Fractal Patterns In Auditory Nerve-Spike Trains

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The pathway for the transfer of information from the inner ear to auditory centers in the mammalian brain is provided by the VIIIth cranial nerve. The neural signal transmitted on individual fibers of this nerve (auditory neurons) has been studied by many researchers, with the goal of gaining insight into the mechanisms of information encoding [1-7]. This signal comprises a series of brief electrical action potentials (nerve spikes), whose amplitudes and energies are widely assumed not to be significant variables [8]. Rather, it is generally accepted that the times of occurrences of these action potentials carry the auditory information. Randomness is involved, since identical experiments lead to differing sequences of nerve spikes [9].

From a mathematical point of view, this neural activity is perhaps best characterized as a stochastic point process [4-6]. A proper description of this point process must include the effects of dead time or absolute refractoriness, which limits the rate at which a neuron can fire. After a relatively brief refractory period, of the order of ms, the neuron may fire again. More precisely, the neuron recovers gradually, over a sick-time (relative refractory) period that lasts tens of ms.

We begin with the simplest case: neural activity in the absence of any external acoustic stimulation. Auditory neurons spontaneously generate nerve spikes under these conditions, albeit at a lower rate than when a stimulus is present.

Traditional Renewal Point Process Models

The mathematical model that has been traditionally used in auditory and other branches of sensory neurophysiology is the homogeneous Poisson point process (HPP) and its close relative, the dead-time-modified Poisson point process (DTMP). Both of these are renewal point processes, which means that they exhibit independent, identically distributed interspike intervals. (The name "renewal" originated in studies pertaining to the replacement or renewal of failed parts such as light bulbs.) These intervals are therefore uncorrelated, and such processes are completely specified by their interspike interval (ISI) histograms.

The theoretical ISI probability density function for the HPP is the simple exponential, $p(t) = \lambda e^{-\lambda t}$, where t is the interspike interval and λ is the rate of the Poisson process. For the firing of a nerve fiber, interspike intervals shorter than a dead-time period τ_d are forbidden by the neuron's refractoriness. This leads to a modified ISI probability density function, $p(t) = \lambda e^{-\lambda(t - \tau_d)}$ for $t > \tau_d$ and $p(t) = 0$ for $t \leq \tau_d$, which is in fact the result for the DTMP.

Figure 1 displays an ISI histogram for the spontaneous neural activity observed on a typical auditory neuron. The approximately straight-line behavior on a semilogarithmic scale demonstrates that the histogram follows an exponential distribution after the dead-time period. Under the assumption that the auditory neural spike train is renewal, the point process that describes it would therefore have to be the DTMP, since it is the unique renewal point process that exhibits exponentially distributed interspike intervals after a dead-time period [10]. This explains the emphasis on the DTMP in auditory theory. However, further investigation reveals that although the DTMP model accurately predicts the ISI histogram, it fails to accord with many other statistical features of auditory nerve-spike data, as explained in this article. The apparent conundrum is resolved by recognizing that the sequence of auditory nerve spikes is, in fact, *not* renewal, despite a long history of papers that espouse the opposite position. Rather, it is characterized by a fractal point process [5, 6] as described below.

Long-Term Correlations

Auditory-nerve spike trains do, in fact, exhibit correlations. The interspike intervals are positively correlated over the long term [5] and often negatively correlated

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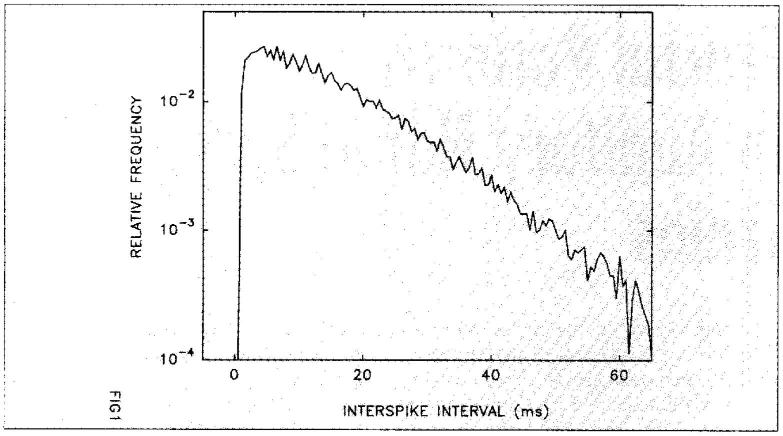


