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The role of V5 (hMT+) in visually guided hand movements: an fMRI study

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Abstract

Electrophysiological studies in animals suggest that visuomotor control of forelimb and eye movements involves reciprocal connections between several areas (striate, extrastriate, parietal, motor and premotor) related to movement performance and visuospatial coding of movement direction. The extrastriate area MT [V5 (hMT+) in humans] located in the 'dorsal pathway' of the primate brain is specialized in the processing of visual motion information. The aim of our study was to investigate the functional role of V5 (hMT+) in the control of visually guided hand movements and to identify the corresponding cortex activation implicated in the visuomotor tasks using functional magnetic resonance imaging. Eight human subjects performed visually guided hand movements, either continuously tracking a horizontally moving target or performing ballistic tracking movements of a cursor to an eccentric stationary target while fixating a central fixation cross. The tracking movements were back-projected onto the screen using a cursor which was moved by an MRI-compatible joystick. Both conditions activated area V5 (hMT+), right more than left, particularly during continuous tracking. In addition, a large-scale sensorimotor circuit which included sensorimotor cortex, premotor cortex, striatum, thalamus and cerebellum as well as a number of cortical areas along the intraparietal sulcus in both hemispheres were activated. Because activity was increased in V5 (hMT+) during continuous tracking but not during ballistic tracking as compared to motion perception, it has a pivotal role during the visual control of forelimb movements as well.

Introduction

Electrophysiological and anatomical studies in the macaque brain have isolated more than 20 visually responsive areas (Essen & Zeki, 1978; Van Essen *et al*., 1981). The theory that visual perception of objects and visual control of action directed at those objects rely on two relatively different parallel streams, a ventral stream and a dorsal stream (Goodale & Milner, 1992), in the primate brain has been widely accepted (Van Essen *et al*., 1992). The dorsal stream, projecting from V1 through areas V2 and V3 to the middle temporal area (MT) and then to additional areas in superior temporal and parietal cortex, processes the physical attributes of stimuli important for localizing objects in space and for the visual guidance of movement towards them, such as the direction and velocity of stimulus motion.

In the dorsal stream, areas that are specialised for motion processing have received particular attention. The motion-selective area MT is located in the fundus of the superior temporal sulcus in macaque monkeys, and cells in this area respond well to the direction and speed of moving stimuli and their inactivation causes deficiencies in motion direction discrimination. The location of human area V5 (hMT+), which most probably corresponds to monkey area MT and its satellite regions MST (Huk *et al*., 2002), is located at the intersection of the ascending limb of the inferior temporal sulcus and the lateral occipital sulcus (Watson *et al*., 1993). The functional importance of area MT for oculomotor behaviour has been elucidated by inactivation studies where the extrafoveal representation of MT has been lesioned irreversibly with ibotenic acid (Newsome *et al*., 1985). In similar ways there are some studies in humans to assess the function of V5 (hMT+): Zihl *et al*. (1991) described that bilateral cortical lesions including area V5 (hMT+) caused a severe impairment in detecting the movement of objects (akinetopsia). Further, virtual lesions of the brain induced by transcranial magnetic stimulation were able to show that the cortex at the temporo-occipital junctions disrupted visual motion detection (Beckers & Zeki, 1995; Theoret *et al*., 2002).

From electrophysiological studies in anaesthetized and in behaving nonhuman primates, a detailed knowledge has evolved about the fundamental processing of sensory and motor information in areas concerned with visuo-motor cognition. The frontal, parietal and occipital lobes consist of a multiplicity of areas with specific connections (Rizzolatti *et al*., 1997). There is growing evidence that in primate cerebral cortex the areas along the 'dorsal pathway' are also involved in the transformation of visual motion information towards a skeleto-motor command. Preliminary results from our group with reversible inactivation of small extrafoveal parts of area MT in a behaving monkey manifested in an impairment of the general performance and a prolonged reaction time for the initiation of arm movements (Gieselmann *et al*., 2001).

Our hypothesis is that the visual extrastriate cortex contributes to the control of visually guided hand movements, comparable to its contribution to the cortical network that controls visually guided eye movements.

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The aim of our study is to investigate the functional role of the human extrastriate visual area V5 (hMT+) in the control of visually guided hand movements and to localize the corresponding cortex activation implicated in the visuomotor tasks by the use of functional MRI (fMRI).

Materials and methods

Subjects

Nine right-handed healthy subjects between 25 and 43 years old (five males, four females, mean age 31 years old), with no history of neurological or psychiatric disease and no structural lesion on cranial MRI, participated in this study. Visual acuity was full in all subjects. Data from one subject had to be excluded because of excessive head motion that could not be corrected by image alignment. All of the subjects gave an informed consent. The studies were performed according to the Guidelines of Helsinki and approved by the Ethics Committee of the Heinrich-Heine-University of Düsseldorf. Right-handedness was assessed by the Edinburgh Handedness Inventory (Oldfield, 1971).

Behavioural tasks

The subjects performed visually guided right hand movements, either continuously tracking a horizontally moving target or ballistically moving a cursor to an eccentric stationary target using an MRI-compatible joystick. Joystick movements were performed with the right hand. The cursor movements were recorded continuously. The visual stimuli were generated by a PC on a high performance graphic card (ELSA Winner 2000 Pro/X, Aachen, Germany). The stimuli were projected (LCD data projector, Sony VPL-S500E) onto a translucinant screen attached in front of the head coil.

