Fall 2015 * Math 430 * Math 635 * Prof. Victor Matveev

Lectures 23-24
The Cable Equation and the Propagation of Action Potential

Without loss of generality, let's start with the Morris-Lecar model. Extending to any conductance-based model such as the Hodgkin-Huxley model, is pretty straightforward

$$\begin{cases} C\dfrac{dV}{dt} = I - G_L\left(V - V_L\right) - G_{Ca}m_\infty\left(V\right)\left(V - V_{Ca}\right) - G_K n\left(t\right)\left(V - V_K\right) \\ \dfrac{dn}{dt} = \dfrac{n_\infty\left(V\right) - n}{\tau_n\left(V\right)} \end{cases}$$

This model is for a single equipotential cell. To simulate an axon with position-dependent potential, think of segmenting it into small pieces ("segments"), each of which is small enough to be approximately equipotential, and therefore well described by the above model. Now, introduce notation for the potential and gating variable of each segment:

$$V_j\left(t\right) \equiv V\left(x_j, t\right)$$
$$n_j\left(t\right) \equiv n\left(x_j, t\right)$$

We assume that the segments are of roughly the same size, so that the capacitance and the conductances are the same for each segment (this assumption could be easily relaxed):

$$\begin{cases} C\dfrac{dV_j}{dt} = -G_L\left(V_j - V_L\right) - G_{Ca}m_\infty\left(V\right)\left(V_j - V_{Ca}\right) - G_K n\left(t\right)\left(V_j - V_K\right) + I_{j-1\to j}^{\text{axial}} + I_{j+1\to j}^{\text{axial}} \\ \dfrac{dn_j}{dt} = \dfrac{n_\infty\left(V_j\right) - n_j}{\tau_n\left(V_j\right)} \end{cases}$$

The only additional terms are $I_{j\pm1\to j}^{\text{axial}}$, the axial currents arriving from the neighboring segments to immediate left and immediate right, which are given by the Ohm's law in terms of the potential differences between neighboring compartments:

$$I_{j\pm1\to k}^{\text{axial}} = G_{\text{axial}}\left(V_{j\pm1} - V_j\right) \qquad \Rightarrow \qquad I_{j-1\to j}^{\text{axial}} + I_{j+1\to j}^{\text{axial}} = G_{\text{axial}}\left(V_{j+1} - V_j\right) + G_{\text{axial}}\left(V_{j-1} - V_j\right)$$
$$= G_{\text{axial}}\left(V_{j+1} - 2V_j + V_{j-1}\right)$$

The equation for the potential of the j-th compartment becomes:

$$C\frac{dV_j}{dt} = -G_L\left(V_j - V_L\right) - G_{Ca}m_\infty\left(V\right)\left(V_j - V_{Ca}\right) - G_K n\left(t\right)\left(V_j - V_K\right) + G_{\text{axial}}\left(V_{j+1} - 2V_j + V_{j-1}\right)$$

Now let's divide the equation by G_L:

$$\tau_m\frac{dV_j}{dt} = -\left(V_j - V_L\right) - \frac{G_{Ca}}{G_L}m_\infty\left(V\right)\left(V_j - V_{Ca}\right) - \frac{G_K}{G_L}n\left(t\right)\left(V_j - V_K\right) + \frac{G_{\text{axial}}}{G_L}\left(V_{j+1} - 2V_j + V_{j-1}\right)$$

Recall that the leak and other membrane conductances are proportional to the cylindrical side surface area of the segment, $A_{side} = 2\pi a\,\Delta x$ (we assume that the segment radius is *a*, and the segment length is Δ*x*):

$$G_{L,K,Ca} = A_{side} g_{L,K,Ca} = 2\pi a\,\Delta x\; g_{L,K,Ca}$$

Where $g_{L,K,Ca}$ are specific conductivities, measured in Siemens per unit area.

In contrast, axial conductances describe the flow of current *inside* the axon, rather than *across* the axon wall. Thus, G_{axial} is inversely proportional to the length of each segment, and directly proportional to the cross section area of the axon:

$$G_{\text{axial}} = g_{\text{axial}} \frac{A_{\text{section}}}{\Delta x} = g_{\text{axial}} \frac{\pi a^2}{\Delta x}$$

Where g_{axial} is the specific axial conductivity, in units of Siemens per meter

Thus, we obtain

$$\frac{G_{\text{axial}}}{G_L} = \frac{g_{\text{axial}} \dfrac{\pi a^2}{\Delta x}}{g_L\; 2\pi a\,\Delta x} = \frac{a\, g_{\text{axial}}}{2\, g_L} \frac{1}{(\Delta x)^2}$$

Denoting $\lambda^2 = \dfrac{a\, g_{\text{axial}}}{2\, g_L}$ and plugging this into the main equation, we obtain:

$$\tau_m \frac{dV_j}{dt} = -\left(V_j - V_L\right) - \frac{G_{Ca}}{G_L} m_\infty(V)\left(V_j - V_{Ca}\right) - \frac{G_K}{G_L} n(t)\left(V_j - V_K\right) + \lambda^2 \frac{V_{j+1} - 2V_j + V_{j-1}}{(\Delta x)^2}$$

One easily recognizes the finite-difference approximation of the second derivative; taking the limit $\Delta x \to 0$, we obtain a partial differential equation:

$$\begin{cases} \tau_m \dfrac{dV(x,t)}{dt} = -\left(V - V_L\right) + \lambda^2 \dfrac{\partial^2 V}{\partial x^2} - \dfrac{G_{Ca}}{G_L} m_\infty(V)\left(V - V_{Ca}\right) - \dfrac{G_K}{G_L} n\left(V_j - V_K\right) \\ \dfrac{dn(x,t)}{dt} = \dfrac{n_\infty(V) - n}{\tau_n(V)} \end{cases}$$

Now, let's consider the passive axon case, $G_K = G_{Ca} = 0$, and shift the zero potential to V_L (i.e. $v = V - V_L$) , which will lead to the so-called cable equation:

$$\tau_m \frac{dv}{dt} = -v + \lambda^2 \frac{\partial^2 v}{\partial x^2}$$

It's instructive to consider the stationary solution, revealing the meaning of parameter λ:

$$\tau_m \frac{dv}{dt} = -v + \lambda^2 \frac{\partial^2 v}{\partial x^2} = 0 \;\Rightarrow\; \frac{\partial^2 v^*}{\partial x^2} = \frac{1}{\lambda^2} v^* \;\Rightarrow\; v^*(x) = v_o\; e^{-x/\lambda}$$

Thus, λ describes the decay of the potential along the length of the axon, due to the loss of charge across the membrane. This parameter is called the *space constant* or the *electrotonic length*. It has the same meaning even for the active axon case, describing the loss of charge due to the leak current, as the action potential is propagating thanks to the active currents.