Refractory Effects in Neural Counting Processes with Exponentially Decaying Rates

PAUL R. PRUCNAL, MEMBER, IEEE, AND MALVIN C. TEICH, SENIOR MEMBER, IEEE

Abstract—The effect of nonparalyzable dead time on Poisson point processes with random integrated rates is studied. The case of exponentially decreasing rate, plus background (pedestal), with a uniformly uncertain starting time is explicitly presented. The decay time is considered to be slow compared to the refractory time. No constraints on the sampling time are imposed for calculating the mean and variance, though for the counting distribution, the sampling time must be short compared to the decay time. The results are expected to be useful in neurobiology, neural counting, psychophysics, photon counting, nuclear counting, and radiochemistry.

I. Introduction

The effects of dead time (refractoriness) on homogeneous (constant rate) Poisson point processes has received considerable attention and has been studied by a number of researchers in neural counting [1]–[6], photon counting [3], [7]–[11], and nuclear counting [3], [12]–[14]. Many cases have been studied in detail, including paralyzable (extended) and nonparalyzable (nonextended) counting under blocked, unblocked, and equilibrium conditions. Attention has also been given to the gradual recovery (sick-time) system [6] and to the variable refractory case [2]. Müller has summarized the results of a number of authors [13], [14] and has compiled a comprehensive and very useful bibliography on refractory effects [15].

Although most of the work on refractoriness cited above is applicable only when the input to the counter is a Poisson point process with constant rate, a few results are also available for the case in which the rate is not constant. Bédard [7], Cantor and Teich [8], Teich and McGill [16], and Saleh *et al.* [17] present expressions for the counting distribution when the rate is a random process. Restrictions are placed on the ratio of coherence to sampling times in each of these cases. The counting distribution has also been calculated when the rate is a known function of time and the sampling time is uniformly uncertain [9], [10]. Expressions were obtained for the mean and the variance of the

Manuscript received August 22, 1982; revised June 13, 1983. This work was supported by the National Science Foundation.

The authors are with the Department of Electrical Engineering, Columbia University, New York, NY 10027.

0018-9472/83/0900-1028$01.00

number of events in a given time interval for a nonextended refractory counter when the input process is Poisson with a rate that is a known function of time [18], and an arbitrary stochastic process [17], [19]. Finally, the interevent probability density was obtained for a shot-noise random rate [20].

The transient behavior of certain neural processes can sometimes be described by a dead-time-modified Poisson point process with a rate that decreases in a typically exponential fashion. The mean and variance for some simple cases of this type have been studied by Müller [21] and Harris [22].

In this correspondence the effect of nonextended refractoriness on Poisson point processes with random integrated rate is studied. The case of exponentially decaying rate plus background (pedestal), with uniformly uncertain starting time, is presented. The decay time is considered to be slow compared to the refractory time. No constraints on the sampling time are imposed for calculations of the mean and variance, whereas for the counting distribution the sampling time must be short compared to the decay time. The case considered is that for which the counter is always connected to the input process; this is the equilibrium counter as opposed to the blocked or unblocked counter. Actually, in the limits where our results are applicable, the number of pulses recorded during a sampling time is much greater than unity, and therefore the differences among blocked, unblocked, and equilibrium counters become negligible, so that our results are indeed valid for all three types of counters.

In Section II, the theory for a dead-time-modified Poisson point process with random integrated rate is presented. The collected results are discussed in Section III. A number of applications in neural counting are presented in Section IV.

II. Theory

Consider a Poisson point process whose rate is a known function of time $\lambda(t)$ in the absence of dead-time effects. The probability $p(n)$ that n events occur, in an interval beginning at time t_0 and of duration T, is then given by the Poisson density function $\mathrm{poid}(n, \mathrm{E}[n])$, defined in the upper left quadrant of Table I. Both the expected value and the variance of n are equal to the integrated rate $M(t_0, T)$.

