UNIVERSITY OF LINCOLN

The Neuronal Cable Theory

CMP9783 – Neural Computing   Week 3

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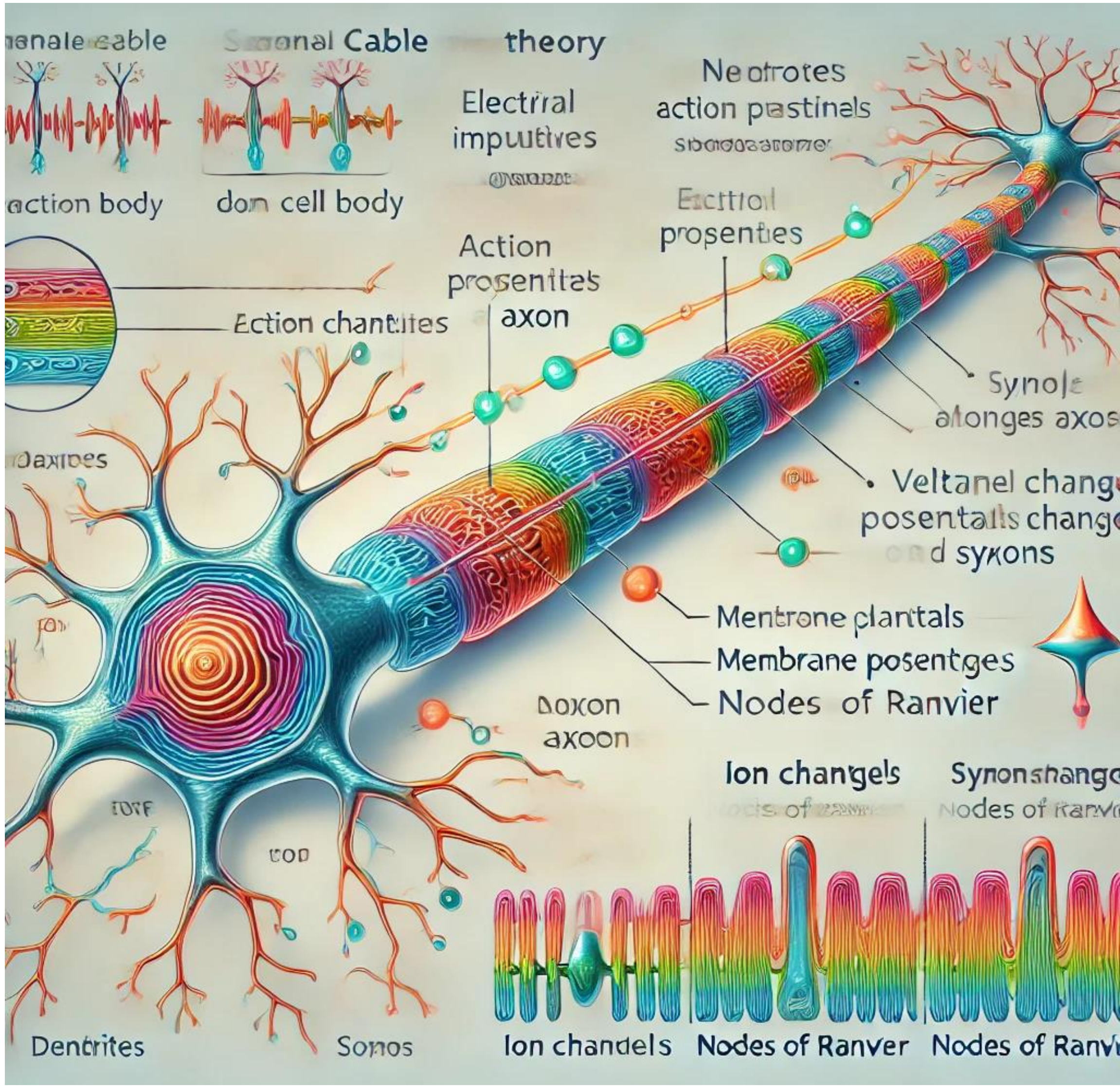
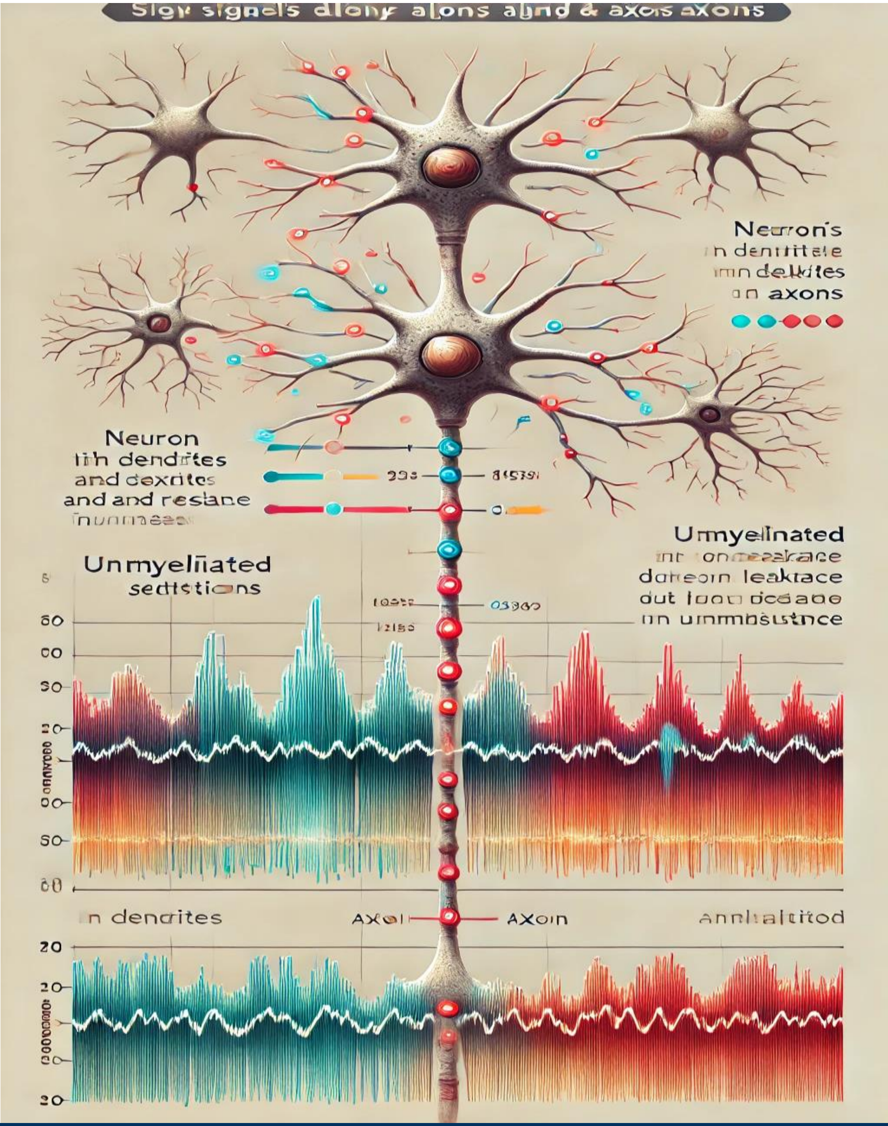
The Neuronal Cable Theory

- It is a mathematical framework used to describe how electrical signals, specifically voltage changes, propagate along passive, elongated neuronal structures like dendrites and axons.
- It models the neuron as a cylindrical cable.
- Its goal is to understand the flow of current and how membrane potentials evolve over time and space in these structures.
- It is a fundamental tool in computational neuroscience.
- It helps explain the electrotonic properties of neurons, especially those with complex dendritic arborizations.



