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Striate Cortex of Monkey and Cat: Contrast Response Function

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SUMMARY AND CONCLUSIONS

1. We measured the responses of 247 neurons recorded from the striate cortex of monkeys and cats as a function of the contrast intensity of luminance-modulated spatial-temporal sine-wave grating patterns to provide a qualitative description and a quantitative mathematical formulation of the contast response function (CRF).

2. Qualitatively, it is possible to provide a general description of the contrast response function for the majority of cells as follows: as the luminance contrast of a pattern increases, the response increases in a relatively linear fashion over approximately 50–60% of the response range (generally less than 1 log unit along the contrast range), the slope of the function then begins a rapid compression to an asymptotic maximum-saturation response level. There is, however, a great deal of variation, from cell to cell, in the exact shape and location of the CRF.

3. Quantitatively, the responses of each cell were analyzed in terms of the least-squares (parameter optimized) best fit using four different mathematical functions: linear, logarithmic power, and hyperbolic ratio. The results of this procedure showed that, across the range of contrasts measured (1.4–56%), the hyperbolic ratio (H ratio) provided the best fit for the vast majority of striate cells: some 70% of the cells were best fitted by the H ratio and further, averaged across all cells, the H ratio produced the least average residual variance.

4. The contrast response function is an important factor when considering the spatial properties of cortical cells; nonlinearities in the CRF (compression and saturation) will necessarily influence the spatial tuning. We therefore measured the CRF at different spatial frequencies and used the parameters of the H ratio to test the predictions of two general classes of models. If the overall gain, compression, and saturation are set by the absolute response level (response-set gain), then the CRFs measured at different frequencies should shift horizontally along the contrast axis. Results show that the measured CRFs (tested on the same cell using different spatial frequencies) were shifted primarily vertically, suggesting that the gain, compression, and saturation were set by the absolute contrast level (contrast-set gain), relatively independent of spatial frequency; in terms of the H ratio, the semisaturation contrast and the exponent were relatively constant in comparison to the asymptotic saturation response. Thus, the spatial frequency response functions are relatively constant when measured at different stimulus contrasts.

5. There is a great deal of variation in the location of the dynamic response range, from cell to cell, along the contrast axis: some cells distribute their dynamic response range over the first 10% of contrast, others the second, etc. (relatively independent of preferred spatial frequency). One might expect this range variation to be an important factor in behavioral contrast discrimination. To provide an indication of the average population response as a function of contrast, all cells were averaged together (percent response relative to each cell's maximum); the slope of the best-fitting power function (0.77) falls well within the range of estimates found for human psychophysical contrast discrimination functions.

INTRODUCTION

The response behavior of sensory systems as a function of stimulus intensity has always

been a fundamental concern of sensory physiology and psychophysics. The mathematical formulations (oftentimes canonized as laws) used to describe the results of such experimentation have been of equal concern and over the decades the source of long-standing debates (33, 34). These and other concerns have led to much research exploring the relations between stimulus magnitude, neural response, and behavioral response. The present study was undertaken to provide a qualitative description and a quantitative mathematical formulation of the responses of visual neurons in the striate cortex of monkeys and cats as a function of stimulus intensity.

Following the pioneering investigations of Hubel and Wiesel (19, 20), striate neurons have been the focal point of much research and in the process many of their important properties have been characterized. However, one important determining factor of the responses of striate cells has received very little experimental attention: namely, the response as a function of luminance contrast (what literature there is will be discussed below). This is somewhat surprising, given that striate cells are exquisitely tuned to respond to specific spatial-temporal variations of luminance contrast.

The recent approaches to vision research that use sine-wave grating stimuli, linear systems analysis, and Fourier mathematics (and the resultant body of research—for general reviews see Refs. 6, 10, 31, 32) provide several good reasons for analyzing the striate cortex contrast response function. The ultimate usefulness of the linear approach and the frequency response descriptions of the visual system rest on the degree to which the system behaves in a linear fashion. While striate neurons have been shown to be linear in certain respects, nonlinearities in the contrast response function will limit the validity and usefulness of any predictions based on the assumption of linearity. In this study, striate neurons were examined under conditions similar to many other physiological and psychophysical experiments. The commonality of methods across a variety of different experiments will undoubtedly make a comparative analysis a more likely possibility. To the extent that the striate cortex plays a role in luminance contrast-dependent visual behavior, the results of this analysis should complement the many relevant investigations (see DISCUSSION below).

METHODS

Preparation

The apparatus and general recording procedures are similar to those more fully described elsewhere (1, 2, 9). Briefly, macaque monkeys (*Macaca fascicularis*) and domestic cats were prepared for chronic experiments some days prior to the first neurophysiological recording: under deep barbiturate anesthesia a rigid plastic pedestal containing a recording chamber was attached to the animal's skull.

On the day of an experiment, the animal was anesthetized with a short-acting barbiturate (thiamylal sodium) and maintained throughout the experiment on 75% N_2O/25% O_2 analgesia. Since no ear, eye, or mouth bars were used, discomfort was minimal. The animals showed no increased aversion to the experimenters or the experimental room as a result of this treatment; those previously tamed remained friendly. During the recording session, the animal rested on a foam-rubber pad with its head held by a plate screwed into the pedestal. It was respired through an endotracheal tube, with the respired CO_2 being maintained at 4.5%. Temperature was maintained within normal limits by means of a thermostatically controlled heating pad; the heart rate was monitored throughout the experiment. The actual experiments ran for about 12 h (1 h preparation, 9 h recording, 2 h recovery).