For example, let the known rate correspond to an exponential function, of maximum value Λ_1 and time constant τ_c, superimposed on a (constant) pedestal of value Λ_0. In that case,

$$\lambda(t) = \Lambda_0 + \Lambda_1 \exp(-t/\tau_c). \tag{1}$$

Integrating the rate function between the limits t_0 and $t_0 + T$ yields

$$M(t_0, T) = \Lambda_0 T + \Lambda_1 \tau_c \exp(-t_0/\tau_c) f_1(T), \tag{2a}$$

where

$$f_1(T) \equiv 1 - \exp(-T/\tau_c). \tag{2b}$$

Now if the integrated rate is a random variable, then n is conditionally a Poisson random variable. The conditioning is removed by taking the expectation with respect to the statistics of $M(t_0, T)$, as illustrated in the lower left quadrant of Table I. The integrated rate may be random by virtue of the rate itself being a random process (in which case the point process is doubly stochastic), or by virtue of t_0 or T being a random variable (in which case the point process is mixed), or any combination of these. If the rate itself is a random process, then the expectation described above is sometimes, but not always [23], difficult to evaluate for arbitrary values of T, and this case will not be considered further here [11], [24, p. 287]. On the other hand, if the rate is deterministic, and t_0 or T is a random variable, the expectation described above is generally straightforward to evaluate with respect to the statistics of t_0 or T [25]–[27].

For example, let t_0 be uniformly distributed over the time interval (t_1, t_2), where $0 < t_1 < t_2$. Taking the expectations with respect to t_0 in the lower left quadrant of Table I yields

$$p(n) = \frac{1}{t_2 - t_1} \int_{t_1}^{t_2} \mathrm{poid}(n | M(t_0, T))\, dt_0 \tag{3a}$$

$$\mathrm{E}[n] = \frac{1}{t_2 - t_1} \int_{t_1}^{t_2} M(t_0, T)\, dt_0 \tag{3b}$$

$$\mathrm{var}[n] = \mathrm{E}[n] - \mathrm{E}[n]^2 + \frac{1}{t_2 - t_1} \int_{t_1}^{t_2} M(t_0, T)^2\, dt_0. \tag{3c}$$

For the specific example where the rate corresponds to a decreasing exponential function superimposed on a pedestal, and t_0 is again uniform, the integrated rate given in (2a) is substituted in (3), and the result is integrated, yielding

$$p(n) = [-\tau_c/(t_2 - t_1)\Gamma(n+1)] \sum_{j=0}^{\infty} (\Lambda_0 T)^j \cdot [\Gamma(n-j, M(t_1, T)) - \Gamma(n-j, M(t_2, T))], \tag{4a}$$

$$\mathrm{E}[n] = \Lambda_0 T - \Lambda_1 \tau_c^2 f_1(T) f_2(t_2, t_1)/(t_2 - t_1), \tag{4b}$$

$$\mathrm{var}[n] = \mathrm{E}[n] - \Lambda_1^2 \tau_c^3 f_1^2(T) f_2(2t_2, 2t_1)/2(t_2 - t_1) - \Lambda_1^2 \tau_c^4 f_1^2(T) f_2^2(t_2, t_1)/(t_2 - t_1)^2. \tag{4c}$$

Here

$$f_2(t_2, t_1) \equiv \exp(-t_2/\tau_c) - \exp(-t_1/\tau_c), \tag{4d}$$

$f_1(T)$ is defined in (2b), $M(t_0, T)$ is defined in (2a), $\Gamma(\cdot)$ is the gamma function, and $\Gamma(\cdot,\cdot)$ is the incomplete gamma function, defined as [28, p. 260, 6.5.3]

$$\Gamma(\alpha, \beta) = \int_{\beta}^{\infty} z^{\alpha - 1} e^{-z}\, dz, \tag{4e}$$

for $\alpha > 0$. For $\alpha = 0$ and $\alpha < 0$, the incomplete gamma function is defined in terms of the exponential integral [28, p. 262, 6.5.15, 6.5.19]. Equations (4a)–(4e) reduce to the results derived by Müller [21, eqs. (9), (17), and (19)] in the limit $T \ll \tau_c$, and in the limit $\Lambda_0 = 0$ reduce correctly to the results of Teich and Card [26].

