Reprinted from Journal of the Optical Society of America A, Vol. 2, page 1115, July 1985

Periodicity of striate-cortex-cell receptive fields

Russell L. De Valois and Lisa G. Thorell

Departments of Psychology and Physiological Optics, University of California, Berkeley, California 94720

Duane G. Albrecht

Department of Psychology, University of Texas at Austin, Austin, Texas 78712

Received December 4, 1984; accepted March 12, 1985

If striate cells had the simple bipartite or tripartite receptive fields (RF's) classically attributed to them, they should be quite broadly tuned for spatial frequency. Most striate-cortex cells, however, are fairly narrowly tuned and would be expected to have more-periodic RF's. We have examined this question in recordings of the responses of cat and monkey striate-cortex cells to gratings of increasingly large number of cycles, all centered on the cells' RF's. Simple cells narrowly tuned for spatial frequency were found to increase their responses with increasing numbers of stimulus cycles beyond the $1\frac{1}{2}$ cycles expected from the classical RF shape. Broadly tuned simple cells were found to have less-periodic RF's. Whereas narrowly tuned complex cells were also found to respond maximally to many stimulus cycles, other more broadly tuned complex cells did as well (possibly reflecting summation across many broadly tuned simple cells without regard to phase). A suppressive region was often seen just outside the excitatory two-dimensional spatial-frequency region, at off orientations and/or off spatial frequencies and around the whole RF in space. Most striate cells can thus be described as having periodic RF's in the space domain such that they fire just to patterns whose local spatial-frequency spectra fall within a compact, restricted, roughly circular two-dimensional spatial-frequency region, with an encircling suppressive region in both the space and the frequency domains.

INTRODUCTION

Striate simple-cell receptive fields (RF's) have been classically described as bipartite or tripartite, with one elongated excitatory area and one adjacent antagonistic area or with a single central excitatory region and antagonistic flanks on either side, respectively; see Hubel and Wiesel.[1] One would expect from linear considerations that such RF shapes would lead to quite broad spatial-frequency tuning. The majority of striate-cortex cells are much more narrowly tuned than would be predicted from such RF shapes; see, for instance, the recordings of Movshon *et al.*[2] from the cat cortex and those of De Valois *et al.*[3] from the monkey. Cells with narrow spatial-frequency tuning would be expected to have more-periodic RF's than those classically described. There are in fact a number of reports of additional excitatory and inhibitory regions in striate RF's, often referred to as sidebands (Bishop *et al.*,[4] Maffei and Fiorentini,[5] Albrecht,[6] De Valois *et al.*,[7] Andrews and Pollen,[8] Kulikowski and Bishop,[9] and Mullikin *et al.*[10]).

The RF structures of cells have usually been determined by mapping the responses to spots or bars flashed in different locations. Such a procedure can be applied only to simple cells; see Hubel and Wiesel[1] (although Movshon *et al.*[2] have usefully examined complex-cell RF's with pairs of bars of various separations). It is also limited by the feeble responses shown by many cells to a small mapping spot or even to a narrow bar, particularly in weaker parts of the RF. We have carried out such conventional mapping experiments and have reported some of the findings.[6,7] However, these classical mapping procedures do not appear to us adequate to answer certain questions of interest concerning the fine structure of cortical-cell RF's.

We have therefore examined the shape of cortical RF's in recordings from simple and complex cells in both cat and monkey striate cortex, using what might be termed functional mapping procedures, so named because the RF is functioning more as a whole unit during these procedures since the mapping stimulus comes close to covering the whole RF simultaneously. We measured the number of functional, alternatively antagonistic regions within cells' RF's by determining the number of stimulus cycles required to produce the greatest response in a cortical cell.

METHODS

The general recording techniques and methods of data analysis have been described fully elsewhere (De Valois *et al.*[3,11]). Single cells were isolated with glass-coated tungsten or platinum–iridium microelectrodes in penetrations through the striate cortex of anesthetized and paralyzed (75% NO_2/25% O_2; gallamine triethiodide 7 mg/kg per h) cats and macaque (*M. fascicularis*) monkeys. When a unit was isolated, the RF of the cell was positioned at the center of the monitor display used to present the stimuli (either by turning the gimbal-mounted recording cage or by moving the display system). After preliminary mapping of the RF with narrow bars and/or small spots, quantitative studies were carried out under computer control. The computer presented patterns on the display monitor while simultaneously analyzing the accompanying spike discharge from the cell.

Each pattern consisted of a luminance-varying grating of a particular spatial frequency and orientation, either drifted across the monitor for 20 cycles or counterphase flickered for 20 cycles at some optimal temporal frequency, generally 2 or

0740-3232/85/071115-09$02.00

4 Hz. The patterns were digitally generated, permitting us to compensate for the nonlinearities of the display oscilloscope. Although gratings of differing orientation could be produced electronically, it was easier to rotate the monitor to change the pattern orientation so as to match the RF of the cell being studied. The computer averaged together (in 5-msec bins) the responses to each of the 20 cycles of stimulus presentation to make a peristimulus–time histogram (PSTH), Fourier analyzed this PSTH on line, and printed out the amplitudes and the phases of the component at zero frequency (DC) and the first five harmonic components of the response. We do not believe that the results reported here were due to the small amount of adaptation produced by the 5- to 10-sec stimulus presentations at the modest contrast levels that we used. As a control for this, however, some data were collected with shorter stimulus presentations, each stimulus being presented twice in random order. Although two short presentations were generally found to produce more total spikes than one long presentation, no differential effects related to the experimental variables were noticed.

