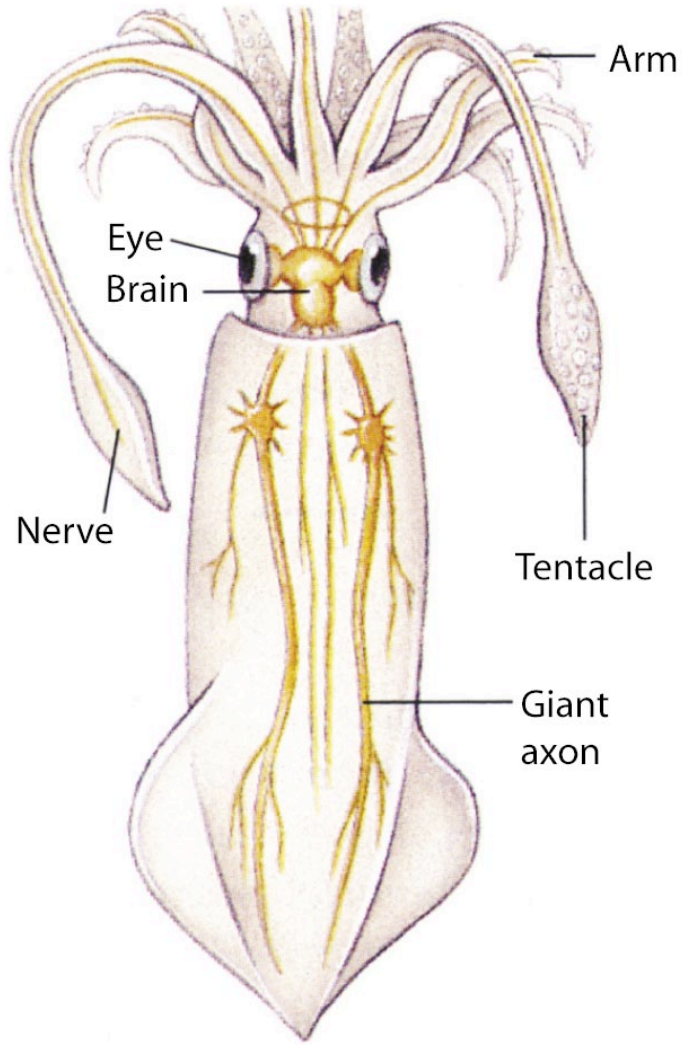
J. Physiol. (1952) 117, 500–544

A QUANTITATIVE DESCRIPTION OF MEMBRANE CURRENT AND ITS APPLICATION TO CONDUCTION AND EXCITATION IN NERVE

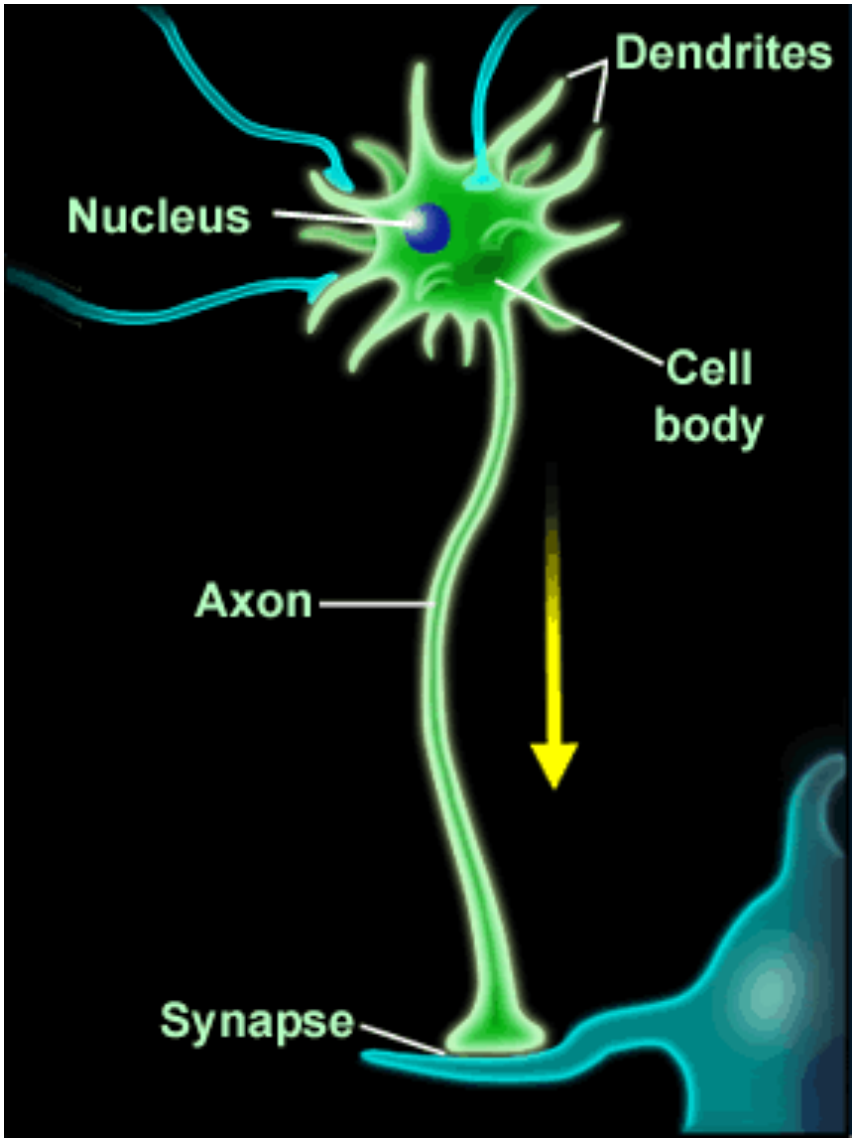
By A. L. HODGKIN and A. F. HUXLEY

From the Physiological Laboratory, University of Cambridge

(*Received* 10 *March* 1952)

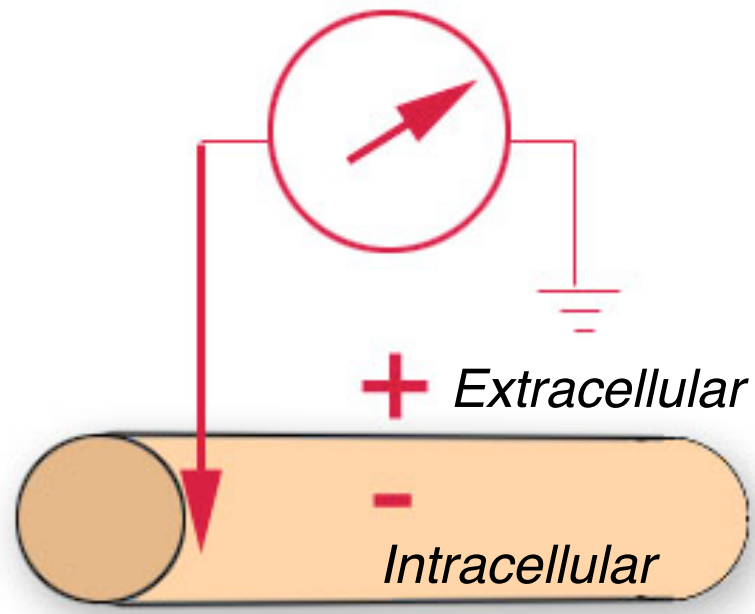


Neurons – Fundamental units of computation



Resting Membrane Potential

- **Difference in voltage between the interior and exterior of a neuron**



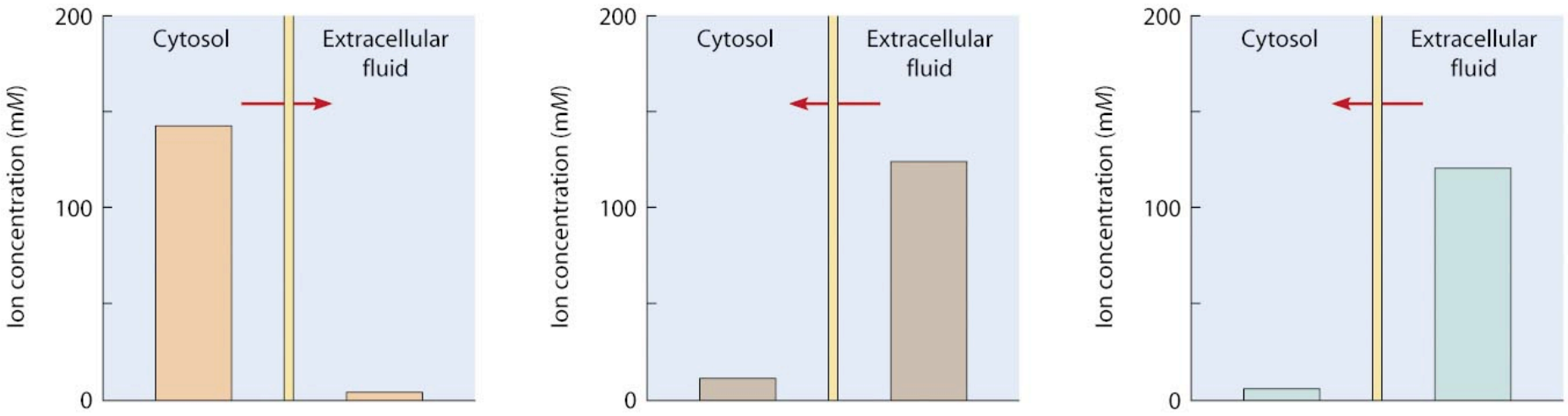
- **Three main players**
  - Salty fluids on either side of the membrane
  - The membrane itself
  - Proteins that span the membrane

Typical Ionic Concentrations

(a) Potassium ions (K^+). K^+ are more concentrated in the cytosol and have a tendency to move out of the cell, leaving behind trapped anions. Membrane potential becomes more negative.

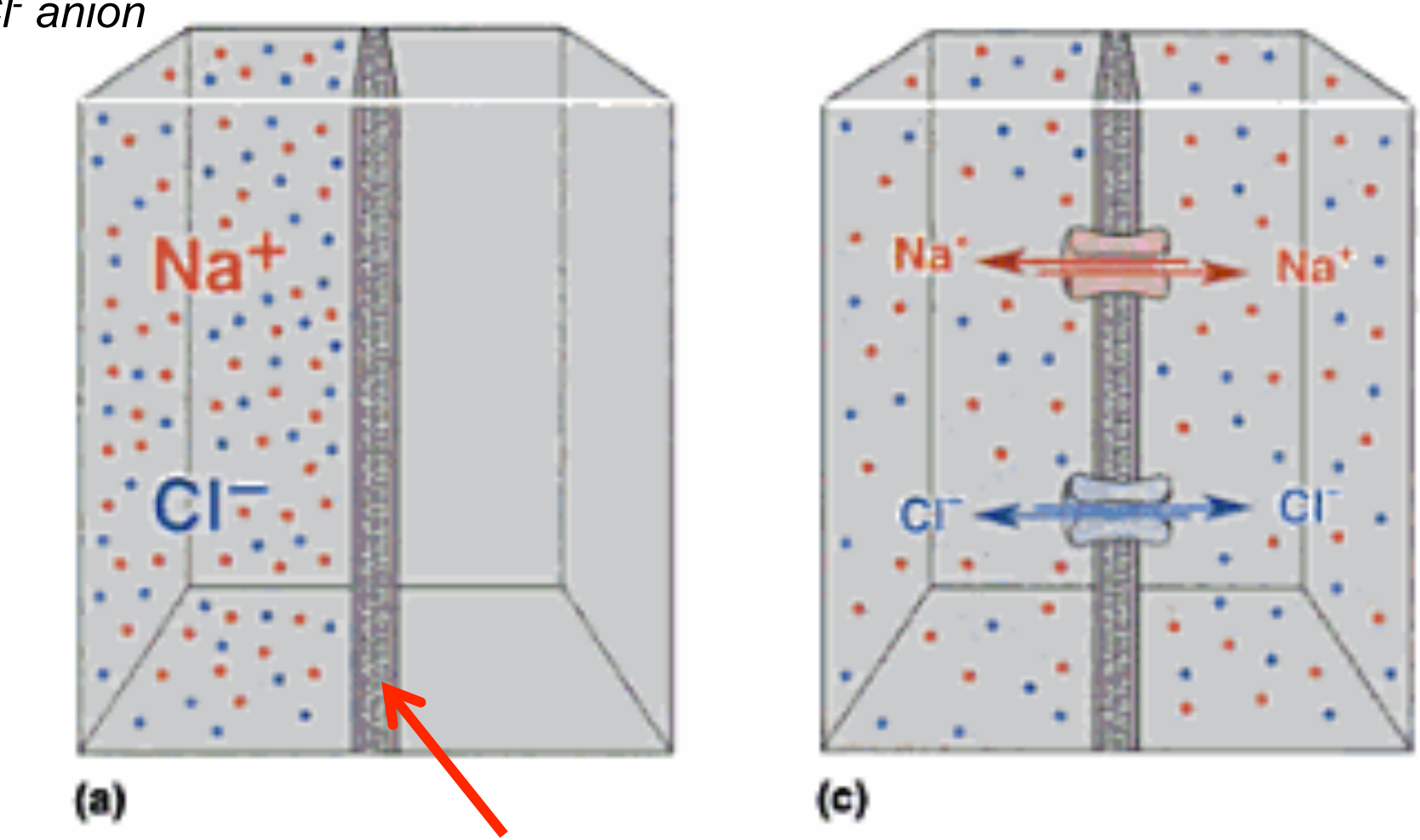
(b) Sodium ions (Na^+). Na^+ are much more concentrated outside the cell than inside and tend to enter the cell. As Na^+ ions enter, they neutralize some excess negative charge in the cytosol, and membrane potential becomes more positive.

(c) Chloride ions (Cl^-). Cl^- usually crosses the membrane together with a permeable cation (normally K^+). As Cl^- enters a cell, it tends to make the membrane potential more negative.



Movements of ions - Diffusion

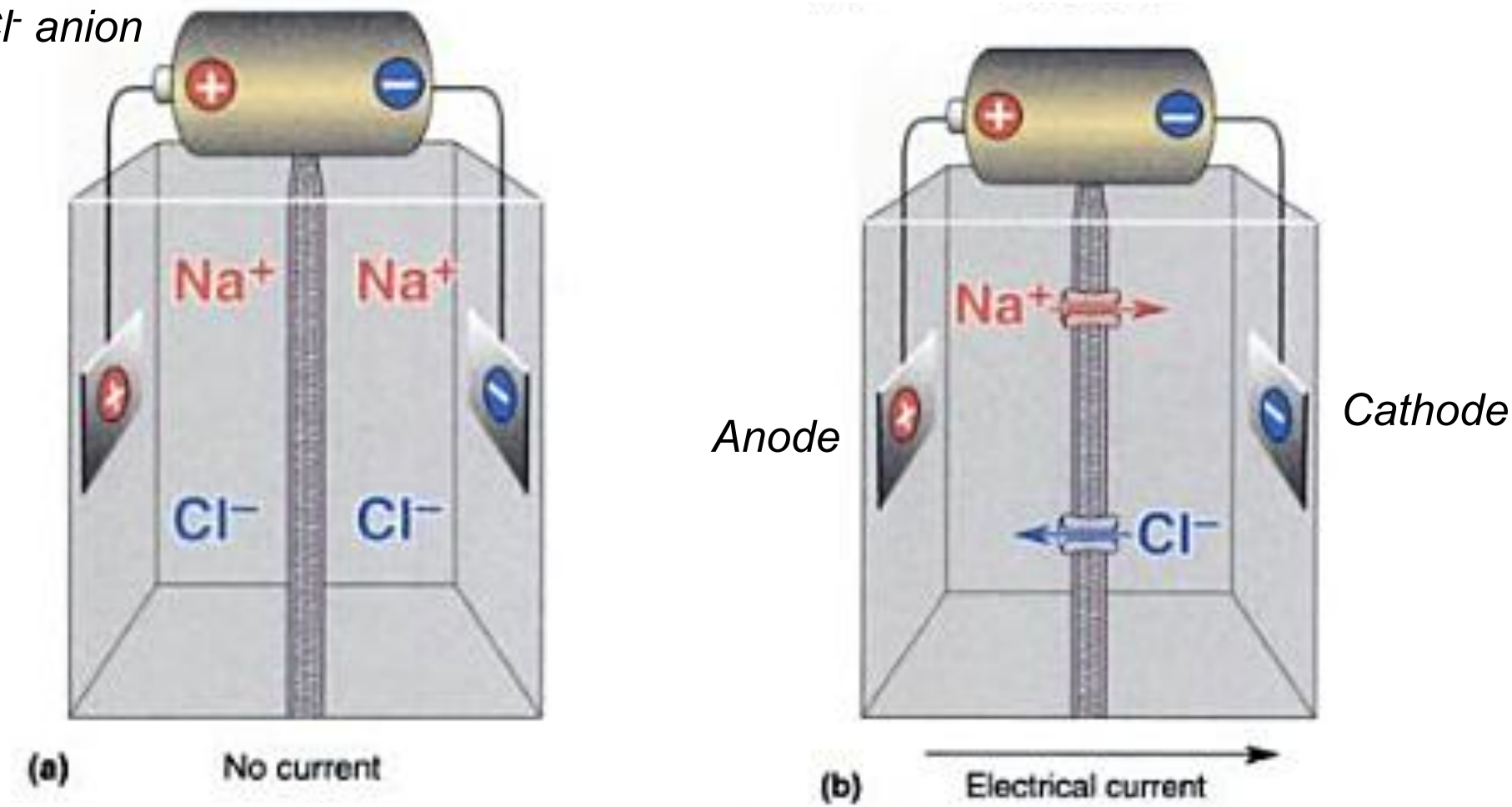
Na^+ cation
Cl^- anion



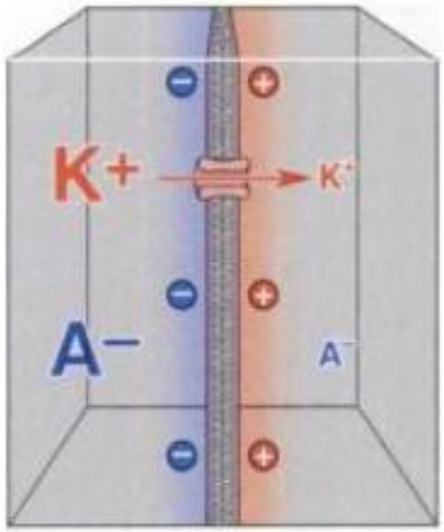
Membrane impermeable to the ions

Movements of ions – Electric Field

Na^+ cation
Cl^- anion

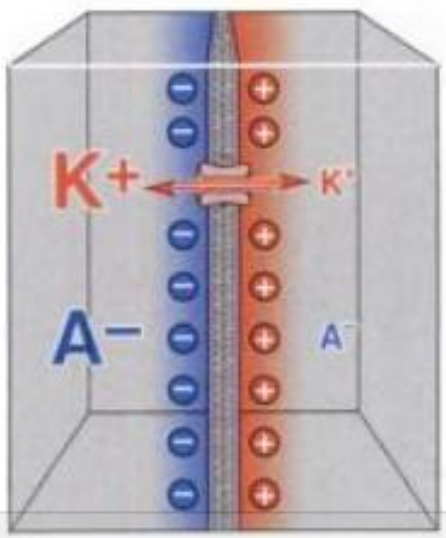


Establishing equilibrium



(b)

Diffusion causes Potassium ions to move from region of higher concentration (intracellular side) to a region of lower concentration (extracellular side)



(c)

A net accumulation of positive charge on the outside and negative charge on the inside retards movement of K^+

An equilibrium is established such that there is no movement of ions and there is a charge difference

Neuroscience, Bear et al. 3rd edition

Reversal potential

- **Nernst Equation**

$$E_{ion} = \frac{RT}{zF} \ln \frac{[ion_{out}]}{[ion_{in}]}$$

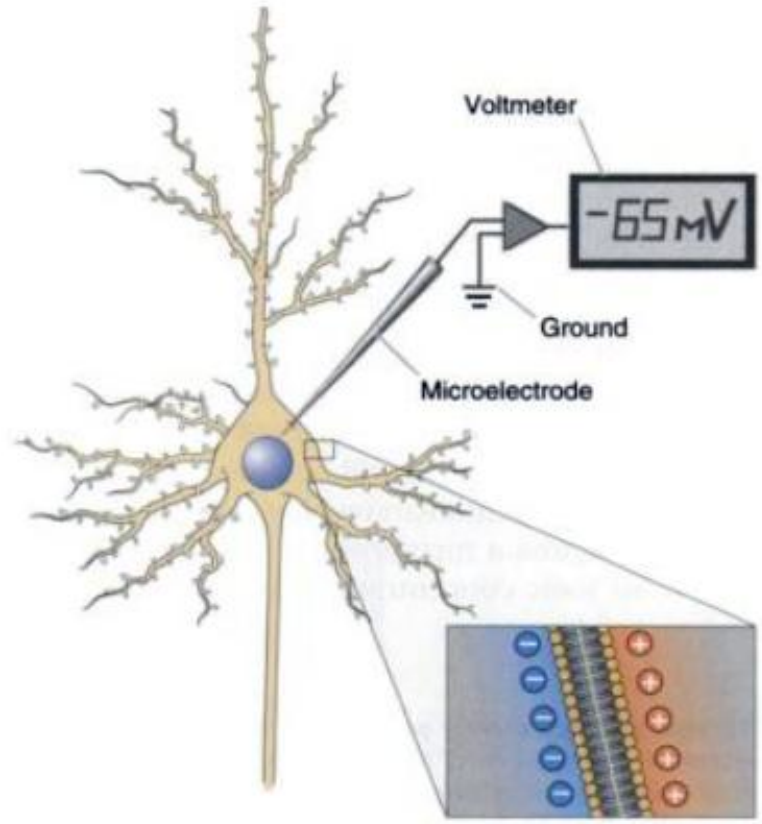
$[ion_{in}]$, $[ion_{out}]$ are ionic concentration inside and outside the cell
T is temperature (Kelvins)
R is gas constant
z is the valence of the ion
F is Faraday's constant: it is the magnitude of electric charge per mole of electrons

Reversal potential at 25C
E_{NA} = 55mV
E_K = -77 mV
E_{CL} = -61 mV

Resting membrane potential

- **Goldman Hodgkin and Katz equation**

$$E_{Na,K,Cl} = \frac{RT}{F} \ln \frac{P_K[K_{out}] + P_{Na}[Na_{out}] + P_{Cl}[Cl_{in}]}{P_K[K_{in}] + P_{Na}[Na_{in}] + P_{Cl}[Cl_{out}]}$$

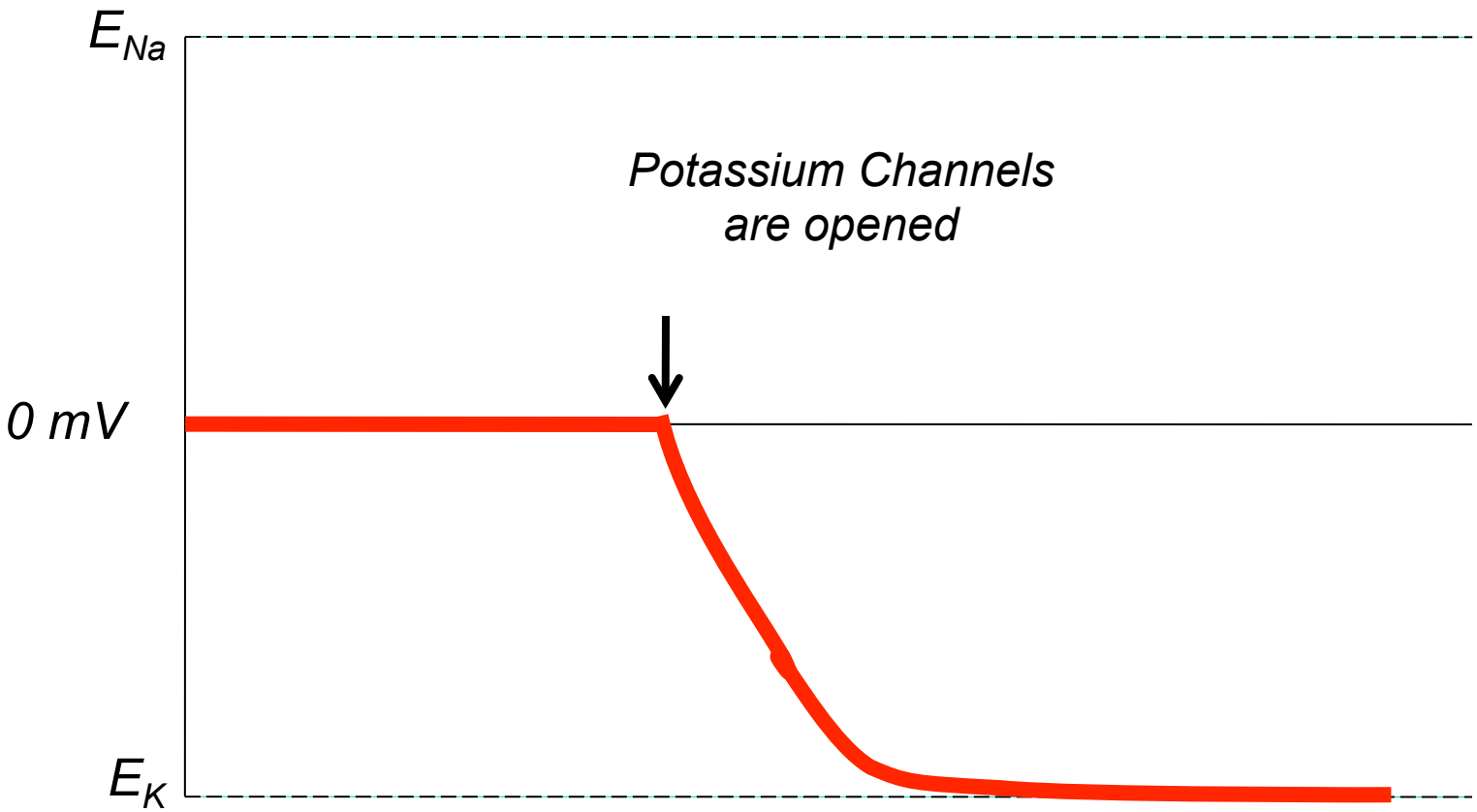


Typical resting membrane potential
V_{rest} = -65 mV

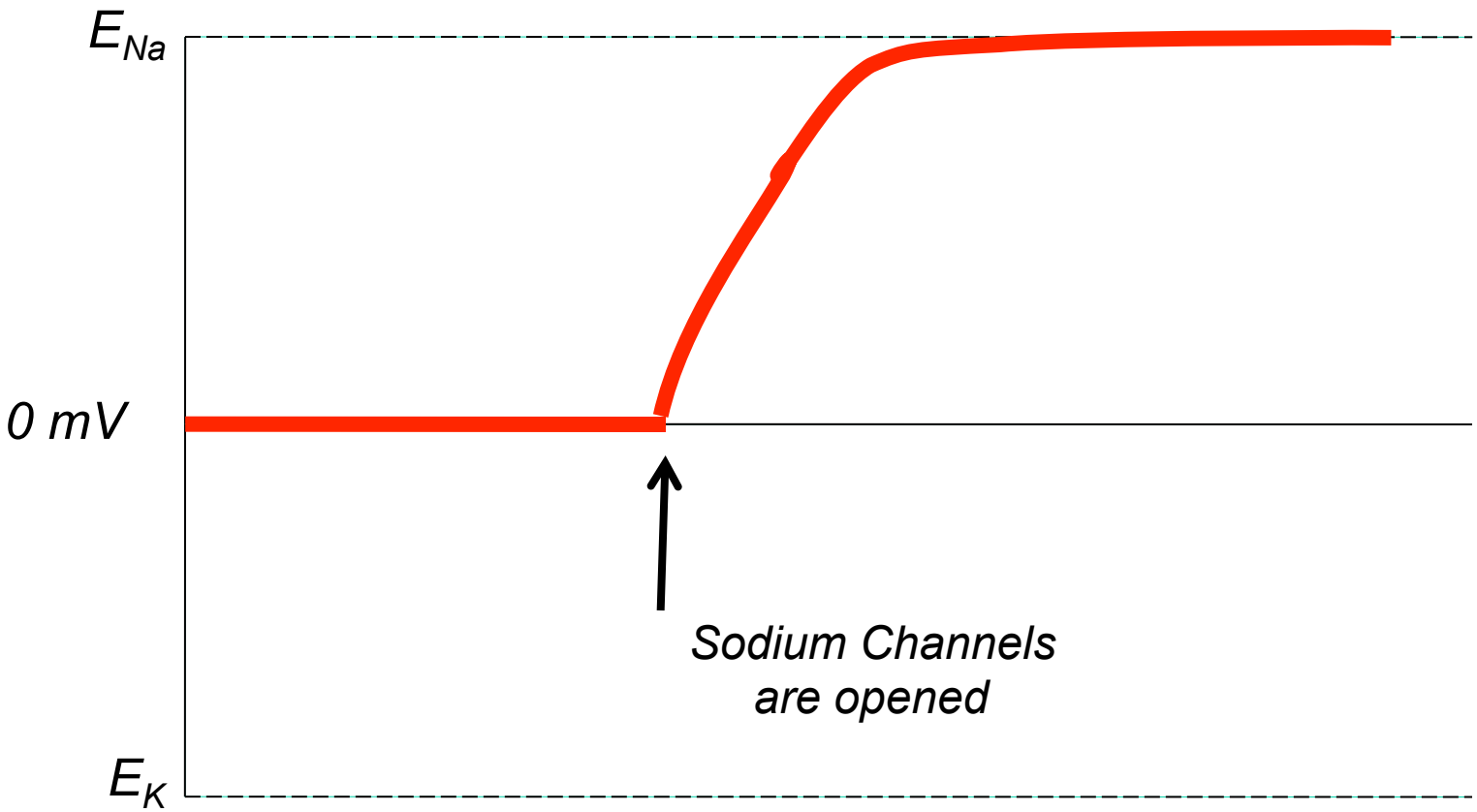
Some terminology

- **Depolarization**
  - Change in cell's membrane potential making the inside of the cell more positive (or less negative) with respect to the cell's outside
- **Hyper-polarization**
  - Change in cell's membrane potential making the inside of the cell more negative (or less positive) with respect to the cell's outside
- **Inward current (example due to Na^+ ions)**
  - Flowing into the cell (considered negative)
- **Outward current (example due to K^+ ions)**
  - Flowing out of the cell (considered positive)
- **Action potential, Spike**
  - An "all or nothing" event during which the membrane potential rapidly rises and for a brief moment V_{inside}-$V_{outside}$ is positive

