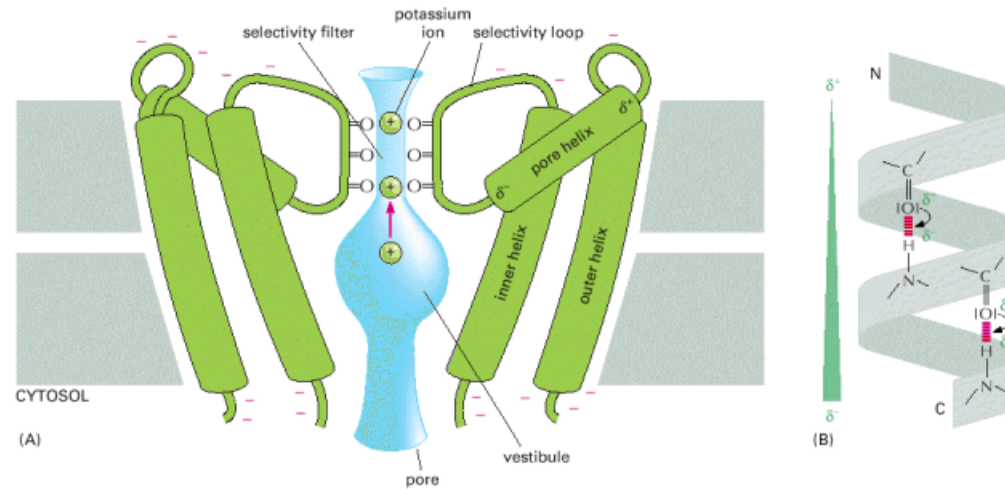
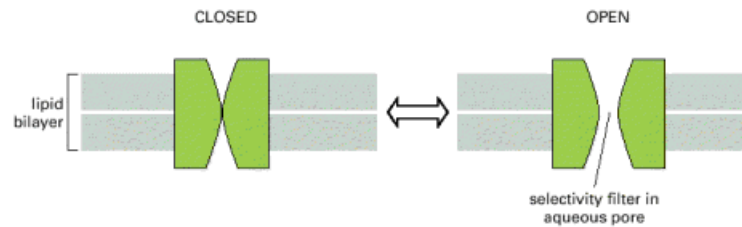


Ιοντικοί δίαυλοι και το δυναμικό της μεμβράνης

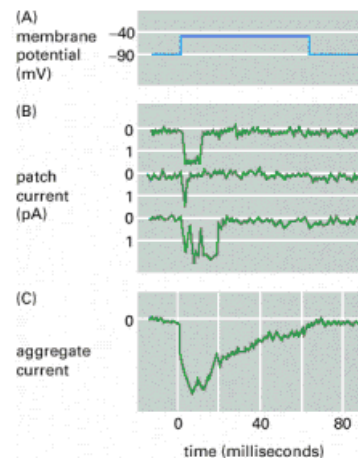
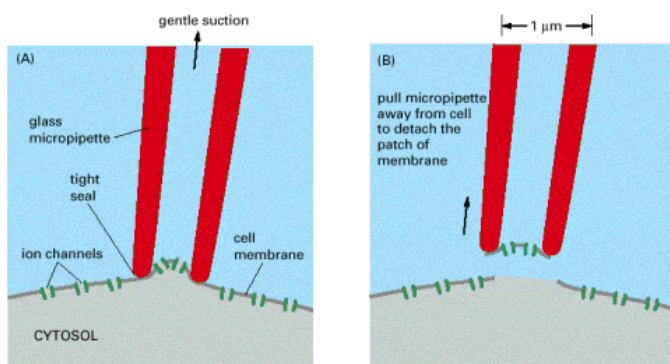
Η δομή ενός βακτηριακού διαύλου K^+



