Announcements:

Piazza is now set up – it is a great discussion tool – use it!

EC-Quiz2 – Monday (7/16) – CH4 (after lecture).

WS3-Equilibrium Potential Due Monday (after lecture).

Midterm 2 – Wednesday – CH3 + WS2 (membrane tutorial)

Boyle OH: Mondays 2-4pm CSB 130 & By appointment

Michael, Tania and Eric’s OH are posted on TritonEd

...ask questions ...discuss ...listen ...learn.
Signup Link:
https://piazza.com/ucsd/summer2018/cogs107a

Piazza Class Link:
https://piazza.com/ucsd/summer2018/cogs107a/home
Questions:

“How much of the detail (particularly relating to formulas and chemical compositions) do I need to know from the labs? All of it? I know basic stuff like the Nernst equation will obviously be on the midterm.”

1. What is the relationship between $[Na]_{0/l}$ & AP?
2. Injected current & AP?
3. Temperature?
4. Equilibrium potential
5. How does I affect AV?
6. Leak conductance?
7. Na/K pump?
THE ACTION POTENTIAL-PART 1

MARY ET BOYLE, PH.D.
DEPARTMENT OF COGNITIVE SCIENCE, UCSD
SIGNALING IN NEURONS – LEARNING OBJECTIVES

Differentiate the resting membrane potential from the action potential.

Describe the means for encoding information in the activity of neurons.

Understand that electrical signaling is the fundamental process that underlies all aspects of brain function.
Membrane: maintain electrical potential

Ions can only diffuse by passing through channels

Example: 1mMKCl
K+ (orange)
same [K+] on each side

When [K+] is not the same in both compartments: concentration gradient

Electrostatic pressure exactly balances with diffusion = equilibrium potential
Membrane: maintain electrical potential

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http://sites.sinauer.com/neuroscience5e/animations/02/neuro5e_0202.swf
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Example: 1mM KCl
K+ (orange)
same [K+] on each side

When [K+] is not the same in both compartments: concentration gradient

Electrostatic pressure exactly balances with diffusion = equilibrium potential
Equilibrium Potential for a single permeant ion

Simplify equation by entering constants

Nernst equation units:
Joules/coulomb
(which is the same as for volts)

Easier to perform calculations using base 10 logarithms and at room temperature

Simplification – yields with having the valence (z) and internal and external ion concentrations as the variables.
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The Nernst Equation

\[ E_{\text{ion}} = \frac{RT}{zF} \ln \frac{[\text{ion}]_o}{[\text{ion}]_i} \]

- \( E_{\text{ion}} \) = Equilibrium potential for the permeant ion
- \( R \) = Universal gas constant (8.31 joules/mole/°K)
- \( T \) = Temperature, in degrees Kelvin (°C + 273)
- \( F \) = Faraday constant (charge per mole: 96,500 coulombs/mole)
- \( z \) = Valence (electrical charge) of the ion
- \( \ln \) = Natural log (log to the base e)
- \([\text{ion}]_o\) = Outside concentration of the ion under consideration
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$$E_{ion} = \frac{\left(8.31 \text{ joules/mole/}^{\circ}\text{K}\right)(293^{\circ}\text{K})}{\left(96,500 \text{ coulombs/mole}\right)z} \ln \frac{[\text{ion}]_o}{[\text{ion}]_i}$$

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\[ E_{\text{ion}} = \frac{58}{z} \log \frac{[\text{ion}]_o}{[\text{ion}]_i} \]
Equilibrium Potential for a single permeant ion

- Simplify equation by entering constants.

Nernst equation units:
Joules/coulomb (which is the same as for volts)

- Easier to perform calculations using base 10 logarithms and at room temperature.

Simplification - yields with having the valence (z) and internal and external ion concentrations as the variables.

**The Potassium Equilibrium Potential**

\[ E_k = \frac{58}{(+1)} \log \frac{20 \text{ mM}}{400 \text{ mM}} \]

To calculate \( E_k \) for a squid axon:

- \( Z \) for \( K^+ = +1 \) (Each \( K^+ \) ion carries a charge of +1)
- \([K^+]_o = 20 \text{ mM}\)
- \([K^+]_i = 400 \text{ mM}\)

\[ E_k = \frac{58}{(+1)} \log \frac{20 \text{ mM}}{400 \text{ mM}} = -76 \text{ mV} \]
The Nernst equation predicted that the $E_k = -76\text{mV}$ (squid).

