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Direction- and velocity-specific responses from beyond the classical receptive field in the middle temporal visual area (MT)

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Abstract. The true receptive field of more than 90% of neurons in the middle temporal visual area (MT) extends well beyond the classical receptive field (crf), as mapped with conventional bar or spot stimuli, and includes a surrounding region that is 50 to 100 times the area of the crf. These extensive surrounds are demonstrated by simultaneously stimulating the crf and the surround with moving stimuli. The surrounds commonly have directional and velocity-selective influences that are antagonistic to the response from the crf. The crfs of MT neurons are organized in a topographic representation of the visual field. Thus MT neurons are embedded in an orderly visuotopic array, but are capable of integrating local stimulus conditions within a global context. The extensive surrounds of MT neurons may be involved in figure-ground discrimination, preattentive vision, perceptual constancies, and depth perception through motion cues.

1 Introduction

We perceive the visual world as an unitary whole, yet one of the guiding principles of more than four decades of neurophysiological research on the visual system has been that neurons respond to stimulation within their classical receptive fields (crfs), which are usually discrete small portions of the total visual field (Hartline 1938). The crfs are organized into a series of topographic representations of the visual field. At least ten areas, each containing a separate map of the visual field, are present in the visual cortex in the owl monkey (see figure 1). It has been widely assumed that perceptual functions that require the integration of inputs over large portions of visual space must be either collective properties of arrays of neurons representing the visual field or else be features of those neurons at the highest processing levels in the visual system, such as those neurons in inferotemporal or posterior parietal cortex that typically possess very large receptive fields and do not appear to be organized in visuotopic maps. These assumptions have been based on results of studies in which receptive fields were mapped with conventional stimuli, spots or bars of light, presented on a featureless background. However, unlike the neurophysiologist's tangent screen, the natural visual scene is rich in features (see figure 2). We thought it would be especially appropriate to study the effects of background motion since the visual field is filled with moving stimuli as the viewer moves through or scans its environment. Neurons in the middle temporal visual area (MT) are specialized for the analysis of moving stimuli, and possess well defined crfs that are organized in a topographic representation of the visual field (Allman and Kaas 1971a; Baker et al 1981; Maunsell and Van Essen 1983a). We have found that the direction and velocity of background textures moving outside the classical receptive field have a profound and selective influence on the responses of MT neurons to stimuli presented within the crf.

2 Methods

2.1 *Subjects*

We recorded from Area MT in three owl monkeys (*Aotus lemurinus griseimembra*: Brumback 1973; Hershkovitz 1983). This is a new taxonomic designation which supersedes the term *Aotus trivirgatus* used in our earlier papers. Our procedures for recording

through a chronically implanted chamber were described in detail in Allman et al (1979) and Baker et al (1981). Under aseptic conditions and general anesthesia (ketamine HCl, 25 mg kg^{-1}), a stainless steel chamber was cemented around an opening in the skull exposing the dura over MT. At the beginning of each experimental session the monkey was tranquilized with a single dose of trifluprom azine (2 mg kg^{-1}), and small doses of ketamine (2 mg kg^{-1} h^{-1}) were used to maintain sedation. The monkey's head was fixed

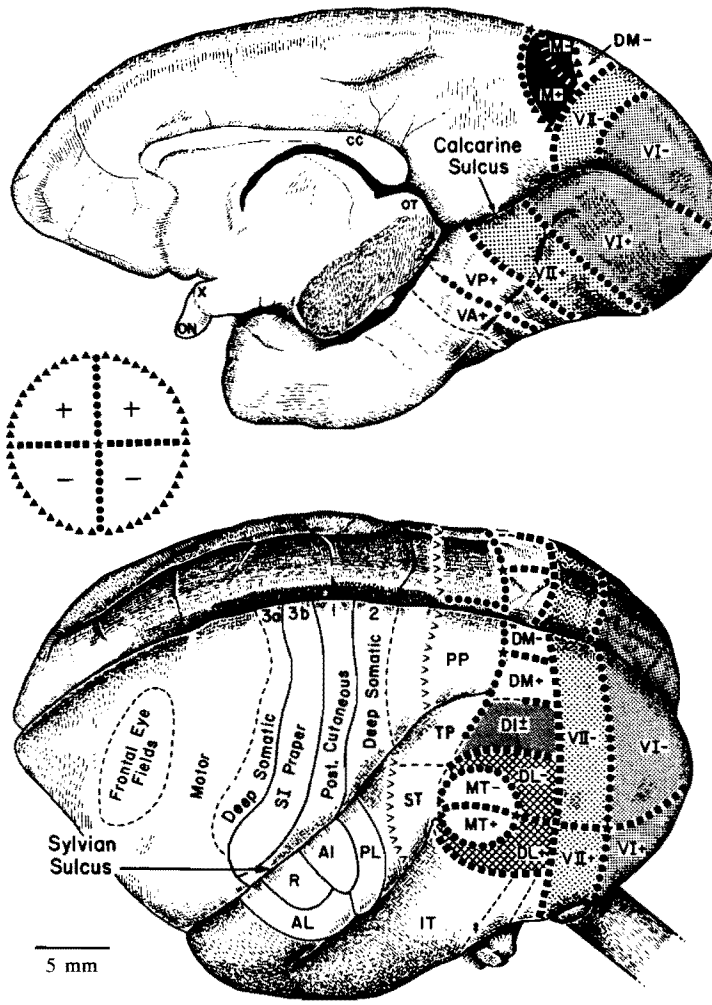

Figure 1. The representations of the sensory domains in the cerebral cortex of the owl monkey. Above is a ventromedial view; below is a dorsolateral view. On the left is a perimeter chart of the visual field. The symbols on this chart are superimposed on the surface of the visual cortex. Pluses indicate upper quadrant representation; minuses, lower quadrants. The row of Vs indicates the approximate border of visually responsive cortex in the parietal and temporal lobes. AI, first auditory area; AL, anterolateral auditory area; CC, corpus callosum; DI dorsointermediate visual area; DL, dorsolateral visual area; DM, dorsomedial visual area; IT, inferotemporal visual cortex; M, medial visual area; MT, middle temporal visual area; ON, optic nerve; OT, optic tectum; PL, posterolateral auditory area; PP, posterior parietal visual cortex; R, rostral auditory area; ST, superior temporal visual area; TP, temporoparietal visual cortex; VA, ventral anterior visual area; V-I first visual area; V-II second visual area; VP, ventral posterior visual area; X, optic chiasm. The cortical visual areas were mapped by Allman and Kaas (1971a, 1971b, 1974a, 1974b, 1975, 1976), and Newsome and Allman (1980); the somatosensory areas by Merzenich et al (1978); and the auditory areas by Imig et al (1977).

with a circular clamp tightened around the steel recording chamber. This clamp was attached to a specially designed chair in which the monkey was restrained in the normal owl monkey sitting posture. The cornea, sclera, and eyelids were topically anesthetized with a long-acting local anesthetic (0.5% dibucaine HCl in contact lens wetting solution), and the pupils were dilated with 1% cyclopentolate HCl solution. After allowing the local anesthetic to take effect, the eyelids were retracted. An eye ring, which was machined to fit the contour of the eye and mounted by an adjustable joint to the apparatus, was cemented to the margin of the cornea with Histoacryl tissue adhesive (n-butyl cyanoacrylate). This method effectively eliminated eye movements during the course of the experimental session. The adhesive was easily removed from the eye without damage at the end of each session. Eye position was monitored by projecting the image of retinal blood vessels in the optic disk onto the screen with an ophthalmoscope (Fernald and Chase 1971). Contact lenses were used to protect the cornea from drying and bring the eye into focus on the television screen which was normally 28.5 cm from the eye.