As we (De Valois *et al.*[3]) and others (Movshon *et al.*[2] and Schiller *et al.*[12]) have pointed out, striate cells fall into two classes on the basis of their responses to drifting-grating patterns, and, with few exceptions, this quantitative dichotomy corresponds to the qualitative distinction first made by Hubel and Wiesel[1] between simple and complex cells. We therefore classified cells on this quantitative basis. A simple cell was taken as one that shows a modulated discharge to the optimal spatial-frequency grating, so that a Fourier analysis of the PSTH shows the largest amplitude in the first harmonic (fundamental). A complex cell, on the other hand, mainly shows an overall, unmodulated increase in firing to an optimal spatial-frequency drifting grating, and thus most of the power in the PSTH is in the DC. Our measurements for drifting gratings then were based on the amplitude of the first harmonic for simple cells and on that of the DC for complex cells. For a counterphase-flickering pattern, the predominant power in the simple-cell response is also at the first harmonic, but that of complex cells is at the second harmonic; these were thus used as measures of the responses to counterphased presentations.

The Tektronix 654 color monitor was viewed behind a circular aperture that subtended 6° at the 172-cm viewing distance used for monkeys or 18° at the 57-cm viewing distance for cats. In each case, the oscilloscope display was surrounded by a white screen maintained at approximately the same luminance as the display face (27 cd/m^2). Between stimulus presentations, the monitor face was always at the mean luminance, as was the background surrounding the delimited gratings. Since the gratings were symmetrical in luminance about the mean level, the space-average luminance of the whole field was thus kept constant throughout the experiment.

The usual procedure for the examination of the extent of periodicity in the RF was to present drifting-grating patterns of the optimal orientation and spatial frequency but of varying numbers of cycles. The RF center was first precisely determined by manually positioning a half-cycle of the optimal grating to produce the maximum response. Since the alignment pattern was drifting, the half-cycle stimulus was in effect a flickering black–white bar. It was usually easy to determine the RF center precisely with this stimulus. With an occasional cell having a well-balanced, odd-symmetric RF, e.g., the cell shown in Fig. 5B below, there would be two equally good RF-center locations for a half-cycle stimulus, the true RF center being halfway between. In those cases, the RF-center location was determined with a one-cycle pattern and only multiples of one cycle presented.

When the choice and the alignment of the stimulus had been accomplished, the program was started. The computer then presented a series of grating patterns, randomly selected, consisting of various numbers of cycles of the cell's peak spatial frequency and orientation, each pattern being centered on the RF. Patterns between 0.5 (a single bar) and 7 cycles were used as well as a full-field grating. All patterns were presented at the same contrast. A contrast level was chosen for each cell such as to produce a large but not maximal response; this was generally between 10 and 30%.

The patterns of multiple cycles looked like extended gratings drifting or flickering behind windows of various widths. The patterns were also windowed along their height, since most striate cells show some decrement in response to patterns that are too long (their hypercomplex property). The typical pattern then was a rectangular patch of grating.

It was critical for the experiment that the stimulus be of the optimal spatial frequency. The cell's spatial-frequency tuning was therefore quantitatively assessed before the experiment proper began. The responses to each of a variety of spatial frequencies were quantitatively measured at each of at least two contrast levels. We judge that we could thereby estimate the peak spatial-frequency tuning to at least ±2%. We do not believe that residual errors within this range could cause any of the quite large response changes that we report here.

Some of the cells studied were directionally selective; others were not. The patterns in all cases were drifted in the optimal direction for the cell. Although we did not make a systematic study of this variable, there were no obvious differences in our data between directional and nondirectional cells with respect to the optimal number of cycles.

A major potential error in this experiment was misalignment of the center of the patterns with respect to the RF center. If, for instance, the patterns in a series were all (mis)centered one cycle to the right of the true RF center, a cell with a true RF size of 1½ cycles would not give its maximum response until the pattern was increased to 3 cycles. We were constantly on guard against this potential problem and took great care to make sure that it did not occur. Not only were we very careful to ensure that the initial alignment on the RF center was correct, but, after each series of stimulus presentations, we redetermined the center location. If the post-stimulus alignment did not coincide with the initial determination, the data were discarded. In the case of many of the cells that gave response maxima to multiple cycles, the experiment was repeated at locations shifted to the one side or the other by one cycle as a control. For every cell with an extended, periodic RF that we include in this report, we assured ourselves at the time of the experiment that the results could not have been due to an alignment artifact.

