Processing of Kinetically Defined Boundaries in the Cortical Motion Area MT of the Macaque Monkey

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SUMMARY AND CONCLUSIONS

1. Electrophysiological recordings of 68 cells in the middle temporal area MT were made in paralyzed and anesthetized macaque monkeys.

2. Testing with our kinetic boundary stimuli always occurred under optimized conditions. To this end, the preferred direction, speed, stimulus position, and stimulus size of each cell were determined by quantitative tests.

3. The orientation selectivity to stationary luminance contrast edges served as a reference by which a response to kinetic boundaries could be compared. We found cells in area MT to be less selective to the orientation of luminance contrast stimuli than to the direction of motion. We confirmed the presence of neurons with preferred orientation aligned with their preferred direction.

4. The responses to kinetic edges defined by motion vectors moving in opposite directions, kinetic gratings with motion vectors in opposite directions, kinetic edges containing coherent motion and a stationary complementary field or coherent motion and a complementary field containing visual dynamic noise were compared. Kinetic boundaries were generated so that the motion vectors moved either parallel or orthogonal to the orientation of the discontinuity. For a cell to be considered as responding to the orientation of a kinetic boundary, it had to exhibit the same preferred orientation when the local motion vectors changed from parallel to orthogonal to the orientation of the kinetic boundary.

5. All cells in area MT changed their preferred orientation by 90° when the coherent motion vectors changed from moving parallel to moving orthogonal to the boundary. This was the case independent of the types of kinetic boundary tested. We concluded that cells in area MT appear to respond to the motion vector over their classical receptive field (CRF) only and were unable to code the orientation of the kinetic boundary.

6. In those cells exhibiting an antagonistic surround, we examined the ability of the cell to code the position of a kinetic boundary. None of the cells tested signaled the position of a kinetic boundary. The side preference of the stimulus of the cells changed from left to right as the motion vectors in the stimulus reversed. This indicates that the cells were only selective for the motion vectors present over their CRF.

7. We found that the directional sensitivity of cells in area MT remained unaltered by the presence of additional motion vectors within the CRF. This suggests that cells in area MT extract a specific motion vector from a spatial configuration of vectors. We further found that the response level of cells in area MT could be related directly to the amount of motion in the nonpreferred direction present in the stimulus.

INTRODUCTION

Anatomic and behavioral experiments place the cortical visual areas (Felleman and Van Essen 1991; Van Essen 1985) into two functionally distinct streams (Ungerleider and Mishkin 1982). The ventral stream, terminating in the inferior temporal lobe, has been primarily associated with form and color perception. The dorsal stream, ending in the posterior parietal lobe, is believed to be involved in image motion and spatial perception.

Anatomic studies place the cortical visual area MT in the dorsal pathway (Desimone and Ungerleider 1986; Maunsell and Van Essen 1983b; Morel and Bullier 1990; Ungerleider and Mishkin 1982). However, area MT is known to have extensive connections with areas forming part of the ventral pathway (Boussaoud et al. 1990; Desimone and Ungerleider 1986; Van Essen et al. 1981, 1992).

Cells in area MT of the owl monkey (Allman and Kaas 1971) and the macaque (Dubner and Zeki 1971; Zeki 1974) are highly selective for moving stimuli. So far, most investigations have concentrated on the direction selectivity (Albright 1984, Maunsell and Van Essen 1983a; Movshon et al. 1985) and speed selectivity (Lagae et al. 1993; Maunsell and Van Essen 1983a; Mikami et al. 1986) of its neurons, although some investigators have found area MT to be sensitive for color (Saito et al. 1989) and selective for orientation (Albright 1984; Maunsell and Van Essen 1983a).

Present studies therefore provide good evidence that area MT is involved in coding direction and speed of retinal image motion. It has been realized that motion information can provide a number of perceptually useful cues (Nakayama 1985). For instance, motion provides feedback information about self motion, thus enabling the animal to guide itself through its environment. Similarly, motion information provides the information necessary to guide eye movement when tracking an object (Kumatsu and Wurtz 1988; Newsome et al. 1985). Motion parallax reveals the spatial layout of the environment, and differential motion can provide cues to the three-dimensional structure of an object. The ability to detect a kinetic boundary provides an animal with a means of breaking the color and/or pattern camouflage adopted by predator and prey alike.