2.2 *Video stimulator*

We developed a video display system with John Power and Michael Walsh of the California Institute of Technology Biology Electronics Shop. The system was based on an Intel 8085 microprocessor and could be controlled either manually through switches and a joystick or through a Nova 2 computer. The display was presented on a Sony KX-2501 RGB monitor (39 cm × 52 cm). The display consisted of a central region of adjustable length, width, and orientation which contained an array of dots. The direction and speed of movement of the dot array could be varied. The dot arrays were produced by a pseudorandom binary sequence generator (PRBS), the motion parameters were generated by the microprocessor. We positioned the central region so that it corresponded to the crf for each neuron. The dots subtended approximately 0.4 deg at a viewing distance of 28.5 cm and the display consisted of 50% bright and 50% dark dots. The surround region contained the same size and density of dots, which were produced by a second PRBS, and the movement of the surround array was controlled by the micro-

Figure 2. Tropical forest habitat of the owl monkey. A family of owl monkeys resides in the tangle of vines, which is viewed from the ground. This photograph was taken by Dave Sivertsen in the Manu National Park in the Peruvian Amazon.

processor independently from the center array. The rectangular border of the center region remained stationary during both center and background movement, and fresh dots continually appeared at the edges of the center and surround so that the screen was continually filled with dots. In addition, we could present more conventional stimuli such as solid bright or dark bars on dark, bright, or random-dot backgrounds.

2.3 *Single neuron recording and analysis*

We penetrated the dura and recorded the activity of single neurons in MT with sterilized glass-insulated platinum-iridium microelectrodes (Wolbarsht et al 1960) advanced with a stepping motor microdrive mounted on a movable stage attached to the chamber. When a neuron with a stable waveform was isolated with a window discriminator, we plotted its crf with hand-controlled stimuli while listening to the neuron's activity over an audio monitor, and then proceeded with the computer-controlled quantitative characterization of the neuron's response properties described in section 3. Each stimulus condition was presented five times, and in each series the stimuli were presented in pseudo-random order. For a 2 to 3 s foreperiod before each stimulus presentation the computer monitored the neuron's firing to measure the rate of spontaneous activity. The neuron's response was calculated by averaging the spikes that occurred during the foreperiod and subtracting this spontaneous rate from the average firing rate during the stimulus presentation period. To allow for response latency, the period for the response calculation ran from 40 ms after the beginning of the stimulus presentation to the end of the presentation. In addition, when we tested with bar stimuli sweeping at the higher speeds, we found that the response often occurred after the end of the brief stimulus-presentation period. So for calculating the response we allowed a minimum period of 250 ms commencing 40 ms after the beginning of the stimulus presentation. The 40 ms delay and 250 ms minimum period were used by Maunsell and Van Essen (1983a) in their study of MT in macaque monkeys.

When we tested the effect of the direction of background movement, we continuously stimulated the cell with a field of random dots moving in its preferred direction and confined to its crf. We calculated the cell's average firing rate during the five 2 s periods before the presentation of each direction of movement of the random-dot background and compared this firing rate, which contained both driven and spontaneous components, with the average firing rate during background movement. These measurements require that the background firing rate resulting from the stimulation of the crf and spontaneous activity be reasonably constant. We excluded from analysis those cells in which the highest firing rate for a foreperiod was more than double the lowest firing rate of all the foreperiods. Sixty-one of the seventy-five MT cells tested for the influence of direction of background movement were acceptable by this criterion, and the data from these 61 cells are described in section 3.1.

When we tested the effect of velocity of background movement in a cell, we first determined the preferred direction and velocity for the optimally shaped bar stimulus, and then we presented the bar moving in the preferred direction at the preferred velocity while simultaneously presenting background movements in the same direction of varying velocity. Instead of driving the cell continuously with the bar stimulus, we presented the optimal bar stimulus together with various background velocities and compared these responses with those obtained when the background was stationary. The background stationary trials were interleaved in the pseudorandom sequence with the other stimulus presentations. This method enabled us to monitor the spontaneous activity during the foreperiod, and thus assess the effect of the velocity of background movement on spontaneous activity separately from the response resulting from the bar stimulus.

In the course of these experiments we derived a visuotopic map for each monkey from the crfs that enabled us to identify the cortical visual areas from which we were recording

by making use of extensive mapping done earlier in owl monkeys (Allman and Kaas 1971a, 1974b). The areal assignment of recording sites was confirmed in two monkeys by identifying recording sites marked with microlesions in MT, which is highly distinctive in histological sections stained for nerve fibers (Allman and Kaas 1971a). These monkeys were deeply anesthetized with a lethal dose of sodium pentobarbital and then perfused with 0.9% saline followed by 3.7% formaldehyde in 0.9% saline. Alternate forty micra frozen sections were stained with cresyl violet for cell bodies and with the Gallyas (1979) method for fibers. The third monkey is in good health and is a successful breeder in our colony.

3 Results

3.1 *Effects of moving stimuli outside the classical receptive field*

For each MT neuron we first mapped its crf with bar and random-dot stimuli and determined its preferred velocity. The term *classical receptive field* (crf) is used instead of *excitatory receptive field* because for many cells the discharge rate is inhibited below the spontaneous rate by conventional stimuli moving against the preferred direction (see the left graph in figure 3 where the response at − 180° was nearly 20% below the level of spontaneous activity). We electronically positioned on the screen a rectangular window of adjustable length, width, and orientation so that it closely corresponded to the crf. We

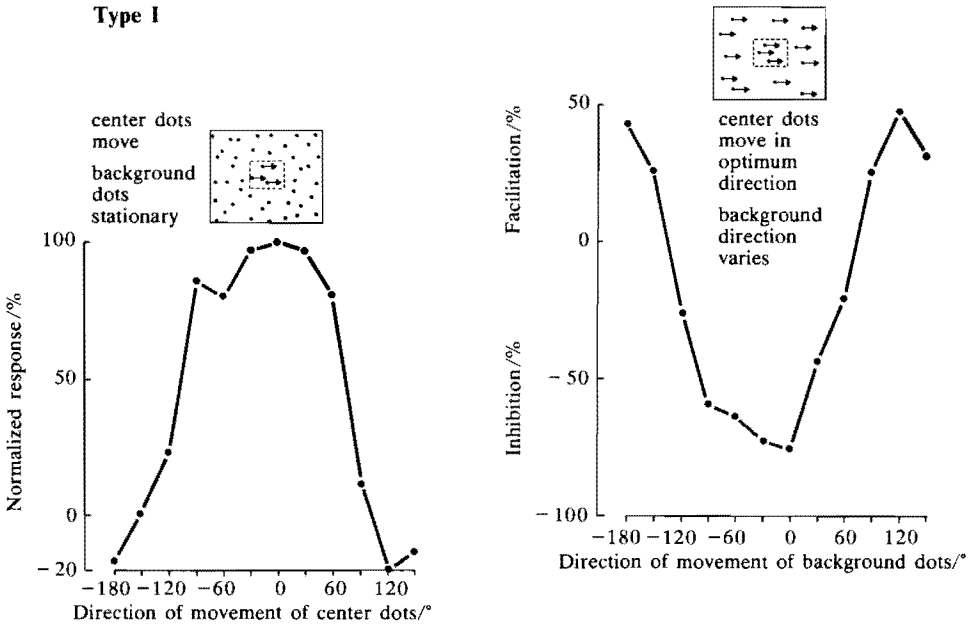

Figure 3. Response properties of a type I neuron (antagonistic direction-selective surround). The left graph depicts the response of the cell, HCMT32B, to twelve directions of movement of an array of random dots coextensive with its crf. The response is normalized so that 0% is equal to the average level of spontaneous activity sampled for 2 s periods before each presentation. Negative percentages in the left graph indicate inhibition relative to the level of spontaneous activity. The response in the optimum direction is 100%. The right graph depicts the response of the cell to different directions of movement in the surround while the crf was simultaneously stimulated with an array moving in the cell's preferred direction. In the right graph the crf was stimulated by the array moving in the optimum direction during the 2 s sample periods preceding background movement; thus a response of 100% in the left graph is equivalent to 0% in the right graph. A value of − 100% in the right graph indicates that the movement in the surround reduced the neuron's firing rate to zero. The stimulus conditions are depicted schematically above each graph. In the experiment the dots were much denser and the background much larger relative to the center than depicted schematically.

examined the neuron's directional preference within its crf by moving random-dot arrays in twelve directions within the window, which was fixed in place and was surrounded by a background of stationary random dots. These data are depicted in the graphs on the left side in figures 3 through 8. To obtain the graphs on the right side of figures 3 through 8, we excited each neuron by presenting random dots moving in its preferred direction within the window and determined the influence of background movement by stimulating the hitherto apparently silent surround with arrays of random dots moving in each of twelve directions. Only the center movement was displayed within the window, and only the background movement was displayed elsewhere on the screen. Both the center and the background dots moved at the same speed, which was approximately the speed for eliciting the optimum response from the crf. Figure 3 illustrates a type I neuron, which possessed a directionally selective crf and an antagonistic directionally selective surround. For type I neurons the preferred direction for the center was the same as the direction of maximum inhibition by movement in the surround.

