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Membrane potential

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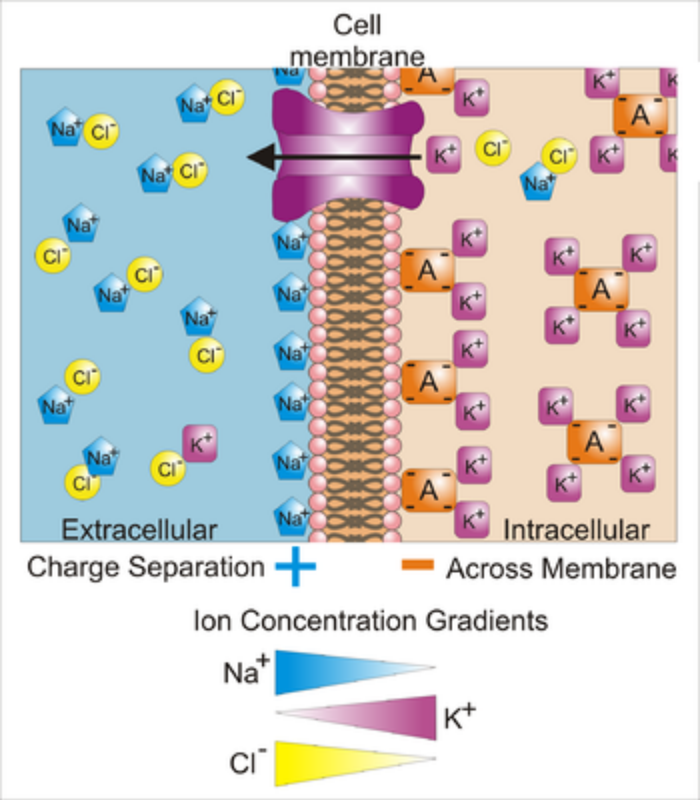

Differences in the concentrations of ions on opposite sides of a cellular membrane lead to a voltage called the **membrane potential**. Typical values of membrane potential are in the range +40 mV to –70 mV. Many ions have a concentration gradient across the membrane, including potassium (K^+), which is at a high concentration inside and a low concentration outside the membrane. Sodium (Na^+) and chloride (Cl^-) ions are at high concentrations in the extracellular region, and low concentrations in the intracellular regions. These concentration gradients provide the potential energy to drive the formation of the membrane potential. This voltage is established when the membrane has permeability to one or more ions. In the simplest case, illustrated here, if the membrane is selectively permeable to potassium, these positively charged ions can diffuse down the concentration gradient to the outside of the cell, leaving behind uncompensated negative charges. This separation of charges is what causes the membrane potential. Note that the system as a whole is electro-neutral. The uncompensated positive charges outside the cell, and the uncompensated negative charges inside the cell, physically line up on the membrane surface and attract each other across the lipid bilayer. Thus, the membrane potential is physically located only in the immediate vicinity of the membrane. It is the separation of these charges across the membrane that is the basis of the membrane voltage. Note also that this diagram is only an approximation of the ionic contributions to the membrane potential. Other ions including sodium, chloride, calcium, and others play a more minor role, even though they have strong concentration gradients, because they have more limited permeability than potassium. *Key*: Blue pentagons – sodium ions; Purple squares – potassium ions; Yellow circles – chloride ions; Orange rectangles – membrane-impermeable anions (these arise from a variety of sources including proteins). The large purple structure with an arrow represents a transmembrane potassium channel and the direction of net potassium movement.

Membrane potential (also **transmembrane potential** or **membrane voltage**) is the difference in electric potential between the interior and the exterior of a biological cell. With respect to the exterior of the cell, typical values of membrane potential range from –40 mV to –80 mV.

All animal cells are surrounded by a membrane composed of a lipid bilayer with proteins embedded in it. The membrane serves as both an insulator and a diffusion barrier to the movement of ions. Ion transporter/pump proteins actively push ions across the membrane and establish concentration gradients across the membrane, and ion channels allow ions to move across the membrane down those concentration gradients. Ion pumps and ion channels are electrically equivalent to a set of batteries and resistors inserted in the membrane, and therefore create a voltage between the two sides of the membrane.

Virtually all eukaryotic cells (including cells from animals, plants, and fungi) maintain a non-zero transmembrane potential,[citation needed] usually with a negative voltage in the cell interior as compared to the cell exterior ranging from –40 mV to –80 mV. The membrane potential has two basic functions. First, it allows a cell to function as a battery, providing power to operate a variety of "molecular devices" embedded in the membrane. Second, in electrically excitable cells such as neurons and muscle cells, it is used for transmitting signals between different parts of a cell. Signals are generated by opening or closing of ion channels at one point in the membrane, producing a local change in the membrane potential. This change in the electric field can be quickly affected by either adjacent or more distant ion channels in the membrane. Those ion channels can then open or close as a result of the potential change, reproducing the signal.

