Distinguishing Subregions of the Human MT+ Complex Using Visual Fields and Pursuit Eye Movements

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Dukelow, Sean P., Joseph F. X. DeSouza, Jody C. Culham, Albert V. van den Berg, Ravi S. Menon, and Tutis Vilis. Distinguishing subregions of the human MT+ complex using visual fields and pursuit eye movements. *J Neurophysiol* 86: 1991–2000, 2001. In humans, functional imaging studies have demonstrated a homologue of the macaque motion complex, MT+ [suggested to contain both middle temporal (MT) and medial superior temporal (MST)], in the ascending limb of the inferior temporal sulcus. In the macaque monkey, motion-sensitive areas MT and MST are adjacent in the superior temporal sulcus. Electrophysiological research has demonstrated that while MT receptive fields primarily encode the contralateral visual field, MST dorsal (MSTd) receptive fields extend well into the ipsilateral visual field. Additionally, macaque MST has been shown to receive extraretinal smooth-pursuit eye-movement signals, whereas MT does not. We used functional magnetic resonance imaging (fMRI) and the neural properties that had been observed in monkeys to distinguish putative human areas MT from MST. Optic flow stimuli placed in the full field, or contralateral field only, produced a large cluster of functional activation in our subjects consistent with previous reports of human area MT+. Ipsilateral optic flow stimuli limited to the peripheral retina produced activation only in an anterior subsection of the MT+ complex, likely corresponding to putative MSTd. During visual pursuit of a single target, a large portion of the MT+ complex was activated. However, during nonvisual pursuit, only the anterolateral portion of the MT+ complex was activated. This subsection of the MT+ cluster could correspond to putative MSTl (lateral). In summary, we observed three distinct subregions of the human MT+ complex that were arranged in a manner similar to that seen in the monkey.

INTRODUCTION

Several neuroimaging studies have localized the human homologue of the monkey motion complex (Tootell et al. 1995b; Watson et al. 1993; Zeki et al. 1991) often referred to as MT+ [the middle temporal (MT) plus other adjacent motion-sensitive areas, including medial superior temporal (MST)]. However, no study has been able to distinguish area MT from MST in humans. Here we show that the two areas can indeed be functionally separated and are adjacent as in the monkey.

Electrophysiology has identified several motion selective regions in the superior temporal sulcus (STS) of the macaque monkey. Two of the most well-studied areas are MT and MST. Area MT has strong projections to adjacent area MST (Desimone and Ungerleider 1986; Maunsell and van Essen 1983) and is typically subdivided into dorsal (MSTd) and lateral (MSTl) subregions. While area MT encodes the basic elements of motion, area MST has higher-order motion-processing abilities and has been implicated in the perception of both object and self-motion (Britten and van Wezel 1998; Tanaka et al. 1993). Macaque area MST has been shown to have considerably larger receptive fields than area MT (Desimone and Ungerleider 1986). The receptive fields of MT cells typically extend only a few degrees into the ipsilateral visual field (Desimone and Ungerleider 1986; Gattass and Gross 1981; Van Essen et al. 1981), while area MSTd neurons have receptive fields that extend well into the ipsilateral visual field (Duffy and Wurtz 1991). Raiguel et al. (1997) recorded neurons in MSTd whose receptive fields extended 30–40° into the ipsilateral field, whereas area MT receptive fields protruded only 10–15° into the ipsilateral field.

Another important criterion to distinguish between MT and MST is extraretinal input related to pursuit eye movements. Newsome et al. (1988), working in the macaque, concluded that MT and MSTl contained a class of cells that provided retinal slip information to the pursuit system. They also observed a second class of pursuit cells in MSTd and MSTl that received extraretinal input related to the execution of pursuit eye movements. These cells maintained activity during pursuit in the absence of a visual target. There is no evidence that area MT receives extraretinal input related to pursuit eye movements. Human functional neuroimaging studies have also demonstrated pursuit related activity within area MT+ (Barton et al. 1996; Petit and Haxby 1999).

The aim of this study was to differentiate between putative human areas MT and MST using high-field, high-resolution fMRI. We found that while contralateral visual motion activated the entire MT+ complex, ipsilateral visual motion only

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produced a significant response in the anterior portion of the MT+ cluster, likely corresponding to putative human MSTd. Additionally we found that while visual pursuit activated most of the MT+ cluster, nonvisual pursuit allowed localization of an area selectively activated by extraretinal signals found at the most anterior point of the human motion complex, possibly corresponding to putative human MSTl.

Preliminary results from this study have appeared previously in abstract form (Dukelow et al. 2000a,b).

METHODS

Subjects

Eight healthy human volunteers (5 male and 3 female) with normal vision were paid for their participation. All subjects gave informed consent in writing and the study was given ethical approval by University of Western Ontario Ethics committee.

Data acquisition

Images were collected using a 4 Tesla Varian Siemens (Palo Alto, CA; Siemens, Erlangen, Germany) Unity Inova whole-body imaging system equipped with whole-body shielded gradients. Functional imaging was carried out using blood oxygenation level dependent (BOLD)-based echoplanar imaging. To provide enhanced signal to noise, a custom-built quadrature radio frequency surface coil (8 cm diam) was placed unilaterally over the right occipital region (centered on MT+). This coil provided excellent signal to noise within the region of interest in only the right hemisphere. Subjects' heads were comfortably supported and restricted by a head vise with padded restraints at the sides of the head and on the forehead.

To locate the MT+ complex, a low-resolution functional localizer was acquired [72 volumes, in-plane resolution = 3.0 mm, 64 × 64, FOV = 19.2 cm, 11 5-mm slices oriented perpendicular to the calcarine, 1.95-s volume-acquisition time, time to repetition (TR) = 0.49 s, 4 shots, time to echo (TE) = 15.0 ms]. During this localizer scan, the subjects viewed alternating stationary and moving dots (16-s epochs, 144-s total). While the subject lay in the scanner, this localizer run was quickly analyzed using a motion minus stationary comparison, and the location of area MT+ was functionally determined. The results of this localizer scan were then used to accurately prescribe the higher resolution slices so they would encompass area MT+.

High-resolution slices were centered on MT+ and acquired with an in-plane resolution of 1.1 mm and slice thickness of 2 mm (128 × 128, FOV = 14 cm, 11 slices, 4-s volume-acquisition time, TR = 1.0 s, 4 shots, TE = 15.0 ms). Fifty-six volumes were acquired in each functional run. At the end of each functional session, high-resolution inversion prepared three-dimensional (3D) T1-weighted anatomical images of the brain (either 32 or 64 slices, 256 × 256, TR = 12.5 ms, TE = 6.5 ms) were collected.

