

## SPATIAL FREQUENCY SELECTIVITY OF CELLS IN MACAQUE VISUAL CORTEX

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**Abstract**—We measured the spatial frequency contrast sensitivity of cells in the primate striate cortex at two different eccentricities to provide quantitative statistics from a large population of cells. Distributions of the peak frequencies and bandwidths are presented and examined in relationship to (a) each other, (b) absolute contrast sensitivity, (c) orientation tuning, (d) retinal eccentricity, and (e) cell type. Simple and complex cells are examined in relationship to linear/nonlinear (that is, X/Y) properties; a procedure is described which provides a simple, reliable and quantitative method for classifying and describing striate cells. Among other things, it is shown that (a) many striate cells have quite narrow spatial bandwidths and (b) at a given retinal eccentricity, the distribution of peak frequency covers a wide range of frequencies; these findings support the basic multiple channel notion. The orientation tuning and spatial frequency tuning which occurs at the level of striate cortex (in a positively correlated fashion) suggests that the cells might best be considered as two-dimensional spatial filters.

### INTRODUCTION

Considerable psychophysical evidence has been accumulated over the past few years indicating that the visual system operates in a quasi-linear fashion over a realistic range of contrasts, and that there are multiple, fairly narrowly tuned, spatial frequency channels (presumably cells selectively sensitive to different restricted portions of the spatial frequency spectrum). These studies (for general reviews see: Sekuler, 1974; Robson, 1975; Braddick *et al.*, 1978; or De Valois and De Valois, 1980) therefore suggest that the visual system up through the striate cortex may be doing a spatial frequency filtering of the visual information.

The earliest physiological studies aimed at providing direct evidence on these points (Campbell *et al.*, 1968; Campbell *et al.*, 1969) did not find the cortical cells in either cat or squirrel monkey to be very narrowly tuned. They did, however, find cortical cells to be more narrowly tuned than those in the lateral geniculate nucleus (LGN), and to show peak sensitivity at different portions of the spatial spectrum. In the experiments reported here, we examined units in the macaque striate cortex. Some of these data were presented earlier (De Valois *et al.*, 1977; Albrecht, 1978). Our contrast sensitivity measurements, from a sizable sample, show that many of the cells are quite narrowly tuned. Other groups have also reported finding cells in the cortex of cat (Maffei and Fiorentini, 1973; Glezer *et al.*, 1973; Ikeda and Wright, 1974; Movshon *et al.*, 1978) and monkey (Schiller *et al.*, 1976b) with narrow spatial tuning; however, with the exception of the study by Movshon *et al.*, on cat

cortical cells, the earlier studies report just the responses to various spatial frequencies at a given contrast (rather than contrast sensitivity measurements) which make their data hard to compare with psychophysical measures.

The primary goal of this study was to provide quantitative population statistics concerning the general nature of the spatial frequency contrast sensitivity functions of macaque striate cells. Such normative physiological data should complement the many relevant psychophysical studies of spatial frequency channels and, in general, should help us assess the relative validity and usefulness of the multiple channel model of visual processing. We were particularly interested in (a) the distributions of peak frequency and bandwidth, (b) the interrelationships between peak frequency, bandwidth, absolute contrast sensitivity and orientation tuning, and (c) the potential variations in cells recorded from two different retinal eccentricities. A secondary goal of this investigation was to analyze the properties of simple and complex cells from the linear/nonlinear (X/Y) perspective. Present methods for classifying different response types seem rather qualitative and provide little indication of the variation which actually exists within a given response type. The procedure we adopted provides a simple, reliable and quantitative method for classifying and describing striate cells.

The experiments reported here are part of a series in which we examined LGN cells (von Blanckensee, 1980), and also measured the behavioral contrast sensitivity of macaque and human observers (De Valois *et al.*, 1974). All these experiments were run at the same adaptation level, using much the same techniques of stimulus presentation, thus permitting comparisons between these two levels in the system as

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well as with the resulting behavioral capabilities. The fact that the macaque and human contrast sensitivities are so similar (De Valois *et al.*, 1974) also facilitates generalizing our physiological measurements of spatial contrast sensitivity to human vision.

