was no main effect of gaze direction, but its critical interaction with the presence of touch was again significant (z value = 2.7; p-corrected = 0.034, see Table 3).

Finally, the *right lingual/fusiform* gyrus also showed an analogous pattern, further replicating Experiment 1 (see Figure 3D). Maximal responses to contralateral-minus-ipsilateral visual targets were detected for multimodal trials during rightward fixation, when left visual targets and touch were presented at the same external location (z value = 4.3; p-corrected = 0.002). Moreover,

when only contralateral left visual targets were considered, there was no main effect of gaze direction (see Table 3), but this again interacted critically with the presence of touch (z value = 2.9; p-corrected = 0.038, see Table 3). Thus, Experiment 2 replicated the spatially specific modulations of visual areas by task-irrelevant tactile stimulation, and its dependence on current gaze direction, while showing that these effects do not require sight of the hand.

In both experiments, our significant crossmodal effects were confined to ventral occipital visual areas (some effects were also detected in the lateral occipital gyrus, but did not survive the statistical threshold for corrected significance). This was also found in our previous study with a similar paradigm (Macaluso et al., 2000b). The reason for the ventral localization of the crossmodal influences on visual cortex needs further investigation. If the visual stimuli were presented lower in the visual field, the crossmodal effects might appear in more dorsal occipital regions. Intriguingly, the only parietal areas to show a main effect of the stimulated visual hemifield (i.e., left posterior parietal cortex) did not show any crossmodal effect. We must note that since our hypotheses and analyses specifically concerned areas showing spatially specific responses to lateralized contralateral visual stimuli, we cannot exclude other regions (e.g., multimodal areas in frontal or parietal cortex and/or subcortical areas, such as the superior colliculus) from playing a more general role in the task.

Our analysis used scan-to-scan variance (fixed ef-

locations). The situation reverses for the right hemisphere (Figures 3B and 3D). Now multimodal spatial correspondence in the contralateral visual field was achieved with gaze directed rightward (see Figure 1), and indeed responses specific to contralateral visual targets with concurrent touch were now significantly larger for rightward fixation (bar 4 versus 3, in the right-side signal plots; see blue arrow). Note that for both hemispheres, these modulations of visual responses specific to contralateral visual targets by spatially congruent touch were indeed dependent on the presence of touch. Gaze direction did not significantly affect these effects when touch was absent (compare bars 1 and 2 within each plot).

Table 4. Reaction Times in the Eight Conditions for the Two Experiments

Touch	Absent				Present			
	Left		Right		Left		Right	
Gaze direction	Left	Right	Left	Right	Left	Right	Left	Right
Side of the visual target	Left	Right	Left	Right	Left	Right	Left	Right
Experiment 1: Hand Visible								
Means	407	414	420	408	441	396	404	395
SD	41	62	66	48	87	64	65	59
Experiment 2: Hand Occluded								
Means	412	402	400	408	372	378	360	373
SD	77	87	82	71	92	94	101	91

Mean reaction times in milliseconds with standard deviations (SD) for the eight experimental conditions, in the two experiments.

fects). Thus, statistical inference concerns the pool of subjects that participated. However, it is encouraging that all the critical effects replicated across the two experiments (with only one subject participating in both).

Overall, these fMRI results indicate that touch can affect visual responses in occipital areas traditionally considered as unimodal, in a spatially specific manner, such that responses specific to contralateral visual stimulation increase when touch is also stimulated at the same location. As discussed elsewhere, this effect may be attributed to crossmodal spatial integration, and/or to crossmodal links in spatial attention (see McDonald et al., 2001; Macaluso et al. 2001). Regardless of this, the main concern of the present paper was to determine whether the crossmodal influence depends on the alignment of tactile and visual stimuli in external space, or simply on their projections to a common hemisphere (c.f. Kinsbourne, 1970). This was tested by manipulating gaze direction. Critically, we found that the crossmodal effects depend on the spatial alignment between visual and tactile events in external space, taking into account current eye-position. Thus, while right-hand tactile stimulation boosted responses to left-visual-field targets under one gaze direction, the same tactile stimulation boosted right-visual-field targets under the other gaze direction. Moreover, note that in the latter case, the concurrent visual and tactile stimuli that led to enhanced activation actually project initially to different hemispheres. Finally, the results of the second experiment (when the stimulated hand was occluded) indicate that these crossmodal effects, and their modulation by current gaze direction, do not require sight of the touched hand.

