Striate Cortex

The terminus of the projection originating in the eye is the enormous sheet of cells in the back of the brain known as the striate cortex. The retina is projected systematically onto the cortex, with hundreds of cells to process the output of each incoming fiber. Striate cells have several characteristics not seen earlier: binocularity, directional selectivity, and much more narrow orientation and spatial frequency selectivity. The nature of striate processing gives a number of clues to how the visual system functions in spatial vision.

ANATOMY OF STRIATE CORTEX

Projection to Striate Cortex

In the primate visual system, the projection from lateral geniculate to striate cortex (the first cortical visual area, and thus also called V1) follows the relatively straightforward pattern seen at earlier levels. All parts of the cerebral cortex are conventionally subdivided into 6 layers, with layer 1 at the cortical surface and layer 6 adjacent to the white matter. The primary destination of the axons of LGN projection cells is layer 4 of the striate (M.E. Wilson & Cragg, 1967), although there are also fibers that go to layers 1, 3, and 6. From V1 the path is much more complex and divergent, the cells in V1 projecting to multiple other cortical and subcortical visual areas. This complexity enters at an earlier level in subprimate mammals. In cat, for instance, geniculate cells project not just to V1, but to V2 and V3 (M.E. Wilson & Cragg, 1967) and to the Clare-Bishop area as well (Graybiel & Berson, 1981). The use of the cat visual system as a model for that of primates is thus considerably weakened at cortical levels.

The left LGN receives the fibers from the temporal portion of the retina of the left eye and the nasal portion of the retina of the right eye; both of these retinal areas are stimulated by light from the right visual field. Since the LGN fibers project only to the cortex on the same side, the projection onto the striate cortex is functionally a completely crossed one: the right visual field activates the left cortex and the left field the right cortex (see Figure 3.8). The cortical
regions receiving projections from near the vertical meridian are interconnected with the corresponding cortical regions in the other hemisphere through the corpus callosum (Myers, 1962; Hubel & Wiesel, 1967).

It was shown in early studies (Talbot & Marshall, 1941) using evoked-potential recordings that there is a systematic retinotopic mapping onto the cortex. That is, different retinal regions project to different cortical areas in a systematic fashion. In the macaque monkey, for instance, the fovea projects to the most lateral striate region, and increasingly peripheral retinal regions (up to about 7°) to more and more medial regions on the cortical surface. Still more peripheral areas project to cortical areas buried within sulci below the cortical surface (Daniel & Whitteridge, 1961). In humans, the whole striate area has migrated medially so that only the foveal projection is left on the outer surface of the cortex.

Retinal receptors are relatively uniformly distributed across the whole retina (considering both rods and cones), thus ensuring an initial faithful, relatively undistorted spatial transformation of the visual world into a physiological representation of it (except that the three-dimensional world is compressed into two dimensions). To a rough first approximation, the image of an object stimulates the same number of retinal receptors whether it is imaged on the fovea or on the periphery. However, under photopic conditions, with only cones active, there are many more central than peripheral units responsive to a given pattern. Beyond the receptors this relationship becomes even more grossly distorted: the image of an object projected to the fovea activates tens or hundreds of times as many ganglion cells as the same image falling on a peripheral region. Further topological transformations take place such that the central regions are further expanded at later neural levels, although neighboring retinal areas remain neighboring in the projection.

Much but not all of the topological transformation of the spatial representation takes place within the retina, from receptors to ganglion cells. It has been shown in cat (Fischer, 1973) that the ganglion cell density falls off in a logarithmic manner with retinal eccentricity. Thus there would be about the same number of ganglion cells in the annular strip between 1 and 2° peripheral as there are in the annulus between 10 and 20° peripheral. The area covered in the projection to the LGN and from there to the cortex was first thought to be about equal for every ganglion cell (Rolls & Cowey, 1970), but recent studies indicate that there is a large additional magnification of the foveal representation in the LGN and again in the cortical projection (Myerson, Manis, Miezin, & Allman, 1977; Connolly & Van Essen, 1984; Van Essen, Newsome, & Maunsell, 1984; Perry & Cowey, 1985). The increased central magnification from retina to LGN, at least, is only in the cells that project to the parvocellular layers (Perry & Cowey, 1985). The eventual cortical magnification of the central retina is such that about 25% of the striate cortex is devoted to processing the central 2.5° of the visual scene (an area roughly equal to that subtended by a 50-cent coin held at arm’s length).

A very powerful procedure for studying functional anatomy is the activity-dependent 2-deoxyglucose (2-DG) technique (Sokolov et al., 1977). The rationale behind this approach is that since glucose is the metabolite of cortical cells,
the more active the cell is, the more glucose it will take up and utilize. A closely related substance, 2DG, is taken up by cells as if it were glucose, but it cannot be metabolized and thus accumulates in the cells. When it is radioactively labeled, its location in the brain can subsequently be determined by autoradiography of the tissue sections. Therefore, if one injects radioactive 2-DG while presenting a particular visual pattern and then slices the brain and prepares it for autoradiography, the cells most responsive to the pattern presented will reveal themselves by their radioactivity.

Using this technique, Tootell, Silverman, Switkes, and R.L. De Valois (1982a) examined the retinotopic projection onto the cortex in macaque monkey. A ring-and-ray pattern was produced on a TV monitor. The rings and rays were made up of small, randomly sized rectangles that flickered in time, with the rings spaced logarithmically (see Figure 4.1A). The monkey was presented with that pattern centered on the fovea while being injected with radioactive 2-DG, and then the cortex was flattened, tangentially sectioned, and placed on X-ray film. An example of the resulting autoradiographs is shown in Figure 4.1B. The logarithmically spaced rings can be seen to activate strips about equally spaced apart on the cortex, and regions stimulated by the rays making up the vertical, horizontal, and oblique meridians can be seen to form almost parallel strips across the cortex. Thus the cortical map reflects a roughly logarithmic transform of the retinal spatial mapping. The varying magnification of the retinal projection at different spatial frequencies, determined from such anatomical experiments or from electrophysiological recordings at different eccentricities, can be specified by the reciprocal of the cortical magnification factor (CMF). The CMF is defined as the number of mm on the cortex to which one degree on the retina projects, and thus its reciprocal is the number of degrees visual angle per mm of cortex. Note, however, that the retinal projection is overlapping, not point-to-point as a simple view of the CMF might lead one to expect. The CMF$^{-1}$ increases linearly with eccentricity, from about 0.15°/mm at the fovea to about 1.5°/mm some 20° peripheral (Hubel & Wiesel, 1974b; Van Essen et al., 1984; Tootell, 1985); see Figure 4.2.

It is to be noted that the fact that the various rays in Figure 4.1B are broken into segments is not related to the checks in the pattern presented. Rather, it reflects the nature of the projection of the two eyes onto the cortex. The ring-and-ray pattern in that experiment was presented to only one eye. Since the two

![Figure 4.2](image.png)

FIG. 4.2 The reciprocal of the cortical magnification factor as a function of eccentricity.
eyes project separately onto the cortex, in alternation over small distances (see discussion of cortical modules at the end of this chapter), what one sees in Figure 4.1B are just the segments related to the stimulated eye, individual ocular dominance columns. The gaps in the activated cortical strips would have been filled in to make continuous bands if both eyes had been stimulated in register by the ring-and-ray pattern. It can be seen that there are certain deviations from a complete log transform in the mapping: the rings in the pattern do not come out as straight lines, but bend increasingly with eccentricity. This is related to the directions taken by the ocular dominance columns in different cortical regions (Tootell et al., 1982a). Since the left-eye, right-eye projections lie side-by-side, the combined module is longer in that direction than in the other. The modules have their long dimension along the vertical meridian, making this then longer than the horizontal meridian.

Not the precise relationship discussed above, but the general expansion of the central retina in the cortical projection, has long been known. The enormous foveal representation relative to that of the periphery raises two questions. One is, how is the processing of information from retinal areas at different distances from the fovea affected by the vastly greater number of cortical cells receiving input from a patch of foveal receptors than from an equal-sized patch of peripheral receptors? The other, related question is, what consequences does this have for visual perception?

With respect to the second question, one extreme position has been stated by E.L. Schwartz (1980). He attributes to the logarithmic conformal mapping of retina onto cortex a major role in itself in the processing of spatial information. Thus, for instance, size constancy might be accounted for on the basis of the fact that as a centrally fixated pattern increases in retinal size (as one approaches it), its cortical projection would only shift laterally, not increase in size, given the logarithmic transform. For instance, the rings in Figure 4.1A can be thought of as a circle at each of 3 different distances; the cortical representations of these circles (see Figure 4.1B) are three roughly equal-length lines displaced laterally with respect to each other. However, Schwartz's model, based on the assumption that information in striate is coded primarily in terms of cortical distances, ignores or minimizes functional differences among neurons. There is by now, however, such an overwhelming amount of evidence for neuronal specificity, for each neuron's being responsive just to certain stimulus characteristics and not to others, that it seems unlikely that a proposal based on a lack of cortical specialization can adequately describe visual pattern analysis within the striate cortex. Schwartz's model has been criticized on other grounds as well (Cavanagh, 1982).

A clear possibility for the variation in physiological processing associated with the increased foveal representation at the cortex is that the RF size of foveally related neurons may be very small and that the RF size of units at increasing eccentricities may become larger and larger. If this were so, and if a constant overlap were maintained between neighboring RFs, then it would clearly require a large number of cells in the foveal area to cover the same region in visual space
encompassed by the RF of a single peripheral ganglion or cortical cell. There is in fact much evidence at both the ganglion cell (Wiesel, 1960; Peichl & Wässle, 1979) and cortical levels (Hubel & Wiesel, 1974b; Dow, Snyder, Vautin, & Bauer, 1981; Van Essen et al., 1984) for an increase in RF size with eccentricity, and this is clearly the principal physiological change with eccentricity.

As an aside, it should be pointed out that the RF size of a cell is often considered to be directly related to its optimum bar width or to its peak spatial frequency tuning. In fact, there is not such a simple relationship. The overall RF size is a joint function of the spatial frequency tuning and the bandwidth of a cell—of the width of the RF center and of the number of sidebands. A narrowly tuned cell would have a larger number of sidebands (see Figure 4.18 below) and thus a larger overall RF size than a more broadly tuned cell that is tuned to the same spatial frequency. Since cells tuned to high spatial frequencies in general are more narrowly tuned (R.L. De Valois, Albrecht, & Thorell, 1982, and Figure 6.12 in this volume) than those responding best to low spatial frequencies, one would expect to find a smaller range of RF sizes than the range of peak spatial frequencies among cells in a given locus. One might also note that the optimum spatial frequency for a cell can be very precisely measured, but this is not true for RF size. Weak sidebands can be easily overlooked and the sensitivity at the edges of the RF falls off gradually, so the overall measured size of the RF can easily vary by a factor of 2:1, depending on the animal's excitability and the response criterion chosen.

Several lines of psychophysical and physiological evidence raise doubts that the differential cortical magnification is solely due to an increase in the RF size of cells (associated with a decrease in their spatial frequency peaks) with eccentricity. The strongest argument against attributing the foveal over-representation purely to peripheral cells' having large RFs and foveal cells' having only small RFs is that our highest sensitivity to almost every visual parameter appears to be highest in the fovea. Specifically, Robson (1975) and Robson and Graham (1981) have shown that one is most sensitive in the fovea not only to high spatial frequencies (which would presumably be detected by cells with small RFs), but to low spatial frequencies (which would be detected by cells with large RFs) as well. There is also both physiological and anatomical evidence, which we will discuss below, that cells with large as well as small RFs are to be found in foveally related parts of the cortex. On the other hand, D.H. Kelly (1984) has shown that if patterns are scaled with eccentricity according to the magnification factor, the whole contrast sensitivity function shifts to lower spatial frequencies, keeping about the same total bandwidth, with increasing eccentricity.

It is possible that some of the enormously magnified representation of the fovea in the cortex is due to a progressive drop in the range of cell peak spatial frequency tuning (and thus to some extent RF sizes) from fovea to periphery. Thus the portion of the cortex related to the fovea may have cells tuned to all spatial frequencies, low as well as high, but those tuned to the highest spatial frequencies may progressively disappear toward the periphery. Likewise, a full range of cells processing color, stereopsis, etc., may be present in the foveal pro-
jection but might become increasingly sparse toward the periphery. Such an arrangement would be consistent with the psychophysical evidence that almost all visual functions are optimal in the fovea.

It can be seen that such a schema is not really inconsistent with the evidence for a change in RF size with eccentricity, since the average RF size would indeed increase as cells with small RFs became fewer peripherally. But cells tuned to a wide range of spatial frequencies, with a wide range of RF sizes, should be found in central loci. Such indeed has been reported (R.L. De Valois, Albrecht, & Thorell, 1982), although more detailed studies of how cells vary with eccentricity would be desirable.

