REFRACTORINESS-MODIFIED FRACTAL STOCHASTIC POINT PROCESSES FOR MODELING SENSORY-SYSTEM SPIKE TRAINS

Steven B. Lowen and Malvin C. Teich

steve6@ctr.columbia.edu
mct2@columbia.edu

Department of Electrical Engineering, Columbia University
500 W. 120th St., New York, NY 10027

Abstract

Fractal stochastic point processes (FSPPs) provide good mathematical models for long-term correlations present in auditory-nerve fibers in a number of species. Simulations and analytical results for FSPPs concur with experimental data over long times. Refractoriness-modified Poisson point processes, in contrast, model only the short-term characteristics of these data. Simulations incorporating refractoriness into FSPP models achieve agreement over all time scales. We now present fully analytical results for a particular FSPP model with refractoriness. Statistics of this model agree closely with computer simulations and auditory data.

Introduction

Certain random phenomena are well described by essentially identical events occurring at discrete times. One example is the registration of action potentials recorded by an electrode near an auditory-nerve fiber [7,8,2]. A (one-dimensional) stochastic point process is a mathematical construction which represents these events as random points on a line. Such a process may be

COMPUTATIONAL NEUROSCIENCE

called fractal when a number of the relevant statistics exhibit scaling with related scaling exponents, indicating that the represented phenomenon contains clusters of points over all (or a relatively large set of) time scales [6,3-5].

The power spectral density (PSD) and the Fano factor (FF) are two statistics which reveal this clustering [5]. The PSD $S(\omega)$ for a point process, as for continuous-time processes, provides a measure of how power is concentrated as a function of the angular frequency ω. The Fano factor $F(T)$, denoted FF, is defined as the variance of the number of counts or events in a specified time window T divided by the mean number of counts in that window. For an FSPP, over a large range of times and frequencies, it can be shown that [5]

$$\begin{array}{lrcl} \text{PSD:} & S(\omega)/\lambda & \approx & 1+(\omega/\omega_0)^{-\alpha} \\ \text{FF:} & F(T) & \approx & 1+(T/T_0)^{\alpha}, \end{array} \tag{1}$$

with λ the average rate of the process, α the fractal exponent ($0 < \alpha < 1$), ω_0 a cutoff frequency, T_0 a cutoff time, and $\omega_0^\alpha T_0^\alpha = \cos(\pi\alpha/2)\Gamma(\alpha+2)$ [5].

The homogeneous Poisson point process (HPP) is perhaps the simplest stochastic point process, being fully characterized by a single constant quantity, its rate. It is not fractal, but serves as a building block for other point processes. With the inclusion of refractoriness (dead- and sick-time effects), the refractoriness-modified Poisson point process (RM-P) proves successful in modeling auditory-nerve spike trains over short time scales. For a fixed refractory period, the RM-P predicts an interevent-interval histogram (IIH) of the form

$$p(t) = \begin{cases} \lambda \exp[-\lambda(t-\tau)] & \text{for } t > \tau \\ 0 & \text{for } t \le \tau, \end{cases} \tag{2}$$

where λ is the original rate of events (before refractory effects), and τ is the refractory period. IIH plots for auditory-nerve fiber firing patterns are often better fit by stochastic dead-time models [11] with exponentially distributed deadtimes [12]; the corresponding RM-P model for this case yields

$$p(t) = \begin{cases} \lambda(1-\lambda\tau)^{-1}\left[\exp(-\lambda t) - \exp(-t/\tau)\right] & \text{for } t > 0 \\ 0 & \text{for } t \le 0. \end{cases} \tag{3}$$

However, the accurate modeling of the self-similar or fractal behavior observed in sensory-system neural spike trains over long times requires a fractal stochastic point process. A number of FSPP models have been developed [5]; we focus on a particular process, the fractal-Gaussian-noise-driven Poisson process (FGNDP) [5]. The FGNDP is important because Gaussian processes are ubiquitous, well understood, and are completely described by their means and autocovariance functions. Thus, only three parameters (including the rate) are required to specify an FGNDP, since, like all FSPPs, it follows Eq. (1). The FGNDP describes the firing patterns of primary auditory afferents quite well over long time scales (several hundred milliseconds and larger) [8], although it does not accurately model neural activity over short time scales.

