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Attention-Regulated Activity in Human Primary Visual Cortex

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[1]*Department of Psychology, Boston University, Boston, Massachusetts 02215;* [2]*Communication Research Laboratory, Tokyo 184;* [3]*Shiraume Gakuen College 184, Tokyo; and* [4]*Frontier, Riken Institute, Saitama 351-01, Japan*

Watanabe, Takeo, Yuka Sasaki, Satoru Miyauchi, Benno Putz, Norio Fujimaki, Matthew Nielsen, Ryosuke Takino, and Satoshi Miyakawa. Attention-regulated activity in human primary visual cortex. *J. Neurophysiol.* 79: 2218–2221, 1998. Effects of attention to a local contour of a moving object on the activation of human primary visual cortex (area V1) were examined. Local cerebral oxygenation changes (an index of neuronal activity) in human area V1 were measured with functional magnetic resonance imaging (fMRI) in conditions including the following two: *1*) when attention was selectively directed toward one side of a moving wedge (the attention condition) and *2*) when the wedges were viewed passively (the passive condition). Activation in area V1 was found to be higher in the attention condition than in the passive condition. To our knowledge, this is the first finding that attention to motion activates as early as area V1. We suggest that attentional activation of area V1 is task dependent.

INTRODUCTION

It has been previously found that cortical cells in primary visual cortex (area V1) of macaque monkeys are sensitive to the normal component of the motion of contours in moving objects (Gizzi et al. 1990). Signals for these local motion directions are subsequently integrated in the middle temporal visual area (area MT) (Movshon et al. 1986; Snowden et al. 1991). Recently, Watanabe has examined effects of attention on the early motion processing and found that attention to a local contour of an object could alter the object's perceived direction of motion (Watanabe 1995). Specifically, when attention was directed to one of the slanted sides of a black wedge translating within a circular aperture (Fig. 1*A*), the wedge was perceived to move in a direction perpendicular to the attended edge as opposed to its overall direction of motion. This finding indicates that a subject may selectively attend to local component motion. Furthermore, it raises the possibility that attention, which presumably originates in higher cortical areas (Corbetta et al. 1991; La Berge 1995; Posner and Petersen 1990), can influence the activity of V1 neurons when this attention is selectively directed to a local motion direction or local contour. However, while attention to motion has been found to activate MT in monkey (Treue and Maunsell 1996) and the MT/MST (the medial superior temporal area) homologue in humans (Culham et al. 1997; O'Craven and Savoy 1997), no study with either animal or human subjects has indicated that attention to motion activates area V1. The purpose of this study was to verify the hypothesis that attention to a local component motion activates area V1 in humans by means of functional magnetic resonance imaging (fMRI).

METHODS

Two adult females and three adult males served as subjects. None of the subjects had any known history of neurological disease. Informed consent was obtained from all the subjects after the nature and possible consequences of the studies were explained.

Task design

In each trial, a cue consisting of one or more beeps was presented accompanied by a gray fixation cross (15.0 cd/m^2) at the center of the screen. One second after its onset, the test stimulus was presented in the passive and attention conditions, while only the fixation cross remained visible in the fixation-only condition. The test stimulus consisted of a black wedge, translating to the right, behind a stationary circular aperture. A cue consisting of a single beep instructed the subject to view the test stimulus passively (passive condition) without attending to either edge, while fixating the gray cross. Two or three beeps instructed the subject to attentively track the left, or right sides of the moving wedge, respectively, while maintaining fixation on the cross (the left and right attention conditions). A four-beep cue instructed the subject to fixate the cross in the dark background (fixation-only condition) to measure the baseline activation level in which visual input is minimum while eyes were fixated. Each subject performed four series of the four conditions. Each series consisted of 40 scans with a complete duration of 164 s.

