STIMULUS SPECIFIC RESPONSES FROM BEYOND THE CLASSICAL RECEPTIVE FIELD:
Neurophysiological Mechanisms for Local–Global Comparisons in Visual Neurons

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INTRODUCTION

We perceive the visual world as a unitary whole, yet one of the guiding principles of nearly a half century of neurophysiological research since the early recordings by Hartline (1938) has been that the visual system consists of neurons that are driven by stimulation within small discrete portions of the total visual field. These classical receptive fields (CRFs) have been mapped with the excitatory responses evoked by a flashed or moving stimulus, usually a spot or bar of light. Most of the visual neurons, in turn, are organized in a series of maps of the visual field, at least 10 of which exist in the visual cortex in primates as well as additional topographic representations in the lateral geniculate body, pulvinar and optic tectum (Allman 1977, Newsome & Allman 1980, Allman & Kaas 1984). It has been widely assumed that perceptual functions that require the integration of inputs over large portions of the visual field must be either collective properties of arrays of neurons representing the visual field, or features of those neurons at the highest processing levels in the visual system, such as the cells 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 the results of the many studies in which receptive fields were mapped with con-

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ventional stimuli, presented one at a time, against a featureless background. However, unlike the neurophysiologist's tangent screen, the natural visual scene is rich in features, and there is a growing body of evidence that in many visual neurons stimuli presented outside the CRF strongly and selectively influence neural responses to stimuli presented within the CRF. These results suggest obvious mechanisms for local–global comparisons within visuotopically organized structures. Such broad and specific surround mechanisms could participate in many functions that require the integration of inputs over wide regions of the visual space such as the perceptual constancies, the segregation of figure from ground, and depth perception through motion parallax. In the first section of this paper, we trace the historical development of the evidence of response selectivity for visual stimuli presented beyond the CRF; in the second, examine the anatomical pathways that subserve these far-reaching surround mechanisms; and in the third, explore the possible relationships between these mechanisms and perception.

STIMULUS SELECTIVITY BEYOND THE CLASSICAL RECEPTIVE FIELD

Retina and Lateral Geniculate Nucleus

Barlow (1953) was the first to probe the apparently silent regions beyond the CRF. While recording from retinal ganglion cells in the frog, he simultaneously turned on a spot of light in the receptive field and a second spot outside the field, and noted that the second spot suppressed the response to stimulation within the receptive field. Kuffler (1953) reported that receptive fields of retinal ganglion cells in the cat were divided into a center and an antagonistic surround. If the cell responded to turning on a spot of light in the center, it responded to turning off a spot in a concentric surrounding region; he also recorded off-centers with on-surrounds. Since stimulation of both the center and the surround gave excitatory responses, both would be parts of the CRF. For the same reason, the CRF would include the "on" and "off" regions for neurons in the lateral geniculate nucleus (Hubel & Wiesel 1961).

McIlwain (1964) activated optic tract axons and lateral geniculate neurons by presenting a flashing spot within their CRFs and found that stimulation with a moving dark spot up to 90° away influenced (usually facilitated) the response. McIlwain termed this phenomenon the "periphery effect" and discovered that it was produced by mechanisms within the retina, since bilateral optic tract section central to the optic tract recording site did not reduce the effect. The effect did not exhibit much selectivity for particular stimuli so long as the movement had sufficient speed and excursion. He also noted that a flashing spot in the classical receptive field was not required for some neurons. Subsequently, Levick et al (1965) and McIlwain (1966) found that the flashing

spot was not necessary in general to observe the increased discharge rate due to movement in the surround. McIlwain (1966) recognized that this observation created a problem as to what to include in the CRF, a quandary that has never been resolved for the periphery effect. Cleland et al (1971) and Ikeda & Wright (1972) found the periphery effect in cat retinal ganglion cells with transient responses and faster axonal conduction velocities but not in cells with sustained responses with slower conduction velocities. Ikeda & Wright (1972) discovered that the periphery effect was suppressed by the presence of stationary contrast within the CRF. It was then determined that the effect could be greatly strengthened in both retinal ganglion cells and lateral geniculate neurons in cats by abruptly shifting a grating that occupied most of the visual field except for the region near the CRF (Kruger & Fischer 1973, Fischer & Kruger 1974). The effect was independent of the direction of displacement of the grating. In the lateral geniculate nucleus in macaque monkeys, Kruger (1977) found the effect in 90% of the neurons in the magnocellular laminae, which respond transiently and with short latencies. The effect was strong and excitatory in magnocellular neurons and was suppressed by steady illumination of the CRF. For neurons in the lateral geniculate parvocellular laminae, which respond in a sustained fashion and at longer latencies, the effect was present in only 30% of the cells and was weak and inhibitory. Also recording from the lateral geniculate nucleus in macaque monkeys, Marrocco et al (1982) demonstrated responses from beyond the CRF for neurons that did not exhibit the periphery effect. By turning on and off a spot in the receptive field and measuring the effect of rotating a radial grating beyond the classical surround, they observed both facilitatory and inhibitory effects that could be abolished by cooling the visuotopically corresponding portions of the striate cortex and thus inactivating the striate-geniculate feedback.