Behavioral Performance

Table 4 shows mean reaction times and standard deviations for the detection of visual targets in the two experiments. Reaction times are divided according to the eight experimental conditions (i.e., visual target in the left or right visual field, for leftward or rightward gaze direction, with or without concurrent touch to the right hand). For each experiment, two separate three-way ANOVAs did not find any significant term (all p 's >0.05). The lack of clear behavioral cueing effects might initially seem surprising, given that previous studies have clearly shown that spatially congruent tactile cues can facilitate certain visual judgements (e.g., Spence et al., 1998). However, it should be noted that the present task was

chosen to optimize the fMRI design, not to provide a detailed psychophysical measure. In fact, responses on just one constant button, using the hand opposite to that which can be tactually stimulated, are unlikely to provide clear behavioral evidence for crossmodal cueing (see Driver and Spence, 1998b; Spence et al., 1998, for further remarks on this). The upside of the null behavioral results in the present study is that the fMRI effects we observed cannot be secondary to differences in behavioral latencies, since the latter differences were not consistently found.

Discussion

The present experiment investigated spatially specific effects of tactile stimulation on responses to concurrent visual stimuli, in visual cortex. Macaluso et al. (2000b) had previously found that spatially congruent touch could boost responses in the lingual and fusiform gyri to a concurrent visual target. Here we presented concurrent, bimodal visuo-tactile stimulations either at the same or at different external locations. Comparing spatially congruent minus incongruent multimodal stimulation, we found enhanced activation of the contralateral lingual/fusiform gyrus, which replicates and extends our previous findings (Macaluso et al., 2000b). Critically, the present design also manipulated gaze direction for the first time. While any spatially congruent multimodal stimulation always occurred at the same external location, this changed its location from one visual hemifield to the other, depending on the current direction of gaze (see Figure 1). Note that such changes of gaze direction are commonplace in daily life, but that they raise the problem of whether different sensory modalities are kept in spatial register across such postural realignments. Our results showed that the crossmodal effects switched hemisphere in accordance with current gaze direction, affecting the lingual/fusiform regions on one side of the brain or the other depending on this (see Figure 3).

These results indicate that the crossmodal spatial interactions are concerned with the spatial alignment of multimodal stimuli in external space (or with respect to the body), rather than simply depending on initial projection of the visual and tactile events to a common hemisphere. Moreover, a second experiment revealed that these effects were not dependent on visibility of the stimulated hand, showing that the location of that hand with respect to current gaze direction still deter-

mined the crossmodal effect even without direct sight of the hand. This indicates a role for extra-retinal information about current posture (presumably via proprioception) in modulating the spatial interactions between touch and vision (see Graziano, 1999).

Several recent studies have also shown that multimodal interactions do not only affect high-order polysensory areas, but can also affect activity in relatively early areas that are traditionally considered to be unimodal (e.g., Sathian et al., 1997; Calvert et al., 1999; Eimer and Driver, 2000; Macaluso et al., 2000b), as here. While some of these crossmodal effects were constrained just by temporal properties of the stimulation (Calvert et al., 1999) or by the type of task required (Sathian et al., 1997), here we present stimulus-driven crossmodal effects that were specifically constrained by the spatial location of the stimuli. This spatial specificity is expressed in the “contralateral-minus-ipsilateral effects” associated with presentation of peripheral visual targets in one visual field versus the other (see Figure 3). Any experimental factor that induces a change in the size of these effects must be affecting visual responses in a *spatially specific* manner. The use of this index, for visual responses that are specific to contralateral visual targets, avoids the possibility of multimodal stimuli and/or gaze direction affecting occipital cortex in some nonspecific way (e.g., any multimodal stimulation simply producing more overall activity than unimodal stimulation).

