

## Relative Refractoriness in Visual Information Processing\*

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**Abstract.** Pulse-interval distributions are obtained for a counting system in which there is a gradual, rather than abrupt, increase in excitability following the registration of a pulse (relative refractoriness). The results are applicable to systems in which Poisson counting would be observed in the absence of such effects, and in which the memory reaches back at most one pulse. Choosing a particular functional form for the recovery function, the theory fits the experimentally measured distribution for the maintained discharge in the cat's retinal ganglion cell. It is also consistent with the notion that Weber's Law emerges from refractoriness in the visual system, as first proposed by van der Velden.

The designation nonparalyzable indicates that pulses arriving at the detector during the dead-time period are ignored; in particular, they neither extend the dead-time period nor further paralyze the counter in any way. At the termination of the dead-time period, the detector is assumed to come fully to life instantaneously and to function as if the dead-time period had not existed.

In visual information processing, the notion of fixed dead time has been incorporated into models dealing with both psychophysical and neurophysiological data. The first such model, perhaps, was developed by van der Velden (1949), who wrote a simple but elegant paper ascribing the emergence of Weber's Law to the dead-time-limited information-transmitting capacity of nerves in the visual system. Aguilar and Stiles (1954) cite van der Velden's model as a possible explanation of their intensity discrimination results. Shortly thereafter, Kuffler et al. (1957) considered a fixed-dead-time model to describe the character of the maintained discharge in the retinal ganglion cell, but they did not pursue this line of reasoning because the calculated pulse-interval distribution (a displaced exponential) did not fit the recorded data well.

Subsequently, Rodieck (1967, 1973) performed a series of experiments on the maintained discharge in the cat and obtained an empirical relationship between the mean and standard deviation of the pulse-interval distribution that was consistent with the notion of a stochastic, rather than a fixed, dead time. Lee (1974) proposed a theoretical neuronal model incorporating stochastic dead time driven by a stationary renewal input process. Souček (1964) and DeLotto and Manfredi (1965a, b) had earlier dealt with the statistical description of nuclear counting systems with variable dead time. Most recently, Teich et al. (1978) fit both experimental pulse-number and pulse-interval distributions using a Poisson-based model that in-

### 1. Introduction

Dead-time-modified pulse counting is important in a number of areas of scientific endeavor, including nuclear particle detection (Parzen, 1962; DeLotto et al., 1964; Müller, 1974), photon counting and optical communications (Bédard, 1967; Cantor and Teich, 1975; Teich and McGill, 1976; Teich and Cantor, 1978; Teich and Vannucci, 1978), and information transmission in neural systems (Ricciardi and Esposito, 1966; Teich and McGill, 1976; Teich et al., 1978). The underlying point process is usually assumed to be Poisson or doubly-stochastic Poisson; the dead time is taken to be fixed and the counter nonparalyzable. Thus, the dead time (or refractoriness period) represents a fixed period of time  $\tau$  after the registration of a pulse, during which the detector is completely ineffective and cannot emit another pulse.

\* This work was supported in part by the National Science Foundation

corporated a nonparalyzable stochastically varying dead time. They found that the variability in refractory-period duration distinctly altered the pulse-interval distribution from that obtainable with a fixed refractory period, but had virtually no effect on the fixed-refractory period pulse-number distribution. Using this model, they were able to fit all of the data on the maintained discharge in the cat's retinal ganglion cell described by Barlow and Levick (1969a,b). Furthermore, they brought together, within a single framework, the work of Rodieck (1967, 1973), Barlow and Levick (1969a,b), and Barlow et al. (1971). Still, this model assumed that at the termination of the random period of time during which the cell does not fire, it instantly comes fully to life.

An alternative to the stochastic absolute refractoriness model proposed by Teich et al. (1978) is a model based on relative refractoriness, in which the responsiveness of the cell increases gradually, rather than suddenly, as it recovers from the discharge of an impulse. Intuitively, the relative refractoriness model provides a more satisfying description of what we might expect of neuronal behavior, since such systems may be expected to take some time to reach full recovery.

