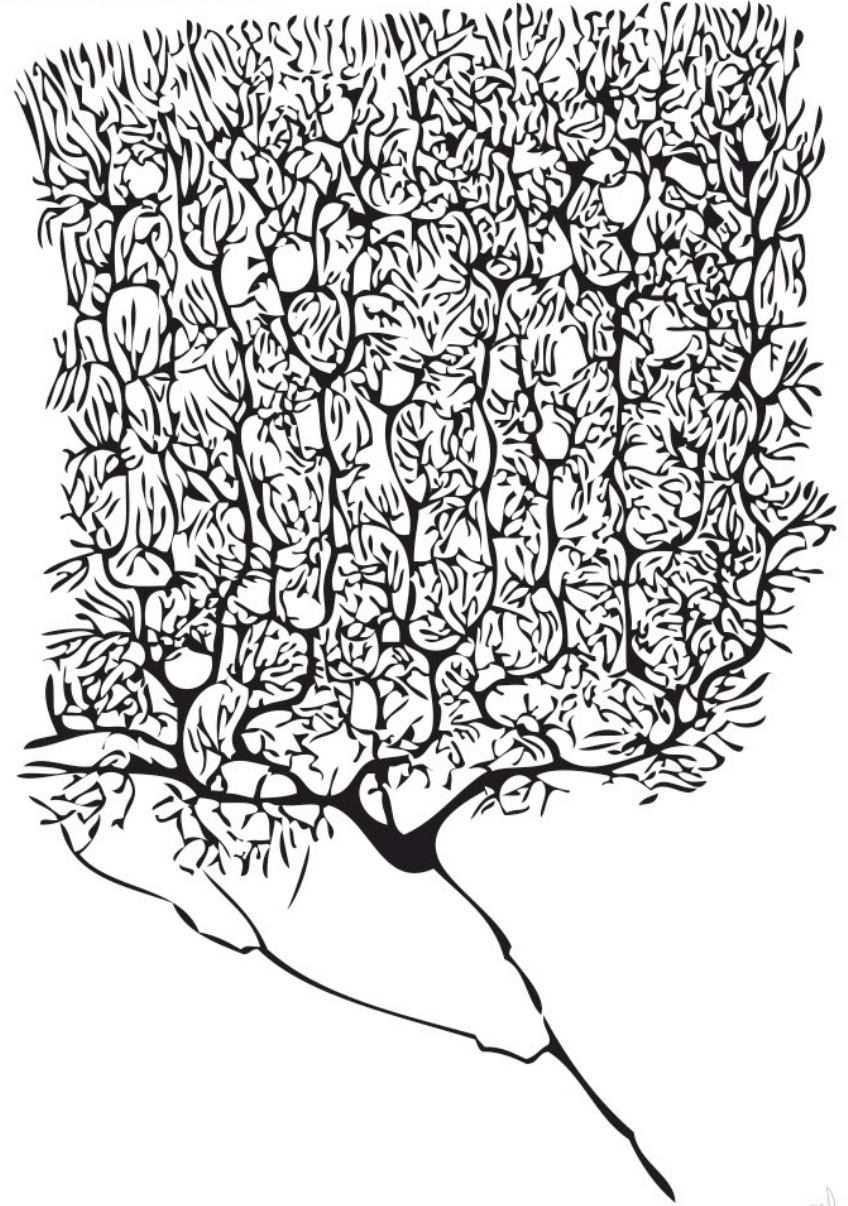


# Cellular Electrodynamics

Santiago Ramón y Cajal (1852-1934)



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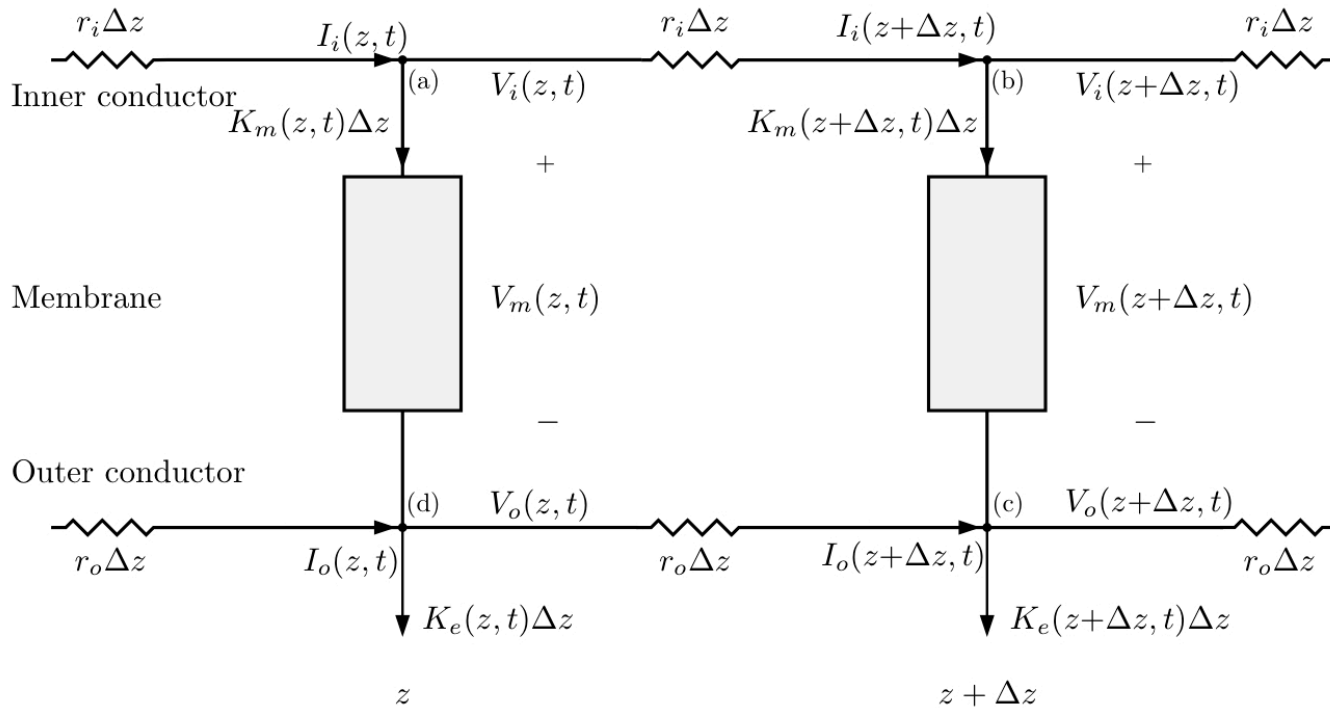
York University  
Winter 2020

BPHS 4080 Lecture X

Reference/Acknowledgement:

- TF Weiss (Cellular Biophysics)
- D Freeman

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## THE Core – Conductor Equation

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

Assumptions/geometry above, along with Kirchoff's & Ohm's Laws lead us to the...

→ Relates spatial change in transmembrane potential to current flowing through the membrane

## Some Implications

Consider no external electrodes  
(i.e.,  $K_e = 0$ ):

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

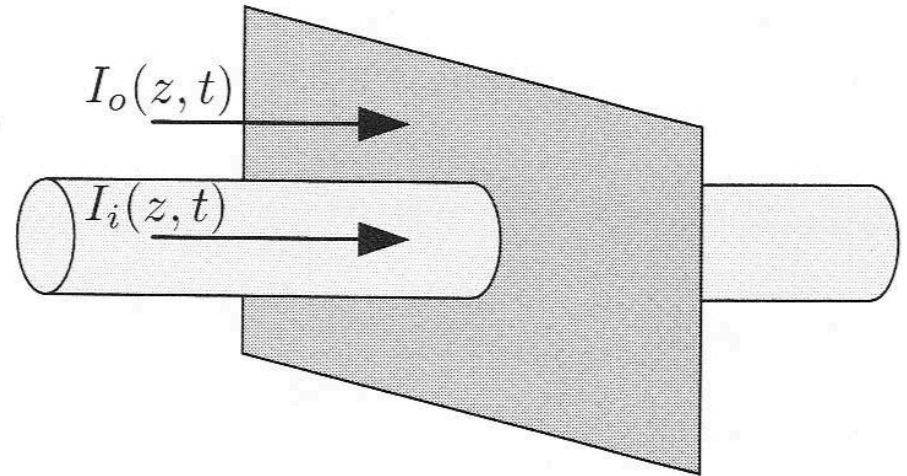


Figure 2.9

**Conservation of charge requires:**  $I_i(z, t) + I_o(z, t) = 0$

### Core – Conductor Equations

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

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

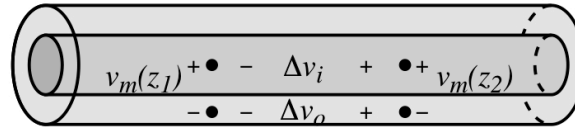
$$\frac{\partial V_i(z, t)}{\partial z} = -r_i I_i(z, t)$$

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

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

## Relation between extracellular and intracellular potentials

Some useful interrelationships...



KVL:

$$v_m(z_2) + \Delta v_o - v_m(z_1) - \Delta v_i = 0$$

$$\Delta v_o - \Delta v_i = v_m(z_1) - v_m(z_2)$$

$$\Delta v_i = - \int_{z_1}^{z_2} r_i I_i dz = -r_i \int_{z_1}^{z_2} I_i dz$$

$$\Delta v_o = - \int_{z_1}^{z_2} r_o I_o dz = -r_o \int_{z_1}^{z_2} I_o dz$$

$$I_o = -I_i$$

$$\Delta v_i = -r_i \int_{z_1}^{z_2} I_i dz = -r_i \int_{z_1}^{z_2} (-I_o) dz = -\frac{r_i}{r_o} \Delta v_o$$

$$\Delta v_o - \Delta v_i = \Delta v_o + \frac{r_i}{r_o} \Delta v_o = v_m(z_1) - v_m(z_2)$$

$$\Delta v_o = \frac{r_o}{r_o + r_i} (v_m(z_1) - v_m(z_2))$$

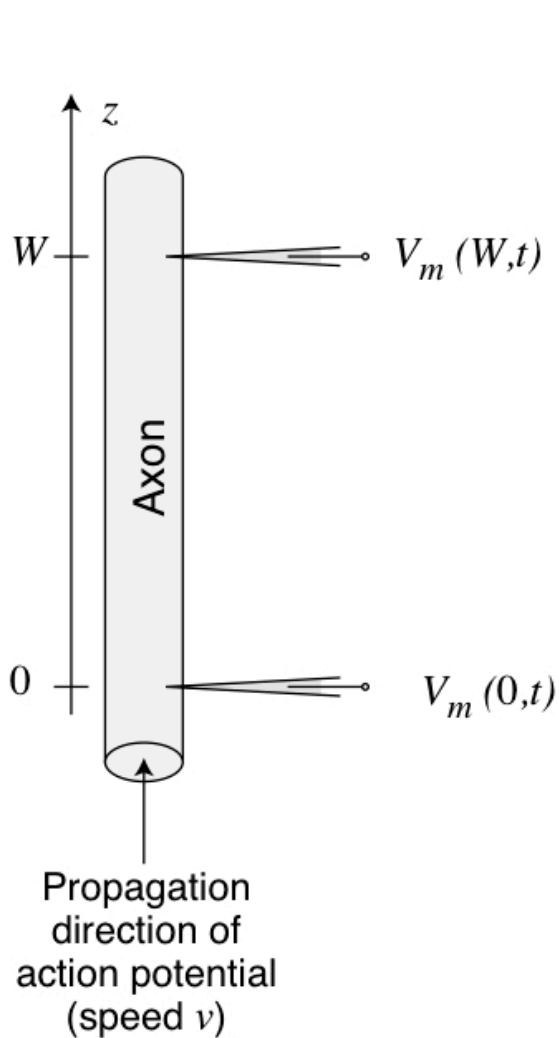
let  $z_1 \rightarrow -\infty$ : then  $v_o(z_1) \rightarrow 0$  and  $v_m(z_1) \rightarrow V_m^o$

$$\Delta v_o = v_o(z_2) - v_o(z_1) = v_o(z_2) = \frac{r_o}{r_o + r_i} (V_m^o - v_m(z_2))$$

