TWO-DIMENSIONAL SPECTRAL ANALYSIS OF CORTICAL RECEPTIVE FIELD PROFILES

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Abstract—Most vision research embracing the spatial frequency paradigm has been conceptually and mathematically a one-dimensional analysis of two-dimensional mechanisms. Spatial vision models and the experiments sustaining them have generally treated spatial frequency as a one-dimensional variable, even though receptive fields and retinal images are two-dimensional and linear transform theory obliges any frequency analysis to preserve dimension. Four models of cortical receptive fields are introduced and studied here in 2D form, in order to illustrate the relationship between their excitatory/inhibitory spatial structure and their resulting 2D spectral properties. It emerges that only a very special analytic class of receptive fields possess independent tuning functions for spatial frequency and orientation; namely, those profiles whose two-dimensional Fourier Transforms are expressible as the separable product of a radial function and an angular function. Furthermore, only such receptive fields would have the same orientation tuning curve for single bars as for gratings. All classes lacking this property would describe cells responsive to different orientations for different spatial frequencies and vice versa; this is shown to be the case, for example, for the Hubel & Wiesel model of cortical orientation-tuned simple cells receiving inputs from an aligned row of center/surround LGN cells. When these results are considered in conjunction with psychophysical evidence for nonseparability of spatial frequency and orientation tuning properties within a "channel", it becomes mandatory that future spatial vision research of the Fourier genre take on an explicitly two-dimensional character.

Psychophysical and physiological studies of spatial vision have generated two diverging modelling approaches which could be, but largely have not been, translated into each other. To a great extent, recent psychophysical work has concentrated on various "channel" hypotheses, sustained by measurements of spatial frequency effects, whereas neurophysiological work has aimed at mapping the geography of single unit receptive fields. This divergence is symbolized by two traditional icons: a vertical sinewave grating on the one hand, and a roving spot or bar of light on the other. The purpose of this paper is to propose and illustrate a method of analysis which can unify psychophysical and physiological work, in proper two-dimensional form, and which clarifies in particular the relationship between the canonical variables of orientation and spatial frequency.

One-dimensional Fourier analysis has been widely applied in psychophysical investigations, sired originally by a series of seminal experiments employing one-dimensional sinewave gratings (Campbell and Robson, 1964, 1968; Sachs *et al.*, 1971). Such analysis has also been used, but to a far lesser extent, in physiological studies of the receptive field profiles of retinal ganglion cells (Enroth-Cugell and Robson, 1966), cortical simple cells (Andrews and Pollen, 1979), and complex cells (Pollen and Ronner, 1975). The shortcoming of purely one-dimensional spectral analysis in both of these spheres is that it fails to capture properties which depend on orientation. Mathematically speaking, current debates about whether or not there occurs a "generalized piece-wise

Fourier analysis in the visual system" (e.g. Tyler, 1978; Glezer, 1979) are meaningless in the absence of a full *two*-dimensional Fourier analysis. Modulation transfer functions and spatial frequency effects have been studied psychophysically for (traditionally) vertical gratings; and neurophysiological MTF's are occasionally measured for gratings inclined at a cell's "preferred" orientation. *But unless a cell's receptive field is circularly symmetric, it is described by no single MTF; its spectrum will scale, shift, or change in shape when studied at other orientations.* In psychophysical terms, the question of whether a "channel" has separable frequency and orientation properties—such that its overall sensitivity function may be expressed as the product of a frequency tuning curve (independent of orientation) and an orientation tuning curve (independent of frequency)—is a critical but unexamined two-dimensional issue which should be resolved at the outset of any discussion regarding the possibility of a Fourier-like decomposition of the visual world.

As a rule, models of cortical receptive fields have been, to date, rather informal notions lacking quantitative specificity. Various general schemes have been proposed for the organization of excitatory and inhibitory influences on cells in Area 17 of cat and monkey (e.g. Hubel and Wiesel, 1962; Bishop *et al.*, 1973; Schiller *et al.*, 1976), but until the recent paper by Rose (1979), there were no explicit quantitative proposals for the weighting functions of cortical receptive fields. Moreover, there has been no general theoretical analysis of the response of cortical cells to the sinewave gratings which have proven so popular in psy-

chophysical experiments. The present paper aims to demonstrate the power of two-dimensional spectral analysis for clarifying receptive field properties both in the space domain and in the spatial frequency domain. For example, we shall see (in one model) that once a basic template is assumed for the center-surround units of the lateral geniculate nucleus (LGN), whose outputs are presumed to provide the summed input to a cortical cell, then exact predictions may be derived for the most fundamental tuning curves of cortical cells (bar orientation, bar length, grating frequency, orientation, and phase) *for any number and configuration of the component LGN fields.* Such predictive power, when applied to empirical work, should prove most beneficial in the development of models of visual mechanisms.