In all conditions the subjects were instructed to keep fixation of a central green fixation spot, which was constantly present in the upper half of the screen above the other stimuli. We used a block design with two visuomotor activation conditions. (1) Manual tracking of the continuously moving target. (2) Moving the cursor fast to an eccentrically upcoming stationary target (ballistic tracking) (Fig. 1). In two further conditions we wished to selectively identify the motor task component by subtracting the visual incoming information only. Therefore, the identical visual signals, consisting of the stored trajectories of the target and the cursor, were presented as replay conditions (3 and 4) while the subjects did not move their hand. Between these conditions, subjects viewed a blank field with the central green cross which served as baseline. Each condition lasted five volumes, giving 20 s per condition. Before scanning, subjects practiced 100 trials of the stimuli to familiarize them with the tasks. The serial order of the conditions was pseudorandomized with the replay conditions always preceded by the visuomotor tasks.

MR scanning

fMRI measurements were performed to measure blood oxygen level dependence (BOLD) activation, which is related to activated neural population (Logothetis *et al.*, 2001), on a 1.5-Tesla clinical scanner (Magnetom Vision, Siemens, Erlangen, Germany) using standard echo planar imaging (EPI) and a standard radio frequency head coil for signal transmission and reception. The following EPI sequences were used: TR 4 s, TE 66 ms, flip angle 90°, voxel size $3 \times 3 \times 4.4\,mm^3$. Twenty-eight consecutive slices (slice thickness 4 mm, interslice gap 0.1 mm) orientated parallel to the anterior–posterior commisure plane and covering the whole brain were acquired. Each subject underwent a high-resolution T1-weighted scan.

Subjects were scanned during two runs, each lasting 15 min. In each run, 250 EPI volumes were acquired. Subjects' eye movements were monitored during scanning using an eyetracker system (Cambridge Research System, Rochester, UK) and hand movements were also monitored during scanning using a custom-made joystick.

A multichannel computer program (EDAS, MH, Erftstadt, Germany) was used to acquire and display the signals derived from the eyetracker as well as the recordings of the hand movements. Trigger of the scanner and trial conditions were recorded and displayed with the same program.

Data analysis

Image analysis was performed using the fMRI analysis software package BrainVoyager 4.9 (Max-Planck-Society, Germany, Goebel *et al.*, 1998). Before statistical inference, the fMRI data sets were

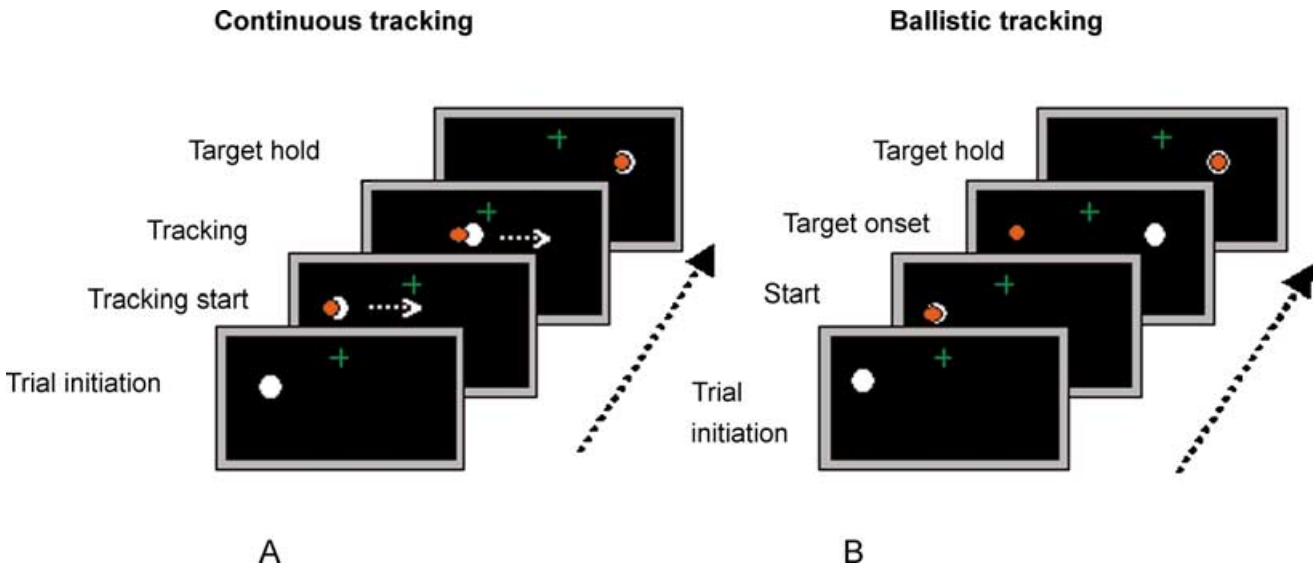

FIG. 1. Representation of the two behavioural tasks: (A) continuous tracking with central fixation (moving target), (B) ballistic tracking with central fixation (moving the cursor fast to an eccentric stationary target). Fixation cross +, cursor, red circle; target, white circle.

