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- Derivation

- Validity

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- Membrane model

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- Interpretation

- Time independent solution

- Time dependent solution

- Cable Model -

Dr. Anjula C. De Silva

anjulads@uom.lk

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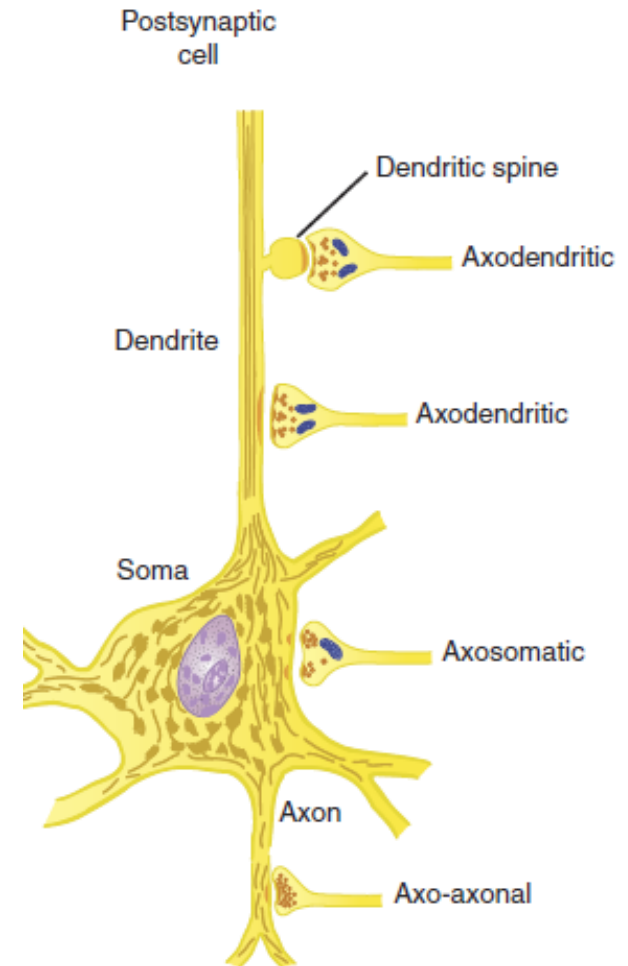
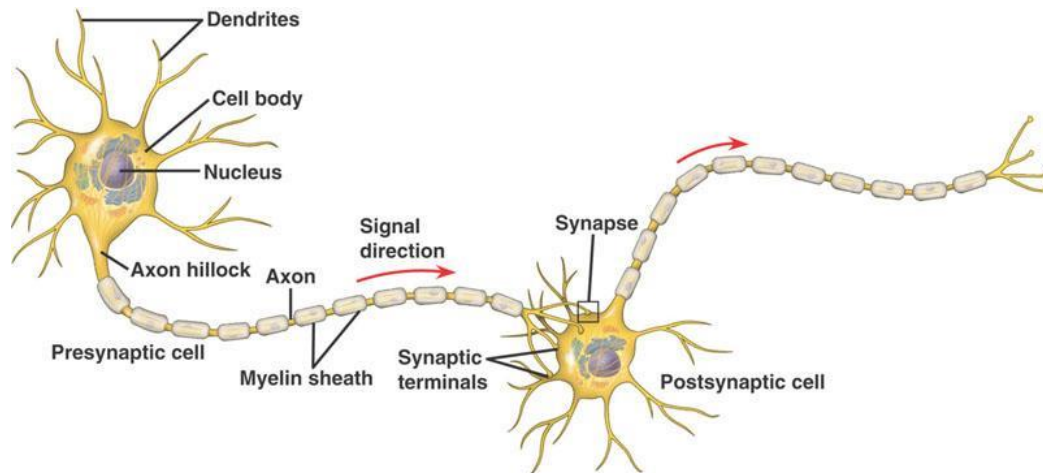
- The intention is to describe how biological conductors behave in terms of more familiar electrical conductors.
- Models used to describe this behaviour
 - Core-conductor model
 - Cable model

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



Synapses

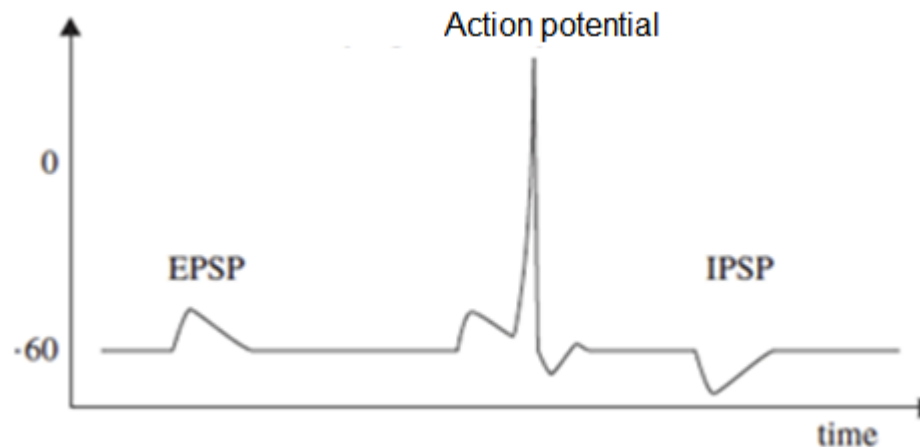
- Neurons communicate through the synaptic cleft by inducing electrical/ionic activity in the adjacent neuron.
- Post synaptic potentials generate as a result of the communication between neurons (cell signalling).





Post synaptic potentials (PSP)

- 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 $\approx 0.5\text{-}1\text{ mV}$
- EPSP or IPSP depends on the neurotransmitter released and the type of postsynaptic receptor activated.