Now consider a Poisson point process whose rate is a known function of time, but where certain events are ignored (or lost) due to refractoriness (dead time). In this way, a given event is followed by a time interval of fixed duration τ_d, during which subsequent events are ignored. It is assumed that the refractory period is not extended by those events which are ignored (nonextended or nonparalyzable case). It is also assumed that $T \gg \tau_d$ so that the distinction between the blocked, unblocked, and equilibrium cases disappears. Let τ_c represent the length of time over which $\lambda(t)$ changes significantly (coherence time). The statistics of n have been obtained under the condition that $\tau_d \ll \tau_c, T$, and are shown in the upper right quadrant of Table I. The probability of n events occurring in the interval $(t_0, t_0 + T)$ has the additional restriction that $T \ll \tau_c$. Under this condition the integrated rate reduces to

$$M(t_0, T) = \lambda(t_0) T. \tag{5}$$

For the example where the known rate corresponds to a decaying exponential function superimposed on a pedestal, the count mean and variance are obtained by substituting the right side of (1) into the integrands in the upper right quadrant of Table I, yielding (under the restrictions specified in Table I)

$$\mathrm{E}[n] = \frac{\Lambda_0 T}{g} + \left(\frac{\Lambda_0 \tau_c}{g} + \frac{\tau_c}{\tau_d}\right) \ln\left[\frac{f_3(t_0 + T)}{f_3(t_0)}\right], \tag{6a}$$

$$\mathrm{var}[n] = \tau_c \left[\frac{\Lambda_0}{g^2}\left(\frac{1}{y_0} - \frac{1}{y_1}\right) + \left(\frac{\Lambda_0}{2g} - \frac{1}{2\tau_d}\right)\left(\frac{1}{y_0^2} - \frac{1}{y_1^2}\right) + \frac{\Lambda_0}{g^3}\left(\ln\frac{y_1}{y_0} + \frac{T}{\tau_c}\right)\right], \tag{6b}$$

TABLE I

COUNTING DISTRIBUTION $p(n)$, MEAN $E[n]$, AND VARIANCE $var[n]$, FOR A POISSON POINT PROCESS WHERE THE INTEGRATED RATE IS KNOWN (TOP HALF) OR RANDOM (BOTTOM HALF), AND WHERE THE STATISTICS ARE UNMODIFIED (LEFT HALF) OR MODIFIED (RIGHT HALF) BY NONEXTENDED FIXED DEAD TIME[a]

	Unmodified by Refractoriness	Modified by Refractoriness (restriction a)	
Known Integrated Rate	$p(n) = \text{poid}(n, E[n]) = E[n]^n \exp(-E[n])/n!$	$p(n)$ (restriction b) $= \sum_{k=0}^{n} \text{poid}(k \mid M(t_0,T)[1-nr]) - \sum_{k=0}^{n-1} \text{poid}(k \mid M(t_0,T)[1-(n-1)r]),$	$n < \frac{T}{\tau_d} = \frac{1}{r};$
		$1 - \sum_{k=0}^{n-1} \text{poid}(k \mid M(t_0,T)[1-(n-1)r]),$	$\frac{T}{\tau_d} \leq n < \frac{T}{\tau_d} + 1;$
		$0,$	$n \geq \frac{T}{\tau_d} + 1$
	$E[n] = M(t_0,T) = \int_{t_0}^{t_0+T} \lambda(t)\,dt$	$E[n] = \int_{t_0}^{t_0+t} \frac{\lambda(t)}{1+\tau_d\lambda(t)}\,dt$	
	$var[n] = E[n]$	$var[n]$ (restriction c) $= \int_{t_0}^{t_0+T} \frac{\lambda(t)}{[1+\tau_d\lambda(t)]^3}\,dt$	
Random Integrated Rate	$p(n) = E[\text{poid}(n \mid M(t_0,T))]$	$p(n)$ (restriction b) $= \sum_{k=0}^{n} E[\text{poid}(k \mid M(t_0,T)[1-nr])] - \sum_{k=0}^{n-1} E[\text{poid}(k \mid M(t_0,T)[1-(n-1)r])],$	$n < \frac{T}{\tau_d};$
		$1 - \sum_{k=0}^{n-1} E[\text{poid}(k \mid M(t_0,T)[1-(n-1)r])],$	$\frac{T}{\tau_d} \leq n < \frac{T}{\tau_d} + 1;$
		$0,$	$n \geq \frac{T}{\tau_d} + 1$
	$E[n] = E[M(t_0,T)]$	$E[n] = E[\int_{t_0}^{t_0+T} \frac{\lambda(t)}{1+\tau_d\lambda(t)}\,dt]$	
	$var[n] = E[n] + var[M(t_0,T)]$	$var[n]$ (restriction c) $= E[\int_{t_0}^{t_0+T} \frac{\lambda(t)}{[1+\tau_d\lambda(t)]^3}\,dt] + E[(\int_{t_0}^{t_0+T} \frac{\lambda(t)}{1+\tau_d\lambda(t)}\,dt)^2] - E[n]^2$	

[a] Restrictions applying to designated equations are: [a] $\tau_d \ll \tau_c, T$ for all cases; [b] $T \ll \tau_c$ and therefore $M(t_0,T) = \lambda(t_0)T$; [c] $(E[\lambda]\tau_d)^2\tau_d/6 \ll \tau_c$.

