Relationship between spatial-frequency and orientation tuning of striate-cortex cells

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If striate cells had the receptive-field (RF) shapes classically attributed to them, their preferred spatial frequencies would vary considerably with orientation. Other models of RF shape would predict a greater independence between orientation and spatial-frequency tuning. We have examined this by recording the responses of cat striate-cortex cells to a wide range of different spatial-frequency and orientation combinations. In almost all cells studied, peak orientation did not consistently vary with spatial frequency, but the majority of cells showed some change in peak spatial-frequency tuning with orientation. The amount of change in peak spatial frequency tended to be greater for cells that were narrowly tuned for orientation. However, cells narrowly (and also very broadly) tuned for spatial frequency tended to show considerable independence of spatial-frequency and orientation tuning, and in all but a few cells the degree of change was less than predicted by the classic RF model. Such cells were found to fire only to patterns whose local spatial spectra fell within a compact, restricted, roughly circular two-dimensional spatial-frequency region. We conclude that the two-dimensional RF shape of striate cells more closely approximates that predicted by a two-dimensional Gabor model or by a Gaussian-derivative model than it does the classic shape based on the output of geniculate cells with aligned RF's.

INTRODUCTION

Over the last 20 years a wide variety of psychophysical and physiological studies have examined the response of the visual system to patterns that vary either in orientation or in spatial frequency. In part the popular use of gratings as stimuli has come about simply because they provide a powerful description of visual performance. Under appropriate conditions, a knowledge of the response to gratings permits one to predict the response to more-complicated stimuli and may provide important insights into the spatial profiles of the channels mediating the response. However, motivating the bulk of this research has been the notion that orientation and spatial-frequency (two-dimensional spatial-frequency) selectivity are fundamental dimensions in the visual analysis of form. In fact, one widely (though by no means universally) accepted model of spatial vision holds that the stimulus is actually encoded and represented according to the two-dimensional spatial-frequency components present in a local area.

In a series of papers Daugman[1,2] has stressed that a great deal can be gained from considering orientation and spatial frequency simultaneously rather than separately. With few exceptions, each of these variables has been examined without regard to the influence of the other, in spite of the obvious two dimensionality of the retinal image and the fact that there is no reason to assume *a priori* that any relationship exists between them. Most investigators seem to have implicitly assumed polar separability of orientation and spatial frequency—that is, that the response to orientation is independent (within a scaling constant) of frequency and vice versa. Such independence, however, would require that the visual system have a particular sort of organization, one that is in fact contrary to many of the more popular notions of how it is organized. It is thus of importance to test this assumption. In this study we have done this by measuring the relationship between the orientation- and the spatial-frequency-tuning properties of single units in the cat striate cortex.

Two of the most striking response properties first seen at cortical levels are those of orientation tuning and spatial-frequency tuning of cells. Hubel and Wiesel[3] first showed that striate cells typically respond only to edges or slits of light of a particular orientation, the orientation preference varying from cell to cell. This orientation tuning has been quantified in both cat and monkey by a number of investigators,[4] the average orientation bandwidths (full width at half-height) being about 45°, with wide variability from cell to cell. That striate cells have much narrower spatial-frequency tuning than units earlier in the pathway has also been shown for both cat and monkey by a number of investigators.[5] The average spatial-frequency bandwidth of striate cells is about 1.4 octaves, again with considerable variation among cells, some being as narrowly tuned as 0.5 octave, whereas others have bandwidths of 2.5 octaves or more.

That striate cells are selective for these two variables suggests that a single unit might respond only over a small, local region of two-dimensional spatial-frequency space. This was partially demonstrated by De Valois *et al.*[6] in the monkey and by Movshon[7] in the cat, by measuring both orientation and spatial-frequency tuning in the same cells. Plotting their results on polar axes, with orientation as the angle and frequency as the distance from the center, De Valois *et al.*[6] showed that the four half-amplitude points (two for each tuning curve) map out the four extremes of an ellipse. Since stimuli whose spatial-frequency spectra fall outside such an ellipse would presumably not elicit a significant response from the cell, the cells would appear to be well characterized as local two-dimensional spatial-frequency filters.

However, these measurements were made only by varying orientation at the cell's preferred spatial frequency and vice versa. Thus significant responses to other, quite different combinations of these variables could not be ruled out.

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Further, within the area over which the cell would clearly respond, the question of how the tuning curve for one variable depended on the value of the other was not addressed.

The question of the relationship between orientation and spatial-frequency tuning is important not only with respect to the adequacy of striate cells as two-dimensional frequency filters but also because it provides important clues about their receptive-field (RF) profiles. The exact shape of cortical RF's has been a subject of great interest and controversy ever since Hubel and Wiesel[3] first suggested that oriented simple cells might arise out of the alignment of a series of center-surround lateral-geniculate-nucleus (LGN) cell inputs. A currently popular alternative is that the profile is described by a Gabor function, a sine wave weighted by a Gaussian envelope (see Ref. 8), expressed in its two-dimensional form by Daugman.[1] Neither of these RF models, as with many other plausible candidates, yields polar-separable frequency spectra.[1] Rather, they predict specific and unique changes in frequency tuning as orientation is varied and vice versa.

As an extreme example of this, Daugman[1] noted that simple elongation of a center-surround unit produces an obviously oriented RF profile but no absolutely preferred orientation. Instead, at each orientation a (different) frequency can be found at which the cell will give the same maximum response. Were such a cell measured only with a range of frequencies at one orientation and with a range of orientations at one frequency, it might mistakenly appear to have a localized spectrum and a uniquely preferred stimulus, when in fact its true spectrum rises to the sample amplitude at every orientation. On the other hand, there are plausible RF profiles that do in fact result in well-localized and polar-separable frequency spectra. For example, such an oriented RF profile could arise through the directional spatial differentiation of an isotropic RF (for instance, a center-surround LGN cell).[2] These various RF models, then, turn out to make what are often rather distinct predictions about the frequency–orientation relationship. An empirical knowledge of this relationship might therefore provide one basis for discriminating between them.

