# Lesson 4. THE PASSIVE AXON

The electrical excitation characteristics of nerve axons are due to the properties of voltage activated $Na^+$ and $K^+$ channels spanning the bilayer membrane. Modeling of these characteristics is complex, so we begin with a simpler case: we model the electrical properties of a simple membrane with channels that are not voltage activated. This can be approximated in the laboratory by applying toxic agents such as. tetrodotoxin and tetraethylammonium, to block the voltage activated channels.

## OBJECTIVES

**1.** To learn how to model flow of ions.

**2.** To model electrical properties of a passive cell membrane.

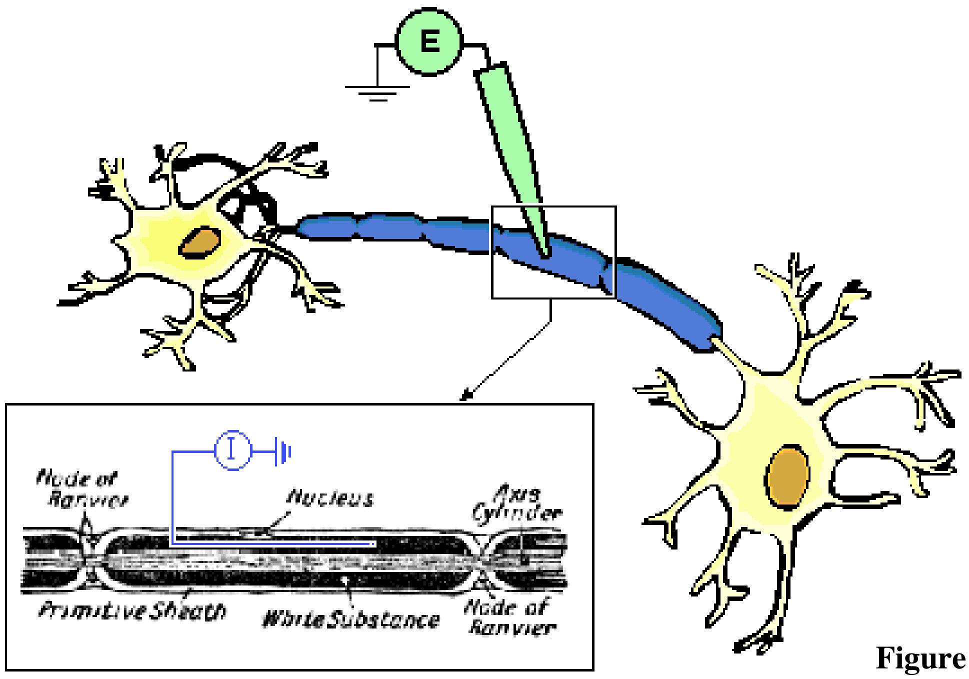


**Figure 1**

## BACKGROUND

In this exercise we treat only passive behavior, so that we will not allow the $Na^+$ and $K^+$ channels to change their properties in response to membrane voltage (see Figure 1). This means that the axon is not excitable; *excitable* axons will be dealt with in a separate problem set.

You will compute the accumulation of net positive charge **Q** on the inner surface of the cell membrane after application a stimulating current, $I_{stim}$ , or after

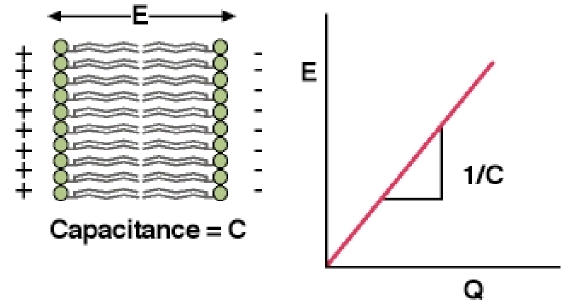


**Figure 2**

changes in concentrations or conductances of ions. The membrane potential, **E** , is then calculated from the electrical capacity of the membrane, **C**, as (see Figure 2)

$$E[\text{volt}] = \frac{Q[\text{Coul / unit area}]}{C[\text{Farad / unit area}]} \qquad (1)$$

