

# Nernst Potential Lecture 5

Sept 18, 2019

- ion wants to equilibrate concentration and pull it down (charge gradient)

## Eg. Potential

- current is due to to concentration gradient balanced by electrical gradient, it's at eq. potential
- Eg potential = Nernst potential

## Nernst Potential

$$\frac{\mu_0^X + KT \ln[X]_i}{\text{chemical potential}} + \frac{z_F F V_i}{\text{electrical potential}} = \text{electrochemical potential}$$

$$V_m = \frac{RT}{z_F F} \ln \frac{[X]_o}{[X]_i} = E_{ion}$$

F = faraday constant

R = gas constant

T = abs. temp in K

z = valence of ion

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

$$E_{ion} = 2.303 \frac{RT}{zF} \log \left( \frac{C_{out}}{C_{in}} \right)$$

$$2.303 \times \frac{RT}{F} = 60 \text{ mV}$$

$$E_{K^+} = 60 \text{ mV} \log \left( \frac{K_o}{K_i} \right)$$

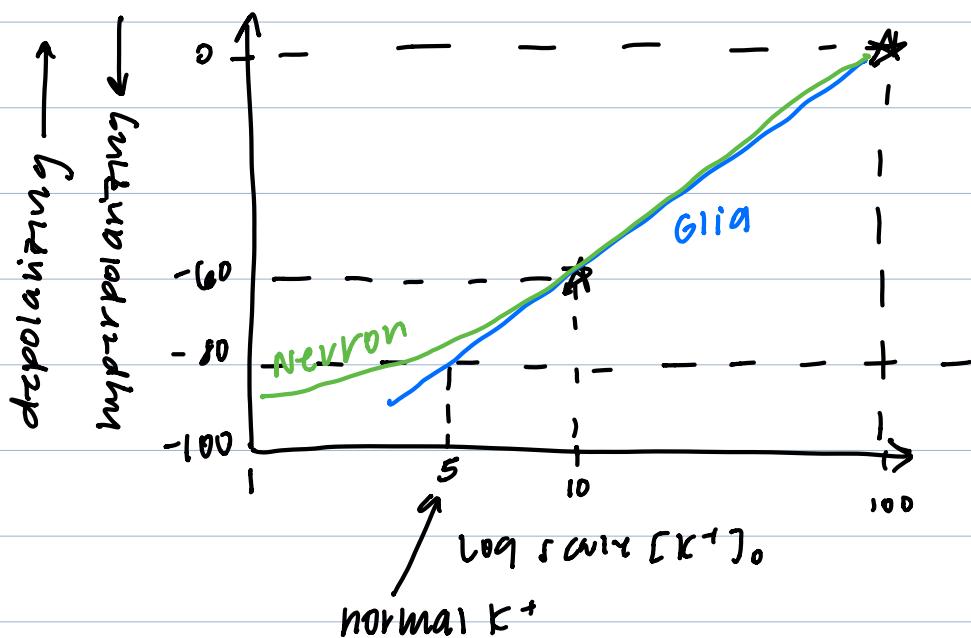
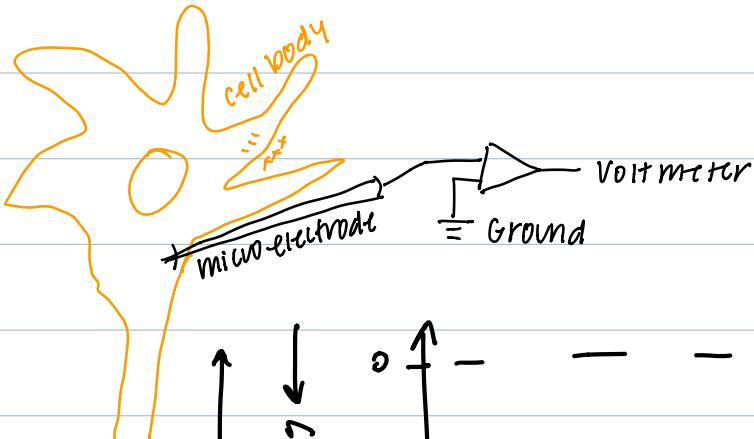
$$E_{Cl^-} = -60 \text{ mV} \log \left( \frac{Cl_o}{Cl_i} \right)$$

$$\text{Formula: } E_{ion} = \frac{60}{z} \log \left( \frac{C_{out}}{C_{in}} \right)$$

## Nernst Potential Ions

outside conc.	inside conc.	ratio out: in	Eg pot (37°C)
K <sup>+</sup>	5 mM	107 mM	-80 mV
Cl <sup>-</sup>	150 mM	13 mM	-65 mV

$\text{Na}^+$	150 mM	15 mM	10 : 1	60 mV
$\text{Ca}^{++}$	2 mM	0.0002 mM	10,000 : 1	120 mV



Goldman-Hodgkin-Katz (GHK) Equation

$$V_{\text{memb}} = \frac{RT}{F} \ln \left( \frac{P_{\text{K}^+} [\text{K}^+_{\text{out}}] + P_{\text{Na}^+} [\text{Na}^+_{\text{out}}] + P_{\text{Cl}^-} [\text{Cl}^-_{\text{out}}]}{P_{\text{K}^+} [\text{K}^+_{\text{in}}] + P_{\text{Na}^+} [\text{Na}^+_{\text{in}}] + P_{\text{Cl}^-} [\text{Cl}^-_{\text{in}}]} \right)$$

In neurons:  $P_{\text{K}^+} : P_{\text{Na}^+} : P_{\text{Cl}^-} = 1 : 0.025 : 0.45$

Nernst:

- eq. w/ net efflux and influx equal

GHK:

- steady state vs not equilibrium condition

Sodium-Potassium Pump

- 70% of ATP consumption

- $3\text{Na}^+$  out,  $2\text{K}^+$  in

## Lecture 5 - Resting Membrane Potential

Pre-class notes for September 19, 2018

Reading: *Neuroscience* by Purves et al., pages **42-46**

If you know the internal and external concentrations of a permeant ion (i.e. one that is freely diffusible across the membrane)- you can calculate what membrane potential ( $V_{mem}$ , or electrical gradient) is needed to maintain that particular concentration gradient by exactly offsetting the diffusional force. This calculation does not explain either 1) how a particular concentration gradient came about or 2) what is the cause of the electrical gradient. But rather it explains what is the membrane potential when a given ion concentration can be maintained in equilibrium. Because typical membrane potentials are negative, there are special terms neuroscientists use to discuss the membrane potential.

**Depolarization** - when the membrane potential of a neuron becomes more positive (or less negative).

**Hyperpolarization** - when the membrane potential of a neuron become more negative.

For a single ion type, we can calculate the **Equilibrium Potential** or **Nernst Potential**, which is the membrane potential when forces caused by the concentration gradient of a particular ion and the cell's electrical gradient are equal and opposite. The equilibrium potential can be determined by the Nernst Equation. At the equilibrium potential there is no net flow (current) for that ion.