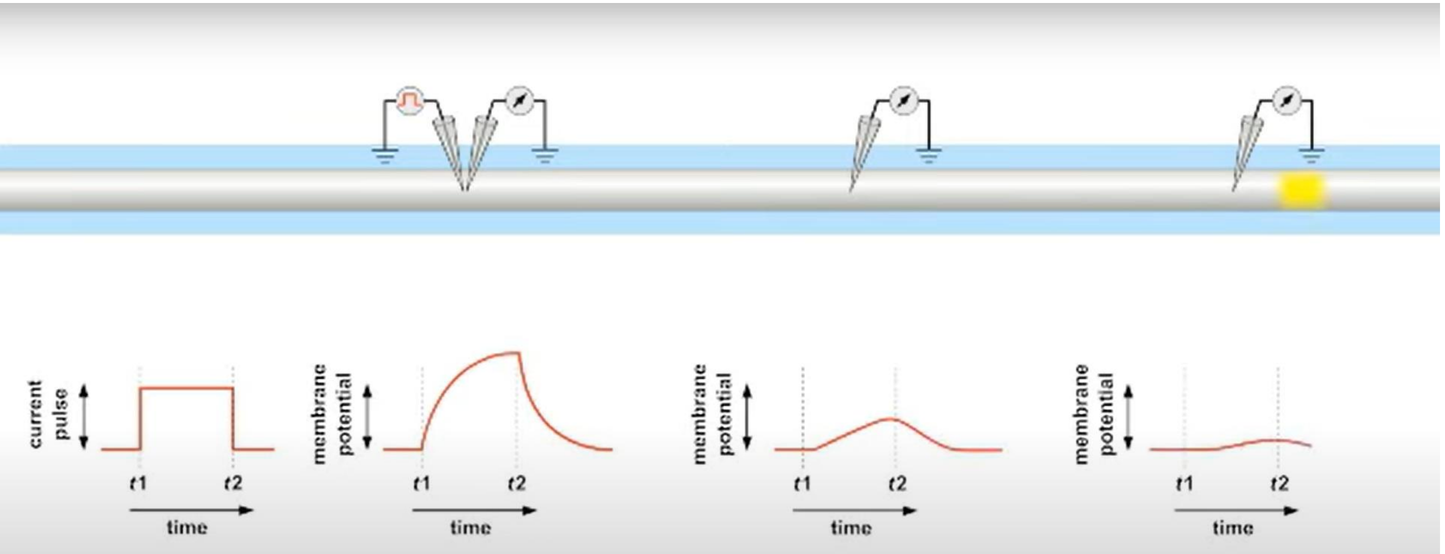
Neuronal Cable Theory - Applications

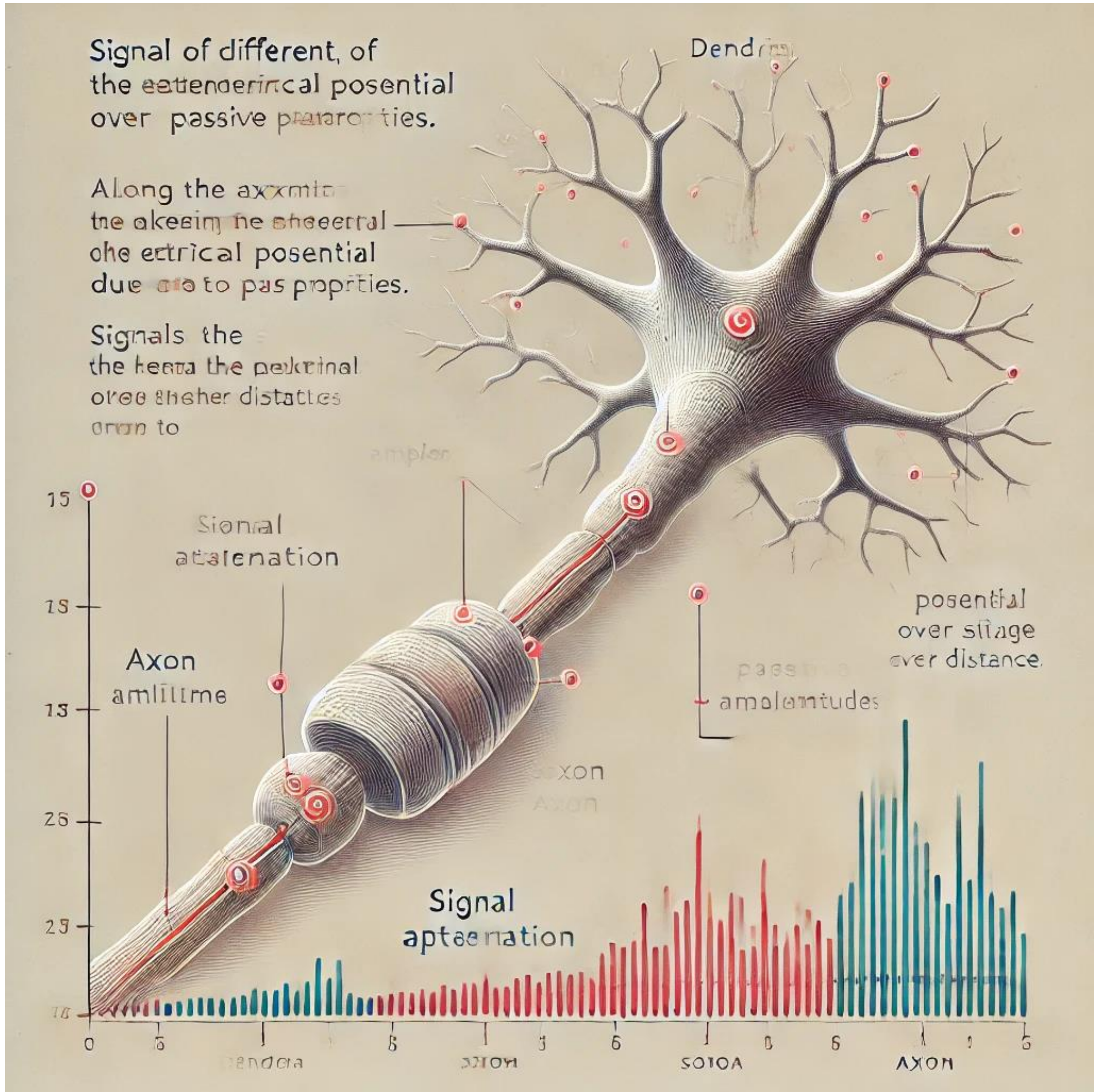
1. **Dendritic Processing**: Helps understand how synaptic inputs on dendrites contribute to overall neuronal output.
2. **Signal Attenuation**: Explains how signals decay as they move along dendrites or axons, particularly in unmyelinated neurons.
3. **Neuronal Modeling**: Provides a foundation for simulating the electrical properties of neurons in computational models, often coupled with active properties (voltage-gated ion channels) for more realistic scenarios.



Key Concepts (1): Passive Electrical Properties

- Cable theory typically assumes the neuron is passive.
- No voltage-gated ion channels are involved in the propagation of the signal.
- The signal diminishes as it travels (attenuation)





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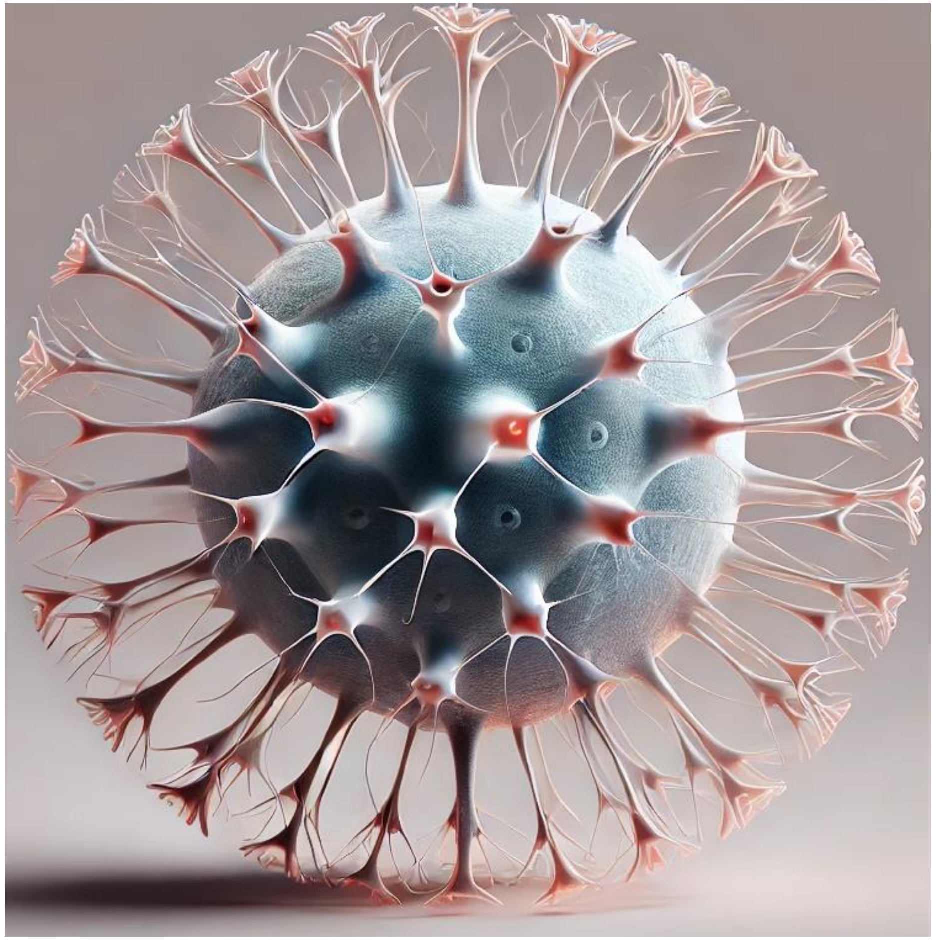
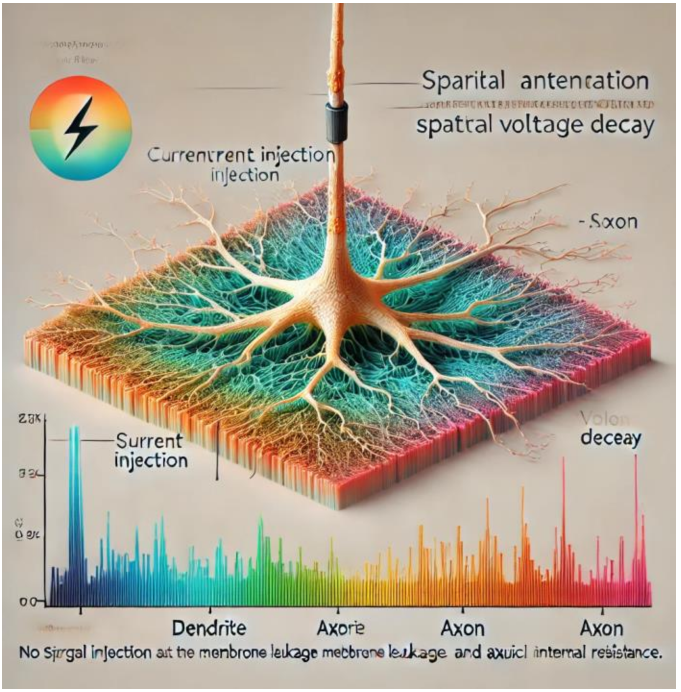
The need for cable theory (1): The neuron as a spherical model

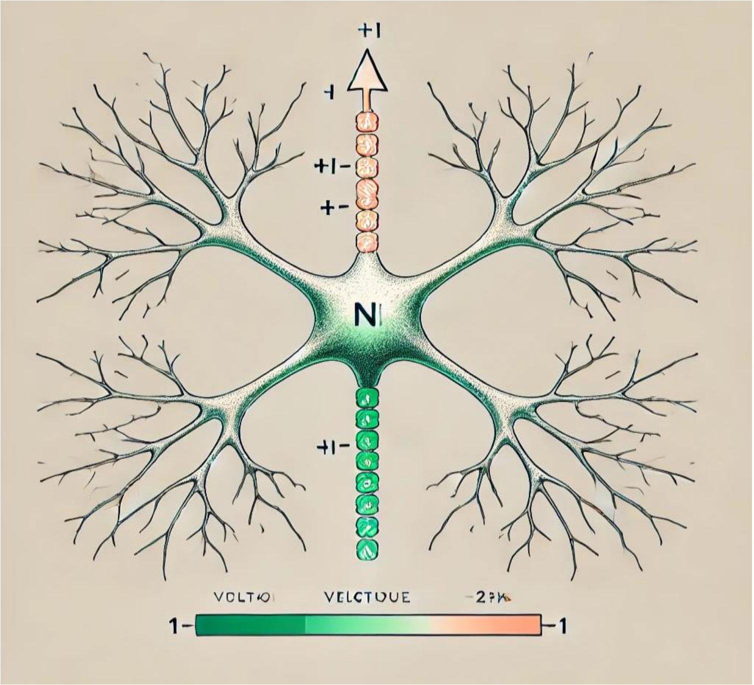


1. Let’s start by assuming that the neuron is a simple spherical cell.
2. Then, the voltage is uniform across the entire volume.
3. This model works well to approximate the behavior of current injections into the cell body (soma), where the spatial spread of the voltage is relatively uniform.

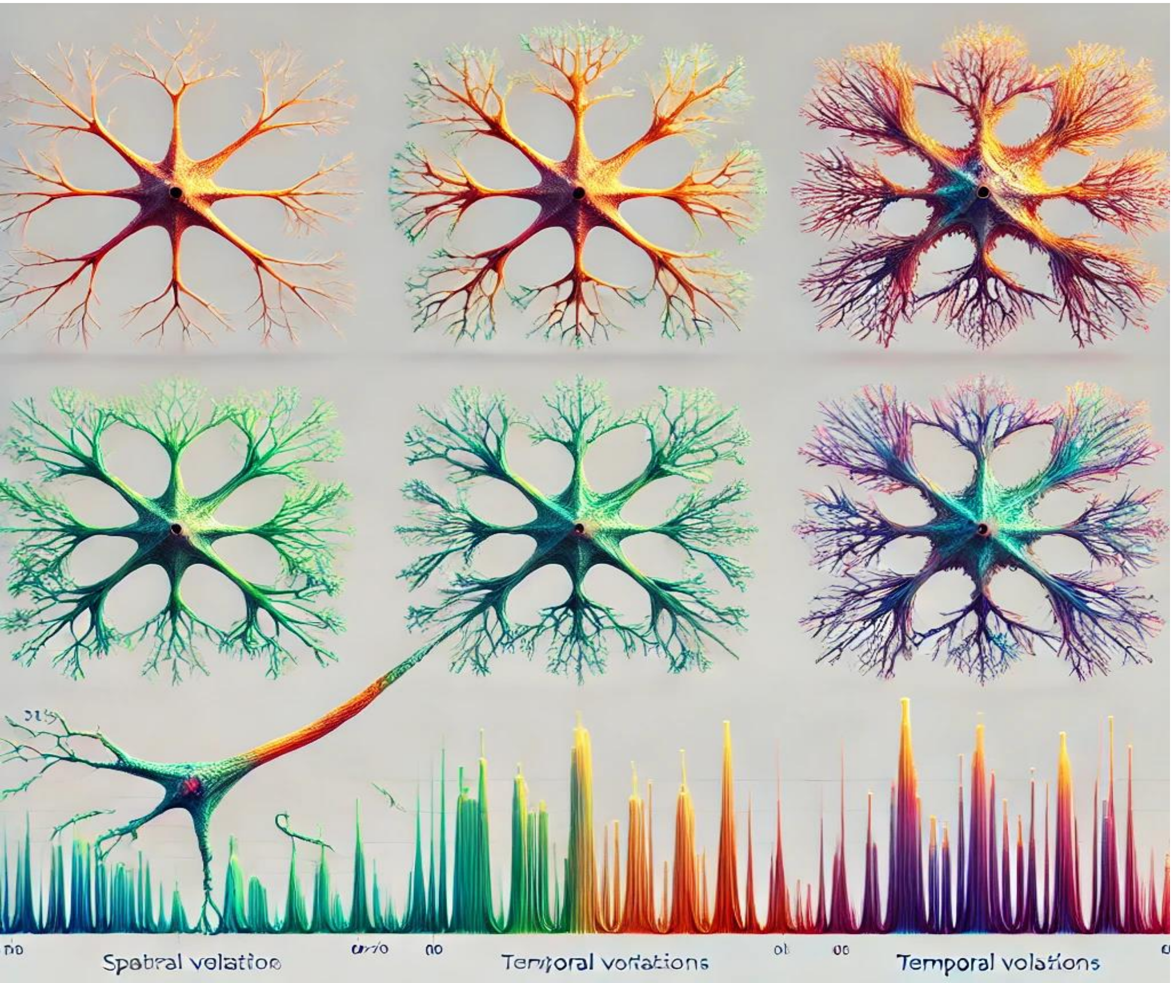
The need for cable theory (2): The case of complex voltage dynamics in the dendrites



- However, for extended structures like dendrites and axons, this simplistic model no longer holds.
- These compartments exhibit complex voltage dynamics that vary with position along their length.
- Particularly in the dendrites, the voltage following a current injection differs significantly as a function of distance from the source.
- This spatial variation occurs because, as the current flows through the dendrite, charges leak out across the membrane, reducing the strength of the signal.