Optic Tectum

Suppressive regions surrounding the CRF for neurons in the optic tectum have been reported in the frog (Grusser-Cornehls et al 1963), the ground squirrel (Michael 1972), the cat (McIlwain & Buser 1968), and the macaque monkey (Wurtz et al 1980). The first evidence for directional selectivity for responses to stimuli presented beyond the CRF was discovered by Sterling & Wickelgren (1969) in the cat optic tectum. They presented a bar moving in the preferred direction in the center and a second bar moving in the surround. When the bar in the surround moved in the same direction as that preferred for the center, the cell was more suppressed than when the bar in the surround moved in the opposite direction. Also recording from the cat optic tectum, Rizzolatti et al (1974) stimulated the CRF and presented a second moving 10° spot at distances as much as 120° away. They found that the suppressive surround was present in 90% of the cells and extended throughout much of the visual

field, although it tended to be stronger in the hemifield ipsilateral to the CRF. Rizzolatti et al also found that the suppressive effect was much stronger if the center and surround stimuli were synchronous. They did not find evidence for a directionally selective influence from the surround and suggested that they were studying a second, broader surround mechanism rather than that described by Sterling & Wickelgren (1969). It is also possible that a single spot stimulus presented in a remote part of the visual field was inadequate to demonstrate selectivity in the distant surround and that a moving pattern subtending a larger area would have been more effective. In the intermediate and deep layers of the optic tectum in pigeons, 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° 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 *random dot background stationary* were very broadly tuned for direction. Frost & Nakayama (1983) found that the surround effect in the pigeon depended on the direction of movement of the center stimulus, such that the direction of greatest suppression by surround movement was the same direction as the movement of the center stimulus.

Visual Cortex

Hubel & Wiesel (1962) described a class of neurons in the first visual area (V–I) in the cat, the simple cells, that like the Kufflerian cells possessed "on" and "off" subregions within their CRFs. Recording from the second (V–II) and third (V–III) visual areas in the cat, Hubel & Wiesel (1965) found a class of neurons, the lower order hypercomplex cells, in which they were able to map out antagonistic regions flanking the CRF. They were unable to obtain a response when they stimulated these regions alone, but when they simultaneously presented a slit stimulus in the CRF and another slit of the same orientation in the antagonistic flank, the response from the first slit was suppressed. Hubel & Wiesel (1965) concluded, "A cell responds when an appropriately oriented line (slit, bar, or edge) is shone or moved anywhere within the activating area, and the response is prevented with similar and simultaneous stimulation of the antagonistic region." They were thus the first to suggest that stimulation of regions beyond the CRF had more than merely a suppressive influence, that it could have a *selective* antagonistic effect. They estimated that the antagonistic flanks extended 2–3° beyond the CRF.

Recording in V–I in the cat, Jones (1970) presented an edge moving in the CRF and measured the effect of moving a second edge at different distances. In 65% of his cells, the second edge exerted an influence from locations beyond the CRF. He observed both inhibitory and facilitatory surround effects, which

in some cases extended 20° from the receptive field although most extended less than 8°. Jones also noted that the more peripheral the location of the CRF, the greater the distance over which a second edge could exert an inhibitory influence. Blakemore & Tobin (1972) described a complex cell with an orientation-selective CRF and an antagonistic orientation-selective surround. They found that the response produced by an optimally oriented bar was abolished by presenting a grating of the same orientation in the surround and was slightly facilitated by an orthogonal grating in the surround.

Bishop et al (1973) studied simple cells in V–I in cats by continuously stimulating the CRF and measuring the effect of test stimuli presented at different locations. Through these techniques they were able to map out powerful but nonorientation selective inhibitory regions that extended 2 to 6° beyond the CRF. Recording intracellularly, Creutzfeldt et al (1974) mapped inhibitory areas 3–4° in diameter that overlapped excitatory areas that were about 2° in diameter. They found that the inhibitory influences were directional and to some extent orientation-selective. Maffei & Fiorentini (1976) found facilitatory and inhibitory regions in the surrounds of both simple and complex cells. They found that the facilitatory surround regions were orientation-selective, but reported that the inhibitory regions were not very selective for orientation. Maffei & Fiorentini also found that the facilitatory and inhibitory surround regions were tuned for the spatial frequency of sine-wave gratings. The inhibition was strongest for the spatial frequency for which the CRF was maximally sensitive. They estimated that the facilitatory and inhibitory surround regions together were three times the size of the CRFs. Fries et al (1977) and Nelson & Frost (1978) found that simple and hypercomplex cells have antagonistic orientation-selective surrounds beyond their CRFs and that these surrounds are also sometimes directionally selective as well. Hammond & McKay (1981) tested the influence of moving random dot patterns on the responses of simple cells stimulated with optimally oriented moving bars. They found antagonistic direction-selective regions that extended beyond the CRFs for the simple cells and were comparable in size to the CRFs of nearby complex cells.

Using a two-stimulus paradigm in V–I in cats that was similar to their experiments in the optic tectum, Rizzolatti & Camarda (1977) found only very weak effects resulting from surround stimulation more than 30° from the CRF. However, in lateral suprasylvian visual cortex, their findings were similar to their previous results in the optic tectum, namely broad inhibitory surrounds that were stronger in the hemifield ipsilateral to the CRF and were not directionally selective. Most neurons in lateral suprasylvian visual cortex are directionally selective (Hubel & Wiesel 1969, Spear & Baumann 1975). Recently, von Grunau & Frost (1983) have tested surround mechanisms in this region with the same methods used in the pigeon optic tectum experiments. In 9 of

11 cells tested quantitatively, they found directionally selective surrounds; the preferred direction for the center was the direction of greatest suppression by the surround, and the opposite direction was either less inhibitory or facilitatory. It is probable in this case, as in the optic tectum, that a moving array of dots subtending a large portion of the visual field is a more effective test for directional selectivity in the surround than a single spot. The moving array of random dots also more closely approximates natural viewing conditions in which the visual image is commonly a texture-filled scene.