The eyes were covered with contact lenses; accommodation was paralyzed, and the natural pupil dilated by applying cyclopentolate hydrochloride. The animal was refracted by streak retinoscopy, corrective lenses were used to focus the stimuli on the retina, and a 3-mm artificial pupil was introduced. The eyes were immobilized by continuous infusion of gallamine triethidiode. Action potentials were recorded from area 17 neurons using glass-coated platinum-iridium microelectrodes. The action potentials were amplified and converted by a window discriminator to standard pulses, which were fed into and analyzed by an on-line computer.

Display

Visual stimuli were generated line by line on either *a*) a Tektronix 654 oscilloscope under the control of a Nova 1220 computer or *b*) a Conrac studio monitor under the control of a PDP11. Tables of luminances to specify each pattern (self-addressing arrays) were stored in the computer and sent to the D/A controlling scope luminance one line at a time, synchronized to the raster scan

of the monitor. Calibration ensured that the grating contrasts used were within the display's linear range (the linear range exceeded 60% contrast, the maximum used was 56%). Patterns were drifted across the scope by changing the starting position in the stimulus array on each successive frame. To rotate the patterns, we placed the scope in a large wheel that rotated the whole unit. The scope face was viewed through a circular aperture in a large white screen maintained at roughly the same mean luminance level (27.4 cd/m^2). The aperture subtended 18° at the 57-cm viewing distance used for cats and 6° for monkeys at a viewing distance of 172 cm.

Experimental procedure

Once the response of a single cell was clearly isolated, its receptive field was located and centered on the display scope. Its preferred orientation, direction of movement, spatial frequency, and temporal frequency were approximately determined by listening to the spike trains while varying these parameters. Bar stimuli were then used to classify the cell as simple or complex according to the criteria of Hubel and Wiesel (19). On the basis of these preliminary measurements, the responses of the cell to various spatial and temporal frequencies were quantitatively assessed with the orientation and direction of motion held constant at the optimum values. (For cells that did not show length inhibition, the grating was kept elongated; for those cells that did show length inhibition, the grating length was decreased to the optimum.)

We then proceeded to measure the contrast response function (for all 247 cells) while all other factors were held constant. Eight different contrasts (1.4, 2.4, 4.0, 6.6, 11.5, 19.0, 33.0, 56.0) were presented in a randomly interleaved fashion. Each presentation consisted of 20 cycles followed by 15 s of no-pattern luminance; cumulative responses at a given contrast consisted of a minimum of 40 repetitions and a maximum of 100. For 22 cells this procedure was repeated using several different test spatial frequencies. The averaged peristimulus time histograms (PSTHs) were collected in 5-ms time bins; from these PSTHs an on-line Fourier harmonic analysis was computed. For complex cells, the average response rate (minus the spontaneous activity), the DC component, was used as the response measure; for simple cells, amplitude of modulation (minus the spontaneous activity), the first harmonic component, was used as the response measure.

RESULTS

The primary goal of this study was to investigate and quantitatively characterize the responses of neurons in the visual cortex of monkeys and cats as a function of the contrast intensity of visual stimuli. To this end, we measured the responses of 247 cells (110 cells from monkey, 137 from cat) to optimal spatial-temporal frequency sine-wave grating patterns presented at different contrasts. In order to characterize the resulting contrast response functions (CRFs) quantitatively, we performed a least-squares fit of the responses of each cell, using several different mathematical formulations. Thus, for example, we asked whether the responses of a particular cell were best fitted by a linear or perhaps a logarithmic function, the criterion for best fit being determined by which function accounted for the largest portion of the variance in response across contrasts (that is, which function produced the least residual variance). Four different functions, shown in Table 1, were used to analyze the responses of all 247 neurons: linear, logarithmic, power, and hyperbolic ratio.

TABLE 1. *Mathematical formulations*

Linear	$R(C) = A + B \cdot C$
Log	$R(C) = A + B \cdot \log_{10}(C)$
Power	$R(C) = A \cdot C^B$
H ratio	$R(C) = R_{max} \cdot (C^n/(C^n + C_{50}^n))$

Contrast response function

A QUALITATIVE DESCRIPTION. To begin, it is important to emphasize that there is a great deal of variation, from cell to cell, with respect to the exact form of the CRF: some cells are, with little doubt, best fitted by a linear function while others are best fitted by a log contrast function, still others by a power function. Furthermore, and perhaps of greater significance, there is a great deal of variation in the dynamic range of contrasts covered by a given cell: some cells distributing their response range from 1 to 10% contrast, others from 10 to 20%, etc. There is also a great deal of variation in the slopes of the CRFs (on log-log coordinates: from less than 1 to greater than 5). The variations noted above, and others, will be quantified in the following sections; however, the variation can be qualitatively seen in Fig. 1 where a variety of typical CRFs are shown plotted on log-log coordinates.