Figure 4 illustrates a type II neuron, which resembled the type I cell but in addition possessed a strong facilitatory peak when the background moved in one direction 90° to the preferred direction for the center.

Figure 5 illustrates a type III neuron, which also possessed a directionally selective crf but was suppressed by all directions of background movement. In this cell we also tested the effect of having the background move in all directions at once like 'snow' on the television screen. This did not suppress the response to center stimulation and suggests that coherent movement of an array of random dots is required for suppression.

Figures 6 through 8 illustrate all of the data points obtained for the three types. In each graph lines connect the median response obtained for each stimulus condition. The data for the three types are summarized in table 1. The three types cannot be distinguished on the basis of the responses from their crfs. Types I and II have directionally selective surrounds with the maximum suppression obtained for background movements in the preferred direction for the center. Type III was suppressed by all directions of background movement with no directional preference. Type II neurons were strongly

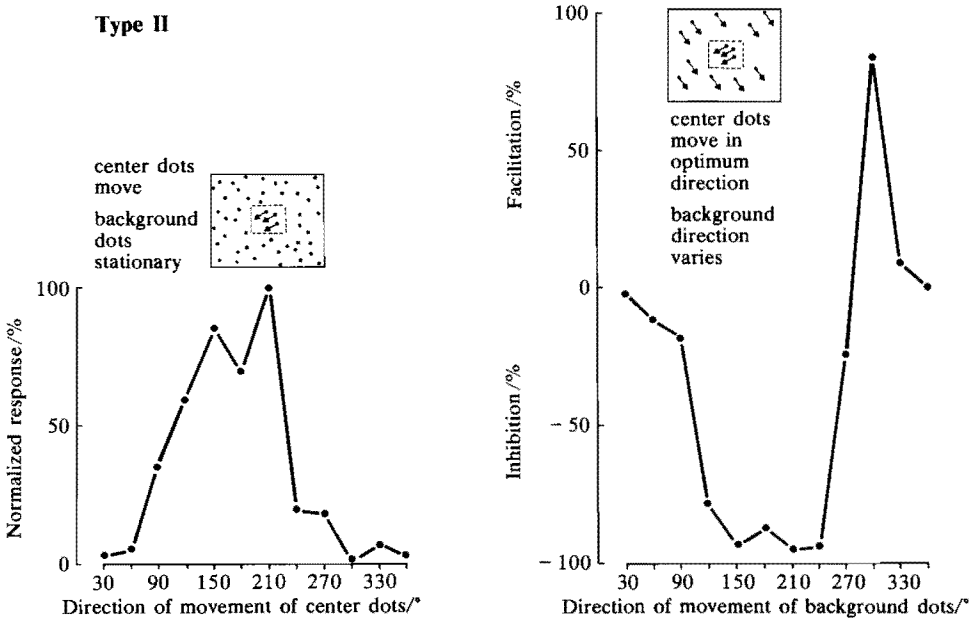

Figure 4. Response properties of a type II neuron, HCMT24E (90° surround facilitator). The schematic diagrams above the graphs depict the optimum stimulus conditions.

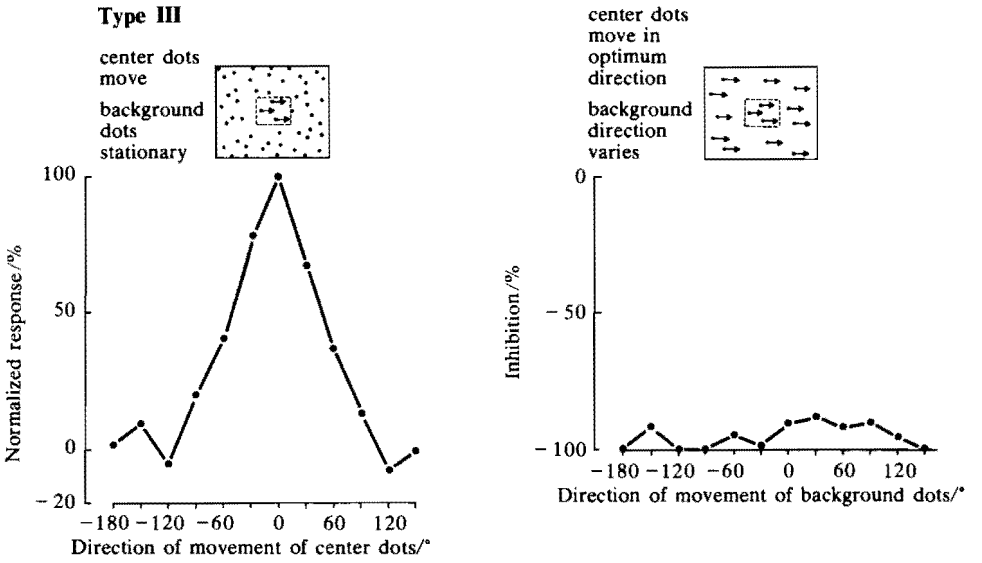

Figure 5. Response properties of a type III neuron, HCMT21K (nondirectional surround inhibitor).

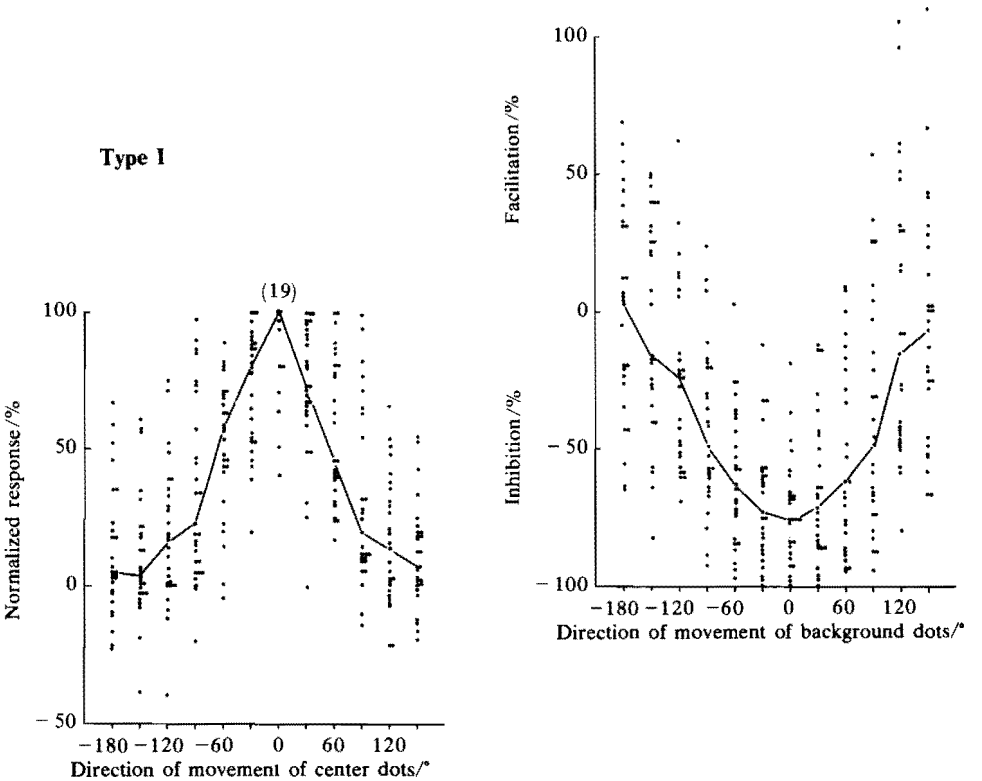

Figure 6. Responses of twenty-seven type I neurons (antagonistic direction-selective surrounds). In the left graph, which depicts responses from the crf with the background stationary, the data have been plotted so that the preferred direction of movement for each cell is set equal to 0° or, in cells with a broad band of preferred directions, the direction in the middle of the band is set equal to 0°. This direction, which also corresponds to the direction of movement driving the center during the presentation of background movements, is also set equal to 0° for each cell in the right graph. A line connects the median responses for each direction in each graph.

facilitated by one direction of shearing background movement that was 90° to the cell's preferred direction. The majority of type I neurons were facilitated by background movement opposite to the preferred direction (180°). In each microelectrode penetration, either type I or type III cells tended to predominate. The five type II cells were found in five separate penetrations mixed with the other types.

