Membrane transport and resting membrane potential

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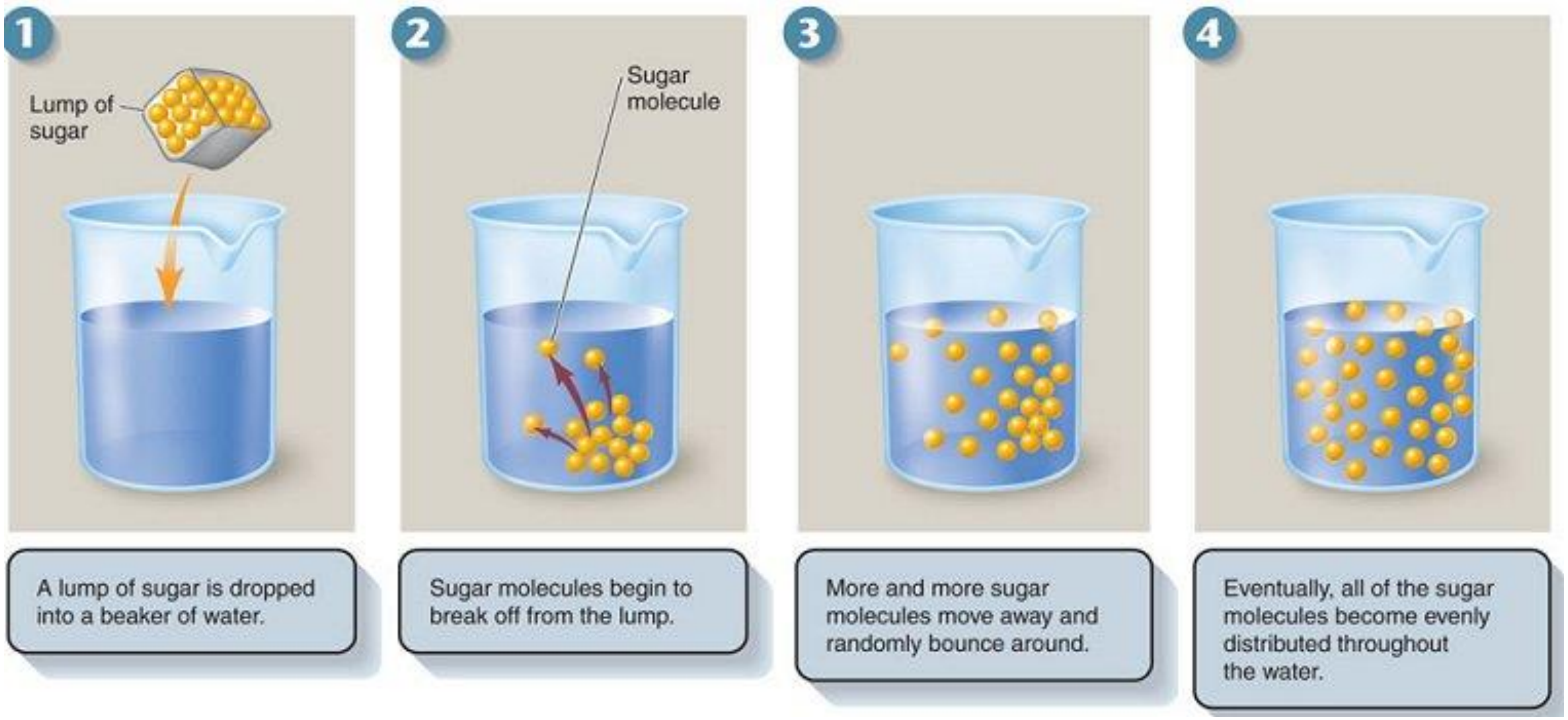
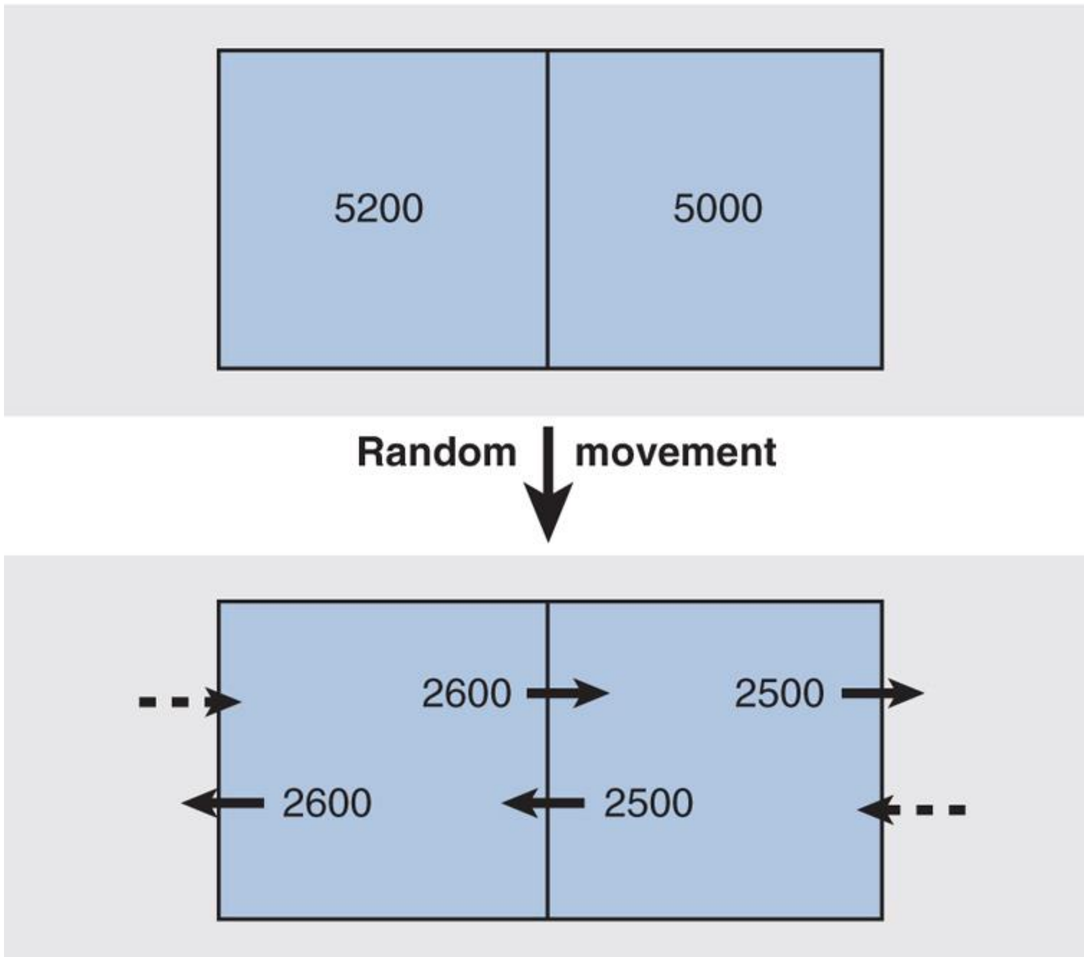
Diffusion

The migration of molecules down a concentration gradient



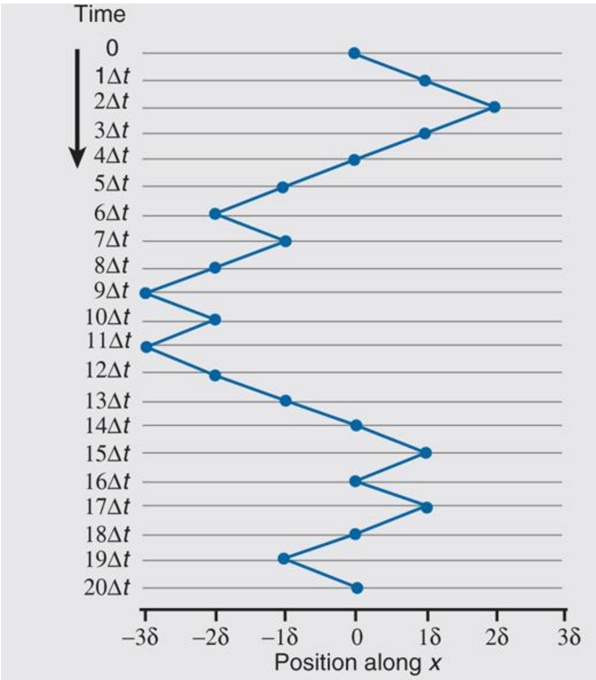
Diffusion



Net movement (100 ⟶) caused by random movement

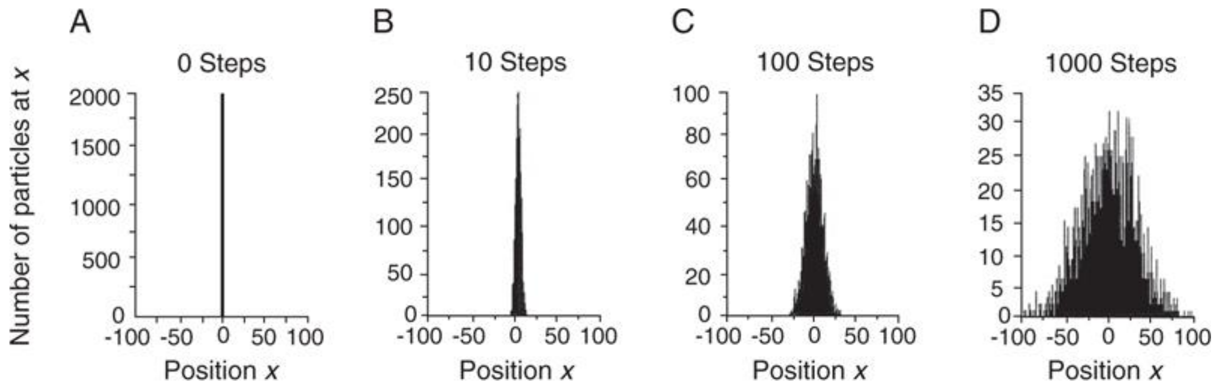
Rate depend on the concentration difference between the two regions

Microscopic movements of molecules



"Random walk" of a single molecule

Spreading of molecules in space by random movements



Time required for diffusion of O_2 over a range of distances

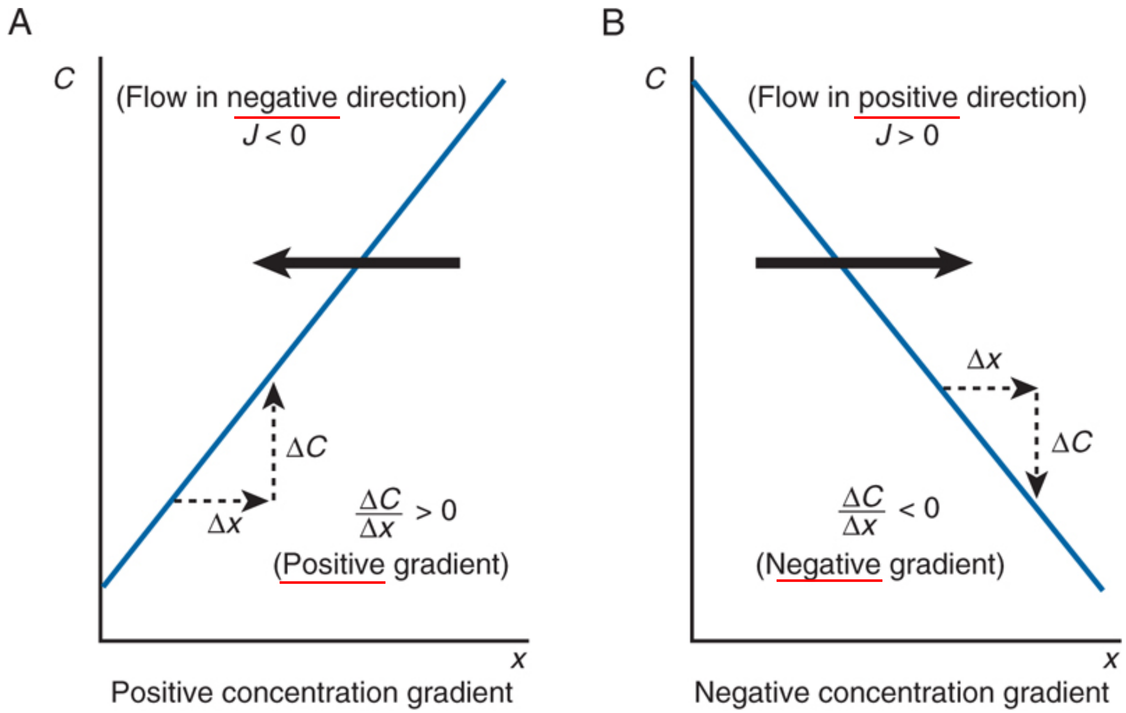
Distance of Diffusion	Approximate Time Required
10 nm	23.8 ns
50 nm	595 ns
100 nm	2.38 μs
1 μm	238 μs
10 μm	23.8 ms
100 μm	2.38 s
1 mm	3.97 min
1 cm	6.61 hours
10 cm	27.56 days

Physiological significance

1. Diameter of mammalian cell ≤ 20 μm
2. Synaptic cleft : 20 ~ 50 nm
3. Circulatory systems in multicellular organism

Direction of the flux

Flux (J): the amount of material passing through unit area per unit time
(단위시간 당 단위면적을 통해 이동하는 물질의 양)



$$J \propto \frac{\Delta C}{\Delta x}$$

$\Delta C / \Delta x$: concentration gradient
J : flux

$$J = -D \frac{\Delta C}{\Delta x}$$

D: diffusion coefficient

Fick's First Law of Diffusion

$$J \propto \frac{\Delta C}{\Delta x}$$

$\Delta C / \Delta x$: concentration gradient ([mol/cm^3]/cm = mol·cm^{-4})
J : flux ([mol/cm^2]/sec)

$$J = -D \frac{\Delta C}{\Delta x}$$

D: diffusion coefficient (cm^2/sec)

$$J = -D \frac{dC}{dx}$$

$$D = \frac{kT}{6\pi\eta R}$$

k: Boltzmann's constant
T: absolute temperature
R: radius of the spherical particle
η: viscosity

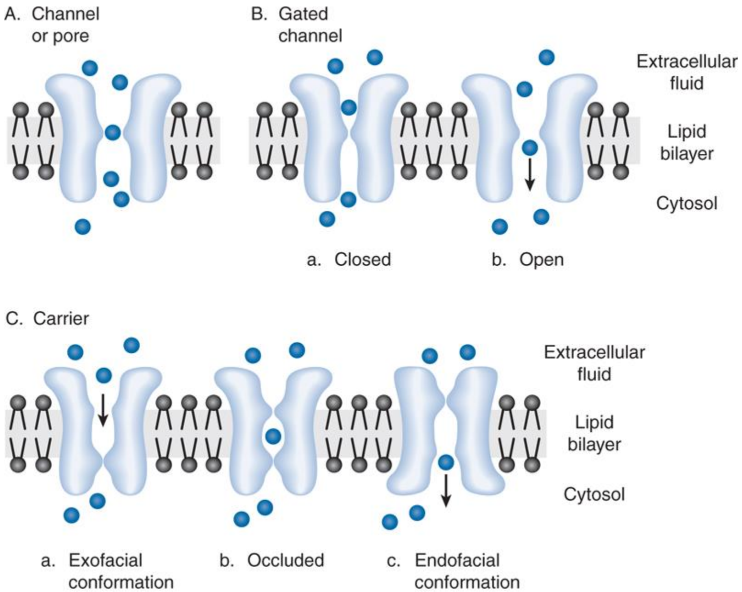
1. Concentration gradient drives diffusion
2. Molecules move from higher concentration to lower concentration
3. Passive process (does not require energy)
4. Net movement of molecules occurs until dynamic equilibrium.
5. Diffusion rate is inversely related to molecular size
6. Diffusion rate is proportional to temperature
7. Diffusion is rapid over short distance but slower over long distance
8. Diffusion rate is proportional to the surface area of the membrane

Transport across biological membrane through channel, carrier, and pump protein

TABLE 2-1

Permeability of Plain Lipid Bilayer Membrane to Solutes

SOLUTE	*P* (cm/sec)	τ*
Water	10^{-4}–10^{-3}†	0.5–5 sec
Urea	10^{-6}	~8 min
Glucose, amino acids	10^{-7}	~1.4 hr
Cl^-	10^{-11}	~1.6 yr
K^+, Na^+	10^{-13}	~160 yr



