

Chapter 1

From Stochastic Resonance to Gabor Functions: An analysis of the probability density function of interspike intervals recorded from visual cortical neurons

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INTRODUCTION

Receptive Fields

The neurophysiologist can readily study the output -- spike trains -- of neurons when they act as channels, but he has only limited access to the functions of the interactive synapto-dendritic process because of the small scale at which the processes proceed. A major breakthrough toward understanding was achieved, however, when Kuffler (1953) noted that he could map the functional dendritic field of a retinal ganglion cell by recording impulses from the ganglion cell's axon located in the optic nerve. This was accomplished by moving a spot of light in front of a paralyzed eye and recording the locations of the spot which produced a response in the axon. The locations mapped the extent of the responding dendritic field of that axon's parent neuron. The direction of response, inhibitory or excitatory, at each location indicated whether the dendrites at that location were hyperpolarizing or depolarizing.

However, spike trains recorded from axons reflect more than the architecture of the functional dendritic field; three separable influences can be identified: 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, Lassoche and Ptito, 1981). The influence of sensory stimuli (influence #1) is obtained, as in the Kuffler experiments, by correlating input with spike train characteristics.

For a given stimulus condition a dendritic environment (influence #2) is generated from the excitatory and/or inhibitory character of the dendritic events per se. 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 can thus be conceived as a processor of stochastic dendritic events which displays its computed output as the statistics of the sequence of inter-spike intervals.

In this paper the analysis of neural activity emphasizes properties of the distribution of inter-spike intervals. A random walk with positive drift model for simulating the interspike interval distribution is used to describe the unknown underlying process. This model incorporates two parameters that specify the temporal distribution of the first passage time of a diffusion process. These parameters, the drift coefficient and barrier height, are derived from the measured mean and standard deviation of the actual neural spike train intervals. The model is therefore a device for describing the underlying process.

If the process generating the interspike interval is stationary, without a temporal change in the probability density, an analysis based on a random walk with drift is potentially relevant. An early study indicated the random walk with positive drift yields an excellent fit to experimental data of inter-spike intervals recorded from spontaneous neural activity (Gerstein and Mandelbrot 1964). There are therefore theoretical and experimental reasons to believe the model based on the first-passage time of a random walk with positive drift realistically describes the process generating spike-train statistics.

When the spontaneous activity of neurons measured by extracellular recordings had been analyzed it was observed that the temporal distributions of inter-spike intervals resemble the distribution of the first passage time of a random walk with drift process (Lansky 1983; Lansky and Lanska 1987; Lansky and Radil 1987; Tuckwell 1976; Tuckwell and Cope 1980; Kryukov 1976; Yang and Chen 1978). The forward Kolmogorov form

of the Fokker-Planck equation provides a formalism whose solution gives the probability density function of the process (Harrison 1985; Karlin and Taylor 1975). The forward equation is recovered whenever any of several types of random noise are assigned as the inputs to the Hodgkin-Huxley equations (Tuckwell 1986). The distribution for the first passage time of random walk with positive drift has also been referred to as the inverse Gaussian distribution (Wasan 1969; Johnson and Kotz 1970).

When viewed as a neuronal-spike generating process, the membrane potential of the neuron changes from the resting potential to threshold, at which time an action potential is initiated; after a brief refractory period the process is reset to the resting potential to begin another drift toward the threshold. In the formal model of spike generation the resting potential is considered the process origin and the threshold voltage as the absorbing barrier. Drift reflects the voltage change resulting from input current and membrane conductance. It is the probability density function of this process that is observed as the sequence of inter-spike intervals recorded extra-cellularly during the experiment. The spike-generating process is influenced by the collective dendritic activity of the neuron. The model process, which is a representation based on the formalism of the forward equation, provides the statistics describing the spike-rain intervals.

METHODS

Subjects

Subjects were eight adult cats obtained from the cattery at the University of California at Davis. A total of 339 spike trains from 110 visual cortical neurons were recorded. Eight spike trains were of sufficient duration and completeness to be useful for the analysis presented here.