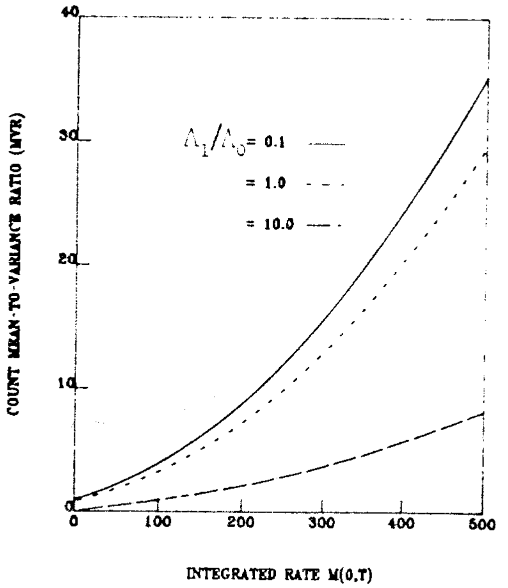

Fig. 1. Count mean-to-variance ratio (MVR) versus integrated rate $M(0, T)$ for known exponential rate (with pedestal) and nonextended refractoriness. The case shown corresponds to $\tau_c = 30$, $\tau_d = 3$, $t_0 = 0$, $T = 300$, $\Lambda_1/\Lambda_0 = 0.1$, 1, and 10.

where

$$g = 1 + \tau_d \Lambda_0 \tag{6c}$$

$$y_0 = 1 + \lambda(t_0) \tag{6d}$$

$$y_1 = 1 + \lambda(t_0 + T) \tag{6e}$$

$$f_3(t) = 1 + \tau_d \lambda(t). \tag{6f}$$

The expression for $p(n)$ is obtained by substituting the right side of (1) directly into the summations in the upper right quadrant of Table I. All of these formulas are subject to the conditions indicated in Table I.

In Fig. 1 we plot the count mean-to-variance ratio (MVR) versus the integrated rate $M(0, T)$ obtained from (6a), (6b), and (2a). The parameters chosen are $\tau_c = 30$, $\tau_d = 3$, $t_0 = 0$, $T = 300$, $\Lambda_1/\Lambda_0 = 0.1$, 1, and 10. It is apparent that the MVR becomes larger as $M(0, T)$ increases. The parameter Λ_1/Λ_0 represents the ratio of the maximum value of the exponential rate to the value of the constant pedestal. In the limit $\Lambda_1/\Lambda_0 \ll 1$, the exponential can be neglected with respect to the pedestal, and we should recover the results for a dead-time-modified Poisson process with constant rate, for which MVR $= \mathrm{E}[n]/\mathrm{var}[n] = [1 + M(0, T)\tau_d/T]^2$, [18]. The curve for $\Lambda_1/\Lambda_0 = 0.1$ illustrated in Fig. 1 does indeed approximate this parabolic behavior. For increasing values of Λ_1/Λ_0, the variation of the integrated driving rate causes the mean-to-variance ratio to decrease for all values of $M(0, T)$. It is well known that dead time deletes highly bunched events more effectively than relatively unbunched events. Thus, the counting efficiency for a dead-time-modified Poisson process of known but variable rate will be reduced below that for the constant-rate case [18]. The behavior of the count variance, which represents the regularization of the pulse train, is more complex [18]. We find from Fig. 1 that increasing values of Λ_1/Λ_0 result in decreasing values of the MVR at all values of $M(0, T)$. This behavior is similar to that produced by other dead-time-modified Poisson processes of known but variable rate [18] and of random rate, as exemplified by the Bose–Einstein distribution [8]. Initially bunched processes retain higher variability (lower MVR) under the effects of dead time than do initially Poisson processes.

