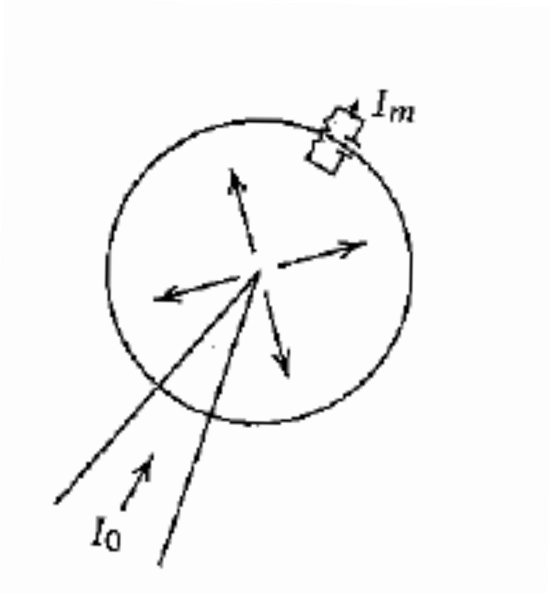
Lecture 3

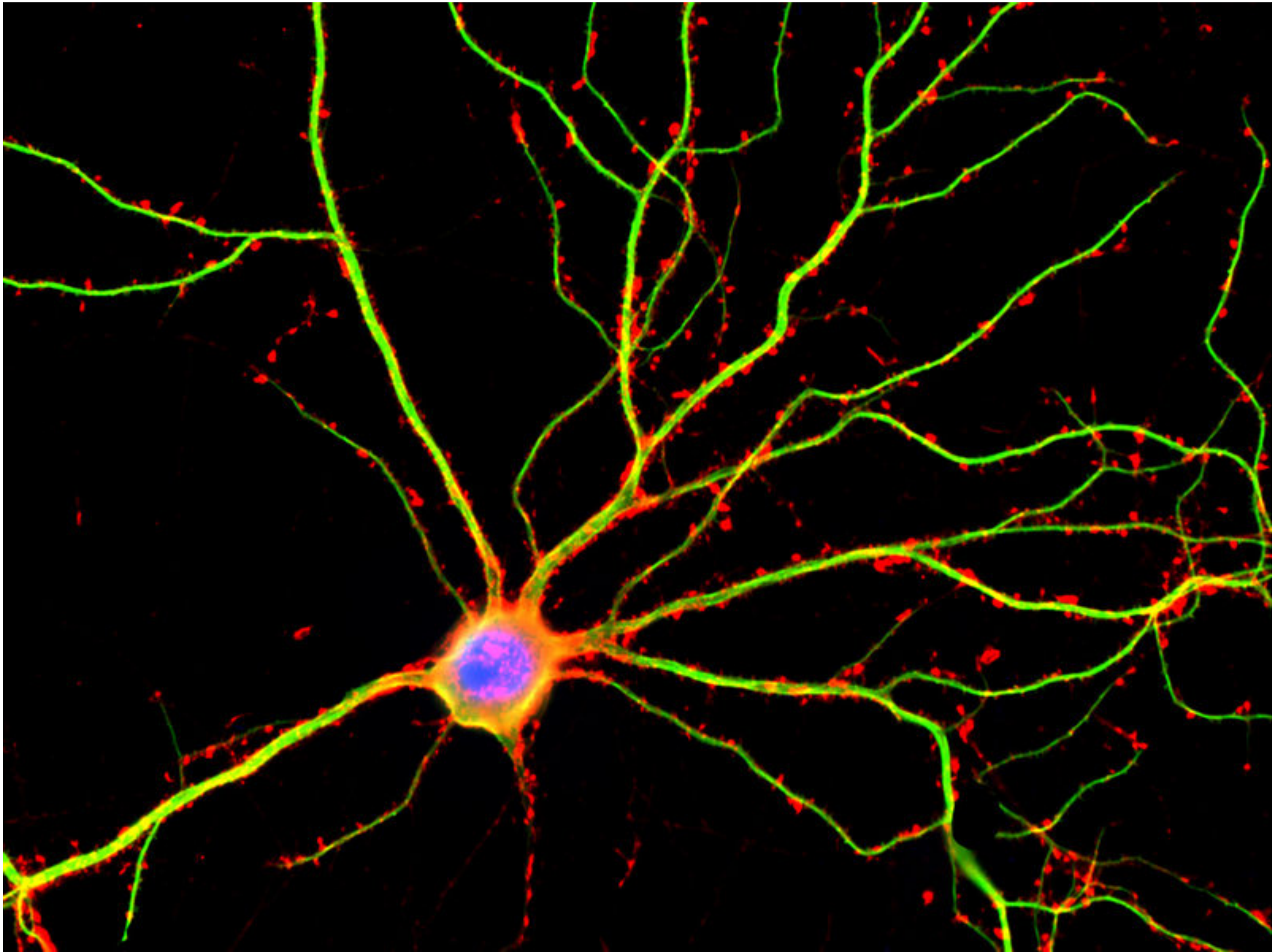
Axial Resistance and Cable Theory

The isopotential cell (RC model)

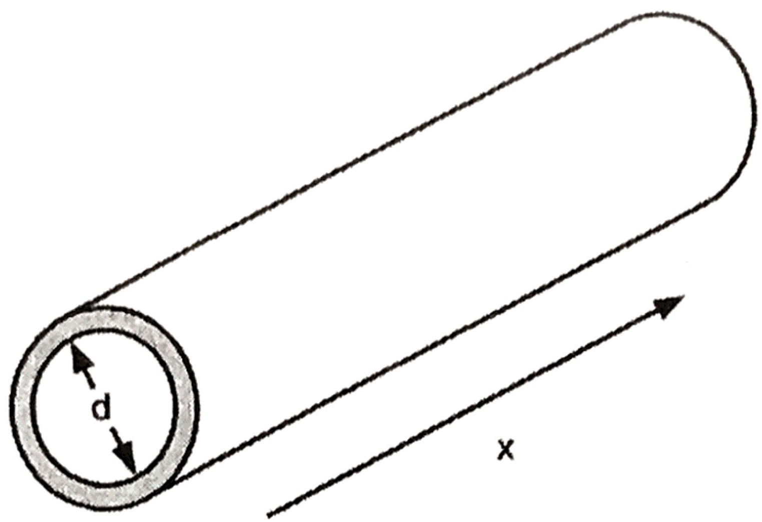


Current injected will distribute uniformly across the surface.

This model made it easy for us to estimate passive membrane properties R_m and C_m, however, we neglected the actual, complex geometry of the neuron.



To model signal propagation along dendrites and axons, we treat them like cables (a thin membrane sheath surrounding an electrically conducting core).



Koch C from *Biophysics of Computation* (1999)

Where d is the diameter, a is the radius and l is the length of the cylinder

Cable Theory

- Lord Kelvin
  - Applied to transatlantic communication cables
  - Ignores voltage gated channels in the membrane (passive)
- Hodgkin and Rushton (1940s)
  - Applied to unmyelinated axons
  - Includes voltage gated channels (active)
- Rall (1960s-1980s)
  - Applied to dendrites (both passive and active)

When we inject current into this cylinder, it can travel across two resistances:

$$r_a = \frac{\rho}{\pi a^2}$$

$$r_m = \frac{R_M}{2\pi a}$$

- r_a is the axial resistance per unit length (Ω/cm)
- r_m is the resistance of a unit length of membrane (Ωcm)
- ρ is the resistivity of cytoplasm (Ωcm)
- R_M is the specific membrane resistance (Ωcm^2)
- a is the radius (cm)

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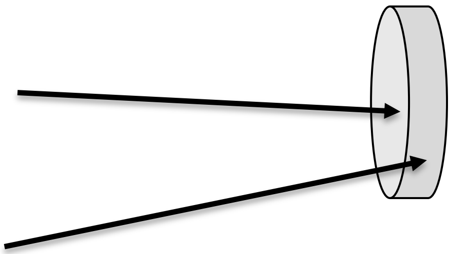

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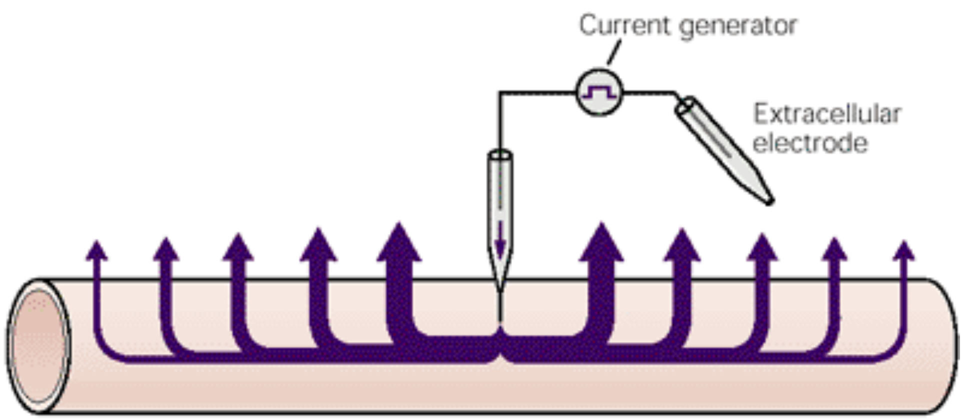
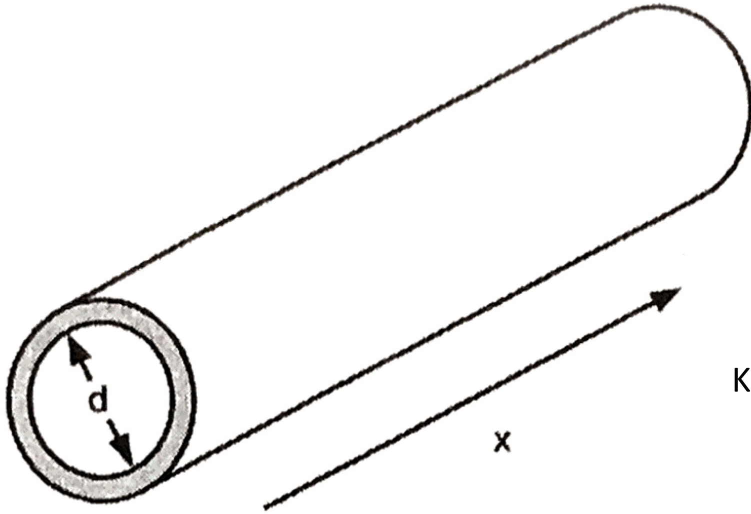
What if we inject current into a cylinder, representing a section of a dendrite or axon?

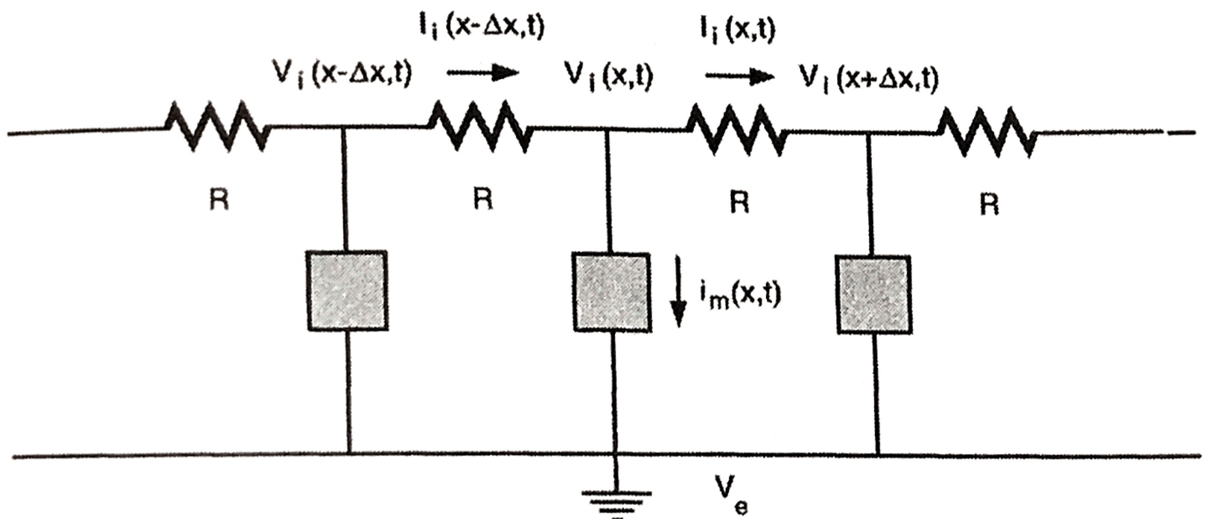


Kandel et al., Principles of Neural Science 2013

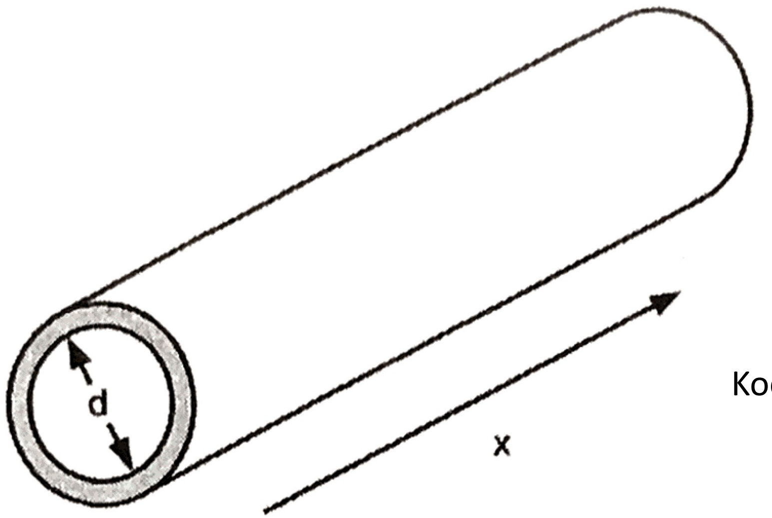
Deriving the cable equation



Koch C from *Biophysics of Computation* (1999)