The traditional concept of a cell's receptive field profile in physiological modelling (e.g. Rodieck, 1965) is a representation of a cell's response characteristics in terms of a functional over the (x, y) plane of visual space. A receptive field profile (rfp) is a bivariate real-valued function $f(x, y)$ which, when multiplied by a like function $s(x, y)$ specifying the stimulus distribution of light intensity and integrated over the plane, yields the response of the cell to that distributed stimulus:

$$\text{response} = k \int\int_{-\infty}^{\infty} s(x, y)f(x, y)\,dx\,dy. \quad (1)$$

Thus, in the simplest case of a small spot of light located at (x_0, y_0) with intensity I_0, the cell's response would be $kI_0f(x_0, y_0)$. A crucial feature of this concept is the assumption of linearity: scaling $s(x, y)$ should identically scale the response, and different stimuli in different regions of the plane should evoke responses that summate. Whether real cortical cells have this property is a matter of considerable debate (e.g. Movshon and Tolhurst, 1975), but for many cells it appears that the assumption may not be too far wrong (Andrews and Pollen, 1979). In any case, as with nearly all current psychophysical work involving sinewave gratings, the usefulness of the present discussion depends almost fatally on the validity of the assumption of linearity.

The cornerstone of the proposed two-dimensional spectral analysis is the calculation of the two-dimensional Fourier transform of a cell's receptive field profile $f(x, y)$:

$$F(u, v) = \int\int_{-\infty}^{\infty} f(x, y)e^{-2\pi i(ux + vy)}\,dx\,dy. \quad (2)$$

By analogy with equation (1), the response of a cell to a stimulus whose two-dimensional Fourier transform is $S(u, v)$ is the product of F and S integrated over the Fourier plane:

$$\text{response} = k \int\int_{-\infty}^{\infty} S(u, v)F(u, v)\,du\,dv. \quad (3)$$

In further analogy with the previous space-domain

example, the simplest Fourier case is that of a stimulus whose two-dimensional Fourier transform $S(u, v)$ is a "small spot" of energy located at (u_0, v_0) with "intensity" I_0. As before, the integration is then trivial and the response of the cell to such a stimulus would be simply $kI_0F(u_0, v_0)$. The great potential of two-dimensional spectral analysis for bridging the gap between traditional physiological and psychophysical experiments now becomes clear: the Fourier "spot stimulus" at (u_0, v_0) in the trivial case above, when complemented with another "spot" at $(-u_0, -v_0)$ and one at $(0, 0)$ having energy $S(0, 0)$, corresponds in the space domain to an inclined sinewave grating whose spatial frequency is

$$\sqrt{u_0^2 + v_0^2},$$

whose orientation is $\arctan(v_0/u_0)$, and whose contrast equals $I_0/S(0, 0)$. In short, inclined sinewave gratings take a trivial case of equation (3). No additional assumptions have been made in introducing the concept of the two-dimensional Fourier transform of a rfp, or in using this surface to predict a cell's responses. Both descriptions (the rfp and its transform) assume linearity of response, and empirically they both require the same magnitude of measurement: namely, spanning independent variables which range over a plane.

To demonstrate the utility of thinking about rfp's in two-dimensional spectral terms, there follow derivations of several crucial predictive properties of a generalized version of the rfp model recently advanced by Rose (1979), as well as for other candidate rfp models to be proposed here. The basic logic of Rose's approach for modelling orientation selective receptive fields traces back to a qualitative notion originally advanced by Hubel and Wiesel (1962), according to which elongated cortical cell profiles are made up of an aligned row of inputs from summated center/surround LGN cells. This scheme was given depth by Rose, who specified the one-dimensional weighting function of each LGN component to be the familiar difference of Gaussians:

$$f(x) = e^{-x^2} - \tfrac{1}{6}e^{-x^2/9}.$$

Presumably each component is rotationally symmetric in the plane, and should therefore be described by the parameterized two-dimensional weighting function

$$f(x, y) = Ae^{-a^2(x^2+y^2)} - Be^{-b^2(x^2+y^2)}$$

as was suggested by Rodieck (1965) for retinal ganglion cell rfp's. The choice of the four parameters should be dictated by four constraints: the spread ratio (b/a) of the excitatory to inhibitory regions; the total volume of the profile; and two scaling constraints (the (x, y) dimension plus height). The volume of the profile, which (from the definition of a rfp) corresponds to the response of the cell under uniform illumination, is given by the double integral of the

profile over the plane. Since most cortical cells have at best a very weak response to uniform illumination (Ikeda and Wright, 1975; Bartlett and Doty, 1974), a useful approximate constraint on the rfp's is that $Ab^2 = Ba^2$, which yields zero volume.

A perspective rendering of such an LGN profile in three dimensions is shown in Fig. 1a, in which the assumptions have been made for zero volume and an excitatory/inhibitory spread ratio of $b/a = 1/2$. Figures 1b and 1c show the result of aligning three and nine such units, as in the Rose scheme for an elongated cortical cell's field whose inputs come from several aligned LGN fields. Figure 1d traces the curves of constant altitude for the profile of 1c, corresponding to the loci of points at which a spot of light would evoke a constant amplitude response. It is clear that such a cortical cell would respond more strongly to a vertical bar of light than to one at any other

orientation, and therefore the cell is orientation selective.