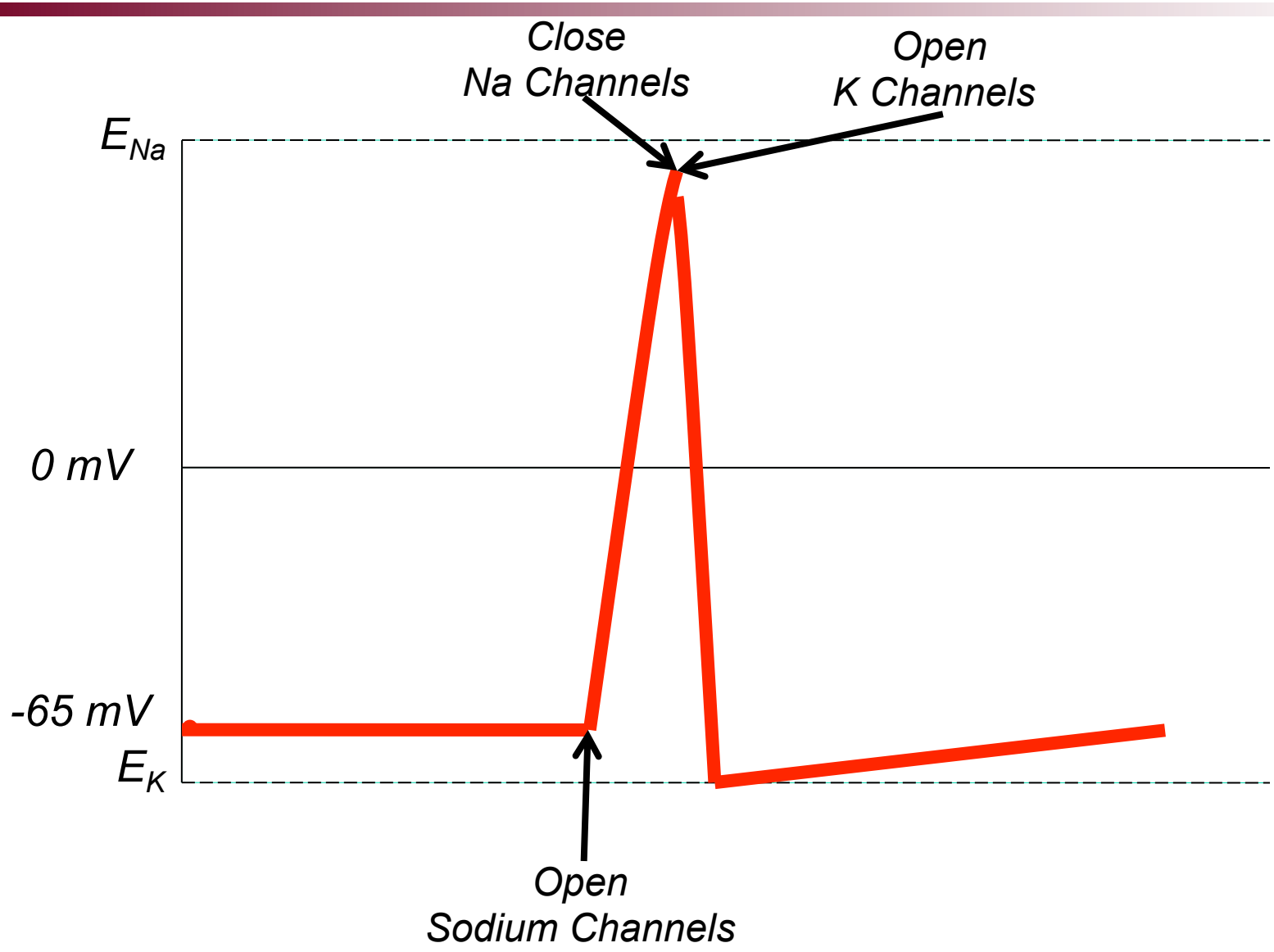
Action Potential



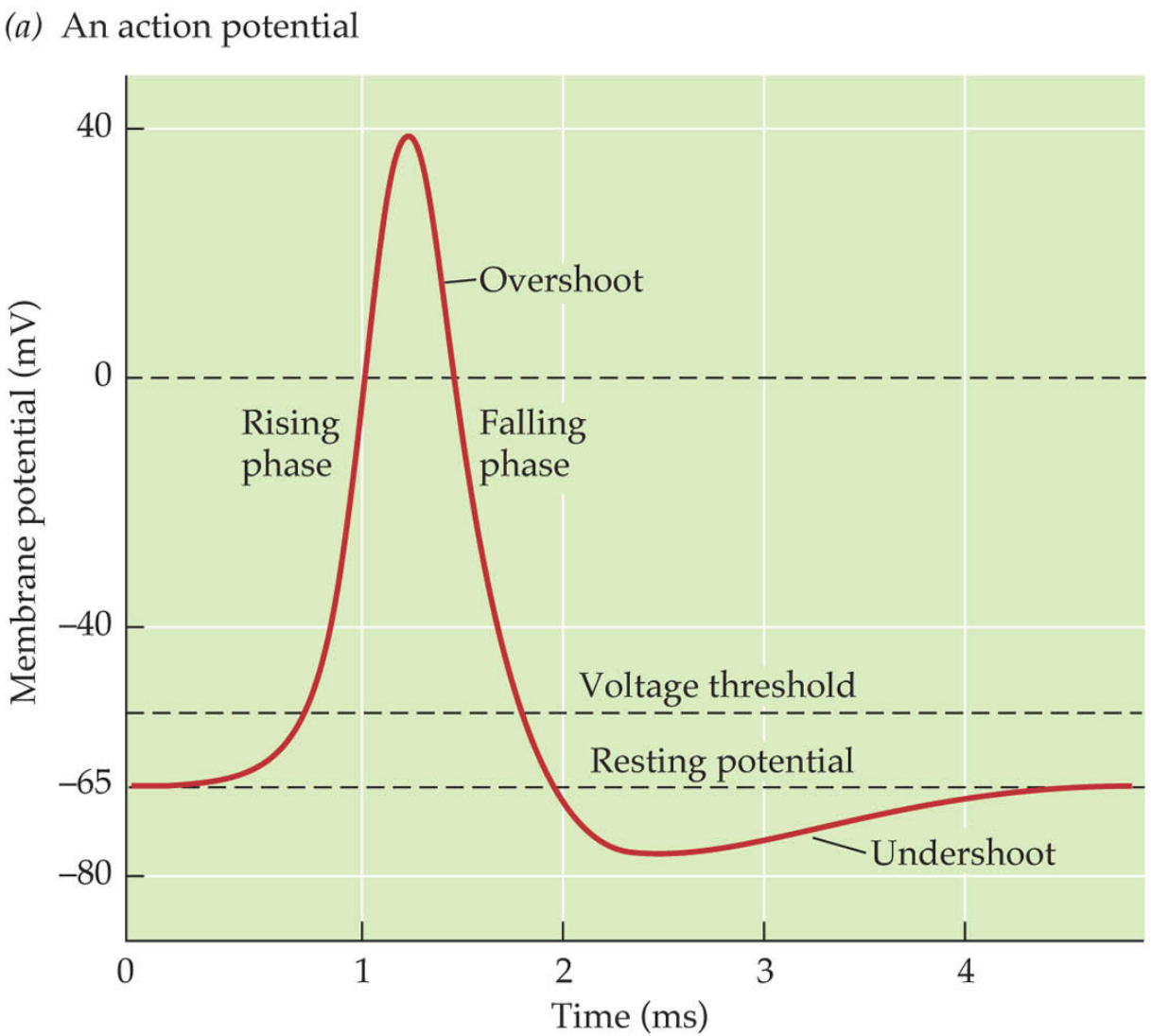
Action Potential



Action Potential



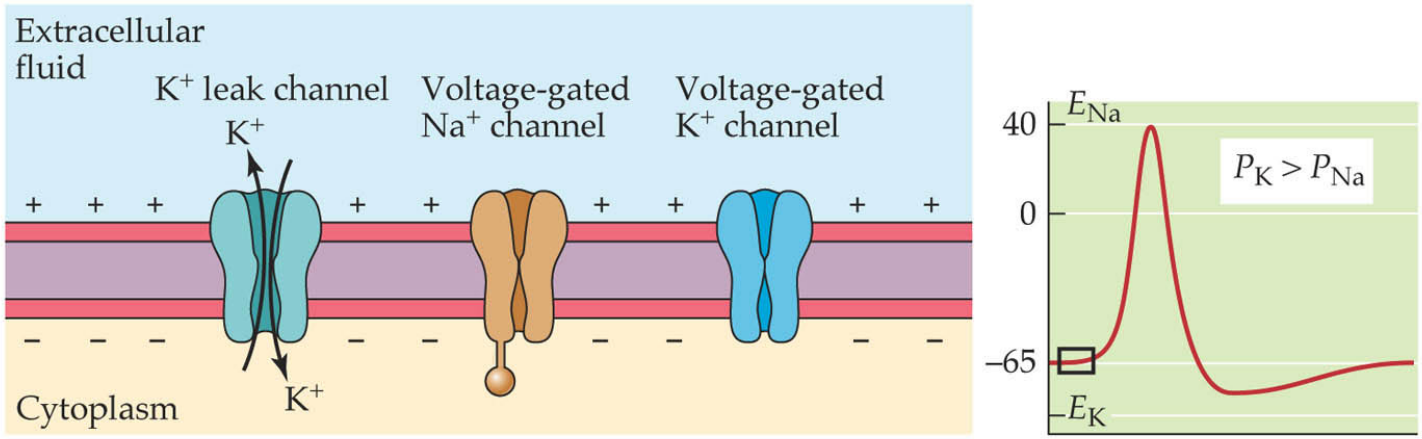
Action Potential



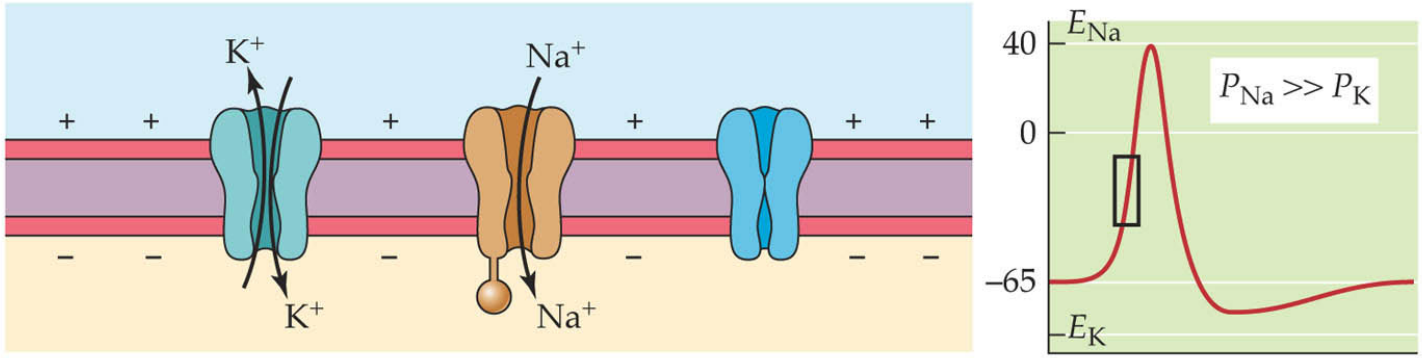
Neuroscience, Bear et al. 3rd edition

Action Potential

(a) Resting membrane potential



(b) Rising phase



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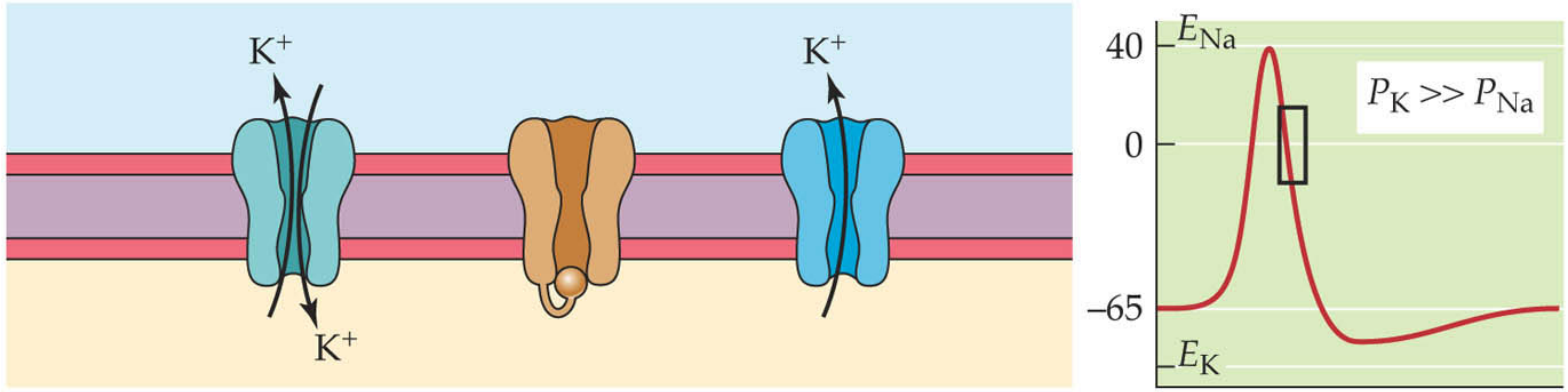
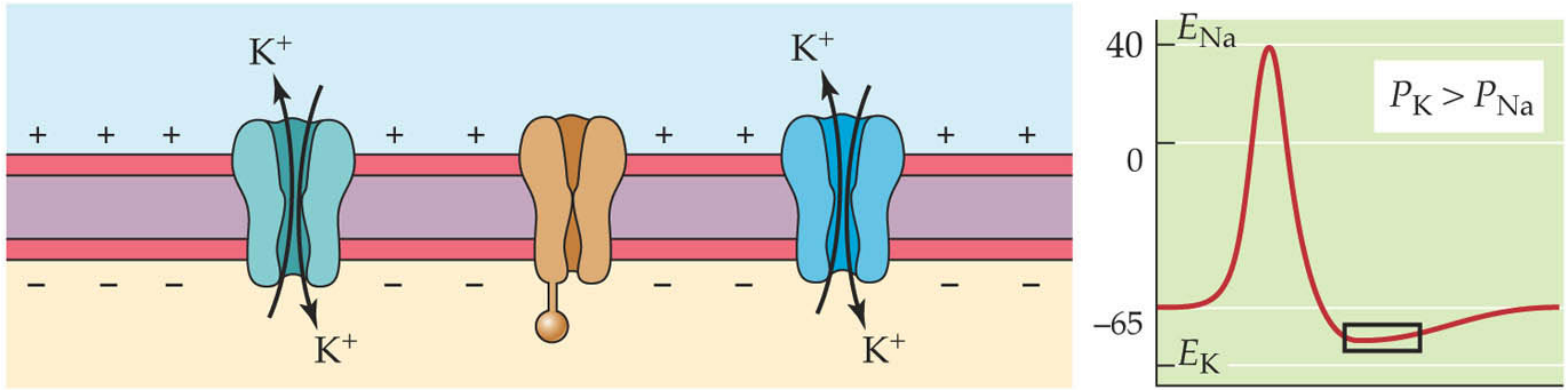
Action Potential

(c) Falling phase



(d) Recovery



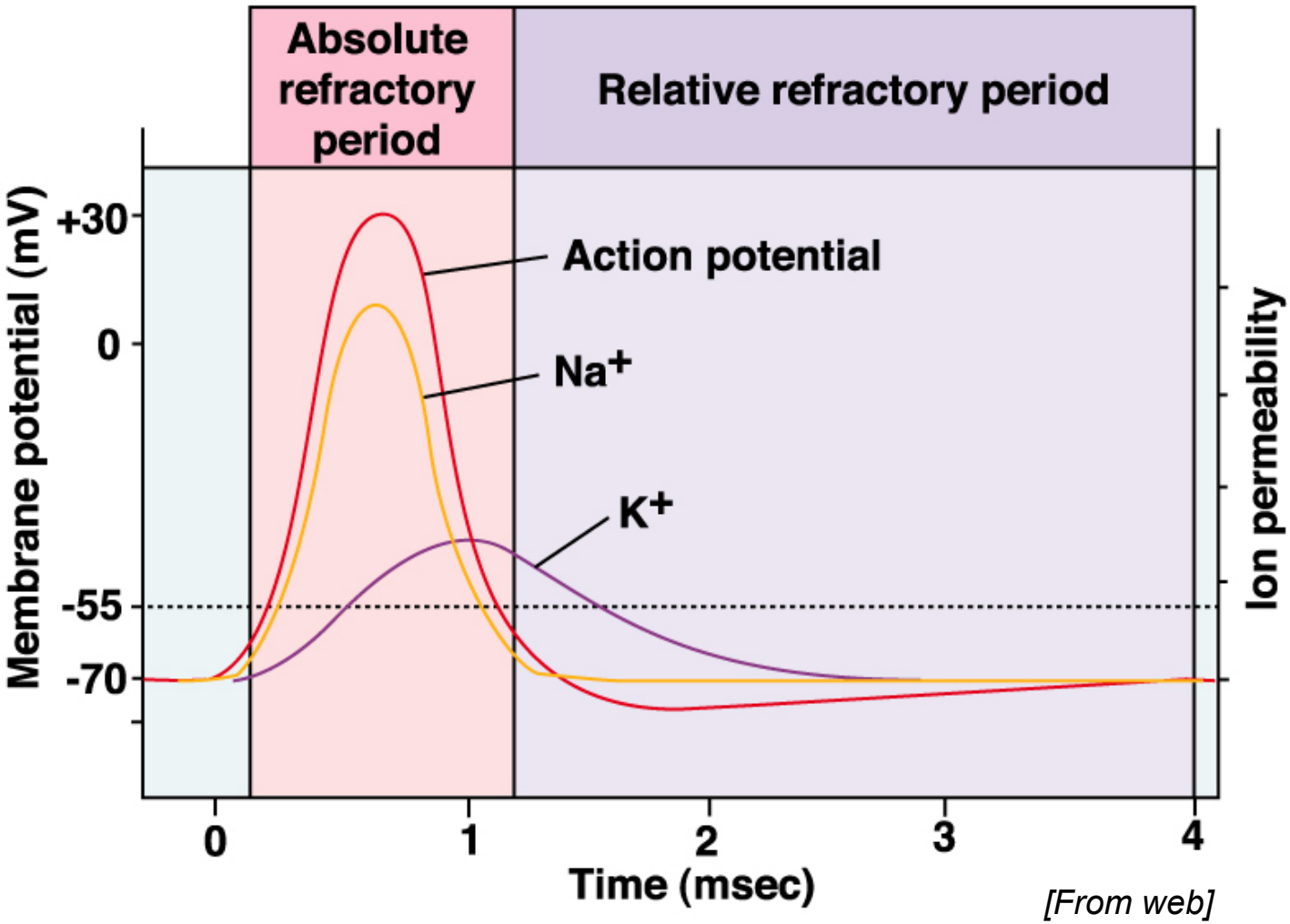
Neuroscience, Bear et al. 3rd edition

Membrane Current and Conductance

- Net movements of ion will cause ionic current I_{ion}
- The number of ion channels open will be proportional to an electrical conductance (g_k, g_{Na}; inverse of resistance)
- Ionic current will flow only as long as membrane potential V_m is not equal to reversal potential E_{ion}

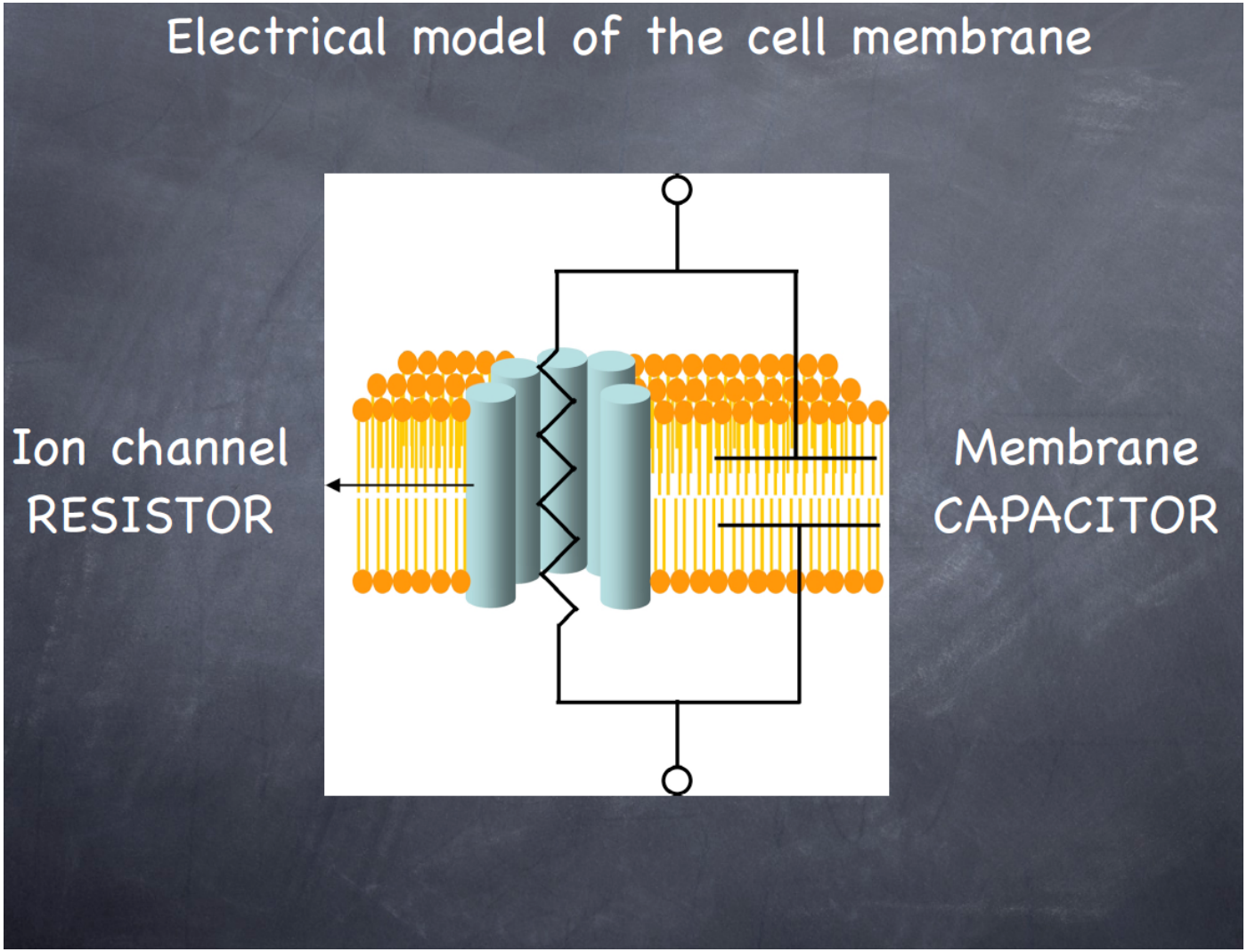
$$I_{ion} = g_{ion} (V_m - E_{ion})$$

Refractory Period



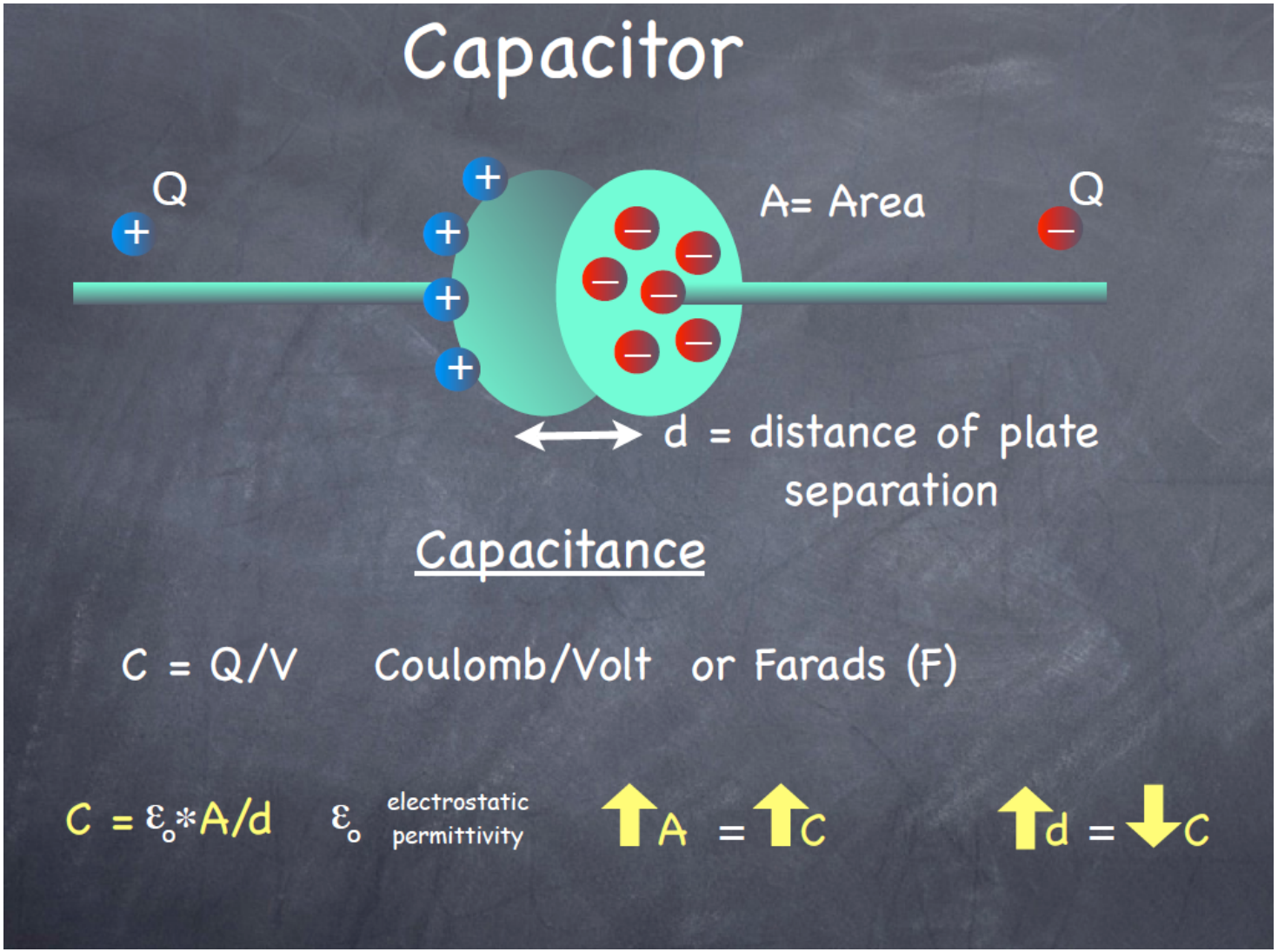
[From web]

Electrical Circuit of a Patch of neuron



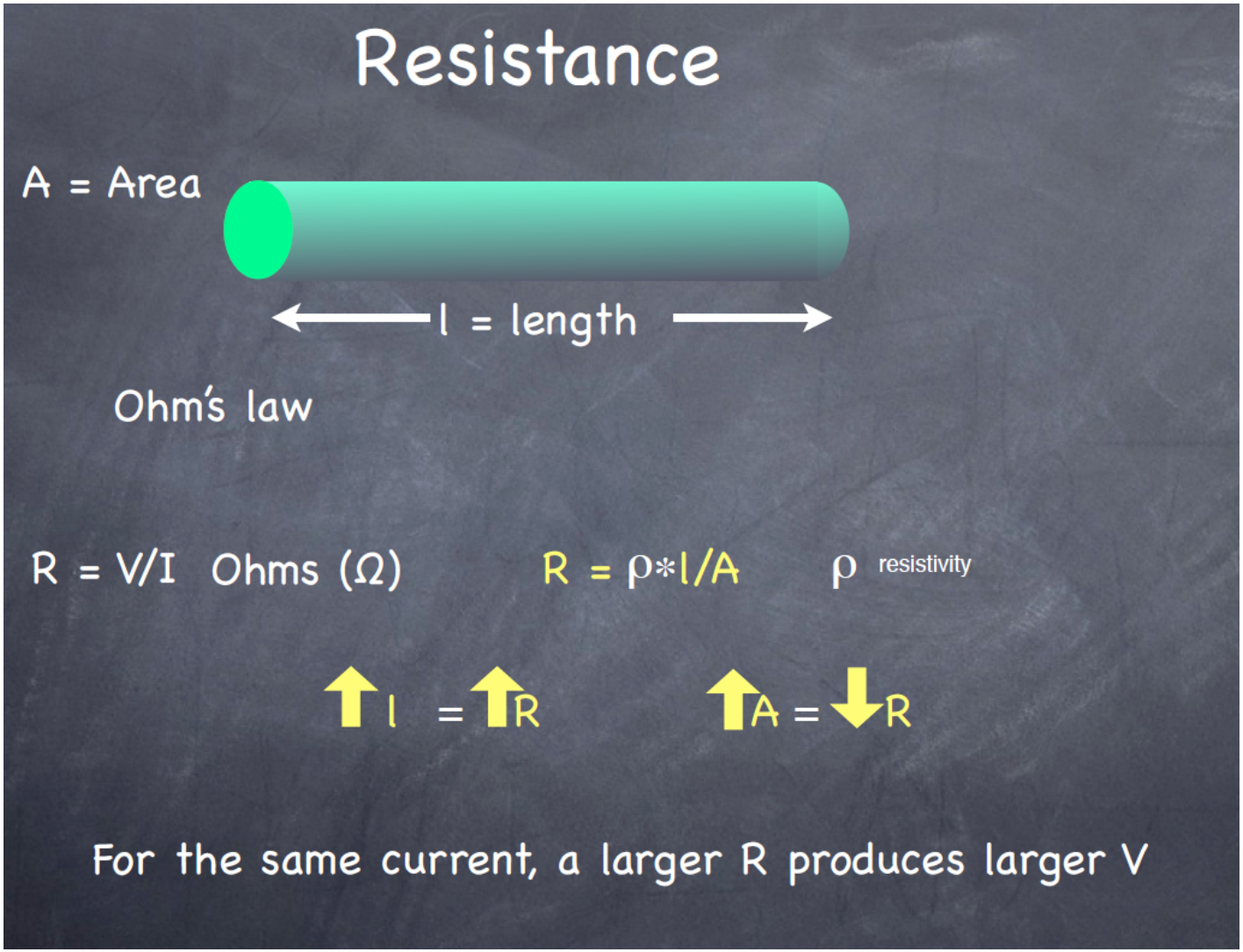
[Notes borrowed from Araneda]