RESULTS

As the number of cycles in a grating pattern centered on the RF of a cell is increased, the response typically increases up

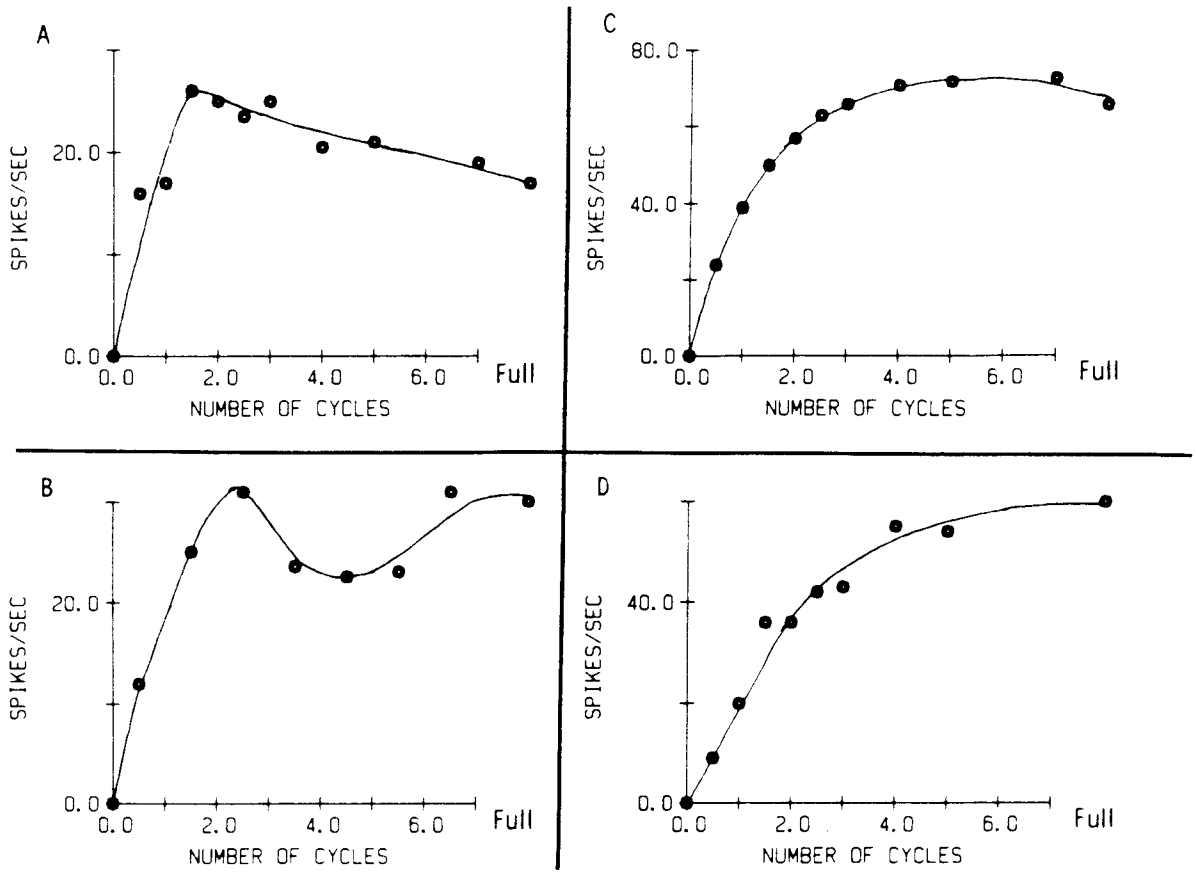

Fig. 1. Responses of four different cells to grating patterns of various numbers of cycles, all centered on the cells' RF's. A and D, Simple cells; B and C, complex cells. Note that the optimum number of cycles varies from A, 1½; to B, 2½; to C, 5½; to D, a full grating (tabulated as 7 cycles). D was the only cell encountered that responded optimally to a full grating.

to a point and then decreases slightly. The main question of interest in this study was the optimum number of cycles (that which produced the largest response) for each of a number of cells. This was found to vary from 1 to about 7 cycles among the cells in our sample, with an average of between 2.5 and 3 cycles. Thus cells were found, on the average, to have five or six separate, alternatively antagonistic RF regions (as opposed to the two or three regions in the classic RF, as was first characterized by Hubel and Wiesel[1]).

A total of 47 cells were studied, 29 simple cells and 18 complex. About two thirds were from cat striate cortex and one third from that of macaque monkey. No differences were seen between these species on the variables examined here, so the data have been pooled.

In Fig. 1 are shown data from four different cells. It can be seen that the cell shown in Fig. 1A increased its response as the number of cycles in the stimulus increased from ½ to 1½ cycles, and then showed a slight decline. This is what one would expect from a cell with the classic RF shape of a center that excited to white and two antagonistic flanks that excited to black. A grating of 1½ cycles (that is, a white bar with a black bar to either side or vice versa, depending on the cell) would optimally stimulate all components of the RF simultaneously to produce the maximum response. Even for cells with the most limited number of RF components, the optimal stimulus was never a single bar but rather three bars (see also Albrecht *et al.*[13]).

Although many cells responded like the one illustrated in Fig. 1A, the responses of others indicated more-periodic RF's. One such cell is illustrated in Fig. 1B. This cell, more typical of the population average, responded optimally to about 2.5 cycles of a grating. It thus gave evidence of about five antagonistic subdivisions within the RF, three regions that excited to white (and inhibited to black) and two regions that excited to black (and inhibited to white).