**Nernst Equation** - used to calculate equilibrium potential for a single ion species ( $E_{ion}$ ).

Depends on the *concentration ratios* of the ions.

$$E_{ion} = \frac{RT}{zF} \ln \frac{[C_{out}]}{[C_{in}]} \quad \longrightarrow \quad E_{ion} = \frac{60mV}{z} \log \frac{[C_{out}]}{[C_{in}]}$$

- R = gas constant (8.31 J/K\*mol)
- T = absolute temperature in degrees Kelvin ( $^{\circ}\text{C} + 273 = \text{K}$ )
- z = valence of ion (i.e. +1, +2 or -1)
- F = Faraday constant (96,500 C/mol)
- to convert natural logs (ln) to base 10 (log) multiply by 2.303  
 $\ln x = 2.303 * \log x$
- at body temp ( $37^{\circ}\text{C}$ ), **2.3RT/F = 60 mV**

Typical concentrations in neurons (do your own calculations to find  $E_{ion}$ ):

Ion	Outside Concentration	Inside Concentration	Ratio O:I	$E_{ion}$ (mV)
Potassium	$[\text{K}^+]_{\text{out}} = 5 \text{ mM}$	$[\text{K}^+]_{\text{in}} = 100 \text{ mM}$	1:20	$E_K \approx -80_-$
Chloride	$[\text{Cl}^-]_{\text{out}} = 150 \text{ mM}$	$[\text{Cl}^-]_{\text{in}} = 13 \text{ mM}$	11.5:1	$E_{\text{Cl}} = \underline{\hspace{2cm}}$
Sodium	$[\text{Na}^+]_{\text{out}} = 150 \text{ mM}$	$[\text{Na}^+]_{\text{in}} = 15 \text{ mM}$	10:1	$E_{\text{Na}} = \underline{\hspace{2cm}}$
Calcium	$[\text{Ca}^{++}]_{\text{out}} = 2 \text{ mM}$	$[\text{Ca}^{++}]_{\text{in}} = 0.0002 \text{ mM}$	10,000:1	$E_{\text{Ca}} = \underline{\hspace{2cm}}$

Glia are typically permeable to only potassium, thus the membrane potential of a glial cell is equal to the the equilibrium potential of K<sup>+</sup> (approximately -80 mV). Neurons however, are permeable to Na<sup>+</sup> and Cl<sup>-</sup> in addition to K<sup>+</sup>. In order to calculate the resting potential in a neuron, we need to take into account the roles of multiple ions that have permeabilities- the Goldman Hodgkin Katz equation is one way to do this. Typical neuronal permeabilities at rest:

$$P_K : P_{Na} : P_{Cl} = 1 : 0.025 : 0.45$$

**Resting Potential** - The membrane potential of a neuron at rest (no action or receptor potentials). Typically ~ -65 mV.

#### Goldman-Hodgkin-Katz (GHK) Equation

- Used to calculate the membrane potential if a cell is *permeable* to multiple ions.

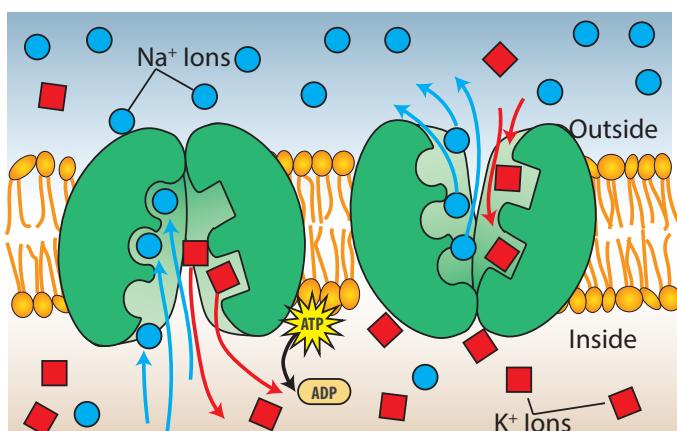
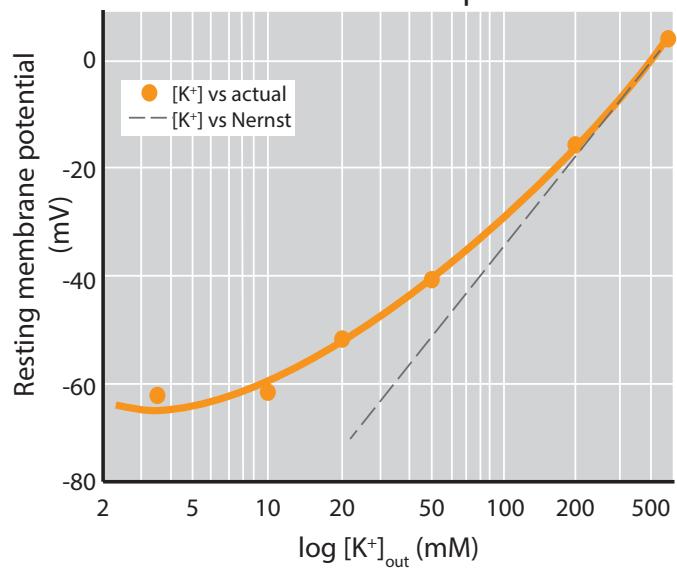
$$V_{memb} = \frac{RT}{F} \ln \frac{P_{K^+}[K_{out}^+] + P_{Na^+}[Na_{out}^+] + P_{Cl^-}[Cl_{in}^-]}{P_{K^+}[K_{in}^+] + P_{Na^+}[Na_{in}^+] + P_{Cl^-}[Cl_{out}^-]}$$

$$V_{memb} = 60mV * \log \frac{P_{K^+}[K_{out}^+] + P_{Na^+}[Na_{out}^+] + P_{Cl^-}[Cl_{in}^-]}{P_{K^+}[K_{in}^+] + P_{Na^+}[Na_{in}^+] + P_{Cl^-}[Cl_{out}^-]}$$

Since the membrane of a glial cell is permeable to only K<sup>+</sup> and the membrane potential is equal to the Nernst potential of K<sup>+</sup>, a glia potential is at **Equilibrium** (when a system has stabilized and all competing forces are balanced without any additional energy expended). At a neuron's resting potential however, none of the ions are at their equilibrium potential. Na<sup>+</sup> will continue to move into the cell down its concentration and electrical gradient and K<sup>+</sup> will continue to leave the cell down its concentration and electrical gradient, thus the cell is at a **Steady State** - when a system is stabilized and concentrations remain constant, but forces may or may not be in equilibrium, some action (in neurons ATP driven Na/K pump) may be needed to remain at steady state.

