Sensitivity to optic flow in human cortical areas MT and MST

A. T. Smith,1 M. B. Wall,1 A. L. Williams2 and K. D. Singh3,*  
1Department of Psychology, Royal Holloway, University of London, Egham TW20 0EX, UK  
2Centre for Cognition and Neuroimaging, Brunel University, Uxbridge, UK  
3Neurosciences Research Institute, Aston University, Birmingham, UK

Keywords: fMRI, human cortical area MST, human cortical area MT, motion, vision

Abstract

The macaque V5/MT complex comprises several sub-regions but little is known of their human homologues. We examined human V5/MT with fMRI in terms of specificity to optic flow stimuli, a key characteristic of macaque MST. Stimuli were large fields of moving dots, forming coherent global flow patterns. Random motion was used as a control. Retinotopic mapping was also conducted. The previously suggested existence of at least two distinct sub-regions, MT and MST, within the V5/MT complex was confirmed. Human MT is activated about equally by all moving dot patterns, including random motion, suggesting that it has little sensitivity to global flow structure. As previously described, this region shows strong signs of retinotopic organization and is only weakly activated by stimuli confined to the ipsilateral hemifield. In human MST, located immediately anterior to MT and strongly driven by ipsilateral stimuli, activation varies markedly with optic flow structure. The strongest activation is produced by complex flow that contains multiple flow components (expansion, contraction and rotation). Single components produce rather less response, while rigid translation and random motion produce less still. The results suggest that human MST is strongly specialized for encoding global flow properties, while human MT is less so.

Introduction

In primates, multiple visual areas have been shown to exist in the posterior cerebral cortex, each with its own representation of visual space. A large literature concerning response properties of neurones in these areas has accrued. In parallel, studies of cortical connectivity have shown clearly that the visual areas are highly and reciprocally interconnected. In the posterior middle temporal gyrus is an area known as V5 or MT (Allman & Kaas, 1971; Dubner & Zeki, 1971) that has a preponderance of neurones sensitive to direction of image motion. There are also several other distinct visual areas in the vicinity of macaque V5/MT which appear to have a greater or lesser degree of specialization for motion. In particular, adjacent to V5/MT lie MST and FST (Desimone & Ungerleider, 1986). MST, like MT, has a preponderance of direction-sensitive cells. Some cells, mostly in the dorsal region (MSTd), respond preferentially to optic flow components (expansion, contraction and rotation) (Duffy & Wurtz, 1991), a property uncommon in MT (Lagaré et al., 1994). FST has fewer direction-sensitive cells and has an input from V4 which MST lacks (Boussaoud et al., 1990), suggesting that it may be as much involved in form as motion analysis. Receptive fields in MST are significantly larger than those of MT, while those in FST are larger again (Desimone & Ungerleider, 1986). Perhaps because of this, the retinotopic organization of MST appears less precise than in MT and less precise still in FST.

The V5/MT homologue in humans has been identified (Zeki et al., 1991; Tootell et al., 1995) and shown to be responsive to coherent global motion (Rees et al., 2000; Braddick et al., 2001). However, in the light of prime neurophysiology and anatomy data, it is widely acknowledged that the relatively large motion-sensitive region that was originally labelled V5 (or MT) in humans is probably a complex of several areas. Indeed, it is often now referred to by names such as 'the V5 complex’ or ‘MT+’. The sub-regions of this complex are difficult to distinguish with fMRI because of their proximity and the fact that, at least in non-human primates, similarities in their response properties outnumber differences.

