LETTER TO THE EDITOR

A Comment on a Retinal Neuron Model

Dear Sir:

In a recent paper published in this journal, Levine and Shefner (1) presented a model for the variability of interspike intervals during the sustained firing of goldfish retinal ganglion cells. The model assumed a noisy spike initiation process in which the time between firings is a random variable equal to the reciprocal of a normally distributed variable. The model was reported to reproduce the experimental result that the coefficient of variation (CV) of the interspike intervals did not change as the mean firing rate changed. It is difficult to see how their model could possess this property when the first two moments of the model's probability density function (PDF) for interspike intervals do not exist. A modification of the underlying PDF will rectify this problem and produce the intended results.

The nonintegrability of the moments of Levine and Shefner's "hypernormal" PDF stems from its $1/t^2$ tail as the interspike time, t, approaches infinity. While the tail could be truncated at some finite time, any such truncation would be totally arbitrary. Although there exist experimental examples where such a slow tail seems justified (2), a more reasonable alternative for this problem would be to choose an underlying PDF whose reciprocal transformation approaches infinity faster than $1/t^2$. One such choice is the gamma PDF

$$p(x) = b^{-(\alpha+1)}/\Gamma(\alpha + 1)x^{\alpha}e^{-x/b}; \quad x > 0, \tag{1}$$

and the PDF of its reciprocal transformation, $t = 1/x$, i.e. the interspike interval PDF,

$$p(t) = b^{-(\alpha+1)}/\Gamma(\alpha + 1)t^{-(\alpha+2)}e^{-1/bt}; \quad t > 0, \tag{2}$$

with $b > 0, \alpha > 1$, and $\Gamma(\alpha + 1) = \alpha!$.

The first and second moments of Eq. 2 clearly exist and a straightforward integration yields a mean interspike interval of $1/\alpha b$ and a CV of $(\alpha - 1)^{-1/2}$. Thus for a fixed α, the CV is indeed independent of the mean firing rate, αb. For moderately large α, say 15, Eq. 1 reasonably approximates a normal distribution (3). As α decreases, the skew and excess of Eq. 1 increase. However, discussion in the above paper indicates that the lack of normality of Eq. 1 may be a desirable property. For 25 unimodal distributions, Levine and Shefner examined the distribution of the reciprocals of the experimental interspike intervals. The third and fourth moments were significantly larger than for a normal distribution.

In Fig. 1, the hypernormal PDF fits for the two unimodal histograms in the above paper are shown together with a fit using Eq. 2. Following Levine and Shefner, we used the mode interval and value of the histogram at the mode to obtain rough estimates for α and b in Eq. 2. A better test of the applicability of Eq. 2 would result if α and b could be estimated from the mean and variance of the recorded interspike intervals. It would be of particular interest to know, say, the first four moments of the firing times for a neuron of a given CV over a range of firing rates. If these moments agreed with the predictions from Eq. 2 with a fixed α, then the interpretation of x in Eq. 1 as proportional to the waiting time for the $(\alpha + 1)^{\text{th}}$ occurrence of a particular type of event at the trigger zone, with the events occurring in a Poisson manner at a mean rate $1/b$, might be worth investigating. In summary, a simple integrate-and-fire model with the CV

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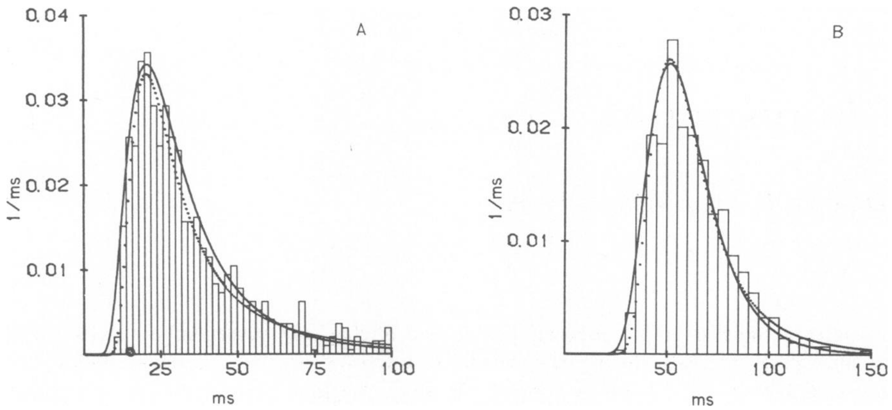

FIGURE 1 Reciprocal gamma (solid curve) and hypernormal (dotted curve) PDF fits for the two unimodal interspike interval histograms in Levine and Shefner (1). Hypernormal PDF parameters are the same as in original text. For the reciprocal gamma PDF of Eq. 2, $\alpha = 3$ and $b = 0.00975$ in *A*, and $\alpha = 11$ and $b = 0.0015$ in *B*.

being independent of the mean firing rate is easily obtained by using the reciprocal transformation suggested by Levine and Shefner.

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