In non-excitable cells, and in excitable cells in their baseline states, the membrane potential is held at a relatively stable value, called the resting potential. For neurons, typical values of the resting potential range from –70 to –80 millivolts; that is, the interior of a cell has a negative baseline voltage of a bit less than one-tenth of a volt. The opening and closing of ion channels can induce a departure from the resting potential. This is called a depolarization if the interior voltage becomes less negative (say from –70 mV to –60 mV), or a hyperpolarization if the interior voltage becomes more negative (say from –70 mV to –80 mV). In excitable cells, a sufficiently large depolarization can evoke an action potential, in which the membrane potential changes rapidly and significantly for a short time (on the order of 1 to 100 milliseconds), often reversing its polarity. Action potentials are generated by the activation of certain voltage-gated ion channels.

In neurons, the factors that influence the membrane potential are diverse. They include numerous types of ion channels, some of which are chemically gated and some of which are voltage-gated. Because voltage-gated ion channels are controlled by the membrane potential, while the membrane potential itself is influenced by these same ion channels, feedback loops that allow for complex temporal dynamics arise, including oscillations and regenerative events such as action potentials

Values of resting membrane potential in most animal cells usually vary between the potassium reversal potential (usually around -80 mV) and around -40 mV. The resting potential in excitable cells (capable of producing action potentials) is usually near -60 mV—more depolarized voltages would lead to spontaneous generation of action potentials. Immature or undifferentiated cells show highly variable values of resting voltage, usually significantly more positive than in differentiated cells.[26] In such cells, the resting potential value correlates with the degree of differentiation: undifferentiated cells in some cases may not show any transmembrane voltage difference at all.

Maintenance of the resting potential can be metabolically costly for a cell because of its requirement for active pumping of ions to counteract losses due to leakage channels. The cost is highest when the cell function requires an especially depolarized value of membrane voltage. For example, the resting potential in daylight-adapted blowfly (*Calliphora vicina*) photoreceptors can be as high as -30 mV.[27] This elevated membrane potential allows the cells to respond very rapidly to visual inputs; the cost is that maintenance of the resting potential may consume more than 20% of overall cellular ATP.[28]

On the other hand, the high resting potential in undifferentiated cells can be a metabolic advantage. This apparent paradox is resolved by examination of the origin of that resting potential. Little-differentiated cells are characterized by extremely high input resistance,[26] which implies that few leakage channels are present at this stage of cell life. As an apparent result, potassium permeability becomes similar to that for sodium ions, which places resting potential in-between the reversal potentials for sodium and potassium as discussed above. The reduced leakage currents also mean there is little need for active pumping in order to compensate, therefore low metabolic cost.

Other values

From the viewpoint of biophysics, the *resting* membrane potential is merely the membrane potential that results from the membrane permeabilities that predominate when the cell is resting. The above equation of weighted averages always applies, but the following approach may be more easily visualized. At any given moment, there are two factors for an ion that determine how much influence that ion will have over the membrane potential of a cell:

1. That ion's driving force
2. That ion's permeability

If the driving force is high, then the ion is being "pushed" across the membrane. If the permeability is high, it will be easier for the ion to diffuse across the membrane.

- **Driving force** is the net electrical force available to move that ion across the membrane. It is calculated as the difference between the voltage that the ion "wants" to be at (its equilibrium potential) and the actual membrane potential (E_m). So, in formal terms, the driving force for an ion = $E_m - E_{ion}$
- For example, at our earlier calculated resting potential of −73 mV, the driving force on potassium is 7 mV : (−73 mV) − (−80 mV) = 7 mV. The driving force on sodium would be (−73 mV) − (60 mV) = −133 mV.
- **Permeability** is a measure of how easily an ion can cross the membrane. It is normally measured as the (electrical) conductance and the unit, siemens, corresponds to 1 $C \cdot s^{-1} \cdot V^{-1}$, that is one coulomb per second per volt of potential.

So, in a resting membrane, while the driving force for potassium is low, its permeability is very high. Sodium has a huge driving force but almost no resting permeability. In this case, potassium carries about 20 times more current than sodium, and thus has 20 times more influence over E_m than does sodium.

However, consider another case—the peak of the action potential. Here, permeability to Na is high and K permeability is relatively low. Thus, the membrane moves to near E_{Na} and far from E_K.

The more ions are permeant the more complicated it becomes to predict the membrane potential. However, this can be done using the Goldman-Hodgkin-Katz equation or the weighted means equation. By plugging in the concentration gradients and the permeabilities of the ions at any instant in time, one can determine the membrane potential at that moment. What the GHK equations means is that, at any time, the value of the membrane potential will be a weighted average of the equilibrium potentials of all permeant ions. The "weighting" is the ions relative permeability across the membrane.

Effects and implications

While cells expend energy to transport ions and establish a transmembrane potential, they use this potential in turn to transport other ions and metabolites such as sugar. The transmembrane potential of the mitochondria drives the production of ATP, which is the common currency of biological energy.

Cells may draw on the energy they store in the resting potential to drive action potentials or other forms of excitation. These changes in the membrane potential enable communication with other cells (as with action potentials) or initiate changes inside the cell, which happens in an egg when it is fertilized by a sperm.

In neuronal cells, an action potential begins with a rush of sodium ions into the cell through sodium channels, resulting in depolarization, while recovery involves an outward rush of potassium through potassium channels. Both these fluxes occur by passive diffusion.