Although the Rose model depicts a cortical cell whose inputs come from *aligned* LGN fields, the present analysis applies to a much more general version of the model, in which n LGN receptive fields are scattered in the plane with their centers positioned at loci (x_i, y_i). Thus the general cortical cell rfp would be described by the function

$$f(x,y) = A \sum_{i=1}^{n} e^{-a^2[(x-x_i)^2+(y-y_i)^2]}$$
$$- B \sum_{i=1}^{n} e^{-b^2[(x-x_i)^2+(y-y_i)^2]}. \qquad (4)$$

The fact that the actual distribution of the (x_i, y_i) loci can be left unspecified here results in great flexibility when applying the results. For example, Creutzfeldt
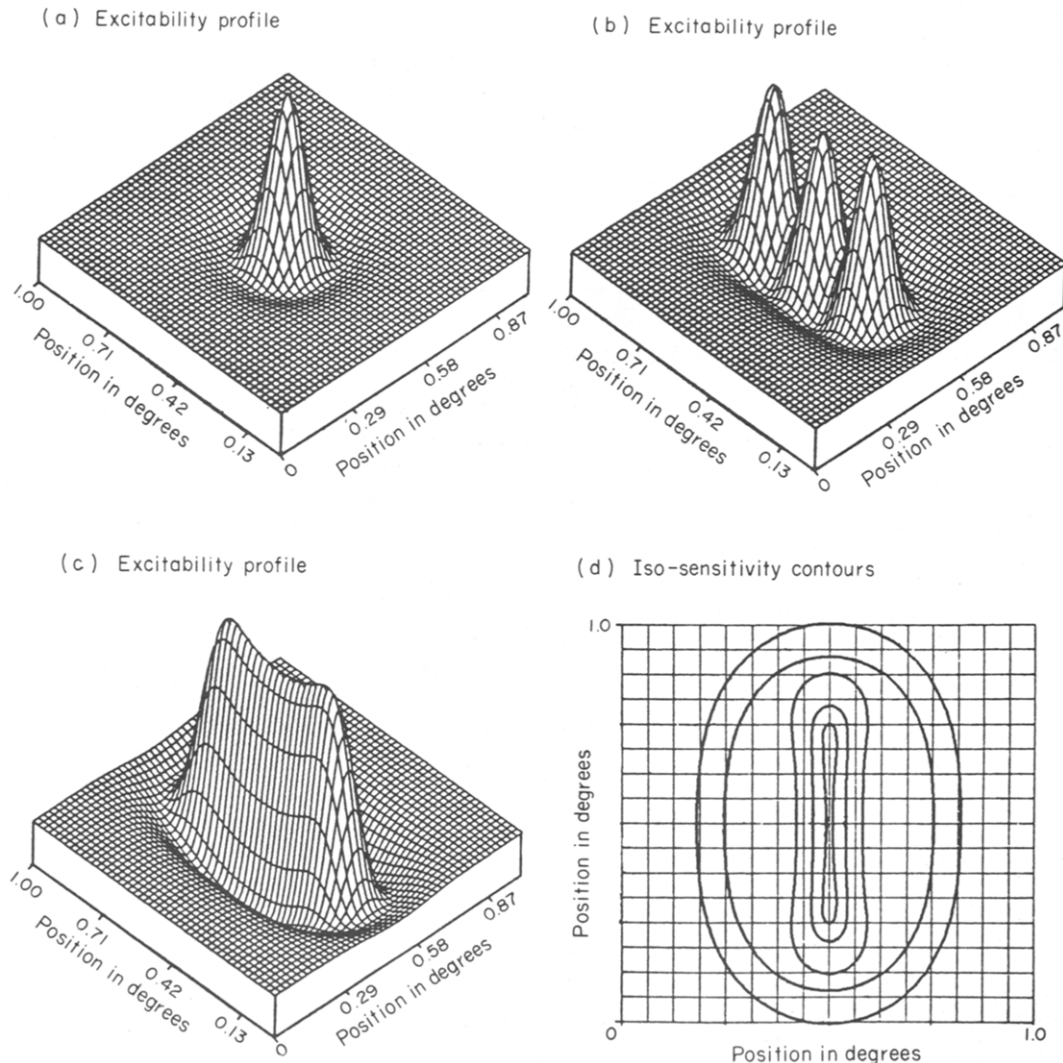

Fig. 1. Theoretical receptive field profiles. (a) A center-surround cell in the lateral geniculate nucleus. (b) A cortical simple cell summating inputs from three and (c) nine LGN cells. (d) Contours of constant altitude for the profile in (c), demonstrating orientation selectivity.

and Ito (1968) reported cells whose receptive fields appeared to be composed of several LGN units scattered randomly in the plane; and Rose (1979, p. 539) suggested that the classical distinction between simple/complex/hypercomplex cell types may be just a matter of the degree of scatter of the underlying LGN fields. The generality of the present analysis absorbs all of these cases: indeed, the resulting expressions for tuning curves will be true of *any* cell whose two-dimensional receptive field profile *could* be represented by a superposition of elementary center/surround components distributed arbitrarily in the plane.

The analytic power of the 2-D transform for treating the problem of cortical receptive field organization is enhanced by the *shift property* of Fourier transforms. If in a cortical hierarchy the profile of a higher-order cell is taken as the sum of the profiles of identical lower-order cells scattered in the field, then the transform of the profile of the higher-order cell is simply the transform of the profile of the characteristic lower-order cell, multiplied by a sum of complex exponentials whose "frequency" parameters are set by the locations of the lower-order cells. It is for this reason that the spectrum of the cortical cell rfp in the "summated inputs" model can be expressed regardless of the configuration of the LGN fields which comprise it. Simplifications result if the distribution of the n LGN rfp loci has even symmetry, such that for every LGN unit located at (x_i, y_i) there corresponds another one located at $(-x_i, -y_i)$; in that case, by application of Euler's formula for complex exponentials, the two-dimensional Fourier transform is purely real. More generally, any real and even function has a Fourier transform which is also real and even.