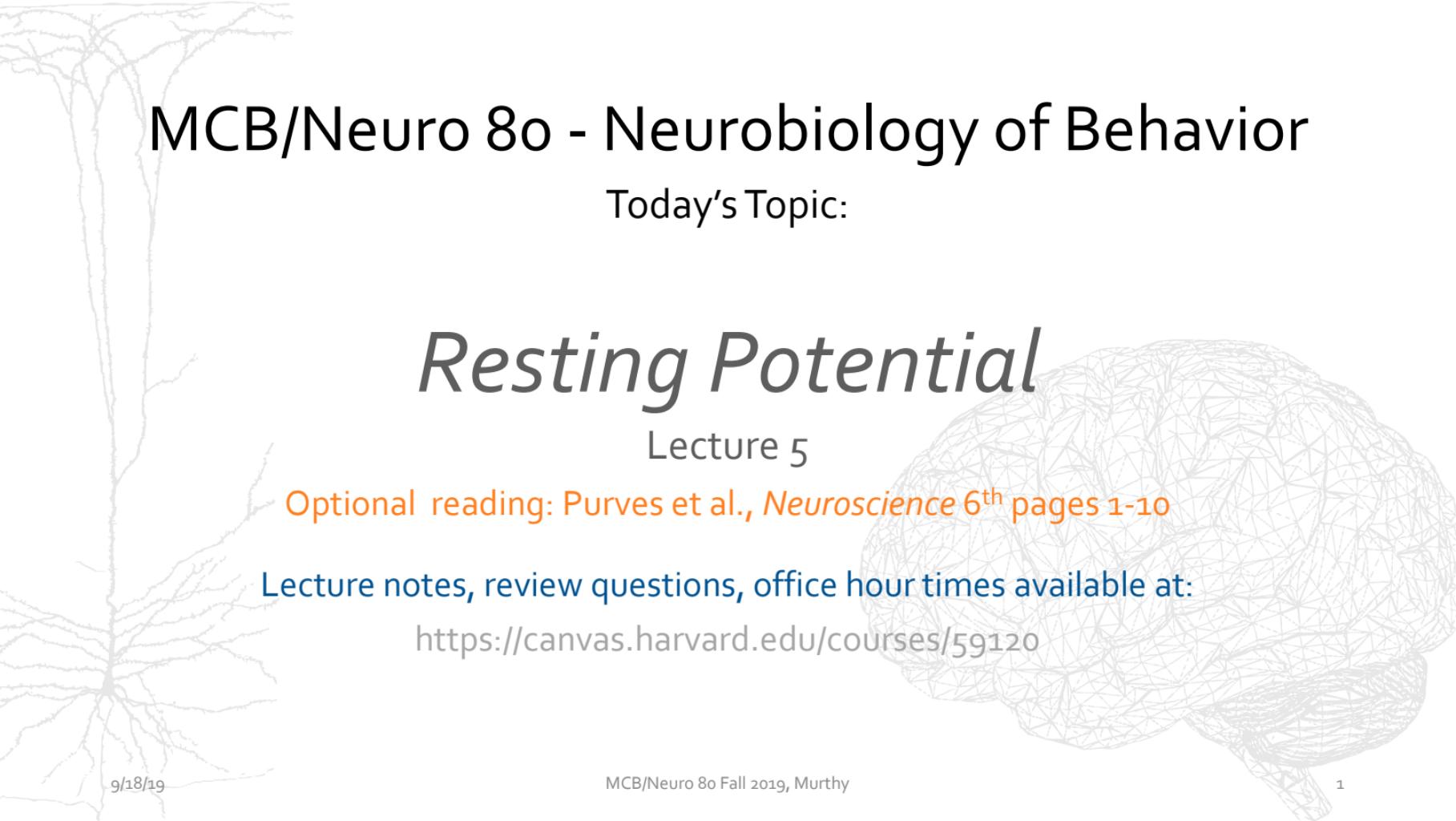
**Sodium Potassium Pump (or ATPase)** is a membrane protein that uses metabolic energy (ATP) to transport ions across the membrane against their concentration gradients. Specifically it pumps 3 Na<sup>+</sup> from inside to outside, then pumps 2 K<sup>+</sup> into the cell. It is responsible for the fact that Na<sup>+</sup> has a higher concentration outside the cell and K<sup>+</sup> has a higher concentration inside the cell. Selective permeability (especially of K<sup>+</sup> "leak" channels) combined with the concentration gradients established by the pump, create the negative resting membrane potential.

Membrane Potential vs External Potassium Concentration in a squid axon



**Learning Objectives:** (By the end of Lecture 5 you should be able answer the following)

1. What two gradients are in balance when an ion is said to be at its equilibrium potential?
2. Draw a graph of neuron's cell membrane potential as a function of changing extracellular potassium concentration (and how it differs from the graph of a glial cell)
3. Recall the equilibrium potentials of potassium, sodium, and chloride and know which way each would flow in a resting neuron.
4. Be able to apply the Nernst and GHK equations and know when to use which equation.
5. Explain how the  $\text{Na}^+/\text{K}^+$  pump functions and why it is necessary.



# MCB/Neuro 80 - Neurobiology of Behavior

## Today's Topic:

# *Resting Potential*

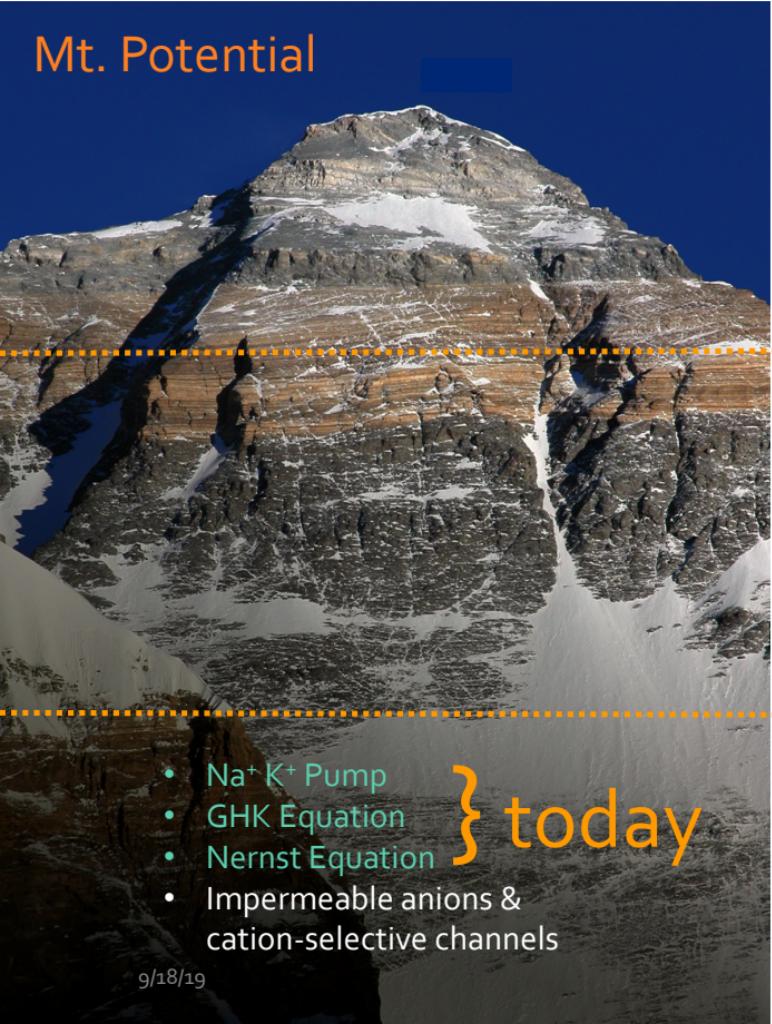
## Lecture 5

Optional reading: Purves et al., *Neuroscience* 6<sup>th</sup> pages 1-10

Lecture notes, review questions, office hour times available at:

<https://canvas.harvard.edu/courses/59120>

# Mt. Potential



- $\text{Na}^+ \text{K}^+$  Pump
  - GHK Equation
  - Nernst Equation
  - Impermeable anions & cation-selective channels
- } today

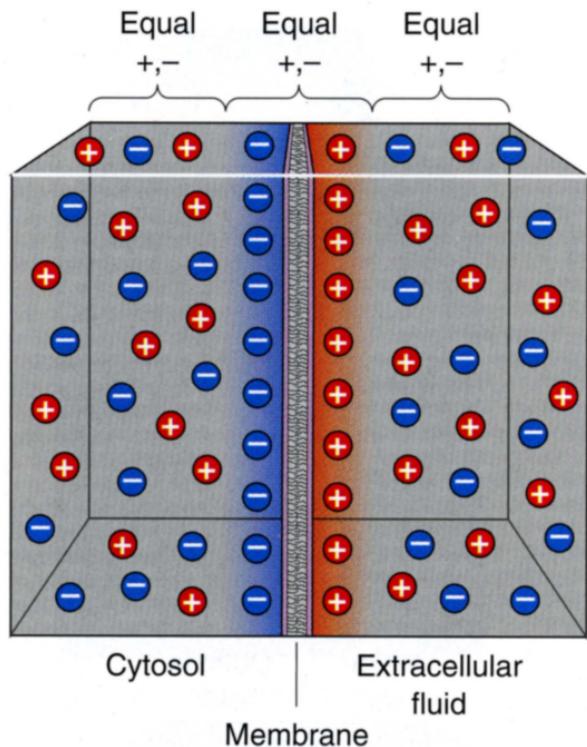
9/18/19

## Synaptic Potential

## Action Potential

## Resting Potential

# What membrane potential is reached when a permeant ion is at equilibrium?



- If you know the internal and external concentrations of the ion that can move across the membrane, you can calculate the membrane potential at equilibrium
- This membrane potential arises from the balance of the two tendencies of the ion:
  - (1) move to equalize the concentration,
  - (2) move towards the opposite charge

# Walther Herman Nernst

(1864-1941)

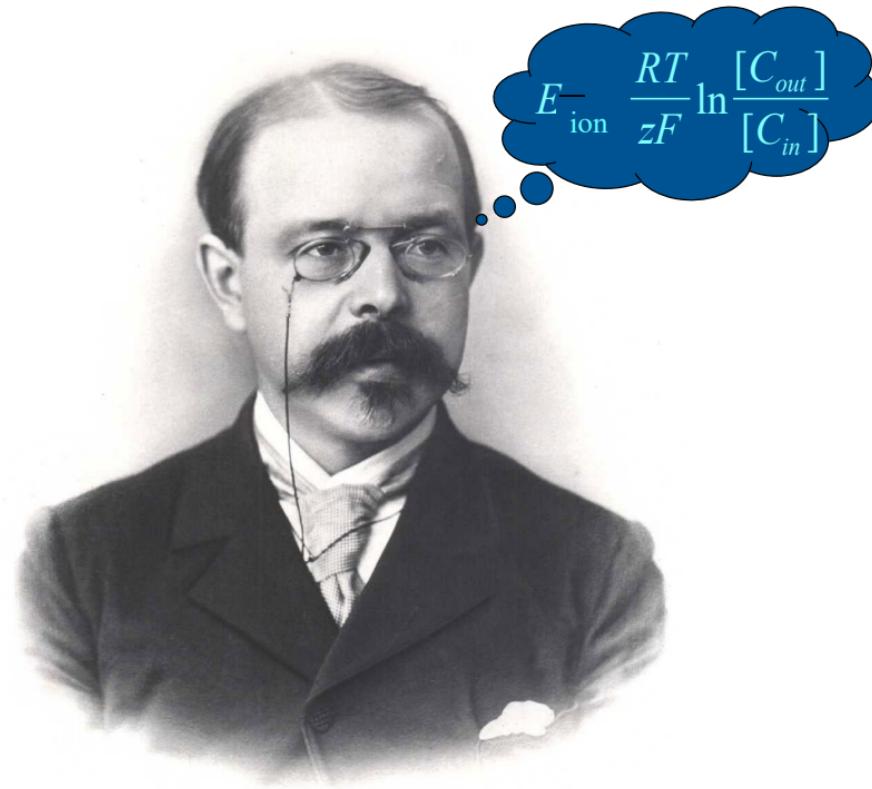
- Nobel in Chemistry-1920  
3<sup>rd</sup> law of thermodynamics
- Invented the electric Piano  
in 1930 ("Neo-Bechstein")



# Walther Herman Nernst

(1864-1941)

- Nobel in Chemistry-1920  
3<sup>rd</sup> law of thermodynamics
- Invented the electric Piano in 1930 ("Neo-Bechstein")
- ☆ Derived the equation now known by his name:  
the **Nernst Equation** or  
**Equilibrium Potential Equation**



W. Nernst.

# Equilibrium Potential

- When the current (i.e., flow of ions) due to the concentration gradient of an ion is exactly counterbalanced by the current due to the electrical gradient across the membrane, the ion has reached its equilibrium potential and there is no net current
- This potential is called the Equilibrium Potential or Nernst Potential of an ion and is calculated by use of the Nernst Equation
- We will come back to the idea of equilibrium potential over and over and over again- so it is important to make sense of this.

**VERY IMPORTANT**

# For the curious (NOT TESTED!)

- The derivation of the Nernst Equation is based on the thermodynamic notion of “electro-chemical potential”.
- At equilibrium, the electro-chemical potential is the same inside and outside. The electro-chemical potential of an ion in a compartment (such as a cell) is affected by the ion’s concentration [X], its charge (z) and the voltage of the compartment (V).

$$\mu_0^X + RT \ln[X]_i + z_X FV_i$$

# For the curious (NOT TESTED!)

- The derivation of the Nernst Equation is based on the thermodynamic notion of "electro-chemical potential".
- At equilibrium, the electro-chemical potential is the same inside and outside. The electro-chemical potential of an ion in a compartment (such as a cell) is affected by the ion's concentration [X], its charge (z) and the voltage of the compartment (V).

inside	outside
$\mu_0^X + RT \ln[X]_i + z_X F V_i$	$= \mu_0^X + RT \ln[X]_o + z_X F V_o$

electrical part	concentration part
$z_X F (V_i - V_o)$	$= RT \ln \frac{[X]_o}{[X]_i}$

**the Nernst equation we know and love** →  $V_m = \frac{RT}{z_X F} \ln \frac{[X]_o}{[X]_i} = E_{ion}$

# Nernst Equation to calculate the Equilibrium potential or $E_{ion}$

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

- R = Gas constant
- T = absolute temperature in degrees Kelvin
- z = valence of ion
- F = Faraday constant
- $E_{ion} = 2.303 \frac{RT}{zF} \log \left\{ \frac{[ion]_{out}}{[ion]_{in}} \right\}$   $2.303 \log X = \ln X$
- $E_{K^+} = 60 \text{ mV} \log \left\{ \frac{[K_o]}{[K_i]} \right\}$   $z=+1, 2.3 \frac{RT}{zF} = 60 \text{ mV}$
- $E_{Na^+} =$
- $E_{Cl^-} =$
- $E_{Ca^{++}} =$

