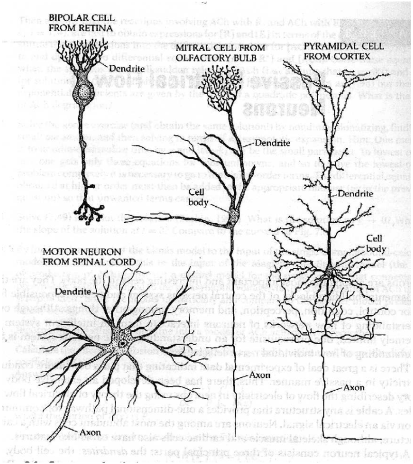
The cable equation A.K.A. the monodomain model

Neurons


BIPOLAR CELL
FROM RETINA
Dendrite
MITRAL CELL FROM
OLFACTORY BULB
Dendrite
Cell
body
PYRAMIDAL CELL
FROM CORTEX
Dendrite
Cell
body
MOTOR NEURON
FROM SPINAL CORD
Dendrite
Axon
Axon
Axon

Electric flow in neurons

The neuron consists of three parts:

- Dendrite-tree, the “input stage” of the neuron, converges on the soma.
- Soma, the cell body, contain the “normal” cellular functions
- Axon, the output of the neuron, may be branched. Synapses at the ends are connected to neighboring dendrites.

The axon has an excitable membrane, gives rise to active conduction. Will first look at conduction in the dentrites, passive conduction.

The cable equation, 4.1

The cell typically has a potential gradient along its length. Radial components will be ignored.

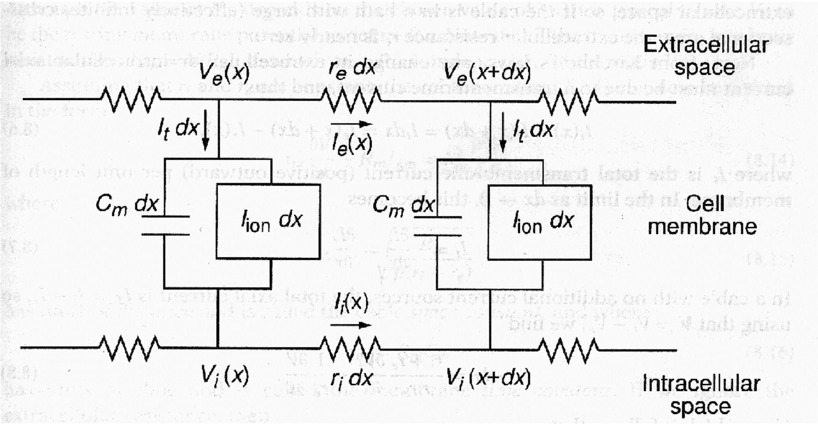
Notation:

V_i and V_e are intra- and extra cellular potential
I_i and I_e are intra- and extra cellular (axial) current
r_i and r_e are intra- and extra cellular resistance per unit length

$$r_i = \frac{R_c}{A_i}$$

where R_c is the cytoplasmic resistivity and A_i is the cross sectional area of the cable.

Discrete cable



Ohmic resistance assumed:

$$V_i(x + \Delta x) - V_i(x) = -I_i(x) r_i \Delta x$$

$$V_e(x + \Delta x) - V_e(x) = -I_e(x) r_e \Delta x$$

In the limit:

$$I_i = -\frac{1}{r_i}\frac{\partial V_i}{\partial x} \quad \text{and} \quad I_e = -\frac{1}{r_e}\frac{\partial V_e}{\partial x}$$

Conservation of current yields:

$$I_i(x) - I_i(x+\Delta x) = -(I_e(x) - I_e(x+\Delta x)) = I_t \Delta x \qquad (1)$$

where I_t is transmembrane current, per unit length. In the limit (1) yields:

$$I_t = -\frac{\partial I_i}{\partial x} = \frac{\partial I_e}{\partial x}$$

We would like to express I_t in terms of V.

$$\frac{1}{r_e}\frac{\partial^2 V_e}{\partial x^2} = -\frac{1}{r_i}\frac{\partial^2 V_i}{\partial x^2} = -\frac{1}{r_i}(\frac{\partial^2 V}{\partial x^2} + \frac{\partial^2 V_e}{\partial x^2})$$

$$(\frac{1}{r_e} + \frac{1}{r_i})\frac{\partial^2 V_e}{\partial x^2} = -\frac{1}{r_i}\frac{\partial^2 V}{\partial x^2}$$

cont.

$$\left(\frac{1}{r_e} + \frac{1}{r_i}\right)\frac{\partial^2 V_e}{\partial x^2} = -\frac{1}{r_i}\frac{\partial^2 V}{\partial x^2}$$

$$\frac{\partial^2 V_e}{\partial x^2} = -\frac{\frac{1}{r_i}}{\frac{1}{r_e} + \frac{1}{r_i}}\frac{\partial^2 V}{\partial x^2} = -\frac{r_e}{r_e + r_i}\frac{\partial^2 V}{\partial x^2}$$

so

$$I_t = \frac{\partial I_e}{\partial x} = -\frac{1}{r_e}\frac{\partial^2 V_e}{\partial x^2} = \frac{1}{r_e + r_i}\frac{\partial^2 V}{\partial x^2}$$

From the membrane model previously derived we have

$$I_t = p(C_m \frac{\partial V}{\partial t} + I_{\text{ion}})$$

where p is the circumference of the cable. The total expression will be in Ampere/meter.

