

The relationship between the Gabor elementary function and a stochastic model of the inter-spike interval distribution in the responses of visual cortex neurons

D. H. Berger and K. H. Pribram

Center for Brain Research and Informational Sciences, Radford University, Box 6977, Radford, VA 24142, USA

Received November 6, 1991/Accepted in revised form January 17, 1992

Abstract. In a previously reported study (Berger et al. 1990) we analyzed distributions of interspike intervals recorded extracellularly from cat visual cortex under four stimulus conditions. Stimuli were gratings differing in orientation and spatial frequency. The probability density function of first passage time for a random walk with drift process, which is defined by its barrier height and drift coefficient, was used to characterize the generating process of axonal discharge under resting and stimulus conditions. Drift coefficient and barrier height were derived from the sample mean and standard deviation of the measured inter-spike intervals. For cells with simple receptive fields, variations in spatial frequency produced changes only in drift coefficient. Variations in barrier height were produced only by changes in orientation of the stimulus. Currently, the method used to analyze these data was implemented in a simulation which displayed the relationship between the interval distribution of impulses, the random walk which represents the time series characteristic of the spike train model and the Gabor filter function which represents the geometry of the receptive field process.

Introduction

Spike trains recorded from visual cortex neurons reflect three separable influences: 1) those, such as the sensory stimuli which characterize the input to the neuron 2) those which parameterize the properties of the ensemble of dendritic activities of the neuron, and 3) those which directly determine the output of the neuron at the axon hillock (Pribram et al. 1981).

For a given stimulus condition a dendritic environment is generated from the excitatory and/or inhibitory character of the dendritic events. The assignment of a weighted rate process to the events of this dendritic microprocess reflects their degree of influence on the

generating of spikes by the cells being examined. The neuron is thus conceived as a processor of stochastic dendritic events which displays its computed output as the statistics of the sequence of inter-spike intervals.

The cells studied in a previous report (Berger et al. 1990) were sufficiently stationary to be analyzed by the spike interval distributions. Such distribution can be used to determine a derived barrier height and drift coefficient process. The first two moments of the sample distribution are sufficient to characterize the underlying diffusion process if stationarity is observed. This property is indicated by the time invariance of the inter-spike interval distributions for a given stimulus condition.

The analyses made in the previous study indicated that inter-spike interval distributions change with different inputs and do this in a consistent and reproducible manner. The changes were reflected in the probability density of the first passage time of the underlying process. Interpretation of these changes was made in terms of a random walk with drift model. The analysis showed that, in the sample of cells studied, the variation of spatial frequency changed only the drift coefficient and that barrier height was changed only by changes in orientation.

The current analysis is undertaken to bring the results of the earlier analysis into formal register with the functional properties of the dendritic fields of visual cortical neurons described by the Gabor filter response (Pribram and Carlton 1986). The Gabor elementary function was initially derived from the fact that the dendritic field of a cortical neuron is spatially limited and that edges produce a greater neural response than would be predicted by a simple Fourier transform of the spatial and temporal frequency characteristics of a grating (Marcelja 1980; Kulikowski et al. 1982). This formulation was supported by the finding that neurons within the same cortical column respond to the cospectrum and quadspectrum i.e., the quadrature of the phase changes produced by the drifting gratings (Pollen and Ronner, 1980). The formulation was generalized to two dimensions to include the role of

orientation of the grating in changing the response of the cortical neuron (Daugman 1980, 1085, 1988).

Pribram (1991, p. 68) has suggested that this formulation can be related to the Gabor filter function which represents the geometry of the receptive field. The signature of coefficients that characterize drift rate can be conceived to represent the coherence among the frequencies of fluctuations of polarizations in the dendritic receptive field. When these coefficients are cross multiplied by probabilities which represent amplitudes, boundary conditions are determined by the orientation of the stimulus display. The result is a probability amplitude modulated set of Fourier coefficients which describe a class of four-dimensional informational hyperspaces such as Hermite polynomials constrained by Gaussians, of which the Gabor function is an elementary example.

