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# Modelling of biological conductors
# - The cable equation -

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# Introduction

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- The intention is to describe how biological conductors behave in terms of more familiar electrical conductors.
- Models used to describe this behaviour
  - Core-conductor model
  - Cable model

  } nerve cells
- Identify limitations of these models and lay a foundation to the more comprehensive model proposed by Hodgkin and Huxley.

# Synapses

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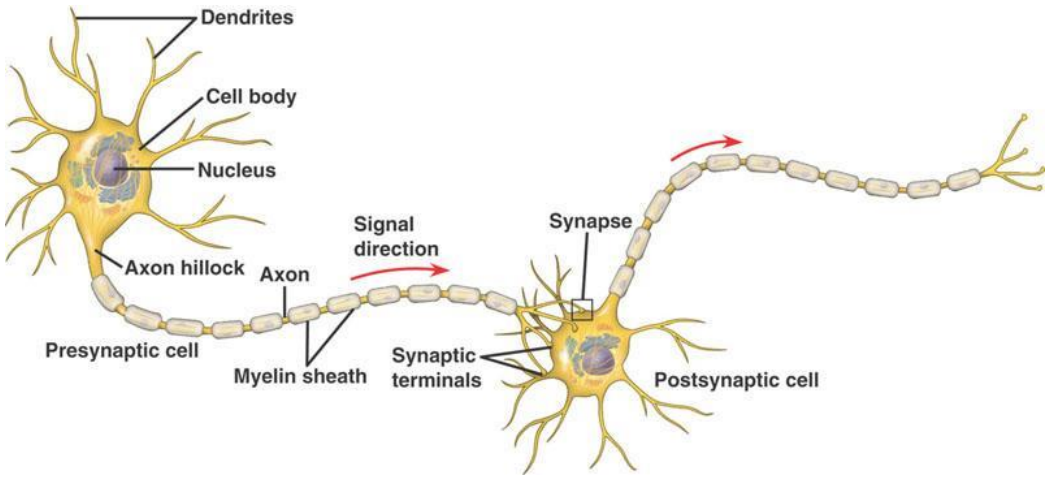
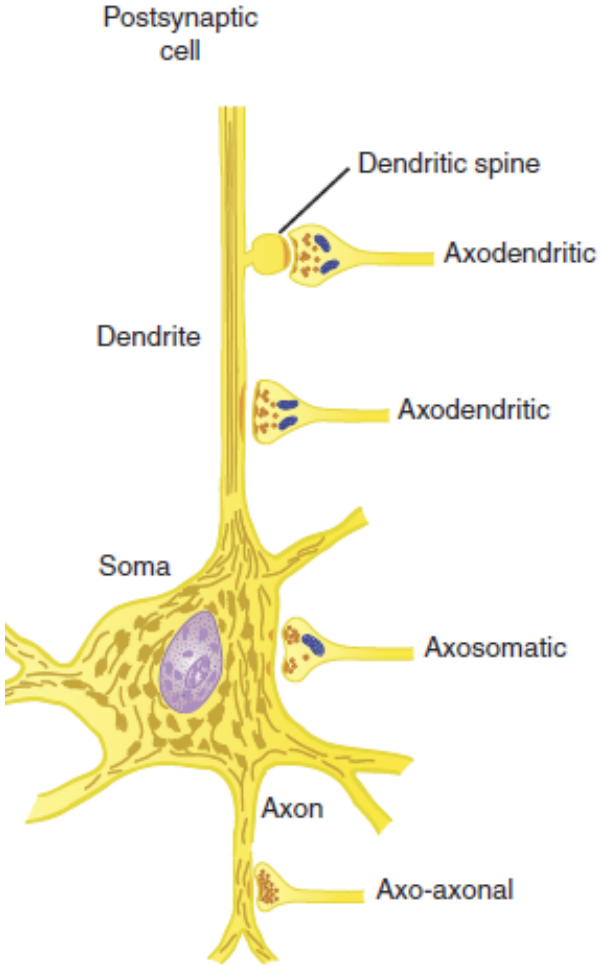
- Neurons communicate through the synaptic cleft by inducing electrical/ionic activity in the adjacent neuron.
  - Post synaptic potentials generate as a result of the communication between neurons (cell signalling).



# Post synaptic potentials (PSP)

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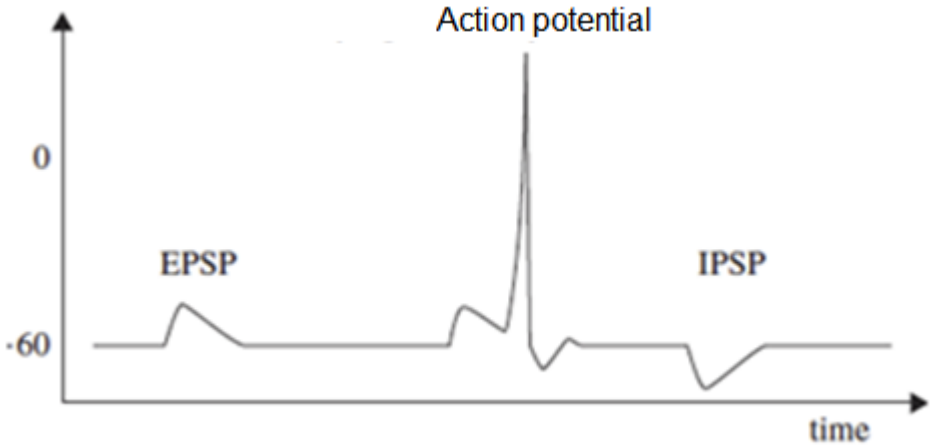
- Post synaptic potentials alter the probability of eliciting an action potential within a neuron at the axon hillock.
- If the post synaptic potential depolarizes the neuron → Excitatory post synaptic potential (EPSP)
  - Increase the probability of an AP
- If the post synaptic potential hyperpolarizes the neuron → Inhibitory post synaptic potential (IPSP)
  - Reduce the probability of an AP
- Amplitude of a single PSP ≈ 0.5-1 mV
- EPSP or IPSP depends on the neurotransmitter released and the type of postsynaptic receptor activated.



# Post synaptic potentials (PSP)

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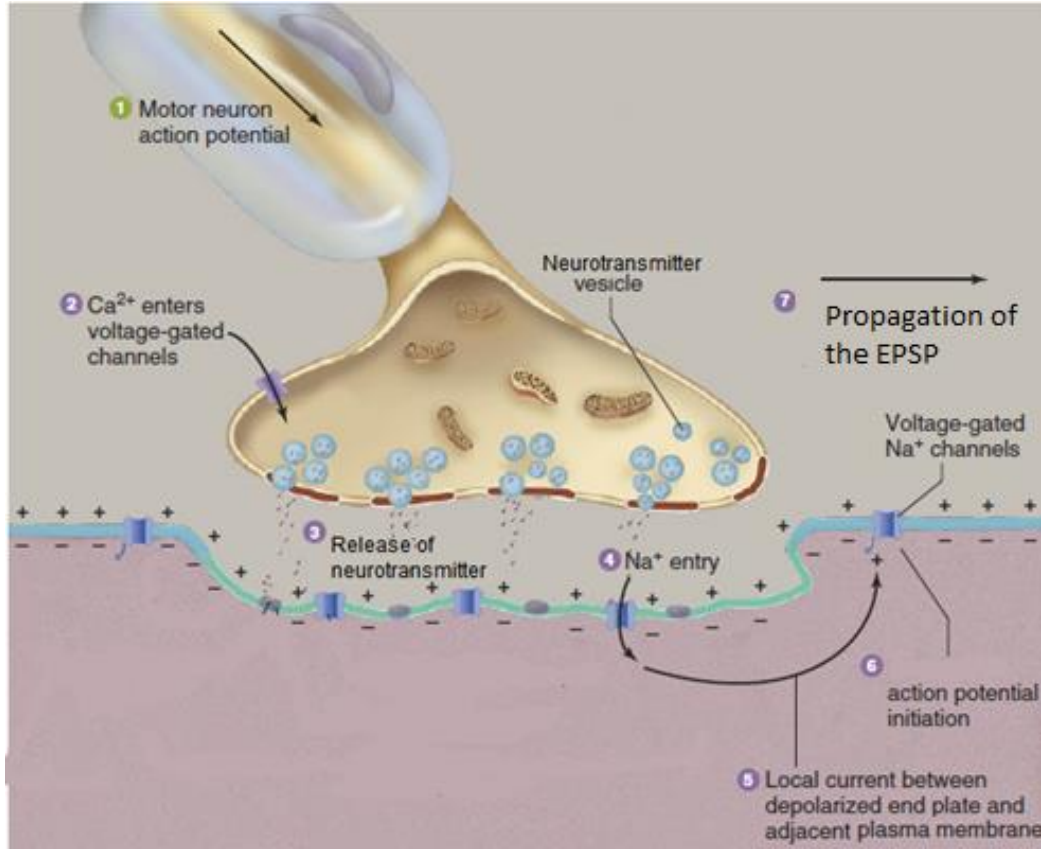
- The AP reaches the presynaptic terminal
  → Initiates the opening of voltage-gated $Ca^{2+}$ channels
- Rapid influx of $Ca^{2+}$ opens vesicles and release the neurotransmitter into the synaptic cleft.
- Depending on the type of neurotransmitter released, an EPSP or an IPSP is initiated in the post synaptic neuron.
  - Excitatory → influx of $Na^{+}$
  - Inhibitory → influx of $Cl^{-}$ and efflux of $K^{+}$

Electron microscope photo of a synaptic terminal.



