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*Research Note*

# Orientation Selectivity in the Cat's Striate Cortex is Invariant with Stimulus Contrast*

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**Summary.** Extracellular responses of single units in striate cortex of the cat were studied quantitatively. Sinusoidal gratings were used as stimuli and the variables of interest were orientation and contrast. Specifically, we wanted to determine if orientation tuning was dependent on contrast. Of 45 cells studied in detail, two basic types of contrast-response pattern were observed, but most patterns were intermediate between these extremes. In one type, responses increased approximately linearly with log contrast while in the second, saturation was found at low contrast levels. For all these cells, orientation tuning characteristics were independent of contrast. An additional observation, made from 14 cells, was that stimuli presented at non-optimal orientations can suppress responses to below the general maintained discharge levels. In eight of these cases, the inhibition was clearly contrast-dependent.

**Key words:** Cat visual cortex – Orientation tuning – Contrast

## Introduction

The relationships between stimulus contrast and responses of visual neurons deserve considerable attention because they must be of fundamental importance in visual function. In X-cells of the retina and LGN, responses appear to be linear at low contrasts, but they vary logarithmically at high contrast levels (Maffei and Fiorentini 1973; Robson 1975). In visual cortex, responses are reported to be linear for about a log unit above threshold until saturation levels are reached, but conclusions from these observations are limited by considerable variability in the data (Tolhurst et al. 1981).

What is clear is that visual neurons do not respond in some simple proportional manner as stimulus contrast is varied. Contrast-response functions may vary considerably with location in the visual pathway, cell type, and absolute contrast levels. One would predict, therefore, that absolute contrast level should affect measurements of other stimulus parameters (Robson 1975). For example, orientation or spatial or temporal tuning properties of cortical cells should vary with contrast level. Specifically, for cells that show saturation, the degree of selectivity for these parameters should be underestimated.

We report here a study designed to test the above hypothesis. We determined the orientation-tuning of cortical cells using sinusoidal gratings of various contrasts. Orientation selectivity was chosen as the variable to be measured because it appears to be the only function which is first elaborated in visual cortex, and in addition, it is a very stable property of cortical cells (Henry et al. 1973; Rose and Blakemore 1974; Hammond et al. 1975).

## Methods

Adult cats (2–4 kg), which were premedicated with injections of atropine and Acepromazine, were anesthetized with halothane while a femoral vein was cannulated. Anesthesia was continued with sodium thioamyl and a tracheal cannula was positioned. A small cranial hole at Horsley-Clarke P4 near the midline was made, and the dura was reflected. The animal was paralyzed with gallamine triethiodide (10 mg/kg · $h^{-1}$) and artificially ventilated with a mixture of $N_2O/O_2/CO_2$ (75 : 24 : 1). Sodium thioamyl was added as required during the experiment so that the EEG contained high amplitude low frequency peaks interspersed with high frequency waves, which we took to indicate an adequate state

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of anesthesia. Peak expired $CO_2$ was held at around 4.5%. Temperature was maintained at about 37.5° C, and EKG and heart rate were monitored.

Prior to recording, topical neo-synephrine and atropine solutions were applied, and contact lenses with 3 mm artificial pupils were placed on the corneas. Spectacle lenses were used in addition to attain conjugacy, between the retinae, a tangent screen and a display TV screen. The screens were 57 cm from the eyes. A reversible ophthalmoscope was used to project retinal landmarks onto the tangent screen. Sinusoidal gratings, displayed on the TV tube, were bright (300 cd/m$^2$) and relatively large (a 10° circular aperture was used to mask the screen). Contrast was linear to values of at least 85%. These gratings were generated by a microcomputer under control of a minicomputer, which was used to run the experiments.

Tungsten-in-glass microelectrodes were advanced into striate cortex through a layer of agar over the brain surface and a wax covering sealed the chamber. Action potentials from individual cells were isolated extracellularly and conventional methods were used to amplify and display impulses by audio and visual devices. Spikes were viewed on a display CRT and a window discriminator selected impulses to be fed to the input buffer of a computer. Small electrolytic lesions were made along each electrode track. At the end of the experiment, animals were deeply anaesthetized and perfused with formalin. Subsequent histological analysis was performed to establish recording sites.