Passive properties of a Neuron



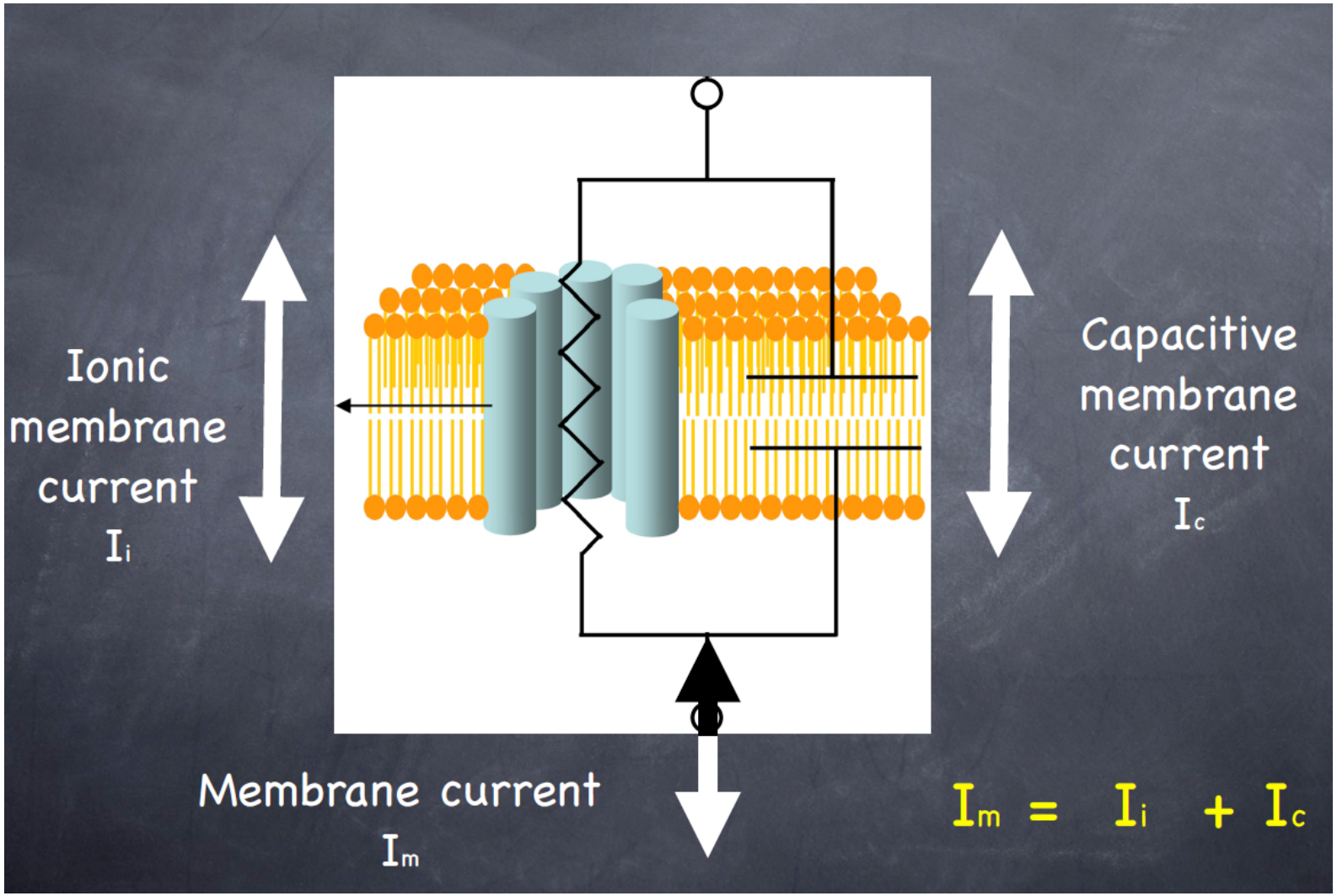
[Notes borrowed from Araneda]

Passive properties of a Neuron



[Notes borrowed from Araneda]

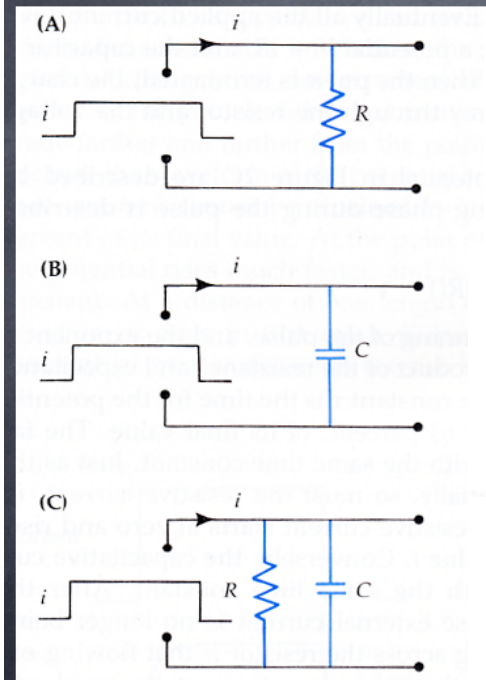
Passive properties of a Neuron



[Notes borrowed from Araneda]

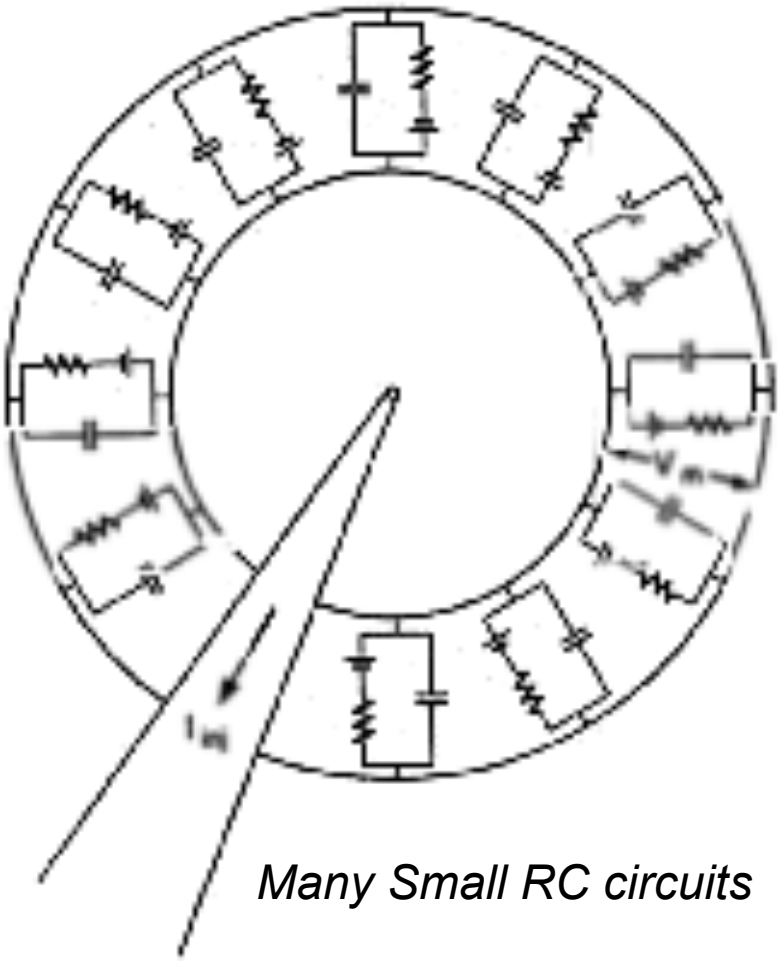
Electrical Circuits with R and C elements

Effects of passing current on circuits containing R and C



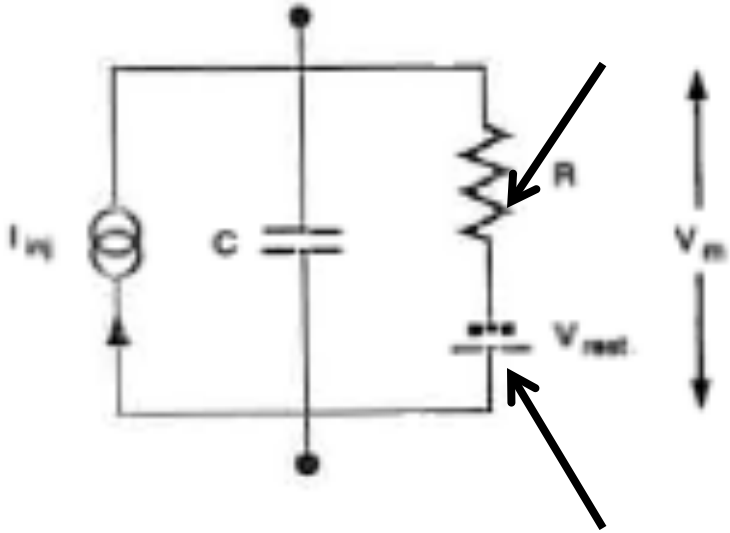
[Notes borrowed from Araneda]

Electrical Structure of Small Passive Neuron



Many Small RC circuits

Resistor mimics ion channel

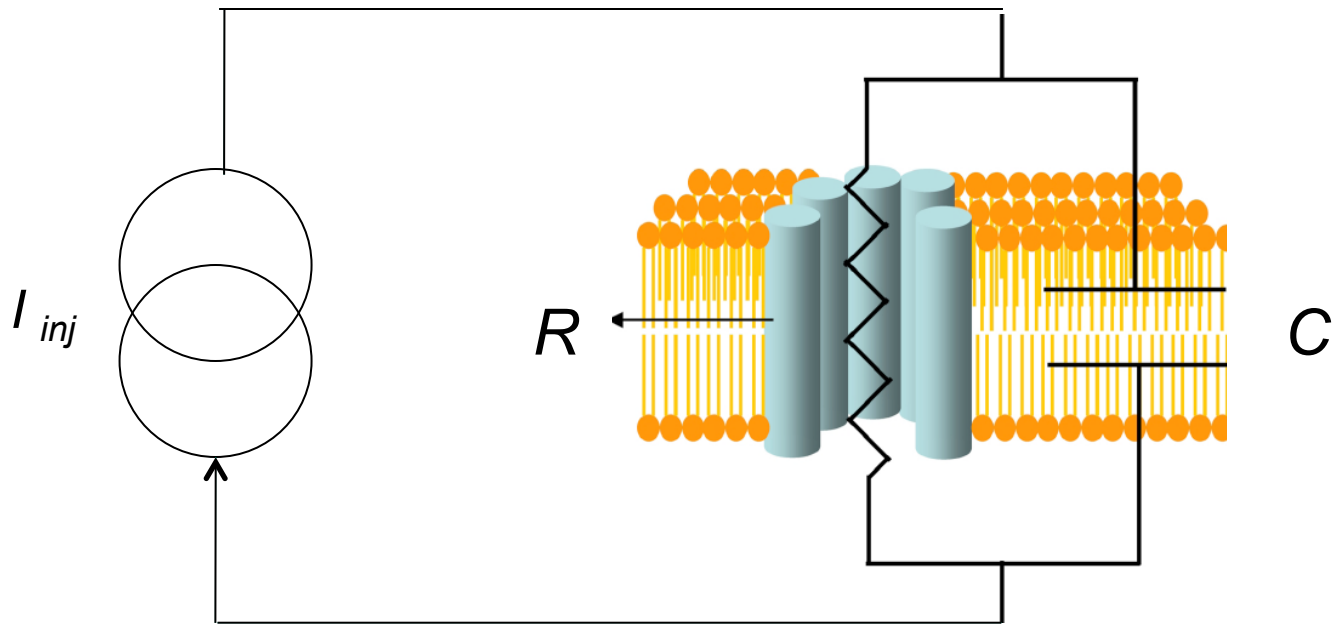


A battery to account for resting membrane potential

Since the cell is so small we can assume same membrane potential everywhere (isopotential)

[Koch, 1999]

Membrane Patch Equation



$$I_{inj} = C\frac{dV_m(t)}{dt} + \frac{V_m(t)}{R}$$

Injected current = Capacitive current + Resistive current

- **Show that the solution is:**

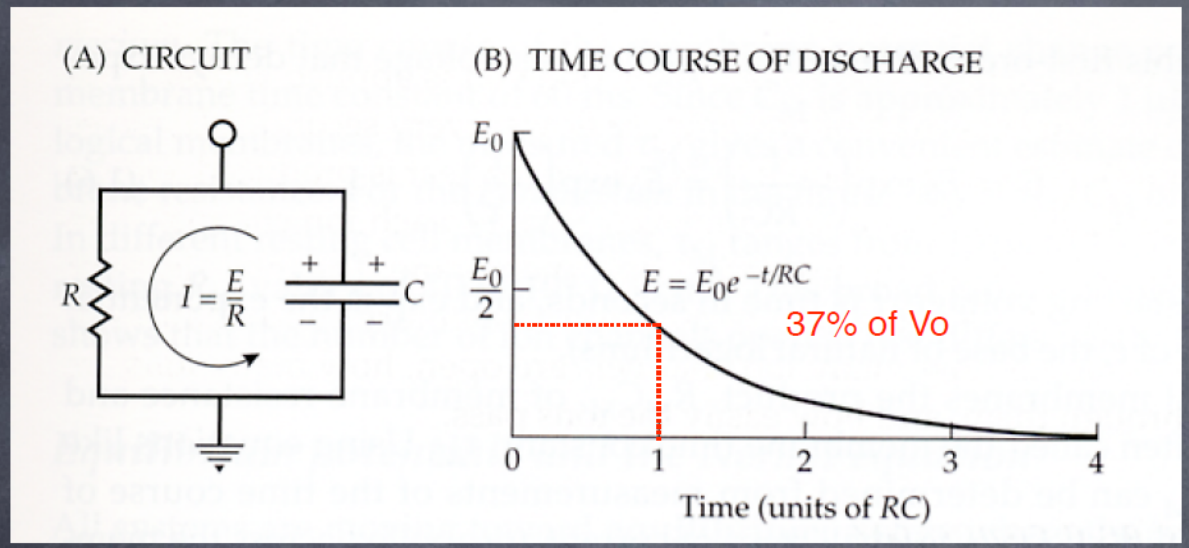
$$V_m(t) = V_\infty(1 - e^{-t/\tau})$$

$$at \quad t = 0 \qquad V = 0$$

$$\tau = RC \qquad V_\infty = I_{inj}R$$

RC Circuit

RC circuits

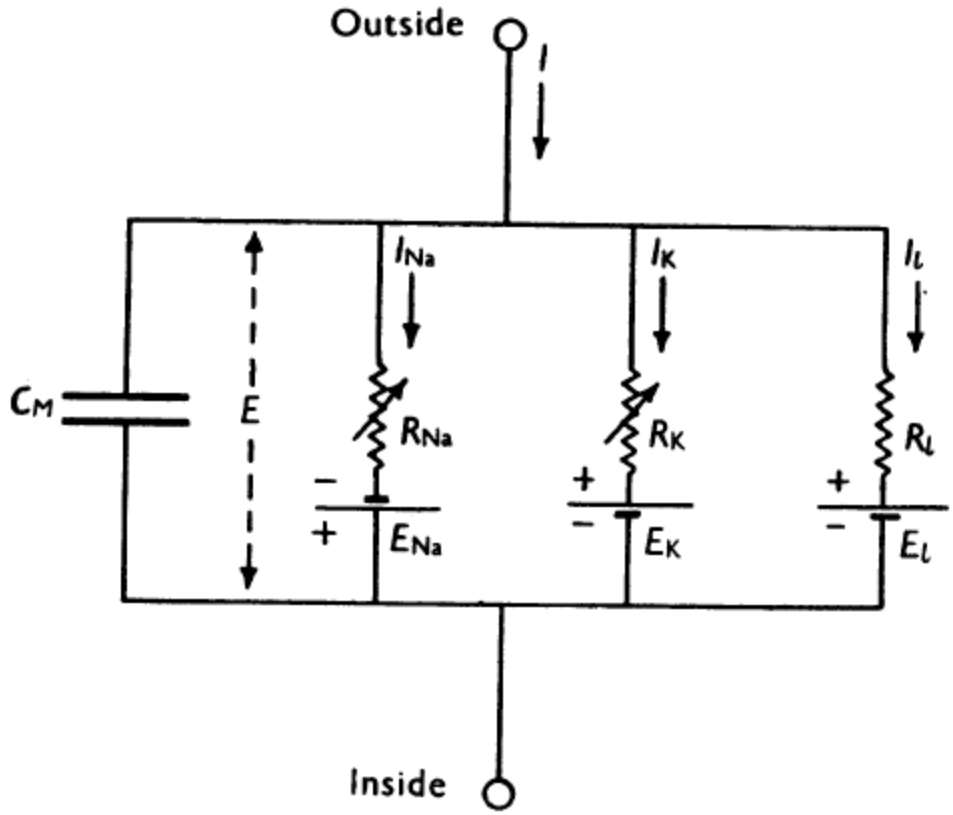


(E and V are the same)

For a rising exponential

$$V = V_0 * (1 - e^{-t/RC})$$

Equivalent circuit



Current is carried through the membrane either by charging the membrane capacitor or by movement of ions through the resistances in parallel with the capacitor.

Currents

$$I = C_M \frac{dV}{dt} + I_i,$$

Total current = Capacitive current + Ionic current

$$I_i = I_{Na} + I_K + I_l.$$

Ionic current = Sodium-Current + Pottasium-Current + Leakage Current (Cl^- and other ions)

Ionic currents

$$I_{\mathrm{Na}} = g_{\mathrm{Na}}\,(E - E_{\mathrm{Na}}),$$
$$I_{\mathrm{K}} = g_{\mathrm{K}}\,(E - E_{\mathrm{K}}),$$
$$I_{l} = \bar{g}_{l}\,(E - E_{l}),$$

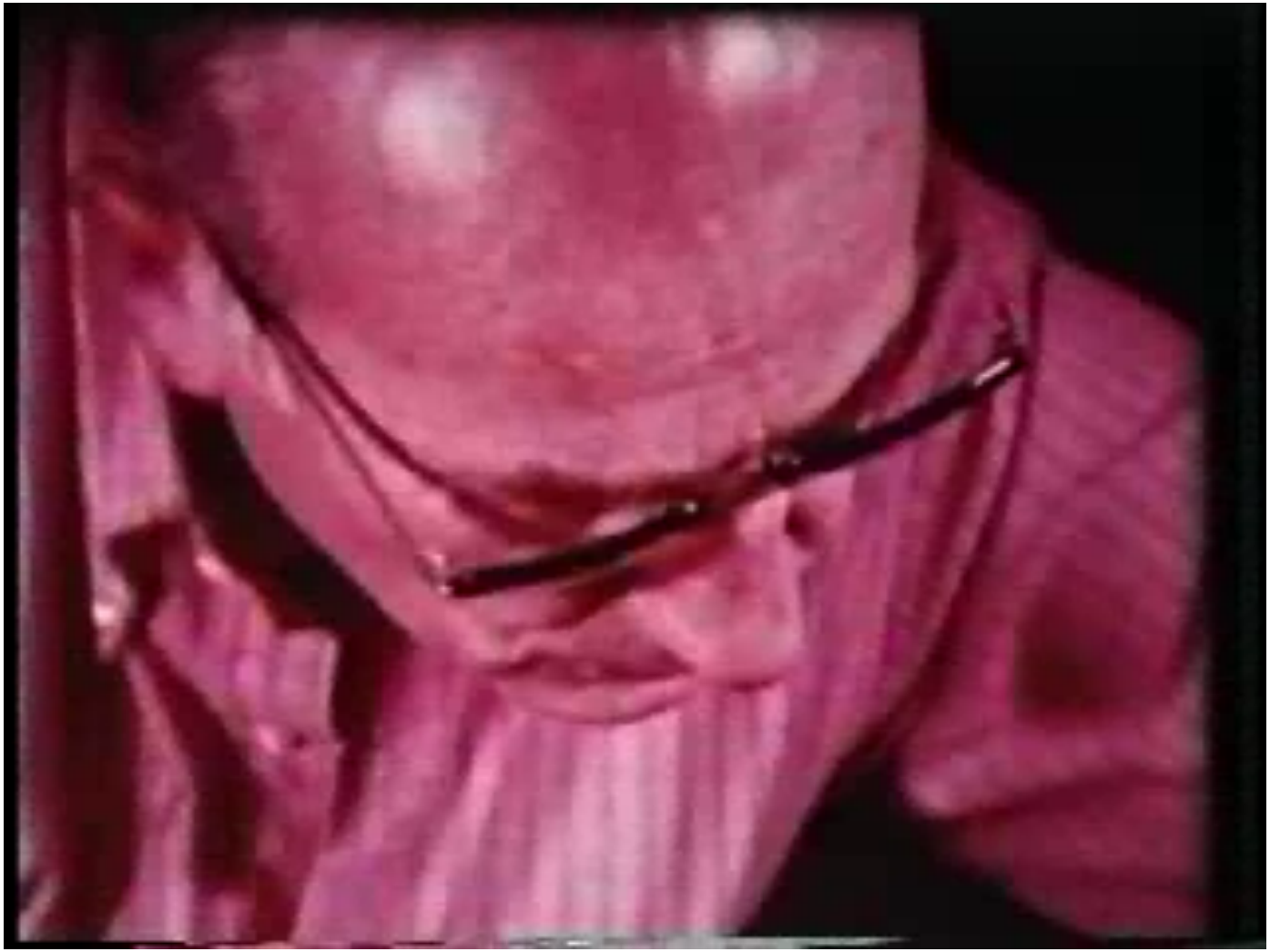
E_{Na}, E_k and E_l are equilibrium or reversal potential for respective ion species
g_{Na}, g_k and g_l are ionic conductances

Notice

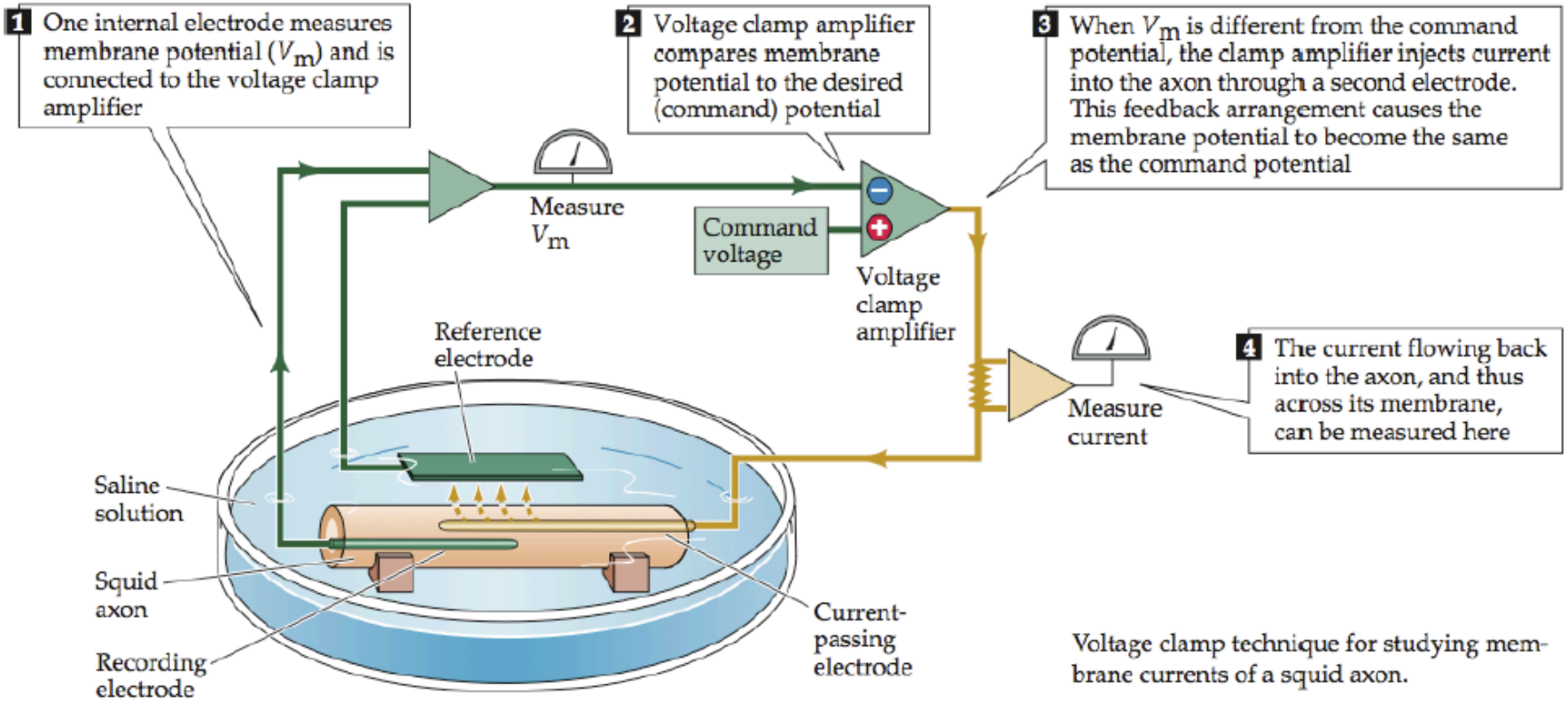
$$\begin{Bmatrix} E_{ion-type} < E & I_{ion-type}\ is\ positive \\ E_{ion-type} > E & I_{ion-type}\ is\ negative \end{Bmatrix}$$

Larger E-E_{ion} the larger the current due to that ionic species

Squid Axon Experiments



Voltage Clamp Technique

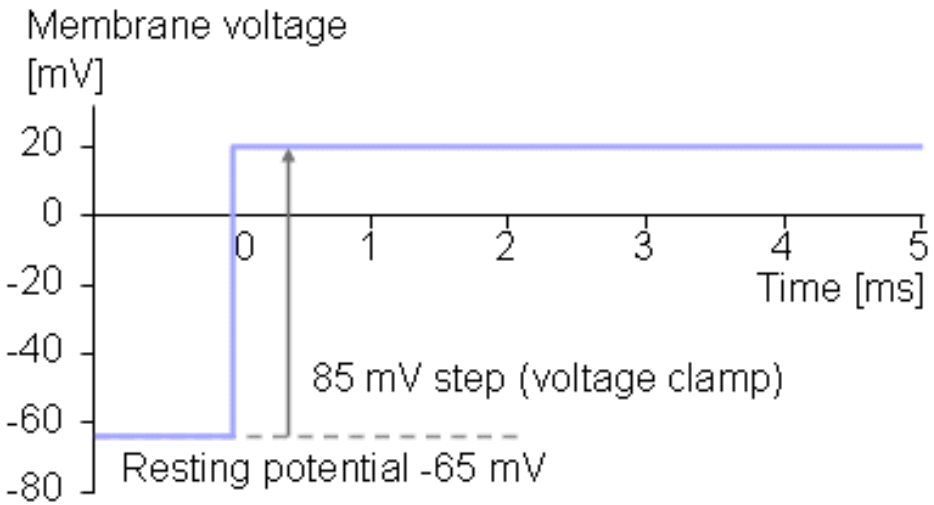


Voltage clamp technique for studying membrane currents of a squid axon.