We are emphasizing the issue because the presence or absence of cells with a wide range of RF sizes at a given retinal locus bears not only on retinocortical mapping, but on the whole issue of multiple spatial channels (see Chapter 6).

**Fine Anatomy of V1**

When the geniculate fibers reach the cortex, they make synaptic contact, mainly with layer 4 cells, over a distance as long as 5,000 μm (Sholl, 1956). The fibers from the magnocellular and parvocellular LGN layers terminate in distinct subregions of cortical layer 4: the magnocellular fibers project to layer 4α while the parvocellular LGN input terminates in layers 4a and 4β (Hubel & Wiesel, 1972). There is also a small input from the parvocellular LGN cells to the upper part of layer 6, and from the magnocellular cells to the lower part of layer 6. Finally, a small projection can be seen ending in layer 3; this perhaps originates in the few scattered interlaminar cells of the LGN.

The synaptic contacts made in both layers 4a and 4c are on the dendritic spines of spiny stellate and spiny pyramidal cells (J.S. Lund, 1973). A magnified view of this geniculostriate synapse reveals rounded synaptic vesicles and a thickened membrane structure, both of which have elsewhere been associated with excitatory synapses (Colonnier, 1968). However, the axosomatic endings on these same cells, from fibers that have an intracortical origin, have the flattened vesicles and distinctive membrane structure often associated with inhibitory synapses (Colonnier, 1968). The anatomical arrangement, then, suggests (but hardly proves) that the first cortical cells have an excitatory input from the geniculate combined with and modified by (lateral) intracortical inhibition. It thus appears quite similar in general plan to the arrangement seen at each of the three preceding synaptic levels, in retina and geniculate.

The stellate cells arborize mainly within layer 4 of the striate, but most of the rest of the interconnections are made predominantly in a direction at right angles to the cortical surface, i.e., vertical. In particular, the large pyramidal cells have dendritic trees that may extend up through all the overlying cortical layers. However, the direction of information flow through the circuitry within the striate cortex is no longer the relatively simple arrangement seen at earlier levels.

Although it is not possible at present to give an entirely satisfactory and clear
picture of the intracortical circuitry, the outputs from the striate area appear fairly straightforward. A distinctive pattern of different projections has been found from each of the output layers (J.S. Lund et al., 1975).

Probably the most important output from the striate cortex, from the point of view of visual perception, is that to other, extrastriate visual areas. Much of this pathway comes from pyramidal cells whose cell bodies are in layers 2 and 3 of V1 (J.S. Lund, 1973), and whose axons go down through the underlying cortical layers to the white matter below layer 6. These cells project to V2, and perhaps to V3, V4, and other extrastriate areas as well.

Layer 4 of the striate cortex is mainly the region in which the LGN afferents terminate. There is, however, a projection from large cells in layer 4b as well as some cells in layer 5 to the middle temporal (MT) extrastriate area. This pathway, which originates in the magnocellular LGN layers, thus seems largely to bypass the main cortical machinery. To a considerable extent there appear to be two separate streams of information through these multiple levels. One goes from retinal α ganglion cells to magnocellular LGN cells to 4ca, 4b, and then to MT. The other goes from retinal β cells through the parvocellular LGN layers to 4cβ, to striate layers 3 and 2, and then to various prestriate regions. In addition to the MT output, the axons of many layer 5 pyramidal cells go to the superior colliculus, forming a major input to this region.

Perhaps 50% of the neurons whose bodies are in the deepest layer (layer 6) send their axons back down to the LGN. This feedback is by no means trivial in amount; there may well be more fibers going from cortex to LGN than there are in the "classical" path from LGN to cortex! This back-projection appears to be strictly retinotopic; that is, a cortical region feeds back to the same geniculate area that projects onto it. Furthermore, the region in layer 6 receiving parvocellular input projects back to the parvocellular LGN layers, and correspondingly for the magnocellular region (J.S. Lund et al., 1975). It is by no means obvious what function is subserved by this feedback.

The feedback from one level to the previous occurs not only from the striate cortex to LGN, but seems to be an almost universal feature of the visual path from this level on. Each of the areas to which V1 cells project sends fibers back to the striate. Even less is understood (if that is possible) about the function of these feedback connections than is understood about the striate-to-LGN feedback.

In addition to the extrastriate projections mentioned above, anatomical evidence (Gilbert & Wiesel, 1979) has been found for fibers going from one region of the striate down into the white matter only to end in another striate locus.

**PHYSIOLOGY OF STRIATE CORTEX**

Of principal concern to us in examining the physiology of the striate cortex in this book will be the different functional types of cells present at this level, and
the spatial response characteristics of the cells, particularly in relation to those at earlier levels. We will discuss these two issues in sequence.

Functional Cell Types

The question of the classification of cells into different functional categories—how many different cell types are present, what the criteria for classification should be, etc.—is an issue that appears to receive much more heated discussion in the literature than is warranted by the problem. Doubtless every cortical cell differs from every other in some way, along some one of a vast number of dimensions. One might dichotomize cortical cells along any one of these dimensions, particularly if one did not ask for nor seek quantitative evidence as to whether the population was indeed dichotomous (or multimodal) along that dimension. In any case, which dimension is chosen as a basis for classifying cells should be to a large extent one of individual choice, in which a critical consideration is how well it fits in with a larger theoretical framework.

Simple and Complex Cells

From our point of view, the most fundamental difference seen among cortical cells is that first pointed out by Hubel and Wiesel (1962), namely between what they termed “simple” and “complex” cells. Not only does the distinction between these cell types have considerable theoretical importance (discussed below), but there is in fact objective evidence (R.L. De Valois, Albrecht, & Thorell, 1982) that it is truly a dichotomous distinction, not just two ends of a continuum.

Hubel and Wiesel (1959, 1962) categorized simple cells as those showing (1) distinct excitatory and inhibitory regions within their RFs (by which they meant excitation or inhibition to increments of light); (2) summation within the excitatory and within the inhibitory regions, so that a stimulus that covers all the excitatory region evokes a larger response than one covering only a portion of the excitatory region; (3) an antagonism between the excitatory and inhibitory areas, so that an increment in light that covers both an excitatory and an inhibitory area evokes less of a response that if it were restricted to the excitatory region alone (indeed, in most cases a stimulus covering both regions is totally ineffective in evoking a response); and (4) an orientation selectivity, that is, a response to a pattern of one orientation but not to one of some other orientation.

Complex cells (Hubel & Wiesel, 1962) were categorized as those showing (1) an absence of discrete excitatory and inhibitory subregions in their RFs (they give on-off responses to increments anywhere within the overall RF); (2) nonetheless, a large excitatory response to a bar of width some fraction (generally about one half to one third) of the total RF width, with no response to a bar covering the whole RF; (3) a response to such an optimal bar wherever it be placed within the RF; and (4) orientation selectivity.

It can be seen that both simple and complex cells have orientation selectivity,
that does not differentiate them. Furthermore, quantitative studies of orientation selectivity (Schiller, Finlay, & Volman, 1976b; R.L. De Valois, Yund, & Hepler, 1982) show there to be a continuum from nonoriented to very narrowly tuned cells. For these reasons, we will discard orientation selectivity as a criterion for distinguishing simple from complex cells. The other criteria, though, reflect basic functional differences between these cell types.

The distinction made by Enroth-Cugell and Robson (1966) between X and Y ganglion cells (see Chapter 3) can be seen to be functionally identical to the simple-complex distinction of Hubel and Wiesel (1962). The three main Hubel and Wiesel criteria for simple cells, listed above, are equivalent to saying that simple cells show linearity of spatial summation, Enroth-Cugell and Robson's criterion for X cells. The defining characteristics of complex cells are equivalent to their not showing linear summation, as is also the case for Y cells. The identity between these classifications would probably have been more readily apparent if the categorization of ganglion cells into X and Y cells had preceded rather than followed the classification of cortical units as simple and complex cells. It should be made clear that saying that X ganglion cells and simple cortical cells have similar summation characteristics, and that so do Y ganglion cells and complex cortical cells, should not be taken to imply that X cells feed into simple cells and Y cells into complex cells in a parallel arrangement, as against simple cells possibly feeding into complex cells in a serial, hierarchical fashion. That issue of the anatomical arrangements will be discussed below, but it is quite separate from the issue of functional characteristics, which is what we are concerned with here.

The basic operational distinction between X and simple cells, on the one hand, and Y and complex cells on the other, is sensitivity to spatial phase. Simple and complex cells are in general sensitive to the same types of stimuli, and in fact have quite similar spatial and orientation selectivities. But a simple cell fires to its optimal pattern when it is in one spatial phase or position, gives no response to it in some other phase, and will be inhibited by it in still another phase. A complex cell, on the other hand, responds to the optimal stimulus regardless of its spatial phase or position within its RF. A simple cell will fire to a white bar in some position; it will be inhibited by a black bar in the same location, and thus maximally distinguishes between increments and decrements (or white and black). A complex cell, on the other hand, will fire to either a white bar or a black bar in the same location, and thus is unable to distinguish between increments and decrements in luminance. Quite the same holds for those simple and complex cells which are also responsive to isoluminant red-green or yellow-blue patterns: simple cells give opposite responses to red and green, but complex cells, while responding to the presence of the pure color pattern, give much the same response to red as to green (Thorell, R.L. De Valois, & Albrecht, 1984); see Chapter 7.

Since cortical cells in general adapt quite rapidly to stationary stimuli, it is convenient to use moving or temporally modulated patterns to study their responses. To examine their contrast sensitivity, then, one can drift gratings of various spatial frequencies across the cell's RF and record the responses. In
response to such a stimulus, a simple cell will give a modulated discharge at the same temporal frequency as the drift rate. When, say, the bright bar goes across the RF center and the dark bars are on the surround, the cell will fire; when, for this cell, the dark bar is on the RF center and the bright bars on the surround, it will be inhibited. Thus it will be excited during one half and inhibited during the other half of each drift cycle (see Figure 4.3A). The peristimulus time histogram (PSTH) of the responses, lined up with respect to the stimulus and averaged over several cycles, will be approximately sinusoidal, a sine wave stimulus producing a sine wave output. A Fourier analysis of the PSTH of the cell’s responses will thus show most of the power to be at the fundamental, at the same frequency as the stimulus, as can be seen in Figure 4.3A. However, most simple cortical cells have little or no maintained firing rate in the absence of stimulation. Therefore, although the discharge rate can readily increase above the maintained rate in the excitatory phase, it cannot decrease much, if any, below the maintained rate during the inhibitory phase. There is therefore inevitably some DC component, some increase in the mean firing rate during stimulation. In the example shown in Figure 4.3A, for instance, the mean firing rate of the cell shifts from 0.0 to 40.0 spikes/sec. In a completely linear system, there would be no increase in mean rate, since the increases and decreases during the two phases would be equal and opposite. The half-wave rectification shown by simple cells

![Graphs showing simple and complex cell responses]

**FIG. 4.3** Averaged response patterns of a simple cell (A) and a complex cell (B) to gratings of optimal spatial frequency drifted across their RFs. The figures below each graph display the results of a Fourier analysis of the peristimulus time histogram in each case, with the amplitude of the DC (mean firing rate), and the amplitude and phase of each of the first five harmonics. Note that the simple cell response shows the most power in the first harmonic (AC), while the complex cell response has its power concentrated in the DC (from R.L. De Valois, Albrecht, & Thorell, 1982, *Vision Res.*, 22, Copyright 1982, Pergamon Journals, Inc. Reprinted with permission).
as a result of their low maintained rates is thus an important nonlinearity in the functioning of the system (Albrecht & R.L. De Valois, 1981); see Chapter 11.

Complex cells give a quite different response to a drifting sine wave. Since a complex cell responds to this pattern (or other patterns) regardless of its position or spatial phase, it shows a continuous, largely unmodulated increase (or decrease) in firing rate while the pattern drifts across its RF (see Figure 4.3B). A Fourier analysis of the PSTH of a complex cell's responses, then, shows most of the power at the DC rather than at the first harmonic. A comparison of the response amplitude at the DC to that at the first harmonic (AC) should thus serve to distinguish a simple from a complex cell on an objective basis. Such a comparison, carried out on a large population of macaque monkey cells, indicates that although there are a few cells whose classification is ambiguous, the overall distribution is clearly bimodal (see Figure 4.4). It can also be seen from this graph that the AC/DC ratios for most simple cells cluster about the value expected from half-wave rectification (1.57).

Another variety of temporally changing stimulus that is useful for studying cortical cell responses is a counterphase flickering grating, that is, a stationary stimulus that is temporally modulated (a standing wave as opposed to a traveling wave). In a sinusoidal counterphase flicker, the pattern is gradually increased then decreased in amplitude, then increased and decreased in amplitude in opposite phase (see Figure 4.5). Thus at any point along the pattern, the light intensity (or the wavelength if it is a color pattern) varies sinusoidally in time.