Finally, if the integrated rate is a random process or random variable, and $T \ll \tau_c$, then n is conditionally a dead-time-modified Poisson random variable. The conditioning is removed by taking the expectation with respect to the statistics of $M(t_0, T)$, as illustrated in the lower right quadrant of Table I. The resulting variance for the modified case is expressed as the expectation of the conditional variance plus the variance of the conditional expectation, as in the unmodified case (see the variance expressions in the lower left and lower right quadrants of Table I). If the conditional expectation is not random, then the variance reduces simply to the expectation of the conditional variance. A number of interesting cases, in which the integrated rate is a random process, have been dealt with previously. $p(n)$ has been obtained for laser light and chaotic light [8], and for interfering superpositions of coherent and chaotic light [16], in the short-counting-time limit ($T \ll \tau_c$). $p(n)$ has also been obtained for a shot-noise rate, under special conditions, in the long-counting-time limit ($T \gg \tau_c$). The result is the Neyman Type-A, which does not conform to the restrictions specified in Table I. The count mean and count variance have also been explicitly calculated, with T arbitrary, for shot-noise light [17] and for chaotic light [19].

As an example in this category that may be useful in neural counting, we now assume that the rate is a known function, but that randomness is introduced by letting t_0 be uniformly distributed over the time interval (t_1, t_2), where again $0 < t_1 < t_2$. The integrated rate is therefore random. Taking the expectation with respect to t_0 in the lower right quadrant of Table I yields

$$p(n) = \begin{cases} \displaystyle\sum_{k=0}^{n} \frac{1}{t_2 - t_1} \int_{t_1}^{t_2} \mathrm{poid}\,(k|M(t_0, T)[1 - nr])\, dt_0 \\ \displaystyle\quad - \sum_{k=0}^{n-1} \frac{1}{t_2 - t_1} \int_{t_1}^{t_2} \mathrm{poid}\,(k|M(t_0, T)[1 - (n-1)r])\, dt_0, & n < \dfrac{T}{\tau_d}; \\ \displaystyle 1 - \sum_{k=0}^{n-1} \frac{1}{t_2 - t_1} \int_{t_1}^{t_2} \mathrm{poid}\,(k|M(t_0, T)[1 - (n-1)r])\, dt_0, & \dfrac{T}{\tau_d} \leqslant n < \dfrac{T}{\tau_d} + 1; \\ 0, & n \geqslant \dfrac{T}{\tau_d} + 1; \end{cases} \tag{7a}$$

$$\mathrm{E}[n] = \frac{1}{t_2 - t_1} \int_{t_1}^{t_2} \int_{t_0}^{t_0 + T} \frac{\lambda(t)}{f_3(t)}\, dt\, dt_0, \tag{7b}$$

$$\mathrm{var}[n] = \frac{1}{t_2 - t_1} \int_{t_1}^{t_2} \int_{t_0}^{t_0 + T} \frac{\lambda(t)}{f_3^3(t)}\, dt\, dt_0 + \frac{1}{t_2 - t_1} \int_{t_1}^{t_2} \left\{ \int_{t_0}^{t_0 + T} \frac{\lambda(t)}{f_3(t)}\, dt \right\}^2 dt_0 - \mathrm{E}[n]^2, \tag{7c}$$

where $r \equiv \tau_d/T$, and where the restrictions specified in Table I apply. For the specific example where the rate corresponds to an exponential function superimposed on a pedestal, the integrated rate given in (2a) is substituted in (7), and the result is integrated, yielding

$$p(n) = \begin{cases} \dfrac{\tau_c}{t_2 - t_1} \displaystyle\sum_{j=0}^{\infty} (\Lambda_0 T[1 - nr])^j \sum_{k=0}^{n} \frac{\Gamma(k-j, M(t_1, T)[1-nr]) - \Gamma(k-j, M(t_2, T)[1-nr])}{\Gamma(k+1)} \\ \quad - \dfrac{\tau_c}{t_2 - t_1} \displaystyle\sum_{j=0}^{\infty} (\Lambda_0 T[1-(n-1)r])^j \\ \quad \cdot \displaystyle\sum_{k=0}^{n-1} \frac{\Gamma(k-j, M(t_1, T)[1-(n-1)r]) - \Gamma(k-j, M(t_2, T)[1-(n-1)r])}{\Gamma(k+1)}, & n < \dfrac{T}{\tau_d}; \\ 1 - \dfrac{\tau_c}{t_2 - t_1} \displaystyle\sum_{j=0}^{\infty} (\Lambda_0 T[1-(n-1)r])^j \\ \quad \cdot \displaystyle\sum_{k=0}^{n-1} \frac{\Gamma(k-j, M(t_1, T)[1-(n-1)r]) - \Gamma(k-j, M(t_2, T)[1-(n-1)r])}{\Gamma(k+1)}, & \dfrac{T}{\tau_d} \leqslant n < \dfrac{T}{\tau_d} + 1; \\ 0, & n \geqslant \dfrac{T}{\tau_d} + 1; \end{cases} \tag{8}$$

