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Analysis of long-range dependence in auditory-nerve fiber recordings

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Rice University, 1994
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Analysis of Long-Range Dependence in Auditory-Nerve Fiber Recordings

by

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A Thesis Submitted in Partial Fulfillment of the Requirements for the Degree Master of Science

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Abstract

The pattern of occurrence of isolated action potentials recorded from the cat’s auditory nerve fiber is modeled over short time scales as a renewal process. For counting times greater than one second, the count variance-to-mean ratio grows as a power of the counting time. Such behavior is consistent with a renewal process driven by a fractal random waveform process (1/f-type spectrum). Based on 108 recordings each 600 seconds long, we conclude that the presence of the fractal noise is independent of characteristic frequency and stimulus level. This noise appears to originate in the cochlear inner hair cells. We measured the low frequency power of the fractal noise, finding its coefficient of variation to decrease as firing rate increases. Such behavior is consistent with multiplicative random variations in the permeability of the hair cell membrane to neuro-transmitter and also with increased level discrimination acuity at high stimulus levels.
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To my mother Rosemary Patricia Kelly and my father Richard James Kelly
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Chapter 1

Introduction

The aim of the research program, of which this thesis forms a part, is to determine the means by which sound is represented and processed in the lower auditory system of mammals. At the biochemical level, researchers model the behavior of nerve fibers by differential equations describing the flows of ions that together constitute the electrical voltages and currents observable in nerve tissue [Hodgkin and Huxley, 1952]. The shapes of measured action potentials differ very little from one to the next, which has led researchers to apply a more abstract model wherein a sequence of action potentials is represented only by the times of occurrence of the action potentials [Siebert, 1970]. Point process theory provides the mathematical tools to interpret such sequences of event times called, in this context, spike trains. Point process models have been used with success in describing short-term statistical properties of spike trains recorded in the auditory-nerve and the lateral superior olive.

The rate of spike generation on the auditory-nerve appears to have substantial variations at frequencies as low as measurements will support [Kumar, 1990]. The resultant power spectrum exhibits the well known “1/f” form, i.e. the power spectrum rises hyperbolically near the frequency origin with some exponent α. This phenomenon came to light as researchers noted the inability of models based on short duration observations to generate data consistent with long duration observations. Teich [1989], and Kumar [1990] have presented point process models which exhibit the long-range correlation associated with 1/f spectra. In the context of a random process, the presence of 1/f “noise” implies that observations distant in time are strongly correlated and the correlation decays according to a power law with separation between observation times. Kumar [1990, p.77] showed that a point process
model having a self-similar, or fractal, correlation structure is consistent with the long-range properties of auditory-nerve observations and his idea forms the basis of the model presented herein.

Validation of long-range dependence models, and the investigation of low frequency phenomena in general, are fundamentally limited by the duration of available experimental data. The purpose of the current study is to produce a refined model of long-range dependence in auditory-nerve recordings by examining a collection of long duration experimental data. The work is based on 108 recordings of auditory-nerve activity under different stimulus conditions that were collected at the Eaton Peabody Laboratory by Bertrand Delgutte and Peter Cariani. The experimental suite was designed to capture long-range phenomena by making observations an order of magnitude longer in duration than typically taken. Each raw data set is 600 seconds in length.

1.1 What is a Point Process?

To study spike trains rigorously, we need to analyze localized events that are distributed in some random fashion across a continuum. A point process is a mathematical model that describes such data by assigning each event to a point in an abstract space appropriately chosen to represent the continuum, $\mathbb{R}^1$ for time, $\mathbb{R}^3$ for space, etc. A fundamental consideration in defining a point process is regularity, which requires that in sufficiently small neighborhoods the probability of having two or more events vanishes and that the probability of one event is proportional to the volume of the neighborhood. Regularity allows sufficient flexibility to model a great variety of phenomena.

As this study concerns the distribution of auditory-nerve action potentials in time, we must define the variables of a temporal point process. The notation generally follows Snyder [1975]. Assume an event occurs at the time origin $t = 0$, and let $N_t$ be the number of events occurring before time $t$. $N_t$ is a realization of the point process.
\{N_t; t \geq 0\}$ and is equivalently represented by a list of event times $w = w_1, \ldots, w_{N_t}$, or inter-event intervals $\tau = \tau_1, \ldots, \tau_{N_t}$.

According to the regularity assumption, the behavior of a point process at each time $t$ is defined by the probability of an event in the immediate neighborhood of $t$

\[
\Pr[N_{t+\Delta t} - N_t = 1] \propto \Delta t \\
= \lambda(t, w) \cdot \Delta t
\] (1.1)

The intensity $\lambda$ may vary with time and be affected by the history of events $w$.

1.1.1 Multiplicative Recovery Model

The multiplicative recovery model is a special case of Eq.1.1 that restricts the intensity to the form

\[
\lambda(t, w) = v_t r(t - w_{N_t})
\] (1.2)

and $r(\tau)$ is usually normalized so that $\lim_{\tau \to \infty} r(\tau) \uparrow 1$. In sequel, all renewal processes are assumed of this form. For the purposes of neural studies, multiplicative recovery conveniently separates the notion of stimulus $v_t$ from the unit's intrinsic properties, which we summarize by the recovery function $r(\tau)$. The point process may be treated as a probabilistic "system" defined by $r(\cdot)$ acting on an "input" $v_t$ and producing "output" $N_t$ (see Fig.1.1). The multiplicative model was introduced in the statistical literature by Aalen [Aalen, 1978] and investigated by Jacobsen [Jacobsen, 1982]. It was introduced in neural studies by Johnson and Swami [1983]. The statistics of renewal processes make frequent use of the following integrals

\[
\Upsilon_{a,b} \equiv \int_a^b v_t \, dt \\
\Lambda_{a,b} \equiv \int_a^b \lambda_t \, dt \\
R(t) \equiv \int_0^t r(\tau) \, d\tau
\]

and the sum

$N_{a,b} \equiv N_b - N_a$. 

1.1.2 Special Cases

Among the models admitted by the multiplicative formulation are several familiar special cases (see Fig. 1.2).

- If the driving function is a constant \( v_t = v \), the process is an ordinary renewal process [Cox, 1962], and the inter-event intervals are independent and identically distributed according to the interval density

\[
 f(\tau) = vr(\tau) \exp(-vR(\tau)) .
\]  

(1.3)

- The Poisson process results if \( r(\tau) = 1, \tau \geq 0 \). Under this condition the number of events in an interval, \( I \), is Poisson distributed with parameter \( \Lambda_I = \int_r v_t dt \), and counts in non-overlapping intervals are independent random variables. If the driving function is constant \( v_t = v \), the homogeneous Poisson process results.

- The deadtime-modified Poisson process is defined by a recovery function that is a shifted step:

\[
 r(\tau) = \begin{cases} 
 0 & \tau < \delta \\
 1 & \tau \geq \delta 
\end{cases} .
\]  

(1.4)

\( \delta > 0 \) is called the absolute deadtime.

Recovery functions that are more general than a shifted step are said to have both absolute and relative deadtime. The relative deadtime refers to the period in which
\( r(\tau) \) is strictly between zero and one: the incremental probability of an event is nonzero but diminished from the value \( u\Delta t \). The point processes of Fig. 1.2 are constructed by generalizing the recovery function and the driving function. The most general process we discuss is the \textit{doubly stochastic renewal process}, explained further in Chapter 2.

![Diagram showing different types of processes](image)

**Figure 1.2** Point Processes having a Multiplicative Intensity

Not all random event processes are accommodated by the framework of multiplicative intensity renewal processes. A model by Miller suggests that the sharp peak observable at the deadtime in the interval histogram and the recovery function is due to a probability \textit{mass} in the interval histogram Eq. 1.3 [Miller and Wang, 1993]. Such a process is not a \textit{regular point process} because for some points in time there exists a nonzero probability of an event that is \textit{independent} of the size of the neighborhood considered to contain the event.
1.1.3 Effective Rate

We wish to develop a notion of the rate of event occurrence for the multiplicative recovery model that is independent of the history of the process. The true rate is $\lambda(t, w)$, but it is usually the case that the history of the process $w$ is unknown and the expectation $E_w[\lambda(t, w)]$ is intractable. However, some statements can be made about the rate of the process near time $t$ that depend only on the driving function and the recovery function.

If the driving function is constant $\nu_t = \nu$, then "under very mild restrictions" [Cox, 1962], the average rate of spike arrival is asymptotically

$$
\lim_{t \to \infty} E[\lambda_t] = E[\tau|\nu]^{-1}
$$

$$
= \left[ \int_0^\infty \tau \nu(t) \exp(-\nu R(t)) \, dt \right]^{-1} \quad (1.5)
$$

$$
= \left[ \int_0^\infty \exp(-\nu R(t)) \, dt \right]^{-1} \quad \text{(by parts).} \quad (1.6)
$$

In fact, if the density of the initial event $w_0$ satisfies a certain equilibrium condition, then $E[\lambda_t] = E[\tau|\nu]^{-1}$ for all $t$ [Cox, 1962, p.55]. We can associate to each recovery function an effective rate function

$$
\lambda^e(\nu) \equiv E[\tau|\nu]^{-1}. \quad (1.7)
$$

Fig.1.3 shows the effective rate function associated with an example piecewise linear recovery function.

We would like to extend the definition of effective rate to accommodate a time-varying driving function. It is convenient to define the instantaneous effective rate

$$
\lambda^e_t \equiv \lambda^e(\nu_t) \quad (1.8)
$$

which bears the following relationship to $E[\lambda_t]$

$$
E[\lambda_t] = E[E[\lambda_t|w_{N_t}]]
$$

$$
\approx E[E[\tau|w_{N_t}]^{-1}] \quad (1.9)
$$
Figure 1.3  Expected Counts of Ordinary Renewal Process
Associated with each recovery function (left) is an effective rate curve (right) which shows the asymptotic rate of generation of events by a homogeneous renewal process defined by recovery function $r(\tau)$ with constant driving level $v$. The recovery function is piecewise linear. The corresponding rate curve is calculated using the error function $\text{erf}(\cdot)$. Locally, the effective rate function is well approximated by an affine function.
\[ \approx \mathcal{E}[\tau | w_{N_i} = t]^{-1} \]
\[ = \left[ \int_0^\infty \tau u_{t+r}(\tau) \exp \left( - \int_0^\tau u_{t+r}(\sigma) \, d\sigma \right) \, d\tau \right]^{-1} \]
\[ \approx \left[ \int_0^\infty \tau u_r(\tau) \exp \left( -u_t \int_0^\tau r(\sigma) \, d\sigma \right) \, d\tau \right]^{-1} \]
\[ = \lambda^e(v_t) \]
\[ = \lambda_i^e. \] (1.11)

The approximations in Equations 1.9, 1.10, and 1.11 are intended to illustrate the differences between the instantaneous rate and instantaneous effective rate \( \lambda_i^e \). The first approximation assumes that the process is always in equilibrium in the sense Cox defined and we may therefore substitute the result Eq.1.5. It is not clear that an inhomogeneous renewal process can maintain equilibrium as its driving function varies. In the second approximation we assume the mean lifetime of the current event \( \tau \) when measured at the time of the last event \( w_{N_i} \) does not differ significantly from its expectation over all values of \( w_{N_i} \). The third approximation simplifies the lifetime density by ignoring variations in the driving function over the duration of the current interval. In short, \( \lambda_i^e \) does not represent the behavior of \( \mathcal{E}[\lambda_i] \) at time scales on the order of the relative deadtime because it ignores the time of the previous event on which \( \lambda_i \) depends heavily. But at time scales longer than the relative deadtime we expect \( \Lambda_{a,b} \approx \int_{a}^{b} \lambda_i^e \, dt \) to be a good approximation. The instantaneous effective rate \( \lambda_i^e \) captures the effects of refractoriness and variation in \( v_t \) on the number of events but ignores the local distribution of the events in time.

1.2 Auditory-Nerve Recordings

We turn now to a general description of our measurements. In mammals, the auditory-nerve forms the only connection between the cochlea, where the transduction of sound occurs, and the central nervous system. Almost all of the 50,000 or so nerve fibers of the auditory-nerve emanate from cochlear hair cells, the electro-mechanical transducers of sound [Kiang et al., 1965]. The cochlea is a mechanically tuned filter bank;
therefore, each hair cell is sensitive to a particular frequency range. Consequently, individual nerve fibers or units have an identifiable characteristic frequency (CF) [Kiang et al., 1965].

Units in the auditory-nerve generate discharges in the absence of sound. Spontaneous rates lower than 1 sp/s and greater than 100 sp/s have been recorded [Kiang et al., 1965, p.95]. Units with a spontaneous rate under 20 sp/s are termed low spontaneous and the remainder high spontaneous units. Liberman has associated variations in the spontaneous rate across units with fiber diameter and with the termination location of fibers at the inner hair cell [Liberman, 1982; Liberman and Simmons, 1985].

In the presence of sound, the rate of spike generation rises monotonically with the sound pressure level along some sigmoid saturating nonlinear curve called the rate-level function. Driven rates are typically less than 300 sp/s.

The cat ear is sensitive between 100Hz and 30kHz. At frequencies lower than 5kHz, there is measurable synchronization between the incoming sound waveform and the probability of occurrence of a spike. The synchronization effect is referred to as time locking.

1.3 Long-range Dependence

Several researchers have found long-range dependence between events in auditory-nerve spike train recordings [Teich and Khanna, 1985; Teich, 1989; Kumar, 1990; Teich et al., 1990b; Kumar and Johnson, 1993]. The pulse number distribution Pr [N_{t,t+T} = n] is the probability of n spikes occurring in a counting time of T seconds. Prompted by an observed invariance of the pulse number distribution (PND) [Teich and Khanna, 1985], Teich [1989] found that the estimated PND from auditory-nerve recordings failed to converge in the expected manner, even for very large data sets. The Fano factor statistic which is the ratio of the variance to the mean of the number of counts in a fixed interval (i.e. var/mean of the PND) shows the changes
in the PND at different counting times. The presence of long-range dependence is indicated by the Fano factor curve which takes a power-law form when applied to long-range dependent data.

Fano factor curves measured from auditory-nerve recordings display the power-law form that indicates long-range dependence. Long-range dependence is associated with non-stationarity and also with large low-frequency variations. Spike rate variations at frequencies much below that of auditory stimulation call into question basic premises about the encoding of sound in the auditory spike strain.

Although deterministic chaos can give rise to long-range dependence, Kumar [1990] showed that, within the context of a doubly stochastic Poisson process model, the observed behavior is not due to deterministic chaos. An alternate explanation provided by Teich [1989] and Kumar [1990] models the auditory-nerve spike train as a doubly stochastic renewal process driven by a random process with hyperbolic power spectrum of the form $1/\alpha$. Processes of this type are termed “$1/f$” after their spectral shape and also fractal after the statistical scaling properties they possess. Though they are widely observed in nature, the analysis of $1/f$ processes is hindered by the fact that they do not formally possess a power spectrum. Kumar [1990] identified the asymptotic slope of the Fano Factor curve with the fractal dimension of the point process and Teich et al. [1990b] noted the apparent increase in the asymptotic slope of the Fano Factor curve when the firing rate of the unit increases under acoustic stimulus.

By modeling the auditory-nerve spike train as a doubly stochastic deadtime-modified Poisson process Teich derives a closed form expression for the Fano factor curve that enables the direct estimation of the fractal dimension and other parameters associated with the point process. Compared to the Fano factor curves of a process that has relative deadtime, the estimated Fano factor curves do not differ significantly at counting times much greater than the relative deadtime.
It is well known that auditory-nerve fibers display relative refractoriness, and thus over the short-term a renewal process with a recovery function models the spike train more accurately than a Poisson or deadtime-modified Poisson process. The difficulty lies in deriving analytic results when the recovery function is not simple. We investigate long-range dependence in auditory-nerve recordings in the setting of a doubly stochastic renewal process model with multiplicative intensity and a general recovery function. Observed interval data are used to estimate the parameters of a $1/f$ driving process and that procedure requires knowledge of the recovery function. The recovery function is estimated from the data.