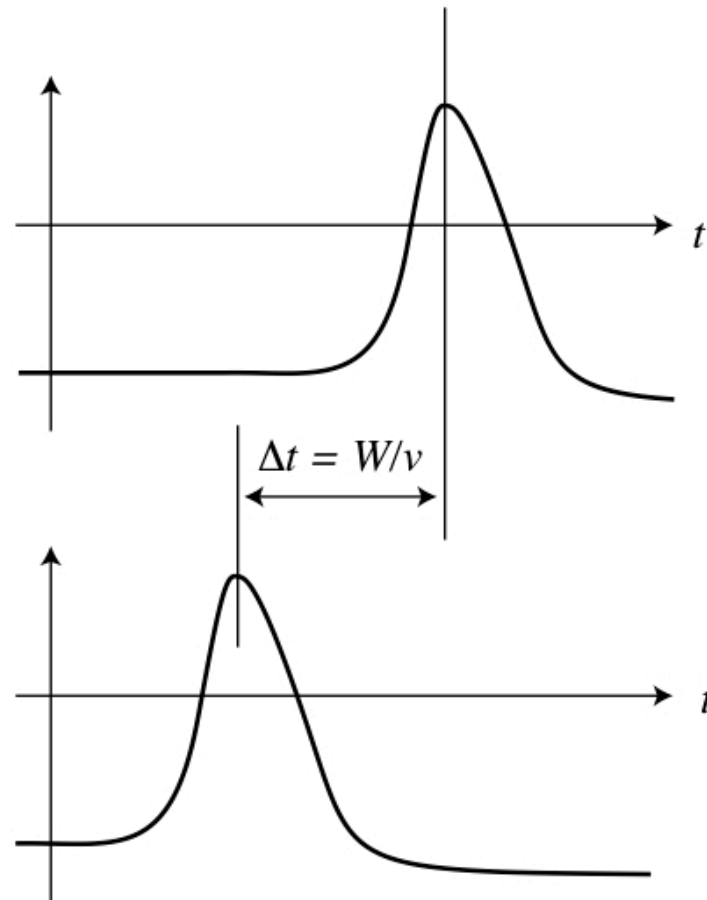
$$v_o(z_2) = -\frac{r_o}{r_o + r_i} (v_m(z_2) - V_m^o)$$

## Propagation at Constant Velocity

Assumption: Membrane potential behaves in a **wave-like** fashion (const. velocity)



$$V_m(z, t) = f\left(t \pm \frac{z}{v}\right)$$

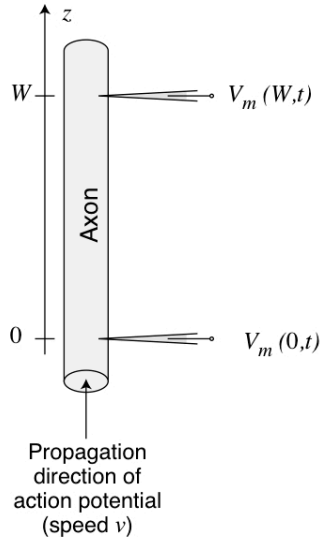


Note: We make an bio-inspired assumption as to the form (i.e., shape) of  $f$  here

# Propagation at Constant Velocity

$$V_m(z, t) = f\left(t \pm \frac{z}{v}\right)$$

“Snapshot” at one specific time  
 → Spatial dependence



“Snapshots” at two different spatial locations  
 → Temporal dependence

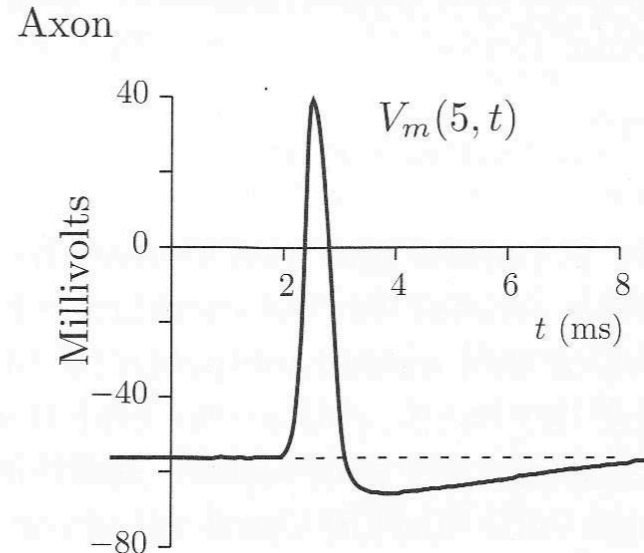
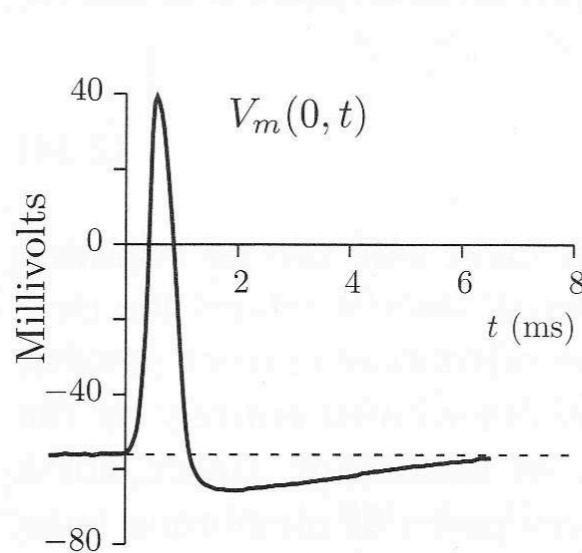
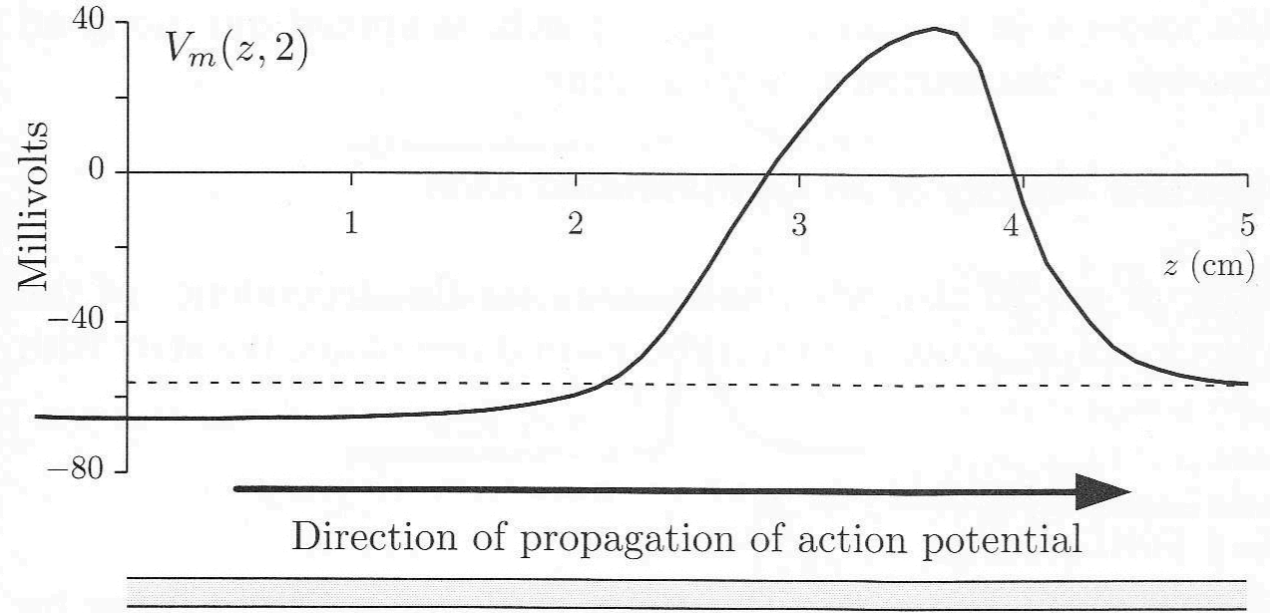


Figure 2.13

## Propagation at Constant Velocity

$$V_m(z, t) = f\left(t \pm \frac{z}{v}\right)$$

Think carefully about what the diacritical dot means here!

$$\frac{\partial V_m(z, t)}{\partial z} = \pm \frac{1}{v} \dot{f}\left(t \pm \frac{z}{v}\right) \quad \text{and} \quad \frac{\partial V_m(z, t)}{\partial t} = \dot{f}\left(t \pm \frac{z}{v}\right)$$

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

**Wave equation**  
(differential form)

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

→ So when we assume a wave propagating at constant velocity, the core conductor model yields explicit time relationships as well

