INTRODUCTION TO NEUROSCIENCE

UNIT NATS 6001

Lecture 2- The ionic basis of membrane potential

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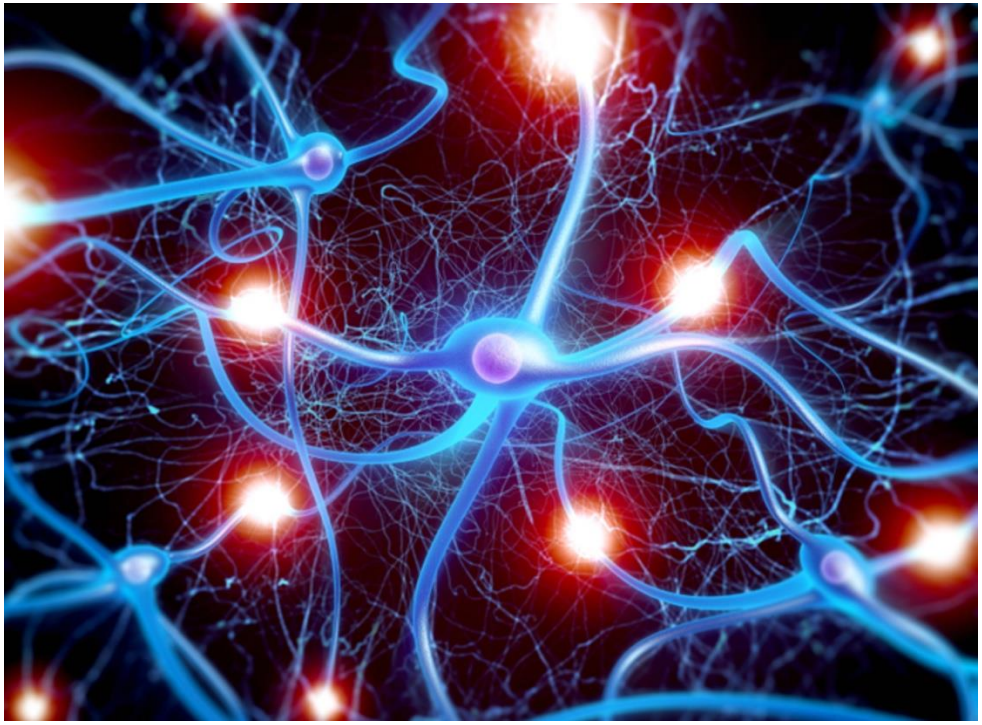
Neural communication

How neurons communicate?

Communication through electrochemical signals

Neurons communicate through electrochemical signals.



To understand the nature of communication in the brain, one must look into the mechanisms governing the neuron excitable membrane

Objectives

- Membrane structure and function
- Transport across membranes (Diffusion, pumps, ion channels)
- The ionic basis of the membrane potential
- Passive and active properties of excitable membranes

What are electrochemical signals?

Signals in which the information is transmitted through ions (chemical) that carry an electrical charge.

Few definitions to start with….

An **ion** is an atom or molecule in which the total number of electrons is not equal to the total number of protons, giving the ion a net positive or negative electrical charge.

Membrane structure and function

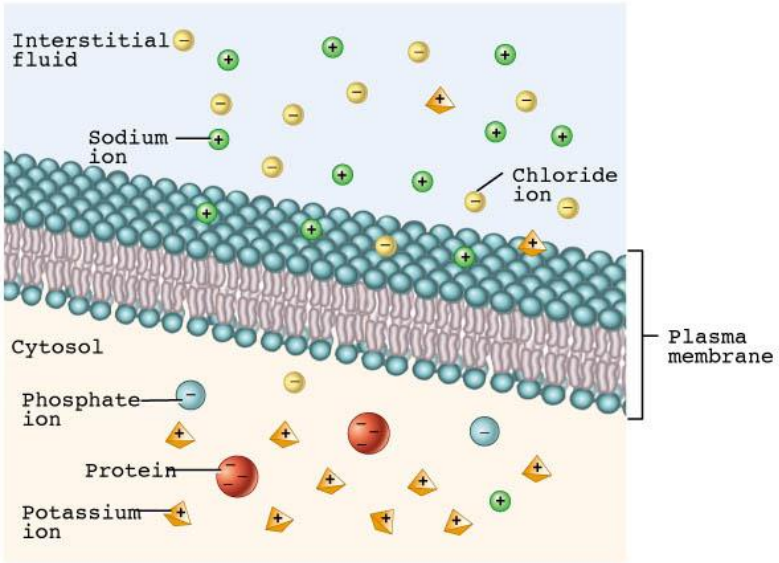
What is the structure of the membrane?

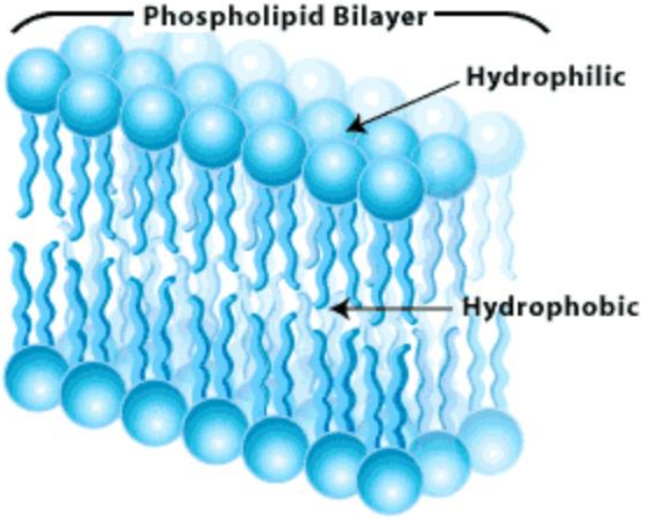
What are the transport pathways to cross the membrane?
(Diffusion vs. active transport)

Membrane structure and function

The cell membrane surrounds the cytoplasm of living cells, physically separating the intracellular components from the extracellular environment

- consists of ***phospholipid bilayer*** with embedded proteins (<10 nM)
- Phospholipids contain a ***hydrophilic*** head and a ***nonpolar hydrophobic*** tail, which creates a barrier.
- ***Selectively permeable*** (controls the movement of substances in and out of cells), and therefore its electrical resistivity is very high.



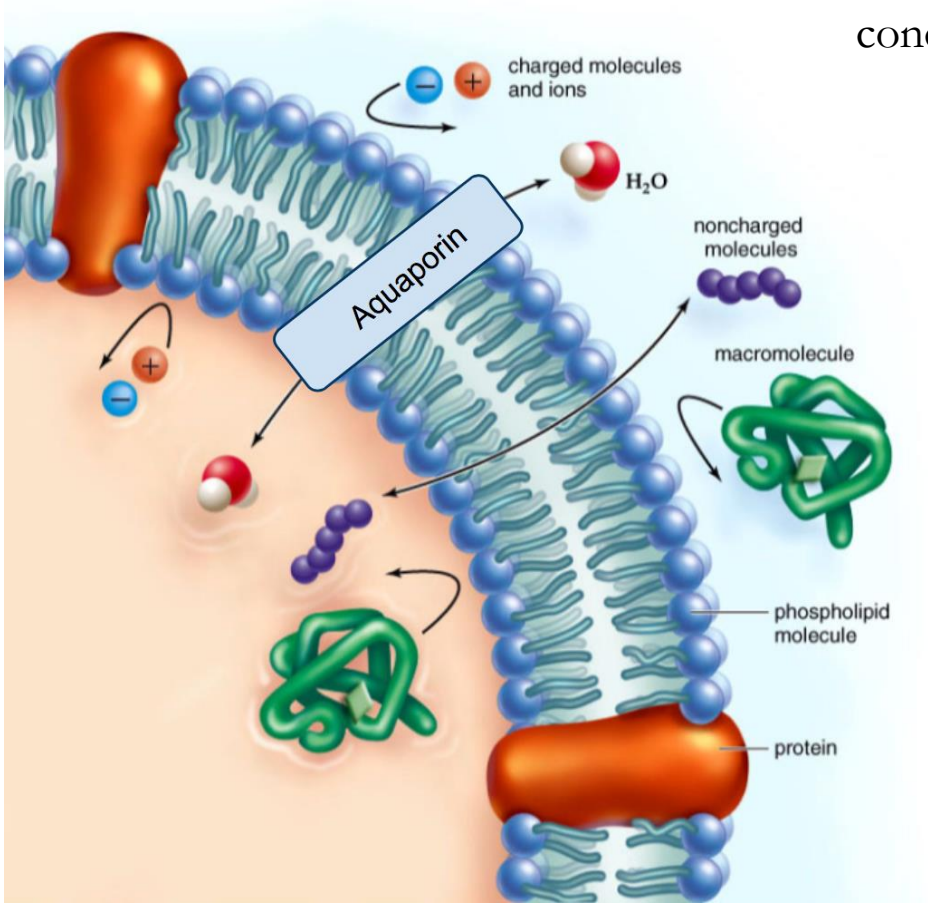


Membrane structure and function

How substances are crossing the membrane?

Transport across membrane

Movement of substances across the membrane can be either "***passive***", occurring without the input of cellular energy, or "***active***", requiring the cell to spend energy in transporting it.



Passive: osmosis and diffusion according to the concentration gradient

Who shall pass (freely)?

Small and uncharged molecules

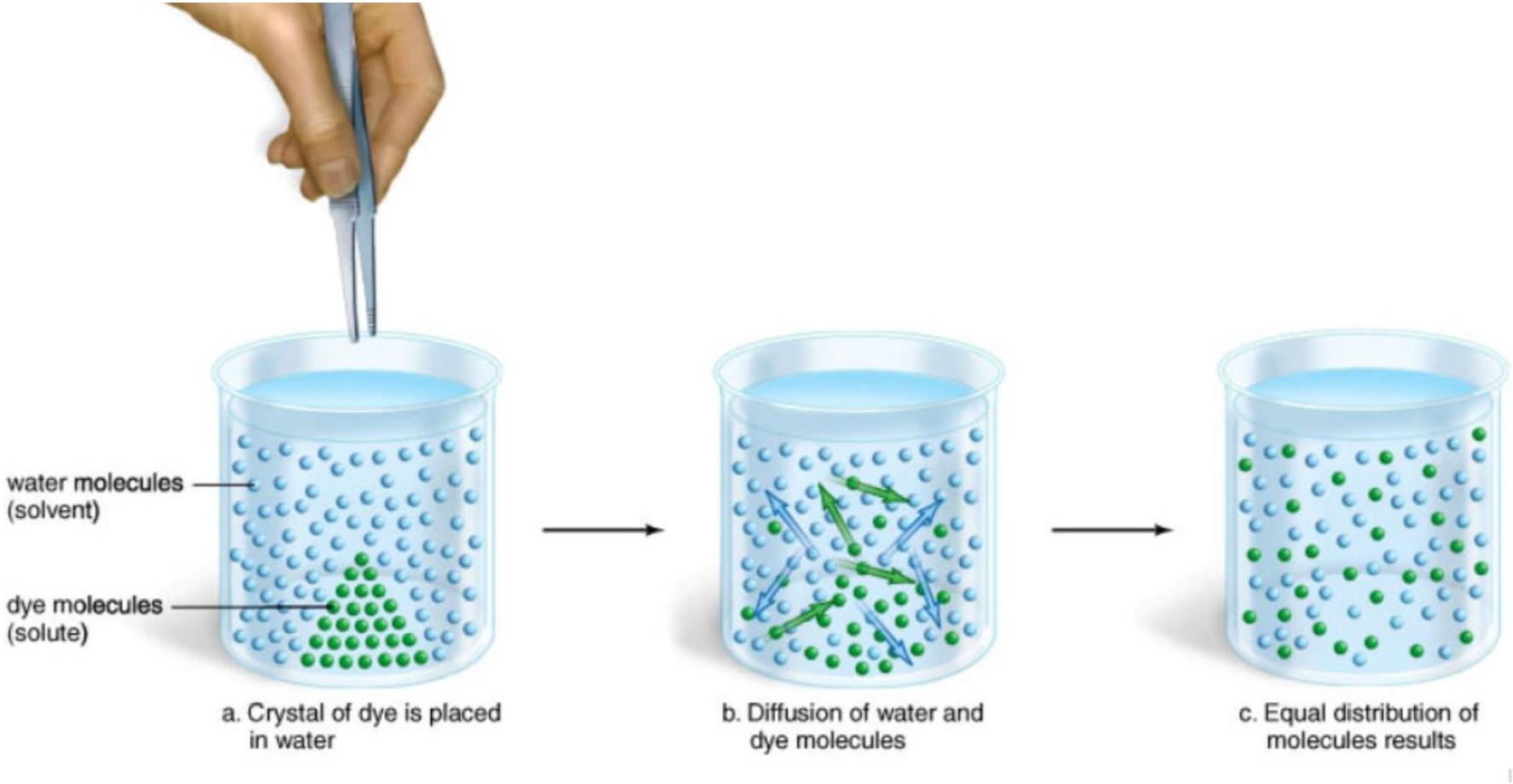
What cannot pass (freely)?