![Graph showing distribution of modulated/unmodulated (AC/DC) response ratios](image)

**FIG. 4.4** Distribution of the modulated/unmodulated (AC/DC) response ratios for a large sample of macaque striate cortex cells. This distribution is clearly bimodal, thus indicating the presence of two distinct populations of cells. Those cells with ratios between 0 and 1 are complex cells; those with ratios greater than 1 are simple cells (from R.L. De Valois, Albrecht, & Thorell, 1982, *Vision Res.*, 22, Copyright, 1982, Pergamon Journals, Inc. Reprinted with permission).
FIG. 4.5  Luminance at different points of a counterphase-modulated grating at different moments in time. The lower part of the figure shows the waveform across space at different instants. Space is represented on the x axis, and time on the y axis. The upper figure simply shows the superposition of these various waveforms to illustrate the fact that the luminance at the nodal points—the axis crossings—does not change.

The amplitude of the oscillation, however, varies along the pattern: it is 0 at the nodal points and maximum halfway between them.

In response to a counterphase flickering stimulus presented in different locations or spatial phases, a simple cell (like a retinal X cell) gives a response that varies with the spatial phase. Consider the case of a cell with a RF consisting of a center that is excitatory to increments and flanks that are excitatory to decrements (and inhibitory to increments), for instance. When the pattern is in a location at which the point of maximum modulation coincides with the RF center, the cell will first show an increase in firing as this part of the pattern is increased in luminance, and then will be inhibited during the second half cycle when the
pattern there is being decreased in luminance (see Figure 4.6A, 225°). With a pattern of optimal spatial frequency, the flanking points of maximum modulation will coincide with the RF flanks. While the luminance is increasing on the RF center (producing excitation), the luminance is decreasing on each flank (also producing excitation), and vice versa during the second half cycle. The center and surround will thus sum to give a large excitatory response during the first half cycle, and inhibition during the second half cycle.

When the pattern is shifted 180° in phase the responses would of course be the same except that the cell is inhibited during the first half and fires to the second half cycle (see Figure 4.6A, 90°). Between these two locations, however, there is a position at which the luminance is increasing in one half of the RF center and in one half of each RF flank, while it is decreasing in the other half of the center and the surrounds throughout the cycle. If the cell shows linear summation of excitation and inhibition within its RF, then, it will give no response to the counterphase flickering pattern in this position or spatial phase. This is clearly the case for the cell whose responses are shown in Figure 4.6A, at 180°. In summary, a simple cell responds to one cycle of an optimally located counterphase flickering pattern of optimal spatial frequency with a sinusoidal output of the same temporal frequency as the stimulus (thus a Fourier analysis of its PSTH would show most of the power at the first harmonic). The amplitude of a simple cell's response varies with spatial phase, the cell giving no response to a counterphase modulation of the pattern in some (null-phase) location.

Shown in Figure 4.6B are the responses of a complex cortical cell to the same counterphase flickering pattern, presented in different locations with respect to its RF. Two differences from the responses of the simple cell are apparent, both of which show that complex cells are not phase specific. First, its responses are the same regardless of the absolute spatial phase of the pattern. Second, the cell responds at twice the temporal modulation frequency of the pattern: it fires when part of the pattern increases in luminance but also when that same part decreases in luminance. A Fourier analysis of the PSTH of a complex cell's responses to a counterphase flicker would show most of the power at the second harmonic, at twice the temporal frequency of the stimulus.

One aspect of counterphase flickering gratings should be mentioned, namely, that such a pattern is mathematically identical to two gratings of identical frequency and half the amplitude drifting in opposite directions. Indeed, observing a counterphase flickering pattern gives one just this visual impression: it is almost impossible to perceive it as flickering in place; rather, it appears to drift first in one direction then in the other. A considerable percentage of both simple and complex cortical cells are direction selective, responding to patterns moving in one direction but not in the opposite direction (Hubel & Wiesel, 1962; Henry & Bishop, 1972; R.L. De Valois, Yund, & Hepler, 1982). Many such cells are actively inhibited by movement in the nonexcitatory direction. From this, one would predict that a strongly direction-selective cell should be rather insensitive to counterphase flickering gratings compared to its response to a grating drifting in the preferred direction, whereas a nondirectional cell should show no such
FIG. 4.6  Responses of a typical simple cell (A) and complex cell (B) to a stationary, counterphase-modulated grating presented at different spatial positions (phase) with respect to the cell's RF. The numbers in the central column represent the displacement (in degrees of phase angle) of each stimulus. Note that the simple cell response shows two distinct peaks, separated in time with respect to the stimulus onset (the stimulus waveforms at various instants are shown in Figure 4.5) and stimulus phase (with maxima separated by 180°), and intermediate null phase. It thus shows linear spatial summation. The complex cell response has two peaks for each stimulus position, with no null phase. It thus responds at twice the temporal frequency of the stimulus modulation and shows very nonlinear spatial summation.
differences. This prediction has been at least partially verified (Cooper & Robson, 1968).

Although we have been emphasizing phase-specificity (in simple cells) and the lack thereof (in complex cells) as the principal defining characteristic of these cell types, it is important to realize that it is absolute phase of patterns (with respect to the cell’s RF) which is being referred to, not the relative position or phase of different parts of the pattern. The fact that complex cells have orientation selectivity for grating patterns indicates that they are sensitive to the relative position or phase of different portions of the grating. Consider a vertical sine wave grating on a TV monitor. If the phase of this pattern were shifted each successive horizontal line of the display by a certain amount, one would have an oblique, not a vertical, grating. A narrowly tuned complex cell that responds to the vertical grating would not respond to the oblique pattern, so it must be sensitive to the position of the pattern at various vertical locations.

**Even- and Odd-Symmetric Receptive Fields**

The cell whose responses were shown in Figure 4.6A is one whose classical RF would consist of an excitatory center (to light increments) and antagonistic flanks (see Figure 4.7A). Some cells of this type also have additional excitatory and inhibitory flanks. Found equally frequently are cells with just the reverse RF structure: their RF to increments would have an inhibitory center and excitatory flanks (see Figure 4.7B). To a counterphase flicker such a cell would give

![Diagram](image)

**FIG. 4.7** Typical simple cell receptive fields as described by Hubel and Wiesel. Cells A and B have even-symmetric receptive fields, with excitatory and inhibitory centers, respectively. Cells C and D have odd-symmetric receptive fields.
responses identical to that of the cell in Figure 4.6A except that they would be shifted 180° in phase. The cell would inhibit to the first half cycle and fire to the second half cycle. The RFs of both of these cell types are symmetrical about their center (or even-symmetric), and are similar in shape to $\frac{1}{2}$ or more cycles of a cosine wave that is damped out with a gaussian fall-off. These cells are thus similar in general symmetrical shape (in one dimension) to the RFs of the X ganglion cells we discussed earlier.

Hubel and Wiesel (1962) also reported the presence of simple cells with a somewhat different RF structure, in which one half of the RF was excitatory and the other half inhibitory (to increments), or vice versa (see Figures 4.7C and D). It can be seen that the RFs of these cells are asymmetric (sometimes termed odd-symmetric), and resemble damped sine rather than damped cosine waves. On close examination, some of these cells also have additional flanks, but the RF is nonetheless asymmetric. The optimal grating positions for such a cell would be shifted 90° in phase relative to that for the cell shown in Figure 4.6A.

In recording from pairs of simple cells isolated at the same time with the same electrode, Pollen and Ronner (1981) found that such pairs often consisted of one even- and one odd-symmetric cell: the responses of these cells to a drifting grating were always 90° out of phase with each other. Since this relationship held despite changes in the spatial frequency of the grating (within the range of frequencies to which the cells were responsive), it must be that the two cells had exactly the same RF location but were of different RF symmetries, rather than being simply two similar cells shifted in RF position with respect to each other.

The resemblance of even- and odd-symmetric RFs to damped cosine and sine waves, respectively, suggests the possibility that cells with such RFs could be analyzing for the cosine and sine components of the waveforms of complex stimuli, acting as localized spatial frequency filters, as we discuss further in Chapters 6 and 8.

**X/Y and Sustained/Transient**

The distinction between simple and complex cells, and between retinal X and Y cells, is in terms of their spatial characteristics. Cells also differ in their temporal characteristics, e.g., in the optimal rate of temporal modulation of a counterphase flicker, or the optimal drift rate of a drifting pattern, and have been categorized as sustained or transient (see Chapter 3). The sustained/Transient distinction is fairly well correlated with the X/Y spatial difference in the case of retinal ganglion cells and LGN cells, but it does not appear to be among cortical cells. It is not in fact clear that there is a dichotomy in the temporal dimension among cortical cells at all. "Sustained" cells respond well to long-duration stimuli, and should thus be sensitive to low temporal frequencies; "transient" cells, on the other hand, should be maximally sensitive to more rapidly changing stimuli, that is, to high temporal frequencies. A quantitative examination of the temporal frequency characteristics of a large sample of cortical cells in monkey (Albrecht, 1978) shows that most cortical cells are quite broadly tuned for different temporal frequencies: they have much broader bandwidths in the tem-
that they would be phase-locked and fire to the grating about their preferred cycles of a 2:1 ratio. Simple cells are thus simple RFs of the X gan-

s, but the RF is such a cell would be more 4.6A.

that the same time with the same frequency consisted of one spatial period of a drifting grat-
ing relationship held for the range of fre-

ven retinal X and Y cells differ in their tem-

polar than in the spatial frequency domain. Furthermore, it is clear that there is a continuum of temporal frequency sensitivity, ranging from cells maximally sensitive to quite low temporal frequencies, e.g., 1 Hz or less, to those tuned to more than 10 Hz, with the majority being maximally sensitive in the 2–8 Hz range. There is no evidence, either within the simple cell population or within the complex cells or within the population as a whole, for a bimodal distribution of temporal properties such as would justify a dichotomy into sustained versus transient cell types. Furthermore, a comparison of the temporal properties of simple versus complex cells also indicates little evidence for any significant temporal differences between these two classes of cells, which differ so drastically in their spatial properties.

**Hypercomplex Cells**

In their first reports of the properties of cells in cat cortex, Hubel and Wiesel (1959, 1962) reported two functional varieties of cells: simple and complex, as we have been discussing. Later (Hubel & Wiesel, 1965) they reported the presence of an additional cell type, which they termed hypercomplex cells. These cells were reported to resemble complex cells except that the length of the optimal oriented line was also a critical factor in determining their response. If the bar was too long at either one or both ends, the response of the cell would be drastically reduced, perhaps even to zero. These cells were thus described as being end-stopped at either one or both ends. Hypercomplex cells, then, respond not to extended bars but to bar segments; not only must the width and orientation of the bar be appropriate, but its length as well.

More recent, quantitative examinations of this type of cell (Schiller, Finlay, & Volman, 1976a; Gilbert, 1977; Kato, Bishop, & Orban, 1978) have forced some modifications of this picture. One is that some so-called hypercomplex cells resemble simple cells in all but their end-stopping; others resemble complex cells. The other is that most cells that would be classified as simple or complex on other grounds in fact show end-stopping to some degree. Although there is some contrary evidence in cat (e.g., Kato et al., 1978), it appears from the data of Schiller et al. (1976a) and from our monkey striate recording that hypercomplex cells are just at one extreme of a continuum of amount of end-inhibition rather than being a discrete cell type.

We have examined the responses of cortical cells to grating patterns of various numbers of cycles, centered on the cells’ RFs (R.L. De Valois, Thorell, & Albrecht, 1985). As one increases the number of cycles of the optimal-frequency grating, a cell’s response increases up to some point, as we will discuss later. However, a still further increase in number of cycles often produces a decrement in response; on occasion the response will go completely to zero for, say, a grating of 7 or more periods. Thus it appears that many cells are not only end-stopped, but side-stopped as well (a property one would not observe, of course, if the RF were explored solely with bars or edges). It might be better to consider that these “hypercomplex” properties reflect the presence of inhibition which extends around the whole RF. In some cells such surround inhibition is rela-
tively weak; in others it is sufficiently strong to completely inhibit the cell if the stimulus pattern encroaches on the surround either by being too long or by having too many cycles (see Figure 4.8). Cortical cells, then, respond optimally to a delimited patch of grating (of some particular orientation and spatial frequency, as discussed below).