In a later session, subjects were rescanned using a birdcage-style head coil to obtain full brain anatomical images. A high-resolution inversion prepared 3D T1-weighted sequence was used (voxel size: 0.86 mm in-plane, 256 × 256, FOV = 22 cm, 256 slices, TR = 11.5–12 ms, TE = 5.5–6.0 ms). Surface coil images were manually realigned to head-coil images using Brain Voyager 3.9 software (Brain Innovation, Maastricht, The Netherlands). Images were convolved to the atlas of Talairach and Tournoux (1988) to obtain coordinates for the regions of interest. Anatomical images from each subject were then segmented at the gray/white matter boundary and inflated for visualization purposes (Goebel et al. 1998).

Visual stimulation

Visual stimuli were presented using a Dell XPS R450 and a NEC MT800 projector at 800 × 600 resolution. Optic flow stimuli were generated using Microsoft Visual Basic (Microsoft, Redmond, WA) with the OpenGL graphics library. Visual pursuit stimuli were made using Director 5 (Macromedia, San Francisco, CA). Subjects lay supine in the magnet, backward (feet first) to allow a projected visual display that subtended a visual angle of 90° wide × 30° tall. They viewed the images back projected on a screen (Da-Lite, Warsaw, IN) through a mirror placed ~5 cm in front of the subjects' eyes and attached to the head vise.

All high-resolution experimental scans lasted 224 s (56 volumes) starting with a control state (either stationary dots or visual fixation) and then alternating between stimulus and control states. Epoch length was 24 s, with the last epoch in each run being 32 s (to allow for shifting of any function to account for hemodynamic lag). Each experimental scan was performed four or more times on each subject.

WIDE FIELD OPTIC FLOW. This stimulus consisted of approximately 1,500 centrifugally moving white dots (screen: 90° wide × 30° tall, dot size = 0.28°, average dot speed = 8.0°/s, dots were replaced as they moved off the screen) on a black background. Both the focus of expansion and the red fixation point were located at the center of the display. The control condition for this experiment was stationary dots. Five subjects were run in this experiment (within the same experimental session, nonvisual pursuit and visual pursuit experiments were also conducted).

CONTRALATERAL/IPSILATERAL OPTIC FLOW. The motion stimulus for this experiment was a radially expanding dot pattern (200 dots, average speed 8.0°/s, white dots on a black background) with the focus of expansion located at the center of the display. However, no dots were displayed in the central 30° of the display. Subjects fixated at center, while dots appeared from 15 to 45° in the periphery in either the contralateral (left) or ipsilateral (right) visual field. The control condition consisted of the identical display, but the dots were stationary. During each scan, epochs alternated as follows: CS-CM-CS-IM-IS-CM-CS-IM-IS (CM, contralateral motion; CS, contralateral stationary; IM, ipsilateral motion; IS, ipsilateral stationary).

As attention has been shown to increase the level of activation observed in MT+ using fMRI (Beauchamp et al. 1997; O'Craven et al. 1997), we incorporated an attentional task into our paradigm to effectively increase our functional signal to noise. At random (~2–5 times in each 24-s motion epoch), the moving dots would accelerate to 14°/s for a short period of time (~80 ms). Subjects were required to press a button when they noticed this acceleration. Each subject's performance was monitored "on-line" to ensure that they maintained attention for the duration of the experiment. Prior to entering the MRI, subjects were shown this acceleration cue to ensure that they could accurately detect it. Subjects were instructed to press the button the same number of times during each stationary condition to control for any activity that might be related to the button press.

Seven subjects participated in this experiment. In a later session, the experiment was repeated in five of these subjects; additionally, the nonvisual pursuit experiment described below was also conducted.

VISUAL PURSUIT. Subjects tracked a white dot (2°) moving pseudosinusoidally (0.35 Hz, horizontal displacement 27°) on a black background. The control condition was fixation of a stationary dot at the center of the display. Five subjects were scanned in this experiment.

NON-VISUAL PURSUIT. Previous studies (Jordan 1970; Lackner and Mather 1981; Levine and Lackner 1979) have shown that subjects are capable of tracking their finger or limb in complete darkness with pursuit eye movements. Subjects were pretested, prior to entering the scanner, to ensure they were able to generate consistent pursuit eye movements in complete darkness by recording their eye movements using the Ober 2 system (Permobil MeditechAB, Sweden). Subjects were instructed to move their finger with a displacement of ~10–12 cm (~30°) at a rate of ~0.25 Hz. One subject, who could not generate consistent pursuit eye movements under these conditions, was not functionally imaged.

During the imaging session, subjects were kept in complete dark-

ness and were instructed to begin by fixating their finger at center position with their arm stationary. They were then cued to change between fixation and pursuit by either a brief (0.5 s) flash of light projected into the magnet room or by an auditory stimulus. Subjects were instructed to smoothly pursue their finger using the same speed and visual angle as they had in the nonvisual pursuit pretest. Each scan began with fixation and alternated between pursuit and fixation. Five subjects were scanned in this experiment.

Data analysis

Analysis was carried out using STIMULATE (Strupp 1996) and BrainVoyager 3.9 (Brain Innovation, Maastricht, The Netherlands) software. Collected images underwent motion correction and linear trend removal. Functional runs within a subject were averaged and analyzed.

Wide field optic flow, visual pursuit, and nonvisual pursuit were analyzed using a voxel-by-voxel cross-correlation analysis to generate functional maps. For the computation of correlational maps, we used reference functions reflecting experimental and control conditions convolved with the hemodynamic response (lag values of 1 corresponding to a 4-s delay). Correlation coefficients were set at a minimum of 0.4 (minimum cluster size = 3). By only considering clusters of three or more contiguous voxels, and by correcting for temporal autocorrelation, the effective P value was <0.005 (Forman et al. 1995). Maps were superimposed on T1-weighted anatomical reference scans. Regions of interest (ROIs) for each experimental condition were chosen based on these correlational analyses.

The contralateral and ipsilateral data sets were analyzed using *t*-tests to compare the only two conditions of interest: contralateral motion minus contralateral stationary or ipsilateral motion minus ipsilateral stationary ($P < 0.05$, minimum cluster = 3). ROIs were generated for putative MT (pMT) based on contiguous voxels found in the ascending limb of the inferior temporal sulcus (Tootell et al. 1995a,b; Watson et al. 1993; Zeki et al. 1991) that were activated significantly by contralateral motion, but *not* activated significantly by ipsilateral motion. ROIs were generated for putative MST (pMST) based on contiguous voxels activated significantly to ipsilateral motion minus stationary.

