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Activation of Area MT/V5 and the Right Inferior Parietal Cortex during the Discrimination of Transient Direction Changes in Translational Motion

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The perception of changes in the direction of objects that translate in space is an important function of our visual system. Here we investigate the brain electrical phenomena underlying such a function by using a combination of magnetoencephalography (MEG) and magnetic resonance imaging. We recorded MEG-evoked responses in 9 healthy human subjects while they discriminated the direction of a transient change in a translationally moving random dot pattern presented either to the right or to the left of a central fixation point. We found that responses reached their maximum in 2 main regions corresponding to motion processing area middle temporal (MT)/V5 contralateral to the stimulated visual field, and to the right inferior parietal lobe (rIPL). The activation latencies were very similar in both regions (~135 ms) following the direction change onset. Our findings suggest that area MT/V5 provides the strongest sensory signal in response to changes in the direction of translational motion, whereas area rIPL may be involved either in the sensory processing of transient motion signals or in the processing of signals related to orienting of attention.

Keywords: attention, direction change, inferior parietal lobe, MEG, motion detection, MT/V5

Introduction

The human brain is equipped with a specialized system devoted to the processing of visual motion. Previous studies in humans have used a variety of visual stimuli and techniques in order to identify the motion processing system components. They have isolated a network of cortical areas that selectively respond to visual displays containing moving objects (Tootell et al. 1995; Anderson et al. 1996; Cornette et al. 1998; Smith et al. 1998; Greenlee 2000; Morrone et al. 2000; Schoenfeld et al. 2002, 2003; Martinez-Trujillo et al. 2005). However, few studies have been devoted to determine the role of different motion processing areas in specific tasks such as the detection of transient changes in motion attributes (Ahlfors et al. 1999; Amano et al. 2006). The present study aims at determining the motion processing areas activated during the detection of transient changes in the direction of translationally moving objects.

In a previous study, Ahlfors et al. (1999) described a cortical network—composed of areas V1, V2, V3A, middle temporal (MT)/V5, and areas of the frontal cortex—maximally activated when a visual pattern composed of concentric rings changed direction of motion (i.e., from expanding to contracting and vice versa). Another recent study, by Amano et al. (2006) used a similar stimulus configuration to study the brain electromagnetic responses during the detection of changes in the expanding/contracting velocity of an optical flow field. They isolated magnetoencephalography (MEG) responses around the temporal–occipital areas evoked by velocity increments with latencies of about 200–290 ms. Such activity was somewhat correlated with subjects' behavioral thresholds in a motion task.

However, it is difficult to generalize the results of these 2 previous studies to the task in which we are interested, that is, the detection of changes in the direction of translational (unidirectional) motion. This is because at least 2 main reasons. First, expanding and contracting optical flow patterns contain different combinations of speeds and directions within the same pattern, and seem to activate different areas within the human motion processing system compared with translational motion (Morrone et al. 2000; Martinez-Trujillo et al. 2005). Second, and related to the previous argument, several studies in nonhuman primates have demonstrated that area MT contains neurons selective for the direction and speed of translational motion (Albright 1984), whereas a different area, medial superior temporal (MST), contains neurons selective for expanding, contracting, and rotating optical flow patterns (Tanaka and Saito 1989; Graziano et al. 1994). In addition, it is known that electrical stimulation of areas MT and MST in nonhuman primates biases animals' performance in different motion tasks depending on whether the task involves translational motion (MT stimulation) or expanding/contracting flow patterns (MST stimulation) (Newsome and Pare 1988; Britten and Wezel 1998). Thus, previous evidence suggests that translational motion and expanding–contracting flow patterns are processed in different cortical areas.

Here, we combine MEG and magnetic resonance imaging (MRI) in 9 healthy human subjects to isolate the motion processing areas activated during the detection of transient changes in the direction of translationally moving random dot patterns (RDP).

Methods

Subjects and Recordings

Nine adult subjects (8 males and 1 female, all right handed) with ages ranging from 21 to 45 (mean = 31 years old) participated in the experiment with their informed consent. All the subjects had normal or corrected-to-normal vision and no signs of neurological or psychiatric disease. Each subject sat upright in a comfortable chair, with eyes open in a magnetically shielded room facing a flat screen on which the visual stimuli were presented. Electromagnetic activity was recorded while subjects performed a visual task (see experimental design) using a whole-head 151 channel CTF-MEG system (VSM MedTech, Ltd, Coquitlam, BC, Canada). The data were collected at a sample rate of 625 samples/s with an on-line band-pass filter of 0–200 Hz.