#### METHODS

##### *Apparatus*

The apparatus and general recording procedures are similar to those more fully described elsewhere (Albrecht, 1978; De Valois *et al.*, 1979; Albrecht and De Valois, 1981). The stimuli were presented by modulating either a Tektronix 602 display oscilloscope (white p4 phosphor), or, in later experiments, a Tektronix 654 monitor. Several types of patterns—gratings of various contrasts and frequencies, black and white bars and edges of various contrasts, gratings or bars delimited in both the *x*- and *y*-axis, etc.—could be presented in any of a variety of ways: flashed on in various stationary locations, drifted across the field, or temporally modulated in counterphase-flicker at any desired rate. The orientation of any of these patterns could be varied, electronically for the 602 scope, or manually for the 654 scope. In the early experiments the patterns were produced by manual control of function generators and the data analyzed by computer off line. For most of the experiments, however, the stimulus presentation was computer controlled and the data analysis was carried out on-line by a NOVA 1200.

##### *Experimental procedure*

There were several subsidiary experiments, but the principal study consisted of measuring the contrast sensitivity of cortical cells in macaque monkey. This was done by drifting spatial sine wave gratings across the cell's receptive field (RF). Every cell was tested at several spatial frequencies, each presented at several contrasts. From the results we determined the contrast sensitivity: the contrast required at each spatial frequency to produce a certain criterion response.

When a cell was isolated, its RF was mapped in the conventional manner with hand-held lights on a tangent screen. From this, we could classify the cell as simple, complex or hypercomplex, using Hubel and Wiesel's (1962) criteria. By definition, simple cell RFs (a) show discrete areas of either on or off firing (b) show summation within the discrete areas and (c) allow qualitative prediction of the responses to moving and flashing stimuli; complex cells (a) fail to display the above properties and (b) generally show mixed on and off responses across the entire RF. Cells with end-zone inhibition (i.e. "hypercomplex") as well as cells with little or no orientation selectivity were categorized using the above criteria and grouped accordingly. Stimuli used to examine cells with end-zone inhibition were delimited in length in accord with the cell's preference. For those cells which could not be un-ambiguously classified with hand-held

Table 1

	Foveal	Parafoveal	Total
Spatial tuning	228	130	358
a.c.-d.c. contrast	220	123	343
Orientation	138	84	222
Null-phase	37	27	64

stimuli, a computerized mapping procedure was used and the resulting RF was then categorized as stated above.

To adequately examine each cell's spatial tuning, preliminary tests were first made to determine the optimal values of orientation and temporal frequency; these were then held constant while the spatial frequency tuning was examined with gratings of various spatial frequency and contrasts. Once this was completed the orientation tuning was quantitatively examined (with spatial and temporal frequency held constant at the optimal values) and then finally the null phase test for linearity was performed (Enroth-Cugell and Robson, 1966).

To carry out the preliminary studies plus the quantitative experiments described took at least an hour; to run them all took several hours and not all cells were held that long. The various subsidiary experiments discussed below, then, were performed on subsamples of our total population of cells. Table 1 provides a summary of cell sample sizes, loci and tests applied.

The recording site could be estimated from the RF locus in relation to the projection of the optic disk, but was more precisely determined from histological examination of the electrode tracks in relation to the 17-18 border and the retinotopic map of Talbot and Marshall (1941). The recording loci varied from the foveal center to 5° peripheral. We wanted to limit the contribution to our data of variations in retinal eccentricity, while examining two different central areas. Therefore, we aimed our probes either close to the foveal projection, or at a slightly parafoveal locus. More than half of the cells (our "foveal" sample) came from cortical loci picking up from 0 to 1.5° away from the fovea; the rest (called "parafoveal") had RFs 3 to 5° away from the fovea.

##### *Data analysis*

The spike discharge was counted in 5 msec time bins over the duration of one stimulus presentation (that is, over one cycle of a drifting grating) and then averaged across the repeated presentations to produce an average response histogram. Since the stimulus was a temporally periodic grating pattern, we could Fourier analyze the histogram to determine the d.c. (average rate of firing) and the amplitude and phases of each of the first five harmonics in the response. Depending on the cell type (see below), we used either the d.c. or the a.c. (the amplitude of the first harmo-

nic, which is of the same period as the stimulus) as the response measure to determine the contrast sensitivity or orientation selectivity of the cell. The a.c. and d.c. measures in each case were the change in the cell's response relative to the a.c. and d.c. shown during no-pattern control trials.

**RESULTS**

*Response types*

Cortical cells are clearly not all the same in their responses to drifting or flickering gratings. There are two principal response types, corresponding to the dichotomy of simple vs complex cells put forth by Hubel and Wiesel (1962; 1968) from their receptive field studies. In many respects, the differences between these cell types are more obvious (and much easier to measure) from their responses to drifting or counterphase flickering gratings than to conventional RF mapping stimuli.