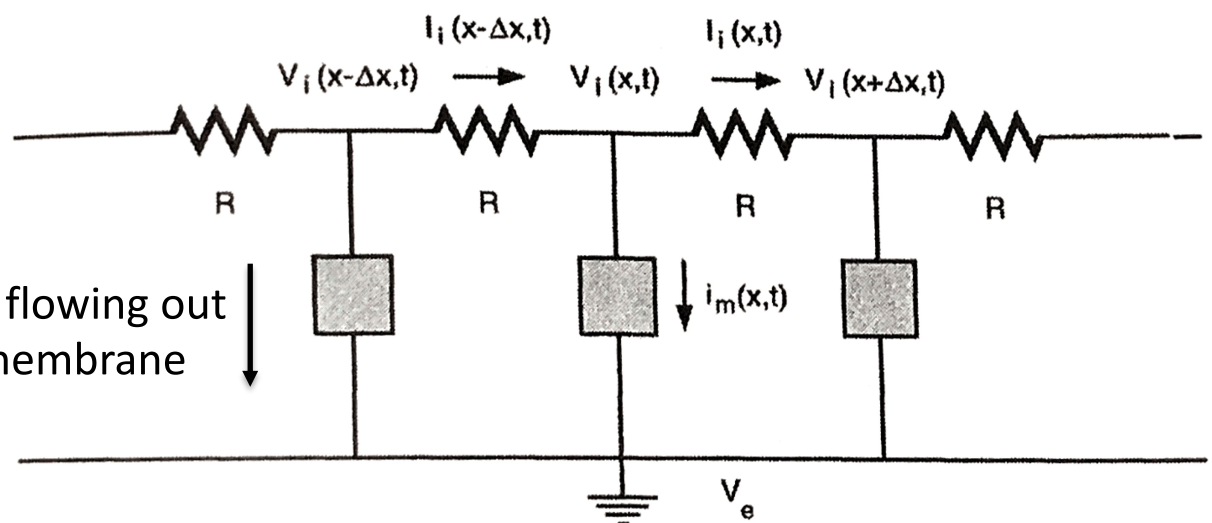


Deriving the cable equation

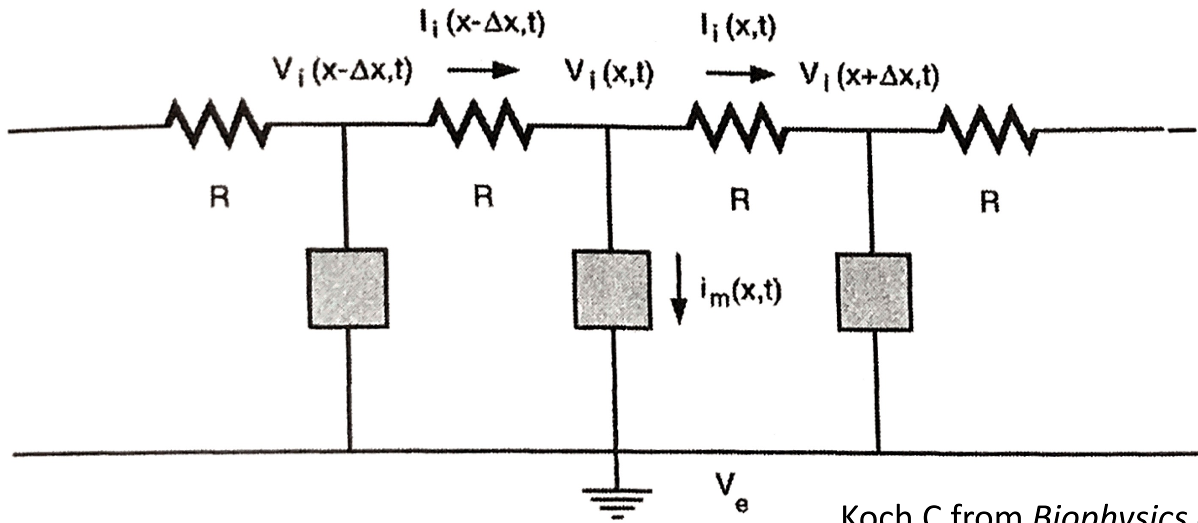


Koch C from *Biophysics of Computation* (1999)

Current flowing down the axon



Current flowing out of the membrane



Koch C from *Biophysics of Computation* (1999)

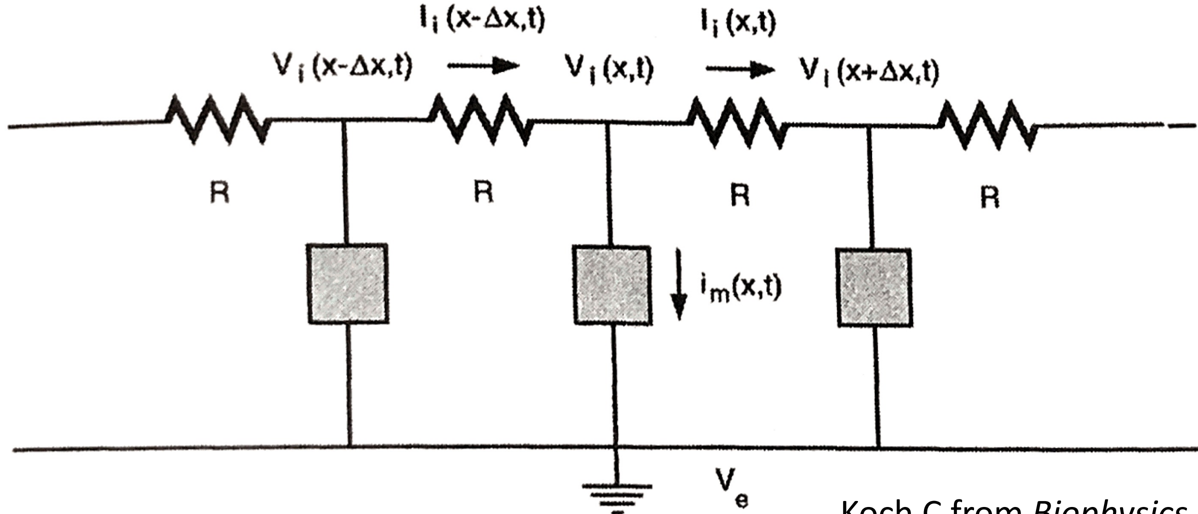
Ohms law $$V_i(x,t) - V_i(x+\Delta x,t) = RI_i(x,t)$$

$$\frac{V_i(x+\Delta x,t) - V_i(x,t)}{\Delta x} = -\frac{RI_i(x,t)}{\Delta x}$$

$$as\ \Delta x \rightarrow 0 \qquad r_a = R/\Delta x$$

$$\frac{\partial V_m}{\partial x}(x,t) = -r_a I_i(x,t) \qquad (1)$$

$$V_m(x,t) = V_i(x,t) - V_e$$



Koch C from *Biophysics of Computation* (1999)

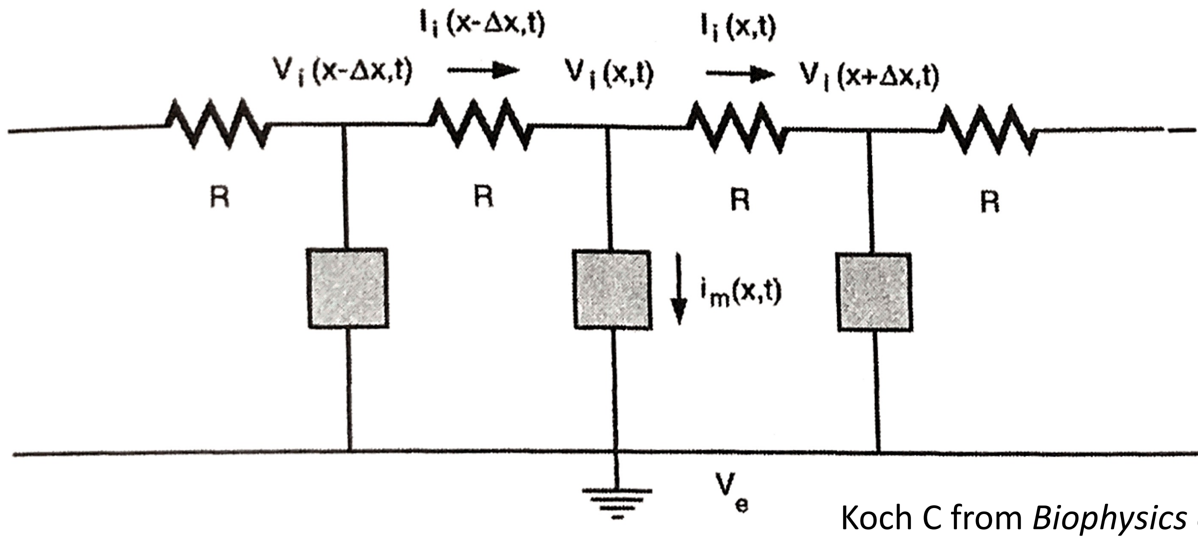
Kirchhoff's conservation of charge

$$-i_m(x,t)\Delta x - I_i(x,t) + I_i(x-\Delta x,t) = 0$$

$$\frac{i_m(x,t)\Delta x}{\Delta x} = \frac{I_i(x-\Delta x,t) - I_i(x,t)}{\Delta x}$$

$$as\ \Delta x\ \rightarrow 0$$

$$-\frac{\partial I_i}{\partial x}(x,t) = i_m(x,t) \qquad (2)$$



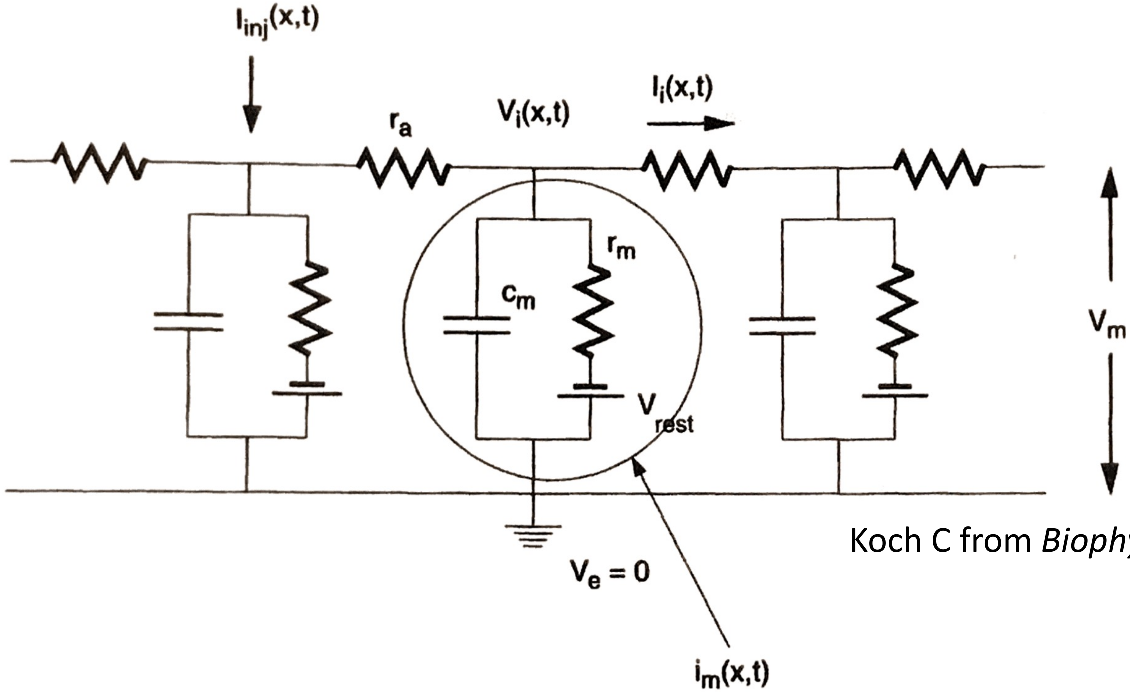
Koch C from *Biophysics of Computation* (1999)

$$\frac{\partial V_m}{\partial x}(x,t) = -r_a I_i(x,t) \qquad (1)$$

$$-\frac{\partial I_i}{\partial x}(x,t) = i_m(x,t) \qquad (2)$$

$$\frac{1}{r_a}\frac{\partial^2 V_m}{\partial x^2}(x,t) = i_m(x,t) \qquad (3)$$

(3) is a second order differential equation that describes the membrane potential in a cable, regardless of what comprises the membrane (black box in the figure).

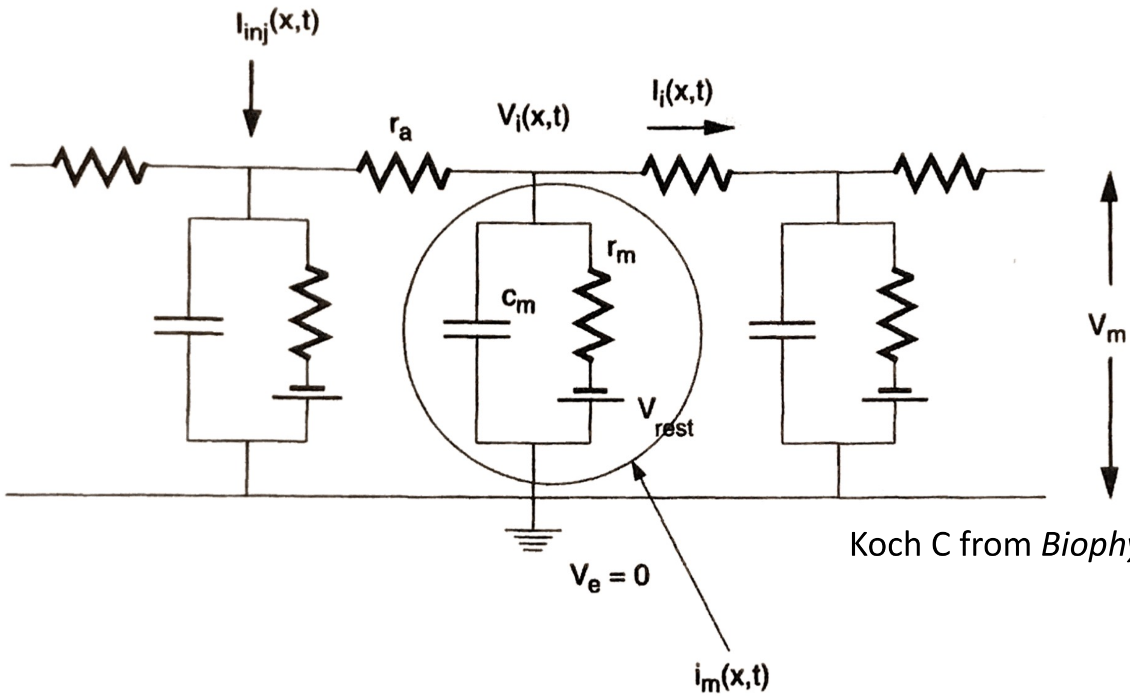


Koch C from *Biophysics of Computation* (1999)

$$i_m(x,t) = \frac{V_m(x,t) - V_{rest}}{r_m} + c_m \frac{\partial V_m(x,t)}{\partial t} - I_{inj}(x,t) \qquad (4)$$

$$\frac{1}{r_a}\frac{\partial^2 V_m}{\partial x^2}(x,t) = i_m(x,t) \qquad (3)$$

$$\frac{1}{r_a}\frac{\partial^2 V_m}{\partial x^2}(x,t) = \frac{V_m(x,t) - V_{rest}}{r_m} + c_m \frac{\partial V_m(x,t)}{\partial t} - I_{inj}(x,t)$$