1. Semilogarithmic plot of relative frequency of interspike intervals for spontaneous auditory neural activity. The data closely follow a straight line for intervals greater than about 4 ms. Bin width is 0.5 ms. The stimulus frequency for which this neuron produces its maximal spike rate is 10.2 kHz. (After Ref. [7].)

over the short term [7]. The auditory spike trains are therefore not renewal, and the DTMP cannot properly describe them [6]. We proceed to show that there is long-term memory at the periphery of the auditory system, requiring a fractal-point-process description for the nerve-spike train [5, 6, 11-15]. Long-term memory appears also to be present at the level of the auditory cortex, as revealed in recent neuromagnetic experiments [16].

Self-Similarity of Neuronal Firing Rates

Perhaps the simplest measure of a sequence of action potentials is its rate: the number of spikes registered per unit time. In auditory neural firings, even this straightforward measure has fractal properties; the fluctuations of the rate do not decrease appreciably even when a very long counting time is used to compute it.

In Fig. 2(a), we illustrate the firing rate of the same auditory neuron as analyzed in Fig. 1. Two different counting times were used to compute the rate: $T = 0.5$ s (solid curve) and $T = 5.0$ s (dashed curve). The total time duration of the solid curve is 15 s (30 consecutive samples, each of 0.5 s) whereas the total time duration of the dashed curve is 150 s (30 consecutive samples, each of 5.0 s). Evidently, increasing the averaging time by a factor of 10 does not appreciably reduce the magnitude of the fluctuations. Long-term fluctuations are present in the spike train.

The firing rate for the same data set, after shuffling (randomly reordering) the intervals, is illustrated in Fig. 2(b). Shuffling removes the correlations among the intervals while exactly preserving their relative frequencies. The $T = 5.0$ s shuffled data (dashed curve) exhibits noticeably smaller fluctuations than does the $T = 0.5$ s shuffled data (solid curve). This reduction in the magnitude of the fluctuations with increased averaging time is typical for nonfractal processes, such as the DTMP, but does not occur with the unshuffled auditory data, as is clear from Fig. 2(a) [6].

Power-Law Behavior of the Fano-Factor Time Curve

Another measure of positive correlations over the long term is provided by the Fano-factor time curve (FFC), which is the variance of the number of neural spikes in a specified counting time T divided by the mean number of spikes in that counting time. In general, the Fano factor, F, varies with the counting time, T.