Two studies have previously examined this question in cat striate cortex (Movshon[7] and Glezer *et al.*[9]). However, results were reported only for a very small number of cells (two and three, respectively, in the two studies) and were limited to the qualitative statements that the tuning for one variable did not (Glezer *et al.*[9]) or did not strongly (Movshon[7]) depend on the value of the other. We therefore decided to reexamine the question more closely and on a larger population.

METHODS

Our recording procedures have been described in detail elsewhere (De Valois *et al.*[6]). Single units in striate cortex were isolated with platinum–iridium microelectrodes in anesthetized, paralyzed cats. The spike responses were sent to a NOVA 4X computer, where they were stored and analyzed.

The sinusoidal gratings used in this study were generated by the computer and a Lexidata display system and were presented on a Tektronix 654 color monitor (though only black–white patterns were used). A white screen with a large circular aperture was placed immediately in front of the monitor and maintained near the average color and the 27-cd/m^2 mean luminance of the display. This aperture subtended 18° at the 57-cm viewing distance. The computer controlled the spatial frequency, contrast, and drift rate of the patterns. To vary orientation, the monitor could be manually rotated in 5° steps.

Once a cell was isolated, its RF was centered on the monitor, and a general exploratory program (providing a variety of patterns) was used to determine the ocular dominance of the unit and its approximate preferred spatial frequency and orientation. Then a preselected range of 10 spatial frequencies [covering 0.16 to 3.8 cycles/deg (c/deg) in 0.5-octave steps] were presented in random order, along with a blank trial to assess the base rate. For narrowly tuned cells, a smaller frequency range with smaller steps was used. The gratings of each spatial frequency were typically presented at a 2-Hz drift rate for a total of 20 cycles. Once such a frequency-response function was measured in this way, a new orientation was randomly selected, and the full frequency series was repeated. A range of orientations spanning ±90° from the optimum was examined in 15° steps for broadly tuned cells and in 5° steps for narrowly tuned units. The full experiment required more than an hour to complete, so many cells were not completely tested. Thus, in addition to complete data from 24 cells (14 simple and 10 complex), we have incomplete information on some dozens of others (which, despite being incomplete, permitted us to be more certain of the generality of the findings).

This study required an analysis of the peaks and the bandwidths of the spatial-frequency- and the orientation-tuning curves for each of the various conditions. Initially the peaks were estimated by eye. Later, a least-squares curve-fitting procedure was used, with the peak and the bandwidth relative to the base rate read off the resulting function. The fitted function was a sixth-order exponential chosen only because it provided reasonable fits over the range of interest and not because it had any theoretical significance. These two procedures yielded essentially the same estimates (they correlated 0.989), so the data presented here are based only on the curve fits.

RESULTS

The quantitative measures reported here are from the population of 24 cells (14 simple and 10 complex) on which we have complete data. The general directions of the results were confirmed on a larger population of cells on which there was incomplete data. The sample population was found to have spatial-frequency bandwidths ranging from 0.90 to 3.13 octaves, with a mean of 1.66 (somewhat broader than the best estimates[6,10] of a population mean of about 1.4 octaves). The full width at half-height orientation bandwidths ranged from 16.6 to 64°, with a mean of 38.4° (somewhat narrower than the population average of about 45°). These (rather small) discrepancies are due to the complex cells in the sample being, on the average, somewhat more narrowly tuned for orientation and more broadly tuned for spatial frequency than usual.

Figure 1 shows the responses of a simple cell to a wide variety of spatial-frequency and orientation combinations (to avoid clutter in the figure, not all the measured curves are presented here). In Fig. 1A, the data are organized into a number of frequency-tuning curves, each measured at a dif-