However, when recording from the axon the resting membrane potential was -65mv? Why?

If the resting membrane potential were only driven by $K$ then we should see the changes in $V_m$ as a function of $[K]_o$.

Note: as $[K]_o$ increases so does $V_m$ ... and eventually $V_m = 0\text{mV}$.

However, the Nernst equation would predict a linear relationship ... What accounts for the difference?
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However, the Nernst equation would predict a linear relationship ... What accounts for the difference?
The discrepancy between $E_r$ and the true resting potential is because there are more than one ion that is permeant.

$K^+$ is the most permeant ion - but $Na^+$ and $Cl^-$ are also leaky at rest.

To calculate the true resting potential - one must incorporate the other permeant ions.

Goldman equation: concentrations and relative permeabilities of multiple ions.

Reformulate the Goldman eq. in terms of permeability of each ion relative to $K$ (b/c it is the dominant ion).

Typical values for relative permeabilities of sodium, potassium and chloride are: $PK:PNa:PCl = 1.00 : 0.04 : 0.45$. 
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The Goldman Equation:

$$E_m = 58 \log \frac{P_K [K^+]_o + P_{Na} [Na^+]_o + P_{Cl} [Cl^-]_i}{P_K [K^+]_i + P_{Na} [Na^+]_i + P_{Cl} [Cl^-]_o}$$

Ratio of external to internal ion concentrations

$$E_m = 58 \log \frac{P_K [K^+]_o + P_{Na} [Na^+]_o + P_{Cl} [Cl^-]_i}{P_K [K^+]_i + P_{Na} [Na^+]_i + P_{Cl} [Cl^-]_o}$$

Permeability coefficients

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$P_{Na}/P_K = \text{permeability of Na}^+ \text{ relative to that of K}^+$

$P_{Cl}/P_K = \text{permeability of Cl}^- \text{ relative to that of K}^+$

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<tbody>
<tr>
<td>outside</td>
<td>20</td>
<td>440</td>
<td>560</td>
</tr>
<tr>
<td>inside</td>
<td>400</td>
<td>50</td>
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\[
E_m = 58 \log \left( \frac{20}{400} + 0.04 \left( \frac{440}{50} \right) + 0.45 \left( \frac{40}{560} \right) \right) = -62 \text{ mV}
\]

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$PK:PNa:PCl = 1.00:0.04:0.45$. 
INTRODUCTION

• Action Potential in the Nervous System
  • Conveys information over long distances
  • Cytosol has negative charge relative to extracellular space
  • Neural code - frequency and pattern
  • Action potential
    • Spike
    • Nerve impulse
    • Discharge
CONSIDER THE FOLLOWING EXPERIMENTAL SETUP:

- **record**
- **stimulate**
- Microelectrode to measure membrane potential
- Microelectrode to inject current
THE EXPERIMENT:

- **record**
- **stimulate**

Diagram showing the process of recording and stimulating neuron activity.
WATCH ANIMATION – ACTION POTENTIAL

http://www.sumanasinc.com/webcontent/animations/content/action_potential.html
Caused by depolarization of membrane beyond threshold
  • “All-or-none”
  • Chain reaction
The Distribution of Ions Across The Membrane

- K\(^+\) more concentrated on inside,
- Na\(^+\) and Ca\(^{2+}\) more concentrated outside

<table>
<thead>
<tr>
<th>Ion</th>
<th>Concentration outside (in mM)</th>
<th>Concentration inside (in mM)</th>
<th>Ratio Out : In</th>
<th>(E_{\text{ion}}) (at 37°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>K(^+)</td>
<td>5</td>
<td>100</td>
<td>1 : 20</td>
<td>-80 mV</td>
</tr>
<tr>
<td>Na(^+)</td>
<td>150</td>
<td>15</td>
<td>10 : 1</td>
<td>62 mV</td>
</tr>
<tr>
<td>Ca(^{2+})</td>
<td>2</td>
<td>0.0002</td>
<td>10,000 : 1</td>
<td>123 mV</td>
</tr>
<tr>
<td>Cl(^-)</td>
<td>150</td>
<td>13</td>
<td>11.5 : 1</td>
<td>-65 mV</td>
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What is the Equilibrium Potential for an Ion?