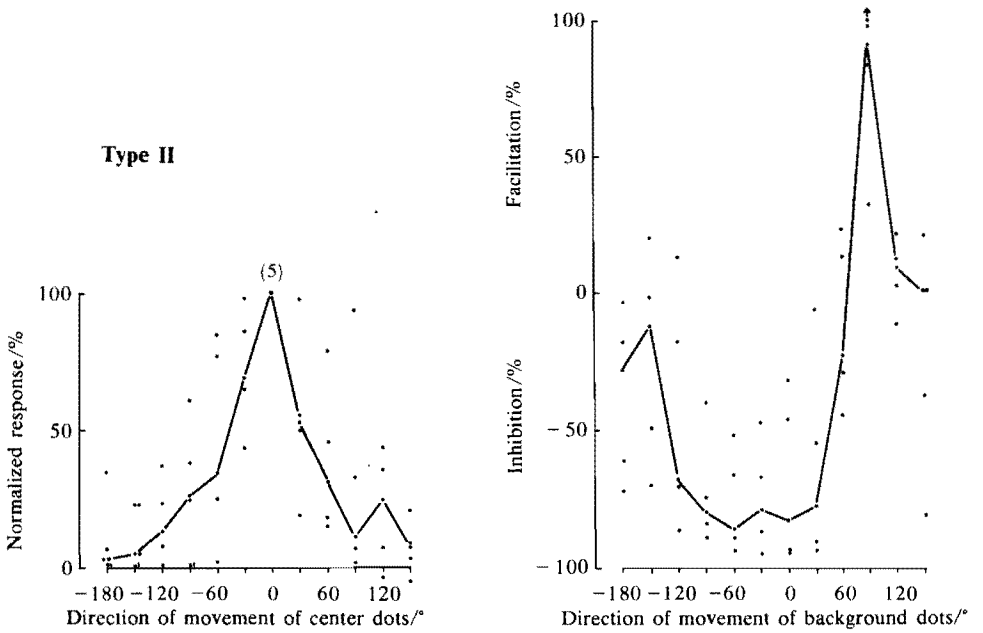

Figure 7. Responses of five type II neurons (90° surround facilitators). The directions have been normalized as in figure 6, but, in addition, the facilitatory peaks have been placed at + 90° although three cells actually had their peaks at − 90°, and the other directions from these three cells have been similarly reversed in both graphs. Small arrows indicate responses falling beyond the limits of the graph.

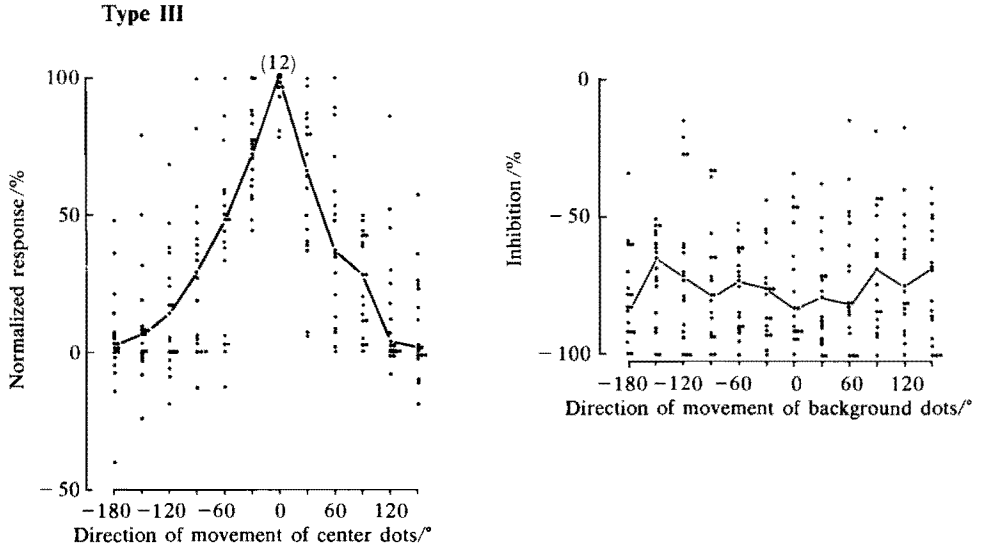

Figure 8. Responses of eighteen type III neurons (nondirectional background inhibitors). The directions have been normalized as in figure 6.

In addition to the three main types, we recorded a cell which responded well to all directions of movement in its crf. When we excited the crf with movement in the preferred 0° direction, the cell behaved like type I with direction-selective background suppression greatest at 0°; when we drove the crf with movement in the 180° direction, the background suppression was greatest at 180°. In another cell the response from the crf was abolished by the presence of a static random-dot surround. In still another cell stimulation of the crf with random dots produced only inhibition. Three cells had irregular mixed patterns of inhibition and facilitation as a result of background stimulation.

Table 1. Types of responses from beyond the crf in MT neurons

Type	Distinguishing features	Number of cells	Percentage of cells
I	directionally selective surround	27	44
II	sharp facilitatory peak for shearing movement in surround in one direction 90° to preferred direction for crt	5	8
III	equal suppression by all directions of movement in the surround	18	30
IV	unresponsive to moving random dots in the surround	5	8
Miscellaneous surround responses		6	10
	Total	61	100

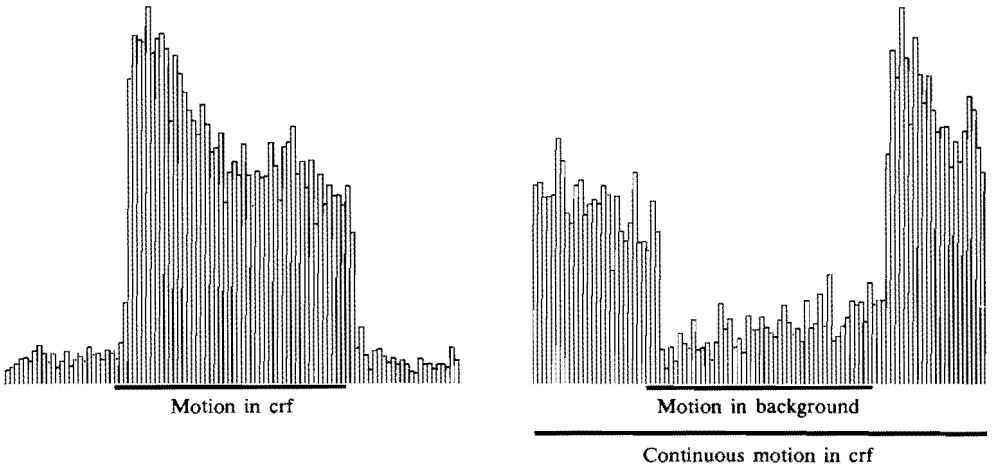

Figure 9. The left histogram illustrates the combined responses of forty-two MT neurons (types I, II, and III) to random dots moving for a 2 s period in the preferred direction within their crfs with the background stationary. In the right histogram the same MT neurons were stimulated continuously with random dots moving in the preferred direction within their crfs and then tested for a 2 s period in which the random dots in the surround also moved in the same direction. Each bin represents 40 ms. The data were based on five stimulus presentations of both conditions to each cell. All of the cells tested with a 2 s period of center and surround stimulation were included in this analysis. The histograms were constructed by normalizing the largest 40 ms bin in the histograms for each cell and then combining the histograms. We were limited in precision for measuring the latency of responses by the cycle time of the video stimulator since the actual beginning of the random dot movement could occur at any time within the 33 ms cycle rather than at the beginning of the cycle as registered by the computer; thus the average latency from the beginning of movement was probably about one half cycle (16.5 ms) shorter than the times illustrated. This delay applies to both the left and right histograms and does not affect the relative delay of the surround response of 40 ms.

Type IV consisted of five cells that showed no effect from surround stimulation; three of these were recorded in their respective penetrations immediately adjacent to type I cells sharing the same crfs and the same directional preferences within their crfs. It is possible that at a higher stage of neural processing the outputs of the type I and type IV cells are compared. Such a comparison would enable the system to determine whether a particular stimulus movement was an isolated occurrence or part of a larger pattern of stimuli moving in one direction (see section 4.4).