# Nernst potentials

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

Outside Conc.	Inside Conc	Ratio Out:In	Eq. Potential (37°C)
$[K^+]_o = 5 \text{ mM}$	$[K^+]_i = 107 \text{ mM}$	1:20	-80 mV

So if the inside of the cell has 20 fold more potassium ( $K^+$ ) than the outside and the cell is permeable to  $K^+$ ,  $K^+$  will rush down its concentration gradient until the inside is -80mV then the negativity inside will attract the low concentration of  $K^+$  outside to flow in so the two gradients are equal (and opposite): in equilibrium

$$E_K^+ = 60 \text{ mV} \log \{[K_o] / [K_i]\}$$

# Nernst potentials

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

Outside Conc.	Inside Conc	Ratio Out:In	Eq. Potential (37°C)
$[K^+]_o = 5 \text{ mM}$	$[K^+]_i = 107 \text{ mM}$	1:20	-80 mV
$[Cl^-]_o = 150 \text{ mM}$	$[Cl^-]_i = 13 \text{ mM}$	11.5:1	-65 mV

So if the inside of the cell has 11.5 fold less Chloride ( $Cl^-$ ) than the outside and the cell is permeable to  $Cl^-$ ,  $Cl^-$  will rush down its concentration gradient until the inside is -65 mV then the negativity inside will repulse the high concentration of  $Cl^-$  outside to flow in so the two gradients are equal (and opposite): in equilibrium

$$E_{Cl^-} = -60 \text{ mV} \log \{[Cl_o] / [Cl_i]\}$$

# Nernst potentials

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

Outside Conc.	Inside Conc	Ratio Out:In	Eq. Potential (37°C)
$[K^+]_o = 5 \text{ mM}$	$[K^+]_i = 107 \text{ mM}$	1:20	-80 mV
$[Cl^-]_o = 150 \text{ mM}$	$[Cl^-]_i = 13 \text{ mM}$	11.5:1	-65 mV
$[Na^+]_o = 150 \text{ mM}$	$[Na^+]_i = 15 \text{ mM}$	10:1	60 mV

Now you try the narrative ...

- $E_{Na^+} = 60 \text{ mV} \log \{[Na_o]/ [Na_i]\}$

The outside of the cell has 10 times more Na<sup>+</sup> than the inside, and the cell is permeable to Na<sup>+</sup>. Na<sup>+</sup> will move \_\_\_\_\_ the cell, until the inside is \_\_\_\_\_

into, -60mV

out of, -60  
mV

into, +60  
mV

out of, +60  
mV

# Nernst potentials

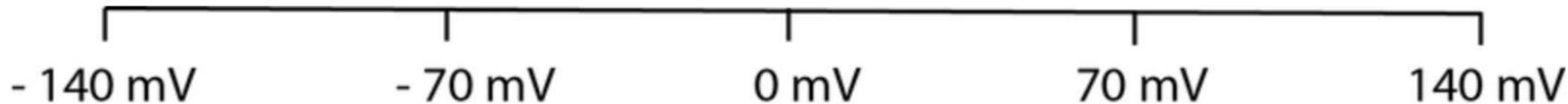
$$E_{ion} = \frac{RT}{zF} \ln \frac{[C_{out}]}{[C_{in}]}$$

Outside Conc.	Inside Conc	Ratio Out:In	Eq. Potential (37°C)
$[K^+]_o = 5 \text{ mM}$	$[K^+]_i = 107 \text{ mM}$	1:20	-80 mV
$[Cl^-]_o = 150 \text{ mM}$	$[Cl^-]_i = 13 \text{ mM}$	11.5:1	-65 mV
$[Na^+]_o = 150 \text{ mM}$	$[Na^+]_i = 15 \text{ mM}$	10:1	60 mV
$[Ca^{2+}]_o = 2 \text{ mM}$	$[Ca^{2+}]_i = 0.0002 \text{ mM}$	10,000:1	

What is the equilibrium potential of  $Ca^{++}$ ?

$$E_{Ca^{++}} = 30 \text{ mV} \log \{[Ca_o]/[Ca_i]\}$$

What is the ECa? [Ca<sub>inside</sub> = 0.0002mM, Ca<sub>outside</sub> = 2mM, Ca is a divalent cation]



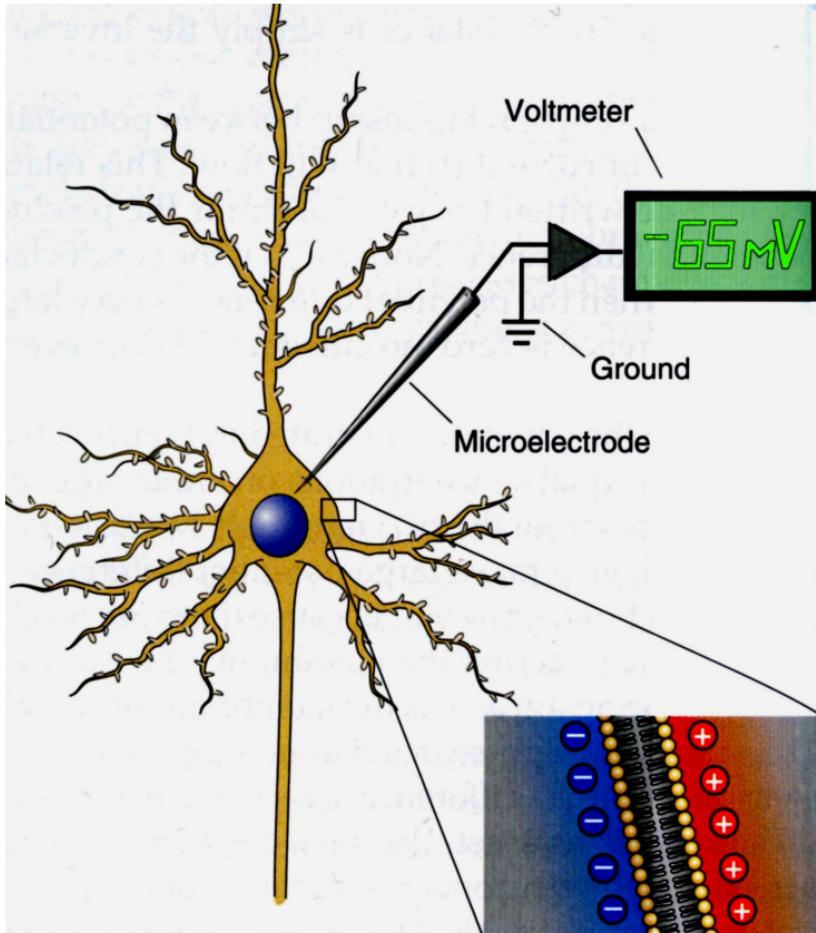
# Nernst potentials

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

Outside Conc.	Inside Conc	Ratio Out:In	Eq. Potential (37°C)
$[K^+]_o = 5 \text{ mM}$	$[K^+]_i = 107 \text{ mM}$	1:20	-80 mV
$[Cl^-]_o = 150 \text{ mM}$	$[Cl^-]_i = 13 \text{ mM}$	11.5:1	-65 mV
$[Na^+]_o = 150 \text{ mM}$	$[Na^+]_i = 15 \text{ mM}$	10:1	60 mV
$[Ca^{2+}]_o = 2 \text{ mM}$	$[Ca^{2+}]_i = 0.0002 \text{ mM}$	10,000:1	120 mV