Data for statistical comparisons across different experimental conditions were generated from the mean time course of all voxels in a particular ROI of an individual subject. These values were then averaged and compared using a paired Student's *t*-test.

Functional maps shown in Figs. 1*B*, 2, and 3 were generated using the general linear model with response to contralateral motion being one predictor and response to ipsilateral motion as a second predictor. This analysis effectively shows the transition from a contralateral motion response in the posterior of the MT+ cluster (pMT) to the anterior of the MT+ cluster (pMST) that responded to both contralateral and ipsilateral motion stimuli.

RESULTS

Response to wide field optic flow

To define the full extent of the MT+ complex, we first examined the response of wide field motion with the expectation that this stimulus should drive most visually responsive cells. As expected, wide field optic flow stimuli (as compared with stationary) produced a robust region of activation at the ascending limb of the inferior temporal sulcus in all subjects (Fig. 1*A*, single subject). On average, an activation volume of 1.43 ± 0.51 (SD) cm^3 was observed. The location of this activation [Talairach Coordinates (x, y, z): 44, −66, 2] was consistent with previous reports of human MT+ (Dupont et al. 1994; McCarthy et al. 1995; Smith et al. 1998; Sunaert et al. 1999; Tootell et al. 1995a,b; Watson et al. 1993; Zeki et al. 1991).

Additionally, optic-flow-related functional activity was observed in the intraparietal sulcus (IPS), the calcarine sulcus (likely corresponding to area V1), the parieto-occipital sulcus (POS), and in the collateral sulcus (for Talairach coordinates see Table 1). Activation within the collateral sulcus (18, −68, −9) was centered near the reported location of motion responsive region LG observed by Sunaert et al. (1999) (18, −81, −11) that they believe corresponds to V8 of Hadjikhani et al. (1998).

Response to contralateral/ipsilateral field optic flow

In this experiment, we compared the responses of the MT+ cluster to peripheral contralateral and ipsilateral optic flow stimuli. As the neurons in macaque area MT have receptive fields that typically do not cross more than 10–15° into the ipsilateral hemifield and MSTd neurons receptive fields that extend much farther into the ipsilateral hemifield, we expected to observe two adjacent areas with differential fMRI signal response properties. Theoretically, pMT should respond to contralateral stimuli only, while a second area, pMST, should respond to both contralateral and ipsilateral stimuli.

Contralateral optic flow stimuli produced a large volume of activation at the ascending limb of the inferior temporal sulcus (Fig. 1*B*, red, orange, and yellow) corresponding to MT+. However, ipsilateral optic flow stimuli consistently produced activation at the anterior end of the MT+ complex (Fig. 1*B*, yellow). As determined by a *t*-test of ipsilateral optic flow minus stationary ($P < 0.05$), an average volume of 0.38 ± 0.61 cm^3 was activated across subjects. Figure 1*B* displays an inflated representation of a single subject's brain. The black line on the inflated brain in Fig. 1*B* represents an ROI from wide field motion collected in a separate imaging session (see Fig. 1*A*). Within the functional maps, red represents voxels that responded significantly ($P < 0.05$) to contralateral but not ipsilateral stimuli, while yellow represents voxels that responded significantly to both contralateral and ipsilateral stimuli. Green voxels, seen in the left hemisphere in the axial slices, are areas that responded significantly ($P < 0.05$) only to what are labeled as "ipsi" stimuli (Fig. 1*B*). On the axial slice view, the posterior to anterior transition from red (contralateral motion response, as illustrated in the time course on the right of Fig. 1*B*) to yellow (both contralateral and ipsilateral motion response) is readily apparent. Because the contralateral/ipsilateral visual stimuli did not cover the central 30° of the visual field, the foveal representation of MT+ may not have been activated.

Figure 2 displays axial scans in five subjects, showing consistent posterior placement of pMT (in red) relative to pMST (in yellow). These areas were consistently found abutting one another as is seen in macaque MT and MST. Table 1 gives the Talairach coordinates of these subjects. On average, putative MT (defined by contralateral motion minus stationary but *not* ipsilateral motion minus stationary) was located at 44, −64, 5, while pMST (defined by ipsilateral motion minus stationary) was located 4 mm anteriorly (45, −60, 5). A paired Student's *t*-test of the Talairach coordinates from each subject revealed that pMST was significantly ($P < 0.01$) anterior to pMT.