3.2 *The latency of the surround response*

The histogram in the top half of figure 9 illustrates the combined responses of forty-two MT neurons (types I, II, and III) to random dots moving in the preferred direction within their crfs with the background stationary. In the lower histogram in figure 9, the same MT neurons were stimulated continuously with random dots moving in the preferred direction within their crfs and then tested for a 2 s period in which the random dots in the surround also moved in the same direction.

The upper histogram in figure 9 indicates that the responses from the crfs began abruptly in the third bin after the onset of movement and ceased just as abruptly in the third bin after the offset of movement. Each bin represents 40 ms. There was a transient response lasting about 600 ms followed by a response subtained through the remainder of the stimulus presentation in the crf. The lower histogram in figure 9 indicates that the inhibitory responses from the surround began abruptly in the fourth bin after the onset of surround movement and ceased just as abruptly in the fourth bin after the offset of surround movement. Thus the response from beyond the crf required somewhat less than 40 ms additional processing time beyond that required for the crf. The lower histogram also indicates that there was a transient rebound in the response from the crf after the offset of background movement.

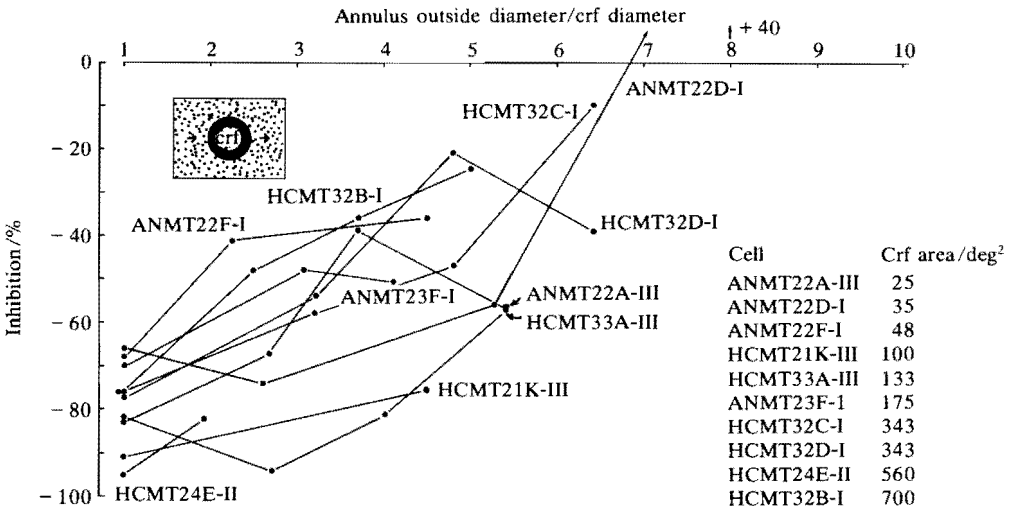

Figure 10. The effects of varying the outside diameter of masking annuli on background inhibition of the response from the crf in ten MT neurons. The stimulus conditions are depicted schematically, but in the experiments the dots were much denser and the surround much larger than are depicted. The dots in the center and background moved in the optimum direction for the crf. The inside diameter of the masking annulus corresponds approximately to the diameter of the crf. The abscissa corresponds to the ratio of the outside diameter of the masking annulus to the diameter of the crf. A value of 1 is equivalent to stimulation without the masking annulus. The cell type is indicated by the roman numeral following the identifying code for each cell. One cell, ANMT22D-I, was facilitated by 40% when a background masking annulus 8 times the diameter of the crf was used. In order to test the larger annuli in some cells we moved the screen to 14.25 cm from the eye.

3.3 *The extent of the surrounds*

We mapped the extent of the surround in eleven cells by systematically masking off parts of the screen with black paper while stimulating both the center and surround with random dots moving in the preferred direction for the center (the direction of maximum inhibition for the surround). In figure 10 the results for ten cells are illustrated in which the crf was surrounded by a masking annulus of variable outside diameter. In only one cell, ANMT22D-I, were we able to create an annulus sufficiently large to eliminate the suppressive effect of movement in the surround, and this was with an annulus 8 times the diameter of the crf. The data suggest that the surrounds are 7 to 10 times the diameter of their crfs. The areas of the crfs of these cells increased with eccentricity and ranged from 25 to 700 deg^2. The smallest surround in this sample would thus be about 1200 deg^2 and some of the others would be enormous (see legend for figure 10). The total hemispherical visual field is approximately 20000 deg^2. Even allowing for considerable tangent error and the possibility that the surrounds were not radially symmetrical about their crfs, it is clear that the surrounds occupied very large portions of the visual field. Finally, in an eleventh cell that is not plotted in figure 10 we found a small but potent suppressive zone less than 4 deg wide flanking the temporal half of a crf 10 deg wide and 5 deg high. This indicates that the surrounds for MT neurons generally, but not always, occupy large portions of the visual field.

3.4 *The influence of background movement on responses to bar stimuli*

In natural conditions stimuli such as bars or edges are often seen against a moving background. We tested bar stimuli moving in twelve different directions on a background of random dots that was stationary or moved in or against the preferred direction for the crf.

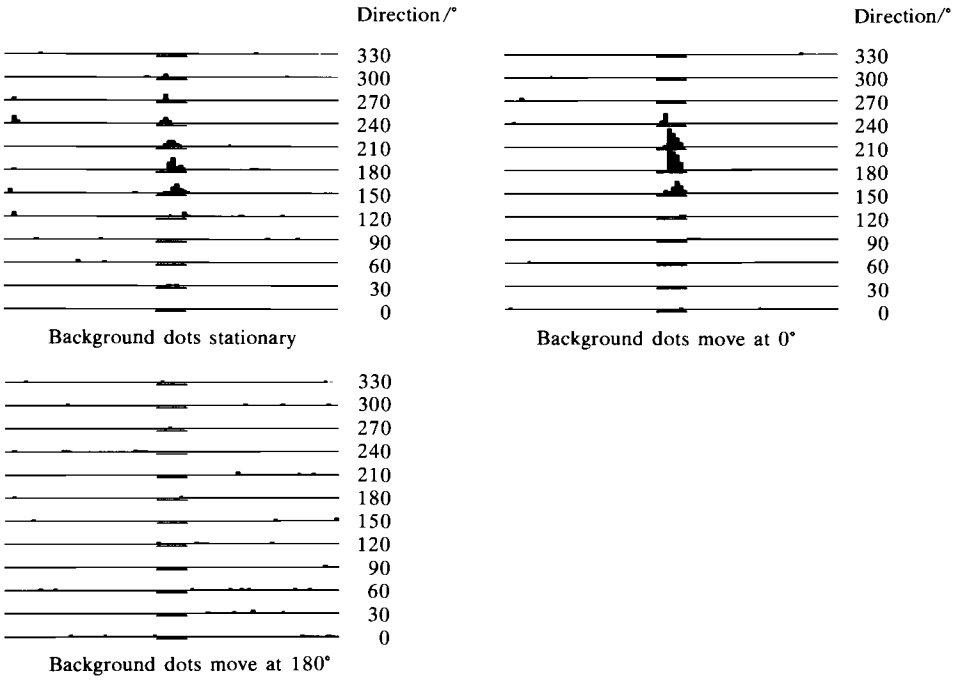

Figure 11. Responses of neuron ANMT17A to a bar moving in different directions superimposed on a background of random dots. The bar was oriented orthogonally to the direction of movement. The results of each of the twelve directions (0° through 330°) are shown in histograms consisting of a fore period, an underscored stimulus presentation period, and an after period. The stimuli were presented in pseudorandom order with each stimulus presented five times. The largest histogram bin contains twenty-six spikes.

This set of stimulus conditions differed from those in sections 3.1 through 3.3 in that both the crf and the surround were stimulated by a continuous sheet of random dots moving in the same direction. In figure 11 the top set of histograms illustrates the response of a MT cell to different directions of bar movement against a stationary random-dot background. The preferred direction of bar movement was 180°. In the middle set of histograms, the background dots were moved against the preferred direction (0°); the response to bar stimuli moving at 180° was enhanced by 110%. The lower set of histograms illustrates that the responses to bar stimuli were abolished by background movement in the preferred direction (180°).