Data collection with fMRI

Local cerebral oxygenation changes were measured with echo-planar imaging using a 1.5 T whole body scanner (Siemens Vision) with a CP head coil (Bandettini et al. 1992; Belliveau 1991; Ogawa et al. 1992). Acquisition parameters were as follows: TE (echo time) = 66 ms, TR (repetition time) = 4.1 s, with an in-plane resolution (pixel size) of 1.80×1.80 mm^2, flip angle = 90°, matrix 128×128, slice thickness = 5 mm, field of view = 230 mm, number of slices = 7, measurement interval = 4.1 s. The test stimulus was projected by means of a SONY CRT projector situated in a control room, through a window, and onto a white screen inside the shielded room housing the fMRI machine. To make functional maps, the pixel-by-pixel correlation between a reference function (comparing the attention and passive conditions) and the signal intensity time course for each pixel of the experimental data (cross-correlation coefficient) was computed. The reference function was a square-wave equal to +1 for one of the attention conditions and −1 for the passive condition (Bandettini et al. 1993; Puetz et al. 1998). Eye movements were measured throughout the experiment with all the five subjects (Ober2 12 parallel system). To reduce artifacts due to head motion, subjects' heads were stabilized with bite-bars, and data were motion corrected using an algorithm (Jiang et al. 1995) adapted from Woods et al. (1992).

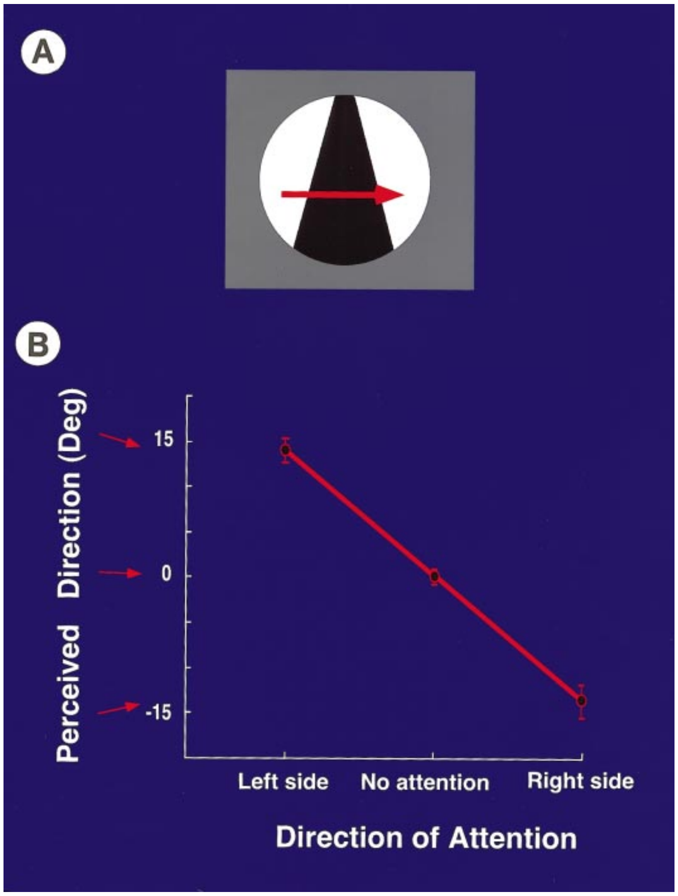

FIG. 1. *A*: test stimulus used in this study. The black wedge (0.5 cd/m^2 in luminance) moved rightward at a speed of 2.5°/s within a white circular aperture (32.0 cd/m^2) against a dark gray background (16.0 cd/m^2). The legs of the wedge subtended 30°. The radius of the circular aperture was 3.75°. Immediately on disappearing from the aperture, a new wedge appeared on the left side of the aperture. A light gray cross (24.5 cd/m^2) was presented in the center of the circle as a fixation point. *B*: results of the psychophysical experiment. When attention is not directed to any particular location or motion, the wedge appears to move in a physically true motion direction (to the right) as represented by the red arrow (*A*). When attention was directed to one of the edges of the wedge, the whole wedge appeared to move perpendicularly to the attended edge.

Psychophysical experiment

To confirm that the wedge is perceived to move in a direction perpendicular to the attended edge (Watanabe 1995), the subjects' behavioral data were collected in the left and right attention conditions and the passive condition. The procedure was similar to that of the fMRI experiments except for the following. *1*) After the offset of the test stimulus, an arrow was presented. The subjects were instructed to adjust the direction of the arrow to the perceived motion direction of the wedge. *2*) The test stimulus was presented on a color video display (Apple M0401, 640 × 480 pixel resolution, 35 kHz in horizontal and 66.7 Hz in vertical scanning frequencies) controlled by a Macintosh IIci.