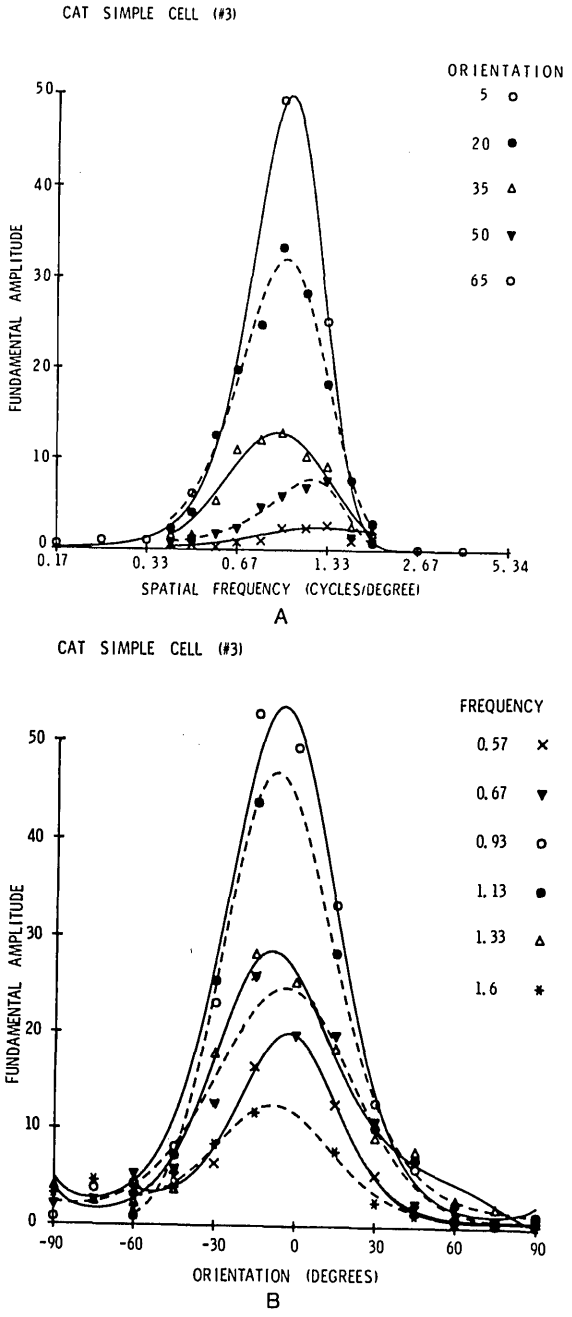

Fig. 1. A, Responses of a simple cell to gratings of each of various spatial frequencies at each of several different orientations. Note that, whereas the response of course decreases at off orientations, the peak spatial-frequency tuning does not change with orientation. B, Responses of the same cell to various orientations at each of several spatial frequencies. Note the invariance of the orientation tuning with spatial frequency.

ferent orientation. In Fig. 1B the same data have been replotted, this time as orientation functions at each of several spatial frequencies.

In several respects, these data are exemplary of all the cells examined. First, as expected, the cell had an absolutely preferred stimulus among the combinations tested, as was true of all cells. In this case it was a grating of 0.97 c/deg (F_{max}) at an orientation of 359.6° (O_{max}). The orientation bandwidth measured at F_{max} was 49.1°, whereas the frequency bandwidth at O_{max} was 0.94 octave. Thus this cell was quite narrowly selective for spatial frequency but slightly more broadly tuned than average for orientation.

The second general point illustrated in Fig. 1A is that for spatial frequencies sufficiently far from F_{max}, no orientation could be found that elicited a significant response. Similarly, it can be seen in Fig. 1B that, at orientations far from O_{max}, no responses could be obtained from gratings of any spatial frequency. Thus this cell (and the others tested) did in fact have well-localized responses in the two-dimensional frequency domain, as the data of De Valois *et al.*[6] clearly suggested. The areas over which the cells responded varied widely depending on their tuning properties, but the critical point here is that the range of stimuli to which any cell was responsive was in fact well predicted simply from a knowledge of the orientation- and the frequency-tuning curves at F_{max} and O_{max}, respectively.

From an inspection of Figs. 1A and 1B, it is clear that all the orientation curves and all the spatial-frequency-tuning curves peak at roughly the same value. For this cell, then, the peak spatial frequency was found to be independent of orientation and vice versa.

This final point has been illustrated by plotting the peaks of the various curves from this cell (cell 3) at the tops of Figs. 2A and 2B. In Fig. 2A the change in peak frequency is plotted as a function of orientation (relative to O_{max}), and in Fig. 2B the change in orientation is plotted as a function of frequency (relative to F_{max}). Also plotted in Fig. 2 are data from three other simple cells, representative of the range of results obtained from the sample. (Cells 3 and 16 form the two extremes of the population, and 4 and 5 are more-typical samples). Complex cells showed essentially the same pattern of results and exhibited a similar range of variability.

It can be seen in Fig. 2 that the curves for cell 3 are reasonably flat, indicating that the preferred value for one of these variables was largely independent of the value of the other, which is the result reported by Movshon[7] and Glezer *et al.*[9]

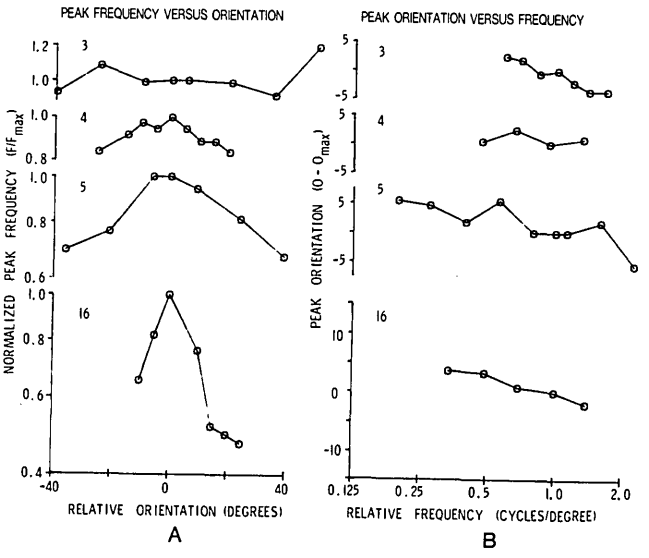

Fig. 2. A, Plots of the peak spatial frequency as a function of orientation and B, peak orientation as a function of spatial frequency for each of four cells. The data from the cell whose detailed data were presented in Fig. 1 (cell 3) are plotted at the top. Note that all cells show orientation peaks that are largely independent of spatial frequency, but some cells (notably cell 16) show considerable change in spatial-frequency tuning at off orientations.

