Vision Res. Vol. 22. pp. 545 to 559. 1982
Printed in Great Britain

0042-6989/82/050545-15$03.00/0
Pergamon Press Ltd

SPATIAL FREQUENCY SELECTIVITY OF CELLS IN MACAQUE VISUAL CORTEX

RUSSELL L. DE VALOIS, DUANE G. ALBRECHT* and LISA G. THORELL
Primate Vision Laboratory, Department of Psychology, University of California, Berkeley, CA 94720, U.S.A.

(*Received* 21 *October* 1980; *in revised form* 14 *May* 1981; *in final form* 18 *September* 1981)

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

* Present address: Department of Psychology, University of Texas, Austin, TX 78712, U.S.A.

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

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

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 cell's 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

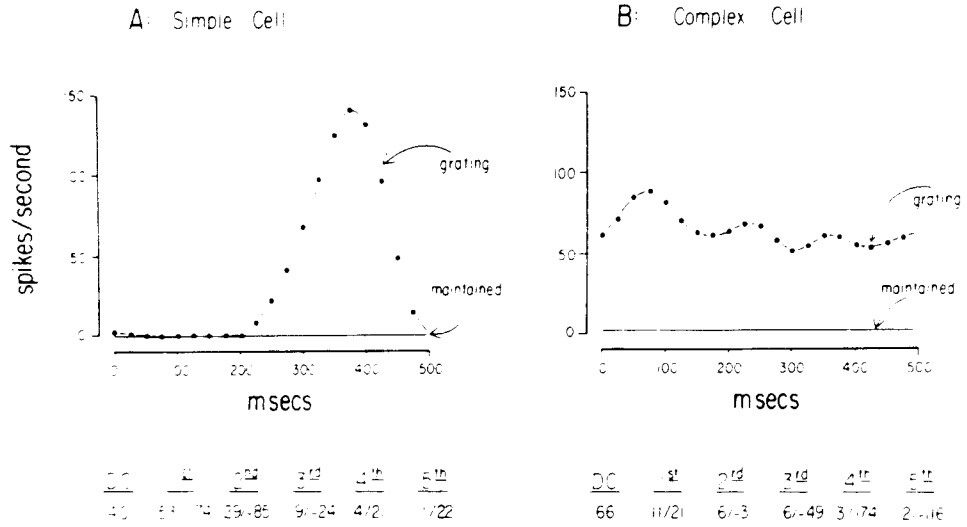

Fig. 1. Response patterns of a representative simple cell (A) and complex cell (B) to gratings drifted across their receptive fields. The response (peri-stimulus time histogram, PSTH) averaged over 20 repetitions of the sinusoidal stimulus is shown above a printout of the d.c. (mean rate of firing) and 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.

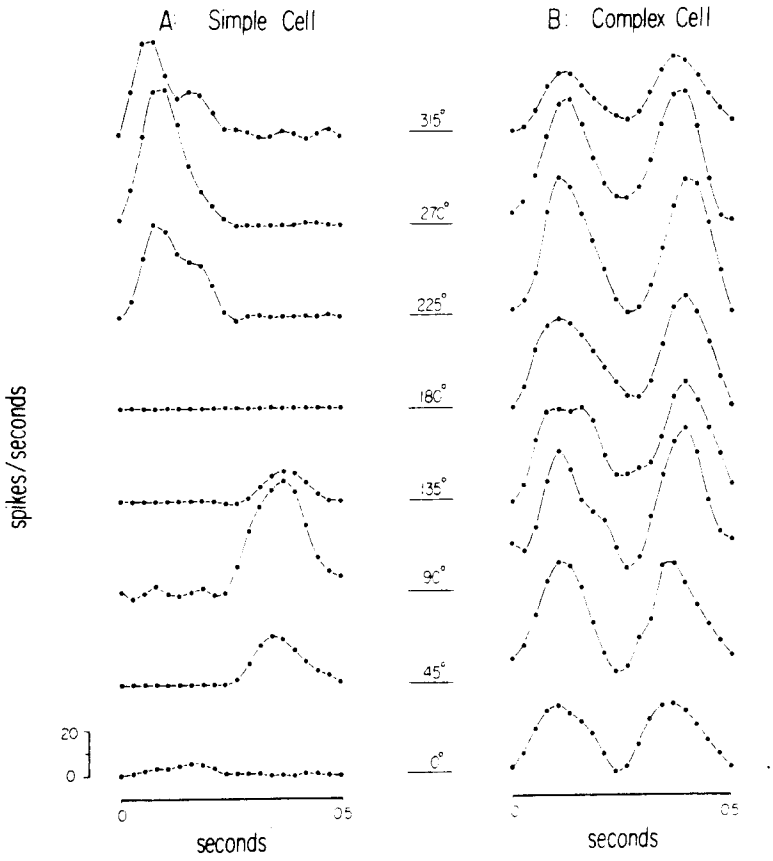

Fig. 2. Response (PSTH) patterns of a representative simple cell (A) and complex cell (B) to a counterphase modulated spatial grating presented in eight different phase positions (each separated by 45°); this corresponds to the Enroth-Cugell and Robson (1966) "null phase test" for spatial summation. 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 and 180°); 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° 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° 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

cell usually showing more of a modulated discharge to lower frequencies, but the d.c. component even there is the most prominent. Figure 1b shows an example of a complex cell's response to a drifting grating. Complex cells also differ from simple cells in that they usually have a higher maintained rate in the absence of any visual pattern (median for our sample: 1.0 spikes/sec).

In response to counterphase flickering gratings presented in various spatial phases (see Fig. 2b), complex cells respond like the retinal Y cells described by Enroth-Cugell and Robson (1966): there is no position at which the cells show a cancellation of excitation and inhibition (that is, a "null response"). Furthermore, the predominant harmonic response is at twice the stimulus flicker frequency, see Fig. 2b; for many complex cells this frequency doubling is virtually the same at every spatial phase, as is the case with the cell shown in Fig. 2b. Another way of considering the frequency doubling is that the cell responds identically to the white and black bars of the grating independent of their position. Frequency doubling and the complete lack of specificity for position of the pattern are consistent with (and predictable from) Hubel and Wiesel's characterization of complex cells; these properties are also the same response properties shown by retinal Y cells.

Evidence relating to a dichotomy of simple/complex (or X/Y). It is unfortunate that physiological investigations so often categorize cells into two or more different response types using qualitative methodology without presenting any quantitative evidence that the distribution of cells was in fact dichotomous rather than just varying uniformily along a continuum. Showing one or more different examples of the responses of the different cell types hardly bears on the issue, since examples drawn from the two ends of a continuum may indeed be very different. Furthermore, prototypical examples provide no indication of the variation which generally exists within a particular cell type.

The sections above are certainly subject to this criticism; the cells were categorized as simple/complex or X/Y using the standard qualitative criteria. Illustrating a population of cells with an exemplar which most closely resembles the mean value of the population is certainly a valid and useful method for communicating the results. However, it is important to provide a quantitative indication of the total population, particularly when arguing for different response types. With this in mind we considered it worthwhile to examine the commonly stated dichotomy (which we implicity assumed) between simple and complex cells or X and Y cells using a more quantitative methodology.

As discussed above, X and Y cells can be differentiated either on the basis of their responses to drifting grating patterns or to counterphase flickering patterns. Since all of our cells were tested with drifting gratings and only a sub-sample with counterphase flicker, we chose the former to examine the distribution of responses. Two issues present themselves: how to compare the a.c. and the d.c. responses, and which particular records to measure to assess the responses of a particular cell.