Some suggestions have been made regarding possible subdivisions of the human V5/MT complex. Several investigators have noted a motion-sensitive region located ventrally with respect to the usual co-ordinates for V5/MT. Morrone et al. (2000) claim that this ventral area responds well to optic flow that changes over time. This raises the possibility that it may be functionally homologous to monkey MSTd. In contrast, Dukelow et al. (2001) found that ipsilateral optic flow stimuli activate only the anterior part of the V5 complex and suggest that this may be MSTd. In addition, they found that ‘non-visual pursuit’ (pursuit that continues after a stimulus disappears) drives only the most anterolateral portion of the V5 complex, which they suggested may be homologous with the lateral portion of primate MST, known as MSTl. Most recently, Huk et al. (2002) clearly identified two areas within the V5 complex. Their ‘MT’ responds to retinotopic mapping stimuli and usually shows signs of a coherent map. This is expected in human V5/MT because primate V5/MT shows a clear (albeit rather coarse) retinotopic organization (van Essen et al., 1981). Their ‘MST’, which is adjacent but more anterior to MT, is defined by a strong response to ipsilateral stimuli, as previously reported (Dukelow et al., 2001).
The various suggestions above can only be partially reconciled. Only one study (Morrone et al., 2000) has claimed to distinguish sub-regions based on specificity to motion stimulus type. One other (Huk et al., 2002), supported by a third (Dukelow et al., 2001), has proposed a division based on presence/absence of retinotopic organization and ipsilateral activation. Each study identifies two areas but they do not appear to correspond. The most detailed account, and that most consistent with primate neurophysiology (Huk et al., 2002), did not examine the functional properties of MT and MST but relied entirely on retinotopic organization. In this study we first employ the techniques reported by Huk et al. (2002) to separate MT and MST based on their two criteria. The purpose was twofold. Primarily, separate definition of the two areas is a necessary foundation for our main experiments but secondly, this is an important study that has not been replicated and is not in complete accord with earlier work. Having defined and identified MT and MST in our participants, we then provide a first account of the functional properties of human MT and MST, in terms of their sensitivity to different types of optic flow.

Materials and methods

Participants

Four healthy volunteers took part (two of each sex; mean age 22.5 years). One (MW) was one of the authors. The others were naive concerning the aims of the study and were paid for their time. All were screened in accordance with standard procedures, local ethical approval was obtained and informed consent was given. The participants were each scanned several times on different occasions and their data were analysed individually.

Stimuli

Visual stimuli were presented via a liquid crystal display projector on a rear-projection screen in the bore of the magnet. The stimuli were viewed monocularly via a custom-built optical device (essentially a low-magnification telescope) whose purpose was to give a larger field of view than is possible in free view. A large-diameter eyepiece lens of short focal length was used to give a circular field of view of diameter 70 deg. The eyepiece lens was aspheric, so there was minimal spherical distortion of the image (which appeared slightly concave). A yellow filter was incorporated to minimize chromatic aberration by eliminating short wavelengths. In this way it was possible to present large optic flow patterns that stimulated most of the visual field. The unstimulated eye was occluded.

All stimuli consisted of high-contrast moving random dot patterns (light dots on a dark background). The dot size was 40 arc min and the dot density was 0.1 dots/deg². Each dot moved in a straight path at a speed of 15 deg/s for a lifetime of 133 ms (10 frames) before disappearing and reappearing at a new, random location. Dots leaving the edge of the stimulus disappeared for the remainder of their lifetime before being replotted. Different dots were repositioned at different times, 10% of the dots being repositioned on each frame update. Global patterns of optic flow were produced by controlling the local motion directions of the dots.

The study had two phases. The first was modelled on the study of Huk et al. (2002) and the stimuli were similar to theirs. The purpose was to identify MT and MST in our participants so that the two areas could be studied independently in the second phase. Two types of stimuli were used, one for retinotopic mapping in V5/MT and one to test for ipsilateral activation. To map polar angle, the 70-deg circular image was filled with dots. Most were static but the dots in one sector (wedge) were made to move alternately inwards and outwards along the radii of the image to form a motion-defined wedge. The width (polar angle) of the wedge was 80 deg. The wedge rotated slowly, in steps of 20 deg, either clockwise or anticlockwise, taking 54 s for a complete revolution. A large, central, static spot provided a fixation point.