Figures 2a and b plot the two-dimensional transform for two special cases in which three and nine component LGN fields are aligned in a vertical row and evenly spaced, as discussed earlier and depicted in Fig. 1b and c. When viewed in polar coordinates with the origin at the center, the surfaces of Fig. 2 are effectively plots of the response amplitude of the cortical cell for a sinewave grating whose spatial frequency

and orientation are given respectively by the polar coordinates (r, θ). By calculating the two-dimensional Fourier transform of equation (4) and expressing it in polar coordinates, it may be shown that the response of a cortical cell whose n LGN input fields are scattered with even symmetry at loci (x_i, y_i), when stimulated by a sinewave grating of frequency r and orientation θ, is

$$F(r, \theta) = \left(\frac{A\pi}{a^2} e^{-r^2/a^2} - \frac{B\pi}{b^2} e^{-r^2 b^2} \right)$$

$$\times \sum_{i=1}^{n} \cos(2\pi[x_i r \cos(\theta) + y_i r \sin(\theta)]). \quad (5)$$

(See footnote* for a discussion of the response dependence on the phase of the grating.) Still more general variants of equation (5) are readily derivable for the case of a cortical cell whose input is a *weighted* sum of LGN fields, or for LGN fields having some *distribution* of size parameters.

For the case of the aligned LGN fields shown in Fig. 1, the resulting cortical cell's modulation transfer function for sinewave gratings of a given orientation may be obtained from Fig. 2 by imagining the vertical cross-section of the surface along a radial path at the appropriate orientation. It is noted that the surfaces of Fig. 2 have zero height at the origin; this property is a reflection of the rfp "zero volume" assumption discussed earlier, since uniform illumination corresponds to a point at the origin of the Fourier plane, namely a "grating" of zero spatial frequency. It is apparent that the MTF's of the alignment model have shapes which vary radically with the orientation of the grating; if the grating has the preferred orientation of a bar of light, then the MTF is unimodal, whereas it ripples for other orientations.

One important property of any alignment model is that the preferred spatial frequency for a grating stimulus—that one for which the cortical cell's response is maximal—is determined only by the assumed template of the individual LGN units; it is independent of both their number and spatial arrangement along the line. By differentiating equation (5) with respect to r and θ, one can show that for any number and arrangement of aligned LGN units, the optimal sinewave grating has orientation $0°$ (the direction of alignment), and spatial frequency

$$r = ab \sqrt{\frac{\ln(A/B) + 4\ln(b/a)}{(b^2 - a^2)}}.$$

Thus the cortical cell's two-dimensional spectral peak is determined solely by the template parameters A, B, a, b of the underlying LGN fields, regardless of either their number or their spatial locations along the axis of alignment.

The number and arrangement of the aligned LGN inputs obviously does, however, affect the sharpness of the cortical cell's orientation tuning curve for inclined sinewave gratings. The plots of equation (5)