subjected to a series of preprocessing operations. The 2-D slice time-course data were registered with the 3-D MP RAGE data sets from the same session and interpolated to the same resolution (voxel size $1\,mm^3$) in order to create volume time course of the fMRI signal. The Siemens slice position parameters of the $T2^*$-weighted measurement (number of slices, 30; slice thickness, 4 mm; distance factor, 0.1; FOV, 256; shift mean, Tra-Cor angle, off-centre read, off-centre, inplane resolution) and parameters of the T_1-weighted 3-D MP RAGE measurement (number of sagittal partitions, 180; resolution, $1 \times 1 \times 1\,mm^3$, shift, off-centre read, off-centre phase) were used for coregistration. For each subject, the structural and functional 3-D data were transformed into Talairach space (Talairach & Tournoux, 1988; Goebel *et al*., 1998). Functional images were realigned to correct for small head movements between scans. Preprocessing of the volume time courses included Gaussian spatial (FWHM 4 mm) and temporal (FWHM 6 s) smoothing as well as the removal of linear trends. With a Gaussian model of the haemodynamic response to generate idealised response functions, which were used as regressors in a multiple regression model, we contrasted epochs for the six different conditions. The overall model fit was assessed using an F statistic. In a random effect analysis all activation areas beyond a voxel level threshold of $P < 0.001$ uncorrected and within clusters of ≥ 50 voxels are reported. Further, we compared the regression parameter beta for the activations specific for continuous and ballistic tracking in the activated visual areas V1/V2 and V5. The beta values result from the best fit of the group data and are a parametric measure of the contribution of each predictor to the total BOLD signal. For anatomical localisation the activated areas were superimposed on the high-resolution 3-D anatomical images. The stereotactic coordinates of the voxel of the local maximum activation were determined. The anatomical localization of these local maxima was assessed with reference to the standard stereoctatic atlas (Talairach & Tournoux, 1988) and prominent sulcal landmarks. Surface rendering, cortex inflation and cortex flattening of the data were also performed as described in more detail elsewhere (Goebel *et al*., 2001; Kriegeskorte & Goebel, 2001).

Results

We wished to identify the different components of the neural network involved in visually guided tracking with the hand. In a first step of analysis we identified the whole network involved in the task using an omnibus statistic before we sorted out the specific subcomponents of the visuomotor integration tasks studied.

Behavioural data

The subjects fixated well and the deviations of the eye movement from the fixation point were $<1^\circ$ (see Fig. 2). Typical hand movements for the continuous and ballistic tracking tasks are shown in Fig. 2.

Activation data

We studied the functional contrasts between the following conditions.

Continuous tracking with fixation vs. central fixation

With this contrast we found a bilateral activation of V5 (hMT+), right more than left (Fig. 3). Increased BOLD response was also observed in the primary visual cortex. In addition, along the intraparietal sulcus different areas showed significant activation, such as bilateral anterior intraparietal area (AIP), ventral intraparietal area (VIP), left lateral intraparietal area (LIP) and posterior intraparietal area (pIP) (Table 1). Furthermore a motor circuit involving left sensorimotor cortex, dorsal premotor cortex left, supplementary motor area (SMA), right inferior premotor cortex, left basal ganglia, bilateral thalamus, and ipsilateral anterior cerebellum and vermis (Fig. 3A) was activated.

Ballistic tracking with fixation vs. central fixation

During visually guided ballistic tracking movements the same areas were activated as during continuous tracking (Table 2). Specifically, there was a significant increase in activation in V5 (hMT+) in both hemispheres, right more than left (Fig. 3B). Also, the motor circuit involving left sensorimotor cortex (SMA), basal ganglia, thalamus and cerebellum as well as the areas along the intraparietal sulcus were activated. In addition, the supramarginal gyrus was activated in a mirror-like fashion in both hemispheres.

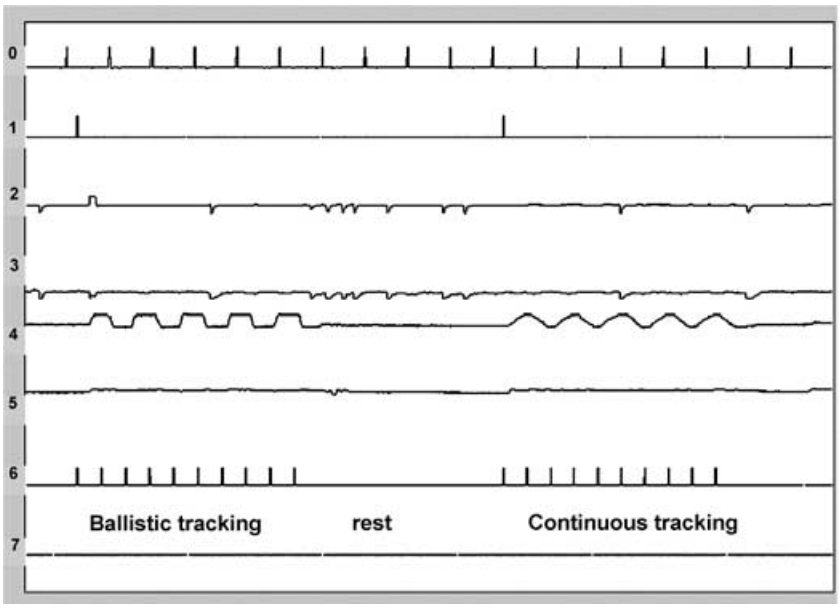

FIG. 2. Subjects' eyes and hand movements were monitored during ballistic tracking and continuous tracking. Channels: 0, scanner trigger; 1, stimuli trigger; 2, eye position X; 3, eye position Y; 4, cursor X; 5, cursor Y; 6, trials per condition.