For comparing contralateral and ipsilateral drive, two circular patches of moving dots could be presented, one on each side of the central fixation point. The patches subtended 15 deg diameter and were centred on the horizontal meridian at an eccentricity of 17.5 deg. The dots within each patch moved alternately inwards and outwards along the radii of the patch. Periods of 15 s in which one patch (either right or left) was present were alternated with 15-s periods in which there was no stimulus (other than the fixation spot).

The second phase of the experiment employed full-field optic flow stimuli of different types. In all cases, a prominent central fixation spot was provided. The key flow components studied were translation, rotation and expansion as these are the properties to which primate MST cells are commonly sensitive (Duffy & Wurtz, 1991). Sensitivity to deformation features strongly in computational analyses of optic flow but MST neurones that respond specifically to deformation are rare (Lagae et al., 1994). The flow patterns employed were as follows.

Translation

All dots moved in the same direction (horizontally), simulating the effect of the observer translating horizontally through a static environment. The purpose was to activate neurones in the MT complex that are selectively sensitive to image translation.

Rotation

All dots moved in concentric circular paths to produce an impression of anticlockwise rotation. This would be consistent with rotation of the observer around the line of sight. Its purpose was to activate neurones that are sensitive to global rotation.

Complex flow

The global flow pattern changed over time. Flow changed gradually from pure clockwise rotation to pure expansion, pure anticlockwise rotation and pure contraction via intermediate spiral flow patterns containing a mixture of radial and rotational flow. The time taken for one cycle was 3 s. This stimulus was modelled on that of Morrone et al. (2000). Its purpose was to activate as many flow-sensitive neurones as possible with a single stimulus.

Random motion

The local direction of each dot was determined at random. The purpose was to provide a control condition in which local motion was present in all directions at all locations, with no global flow structure.

Data acquisition

Images were acquired with a 3T MR scanner (Magnetom Trio, Siemens, Erlangen, Germany) equipped with an eight-channel array headcoil. Functional images were acquired with a standard
gradient-echo, echoplanar (EPI) sequence (TR, 1500 ms; TE, 31 ms; flip angle, 90 deg; voxel size, $2.5 \times 2.5 \times 2.5$ mm; coronal slices, partially parallel acquisition, GRAPPA; Griswold et al. 2002; acceleration factor, 2). Only the posterior portion of the brain was imaged. Functional volumes were acquired continuously during each experimental run. A high-resolution (1 mm) three-dimensional anatomical scan (MP-RAGE, Siemens) of the whole brain was also acquired.

Procedure

Each participant was scanned on several different occasions over a number of weeks. Each session consisted of eight to 10 functional scans lasting either 4 or 4.5 min each, interspersed with short rest periods. For the study of sensitivity to optic flow, a block design was employed (16 blocks of 15 s, total 4 min) in which either two types of optic flow were alternated or one was alternated with a blank field (see Results for details). For retinotopic mapping, five cycles of wedge rotation were presented (total 4.5 min). To obtain improved results, each stimulus condition was repeated at least three times and the results were averaged. Anatomical scans were also obtained at least three times and averaged to provide improved grey/white matter segmentation.

Analysis

Pre-processing of the data was performed using SPM2 (Wellcome Department of Cognitive Neurology, London, UK). This involved: (i) realignment of each EPI volume to match the first volume in the first run of the scan session, providing correction for head motion; (ii) coregistration of each series with the first series of the first scanning session to enable averaging of experimental conditions across sessions and (iii) spatial smoothing by convolution with a three-dimensional Gaussian kernel of FWHM 5 mm.

Analysis was performed in different ways for different purposes. For all block designs, the time-courses were modelled in SPM2. Each 4-min run contained only two different stimuli. In each voxel, the difference in the magnitude of activation between the two stimuli was estimated by modelling the data in terms of the SPM contrast between the two. The model was a boxcar (squarewave) function, smoothed by convolution with a synthetic haemodynamic temporal impulse response function (SPM’s ‘canonical HRF’). High-pass temporal filtering (cut-off frequency 0.017 Hz) was applied to each time-series to reduce the effects of low-frequency temporal noise.