Incorporating refractory effects into the fractal behavior of the FGNDP yields the refractoriness-modified version (RM-FGNDP), a new model which does indeed mimic auditory-nerve behavior over all time and frequency scales. Fortuitously, for the parameter ranges employed in modeling these spike trains, the effects of the fractal fluctuations are minimal over the time scales where refractoriness dominates, and vice versa. Since these two effects may be decoupled, asymptotic expressions for small and large time scales remain accurate at intermediate times, simplifying the mathematical results considerably. In particular, the predicted IIH plots do not differ appreciably from those of the (non-fractal) RM-P models and therefore resemble the data closely.

The FF and PSD for the RM-FGNDP, in contrast, do differ appreciably from those of both the (non-fractal) RM-P and (non-refractory) FGNDP models. For exponentially distributed stochastic refractory periods, the FF becomes

$$F(T) \approx \begin{cases} \dfrac{1+(\lambda\tau)^2}{(1+\lambda\tau)^2} + \dfrac{2\lambda\tau^2}{T(1+\lambda\tau)^3}\left[1-\exp(\lambda T + T/\tau)\right] & \text{for } \lambda T \le 1 \\ \dfrac{2\lambda\tau^2}{(1+\lambda\tau)^3}T^{-1} + \dfrac{1+(\lambda\tau)^2}{(1+\lambda\tau)^2} + \dfrac{T_0^{\alpha}}{(1+\lambda\tau)^3}T^{\alpha} & \text{for } \lambda T > 1 \end{cases} \tag{4}$$

for steady-state (equilibrium) counting. [For Eqs. (4–7) the parameters are as in Eqs. (1) and (2).] For a fixed refractory period, the FF assumes the form

$$F(T) \approx \begin{cases} 1 - \dfrac{\lambda T}{1+\lambda\tau} & \text{for } \lambda\tau \le 1 \\ 3 - \dfrac{\lambda T}{1+\lambda\tau} + \dfrac{2}{\lambda T}\left[\exp(\lambda\tau - \lambda T) - (1+\lambda\tau)\right] & \text{for } 1 < \lambda\tau \le 2 \\ \dfrac{\lambda\tau^2(6+4\lambda\tau+\lambda^2\tau^2)}{6(1+\lambda\tau)^3}T^{-1} + \dfrac{1}{(1+\lambda\tau)^2} + \dfrac{T_0^{\alpha}}{(1+\lambda\tau)^3}T^{\alpha} & \\ & \text{for } \lambda\tau > 2. \end{cases} \tag{5}$$

For the RM-FGNDP model with fixed refractoriness, the PSD becomes

$$S(\omega) \approx \frac{\lambda\omega^2(1+\lambda\tau)^{-1}}{\omega^2 + 2\lambda\omega\sin(\omega\tau) + 2\lambda^2[1-\cos(\omega\tau)]} + (1+\lambda\tau)^{-3}(\omega/\omega_0)^{-\alpha} \tag{6}$$

over all frequencies, in accordance with results obtained by [1]. For stochastic refractoriness, the corresponding PSD assumes the form

$$S(\omega) \approx \frac{\lambda}{1+\lambda\tau}\frac{1+(\lambda\tau)^2+(\omega\tau)^2}{(1+\lambda\tau)^2+(\omega\tau)^2} + (1+\lambda\tau)^{-3}(\omega/\omega_0)^{-\alpha}. \tag{7}$$

Eliminating the terms involving T_0 and ω_0 in Eqs. (4–7) yields the corresponding RM-P (non-fractal) results.

Methods

A spontaneous recording of duration $L = 600$ sec was obtained from a cat auditory-nerve fiber with a characteristic frequency of 3926 Hz, a threshold of 19.3 dB SPL, and a spontaneous firing rate of 75 spikes/sec. Data collection methods have been described previously [2, and references therein]. The initial 100 sec of data was discarded to ensure stationarity of the remaining data. The IIH and the FF were computed from this data. Parameters for the RM-P, the FGNDP, and the RM-FGNDP models were fit to these experimental plots using the Levenberg-Marquardt algorithm.

Results

The IIH plot for the auditory data is presented in Fig. 1, together with the predictions of the three models. The RM-P and RM-FGNDP models coincide and closely follow the data, while the FGNDP model does not. The IIH reveals information about shorter time scales only (on the order of an interevent time) so short-time effects, such as refractoriness, are important for the IIH.