To classify a particular cell as X or Y, we chose the a.c./d.c. ratio. For the a.c. (amplitude of the fundamental) and the d.c. (mean firing rate) measures, we subtracted out the average a.c. and d.c. responses during the no-stimulus control trials. It is important to note that the resulting a.c. and d.c. responses index the changes in the responses produced by the stimulus presentations, not the absolute levels *per se*. Thus for example the d.c. component of a linear X cell with a high maintained rate of firing would be unaffected during the cell's response to a drifting sine wave grating: the response would be an equal modulation above and below the maintained rate, the average remaining the same.

An a.c./d.c. ratio of more than one would indicate an X cell, less than one a Y cell. Although there is no upper limit to the a.c./d.c. ratio, one would not expect extreme values since such would be possible only if the X cells showed a high maintained rate of firing. Cortical cells in general have low or even zero maintained rates and a d.c. component must necessarily accompany any a.c. response. The expected value from half wave rectification in an X cell with zero maintained firing rate is 1.57.

The question of which records to analyze in categorizing a cell as X or Y arises because a cell does not respond to all spatial frequencies and one obviously wants to measure only at the points at which there is a significant response. But the maximum a.c. and d.c. responses may not occur at the same spatial frequency; chosing which record to measure could thus bias the results. We therefore selected, from the responses to a range of spatial frequencies of moderate contrast, those three spatial frequencies to which the cell showed the largest combined a.c. and d.c. responses. In the cat retina, Hochstein and Shapley (1976) have found that Y cells tend to show large a.c. responses at low spatial frequencies and d.c. responses at high. This is less true at the cortex; in general, the a.c./d.c. ratio is relatively invariant across frequency.

Figure 3 shows the distribution of cells with respect to the a.c. vs d.c. responses. The X-cells cluster about 1.57, as would be expected from half wave rectification. The Y cells are distrubuted around 0.5 and there are some ambiguous cells with almost equal a.c. and d.c. responses. From this we can conclude that the distribution is bimodal; that is, the distribution is composed of two separate populations indicating two discrete cortical cell types. In our sample, some 61% of the cells had larger a.c. than d.c. responses (X cells or simple cells); the remaining 39% of the cells showed larger d.c. responses (Y cells or complex cells).

Spatial contrast sensitivity

General nature of the spatial tuning. Cells in the

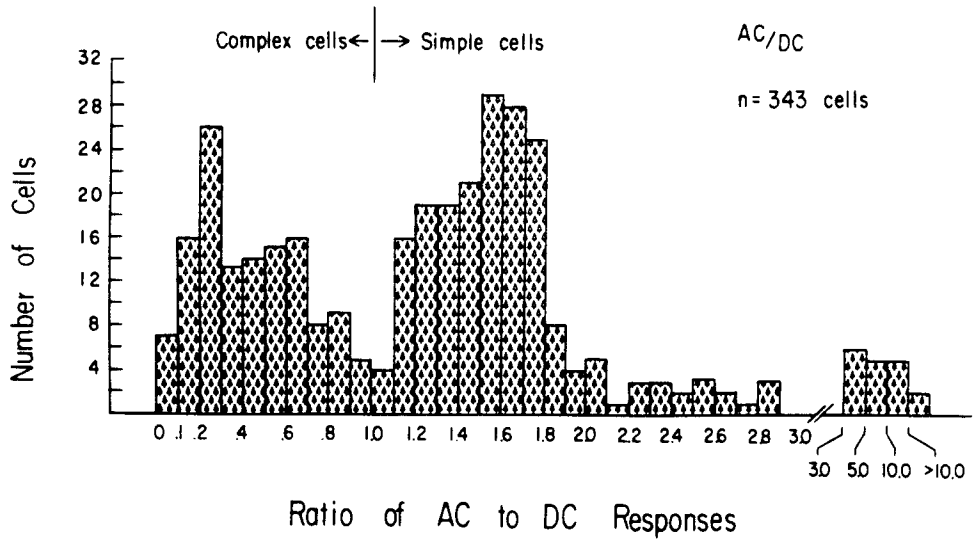

Fig. 3. Distribution of the a.c./d.c. ratio for all cells measured (n = 343). Those cells whose d.c. is larger than the a.c. (that is, Y cells) fall between 0.0 and 1.0; those cells whose a.c. is larger than the d.c. fall above 1.0. It is clear that the distribution is best described as bimodal indicating the presence of two distinct populations of cells.

lateral geniculate nucleus (LGN) are generally very broadly tuned, showing sharp high frequency attenuation but only a very gentle drop in sensitivity to low frequencies (Campbell *et al.*, 1969; von Blanckensee, 1980). By contrast, the vast majority of cortical cells are considerably more narrowly tuned, showing sharp low frequency as well as high frequency attenuation. Most cells thus have a distinct band-pass characteristic, see for example the cells shown in Fig. 4. This is true for both simple and complex cells.

The data shown in Fig. 4 are plotted on a log spatial frequency or octave scale; when so plotted, the cells tuned to different spatial frequency ranges have the same approximate range of shapes and bandwidths (although see below for an interesting deviation from this); that is what one would expect if the cells had the same RF shape regardless of the RF size (see discussion below).

Bandwidths. One of the principal points of this study was to establish the actual spatial bandwidths of primate cortical cells. Estimates of "channel bandwidth" from various types of psychophysical investigations have varied from less than 0.5 octaves (Sachs *et al.*, 1971) through 1.2 octaves (Blakemore and Campbell, 1969) to 2.0 octaves (Wilson, 1978). Most of the previous physiological studies (Campbell *et al.*, 1969; Maffei and Fiorentini, 1973; Schiller *et al.*, 1976b) have reported only spatial frequency response functions. Without knowing the contrast response function of a cell, one cannot determine the cell's contrast sensitivity—the appropriate measure to compare with the psychophysical data. We therefore have measured the responses of each cell to gratings of several contrasts and from these data determined the cell's contrast sensitivity: the contrast required for a fixed criterion response size. From the contrast sensitivity function we then measured, in octaves, the full bandwidth at half amplitude. For example, a cell might have had a maximum contrast sensitivity of 50 at 7 c/deg. The spatial frequency which produced a contrast sensitivity of 25 (half amplitude) to each side of the peak would then be determined. If these were, say 5 and 10 c/deg, the cell's full bandwidth at half amplitude would be 1.0 octave.

In Fig. 5 are shown the distributions of bandwidths of our cortical cell population, broken down into foveal-parafoveal and X (simple) and Y (complex) cells. It can be seen that the range of bandwidths is

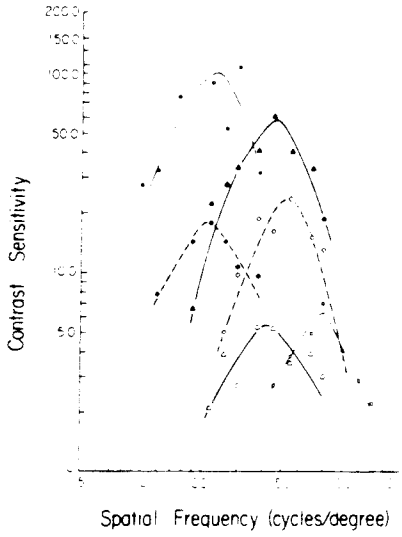

Fig. 4. Spatial frequency tuning curves of six striate cells recorded during the same electrode penetration. Symbols indicate the contrast sensitivity of each cell (the reciprocal of the contrast required to reach a constant response criterion) plotted as a function of spatial frequency; the curves were fitted by eye. Note the variation in peak tuning, bandwidth and sensitivity for this sample of cells (all of which pick-up from the same retinal locus).

