Notes on Noise and First-Passage Times - Larry Abbott

The Model

The membrane potential V, obeys the stochastic, first-order differential equation.

$$\tau \frac{dV}{dt} = V_\infty - V + \eta(t) \,, \tag{1.1}$$

where $V_\infty = V_{\text{rest}} + I$, for constant I. In addition, when V reaches a threshold value, V_{th}, an action potential is generated and V is reset to a lower value V_{reset}.

η is a white-noise random variable satisfying (see the following section),

$$\langle \eta(t) \rangle = 0 \quad \text{and} \quad \langle \eta(t)\eta(t') \rangle = 2D\delta(t - t') \,. \tag{1.2}$$

D is a constant with dimensions of voltage squared multiplied by time.

The problem is to compute the average time between resets, that is, the average time it takes for V to travel from V_{reset} to reach, for the first time, V_{th}.

White Noise

A white noise stimulus, $\eta(t)$, has zero mean

$$\langle \eta(t) \rangle = 0 \,, \tag{1.3}$$

where the brackets stand for the average over multiple trials. This equation applies for all t values. In addition to the above equation, white-noise is characterized by averages of pairs of η variables. When $t \neq t'$, $\eta(t)$ and $\eta(t')$ are completely independent, so the average value of their product (again averaged over a large number of different white-noise trials), which is their cross-correlation, is zero. This is stated as

$$\langle \eta(t)\eta(t') \rangle = 0 \quad \text{if} \quad t \neq t' \,. \tag{1.4}$$

On the other hand, if $t = t'$, the value of $\langle \eta^2(t) \rangle$ is proportional to $1/\Delta t$, assuming, for the moment, that time is divided into discrete bins. The reason for this proportionality is that it prevents the fluctuations from averaging out in the $\Delta t \to 0$ limit. Consider the average of η over a time period of duration T,

$$\overline{\eta}(t) = \frac{\Delta t}{T} \sum_{i=1}^{T/\Delta t} \eta(t + (i-1)\Delta t) \,. \tag{1.5}$$

This quantity has zero mean, $\langle\overline{\eta}\rangle = 0$, and variance

$$\langle\overline{\eta}^2\rangle = \left(\frac{T}{\Delta t}\right)\left(\frac{\Delta t}{T}\right)^2 \langle\eta^2\rangle = \left(\frac{\Delta t}{T}\right)\langle\eta^2\rangle\,. \tag{1.6}$$

Thus, for consistency across scales, we must require that

$$\langle\eta^2\rangle \propto \frac{1}{\Delta t}. \tag{1.7}$$

The constant of proportionality is written, by convention, as $2D$.

The function that is zero except when its argument is zero and then is $1/\Delta t$ at that point is the δ function, defined by

$$\int dt\,\delta(t) = 1 \quad \text{and} \quad \int dt\, f(t)\delta(t-t') = f(t')\,. \tag{1.8}$$

In other words, $\delta(t-t')$ is zero when $t \neq t'$ and is infinite when $t = t'$ in such a way that its total integral over time is one. Thus,

$$\langle\eta(t)\eta(t')\rangle = 2D\delta(t-t')\,. \tag{1.9}$$

D is called the diffusion constant and has the units of voltage squared multiplied by time.

Physical processes typically produce filtered versions of white noise. Consider, the membrane potential satisfying 1.1 for a neuron that is not spiking. Then, take $t = 0$ as an arbitrary time point,

$$V(0) = V_\infty + \frac{1}{\tau}\int_{-\infty}^{0} dt'\,\eta(t')e^{t'/\tau}\,, \tag{1.10}$$

so

$$\langle V(t)\rangle = \langle V(0)\rangle = V_\infty \tag{1.11}$$

and

$$\begin{aligned}\sigma_V^2 &= \langle(V(t)-V_\infty)^2\rangle = \langle(V(0)-V_\infty)^2\rangle \\ &= \frac{1}{\tau^2}\int_{-\infty}^{0} dt' \int_{-\infty}^{0} dt''\,\langle\eta(t')\eta(t'')\rangle e^{(t'+t'')/\tau} = \frac{2D}{\tau^2}\int_{-\infty}^{0} dt'\,e^{2t'/\tau}\,.\end{aligned} \tag{1.12}$$