Large and charged molecules

Active: Transporters and pumps activation to move ions against their concentration gradient

Transport across membrane - diffusion

Passive transport – diffusion of molecules, from areas of high concentration to areas of low concentration according to a concentration gradient.



Transport across membrane - diffusion

Can we force diffusion against the concentration gradient?

Yes, but it's going to cost you! (with ATP coins)

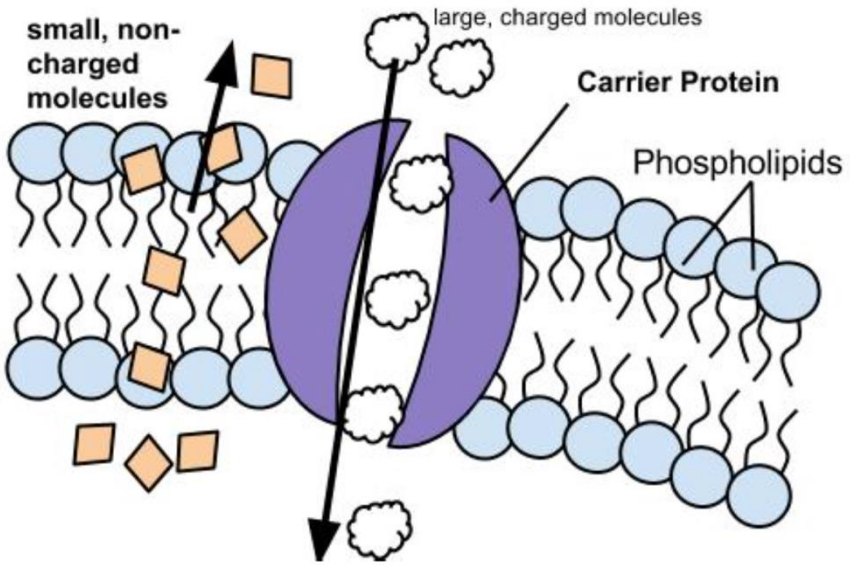
Facilitated diffusion transport

How particles diffuse through an impermeable membrane?

Facilitated diffusion transport

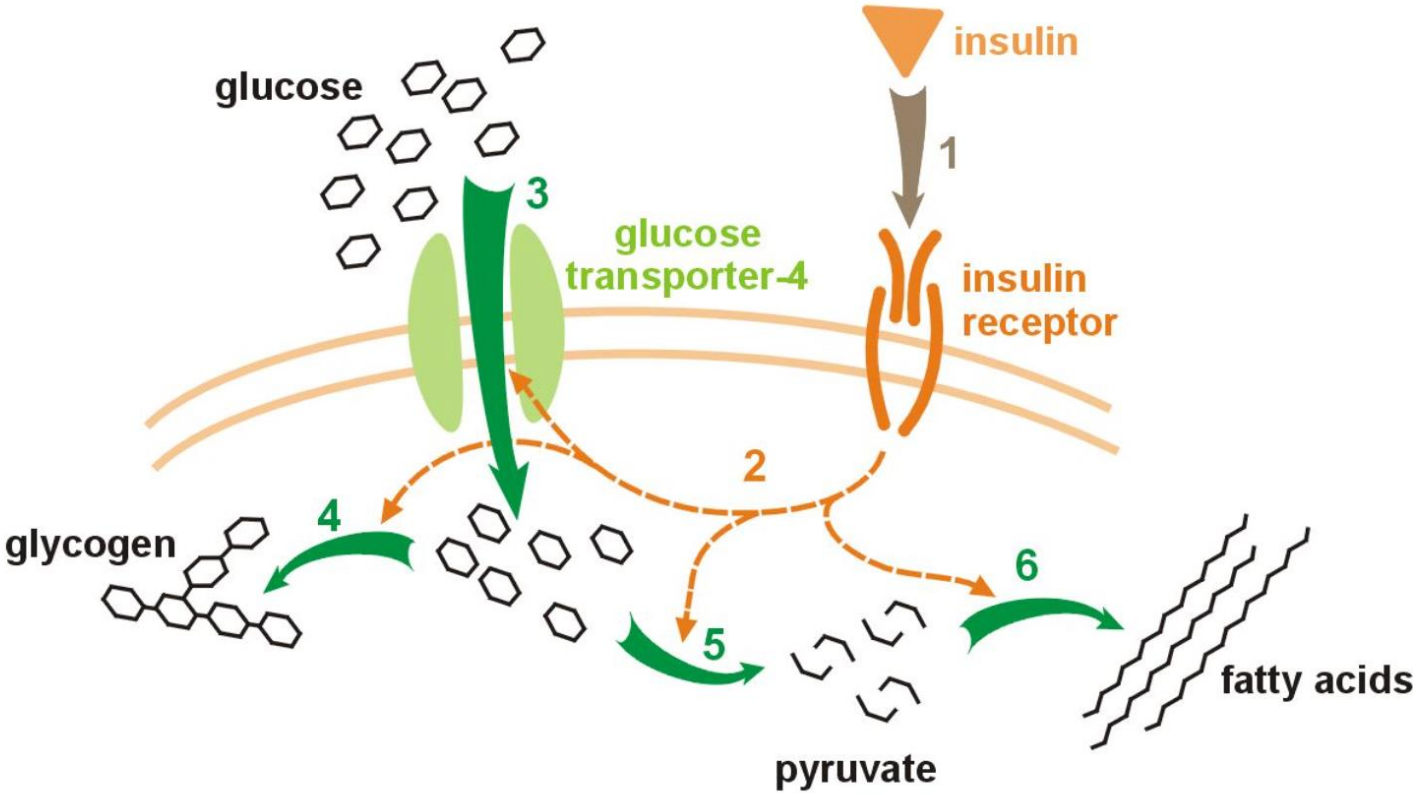
Diffusion that requires the assistance of proteins (channels), yet it is ***passive*** as molecules moving along the concentration gradient.

Membranes have gates



Facilitated diffusion transport

Glucose transporters (GLUT) are a wide group of membrane proteins that facilitate the transport of glucose over a plasma membrane.

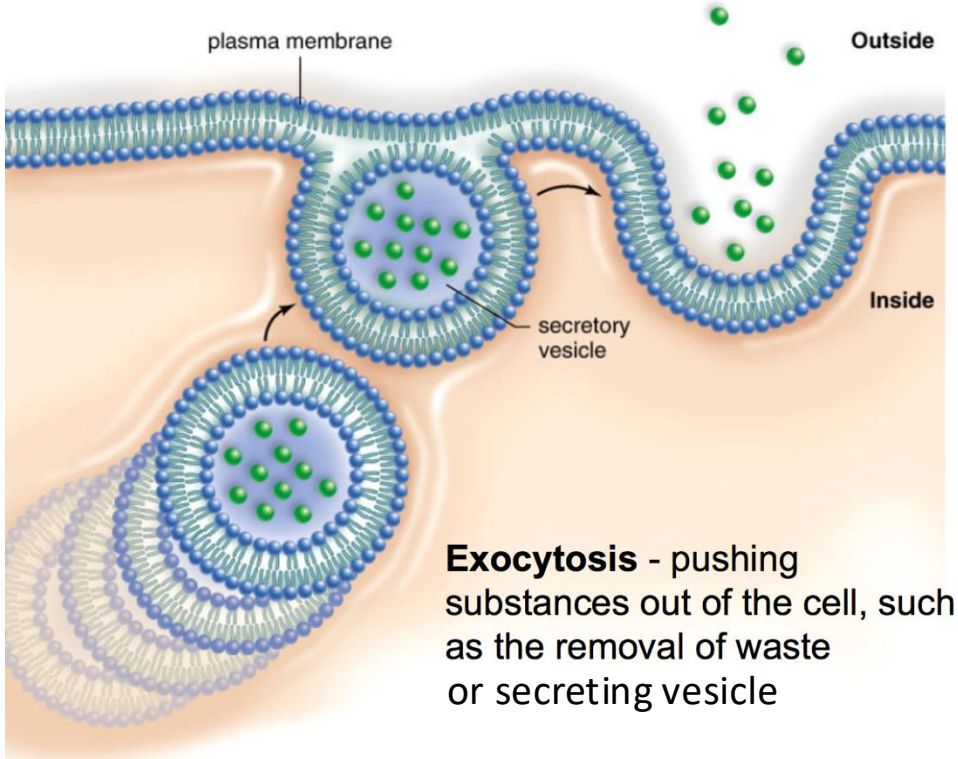


Transport across membrane - active transport

Transport of molecules "up-hill", against the concentration gradient, which requires energy

Three processes:

- Endocytosis/Exocytosis
- Primary active transport (pumps – ATPase)
- Secondary active transport (Cotransporters, symporters)

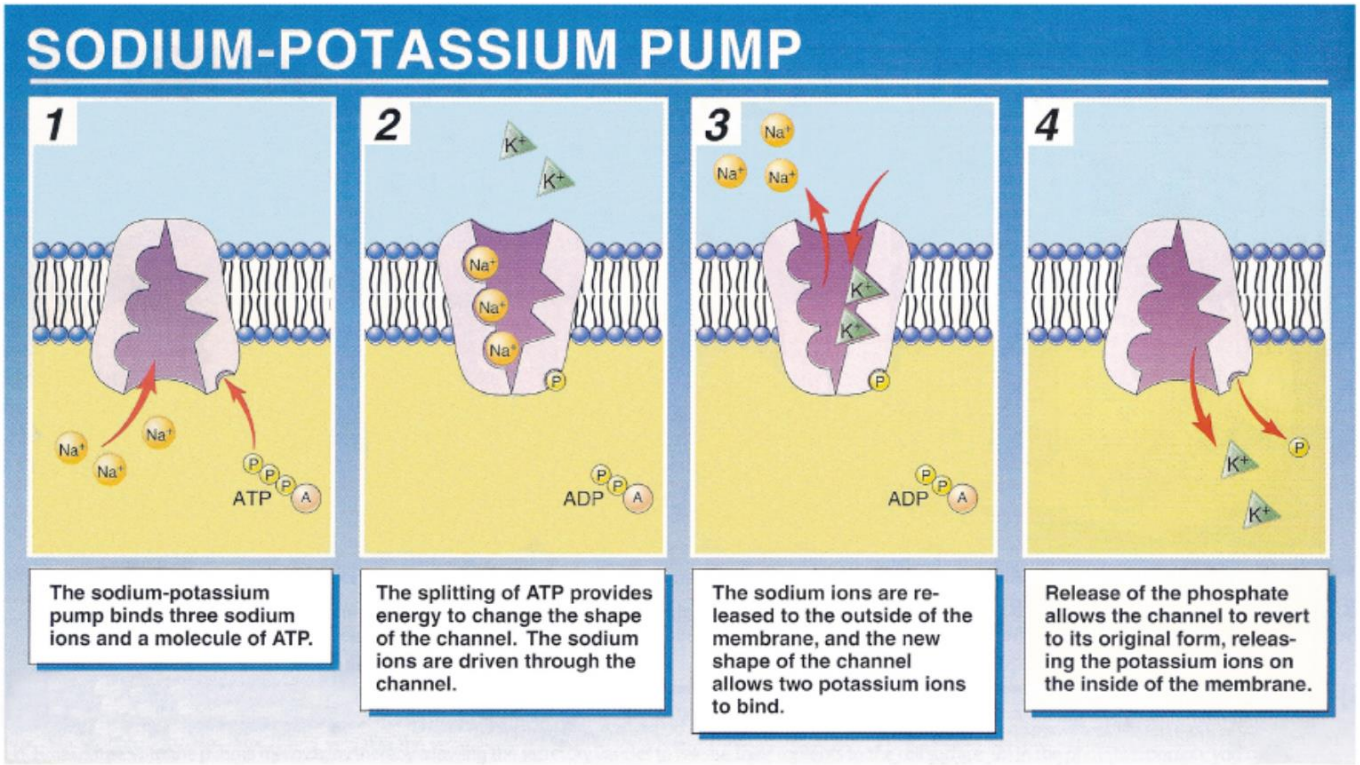


Active transport – primary active transport

Primary active transport directly uses metabolic energy (***ATP***) to transport molecules across a membrane, ***against their gradient concentration***