# Neurotransmitters

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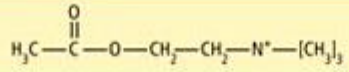
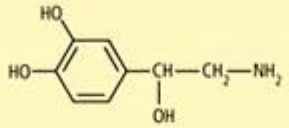
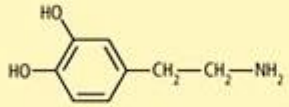
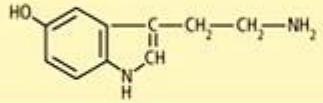
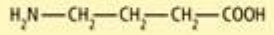
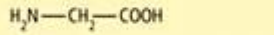
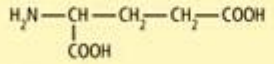
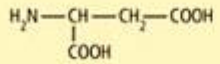
- Information processing and storage occur within the synaptic cleft as a result of the type of neurotransmitter released.
- Types of neurotransmitters

| Neurotransmitter | Structure | Functional Class |
|---|---|---|
| **Acetylcholine** |  | Excitatory to vertebrate skeletal muscles; excitatory or inhibitory at other sites |
| **Biogenic Amines** | | |
| Norepinephrine |  | Excitatory or inhibitory |
| Dopamine |  | Generally excitatory; may be inhibitory at some sites |
| Serotonin |  | Generally inhibitory |
| **Amino Acids** | | |
| GABA (gamma aminobutyric acid) |  | Inhibitory |
| Glycine |  | Inhibitory |
| Glutamate |  | Excitatory |
| Aspartate |  | Excitatory |
| **Neuropeptides** (a very diverse group, only two of which are shown) | | |
| Substance P | Arg—Pro—Lys—Pro—Gln—Gln—Phe—Phe—Gly—Leu—Met | Excitatory |
| Met-enkephalin (an endorphin) | Tyr—Gly—Gly—Phe—Met | Generally inhibitory |

Acetylcholine: pain, memory, chemosensory (smell and taste) Monoamines

Norepinephrine: modulation of sleep and wakefulness

Dopamine: body movements

Serotonin: modulation of sleep and wakefulness

# Spatial summation of EPSP and reaching the threshold

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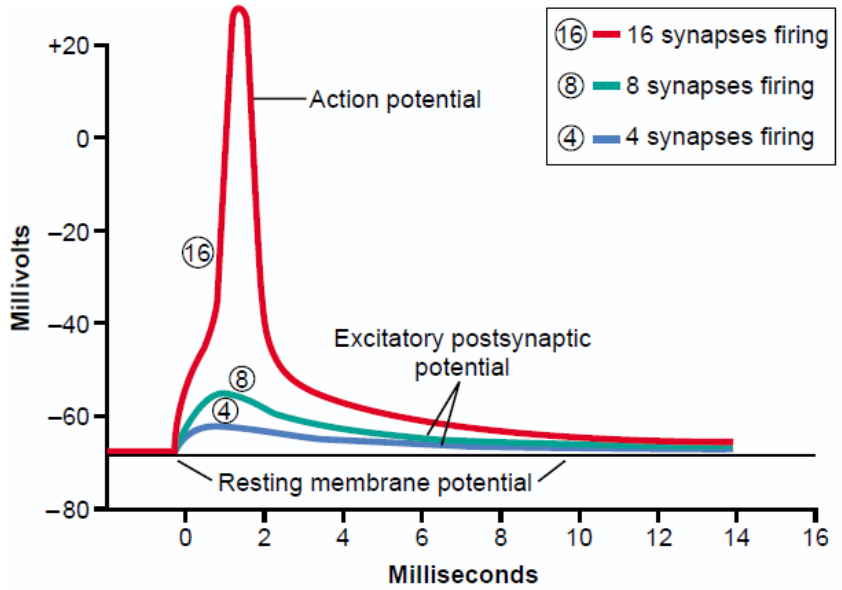
- A single EPSP can never initiate an action potential
  - Single EPSP ➔ 0.5-1 mV
  - Duration
    - 1-2 ms rising time while the $Na^+$ gates are open
    - 15 ms decay time to leak excess $Na^+$ through the pump
- The highly conductive soma summate all the neuronal excitations that occur in the soma and dendrites
- When the total EPSP becomes large enough
  - Threshold for firing is reached
  - An action potential will generate at the axon hillock



# Core conductor model

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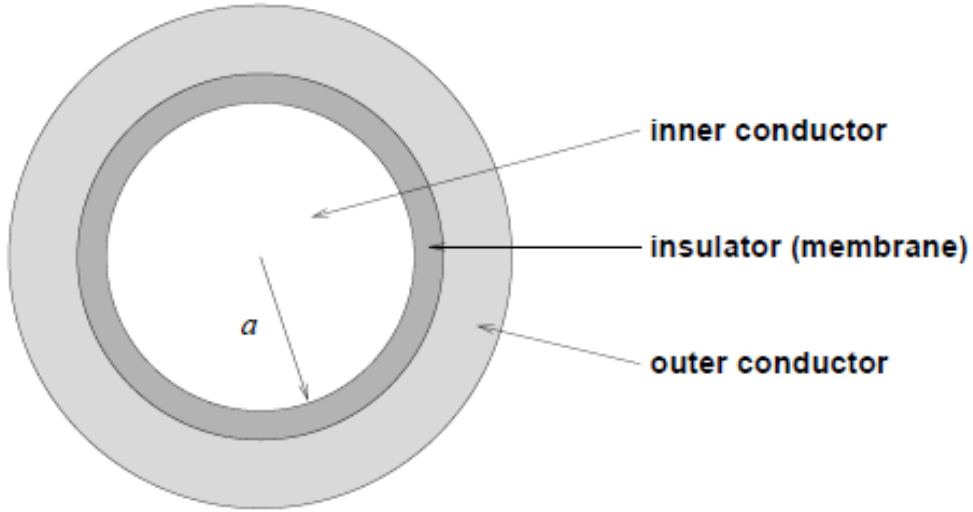
- First derived by William Thomson (1824-1907), later Lord Kelvin, during his involvement with the laying, design and analysis of the first Trans-Atlantic telegraph cables beginning in 1854.
- The cable equation is based on the simple notion of transverse current leakage between an inner and outer conductor due to an imperfect insulator when there is a longitudinal flow of current within the inner conductor.



# Cylindrical conductor

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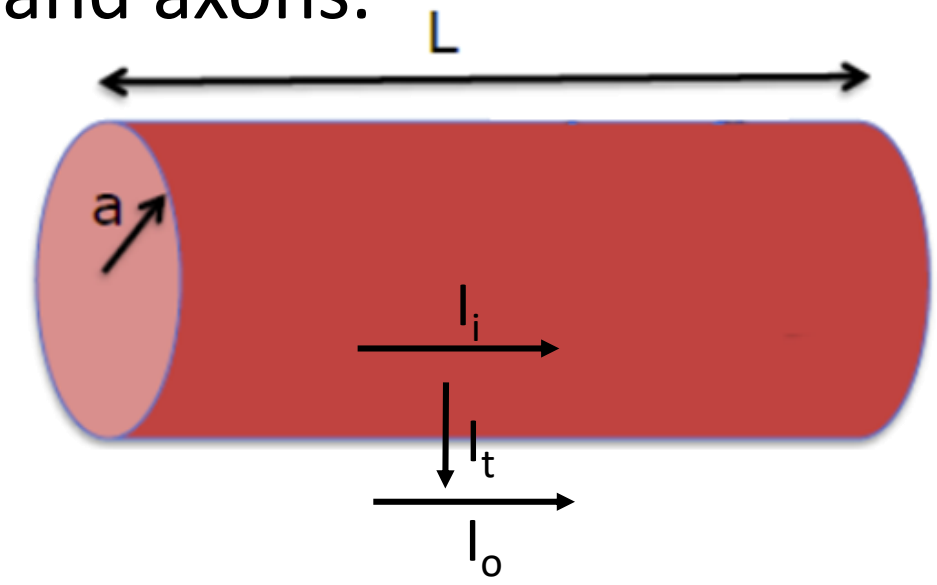
- Appropriate to describe long cylindrical neuronal dendrites and axons.




