Models of Neurons 1: The membrane potential

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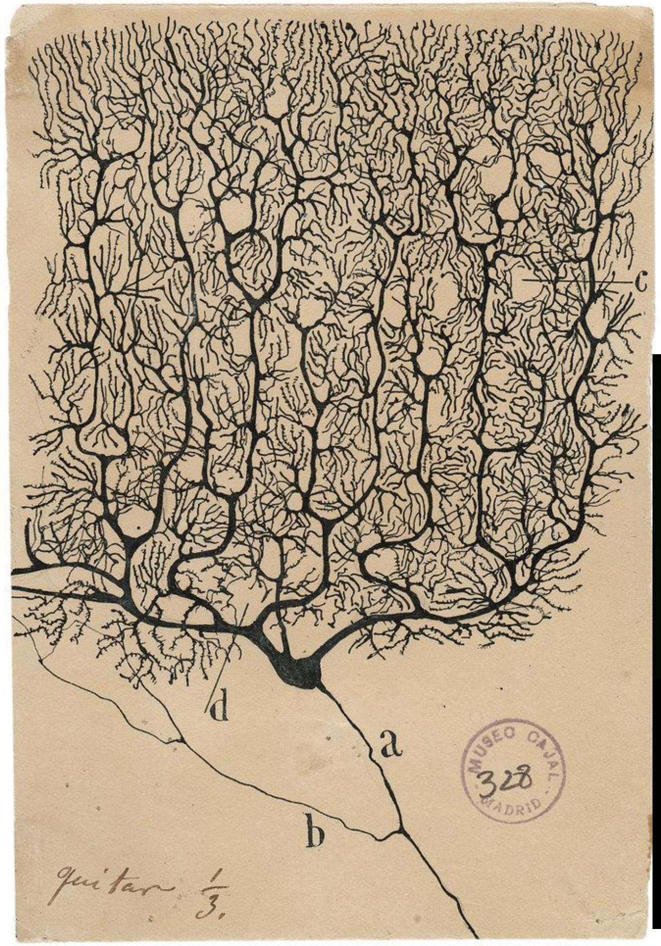
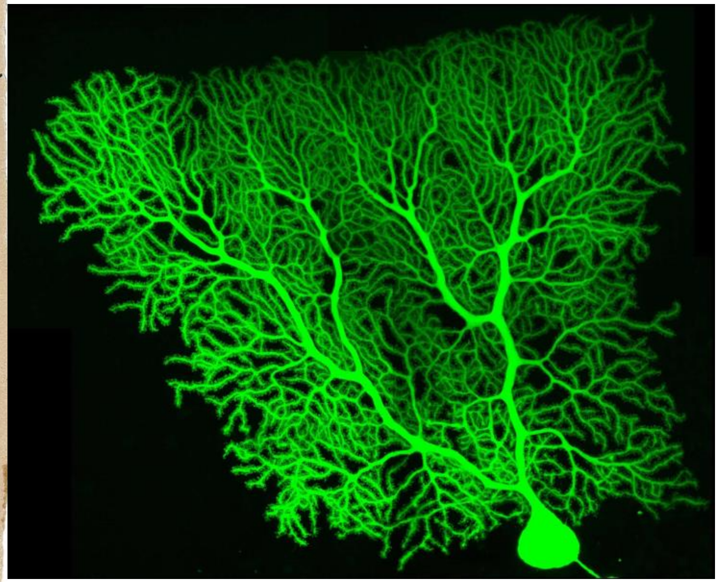
Computational Neuroscience (Lecture 3, 2024/2025)

Outline of Lecture

- Overview of neurons (recap)
- Cell membranes, ions and ion channels
- The membrane potential (voltage)
- The reversal and resting potentials
- Passive membrane potential dynamics





Purkinje neurons. Left: drawing by Ramon y Cajal
Right: Image of a real one

Overview of Neurons

- Neurons are cells, just like in the rest of the body (the fact that neurons are discrete cells rather than a continuous net was first demonstrated by Ramon y Cajal, Nobel Prize 1906)
- Unlike other cells, neurons have dendrites, a soma, and an axon.

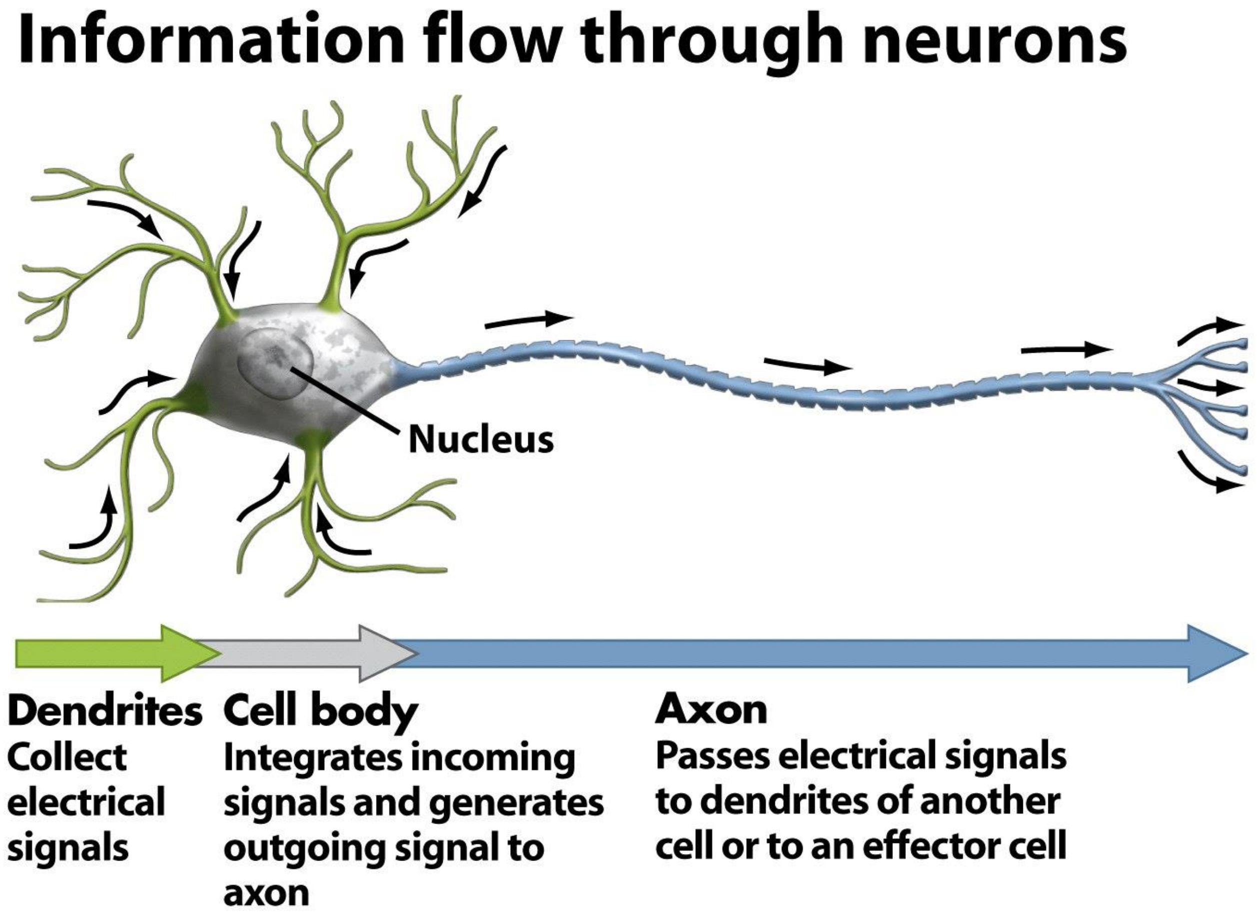
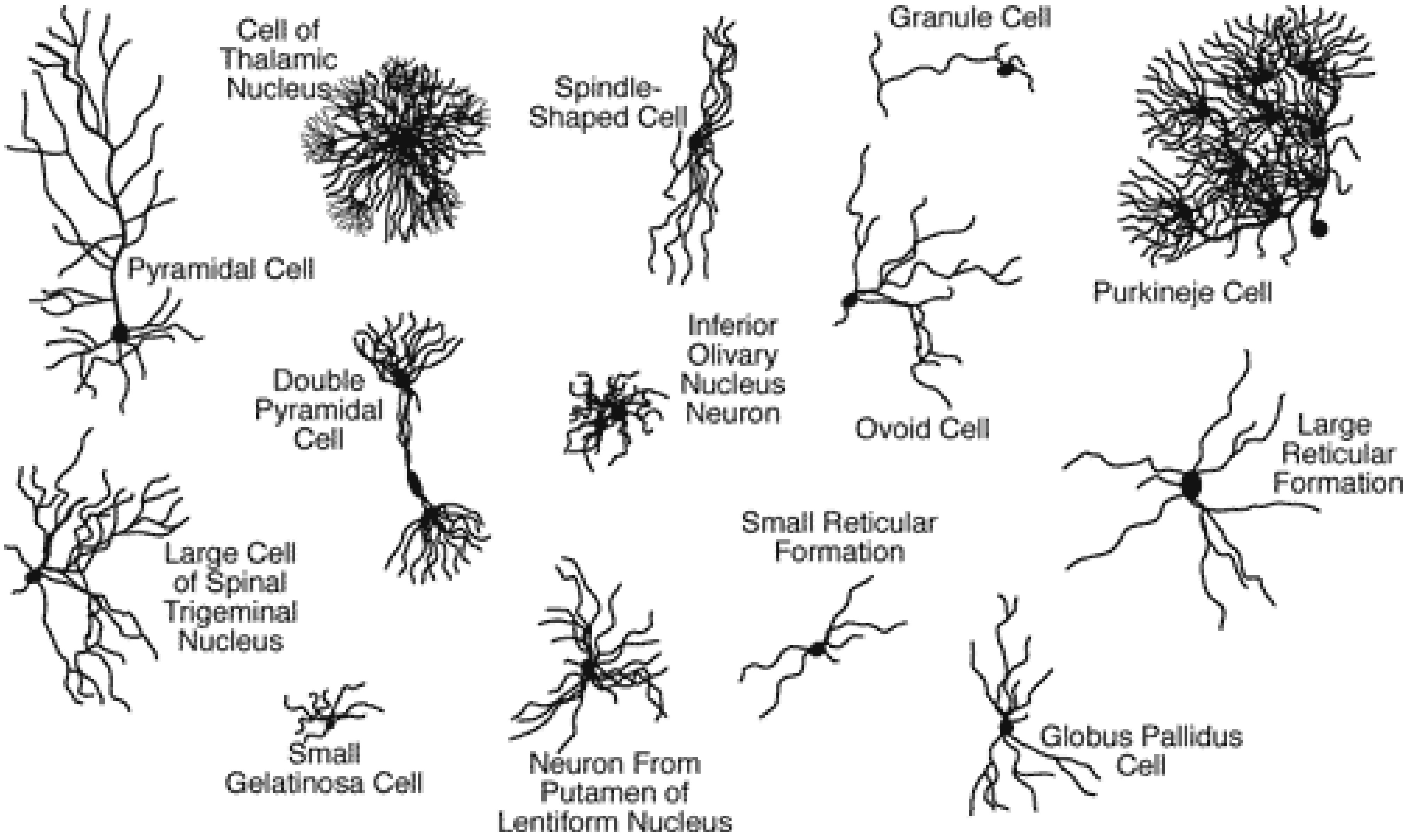


Figure 45-2b Biological Science, 2/e

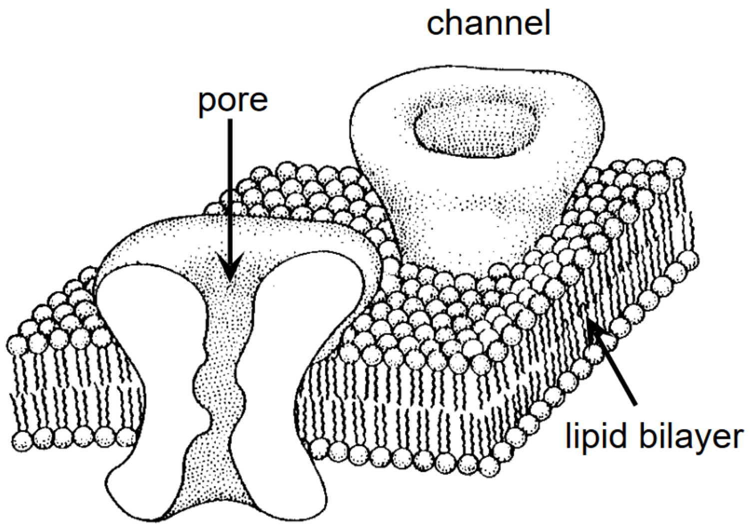
Overview of Neurons

- There are many types of neuron with varying morphologies, biophysical properties and computational functions



The Cell Membrane

- A neuron is like a bag of ions and other molecules. The membrane is made of a lipid bilayer, which itself is impermeable to most of these ions and molecules
- Outside the neuron is the extracellular medium, which also contains various ions and molecules
- The cell membrane has various ion channels through which ions can sometimes pass in or out. Ion channels can open and close, changing the permeability of the membrane to specific ionic species