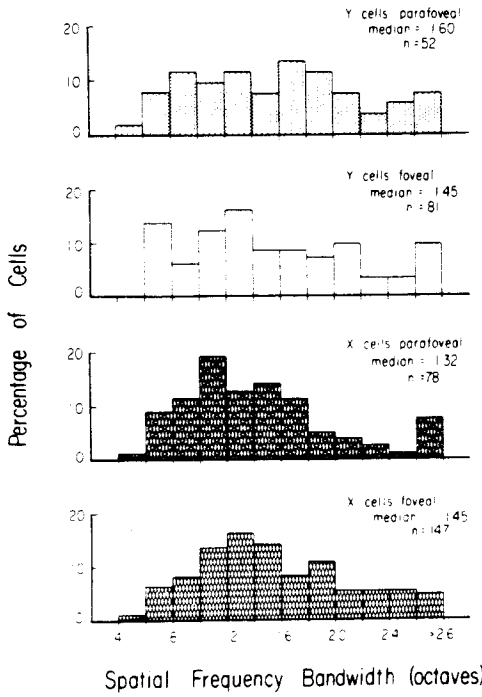

Fig. 5. Distributions of the full bandwidths at half amplitude (in octaves) of the spatial frequency tuning functions. The total population is segregated into X (simple) cells and Y (complex) cells recorded from the foveal and parafoveal areas. Note that there is no difference in the bandwidths of the foveal and parafoveal sample and that while the simple cells are slightly more narrowly tuned than the complex, the difference is not statistically significant. The median bandwidth was 1.4 octaves for simple cells and 1.5 octaves for complex cells.

very large. Most of the cells have bandwidths between 1.0 and 1.5 octaves, but there are a number of very narrowly tuned cells with bandwidths of less than an octave; and a sizable population of broadly tuned cells with bandwidths as large as 2.0 octaves. The distribution of the bandwidths of cortical cells, however, overlaps very little with the much more broadly tuned LGN cells.

The median bandwidth for simple cells (both foveal and parafoveal) is about 1.4 octaves, very close to that predicted from the Blakemore and Campbell selective spatial frequency adaptation experiment. It should be emphasized that there is a considerable spread of the tuning curves, however, so that any statement about "the" channel bandwidth of the visual system is of questionable validity.

As demonstrated in Fig. 5, the complex cells cover roughly the same range of bandwidths as simple cells, but on the average are slightly more broadly tuned. For neither simple or complex cells is there any difference in narrowness of tuning between the foveal and parafoveal populations.

Peak spatial frequency. One of the principal issues at question with respect to the visual system's doing a spatial frequency analysis of visual space is the presence of multiple spatial frequency channels at each locus in the visual field. Psychophysical studies using extended gratings provide ambiguous information on this question since different spatial frequency bands might be operating in different retinal regions. The same would be true if recordings from different degrees of eccentricity were pooled together. It was specifically to address this point that we restricted our sample of the cortex to two distinct limited cortical loci. By looking at just the foveal sample or just the parafoveal sample, we can consider the characteristics of a population of cells all picking up from the same region in space.

In Fig. 6 it can be seen that the cells within each of these samples are tuned to a wide range of spatial frequencies, covering overall at least 4 octaves and with a sizable portion spread over a 2 octave range. Some cells picking up from the foveal area respond maximally to as low as 0.5 c/deg; others, with overlapping RFs, peak as high as 15 c/deg. The more narrowly tuned cells within these populations tuned to different spatial frequencies would thus be responding to totally non-overlapping ranges of spatial frequencies.

The fact that cells with overlapping RF locations may have quite different spatial frequency tuning is seen most dramatically when two such cells are

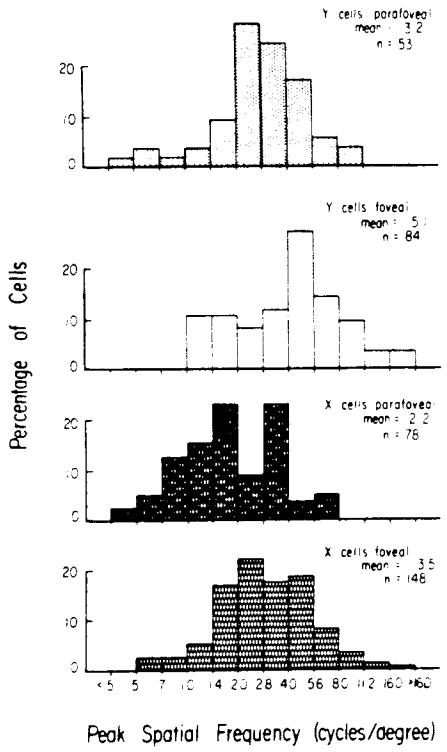

Fig. 6. Distributions of the peaks of the spatial frequency tuning functions. The total population was segregated into X (simple) and Y (complex) cells recorded from the foveal and parafoveal areas. Note that the foveal sample extends into higher frequencies than the parafoveal sample as does the Y cell sample in comparison to the X cell sample (both of these trends are statistically significant). The mean was 3.0 for the X cell population and 4.4 for the Y cell population.

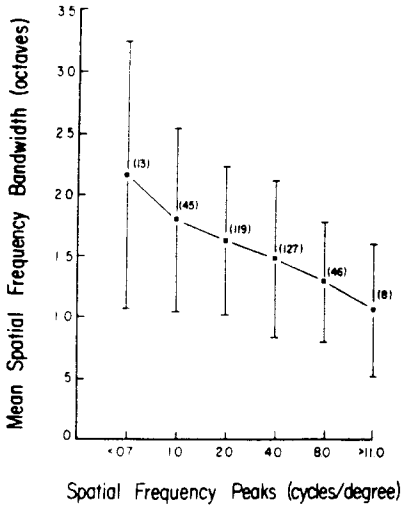

Fig. 7. Mean spatial frequency bandwidth (in octaves) plotted as a function of the spatial frequency peak. One standard deviation is plotted on each side of the means and the number of cells which comprise each mean is indicated within the parentheses. Note the negative correlation between bandwidth and peak tuning.

encountered successively on a single probe through the cortex. In general, successive cells within a probe have similar spatial frequency (and orientation) tuning. On occasion, however, we have recorded from two cells simultaneously, one close to the electrode and one more distant and heard them firing in counterpoint to gratings of different spatial frequency: one firing to low spatial frequencies but not at all to higher spatial frequencies while the other firing to high but not low spatial frequencies.

It should be noted in Fig. 6 that the distributions of peak spatial frequency for simple and complex cells are quite the same within each cortical region (there is a slight difference, as discussed below), but both populations are shifted away from high spatial frequencies as one goes further peripheral. It might also be noted that the number of cells tuned to each spatial frequency range corresponds roughly at least to the overall behavioral contrast sensitivity function of the macaque at this mean luminance level. Finally, one might point out that the distributions of peak frequencies to which the cells are tuned appear continuous. There is no evidence to support the notion (Wilson, 1978) of cells being tuned to just 3 or 4 different spatial frequencies.

