

Mathematical description of the responses of simple cortical cells*

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On the basis of measured receptive field profiles and spatial frequency tuning characteristics of simple cortical cells, it can be concluded that the representation of an image in the visual cortex must involve both spatial and spatial frequency variables. In a scheme due to Gabor, an image is represented in terms of localized symmetrical and antisymmetrical elementary signals. Both measured receptive fields and measured spatial frequency tuning curves conform closely to the functional form of Gabor elementary signals. It is argued that the visual cortex representation corresponds closely to the Gabor scheme owing to its advantages in treating the subsequent problem of pattern recognition.

INTRODUCTION

Simple cells in the visual cortex have spatially localized receptive fields, which consist of distinct elongated excitatory and inhibitory zones. The cells, therefore, respond strongly to specifically oriented lines or edges positioned in their receptive fields. This initial description of simple cortical cells, due to Hubel and Wiesel,¹ captures the basic elements of their receptive field organization. A detailed description of that organization is, however, more complex.^{2,3}

Alternatively, the response of cortical cells can be studied in the spatial frequency domain.^{4,5} It is found that the cells are tuned to specific spatial frequencies, with the bandwidth of the order of one octave. The results are analogous to earlier psychophysical experiments,⁶ which have found evidence that the visual scene is analyzed in terms of independent spatial frequency channels.

The well-defined spatial frequency tuning of simple cortical cells naturally leads to an assumption that the visual cortex acts as a spatial frequency analyzer.⁷ Strictly interpreted, the assumption should mean that the visual cortex performs a two-dimensional Fourier transformation of the visual scene. This, however, could only be partially true, because of the rather large bandwidth of cortical cells. Equivalently, receptive fields of cortical cells are too localized to be able to perform a proper spatial frequency analysis. This difficulty in description is well appreciated,⁸ and is qualitatively expressed by the term "piecewise spatial frequency analysis."

For a linear system, spatial response and spatial frequency response are best described using an analogous language. For simple cortical cells, the experiments point out that the response to a narrow bar stimulus is localized in a spatial receptive field. The response to the analogous stimulus in the spatial frequency domain elicits again a localized response (i.e., the spatial frequency tuning curve). The representation of the image in the visual cortex must, therefore, involve both spatial and spatial frequency variables in its description. It is a representation intermediate between the spatial sampling and the Fourier transformation.

Many mathematical schemes could provide a simultaneous description of the response in both spatial and spatial frequency domains. However, one such scheme due to Gabor⁹ has a special significance. It is the scheme where an arbitrary function is expanded in terms of symmetrical and antisym-

metrical "elementary signals," which have the important property that they are maximally localized in space and in spatial frequency.

The introduction of a mathematically more precise description of visual cortex channels should have many advantages in discussions of visual perception or processing of visual information. But perhaps most important is the fact that description in terms of Gabor signals points out a feature of the visual cortex representation that has not been previously recognized: the simultaneous maximal localization in space and in spatial frequency. This feature is likely to be a significant factor in future understanding of pattern recognition pathways.

The following section gives a brief formal description of the Gabor representation, while the last section gives a comparison between the experimental results on simple cortical cells and the mathematical formalism. Before continuing with that program, it is appropriate to list all the assumptions and approximations that will be used.

A crucial requirement is a linear spatial summation across the receptive field. The linearity properties of visual cortex neurones have recently been reexamined by Movshon *et al.*^{10,11} Since striate cortex neurones do not have much maintained activity, a response to a drifting grating is a rectified sine wave, with the neurones silent for about half the stimulus cycle. Except for that rectification at the output, a great majority of simple cells have shown linear spatial summation. The behavior of complex cells was very far from linear. Background activity of cortical cells can be increased by the addition of visual noise to the stimulus pattern.¹² In those conditions, the behavior of simple cells was found to be linear.

Since different spatial orientations of the stimuli correspond to independent channels, the analysis can be approximately discussed as a one-dimensional problem. For simple cells, that approximation is justified by the absence of strong inhibition or other unusual properties in the end-zone region.¹³

A number of other important properties of the response of simple cells could not be taken into account in this initial analysis. These include a preferred direction of the stimulus movement, coding of color information, or actual neural connections that give rise to the measured receptive fields.