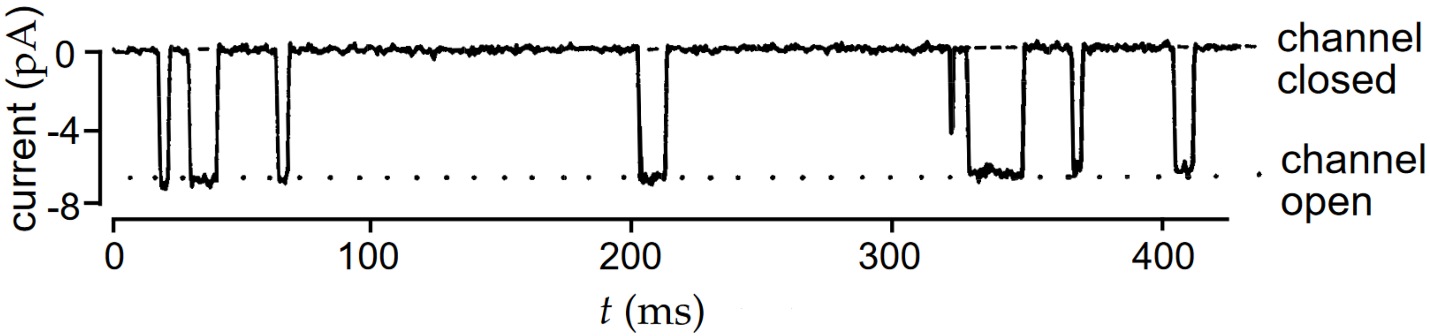
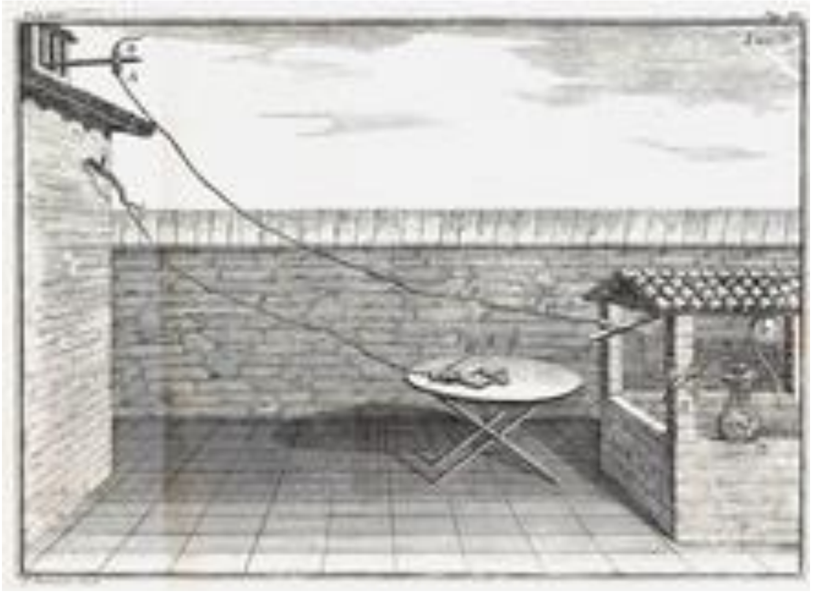
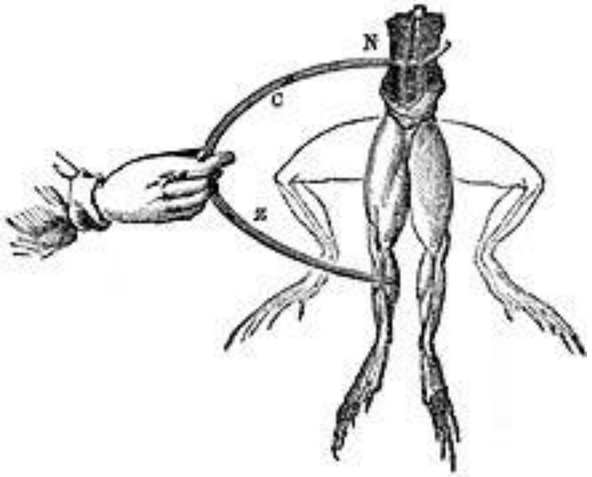


Figure 5.1 A schematic diagram of a section of the lipid bilayer that forms the cell membrane with two ion channels embedded in it. The membrane is 3 to 4 nm thick and the ion channels are about 10 nm long. (Adapted from Hille, 1992.)

Some History: "Animal Electricity"/Galvanism

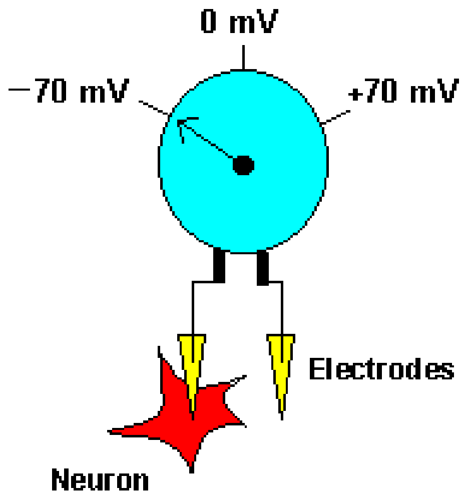
- Galvani (1700s) first demonstrated that the nervous system is electrically active
- He showed that an applied voltage would cause the legs of a frog to twitch
- The action potential was measured much later (Bernstein, 1865) and the first intracellular recording was by Hodgkin and Huxley in 1939.



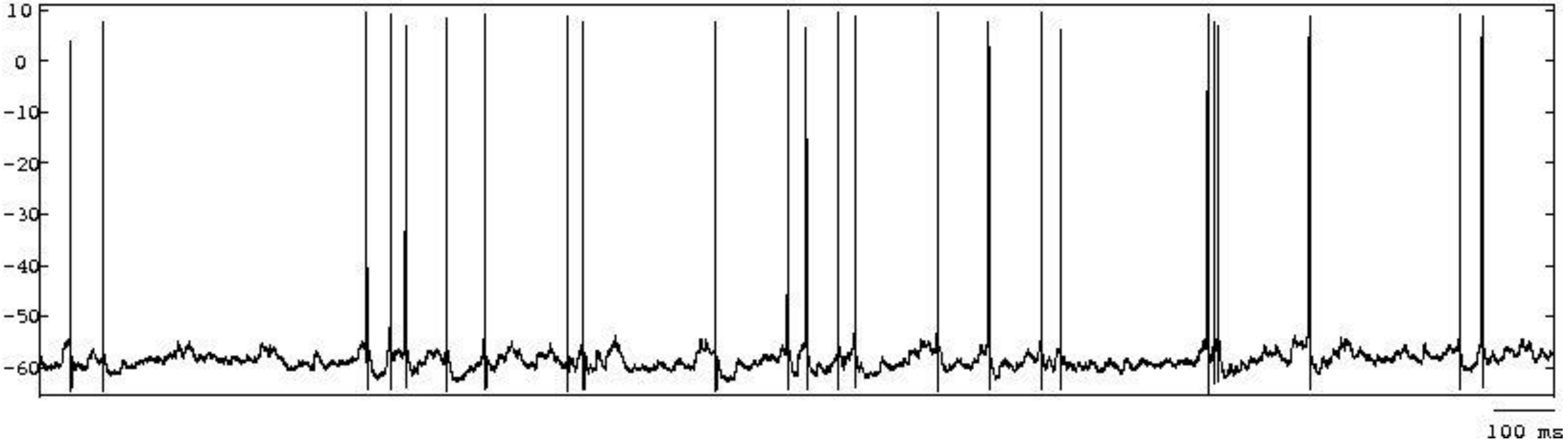


The Membrane Potential

- One can measure a voltage (or “potential”) across the cell membrane of a neuron
- This membrane voltage responds to injected current via either graded changes (“subthreshold”) or action potentials/spikes

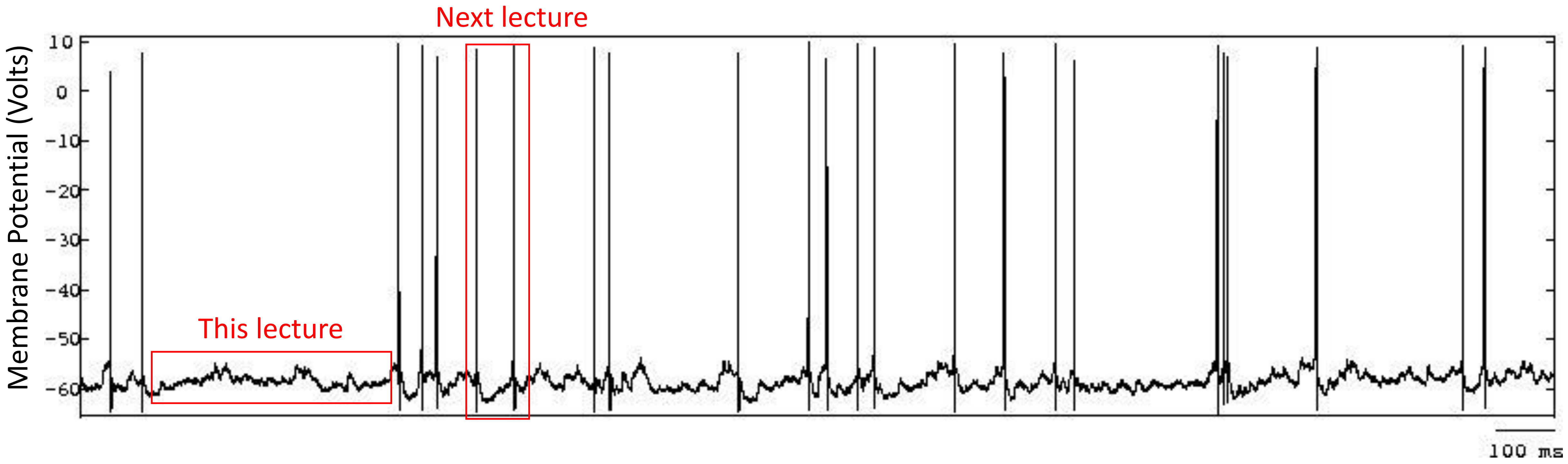


Membrane Potential (Volts)



How is the Membrane Potential Generated?

- How do neurons maintain a voltage across their cell membrane? How does the membrane potential respond to injected current?
- Subject of this lecture…
- How are action potentials generated? Subject of next lecture…



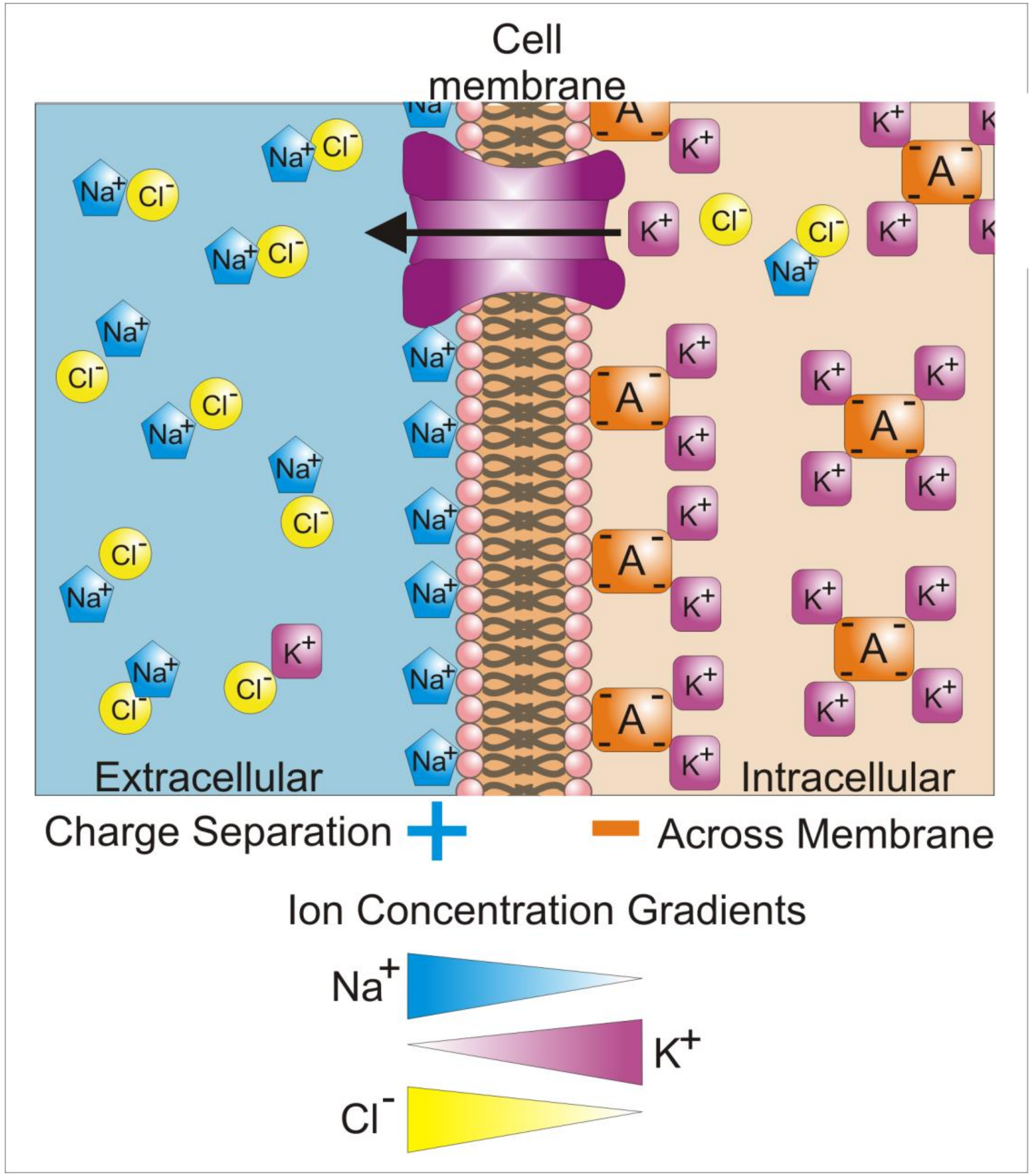
Ionic Basis of the Membrane Potential

- Neurons maintain a concentration difference of various ionic species across their membrane (mostly Na+, K+, Cl-)