Interrelationships

It is of some interest to examine the interrelationships among the variables of peak spatial tuning, narrowness of tuning, absolute contrast sensitivity and orientation tuning. In Figs 7 and 8 we present data relevant to these questions.

Bandwidth and spatial frequency peak. Are there differences in the bandwidths of cells tuned to different spatial frequency ranges? In Fig. 7 we have plotted the relationship between these two variables. While there are narrowly and broadly tuned cells peaking at each spatial frequency, there is a correlation between peak tuning and bandwidth (-0.3, significant beyond the 0.001 level): cells tuned to high spatial frequencies tend to be more narrowly tuned (on an octave scale) than those tuned to lower spatial frequencies. For instance, the median bandwidth of cells tuned to frequencies higher than 5 c/deg is 1.2 octaves, whereas those tuned to low frequencies (less than 2 c/deg) have a median bandwidth of 1.7 octaves. (It should not be forgotten that plotted on a *linear* spatial frequency scale, cells tuned to low spatial frequencies would be much more narrowly tuned; see discussion below.)

Contrast sensitivity and spatial tuning. There is essentially no relationship between absolute contrast sensitivity and peak spatial frequency: cells tuned to different spatial frequency ranges do not differ in their contrast sensitivity. Knowing this and referring back to the distribution of the numbers of cells at each spatial frequency range (Fig. 6), we can conclude that the shape of the overall behavioral sensitivity function probably reflects the variation in numbers of cells tuned to each spatial frequency rather than variations in the absolute sensitivity. There is a slight correlation (-0.15, significant at the 0.01 level of confidence) between absolute contrast sensitivity and spatial bandwidth: the more narrowly tuned cells are slightly more sensitive than the more broadly tuned cells.

Orientation and spatial tuning. Finally, we can consider the relationship between narrowness of orientation and spatial frequency tuning by examining those cells in which both orientation and spatial frequency tuning were quantitatively measured: see Fig. 8. A very significant positive correlation is seen (0.5, significant beyond the 0.001 level): cells that are nar-

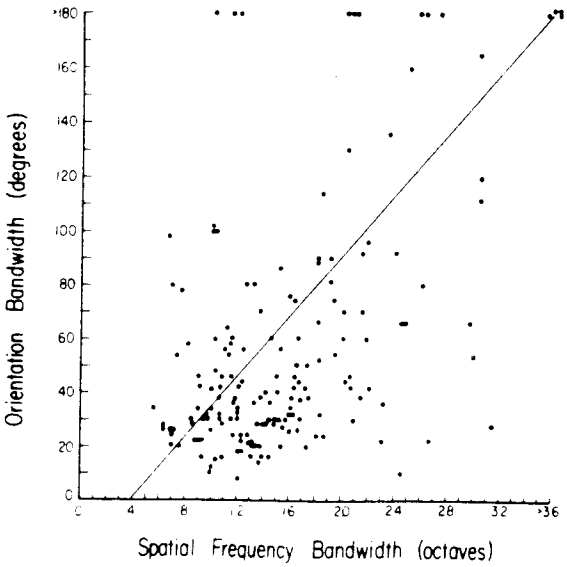

Fig. 8. Scatterplot showing the orientation bandwidth and the spatial frequency bandwidth of each cell ($n = 168$). The best fitting (least squares) line is drawn. There is a positive correlation of 0.5 (which is statistically significant).

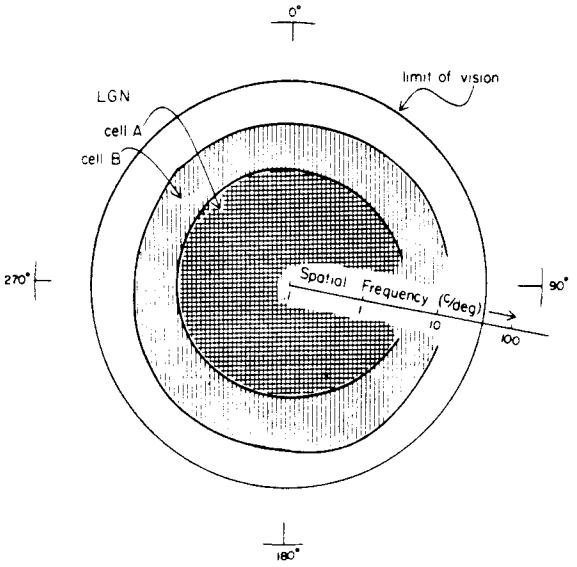

Fig. 9. Two-dimensional polar plot of spatial frequency and orientation for a pair of representative LGN cells. Orientation varies radially (around the circumference) and spatial frequency increases from the center along any radius. As can be seen, the typical LGN cells respond across a broad range of spatial frequencies at all orientations.

rowly tuned for orientation are also, on the average, narrowly tuned for spatial frequency. This is the largest correlation we found between any of the variables we measured.

Spatial frequency and orientation tuning

Cortical cells differ dramatically from LGN cells in being narrowly tuned for orientation and for spatial frequency. The difference in orientation tuning of LGN and cortical cells was of course first found by Hubel and Wiesel (1959). They also noticed, but did not emphasize, that the cells were somewhat more narrowly tuned for bar width, that is more narrowly tuned spatially than are LGN cells. Cortical cells are indeed somewhat more narrowly tuned for bar width than are LGN cells, but it is not a large difference. However, if one compares their respective tuning for *spatial frequency*, the difference between LGN and cortical cells is as dramatic as it is for orientation.

The combined spatial frequency and orientation tuning of cells can be conveniently (and informatively) shown in a polar plot, see Figs 9 and 10, in which the orientation is given by any particular radial axis and spatial frequency increases from the center along the radial axis. Such a plot bears more than a passing relation to an optical 2-dimensional Fourier spectrum. On such a polar graph, LGN cells (as shown in Fig. 9) cover a disc shaped region in 2-dimensional spatial frequency space centred on the origin: they respond to d.c. (full field or ambient illumination) and to all spatial frequencies up to their particular cut-off frequencies; they also respond to all orientations of a pattern. A similar plot for cortical cells would show them responding to narrow regions of frequency and orientation. For instance, in Fig. 10a we have plotted the combined spatial frequency and orientation (or the 2-dimensional spatial frequency) tuning of all the narrowly tuned cells recorded in one monkey in which a series of recordings were made in a one degree parafoveal region. It can be seen that the various cells altogether cover a good share of 2-dimensional frequency space, each sensitive to a limited portion of it. Presumably, still further probes within this same cortical area would have found cells tuned to still other orientations and spatial frequencies. It seems reasonable to assume that the total cell population in a given small cortical region (about 1 mm square, Hubel and Wiesel, 1974), would contain narrowly tuned cells selective for every 2-dimensional spatial frequency locus.

DISCUSSION

Simple vs *complex cells*

Our results agree with those of Hubel and Wiesel (1962) in finding two different types of cells in the cortex, corresponding to what they term simple and complex cells. In addition, however, our measures of the response properties of these cells provide objective and quantitative criteria for categorizing and describing the two types of cells (while also providing an index of the variation which exists within each cell type).