**Temporal Frequency Versus Velocity**

While receptors and neurons early in the visual path respond best to changing visual stimuli, most also respond well, for some seconds, to a static stimulus as well. Cortical neurons, however, give almost no sustained response to a stationary, unchanging pattern. Therefore their properties are usually examined by

![Graphs showing responses of four striate cortex cells to gratings of optimal spatial frequency and varying numbers of cycles.](image)

**FIG. 4.8** Responses of four striate cortex cells to gratings of optimal spatial frequency and varying numbers of cycles. Note that each of these side-stopped cells responds best to a grating patch made up of only a few cycles. In each case, increasing the number of cycles (and thus the width of the overall stimulus pattern) produces some diminution of the response. On occasion (cells C and D) increasing the number of cycles still further leads to a secondary increase in the response, suggesting possible disinhibition. Not all cells show side stopping; see Figure. 4.15 for counterexamples (from R.L. De Valois, Thorrell, & Albrecht, 1985, *J. Opt. Soc. Am. A*, 2, 1115–1123. Reprinted with permission).
moving a pattern back and forth across the cell’s RF. In early studies, in which the
typical pattern was a light or dark bar, the temporal properties of the stim-
ulus were specified in terms of its velocity (amount of movement per unit time;
for visual stimuli the number of degrees of visual angle per second). Some cells
were found to respond best to rapidly moving bars, others to slowly moving
bars, so cells were characterized by their velocity tuning properties. However,
there are two confounded variables in such a stimulus presentation: rate of
movement, and rate of change in luminance or color. It is not clear from such
studies whether movement or temporal change is the crucial variable for con-
tinued activity of the cell, or along which dimension cortical cells are selective.

It is of course possible to separate the movement versus temporal change vari-
ables by comparing responses to moving patterns versus ones flickered on and
off in place, the latter producing only temporal change whereas the former have
both movement and temporal change. It is also possible to assess which is the
crucial variable for the cells’ selectivity by using moving gratings patterns of dif-
ferent spatial frequencies. Consider two gratings of 1 and 2 c/deg. If the 1-c/deg
black-white grating is moved constantly at a particular rate, it will have a velo-
city of 1 deg/s (each bar moving 1 deg visual angle per second); at each point in
the field there will also be a temporal luminance change at 1 c/s (1 Hz). If one
now moves the 2-c/deg grating at a velocity of 1 deg/s, each point in the visual
field will have a temporal modulation of not 1 but 2 Hz, twice the temporal
frequency of the 1-c/deg grating moved at the same velocity. Correspondingly,
of course, if the two gratings have the same temporal frequency, the lower spatial
frequency pattern will have twice the velocity of movement as the other. Thus,
temporal frequency = (velocity) × (spatial frequency).

Using either of these techniques (flicker versus movement; moving gratings
of different spatial frequency), one can ask the question of whether temporal
frequency or velocity is the crucial variable for cortical cells. The answer is quite
clear: for almost all striate cells, it is temporal frequency, not velocity. Most cells
do not require a moving stimulus, but respond well to a stationary flickering
pattern; and they are tuned to a particular temporal frequency range, not to a
certain range of velocities. Thus a cell tuned spatially to, say, 1.4 c/deg might
give equal (but smaller) responses to each of the two patterns of 1 and 2 c/deg
discussed above. When tested with a 1-c/deg grating moving at various rates and
temporal frequencies, it might respond best to a 3-Hz pattern, and not respond
to the grating when it has a temporal frequency of less than 1 or more than 8 Hz
(as discussed above, this can of course be restated to say that it responds best to
a 3-deg/s movement and cuts off at 1 and 8 deg/s velocities). When tested with
moving 2-c/deg gratings, however, it will be found to again respond best to 3 Hz
and cut off at 1 and 8 Hz, although these are now of course quite different velo-
cities. It is thus apparent that it is tuned to a certain range of temporal frequen-
cies, not to a certain velocity range.

Considered in terms of naturalistic stimuli, these properties of striate neurons
are rather paradoxical. When a pattern such as a branch moves, the broad range
of different spatial frequency components of which it is composed all move at
the same velocity, but at very different temporal frequencies. One would therefore think that a system concerned with detecting movement, or utilizing movement information for form vision, would be velocity tuned. Some velocity-tuned cells have in fact been found (Movshon, Adelson, Gizzi, & Newsome, 1985) in areas V2 and MT, leading to the supposition that these regions, but not most of the striate cortex, may be specifically involved with movement analysis. Whether such velocity tuning is found among the subclass of striate cells that form the V2-MT projection (e.g., layer 4b of striate), or whether it is an emergent characteristic of processing past the striate is at present unknown.

Ocular Dominance and Binocularity

The ipsilateral and contralateral inputs to the cortex in monkey are totally discrete, and the initial cortical cells in layer 4 are largely monocular (Hubel & Wiesel, 1968). The separate projection of the eyes, in ocular dominance columns arranged in strips across the cortex, can be seen in Figures 4.1B and 4.22, and is discussed more extensively below. The remainder of the cortical cells in the upper and lower cortical layers are largely binocular, responding to stimulation of the appropriate region in either eye. Overall, about 80% of cortical neurons in both monkey and cat are binocular, the most common type being equally responsive to either eye (Hubel & Wiesel, 1962, 1968). It should be noted that the usual tests of binocularity—whether a cell can be driven by either eye alone—may considerably underestimate the true extent (and nature) of binocularity. Many cells cannot be driven by stimulation of, say, the left eye alone, but their responses to stimulation of the right eye are significantly modified by concurrent patterns in the apparently nonresponsive eye (von der Heydt, Adorjani, & Häny, 1977; Poggio & Fischer, 1977).

The joining of the inputs from the two eyes onto one cell within the cortex clearly provides a mechanism by which we can see a single visual world despite having two separate eyes. It can potentially do more than that: since each eye gets a slightly different view of three-dimensional objects, it is possible to gain information about depth from an appropriate comparison of the activity in the two eyes. Such a process (termed stereopsis) is known from psychophysical experiments to be an important source of depth information.

The image of a fixated point will fall on the fovea of each eye; other points that are at roughly the same depth will fall on corresponding points in the two eyes, e.g., 2.3° away from the fovea in each eye, etc. Objects nearer or farther than the fixation depth, however, will fall on disparate retinal points, the amount of the disparity between the two eyes being proportional to the distance away from the fixation plane, and the sign of the disparity indicating nearer or farther depths.

If various cortical binocular cells received inputs from the two eyes that systematically varied, from cell to cell, in relative disparity, these various units would be activated by objects at various depths. For instance, a unit that
One would therefore utilize moving some velocity, some movement analysis, or some striate cells that are an emergent activity and the RFs of the cells being equal, or the cells being modulated by the other eye alone, only modified by the visual field left eye alone, only modified by the visual field right eye alone. Therefore, within the cortex, it is possible to gain activity in the psychophysical world despite since each eye points in the two nearer or farther points, the image of the distance activating nearer or farther.

Two eyes that activate various units are, a unit that received inputs from exactly corresponding points would be activated by an object on the fixation plane; one that received inputs from just slightly disparate points would be activated by objects just slightly in front of or behind the fixation plane, etc.

That such a cortical organization exists in cat striate cortex was first proposed by Barlow, Blakemore, and Pettigrew (1967) and Nikara, Bishop, and Pettigrew (1968). They plotted the RFs of binocular cortical cells in one eye and then the other and found a considerable scatter between the RF loci in the two cases. From this they concluded that each of these cells could be involved in signaling about patterns at slightly different depths; that is, that there were a large number of different depth channels for each retinal locus.

The validity of physiological studies of stereopsis depends on control of eye position. If the eyes moved differentially in the course of a recording experiment, the RFs in the two eyes would appear scattered even if they all in fact came from corresponding points in the two eyes. Hubel and Wiesel (1970) suggested that such was the case, since with careful monitoring of eye position they found the binocular cells in both cat and monkey to have corresponding RFs with negligible disparity. A recent study (Poggio & Fischer, 1977), in which eye movements were controlled by training the monkey to fixate the target, found results that partially agreed with both these opposing positions. They report that most binocular cells have zero disparity between their inputs from the two eyes, but are very sensitive to disparity differences. Such cells, then, would signal about objects in the fixation plane, and would give very precise depth information at that depth. In addition, Poggio and Fischer report cells that are much more broadly tuned, one group tuned to depths in front of and another group to depths behind the fixation plane. This study then agrees with that of Hubel and Wiesel in finding coincident RFs for most binocular striate cells, rather than the variety of disparities reported earlier, but they agree with Pettigrew and collaborators (Barlow et al., 1967; Nikara et al., 1968) in finding that most striate cells in fact appear to be concerned with signaling binocular depth.

Spatial Properties of Cortical Cells

Orientation Selectivity
The most striking finding of Hubel and Wiesel's (1959) study of cortical cells was that the vast majority of cells were selective for patterns of a specific orientation, the particular optimum orientation varying from cell to cell. This was an important finding because it was so unexpected, and also because it made clear that the cortical cells were doing something quite different from those cells which came before. The RFs of cells from receptors through the LGN are characterized by radial symmetry—the very antithesis of an orientation-specific structure. This finding of cortical cell orientation selectivity therefore produced a considerable change in thought about cortical functioning.

Hubel and Wiesel (1962) not only discovered that most cortical cells have
orientation selectivity, but they also postulated an influential model of how the cells might acquire such selectivity—namely, by summing the outputs of LGN cells whose RFs were in different but aligned spatial locations. This model is discussed more extensively below.

The early studies of orientation selectivity of cortical cells involved a qualitative assessment of their properties; more recently there have been several quantitative studies of large samples of cortical cells in both cat (Henry, Dreher, & Bishop, 1974) and monkey (Schiller et al., 1976b; R.L. De Valois, Yund, & Hepler, 1982). These studies make it clear that the degree of orientation selectivity varies considerably from cell to cell, between the two extremes of orientationally nonselective units (see Figure 4.9B) to very narrowly tuned ones (see

![Image](image_url)

Figure 4.9A). Shown in Figure 4.9C is a cortical cell with average (median) narrowness of tuning (R.L. De Valois, Yund, & Hepler, 1982). It can be seen that this cell is not direction selective; it responds about equally well to movement in either direction of a grating of optimal orientation. The cell whose responses are plotted in Figure 4.9D, on the other hand, responds to a pattern at 90°, but only if it moves to the right; the cell is unresponsive to a leftward moving pattern (which would be plotted at 270°).

The cells whose responses are plotted in Figs. 4.9A, C, and D appear to have a response minimum at 90° away from the optimum orientation. However, the minimum response is actually at the “flanks” of the excitatory orientations. In the case of a broadly tuned cell, this would be about 90° away, but in the case of many narrowly tuned cells the minimum is considerably closer to the peak than that, with the response slightly increasing 90° away (see Figure 4.10). It can be

shown for cells that have a maintained discharge that there is not just an absence of response at off-orientations, but active inhibition. It appears, then, that the orientation tuning involves not just a summation across cells with different RF locations, as in the Hubel and Wiesel (1962) model, but an active inhibitory process which may be maximum between cells tuned to neighboring orientations. This question, along with more direct evidence bearing on it, is discussed further below.

The selectivity of a cell along a particular dimension is conventionally quantified by its bandwidth: the distance between the points to either side of the peak at which the response falls to half its maximum peak response. Thus a cell that gave its maximum response of 100 spikes to a pattern at 90° and dropped to 50 spikes at 70 and 110° would have an orientation bandwidth of 40°.

In Figure 4.9 examples are given of cells with varying orientation bandwidths. In Figure 4.11 are presented distributions of bandwidths for four samples of macaque cells: simple and complex cells from foveal and from near nonfoveal cortical regions. It is clear that there is a wide range of orientation tuning among cortical cells, with the median bandwidth being about 45°. It can also be seen that there is little or no difference in bandwidths between foveal and parafoveal cells, but that simple cells are on the average slightly more narrowly tuned than complex cells. These results agree well with most other quantitative studies of orientation tuning of cortical cells in monkey (Schiller et al., 1976b) and cat (Henry, Bishop, & Dreher, 1974). It appears that cat cortical cells on the average are a little more narrowly tuned than those in monkey.

FIG. 4.11 Distributions of orientation bandwidths from four samples of macaque monkey striate cortex cells. A represents foveal simple cells; B, foveal complex cells; C, parafoveal simple cells; D, parafoveal complex cells. Note that there are no striking differences between simple and complex cells, or between foveal and parafoveal samples (from R.L. De Valois, Yund, & Hepler, 1982, Vision Res., 22, 531–544: Copyright 1982, Pergamon Journals, Inc. Reprinted with permission).
Cortical cells are found tuned to every orientation around the clock, cells with these various peak sensitivities being arranged in systematic order within the cortex. In the foveal projection area of monkey cortex, there are somewhat more cells tuned to vertical and horizontal than to oblique orientations (Mansfield, 1974; R.L. De Valois, Yund, & Hepler, 1982). This provides a likely basis for our slightly greater sensitivity to vertical-horizontal patterns than to oblique ones (Campbell, Kulikowski, & Levinson, 1966).