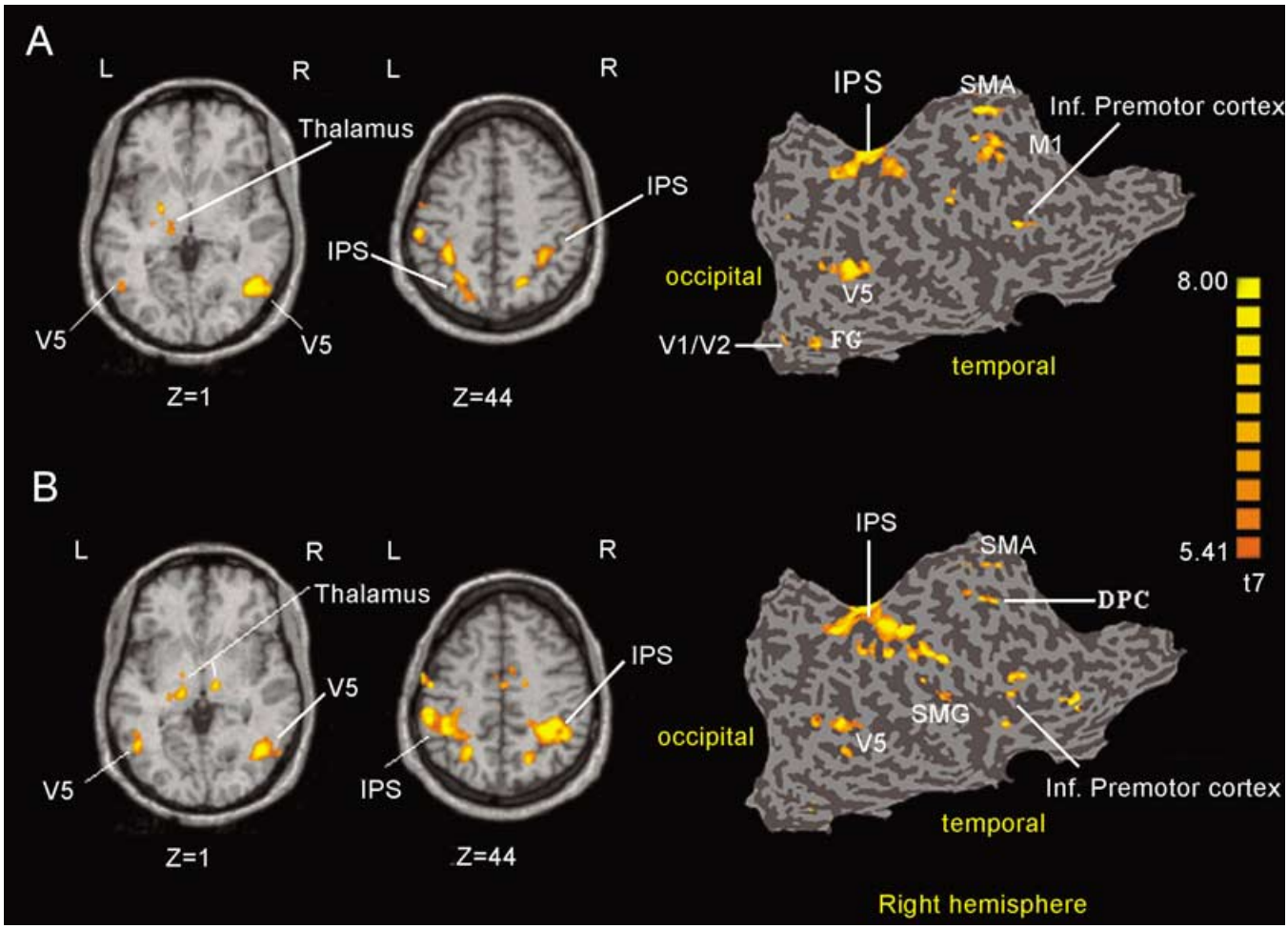

FIG. 3. (A) Continuous tracking of a visual target while subjects were fixating a central fixation spot. The axial slices and flattened representation of the reconstructed right cortical hemisphere show activation in V5 (hMT+) bilateral, basal ganglia, thalamus, inferior premotor cortex, fusiform gyrus, V1/V2, SMA, sensorimotor cortex and intraparietal cortex (IPS). (B) Ballistic tracking of a visual target while subjects were fixating a central fixation spot. The axial slices and flattened representation of the reconstructed right cortical hemisphere show activation in V5 (hMT+) bilateral, thalamus, dorsal premotor cortex, supramarginal gyrus, inferior premotor cortex, SMA, sensorimotor cortex and intraparietal cortex. Data threshold is at $P < 0.001$ (uncorrected). R, right; L, left; FG, fusiformis gyrus; SMA, supplementary motor area; SMG, supramarginal gyrus; DPC, dorsal premotor cortex; M1, motor cortex; V1/V2, early visual areas.