In primates, the middle temporal visual area contains a high concentration of directionally selective neurons (Baker et al 1981, Maunsell & Van Essen 1983a). We have investigated surround mechanisms in the middle temporal area in the owl monkey (Miezin et al 1982, Allman et al 1984a). Middle temporal neurons are very responsive to moving random dot patterns. We stimulated the CRF with random dots moving in the preferred direction and at the preferred velocity and tested the effect of different directions of random dot movement in the surround. Forty-four percent of our middle temporal cells had antagonistic directionally selective surrounds and half of these cells were facilitated by background movement in the direction opposite to that preferred by the center (see Figure 1). An additional 8% were maximally suppressed by background movement in the preferred direction for the center but were powerfully and specifically facilitated by a shearing background movement in one direction 90° to the preferred direction for the center. This specific facilitation indicates that center–surround relations are not limited to simple antagonistic interactions. Another 30% of our middle temporal cells were suppressed by all directions of movement. Finally, 8% showed no effect from surround stimulation; these cells were often recorded immediately adjacent to cells with directionally selective surrounds and shared with these adjacent cells the same CRFs and the same directional preferences. It is possible that at a higher stage of neural processing the outputs of these two types of 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.

The histogram in the top half of Figure 2 illustrates the combined normalized response of 42 middle temporal neurons of all three types to random dots moving in the preferred direction within their CRFs with the background stationary. The responses from the CRFs began abruptly in the third bin following the onset of movement and ceased abruptly in the third bin following the offset of movement. Each bin represents 40 msec. There was a transient response lasting about 600 msec, followed by a response sustained throughout the remainder of the stimulus presentation in the CRF. The lower histogram in Figure 2 indicates that the inhibitory responses from the region beyond the CRF began abruptly in the fourth bin following the onset of background
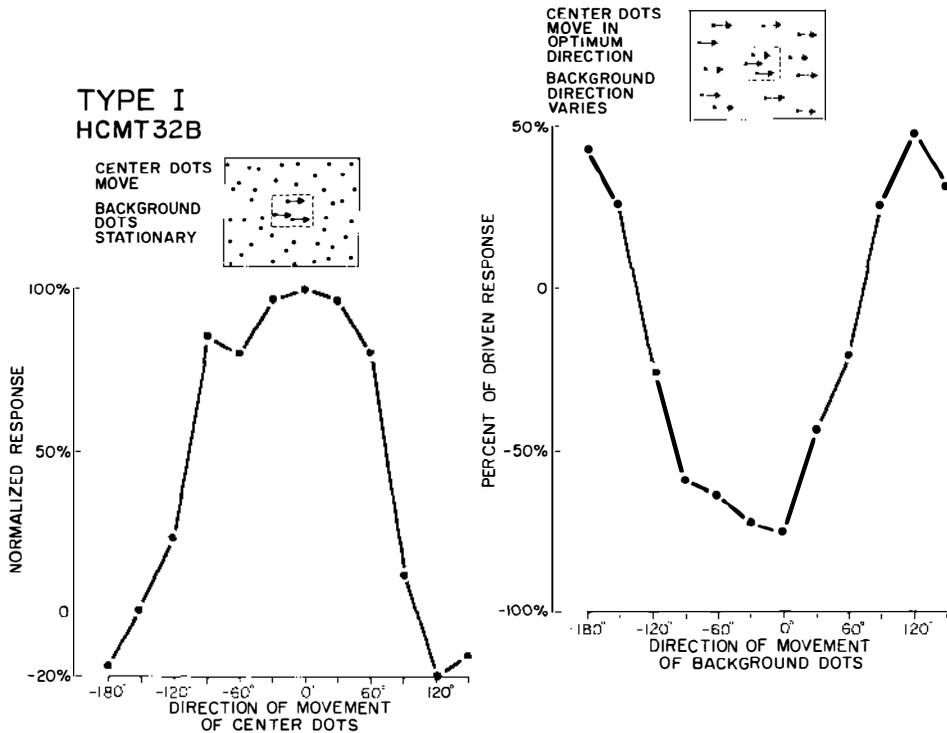
Figure 1 Direction-selective neuron with an antagonistic direction-selective surround recorded from middle temporal area in the owl monkey. The *left graph* depicts the response of the cell to 12 directions of movement of an array of random dots within an area coextensive with its CRF. The response is normalized so that 0% is equal to the average level of spontaneous activity sampled for 2-sec periods before each presentation. Negative percentages in the left graph indicate inhibition relative to the level of spontaneous activity. In the left graph, the response to the optimum direction is 100%. The *right graph* depicts the response of the cell to different directions of background movement while the CRF was simultaneously stimulated with an array of dots 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-sec sample periods preceding background movement, and thus a response of 100% in the left graph is equivalent to 0% in the right graph. The stimulus conditions are depicted schematically above each graph. In the experiment, the dots were 50% dark–50% light and the background was much larger relative to the center than is depicted schematically.