Functional maps generated for pMT and pMST were also

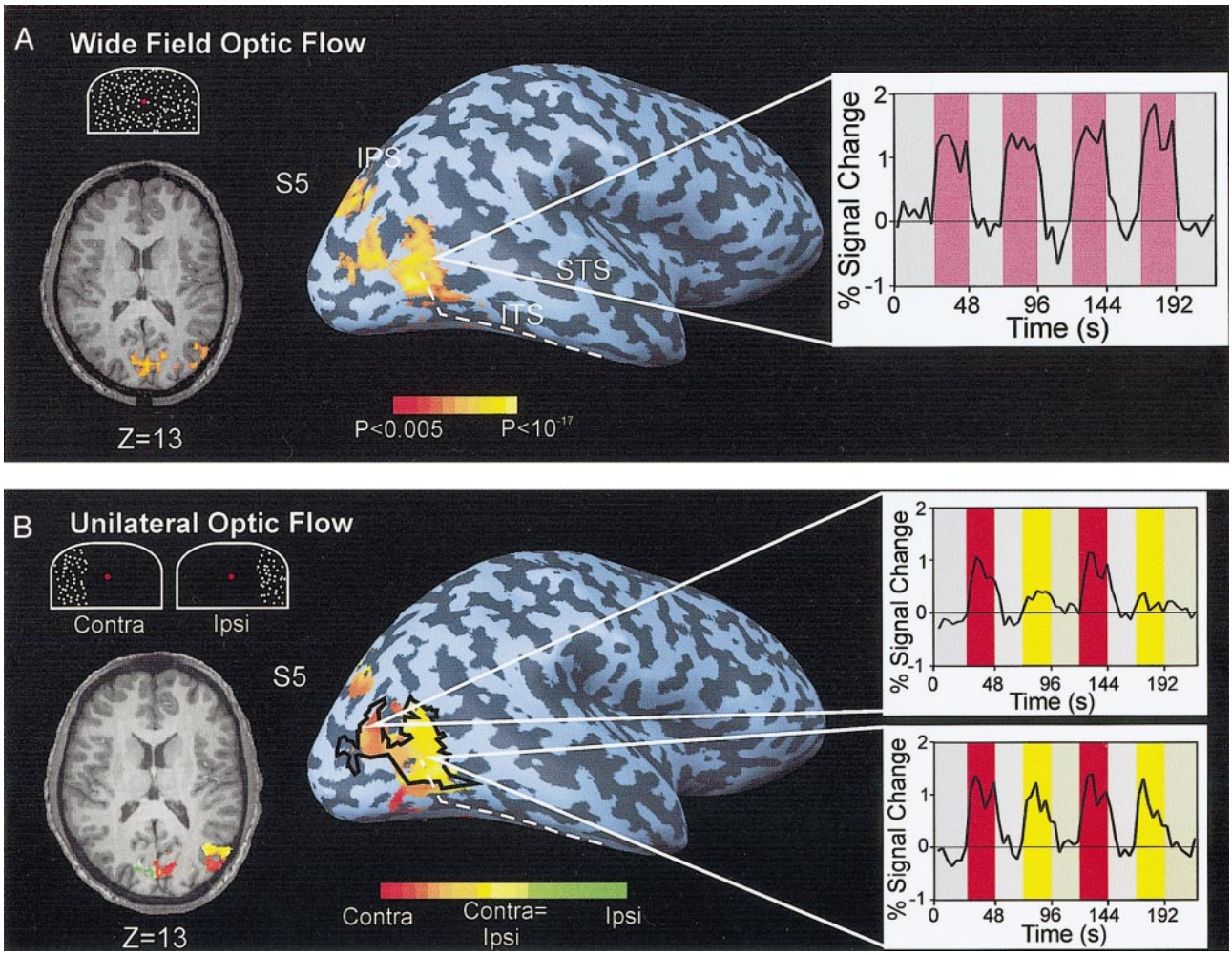

FIG. 1. *A*: activation observed by comparing wide field optic flow minus stationary correlation ($P < 0.05$) in *subject 5* on both the inflated brain and an axial slice. Activation is observed in area MT+ [the middle temporal (MT) plus other adjacent motion-sensitive areas, including medial superior temporal (MST)] in the ascending limb of the inferior temporal sulcus (ITS, outlined on the inflated brain with a dashed white line). It should be noted that this subject had one of the larger volumes of MT+ activation in our study. *Right*: the time course from area MT+. Within the time-course window, gray represents the periods in which the subject was presented with stationary dots, while purple represents the periods in which the subject was presented with wide field optic flow. *B*: a comparison of the activation produced by peripheral contralateral and ipsilateral optic flow is presented on both inflated brains and axial slices. A general linear model was used to generate this display of the functional maps. The 1st regressor examined the variance in the time course accounted for by contralateral motion. The 2nd regressor examined the variance in the time course accounted for by ipsilateral motion. The color bar found at the *bottom* of the figure represents the relative variance in the signal time course accounted for by contralateral versus ipsilateral regressors. This bar displays the transition from red (contralateral motion response only) to yellow (both contralateral and ipsilateral motion response) to green (ipsilateral motion response only). All activity displayed has met a minimum criteria of $P < 0.05$. A black line on the inflated brain represent the same subject's region of interest (ROI) from wide field motion on a separate day and session (*A*). Signal time courses are displayed to the right of the inflated brains for the both posterior portions of MT+ [putative MT (pMT), see *top time course* in *B*] and the anterior portions [putative dorsal MST (pMSTd), see *bottom time course* in *B*]. Within each of the time-course windows in *B*, gray represents stationary periods, red represents contralateral motion presentation, and yellow represents ipsilateral motion presentation. From the time courses, it is clear that the posterior portion of the MT+ cluster is modulated strongly by contralateral motion only, whereas the anterior portion of the MT+ cluster is modulated by both contralateral and ipsilateral motion. These time courses would be expected based on the analysis that was performed. STS, superior temporal sulcus; IPS, intraparietal sulcus.

consistent within subjects across different imaging sessions. Figure 3 shows functional maps from two subjects, scanned ~1 yr apart, that are nearly identical. It should be noted that while in Fig. 3*B* (*left*) activation in the posterior calcarine sulcus is observed, activation is not observed on the *right side* of the figure. This is due to orientation of the slice prescription, which was centered on pMT and incidentally excluded the posterior calacarine area in the later scanning session (*right*).

The averaged signal time courses for pMST across the seven subjects tested are presented in Fig. 4. Area pMST displayed a strong signal in both contralateral and ipsilateral motion in all subjects. As one might expect, assuming that MST neurons' receptive field centers are located in the contralateral visual field, the pMST group average for contralateral motion activity was still significantly greater ($P < 0.05$) than ipsilateral-motion-related activity.

In addition to activity within the inferior temporal sulcus, contralateral motion produced robust activity within the IPS,

TABLE 1. *Talairach coordinates of areas pMT and pMST in individual subjects*

	pMT			pMST			Difference		
Subject	*x*	*y*	*z*	*x*	*y*	*z*	*x*	*y*	*z*
S1	48	−58	9	45	−54	11	3	−4	−2
S2	44	−60	2	49	−59	3	−5	−1	−1
S3	45	−64	2	45	−59	1	0	−5	1
S4	41	−66	5	42	−61	5	−1	−5	0
S5	43	−72	9	46	−68	7	−3	−4	2
Mean ± SD	44 ± 3	−64 ± 7	5 ± 4	45 ± 3	−60 ± 5	5 ± 4	−1 ± 3	−4* ± 2	0 ± 2

Talairach coordinates for *subjects 1–5* for their putative middle temporal (pMT) and the putative medial superior temporal (pMST) region of interest (ROI). pMST was found to be consistently and significantly ($P < 0.01$) anterior to pMT. Difference refers to the difference between the pMT coordinates and the pMST coordinates. *, significant difference $P < 0.01$ in the *y* (anterior/posterior) coordinate. Neither the lateral (*x*) coordinates nor vertical (*z*) coordinates showed significant differences.

the calcarine sulcus, the POS, and the collateral sulcus (for Talairach coordinates see Table 2). The only other area in the right hemisphere that responded positively to ipsilateral motion was located in the IPS. However, signal increases to ipsilateral motion were only observed in three of seven subjects in the IPS. This area might bear some homology with the macaque ventral intraparietal area (VIP), as VIP receptive fields characteristics have been shown to be similar to those in MSTd (Schaafsma and Duysens 1996), but a recent study has suggested that human VIP is located much more anteriorly in the IPS (Bremmer et al. 2001).