Active transport – primary active transport

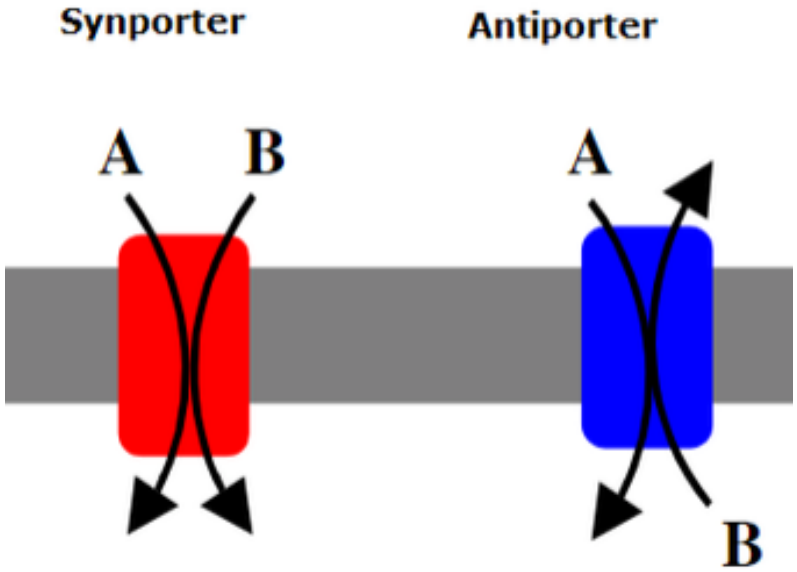
- ***Na⁺/K⁺* pump** moves three molecules of sodium out of the cell and gets two molecules of potassium into the cell, against the concentration gradient. As it generates a net current, it is also electrogenic.
- Slow (small currents) – produce <1% than the Na^+ current through the Na^+ channels.
- One of the most important pumps in our body, why?
  It is responsible for maintaining the trans-membrane concentration gradient



Active transport – secondary active transport

In ***secondary active transport***, one molecule moves ***along*** its electrochemical gradient, allowing a different molecule to move ***against*** its own electrochemical gradient.

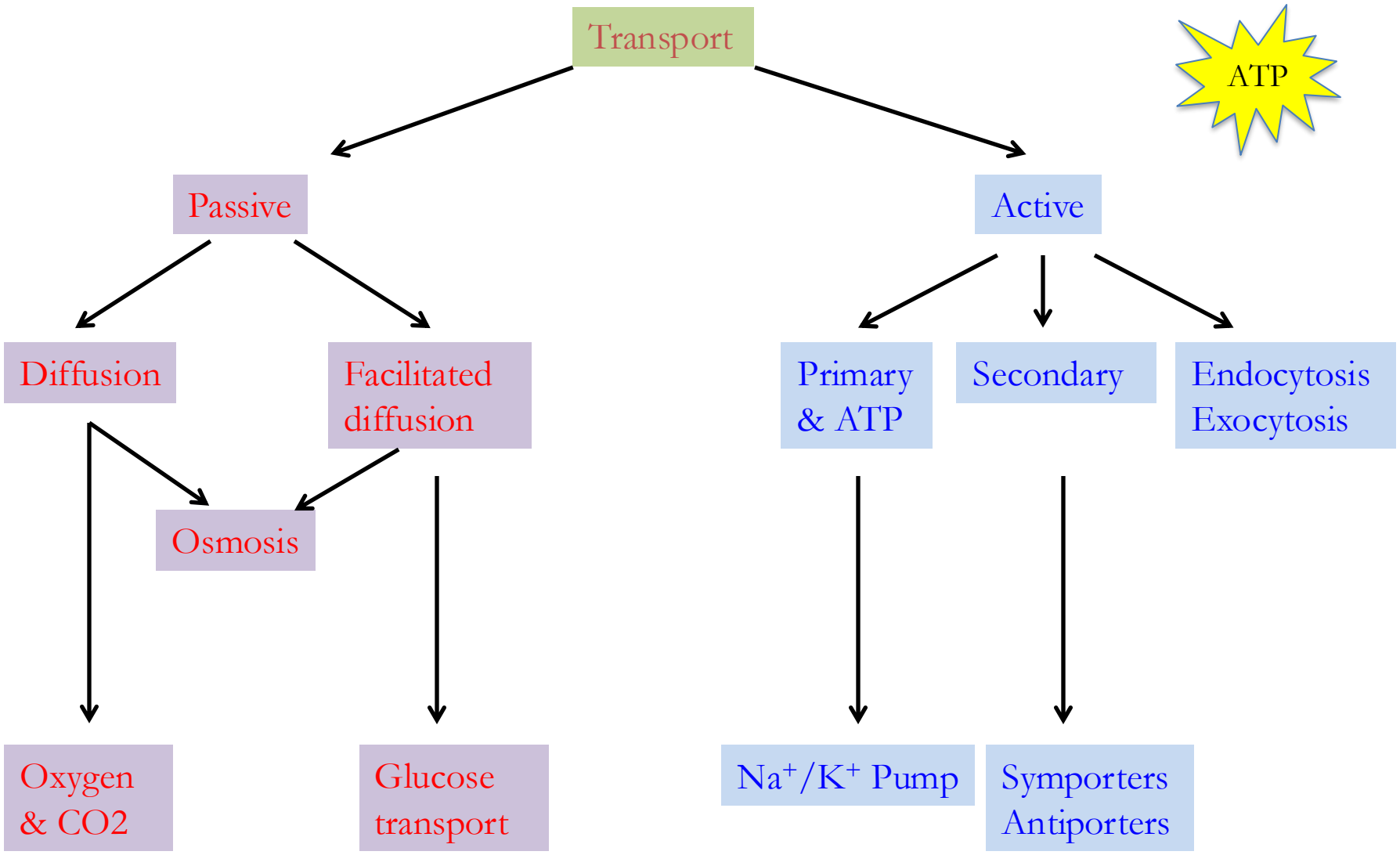
This movement is in contrast to primary active transport, in which all solutes are moved against their concentration gradients, fueled ***by ATP***.



Na-K-Cl cotransporter

Na^+/Ca^{2+} exchanger

Transport across membrane – summary



Particle movement through membranes

Which transport mechanism is most efficient?

- Energy cost
- Distance

Measuring diffusion

Diffusion is the most cost efficient way (free), however distance wise…

Adolf Fick, 1855

Fick's I[st] law of diffusion - In Aqueous diffusion, uncharged particles (no electrical energy), move only by the chemical energy, along the concentration gradient

Diffusion of substance S

Difference in concentration of substance S

J_s –flux – mole /(cm^2 * s)
C_s - local concentration - mole / cm^3
D_s - diffusion coefficient (of S) – cm^2/s

Rate of transport (flux density)

$$J_s = - D_s \frac{dC_s}{dx}$$

Diffusion coefficient of substance s

Concentration gradient

Distance between two points

According to Fick's law, the time required for a given concentration is a power of the distance J_s = mole /(cm^2 * s)

Diffusion rates according to Fick's law

The time required for a given concentration is a power of the distance

Time		Diff. path	Distance	
microsecond	1μs	Membrane width	10 nm	10^{-8}m
second	1 s	Neuron length (soma)	10 μm	10^{-5}m
2.77 hours	10^{4}s	Axon/dendrite length CNS	1 mm	10^{-3}m
277.7 hours	10^{6}s	Within a tissue/ organ	1cm	10^{-2}m
115740 days	10^{10}s	Communication in the body	1m	1m

Summary diffusion

- Diffusion is effective for particle movement only for a short distance.
- In order to move a diffusional signal along the human body (1 m) it will take decades.
- The common biological solution to increase diffusion rate is by increasing the diffusion area, by folds, cilia, microvilli.

In order to transmit signals to long distances in a short time, we need a different mechanism (clue- electrical activity)

Neurons have excitable membrane

In order to respond to the ever-changing environment, neurons need fast communication

- As **diffusion** is not the fastest pathway to transfer molecules and thus signals, neurons use active transport of ***electrochemical*** signals

  *"**electrochemical signals** are signals in which the information is transmitted through ions (chemical) that carry an electrical charge"*

  Two forces impact ion movement through membranes:

  - Chemical force (concentration gradient)
  - Electrical force (Charge gradient)

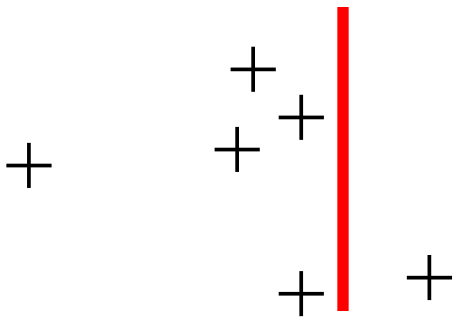
  Both forces create the membrane potential. They are independent of each other and under certain conditions may contradict each other.

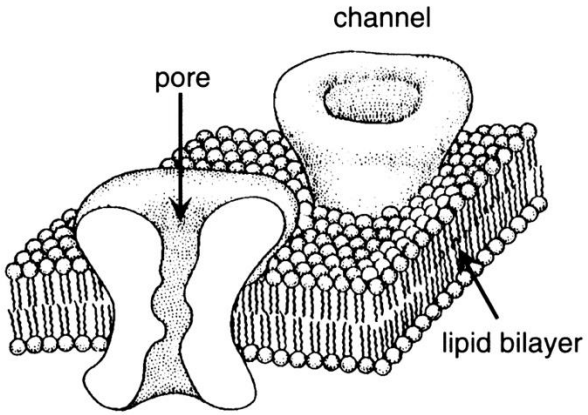
Ions channels and signaling

What are electrochemical signals?