RESULTS

The results of the psychophysical experiment show that when attention was directed to one of the slanted sides of a black wedge translating within a circular aperture, the subjects perceived the wedge move in a direction almost perpendicular to the attended edge as opposed to its overall direction of motion (Fig. 1). The maps (Fig. 2,*A* and *B*) of one representative subject shows that activities in area V1 are significantly higher in the left (*A*) and the right (*B*) attention condition than in the passive condition. The same tendency was found with the other four subjects. The mean time courses averaged across four series and over five subjects in Fig. 3 indicate that magnetic resonance (MR) signals in the attention conditions are significantly higher than in the passive and fixation-only conditions. The difference in amount of MR signals between the passive and fixation-only conditions is regarded as the activation caused by a mere presence of the test stimulus.

DISCUSSION

Selective attention to a single line orientation has previously been found to enhance V1 cell activity in a monkey (Motter 1993). However, the activity we have found in area V1 when attention was directed to local component motion is noteworthy for another reason. To our knowledge, this is the first finding in humans of enhanced V1 activity produced by *selective attention to motion.*

We considered the question of whether the activation increase in the area V1 would also be observed with a stationary stimulus. Brain activity was measured with a stimulus in which a stationary wedge was presented at the right, left, or center of the aperture while the subject gazed at a central fixation point. Here we found the activity of area V1 to be as low as in the passive condition. This confirmed that the activation in area V1 found in the main experiment was the result of attention to local motion and not merely a particular location or orientation.

Figure 2 shows that the activation of a representative subject is not confined to the region representing the central 7.5° of visual field across which the wedge passed. Highest activations in V1 with this subject are only in the central region, however. The locations of the activations outside the region for the central visual field were not constant across all the subjects. Thus these activations could be regarded as noises.

The experiment was not designed to measure the activity of the MT/MST human homolog. Thus the activities in only a portion of the area were measured in each subject. In five of the six subjects, the regions corresponding to the MT/MST homologues were bilaterally more activated in both attention conditions than in the passive condition.

It is noticeable that four of the five subjects showed that activity on the side of V1 contralateral to the *attended* side of the wedge was more extensive than the side ipsilateral to attention (Fig. 2). The remaining one subject did not show such a lateralization. We have considered the possibility that small eye movements could account for the activation pattern seen if the subjects shifted their eyes predominantly or exclusively in the direction of the attended edge when the edge was very close to the center of gaze. However, this is not likely for the following reasons. First, although small pursuit movements were observed in the passive and the attention conditions, no significant difference was found in the amplitude or pattern of the movement among these conditions. Second, the eye movements