and

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

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

Connecting action potential-type waves to the core conductor model

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

and

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

$$I_i(z, t) + I_o(z, t) = 0$$

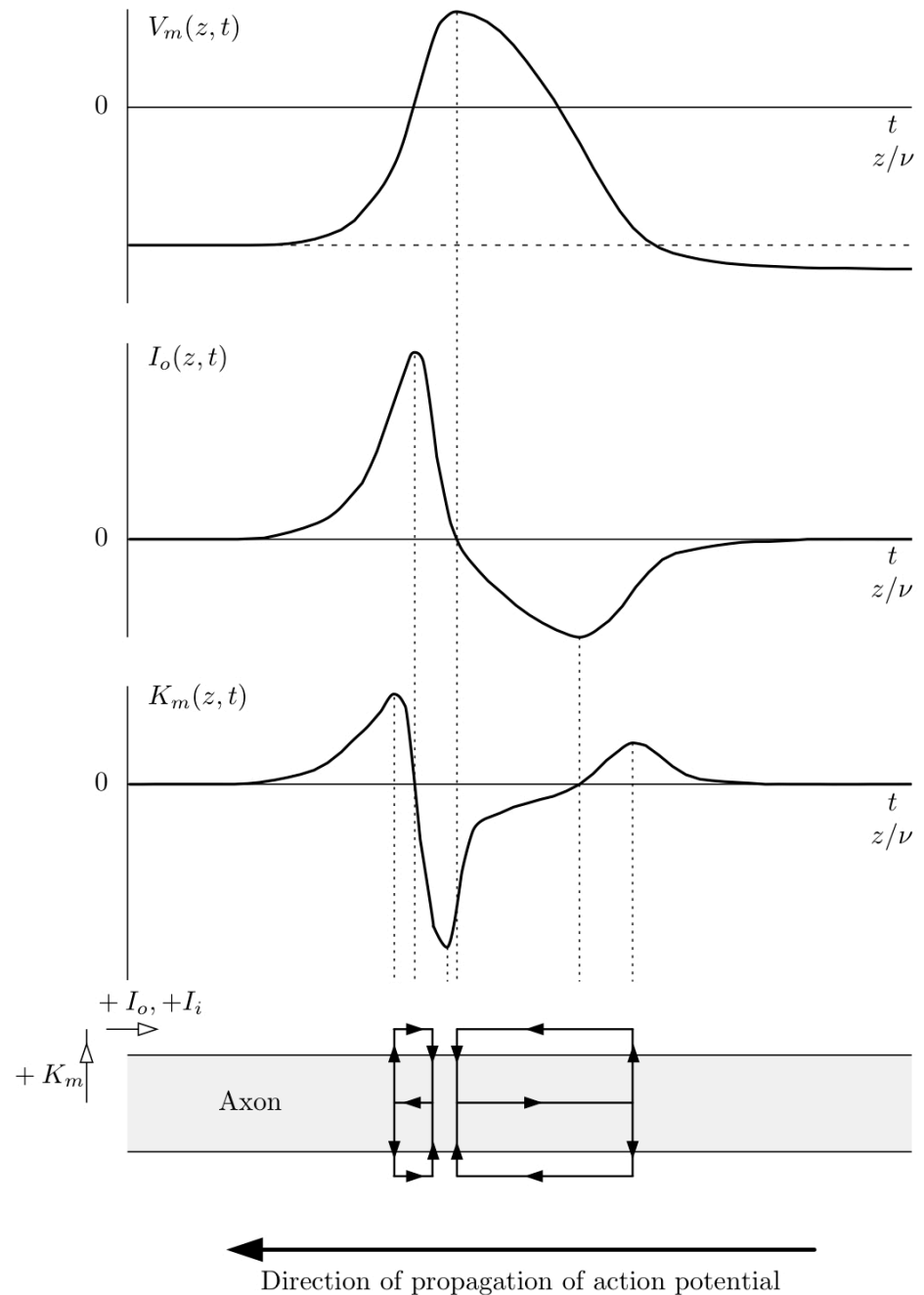


Figure 2.12



## Conduction Velocity (unmyelinated axon)

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

$$J_m(z, t) = K_m(z, t) / (2\pi a)$$

$$\frac{\partial^2 V_m(z, t) / \partial t^2}{J_m(z, t)} = 2\pi a (r_o + r_i) v^2$$

Left-side: constant, only depends upon electrical properties of membrane per unit area

Right-side: constant, velocity depends only upon axon diameter and fluid resistances

Conduction Velocity (unmyelinated axon)

$$\frac{\partial^2 V_m(z, t) / \partial t^2}{J_m(z, t)} = 2\pi a(r_o + r_i)v^2$$

Changing resistivity affects conduction velocity

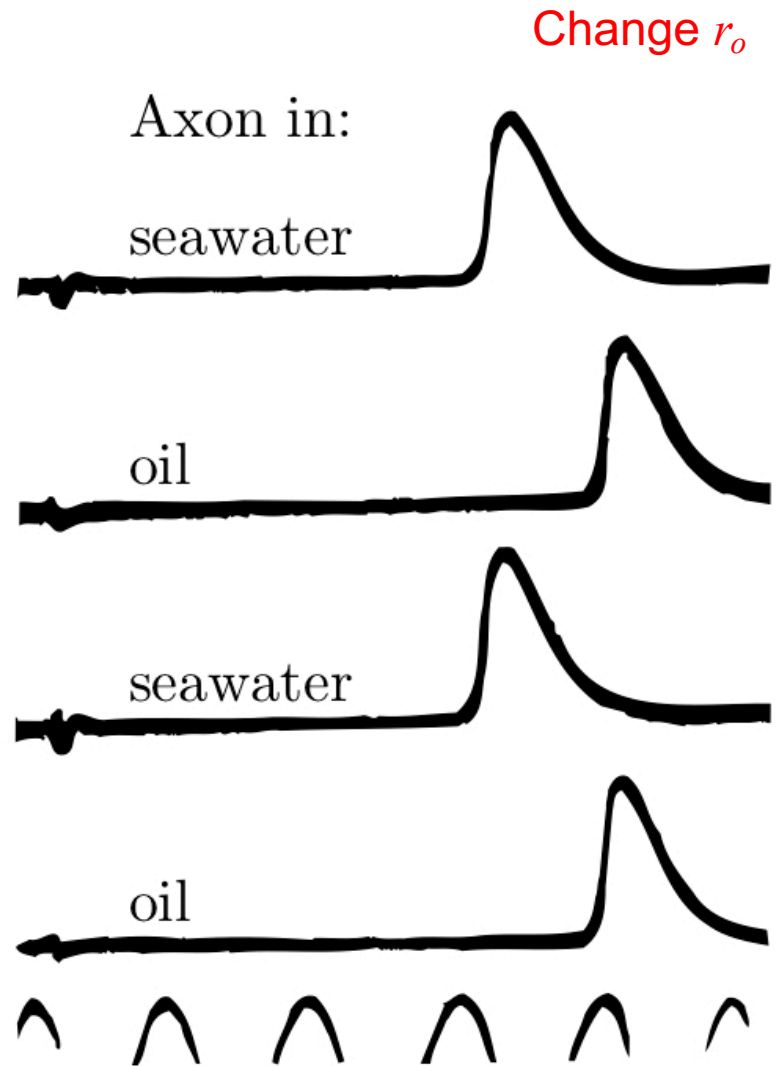
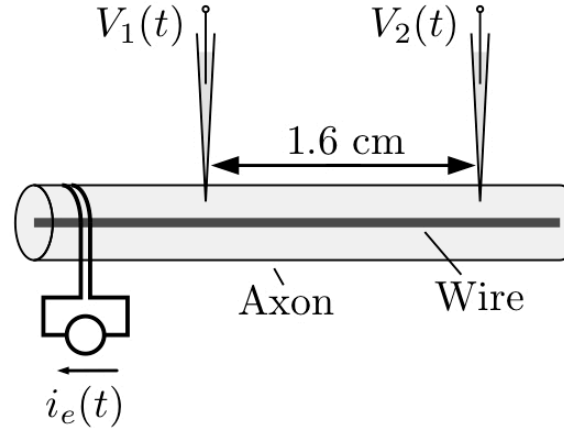
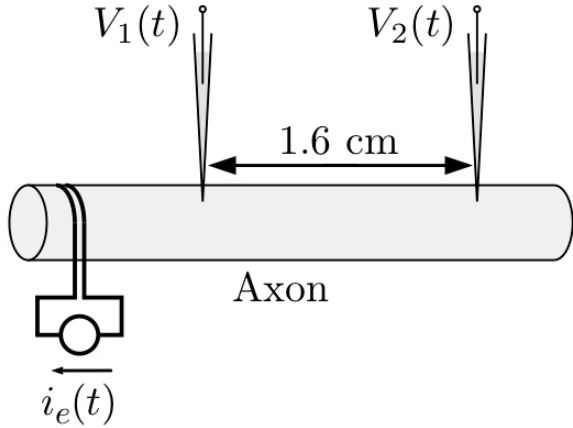


Figure 2.14

Conduction Velocity (unmyelinated axon)

Change  $r_i$



Inner wire essentially acts like a short

$$\frac{\partial^2 V_m(z, t) / \partial t^2}{J_m(z, t)} = 2\pi a(r_o + r_i)v^2$$

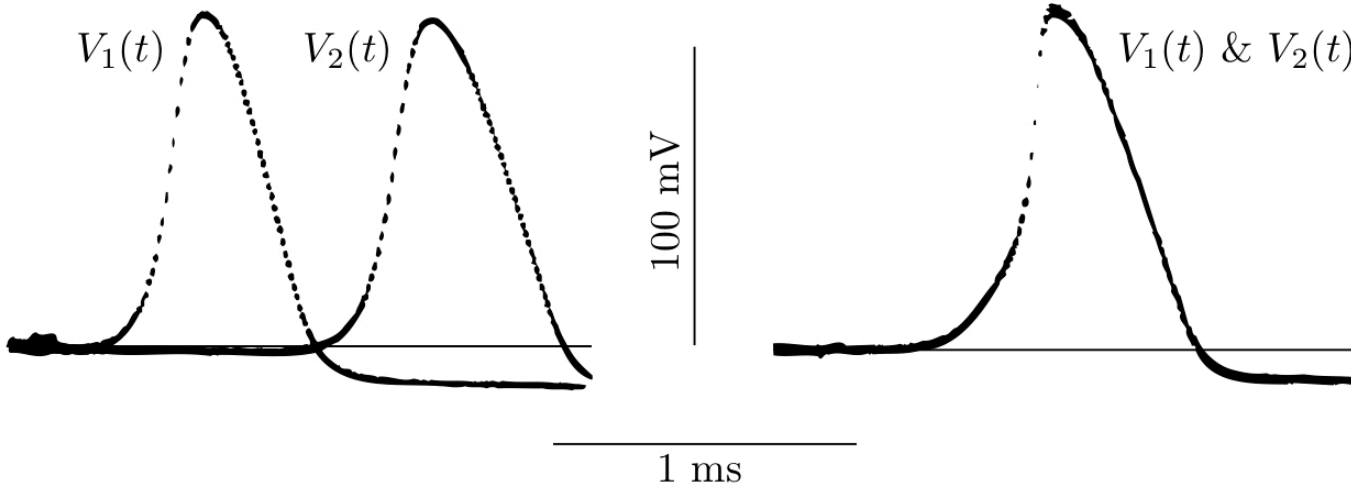


Figure 2.15

→ 'Space clamp'