Electrochemical signals (currents) are made of ions flowing into and out of the cell through **ion channels** embedded in the neuronal membrane

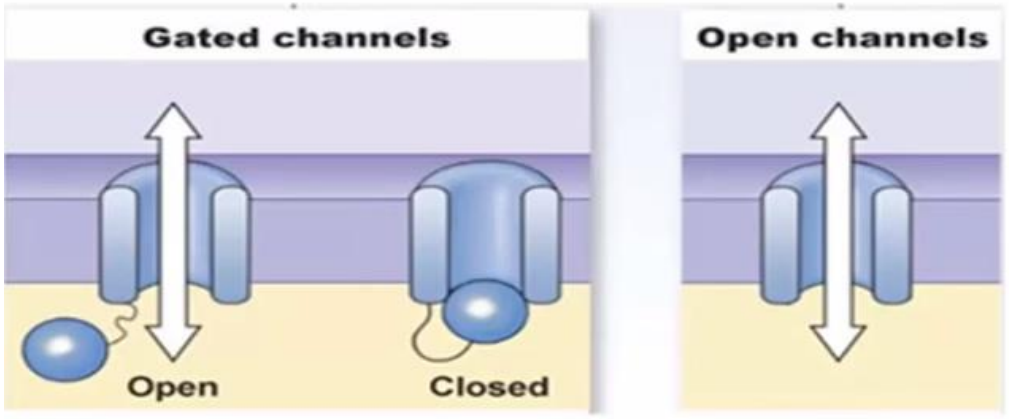
- We have many types of ion channels embedded in the membrane and they all selective to one or few ions.
- Note the difference to *pumps/transporters which are also membrane proteins*
- Ions carry the electrical charge which generate the current flow





Properties of Ion channels

- **Ion channels** are pore-forming membrane proteins that allow high rate of ion (10^6) transport down the electrochemical potential. (unlike pumps with low rate)
- Involved in establishing a **resting membrane potential**, shaping **action potentials** and other electrical signals by **gating** the flow of **ions** across the cell membrane.
- Current flow across the membrane is determined by the amount of time the channels are open and is passive (driven by concentration gradients; uniporters)
- Two types of ion channels: **Leak channels** and **gated channels**



Properties of Ion channels

- **leak channels –** randomly gated with no actual event that opens the channel**.**
- **Gated channels** -opens following a cue, which can be chemical, mechanical or electrical.
- **Channels** experience a conformational change that can either open or close the channel pore.
- Channels have a characteristic ***mean open time***
- Some channels are ***deactivated*** by a stimulus
- Channel ***activation*** or ***deactivation*** means increase or decrease in ***the probability of opening*** following a stimulus (opening time remains random)
- The channel **conductance** depends on two factors: **electrochemical gradient** across the membrane and the **permeability** of the channels to the ion
- **Channel Selectivity** – Most ion channels are specific to one or two ions, but there are channels that are selective to anions/cations and some channels that specific to size

Properties of Ion channels

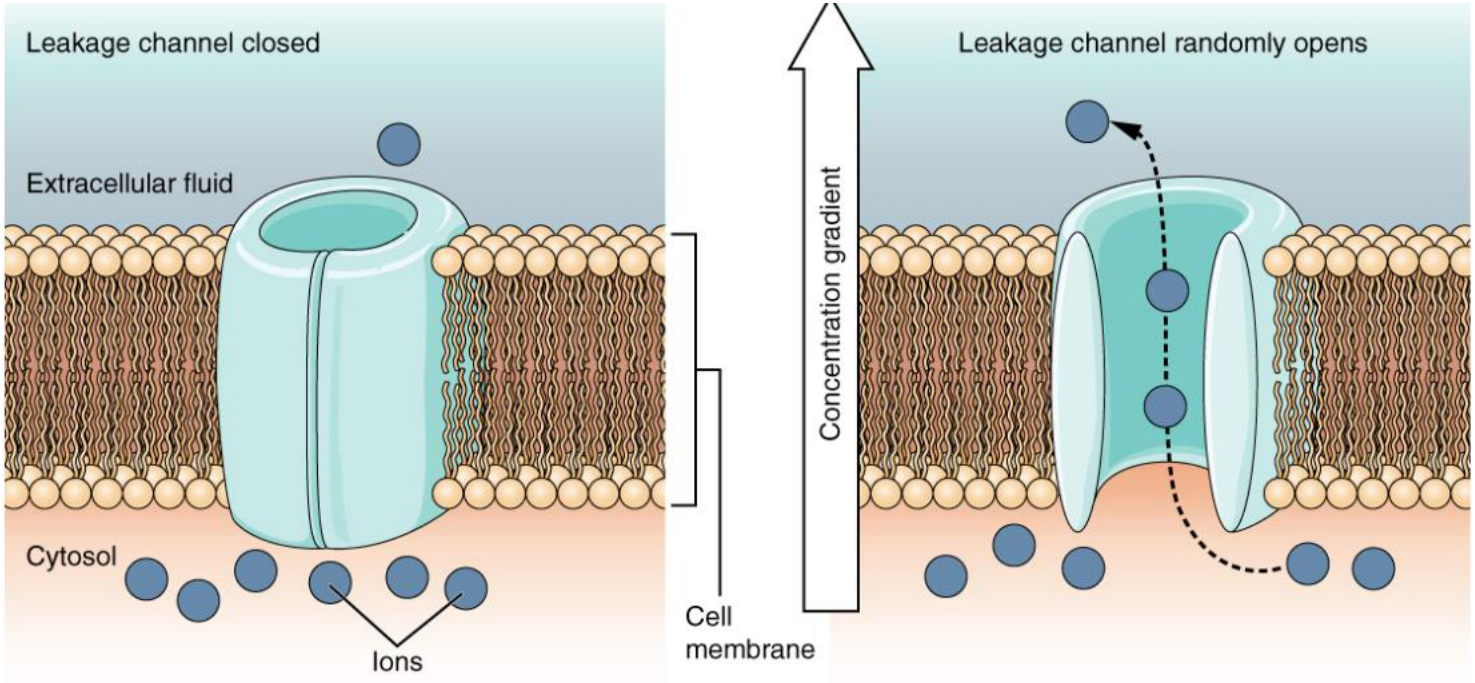
- Channels can go to inactivation state (despite continuous stimulus) that sometimes called ***desensitization*** (while the stimulus last)

- Channels can be between cells (connexons)

Leak channels

Several types of leak channels (Water, K^+, Na^+). As there is no actual event that opens the channel**,** some considered them as constantly open.

The ions will flow according to the electrochemical gradient



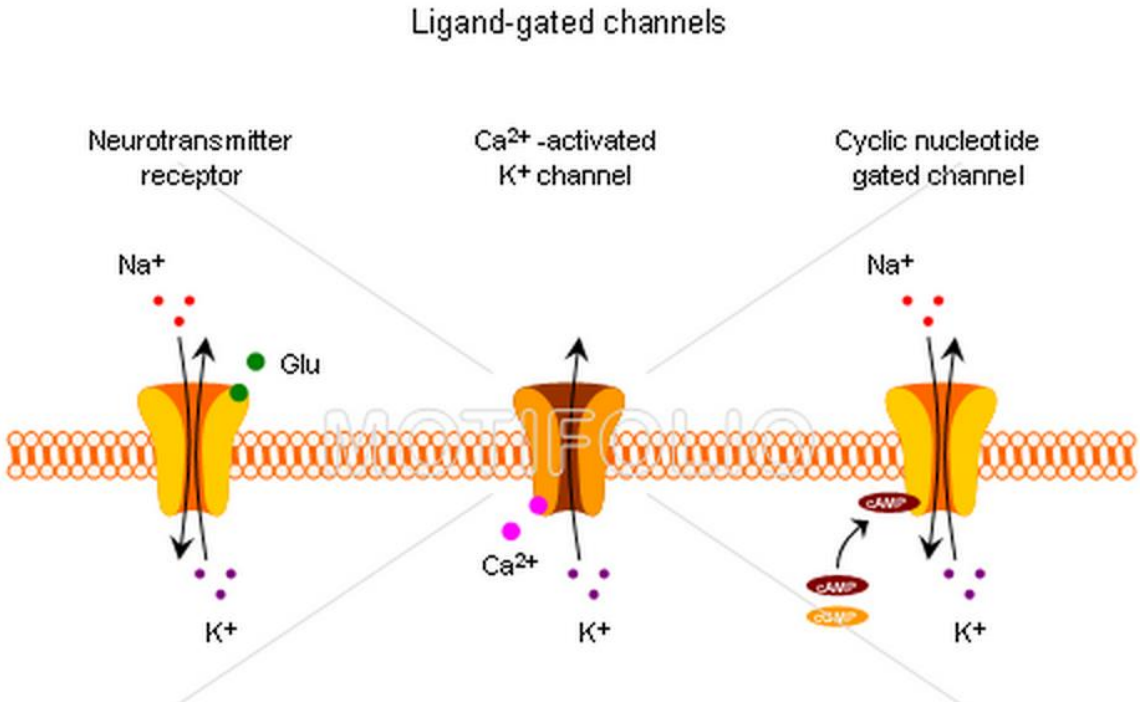
Gated channels

Three types of gated channels – classified according to the stimulus that activates them

ligand gated channels
voltage gated channels
mechanically gated channels

Types of gated channels – Ligand gated

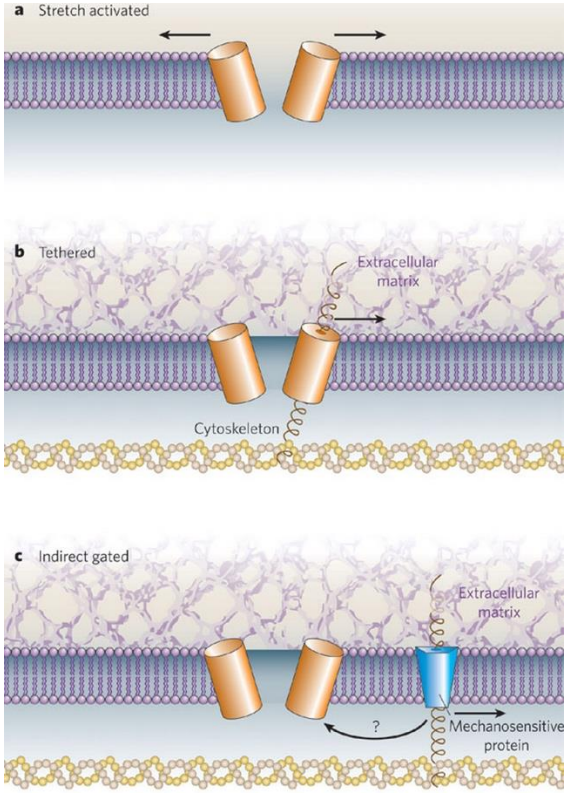
- **Ligand** – a molecule that binds to the channel by non-covalent bonds.
- Ligand gated channels requires the physical connection of the ligand to it's binding site on the channel (also include the "second messengers channels").
- The binding of the ligand to the channel forms a ***conformational*** change that opens the pore site of the channel, which remains open as long as the ligand is connected



Gated channels - mechanical

- **Mechanical** gated channels requires physical activation such as stretch.