**Spatial Frequency Selectivity**

In their first recordings from cat cortex, Hubel and Wiesel (1959, 1962) reported that cortical cells were somewhat more selective for the width of patterns than were ganglion cells. In particular, they noted that striate cells would give no response to a bar covering the whole RF, whereas at earlier levels a cell will typically give an attenuated "center" response to such a pattern. However, these differences in spatial characteristics were not very dramatic with the bar and edge stimuli Hubel and Wiesel used, much less striking than the differences in orientation tuning of cortical versus retinal cells. As discussed further in Chapter 6, though, this apparent absence of a large difference in spatial tuning was due to the fact that the cells were only tested with bars and edges—stimuli which have broad spatial frequency spectra. If cells are examined with spatially narrow-band stimuli, the differences in spatial tuning between cortical and retinal cells are as dramatic as are their differences in orientation tuning.

Retinal ganglion cells and LGN cells are rather broadly tuned for spatial frequency (see Chapter 3). The first studies of the spatial frequency tuning of cat (Campbell, Cooper & Enroth-Cugell, 1969; Maffei & Fiorentini, 1973) and monkey cortex (R.L. De Valois, K.K. De Valois, Ready & von Blanckenee, 1975; Schiller, Finlay, & Volman, 1976; R.L. De Valois, Albrecht, & Thorrell, 1977; Albrecht, 1978) found many cells to be much more narrowly tuned. Cells at subcortical levels have sharp high spatial frequency cuts, but only gentle decreases in sensitivity to low spatial frequencies; most cortical cells, on the other hand, have fairly sharp attenuation at both low and high spatial frequencies (see Figure 4.12). Cortical cells thus have a distinctly band-pass spatial frequency characteristic, as opposed to the almost low-pass characteristic of LGN and ganglion cells' spatial frequency tuning.

Spatial frequency selectivity, like orientation selectivity, can be quantitatively specified by the cell's bandwidth, the spatial frequency distance between the points to either side of the cell's peak frequency at which the response falls to half maximum. The spatial frequency bandwidths of cortical cells tuned to different spatial frequency ranges have bandwidths which are roughly constant on a ratio, or logarithmic, scale. Thus a typical narrowly tuned cell may have high and low spatial frequency half maxima which are in a 2:1 ratio, regardless of whether a cell is tuned to 1 c/deg, in which case the low and high cuts would be, say, 0.7 and 1.4 c/deg, or tuned to 10 c/deg with low and high cuts of 7 and 14 c/deg. This is in fact what one would expect from a constant RF shape (in terms of the number of oscillations in the RF) regardless of the RF size. Therefore it

is customary to specify spatial frequency bandwidths on a logarithmic scale, in terms of octaves (a term taken over, of course, from music where it refers to a 2:1 ratio of frequency). Formally, the bandwidth is

\[
\frac{\log F_h - \log F_l}{\log 2}
\]

where \( F_h \) and \( F_l \) are the high- and low-frequency half-amplitude points, respectively.

In Figure 4.13 is shown the distribution of spatial frequency bandwidths for a population of macaque cortical cells (R.L. De Valois, Albrecht, & Thorell, 1982). It can be seen that a small subsample has broad spatial tuning similar to LGN cells, but that most are much more narrowly tuned, the median spatial frequency bandwidth being about 1.4 octaves. A sizable fraction (about one third) of the cells have bandwidths between 0.5 and 1.2 octaves, quite narrowly

tuned indeed, given the overall range of more than 8 octaves to which we are sensitive. Similar distributions of bandwidths have been reported in other quantitative studies of cortical cells in both cat (Movshon, Thompson, & Tolhurst, 1978c) and monkey (Schiller et al., 1976c; Albrecht, 1978; Kulikowski & Bishop, 1981).

Hubel and Wiesel (1962) described the RF of one common type of cortical simple cell as having an excitatory center (to an increment) and antagonistic flanks. Qualitative RF maps such as those they presented (see Figure 4.7) are incomplete in giving no indication of the relative strength of excitation and of inhibition to increments in various subregions (and in fact making the excitation appear to be uniform across the center and the inhibition uniform across the surround). Quantitative measures of the RF of a typical broadly tuned simple cell, however, reveal a cross-sectional profile that oscillates smoothly from excitation to inhibition (see Figure 4.14C). It can be seen that a cross section through the center of the RF of such a broadly tuned cell has a shape similar to that of the X ganglion or bipolar cell diagrammed in Figure 3.16 except that the surround is much stronger in the case of the cortical cell, so that uniform stimulation across the RF gives little if any response.
FIG. 4.14 Quantitative simple cell receptive field profile (space domain) and corresponding spatial frequency tuning function. The RF profile was measured by recording the responses (y axis) to a narrow, flickering black-white bar in different spatial positions (x axis). The solid lines in the column on the left represent the RF profiles predicted by measuring the response to gratings of different spatial frequencies (right). The data points are actual responses (from Albrecht, 1978. Reprinted by permission).

Insofar as the visual system is linear, one can go from the space domain to the spatial frequency domain by the Fourier transform, and predict from the RF shape of cells what their spatial frequency tuning should be, or vice versa by the inverse Fourier transform. There have been several reports of success in making such predictions for both cat and monkey simple cells (R.L. De Valois, Albrecht, & Thorell, 1978; Movshon, Thompson, & Tolhurst, 1978a; Albrecht, 1978;
Kulikowski & Bishop, 1981). On the other hand, Schiller et al. (1976c) failed to confirm this for the cells they tested. Linear summation across RF profiles such as those shown in Figure 4.7 would give bandpass spatial frequency tuning functions with bandwidths of roughly 1.2 to 2 octaves, depending on the weighting of center and surround. One such cell, shown in Figure 4.14C, was found to have a spatial frequency bandwidth of 1.3 octaves. Such RFs, then, can account for the more broadly tuned half of the cortical population. It would not, however, account for those numerous cells with bandwidths of less than one octave. The linear prediction for such cells (Albrecht, 1978; R.L. De Valois et al., 1978; Kulikowski, Marcelja, & Bishop, 1982) is of an RF with additional excitatory and inhibitory regions, that is, with multiple oscillations in the RF, rather than just $\frac{1}{2}$ as in the classic Hubel and Wiesel model.

There are two types of evidence that cortical cells with such multiple-oscillatory RFs exist, and that they are those cells with narrow spatial frequency bandwidths. One is that direct RF mapping with a small spot or bar has revealed additional sidebands in the case of many cortical cells (R.L. De Valois et al., 1978; Movshon, Thompson, & Tolhurst, 1978b; Andrews & Pollen, 1979; Mulkkin, Jones, & Palmer, 1984). The results from such an experiment (Albrecht, 1978) are shown in Figure 4.14. From the spatial frequency tuning of each of these three cells (see right hand columns), RF profiles were predicted by the reverse Fourier transform (see lines in left hand column). The actual determinations of the RF profiles by mapping with a thin flickering line (data points in left column) are seen to fit the predicted curves quite well. The cells shown in Figures 4.14A and B have quite narrow spatial frequency tuning, with bandwidths of 0.8 and 0.9 octaves, respectively (see Figures 4.14D and E). The cross sections of their RFs are seen to have additional oscillatory sidebands.

A second type of evidence for multiple-oscillatory RFs for narrowly tuned cells comes from determining the number of cycles of a grating that produce the largest response from a cell. If a cell has a classic RF with one excitatory and two inhibitory regions, such as that shown in Figure 4.14C, increasing the number of cycles of a grating above $\frac{1}{2}$ cycles should produce no further increase in response. However, if there are additional sidebands, such as shown by those cells in Figures 4.14A and B, the response of the cell should continue to rise as additional numbers of cycles are added to a grating.

We (R.L. De Valois et al., 1985) find that such is usually the case (see Figure 4.15), and that cells that prefer more than 2 cycles of gratings are more narrowly tuned than those that respond maximally to less than 2 cycles, as would be predicted. If one considers just the 30% subpopulation of simple and complex cells that are narrowly tuned, with spatial frequency bandwidths less than 1.2 octaves, the average number of cycles in the optimum grating is 3.3, considerably more oscillatory than the classic 1.5-cycle RF.

We might note that if it makes little sense, as is discussed in Chapter 6, to consider even classic simple cells as bar detectors (as opposed to spatial frequency filters), it makes even less sense to so characterize a cell with a multiple-lobed, oscillating RF.

Cortical cells have been found to be tuned to a wide range of spatial frequen-
cies. As discussed earlier, there are two possible bases for such a range, with entirely different implications. One is that these differences in peak tuning might reflect a foveal-peripheral gradient in spatial frequency tuning. Foveal cells might be sensitive to high spatial frequencies (and, on the average, have small RFs), whereas cells located increasingly peripherally might be tuned to increasingly lower spatial frequencies (having generally larger and larger RFs). The other possibility is that there are cells tuned to each of a wide range of spatial frequencies present at each cortical locus (just as there are cells tuned to the complete range of orientations at each locus).

These two possibilities have quite different consequences for vision. Variations in spatial frequency tuning related just to eccentricity would account for the progressive loss of acuity with increasingly peripheral fixation, but would not provide a mechanism for processing complex visual stimuli by using multiple spatial frequency channels for each retinal locus. On the other hand, if cells with a wide range of peak spatial frequencies were all located in each cortical region, the substrate for multiple spatial channels would be present.
Hubel and Wiesel (1974b) indicate that the RF size of cortical units varies considerably with eccentricity, although their data also show some degree of variation in RF size at a given locus. As discussed earlier, RF size is also partially related to spatial frequency tuning. Quantitative measures of the spatial tuning characteristics of a large population of foveally related cells in monkey (R.L. De Valois, Albrecht, & Thorell, 1982) have clearly shown that cells tuned to each of a very wide range of spatial frequencies (over at least a 5-octave range), are all present in this one cortical locus. It is notable that cells tuned to very low spatial frequencies (as low as 0.5 c/deg) are found in the foveal projection region. The same was found to hold for a somewhat more peripheral site, except that cells tuned to the highest spatial frequencies were far fewer here (see Figure 4.16). With the progressive elimination of high spatial frequency cells with increasing eccentricity, the average RF size would increase with eccentricity, thus perhaps accounting for Hubel and Wiesel's (1974b) results, although more data would be desirable from far peripheral sites. But it is very clear that the cells in any one region do in fact encompass a wide range of peak spatial frequencies.

This point is supported also by 2-DG studies of spatial frequency organization in cat (Tootell, Silverman, & R.L. De Valois, 1981). The pattern of uptake seen with stimulation by a high spatial frequency pattern extends from the central region only part of the way to the peripheral cortex, not as far peripherally as the stimulus itself actually extends. A low spatial frequency pattern, on the other hand, produces columns extending over the whole stimulated area, including specifically the very central projection region. Thus both low and high spatial frequencies stimulate the foveally related cortex, but only low spatial frequencies the far periphery.

An anatomical characteristic which may be related to this progressive narrowing of the spatial frequency range with eccentricity is the progressive thinning of the peripheral cortex. In the far periphery it may only be about 40% as thick as it is in the central projection region. This could reflect a decrease in the total number of cells due to the elimination of cells tuned to high spatial frequencies. The distribution of peak spatial frequencies shown in Figure 4.16 indicates that most cells in the foveal area are tuned to the mid spatial frequency range at a photopic testing luminance. The distribution of cells can be seen to approximate the shape of the CSF at this luminance, with its maximum sensitivity at 1 to 6 c/deg and lower sensitivity to both low and high spatial frequencies.

The spatial frequency bandwidth of cortical cells is consistently related to their peak spatial frequency (Kulikowski & Bishop, 1981; R.L. De Valois, Albrecht, & Thorell, 1982): cells tuned to high spatial frequencies have on the average a somewhat narrower octave bandwidth than those tuned to lower spatial frequencies (see Figure 6.11). On an absolute frequency scale, of course, quite the reverse is true: the bandwidth in c/deg of cells tuned to low spatial frequencies is much narrower.

Simple and complex cells have very similar spatial frequency bandwidths, with simple cells slightly more narrowly tuned on the average than complex
FIG. 4.16  Peak spatial frequency tuning for samples of foveal and parafoveal cells in macaque striate cortex. The top panel shows the distribution of peak frequencies for the foveal sample. The middle panel has corresponding data for a parafoveal sample. The lower panel illustrates the difference between the two distributions. Note that the foveal sample has a higher proportion of cells tuned to high spatial frequencies (from R.I. De Valois, Albrecht, & Thorell, 1982, Vision Res., 22, 545-559. Copyright 1982, Pergamon Journals, Inc. Reprinted by permission).
cells. The distributions overlap almost completely. These results are in agreement with other quantitative studies of cat (Movshon et al., 1978c) and monkey cortical cells (Schiller et al., 1976c).

Finally, the peak spatial frequency sensitivities of simple and complex cells are also similar (R.L. De Valois, Albrecht, & Thorell, 1982); see Figure 4.17.