In an experiment in which area MT was surgically removed in macaque monkeys, Marcar and Cowey (1992) found that the animals performed poorly on a shape discrimination task based on the detection of kinetic boundaries. The lesion had no effect, however, on the animal’s ability to perform the shape discrimination task based on the detection of a luminance contrast boundary. This finding has been confirmed by work in this laboratory with monkeys judging orientation of kinetic boundaries (K. Lauwers, R. C. Saunders, B. De Bruyn, R. Vogels, and G. A. Orban, unpublished results). Electrophysiological studies have reported cue-in-
variant shape selectivity in area TE (Sáry et al. 1993), whereas cells selective for the orientation of non-Fourier boundaries have been reported in area V4 (Logothetis and Charles 1990). Both areas TE and V4 form part of the ventral stream of visual processing, whereas area MT forms part of the dorsal stream.

These findings led us to pursue the suggestion of Marcar and Cowey (1992) that the perception of kinetic boundaries requires the visual system to integrate information from area MT into the ventral stream. This view is supported by a psychophysical investigation of Berkley et al. (1994), who reported that kinetic boundaries and luminance contrast boundaries interact in the human visual system in the tilt aftereffect.

The receptive field organization of some cells in area MT, where the "classical" receptive field (CRF) is modified by an inhibitory surround (Allman et al. 1985; Born and Tootell 1992; Lagae et al. 1989; Saito et al. 1986), makes these cells selective to differential motion and thus suited for processing kinetically defined contours. This suggests two alternatives: either the role of area MT is limited to preprocessing motion information leading to the coding of orientation of kinetic boundaries and some other cortical visual area performs the conversion of a motion signal into an orientation signal for kinetic boundaries, or the conversion occurs in area MT itself. If the latter hypothesis is true, then cells should be found in area MT that are able to signal the orientation of a kinetic boundary.

Reports that signals in area MT relating to luminance-defined orientation are weak do not necessarily imply that signals relating to kinetic boundary orientation will be weak also. A direct link between the responses to luminance-defined orientation and kinetic boundary orientation can only be made if it is assumed that the convergence of the two types of signals occurs in area MT and that areas where cue-invariant orientation signals have been observed receive these signals from area MT. Even if cells in area MT do not code the orientation of a kinetic boundary, they may still be able to signal a much simpler aspect, namely the position of a kinetic boundary. Our investigation set out to determine whether cells in area MT could code the orientation and/or position of a kinetic boundary. Our initial results have been presented in the form of an abstract (Marcar et al. 1991).

**METHODS**

**Animal preparation**

Extracellular recordings were made in area MT of six male macaque monkeys (*Macaca fascicularis*) weighing between 4.2 and 5.1 kg. Animals were prepared for acute recording following the methods of Lagae et al. (1994). Because the methodology has already been described in Lagae et al. (1994), only the differences will be discussed here.

**Stimulus**

The stimuli consisted of stationary contrast luminance square-wave gratings (0.8, 1.6, and 3.2 cycles/°) and edges with a luminance value of 47 cd/m² for the white parts and 0.2 cd/m² for the dark parts. Random dot patterns (RDPs) moving in the frontoparallel plane and kinetic edges and gratings generated using RDPs moving in the frontoparallel plane were used. The RDP subtended an angle of 25 x 25° at 0.57 m with a resolution of 512 x 512 pixels. It consisted of single, pixel-sized dots, with each dot subtending an angle of 0.3 arc min and a dot density of 25% white dots (47 cd/m²) on a dark background (0.2 cd/m²). All stimuli were generated using a Microvax II Workstation and saved on disk. The dot size and density chosen avoided static occlusion and deformation cues. We nevertheless examined all our kinetic boundary stimuli for unintended aggregations of dots. If some salient aggregation was noted, the stimulus was generated again in such a way that the unwanted cue was removed. Movies consisting of 32 or 64 frames were selected by the STIMUL program running on a PDP/11/70 (Maes and Orban 1980) and presented at a 100-Hz refresh rate using the GOULD 9000 image processor on a monitor (BARCO CDCT 6551).