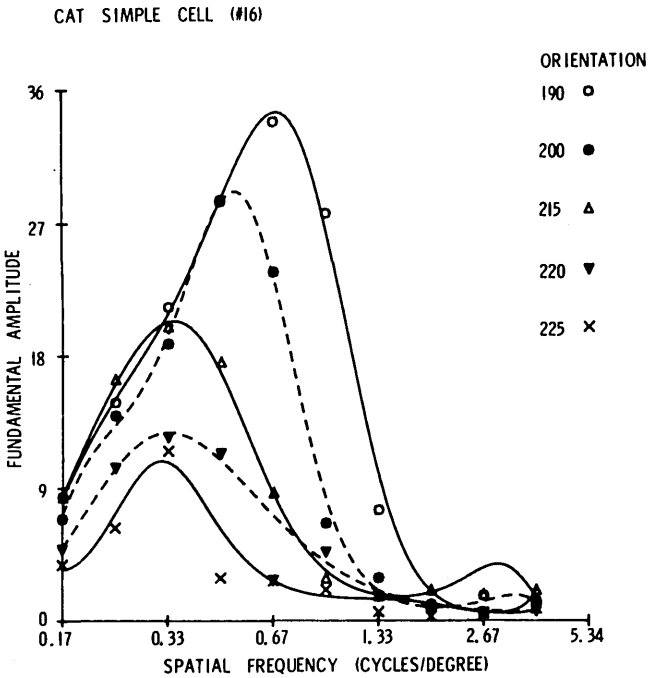

Fig. 3. Responses of the cell that showed the most extreme shift in spatial-frequency tuning (to lower frequencies) at off orientations.

With regard to preferred orientation (Fig. 2B), this seemed to be a general property of the cells in our sample. They showed no strong change in peak orientation tuning as spatial frequency was varied (the curves for three of the cells in Fig. 2B actually suggest a slight but consistent change in peak, but this trend was not found in the majority of our cells). However, when preferred spatial frequency was examined as a function of orientation, an invariant peak was *not* observed. The results from cell 3 represent more of an exception than a rule. Most cells actually showed a consistent and symmetric shift toward lower peak frequencies as orientation was varied away from O_{max} on either side.

In Fig. 2A, this trend is most clearly seen in the curve for cell 16, which exhibited the largest changes found. At just 15° away from O_{max}, the frequency-tuning function peaked at a frequency that was only half of that of F_{max}. Several of the modulation transfer functions (MTF's) for cell 16 have been plotted in Fig. 3, where the steady shift toward lower frequencies at off orientations is readily apparent. The fact that a similarly large change in preferred orientation does not occur is suggested in this figure by the fact that the function at 190° is generally higher than the other curves over most of the frequency range.

The majority of cells fell between the extremes set by cells 3 and 16. That is, they showed a moderate change in peak spatial frequency (toward lower frequencies) as orientation was varied, while showing little consistent change in preferred orientation as frequency was varied. Since the frequency changes were found to be symmetrical around O_{max}, + and − orientation changes have been averaged together in further analyses.

Considerable individual differences in the degree of independence between spatial frequency and orientation was found in our sample, as evidenced by the extreme cases illustrated in Figs. 1 and 3. This raises the question of what might account for these differences. Since the cells varied considerably in their orientation and spatial-frequency selectivities, we looked to this for a possible explanation. Of the cells illustrated in Fig. 2, for instance, cell 3 was narrowly tuned for spatial frequency and broadly tuned for orientation, whereas cell 16 was narrowly tuned for orientation and broadly tuned for spatial frequency.

To examine this on the population as a whole, the entire sample was divided into four groups, each spanning a different range of bandwidths, and the average change in frequency within each group was plotted as a function of orientation (see Fig. 4). These averages include the results of both simple and complex cells, because separate examinations of the two groups revealed no significant differences in the general pattern of results. However, it should be noted that the theoretical considerations motivating this analysis were developed only with the linear simple cells in mind.

From Fig. 4 it is apparent that the group with the narrowest orientation tuning exhibited the largest change in frequency (Fig. 4D), whereas the group with the broadest orientation tuning showed little change, consistent with the examples of cells 3 and 16. However, it does not appear to be a particularly strong relationship, for the two medium groups actually showed the reverse trend. Also shown in this figure (dashed lines) are theoretical predictions from the aligned-LGN model of striate RF's, to which we shall return later. Here we merely note that the agreement with the data is not very close.

In Fig. 5 are plotted results for the cells grouped into four frequency- (rather than orientation-) bandwidth classes. This time the slight trend is seen that those cells either very narrowly or very broadly tuned for spatial frequency show little change in peak frequency at off orientations.

It is possible that neither the orientation nor the frequency bandwidths considered alone provide a particularly strong indicator of a cell's frequency–orientation relationship, simply because the two bandwidths jointly determine the relationship

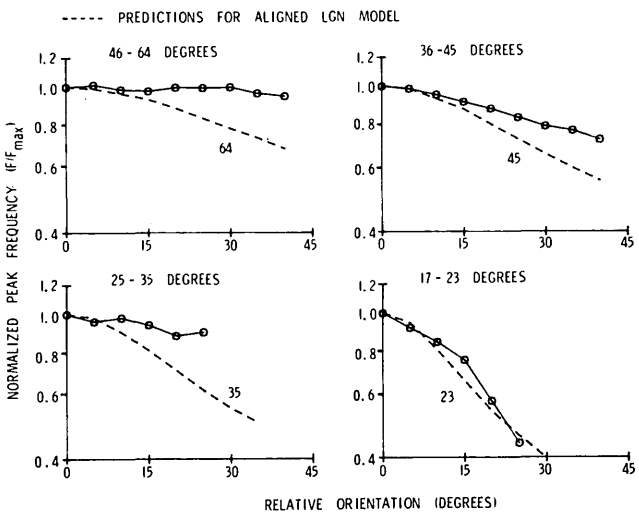

Fig. 4. Shift in peak spatial frequency with change in orientation. Data are from all cells tested, grouped by their orientation bandwidths. Also plotted (dashed lines) are the predictions from the classic aligned-LGN model. Note that, with the exception of the cells most narrowly tuned for orientation, the amount of spatial-frequency change is much less than that predicted by this model.