1.4 Contribution of the Thesis

A closed form expression for the Fano factor curve of the doubly stochastic Poisson process is well known. Teich has derived an expression for the Fano factor curve of the doubly stochastic deadtime-modified Poisson process.

We consider the doubly stochastic renewal process that has a general recovery function. Six new ideas are presented. 1) A lower bound is found for the Fano factor curve of the doubly stochastic renewal process. 2) The lower bound is employed in a new approximation for the Fano factor curve. 3) By modeling the short-term behavior of the process, we are able to extend toward smaller values the range of counting times for which power-law dependence is known to hold. 4) This new knowledge of the short-term dependence of the process enables us to propose reasonable bounds for the power of the fractal component of the process. 5) Measurements show that the relative contribution of the fractal component to the whole process diminishes as the rate of nerve firing increases. This relationship has implications for a hypothetical model of sound transduction in the inner hair cells of the cochlea. 6) The downward trend in the power of the random component of the spike rate of the process as a function of mean spike rate parallels the increasing acuity of the auditory system in intensity discrimination as a function of stimulus level.
Chapter 2

The Fano Factor of a Point Process

The Fano factor or index of dispersion of a nonnegative random variable $X$ is defined to be the ratio of the variance to the mean [Fano, 1947].

$$\mathcal{F}(X) \equiv \frac{\operatorname{var}[X]}{\mathcal{E}[X]}$$  \hspace{1cm} (2.1)

It has been used [Teich et al., 1990b; Teich, 1989; Kumar and Johnson, 1993; Teich et al., 1990a] as an indicator of fractal correlation in point processes and as such is central to our study.

2.1 Properties of the Estimator

Naturally, the Fano factor is estimated as the ratio of the sample variance to the sample mean. Given a vector of observations $x = \{x_1, x_2, \ldots, x_N\}$ from a vector of positive random variables $X = \{X_1, X_2, \ldots, X_N\}$, we define

$$m(x) \equiv \frac{1}{N} \Sigma_{i=1}^{N} x_i$$  \hspace{1cm} (2.2)

$$s^2(x) \equiv \frac{1}{N} \Sigma_{i=1}^{N} x_i^2 - m(x)^2$$ and \hspace{1cm} (2.3)

$$\mathcal{F}_{\text{sample}}(x) \equiv \frac{\frac{N}{N-1} s^2(x)}{m(x)}.$$  \hspace{1cm} (2.4)

Under what conditions is $\mathcal{F}_{\text{sample}}(x)$ a good estimator of $\mathcal{F}(X_i)$ (for some $i$)? We limit our answer to this question to an investigation of the properties of the quantity

$$\mathcal{F}_{\text{th}} \equiv \frac{\frac{N}{N-1} \mathcal{E} s^2(X)}{\mathcal{E} m(X)},$$  \hspace{1cm} (2.5)

because the expectation $\mathcal{E} \mathcal{F}_{\text{sample}}(X)$ is generally intractable. $\mathcal{F}_{\text{th}}$ is a zeroth order Taylor series approximation of $\mathcal{E} \mathcal{F}_{\text{sample}}(X)$ expanded about $\mathcal{E} m(X)$. Without making assumptions on the stationarity or dependence structure of the sequence $X_i$, $\mathcal{F}_{\text{th}}$
can be expressed

\[
\mathcal{F}_{th} = \frac{\sum_{i=1}^{N} \text{var}[X_i]}{\sum_{i=1}^{N} \mathbb{E} X_i} + \frac{N}{N(N-1)} s^2(\{\mathbb{E} X_i\}) + \frac{1}{N} \sum_{i\neq j}^{N} \text{cov}[X_i, X_j] \\
= \frac{\sum_{i=1}^{N} \text{var}[X_i]}{\sum_{i=1}^{N} \mathbb{E} X_i} + \mathcal{F}_{\text{sample}}(\mathbb{E} \mathbf{X}) + \frac{1}{N} \sum_{i=1}^{N} \mathbb{E} X_i
\]

(2.6)

The quantity of interest is \( C_1 \) which Theorem 2.1 (below) shows to be bounded by the largest and smallest Fano factors among the random variables \( \{X_i\} \). Thus if the sequence is wide-sense stationary, \( C_1 = \mathcal{F}(X) \).

**Theorem 2.1**

\[
\min_i \mathcal{F}(X_i) \leq \frac{\sum_{i=1}^{N} \text{var}[X_i]}{\sum_{i=1}^{N} \mathbb{E} X_i} \leq \max_i \mathcal{F}(X_i)
\]

(2.7)

**Proof.** For positive numbers \( a, b, c, d \) satisfying \( \frac{a}{c} \leq \frac{b}{d} \) the inequality

\[
\frac{a}{b} \leq \frac{a + c}{b + d} \leq \frac{c}{d}
\]

holds and extends by induction to higher order sums of positive numbers such as appear in Eq. 2.7. \( \square \)

Insofar as \( \mathcal{F}_{th} \) represents \( \mathcal{E} \mathcal{F}_{\text{sample}}(X) \), Eq. 2.6 shows that in measuring the Fano factor:

- the estimate cannot distinguish between the inherent variance of the samples (\( C_1 \)) and variations among the means of the random variables sampled (\( C_2 \))
- covariance between samples biases the estimate (\( C_3 \))
- when the random variables are independent (\( C_3 = 0 \)) and identically distributed (\( C_2 = 0, \ C_1 = \mathcal{F}(X) \)), inequality 2.7 implies that measurements are unbiased
2.2 Fano Factor as a Measure of Dependence

Recall the pulse number distribution (PND) which is the probability mass function $\Pr(N_{i,t+T} = n)$ of the number of events observed in a counting time $T$. The motivation to use the Fano factor as a measure of long-range variation in point processes comes from Teich [1989] who observed that PND histograms of auditory nerve data exhibit erratic behavior in $T$ even for very large data sets. The Fano factor

$$F_N(T) = \frac{\text{var} [N_{i,t+T}]}{\mathcal{E} N_{i,t+T}}$$

of the counts in time $T$ summarizes the shape of the PND at counting time $T$ so that the curve $F_N(T) \text{ vs. } T$ shows the changes in the PND over different counting times. For sums of positive, independent, and identically distributed random variables, the variance increases in proportion to the mean; but Fano factor curves of auditory nerve counts show that the observed variance increases faster than the mean at long time scales. Hence either the counts in non-overlapping counting bins are not independent or they are not identically distributed. If the point process of the auditory nerve is assumed stationary, we must conclude that the excess variance in the counts at long counting times arises from dependence in the data over long time scales.

For a homogeneous Poisson process, the counts $N_{i,t+T}$ are Poisson distributed with parameter $\Lambda_{i,t+T} = \int_{t}^{t+T} v_s \, ds$. The Poisson distribution has equal mean and variance, hence the Fano factor of such a process is identically 1 for all values of the counting time $T$. Although the Fano factor of an inhomogeneous Poisson process is also unity, the sample Fano factor, if applied to a single sample path is biased by the variations of $\int_{t}^{t+T} v_s \, ds$ (each bin begins at a different value of $t$).

The Fano factor of a homogeneous renewal process is difficult to find in closed form, but its asymptotic value is related to the interval density (Eq. 1.3) by [Cox and Lewis, 1966, p.72]

$$\lim_{T \to \infty} \frac{\text{var} [N_T]}{\mathcal{E} N_T} = \frac{\text{var} [\tau]}{(\mathcal{E} \tau)^2}.$$  \hspace{1cm} (2.8)
By Eq. 2.8, the asymptotic Fano factor for a deadtime modified Poisson process is less than unity: the deadtime simply shifts the exponential density thereby increasing the mean with no change of variance. Processes with Fano factor less than one are called sub-Poisson. All of the homogeneous renewal processes generated by recovery functions that we have measured from auditory-nerve fiber recordings are sub-Poisson.

Fig 2.1 shows typical Fano factor curves for a set of homogeneous renewal processes. At short counting times (for which only zero or one events may be expected in each bin), a renewal process is indistinguishable from a homogeneous Poisson process and thus has a Fano factor of 1. At longer counting times the Fano factor curve usually tends monotonically towards its asymptotic value. The presence of absolute and relative deadtime truncates the tail of the Poisson-like pulse number distribution causing the counts to be clustered more closely about the mean than for a Poisson process. The sub-Poisson nature of these homogeneous renewal processes is especially apparent when the driving function is large enough to force the mean inter-event interval close to the absolute deadtime.

2.3 Fano Factor of a Doubly Stochastic Renewal Process

Consider now a renewal process whose driving function \( v_t \) is a realization of the random process \( \{v_t; t \geq 0\} \). Such a process is called a doubly stochastic renewal process.

In the special case of a doubly stochastic Poisson process, we have \( \lambda_t = v_t \) and Cox [1962] and Snyder [1975] have shown that for an interval \( I = [t, t + T) \)

\[
\mathcal{E} N_I = \mathcal{E} \Lambda_I
\]

and

\[
\text{var} [N_I] = \mathcal{E} \Lambda_I + \text{var} [\Lambda_I]
\]

so that

\[
\mathcal{F}_N(T) = 1 + \mathcal{F}_\Lambda(T).
\]

In the remainder of the section, we develop a similar result for doubly stochastic renewal processes. The result, which we show via simulation to hold approximately,
Figure 2.1  Fano Factor of a Homogeneous Renewal Process

For recovery functions similar to that shown in the inset, the variance-to-mean ratio of the counts of a homogeneous renewal process typically declines with the counting time from unity to some value between zero and one. Although the curve is uniquely determined by the recovery function and the driving function value, it is evaluated by simulation. The point process simulator is described in Johnson and Linebarger [1984]. The simulator requires a piecewise linear specification of the recovery function (see inset), and sample values of the driving function over the whole simulation period (50\(\mu\)s time step was used). For each curve above, a constant valued driving function was used, together with recovery function shown, to generate 1000s of simulated homogeneous renewal process data. The driving function values appear in the legend. The simulated data consist of a list of positive real numbers representing the interevent intervals. Each point of each Fano factor curve is evaluated by partitioning total simulation time into non-overlapping bins of duration \(T\)s then counting the number of events that fall in each bin. The result is a list of \([T_{\text{total}}/T]\) integers, from which the Fano factor is estimated as the ratio of the sample variance to the sample mean.
is

\[ \mathcal{F}_N(T) \approx L(T, \bar{\nu}) + \mathcal{F}_{A^*}(T) \]  \hspace{1cm} (2.12)

where \( L(T, \bar{\nu}) \) is a lower bound on the Fano factor, and \( \Lambda^*_f \) is the integrated instantaneous effective rate. The lower bound is a function of the counting time \( T \) and the time-averaged mean of the driving process, denoted \( \bar{\nu} \) (a scalar). The bound follows from a lower bound on \( \text{var} [N_{t,t+T}] \) presented next.

2.3.1 Lower Bound on Variance of \( N_{t,t+T} \)

It is intuitively reasonable that variation of the counting function \( N_{t,t+T} \) of an inhomogeneous renewal process is intimately related to variations of the driving function \( \nu_t \). For the doubly stochastic Poisson process, that relationship is implicitly expressed by Eq. 2.11. Note that the variance of the counting process \( \text{var} [N_{t,t+T}] \) is minimized when the driving function is deterministic (i.e. \( \text{var} [Y_{t,t+T}] = 0 \)). Is this also true for doubly stochastic renewal processes?

Here we show that the count variance of a renewal process is also minimized by a deterministic driving function, and further, if the integrated driving process has stationary increments, then the count variance is minimized by a constant driving function. The method of proof is first to construct a driving function as a mixture of a deterministic function with a zero-mean random process. We then show that the mixture resulting in the minimal count variance has no contribution from the random process: Deterministic input yields the minimal variance output.

Consider a doubly stochastic Poisson process driven by the random process \( \nu_t = m(t) + \eta(t) \). Let \( \eta \) be a zero-mean random process that satisfies \( \text{var} \left( \int_0^T \eta dt \right) = 1 \) and let \( m \) be a deterministic function. Then \( \text{var} [N_{t,t+T}] \) as a function of the scalar \( \epsilon \) is

\[ \text{var} [N_{t,t+T}] = \int_t^{t+T} m(\sigma) \, d\sigma + \epsilon^2 \]  \hspace{1cm} (2.13)

with first derivative

\[ \frac{d}{d\epsilon} \text{var} [N_{t,t+T}] = 2\epsilon \]  \hspace{1cm} (2.14)
and second derivative \[ \frac{d^2}{d\epsilon^2} \text{var} [N_{t,t+T}] = 2. \] (2.15)

The root of Eq. 2.14 shows that \( \epsilon = 0 \) is a stationary point of the variance and the positive second derivative shows that \( \epsilon = 0 \) is, in fact, a minimizer. A result similar to Eq. 2.14, which applies to doubly stochastic point processes with nontrivial recovery properties, is stated in the following theorem (proven in Appendix A).

**Theorem 2.2** Let \( \{N_t; t \geq 0\} \) be a doubly stochastic renewal process with bounded recovery function \( r(t) \) and driving function \( v_t = m(t) + \epsilon \eta(t) \) where \( m(t) > 0 \) is a deterministic function, \( \eta(t) \) is a bounded zero mean random waveform process, and \( \epsilon \) is a scalar. Let \( 0 \leq r(t) < R \) and \( |\eta(t)| < B \) and let \( \epsilon \) be chosen so that \( v_t > \delta > 0 \) \( \forall t \) for some small \( \delta \).

Then, as a function of \( \epsilon \), \( \text{var} [N_{t,t+T}] \) has a stationary point at \( \epsilon = 0 \).

The so-called "second derivative test" that distinguishes among maxima, minima, and saddle points is not easily extended to doubly stochastic point processes with general recovery functions, but the special case of the Poisson process suggests that \( \epsilon = 0 \) indeed minimizes the count variance. If \( \{Y_t; t \geq 0\} \) is constrained to have stationary increments, it follows that the choice \( v_t \) that minimizes the output variance is the constant function.

Incorporating the lower bound on the variance of \( N_{t,t+T} \), we see that the ordinary or homogeneous renewal process has the minimal Fano factor among all renewal processes that share the same recovery function and mean rate. For a given recovery function, denote this lower bound curve \( L(T, \bar{v}) \).