The following account provides a formal delineation of this model by virtue of a simulation performed on a computer.

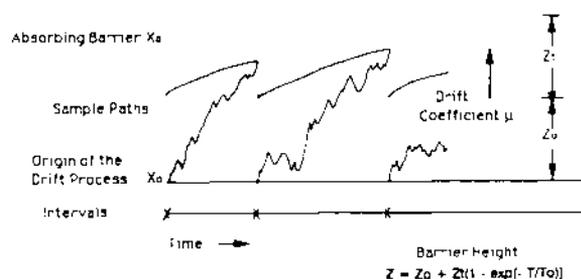
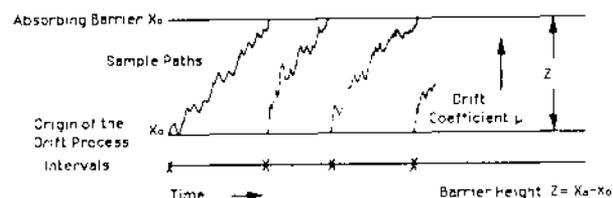
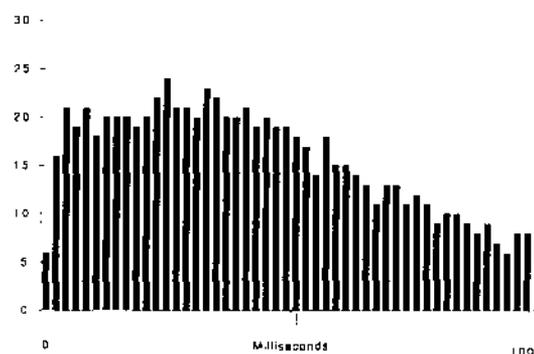
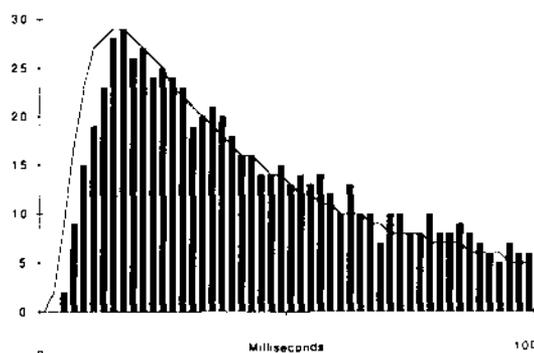


Fig. 1. a Random walk with positive drift is illustrated for drift coefficient μ and barrier height Z . The first passage time of this process generates the intervals that correspond to inter-spike intervals of neural action potentials. The process starts with a random walk at the origin X_0 . It proceeds to the absorbing barrier X_a with a drift rate determined by the drift coefficient μ . When the absorbing barrier is reached the process is restarted and another walk is initiated. The first passage time defines an interval that corresponds to the time between occurrences of action potentials in extracellularly recording neurons. The analytic solution for the probability distribution function is shown in the right hand side of **a**, imposed on the simulated histogram for a drift coefficient

The formal model

Features of the dendritic computation are reflected in the statistical properties of neural spike-trains (Kryukov 1978; Kirilov et al. 1989; Pribram 1991, Lecture 1). The simulation performed here is based on the finding that the dendritic receptive field is tuned to approximately an octave of spatial frequency and is selective in its response to the orientation of the sensory input (Campbell and Blakemore 1969; DeValois et al. 1985; Lassonde et al. 1981). The orientation of the sinusoidally varying input of the simulation represents the drifted dark and light bars of the gratings used during the actual experiments; the output represents the interresponse interval distributions actually recorded.

