Models of Spiking Neurons

In this module we will examine the voltage-gated channels that support action-potential generation. A well known reduction to a two-variable system will be used to demonstrate a Type II neuron - one that cannot fire slower than a certain frequency. A simple one-dimensional model will be used to demonstrate a Type I neuron - one that can fire at an arbitrarily low frequency.

Mathematical Physiology, Keener and Sneyd. Chapter 4 p116-142. Springer.
Theoretical Neuroscience, Dayan and Abbott. Chapter 5 p173-175. MIT Press
Spiking Neuron Models, Gerstner and Kistler. Chapter 3 p69-91. Cambridge University Press

• The Fitzhugh-Nagumo Model

The full non-linear dynamics of the 4 coupled equations that make up the Hodgkin-Huxley (HH) model of a spike are too complicated to extract much from analytically. Reductions of the model typically involve a fast voltage equation which encompasses the subthreshold and run-up to the top of the spike, and a slower, negative feedback variable that repolarises the neuron. One such two-variable "toy" model that has similarities with the HH model is the Fitzhugh-Nagumo model with an equation for a voltage-like variable V and a second variable W

$$\frac{dV}{dt} = V - \frac{V^3}{3} - W + I \quad (1)$$

$$\frac{dW}{dt} = \epsilon\left(b_0 + b_1 V - W\right). \quad (2)$$

Here ϵ is small constant that leads to a dynamics for the W variable that is much slower than for the voltage variable V. The nullclines for the system are

$$W_1 = V - \frac{V^3}{3} + I \quad \text{and} \quad W_2 = b_0 + b_1 V. \quad (3)$$

The fixed point (V_*, W_*) is at the intersection of these cubic and linear equations. We assume that $b_1 > 1$ so the gradient of W_2 is always greater than W_1 and there is only one fixed point. The direction of flow on the nullclines is such that damped oscillatory solutions, and fully oscillating solutions can be expected. We will now examine where the domains of these two cases lie.

Following the method that we used to analyse subthreshold voltage-gated channels we linearise the equations by inserting $V = V_* + v$ and $W = W_* + w$, and keeping terms only to first order in v and w:

$$\frac{dv}{dt} = v(1 - V_*^2) - w \quad \text{and} \quad \frac{dw}{dt} = \epsilon\left(b_1 v - w\right). \quad (4)$$

The eigenvalues of this system are given by the equation

$$\lambda^2 + \lambda\left(V_*^2 - 1 + \epsilon\right) + \epsilon\left(b_1 + V_*^2 - 1\right) = 0. \quad (5)$$

If we assume that damped solutions exist, so that λ is imaginary, the system will destabilise into spontaneous oscillations when

$$\left(V_*^2 - 1 + \epsilon\right) < 0 \quad (6)$$

which for small ϵ yields $V_*^2 < 1$. Hence, if the fixed point is between the minimum and maximum of W_1 there are spontaneous oscillations. For small ϵ these oscillations loop from the

W_1 minimum at $V = -1$, move in the direction of increasing voltage until the W_1 line is hit (at a value $V > 1$. The W_1 nullcline is then followed up (increasing W, decreasing V to the W_1 maxima at $V = 1$) at which point it moves quickly in the direction of decreasing voltage until the W_1 nullcline is again hit, at which point the voltage relaxes down to $V = -1$ and the oscillation restarts. The period is finite and so the neuron starts to fire at a finite frequency once the critical current is reached. A neuron that starts to fire at a non-zero rate, once a threshold has been passed, is called a Type II neuron - it cannot fire at a rate below this frequency.

• The Mechanism Behind Type I Neuron Models

Another two variable model which can spontaneously oscillate is the Morris-Lecar model. This has a similar structure except that a transition occurs from 3 fixed points to 1 unstable fixed point. At the point of transition, two fixed points collide because the nullclines of this model are at a tangent. At this point one of the eigenvalues becomes zero (not just the real part, as was the case for the Fitzhugh-Nagumo model). On the other side of the transition, when the two curves are no longer at a tangent but just miss each other, there are spontaneous oscillations. When the trajectory passes near to where the tangent was it slows down dramatically, because the eigenvalue, though now positive, is still very close to zero. In this case the period can be made arbitrarily long, and the neuron can fire at an arbitrarily low rate. This is called a Type I neuron.