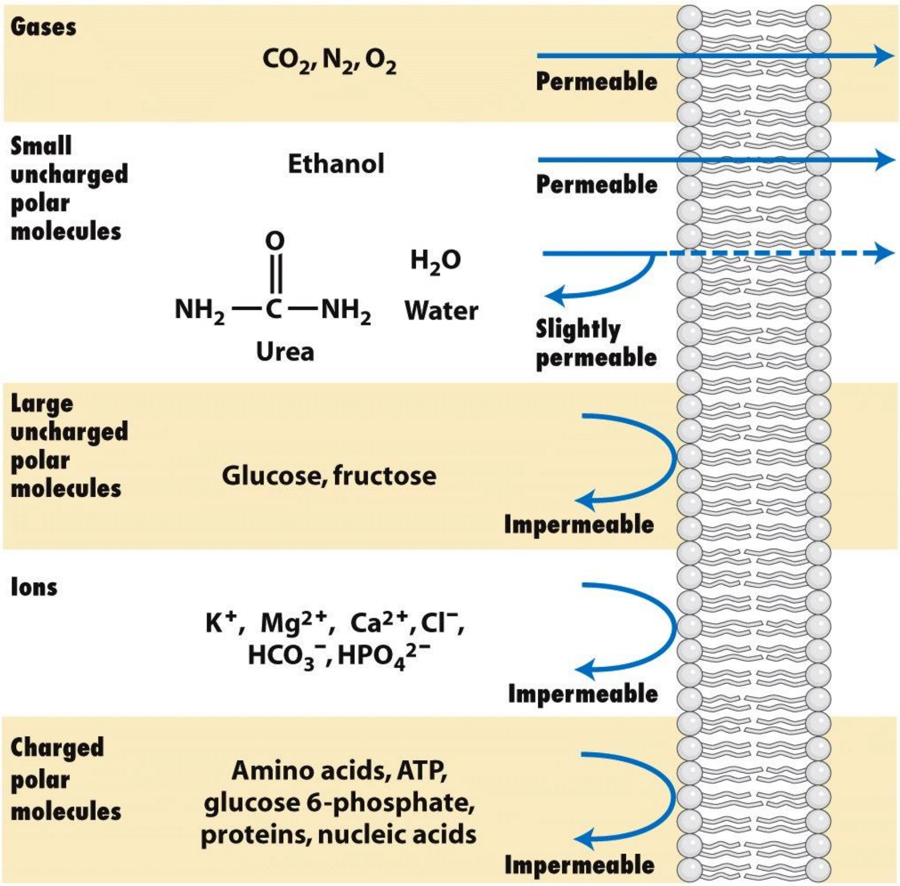
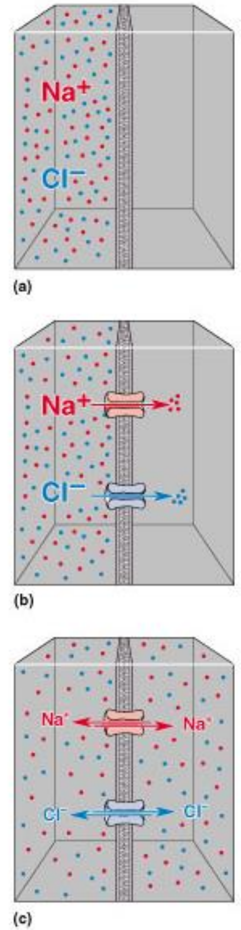


Figure 11-1
Molecular Cell Biology, Sixth Edition

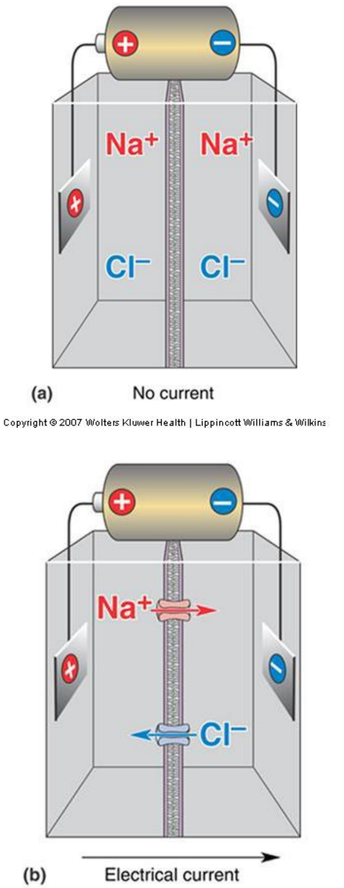
A pure artificial phospholipid bilayer is permeable to <u>small hydrophobic molecules</u> and <u>small uncharged polar molecules</u>.

Movements of ions

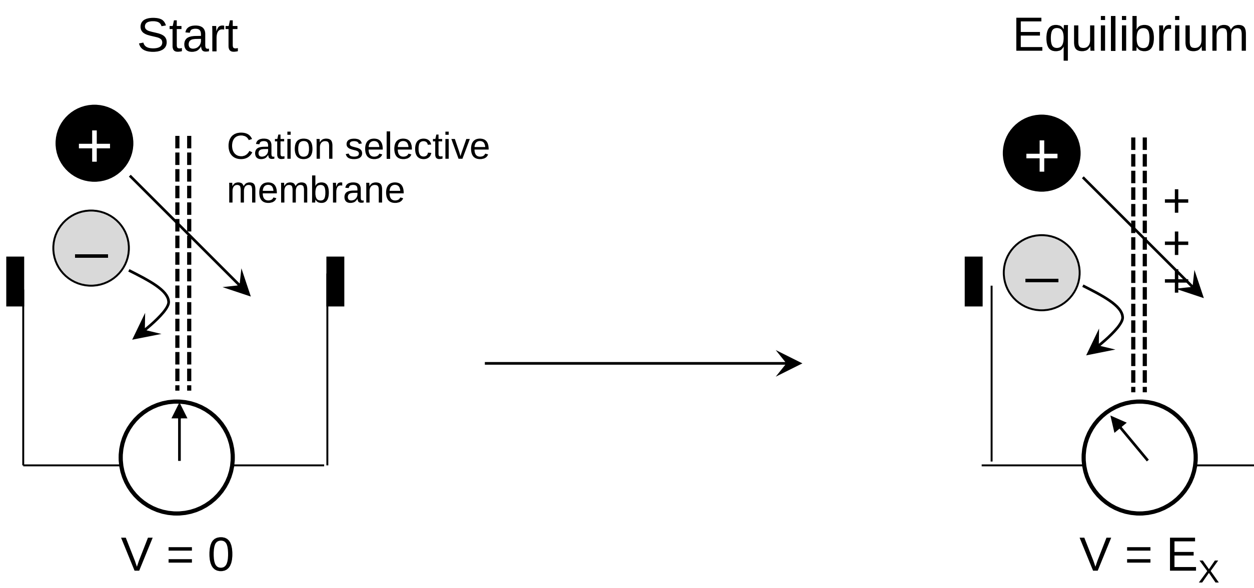
1. Diffusion (Chemical gradient)

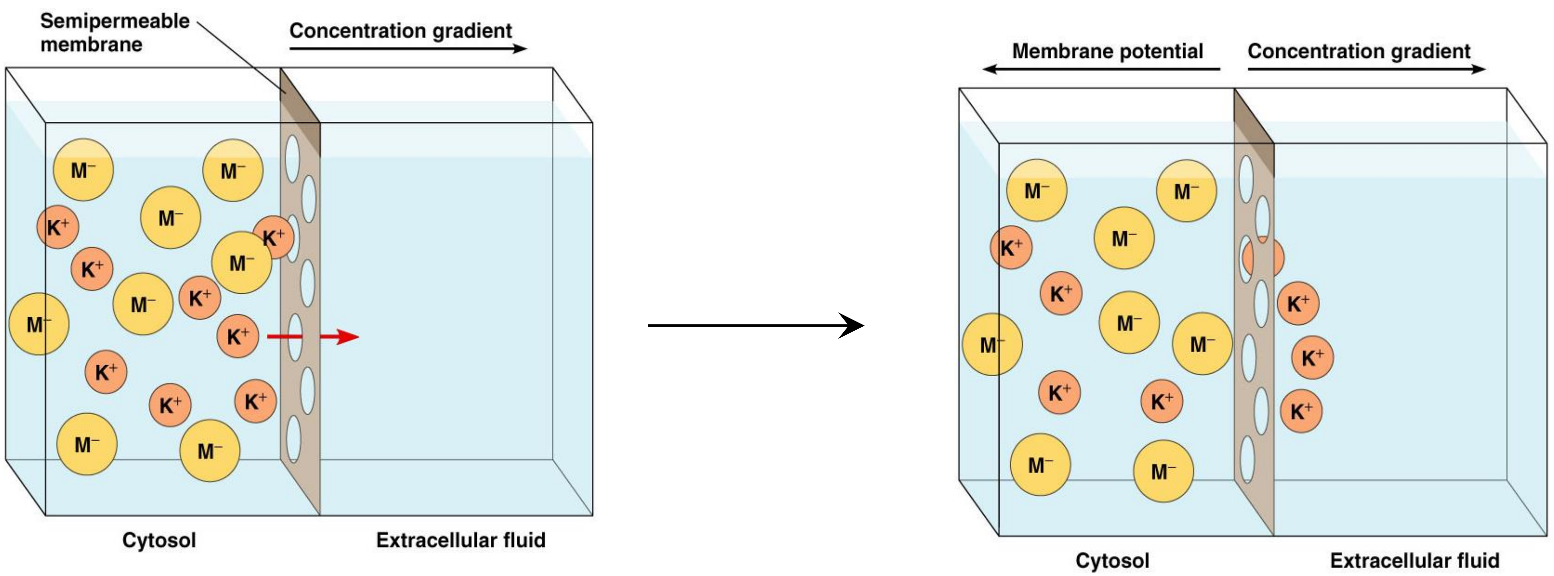


2. Electricity (Electrical gradient)



Diffusion potential

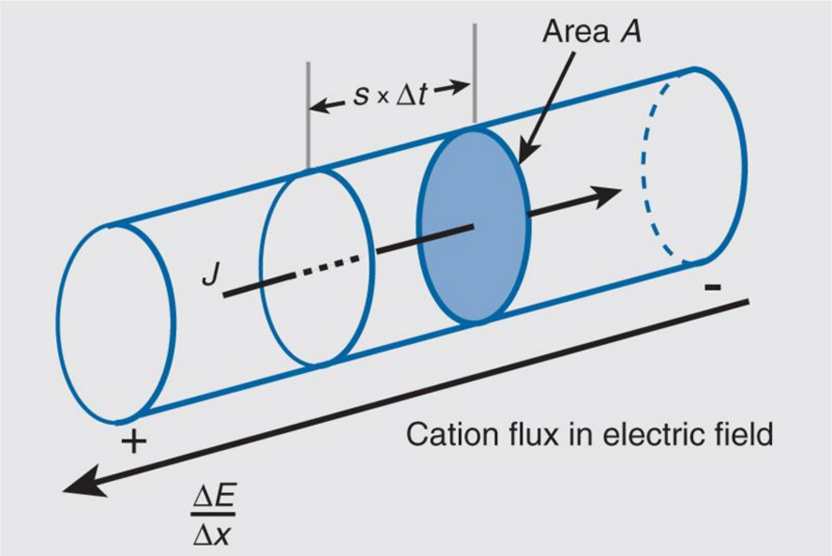




Movement of ions driven by electrical potential gradient

Electric field (force, electrical potential gradient) → movement of ions

Speed of ion movement ∝ strength of the electric field, charge on the ion



$\Delta C/\Delta x$: concentration gradient (mol/cm)

$\Delta E/\Delta x$: electrical potential gradient (V/cm)

$$s = uz\,\frac{\Delta E}{\Delta x}$$

s : 이온의 이동 속도 (cm/sec)
u : ionic mobility (cm^2/sec/V)
단위전위기울기(전기장, V/cm)에서 이온의 이동속도(cm/sec)

Total number of moles of ion : $C \times s \times \Delta t \times A$ $\quad (cylindrical\ volume = s\Delta t \times A)$

$$J_{electr} = -[(C \times s \times \Delta t \times A)/A]/\Delta t = -C \times s$$

$$= -uzC\,\frac{\Delta E}{\Delta x} = -uzC\,\frac{dE}{dx}$$

Nernst equation

$$J_{total} = J_{diffusion} + J_{electr} = -D\frac{dC}{dx} - uzC\frac{dE}{dx}$$

$J_{diffusion}$: flux driven by the chemical gradient
$J_{electric}$: flux driven by the electrical gradient

At equilibrium, $-D\frac{dC}{dx} - uzC\frac{dE}{dx} = 0$,

$$uzC\frac{dE}{dx} = -D\frac{dC}{dx} \quad , D\text{(diffusion coefficient of ion)}=\frac{uRT}{F}$$

$$uzC\frac{dE}{dx} = -\frac{uRT}{F}\frac{dC}{dx}$$

$$\frac{dE}{dx} = \frac{-RT}{zF}\frac{1}{C}\frac{dC}{dx}$$

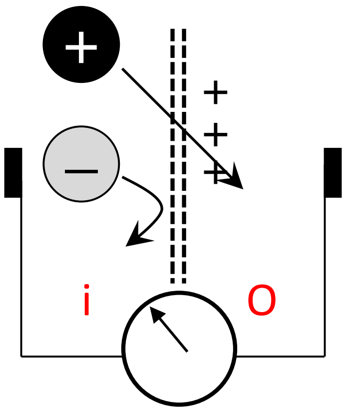
$$\int_{x1}^{x2}\frac{dE}{dx}dx = \frac{-RT}{zF}\int_{x1}^{x2}\frac{1}{C}\frac{dc}{dx}dx$$

$$E_2 - E_1 = \frac{-RT}{zF}(\ln C_2 - \ln C_1)$$

$$= \frac{-RT}{zF}\ln\frac{C_2}{C_1} = \frac{RT}{zF}\ln\frac{C_1}{C_2}$$

u: mobility of the ion
R: gas constant
T : temperature
F : Faraday constant

Equilibrium



$V = E_X$

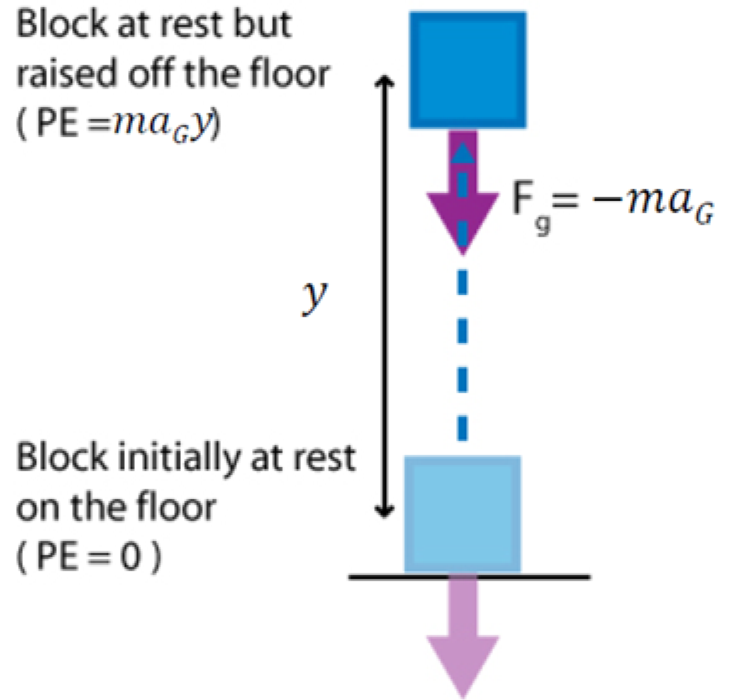
Force and potential energy

$$F_G = -ma_G \quad (a_G = 9.8\ \mathrm{m/s^2})$$

(gravitational force)

$$PE_G = ma_G y \quad (PE_G = 0 \text{ when } y = 0)$$

(gravitational potential energy)



