Populations of Neurons

In this module we calculate the distribution and firing rate of a populations of unconnected neurons receiving fluctuating synaptic input, each with different realisations of the synaptic noise, but with the same mean and variance.

Spiking Neuron Models, Gerstner and Kistler. Chapter 5 p178-188. Cambridge University Press

• General Framework

We consider a situation in which there are many neurons receiving similar input. We are interested in the probability density $P(V,t)$ of finding a neuron with a voltage V at time t. We first derive the continuity equation which is a result related to the conservation of voltage trajectories. Let $J(V)$ be the current of neuronal voltage trajectories that cross a voltage V in a time t from below. The number of trajectories that enter and leave the voltage range $V \to V+\delta V$ in a time δt is $(J(V)-J(V+\delta V))\delta t$. This must be equal to the rate of increase of the probability $P(V,t)\delta V$ finding a neuron in this voltage range, and so taking the continuum limit we get

$$\frac{\partial P}{\partial t} + \frac{\partial J}{\partial V} = 0. \tag{1}$$

We now need to derive the specific form of the current J for spiking neurons (in the limit of fast synapses - see Week 7 notes). When the synapses are fast we can write the voltage as

$$\tau_0 \frac{dV}{dt} = E_0 - V + \sigma_V \sqrt{2\tau_0}\xi(t). \tag{2}$$

The current has two components; a drift component that is proportional to the average voltage "velocity"

$$J_{drift} = \frac{dV}{dt}P = \frac{(E_0 - V)}{\tau_0}P, \tag{3}$$

and a component coming from the fluctuations that is proportional to the gradient of the density

$$J_{fluct} = -\frac{\alpha^2}{\tau_0}\frac{dP}{dV}. \tag{4}$$

The prefactor α^2 of the "diffusive" term can be extracted by considering a situation where the net current is zero (such as when the population of neurons is in equilibrium and there is no threshold)

$$0 = J = J_{drift} + J_{fluct}. \tag{5}$$

Under these circumstances it must be that:

$$(V - E_0)P = -\alpha^2 \frac{dP}{dV}. \tag{6}$$

Multiplying this equation by voltage V and integrating over the entire voltage range gives that $\langle V\rangle^2 - E_0^2 = \sigma_V^2 = \alpha^2$, and hence the current can be written

$$\tau_0 J = (E_0 - V) - \sigma_V^2 \frac{dP}{dV}. \tag{7}$$

Combining the current and continuity equation yields the Fokker-Planck equation

$$\tau_0 \frac{\partial P}{\partial t} = \sigma_V^2 \frac{\partial^2 P}{\partial V^2} + \frac{\partial}{\partial V}\left(\left(V - E_0\right)P\right). \qquad (8)$$

• The Firing Rate of a Population of LIF Neurons

We will now include a threshold for a spike at V_{th} and a reset at V_{re}. If a neuron reaches V_{th} its voltage is instantly reset to V_{re} so that $P(V_{th}) = 0$. We will consider the steady state case such that $\partial P/\partial t = 0$. Because of the threshold-reset condition the probability density of finding a neuron at V_{th} is zero and the current of neurons across the threshold must be equal to the steady-state firing rate r which is the quantity of interest. Evaluating the current equation (7) at threshold yields

$$r = J(V_{th}) = \frac{E_0 - V_{th}}{\tau_0} P(V_{th}) - \frac{\sigma_V^2}{\tau_0} \left.\frac{\partial P}{\partial V}\right|_{V_{th}} = -\frac{\sigma_V^2}{\tau_0} \left.\frac{\partial P}{\partial V}\right|_{V_{th}}. \qquad (9)$$

This current is reinserted at V_{re} and in the steady state, the currents near the rest must sum to zero; the incoming trajectories equal the outgoing trajectories

$$J_{re-} + r = J_{re+}. \qquad (10)$$

The current below rest must be equal to zero because no neurons have voltages that go off to $-\infty$ (they always drift back). If we are in the steady state situation it must be, from equation (1), that the current is a piecewise constant of voltage and hence we have

$$J = r\theta(V - V_{re}) \quad \text{for } V \le V_{th}. \qquad (11)$$

To simplify the analysis we use the notation $x = (V - E_0)/\sigma_V$ and $P(V)dV = p(x)dx$. The current equation (7) can therefore be written

$$-\tau_0 r\theta(x - x_{re}) \quad = \quad xp + \frac{\partial p}{\partial x} = e^{-x^2/2}\frac{\partial}{\partial x}\left(e^{x^2/2}p\right) \qquad (12)$$

where $x_{re} = (V_{re} - E_0)/\sigma_V$. We now multiply both sides by the exponential prefactor and integrate from x to $x_{th} = (V_{th} - E_0)/\sigma_V$ to yield

$$p(x) = \tau_0 r e^{-x^2/2} \int_x^{x_{th}} dy e^{y^2/2} \theta(y - x_{re}). \qquad (13)$$