Kinetic boundaries were generated with at least one motion vec-
The presence of a modulatory field around the CRF of some cells in area MT (Allman et al. 1985; Born and Tootell 1992; Saito et al. 1986) renders them particularly suitable for the processing of kinetic boundaries. Our summation test enabled us to identify those cells with an antagonistic surround. We defined them as those cells that reduced their firing rate to ~50% of their maximum response as the diameter of a moving RDP was increased. We considered the possibility that cells with an antagonistic surround may be able to signal the position of a kinetic boundary without necessarily being selective for the orientation of the boundary. We therefore examined the effect of placing the kinetic boundary in different parts of the receptive field for cells with an antagonistic surround. For this purpose we employed a stimulus in which a uniform RDP: a direction test using 16 different directions at three different speeds; a CRF mapping test (CRF map) using 25 different positions in a 5 × 5° grid with a stimulus size of 5 × 5°; or a 2.5 × 2.5° grid with a stimulus size of 2.5 × 2.5°; and an area summation test using eight different stimulus diameters (for details see Lagae et al. 1994).

Before tests with kinetic boundaries were undertaken, the preferred direction of motion of the cell, as well as its velocity preference, the center of its receptive field, and the optimum stimulus size were determined by three preliminary quantitative tests using a uniform RDP: a direction test using 16 different directions at three different speeds; a CRF mapping test (CRF map) using 25 different positions in a 5 × 5° grid with a stimulus size of 5 × 5°, or a 2.5 × 2.5° grid with a stimulus size of 2.5 × 2.5°; and an area summation test using eight different stimulus diameters (for details see Lagae et al. 1994).

Quantitative testing

Our principal test was designed to compare the orientation selectivity of MT cells to kinetic edges in which the motion vectors ran parallel to the orientation of the boundary and to kinetic edges in which motion vectors ran orthogonal to the orientation of the boundary. The eight orientations used spanned 180° in steps of 22.5°, and the edges were always positioned such that they bisected the CRF. Each orientation was presented twice, because the movie used to display the kinetic boundary was first run forward (go) and then backward (back). In the initial experiments (1/3 of the cells tested), the parallel and orthogonal conditions were tested separately, whereas in two thirds of the cells tested, the conditions were interleaved.

The three types of kinetic edges used are illustrated schematically in Fig. 2. In the first, standard type of kinetic boundary the RDPs moved in opposite directions (antiphase condition); in the second, the coherent motion was paired with a stationary dot field (stationary condition). In the third type, the coherent motion was paired with visual dynamic noise (VDN condition). In the latter two types of kinetic boundaries two series of movies were used: one that contained the coherently moving dots in the lower half of the visual field while the stationary or VDN dot pattern occupied the upper half of the visual field, and a second in which the locations of the patterns were reversed. Although only the complete sets of stimuli for the stationary conditions are shown in Fig. 2, the boundaries for the VDN condition were identical to these except that the stationary dots were replaced with VDN.

Besides the boundaries discussed above, cells were also tested with kinetic gratings. The kinetic grating stimulus consisted of a number of kinetic edges defined by stripes of random dots moving along the cell’s preferred and nonpreferred axes. Neighboring stripes always containing motion in opposite directions (see Fig. 5A). The spacing between the kinetic edges making up the kinetic grating stimulus was 0.8°. In our investigation of area MT, the kinetic edge with motion vectors moving in opposite directions served as our standard kinetic boundary type.
The last two positions were located outside of the cell's CRF but within its surround. Figure 3 provides an illustration of the different position of the kinetic edge. The circle represents the border of the CRF derived from the summation test, whereas each numbered line indicates the position of the kinetic boundary. In this test the kinetic edge could be parallel or orthogonal to the motion vectors, which were aligned with the preferred direction of the neuron. As with the kinetic boundary stimulus, each condition was tested twice with the movie generating the boundary being presented forward (go) and then backward (back).

Data analysis

To determine the response strength to the experimental condition presented, we calculated the median value (over presentations) of the average firing rate in the response window, which was shifted by 50 ms after the stimulus onset and continued for the same amount of time after the stimulation stopped. This shift was applied to all conditions, because our stimulus presentation time of 320 ms was sufficiently long to render any changes in response onset insignificant (Lagae et al. 1994). The response level, characteristic of the neuron in a test, was defined as the maximum response in the luminance or kinetic boundary responses. The preferred orientation and the orientation selectivity index were also calculated on the basis of the responses to the eight orientations used. The angle $\theta$ in this case is a factor of twice the orientation step (22.5°).

