Graded Effects of Spatial and Featural Attention on Human Area MT and Associated Motion Processing Areas

MICHAEL S. BEAUCHAMP,[1] ROBERT W. COX,[2] AND EDGAR A. DEYOE[3]
[1]*Program in Neurosciences, University of California, San Diego, La Jolla, California 92093;* [2]*Biophysics Research Institute, Medical College of Wisconsin; and* [3]*Department of Cellular Biology and Anatomy, Medical College of Wisconsin, Milwaukee, Wisconsin 53226*

Beauchamp, Michael S., Robert W. Cox, and Edgar A. DeYoe. Graded effects of spatial and featural attention on human area MT and associated motion processing areas. *J. Neurophysiol.* 78: 516–520, 1997. Functional magnetic resonance imaging was used to quantify the effects of changes in spatial and featural attention on brain activity in the middle temporal visual area and associated motion processing regions (hMT+) of normal human subjects. When subjects performed a discrimination task that directed their spatial attention to a peripherally presented annulus and their featural attention to the speed of points in the annulus, activity in hMT+ was maximal. If subjects were instead asked to discriminate the color of points in the annulus, the magnitude and volume of activation in hMT+ fell to 64 and 35%, respectively, of the previously observed maximum response. In another experiment, subjects were asked to direct their spatial attention away from the annulus toward the fixation point to detect a subtle change in luminance. The response magnitude and volume dropped to 40 and 9% of maximum. These experiments demonstrate that both spatial and featural attention modulate hMT+ and that their effects can work in concert to modulate cortical activity. The high degree of modulation by attention suggests that an understanding of the stimulus-driven properties of visual cortex needs to be complemented with an investigation of the effects of task-related factors on visual processing.

INTRODUCTION

Visual attention allows the brain to use its limited processing capacity to analyze the visual information most relevant for the current behavioral task. Objects can be selected for processing on the basis of their position in the visual field (spatial attention) or of other attributes, such as speed or color (featural attention). Although several recent studies have demonstrated modulation of brain activity by either featural attention (Corbetta et al. 1991; Haxby et al. 1991) or spatial attention (Treue and Maunsell 1996), the degree and extent to which they interact is not well understood.

To explore these issues, we used functional magnetic resonance imaging (FMRI) to quantify the effects of spatial and featural attention on activation in the middle temporal area complex (hMT+) of human volunteers. The middle temporal area is known from studies in nonhuman primates to be an important locus for the processing of visual motion. In a previous study, we identified a dorsal strip of human visual areas, including hMT+, that was selectively activated when subjects discriminated between point speeds in each half of a motion-defined annulus (Beauchamp and DeYoe 1995a). In the experiments reported here, subjects viewed the annulus while performing tasks designed to distribute the subjects' visual attention differently.

METHODS

FMRI was used to record changes in blood oxygenation and flow evoked by brain activity in human subjects ($n = 8$) engaged in a visual discrimination task (for details see DeYoe et al. 1996). During each magnetic resonance (MR) scan series, 102 echoplanar brain volumes were collected (repetition time = 2 s, in-plane resolution = 3.75 × 3.75 mm, 10 axial slices 8 mm in thickness spanning visual cortex; up to 3 repetitions of each condition averaged to increase signal-to-noise ratio). Active brain regions were determined by cross-correlating each voxel's MR time series with reference waveforms representing the neuronal-hemodynamic response to the stimulus. Response magnitude was calculated as the amplitude of the best-fit reference waveform (e.g., Fig. 2*A, insets*). Correlation values exceeding a statistical significance of $P \leq 1 \times 10^{-6}$ indicated valid responses. Activation maps were interpolated to 1-mm^3 resolution and overlaid on high-resolution anatomic MR images. Brain locations are reported as X, Y, Z coordinates (left to right, anterior to posterior, inferior to superior), in millimeters, in the standardized system of Talairach and Tournoux (1988).

During each FMRI scan series, subjects maintained fixation on a central square while viewing an annulus (10–20° eccentricity) defined by coherent motion, with or without color, which alternated with a full field of incoherent points for five ON/OFF cycles (Fig. 1). During "ON" periods, subjects performed one of three tasks. *1*) Subjects indicated by button press which half of the annulus contained faster moving points. This directed spatial and featural attention to the speed of points in the annulus (S+F+). *2*) Subjects indicated which half contained "yellow" points. This directed spatial attention to the annulus but featural attention away from speed (S+F−). *3*) Subjects indicated whether the fixation square increased or decreased in brightness. This directed both spatial and featural attention away from the speed of points in the annulus (S−F−). During the "OFF" periods of all tasks, subjects were instructed to respond randomly at the same rate as during ON periods to reduce phasic activity in motor areas.