FIG. 4.17 Distributions of peak spatial frequency sensitivities for samples of simple and complex cells. Note that while there are both simple and complex cells tuned to all spatial frequency regions, the cells tuned to the highest frequencies are most often complex cells (from R.L. De Valois, Albrecht, & Thorell, 1982, Vision Res., 22, 545–559. Copyright 1982, Pergamon Journals, Inc. Reprinted by permission).
There are both simple and complex cells in the foveal projection area that are tuned to low, middle, and high spatial frequencies. Overall, however, complex cells are tuned to slightly higher spatial frequencies than are simple cells. It can be seen in the lower panel of Figure 4.17 that at high spatial frequencies the percentage of complex cells exceeds that of simple cells, so that, for instance, 10% of the complex cells in the sample collected by De Valois, Albrecht and Thorell, 1982, had spatial frequency peaks over 8 c/deg, whereas only 3% of simple cells were tuned to these very high spatial frequencies. This finding is consistent with the relative phase insensitivity of vision at high spatial frequencies (see Chapter 8), but it is surprising considering the fact that at subcortical levels the cells comparable to complex cells (the Y cells) have large RFs and are tuned to lower spatial frequencies than are X cells. However, it is by no means clear what the relation is between retinal and cortical cell types, as is discussed below.

Relation Between Spatial Frequency and Orientation
Spatial frequency and orientation are closely related to each other in terms of two-dimensional spatial frequency analysis (see Chapter 9). It is thus of particular interest to consider the relationship between the tuning of cells along these two parameters. There have been two studies (Movshon et al., 1978; R.L. De Valois, Albrecht, & Thorell, 1982) which have quantitatively measured both the orientation and the spatial frequency tuning of a large sample of cells (in cat and monkey cortex, respectively). Both studies found a strong positive correlation between narrowness of tuning of cells along these two dimensions. Cells that are narrowly tuned for orientation tend likewise to be narrowly tuned for spatial frequency. Cells with very broad spatial frequency tuning, e.g., > 2 octaves, tend to be nonoriented.

Putting together the outputs of the two eyes into a binocular organization is certainly one major feature of striate cortical processing. The other main accomplishments at this level appear to be that of developing orientation and spatial frequency selectivity (which together constitute two-dimensional spatial frequency selectivity) in multiple channels. Since there are multiple synaptic levels within the striate, it is possible that the cells with differing narrowness of two-dimensional spatial frequency tuning may be at different stages in this process. Indeed, Hubel and Wiesel (1968) have shown that most of the nonoriented cells are in layer 4, the input layer of the cortex. On the other hand, it is conceivable that there is some functional benefit to the system to have cells with varying narrowness of tuning: the cells with narrow and those with broad spatial tuning may subserve different visual roles.

A two-dimensional spatial frequency filtering would require some degree of independence between spatial frequency and orientation tuning. To encode faithfully the presence of a certain range of spatial frequencies in the local stimulus, a cell should show the same spatial frequency tuning regardless of the orientation of the test grating, and vice versa. As pointed out by Daugman (1980), the classic Hubel and Wiesel (1959, 1962) model of a cortical simple cell RF (made by summing the outputs of an aligned group of LGN cells) would be
expected to show very different spatial frequency tuning at off-orientations, compared to those shown at the peak orientation. Therefore, a cell with this “classic” RF shape would not have any single two-dimensional spatial frequency range to which it would confine its responses. This is obviously not at all what would be desired for a two-dimensional spatial filter. On the other hand, a two-dimensional Gabor function RF (a sinusoidal tapered by a gaussian in both x and y) would show fairly constant spatial frequency tuning regardless of orientation.

Tests of the responses of cells to gratings of a wide range of spatial frequencies and orientations (Webster & R.L. De Valois, 1985) show that actual striate cells behave much as would be predicted if the RFs approximated a two-dimensional Gabor function: they show some but only slight change in spatial frequency tuning with variations in orientation. From these measures of cells’ responses to various spatial frequencies at multiple orientations, and vice versa, one can determine the precise response characteristic in the frequency domain, and the space RF by the inverse Fourier transform of this. An example of such a two-dimensional RF is given in Figure 4.18. It can be seen in Figure 4.19 that the RF shape of a typical cell closely approximates a Gabor function in both x and y.

Variations With Eccentricity

The characteristics of cells at different visual eccentricities unfortunately have not been as extensively studied as one would like. We have already mentioned that the average peak spatial frequency of cells shifts to lower frequencies with increasing eccentricity (and thus the RF size in general goes up), but that this most likely results from a progressive loss of cells tuned to high spatial frequencies, low-frequency cells being found in all cortical areas. The orientation peaks also change somewhat with eccentricity (Mansfield, 1974; R.L. De Valois, Yund, & Hepler, 1982), with an even balance between vertical and horizontal cells versus oblique ones found peripherally, and an imbalance toward the former found in the foveal projection regions.

Although the peak spatial frequency and orientation tuning of cells changes with eccentricity, the narrowness of tuning does not appear to do so, at least within the fovea and near parafovea (R.L. De Valois, Yund, & Hepler, 1982). Parafocal cells appear to be performing as precise an analysis of stimuli as foveal cells, although over a more restricted (and lower, on the average) spatial frequency range.

In an extensive study of cat striate cortical cells at different eccentricities, J.B. Wilson and Sherman (1976) found that the proportion of simple cells to complex cells falls off drastically with eccentricity (although one study has failed to confirm this finding; Berman & Payne, 1982). If this is so, the central (equivalent to the foveal) cortex has mainly simple cells and the far periphery almost exclusively complex cells. As Wilson and Sherman point out, the same relationship holds in the retina between X and Y cells, which are functionally similar to cortical simple and complex cells, respectively. The possible relevance of this to color and phase specificity of vision at different eccentricities is discussed in Chapters 7 and 8.
FIG. 4.18 Three-dimensional representations of the RF profiles (in both space and frequency domains) of a fairly narrowly tuned cat simple cell. In the frequency domain plot it can be seen that the cell responds to a delimited, compact range of spatial frequencies. Note in the space domain plot that this cell has an oscillatory RF with multiple lobes along the x axis and is elongated in the y direction (from Webster & R.L. De Valois, 1985, *J. Opt. Soc. Am. A, 2*, 1124–1132. Reprinted by permission).
Functional Architecture

Interrelation of Functional Cell Types

The manner in which cortical cells are interconnected is a major question for cortical physiology and anatomy, but is of somewhat lesser concern with respect to the topics we are covering here. Hubel and Wiesel (1959, 1962) first suggested what is now the classical model of interrelations among cortical cell types. We will briefly discuss this model and the evidence for and against it.
The Hubel and Wiesel model (which, we should note, they have repeatedly emphasized was put forth only as a tentative working hypothesis) is that there is a systematic, hierarchical order of cells in the cortex, as is present in the retina with receptors—bipolars—ganglion cells. In cortex, they propose that simple cells are formed by ordered arrays of LGN cell inputs and in turn form the input to complex cells. The complex cells then feed together to produce hypercomplex cells, which presumably are the output cells that project to other levels. Since many nonoriented cells were found in monkey cortex, Hubel and Wiesel amended this description (which was initially based on their recordings in cat cortex) to add a fourth level in primate, consisting of nonoriented cells, between LGN and simple cells, (Hubel & Wiesel, 1968). Since in recent formulations they have questioned, as have others (Schiller et al., 1976a), whether hypercomplex cells constitute a separate category of cell, the central tenet of their proposal is that of a hierarchical relationship between simple and complex cells.

A second aspect of Hubel and Wiesel’s (1962) model of cortical organization is that each of these cell types receives only excitatory inputs from the preceding level, and that the critical response characteristics of both simple and complex cells are determined by the RF locations of the cells providing these excitatory inputs. Thus simple cells produce their orientation selectivity by summing inputs from a number of LGN cells (or nonoriented cortical cells) whose RFs are systematically displaced spatially with respect to each other in a row at a particular orientation. The RF of the simple cell, then, would be the sum of the RFs of the input cells. A similar arrangement is envisioned in which complex cells sum together the outputs of simple cells whose RFs are displaced laterally with respect to each other.

Much evidence has been brought to bear, pro and con, on each of these aspects of the influential Hubel and Wiesel model of cortical architecture. It is at present not clear to what extent the basic hierarchical model must be modified or discarded (D. Rose, 1979); the weight of evidence clearly supports a major modification of the purely excitatory aspect of the model, however.

Hubel and Wiesel (1959, 1962) described and differentiated simple from complex cortical cells before Enroth-Cugell and Robson (1966) distinguished between retinal X and Y cells. If the order had been reversed it would perhaps have been more apparent that simple cells are functionally similar to X cells in terms of spatial summation, and complex cells to Y cells. The possibility of simple and complex cells being arranged in parallel rather than serially might have therefore been given more serious consideration. There is considerable evidence for at least a partially parallel arrangement. It has often been shown (e.g., Hoffman & Stone, 1971; Stone, 1972; Bullier & Henry, 1979a, 1979b, 1979c; Henry, Harvey, & J.S. Lund, 1979) that many complex cells, as well as many simple cells, receive a direct monosynaptic input from the LGN. But Bullier and Henry found that both X and Y geniculate cells feed into both simple and complex cortical cells, so the cortical dichotomy is not just an extension of the earlier X-Y separation. Further evidence for parallel processing in the cortex is the finding by Gilbert (1977) that as many as 40% of the cells in the main striate input layer,
layer 4c, are complex cells. Furthermore, some complex cells have response properties that are not seen in simple cells and that cannot readily be derived from a summation of simple cell inputs: they respond to random dot patterns and other complex textures to which simple cells do not respond (Hammond & MacKay, 1975); some complex cells respond to higher velocities of stimulus movement than any simple cells do (Movshon, 1975); few complex cells show inhibition by off spatial frequencies, although virtually all simple cells do (K.K. De Valois & Tootell, 1983). All of this rather convincingly argues that at least some, if not all, complex cells must have a direct input that does not come solely from simple cells.

There is also convincing evidence that simple as well as complex cells must feed on to later centers, counter to the hierarchical model in which only complex (or hypercomplex) cells project out of striate cortex. The most compelling evidence is that we certainly have absolute phase-specificity in our visual perception, and ability to distinguish black from white (and red from green and blue from yellow); see Chapters 7 and 8. Since only simple cells are phase specific, however, their output must go on to later centers, not just end on complex cells, which have no phase specificity in this sense. The same argument holds with respect to cells in V4 or elsewhere with color specificity (Zeki, 1973), which they could not have if their input were purely from complex cells.

We can thus safely conclude that the phase-specific simple cells and non-phase-specific complex cells must to some degree be in parallel in the striate, both in their inputs and in their outputs. As we argue elsewhere in this book, each of these cell types is carrying useful, and quite different, kinds of visual information. The presence of both of their distinctive characteristics is evident in the ultimate visual percept. One need not conclude, however, that simple and complex cells form totally parallel paths from retinal and geniculate X and Y cells, respectively. It is entirely possible that some complex cells are constructed from simple cell inputs, as Hubel and Wiesel suggest, while others receive a direct Y-cell input from the LGN; or both simple cells and LGN Y cells might feed into complex cells in general. A detailed discussion of various possible models is to be found in D. Rose (1979).

There are a number of observations which suggest that complex cells are at least partially constructed within the cortex, as Hubel and Wiesel proposed, rather than just being the cortical component of the Y-cell path. One is that whereas Y cells are very rare in the retina (perhaps 3% in cat retina), complex cells constitute approximately 50% of the cortical population. Another is the fact (discussed earlier) that complex cells are tuned on the average to higher spatial frequencies than are simple cells (R.L. De Valois, Albrecht, & Thorell, 1982), whereas retinal Y cells are tuned to lower spatial frequencies on the average than are retinal X cells. Finally, complex cells have certain properties, e.g., sensitivity to binocular disparity and to the two-dimensional Fourier spectral components of patterns (K.K. De Valois, R.L. De Valois, & Yund, 1979), which would not be expected if they received input only from LGN Y cells, but would be if they were built up at least partially from cortical simple cells.
Although these are important questions of physiological and anatomical organization, they are secondary from our point of emphasis here on functional properties. The critical consideration with respect to spatial vision is that there are two different cortical systems, however constructed, one with and one without spatial phase specificity.

A second aspect of the Hubel and Wiesel (1962) hierarchical model is its postulate that cortical cells gain their response properties from the precise architectural arrangement of RFs of cells at the preceding stage. For instance, the orientation selectivity of simple cells is assumed to arise from excitatory inputs from specific LGN cells whose RFs are systematically displaced with respect to each other. An alternative possibility is that much if not all of the orientation and spatial frequency tuning is produced by intracortical inhibitory interactions.