In this paper we consider the suitability of a model based on relative refractoriness in visual information processing. In particular, we obtain an expression for the pulse-interval distribution for a Poisson process modified by relative refractoriness. We demonstrate that the latter can be used to fit an experimental pulse-interval distribution for the maintained discharge in the cat's retinal ganglion cell. Our model also leaves unchanged the arguments used by van der Velden in ascribing Weber's Law to dead-time effects in the neural channel.

## 2. Theory

In the generally recognized model of a Poisson counter that retains no memory of previous discharges and responds to a continuous stimulus  $I(t)$  by emitting pulses at a mean rate  $\lambda$  proportional to the excitation, the proportionality factor is a fixed detection efficiency  $\alpha$ . The differential probability that the stimulus evoke a response within time  $dt$  of  $t$  is then  $\alpha I(t)dt$ , regardless of previous responses. In the treatments of fixed dead time, this relation is modified to grant the detector some memory of the previous response, to the extent that the differential probability of response becomes  $\alpha I(t)dt$  only after a dormant period  $\tau$ . In contrast to these models, we now assume that the differential probability includes an efficiency factor  $\alpha$  that depends on the elapsed time  $t - t_0$  since the last response at time

$t_0$ . The mean response rate  $\lambda$  is still linearly proportional to the stimulus  $I(t)$ , but with a time-dependent efficiency:

$$\lambda dt = \alpha(t - t_0)I(t)dt. \quad (1)$$

For simplicity, the recovery function  $\alpha(t)$  of the detection efficiency is assumed to have been reset to zero at  $t=0$ , immediately after the last impulse, and then to increase to an eventual saturation level  $\alpha_0$ . The recovery extends over a time period of partial responsiveness, characterized by a time scale  $\tau$ , of the order of the usual relative refractory period or dead time. We may refer to this time colloquially as the sick time rather than the dead time. The model is that of a renewal point process (Cox, 1962; Cox and Lewis, 1966).

With the additional assumption that no more than one response pulse can be generated during the infinitesimal observation time  $dt$ , it follows from (1) that the conditional probability that no count be registered within the time  $dt$  at time  $t$ , given that none was recorded since the last one at time  $t_0$ , is  $(1 - \lambda dt)$ . Consequently, if  $p_0(t, t_0)$  is the probability that no response occur in the interval from  $t_0$  to  $t$ , then

$$p_0(t + dt, t_0) = p_0(t, t_0) [1 - \alpha(t - t_0)I(t)dt] \quad (2)$$

by the rule governing conditional probabilities. This integrates to

$$p_0(t, t_0) = \exp \left[ - \int_{t_0}^t \alpha(t' - t_0)I(t')dt' \right]. \quad (3)$$

This result for the probability of zero counts in the interval from  $t_0$  to  $t$  generalizes the Poisson formula to the case of a time-varying responsiveness.

The pulse-interval distribution,  $P(t, t_0)$ , can be readily observed and calculated. Since the cumulative probability that the interval between pulses exceed  $t - t_0$  is identical to the probability that no pulse be registered in this interval,

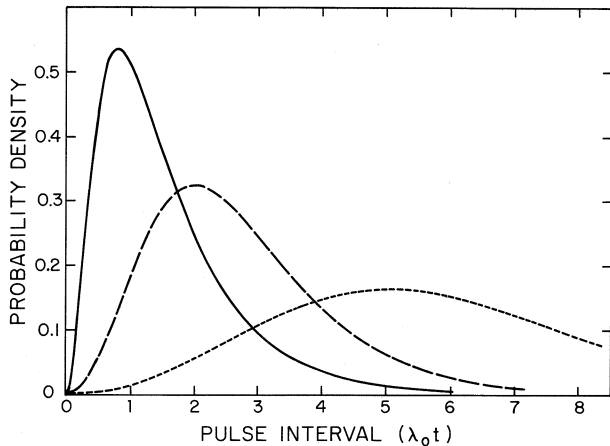
$$p_0(t, t_0) = \int_t^\infty P(t', t_0)dt' \quad \text{or} \quad P(t, t_0) = -\partial p_0(t, t_0)/\partial t, \quad (4)$$