Our classification procedure is based upon the Enroth-Cugell and Robson (1966) X-Y distinction, rather than on mapping with discrete spots. However, the criteria for X cells and for simple cells are in fact basically the same; furthermore, in every case in which we could clearly categorize a cell as a simple cell by RF mapping, our objective criterion (a.c./d.c. ratio) classified it as an X cell. The fundamental property of a simple cell, in Hubel and Wiesel's schema, is that the RF is composed of spatially discrete excitatory and inhibitory regions. It is precisely this which causes X cells to produce a modulated discharge as a grating is drifted across the RF; the cell fires when the white bar goes across the excitatory region and inhibits when the black bar goes across this region. The fundamental property of a complex cell, on the other hand, is that it fires similarly to a stimulus regardless of its location within the RF. Again, it is precisely this property which causes Y cells to produce an unmodulated discharge as a grating is drifted across the RF.

The proportions of simple vs complex we find are quite different from those initially reported in monkey cortex by Hubel and Wiesel (1968). They found roughly 9% simple and 65% complex cells in macaque striate (they classified the remainder as hypercomplex or non-oriented). Considering just the simple and complex cells alone, the percentages become 12% simple and 88% complex. Our sample, on the other hand, shows 61% simple and 39% complex cells. Our

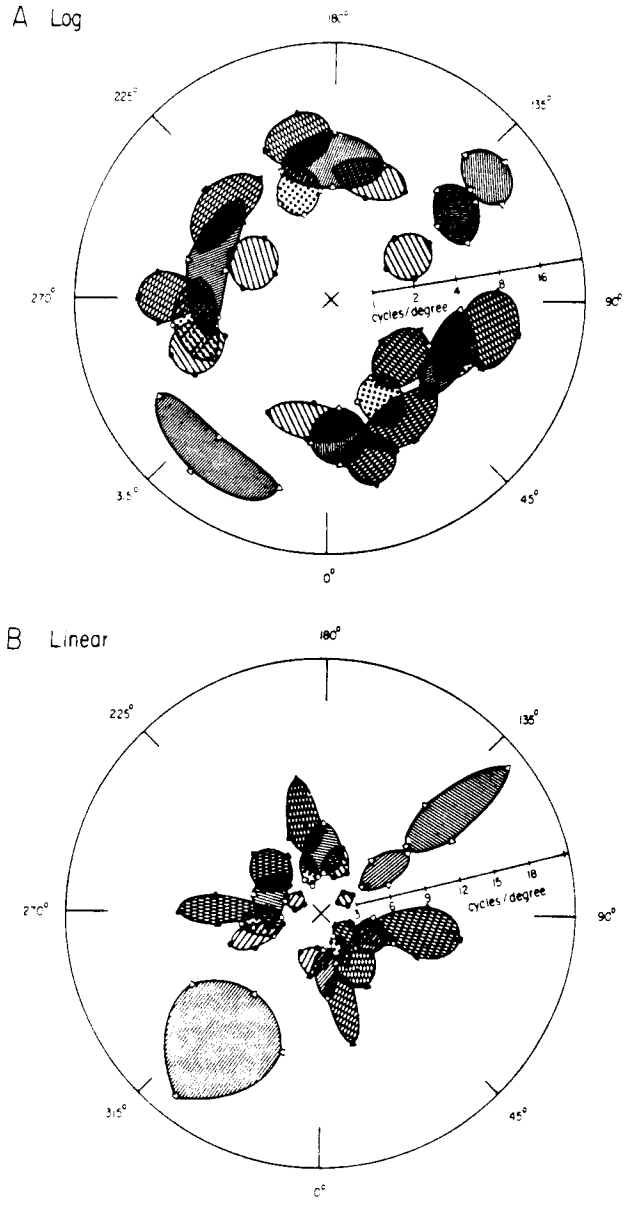

Fig. 10. Two-dimensional (orientation and spatial frequency) polar plots of all the narrowly tuned striate cells recorded from in one monkey at a 1° parafoveal eccentricity. The spatial frequency bandwidths are plotted on both a log scale (A) and a linear scale (B). It can be seen that on an octave scale (log plot) the cell's bandwidths are roughly independent of spatial frequency (although slightly more narrowly tuned at high frequencies). However, on a linear scale the spatial frequency bandwidths are much narrower for cells tuned to low spatial frequencies than those tuned to high.

percentages are virtually the same as those reported by Movshon *et al.* (1978a) in the cat (57% simple), and similar to those of Schiller *et al.* (1976a) in the monkey (42% simple cells). There are a number of factors, one or more of which might account for the discrepency: classification of cells; electrode properties; and degree of eccentricity of the recording site within the striate cortex.

If cells of different response types were of different anatomical sizes, as indeed Kelly and Van Essen (1974) argue, larger electrodes might selectively record a higher percentage of large cells, presumably complex cells. Our electrodes were probably smaller both in tip diameter and in exposed tip than Hubel and Wiesel's and we might thus have more easily isolated smaller cells (presumably simple cells) than they did.

Another possible explanation of why we obtained so many more simple cells relative to complex cells than did Hubel and Wiesel (1968) is that our recordings were all from the foveal or near parafoveal projection sites, whereas their probes were on the average considerably more eccentric in locus. Wilson and Sherman (1976) have found in the cat that the proportion of complex cells increases dramatically with eccentricity (as does the proportion of Y cells in the

retina, incidentally). If the same relation holds in monkey cortex it could account for the discrepancy. Our foveal sample in fact had 37% complex cells and our parafoveal subsample 42%.

Phase selectivity

One fundamental distinction between simple and complex cells is that of sensitivity to spatial phase (as illustrated in Fig. 2). Simple or X cells are phase-specific. They either fire, respond not at all, or inhibit to a pattern, depending on the location of the pattern with respect to the cell's RF. Simple cells are thus very sensitive to the spatial phase of a grating pattern. Complex or Y cells, on the other hand, respond similarly to a pattern regardless of its location with respect to the cell's RF and therefore show no phase selectivity to a grating pattern.

Comparison to X and Y cells in the LGN

Since X and Y cells have been reported in the retina, in the LGN and in the cortex, it is natural to consider whether these could constitute parallel pathways all the way through the system (as opposed to Hubel and Wiesel's suggestion that simple cells are combined within the cortex to form complex cells in a hierarchical organization). The data reported here provide some evidence for and against each of these theoretical notions.

Given strictly parallel systems of X and Y cells from retina through striate, one might have expected to find equivalent proportions in the retina, LGN, and cortex. We find that 39% of the striate neurons are Y cells whereas only about 3% of cat retinal ganglion cells are reported to be Y cells (Enroth-Cugell and Robson, 1966). In the monkey geniculate Y cells are found only amongst the few cells in the two magnocellular layers, and even there they may not constitute the total population (Dreher *et al.*, 1976; Kaplan and Shapley, 1980). Such cell types are clearly much more prevalent in the cortex.

A second argument against completely parallel systems is that simple and complex cells have very similar tuning characteristics. Simple cells are slightly, but only slightly, more narrowly tuned than complex cells in both spatial frequency and orientation. While this is of course not a strong argument against a parallel organization, it is what one might expect if complex cells were just summing simple cells in a hierarchical manner.

There are, on the other hand, several strong arguments against a strictly hierarchical structure. Hoffman and Stone (1971) have shown in the cat that some complex cells (as well as some simple cells) receive monosynaptic geniculate input, an arrangement which is obviously incompatible with a strict hierarchical organization. One can also argue to the same end from the response characteristics of simple and complex cells. It is easy to see how one could combine X (or simple) cells form a Y (or complex) cell. This could take place within the cortex or from geniculate to cortex. It would be most difficult and unlikely, however, to have the reverse, namely, very non-linear geniculate Y cells combined to produce a linear X cell. Yet that is what Gilbert and Wiesel (1979) explicitly propose. Surely at least some of the cortical complex cells must be receiving input from the earlier Y cells.