The most extensively periodic RF's that we encountered were those of cells that responded optimally to about 5 to 7 cycles of a grating, such as those illustrated in Figs. 1C and 1D. The classic tripartite RF does not even closely approximate the RF structure that must underlie this summation over multiple cycles, nor could such cells with more than a dozen alternating subdivisions within their RF's reasonably be described as bar detectors. Not coincidentally, the simple cell shown in Fig. 1D was quite narrowly tuned, with a spatial-frequency bandwidth of about 1.0 octave. It was thus toward the lower end of the spatial-frequency bandwidths found among cat and monkey striate cells. The complex cell shown in Fig. 1C, on the other hand, had very broad spatial-frequency tuning (bandwidth = 2.2 octaves), despite the fact that it summed over many cycles of the stimulus.

Figure 2 shows the distribution of optimal number of cycles for the total population of cat and monkey simple and complex cells. It can be seen that many cells reached their maximum response at about 1½ cycles of a grating pattern. However, a significant number of striate cells, both simple and complex, gave evidence of additional components to their RF's by responding better to more extensively periodic stimuli. In our sample, some 76% of the simple cells and 78% of the complex

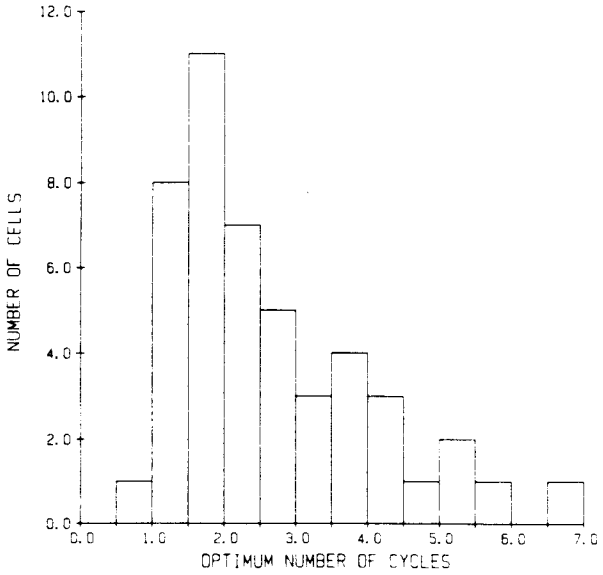

Fig. 2. A histogram of the optimum number of cycles for the whole population of 47 simple and complex cells.

cells were found to have more-periodic RF's than would be expected from the classic bipartite or tripartite RF shapes.

Insofar as a cell shows linear summation within its RF, one should be able to predict the RF cross section of the cell from its spatial-frequency tuning by the inverse Fourier transform (and vice versa from the Fourier transform). We have shown that, for a few monkey-cortex simple cells, one can in fact do this (De Valois *et al.*[7] and Albrecht[6]), as have others for cat striate units (Andrews and Pollen,[8] Kulikowski and Bishop,[9] and Movshon *et al.*[2]). Cells with a tripartite RF should show spatial-frequency bandwidths of 1.6 octaves or more, depending on the weighting of excitation and inhibition. Fewer than half of striate cortical cells have bandwidths this broad (De Valois *et al.*[3]), most being more narrowly tuned, and many have bandwidths of less than an octave. Such narrowly tuned cells would be expected to have RF's with greater spatial periodicity.

That cells with narrower spatial-frequency tuning have more-periodic RF's than do more-broadly tuned cells is clearly the case for simple cells, as is shown in Fig. 3, in which we plot the optimum number of cycles against spatial-frequency bandwidths for all our simple cells. As expected from linear considerations, there is a high correlation (−0.66) between spatial-frequency bandwidth of simple cells and optimum number of cycles. If the population is divided into those cells with optimum number of cycles of less than two versus the more-periodic cells, there is only one exception to the finding that the relatively nonperiodic cells all have spatial-frequency bandwidths of more than 1.2 octaves, whereas the more-periodic cells all have bandwidths of less than 1.2 octaves. There are no broadly tuned periodic simple cells and only one narrowly tuned aperiodic cell.

In Fig. 4 a comparable plot of optimum number of cycles versus spatial-frequency bandwidth is shown for complex cells. It can be seen that narrowly tuned complex cells respond optimally to multiple cycles and that those that respond best to few cycles are all broadly tuned, as was true for simple cells as well. However, we also found that many broadly tuned complex cells respond best to highly periodic patterns. As we discuss later, this could be accounted for if such a periodic but broadly tuned complex cell were summing the outputs of broadly tuned simple cells in different locations without respect to their phase relationships.

As can be seen in Figs. 3 and 4, complex cells on the average respond optimally to somewhat more-extensive periodic patterns than do simple cells. The average optimum number of cycles for simple cells is 2.4; for complex cells it is 3.0 cycles. Despite this, the simple cells in our sample were, on the whole, more narrowly tuned for spatial frequency than were complex cells (average bandwidths of 1.26 versus 1.71 octaves for simple