Two different experiments were performed to assess the effects of spatial and featural attention. Within each experiment, subjects' attention was manipulated by modifying the task while the stimulus remained identical. In the first experiment, subjects viewed an annulus defined by coherent motion and color, and made speed (S+F+) and color (S+F−) discriminations in successive scan series. This manipulation isolated the effects of featural attention, because spatial attention remained fixed on the annulus. In the second experiment, subjects viewed an annulus defined by motion, and in successive scan series attended the speed of points in the annulus (S+F+) or the brightness of the central fixation point

0022-3077/97 $5.00

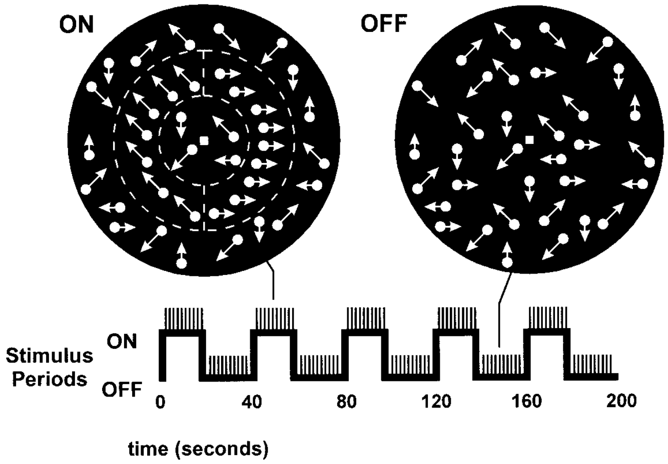


FIG. 1. Schematic illustration of visual stimulus during each 200-s magnetic resonance (MR) scan series (thick line). A new stimulus, consisting of a fixation square and 608 moving points (arrows: point velocity vectors), was generated every 2 s (tick marks). During "ON" periods, the points within a vertically divided annulus-shaped region (– – –) moved coherently with different velocities in each half (each half's points could also have a color that differed from background). During "OFF" periods, all points were white and moved incoherently.

(S−F−). This manipulation revealed the combined effects of spatial and featural attention.

To measure the effects of attention, we compared the volume and intensity of hMT+ activation between conditions. A combined region of interest (ROI) was defined as two cubic volumes (edge length 20 mm) centered on the average location of hMT+ in each hemisphere (illustrated in Fig. 2*C*). The location of hMT+ was estimated as the point of peak intensity in the S+F+ average activation map, with coordinates of ±42, 77.5, 4.5.

A relationship between visual stimulus rate and neuronal metabolic activity has been demonstrated with measurements of cerebral blood flow (Fox and Raichle 1984) and MR response amplitude (Belliveau et al. 1992). The amplitude of MR response has also been shown to increase monotonically with stimulus rate for auditory (Binder et al. 1994) and motor (Rao et al. 1996) tasks. Therefore amplitude of MR response is our preferred measure of activation. The intensity of activation in each attentional condition was determined by averaging the MR response amplitude of ROI voxels that were active in any condition. As another measure of activation, the volume of active hMT+ cortex was measured as the number of active 1-mm^3 voxels inside the ROI (e.g., Kim et al. 1993). However, the threshold used to determine each voxel's statistical significance introduces a nonlinearity, meaning that the number of active voxels does not necessarily increase with increased activity.

RESULTS

When subjects discriminated between point speeds in each half of the motion-defined annulus (S+F+), hMT+ was strongly active (Fig. 2, *left*). As shown in Fig. 2*A*, *left*, the alternation between the speed task in ON periods and incoherently moving points in OFF periods produced a robust cyclic response in an individual subject hMT+ voxel time series at location −36, 80, 4. For the subject illustrated in Fig. 2*B*, hMT+ was located in the lateral occipital sulcus. In addition to hMT+, activation can be seen extending dorsally along a strip to posterior parietal cortex (primary visual cortex responded in both ON and OFF periods and so was not phasically active). hMT+ was active in all subjects performing the speed task. Figure 2*C*, *left*, illustrates the average activity in six subjects at the location of peak intensity in hMT+ ($z = 5$ mm).