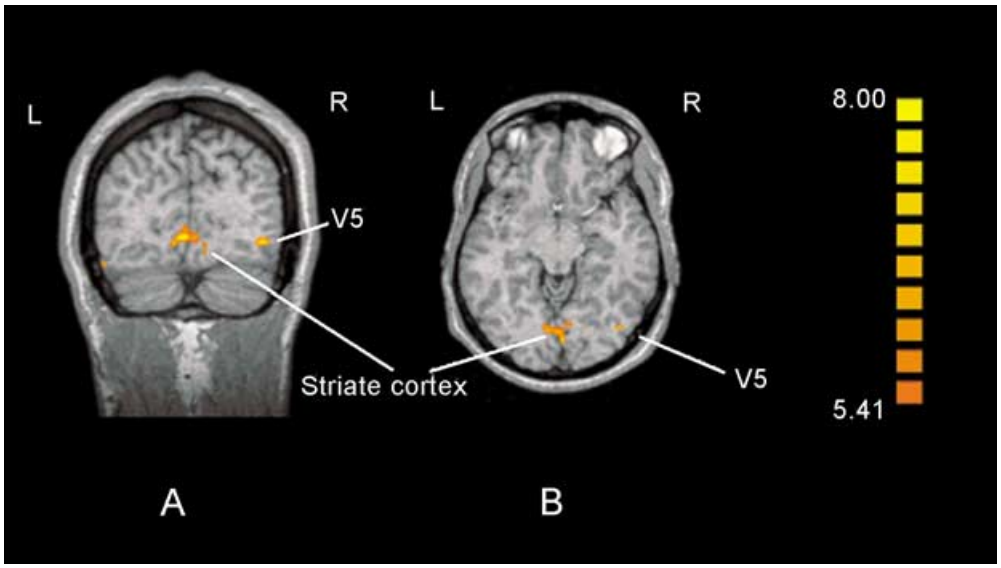

FIG. 4. Continuous tracking movements vs. ballistic tracking movements while subjects were fixating a central fixation spot. It shows significant activation in V5 (hMT+) right and in early visual areas. (A) Coronal slice. (B) Axial slice. Data threshold at $P < 0.001$ (uncorrected). R, right; L, left.

TABLE 1. Activations related to continuous tracking with fixation vs. fixation

Area	x	y	z	t_7-value	Voxels
V5 (hMT+) (R)	45	−61	4	15.92	3497
V5 (hMT+) (L)	−48	−59	4	9.26	235
Early visual areas	1	−74	−12	9.45	500
S1 (L)	−46	−34	55	14	888
AIP (R)	33	−39	44	8.64	1206
AIP (L)	−33	−39	42	10.07	670
VIP (R)	32	−42	45	10.01	1517
VIP (L)	−31	−45	48	10.11	787
LIP (L)	−41	−40	56	15.45	2338
pIP (R)	20	−60	52	13.55	2653
pIP (L)	−31	−51	54	16.14	3763
M1 (L)	−34	−22	58	17.28	9424
SMA	1	−11	55	14.56	2798
Premotor cortex (L)	−55	2	40	7.02	304
Inf. premotor cortex (R)	50	7	13	12.18	402
Putamen (L)	−21	−6	7	14.86	948
Thalamus (R)	20	−8	11	11.38	466
Thalamus (L)	−14	−16	6	12.19	818
Ant. Cerebellum (R)	11	−52	−18	45.81	14636
Post. Cerebellum (L)	−29	−44	−27	12.73	1634

Coordinates are in standard stereotaxic space (Talairach & Tournoux, 1988) and refer to maximally activated foci as indicated by the highest t score within an area of activation ($P < 0.001$, uncorrected, random effect analysis). AIP, anterior intraparietal cortex; VIP, ventral intraparietal cortex; LIP, lateral intraparietal cortex, M1, primary motor cortex; pIP posterior parietal cortex; SMA, supplementary motor area; S1, sensory cortex.

TABLE 3. Common activations in continuous and ballistic tracking with fixation

Area	x	y	z	t_7-value	Voxels
V5 (hMT+) (R)	42	−61	4	11.49	1531
V5 (hMT+) (L)	−47	−59	4	7.21	182
S1 (L)	−46	−33	53	16.21	2348
AIP (R)	34	−38	44	8.89	1195
AIP (L)	−34	−40	43	7.89	383
VIP (R)	33	−40	46	8.27	552
VIP (L)	−31	−43	48	8.60	786
LIP (L)	−41	−36	55	16.21	2691
pIP (R)	21	−58	52	15.53	1880
pIP (L)	−30	−52	59	14.15	4466
M1 (L)	−36	−23	58	26.25	8406
SMA (L)	−2	−13	53	13.78	1513
Dorsal premotor cortex (R)	17	−12	56	10.95	701
Dorsal premotor cortex (L)	−16	−17	59	16.97	1810
Inf. Premotor cortex (R)	49	6	13	9.22	239
Putamen (L)	−21	−5	6	11.32	592
Thalamus (L)	−16	−15	6	10.98	845
Ant. Cerebellum (R)	10	−50	−19	20.79	8009

Coordinates are in standard stereotaxic space (Talairach & Tournoux, 1988) and refer to maximally activated foci as indicated by the highest t score within an area of activation ($P < 0.001$, uncorrected, random effect analysis). AIP, anterior intraparietal cortex; VIP, ventral intraparietal cortex; LIP, lateral intraparietal cortex, M1, primary motor cortex; pIP, posterior parietal cortex; SMA, supplementary motor area; S1, sensory cortex.