# Membrane potential measurement

- Intracellular microelectrode compares inside cell to ground. Hollow glass pipette with tip open filled with a high salt solution connected to a voltmeter
- The membrane potential at “rest” is the resting potential
- Around -65 to -80 millivolts ( $\text{mV} = 10^{-3}$  volts) depending on which particular cell



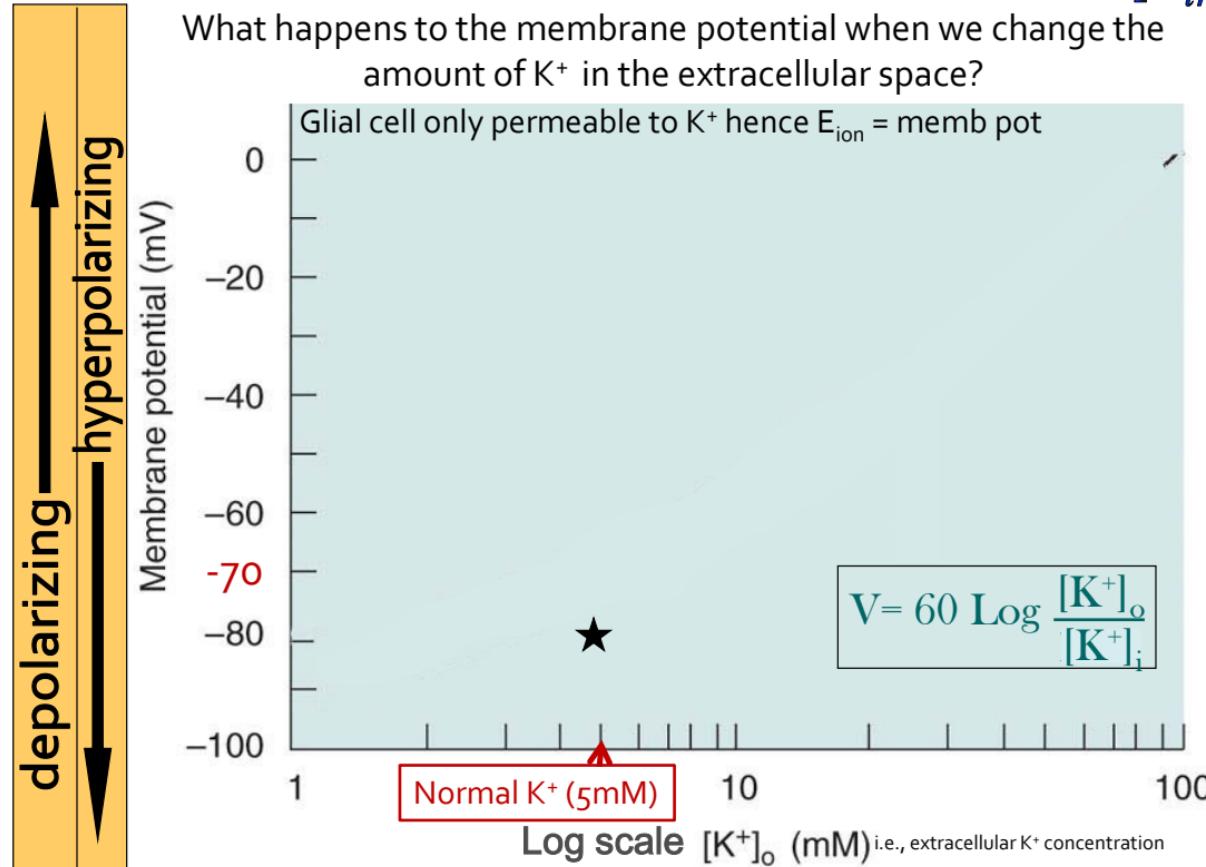
In glial cells because leak K<sup>+</sup> channels are the only ion selective channels, thus the membrane potential (V<sub>m</sub>) is equal to the potassium equilibrium (Nernst) potential (E<sub>K</sub>)

In Glia:  $V_m = 60 \log [K]_{out} / [K]_{in}$   
[K]<sub>in</sub> = 100 mM always

# Nernst Equation

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

What happens to the membrane potential when we change the amount of  $K^+$  in the extracellular space?



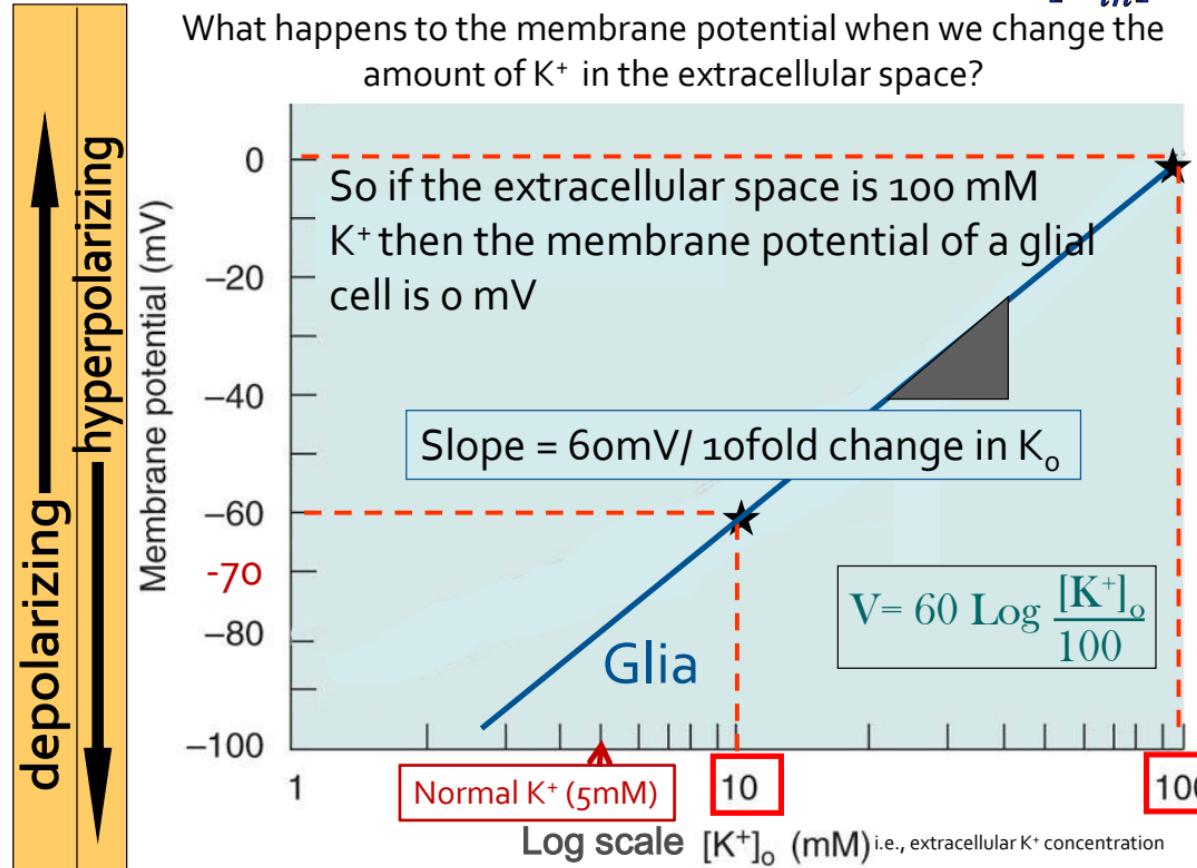
# What will the resting potential of a glial cell be if we raise the extracellular K concentration to 100mM?