$I_o$ = longitudinal current in the outer conductor
$I_i$ = longitudinal current in the inner conductor
$I_t$ = trans-membrane current
$I_t/L = K$ = trans-membrane current per unit length
a = radius
L = length

# Assumptions

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- The cell membrane is a cylindrical boundary of finite thickness separating the intra-cellular fluid (ICF) and the extra-cellular fluid (ECF).
- The ECF and ICF are homogeneous and Ohmic.
- All electrical variables are independent of $\hat{\phi}$.
- Currents in the inner and outer conductors will flow only in the longitudinal ($\hat{z}$) direction.
- Trans-membrane current flows only in the radial ($\hat{r}$) direction.
- Variation in the potential occurs radially.

# Derivation of the core conductor model


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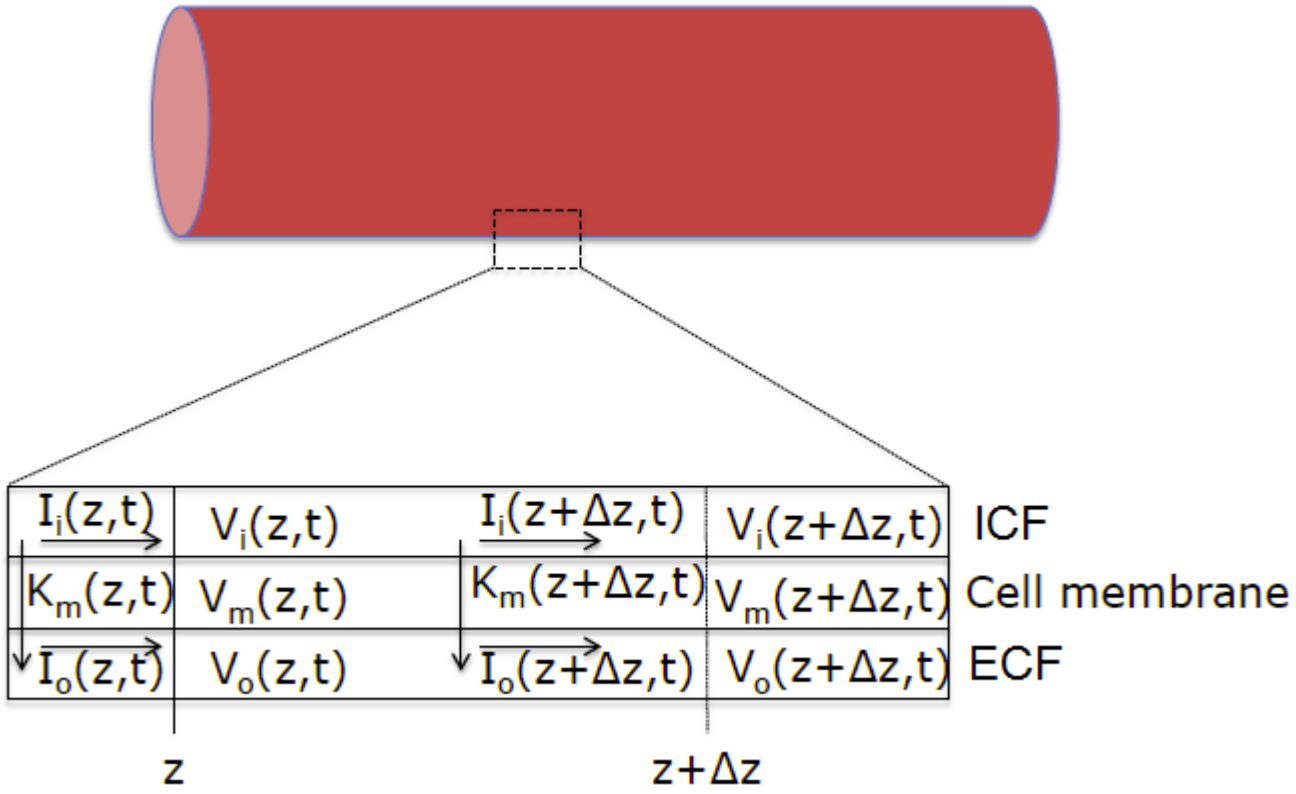


- Consider an infinitesimal segment along the $\hat{z}$ direction $\Delta z$

# Definitions

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$I_i$ = current inside the conductor/cell

$I_o$ = current outside the conductor/cell

$K_m$ = membrane current per unit length

$K_e$ = external current applied (e.g. by electrode)

$r_o$ = resistance per unit length outer conductor

$r_i$ = resistance per unit length inner conductor

$a$ = radius of the conductor/cell

# Equivalent circuit

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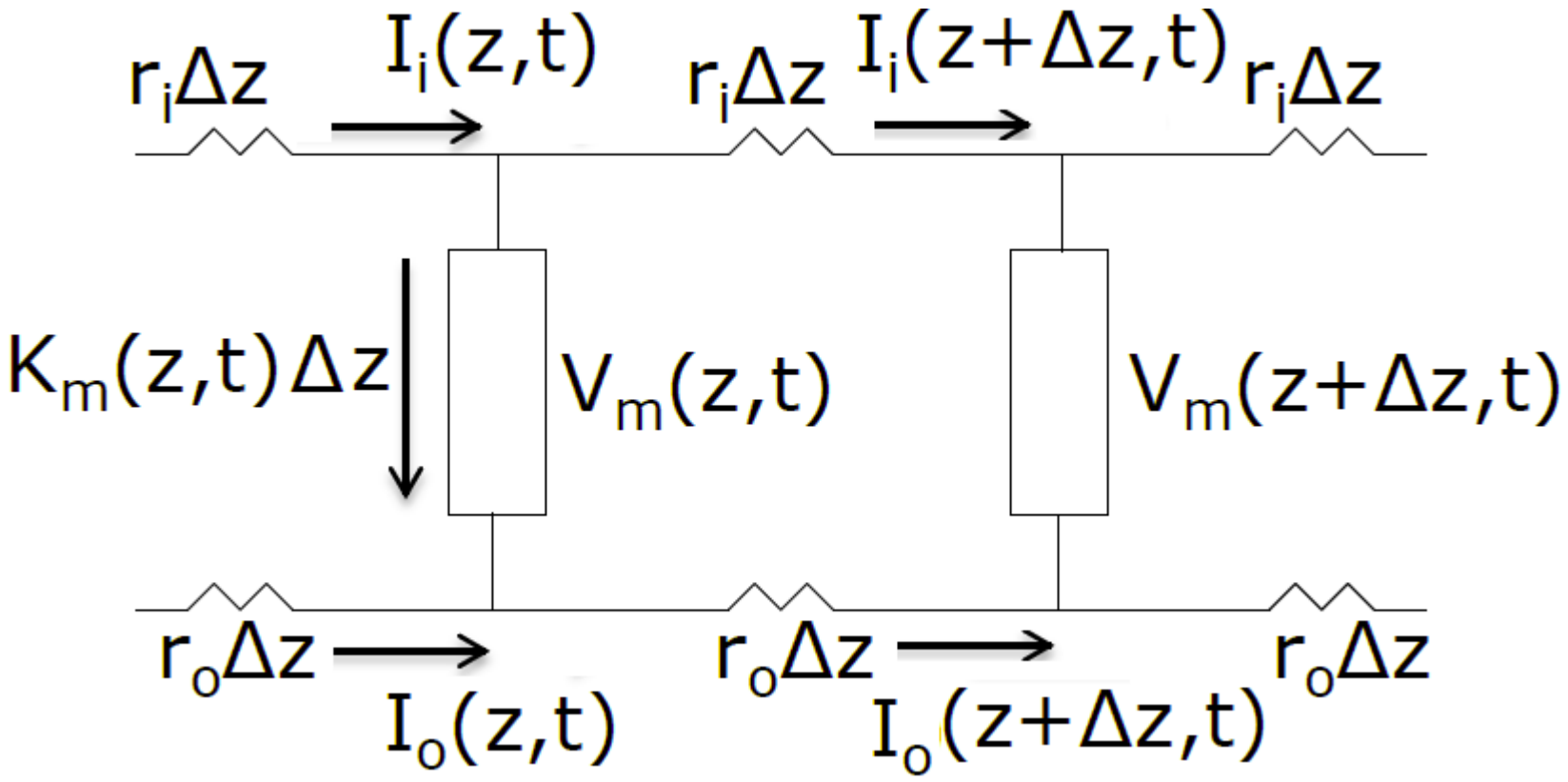