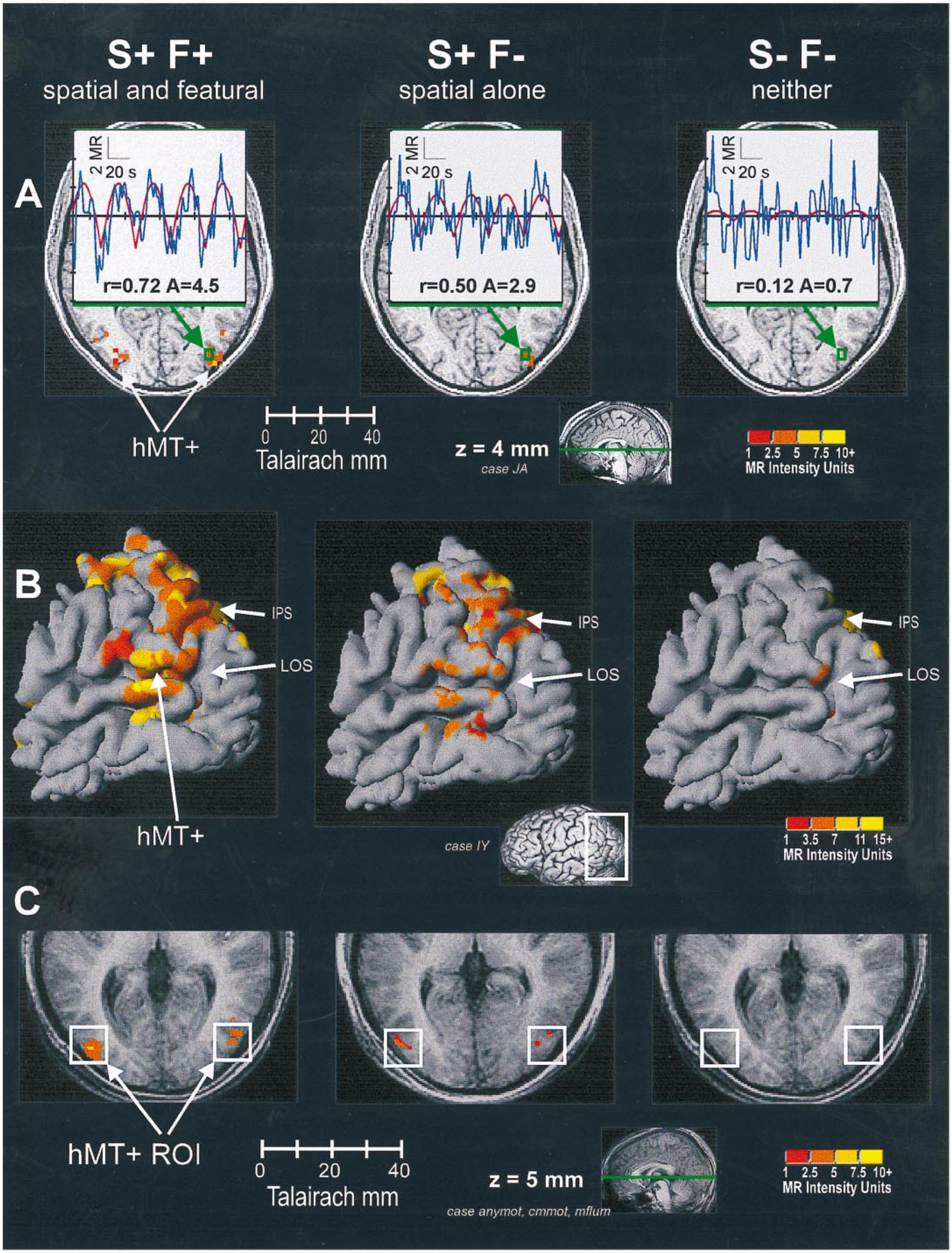
When subjects' featural attention was directed away from speed and toward annulus color (S+F−) in the first experiment (Fig. 2, *middle*) hMT+ was only moderately active. For the voxel shown in Fig. 2*A*, the response dropped to 64% of its intensity in the S+F+ condition. For all ROI voxels in this subject, intensity was reduced to 59% of the S+F+ intensity with a corresponding decrease in activated volume to 30% of the S+F+ volume. Decreases in volume and intensity of activation throughout the extent of hMT+ (and other regions of the dorsal motion processing strip) are illustrated for another subject in Fig. 2*B*, *middle*. Across all subjects, a similar decrease in hMT+ intensity and volume was observed with an average intensity that was 64 ± 6% (mean ± SE) and a volume that was 35 ± 11% (mean ± SE) of the S+F+ value. The average activity from six subjects illustrates the reduced extent and intensity of activity in hMT+ (Fig. 2*C*, *middle*).