#### 2.3.2 Sum Approximation

The approximation is

\[ \mathcal{F}_N(T) \approx L(T, \bar{v}) + \mathcal{F}_A(T). \] (2.16)

In the special case of a Poisson process, we have \( L(T, \bar{v}) = 1 \) and the approximation reduces to Eq. 2.11. Fig. 2.2 compares the measured Fano factor of a simulated ex-
ample with the sum suggested by Eq. 2.16. The approximation was tested for fractal driven renewal processes with piecewise linear recovery functions estimated from auditory nerve spike trains and at rates typical of auditory nerve fibers. The measured Fano factor of the point process is slightly less than suggested by the approximation at short counting times, and slightly greater at long counting times. At short counting times and high rates the excess is as much as 25%. Subsequent analysis therefore limits the minimum counting time at which the approximation is employed.
Figure 2.2 An Approximation to the Fano Factor Curve

The figure is based on 840s of simulation of a fractal driven multiplicative intensity renewal process with the recovery function shown in the inset of Fig. 2.1. The top row shows the effect of increased deadtime with respect to the middle row and the bottom row shows the effect of increased rate. The recovery function $r(\tau)$ has absolute deadtime $0.65 ms$ and relative deadtime less than $32 ms$. Each plot at left shows the lower bound $L(T, \nu)$ generated by simulation from the known recovery function and the calculated output Fano factor $F_{\lambda^*}(T)$ as dotted curves. The sum of the two curves gives the approximation to $F_N(T)$ shown as a dashed line. The actual Fano factor curve of the counts $F_N(T)$ is the solid line. The curves at right show the relative error in the estimate of $F_N(T)$. Although the error may be as high as 25% at low counting times and high rates, the effect is moderated by the fact that we do data fitting on the log-log scale. The Fano factor of the effective rate is calculated from the same realization of the driving process used in the point process simulation; the curve is measured after passing the driving function through the memoryless nonlinearity $\lambda^*(\nu)$ that corresponds to $r(\tau)$. 
Chapter 3

A Model of Auditory-nerve Activity

Figure 3.1  Fano Factor of Unit ct-18-94

We have so far only hinted at the connection between long-range dependence, 1/f-noise, and our concern with the Fano factor. Fano factor curves measured from auditory-nerve recordings generally have the shape of the curve shown in Fig. 3.1. The asymptotically linear behavior exhibited by $\mathcal{F}_N(T)$ on the log-log scale corresponds to the power-law relationship

$$\mathcal{F}_N(T) \longrightarrow T^D$$
for some $D$ in the range $0 \leq D \leq 1$. For simplicity let us assume that $\{N_t; t \geq 0\}$ is a doubly stochastic Poisson process and that its driving process $\{v_t; t \geq 0\}$ is wide-sense stationary. Then for large counting times we have

$$\text{var } [N_{t,t+T}] \propto T^{D+1}$$

because $\mathcal{E}[N_{t,t+T}] = \mathcal{E}[T_{t,t+T}] = \tau T$. It follows from Eq. 2.11 that for large counting times, i.e. $T > T_{\text{min}}$, the variance of the integrated driving process must also obey the power-law

$$T^{D+1} \propto \text{var } [T_{t,t+T}]$$

$$= 2T \int_0^T \left(1 - \frac{\sigma}{T}\right) C_v(\sigma) d\sigma \quad ; \quad T > T_{\text{min}}$$

where $C_v(T) \equiv \mathcal{E}[v_tv_{t+T}] - \mathcal{E}[v_t]^2$ is the covariance function of the driving process. Taking two derivatives with respect to $T$ shows that the tails of the covariance function decay according to

$$C_v(T) \propto T^{-D-1} \quad ; \quad T > T_{\text{min}}$$

and this is necessarily accompanied by a power spectrum which rises hyperbolically at the origin. The generalized Laplace transform pair $t^{D-1} \leftrightarrow \Gamma(D)s^{-D}$ indicates that the associated power spectrum has the form $f^{-D}$. That result presents some difficulty because $f^{-D}$ is not integrable and hence does not represent a valid power spectrum. Although our assumption that the driving process is a conventional second-order process does not stand, Wornell [1990] has defined a notion of stationarity based on the invariance of the wavelet coefficients of a random process that is well suited to $1/f$ processes.

### 3.1 The Doubly Stochastic Renewal Model

Despite these formal considerations, we have at least established the motivation for a point process model of auditory-nerve spike generation as doubly stochastic point process driven by a $1/f$ type random waveform process. Kumar, Teich, and Johnson
[Kumar, 1990; Teich et al., 1990a; Kumar and Johnson, 1993] have suggested models of spike generation with the basic form shown in Fig. 3.2. The refractory property of

\[ 1/f \text{ process} \rightarrow \begin{array} \text{\quad} \\
\end{array} \rightarrow \begin{array} \text{\quad} \\
\end{array} \rightarrow \begin{array} \text{\quad} \\
\end{array} \]

**Figure 3.2** Fractal Doubly Stochastic Point Process Model

The figure shows a point process model that accounts for the scaling behavior of the count variance and thus gives rise to the asymptotically linear Fano factor curve shown schematically at the far right. From left to right: a $1/f$ or fractal process drives a point process to generate a spike train with the required temporal patterns. In particular we consider the case that the driving waveform process is the (discretely differenced) fractional Gaussian noise ($fGn$) described by [Mandelbrot and Van Ness, 1968] and the point process has a general recovery function. Teich et. al. treat the cases, in combination and separately, that the waveform process is shot noise, that the waveform process is $fGn$, that the point process is Poisson, and that the point process is a deadtime modified Poisson process [Teich et al., 1990a; Teich, 1992].

neurons is well known but has not been fully incorporated into studies of long-range dependence due to the difficulty of the analysis. Teich has examined the absolute deadtime case and Johnson and Kumar the Poisson case. Although unproven, the approximation Eq. 2.16 that we have shown by simulation is precisely the tool that allows us to include general refractory behavior in the analysis of auditory-nerve recordings based on the model of Fig. 3.2.

### 3.2 Self-Similar Random Processes

A class of random processes that has a correlation function of the form

\[ C_x(T) \propto T^{D-1}, \quad \frac{1}{2} < D < 1 \]

are the *self-similar* random processes, which, by definition, have the property that

\[ \{x_t; t \geq 0\} \overset{id}{=} \{a^{-H}x_{at}; t \geq 0\}. \quad (3.1) \]
Scaling the time axis by a factor $a > 0$ results in a process equal in distribution to the original save for an amplitude scaling of the form $a^{-H}$. This specification is actually quite restrictive. For Gaussian random processes, together with a requirement of mean square continuity, it is sufficient to specify the fractional Brownian motion process introduced by Mandelbrot and Van Ness [1968], that has become a standard model of a $1/f$ process. Fractional Brownian motion ($fBm$) is a formally defined fractional integral of white noise which takes as special cases white noise, Brownian motion, and a range of processes in between based on the self-similarity parameter $H$. By assuming the integrated driving process $\Upsilon_t$ is fractional Brownian motion, the similarity condition Eq. 3.1 can be used to derive the scaling behavior of $\text{var}[\Upsilon_{t,t+T}]$. It follows that the driving process $\{v_t; t > 0\}$ is well modeled as the derivative of $fBm$ or fractional Gaussian noise ($fGn$). The restriction $\frac{1}{2} < D < 1$ is not necessary for $fGn$ but rather indicates that we have invoked the self-similar random process model in order to explain long-range variations in the observed data, and it is only in this range of the fractal dimension that the covariance function of fractal Gaussian noise has the required “heavy-tailed” shape. Fractal dimensions less than one half correspond, in round terms, to derivatives of white noise and such high frequency phenomena are not of interest here.

Processes that display the general self-similarity suggested by Mandelbrot and Van Ness, or only the covariance self-similarity above, have been termed fractal. This corresponds to the use of the term for deterministic sets which display similarity over a range of scales. The type of point process described in Fig. 3.2 is best termed fractal intensity point process because it is not in its realizations that scaling behavior is readily apparent, but in its intensity.

### 3.3 Simulation

The simulations used to generate $fGn$ for Fig. 2.2 and throughout the study are generated by the fast wavelet-based algorithm introduced by Wornell [1990]. The
algorithm for simulating an inhomogeneous renewal process is the one used by Johnson and Linebarger [1984]. Unless noted otherwise, the time step for all simulations is 50\(\mu\text{s}\).
Chapter 4

Processing Spike Train Measurements

The purpose of this study is to understand the origin of the long-range dependence observed in single auditory-nerve fiber recordings. Under the doubly stochastic renewal process model with multiplicative driving function, the low-frequency behavior of the point process follows from the statistics of the driving process. This leads us to the immediate goal of measuring the fractal dimension $D$ and the fractal height $K$ in the expression

$$\mathcal{F}_T(T) = KT^D.$$ 

Estimates of $K$ and $D$ are obtained by a procedure described in this chapter. The coefficient of variation of the integrated driving process $CV[T_0,T]$ is directly computable from $K$, $D$, and an estimate $\bar{u}$ of $\bar{E}[u]$. Using $CV[T_0,T]$ and the power-law structure of the covariance function, we compute reasonable bounds for the $CV$ of the driving process itself $CV[u]$. 

The procedure begins with data collection and screening. For each acceptable recording, an estimate of $\mathcal{F}_N(T)$ calculated directly from the measured series of inter-event intervals. Among point processes with the same recovery function and mean rate, there is a lower bound on $\mathcal{F}_N(T)$ that can be estimated indirectly via a maximum likelihood estimate of the recovery function governing the observations (assuming a multiplicative recovery model). The estimated lower bound $\hat{L}(T, \bar{v})$ is then subtracted from the approximation

$$\mathcal{F}_N(T) \approx L(T, \bar{v}) + \mathcal{F}_N^*(T).$$
yielding an estimate of $\mathcal{F}_T(T)$. $\mathcal{F}_T(T)$ is estimated from $\mathcal{F}_T^*(T)$ using a linear approximation to the effective rate function (recall $\lambda^*_T = \lambda^*(v_T)$, Section 1.1.3). Fig. 4.1 outlines the method. Estimates are denoted by "*" throughout.

4.1 Data Collection

For each auditory nerve unit, the data consist of a set of recordings at different stimulus levels. The stimulus is a pure sinusoid presented at the unit's characteristic frequency; its level is measured in dB with respect to the threshold level of the unit. The protocol called for a 600 second duration recording to be made first with no stimulus, then at $+15$ dB with respect to threshold, at $+40$ dB, and at $+5$ dB, in that order. Most units did not last through the entire protocol. The database consists of 108 recordings of varying lengths from 50 units.

The recordings were made from one barbiturate anesthetized cat by Bertrand Delgutte and Peter Cariani at the Eaton Peabody Laboratory of the Massachusetts Eye and Ear Infirmary. The electrodes used were glass micro-pipettes, and a description of the techniques may be found in [Delgutte, 1990]. The time of each spike is measured and recorded as an integer number of microseconds after the beginning of the recording run. The absolute spike times in microseconds were then converted into inter-spike intervals in seconds and stored as double-precision floating point numbers. The remainder of the processing was performed in double-precision.

4.2 A Test for Consistence with Mean Stationarity

Following the collection of the data, the next step is screening for the presence of trends in each recording. Chapter 2 shows that the Fano factor estimator is a combination of the actual Fano factor with the "Fano factor" of the means of the random variables used in the estimate. In this section we describe a consistency test for disqualifying those portions of each recording during which the rate of spike arrival does not appear mean-stationary. This precaution reduces the bias of the Fano factor
Figure 4.1 Estimation Method
The fractal dimension $D$ and fractal height $K$ of a fractal intensity renewal process are estimated by the nine steps illustrated. The graphs to the right of each processing block show the intermediate results of each stage.
estimate ($C_2$ in Eq. 2.6). A frequently observed form of non-stationarity in auditory nerve recordings is adaptation: a gradual decrease in the rate of occurrence of spikes following stimulus onset. The rate of unit L-19-6 in Fig. 4.2 exhibits adaptation. The figure also shows the portion accepted by the consistency test.

The stationarity test finds the largest contiguous segment of a unit recording which is consistent with statistics calculated from a starting segment of the recording. The data are assumed to be generated from a doubly stochastic renewal process whose driving process obeys the covariance law $\text{cov} [v_i, v_{i+T}] \propto T^{D-1}$ for large $T$. In the Poisson case, the statistics of the generated inter-event intervals $\{\tau_i\}$ approximately have a similar heavy-tailed covariance function with the same exponent (Appendix B). By assuming that a fractal driving process for a doubly stochastic renewal process also gives rise to intervals with power-law covariance, we are able to conduct the stationarity check in terms the inter-event intervals themselves rather than counts of events.

From the sequence of intervals $\{\tau_i\}$, we construct a shorter sequence $\{s_j\}$ by summing each $m$ adjacent intervals $s_j = \tau_{jm} + \tau_{jm+1} + \cdots + \tau_{jm+m-1}$. Each such sum we call a frame of intervals. Let the column vector $S_{p,q} \equiv (s_p, \ldots, s_q)'$ represent a segment of the recording comprised of several adjacent frames and let the matrix $C \equiv \mathcal{E}[S_{p,q}S_{p,q}'] - \mathcal{E}[S_{p,q}]\mathcal{E}[S_{p,q}']'$ be the covariance matrix of the segment. The elements of $C$ are $c_{ij} = \text{cov} [s_i, s_j]$. The method works by establishing error bounds at two standard deviations about the mean from estimates of the mean and variance of the frames of $S_{p,q}$. Neighboring frames $\{s_{p-2}, s_{p-1}\}$ and $\{s_{q+1}, s_{q+2}, \ldots\}$ are joined to the initial segment one by one, while keeping a running total of the number of frames that lie outside the bounds. The initial segment $S_{p,q}$ is “grown” in this way until the allowed number of outliers have been included (4.5% for two standard deviations assuming normal data). The resulting segment $S_{u,v}$, with $u < p < q < v$, is denoted $S_{p,q}^{*}$ to indicate that it is longest segment consistent with the assumption that $S_{p,q}$ is mean-stationary.
Figure 4.2  Adaptation and Stationarity

Unit L-19-6 displays an exponential-like decay of spike rate termed adaptation. Adaptation appears at the onset of recordings of stimulated units and is the primary motivation for the development of the stationarity-consistency check. The check provides objective criteria to distinguish between trends and the trend-like low frequency oscillations typical of 1/f processes. Based on bounds established in the segment $497 < t < 563s$, the stationarity-consistency check accepts the segment $200 < t < 600s$. Although a portion of the accepted segment could be read as an extension of the decaying trend in the initial part of the recording, the accepted portion viewed alone appears free of trends.
The unknown variance $\sigma^2$ is estimated by assuming $C = \sigma^2 C_0$, where $C_0 = (c_{ij}^0)$ models power-law correlation of known dimension and unit power: $c_{ij}^0 = (|i-j| + 1)^{D-1}$. For normally distributed $s_i$, the maximum likelihood estimate of the variance is $\hat{\sigma}^2 = \frac{1}{N}(S_{p,q}^* - \bar{s})C_0^{-1}(S_{p,q}^* - \bar{s})$, where $\bar{s}$ is the sample mean of $S_{p,q}^*$.

The algorithm proceeds by exhaustively searching (over all $p < q$) for the longest duration segment $S_{p,q}^*$ that satisfies the following *ad hoc* criteria. Threshold values appear in parentheses.

- $\text{length}(S_{p,q}^*)/\text{length}(S_{p,q}) > a \quad (a = 1.1)$
  If the starting segment lies in a portion of the recording that is so non-stationary that very few frames can be said to be consistent with the local statistics, then the assumption that the starting segment is stationary is suspect.

- $\text{length}(S_{p,q}^*)/\text{length}(S_{p,q}) < b \quad (b = 8)$
  If the starting segment grows too much, then perhaps the starting segment is very non-stationary and consequently established very loose bounds.

- $\text{length}(S_{p,q})/\text{length}(\text{recording}) < c \quad (c = 0.25)$
  An upper bound on the length of the initial segment prevents us from being too greedy with the assumption that the initial segment is mean stationary.

- $\text{var}[r \in S_{p,q}] / \left( \max_{m=p-q} \text{var}[r \in S_{m,n}] \right) < d \quad (d = 0.7)$
  We eliminate from consideration those starting segments for which the sample variance of the contained intervals is large with respect to all other segments of the same length in the recording. The condition eliminates initial segments that contain apparent discontinuities in the mean.

In each case length refers to the number of frames in the specified segment. The default frame size used was $m = 50$ intervals and the fractal dimension used to construct $C_0$ was $D = 0.65$. That value is at the low end of the range of fractal dimensions measured from the data (typically $D \approx 0.75$, see Section 5.2) however the
error bounds expand quickly at higher dimensions so that at $D = 0.85$ all of the data in Fig. 4.2 might be admitted despite the evident trend.

Aggregating the interval sequence into frames has two advantages over testing the interval sequence directly. Primarily, it permits the use of the pure power-law model $C_0$ and thereby the inclusion the fractal dimension in the establishment of the error bounds. Positively correlated data generally have looser bounds than those one might calculate using the sample variance (which assumes independence). The power-law behavior of our observations is evident for counting durations greater than about one second (Fig. 3.1). Whereas long time lags correspond to large index lags in the interval sequence $\{\tau_i\}$, one expects that if enough intervals are aggregated into each frame (i.e. $E[s_i] > 1$) then power-law correlation will be present between frames that are separated by a small number of lags in the frame sequence, perhaps even adjacent frames. Indeed this is required by the model covariance matrix $C_0$ which assumes power-law covariance beginning with the very first lag. Hence $C_0$ is a better model of the covariance of $\{s_i\}$ than it could be for $\{\tau_i\}$. The second advantage concerns the applicability of the formula for the estimated variance. We may not assume that the density of each $s_j$ is simply the $m$-fold convolution of the exponential-like density of $\tau$ because the intervals $\tau_i$ are correlated; nonetheless, for large $m$, we expect some smoothing and anticipate that the Gaussian assumption used for the maximum likelihood estimate of the variance is not entirely inappropriate.

