Visual Cortical Neurons: Are Bars or Gratings the Optimal Stimuli?

Abstract. *Neurons in the visual cortex of monkeys and cats have been characterized as either (i) bar and edge detectors or (ii) cells selective for certain spatial frequencies. To assess which of these functional descriptions is more accurate, we measured (i) the selectivity and (ii) the responsivity-sensitivity of these neurons to bars of various widths and gratings of various spatial frequencies. All of the cells recorded from were considerably more selective along the dimension of spatial frequency than along the dimension of bar width. Further, most were more responsive and sensitive to the grating of optimal frequency than to the bar of optimal width.*

In their pioneering recordings from cells in the cat and monkey visual cortex, Hubel and Wiesel (*1*) described the cortical cells as responding optimally to bars and edges. The optimal stimulus appeared to consist of an elongated object of a specified orientation, some cells being maximally sensitive to edges and others to white or black bars. Those cells optimally sensitive to bars were reported to be selective for bar width, being more narrowly tuned spatially than were cells at lower levels. On the basis of these results, others (*2*) have developed models of the spatial processing of the visual system in which "simple" cortical cells analyze the visual world into bars and edges of varying orientations, widths, and locations; later cells, in a hierarchical organization, presumably combine these characteristics in various arrangements to represent the visual objects in our perceptual world.

A different model of how the visual system might analyze visual space was proposed by Campbell and Robson (*3*), who treated it as a quasi-linear system. They have suggested that the visual system may analyze the world not into such seminaturalistic objects as bars and edges, but rather into spatial frequency components, with each cell being selective for a certain range of spatial frequencies. Linear summation of excitation and inhibition within receptive fields (RF) with spatially antagonistic regions would give the cells the characteristics of spatial frequency filters. The visual system may thus operate on the distribution of light across visual space in much the same way that the cochlea is presumed to operate on the temporal pattern of sound waves impinging on the ear, breaking down the complex wave into its sine-wave components. Considerable psychophysical evidence supporting the spatial frequency filter model of visual organization has been obtained (*4–6*).

As Hubel and Wiesel's initial recordings indicated and as many have since further demonstrated (*7*), bars and edges drive cortical cells well. Virtually any cortical cell will respond vigorously to a bar or an edge in the appropriate location and orientation. Furthermore, many cells are somewhat selective for bar width, responding better to some widths than to others. On the other hand, we (*8*) and others (*9*) have shown that cortical cells also respond well to sinusoidal grating patterns and that many cells are narrowly tuned in the spatial frequency domain. Thus each of these alternative ways of describing cortical cells has some physiological support. This is not surprising, since gratings of different frequencies can be thought of as bars of different widths; a bar-detector model would predict that cells should respond to such patterns. On the other hand, a bar, like any other stimulus, can be broken down into its spatial frequency components; one would expect from a linear systems analysis that cells responsive to almost any particular spatial frequency band would respond to the broad range of spatial frequencies present within the spectrum of a single bar.

Both models thus have some validity as a characterization of cortical cell behavior. We now pose the question of which model seems to be a better descriptor of the activity of cells in the striate cortex. There are two ways by which we might decide this question. One is by considering the responsivity or sensitivity of the cells to these patterns. The optimum stimulus for a cell is conventionally considered to be that which evokes the largest response. To which are cortical cells the more sensitive, and which produces the more vigorous responses from them—a bar of the optimum width and orientation or a sine-wave grating pattern of the optimum spatial frequency and orientation? The other critical question is the selectivity of the cells: Along which dimension, bar width or spatial frequency, are the cortical cells more narrowly tuned? Both models of cortical organization postulate that the cells analyze the visual environment into elements, with each cortical cell responsive to only a selective range within the dimension. Within which of these dimensions, bar width or spatial frequency, are cortical cells in fact more selective?

To make such comparisons of bars and gratings, one must equate the stimuli in width and contrast. The appropriate relation between bar width and spatial frequency is readily established. One can consider a sine-wave grating pattern as alternate black and white bars; the bar of equivalent width is equal to a half cycle of the grating. The contrast of a grating is conventionally described by the Michelson contrast, $(max - min)/(max + min)$, where *max* and *min* are the luminance of the peak and trough, respectively. The contrast of a bar is most widely defined as $\Delta I/I$, where ΔI is the luminance increment of the bar with respect to its background, I. These specifications of contrast for bar and grating are equivalent (*10*); we therefore equated the patterns for contrast on this basis.

The experimental procedure was to examine the responses of single cells in the striate cortex of the macaque monkey and the cat, the cells being isolated with platinum-iridium microelectrodes.