RESULTS

Data set

We obtained recordings for our standard kinetic boundary from 68 cells of area MT. Their location within area MT was confirmed using myeloarchitectonic criteria (Desimone and Ungerleider 1986; Van Essen et al. 1981). Several electrolytic lesions were made in the course of a penetration and their location along the track was noted. This enabled us to determine the shrinkage of the brain after perfusion and also enabled us to accurately determine the laminar position of each cell using sections stained for Nissl substance using the cresyl violet dye. Of our sample of 68 cells, 37 were located in the superficial cortical layers II and III and 20 in layer IV, with the remaining 11 cells belonging to the deep cortical layers V and VI. The eccentricities ranged from 0.5 to 32.0°, with a median of 9.7° (Q1: 6.2; Q3: 14.0). The median direction index $i = 1 - (\text{nonpreferred response/preferred response})$ of our sample population of 68 cells was 1.00 (Q1: 0.96; Q3: 1.00). This result is the same as that reported by Lagae et al. (1994). The median directional sensitivity index was 76 (Q1: 59; Q3: 85) (see Fig. 4A). The median response at the preferred direction (i.e., response level) was 35 spikes/s (Q1: 22; Q3: 70; see Fig. 4B).

Orientation of kinetic boundary

For a cell to qualify as selective for the orientation of a kinetically defined boundary, three criteria had to be met. The first criterion was that the cell had to have a reasonable orientation selectivity when tested with kinetic boundaries. Only those cells with a sensitivity index $\geq$15 were considered for further analysis. This SI limit ensured that the response orthogonal to the best orientation was less than half the response to the best orientation. Second, the orientation response should not vary when the direction of the motion vectors changed from moving parallel to moving orthogonal to the orientation of the boundary. We reasoned that cells selective to the local motion vectors would shift their preferred orientation by 90°, reflecting the change in the local motion vectors when they changed from moving orthogonal rather than parallel to the orientation of the discontinuity. The final condition was that the calculated preferred orientations for the kinetic and luminance contrast boundaries should match. In both conditions two and three, the difference in preferred orientation was permitted to vary by 31°, following the convention of Albright (1984).

Figure 4C shows that only 10% of cells (7 cells) could not be used to test the selectivity of MT cells to kinetic boundaries because their SI values were <15. The median
SI for the parallel condition was 32 (Q1: 15; Q3: 45), whereas the median SI for the orthogonal condition was 26 (Q1: 18; Q3: 44). The distribution of the orientation selectivity index in Fig. 4C was obtained by pooling the data from the parallel and the orthogonal condition, which yielded a median SI of 32 (Q1: 16; Q3: 45). This value is not very different from the median SI for the two conditions taken separately. Comparing the response levels of the direction test with the response level obtained with our standard kinetic boundary showed a marked drop in the response rate for the kinetic boundary. The median response rate for the parallel condition was 17 spikes/s (Q1: 8; Q3: 32); the median response rate for the orthogonal condition was also 17 spikes/s (Q1: 10; Q3: 27). The distribution of the response levels shown in Fig. 4D is based on the pooled sample for the parallel and orthogonal conditions of the standard kinetic boundary. The median response level for our standard kinetic edge was 17 spikes/s (Q1: 8; Q3: 31). This value too did not differ very much from the response levels of the parallel and the orthogonal conditions separately.

We also tested 45 cells with a kinetic grating. Kinetic grating stimuli generally reduced the orientation selectivity of the cells [median orientation selectivity index was 20 (Q1: 12; Q3: 35)] as well as the response level [median response level was 13 spikes/s (Q1: 7; Q3: 25)].

Although most cells met our first condition, all cells changed their preferred orientation by ~90° when the local motion vectors changed by 90° and thus failed to meet our second condition. The response properties of cell 6609, shown in Figs. 5–7, is representative of all cells from which we recorded in area MT. This cell had a relatively small receptive field, as shown in Fig. 5A. It also exhibited an antagonistic surround, as indicated by the summation test of Fig. 5B. Testing of orientation selectivity for kinetic boundaries was therefore reduced to a central aperture of 6.4° by inserting a occluding mask over the monitor. The directional selectivity of this cell was 85, a value close to the median value of a sample population.