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* Since the Fourier transform is in general a complex function, a complete spectral representation would usually require plotting not one but two surfaces: one showing the real part and the second showing the imaginary part of the transform, or (more usefully), one surface showing the amplitude spectrum and the second surface showing the phase spectrum. But all of the theoretical rfp's presented in the figures have even symmetry (and are real), and consequently their Fourier transforms are purely real. For this reason, the response of the receptive fields to phase shifted gratings is the same function of spatial frequency regardless of the phase of the grating, except for a multiplicative constant. In particular, if a grating is shifted in phase (from cosine phase) by an amount θ, the effect is equivalent to uniformly multiplying the cell's response surface by $\cos(\theta)$. In summary, for rfp's possessing even symmetry, the shape of their frequency response surfaces does not depend on the phase of the grating except for a multiplicative constant.
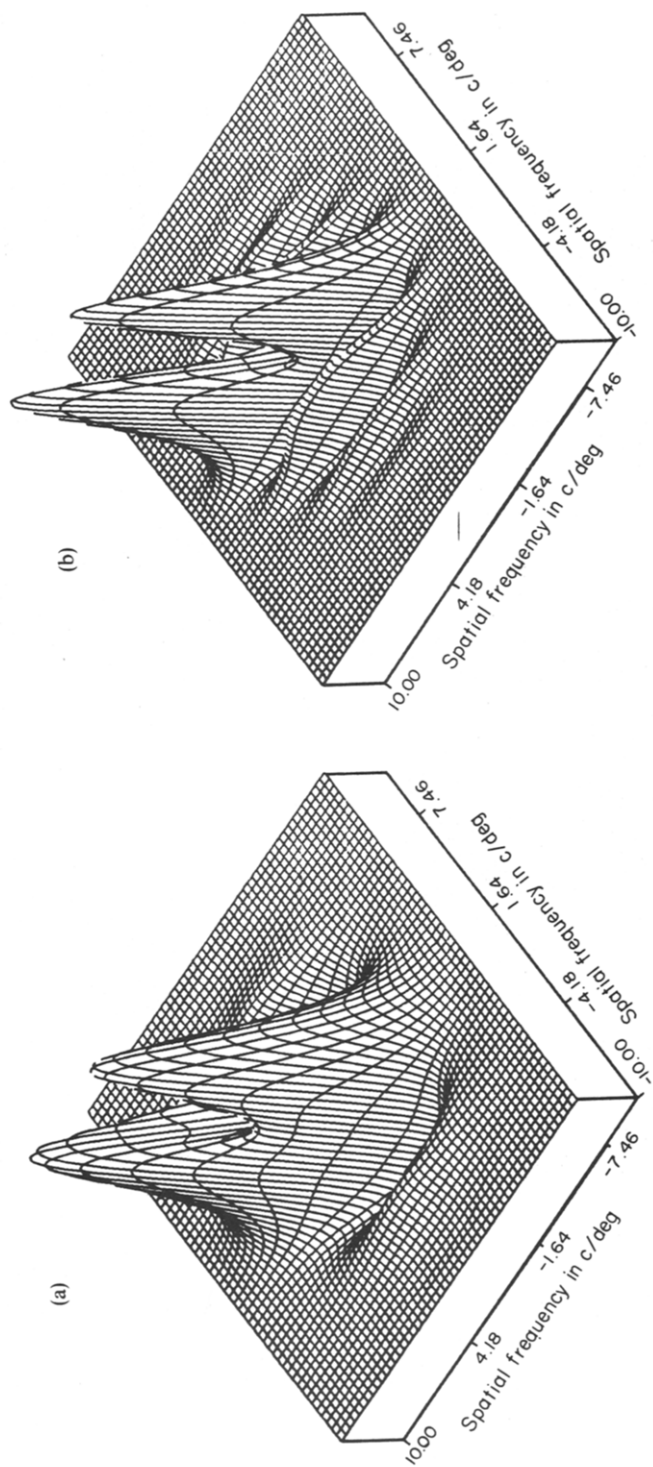
Fig. 2. Two-dimensional Fourier transform of the theoretical receptive field profile of an orientation selective simple cell receiving inputs from (a) three and (b) nine aligned LGN fields. Viewed in polar coordinates, the height of each surface at a point (r, θ) corresponds to the cell's relative response to a sinewave grating having spatial frequency r and orientation θ.

in Fig. 3 show such tuning curves for cortical cells comprised of three and nine aligned and evenly spaced LGN fields, in response to an inclined sine waves grating whose spatial frequency was arbitrarily given the "optimal" value expressed above. Increasing the number of evenly spaced LGN subfields is seen to sharpen and modulate the tuning curve. Geometrically, the curves of Fig. 3 correspond to the intersection of the surfaces in Fig. 2 with an upright cylinder whose radius is the spatial frequency in question. The fact that the model's tuning curves in Fig. 3 are smooth at the top and undulate, is contradicted by the observation of Campbell et al. (1968) and of Ikeda and Wright (1975) that the spike frequency of cat cortical cells decreases linearly with the angle of a sinewave grating away from its optimal orientation.

Rose (1979) provides the results of a numerical simulation of a bar length tuning experiment (in the direction of elongation) for his one-dimensional profile and so that property will not be pursued here, although it should be mentioned that an exact expression in terms of the function erf(x) can be derived for the bar length tuning curve in any orientation and for any two-dimensional arrangement of the LGN units. Such a length tuning curve is a very valuable function to map out empirically, because its derivative (under the assumption of linearity) is precisely the rfp in the direction of bar-lengthening, thus yielding a set of radial cross-sections.

An exact expression for the bar orientation tuning curve may be derived via equations (3) and (5) plus the fact that the two-dimensional spectrum of a long, thin bar inclined at some angle $\theta' - \frac{\pi}{2}$ is itself a line, expressible in polar coordinates by a delta function of orientation: $S(r, \theta) = \delta(\theta^1 - \theta)$. (If the stimulus were described with finite width and length, or if one were interested in a "bar width" tuning curve, the stimulus

Fig. 4. Bar orientation tuning curves for the theoretical cortical cells described in the text and in Figs 2 and 3. The curves correspond to equation (6).

spectrum would be described by sinc functions.) By inserting equation (5) into a polar version of equation (3) it emerges that the bar orientation tuning curve for the cortical cell whose inputs come from some random distribution of n LGN fields scattered around in loci (x_i, y_i) is

$$f(\theta') = \frac{A\pi^{3/2}}{a} \sum_{i=1}^{n} e^{-\pi^2 a^2 [x_i \cos(\theta') + y_i \sin(\theta')]^2}$$

$$- \frac{B\pi^{3/2}}{b} \sum_{i=1}^{n} e^{-\pi^2 b^2 [x_i \cos(\theta') + y_i \sin(\theta')]^2} \qquad (6)$$

where $\theta' - \frac{\pi}{2}$ is the bar orientation. Figure 4 shows plots of equation (6) for the same two cases of three and nine component subfields that have been depicted throughout. The adequacy of the alignment model in this respect, for predicting empirical bar orientation tuning curves, is quite high.

It should be emphasized that the foregoing spectral analysis of the alignment model has shown that the preferred orientation both of a bar of light and of a sinewave grating with arbitrary spatial frequency is always in the direction of alignment (with the exception of certain "special" spatial frequencies if the LGN fields are evenly spaced, in which case there exist multiple equally preferable orientations as revealed by the submaxima in Fig. 2). The property that there never exists an absolutely preferred orientation other than that of alignment, for any spatial frequency, is by no means true of all plausible models of cortical rfp's, surprisingly, as will be seen in Fig. 5.