Nevertheless, if basic elements of a description of the cortical representation can presently be established, it will be an easier task in the future to complete the scheme with the incorporation of the important features which are currently being omitted.

GABOR REPRESENTATION

In the Gabor representation⁹ an arbitrary function $F(x)$ is expanded in terms of symmetrical and antisymmetrical elementary signals

$$S_s(x) = \exp[-(x - x_m)^2/4\sigma^2] \cos[2\pi f_n(x - x_m)], \quad (1a)$$

$$S_a(x) = \exp[-(x - x_m)^2/4\sigma^2] \sin[2\pi f_n(x - x_m)]. \quad (1b)$$

The signals shown above are centered at the position $x = x_m$ and the spatial frequency $f = f_n$, with the Gaussian envelope described by the standard deviation σ .

For any signal, one can define the effective spread of a signal in space as

$$\Delta x = [2\pi \overline{(x - \bar{x})^2}]^{1/2}, \quad (2a)$$

and the effective spread in spatial frequency (or the frequency width) as

$$\Delta f = [2\pi \overline{(f - \bar{f})^2}]^{1/2}. \quad (2b)$$

The horizontal bars denote average values, and the numerical factors of 2π have been introduced in order to obtain an exact correspondence between area occupied in the x - f space and the information-carrying capacity of the signal. The Gabor elementary signals then satisfy

$$\Delta x \Delta f = 1/2, \quad (3)$$

while for any other function, $\Delta x \Delta f > 1/2$.

In the following brief description of the expansion in terms of elementary signals, it is convenient to use complex notation and write the normalized signal as

$$\psi(x; x_m, f_n) = (2\pi\sigma^2)^{-1/4} \exp[-(x - x_m)^2/4\sigma^2 + 2\pi i f_n(x - x_m) + i\phi]. \quad (4)$$

An arbitrary function $F(x)$ is then represented as a sum over the elementary signals

$$F(x) = \sum_m \sum_n G_{mn} \psi(x; x_m, f_n). \quad (5)$$

x_m and f_n are regularly spaced, with the sampling density conforming to the sampling theorem. In the original work, Gabor did not discuss the question of completeness of the set of functions $\psi(x; x_m, f_n)$ or present an expression for evaluation of the coefficients G_{mn} . This has resulted in some confusion, where several authors¹⁴⁻¹⁶ have considered the Gabor expansion to be an approximate representation of the original function.

However, expansion in terms of functions $\psi(x; x_m, f_n)$ has a long history. It was used by von Neumann,¹⁷ who also has stated that the set $\psi(x; x_m, f_n)$ is complete. An exact continuous version of the same expansion is well known in quantum optics¹⁸ and in information theory.¹⁴⁻¹⁶ It is easily proven that the function $F(x)$ can be exactly represented as an integral over the elementary signals¹⁴

$$F(x) = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} g(x_m, f_n) \psi(x; x_m, f_n) dx_m df_n, \quad (6)$$

where the expansion function $g(x_m, f_n)$ is given by

$$g(x_m, f_n) = \int_{-\infty}^{\infty} \psi^*(x; x_m, f_n) F(x) dx. \quad (7)$$

In the case of discrete expansion, the standard way of determining the coefficients G_{mn} is to multiply Eq. (5) by $\psi(x; x_p, f_q)$ and integrate over x . This leads to a set of linear equations for G_{mn} in terms of $g(x_m, f_n)$

$$g(x_m, f_n) = \sum_p \sum_q \left(\int_{-\infty}^{\infty} \psi^*(x; x_m, f_n) \psi(x; x_p, f_q) dx \right) G_{pq}. \quad (8)$$

If density of positions x_m and frequencies f_n is higher than or equal to that given by the sampling theorem, the set $\psi(x; x_m, f_n)$ is complete and the Gabor expansion scheme is exact.^{19,20} The scheme is also applicable with a nonperiodic spacing of mean positions and mean spatial frequencies, as long as the requirement that elementary cells of area $\Delta x_m \Delta f_n = 1/2$ associated with each sampling point cover all of the required region in x - f space.

Since distant signals have no overlap, and neighboring signals have only a weak overlap, the major contribution to the sum in Eq. (8) comes from the $p = m, q = n$ term. It follows that

$$G_{mn} \simeq g(x_m, f_n). \quad (9)$$

However, for the present purpose it is sufficient to note that the coefficients $g(x_m, f_n)$ contain full information about the function $F(x)$.