Figure 12 is a two-dimensional plot of the responses of forty-eight MT neurons that were stimulated with a bar moving in the preferred direction superimposed on a random-dot background that was moving either in or opposite to the preferred direction. All but one of the cells were inhibited by the background moving in the preferred direction. 56% were inhibited by the background moving against the preferred direction; the remaining 44% were facilitated. The data in figures 11 and 12 indicate that background movement has a profound influence on the responses of MT neurons to moving bar stimuli. Figure 11 also shows that background movement in the opposite direction can influence the *sharpness of tuning* of the responses to bar stimuli moving in different directions since the responses to the non-optimal directions of 120°, 270°, and 300° that were present when the background was stationary were virtually abolished when the background dots moved at 0°. By applying a tuning index developed in an earlier paper (Baker et al 1981) it was found that this effect was characteristic of MT neurons. Baker et al (1981) found an average tuning index of 0.567 with a standard deviation of 0.246 for one hundred and twenty-nine owl monkey MT neurons. Maunsell and Van Essen (1983a) found an average tuning index of 0.557 with a standard deviation of 0.329 for one hundred and

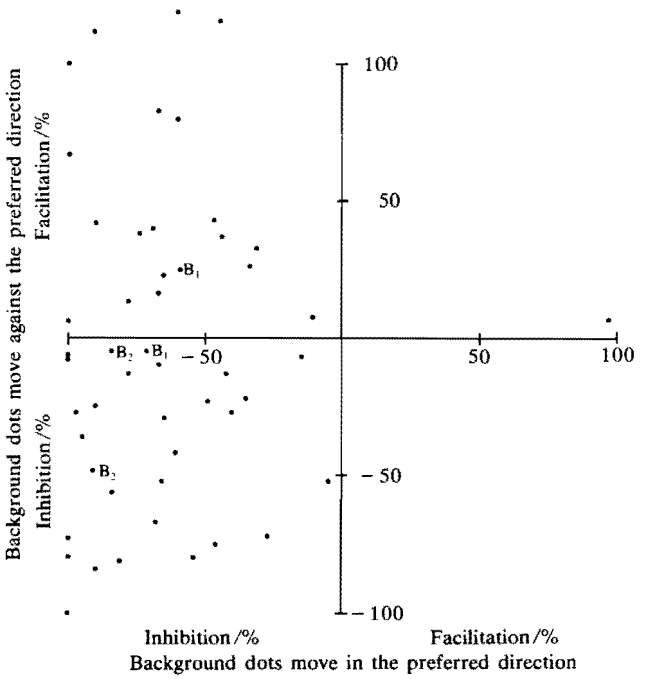

Figure 12. The effect of background movement in and opposite to the preferred direction on the responses of forty-eight MT neurons to a bar moving in the preferred direction. Two cells (B_1 and B_2) were bidirectional and had two preferred directions of motion that were opposite (180°) to one another. Two points were plotted for each of these cells since they were tested with both of their preferred directions of bar movement.

sixty-three macaque monkey MT neurons. Both of these studies were done with conventional bar stimuli moving in different directions against a featureless background. We tested the influence of the background in forty-six MT cells. With a stationary random-dot background, the average tuning index was reduced to 0.44 with a standard deviation of 0.14. With the background moving opposite to the preferred direction for the center (180°), the tuning index was 0.51 with a standard deviation of 0.14. The average tuning index was statistically significantly higher with the background moving opposite to the preferred direction than when the background was stationary ($p < 0.005$), but it was still significantly lower than when the stimuli were presented on a featureless screen ($p < 0.05$). Thus the presence of a stationary random-dot background reduces the sharpness of tuning for direction of bar movement in MT neurons, but this reduction is much less if the background is moving against the preferred direction.

3.5 *Effects of the velocity of background motion*

We also tested the effects of varying the velocity of background motion on the response to a bar moving in the preferred direction. In figure 13 the left graph illustrates the velocity tuning curve for a neuron tested with a bar stimulus of optimum length, width, and contrast moving in the cell's preferred direction against a background of stationary random dots. The cell's preferred velocity was 16 deg s^{-1}. In the right graph in figure 13, we presented the bar at 16 deg s^{-1} and tested the effects of varying the velocity of the random-dot background, which was moving in the same direction. The result was profound inhibition produced by background stimulation at the preferred velocity of 16 deg s^{-1}. Five of the eighteen MT cells tested exhibited this V-shaped pattern with the maximum inhibition resulting when the background dots moved at the preferred velocity for the bar stimulus. However, as is illustrated in figure 14, for the population of eighteen MT neurons, inhibition tended to increase with increasing background velocity. Interestingly, the V-shaped pattern with maximum inhibition at the preferred velocity was found in the majority (20/39) of cells tested in the second visual area (V-II) in the owl monkey (Allman et al 1985b).

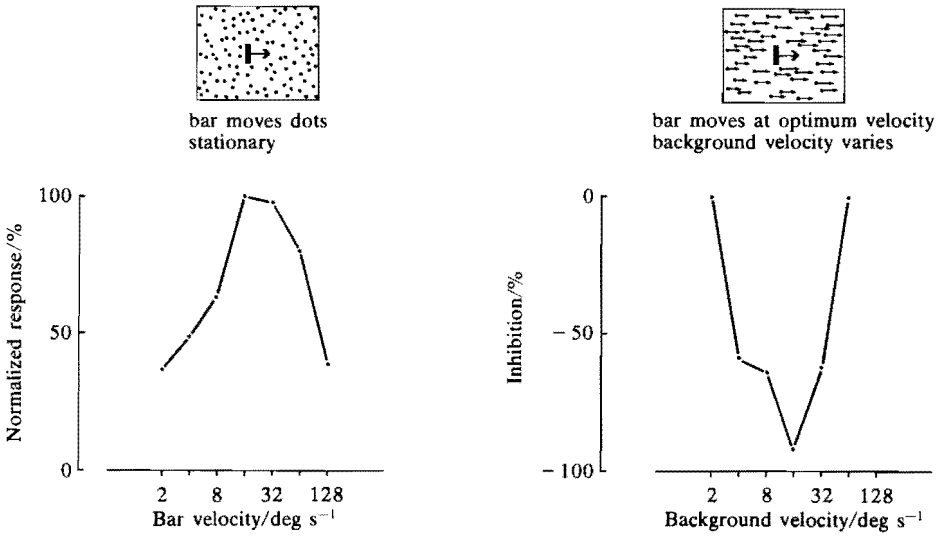

Figure 13. The effect of bar and background velocity on neuron HCMT33C. The left graph is a velocity tuning curve for a bar moving in the optimum direction with the background stationary. The right graph is a velocity tuning curve for background movement in the same direction while simultaneously presenting the bar moving at the optimum velocity (16 deg s^{-1}). The stimulus conditions are depicted schematically above the graphs, but in the experiment the dots were much denser and the surround larger.

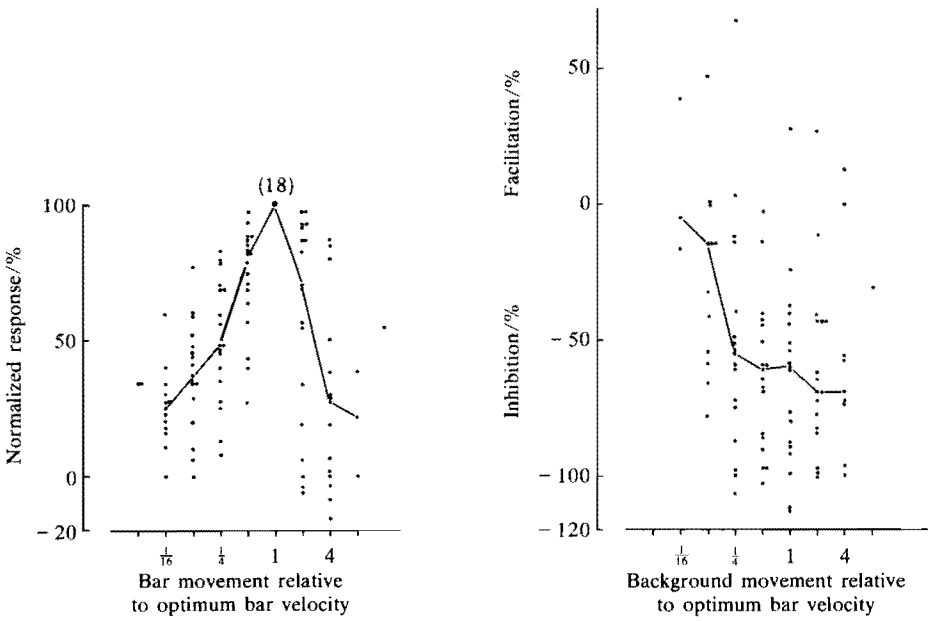

Figure 14. Center and surround velocity responses for eighteen MT neurons. The preferred velocities for these cells ranged from 8 to 32 deg s^{-1} with an average of 25.3 deg s^{-1}. In both graphs a line connects the median response for each velocity. In both the left and right graphs spontaneous activity was sampled during a period prior to the presentation of each stimulus. In the data collection for each cell in the right graph, the bar moving at the preferred velocity against the stationary background was presented interleaved among the other stimulus conditions in which the background moved at different velocities. In the right graph the response to the control condition of the bar moving at the preferred velocity against a stationary background was set equal to zero. Thus it is possible to calculate the response and the spontaneous activity separately, and in the right graph values below − 100% indicate that the response to the bar was entirely suppressed and in addition there was some inhibition below the spontaneous firing rate. In the background velocity experiments, the background dots stimulated both the crf and the surround; however, in these experiments covering the surround usually eliminated or greatly reduced the inhibitory effect of background movement.