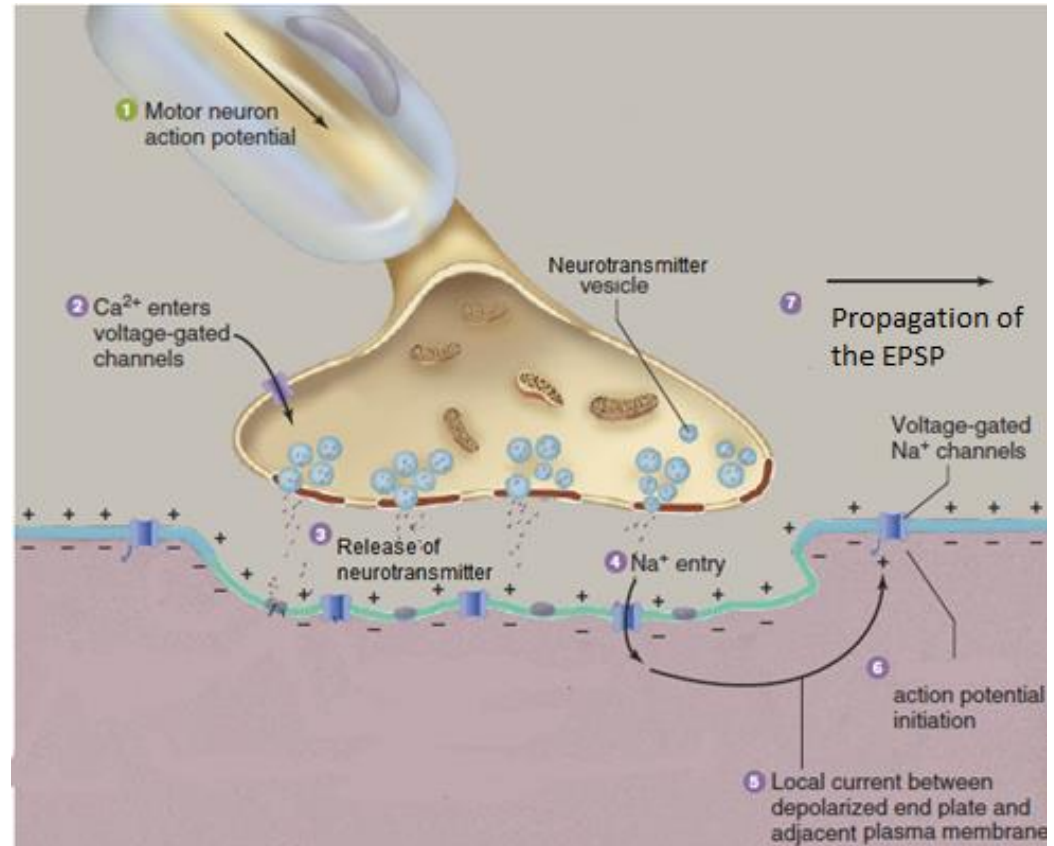


Post synaptic potentials (PSP)

- 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^+



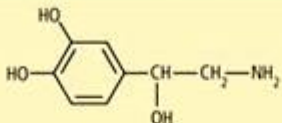
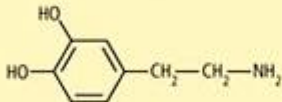
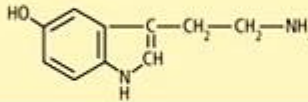
Electron microscope photo of a synaptic terminal.





Neurotransmitters

- 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	$\text{H}_3\text{C}-\overset{\text{O}}{\parallel}{\text{C}}-\text{O}-\text{CH}_2-\text{CH}_2-\text{N}^+-(\text{CH}_3)_3$	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)	$\text{H}_2\text{N}-\text{CH}_2-\text{CH}_2-\text{CH}_2-\text{COOH}$	Inhibitory
Glycine	$\text{H}_2\text{N}-\text{CH}_2-\text{COOH}$	Inhibitory
Glutamate	$\text{H}_2\text{N}-\underset{\text{COOH}}{\underset{ }{\text{CH}}}-\text{CH}_2-\text{CH}_2-\text{COOH}$	Excitatory
Aspartate	$\text{H}_2\text{N}-\underset{\text{COOH}}{\underset{ }{\text{CH}}}-\text{CH}_2-\text{COOH}$	Excitatory
Neuropeptides (a very diverse group, only two of which are shown)		
Substance P	$\text{Arg}-\text{Pro}-\text{Lys}-\text{Pro}-\text{Gln}-\text{Gln}-\text{Phe}-\text{Phe}-\text{Gly}-\text{Leu}-\text{Met}$	Excitatory
Met-enkephalin (an endorphin)	$\text{Tyr}-\text{Gly}-\text{Gly}-\text{Phe}-\text{Met}$	Generally inhibitory