An equilibrium potential for an ion is - the membrane potential that results if a membrane is selectively permeable to that ion alone.
Examples:
Current membrane potential is $V_m$; If $g_{C^+} \gg 0$, which way would ion $C^+$ go?

- a. $C^+$ would go into the cell
- b. $C^+$ would leave the cell
- c. $C^+$ would neither enter nor leave the cell
- d. Cannot tell, not enough information.
Current membrane potential is $V_m$; If $g_{C^+} >> 0$, which way would ion $C^+$ go?

- a. $C^+$ would go into the cell
- b. $C^+$ would leave the cell
- c. $C^+$ would neither enter nor leave the cell
- d. Cannot tell, not enough information.
Current membrane potential is $V_m$; If $g_{C^+} = 0$, which way would ion $C^+$ go?

<p>| | |</p>
<table>
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Current membrane potential is \( V_m \);

If \( g_{w-} \gg 0 \), what would happen to the membrane potential?

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<tr>
<td>a.</td>
<td>( V_m ) would approach ( E_w ) and become more positive</td>
</tr>
<tr>
<td>b.</td>
<td>( V_m ) would approach ( E_w ) and become more negative</td>
</tr>
<tr>
<td>c.</td>
<td>( V_m ) would become more positive than ( E_w )</td>
</tr>
<tr>
<td>d.</td>
<td>Cannot tell, not enough information.</td>
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Current membrane potential is $V_m$; If $g_{W^-} = 0$, which way would ion $W^-$ go?

- a. $W^-$ would go into the cell
- b. $W^-$ would leave the cell
- c. $W^-$ would neither enter nor leave the cell
- d. Cannot tell, not enough information.
Current membrane potential is $V_m$; If $g_{W-} \gg 0$, which way would ion $W-$ go?

- a. $W-$ would go into the cell
- b. $W-$ would leave the cell
- c. $W-$ would neither enter nor leave the cell
- d. Cannot tell, not enough information.
Examples:

$mV$

$E_{C+}$

$mSec$
Examples:

$E_w$ vs. $t_{\text{mSec}}$

$V_m$
Examples:

\[ \text{mV} \]

\[ E_{W-} \]

\[ \text{mSec} \]
Examples:

$E_{K^+}$

$-80$ mV

$mSec$
Examples:
Examples:

\[ E_{Na^+} \quad 62 \text{mV} \]

\[ E_{K^+} \quad 80 \text{mV} \quad \text{mSec} \]
Examples:
THE UPS AND DOWNS

Rising phase
Overshoot
Falling phase
Undershoot
Recovery

resting potential

overshoot
undershoot
recovery

rising phase
falling phase

(a) Time (msec)

Membrane potential (mV)
A CLOSER LOOK AT ACTION POTENTIALS

- Artificially inject current into a neuron using a microelectrode
FIRING FREQUENCY = MAGNITUDE OF \( I \)
1. water (in cytosol and extracellular fluid; polar);
2. ions (monovalent, divalent, cation, anion; Na⁺, K⁺, Ca²⁺, Cl⁻);
3. phospholipid bilayer (phospholipids have polar, hydrophilic heads and nonpolar, hydrophobic tails);
4. proteins (enzymes, cytoskeleton, receptors, channel proteins, ion pumps).

### Cast of Molecules

#### Ion Channels
1. Ion channels • membrane-spanning proteins (have hydrophobic bodies and hydrophilic tails);
2. ion-specific • no ATP needed;
3. movement directed by diffusion along concentration gradients

#### Ion Pumps
1. Ion pumps • membrane-spanning proteins • ATP is needed;
2. movement against concentration gradient •
3. Examples: sodium-potassium pump; calcium pump
1. the membrane possesses channels permeable to the ions.
2. there is a concentration gradient across the membrane

**Movement of Ions**

**Diffusion**
1. the membrane possesses channels permeable to the ions,
2. there is a concentration gradient across the membrane

**Electricity**
1. the membrane possesses channels permeable to the ions,
2. there is an electrical potential difference across the membrane

**Current (I)**
1. movement of electrical charge • flows in the direction of cations (i.e. sodium ions)

**Potential (V)**
1. Potential (V) • voltage, or the force exerted on charged particles •
2. the amount of force reflects difference in charge between anode and cathode;
3. greater difference, greater force

**Conductance (g)**
1. relative ability of charge to migrate; inverse of resistance •
2. depends on the number of particles available to carry charge
3. depends on the number of channels
Movement of Ions