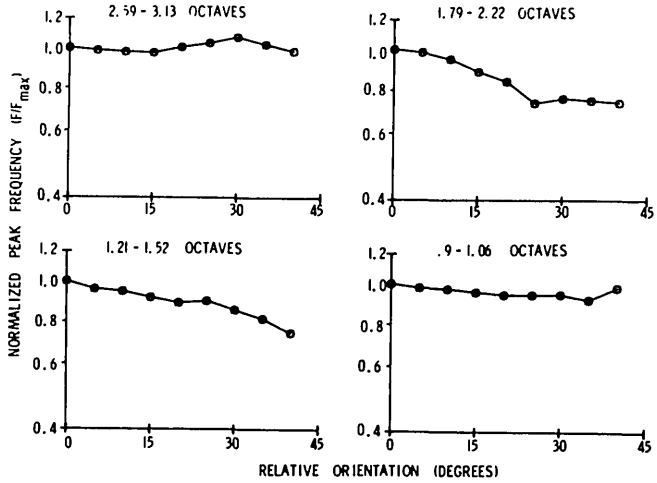

Fig. 5. Peak spatial frequency as a function of orientation. Data from all cells, grouped by their spatial-frequency bandwidths. Note that the cells most narrowly tuned for spatial frequency show invariant frequency tuning with orientation, as do the most broadly tuned cells.

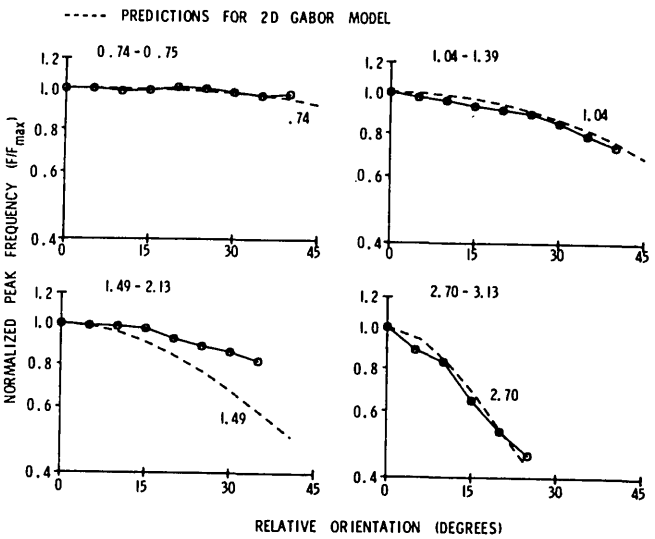

Fig. 6. Peak spatial frequency as a function of orientation of cells grouped by their aspect ratios (relative spatial-frequency versus orientation tuning). Note that the cells with small aspect ratios (those relatively more narrowly tuned for spatial frequency than for orientation) show little dependence of frequency on orientation. Also plotted are the predictions for Gabor RF's. It can be seen that the data in general fit this model quite well.

and must therefore be considered together. For this reason, we calculated for each cell an assumed aspect ratio, see Daugman.[2] As was mentioned in the introduction, if the four half-amplitude points (two for each bandwidth) are plotted on polar coordinates and connected by a smooth curve, the result is a crude ellipse. The aspect ratio is the ratio of the two axes of this ellipse. To compare different cells, we rotate each through frequency space until $O_{max} = 0°$, so the ellipse is centered on the x axis, and define the aspect ratio as

$$\mathrm{AR} = \frac{\text{length of ellipse's axis along } x \text{ axis}}{\text{length of ellipse's axis along } y \text{ axis}}.$$

This value is equivalent to

$$\mathrm{AR} = \frac{(2^{\Delta W} - 1)}{(2^{\Delta W} + 1)} \times \frac{1}{\sin(\Delta O_{1/2})},$$

where $\Delta O_{1/2}$ is the orientation half-bandwidth and ΔW is the spatial-frequency full bandwidth. This provides an adequate measure of the relative tuning in these two dimensions but indicates nothing about the absolute tuning of either. According to this convention, a cell with an aspect ratio of less than 1 is relatively more narrowly tuned for frequency than orientation, whereas a cell with a ratio greater than 1 has greater relative orientation selectivity.

The aspect ratios calculated in this way were found to range from 0.7 to 3.1, with a mean of 1.45. In this particular population, simple cells tended to have smaller ratios than did complex cells, a reflection of the fact that our complex-cell sample was unusually broadly tuned for spatial frequency. Again, the cells were divided into four groups, and the variations in frequency tuning at increasingly off orientations are plotted in Fig. 6. The resulting relationship is quite systematic. The only cells that show a pronounced change in spatial-frequency tuning at off orientations are those with a large aspect ratio (cells relatively much more selective for orientation than for spatial frequency). The two middle groups showed intermediate amounts of change but were not distinguishable from each other. As we discuss in the next section and as can be seen from the dashed lines, these results are in fair agreement with predictions from a two-dimensional Gabor model of RF shape.

DISCUSSION

Our results suggest that single striate units have the following two-dimensional tuning characteristics. First, the responses of these cells are well localized within the spatial-frequency domain, as was suggested by several earlier studies. In every case, the range of stimuli to which the cell responded could have been well predicted from a knowledge of the orientation-tuning curve at the preferred spatial frequency and vice versa. Stimuli that fell outside the boundaries defined by these tuning curves invariably failed to elicit a significant response. As Daugman[2] has noted, this is not a result predicted by many otherwise plausible RF models, including at least the simplest interpretation of the aligned-LGN-cell model of Hubel and Wiesel.[3]

Second, over the range of stimuli to which a cell is responsive, the preferred orientation is not strongly dependent on the spatial frequency at which it is measured. However, a quite different result was obtained when preferred spatial frequency was examined as a function of orientation. The majority of cells showed consistent changes in the peak of the frequency-tuning functions as orientation was varied away from the optimum, although the amount of change was quite different for different cells. The relationship between peak frequency and orientation had the following important properties: (1) The shift with off orientations was almost invariably toward lower-spatial-frequency values; (2) it was symmetric and largely monotonic with orientation, orientations further and further to either side of optimum resulting in increasingly lower-frequency peaks; and (3) the degree of change was at least loosely related to the tuning properties of the cell, cells relatively more selective for spatial frequency than for orientation showing the least change (i.e., the greatest degree of independence of spatial frequency and orientation).