Experimental Design

Each experimental trial consisted of the presentation of a moving RDP (black dots on a white background within a circular aperture of 7.6° diameter) randomly appearing either to the right or to the left of

a central fixation cross, at an eccentricity of 7.6° during a time interval of 500 ms. Subjects were required to fixate the cross during the whole trial and to determine whether a change in the direction of the moving RDP (40° intensity and 200 ms duration) was clockwise or counterclockwise (Fig. 1*a*). In order to avoid adaptation to the same motion direction, the RDP could move—from trial to trial—either upwards or downwards (50% of the times in each direction). The dots had 100% coherence and there were on average 5 dots per degree^2 within the area covered by the pattern. The dot's size was 0.003°^{2}. The viewing distance was 57 cm. A luminance change on the back-projection screen (not visible to the subject) was detected by a photo-resistor circuit that sent a transistor transistor logic pulse to the acquisition computer to mark onset and offset of motion direction change.

In order to avoid overlap between the activity due to the motor response (key press) and the activity due to the change in the direction of the visual stimulus we instructed the subjects to respond once the stimulus presentation had finished and always with their right hand. They were explicitly told that this was not a reaction time task. Due to these factors there was a considerable variability in the subject's reaction time, which was in many cases longer than a second. Because neuromagnetic activity preceding motor responses typically begins 500–600 ms prior to movement onset (Cheyne et al. 2006) we did not expect to detect significant motor area activations in the time window of analysis for the period of direction change.

MEG Analysis

We applied the event-related Synthetic Aperture Magnetometry (erSAM) beamformer algorithm (Cheyne et al. 2006) to image instantaneous changes in source activity throughout the brain in order to describe spatiotemporal patterns of brain activity accompanying the detection of transient changes in motion direction. The SAM algorithm (Robinson and Vrba 1999) was recently introduced as a novel source localization method for detecting the time course and location of multiple neural sources. This method comprises an adaptive or data-driven linear inverse localization method based on minimum-variance beamforming and has been successfully used to create differential images of source power in narrow frequency bands over short time intervals (for review see Hillebrand et al. 2005). This approach has a number of advantages over conventional equivalent current dipole modeling methods, as they do not require that the number of active sources be specified a priori and can suppress contributions from noise sources such as eye movements. Recently, this technique has been modified to calculation of source power at single time points to image time-locked activity associated with evoked response activity with the ability to differentiate cortical sources separated by distances as small as 5–10 mm (Cheyne et al. 2006).

Volumetric erSAM images were computed by scanning a volume covering the entire brain with a grid spacing of 2 mm and were calculated at 5-ms increments preceding and following the period of direction change. These images were then spatially normalized to the Montreal Neurological Institute (MNI) (T1) template brain using SPM2 (Welcome Institute of Cognitive Neurology, London, UK). Linear and nonlinear warping parameters were obtained from each individual's coregistered T_1-weighted MR scans and used to warp individual erSAM images standardized stereotactic space, prior to averaging across subjects. The resulting group images were thresholded using a non-parametric permutation test (Nichols and Holmes 2002; Singh et al. 2003) based on images created during the baseline period to avoid bias due to the nonuniform distribution of source power in the functional erSAM images (Chau et al. 2004). No spatial or variance smoothing was applied. Thresholded images were then superimposed on the MNI template brain (Collins et al. 1994) and viewed with the mri3dX program (http://www.aston.ac.uk/lhs/staff/singhkd/mri3dX/mri3dX.jsp). Talairach coordinates of peaks activations were determined from the normalized images using the MNI to Talairach daemon (Lancaster et al. 2000). Peak activations in the group-averaged data were then used to generate source waveforms based on each subject's data using an inverse transformation from Talairach coordinates to locations in the individual subject's head-based (MEG) coordinate system and then averaged across subjects in order to view the entire time course of activity for these locations.

