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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 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

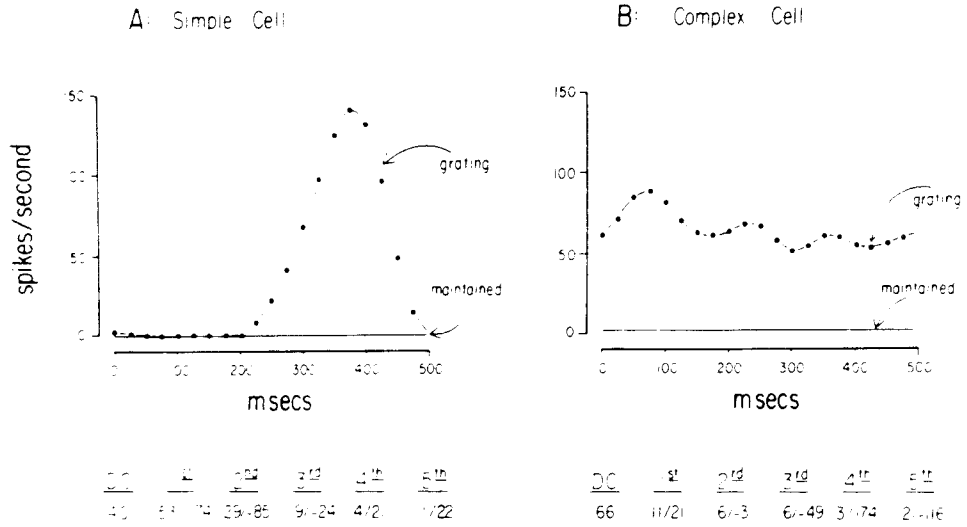

Fig. 1. Response patterns of a representative simple cell (A) and complex cell (B) to gratings drifted across their receptive fields. The response (peri-stimulus time histogram, PSTH) averaged over 20 repetitions of the sinusoidal stimulus is shown above a printout of the d.c. (mean rate of firing) and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

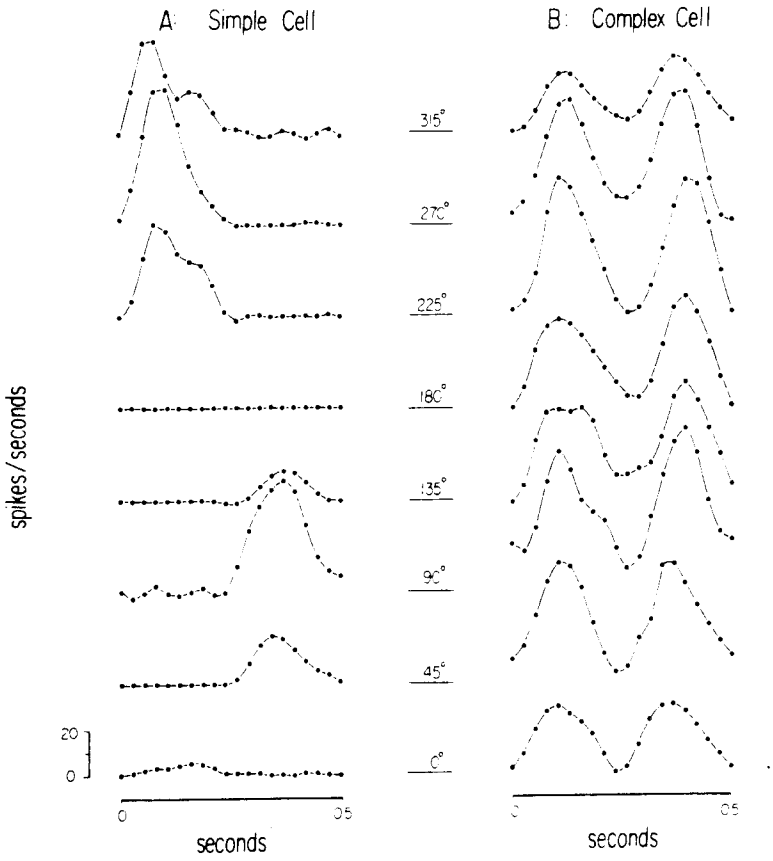

Fig. 2. Response (PSTH) patterns of a representative simple cell (A) and complex cell (B) to a counterphase modulated spatial grating presented in eight different phase positions (each separated by 45°); this corresponds to the Enroth-Cugell and Robson (1966) "null phase test" for spatial summation.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