*Simple cells.* Cells classified by Hubel and Wiesel RF mapping procedures to be simple cells respond to a sine wave grating drifting across their RF with a modulated discharge at the same frequency as the drift rate. If the average response histogram of such a cell is Fourier analyzed, therefore, most of the power is at the 1st harmonic. Typically, however, simple cells have little or no maintained discharge (the median maintained rate for our total sample of simple cells was 0.25 spikes/sec). Any modulated firing must therefore produce (a) an increase in mean firing (d.c. component) and (b) some higher harmonic distortion mainly because of the effective half-wave rectification:

the cell cannot fire less than 0 spikes/second during the trough. A typical response of a simple cell to a drifting grating pattern is shown in Fig. 1a, together with the amplitudes and phases of the first five Fourier harmonic components. As can be seen this cell provided an excitatory response during one half cycle of the pattern but due to the lack of a maintained discharge the cell's response could not reflect the second half cycle of the pattern; those few simple cells which possess a maintained discharge show an inhibitory response during this half cycle of the stimulus (see Albrecht, 1978, for a discussion of this issue).

The other type of grating presentation we used was a stationary counterphase flickering grating pattern (with spatial and temporal frequency held constant at the optimal values) presented at 8 different phase positions each separated by 45 degrees spatial phase angle. This type of presentation, first used by Enroth-Cugell and Robson (1966) to test the linearity of spatial summation, invariably produced from simple cells the type of results shown in Fig. 2a. At the position where the white bar of the grating was centered on the excitatory portion of the RF (second line from the top, 270° spatial phase), the cell gave a large response to the first half of the temporal cycle of the counterphase flicker. During this half of the cycle, the amount of light in the central area of the RF was being increased while the amount of light on each inhibitory flank was being simultaneously decreased; this condition produced the maximum response from the cell. During the second half of the temporal stimulus cycle, the light over the center of the RF decreases while the light over the flanking areas increases; this produces

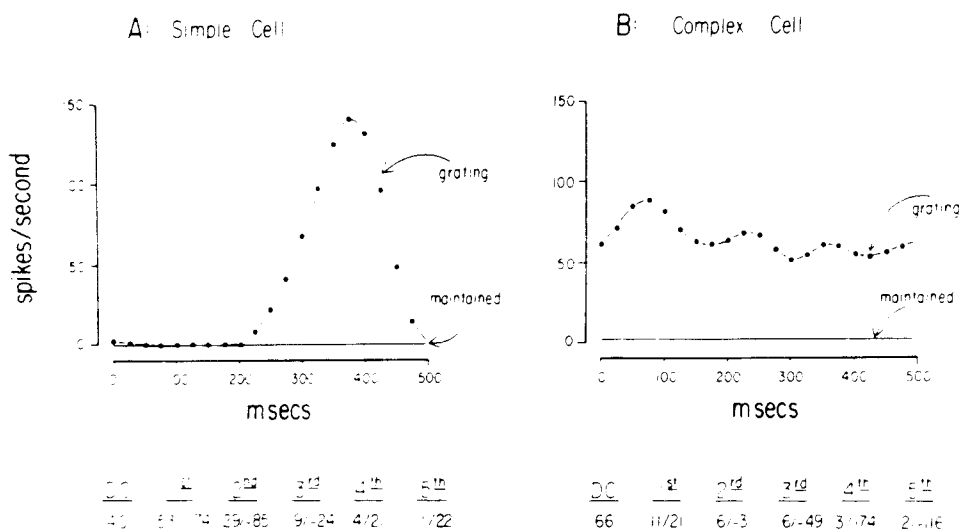


Fig. 1. Response patterns of a representative simple cell (A) and complex cell (B) to gratings drifted across their receptive fields. The response (peri-stimulus time histogram, PSTH) averaged over 20 repetitions of the sinusoidal stimulus is shown above a printout of the d.c. (mean rate of firing) and the first five harmonic components (amplitude:phase). The average maintained discharge in the absence of any visual stimulus is also displayed for each cell. Note that the simple cell's response to the drifting grating shows a discharge pattern which modulates in synchrony with the fundamental temporal cycle of the stimulus, therefore most of the power appears in the 1st harmonic. The complex cell's response, on the other hand, shows an overall increase in the mean rate of firing with little modulation, therefore the response appears in the d.c. component with little power in the harmonics.