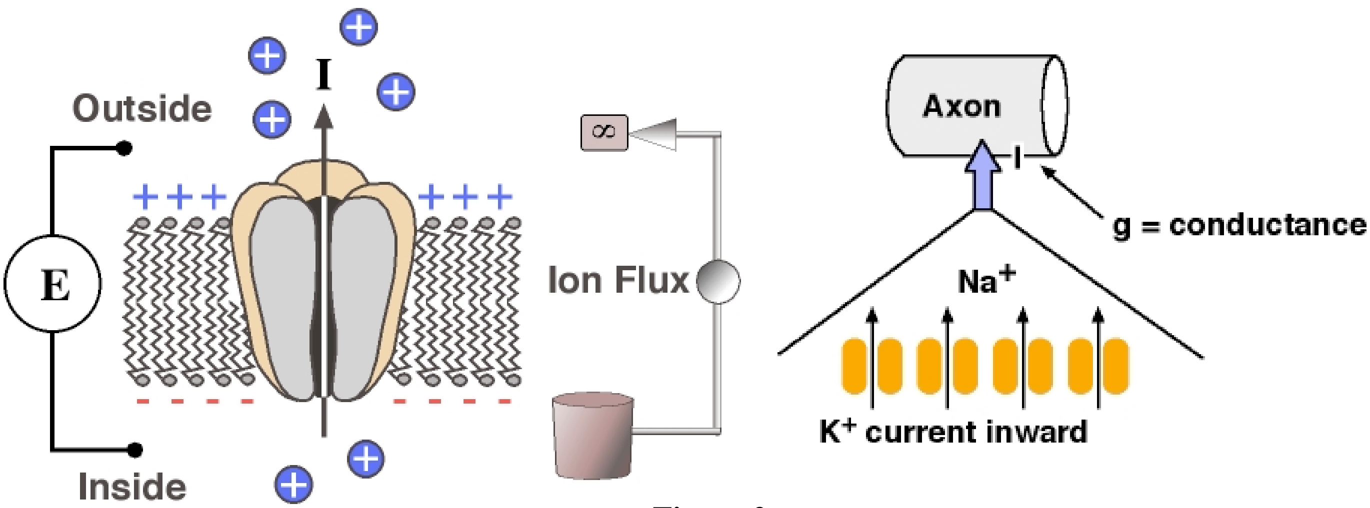


**Figure 2**

The intracellular charge changes as a result of $Na^+$, $K^+$, and "leakage" ions flowing in or out of the cell. Denoting the flow of any ion species (□) *out of the cell* by $I_x$, we have:

$$I_K = g_K(E - E_K)$$
$$I_{Na} = g_{Na}(E - E_{na})$$
$$I_L = g_L(E - E_L) \qquad (2)$$

By convention, positive current is always defined as positive charge moving out of the cell. The $g_x$'s are conductances (= 1/resistance); they are proportional to the number of channels available to that ion species. The $E_x$ are equilibrium potentials. They are the value of the membrane potential (inside - outside) that would be required to prevent any diffusion of ion x across the membrane. Thus they are a measure of the concentration ratio on the two sides of the membrane.[1]*:*

In addition to the ion currents the experimenter may impose a stimulating flow of positive charge into the cell. If this imposed current has the form of a square wave, it has the form:

$$I_{step} = Intensity*SQUAREPULSE(\text{ontime, duration}) \qquad (3)$$

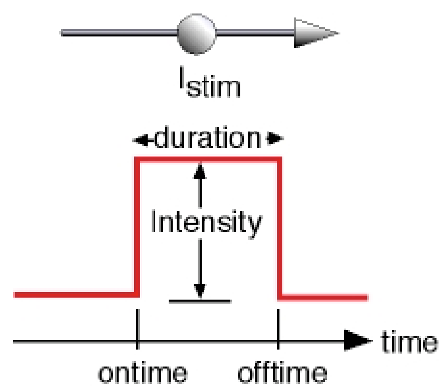


**Figure 3**

**SQUAREPULSE** is either 0 or 1, so that the *Intensity* specifies the height of the pulse. The off time is not specified, instead the *duration* of the pulse is required.

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[1] For ions with a single positive charge (e;.g. $Na^+$ or $K^+$) the membrane potentials are related to the ion concentrations by the *Nernst equation*: $E_X = -RT/F \ln([c]_{in}/[c]_{out}) \approx -25 \cdot \ln([c]_{in}/[c]_{out})$. We will meet this equation again later.