• Canonical Type I Neuron Model

There is a simple one-dimensional model that shows Type I behaviour. The voltage equation takes the form

$$\frac{dV}{dt} = qV^2 + I \tag{7}$$

where $q > 0$. This dynamics allows the voltage to run off to infinity in finite time. We supplement the equation by stating that if the voltage is at $+\infty$ we re-insert it at $-\infty$. This will allow oscillations, and something that looks a bit like a spike. We will now examine the fixed point structure of equation (7) and consider its possible dynamics.

Subthreshold response and excitability. When $I < 0$ there are two fixed points, at

$$V_* = \pm\sqrt{\frac{-I}{q}}. \tag{8}$$

The lower fixed point is stable and the upper unstable, as can seen from the eigenvalues at these fixed points:

$$\lambda_\pm = \pm 2\sqrt{-Iq}. \tag{9}$$

If the voltage is between $-\infty$ and $\sqrt{-I/q}$ it will relax to the stable fixed point. However if the voltage is above the unstable fixed point $V > \sqrt{-I/q}$ the voltage will go off to $+\infty$, be reinserted at $-\infty$ and then relax to the fixed point. For $I < 0$ the model has a stable fixed point but is *excitable*, synaptic pulses that add up to a total voltage larger than $2\sqrt{-I/q}$ will cause the neuron to fire once.

Approach to the critical point. As $I \to 0$ the eigenvalues approach 0. Because the response of the system near the fixed point are governed by a time-scale that is the inverse of the eigenvalue, the dynamics become very slow near V_* (which also approaches 0). At $I = 0$ the stable and unstable fixed points "collide" and annihilate, and so for $I > 0$ no fixed point exists. The derivative is always positive and all motion is towards more positive V. For small positive I the dynamics are still very slow near $V = 0$ as can be seen by directly evaluating the voltage rate of change (7) at $V = 0$ which scales with I.

Spontaneous oscillations. We will now derive the form for the oscillations for the unstable case when $I > 0$. On rescaling voltage by $V = x\sqrt{I/q}$ and time by $t = s/\sqrt{qI}$, the dimensionless voltage equation becomes

$$\frac{dx}{ds} = x^2 + 1. \tag{10}$$

The solution of this equation between times s_a, s_b and voltages x_a, x_b is

$$\arctan(x_b) - \arctan(x_a) = s_b - s_a \tag{11}$$

and if, when $s_a = 0$ we have $x_a = 0$, then the voltage takes the simple form

$$x = \tan(s) \quad \text{or} \quad V = \sqrt{\frac{I}{q}}\tan\left(t\sqrt{Iq}\right). \tag{12}$$

From this it is straightforward to extract the period of the oscillation, which is the time it takes to go from $0 \to \infty$ and then $-\infty \to 0$. This is just

$$T = \frac{2}{\sqrt{Iq}}\lim_{V\to\infty}\left(\arctan\left(V\sqrt{\frac{q}{I}}\right)\right) = \frac{\pi}{\sqrt{Iq}} \tag{13}$$

which gives a firing rate r that scales with the square-root of the current

$$r = \frac{\sqrt{Iq}}{\pi}. \tag{14}$$

This is an example of a Type I neuron model - it can fire at arbitrarily low frequency.

There is a nice remapping of the model onto a variable that measures the phase of the oscillation. This avoids some of the infinities that appear in the model:

$$V = \tan\left(\frac{\theta}{2}\right). \tag{15}$$

If the initial condition has the voltage at zero we get spikes (discontinuities in the original voltage model at $\theta = n\pi$ where n counts over the integers. The corresponding differential equation is

$$\frac{d\theta}{dt} = q(1 - \cos(\theta)) + I(1 + \cos(\theta)) \tag{16}$$

which in this form is known as the theta model.