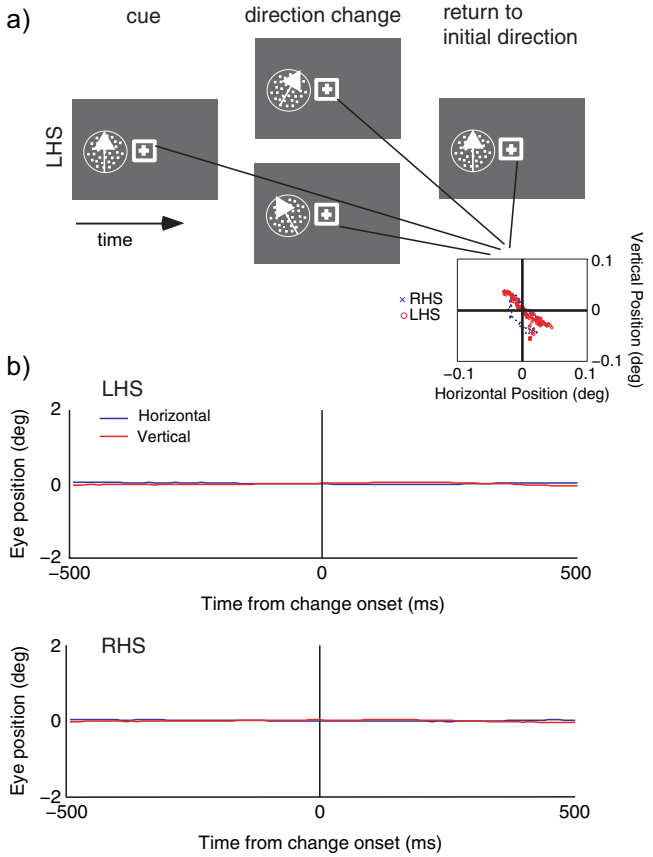

Figure 1. (*a*) Task and stimulus configuration. The trial started with the onset of an RDP moving either upwards or downwards (left panel). After 500 ms, the RDP changed direction 40° to the right or to the left of the initial direction (middle panels). After 200 ms, the pattern returned to its original direction. In a 2-alternatives forced choice subjects indicated (by pressing a key) whether the direction change was to the right or left relative to the initial motion direction. The panel on the bottom right illustrates the average eye position in one subject for the cases in which the stimulus was presented on the left (LHS, red circles) and on the right (RHS, blue crosses). The abscissa represents horizontal and the ordinate vertical position in degrees. (*b*) Average horizontal (blue) and vertical (red) eye position signals (ordinate) as a function of time from direction change onset (abscissa) for the LHS (top panel) and the RHS (bottom panel) for the same subject.

Eye Position Analysis

In order to minimize the probability that subjects move their eyes during the MEG recordings sessions we trained them in advance on the same task outside the MEG setup. We instructed each subject to keep gaze steady on the fixation cross during the trials and covertly attend to the moving RDP. Subjects learned to do so very quickly after a few trials of the first training session. Once this stage was achieved we proceeded to schedule the MEG recording sessions. Although we did not record the eye positions inside the MEG setup (due to the amount of noise introduced by our eye-tracking devices on the MEG recordings), we did so during the training sessions in some of the subjects using a video-based head-mounted eye-tracking system (Chronos, Inc, Berlin, Germany) and a bite bar to immobilize the subjects' head. The task during these sessions was identical to the one inside the MEG setup.

Figure 1 shows averaged eye position data recorded outside the MEG setup from the same subject appearing in Figure 2. The panel in "*a*" shows a scatter plot of vertical against horizontal eye position signals on a window of 0.1° radius in both axes. The red data points illustrated the average on left hemifield stimulation (LHS) trials and the blue points on right hemifield stimulation (RHS) trials. The points overlap considerably. The panels in "*b*" show plots of vertical and horizontal position signals as a function of time from the direction change onset for the LHS and RHS. Averaged changes in eye position during the entire stimulus period

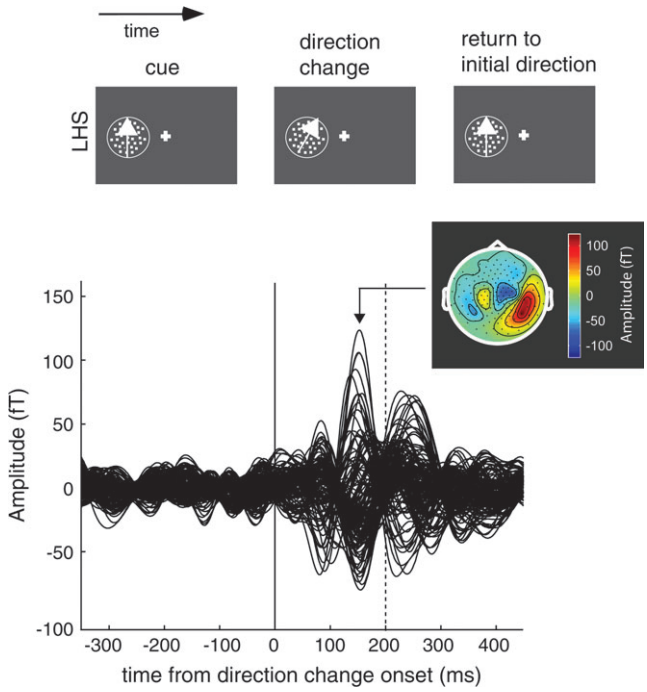

Figure 2. Example subject. The top panels represent the stimulus sequence for LHS trials. In the bottom graph, the ordinate displays the intensity/amplitude of the electromagnetic activity (in fT) and the abscissa the time from direction change onset in milliseconds in all the channels superimposed. The activity in each channel was averaged across all trials. The smaller panel on the top right shows the distribution of intensities (relative to each channel location) on a sketch of the subject's head. The color scale indicates the amplitude values in fT.

were smaller than 0.1°. This result was similar for 3 other subjects whose eye positions were recorded outside the MEG setup (data not shown).