### 4.3 Recovery Function Estimate

This section describes the method by which we estimate the recovery function of an inhomogeneous point process governed by the multiplicative intensity model

$$\lambda_t = \nu(t - w_N(t))$$

introduced in Section 1.1.1.
The log-likelihood of a realization of the process is

$$l(\tau) = \sum_{i=1}^{N} \left( \log(v_{w_i}r(\tau_i)) - \int_{0}^{\tau_i} u_{w_{i-1}+\sigma}r(\sigma)d\sigma \right)$$  \hspace{1cm} (4.1)$$

where $\tau = \tau_1, \tau_2, \ldots, \tau_N$ is the vector of observed inter-event intervals and $w_i$ are the event times. In Eq. 4.1, both the recovery function $r(\tau)$ and the driving function $v_t$ are unknown. For the maximum likelihood estimate, each is given a parameterization having sufficient flexibility to allow a wide range of functions but few enough parameters so that some smoothing is attained from our $N$ measurements.

We have chosen to parameterize the recovery function as a piecewise linear function described by $m$ pairs $(x_i, y_i)$ called knots with $x_0 < x_1 < \cdots < x_{m-1} < x_m = \infty$ and $y_i > 0$ for all $i$, and $y_{m-1} = y_m = 1$. The driving function is assumed to be constant over each inter-event interval, i.e. piecewise constant. We denote by $v^i$ the unknown driving level during the $(i+1)^{th}$ interval $\tau_i$, that is $v_t = v^i$ for $t \in [w_i, w_{i+1})$, $i = 0, \ldots, N-1$. The model has $N + 2m - 1$ free parameters, a number which exceeds the $N$ interval measurements; we therefore introduce a smoothness constraint on the driving function. In particular, assume that the driving function $v_t$ is constant over $k$ adjacent intervals. We define the driving function parameters $\{d_j\}_{j=0}^{N/k-1}$ so that

$$d_{[i/k]} = v^i, \hspace{1cm} i = 0, \ldots, N - 1.$$  \hspace{1cm} (4.2)$$

The final model has $[N/k]$ parameters that describe the driving function plus $2m - 1$ parameters that describe the recovery function. The order of the model is controlled by the smoothing parameter $k$.

The maximum likelihood estimate of the driving function parameters $\{d_j\}$ can be found analytically by substituting Eq. 4.2 into Eq. 4.1 and setting the partial derivative to zero:

$$d_j = \frac{1}{R(\tau_{jk}) + R(\tau_{jk+1}) + \cdots + R(\tau_{jk+k-1})}$$

where $R(\tau) \equiv \int_{0}^{\tau} r(\sigma)d\sigma$.  \hspace{1cm} (4.3)
Using Eq. 4.3, and ignoring constants, the log-likelihood simplifies to

\[ l(\tau, x, y) = \sum_{j=0}^{N/k-1} \sum_{i=1}^{k} \log \left( \frac{r(\tau_{jk+i})}{\sum_{p=1}^{k} R(\tau_{jk+p})} \right) \] (4.4)

where \( \tau \) is the vector of observed inter-spike intervals, \( x \) is a vector specifying the \( x \)-values of the knots of the recovery function and \( y \) is a vector specifying the corresponding values of the recovery function. The dependence of \( l(\tau, x, y) \) on \( x \) and \( y \) in Eq. 4.4 is implicit in the definitions of \( r(\cdot) \) and \( R(\cdot) \). The analytic result for \( \hat{d}_j \) (Eq. 4.3) reduces the maximum likelihood optimization to a search over the parameter spaces of \( x \) and \( y \). Notice in Eq. 4.4 that two functions that differ by a multiplicative constant have the same likelihood: \( l(\tau, x, y) = l(\tau, x, ay) ; a \neq 0 \). If \( y \) is scaled up by \( a \) then the corresponding driving function is scaled down by \( a \), the product is fixed. In effect, the optimization chooses a hazard function to fit the data and the decomposition hazard = drive \( \times \) recovery is arbitrary.

A gradient based search technique is used to find the optimizer of Eq. 4.4. If \( x \) is treated as a free parameter, the optimization has many local maxima that cause the search algorithm to terminate without much change from the initial \( x \)-values. The optimization therefore is performed with \( x \) fixed. The \( x \)-values are chosen to equally partition the distribution of the observed data (as a quantizer would), with extra knots added near the deadtime to describe details of the recovery function near the deadtime, see Fig. 4.3. After the optimization converges, the result is normalized by \( y_m \) to give a recovery function that is asymptotically 1. The algorithm did not always converge when the smoothing parameter was small \((k < 10)\). We offer no proof that the likelihood is a concave function of \( y \) for a fixed choice of \( x \), however optimizations performed in that mode terminated at the same maximizer for all initial conditions used. In approaching the same estimation problem, Kooperberg and Stone [1993] parameterized the logarithm of the recovery function and their choice yields a provably concave optimization.
Figure 4.3 Knot Location
Optimization to find the maximum likelihood estimate of a piecewise linear recovery function is performed over the y-values of the knots defining the recovery function. The histogram of the observed intervals, above, is used to select x-values for the knots, indicated with vertical hash marks. A knot is placed at the estimated deadtime, followed by seven knots spaced 0.2ms apart. These closely spaced knots enable the resultant estimate to describe the sharp peak in the hazard function which is observed in many units. The remaining knots describe the smoother part of the hazard function and are placed so as to divide the remaining probability mass into equal parts. The histogram shown results from a simulation further described in Fig. 4.5.
4.3.1 Deadtime Estimation

If two renewal processes share the same recovery function but have different absolute deadtimes, i.e. \( r_1(\tau + \delta_1) = r_2(\tau + \delta_2) = r(\tau) \), it can be shown that the deadtime carries through the maximum likelihood analysis so that \( \hat{\tau}_j(\tau) = \hat{\tau}(\tau - \delta_j); \quad j = 1, 2. \) Therefore it is a matter of convenience whether to estimate the absolute deadtime separately then proceed with the estimation of \( r(\cdot) \) using the adjusted measurements \( \tau_i - \hat{\delta} \), or to estimate the entire recovery function directly. We estimate the absolute deadtime before the recovery function so that the knot locations can be chosen to capture details of the recovery function that appear near the absolute deadtime (see Fig. 1.3 and Fig. 2.1 inset).

The sharp peak that appears in some recovery functions is located at about 1 ms [Miller and Wang, 1993], therefore we search for the absolute deadtime in the range \( 0.5 < \delta < 5 \text{ ms} \) and, if the deadtime appears to be greater than 5 ms, the first knot is placed at 5 ms. For a driven unit the deadtime is usually not less than 0.6 ms. The maximum likelihood estimate of the absolute deadtime for a homogeneous renewal process is simply the smallest observed interval \( \tau_{\text{min}} \). That estimate is not appropriate to the data because the recordings contain some very short intervals (as low as 0.2 ms) which appear to arise from false triggers in the recording procedure. In addition to its use in positioning the knots, the estimated deadtime provides a threshold to detect false triggers. False triggers must be removed from the data set (by combining overly short intervals with their neighbors) in order for the likelihood function in Eq. 4.4 to be defined for all intervals. In this application therefore, it is essential that the deadtime estimate be negatively biased in order to avoid erroneously classifying spikes as false triggers. Note that the exponential-like interval density is largest precisely at the deadtime, hence a small overestimate of the deadtime leads to a large number of mis-classified events. The estimate is found by examining intervals shorter than 5 ms and applying the maximum likelihood technique shown in Fig. 4.4 subject to the constraint \( \tau_{\text{min}} < \hat{\delta} < 5 \text{ ms} \). We assume that short intervals (less than 5 ms)
**Figure 4.4 Deadtime Estimation with False Triggering**

Very short intervals (less than 0.2ms) in the data appear to correspond to noise events during experimental recording. For an ideal renewal process, the maximum likelihood estimate of the deadtime is simply the shortest observed interval, but in the presence of noise we must seek an alternative estimate. We assume that short intervals (less than 5ms) are distributed according to a density that is a mixture of a uniform and a shifted exponential ($\alpha \times \text{uniform} + (1 - \alpha) \times \text{exponential}$). The maximum likelihood shift for the observed data serves as an estimate of the absolute deadtime. As the uniform component $\alpha$ of the mixture is reduced, the deadtime estimate moves toward the minimum interval i.e. toward the maximum likelihood estimate for noise-free observations.
are distributed according to a density that is a mixture of a uniform and a shifted exponential density \((\alpha \times \text{uniform} + (1 - \alpha) \times \text{exponential})\) and find the maximum likelihood shift for the observed data. As \(\alpha\) is reduced, the deadtime estimate moves toward the minimum interval, i.e. toward the maximum likelihood estimate for noise-free observations. The value \(\alpha = 0.01\) provided satisfactory results. If a more accurate estimate of the deadtime were required, one might consider maximizing the likelihood over both \(\delta\) and \(\alpha\), and perhaps also seek out the origins of false triggers in the recording process.

### 4.3.2 Smoothing

Part of the estimation procedure is the choice of the smoothing parameter \(k\). In effect, it determines the extent to which variations in the data are explained by variations of the driving function, and in a less intuitive but necessarily complementary fashion, the extent to which they are explained by the recovery function.

The hazard function \(\phi(\tau)\) is related to the interval density \(f(\tau)\) by the identity

\[
\phi(\tau) = \frac{f(\tau)}{1 - F(\tau)} \tag{4.5}
\]

where \(F(\tau) = \int_{0}^{\tau} f(\sigma) \, d\sigma\). The usual recovery function estimate is a normalization of Eq. 4.5 based on the histogram estimate of the interval density \(f(\tau)\). The implicit assumption is that the driving function is a constant, which Kumar [1990] has shown is an implausible model of auditory nerve data. Our parameterization of the driving function allows the recovery function to be estimated without assuming a constant driving function. Fig. 4.5 shows, as one expects, that for large values of \(k\) the maximum likelihood hazard function estimate agrees with the histogram based estimate. The piecewise linear estimate of \(r(\cdot)\) has another advantage over the histogram based estimate: it provides a definition of \(r(\tau)\) for the whole range \(\tau \in [0, \infty)\) required for simulation. The histogram based estimate becomes noisy for large values of \(\tau\) corresponding to the tails of the interval density, and although the maximum likeli-
Figure 4.5 Effect of Smoothing on the Hazard Function Estimate
Due to the multiplicative ambiguity of the recovery function, it is easier to consider the hazard function when making comparisons. The figure compares the maximum likelihood piecewise linear estimate of the hazard function, the histogram estimate of the hazard function, and the actual hazard function based on a 600s simulation using the driving function \( v_t = 50 + 25 \sin(2\pi ft) \) with \( f = 0.02 \text{ Hz} \). The sequence of graphs shows the effect of the smoothing parameter \( k \) on the maximum likelihood estimate of \( \phi(\tau) \). As \( k \) increases, the final value of the hazard function decreases, and this behavior is typical. Based on the known driving function, we can judge the validity of the assumption that the driving function remains constant over a typical \( k \)-interval period. \( k = 3 \) corresponds to about 0.0017 cycles of the sinusoid, over which the driving function deviates less than 0.1% of its value. The assumption of constancy appears valid, however the small value of \( k \) results in a high model order that renders the optimization problem poorly conditioned. Conversely, \( k = 400 \) allows a change in the driving function of about 10% over the time it is assumed to be constant and, although the optimization is well conditioned, the assumption is less accurate. Here \( k = 35 \) and \( k = 118 \) seem to find a satisfactory middle ground between the competing effects, but there is no guarantee for a given problem that the middle ground exists. For example, the constant driving level assumption is not consistent with variations at frequencies of typical auditory stimuli (see Section 4.8.1).
hood estimate has the advantage of being defined in the tail region, its value there is sensitive to the choice of the smoothing parameter $k$.

We now have an estimate of the recovery function, albeit parametric in $k$, which together with results from Chapter 2 enables us to estimate the fractal parameters $D$ and $K$.

4.4 Output Fano Factor Curve

The estimated recovery function $\hat{r}(T)$ can be used to find the lower bound of the Fano factor curve $\hat{L}(T, \bar{v})$ and thereby to estimate the quantity

$$\hat{F}_x(T) \approx \hat{F}_N(T) - \hat{L}(T, \bar{v})$$

which we call the output Fano factor curve.

The lower bound $L(T, \bar{v})$ is the Fano factor curve that corresponds to a homogeneous renewal process having the recovery function $\hat{r}(\tau)$ and driven by the constant value $\bar{v}$. The driving level $\bar{v}$ is chosen to yield the same spike rate $\bar{\lambda}$ as the observed process by solving Eq. 1.7 for $\bar{\lambda} = N_{\text{total}}/T_{\text{total}}$.

Together, $\bar{v}$ and $\hat{r}(\tau)$ define a homogeneous renewal process and although the associated Fano factor curve follows uniquely from the process definition, direct calculation of it requires infinite-order convolutions. The difficulty is avoided by using $\bar{v}$ and $\hat{r}(\tau)$ to simulate the process. $\hat{L}(T, \bar{v})$ is the the Fano factor curve measured from a simulated realization of the homogeneous renewal process defined by $\bar{v}$ and $\hat{r}(\tau)$.

4.5 Correction Based on Counting Efficiency

The question remains, how do we obtain an estimate of the input Fano factor curve $F_T(T)$ from the output Fano factor curve $F_{x}(T)$? Consider a linearization of the effective rate function Eq. 1.7 so that

$$\lambda^e(v) \approx av + b.$$
By mean-stationarity, $\mathcal{E}[\Lambda_t^2] = \bar{\lambda} t$ and $\mathcal{E}[T_i] = \bar{u} t$. It follows directly that

$$\mathcal{F}_T(T) \approx \mathcal{F}_{\lambda^*}(T) \left( \frac{\bar{\lambda}}{a(\lambda - b)} \right). \quad (4.6)$$

The correction $\left( \frac{\bar{\lambda}}{a(\lambda - b)} \right)$ is calculated by estimating the effective rate as $\bar{\lambda} = N_{\text{total}}/T_{\text{total}}$ and linearizing the effective rate curve about $\lambda^*(v) = \lambda$ to find $a$ and $b$.

### 4.6 Estimating the Fractal Parameters (summary)

The fractal height $K$ and fractal dimension $D$ are estimated by combining the results of Sections 4.3–4.5. Fig. 4.1 reviews the estimation strategy. $K$ and $D$ are the coefficients of a linear fit of the input Fano factor curve $\mathcal{F}_T(T)$ vs. $T$ (on a log-log scale). The input Fano factor curve results from a multiplicative correction to the output Fano factor curve. The output Fano factor curve is the amount the observed Fano factor curve exceeds its own lower bound. The lower bound is generated via simulation from the maximum likelihood estimates of the recovery function and the absolute deadtime.

### 4.7 Fractal Noise Strength

In this section we relate the fractal parameters to a more familiar quantity: the coefficient of variation. The coefficient of variation $(CV)$ of a positive random variable is defined as the ratio of the standard deviation to the mean.

$$CV = \frac{\text{standard deviation}}{\text{mean}}$$

The squared coefficient of variation corresponds to the reciprocal signal-to-noise ratio

$$CV^2 = \frac{1}{SNR}.$$

Reasonable bounds for the $CV$ of the integrated driving process and the driving process can be derived from the fractal height and the fractal dimension.
Assuming that auditory nerve spike trains are well modeled as a multiplicative renewal process driven by a mean-stationary random process \{v_t; t \geq 0\}, the power-law behavior of the Fano factor can be expressed in terms of the variance of the integrated driving process

\[
\text{var} [Y_{t,t+T}] = \text{var} [Y_{0,1}] T^{D+1}; \quad T_{\text{min}} < T < T_{\text{max}}.
\] (4.7)

We assume \( K \) and \( D \) are known, as is the mean driving level \( \bar{v} \). \( T_{\text{max}} \) and \( T_{\text{min}} \) are unknown but it appears that the power-law form of the Fano factor curve persists for counting times as large and as small as observations permit the measurement of the input Fano factor. The longest recording we have is 1800s (unit ct-18-94) for which \( T_{\text{max}} > 180 \text{s} \). \( T_{\text{min}} \) is more difficult to estimate because of negative serial correlation in the data, and the ambiguity introduced by smoothing make Fano factor measurements at counting times less than 0.7s uncertain. However, Unit L-19-5 in Figure 4.9 appears to have \( T_{\text{min}} < 0.2 \text{s} \) after compensating for serial dependence. For subsequent analysis we assume \( T_{\text{min}} = 0.2 \text{s} \) and \( T_{\text{max}} > 100 \text{s} \).