- This concentration difference creates a membrane potential (or voltage) due to the net imbalance of charge

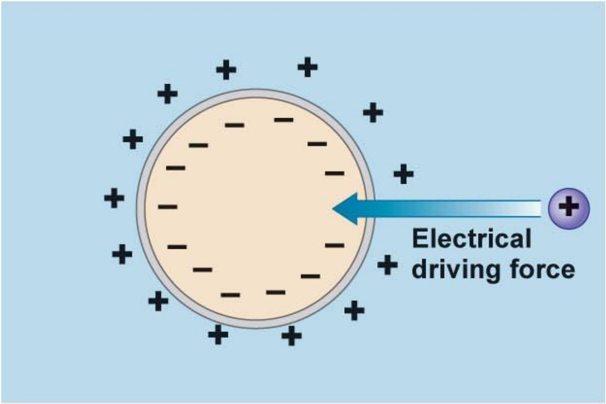
- The membrane contains various ion channels, some of which are selectively permeable to specific species of ion

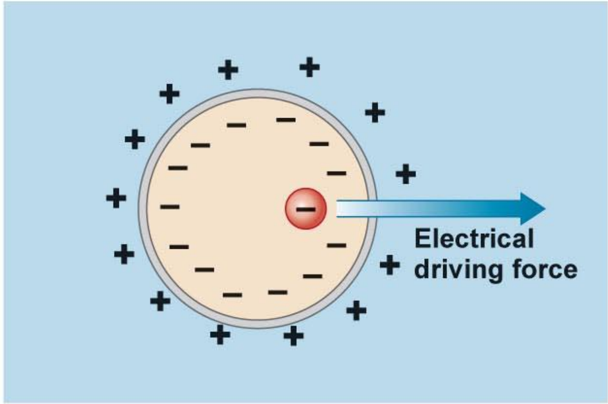
- Ion channels may open or close depending on membrane voltage or on the binding of neurotransmitter to the membrane



Electrical and Chemical Driving Forces

- Ions are subject to an electrical driving force when a voltage is applied (force = charge x voltage, $F=qV$)





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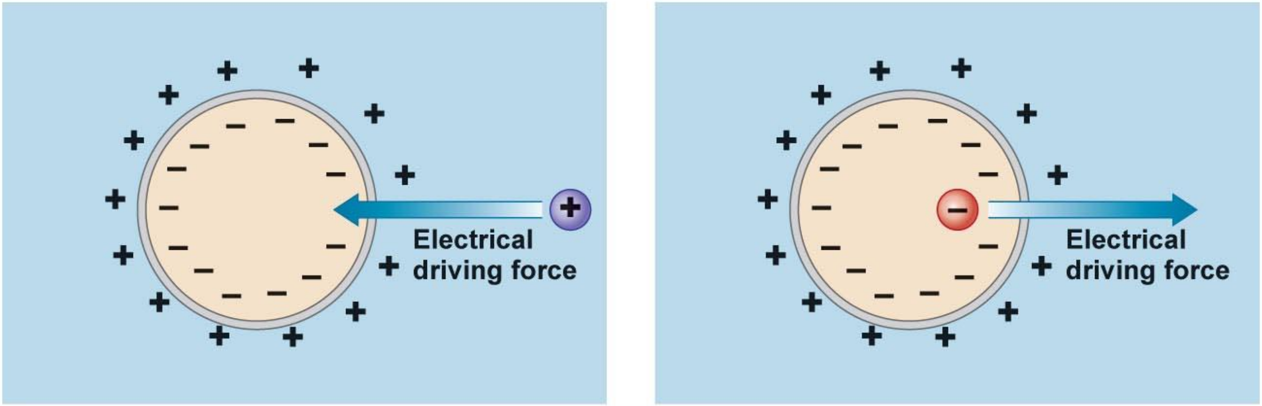
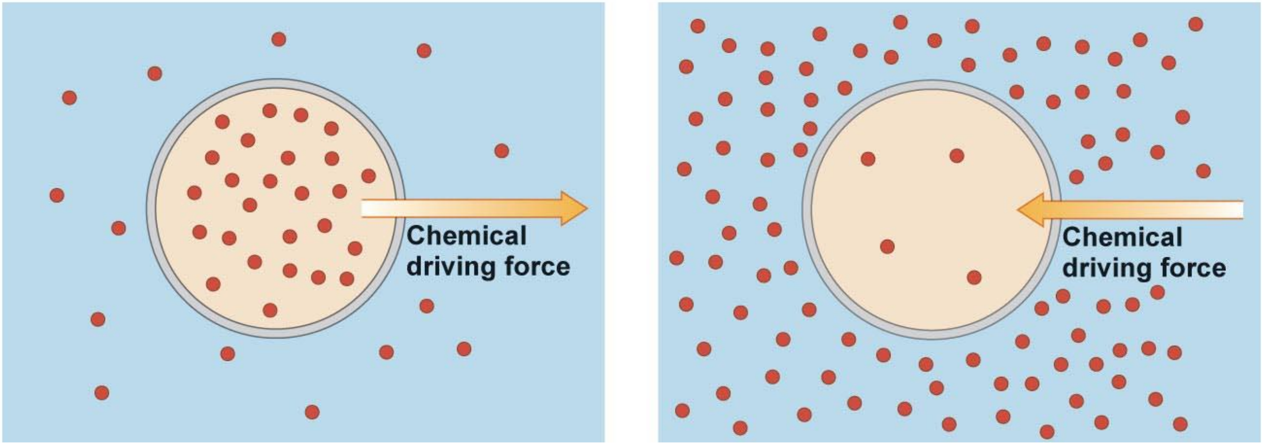


- In the absence of any applied forces (e.g., for uncharged particles), ions flow along their concentration gradient due to random thermal fluctuations (passive diffusion/chemical driving "force")



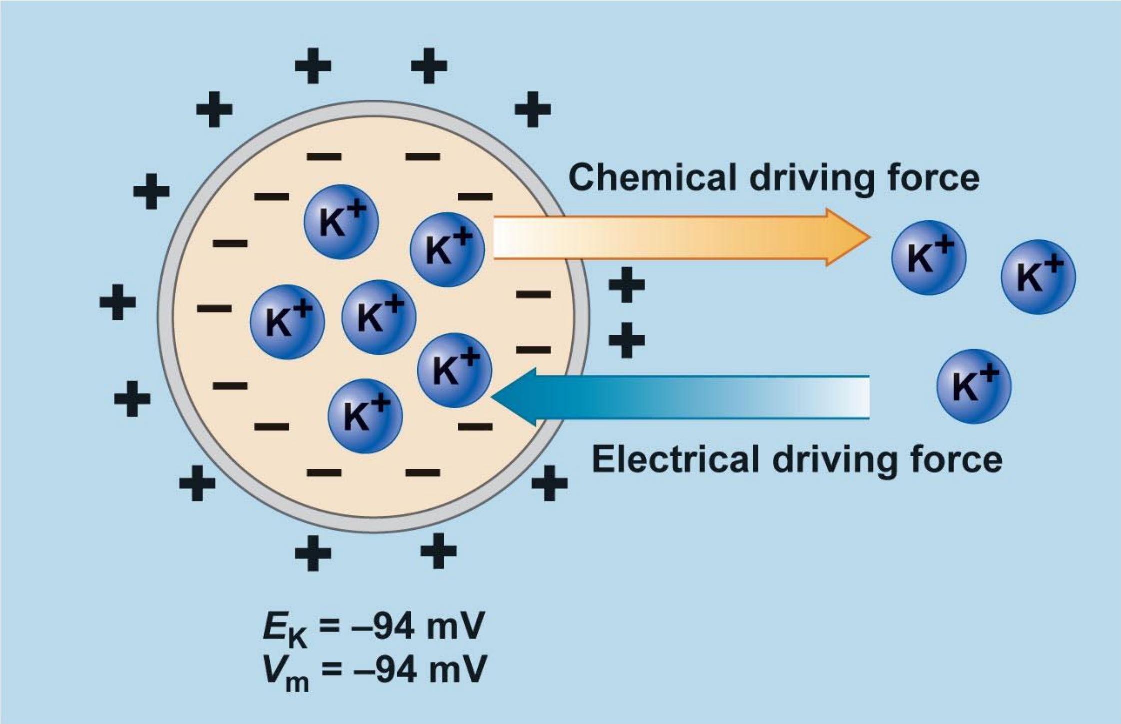
The Reversal Potential

- When both electrostatic force and concentration gradients exist, there is a certain voltage at which the chemical driving force and the electrical driving force exactly cancel

- This voltage is called the reversal potential

- The reversal potential is the voltage at which no net ionic current will flow across the cell membrane

- If the membrane potential is not equal to the reversal potential, ions will flow across the membrane (assuming it is permeable to those ions)



The Nernst Equation

- The Nernst Equation gives the voltage at which no net current will flow across the cell membrane, for a given concentration of ions inside and outside the cell (called the reversal potential)

$$E = \frac{RT}{zF} \ln \frac{[\text{ion outside cell}]}{[\text{ion inside cell}]}$$

- The reversal potential *E* depends on the charge per ion *z*, the logarithm of the concentration ratio, the temperature *T,* and two physical constants *(*the Universal Gas Constant *R* and Faraday's Constant *F).*

- This equation can be derived in several ways, see course textbooks if interested

The Reversal Potential – Worked Example

- Plugging in R=8.31 Joule/mol Kelvin, F=96480 Coulomb/mol, (these are known constants) and setting T=37 Celsius (or 310 Kelvin), gives:

$$E = \frac{RT}{zF} \ln \frac{[\text{ions outside}]}{[\text{ions inside}]} \approx \frac{27\text{mV}}{z} \ln \frac{[\text{ions outside}]}{[\text{ions inside}]}$$

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- Potassium (K) ions have z=+1, and have a concentration outside and inside of 20 and 400 milli mol respectively, which gives:

$$E_K = 27mV \ln \frac{20}{400} \approx -80mV$$

- Temperature and ionic concentration vary across species and cell types, leading to different reversal potentials

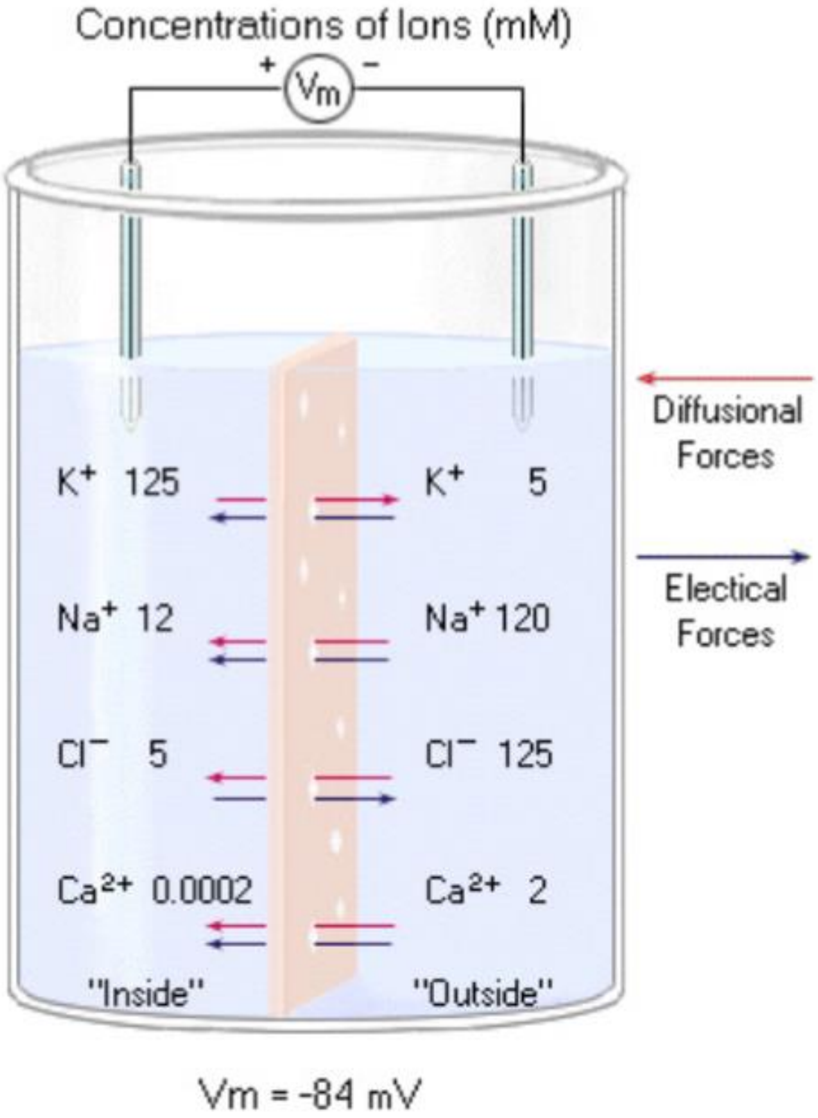
The Reversal Potential

Ion	Concentration Gradient	Reversal Potential E_i
K^+	higher inside	$\sim -75\text{mV}$
Cl^-	higher outside	$\sim -65\text{mV}$
Na^+	higher outside	$\sim 50\text{mV}$
Ca^{2+}	higher outside	$\sim 150\text{mV}$