Our results disagree to some extent with those of Movshon[7] and Glezer *et al.*,[9] who concluded that peak spatial frequency

does not depend on orientation. It should be noted, however, that their conclusions were based on data from a limited number of cells. It is possible that they happened to examine cells for which this was in fact the case, for indeed in our sample a few cells had largely invariant peaks. Further, for the majority of our cells, the changes in peak frequency at off orientations were actually rather small, so that it is often true that—to a first approximation—the peaks do not depend strongly on the orientation. However, on closer examination a significant and highly systematic dependence is in fact apparent.

This study was largely motivated by Daugman's[1] suggestion that information on the spatial-frequency–orientation relationship might be used to discriminate among various models of RF shape. To this end, we calculated the predicted changes in peak spatial frequency as a function of orientation for the Hubel–Wiesel[3] aligned-LGN-cell model and for a Gabor model.

Before considering these, we might first note that our results clearly argue against a RF model based on simple elongation of a center-surround LGN cell. As was mentioned earlier, such a cell would show the same peak amplitude of response at all orientations, although to a different frequency depending on the orientation.[1] In contrast, all our cells had responses that were well localized in the frequency domain and always appeared to have only one absolutely preferred frequency and orientation.

To calculate predictions for the aligned-LGN-cell model, each LGN unit was constructed from a difference of two Gaussians, a narrow excitatory one overlapped by a broader inhibitory one, as in the Rodieck[11] ganglion-cell model. These two Gaussians were weighted so that the resultant center-surround unit would give zero net response to full-field illumination (as cortical units in fact do). This gives them a fixed spatial-frequency bandwidth of 1.93 octaves. A large number of these units were then aligned and evenly spaced to produce the presumptive cortical RF, with the orientation tuning simply controlled by varying the length of the RF. This is essentially one of the cases considered by Daugman,[1] and reference should be made to his Figs. 1 and 2 to see the RF and its Fourier transform.

The dashed lines in Fig. 4 show the predictions from this model in comparison with the actual data. It can be seen that the predicted curves behave qualitatively in a manner similar to the observed data, but that (except for the most narrowly tuned cells) the amount of change in spatial-frequency peak with change in orientation is much greater than that observed.

In addition to not giving a close approximation to the results reported here, the aligned-LGN-cell model is not in accord with the narrow spatial-frequency tuning seen in a sizable fraction of cortical cells or with the related findings of multiple subregions within the RF's of many cortical units. These findings are easily accounted for by the Gabor model, in which the RF is simply a sine wave weighted by a two-dimensional Gaussian envelope. The broader the Gaussian along the sine wave's axis of modulation is, the more periods will fall under the envelope and thus the more subdivisions to the RF (and the narrower the spatial-frequency tuning).

In the general case, the Gabor filter will have a different envelope in the two dimensions. If the underlying sine wave is vertically oriented, a broader envelope in the vertical dimension will result in relatively greater selectivity for orientation than for spatial frequency, because the RF will contain a small number of long subregions. This would correspond to a space-domain aspect ratio of less than 1 and, because the two are inversely related, to a frequency-domain aspect ratio of greater than 1. Alternatively, a broader horizontal envelope will produce relatively narrower spatial-frequency tuning and will have an aspect ratio in the frequency domain of less than 1.

The dashed curves in Fig. 6 represent the predicted changes in peak spatial frequency for two-dimensional Gabor filters with different aspect ratios. It can be seen that these predictions provide quite a close fit to three of the four observed curves. Unlike the aligned-LGN model, the Gabor model can readily account for the almost orientation-invariant preferred frequencies observed in those cells with smaller aspect ratios. This model can also, of course, account for the wide range of spatial-frequency bandwidths found among striate cells, in particular the occurrence of narrowly tuned cells. Further, it also readily predicts the cells' localized response area in the spatial-frequency domain, where the aligned-LGN model does not.

Neither of these models has RF's that yield polar-separable spectra, nor do our data in general show polar separability. For at least the simplest conception of single striate-cortex units as two-dimensional spatial-frequency filters, it would seem that, if the cells had independent tuning functions for spatial frequency and orientation, these two variables could be encoded with the least ambiguity. However, in many of the cells this confounding of variables does indeed exist. (There are other much more formidable sources of ambiguity in the cells' responses, however; notably the contrast dependence of their responses.)

In this regard, it is interesting to note that the cells exhibiting the greatest change in spatial frequency with orientation are those least efficient in encoding frequency, because they are narrowly tuned for orientation but broadly tuned for frequency. These cells were in fact *best* suited to encode the orientation of a grating, regardless of its frequency. On the other hand, the cells with the most invariant spatial-frequency preference (and therefore most effective for signaling spatial frequency independent of orientation) tended to be those most narrowly tuned for spatial frequency. De Valois *et al.*[6] suggested that those cells narrowly tuned in both dimensions are probably the most critical for spatial vision and pointed out that the positive correlation between the orientation and the spatial-frequency bandwidths supports this view. However, the present results suggest that there are certain distinct advantages to narrow tuning in only one dimension. The potential role of such cells in the analysis of form should not be overlooked.