Results

We recorded the MEG activity in 9 normal human subjects while they discriminated the direction of a transient change in a translationally moving RDP located either to the left or to the right of a central fixation point (Fig. 1*a*). For all subjects, performance (proportion of correct responses) in both, the LHS and RHS, presentation was close to 100%; therefore all trials were included in the analysis. Figure 2 shows an example of the average MEG signals in one subject (S1) as a function of time from direction change onset in trials where the stimulus was presented on the left visual hemifield.

The graph at the bottom shows the amplitude of the magnetic field activity in femtotesla (fT) as a function of time from direction change onset in milliseconds in all the channels superimposed. Clearly, the transient direction change evoked an electromagnetic response that lasted about 200 ms and reached its highest amplitude at about 140 ms after the change onset over the right hemisphere, that is, contralateral to the stimulated visual hemifield (Fig. 2, panel on the top right). For the rest of the subjects, the results were very similar (data not shown).

In order to obtain a more precise localization of the activity evoked by the direction change, we conducted group erSAM analysis by averaging the images at selected latencies over all subjects after normalization to a standard brain template (see Methods). Figure 3(*a*) shows snapshots spaced every 10 ms of the regions maximally activated (yellow) during the time intervals from 120 to 150 ms after the direction change. The top panels represent the LHS and the middle panels the RHS.

At 120 ms after the direction change onset, the areas maximally activated are localized in the region corresponding to the temporal–occipital junction–middle temporal gyrus contralateral to the stimulated hemifield (left most panels in Fig. 3*a*). This activation remains localized to approximately the same region during the next 30 ms. Additionally, about 10 ms later, an area at the same anatomical location but ipsilateral to the stimulated visual field was also activated. The Talairach coordinates of peaks of activity identified in the group-averaged erSAM images, taken at 140 ms after the direction change onset, appear in Table 1. Although our permutation test revealed a pseudo-*Z* noise level of approximately 0.4–0.5 using baseline data ($P < 0.005$) only those peaks with a pseudo-*Z* value greater than 1.0 were selected for further analysis.

The second interesting finding in this figure is the existence of an area of activation located approximately in the region corresponding to the right inferior parietal lobe (rIPL). For the LHS, this activation can be seen at about 120 ms after direction change onset and for the RHS at about 130 ms. The Talairach coordinates of this rIPL area for both the LHS and the RHS are depicted in Table 1. They are very similar in both cases (51, –47, 26 for the LHS and 53, –41, 28 for the RHS), suggesting that stimulation of either hemifield generally elicited rIPL activation.

We further examined peak activations for areas MT/V5 and rIPL at 140 ms from stimulus onset that were large enough to be identified in individual subjects (rIPL peak could not be identified in one subject). These data are shown in Table 2. During LHS the average peak location across subjects was 38 ± 6, –63 ± 6, 22 ± 14 for the right middle temporal gyrus and 54 ± 6, –40 ± 9, 22 ± 7 for the rIPL. During RHS it was –41 ± 5, –62 ± 2, 19 ± 6 for the right middle temporal gyrus and 54 ± 6, –38 ± 9, 25 ± 9 for the rIPL. Note that these locations were similar to the location of peaks as identified in the group-averaged images shown in Table 1. Also, the locations of MT/V5 identified in the erSAM images were quite consistent across conditions and similar in anatomical location to that reported for human MT/V5 based on analysis of sulcal patterning in structural MRI (Dumoulin et al. 2000).

The time course of the evoked electromagnetic responses at the regions appearing in Table 1 is shown in Figures 3(*b*) and 4. The time corresponding to the snapshots appearing in Figure 3(*a*) are indicated by vertical dashed lines. For the case of LHS, the response amplitude was stronger in the rIPL followed by the left MT/V5 and finally by the right MT/V5. For the case of the RHS, the response was stronger in the left MT/V5 followed by the rIPL and the right MT/V5. In this latter case, the maximum of the rIPL activation seems to occur later than the one of the left MT/V5 activation. Thus, generalizing the findings in this figure, we found that stimulation of one visual hemifield evokes activation of area MT/V5 contralateral to the stimulated field and activation of the rIPL independently of the stimulated field. We also found some weaker activation of area MT/V5 ipsilateral to the stimulated field.