movement and ceased abruptly in the fourth bin following the offset of background movement. Thus the response from beyond the CRF required somewhat less than 40 msec 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 following the offset of background movement.
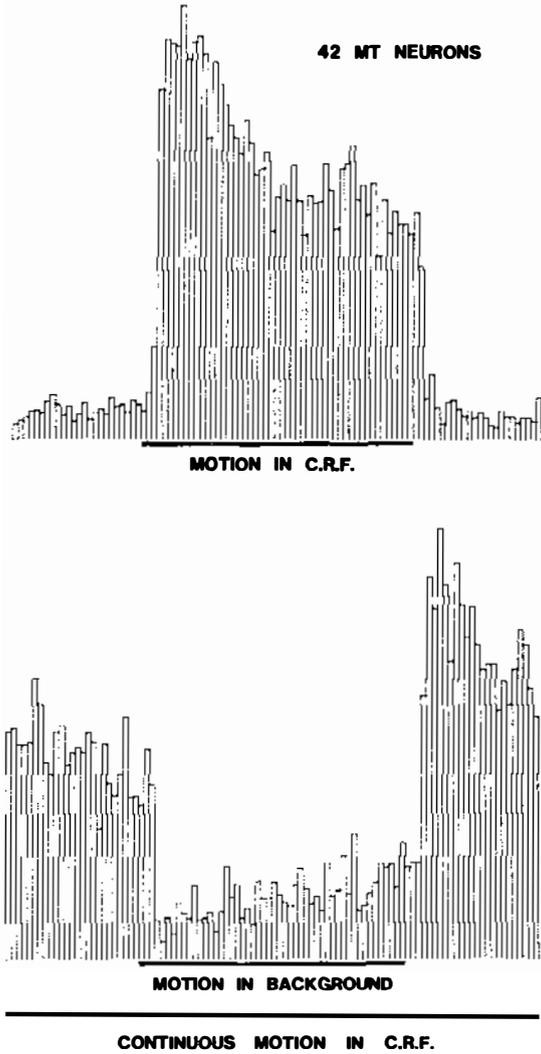
42 MT NEURONS

MOTION IN C.R.F.

MOTION IN BACKGROUND

CONTINUOUS MOTION IN C.R.F.

Figure 2   The *top histogram* illustrates the combined responses of 42 middle temporal neurons to random dots moving for a 2-sec period in the preferred direction within their CRFs, with the background stationary. In the *lower histogram*, the same middle temporal neurons were stimulated continuously with random dots moving in the preferred direction within their CRFs and then tested for a 2-sec period in which the random dots in the surrounding regions also moved in the same direction. Each bin represents 40 msec. The histograms were constructed by normalizing with the largest 40 msec bin in the histogram for each cell and then combining the histograms.

Background movement also has a profound influence on responses of middle temporal neurons to moving bar stimuli. Figure 3 illustrates that background movement in the preferred direction (180°) can totally abolish the response to bar stimuli, whereas background movement in the anti-preferred direction (0°) can powerfully facilitate such responses. Background movement in the preferred direction inhibited nearly all middle temporal neurons; background movement in the anti-preferred direction facilitated 44% of middle temporal neurons. Figure 3 also shows that the background movement can influence the *sharpness of tuning* of the responses to bar stimuli moving in different directions, because the responses to the nonoptimal directions of 120°, 270°, and 300° that were present when the background was stationary were virtually abolished when the background dots moved at 0°.

In the foregoing experiments, the random dots in the surround moved at the same speed as in the center. We discovered that the velocity of the random dots moving in the preferred direction in the background also influenced the response to bar stimuli. In Figure 4 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° per second. In the right graph in Figure 4, the bar moved at 16° per second and the velocity of the random dot background was varied. The result was profound inhibition produced by background stimulation at the preferred velocity of 16° per second. About one-third of middle temporal cells exhibited this V-shaped pattern; the maximum inhibition resulted when the background dots moved at the preferred velocity for the bar stimulus; in the remaining middle temporal cells the inhibition tended to decrease with background velocity. The V-shaped velocity for the CRF is characteristic of the majority of V–II neurons in the owl monkey (Allman et al 1984b).

We mapped the extent of the surround in ten middle temporal cells by masking off parts of the screen while stimulating both the center and surround with random dots moving in the preferred direction at the preferred velocity. Figure 5 illustrates the results. The CRF was surrounded by a masking annulus of variable outside diameter. In only one cell in this series, ANMT22D–I, were we able to create an annulus sufficiently large to eliminate the suppressive effect of background movement, and this was with an annulus eight times the diameter of the CRF. The data suggest that the surrounds are seven to ten times the diameter of the CRFs of middle temporal neurons. The areas of the CRFs for these cells increased with eccentricity and ranged from 25 to 700 deg^2. The smallest surround in this sample of middle temporal neurons would thus be about 1200 deg^2 and the others would range upward, with the largest including virtually the whole visual field.
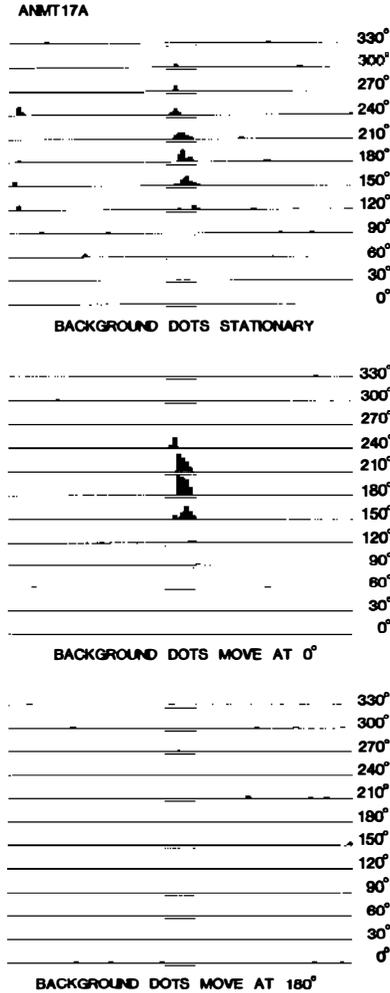
Figure 3   The responses of a middle temporal neuron to a bar moving in different directions superimposed on a background of random dots. The bar was oriented orthogonally to the direction of movement. The results of each of the 12 directions (0° through 330°) are shown in histograms consisting of a fore period, an underscored stimulus presentation period, and an after period. The largest histogram bin contains 26 spikes.