Two alternative and plausible models for orientation selective cortical rfp's are depicted in Fig. 5, along with their respective Fourier transforms. (The details of functional form for these elliptical Gaussians will not be pursued here, but it should be mentioned that for these models, also, spectral methods permit the derivation of predictive tuning curves for bar length, bar orientation, and grating frequency, orientation, and phase.) The outstanding difference
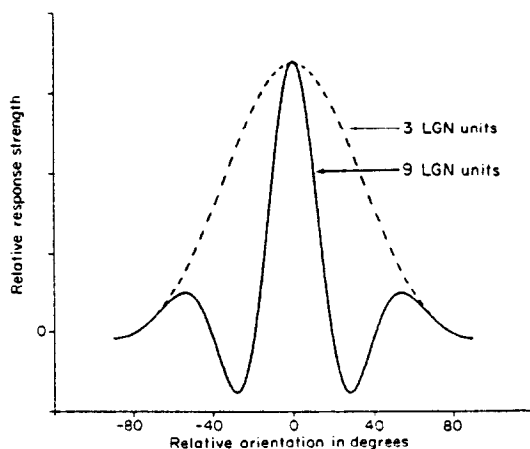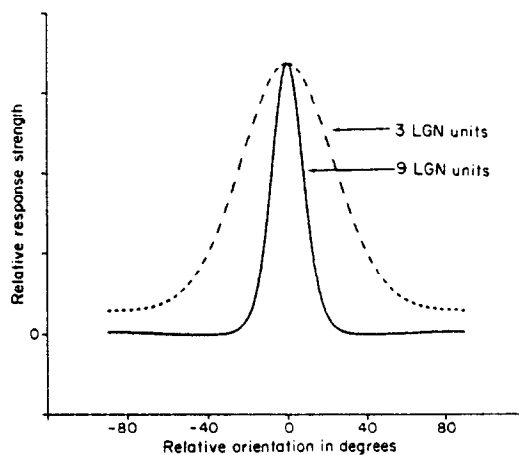

Fig. 3. Grating orientation tuning curves for the theoretical cortical cells described in the text and in Fig. 2. The curves correspond to equation (5) with spatial frequency held constant at the value to which the cell gives its overall best response in the preferred bar orientation.

(a)

Excitability profile

2-D Fourier transform of profile

(b)

Excitability profile
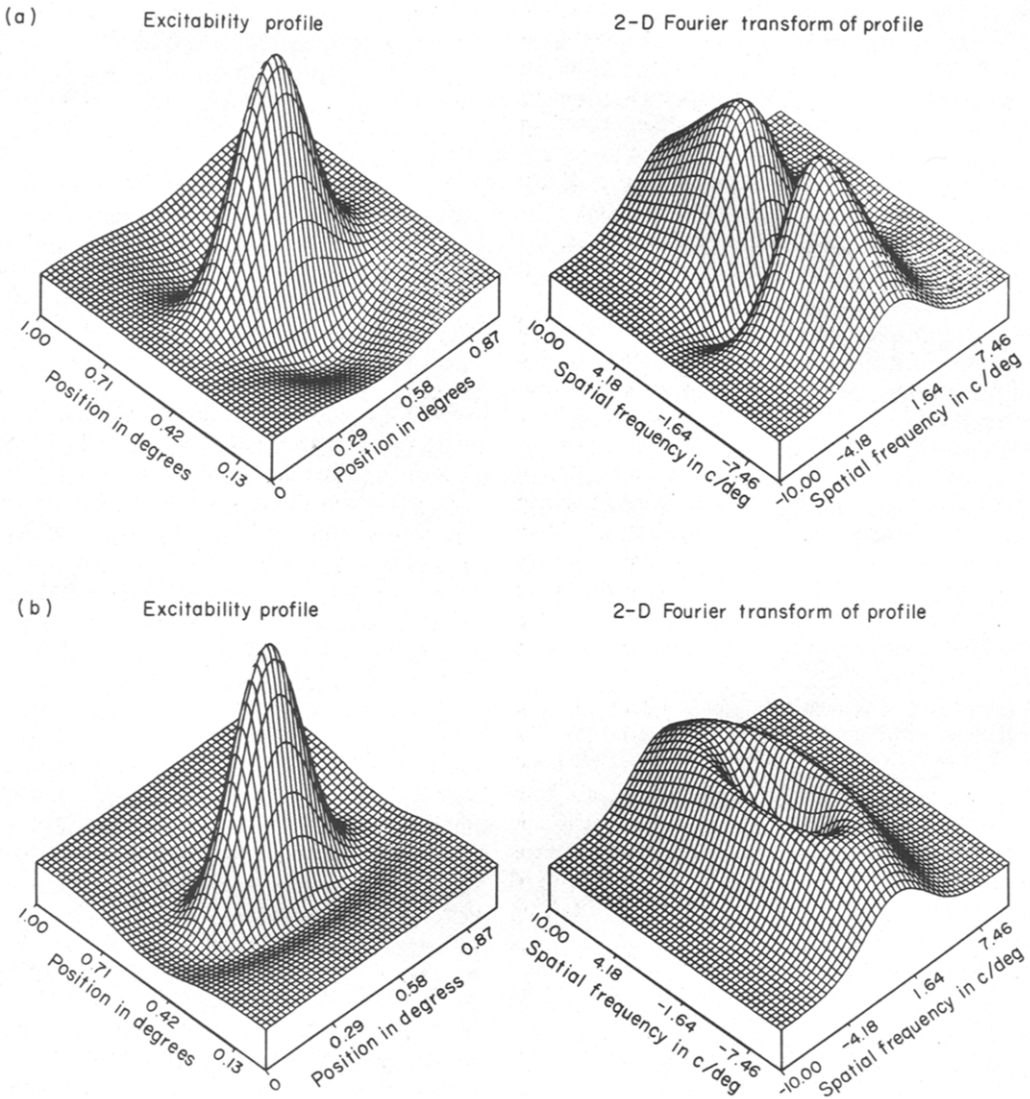
2-D Fourier transform of profile