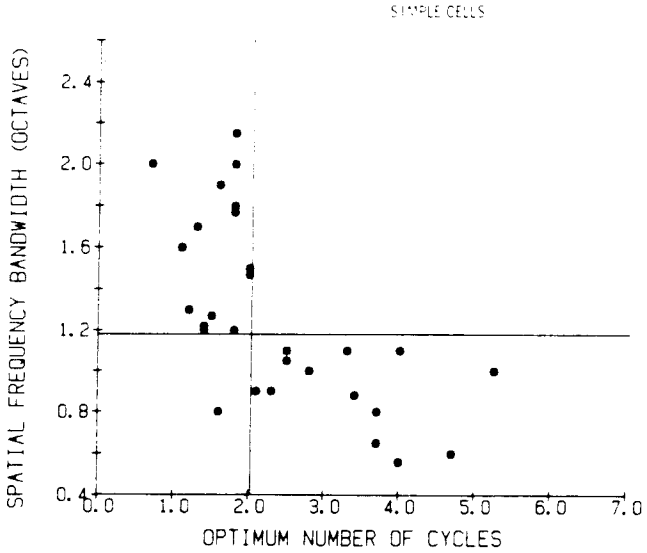

Fig. 3. A plot of the minimum number of cycles versus the spatial-frequency bandwidth for all the simple cells in our sample. The lines are arbitrarily drawn to divide the x axis into aperiodic versus periodic cells and the y axis into narrowly versus broadly tuned cells. It can be seen that, when so divided, the whole population with one exception falls into narrowly tuned periodic cells (bottom right) and broadly tuned aperiodic cells (top left).

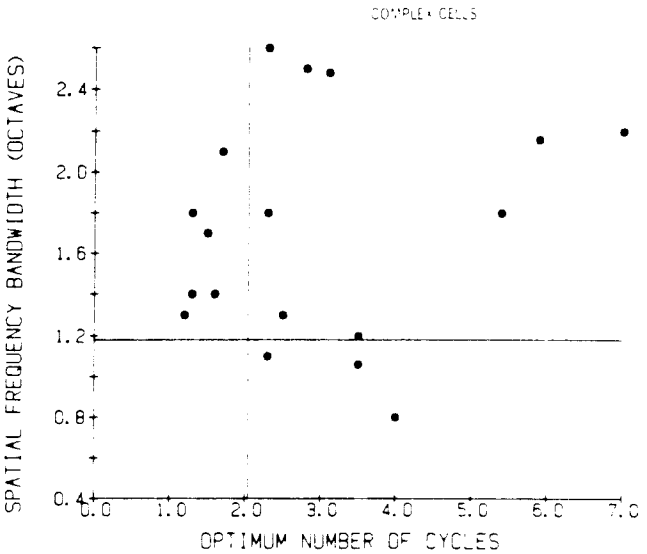

Fig. 4. A plot of the optimum number of cycles versus the spatial-frequency bandwidth for all the complex cells in our sample. When the axes are divided at the same points as in Fig. 3, it can be seen that there are many complex cells that are periodic but broadly tuned, a class not seen among simple cells.