so that

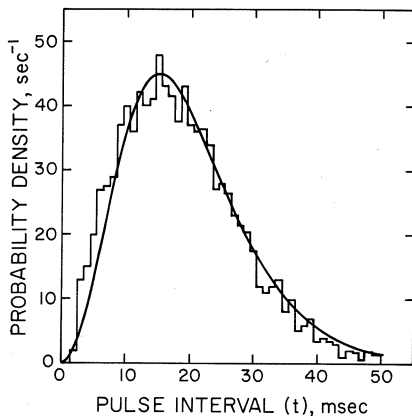
$$P(t, t_0) = \alpha(t - t_0)I(t) \exp \left[ - \int_{t_0}^t \alpha(t' - t_0)I(t')dt' \right]. \quad (5)$$

The full counting distribution,  $p_n(t, t_0)$ , is also obtainable from  $p_0(t, t_0)$ , by iterated integration. These results are the usual ones for renewal processes.

In what follows, we restrict the discussion to a constant level of stimulus  $I(t) = I_0$ , whereupon the



**Fig. 1.** Pulse-interval probability density functions generated by the recovery function  $r(x) = x^2/(1+x^2)$ . The asymptotic rate parameter is  $\lambda_0$  and the mean number of counts lost during the recovery time  $\tau$  is  $\lambda_0\tau = v$ .  $v = 0.5$  for the solid curve,  $v = 2.0$  for the dashed curve,  $v = 8.0$  for the dotted curve



**Fig. 2.** Theoretical fit (solid curve) to experimental pulse-interval distribution for the maintained discharge in the retinal ganglion cell of the cat (on-center unit). The theoretical curve is based on the recovery function  $r(x) = x^2/(1+x^2)$ . Only one point of the curve (the peak) is fitted to the experimental histogram. Data adapted from Fig. 9 of the paper by Barlow and Levick (1969b)

probability distributions become homogeneous in time. Also, the efficiency factor can be expressed in terms of a recovery function  $r(x)$  that is normalized to unit steady-state level and to unit time scale. Then the pulse-interval distribution becomes

$$P(t|\tau) = \alpha_0 I_0 r(t/\tau) \exp \left[ -\alpha_0 I_0 \tau \int_0^{t/\tau} r(x) dx \right]. \quad (6)$$

Since  $\alpha_0 I_0 = \lambda_0$  is the ultimate mean count rate at full efficiency,  $\alpha_0 I_0 \tau = v$  is interpretable as the mean number of counts lost during the recovery time  $\tau$ .

The asymptotic behavior of this distribution is the usual Poisson result

$$P(t|\tau) \sim P_0 e^{-\lambda_0 t} \quad (t \gg \tau), \quad (7)$$

where  $P_0 = \lambda_0 \exp(vA)$  and  $A = \int_0^\infty [1-r(x)] dx$ . For time intervals shorter than  $\tau$ , the distribution reflects the recovery process:

$$P(t|\tau) = \lambda_0 r(t/\tau) \quad (t \ll \tau), \quad (8)$$

so that measurements of the distribution for short intervals are actually observations of the recovery function. Furthermore, the pulse-interval distribution peaks at time  $t_m = \xi\tau$ , where  $\xi$  may be found as that value of  $x$  for which

$$\frac{d}{dx} \left( \frac{1}{r(x)} \right) = -v. \quad (9)$$

Figure 1 presents the pulse-interval distributions to be expected if the form of the recovery function be selected as

$$r(x) = x^2/(1+x^2). \quad (10)$$

Some considerations that guide the selection of this form of renewal intensity will be discussed below in relation to the experimental data to be modeled. This choice yields the family of distributions

$$P(t|\tau) = \lambda_0 e^{-\lambda_0 t} [t^2/(t^2 + \tau^2)] \exp[\lambda_0 \tau \tan^{-1}(t/\tau)], \quad (11)$$

shown for various values of the lost-count parameter  $v = \lambda_0 \tau$ .