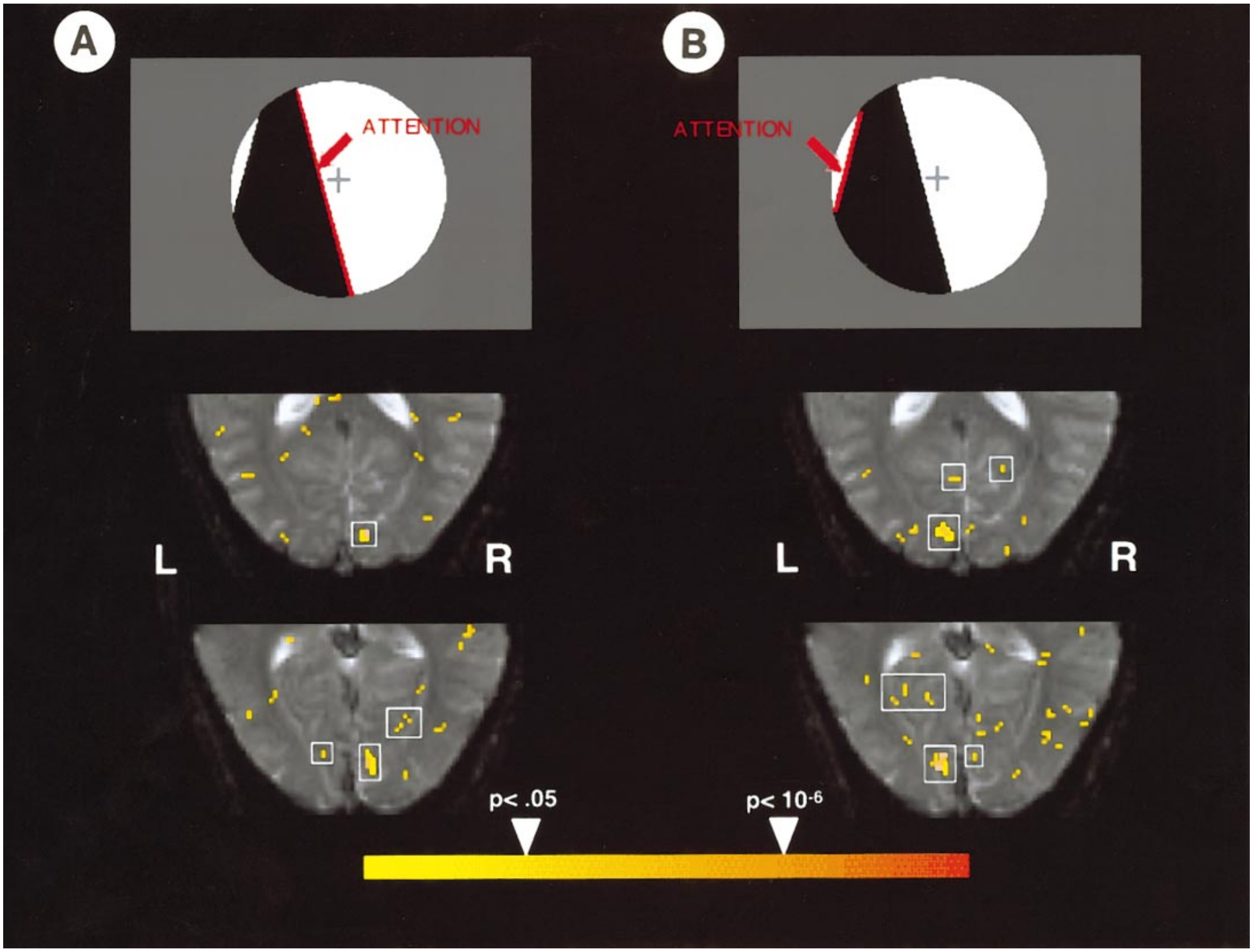

FIG. 2. Functional maps of a representative subject were superimposed on a T1 image of the posterior part of the brain of the subject. The maps of 2 representative slices at 5 mm (*middle*) and 10 mm (*bottom*) above the AC-PC line are shown. Those on the *left* or *right* are the results of the comparisons between the left attention and passive conditions or between the right attention and passive conditions, respectively. The activations in area V1 are indicated by surrounding white frames. Area V1 was functionally located (Engel et al. 1994; Sereno et al. 1994). L and R, left and right sides of the brain, respectively. Posterior portions are shown at the *bottom* of the figure.

occurred irrespective of whether a side of the wedge was close to the center of gaze or not. Thus they did not occur predominantly or exclusively when the edge was close to the center of gaze. Third, basically the same activation patterns were obtained with the five subjects when the wedge was white in a white aperture.

The activation of the side contralateral to attention would be obtained if the activation occurred with respect to the axis of an attended object. However, the side ipsilateral to attention was also found to be activated, although it was less extensive than the contralateral side. In addition, the results of one subject did not show this tendency. Thus more systematic study is necessary to draw any conclusion about the cause of the lateralization.

Does attention to motion always activate area V1? Using five subjects, we also tested the case in which attention was directed to a moving object as a whole. Ten black disks (0.5 cd/m^2), 0.5° in radius, were presented bouncing at the speed of 15°/s in a white background (32 cd/m^2) within a black square frame (10 × 10°). In an attention condition, subjects attentionally pursued only one of them while gazing at the fixation cross presented in the center of the display. Only the bilateral regions homologous to MT/MST, but not area V1, showed a significant difference in activity between the attention and passive conditions. The difference in results between attention to local component motion and attention to a moving object as a whole, suggests that the area activated by attention depends on the aspect of motion (i.e., local component motion vs. object motion) to which attention is directed.