The cell shown in Figs. 6 and 7 summarizes the general findings of our investigation into the orientation selectivity of cells in area MT to kinetically defined boundaries. Figure 6, A and B, shows that although there are large differences in the response rates to the two stimuli, the cell's calculated preferred orientation for a luminance contrast boundary was close to its calculated preferred direction of motion, 148° versus 168°. To complete the circle, each data point obtained from the orientation test, stationary luminance, or kinetic boundary was plotted twice (Maunsell and Van Essen 1983a). This cell was classified as a type II cell, following the convention of Albright (1984), because its preferred orientation was within 30° of its preferred direction of motion.

Figure 6, C–F, shows the cell's response to the standard kinetic edge and the kinetic grating. The data at each orientation were obtained by averaging the response of the cell to the go and back conditions. Figure 6, C and E, shows that the cell's preferred orientation shifts by 89° when the motion vectors change from moving parallel to moving orthogonal to the orientation of the standard kinetic edge. The same applies to the kinetic grating shown in Fig. 6, D and F (86° shift). The orientation selectivity index and the calculated preferred orientation are shown below each polar plot.

For the purpose of analysis of the additional kinetic boundaries, the two halves of the CRF were labeled as strong or weak, depending on the response level obtained when the
coherently moving RDP stimulated that particular half of the CRF. Comparing Fig. 7, A and B, shows that the preferred orientation for the strong half of the CRF, when tested with the kinetic boundary stimulus containing a stationary RDP, shifted by 86° between the parallel and orthogonal conditions. Figure 7, C and D, represents the orientation response to the same stimulus for the weak half of the CRF. Here, too, a shift in the preferred orientation of 89° can be seen between the parallel and orthogonal condition. Figure 7, E and F, shows that there is a shift of 87° in the preferred orientation of the strong half of the CRF between the parallel and orthogonal conditions of the kinetic boundary stimulus containing VDN. A shift of 83° in the preferred orientation between the parallel and orthogonal conditions of the kinetic boundary stimulus containing VDN in the weak half of the CRF can be seen in Fig. 7, G and H.

Figure 8A shows that the shift in the apparent orientation preference of our sample population to the standard kinetic edge clusters around 90°. The same is true for the kinetic grating shown in Fig. 8B. In determining the shift in preferred orientation for the kinetic edges containing either stationary dots or VDN, we averaged the calculated preferred orientation of the two halves of the CRF. Figure 8, C and D, shows that their shift too clusters around 90°. In fact, irrespective of the type of kinetic boundary used, the majority of cells in area MT changed their preferred orientation by nearly 90° and no cell was observed that changed its preferred orientation by <40°.

In analyzing the shift in preferred orientation, we pooled the data for all cortical layers. Lagae et al. (1989) have shown that there was processing occurring between the different cortical layers of area MT. Comparing the shift across all layers of area MT may have obscured the presence of laminar differences. We therefore examined whether there were any laminar differences in the shift in preferred orientation between the parallel and orthogonal conditions of the standard kinetic boundary. We found that the superficial layers (II and III), the input layer (IV), and the deep layers (V and VI) all showed the same median shift in orientation preference of ~90° (Fig. 9). This indicates no preferential selectivity to the orientation of kinetic boundaries across the cortical layers of area MT.

Position of kinetic boundary

In those cells with an antagonistic surround, any selectivity to the position of a kinetic boundary was predicted to result in one of the seven positions yielding a much higher response than the others, irrespective of the local motion vectors. Figure 10A shows the receptive field of such a cell with an antagonistic surround (cell 6605). The summation test shown in Fig. 10B confirmed the presence of a strong antagonistic surround. In contrast to the orientation testing with kinetic edges, no mask was inserted over the monitor, because we were interested in the interaction between the CRF and its surround. Figure 11 shows the response of cell 6605 to the seven positions in which the kinetic boundary was presented. Instead of responding to one specific location,
the positions eliciting the higher activity levels switched from one side to the other when the direction of the local motion vectors was reversed. This was a general finding, as shown in Fig. 12. The responses for each cell were normalized to a best response to either the go or the back conditions. Figure 12A shows the median response for the seven positions of the kinetic boundary for 24 cells. Note that the local motion vectors were always orientated parallel to the cell's preferred direction of motion (see Fig. 3A). Figure 12B shows the median response for each position for nine cells where the boundary was located orthogonal to the motion vectors (see Fig. 3B). From Figs. 11 and 12 it is apparent that the optimal positions shift from the left to the right side and from the upper to the lower area of the CRF when the direction of the local motion vectors was reversed. This is a clear indication that cells in area MT respond to the motion vectors present over their CRF only.