where $M(t_0, T)$ is defined in (2a), $\Gamma(\cdot)$ is the gamma function, and $\Gamma(\cdot, \cdot)$ is the incomplete gamma function defined in (4e). The expected value and variance of n can be obtained in a similar manner, as was done by Müller [21], [29] for the case $T \ll \tau_c$.

III. Summary of Results

The results of this correspondence, that are new or generalized, are summarized in Table II. Next to each case in the table are shown the restrictions that apply to the statistical quantities that were calculated, and reference to the corresponding equations in the text, Table I, and Fig. 1.

Much of the previous work on the doubly stochastic Poisson counting distribution, with and without refractoriness, has carried out the appropriate expectations on a case-by-case basis (e.g., see [26]), with respect to the rate, starting time, or sampling time. This presentation has unified the previous work by carrying out expectations, wherever possible, with respect to the integrated rate. An exception to this is the case of the modified variance, which cannot simply be represented as the expectation of the unmodified variance. In particular, for the modified variance with random integrated rate (Table I, lower right quadrant), the correlation properties of the rate must be taken into consideration.

It is expected that the results incorporating uniformly uncertain sampling time will prove useful for experiments where the phase of the known rate function is uncertain, or where the starting time of the sampling interval cannot be measured with great precision.

IV. Applications in Neurobiology and Neurophysiology

The calculations carried out in this paper should be applicable to a number of problems in neurobiology and neurophysiology.

As an example in neurobiology, the amplitude of the postsynaptic potential (PSP) for certain neurons sometimes follows an approximately exponential time course during habituation and sensitization. This has been discussed by Castellucci *et al.* [30]–[32] for the gill-withdrawal reflex evoked by a weak tactile stimulation of the siphon skin in the marine mollusk *Aplysia californica*. Since the PSP is induced by the flow of discrete chemical neurotransmitter packets (quanta) across a synapse, when the underlying statistics of the quanta are Poisson, as they appear to be at

TABLE II
New or Generalized Results for the Counting Distribution $p(n)$, Mean $E[n]$, and Variance $\mathrm{var}[n]$[1]

Case	Restrictions for: $p(n)$	$E[n]$	$\mathrm{var}[n]$	Refer to:
Known rate, exponential with pedestal; unmodified	d	d	d	Table I, upper left; (2a), (2b)
Uniformly uncertain starting time; arbitrary rate parameter; unmodified	d	d	d	(3a), (3b), (3c)
Uniformly uncertain starting time; exponential with pedestal; unmodified	d	d	d	(4a), (4b), (4c)
Known rate, exponential with pedestal; nonextended refractoriness	a, b	a	a, c	Table I, upper right; (1), (6a)–(6f); Fig. 1
Uniformly uncertain starting time; arbitrary rate parameter; nonextended refractoriness	a, b	a	a, c	(7a), (7b), (7c)
Uniformly uncertain starting time; exponential with pedestal; nonextended refractoriness	a, b	a	a, c	Table I, lower right; (8)

[1]Restrictions for the validity of results are as follows: [a]$\tau_d \ll \tau_c, T$; [b]$T \ll \tau_c$; [c]$(E[\lambda]\tau_d)^2\tau_d/6 \ll \tau_c$; [d]no restrictions.

sufficiently low arrival rates [33], the Poisson point process with known exponential rate and a pedestal will provide an appropriate description for quantal arrivals in the presence of habituation and sensitization. The counting distribution, mean, and variance for this case are presented in Table I, upper left quadrant, along with (2a) and (2b). In the case where the starting time is uniformly uncertain, or exhaustive sampling is used, (4a), (4b), and (4c) apply. Since a pedestal is incorporated into our calculations, they are more suitable for this case than are the calculations of Teich and Card [26].