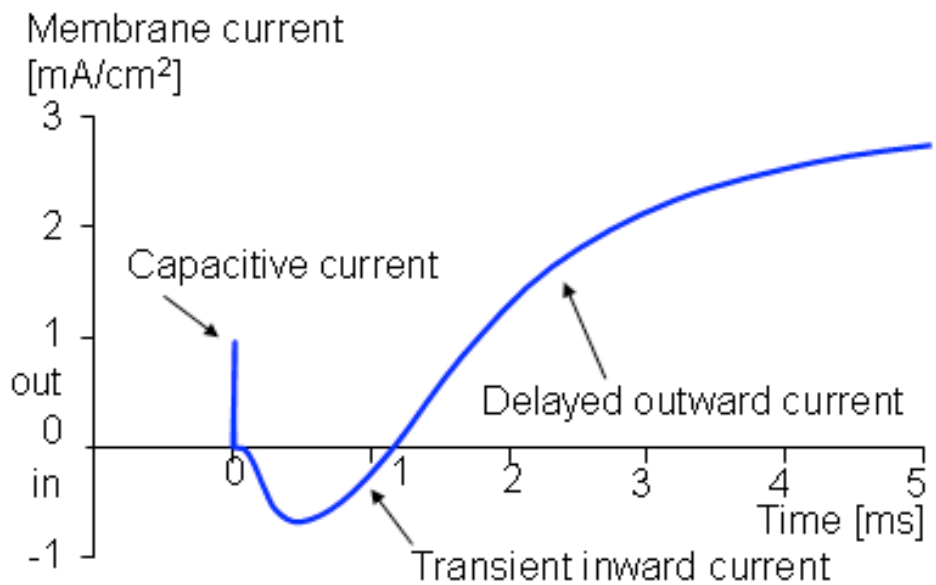
Hodgkin Huxley Experiments

Voltage Clamp

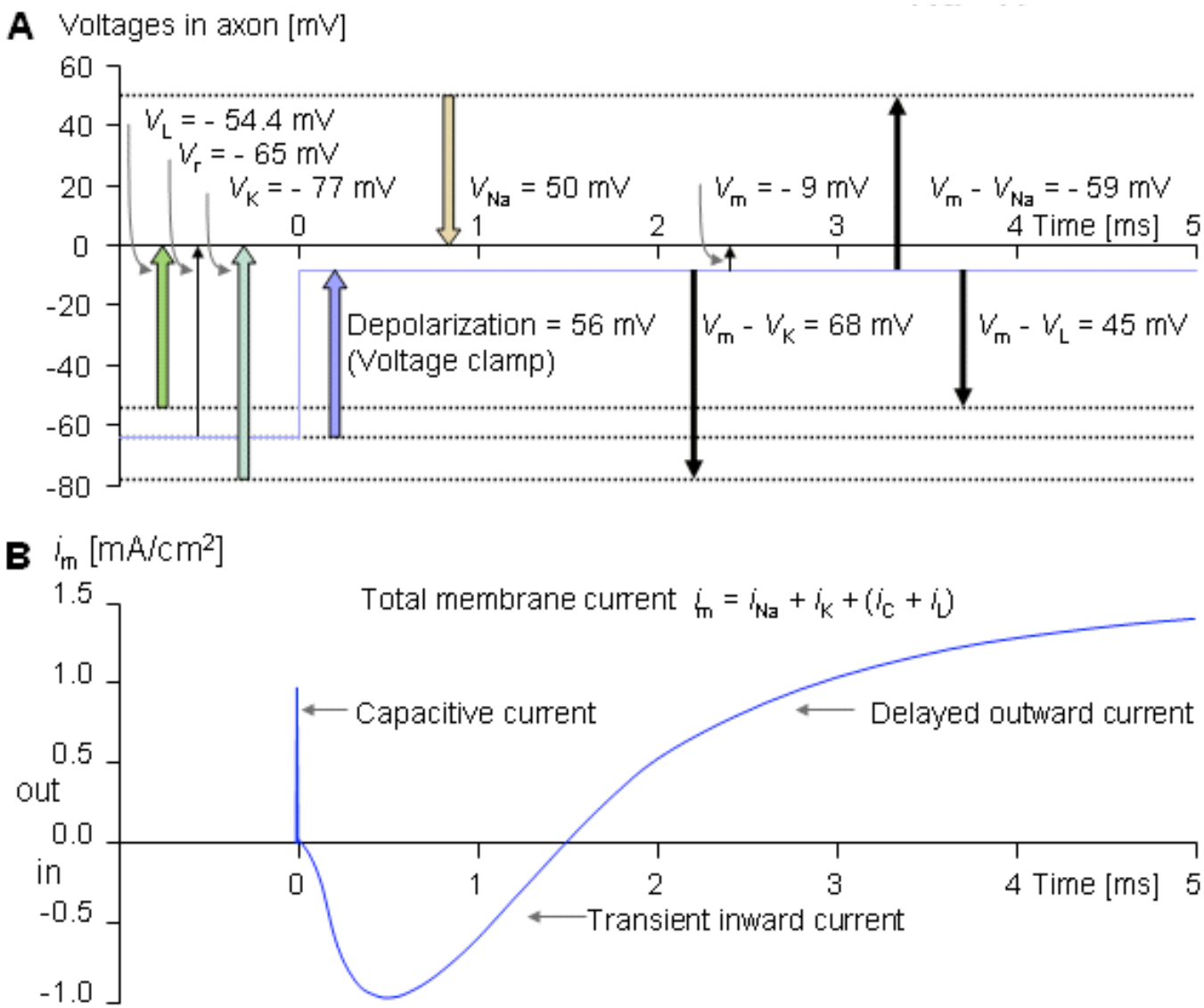
Potential inside the membrane



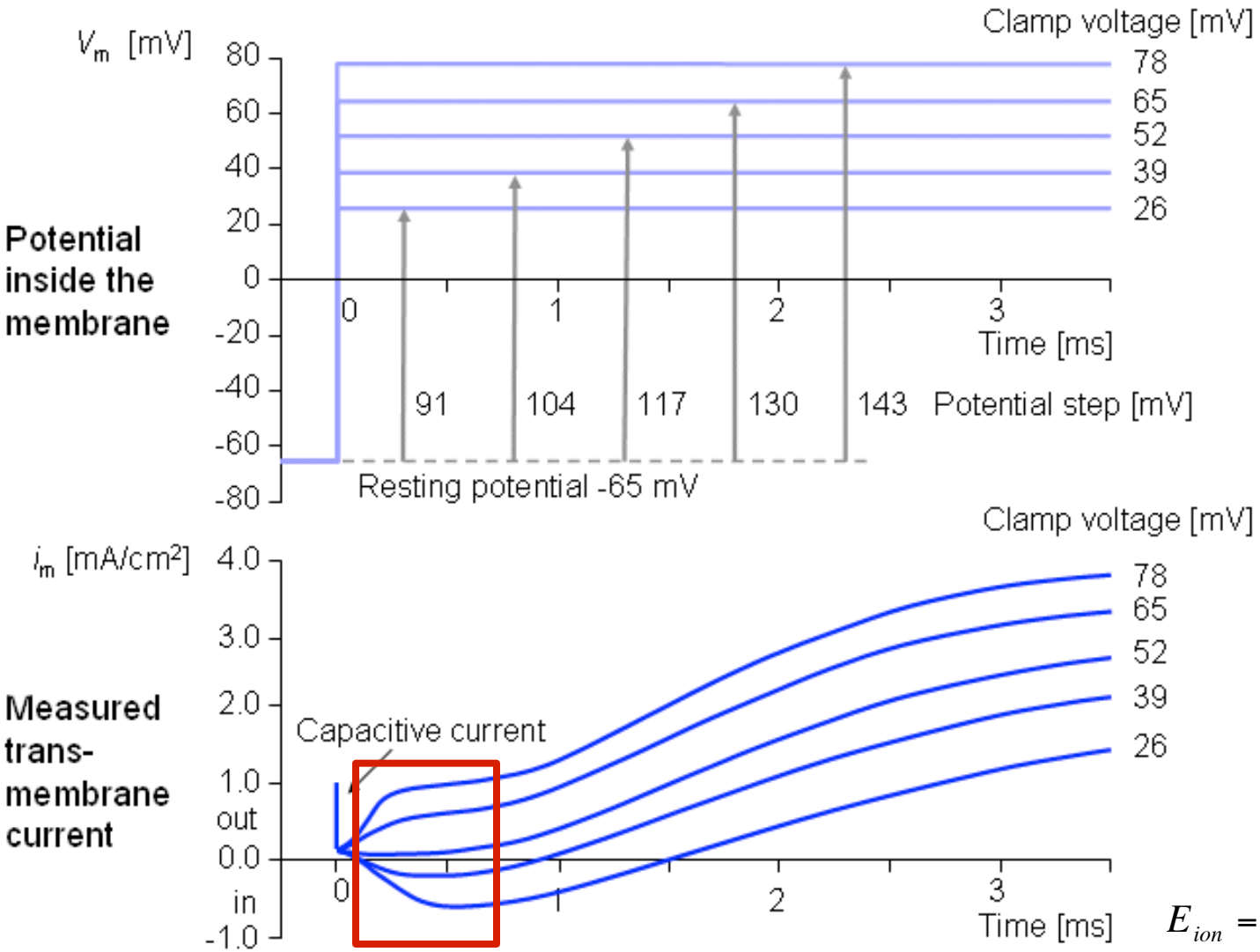
Measured trans-membrane current



Measuring individual ionic currents



Voltage Clamp

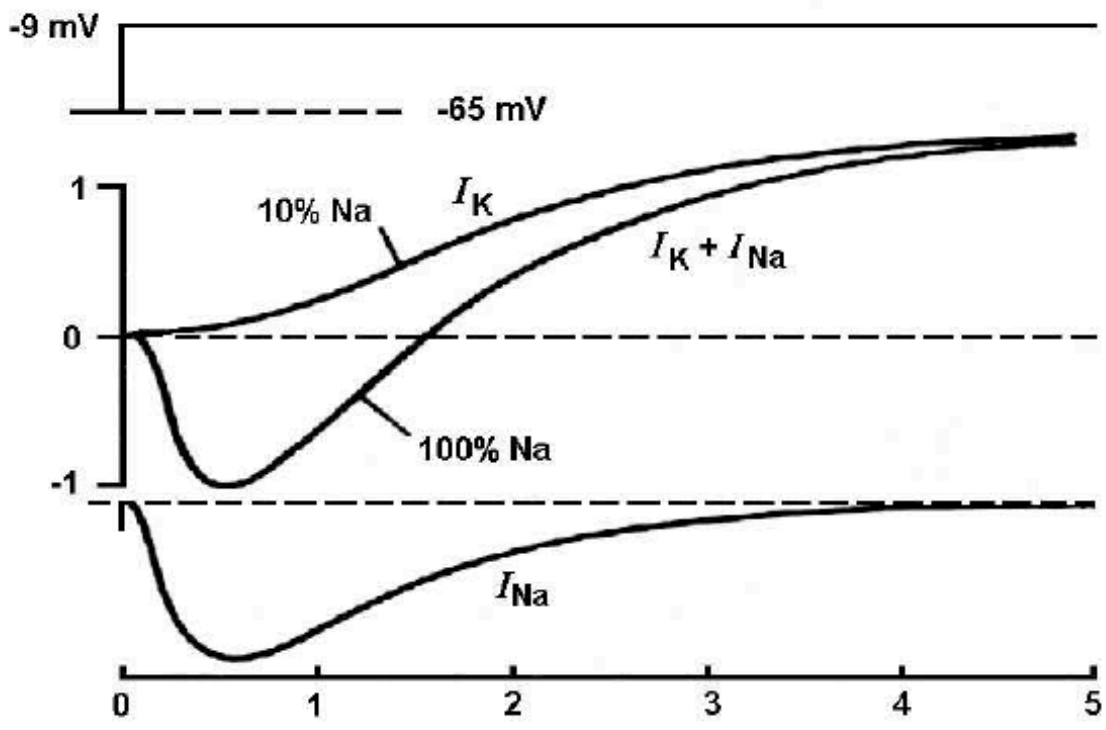


Outward current is monotonic as you move away from K reversal Potential (-77mV)

$$E_{ion} = \frac{RT}{zF} \ln \frac{[ion_{out}]}{[ion_{in}]}$$

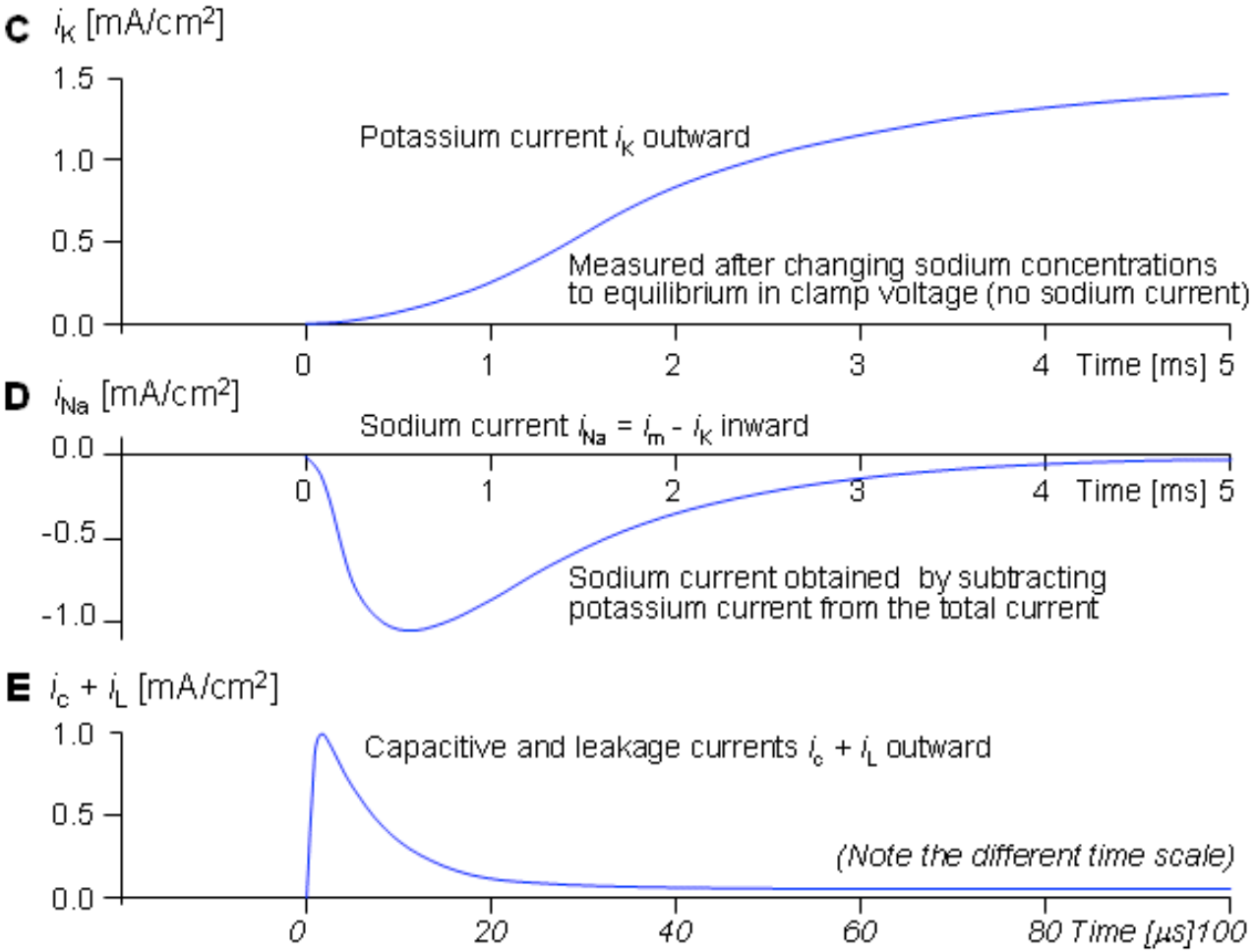
Inward current become smaller as Clamp voltage gets close to Na Reversal Potential (+55mV) and flips sign for larger depolarizations

Voltage Clamp (continued …)



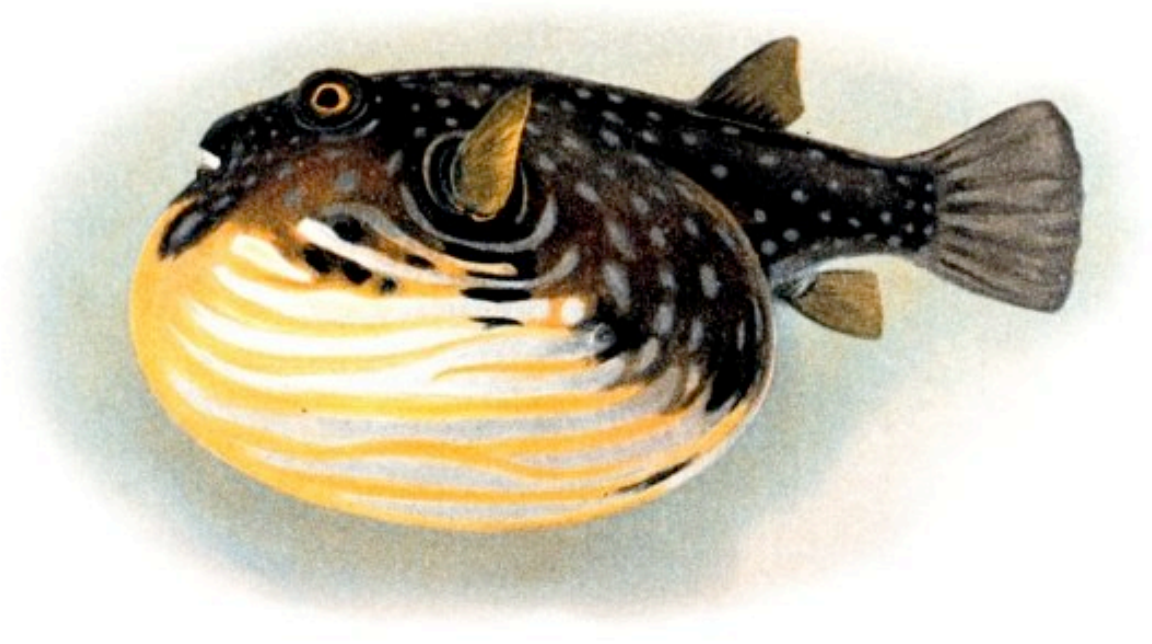
Measuring individual ionic currents

- **Selective measurement of the K ion flow alone is possible by utilizing a voltage clamp step corresponding to the Na Nernst potential.**



Pharmacological agents

Puffer fish



Lips and tongue tingles, hands feel numb and trouble making movements

Tetrodotoxin (TTX) – blocks voltage-gated Na channels

Pharmacological agents

Scorpion toxin

Scorpion toxin blocks voltage-gated K channels

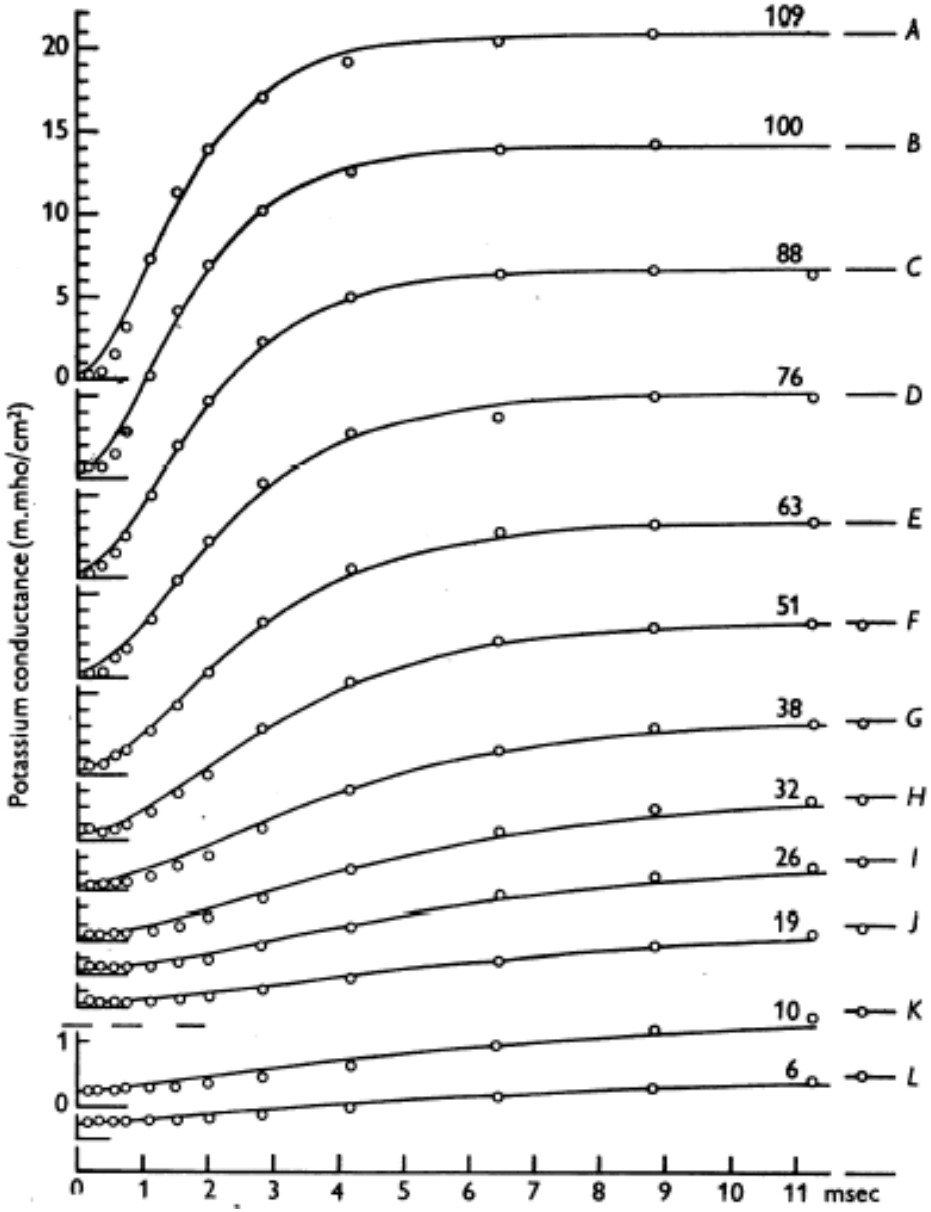
Another popular blocker is tetraethylammonium (TEA)

Hodgkin Huxley

- **One of the most important contributions of Hodgkin and Huxley was their detailed discussion of membrane kinetics**

- **The model was not formulated from fundamental principles but rather from theoretical insights and curve fitting**

Dynamics of K Conductance (3)



How do K conductance change with V?

Becomes more rapid at higher depolarization

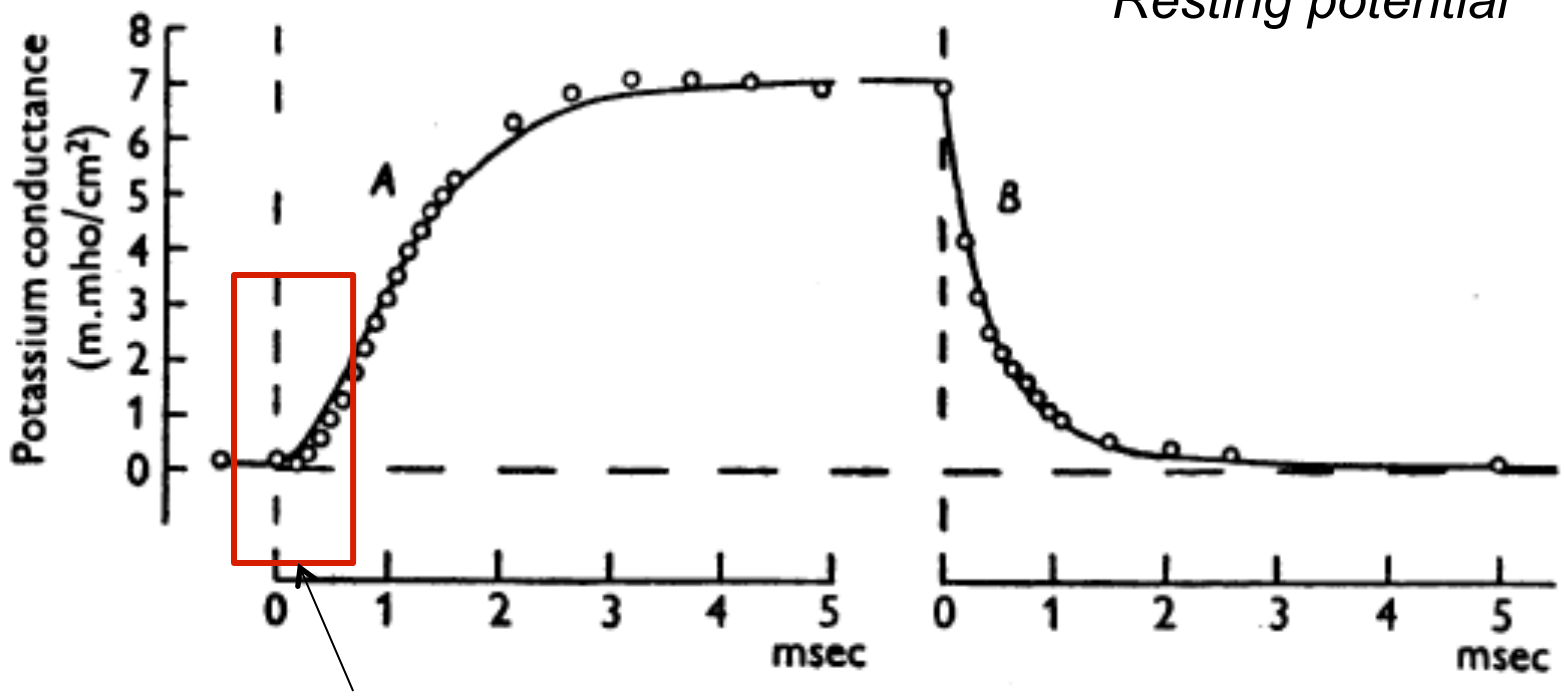
Does K conductance ever return back to baseline?

No!

K conductance

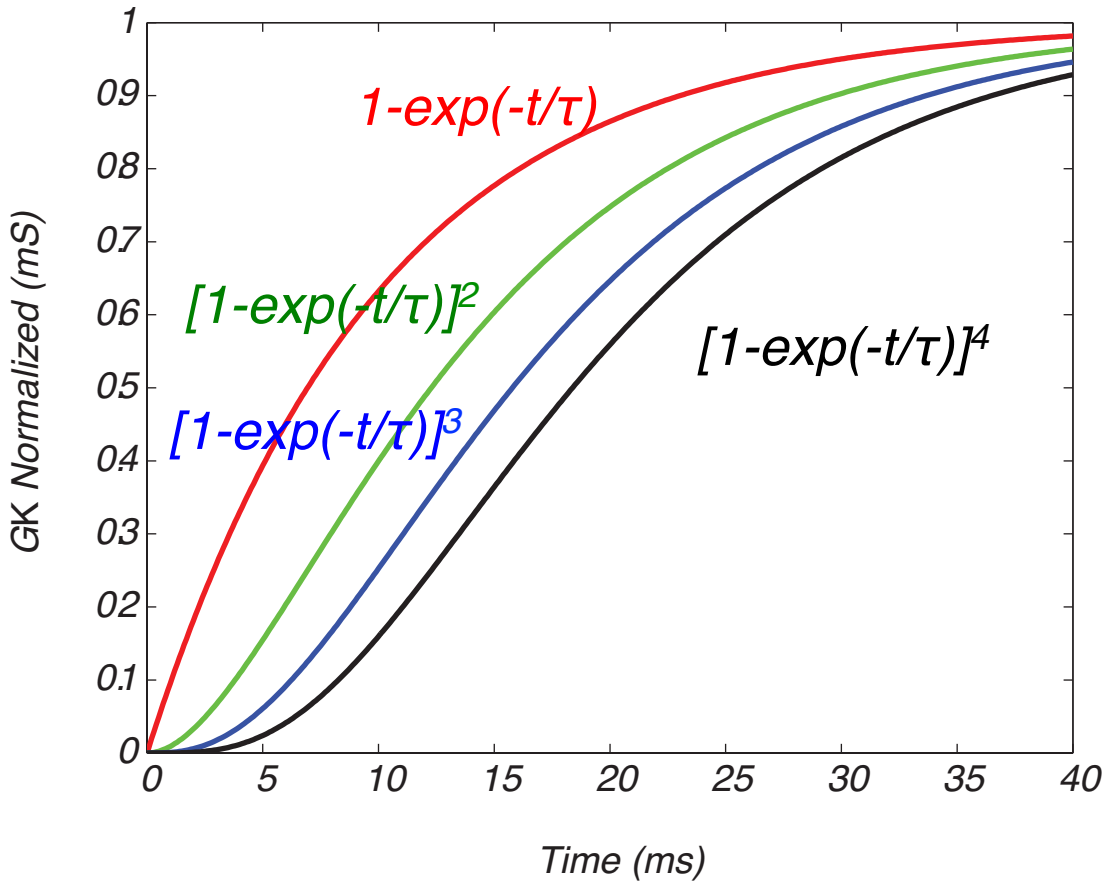
Depolarization to 25 mV

Repolarization back to Resting potential

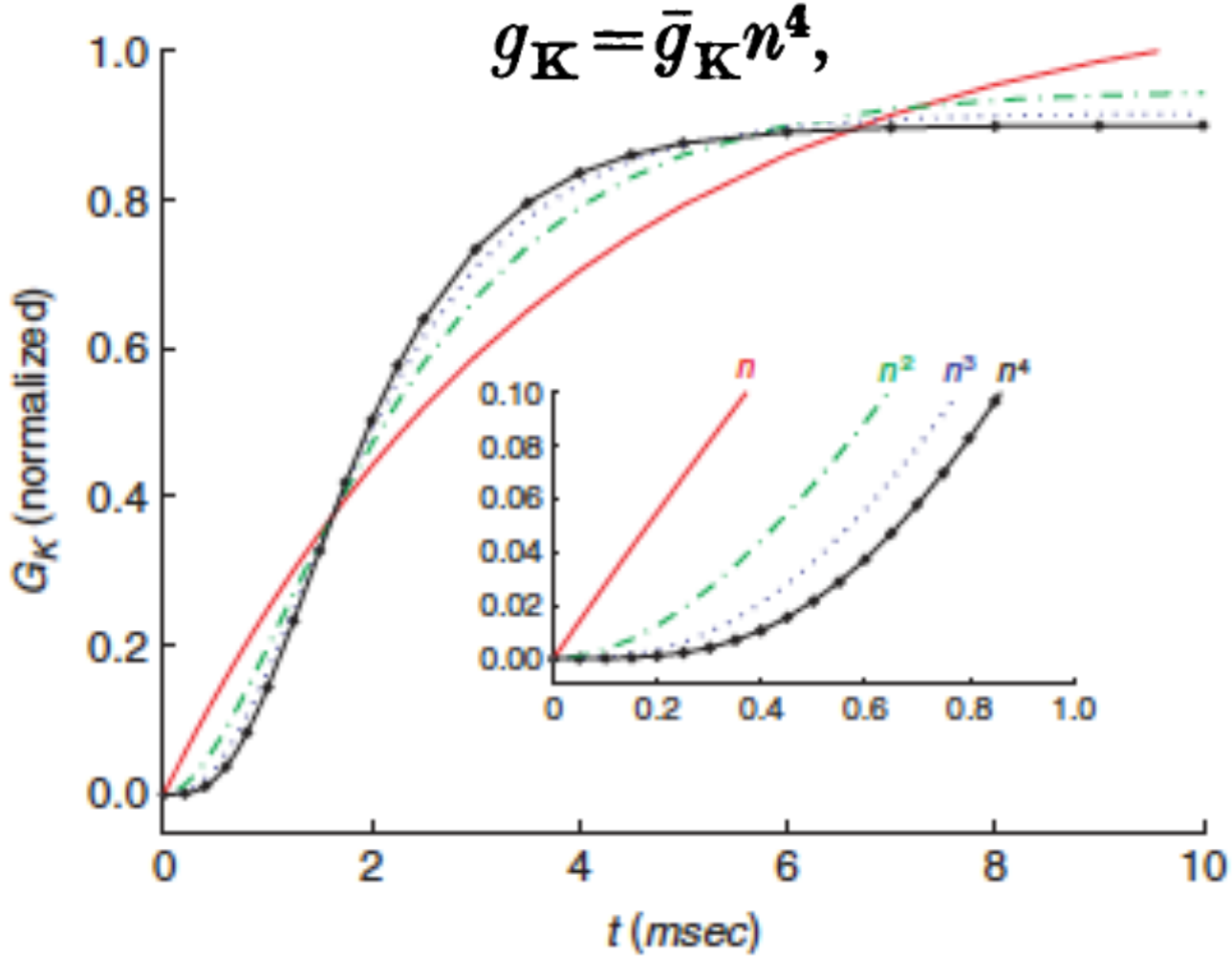


Inflexion of the curve

What's the best fit?