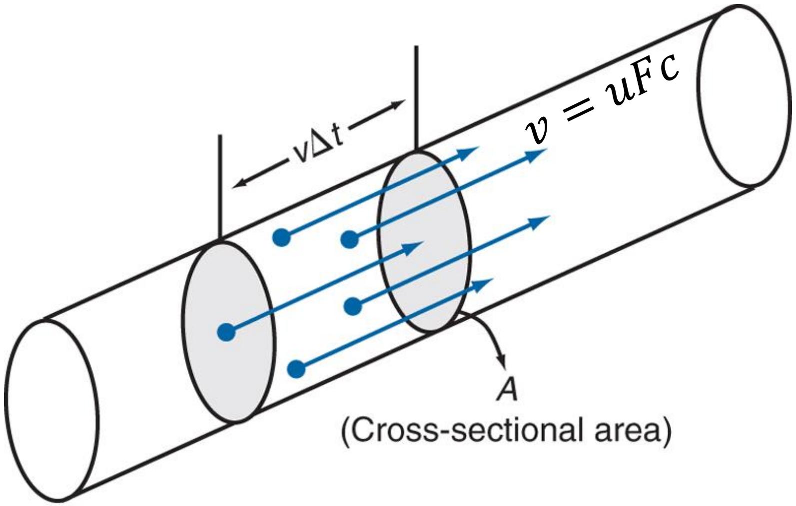
$$\text{Gradient of potential energy} = \frac{dPE_G}{dy} = ma_G = -F_G$$

Chemical potential energy

Concentration gradient gives rise to a chemical force

Gradient of potential energy

$v = uFc$ — v: velocity of molecule; u: mobility coefficient; F_c: chemical force



$$J = \frac{moles\ of\ S/A}{\Delta t} = \frac{[S]\times A \times (v\Delta t)/A}{\Delta t}$$

$$= [S]v = [S]uF_c \quad (u = D/RT)$$

$$J = -D\frac{d[S]}{dx} \qquad \text{(Fick's first law)}$$

$$F_c = -RT\frac{1}{[S]}\frac{d[S]}{dx} = -RT\frac{d\ln[S]}{dx}$$

$$\frac{du_s}{dx} = -Fc = RT\frac{d\ln[S]}{dx}$$

$$u_s = constant + RTln[S]$$

Chemical potential energy $\mu_S = \mu_S^0 + RT\ln[S]$

μ_S^0 : chemical potential energy of solute at the reference concentration (1 M)

Electrical potential energy

Electrical potential energy of single ion $= zeV$

z :charge
e : 1.602 X 10^{-19} coulomb
V :Voltage

Electrical potential energy of one mole of ion $= zFV$

F :N_A X e

μ_x (electrochemical potential energy) = μ_x^0 + RT ln[X] + zFV

Electrochemical potential of solutes inside and outside a cell

μ_x (electrochemical potential energy) = μ_x^0 + RT ln[X] + zFV

For glucose (z=0)

$$\mu_{G,i} = \mu_G^0 + RT \ln[G]_i$$

$$\mu_{G,O} = \mu_G^0 + RT \ln[G]_O$$

For sulfate ion (SO_4^{2-} , z=-2)

$$\mu_{SO4^{2-},i} = \mu_{SO4^{2-}}^{0} + RT \ln[SO_4^{2-}]_i - 2FV_m$$

$$\mu_{SO4^{2-},O} = \mu_{SO4^{2-}}^{0} + RT \ln[SO_4^{2-}]_O$$

Electrochemical potential energy

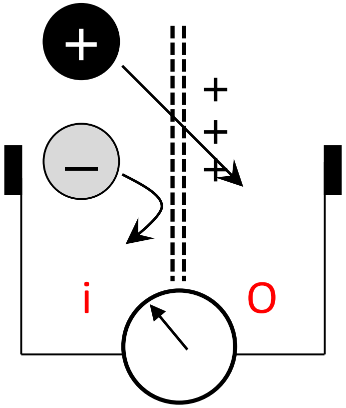
Chemical potential energy = μ_x^0 + RT ln[X]

Electrical potential energy = zFV

μ_x^0 : chemical potential energy at [X] = 1M
R: gas constant
T : temperature
z : electrical charge
F : Faraday constant
V: electrical potential

μ_x (electrochemical potential energy) = μ_x^0 + RT ln[X] + zFV

Equilibrium



At equilibrium, $\mu_{x,i} = \mu_{x,o}$ (no net electrochemical force)

$$\mu_{x,i} = \mu_x^0 + RT \ln[X]_i + zFV_i$$
$$\mu_{x,o} = \mu_x^0 + RT \ln[X]_o + zFV_o$$

$$\mu_x^0 + RT \ln[X]_i + zFV_i = \mu_x^0 + RT \ln[X]_o + zFV_o$$
$$zFV_i - zFV_o = RT \ln[X]_o - RT \ln[X]_i$$

$$V_i - V_o = V_m = \frac{RT}{zF} \ln \frac{[X]_o}{[X]_i}$$, where $V_o = 0$ mV

Nernst equation

Nernst Equation

$$E_x = \frac{RT}{zF} \ln \frac{[X]_o}{[X]_i} = \frac{58}{z} \log \frac{[X]_o}{[X]_i}$$

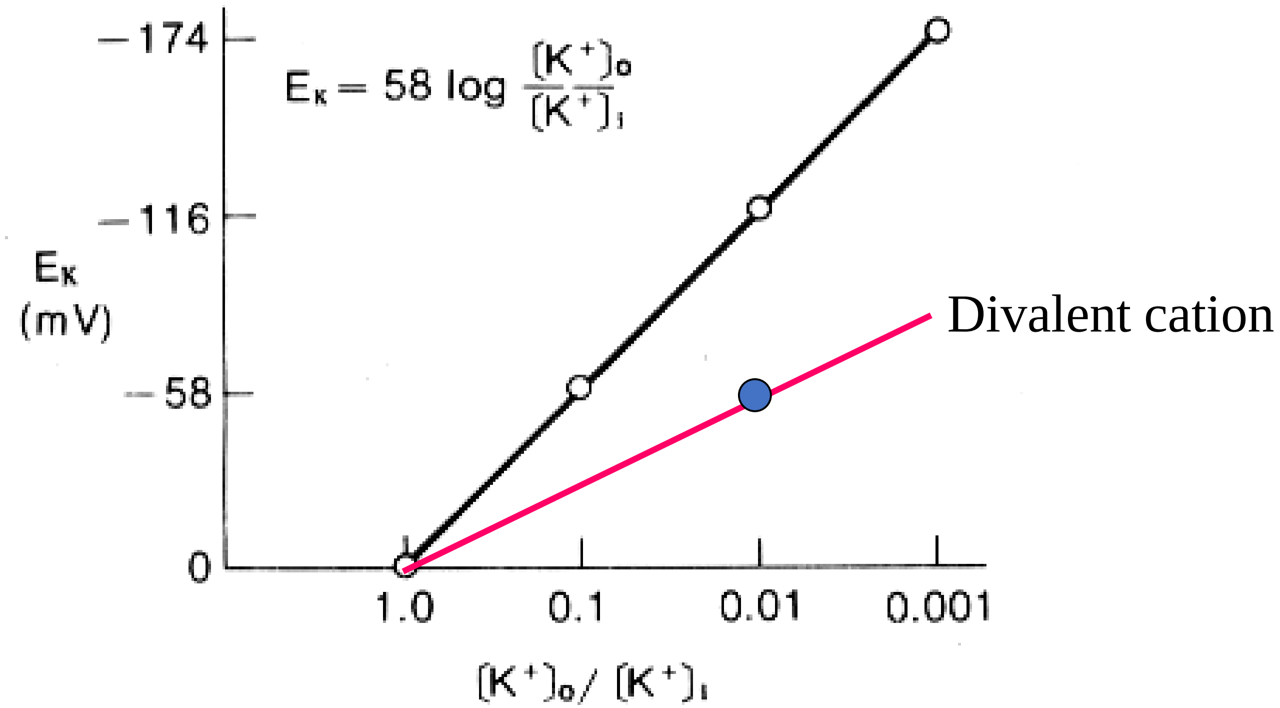
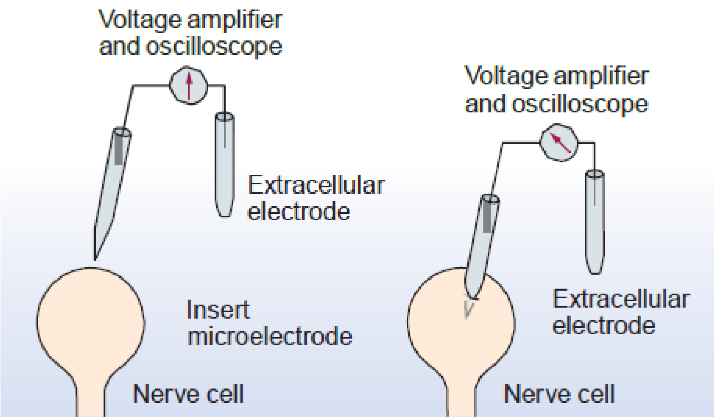
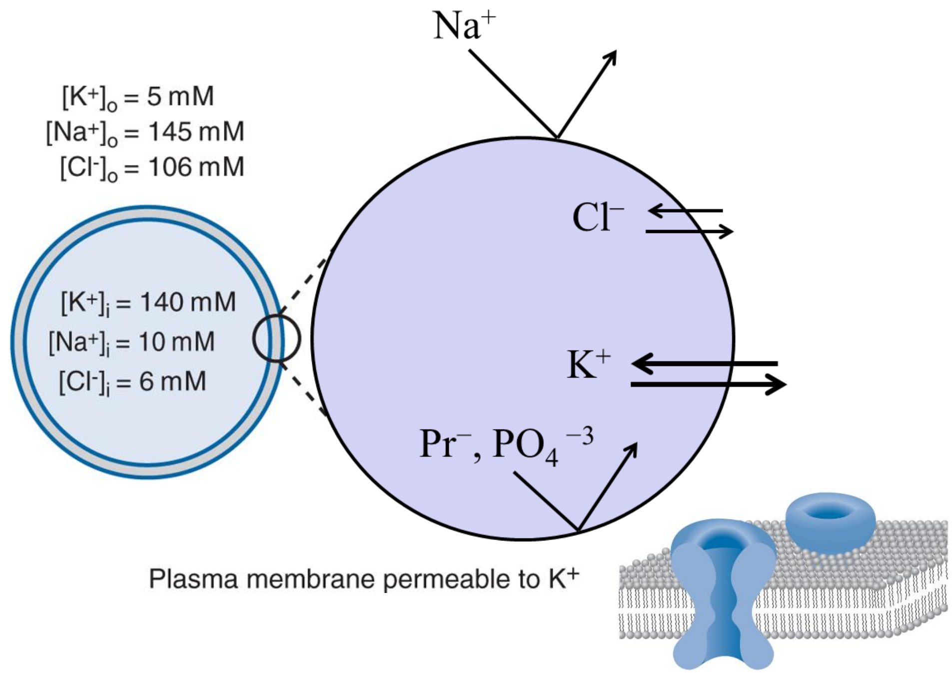


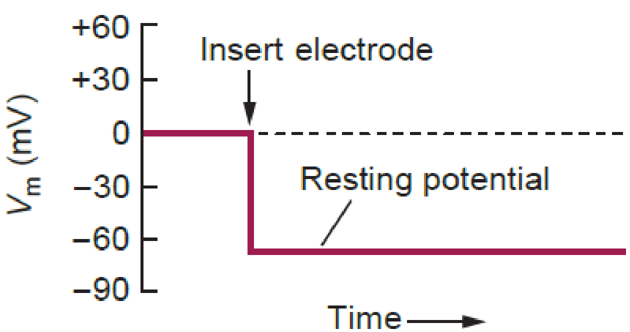
그림 2-13. K^+의 평형전압과 $[K]_o/[K]_i$ 비율과의 관계.

평형 전압은 두 구분 농도비의 대수 값에 비례함

Resting membrane potential







Nernst equation $$E_{eq} = \frac{RT}{zF} \ln \frac{[X]_o}{[X]_i}$$

$$E_K = \frac{61.5}{+1} \log \frac{5}{140} = 61.5(-1.45) = -89.1 \text{ mV}$$

$$E_{Na} = \frac{61.5}{+1} \log \frac{145}{10} = 61.5(+1.16) = +71.5 \text{ mV}$$

결국 휴지상태에서 투과도가 높은 이온의 전기화학적 평형전압이 휴지막전위 형성에 크게 기여한다.

Solute composition of intracellular and extracellular fluids

(in mM)	In	Out
K^+	**155**	5
Na^+	12	**145**
Ca^{2+}	<0.0002	2
Cl^-	4	110
HCO_3^-	8	27
Pr^-	64	15
PO_4^{-3}	90	2

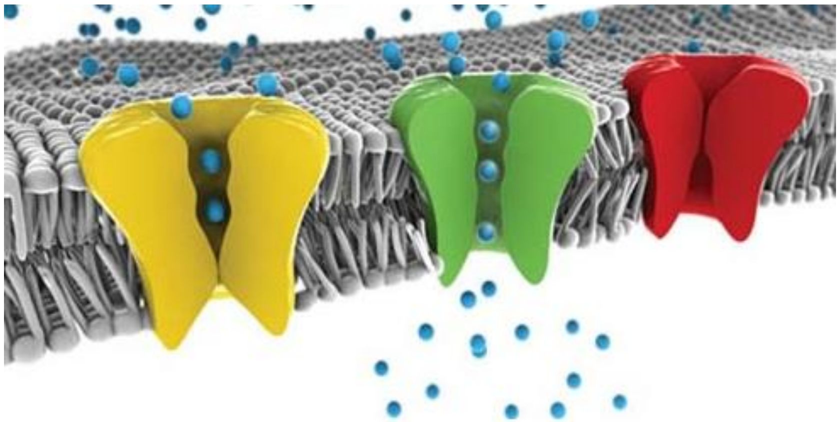
$$E_{eq} = \frac{RT}{zF} \ln \frac{C_{out}}{C_{in}}$$

$$E_{eq} = \frac{2.303\, RT}{zF} \log \frac{C_{out}}{C_{in}}$$

at 37 °C, RT/F = 26.7 mV

$$E_{eq} = \frac{26.7}{z} \ln \frac{C_{out}}{C_{in}}$$

$$E_{eq} = \frac{61.5}{z} \log \frac{C_{out}}{C_{in}}$$



Ion movement needed to establish a physiological membrane potential (−60 mV)

Cell radius (spherical), r = 10 μm
Membrane area: $4\pi r^2$ = 1257 μm^2 = 1.257×10^{-5} cm^2
Cell volume: $4/3\ \pi r^3$ = 4189 μm^3 = 4.189×10^{-12} L = 4.2 pL

Membrane capacitance: C_m = 1 $\mu F/cm^2$ × 1.257×10^{-5} cm^2 = 1.257×10^{-11} F = 12.57 pF

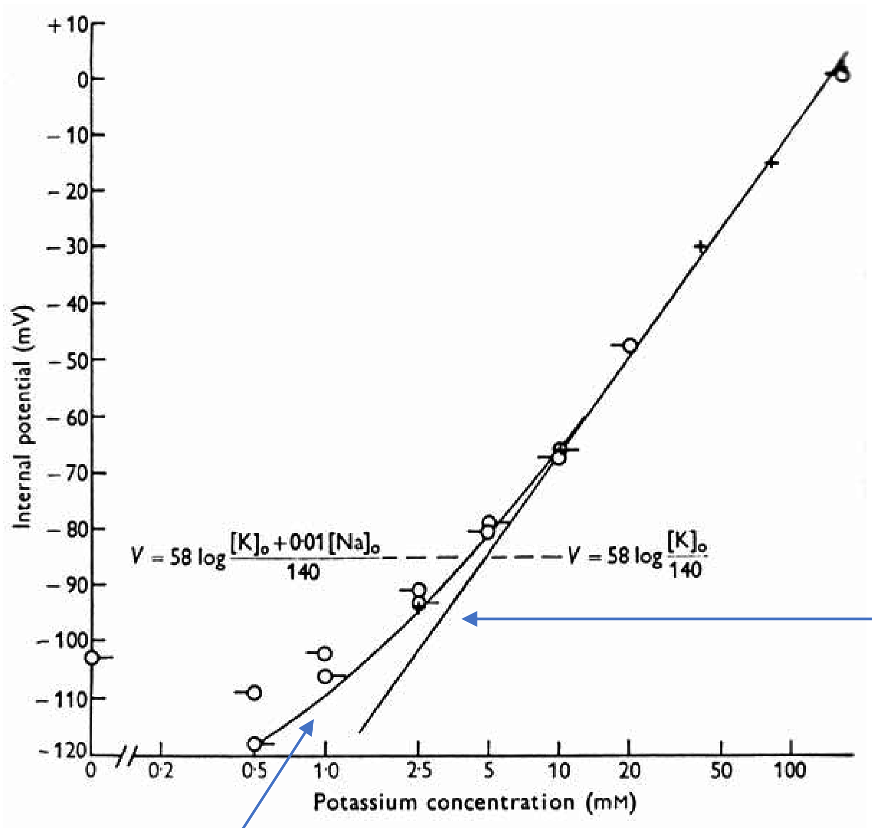
q **(electrical charge, coulomb) = C (capacitance, farad) × V (electrical potential, volt)**