Koch C from *Biophysics of Computation* (1999)

$$\frac{1}{r_a}\frac{\partial^2 V_m}{\partial x^2}(x,t) = \frac{V_m(x,t) - V_{rest}}{r_m} + c_m\frac{\partial V_m(x,t)}{\partial t} - I_{inj}(x,t)$$

$$\frac{r_m}{r_a}\frac{\partial^2 V_m}{\partial x^2}(x,t) = (V_m(x,t) - V_{rest}) + c_m r_m\frac{\partial V_m(x,t)}{\partial t} - r_m I_{inj}(x,t)$$

$$\boxed{\lambda^2\frac{\partial^2 V_m}{\partial x^2}(x,t) = \tau_m\frac{\partial V_m(x,t)}{\partial t} + (V_m(x,t) - V_{rest}) - r_m I_{inj}(x,t)} \qquad (5)$$

Where the **time constant** $\tau_m = c_m r_m$ and the **length constant** $\lambda = \sqrt{\frac{r_m}{r_a}}$

Linear cable equation

$$V(x,t) = (V_m(x,t) - V_{rest})$$

$$\boxed{\lambda^2 \frac{\partial^2 V}{\partial x^2}(x,t) = \tau_m \frac{\partial V(x,t)}{\partial t} + V(x,t) - r_m I_{inj}(x,t)} \qquad (6)$$

$$\lambda = \sqrt{\frac{r_m}{r_a}} = \sqrt{\frac{aR_M}{2R_A}} \quad \textit{space or length constant}$$

$$\tau_m = r_m c_m = R_m C_m = R_M C_M \quad \textit{membrane time constant}$$

Guide for capacitance and resistance

C_M is specific membrane capacitance (μF/cm^2)

$$C_m = C_M \bullet 2\pi a l \quad (\mu\text{F})$$

$$c_m = C_m / l = C_m / \Delta x \quad (\mu\text{F/cm})$$

R_M is specific membrane resistance (Ωcm^2)

$$R_m = R_M / (2\pi a l) \quad (\Omega)$$

$$r_m = R_m l = R_m \Delta x \quad (\Omega\text{cm})$$

R_A is specific axial resistance (Ωcm)

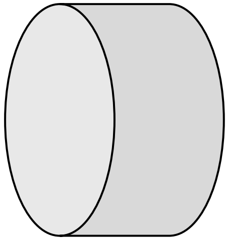
$$R_a = (l R_A) / (\pi a^2) \quad (\Omega)$$

$$r_a = R_a / l = R_a / \Delta x \quad (\Omega\ /\text{cm})$$

- Where a is the radius and l is the length of the cylinder

Linear cable assumptions

- Membrane current is a linear function of the membrane potential (ignore active currents)
- No current flow in the radial direction inside the dendrite/axon (only across the membrane)
- Membrane parameters are uniform
- Extracellular space is isopotential (r_e ignored)



Solutions to the cable equation

- Solutions to the cable equation depend on the initial conditions (IVP) and the boundary conditions (IBP).
- In practice, this equation is solved using numerical integration methods.
- However, analytical solutions of this equation exist for very simple cases. We are going to review some of them as they give us insight into how voltage spreads across the cable (dendrite/axon).
  - Infinite, semi-infinite and finite length cables
    - <u>Steady state solutions</u>
    - <u>Transient solutions</u>

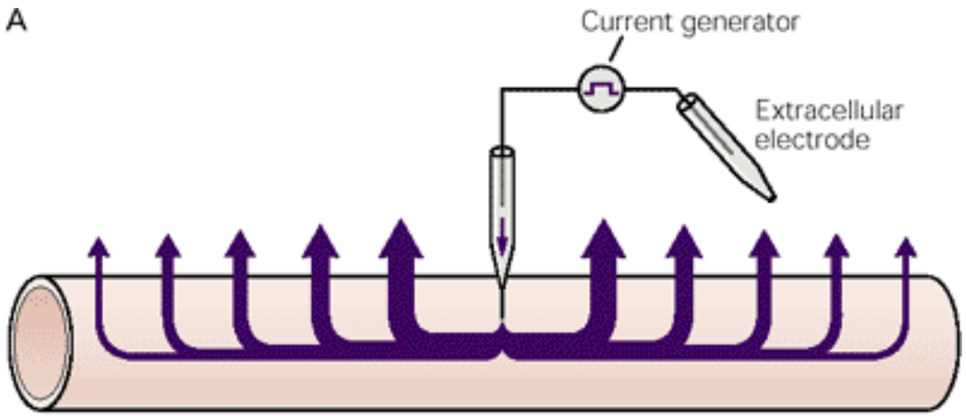
Steady state: Linear cable equation

$$\boxed{\lambda^2 \frac{\partial^2 V}{\partial x^2}(x,t) = \cancel{\tau_m \frac{\partial V(x,t)}{\partial t}} + V(x,t) - r_m I_{inj}(x,t)}$$

$$\lambda = \sqrt{\frac{r_m}{r_a}} = \sqrt{\frac{aR_M}{2R_A}} \qquad \textit{space or length constant}$$

$$\tau_m = r_m c_m = R_m C_m = R_M C_M \qquad \textit{membrane time constant}$$

Infinite cable: steady state solution



$$\lambda^2 \frac{\partial^2 V}{\partial x^2}(x,t) = V(x,t) - r_m I_{inj}(x,t)$$

$|x| \to \infty$

Kandel et al., Principles of Neural Science 2013

Infinite cable: steady state solution

For an ordinary differential equation in the form

$$\frac{d^2V}{dX^2} - V = 0$$

The general solution is

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

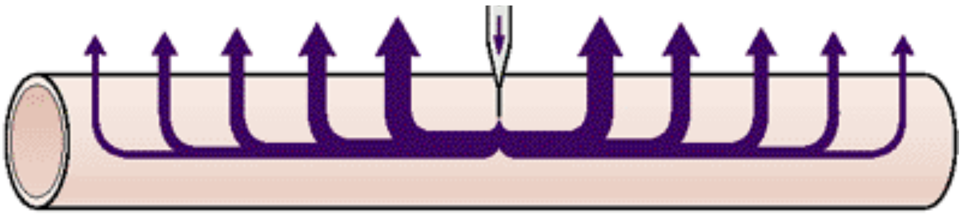
Infinite cable: steady state solution

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

Make X = x/λ

Boundary conditions for an infinitely long cylinder:

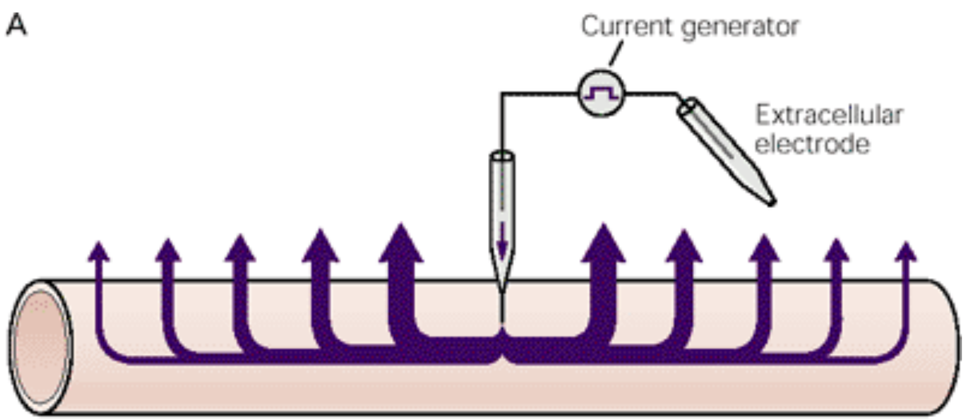
- V=0 at $X = \pm\infty$
  A=0
- V=V_0 at X=0
  B=V_0



Then our final solution is:

$$V(x) = V_0 e^{-|x|/\lambda}$$

Infinite cable: steady state solution



$|x| \rightarrow \infty$

$$\lambda^2 \frac{\partial^2 V}{\partial x^2}(x,t) = V(x,t) - r_m I_{inj}(x,t)$$

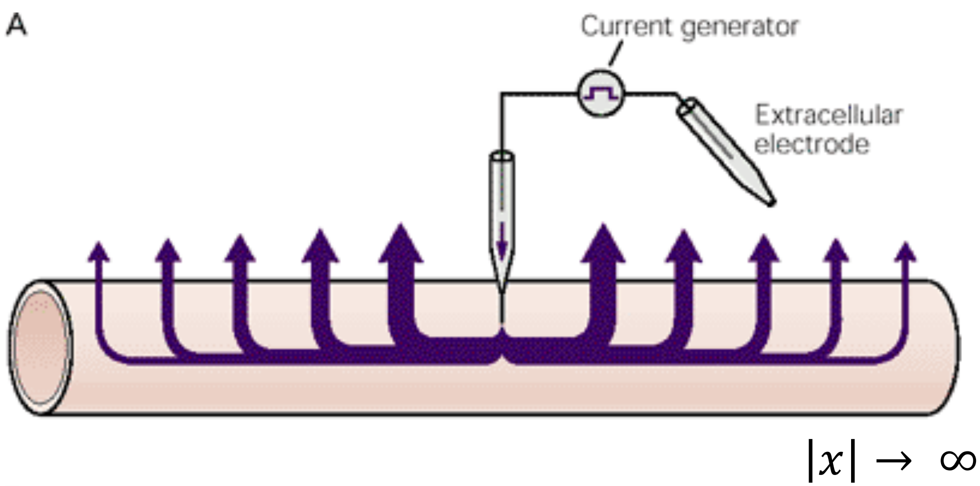
$$V(x) = V_0 e^{-|x|/\lambda}$$

$$V_0 = \frac{I_0 r_m}{2\lambda}$$

$\lambda = \sqrt{r_m / r_a}$ = length constant

Kandel et al., Principles of Neural Science 2013

What is the input resistance R_{in}?

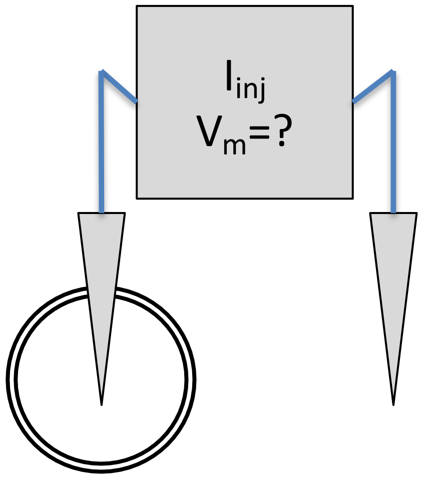


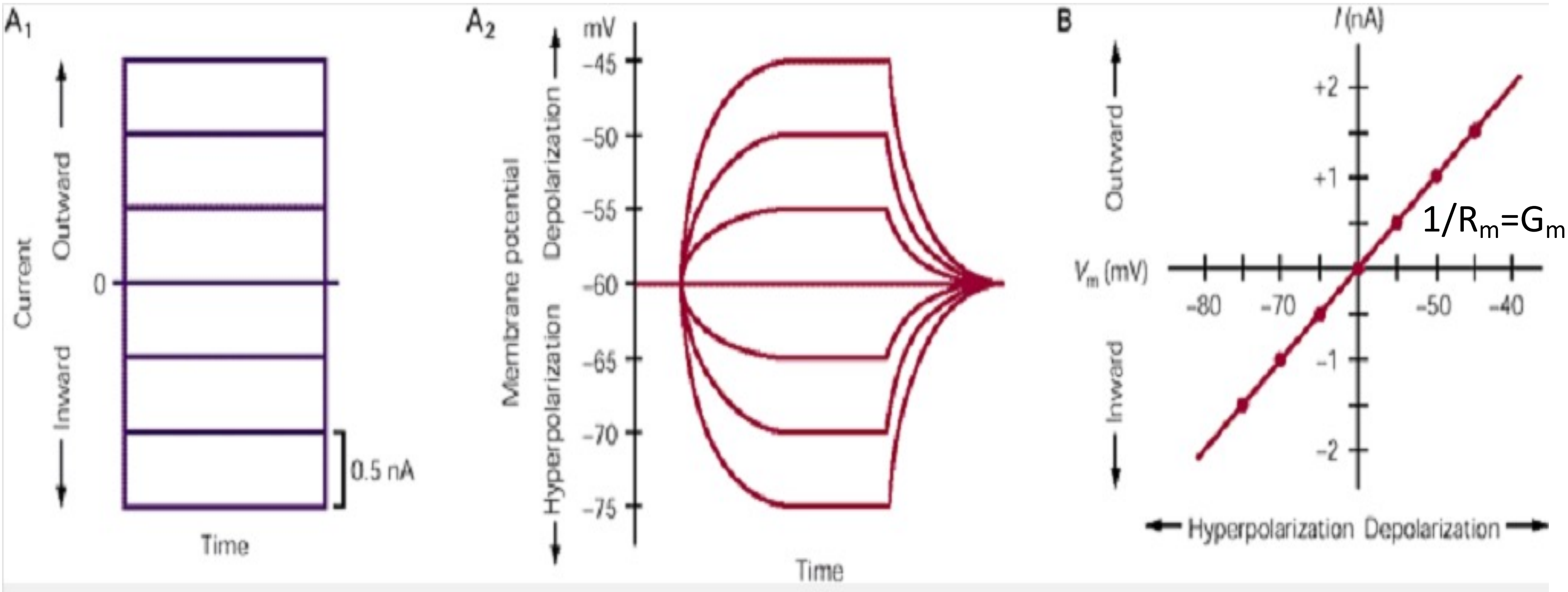
When injecting into a cable what is the input resistance – **the resistance at the site of current injection** (essentially the resistance "seen" by the injection electrode)?