### 3. Application to the Ganglion-Cell Discharge

The above class of pulse-interval distributions was fitted to the experimental data obtained from the maintained discharge in the retinal ganglion cell of the cat for an on-center unit (Barlow and Levick, 1969b). To fit one of the theoretical distributions to the experimental histogram, it suffices to fit one point of the data. That point is chosen to be the peak of the observed distribution. This most-likely pulse interval is the one known experimentally with the greatest precision. For the case illustrated in Fig. 2, it occurred at  $t_m = 15$  ms, with an observed peak probability  $p_m$  of about  $45 \text{ s}^{-1}$ . From (9), using the model recovery function (10), this peak should occur at  $\xi = (2/v)^{1/3}$ . The dimensionless product  $p_m t_m$  is 0.675 experimentally and depends theoretically only on the ratio  $t_m/\tau = \xi$ , through

$$p_m t_m = \frac{2}{1 + \xi^2} \exp \left[ \frac{2}{\xi^3} (\tan^{-1} \xi - \xi) \right]. \quad (12)$$

Solving for  $\xi$  yields 0.950, which determines the recovery time scale  $\tau = 15.8$  ms, the mean count loss

$v=2.33$ , as well as the ultimate mean pulse rate  $\lambda_0=148\text{ s}^{-1}$ . Note that this pulse rate is only the steady-state value and differs from the experimental mean rate, which is affected by the depressed excitability. The theoretical pulse-interval distribution fitted to the observed peak interval is thus fully determined and is seen to fit the entire histogram quite well. No reasonable fit is obtainable with the usual model of a fully unresponsive fixed refractory period, which would predict a precisely exponential distribution, delayed by a dead time  $\tau$ . The experimental evidence here clearly favors the gradual-recovery model though it is also consistent with the stochastically varying absolute dead-time model considered by Teich et al. (1978).

#### 4. Discussion

For the practical purpose of fitting experimental data, it should be noted that while the theoretical distribution is not very sensitive to the precise shape of the recovery function, such as that selected in (10), only certain classes of functions will be found to fit at all. For example, a recovery function  $r(x)$  that begins linearly in  $x$ , rather than quadratically as in (10), can not reach the experimental peak value fitted in Fig. 2. The asymptotic behavior of (6) is such that if  $r(x)\sim x^n$  for  $x\rightarrow 0$ , then the product  $p_m t_m$  will not exceed  $n \exp\left\{-[n/(n+1)]\right\}$ . This precludes any recovery function that begins linearly for the observed histogram, since the experimental product  $p_m t_m$  exceeded  $e^{-1/2}=0.607$ . Further guidance in choosing the recovery function is provided by (8), which is directly observable in the experimental data, if short time intervals are measured sufficiently frequently. As used here, the particular recovery function in (10) is merely representative of a class of functions that rise gradually to their steady-state levels. If of interest to note that the zero-initial-slope form, as in (10), but not the linear-rise version, is consistent with the presence of a short absolute refractory period following the registration of a pulse (in accord with experimental observation).

The gradual recovery model presented here may be compared with the time-varying threshold models discussed by Holden (1976). The recovery function and the threshold variation are complementary in the sense that  $[1-r(x)]$  can serve as a normalized version of the  $V_0(t)$  threshold function (Holden, 1976). A number of models quite different in character have also been developed (see, for example, Levine and Shefner, 1977; Smith, 1979).

Not all possible features of a pulse train are accounted for in the proposed model. For example,

negative serial correlation coefficients (Kuffler et al., 1957; Rodieck, 1967) are not incorporated in the model, which assumes that the recovery function always resets to zero upon registration of a pulse. A more complex model to account for this effect can easily be envisioned.

#### 5. Conclusion

In short, a gradual increase of excitability following the registration of a pulse, rather than a sudden but delayed increase, can be incorporated into a mathematical model to provide useful pulse-interval distributions for the maintained discharge in the cat's retinal ganglion cell. Furthermore, as with any renewal process, the pulse-number distributions for relative and absolute refractoriness should deviate little from each other, so that the association of Weber's Law with dead time, as offered by van der Velden (1949), should remain valid. The relative-refractoriness model thus provides a suitable description of certain neurophysiological and psychophysical aspects of visual information processing. Although the stochastically varying absolute dead-time model (Teich et al., 1978) also provides an adequate description for these data, the relative refractoriness model is more in consonance with the known behavior of neural systems (Holden, 1976).

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Received: March 10, 1980

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