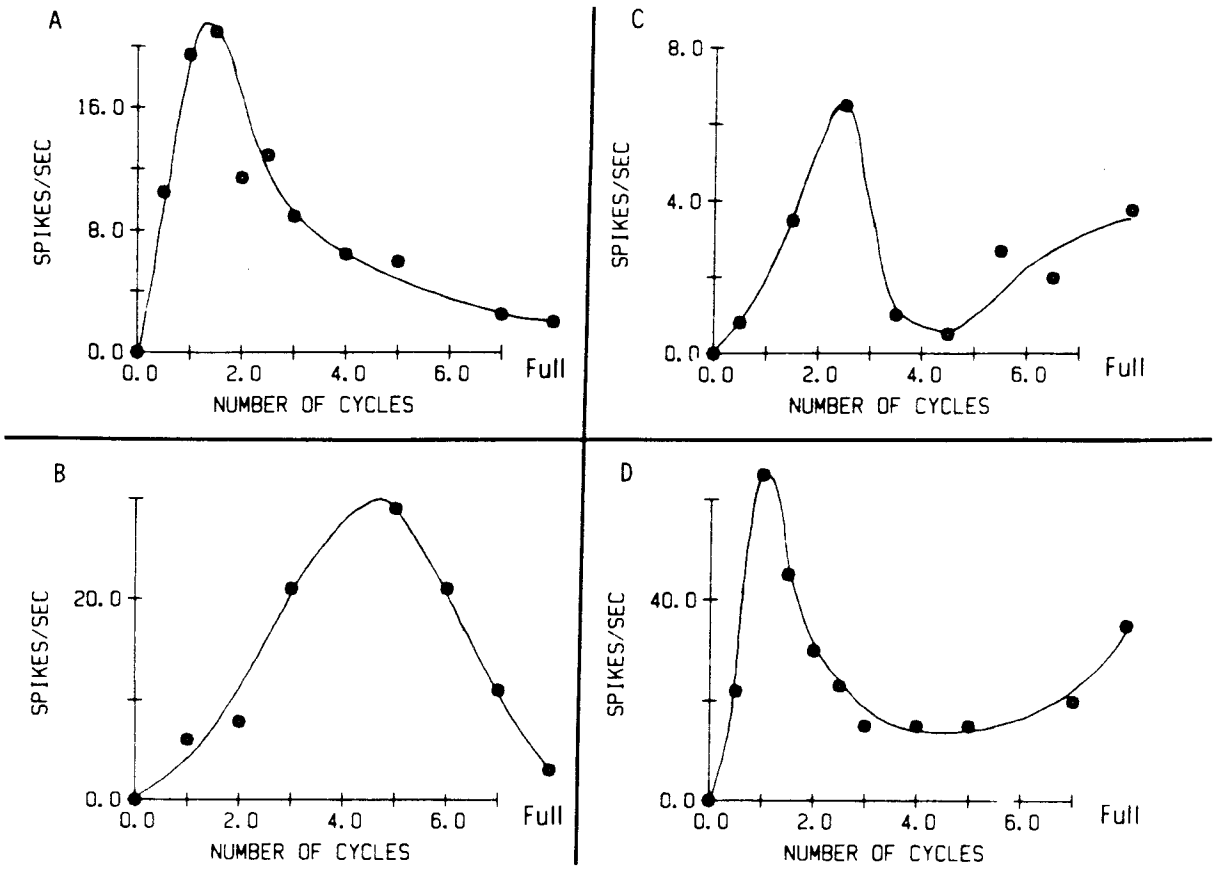

Fig. 5. Further examples of the responses of individual cells to varying numbers of cycles of gratings centered on their RF's. All these cells show profound side stopping: Inhibition when the grating patch exceeds a certain optimum number of cycles. A, a complex cell, and B, a simple cell, each show almost no response to a full-field grating. C and D, simple cells, show profound inhibition at intermediate grating-patch sizes, then disinhibition from still more-extensive patterns.

and complex cells, respectively). If we accept the rather arbitrary division of the cell population, as shown by the lines in Figs. 3 and 4, into narrowly tuned cells (with spatial-frequency bandwidths of less than 1.2 octaves) and broadly tuned units, we find that the narrowly tuned simple and complex cells are very similar. The average spatial-frequency bandwidth of this narrowly tuned sample is 0.9 octave in each case, and the average optimum number of cycles in a grating patch is 3.3.

Hubel and Wiesel[1] discovered that some complex striate cells were greatly inhibited, in fact often would not respond at all, if the stimulus bar extended in length beyond a certain point. They termed this "end stopping" and called the most extreme of such end-stopped units "hypercomplex cells." It is now generally accepted (e.g., Gilbert[14]) that end stopping is also found in cells that would otherwise be classified as simple cells as well as in certain complex cells and that end stopping is present to a greater or a lesser extent in many cells.

When tested with gratings of various numbers of cycles, most striate-cortex cells show what one might call side stopping, by analogy with the end-stopping or hypercomplex property discussed above. This is doubtless related to the "suppressive surround" reported by Maffei and Fiorentini.[5] If a grating patch exceeds a certain number of cycles, the response may decrease or in the extreme case drop out entirely. This is a property that one would never discover with a single-bar stimulus, for it is to be emphasized that what is being varied is not the width of the individual bars in the grating but the overall width of the grating patch.

Examples of sidestopping can be seen in Figs. 2A–2C. In all those cases, the response of the cell dropped slightly when the grating patch exceeded the optimum number of cycles. Some cells show more-extreme side stopping than this, inhibition of the same degree as the end stopping seen in those cells that Hubel and Wiesel[1] termed hypercomplex. Examples of this are shown in Figs. 5A and 5B. Each of these cells gave a large response to the optimum grating patch but then showed a considerable reduction in response as the patch was made still wider. Each gave almost no response to a full-field grating. It should be noted that even in these cases the optimal stimulus was *not* a single bar but rather a grating patch of a certain number of cycles; in the case of the cell in Fig. 5B this was a patch of 4 cycles or 8 bars. Side stopping as illustrated here was found in both simple and complex cells. Inhibitory interactions that may be related to this side stopping have found by others (Creutzfeldt *et al.*[15] and Maffei and Fiorentini[5]).

Both the amount and the characteristics of the side stopping were found to vary from cell to cell. For many cells there was a drop in response when the grating patch exceeded the optimum number of cycles, but a still further width increase would bring the response back up a greater or a lesser amount. A small dip of this sort is seen in Fig. 1B, in which the responses to 3.5, 4.5, and 5.5 cycles were clearly lower than that to 2.5, but the responses to 7.5 cycles and to a full grating were

back up. Some cells, illustrated in Figs. 5C and 5D, show a drop almost to zero at intermediate grating-patch widths but then some increase to still more extensive gratings. This rise after a drop at intermediate values suggests disinhibition from more distant regions.

There was considerable variation in the amount of side stopping found in the sample of striate-cortex cells. The percentage drop in response from that shown to the optimal grating patch down to that produced by a full-field grating varied between 0 and 98% across cells, with a mean of 35% for simple cells and 24% for complex cells. That is, simple cells on the average showed 65% as large a response to a full-field grating as to the optimum grating patch and complex cells 76%.

The presence of both end stopping and side stopping in striate-cortex cells suggests that they may be related. Cells may respond optimally to a two-dimensional grating patch of a certain overall size (not to be confused with its spatial-frequency selectivity), the response being suppressed if the patch extends beyond the preferred region in either length (end stopping) or width (side stopping). In other words, there may be a suppressive region, weak in some cells and strong in others, extending all around the RF.