For retinotopic mapping, a different analysis was employed based on standard procedures (Sereno et al., 1995). For each stimulus run, the temporal phase of the response to the wedge of moving dots was obtained by fitting a sinusoid to the time-series for each voxel and taking its phase as an indicator of visual field position of the neurones in that voxel. Custom software was used for this computation. The resulting phases were averaged across equal numbers of runs in which the wedge moved clockwise and anticlockwise, so as to cancel the effect of the haemodynamic delay on measured phase (Smith et al., 1998).

In all cases, results were visualized and regions of interest (ROIs) were defined on the two-dimensional grey matter surface rather than in the three-dimensional brain. Based on the three-dimensional anatomical scan, the grey matter was segmented with mrGray (Stanford Tools; http://white.stanford.edu/~brian/mri/segmentUnfold.htm). A circular patch of grey matter that included the V5 complex was then flattened to produce a flatmap. Finally, functional data were superimposed as colours on the flatmap with mri3dX (http://www.jiscmail.ac.uk/lists/mri3dX.html). The same software was used to define ROIs and to calculate mean activation values across the voxels in each ROI.

Results

Definition of MST from ipsilateral activation

Presenting a motion patch separately in the right and left hemifields provided good differentiation of MST and MT in five of the eight hemispheres studied. In two others, indicative signs were obtained that allowed definition of MST when taken in conjunction with data from the other experiments but might not be reliable when taken alone. In the eighth hemisphere, there was activity in the V5/MT complex but no reliable difference between contralateral and ipsilateral stimulation. There was also no differentiation in terms of retinotopic organization or optic flow. This hemisphere was therefore excluded from all further analysis.

Figure 1 shows results from both hemispheres of one participant as a pseudo-colour overlay on a flattened representation of the lateral occipital cortex. Contralateral stimulation yields a large active region corresponding to the V5/MT complex. Also apparent is activity in the most dorsolateral of the standard retinotopic areas, V3A. The gap between these two regions is the lateral occipital area, which is not strongly activated by meaningless patterns. With ipsilateral stimulation, only a relatively small sub-region of the V5/MT complex is active; this is the region identified as human MST by Huk et al. (2002). Area MT is not significantly activated. MST is adjacent to MT and positioned further away from V3A on the grey matter surface. This was a consistent finding across all seven hemispheres in which a division was evident. The approximate borders of the two areas, drawn by eye with no attempt to define the precise shape and extent of the regions, are shown by black outlined. The borders of the regions are highly dependent on the threshold adopted and so precise definition is not realistic. The approximate locations of the centres of the two areas in each hemisphere are indicated in a three-dimensional-rendered image (Fig. 1, right panel). The approximate extent of the grey matter covered by the two areas is identified, for one hemisphere of the same brain, in Fig. 2. The location of the V5 complex, in terms of the local gyral anatomy, is consistent with that described in detail by Dumoulin et al. (2000).

These results replicate and are broadly in line with those of Huk et al. (2002). We found that the size of MST is about equal to that of MT, whereas they reported that it is rather smaller. However, the apparent size of MST, based on ipsilateral drive, is dependent on the sensitivity of the acquisition and the threshold applied to the results as the active area tends to shrink towards its centre as the threshold is raised. Thus, neither study gives truly reliable estimates of the size of MST.

Retinotopic organization of MT and MST

The second criterion used by Huk et al. (2002) to differentiate human MT and MST is that MT contains a clear and orderly retinotopic map of the contralateral hemifield, whereas MST does not (or at least none could be demonstrated with fMRI). Finding a retinotopic map in MT is more demanding, in terms of spatial precision, than demonstrating the presence or absence of ipsilateral activation and our success rate was correspondingly lower. Figure 3 shows the most compelling examples. In the left panel, a clear map of polar angle is seen in MT, covering the entire contralateral hemisphere. In MST, a patch of colour is seen, indicating that there is modulation of the response with stimulus
position, but there is no clear retinotopic map. In the right panel, the result is similar but less robust in MT and there is no significant position dependency in MST. The other five hemispheres also show position-dependent activation in MT and sometimes MST but with varying degrees of orderliness in MT and little or none in MST. This, too, is in line with the results of Huk et al. (2002). Their maps always tended to exclude the extremes of the colour scale (the upper and lower vertical meridians), indicating some regression to the mean, and some cases showed position-dependent activation without a compelling structure. Obtaining a phase map within MT is at the edge of the resolution obtainable with standard fMRI procedures.