Fig. 5. Two alternative models of elongated cortical receptive fields, and their two-dimensional transforms. (a) With inhibition limited to the two flanks, as suggested by Bishop *et al.* (1973), Glezer *et al.* (1973), and Schiller *et al.* (1976), the predicted spectrum is in reasonable agreement with experiments using inclined sinewave gratings. (b) If inhibitory regions extend into the axis of elongation, the profile shown has a spectrum with the unique property that for *every* orientation, there can be found a spatial frequency which will evoke the cell's maximum response for the best grating at *any* orientation. Therefore this theoretical receptive field profile can probably be rejected on spectral grounds.

between the two rfp's in Fig. 5 is that in the first case the inhibitory regions exist only on the two flanks, whereas in the second case the inhibitory regions extend on all sides of the elongated excitatory zone. This difference produces a dramatic effect on the two spectra. The first spectrum, which grossly resembles those of Fig. 2 in having two main peaks, indicates that for sinewave gratings inclined perpendicular to the preferred orientation there is no spatial frequency which evokes much response. However, the spectrum of the second receptive field indicates that for *every* orientation, there can be found a frequency which will evoke the maximal response possible for *any* orientation. *In other words, this is an example of an elongated receptive field which has no "preferred" orientations for sinwave gratings; all orientations will do equally well, provided the frequency changes accordingly.* (See footnote* for a clarification of the family of rfp's whose "elongation" renders them sharply selective for bar orientation but not at all selective for grating orientation, as in the case of Fig. 5b.)

Although the elongated profile of Fig. 5b looks plausible enough in the space domain, it can probably be rejected on spectral grounds. It has generally been reported (Campbell *et al.*, 1968; Ikeda and Wright, 1975; DeValois *et al.*, 1979) that the response of cortical cells to gratings orthogonal to the preferred bar orientation is nil, although in none of these

studies was frequency varied systematically at each orientation as would be required conclusively to reject the kind of profile in Fig. 5b. It is difficult to prove mathematically, but some exercise of intuition while inspecting Fig. 5 suggests that nil response to orthogonal gratings of *all* spatial frequencies would not be obtained if, as in Fig. 5b, there were significant inhibitory flanks extending also into the axis of elongation. This relationship between the locations of inhibitory zones and the response to inclined gratings emphasizes the importance of incorporating spectral considerations when modelling rfp's.

For the reasons illustrated above, it would be very useful in neurophysiological recordings to map out the regions of the Fourier plane in which cells are responsive. "Iso-sensitivity contours" of the sort shown in Fig. 1d, but instead in the Fourier plane, would provide important constraints in physiological model building and would also help build a bridge to the body of results from psychophysics. If points in the Fourier plane were connected which correspond to stimuli evoking a constant amplitude neural response, the resulting iso-sensitivity contours would correspond to the intersection of the two-dimensional Fourier transform of the cell's rfp with a horizontal plane whose height is the response criterion adopted by the experimenter. DeValois *et al.* (1977) presented their data for inclined gratings in this form, and it was apparent that the cells had a "localized responsiveness" in the Fourier plane. If one begins with this constraint as the essential characteristic of cortical cells, and if one models this property as in Fig. 6b with displaced spectral Gaussians, then inverse Fourier transformation yields the corresponding space domain rfp shown in Fig. 6a. The periodic structure of this rfp is consistent with the observations of several investigators that both simple and complex cells show "a distinctly periodic structure, with additional sidebands beyond those seen in the initial studies..." (DeValois *et al.*, 1979, p. 484; see also Pollen and Ronner, 1975).