The similarity of the activation pattern during ballistic as compared with continuous tracking was demonstrated formally in a conjunction analysis (Table 3). Again, V5 (hMT+) was active in both hemispheres, as were the AIP, VIP, left LIP and pIP in both hemispheres, and a cortico-subcortical motor circuit including the sensorimotor cortex, premotor cortex, striatum and cerebellum. In a further step we investigated whether there are differences between continuous and ballistic tracking. We therefore studied the following contrast:

TABLE 2. Activations related to ballistic tracking with fixation vs. fixation

Area	x	y	z	t_7-value	Voxels
V5 (hMT+) (R)	42	−60	3	13.47	2581
V5 (hMT+) (L)	−46	−56	5	13.36	1108
S1 (L)	−47	−29	53	24.64	3433
Supramarginal gyrus (R)	36	−32	27	10.833	1260
Supramarginal gyrus (L)	−43	−30	27	9.44	902
AIP (R)	33	−37	43	12.15	3030
AIP (L)	−35	−39	46	18.12	2544
VIP (R)	32	−43	46	12.15	2242
VIP (L)	−33	−44	51	22.22	6132
LIP (L)	−39	−42	55	27.63	3055
pIP (R)	22	−58	52	16.26	3121
pIP (L)	−27	−57	53	17.03	3673
M1 (L)	−38	−19	55	18.94	2803
SMA (L)	−3	−14	53	13.43	1772
Dorsal premotor cortex (R)	18	−10	57	12.15	939
Dorsal premotor cortex (L)	−18	−18	59	15.26	1812
Inf. Premotor cortex (R)	43	6	9	11.29	868
Putamen (R)	23	2	4	8.11	209
Putamen (L)	−24	−8	9	9.72	973
Thalamus (R)	8	−14	2	11.86	385
Thalamus (L)	−17	−20	5	16.39	1370
Ant. Cerebellum (R)	10	−50	−19	20.82	9160
Post. Cerebellum (L)	−19	−61	−19	8.65	624

Coordinates are in standard stereotaxic space (Talairach & Tournoux, 1988) and refer to maximally activated foci as indicated by the highest t score within an area of activation ($P < 0.001$, uncorrected, random effect analysis). AIP, anterior intraparietal cortex; VIP, ventral intraparietal cortex; LIP, lateral intraparietal cortex, M1, primary motor cortex; pIP posterior parietal cortex; SMA, supplementary motor area; S1, sensory cortex.

Continuous tracking with fixation vs. ballistic tracking with fixation

This contrast revealed significant activations that were restricted to visual areas: activated were the early visual areas and V5 (hMT+) on the right (Fig. 4, Table 4). In contrast, a comparison in the opposite direction (ballistic tracking with fixation vs. continuous tracking with fixation) showed no ($P > 0.1$) area of higher activation.

These results raised the question of whether the activation of V5 (hMT+) was due to the larger visual input during continuous tracking or whether V5 (hMT+) potentially also participated in programming of the tracking hand movements. Therefore, we contrasted the two tracking conditions with their corresponding replay conditions. Because the replay conditions were identical to the visual input related to the trajectories of the target and the cursor as in the tracking conditions, an enhanced activity in V5 (hMT+) would indicate the visuomotor components in the tracking conditions:

Continuous tracking with fixation vs. replay

In fact, our results showed significant bilateral activations in area V5 (hMT+), on the right more than on the left (Table 4). This was reflected in each of the eight individuals. Also, the primary visual cortex was activated. It should be noted that both during the active and the control task the subjects fixated the fixation cross in the centre of the screen.

Ballistic tracking with fixation vs. replay

Again, an increased BOLD response was shown in area V5 (hMT+) right, but in this contrast only on the right (Table 4). Overall, the activations were less prominent than during continuous tracking.

Beta values analysis

We did an additional parametric analysis with calculation of beta values to compare these regression parameter betas for the activations

specific for continuous and ballistic tracking. The beta value in area V5 (hMT+) during the replay condition of continuous tracking was less than during continuous tracking. However, the beta value during the replay condition of ballistic tracking was higher than during ballistic tracking. Furthermore, the beta values in area V1/V2 showed the same behaviour as in V5 (hMT+) (Fig. 5).

Thus, the activations had different systematic load changes in the different conditions suggesting a task-specific impact of sensorimotor control rather than a systematic effect related to different loads of attention.

Discussion

In this study we were able to show that V5 (hMT+) has both a perceptive and an executive role for the control of visually guided hand movements. When we contrasted the continuous tracking condition vs. the ballistic tracking condition (Fig. 4), central fixation and object tracking were present in both tasks, while the difference was in the target and cursor movements. Due to the long path of the motion signals across the visual field, there was a greater visual input during continuous tracking than during ballistic tracking which yielded a greater activation of V5 (hMT+). Also, V1/V2 became activated in this contrast, probably due to its role in visual guidance of hand movements (Dohle *et al*., 2004). During the continuous tracking condition a stronger feedback is also available. Furthermore, V5 (hMT+) also became activated when we contrasted the tracking conditions with the corresponding replay conditions. In this contrast both visual motion signals (cursor and target) were expected to be cancelled, while an activation of V5 (hMT+) should show its role for the control of visually guided hand movements. In fact, this was the case, substantiating our hypothesis.

Different visual areas in the extrastriate cortex that respond selectively to moving stimuli have been identified (Newsome *et al*., 1988; Albright, 1989). It was known that the area V5 (hMT+) is specialised in the processing of visual motion information in primate and human (van Essen *et al*., 1981; Watson *et al*., 1993). Earlier fMRI studies (Tootell *et al*., 1995) found that area V5 (hMT+) in humans responded selectively to moving (compared to stationary) stimuli. Lesions in area MT mainly affect ocular tracking movements and has little effect on visually guided saccades (Newsome *et al*., 1985).