Curiously, the orientation of the retinotopic map within MT is not consistent. In AL, right hemisphere (Fig. 3, left panel), it is clear that polar angle changes in the direction parallel to the MT/MST boundary. The upper quadrant of the visual field (blue/purple) is represented ventrally within MT and the lower quadrant (orange/green) is represented dorsally. This organization mirrors that found in areas V1–V3. In MW, right hemisphere (right panel), polar angle again changes in the direction parallel to the boundary but now upper field locations appear to be represented dorsally. Inspection of the data of Huk et al. (2002) (their figures 3 and 4) also shows variability in the apparent orientation of the map in MT. Their clearest example (ARW, right hemisphere) shows the upper field represented dorsally, in line with our MW. This is also the case for two other hemispheres (their
ARW right and DJH left) but their DJH right shows a clear organization running broadly orthogonal to the boundary. Their remaining hemispheres are ambiguous in this respect, as are several of our own. It is unclear whether these differences are real or simply an artefact of limited resolution, imperfections in the flatmap or in the correspondence between the functional voxels and flatmap. Imaging with higher precision will be necessary in order to resolve this issue. Here, we simply use the presence of greater position dependence in MT than MST as an additional criterion for defining the two areas, prior to studying their sensitivity to optic flow.

**Specificity for optic flow**

Having defined human MT and MST, the strength of the response to various optic flow stimuli in each region was assessed by defining a ROI on the flatmap corresponding to each of the two areas and computing the mean activation (percent signal change) averaged across all voxels falling within the region. The values obtained were then averaged across the seven (of eight) hemispheres in which MT and MST could be distinguished. These average activation values are shown in Fig. 4.

When an optic flow pattern was alternated with a blank field (Fig. 4a), responses to all flow patterns were obtained in both MT and MST. This is also evident in Fig. 5, which shows results for one hemisphere as pseudo-colour overlays on a flatmap. Responses were generally larger in MST than MT. This could be because MST was more optimally activated but it may simply reflect an artefact of the ROIs selected, as mean activation magnitude of an ROI depends heavily on which voxels are included.

Figure 4a shows that, in both MT and MST, the weakest activations were produced by random motion and translation. A relatively weak response to random motion is expected and, if anything, it is surprisingly strong. The equally weak response to translation is not expected as previous studies have reported that neurones in macaque MT and MST respond more strongly to coherent translation than to random motion (Britten et al., 1993) and the same is true in previous fMRI studies of the human V5/MT complex (Rees et al., 2000). This issue will be considered in the Discussion.

The strongest activations, in both MT and MST, were obtained with expansion, rotation and the complex time-varying pattern in which expansion and rotation were combined. In MT, the responses to these three stimuli were similar in magnitude. In MST, the complex stimulus caused a greater response than pure expansion or rotation. ANOVA showed that this difference between the two areas is statistically significant. A two-way ANOVA based on the five stimuli in Fig. 4a showed a significant interaction between visual areas (MT/MST) and stimulus \((F_{4,12} = 3.3, P < 0.05)\). As it may not be appropriate to regard the two hemispheres of one brain as independent, this and related analyses were based on data for four people with left and right pooled, rather than seven hemispheres. In practice, the two measures are probably largely independent, so this approach is conservative. Post-hoc t-tests show that the interaction reflects a difference between MT and MST for the complex stimulus \((t_3 = 3.0, P < 0.05)\) but not for expansion or rotation.