Two further points should be noted. First, the lingual/fusiform region, where the critical crossmodal effects were found, did not show any main effect of tactile stimulation. As expected, touch on the right hand directly activated only somatosensory areas, in the left postcentral region and parietal operculi (see Figures 2C and 2F). No such effect was found in the lingual/fusiform region, consistent with traditional views that this is a unimodal visual region that does not respond directly to touch *per se*. Second, the response of this lingual/fusiform region to visual stimuli depended strongly on which *retinal* hemifield these targets appeared in (see Figures 2A, 2B, 2D, and 2E, where visual responses are displayed according to the visual hemifield stimulated). These two observations, together with the anatomical localization of the clusters in posterior occipital cortex, seem consistent with the proposal that the crossmodal influences we report here affect unimodal visual cortex, as traditionally conceived.

Different sensory modalities initially encode stimulus position according to different coordinate systems (i.e., retinal coordinates in early visual areas, and somatotopic coordinates for tactile areas), raising the question of how the different senses can communicate to produce spatially specific interactions, such as those observed here. Moreover, changes of posture, such as shifts in gaze, mean that a particular somatotopic location will not invariably correspond to a fixed retinal location in external space (nor vice versa), thus raising the issue of whether crossmodal links may “re-map” across postural changes. Here we showed with fMRI that crossmodal effects of touch upon human visual cortex do indeed re-map across changes in gaze direction, such that while touch on the right hand can boost responses to a visual target in the right visual field (activating the

left lingual/fusiform gyri) under one gaze posture, the same touch can instead boost a left-visual-field target (now activating the right lingual/fusiform gyri) for another gaze direction. Moreover, this effect does not require sight of the stimulated hand, suggesting a role for a third modality (i.e., proprioceptive information about current eye position) in modulating the spatial links between touch and vision.

A combination of extra-retinal signals about current gaze direction, together with spatial information from visual and somatosensory modalities, may arise in higher association areas, with the outcome then being relayed to lower sensory specific areas via back-projections. It is already known that activity in several parietal and premotor areas combines information from vision, audition, or touch, together with extra-retinal signals about current eye position, to produce “gain-field” modulation of sensory responses (e.g., Andersen et al., 1997; Bremmer et al., 2001b). Although such effects have often been studied in relation to sensorimotor transformations in motor tasks (e.g., DeSouza et al., 2000; Snyder, 2000), similar mechanisms might operate to solve the coordinate transformations required for crossmodal sensory integration (Bremmer et al., 2001b). The anatomical overlap between brain regions that contain multimodal neurons (e.g., Graziano and Gross, 1995; Duhamel et al., 1998) and those showing gain-field modulations by current posture (e.g., Striccanne et al., 1996; Andersen et al., 1997) may accord with this.

Some studies have found modulation by gaze direction even for visual occipital neurons (e.g., Galletti and Battaglini, 1989; Rosenbluth and Allman, 2002). However, it is thought that the gaze directions signals producing such effects may be relayed from higher parietal and/or frontal areas to such lower visual areas (e.g., Andersen et al., 1997; Rosenbluth and Allman, 2002). This would accord with our current proposal that integrated signals relating current posture to the location of multimodal stimuli in external space may reach occipital cortex from higher order areas (see also Macaluso and Driver, 2001). However, it should be noted that the present effects were not simply due to gaze posture modulating visual responses directly. Instead, the influence of gaze direction was most pronounced for the crossmodal effect of touch upon vision (see Figure 3). The purely visual responses in the lingual/fusiform gyri (i.e., in the absence of touch) were mainly determined just by the retinal hemifield of the visual target. Gaze direction had a stronger effect on the lingual/fusiform gyri contralateral to the visual target when tactile stimulation was also present.

Our results show that concurrent stimulation in touch boosted activity in visual cortex specifically when presented at the same external location as the visual target. Shifting the direction of gaze reversed which visual hemifield (and hence which hemisphere) was boosted by a right-hand touch. Further variations on our paradigm could shift the hand in space, instead of the direction of gaze, to test whether this can also induce an analogous “re-mapping” of the crossmodal influences.

In conclusion, our results confirm that crossmodal spatial interactions between touch and vision can affect brain activity in visual cortex (see also Macaluso et al., 2000b). These interactions are spatially specific, with

tactile stimuli at the same external location as visual events boosting responses to these visual targets in contralateral visual cortex, while multimodal stimulation at different external locations does not (see Figures 3A–3D). Critically, the present experiment also shows that these multimodal interactions take current gaze direction into account, even though they affect posterior visual areas that are traditionally thought to code visual space primarily in relation to the retina.