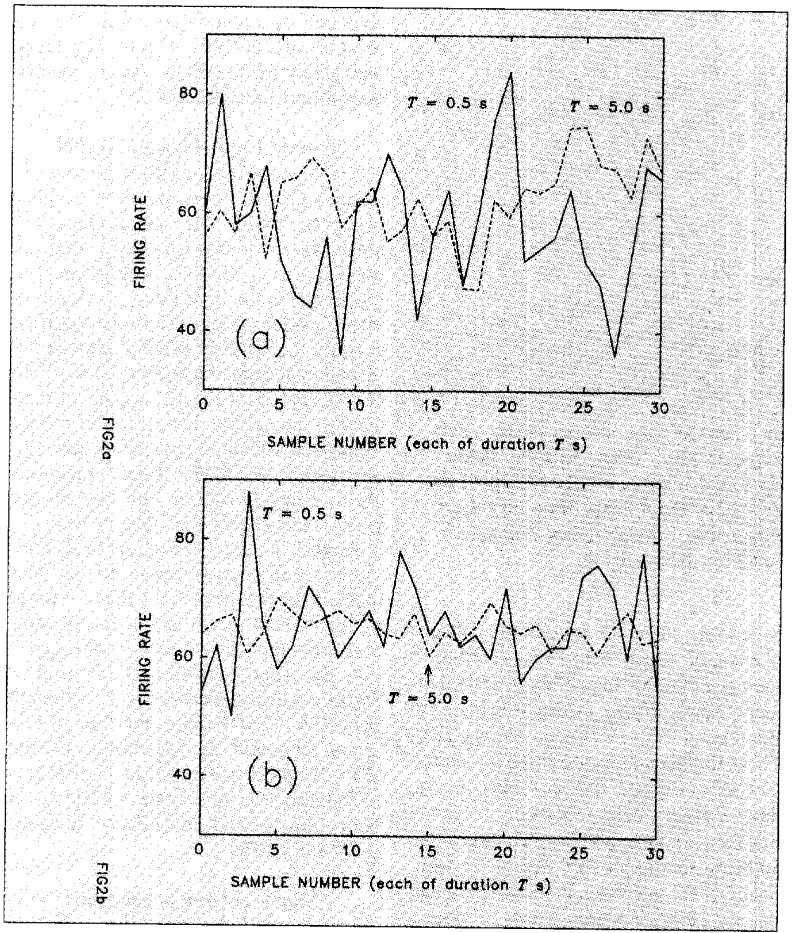
Figure 3 shows the experimental FFC, again for this same spontaneously firing neuron (solid curve). The Fano factor increases steadily for counting times greater than about 100 ms, and exceeds a value of 10 for counting times in excess of 30 s. Since the FFC approximates a straight line for sufficiently large counting times on this doubly logarithmic plot, it is well fit by an increasing power-law function of the counting time, $F(T) \sim T^{\alpha}$ ($\alpha = 0.68$ for this particular neuron). This monotonic, power-law increase indicates the presence of fluctuations on many time scales, and the exponent α is the dimension of the fractal point process [5, 6]. For large counting times, all auditory nerve-spike trains examined to date exhibit Fano factors that increase as power-law functions of the counting time, with $0 < \alpha < 1$ [5, 6, 11-15]. For the DTMP process, in contrast, the Fano factor may never exceed unity for any counting time.

A plot of the FFC alone does not determine whether this large Fano factor arises from the distribution of the interspike intervals or from their ordering. This issue is resolved by shuffling the interspike intervals and then replotting the Fano-factor time curve. FFCs constructed from shuffled data retain information about the relative sizes of the intervals only; all correlations and dependencies among the intervals are destroyed by the shuffling process. The non-solid curves in Fig. 3 illustrate five successive shufflings. All of the FFCs for the shuffled interspike intervals behave like the DTMP, approaching a value less than unity for large counting times. This illustrates that it is the ordering of the intervals, which in turn reflects correlations in the spike occurrences, that gives rise to the power-law growth of the FFC.

The FFC provides a sensitive test for the presence of fractal variability, detecting it even when it cannot be discerned in visual representations of the nerve-spike train. This variability also manifests itself in other statistical measures, perhaps the most familiar of which is the power spectral density (PSD). For low frequencies, f, (corresponding to long time scales T) the PSD varies in a decreasing fractional power-law fashion with frequency, $S(f) \sim f^{-\alpha}$ with the same power-law exponent, α, as in the FFC. Thus the auditory-nerve spike-train data exhibits $1/f$-type noise [14].