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

Norepinephrine: modulation of sleep and wakefulness

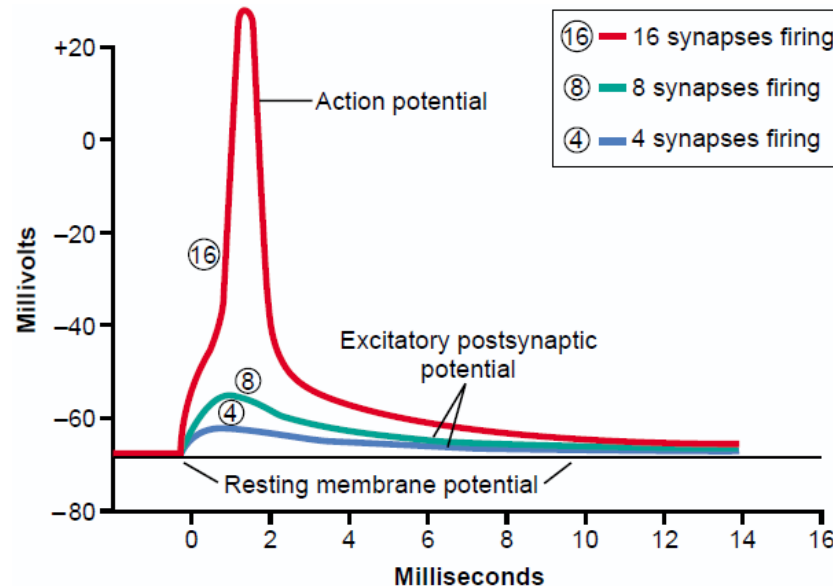
Dopamine: body movements

Serotonin: modulation of sleep and wakefulness



Spatial summation of EPSP and reaching the threshold

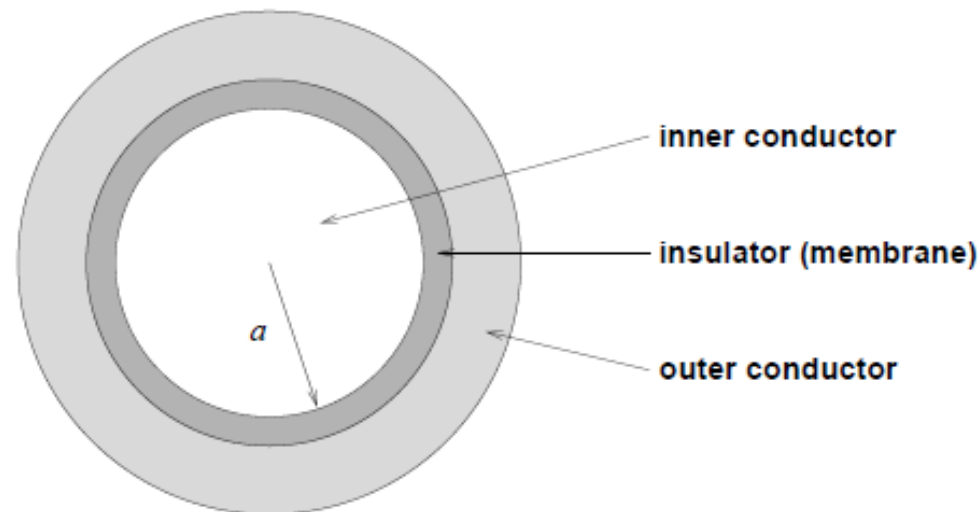
- A single EPSP can never initiate an action potential
 - Single EPSP → 0.5-1 mV
 - Duration
 - 1-2 ms rising time while the Na^+ gates are open
 - 15 ms decay time to leak excess Na^+ through the pump
- The highly conductive soma summate all the neuronal excitations that occur in the soma and dendrites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





Core conductor model

- 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.



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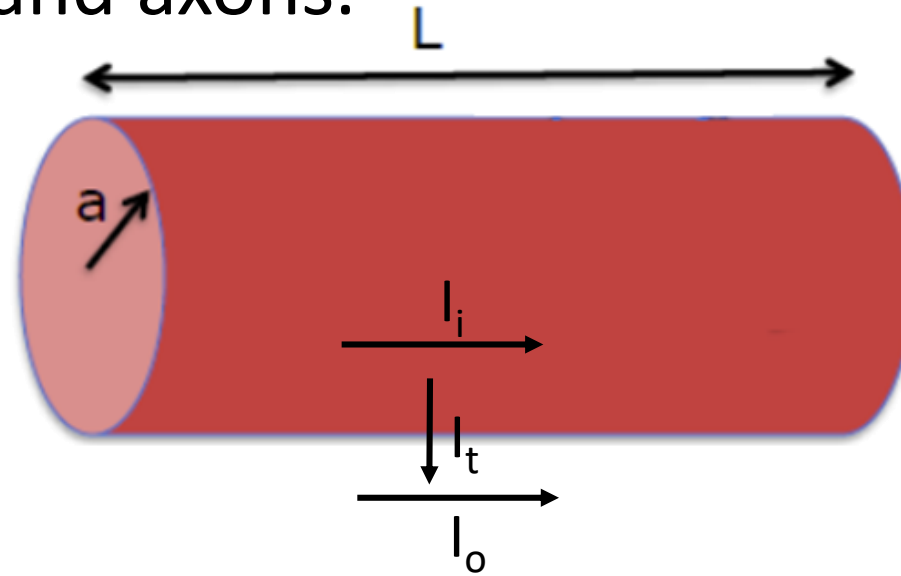
-Time independent solution

-Time dependent solution



Cylindrical conductor

- 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

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Assumptions

- 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.

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Derivation of the core conductor model

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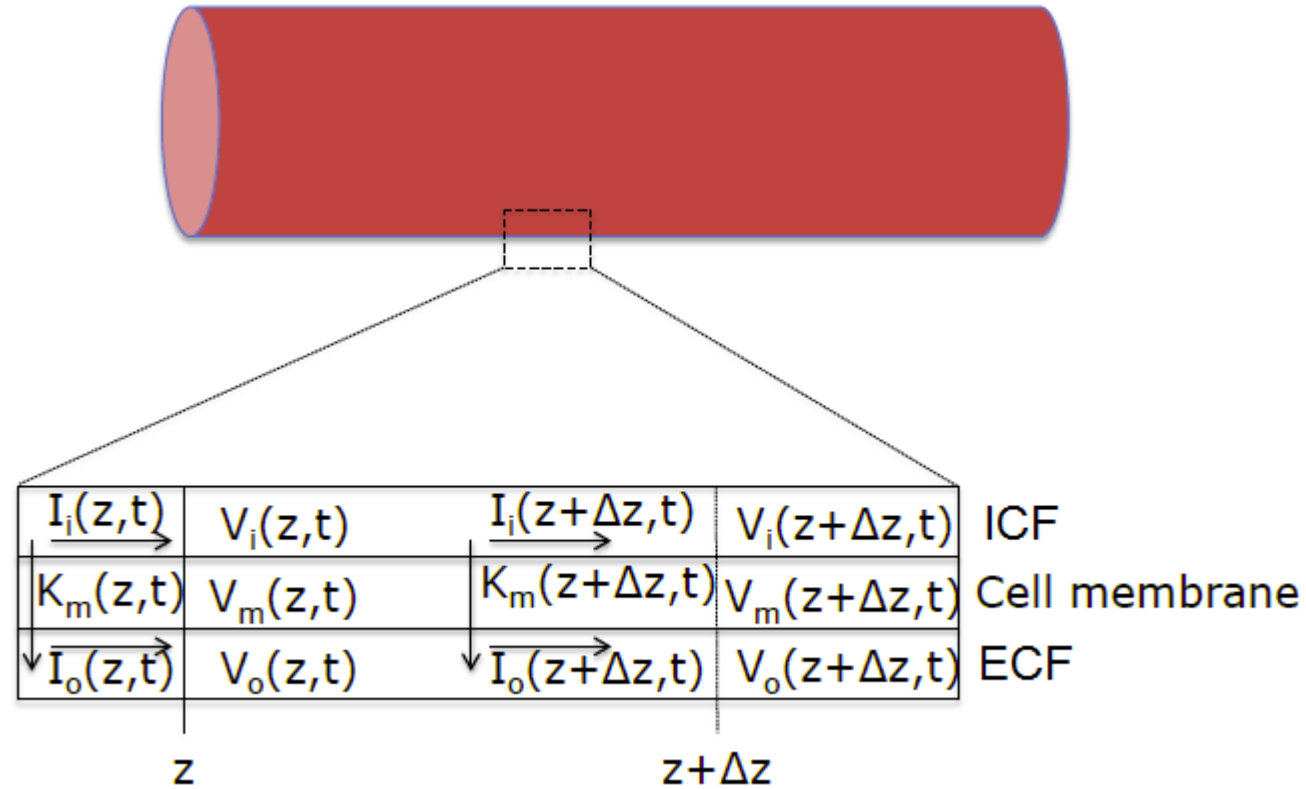
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- Consider an infinitesimal segment along the \hat{z} direction Δz