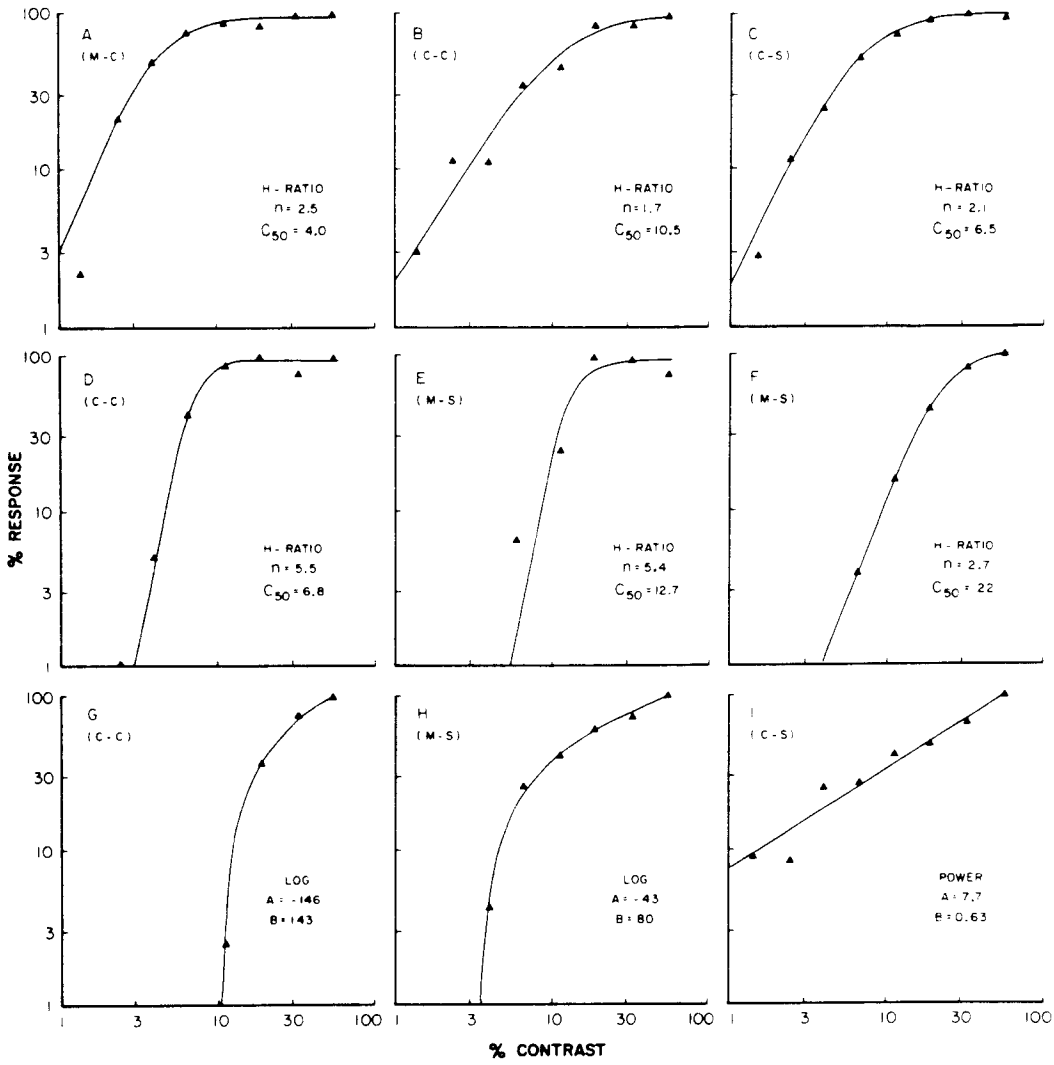

FIG. 1. Contrast response functions for nine representative striate neurons; percent response (relative to the maximum response) is plotted on log-log coordinates as a function of the luminance contrast of spatial-temporal sine-wave grating patterns. The smooth curve drawn through responses of each cell is the best-fitting function of four candidates (H ratio, log, linear, power). As can be seen, there is a great deal of variation from cell to cell with respect to the exact shape and relative position of each cell's contrast response. Some cells are best fitted by a log function, others by a power function; however, most are best fitted by the hyperbolic ratio. Note the variation in the position (along the contrast axis) where the dynamic response range is distributed. Animal type (monkey or cat) and cell type (simple or complex) are specified in the upper left corner of each graph (animal type-cell type); variations in this regard will be presented below (the few cells shown here should not be taken as indicative of any cell-type trends).

The responses of each of the nine cells shown in Fig. 1 were analyzed for a least-squares fit using the four functions shown in Table 1; the line drawn through the measured responses of each cell represents the best fit of the four (the function and the parameters are as specified). The six cells shown in *A–F* are typical examples of striate CRFs best fitted by the hyperbolic ratio; as will be shown below, this function proved to be the best descriptor of the CRF for the overwhelming majority of striate cells. The cells shown in *G* and *H* were best fitted by a log contrast relationship; the responses

shown in *I* were best fitted by a power function. Quantitative normative statistics will be presented below concerning how the entire population of cells and the various subgroups (cat, monkey, simple, complex) were distributed among the four functions. Again, the point we wish to emphasize (and illustrate in Fig. 1) is the variation from cell to cell with respect to the form of the CRF.

Nevertheless, it is possible to provide a general qualitative description that applies to the majority (some 80–90%) of the striate contrast response functions. In general then, as the contrast of a grating pattern increases, the response of a striate cell increases in a relatively linear (possibly logarithmic, see DISCUSSION below) fashion; the slope of this linear increase is steep and thus covers a restricted contrast range (generally less than 1 log unit of contrast). At approximately 50–60% of the maximum response of a cell, the slope of the function begins a rapid decline; that is, the function begins an accelerating compression. Ultimately, the response totally saturates (the slope hyperbolically approaches zero) and remains at the saturated level or, in some cases, actually decreases to some extent.