The simulation begins by modeling the relation between input and output with a fixed barrier height. At the process origin, X_0 , random walk with positive drift proceeds toward the absorbing barrier at X_a (Fig. 1a). The distance from the origin to the absorbing



$\mu = 0.1$ and a barrier height $Z = 10.0$ which are typical for cortical neurons. **b** The added structure of the moving boundary simulates the existence of channel kinetics which differentiate different neurotransmitter types. In this case a moving barrier is a function of time and is reset at each first passage event. This produces a distinctly different form of histogram that closely resembles measured inter-spike interval histograms from visual cortical cells. The values of the added parameters can be determined from least-square analysis of inter-spike interval histograms of extra-cellularly recorded cortical neurons. The case illustrated in the right hand side of **b** is for $Z_0 = 4.0$, $Z_1 = 10.0$, $T_0 = 12.0$ and $\mu = 0.20$. 10,000 intervals were simulated for both histograms

barrier, $Z = X_a - X_o$, defines the barrier height (Tuckwell 1976). When the absorbing barrier is reached an event is recorded that indicates a temporal interval in analogy to the interval between occurrences of an action potential in a neuron. The statistical properties of these intervals are described by the stochastic differential equation (Kolmogorov forward equation)

$$\frac{\partial P}{\partial T} = -\mu \frac{\partial P}{\partial X} + \frac{\sigma^2}{2} \frac{\partial^2 P}{\partial X^2} \quad (1)$$

The drift coefficient μ , barrier height, Z , and the normalized variance parameter, $\sigma^2/2 = 1.0$ characterize the probability density function of the first passage time of random walk with positive drift which is given by the following expression.

$$P(\mu, Z, \sigma, T) = \frac{Z}{\sqrt{2\pi\sigma T^{3/2}}} \exp\left\{-\frac{(Z - \mu T)^2}{2\sigma^2 T}\right\} \quad (2)$$

The mean rate for this process is given by

$$R_m = \mu/Z \quad (3)$$

The Hodgkin-Huxley model has been found to yield the Kolmogorov forward equation for a variety of such noise models of input currents (Tuckwell 1986).

A modification of the model using a moving barrier was then implemented. This modified model resulted in interspike interval histograms that more closely resemble the measured data from actual neurons when compared by least square error between the simulated and the experimentally observed interspike interval histogram. The barrier height in the modified model is time dependent and is reset to an initial value of Z_o at each occurrence of an absorbing event. This modification to the process is seen in Fig. 1b and is referred to as a moving barrier model. The barrier height for this model process is determined by

$$Z = Z_o + Z_i(1 - \exp(-T/T_o)) \quad (4)$$

This added structure is motivated by the following observations. The barrier height can be considered an analog of the dendritic membrane potential and is reset after each depolarization. However, a consequence of channel kinetics is to produce a characteristic time constant, T_o , for this reset process to be achieved. Whole-cell noise analysis has found a time constant of a single exponential fit for glutamate receptors of approximately 5 ms and approximately 20 ms for GABA receptors (Cull-Cand and Usowicz 1989). Other investigators have found similar values in different preparations (Barker and Owen 1986). Membrane potential shifts have been found to be associated with GABA-activated channels and their associated chloride reversal potentials (Williams et al. 1989). These features are incorporated into the model as shifts in the barrier height parameter and result in the observed signatures of orientation change resulting in barrier height shifts from presumed GABA mediated inhibition.

An explanation of the interaction of spatial frequency and orientation on the response of cortical neurons can now be made in terms of these findings.

Excitatory glutamate receptors could be involved in the suppression of non-optimal spatial frequency. However, an additional mechanism would be required to account for orientation selectivity (Ramoia et al. 1986). This additional mechanism has been demonstrated to be GABA related (Sillito et al. 1980). Thus, it is possible that glutamate receptors in the synapto-dendritic receptive field determine drift rate in our model while GABA determines the (barrier) height of the moving boundary.

The Gabor function

The drift coefficient and barrier height parameters as functions of spatial distribution and orientation will now be shown to be consonant with the Gabor elementary function. The analysis is based on the assumption that the inputs to dendritic receptive fields are transformed into a specific drift coefficient and barrier height that in turn produce a characteristic configuration of neuronal-spike interval histogram.