## Conduction Velocity (unmyelinated axon)

Assume  $r_i \gg r_o$

$$2\pi a r_i v^2 = \kappa_m$$

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

$$v = \sqrt{\frac{\kappa_m a}{2\rho_i}}$$

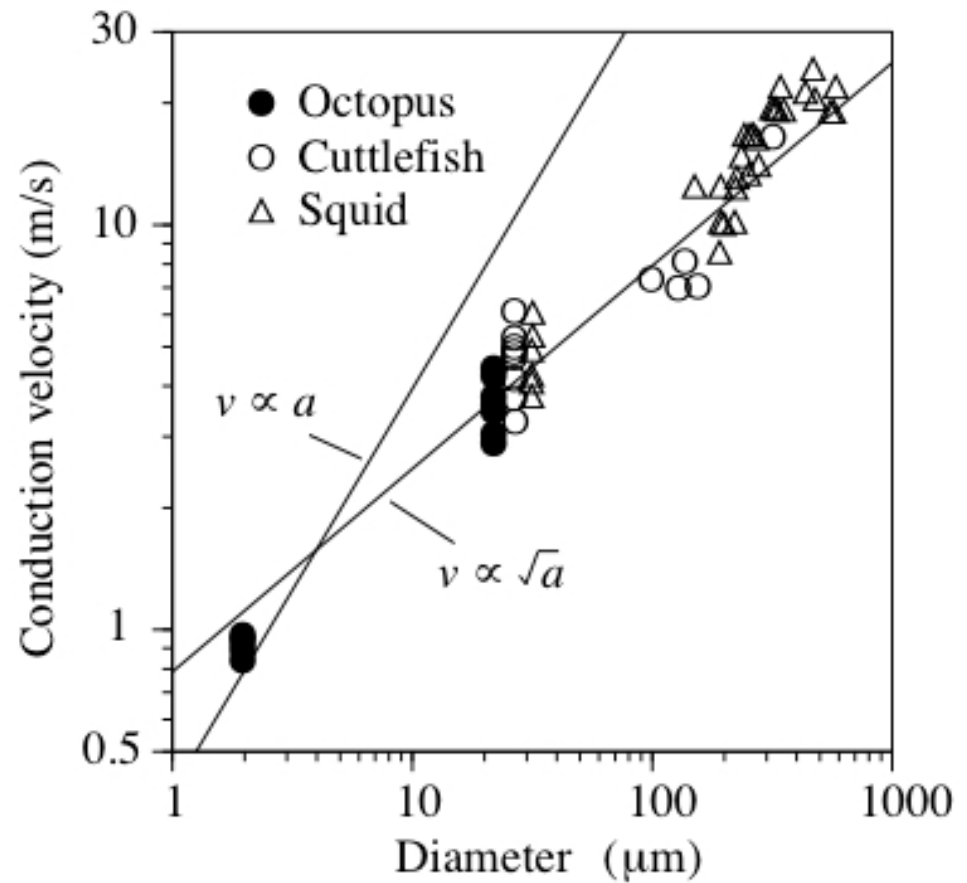


Figure 2.16

→ thicker axons = faster propagation

## Core Conductor Model

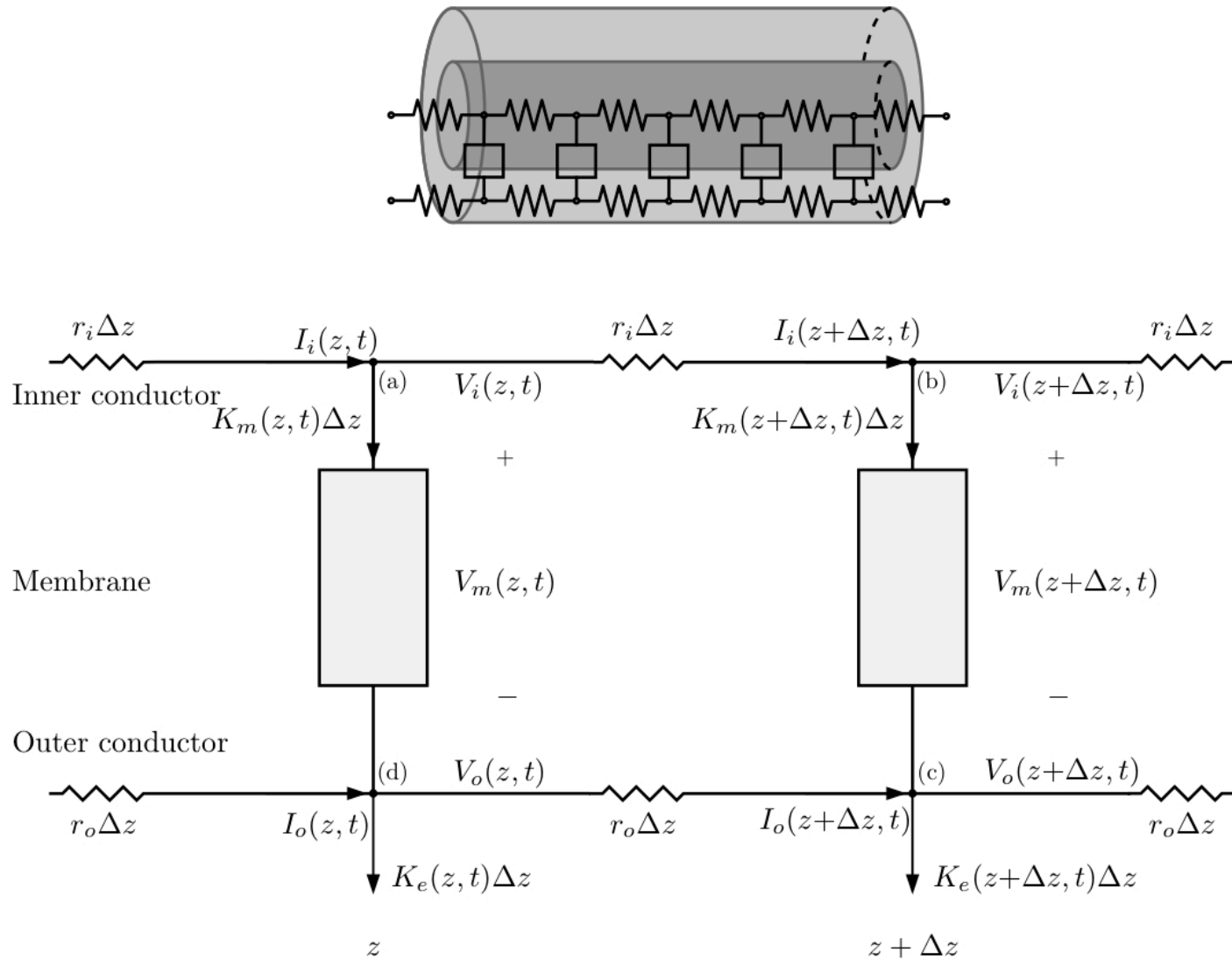
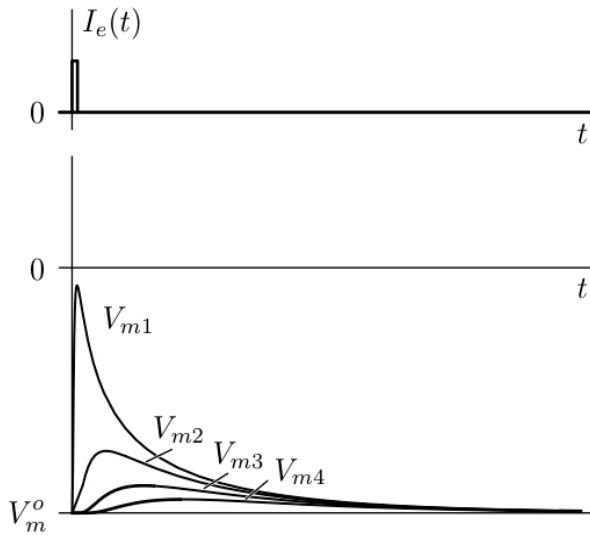
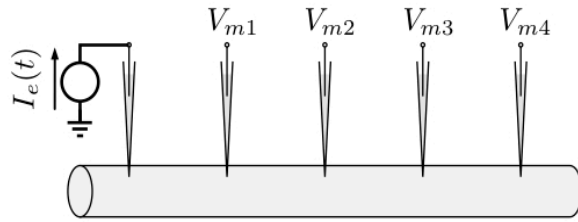
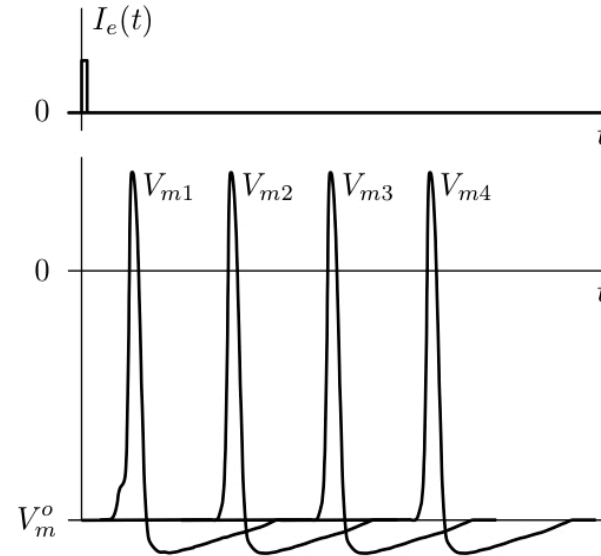
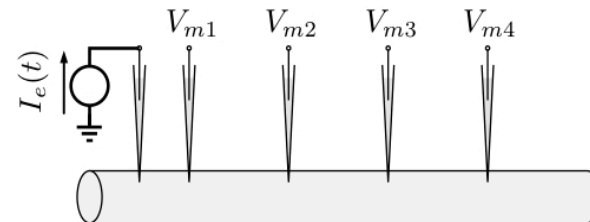


Figure 2.7

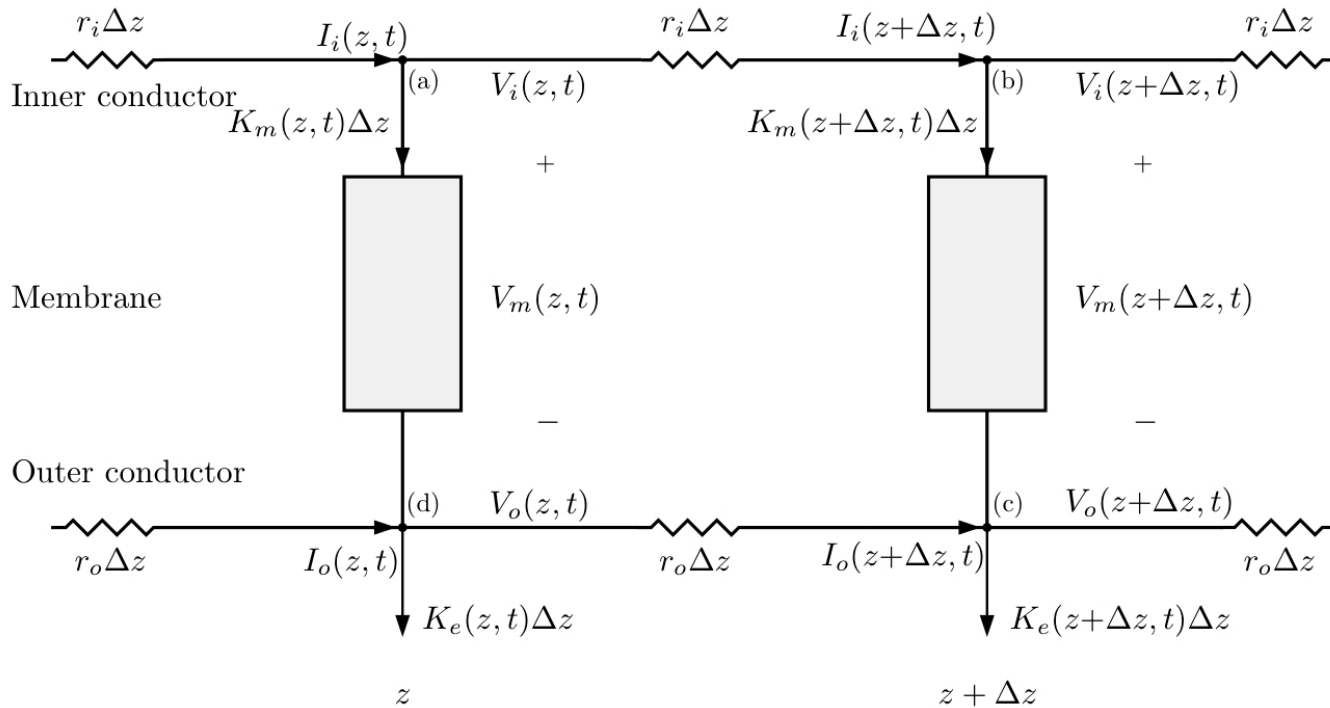
Decremental conduction



Decrement-free conduction



**Core-Conductor Model** (starting point) → Model for electrically large cells

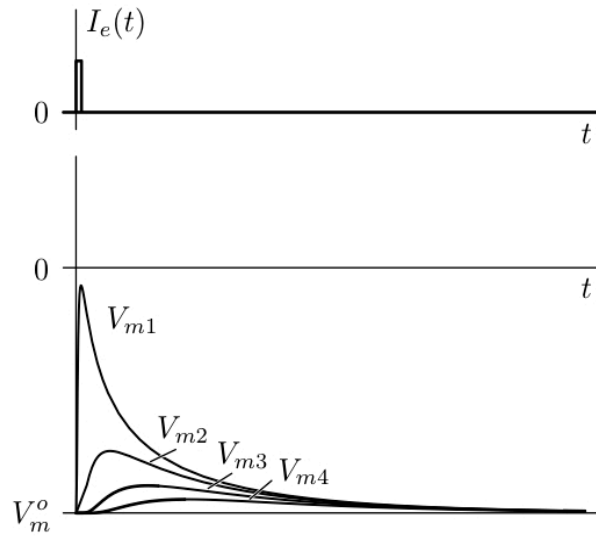
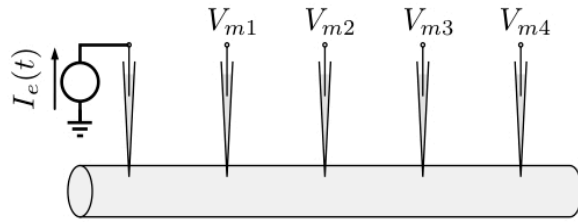