Why n^4?


$g_K = \bar{g}_K n^4,$
1.0
0.8
0.6
0.4
0.2
0.0
G_K (normalized)
0
2
4
6
8
10
t (msec)
n
n^2
n^3
n^4
0.10
0.08
0.06
0.04
0.02
0.00
0
0.2
0.4
0.6
0.8
1.0

Dynamics of K conductance (1)

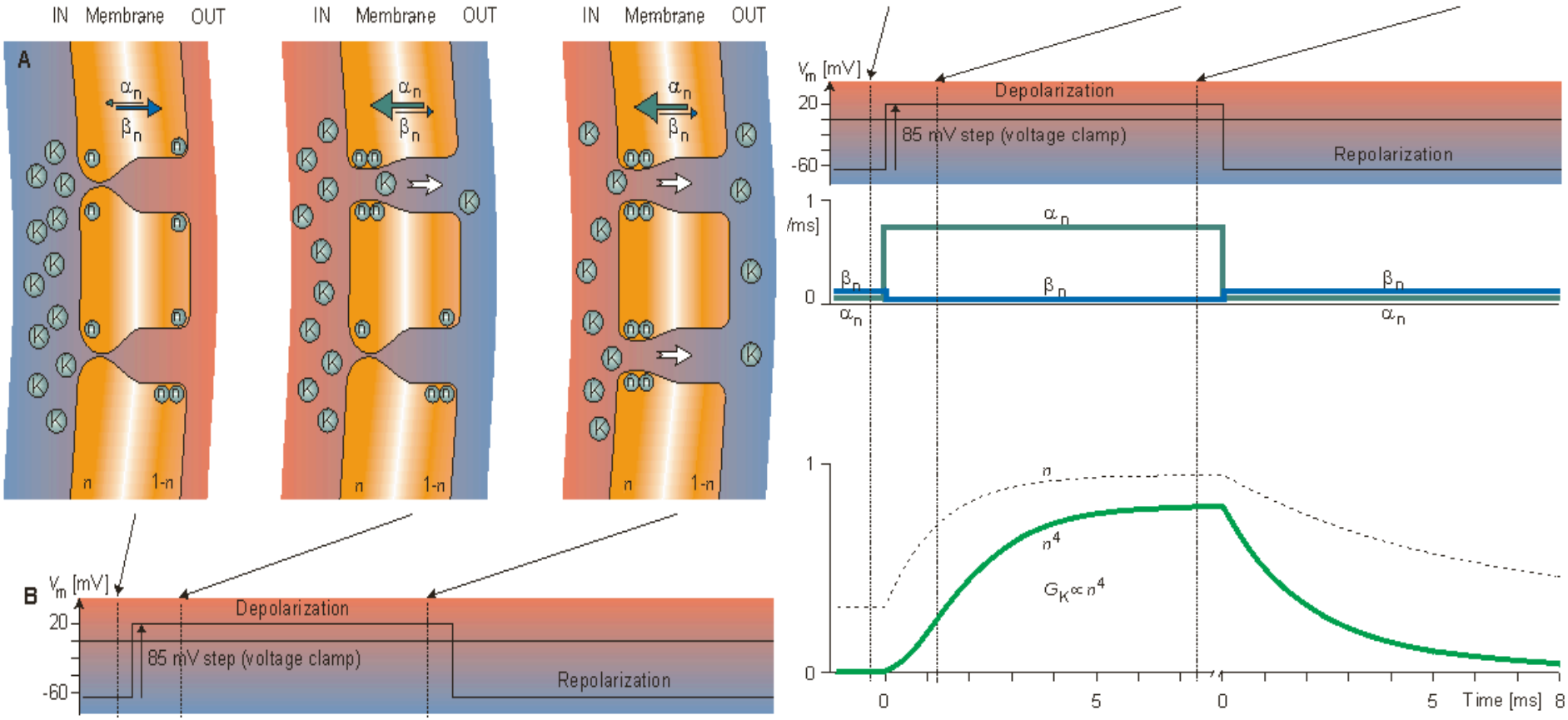
- **Hodgkin-Huxley assumed that there is only one variable that determines the dynamics of potassium conductance**

$$g_K = \bar{g}_K n^4,$$

$\bar{g}_K$ *is a constant*

- **What does n^4 represent?**
  - That K ions cross membrane only when four particles occupy a certain region of the membrane

Dynamics of K conductance (1)



www.bem.fi/book/04/04.htm

Dynamics of K Conductance (2)

$$\frac{dn}{dt} = \alpha_n (1 - n) - \beta_n n,$$

- α_n represents of transfer from outside to inside
- β_n represents of transfer from inside to outside

- **The solution of this first order ODE that satisfies the boundary condition $n=n_0$ at $t=0$ is:**

$$n = n_\infty - (n_\infty - n_0)\exp\left(\frac{-t}{\tau_n}\right)$$

$$n_\infty = \frac{\alpha_n}{\alpha_n + \beta_n}$$

$$n_0 = \frac{\alpha_0}{\alpha_0 + \beta_0}$$

$$\tau_n = \frac{1}{\alpha_n + \beta_n}$$

HW Pblm

Dynamics of K Conductance (3)

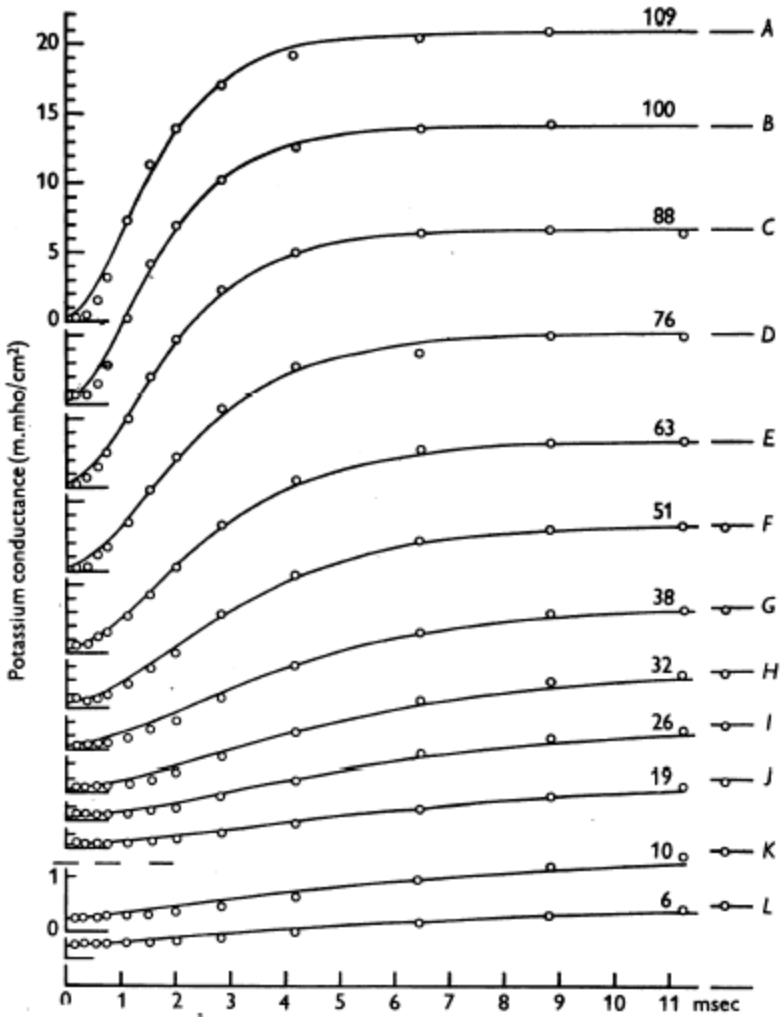


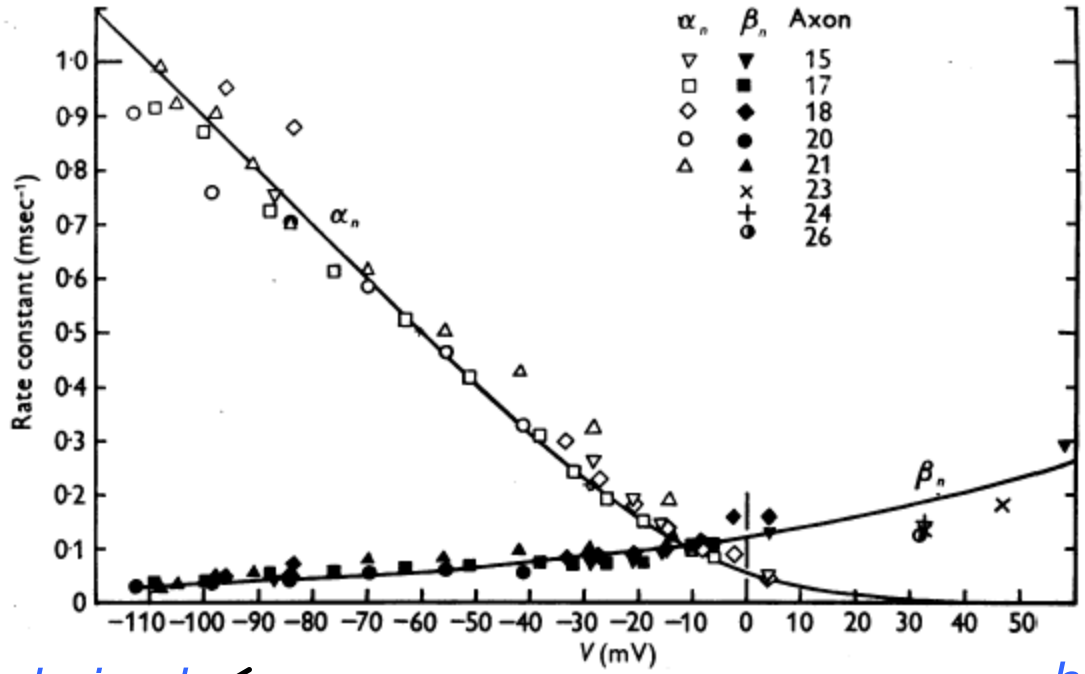
Fig. 3. Rise of potassium conductance associated with different depolarizations. The circles are experimental points obtained on axon 17, temperature 6–7° C, using observations in sea water and choline sea water (see Hodgkin & Huxley, 1952*a*). The smooth curves were drawn from eqn. (11) with $g_{K0}=0{\cdot}24$ m.mho/cm² and other parameters as shown in Table 1. The time scale applies to all records. The ordinate scale is the same in the upper ten curves (*A* to *J*) and is increased fourfold in the lower two curves (*K* and *L*). The number on each curve gives the depolarization in mV.

$$g_K = \bar{g}_K n^4,$$

$$n = n_\infty - \left(n_\infty - n_0\right)\exp\left(\frac{-t}{\tau_n}\right)$$

$$g_K = \{(g_{K\infty})^{\frac{1}{4}} - [(g_{K\infty})^{\frac{1}{4}} - (g_{K0})^{\frac{1}{4}}]\exp(-t/\tau_n)\}^4,$$

Rate constants α_n, β_n(6)

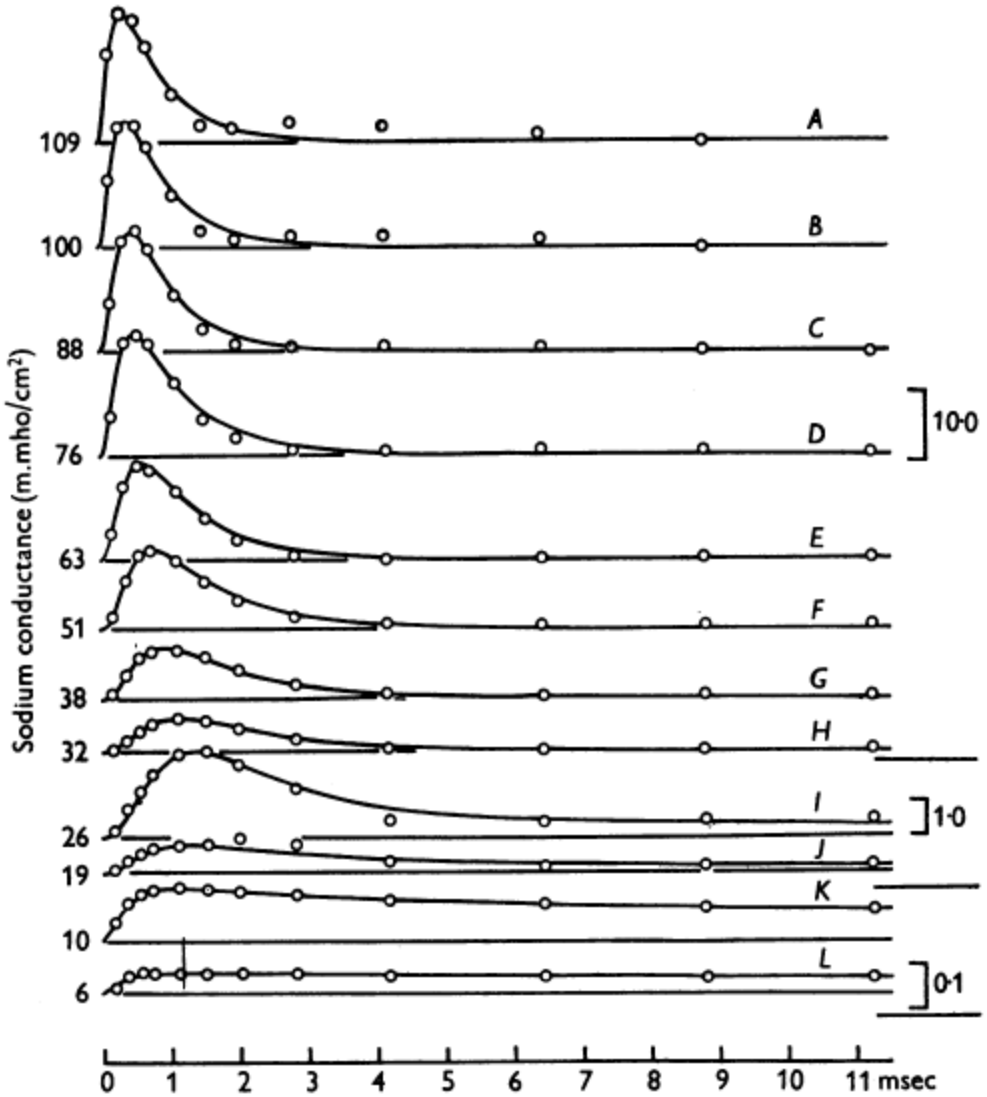


depolarized ← → *hyperpolarized*

$$\alpha_n = 0{\cdot}01\,(V+10) \Big/ \left[\exp\frac{V+10}{10} - 1\right],$$

$$\beta_n = 0{\cdot}125\,\exp\,(V/80),$$

Dynamics of Na Conductance (5)



How does Na conductance change with V?

Becomes more rapid at higher depolarization

Does Na conductance ever return back to baseline?

Yes!

Are the rising and falling portions of the curves similar?

No!

Dynamics of Na Conductance (1)

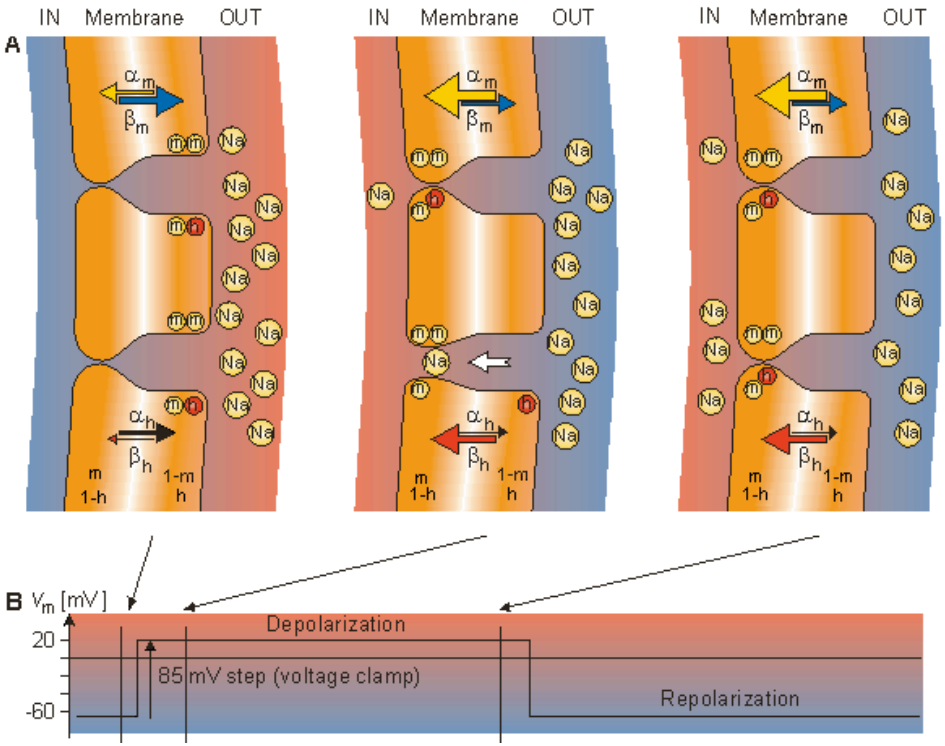
- **Hodgkin-Huxley assumed that there are two variables that determine the dynamics of sodium conductance**

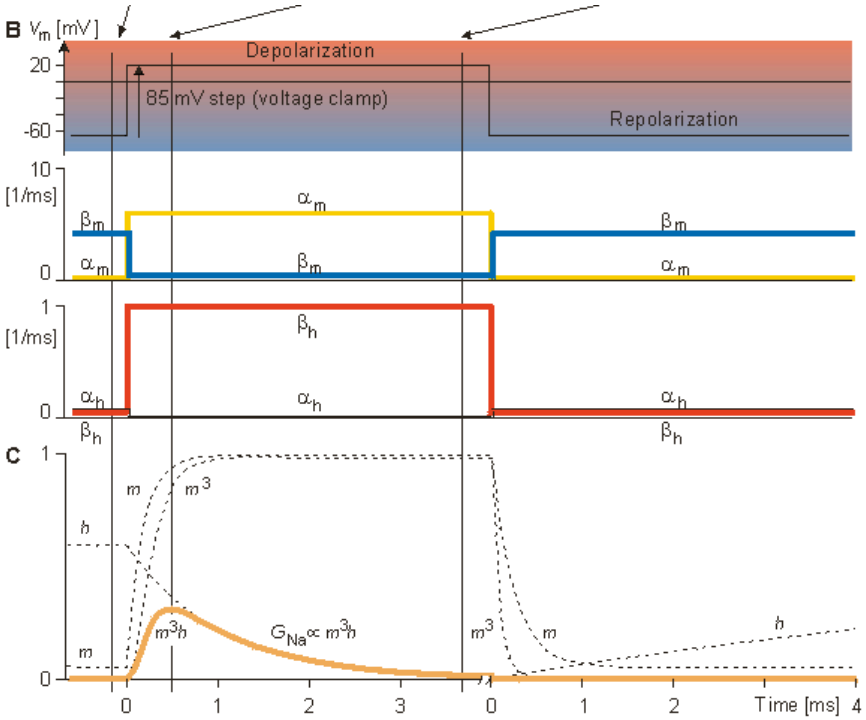
$$g_{\mathrm{Na}} = m^3 h \bar{g}_{\mathrm{Na}},$$

$\bar{g}_{Na}$ *is a constant*
m represents the proportion of activating molecules on the inside
h represents the proportion of inactivating molecules on the outside

- **What does m^3h represent?**
  - That sodium conductance is proportional to the number of sites on the inside of the membrane which are occupied simultaneously by three activating molecules (m^3) and not blocked by an inactivating molecule (m^3h).

Dynamics of Na Conductance (1)





www.bem.fi/book/04/04.htm

Dynamics of Na Conductance (2)

- **The two variables obey the following first order differential equation**

$$\frac{dm}{dt} = \alpha_m (1 - m) - \beta_m m,$$

$$\frac{dh}{dt} = \alpha_h (1 - h) - \beta_h h,$$

- **α_m or β_h represents of transfer from outside to inside**
- **β_m or α_h represents of transfer from inside to outside**

Dynamics of Na Conductance (3)

- **Solving the first order differential equation**

$$m = m_\infty - (m_\infty - m_0)\exp(-t/\tau_m), \qquad h = h_\infty - (h_\infty - h_0)\exp(-t/\tau_h),$$

$$m_\infty = \alpha_m/(\alpha_m + \beta_m) \qquad h_\infty = \alpha_h/(\alpha_h + \beta_h)$$

$$\tau_m = 1/(\alpha_m + \beta_m), \qquad \tau_h = 1/(\alpha_h + \beta_h).$$

- **At t=0; m =m_0, h =h_0**

Dynamics of Na Conductance (4)

- **HH noted that in resting state, sodium conductance is negligble, so we can neglect m_0, and inactivation in nearly complete if V< -30mV and h_α can also be neglected**

$$g_{\mathrm{Na}} = g'_{\mathrm{Na}} \left[1 - \exp\left(-t/\tau_m\right)\right]^3 \exp\left(-t/\tau_h\right),$$

where $$g'_{\mathrm{Na}} = \bar{g}_{\mathrm{Na}} m_\infty^3 h_0$$

is the value of sodium conductance if *h* remained in its resting level h_0

Dynamics of Na Conductance (5)

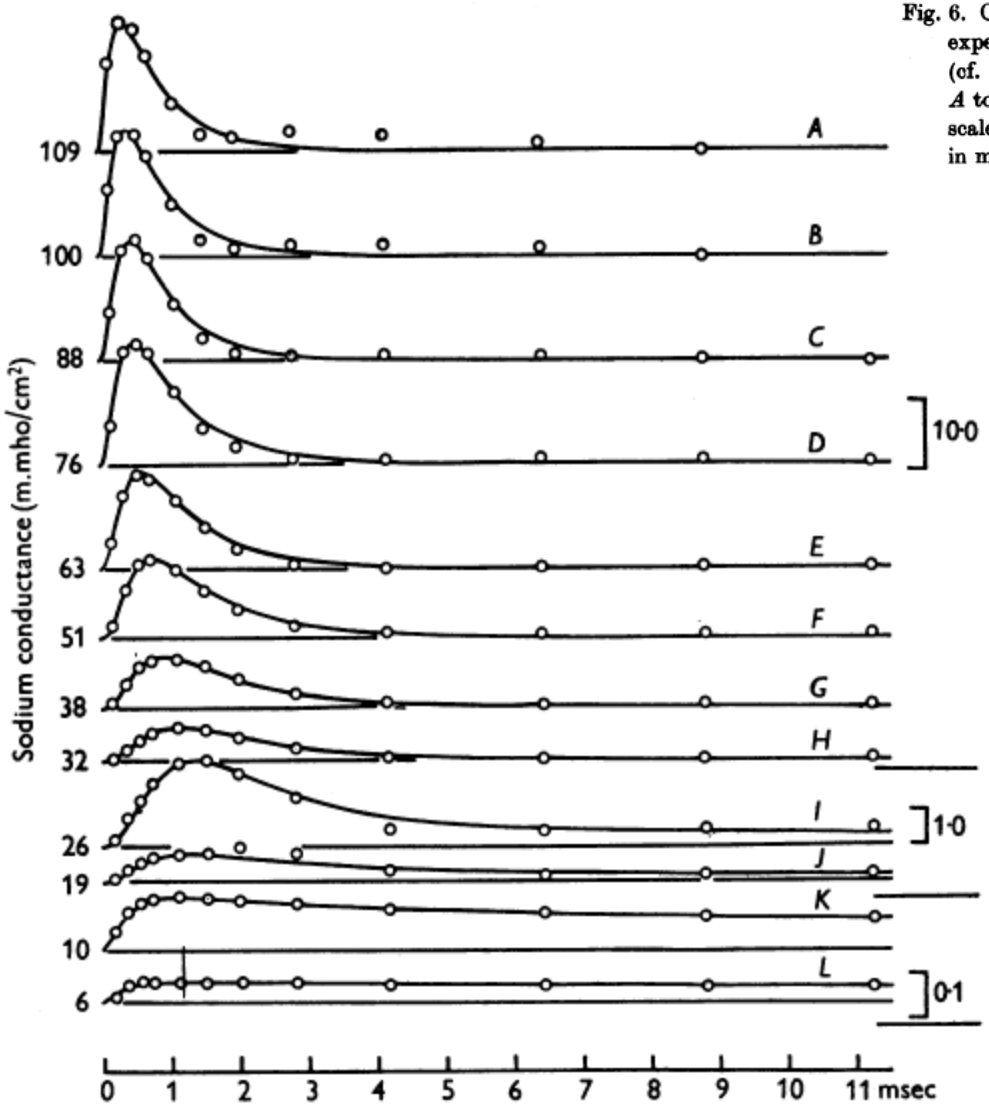
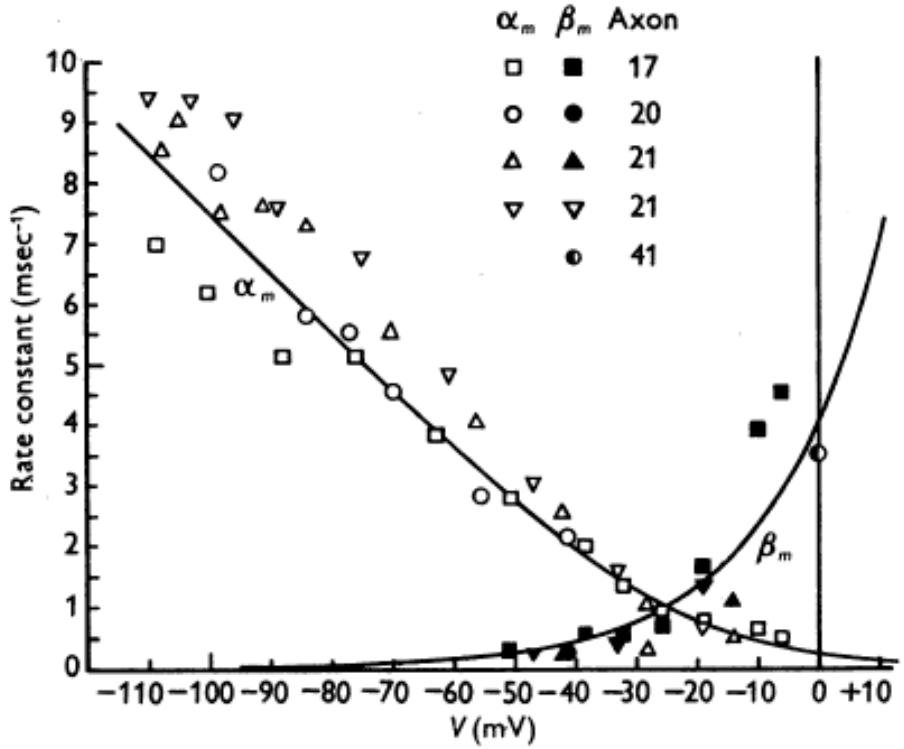


Fig. 6. Changes of sodium conductance associated with different depolarizations. The circles are experimental estimates of sodium conductance obtained on axon 17, temperature 6–7° C (cf. Fig. 3). The smooth curves are theoretical curves with parameters shown in Table 2; *A* to *H* drawn from eqn. 19, *I* to *L* from 14, 17, 18 with $\bar{g}_{Na} = 70{\cdot}7$ m.mho/cm². The ordinate scales on the right are given in m.mho/cm². The numbers on the left show the depolarization in mV. The time scale applies to all curves.

