First passage time

Consider a 1-d neuron model that is driven by noise:

$$\frac{dV}{dt} = f(V) + \sigma \frac{dW}{dt}$$

where W is a white-noise process with mean zero and unit variance. The second moment is $< (\Delta V)^2 >= \sigma^2 \Delta t$ in small time intervals. The mean $< \Delta V >= f(V)\Delta t$. This is a scalar model (for example if $f(V) = I - V$, it is the integrate-and-fire model). Suppose that when $V(t)$ hits V_{spike} then it is set to V_{reset}. You can try to simulate this using Eulers method:

$$\Delta V = f(V)\Delta t + \sqrt{\Delta t}\sigma\eta$$

where η is drawn from a gaussian distribution with zero mean and unit variance. Here is an XPP file for the simulation:

```
f(v)=I-V
wiener w
V'=f(V)+sig*w
init V=0
par I=0,sig=1
@ meth=euler,total=200
done
```

Note that XPP takes care of the square root of of the time step autoimatically when you use "wiener" parameters. You can get XPP to integrate this equation until it hits `vspike`. Click on Numerics Poincare. Then choose Section with `V` as the variable, 1 as the section, and `y` to Stop-on-section. Each time you integrate the equations, you get one point, the time at which it hit. Escape to the main menu and click on Initconds range. Range over V for 200 steps starting at 0 and ending at 0 and choosing "N" for reset storage. This will give you 200 instances of the simulation. Click on Numerics Stochastic Stat and choose `t` and it will give you a mean of about 5 or so. Thus the mean firing rate is about 0.2. is there a better way to do this? Of course!

In absence of noise, you already looked at the firing properties of this for the I&F model and for $f(V) = V^m + I$. However, if there is noise, then it is possible for the neuron to fire even for the cases when there is a stable rest state. Thus, we can ask what the mean time until firing will be if the neuron is currently at V. Call this $T(V)$. Clearly $T(V_{spike}) = 0$. The mean firing rate of the neuron is: $R = 1/T(V_{reset})$ since this is the average amount of time from reset until firing again. I now present a short derivation for this based on notes from Larry Abbott. Suppose that on a given trial, the potential moves from V to $V + \Delta V$ in time Δt. Then on average, $< T(V + \Delta V) >= T(V) - \Delta t$. (Note that ΔV is a random variable but $T(V), V, \Delta t$ are not.) Expanding, in small ΔV, we get:

$$T(V + \Delta V) \approx T(V) + \Delta V T'(V) + \frac{1}{2}(\Delta V)^2 T''(V) + \ldots.$$

Taking the mean and using the above facts about ΔV, we get:

$$\frac{\sigma^2}{2}T''(V) + f(V)T'(V) = -1$$

as $\Delta t \to 0$. This is a linear differential equation which satisfies the boundary condition, $T(V_{spike}) = 0$. What is the other condition? Since there is no lower bound for V (that is V can be driven arbitrarily low), we want $T'(-\infty) = 0$. As an exercise, you should compute the first passage time for the I&F model as a double integral and use this to write an expression for the firing rate, $1/T(V_{reset})$. For the most part, these kinds of expressions are pretty worthless since it is so hard to evaluate the integrals. So instead, we can do this numerically by solving the boundary-value problem. We replace the semi-infinite interval with $(-A, V_{spike})$ where we choose A large. Then we must solve the above ODE with $dT/dV = 0$ at $V = -A$ and $T(V_{spike}) = 0$. XPP can solve boundary value problems either with AUTO or on its own using a method called shooting. Since the BVP is linear, it usually converges in one try. XPP can also solve BVPs over a range. however, it only keeps the values of the end-points. We actually want $T(V_{reset})$ which is an interior point. So, we split the interval $(-A, V_{spike})$ into two intervals $(-A, V_{reset})$ and (V_{reset}, V_{spike}). Then we rescale these intervals to the same size and solve boundary value problems on each of them, matching the right-hand of the lower interval with the left-hand of the upper interval. Here is an XPP file I have created for this:

```
# first passage set up to compute the firing times
# this is defined on an interval [0,1]
# and split up to get the interior value
#
par I=-1,sig=1,vreset=-1,vspike=10,a=10
b=(vreset+a)
c=(vspike-vreset)
# ok - here it is
# u is lower and w is upper interval
# s lies between 0 and 1
# u(s=0) = T(-A)
# u(s=1) = w(s=0)=T(V_reset)
# w(s=1) = T(V_spike)
# gotta write it as a system
du/dt=up
dup/dt=-2*b*b/sig-2*f(-a+b*s)*up*b/sig
dw/dt=wp
dwp/dt=-2*c*c/sig-2*f(vreset+c*s)*wp*c/sig
ds/dt=1
# 5 equations - 5 boundary conds
# du/ds=0 at s=0
bndry up
# w=0 at s=1
```

```
bndry w'
# du/ds(1)=dw/ds(0)
bndry up'-wp
# u(1)=w(0)
bndry u'-w
# s=t
bndry s
# set up some numerics
@ total=1,dt=.005
# here is f, dont want to forget  f
f(x)=x^2+I
done
```

Give it a whirl!