No assumptions made about membrane!

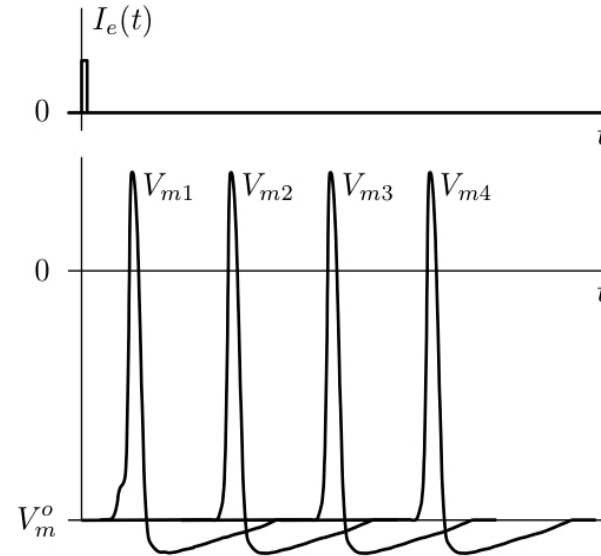
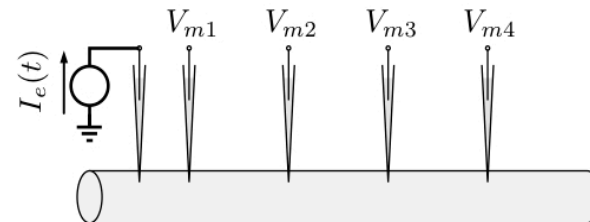
## THE Core – Conductor Equation

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

Decremental conduction



Decrement-free conduction



Note dynamics of response....



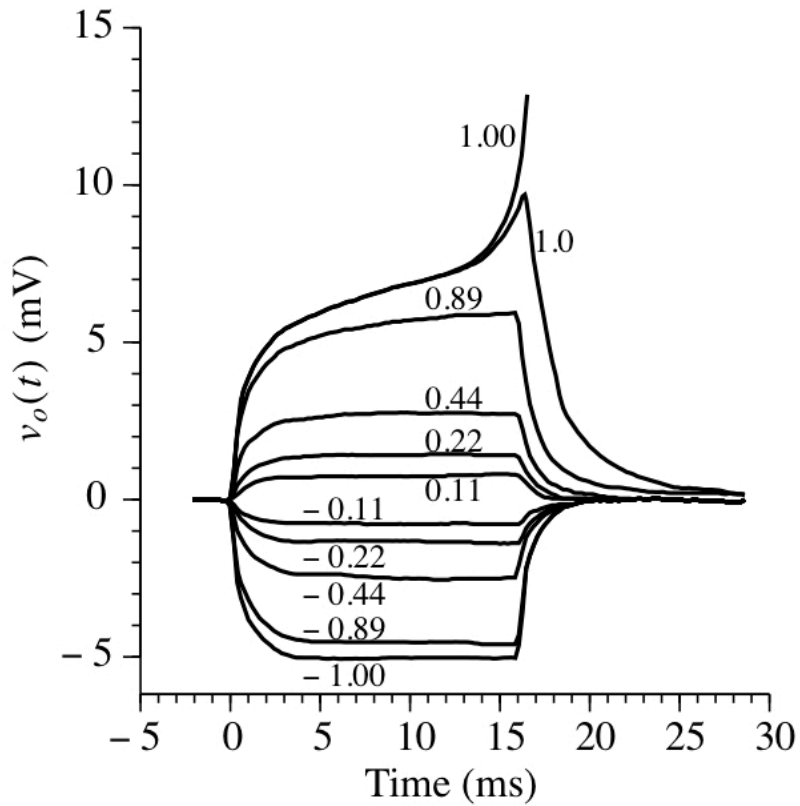


Figure 3.1

1. Linear (to a point)

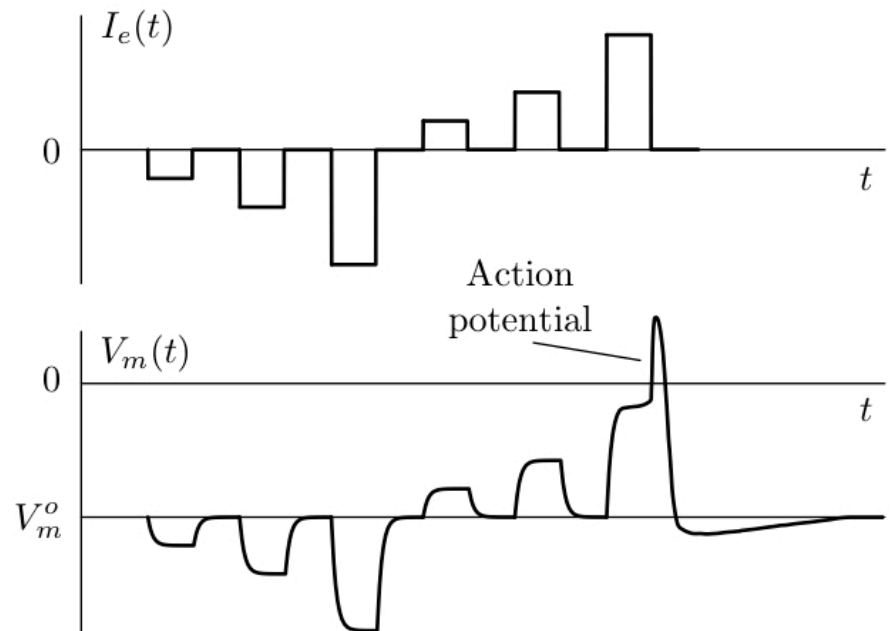
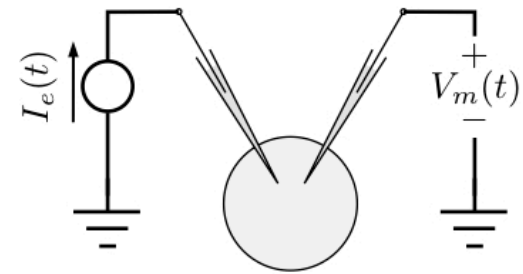


Figure 1.8

2. Delay apparent

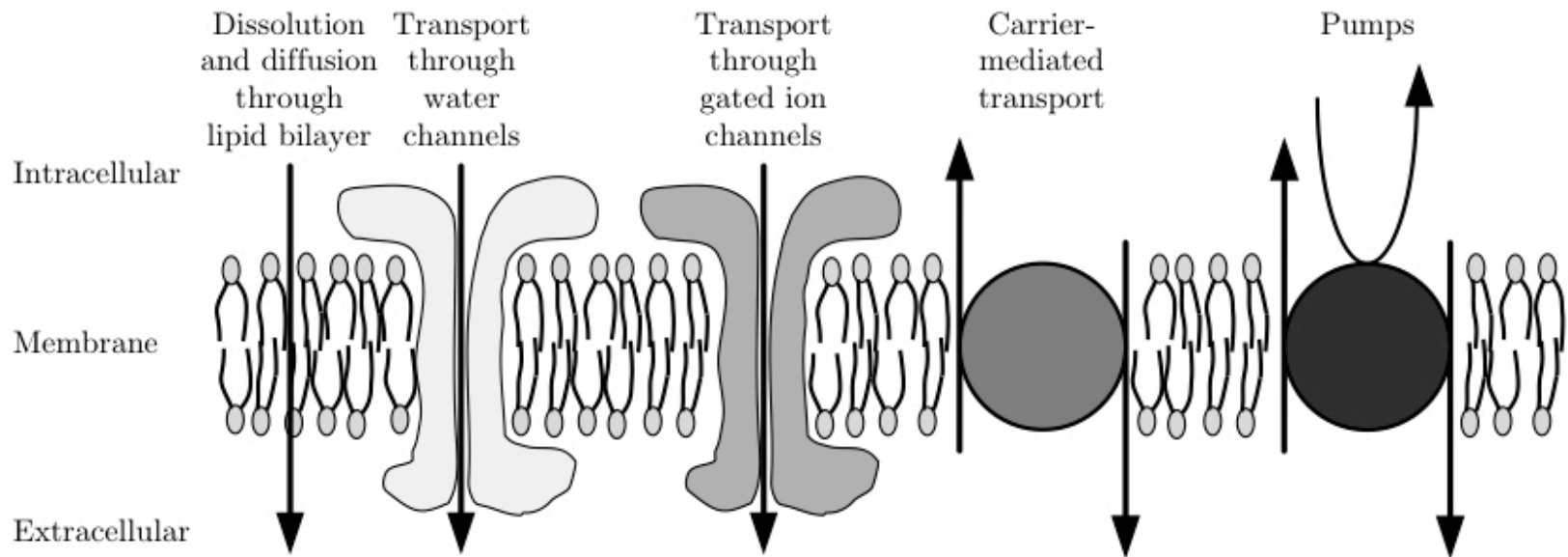
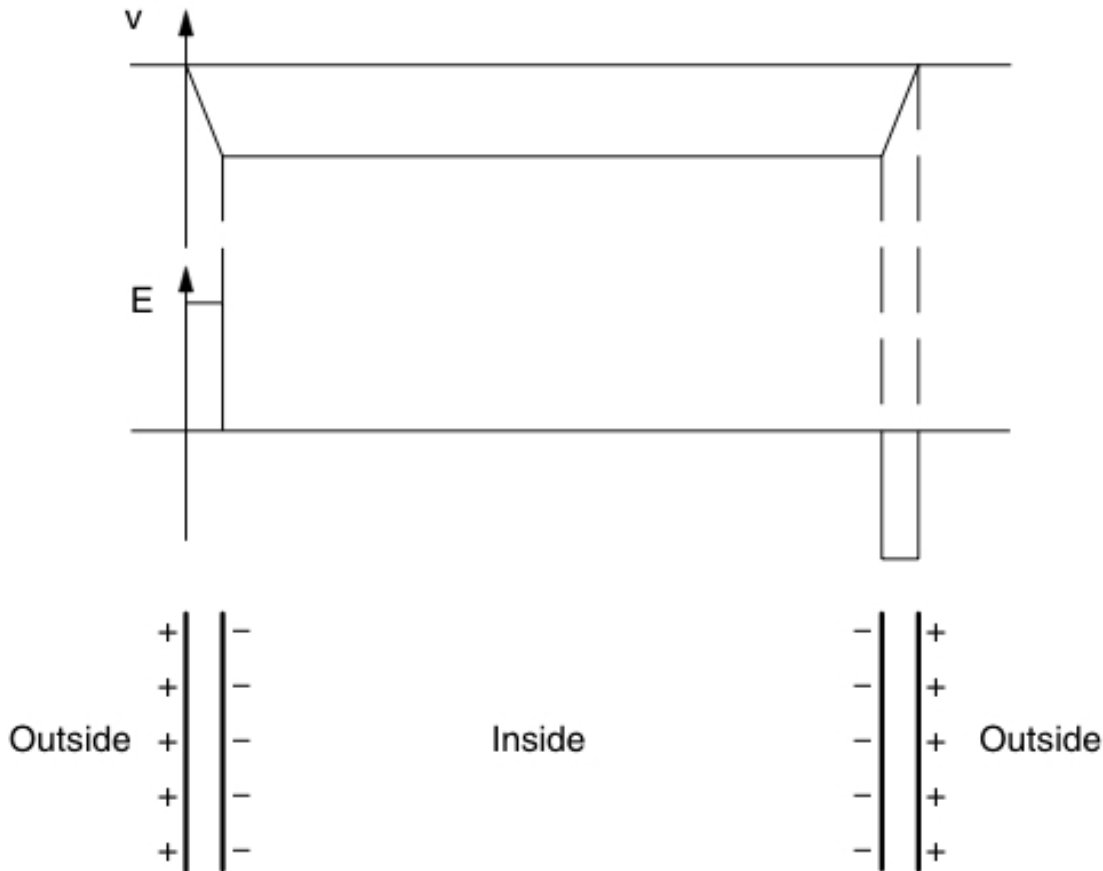