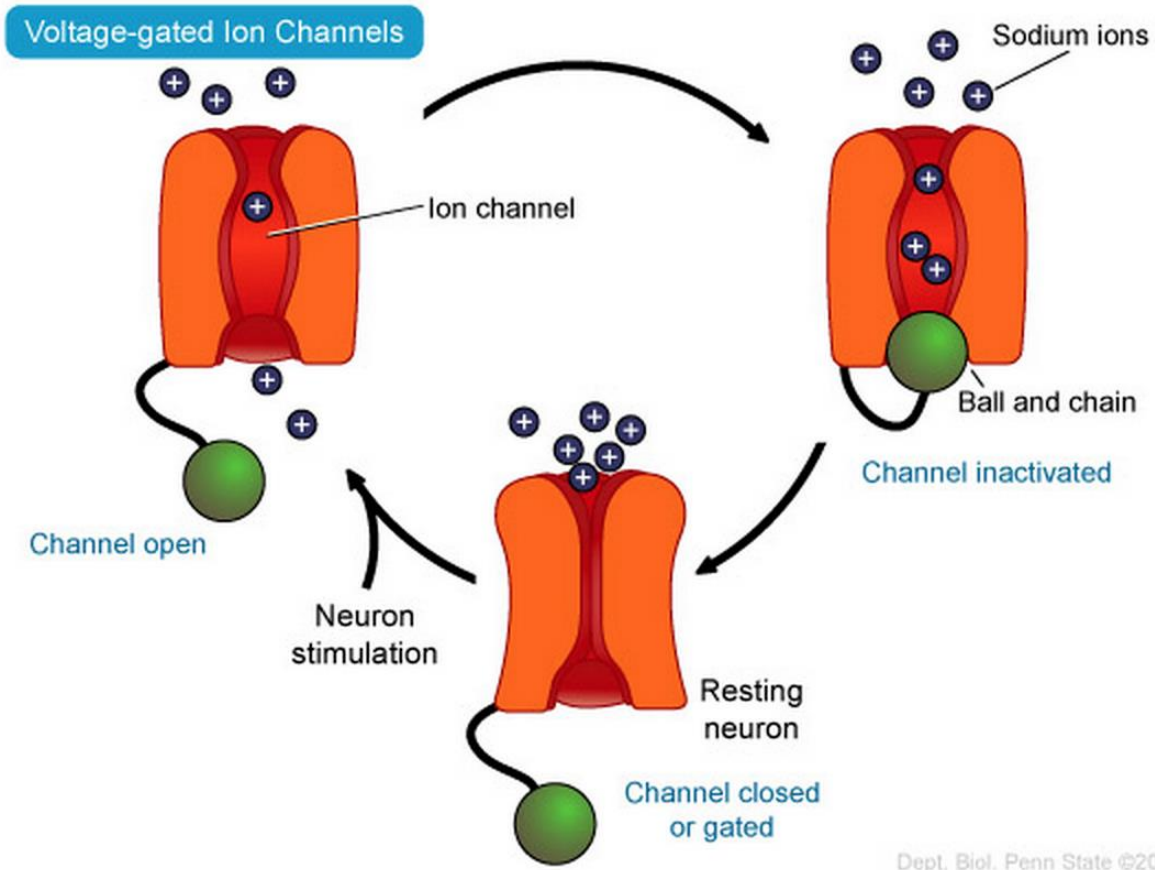
- The stretch leads to mechanical opening of the channel, which remains open as long as the mechanical force is applied



Gated channels - voltage

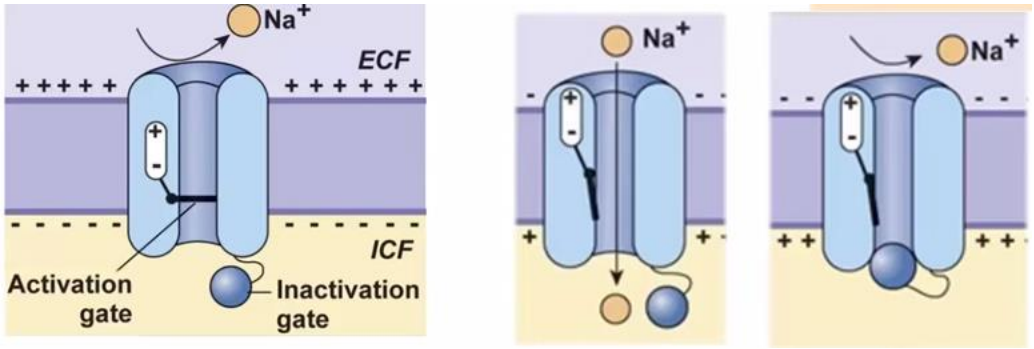
- **Voltage** gated channels that respond to changes in the membrane potential

- The pore is blocked by a charged component. A change in the membrane potential leads to conformational change that open the pore site.



Functional states of ion channels

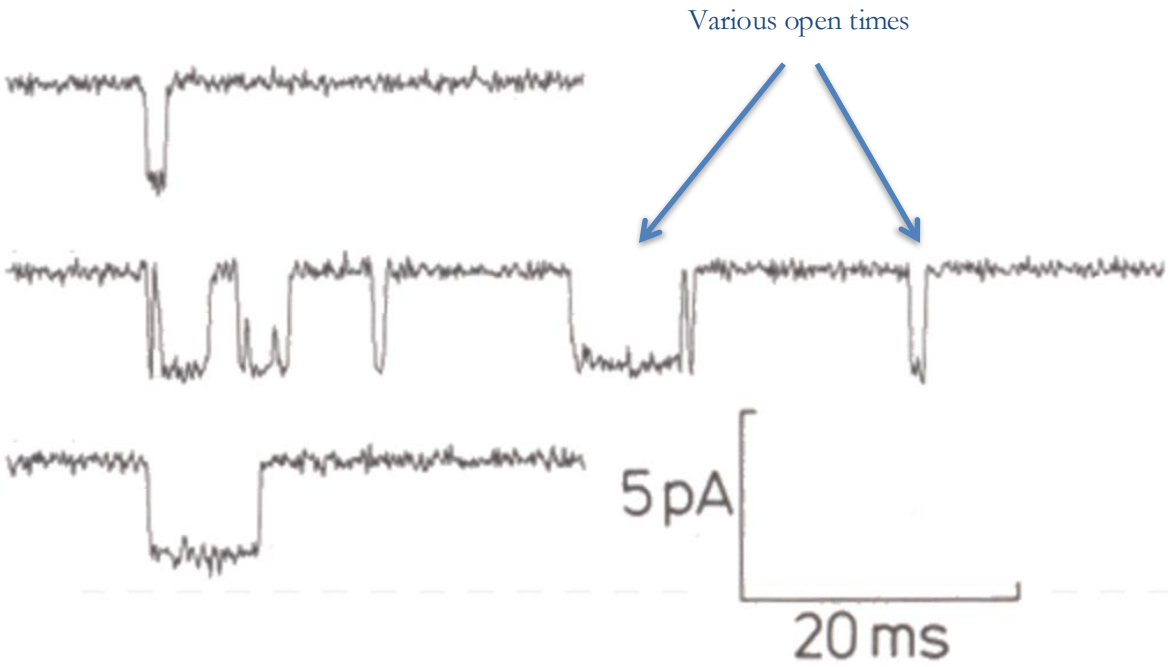
Ion channels can be open, closed or inactivated (only some of them, which are essential for the generation *of action potential*).

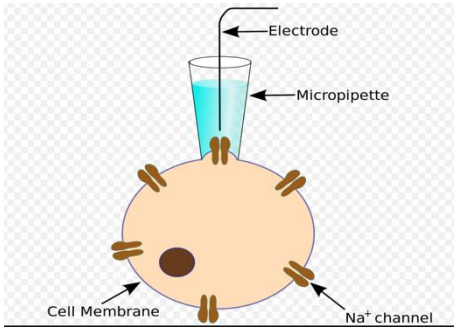


Closed (rest) → Open → Inactivated

Functional states of ion channels

The transition between open and closed states occur ***virtually instantly*** and lead to microscopic currents that can be measured through a patch electrode

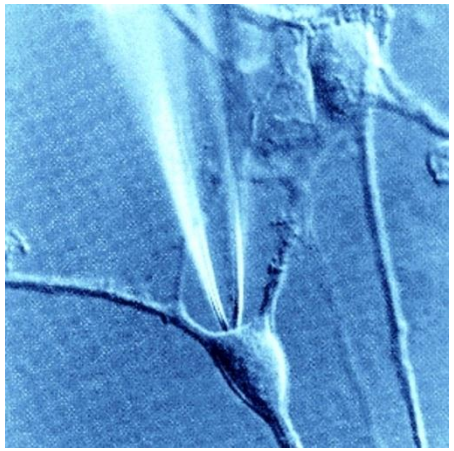




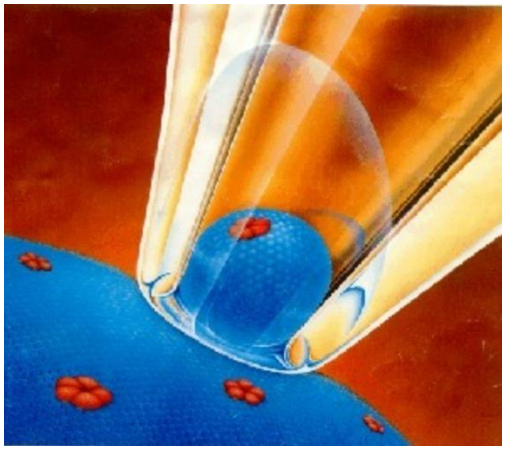
Current flow through ion channels

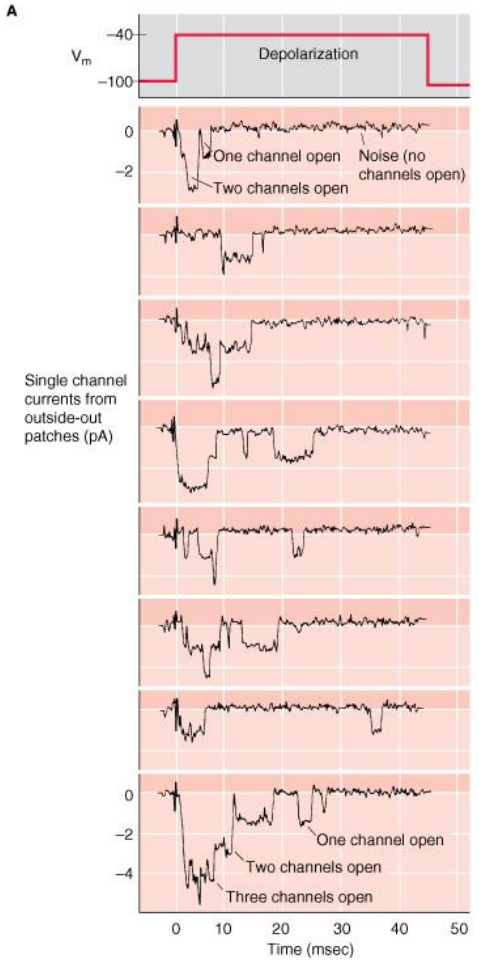
Accumulation of ***microscopic*** currents (single channel) occurring at the same time (stimulus) result in a ***macroscopic current*** (recorded from the whole cell).

Whole cell recording



Single channel recording

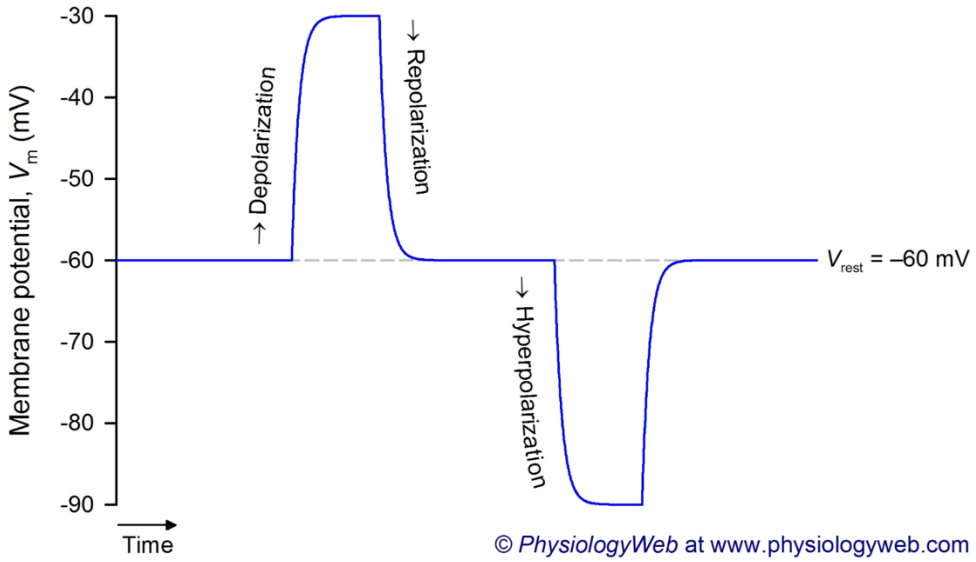




Current flow through ion channels

A current flow through the membrane can lead to:

- **Hyperpolarization** – making the cell membrane potential more negative
- **Depolarization** – making the cell membrane potential less negative



Summary ion channels

- Electrical signals in the nervous system are generated by movement of ions through aqueous pores of membrane proteins known as ion channels
- Channels varies in their selectivity
- Channels fluctuate between open and closed states
- Channels can be classified by their mode of activation: stretch/ voltage/ ligand - activated
- The movement of ions through channels is passive and depends on the concentration gradients and electrical field (The Nernst potential)