When subjects attended to the fixation square rather than the annulus and made brightness rather than speed discriminations (S−F−), little activity was observed in hMT+ (Fig. 2*A*, *right*). For the illustrated voxel (Fig. 2*A*, *right*), there was virtually no response, and no voxels in the hMT+ ROI reached statistical validity. The intensity of the remaining activity was only 34% of the intensity in the S+F+ condition. Similar results are illustrated in the activation map for another subject (Fig. 2*B*, *right*) with only a single voxel in the hMT+ ROI responding. Across subjects, the intensity in hMT+ averaged 40 ± 3% (mean ± SE), and volume averaged 9 ± 3% (mean ± SE) of the S+F+ value. In an axial slice through the average data set, no statistically significant hMT+ activity was observed (Fig. 2*C*, *right*).

Figure 3 summarizes the results across the three attentional conditions. hMT+ activity was maximal in the S+F+ condition of both experiments. When spatial attention remained directed to the annulus (S+F−), a moderate level of hMT+ activation was observed. When both featural and spatial attention were directed away from the speed of points in the annulus (S−F−), little hMT+ activation was observed.

One possible concern was that the different levels of attentional modulation might be due to differences in the visual stimulus between the two experiments. To control for this possibility, the two stimuli were integrated into a single stimulus containing a motion- and color-defined annulus and a brightness-varying fixation point, and the three conditions (S+F+, S+F−, and S−F−) were repeated with two subjects. A similar graded effect of attention was observed (average S+F− intensity = 64%, volume = 48%; average S−F− intensity = 25%, volume = 2%, of the S+F+ value).

A second concern was that differences in attentional modulation might be due to the effects of task difficulty. Although the accuracy of responses was well matched within each experiment (1st experiment: S+F+ vs. S+F−, 99.6% vs. 95.6%; 2nd experiment: S+F+ vs. S−F−, 82.5% vs. 82.9%), the accuracy difference between experiments suggests that the second experiment was more difficult. Previous work, however, has demonstrated that more difficult tasks yield greater activation, not less activation (Rao et al. 1996).


S+ F+
spatial and featural
S+ F-
spatial alone
S- F-
neither
A
2 MR
20 s
r=0.72 A=4.5
r=0.50 A=2.9
r=0.12 A=0.7
hMT+
0 20 40
Talairach mm
z = 4 mm
case JA
1 2.5 5 7.5 10+
MR Intensity Units
B
IPS
LOS
hMT+
case IY
1 3.5 7 11 15+
MR Intensity Units
C
hMT+ ROI
0 20 40
Talairach mm
z = 5 mm
case anymot, cmmot, mflum
1 2.5 5 7.5 10+
MR Intensity Units

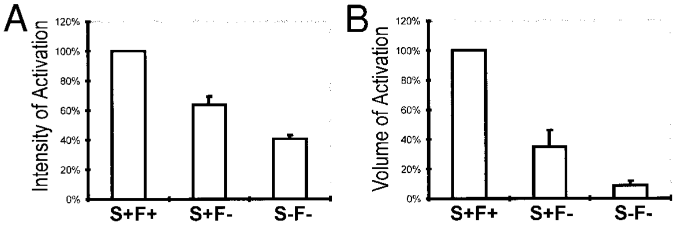


FIG. 3. Mean effects of attention on intensity (*A*) and volume (*B*) of hMT+ activation in 6 subjects during 3 attentional conditions. Magnitudes are expressed as % of response obtained during the S+F+ condition (error bars: means ± SE).

Since we observed less activation in the more difficult task, difficulty cannot account for the observed differences.

A third concern was that the observed attentional modulation could be influenced by the location of the ROI used in the analysis. Therefore the analysis was repeated with the use of an ROI based on an independent estimate of the location of hMT+. A meta-analysis of eight studies found an average lateral occipital focus for motion processing of ±42, 70, 3 (Cheng et al. 1995; Corbetta et al. 1991; Dupont et al. 1994; McCarthy et al. 1995; Tootell et al. 1995a,b; Watson et al. 1993; Zeki et al. 1991, 1993). When these coordinates were used as the center of the ROI, nearly identical attentional modulation was observed, with average S+F− intensity = 63 ± 6% (mean ± SE) and volume = 23 ± 11% (mean ± SE) of the S+F+ value; and average S−F− intensity = 38 ± 3% (mean ± SE) and volume = 10 ± 4% (mean ± SE) of the S+F+ value.