Figure 2.19

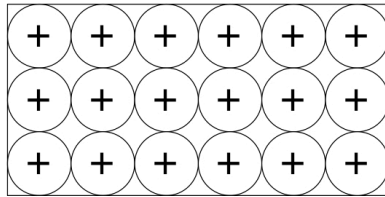
Idea: Membrane not only allows for charge transport, but also charge separation

## Cell Membrane = Capacitor

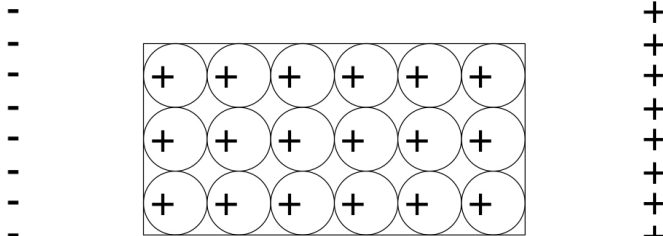


- Steady-state electrodiffusion cause charge buildup on both sides of membrane
- Charge separation acts like parallel-plate capacitor  
( $C \sim 1 \mu\text{F}/\text{cm}^2$ )

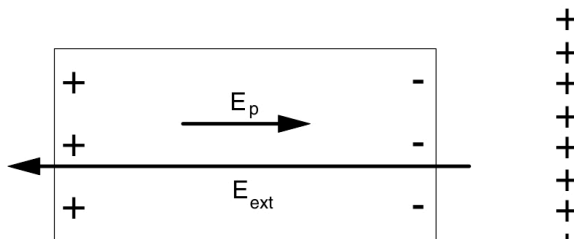
# Lipid Bilayer = Dielectric



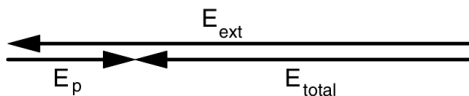
(a)



(b)



(c)

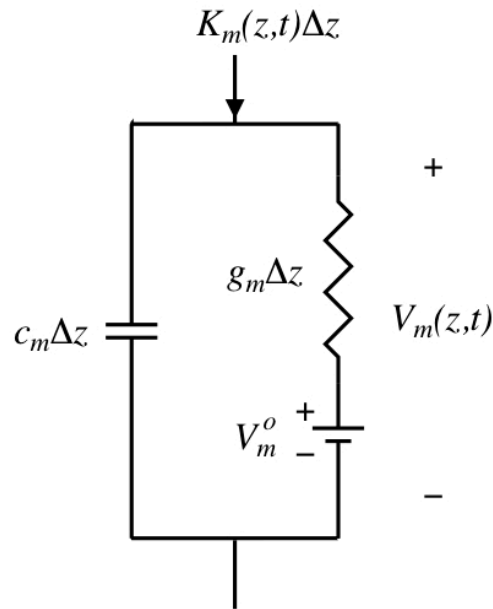
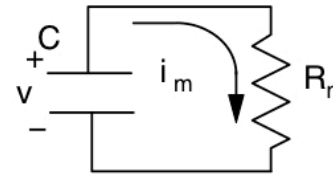
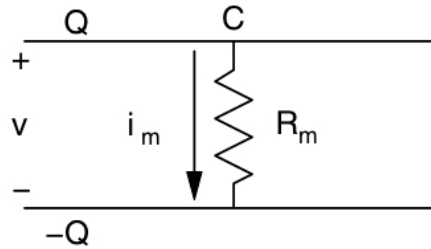
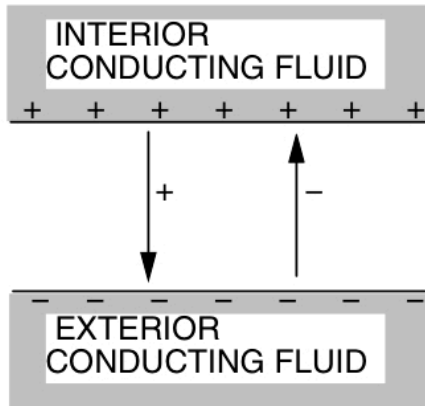


(d)

- Lipid bilayer is an insulator  
(i.e., acts as a dielectric w/ const.  $\kappa$ )

-  $\kappa \sim 3-7$ , meaning more charge separation can occur (higher capacitance)

# Circuit Representation

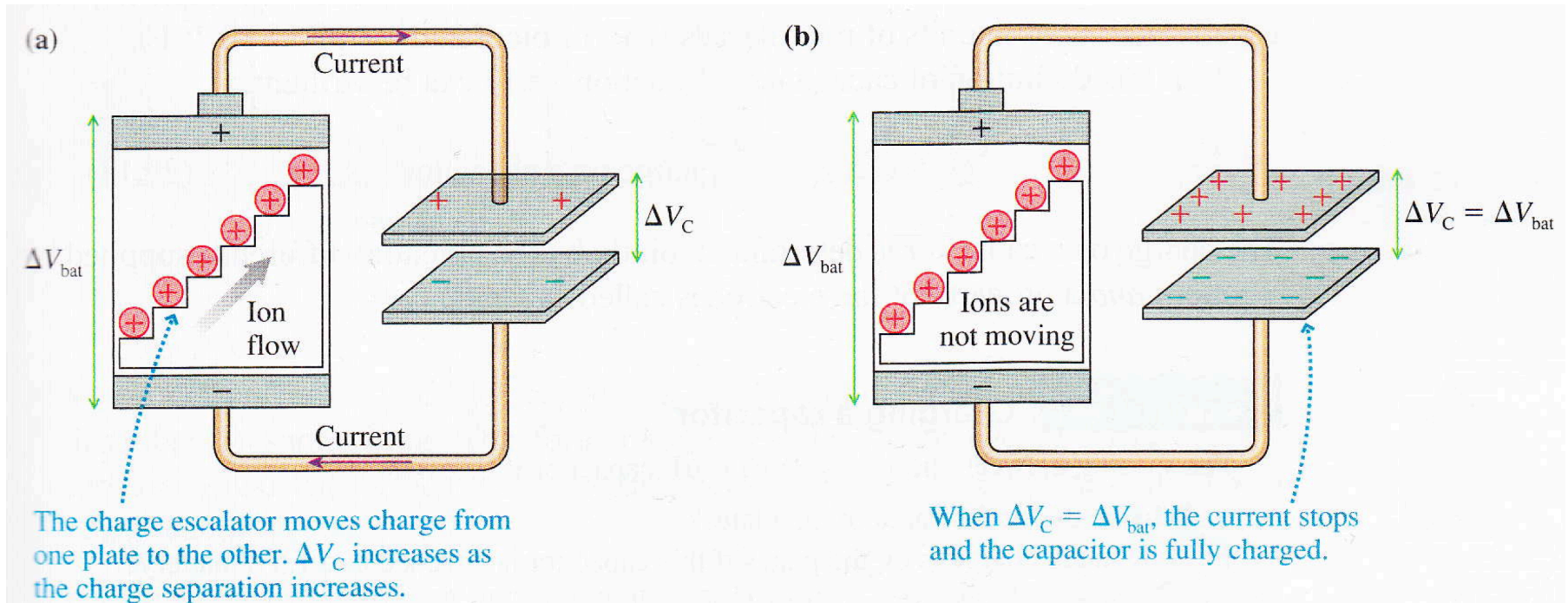


Resistor and capacitor in series  
 → RC time constant

Figure 3.6

## Review: Capacitance

- Charging a parallel-plate capacitor



$$Q = C \Delta V_C \quad (\text{charge on a capacitor})$$

→ Stored charge is proportional to potential difference. Constant of proportionality is characterizes the “capacitance”

## Review: RC Circuits

KVL (combined w/ Ohm's law):

$$\Delta V_{\text{cap}} + \Delta V_{\text{res}} = \frac{Q}{C} - IR = 0$$

$$I = -\frac{dQ}{dt}$$

Negative because resistor current removes charge from capacitor

$$\frac{dQ}{dt} + \frac{Q}{RC} = 0 \qquad \frac{dQ}{Q} = -\frac{1}{RC} dt$$

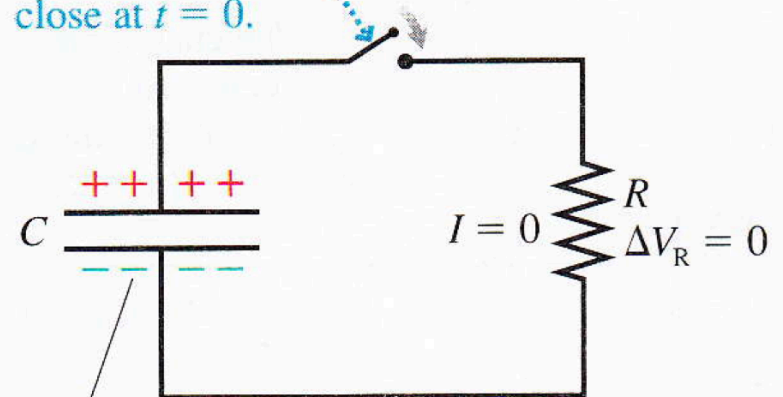
$$\int_{Q_0}^Q \frac{dQ}{Q} = -\frac{1}{RC} \int_0^t dt$$

$$\ln Q \Big|_{Q_0}^Q = \ln Q - \ln Q_0 = \ln \left( \frac{Q}{Q_0} \right) = -\frac{t}{RC}$$

$$Q = Q_0 e^{-t/RC}$$

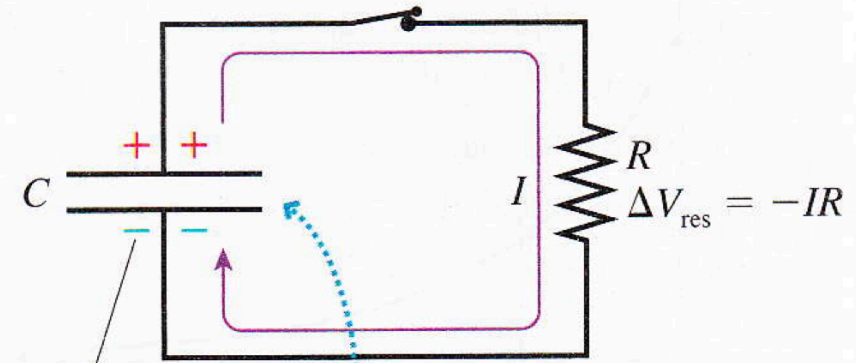
(a) Before the switch closes

The switch will close at  $t = 0$ .