COMPARISON WITH EXPERIMENTS AND DISCUSSION

In the visual cortex, information about the visual world is represented in an abstract form, as a set of excitation levels of different cells. The excitation levels are obtained through a convolution of the visual scene with a receptive field of the corresponding cell. If the visual cortex representation were identical to one of the two familiar schemes, those excitation levels would correspond to spatial samples of the visual image, or to two-dimensional Fourier coefficients of the image.

The same general principles are valid for a representation in terms of the Gabor expansion, Eq. (5). The excitation levels should then correspond to the coefficients of the expansion, and according to Eq. (7) receptive fields should have the form of Gabor elementary signals, Eq. (1).

Elementary signals have the same functional form in terms of either spatial or spatial frequency variables. In other words, a Fourier transform of the spatial receptive field, Eq. (1) has again the same functional form of a product of a Gaussian function and a sine or a cosine function. However, as noted in the Introduction, only a positive part of the stimulus cycle is normally observed. In most experiments with a drifting grating, the spatial phase is not recorded. In that case, one would measure only a Gaussian envelope of the corresponding elementary signal.

A number of experimental studies on simple cortical cells could now be examined in order to find out if the cortical

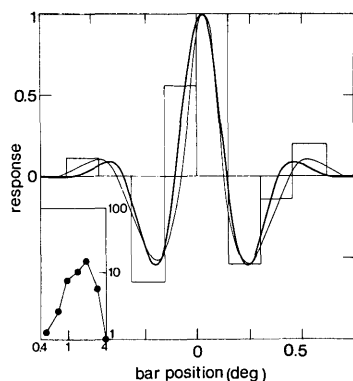


FIG. 1. Comparison of the experimentally measured response of a simple cell in the visual cortex [Movshon *et al.*, Ref. 10, Fig. 9(b)] and the functional form of the elementary signal, Eq. (1a). A response measured in the spatial domain (histogram) and in the frequency domain (inset, spatial frequency scale in cycles/deg) is compared with a theoretical functional form (heavy line). A symmetrical Fourier transform of the measured frequency response is shown as a thin line (Movshon *et al.*, Ref. 10). Both spatial response curves have been translated sideways arbitrarily to fit the data. Least-squares-fit parameters: $f_n = 2.00$ cycles/deg; $\sigma = 0.15$ deg ($\Delta f = 1.31$ cycles/deg).

representation is close to the Gabor expansion. First, it should be noted that Gabor elementary signals correspond to symmetrical receptive fields and antisymmetrical receptive fields. Such fields are experimentally found; the importance of that fact has been emphasized by Tolhurst.²¹

The response of cortical cells to different spatial frequencies has been reported in a number of studies.^{4,6,7,22} The earlier reports did not distinguish, or did not fully distinguish, between different cell types. Nevertheless, spatial frequency tuning curves that come very close to the expected Gaussian envelope of a Gabor signal have been recorded in most of the experiments. Ikeda and Wright²² distinguish between simple-sustained and simple-transient cortical cells. The responses of simple-sustained cortical cells (Fig. 2 of Ref. 22) are very well described by a Gaussian functional form.

Few recent studies where both spatial and spatial frequency responses have been measured on the same cells are particularly useful for comparison with the theory. Figures 1 and 2 show a least-squares fit of the functional form Eq. (1) to the experimental results on simple cortical cells of the cat.¹⁰ A

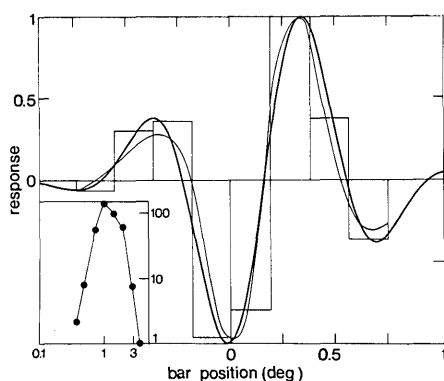


FIG. 2. Comparison of a response of a cell with an antisymmetric receptive field [Movshon *et al.*, Ref. 10, Fig. 9(d)] and the elementary signal, Eq. (1b). The notation corresponds to that in Fig. 1. Least-squares-fit parameters: $f_n = 1.27$ cycles/deg; $\sigma = 0.27$ deg ($\Delta f = 0.73$ cycles/deg).