Reversal Potential - Summary

- Neurons have ions inside and outside, but with different concentrations
- Two effects cause ions to move across the membrane: diffusion and electric force
- The reversal potential is the voltage across the cell membrane at which no net current will flow, for a given species of ion
- It depends on the concentration of the ions inside and outside the cell, on the temperature, and the ionic charge
- We can calculate the reversal potential using the Nernst equation

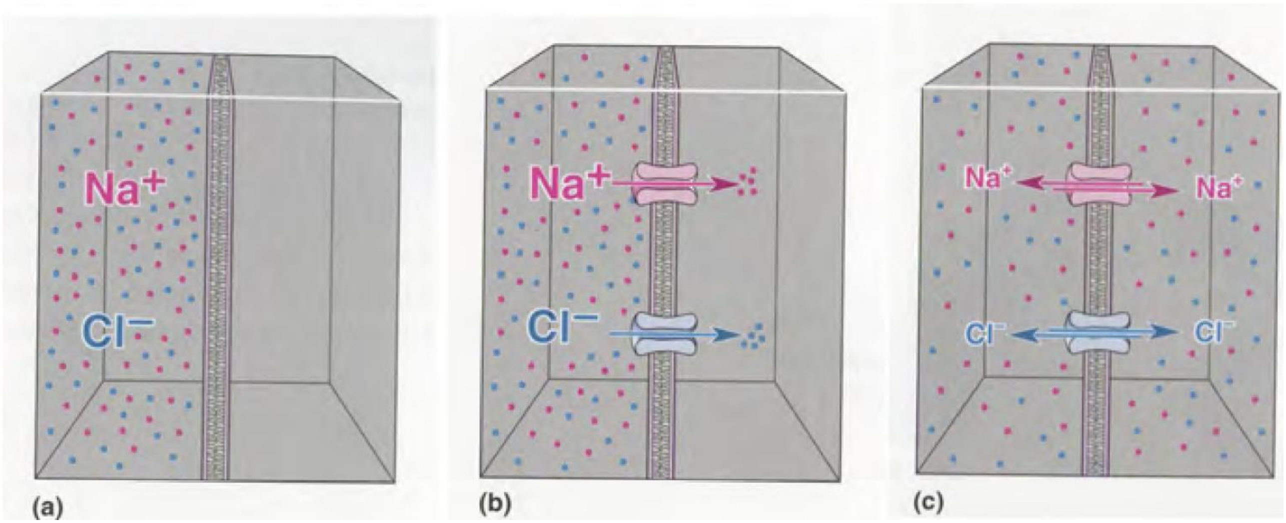
Typical Ion Concentrations for Mammals



Permeable vs Semi-Permeable Membranes

Example 1: A box contains sodium and chloride on one side of a permeable membrane. Eventually they diffuse uniformly throughout the box, and no membrane potential is produced.

Permeable membranes (pointless!)



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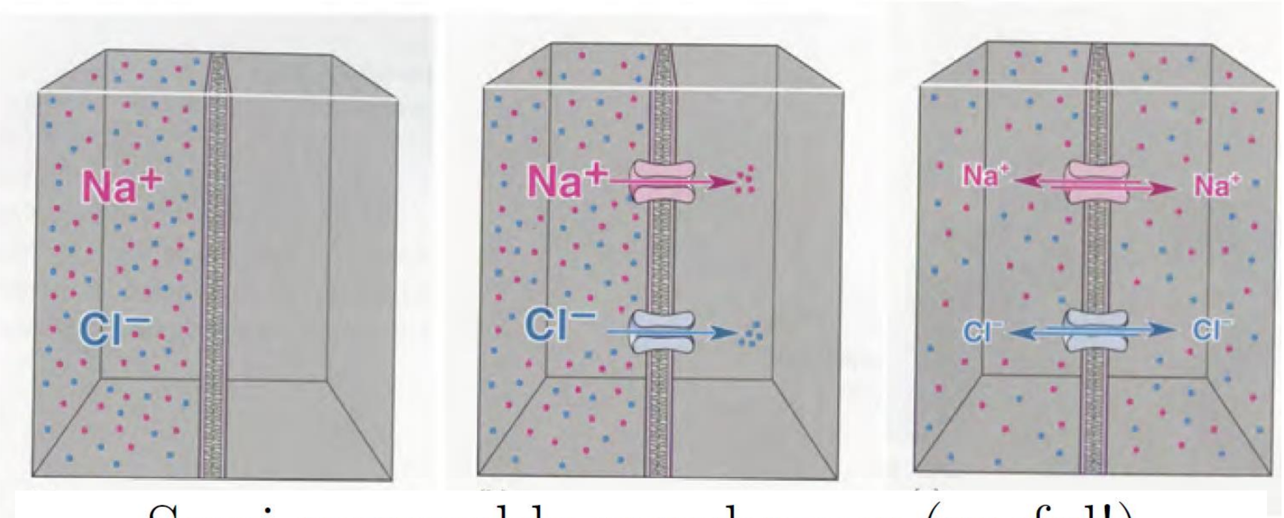
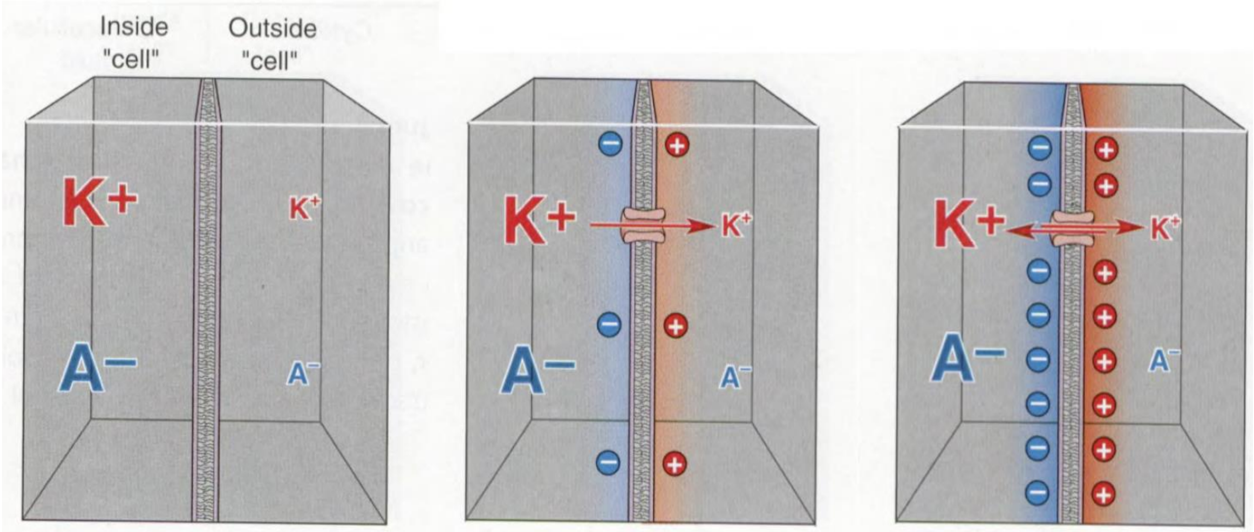


Example 2: The box contains potassium and another ion A, and the membrane is permeable only to potassium. Potassium flows down the concentration gradient, and creates a charge difference and therefore a membrane potential

Semi-permeable membranes (useful!)



The Resting Potential

- When multiple species of ion are present, the voltage at which no net current flows across the membrane is the cell's resting potential (Goldman-Hodgkin-Katz equation)

$$E_m = \frac{RT}{F} \ln \frac{P_{Na^+}[Na^+]_{out} + P_{K^+}[K^+]_{out} + P_{Cl^-}[Cl^-]_{in}}{P_{Na^+}[Na^+]_{in} + P_{K^+}[K^+]_{in} + P_{Cl^-}[Cl^-]_{out}}$$

- *P* = permeability of membrane to ions of each species
- The above equation considers three main ionic species (sodium, potassium and chloride), but generalises straightforwardly to any number of ionic species
- The relative concentrations of each ionic species, together with their membrane permeabilities, determine the resting potential
- The resting potential of neurons in the brain is roughly -70 mV (between the reversal potential of potassium and chloride)

The Resting Potential: An Illustration

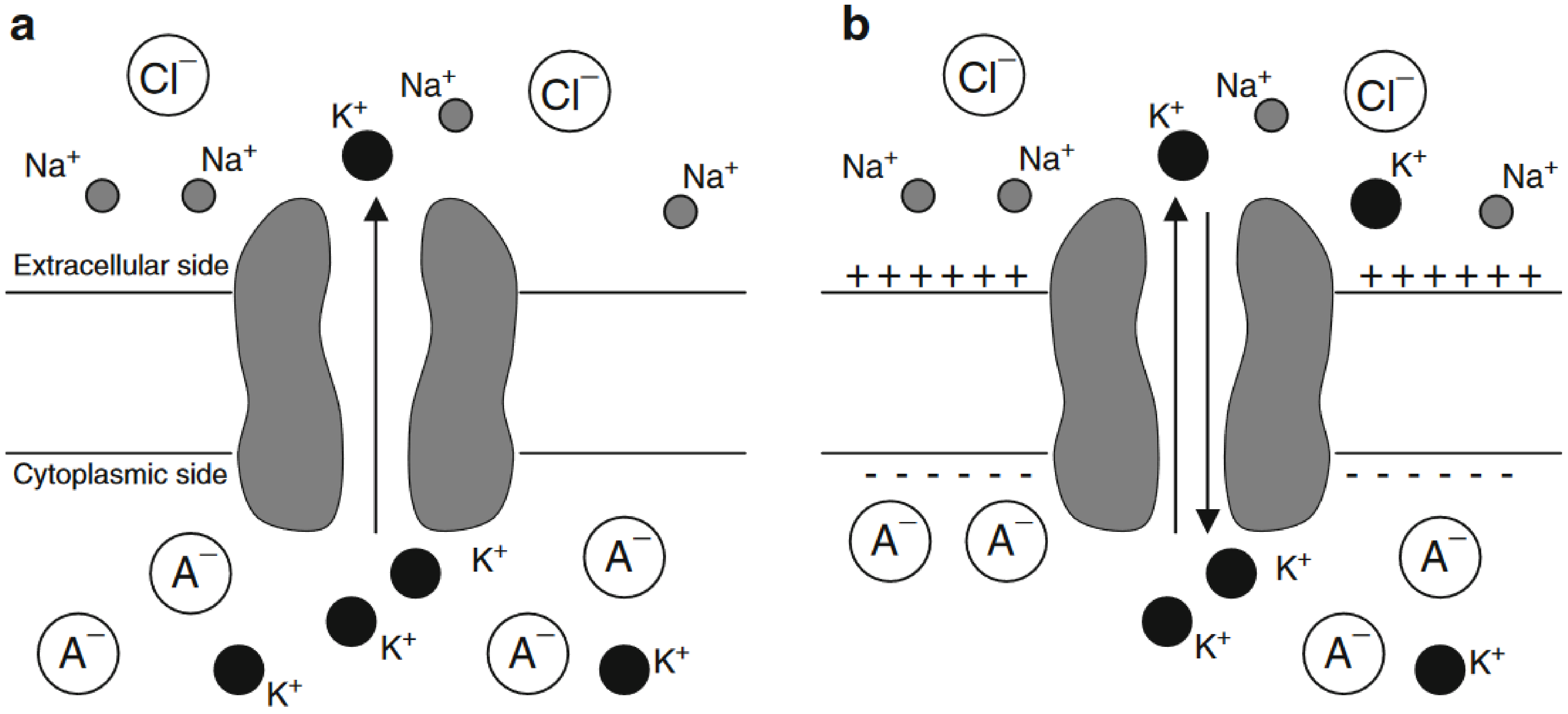


Fig. 1.1 The K^+ flux is determined by both the K^+ concentration gradient and the electrical potential across the membrane. (**a**) For a cell that is permeable only to K^+, the concentration gradient of K^+ moves K^+ ions out of the cell. (**b**) The continued efflux of K^+ builds up an excess of positive charge on the outside and an excess of negative charge on the inside. At equilibrium, the electrical and chemical driving forces are equal and opposite