Charge  $Q_0$   
 $\Delta V_0 = Q_0/C$

(b) After the switch closes



Charge  $Q$   
 $\Delta V_{\text{cap}} = Q/C$

The current is reducing the charge on the capacitor.

## Review: RC Circuits

$$Q = Q_0 e^{-t/RC}$$

$$Q = C \Delta V_C$$

$$\tau = RC$$

$$\Delta V_C = \Delta V_0 e^{-t/\tau}$$

“RC time constant”

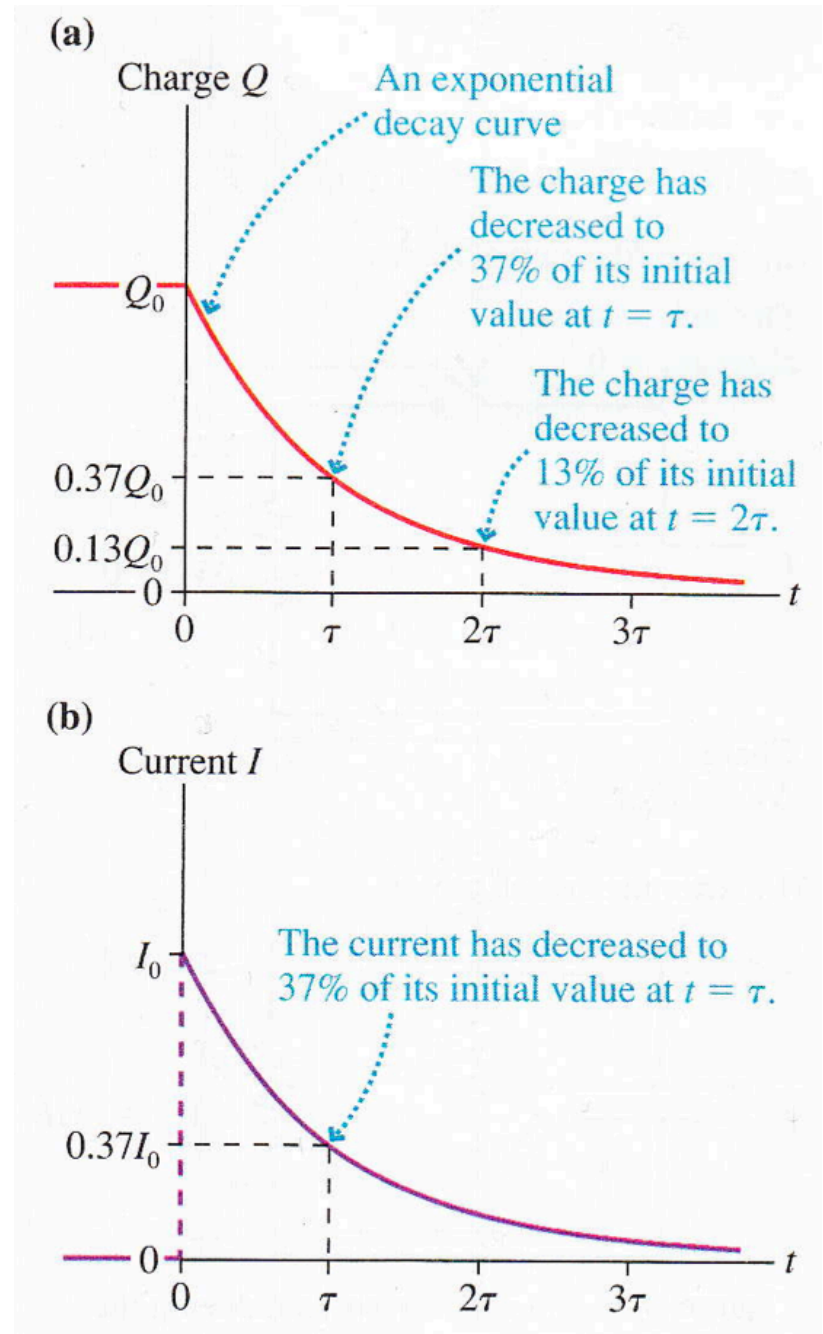
→ Resistor dissipates energy stored in the capacitor

Current through the capacitor?

$$I = \frac{dQ}{dt}$$

$$I_C = C \frac{dV_C}{dt}$$

$$Q = C V_C$$





# Review: RC Circuits

**DC** (some energy initially stored via charged capacitor) → **KCL**

$$C \frac{dV}{dt} + \frac{V}{R} = 0$$

$$V(t) = V_o e^{-\frac{t}{RC}}$$

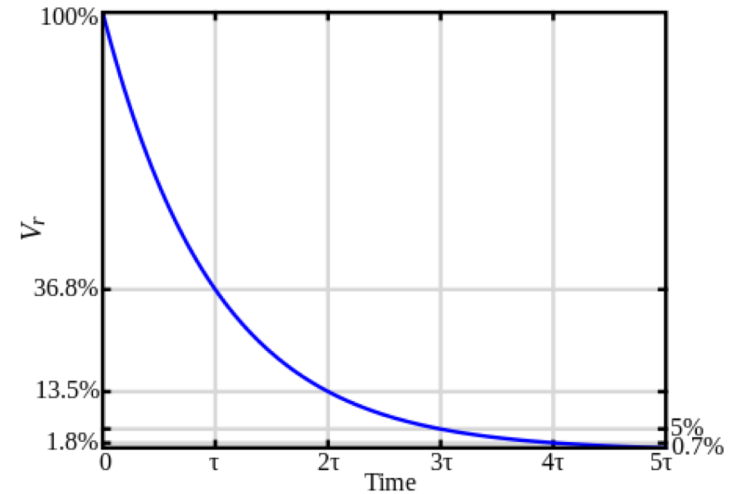
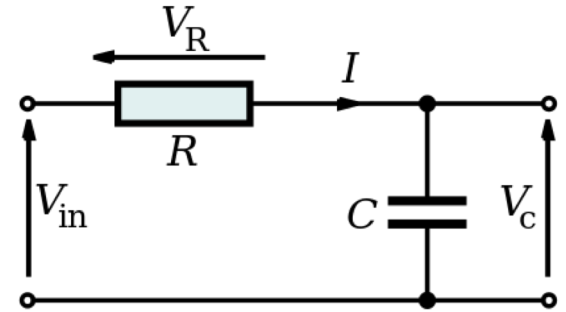
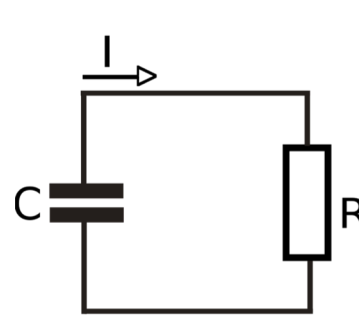
$$\tau = RC$$

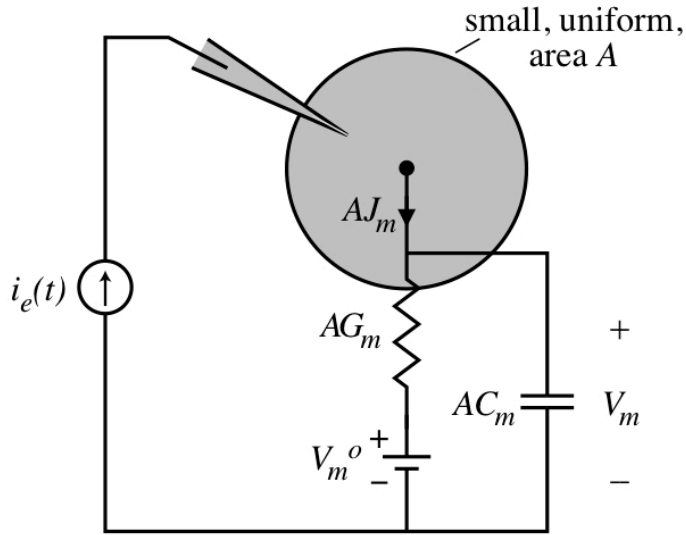
“RC time constant”