Change in the Firing Pattern Induced by the Presence of a Stimulus

The FFC for this same auditory neuron is shown in Fig. 4 when the ear is stimulated by a continuous tone (solid curve). The spontaneous FFC shown in Fig. 3 is replotted for comparison (dashed curve). The shapes of the FFCs are similar. However, the minimum value of the Fano factor is reduced under stimulation, because dead time regularizes the spike train more effectively when the rate is higher, thereby reducing the count variance. The estimated Fano-factor power-law exponent also increases under stimulation [6, 11, 17]; for this particular neuron, it rises from 0.68 to 0.85 when the tone is applied. Figure 5 illustrates the increase in fractal dimension engendered by stimulation for a number of auditory neurons. It is apparent that an acoustic stimulus serves to alter



2. (a) Spontaneous firing rate of the same auditory neuron as illustrated in Fig. 1. Two different counting times were used to compute the rate: $T = 0.5$ s (solid curve) and $T = 5.0$ s (dashed curve). (b) Firing rate of the shuffled data.

the *pattern* of action-potential firing as well as its *rate* [5, 6].

Neural Information Processing with Fractal Nerve Spikes

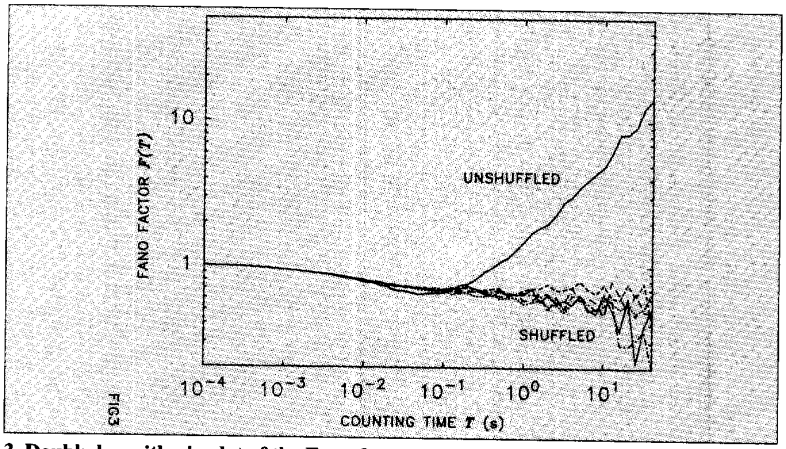
The auditory nerve-spike train appears to sample an information-carrying signal [18, 19]. Fractal nerve-spike occurrences may serve to sample fractal signals and natural fractal noises in an efficient correlated manner [5, 6]. Indeed, both the instantaneous audio power of music and speech, and the instantaneous frequency (rate of zero crossings) of music, exhibit fractal ($1/f$-type) properties over a substantial range of low frequencies [20].

Psychophysical tasks, such as intensity discrimination and loudness estimation, can be understood in terms of the relationship of the count standard deviation to the count mean of an underlying point process representing collected neural activity at a central auditory locus [21, 22]. The signal-to-noise ratio (SNR = mean number of counts divided by the Fano factor) has a positive slope for all counting times T. However, the SNR begins to saturate for values of T near the minimum of the Fano-factor time curve, which typically occurs in the range of 50 to 500 ms. Further increase in the counting time enhances the signal-to-noise ratio only slightly, and it does so at the expense of added response time. Thus, information processing tasks that require rapidity of response, yet low noise, for good performance are best served by using integration time in this range. On the other hand, tasks that require a slower response time, such as thoser involving memory, make use of longer integration times and benefit from the concomitant increase in SNR.

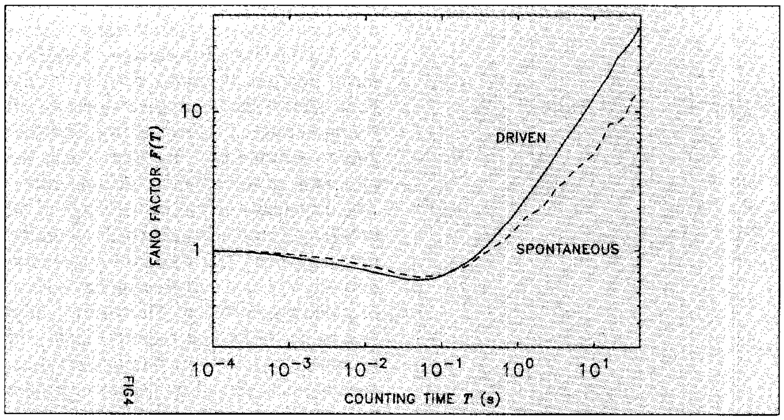
Biophysical Origin of the Fractal Behavior

There are a number of possible origins of the observed fractal behavior [23]: (1) slow decay of intracellular calcium in the hair-cell receptor; (2) fractal ion-channel statistics [5, 24]; and (3) self-organized criticality in ion-channel behavior.