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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



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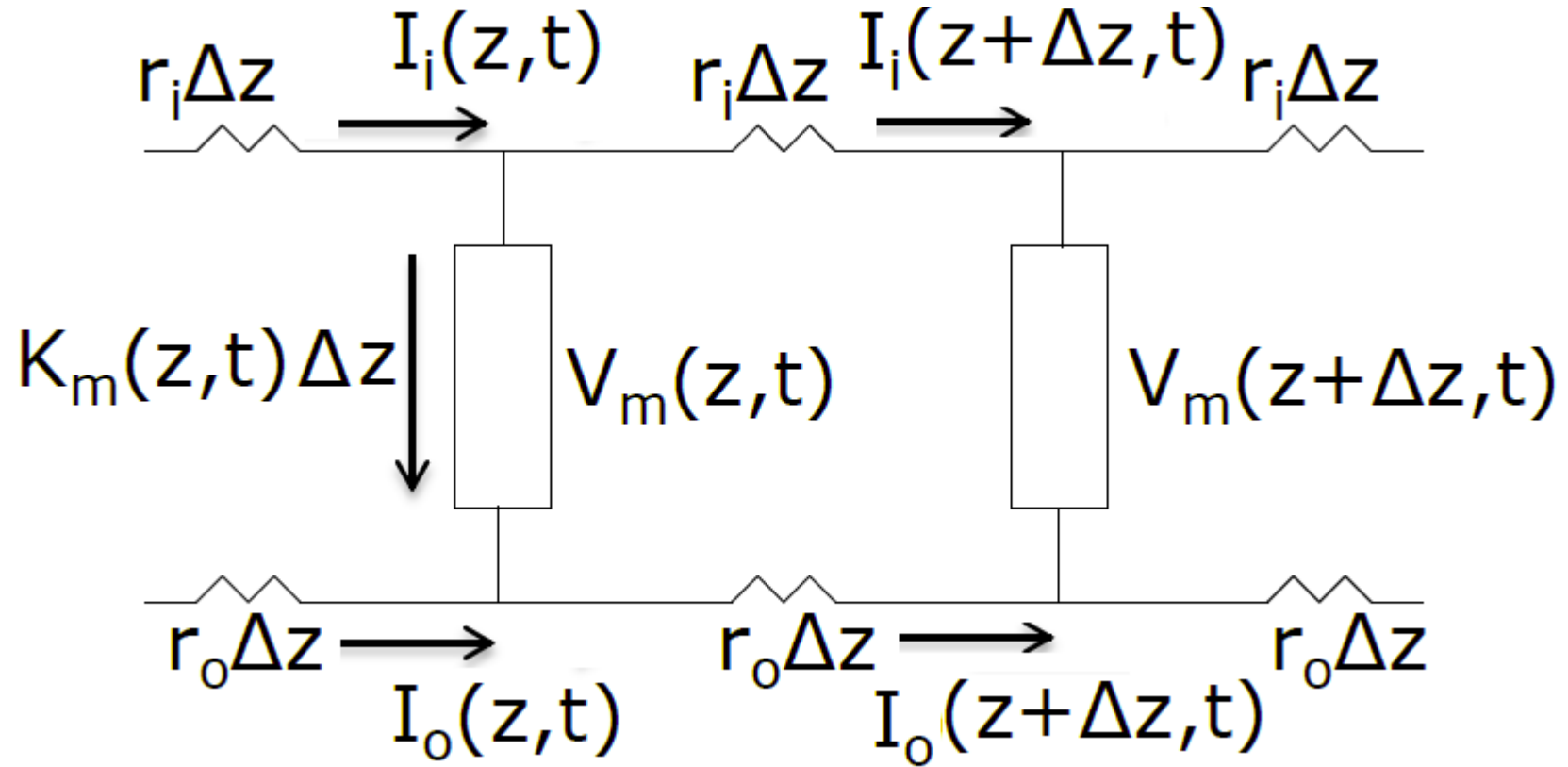
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- Consider an infinitesimal segment along the \hat{z} direction Δz



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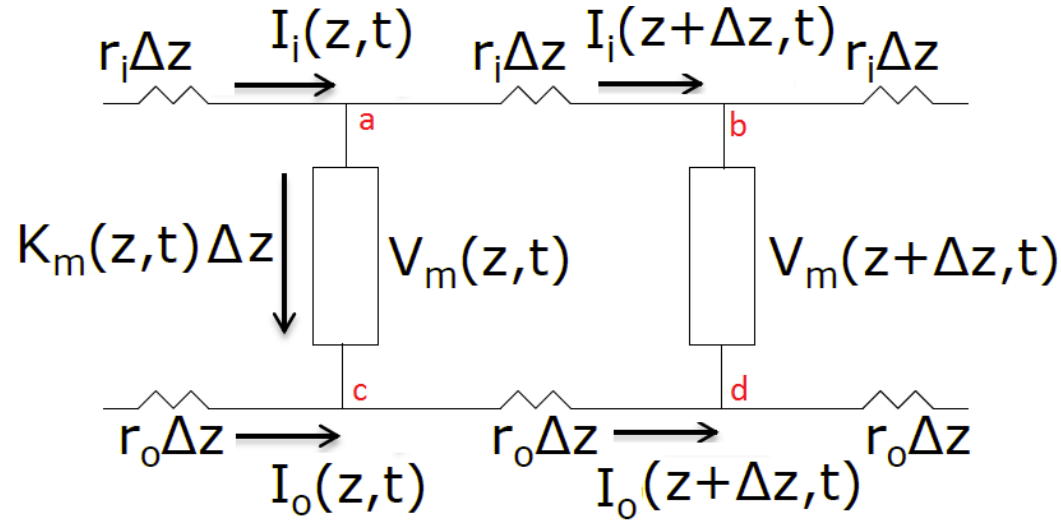
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From KCL at node **a**:

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

From KCL at node **c**:

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



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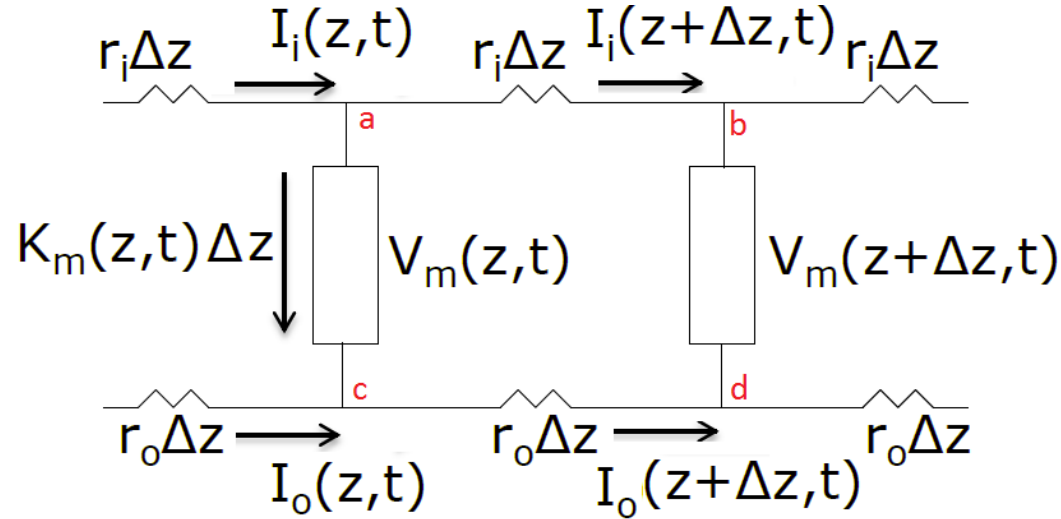
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From Ohm's law inside the cell:

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

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

- Rearranging and dividing by Δz :

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

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

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

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

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Analysing the equivalent circuit

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

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

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

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

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

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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:

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



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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 $K_e=0$

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

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

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

- 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:

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





Observations from APs

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

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

- Therefore:

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

- and:

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

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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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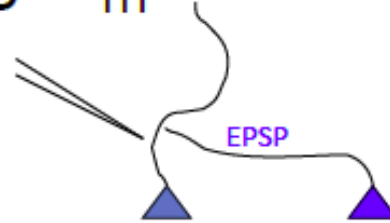
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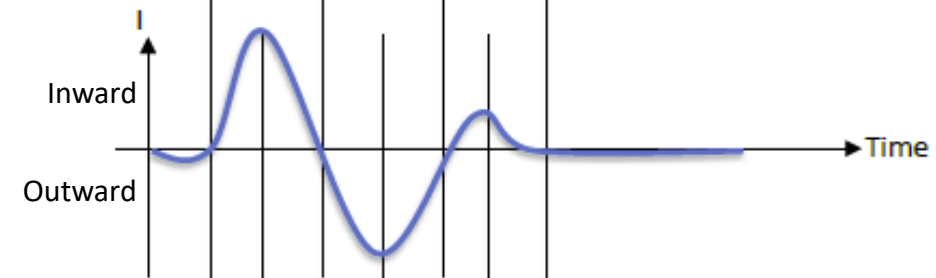
-Time independent solution

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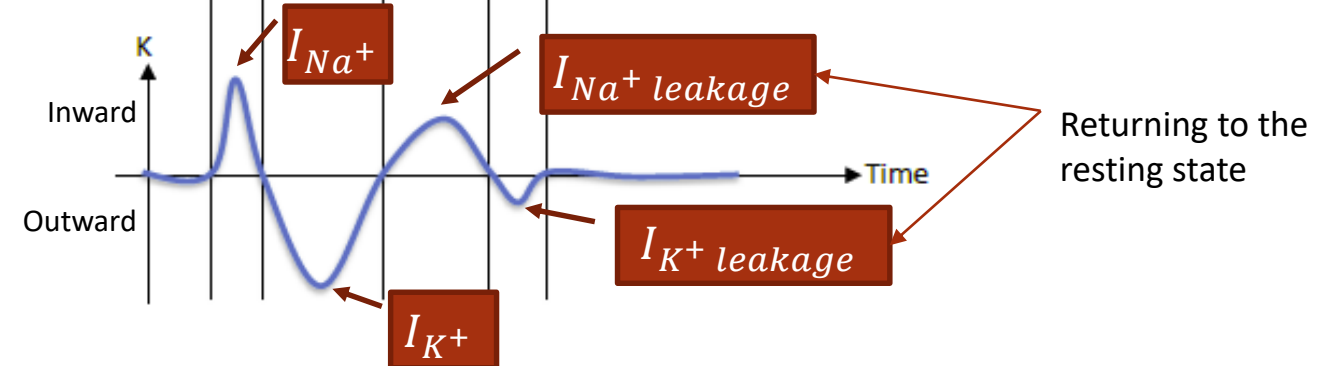
- Plotting V_m :



- Plotting I_o :



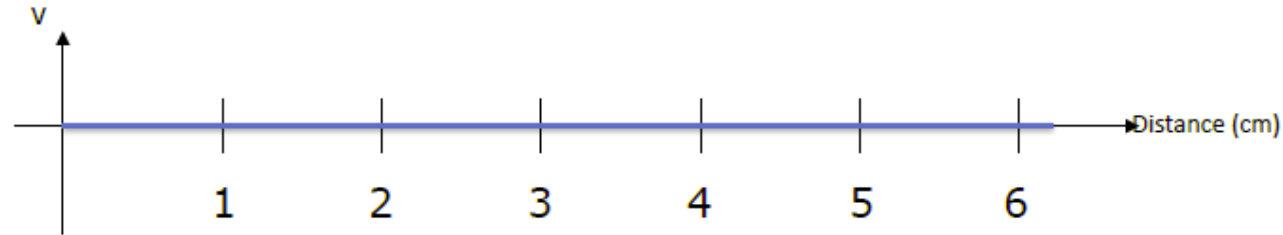
- Plotting K_m :