- Consider an infinitesimal segment along the $\hat{z}$ direction $\Delta z$

# Analysing the equivalent circuit


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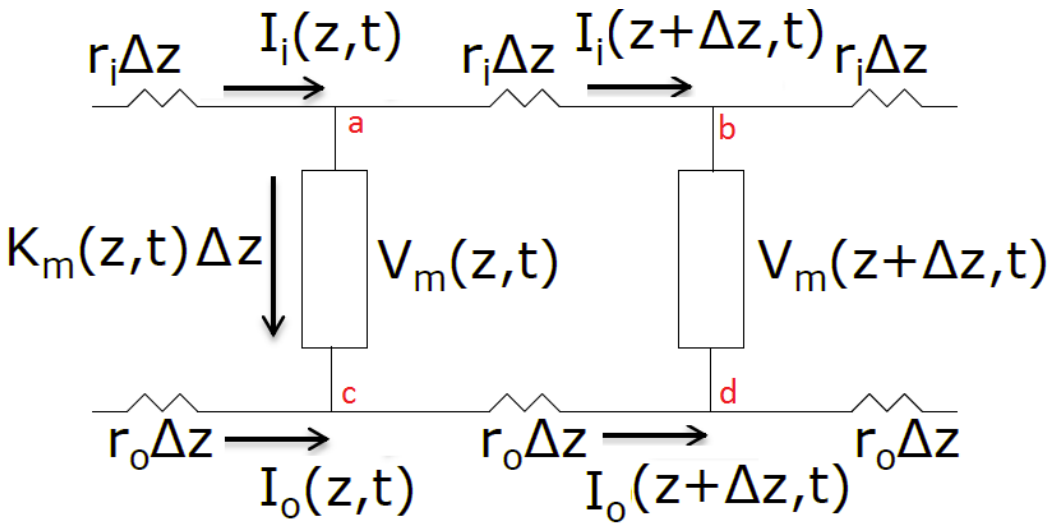


From KCL at node a:

$$I_i(z,t) = I_i(z+\Delta z,t) + K_m(z,t)\Delta z$$

From KCL at node c:

$$I_o(z,t) + K_m(z,t)\Delta z = I_o(z+\Delta z,t) + K_e(z,t)\Delta z$$

# Analysing the equivalent circuit


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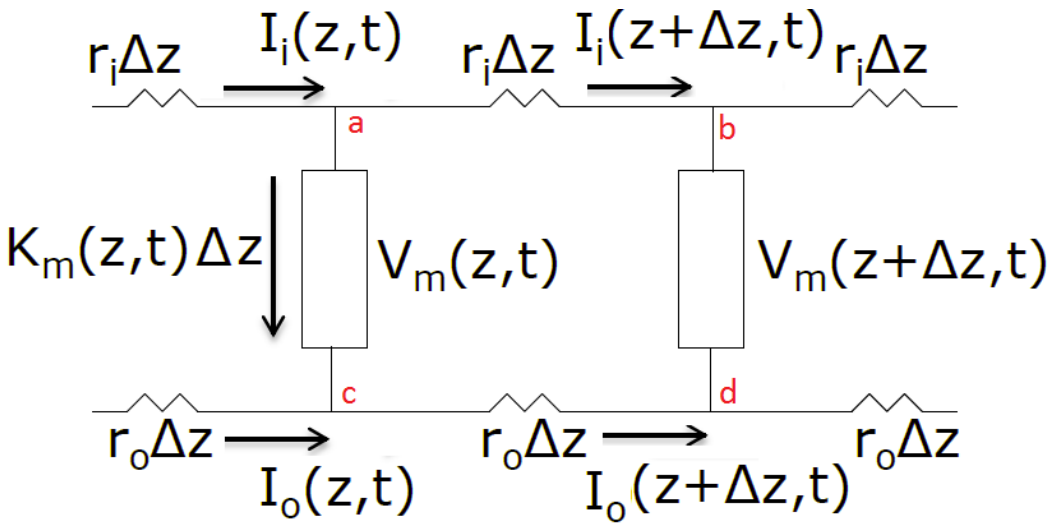


From Ohm's law inside the cell:

$$V_i(z,t) - V_i(z+\Delta z,t) = r_i \Delta z I_i(z+\Delta z,t)$$

From Ohm's law outside the cell:

$$V_o(z,t) - V_o(z+\Delta z,t) = r_o \Delta z I_o(z+\Delta z,t)$$

# Analysing the equivalent circuit

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- Rearranging and dividing by $\Delta z$:

$$\frac{I_i(z+\Delta z,t)-I_i(z,t)}{\Delta z}=-K_m(z,t)$$

$$\frac{I_o(z+\Delta z,t)-I_o(z,t)}{\Delta z}=K_m(z,t)-K_e(z,t)$$

$$\frac{V_i(z+\Delta z,t)-V_i(z,t)}{\Delta z}=-r_i I_i(z+\Delta z,t)$$

$$\frac{V_o(z+\Delta z,t)-V_o(z,t)}{\Delta z}=-r_o I_o(z+\Delta z,t)$$

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- Taking the limit as $\Delta z \to 0$:

$$\frac{\partial I_i(z,t)}{\partial z} = -K_m(z,t) \quad (1)$$

$$\frac{\partial I_o(z,t)}{\partial z} = K_m(z,t) - K_e(z,t) \quad (2)$$

$$\frac{\partial V_i(z,t)}{\partial z} = -r_i I_i(z,t) \quad (3)$$

$$\frac{\partial V_o(z,t)}{\partial z} = -r_o I_o(z,t) \quad (4)$$

# Analysing the equivalent circuit

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- Noting:

$$V_m(z,t) = V_i(z,t) - V_o(z,t)$$

$$\therefore \frac{\partial V_m(z,t)}{\partial z} = \frac{\partial V_i(z,t)}{\partial z} - \frac{\partial V_o(z,t)}{\partial z}$$

- Substituting (3) and (4) yields:

$$\frac{\partial V_m(z,t)}{\partial z} = -r_i I_i(z,t) + r_o I_o(z,t)$$

# Analysing the equivalent circuit

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- Differentiating again w.r.t. z yields:

$$\frac{\partial^2 V_m(z,t)}{\partial z^2} = r_o \frac{\partial I_o(z,t)}{\partial z} - r_i \frac{\partial I_i(z,t)}{\partial z}$$

- Substituting (1) and (2) yields:

$$\frac{\partial^2 V_m(z,t)}{\partial z^2} = (r_o + r_i) K_m(z,t) - r_o K_e(z,t)$$

- Which is the core conductor equation!

# When there's no external stimulating current $K_e$=0

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- With no external current, $K_e = 0$, therefore:

$$\frac{\partial^2 V_m(z,t)}{\partial z^2} = (r_o + r_i) K_m(z,t)$$

$$\therefore K_m(z,t) = \frac{1}{(r_o + r_i)} \frac{\partial^2 V_m(z,t)}{\partial z^2} \qquad (5)$$

- Setting $K_e$=0, and substituting into (2):

$$\frac{\partial I_o(z,t)}{\partial z} = \frac{1}{(r_o + r_i)} \frac{\partial^2 V_m(z,t)}{\partial z^2}$$

  - Integrating:

$$I_o(z,t) \propto \frac{1}{(r_o + r_i)} \frac{\partial V_m(z,t)}{\partial z} \qquad (6)$$

# Observations from APs

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- If an AP propagates at a constant velocity $v$, the space gets dependent on the time.

$$[v] = \frac{z}{t} \quad \rightarrow \quad \partial z = v \partial t$$

- Therefore:

$$\frac{\partial V_m(z,t)}{\partial z} = \frac{1}{v} \frac{\partial V_m(z,t)}{\partial t}$$

- and:

$$\frac{\partial^2 V_m(z,t)}{\partial z^2} = \frac{1}{v^2} \frac{\partial^2 V_m(z,t)}{\partial t^2}$$

# Observations from APs

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- Substituting into (5) and (6):

$$K_m(z,t) = \frac{1}{(r_o + r_i)v^2} \frac{\partial^2 V_m(z,t)}{\partial t^2}$$

- and:

$$I_o(z,t) = \frac{1}{(r_o + r_i)v} \frac{\partial V_m(z,t)}{\partial t}$$

- We have shift to the derivative w.r.t. time from the derivate w.r.t. space.
- Easy for inspectional conclusions.