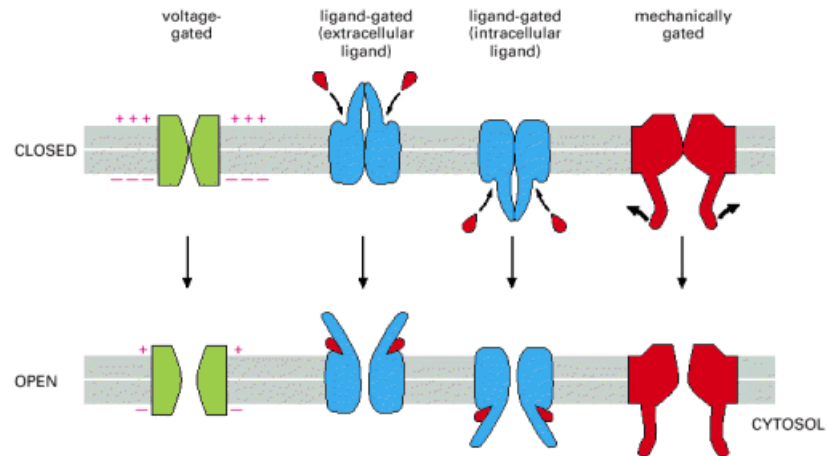
Ένας τυπικός διάυλος ιόντων μεταπίπτει
από κλειστή σε ανοιχτή διαμόρφωση και
αντιστρόφως



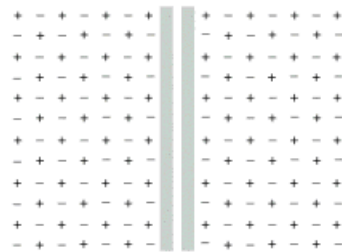
Καταγραφή καθήλωσης δυναμικού



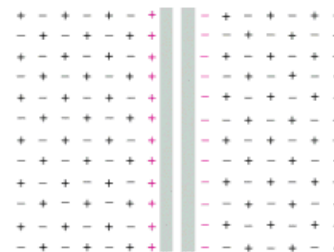
Ελεγχόμενοι ιοντικοί διάυλοι



Η κατανομή των ιόντων δημιουργεί το δυναμικό της μεμβράνης

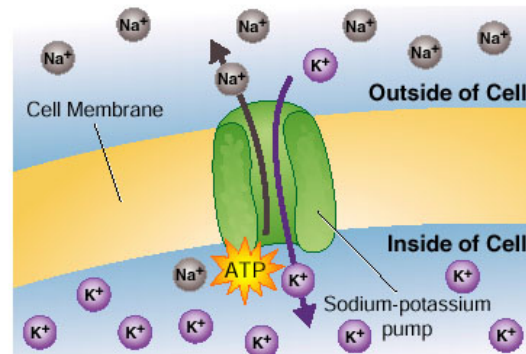


exact balance of charges on each side of the membrane; membrane potential = 0

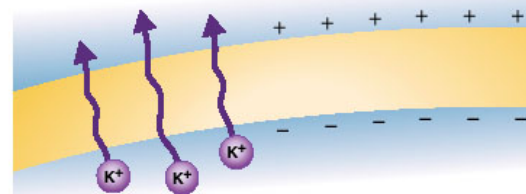


a few of the positive ions (*red*) cross the membrane from right to left, leaving their negative counterions (*red*) behind; this sets up a nonzero membrane potential

Ο ρόλος του K^+ στη δημιουργία του δυναμικού της μεμβράνης



A A protein pump in the neuron cell membrane uses the energy of ATP to pump Na^+ out of the cell, and at the same time to pump K^+ in.



B The cell membrane is leakier to K^+ than it is to Na^+ . Because more positive charges leak out of the cell than leak in, the inside of the cell becomes negatively charged with respect to the outside.

Η εξίσωση του Nernst

THE NERNST EQUATION AND ION FLOW

The flow of any ion through a membrane channel protein is driven by the **electrochemical gradient** for that ion. This gradient represents the combination of two influences: the voltage gradient and the concentration gradient of the ion across the membrane. When these two influences just balance each other the electrochemical gradient for the ion is zero and there is no net flow of the ion through the channel. The voltage gradient (membrane potential) at which this equilibrium is reached is called the **equilibrium potential** for the ion. It can be calculated from an equation that will be derived below, called the **Nernst equation**.