In addition to activation of MT/V5 and rIPL we detected weaker activations in both the left IPL and bilaterally in the cuneus (Table 1). In order to further test whether the rIPL activation was independent of the stimulated visual hemifield, we plotted source activity evoked in the rIPL and left IPL areas during both LHS and RHS. These data appear in Figure 4(*a*). Clearly, the activity was always stronger over the rIPL than over

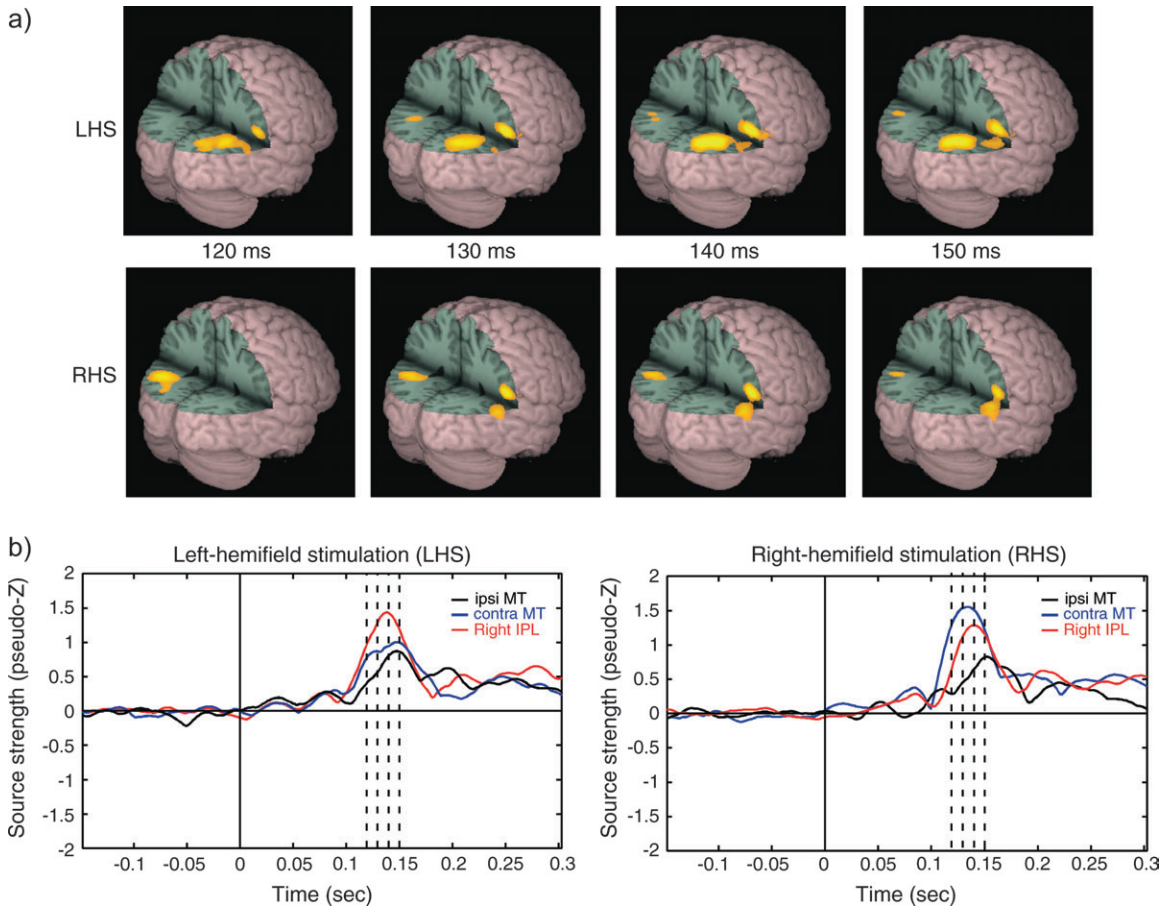

Figure 3. (*a*) Maps of brain activity given by the erSAM analysis pooled across subjects and normalized to the MNI template (see Methods) spaced every 10 ms over the intervals from 120 to 150 ms after the direction change onset. The upper panels represent the LHS and the lower panels the RHS. The yellow color indicates the locations where activity reached its maximal amplitude. (*b*) Time course of the activity at the regions of maximal amplitude for LHS (left panel) and RHS (right panel). The colors indicate the activity corresponding to the different regions. The dashed lines indicate the times at which the images shown on the upper panels were taken. The coordinates of these regions are the ones appearing in Table 1.

the left IPL, independently of the stimulated visual hemifield. The time courses of left and right cuneus activation for both conditions are plotted in Figure 4(*b*), showing activity in the cuneus contralateral to the hemifield of stimulation peaking around 150 ms after direction change and preceded by smaller peaks at about 70–100 ms. There were also weaker and somewhat delayed peaks in the ipsilateral hemisphere.