Bilateral extrastriate damage to areas that include the human homologue of MT caused a patient to have a specific deficit in motion vision (akinetopsia) (Zihl *et al*., 1983, 1991). A study by Schenk *et al*. (2000) with the same patient as in Zihl's study demonstrated impairment not only in motion perception but also in action during ballistic tracking movements.

Focal electrical stimulation in the human posterior temporal lobe selectively impaired the perception of motion in one direction, and the direction was found to depend on the brain area stimulated (Blanke *et al*., 2002).

The hypothesis of our study is that the visual extrastriate cortex contributes not only to ocular tracking movements but also to certain aspects of the control of visually guided hand movements. For this reason, we designed our experiment to assess the functional role of V5 (hMT+) in visually guided hand movements and to localize the corresponding cortex activation during visually guided hand movements. To separate the influence of arm movements, replay conditions were used in our study where only visual motion of the identical target and cursor trajectories on the screen had to be watched.

Activation of V5 (hMT+)

Our results indicate that visual monitoring during tracking with central fixation implicitly requires the involvement of area V5 (hMT+).

The activation was increased significantly during visually guided continuous tracking movements in comparison to the replay of the identical visual scene. Ballistic tracking vs. replay also showed an activation in V5 (hMT+), but less than during continuous tracking, which agrees with the greater activation of V5 (hMT+) when visually guided continuous tracking is contrasted with visual guided ballistic tracking (Fig. 4). V5 (hMT+) activation in all of these cases is much stronger on the right than on left side (Fig. 5, Table 4). This is in agreement with the suggestion that the human right hemisphere appears privileged in processing spatial visuomotor information (Kertzman *et al*., 1997; Coghill *et al*., 2001).

In the pure visual motion task with fixation, we confirmed strong activation in early visual areas and moderate activation in V5 (hMT+) bilaterally. With this study we have, however, demonstrated the importance of V5 (hMT+) in visuomotor integration and not only in visual motion analysis. Primate studies (Treue & Maunsell, 1996) demonstrate that activity in the V5 complex (middle temporal region) can be modulated by attention. The effect of attention alone, however, is not sufficient to account for the present results. Subjects were instructed to attend to the motion of the cursor and target in the visuomotor tasks as well as in the visual tasks, so that the large effects (Fig. 5, Table 4) found here can hardly be accounted for by slight differences in attentional demands between the two tasks. By comparing visually guided continuous tracking movements with the ballistic tracking movements (center out) a significant increase of activation in V5 (hMT+) was also seen, but the attentional requirements in both tasks should be similar. We cannot, however, rule out completely the possibility that different attentional loads could be partially responsible for the enhancement of brain activation found during continuous tracking in the visuomotor tasks. However, a study by Culham *et al*. (1998) reported that attentional enhancement was weak in the MT complex, when they compared attentive tracking and passive viewing. Along the same line, Orban (2001) and Chawla *et al*. (1999) showed only a modest transient activity increase in the area V5 (hMT+) when the subjects attended infrequent speed changes.

As illustrated in Fig. 5, we can show that the activation in MT had higher beta values during continuous tracking than during the corresponding replay condition, while the opposite was true for

TABLE 4. Activations specific for continuous and ballistic tracking

	Continuous tracking vs. ballistic tracking					Continuous tracking vs. replay					Ballistic tracking vs. replay				
Area	*x*	*y*	*z*	*t*-value	Change (%)	*x*	*y*	*z*	*t*-value	Change (%)	*x*	*y*	*z*	*t*-value	Change (%)
V5 (hMT+) (R)	40	−69	−7	7.79	0.23	49	−56	−1	7.80	0.23	41	−50	−1	5.00 *	0.13
V5 (hMT+) (L)						−56	−65	−2	7.10	0.33					
Early visual a.	0	−71	−5	8.94	0.38	3	−75	−10	7.28	0.43					

Coordinates are in standard stereotaxic space (Talairach & Tournoux, 1988) and refer to maximally activated foci, as indicated by the highest *t* score within an area of activation (data threshold at $P < 0.001$ except $^{*}P < 0.01$, uncorrected, random effect analysis).

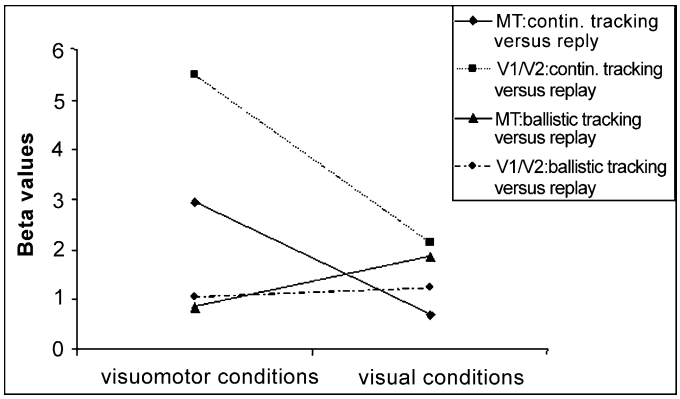

FIG. 5. Graphic representation of the GLM beta weights in area V5 (hMT+) and V1/V2 during the four conditions. Continuous tracking vs. replay V1/V2, $P < 0.05$; V5 (hMT+), $P < 0.05$. Ballistic tracking vs. replay V1/V2, $P = 0.91$; V5 (hMT+), $P = 0.67$.