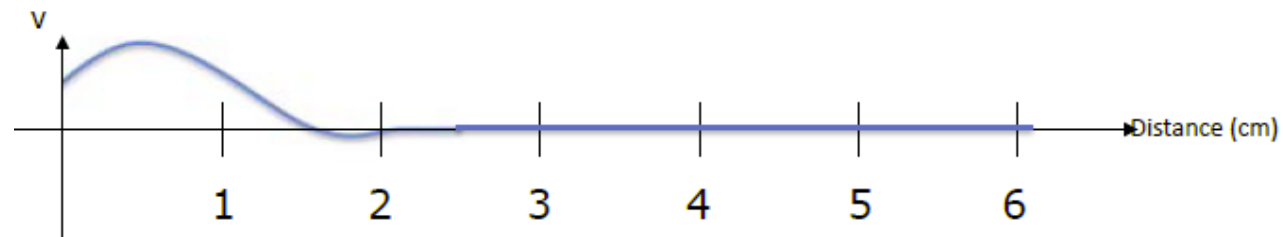


Observations from APs (space variations)

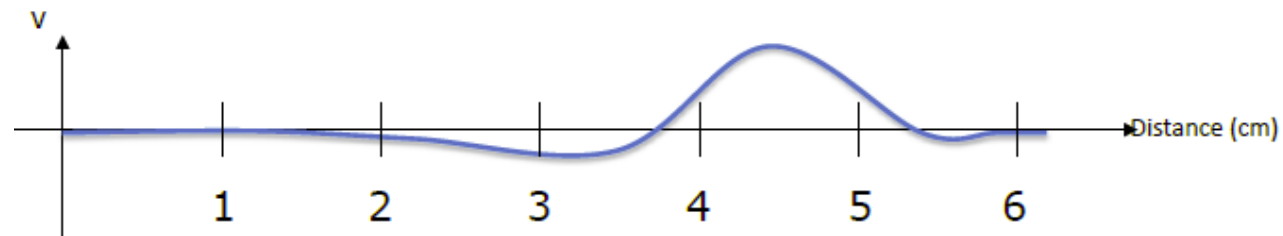
- Spatial variation of an action potential



Plotted at time $t = 0$ ms



Plotted at time $t = 1$ ms



Plotted at time $t = 2.5$ ms

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Core-conductor equation

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

- 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.

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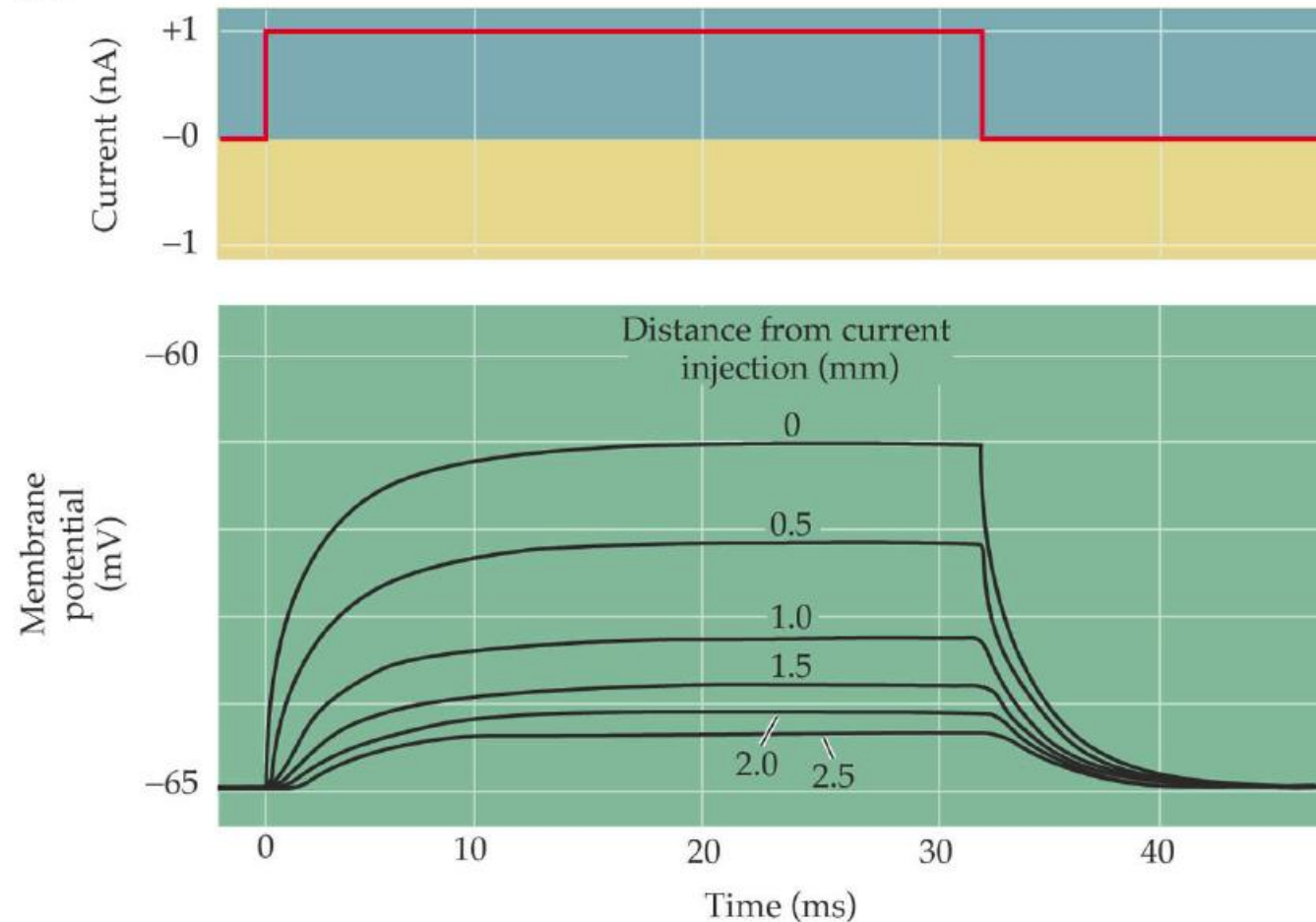
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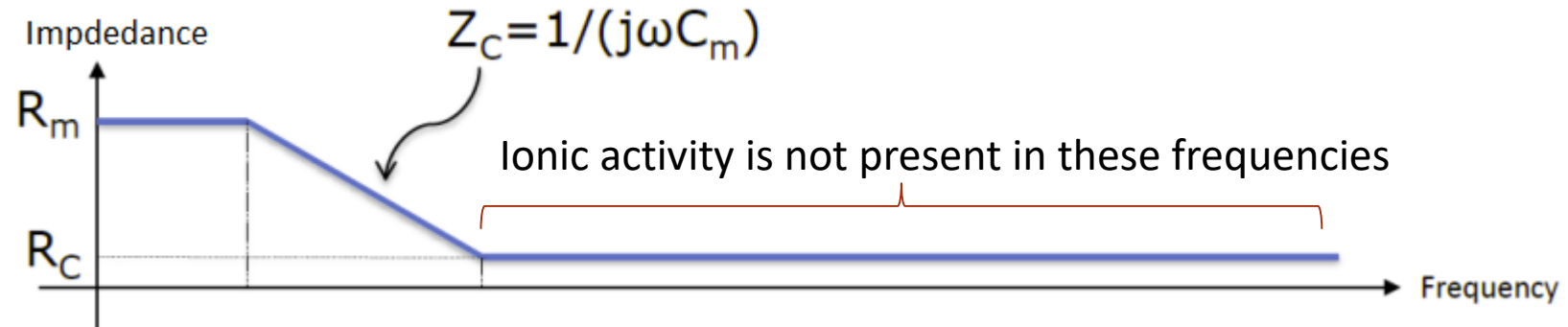
Behaviour of V_m