The Resting Potential: A Worked Example

- As before, we have RT/F = 27 mV (at T=37 Celsius)

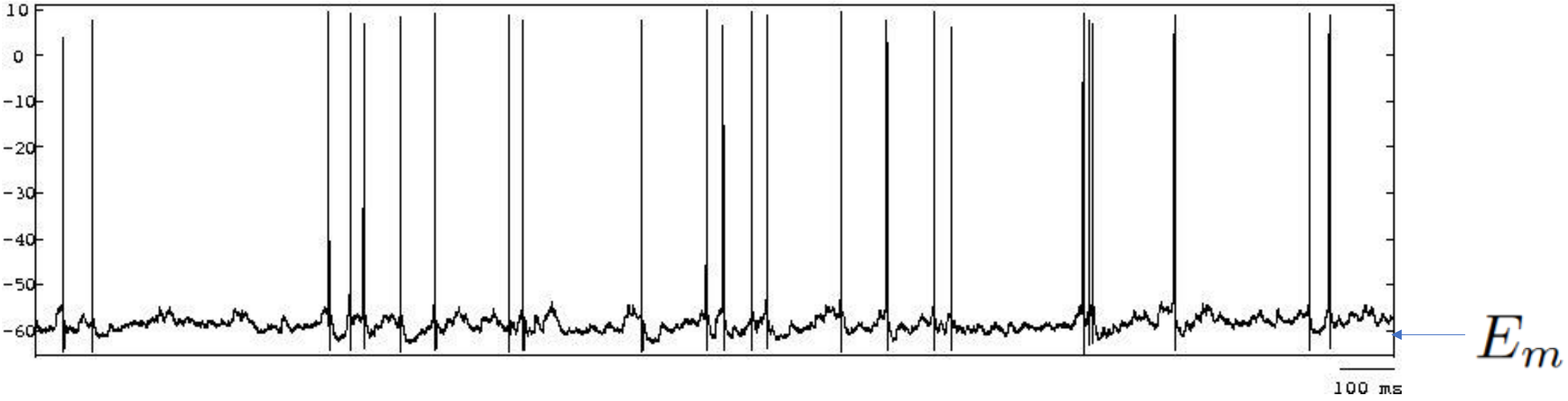
- Typical ratios for the ionic permeabilities are $P_K : P_{Na} : P_{Cl}$ = 1 : 0.05 : 0.45 (so highly permeable to potassium, highly impermeable to sodium)

- The concentrations are roughly: Potassium 400:20, Sodium 50:440, Chloride 52:560 (inside:outside – measured in squid!)

- Plugging this into Goldman-Hodgkin-Katz gives the resting potential:

$$E_m = 27\text{mV} \ln \frac{0.05 \times 440 + 1 \times 20 + 0.45 \times 52}{0.05 \times 50 + 1 \times 400 + 0.45 \times 560} \approx -62mV$$

The Resting Potential: A Worked Example



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The Resting Potential - Summary

- The resting potential is the voltage across the cell membrane at which no net current will flow

- The resting potential depends on the membrane permeability to each ionic species, and the concentration of each species inside and outside the cell

- The resting potential is described by the Goldman-Hodgkin-Katz equation, a generalisation of the Nernst equation

- In neurons, the resting potential is mostly determined by potassium (K) and chloride (Cl), to which the membrane is highly permeable

Ionic Current Flow

- So far we have discussed the reversal and resting potentials, defined as the voltage at which *no current flows* across the cell membrane

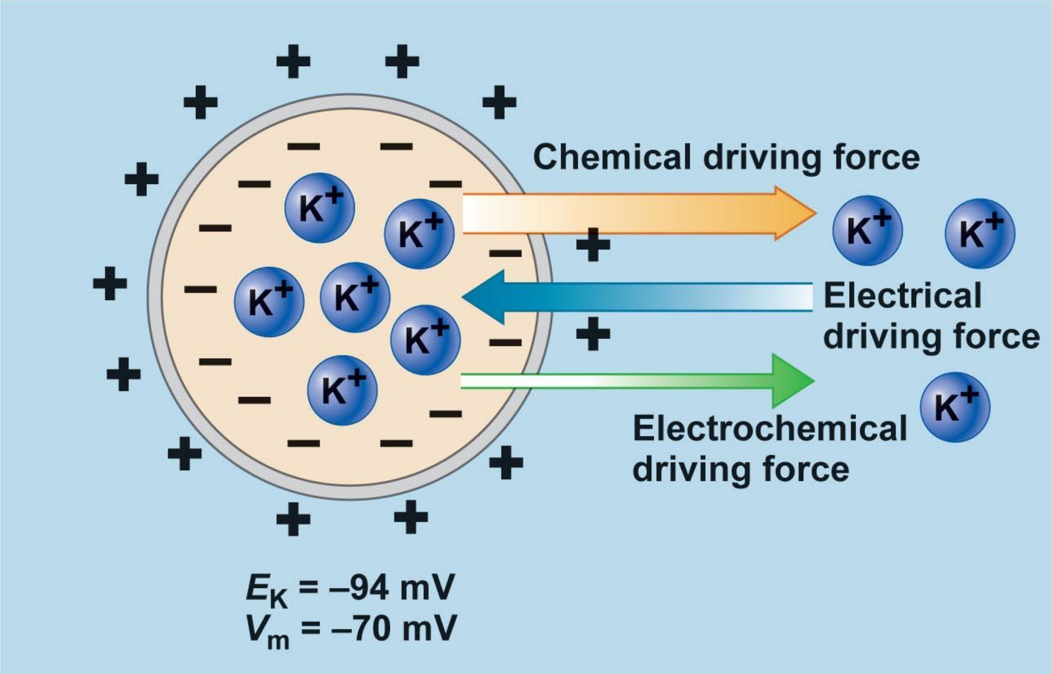
- However, cells are dynamic – their membrane potential fluctuates in response to external input, and they are rarely at resting/reversal potential

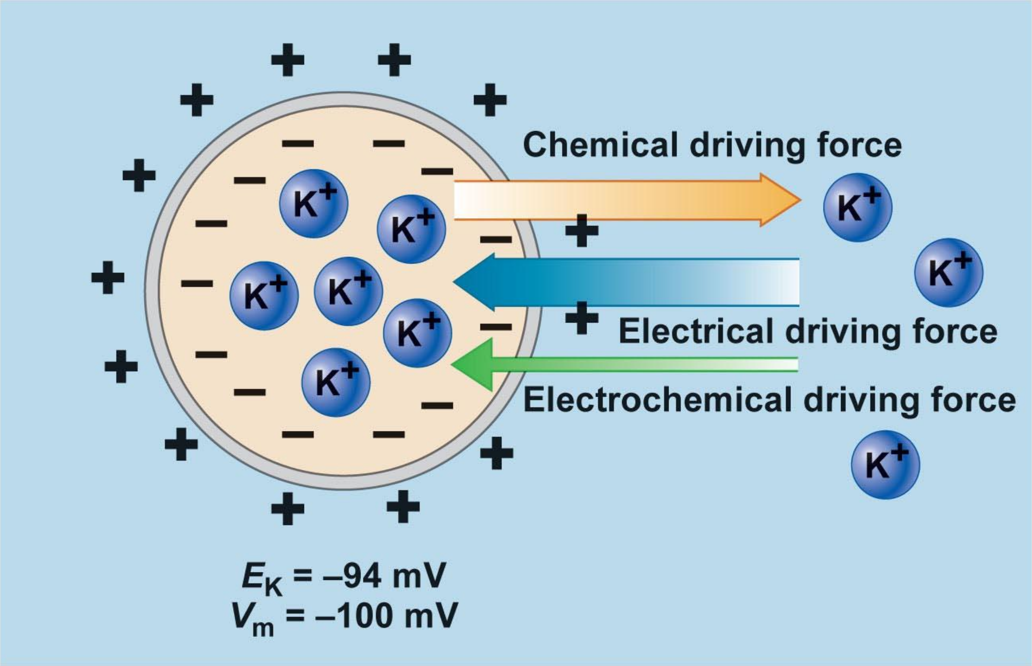
- What happens when the membrane potential is not at the reversal/resting potential? How much current will flow across the cell membrane?

- We can model this using Ohm's law!

Reversal Potential and Ionic Current Flow

- When the membrane potential is not at the resting/reversal potential, ionic currents will flow across the cell membrane
- The figure below shows the simple case where only one ionic species is present
- Current flows in/out when the electric and chemical driving force do not balance, creating a net electrochemical driving force





Ohm's Law

- Ohm's law relates the current flow *I* through a material to its resistance *R*, as a function of the voltage *V* applied:

$$V = IR$$

- The resistance is an intrinsic property of the material (e.g., metal, rubber, cell membranes). It is often more convenient to work with the conductance *g*:

$$g = 1/R \implies I = gV$$

- Ohm's law assumes a linear relationship between voltage and current, but this isn't always the case in the real world (non-Ohmic resistors)

- Note: in electronics, current is flow of electrons. In neurons, current is flow of both positively and negatively charged ions!

Ohm's Law Model for Ionic Current Flow

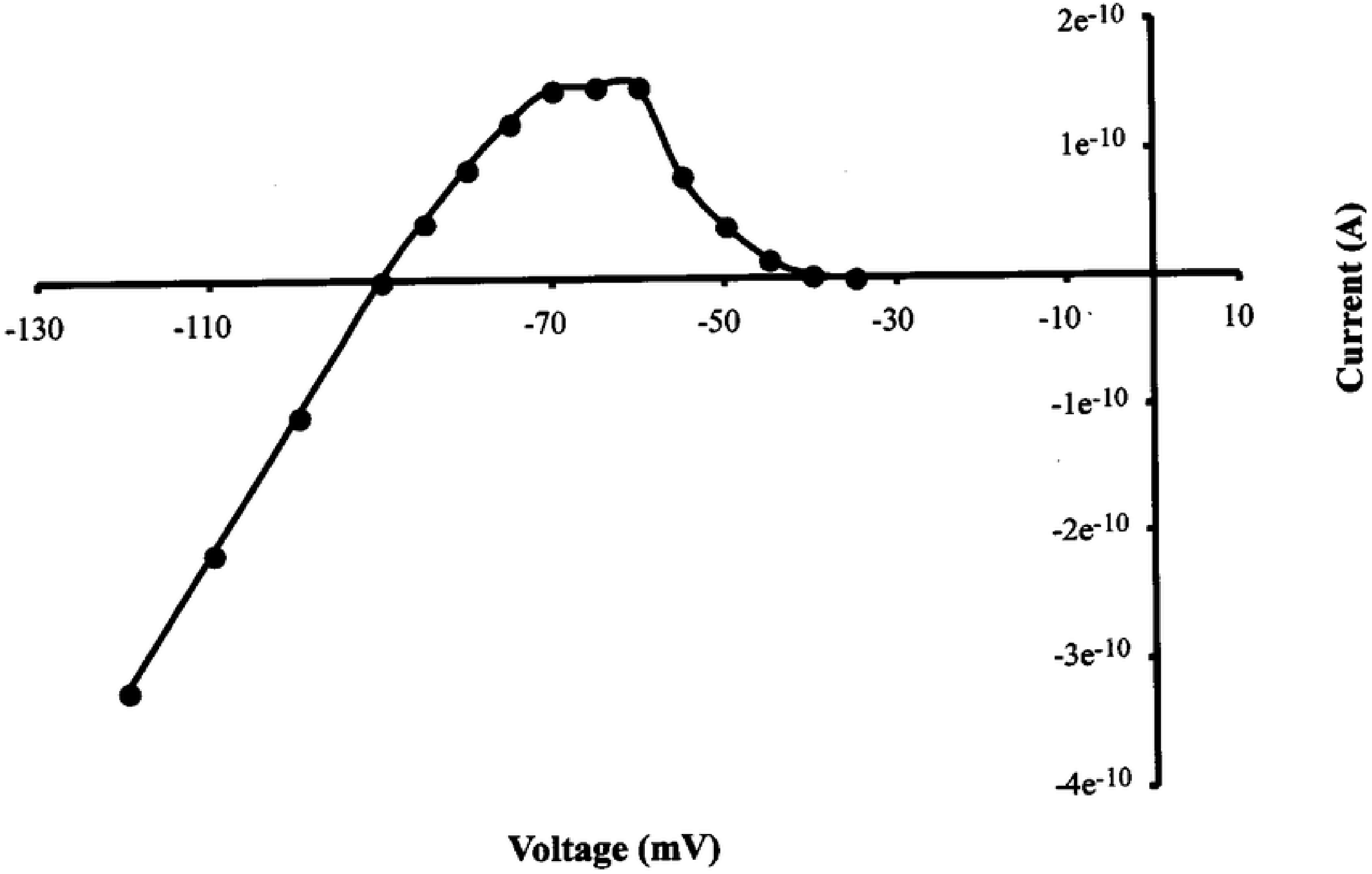
- We can use Ohm's law to determine the ionic current flow through the cell membrane:

$$V - E = IR = I/g \implies I = g(V - E)$$

- Where *g* is the membrane conductance (related to its permeability to ions), *E* is the reversal potential for the ionic species under consideration. Note the offset by *E* in this variant of Ohm's law.