In our previous study changes in spatial frequency were indexed solely by changes in drift coefficient. While change in barrier height is determined only by orientation. Here an indexing method is used to simulate the same model of influencing the distribution of the output. A ten second sequence of intervals is modeled by an algorithm that simulates the inter-spike intervals by a random walk to the moving barrier. The overall behaviour of the model can be seen in effects of orientation change (Fig. 2a) and change in spatial frequency (Fig. 2b). The effect of non-optimal orientation on spatial frequency tuning and non-optimal spatial frequency on orientation responses are seen to reflect measured characteristics (Webster and DeValois 1985).

There is thus a constant set of parameters for the barrier height for a given orientation; the drift coefficient is generated from the spatial frequency. The variations of drift coefficient and the orientation parameters for the barrier height are shown in the following equations

$$Z_o(\theta) = 2.0 \cos(|\theta| - \pi/2) + 3.0 \quad (5)$$

$$Z_i(\theta) = 2.0 \cos(|\theta| - \pi/2) + 3.0 \quad (6)$$

$$T_o(\theta) = 7.0 \cos(|\theta| - \pi/2) + 8.5 \quad (7)$$

$$\mu(\theta, f) = 0.2 \exp(-2.0\theta^2) \exp(-4.0(f-1)^2) \quad (8)$$

In these equations, the inputs are temporally fixed and a continuous stream of outputs of inter-spike intervals are generated by the model neuron. The calculated drift coefficient and barrier height values are then used in the simulation to generate the interspike intervals that constitute the output. Different spatial frequencies of input are used to produce different response rates for different normalized input spatial frequencies. Surrounding flanks simulate inhibition by decreasing the incremental value of the drift coefficient for the edges of the regions examined. This reflects the spatial property of the receptive field and therefore selectivity represents the orientation in our simulation. The μ parameters of

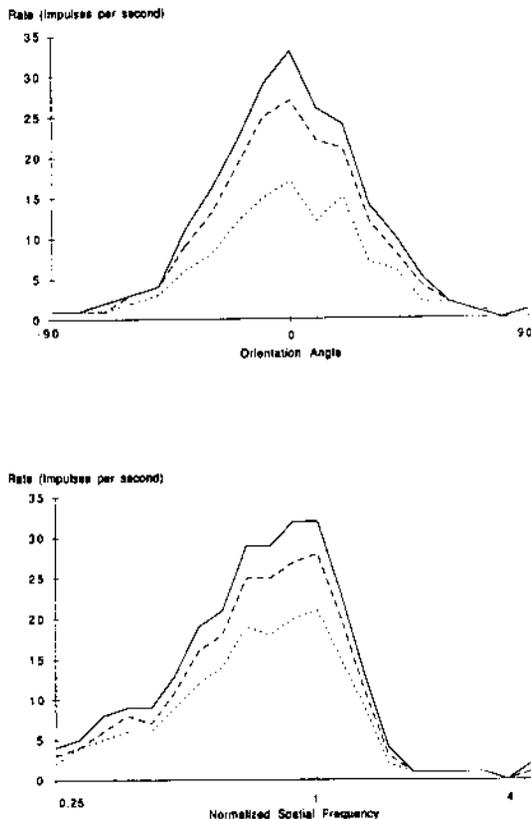


Fig. 2. **a** The model output for the case of variable orientation using the model described in the text. Two additional cases for non-optimal spatial frequency are also seen. The tuning curve is characteristic of one type of receptive field in the visual cortex. The variations of the barrier height with orientation change are given in the text. **b** The drift coefficient of the model neuron was calculated from the filter function of the Gabor model. The normalized spatial frequency of 1.0 corresponds to the optimal case of best alignment at the characteristic frequency and yields the highest drift coefficient. This results in the highest rate of output interval generation. The response of the filter is seen as the average rate of the unit outputs for the normalized spatial frequency. Two conditions of non-optimal orientations are also illustrated in the figure

each neuron are thus determined by the center-excitation, flank-inhibition configuration of the Gabor filter function.

