LETTER TO THE EDITOR

Neural 1/f Noise and Membrane Models

Dear Sir:

Measurements of inherent electric fluctuations across various nerve membranes have disclosed that a large part of this neural noise has a power spectrum inversely proportional to frequency, $S(f) \propto 1/f$ (Derksen, 1965; Verveen and Derksen, 1968; Poussart, 1971; Siebenga and Verveen, 1972; Fishman, 1973). Membrane models published in this Journal have apparently yielded such $1/f$ spectra in computer simulations (Offner, 1971 *a*, *b*, 1972 *b* [last sentence]). It seems worth remarking here that these models do not actually yield $1/f$ noise, particularly since this will illustrate some hazards of computer simulation (Bird, 1974).

The neural $1/f$ noise is connected with potassium flux rather than conductance (Derksen and Verveen, 1965), and hence, is perhaps of less immediate interest than the $1/(f^2 + \text{constant})$ component now assigned to potassium channels (Siebenga et al., 1973; Fishman, 1973). However, the $1/f$ component remains a neural phenomenon in need of a quantitative theory, no less a mystery than the ubiquitous $1/f$ spectra found in all sorts of other systems (Bell, 1960; Mandelbrot and Wallis, 1969; Scarf, 1970).

It is important, therefore, to consider carefully the noise properties of membrane models. We report here on a complete analysis (Bird, 1974) for two random-walk computer simulations (Offner, 1970, 1972 *a*) which seemed to yield $1/f$ noise spectra. The $1/f$ result has been questioned, but then was reasserted in modified form, in some previous discussion (Hawkins, 1972; Offner, 1972 *a*). Our analysis conclusively resolves the issue, not only proving the $1/f$ assertions to be invalid, but also demonstrating the source of error to be the limitations of computer simulation.

The apparent $1/f$ simulation seemed peculiar to us, since we could see that the models were both closely related to classical diffusion models (Langevin-Ehrenfest-Schrödinger-et al. ii, see Bird, 1974) which are known to give relaxation, not $1/f$, spectra. Consequently, we combined the two models in question into a single Markov process. This generalized model we then succeeded in solving analytically for the noise power spectrum. Details of the calculation are presented in Bird (1974).

Our analytical solution showed that both models yield the same form of expected noise power spectrum,

$$S(f) \propto \frac{1}{f_c^2 + (\sin \pi f \tau)^2/\pi^2 \tau^2}, \qquad (1)$$

where f_c is a characteristic frequency (~ 0.03 per time-step in Offner's simulations) and τ is the computer time-step. This spectrum is discussed fully in Bird (1974). Its salient feature is that the $(\sin \pi f \tau)^2/\pi^2\tau^2$ in the denominator flattens steadily from f^2 at low frequency ($f\tau \ll 1$) towards f^0 behavior at the Nyquist limit ($f\tau = \frac{1}{2}$).

Consequently, for any finite computation ($\tau \neq 0$, number of steps $N \neq \infty$), Eq. 1 predicts approximate $1/f$ behavior over a broad region near 3/4 the Nyquist frequency. Further, this $\sim 1/f$ region will broaden as the simulation is lengthened ($N \propto 1/\tau$ increased), proportionally with the number of computer steps N (not just with $\sqrt{N}$ as Offner 1972 *a* suggests). This is consistent with what was reported for the computer simulations, and from which it seemed that more computer time might yield true $1/f$ spectra (Offner, 1972 *a*).

However, for the continuum limit of infinite computation ($N \rightarrow \infty$ and $\tau \rightarrow 0$), Eq. 1 predicts $S(f) \rightarrow 1/(f_c^2 + f^2)$, which is the familiar relaxation form. What happens to the above $\sim 1/f$ region is that, while it broadens with $N \rightarrow \infty$, it moves out towards infinite frequency in this continuum limit (as depicted in the figure in Bird, 1974). In other words, the $\sim 1/f$ region that appears in the simulations is but a computer phantom that fades away in the light of analysis.

In sum then, analysis finds that *both* models: (*a*) are *classic* Brownian motion analogs; (*b*) are *identical* as regards the form of their noise spectra; and (*c*) show $\sim 1/f$ behavior only as an *artifact* of the computer simulations. While limited computation can appear to simulate $1/f$ noise, the unlimited analysis gives just $1/(f^2 + f_c^2)$ noise.[1]

This work contributes to the quest for a theory of neural $1/f$ noise only in the minor way of pointing out impediments due to erroneous models. In that connection, let us note the stated motivation of Offner (1971 *a, b*) for calling attention to the apparent $1/f$ noise in his random-walk models, namely, to show a viable alternative to the queuing feature of the Hodgkin-Huxley (1952) model. However, a perusal of the literature will show that queuing is not necessary, nor indeed even sufficient, to quantitatively explain $1/f$ noise. Therefore, neural $1/f$ noise remains in search of a theory.

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[1]Since the one test specifically quoted to this Journal (Offner, 1971 *a*) seems to show almost *exact* $1/f$ behavior for the computer solutions, in conflict with the analytical prediction of Eq. 1, it is necessary to examine that test more closely. It consists in computing from the simulation data the partial sums $\sum kS(k)$ (where $k \equiv 1{,}000\ f\tau$) for k = 31-210 and 211-390, and forming their ratio which would be exactly 1 for a true $1/f$ spectrum. For comparison, a pure relaxation spectrum would give a ratio 2.7, and the prediction of Eq. 1 for an ensemble of simulations is 2.0. Now the quoted results of the test were 325.4/319.6 = 1.02, very close to $1/f$ behavior, but that is in error (cf. parenthetic remark in Hawkins, 1972). Actually, from Table I in Offner (1970) one computes 511.1 for 31-210 and 319.5 for 211-390, whose ratio is 1.6. But more significantly, if one takes instead the sums for 31-180 and 181-330, one finds a ratio of 2.4. Thus, this test is really inconclusive. Moreover, the wide range of ratios (1.6-2.4) reflects the unreliability of a simulation technique that uses single numerical realizations of a random model (Offner, 1970). Recently, Alberding (1973) has done the simulation (applicable to one model) reliably, by using Monte Carlo ensembles. His results directly confirm the predictions of Eq. 1 (cf. Bird, 1974).

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