- This equation is only an approximation, in reality I-V curves are not linear (non-Ohmic)

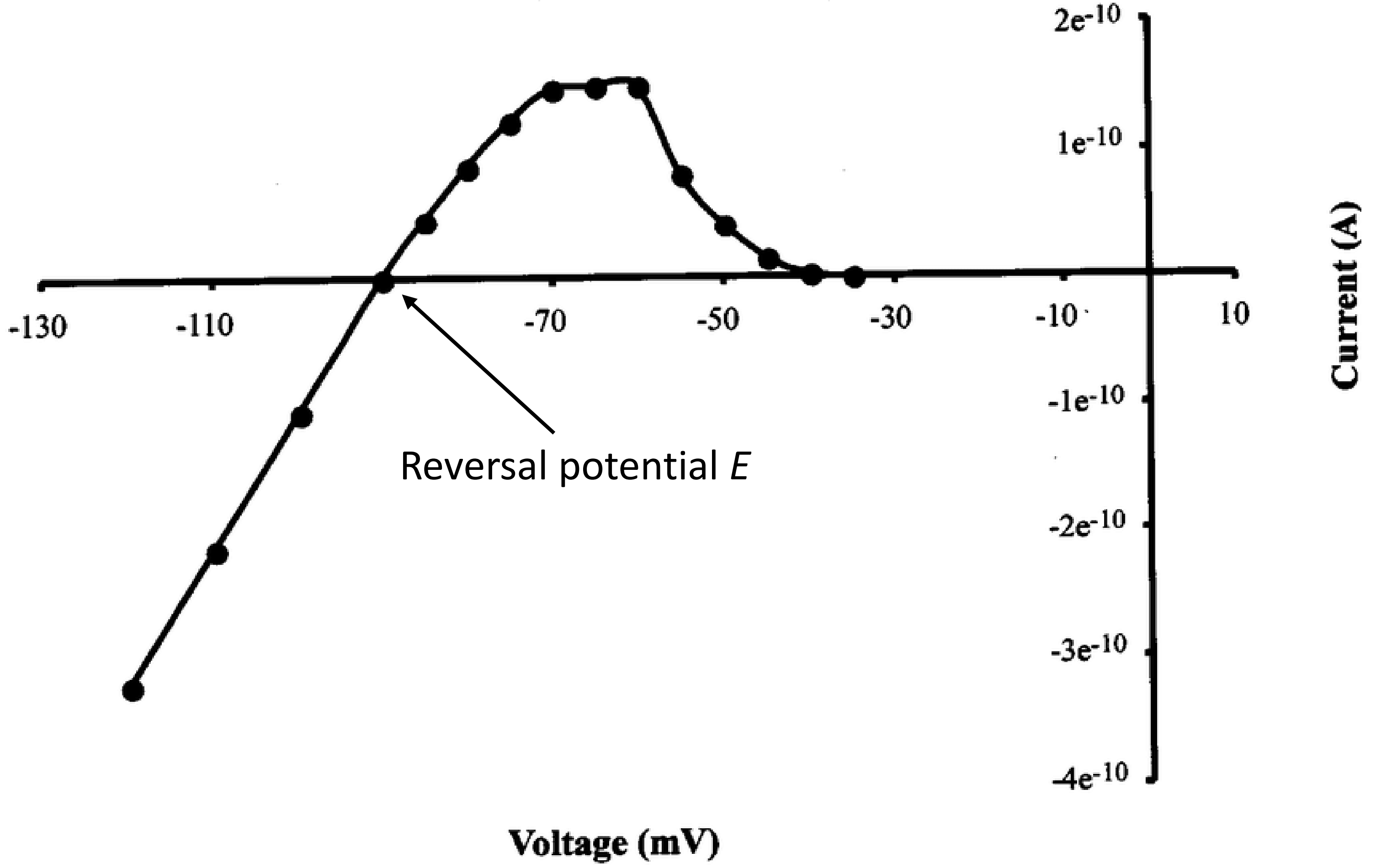
Example Ionic Current - Potassium



Example Ionic Current - Potassium

$$I = g(V - E)$$

Potassium has a reversal potential around -70 to -90 mV.



Example Ionic Current - Potassium

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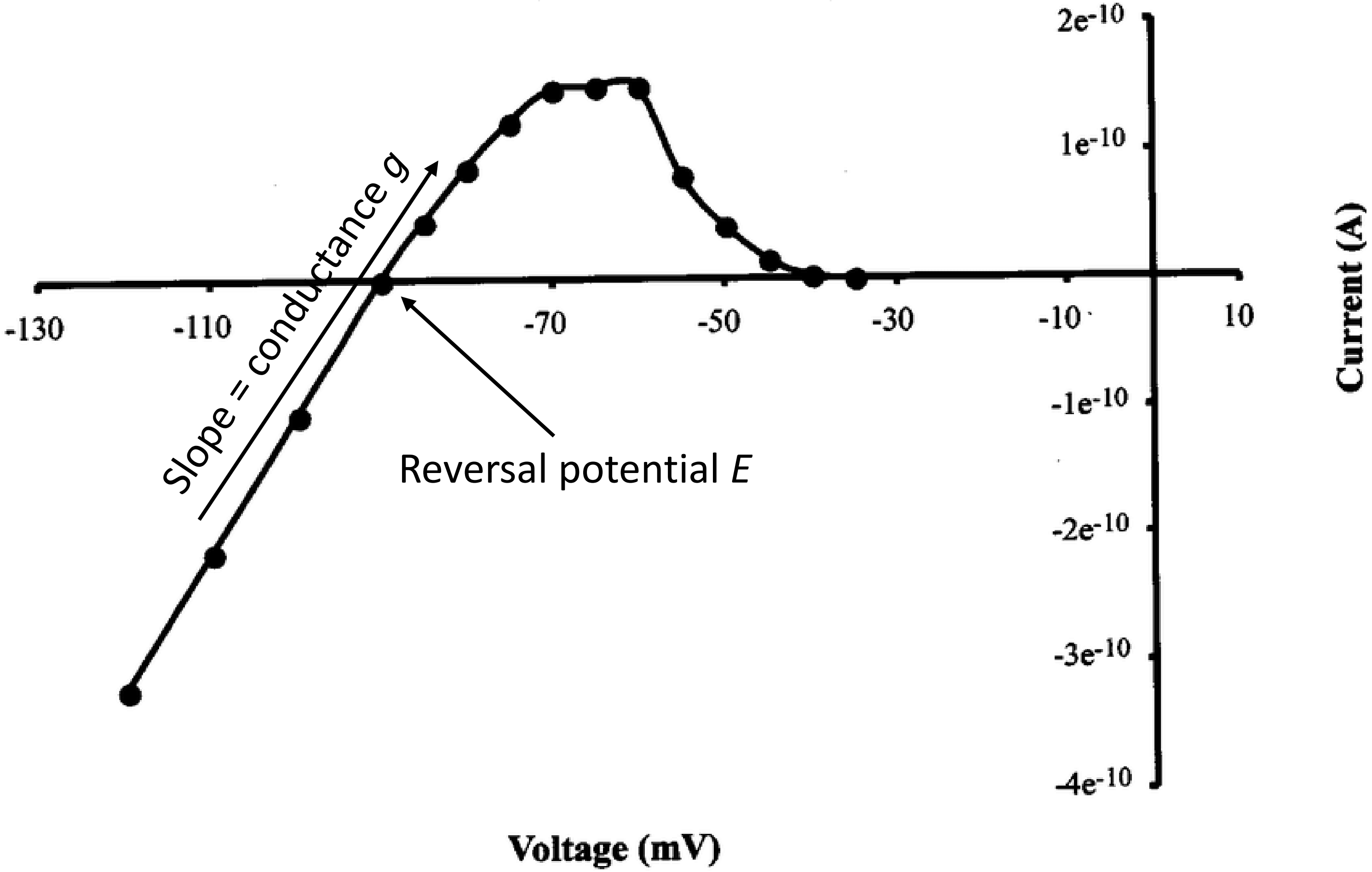
The linear Ohm's law approximation is a good model for voltages around the reversal potential, but breaks down for higher voltages

(in this particular case…)



Resting Potential and Ionic Current Flow

- At the resting potential, each ionic species *i* typically has a net flow through the membrane - but the total current over all ionic species sums to zero:

$$I_m(V) = \sum_i I_i(V)$$

$$I_i(V) = g_i(V - E_i)$$

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- Away from the resting potential, a net current flows:

$$I_m = \sum_i g_i(V - E_i) = g_m(V - E_m) \implies g_m = \sum_i g_i$$

- Again, Ohm’s law does not always hold! This is just an approximation…

Ionic Current Flow - Summary

- When the membrane potential is away from the reversal potential of an ionic species, ions will flow across the membrane (if it is permeable to that ion…)
- This current flow can be approximated by Ohm's law
- At the resting potential, the total membrane current is zero, but there can still be currents for each species of ion that cancel in sum
- Away from the resting potential, the total current can be modelled by a single membrane conductance g_m and resting potential E_m, ignoring individual ionic species

Passive Membrane Potential Dynamics

- So far we have discussed the reversal and resting potential, and the current that flows across the membrane when the neuron is away from these potentials

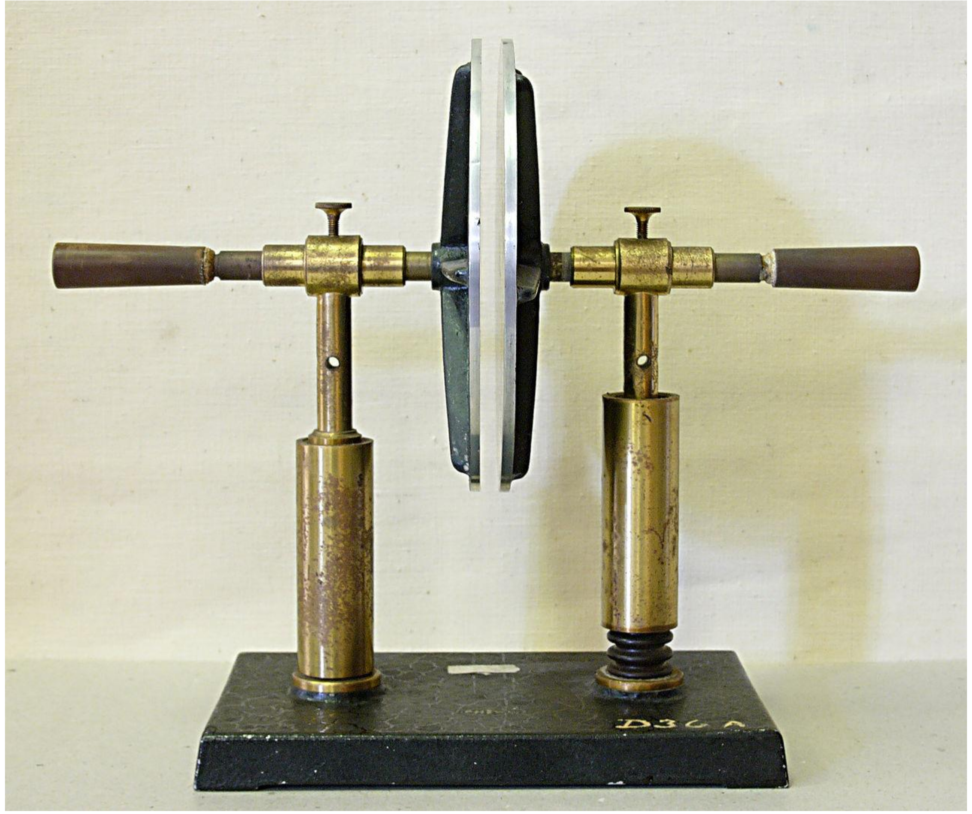
- How will the membrane potential change when current flows into or out of the neuron? What happens if we inject current through an electrode for example?