The two-dimensional rfp of Fig. 6, whose functional form corresponds to a spatial "tone-burst" within a Gaussian envelope, comes close to possessing the property that spatial frequency and orientation are separable variables. The mechanisms of Figs 1–5, however, stand in stark contrast: they would subserve "channels" responsive to frequency bands which depend on orientation, or stated another way, responsive to orientation bands which depend on frequency. Because this issue of separability remains (through inattention) unresolved, it may be meaningless to refer simply to a "channel's center frequency"; we have seen in Figs 1–5 that the spectra of physiologically plausible rfp's have bandwidths and center frequencies which depend on orientation. With few exceptions (e.g. Blakemore and Nachmias, 1971; Mostafavi and Sakrison, 1976), this point seems to have been overlooked in psychophysics, perhaps because of the longstanding use of *uniformly oriented* (namely verti-

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* There exists a general family of elongated receptive field profiles which are orientation selective for bars but not for gratings, meaning that their response to gratings has the property that for *every* orientation, a frequency may be found which will evoke the maximum response possible for the best grating at *any* orientation. One family of rfp's possessing this property consists of those functions whose two-dimensional Fourier transforms $F(u, v)$ may be expressed in polar coordinates such that $F(r, \theta) = F[a(\theta)r, o]$ for some anisotropy function $a(\theta)$. Thus, all radial cross-sections of such spectral surfaces are identical except for a factor which scales the r coordinate by a constant; this constant depends on the θ coordinate and it specifies how spatial frequency must change with orientation in order to maintain a given response amplitude. (Clearly, such spectra are not separable into a product function $F[r, \theta] = G[r]H[\theta]$.) An example of two-dimensional functions possessing this property of radial scaling is the family of elliptical Gaussians, an illustration of which is seen in Fig. 5b. The integral of the profile along any radial line is positive and depends on orientation, and therefore the profile is selective for bar orientation; but the maximum of the spectrum is a continuous locus of points, so no grating orientation is *absolutely* preferred (except for at a *particular* frequency.) For the spectral surface shown, the anisotropy function is

$$a(\theta) = \sqrt{\cos^2(\theta) + x^2 \sin^2(\theta)}$$

where the elongation (eccentricity) of the elliptical Gaussians is 1-α.

The theoretical existence of such families of receptive field profiles, which have a strong preference for grating orientation but no general preference for grating orientation, reveals the folly of drawing inferences about spectral "orientation channels" on the grounds of neurophysiological tuning curves for inclined bars.

(a) Excitability profile

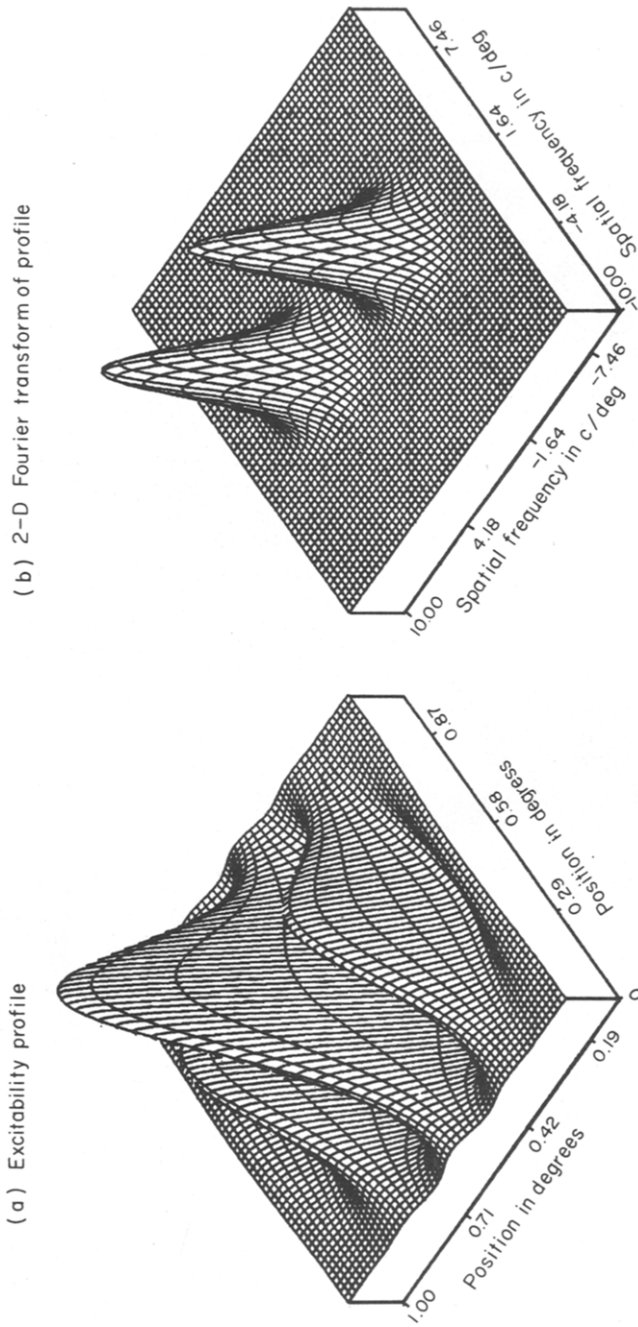(b) 2-D Fourier transform of profile

Fig. 6. (a) Model of a receptive field profile as a spatial tone-burst, and (b) its two-dimensional Fourier transform. The model captures the property of "periodic excitability" as described for both simple cells and complex cells by DeValois *et al.* (1979) and Pollen and Ronner (1975), as well as the spectral property of "localized responsiveness" in the Fourier plane, as described by DeValois *et al.* (1977, 1979).

cal) sinewave gratings. Likewise, neurophysiological experiments employing gratings inclined only in the cell's preferred bar orientation invite misleading conclusions. Because the theoretical connection between spatial frequency and orientation has been largely neglected up to the present time, much "channel" modelling of how the two-dimensional retinal image is analyzed has been, in large measure, effectively a one-dimensional discussion.

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