Once a cell was isolated, its receptive fields were plotted manually. Ocular dominance, orientation limits, direction selectivity and velocity characteristics were determined subjectively. A front surface mirror was then positioned to place the receptive field of the dominant eye in the center of the TV screen. The other eye was occluded. Short quantitative trials were then run, prior to the main experiment, to determine preferred orientation, spatial, and temporal frequencies. A response versus contrast curve was then obtained, using the preferred stimulus values. The main experiment was typically run over a range of contrasts of around 0.82 log units. The highest and lowest contrasts generally used were 80% and 2–10%, respectively. The central measurements required responses to a stimulus set comprised of 28 or 30 variables (4–5 contrasts at equal intervals along a log scale, as a function of 6–7 orientations). All stimulus conditions were randomly interleaved. Included in the set was a null or blank presentation consisting of a field of uniform luminance, i.e., zero contrast to measure maintained discharge levels. Each stimulus was presented ten times, for 4 s per trial, and trials were preceded by a 1-s foreperiod during which no stimulus was presented. Responses to the stimuli were accumulated in 256 bin histograms representing 2 s. Responses to the gratings were Fourier transformed, to obtain the amplitude at the D.C. level (zero frequency component) or the first harmonic of the temporal modulation rate used. The larger of these values was used to specify responses.

## Results and Discussion

We have obtained complete data, as described above, for 45 cells. For each cell, a given set of data may be analyzed from two points of view: by examining the effects of contrast upon orientation tuning, or by observing the effects of orientation on contrast-response curves. Examples of the first type of analysis are shown in Fig. 1a and c. In Fig. 1a, orientation tuning curves are given for contrast levels of 10%, 20%, 40%, and 80%. Some degree of saturation is evident between the upper two curves (40% and 80%) but below that, response is an approximately linear function of log contrast. Note that all four curves peak at around the same orientation. Responses from a different type of cell are shown in Fig. 1c. Once again, four contrast levels were used (10%, 20%, 40%, and 80%). In this case, saturation occurs at much lower values, and responses are only slightly reduced at a contrast of 10%. What is striking here is that, relatively, saturation applies to all orientations tested, in the sense that no increase in response is found as contrast is increased.

Using responses of these same two cells, the second form of analysis is illustrated in Fig. 1b and d. In Fig. 1b contrast-response functions are given at optimal (top curve) and sub-optimal (lower six curves) orientations. For all orientations, responses vary approximately linearly with log contrast, and slopes decrease monotonically with reduced peak response levels. Contrast-response functions for the other cell, shown in Fig. 1d, also vary approximately linearly with log contrast, but in this case, slopes are relatively flat for all orientations. Once again, this demonstrates the remarkably uniform relative saturation at suboptimal as well as optimal orientations.

The orientation tuning curves and contrast-response functions shown in Fig. 1 represent two basic patterns that we observed. Response patterns of most cells were generally intermediate between these two types. Differentiation could not be made on the basis of receptive field classification. We classified 19

**Fig. 1. a, c** Orientation tuning curves are shown for two simple cells from which responses were obtained to presentations of sinusoidal gratings at the following contrast levels: 10% (*open circles*), 20% (*asterisks*), 40% (*crosses*), 80% (*filled circles*). In these and succeeding graphs, dashed lines indicate spontaneous discharge levels. Response patterns of these cells are quite different, but in both cases preferred orientation and bandwidth remained constant over the range of contrasts tested. The data of **a** and **c** are replotted in **b** and **d**, respectively, to illustrate the different response patterns of the two cells. Now, contrast, on a log axis, is the variable and response functions are plotted for the seven orientations shown on the left. Preferred orientation is at the top and successively lower curves represent increasing angular distances from the optimal value. Note that the functions in **b** are approximately linear but the slopes change markedly from steep at the top to shallow or flat on the bottom. The functions in **d**, on the other hand, are nearly all flat indicating response saturation at relatively low contrasts. Summaries of data from these cells and all others studied are given in **e** and **f**. For each cell, preferred orientations and orientation tuning characteristics (half-widths at half-heights) were noted for all contrast levels. Then the slopes were computed of linear regression fits of preferred orientation and tuning widths as functions of contrast. The distributions of these slopes for orientation and tuning are shown in the histograms of **e** and **f**, respectively. Most slopes are close to zero indicating that these functions are relatively constant as contrast is varied