Very recently Tanaka et al (1984) recorded from the middle temporal area in macaque monkeys. The response to a moving bar was suppressed by background movement in the same direction in one half of their middle temporal neurons; one-quarter were facilitated by background movement in the opposite direction. In these neurons the effective zone extended well beyond the CRF.
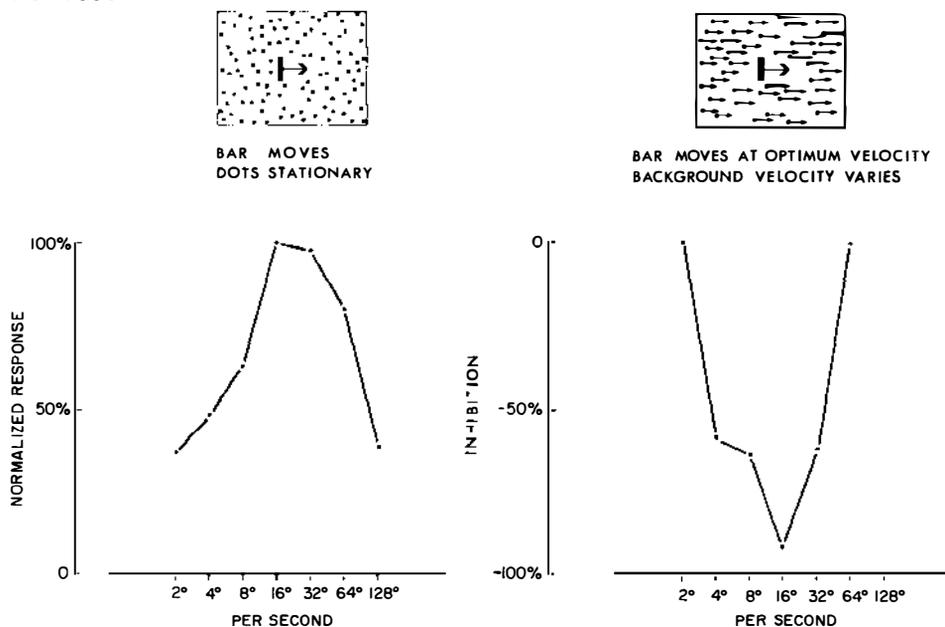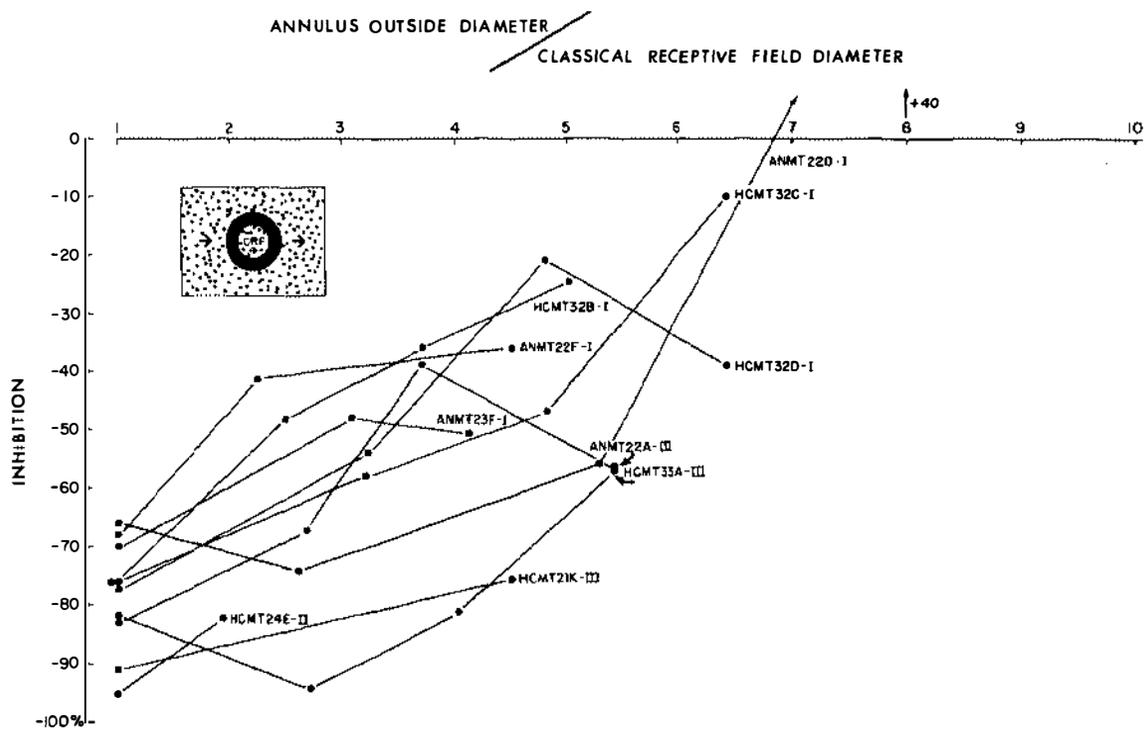
HCMT33C