The results of the experiment using a moving wedge do not themselves rule out the possibility that the observed modulation is due to different levels of arousal between the passive and attention conditions. However, in the experiment using bouncing disks the arousal difference that should be the same or similar to that in the wedge experiment did not

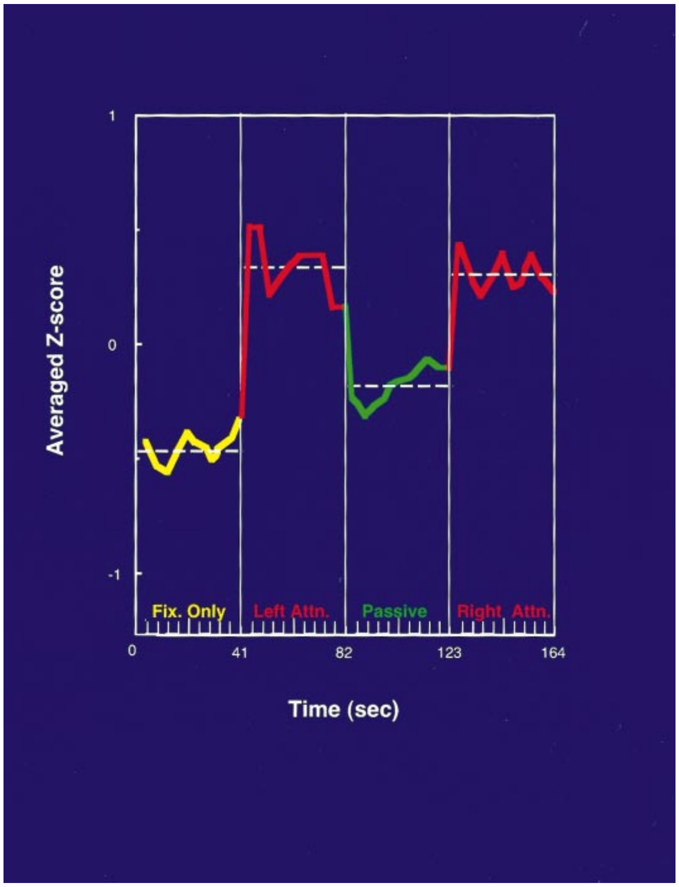

FIG. 3. Mean time courses for 4 conditions for both sides of area V1. The ordinate represents the averaged *z*-scores across the subjects. *Z*-scores were computed based on magnetic resonance (MR) signals of all the voxels in 4 cycles of trial repetitions in each subject. The abscissa shows time measured in number of functional magnetic resonance imaging images collected.

result in an activation of V1. Thus, we conclude that arousal is not the main effect observed.

Recently, it has been suggested that attention operates on relatively high-level visual processing. Lu and Sperling (1995) suggest that attention plays no role in the perception of energy-based motion called ''first order motion.'' However, the results of the present study suggest that attention can modulate energy-based, local motion processing as early as V1 if a task requires it. On the other hand, the results are in accordance with the hypothesis made by Sakai and Miyashita (1993) that attention activates V1 when it is directed to a local feature.

In conclusion, we found that attention to local component motion activates V1 and the MT/MST homologue, whereas attention to an integrated motion activates only the MT/MST homologue. The results suggest that the activation in V1 as a result of attention to motion depends on the type of motion to which attention is directed.

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REFERENCES

BANDETTINI, P. A., JESMANOWICZ, A., WONG, E. C., AND HYDE, J. S. Processing strategies for time-course data sets in functional MRI of the human brain. *Magn. Reson. Med.* 30: 161–173, 1993.

BANDETTINI, P. A., WONG, E. C., HINKS, R. S., TIKOFSKY, R. S., AND HYDE, J. S. Time course EPI of human brain function during task activation. *Magn. Reson. Med.* 25: 390–397, 1992.

BELLIVEAU, J. W., KENNEDY, D. N., JR., MCKINSTRY, R. C., BUCHBINDER, B. R., WEISSKOFF, R. M., COHEN, M. S., VEVEA, J. M., BRADY, T. J., AND ROSEN, B. R. Functional mapping of the human visual cortex by magnetic resonance imaging. *Science* 254: 716–719, 1991.