The Nernst equation is

$$V = \frac{RT}{zF} \ln \frac{C_o}{C_i}$$

where

- V = the equilibrium potential in volts (internal potential minus external potential)
- C_o and C_i = outside and inside concentrations of the ion, respectively
- R = the gas constant ($2 \text{ cal mol}^{-1} \text{ K}^{-1}$)
- T = the absolute temperature (K)
- F = Faraday's constant ($2.3 \times 10^4 \text{ cal V}^{-1} \text{ mol}^{-1}$)
- z = the valence (charge) of the ion
- \ln = logarithm to the base e

The Nernst equation is derived as follows:

A molecule in solution (a solute) tends to move from a region of high concentration to a region of low concentration simply due to the random movement of molecules, which results in their equilibrium. Consequently, movement down a concentration gradient is accompanied by a favorable free-energy change ($\Delta G < 0$), whereas movement up a concentration gradient is accompanied by an unfavorable free-energy change ($\Delta G > 0$). Free energy is introduced and discussed in Panel 14-1, p. 784.) The free-energy change per mole of solute moved across the plasma membrane (ΔG_{mem}) is equal to $-RT \ln C_o/C_i$. If the solute is an ion, moving it into a cell across a membrane whose inside is at a voltage V relative to the outside will cause an additional free-energy change (per mole of solute moved) of $\Delta G_{\text{el}} = zFV$. At the point where the concentration and voltage gradients just balance, $\Delta G_{\text{mem}} + \Delta G_{\text{el}} = 0$ and the ion distribution is at equilibrium across the membrane. Thus,

$$zFV - RT \ln \frac{C_o}{C_i} = 0$$

and, therefore,

$$V = \frac{RT}{zF} \ln \frac{C_o}{C_i} = 2.3 \frac{RT}{zF} \log_{10} \frac{C_o}{C_i}$$

For a univalent ion,

$$2.3 \frac{RT}{F} = 58 \text{ mV at } 20^\circ\text{C} \text{ and } 61.5 \text{ mV at } 37^\circ\text{C}$$

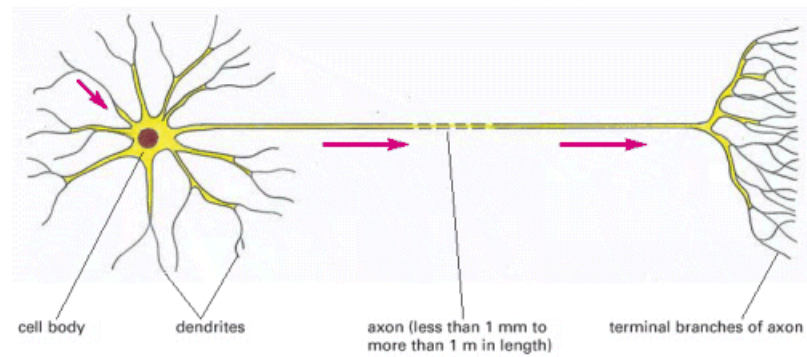
Thus, for such an ion at 37°C , $V = +61.5 \text{ mV}$ for $C_o/C_i = 10$, whereas $V = 0$ for $C_o/C_i = 1$.

The K^+ equilibrium potential (V_K), for example, is $61.5 \log_{10}([\text{K}^+]_o/[\text{K}^+]_i)$ millivolts ($\sim 99 \text{ mV}$ for a typical cell where $[\text{K}^+]_o = 5 \text{ mM}$ and $[\text{K}^+]_i = 140 \text{ mM}$). At V_K , there is no net flow of K^+ across the membrane. Similarly, when the membrane potential has a value of $61.5 \log_{10}([\text{Na}^+]_o/[\text{Na}^+]_i)$, the Na^+ equilibrium potential (V_{Na}), there is no net flow of Na^+ .

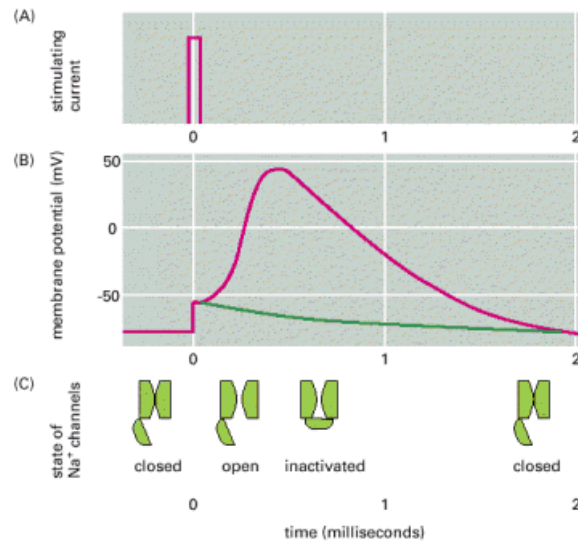
For any particular membrane potential, V_m , the net force tending to drive a particular type of ion out of the cell, is proportional to the difference between V_m and the equilibrium potential for the ion; hence, for K^+ it is $V_m - V_K$ and for Na^+ it is $V_m - V_{Na}$.