# Observations from APs (time variations)

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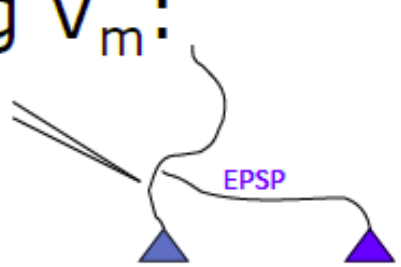
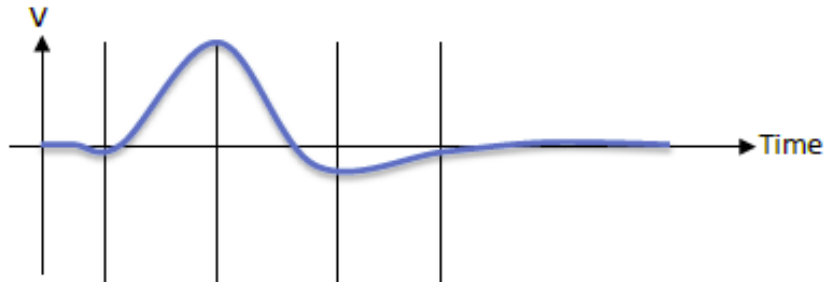
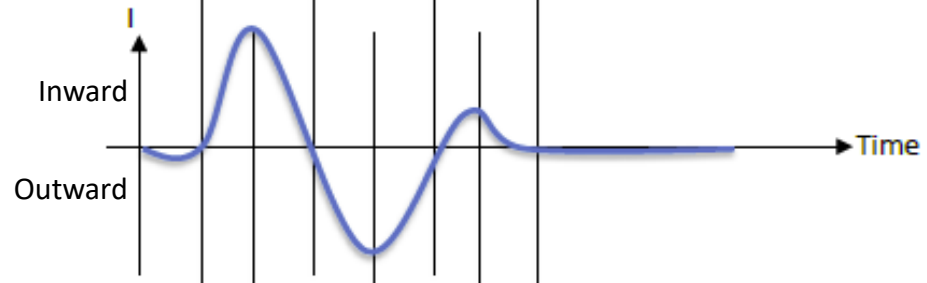
- Plotting $V_m$:

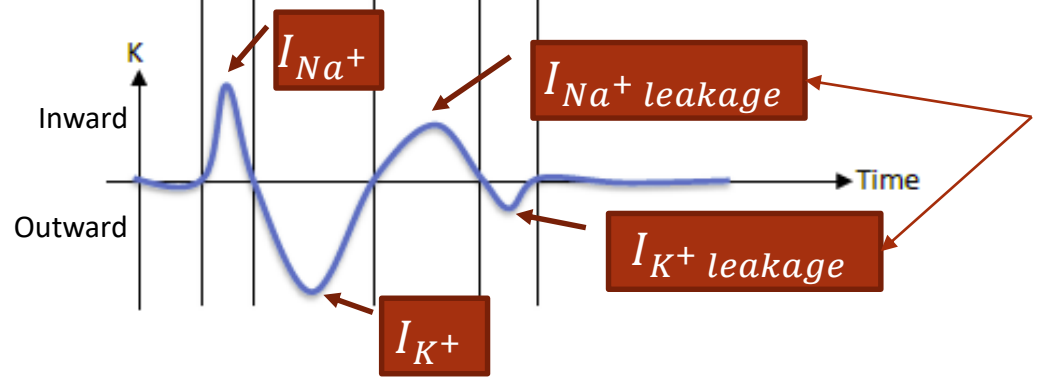



- Plotting $I_o$:




- Plotting $K_m$:




Returning to the resting state

# Observations from APs (space variations)

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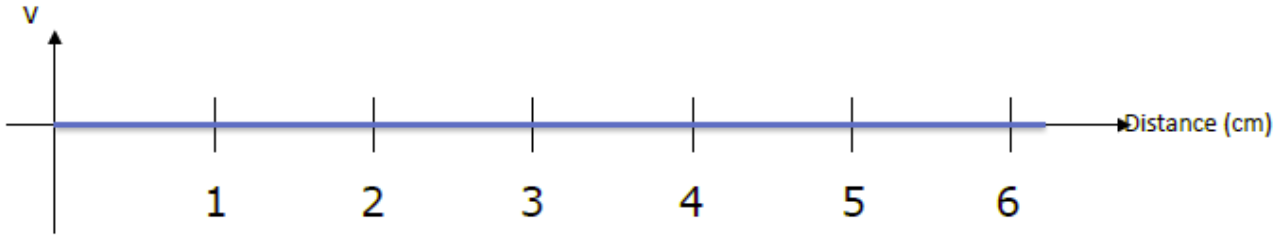
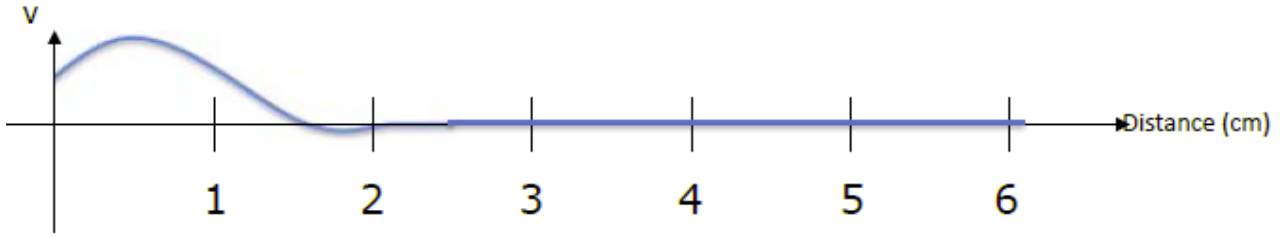
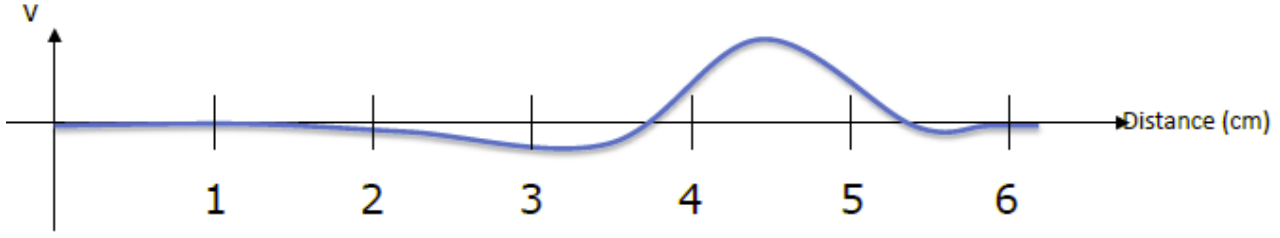
- Spatial variation of an action potential




Plotted at time t = 0 ms




Plotted at time t = 1 ms




Plotted at time t = 2.5 ms

# Core-conductor equation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$$\frac{\partial^2 V_m(z,t)}{\partial z^2} = (r_o + r_i) K_m(z,t) - r_o K_e(z,t)$$

- Explains the relationship between the membrane voltage and the membrane current (also the effect of an external current).
- However, $V_m$ and $K_m$ are unknowns.
- Need another equation which involves these unknowns.
- Transmembrane impedance (which we represented as a black box) can be used for this.

# Behaviour of $V_m$

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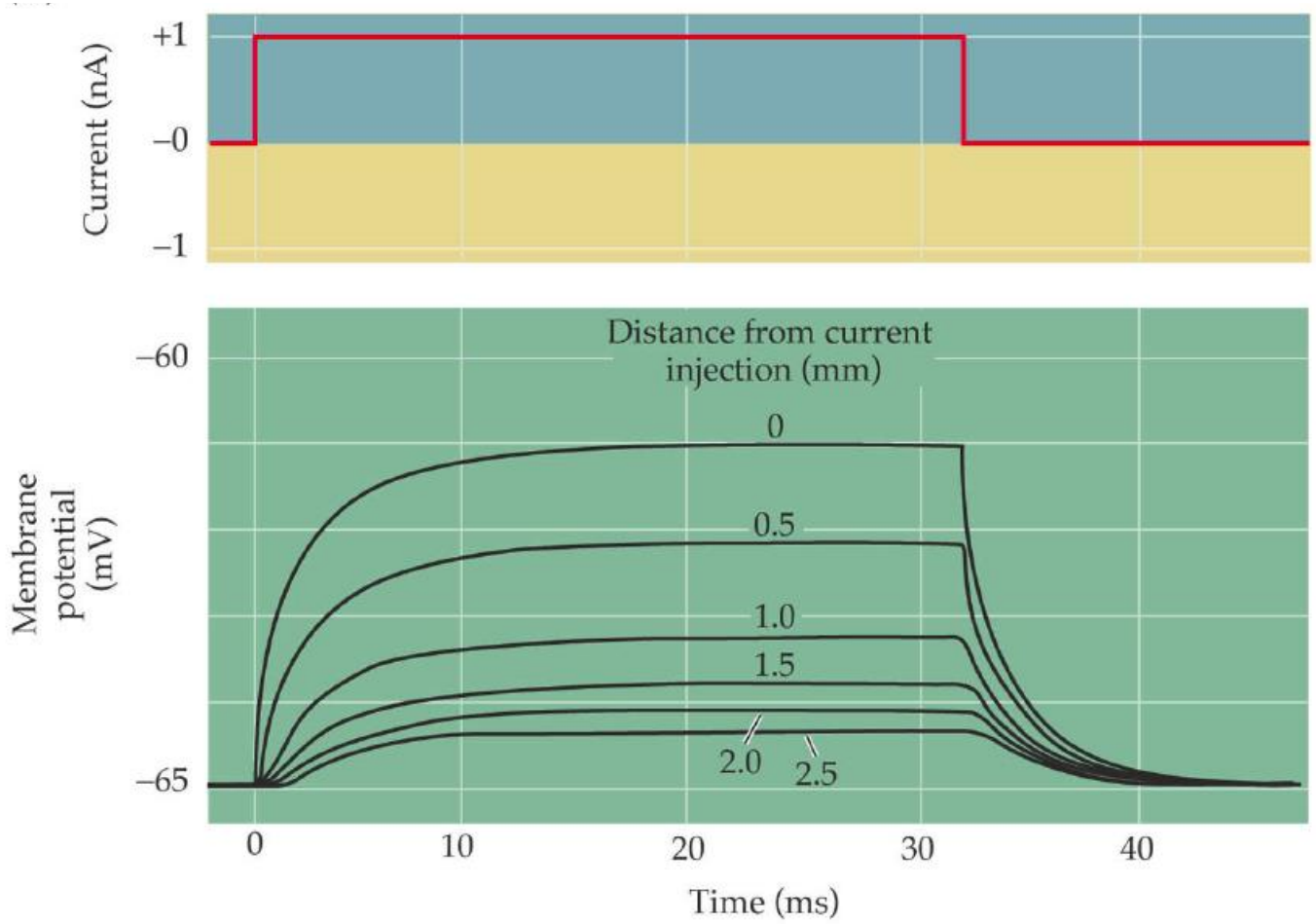
- There is an attenuation and a delay in the current that flows in the membrane.