Ohm’s Law

\[ I = gV \]
\[ V = IR \]

Neuro version of Ohm’s Law:

\[ I_{ion} = g_{ion} \times (V_m - E_{ion}) \]
THE ACTION POTENTIAL, IN THEORY

- Depolarization (influx of Na\(^+\)) and repolarization (efflux of K\(^+\))
- Membrane Currents and Conductances
  - Current
    - The net movement of K\(^+\) across membrane
  - Potassium channel number
    - Proportional to electrical conductances
  - Membrane potassium current
    - Flow and driving force
Action Potential has 6 phases:

1. Resting
2. Rising
3. Overshoot
4. Falling
5. Undershoot
6. Recovery
1. Resting leak

Diagram:

1. Resting potential
2. Rising phase
3. Overshoot phase
4. Falling phase
5. Undershoot phase
6. Recovery

Leak potassium channel
2 Rising v Na⁺

Diagram showing phases of a voltage trace:
1. Resting potential
2. Rising phase
3. Overshoot phase
4. Falling phase
5. Undershoot phase
6. Recovery
3 overshoot

\[ g_{Na} \to 0 \]

\[ g_{K} \gg 0 \]
4 Falling

\[ g_{K} \gg 0 \Rightarrow \text{v}_{K}^{+} \]

\[ g_{Na} = 0 \]
5 undershoot
Recovery

$\text{K}^+$ channels close
At rest, which ion channels are open?

a. Voltage-gated Na+ channels
b. Voltage-gated K+ channels
c. K+ leak channels
d. None of the channels.
e. All of the channels.
**Action Potential**

**Depolarization**
1. A change in membrane potential from normal resting value to less negative value
2. Increasing extracellular potassium ions depolarizes cells

**Threshold**
1. Critical level of depolarization that is needed to trigger action potential
2. Membrane potential must depolarize beyond threshold to fire action potential
3. Action potentials are “all or none.”

**Firing Frequency**
1. If more current is injected, size of action potentials do not change, firing rate increases
2. Maximum firing frequency is 1000 Hz.
3. Absolute refractory period is 1 msec.
What is the threshold potential?

<table>
<thead>
<tr>
<th></th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>a.</td>
<td>Critical level of depolarization that is needed to trigger action potential</td>
</tr>
<tr>
<td>b.</td>
<td>The membrane potential associated with VK+ channels</td>
</tr>
<tr>
<td>c.</td>
<td>The membrane potential associated with K+ leak channels</td>
</tr>
<tr>
<td>d.</td>
<td>None of above</td>
</tr>
</tbody>
</table>
What determines firing frequency?

a. Amount of current injected
b. The absolute refractory period
c. All of the above
d. None of above
• Na-K pump
• K channels
• Na channels

Pump works continuously to keep the concentration gradients.

Initial Conditions:
• K ratios: $K_i[20]:K_o[1]$
• Na ratios: $Na_i[1]:Na_o[10]$
• $E_K = -80\text{mV}$
• $E_{Na} = 62\text{mV}$
• $g_K = 0\text{mV}$
• $V_m = 0\text{mV}$

$I_k = g_k(V_m - E_k)$
$= g_k(0 - (-80\text{mV}))$
$= g_k(80\text{mV})$
$= 0 \times (80\text{mV})$
$= 0\text{mV}$
Net movement of K is an electrical current ($I_k$).

- The number of K channels is proportional to the conductance ($g_k$).
- Membrane potassium current will flow as long as $V_m \neq E_k$.
- Recall: driving force is defined as: $V_m - E_k$.

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

$$I = gV \quad \text{(Ohm’s Law)}$$

Relationship between ionic driving force, ionic conductance and the amount of ionic current that will flow.

$$I_k = g_k(V_m - E_k)$$
At equilibrium there is no net potassium current because:

- $V_m = E_k$
- Even though $g_k > 0 \text{mV}$

$$I_k = g_k(V_m - E_k) = g_k(0 \text{mV}) = 0 \text{mV}$$
Initial Conditions:
- K ratios: $K_i[20]:K_o[1]$
- Na ratios: $Na_i[1]:Na_o[10]$
- $E_{Na} = 62$mV
- $E_k = -80$mV
- Permeable only to K
- $V_m = E_k$