The number of ions that go to form the layer of charge adjacent to the membrane is minute compared with the total number inside the cell. For example, the movement of 6000 Na^+ ions across $1 \mu\text{m}^2$ of membrane will carry sufficient charge to shift the membrane potential by about 100 mV. Because there are about 3×10^7 Na^+ ions in a typical cell ($1 \mu\text{m}^2$ of bulk cytoplasm), such a movement of charge will generally have a negligible effect on the ion concentration gradients across the membrane.

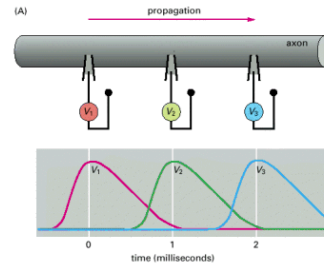
Νευρώνες



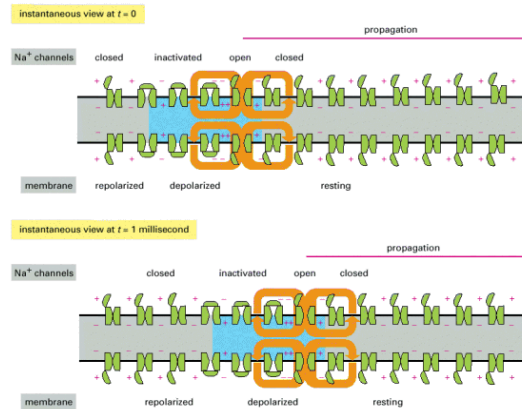
Ένα δυναμικό ενέργειας



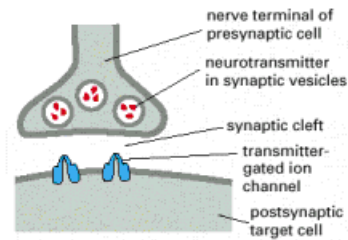
Μετάδοση ενός δυναμικού ενέργειας κατά μήκος ενός άξονα



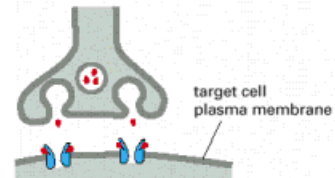
(B)



