DOING PHYSICS WITH MATLAB

NEURON MEMBRANE CURRENTS

REVERSAL (NERNST – EQUILIBRIUM) POTENTIALS

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MATLAB

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INTRODUCTION

Electrical activity in neurones is sustained and propagated by ion currents through neurone membranes as shown in figure 1. Most of these transmembrane currents involve four ionic species: sodium Na^+, potassium K^+, calcium Ca^{2+} and chloride (Cl^-). The concentrations of these ions are different on the inside and outside of a cell. This creates the electrochemical gradients which are the major driving forces of neural activity. The **extracellular** medium has high concentration of Na^+ and Cl^- and a relatively high concentration of Ca^{2+}. The **intracellular** medium has high concentration of K^+ and negatively charged large molecules A^-. The cell membrane has large protein molecules forming **ion channels** through which ions (but not A^-) can flow according to their electrochemical gradients.

The concentration asymmetry is maintained through

Passive redistribution: The impermeable anions A^- attract more K^+ into the cell and repel more Cl^- out of the cell.

Active transport: Ions are pumped in and out of the cell by ionic pumps. For example, the Na^+/K^+ pump, which pumps out three Na^+ ions for every two K^+ ions pumped.

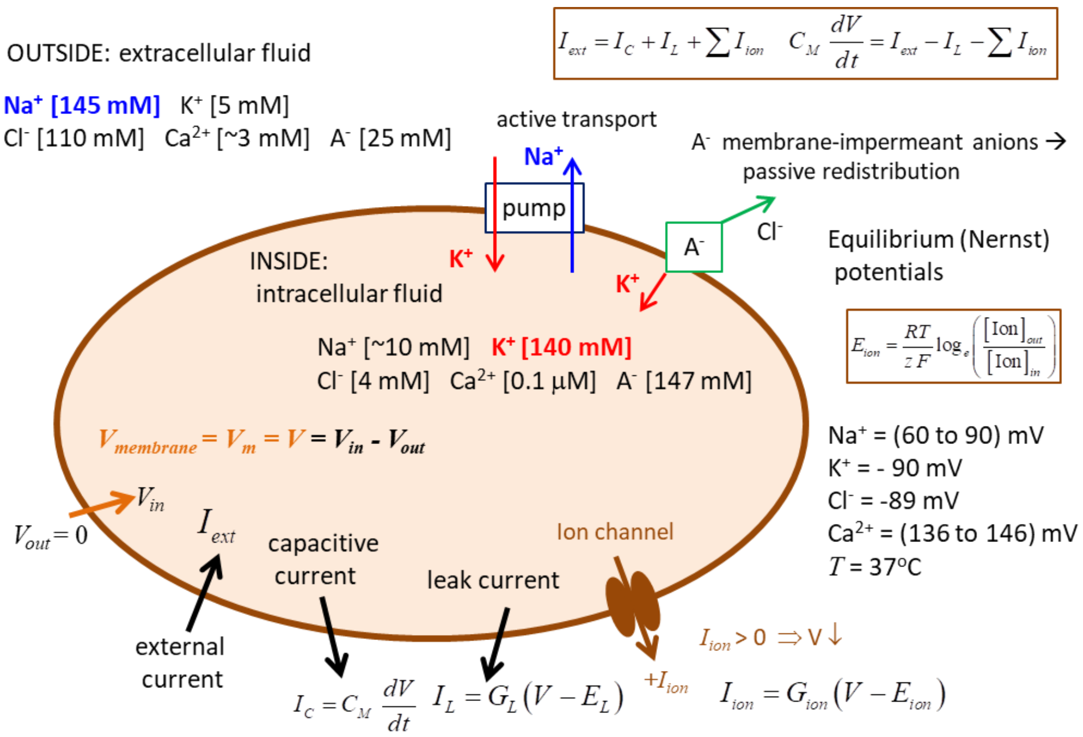


Fig. 1. Electrophysiology of a neurone.

Nernst or Equilibrium Potential

There are two forces that drive each ion species through the membrane channel.

Concentration gradient: ions diffuse down the concentration gradient. For example, the K^+ ions diffuse out of the cell because K^+ concentration inside is higher than outside.

Electric potential gradient: as ions diffuse across the membrane a charge imbalance occurs producing a potential difference between the inside and outside of the cell. For the K^+ ions exiting the cell, they carry positive charge with them and leave a net negative charge inside the cell (consisting mostly of impermeable anions A^-), thereby producing the outward K^+ current.