DISCUSSION

There are several important results reported here. *1*) Spatial and featural attention can modulate activity in hMT+. *2*) The combined effects of spatial and featural attention provide greater modulation than featural attention alone. *3*) The combined effects can be large enough to reduce stimulus-evoked activation of hMT+ to a small fraction of the maximum response observed under optimal attentional conditions.

These results are consistent with reports of middle temporal area modulation by spatial attention in macaque monkeys (Treue and Maunsell 1996) and by featural attention in humans (Beauchamp and DeYoe 1995b; Corbetta et al. 1991; Haxby et al. 1991; O'Craven et al. 1995). The present results, however, show that both types of attention can modulate visual system activity in the human at least as early as hMT+. If the anatomic connections of hMT+ are comparable with those of the middle temporal area in the macaque, this may be as early as one or two synapses away from primary visual cortex. At the very least, this suggests that task-related ''top-down'' influences can have a major effect on the processing of ''bottom-up'' signals from the retina early in the cortical processing network. hMT+ could be one site in which visual attention acts to dynamically enhance motion information when it is relevant to the visual task at hand.

M. S. Beauchamp thanks J. Hyde and coadvisors, T. Albright, and E. A. DeYoe.

This work was supported by National Institutes of Health Grants EY-10244 and MH-51358 and a Howard Hughes Medical Institute Fellowship to M. S. Beauchamp.

Address reprint requests to E. A. DeYoe.

Received 30 January 1997; accepted in final form 26 March 1997.

REFERENCES

BEAUCHAMP, M. S. AND DEYOE, E. A. FMRI of human visual cortex: selective activation by motion-defined figures (Abstract). *Proc. Soc. Magn. Reson. Med.* 3: 853, 1995a.

BEAUCHAMP, M. S. AND DEYOE, E. A. FMRI reveals feature-specific attentional modulation of area MT, V3/V3A and parietal visual areas. *Soc. Neurosci. Abstr.* 21: 1760, 1995b.

BELLIVEAU, J. W., KWONG, K. K., KENNEDY, D. N., BAKER, J. R., STERN, C. E., BENSON, R., CHESLER, D. A., WEISSKOFF, R. M., COHEN, M. S., TOOTELL, R. B., FOX, P. T., BRADY, T. J., AND ROSEN, B. R. Magnetic resonance imaging mapping of brain function. Human visual cortex. *Invest. Radiol.* 27, *Suppl.* 2: 59–65, 1992.

BINDER, J. R., RAO, S. M., HAMMEKE, T. A., BANDETTINI, P. A., FROST, J. A., AND HYDE, J. S. Effects of stimulus rate on signal response during functional magnetic resonance imaging of auditory cortex. *Cognit. Brain Res.* 2: 31–38, 1994.

CHENG, K., FUJITA, H., KANNO, I., MIURA, S., AND TANAKA, K. Human cortical regions activated by wide-field visual motion: an $H_2{}^{15}O$ pet study. *J. Neurophysiol.* 74: 413–427, 1995.

CORBETTA, M., MIEZIN, F. M., DOBMEYER, S., SHULMAN, G. L., AND PETERSEN, S. E. Selective and divided attention during visual discriminations of shape, color, and speed: functional anatomy by positron emission tomography. *J. Neurosci.* 11: 2383–2402, 1991.

DEYOE, E. A., CARMAN, G., BANDETTINI, P., GLICKMAN, S., WIESER, J., COX, R., MILLER, D., AND NEITZ, J. Mapping striate and extrastriate visual areas in human cerebral cortex. *Proc. Natl. Acad. Sci. USA* 93: 2382–2386, 1996.

DUPONT, P., ORBAN, G. A., DE BRUYN, B., VERBRUGGEN, A., AND MORTELMANS, L. Many areas in the human brain respond to visual motion. *J. Neurophysiol.* 72: 1420–1424, 1994.

FOX, P. T. AND RAICHLE, M. E. Stimulus rate dependence of regional cerebral blood flow in human striate cortex, demonstrated by positron emission tomography. *J. Neurophysiol.* 51: 1109–1120, 1984.