# Nernst Equation

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

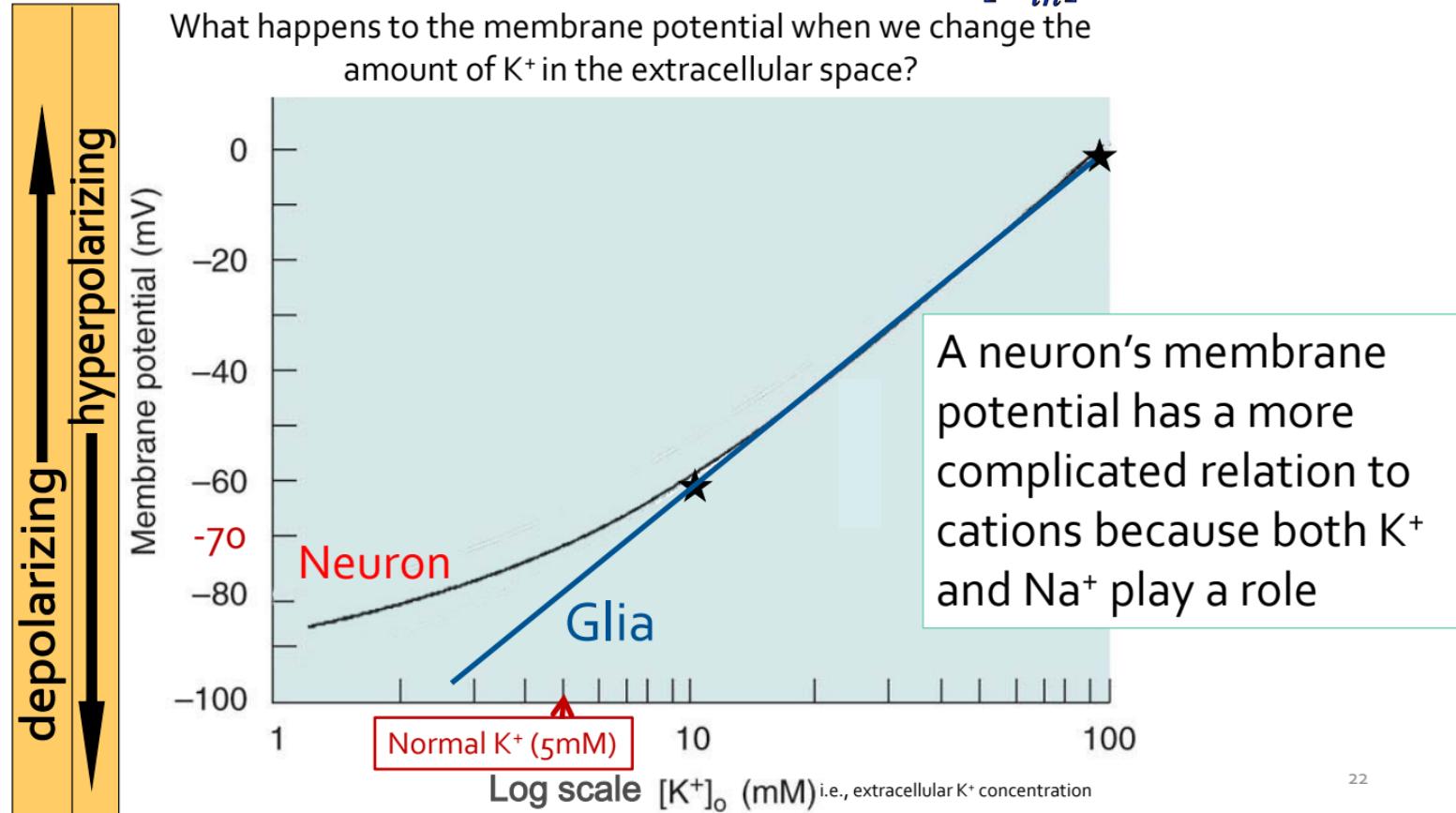
What happens to the membrane potential when we change the amount of  $K^+$  in the extracellular space?



# Nernst Equation

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

What happens to the membrane potential when we change the amount of K<sup>+</sup> in the extracellular space?

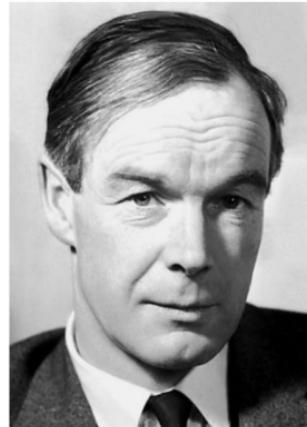


# Goldman-Hodgkin-Katz Equation (GHK)

How to figure our resting potential when multiple different ions are permeable?  
Nernst potential (one ion) wont help



David Goldman



Alan Hodgkin  
of action potential  
fame



Bernard Katz  
of synapse  
fame

# GHK Equation: how to calculate membrane potential if multiple ions are permeable

$$V_{\{memb\}} = \frac{RT}{F} \ln \frac{[K_{out}^+]}{[K_{in}^+]}$$



- In order to calculate the resting potential in a neuron we need to take account of the roles of multiple ions that have permeabilities- the **Goldman Hodgkin Katz** equation is one way to do this.
- In glial cells the permeability to  $\text{Na}^+$  and  $\text{Cl}^-$  is negligible, so equation reduces to Nernst
- In neurons there is small but significant permeability to  $\text{Na}^+$  and  $\text{Cl}^-$  so their equilibrium potentials need to be taken into account:
- $P_K:P_{\text{Na}}:P_{\text{Cl}} = 1: 0.025: 0.45$

$$V_{\{memb\}} = \frac{RT}{F} \ln \frac{P_{K^+}[K_{out}^+] + P_{Na^+}[Na_{out}^+] + P_{Cl^-}[Cl_{in}^-]}{P_{K^+}[K_{in}^+] + P_{Na^+}[Na_{in}^+] + P_{Cl^-}[Cl_{out}^-]}$$

- If the permeability to  $Na^+$  suddenly increased to many fold higher than the permeability to  $K^+$
- Then what happens to the membrane potential?

