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On Stochastic Models of the Activity of Single Neurons

Stein (1965, 1967) considered a realistic model of nerve membrane potential which had jumps either up or down when excitatory or inhibitory synaptic events occurred and which at other times decayed exponentially to the resting level. In view of the "quantal" nature of synaptic transmission it is probably best to present Stein's model in its general form with a discrete distribution of post-synaptic potential (p.s.p.) amplitudes.

Let the level of depolarization at time t be $X(t)$ and suppose there are n independent synaptic inputs with p.s.p. amplitudes ε_i (which may be positive or negative) and with Poisson rate parameters λ_i. If we set

$$\Lambda = \sum_i \lambda_i,$$

then the conditional distribution of the p.s.p. amplitude ε, given that a p.s.p. occurred, is $\Pr\{\varepsilon = \varepsilon_i\} = \lambda_i/\Lambda$. The model can be presented as the stochastic differential equation of a Markov process. We let Π_λ denote a Poisson process of rate parameter λ. Then we have

$$\mathrm{d}X(t) = -\sigma X(t)\,\mathrm{d}t + \sum_i \varepsilon_i\,\mathrm{d}\Pi_{\lambda_i}(t), \tag{1}$$

where σ is the reciprocal of the time constant of the membrane.

The moments of $X(t)$ in the absence of threshold can be readily found without finding characteristic functions. If $Y(t) = \mathrm{e}^{\sigma t}X(t)$, then this process satisfies

$$\mathrm{d}Y(t) = \mathrm{e}^{\sigma t}\sum_i \varepsilon_i\,\mathrm{d}\Pi_{\lambda_i}(t). \tag{2}$$

$Y(t)$ is thus the sum of n temporally inhomogeneous independent Poisson processes and its expectation is

$$E\left[\int_0^t \mathrm{e}^{\sigma t'}\sum_i \varepsilon_i\,\mathrm{d}\Pi_{\lambda_i}(t')\right] = \sum_i \frac{\lambda_i\varepsilon_i}{\sigma}(\mathrm{e}^{\sigma t}-1), \tag{3}$$

while its variance is

$$\mathrm{Var}\left[\int_0^t \mathrm{e}^{\sigma t'}\sum_i \varepsilon_i\,\mathrm{d}\Pi_{\lambda_i}(t')\right] = \sum_i \frac{\lambda_i\varepsilon_i^2}{2\sigma}(\mathrm{e}^{2\sigma t}-1). \tag{4}$$

It follows immediately that

$$E[X(t)] = \frac{1}{\sigma}\sum_i \lambda_i\varepsilon_i(1-\mathrm{e}^{-\sigma t}), \tag{5}$$

$$\mathrm{Var}\,[X(t)] = \frac{1}{2\sigma}\sum_i \lambda_i\varepsilon_i^2(1-\mathrm{e}^{-2\sigma t}). \tag{6}$$

To find the time between action potentials one needs the random variable T_θ which is the time at which $X(t)$ first reaches or exceeds the threshold depolarization θ. If $T_m(x)$ denotes the mth moment of the first passage time for an initial value x, then we have the recurrence relations (Tuckwell, 1976)

$$-\sigma x \frac{dT_m}{dx} + \sum_i \lambda_i T_m(x+\varepsilon_i) - \Lambda T_m(x) = -mT_{m-1}(x), \tag{7}$$

for $m = 1, 2, \ldots$, and $T_0(x) = 1$. The time between action potentials then has mth moment $T_m(0)$ (ignoring the refractory period) and the first moment has been found in a few cases when θ is relatively small (Tuckwell, 1975), and there is a single excitatory input. With excitation only, one solves equation (7) with the conditions that $T_m(x) = 0$ for $x \geqslant \theta$, $T_m(x)$ continuous on $(0, \theta)$ and that $T_m(x)$ possesses a finite limit as x approaches zero from above. The case where there is an exponential distribution of excitatory inputs has recently been treated by Tsurui & Osaki (1976).

When there is inhibition as well as excitation the problem is more complicated, not only because the equations (7) are harder to solve, but because when $X(t)$ leaves $(0, \theta)$ an action potential will not occur if the exit was at zero. The Ornstein–Uhlenbeck diffusion approximation $\hat{X}(t)$, which satisfies the stochastic equation

$$d\hat{X}(t) = \left[-\sigma\hat{X}(t) + \sum_i \lambda_i\varepsilon_i\right] dt + \left(\sum_i \lambda_i\varepsilon_i^2\right)^{\frac{1}{2}} dW(t), \tag{8}$$

where $W(t)$ is a standard Wiener process has been studied by various authors (Roy & Smith, 1969; Sugiyama, Moore & Perkel, 1970; Capocelli & Ricciardi, 1971; Matsuyama, Shirai & Agizuki, 1974) and the first moment of the time at which $\hat{X}(t)$ first leaves $(-\infty, \theta)$ has been derived. Since in reality the neuron cannot achieve exceedingly large hyperpolarizations, it seems that this approach will only be valid if $\hat{X}(t)$ does not spend much time at large negative values. This will occur when the inhibition is weak in comparison with the excitation.

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