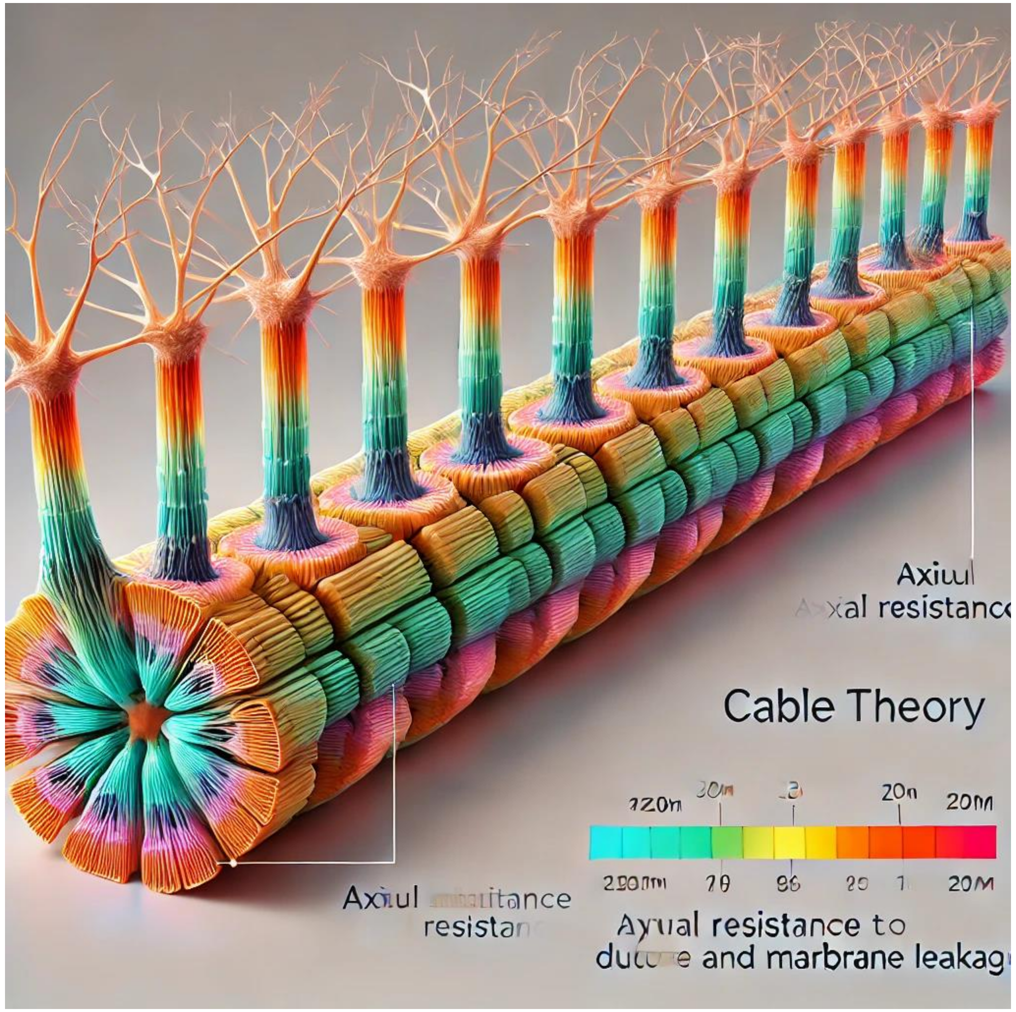


The need for cable theory (3): The case of complex voltage dynamics in the dendrites



- Dendrites, often the primary sites of current injection – whether via synapses or sensory inputs – require a more sophisticated model to capture the spatial and temporal variations in membrane potential.
- Unlike the soma, where voltage can remain relatively uniform, dendritic voltages are affected by their elongated geometry and branching structure, leading to varying voltages across different dendritic branches at any given time.

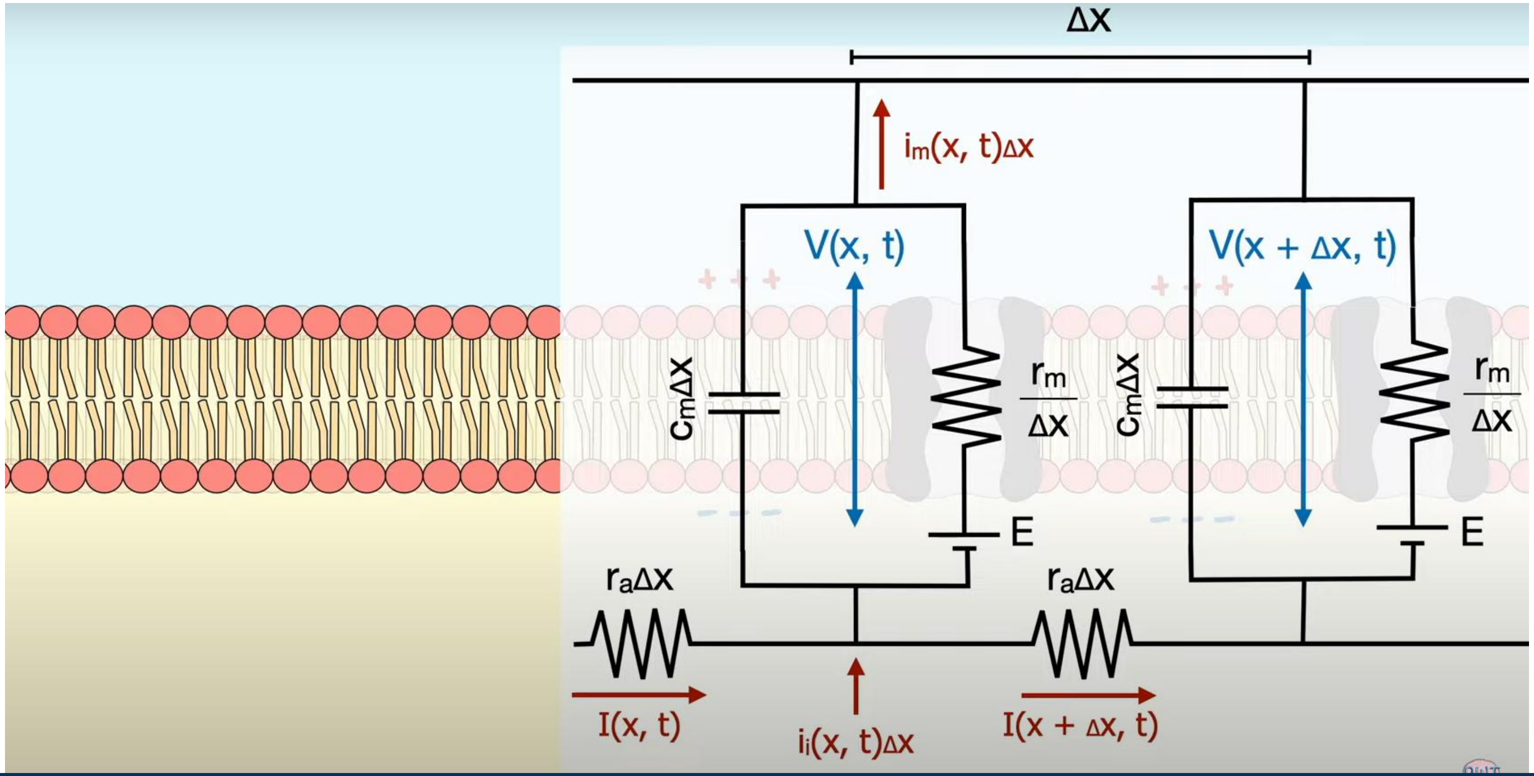
The need for cable theory (4): Approximating the dendrites as 3-D cylinders



- To accurately model the behavior of voltages in dendrites, we need a different framework.
- This should accommodate the electrical and spatial properties of these elongated structures.
- Dendrites can be geometrically complex.
- To approximate their three-dimensional shape, we can model them as cylinders.
- This approximation provides a foundation for applying the neuronal cable theory.
- The compartments represent the structure of dendrites.
- Color gradients indicate the voltage attenuation.

Key Concepts (2): Resistances & Capacitances

- **Membrane resistance**: Describes how easily current can flow across the neuronal membrane.
- **Axial (internal) resistance**: Represents how easily current can flow longitudinally within the neuron.
- **Membrane capacitance**: Models the ability of the membrane to store charge, affecting how quickly the membrane potential can change.