Figure 4   The effect of center and background velocity on a neuron recorded from the middle
temporal area in the owl monkey. The *left graph* is a velocity-tuning curve for a bar moving in
the preferred direction with the background stationary. The *right graph* is a velocity-tuning curve
for background movement while simultaneously presenting the bar moving at the optimum veloc-
ity (16° per second). In the background velocity experiments, the background dots stimulated
both the CRF and the surround; however, in these experiments covering the surround eliminated
or greatly reduced the inhibitory effect.

There is a strong quantitative similarity in other aspects of the functional
properties of middle temporal neurons recorded from the macaque and the
owl monkeys (Baker et al 1981, Maunsell & Van Essen 1983a, Albright 1984).
It remains to be seen whether the lower incidence of cells influenced by moving
background in the macaque middle temporal area reflects a genuine functional
difference or amthodological difference between the studies conducted in the
two species.

Recent recordings from neurons in the V4 complex in macaque monkeys
have revealed broad surround regions tuned for orientation, spatial frequency,
and color (Desimone et al 1984, R. Desimone and S. J. Schein, personal
communication). Moran et al (1983) found that while the CRFs for V4 cells
located near the vertical meridian extended an average of only 0.6° into the
ipsilateral hemifield, the inhibitory surrounds extended at least 16° into the
ipsilateral hemifield. This suppression by stimulation in the ipsilateral hemi-

field was greatly reduced by section of the corpus callosum. Zeki (1983a,b) reported two types of neurons in macaque V4: wave-length selective and color-coded. The responses of the first type were highly dependent on the wavelength of light illuminating the CRF. The responses of the color-coded cells depended on the natural color of the object in the CRF under normal illumination, but not on the spectral content of the light reflected from the object. Thus, the color-coded cells exhibited color constancy over a certain range of illumination conditions. The response of the color coded cells depended on the color of objects located outside the CRF, which indicated that they possess surround mechanisms with complex and as yet undetermined properties (Zeki 1983b). The influence of the surround on the color of an object was limited to the ipsilateral hemifield in a corpus-callosum sectioned human (Land et al 1983), which restricts the locus of the effect to the cortex, but regions other than the V4 complex, particularly V–II and the ventral posterior area (VP), may be involved as well (Burkhalter & Van Essen 1982).

Finally, von der Heydt et al (1984) discovered that about one third of the neurons in V–II in awake macaque monkeys respond to illusory contours when the real contours evoking the response were located entirely outside the CRF. V–I neurons were unresponsive under the same conditions. The perception of illusory contours might be considered as a type of constancy, 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, in which primates evolved, abounds with occluding foliage and branches, and the ability to reconstruct surfaces that are partially hidden from view would be very adaptive.

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 that are organized into an orderly representation of auditory space in the midbrain nucleus mesence-phalicus lateralis (MLD) (Knudsen & Konishi 1978a). These receptive fields are mapped in the owl's auditory space by moving a sound source in an

Figure 5 The effect of varying the outside diameter of masking annuli of surround inhibition of the response from the CRF in 10 neurons recorded from middle temporal area in the owl monkey. The stimulus conditions are depicted schematically, but in the experiments, the dots were 50% dark–50% light and the surround was much larger. The dots in the center and surround 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 areas of the CRFs were: ANMT22A–III = 25 deg^2; ANMT22D–I = 35 deg^2; ANMT22F–I = 48 deg^2; HCMT21K–III = 100 deg^2; HCMT33A–III = 133 deg^2; ANMT23F–I = 175 deg^2; HCMT32C–I = 343 deg^2; HCMT32D–I = 343 deg^2; HCMT24E–II = 560 deg^2; HCMT32B–I = 700 deg^2.

anechoic chamber. Knudsen & 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 exists in the middle temporal area and other visual structures.

Summary of Responses from Beyond the Classical Receptive Field

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 direction and velocity of movement, orientation, spatial frequency, and
wavelength) are matched in some neurons 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. One significant parameter,
relative depth between the center and the surround, has yet to be investigated,
but we predict the existence of neurons with antagonistic surround mechanisms
tuned for depth. The "periphery effect" and the responses to illusory contours
indicate that under some conditions, excitatory responses can be obtained from
apparently silent surrounds without any direct stimulation of what would nor-
mally be considered the CRF. Thus, the concept of the CRF, as useful as it
is, does have some vexing limitations.