Finally, one can argue strongly on psychophysical grounds against a purely hierarchical arrangement in which simple cells serve only as inputs to complex cells, and complex cells carry the only output from the striate cortex. This does not seem logically possible since simple, but not complex, cells possess certain properties which must be maintained throughout the whole system. Specifically, as shown in Fig. 2, simple cells are phase specific: they respond in opposite directions to white and black, in the same location and thus differentiate between them. Complex cells, on the other hand, are not phase specific: they respond identically to white and black in the same location. The phase specificity of human vision and our ability to tell white from black cannot be explained if complex cells carry the sole output from the striate cortex.

We would therefore conclude that at least some of the cortical complex cell input must be from geniculate Y cells. But the great prevalence of complex cells, if nothing else, suggests that many of these must have an X cell input in addition to or instead of an input from Y cells. We can even more firmly conclude, however, that simple cells as well as complex cells must project to later levels. In fact, many of our perceptual capabilities reflect the attributes of simple cells much more than of complex cells.

Spatial frequency tuning of cortical cells

The principal point of these experiments was to determine the nature of the spatial frequency tuning of macaque cortical cells to luminance varying patterns. The results clearly show that whereas most geniculate cells show essentially a low pass filter characteristic, with sharp high spatial frequency attenuation but only a gentle low frequency drop, most cortical cells have a bandpass characteristic with sharp high and low spatial frequency attenuation. Thus while most geniculate cells respond to virtually the whole range of spatial frequencies to which the visual system is sensitive at that eccentricity, each cortical cell fires to only a limited subset of those spatial frequencies. Different cortical cells within an area respond to different spatial frequency ranges, often a range not overlapping that of a nearby cell picking up from the same retinal region. In this respect, as in many others, the situation is similar to the orientation organization (familiar from the work of Hubel and Wiesel, 1959, 1962). That is, geniculate cells respond over the whole range of orientations, whereas cortical cells respond to a limited subset of orientations, the particular orientation range varying from one cell to

another within the group of cells picking up from a given retinal region.

Two-dimensional spatial frequency filtering

Looked at from the point of view of spatial frequency filtering, the spatial frequency and orientation tuning of cortical cells are not separate phenomena, but are different aspects of a single process, namely, that of producing a 2-dimensional spatial frequency filter. The strong positive correlation between the spatial frequency and the orientation tuning of cells would lend further support to this notion. Although it is convenient in initially examining the cortical organization to use such 1-dimensionally varying stimuli as elongated bars and gratings, one should not forget that most visual stimuli vary in two dimensions (ignoring depth). Any 2-dimensionally varying stimulus is uniquely specified by its 2-dimensional spatial frequency spectrum, which can be thought of as the spatial frequencies present at each of the various orientations. Any visual stimulus could thus be uniquely specified by the relative firing rates of an array of cortical cells each with a particular 2-dimensional spatial frequency bandpass.

We find that the spatial frequency bandwidths vary at most over a 2:1 range with spatial frequency peak, when the bandwidths are measured in octaves, see Fig. 7. This is what one would expect if the *shapes* of the RFs of cells were much the same regardless of their center sizes. A cell with an excitatory center and two strong antagonistic flanks might have a bandwidth of, say 1.5 octaves, regardless of whether the center diameter was 5′ or 50′. If either of these cells had additional sidebands their spatial frequency bandwidths might now be 0.8 octaves in each case. There is a clear analogy here to a similar situation in the auditory system: the temporal frequency bandwidths of cochlear cells are much the same regardless of the temporal frequency to which the cells are tuned.

The consequence of roughly equal octave bandwidths regardless of spatial frequency peak, however, is that cells tuned to various spatial frequencies would have quite different tuning on a linear scale. (A one octave bandwidth centered at 0.5 cycles would be a linear bandwidth of less than 1 c deg; a one octave bandwidth centered at 16 c deg would be a linear bandwidth of about 10 c deg.) Again, the analogy to the auditory system is clear. In Fig. 10b we have plotted the same cells shown in Fig. 10a on a linear scale. As can be seen, the cells tuned to low spatial frequencies have much narrower bandwidths when plotted on a linear scale. Compare, for instance, the three cells tuned to about 125 deg orientation. On a log scale (Fig. 10a) they have about equal bandwidths, but on a linear scale (Fig. 10b) the spatial bandwidths vary drastically with the location of the bandpass along the frequency axis. It would thus appear that low spatial frequency information would be processed with considerably greater precision than that at high spatial frequencies. However, the numbers of cells tuned to various spatial frequency regions would be as important as narrowness of tuning of the individual units in determining the capability of the system.

Narrowness of tuning

Many discussions of whether cortical cells could be doing a spatial frequency analysis of visual space (and how such an analysis might take place) hinge on the narrowness of the spatial frequency tuning of cortical cells. Given the wide range of spatial frequency bandwidths exhibited by both simple and complex cells, one cannot speak of *the* bandwidth of cortical cells. We would argue that while it is not yet clear why there is such a wide range of spatial bandwidths (although, see Albrecht, 1978, for a discussion of this issue), it is reasonable to suppose that the most narrowly tuned cells are the critical ones for detailed spatial analysis. Geniculate cells are broadly tuned in both orientation and spatial frequency, and the main process we can see occurring at the striate cortex is that of producing cells which are much more narrow in their tuning along both the spatial frequency and orientation dimensions, that is, narrow in their 2-dimensional spatial frequency bandpass.

Wilson (1978) has proposed a model of spatial processing based on the assumption that cortical cells have bandwidths of about 2 octaves, and that they peak at just 4 discrete spatial frequencies. The latter assumption is clearly contrary to our findings: cells in a given locus show a continuum of spatial frequency peaks over a range of more than 3 octaves in the foveal area, as can be seen in Fig. 6 above. An assumption of 2 octaves bandwidths is not necessarily contrary to the physiological results—there clearly are some cortical cells with spatial frequency tuning that broad—but there is little reason to assume that only the most broadly tuned cells, those which resemble geniculate cells, are the ones involved in spatial processing. The comparable situation with respect to orientation would be to postulate that the cortical cells involved in spatial processing are those with little or no orientation tuning. There are indeed non-oriented cortical cells, but again they are atypical of cortical cells in general and resemble precortical cells. Orientation and spatial frequency sharpening appear to be the main activities which take place at the level of the striate cortex; this fact should not be ignored. It is worth noting that since orientation and spatial frequency tuning are strongly correlated, the assumption of a 2+ octave spatial frequency bandwidth would imply very broad orientation tuning: in our sample, the cells with 2+ octave spatial frequency bandwidths have an average orientation bandwidth of 130 deg!

It would seem more reasonable to incorporate the *most* narrowly tuned cells (which appear to be the end product of the striate processing) into models of spatial vision. We might therefore examine that population, taking it rather arbitrarily as consisting of those

cells which are narrower than the median in both spatial frequency and orientation tuning, that is, in 2-dimensional spatial frequency tuning. This would therefore be the population of cells with frequency bandwidths of 1.4 octaves or less and orientation bandwidths of less than 42°. Since these properties are positively correlated (with a chi square significance at the 0.001 level), the resulting population is 31.5% of the cells. This "narrowly tuned" subgroup has an average spatial frequency bandwidth of 1.07 octaves and an average orientation bandwidth of 26°.