Does the membrane resistance (R_m) equal the input resistance (R_{in})?

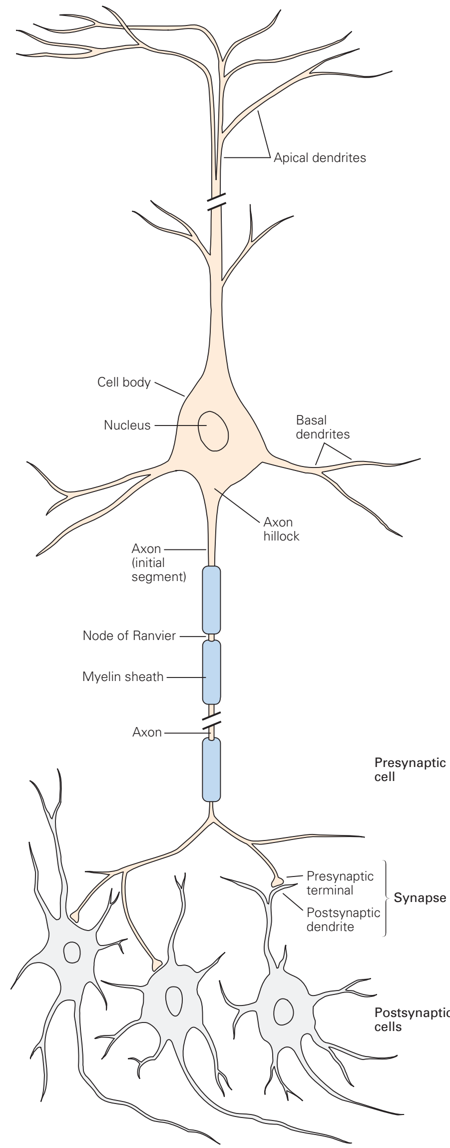
Kandel et al., Principles of Neural Science 2013

Current Injection





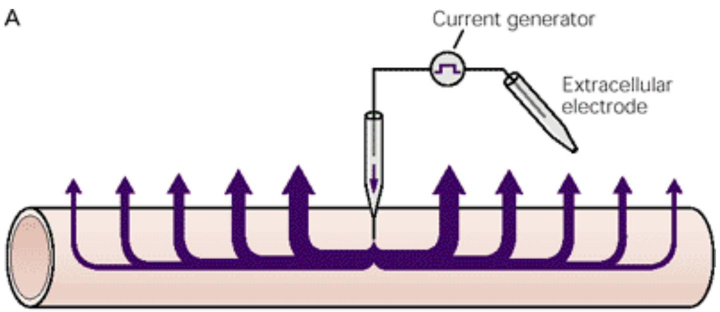
For an isopotential, spherical cell, $R_{in}=R_m$



Kandel et al., Principles of Neural Science 2013

For a real neuron, R_{in} needs to account for r_m and r_a

Infinite cable: Input Resistance and Input Conductance



$|x| \rightarrow \infty$

$$V(x) = V_0 e^{-|x|/\lambda}$$

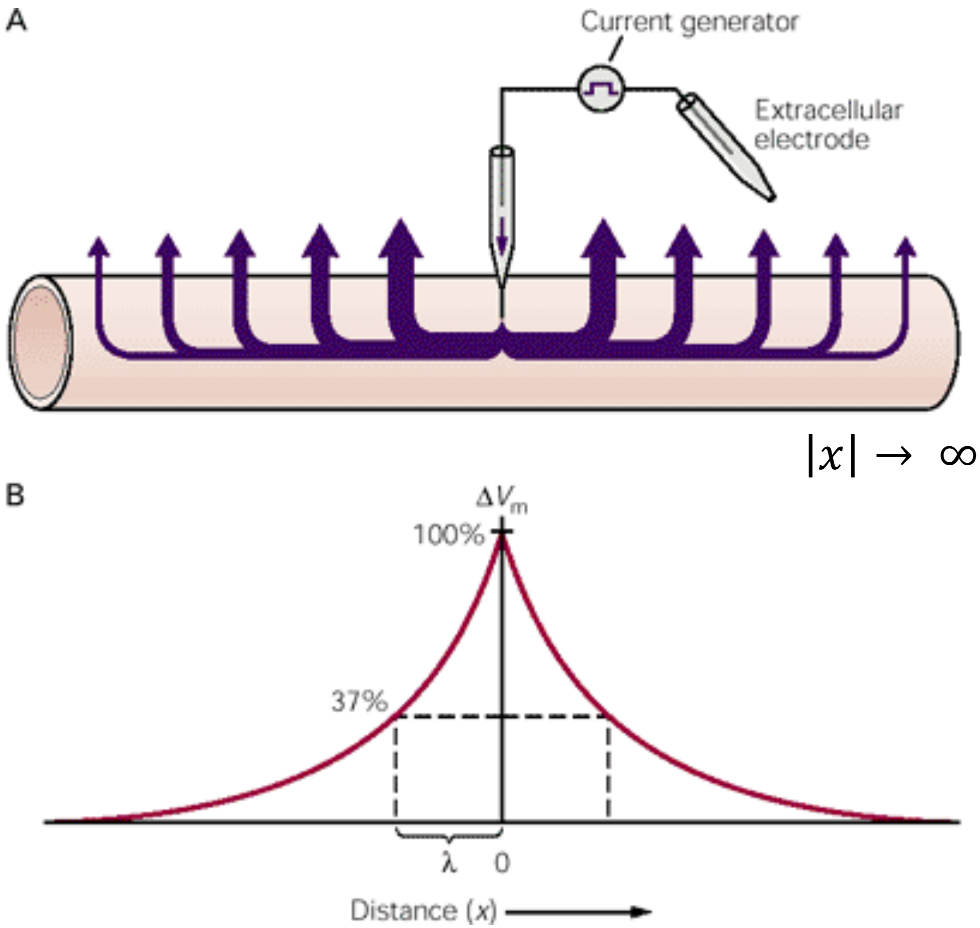
$$V(x) = \frac{I_0 r_m}{2\lambda} e^{-|x|/\lambda}$$

$$\text{Input resistance } R_{in} = \frac{V(0)}{I_0} = \frac{r_m}{2\lambda} = \frac{r_a \lambda}{2} = \frac{\sqrt{R_M R_A}}{\pi d^{3/2}}$$

$$\text{Input conductance: } G_{in} = \frac{\pi d^{3/2}}{\sqrt{R_M R_A}}$$

Where *d* is the diameter

Infinite cable: how does the voltage change across space?



$|x| \rightarrow \infty$

$$\lambda^2 \frac{\partial^2 V}{\partial x^2}(x,t) = V(x,t) - r_m I_{inj}(x,t)$$

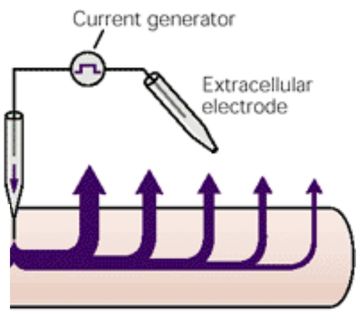
$$V(x) = V_0 e^{-|x|/\lambda}$$

$$V_0 = \frac{I_0 r_m}{2\lambda}$$

$\lambda = \sqrt{r_m / r_a}$ = length constant

Kandel et al., Principles of Neural Science 2013

Semi-infinite cable: steady state solution



$x \to \infty$

$$V(x) = V_0 e^{-x/\lambda}$$

$$V(x) = \frac{I_0 r_m}{\lambda} e^{-x/\lambda}$$

$$\text{Input resistance } R_{in} = R_\infty = \frac{V(0)}{I_0} = \frac{r_m}{\lambda} = r_a \lambda = \frac{2\sqrt{R_M R_A}}{\pi d^{3/2}}$$

$$\text{Input conductance: } G_{in} = G_\infty = \frac{\pi d^{3/2}}{2\sqrt{R_M R_A}}$$

Where *d* is the diameter

Is the spatial rate of voltage decay along the length of an axon faster if it has a small radius or large radius (assuming V_0 is the same)?

$$V(x) = V_0 e^{-x/\lambda}$$

$$\lambda = \sqrt{r_m/r_a}$$

$$r_a = \frac{\rho}{\pi a^2}$$

$$r_m = \frac{R_M}{2\pi a}$$

- a is the radius

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$$\lambda = \sqrt{r_m / r_a}$$

$$r_a = \frac{\rho}{\pi a^2}$$

$$r_m = \frac{R_M}{2\pi a}$$

$$2a_1 = a_2$$

$$\lambda_1 \; \begin{matrix} > \\ = \\ < \end{matrix} \; \lambda_2$$

?

- a is the radius

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$$\lambda = \sqrt{r_m/r_a}$$

$$r_a = \frac{\rho}{\pi a^2}$$

$$r_m = \frac{R_M}{2\pi a}$$

- a is the radius

$$2a_1 = a_2$$

$$\lambda_1 = \sqrt{\frac{R_M \pi a_1^2}{\rho 2 \pi a_1}} = \sqrt{\frac{R_m a_1}{\rho 2}}$$

$$\lambda_2 = \sqrt{\frac{R_m \pi (2a_1)^2}{\rho 2 \pi 2a_1}} = \sqrt{\frac{R_m a_1}{\rho}}$$

$$\lambda_2 > \lambda_1$$

Is the spatial rate of voltage decay along the length of an axon faster if it has a small radius or large radius (assuming V_0 is the same)?

$$V(x) = V_0 e^{-x/\lambda}$$

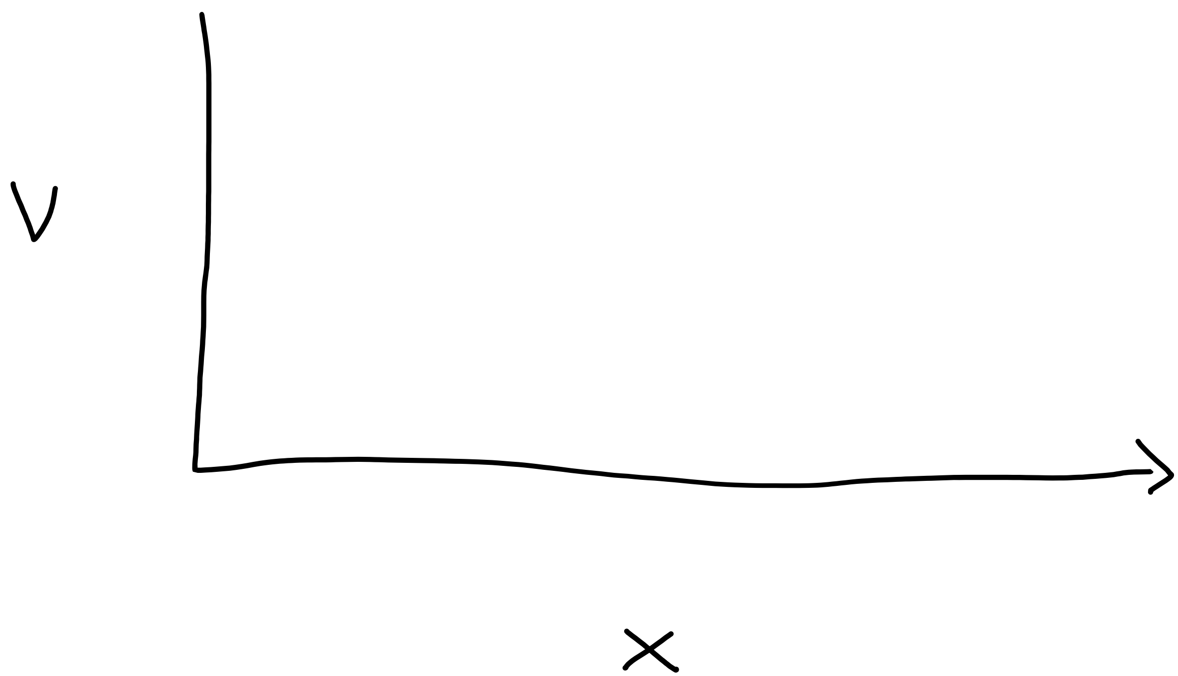
$$\lambda = \sqrt{r_m / r_a}$$

$$r_a = \frac{\rho}{\pi a^2}$$

$$r_m = \frac{R_M}{2\pi a}$$

- a is the radius

$x = \lambda \qquad V = V_0 e^{-1} = 0.368 V_0$



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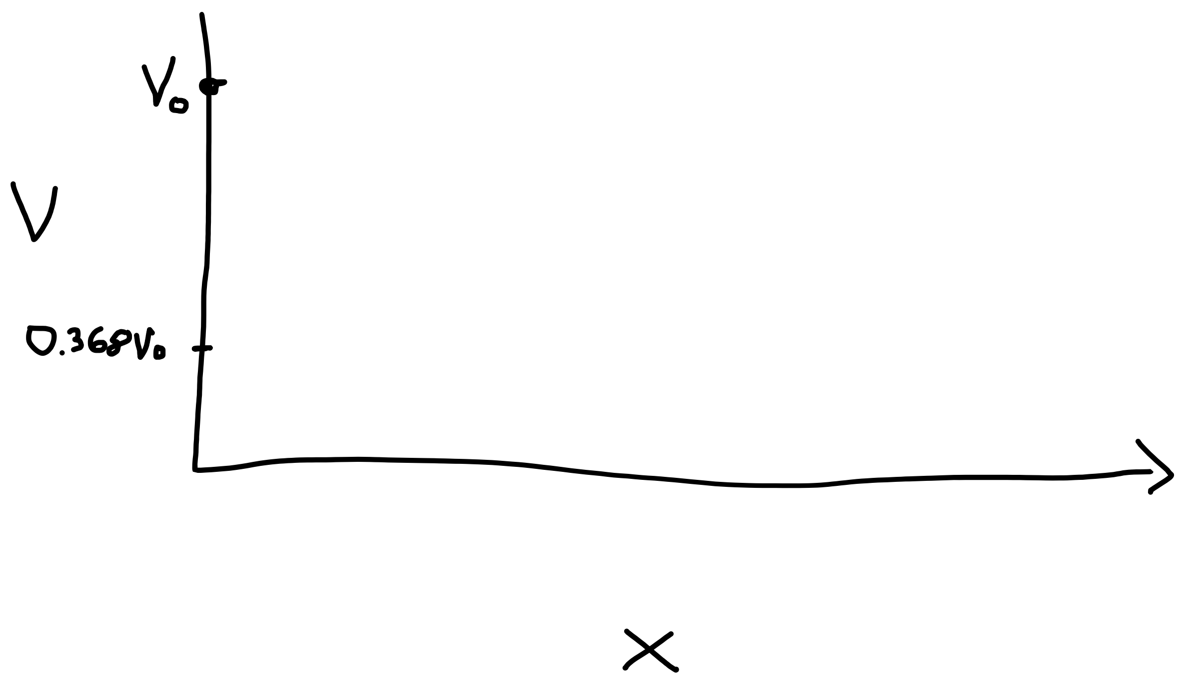
$$V(x) = V_0 e^{-x/\lambda}$$

$x = \lambda \quad V = V_0 e^{-1} = 0.368 V_0$

$$\lambda = \sqrt{r_m / r_a}$$

$$r_a = \frac{\rho}{\pi a^2}$$

$$r_m = \frac{R_M}{2\pi a}$$



- a is the radius

Is the spatial rate of voltage decay along the length of an axon faster if it has a small radius or large radius (assuming V_0 is the same)?