**Stationary contrast luminance and direction response**

Comparing the median SI of Fig. 4A with the median orientation selectivity index for the luminance contrast boundary of Fig. 13A shows a clear reduction in selectivity. The median response levels for the direction test shown in Fig. 4B with the response level to the stationary luminance contrast stimulus in Fig. 13B clearly show that on average the cells of area MT are much less sensitive to luminance contrast boundaries than they are to direction of RDP motion. The median values given below are obtained from a subpopulation of cells that were tested with both types of stimuli.

**FIG. 6.** Responses of cell 6609 to uniform motion in 16 directions (A), a stationary luminance contrast stimulus (B), and our standard kinetic edge (C and D) and kinetic grating stimulus (E and F), in the form of polar plots. The cell shows a preferred orientation parallel to its preferred direction of motion, thus making it a type II cell (Albright 1984). The data for the orientation tests (stationary luminance contrast and kinetic boundaries) were plotted twice, following the convention Maunsell and Van Essen (1983a,b) to complete the circle. The direction or orientation selectivity index (SI) value for each test and the calculated preferred direction or preferred orientation is shown below the appropriate polar plot.

**FIG. 7.** A–D: responses of the strong and weak half of the CRF of cell 6609 (same cell as Fig. 6) to the kinetic edges containing stationary dots, shown as polar plots. E–H: responses to the kinetic edge containing VDN. Following the convention of Maunsell and Van Essen (1983a,b), the data points for the orientation tests were plotted twice to complete the circle. The sensitivity index and calculated preferred orientation for each half of the CRF are shown below the appropriate polar plot. KE, kinetic edge.
FIG. 8. Distribution of the differences in preferred orientation for the kinetic boundary stimuli when the local motion vectors ran parallel or orthogonal to the orientation of the discontinuity. The change in preferred orientation clusters around 90° with both the kinetic edge (A: N = 61) and the kinetic grating (B: N = 41). The same observation was made for the kinetic boundaries containing either stationary random dots (C: N = 27) or VDN (D: N = 24). The change in the preferred orientation clusters around 90°.

The median SI and median response at optimal direction are not very different from the values of the whole population shown in Fig. 4. The median orientation selectivity index of 32 (Q1: 17; Q3: 50) is clearly smaller than the median direction SI of 73 (Q1: 57; Q3: 84). The response level at optimal orientation was smaller [median response 14 spikes/s (Q1: 9; Q3: 19)] compared with the response at optimal direction [median 31 spikes/s (Q1: 19; Q3: 65)]. However, this should not distract from the fact that some cells in area MT are clearly selective to the orientation of luminance contrast stimuli. Comparing the preferred orientation of cells in area MT with their respective preferred direction (see Fig. 14) yields a proportion of 28% type II cells, that is, cells in which the preferred orientation did not differ by >30° from the preferred direction of motion.

Investigation of the interaction of motion vectors on direction tuning

During our investigation we restricted our stimulus to the CRF by placing an occluding mask in front of the monitor. This enabled us to reorganize the kinetic edge data to examine the effect of different motion vectors in the two halves of the CRF on the directional selectivity and responsiveness of the cells. We arbitrarily divided the CRF into top and bottom rather than left and right.

Figure 9, A–F, shows how the data from the parallel and orthogonal conditions of the kinetic edge stimuli were reorganized to obtain the required motion vector for the lower half of the CRF. The larger circle in each panel represents the CRF, whereas the smaller circles indicate the kinetic boundary that provided the local motion vector at that location. The dot pattern in the larger circles of Fig. 15 represents the part of the CRF containing a moving RDP, with a reversal of contrast being representative of a reversal in the direction of motion. Each half of the CRF was labeled...
as either strong or weak, depending on its response level to the moving RDP.

As described above, we calculated an SI for each cell.

Because our standard kinetic boundary contained motion in opposite directions and the formula for calculating the SI is particularly sensitive to motion in the opposite direction, we felt that this would lead to an unfair appraisal of the directional selectivity from these data. We consequently calculated a truncated SI based on 8 directions including the optimum direction, rather than all 16 directions of motion. Figure 15, D–F, shows the standard kinetic edge stimuli that provided the data for cells with a preferred direction of motion from left to right, diagonally, and vertically upward, respectively.