The FF for the data is presented in Fig. 2, together with the predictions of the three models. Plots of the FF for the two fractal models (FGNDP and RM-FGNDP) were multiplied by $1 - (T/L)^{1-\alpha}$, where L is the duration of the recording, to compensate for the finite recording length [5]. The RM-P model follows the data for short times only; the FGNDP agrees with the data over long times, but not short ones. However, predictions of the RM-FGNDP model closely follow the FF for the experimental data over all time scales. Thus the FF, which displays information over all time scales, indicates that the RM-FGNDP model is superior to all previous models.

The PSD predicted by the RM-FGNDP model accords with that of the data over all frequency scales, as do all other statistics examined to date. In contrast, predictions of the RM-P and FGNDP do not. One particularly robust statistic is the Allan factor $A(T)$, denoted AF, which is defined as the variance of the *difference* in the number of counts in adjacent windows of duration T divided by the mean number of counts. The AF proves superior to the FF in some respects, often providing superior estimates of α, for example [9]. The AF and the FF are simply related by $A(T) = 2F(T) - F(2T)$, so that expressions for the AF may be obtained directly from Eqs. (4) and (5).

Finally, the RM-FGNDP process with different parameters provides a fair fit to data collected from neurons in the visual system of the cat, using these same

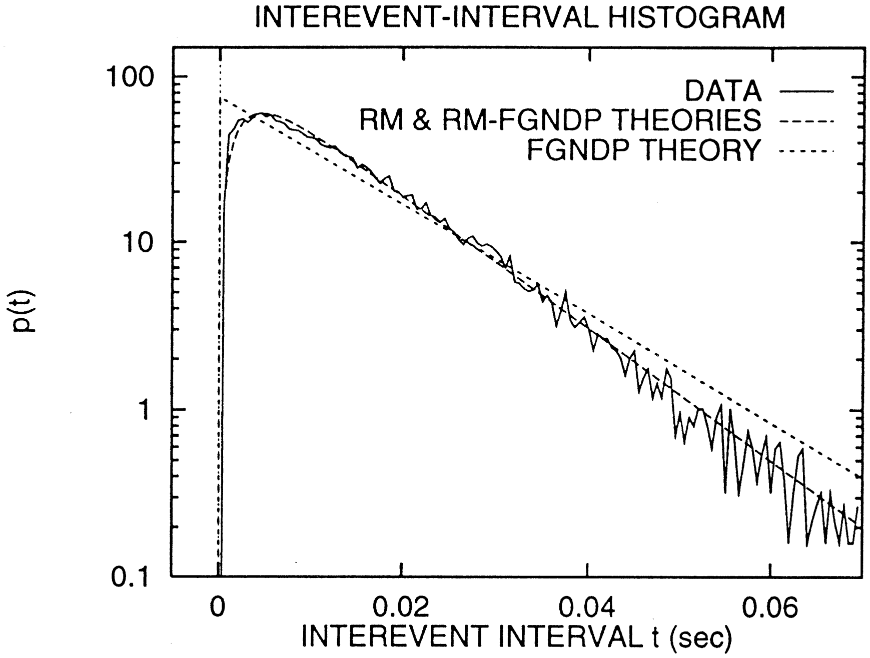

Figure 1: *Semi-logarithmic plot of the interevent-time histogram (IIH) for the auditory neural data (solid curve), with least-squares fits from the RM-P and RM-FGNDP (long-dashed curve) and FGNDP (medium-dashed curve) models. Models incorporating refractoriness follow the data closely; the FGNDP does not.*