Apparatus

The stimulus, consisting of sine wave gratings of variable spatial frequency, drift velocity and contrast, was displayed on a Tektonix type 602 XY oscilloscope. Orientation of gratings was varied mechanically. The display was maintained at a distance of 50 cm from the subject's head. The neural response was picked up using Haer tungsten microelectrodes with impedance from one to six MegaOhms. A combination of an RCA 3140IC chip provided first amplification, constant input current of 5 picoamps, and a low output impedance. This device was fastened via alligator clip directly to the electrode. A large bore hypodermic needle inserted through the animal's scalp provided the ground. The signal was transmitted to the input of a Grass P511 J AC preamplifier with gain set at 10k, low pass at 3 Hz, high pass at 300 Hz, and a 50 Hz notch filter. This combination of settings allowed operation without a Faraday cage although partial screening around the animal's head was sometimes necessary. The output of the Grass amplifier was divided: one output went to an A-to-D converter input of PDB11 computer; another went to an adjustable Schmitt trigger; a third to a Tektronix model 5111A oscilloscope; and a fourth to an audio monitor. The output of the Schmitt trigger, set to fire when a spike appeared above background noise, was in turn sent to the alternate trace of the oscilloscope and audio monitor. A software window discriminator allowed setting two voltage windows for accepting spikes. Two separate records of interspike intervals were thus kept when two units were defined. Interspike interval lengths were rounded to the nearest millisecond.

Surgical Procedures

Craniotomy and implantation of two 6.5 mm tubular electrode chambers were performed under halothane anesthesia and sterile conditions. A 1/4"-20 bolt was embedded in a cranial cap made of dental acrylic and fastened to the skull by four to six stainless steel screws. Trepine holes were centered at stereotaxic coordinates posterior 2.0 cm and left and right 0.5 cm. The trephine holes were thus placed over areas 17 and 18, and included, at their medial margins, cells activated by stimuli in the midline of the cat's visual field. It is these cells from which most of the recordings were made.

Experimental Procedures

The animal was allowed to recover from surgery for at least one week. On the morning of the experiment subjects were anesthetized with Ketamine and Valium, intubated, and fastened to the Kopp stereotactic apparatus by the head bolt. Subjects were paralyzed with 10 mg/kg Flaxedil to prevent muscle action. Respiration and temperature were stably maintained; heart rate and anal temperature were recorded every 15 min. Subsequent medication during the experimental session was limited to intravenously administered Valium and Flaxedil, titrated to the condition of the animal: Valium was administered when heart rate began to rise; Flaxedil was administered when hind leg muscle tension began to increase. One electrode chamber was opened and coordinates for the placement of the electrode were determined. Contact lenses with zero correction were inserted in both eyes, the eye ipsilateral to the recorded hemisphere was occluded. The electrode was then set with the stereotax to touch the surface of the brain where a small cut in the dura had been made.

The experimental room was darkened and recording commenced. A Wells hydraulic drive was used to slowly lower the electrode. A small flashlight, masked to project an oblong patch of light onto a ground glass or white paper screen at about 20 cm distance from the cat, was used as a search stimulus. When a responding unit was found an unaltered flashlight was used to illuminate a 50 cm by 38 cm stimulus card with 2.5 cm wide alternating black and white stripes, to hand-map the response of the unit. For this study only spike trains from cells whose receptive fields showed "simple" properties were used. The XY display monitor was positioned at the orientation which provided the best response of the unit. Using maximum contrast (0.8 on a scale where 1 equals maximum brightness on a background of total darkness) the frequency of the sine wave gratings and the velocity of their drift were varied until a maximum response was obtained; the direction of movement of black and white stripes over the visual field was reversed to check for directional selectivity.

Testing Procedures

The intent of the experiment was to contrast the stimulus which included the maximal response (determined by an online sample as the histogram with maximum amplitude) with suboptimal stimuli whose parameters were changed over one dimension at a time. After the optimal stimulus parameters had been determined, the experimental procedure was as follows: Recordings were made while the animal was in darkness; then the optimal condition was displayed twice; then again the dark-condition. After this, the variations of single stimulus parameters were carried out in the following order: variation 1; darkness; variation 1; darkness; variation 2; darkness; variation 2; darkness; variation 3; darkness; variation 3; darkness; etc., until all effective values of that variable

were explored. At this point a new stimulus parameter was varied leaving the previously manipulated variable at optimum. The dark conditions preceding and following each comparison made it possible to detect linear drift of the spontaneous firing rate and to search later for stationarity in an analysis of covariance of firing rates. Presenting the optimal condition each time before and after a series of variations allowed for additional tests of stationarity for the conditions with stimulation. The first stimulus variable to be systematically changed was spatial frequency; the next was the velocity of the grating (temporal frequency); systematic changes in orientation and contrast followed if the unit held up long enough. After completion of the procedure search began for a second unit, and the sequence was repeated. When an electrode track was no longer productive the electrode was moved 2 mm laterally, or moved to the other chamber to begin a new search. After about four hours the administration of Flaxedil was discontinued and the animal allowed to recover.