The positive and negative charges accumulate on the opposite sides of the membrane
surface creating an electric potential gradient across the membrane. This potential difference is called the transmembrane potential or **membrane voltage**

(1) $V \equiv V_M = V_{in} - V_{out}$

where the extracellular potential is the reference potential such that $V_{out} = 0 \text{ V}$.

This potential slows down the diffusion of K^+, since K^+ ions are attracted to the negatively charged interior and repelled from the positively charged exterior of the membrane. At some point an equilibrium is achieved. When the concentration gradient and the electric potential gradient exert equal and opposite forces on the ions, the net cross-membrane current is zero.

The value of such an **equilibrium potential** depends on the ionic species and it is given by the **Nernst equation**

(2) $$E_{ion} = \frac{RT}{zF} \log_e \left(\frac{[Ion]_{out}}{[Ion]_{in}} \right)$$

where $[Ion]_{in}$ and $[Ion]_{out}$ are concentrations of the ions inside and outside the cell respectively, R is the universal gas constant (R = 8.3155 $J.mol^{-1}.K^{-1}$), T is temperature in degrees Kelvin, F is Faraday's (F = (96 485 $C.mol^{-1}$), z is the valence of the ion (z = 1 for Na^+ and K^+, z = -1 for Cl^-, and z = 2 for Ca^{2+}). E_{ion} is also called the **reversal potential**.

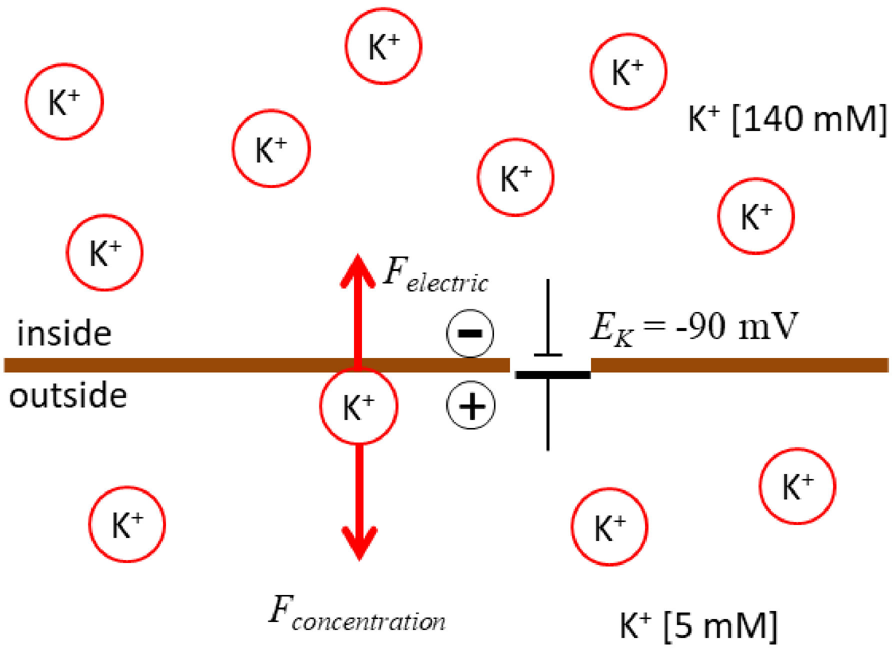
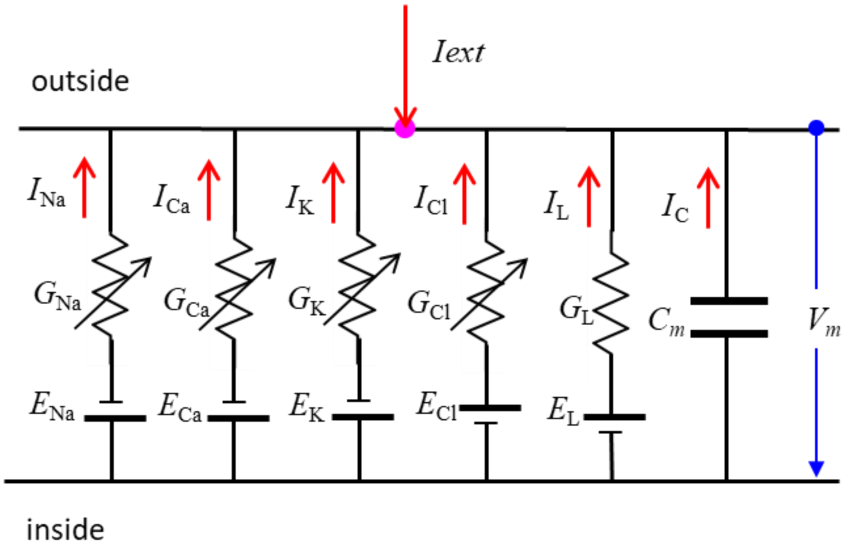


Fig. 2. Diffusion of K^+ ions down the concentration creates an increasing electric force directed in the direction opposite to the force due to the concentration difference until the diffusion and electrical forces balance each other.