Passive and active electrical properties of neurons

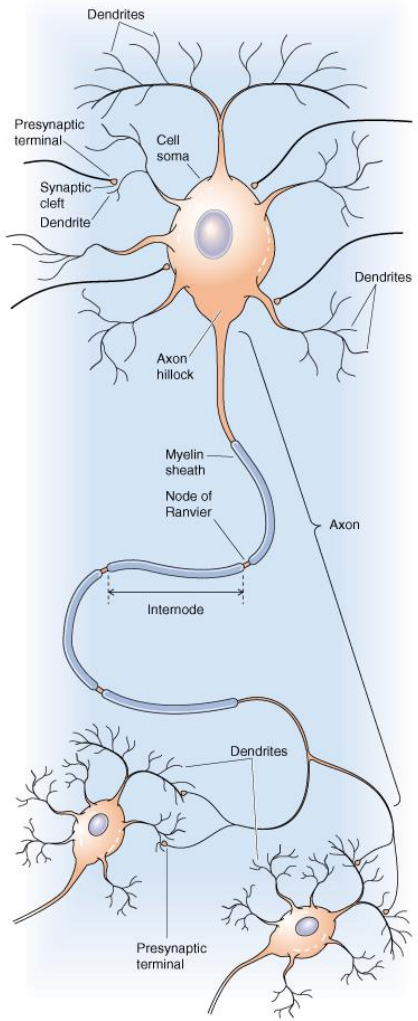
Objectives:

- The ionic basis of the resting membrane potential
- Passive membrane properties
- Active membrane properties and action potential
- Hodgkin-Huxley experiments and model

Excitable membranes

Basic terms about excitable membranes

Resting Membrane potential

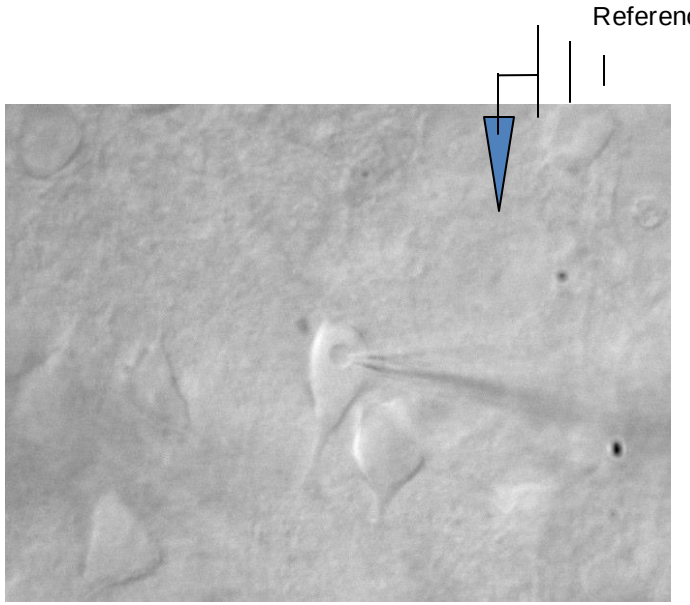


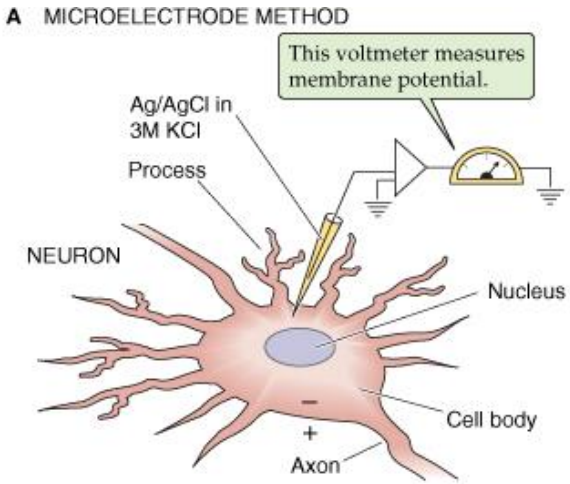
Defined as the potential difference, measured in mV, across a cell membrane. Usually the membrane potential of a neuron is around **-65 mV**.

We refer to the membrane potential as isopotential, although minor differences between compartments do occur.

Membrane potential:

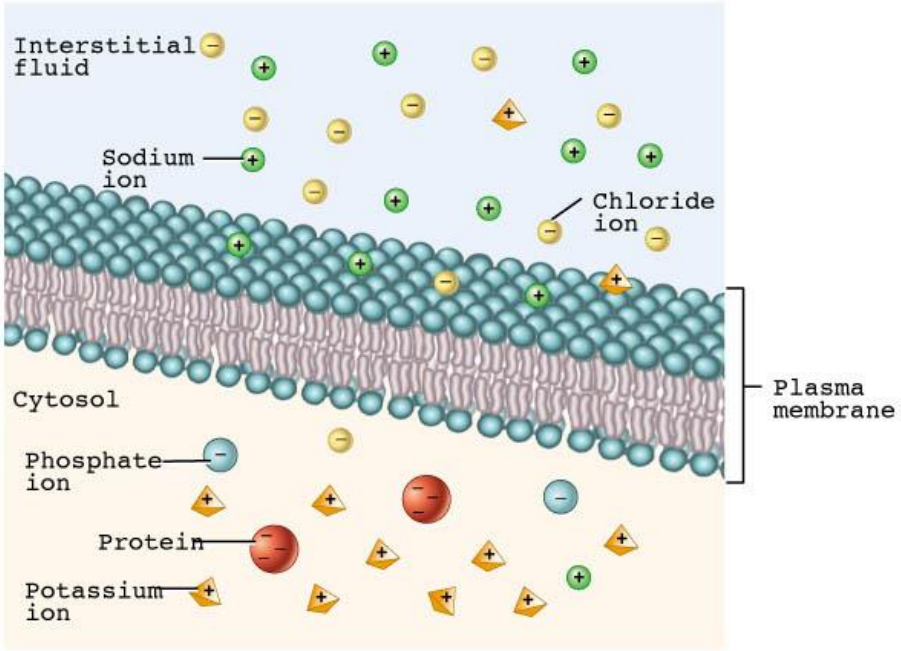
The membrane potential is measured by inserting a microelectrode through the cell membrane and measuring the voltage of the interior relative to the exterior of the cell.





Membrane potential:

The membrane potential is determined by **the relative fluxes of Na^+, K^+ and Cl^- ions** through specific ion channels in the cell membrane



Membrane potential:

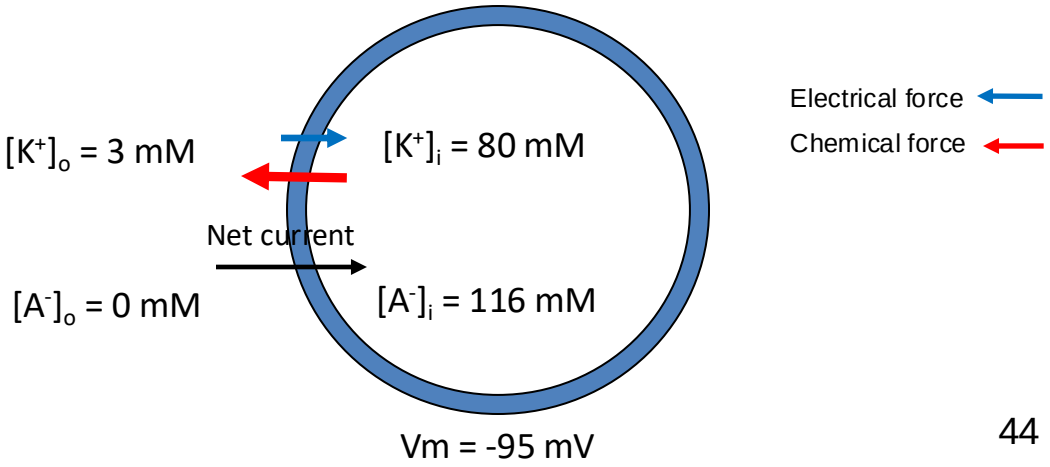
Resting membrane potential depends on the relative conductance (or permeabilities) of the membrane to major ions, and on the equilibrium potential for these ions.

The equilibrium potential (E_i) is the membrane potential at which the **net influx** of a certain ion through the membrane is **zero**. At the **ion** equilibrium potential, its ***electrical gradient*** is equal and opposite to its **chemical concentration gradient** and therefore there is no net ionic flow across the membrane**.** It is the ion "battery", and the ions will always move towards their **(E_i)**.

E_{K+} = -90 mV

E_{Na+} = +47 mV

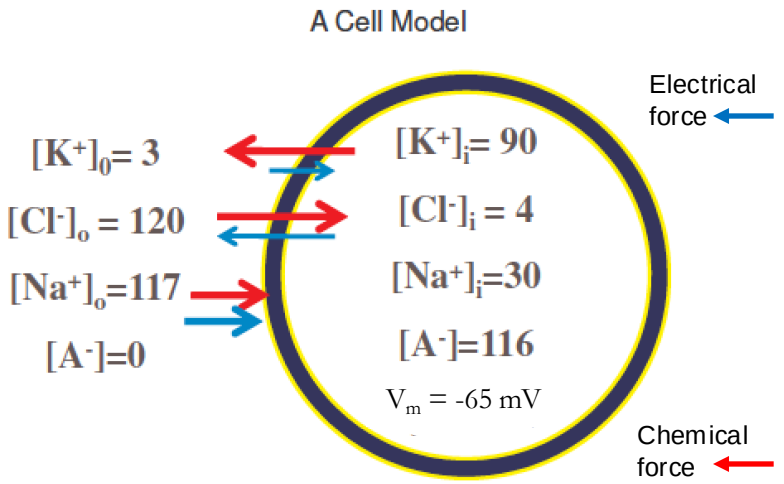
E_{cl-} = -60 mV



Membrane potential:

What happens when the membrane is permeable to more than one ion?

Interior of cell is ~ -65 mV relative to the exterior



How the resting membrane potential stays at -65mV?

The membrane potential is maintained through active transport of Na^+ and K^+ via the Na-K pump

The forces that creates the membrane potential

Nernst equation - equation describing the **Equilibrium potential (E_i)** for a particular ion.

Electrical force Chemical force

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

Walther H. Nernst
1920 – Nobel prize

Equilibrium potential (E_i) - the transmembrane voltage at which the ***electrical gradient (E)*** is equal and opposite to the concentration gradient for a particular ion (no net ionic flow across the membrane) **.** It is the ion "battery", and the ions will always move towards their (E_i).

where **R** is the gas constant, **T** is the temperature in degrees Kelvin, **z** is the valence of the ionic species, and **F** is the Faraday constant.