Charge (q) = 12.57 pF × 0.060 V = 0.754 pCoulb
F = (1.6×10^{-19} coulomb) × (6.02×10^{23} mol^{-1}) = 96,485 coulombs/mol

Amount of K+ moved: 0.754 pCoulb / (96,485 Coulb / 1 mole) = 0.78×10^{-5} pmole = 0.78×10^{-17} mole
Concentration change: 0.78×10^{-5} pmole / 4.2 pL = 1.9 μM

K+ content in cell: (0.14 mole / L) × (4.189×10^{-12} L) = 5.864×10^{-13} mole
Fraction of K+ content moved out: (0.78×10^{-17} mole) / (5.864×10^{-13} mole) = 1.33×10^{-5} = 13 / 1,000,000

Membrane potential and equilibrium potential for K^+



Nernst eq. for K^+

$$V_m = 58 \log \frac{[K^+]_o + \alpha [Na^+]_o}{[K^+]_i + \alpha [Na^+]_i} (mV)$$

where $\alpha = P_{Na} / P_K$

Goldman-Hodgkin-Katz (GHK) equation

- The membrane is homogenous
- Ions cross the membrane independently of one another
- Electrical gradient across the membrane is linear (“constant field theory”)

$$V_m = \frac{RT}{F} \ln \frac{P_k[K^+]_o + PN_a[Na^+]_o + PC_l[Cl^-]_i}{P_k[K^+]_i + P_{Na}[Na^+]_i + PC_l[Cl^-]_o}$$

$$K^+ \text{ efflux} = J_K^{in \rightarrow out} = P_K[K^+]_i$$

$$K^+ \text{ influx} = J_K^{out \rightarrow in} = P_K[K^+]_o$$

$P_K = 1$, $P_{Na} = 0.02$, $P_{Cl} = 0.5$, $RT/F = 26.7$ mV at 37 ℃

$$V_m = 26.7 \ln \frac{1(5) + 0.02(145) + 0.5(6)}{1(140) + 0.02(10) + 0.5(106)} = -76.8 \text{ mV}$$

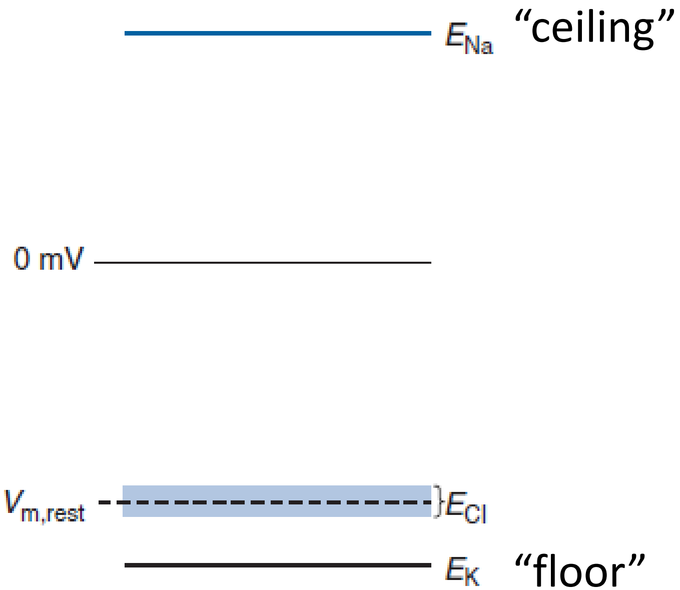
$$E_{Cl} = -76.8 \text{ mV}.$$

$$V_m = \frac{RT}{F} \ln \frac{P_K[K^+]_o + P_{Na}[Na^+]_o}{P_K[K^+]_i + P_{Na}[Na^+]_i}$$

$$= 26.7 \ln \frac{1(5) + 0.02(145)}{1(140) + 0.02(10)} = -76.8 \text{ mV}$$

Goldman-Hodgkin-Katz (GHK) equation

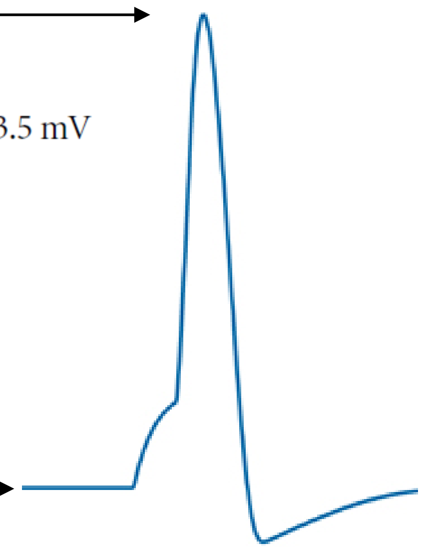
$$V_m = \frac{RT}{F} \ln \frac{P_k[K^+]_o + PN_a[Na^+]_o + PC_l[Cl^-]_i}{P_k[K^+]_i + P_{Na}[Na^+]_i + PC_l[Cl^-]_o}$$



$P_K : P_{Na} : P_{Cl} = 1.0 : 20 : 0.45$ →

$$V_m = 26.7 \ln \frac{1(5) + 20(145) + 0.5(6)}{1(140) + 20(10) + 0.5(106)} = +53.5 \text{ mV}$$

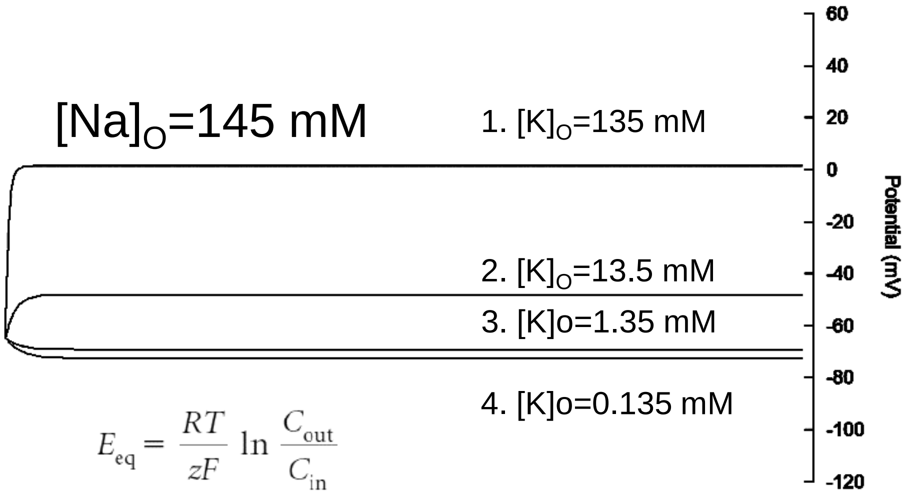
$P_K : P_{Na} : P_{Cl} = 1.0 : 0.04 : 0.45$ →



When $P_{Na} = P_{Cl} = 0$ or $P_K >> P_{Na}, P_{Cl}$

$$V_m = \frac{RT}{F} \ln \frac{[K^+]_o}{[K^+]_i} = EK$$

Nernst equation vs. GHK equation



$$E_{eq} = \frac{RT}{zF} \ln \frac{C_{out}}{C_{in}}$$

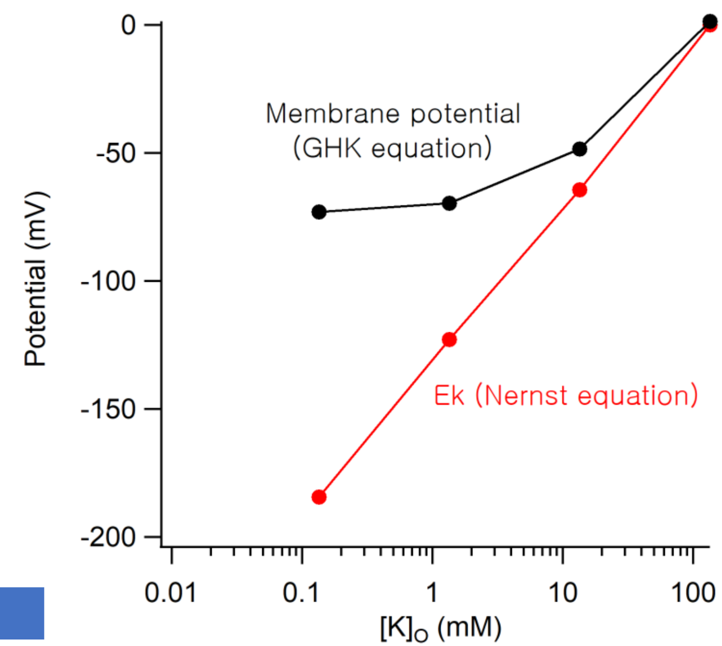
$$E_{eq} = \frac{26.7}{z} \ln \frac{C_{out}}{C_{in}}$$

$$E_{eq} = \frac{61.5}{z} \log \frac{C_{out}}{C_{in}}$$

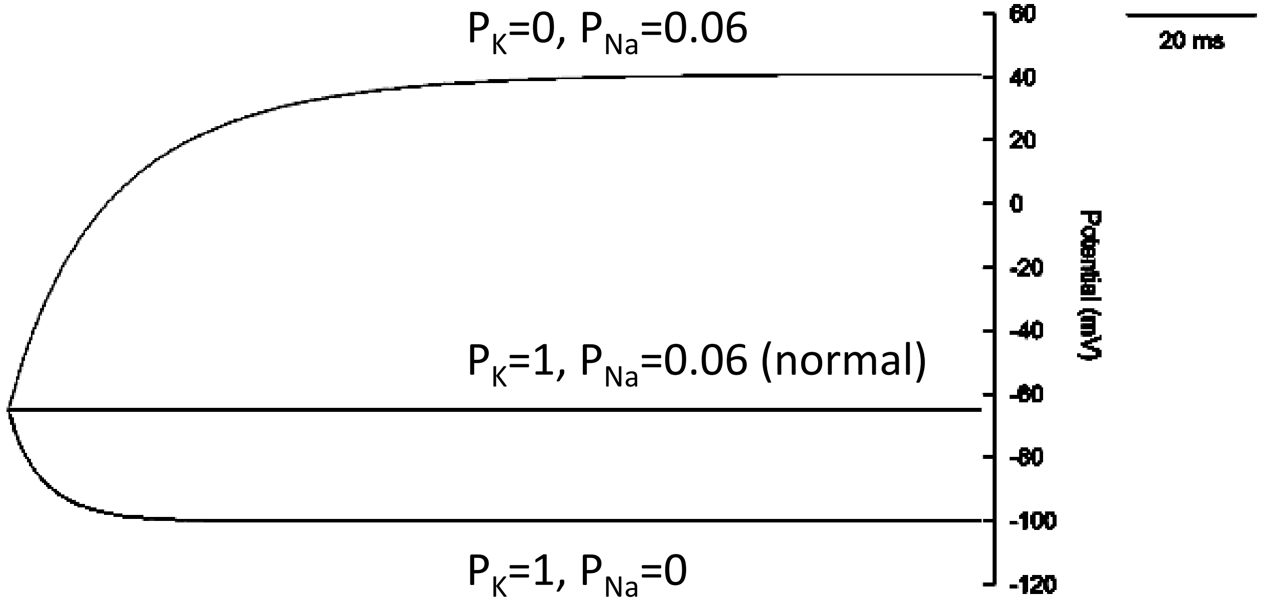
P_K=1, P_{Na}=0.06

$$V_m = \frac{RT}{F} \ln \frac{P_k[K^+]_o + P_{Na}[Na^+]_o}{P_k[K^+]_i + P_{Na}[Na^+]_i}$$

$[K]_O$	E_K (Nernst)	V_m (GHK)
135	0	1.3
13.5	-61	-49
1.35	-123	-70
0.135	-184	-73



Effects of changing P_k and P_{Na} on membrane potential



$$V_m = \frac{RT}{F} \ln \frac{P_k[K^+]_o + P_{Na}[Na^+]_o}{P_k[K^+]_i + P_{Na}[Na^+]_i}$$

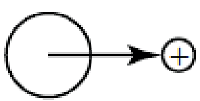
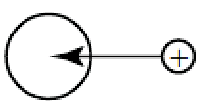
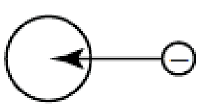
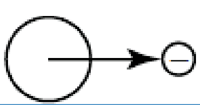
$[K]_O$	$[K]_i$	$[Na]_O$	$[Na]_i$
135 mM	3.1 mM	145 mM	31 mM

Ionic fluxes and ionic currents

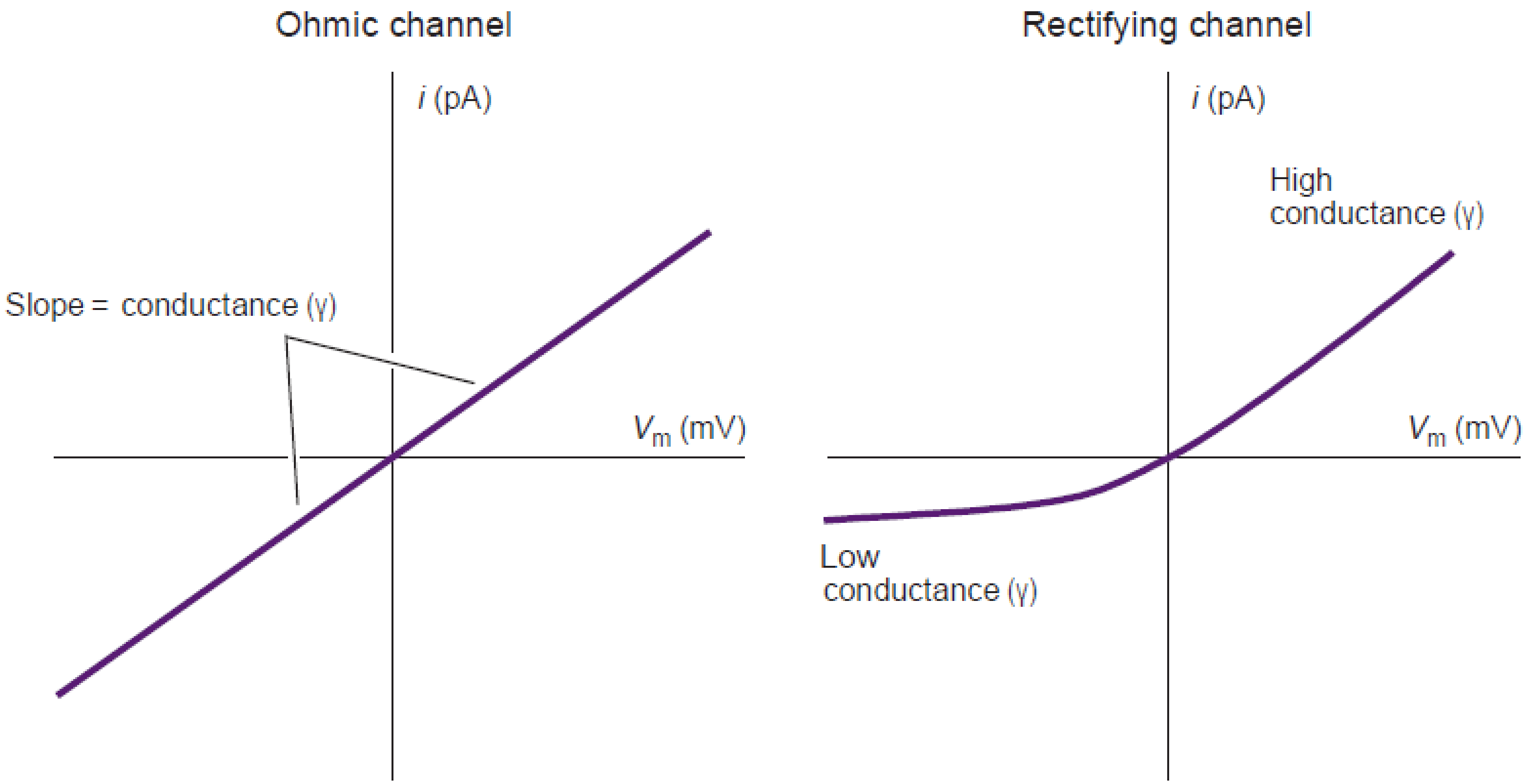
Ionic flux (J)	Ionic current (I)
number of moles of ions moving through a unit area of membrane per unit time	Movement of charges per unit time
[mol/cm^2]/sec	Coulombs/sec, A

$$I = zF \times J \times A_{mem}, \quad \text{where } F=96{,}485 \text{ coulombs/mol}$$