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





Complex impedance measurement



- 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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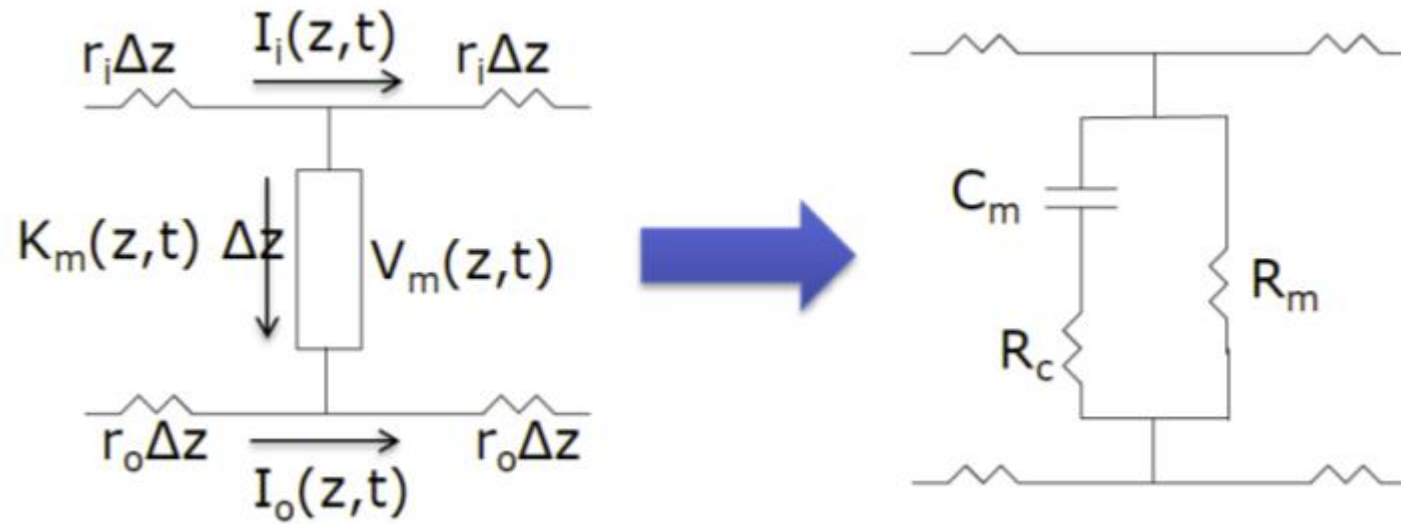
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Derivation of the cable equation

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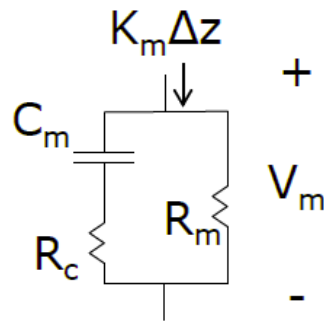
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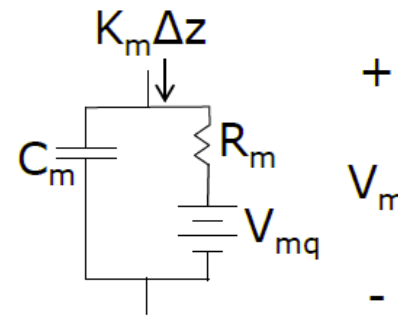
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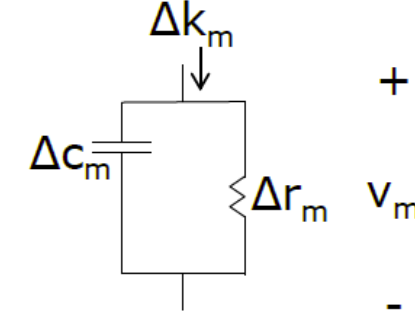
Cable model



Total variables



Incremental variables



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



Derivation of the cable equation

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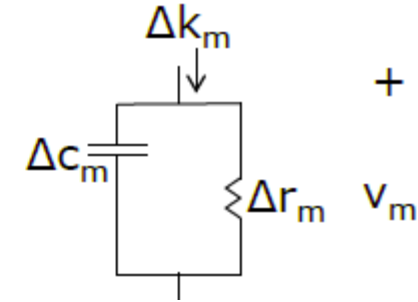
- Variables

- 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 = $V_{mq} + v_m$



Derivation of the cable equation

- Applying KCL to local circuit:



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

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

- 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:

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

- 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

- Subtracting (9) from (8):

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

- = 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 .