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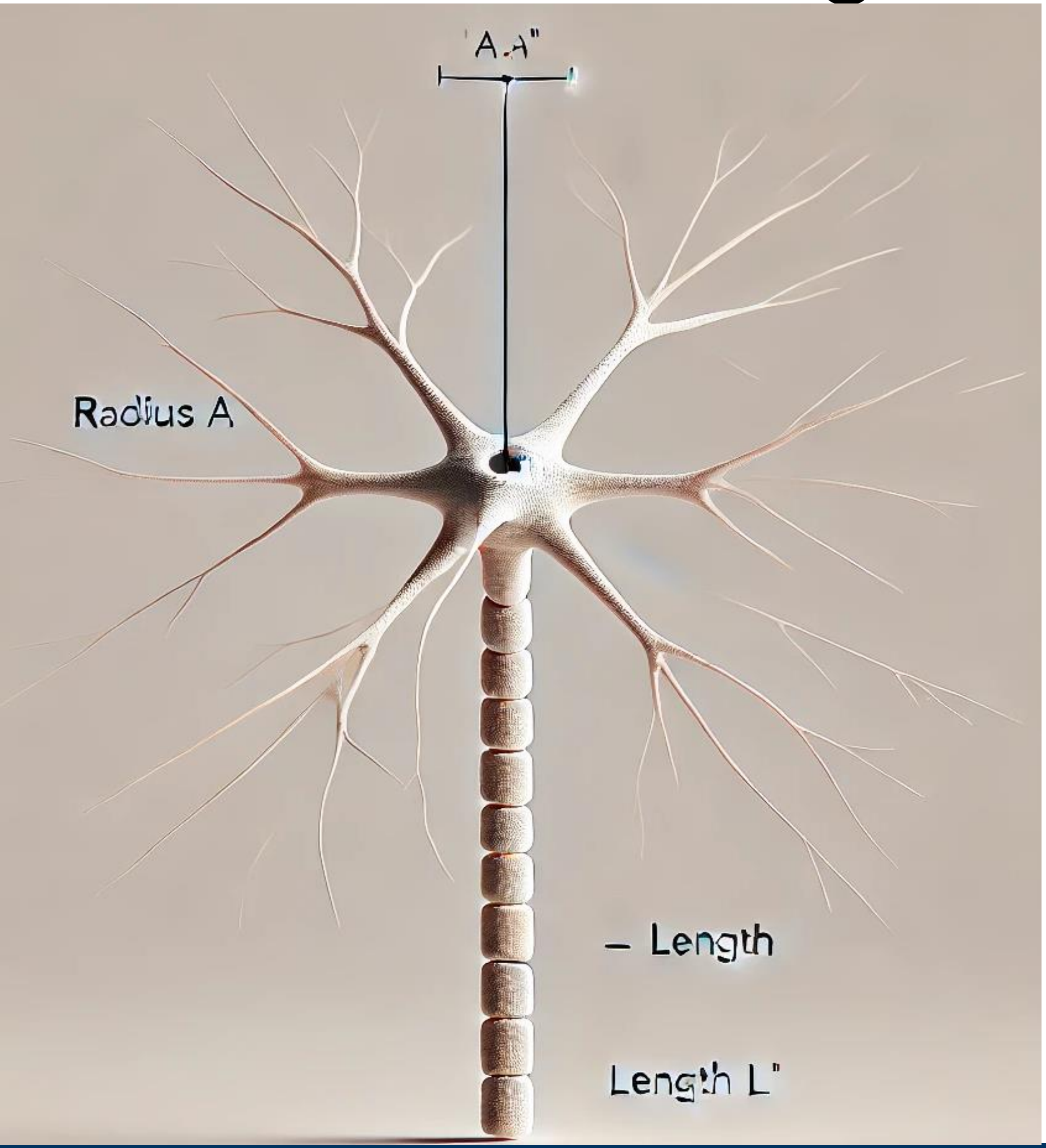
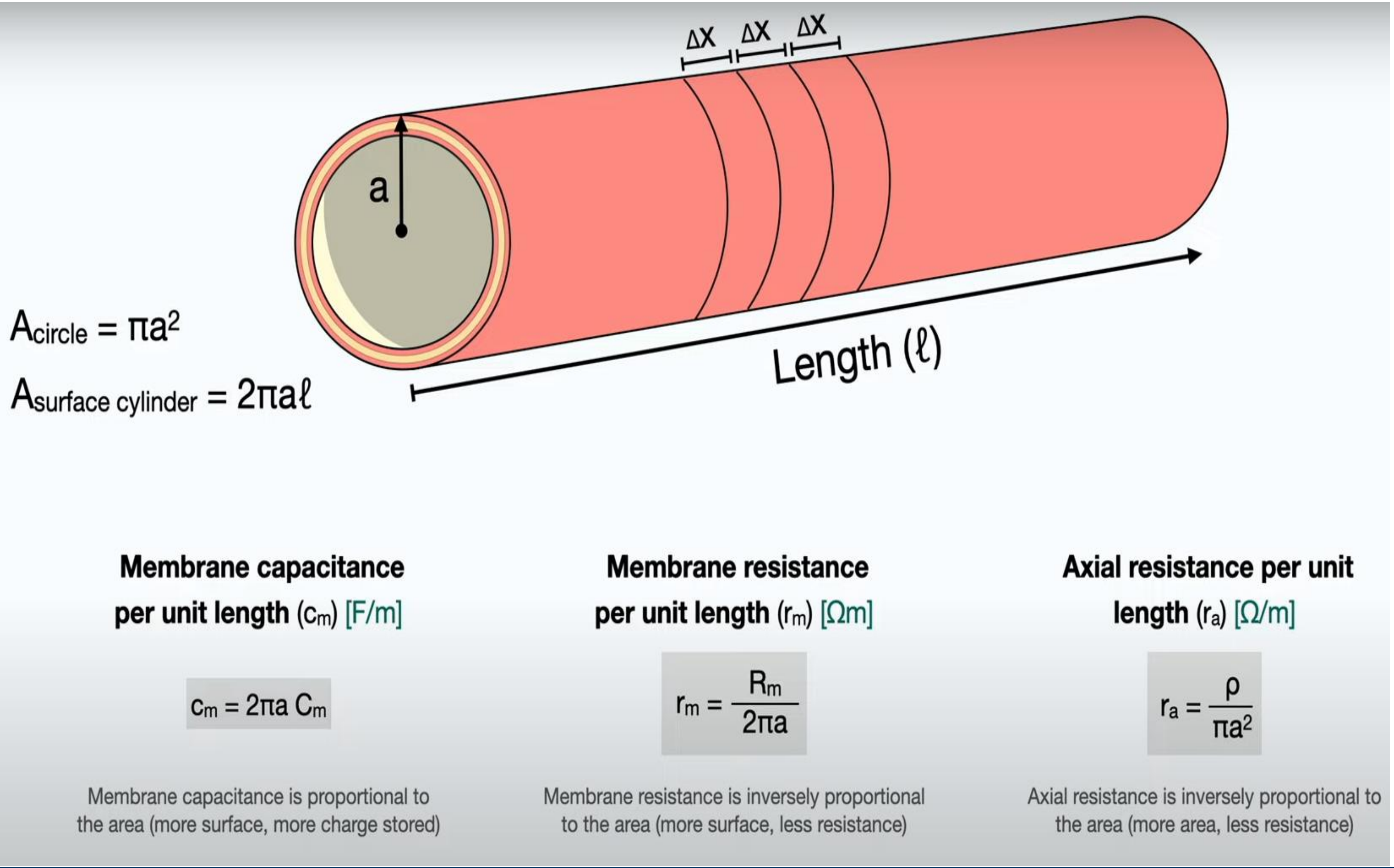
Modeling dendrites as cylinders



When dendrites are modeled as cylindrical structures, we make several simplifying assumptions to capture their behavior mathematically:

1. **Cylindrical Geometry**
   - Dendrites are modeled as straight or slightly branched cylinders of length L and radius α.
   - The membrane of the dendrite forms the outer boundary of the cylinder, and the interior contains cytoplasm (intracellular medium) with a certain resistance to current flow.
2. **Current Flow**
   - Current flows longitudinally through the interior of the dendrite (axial current).
   - A portion of this current leaks out across the membrane into the extracellular space (transmembrane current).

Useful geometric equations



1. The radius (**α**) of the cylinder (dendrite) affects the amount of cytoplasmic space available for current to flow longitudinally.
2. The length (**L**) of the dendrite affects how far the signal can propagate before attenuating.

Resistance per Unit Length (R_i)

- The axial (internal) resistance $\mathbf{R_i}$ is the resistance to current flow within the cytoplasm of the dendrite.
- It depends on the resistivity of the intracellular medium $\boldsymbol{\rho_\iota}$ (measured in ohm × meters) and the dendrite's radius **α**.
- It is expressed as resistance per unit length: $$R_i = \frac{\rho_i}{\pi a^2}$$

Where:

- ❖ $\boldsymbol{\rho_\iota}$ is the specific resistivity of the cytoplasm (in ohm × meters).
- ❖ **α** is the radius of the dendrite (in meters).
- ❖ $\boldsymbol{\pi a^2}$ is the cross-sectional area of the dendrite through which current flows.

This equation indicates that the **larger** the radius **α**, the **lower** the **resistance** to current flow along the length of the dendrite.

Membrane Resistance per Unit Length (R_m)

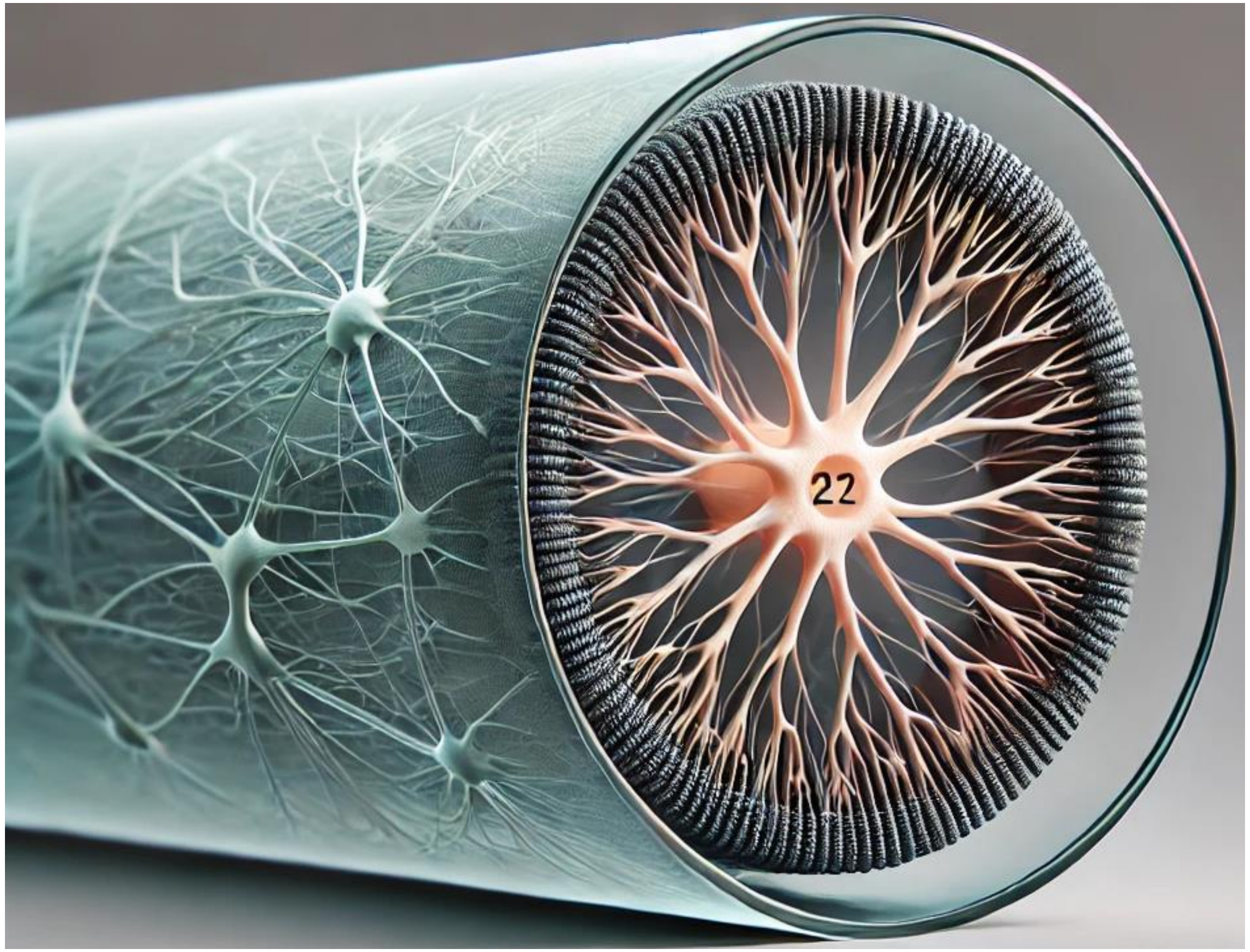
- The membrane resistance $\mathbf{R_m}$ is the resistance to current flowing across the dendritic membrane (from the inside to the outside).
- It depends on the membrane's specific resistance r_m (measured in ohm × meters^2) and the surface area of the cylindrical segment per unit length:
- It is expressed as resistance per unit length:

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

Where:

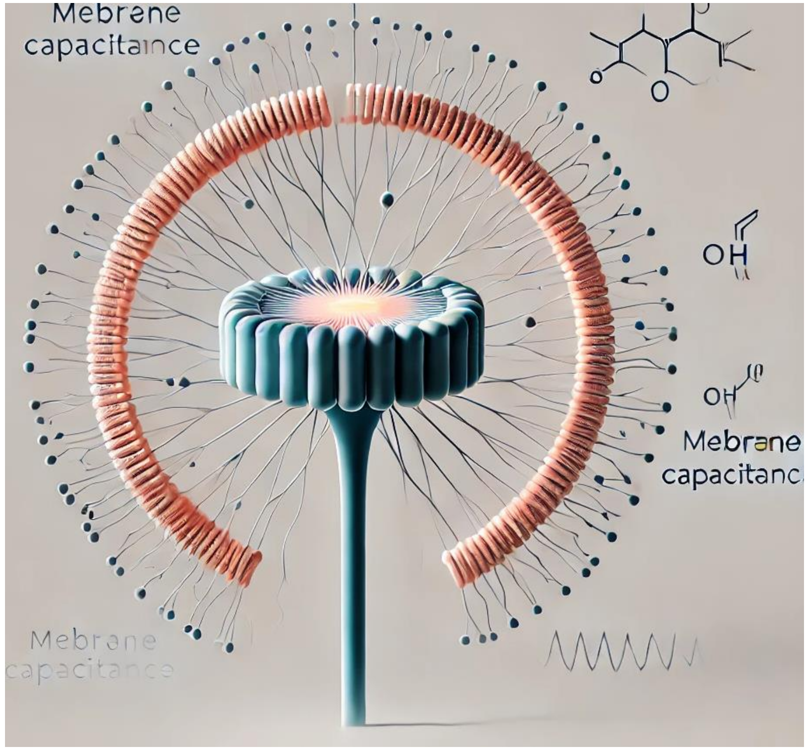
❖ $\mathbf{r_m}$ is the specific membrane resistance (in ohm × meters^2).

❖ **2πa** is the circumference of the cylindrical dendrite per unit length, representing the surface area of the membrane through which current can leak.



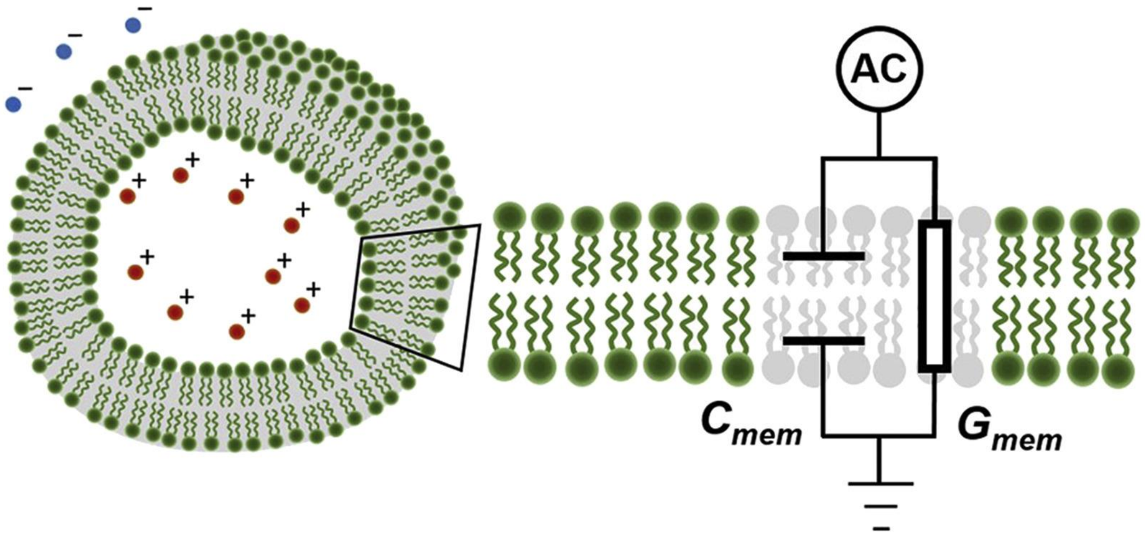
Membrane Capacitance per Unit Length (R_m)

- It represents the ability of the membrane to store charge.
- It is modeled as a capacitor.
- It depends on the specific capacitance c_m (in farads per square meter) and the surface area per unit length of the cylinder: $C_m = 2\pi a c_m$



Where:

❖ $\mathbf{c_m}$ is the specific membrane capacitance (in farads per square meter).
❖ **2πa** is the surface area of the membrane per unit length.



https://doi.org/10.1016/j.bpj.2017.08.006

Summary of the formulas & Interpretation of parameters

- Axial resistance per unit length:

$$R_i = \frac{\rho_i}{\pi a^2}$$

- Membrane resistance per unit length:

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

- Membrane capacitance per unit length:

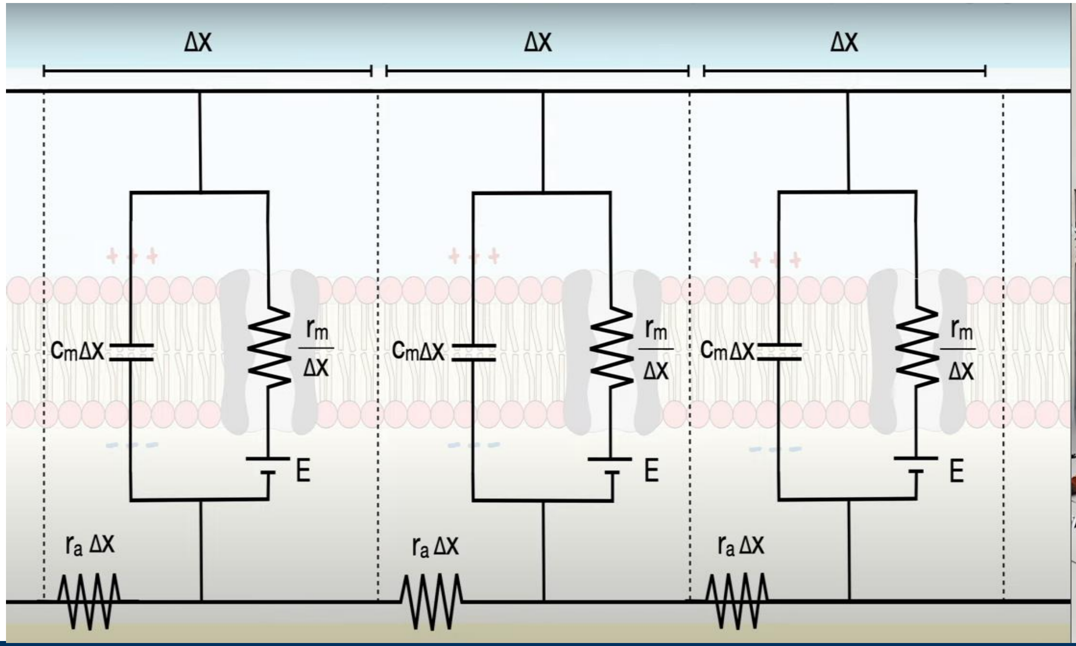
$$C_m = 2\pi a c_m$$

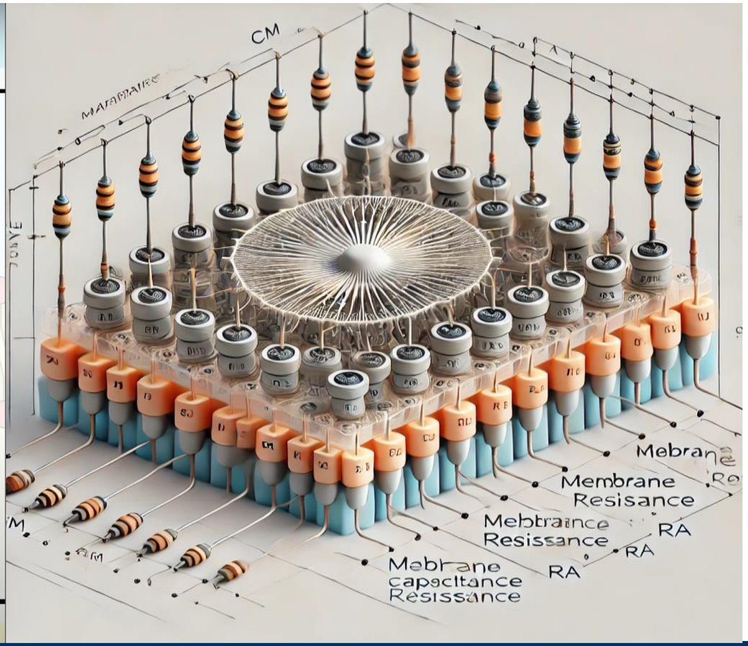
- **Axial Resistance R_i:**
  - Higher resistance means that the current will attenuate more rapidly as it flows along the length of the dendrite.
  - A smaller dendritic radius **α** will lead to higher axial resistance and thus faster signal attenuation.
- **Membrane Resistance R_m:**
  - Higher membrane resistance means fewer current leaks out of the membrane as the signal propagates along the dendrite.
  - If the membrane resistance is low, more current will leak out, leading to signal decay.
- **Membrane Capacitance C_m:**
  - Higher capacitance means that the membrane can store more charge.
  - This affects how quickly the membrane potential can change in response to an injected current.

The Electric Circuit Model

Each small segment of the dendrite can be represented by an electrical circuit that includes:

1. A **resistor** to represent the **axial (internal) resistance R_i**, which models how difficult it is for current to flow along the length of the dendrite.
2. A **resistor** to represent the **membrane resistance R_m**, which models how easily current leaks out of the membrane.
3. A **capacitor** to represent the membrane capacitance C_m which models the membrane's ability to store charge.
4. The **voltage E** represents the **resting potential** or **reversal potential** of the membrane. It is the voltage at which there is **no net flow** of ions across the membrane (the driving force for ion flow is zero)





To model the entire dendrite, we can chain together many such segments, with axial resistance connecting each adjacent segment.