Based on the GHK equation what would happen to a neuron's membrane potential if the Na permeability suddenly increased to be many fold higher than the K permeability?

no change

the cell would hyperpolarize

the cell would depolarize

another answer

$$V_{\{memb\}} = \frac{RT}{F} \ln \frac{P_{K^+}[K_{out}^+] + P_{Na^+}[Na_{out}^+] + P_{Cl^-}[Cl_{in}^-]}{P_{K^+}[K_{in}^+] + P_{Na^+}[Na_{in}^+] + P_{Cl^-}[Cl_{out}^-]}$$

- If the permeability to  $Na^+$  suddenly increased to many fold higher than the permeability to  $K^+$
- Then what happens to the membrane potential?
- Cell would move from -70 mV towards +60 mV (i.e., depolarize)
- That is what happens during an action potential- more on this next time
- If the permeability to  $Cl^-$  increased, then what would happen?

# If Chloride permeability increased in a neuron what would happen to the membrane potential?

nothing

cell would depolarize

cell would hyperpolarize

another answer

$$V_{\{\text{memb}\}} = \frac{RT}{F} \ln \frac{P_{K^+}[K_{out}^+] + P_{Na^+}[Na_{out}^+] + P_{Cl^-}[Cl_{in}^-]}{P_{K^+}[K_{in}^+] + P_{Na^+}[Na_{in}^+] + P_{Cl^-}[Cl_{out}^-]}$$

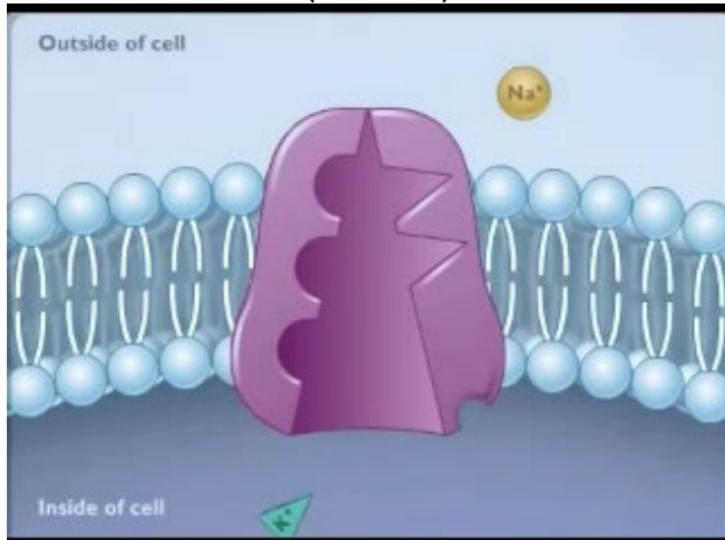
- If the permeability to  $Na^+$  suddenly increased to many fold higher than the permeability to  $K^+$
- Then what happens to the membrane potential?
- Cell would move from -70 mV towards +60 mV (i.e., depolarize)
- That is what happens during an action potential- more on this next time
- If the permeability to  $Cl^-$  increased, then what would happen?
- Then, cell would be clamped at a negative membrane potential (-65 mV) which is  $V_{rest}$  so there would be no change. (Inhibitory synapses)

# Problem of changing concentrations of K<sup>+</sup> & Na<sup>+</sup>

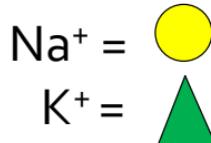
- There is a subtle difference between the Nernst and GHK equations: unlike a Nernst potential which reaches **equilibrium** with the net efflux and influx of an ion equal, the GHK represents a **steady state** but not an equilibrium condition.
- At -65mV (~Vrest), Na<sup>+</sup> will continue to move into the cell down its concentration and electrical gradient and K<sup>+</sup> will continue to leave the cell down its concentration and electrical gradient.
- Eventually the concentration differences across the membrane for these two ions differences would disappear- which would have disastrous consequences for neural signaling
- Thus there needs to be a means to maintain a high concentration of K<sup>+</sup> inside and a low concentration of Na<sup>+</sup> inside.

# Sodium Potassium Pump

(Cartoon)



<https://www.youtube.com/watch?v=Gsxn4giVnhE>



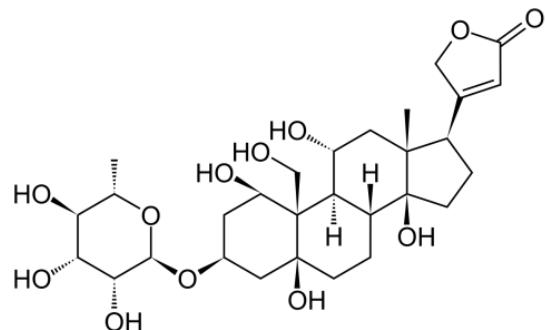
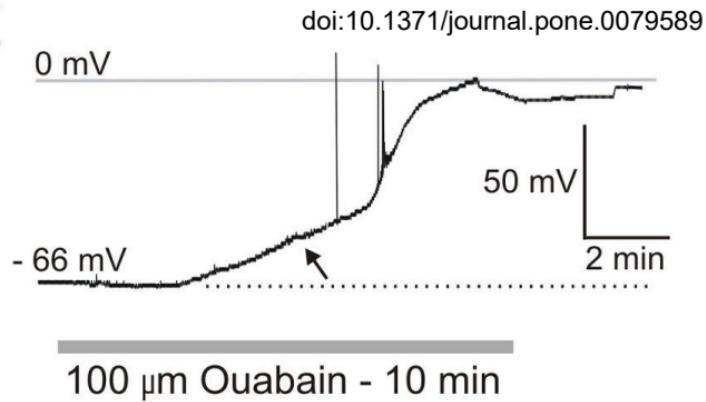
- The pump is an ATPase.
- 70% of all energy consumption (ATP conversion to ADP) in brain is used to pump Na<sup>+</sup> out and K<sup>+</sup> back into neurons. This ATP is generated by glycolysis which is dependent on Oxygen.
- The pump is electrogenic : it sends 3Na<sup>+</sup> out for 2K<sup>+</sup> in. Thus it tends to make the inside more negative (10s of mVs) as well as maintain the concentration gradient.

# Molecules as Machines

(More accurate version of Na/K ATPase)

- Yellow circle: Sodium
- Purple circle: Potassium

# Ouabain, a poison that blocks Na-K pump



*Strophanthus gratus* plant

# Learning Objectives

1. What two gradients are in balance when an ion is said to be at its equilibrium potential?
2. Draw a graph of neuron's cell membrane potential as a function of changing extracellular potassium concentration (and how it differs from the graph of a glial cell)
3. Recall the equilibrium potentials of potassium, sodium, and chloride and know which way each would flow in a resting neuron.
4. Be able to apply the Nernst and GHK equations and know when to use which equation.
5. Explain how the  $\text{Na}^+/\text{K}^+$  pump functions and why it is necessary.