### 4.7.1 Driving Process Covariance

If we define the covariance of the driving process as \( C_v(T) \equiv \mathcal{E} [v_t v_{t+T}] - \bar{v}^2 \), then \( \text{var} [Y_{0,T}] \) is

\[
\text{var} \left[ \int_0^T v_t dt \right] = \int_0^T \int_0^T C_v(|t-s|) ds \, dt.
\]

Taking two derivatives of Equation 4.7 reveals that

\[
C_v(T) = \frac{D(D+1)}{2} \text{var} [Y_{0,1}] T^{D-1}; \quad T_{\text{min}} < T < T_{\text{max}},
\] (4.8)

where \( \text{var} [Y_{0,1}] = K \bar{v} \) is known. The variance of the process, \( C_v(0) \), is of particular interest. By the Cauchy-Schwarz inequality, \( C_v(0) \geq C_v(T) \) for all \( T \), which provides the lower bound

\[
\text{var} [v_t] \geq \frac{D(D+1)}{2} \text{var} [Y_{0,1}] T_{\text{min}}^{D-1}.
\] (4.9)
Because $\mathcal{E}[\nu_i] = \mathcal{E}[\Upsilon_{0,1}]$, we can obtain a lower bound on the coefficient of variation of the driving process

$$CV[\nu_i] \geq CV[\Upsilon_{0,1}] \sqrt{\frac{D(D+1)}{2} T_{\text{min}}^{D-1}}.$$  \hfill (4.10)

For $T_{\text{min}} = 0.2s$ and $1/2 < D < 1$, the radical is $\approx 1$. Note that $CV[\Upsilon_{0,1}] = \sqrt{K/\bar{v}}$ is known.

4.7.2 Low Frequency Power

A stronger statement than the lower bound Eq. 4.10 can be made by considering a filtered version of the driving process. Lowpass filtering eliminates the frequency components of the driving process that correspond to the short lags of $C_\nu(T)$ where measurements are lacking (i.e. $T < T_{\text{min}}$ in Eq. 4.8). Define $\{\nu_i'; t \geq 0\}$ to be the random process that arises from passing $\nu_i$ through an ideal lowpass filter with cutoff $f$ cycles per second. Then $CV[\nu_i']$ measures the low frequency variability of $\{\nu_i; t \geq 0\}$ where

$$CV[\nu_i'] \equiv \sqrt{\frac{\text{var} [\nu_i']}{\bar{v}}}.$$

By Parseval's relation

$$\text{var} [\nu_i'] = \int_{-\infty}^{\infty} \frac{\sin(2\pi f T)}{\pi T} C_\nu(T) dT.$$

Thus uncertainty in $C_\nu(\cdot)$ can be expressed as uncertainty in $\text{var} [\nu_i']$.

Although the covariance function $C_\nu(T)$ is unknown for $T$ outside $T_{\text{min}} < |T| < T_{\text{max}}$, some bounds can be suggested. Define the power-law function

$$C_\nu^p(T) \equiv C_\nu(1) |T|^{D-1} \text{ for all } T,$$

and the "truncated" power-law

$$C_\nu'(T) \equiv \begin{cases} C_\nu(1) T_{\text{min}}^{D-1} & |T| < T_{\text{min}} \\ C_\nu(1) |T|^{D-1} & T_{\text{min}} \leq |T| \leq T_{\text{max}} \\ 0 & |T| > T_{\text{max}} \end{cases}.$$
Figure 4.6 Covariance Function of the Driving Process

The covariance function $C_v(T)$ of the driving process obeys a power-law $|T|^{p-1}$ over the lags for which it is known $T_{\text{min}} < |T| < T_{\text{max}}$. For other lags it is assumed to lie below the continuation of the power-law and above the "truncated" power-law whose shape is shown. Note that the truncated power-law is not a positive-definite function and therefore not a valid covariance function, however there is a covariance function shown in the figure that is a valid positive-definite extension of $C_v$ found by alternating projection (Papoulis' algorithm) with the truncated power-law as a starting point.
These are shown in Figure 4.6. We may reasonably assume the true covariance function lies below $C_v^p(\cdot)$ in the undefined regions because near the origin the power-law rises to infinity, and in the tails the power-law decays slowly. With less certainty we may suggest that the true covariance lies above the truncated power-law: at least $C_v(0) \geq C_v^t(0)$ is required for positive definiteness. The constant $C_v(1)$ ensures that the three functions match in the known region. If we assume our suggested bounds indeed apply, the inequality $C_v^t(T) \leq C_v(T) \leq C_v^p(T)$ viewed through Parseval's relation becomes

$$\int_{-\infty}^{\infty} \frac{\sin(2\pi f T)}{\pi T} C_v^t(T) dT \leq \text{var} [v'_f] \leq \int_{-\infty}^{\infty} \frac{\sin(2\pi f T)}{\pi T} C_v^p(T) dT$$

provided $f$ is chosen to ensure $T_{\text{min}}$ falls within the first lobe of the sinc function, i.e. $f < \frac{1}{2T_{\text{min}}}$. The upper bound is

$$\text{var} [\gamma_{0,1}] \times \left( D(D + 1) \frac{\Gamma(D - 1) \sin(\frac{1}{2} \pi(D - 1))}{\pi (2\pi f)^{D-1}} \right)$$

and the lower bound is

$$\text{var} [\gamma_{0,1}] \times D(D + 1) \left( \frac{\Gamma(D - 1) \sin(\frac{1}{2} \pi(D - 1))}{\pi (2\pi f)^{D-1}} - \int_{0}^{T_{\text{min}}} \frac{\sin(2\pi f T)}{\pi T} (T^{D-1} - T_{\text{min}}^{D-1}) dT \right)$$

where $\text{var} [\gamma_{0,1}] = K \nu$ is known. The lower bound also contains a term of the form $-\int_{T_{\text{max}}}^{\infty} \frac{\sin(2\pi f T)}{\pi T} T^{D-1} dT$, but for $T_{\text{max}} > 100s$ and $f = 1 \text{ Hz}$, its value is negligible. Bounds on the coefficient of variation $CV[v'_f]$ of the filtered driving process can be expressed in terms of the known quantity $CV[\gamma_{0,1}]$. The bounds are shown in Fig. 4.7 for $T_{\text{min}} = 0.2s$ and $f = 1 \text{ Hz}$.

4.8 Performance of Estimators

4.8.1 Recovery Function

Fig. 4.5 compares estimated hazard $\hat{\hat{r}}(\tau)$ function to the known hazard function $\phi(\tau) = 50r(\tau)$ and the histogram-based hazard function estimate $\hat{\phi}(\tau)$ for a range of smoothing parameters. For small intervals, both estimates successfully approximate
Figure 4.7 Bounds on the CV of the filtered Driving Process

The coefficient of variation $CV[u'_f]$ of the lowpass filtered driving process can be estimated from the measurable quantity $CV[\Gamma_{0,1}]$. The figure shows upper and lower bounds on the ratio $CV[u'_f]/CV[\Gamma_{0,1}]$ that follow from the assumed bounds on $C_v$ shown in Fig. 4.6. $CV[\Gamma_{0,1}] = \sqrt{K/\delta}$. 
the actual hazard function regardless of the smoothing parameter $k$. $\tilde{\nu}(\tau)$ is more sensitive to the choice of $k$ for longer lifetimes $\tau$. There we find that $\tilde{\nu}(\tau)$ overestimates $\phi(\tau)$ for small $k$ and may underestimate $\phi(\tau)$ for large $k$, but the effect is asymmetric as the overestimate may be very large and the underestimate is usually slight. For the intensities and recovery functions of this study, the useful range of $k$ is about $20 \leq k \leq 100$.

Increasing the smoothing parameter has a dual effect: It reduces the assumed class of driving functions of the process, and it improves the numerical conditioning of the maximum likelihood optimization. Experiments in which the driving function was designed to correspond to a low smoothing value ($k = 3$), i.e. with poor conditioning but an accurate optimization constraint, display the same behavior shown in Fig. 4.5. That is, the best results in estimating $r(\tau)$ were obtained with a large smoothing value clearly inconsistent with the actual driving function. Therefore it seems that $k$ should be chosen first to avoid the large positive bias that accompanies under-smoothing, and then for consistency with known features of the driving function.

Suppose the smoothness constraint provides an accurate description of the driving function. What is the highest frequency $f$ consistent with a particular choice of $k$? The smoothness assumption requires that the driving function remain constant for $k$ intervals, or about $(k/\lambda)s$. The period over which we are willing to grant that the driving function remains relatively constant will certainly be less than the period of its highest frequency component. Thus

$$k/\lambda < 1/f.$$  

The smoothing parameter strongly affects the numerical condition of the gradient-based search for $\hat{r}(\cdot)$. It searches over $N/k + 2m - 1$ parameters using $N$ data points; for small $k$, the problem is ill-posed. For practical purposes, the search requires a minimum amount of smoothing in order to converge. The effect of enforcing a lower
bound $k_{\text{min}}$ on the smoothing parameter is to place an upper bound on $f$.

$$k > k_{\text{min}} \implies f < \frac{\lambda}{k_{\text{min}}}.$$  

Our auditory nerve recordings have $\lambda < 200$ and our experiments show that $k_{\text{min}} \approx 20$, therefore the highest frequency for which the smoothness assumption is consistent with the driving function is about 10 Hz. In short, the non-constant nature of the driving function in the formulation of the maximum likelihood problem does not accommodate variations on the order of typical auditory stimuli, but it does accommodate the very low frequency variations associated with fractal processes.

### 4.8.2 Input Fano Factor

Under proper conditions the estimate of the input Fano factor curve can be very good: see Fig. 4.8. The estimate shows the same lopsided sensitivity to the smoothing parameter as the renewal function estimate. With insufficient smoothing, the estimate of the Fano factor curve is positively biased, and in terms of a linear fit, the experiments shown in Fig. 4.8 indicate that the fractal height will be overestimated and the fractal dimension underestimated.
Figure 4.8 Estimates of the Input Fano Factor Curve $\mathcal{F}_T(T)$

The figure compares estimates of the input Fano factor $\mathcal{F}_T(T)$ as a function of three variables: the coefficient of variation, the mean driving level, the smoothing parameter $k$. Each plot shows the actual input Fano factor along with estimates generated from 1000s of simulated point process data using five different smoothing values. Simulations shared the same recovery function (estimated from unit ct-18-94) but were driven by fractal noise realizations with different means and variances. The estimator has strong positive bias for small values of $k$ and slight negative bias for large values (the prominent dashed line is $k = 3$). The effect of negative bias is evident at short counting times $T < 0.1$. Graphs in the same row share the same mean driving level $E[u]$ ($A=32$, $B=64$, $C=128$, $D=256$) and graphs in the same column share the same coefficient of variation $CV[u]$ ($CV_A = 0.27$, $CV_B = 0.15$). At the same driving level, the estimator is less noisy for the larger $CV$ process (at left). At the same $CV$ the estimator shows less noise at higher rates (downward). Note that the Fano factor scales with both rate and variance and it appears that the estimate is less noisy when the Fano factor is larger, whether due to rate increase or variance increase. Thus it is inherently difficult to estimate the input Fano factor at short counting times.
4.8.3 Negative Serial Dependence

In some cases the estimated "lower bound" $L(T, \bar{v})$ actually exceeds the estimated Fano factor $\mathcal{F}_N(T)$ in apparent contradiction of Theorem 2.2 that established the lower bound (see Fig. 4.9). The statement of the theorem requires that

1. the driving process is positive and bounded,
2. the recovery function is bounded, and
3. the process is a doubly stochastic renewal process.

In what way are the data observed from auditory-nerve fibers inconsistent with the conditions of the theorem? The first condition is satisfied for any particular realization of the driving process. If the model of Miller and Wang [1993] is correct then the second condition is not met because a probability mass in the interval density implies a "delta function" in the recovery function. One would expect the resulting effect to appear in Fig. 4.9 at counting times on the order of the deadtime, but the bound exceeds the measured Fano factor in the range $10 < T < 180 \text{ ms}$ which is an order of magnitude greater than the deadtime (compare the solid line with the dash-dot-dash line). In what way then are the observations not well modeled by a doubly stochastic renewal process? Auditory Nerve spike trains may display negative serial correlation [Lowen and Teich, 1992] as measured by the correlation coefficient

$$\rho \equiv \frac{\text{cov} [\tau_n, \tau_{n+1}]}{\text{var} [\tau_n]}.$$ 

Although the serial dependence is mild ($|\rho| \leq 0.1$), its presence cannot be modeled by an inhomogeneous renewal process and consequently Theorem 2.2 does not apply.

Figure 4.10 shows the effect of processing interval data that have negative serial correlation under the assumption that they do not. That is, we applied the methods of Fig. 4.1 to simulated data generated with known serial correlation ($\rho = -0.84$).
Figure 4.9  Data Sets do not Obey Lower Bound

The figure shows two approaches to estimating the input Fano factor for unit L-19-5. If correlation between adjacent intervals is ignored, the estimated lower bound (dotted-dash) exceeds the measured Fano factor (solid) in the range $0.001 < T < 0.2s$. Although the difference curve is linear at large $T$, it twists downward toward $-\infty$ near $T = 0.2s$. The input Fano factor estimate (labeled "without serial correlation") results from applying the efficiency correction of Eq. 4.6 to the difference curve, only considering the portion of the difference curve that exceeds 1/2. The second approach assumes that serial correlation arises from a conditional shifting of the recovery function based on the length of the previous interval. Under that assumption, a new lower bound is estimated that corresponds to a homogeneous renewal process with shifting-induced serial correlation that has the same correlation coefficient and recovery function as the original data. The new bound is better than the old but does not truly form a lower bound. The difference curves generated by the two lower bounds are similar where they exceed 1/2 however the resulting estimates of the input Fano factor curve differ because the efficiency corrections for the two methods are different. Here $K$ is estimated 30% smaller when serial correlation is ignored. Subsequent calculation use $\sqrt{K}$, therefore an error as large as 15% may be propagated.
Figure 4.10  Serial Correlation Biases Parameter Estimates

Figure 4.9 shows that the the lower bound established by Theorem 2.2 does not apply to auditory-nerve data. Although there are several ways that the observed intervals might not constitute a valid renewal process, Fig. a) shows that the presence of negative serial correlation between intervals causes the lower bound to rise above the measured Fano factor in a fashion similar to that observed in the data (Fig. 4.9). The figure is based on simulation of a fractal driven renewal process that has shifting-induced serial correlation ($\rho = 0.84$) and a homogeneous renewal process with no serial correlation. Fig. b) shows that if one proceeds with the estimation regardless, it is likely that the fractal dimension $D$ will be overestimated and the fractal height $K$ will be underestimated. The actual input and output Fano factor curves are solid lines, and the lower bound, difference curve, and corrected difference (i.e. the final estimate of $F_T(T)$) are dashed lines. The effect on the fractal dimension can be controlled by only considering the difference curve where it exceeds a threshold (1/2).
using a typical recovery function. The simulation uses the renewal model

\[ \Pr [N_{t+\Delta t} - N_t = 1|w; u_t, t \geq 0] \approx \begin{cases} 0 ; & t - w_{N_t} + a - b \tau_{N-1} \leq \delta \\ v_t r(t - w_{N_t} + a - b \tau_{N-1}) \Delta t ; & \text{otherwise} \end{cases} \]

in which serial correlation is induced by shifting the recovery function [Zacksenhouse, 1993]. The recovery function shifts to the left following a long interval and to the right after a short one. The first line above, in which \( \delta \) is the absolute deadtime, prevents evaluation of the recovery function at a negative argument following a very long interval. Zacksenhouse has shown that a modified version of the basic shifting model thoroughly describes the refractory behavior of unit recordings from the lateral superior olivary complex. It is not our intention to imply that the model can be transferred to auditory-nerve unit recordings without further study but rather we have used the shifting model as a simple method of generating serially correlated intervals having a prescribed recovery function. Fig. 4.10a shows in detail that the resulting estimate of \( L(T, \bar{v}) \) rises above the Fano factor curve for some values of \( T \) and thus serial correlation could account for the fact that some data sets do not obey Theorem 2.2. If we proceed with the estimation, ignoring serial correlation, then it is likely that the fractal dimension will be overestimated due to distortion of the difference curve \( \log(\mathcal{F}_N(T) - L(T, \bar{v})) \) as the argument of the log approaches negative values, see Fig. 4.10b. The corrected difference curve appears only for values of \( T \) where \( \mathcal{F}_N(T) - L(T, \bar{v}) > 0.5 \) to show that such a thresholding can reduce the distortion and give rise to a reasonably straight line on which to perform the linear fit that yields the fractal parameters.