Take for example one of the cells shown in Fig. 1 (say Fig. 1*C*). Over a contrast range of 1–8%, the responses of this cell cover some 60% of the cell's total response range in a relatively linear fashion. However, beyond this linear range the cell distributes the remaining 40% of its dynamic response range over a contrast range from 8 to 30%; beyond 30% contrast the response is saturated and virtually static. Thus, for this cell, over a little less than 1 log unit of contrast the response was essentially linear, and then over the next 0.5 log unit of contrast the response was compressing to a saturated maximum response thereafter. While this general characterization is not applicable to all striate cells, as will be shown below, it is a good general descriptor for some 80–90% of the total population.

The cells shown in Fig. 1 have been labeled as cat, monkey, simple, or complex; however, these should not be taken as necessarily exemplary of any variation among the cell classes. As will be seen, the similarities among these different cell groups far exceed the differences. All the data presented in the following tables will be broken down in terms of these groups. A discussion of the general trends for all cells will precede a final discussion of group differences.

CLASSICAL FUNCTIONS. The search for a general function to describe the intensity response behavior of sensory systems adequately has a long history. The two functions that seem to have received the greatest amount of attention are the log function, or Fechner's law (14), and the power function, or Stevens' law (34). We felt it was important to analyze the contrast-intensity response function of striate neurons from the perspective of these two functions in addition to a strict linear function (the relative fit of the hyperbolic ratio will be analyzed below).

We therefore analyzed all of the 247 cells with respect to the least-squares best fit of a linear, log, and power relation (refer to Table 1). A breakdown of how many cells were best fitted by each of the three candidate functions is shown in Table 2. It should be clear from this data that across all subgroups a log function provides the best fit (compared to a linear or power function) for the vast majority of striate cells (some 80%).

If we look at the data from the total population in a slightly different way, by analyzing the residual variance unaccounted for after finding the best-fit parameters for each function, we find that the average residual per point is 271 ± 14 (SE) for linear, 204 ± 11 (SE) for power, and 120 ± 8 (SE) for log. We can therefore conclude that over the contrast range tested (1–56%), a log function in comparison to a linear or power function provides a much better fit to the contrast response function of striate cells.

Given that the responses of most striate cells tend to compress and saturate at higher response rates, as described above, it is not too surprising that a log function should fit better than a linear function. If we were to restrict the analysis to the beginning portion of the CRF (say the first log unit of contrast), the analysis could potentially produce rather different results (see DISCUSSION). However, demonstrating that a log or linear function provides a better fit over a (judiciously selected) restricted range becomes somewhat untestable (particularly since, as

TABLE 2. *Percentage distributions of best fits*

	All Cells			Cat Cells			Monkey Cells		
	Total (247)	Simple (155)	Complex (92)	Total (137)	Simple (83)	Complex (54)	Total (110)	Simple (72)	Complex (38)
Linear	6	7	3	4	6	2	7	8	5
Log	81	79	86	86	84	87	78	74	84
Power	13	14	11	10	10	11	15	18	11

The best-fitting (parameter optimized) linear, log, and power functions were derived for the responses of each cell individually and then the residual variance was compared. Shown are percentage of cells best fitted (least residual variance) by linear, log, and power functions, broken down across the various subgroups. Thus the first three columns provide the percentages for all cells, the second three columns show all cat cells, the last three columns show all monkey cells. As can be seen, given these three functions and responses over a range of 1-56%, some 80% of the population is best fitted by a log function. Values in parentheses are numbers of cells.

one restricts the range, the actual differences expected are not very large—given small perturbations, many nonlinear intensity response functions are well approximated by a linear function).

HYPERBOLIC RATIO. As discussed above, the contrast response data from striate cells can be qualitatively described as linear over a restricted range, then showing gradual compression, and finally total saturation. This type of behavior is quite adequately characterized by a hyperbolic function (H ratio) of the form

$$\text{response}(C) = R_{max} \cdot (C^n/(C^n + C_{50}^n))$$

where R_{max} refers to the maximum response rate, C_{50} refers to the semisaturation contrast (the contrast required to produce 50% of the cell's maximum response), and n, the exponent, refers to the rate at which the changes occur. This function was first used by Naka and Rushton (30) to fit voltage-intensity data from retinal S potentials. It has since been used to describe the intensity response functions of retinal neurons in a wide variety of vertebrate species (4, 5, 11, 13, 16, 22, 37) in addition to luminance sensitivity measured in human psychophysical studies (3, 15, 17, 18).

We wished to determine the validity of using this relationship as a general descriptor of the contrast response behavior of striate neurons. We therefore began by asking two experimental questions: *a*) which of the four functions, linear/log/power/hyperbolic, provided the best fit for the largest proportion of neurons; and *b*) which of the four accounted for the largest proportion of the variance in response across contrast (that is, which produced the least average residual variance across all cells).