What’s happening to Na?
Driving force for Na:
\[ = [V_m - E_{Na}] \]
\[ = -80$mV $- 62$mV \]
\[ = -142$mV \]
Open the Na channels:
• $g_{Na} = \text{very high}$
• High driving force for Na
  $= [V_m - E_{Na}] = -142\text{mV}$

Stage is set to have a high Na current

$\mathbf{I}_{Na} = g_{Na}(V_m - E_{Na})$

$V_m \rightarrow E_{Na} = 62\text{mV}$
Na channels quickly close & K channels remain open

- \( g_{Na} = 0 \)
- High driving force for K
  \[
  \text{High driving force for K} = [V_m - E_K] \\
  \approx [40 - (-80)] \approx 120 \text{mV}
  \]

Dominant ion: K

\[
I_K = g_K(V_m - E_K) \\
V_m \rightarrow E_K = -80 \text{mV}
\]
K channels remain open

- \( g_{Na} = 0 \)
- Resting membrane potential
  \[ V_m = E_K = -80 \text{mV} \]

Dominant ion: K

\[
I_K = g_K(V_m - E_K)
\]

\( V_m \rightarrow E_K = -80 \text{mV} \)
“The movie shows that the amplitude of the action potential depends on the value of $E_{Na}$.”

- An action potential is generated in three different concentrations of external [Na]:
  - 140 mM (the normal value),
  - 70 mM and
  - 14 mM.
- The internal [Na] is 14 mM.
- The three corresponding values of $E_{Na}$: (red lines)
  - 55 mV
  - 39 mV
  - 0 mV
VOLTAGE CLAMP - TECHNIQUE

• Determine the relative contribution of Na$^+$ and K$^+$ to the action potential

• Voltage Clamp → “clamp” $V_m$ at any value
  • Look at the changes in membrane conductance as a function of membrane potential
    • Measure Na$^+$, K$^+$, Cl$^-$, and Ca$^{++}$ currents
  • Kenneth C. Cole – invented
  • Hodgkin and Huxley (1950s)
    • Giant squid axon
    • Nobel Prize
Voltage Clamp: “Clamp” membrane potential at any chosen value

Rising phase → transient increase in $g_{Na}$, influx of Na$^+$ ions

Falling phase → increase in $g_K$, efflux of K$^+$ ions

Existence of sodium “gates” in the axonal membrane
VOLTAGE CLAMP
A glass pipette with a very small opening is used to make tight contact with a tiny area, or patch, of neuronal membrane.

After the application of a small amount of suction to the back of the pipette, the seal between pipette and membrane becomes so tight that no ions can flow between the pipette and the membrane. Thus, all the ions that flow when a single ion channel opens must flow into the pipette. The resulting electrical current, though small, can be measured with an ultrasensitive electronic amplifier connected to the pipette.

When the interior of the pipette becomes continuous with the cytoplasm of the cell. One can measure the electrical potentials and currents from the entire cell and is therefore called the whole-cell recording method. The whole-cell configuration also allows diffusional exchange between the pipette and the cytoplasm, producing a convenient way to inject substances into the interior of a “patched” cell.

Thus, all the ions that flow when a single ion channel opens must flow into the pipette. The resulting electrical current, though small, can be measured with an ultrasensitive electronic amplifier connected to the pipette.
THE VOLTAGE-GATED SODIUM CHANNEL

- Structure: single long polypeptide with four transmembrane domains (I-IV) and ion-selective pore

Each domain consists of six transmembrane alpha helices (S1-S6)

Pore loop is a selectivity filter.
The ion water complex is used to select Na\(^+\) and exclude K\(^+\).

Conformational changes of the voltage gated sodium channel as a function of membrane potential.
“This movie illustrates the exquisite sensitivity of the stimulus current amplitude for generation of an action potential.

• A brief current pulse of 0.06564 nA injected into a patch of membrane causes a subthreshold response
• but a second stimulus (0.06565 nA) is suprathreshold and generates an impulse.

➢ A change of 0.00001 nA in stimulus current strength can change the membrane's response from "none" to "all" after a long “decision time.”

➢ The subthreshold response lingers for several milliseconds after the stimulus before the K current wins the battle with the Na current and the voltage returns to rest.

➢ The suprathreshold response also lingers after the stimulus, but the Na current is clearly gaining on the K current.