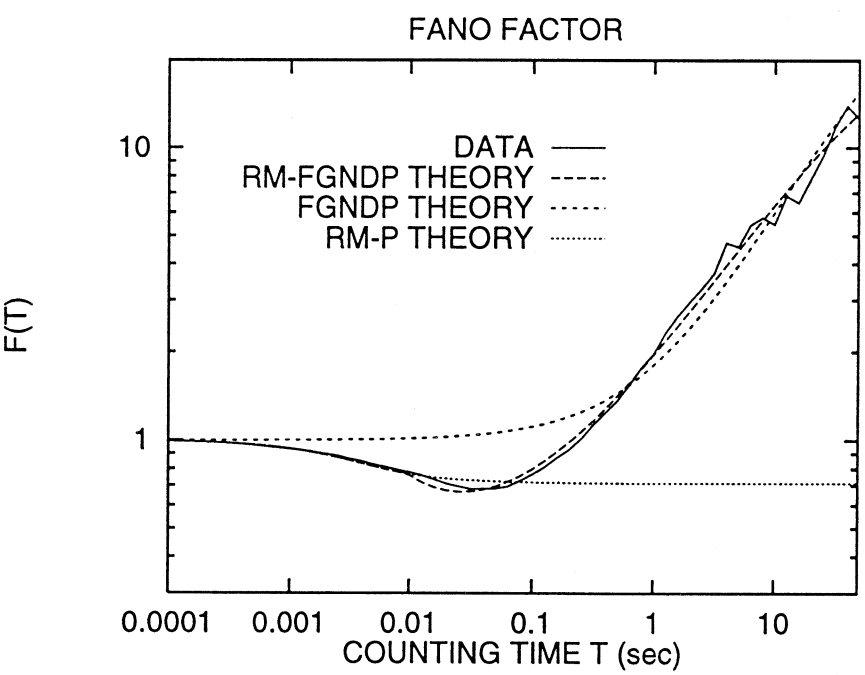

Figure 2: *Doubly logarithmic Fano factor (FF) plot for the auditory neural data (solid curve), with least-squares fits from the RM-FGNDP (long-dashed curve), FGNDP (medium-dashed curve), and RM-P (short-dashed curve) models. Only the RM-FGNDP accurately models the data.*

statistics. However, a similar process, based on a gamma renewal process instead of a Poisson substrate, appears to fit the data extremely well [10].

Summary and Conclusions

Over all time scales, the statistics of the refractoriness-modified fractal-Gaussian-noise-driven Poisson point process model with stochastic refractory periods match those of experimental data collected from cat auditory-nerve fibers. A close relative of the RM-FGNDP also performs well in modeling cat visual-system neuronal firing patterns.

Supported by the Whitaker Foundation under Grant No. CU01455801 and by the Office of Naval Research under Grant No. N00014-92-J-1251.

References

[1] Frontera, F., and Fuligni, F. 1978 The effect of dead time on the power spectral density estimates of discrete time series. Nucl. Instr. Meth. 157:557–561.

[2] Kelly, O. E., Johnson, D. H., Delgutte, B., and Cariani, P. 1995 Fractal noise strength in auditory-nerve fiber recordings. J. Acoust. Soc. Am. (submitted) preprint.

[3] Lowen, S. B., and Teich, M. C. 1991 Doubly stochastic Poisson point process driven by fractal shot noise. Phys. Rev. A 43:4192–4215.

[4] Lowen, S. B., and Teich, M. C. 1993 Fractal renewal processes generate $1/f$ noise. Phys. Rev. E 47:992–1001.

[5] Lowen, S. B., and Teich, M. C. 1995 Estimation and simulation of fractal stochastic point processes. Fractals 3:183–210.

[6] Mandelbrot, Benoit B., *The Fractal Geometry of Nature.* New York: Freeman, 1983.

[7] Teich, M. C. 1989 Fractal character of the auditory neural spike train. IEEE Trans. Biomed. Eng. 36:150–160.

[8] Teich, Malvin C., "Fractal neuronal firing patterns." In *Single Neuron Computation,* T. McKenna, J. Davis, and S. Zornetzer, eds. Boston: Academic, 1992, pp. 589–625.

[9] Teich, Malvin C., "Estimating the fractal exponent of point processes in biological systems using wavelet- and Fourier-transform methods," In *Wavelets in Medicine and Biology,* A. Aldroubi and M. Unser, eds. Boca Raton, FL: CRC Press, 1996 (in press).

[10] Teich, M. C., Heneghan, C., Lowen, S. B., Ozaki, T., and Kaplan, E. 1995 Fractal character of the neural spike train in the visual system of the cat. J. Opt. Soc. Am. A (submitted) preprint.

[11] Teich, M. C., Matin, L., and Cantor, B. I. 1978 Refractoriness in the maintained discharge of the cat's retinal ganglion cell. J. Opt. Soc. Am. 68:386–402.

[12] Young, E. D., and Barta, P. E. 1986 Rate responses of auditory nerve fibers to tones in noise near masked threshold. J. Acoust. Soc. Am. 79:426–442.