During ipsilateral stimuli, we observed significant ($P < 0.05$) signal decreases along the calcarine sulcus (V1). In some subjects, we also observed signal decreases in other higher order visual areas—the parieto-occipital sulcus (3 of 7 subjects) and the collateral sulcus (2 of 7 subjects).

Response to visual pursuit

Newsome et al. (1988) found that cells in macaque MT and MSTl responded to the retinal slip associated with smooth pursuit eye movements, while certain cells in MSTl and MSTd responded to the "nonvisual" or extra-retinal component of pursuit eye movements.

In our experiment, pursuit of a small moving dot produced robust activation in most of MT+ (see Table 2 for Talaraich coordinates; average size = 1.94 ± 1.15 cm^3) in all subjects. As shown in the time course in Fig. 5*A*, the MT+ signal is strongly modulated during visual pursuit. This is consistent with previous fMRI reports (Barton et al. 1996; Petit and Haxby 1999), suggesting that visual pursuit produced significant activation of MT+.

Additionally, we observed activity within the fundus of the IPS in each subject, corresponding in location to that activated during optic flow stimulation. Activity was also observed in the calcarine sulcus, the POS, and the collateral sulcus during visual pursuit. Activity within the calcarine sulcus means a greater activation when pursuing the small moving dot than when fixation of the same stationary target, the greater activity may be due to the presence of retinal slip during the visual pursuit task.

Response to nonvisual pursuit

In the macaque, area MT and MST can be distinguished by their response to extraretinal pursuit signals (Newsome et al. 1988). Macaque MST cells, but not MT cells, are known to continue to respond during pursuit eye movements, even after a visual pursuit target disappears (Newsome et al. 1988). To mimic this, we had subjects generate pursuit in complete darkness while attempting to track the sinusoidal displacements of their finger. This nonvisual pursuit task produced a much smaller volume (0.44 ± 0.48 cm^3) of activation than visual pursuit, occurring in the anterolateral portion (see Talaraich coordinates in Table 1) of the MT+ complex in all subjects. Figure 5*B* shows an individual subject's activation

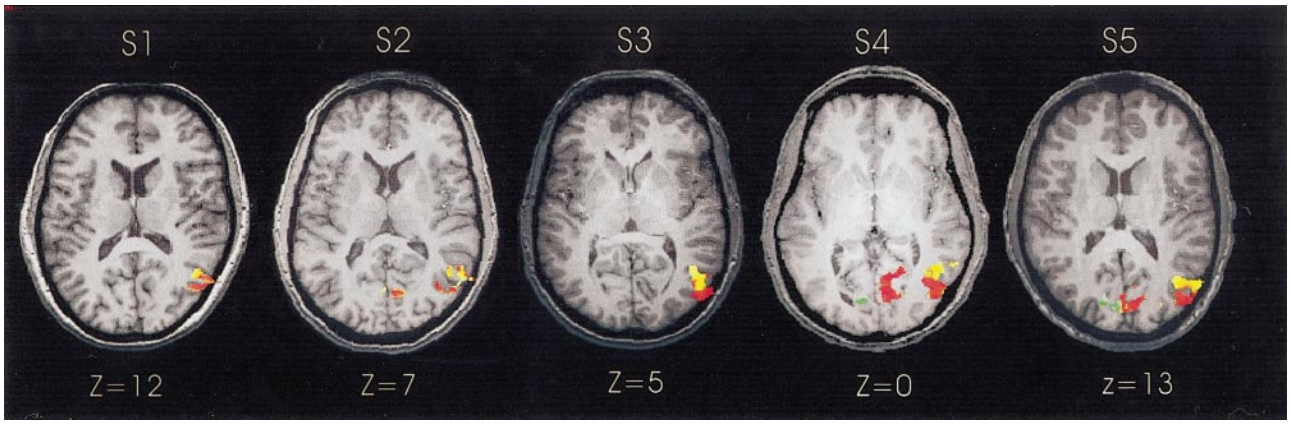

FIG. 2. Axial slices from 5 subjects (*S1–5*) showing that pMT (in red) was consistently located posteriorly to pMST (in yellow) across all subjects. Activation color coding is the same as in Fig. 1*B*. All activity displayed has met a minimum statistical criteria of $P < 0.05$.

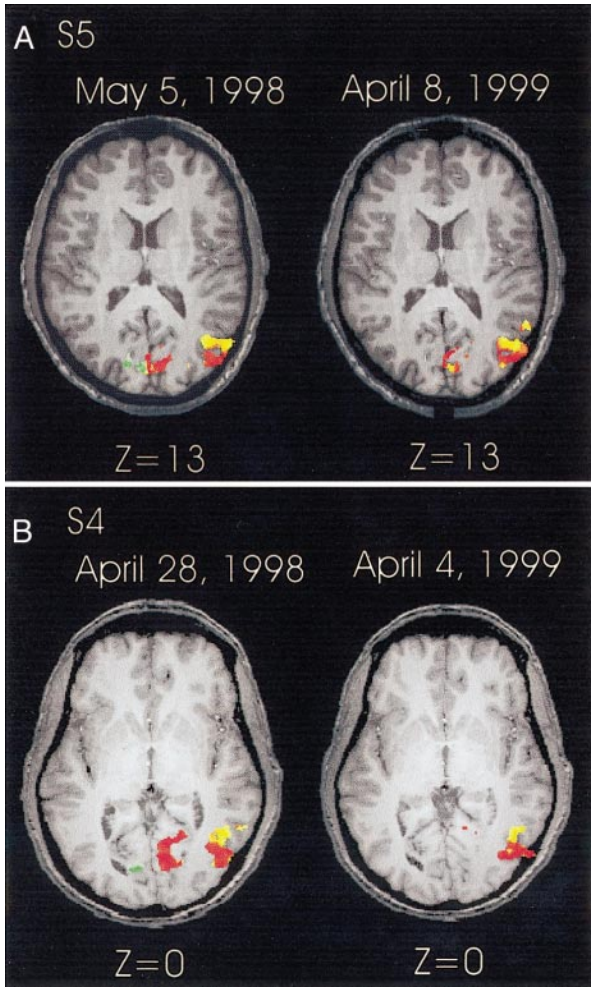

FIG. 3. Axial slices from 2 subjects, *5* (*A*) and *4* (*B*), showing replicability of maps in separate sessions dating almost a year apart. Activation color coding is the same as in Fig. 1*B*. These maps show remarkable consistency of the location of pMT and pMST within subjects. Maps were constrained to the same statistical criteria ($P < 0.05$). Small variations in maps may be due to slight differences in coil placements and slice selection in the different imaging sessions.

and signal time course for this nonvisual pursuit task. The ROI here was consistently located at the anterior portion of the visual pursuit ROI. As seen in the individual time-course plots, the signal within this area was strongly modulated by the nonvisual pursuit task.