Figure 16A shows that the median SIs for the 20 cells for which data from all three types of kinetic boundaries were available did not differ significantly. Neither did the differences in the SI between the strong and the weak half of the CRF (paired t-test: stationary, \( P = 0.13 \); VDN, \( P = 0.08 \)).

Although we found little difference in the SIs of the strong and weak halves of the CRF, we did observe differences in the responsiveness of the two halves of the CRF (see Fig. 16B). Direct evidence for this asymmetry was obtained in the present experiments and in a previous study (Lagae et al. 1994). The response contour plot of cell 6609 (see Fig. 5A) reveals a good symmetry between the two halves of the CRF, whereas the response contour plot of cell 6605 (see Fig. 10A) shows a marked asymmetry. This is reflected in the response strength of the two halves of the CRF. The two CRF halves of cell 6609 show little difference (strong: 64.9 spikes/s; weak: 62.2 spikes/s), whereas cell 6605 exhibits an appreciable differences in the response level of the two CRF halves (strong: 73.0 spikes/s; weak: 56.4 spikes/s).

Comparing the median response levels of the strong half
of the CRF, we found that the differences in the response level depended on the amount of motion in the nonpreferred direction (Page test: $L = 261.5$, $k = 3$, $N = 20$, $P < 0.001$; see Siegel and Castellan 1988).

Comparing Fig. 16B with Fig. 4B reveals little difference in the median response level of the direction test and the antiphase kinetic boundary. This result seems surprising because in Fig. 4 the median response level for the optimal orientation of the antiphase kinetic edge (see Fig. 4D) was clearly lower than the median response level at optimal direction (see Fig. 4B). This difference can be attributed to the manner in which we calculated the response strength in the two cases. When we examined the orientation selectivity to kinetic boundaries we combined the data from the go and back conditions, whereas in Fig. 16 we were interested in the direction response of the cell so the data for the go and back conditions were treated separately.

**FIG. 12.** A: normalized median response for the 7 horizontal positions across the CRF of 24 cells. B: normalized median response level for the 7 vertical positions across the CRF of 9 cells. Conventions as in Fig. 11.

**DISCUSSION**

**Kinetic boundary responses**

There is, as far as we know, presently no work that has examined the ability of cells in area MT to code orientation or position of kinetically defined discontinuities. There is evidence that area MT plays an important role in the perception of kinetic boundaries (Marcar and Cowey 1992; Regan et al. 1992), but to date no direct physiological evidence has been available. In one study the responses of a small
The main finding of that study was that stimuli containing a motion discontinuity evoked a weaker response than did uniform motion. This decrease was more marked when the stimulus contained five discontinuities than in the case where there was only a single discontinuity present. Our investigation replicates these findings. Furthermore, we, like Snowden et al., found a large difference in the level of suppression elicited by motion in the nonpreferred direction between the two halves of the CRF. Snowden et al. averaged the data for the two halves and obtained an average \((n = 12)\) suppression index of 0.36 (estimated from their Fig. 10). Use of the median of the data of Fig. 4B and the median response at optimal direction gives an average suppression index of 0.51.

From our results it appears that although cells in area MT of the macaque may have the properties for processing kinetic boundaries (Allman et al. 1985) and play an important role in their perception (Marcar and Cowey 1992), they do not themselves code the orientation of kinetic boundaries. They are equally insensitive to the position of a kinetic boundary. Even those cells in area MT that have a surround are unable to signal even the position of a kinetic boundary.

The finding that cells in area MT are not themselves sensitive to the orientation or position of kinetically defined boundaries but participate in their processing (Marcar and Cowey 1992) suggests that the role of cells in area MT is limited to establishing a reliable indication of the direction of motion within their CRF (Albright 1984; Movshon et al. 1985; Rodman and Albright 1989) and sending this preprocessed motion signal to cortical visual areas in the ventral stream.

Selectivity for orientation of kinetically defined boundaries has been observed in area V2 (Marcar et al. 1992) and in area TE (Sáry et al. 1995). In addition, TE neurons have been shown to be selective for kinetically defined patterns (Sáry et al. 1993). This scheme is supported by the anatomic evidence showing extensive, direct connections between area MT and area V2 (Shipp and Zeki 1989) and indirect connections between area MT and IT (Van Essen et al. 1992).

