

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 contrast 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 re-

sults 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% N₂O/25% O₂ 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 CO₂ 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 triethiodide. 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/m²). 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

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

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.

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.

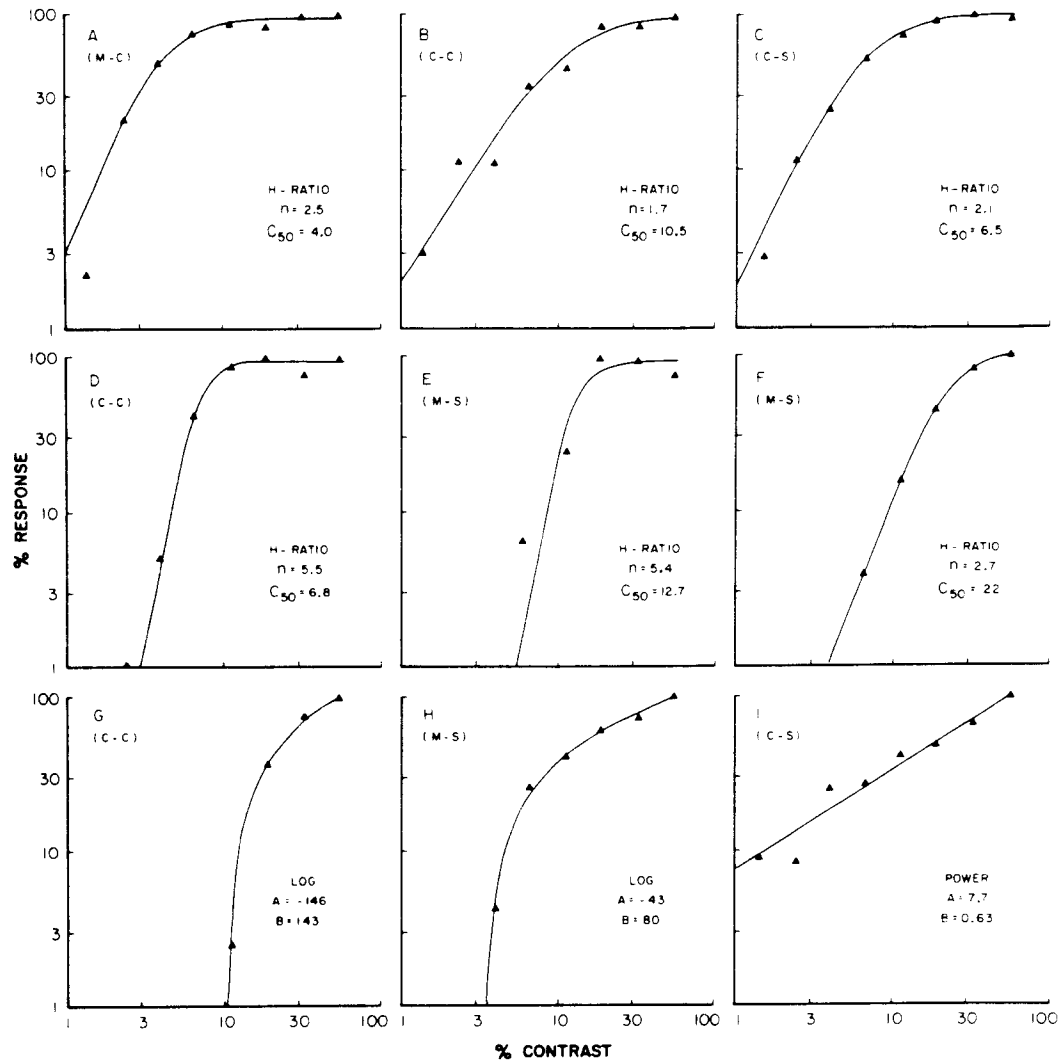


FIG. 1. Contrast response functions for nine representative striate neurons; percent response (relative to the maximum response) is plotted on log-log coordinates as a function of the luminance contrast of spatial-temporal sine-wave grating patterns. The smooth curve drawn through responses of each cell 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. 1C). 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 pre-

sented 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