The answer to the first question is shown in Table 3. Of the four functions, the hy-

TABLE 3. *Percentage distributions of best fits*

	All Cells			Cat Cells			Monkey Cells		
	Total (247)	Simple (155)	Complex (92)	Total (137)	Simple (83)	Complex (54)	Total (110)	Simple (72)	Complex (38)
Linear	4	5	3	3	4	2	5	5	5
Log	19	19	19	21	20	22	15	17	13
Power	7	8	5	6	5	7	9	13	3
H ratio	70	68	73	70	71	69	71	65	79

The best-fitting (parameter optimized) linear, log, power, and H ratio functions were derived for the contrast responses of each cell individually and then the residual variance was compared. Shown are the percentage distributions of the cells best fitted by each of the four functions (broken down across animal type and cell type as in Table 2). Values in parentheses are numbers of cells.

perbolic ratio provides the best fit for some 70% of the cells and a log function for some 19%. This general trend is seen across all groups: monkey, cat, simple, complex. The answer to the second question is shown in Fig. 2, where the distributions of residual variance are shown for each function type; the means and standard errors associated with these distributions are shown in Table 4 broken down for the various subgroups. From these results it becomes clear that the hyperbolic ratio is by far the best general descriptor for the striate cell contrast response functions. The average residual variance per data point was 38.4 ± 3.5 (SE); the log function is not really a very close second (120 ± 7.8 (SE)).

To help illustrate the type of fit these four functions are providing for a typical striate cell, the data points for a particular cell are shown in Fig. 3 plotted on linear-linear coordinates with the best fitting *a*) linear function, *b*) log function, *c*) power function, and *d*) H ratio. As can be seen, a strictly linear function over the entire range provides a very poor fit; as will be shown below, when the analysis is restricted to the first 1 log unit of contrast, both a linear relationship as well as a log relationship provide reasonable fits. Over a larger range of contrasts, a log function provides a much better fit than a strict linear function, since it not only characterizes the first few responses quite adequately, but then turns (concave downward) to accommodate the compression and saturation of the cell's response. The log compression, however, is not nearly rapid enough to accommodate the cell's accelerating compression. The values of the parameters of the power function that best fit these data points result in a function that compresses much like a log function (concave downward). Of the four, the H ratio provides the best total description of the linear dynamic range in addition to the nonlinear compression and saturation that this cell shows.

The values of the parameters of the hyperbolic function vary considerably from cell to cell, as would be expected given the qualitative differences that can be seen in the CRFs of different cells. These values can be used to quantify some of this variation in a useful way. The semisaturation constant is an excellent indication of the overall sensitivity of each cell, since it tells us the contrast required to reach a fixed criterion of response (namely 50% of the maximum response); furthermore, the semisaturation constant falls on the linear portion of the dynamic range. The distributions of the values of all three parameters are shown in Fig. 4 for all cells, and the means and standard errors across all subgroups are shown in Table 5; this analysis includes all cells except some 9% of the cells that produced values of C_{50} that exceeded 100% contrast. An analysis of these cells with a semisaturation constant in excess of 100% contrast showed that they were best fitted by either a strict linear func-

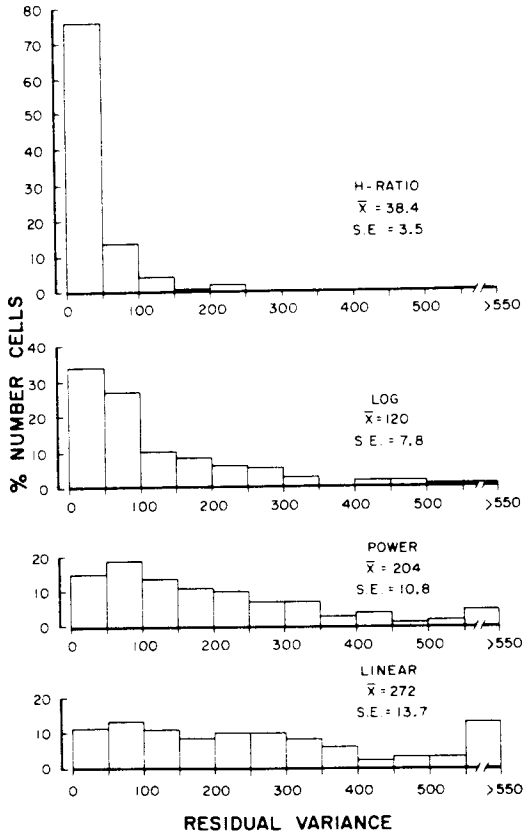

FIG. 2. Distributions showing the average variation between the measured responses and the predicted responses (following parameter optimization). Responses of each cell were fitted by the four functions (linear, log, power, hyperbolic ratio) and then the squared deviation per point was indexed. While some cells are best fitted by a linear relationship, others by a power function or log function, averaged across all cells, the H ratio provides a better description of striate cell contrast response functions.

TABLE 4. *Average residual variance*

	All Cells			Cat Cells			Monkey Cells		
	Total (247)	Simple (155)	Complex (92)	Total (137)	Simple (83)	Complex (54)	Total (110)	Simple (72)	Complex (38)
Linear	271 ± 14	251 ± 16	305 ± 25	279 ± 18	267 ± 21	299 ± 33	262 ± 21	235 ± 25	315 ± 38
Log	120 ± 8	113 ± 9	132 ± 14	104 ± 9	96 ± 19	117 ± 18	141 ± 13	134 ± 16	154 ± 21
Power	204 ± 11	189 ± 13	230 ± 19	186 ± 13	174 ± 14	204 ± 24	228 ± 18	207 ± 23	268 ± 31
H ratio	38 ± 4	37 ± 5	41 ± 6	34 ± 5	34 ± 6	35 ± 7	43 ± 6	41 ± 7	48 ± 10

After finding the best-fitting (parameter optimized) linear, log, power, and H ratio functions for each cell, the residual variance was computed. Shown is the residual variance ± SE per point, averaged across all cells (as well as broken down into the subgroups) for each function. Values in parentheses are number of cells.

tion (6/22) or a power function with parameters that force a C_{50} greater than 100. The hyperbolic function will fit these data points; however only half of the function (primarily the linear portion) appears in the range of measured contrasts.