This equation gives the probability density as function of the unknown firing rate r. We can use the fact that the integral of $p(x)$ must be one to fix the rate

$$1 = \int_{-\infty}^{x_{th}} p(x)dx = \tau_0 r \int_{-\infty}^{x_{th}} dx e^{-x^2/2} \int_x^{x_{th}} dy e^{y^2/2}\theta(y - x_{re}) = \tau_0 r \int_{x_{re}}^{x_{th}} dy \int_{-\infty}^{y} dx e^{y^2/2} e^{-x^2/2}. \qquad (14)$$

If substitute $x = y - z$ we reduce the identity further to

$$1 = \tau_0 r \int_{x_{re}}^{x_{th}} dy \int_0^{\infty} dz e^{yz - z^2/2} = \tau_0 r \int_0^{\infty} \frac{dz}{z}\left(e^{x_{th}z} - e^{x_{re}z}\right) e^{-z^2/2}. \qquad (15)$$

Hence we can write the firing rate as

$$r = \frac{1}{\tau_0 Z} \quad \text{where} \quad Z = \int_0^{\infty} \frac{dz}{z}\left(e^{x_{th}z} - e^{x_{re}z}\right) e^{-z^2/2}. \qquad (16)$$

• The Steady-State Firing Rate in Various Limits

The form of the firing rate (16) must be analysed numerically as it is not possible to find the integral in the form of analytical functions. The first case we consider is that of low noise and $E_0 > V_{th}$ so that $x_{th} \ll 0$ and $x_{re} < x_{th} \ll 0$. In this case the exponentials in Z decay rapidly and we need not consider the gaussian envelope:

$$Z \simeq \int_0^\infty \frac{dz}{z}\left(e^{x_{th}z} - e^{x_{re}z}\right) = \int_{x_{re}}^{x_{th}} dx \int_0^\infty dz e^{xz} = \log\left(\frac{x_{re}}{x_{th}}\right) \quad (17)$$

which gives the firing rate in this limit as

$$r \simeq \frac{1}{\tau_0 \log\left(\frac{E_0 - V_{re}}{E_0 - V_{th}}\right)} \quad (18)$$

which is in agreement with the deterministic firing case previously calculated. At this order there is no effect of the noise - to account for this the gaussian envelope in (16) must be expanded to second order in y and the steps repeated. We now consider the case of subthreshold drive $E_0 < V_{th}$ where it is the (weak) fluctuations that cause the spikes. In this case $x_{th} \gg 0$ and it proves convenient to rewrite Z as follows:

$$Z = \int_0^\infty \frac{dz}{z}\left(e^{x_{th}^2/2} e^{-(z-x_{th})^2/2} - e^{x_{re}^2/2} e^{-(z-x_{re})^2/2}\right). \quad (19)$$

If $x_{re} > 0$, then because $x_{th} > x_{re}$ we have $e^{x_{th}^2/2} \gg e^{x_{re}^2/2}$ and the second term in the integral may be dropped. If $x_{re} < 0$ the second term may again be neglected as the integral of z runs from 0. That the reset is unimportant is unsurprising because in the limit of subthreshold firing, when the noise is weak, the time to spike is dominated by the time from rest E_0 to threshold V_{th}, not from the post-spike equilibration from reset V_{re} to rest E_0. Hence

$$Z \simeq e^{x_{th}^2/2} \frac{1}{x_{th}} \int_0^\infty dz e^{-(z-x_{th})^2/2} = e^{x_{th}^2/2} \frac{\sqrt{2\pi}}{x_{th}} \quad (20)$$

which gives a firing rate for the limit $V_{th} - E_0 \ll \sigma_V$

$$r \simeq \frac{1}{\tau_0} \frac{(V_{th} - E_0)}{\sqrt{2\pi\sigma_V^2}} \exp\left(-\frac{(V_{th} - E_0)^2}{2\sigma_V^2}\right). \quad (21)$$