We have not systematically studied both end stopping and side stopping in the same cells for our whole population, but we have done so on a subsample of cells. In general, we find that they are in fact related: Cells that are powerfully inhibited if a bar or grating is too long also tend to be strongly inhibited if the grating patch is too wide, with too many cycles in it. An example is the cell in Fig. 5B, which would have been termed hypercomplex by Hubel and Wiesel since it gave essentially no response to a bar or a grating that was too long. It was also, of course, side stopped, as is illustrated in the figure. Other cells were found to respond well to a grating that extended beyond the RF in every direction.

DISCUSSION

Periodic Receptive Fields

One of the principal findings of this study was that sizable proportions of both simple and complex cells appear to have periodic RF's, as is indicated by their preference for multiple-cycle gratings. Such periodic RF's are of course what would be expected if these cells were functioning as spatial-frequency filters, detecting periodicities in a local patch of the visual field. Such periodic RF's are not at all what would be demanded by bar and edge models nor by zero-crossing detectors, such as those postulated by Marr.[16] Marr did in effect postulate multiple spatial-frequency channels (as of course Campbell and Robson[17] had earlier), but ones with extremely broad spatial tuning, as an initial coarse filter before the zero-crossing detectors. There are cells in the striate cortex with the broad spatial-frequency (and orientation) tuning that Marr postulated, but it seems strange to have a role in pattern processing only for such geniculatelike cells while ignoring the numerous cells with narrow spatial-frequency and orientation tuning. To do so overlooks the primary transformation that the physiology indicates takes place in the striate cortex.

Relation of Periodicity to Spatial-Frequency Tuning

Insofar as there is linear summation within a cell's RF, the extent of periodicity in its RF should be related to the narrowness of its spatial-frequency tuning, as is given by the Fourier transform and its inverse. A cell with the classic tripartite RF, a center with two antagonistic flanks, would be expected to have a spatial-frequency bandwidth of 1.6 octaves or more; cells with bandwidths of 1.2 octaves or less would be expected to have more-periodic RF's. This is exactly what we found in the case of simple cells: The spatial-frequency bandwidths were closely related to the periodicities of the cells' RF's. Given a judicious choice of cuts in the distribution, there are virtually no exceptions to the rule that simple cells narrowly tuned for spatial frequency have quite periodic RF's and that broadly tuned simple cells have less-periodic RF's. One does not see broadly tuned periodic simple cells or narrowly tuned aperiodic ones.

The same relation was not found among complex striate cells. One quadrant in the 2×2 matrix of spatial bandwidth versus RF periodicity that is forbidden from linear considerations was indeed empty: We found no narrowly tuned nonperiodic complex cells. But another quadrant that was empty for simple cells—broadly tuned periodic cells—contained a large proportion to the complex-cell population. The most straightforward hypothesis to explain this finding is that such complex cells are summing the outputs of broadly tuned simple cells whose RF's are in neighboring loci, but doing so without respect to the spatial-phase relationships among the subunits. Narrow spatial-frequency tuning would only result from summing multiple subregions in an RF if the different subregions were precisely spaced and in the appropriate phase relations with respect to each other; but complex cells are not phase specific (De Valois *et al.*[3]), giving mainly DC responses to a drifting grating.

Pollen and Ronner[18] reported that many complex cells had extremely periodic RF's, from which they concluded that complex cells must be extremely narrowly tuned. Our results support their finding of great periodicity among many complex cells, but we found in this study that on the average complex cells are less narrowly tuned than simple cells for spatial frequency, as we and others had earlier reported as well (Movshon *et al.*[19] and De Valois *et al.*[3]).

Negative Maintained Discharge

As judged by their optimal response to multiple cycles, about three quarters of the simple cells in our sample were found to have RF's more periodic than the classic RF shape of center plus two antagonistic flanks. The question immediately arises as to why such a periodic RF structure was not noted in early RF-mapping experiments. In general, such sidebands are not obvious, often being so weak as to be revealed only by averaging over a large number of stimulus presentations, so it is not surprising that qualitative RF mapping does not reveal multiple sidebands. One would be quite wrong in concluding from this that they are unimportant in the cells' behavior, however. The much larger responses that some cells give to 3 or even 5 cycles than to only $1\frac{1}{2}$ cycles of a grating argues that the sidebands must play an important role in the cells' responses to naturalistic patterns, which are usually quite extended in space (sidebands are also, of course, critical for producing the narrow spatial-frequency tuning seen in these cells).

One reason why sidebands in RF's are not obvious is that cortical cells may well have a negative maintained-discharge level. Cells in the lateral geniculate nucleus have a maintained discharge that may average 10 spikes/sec or so, and the

rate may fluctuate between 0 and 20 spikes/sec. Simple cortical cells usually show almost no maintained discharge, often going many seconds without firing a single spike. If their membrane potentials vary as much as those of geniculate cells, they must be tonically clamped at a level equivalent to a maintained discharge of −10 spikes/sec or so, some distance below threshold (Bishop *et al.*[20] also suggested an effective negative maintained rate for cortical cells, as did Movshon *et al.*[2] in a different context).