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- a is the radius

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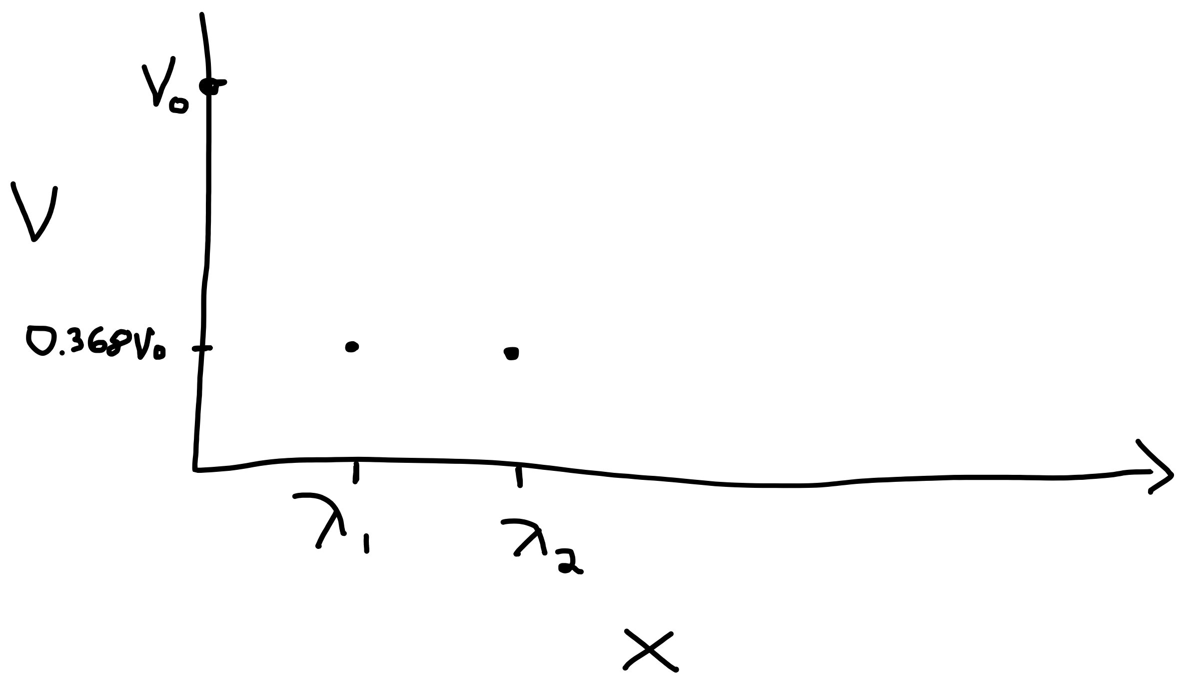
$\lambda_2 > \lambda_1$



Is the spatial rate of voltage decay along the length of an axon faster if it has a small radius or large radius (assuming V_0 is the same)?

$$V(x) = V_0 e^{-x/\lambda}$$

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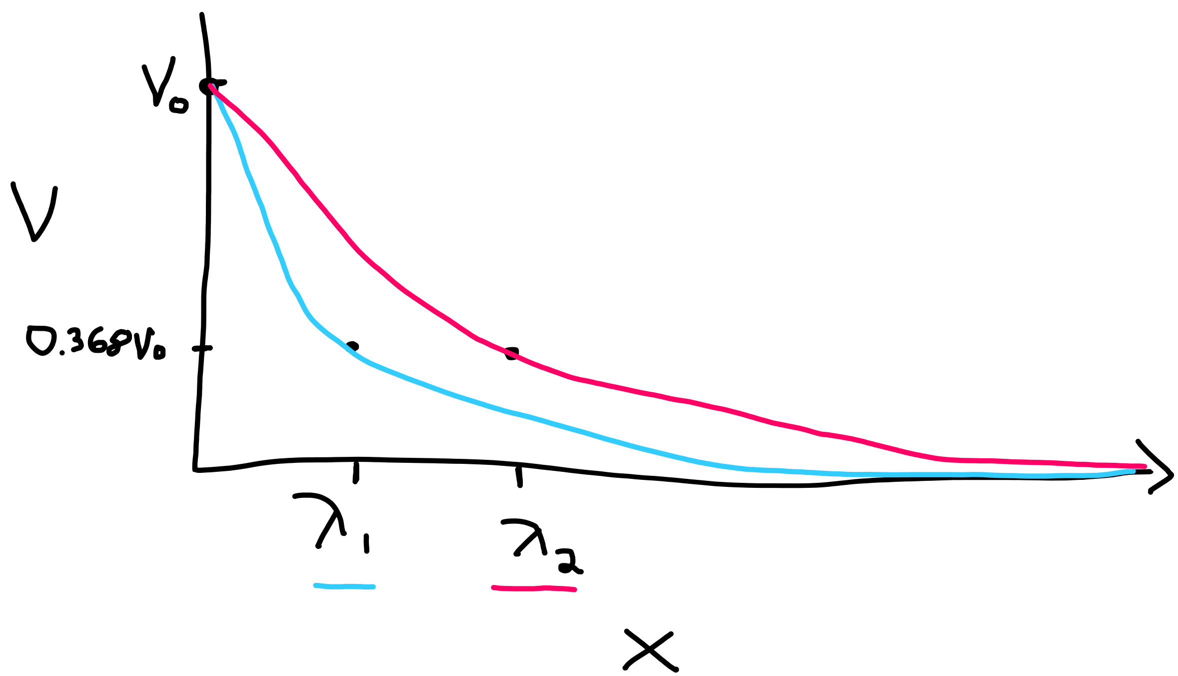
- a is the radius

$x = \lambda$ $V = V_0 e^{-1} = 0.368 V_0$

$\lambda_2 > \lambda_1$



Possible end conditions

- Infinite
- Sealed end ($dV/dx = 0$)
- Clamped end (V = clamped value)
- Leaky end (let some current escape)

Dimensionless form of linear cable equation

$$\boxed{\lambda^2 \frac{\partial^2 V}{\partial x^2}(x,t) = \tau_m \frac{\partial V(x,t)}{\partial t} + V(x,t) - r_m I_{inj}(x,t)}$$

$$\lambda = \sqrt{\frac{r_m}{r_a}} = \sqrt{\frac{aR_M}{2R_A}} \quad \textit{space or length constant}$$

$$\tau_m = r_m c_m = R_m C_m = R_M C_M \quad \textit{membrane time constant}$$

Put into a dimensionless form:

$$X = \frac{x}{\lambda}, T = \frac{t}{\tau_m}$$

$$\boxed{\frac{\partial^2 V(X,T)}{\partial X^2} = \frac{\partial V(X,T)}{\partial T} + V(X,T) - \frac{I_{inj}(X,T)}{\lambda c_m}}$$

- a is the radius

General steady state solution for all end conditions

l is length of the cable
L is the dimensionless length (electrotonic length): $L = \dfrac{l}{\lambda}$

$$V(X=0) = V_0$$

$$B_L = \frac{G_L}{G_\infty}$$

Conductance at the end of the cable

Conductance of semi-infinite cable

$$V(X) = V_0 \frac{\cosh(L-X) + B_L \sinh(L-X)}{\cosh(L) + B_L \sinh(L)}$$

- Hyperbolic sine:

$$\sinh x = \frac{e^x - e^{-x}}{2} = \frac{e^{2x} - 1}{2e^x} = \frac{1 - e^{-2x}}{2e^{-x}}.$$

- Hyperbolic cosine:

$$\cosh x = \frac{e^x + e^{-x}}{2} = \frac{e^{2x} + 1}{2e^x} = \frac{1 + e^{-2x}}{2e^{-x}}.$$

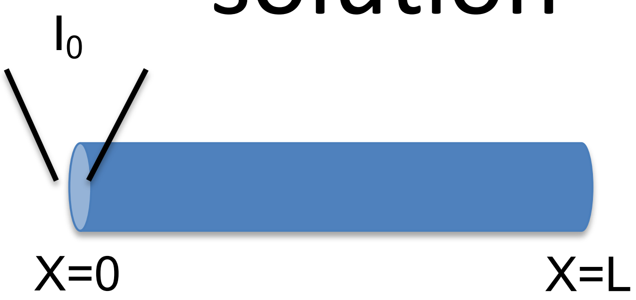
- Hyperbolic tangent:

$$\tanh x = \frac{\sinh x}{\cosh x} = \frac{e^x - e^{-x}}{e^x + e^{-x}} =$$

$$= \frac{e^{2x} - 1}{e^{2x} + 1} = \frac{1 - e^{-2x}}{1 + e^{-2x}}.$$

From Hyperbolic Functions, wikipedia.org

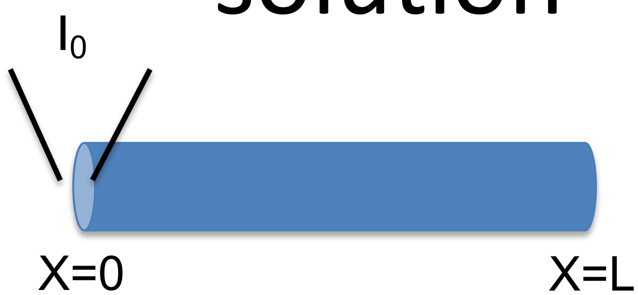
Finite Cable: steady state, sealed end solution



- Resistance at X=L is ~ infinite (G_L is very small)
- I(X=L)=0
- dV/dX = 0 at X = L

$$V(X) = V_0 \frac{\cosh(L-X) + B_L \sinh(L-X)}{\cosh(L) + B_L \sinh(L)}$$

Finite Cable: steady state, sealed end solution



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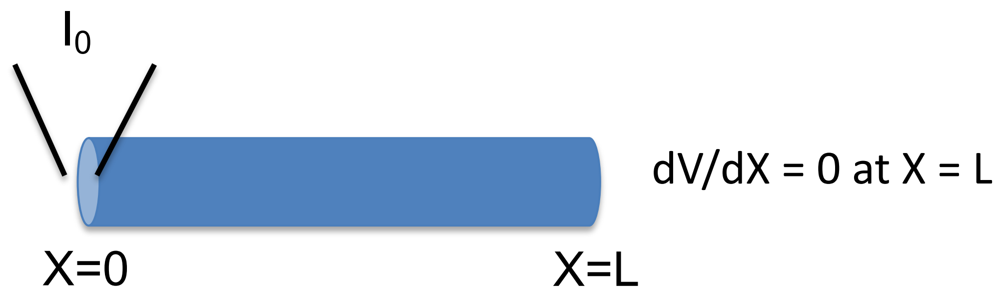
$$V(X=0) = V_0$$

$$B_L = \frac{G_L}{G_\infty}$$

- If we seal the end, $G_L << G_\infty$ so $B_L \approx 0$

$$V(X) = V_0 \frac{\cosh(L-X)}{\cosh(L)}$$

Input conductance, steady state, sealed end solution



$$G_\infty = \frac{\pi d^{3/2}}{2\sqrt{R_M R_A}}$$

$$G_{in} = G_{sealed} = G_\infty \tanh(L) = G_\infty \frac{\sinh(L)}{\cosh(L)}$$

tanh(L) goes to one with increasing L

Finite Cable: steady state, clamped (shorted) end solution

- V(L) = 0
- Resistance at X=L is very small

$$V(X) = V_0 \frac{\cosh(L-X) + B_L \sinh(L-X)}{\cosh(L) + B_L \sinh(L)}$$

Finite Cable: steady state, clamped (shorted) end solution

- V(L) = 0
- Resistance at X=L is very small

$$V(X) = V_0 \frac{\cosh(L - X) + B_L \sinh(L - X)}{\cosh(L) + B_L \sinh(L)}$$

$$V(X=0) = V_0$$

$$B_L = \frac{G_L}{G_\infty}$$

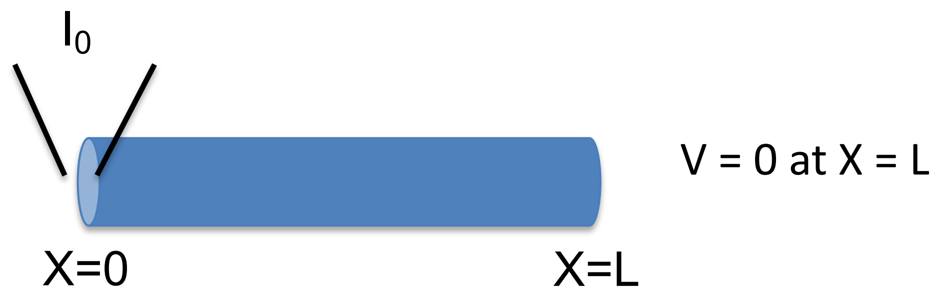
- If we clamp the end to zero (short-circuit)