Sign Conventions for Fluxes and Currents

FLOW OF POSITIVE OR NEGATIVE IONS RELATIVE TO CELL	DIRECTION AND SIGN OF FLUX, J	DIRECTION AND SIGN OF CURRENT, I
	Outward, negative ($J < 0$)	Outward, positive ($I > 0$)
	Inward, positive ($J > 0$)	Inward, negative ($I < 0$)
	Inward, positive ($J > 0$)	Outward, positive ($I > 0$)
	Outward, negative ($J < 0$)	Inward, negative ($I < 0$)

Current–voltage relationship

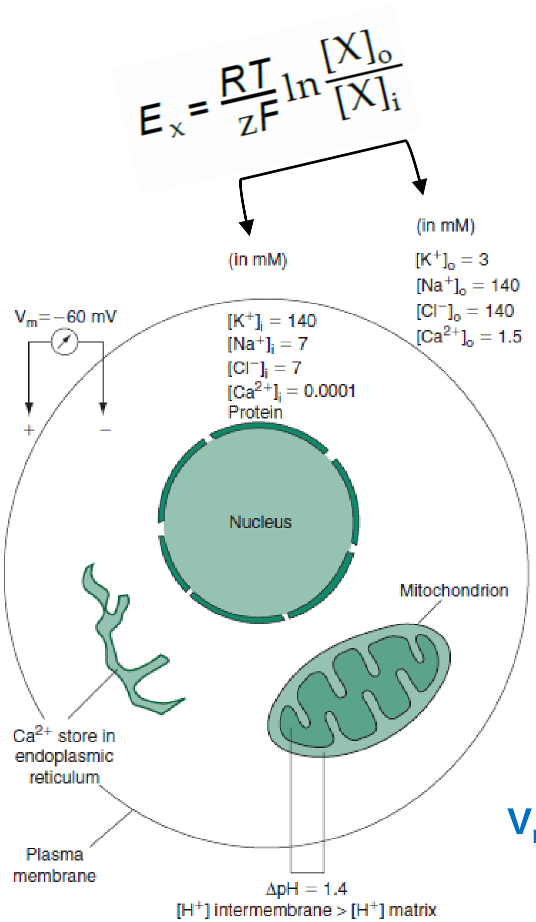


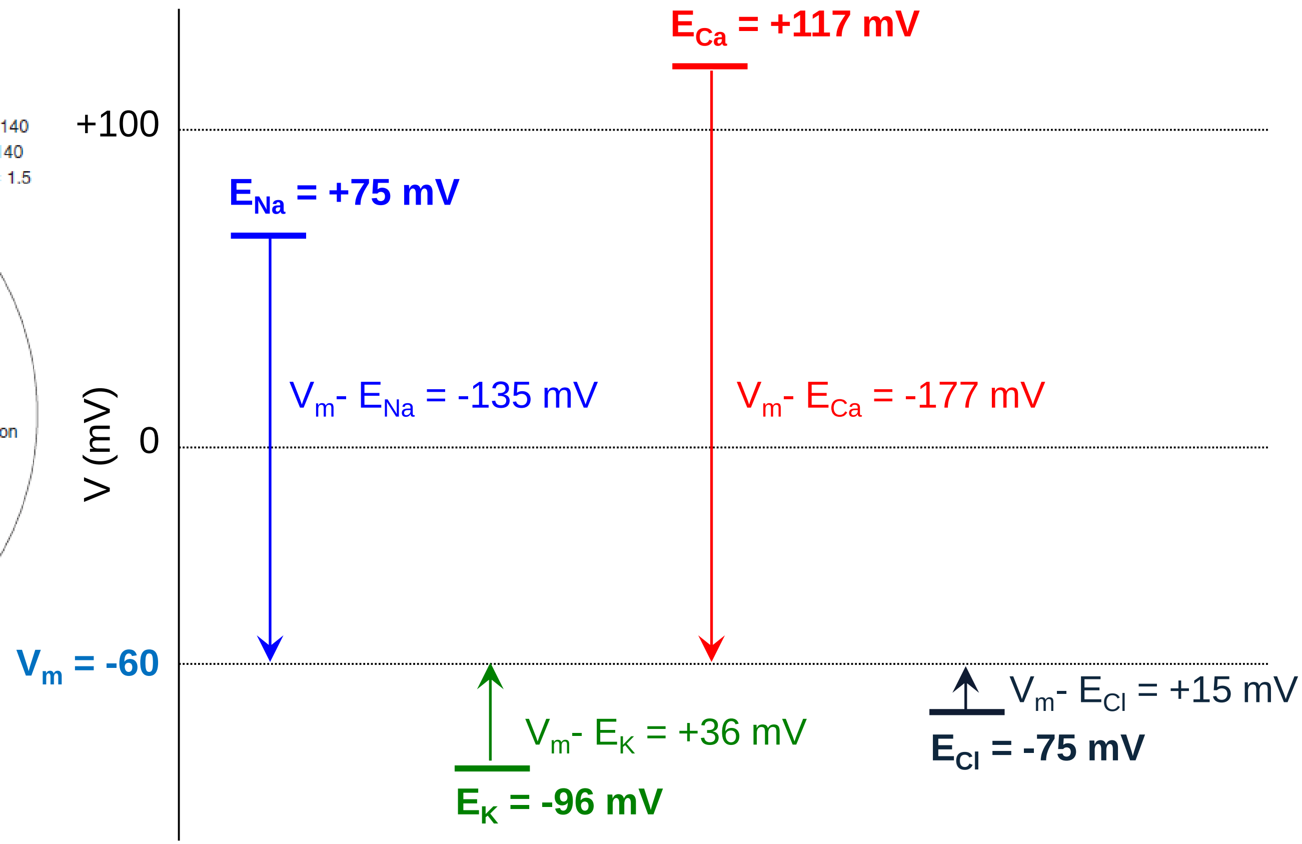
Ohm’s law

$i = V/R$ or $i = \gamma \times V$ (conductance: $\gamma = 1/R$)

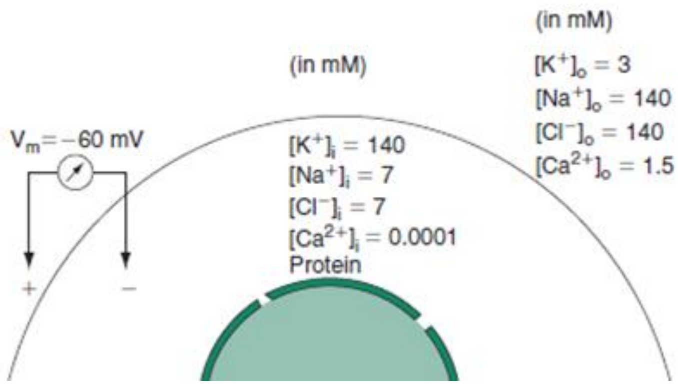
Electrochemical driving force (Electromotive force, EMF)

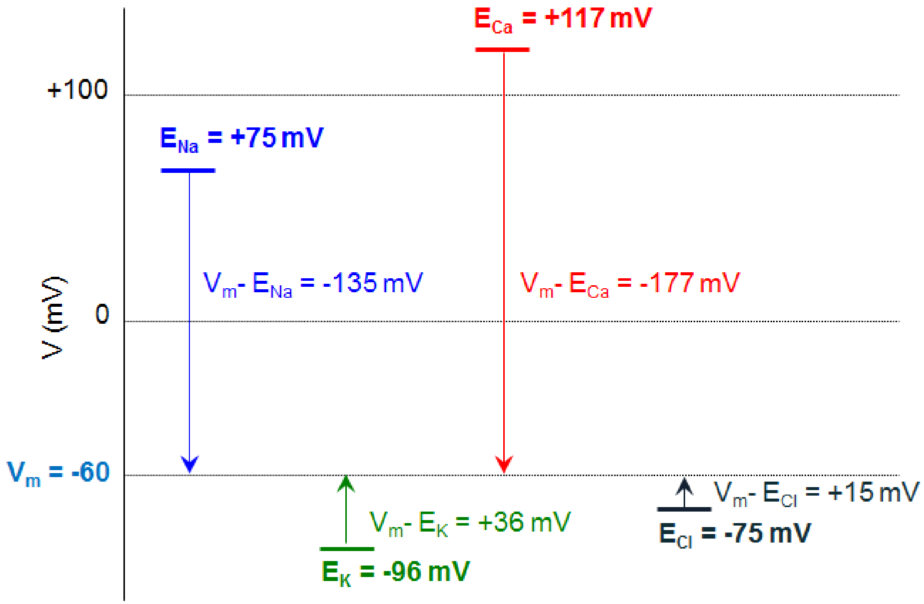
$$EMF = V_m - E_X$$

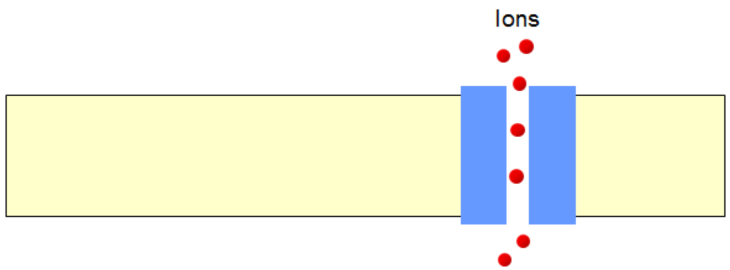




Ionic currents through ion channels







$$I_X = G_X (V_m - E_X)$$

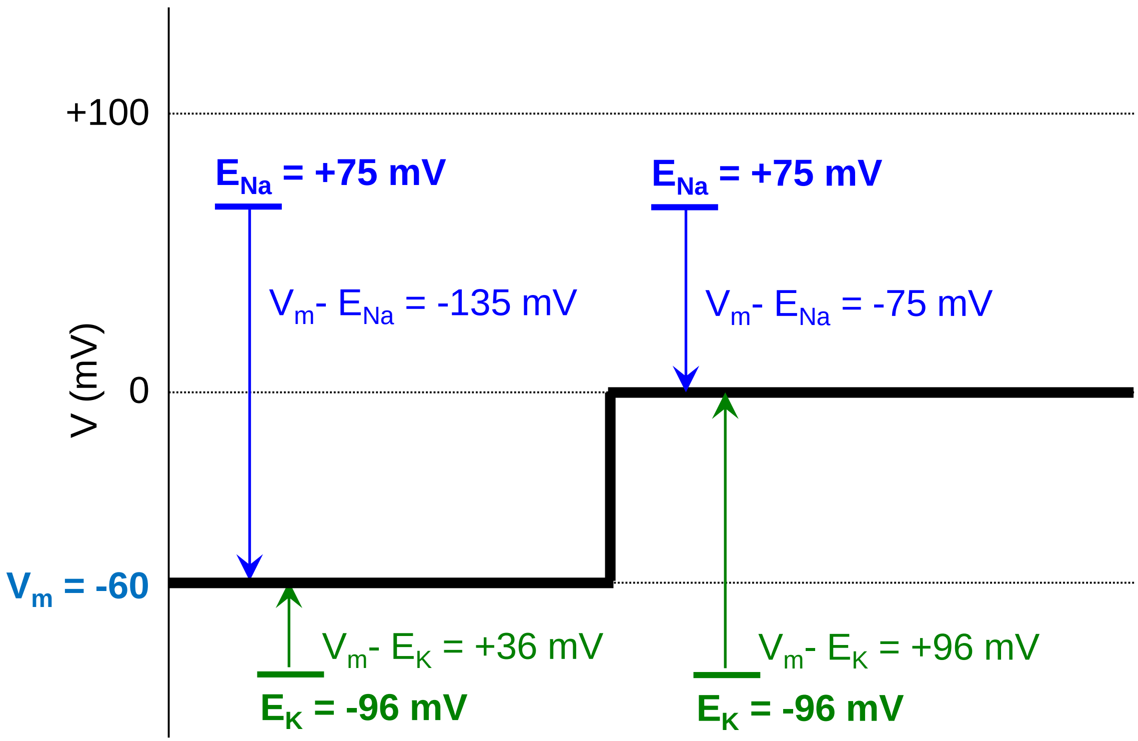
Current (A) = conductance (S) × electromotive force (V)

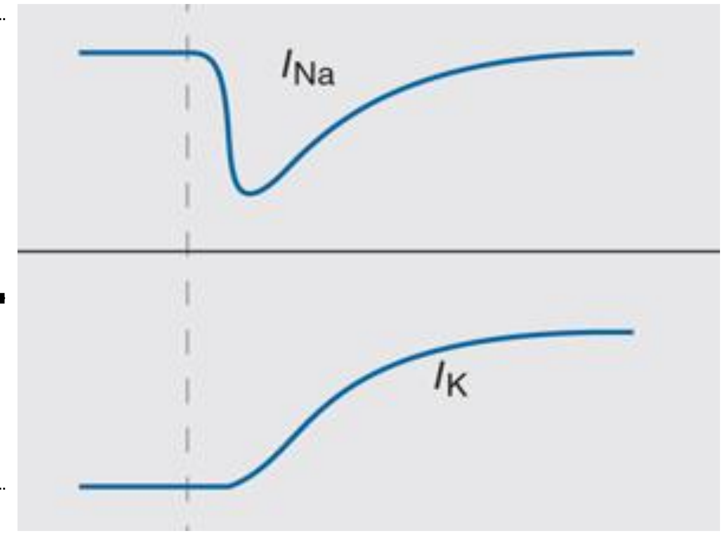
Ohm's law

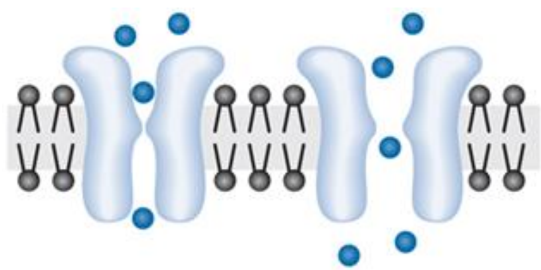
$I = V/R$ or $I = \gamma \times V$

$$I_{Na} = G_{Na} (V_m - E_{Na}) = -135 \times G_{Na}$$
$$I_K = G_K (V_m - E_K) = +36 \times G_K$$
$$I_{Cl} = G_{Cl} (V_m - E_{Cl}) = +15 \times G_{Cl}$$
$$I_{Ca} = G_{Ca} (V_m - E_{Ca}) = -177 \times G_{Ca}$$

Voltage- and time-dependent ion channel currents







$$I_X = G_X (V_m - E_X)$$

Current (A) = conductance (S) × electromotive force (V)