Discussion

The main contribution of the present study was to isolate the brain regions maximally activated during the discrimination of transient direction changes in translational motion. These regions were 1) areas in the middle temporal gyrus and cuneus, more strongly activated in the hemisphere contralateral to the stimulated visual hemifield, and 2) an area in the rIPL.

A previous study using MEG and functional MRI (fMRI) has demonstrated activation of an area located near the occipito-temporal junction by changes in the direction (expansion to contraction and vice versa) of an optical flow pattern (Ahlfors et al. 1999). The Talairach coordinates of that region for 3 subjects tested in that study (right hemisphere s1: 45, −57, 14; s2: 33, −69, 1; s3: 44, −50, 2; left hemisphere, s1: −43, −73, 20; s2: −49, −69, 7; s3: −36, −67, 11) are very similar to the ones depicted in Table 1 of the present study. This suggests that the activation resulting from changes in the direction of translationally moving RDP isolated in our study corresponds to the one previously isolated by Ahlfors et al. (1999). This region seems to correspond to human area MT/V5.

Interestingly, in our study we found a clear bias toward activation of MT/V5 contralateral to the stimulated hemifield, whereas Ahlfors et al. (1999) did not report such a bias. A

Table 1
Peak Activations in Group erSAM Images (t = 140 ms)

Talairach coordinates (mm)			pseudo-Z	Brain region
x	y	z		
LHS				
50	−47	26	1.75	IPL (R)
38	−61	20	1.51	Middle temporal gyrus (R)
24	−78	5.6	1.25	Cuneus (R)
−40	−61	21	1.10	Middle temporal gyrus (L)
RHS				
−42	−63	20	1.92	Middle temporal gyrus (L)
53	−41	28	1.58	IPL (R)
−20	−77	17	1.48	Cuneus (L)
51	−50	14	1.18	Middle temporal gyrus (R)
−46	−30	25	1.04	IPL (L)

Note. Mean locations and magnitudes of the 6 largest peak activations (pseudo-$Z > 1.0$) in the group-averaged erSAM images occurring 140 ms after onset of motion direction change.

Table 2
Peak Activations in Individual erSAM Images (t = 140 ms)

Subject	LHS								RHS							
	Middle temporal gyrus (R)				Inferior parietal lobule (R)				Middle temporal gyrus (L)				Inferior parietal lobule (R)			
	Talairach coordinates (mm)			pseudo-Z	Talairach coordinates (mm)			pseudo-Z	Talairach coordinates (mm)			pseudo-Z	Talairach coordinates (mm)			pseudo-Z
	x	y	z		x	y	z		x	y	z		x	y	z	
1	40	−54	23	1.64	54	−51	25	2.61	−38	−65	20	3.97	50	−53	27	2.16
2	44	−66	14	3.18	-	-	-	-	−38	−64	14	2.75	56	−30	33	0.62
3	34	−66	11	2.56	50	−36	24	4.54	−46	−65	18	2.57	48	−34	22	3.52
4	28	−60	12	2.22	58	−42	13	2.53	−44	−62	14	2.09	66	−27	16	2.13
5	34	−68	11	2.37	54	−32	31	2.40	−46	−60	10	2.41	52	−40	28	2.30
6	34	−57	23	1.15	60	−30	24	4.06	−34	−59	29	1.97	60	−32	24	3.57
7	34	−69	27	3.03	56	−32	22	1.60	−48	−61	20	1.45	48	−31	42	1.25
8	50	−70	27	0.51	42	−49	28	1.27	−40	−61	25	1.72	50	−48	13	1.78
9	46	−58	16	1.91	58	−50	12	2.26	−38	−59	21	2.67	56	−44	22	1.95
Mean	38	−63	22	2.04	54	−40	22	2.66	−41	−62	19	2.40	54	−38	25	2.14
SD	7	6	14		6	9	7		5	2	6		6	9	9	

Note. Locations and magnitudes of peak activations for the contralateral MT/V5 (middle temporal gyrus) and right hemisphere IPL sources occurring 140 ms after onset of motion direction change are shown for individual subjects. The mean and standard deviation (SD) of the source locations are also shown for the x (left–right), y (posterior–anterior), and z (inferior–superior) directions in the Talairach coordinate system.