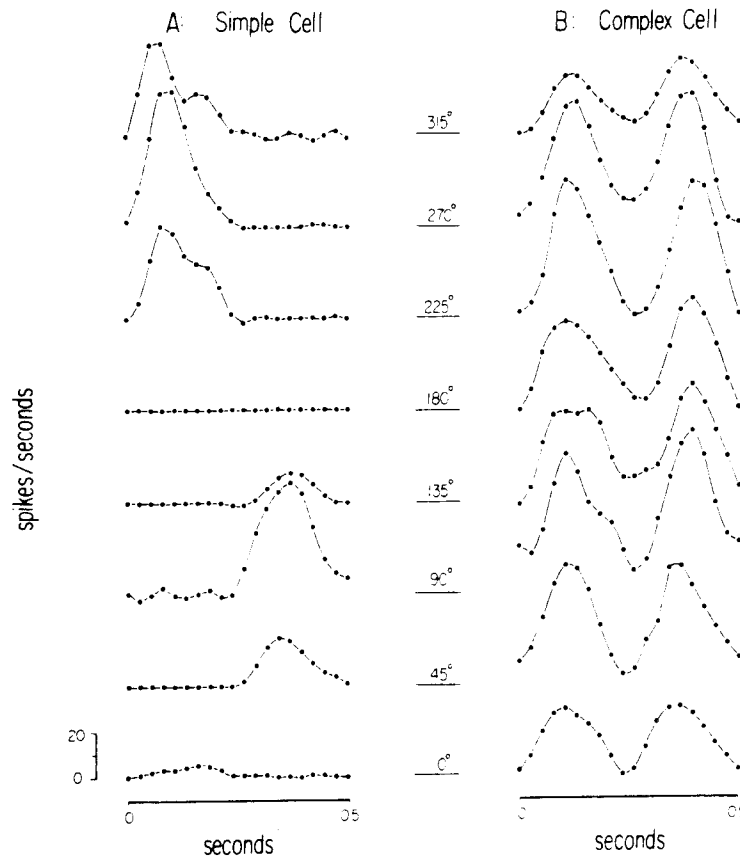


Fig. 2. Response (PSTH) patterns of a representative simple cell (A) and complex cell (B) to a counterphase modulated spatial grating presented in eight different phase positions (each separated by  $45^\circ$ ); this corresponds to the Enroth-Cugell and Robson (1966) "null phase test" for spatial summation. For ease of viewing, the responses have been vertically displaced by a constant amount (as indicated by the central markers). Note that the simple cell modulates its discharge in synchrony with the fundamental temporal cycle of the stimulus and shows two "null phase positions" (at  $0^\circ$  and  $180^\circ$ ); this indicates linearity of spatial summation. The complex cell, on the other hand, modulates its response at twice the fundamental and shows no "null phase positions", thus indicating non-linear spatial summation.

no firing of action potentials from the cell presumably because the cell is maximally inhibited. Those few simple cells mentioned above which did have a maintained discharge showed an inhibition of the maintained discharge during this half cycle. At  $90^\circ$  spatial phase (third line from the bottom) the cell gives the same response except that the light on the RF center decreases during the first half cycle and then increases during the second half cycle: this produces no response (inhibition) followed by maximum response (excitation). At  $90^\circ$  phase shifts away from these positions of maximum response, however, the cell shows "null responses" (bottom and 4th line down), that is, it gives virtually no response to either half cycle of the flickering pattern. In this spatial phase, the grating is so positioned with respect to the RF that while the light is increasing in one half of the excitatory center it is decreasing in the other half by precisely the same amount. This symmetrical relationship applies to each inhibitory flank as well.

The fact that simple cells give little or no response to the flickering grating at these "null positions" indicates linearity of spatial summation. This is in accord

with Hubel and Wiesel's (1959) statement that simple cells show summation within the excitatory and inhibitory regions. Linearity of spatial summation, however, is also the defining characteristic of X-cells (Enroth-Cugell and Robson, 1966). Simple cortical cells behave just like retinal (and LGN) X-cells not only to the counterphase flickering grating patterns but also to the drifting grating patterns discussed earlier (they modulate their discharge in synchrony with the fundamental temporal period of the stimulus). While there are cells which are difficult to classify, we found that every cell classified as a simple cell by Hubel and Wiesel's criteria was classified as an X-cell by Enroth-Cugell and Robson's criteria.

*Complex cells.* Complex cells respond quite differently from simple cells to both drifting and counterphase flickering grating patterns. Their main response to drifting gratings (see Fig. 1b) is an overall increase in mean firing with little or no modulated response. The d.c. component is thus always larger than the fundamental or any of the higher harmonic components. The proportion of d.c. to modulated response sometimes varies with spatial frequency, the