ballistic tracking. Similar results were obtained for area V1/V2. Thus, the comparison of the beta values showed that the imaging data were more homogenous in the continuous tracking condition than in the corresponding replay condition (V1/V2, $P < 0.05$; V5 (hMT+), $P < 0.05$). In contrast, the response was as heterogeneous in the ballistic tracking condition as in the corresponding replay condition (V1/V2, $P = 0.91$; V5 (hMT+), $P = 0.67$) and this was probably due to a shorter engagement of V5 during the short period of time needed to execute the ballistic tracking movement. Therefore, this comparison of data accords with the hypothesis of a task-specific top-down modulation of these areas related to visuomotor control, whereas a single effect that could be due to a systematically higher load of attention during visuomotor control could be ruled out.

Activation pattern during visually guided hand movements

Our results show that the pattern of activation during visually guided hand movements include amongst others extrastriate areas and in particular posterior parietal cortex (PPC) (Fig. 3). PPC is densely interconnected with MT in non-human primates (Ungerleider & Desimone, 1986) and plays a critical role in integrating visual and somatic inputs (Savaki *et al*., 1997). Bilateral damage to the posterior parts of the parietal lobes causes severe impairments in spatial selective attention and visuomotor control (Harvey *et al*., 1995). Patients with lesions centered in posterior superior parietal cortex may have optic ataxia in which they cannot use visual information for accurate control of visually guided hand movements or to accurately reach targets (Perenin & Vighetto, 1988; Grafton *et al*., 1992).The posterior parietal lobe system is important for the visuomotor control of reaching in space (Desmurget *et al*., 1999) and for the visual processing required in the initiation of actions such a grasping, saccadic and pursuit eye movements and whole-body locomotion (Jeannerod, 1994; Milner, 1998). The extrastriate visual regions provide the visual information necessary to reach out and accurately touch an object. Because these regions project to PPC and PPC receives additional visual information from the pulvinar, it is within PPC that the integration of visual and somatomotor coordinates most probably occurs. For the hand used to reach, more contralateralized activity occurred within cortical motor areas and the PPC (Kertzmann *et al*., 1997). We found PPC activation bilaterally, although much more highly left than right. This left-sided activation was, however, stronger in visually guided ballistic tracking movements than during continuous tracking.

The study of AIP (anterior lower bank of the intraparietal sulcus) showed that many of its neurons discharge during finger and hand movements (Sakata *et al*., 1997). The AIP seems to play an intermediate role, as it processes information required for initiating hand–object interaction (Binkofski *et al*., 1999). We can confirm this result because in our tasks a bilateral increase of activation in this area was shown. The same results were obtained for the area VIP (ventral intraparietal area). Within the intraparietal sulcus, area VIP has been defined as the principal projection area from the MT (Maunsell & Essen, 1983). Its neurons have been shown to respond selectively to the direction and speed of moving visual stimuli (Duhamel *et al*., 1992; Colby *et al*., 1993). This area seems to process eye and head movement-related information by relating the different components of an entire action to each other in head-centered coordinates (Culham *et al*., 2001). The area VIP also processes polymodal motion including visual, acoustic and somatosensory information in humans and monkeys (Bremmer *et al*., 2001).

Classen *et al*. (1998) have shown that optic ataxia can occur following a thalamic hemorrhage. They suggest that the thalamic lesion interrupts a route for visual information going from the parietal cortex, via the pons, cerebellum and thalamus, to the frontal lobes. In both our visuomotor tasks the activation of the basal ganglia and thalamus was increased significantly. This is consistent with the studies of visually guided movements of Ellermann *et al*. (1998) and Kertzman *et al*., 1997). Thalamic activation also suggests that this nucleus is an important subcortical target of the dorsal stream. The activation foci we observed in the thalamus are most probably within the pulvinar, which is involved in sensorimotor integrative functions. We showed in all visuomotor conditions in our study that the anterior cerebellum (right more than left) and the vermis were activated. Lesions and inactivation of the cerebellar hemispheres disrupt visually guided reaching movements (Stein & Glickstein, 1992). The activation of the cerebellum demonstrates the implication of the cortico-ponto-cerebellar pathway in visually guided movements.

Our study confirmed that visuomotor tasks require the involvement of a large-scale sensorimotor network which includes parietal cortex, in particular posterior parietal cortex, insula, premotor cortex, motor cortex and cerebellum as well as subcortical structures such as basal ganglia and thalamus. More importantly, our study aimed to clarify the human cortical mechanism of visuomotor integration and we showed the role of area V5 (hMT+) in the dorsal stream in transforming visual information into motor behaviour for visual guidance of hand movements.

In conclusion, V5 (hMT+) has a pivotal role not only for the perception of visual motion but also for the control of visually guided forelimb movements. A further study is in progress investigating the role of V5 (hMT+) for pursuit and pursuit tracking (Kleiser *et al*., 2002).

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Abbreviations

AIP, anterior intraparietal area; BOLD, blood oxygen level dependence; EPI, echo planar imaging; fMRI, functional magnetic resonance imaging; MT, middle temporal area; LIP, lateral intraparietal area; pIP, posterior intraparietal

area; SMA, supplementary motor area; VIP, ventral intraparietal area; PPC, posterior parietal cortex.

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