$$g_{Na} = g'_{Na}\,[1 - \exp(-t/\tau_m)]^3 \exp(-t/\tau_h),$$

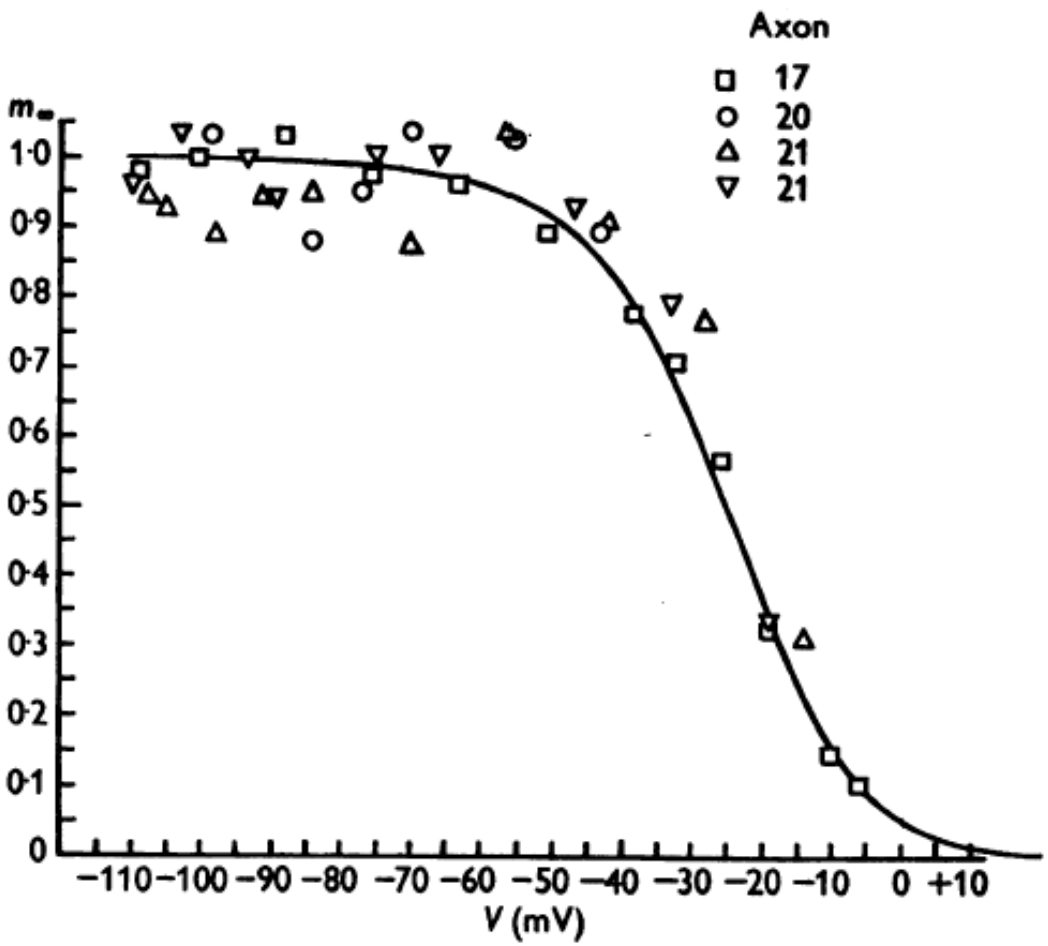
Rate constants α_m, β_m(6)



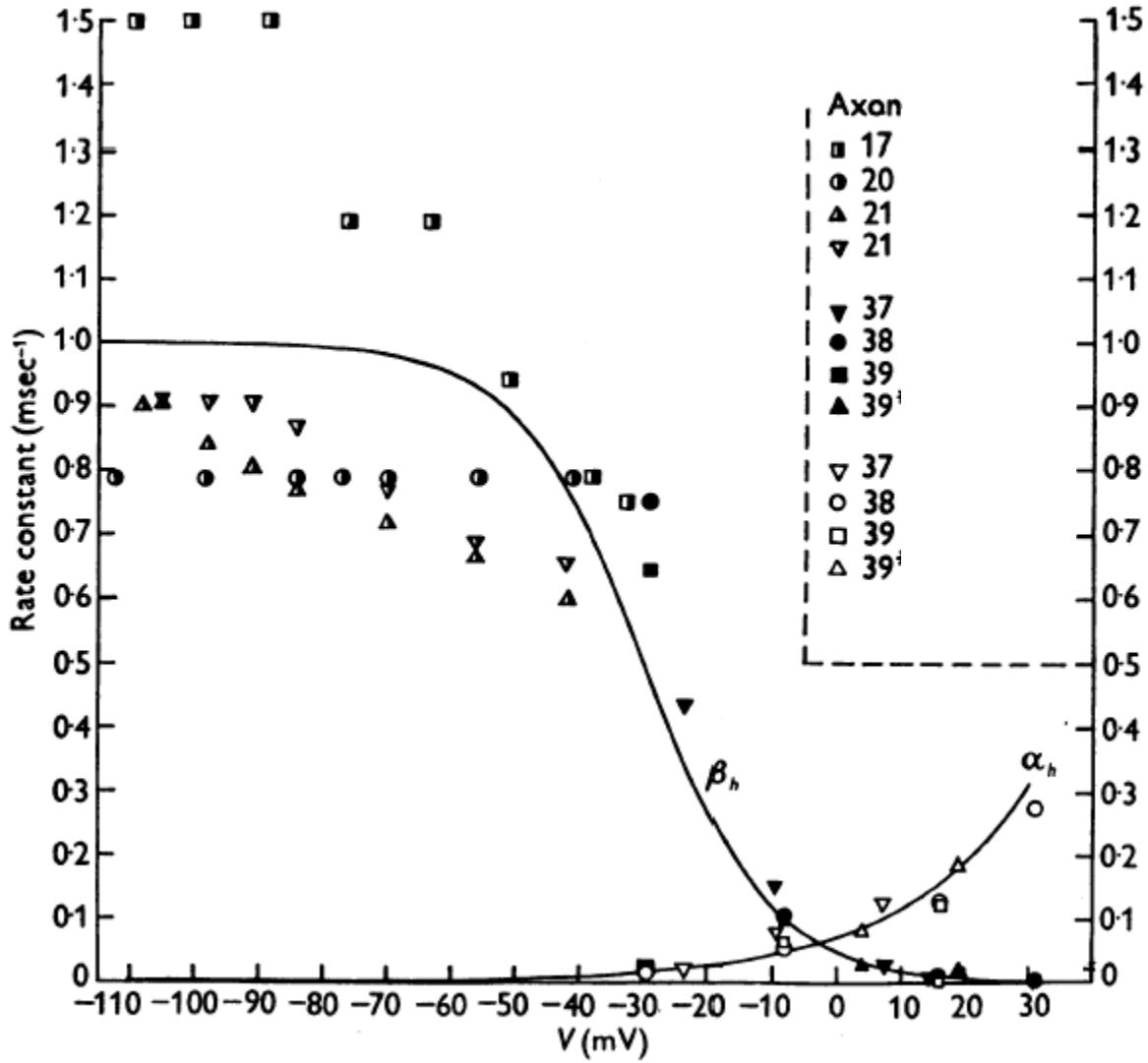
$$\alpha_m = 0{\cdot}1\,(V+25)\Big/\left(\exp\frac{V+25}{10}-1\right),$$

$$\beta_m = 4\,\exp\,(V/18),$$

How does activation variable m change with V?(7)



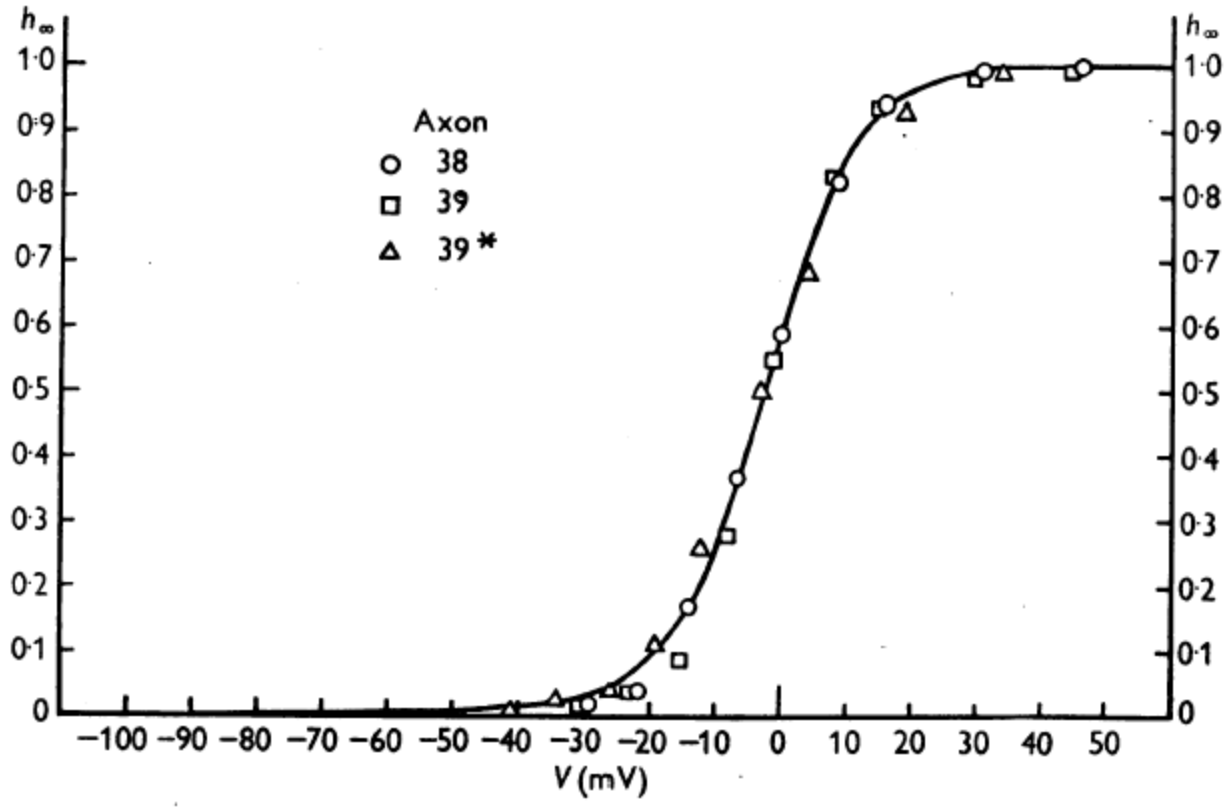
Rate constants α_h, β_h(8)



$$\alpha_h = 0{\cdot}07 \exp(V/20),$$

$$\beta_h = 1 \Big/ \left(\exp \frac{V+30}{10} + 1\right).$$

How does activation variable h change with V?(9)



Putting pieces together – HH model

$$I = C_M \frac{dV}{dt} + \bar{g}_K n^4 (V - V_K) + \bar{g}_{Na} m^3 h (V - V_{Na}) + \bar{g}_l (V - V_l),$$

where

$$dn/dt = \alpha_n (1 - n) - \beta_n n,$$

$$dm/dt = \alpha_m (1 - m) - \beta_m m,$$

$$dh/dt = \alpha_h (1 - h) - \beta_h h,$$

$$\alpha_n = 0{\cdot}01\ (V + 10) \Big/ \left(\exp \frac{V + 10}{10} - 1 \right),$$

$$\beta_n = 0{\cdot}125 \exp (V/80),$$

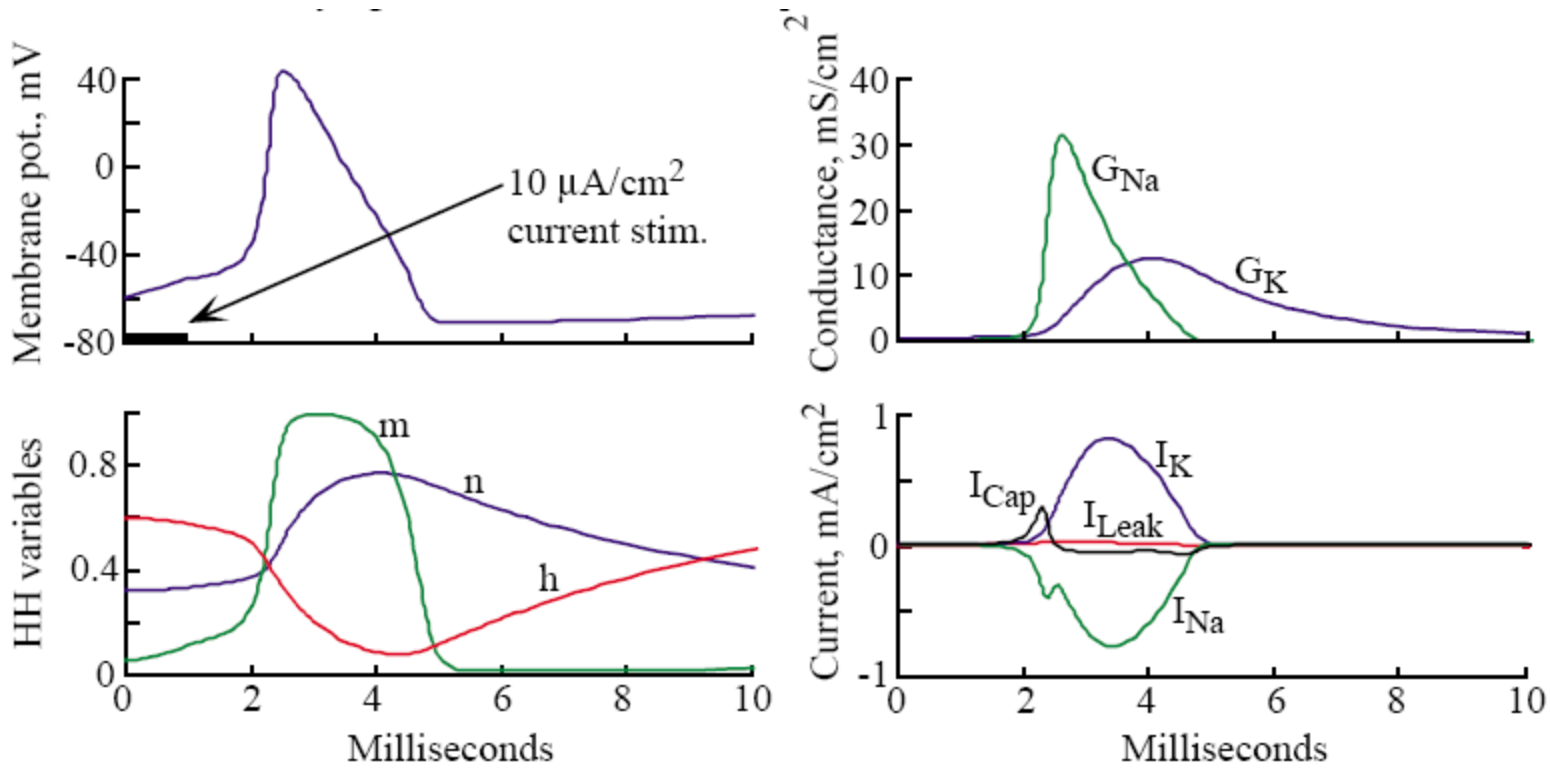
$$\alpha_m = 0{\cdot}1\ (V + 25) \Big/ \left(\exp \frac{V + 25}{10} - 1 \right),$$

$$\beta_m = 4 \exp (V/18),$$

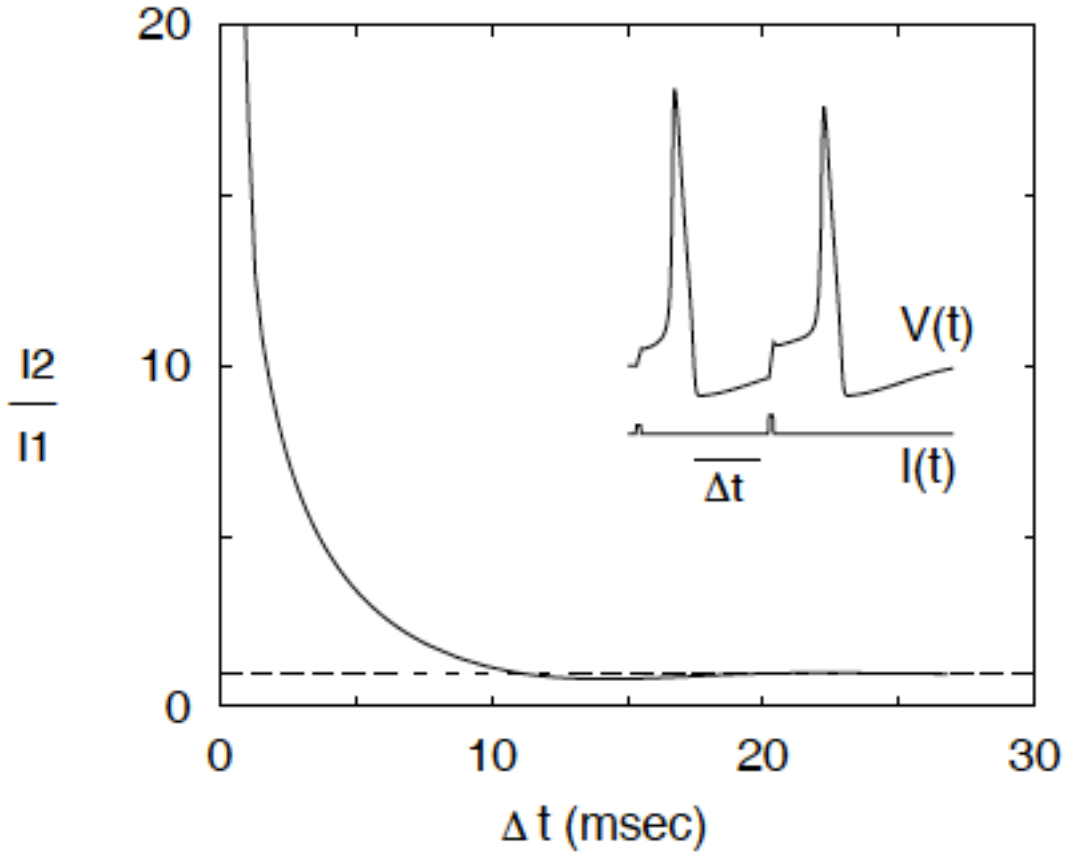
$$\alpha_h = 0{\cdot}07 \exp (V/20),$$

$$\beta_h = 1 \Big/ \left(\exp \frac{V + 30}{10} + 1 \right).$$

Time courses of HH variables



Refractory Period

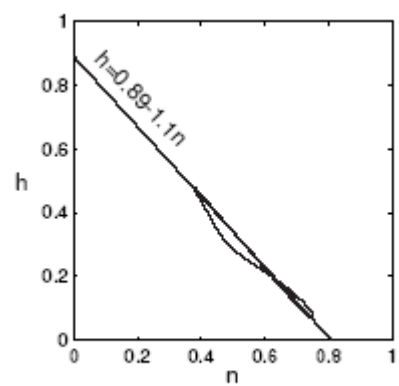


HH model - Summary

- **Models a patch of membrane**
- **Assumes isopotential i.e. the membrane potential is constant across the patch**
- **The number of channels is large enough that individual gating events are averaged out and the Na and K currents are smooth population currents**
- **The channels are not arranged in anyway which allows local interaction among small number of channels**

Reducing HH models

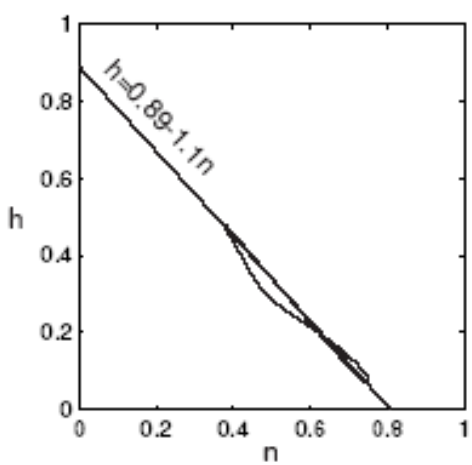
- **State variables of HH eqns : [V, m, n, h]**
- **Most reduction rely on two simplifications**
  - Time constants are very different
  - *m* changes so fast compared to *n* and *h* that you don't need a ODE to describe it (removes one ODE)
  - *n+h* is almost a constant; so we can eliminate one more variable
  - Now the reduced HH will have state variable [V, w]; V – fast variable (membrane potential) and w – slow variable (potassium activation)

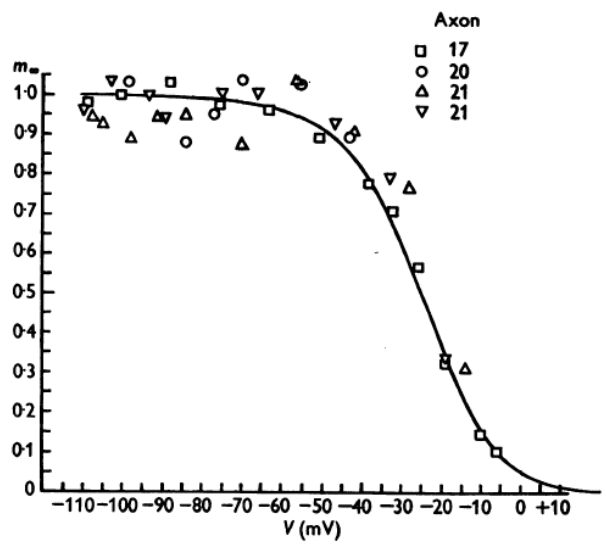


Reducing HH models(2)

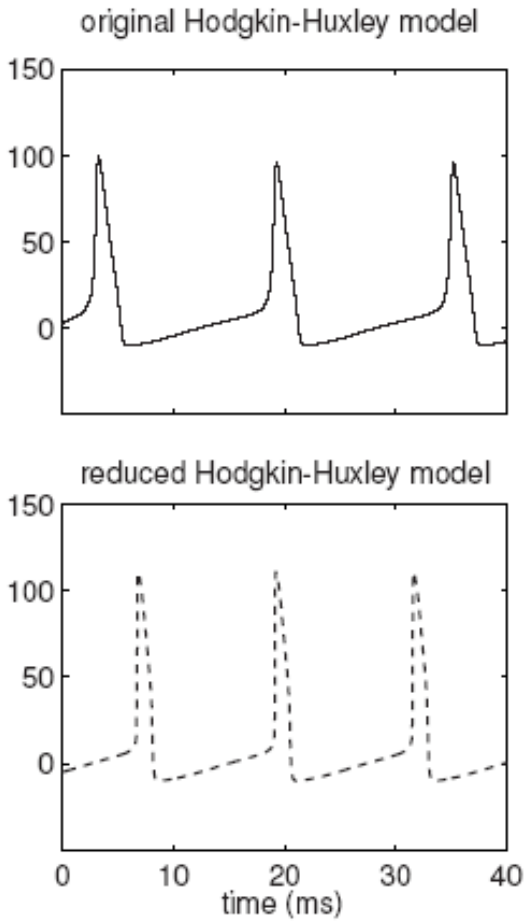
Original $$C\dot{V} = I - \overbrace{g_{\mathrm{K}} n^4 (V - E_{\mathrm{K}})}^{I_{\mathrm{K}}} - \overbrace{g_{\mathrm{Na}} m^3 h (V - E_{\mathrm{Na}})}^{I_{\mathrm{Na}}} - \overbrace{g_{\mathrm{L}} (V - E_{\mathrm{L}})}^{I_{\mathrm{L}}}$$

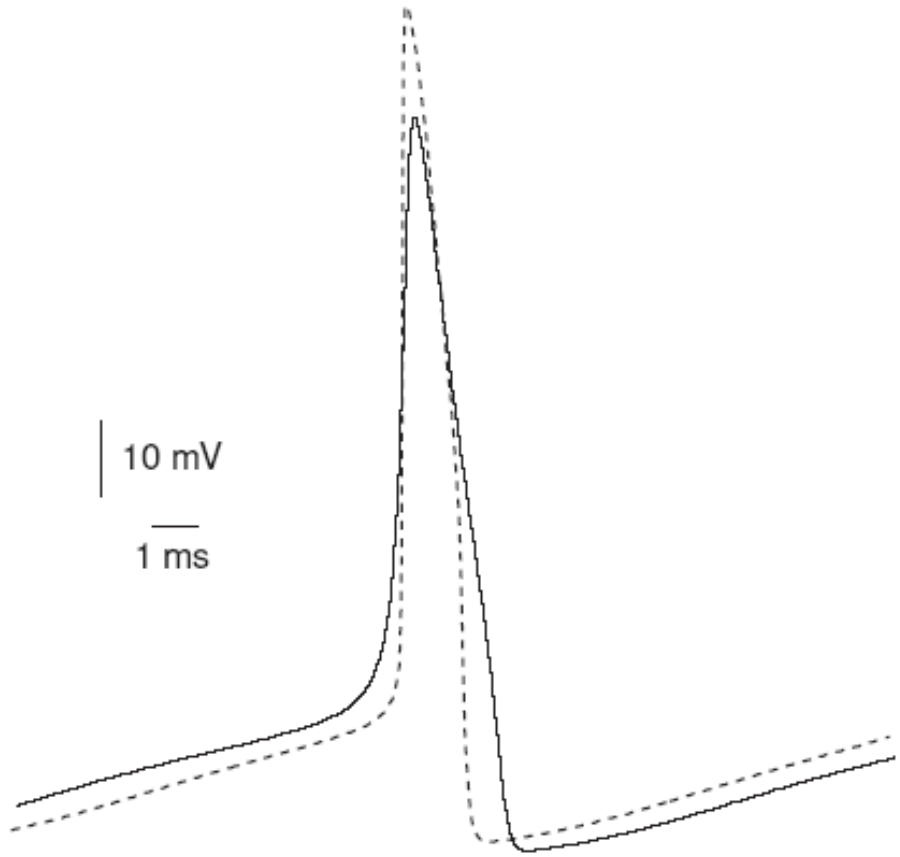
Reduced $$C\dot{V} = I - \overbrace{g_{\mathrm{K}} n^4 (V - E_{\mathrm{K}})}^{I_{\mathrm{K}}} - \overbrace{g_{\mathrm{Na}} \underline{m_{\infty}^3(V)} \underline{(0.89 - 1.1n)} (V - E_{\mathrm{Na}})}^{\text{instantaneous } I_{\mathrm{Na}}} - \overbrace{g_{\mathrm{L}} (V - E_{\mathrm{L}})}^{I_{\mathrm{L}}}$$





Reducing HH models(3)

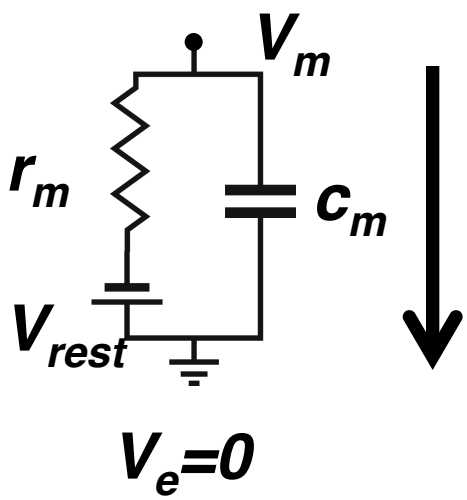




Linear Cable Equation

Action Potential Propagation

Transmembrane current across unit length of the axon

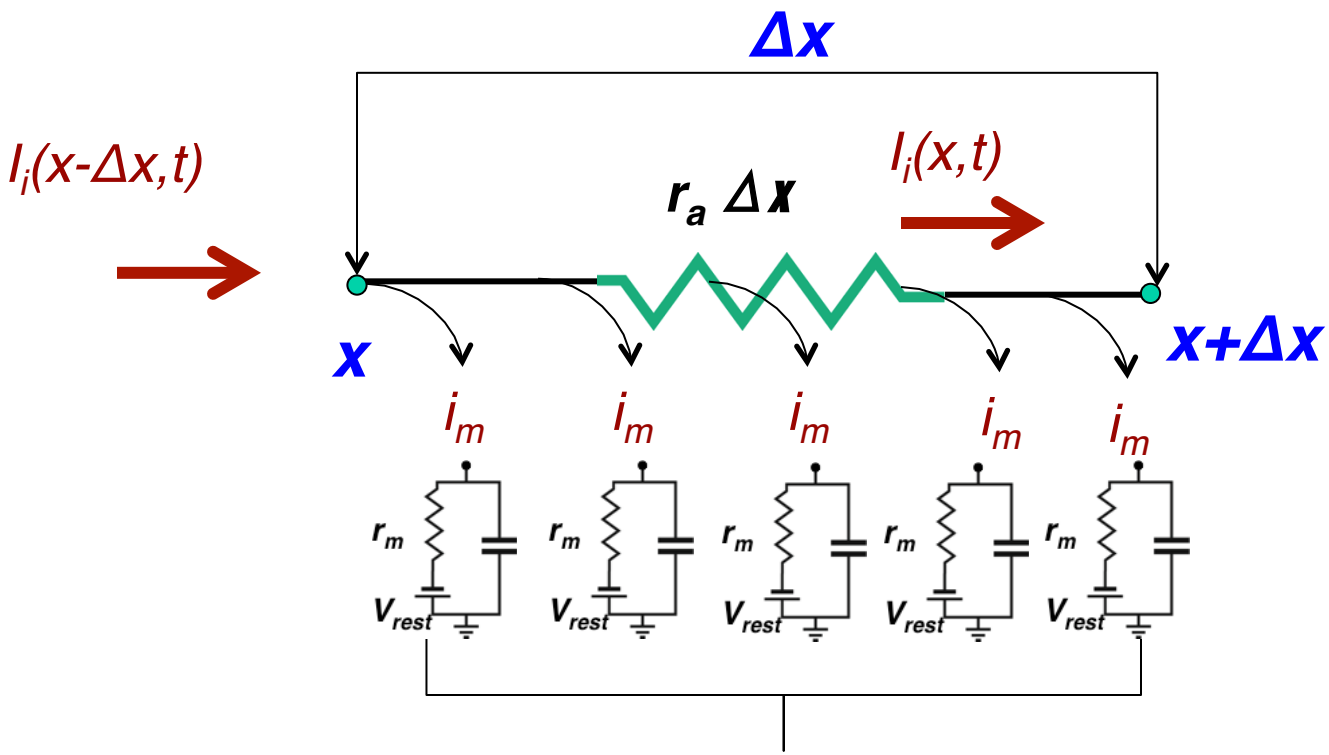


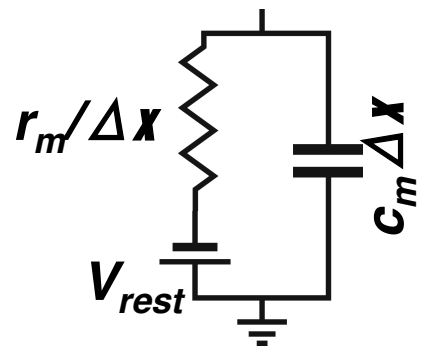
$$i_m = \frac{V_m - V_{rest}}{r_m} + c_m \frac{dV_m}{dt}$$

i_m – Transmembrane current per unit length (A/cm)
r_m – membrane resistance per unit length (Ωcm)
c_m –membrane capacitance per unit length (F/cm)