Analytic Procedures

The temporal stability of the distribution of inter-spike intervals is essential to all consideration of reproducibility of experimental results. If this criterion is not met, either some aspect of the experimental preparation is changing, or the instrumentation is not recording the activity correctly. If the conditions of time invariance for the distribution of inter-spike intervals and a low level of first order auto-correlation are met, a two-parameter fit of the data can be based on the random walk with drift model of neural activity. This approach uses the derived values of drift coefficient and barrier that can generate probability densities which have the same mean and variance as the measured spike trains.

Calculated values of mean and standard deviation from the measured inter-spike intervals were determined from the following expressions:

The mean of the measured inter-spike intervals,

$$T_m = \sum_{i=1}^N \frac{T_i}{N} \quad (1)$$

The standard deviation of the measured inter-spike intervals,

$$S_d = \left\{ \sum_{i=1}^N \frac{(T_i - T_m)^2}{(N-1)} \right\}^{1/2} \quad (2)$$

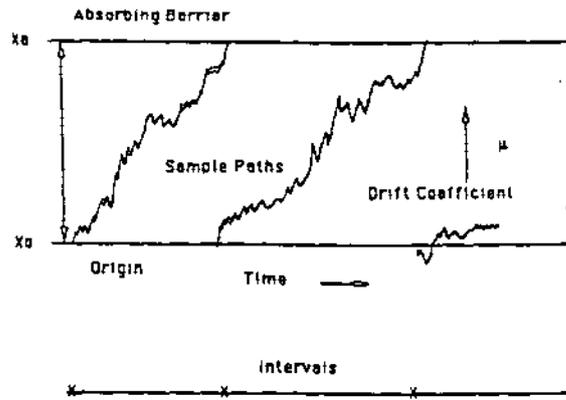


Fig 1. First passage time of random walk with drift is illustrated for positive drift coefficient μ and barrier height $Z = X_a - X_0$. The probability distribution function for the first passage time intervals is determined by these parameters

The random walk with positive drift process is illustrated in Fig. 1. A sample path beginning with the origin at X_0 is seen to advance towards the absorbing barrier at X_a . The distance between the origin and the absorbing barrier, $Z = X_a - X_0$, will always be referred to as the "barrier height" in this paper. The problems are to determine 1) the density of this processing path, 2) its first moment or expectation value, and 3) the second moment from which the variance is calculated. Using sample values for the mean inter-spike interval T_m and the standard deviation S_d then the drift coefficient μ and barrier

height Z can be derived for the first passage time of random walk with positive drift process. A normalized diffusion constant, $\sigma^2/2=1.0$, is assumed in the derivation of the drift coefficient and barrier height. This normalization scales the process to ensure the consistency of the units of the derived parameters.

The solution of the forward equation, Eq. (3), is the probability density function of the first passage time of random walk with positive drift.

$$\frac{\partial P}{\partial t} = -\mu \frac{\partial P}{\partial x} + \frac{\sigma^2}{2} \frac{\partial^2 P}{\partial x^2}. \quad (3)$$

The probability density function that is a solution of the forward equation is given by:

$$P(\mu, Z, \sigma; t) = \frac{Z}{\sqrt{2\pi\sigma^2 t^{3/2}}} \exp\left\{-\frac{(Z-\mu t)^2}{2\sigma^2 t}\right\}. \quad (4)$$

The first moment or expectation value the second moment and the variance of the probability density function are given by Eqs. (5), (6) and 7).

$$E[t] = \frac{Z}{\mu} \quad (5)$$

$$E[t^2] = \frac{\sigma^2 Z}{\mu^3} + \frac{Z^2}{\mu^2} \quad \frac{\sigma^2}{2} = 1.0 \quad (6)$$

$$E[t^2] - E[t]^2 = \frac{2Z}{\mu^3}. \quad (7)$$

To obtain derived values of drift coefficient μ and barrier height Z , the sample mean, T_m , is set equal to the expectation value of the probability density function and the sample standard deviation S_d is set equal to the square root of the variance of the probability density function. In this way a calculated probability density function with the same mean and variance of the measured inter-spike interval distribution is obtained. The

derived drift coefficient of the model process is given by equation (8) and the derived barrier height is given by Eq. (9).

$$\mu = \frac{\sqrt{2T_m}}{S_d} \quad (8)$$

$$Z = \mu T_m. \quad (9)$$

The main objective of this report is to illustrate the activity of neurons under different stimulus conditions as graphs of Z and μ ; this will provide insight into the changes in the spike-generating process. If sufficient stationarity during recording of experimental data is observed it is believed that this method for investigating neural activity will yield a substantially correct description of the inter-spiked interval statistics in a concise form.