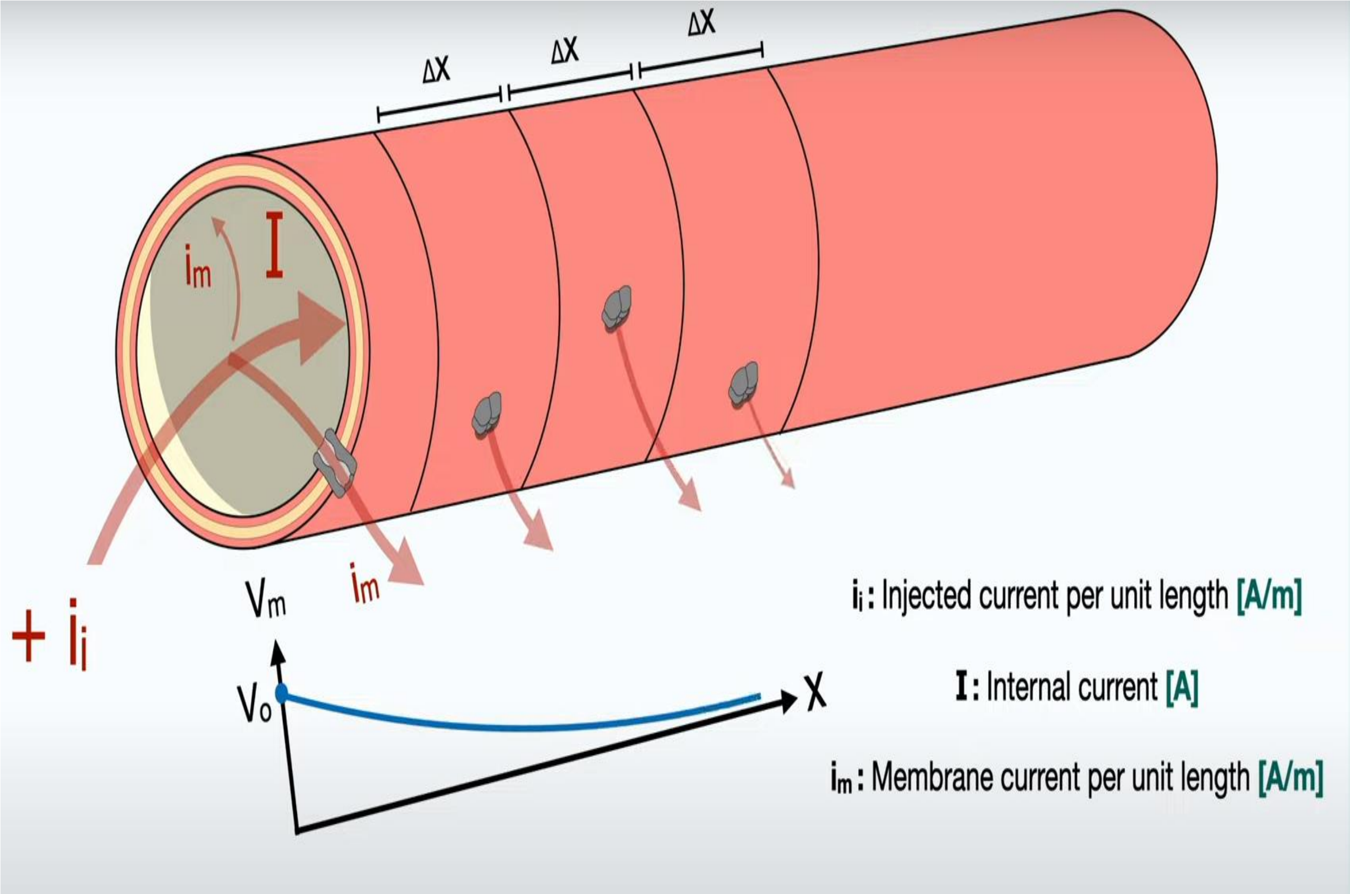
https://www.youtube.com/watch?v=2VzAY8pEbEE&t=195s

Current Injection

To understand the currents and voltages in this system, let's think conceptually about what happens when we inject the current into a small region of the dendritic cylinder of length **Δx**.

Assume we inject positive charges inside the neuron, where the resting membrane potential is typically negative.

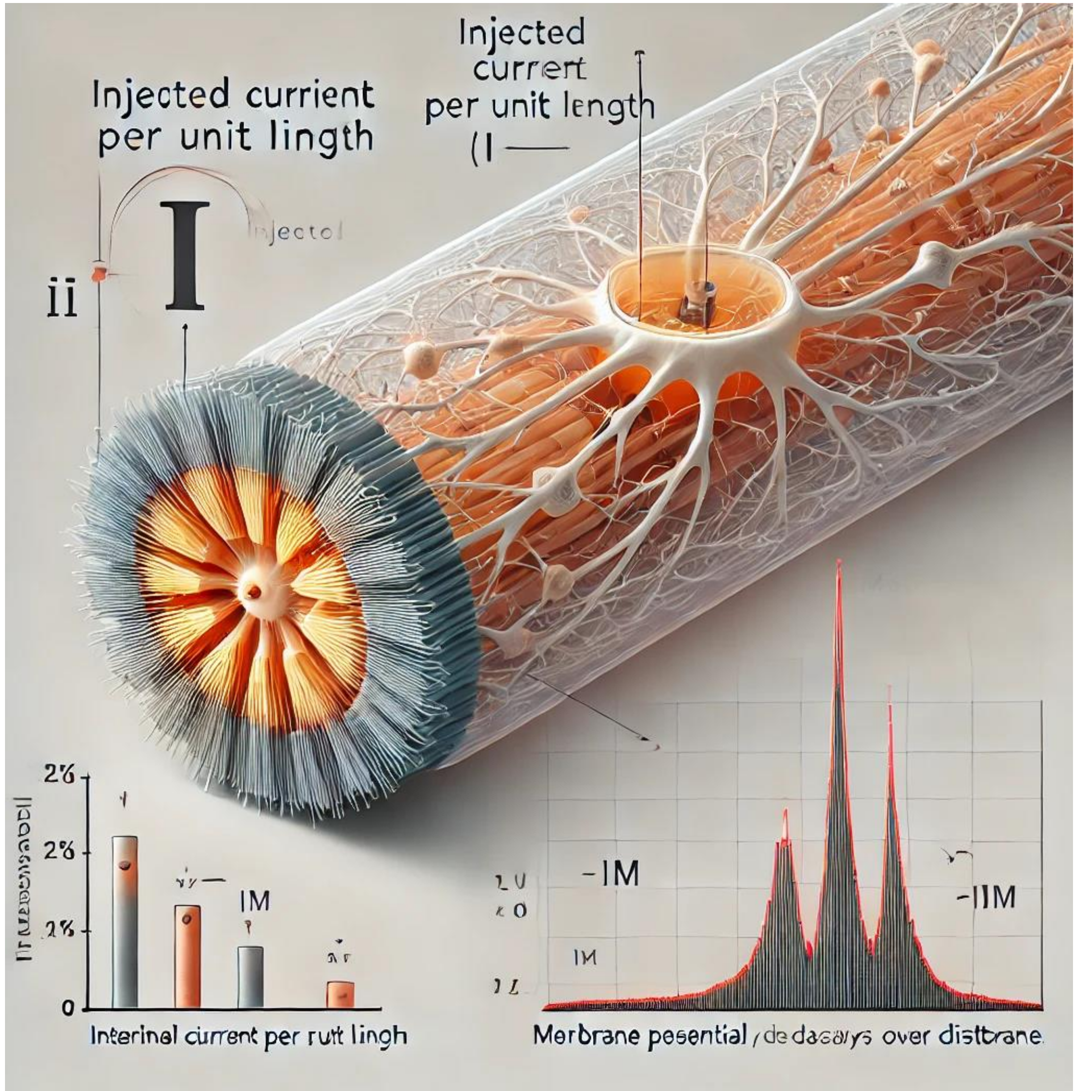
At the site of current injection, the voltage rises, creating a localized region with a higher voltage of $\mathbf{V_0}$ relative to the extracellular space.



The three (3) current pathways

As these charges move and spread out, they have three main paths they can follow:

1. **Axial Current (I)**: The charges can continue to flow through the cytoplasm of the dendrite. This movement is driven by the potential difference between adjacent regions of the cylinder. The axial current **I**, is governed by the axial resistance $\mathbf{R_i}$, which limits how easily charges can move from one region to the next.
2. **Membrane Leak Current**: Some of the charges leak out across the membrane through ion channels. This forms a **leak current** across the membrane, driven by the difference between the membrane potential and the equilibrium potential **E**. The membrane resistance $\mathbf{R_m}$ controls how much current can leak out at any given point along the membrane.
3. **Membrane Capacitive Current:** Charges can also be temporarily stored by the membrane as they accumulate on either side of the membrane. This is modeled by the membrane capacitance $\mathbf{C_m}$. The membrane capacitance affects how quickly the voltage at a particular point can change, as the membrane takes time to accumulate or release change.



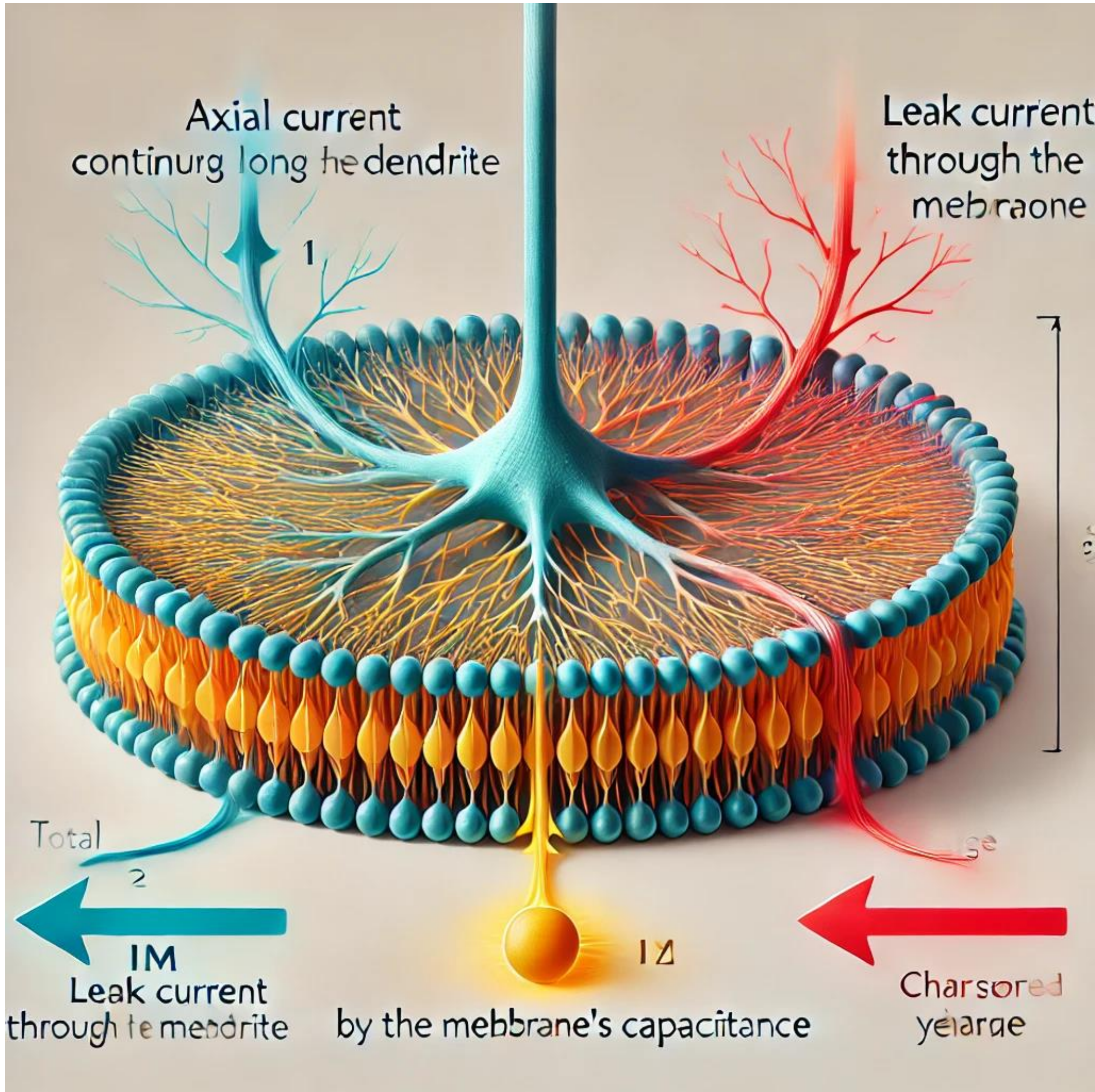
The total membrane current (I_m)

These latter two components – the leak current and the capacitive current – combine to form the **total membrane current (I_m),** which describes the total flow of charge across the membrane at any point.

As charges flow through the cytoplasm they are continually faced with the same options:

1. **Continue flowing axially**
2. **Leak out through the membrane**
3. **Be stored by the membrane's capacitance**

Over time, more and more charge leaks out, which causes the membrane potential to decay back towards the resting potential.