The total 1D cable model is then:

$$p(C_m \frac{\partial V}{\partial t} + I_{\text{ion}}(V)) = (\frac{1}{r_e + r_i} \frac{\partial^2 V}{\partial x^2})$$

Dimensionless form

We can scale the variables to reduce the number of parameters. Defines a membrane resistance:

$$\frac{1}{R_m} = \frac{\Delta I_{\text{ion}}}{\Delta V}(V_0)$$

where V_0 is the resting potential. Multiplication with R_m

$$C_m R_m \frac{\partial V}{\partial t} + R_m I_{\text{ion}} = \frac{R_m}{p(r_i + r_e)} \frac{\partial^2 V}{\partial x^2}$$

Here we have assumed r_i and r_e constant.

Defining $f = -R_m I_{\text{ion}}$, $\tau_m = C_m R_m$ (time constant) and $\lambda_m^2 = R_m/(p(r_i + r_e))$ (space constant squared) we can write

$$\tau_m \frac{\partial V}{\partial t} - f = \lambda_m^2 \frac{\partial^2 V}{\partial x^2} \qquad (2)$$

Introduces the dimensionless variables:

$$T = t/\tau_m \quad \text{and} \qquad X = x/\lambda_m$$

We can then write:

$$\frac{\partial V}{\partial T} = f + \frac{\partial^2 V}{\partial X^2} \tag{3}$$

A solution $\hat{V}(T, X)$ of (3) will imply that $V(t, x) = \hat{V}(t/\tau_m, x/\lambda_m)$ will satisfy (2).

The reaction term, 4.2

The form of f depends on the cell type we want to study.

For the axon $I_{\text{ion}}(m, n, h, V)$ of the HH-model is a good candidate.

For the dendrite, which is non-excitable, a linear resistance model is good. Shift V so $V = 0$ is the resting potential:

$$\frac{\partial V}{\partial T} = \frac{\partial^2 V}{\partial X^2} - V$$

Need boundary and initial values. Initially at rest:

$$V(X, 0) = 0$$

Boundary conditions

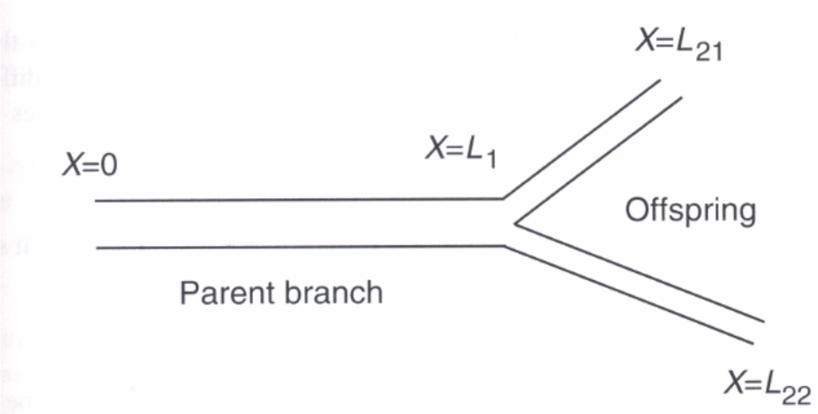
Types of boundary conditions:

- Dirichlet: $V(x_b, T) = V_b$, voltage clamp.
- Neumann: $\frac{\partial V}{\partial X} = -r_i \lambda_m I$, current injection.

Justification:

$$\frac{\partial V_i}{\partial x} = -r_i I_i \Rightarrow \frac{\partial V}{\partial x} - \frac{\partial V_e}{\partial x} = -r_i I_i \overset{r_e = 0}{\Longrightarrow} \frac{\partial V}{\partial x} = -r_i I_i$$

Branching structures, 4.2.3



Linear cable equation used in each branch:

$$\frac{\partial V}{\partial T} = \frac{\partial^2 V}{\partial X^2} - V$$

General solution in the steady state:

$$V = Ae^{-X} + Be^{X}$$

Two parameters per branch, six in total to determine.
Three taken from boundary conditions: current injection in X=0 and voltage clamp at $X = L_{21}$ and $X = L_{22}$.
Two more from continuity of voltage:

$$V_1(L_1) = V_{21}(L_1) = V_{22}(L_1)$$

The sixth condition is obtained from continuity of current:

$$\frac{1}{R_{1,in}}\frac{dV_1}{dX} = \frac{1}{R_{21,in}}\frac{dV_{21}}{dX} + \frac{1}{R_{22,in}}\frac{dV_{22}}{dX}$$

where the input resistance is

$$R_{in} = \lambda_m r_i = \sqrt{\frac{R_m}{pr_i}\frac{R_c}{A_i}}$$

Assuming a circular crossection:

$$R_{in} = \frac{2}{\pi}\sqrt{R_m R_c} d^{-3/2}$$

If R_m and R_c is not changing the condition becomes:

$$d_1^{3/2}\frac{dV_1}{dX} = d_{21}^{3/2}\frac{dV_{21}}{dX} + d_{22}^{3/2}\frac{dV_{22}}{dX}$$

Equivalent cylinders

With certain assumptions the dendrite tree can be modelled with a single cable equation. $L_{21} = L_{22}$, and they have the same boundary conditions:
This gives $V_{21} = V_{22}$ and thus:

$$d_1^{3/2} \frac{dV_1}{dX} = (d_{21}^{3/2} + d_{22}^{3/2}) \frac{dV_{21}}{dX}$$

The critcal assumption is then:

$$d_1^{3/2} = d_{21}^{3/2} + d_{22}^{3/2}$$

If so, then we can use a single equation for the whole system. Similar arguments can be made for more complex branching.