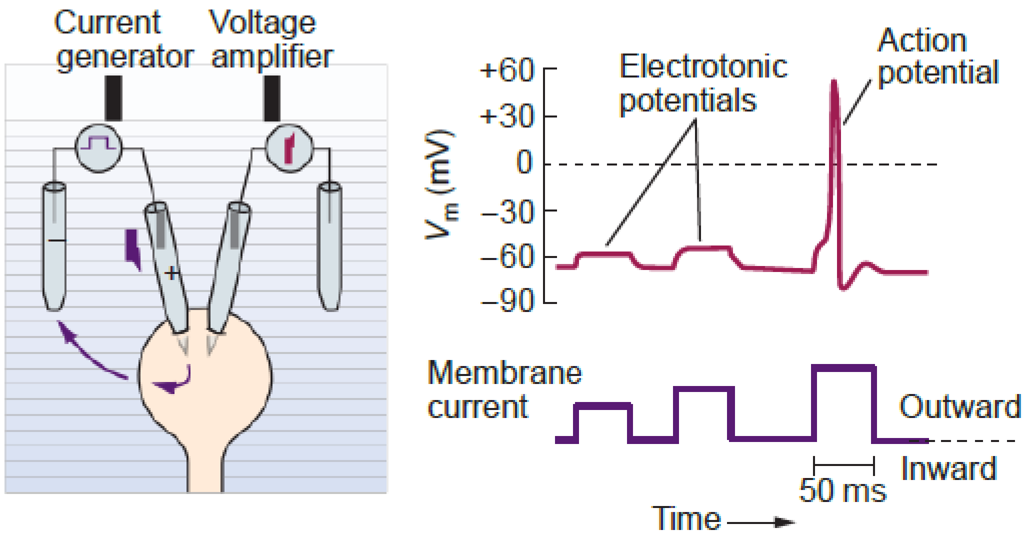
Passive electrical properties

- properties that are fixed, or constant, near the resting potential of cell
- determines the time course and spread of electrical activity
  → electrotonic potential
- Ex. Membrane resistance, membrane capacitance, axial resistance

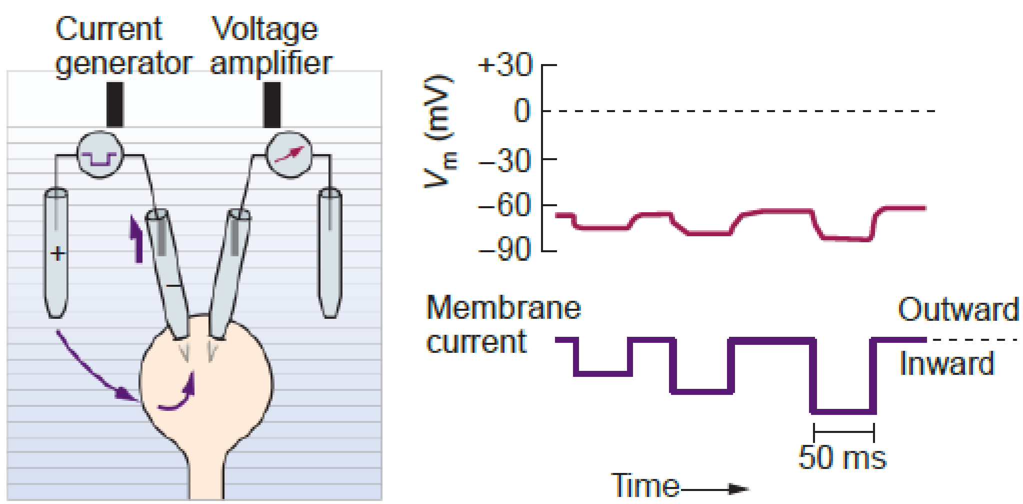
Electrotonic potentials (전기긴장성 전압)

-Passive response of membrane
-Do not lead to the opening of ion channels

Opening of voltage-gated ion channels

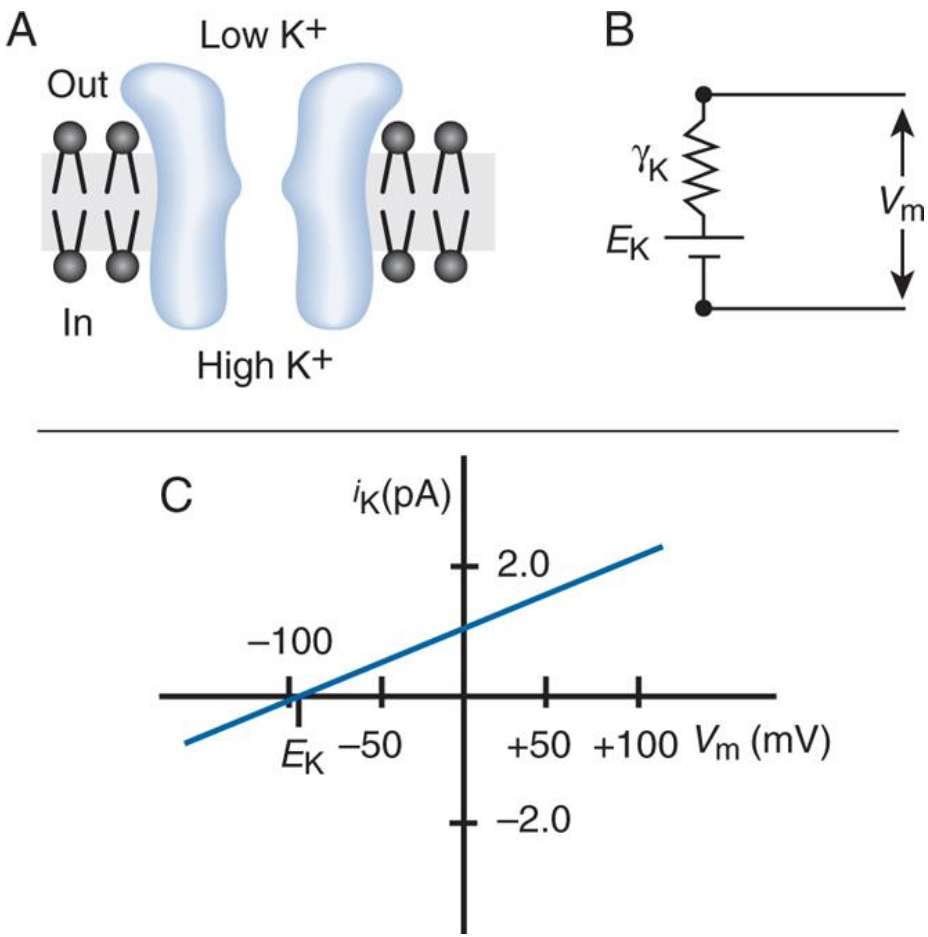


Depolarization



Hyperpolarization

Equivalent circuit of a membrane has a resistor in parallel with a capacitance



Ohm's Law

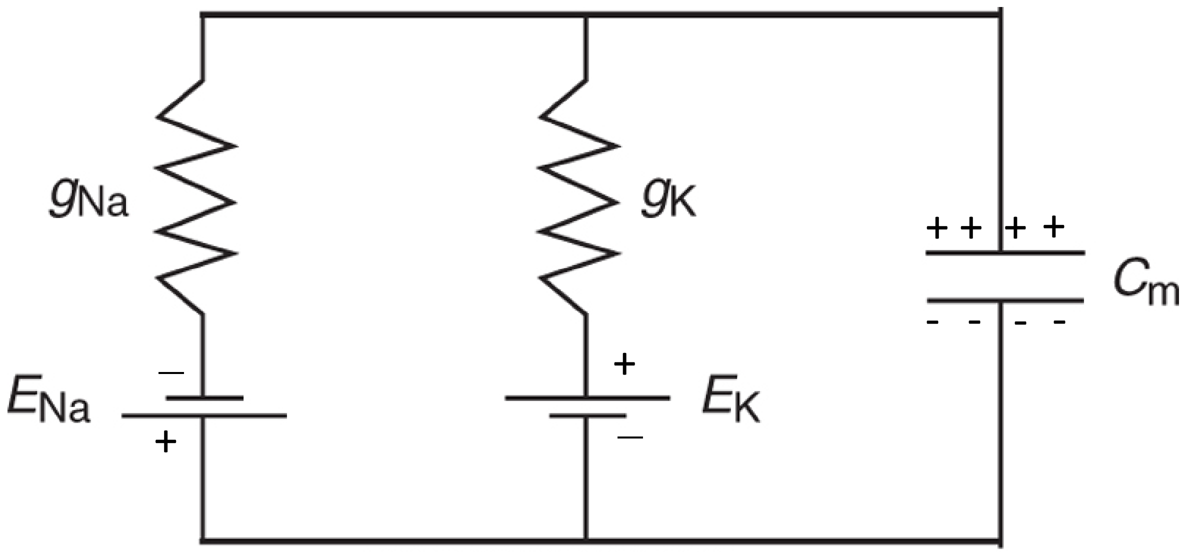
$$I = \frac{V}{R} = g \times V$$

$$i_K = \gamma_K(V_m - E_K)$$

$$I_K = g_K(V_m - E_K)$$

$$g_K = N_O \times \gamma_K$$

Equivalent circuit of a membrane containing many open Na^+ and K^+ channels



$$q = C_m \times Vm \qquad \frac{dq}{dt} = C \times \frac{dV}{dt} \text{ or } I_c = C \times \frac{dV}{dt}$$

Biological membrane $C_m = 1\ \mu F/cm^2$ (1 F= 1 Coulomb/V)

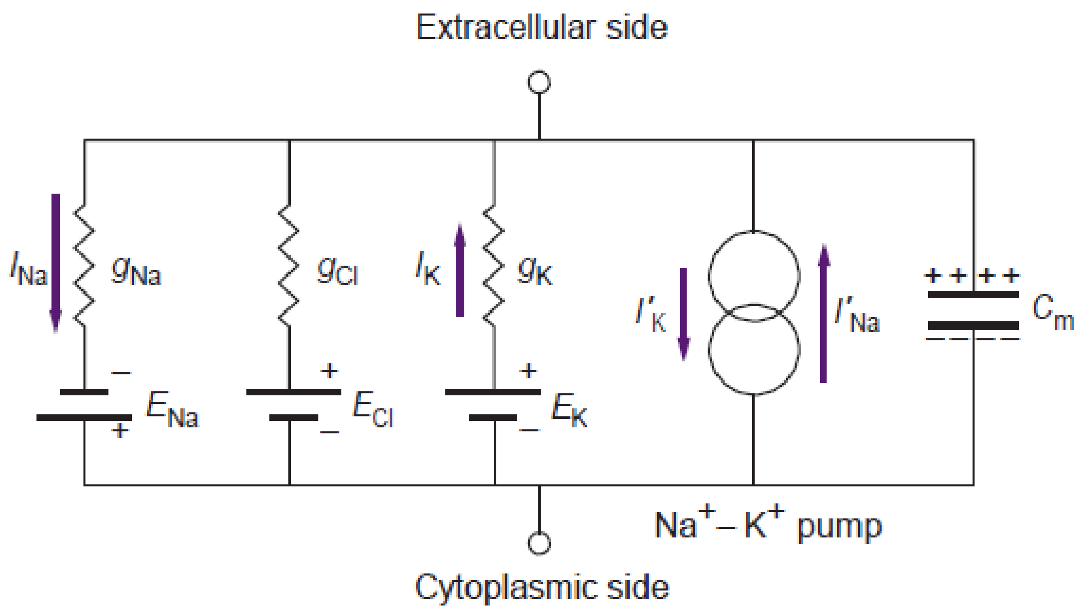
$$A_{cell} = \pi d^2 \qquad d = 10\ \mu m$$

$$A_{cell} = 3.1 \times 10^{-6}\ cm^2$$

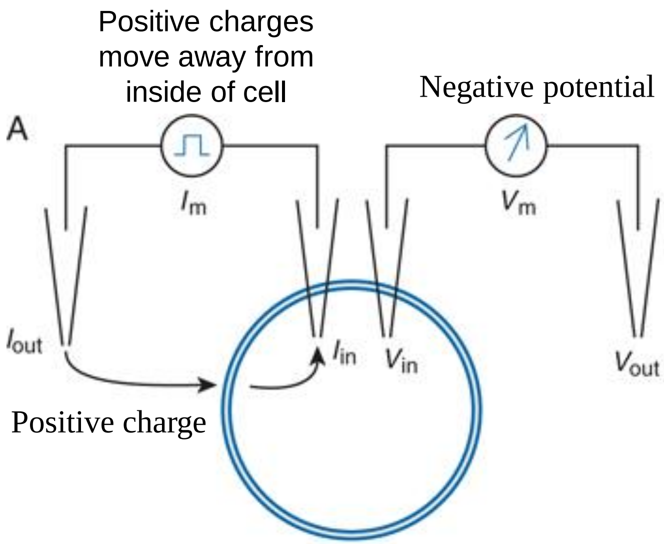
$$C_{cell} = C_m \times A_{cell}$$

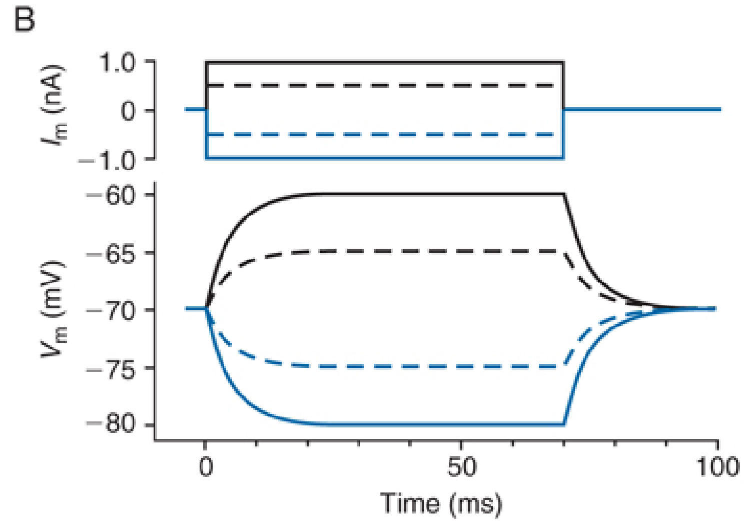
$$= 10^{-6}\ F{\cdot}cm^{-2}\ (3.1 \times 10^{-6}\ cm^2)$$
$$= 3.1 \times 10^{-12}\ F = 3.1\ pF$$

Equivalent circuit of a cell membrane

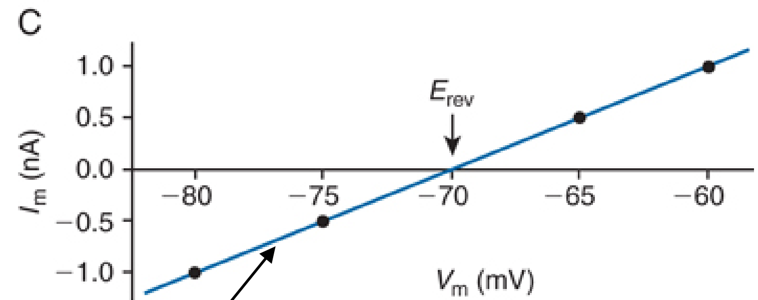


Passive properties of membranes





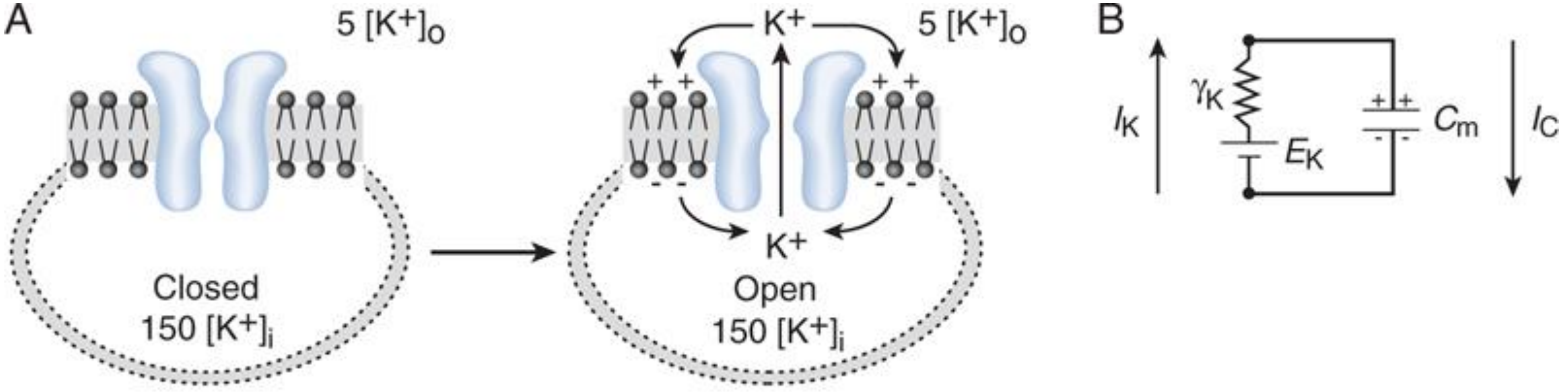
$R_{in} = \Delta V / \Delta I$



linear I-V relationship
(in the steady state)

resting conductance

Current flow through a channel alters the charge distribution across the membrane