A point worth developing here concerns the search for a general mathematical formulation (general, accurate, and simple).

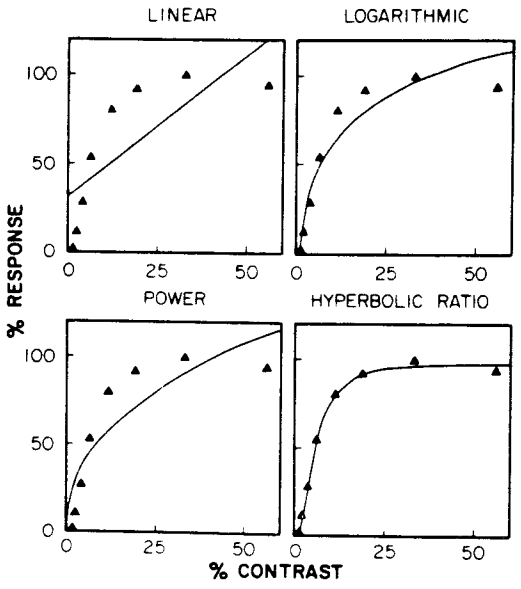

FIG. 3. Responses of a typical striate cell as a function of contrast are plotted on linear-linear coordinates showing the best-fitting (parameter optimized) linear, log, power, and hyperbolic relationships. As can be seen, the H ratio provides the best description of the typical CRF: a linear increase over a restricted range followed by accelerating compression to ultimate saturation. While a log function and power function do show response compression, the compression does not accelerate or saturate. A linear function, over the entire range of contrasts measured, is clearly inappropriate (see Fig. 14 for an analysis of linearity over a restricted range).

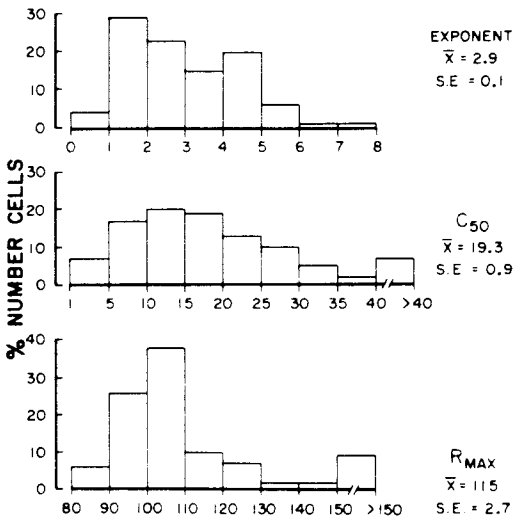

FIG. 4. Distribution of the optimized parameters of the hyperbolic relationship for each cell (save 22, or 9%, with C_{50} in excess of 100%; see text). Each cell has a slightly different set of values. The exponent specifies the rate of change, or slope of the function; the C_{50}, or semisaturation constant, moves the curve horizontally and provides a good index of the contrast sensitivity at half the maximum response; R_{max} specifies the saturation point (values greater than 100 indicate that some cells had not yet reached saturation at the highest contrast measured).

TABLE 5. *H ratio constants*

	All Cells			Cat Cells			Monkey Cells		
	Total (225)	Simple (139)	Complex (86)	Total (127)	Simple (77)	Complex (50)	Total (98)	Simple (62)	Complex (36)
Exponent	2.9 ± 0.1	2.8 ± 0.1	3.0 ± 0.16	2.5 ± 0.12	2.5 ± 0.15	2.6 ± 0.2	3.4 ± 0.13	3.3 ± 0.17	3.5 ± 0.2
Semi-saturation	19.3 ± 0.9	19.8 ± 1.2	18.6 ± 1.5	15.5 ± 1.06	15.2 ± 1.25	16.0 ± 1.9	24.0 ± 1.5	25.0 ± 2.0	22.1 ± 2.5
Maximum	115.0 ± 2.7	117.0 ± 4.0	111.7 ± 3.2	111.0 ± 2.2	111.0 ± 2.7	111.0 ± 3.8	120.0 ± 5.7	124.0 ± 8.4	112.0 ± 5.5

Values are averages of means ± SE of the optimized parameters of the best-fitting hyperbolic relationship computed for each cell (save 22, or 9% of the population, with C_{50} in excess of 100%; see text). Values in parentheses are numbers of cells.

While the H ratio may be well suited to accommodate some 70% of the total population of cells, its value would be diminished if it was grossly inaccurate in describing the rest of the population. Fortunately, this is not the case. Those CRFs that are best fitted by a log function or a power function with an exponent less than 1.0 are quite adequately described by the H ratio as well; the ultimate saturation is simply moved to higher contrasts. The point is that, with the goal of parsimony in mind, it is possible to describe some 90% of all striate cells using the H ratio; the increase in residual variance (as indicated in Fig. 2 and Table 4) is reasonably small.