Up to this point, our analysis has centered on the behavior of cells in the frequency domain. We would like briefly to consider instead the space domain. The RF's implied by our data can be constructed by calculating the inverse Fourier transforms of the cells' frequency responses. To do this required making certain assumptions that were not totally justified, but the deviations from them are probably not critical for our purposes. These included the assumptions that the response was a linear function of contrast (deviations from this around the middle-contrast range that we picked are minor, judging from our previous measures) and that the RF's were all in cosine phase (in the absence of any actual phase measurements).

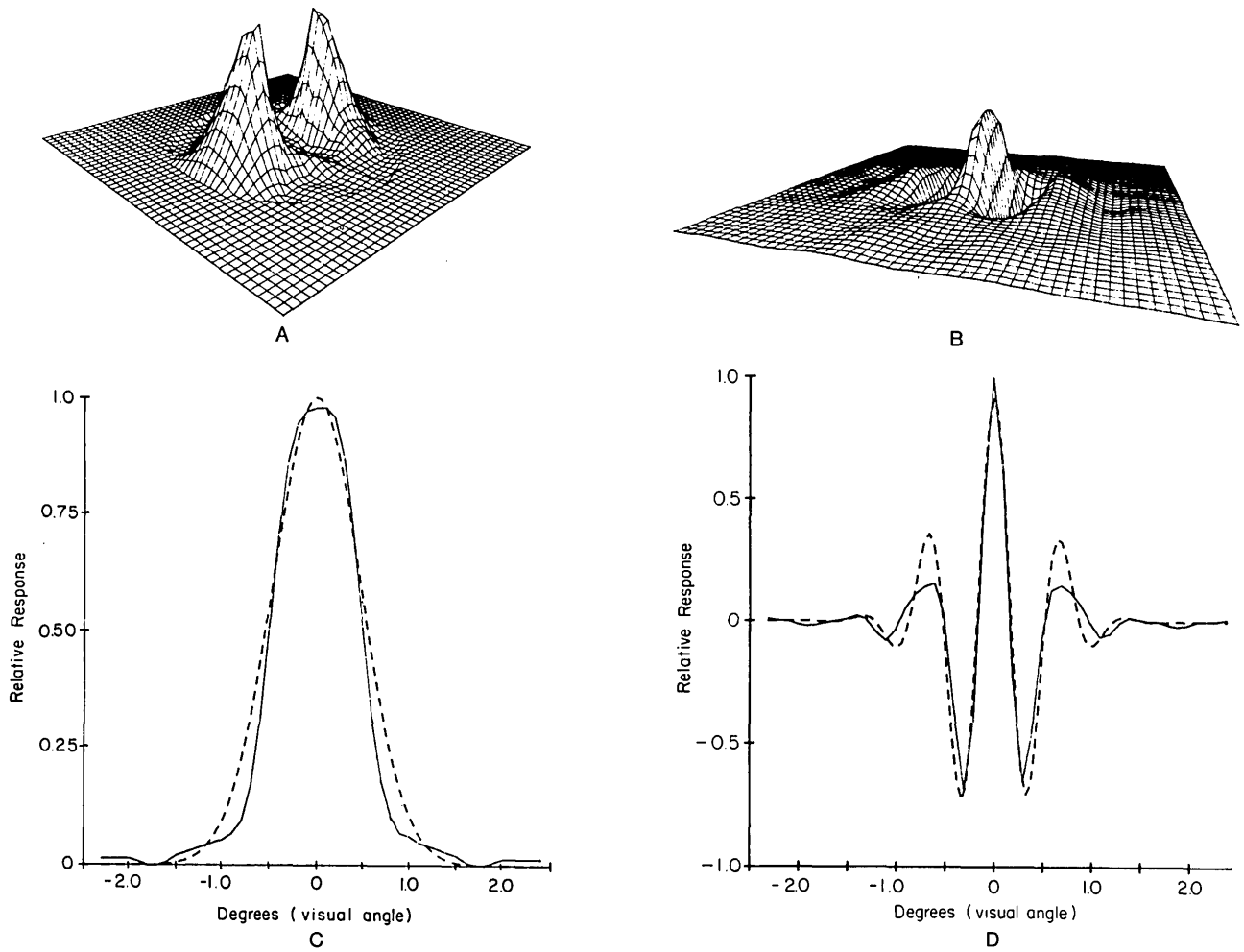

Fig. 7. A, Two-dimensional spatial-frequency plot of the responses of cell 3. Note that the cell responds to only a restricted two-dimensional spatial-frequency region. Note also the indication of a surrounding inhibitory region in the frequency domain (at higher spatial frequencies). B, The receptive field in the space domain for this cell, calculated by the inverse Fourier transform. Note the oscillations in the RF for this narrowly tuned (0.94-octave) cell. C and D, Cross sections through the RF of this cell in x and y along with the best-fitting Gabor function (dashed lines).

The two-dimensional spatial-frequency spectra and resultant RF's for two of the simple cells characterized in Fig. 2 are plotted in Figs. 7 and 8: cell 3, which had narrow spatial-frequency tuning, and cell 5, which was quite broadly tuned for both spatial frequency and orientation. It can be seen (Figs. 7A and 8A) that both cells responded to only a limited, compact, two-dimensional spatial-frequency range. In the space-domain RF plots, the narrow spatial-frequency tuning (0.94 octave) of cell 3 translates into multiple oscillations in the RF (Fig. 7B), whereas that for the broadly tuned (1.94-octave) cell 5 has just a central subregion and two antagonistic flanks (Fig. 8B).