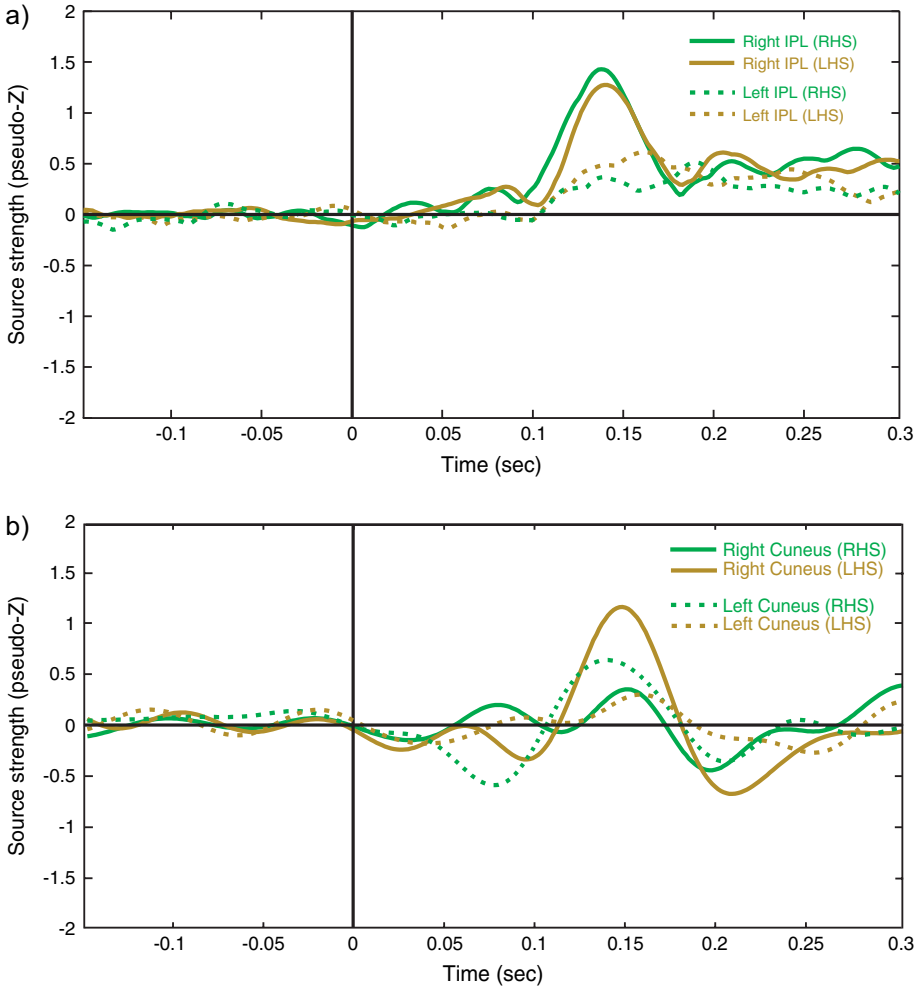

Figure 4. Time course of activity for sources identified in the right and left IPL (*a*) and right and left cuneus (*b*) during the LHS and RHS conditions. The abscissa represents time from direction change onset in milliseconds and the ordinate the intensity of the activation (in pseudo-Z values). Different hemispheres (right and left) are shown by solid and dashed traces, and stimulation sides (right and left hemifield) are shown by green and yellow traces, respectively. The coordinates of these regions are the ones appearing in Table 1.

possible explanation for this difference between the results of the 2 studies is that although we used translationally moving RDPs, these authors used a more complex optical flow stimulus (expansion and contraction). Our stimuli likely activated a high proportion of MT/V5 neurons with receptive fields contralateral to the stimulated visual field, whereas the complex optical flow stimuli use by Ahlfors et al. mainly activated MT/V5 neurons with large receptive fields covering both hemifields.

This latter type of neuron may be more similar to optical flow selective neurons in area MST of nonhuman primates (Tanaka and Saito 1989; Graziano et al. 1994).

An argument in favor of this hypothesis is that the MT/V5 activation contralateral to the stimulated visual field, started at about 120 ms, that is, about 10 ms earlier than the activation within MT/V5 ipsilateral to the stimulated hemifield (see Fig. 3*a*) and it is already known that activation latencies within area MT of nonhuman primates are somewhat shorter than within area MST (Schmolesky et al. 1998). Additionally, human fMRI studies have demonstrated that expanding–contracting stimuli activate a different region of the human MT/V5 complex when compared with translational motion (Morrone et al. 2000) and also that stimulation of one visual hemifield selectively activates a region of the human MT/V5 complex in the contralateral hemisphere (Dukelow et al. 2001; Huk et al. 2002). Thus, it is very likely that changes in the direction of our translationally moving RDPs strongly activated the regions of human MT/V5 that encode translational motion and that such regions are mainly located within the hemisphere contralateral to the stimulated visual hemifield.

