

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 Wiesel¹ (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% NO₂/25% O₂; 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

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 Wiesel¹ 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/m²). 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 occa-

sional 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 $\pm 2\%$. 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 $1\frac{1}{2}$ 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

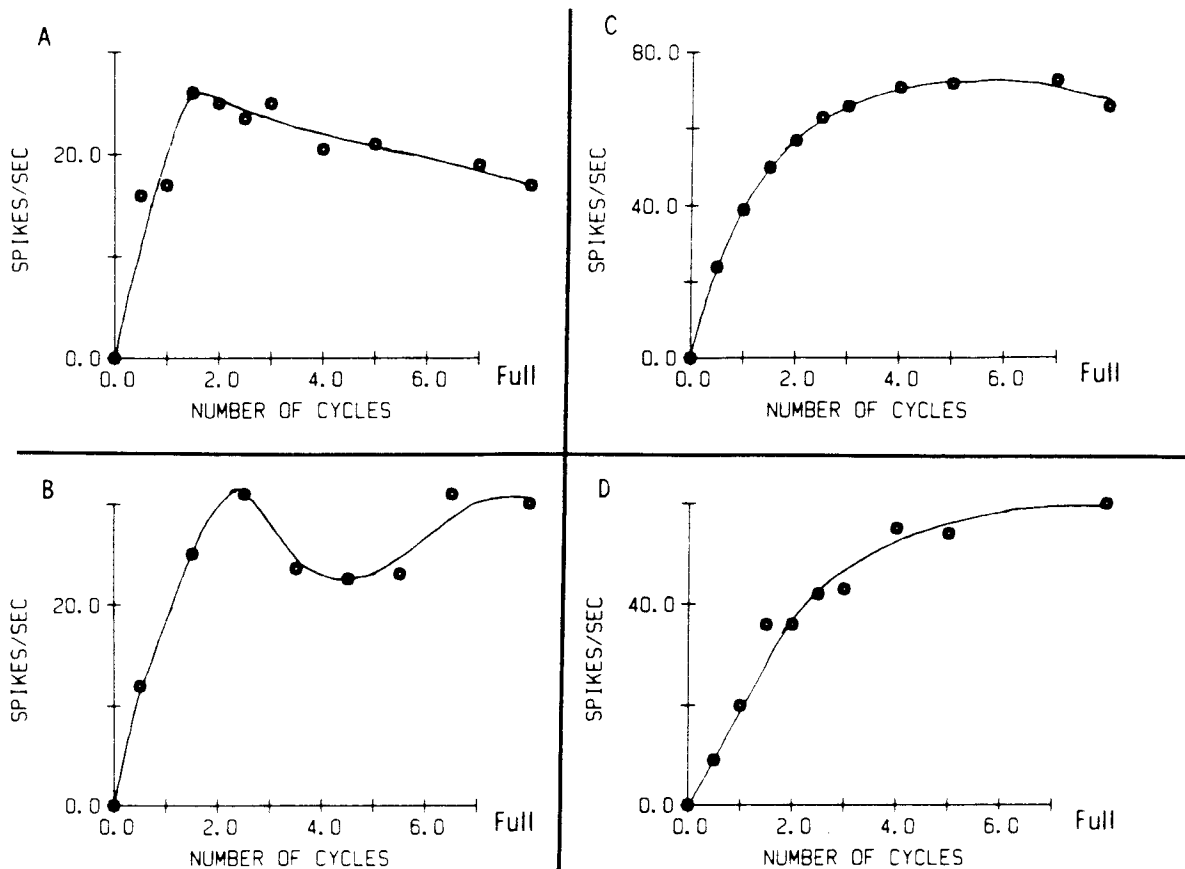


Fig. 1. Responses of four different cells to grating patterns of various numbers of cycles, all centered on the cells' RF's. A and D, Simple cells; B and C, complex cells. Note that the optimum number of cycles varies from A, $1\frac{1}{2}$; to B, $2\frac{1}{2}$; to C, $5\frac{1}{2}$; to D, a full grating (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 Wiesel¹).

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 $\frac{1}{2}$ to $1\frac{1}{2}$ 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 $1\frac{1}{2}$ 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 $1\frac{1}{2}$ 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