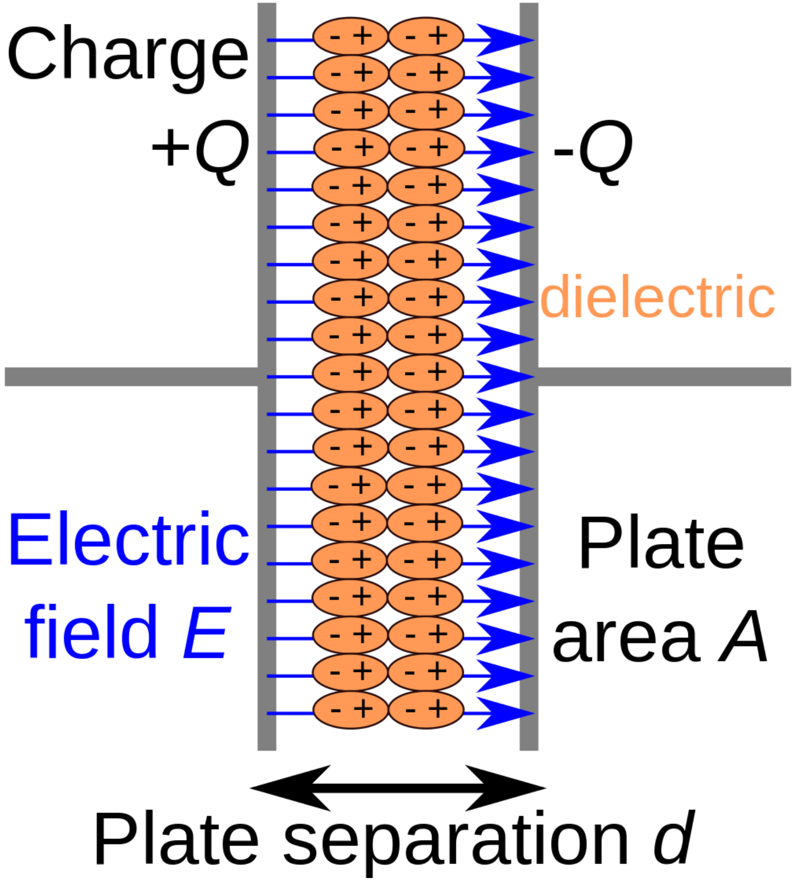
- Understanding this process is critical to understanding how neurons compute – neurons communicate by injecting current into each other via synapses

- This process can be modelled using two simple concepts from physics – capacitance, and current as the rate of change of charge with time

Capacitance

- A capacitor is two conductors separated by an insulator (e.g., metal plates + air)
- When a voltage *V* is applied across the capacitor, charge *Q* builds up. We define the capacitance as $C = Q/V$, i.e. amount of charge per applied voltage





Capacitance and Current

- When current is applied, it takes time for charge to build up on the capacitor (i.e. for the capacitor to “charge”). How can we model this?

- We use two facts:

1) the definition of capacitance: $Q = CV$

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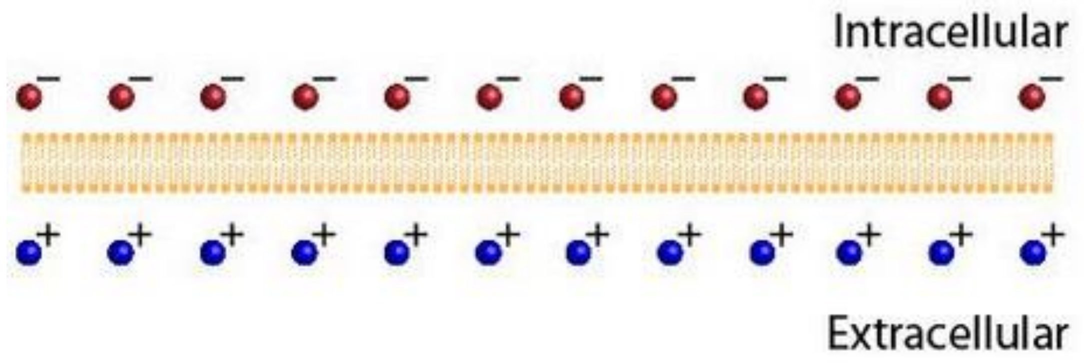
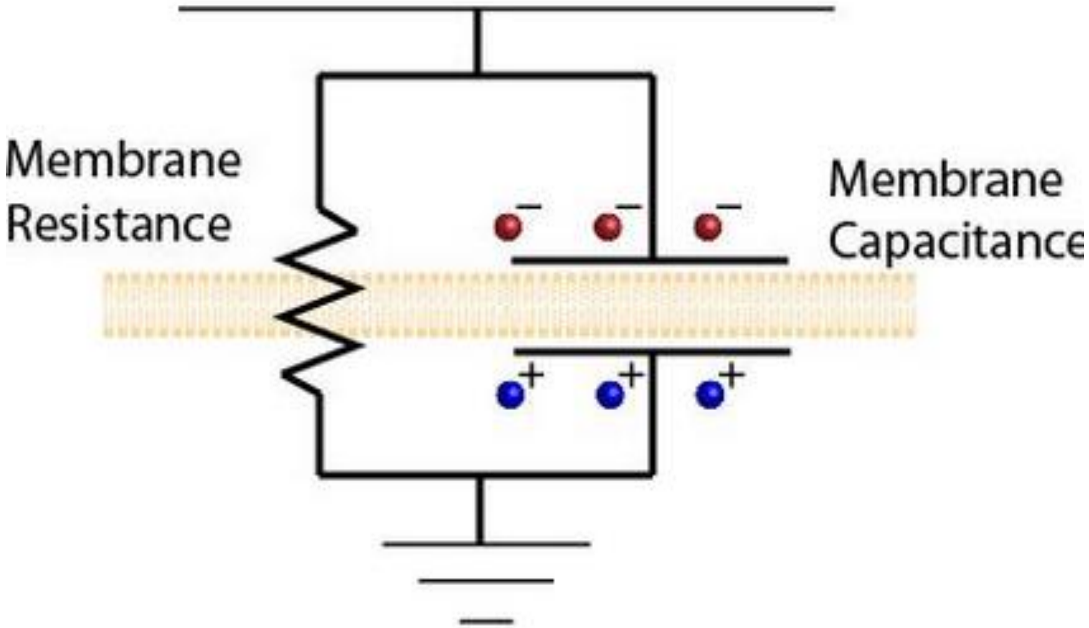
Equivalent Circuit Model for Membrane Potential

- We now consider how membrane currents influence the membrane potential
- The cell membrane is an insulator separating two conducting fluids, i.e. a capacitor
- Using our equations for capacitors and current flow, we get:

$$Q = C_m V \qquad C_m \frac{dV}{dt} = \frac{dQ}{dt} = -I_m$$





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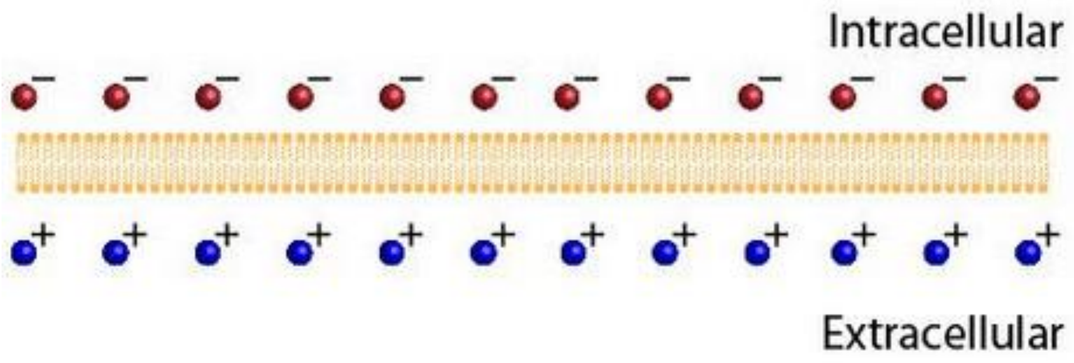
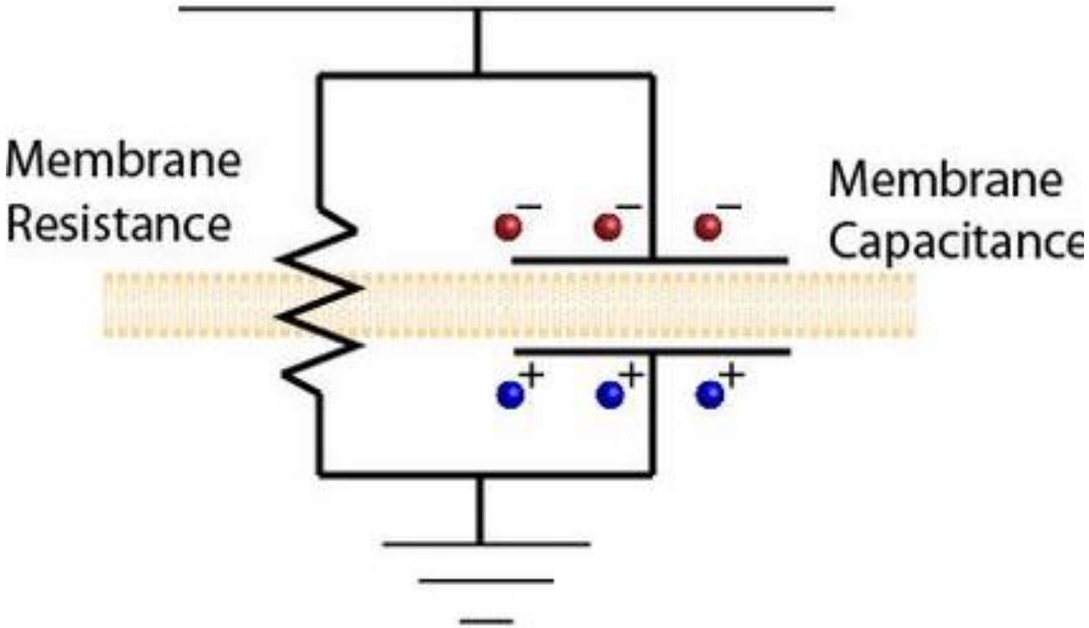
Negative sign defines outward flow as positive





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Membrane Potential Dynamics

- Various factors can cause current to flow across the membrane:

- Ions flowing through permanently open ion channels (passive/leak currents)

- Ions which flow through synaptic ion channels (synaptic input currents)

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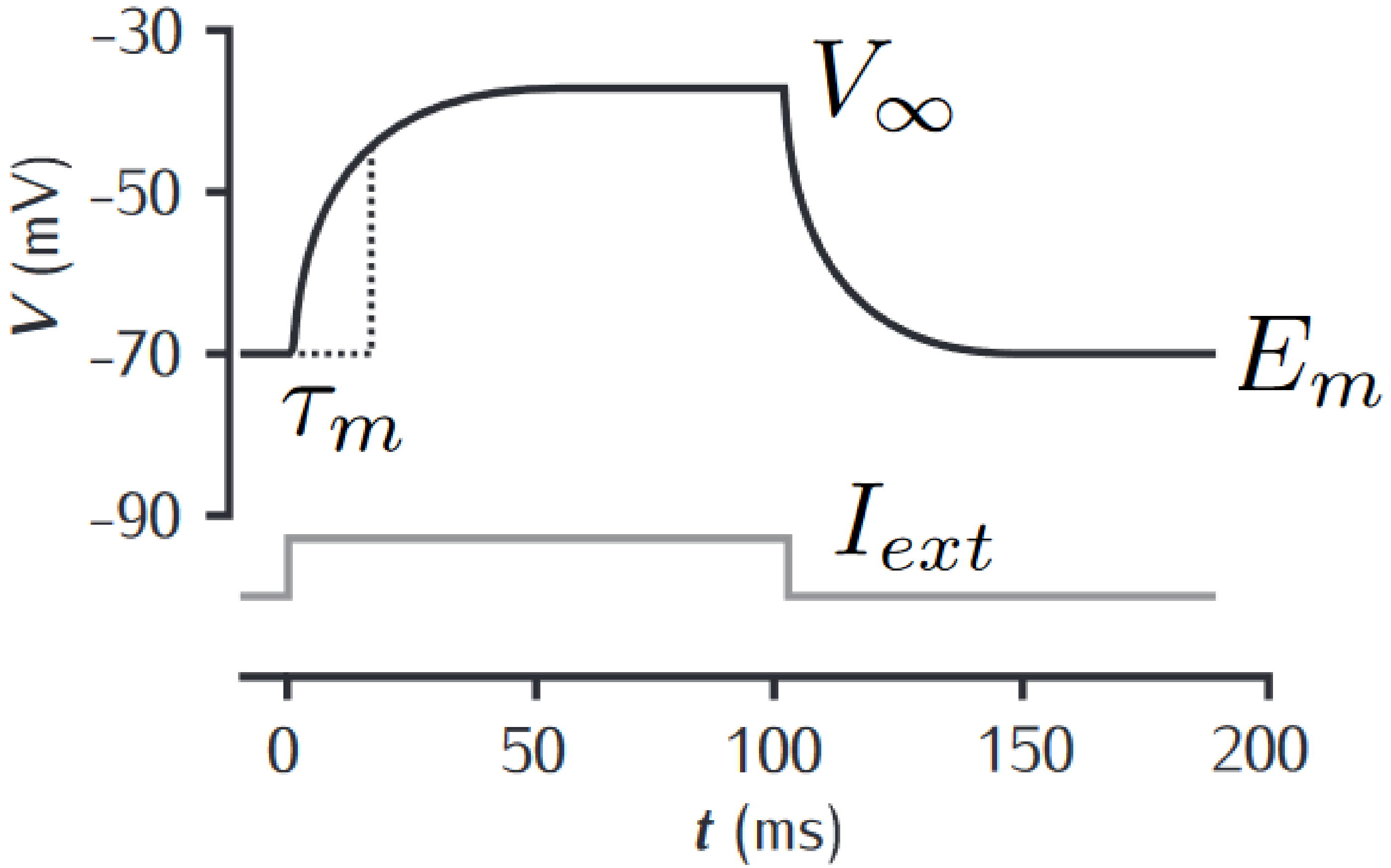
Decay of initial membrane potential towards resting potential

Low-pass filter of external current input (also called a "leaky integrator")