➢ It finally wins the battle and an action potential is generated.”
What is the state of the VNa+ channel?

a. open
b. closed
c. inactive
d. None of above
Patch-clamp sealing the tip of an electrode with a very small patch of neuronal membrane.

Ionic currents across membrane can be measured as the membrane potential is clamped at any desired value. (e.g. -65mV & -40mV)

Ideal situation: only one channel in the patch – study properties of channel.

Characteristics of voltage gated Na⁺ channels:

Open with a little delay
Stay open for about 1msec
Become inactive (close)
Cannot reopen until membrane potential returns to a negative value.
"The Squid and its Giant Nerve Fiber" was filmed in the 1970s at Plymouth Marine Laboratory in England. This is the laboratory where Hodgkin and Huxley conducted experiments on the squid giant axon in the 1940s.
TWO WAYS TO RECORD THE AP

intracellular

extracellular
DIFFERENCES BETWEEN INTRACELLULAR AND EXTRACELLULAR RECORDINGS

Intracellular
- Electrode inside the neuron detects the AP in the positive direction relative to the resting (-65mV) potential.
- AP → Na+ enter the cell from the extracellular fluid.
- Recording a single neuron.

Extracellular
- Electrode is outside – connected to ground – electrical potential is 0mV
- When the AP comes along, Na leaves the extracellular fluid to enter the neuron.
- Biphasic spike: negative peak from one input + positive peak from the other input
- Bundles of axons – multiple spikes from different axons with different diameters.
GIANT AXONS IN THE EARTHWORM

REFRACTORY PERIOD

Two stimulating pulses
Vary the time delay for the second pulse
Decrease interval between pulses
The interval at which the second pulse cannot be initiated is the refractory period.
Passive Membrane Properties

Mary ET Boyle, Ph. D.
Department of Cognitive Science
Sub-threshold current injection in unmyelinated axon.

Watch the membrane potential change as the current injected spreads passively.
Injected current spreads passively along the axon.

Potential (V_m) responses recorded along the axon.

The effects of the current injection attenuate with distance.

Notice V_m decreases because the current leaks out.
Axon

Stimulate

The potential decays exponentially with increasing distance.
Passive membrane conductance decays over distance

A current-passing electrode produces a current that yields a sub-threshold change in membrane potential, which spreads passively along the axon.

Potential responses recorded at the positions indicated by microelectrodes.

With increasing distance from the site of current injection the amplitude of the potential change is attenuated as current leaks out of the axon.

Relationship between the amplitude of potential responses and distance.
Passive flow of current affects all aspects of electrical signaling in nerve cells.

Passive current flow varies with distance along a neuron.

\[ V_x = V_0 e^{-\frac{x}{\lambda}} \]

- \( V_x \) is the voltage response at any distance \( x \) along the axon.
- \( V_0 \) is the voltage change at the point where current is injected into the axon.
- \( e \) is the base of natural logarithms (approx. 2.7).
- \( \lambda \) is the length constant of the axon.
Exponential Function: plot: relative reduction in amplitude over distance

Superimposed responses to current pulse from different distances along the axon (see previous slides)
$V_x$: voltage response at distance $x$

$V_0$: voltage response at current inj.

$V_x = V_0 e^{-x/\lambda}$

Distance from current injection (mm)

Graph shows the relationship between $V_x / V_0$ and distance from current injection, with $V_x = V_0 e^{-x/\lambda}$ as the exponential function. The graph illustrates how the voltage response decreases as the distance from the current injection point increases, with a significant reduction at $0.4$ of the original voltage ($37\%$) at a distance of $1.0$ mm. The inset graph shows superimposed responses to current pulse from different distances along the axon, indicating the relative reduction in amplitude over distance.
current injection

distance $x$ - along axon
$V_x$: voltage response at distance $x$

$V_0$: voltage response at current inj.

Recall: $e = 2.7$

$x$ is the distance along the axon where $V_0$ decays to 37% (or $1/e$).

$L$ is the length constant.

$V_x = V_0 e^{-x/L}$
What does the length constant (\( \lambda \)) tell us:

\( \lambda \) tells us how far passive current flows before it leaks out.

\[ \Rightarrow \text{the leakier the axon, the smaller the } \lambda \text{ value!} \]
Key Properties of the Action Potential

- Threshold
- Rising phase
- Overshoot
- Falling phase
- Undershoot
- Absolute refractory period
- Relative refractory period