The variance of the variable V from this equation is thus given by

$$\sigma_V^2 = \frac{D}{\tau}\,. \tag{1.13}$$

Suppose we know the value of V at time t, $V(t)$. What will the value be a short time Δt later. We denote this by $V(t+\Delta t)$, but we cannot determine its value unless we know what the random variable η is doing. However, we can compute its average value $\langle V(t+\Delta t)\rangle$. Actually, we will compute the average of $\Delta V = V(t+\Delta t) - V(t)$ instead. To do this we integrate equation 1.1 over the small interval from t to $t+\Delta t$,

$$\int_t^{t+\Delta t} dt' \, \frac{dV(t')}{dt'} = \Delta V = \frac{1}{\tau} \int_t^{t+\Delta t} dt' \left(V_\infty - V(t') + \eta(t') \right) . \tag{1.14}$$

Taking the average of both sides of this equation, and recalling that $\langle \eta \rangle = 0$, we find

$$\langle \Delta V \rangle = \frac{1}{\tau} \int_t^{t+\Delta t} dt' \left(V_\infty - V(t') \right) . \tag{1.15}$$

Finally, for small Δt, we can approximate the integral as the integrand times Δt, so we obtain the final result

$$\langle \Delta V \rangle = \left(V_\infty - V(t) \right) \left(\frac{\Delta t}{\tau} \right) , \tag{1.16}$$

where in this and the following equations ΔV stands for $\Delta V(t)$.

We can also compute

$$\langle (\Delta V)^2 \rangle = \frac{1}{\tau^2} \int_t^{t+\Delta t} dt' \int_t^{t+\Delta t} dt'' \left\langle \left(V_\infty - V(t') + \eta(t') \right) \left(V_\infty - V(t'') + \eta(t'') \right) \right\rangle . \tag{1.17}$$

Taking the averages and using equation 1.9 we find

$$\langle (\Delta V)^2 \rangle = \frac{1}{\tau^2} \int_t^{t+\Delta t} dt' \int_t^{t+\Delta t} dt'' \left((V_\infty - V(t'))(V_\infty - V(t'')) + 2D\delta(t'-t'') \right) , \tag{1.18}$$

which gives, integrating over the δ function and using the same approximation as before,

$$\langle (\Delta V)^2 \rangle = \left(V_\infty - V(t) \right)^2 \left(\frac{\Delta t}{\tau} \right)^2 + 2\sigma_V^2 \left(\frac{\Delta t}{\tau} \right) . \tag{1.19}$$

Furthermore, for small Δt, we can ignore the term of order $(\Delta t)^2$ relative to the term linear in Δt and write

$$\langle (\Delta V)^2 \rangle = 2\sigma_V^2 \left(\frac{\Delta t}{\tau} \right) . \tag{1.20}$$

Results 1.16 and 1.20 are needed for the first-passage time calculation.

The Mean First-Passage Time

We denote the average first-passage from an arbitrary value V to the threshold as $T(V)$, so that the mean first-passage time we seek is $T = T(V_{\text{reset}})$. Suppose that, on a given trial, the variable satisfying equation 1.1 moves from V to $V + \Delta V$ in time Δt. On average, the time it takes to get to the threshold from $V + \Delta V$ must be Δt less than the time it takes from V, so

$$\langle T(V + \Delta V)\rangle = T(V) - \Delta t\,. \tag{1.21}$$

Expanding in a Taylor series,

$$\langle T(V + \Delta V)\rangle \approx T(V) + T'(V)\langle \Delta V\rangle + \frac{1}{2}T''(V)\langle (\Delta V)^2\rangle\,, \tag{1.22}$$

where the primes denote derivatives with respect to V. Using equations 1.16 and 1.20, we find, from 1.21, that

$$\sigma_V^2(V)T''(V)\left(\frac{\Delta t}{\tau}\right) + (V_\infty - V)T'(V)\left(\frac{\Delta t}{\tau}\right) + \Delta t = 0\,, \tag{1.23}$$