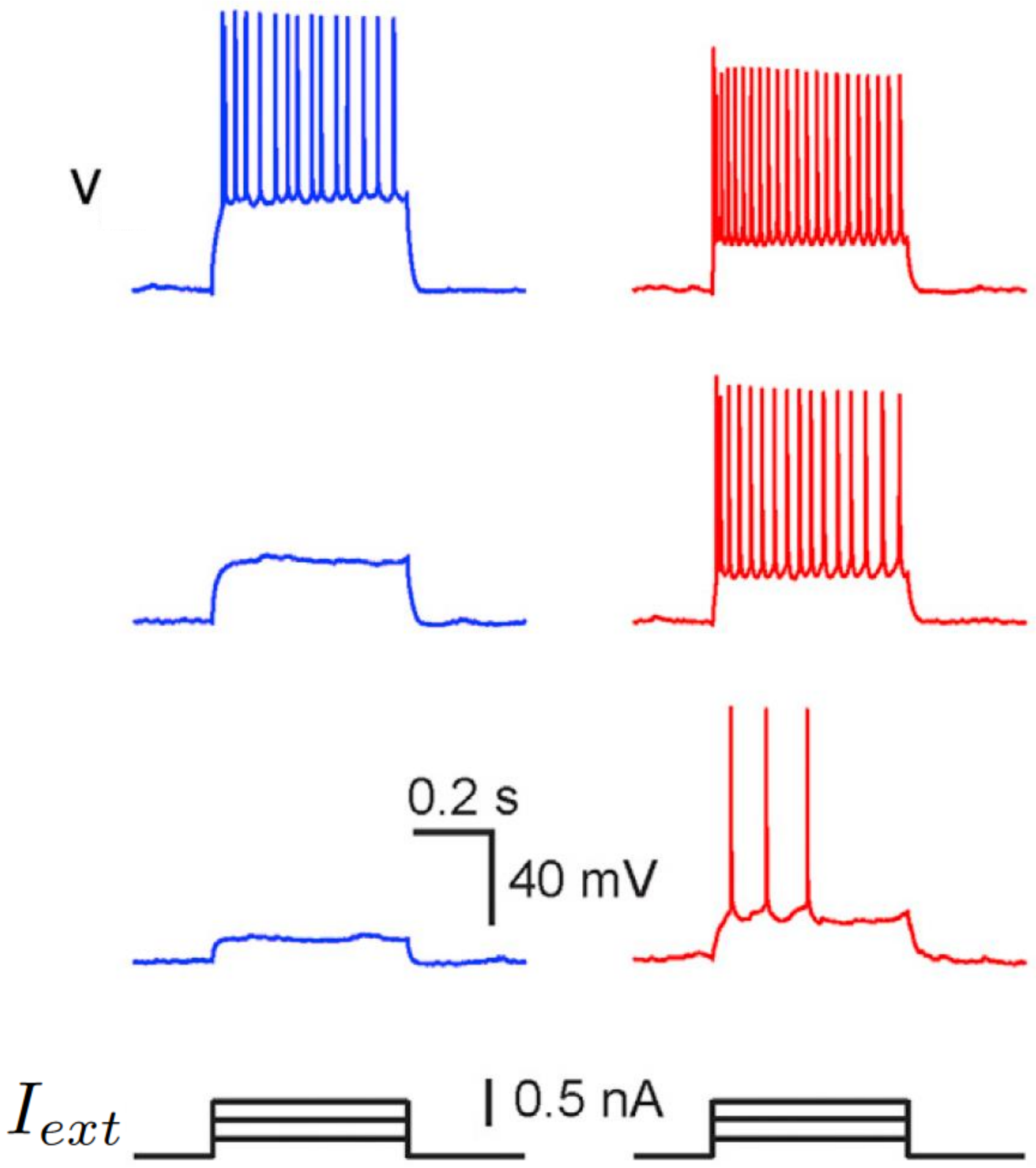
Response to Step Current

$$\tau_m \frac{dV}{dt} = -(V - E_m) + I_{ext}/g_m$$



Derivation: see additional slides

Response of Real Neurons to Step Current



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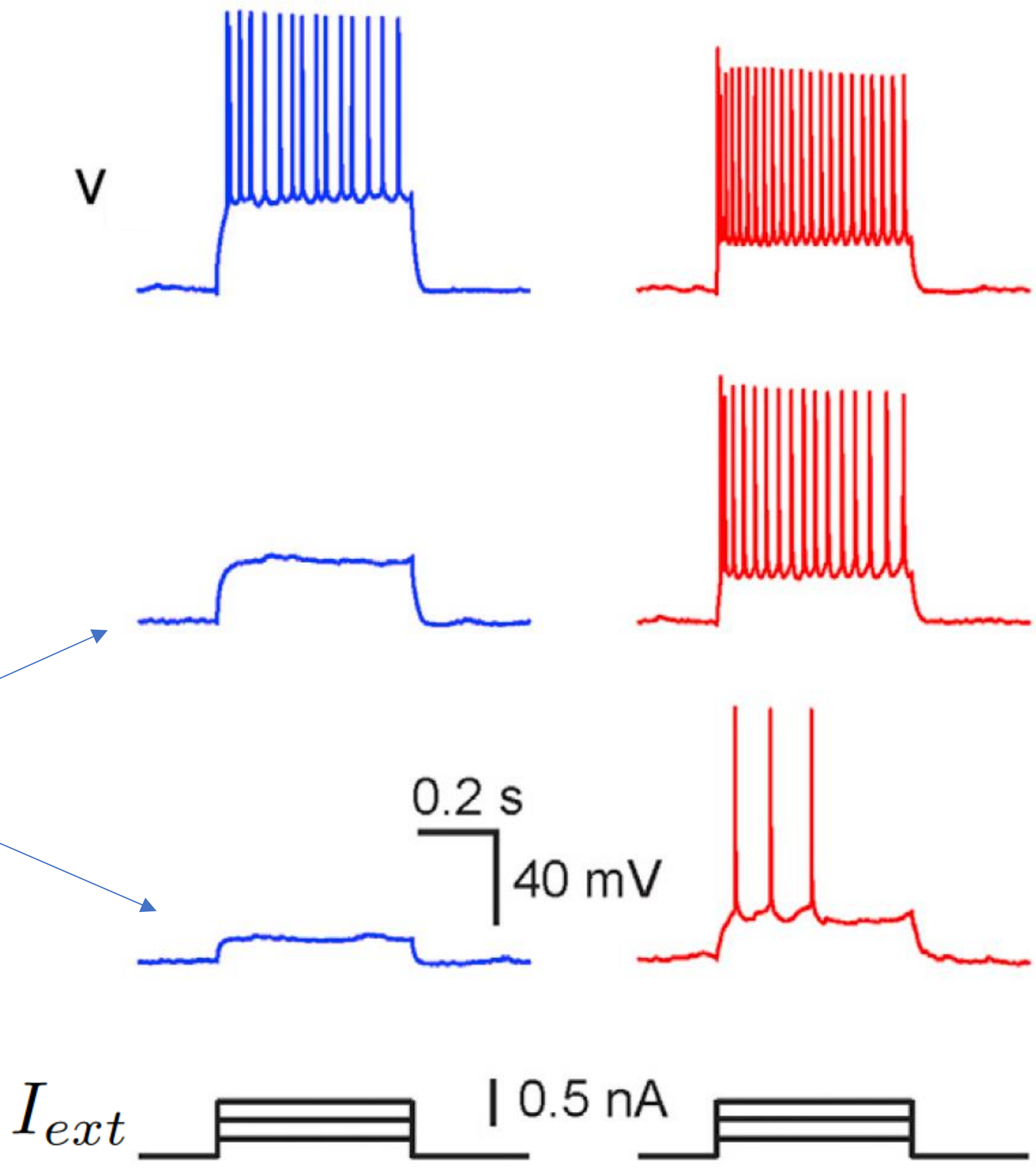
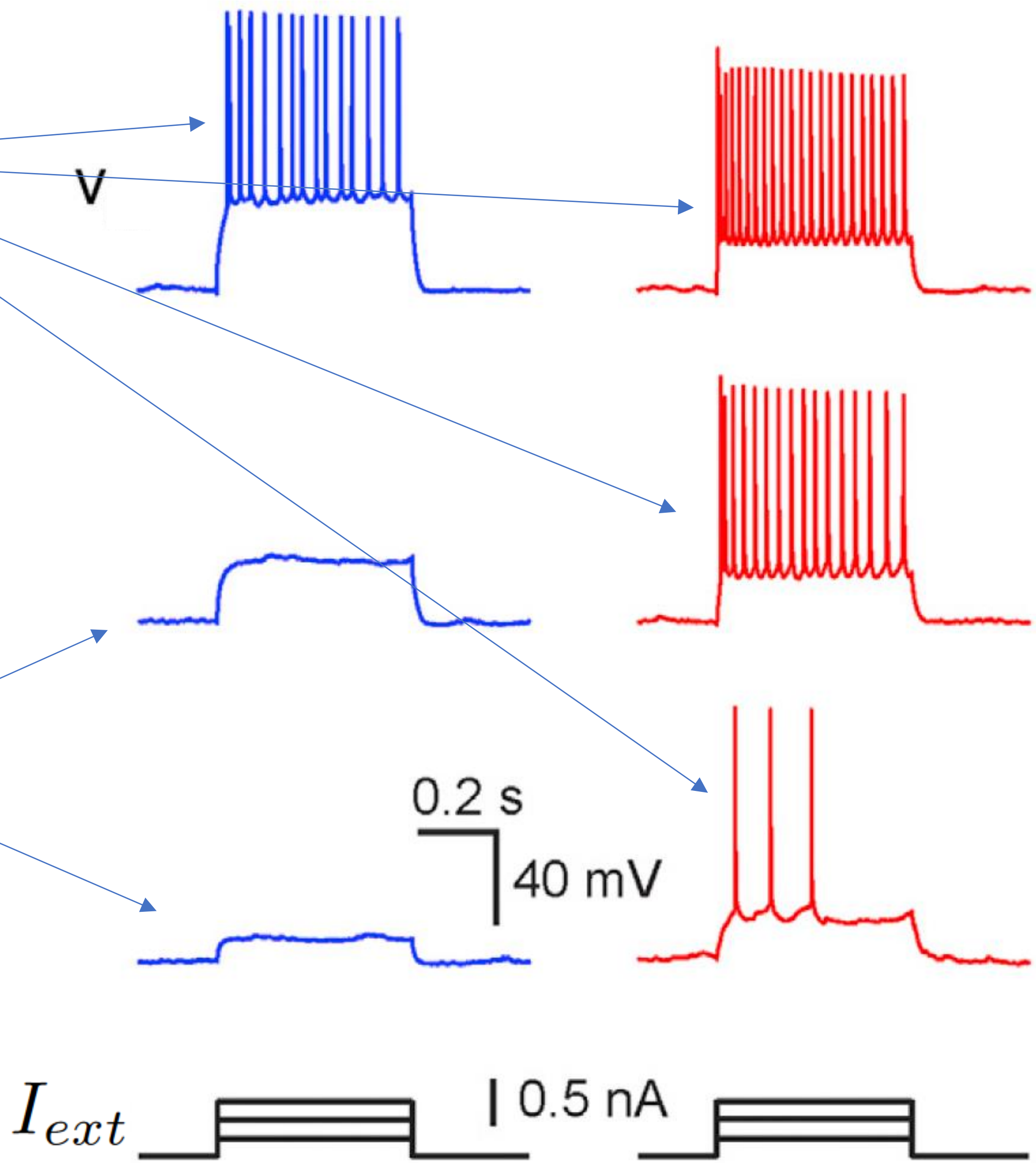


Well described by passive membrane dynamics equation

Response of Real Neurons to Step Current

Not explained by passive membrane dynamics equation

Well described by passive membrane dynamics equation



Passive Membrane Potential Dynamics - Summary

- Assumptions: model membrane currents using Ohm's law and model relationship between current and voltage by treating the cell membrane as a capacitor
- Solution: membrane potential is equal to the external input current integrated with an exponential filter
- Predicts that membrane potential has slow dynamics (~20 ms timescale) and acts as low pass filter of external input current
- Valid approximation for small deviations of membrane potential away from resting potential, can't account for the action potential (~1 ms timescale)
- Next lecture: active membrane potential dynamics, Hodgkin-Huxley model of the action potential

Bibliography

- *Neuronal Dynamics Ch. 1* (Gerstner et al.) https://neuronaldynamics.epfl.ch/online/index.html
- *Theoretical Neuroscience Ch. 5-6* (Dayan and Abbott)
- *Mathematical Foundations of Neuroscience Ch. 1* (Ermentrout and Terman)
- *Dynamical Systems in Neuroscience Ch. 1-2* (Izhikevich) https://www.izhikevich.org/publications/dsn.pdf

Steady State Solution

- For a constant current input, the passive membrane dynamics will settle into a constant membrane potential
- Derivation 1 - Solve equation for case of constant current input *Iext*, then take limit of large *t:*

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- Derivation 2 – set derivative to zero and solve for *V:*

$$\tau_m \frac{dV}{dt} = -(V - E_m) + I_{ext}/g_m = 0$$