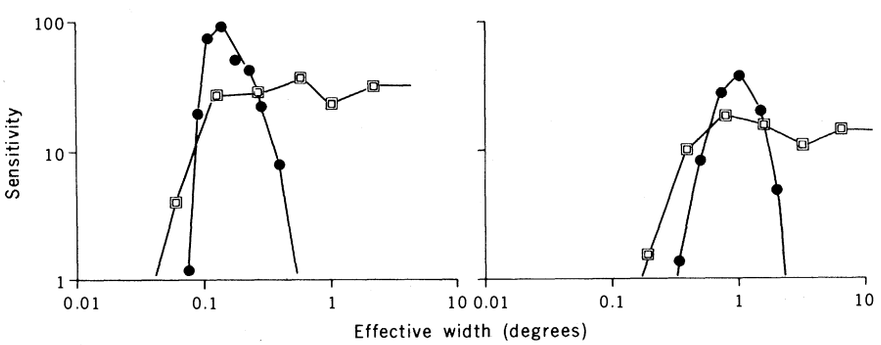

Fig. 1. Selectivity functions for bars (squares) and gratings (circles) of two striate neurons. (A) Macaque monkey simple cell. (B) Cat complex cell. Contrast sensitivity (the reciprocal of the contrast required to reach a constant response criterion near threshold) is plotted as a function of effective width (for gratings, the effective width is equal to the width of one half of one period). There is little selectivity for bars and essentially no drop in the sensitivity as bar width increases. In contrast, the cells are sensitive to only a limited range of spatial frequencies and are therefore selective for gratings.

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The animals were paralyzed to prevent eye movements. The conventional recording procedures have been described (*8, 11*).

The animal faced an oscilloscope screen on which were displayed the stimulus patterns. At the viewing distances, the 8- by 10-cm display scope (Tektronix 602, white P4 phosphor) subtended a visual angle of 16° at 27 cm for cat and 5.3° at 87 cm for monkey. The animal's eyes were refracted, and supplementary lenses were used to focus the patterns on the retina. The animal was turned to center the RF of the cell on the oscilloscope screen, and then the stimuli were presented.

We initially performed a number of subsidiary experiments including conventional RF mapping, which allowed us to classify the cell as simple or complex according to Hubel and Wiesel's criteria. Then we compared the cell's responses to bars and gratings. The gratings were drifted across the cell's RF at a constant number of cycles per second (usually 2 Hz), regardless of the spatial frequency. The bars were also moved across the RF, each going back and forth at a constant rate, one chosen to be optimum for that cell. Spikes were averaged over several (generally 20) repetitions of the stimulus. From these averaged data we could calculate the maximum firing rates and contrast sensitivity functions. In each case, only the responses at the optimal orientation and direction of movement were used. Both stimulus presentation and response analysis were under computer control.

To actually compare bars and gratings, we determined the contrast sensitivity function for each; that is, we determined what stimulus contrast was required for a certain size response at different bar widths in the one case and at different spatial frequencies in the other. To do this, we presented gratings at several contrasts (between 1 and 95 percent) at each of a number of spatial frequencies. The spatial frequency spectrum was tested from 0.5 to 23.0 cycles per degree in monkey and 0.15 to 5.0 cycles per degree in cat. For the bar stimuli, different bar widths were presented at several contrasts between 1 and 95 percent. From the data we determined the contrast required at each bar width and at each spatial frequency for a given criterion of response amplitude.

Without exception, all 96 simple and complex cells from which we recorded in both cat and monkey were more selective for gratings of various spatial frequencies than for bars of equivalent bar widths (Fig. 1). The cells responded to only a narrow range of spatial frequencies, whereas they responded almost uniformly to all bar widths. The fineness of spatial frequency tuning of cat and monkey cortical cells (*8*) ranges from about 0.5 octaves to more than 2 octaves (full bandwidth measured at half amplitude). Thus, although the cells vary considerably in narrowness of spatial tuning, even the most broadly tuned cells responded to only about half of the total range of spatial frequencies studied. We found no cells, however, that responded to only such a limited range of bar widths. Some of the cells were somewhat selective for bar width, in that they gave slightly larger responses to some bar widths than to others, but they all responded to a wide range of bars, even to extremely broad ones.

Table 1. Responsivity and sensitivity. Mean (± standard deviation) response ratios at equal contrast and mean contrast ratios at equal response.