  V = 0 at X = L

  $G_L >> G_\infty$ so $B_L >> 1$

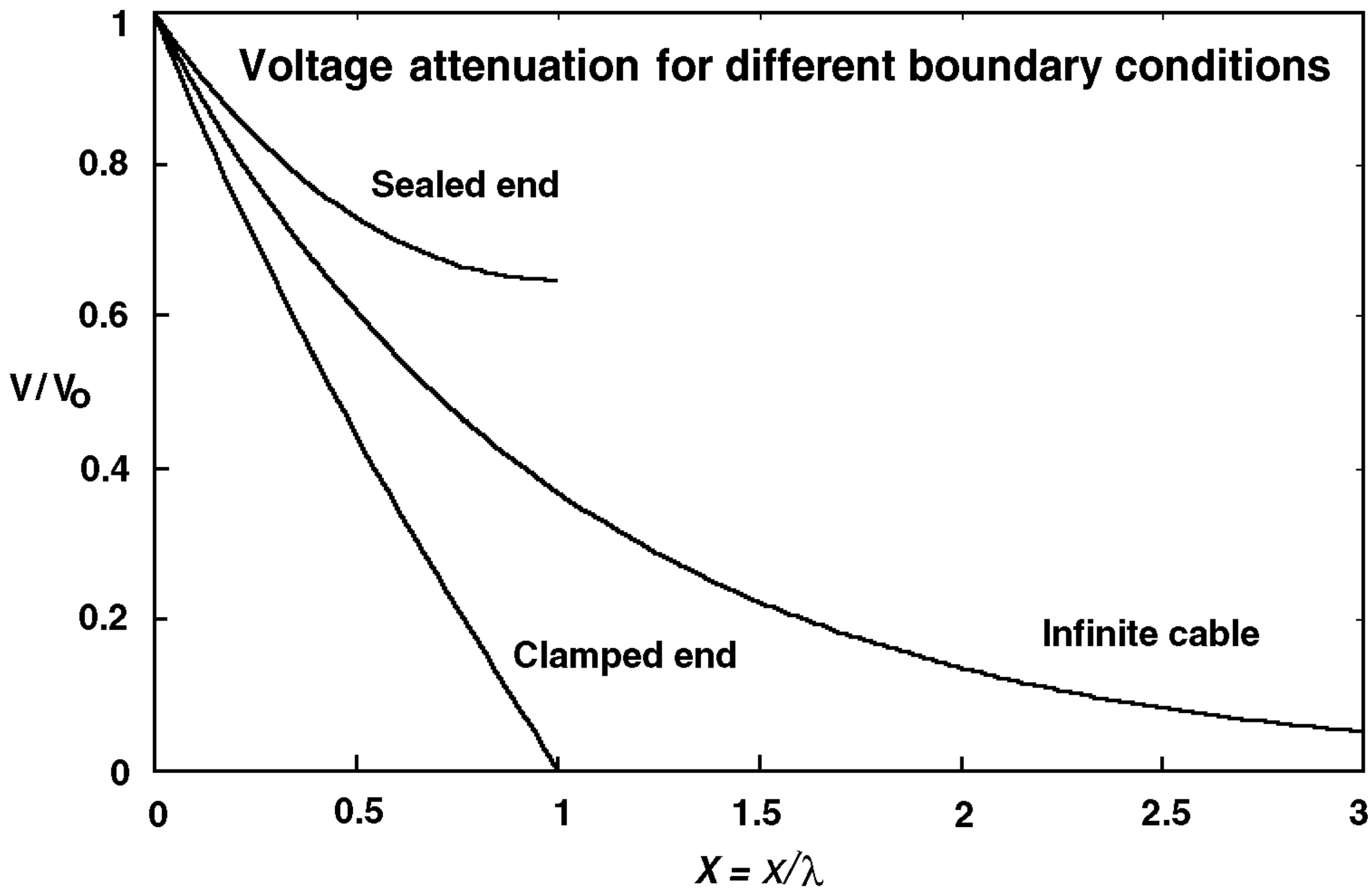
$$V(X) = V_0 \frac{\sinh(L - X)}{\sinh(L)}$$

Input conductance, steady state, clamped (shorted) end solution



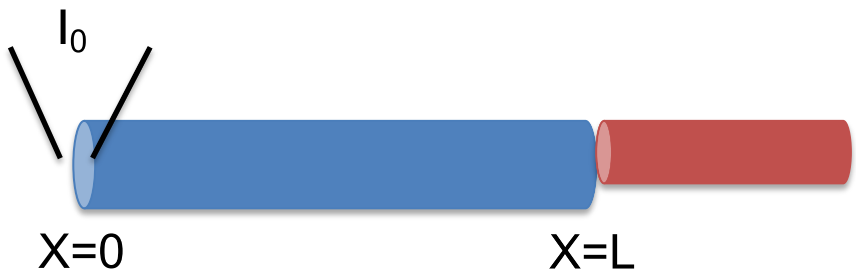
$$G_\infty = \frac{\pi d^{3/2}}{2\sqrt{R_M R_A}}$$

$$G_{in} = G_{clamped} = G_\infty \coth(L) = G_\infty \frac{\cosh(L)}{\sinh(L)}$$



Segev I., Cable and Compartmental Models
of Dendritic Trees

Finite Cable: steady state solution with a leak conductance (step 1 in modeling dendritic trees)



- $V(L) = V_L$
- $dV(L)/dx = V_L G_L$

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Finite Cable: steady state solution with a leak conductance (step 1 in modeling dendritic trees)

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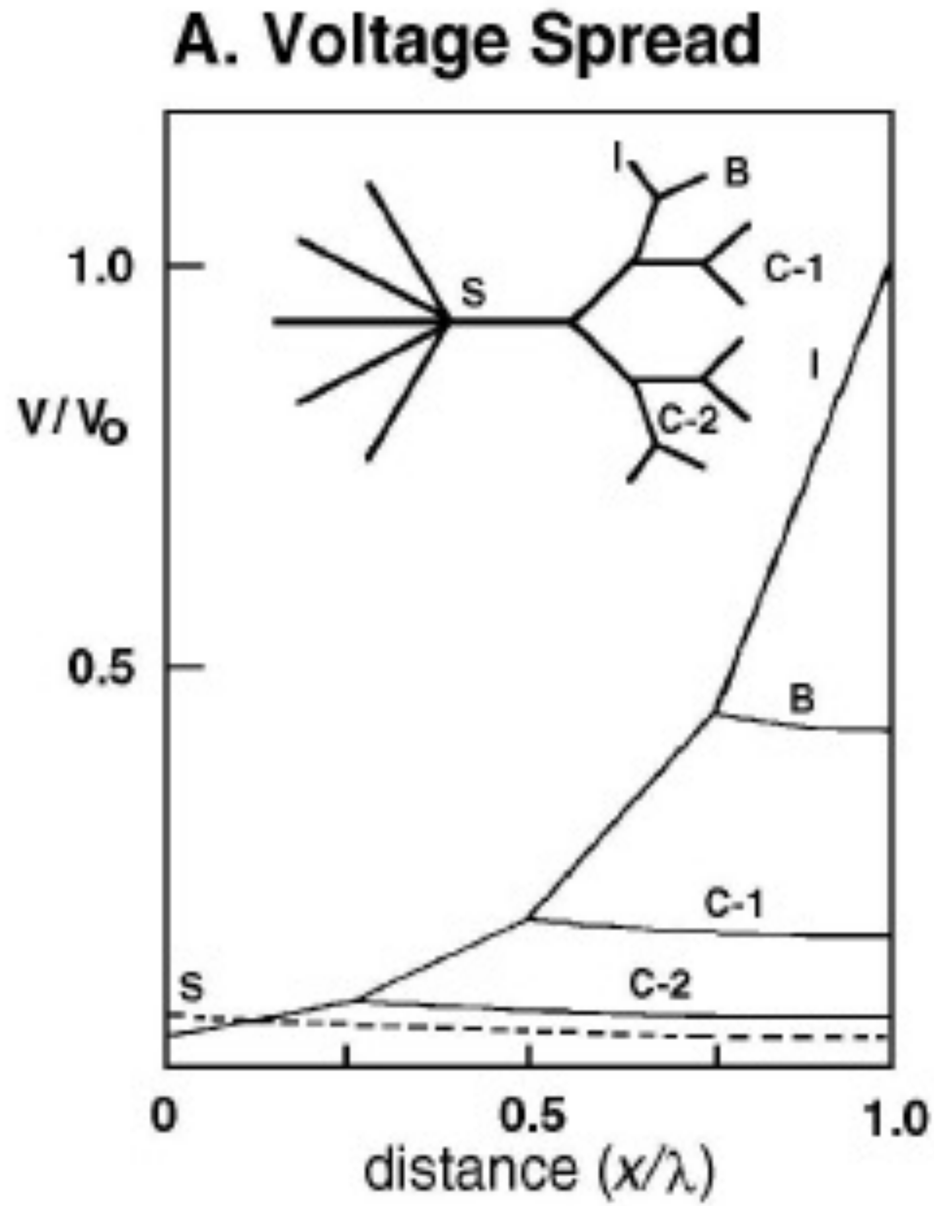
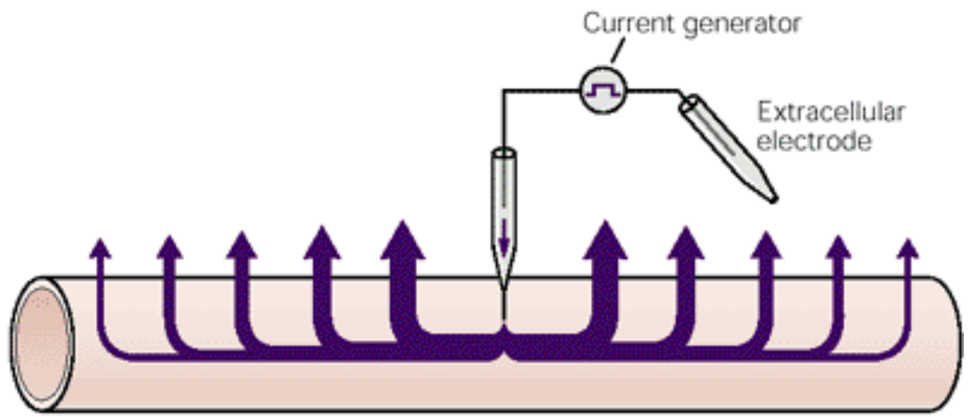
$$G_{in} = G_{leak} = G_\infty \frac{G_L + G_\infty \tanh(L)}{G_\infty + G_L \tanh(L)}$$



From “Cable and Compartmental Models of Dendritic Trees” by Idan Segev

What about time?



Solution for an instantaneous pulse of current in a cable

Dimensionless cable equation:

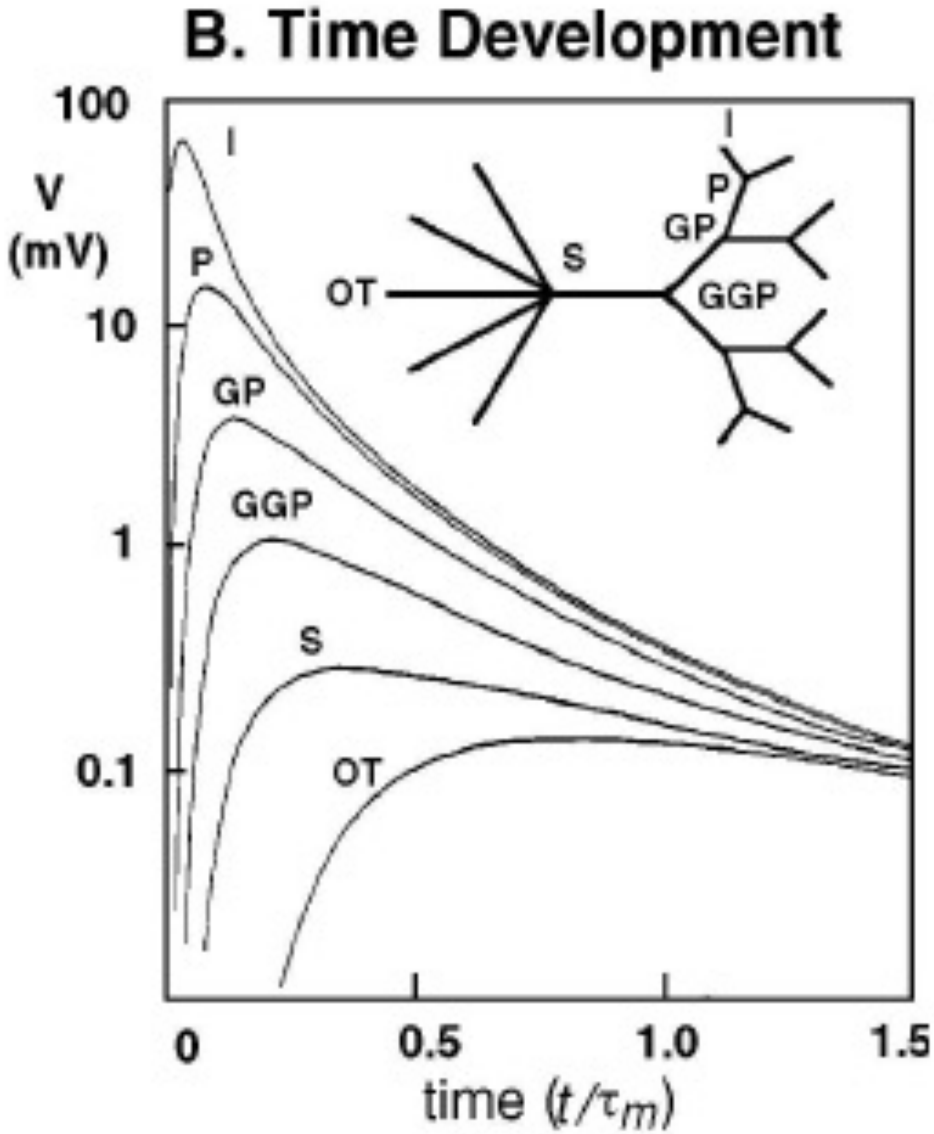
$$\boxed{\frac{\partial^2 V(X,T)}{\partial X^2} = \frac{\partial V(X,T)}{\partial T} + V(X,T) - \frac{I_{inj}(X,T)}{\lambda c_m}}$$

$$X = \frac{x}{\lambda}, T = \frac{t}{\tau_m}$$

Solution for an infinite end ($L \rightarrow \infty$) in response to a brief current injection:

$$V(X,T) = \frac{I_0 r_m}{2\lambda(\pi T)^{1/2}} e^{\frac{-X^2}{4T}} e^{-T}$$

Here, a charge Q_0 is breifly applied at $X = 0$
and $I_0 = Q_0/\tau_m$



From “Cable and Compartmental Models of Dendritic Trees” by Idan Segev

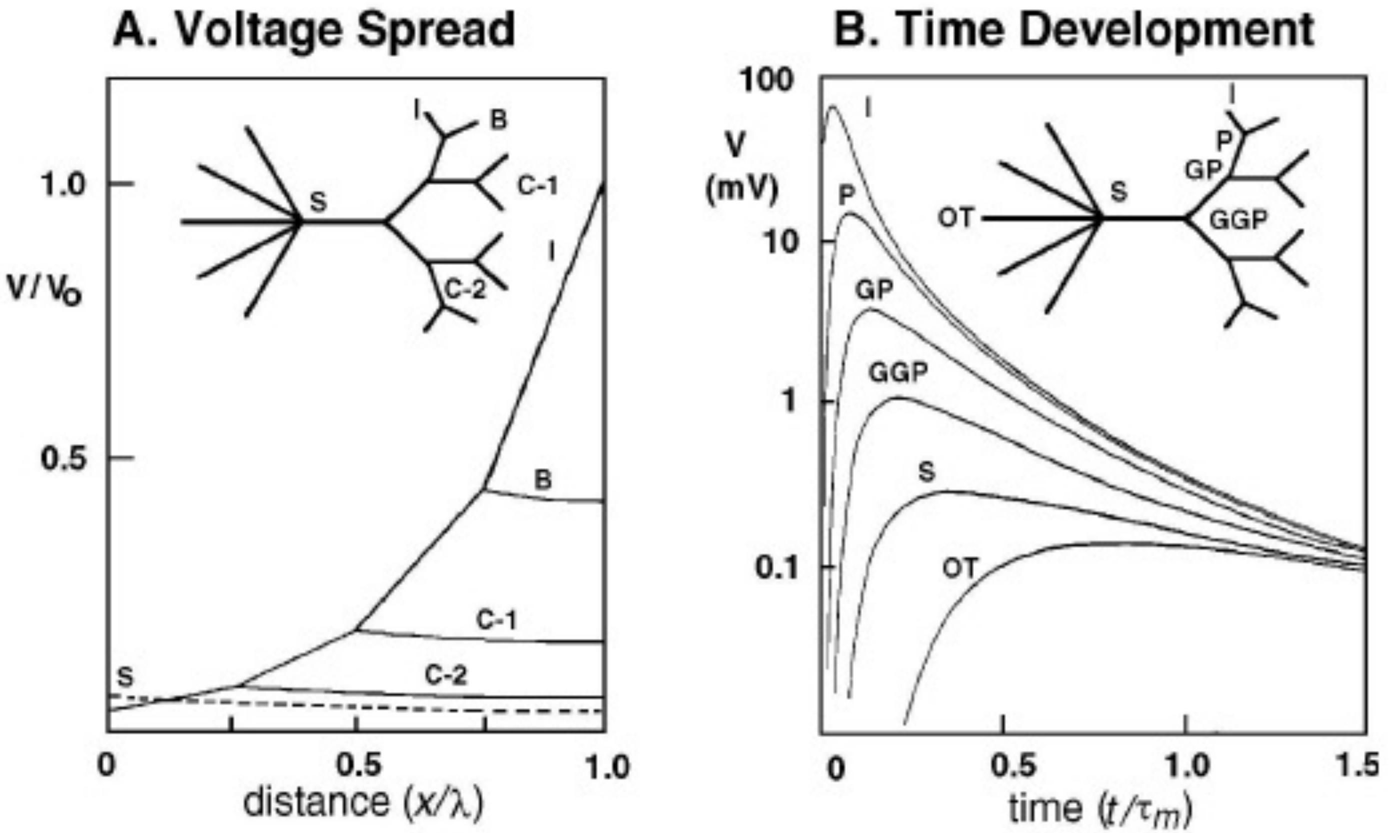


Figure 5.3 The voltage spread in passive dendritic trees is asymmetrical (A); its time-course changes (is broadened) and the peak is delayed as it propagates away from the input site (B). Solid curve in (A) shows the steady-state voltage computed for current input to terminal branch I. Large attenuation is expected in the input branch whereas much smaller attenuation exists in its identical sibling branch B. The dashed line corresponds to the same current when applied to the soma. Note the small difference, at the soma, between the solid curve and the dashed curve, indicating the negligible "cost" of placing this input at the distal branch rather than at the soma. (Data replotted from Rall and Rinzel (1973).) In (B), a brief transient current is applied to terminal branch I and the resultant voltage at the indicated points is shown on a logarithmic scale. Note the marked attenuation of the peak voltage (by several hundredfold) from the input site to the soma and the broadening of the transient as it spreads away from the input site. (Data replotted from Rinzel and Rall (1974).) Dendritic terminals have sealed ends in both (A) and (B).

From "Cable and Compartmental Models of Dendritic Trees" by Idan Segev

Contribution of time constant and length constant to integration

- “integration” – how the neuron processes its inputs.

Significance of τ_m on temporal integration

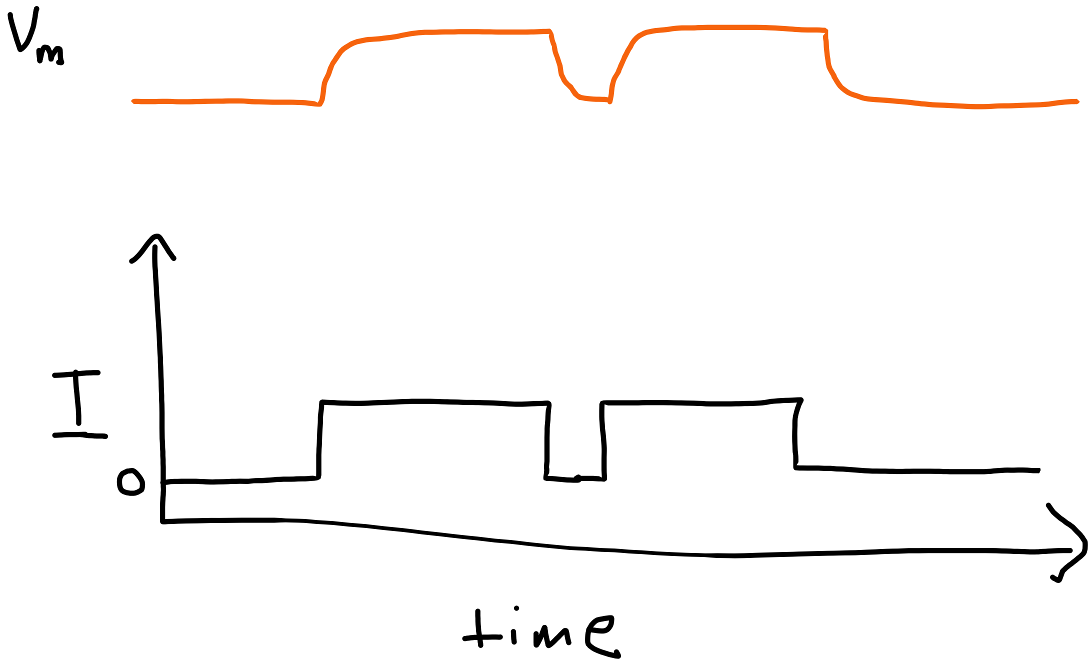
- Why do we care about this?

Significance of τ_m

If two synaptic inputs occur at the same location but are separated by a time t, will we get larger V_m halfway between the two time points with a large or small τ_m?

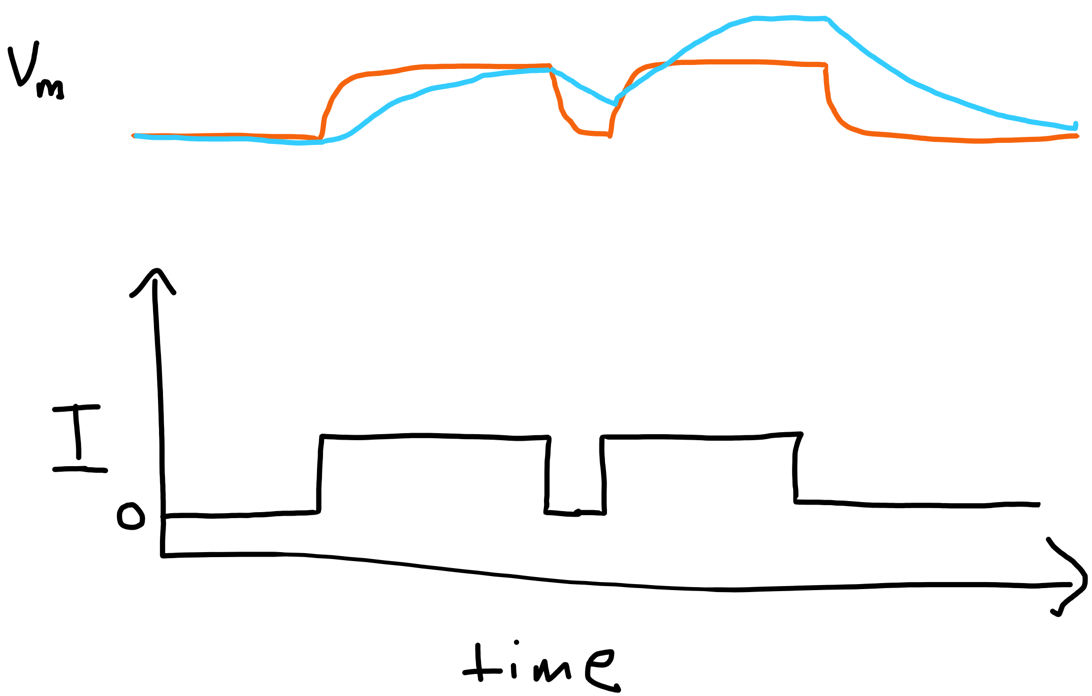
Significance of τ_m

$\tau_1 < \tau_2$



Significance of τ_m

$\tau_1 < \tau_2$



Significance of λ on spatial integration

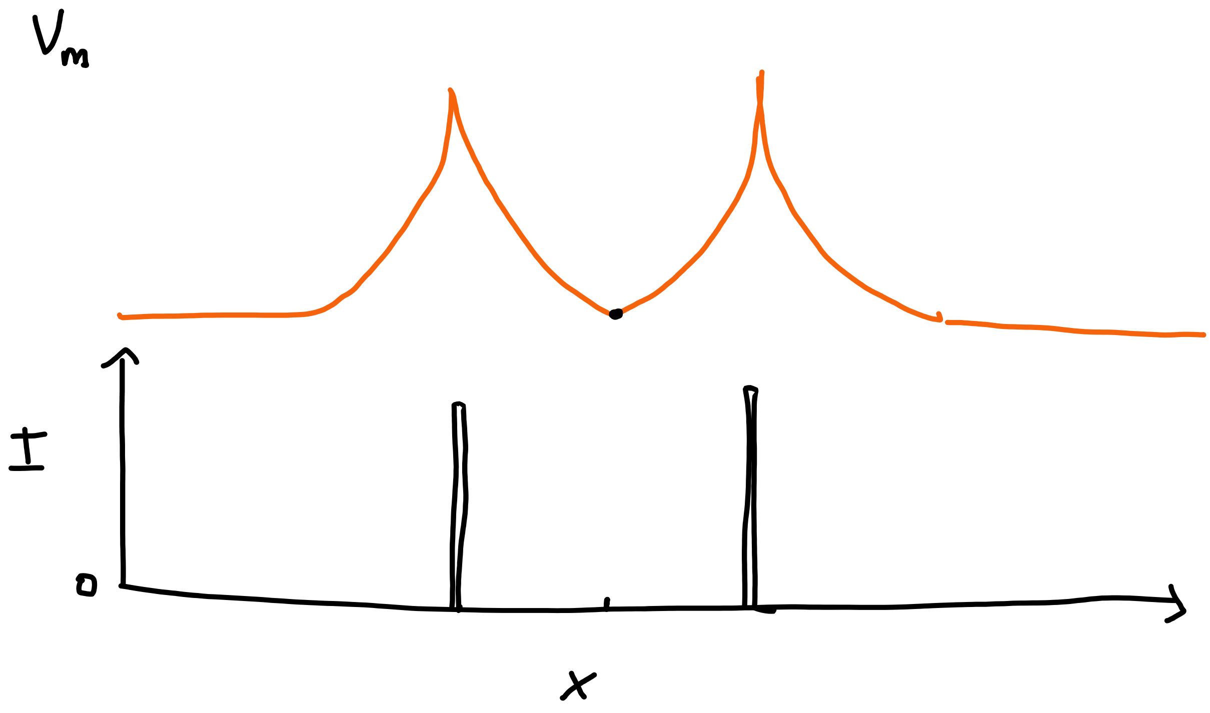
- Why do we care about this?

Significance of λ

If two synaptic inputs occur simultaneously and are separated by a distance *l*, will we get a larger V_m halfway between the two points of a dendrite with a large or small λ?