Μια χημική σύναψη

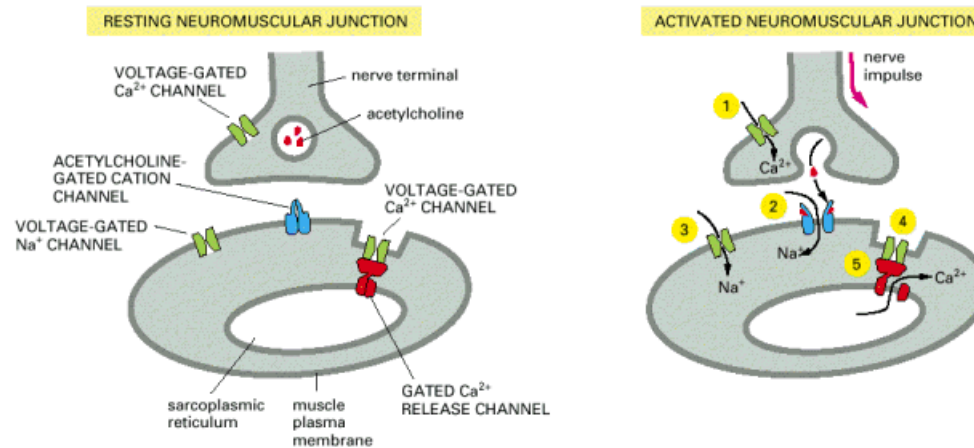


RESTING CHEMICAL SYNAPSE

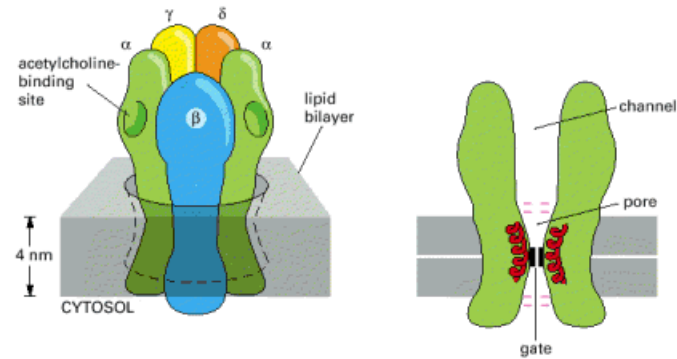


ACTIVE CHEMICAL SYNAPSE

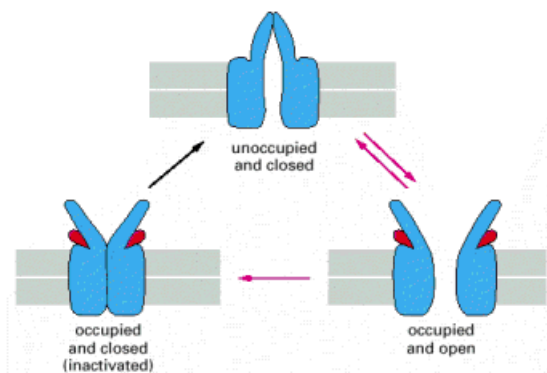
Ιοντικοί δίαυλοι στη νευρομυϊκή συμβολή



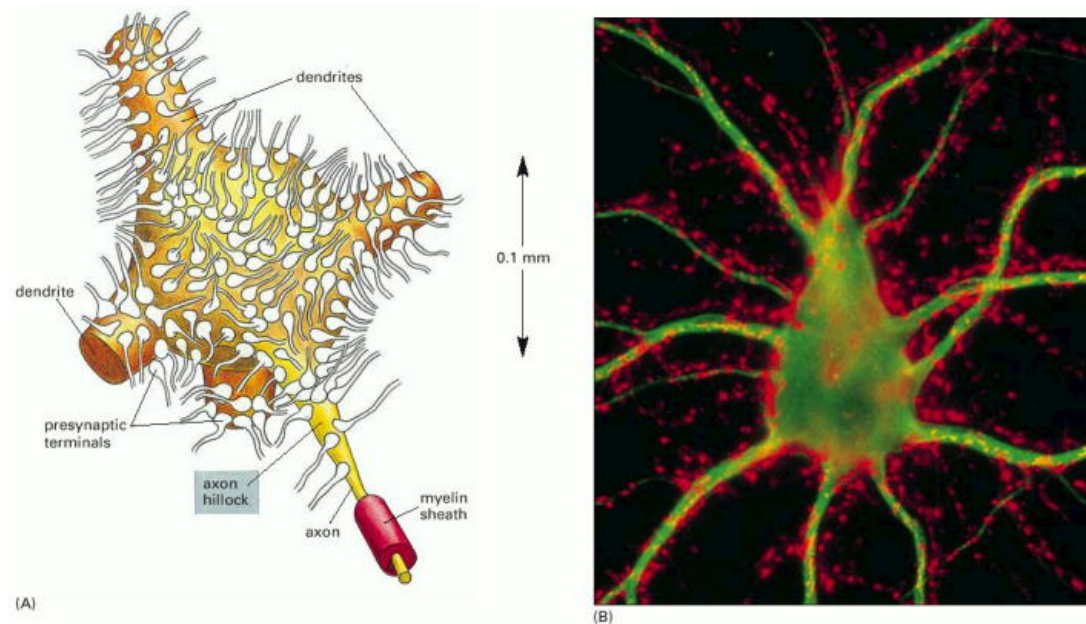
Μοντέλο για τη δομή του υποδοχέα της ακετυλοχολίνης



Ο υποδοχέας της ακετυλοχολίνης



Συνάψεις στο κυτταρικό σώμα και στους δενδρίτες ενός κινητικού νευρώνα της σπονδυλικής στήλης