Voxels activated strongly by nonvisual pursuit had only weak activation for contralateral motion and even less for ipsilateral motion in the peripheral retina (Fig. 6*A*). Nonvisual pursuit ROIs overlapped with ipsilateral motion ROIs in only two of five subjects. Within these two subjects, only 12% of the ipsilateral voxels overlapped with those in the nonvisual pursuit ROI. On average, the nonvisual pursuit ROI was found slightly anterior, lateral, and inferior to the ipsilateral motion ROI (Talairach coordinates: nonvisual pursuit: 47, −58, 3 vs. ipsilateral: 45, −60, 5). However, a paired Student's *t*-test revealed that differences in coordinates between the ipsilateral and nonvisual pursuit ROIs were not significant ($x = P < 0.24$, $y = P < 0.16$, $z = P < 0.14$).

The voxels activated by nonvisual pursuit were also strongly active to both wide field optic flow (which unlike the ipsilateral and contralateral optic flow, stimulated the fovea), and by visual pursuit (Fig. 6*B*).

DISCUSSION

Several studies (McCarthy et al. 1995; Tootell et al. 1995b; Watson et al. 1993; Zeki et al. 1991) have shown that moving visual stimuli preferentially activate an area in the lateral occipito-temporal cortex of humans. This area has been named MT+ because it likely represents a complex of distinct areas that include both the human homologues of MT and MST. Our study shows that this assumption was indeed correct. It demonstrates that MT+, which typically lies in the ascending limb of the inferior temporal sulcus, is made up of two parts: pMT and more anterior but immediately adjacent pMST. pMST in turn, can be separated into two adjacent parts, a posteromedial part that is activated by optic flow in the peripheral contralateral and ipsilateral visual field and an anterolateral part that is activated during nonvisual pursuit eye movement.

Area MT versus area MST

We observed a posterior area in the MT+ complex that responded to wide field motion, contralateral motion and visual pursuit, but not to motion in the peripheral ipsilateral visual field. This area displays properties typically found within the neurons of macaque area MT: receptive fields constrained mostly to the contralateral visual field (Desimone and Ungerleider 1986; Gattass and Gross 1981; Van Essen et al. 1981) and responsiveness to visual pursuit (Newsome et al. 1988). As such, this area most closely corresponds to the human homologue of macaque MT.

In the macaque, area MT is located on the lateral bank and floor of the caudal STS (Desimone and Ungerleider 1986; Gattass and Gross 1981; Montero 1980; Ungerleider and Mishkin 1979; Van Essen et al. 1981; Weller and Kaas 1983; Zeki 1969, 1971, 1975), while MST is located on the upper bank of the caudal STS and a small part of the adjacent floor (Desimone and Ungerleider 1986) with the posterior of MST bordering on MT. In humans, MT+ is typically found in the inferior temporal sulcus but has also been shown to be located in the lateral occipital sulcus and at the junction of these two

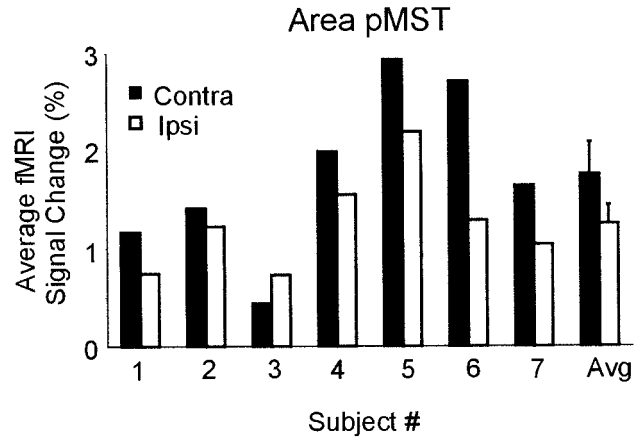

FIG. 4. Average percent signal change from area putative MST during both contralateral (■) and ipsilateral (□) motion stimuli. *Left*: individual subjects; *right*: the average (Avg) of all subjects. Error bars indicate SE. Although there was a large ipsilateral signal change in pMST, it was still significantly ($P < 0.05$) smaller than the signal change to a contralateral motion stimulus.

TABLE 2. *Talairach coordinates of observed activation experimental conditions*

Anatomic Location	WF-Stat			C-Stat			I-Stat			VP-Fix			NVP-Fix		
	x	*y*	*z*	*x*	*y*	*z*	*x*	*y*	*z*	*x*	*y*	*z*	*x*	*y*	*z*
ITS	44	−66	2	44	−64	5	45	−60	5	45	−66	2	47	−58	3
IPS	25	−79	22	25	−73	23	26	−70	24*	24	−78	23			
Col.S.	18	−68	−9	13	−60	−5				12	−61	−4			
POS	14	−77	24	11	−74	24				16	−74	21			

The center of activity in all of the observed regions in each functional subtraction. WF, wide field optic flow; Stat, stationary dots; C, contralateral optic flow; I, ipsilateral optic flow; VP, visual pursuit; Fix, fixation; NVP, nonvisual pursuit; Col.S., collateral sulcus; POS, parietoccipital sulcus; IPS, intraparietal sulcus. Inferior temporal sulcus (ITS) represents activity within MT+. *, activation was observed in only 3 subjects during this experiment.

sulci (DuMoulin et al. 2000). A positron emission tomography (PET) study (de Jong et al. 1994) examining coherent and incoherent motion has suggested that human MST may be separated from human area MT. In contrast, our study suggests that the arrangement in humans is very similar to that in the monkey with pMT being located posterior and adjacent to pMST in the ITS (see Figs. 1*B*, 2, and 3). This finding is consistent with preliminary human neuroimaging reports from other groups (Khan et al. 1999; Tootell et al. 1996).