More analysis. It is pretty straightforward to solve the first passage time analytically. Let me call $v_{spike} = \theta$ and $v_{reset} = \phi$ for notational simplicity. Let $F(V) = \int f(V)$. Then the solution to

$$\frac{\sigma^2}{2}T'' + f(V)T' = -1, \quad T(\theta) = 0, \quad T'(-\infty) = 0$$

is

$$T(V) = \frac{2}{\sigma^2}\int_V^\theta e^{\frac{-2F(x)}{\sigma^2}} \int_{-\infty}^x e^{\frac{2F(y)}{\sigma^2}} dy\ dx.$$

An alternate formulation is to compute the flux for the Fokker-Planck equation. Let me lay this out briefly for a general Markov process and then apply it to the noisy oscillator. Let $P(v,t)dv$ be the probability of finding $v \in (v, v+dv)$ at time t. Let $R(y,v)$ denote the rate at which a jump of size y is made given you are at state v. Then we write down the evolution of P through the Master equation:

$$\frac{\partial P}{\partial t} = \int R(y, v-y)P(v-y,t) - R(y,v)P(v,t)\ dy.$$

The first term sums up all jumps of length y that take you to v. The second is all the jumps taking you away from v. We can write

$$R(y,v-y)P(v-y,t) = R(y,v)P(v,t) - y[R(y,v)P(y,v)]_v + \frac{y^2}{2}[R(y,v)P(v,t)]_{vv} + \ldots$$

using Taylor's theorem. We can interchange the integral and the derivative (they are both linear and they commute) so that we get

$$\frac{\partial P}{\partial t} = -[\int yR(y,v)dyP(v,t)]_v + \frac{1}{2}[\int y^2R(y,v)dyP(v,t)]_{vv} + \ldots.$$

Now note that the first term $\int yR(y,v)dy$ is the mean jump size per unit time and the second term is the second moment of the jump size per unit time.

Higher order terms are higher moments of the jump size per unit time. Recall from the first paragraph in this note that the mean jump size in time Δt is $f(V)\Delta t$ and the second moment is $\sigma^2 \Delta t$. Higher moments will be of the order of $(\Delta t)^s$ where $s \geq 3/2$. Dividing by Δt and letting it go to zero, we see that all but the first two moments go to zero. Thus, for our little noisy neuron, the probability evolves as:

$$\frac{\partial P}{\partial t} = -[f(v)P(v,t)]_v + \frac{\sigma^2}{2}[P(v,t)]_{vv}.$$

This is called the Fokker-Planck equation. We have $P(\theta, t) = 0$ since whenever we hit this boundary, we are reset. We also have $P(-\infty, t) = 0$ and

$$\int_{-\infty}^{\theta} P(v,t)\ dv = 1$$

for normalization. The steady state satisfies:

$$[f(v)P(v) - \frac{\sigma^2}{2}P'(v)]' = 0$$

along with the boundary conditions and normalization. Integrating this once, we get

$$f(v)P(v) - \frac{\sigma^2}{2}P'(v) = J$$

where J is a constant called the flux. Note that at $v = \theta$, J is the rate at which the voltage crosses θ, so that it is the firing rate! We must be careful about the reset after firing. For $v < \phi$ there is no flux, $J = 0$ since nothing is coming in at that end other than the leakage from the noise. For $v > \phi$, J will be nonzero in general due to re-injection after firing. So, we will solve this in two pieces. Thus we must solve the following system of ODEs:

$$\begin{aligned}
f(v)P_-(v) - \frac{\sigma^2}{2}P_-'(v) &= 0 \quad -\infty < v < \phi \\
f(v)P_+(v) - \frac{\sigma^2}{2}P_+'(v) &= J \quad \phi < v < \theta \\
P_-(-\infty) &= 0 \\
P_-(\phi) &= P_+(\phi) \\
P_+(\theta) &= 0 \\
\int_{-\infty}^{\phi} P_-(v)\ dv + \int_{\phi}^{\theta} P_+(v)\ dv &= 1.
\end{aligned}$$

The solution to this depends on a single constant J and this constant is determined by the normalization. After a bit of simple integration, we find:

$$\begin{aligned}
J^{-1} &= \frac{2}{\sigma^2}\int_{-\infty}^{\phi} e^{\frac{2F(x)}{\sigma^2}}\ dx \int_{\phi}^{\theta} e^{\frac{-2F(y)}{\sigma^2}}\ dy \\
&+ \frac{2}{\sigma^2}\int_{\phi}^{\theta} e^{\frac{2F(x)}{\sigma^2}} \int_{x}^{\theta} e^{\frac{-2F(y)}{\sigma^2}}\ dy\ dx.
\end{aligned}$$

Homework

1. Show that $J^{-1} = T(\phi)$.
2. Compute $T(\phi)$ for the simplest model, $f(v) = I$.
3. Compute $P_{\pm}(v)$ for this simple model as well.