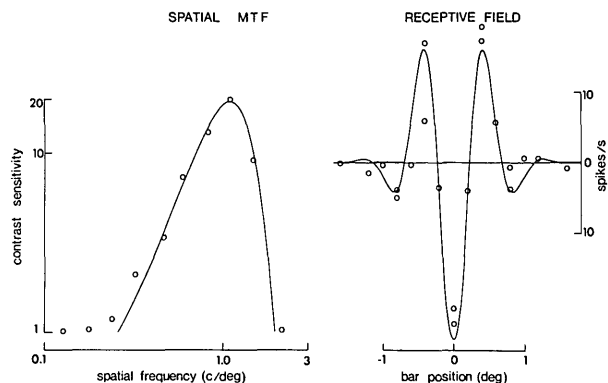


FIG. 3. Comparison of the response of a simple X cell from a monkey visual cortex (De Valois *et al.*, Ref. 24, Fig. 4) and the functional form of Gabor elementary signals. A least-squares-fit to the contrast sensitivity data as a function of spatial frequency is shown on the left-hand side. A Fourier transform of the elementary signal that fits the contrast sensitivity data is shown on the right-hand side, together with the measurements of a response to a narrow bar stimulus. Mean spatial frequency and width of a Gaussian envelope are determined from the fit to the contrast sensitivity data; normalization and horizontal translation of the transformed elementary signal are arbitrary. Least-squares-fit parameters: $f_n = 1.09$ cycles/deg; $\sigma = 0.24$ deg ($\Delta f = 0.61$ cycles/deg).

shifted Gaussian curve was fitted to the data points in the frequency domain, and its symmetrical or antisymmetrical Fourier transform was plotted together with the measured spatial response. In the case of a symmetrical receptive field the procedure has slightly overestimated the mean spatial frequency, but otherwise the agreement between the measured and the theoretical functional form is excellent.

In another recent work on simple cortical cells of the cat, Andrews and Pollen²³ have measured for several cells both the amplitude and the phase of the response to a drifting grating. In principle, such measurements contain more information on the cell response. Unfortunately, the authors do not show the measured phase for any of the simple-sustained cells. Their measurements in the spatial domain are only qualitative, and the comparison with their data is thus less conclusive.

Spatial and spatial-frequency responses of simple cortical cells of the monkey have been described by De Valois *et al.*²⁴ Their data on the spatial frequency tuning and receptive field of a simple X cell have been compared with the functional form of Gabor elementary signals in Fig. 3. A very close agreement suggests again the advantage of a description of the visual cortex representation in terms of the Gabor expansion.

In the most recent work, Maffei *et al.*¹² have measured responses of simple cortical cells to a passage of a narrow bar or a sinusoidal grating stimulus in the presence of a visual noise. The superimposed visual noise ensures a background activity of a cell, which was found to lead to a linear behavior. Experimental results, which are similar to those of Ref. 10 or Ref. 24, are again in very good agreement with the functional form of Gabor elementary signals. Maffei *et al.*¹² also present a compelling argument to the effect that descriptions of simple cortical cells in terms of spatial feature detectors or in terms of spatial frequency channels are not contradictory. This fact is formally expressed in the Gabor representation scheme,

which is symmetrical in spatial and spatial frequency variables.

Why should the visual cortex analyze information in terms of Gabor elementary signals? I believe that the answer must be sought in the particular property of Gabor signals to provide the best *local* description of the most important elements of the image. Let us consider a typical visual scene, which largely consists of lines and edges interspersed with areas of uniform illumination. The information that is crucial in the task of pattern recognition is contained in the data on positions and orientations of lines and edges. Extraction of such data is the first task in current engineering efforts in artificial pattern recognition systems. In the Gabor representation, a localized edge or line stimulus will elicit a response from only a few cells. With either pure spatial sampling or pure frequency analysis, an identical stimulus would elicit a response from many cells. In the language of pattern recognition theories (e.g., Ref. 25) the representation in terms of elementary signals provides a powerful method of extraction of significant features in the visual world.

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