Our results are also applicable to a number of problems involving the statistics of neural spike generation in neurophysiology. Spike trains have been recorded from single optic nerve fibers in the frog [34] and cat [35], after the onset of a step-function light stimulus. Many of these cells display an instantaneous spike frequency that is roughly describable by an exponentially decaying function, with a pedestal. The counting statistics for this case are again found in Table I, upper left quadrant, together with (2a) and (2b), if a Poisson-based model is assumed and the effects of refractoriness are ignored. At high stimulus levels, the maintained-discharge retinal ganglion cell spike train in the cat is well modeled by a Poisson process modified by nonextended (stochastic or relative) refractoriness [2], [6]. We would therefore expect that the nonstationary neural spike statistics in response to an onset (or offset) of the stimulus, will approximately correspond to the results presented in Table I, upper right quadrant, together with (1), (6a)–(6f), and Fig. 1. If the starting time of the exponential rate is uniformly uncertain, then (8) applies instead.

It would appear that many of these results will also apply to the spike trains recorded at primary VIII-th nerve fibers in the mammalian auditory system [36], [37]. This is expected to be particularly true at acoustic frequencies greater than about 5 kHz, where phase locking does not appear to be an important determinant of the neural spike statistics. Other areas of application include psychophysics, photon counting, nuclear counting, and radiochemistry.