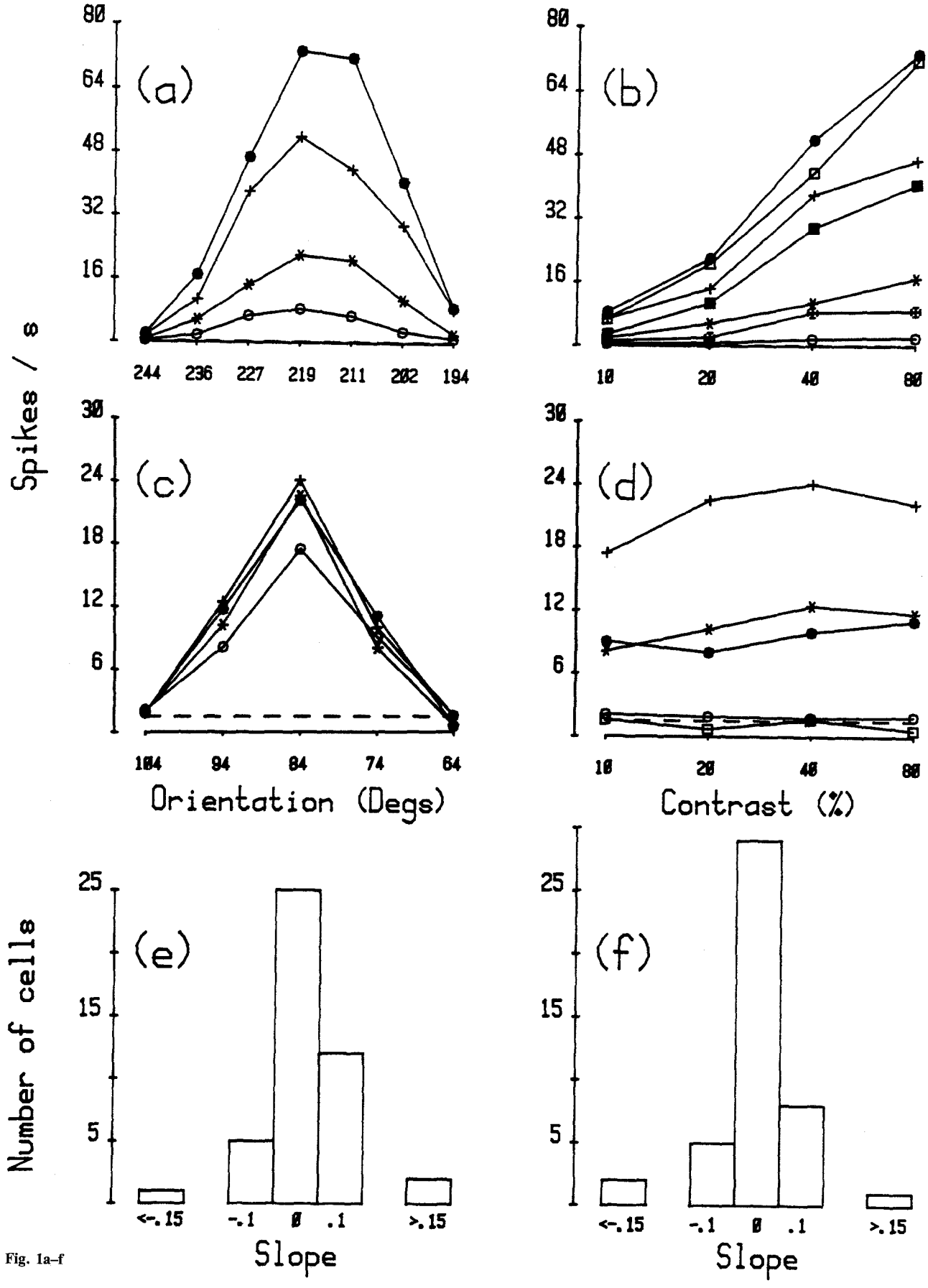
(a)
(b)
(c)
(d)
(e)
(f)
Spikes / s
80
64
48
32
16
244 236 227 219 211 202 194
10 20 40 80
30
24
18
12
6
184 94 84 74 64
Orientation (Degs)
Contrast (%)
Number of cells
25
15
5
<-.15 -.1 0 .1 >.15
Slope