4 Discussion

4.1 *Stimulus selectivity beyond the classical receptive field*

The first evidence for directional selectivity for responses to stimuli presented beyond the crf was discovered by Sterling and Wickelgren (1969) in the optic tectum of the cat. This cell was stimulated with a bar moving in the preferred direction within the crf and a second bar just outside the crf. When the bar outside the crf moved in the preferred direction for the center, the cell was more suppressed than when it moved in the opposite direction. In the intermediate and deep layers of the optic tectum of the pigeon Frost et al (1981) stimulated the crf with a moving spot and tested the effect of presenting different directions of movement of random-dot patterns in the surround. They found that the surrounds were directionally selective and were more than 100 deg in diameter. Many of the cells were facilitated by background movement opposite to the direction of spot movement in the center. The responses from the crf *with the background stationary* were very broadly tuned for direction, and Frost and Nakayama (1983) found that the surround effect depended on the direction of movement of the center stimulus such that the direction of greatest suppression by surround movement was the same as that of the movement of the center stimulus.

Neurons in lateral suprasylvian visual cortex in the cat are directionally selective (Hubel and Wiesel 1969; Spear and Baumann 1975), and recently von Grunau and Frost

(1983) have tested surround mechanisms for neurons in this region with the same methods as those used in the pigeon work described above. In nine of eleven cells tested quantitatively they found directionally selective surrounds with the preferred direction for the center being the direction of greatest suppression by the surround and the opposite direction being either less inhibitory or facilitatory. These cells would thus resemble our type I. They concluded that the surrounds were large, although data for only one cell were reported. Portions of lateral suprasylvian visual cortex in the cat have sometimes been considered homologous with MT in primates (see discussion in Baker et al 1981). Very recently Tanaka et al (1984) have recorded from MT in macaque monkeys. The response to a moving bar was suppressed by background movement in the same direction in one half of their MT neurons; one quarter were facilitated by background movement in the opposite direction. In these neurons the effective zone extended well beyond the crf.

We believe that the tuned antagonistic surround effects should be considered distinct from apparently nonspecific facilitatory and inhibitory effects such as those described by McIlwain (1964) and others for cells in the retina and lateral geniculate nucleus. However, these subcortical effects may contribute to the nonspecific effects seen at higher levels. There also is evidence that some of the surround effects observed in the lateral geniculate nucleus may be due to descending inputs from the visual cortex (Marrocco et al 1982). Most of the known response properties described in the studies carried out within the crf of neurons at various levels in the visual system (selectivity for stimulus direction and velocity of movement, orientation, spatial frequency and phase, and color) are matched by antagonistic tuned mechanisms in the surrounding parts of the visual field from which no direct response can be obtained, but which nonetheless exert a strong influence on the responses obtained from stimuli presented within the crf (see Allman et al 1984a for review). One significant parameter—relative depth between the center and surround—has yet to be investigated, but we predict the existence of neurons with antagonistic surround mechanisms tuned for depth. It would be interesting in view of the multiple mechanisms capable of producing depth perceptions (binocular disparity, motion parallax, motion occlusion, perspective, etc) to determine how these different cues for depth might interact in the surround to influence the response from the crf. Opponent processes have a long history in vision research dating back into the nineteenth century with Hering's theory of color vision (see Hering 1879/1942) and to Kuffler's (1953) discovery of antagonistic center-surround organization in retinal ganglion cells, which of course differs from the work under discussion here in that responses can be obtained by stimulation of either the center or the surround and thus both lie within the crf.

Another intriguing issue is the degree to which antagonistic surround mechanisms are 'relativistic' as in the case of the deep optic tectum neurons recorded by Frost and Nakayama (1983) where the directional selectivity of the surround depended on the direction of movement of the stimulus within the crf. We found two cells in MT and three in V-II that were bidirectional with the two preferred directions 180° opposite to one another. These cells possessed directionally tuned antagonistic surrounds that depended on the direction of center movement. This question also arises in the velocity domain, and we are currently investigating whether the velocity of greatest suppression by surround stimulation depends upon the velocity used to stimulate the center. Another 'relativistic' question emerges from the observation that the direction and velocity of the background influences the apparent direction and velocity of the center stimulus. For example, if the center stimulus is moving horizontally and the background is moving vertically upward, the apparent direction of the center stimulus rotates downward by 30° to 40°. We have demonstrated that the movement of the background opposite to the preferred direction significantly sharpens the tuning of the center stimulus relative to the

stationary background condition; however, it would be interesting to determine whether direction or velocity preferences for center stimuli ever shift in a manner similar to the perceived changes that occur when background stimuli are altered.

4.2 *Anatomical connections subserving cortical surround mechanisms*

In the first visual area (V-I) in monkeys, horizontal intrinsic fibers in the stria of Gennari extend 3 mm or more from the margins of lesion or injection sites (Fisken et al 1975; Rockland and Lund 1983), which is beyond the 2 mm maximum distance that would be expected for connecting a cell with adjacent cells that would share portions of its crf (Hubel and Wiesel 1974). It is particularly interesting that the horizontal connections are most extensive for V-I in the stria of Gennari since this layer receives an input from the magnocellular laminae of the lateral geniculate nucleus via neurons in layer 4C-alpha (Hubel and Wiesel 1972; Lund et al 1975), contains a high proportion of directionally selective neurons (Dow 1974; Livingstone and Hubel 1984), and projects to MT (Lund et al 1975; Spatz 1977; Tigges et al 1981; Maunsell and Van Essen 1983b). Montero (1980) found by using two separate tracers that the input from V-I to MT terminates in a series of bands within partially overlapping projections from adjacent sites in V-I. These partially overlapping projections may contribute, possibly via interneurons, to the large surrounds in MT. Maunsell and Van Essen (1983b) injected tritiated proline in MT and found intrinsic horizontal connections extending about 3 mm from the margin of the injection site, which because of the relatively small size of MT would cover much of the representation of the visual hemifield, and thus could also contribute to the large surrounds. Although the transcallosal connections of MT are much heavier near the representation of the vertical meridian, they extend throughout most of the area (Newsome and Allman 1980), and thus may contribute to the portion of the surround extending into the opposite half of the visual field as do the transcallosal connections of V4 complex (Moran et al 1983).

The visual system contains many descending pathways (Tigges et al 1981; Maunsell and Van Essen 1983b) which could contribute to surround mechanisms in the recipient structure. The crfs in the higher area typically are larger than those at a comparable eccentricity in the lower area, and thus the crfs in the higher area might match the dimensions of the true receptive field including the surround in the lower area (F Crick, personal communication). Marrocco et al (1982) have demonstrated that interruption of the striate-geniculate pathway by cooling striate cortex eliminates surround responses from regions beyond the crf in many lateral geniculate neurons. Small injection sites in the superior temporal visual area (ST) project to the entire extent of the ipsilateral MT in the owl monkey (Weller and Kaas 1983) and may be another source of the large surrounds present for neurons in MT. Finally another potential source is input from subcortical structures such as the pulvinar.