One strong bit of evidence for a prominent role for cortical inhibition is the great prevalence of inhibitory synapses of intracortical origin on all cortical cells. Recording intracellularly from cortical cells, Creutzfeldt, Kuhnt, and Benevento (1974) found large inhibitory as well as excitatory postsynaptic potentials. Lee, Cleland, and Creutzfeldt (1977) also found that the excitatory RF region of striate cells is essentially circular, not elongated, so that the orientation tuning must be a result of inhibitory inputs. In cells with sufficient maintained discharge for a decrease in firing to be seen, strong inhibitory responses are found to stimuli of off-orientations in both simple and complex cells (R.L. De Valois, Yund, & Hepler, 1982). The same is true for spatial frequency: frequencies off the peak of a cell’s preferred spatial frequency (particularly higher spatial frequencies) are often found to profoundly inhibit the cell (K.K. De Valois, 1978; K.K. De Valois & Tootell, 1983).

The strongest direct evidence for a prominent role for intracortical inhibition in producing orientation and direction selectivity comes from observing the effects of blocking the presumed inhibitory transmitters (Sillito, 1975; Sillito, Kemp, Milson, & Berardi, 1980). There is good evidence that GABA serves as an inhibitory transmitter in the cortex; if an agent (bicuculine) that blocks GABA is injected in the vicinity of the recording electrode, most cells soon show a greatly decreased direction and orientation selectivity. Some become completely nonoriented. Since the excitatory inputs are presumably not affected by bicuculine, they must not be providing the orientation tuning.

One of the attractions of the idea that striate cells gain their selectivities by intracortical interactions rather than by a very precise set of inputs from earlier levels is that the neural connections involved (and thus the requirements for genetically specifying them) would be greatly simplified (Swindale, 1979). It would also provide a good rationale for the systematic arrangement of cortical cells by orientation and spatial frequency, with cells tuned to neighboring regions along these dimensions being located next to each other. To sharpen their tuning, cells would require inhibitory inputs from other cells with slightly different selectivities. This would be simplified with systematic columnar arrangements.
Modular Structure and Columnar Organization

A modular organization of the striate cortex was first found by Hubel and Wiesel (1962, 1974a) in single-cell recording experiments in both cat and monkey. In recording with an electrode penetration at right angles to the cortical surface, they found that successive cells had certain response characteristics in common. Specifically, the peak orientation tuning and the laterality of the cells (whether the cells were responsive just to the contralateral eye, just to the ipsilateral eye, or to both) in a "column" through the cortex would all be nearly the same. A probe through an adjacent region would encounter cells with RFs that overlapped with those of the cells in the first column, but that had a quite different orientation peak and/or laterality of response (these being the two variables on which they concentrated). The cortical arrangement was most clearly delineated with the use of oblique or tangential probes, more parallel to the cortical surface. Figure 4.20 shows the results from one such experiment (Hubel & Wiesel, 1974a) in which each successive cell in an oblique traverse had a slightly different peak orientation. It can be seen that the peak orientations repeat after about 0.8 mm across the cortex. This cortical expanse, which contains cells tuned to the full range of orientations, was termed by Hubel and Wiesel an orientation hypercolumn.

In recordings made from layer 4 cells, Hubel and Wiesel (1974a) also found evidence for ocular dominance hypercolumns. The cells along a tangential probe for about 0.5 mm might have an ipsilateral eye preference, then for the next 0.5 mm the contralateral eye would be dominant. Such an ocular dominance orga-

![Diagram](https://example.com/diagram.png)

FIG. 4.20 Orientation tuning of successively encountered cells during an oblique electrode penetration of monkey striate cortex. Note the systematic variation of orientation tuning with distance as the electrode traverses cortical columns (from Hubel & Wiesel, 1974a. Reprinted by permission).
nization is present in both cat and monkey, but it is clearer in the latter. In the
approximately 1-mm extent across the cortex of such an ocular dominance
hypercolumn, there would be two orientation hypercolumns, one for each eye.
Hubel and Wiesel also reported that the cells within such hypercolumns have
overlapping RFs; going still further across the cortex one would encounter the
same sequence of orientation and laterality changes again, but with the RF loca-
tion of the cells shifted to a neighboring (though partially overlapping) region of
the visual field. There is also anatomical evidence for such ocular dominance
columns in the human visual cortex (Hitchcock & Hickey, 1980).

Although ocular dominance and orientation hypercolumns were first found in
recording experiments, the organization across the whole cortex can be more
readily established in anatomical experiments. The ocular dominance organi-
ization was clearly revealed in an experiment in which radioactive proline was
injected into one eye of a monkey (Wiesel, Hubel, & Lam, 1974). Proline is
transneuronally transported to the cortex. Autoradiography of the cortex then
reveals the regions where the inputs from the labeled eye project. It was also
shown by a reduced silver staining of the cortex (Le Vay, Hubel, & Wiesel,
1974); see Figure 4.21. Seen in cross section the ocular dominance organization
is columnar (although only pronounced in layer 4). In tangential sections of the
cortex, however, these columns form strips across the cortex of a constant width,
but taking fairly random directions. The ocular dominance organization can also
be seen in 2-DG studies. If only one eye is stimulated, the cortical cells and
processes responsive to that eye will take up the radioactive 2-DG and be
revealed by autoradiography. This can be seen in the retinotopic study illus-
trated in Figure 4.1. Only one eye was stimulated by the ring-and-ray pattern in

![Diagram of ocular dominance slabs in monkey striate cortex](image)

**FIG. 4.21** Ocular dominance slabs in monkey striate cortex reconstructed from tangen-
tial sections, using a reduced silver stain (from Le Vay, Hubel & Wiesel, 1975. Reprinted
by permission).
that experiment. The small dark square within each module is the ocular dominance column related to the stimulated eye; the adjacent nonradioactive region is that connected with the unstimulated eye.

Hubel, Wiesel, and Stryker (1978) used this 2-DG technique to examine the orientation arrangement across the cortex. Stimulation with a pattern of a single orientation was found to produce a columnar pattern of 2-DG uptake in a cross section through the cortex. In a tangential section through the cortex, these columns were seen to combine into strips across the cortical surface. By combining proline injection into one eye and the 2-DG technique with a single-orientation stimulus pattern during injection, it is possible to see the relationship between the ocular dominance and the orientation slabs. These slabs appear to intersect at random angles rather than in a simple systematic way that would make it conceptually easy to visualize. Nonetheless, the arrangement is such that nearby regions related to each eye would include cells tuned to every orientation.

The picture thus far in cat cortex is of a block of cells about 0.5 mm on a side related to one eye and consisting of strips of cells of common orientation selectivity so that across one edge of the block there would be cells tuned to each orientation in turn. Adjacent to this in some direction would be a corresponding block related to the other eye. These two orientation hypercolumns and one ocular dominance hypercolumn together would constitute what we shall term a cortical module (CM), since it appears to consist of all the cortical cells with different functional properties and selectivities that are processing information from one general area of the visual world.

What about the other dimension across the cortical surface? Are all the cells in a given orientation slab within an ocular dominance column alike in other characteristics, or is another dimension arranged in columnar strips at right angles to orientation? There is evidence that another dimension, namely, spatial frequency, is in fact laid out across the cortex in a manner similar to that found for orientation. If, using the 2-DG technique, one presents a cat with a pattern consisting of every orientation (presented sequentially) but only a single spatial frequency, a cortical pattern very similar to that seen with presentation of just a single orientation at every spatial frequency is obtained (Tootell, Silverman, & R.L. De Valois, 1981; Silverman, 1984). In cross section, columns of 2-DG uptake are seen going through all cortical layers, indicating a columnar spatial frequency organization (see Figure 4.22). The distance between spatial frequency columns (a spatial frequency hypercolumn) is roughly 1 mm, about the same as an orientation hypercolumn. In tangential sections, it can be seen that the cells tuned to a single spatial frequency are arranged in slabs or bands across the cortical surface, again similar to the pattern seen for orientation. However, the directions of the orientation and spatial frequency slabs differ from each other (Silverman, 1984). The orientation slabs in cat appear to run at right angles to the vertical meridian at the V1–V2 border, but the spatial frequency slabs appear to radiate out more from the area centralsis projection region. Such an arrangement would produce a regular intersection of spatial frequency and orientation slabs. Such a model is diagrammed in Figure 4.23. When an animal is presented
FIG. 4.22 Autoradiographs from a 2-DG study of spatial frequency organization in cat striate cortex. In A is a cross section through the cortex of an animal exposed to a pattern of all orientations but only a single spatial frequency, 1.8 c/deg (a high spatial frequency for a cat). Columns of high 2-DG uptake can be seen around the right-hand arrow, which indicates the cortical representation of the center of the retina. The visual pattern extended all the way out to the peripheral region indicated by the left-hand arrow, but columnar uptake to this high spatial frequency pattern is seen only in the region of the area centralis. In B is a cross section through the cortex of a control animal that was shown a pattern of all spatial frequencies at all orientations. Note the absence of columns. In both A and B continuous high 2-DG uptake can be seen in the cortical input layer, layer 4. The calibration bar is 2 mm. The bubbles in both A and B are histological artifacts (from Tootell et al., 1981, Science, 214, 813–815. Copyright 1981, AAAS. Reprinted by permission).

with a single spatial frequency at a single orientation, only those cells sensitive to that particular spatial frequency and that particular orientation should be activated, and thus just the intersections between these two cortical organizations should be seen. Such is the case. In tangential sections of the cortex of a cat exposed to one spatial frequency at one orientation one sees a leopard-like dot pattern rather than the zebra-like stripe pattern seen with either of these variables alone. That the spatial frequency and orientation organizations are sys-
The organization in cat striate cortex exposed to a pattern of spatial frequency is indicated by the regularity of the intersection points seen in such a section.

In macaque monkey cortex, there also appears to be a systematic modular arrangement of ocular dominance, orientation, and spatial frequency, but with somewhat different pattern from that in cat. One striking peculiarity of the primate striate cortex, as opposed to that of the cat, is that there is a very non-uniform distribution of cytochrome oxidase (cyt-ox), a metabolic enzyme found in the mitochondria of cells (Horton & Hubel, 1981; Horton & Hedley-White, 1984). If a tangential slice through the cortex is stained for cyt-ox, numerous spots or blobs are seen (see Figure 4.24). These cyt-ox-rich blobs are most prominent in layer 3, but they are also apparent in the other cortical layers, with the possible exception of layer 4 (Horton, 1984). They are associated with a fine LGN projection, which can be seen in fiber stains of layer 3 of the flattened cortex (Tootell, Silverman, R.L. De Valois, & Jacobs, 1983). The cyt-ox blobs are fairly regularly spaced at ca. 0.5 mm separation, and there are a total of about 5,000 of them across the whole striate cortex.

Although the cyt-ox blobs associated with one eye disappear with long-term enucleation, their appearance does not depend on the short-term nature or level
of visual activity. They can thus be used as landmarks on the otherwise uniform-appearing striate cortex, to help in the elucidation of the cortical functional architecture. With the 2-DG technique, the orientation organization can be seen in one animal and the spatial frequency in another, but in the absence of cortical landmarks one cannot tell how these are related to each other. However, since one can combine 2-DG autoradiography and cyt-ox staining on the same brain section (Silverman & Tootell, in preparation) the interrelations among the various types of functional organization can be obtained by seeing how each in turn is related to the cyt-ox blobs.

In one such experiment, a pattern of all spatial frequencies at all orientations was presented to one eye, to activate all the cells in one set of ocular dominance columns. An autoradiographic section was then computer processed and dichotomized into low-uptake and high-uptake regions. The results were ocular dominance stripes across the cortex that had the appearance of zebra stripes. When the cyt-ox uptake pattern from this same brain section was similarly treated, the result was the pattern of cyt-ox blobs scattered across the striate. When these two patterns were superimposed, it could be seen that the cyt-ox blobs are located right in the middle of the ocular dominance columns, either in the middle of the ocular dominance strips from the unactivated eye or that from the activated eye (Switkes, Tootell, Silverman, & R.L. De Valois, 1986). There thus are two blobs for each ocular dominance hypercolumn, and two or four for each CM, depending on one's model.