Good to know (but not must)

PHYSICAL CONSTANTS

Avogadro's number **N** = 6.022×10^{23} mol^{-1}

Elementary charge **e** = 1.6022×10^{-19} C

Farady's constant **F** = 9.648×10^{4} C/mol

Absolute Temperature T (**K**) = 273.16 Celsius

Gas Constant **R** = 1.987 cal K^{-1} mol^{-1} (in energy units) = 8.315 J K^{-1} mol^{-1}

One joule 1J = 1 kg m^2 s^{-2} = 0.2389 cal

Good to know (but not must)

PHYSICAL CONSTANTS

- Mole of atoms contains Avogadro's number (**N**=6.02 x 10^{23}) of protons and same number of electrons
- Quantity of charge (***Q***) is measured in coulombs (C) where the charge of a proton is **e** = 1.6 x 10^{-19} C.
- The charge of 1 Mole of electrons is called the **Faraday Constant**, **F**. It is calculated by multiplying the charge of one electron by the Avogadro **number**.
- Charge can move. A net flow of charges is current **(I)**
- Current is measured in Amperes (Amp = 1 coulomb per second = 6.24 x 10^{18} **e**)
- Electric potential difference is measured by voltage (Volts/(**V**)
- Resistance (**R**) is the opposition to the current flow, measured by Ohms (**Ω**)
- Conductance (**G**) defined as the ease of current flow. Measured in Siemens (**S**) and is opposite of the resistance **G**=1/**R**
- **Ohm's** law – The current (***I***) in amps (A) is equal to the voltage (***V***) in volts (V) divided by the resistance *R* in ohms. V=IR

Nernst equilibrium

Back to the model cell ...

$$E_X = \frac{RT}{zF} \ln \frac{[X]_2}{[X]_1}$$

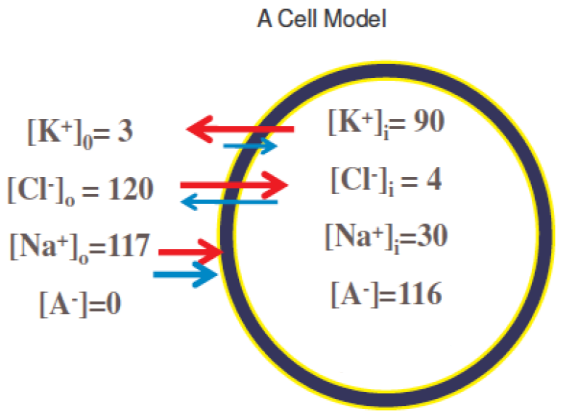
$\mathbf{E_x}$ = V_1-V_2 - The potential in compartment 1 relative to compartment 2

When T is room temperature (20 C^0) and when the natural logarithm is replaced with base 10 logarithm the equation can be simplified to:

$$E_X = \frac{58}{z} \log \frac{[X]_2}{[X]_1}$$

Thus, the Equilibration potential for K^+ in our model cell is

$$E_k = 58 \log \frac{3}{90} = -85mV$$



Nernst equilibrium

From Nernst equation, one can see that the ionic equilibrium is highly dependent on the Ion concentrations and temperature.

At room temperature (20 C^0) $\frac{RT}{zF}$ = 58 mV; at body temperature (37 C^0) $\frac{RT}{zF}$= 61 mV

Ion	Symbol	The Nernst equation
Potassium	K+	$E_k = 61.54\times10^{-3}\log \frac{[K+]_o}{[K+]_i}$
Sodium	Na+	$E_{Na} = 61.54\times10^{-3}\log \frac{[Na+]_o}{[Na+]_i}$
Choline	Cl-	$E_{Cl} = -61.54\times10^{-3}\log \frac{[Cl+]_o}{[Cl+]_i}$
Calcium	Ca^2+	$E_{Ca} = 30.77\times10^{-3}\log \frac{[Ca+]_o}{[Ca+]_i}$

Nernst equilibrium

Typical ionic concentration and gradients (can vary between cells)

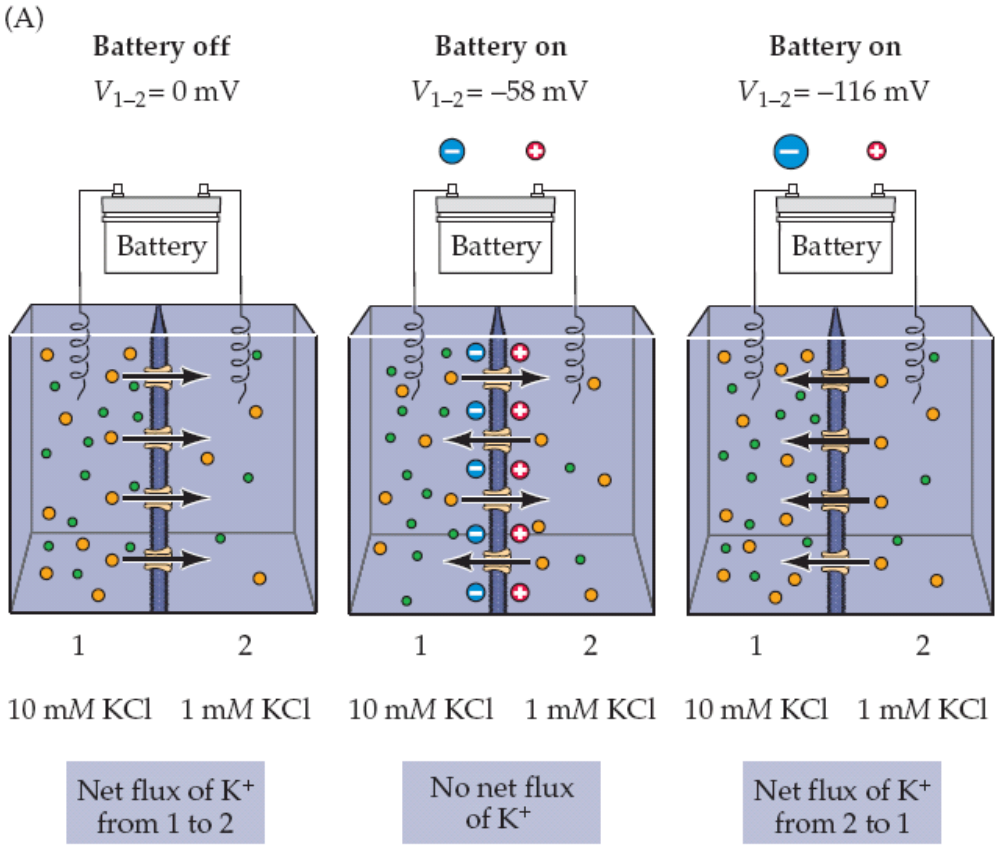
Ion	Extracellular concentration (mM)	Intracellular concentration (mM)	E_{nernst} (mV) at 37 C^0
Na^+	145	12	+67
K^+	4.5	155	-95
Ca^{2+}	1.2	10^{-4}	+123
Cl^-	116	4.2	-89

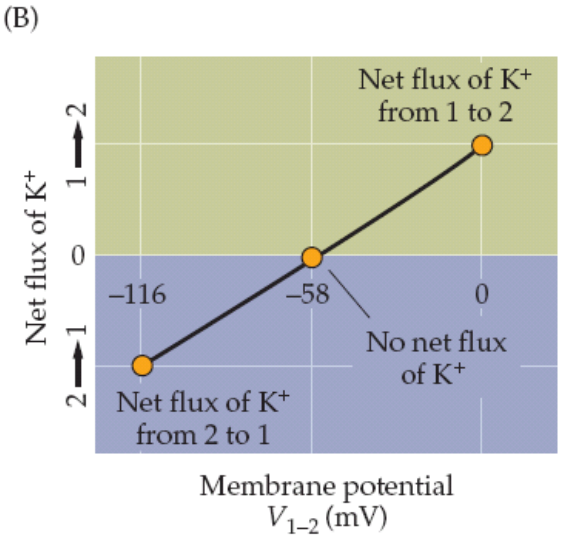
Nernst equilibrium

How the ionic flux will behave once we will change the membrane potential?

Nernst equilibrium

The effect of voltage on current flow through a permeable selective membrane





The driving force = V_m-V_{eq}

Thus

Current is proportional to V_m-V_{eq}

When the membrane potential is forced by a battery that is more negative than its Nernst potential, ions move into the cell (from 2 to 1) since they are driven more by the negative field. When the potential is more positive than the Nernst potential they move from 1 to 2.

Nernst equilibrium

Example of problems (might be in the quiz)

1. The external concentration of Na^+ is 20 times larger than the concentration inside the cell. What is the equilibrium potential of Na^+ at 20 C^0?

$$E_{Na} = 58 \log \frac{20}{1} = 58 * 1.3 = 75.4 mV$$

2. A membrane is permeable only to chloride, the equilibrium potential is -60 mV and you were asked to reduce it by 10 mV by changing the concentration outside (side 2). Assuming that the concentration inside (compartment 1) is 10 mM, what should be the new concentration of Cl^- outside?

$$E_{Cl} = -58 \log \frac{x}{10} = -70 mV$$

$$\frac{x}{10} = 10 \wedge 1.2069 = 16.102$$

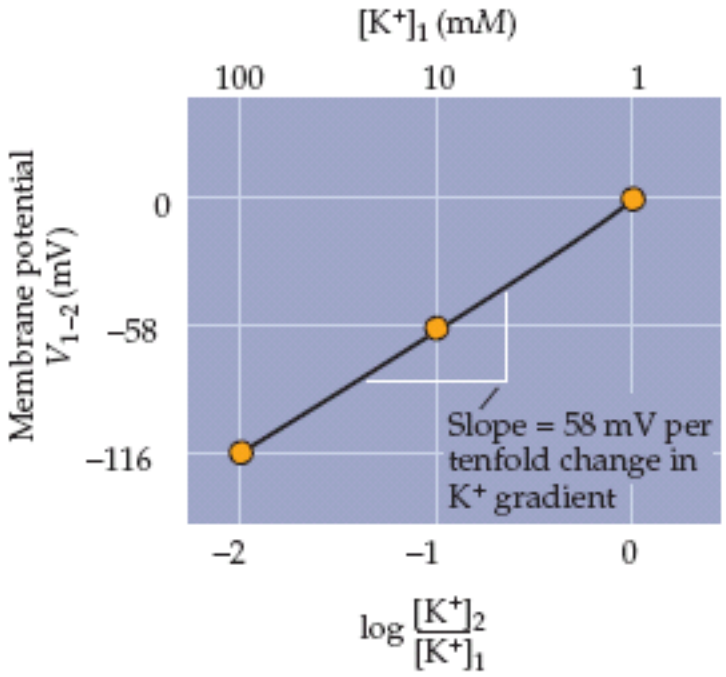
$$\log \frac{x}{10} = \frac{-70}{-58} = 1.2069$$

$$x = 161.02 \text{ mM}$$

Resting membrane potential

According to Nernst equation:

The relation of voltage and concentration are such that for every 10 fold change in K^+ gradient the slope will be equal to 58 mV (at 20 Celsius).



$$E_X = \frac{58}{z} \log \frac{[X]_2}{[X]_1}$$

($[K^+]_2$ is 1 mM)

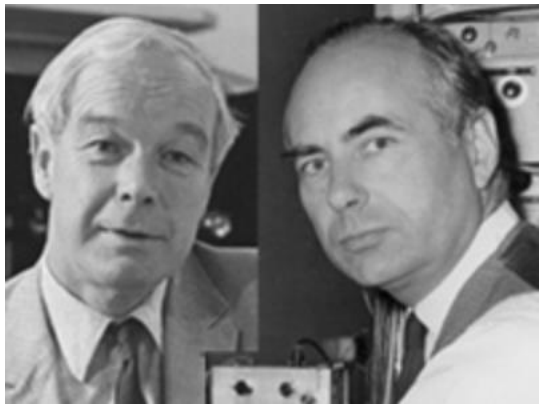
Nernst equilibrium

Remember:

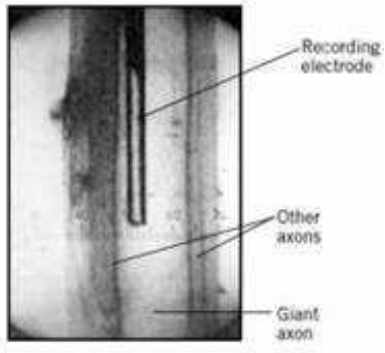
- At Nernst equilibrium, the net influx of the ions is 0 as the electrical and chemical forces opposing and canceling each other.
- If the membrane is not permeable to any ion, there will be no current
- If the valence of ion is 2 (like Ca^{2+}), the potential across the membrane will be half of the univalence ion (hence 29 mV at room temperature)
- If the membrane is permeable to only one ion, its equilibrium potential will be equal to the membrane potential

Resting membrane potential

What will be the electrochemical equilibrium when the membrane is permeable to more than one ion? **This is exactly what H&H asked**



"it's the squid that really ought to be given the Nobel Prize"
Hodgkin, A.L., 1973



- Alan L. Hodgkin and Andrew F. Huxley first to record **resting membrane potential** from living neuron using an amplifier at 1939
- Used squid giant axon because 0.5 mm in diameter
- Electrode inserted longitudinally, so that tip far from injured point of entry, which was tied off to prevent loss of ions from interior of cell