Experimental Procedures

Subjects

Six right-handed volunteers participated in the first experiment (mean age of 26 years; range 21–33). Five different subjects plus one subject from the first group participated in the second experiment (mean age of 30 years; range 21–43). After receiving an explanation of the procedures, subjects gave written informed consent. The study was approved by the Joint Ethics Committee of the Institute of Neurology and the National Hospital for Neurology & Neurosurgery.

Paradigm

Functional MRI data were acquired as subjects detected peripheral visual targets while maintaining fixation at one of two off-center locations (see Figure 1). Eight event types were organized in a $2 \times 2 \times 2$ factorial design. One factor was the direction of fixation with respect to the head/body (leftward or rightward). The second factor was the retinal hemifield of the peripheral visual target, either left or right of the position that was fixated. The third factor was the presence or absence of unseen tactile stimulation to the right index finger, held in a fixed position on the mid-sagittal plane. In the first experiment, the centrally placed right hand was visible to the subject throughout the experiment; while in the second experiment it was completely occluded with a black panel.

This design allowed us to investigate the effect of presenting visual and tactile stimuli either at the same external location (multimodal spatial correspondence) or in different locations, as in Macaluso et al. (2000b), but while also manipulating for the first time which particular retinal visual location fell at the same position in external space as the fixed tactile stimulation (see Figure 1). Hence, we could establish whether the effects of multimodal spatial congruence in visual cortex (see Macaluso et al., 2000b) simply relate to visual and tactile stimulations being delivered to the same hemisphere; or if they depend instead on the alignment of the stimuli in external space.

Stimuli and Task

Subjects lay in the scanner with the right hand resting on a rigid plastic support. The index finger was aligned to the head/body midline (see Figure 1). Two LEDs were placed approx. 7.5° to the left and right of the head/body midline. These served as potential fixation points (marked as “+” in Figure 1). Three clusters of adjoining LED-pairs each served as potential visual targets in peripheral vision. One cluster was placed centrally with respect to the head/body (position 2 in Figure 1), in close spatial proximity with the right index finger that could be stimulated tactually. The other two LED clusters were placed approximately 15° to the left and to the right of the central midline (positions 1 and 3, respectively, in Figure 1). The scanner environment was dimly lit and subjects viewed all LEDs through a mirror system. In the first experiment only, the subject could also see the centrally placed right hand. In the second experiment, the right hand was occluded with a black panel (the scanner environment was still dimly lit, but the right hand could no longer be seen and the wide occluding panel did not mark its location). The mirror system comprised two mirrors placed on top of the whole-head RF coil, such that the whole scene could be viewed without any mirror-image reversal. A third mirror was also placed on top of the RF coil, to allow monitoring of eye position throughout the experiment (see below).

The visual targets consisted of brief flickers (300 ms, 10 Hz) of an LED cluster at 7.5° eccentricity, unpredictably to either the left

or right of current fixation (position 1 or 2 during left fixation, and 2 or 3 for right fixation; note that these possibilities were retinally equivalent). On an unpredictable half of the trials, tactile stimulation to the right index finger (unseen vibration for 300 ms at 130 Hz) was delivered concurrently with the visual target. The tactile stimulations were not visible and did not predict the side of the visual targets, which were still equally likely to be in either the left or right retinal hemifield. Spatially congruent multimodal trials (i.e., same location in external space for concurrent visual and tactile stimulation) and spatially incongruent multimodal trials (different locations in external space) were intermingled, together with trials of visual stimulation only, all in a random sequence of equiprobable trial types. The only factor that was predictable was the position where fixation was required, which alternated between the two possibilities (marked with “+” in Figure 1) every eight trials (i.e., every 40 s).

During each scanning session, one or the other of the two fixation LEDs was always illuminated to indicate the currently required fixation. Subjects were required to maintain gaze at the illuminated fixation LED, and to detect any peripheral visual onsets (targets) without deviating gaze. These targets occurred every 4.5–5.5 s (uniform random distribution in this range). Regardless of the side of the visual targets, and the presence of any tactile stimulation, the task was to press a button with the index finger of the left hand, which could never be seen, in response to each visual target. In the first experiment, each subject underwent two scanning sessions during each of which 160 trials were presented (80 for each fixation position: with 20 events in each retinal hemifield without touch, and 20 events per hemifield with concurrent tactile stimulation on the right hand, in random order). In the second experiment, each subject underwent three scanning sessions, with 96 trials per session (same proportions of each trial type as in Experiment 1).