Selectivity to the orientation of non-Fourier boundaries (van Santen and Sperling 1984) has also been reported for area V4 (Logothetis and Charles 1990) and in area V1 (Gawne et al. 1994). Area MT has also been found to be

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**Fig. 15.** How data from the different types of kinetic edges were reorganized to obtain the different directional motion vectors limited to 1/2 of the CRF. Numbers: directions of motion in the lower half of the CRF.

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**Fig. 16.** A: median truncated SI and the quartiles of the 2 halves of the CRF for those cells for which tests for all kinetic boundaries were tested \((N = 20)\). The response strength to the coherent motion in the stationary kinetic boundary stimulus served as the criterion for classifying the CRF half as the strong or weak response half-field. The reconstructed sensitivity index based on strong half or the weak half of the CRF was calculated using the method described in the text and represented by Fig. 15, D–F. B: median response levels and the quartiles to motion in the unit's preferred direction for the strong and weak response half-fields.
Responses to luminance contrast stimuli

Cells in area MT were clearly found to exhibit orientation tuning to stationary luminance contrast stimuli, confirming the results obtained by Albright (1984). In our study, as in that of Albright (1984), responses to stationary stimuli were much weaker than those to moving stimuli. The median orientation selectivity index in our study was much smaller than the median SI. This is apparently in contradiction with the study by Albright (1984), where a narrower bandwidth was observed for orientation tuning than for direction tuning. This difference can be accounted for by the methods used to measure selectivity. The SI reflects primarily influenced response to opposite directions of motion. Consequently it correlates less well with the bandwidth measurement than the orientation selectivity index, which primarily reflects differences in response to orthogonal orientations. Both our study and that of Albright (1984) show less selectivity for orientation than for direction of motion. The advantages of the selectivity index are that it provides an indication of direction selectivity and bandwidth in one measure. Also, it uses all data points and can be applied to cells that exhibit poor tuning and for which no bandwidth can be calculated (Albright 1984; Snowden et al. 1992). The proportion of cells in our study with their preferred orientation close to their preferred direction of motion (type II cell of Albright 1984) was 28%, a value very similar to the 29% reported by Albright (1984).

Interaction between motion vectors in the CRF and their effect on direction tuning

The cell's directional selectivity was little influenced by the presence of a different type of motion vector in the other half of the CRF. Examining how one type of motion vector can influence the directional tuning of a cell is effectively the opposite of the method previous studies have employed to study the interaction between different parts of the CRF. In these studies (Britten and Newsome 1990; Snowden et al. 1991) the effect of a second motion vector on the cell's response to an optimal stimulus was examined. The conclusions drawn from our results are in agreement with those of Lagae et al. (1994). Lagae et al. (1994) showed that cells in area MT responded to the presence of their preferred translation motion vector even when it formed part of an optic flow component. The optic flow component stimulus employed by Lagae et al. (1994), unlike our kinetic edge stimulus, did not contain any perceptual discontinuity. Independent of the type of stimulus used, cells in area MT extract a specific motion vector from a spatial configuration of motion vectors.

Snowden et al. (1991) reported that the amount of suppression in transparent and kinetic displays correlated with the amount of motion in the nonpreferred direction. Our data confirm their finding. Stationary dots in the complementary half of the CRF yielded the least suppression and thus the highest median response rate, whereas VDN and motion in the opposite direction in the complementary half of the CRF resulted in a progressively larger suppression and lower median response levels.

Concluding remarks

From our discussion it would appear that the role of area MT neurons is to extract from the visual scene the motion vector with the speed and direction to which they are tuned. This may seem a very limited function, although it is perhaps worth remembering that determining the true direction of motion of an object is no trivial matter. Obtaining a robust representation of local motion requires an invariance of direction and speed selectivity for other parameters. Physiological evidence for this invariance in area MT has been obtained to a certain degree (Albright 1992; Lagae et al. 1993; Movshon et al. 1985; Olivaria et al. 1992; Xiao et al. 1993).

Our investigation illustrates that an understanding of the role that area MT plays in visual perception will depend as much on a thorough knowledge of its speed and direction selectivity as on an appreciation of the way in which speed- and direction-related signals are further processed within its subcompartments and the use other cortical visual areas make of the signals they receive from area MT.

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