or

$$\sigma_V^2 T''(V) + (V_\infty - V)T'(V) + \tau = 0\,. \tag{1.24}$$

Defining

$$f(V) = -\frac{(V_\infty - V)^2}{2\sigma_V^2} \quad \text{so that} \quad f'(V) = \frac{V_\infty - V}{\sigma_V^2}\,, \tag{1.25}$$

we can write down the solution to this equation using standard integration factors,

$$T'(V) = -\left(\frac{\tau}{\sigma_V^2}\right)e^{-f(V)}\int_{-\infty}^{V} dy\ .e^{f(y)}\,, \tag{1.26}$$

Integrating the above result, we find

$$T(V) = -\left(\frac{\tau}{\sigma_V^2}\right)\int_{V_{\text{th}}}^{V} dx\, e^{-f(x)}\int_{-\infty}^{x} dy\, e^{f(y)}\,, \tag{1.27}$$

where we have imposed the additional boundary condition $T(V_{\text{th}}) = 0$, which means that once you are there it takes no time to get there. This means that the answer we seek is

$$\begin{aligned} T &= \left(\frac{\tau}{\sigma_V^2}\right)\int_{V_{\text{reset}}}^{V_{\text{th}}} dx\, e^{-f(x)}\int_{-\infty}^{x} dy\, e^{f(y)} \qquad (1.28)\\ &= \left(\frac{\tau}{\sigma_V^2}\right)\int_{V_{\text{reset}}}^{V_{\text{th}}} dx\,\exp\left(\frac{(V_\infty - x)^2}{2\sigma_V^2}\right)\int_{-\infty}^{x} dy\,\exp\left(-\frac{(V_\infty - y)^2}{2\sigma_V^2}\right)\,. \end{aligned}$$

Changing variables $y \to y\sqrt{2}\sigma_V + V_\infty$ and $x \to x\sqrt{2}\sigma_V + V_\infty$, we find

$$T = 2\tau \int_{(V_{\text{reset}}-V_\infty)/\sqrt{2}\sigma_V}^{(V_{\text{th}}-V_\infty)/\sqrt{2}\sigma_V} dx\, \exp(x^2) \int_{-\infty}^{x} dy\, \exp(-y^2)\,. \tag{1.29}$$

Using the fact that

$$\int_{-\infty}^{x} dy\, \exp(-y^2) = \frac{\sqrt{\pi}\,(1+\text{erf}(x))}{2}\,, \tag{1.30}$$

we obtain the result

$$T = \tau\sqrt{\pi} \int_{(V_{\text{reset}}-V_\infty)/\sqrt{2}\sigma_V}^{(V_{\text{th}}-V_\infty))/\sqrt{2}\sigma_V} dx\, \exp(x^2)\,(1+\text{erf}(x))\;. \tag{1.31}$$

Useful Numerical Approximation

The integral in equation 1.31 is difficult to compute numerically because of the nature of the integrand $\exp(x^2)(1+\text{erf}(x))$. To compute this integral using standard methods, use the following approximation.

$$\exp(x^2)(1+\text{erf}(x)) \approx \begin{cases} f_1 & \text{if } x \le 0 \\ 2\exp(x^2) - f_1 & \text{if } x > 0\,, \end{cases} \tag{1.32}$$

where

$$f_1 = t\exp(\alpha)\,, \qquad t = \frac{1}{1+0.5|x|}\,, \tag{1.33}$$

and

$$\alpha = a_1 + t(a_2 + t(a_3 + t(a_4 + t(a_5 + t(a_6 + t(a_7 + t(a_8 + t(a_9 + ta_{10})))))))) \tag{1.34}$$

with

$$\begin{aligned} a_1 &= -1.26551223 & a_2 &= 1.00002368 & a_3 &= 0.37409196 \\ a_4 &= 0.09678418 & a_5 &= -0.18628806 & a_6 &= 0.27886087 \\ a_7 &= -1.13520398 & a_8 &= 1.48851587 & a_9 &= -0.82215223 \\ & & & & a_{10} &= 0.17087277 \end{aligned} \tag{1.35}$$