EXPERIMENTAL RESULTS

The methods described were applied to the inter-spike intervals of recorded data for eight cells that were under similar experimental conditions. The four conditions can be summarized as follows:

- Condition 1. No stimulus presentation and a corresponding spontaneous neural discharge-rate.
- Condition 2. Orientation change with the same spatial frequency as Condition 4.
- Condition 3. Spatial frequency change with the same orientation as Condition 4.
- Condition 4. Condition of orientation and spatial frequency for maximal discharge rate.

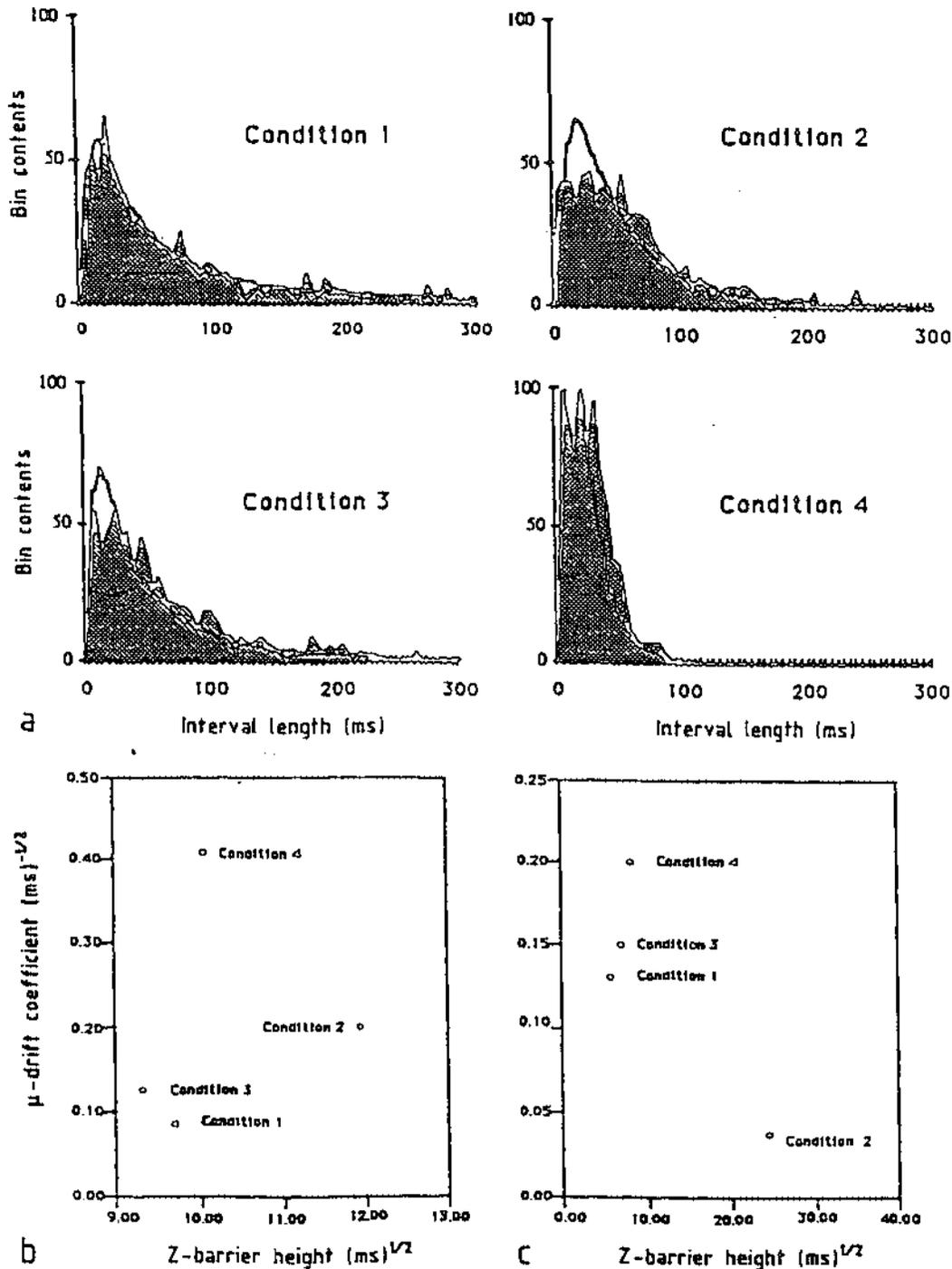


Fig. 2 a The interspike interval histograms for the four stimulus conditions are shown by the shaded areas. The solid line shows the calculated pdf for the first passage time of random walk with positive drift with the same mean and variance as the measured histograms. b The barrier height and drift coefficient for the cell with the interspike interval histograms illustrated in a is shown. c Another cell is presented which shows a large increase in barrier height for the 90 degree orientation change of Condition 2

The inter-spike interval histograms for a selected cell are shown in Fig. 2a. These histograms show that a given stimulus condition results in a unique distribution of interspike intervals. Figure 2b illustrates the derived values of drift coefficient μ and barrier height Z for this cell. For condition 2, for which the stimulus orientation is changed by 90 degrees relative to conditions 3 and 4, an increase in barrier height Z is seen for the

process. Another cell with an even greater Z shift is shown in Fig. 2c. The condition 3 for change in the spatial frequency is primarily associated with a decrease in drift coefficient μ in both figures. The Z and μ values shown in Fig. 2b were evaluated for 800 measured intervals for each of the four conditions. The statistical significance of the change in Z values between condition 2 and condition 3 of Fig. 2b is an important issue. To examine this problem the measured intervals were divided into ten equal segments of 72 intervals each for both condition 2 and condition 3. The mean and variance of the derived values of Z of each collection of intervals was calculated. The results of a one-tail T -test showed the confidence level for eighteen degrees of freedom to be $T=2.09$, $P<0.05$). This would indicate that the Z shift is statistically significant and that changes in orientation and spatial frequency are indexed separately. (Sillito et al. 1980; Romoa et al. 1986). The limits of hyperpolarization and depolarization correspond to changes in the barrier height of the process if other factors are unchanged.