DYNAMIC RANGE VARIATION. There is a great deal of variation from cell to cell in the absolute location of the dynamic response range along the contrast axis; different cells respond over different ranges of contrast. This variation is illustrated in Fig. 5 where the contrast response functions for four different cells are shown; these cells all had very similar spatial frequency tuning and were all encountered during the same electrode penetration. As can be seen, the dynamic response range of each cell covers a slightly different range of contrasts. At a given low contrast, one cell may already be saturated, another silent, and a third may be optimally positioned such that the contrast falls within the dynamic linear range. Such range variation could be an important factor in behavioral contrast discrimination; in general, when considering the activation of a large population of cells, increasing the contrast of a grating produces an increase in both *a*) the overall number of action potentials produced as well as *b*) the overall number of cells responding.

To provide a quantitative indication of this range variation for the total population of cells we computed (from the best-fitting function for each individual cell) the contrast required to reach 50% of each cell's maximum response (that is, we computed the semisaturation contrast); the values were

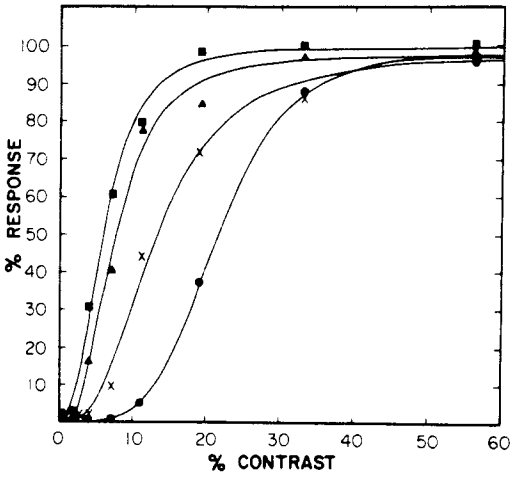

FIG. 5. Contrast response functions of four striate cells plotted on linear-linear coordinates to illustrate the variation that occurs, from cell to cell, in the location of the dynamic portion of the response range, along the contrast axis. These four cells had similar spatial tuning and were encountered during a 1-mm penetration perpendicular to laminae. One cell begins responding at 1% contrast and saturates by 10%; another cell does not begin responding until 10% contrast.

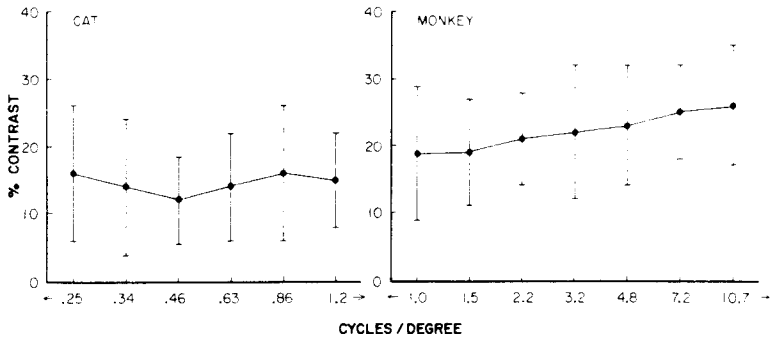

FIG. 6. To quantify the range variation, the average semisaturation contrast (the contrast required to reach 50% of a cell's maximum response) is plotted conjointly with (as a function of) preferred spatial frequency (cells recorded from cat cortex are averaged together in the left panel, monkey cells in the right panel). One standard deviation is plotted on each side of the mean to indicate the variation in the location of the dynamic response range that occurs, from cell to cell, across the range of preferred frequencies. Such range variation indicates that cells distribute their limited dynamic response ranges over different restricted contrast ranges: multiple channels along the contrast axis.

then averaged over sequential frequency intervals. The results of this analysis are shown in Fig. 6, where the means and standard deviations of the semisaturation contrasts are plotted as a function of spatial frequency. As can be seen, the standard deviations indicate the variation that occurs, from cell to cell, in the location of the dynamic range; further, the average values indicate that these distributions are very similar across the range of preferred spatial frequencies.

Contrast response and spatial tuning

While some of the CRFs of neurons in the striate cortex are in fact strictly linear (some 5% of the total population across the range of contrasts measured), the vast majority have a dynamic linear response range only over a limited contrast range (generally less than 1 log unit of contrast, depending on the cell's particular exponent and semisaturation contrast). Outside of the linear range, the cells are *a*) essentially silent, *b*) completely saturated at the maximum, or *c*) in the process of nonlinear compression to the asymptotic level. In other words, beyond their respective dynamic linear range, the CRFs of most striate cells are quite nonlinear (the range of the latter generally exceeding the former).

Given compression and saturation of the contrast response function, it is appropriate and important to ask what the consequences of such nonlinearities might be on the spatial processing of striate cells. What sort of responses might one expect when the contrasts of a given spatial pattern exceed the linear range of a given cell. To test several different possibilities, we measured the CRFs of 22 cells at several different spatial frequencies and then analyzed the data using the hyperbolic equation, which is capable of distinguishing different models (cf. Refs. 17, 18 and Ref. 15).