# Complex impedance measurement

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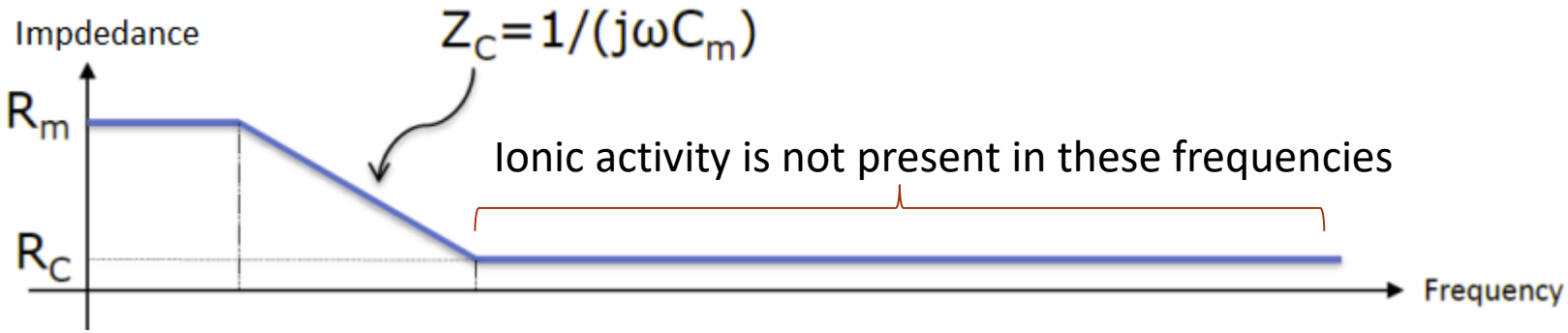


- $R_m$ results from finite resistivity of the neuronal membrane.
- $C_m$ results from the membrane capacitance.
- $R_C$ results from small impedance of the intracellular cytoplasm.

# The membrane equivalent circuit

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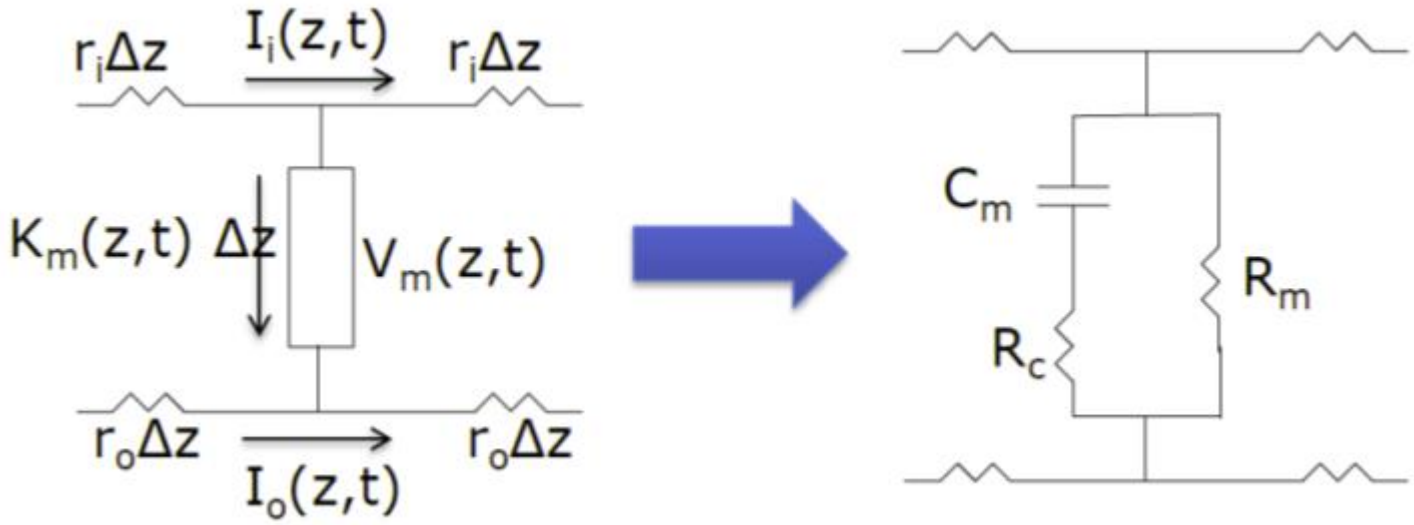

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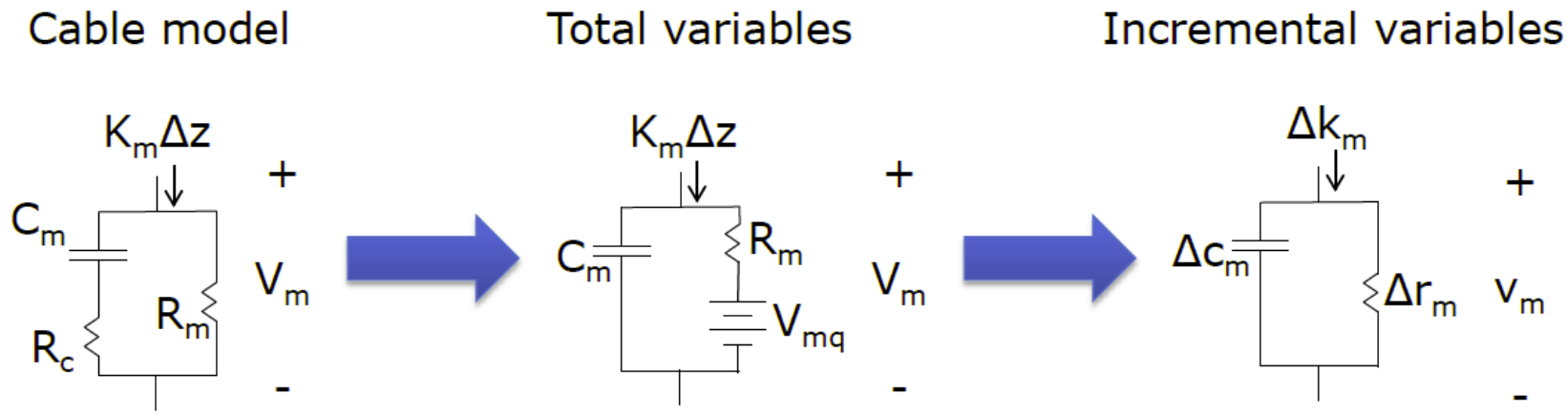


- Total variables
  - $R_c$ disregarded since frequencies which activate this is not biologically available.
  - $V_{mq}$ quiescent membrane potential ≡ Nernst potential
- Incremental variables
  - We're interested only in changing parameters (lowercase letters)

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- Variables
  - $C_m$ = total membrane capacitance
  - $c_m$ = membrane capacitance per unit length
  - $R_m$ = total membrane resistance
  - $r_m$ = membrane resistance per unit length
  - $K_m$ = total membrane current per unit length
  - $k_m$ = local current change from quiescent
  - $V_{mq}$ = resting or quiescent membrane potential
  - $v_m$ = local voltage change from quiescent
  - $V_m$ = average membrane potential = $V_{mq} + v_m$