Action Potential Propagation

Transmembrane current across Δx units of the axon





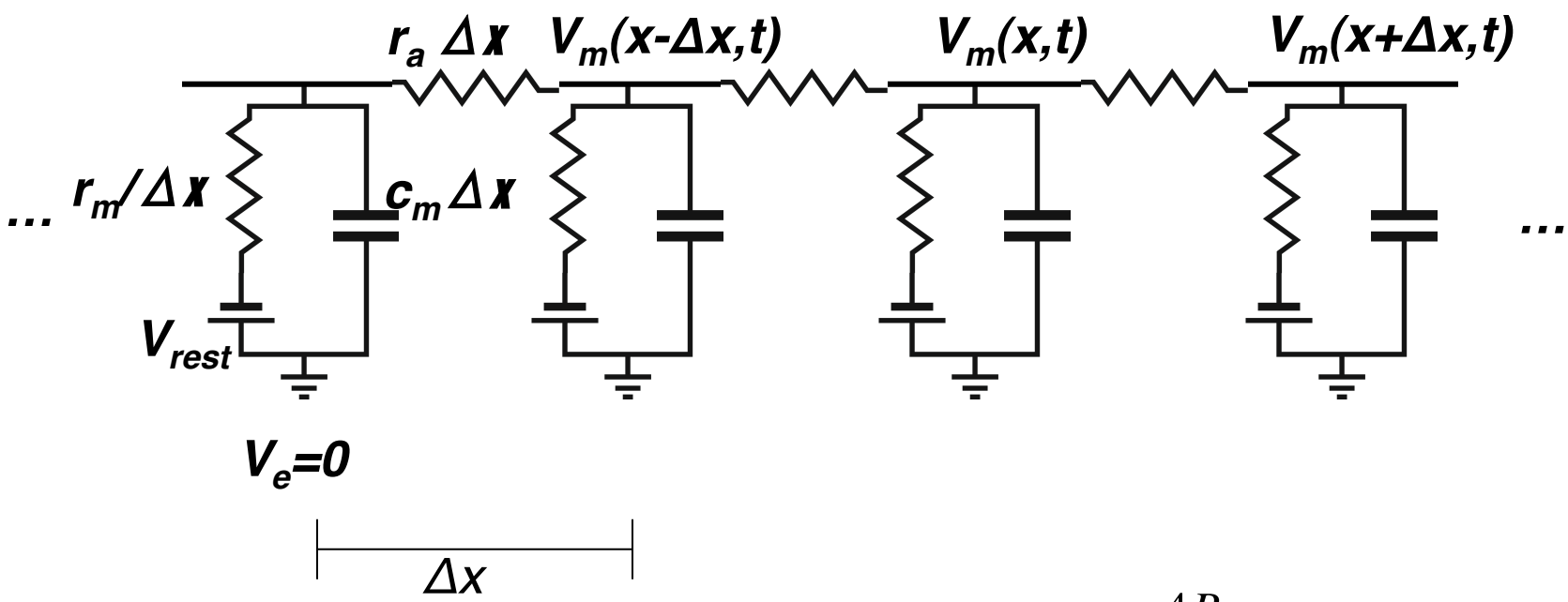
= unit transmembrane current (i_m) times Δx

The total membrane resistance in a fiber of length Δx is: $r_m/\Delta x$

The total membrane capacitance in a fiber of length Δx is: $c_m\Delta x$

Action Potential Propagation

Plug membrane together: get linear cable



$$r_a = \frac{4R_a}{\pi d^2} \quad \Omega / cm$$

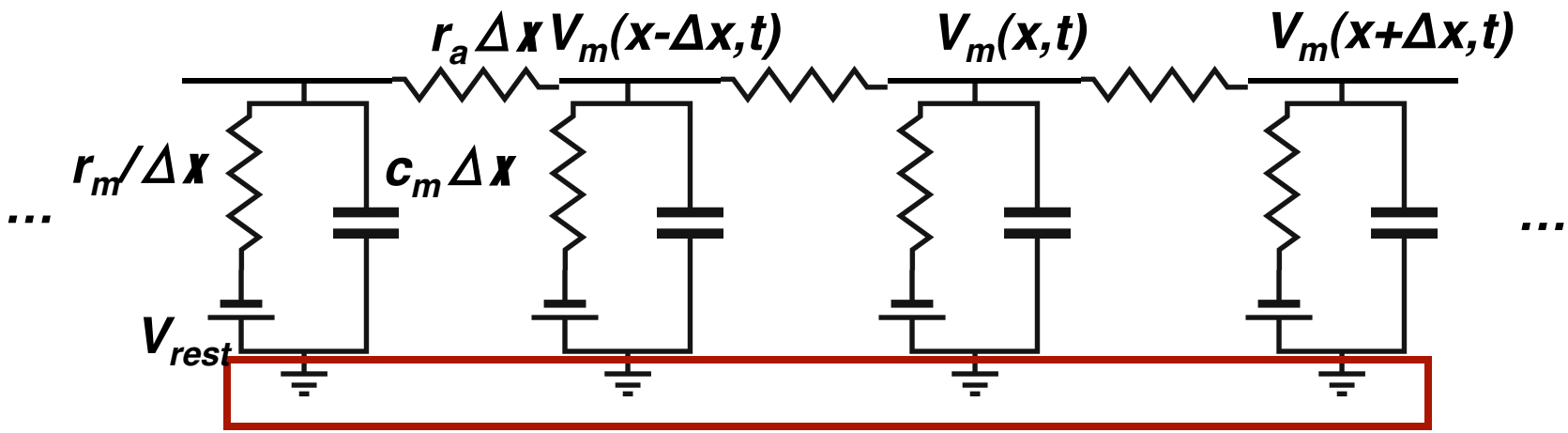
$$r_m = \frac{R_m}{\pi d} \quad \Omega \cdot cm$$

$$c_m = C_m \cdot \pi d \quad F / cm$$

R_a - intracellular resistivity (Ωcm)
R_m - specific membrane resistance (Ωcm²)
C_m - specific membrane capacitance (F/cm²)

Action Potential Propagation

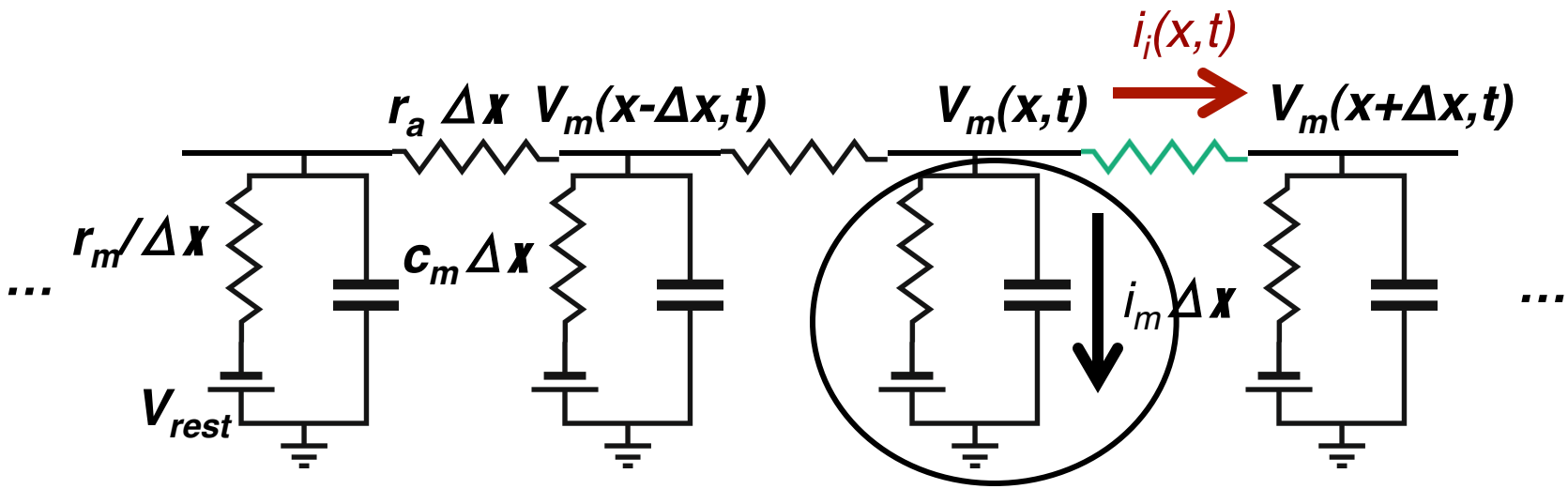
Plug membrane together: get linear cable



Note: Constant V_e is an assumption

Action Potential Propagation

Plug membrane together: get linear cable



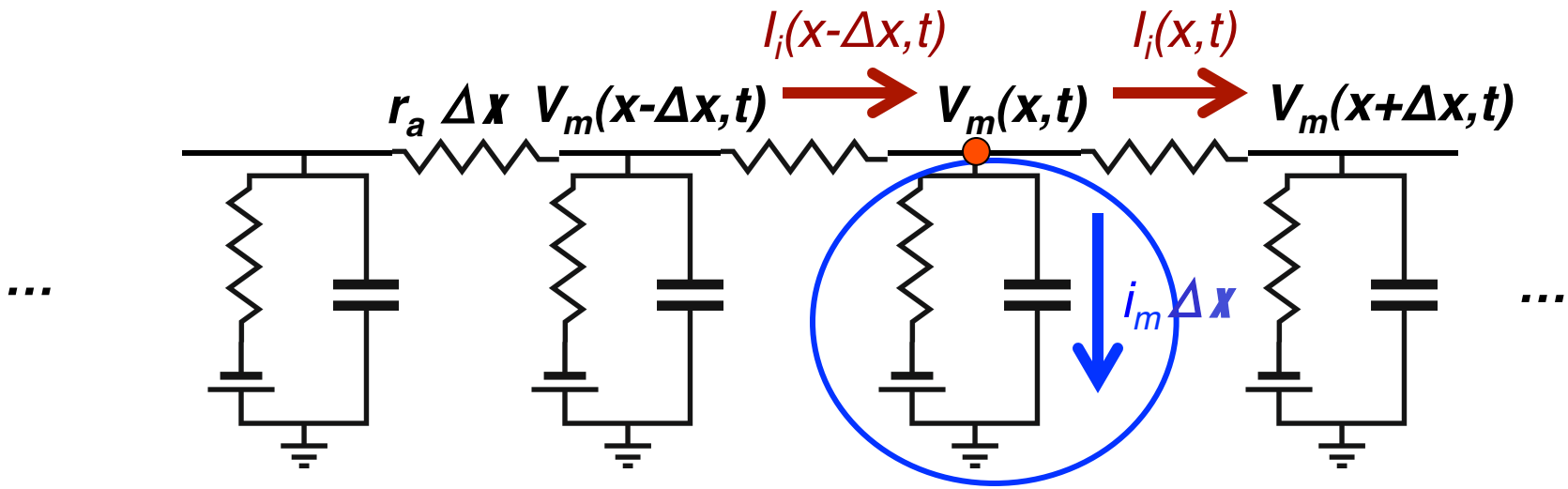
$$V_m(x,t) - V_m(x+\Delta x,t) = r_a \cdot \Delta x \cdot i_i(x,t)$$

$$\lim it \quad \Delta x = 0 = \frac{V_m(x,t) - V_m(x+\Delta x,t)}{\Delta x} = \frac{\partial V_m}{\partial x}(x,t) \quad = -r_a \cdot I_i(x,t)$$

Eqn 1

Action Potential Propagation

Plug membrane together: get linear cable



By applying Krichhoff's current law at node x

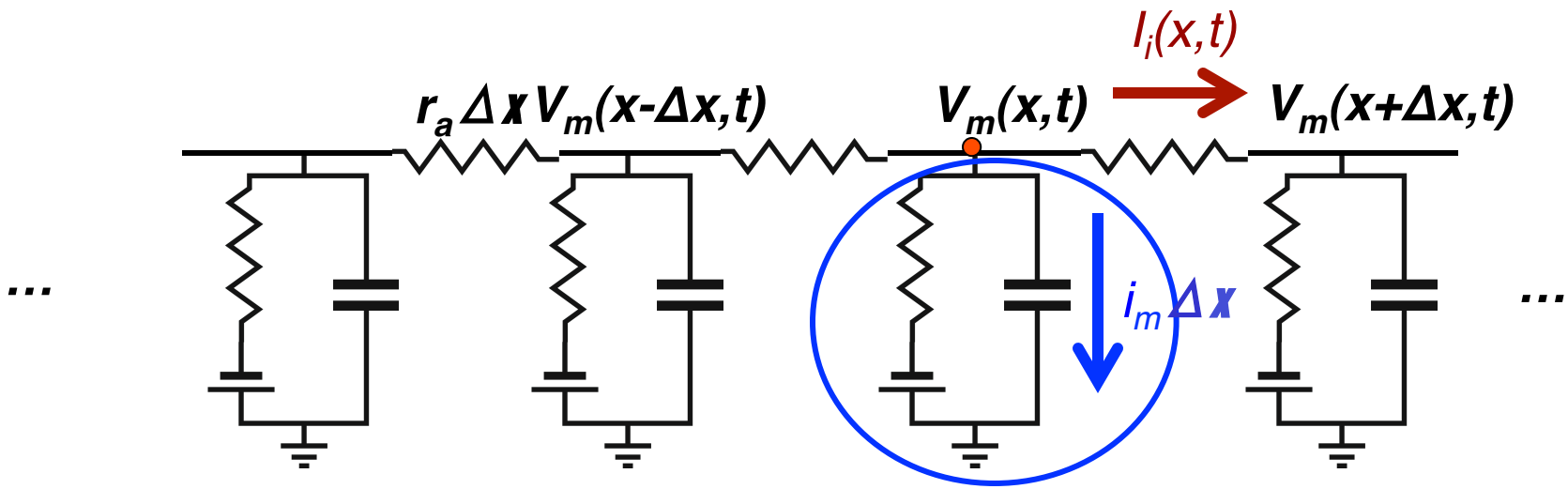
$$i_m(x,t)\Delta x + I_i(x,t) - I_i(x-\Delta x,t) = 0$$

$$\lim it\ \Delta x = 0 \quad -\frac{\partial I_i}{\partial x}(x,t) \quad = i_m(x,t)$$

Eqn 2

Linear Cable Equation

Plug membrane together: get linear cable



$$\lim it\ \Delta x = 0 \quad \frac{\partial V_m}{\partial x}(x,t) = -r_a \cdot I_i(x,t)$$

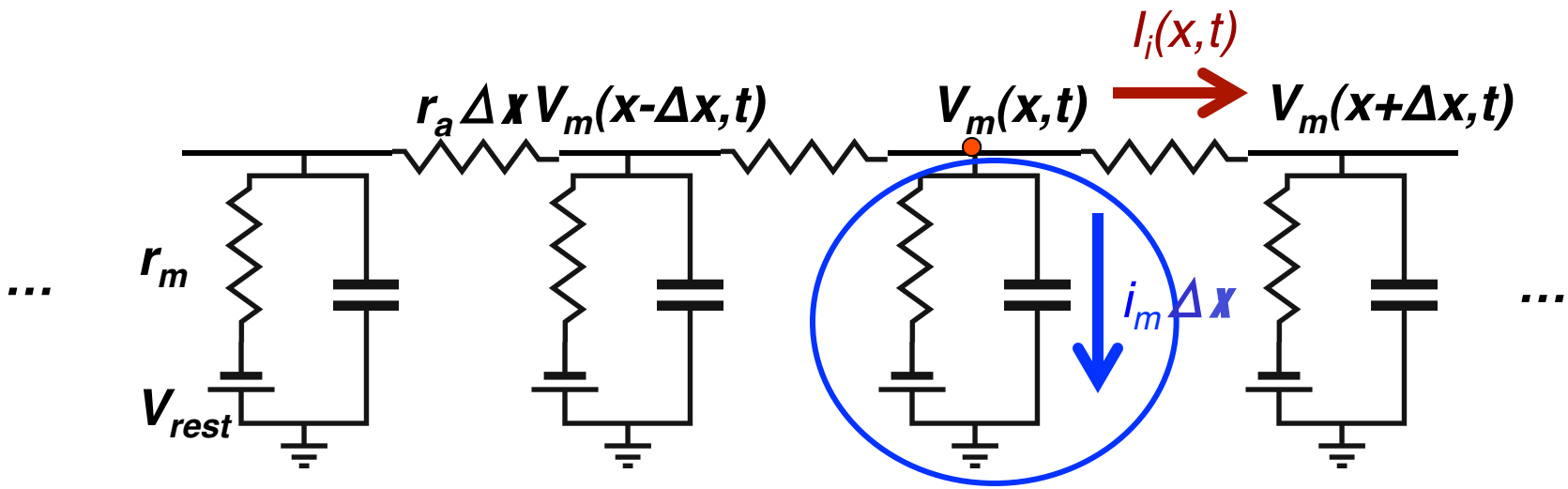
Substitute

$$\lim it\ \ \Delta x = 0 \quad -\frac{\partial I_i}{\partial x}(x,t) = i_m(x,t)$$

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

Linear Cable Equation

Plug membrane together: get linear cable

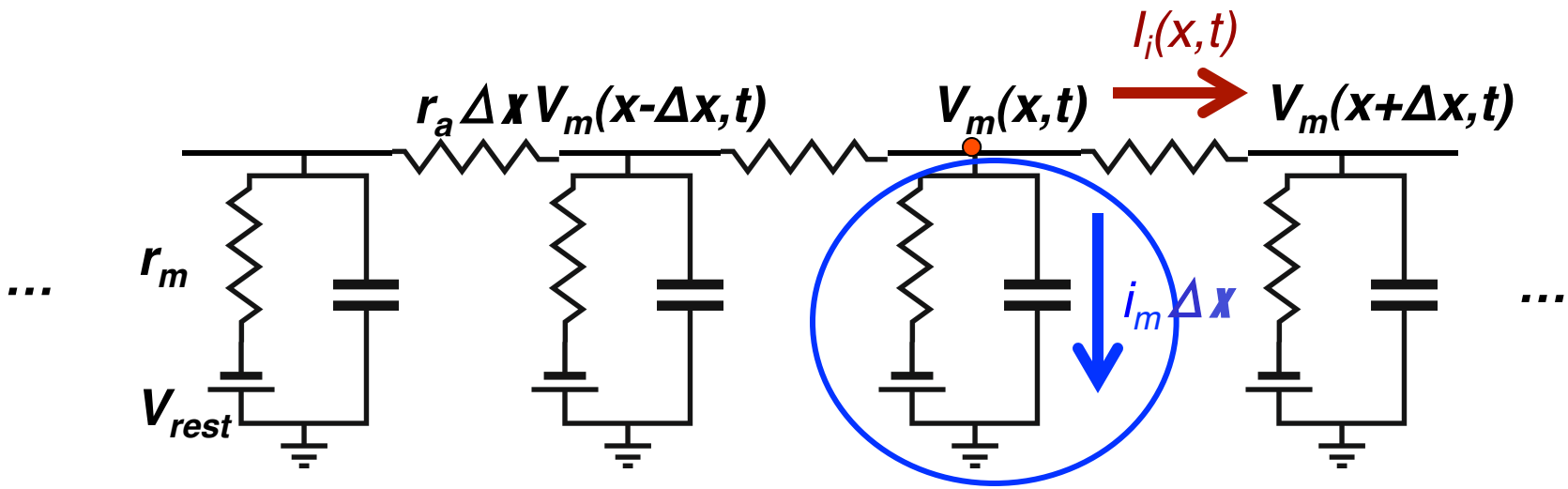


If electrical nature of the membrane is constant, then

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

Linear Cable Equation

Plug membrane together: get linear cable



Multiplying both sides by r_m we get:

$$\lambda^2 \frac{\partial^2 V_m(x,t)}{\partial x^2} = V_m(x,t) - V_{rest} + \tau_m \frac{\partial V_m(x,t)}{\partial t} \qquad \lambda = \sqrt{(r_m / r_a)} \qquad \tau_m = r_m c_m$$

λ – steady state space constant

τ -Membrane time constant

Space and Time constants

$$\lambda = \sqrt{r_m / r_i} = \sqrt{\frac{R_m}{2\pi a} \Big/ \frac{R_i}{\pi a^2}} = \sqrt{R_m a / 2R_i}$$

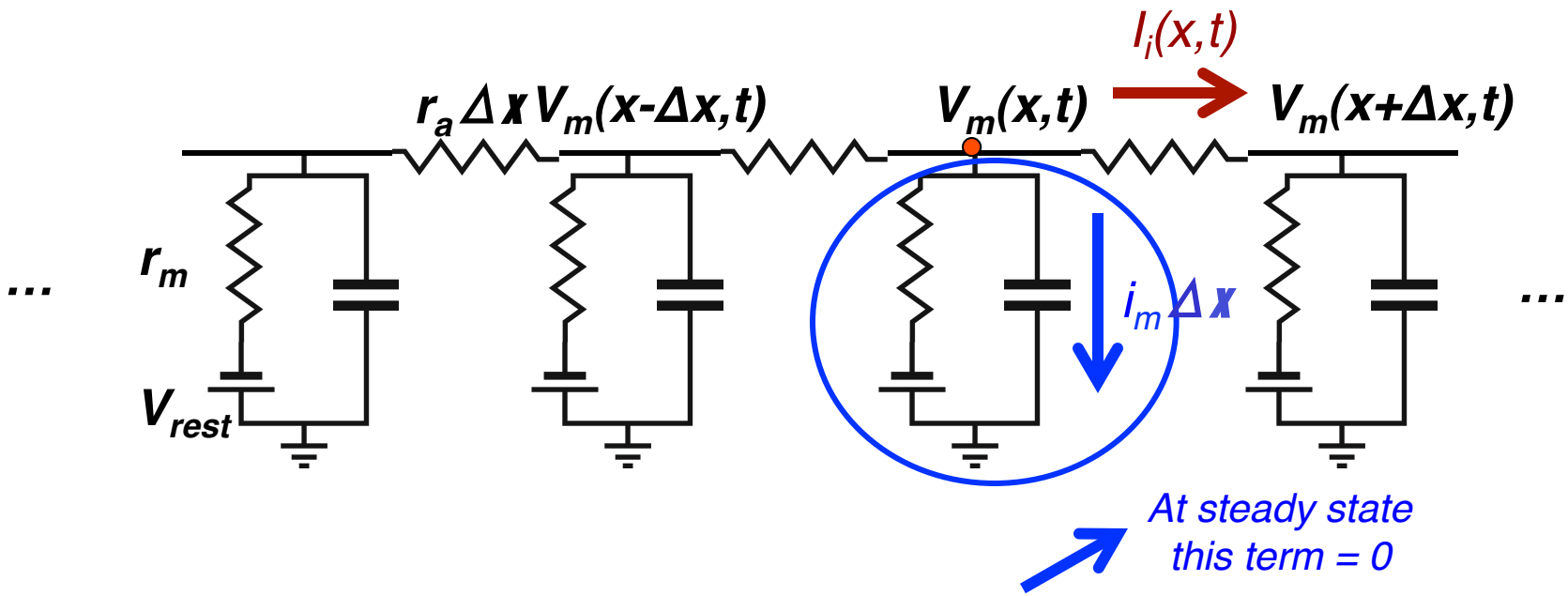
- **Space constant increases with square root of the axon radius**

$$\tau_m = r_m c_m = \frac{R_m}{2\pi a} \cdot C_m 2\pi a = R_m C_m$$

- **Time constant does not depend on axon size**

Steady-State Solutions

Plug membrane together: get linear cable



$$\lambda^2 \frac{\partial^2 V_m(x,t)}{\partial x^2} = V_m(x,t) - V_{rest} + \tau_m \frac{\partial V_m(x,t)}{\partial t}$$

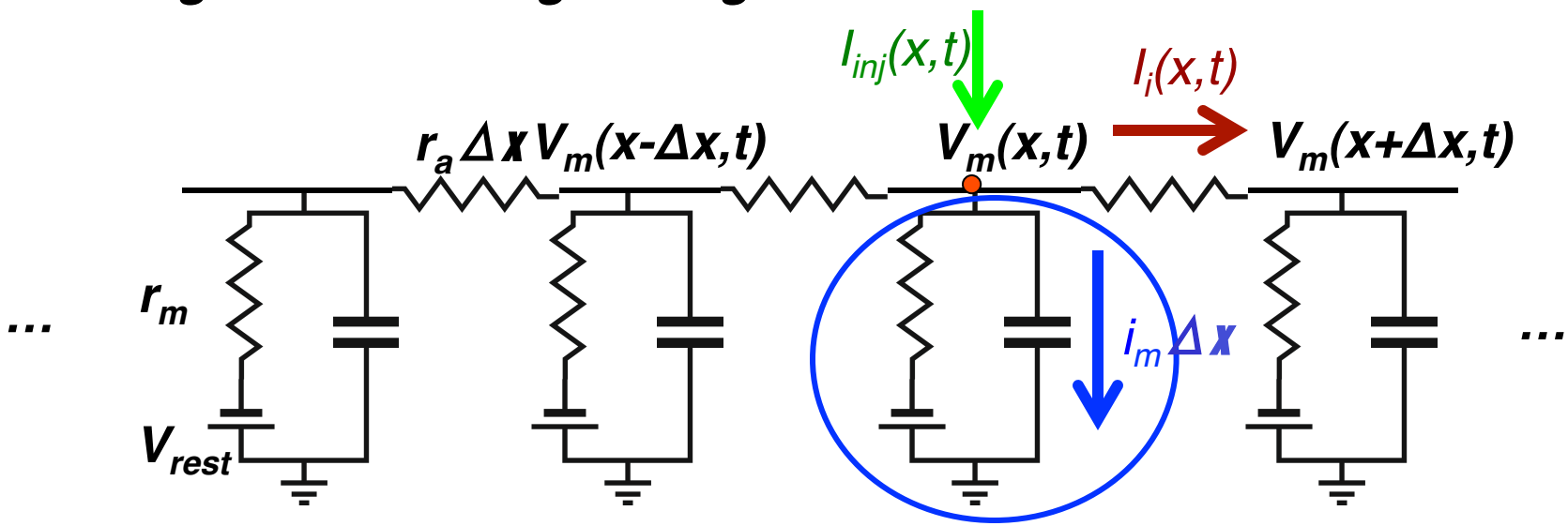
$$\lambda = \sqrt{(r_m / r_a)}$$

$$\tau_m = r_m c_m$$

$$\boxed{\lambda^2 \frac{d^2 V(x)}{dx^2} = V(x) \qquad (V = V_m - V_{rest})}$$

Steady-State Solutions

Plug membrane together: get linear cable

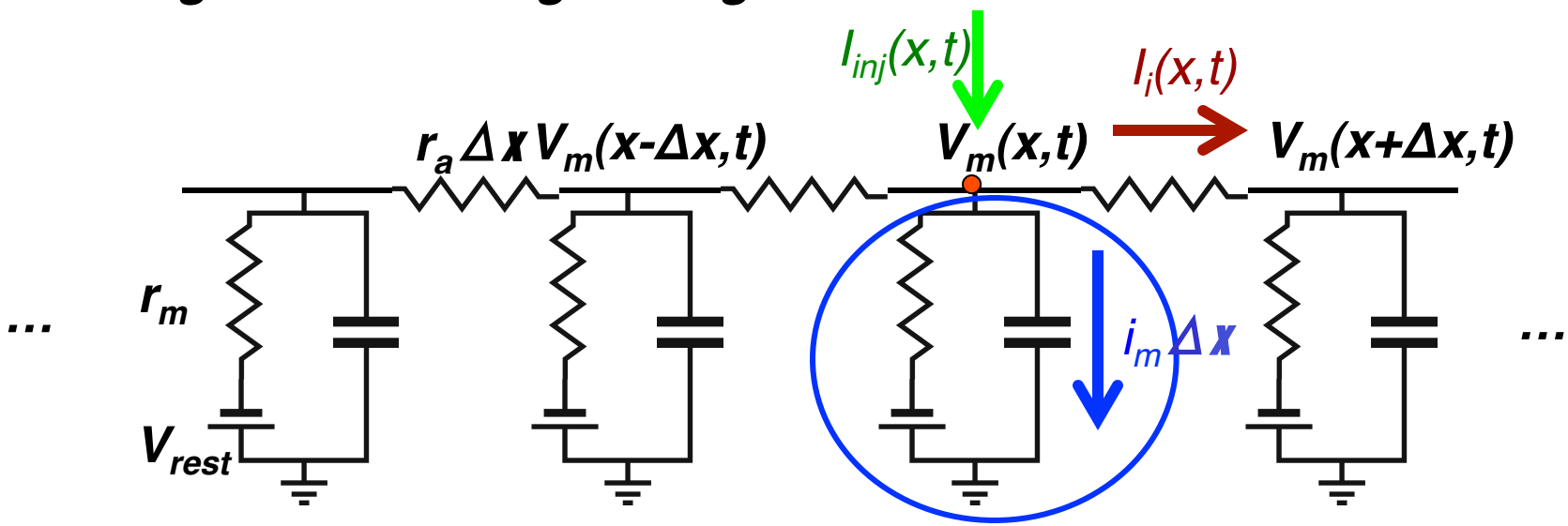


$$i_m(x,t) = \frac{V_m(x,t) - V_{rest}}{r_m} + c_m \frac{\partial V_m(x,t)}{\partial t} - I_{inj}(x,t)$$