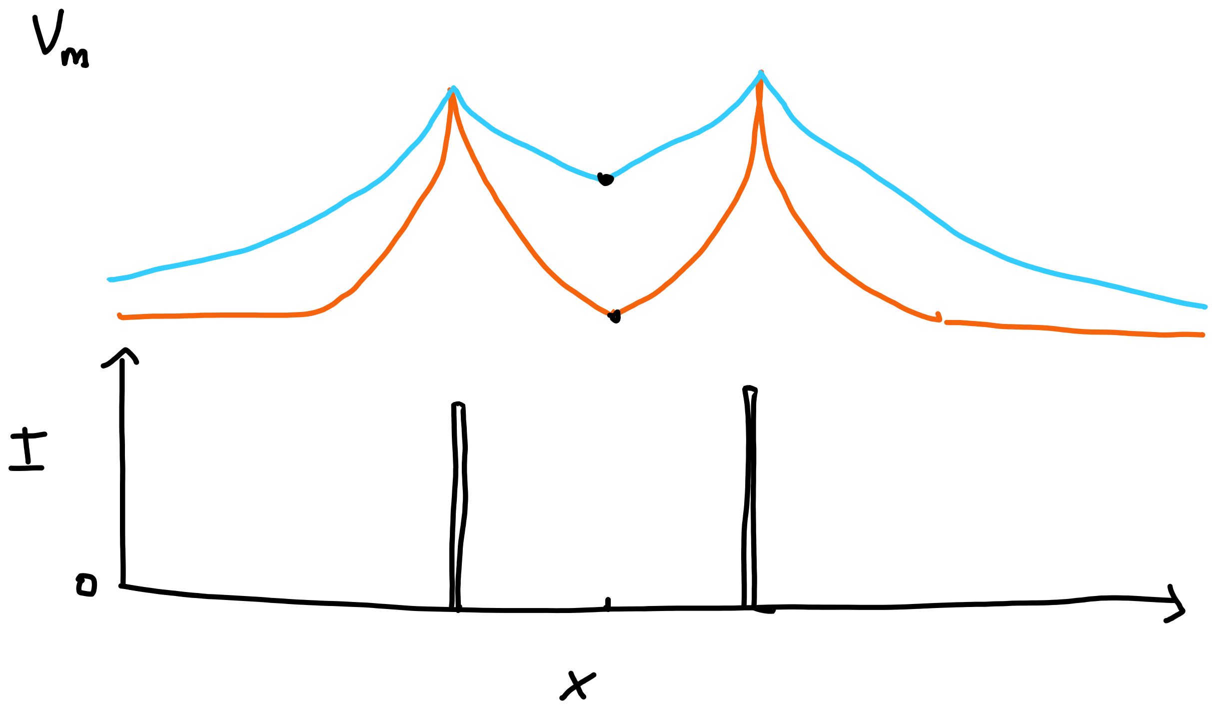
Significance of λ

$\lambda_1 < \lambda_2$



Significance of λ

$\lambda_1 < \lambda_2$



Our cable model suggest signals are delayed as they travel from their initiation site

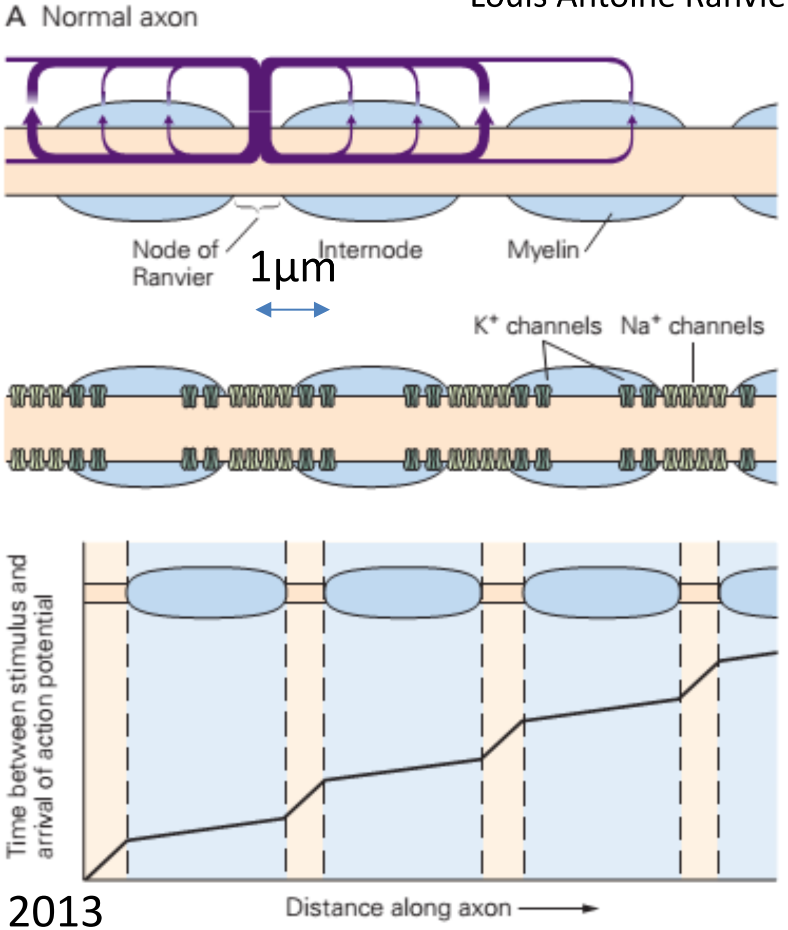
How can you increase the speed?

- Change geometry
- Insulate the axon (saltatory conduction)

Saltatory Conduction

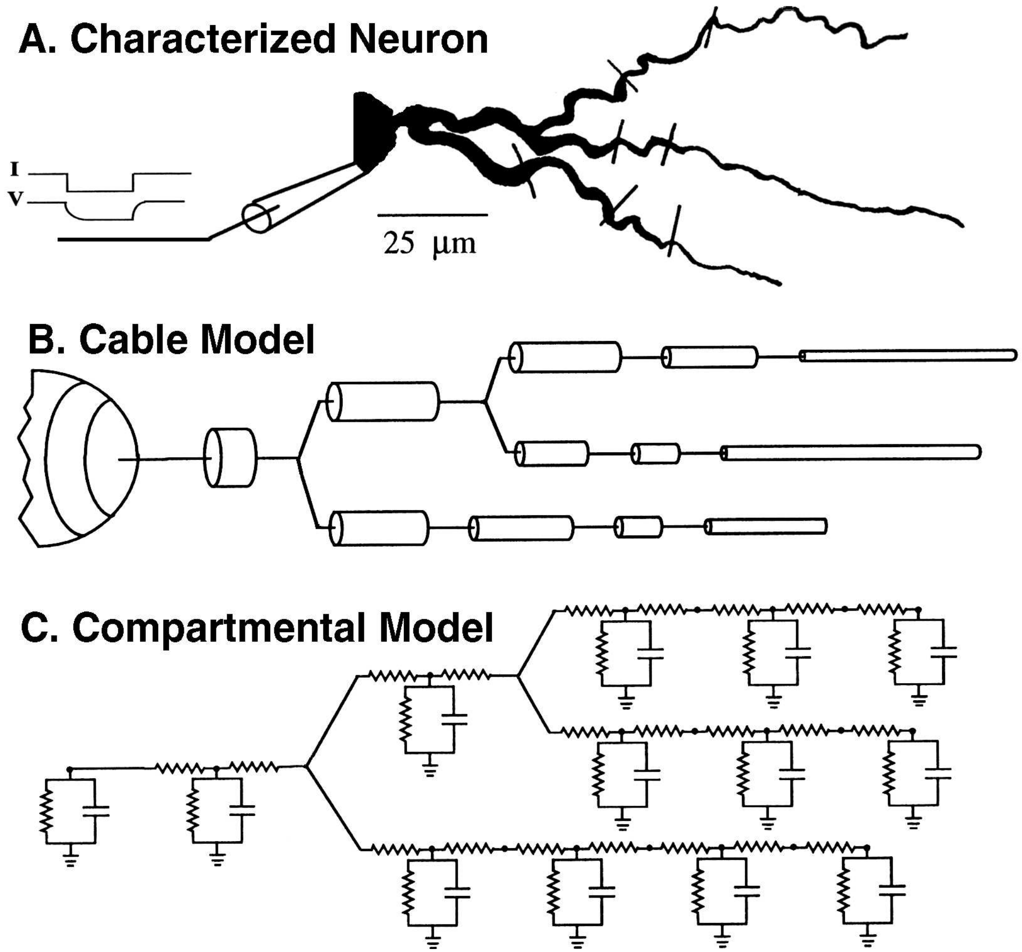

Louis Antoine Ranvier

- Myelin increases membrane resistance and decreases membrane capacitance
- Densely packed voltage-gated Na^+ channels at Nodes of Ranvier "boost" signal

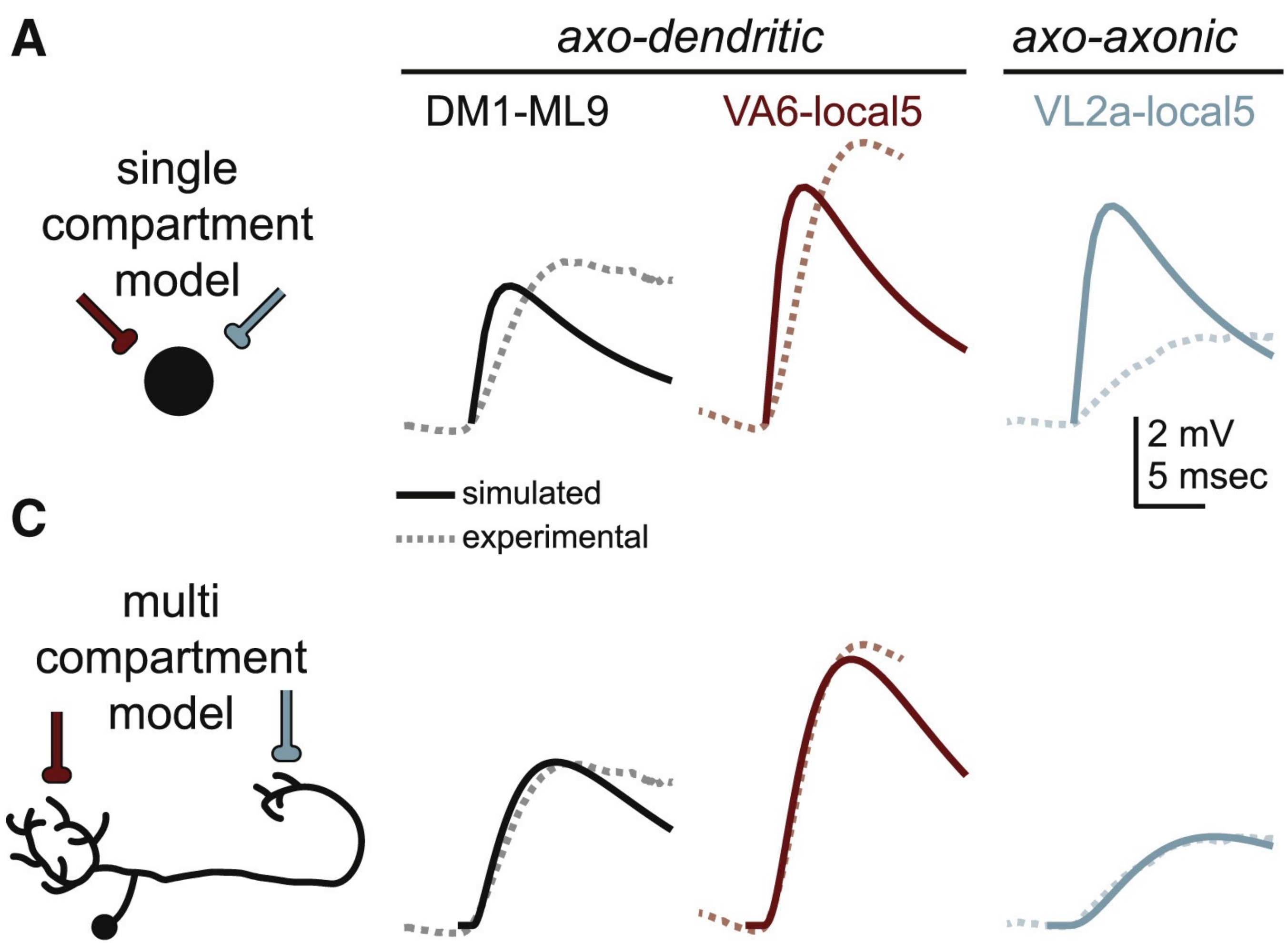


Kandel et al., Principles of Neural Science 2013

Modeling real neurons

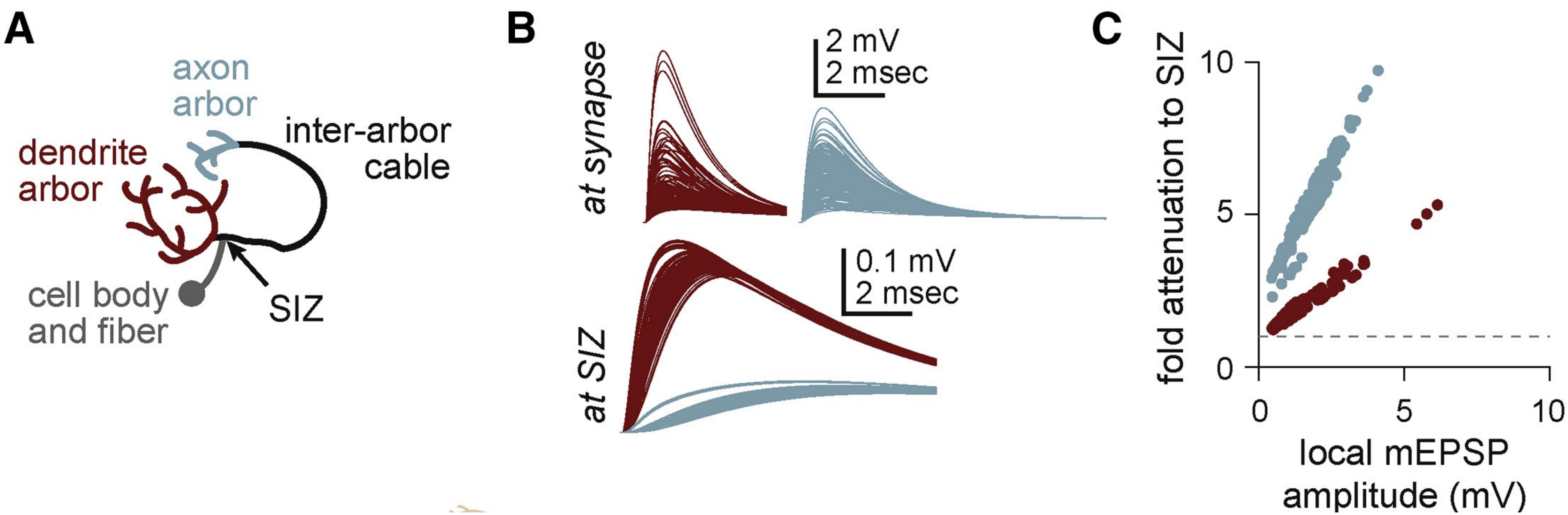


http://www.genesis-sim.org/GENESIS/iBoG/iBoGpdf/chapt5.pdf



Liu et al. Current Biology 2021 https://doi.org/10.1016/j.cub.2021.11.056

Does synapse location matter?



Liu et al. Current Biology 2021 https://doi.org/10.1016/j.cub.2021.11.056

Additional Reading For Today

Neuron

Obituary

Wilfrid Rall (1922–2018)

Chapter 1

The Hodgkin–Huxley Equations

G.B. Ermentrout and D.H. Terman, *Mathematical Foundations of Neuroscience*,
Interdisciplinary Applied Mathematics 35, DOI 10.1007/978-0-387-87708-2_1,

For Next Time

- Quiz 2 (online, open book/notes)
  - Modeling a neuron as an RC circuit
  - How to calculate R and C if you inject a current step into an isopotential cell.
  - Semi-infinite cable solution
  - How does lambda (length constant) affect the spatial rate of decay?
- Remember: Lab 2 is due on Monday at 11:59pm