Cortical integration region

Over a given cortical area, all the cells deal with a specific retinal region and thus have overlapping RFs. We may term this a "Cortical Integration Region" (CIR). Such an analytic unit would contain a complete orientation hypercolumn and one complete ocular dominance hypercolumn (Hubel and Weisel, 1974) and we would argue a complete spatial frequency hypercolumn. Such a CIR might cover a 1 mm square of cortical surface and contain about 100,000 cells. The narrowly tuned cells within such a CIR would then consist of circa 32,000 cells for some 20 different orientations (Hubel and Wiesel, 1962). So while it would appear from our histograms (Fig. 6) that there are relatively few narrowly tuned cells, this would nevertheless (given the assumptions above) provide some 1600 narrowly tuned cells per orientation tuned to various spatial frequencies over a 3 or so octave range of peak spatial frequencies. One must consider, however, that it would require several cells tuned to high spatial frequencies (and thus generally with small RFs) to cover the area encompassed by the RF of a cell tuned to low spatial frequencies. This is assuming different locations for the RF centers of the high spatial frequency cells, so that several of them jointly would cover the visual region subtended by the hypercolumn as a whole. Such an arrangement would necessitate more cells tuned to high than to low spatial frequencies. This is in fact true if one considers the low-to-middle spatial frequency range from say 0.5–3.0 c/deg. Since it is not true above that point, however, one would have to conclude that very high spatial frequencies are not processed with the same precision as the low and middle frequency range.

Simple and complex cell tuning

In discussing the spatial frequency tuning of cat cortical cells, Maffei and Fiorentini (1973; Maffei, 1978) have stated that simple cells are narrowly tuned for spatial frequency, whereas complex cells are not. Furthermore, the sample data they presented to illustrate this point show only a small range of spatial bandwidths for each of these cell types, the range of bandwidths of simple and complex cells not even overlapping.

Our data, along with that of others who have presented the actual distributions of all their cells (Schiller *et al.*, 1976; Albrecht, 1978; Movshon *et al.*, 1978), do not agree with either of these points. We find that, far from all having the same tuning, both simple and complex cells have a wide range of bandwidths, varying from 0.6 to over 2.5 octaves. And while simple cells are on the average more narrowly tuned than complex cells, the difference is very slight indeed, and not statistically significant ($P = 0.16$). It is considerably more accurate to say that simple and complex cells have much the same spatial frequency bandwidths.

Although simple and complex cells turn out to have very similar spatial frequency bandwidths, they are significantly different in their peak tuning. The mean spatial frequency peak of simple cells is 3.0 c/deg, and of complex cells 4.4 c/deg, a difference significant beyond the 0.001 level of confidence. Higher peak tuning of complex cells is seen both within the foveal and within the parafoveal sample. About 80% of the cells tuned to the very highest spatial frequencies, with peaks above 8 c/deg, are complex cells.

The higher spatial tuning of complex or Y cells than simple cells may appear strange, given the evidence at retinal levels that Y cells have larger receptive fields (Enroth-Cugell and Robson, 1966). There are two things to be said, however. One is that probably not all cortical Y cells are directly related to retinal and geniculate Y cells but are constructed *de novo* within the cortex, as discussed above. They should thus not be expected to bear the same relation to X cells as was true in the retina. The other is that the size of a cell's RF is not simply related to its optimal spatial tuning. In the case of complex cells the relation is weak indeed: as pointed out by Hubel and Wiesel (1962), the optimum bar width for a complex cell is less than the overall width of the RF. In the case of simple cells, the overall RF width is related both to the optimum spatial frequency and the narrowness of tuning (Albrecht, 1978; De Valois *et al.*, 1978). We find that the RF center width is correlated with the optimal spatial frequency (in agreement with Movshon *et al.* but in contradiction with Schiller *et al.*). Narrowly tuned cells, however, have additional sidebands and thus wider RFs than broadly tuned cells with the same peak spatial frequency sensitivity.

Foveal vs *parafoveal cells*

This study was not intended as a parametric examination of cortical activity as a function of retinal eccentricity of input; on the contrary, we attempted to limit our recording sites to just two regions neither very far from the fovea. Nonetheless, we can come to some conclusions from a comparison of our foveal and parafoveal samples. The main result seen is that of considerable similarity between the cells picking up from these different retinal areas. Foveal and parafoveal cells have about the same proportion of simple and complex cells, the same narrowness of spatial frequency and orientation tuning and each cover a wide range of orientations and spatial frequencies. The

most important differences we find are that the parafoveal sample does not include cells tuned to the very highest spatial frequencies. Since cells peaking at very low spatial frequencies are found in both the foveal and the parafoveal sample, the total range of spatial frequency peaks is narrower in the parafoveal region. It should be emphasized that cells with even very low spatial frequency tuning are found in the foveal projection; it is only the progressive loss of high frequency cells which moves the mean peak tuning to lower frequencies with increasing eccentricity.

Cortical cells as spatial frequency filters

The presence of narrow tuning for sine wave gratings in monkey cortex has also been reported by Schiller *et al.*, 1976. They also observed that while the cells are quite narrowly tuned for sine wave gratings, they are broadly tuned for square wave gratings. From this they conclude that what cortical cells are really interested in are bars or square wave gratings, and that a system sensitive to sine waves would be useful in dealing only with fuzzy, blurred patterns. We believe for several reasons that our results and those of Schiller *et al.* in fact *support* a spatial frequency analysis model of cortical processing.

First, the narrow tuning for sine wave gratings and broad tuning for square waves is exactly what one would expect from the respective Fourier spectra of these patterns, given cells with narrow spatial frequency tuning. A sine wave grating has only a limited spatial frequency spectrum (only one frequency if it has an infinite extent, a narrow range of frequencies for a pattern of a few cycles) whereas a square wave grating is composed of a broad range of frequencies (a fundamental and all of the odd harmonics). A cortical cell tuned to, say, 2–5 c/deg would (by definition) respond to square wave gratings whose fundamental fell within that range; such a cell would also respond to square wave gratings of lower spatial frequencies since all the lower frequency patterns would have higher harmonics within the 2–5 c/deg bandpass of the cell. This is exactly what is found.

Secondly, a related point is that cells tuned to only a limited range of spatial frequencies would *not* be restricted in usefulness only for responding to blurred patterns. The fundamental theorem of Fourier analysis, in fact, is that *any* pattern can be analyzed into sine wave components (given linearity). Sine waves are not present only in blurred, fuzzy patterns!

Thirdly, the fact that cortical cells are much more narrowly tuned for sine wave gratings than they are for bars (Albrecht *et al.*, 1980) or square wave gratings (Schiller *et al.*, 1976) does not argue *against* sine wave gratings as the basic unit of cortical analysis, but just the reverse. If a complex stimulus is to be analyzed into elements along some dimension, one clear requirement is units which are highly selective (that is, narrowly tuned) along that dimension. In an analogous situation in the auditory system, for instance, units in the cochlea are very selective to temporal sine waves of different frequencies, but they all respond to clicks of various widths. From this, one reasonably concludes that the auditory system is analyzing the incoming sound wave into different sine wave frequencies, but not into click width. Bars are "spatial clicks" (in that spatial bars, like temporal clicks, have very broad Fourier spectra); the broad bandwidths cortical cells have for bars and square wave gratings argue that these cannot be the units of visual analysis. In contrast, the relatively narrow bandwidths cortical cells have for spatial frequency and orientation argue that 2-dimensional spatial frequencies might well be the units of visual analysis at this level in the system.