The volume of activation we observed for human MT seems relatively consistent with what might be predicted from the literature on both monkeys and humans. Van Essen et al. (1981) measured the surface area of macaque MT to be 0.33 cm^2 with a cortical thickness of 1.5 mm (equivalent volume =

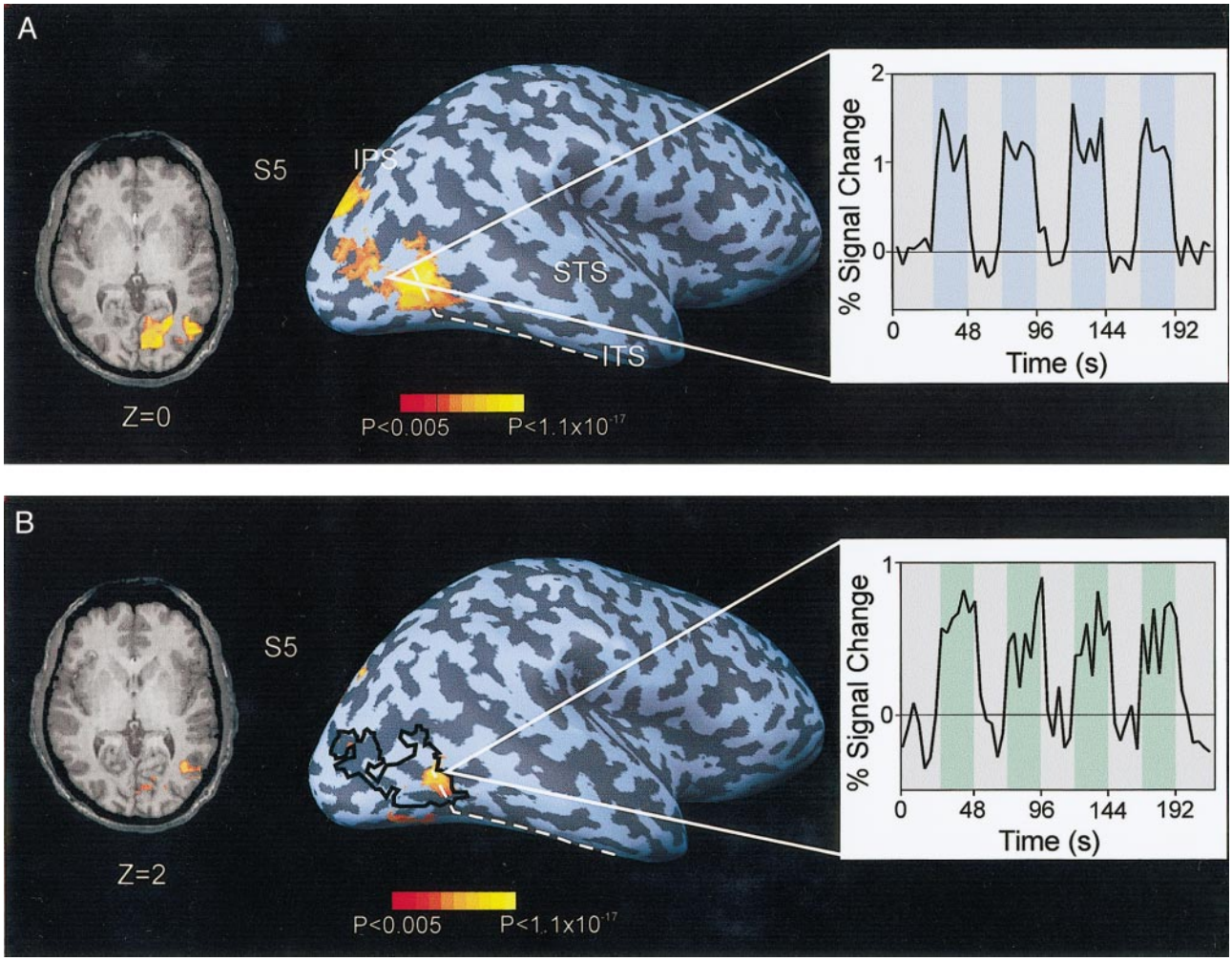

FIG. 5. *A*: activation produced by the visual pursuit task minus fixation correlation ($P < 0.05$) in *subject 5*. *Right*: time course from area MT+. Gray represents periods in which the subject was fixating, while blue represents periods in which the subject pursued a small dot. It should be noted that the activity observed in this condition is likely a combination of both visual pursuit activity as well as retinal slip. *B*: activation produced by nonvisual pursuit minus fixation ($P < 0.05$) correlation by same subject. A small subset of voxels at the anterior of MT+ was activated in response to nonvisual pursuit. *Right*: signal time course is presented with nonvisual pursuit periods marked by green and fixation marked by gray. Some activity also appears visual cortex, but only in this subject. Black lines on the inflated brain represent the visual pursuit ROI generated in the same subject during the same experimental session.