Fig. 1a–f

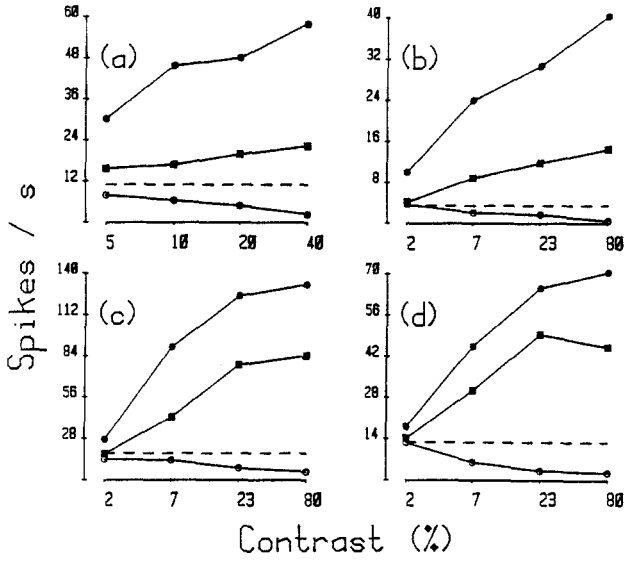


**Fig. 2a–d.** Responses of four complex cells are given for gratings at the contrast levels indicated. Sweeps at three different orientations were used to obtain the functions shown for each cell. The orientations used were optimal (*filled circles*), moderately suboptimal (*filled squares*, ± 25°, 31°, 39°, 65° in **a, b, c,** and **d,** respectively) and substantially suboptimal (open circles, ± 50°, 47°, 59°, and 83° in **a, b, c,** and **d,** respectively). Note that contrast dependent inhibition was present in each case when the most inappropriate orientation was used, and that responses were below the spontaneous levels (*dashed lines*) as determined with blank stimuli (see Methods)

cells as simple and 26 as complex but contrast-response patterns were independent of these categories. In the case of the first pattern, Fig. 1a and b, the responses are approximately proportional to log contrast but the proportionality (slope) is a function of stimulus orientation. In the second (Fig. 1c and d), the cell is relatively insensitive to changes in contrast at all orientations. However, in both these cases, inspection of Fig. 1 suggests that orientation tuning properties may remain relatively unaffected as contrast is changed. Returning to the hypothesis stated at the outset, we now consider these tuning properties in detail. We have determined preferred orientations and tuning characteristics at each contrast level, for the population of cells we studied. In accordance with previous procedures we calculated linear regression fits around peak responses to estimate preferred orientations and half-width at half-height values (Henry et al. 1973; Rose and Blakemore 1974). Linear regression fits were then computed between these quantities and contrast. If the data of Fig. 1a–d are typical, then the slopes of these regression fits should be quite flat. Slopes of zero would indicate that contrast changes have insignificant effects on orientation tuning and preference.

The distributions of slopes for all 45 cells recorded are given in Fig. 1e and f. In Fig. 1e, the histogram represents slopes of regression fits to preferred orientation vs. contrast values. Data of Fig. 1f, similarly, are regression fit slopes of tuning (half-width at half-height) characteristics versus contrast values. In both cases, it is clear that the histograms peak markedly around a slope of zero. For only two cells, tuning patterns were marginally different from zero ($t = 15$, $p < 0.05$; $t = 14.3$, $p < 0.05$) and, in these cases, tuning sharpness appears, counterintuitively, to decrease slightly as contrast increases. Aside from these exceptions, the results illustrated in the histograms suggest that orientation preference and tuning characteristics remain remarkably constant as contrast is altered.

In addition to this central finding, one other feature of the data we analyzed is worth noting. Of the 45 cells we studied, 19 had substantial maintained discharge levels. For 14 of these cells, stimuli presented at nonoptimal orientations were inhibitory in that responses were clearly below maintained levels. For eight of these 14 cells, all of which had relatively high spontaneous levels (mean = 11.3 impulses/s, SD = 5.9), this inhibition was markedly contrast dependent. Typical responses from this group of cells, all classified as complex, are illustrated in Fig. 2.

In summary, we have found that orientation preference and tuning characteristics of cortical cells are stable as contrast is varied. This holds over very wide ranges of contrast, nearly 2 log units, as well as near threshold levels. The implication of these results is that threshold and suprathreshold stimulus contrast levels should produce highly correlated responses of cortical cells. This appears to hold in the case of spatial frequency preference and bandwidth (Movshon et al. 1978). Our present findings do not support the hypothesis stated at the outset, that orientation tuning properties of cortical cells should vary with contrast.

Perhaps the most intriguing finding of our experiments is related to the contrast-response functions that showed clear saturation. What is striking here is that relative saturation was evident at all orientations tested. These cells may receive a strong non-oriented excitatory input which causes saturation prior to the process of orientation selectivity, which is thought to be largely inhibitory (Creutzfeldt et al. 1974; Nelson and Frost 1978; Sillito 1979; Tsumoto et al. 1979). This could be due to saturation at the LGN as suggested in another study of cortical response functions (Henry et al. 1978). Cells which do not show saturation may have relatively weak excitatory input.

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