Membrane Currents

We can model the movement of ions across the membrane as an electric circuit as shown in figure 3.



Kirchhoff's Current Law:
at a junction

$$\sum I = 0$$

$$I_{Na} + I_{Ca} + I_K + I_{Cl} + I_L + I_C - I_{ext} = 0 \qquad I_C = C_M \, dV_M$$

$$dV_M / dt = \left(I_{ext} - I_{Na} - I_{Ca} - I_K - I_{Cl} - I_L \right) / C_M$$

Fig. 3. Equivalent circuit representation of a nerve cell membrane.

In the neuroscience literature, there is often some confusion and inconsistencies in the use of scientific language and the units used for physical quantities. For example, the terms conductance and conductance per unit area are often not distinguished and g maybe the conductance or conductance per unit area with units S or S.cm^{-2}. In Izhikevich's book, he gives the current in μA.cm^{-2}, which is clearly wrong.

In the Scripts to model the dynamic behaviour of neurones, S.I. units are used for all input parameters and calculations. However, results may be expressed in non S.I. units, for example, mV for voltage.

The current through a resistive element can be expressed by the equation

(3) $I = V / R = GV$

I current [ampere A]

V potential difference [volts V]

R resistance [ohm Ω]

G conductance [Siemens S 1 S $= \Omega^{-1}$]

This equation can also can also be expressed in expressed in terms of the current density

(4) $J = gV \quad J = I / A \quad g = G / A$

A area [m]

J current density [A.m^{-2}]

g specific conductance [S.m^{-2}]

The major ion currents shown in figure 2, can be expressed as

(5) $I_X = G_X\,(V_M - E_X) \quad J_X = g_X\,(V_M - E_X)$

X ion (e.g. Na^+ K^+ leakage)

V_M membrane potential (voltage) [volt V]

E_X equilibrium (Nernst) potential [V]

When the conductance is constant, the current is said to be **ohmic**. In general, ionic currents in neurones are not ohmic, since the conductance may depend upon time, membrane potential, and pharmacological agents (e.g. neurotransmitters). It is the time-dependent variation of conductances that allow a neurone to generate an action potential (spike).

The membrane acts like a capacitor – an insulator (membrane) surrounded by the extracellular and intracellular fluids (conductive plates). When the membrane potential changes, a current is generated to charge or discharge the capacitor. The capacitor current is given by the time derivative of the voltage

(6) $$I_C = C_M \frac{dV_M}{dt} \qquad J_C = c_M \frac{dV_M}{dt} \qquad c_M = \frac{C_M}{A}$$

C_M capacitance [F]

c_M specific capacitance [F.m^{-2}]

The equivalent circuit to represent the electrical properties of membranes is shown in figure 3. According to Kirchhoff's Current Law, the sum of the currents entering and leaving a junction must add to zero. Hence across the membrane

(7) $\quad I_{\mathrm{Na}} + I_{\mathrm{Ca}} + I_{\mathrm{K}} + I_{\mathrm{Cl}} + I_{\mathrm{L}} + I_{\mathrm{C}} - I_{\mathrm{ext}} = 0 \qquad I_C = C_m \, dV_M \, / \, dt$

Therefore, we can write an "equation of motion" to describe the dynamical system of a neurone as

(8) $\quad dV_M \, / \, dt = \left(I_{\mathrm{ext}} - I_{\mathrm{Na}} - I_{\mathrm{Ca}} - I_{\mathrm{K}} - I_{\mathrm{Cl}} - I_{\mathrm{L}} \right) / \, C_M$

Note: $I_{\mathrm{Na}} < 0, \quad I_{\mathrm{Ca}} < 0$ are inward currents (outside to inside)

$I_{\mathrm{K}} > 0, \quad I_{\mathrm{Cl}} > 0$ are outward currents (inside to outside)

The membrane potential is typically bounded by the equilibrium potentials

$$E_{\mathrm{K}} < E_{\mathrm{Cl}} < V_M < E_{\mathrm{Na}} < E_{\mathrm{Ca}}$$

One example of the application of equation (8) is the Hodgkin-Huxley Model.

For different models of a neurone, equation (8) can be solved using the Matlab ordinary differential equation solver **ode45**.