ANATOMICAL CONNECTIONS AND SURROUND SPECIFICITY

Dowling & Boycott (1966) suggested that McIlwain's (1964) periphery effect
was mediated by amacrine cells, since there are serial amacrine–amacrine and
amacrine–ganglion cell synapses that could transmit the effect across the ret-
ina. Werblin's (1972) intracellular recordings demonstrated that amacrine cells
were depolarized by remote retinal stimulation. These results suggest that
responses from beyond the CRF also might be mediated by serial chains of
interneurons at higher levels in the visual system. Although this remains a
valid possibility, there is an increasing body of anatomical data indicating that
cortical neurons extend their axons horizontally beyond the dimensions that
would correspond to their CRFs. Recently, Rockland et al (1982) injected the
neural tracer, horseradish peroxidase, into V–I in tree shrews and found hor-
izontal connections arrayed in periodic stripes in layers I–III throughout a

large portion of this area. Rockland et al and Mitchison & Crick (1982) have proposed several schemes for the elaboration of receptive field mechanisms on the basis of this intrinsic connectivity. Since the CRFs in V–I in tree shrews are small and in precise visuotopic order (Kaas et al 1972), these periodic intrinsic connections are probably related to surround mechanisms beyond the CRF. The striking similarity of this striped pattern of intrinsic connectivity with the topographic distribution of orientation preferences revealed by single neuron recording and metabolic uptake of 2-deoxyglucose in V–I in tree shrews (Humphrey & Norton 1980, Humphrey et al 1980) suggests that this intrinsic connectivity is related to orientation preferences. Since most surround mechanisms are antagonistic, it is likely that this intrinsic connectivity participates in elaboration of antagonistic orientation-selective surrounds, possibly mediated by inhibitory interneurons. Such antagonistic orientation-selective surrounds have often been found for visual cortex neurons in cats. Gilbert & Wiesel (1983) injected single neurons in V–I in cats with horseradish peroxidase and found that the axons extended horizontally over distances of up to 4 mm and that collaterals within the axonal fields were distributed in repeating clusters with an average periodicity of about 1 mm. This pattern of clustered axonal collateralizations may also be related to the elaboration of stimulus-specific surround mechanisms.

In V–I in monkeys, horizontal intrinsic fibers extend well beyond the distance of about 2 mm that would be expected for connecting a cell with adjacent cells sharing portions of its CRF (Hubel & Wiesel 1974). Fisken et al (1975) made small lesions in V–I and traced degenerating fiber 1.5 to 2 mm horizontally in most layers, except in the stria of Gennari, where fibers extended horizontally for up to 4 mm. More recently Rockland & Lund (1983) injected horseradish peroxidase in V–I in macaque and squirrel monkeys and found a periodic lattice-like pattern of dense connections extending 2 mm from the margin of the injection in layers II–III and 3 mm in the stria of Gennari. Similar lattice-like patterns of intrinsic connections have been found to extend 2 to 3 mm in V2 and 3.5 to 4 mm in V4 in monkeys (Rockland 1983). These patterns of connectivity may participate in the elaboration of stimulus-specific surround mechanisms. It is particularly interesting that the horizontal connections are most extensive for V–I in the stria of Gennari, as this layer receives an input from the magnocellular laminae of the lateral geniculate nucleus via layer IV–C–α (Hubel & Wiesel 1972, Lund et al 1975), contains a high proportion of directionally selective neurons (Dow 1974, Livingstone & Hubel 1984), and projects to the middle temporal area (Spatz 1975, Lund et al 1975, Tigges et al 1981, Maunsell & Van Essen 1983b). Montero (1980) found by using two separate tracers that the input from V–I to the middle temporal area terminates in a series of bands within partially overlapping projections from adjacent sites in V–I. These partially overlapping striate projections may con-

tribute, possibly via interneurons, to the large direction selective surrounds in the middle temporal area. Small injections of tritiated proline in the middle temporal area have revealed extensive connections within the area that also terminate in a series of bands, and thus could also contribute to large direction-selective surrounds (Maunsell & Van Essen 1983b, Weller et al 1984). Although the transcallosal connections of the middle temporal area are much heavier near the representation of the vertical meridian, they extend throughout most of the area (Newsome & Allman 1980) and thus may contribute to the portion of the surround extending into the opposite half of the visual field as do transcallosal connections in V4 (Moran et al 1983). Large portions of the V4 complex are richly supplied with callosal connections (Van Essen et al 1982).

Another source of stimulus-specific input to surrounds is from noncortical structures. Sherk & LeVay (1983) found that unilateral destruction of the claustrum in cats resulted in a 50% reduction in the number of end-stopped cells in the ipsilateral V–I with other visual response properties apparently unaffected. End-stopping is produced by inhibitory regions flanking the CRF (Hubel & Wiesel 1965). Neurons in the visual claustrum of the cat are arranged in a representation of the visual field (LeVay & Sherk 1981) and respond best to long bars or slits with a definite preferred orientation (Sherk & LeVay 1981). Thus, neurons in the visual claustrum seem well suited to provide input, possibly through cortical interneurons, to antagonistic orientation-specific surrounds in the visual cortex (Sherk & LeVay 1983). Comparable experiments have not been conducted in primates; however, the claustrum has been found to project to the visual cortex in galagos (Carey et al 1979) and baboons (Riche & Lanoir 1978). Another possible source of stimulus-specific input to visual cortical surrounds is from the pulvinar. The pulvinar contains several topographic representations of the visual field (Allman et al 1972, Gattass et al 1978, Bender 1981) and many direction- and orientation-selective neurons (Gattass et al 1979, Bender 1982).