0 mV

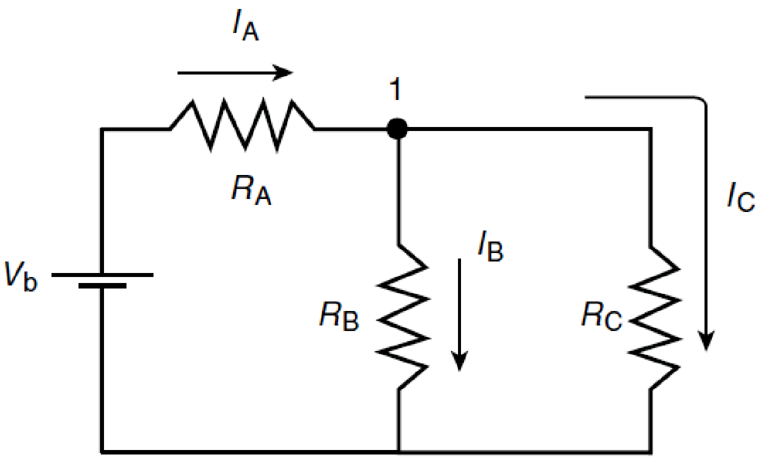
-90 mV

outward I_K → V_m moves negative direction → inward I_C

Kirchhoff's Law

1. Kirchhoff's Current Law
-The principle of conservation of electric charge

2. Kirchhoff's Voltage Law
-The principle of conservation of energy



$$I_A = I_B + I_C$$

$$I_A \times R_A + I_B \times R_B - V_b = 0$$

$$I_C \times R_C - I_B \times R_B = 0 \quad \text{or} \quad I_C \times R_C = I_B \times R_B$$

$$I_A = \frac{V_b - I_B \times R_B}{R_A}$$

$$\frac{V_b - I_B \times R_B}{R_A} - I_B - I_B \times \frac{R_B}{R_A} = 0$$

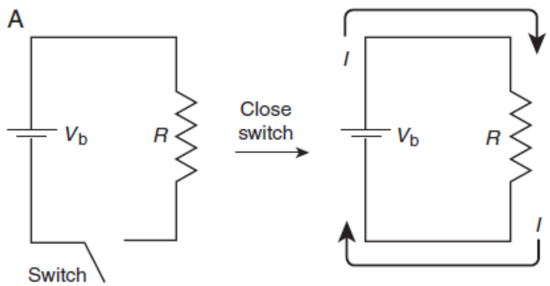
$$I_B = \frac{V_b}{R_A + R_B + \frac{R_A \times R_B}{R_C}}$$

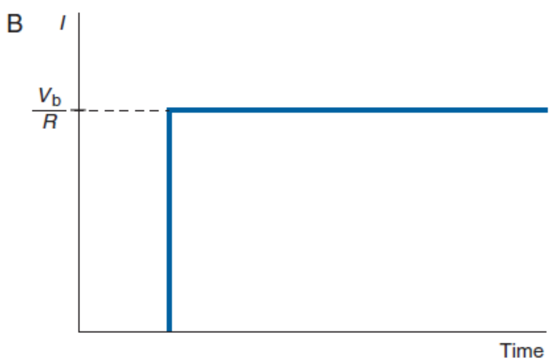
$$\begin{pmatrix} 1 & -1 & -1 \\ R_A & R_B & 0 \\ R_A & 0 & R_C \end{pmatrix} \begin{pmatrix} I_A \\ I_B \\ I_C \end{pmatrix} = \begin{pmatrix} 0 \\ V_b \\ V_b \end{pmatrix}$$

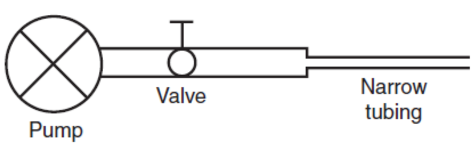
If $V_b = 10$ V, $R_A = 10\ \Omega$, $R_B = 10\ \Omega$, $R_C = 20\ \Omega$

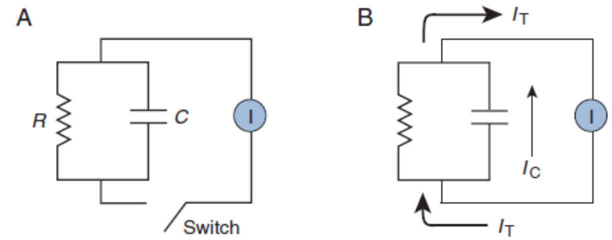
$I_A = 0.6$ A, $I_B = 0.4$ A, $I_B = 0.2$ A

Parallel R-C circuit

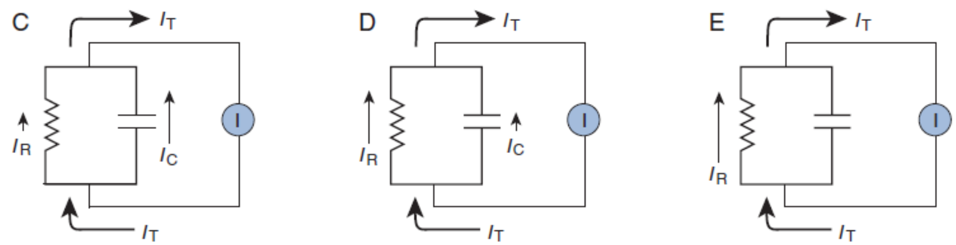


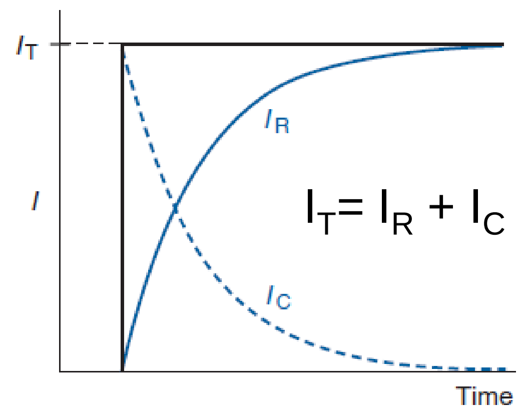


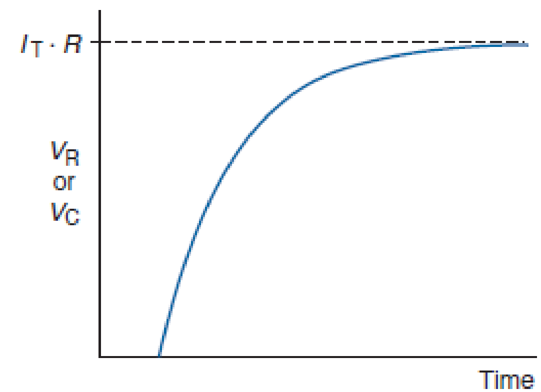


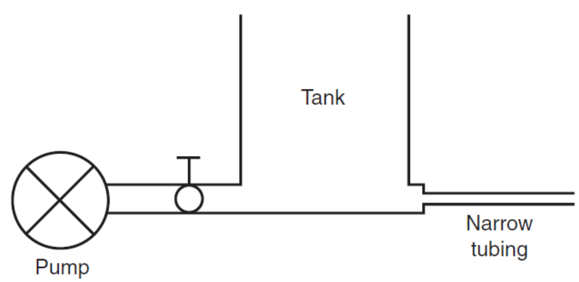


1. charge separation
2. development of V_C
3. $V_C = V_R$

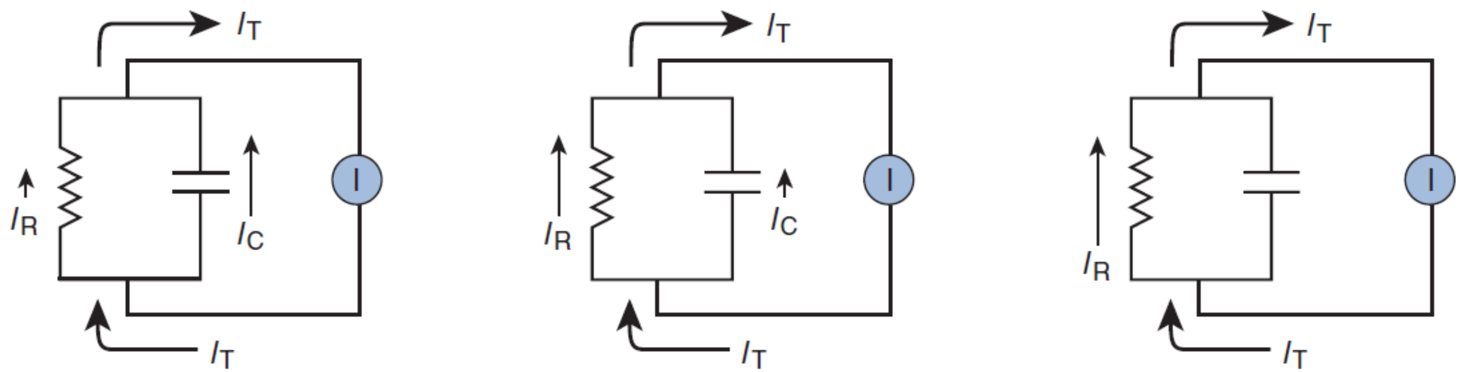








Time course of V_m changes in parallel R-C circuits



$$I_T = I_R + I_C = \frac{V_R}{R} + C\frac{dV_C}{dt}$$

$$V_m = V_R = V_C \;, \quad I_T = \frac{V_m}{R} + C\frac{dV_m}{dt}$$

$$V_m = e^{-\frac{t}{RC}} \int e^{\frac{t}{RC}} \left(\frac{I_T}{C}\right) dt = e^{-\frac{t}{RC}} \left[\frac{I_T}{C} \cdot e^{\frac{t}{RC}} \cdot RC + Const\right] \qquad Const = -I_T R.$$

$$V_m = I_T R\left[1 - e^{-\frac{t}{RC}}\right] \;, \quad V_m(t) = V_{m,\infty}\left[1 - e^{-\frac{t}{\tau_m}}\right]$$

$$\tau_m = R \times C \text{ and } V_{m,\infty} = I_T \times R$$

$$I_R(t) = \frac{V_m(t)}{R} = \frac{V_{m,\infty}}{R}\left[1 - e^{-\frac{t}{\tau_m}}\right] = I_T\left[1 - e^{-\frac{t}{\tau_m}}\right]$$

$$I_C(t) = C\frac{dV_m(t)}{dt}$$

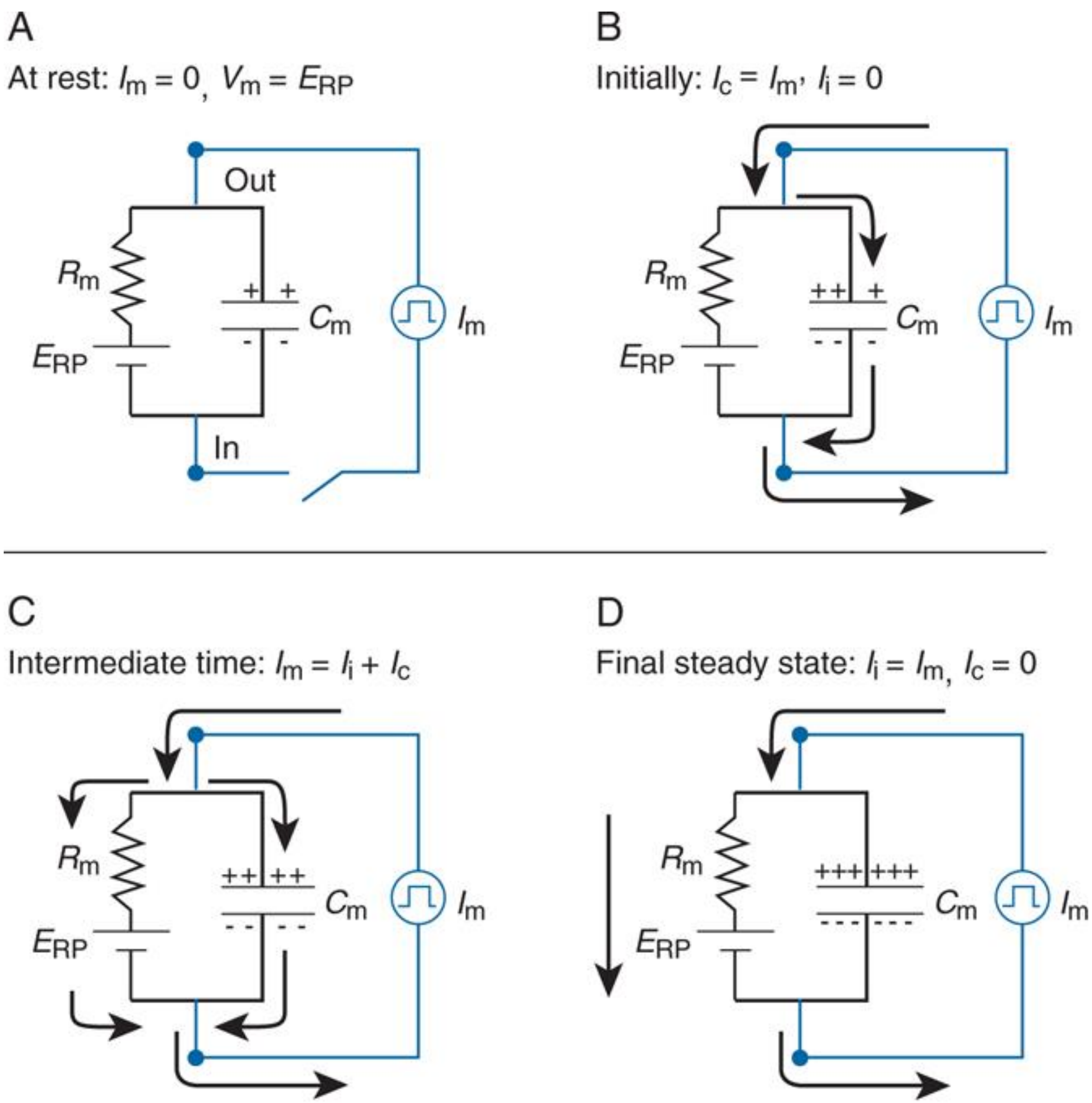
$$\frac{dV_m(t)}{dt} = V_{m,\infty}\frac{d}{dt}\left[1 - e^{-\frac{t}{\tau_m}}\right]$$

$$= \frac{V_{m,\infty}}{\tau_m} \cdot e^{-\frac{t}{\tau_m}}$$

$$I_C(t) = \frac{CV_{m,\infty}}{\tau_m} e^{-\frac{t}{\tau_m}} = \frac{CI_T R}{CR} e^{-\frac{t}{\tau_m}}$$