References

- Barker JL, Owens DG (1986) Electrophysiological pharmacology of GABA and diazepam in cultured CNS neurons. In: Olsen CW, Venter IC (eds) Benzodiazepine/GABA receptors and chlorides channels: structural and functional properties. Liss, New York, pp 135-165
- Berger D, Pribram KH, Wild H, Bridges C (1990). An analysis of neural spike-train distributions: determinants of the response of visual cortex neurons to changes in orientation and spatial frequency. *Exp Brain Res* 80:129-134
- Campbell FW, Blakemore C (1969) On the existence of neurons in the human visual system selectively sensitive to the orientation and size of retinal images. *J Physiol* 203:237-260
- Cull-Candy SG, Usowicz MM (1989) Whole-cell current noise produced by excitatory and inhibitory amino acids in large cerebellar neurones of the rat. *J Physiol* 415:533-553
- Daugman JG (1980) Two-dimensional spectral analysis of cortical receptive field profiles. *Vision Res* 20:847-856
- Daugman JG (1985) Uncertainty relation for resolution in space, spatial frequency, and orientation optimized by two-dimensional visual cortical filters. *J Optom Soc Am A* 2:1160-1169
- Daugman JG (1989) Complete discrete 2-d Gabor transforms by neural networks for image analysis and compression. *IEEE Trans Acoust Speech Signal Process* 36:1169-1179
- DeValois RL, Albrecht DG, Thorell LG, (1982) Spatial frequency selectivity of cells in the macaque visual cortex. *Vision Res* 22:545-559
- DeValois RL, Thorell LG, Albrecht DG (1985) Periodicity of striate-cortex-cell receptive fields. *J Optom Soc Am A* 2:1115-1123
- Gerstein GL, Mandelbrot B (1964) Random walk models for the spike activity of a single neuron. *Biophys J* 4:41-68
- Kirilov AB, Borisyuk GN, Borisyuk RM, Kovalenko Yel, Makarenko VI, Chulaevsky VA, Kryukov Vi (1989) A model oscillator for a unified submodule. In: Touretzky DS (ed) *Advances in neural information processing systems*. Morgan Kaufmann, San Mateo Calif pp 560-567
- Kryukov VI (1978) Markov interaction processes and neuronal activity. In: Dold A, Eckmann B (eds) *Lecture Notes in Mathematics*, Vol 653: Locally interacting systems and their applications in biology. Springer, Berlin Heidelberg New York, pp 122-139
- Kulikowski JJ, Marcelja S, Bishop P (1982) Theory of spatial position and spatial frequency relation in the receptive fields of simple cells in the visual cortex. *Biol Cybern* 43:187-198
- Lassonde MC, Püto M, Pribram Kh (1981) Intracerebral influences on the microstructure of visual cortex. *Exp Brain Res* 43:131-144
- Marcelja S (1980) Mathematical description of the responses of simple cortical cells. *J Optom Soc Am* 70:1297-1300
- Pribram KH (1991) *Brain and perception: holonomy and structure in figural processing*. Erlbaum, Hillsdale NJ
- Pribram KH, Carlton EH (1986) Holonomic brain theory in imaging and object perception. *Act Psychol* 63:174-210
- Romoa AS, Shalden M, Skottun BC, Freeman RD (1986) A comparison of inhibition in orientation and spatial frequency of cat visual cortex. *Nature* 321:237-239
- Shapley R, Lennie P (1985) Spatial frequency analysis in the visual system. *Ann Rev Neurosci* 8:547-583
- Sillito AM, Kemp JA, Milson JA, Berardi N (1980) A re-evaluation of the mechanisms underlying simple cell orientation selectivity. *Brain Res* 194:517-520
- Tuckwell HC (1976) On the first-exit time problem for temporally homogeneous Markov processes. *J Appl Prob* 13:39-48
- Webster MA & DeValois RL (1985) Relationship between spatial-frequency and orientation tuning of striate-cortex cells. *J Optom Soc Am A* 2:1124-1132
- Williams PJ, MacVicar BA, Pittman QJ (1989) Identification of a GABA-activated chloride-mediated synaptic potential in rat pars intermedia. *Brain Res* 483:130-134