HAXBY, J. V., GRADY, C. L., HORWITZ, B., UNGERLEIDER, L. G., MISHKIN, M., CARSON, R. E., HERSCOVITCH, P., SCHAPIRO, M. B., AND RAPOPORT, S. I. Dissociation of object and spatial visual processing pathways in human extrastriate cortex. *Proc. Natl. Acad. Sci. USA* 88: 1621–1625, 1991.

KIM, S. G., ASHE, J., HENDRICH, K., ELLERMANN, J. M., MERKLE, H., UGURBIL, K., AND GEORGOPOULOS, A. P. Functional magnetic resonance imaging of motor cortex: hemispheric asymmetry and handedness. *Science Wash. DC* 261: 615–617, 1993.

MCCARTHY, G., SPICER, M., ADRIGNOLO, A., LUBY, M., GORE, J., AND ALLISON, T. Brain activation associated with visual motion studied by functional magnetic resonance imaging in humans (Abstract). *Hum. Brain Map.* 1, *Suppl.*: 60, 1995.

O'CRAVEN, K. M., SAVOY, R. L., AND ROSEN, B. R. Attention modulates

FIG. 2. Activity in the probable human homologue of macaque middle temporal area and associated motion processing areas (hMT+) during 3 attentional conditions. *Left*: spatial attention directed to location of annulus and featural attention directed to speed of points in annulus (S+F+). *Middle*: spatial attention directed to annulus, featural attention directed to color of points in annulus (S+F−). *Right*: attention directed to luminance at fixation point (S−F−). Color scale: amplitude of MR response. *A*: axial slice through individual subject with inset graphs of MR time course (blue graph line) and reference waveform (red line) from single voxel (green square), with amplitude (A) and correlation (r) of response indicated. *B*: single subject's activity mapped to occipital lobe reconstruction (lateral view). *C*: axial slice through average (*n* = 6) data sets, showing hMT+ region of interest (ROI; white box). IPS, intraparietal sulcus; LOS, lateral occipital sulcus.

fMRI activation in human MT/MST. *Soc. Neurosci. Abstr.* 21: 1988, 1995.

RAO, S. M., BANDETTINI, P. A., BINDER, J. R., BOBHOLZ, J. A., HAMMEKE, T. A., STEIN, E. A., AND HYDE, J. S. Relationship between finger movement rate and functional magnetic resonance signal change in human primary motor cortex. *J. Cereb. Blood Flow. Metab.* 16: 1250–1254, 1996.

TALAIRACH, J. AND TOURNOUX, P. *Co-Planar Stereotaxic Atlas of the Human Brain.* New York: Thieme, 1988.

TOOTELL, R. B., REPPAS, J. B., DALE, A. M., LOOK, R. B., SERENO, M. I., MALACH, R., BRADY, T. J., AND ROSEN, B. R. Visual motion aftereffect in human cortical area MT revealed by functional magnetic resonance imaging [see comments]. *Nature Lond.* 375: 139–141, 1995a.

TOOTELL, R. B., REPPAS, J. B., KWONG, K. K., MALACH, R., BORN, R. T., BRADY, T. J., ROSEN, B. R., AND BELLIVEAU, J. W. Functional analysis of human MT and related visual cortical areas using magnetic resonance imaging. *J. Neurosci.* 15: 3215–3230, 1995b.

TREUE, S. AND MAUNSELL, J.H.R. Attentional modulation of visual motion processing in cortical areas MT and MST. *Nature Lond.* 382: 539–541, 1996.

WATSON, J. D., MYERS, R., FRACKOWIAK, R. S., HAJNAL, J. V., WOODS, R. P., MAZZIOTTA, J. C., SHIPP, S., AND ZEKI, S. Area V5 of the human brain: evidence from a combined study using positron emission tomography and magnetic resonance imaging. *Cereb. Cortex* 3: 79–94, 1993.

ZEKI, S., WATSON, D. G., AND FRACKOWIAK, R.S.J. Going beyond the information given: the relation of illusory visual motion to brain activity. *Proc. R. Soc. Lond. B Biol. Sci.* 252: 215–222, 1993.

ZEKI, S., WATSON, J. D., LUECK, C. J., FRISTON, K. J., KENNARD, C., AND FRACKOWIAK, R. S. A direct demonstration of functional specialization in human visual cortex. *J. Neurosci.* 11: 641–649, 1991.