References

[1] L. M. Ricciardi and F. Esposito, "On some distribution functions for non-linear switching elements with finite dead time," *Kybernetik*, vol. 3, pp. 148–152, 1966.
[2] M. C. Teich, L. Matin, and B. I. Cantor, "Refractoriness in the maintained discharge of the cat's retinal ganglion cell," *J. Opt. Soc. Amer.*, vol. 68, pp. 386–402, 1978.
[3] G. Vannucci and M. C. Teich, "Equivalence of threshold detection with and without dead time," *Appl. Opt.*, vol. 18, pp. 3886–3887, Dec. 1979.
[4] M. C. Teich and G. Lachs, "A neural counting model incorporating refractoriness and spread of excitation. I. Application to intensity discrimination," *J. Acoust. Soc. Amer.*, vol. 66, pp. 1738–1749, 1979.
[5] G. Lachs and M. C. Teich, "A neural counting model incorporating refractoriness and spread of excitation. II. Application to loudness estimation," *J. Acoust. Soc. Amer.*, vol. 69, pp. 774–782, Mar. 1981.
[6] M. C. Teich and P. Diament, "Relative refractoriness in visual information processing," *Biol. Cybern.*, vol. 38, pp. 187–191, 1980.
[7] G. Bédard, "Dead-time corrections to the statistical distribution of photoelectrons," *Proc. Phys. Soc.*, vol. 90, pp. 131–141, 1967.
[8] B. I. Cantor and M. C. Teich, "Dead-time corrected photocounting distributions for laser radiation," *J. Opt. Soc. Amer.*, vol. 65, pp. 786–791, July 1975.
[9] M. C. Teich and B. I. Cantor, "Information, error, and imaging in deadtime-perturbed doubly-stochastic Poisson counting systems," *IEEE J. Quantum Electron.*, vol. QE-14, pp. 993–1003, 1978.
[10] M. C. Teich and G. Vannucci, "Observation of dead-time-modified photocounting distributions for modulated laser radiation," *J. Opt. Soc. Amer.*, vol. 68, pp. 1338–1342, Oct. 1978.
[11] B. E. A. Saleh, *Photoelectron Statistics*. New York: Springer-Verlag, 1978.
[12] I. DeLotto, P. F. Manfredi, and P. Principi, "Counting statistics and dead-time losses, Part 1," *Energ. Nucl.* (Milan), vol. 11, pp. 557–564, 1964.
[13] J. W. Müller, "Dead-time problems," *Nucl. Instrum. Methods*, vol. 112, pp. 47–57, 1973.
[14] ——, "Some formulae for a dead-time-distorted Poisson process," *Nucl. Instrum. Methods*, vol. 117, pp. 401–404, 1974.
[15] J. W. Müller, Ed., "Bibliography on dead time effects," Rep. BIPM-81/11, Bureau International des Poids et Mesures, Sèvres, France, 1981.
[16] M. C. Teich and W. J. McGill, "Neural counting and photon counting in the presence of dead time," *Phys. Rev. Lett.*, vol. 36, pp. 754–758, 1473, Mar. 1976.
[17] B. E. A. Saleh, J. T. Tavolacci, and M. C. Teich, "Discrimination of shot-noise-driven Poisson processes by external dead time: Application to radioluminescence from glass," *IEEE J. Quant. Electron.*, vol. QE-17, pp. 2341–2350, Dec. 1981.
[18] G. Vannucci and M. C. Teich, "Effects of rate variation on the counting statistics of dead-time-modified Poisson processes," *Opt. Commun.*, vol. 25, pp. 267–272, May 1978.
[19] ——, "Dead-time-modified photocount mean and variance for chaotic radiation," *J. Opt. Soc. Amer.*, vol. 71, pp. 164–170, Feb. 1981.
[20] M. C. Teich and B. E. A. Saleh, "Interevent-time statistics for shot-noise-driven self-exciting point processes in photon detection," *J. Opt. Soc. Amer.*, vol. 71, pp. 771–776, June 1981.
[21] J. W. Müller, "Counting statistics of short-lived nuclides," *J. Radioanal. Chem.*, vol. 61, pp. 345–359, 1981.
[22] C. M. Harris and B. K. Selinger, "Single-photon decay spectroscopy. II. The pile-up problem," *Aust. J. Chem.*, vol. 32, pp. 2111–2129, 1979.
[23] B. E. A. Saleh and M. C. Teich, "Multiplied-Poisson noise in pulse, particle, and photon detection," *Proc. IEEE*, vol. 70, pp. 229–245, 1982.
[24] D. L. Snyder, *Random Point Processes*. New York, Wiley, 1975.
[25] P. Diament and M. C. Teich, "Photoelectron counting distributions for irradiance-modulated radiation," *J. Opt. Soc. Amer.*, vol. 60, pp. 682–689, 1970.
[26] M. C. Teich and H. C. Card, "Photocounting distributions for exponentially decaying sources," *Opt. Lett.*, vol. 4, pp. 146–148, May 1979.
[27] P. R. Prucnal and H. C. Card, "Effects on VLSI yield of doubly-stochastic impurity distributions," *IEEE Trans. Rel.*, vol. R-31, pp. 185–190, June 1982.
[28] M. Abramowitz and I. A. Stegun, Eds., *Handbook of Mathematical Functions*. Washington, DC: U.S. Government Printing Office, 1965.
[29] J. W. Müller, "Espérance et variance pour une source décroissante avec temps mort non cumulatif," Rep. BIPM WPM-212, Bureau International des Poids et Mesures, Sevres, France, 1979.
[30] V. Castellucci, H. Pinsker, I. Kupfermann, and E. R. Kandel, "Neuronal mechanisms of habituation and dishabituation of the gill-withdrawal reflex in *Aplysia*," *Science*, vol. 167, pp. 1745–1748, 1970.
[31] V. Castellucci and E. R. Kandel, "A quantal analysis of the synaptic depression underlying habituation of the gill-withdrawal reflex in *Aplysia*," in *Proc. Nat. Acad. Sci. USA*, vol. 71, pp. 5004–5008, 1974.
[32] J. H. Byrne, V. F. Castellucci, and E. R. Kandel, "Contribution of individual mechanoreceptor sensory neurons to defensive gill-withdrawal reflex in *Aplysia*," *J. Neurophysiol.*, vol. 41, pp. 418–431, 1978.
[33] J. del Castillo and B. Katz, "Quantal components of the end-plate potential," *J. Physiol.* (London), vol. 124, pp. 560–573, 1954.
[34] H. K. Hartline, "The response of single optic nerve fibers of the vertebrate eye to illumination of the retina," *Amer. J. Physiol.*, vol. 121, pp. 400–415, 1938.
[35] H. B. Barlow and W. R. Levick, "Changes in the maintained discharge with adaptation level in the cat retina," *J. Physiol.* (London), vol. 202, pp. 699–718, 1969.
[36] N. Y. S. Kiang, T. Watanabe, E. C. Thomas, and L. F. Clark, *Discharge Patterns of Single Fibers in the Cat's Auditory Nerve* (Research monograph no. 35). Cambridge, MA: MIT Press, 1965.
[37] R. L. Smith and M. L. Brachman, "Adaptation in auditory-nerve fibers: A revised model," *Biol. Cybern.*, vol. 44, pp. 107–120, 1982.

0018-9472/83/0900-1033$01.00