It is tempting to hypothesize that a sum approximation, similar to Eq. 2.16, can be formulated for renewal processes with serial correlation. The idea is supported by the simulations shown in Fig. 4.11. It appears from simulations that when a fractal intensity renewal process is modified to have serial correlation induced by shifting then a lower bound on the Fano factor is provided by the Fano factor of a homogeneous renewal process similarly modified.
Figure 4.11 Sum Approximation for Serially Correlated Data

The figure illustrates that a modified version of the “sum rule” (Eq. 2.16) may apply to serially correlated renewal processes. Intervals with negative serial correlation are generated by using a shifting model in which the recovery function is conditioned on the previous interval length $r(\tau|\tau_{N-1}) = r_o(\tau - a + b\tau_{N-1})$. The solid lines show the Fano factor curves of the fractal driving process and the serially correlated renewal process that it generates. The Fano factor curve of a homogeneous renewal process generated by the same shifting model (dotted) lies below the Fano factor of the fractal driven process. The efficiency correction that must be applied to the difference curve to form the final estimate of the input Fano factor differs in from Eq. 4.6 in that the effect of serial correlation must be incorporated into the effective rate curve. The method applies only to shifting-induced serial correlation.
Return now to Fig. 4.9 in which the Fano factor curve of the driving process has been estimated first by ignoring serial correlation then by the method that Fig. 4.11 suggests. Of the two estimates, the line estimated by ignoring serial correlation has a steeper slope (larger fractal dimension estimate), but because of thresholding the difference in slopes is slight. The most evident difference between the two techniques in the example of Fig. 4.11 is that the fractal height $K$ calculated by ignoring serial correlation is approximately 30% smaller than the fractal height calculated using the technique that incorporates serial correlation. The difference arises in the correction term of Eq. 4.6. In the case of a renewal process with shifting-induced serial correlation, the mean driving level that generates a particular spike rate depends on the correlation coefficient. In addition, the recovery function and hence the effective rate function for the shifting model differs from that of the direct model, because the former is estimated from a "whitened" interval sequence.

In expressions for the coefficient of variation the fractal height appears as $\sqrt{K}$ and therefore a 30% error in $K$, as was measured from unit L-19-5, amounts to a 15% error in the coefficient of variation. Fifty-four of sixty-five units have an estimated correlation coefficient smaller in magnitude than Unit L-19-5 for which $\hat{\rho} = -0.075$. The decision to remain with the basic estimation technique at the cost of such possible errors was motivated in part by the arbitrariness of the shifting model and in part by the difficulty of determining automatically the coefficient values of the shifting model. Shifting is the simplest serial correlation model, but it does not accommodate for example the sharp peak visible in measured recovery functions near the absolute deadtime (see Fig. 2.1 inset).

4.8.4 Coefficient of Variation of the Filtered Driving Process

Estimates of the filtered coefficient of variation $CV[u^j]$ are generally larger than the actual value in the examples shown in Fig. 4.12. The figure does not show enough simulations to see the distribution of the estimation errors, but it appears
The figure shows the performance of the $CV[v^f]$ estimator at different rates. The effect of unmodeled negative serial correlation is also shown. For each pair of data points, 1000s of point process data were simulated, and the resulting intervals used to estimate the recovery function etc. The actual recovery function used was estimated from the unit L-19-5 considered in Fig. 4.9. Both $CV[v^f]$ and $E[v]$ are estimated for each point. For a multiplicative renewal process examples (without serial correlation), the $CV[v^f]$ is larger than the true value and the difference appears to decrease with increased smoothing. The estimated driving level is consistently underestimated and the error increases with the driving level but is not strongly affected by smoothing (the actual driving levels were 2, 5, 10, 20, 50, 100, 200, and 500). Fig. 4.13 shows fractal dimension estimates for the same set of simulations.
that the estimator with more smoothing performs better at low rates. The effect of unmodeled negative serial correlation is larger at low rates but no strong pattern emerges. Because negative serial correlation only appears in the actual recordings at rates above 37 sp/s, it may play little role in the final $CV$ estimates. Note that the $x$-coordinate of each data point in the figure is also estimated, and negative bias arises there in part because of the multiplicative ambiguity in the definition of the driving function. The coefficient of variation, however, is invariant to amplitude scalings: $CV[\tilde{Q}] = CV[\tilde{a}Q]$, and thus is not affected by the ambiguity.

4.8.5 Fractal Dimension

The fractal dimension and the squared coefficient of variation are the estimated slope and intercept of a line drawn on a log-log scale through the estimated input Fano factor curve, and therefore the two estimates are very strongly negatively correlated. The negative correlation is apparent in comparing the dimension estimates of Fig. 4.13 to the filtered $CV$ estimates of Fig. 4.12. Fig. 4.13 shows the fractal dimension estimate as a function of estimated mean driving level for two levels of smoothing. The bias of the estimate is generally negative and especially so at low rates. The errors are largest at low rates and appear to be improved by increased smoothing.

4.8.6 Practical Checks

At some stages in the estimation we eliminated from consideration recordings for which it seemed that the accuracy of the final result would be questionable. The first such step is the check for consistency with mean-stationarity described in Section 4.2. Let $T_{stat}$ be the length of the stationary-consistent segment. Recordings with no stationary-consistent segment were eliminated. The search for the maximum likelihood estimate of the recovery function performs badly on recordings with few intervals. (In Fig. 4.12 and Fig. 4.13 the data points for the $\bar{v} = 2$ simulation with serial
Figure 4.13 Estimates of the Fractal Dimension

The figure shows the performance of the fractal dimension estimator on simulated fractal intensity renewal processes. All of the simulations were produced by the same sample path of the $1/f$ driving process scaled to achieve different rates. At each driving level, two simulations were performed using the same recovery function: one with shifting-induced serial correlation and one without serial correlation. Fractal dimensions were estimated without modeling serial correlation. Comparison with Fig. 4.12 shows that the errors in estimates of $D$ and $CV[u^f]$ are generally of opposite sign. The magnitude of errors in fractal dimension estimates appear to be smaller at higher rates.
correlation are missing because the search failed to converge.) If less than 1000 events remained after stationarity checking, the recording was eliminated.

The fractal parameters arise from a linear fit on a log-log scale. The fit begins at the smallest value of the counting time that satisfies

$$\mathcal{F}_{\Lambda^c}(T_1) > 0.5 \quad \text{and} \quad T_1 > 0.2s;$$

and ends at $T_2 = T_{\text{stat}}/10$. We require that the linear fit be to at least 1/2-decade of data; if $\log_{10}(T_2/T_1) < 1/2$ the recording was eliminated. If $T_{\text{stat}} < 200s$ the recording was eliminated. Recordings for which the residual of the least squares linear fit to the Fano factor curve over the range $T_1 < T < T_2$ exceeded 0.18 per data point were eliminated.

Serial correlation invalidates the lower bound and in Fig. 4.9 and Fig. 4.10b we see that the effect of errors in the lower bound estimate is asymmetric. If the estimated lower bound $\hat{L}(T, v)$ is too small then a corresponding error is incurred in the estimate of $\hat{\mathcal{F}}^r_\Lambda(T) = \hat{\mathcal{F}}_N(T) - \hat{L}(T, v)$, but if $\hat{L}(T, v)$ is too large then the difference is negative and the estimate of $\hat{\mathcal{F}}^r_\Lambda(\cdot)$ is strongly distorted on the log-log scale. The effect of unmodeled negative serial correlation is mitigated in three ways.

1) Experiments show that in the absence of serial correlation the estimated recovery function (Fig. 4.5), the estimated fractal dimension (Fig. 4.13), and the estimated filtered coefficient of variation (Fig. 4.12) are all improved by a high choice for the smoothing parameter. However strong smoothing that results in more Poisson-like recovery functions (shorter relative deadtime) also gives a high lower bound, i.e. closer to unity. In order to allow for some unmodeled negative serial correlation we chose a moderate value for the smoothing parameter ($k = 100$) that results in conservative estimate of $L(T, v)$ and reduces the incidence of the lower bound "puncturing" the observed Fano factor curve. 2) The condition Eq. 4.11 ensures that the the most distorted portion of $\hat{\mathcal{F}}^r_\Lambda(T)$ is not included in the linear fit. 3) Recordings with an estimated serial correlation $|\hat{\rho}| > 0.11$ were eliminated.
The histogram of estimated fractal dimensions Fig. 5.8 highlights the difficulty of the estimation problem. Each of the dimensions counted in the histogram comes from a recording that passed all of the tests discussed and yet two measurements (of 65) fall outside the hard bounds $1/2 < D < 1$. Closer examination of those recordings revealed no a priori justification to remove them from consideration.

4.9 Summary

We have established an estimation technique for the parameters of doubly stochastic renewal process that models the auditory nerve spike train. The renewal process uses the multiplicative recovery model

$$\Pr [N_{t+\Delta t} - N_t = 1 \mid w; u_t, t \geq 0] = u_t r(t - w_{N_t}) \Delta t + o(\Delta t)$$

where $\{u_t; t \geq 0\}$ is assumed to be a random process with a power-law spectrum. The estimation has three steps: i) discard data that does not appear stationary in the mean, ii) estimate the recovery function $r(\tau)$ from the remaining data, and iii) estimate the parameters of the power-law spectrum. The estimate of the recovery function, and therefore the subsequent analysis, is based upon a smoothed maximum likelihood optimization with an arbitrary smoothing parameter.

Measured intervals from the auditory nerve spike train may display mild negative serial correlation that the model does not accommodate. The estimation errors that result primarily affect the ability to estimate the covariance properties of the process at short lags. The measured spectral parameters can be related to the coefficient of variation of the driving process and a lowpass filtered version of the driving process.
Chapter 5

Results

More than one-hundred primary auditory nerve fiber recordings were analyzed by the method described in Chapter 4. This chapter describes the fractal dimension and filtered \( CV \) measurements of the 65 recordings that passed all of the checks described in Section 4.8.6.

Auditory nerve units are generally classified into four subgroups by their characteristic frequency (\( \geq 3000 \text{ Hz} \)) and spontaneous rate (\( \geq 20 \text{ sp/s} \)). The database includes units with a characteristic frequency as low as 500 Hz and as high as 10 kHz, with the bulk of the units having their CF in the range 1 kHz – 5 kHz. See Fig. 5.1. The majority of the units represented in the database are high spontaneous units as shown in Fig. 5.2.

The division by spontaneous rate at 20 sp/s is a natural consequence of the bimodal spontaneous rate distribution. The division by CF at 3000 Hz is somewhat more arbitrary and is intended to distinguish units that are likely to phase lock under stimulus (i.e. low CF units) from those that will not phase lock. Units can display some degree of phase locking at frequencies as high as 5000 Hz. Our division at 3000 Hz intentionally favors the observed data and we use it with the interpretation more vs. less phase locking rather than some vs. none.

Note that the distribution of units in Fig. 5.1 and Fig. 5.2 is different from the distribution of data. Ideally, four 600s recordings would have been made from each unit, but most units provided less than four runs and most runs yield less than 600s of stationary-consistent data. The majority of units provided one run (spontaneous) or two runs (spontaneous and +15 dB stimulus).
Figure 5.1  Histogram of Characteristic Frequencies
The 65 recordings in the database come from 37 different units. The figure shows the
distribution of the characteristic frequencies of the 37 units.

Figure 5.2  Histogram of Spontaneous Rates
Twenty-seven of the 37 units in the database possess a spontaneous run that has a
stationary-consistent segment that passes all checks. The distribution of spontaneous
rates among the 27 units is shown.
5.1 Coefficient of Variation of the Filtered Driving Process

Fig. 5.3 is our main result. The estimated coefficient of variation of the filtered driving process is plotted against the estimated mean of the driving process for the four unit populations. There is a gap in the observations for units with a driving level in the range $15 < \bar{v} < 46$ corresponding to rates in the range $15 < \bar{\lambda} < 38 \text{sp/s}$. After lowpass filtering at 1 Hz, the driving process has a coefficient of variation in the range $0.06 < CV[v^L] < 0.36$, but Fig. 4.12 indicates that $CV$ measurements at driving levels less than 10 may have positive bias. In view of Fig. 4.12, we might judge that the highest noise strength is closer to 0.25 than 0.36. $CV = 0.06$ corresponds to $SNR = 278$ and $CV = 0.25$ corresponds to $SNR = 16$.

The results of Fig. 5.3 are shown for each population separately in Fig. 5.4. Whereas only the upper bound on $CV[v^L]$ is shown in Fig. 5.3, Fig. 5.4 shows both upper and lower bounds. We caution that these are not error-bars in the usual sense because they only reflect one source of uncertainty in the measurement and the measurements are still dependent on the accuracy of the estimated $CV$ of the integrated driving process $CV[T_{0,1}]$.

Performance tests of the estimators in Section 4.8 show that the estimate $\bar{v}$ of $E[v]$ is negatively biased at high rates. This is due in part to the multiplicative ambiguity in factoring the recovery function out of the hazard function. The ambiguity does not affect estimates of the coefficient of variation. Fig. 5.5, showing estimates of $CV$ vs. rate on the output side of the point process, is intended to present the same information as Fig. 5.3 without negative bias on the x-axis. Fig. 5.5 and Fig. 5.3 have essentially the same shape and thus the effect of the bias has not changed the qualitative relationship seen between the variables.

Fig. 5.6 shows the $CV$ vs. rate curves among the four populations by unit. Runs from the same unit at different stimulus levels are connected by a solid line and data points with the same stimulus level share the same symbol. The effect of increased
Figure 5.3  CV of the Driving Process vs. Mean Driving Level

The coefficient of variation of the filtered driving process is in the range $0.06 < CV[v'_T] < 0.36$ and generally decreases as the mean value of the driving function increases. $CV[v'_T] \approx 0.15$ is a typical value. The upper bound for each measurement is plotted.
Figure 5.4 CV vs. Driving Level in Different Unit Populations

Estimates of the coefficient of variation of the filtered (1 Hz) driving process $CV[\nu_i]$ are shown with error bars corresponding to the assumed bounds on the covariance function $C(\nu_i)$ at short lags (Fig. 4.7). The unit population is partitioned by spontaneous rate ($\gtrsim 20$ sp/s) and characteristic frequency ($\gtrsim 3000$ Hz).
Figure 5.5 CV of the Intensity vs. Mean Intensity

The coefficient of variation of the intensity process is in the range $0.05 < CV[\lambda_t] < 0.34$ and generally decreases as the rate of spike generation increases. $CV[\lambda_t] \approx 0.13$ is a typical value.
stimulus is to decrease the filtered $CV$, but the filtered $CV$ seems dependent on the firing rate that results from stimulation rather than the stimulus level.