REFERENCES

Albrecht D. G. (1978) *Analysis of Visual Form.* Doctoral Dissertation, University of California, Berkeley.

Albrecht D. G. and De Valois R. L. (1981). Striate cortex responses to periodic patterns with and without the fundamental harmonics. *J. Physiol.* In press.

Albrecht D. G., De Valois R. L. and Thorell L. G. (1980) Visual cortical neurons: are bars or gratings the optimal stimuli? *Science* **207**, 88–90.

Blakemore C. and Campbell F. W. (1969) On the existence of neurones in the human visual system selectively sensitive to the orientation and size of retinal images. *J. Physiol.* **203**, 237–260.

von Blanckensee H. (1980) Spatio-temporal properties of cells in monkey lateral geniculate nucleus. Ph.D. Dissertation, University of California, Berkeley.

Braddick O., Campbell F. W. and Atkinson J. (1978) Channels in vision: basic aspects. In *Handbook of Sensory Physiology* (Edited by Held R., Leibowitz H. W. and Teuber H.-L.), Vol. 7, pp. 3–38. Springer, Berlin.

Campbell F. W., Cooper G. F. and Enroth-Cugell C. (1968) The spatial selectivity of visual cells of the cat. *J. Physiol.* **203**, 223–235.

Campbell F. W., Cooper G. F., Robson J. G. and Sachs M. B. (1969) The spatial selectivity of visual cells of cat and the squirrel monkey. *J. Physiol.* **204**, 120–121P.

De Valois K. K., De Valois R. L. and Yund E. W. (1979) Responses of striate cortex cells to grating and checkerboard patterns. *J. Physiol.* **291**, 483–505.

De Valois R. L. and De Valois K. K. (1980) Spatial vision. *Ann. Rev. Psychol.* **31**, 309–341.

De Valois R. L., Albrecht D. G. and Thorell L. G. (1977) Spatial tuning of LGN and cortical cells in the monkey visual system. In *Spatial Contrast* (Edited by Spekreijse H. and van der Tweel H.), pp. 60–63. Elsevier, Amsterdam.

De Valois R. L., Albrecht D. G. and Thorell L. G. (1978) Cortical cells: bar and edge detectors, or spatial frequency filters? In *Frontiers in Visual Science* (Edited by Cool S. J. and Smith E. L.), pp. 544–556. Springer-Verlag, New York.

De Valois R. L., Morgan H. and Snodderly D. M. (1974) Psychophysical studies of monkey vision III. Spatial luminance contrast sensitivity tests of macaque and human observers. *Vision Res.* **14**, 75–81.

Dreher B., Fukada Y. and Rodieck R. W. (1976) Identification, classification and anatomical segregation of cells with X-like and Y-like properties in the lateral geniculate nucleus of old-world primates. *J. Physiol.* **258**, 433–452.

Enroth-Cugell C. and Robson J. G. (1966) The contrast

sensitivity of retinal ganglion cells of the cat. *J. Physiol.* **258,** 517–552.

Gilbert C. D. and Wiesel T. N. (1979) Morphology and intracortical projections of functionally characterized neurones in the cat visual cortex. *Nature* **280,** 120–125.

Glezer V. D., Ivanoff V. A. and Tscherbach T. A. (1973) Investigation of complex and hypercomplex receptive fields of visual cortex of the cat as spatial frequency filters. *Vision Res.* **13,** 1875–1904.

Hochstein S. and Shapley R. M. (1976) Quantitative analysis of retinal ganglion cell classifications. *J. Physiol.* **262,** 237–264.

Hoffman K.-P. and Stone J. (1971) Conduction velocity of afferents to cat visual cortex: correlation with cortical receptive field properties. *Brain Res.* **32,** 460–466.

Hubel D. H. and Wiesel T. N. (1959) Receptive fields of single neurones in the cat's striate cortex. *J. Physiol.* **148,** 574–591.

Hubel D. H. and Wiesel T. N. (1962) Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *J. Physiol.* **160,** 106–154.

Hubel D. H. and Wiesel T. N. (1968) Receptive fields and functional architecture of monkey striate cortex. *J. Physiol.* **195,** 215–243.

Hubel D. H. and Wiesel T. N. (1974) Uniformity of monkey striate cortex: a parallel relationship between field size, scatter and magnification factor. *J. comp. Neurol.* **158,** 295–306.

Ikeda H. and Wright M. J. (1975) Spatial and temporal properties of "sustained" and "transient" neurones in area 17 of the cat's visual cortex. *Expl Brain Res.* **22,** 363–383.

Kaplan E. and Shapley R. M. (1980) X and Y cells in the lateral geniculate nucleus of the macaque monkey. *Invest. Ophthal. visual Sci. (Suppl.)* **19,** 41.

Kelly J. P. and Van Essen D. C. (1974) Cell structure and function in the visual cortex of cat. *J. Physiol.* **238,** 515–547.

Maffei L. (1978) Spatial frequency channels: neural mechanisms. In *Handbook of Sensory Physiology* (Edited by Held R. *et al.*), Vol. 7, pp. 39–66. Springer, Berlin.

Maffei L. and Fiorentini A. (1973) The visual cortex as a spatial frequency analyzer. *Vision Res.* **13,** 1255–1267.

Movshon J. A., Thompson I. D. and Tolhurst D. J. (1978a) Spatial summation in the receptive fields of simple cells in the cat's striate cortex. *J. Physiol.* **283,** 53–77.

Movshon J. A., Thompson I. D. and Tolhurst D. J. (1978b) Spatial and temporal contrast sensitivity of neurones in areas 17 and 18 of the cat's visual cortex. *J. Physiol.* **283,** 101–120.

Robson J. G. (1975) Receptive fields: neural representation of the spatial and intensive attributes of the visual image. In *Handbook of Perception* (Carterette E. C. and Friedman M. P.), Vol. 5, pp. 81–112. Academic Press, New York.

Sekuler R. (1974) Spatial vision. *Ann. Rev. Psychol.* **25,** 195–232.

Sachs M. B., Nachmias J. and Robson J. G. (1971) Spatial frequency channels in human vision. *J. opt. Soc. Am.* **43,** 1120–1128.

Schiller P. H., Finlay B. L. and Volman S. F. (1976a) Quantitative studies of single-cell properties in monkey striate cortex. I. Spatiotemporal organization of receptive fields. *J. Neurophysiol.* **39,** 1288–1319.

Schiller P. H., Finlay B. L. and Volman S. F. (1976b) Quantitative studies of single cell properties in monkey striate cortex. III. Spatial frequency. *J. Neurophysiol.* **39,** 1334–1351.

Talbot S. A. and Marshall W. H. (1941) Physiological studies on neural mechanisms of visual localization and discrimination. *Am. J. Ophthal.* **24,** 1255–1264.

Wilson H. R. (1978) Quantitative prediction of line spread function measurements: implications for channel bandwidths. *Vision Res.* **18,** 493–496.

Wilson J. B. and Sherman S. M. (1976) Receptive-field characteristics of neurons in cat striate cortex: changes with visual field eccentricity. *J. Neurophysiol.* **39,** 512–533.