**AC** (sinusoidally-driven at  $\omega$ , steady-state) → **KVL**

$$Z = R - \frac{i}{\omega C}$$

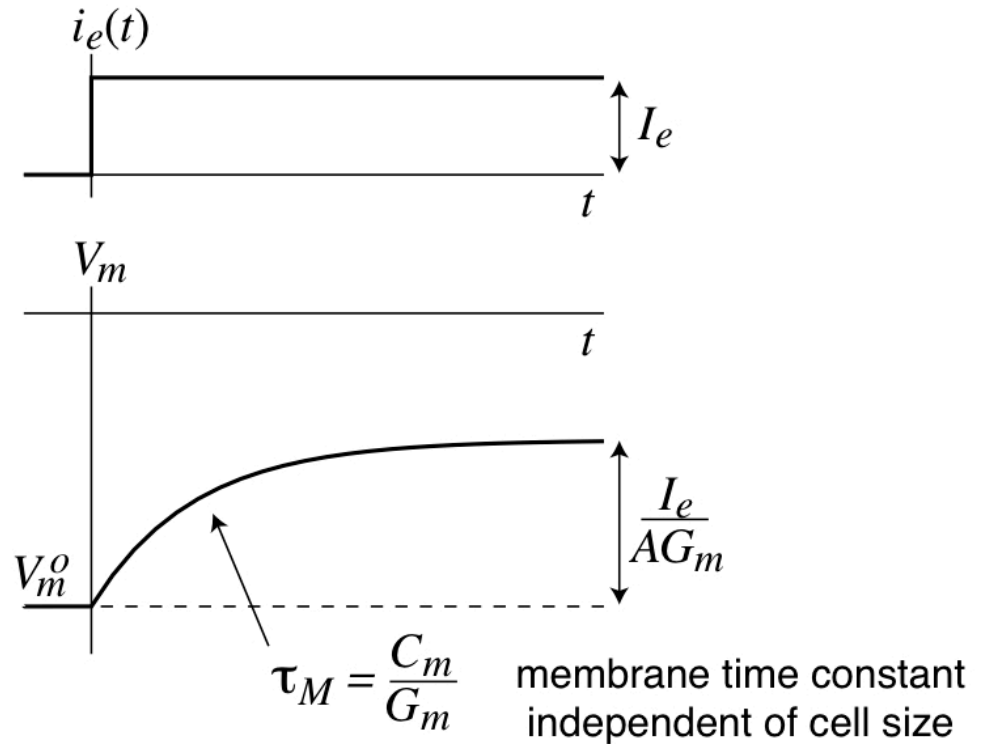
Think: RLC without the inductor

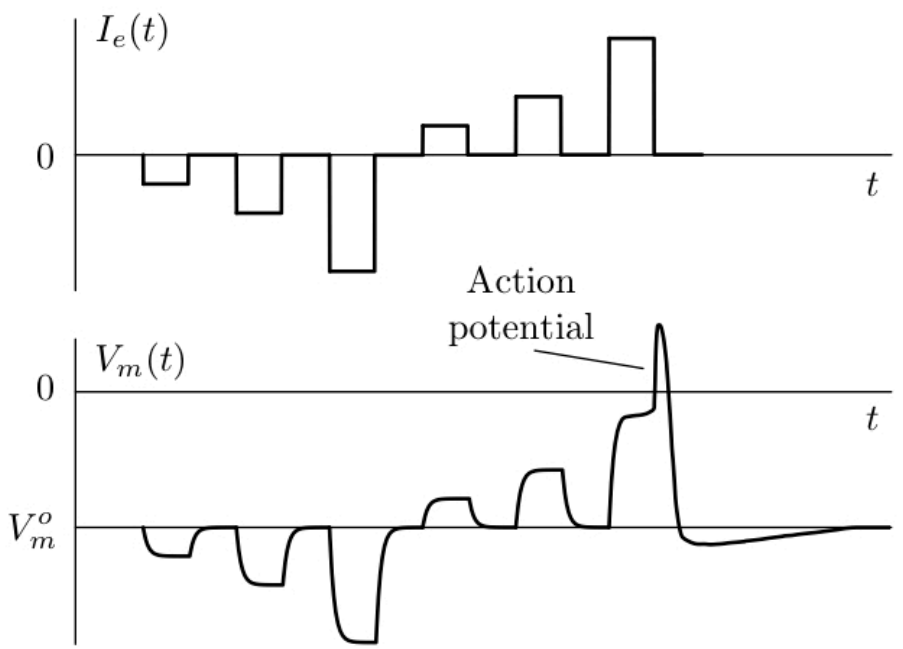
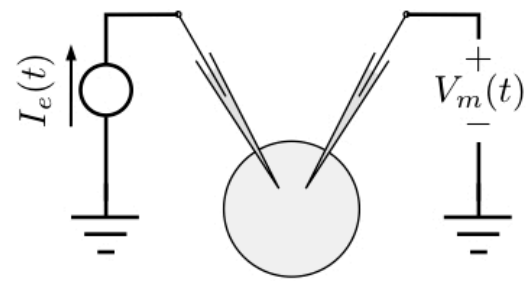
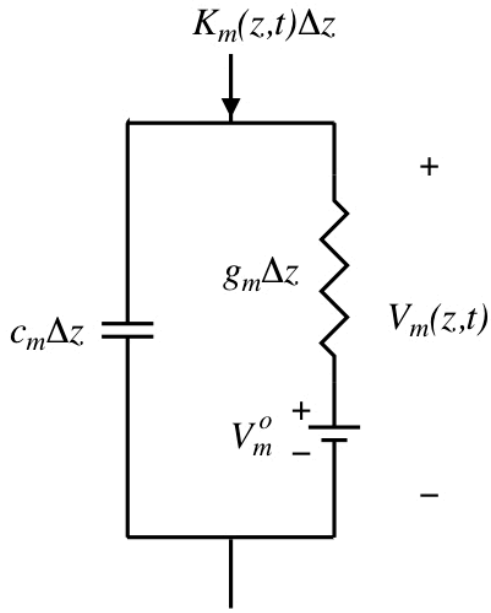




$$i_e(t) = AJ_m = AC_m \frac{dV_m}{dt} + AG_m(V_m - V_m^o)$$

$$\frac{AC_m}{AG_m} \frac{dV_m}{dt} + V_m = V_m^o + \frac{i_e(t)}{AG_m}$$





→ Delay explained  
(but not action potentials yet!)

Figure 1.8

## Cable Model - History

- First solved by William Thomson (aka Lord Kelvin) in ~1855
- Motivated by Atlantic submarine cable for intercontinental telegraphy

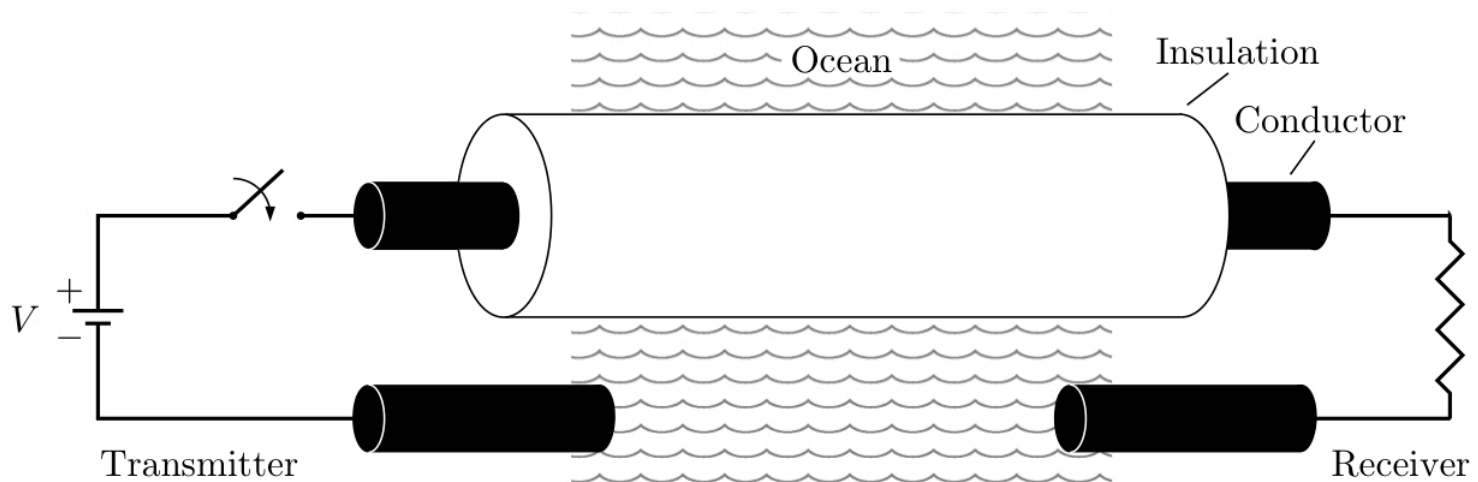


Figure 3.8

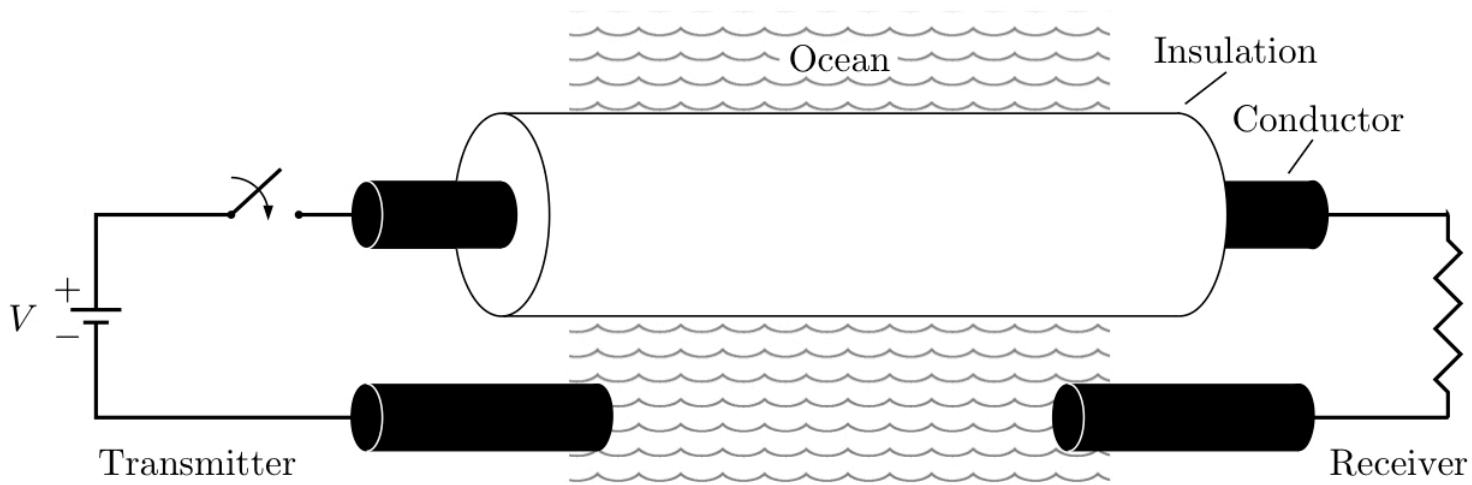


Figure 3.8

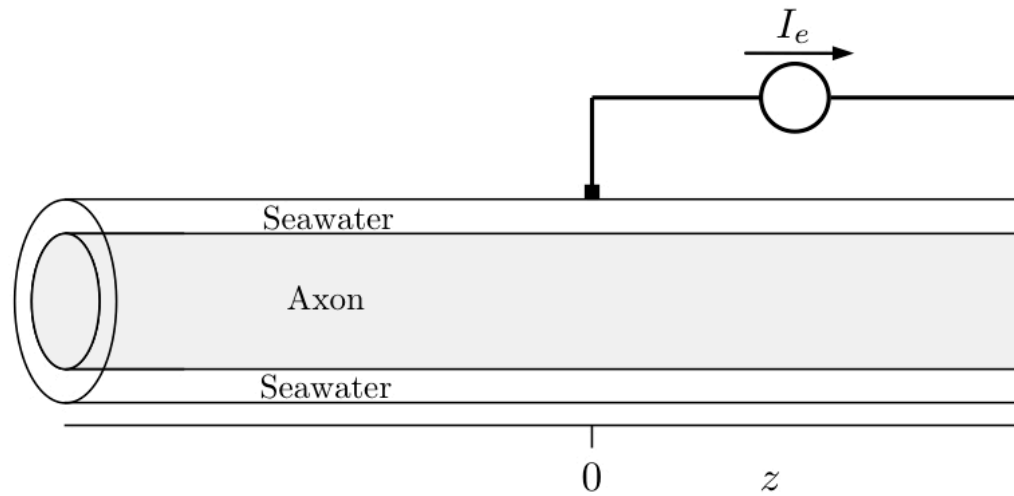


Figure 3.9

## Cable Model - Overview

- Uses the Core Conductor model as underlying basis
- Assumes membrane that it can be described as a parallel capacitance and conductance
- Linear

### Core Conductor Model