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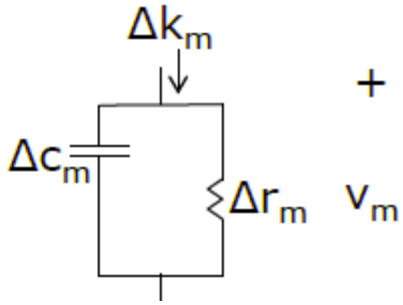
- Applying KCL to local circuit:




$$k_m(z,t)\Delta = \frac{v_m(z,t)}{r_m\Delta} + c_m\Delta\frac{\partial v_m(z,t)}{\partial t}$$

$$\therefore k_m(z,t) = g_m v_m(z,t) + c_m\frac{\partial v_m(z,t)}{\partial t} \qquad (7)$$

- This equation shows the relationship between membrane voltage and current through the membrane.
- Two unknowns: $g_m, c_m$

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- Recall the core conductor equation:

$$\frac{\partial^2 V_m(z,t)}{\partial z^2} = (r_o + r_i) K_m(z,t) - r_o K_e(z,t)$$

- Which, in terms of incremental variables is:

$$\frac{\partial^2 \left(V_{mq}(z,t) + v_m(z,t)\right)}{\partial z^2} = (r_o + r_i)\left(K_{mq}(z,t) + k_m(z,t)\right) - r_o\left(K_{eq}(z,t) + k_e(z,t)\right) \quad (8)$$

- When in the quiescent state, $v_m = k_m = k_e = 0$

$$0 = (r_o + r_i) K_{mq}(z,t) - r_o K_{eq}(z,t) \quad (9)$$

# Derivation of the cable equation

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- Subtracting (9) from (8):

$$\frac{\partial^2 v_m(z,t)}{\partial z^2} = (r_o + r_i) k_m(z,t) - r_o k_e(z,t) \qquad (10)$$

- = core conductor for incremental variables
- Substituting (7) into (10):

$$\frac{\partial^2 v_m(z,t)}{\partial z^2} = (r_o + r_i)\left( g_m v_m(z,t) + c_m \frac{\partial v_m}{\partial t} \right) - r_o k_e(z,t)$$

- This is the cable equation.
- This presents the relationship between the change in the membrane voltage and the variables around that except the membrane current.
- This shows only the passive membrane activity (PSP) not active activity (AP) with constant $g_m$ and $c_m$.

# Interpreting the cable equation

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- Measured voltage signals are further governed by a time constant: $\tau = r_m c_m$
  - The decay in passive voltage (ion diffusion) over time
- And a space constant: $\lambda = \sqrt{\frac{1}{(r_i + r_o) g_m}}$
  - The decay in passive voltage (ion diffusion) along the membrane (z axis)
    - Substituting:

$$\lambda^2 \frac{\partial^2 v_m(z,t)}{\partial z^2} = v_m(z,t) + \tau \frac{\partial v_m(z,t)}{\partial t} - \lambda^2 r_o k_e(z,t) \quad (11)$$

- We can find the behaviour of the membrane voltage as a function of the time and distance as long as it does not go beyond the threshold voltage (AP).
  - Since $Na^+$ and $K^+$ channels open, $g_m$ is going to be time dependent.

# Solving the cable equation

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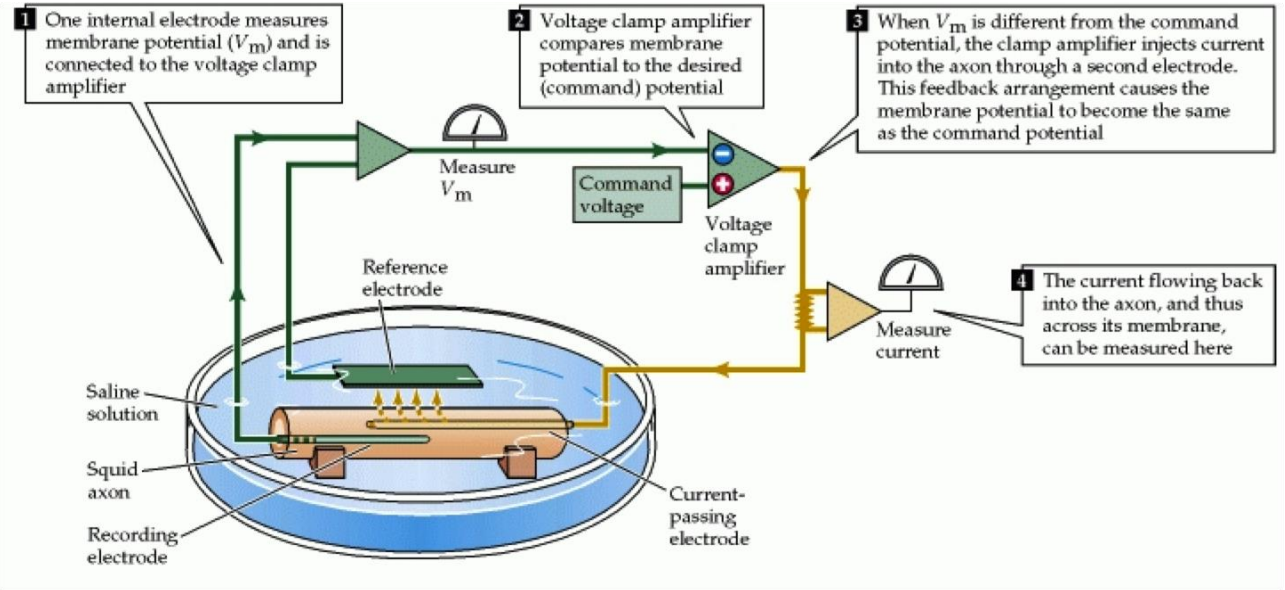
- There are two ways of solving:
  - Time independent i.e.
    - Voltage clamp

$$\partial v_m / \partial t = 0$$




  - Time dependent i.e.
    - Normal neural function

$$\partial v_m / \partial t \neq 0$$

# Time independent solution

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(11) Can be rewritten as

$$\lambda^2 \frac{\partial^2 v_m(z,t)}{\partial z^2} = v_m(z,t) - \lambda^2 r_o k_e(z,t)$$

$$\therefore \lambda^2 \frac{\partial^2 v_m(z,t)}{\partial z^2} - v_m(z,t) = -\lambda^2 r_o k_e(z,t) \qquad (12)$$

To solve, set $K_e = 0$

$$\therefore \lambda^2 \frac{\partial^2 v_m(z,t)}{\partial z^2} - v_m(z,t) = 0$$

Solution: $v_m(z,t) = Ae^{-z/\lambda}$

Substitute this back in the (12) and find $A$

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- It is obvious that the solution is not time dependent

$$v_m(z,t) = Ae^{-z/\lambda}$$

- If there's a PSP on a dendrite or on soma, it'll gradually diffuse (exponentially) over space.
- However, what we're interested in is how a set of PSPs move towards the axon hillock over time and contribute to the generation of the AP.
- Remember, cable model can only explain pre-threshold activity within the membrane (cannot explain the AP).

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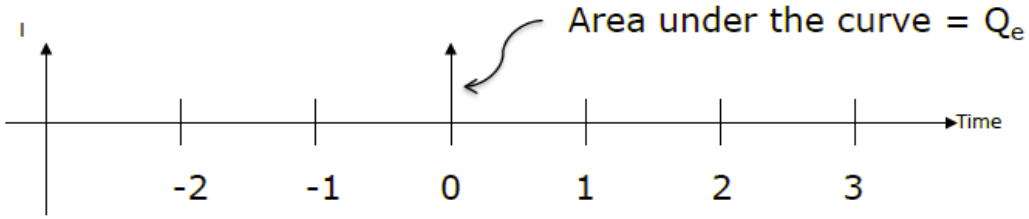
- Time dependent i.e. $\frac{\partial v_m}{\partial t} \neq 0$
- Assume that the stimulus current from the electrode $k_e$, is equal to the impulse function:

$$k_e(z,t) = Q_e \delta(z,t)$$

  - Where $Q_e$ is the total amount of charge delivered




- In this case

$$\int_{t=-\infty}^{\infty} \int_{z=-\infty}^{\infty} k_e(z,t)\,dz\,dt = Q_e$$

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- Let us also define normalized variables:

$$\lambda' = z/\lambda \quad \& \quad \tau' = t/\tau$$

- Therefore:

$$v_m(z,t) = v_m(\lambda'\lambda, \tau'\tau) = v_m'(\lambda', \tau')$$

- Similarly:

$$k_e(z,t) = k_e(\lambda'\lambda, \tau'\tau) = k_e'(\lambda', \tau') = \frac{Q_e}{\lambda\tau}\delta(\lambda', \tau')$$

This is as a result of

$$\int_{\tau'=-\infty}^{\infty} \int_{\lambda'=-\infty}^{\infty} Q_e \delta(\tau', \lambda')\, \lambda\tau\, d\tau' d\lambda' = \lambda\tau Q_e$$

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- We can now rewrite the cable equation:

$$\lambda^2 \frac{\partial^2 v_m(z,t)}{\partial z^2} = v_m(z,t) + \tau \frac{\partial v_m(z,t)}{\partial t} - \lambda^2 r_o k_e(z,t) \quad (11)$$

- To:

$$\frac{\partial^2 v_m'(\lambda',\tau')}{\partial \lambda'^2} = v_m'(\lambda',\tau') + \frac{\partial v_m'(\lambda',\tau')}{\partial \tau'} - \frac{\lambda r_o Q_e}{\tau} \delta(\lambda',\tau') \quad (13)$$

- Now we have eliminated the constant on the second derivative term.