# Procedure

We begin with a simple cell that that illustrates the passive (non-excitable) properties of nerves. We assume that the conductance of each ion remains constant;, i.e. they do not depend on voltage and they do not change with time. We are given the data in **Table 1**.

| QUANTITY | SYMBOL | UNITS | VALUE |
|---|---|---|---|
| **membrane capacity** | $C_m$ | μfarad/cm$^2$ | 1 |
| **Equilibrium potential for K$^+$** | $E_K$ | mV | -77 |
| **Equilibrium potential for Na$^+$** | $E_{Na}$ | mV | 50 |
| **Equilibrium potential for L$^+$** | $E_L$ | mV | -54.4 |
| **resting potential** | $E_r$ | mV | -65 |
| **K$^+$ conductance** | $g_K$ | mmho/cm$^2$ | 0.425 |
| **Na$^+$ conductance** | $g_{Na}$ | mmho/cm$^2$ | 0.0167 |
| **leakage conductance** | $g_L$ | mmho/cm$^2$ | 0.3 mmho/cm$^2$ |

**Table 1.** Data for the passive axon.

**1.** Simulate the response of the membrane potential $E$ when you stimulate the cell with a square wave of 100 μamps with a 10 msec. duration. Set up your simulation by using a reservoir for charge Q on the internal surface of the membrane. Flows out of the reservoir are given by the currents $I_K$, $I_{Na}$, $I_L$ of equations (2) and $I_{stim}$ of equation (4). The value of E is obtained from Q via equation (1) (use a converter). Plot **E** and **I**stim vs. time**.** Note that the system is linear: it depends only on the first power of *E*. The cell responds with a single time constant. What is its magnitude? Is the response all or none? Is there a threshold?

**2.** Illustrate the sensitivity of the system (speed of response and final steady state resting potential) when you change the parameters listed below. An easy way to do this is to use the **Batch Runs** command. Begin by making simultaneous plots of 0.1, 1. 5, and 25 times the normal value given in the table for each parameter. This can be done by choosing **Geometric Series** and setting the maximum and minimum values for the specific parameter you are investigating. As you see your results you may want to change these values to illustrate some particular point. Parameters to change are the membrane capacity, $C_m$, the number of open sodium and potassium channels, $g_{Na}$ and $g_K$.

**3.** Set $I_{stim} = 0$ and assume that by some means the resting potential has been set to zero (E = 0 at t = 0); i.e. the membrane has been "short circuited". Suddenly the short is removed and the membrane is allowed to charge up to its normal resting potential.

(a) Simulate the time course of this experiment.

(b) How much charge in Coulombs moved in to accomplish this? Using the Faraday constant, translate this into moles of positive ions.

(c) Show that no matter where you place the initial value of the membrane charge (and corresponding membrane potential) the potential always returns to the same value.

(d) Show that changing the capacitance $C_m$ will change the speed of response but will not effect the final value. How does the speed of response (increase/decrease) when $C_m$ increases?

(e) Show that changing the conductances *in the same proportion* (i.e. increase all of them by a factor of 10x) will also change the speed of response but will not effect the final value. How does the speed of response (increase/decrease) when conductances increases?

**Save the model**! You will use it next time to patch in voltage activated channels and simulate nerve excitation.

# APPENDIX: Units

Capacitance is *defined* as the ratio of the charge on a capacitor to the voltage required to build up that charge:

$$C \text{ [farads]} = Q \text{ [Coul]} / V \text{ [volts]}$$

However, farads and volts are much too large to be convenient in physiology, so we use microfarads [μf] and millivolts [mV] instead. However, if we measure C μf and E in mV, then we must use Q in nanoCoulombs [nCoul] ($10^{-9}$ Coul). That is,

$$Q \text{ [nCoul]} = C \text{ [}\mu\text{f]} \times V \text{ [mV]}$$

$$\text{i.e. Coul} = 10^{6}\ \mu\text{farads} \times 10^{3}\text{ mV} = 10^{9}\ \mu\text{farads} \times \text{mV}$$

$$10^{-9}\text{ Coul} = \text{nCoul} = \mu\text{farads x mV}$$

Conductance is defined by Ohms law: I [amp] = g [mho] × E [volt], where the conductance, g [mho] = 1/resistance [ohm]. If we use the units of conductance (mmho), current (μamps) and time (msec), then

$$\text{amps} = \text{Coul/sec} = \text{mho x volts} = 10^{3}\text{ mmho} \times 10^{3}\text{ mV}$$

So $10^{-6}$ Coul/sec = $10^{-9}$ Coul/msec = mmho x mV. Thus to keep the units of Q in nCoul, we must measure time in msec.

Thus the charge that appears in a reservoir will be in terms of *nCoul*.. To convert this charge to *moles* we use the *Faraday constant* ***F* = 96, 485 Coul/mol** (the charge on a mole of particles). When a reservoir has charge Q, the implication is that this is Q [nCoul] = Q × $10^{-9}$ [Coul]. The corresponding number of moles of *univalent* ions is given by Q × $10^{-9}$ [Coul] / 96,485.