Το καλαμάρι αποκαλύπτει τα μυστικά της μεμβρανικής διαγεροσιμότητας

1. Action potentials are recorded with an intracellular electrode
 The squid giant axon is about 0.5-1 mm in diameter and several centimeters long. An electrode in the form of a glass capillary tube containing a conducting solution can be thrust down the axis of the axon so that its tip lies deep in the cytoplasm. With its help, one can measure the voltage difference between the inside and the outside of the axon—that is, the membrane potential—as an action potential sweeps past the electrode. The action potential is triggered by a brief electrical stimulus to one end of the axon. It does not matter which end, because the excitation can travel in either direction; and it does not matter how big the stimulus is, as long as it exceeds a certain threshold: the action potential is all or none.

2. Action potentials depend only on the neuronal plasma membrane and on gradients of Na⁺ and K⁺ across it
 The three most plentiful ions, both inside and outside the axon, are Na⁺, K⁺, and Cl⁻. As in other cells, the Na⁺/K⁺ pump maintains a concentration gradient: the concentration of Na⁺ is about 9 times lower inside the axon than outside, while the concentration of K⁺ is about 20 times higher inside than outside. Which ions are important for the action potential?
 The squid giant axon is so large and robust that it is possible to extrude the cytoplasm from it, like toothpaste from a tube, and then to perfuse it internally with pure artificial solutions of Na⁺, K⁺, and Cl⁻ or SO₄²⁻. Remarkably, if (and only if) the concentrations of Na⁺ and K⁺ inside and outside approximate those found naturally, the axon will still propagate action potentials of the normal form. The important part of the cell for electrical signaling, therefore, must be the plasma membrane; the important ions are Na⁺ and K⁺; and a sufficient source of free energy to power the action potential must be provided by their concentration gradients across the membrane, because all other sources of metabolic energy have presumably been removed by the perfusion.

3. At rest, the membrane is chiefly permeable to K⁺; during the action potential, it becomes transiently permeable to Na⁺
 At rest the membrane potential is close to the equilibrium potential for K⁺. When the external concentration of K⁺ is changed, the resting potential changes roughly in accordance with the Nernst equation for K⁺ (see Panel 11-2). At rest, therefore, the membrane is chiefly permeable to K⁺; K⁺ leak channels provide the main ion pathway through the membrane.
 If the external concentration of Na⁺ is varied, there is no effect on the resting potential. However, the height of the peak of the action potential varies roughly in accordance with the Nernst equation for Na⁺. During the action potential, therefore, the membrane appears to be chiefly permeable to Na⁺; Na⁺ channels have opened. In the aftermath of the action potential, the membrane potential reverts to a negative value that depends on the external concentration of K⁺ and is even closer to the K⁺ equilibrium potential than the resting potential is: the membrane has lost most of its permeability to Na⁺ and has become even more permeable to K⁺ than before—that is, Na⁺ channels have closed, and additional K⁺ channels have opened.

4. Voltage clamping reveals how the membrane potential controls opening and closing of ion channels
 The membrane potential can be held constant ("voltage clamped") throughout the axon by passing a suitable current through a bare metal wire inserted along the axis of the axon while monitoring the membrane potential with another intracellular electrode. When the membrane is abruptly shifted from the resting potential and held in a depolarized state (A), Na⁺ channels rapidly open until the Na⁺ permeability of the membrane is much greater than the K⁺ permeability; they then close again spontaneously, even though the membrane potential is clamped and unchanging. K⁺ channels also open but with a delay, so that the K⁺ permeability increases as the Na⁺ permeability falls (B). If the experiment is now very promptly repeated, by returning the membrane briefly to the resting potential and then quickly depolarizing it again, the responding is different: prolonged depolarization has caused the Na⁺ channels to enter an inactivated state, so that the second depolarization fails to cause a rise and fall similar to the first. Recovery from this state requires a relatively long time—about 10 milliseconds—spent at the polarized (resting) membrane potential.
 In a normal unclamped axon, an influx of Na⁺ through the opened Na⁺ channels produces the spike of the action potential; inactivation of Na⁺ channels and opening of K⁺ channels bring the membrane rapidly back down to the resting potential.