What about the relationship between the blobs and other functional group-
ings? The evidence is clearest in the case of spatial frequency (Tootell, Silverman, Switkes & R.L. De Valois, 1982b). A stimulus containing all spatial frequencies at all orientations produces an almost uniform cortical uptake pattern in a 2-DG experiment, with just slight inhomogeneities due to the cyt-oxy blobs to be seen in tangential sections. A pattern of just a low spatial frequency (e.g., 1 c/deg) at all orientations, on the other hand, produces a very dot-like 2-DG uptake pattern extending across the whole stimulated cortex. The low spatial frequency 2-DG dots are superimposed on the cyt-oxy blobs when the 2-DG and cyt-oxy patterns from the same section are superimposed. When a high spatial frequency, e.g., 8 c/deg, is used, the cortical pattern is very different. First of all, the high spatial frequency pattern only extends out a small distance into the periphery, rather than covering the whole cortex related to the retinal areas stimulated. Second, the pattern seen in tangential sections is also very different from the low-frequency pattern: it looks like an array of doughnuts. When superimposed on the cyt-oxy blobs from the same section, the high spatial frequency doughnut pattern is seen to lie all around the blobs, which coincide with the holes in the doughnuts. Most interesting is the pattern seen with an intermediate spatial frequency of 3 c/deg. Stimulation in a 2-DG experiment with that spatial frequency produces uptake in the whole 6° stimulated area, but the pattern varies with eccentricity. In the foveally related cortex it is dotty (like a low spatial frequency pattern), whereas in the peripheral cortex it is like doughnuts (like a high spatial frequency pattern). It thus appears that the spatial frequency organization in the CM is a radial one, with low spatial frequencies (low frequencies for that eccentricity) in the center of the module, coinciding with the cyt-oxy blob, and high spatial frequencies increasingly farther out.

The orientation organization in monkey is quite different from that for spatial frequency. In cross section through the cortex both are columnar, but stimulation with one orientation at all spatial frequencies produces stripes in tangential sections that skirt but do not go through the cyt-oxy blobs. The patterns for different orientations presumably go in different directions within a CM. The overall two-dimensional spatial frequency (spatial frequency by orientation) pattern within a CM, then, bears some resemblance to a two-dimensional spectral polar plot, with orientation at different axes and spatial frequency increasing radially out from the center (see Figure 4.25).

Livingstone and Hubel (1984) report that the basic organization with respect to the cyt-oxy blobs is related to color, with color-selective cells in the blobs and not outside. Their color experiments are confounded with spatial frequency, however, since they have used low spatial frequency chromatic patterns to test for color selectivity. A low spatial frequency color pattern does indeed produce 2-DG uptake on the blobs, but so does a low spatial frequency isochromatic luminance-varying pattern. And a high spatial frequency color grating of 6 c/deg activates cortical regions outside the blobs (Tootell et al., in preparation).

One problem that is not completely understood is the relationship between the functional organization of the cortex (ocular dominance, orientation, and spatial frequency hypercolumns) and the retinotopic mapping onto the cortex.
Retinotopic mapping implies that neighboring cortical areas represent neighboring retinal locations, but the functional mapping indicates that a neighboring cortical area may contain cells with a different orientation, spatial frequency, or ocular dominance selectivity. How does the brain avoid being able to see only one orientation at one location, and another orientation at a neighboring location, etc.? This may not be that much of a problem, for several reasons. One is that it is not clear to what extent the retinotopic mapping extends down to small cortical distances. There is some evidence for a shift in RF location with small displacements in cortical recording loci, particularly in layer 4, but there are also reports of considerable scatter in RF center locations within a given column (Hubel & Wiesel, 1974b). It may be that the retinotopic mapping only provides relatively coarse positional information, finer localization (other than in layer 4) being encoded in other ways, e.g., in terms of phase (see Chapter 8).

Another reason that there may not be a conflict between retinotopic and functional mapping in the cortex is that the cortical modules are very small with respect to the RFs of most cells. In the foveal center, for instance, the distance
between neighboring CMs may correspond to only 0.15° visual angle (see earlier discussion of cortical magnification factor). This corresponds to the RF diameter of a cell tuned to about 20 c/deg (with an oscillating RF consisting of 2 or more cycles of excitation and inhibition). There are very few cortical cells tuned to higher spatial frequencies than that; the RFs of all the 99+% of cells tuned to lower spatial frequencies would extend not only over neighboring orientation columns but also across whole neighboring CMs. In fact, a foveal cell tuned to some low spatial frequency, say 0.5 c/deg, will have an RF covering the regions of visual space analyzed by dozens, if not hundreds, of neighboring CMs. In the periphery, each CM covers a larger retinal area, but the RFs of the highest frequency cells would be correspondingly larger. There would not, then, be any gaps in the visual field for certain classes of stimuli.

The overall model we have arrived at suggests that the primate striate cortex is divided up into perhaps 2,000 to 3,000 CMs, each about 0.5 by 0.7 mm, across the cortical surface. Each CM processes information from a particular, different locus in the visual field, to a considerable degree overlapping with that represented in the neighboring CMs. The RFs of cells tuned to the very highest spatial frequencies within a CM may overlap minimally with those in the neighboring CMs, but the vast majority of cells, those tuned to middle and low spatial frequencies, will have RFs that overlap many neighboring CMs. The size of the CMs is fairly constant across the cortex (slightly smaller in the periphery), but the distance across the visual field between adjacent CM centers varies greatly with retinal eccentricity, from about 0.1° visual angle in the case of foveally related CMs, to several degrees for those related to far peripheral regions. Each CM contains perhaps 100,000 to 200,000 cells, and consists of an arrangement of orientation columns intersecting with spatial frequency columns. Since orientation by spatial frequency is the same as two-dimensional spatial frequency (see Chapter 9), this means that within each CM are cells tuned to each of the many regions in two-dimensional spatial frequency space. Those tuned to a given two-dimensional spatial frequency region at a given location in space are all arranged in a column through all six cortical layers. This whole array is duplicated within the CM, once for each eye, the separation of the inputs from the eyes being considerable in layer 4, but much less in upper and lower layers, thus providing for the possibility of extracting information about the third dimension as well (see Chapter 10).

Color in Cortex

We are not concerned in this book with color processing per se: that deserves and has received volumes devoted to it alone. Rather, we consider color only in relation to spatial vision. However, since we believe color to play an important role in spatial vision, we need to examine the spatial processing of color-varying, as well as luminance-varying, stimuli. Almost all studies of the cortical processing of spatial information have used just luminance-varying patterns (under-
standably so, of course, in studies of cat cortex). Thus relatively little is known about color-spatial processing.

The cells in the macaque LGN (see Chapter 7) have a low-pass spatial frequency characteristic in response to pure color stimuli. LGN cells, which show a modest low spatial frequency drop to luminance-varying patterns, show no low-frequency attenuation at all to color-varying stimuli (R.L. De Valois, Snodderly, Yund, & Hepler, 1977). Most cortical cells, on the other hand, show a band-pass spatial frequency characteristic both to luminance-varying and to color-varying gratings (Thorell, 1981; Thorell et al., 1984). A given cell may respond optimally to a red-green grating of 2 c/deg, with considerably less sensitivity to red-green gratings of either higher or lower spatial frequency, giving no response at all to patterns above, say, 4 or below 1 c/deg.

To a first approximation the tuning characteristics of cortical cells to pure color-varying patterns are the same as those to pure luminance-varying patterns we have been considering up to now. Most cells have fairly narrow spatial frequency bandwidths, and cells tuned to a variety of spatial frequencies are to be found in a CM (Thorell et al., 1984). The cells also show orientation selectivity to pure color patterns, with about the same orientation bandwidths as are shown to luminance patterns. Within a cortical region, cells are found with peak sensitivities to each of the various orientations for color patterns, as was found for luminance-varying patterns.

As discussed earlier, stimulation with luminance-varying patterns reveals two fundamentally different varieties of cortical cells: simple and complex cells. Both of these cell types are also to be found among those responsive to pure color patterns. For instance, some (simple) cells will fire to red on green and inhibit to green on red at the same RF location (the red and green being equated for luminance). Other (complex) cells will fire both to red on green and to green on red at the same RF location (R.L. De Valois, 1972; Thorell et al., 1984). The distinctions made earlier between the responses of simple and complex cells to drifting and to counterphase-flickering luminance gratings also apply to their responses to isoluminant color gratings.

There have been reports that there is a dichotomy among cortical cells, some responding to color stimuli and others to luminance patterns (Gouras, 1974; Michael, 1978a, 1978b, 1978c). We find, on the contrary, that most of the same cells respond to both color and luminance patterns, as was true also for the LGN. Specifically, about 80% of foveal macaque cortical cells respond both to luminance-varying and to color-varying patterns, and show much the same responses to each (Thorell et al., 1984). Smaller percentages respond to only one or the other.

Although, as we have been pointing out, cortical cells to a first approximation show similar responses to pure color as to pure luminance patterns, there are certain differences. Although most cells have similar color and luminance spatial frequency bandwidths, when they differ it is almost always in the direction of a broader color tuning resulting from less low-frequency attenuation (Thorell et al., 1984). Furthermore, fewer of the cells tuned to the highest spatial frequencies
are color responsive. The net effect of these two differences is that the color sensitivity averaged across all cells is shifted to lower spatial frequencies and shows little decrease in sensitivity to low spatial frequencies, compared with the overall responses to luminance patterns (Thorell et al., 1984). This is in agreement with the difference between the color and luminance behavioral contrast sensitivity function (see Chapter 7).

Later Cortical Areas

Our discussion so far has been restricted to the striate cortex, to only the first of at least a half dozen cortical regions that have been anatomically and physiologically identified as being involved with the processing of visual information. It would clearly be desirable to understand the anatomy and physiology of these later centers and how they further process visual information. We believe, however, that it is premature for that endeavor, since not enough is understood either of the detailed physiology of these later centers or of the likely functional processes, relevant to spatial vision, that operate at those levels.

One issue with respect to post-striate physiology that seems worth raising, however, is the evidence for or against a progressive hierarchical arrangement of cells in subsequent visual areas. That is, is visual information processed serially through the striate, then successively through cells in V2, V3, . . . , or are the later areas more in parallel, each dealing with a different subset of the total? A serial arrangement was rather suggested by the early results of Hubel and Wiesel in which they found mainly simple and complex cells in V1, but mainly complex and hypercomplex cells in V2 and V3 of cat (Hubel & Wiesel, 1965). Since they were arguing for a serial arrangement of simple to complex to hypercomplex cells, these findings supported a serial arrangement in later levels. This position was built upon by others to construct perceptual models of increasingly specific feature detectors (Neisser, 1967; Lindsay & Norman, 1972). The actual increases in specificity of units in V2 and V3 compared with V1, however, did not seem to be nearly as great as demanded by these models.

Recent studies of the anatomical connections among the various poststriate areas indicate a combination of serial and parallel processing, with an emphasis on the latter. Cells in V1 project to a number of other regions, in a parallel fashion, with many of these outputs coming from different laminae of V1. The best worked out of these are the projections from layer 2 and 3 cells of V1 to V2; from layer 4b and 5 cells to MT; from other layer 5 cells to the superior colliculus; and from layer 6 cells to the LGN (J.S. Lund et al., 1975). There have also been reports of V1 projections to V3 and V4 (Zeki, 1978). In addition, the various poststriate regions appear to differ considerably in the retinal regions represented (Allman, Baker, Newsome, & Petersen, 1981). In MT different retinal eccentricities are more uniformly represented than is the case with V1 (which, as we have noted, has a great magnification of the foveal retina), whereas another poststriate region, DL (dorsolateral), is largely restricted to processing
input just from the central retina. All of this suggests a parallel organization, of different poststriate (and subcortical) regions receiving and further analyzing different aspects of the information in V1. On the other hand, there are also projections from V2 to MT, which in turn projects to the inferotemporal cortex (IT), to form a serial series V1 to V2 to MT to IT; there is also a serial path from V1 to V2 to V4 to IT.

Physiological studies also suggest that poststriate areas are specialized for dealing with subportions of the total visual information, in a combined serial and parallel arrangement (Zeki, 1973, 1978; Allman et al., 1981; Van Essen & Maunsell, 1983). Specifically, cells in MT (also termed the superior temporal sulcus movement area, and V5, by Zeki, 1978) appear to be particularly involved with the analysis of stimulus movement. Virtually all the cells here are direction sensitive, and they appear to be selective for movements in particular directions in the frontoparallel plane or in depth (Zeki, 1974, 1978). Furthermore, some at least appear to be putting together information about the movement direction of various spatial frequency components of an object into a response to the overall pattern movement direction (Movshon et al., 1985).

Cells in V2, on the other hand, have been reported to be selective for stereoscopic depth (Hubel & Wiesel, 1977; Proietto & Fischer, 1977). Finally, the cells in V4 have been reported to be color-selective (by Zeki (1973); he reported not only visual motion, but also that they are arranged in color columns. Although these reports on V4 have been disputed (Schein, Marrocco, & de Monasterio, 1982), no one questions that there are great differences in the functional characteristics of the cells located in the various poststriate areas.

The physiological evidence, then, along with the nature of the anatomical projections, suggests that the visual information after V1 is processed more in a parallel than in a serial arrangement. From the point of view of spatial vision, however, there is a paucity of physiological information from poststriate areas to indicate the nature of these later processing steps. The generally parallel anatomical organization, however, suggests that there may be a limited number of synaptic levels beyond V1 for the processing of spatial information.