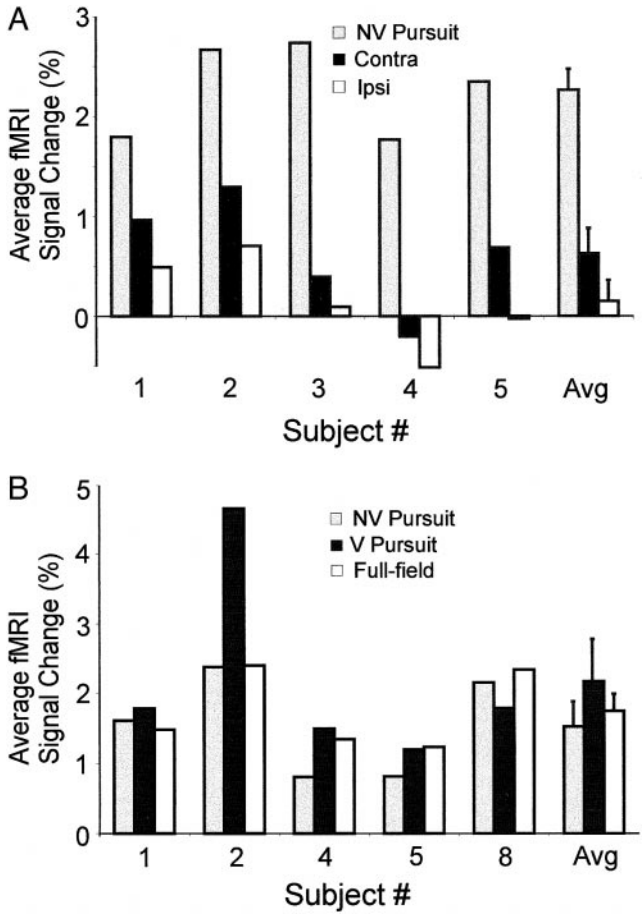

FIG. 6. *A*: average signal change activity plotted for the nonvisual pursuit ROI [defined in a nonvisual pursuit minus fixation correlation ($P < 0.05$)] during contralateral motion (black bars), ipsilateral motion (white bars) and nonvisual pursuit (light gray bars). Individual subjects are presented on the left and the average (Avg) data are presented on the right. The nonvisual pursuit condition was significantly higher ($P < 0.01$, paired *t*-tests) than both contralateral and ipsilateral motion. Thus the nonvisual pursuit region is only weakly activated by motion stimuli in the peripheral retina. *B* displays the average signal change activity plotted for the nonvisual pursuit ROI during visual pursuit (black bars), wide field motion (dark gray bars) and nonvisual pursuit (light gray bars). Data for graphs in *A* and *B* were collected in separate imaging sessions. The nonvisual pursuit region is activated in all three conditions. On average, there are no significant differences in signal change between any of the conditions.

0.495 cm^3). We observed an average volume of activation of 1.43 cm^3 for human area MT+ and 0.38 cm^3 for pMST. Hence, our pMT was 1.05 cm^3, approximately double the volume that was observed in the macaque. Tootell and Taylor (1995), using various staining techniques postmortem, reported that human area MT was $\sim 1.2 \times 2.0$ cm. While we measured volume and not surface area, the sizes we observed seem slightly smaller than Tootell's but still within what one might expect to find for human area MT using fMRI.

Tootell et al. (1998) observed activation throughout area MT+ in response to ipsilateral stimuli. Although this may seem inconsistent with our current findings, we suggest a possible reason for the difference: The ipsilateral stimuli used by Tootell et al. (1998) were presented immediately adjacent to the central fixation point while our stimuli were located 15° of visual angle into the periphery. Some MT cells have been shown to be activated by motion up to 10–15° into the periphery (Desimone and Ungerleider 1986; Gattass and Gross 1981; Raiguel et al. 1997; Van Essen et al. 1981). It should be noted, however, our results are similar to Tootell et al.'s (1998) in early visual areas (V1, V2), as we also observed significant signal reductions when stimuli were moved in the ipsilateral field.

Area MSTd versus area MSTl

In the macaque, MST is typically divided into MSTl and MSTd. Eifuku and Wurtz (1999) have proposed that the characteristics of MSTl neurons are appropriate for segmenting the motion of a small object from background, while MSTd neurons have characteristics consistent with a mechanism for the analysis of optic flow. Several lines of evidence support this proposal (see Eifuku and Wurtz 1999). Important to the present study, MSTl responds better to small moving spots, while MSTd responds preferentially to large moving patterns (Komatsu and Wurtz 1988). MSTl receptive fields have been shown to be smaller than those of MSTd (Tanaka et al. 1993). As well, MSTd neurons respond robustly to the components of large optic flow stimuli (Andersen et al. 1990; Duffy and Wurtz 1991; Saito et al. 1986), whereas there is no evidence that MSTl neurons do this. Interestingly, stimulation and lesions of MSTl alter the maintenance of smooth pursuit eye movements, whereas stimulation and lesions to MSTd do not (Dursteler and Wurtz 1988; Dursteler et al. 1987; Komatsu and Wurtz 1989).

Our study would suggest that the anterior MT+ complex in humans is also subdivided into two areas. The first area responded strongly to optic flow falling on both the contralateral and ipsilateral peripheral retina and shares similarities with the response properties to those neurons recorded from macaque MSTd, i.e., large receptive fields, strong response to optic flow. The second area, typically found slightly anterolaterally and inferior to the first, was selectively activated during nonvisual pursuit, responded strongly to wide field motion that included the fovea and to visual pursuit. This area shares similarities with monkey area MSTl, i.e., pursuit response and response to foveal stimuli. Taken together, these findings suggest the organization of the human motion complex is reasonably consistent with that observed in the macaque.

Activation within the IPS

Within the fundus of the macaque IPS exists VIP (Colby et al. 1993), an area known to receive input from both MT (Blatt et al. 1990; Maunsell and van Essen 1983; Ungerleider and Mishkin 1979) and MSTd (Baizer et al. 1991; Boussaoud et al. 1990). Neurons within this area respond strongly to visual motion stimuli (Bremmer et al. 2000; Colby et al. 1993; Duhamel et al. 1991), pursuit eye movements (Colby et al. 1993), and tactile stimuli (Colby and Goldberg 1999). Additionally, neurons in VIP have demonstrated receptive field characteristics similar to those observed in MSTd (Schaafsma and Duysens 1996). We observed activation within the fundus of the human IPS in response to both optic flow and pursuit stimuli (see Figs. 1, *A–C*, and 5*A*). Other imaging studies have produced similar results: Sunaert et al. (1999) observed activation in response to motion stimuli in a similar location [which they called VIPS (24,−76,28)], while Petit and Haxby (1999) observed pursuit responses in this region (28,−69,39).

Although this area appears to have some properties consistent with a macaque area VIP, a recent study claims to have mapped the human homologue of VIP depicts an area that is much more anterior along the IPS (Bremmer et al. 2001). The area that we have observed in the IPS definitely needs further investigation to characterize its field properties.

Conclusions

To date, researchers have been unable to separate human area MT from MST. Previous human neuroimaging work has studied the effects of visual motion processing (McCarthy et al. 1995; Smith et al. 1998; Tootell et al. 1995b; Watson et al. 1993; Zeki et al. 1991), the motion aftereffect (Culham et al. 1999; He et al. 1998; Tootell et al. 1995a), implied motion (Kourtzi and Kanwisher 2000), apparent motion (Goebel et al. 1998; Kaneoke et al. 1997), attention to motion (Beauchamp et al. 1997; O'Craven et al. 1997), and pursuit eye movements (Barton et al. 1996; Petit and Haxby 1999) on the MT+ complex. Our results indicate that the human MT+ complex can be teased apart, separating the human pMST from adjacent area pMT through the use of ipsilateral optic flow and nonvisual pursuit stimuli. This demonstrates that the human motion complex is organized in a similar manner to that of the macaque. The dissociation of human area MST from MT will allow future evaluation of the differential contributions of these areas to the many aspects of motion processing.

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