The greater response to the complex flow pattern in MST suggests that MST may contain different neurone populations sensitive to rotation and expansion, both of which respond to the time-varying stimulus. Also, the complex stimulus contains both expansion and contraction, and rotation in both directions, whereas the single stimuli contain only one component. It is conceivable that putative human MST encodes the temporal structure of changing flow patterns but it is not necessary to invoke such a mechanism to explain the results and it is not thought that primate MST has such properties (Paolini et al., 2000).

**Fig. 4.** Mean relative activation in each of the nine stimulus comparisons that were conducted in the main experiment, averaged across seven hemispheres. Activation values reflect the difference between the two block types in each condition. Percent signal change was calculated based on the mean value over the relevant region of interest. (a) Conditions in which optic flow was contrasted with a blank field; (b) conditions in which optic flow was contrasted with random motion. Error bars show ± 1 SEM.
Differential activation between coherent optic flow and random motion was also assessed, based on separate scans in which two patterns were interleaved. The results are shown in Fig. 4b. In MT, expansion, rotation and complex flow all give similar levels of differential activation. Translation gives no differential activity. Indeed, the mean is negative, reflecting the average of some hemispheres with small positive activations (translation > random) and some with small negative activations (random > translation). In MST, the pattern is similar but the differential activation is larger, particularly for the complex time-varying stimulus. A two-way ANOVA based on the four conditions in Fig. 4b gave a significant interaction between visual areas (MT/MST) and stimulus ($F_{3,9} = 6.5, P < 0.02$).

Post-hoc t-tests show significant differences between MT and MST for the complex stimulus ($t_5 = 6.3, P < 0.01$), expansion ($t_5 = 5.9, P < 0.01$) and rotation ($t_5 = 3.2, P < 0.05$) but not translation. These results indicate clear sensitivity to global flow properties in MST but not MT. However, the fact that three of the four flow patterns give greater activity than random motion in MT suggests that there may also be some degree of global motion specificity in MT.

The flatmaps in Fig. 6 illustrate the fact that complex flow gives much greater activation than random motion in MST. This comparison is shown for all seven hemispheres analysed. In all cases, MST shows significantly greater activation by flow than random motion across most or all of its area, in accordance with Fig. 4b. In the case of MT,
the difference between the two conditions is much weaker and fails to reach statistical significance in all but a handful of voxels.

The results shown in Fig. 4b are very much in line with those from the comparison of the same optic flow patterns with a blank field (Fig. 4a). It should be noted that this is not inevitable as the differential results are not derived from the single-stimulus data but from separate scans in which two stimuli were directly contrasted.

Overall, the mean responses were consistently larger in MST than in MT. This is confirmed by a two-way ANOVA based on all of the data in Fig. 4a and b combined, which gave a significant main effect of visual area (F1,13 = 17.3, P < 0.05). The same analysis gave a significant interaction between visual area and stimulus comparison (F6,24 = 2.4, P < 0.05), showing again that MT and MST were differentially affected by the type of stimulus.

Discussion

Flow specificity in human MST

We have confirmed the existence in human cerebral cortex of two distinct motion-sensitive areas (Dukelow et al., 2001), dubbed MT and MST by analogy with the primate areas of the same names. We tested whether the two areas differ in their specificity to the global structure of optic flow patterns and found that they do. Just as in monkey cortex, MST has greater specificity than MT to global expansion and rotation of a dot pattern in which the individual dots only ever translate. This finding strengthens the belief that the two human areas are functionally homologous with the two homonymous primate areas.

This tidy conclusion must immediately be qualified, however. In primates, the grey matter in the region of V5/MT has been subdivided into numerous distinct regions, defined by a combination of anatomy, connectivity and response properties. Indeed, the exact number and boundaries of these regions are not yet clearly established. Even within MST, there is some uncertainty and disagreement concerning sub-divisions such as MSTd and MSTl (dorsal and lateral), their locations and functions. To demonstrate a large (approx. 200 mm²) region of the human grey matter sheet that appears functionally uniform in one set of experiments and call it MST may well prove to be a serious oversimplification.