Fig. 5.7 shows the coefficient of variation of the filtered driving process as a function of the characteristic frequency. No relationship is apparent.
Figure 5.6  CV of the Driving Process for each Unit
Each line represents recordings of a single unit under different stimulus conditions. Units were stimulated by continuous tone at CF: "o" = spontaneous, "+" = 5 dB (with respect to threshold), "x" = 15 dB, and "*" = 40 dB.
Figure 5.7 CV vs. CF
The coefficient of variation is shown as a function of the characteristic frequency of the unit under test. The error bars on the CV measurement correspond to the uncertainty in the low lag behavior of the driving process autocorrelation function (see Fig. 4.7).
5.2 Fractal Dimension

The fractal dimension $D$ is related to the frequency content of the fractal noise process. For fractional Brownian motion, the dimension $D = 1/2$ corresponding to white noise serves as a dividing line between negatively and positively correlated random processes and also between processes characterized by excess high frequency power and processes with excess low frequency power (long-range dependence). Processes described by $0 < D < 1/2$ are fractional derivatives of white noise, while those with dimension $1/2 < D < 1$ fractional integrals of white noise. The latter group of processes, when transformed to be nonnegative, serve as a model class for the driving process $\{v_t; t > 0\}$. Most of the estimated dimensions shown in Fig. 5.8 fall in the range $1/2 < D < 1$ predicted by the long-range dependence model. Measurements outside the expected interval are assumed to result from estimation errors because the limits $D = 1/2$ and $D = 1$ are “hard” in the sense that no point process can theoretically have $D > 1$ and processes with $D < 1/2$ are fundamentally different from those with $D > 1/2$. The median fractal dimension is $D = 0.773$. Fig. 5.9 shows no clear relationship between the fractal dimension and the mean driving level.

Fig. 5.10 compares the estimated dimension $D$ of the fractal noise process to its estimated strength $CV[v^f]$. The two quantities are apparently negatively correlated, but before drawing any conclusions on this point, compare Fig. 4.12 and Fig. 4.13 to one another. The dimension estimator and the $CV$ estimator are strongly negatively correlated at low rates. The two estimates are the slope and square root of the intercept of a straight line fitted through the data and therefore errors in the dimension estimate and $CV$ estimate are naturally complementary.
Figure 5.8  Estimated Fractal Dimensions

The range $0.539 < D < 0.955$ contains 90% of the data, or 59 of 65 runs. $Mean(D) = 0.749$ and $median(D) = 0.773$. The long-range dependence model requires $\frac{1}{2} < D < 1$ and all but two of the measured dimensions shown fall within that range. The low outlier corresponds to a 220s recording of a 7.6 sp/s unit (L-54-2). At very low rates even a long recording does not provide a sufficient number of events to estimate the recovery function well and as a consequence the variance of the dimension estimator increases (see Fig. 4.12 and Fig. 4.13). The overestimated $D$ (unit L-18-4) may be attributed to serial correlation ($\hat{\rho} = -0.08$) as discussed in Section 4.8.3 or perhaps to very strong phase locking observed in the unit (stimulus level = 40 dB at $CF = 2108$ Hz). Phase locking can distort the recovery function estimate: it may be non-monotonic, having an indentation at an interval length that corresponds to a fraction of the period.
Figure 5.9 Fractal Dimension vs. Driving Level
Each line represents recordings of a single unit under different stimulus conditions. Units were stimulated by continuous tone at CF: “o” = spontaneous, “+” = 5 dB (with respect to threshold), “x” = 15 dB, and “o” = 40 dB.
Figure 5.10 Fractal Dimension vs. $CV[v^f]$

The figure shows fractal dimension estimates plotted against estimates of the filtered coefficient of variation for the sixty-five recordings. The set of recordings is divided into low, medium, and high rate runs by the estimated mean value of the driving process. Large fractal dimensions are associated with small $CV$s. The negative serial correlation of the estimators is especially evident at low rates.
Chapter 6

Conclusions

We have established that the firing rate of each auditory-nerve fiber possesses a component that is not determined by the stimulus and this we have modeled as a fractal random process. Spike generation is modeled as a renewal process driven by a random waveform process \( \{v_t; t \geq 0\} \). The driving process requires a power-law spectrum in order to describe the data [Kumar, 1990]. This section presents a more specific description of that driving process.

6.1 The Coefficient of Variation of the Driving Process

A discernible relationship exists between the mean of the driving process and the magnitude of its "fractal noise" content as measured by the coefficient of variation. We find the coefficient of variation of the driving process at frequencies less than 1 Hz to lie in the range \( 0.06 < CV[v'_t] < 0.36 \). At driving levels greater than \( \mathcal{E}[v] = 40 \), where the estimator appears to have smaller errors, all of the observations are in the range \( 0.06 < CV[v'_t] < 0.26 \). The latter range can be expressed in terms of the signal-to-noise ratio \( 15 < SNR < 278 \). The bounds suggested by one standard deviation are \( \lambda = \bar{\lambda} \pm 17\% \) at low spike rates (~ 40 sp/s) and \( \lambda = \bar{\lambda} \pm 8\% \) at high rates (~ 100 sp/s).

6.1.1 Rate Variation Masks Stimulus Level Changes

At a particular mean firing rate, Fig. 5.5 indicates the typical size of the non-stimulus-related rate variations. It follows that a sufficiently small change in the mean rate, due to a small increase or decrease of the stimulus level, might not distinguish itself from
fractal variations. Figure 6.1, based on the rate-level functions of two units presented in [Sachs and Abbas, 1974], shows that the non-stimulus-related component in the rate of individual auditory-nerve fibers may be a determining factor of the precision with which the auditory system detects level changes of pure tones. The psychophysical measure of precision is the just noticeable difference or difference limen. It is defined as the smallest detectable change $\Delta L$ in a stimulus of size $L$. Weber’s law states that the difference limen is proportional to the size of the stimulus $\Delta L \propto L$ and therefore the difference limen is a constant when expressed in decibels with respect to stimulus level ($\Delta L_{dB} = 10 \log_{10}\left(\frac{L+\Delta L}{L}\right)$). Weber’s law does not apply for detecting the level of pure tones, in fact the acuity of the ear in detecting level changes improves as the level $L$ increases [Viemeister and Bacon, 1988]. The table in Fig. 6.1 compares the size of stimulus change ($\Delta$stim) that corresponds to one standard deviation of the spike rate to the difference limen at a comparable stimulus level. Note that the size of stimulus change masked by random rate fluctuations decreases as the stimulus level increases, in the same fashion as the difference limen. The stimulus change was arbitrarily made to correspond to one standard deviation which coincidentally yields numbers comparable in size to the difference limen: roughly 1.5 dB. The stimulus level used to determine $\Delta$stim is not the same as that reported for difference limen measurements: In the left-hand column, “dBTh” is decibels with respect to the threshold of the auditory-nerve unit and the threshold is defined in terms of increased firing rate for that fiber [Sachs and Abbas, 1974]. In the right-hand column, “dBSL” is decibels of sensation level above an absolute threshold reported by a particular subject for that sound. The latter measure therefore includes contributions of the whole auditory system including cognitive functions. Calibration of the right-hand column to the rest of the chart is therefore imprecise but it does not alter the conclusion that $\Delta L$ and $\Delta$stim are similar in size and behavior.
<table>
<thead>
<tr>
<th>stimulus level $L$</th>
<th>unit 11.7</th>
<th>unit 8.02</th>
<th>difference limen $\Delta L_{dB}$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>rate</td>
<td>$CV$</td>
<td>$\Delta$stim</td>
</tr>
<tr>
<td>5 dBTh</td>
<td>45 sp/s</td>
<td>0.154</td>
<td>2.06 dB</td>
</tr>
<tr>
<td>10</td>
<td>87</td>
<td>0.098</td>
<td>1.93</td>
</tr>
<tr>
<td>15</td>
<td>136</td>
<td>0.033</td>
<td>0.96</td>
</tr>
</tbody>
</table>

**Figure 6.1** Rate Variation Masks Stimulus Level Changes

We find the size of stimulus level fluctuation ($\Delta$stim) that corresponds to (plus-or-minus) one standard deviation of the spike rate by combining the results of Fig. 5.5 with rate level functions for two units presented in Fig. 3 of [Sachs and Abbas, 1974]. At stimulus level 5 dBTh, the firing rate of unit 11.7 is 45 sp/s. The corresponding coefficient of variation, read from a least-squares fit line through the data of Fig. 5.5, is $CV[\lambda_t] \approx 0.154$ at $\lambda = 45$. One standard deviation then is $45 \times 0.154 = 6.9$ sp/s. From the rate-level function of unit 11.7, the range 45±6.9 corresponds to a 2.06 dB range of stimulus levels. The difference limen values are the average for three human subjects indicating a level change in a 1 kHz tone with 70.7% correct responses (from Fig. 2 of [Viemeister and Bacon, 1988]). Intensity variations in the range ±1σ mask stimulus variations of a size similar to the difference limen: $\sim 1.5dB$. More importantly, the decreasing trend in $\Delta$stim as a function of stimulus level matches the trend of the difference limen. The two measures are not directly comparable because $\Delta$stim is derived from individual units whereas $\Delta L$ is a subjective measure to which the whole auditory system may contribute. The chart is empty where linear extrapolation of Fig. 5.5 would yield a negative value for the coefficient of variation. The problem arises because the coefficient of variation decreases as the rate increases and the rate-level functions of Sachs and Abbas, based on short recordings, show rates much higher than seen in the fully adapted units of our data set. The chart could be improved by using rate-level function measured from units after a long period of continuous tone stimulation.

**6.1.2 Fractal Effect is Independent of Spontaneous Rate and CF**

The $CV$ appears to depend only on the mean driving level and is independent of the characteristic frequency and the spontaneous rate of the unit under study. In Fig. 5.3 the data fall into two clusters (to the left and right of $E[v_t] = 20$). The tightly clustered high rate data points include low and high spontaneous units and low and high CF units. At low rates in Fig. 5.3, where there are only low spontaneous units, we see low and high CF units with similar $CV$s, but the clustering is less evident.
If the fractal process is indeed parameterized by the rate and invariant to the characteristic frequency, what can we infer about its origin? The well-known tonotopic organization of the basilar membrane [Kiang et al., 1965] gives structural meaning to a unit's characteristic frequency: It indicates the relative location of the hair cell driving the unit. For the fractal process to be invariant to hair cell location implies either that the fractal process originates at the hair cell level "after" the basilar membrane, or that the fractal process is present in the vibrations of the basilar membrane and propagates in such a fashion as to be invariant at different destinations. Simplicity favors the former explanation.

Fig. 5.3 shows that the noise content of the driving function is independent of spontaneous rate. Auditory nerve fibers that display low spontaneous activity have a smaller diameter than high spontaneous fibers, and the two types terminate at different locations on inner hair cells [Liberman, 1982; Liberman and Simmons, 1985]. The presence of fractal noise and its CV appear to be independent of these factors. The most plausible explanation is that the fractal phenomenon observed on the auditory nerve originate either in the hair cells or at the synaptic function between the hair cells and the primary auditory nerve fibers.

If the fractal variation originates at each hair cell then it is reasonable to conclude that separate hair cells generate independent fractal processes. There remains the possibility that the variations stem from a metabolic influence shared among hair cells. Note that the data show dependence extending over more than 60s which exceeds both the cardiac and respiration periods.

6.1.3 Structural Considerations

Two standard noise models employed in engineering are the additive noise model, observation = signal + noise, and the multiplicative noise model, observation = signal x noise. By noise, we mean a source of random behavior. For a fixed noise variance, the two structures are easily distinguishable by the effect of the signal
magnitude on the coefficient of variation. Let the observation be \( v = \bar{v} + \eta \) where \( \bar{v} = \mathcal{E}[v] \) is the signal and \( \eta \) is a zero-mean random noise with constant variance \( \text{var}[\eta] = \sigma^2_{\eta} \), then \( CV[v] \) vs. \( \mathcal{E}[v] \) is a hyperbolic curve
\[
CV[v] = \frac{\sqrt{\text{var}[\bar{v} + \eta]}}{\mathcal{E}[v]} = \frac{\sigma_{\eta}}{\mathcal{E}[v]} = \text{constant}.
\]
In the multiplicative case, the observations are \( v = \bar{v} \cdot \eta \) where \( \eta \) has unit-mean. The resulting coefficient of variation is independent of the signal level
\[
CV[v] = \frac{\sqrt{\text{var}[\bar{v} \eta]}}{\mathcal{E}[\bar{v} \eta]} = \frac{\sqrt{\bar{v}^2 \sigma^2_{\eta}}}{\bar{v}} = \sigma_{\eta} = \text{constant}.
\]
What curve best describes \( CV[v_1'] \) as a function of \( \mathcal{E}[v] \)? The data of Fig. 5.3 clearly fall into a clustered high-rate region and a low-rate region. The sharp drop in \( CV[v] \) for \( \mathcal{E}[v] > 40 \) in Fig. 5.3 suggests an additive noise model at high rates. The best fit hyperbola has the form \( \mathcal{E}[v]^{-0.64} \) rather than \( \mathcal{E}[v]^{-1} \); note that the data do not cover a sufficient range of values to estimate this exponent accurately. The spread of the low rate observations and the gap in observations for \( 15.0 < \mathcal{E}[v] < 45.6 \) makes it difficult to hypothesize curve fit at low rates, but the low-rate data points do not lie on the hyperbola that might extend from the high-rate region.

The fractal noise does not appear to obey these simple models directly. Johnson [1980] proposed that the rectifier effect of the hair cell is best modeled as an exponential function. Consequently, we anticipate that any additive noise that originates before rectification in the hair cell appears in auditory nerve statistics as a multiplicative noise. We show in Section 6.1.4 that the measurements of Fig. 5.3 are consistent with multiplicative noise embedded in a model of the hair cell transduction mechanism. This interpretation requires that the noise source be embedded in the rectification mechanism.

### 6.1.4 Mechanical to Neural Transduction in the Auditory Receptor

The decrease of the filtered driving process coefficient of variation with increasing rate (Fig. 5.3) is consistent with several models of hair cell mechano-electrical transduction
[Schroeder and Hall, 1974; Meddis, 1986; Meddis, 1988]. These models describe the course of events by which acoustic stimuli presented at the cochlear hair cells result in a probabilistic spike train on the auditory nerve based on the modulated release of transmitter into the synaptic cleft. The transmitter is the assumed chemical agent that, when present in sufficient quantity and when the nerve is susceptible, causes the nerve to fire. The role of the stimulus is to modulate the permeability of the hair cell membrane to the release of transmitter. The permeability function $k(s)$ rectifies bipolar sound pressure variations $s(t)$ into a non-negative waveform. Meddis’ “model B” is governed by a set of 3rd order ODEs that regulate the flow of transmitter among three reservoirs: the free transmitter pool, the synaptic cleft, and the reprocessing store. The main motivation for the model is that with the proper choice of constants it can reproduce many short-term phenomena present in auditory nerve observations, in particular adaptation.

Schroeder and Hall [1974] observe that “the firing probability is asymptotically independent of signal amplitude.” In fact, in their model as well as Meddis’, the steady-state amount of transmitter in the synaptic cleft is entirely determined by the constants of the model and the mean rectified stimulus level. In the notation of model B, the steady state level of transmitter in the synaptic cleft is

$$c = \frac{k}{r + l + kl/y}$$

(6.1)

$$0 < k < 1000, \quad r = 16667, \quad l = 1250, \quad y = 11.11$$

and $c$ is proportional to the driving level $v$. Our measurements indicate that under constant stimulus the driving level $v$ (hence $c$ above) experiences random variations over long time scales ($1s < t < 60s$). The transmitter dynamics of model B are deterministic, however the possibility that the model parameters may exhibit slow random variations is not inconsistent with Meddis’ findings because that model describes short term phenomena of duration less than 300ms. For the 600s recordings of this study, model B may be considered to be continually at equilibrium. Consequently the firing rate for a long recording must track the equilibrium point of the model expressed in
Eq.6.1. We consider the possibility that each of the “constants” of Eq.6.1, is in fact a random parameter with a constant coefficient of variation, and ask the question: What is the coefficient of variation of the driving level \( CV[c] \) \((= CV[u])\) that results? How does it vary with the mean driving level \( c \) \((\propto \E[u])\)? The relative sensitivity of \( c \) to each model parameter is

\[
\frac{CV[c]}{CV[l]} = \frac{l}{c} \frac{\partial c}{\partial l} = \frac{l}{r + l} \left(1 + \frac{c}{y}\right)
\]

\[
\frac{CV[c]}{CV[y]} = \frac{k}{c} \frac{\partial c}{\partial y} = \frac{l}{y}
\]

\[
\frac{CV[c]}{CV[k]} = \frac{k}{c} \frac{\partial c}{\partial k} = 1 - \frac{c}{y}
\]

\[
\frac{CV[c]}{CV[r]} = \frac{r}{c} \frac{\partial c}{\partial r} = \frac{r}{r + l} \left(1 - \frac{l}{y}\right)
\]

The last two equations show the diminishing sensitivity with mean (i.e. with \( c \)) indicated by our observations. The parameter \( k \) is the membrane permeability and parameter \( r \) controls the rate at which transmitter metabolites are recycled from the synaptic cleft by the hair cell. A plausible explanation of the the observations of Fig. 5.3 (that the driving process has a smaller \( CV \) at high rates) is provided by the possibility that the membrane permeability, though modulated by the stimulus also has a multiplicative (i.e. constant \( CV \)) random component with long term memory. In particular, Fig. 6.2 shows the effect that \( CV[k] = 0.253 \) could be expected to have on the \( CV[u] \) vs. \( \E[u] \) curve. A similar property in the recovery rate \( r \) also explains the data.