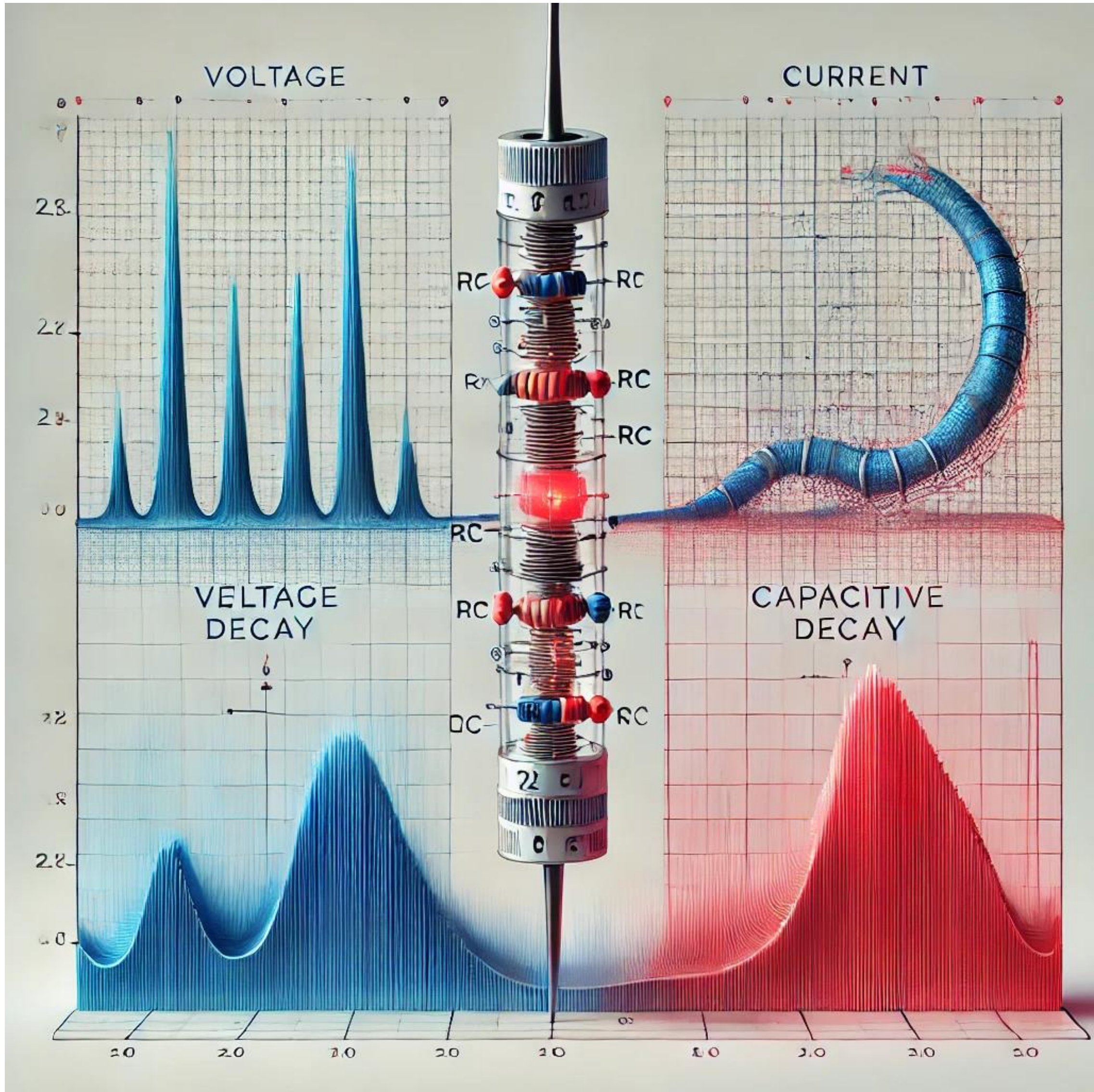


The voltage decay

This decay of voltage happens in two ways:

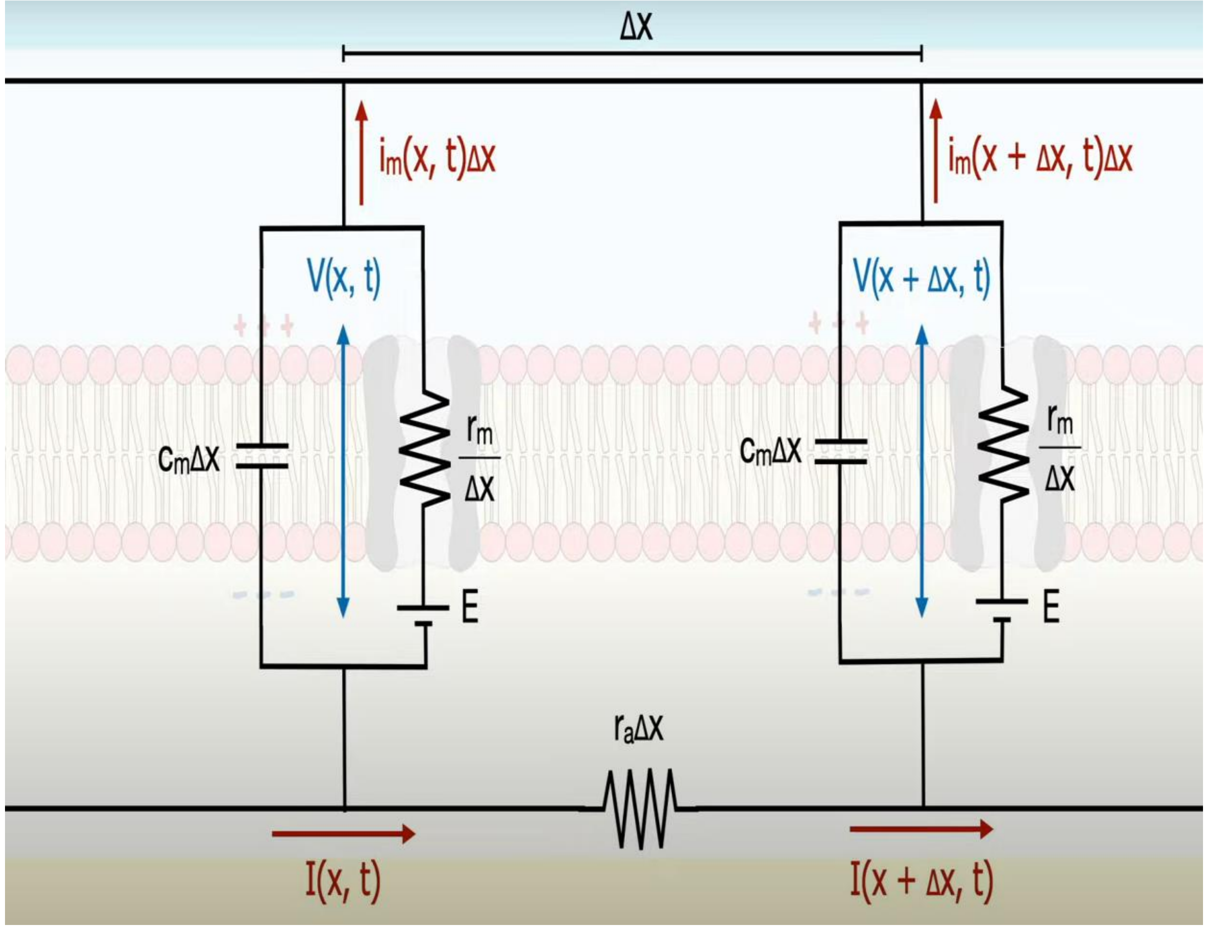
1. **Over time**: As charges leak out or are stored by the membrane capacitance, the voltage at a given point decreases with time.
2. **Over distance**: As the charges move farther from the point of injection, the voltage also decreases, due to both the axial resistance and the continual leakage of current across the membrane.

- ❑ Both the current and voltage diminish as functions of time and distance.
- ❑ The further you move away from the site of current injection, the smaller the voltage becomes.
- ❑ It eventually returns to the resting potential.
- ❑ The current flowing along the dendrite progressively decreases due to membrane leakage.



Circuit Model Explanation

- Let’s assume the left circuit represents a small segment of a dendrite at position **x**, with the membrane potential across the membrane denoted as **V(x, t)**.
- The right circuit represents an adjacent segment, located a distance **Δx** away from the left segment, with the membrane potential at that position denoted as **V(x+Δx, t)**.



Key Circuit Components

1. **Membrane Potential V(x, t)**:
   - The voltage across the membrane at position **x** and time **t**.
   - It is influenced by the axial current, membrane resistance, membrane capacitance and the equilibrium potential **E**.
2. **Axial Resistance $r_a\Delta x$**:
   - This resistance represents the difficulty for the current to flow through the cytoplasm along the length of the dendrite.
   - It connects adjacent segments and limits the flow of current between them.
   - The total axial resistance increases with the segment length **Δx** where **r_a** is the specific axial resistance per unit length.
3. **Membrane Capacitance $C_m\Delta x$**:
   - The membrane capacitance allows charge to be stored on either side of the membrane, influencing how quickly the membrane potential can change.
   - Like axial resistance, it is proportional to the length of the segment **Δx**.
4. **Membrane Resistance $r_m\Delta x$**:
   - This represents the leakiness of the membrane, controlling how much current leaks out across the membrane.
   - It is also proportional to the length of the segment **Δx**.
5. **Equilibrium (or reversal) Potential E:**
   - It acts like a battery that determines the direction and magnitude of current flow through the membrane.
   - The difference between the membrane potential **V(x, t)** and the equilibrium potential **E**, drives the membrane current.

Circuit Currents

1. **Axial Current I(x, t)**:
   - This is the current flowing longitudinally through the cytoplasm, from the left segment to the right.
   - The current depends on the potential difference between adjacent segments, i.e. between **V(x, t)** and **V(x+ Δx, t)**, and is influenced by the axial resistance $r_a\Delta x$.
2. **Membrane Current I_m(x, t)**:
   - This represents the total current flowing across the membrane in a given segment.
   - The membrane current has two components:
     A. **Leak Current**: Flow of ions through the membrane channels, driven by the difference between **V(x, t)** and **E**, and controlled by the membrane resistance $r_m\Delta x$.
     B. **Capacitive Current**: Current due to the charging and discharging of the membrane capacitance $C_m\Delta x$, which influences how quickly the membrane potential changes.
3. **Current Injection**:
   - The injected current in this model is per unit length of the dendrite.
   - This means that when a current is injected into a small segment of the dendrite, the amount of current is proportional to the length of the segment **Δx.**
   - The membrane potential at the injection site will be **V(x, t)**
   - It will then spread and decay as the current flows axially and leaks across the membrane.

Key Concepts (3): The cable equation

- It is the central result of cable theory.
- This is a partial differential equation (PDE) that describes the spatial and temporal distribution of membrane potential along a cylindrical neuron.

$$\frac{\partial V(x,t)}{\partial t} = \frac{1}{R_m C_m}\left(\frac{\partial^2 V(x,t)}{\partial x^2}\right) - \frac{V(x,t)}{R_m C_m}$$

Where:

- **V(x,t)** is the membrane potential at position x and time t
- $\mathbf{R_m}$ is the membrane resistance
- $\mathbf{C_m}$ is the membrane capacitance

Step 1: Axial Current Flow I(x, t)

- Consider a small segment of the dendrite of length **Δx** and axial resistance **r_aΔx**.
- The axial current flowing through the cytoplasm from position **x** to position **x+Δx** is denoted **I(x,t)**.
- The current flowing at position x is related to the change in membrane potential along the dendrite:
$$I(x,t) = -\frac{V(x+\Delta x,t) - V(x,t)}{r_a \Delta x}$$
- This equation follows from Ohm's law, where **r_a** is the axial resistance per unit length.
- As **Δx → 0,** this becomes
$$I(x,t) = -\frac{\partial V(x,t)}{\partial x}\frac{1}{r_a}$$
- The negative sign indicates that current flows from high to low potential.