Cell	Ratio	
	Response (grating:bar)	Contrast (bar:grating)
Simple	2.2 ± 0.7	2.2 ± 0.9
Complex	1.8 ± 0.8	1.7 ± 0.7

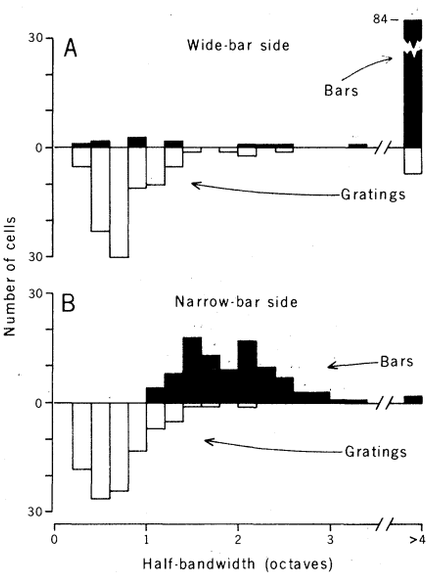

Fig. 2. Bandwidths for bar selectivity functions (dark bins) and grating selectivity functions (clear bins) taken from the entire sample (N = 96) of monkey and cat cortical neurons. (A) Bandwidth (at half amplitude) from the peak of the selectivity curve to the drop in sensitivity (to half the maximum) at the wide-bar/low-frequency end of the x axis. Most bar selectivity functions do not drop to half maximum at this end and, therefore, the bandwidth is large (greater than 4 octaves). The median bandwidth for the grating selectivity functions at the low-frequency (large effective width) end of the axis is 0.7 octaves. (B) Bandwidth (at half amplitude) from the peak of the curve to the narrow-bar/high-frequency end of the (effective width) x axis. The median bandwidth for the bar selectivity function is 2 octaves; the median bandwidth for the grating selectivity function is 0.6 octaves.

The large and consistent difference in the selectivity of cells for bar widths versus spatial frequency is shown in Fig. 2, which gives a quantitative index of the selectivity for each of the cells in our sample. There is essentially no overlap between the two distributions; every cell is far more selective for spatial frequency than for bar width. Although all of the data in Fig. 2 were obtained with bars and gratings drifted across the cells' RF's, the conclusions are not restricted to that condition. Many cells were also tested with stationary patterns flashed on in various locations with respect to the cell's RF. We found with these stationary presentations, as we had with drifting patterns, that every cell tested was more selective for spatial frequency than for bar width.

Examining only stimuli centered on the cell's receptive field does not give an accurate indication of the cell's selectivity. In the real world, of course, stimuli are not all centered on receptive fields. The real questions—given stimuli of various widths and locations—are, What information is carried by the cortical cell's firing at a certain rate? What information could some later cell obtain from it about the nature of the stimulus? The answer, from our data, is that very little information is being transmitted about the specific bar width in the field, since a cell, for instance, will discharge similarly to a very narrow bar centered on the RF and to broad bars whose edges are optimally located on the RF. The cortical cell does, however, transmit precise information about the spatial frequency of patterns within its portion of the visual world, since it will respond only to spatial frequencies within its band-pass.

The responsivity of cells to bars and gratings also differed. An occasional cell responded more to bars than to gratings of the same contrast, but for the vast majority of cortical cells the converse was the case: They gave a larger response to a grating of the optimal frequency than to a bar of the optimal width. This was true for both simple and complex cells; the only exceptions among 114 cells were four complex and two simple cells. The two cells shown in Fig. 1 are both more sensitive to the optimal grating than to any width of bar. The relative responsiveness of all the cells in our sample to bars and gratings of optimum size is shown in Table 1. The cells were approximately twice as responsive and sensitive

to gratings as to bars. This is a relatively small difference in sensitivity, but it is in fact about the size predicted from the spatial frequency spectra of the patterns: If a larger difference had been found it would not have been stronger evidence for spatial filtering, but evidence against it.

The greater selectivity and responsivity of cells to gratings than to bars is predictable from a consideration of them as a spatial frequency filters. A single bar of any width has a broad spatial frequency spectrum, covering virtually the whole spatial frequency range studied. Cortical cells are responsive to only a limited range of spatial frequencies, but would be expected to respond to bars of all the widths because all have in their spectra spatial frequencies within the cell's sensitivity range. Cells should thus be, as we have found, selective for spatial frequencies but not for bars (*12*).