CORBETTA, M., MIEZIN, F. M., 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.

CULHAM, J. C., CAVANAGH, P., KANWISHER, N. G., BRANDT, S., DALE, A. M., AND TOOTELL, R.B.H. Attentive tracking of moving targets produces parietal activation revealed by functional magnetic resonance imaging. *Invest. Ophthalmol. Vis. Sci. (Suppl.),* 38: 1174, 1997.

ENGEL, S. A., RUMELHART, D. E., WANDELL, B. A., LEE, A. T., GLOVER, G. H., CHICHILNISKY, E. J., AND SHADLEN, M. N. fMRI of human visual cortex. *Nature* 369: 525, 1994.

GIZZI, M. S., KATZ, E., SCHUMER, R. A., AND MOVSHON, J. A. Selectivity for orientation and direction of motion of single neurons in cat striate and extrastriate visual cortex. *J. Neurophysiol.* 63: 1529–1543, 1990.

JIANG, A., KENNEDY, D. N., BAKER, J. R., WEISSKOFF, R. M., TOOTELL, R.B.H., WOODS, R. P., BENSON, R. R., KWONG, K. K., BRADY, T. J., ROSEN, B. R., AND BELLIVEAU, J. W. Motion detection and correlation in functional MR imaging. *Hum. Brain Mapp.* 3: 1–12, 1995.

LABERGE, D. *Attentional Processing—The Brain's Art of Mindfulness.* Cambridge: Harvard University Press. 1995.

LU, Z.-L. AND SPERLING, G. Attention-generated apparent motion. *Nature* 377: 237–239, 1995.

MOTTER, B. C. Focal attention produces spatially selective processing in visual cortical areas V1, V2 and V4 in the presence of competing stimuli. *J. Neurophysiol.* 70: 909–919, 1993.

MOVSHON, J. A., ADELSON, E. H., GIZZI, M. S., AND NEWSOME, W. T. The analysis of moving visual patterns. In: *Pattern Recognition Mechanisms,* edited by C. Chagas, R. Gattas, and C. Gross. New York: Springer-Verlag, 1986, p. 117–151.

O'CRAVEN, K. M. AND SAVOY, R. L. Attentional modulation of activation in human MT shown with functional magnetic resonance imaging (FMRI). *Neurone.* 18: 591–598, 1997.

OGAWA, S., TANK, D. W., MENON, R., ELLERMAN, J. M., KIM, S.-G., MERKLE, H., AND UGURBIL, K. Intringic signal changes accompanying sensory stimulation: functional brain mapping with magnetic resonance imaging. *Proc. Natl. Acad. Sci. USA* 89: 5951–5955, 1992.

POSNER, M. I. AND PETERSEN, S. E. The attention system of the human brain. *Annu. Rev. Neurosci.* 13: 25–42, 1990.

SAKAI, K. AND MIYASHITA, Y. Visual imagery: an interaction between memory retrieval and focal attention. *Curr. Opin. Neurobiol.* 3: 166–170, 1993.

SERENO, M. I., DALE, A. M., REPPAS, J. B., KWONG, K. K., BELLIVEAU, J. W., BRADY, T. J., ROSEN, B. R., AND TOOTELL, R.B.H. Borders of multiple visual areas in humans revealed by functional magnetic resonance imaging. *Science* 268: 889–893, 1994.

SNOWDEN, G. R., TREUE, S., ERICKSON, R. E., AND ANDERSEN, R. A. The response of Area MT and V1 neurons to transparent motion. *J. Neurosci.* 11: 2768–2785, 1991.

STONER, G. R. AND ALBRIGHT, T. D. Neural correlates of perceptual motion coherence. *Nature* 412: 412–414, 1992.

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

WATANABE, T. Motion aftereffects show that attention may selectively activate local motion units located in V1. *Invest. Ophthalmol. Vis. Sci.* 36: 3929, 1995.

WOODS, R. P., CHERRY, S. R., AND MAZZIOTTA, J. C. Rapid automated algorithm for aligning and reslicing PET images. *J. Comput. Assist. Tomogr.* 16: 620–633, 1992.