The first two of these models may be cast in the form of a (dead-time-modified) fractal point process; we develop the second as follows. Ion channels switch between two states (open and closed), and the dwell-time distributions often obey power-law forms over a wide range of dwell times [5, 24]. Hair cells contain K$^+$-ion channels that open and close in a fractal fashion, and a fractal renewal process is expected to describe the K$^+$-ion con-



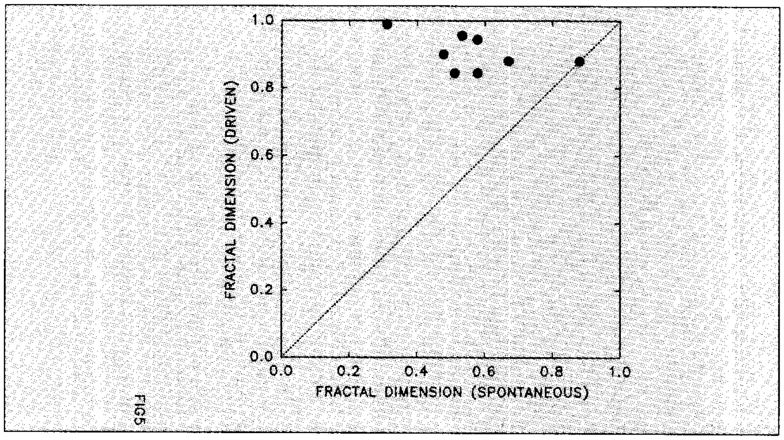
3. Doubly logarithmic plot of the Fano-factor time curve (FFC) for the same auditory neuron as illustrated in Figs. 1 and 2. For counting times of about 1 s and larger, the curve for the unshuffled data is approximately a straight line, representing a fractional power-law increase in the Fano factor. The curve for the shuffled data behaves like that of a DTMP. (After Ref. [7].)



4. Fano-factor time curve for this same neuron when the ear is stimulated by a continuous tone at the neuron's most sensitive frequency (10.2 kHz). The Fano-factor time curve for the spontaneous firing, shown in Fig. 3, is again plotted here for purposes of comparison (dashed curve). The shapes of the Fano-factor time curves are similar for the spontaneous and driven firing; however, the power-law exponent α increases from 0.68 for spontaneous firing to 0.85 for driven firing.

centration within the cell [25, 26]. Since each channel returns to the same physical configuration when it opens, the openings can be reasonably represented as a renewal process. Therefore, it is plausible to conclude that the dwell times in the open state are independent of each other and identically distributed; the same argument holds for the dwell times in the closed state.

Consider the case of independent fractal ion channels [24]. Since there are many such channels, the sum of these fractal renewal processes converges to fractal Gaussian noise (FGN) as a result of the central limit theorem [25, 26], with an empirical fractal exponent that lies between zero and unity. Indeed, the voltages of excitable tissue membranes at rest have long been known to exhibit 1/*f*-type fluctuations, which have in turn been traced to fluctuating K^+-ion concentrations [27]. These fluctuations establish the intracellular Ca^{++}-ion concentration, which, in turn, determines the neurotransmitter secretion that then produces a FGN excitation of the auditory neuron proportional to the original FGN K^+-ion concentration. Assuming that an auditory neuron would produce a homogeneous Poisson point process in the presence of a steady concentration of neurotransmitter (if it were possible to so excite it), then with fluctuations as described above, it would generate action potentials as a doubly stochastic Poisson point process (DSPP), with the stochastic rate given by the FGN-varying neurotransmitter concentration [28].