For each of these cells, cross sections along the two primary axes of the RF are also presented (Figs. 7C and 7D and 8C and 8D), along with the best-fitting two-dimensional Gabor functions. For the axis orthogonal to the RF's modulation this is the best-fitting (least-squares) Gaussian. For the modulated cross section, the spatial frequency yielding the largest measured response was chosen, and then its best-fitting Gaussian envelope was calculated.

It is difficult to evaluate exactly how good these fits are or how important the observed discrepancies. To a first approximation, however, the two-dimensional Gabor model clearly appears to capture the essential characteristics of these curves, just as it predicted the general-response characteristics in the frequency domain. This is impressive when one considers the diverse properties of the cells in this sample. The fact that the model is sufficiently general to account for this diversity without compromising its simplicity clearly makes it a useful, if not entirely accurate, description of these results.

There are, of course, other possible RF models that may fit our data even better than a Gabor model, e.g., the Gaussian-derivative model of Young and Marrocco,[12] which is a close approximation to a Gabor model but which might perhaps be more plausibly constructed from known anatomical and physiological processes. We have not attempted to make detailed predictions for Gaussian-derivative RF's, but it is of interest to note that a Gabor model predicts that the zero crossings in an oscillating RF should all be equally spaced, since it is just a tapered sine wave in cross section. The Gaussian-derivative model, on the other hand, predicts that the successive sidebands should be increasingly widely spaced out. The slight deviations from the Gabor prediction seen in Fig. 7D are in the direction predicted from the Gaussian-derivative model.

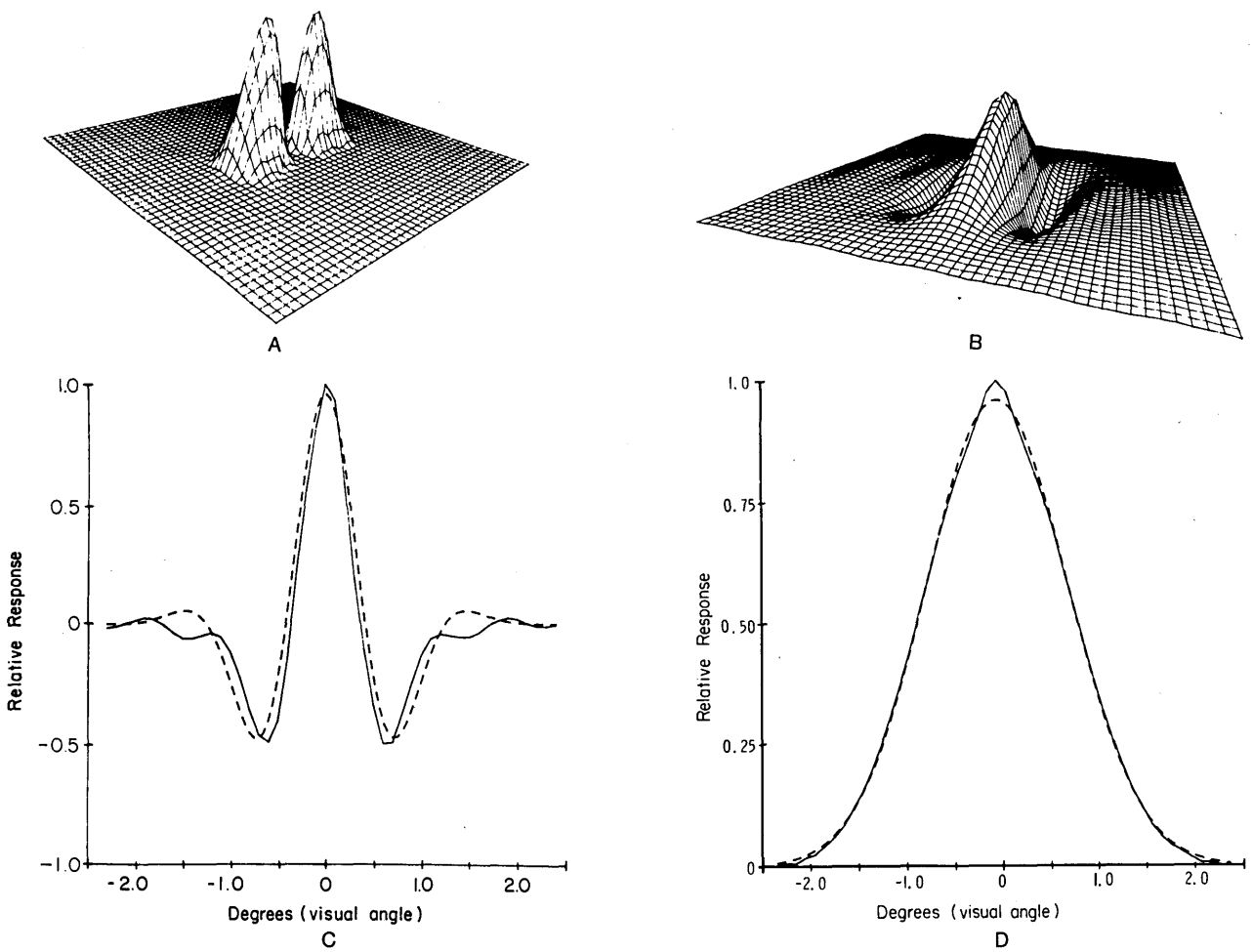

Fig. 8. A, Two-dimensional spatial-frequency plot of the responses of cell 5 [a cell broadly tuned (1.94 octaves) for spatial frequency]. Note, nonetheless, that the cell responds only within a restricted two-dimensonal spatial-frequency region. B, The computed RF for this cell. Note the absence of multiple sidebands. C and D, Cross sections through the RF of this cell, with the predictions from the Gabor model in dashed lines.

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