One simple model, response-set gain, would place the burden of the nonlinear compression and saturation on the final common response-generating mechanism of the individual striate neuron: the gain is set by the response level (Robson (31) discusses similar theoretical issues and some of the consequences of such a model; see also Evans (12) for a similar discussion in reference to the auditory system). This compression would be applied after the spatial summation had occurred. Thus, for example, a given cell may have a restricted response range and a fixed maximum response (R_{max}) beyond which it cannot be expected to operate; it therefore compresses any and all excitation, independent of other stimulus variables (e.g., spatial frequency, temporal frequency, orientation, etc.) solely on the basis of how far up the response axis a certain response had moved. Such a mechanism can potentially result in the cell producing equivalent responses to optimal stimuli (presented at or beyond the saturation level) and nonoptimal stimuli (presented at high contrast); once an optimal stimulus produces the maximum re-

sponse, nonoptimal stimuli can catch up if their contrast is raised.

Given such a mechanism, which has been demonstrated for other visual neurons (25), one would expect the CRFs measured at different spatial frequencies to shift to the right horizontally as the spatial frequency is varied from the optimum value. Or, in terms of the hyperbolic relationship, the maximum rate of firing (R_{max}) and the exponent (n) would be expected to remain constant and only the semisaturation constant (C_{50}) should increase (directly proportional to the frequency attenuation factor). Such a scheme would have the desirable quality of producing (from a nonlinear CRF) identical spatial-frequency sensitivity curves independent of the response criterion used (the sensitivity ratio between different frequencies would remain constant, at least up to saturation). Since the nonlinear gain is determined by the response, if we hold the response level constant, the effect of the nonlinearity should be nullified (cf. Ref. 31).

A second model, contrast-set gain, would place the burden of the nonlinear compression and saturation on a mechanism that precedes the striate response generation and possibly even the spatial summation of the light distribution: the gain is set by the contrast level. It is possible that some mechanism prior to the striate neuron (or at least prior to the neuron's response) clips or compresses the potential excitation more as a function of the luminance contrast and not the actual response level. If the input to the

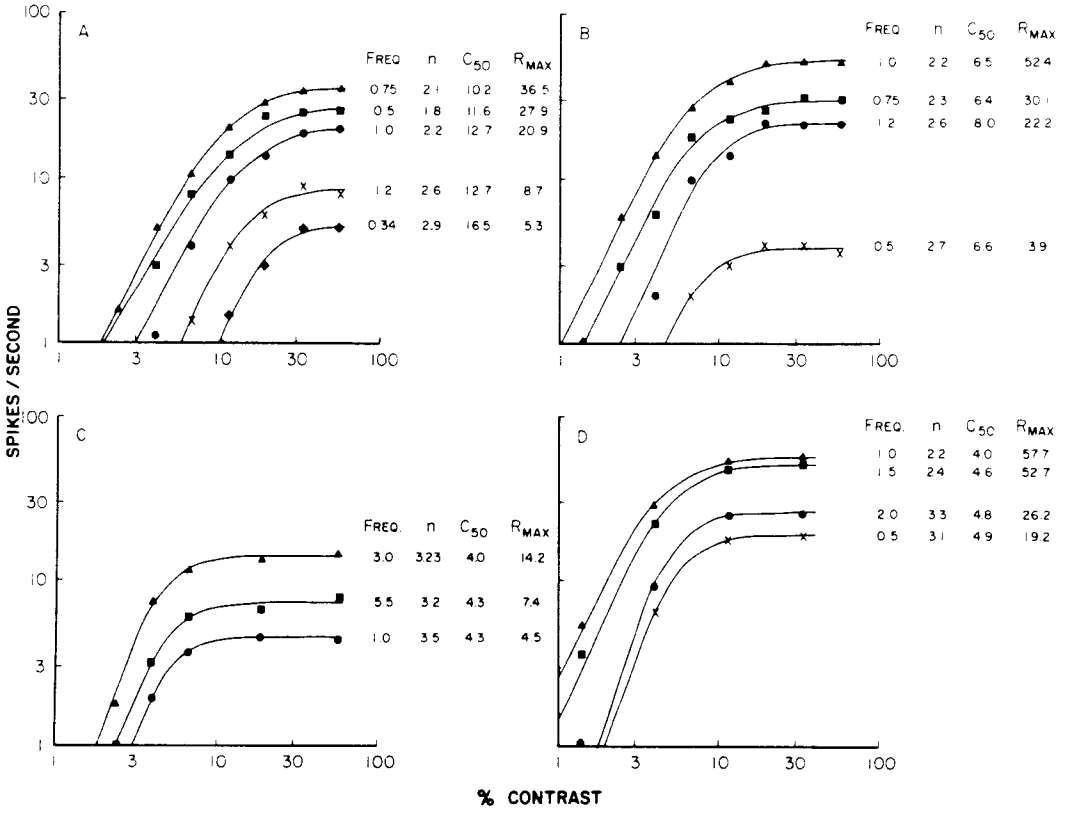

FIG. 7. Contrast response functions for four cells measured using several different test spatial frequencies. The best-fitting H ratio was found for each test frequency; values of parameters, along with the test frequencies, are shown to the right of each curve. Qualitatively, curves appear to shift vertically downward along the response axis as the frequency is varied from the optimum value. Quantitatively, this effect is seen in values of parameters of the best-fitting H ratios: within a given cell, the exponent and the semisaturation contrast are relatively constant across spatial frequency in comparison to R_{max} (which varies considerably). Such vertical shifts preserve the relative frequency response function independent of contrast. These results are more consistent with a contrast-set gain mechanism as opposed to a response-set gain.