A second finding in this study, the activation of the rIPL with approximately the same latency and intensity as the MT/V5 activation, is somewhat more difficult to relate to previous studies. We consider at least 2 possible interpretations. First, it is possible that neurons within this human area have similar properties as MT/V5 neurons, that is, they are direction selective and respond to changes in the direction of motion shown inside their receptive field. Second, it is possible that neurons in this area play a more general role and react to transient events that automatically attract our attention toward potentially relevant targets. In favor of the latter argument it is well documented the role of IPL on attention. Patients with lesions of the rIPL suffer from Visuospatial Neglect (Mort et al. 2003). In favor of the first argument, a recent fMRI study has reported bilateral activation of the IPL during responses to visual motion (Claeys et al. 2003). In our study, although we detected weak left hemisphere IPL activation, the responses were clearly dominant over the rIPL, independently of the stimulated visual hemifield.

An interesting finding in our study is that during RHS, the activation within area MT/V5 clearly preceded the rIPL activation (Fig. 3*a*). This may suggest that sensory signals processed within area MT/V5 may be the source for the rIPL activation. If one considers that the rIPL is involved in orienting attention (Mort et al. 2003), one may hypothesize that this area receives sensory signals from MT/V5 regarding the spatial location of potentially relevant targets (i.e., visual objects that abruptly change direction) and then it sends feedback signals that modulate the sensory processing of relevant information in visual areas (Friedman-Hill et al. 2003). It is also possible that other sensory areas that process different visual features also inform the parietal lobe about transient changes on those features. From this, one would predict that transient changes in a given visual feature would first activate sensory areas selective for that feature and then the rIPL. This prediction, however needs further testing.

Finally, there could be at least 2 other possible explanations for the activity peaks we have isolated in the present study. First, it is possible that such peaks are related to motor processing of the key-press responses (Cheyne et al. 2006). Second, it is possible that they will be due to an anticipatory signal arising in areas MT/V5 and rIPL because subjects could have predicted in advance the time at which the direction change occurred (Janssen and Shadlen 2005).

We consider the former explanation unlikely because it was a considerable amount of variability in the subjects' reaction time, which was in the majority of trials larger than 1 s. Additionally, the latencies and distribution of the activity peaks we observed are very similar to latencies reported by other authors for changes in the direction of optical flow patterns in area MT/V5 (Ahlfors et al. 1999) and considerably shorter than the ones reported for motor or premotor responses (Cheyne et al. 2006) when considering the subjects' reaction time.

The second interpretation that the activity peaks over areas MT/V5 and rIPL could be related to an anticipatory signal; we consider it unlikely for the following reasons. First, the activity peaks seem to occur at different times in MT/V5 and in rIPL (Fig. 3), with the former peak preceding the latter. This is particularly notorious for the case of RHS. Our interpretation of this finding is that the signal caused by the direction change likely travels bottom-up in the hierarchy of visual processing (from MT/V5 to rIPL). On the other hand, an anticipatory (top-down) signal will likely show the inverse pattern because it will likely arise first in the rIPL or some other higher area and then in MT/V5. Secondly, anticipatory signals associated to visual attention and isolated using EEG techniques usually precede the target onset (Sauseng et al. 2005). In our data, the peaks of activity were clearly after the direction change onset.

So far, we have focused on the discussion of the activity peaks found over the regions corresponding to MT/V5 and rIPL, which were the major activity peaks found at the level of the pooled data and the individual subjects. However, we also found some activation over the region corresponding to the cuneus contralateral to the hemifield of stimulation. This was more evident when pooling the data from all subjects than at the level of individual subjects (see Table 1 and Fig. 4*b*). Although weaker activity was observed in the ipsilateral cuneus this was somewhat delayed in time suggesting the cuneus activation was largely lateralized to the contralateral hemisphere. We speculate that this cuneus activation may represent either the time course of the sensory signal traveling the motion processing pathways (early peaks) or perhaps the combination of sensory and more cognitive influences such as attention (later peaks).

Our findings are compatible with the ones reported by other studies using different techniques and stimulus types (Dupont et al. 1994; Shulman et al. 1998; Vanni et al. 2001; Servos et al. 2002; Cant and Goodale 2006; Wittfoth et al. 2006). Interestingly, it has been suggested that the human cuneus may represent the link between signals originated in the striate cortex and those arising in extrastriate areas (Vanni et al. 2001). It has been also proposed that areas of the human cuneus may correspond to visual area V3 (Shulman et al. 1998). In our data, the cuneus activation was present but it was less robust than the peaks found at the level of MT/V5 and rIPL. Future studies are needed in order to address the specific role of this human area in vision and motion processing.

In summary, our results suggest that human area MT/V5, together with the rIPL plays an important role in the detection of transient changes in the direction of translational motion. Our novel spatiotemporal analysis also provides a useful method to study the time course of cortical activation during tasks such as the detection of transient sensory events.

Notes

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