The histogram of the intervals shown in Fig. 2a has some peaks and troughs in the distributions. It is of interest to determine if this structure is a permanent feature related to the stimulus conditions or if it an unrelated artifact. An extensive examination of histograms using segmented data and auto-correlograms did not reveal any permanent feature that could be attributed to the representation of relevant information. The structure of the probability density function derived from the measured histograms appears to contain all the significant information in terms of representation of the stimulus. Clearly a sufficiently low rate of temporal change in the stimulus conditions would create variations in the probability density function and auto-correlograms but under the nearly

stationary conditions of these experiments no temporal sequences provided evidence for an additional mode of stimulus representation.

THE GABOR FUNCTION

An additional analysis was undertaken to bring the results of the previous analysis into formal register with the functional properties of the dendritic fields of visual cortical neurons described by their 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 & 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, 1985, 1988).

Pribram (1991, p. 678) has suggested that the formal model presented above 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 drift coefficient and barrier height parameters, 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 analysis changes in spatial frequency were indexed solely by changes in drift coefficient, while change in barrier height was determined only by orientation. Here an indexing method is used to simulate the same mode 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 behavior 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.

$$Z_0(\Theta) = 2.0 \cos (\Theta - \pi/2) + 3.0 \quad (11)$$

$$Z_t(\Theta) = 2.0 \cos (\Theta - \pi/2) + 3.0 \quad (12)$$

$$T_0(\Theta) = 7.0 \cos (\Theta - \pi/2) + 8.5 \quad (13)$$

$$\mu(\Theta, f) = 0.2 \exp (-2.0\Theta^2) \exp (-4.0(f-1)^2) \quad (14)$$

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 orientation in our simulation. The μ parameters of each neuron are thus determined by the center-excitation, flank-inhibition configuration of the Gabor filter function.

CONCLUSION

As noted in the 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, Lassonde and Ptito 1981). Receptive field properties (#2 above) can be characterized as filters resonating to spatial (and temporal) frequencies (DeValois and DeValois 1988) which are specified as sinusoids in the spectral domain. These sinusoids are limited by a Gaussian envelope which reflects the spatial characteristic of the receptive field, specifically, orientation. The result is best described as a Hermitian of which the Gabor elementary function is a basic example. (Marcelja 1980; Pribram and Carlton 1986; Daugman 1988). The analyses undertaken in this study indicates that these two separable characteristics of the receptive dendritic

field, responses to changes in spatial frequency and orientation, have different effects on the processes generating neural impulses at the axon hillock.

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