$$= I_T \, e^{-\frac{t}{\tau_m}}$$

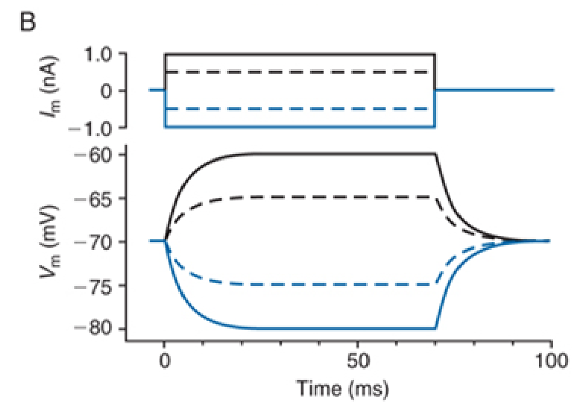
Passive properties of the membrane

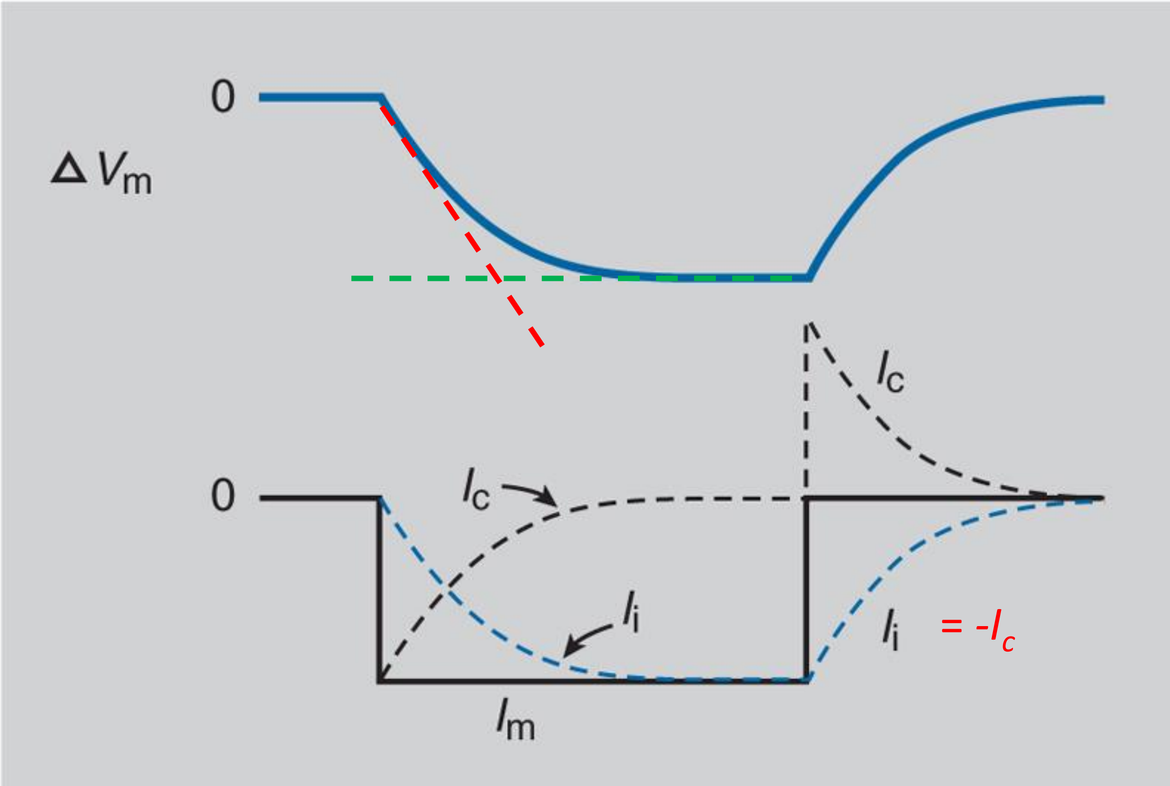


$$V_m - E_{RP} = 0$$

↓

$$V_m - E_{RP} < 0$$





$$I_M = I_C + Ii$$

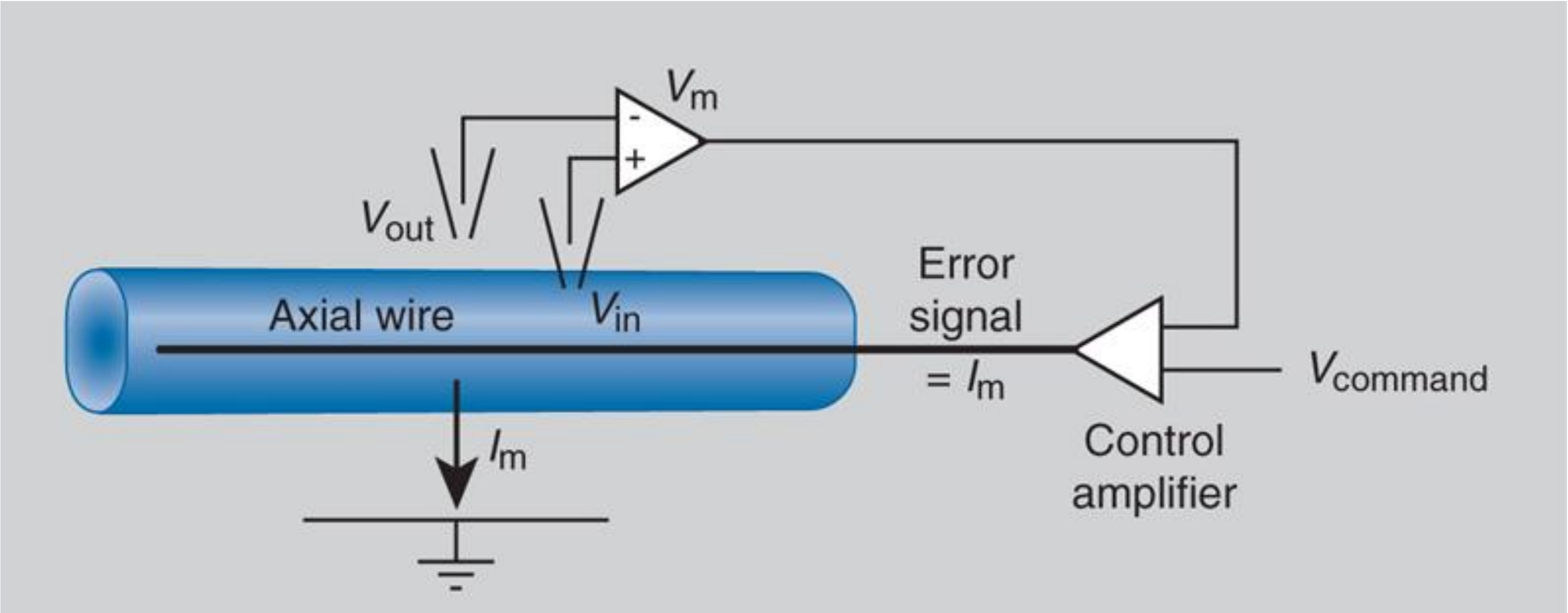
$$= C\frac{dv}{dt} + \frac{V_M}{R}$$

$$\Delta V_m(t) = \Delta V_{m,\infty}(1 - e^{-t/\tau}) = I_m R_m(1 - e^{-t/\tau})$$

$$\tau = R \times C, \ \Delta V_{m,\infty} = I_m \times R_m$$

If $\tau = t$, $\Delta V_m = 0.63\Delta V_{m,\infty}$

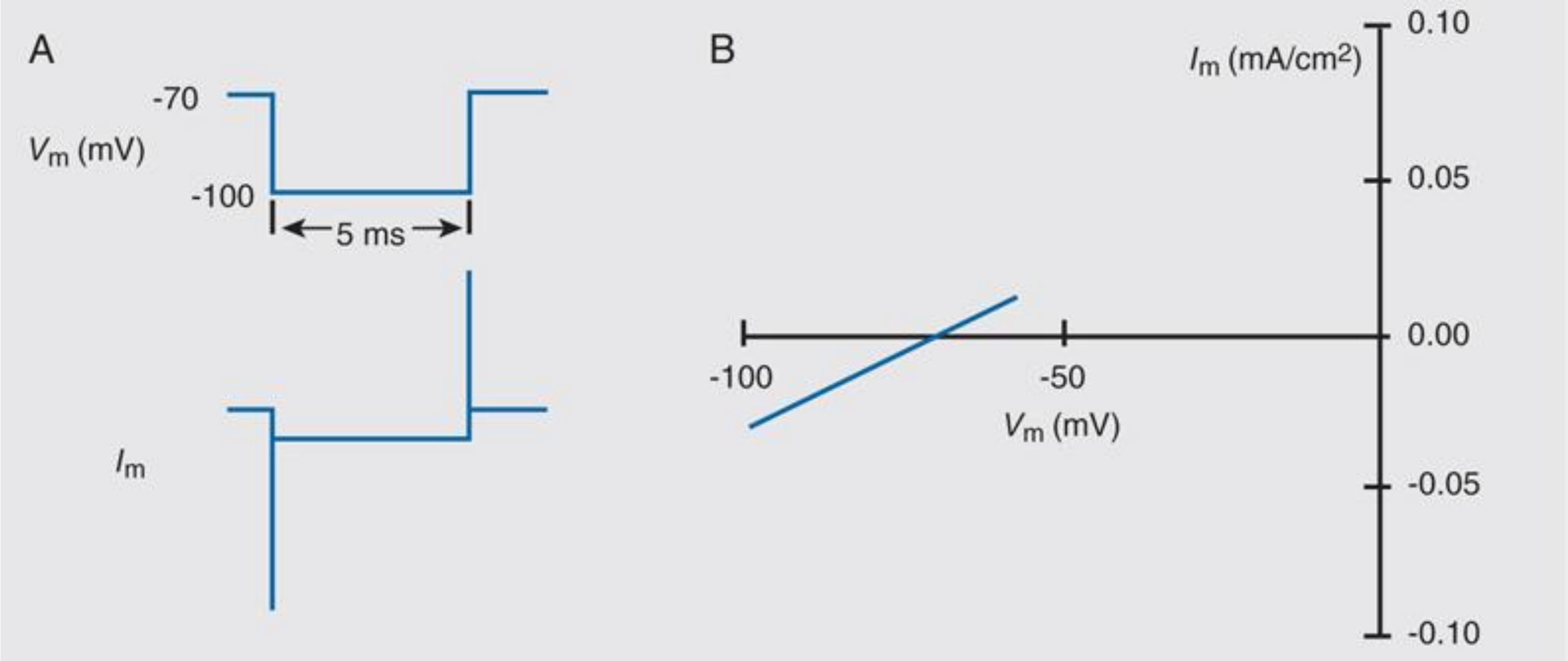
Voltage clamp



$$I_M = I_C + Ii$$

$$= C\frac{dv}{dt} + \frac{V_M}{R}$$

Passive responses by hyperpolarizing and small depolarizing voltage step

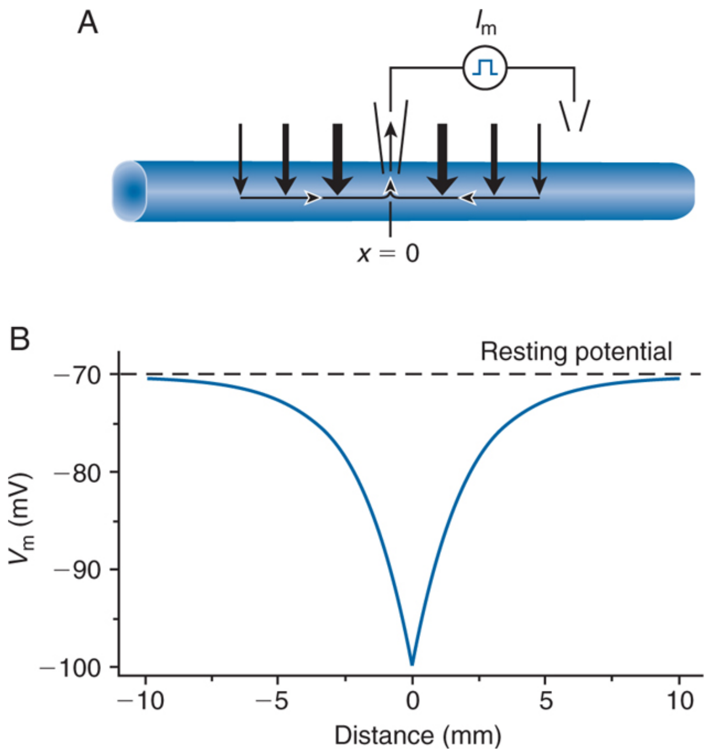


$$I_M = I_C + Ii$$

$$= C\frac{dv}{dt} + \frac{V_M}{R}$$

Electrotonic conduction

Passive flow of electric potential along the membrane



Cable equation

$$\Delta V_m(x) = \Delta V_0 e^{\left(\frac{-x}{\lambda}\right)}$$

$$\lambda \text{ (length constant)} = \sqrt{\frac{r_m}{r_i + ro}} \approx \sqrt{\frac{r_m}{r_i}}$$

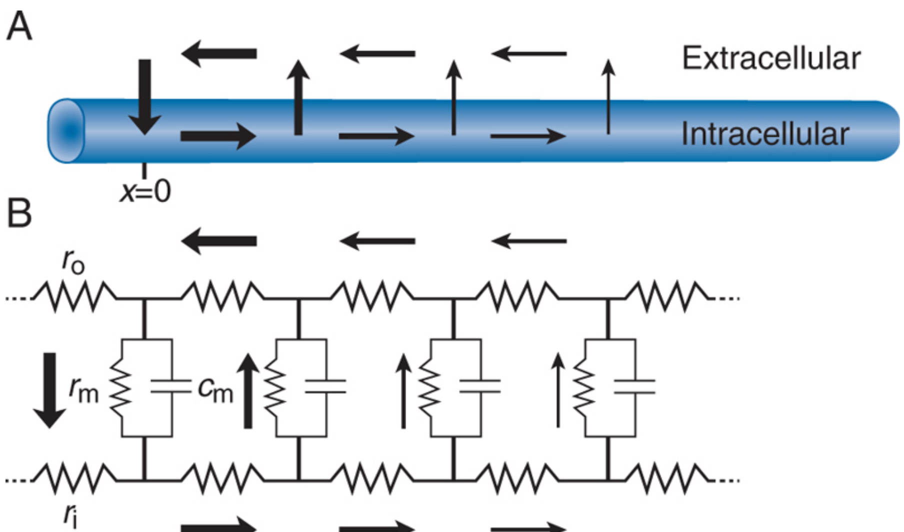
r_m=membrane resistance (Ω × cm)
r_i = intracellular resistance (Ω /cm)
r_o =extracellular resistance (Ω /cm)
λ = length constant (cm)

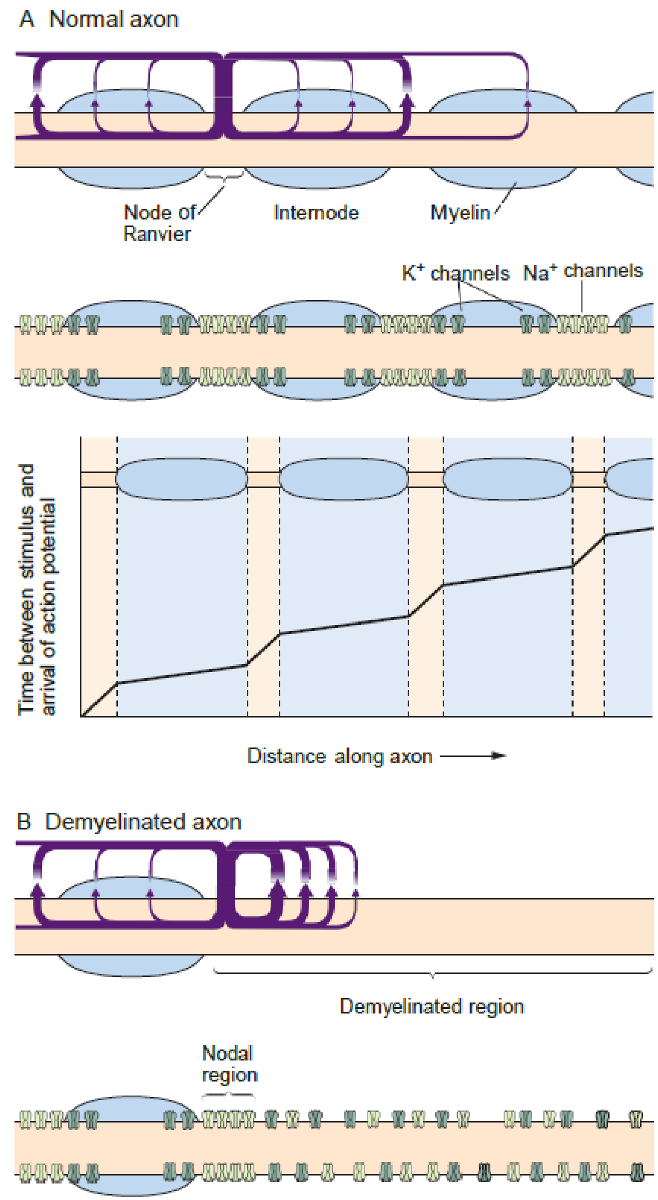
R_m=membrane resistance (Ω × cm^2)
= r_m × circumference (π × d)

ΔV_m at a distance λ

$$\Delta V(\lambda) = \Delta V_0 e^{\left(\frac{-\lambda}{\lambda}\right)} = \Delta V_0 e^{-1} = 0.37\Delta V_0$$

Myelin sheath decreases capacitance and increases electrical resistance across the cell membrane





$$\lambda \text{ (length constant)} = \sqrt{\frac{r_m}{r_i + ro}} \approx \sqrt{\frac{r_m}{r_i}}$$