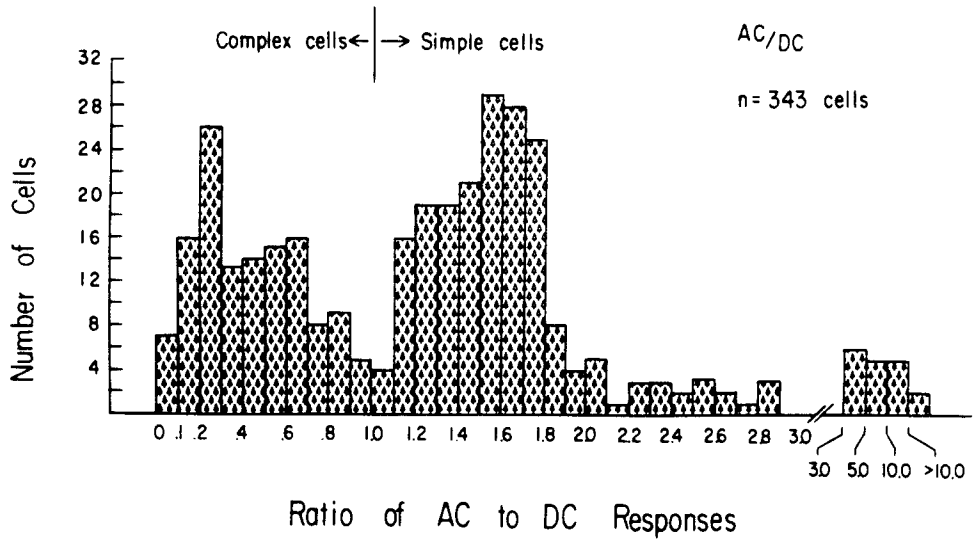

Fig. 3. Distribution of the a.c./d.c. ratio for all cells measured (n = 343). Those cells whose d.c. is larger than the a.c. (that is, Y cells) fall between 0.0 and 1.0; those cells whose a.c. is larger than the d.c. fall above 1.0. It is clear that the distribution is best described as bimodal indicating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

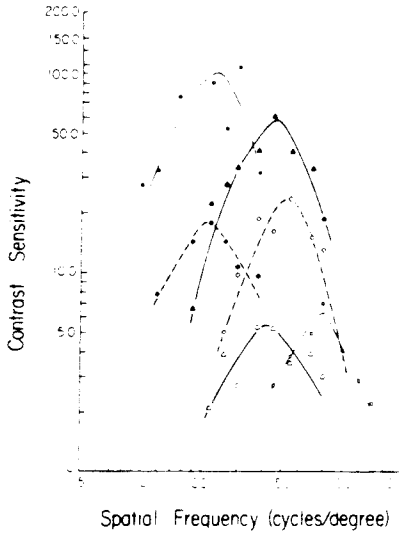

Fig. 4. Spatial frequency tuning curves of six striate cells recorded during the same electrode penetration. Symbols indicate the contrast sensitivity of each cell (the reciprocal of the contrast required to reach a constant response criterion) plotted as a function of spatial frequency; the curves were 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).

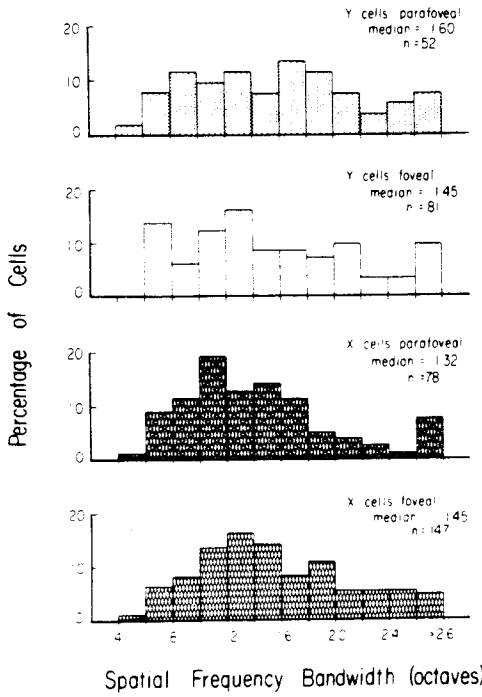

Fig. 5. Distributions of the full bandwidths at half amplitude (in octaves) of the spatial frequency tuning functions. The total population is segregated into X (simple) cells and Y (complex) cells recorded from the foveal and parafoveal areas. Note that there is no difference in the bandwidths of the 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