Step 2: Conservation of Current

- The current that enters a small segment of the dendrite at position **x** must equal the current that leaves at position **x+Δx** plus any current that leaks across the membrane**.**
- By the principle of conservation of charge, the difference in axial between **x** and **x+Δx** must be equal to the membrane current **I_m(x,t):**

$$\frac{\partial I(x,t)}{\partial x}\Delta x = I_m(x,t)\Delta x$$

- Simplifying this, we get: $\frac{\partial I(x,t)}{\partial x} = I_m(x,t)$

- This means that the membrane current at position x is determined by the rate of change of axial current at that position.

Step 3: Membrane Current $I_m(x,t)$

- The total membrane current **I_m(x, t)** consists of two components:
  1. **Leak current** through the membrane channels, driven by the difference between the membrane potential **V(x,t)** and the equilibrium potential **E**, controlled by the membrane resistance.
  2. **Capacitive current** due to the charging or discharging of the membrane capacitance.

- The **leak current** is given by: $I_{leak}(x,t) = \frac{V(x,t) - E}{r_m \Delta x}$

  Where **r_m** is the membrane resistance per unit length, and **E** is the equilibrium potential.

- The **capacitive current** is given by: $I_{cap}(x,t) = C_m \frac{\partial V(x,t)}{\partial t}$

  Where **C_m** is the membrane capacitance per unit length.

- Thus, the **total membrane current I_m(x, t)** is the sum of these two components:

$$I_m(x,t) = C_m \frac{\partial V(x,t)}{\partial t} + \frac{V(x,t) - E}{r_m}$$

Step 4: Combining Axial and Membrane Currents

- We now combine the expressions for the **axial** and **membrane** current.
- From step 2, we know: $$\frac{\partial I(x,t)}{\partial x} = I_m(x,t)$$
- Substituting the expression for **I(x, t)** from step 1: $$-\frac{\partial}{\partial x}\left(\frac{1}{r_a}\frac{\partial V(x,t)}{\partial x}\right) = C_m\frac{\partial V(x,t)}{\partial t} + \frac{V(x,t)-E}{r_m}$$
- Simplifying: $$\frac{1}{r_a}\frac{\partial^2 V(x,t)}{\partial x^2} = C_m\frac{\partial V(x,t)}{\partial t} + \frac{V(x,t)-E}{r_m}$$

Step 5: The Cable Equation

- The **final cable equation** describes the membrane potential as a function of both time and space:

$$\frac{\partial^2 V(x,t)}{\partial x^2} = \lambda^2 \left(\tau \frac{\partial V(x,t)}{\partial t} + V(x,t) - E\right)$$

Where:

- $\lambda = \sqrt{\frac{r_m}{r_a}}$ is the **length constant**, which determines how far the voltage travels before decaying significantly.
- **$\tau = r_m C_m$** is the **time constant**, which determines how quickly the membrane potential responds to changes in current.

- This is the cable equation, a partial differential equation that describes how the membrane potential changes over time and space in a passive neuron, like a dendrite or an axon.

Key Concepts (4): Cable Theory Constants

1. **Length Constant (λ):**
   - This is a measure of how far the voltage signal travels before attenuating significantly.
   - It depends on the membrane and axial resistances.
   - A larger length constant means the signal travels farther before decaying.
2. **Time constant (τ):**
   - It is a measure of how quickly the membrane potential responds to changes in current.
   - It depends on membrane resistance and capacitance.

Interpretation & Key Insights

- The term $\frac{\partial^2 V(x,t)}{\partial x^2}$ describes the **spatial change** in voltage, indicating how the membrane potential varies with position along the dendrite.
- The term $\tau \frac{\partial V(x,t)}{\partial t}$ represents the **temporal change** in voltage, accounting for how the membrane potential evolves over time.
- The term **V(x, t) – E** describes the **leak current** through the membrane, which drives the potential back toward the equilibrium potential.

- **Spatial Decay**: The voltage attenuates as it travels along the dendrite, and this attenuation is governed by the length constant λ. A larger λ means the signal can travel farther before decaying.
- **Temporal Decay**: The membrane potential relaxes back to its resting value over time, governed by the time constant τ. A larger τ means the potential takes longer to decay.

Key Steps for Solving the Cable Equation

1. **Discretize the Dendrite**: Break the dendrite into small segments of length **Δx** and calculate the voltage **V(x, t)** at each segment over time.
2. **Finite Difference Method**: Use the finite difference method to approximate the spatial and temporal derivatives in the cable equation.
3. **Numerical Integration**: Use an explicit time-stepping method (e.g. Euler) to numerically integrate the equation over time.
4. For simplicity we assume the equilibrium potential **E=0**. The equation becomes: $\frac{\partial^2 V(x,t)}{\partial x^2} = \lambda^2 \tau \frac{\partial V(x,t)}{\partial t} + \lambda^2 V(x,t)$
5. We discretize both space and time:
   - **Space**: Discretize **x** into small intervals **Δx**.
   - **Time**: Discretize **time** into small steps **Δt**.
6. Using the finite difference approximation for the spatial derivative and a forward Euler method for time integration:
   - The second derivative with respect to space: $\frac{\partial^2 V(x,t)}{\partial x^2} \approx \frac{V(x+\Delta x,t) - 2V(x,t) + V(x-\Delta x,t)}{(\Delta x)^2}$
   - The time derivative: $\frac{\partial V(x,t)}{\partial t} \approx \frac{V(x,t+\Delta t) - V(x,t)}{\Delta t}$

Matlab Simulation: Parameters

1. Length of the dendrite (**L**)
2. Number of spatial points along the dendrite (**N_x**)
3. Spatial step size (**dx**)
4. Total simulation time (**T**)
5. Time step size (**dt**)
6. The length constant of the cable equation (**λ**)
7. The time constant of the cable equation (**τ**)

```
% Parameters
L = 1;                  % Length of the dendrite (in space units)
Nx = 100;               % Number of spatial points
dx = L / (Nx - 1);      % Spatial step size
T = 1;                  % Total simulation time (in time units)
dt = 0.0001;            % Reduced time step size for stability
Nt = T / dt;            % Number of time steps

% Cable equation parameters
lambda = 0.1;           % Length constant (in space units)
tau = 0.05;             % Time constant (in time units)
```

Matlab Simulation: Stability Condition

1. For stability, the ratio of the time step **Δt** to the spatial step **Δx** must satisfy a condition similar to the **Courant** condition for the diffusion equation.
2. Specifically, you need: $$\frac{\lambda^2 \Delta t}{\Delta x^2} < \frac{1}{2}$$
3. This ensures that the propagation of the voltage is stable over time.
4. If this condition is not satisfied, the solution can "**blow up**".
5. Decrease the time step size **Δt** to ensure stability.
6. Ensure that the length constant **λ** and the time constant **τ** are within realistic biological ranges.

Parameters Explanation

1. **Length of the dendrite (L = 3):** This defines the **physical length** of the dendrite you are simulating. A value of 3 can be interpreted as 3 arbitrary length units (e.g. micrometers). This length is reasonable for visualizing voltage propagation along a segment of a dendrite.
2. **Number of spatial points (N_x = 150):** This is the **spatial resolution** of your simulation. The dendrite is divided into 150 points along its length, meaning each point corresponds to a segment of the dendrite where the voltage is calculated.
3. **Spatial Step Size (dx):** The **distance between two adjacent spatial points** along the dendrite, calculated as: This provides the physical size of each segment of the dendrite in your simulation. It ensures the dendrite is divided into equal intervals for the numerical calculation. $$dx = \frac{L}{Nx - 1}$$
4. **Total Simulation Time (T=1):** The **duration** of the simulation. You are simulating the voltage propagation along the dendrite for 1 time unit (this could represent milliseconds or seconds in a biological context).
5. **Time Step dt = 0.00005**: This is the time resolution of the simulation. The small value of dt ensures numerical stability when solving the cable equation over time. This value ensures smooth and accurate voltage propagation without instability or numerical artifacts.
6. **Number of Time Steps N_t**: The number of time steps over which the simulation will run. Calculated as Nt = T / dt, this ensures that the simulation covers the total time specified.

Cable Equation Parameters

- **Length Constant (λ = 0.2)**: It is crucial in determining how **far** the voltage spreads along the dendrite before decaying. In the biological context, the length constant is defined as: $\lambda = \sqrt{\frac{r_m}{r_a}}$, where $\mathbf{r_m}$ is the membrane resistance and $\mathbf{r_a}$ is the axial resistance. A higher value of **λ** means the voltage spreads further before it decays, while a lower value indicates more rapid decay along the length of the dendrite. In this case, **λ = 0.2**, allows moderate propagation and decay.
- **Time Constant (τ = 0.8):** It describes how **quickly** the membrane potential returns to its resting state after a change. In biological terms, it is defined as $\boldsymbol{\tau = r_m \times C_m}$, where $\mathbf{C_m}$ is the membrane capacitance. A **larger** time constant indicates that the voltage **decays more slowly** over time. The specific value (**τ = 0.8**) suggests that the voltage will decay slowly, maintaining the propagation over time.

Initial Conditions: Voltage Spikes:

- **Voltage Array (V):** The array *V* represents the **voltage at each point along the dendrite** at any given time. It is initialized with zeros, meaning the dendrite starts in a resting state (no voltage) everywhere.
- **Spike Definition**:
  - You are defining a **voltage spike** at the middle of the dendrite (position: **round(Nx/2)**) with an **amplitude** of 2. This simulates an initial disturbance (injection of current or synaptic input) at the midpoint of the dendrite.
  - **Additional** possible spikes are currently commented out in the code. If activated, they would place **additional voltage spikes at different positions** (one-third and one-fifth along the dendrite) with different amplitudes.
- **Matrix for storing results (V_history)**: This matrix stores the voltage at each spatial point at every time step of the simulation. It will later be used to visualize how the **voltage propagates and decays over time**.

```
V(round(Nx/2)) = 2;  % First spike in the middle with amplitude 2
```

Numerical Solution Using Finite Difference Method

- This loop solves the equation using the finite difference method.
- At each time step, the new voltage value at each spatial point is calculated based on the values of the neighboring points and the parameters **λ** and **τ**.
- The following term updates the voltage at point x based on the **difference in voltage** between neighboring points (spatial propagation) and the **leakage of voltage** over time (temporal decay):

```
% Simulation loop
for t = 1:Nt
    V_new = V;  % To store the new values of V
    for x = 2:Nx-1
        % Update the voltage using the cable equation
        V_new(x) = V(x) + dt * (lambda^2 / dx^2) * ...
                   (V(x+1) - 2*V(x) + V(x-1)) - dt/tau * V(x);
    end

    % Update V and store the result for this time step
    V = V_new;
    V_history(:, t) = V;
end
```

```
% Update the voltage using the cable equation
V_new(x) = V(x) + dt * (lambda^2 / dx^2) * ...
           (V(x+1) - 2*V(x) + V(x-1)) - dt/tau * V(x);
```

Voltage Propagation Plot

- This code generates a 2D heatmap where the **x-axis represents time**, and the **y-axis represents position** along the dendrite.
- The **color intensity** represents the voltage at each position and time.
- The ‘**caxis([0 0.2])**’ sets the colour limits, enhancing the contrast to better visualize the voltage changes.

```
figure;
imagesc(0:dt:T, 0:dx:L, V_history);
xlabel('Time (t)');
ylabel('Position (x)');
title('Voltage propagation with two spikes');
colorbar;
caxis([0 0.2]);  % Adjust the color limits to improve contrast
```