The greater responsivity of cortical cells to gratings of the optimal spatial frequency than to bars of optimal width is also predictable from the spatial frequency selectivity of the cell. In the space domain, the RF of a cortical cell has not just a central excitatory region, but also inhibitory (antagonistic) flanks (*1*). In addition, narrowly tuned cells have further excitatory and inhibitory side bands (*8*), as would be predicted by their fine selectivity for sine waves. Both the inhibitory flanks and the additional side bands should make a grating a more effective stimulus than a bar, which excites only the RF center. Looked at in the frequency domain, a bar, with its broad spatial frequency spectrum, has much of its power at frequencies other than those to which a given cell is sensitive. It is thus less effective in driving the cell than is a grating, which has a limited frequency spectrum within the cell's sensitivity range.

Our data show that while cells in the striate cortex have been characterized as either bar and edge detectors or as cells selective for certain spatial frequencies, the latter is by far the more accurate descriptor of their behavior. Gratings are in fact the stimuli to which most cortical cells give their largest responses and to which they are the most sensitive; furthermore, all cortical cells are much more selective along the dimension of spatial frequency than they are along the dimension of bar width.

DUANE G. ALBRECHT*
RUSSELL L. DE VALOIS
LISA G. THORELL

Department of Psychology, University of California, Berkeley 94720

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10. If the mean level of a grating is taken as I, the peak of the wave is $I + \Delta I$ and the trough is $I - \Delta I$. Thus the contrast becomes:

$$\frac{(I + \Delta I) - (I - \Delta I)}{(I + \Delta I) + (I - \Delta I)} = \frac{2\Delta I}{2I} = \frac{\Delta I}{I}$$

This method of equating the contrast of the bars has also been used by others (*6*).
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12. Sullivan, Georgeson, and Oatley (*6*) came to similar conclusions on purely psychophysical grounds. They found that adaptation to a grating selectively adapted only nearby spatial frequencies, whereas adaptation to a bar adapted all bar widths nonselectively. P. H. Schiller, B. L. Finlay, and S. F. Volman [*J. Neurophysiol.* **39**, 1334 (1976)] also found greater selectivity to gratings than to bars, although contrasts were not matched for bars and gratings and only response functions at a single contrast were obtained.
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* Present address: Department of Psychology, University of Texas, Austin 78712.

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Nonvolatile Mutagens in Drinking Water: Production by Chlorination and Destruction by Sulfite

Abstract. *In concentrates of water produced in a laboratory simulation of a drinking water treatment process, direct-acting, nonvolatile mutagens were readily detected by means of the Ames* Salmonella *test. The mutagens were shown to be produced by the chlorination process. Treatment of the water with chloramine resulted in less mutagenic activity than treatment with free chlorine. Dechlorination of drinking water with sulfite sharply reduced the mutagenic activity. Treatment with sulfur dioxide is proposed as an effective, inexpensive method of reducing the direct-acting mutagenic activity of drinking water and of aqueous industrial effluents.*

Although there is concern over the presence of low levels of mutagens and carcinogens in drinking water (*1*), and especially over the ubiquitous appearance of chloroform after chlorination (*1, 2*), little is known about the nonvolatile organic compounds present in drinking water (*1*).

Pelon *et al.* (*3*) used the Ames *Salmonella* test (*4*) to detect low levels of direct-acting mutagens (not requiring enzymatic activation) and promutagens (requiring enzymatic activation) in unconcentrated water from the lower Mississippi River. Several subsequent studies (*5–7*) found mutagens in concentrates of several U.S. drinking waters. Glatz *et al.* (*6*) and Hooper *et al.* (*7*) suggested that in several water supplies, treatment processes such as chlorination might generate mutagenic activity. Chlorination is known to produce chloroform (*8*) in drinking water as well as mutagens in the bleaching effluents from softwood kraft pulp (*9*). The experiments we have conducted show that chlorination produces nonvolatile mutagens in drinking water and that treatment of chlorinated water with sulfite reduces mutagen levels significantly.

Water that had been softened with lime was taken from a municipal treatment plant, and the treatment that would have been followed there was followed in the laboratory (*10*). All samples (40 to 80 liters each) were treated in a similar manner except that several different procedures were used for chlorination and dechlorination. Organic compounds present in the water were adsorbed to the nonpolar resin, Amberlite XAD-4, according to the method of Glatz *et al.* (*6*). We used acetone and then methylene chloride (*11*) for desorption of these compounds and removed the solvent (and volatiles) by rotary evaporation of the samples to dryness. The residual organic compounds were dissolved in a volume of dimethyl sulfoxide (DMSO) equal to about 1/20,000th that of the original water. Samples of the water concentrate were assayed by the Ames *Salmonella* plate test (*4*).

We used several strains of *Salmonella typhimurium* for this test. The Ames test strain TA100 showed the highest rever-

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