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- Finally, let us define a new variable:

$$w_m\left(\lambda',\tau'\right)=v_m'\left(\lambda',\tau'\right)e^{\tau'}$$

- Noting that:

$$\frac{\partial^2 w_m\left(\lambda',\tau'\right)}{\partial\lambda'^2}=\frac{\partial^2 v_m'\left(\lambda',\tau'\right)}{\partial\lambda'^2}e^{\tau'} \qquad (14)$$

- And:

$$\frac{\partial w_m\left(\lambda',\tau'\right)}{\partial\tau'}=v_m'\left(\lambda',\tau'\right)e^{\tau'}+\frac{\partial v_m'\left(\lambda',\tau'\right)}{\partial\tau'}e^{\tau'} \qquad (15)$$

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- Substituting (14) and (15) into (13):

$$\frac{1}{e^{\tau'}}\frac{\partial^2 w_m\left(\lambda',\tau'\right)}{\partial\lambda'^2}=\frac{1}{e^{\tau'}}\frac{\partial w_m\left(\lambda',\tau'\right)}{\partial\tau'}-\frac{\lambda r_o Q_e}{\tau}\delta\left(\lambda',\tau'\right) \quad (16)$$

- If we set $Q_e$ to zero, this reduces to:

$$\frac{\partial^2 w_m\left(\lambda',\tau'\right)}{\partial\lambda'^2}=\frac{\partial w_m\left(\lambda',\tau'\right)}{\partial\tau'}$$

- Which is in the form of a second order homogeneous differential equation

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- Solving by inspection:

$$w_m\left(\lambda^{'},\tau^{'}\right)=\frac{A}{\sqrt{4\pi\tau^{'}}}e^{-\lambda^{'2}/4\tau^{'}}$$

$$\therefore v_m^{'}\left(\lambda^{'},\tau^{'}\right)=\frac{A}{\sqrt{4\pi\tau^{'}}}e^{-\lambda^{'2}/4\tau^{'}}e^{-\tau^{'}}$$

$$\therefore v_m\left(z,t\right)=\frac{A}{\sqrt{4\pi\left(t/\tau\right)}}e^{-\left(z/\lambda\right)^2/\left(4t/\tau\right)}e^{-t/\tau} \qquad (17)$$

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- To find A, rearrange (16) into:

$$\frac{\partial^2 w_m(\lambda',\tau')}{\partial \lambda'^2} = \frac{\partial w_m(\lambda',\tau')}{\partial \tau'} - \frac{\lambda r_o Q_e}{\tau}\delta(\lambda',\tau')e^{\tau'}$$

$$\frac{\lambda r_o Q_e e^{\tau'}}{\tau}\int_{-\infty}^{\infty}\delta(\lambda',\tau')d\lambda'$$

$$\frac{\lambda r_o Q_e}{\tau}e^{\tau'}\delta(\tau') = \frac{\lambda r_o Q_e}{\tau}\delta(\tau')$$

$$f(x)\delta(x-a) = f(a)\delta(x-a)$$
$$e^{\tau'}\delta(\tau'-0) = e^0\delta(\tau'-0)$$
$$e^{\tau'}\delta(\tau') = \delta(\tau')$$

- Integrate w.r.t. $\lambda'$

$$\int_{-\infty}^{\infty}\frac{\partial^2 w_m(\lambda',\tau')}{\partial \lambda'^2}d\lambda' = \int_{-\infty}^{\infty}\frac{\partial w_m(\lambda',\tau')}{\partial \tau'}d\lambda' - \frac{\lambda r_o Q_e}{\tau}\int_{-\infty}^{\infty}\delta(\lambda',\tau')e^{\tau'}\,d\lambda'$$

- According to (5), membrane current over a large distance is zero as the charged ions going into the membrane should be equal to that of going out.

$$\int_{-\infty}^{\infty}\frac{\partial^2 w_m(\lambda',\tau')}{\partial \lambda'^2}d\lambda' \propto \int_{-\infty}^{\infty}\frac{\partial^2 V_m(z,t)}{\partial z^2}\,dz \propto \int_{-\infty}^{\infty}K_m(z,t)\,dz = 0$$

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$$\therefore \int_{\lambda'=-\infty}^{\infty} \frac{\partial w_m(\lambda', \tau')}{\partial \tau'} d\lambda' = \frac{\lambda r_o Q_e}{\tau} \delta(\tau')$$

- Rearranging the order of integration:

$$\frac{d}{d\tau'} \int_{-\infty}^{\infty} w_m(\lambda', \tau') d\lambda' = \frac{\lambda r_o Q_e}{\tau} \delta(\tau')$$

$$\frac{d}{d\tau'} \int_{-\infty}^{\infty} w_m(\lambda', \tau') d\lambda' = \frac{d}{d\tau'} \int_{-\infty}^{\infty} \frac{A}{\sqrt{4\pi\tau'}} e^{-\lambda'^2/4\tau'} d\lambda' = \frac{d}{d\tau'} Au(\tau') = A\delta(\tau')$$

$$\therefore A = \frac{\lambda r_o Q_e}{\tau} \qquad (18)$$

Hint→ $\int_{-\infty}^{\infty} e^{-ax^2} \, dx = \sqrt{\frac{\pi}{a}} \quad (a > 0)$

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- Substituting (18) into (17)

$$v_m(z,t) = \frac{\frac{\lambda r_o Q_e}{\tau}}{\sqrt{4\pi\left(t/\tau\right)}} e^{-\left(z/\lambda\right)^2/\left(4t/\tau\right)} e^{-t/\tau}$$

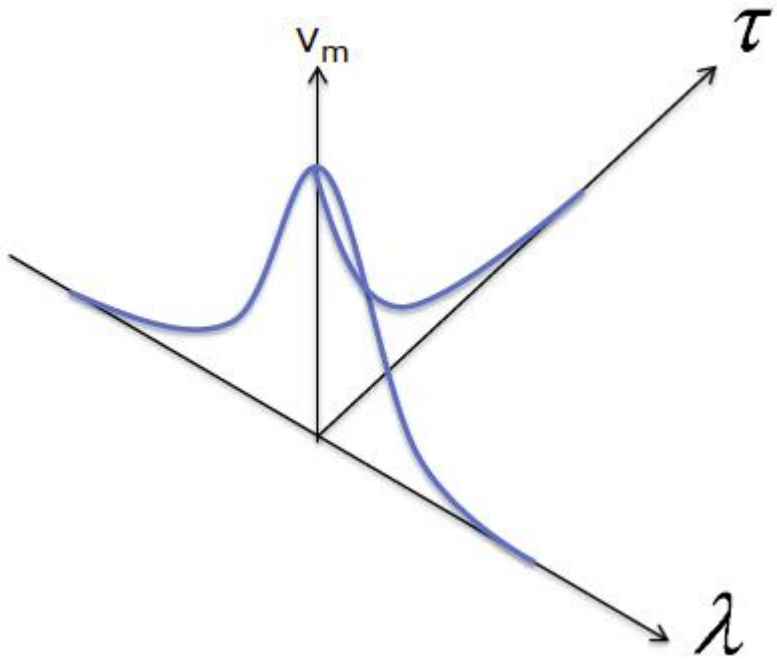
$when\ z = 0;$

$$v_m(t) = \frac{\alpha}{\sqrt{t}} e^{-t/\tau}$$

$when\ t = \tau;$

$$v_m(z) = \beta e^{-\theta z^2}$$

where $\alpha, \beta, \theta$ are constants



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- We can obtain the spatial and temporal information of the membrane potential that has resulted from a PSP.
- If we know
  - **where** the PSPs that are activating within the dendritic tree and the soma and
  - **when** they're activating

  it is possible to mathematically estimate the resultant membrane voltage at the axon hillock.
- If this has reached the threshold, an action potential will generate and travel through the axon toward synapses.
- However, by the time AP is generated $r_m$, $c_m$ become functions of time as a result of the activation ionic gates thus cable model is no longer valid.
- Hodgkin and Huxley presented the model which explains this AP phenomena.