Even the definition of human MT applied here and by Huk et al. (2002) should not be regarded as watertight. Still lacking is a clear, repeatable demonstration of a single representation of contralateral visual space in this region. Macaque V5/MT has a clear retinotopic organization that has been specified in detail and independently verified in several laboratories (e.g. Gattass & Gross, 1981; van Essen et al., 1981). The fovea is represented at a single location, different polar angles are represented along lines radiating from this point and iso-eccentricity lines form curves that are orthogonal to the polar angle lines. In short, the shape of the map resembles the visual space it represents, although with distortion at the edges and with a decline in magnification factor as eccentricity increases. Neither our study nor previous fMRI work has come close to specifying the organization of human MT at this level of detail. We saw very clear signs that a retinotopic organization exists but, even when polar angle appears to vary in an orderly way in one hemisphere, the organization may appear different in another. Retinotopic mapping is particularly difficult in this region, not only because the area devoted to one map of space is much less than in V1/V2 but also because the cortex tends to be highly convoluted in this vicinity (Zilles et al., 1989). The latter point can be seen clearly in Fig. 2, which shows the locations of the MT and MST ROIs in one hemisphere transposed to the three-dimensional grey matter surface. This level of convolution is typical and the form of the convolutions is not consistent across hemispheres, even within the same brain. As functional voxels are relatively large (2.5 mm in our case), small-scale convolutions lead to disproporti- rate errors that arise when a voxel straddles both banks of a small sulcus. The problem is compounded by the fact that small errors in coregistration and the minor distortions that are inherent in echo-planar imaging can cause large errors in terms of visual field location.

Even without these problems, the inherent spread of the BOLD response and the strong contribution of draining veins would impose a limit to spatial resolution of retinotopic mapping. All of these problems exist in V1–V3 but are manageable because (i) the magnification factor is greater in these areas and (ii) receptive fields are smaller and the map is therefore more precise. Current BOLD methodology may not permit accurate documentation of retinotopic maps in V5/MT, no matter how many stimulus repetitions are presented and averaged, even when higher field strengths and smaller voxels are used. A key limitation is BOLD spread due to the contribution from draining veins. Various promising methods for improving resolution are currently being researched (e.g. Menon, 2002; Lu et al., 2004) but, until methods are developed that are capable of yielding clear, detailed maps in small areas of tissue, it remains possible that what we refer to as MT may, in fact, contain more than one representation of space even after MST has been hived off. This is even more true of MST itself. In primate MST, retinotopic organization is coarser than in MT (e.g. Gattass & Gross, 1981) and MST cells have receptive fields that extend well into the ipsilateral visual field (e.g. Albright & Desimone, 1987; Tanaka & Saito, 1989). The next advance is likely to be the division of MT+ into a definitive area MT and an MST complex (MST+). At the very least, MST+ is expected, on the basis of primate physiology, to contain two sub-regions (MSTd and MSTl). Primate FST would also be expected to respond to our stimuli (although not necessarily with flow specificity). Indeed, in an fMRI study of macaque motion areas, Orban et al. (2003) found that motion-related activation in FST equalled that in MT. We saw no additional active regions in our data that might correspond to FST and so presumably human FST, if it exists, is part of the complex which we have labelled MST. If so, the name will need to be revised.

Attention and eye movements

A possible interpretation of the results is that greatest activation was obtained for the complex flow stimulus simply because it is the most interesting and therefore attracts greater attention than the others. It is well known from both neurophysiological and fMRI work that attention causes modulation of response gain in all of the visual areas. This includes MT and MST (e.g. O’Craven et al., 1999; Treue & Trujillo, 1999). There may indeed be an element of attentional modulation reflected in our data but it is unlikely to explain the entire pattern of results. Firstly, an attentional explanation would require modulation to be three to four times greater in MST than MT in order to explain the results for the complex stimulus in Fig. 4b. This seems unlikely. Secondly, attentional modulation of some 900% would be required to explain the difference between complex motion and translation in Fig. 4b. This too is implausible. It is much more likely that our results reflect sensitivity to the global structure of the stimuli.