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

Steady-State Solutions

Plug membrane together: get linear cable

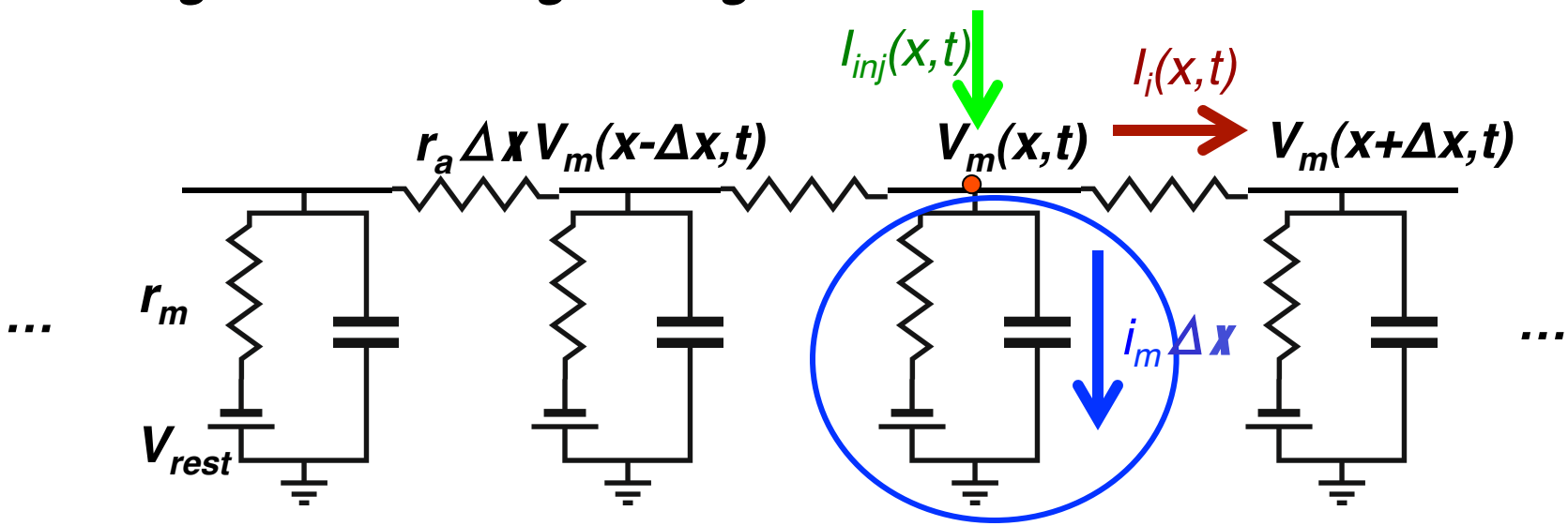


$$\frac{1}{r_a}\frac{\partial^2 V_m(x,t)}{\partial x^2}(x,t) = i_m(x,t)$$

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

Steady-State Solutions

Plug membrane together: get linear cable

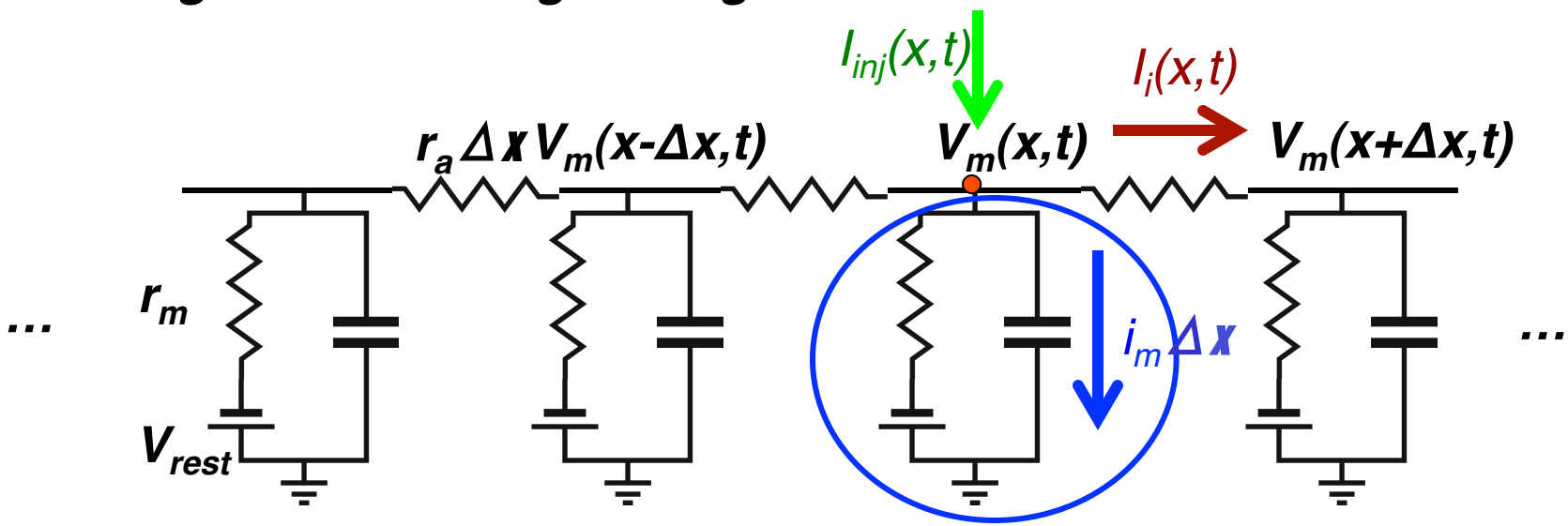


$$\frac{1}{r_a}\frac{\partial^2 V_m(x,t)}{\partial x^2}(x,t) = \frac{V_m(x,t) - V_{rest}}{r_m} + c_m \frac{\partial V_m(x,t)}{\partial t} - I_{inj}(x,t)$$

At steady state $$\lambda^2 \frac{d^2 V(x)}{dx^2} = V(x) - r_m I_{inj}(x,t) \qquad (V = V_m - V_{rest})$$

Steady-State Solutions

Plug membrane together: get linear cable



$$\lambda^2 \frac{d^2V(x)}{dx^2} = V(x) - r_m I_{inj}(x)$$

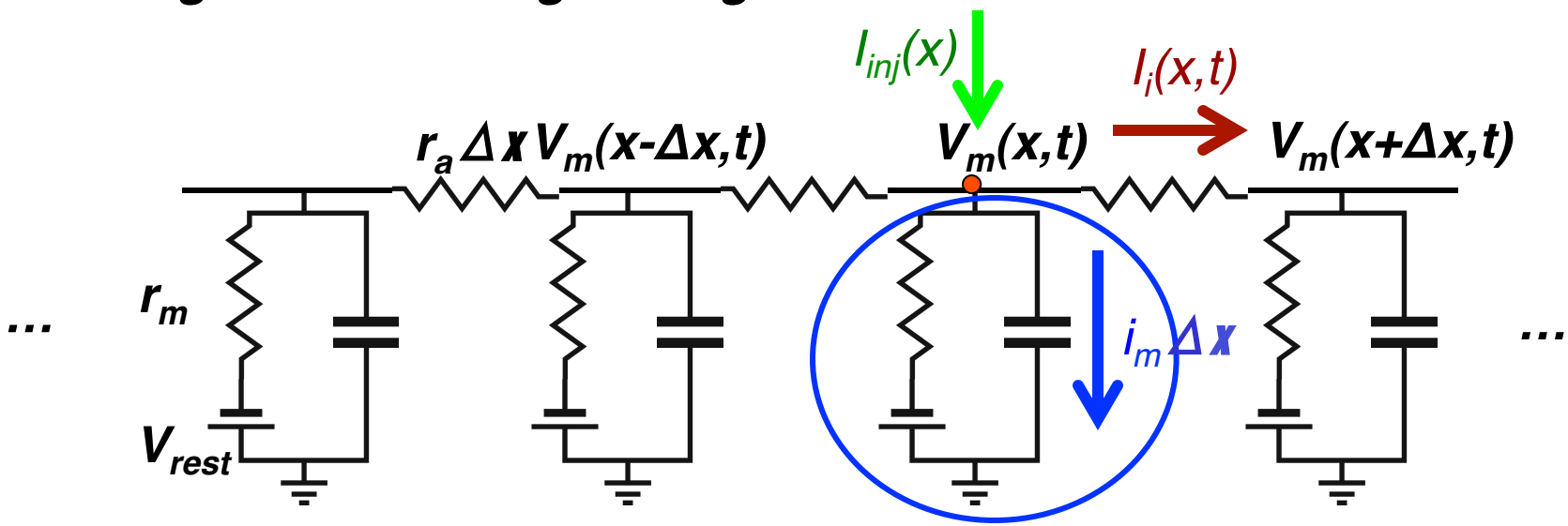
a general solution to this ODE for constant current applied at x

$$\boxed{V(x) = A\exp(x/\lambda) + B\exp(-x/\lambda)}$$

A and B are constants will depend on the boundary conditions

Steady-State Solutions

Plug membrane together: get linear cable



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

For boundary-value solutions it is often convenient to use another pair of solutions to the second-order ordinary differential equation

$$V(x) = A\exp(x/\lambda) + B\exp(-x/\lambda)$$

$$V(x) = A\cosh(x/\lambda) + B\sinh(x/\lambda)$$

$$\cosh(x) = \frac{\exp(x) + \exp(-x)}{2}$$

$$\sinh(x) = \frac{\exp(x) - \exp(-x)}{2}$$

Case 1: Infinite Cable

$$\lambda^2 \frac{d^2V(x)}{dx^2} = V(x) - r_m I_{inj}(x)$$

$$V(x) = A\exp(x/\lambda) + B\exp(-x/\lambda)$$

For the case in which the cable extends from -∞ to +∞ we require V (-∞) = V (∞) = 0. What should be values of A and B to obey this boundary conditions?

For x > 0; A = 0 and B = V_0 (where V_0 is the membrane voltage at the site of current injection)
Similarly for x<0; A = V_0 and B = 0

$$\boxed{V(x) = V_0 \exp(-|x|/\lambda)}$$

Case 2: Sealed End Cable

$$\lambda^2 \frac{d^2V(x)}{dx^2} = V(x) - r_m I_{inj}(x)$$

$$V(x) = A\cosh(x/\lambda) + B\sinh(x/\lambda)$$

The idea for sealed end is that current should not flow across a boundary at length x = l

$$\left.\frac{dV}{dx}\right|_{x=0} = -r_a I_{inj} \qquad At \quad x = 0 \quad -r_a I_{inj} = \frac{B}{\lambda}$$

$$\left.\frac{dV}{dx}\right|_{x=l} = 0 \qquad B = -r_a I_{inj}\lambda$$

$$V(x) = A\cosh(x/\lambda) + B\sinh(x/\lambda)$$

$$\frac{dV(x)}{dx} = \frac{A}{\lambda}\sinh(x/\lambda) + \frac{B}{\lambda}\cosh(x/\lambda)$$

$$At \quad x = l \quad -0 = A\sinh(l/\lambda) + B\cosh(l/\lambda)$$

$$A = -B\coth(l/\lambda)$$

$$A = r_a I_{inj}\lambda\coth(l/\lambda)$$

Case 2: Sealed End Cable

$$\lambda^2 \frac{d^2V(x)}{dx^2} = V(x) - r_m I_{inj}(x)$$

$$V(x) = A\cosh(x/\lambda) + B\sinh(x/\lambda)$$

The idea for sealed end is that current should not flow across a boundary at length x = l

$$\left.\frac{dV}{dx}\right|_{x=0} = -r_a I_{inj}$$

$$\left.\frac{dV}{dx}\right|_{x=l} = 0$$

$$B = -r_a I_{inj}\lambda$$

$$A = r_a I_{inj}\lambda\coth(l/\lambda)$$

$$V(x) = A\cosh(x/\lambda) + B\sinh(x/\lambda)$$

$$V(x) = r_a I_{inj}\lambda[\coth(l/\lambda)\cosh(x/\lambda) - \sinh(x/\lambda)]$$

$$V(x) = \frac{r_a I_{inj}\lambda}{\sinh(l/\lambda)}[\cosh(l/\lambda)\cosh(x/\lambda) - \sinh(l/\lambda)\sinh(x/\lambda)]$$

Case 2: Sealed End Cable

$$\lambda^2 \frac{d^2V(x)}{dx^2} = V(x) - r_m I_{inj}(x)$$

$$V(x) = A\cosh(x/\lambda) + B\sinh(-x/\lambda)$$

The idea for sealed end is that current should not flow across a boundary at length x = l

$$\left.\frac{dV}{dx}\right|_{x=0} = -r_a I_{inj}$$

$$\left.\frac{dV}{dx}\right|_{x=l} = 0$$

$$B = -r_a I_{inj}\lambda$$

$$A = r_a I_{inj}\lambda\coth(l/\lambda)$$

$$V(x) = A\cosh(x/\lambda) + B\sinh(-x/\lambda)$$

$$V(x) = r_a I_{inj}\lambda[\coth(l/\lambda)\cosh(x/\lambda) - \sinh(x/\lambda)]$$

$$V(x) = \frac{V_m(0)\cosh[(l-x)/\lambda]}{\cosh(l/\lambda)} \qquad 0 \le x \le l \quad sealed \qquad x = l$$

$$V_m(0) = r_a I_{inj}\lambda\coth(l/\lambda)$$

Case 3: Killed End Cable

$$\lambda^2 \frac{d^2V(x)}{dx^2} = V(x) - r_m I_{inj}(x)$$

$$V(x) = A\cosh(x/\lambda) + B\sinh(-x/\lambda)$$

The idea here is that one of a boundaries is clamped to resting membrane potential

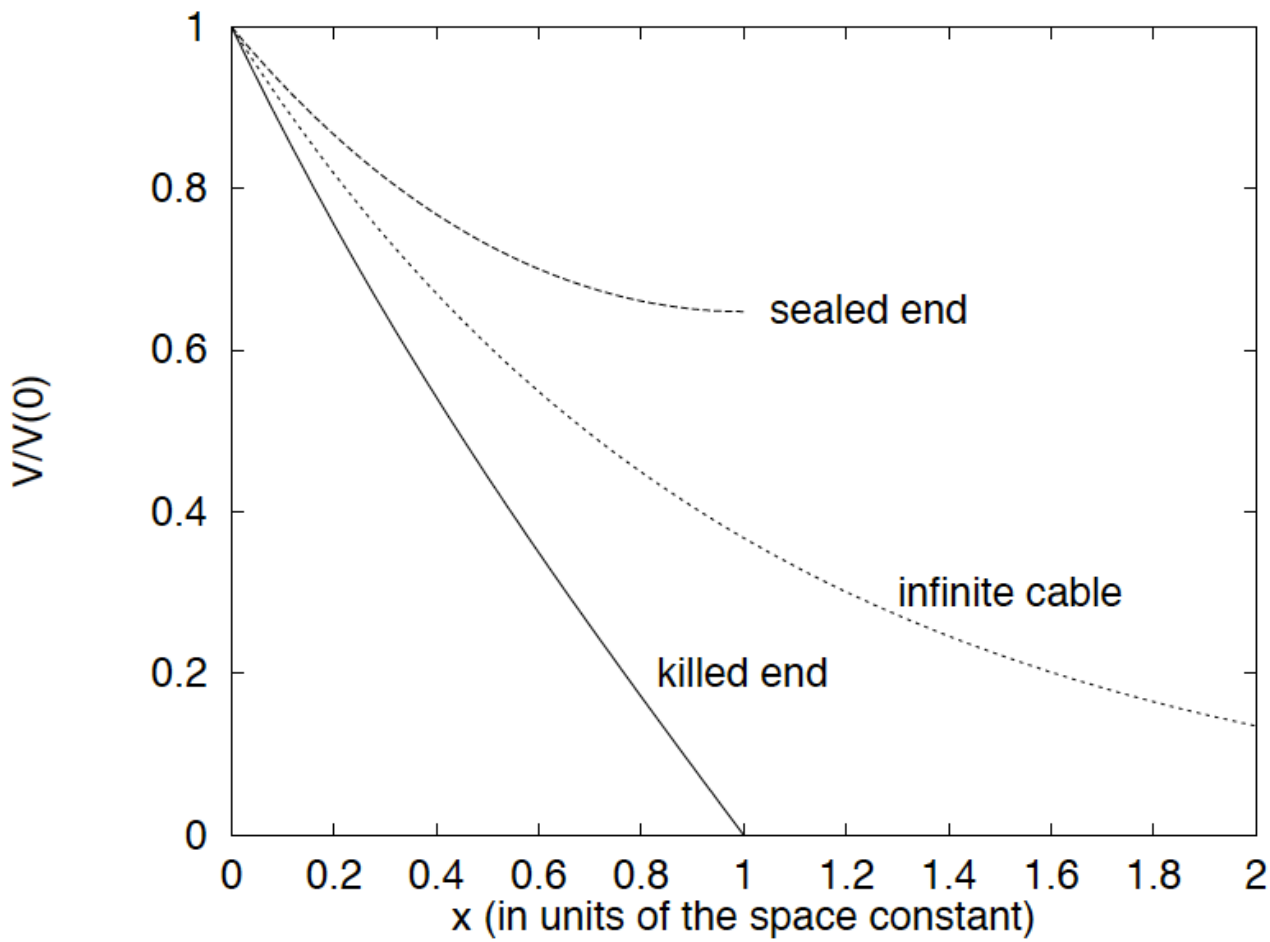
$$\left.\frac{dV}{dx}\right|_{x=0} = -r_a I_{inj}$$

$$V(l) = 0$$

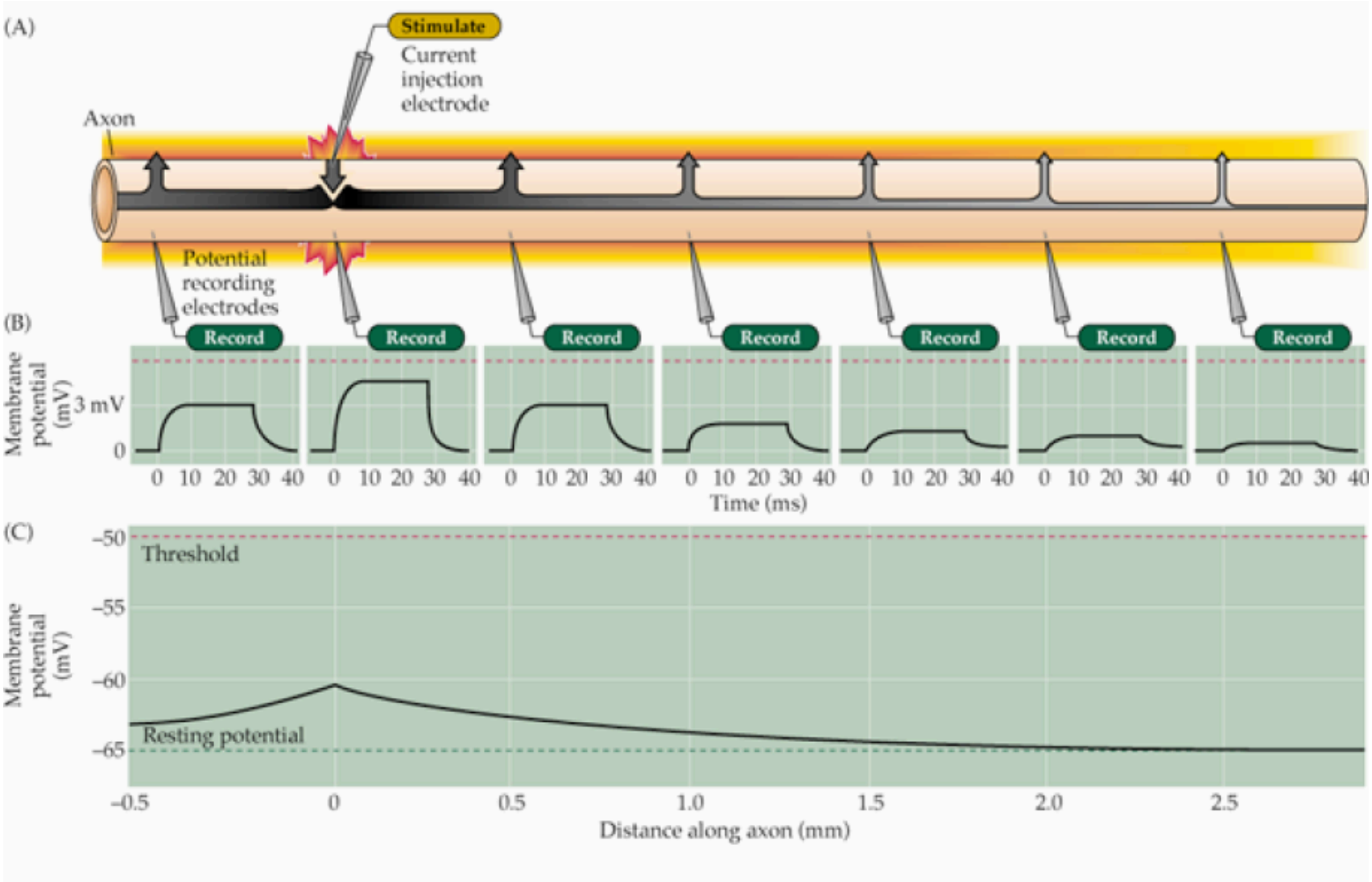
$$V(x) = \frac{V_m(0)\sinh[(l-x)/\lambda]}{\sinh(l/\lambda)} \qquad 0 \le x \le l \quad killed \quad end \quad x = l$$

$$V_m(0) = r_a I_{inj} \lambda \tanh(l/\lambda)$$

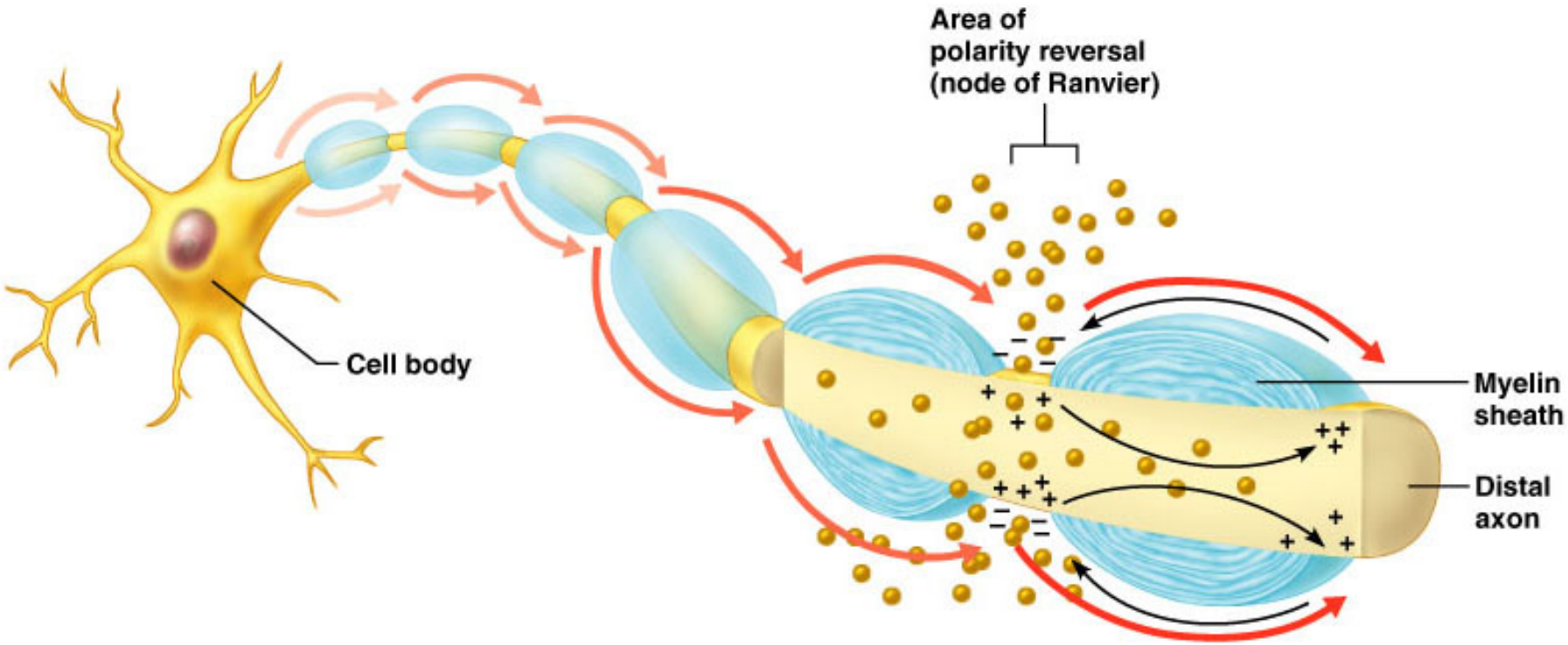
Cable Equation Solutions



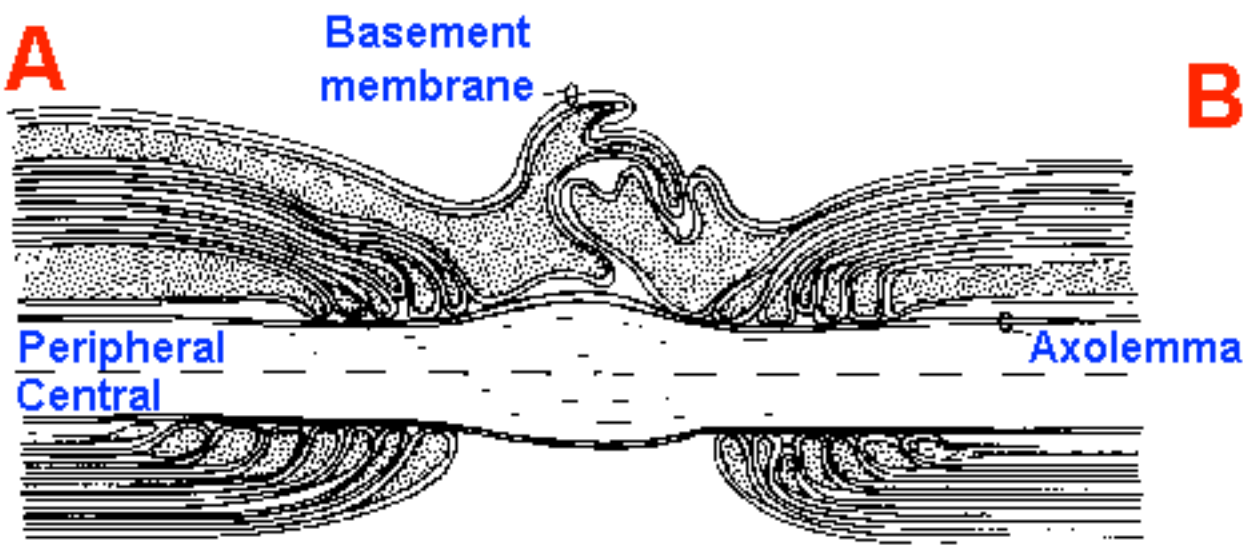
Propagation of AP along an axon

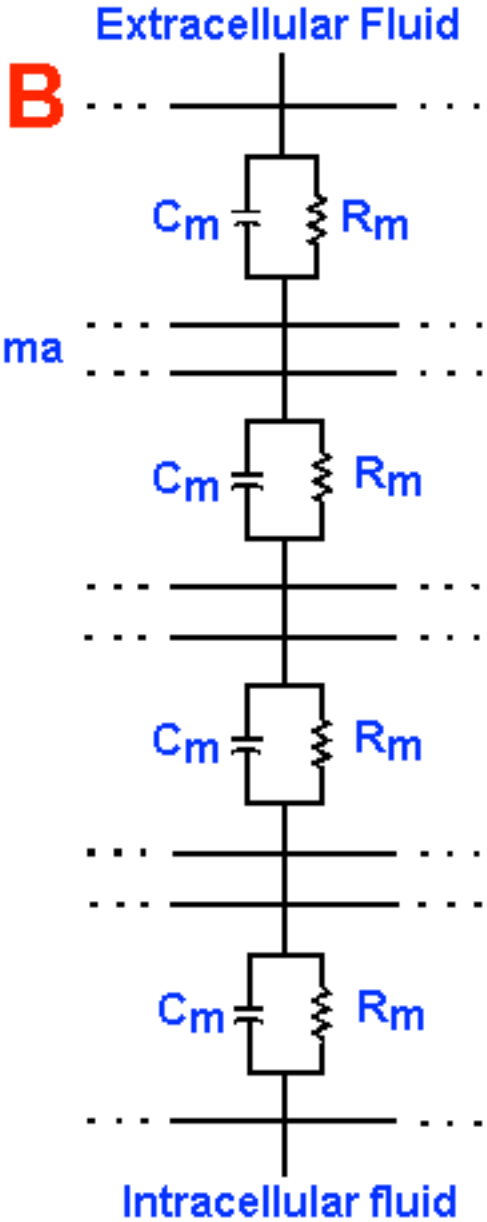


Saltatory Conduction



Saltatory conduction in myelinated axons





The Physiology of Excitable Cells. Cambridge: Cambridge Univ. Press, 1971