The visual system contains many descending pathways (Tigges et al 1981, Maunsell & Van Essen 1983b), such as from the middle temporal area to V–I and V–II, 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 (1 982) has 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 project to the entire extent of the ipsilateral middle temporal area in the owl monkey (Weller et al 1984) and may be another source of the large surrounds present for neurons in this structure.

In summary, surround mechanisms have been demonstrated to be mediated by (*a*) transcallosal connections with the representation of the opposite hemifield, (*b*) input from the claustrum, (*c*) descending input. In addition, it is very likely that intrinsic connections with adjacent parts of the visuotopic map that extend beyond the neurons's CRF contribute to surround mechanisms. All of these connections subserving surround mechanisms may be further mediated by interneurons. Finally, it should be pointed out that although we emphasize in the chapter anatomical connections that transcend the topographic organization of the CRFs, a great many connections do reflect the visuotopic organization of CRFs. This, of course, has been the subject of considerable investigation (for recent research in primates see Weller & Kaas 1983).

SURROUNDS AND PERCEPTION

Stimulus Selectivity Beyond the Classical Receptive Field and Figure–Ground Discrimination

Stimulus-specific responses from beyond the CRF seem ideally suited for discriminating figure from ground and preattentive vision (Treisman & 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 msec (Julesz 1984), which is slightly longer than the time required for the response from the regions beyond the CRF to influence the response from within the CRF in middle temporal neurons (see Figure 2).

Stimulus Selectivity Beyond the Classical Receptive Field 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 that 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 in the environment, yet the system's task is to determine the motion of objects relative to other objects and to the observer.

In both cases more than just information restricted to a small locality on the retinal surface is required to make veridical judgments. Land's (1959a,b, 1983) experiments indicate that the system compares the wavelength composition of the light reflected by the 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. 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 (von Helmholtz 1925), 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 implemented through surround mechanisms.

The neurons in several of the extrastriate cortical visual areas have properties that seem well suited for performing the local–global comparisons that serve as the basis of perceptual constancy functions and the discrimination of figure from background. They possess large stimulus-specific surrounds that extend well beyond their CRFs and are capable of comparing stimuli present within their CRFs and other stimuli present throughout large portions of the visual field. Their CRFs are embedded in representations of the visual field that may provide the spatial structure to the perceptual image. Recently Ingle & Shook (1984) found that area 18 lesions in gerbils produced a selective deficit in the animal's ability to make local–global comparisons. It is remarkable that more than 40 years ago Kluver (1942) proposed on the basis of behavioral deficits in monkeys following occipital lobectomy that the visual cortex is necessary for spatial discrimination and perceptual constancies. He made the analogy that just as mechanisms have evolved to maintain a constant internal physiological environment in higher organisms, which create for them an independence from external environmental conditions, similarly the perceptual constancy functions of the visual cortex "guarantee varying degrees of freedom from the visual milieu." Such constancy mechanisms are of enormous adaptive value but are energetically and computationally very expensive, and yield only a partial independence from the physical environment. For example, common experience reminds us that objects may in some instances appear differently colored under different lighting conditions.

Surround Mechanisms and the Perception of Depth Through Motion

Von Helmholtz (1925) 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 & 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." Von Helmholtz (1925) 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 & Loomis (1974) postulated a simple neural mechanism that could serve as the basis for the analysis of optical flow patterns that occur as a viewer moved 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. In our studies of neurons in the middle temporal area (Allman et al 1984a) and V–II (Allman 1984b), we have provided the first experimental confirmation of this hypothesis in the discovery of neurons sensitive to background movement. It is easy to imagine how an antagonistic velocity-selective center-surround mechanism, as first proposed by Nakayama & Loomis and demonstrated in our study, could subserve the spatial, velocity-discriminating function required for depth perception through motion parallax or optical flow patterns. It should be pointed out that the characteristic symmetrical V-shaped background velocity tuning curves obtained from the majority of V–II and one third of middle temporal 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, these neurons could register the relative magnitude of the depth difference between center and surround but not whether the center was nearer or farther than the background. The middle temporal cells in which inhibition simply increases with background velocity might help to resolve this ambiguity.

The velocity–distance relationship postulated by von Helmholtz (1925) obtains only when the observer fixates on very distant objects. If the observer fixates on an object at a given depth while he or she 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). Rogers & Graham (1979) produced compelling, unambiguous depth illusions based on motion parallax with random dot patterns displayed on an oscilloscope screen that confirmed the depth relationships predicted by this optical configuration. There exists additional motion-related depth information in the visual scene described so graphically by von Helmholtz (1925). 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.

CONCLUSIONS

The function of the visual system is not merely to create a set of precise neural analogues of the optic 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,b, 1983), and Ramachandran & 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 total receptive fields (TRFs) for many neurons in these maps may be much larger and even extend throughout much of the visual field. The TRFs 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 middle temporal neurons that are strongly facilitated by background motion shearing at 90° to the preferred direction for the CRF, by the responses to illusory contours in V–II (von der Heydt et al 1984), and by the influence of background color patches on the properties of color-coded neurons in the V4 complex (Zeki 1983b). The successful exploration of these complex surround mechanisms calls for collaboration among psychophysicists, mathematical modelers, and neurophysiologists. There exist some very promising beginnings for this endeavor (Horn 1974, Nakayama & 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 the perceptual processes.

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