### 6.2 Adaptation

We have suggested that the long recordings in which fractal dependence can be measured in some way track the equilibrium of the hair cell. This statement does not imply a connection between adaptation and the fractal effect. In fact, the very opposite is true. Fractal dependence is measured in recordings of spontaneous activity as well as driven activity. Spontaneous activity lacks adaptation but shows fractal
Figure 6.2 Agreement with Meddis model

In equilibrium, the neuro-transmitter based model of [Meddis, 1988] shows decreasing sensitivity to variations in the membrane permeability as the amount of transmitter in the synaptic cleft $c$ (proportional to $\mathcal{E}[v]$) increases. The model proposes the transmitter flow into the synaptic cleft is a constant $q$ times the membrane permeability $k$ which is signal modulated. In the context of the low frequency variations associated with fractal noise, we consider the possibility that the flow $k$ is a random process at time scales beyond those modeled in the original paper (300ms). The figure shows the coefficient of variation expected in the driving process $CV[v]$ under the assumption that the coefficient of variation of the permeability $k$ is constant ($CV[k] = 0.253$ is shown). Increasing $c$ diminishes the sensitivity of the cleft pool size $c$ to variations of the transmitter inflow $kq$. The solid line is the $CV[v]$ predicted by Meddis' model. Note from Fig. 4.12 that $\mathcal{E}[v]$ has strong negative bias at high rates suggesting that the true data lie closer to Meddis' prediction than shown.
variation. Driven activity shows rate adaptation and fractal variation, but we must select segments of each recording that do not exhibit adaptation in order to measure the parameters of the fractal process.

6.3 Fractal Dimension

Several researchers have noted that the fractal dimension increases as the firing rate increases. The distinction between the Fano factor curve of the counts (\( \text{var} [N_T] / \mathcal{E}[N_T] \)) and the Fano factor curve of the driving process (\( \text{var} [T_T] / \mathcal{E}[T_T] \)) is important. The first is a statistic of the data, whereas the second is a model-based estimate that depends on the applicability of doubly stochastic renewal process model. Asymptotically, both curves have a slope equaling the fractal dimension (on a log-log plot). For finite data sets, the slope measured from the count curve is less than the slope measured from the driving process curve; the difference is attributable, in part, to the refractory properties of the point process. As an estimator of the driving process dimension, the slope measured from the count curve has negative bias, and the bias diminishes as the rate increases. Referring to the slope of the Fano-time curve of the counts, Teich et. al. [1990b] report an increased fractal dimension under stimulation compared to that measured from spontaneous activity. This effect alone does not imply a change in the dimension of the driving process under a doubly stochastic model and may be due to reduced negative bias. The pertinent question is whether the dimension of the driving process changes under stimulus, and the answer requires dimension estimates that incorporate the biasing effect of refractoriness. Using such a method, Teich [1992] has found that the fractal dimension of the driving process increases with rate. Fig. 5.9 neither supports nor contradicts that hypothesis.

6.4 Future Work

Our main results follow from the estimation technique developed in Chapter 4. Three improvements are suggested here.
The chief shortcoming of the technique is the arbitrariness of the smoothing parameter. What is needed is an additional consistency check between the data and the estimated recovery function. The current model reproduces the firing rate and the hazard function of the original data over the range of intervals present in the data.

The estimate $\bar{u}$ of the mean value of the driving function $E[v]$ has strong negative bias (Fig. 4.12), due in large part to the fact that at high rates the intervals of the process are seldom long enough to "sample" the plateau portion of the recovery function. It may be possible, within the variable intensity framework of the recovery function estimation step, to adjoin data records from the same unit at different stimulus levels (Eq.4.3). In this way, the plateau level of the hazard function can be established by data from spontaneous activity and the small interval detail of the recovery function can be established by the data from stimulated activity. This strategy assumes that the recovery function is invariant to changes in the firing rate, an assumption implicit in the multiplicative renewal process model driven by a non-constant function. Having made the assumption, we should have its full benefit.

The Fano factor estimates are sensitive to unmodeled serial correlation (see Fig. 4.10). We have not thoroughly investigated the possibility, presented in Fig. 4.9, that the effects of negative serial correlation can be accounted for in the estimate of the driving process Fano factor curve. That effort might require a serial correlation model for the auditory nerve activity akin the LSO model by Zacksenhouse [1993].

Two new types of data are needed. First, the methods of this study should be applied to units with a firing rate in the range $14.5 < \lambda < 37.8$ sp/s, driven or spontaneous. The key figures (Fig. 5.3 and Fig. 5.5) lack data in that range. Second, a thorough investigation of the relationship between the difference limen for level discrimination and the rate variability of primary auditory-nerve fibers requires measurements of the rate-level functions for adapted units. The rate-level functions used to make Fig. 6.1 are based on 400 ms stimulus presentations and therefore have higher rates than are typically found in long continuous tone recordings. In order the con-
struct a function that measures the coefficient of variation as a function of stimulus level, we must combine the $CV$ versus rate data of Fig. 5.5 with rate-level functions measured after prolonged stimulus by a pure tone.

The source of long-range memory in the auditory periphery lies within the inner hair cells. Experiments and models directed at the source of this fractal variation must distinguish between stimulus induced variation and non-stimulus induced variation in the cellular quantities that control transmitter release.

It is an open question whether a fractal model of auditory nerve activity must possess a single fractal dimension $D$. Teich [1992] states that different sections of a single recording may yield differing estimates of $D$ but this could be attributed to variance of the estimator rather than variance of the actual parameter $D$. 
Appendix A

Lower Bound for $\text{var}[N_{t,t+T}]$

**Theorem A.1** Let $\{N_t; t \geq 0\}$ be a doubly stochastic renewal process with bounded recovery function $r(t)$ and driving function $s(t) = m(t) + \epsilon \eta(t)$ where $m(t) > 0$ is a deterministic function, $\eta(t)$ is a bounded zero mean random waveform process, and $\epsilon$ is a scalar. Let $0 \leq r(t) < R$ and $|\eta(t)| < B$ and let $\epsilon$ be chosen so that $s(t) > \delta > 0 \forall t$ for some small $\delta$. Then, as a function of $\epsilon$, $\text{var}[N_{t,t+T}]$ has a stationary point at $\epsilon = 0$.

**Proof.** Without loss of generality, consider the interval $[0, T)$. The idea of the proof is to show that the partial derivative with respect to $\epsilon$ of each mass of the probability mass function $p(N_T = n)$ vanishes at $\epsilon = 0$. For a doubly stochastic renewal process the joint density of the number of events $N_T$, and their occurrence times $w = \{w_1, \ldots, w_{N_T}\}$ in the interval $[0, T)$ is given by Snyder [1975, p.64]:

$$p(N_T = n; w|\eta; \epsilon) = \exp \left(- \int_0^T s(\alpha)r(\alpha - w_{N_\alpha}) \, d\alpha + \int_0^T \log(s(\alpha)r(\alpha - w_{N_\alpha})) \, dN_{\alpha} \right)$$

with first derivative

$$\frac{d}{d\epsilon} p(N_T = n; w|\eta; \epsilon) = \left[- \int_0^T \eta(\alpha) r(\alpha - w_{N_\alpha}) \, d\alpha + \int_0^T \frac{\eta(\alpha)}{s(\alpha)} dN_{\alpha} \right] \times$$

$$p(N_T = n; w|\eta; \epsilon). \quad (A.1)$$

Assuming that the order of the integrations and differentiation can be changed, Eq. A.1 can be used to find $\frac{d}{d\epsilon} p(N_T = n)$.

$$\frac{d}{d\epsilon} p(N_T = n) = \frac{d}{d\epsilon} E p(N_T = n|\eta; \epsilon) \quad (A.2)$$

$$= \frac{d}{d\epsilon} E \int p(N_T = n; w|\eta; \epsilon) \, dw \quad (A.3)$$
\[
\frac{d}{d\epsilon} \int \mathcal{E} p(N_T = n; w|\eta; \epsilon) \, dw \\
= \int \frac{d}{d\epsilon} \mathcal{E} p(N_T = n; w|\eta; \epsilon) \, dw \\
= \int \mathcal{E} \frac{d}{d\epsilon} p(N_T = n; w|\eta; \epsilon) \, dw
\]

(A.4) (A.5) (A.6)

In order to evaluate Eq. A.6 at \( \epsilon = 0 \) it is sufficient to evaluate the expectation of Eq. A.1 at \( \epsilon = 0 \). Note that for \( \epsilon = 0 \), \( s(t) = m(t) \) and \( w \) becomes independent of \( \eta \).

\[
\mathcal{E} \left. \frac{d}{d\epsilon} p(N_T = n; w|\eta; \epsilon) \right|_{\epsilon=0} = \\
\mathcal{E} \left\{ -\int_0^T \eta(\alpha) r(\alpha - w_{N\alpha}) \, d\alpha + \int_0^T \frac{\eta(\alpha)}{s(\alpha)} \, dN\alpha \right\} p(N_T = n; w|\eta; \epsilon) \\
= \mathcal{E} \left[ -\int_0^T \eta(\alpha) r(\alpha - w_{N\alpha}) \, d\alpha + \int_0^T \frac{\eta(\alpha)}{m(\alpha)} \, dN\alpha \right] p(N_T = n; w|\eta; \epsilon) \\
= \left[ -\int_0^T \mathcal{E} \eta(\alpha) \mathcal{E} r(\alpha - w_{N\alpha}) \, d\alpha + \int_0^T \frac{\mathcal{E} \eta(\alpha)}{m(\alpha)} \, dN\alpha \right] p(N_T = n; w|\eta; \epsilon) \\
= 0
\]

The last step follows from the assumption \( \mathcal{E} \eta(t) = 0 \). Thus \( \frac{d}{d\epsilon} p(N_T = n) \big|_{\epsilon=0} = 0 \) and \( \frac{d}{d\epsilon} \text{var} [N_{t,T+t}] = 0 \) as claimed.

Eq. A.4 follows from Fubini's theorem and the boundedness of \( p(N_T = n; w|\eta; \epsilon) \). Eq. A.5 and Eq. A.6 require the Lebesgue Dominated Convergence Theorem. In Eq. A.6, the interchange of \( \frac{d}{d\epsilon} \) and \( \mathcal{E}_\eta \) requires that \( \frac{d}{d\epsilon} p(N_T = n; w|\eta; \epsilon) \) is bounded over \( \epsilon \) and \( \eta \) for fixed \( w \).

\[
\left| \frac{d}{d\epsilon} p(N_T = n; w|\eta; \epsilon) \right| \leq \int_0^T |\eta(\alpha)| r(\alpha - w_{N\alpha}) \, d\alpha + \sum_{i=1}^n \frac{\eta(w_i)}{s(w_i)} \right\} \leq TBR + \frac{n}{\delta} B
\]

(A.7) (A.8)

and \( w \) being fixed, fixes \( n \) and the interchange is justified. In Eq. A.5 we may interchange \( \frac{d}{d\epsilon} \) with \( \int dw \) provided \( \frac{d}{d\epsilon} \mathcal{E} p(N_T = n; w|\eta; \epsilon) \) is bounded over \( \epsilon \) and \( w \).

We again interchange \( \frac{d}{d\epsilon} \) and \( \mathcal{E}_\eta \) and the boundedness requirement becomes

\[
\left| \mathcal{E} \frac{d}{d\epsilon} p(N_T = n; w|\eta; \epsilon) \right| < \mathcal{E} \left| \frac{d}{d\epsilon} p(N_T = n; w|\eta; \epsilon) \right|.
\]

(A.9)

The argument of the term at right is bounded by A.8 which is independent of \( \eta \).
Appendix B

Interval Covariance of Fractal Intensity Poisson Process

Let \( \{N_t; t \geq 0\} \) be a doubly stochastic Poisson process with intensity process \( \{u_t; t \geq 0\} \) which has the property that \( \text{cov}[u_t, u_{t+T}] \propto T^{-h} \) for some \( h > 0 \) when \( T \) is large. The following analysis shows that, provided \( u_t \) is slowly varying, the approximation \( \text{cov}[\tau_i, \tau_{i+m}] \propto m^{-h} \) holds.

Consider \( \{\tau_i\} \) as a sequence of conditionally independent random variables, each distributed according to a parametric density with parameter \( u_i \), then

\[
\text{cov}[\tau_i, \tau_{i+m}] = \mathcal{E}[\mathcal{E}[\tau_i \mid \tau_{i+m} \mid u_i, u_{i+m}]] - \mathcal{E}[\tau_i] \mathcal{E}[\tau_{i+m}]
\]

\[
= \mathcal{E}[\mathcal{E}[\tau_i \mid u_i] \mathcal{E}[\tau_{i+m} \mid u_{i+m}]] - \mathcal{E}[\tau_i] \mathcal{E}[\tau_{i+m}].
\]

It follows that if \( \tau_i \) are exponentially distributed with parameter \( u_i \) then

\[
\text{cov}[\tau_i, \tau_{i+m}] = \text{cov}\left[\frac{1}{u_i}, \frac{1}{u_{i+m}}\right]
\]

exactly. A first order expansion of \( 1/x \) about \( \bar{u} \equiv \mathcal{E}[u] \) gives the result

\[
\text{cov}[\tau_i, \tau_{i+m}] \approx \frac{\text{cov}[u_i, u_{i+m}]}{\bar{u}^4}.
\]

At this point we need simply make the connection that \( u_i \approx u_{w_{i-1}} \) and retrace our steps to verify the argument. (Recall \( w_i \) is the time of occurrence of the \( i^{th} \) event.) Two approximations arise. First, \( \tau_i \) and \( \tau_{i+m} \) cannot be independent because \( \tau_i < w_{i+m} \), but their asymptotic independence can be shown easily. Second, we approximate that \( \mathcal{E}[\tau_i] = u_{w_{i-1}}^{-1} \) which holds if \( u_i \) varies slowly enough that it may be treated as constant for a duration of \( O(1/\bar{u}) \).
Figure B.1 Power-Law Spectrum of Poisson Intervals
A sequence of frames is constructed by adding each 20 adjacent intervals (without overlap) of a doubly stochastic Poisson process driven by a $1/f$ process. The figure shows that the reciprocal intensity process, and the frame sequence inherit the "$1/f$" structure of the intensity process. The $y$-axis is not to scale.
Figure B.2 Assumptions for the Power-Law Spectrum of Intervals

The derivation of long-range power-law correlation for intervals of fractal intensity Poisson process (Fig. B.1) relies on the assumption that the driving process is slowly varying (smooth). However, point processes are intrinsically integrators and the first two traces show that the approximation holds whether or not the driving process is actually smooth. The smoothed intensity was lowpass filtered at 200Hz. The third trace shows that the power-law trend in the spectrum of the interval sequence disappears below the “Poisson” noise floor at high frequencies. Averaging via construction of the frame sequence, as for the first two traces, ensures that the power-law structure appears at all frequencies. The fourth trace is included to demonstrate that power-law driving functions generate power-law correlated intervals for renewal processes as well as the Poisson processes considered in the first three traces. The fourth trace shows the spectrum of the frame sequence constructed from the intervals of unit L-19-3.
Bibliography