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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:

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

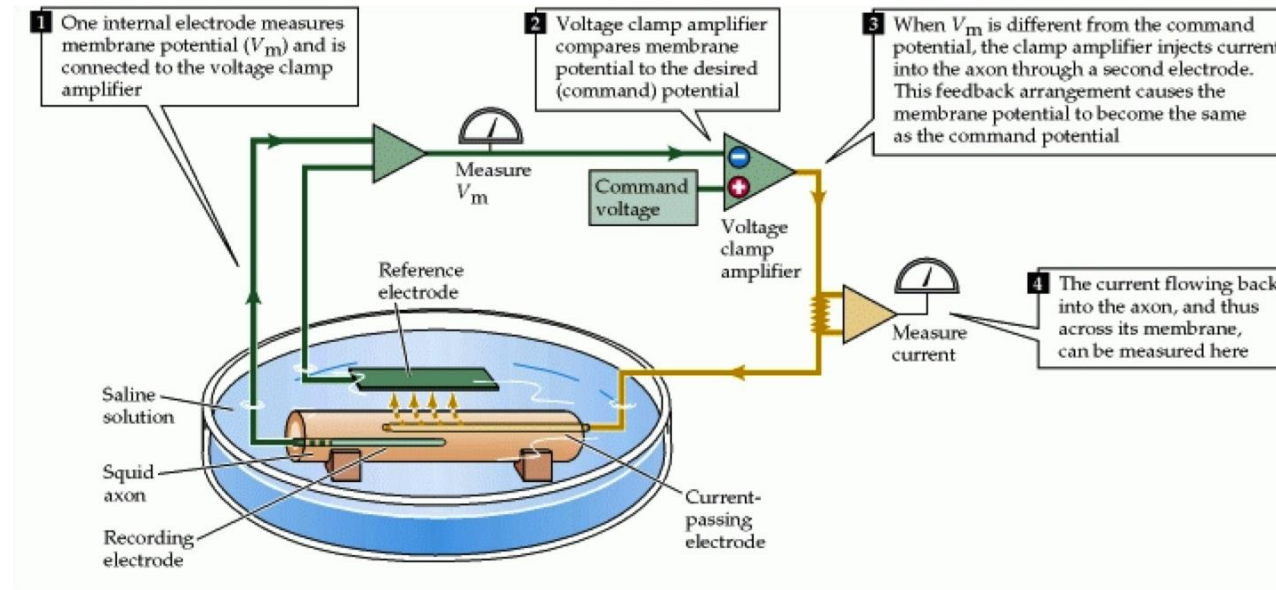
- We can find the behaviour of the membrane voltage as a function of the time and distance as long as it does not go beyond the threshold voltage (AP).
 - Since Na^+ and K^+ channels open, g_m is going to be time dependent.



Solving the cable equation

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

$$\frac{\partial v_m}{\partial t} = 0$$



- Time dependent i.e.
 - Normal neural function

$$\frac{\partial v_m}{\partial t} \neq 0$$



Time independent solution

(11) Can be rewritten as

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

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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Time independent solution

- 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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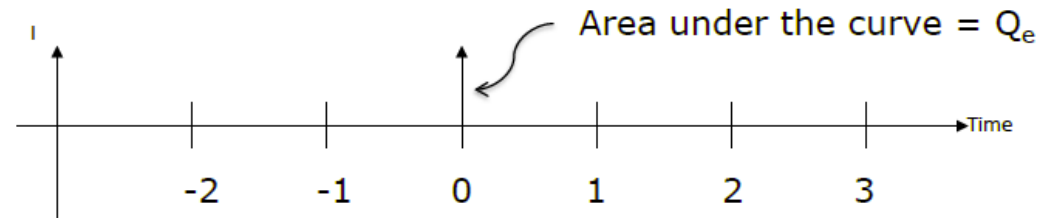


Time dependent solution

- 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

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



Time dependent solution

- 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

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



Time dependent solution

- 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:

$$w_m(\lambda', \tau') = v'_m(\lambda', \tau') e^{\tau'}$$

- Noting that:

$$\frac{\partial^2 w_m(\lambda', \tau')}{\partial \lambda'^2} = \frac{\partial^2 v'_m(\lambda', \tau')}{\partial \lambda'^2} e^{\tau'} \quad (14)$$

- And:

$$\frac{\partial w_m(\lambda', \tau')}{\partial \tau'} = v'_m(\lambda', \tau') e^{\tau'} + \frac{\partial v'_m(\lambda', \tau')}{\partial \tau'} e^{\tau'} \quad (15)$$



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

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

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

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

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



Time dependent solution

- Solving by inspection:

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

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

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

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- To find A, rearrange (16) into:

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

- Integrate w.r.t. λ'

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

- 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.



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

$$\begin{aligned} \frac{\lambda r_o Q_e e^{\tau'}}{\tau} \int_{-\infty}^{\infty} \delta(\lambda', \tau') d\lambda' \\ \frac{\lambda r_o Q_e}{\tau} e^{\tau'} \delta(\tau') = \frac{\lambda r_o Q_e}{\tau} \delta(\tau') \\ f(x) \delta(x - a) = f(a) \delta(x - a) \\ e^{\tau'} \delta(\tau' - 0) = e^0 \delta(\tau' - 0) \\ e^{\tau'} \delta(\tau') = \delta(\tau') \end{aligned}$$



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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:

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

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

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

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



Time dependent solution

- Substituting (18) into (17)

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

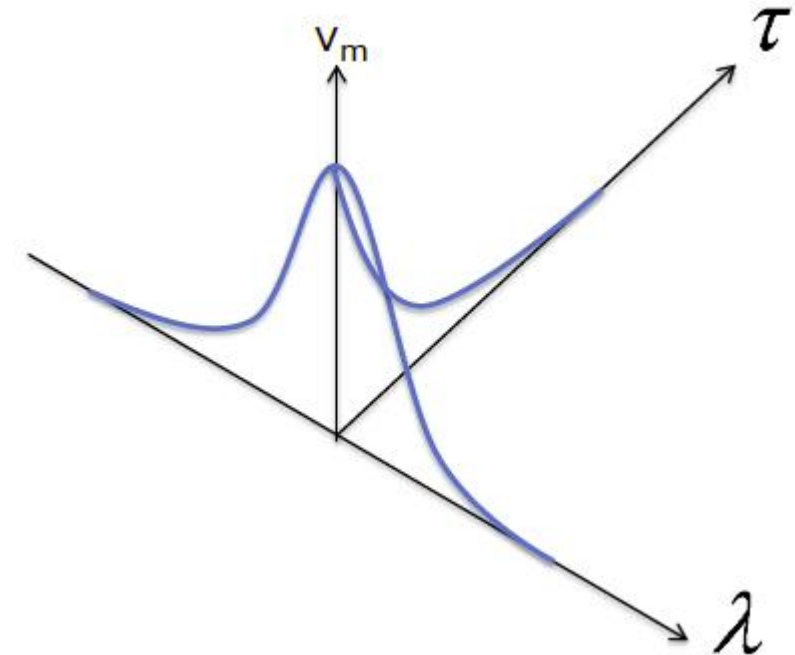
when $z = 0$;

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

when $t = \tau$;

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

where α, β, θ are constants





Time dependent solution interpretation

- 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 activatingit 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.

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