It is also unlikely that our results reflect differential patterns of eye movement. It was not practical to monitor eye position with the optical viewing device in place. However, rotation, expansion and complex...
flow do not pose a problem for eye stability and it is not expected that the responses to them would alter greatly even if fixation was poor. The only stimulus liable to cause eye movements is translation. Following eye movements would reduce retinal speed and it is conceivable that this contributed to the relatively weak responses to translation. However, (i) participants did not report problems fixing and (ii) tracking the dots was prevented by the limited lifetime of the dots.

**Motion coherence**

One feature of our results is at odds with some previous studies. Two studies (Rees et al., 2000; Braddick et al., 2001) have documented the sensitivity of the human V5/MT complex to motion coherence. In these studies, a random-dot kinematogram was presented which was similar to ours in that each dot translated in a single direction and had a limited lifetime. Dots moved either in a common direction (signal) or else in random directions (noise). The proportion of signal dots was then varied between 100% (the whole pattern translating rigidly) and 0% (random motion). It has been shown (Newsome & Paré, 1988) that global motion (translation) is readily perceived with quite low levels of coherence (around 5%), indicating the existence of a global motion mechanism that integrates direction signals across space. Rees et al. (2000) reported a strong, positive relationship between BOLD signal strength and motion coherence in V5/MT (but no such relation in V1). Our ‘translation’ and ‘random’ conditions correspond to 100 and 0% coherence, respectively, in this framework. However, we did not find that translation yields stronger activity than random motion in either MT or MST. Indeed, we obtained a clear demonstration that it does not. Although this conflicts with the above studies, it is in agreement with the findings of McKeefry et al. (1997) who compared responses to coherent and incoherent motion using PET and found that responses to incoherent motion were as large as, or larger than, those to coherent motion.

The reason for these different results is not obvious. Either result can be reconciled with the underlying physiology. On the one hand, a translating stimulus has a single direction of motion and is therefore expected to activate only a minority of direction-sensitive neurones in MT and MST. In a random motion stimulus, all directions are present and many direction-selective neurones may be driven, giving a strong summed response. On the other hand, neurones may not respond in this way because primate MT neurones are typically suppressed by the presence of motion in the non-preferred direction (Snowden, 1989) while Heeger et al. (1999) have provided fMRI evidence for similar suppression in the human MT complex. Such suppression could lead to results more like those of Rees et al. (2000). However, a weak response will still occur if suppression is not total and this weak response will be present in many neurones, so the total activation summed across all neurones in a voxel could still be as great for random motion as for translation. McKeefry et al. (1997) speculated that their failure to find stronger activation for coherent motion may reflect the action of suppressive surrounds. One feature shared by our study and theirs is the use of a large field of view. They used 20 × 26 deg and we used 70 deg diameter. These image sizes are comfortably bigger than the largest receptive fields in primate V5/MT and bigger than most in MST. Thus, surround effects will be in play for virtually all neurones that possess this property. In the two studies that found greater responses for coherent motion, the stimulus was smaller [4 and 12.5 deg for Rees et al. (2000) and Braddick et al. (2001), respectively] and surround influences may have been significantly reduced in cells with large receptive fields, particularly in the case of Rees et al. (2000), leading to stronger responses in the preferred direction. However, this is speculation. As global translation is an important example of optic flow, corresponding as it does to linear motion of the body through the environment (or, to a first approximation, rotation of the head with static body), it will be important to reach a fuller understanding of specificity for translating global flow in the sub-regions of the MT complex.

**Acknowledgements**

This work was supported by a grant to A.T. from The Wellcome Trust (GRO70500). The results have previously been reported in abstract form (Smith et al., 2004).

**Abbreviation**

ROI, region of interest.

**References**