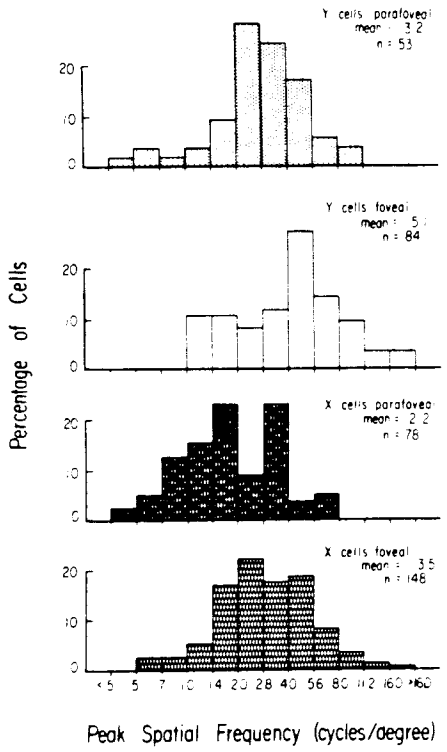

Fig. 6. Distributions of the peaks of the spatial frequency tuning functions. The total population was segregated into X (simple) and Y (complex) cells recorded from the foveal and parafoveal areas. Note that the foveal sample extends into higher frequencies than the parafoveal sample as does the Y cell 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.

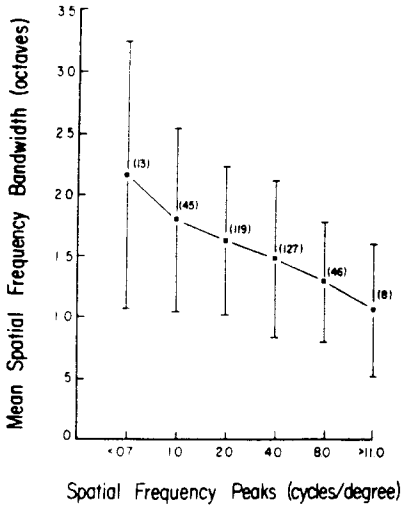

Fig. 7. Mean spatial frequency bandwidth (in octaves) plotted as a function of the spatial frequency peak. One standard deviation is plotted on each side of the means and the number of cells which comprise each mean is indicated within the parentheses. Note the negative correlation between bandwidth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

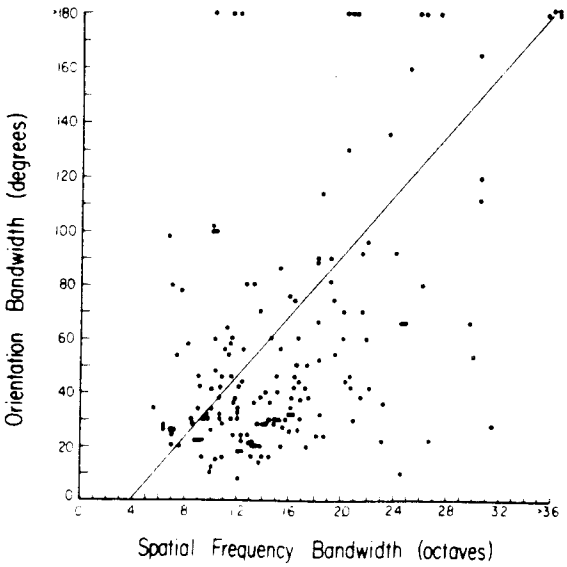

Fig. 8. Scatterplot showing the orientation bandwidth and the spatial frequency bandwidth of each cell ($n = 168$). The best fitting (least squares) line is drawn. There is a positive correlation of 0.5 (which is statistically significant).