Resting membrane potential

Julius Bernstein
(1839-1917)

The first physiologist to suggest that resting potential exists across neuronal membrane

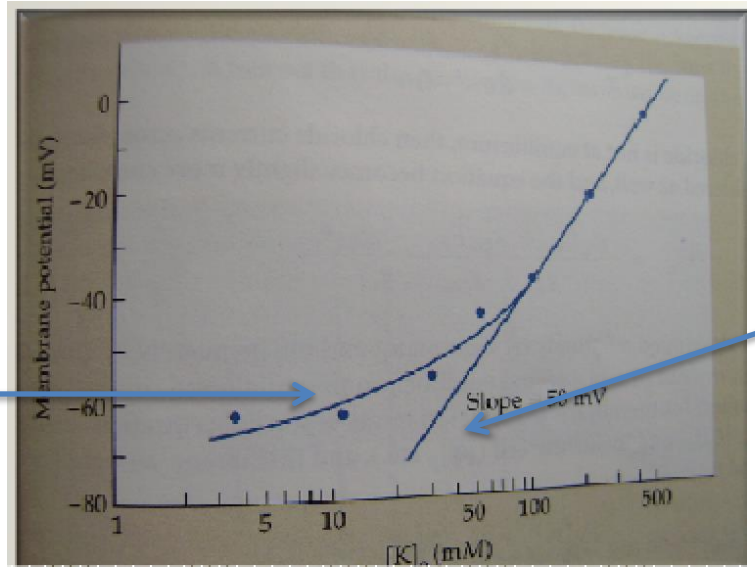
The "Bernstein hypothesis" postulated that nerves are normally polarized with positive ions on the outside and negative ions inside and that the current he measured was the change in this polarization.

Resting membrane potential

In 1902, ***Julius Bernstein*** proposed that

"the resting membrane potential (or "membrane breakdown") is the result of an ***unequal distribution of K^+ ions*** *between the extracellular to the intracellular fluids"*

Therefore – **H&H** Changed the extracellular K^+ concentration by 10 folds, expecting to see a change of the membrane potential by 58mV



Reality

Expected slope

The experimental results of H&H were different….why?

Resting membrane potential

Hodgkin – Huxley conclusions:

- The membrane potential is strongly, but not exclusively dependent on the potassium concentration ratio.
- Why the Nernst equation does not "work" ?
  The previous assumption of no permeability to sodium ions is **NOT** correct
- A real cell membrane has a permeability to sodium that ranges between 1-10% of its permeability to potassium
- As there is no permeability ratio in Nernst equation (the ratio permeability is 100% as there is only one ion), a more elaborated equation is needed…

Goldman Hodgkin Katz (GHK) equation (1943)

Goldman equation - Resting membrane potential (V_m) depends on the **relative conductances** (or permeabilities) of the membrane to the major ions (Na^+, K^+ and Cl^-), and on the **equilibrium (Nernst) potential** for these ions, which determine their fluxes through the membrane.

$$V = 58 \log \frac{P_K [K]_2}{P_K [K]_1}$$

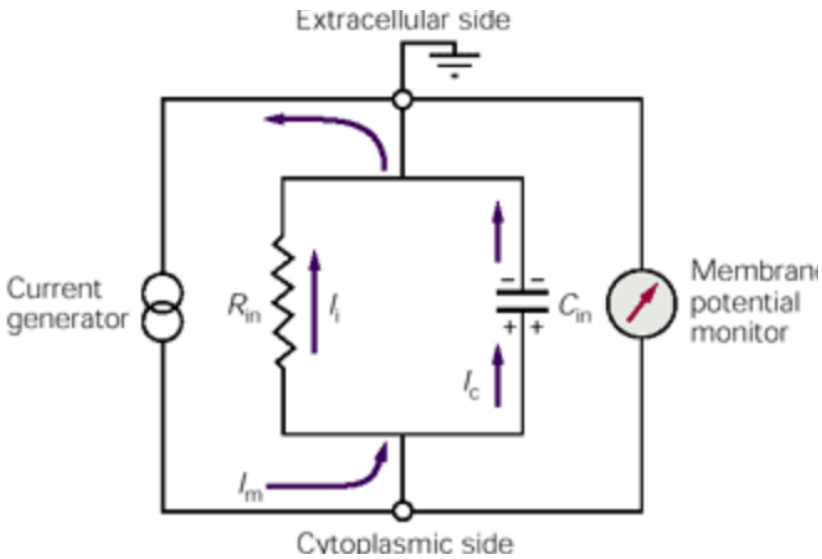
Nernst equation

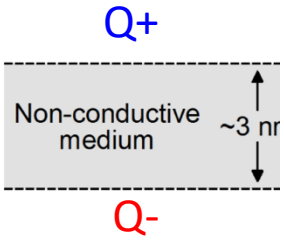
- GHK equation is an extended version of the Nernst equation.
- When the membrane is permeable to only one ion, GHK = Nernst
- The valence factor (z) has been eliminated in GHK , hence the concentration gradient of the negative ion Cl^- has been inverted
- At a stable condition, the net current of each individual ion will be zero

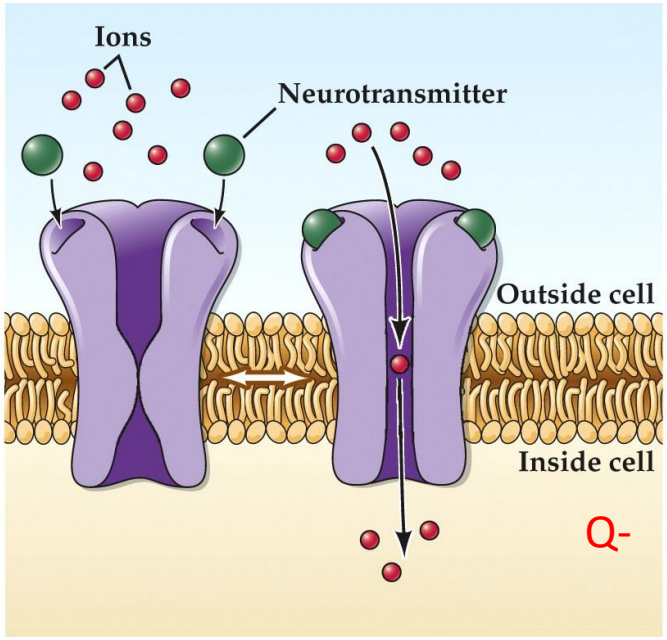
Passive membrane properties Equivalent electrical circuit

One way of looking on membranes is as an electrical circuit

The neuronal membrane act as an RC circuit, in which the phospholipid bilayer is the "**C**apacitor" and the ion channels are the "**R**esistors".







An **electric current** is a flow of electric charge. In neurons the electric charge is carried by ions through ion channels, hence resistors

Passive membrane properties Equivalent electrical circuit

- If a membrane act as an ***electrical circuit***, we can use "electrical" equations to calculate currents and conductances through the membrane, which are easier to measure than permeability and ion movement.

- ***Conductance*** depends on concentration as well as permeability. For example, permeability could be high (many open channels) but if only a few ions are present, then that ion species can't carry much current.

- Permeability and conductance are related but not the same.

  Permeability is the ease with which an ion can pass through the membrane.
  Conductance is the ability of a given ion to carry electrical current across the membrane.

- Currents are measured and conductances calculated in voltage or patch clamp.

- Measuring permeability requires some way of observing ion movement itself. In practice, neurophysiologists generally use the "***equivalent electrical circuit***" method because it involves parameters that are more readily available.

Membrane as a Capacitor Equivalent electrical circuit

Physics 101

Capacitance is measured in Farad (***F***). One farad is the capacitance of a capacitor when charged with one coulomb of electricity, and there is a potential difference of one volt.

Cap*acitance* ***C=Q/V*** (Coulomb/Volt) = 1 Farad

Charge ***Q=C*V*** (Coulomb)

Current ***dQ/dt= I*** (coulomb/sec) = 1 Amp

The current flowing through a capacitor

$$I = C * \frac{dV}{dt}$$

Changes of voltage over time

Ohm’s law

Physics 101

There is a direct proportionality between the potential difference (voltage) applied across a conductor and the resultant electric current. This relationship is known as ***Ohm's law***.

$$V=I*R$$

Georg Simon Ohm
1789 – 1854

V=Voltage - electric potential difference (Volts/V)

I= Current – flow of electric charge (Amperes/A)

R=Resistance – opposition to current flow (Ohms/Ω)

G = Conductance – Inverse of resistance (G=I/R), measured in Siemens (S)

Passive membrane properties Equivalent electrical circuit

From Ohm's law $V = IR$ or $I = gV$

As the ***driving force*** for a certain ion is the difference between the membrane potential (V_m) to its equilibrium potential (E_i), we can write the equation as

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

Resting membrane potential

Nernst equilibrium potential

From Kirchhof law, at resting membrane potential $I_m = 0$

$$I_K + I_{Na} + I_{cl} = I_m = 0$$

Therefore

$$g_{Na}(V_m - E_{Na}) + g_K(V_m - E_K) + g_{Cl}(V_m - E_{Cl}) = I_m = 0$$

Passive membrane properties Equivalent electrical circuit

$$g_{Na}(V_m - E_{Na}) + g_K(V_m - E_K) + g_{Cl}(V_m - E_{Cl}) = I_m = 0$$

If we will rescue the V_m , we will get the ***constant field equation***

$$V_m = \frac{g_{Na} * E_{Na} + g_{Na} * E_{Na} + g_{Cl} * E_{Cl}}{g_{Na} + g_K + g_{Cl}}$$

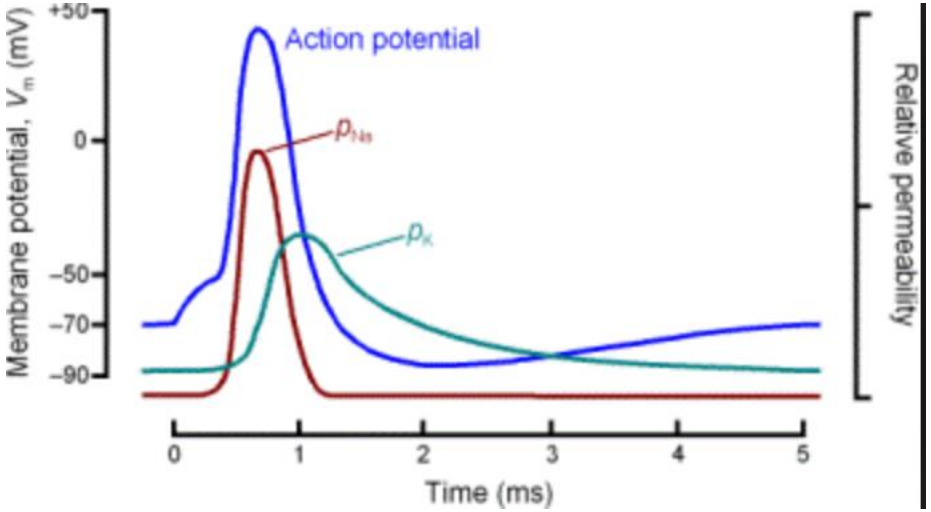
Which is equivalent to GHK equation

$$V = 58 \log \frac{P_K[K]_2 + P_{Na}[Na]_2 + P_{Cl}[Cl]_1}{P_K[K]_1 + P_{Na}[Na]_1 + P_{Cl}[Cl]_2}$$

Resting membrane potential

What would happen if the membrane permeability to Na^+ will increase?

$$V = 58 \log \frac{P_K[K]_2 + P_{Na}[Na]_2 + P_{Cl}[Cl]_1}{P_K[K]_1 + P_{Na}[Na]_1 + P_{Cl}[Cl]_2}$$



Further reading

From neuron to brain – chapters 4,8 “Ion channels and signaling”
Neuroscience – chapters 1, 2

Check point