4.3 *Stimulus selectivity beyond the crf and figure–ground discrimination*

Stimulus-specific responses from beyond the crf seem ideally suited for discriminating figure from ground and preattentive vision (Treisman and Gelade 1980; Julesz 1981). Julesz's elementary units of figure–ground discrimination, the 'textons', are based on differences in motion, color, orientation, etc that are strikingly similar to the tuned antagonistic interactions between the crf and the background in visual cortical and tectal neurons. This preattentive system is capable of guiding focal attention with a latency of about 50 ms (Julesz 1984), which is slightly longer than the time required for the response from the regions beyond the crf to influence the response within the crf in MT neurons (see figure 9).

4.4 *Stimulus selectivity beyond the crf and perceptual constancies*

The function of the visual system is to extract behaviorally significant features embedded in a complex optical array over a very broad range of environmental conditions. Its first task is to discriminate discontinuities in the optic array. Local antagonistic center-surround mechanisms clearly have this role. A second and more difficult task is to make good estimates of the qualities of objects in the visual field, their color and motion for example, on the basis of rather imperfect optical information imaged on the photoreceptor layer of the retina. Thus the wavelength composition of the retinal image will depend on environmental lighting conditions which may vary enormously, yet the behaviorally significant task may involve judging the ripeness of fruit based on its color. Retinal image motion can be produced by movement of the eye, movement of the animal, or movement of the environment, yet the system's task is to determine the motion of objects relative to other objects and the observer. In both cases more than just information restricted to a small locality on the retinal surface is required to make veridical judgements. Land's (1959a, 1959b, 1983) experiments indicate that the system compares the wavelength composition of the light reflected by an object with that of other objects in the surrounding visual field and is able to extract color constancy over a broad range of lighting conditions. The determination of the motion of objects in the environment similarly requires the integration of motion information over a large portion of the visual field, and to determine object motion relative to the observer requires further input concerning eye and head position. These position inputs are usually thought to be derived from motor commands to the eye muscles (Helmholtz 1909/1962), from the vestibular system, and perhaps from proprioceptors in the eye muscles; however another parallel source of position information could be derived from the visual image itself (Gibson 1966; Koenderink 1984) and possibly implemented through comparisons between the crf and its surround.

4.5 *Background motion and depth perception*

Helmholtz (1909/1962) observed:

> "Suppose, for instance, that a person is standing still in a thick woods, where it is impossible for him to distinguish, except vaguely and roughly, in the mass of foliage and branches all around him what belongs to one tree and what to another, or how far apart the separate trees are, etc. But the moment he begins to move forward, everything disentangles itself, and immediately he gets an apperception of the material contents of the woods and their relations to each other in space, just as if he were looking at a good stereoscopic view of it."

Nakayama and Loomis (1974) have suggested a division of labor between *stereopsis* and *kineopsis*:

> "Retinal disparity, based on a relatively small interpupillary distance, probably controls behavior which is directed at the near environment; whereas optical velocity information (kineopsis), based on much greater displacements of a single eye, controls more distantly directed behavior."

Helmholtz (1909/1962) concluded:

> "the apparent angular velocities of objects in the field of view will be inversely proportional to their real distances away; and, consequently, safe conclusions can be drawn as to the real distance of the body from its apparent angular velocity".

Nakayama and Loomis (1974) postulated a simple neural mechanism which could serve as the basis for the analysis of optical flow patterns that occur as a viewer moves through its environment with the images of objects located at different distances from the viewer moving at different velocities across the retina. They hypothesized the existence of a class of neurons possessing a velocity-selective center with an antagonistic velocity-selective surround. Such neurons would be suppressed by an optical flow field of uniform velocity

but would detect differential velocities such as would result from sweeping past objects at different distances from the viewer. We have provided the first experimental confirmation of this hypothesis in the discovery of neurons sensitive to the velocity of background movement. It is easy to imagine how an antagonistic velocity-sensitive center–surround mechanism, as first hypothesized by Nakayama and Loomis (1974) and found for some neurons in our study, could subserve the spatial, velocity-discriminating function required for depth perception through motion parallax or optical flow patterns. However, the characteristic symmetrical V-shaped background velocity tuning curves obtained for the majority of V-II and some MT neurons do not discriminate between the condition in which the background movement is faster than the preferred velocity and the condition in which the background movement is slower than the preferred velocity. Thus they could register relative magnitude of the depth difference but not whether the center was nearer or farther than the background. The MT cells in which inhibition simply increases with background velocity might help to resolve this ambiguity.

The velocity–distance relationship postulated by Helmholtz (1909/1962) obtains only when the observer fixates at very distant objects. If the observer fixates on an object at a given depth while he is in motion, objects beyond the fixation plane will move in the same direction as the observer while objects nearer than the fixation plane will move in the opposite direction (Gordon 1965). This cue is utilized in depth perception through motion parallax (Rogers and Graham 1979) and may be analyzed by MT type I neurons, which would be facilitated by stimuli moving in opposite directions nearer and beyond the fixation plane. There exists additional motion-related depth information in the visual scene described so graphically by Helmholtz (1909/1962). As Gibson (1979) has emphasized, the disappearance or emergence of background from behind an occluding surface is a strong cue for depth. The depth percept elicited by kinetic occlusion is very powerful and can override conflicting stereoscopic cues (Royden et al 1984). The antagonistic direction-selective center–surround mechanism may serve the computations for depth perception through kinetic occlusion by helping to identify which surfaces in an array are in motion with respect to other surfaces.

4.6 *Other surround effects*

Recently, von der Heydt et al (1984) have discovered that some neurons in V-II in awake macaque monkeys respond to illusory contours where the real contours evoking the response are located entirely outside the crf. V-I neurons were unresponsive under the same stimulus conditions. This result indicates that under some conditions stimulation of regions beyond the crf is sufficient by itself to evoke an excitatory response. The perception of illusory contours might be considered as a type of constancy function since the visual system is interpolating a continuous contour from an interrupted contour, which under natural conditions would be produced by a partially occluding surface. The tropical forest environment, where primates evolved, abounds with occluding foliage and branches, and the ability to reconstruct surfaces that are partially hidden from view would be very adaptive. Integrative mechanisms extending beyond the crf may underlie a number of possibly related phenomena such as the influence of unambiguous movement in the surround on the perceived direction of ambiguous movement in the center of a display (Ramachandran and Anstis 1983).

Extensive surrounds beyond the crf are not limited to the visual system. Barn owls, which hunt in darkness using sound localization, possess auditory neurons with sharply defined spatial receptive fields which are organized into an orderly representation of auditory space in the midbrain nucleus MLD (Knudsen and Konishi 1978a). These receptive fields are mapped in the owl's auditory space by moving a sound source in an anechoic chamber. Knudsen and Konishi (1978b) probed the regions beyond these receptive fields by stimulating the MLD neurons with a sound source located in the crf

and measuring the effect of moving a second sound source through the remainder of the auditory field in a manner analogous to our experiments. By using this technique they demonstrated that the second sound source had an inhibitory effect throughout most of auditory space beyond the crf. Thus neurons in the owl's auditory-space-mapped MLD would be capable of making the same sort of local-global comparisons within a representation of space that exist in MT and other visual structures.

5 Conclusions

The function of the visual system is not merely to create a set of precise neural analogs of the optical image on the photoreceptors, but, beyond this, to reconstruct behaviorally significant features of the visual environment on the basis of imperfect and unconstant optical stimuli. Gibson (1950, 1966, 1979), Land (1959a, 1959b, 1983), and Ramachandran and Anstis (1983) have emphasized the influence of the context of the whole visual field on perception at any one locality within the field. The brain contains many maps of the visual field, as revealed by the topographic organization of crfs, but the true receptive fields for many neurons in these maps may be much larger and even extend throughout much of the visual field. The crfs and their surrounds provide mechanisms for local-global comparisons embedded in visuotopic matrices that may serve as the basis for many functions in vision such as the perceptual constancies, figure-ground discrimination, and depth perception through motion. The surrounds explored thus far usually exert selective antagonistic influences on their crfs, but the existence of more complex surround mechanisms is indicated by the type II neurons in MT, the responses to illusory contours in V-II (von der Heydt et al 1984), and the influence of background color patches on the properties of neurons in the V4 complex (Zeki 1983). The successful exploration of complex surround mechanisms calls for collaboration among psychophysicists, mathematical modelers, and neurophysiologists for which there exist some very promising beginnings (Horn 1974; Nakayama and Loomis 1974; Ballard et al 1983; Land 1983; Reichardt et al 1983). The exploration of surround mechanisms will be vital to our understanding of the role that each cortical visual area plays in perceptual processes.

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