Image Acquisition

Functional images were acquired with a 2 Tesla Magnetom VISION MRI scanner (Siemens, Erlangen, Germany). BOLD (blood oxygenation level dependent) contrast was obtained using echo-planar $T2^*$ weighted imaging (EPI). The acquisition of 32 transverse slices gave coverage of the whole cerebral cortex (voxel size was $3 \times 3 \times 3$ mm). Because of the use of different readout gradients, the repetition time of Experiment 1 was 2.93 s, while repetition time in Experiment 2 was 2.43 s.

Data Analysis

Event-related fMRI data were analyzed with SPM99 (www.fil.ion.ucl.ac.uk). For each subject, acquisition timing was corrected using the middle slice as reference (Henson et al., 1999). Functional volumes (546 for the first experiment, and 603 for the second experiment) were realigned with the first volume of each subject. To allow inter-subject analysis, images were normalized to the Montreal Neurological Institute (MNI) standard space (Collins et al., 1994), using the mean of the 546 (or 603) functional images. All images were smoothed using a 10 mm isotropic Gaussian kernel.

The data were analyzed independently for each experiment, using a fixed-effects model. For each voxel, data were best-fitted (least square) using a linear combination of the effects of interest. These were the timing of the eight event types (i.e., given by crossing the following factors: side of fixation \times visual field of the target \times presence of touch), convolved with the SPM99 standard hemodynamic response function (HRF). The sustained effect of maintaining fixation either to the left or to the right of the body midline was modeled with a box-car function (again convolved with the HRF), plus its derivative. Additionally, for ten out of twelve subjects (five for each experiment), any trials containing losses of fixation were modeled separately (see below). This should ensure that the effects we report were not produced by unintended changes of visual input.

Linear compounds (contrasts) were used to compare the parameters of the multiple regression for the different conditions (excluding trials containing losses of fixation). Given the large number of voxels tested, the Theory of Gaussian Fields was used to assign corrected *p* values (Worsley et al., 1996). For the main effects of retinal hemifield for the visual target, or presence of task-irrelevant touch, correction at cluster level was employed (cluster size determined by setting SPM-map thresholds at *p*-uncorrected = 0.001). For the

effect of multimodal spatial correspondence upon visual responses (i.e., multimodal stimulation at the same external location versus at different external locations), the volume of interest was confined to those voxels showing a main effect of retinal hemifield for the visual target. These were posterior regions symmetrical in the two hemispheres (see Results section), with the exception of posterior parietal cortex that activated only in the left hemisphere for the comparison of right- minus left-visual-field stimulation.

Additional follow-up tests were then performed within the clusters showing an effect of spatial correspondence during multimodal stimulation. These comprised separate tests for stimulation of each retinal hemifield. In the left hemisphere, we tested for the main effect of leftward minus rightward fixation during right-visual-field stimulation, and whether this was modulated (amplified) by the presence of touch (interaction term). In the right hemisphere, we tested for a main effect of rightward fixation during left-visual-field stimulation, and the interaction between this and the presence of touch. In both cases, corrected *p* values were assigned according to the size of volumes that were activated for the effect of spatial correspondence during multimodal stimulation (see above).

Eye Tracking

Eye position was monitored using an ASL Eye-Tracking System (Applied Science Laboratories, Bedford), with remote optics (Model 504, sampling rate = 60 Hz) that was custom-adapted for use in the scanner. Due to technical difficulties with the first subject in both experiments, reliable eye tracking data were available throughout all scanning sessions for five out of six subjects in each experiment. Thus, eye tracking data were included in the fMRI analysis for ten out of twelve subjects. Maintenance of gaze direction was considered in a 1 s time window that included 500 ms pre-stimulus interval, the 300 ms period when the stimuli were delivered, and a 200 ms post-stimulus interval. After removing blinks, losses of fixation were identified as changes in horizontal eye position greater than 2°.

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