5. Fractal dimension α of the nerve-spike train for several auditory neurons, under conditions of continuous-tone-driven and spontaneous firing. The increase in α reveals that stimulation serves to alter the pattern of action-potential firing as well as the rate of firing. (After Ref. [6]).

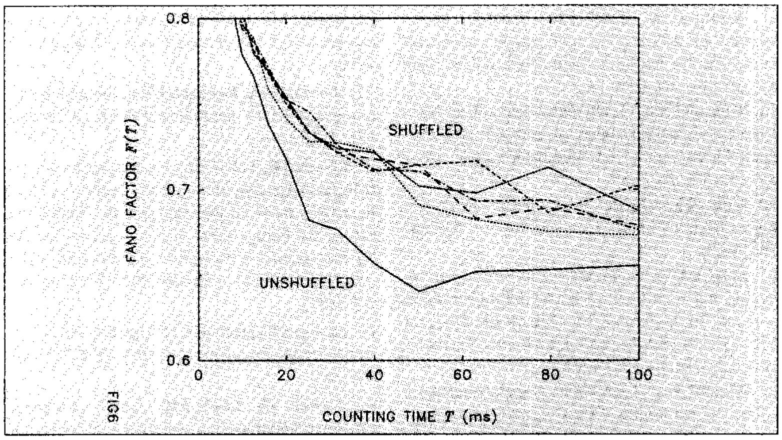
Fractal Point-Process Model

Using the FGN process as the stochastic rate of a Poisson point process yields a particular DSPP, the fractal-Gaussian-noise-driven doubly stochastic Poisson point process (FGNDP). A refinement to this model is the imposition of refractory effects, which yields a dead-time modified version, the DTM-FGNDP. Although the inclusion of dead time makes it difficult to obtain analytical results, we have managed to incorporate the effects of refractoriness in simulations of the process. In contrast to the DTMP, these simulations are in excellent accord with the data for every statistical measure that we have examined [6, 12, 14, 29]. For practical simulations, it often proves easier to use other mathematical formulations that converge to the FGNDP, such as the fractal-shot-noise-driven Poisson point process [12, 30], and superpositions of independent fractal renewal processes [25]. Although the DTM-FGNDP is not amenable to analytical treatment, the FGNDP is, and the FGNDP fits all of the statistical measures of the data over time scales of 100 ms or larger, where dead-time effects are unimportant [12, 30].

Short-Term Correlations

Aside from the positive correlation over long times, there is also a small but significant correlation over times scales on the order of tens of ms. Figure 6, which is a magnification of Fig. 3 (but plotted with linear coordinates), shows this effect. Again, the FFCs for the shuffled intervals are repeatably different from those of the original data, and they are closer to unity. For this particular neuron, and in this range of counting times, *T*, the FFC increases with shuffling, indicating anticorrelation in the original interspike intervals. For this neuron, then, long intervals are more likely to be followed by short intervals and vice versa. Many of the auditory neurons studied behave this way [7, 31]. The short-term correlation appears to arise from a form of refractoriness with memory that extends over a few interevent times. Such models have been satisfactorily employed for clicks [32] and for tone bursts [33], for which nonrenewal, and indeed nonstationary, behavior occurs.

We conclude that over the short term, as well as over the long term, neural activity on auditory-nerve fibers cannot be modeled as a renewal point process.



6. Doubly linear plot of the Fano-factor time curve (FFC) for this same neuron, for counting times shorter than 100 ms. The values for the shuffled data resemble each other but are consistently closer to unity than the curve for the unshuffled data. (After Ref. [7]).

Rather, the firings are characterized as a fractal point process modified by refractoriness with memory.

Acknowledgement

This work was supported by the Office of Naval Research under Grant N00014-92-J-1251, and by the Joint Services Electronics Program through the Columbia Radiation Laboratory.

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