Such a hypothetical negative maintained rate would effectively mask the presence of sidebands in a conventional RF-mapping experiment but not in our number-of-cycles experiment or in normal vision. Consider, for instance, a periodic simple cell with an RF consisting of a central, elongated, excitatory region and two additional, increasingly weak, excitatory sidebands to either side (plus of course the interspersed antagonistic regions to form a total of nine subregions). A bar flashed onto the RF center is assumed to produce 20 units of excitation; one on either of the adjacent excitatory flanks 8 units of excitation; and 3 units on either far flank. If such a hypothetical cell were clamped at −10 spikes, only the main central excitatory strip in the RF would be seen by conventional RF mapping, a bar flashed here producing 10 spikes (−10 + 20 = 10). In our number-of-cycles experiment, however, the presence of these flanks would be readily apparent. A half-cycle of a grating (a bar) would, as above, produce 20 units of excitation and thus 10 spikes. A grating of 2½ or 3 cycles would stimulate the center plus each adjacent excitatory flank, producing 36 units of excitation (20 + 8 + 8 = 36) and thus 26 spikes (−10 + 36 = 26). Adding another 2 cycles to bring in the far flanks would add another 6 spikes for a total of 32 spikes. The response would thus go from 10 to 26 to 32 spikes/sec with increases from 1½ to 2½ to 3½ cycles of the stimulus.

One might note in passing that we are merely utilizing linear summation here to explain a response pattern that first sight appears to involve facilitation (a multiplicative interaction such that two stimuli together produce a bigger response than the sum of the individual responses to them). Other situations that appear to reflect facilitation, e.g., the common finding that binocular stimulation produces a larger response from a striate cortical cell than the sum of the same stimuli to each eye alone, may have a similar explanation.

Maffei and Fiorentini,[5] by comparing the responses of cat striate cells to stimulation of the classic RF alone with the effects of stimulating the RF plus the surrounding nonresponsive region, found evidence for both inhibitory and facilitatory effects of the far surround. Our results are to some extent consonant with theirs, in that we find both increases and decreases in activation from regions outside the classic RF. However, they report that about half of the striate cells have an inhibitory surround and the rest a facilitatory one, whereas we find both excitatory and inhibitory areas within the far surrounds of the RF's of the same cells. Furthermore, we find from our data, that the excitatory effects are from nearby regions, which we interpret as being part of the RF in the usual sense. As is discussed above, we interpret this excitation not as facilitation from nonresponsive regions but as the contribution from the sidebands of the RF, which could be readily mapped were it not for a negative maintained level. The suppression, our results make clear, comes from more-extensive surrounding regions and is present in virtually all cells.

Inhibitory Inputs

Virtually all recent investigations of cortical units have found evidence for inhibitory effects of various stimuli on cortical-cell responses. It is becoming increasingly apparent that such inhibition is largely intracortical and that it serves many functions including an important role in giving cells their tuning characteristics (see, e.g., Creutzfeldt *et al.*,[15] Sillito,[21] and De Valois and Tootell[22]). Our examination of the effect of increasing the number of cycles in a grating gives strong evidence for inhibition from the sides of the RF (as opposed to the ends of the RF in the case of the hypercomplex property of cells). It was not the primary intent of this study to examine such inhibition in detail, but our results suggest that side stopping and end stopping are related. Some cells show little evidence for inhibition when either the bars in a grating are lengthened or the number of cycles is increased. Other cells (which Hubel and Wiesel[1] would term hypercomplex cells) are powerfully inhibited either by lengthening the bars or by increasing the number of cycles in the grating. It therefore appears that the excitatory region of the RF is surrounded in visual space by a suppressive area of greater or lesser strength in different cells, the so-called hypercomplex property being only one aspect of this surround suppression.

In almost all cells, when more than a certain number of cycles was added to a grating a response decrement was produced, presumably as the grating invaded the surrounding inhibitory region. In many cells, still further increases in the number of cycles diminished the inhibition, so that a cell might respond best to 2 cycles, much less to 4 cycles, and at an intermediate extent to a full grating. It thus appears that the inhibition comes from an annular band just around the RF and that stimulation of still more-distant locations produces disinhibition. That is, these results would be expected if the quite distant surround inhibits the near (inhibitory) surround, so that stimulation with a full grating would produce less net surround inhibition than would a less-extensive grating patch.

We had shown earlier (De Valois *et al.*[7] and Albrecht *et al.*[13]) that striate neurons are not only much more selective for gratings of various spatial frequencies than for bars of various widths but that they are also somewhat more responsive to the optimal spatial-frequency grating than to the optimal width bar. It is apparent from the results of the present study that, had we earlier compared responsivity of cortical cells to bars versus gratings of limited numbers of cycles (instead of full-field gratings), the superiority of the periodic patterns would have been even greater, because a full-field grating often brings in some of the suppressive surround. All the cells in the present study were much more responsive to a delimited periodic pattern than they were to a half-cycle grating, that is, a single bar (the usual bar, a half-cycle of a square wave, would be marginally more effective than a half-cycle sine wave). On the average, the optimal grating–bar response ratio was found to be 2.4 for simple cells and 3.0 for complex cells.

We have been discussing inhibition from certain spatial locations around the RF. There is in addition evidence for inhibition from certain two-dimensional spatial-frequency bands (De Valois and Tootell[22] and De Valois *et al.*[23]). One sometimes finds a cell with a maintained discharge that fires to a pattern of some spatial frequency and orientation but that is actively inhibited by the presentation of a grating pattern