Box 17.1 Sensory signal amplification

Sensory signal amplification refers to the ratio between the energy associated with the stimulus output and the energy of the stimulus input. For example, if one action potential is triggered in the sensory receptor in response to a stimulus, then the amplification factor in the sensory receptor is calculated as the ratio between the energy associated with the action potential and the energy of the stimulus that *triggered* the action potential.

Let us first estimate the energy associated with the generation of one action potential. This energy is derived primarily from sodium ions (Na^+) entering the axoplasm down an electrochemical potential difference and potassium ions (K^+) crossing the membrane in opposite direction. We discuss in section 16.2.4 that the amount of Na^+ and K^+ that cross the membrane of a squid axon (in opposite directions) during one action potential is about 4×10^{-12} mol per 1 cm^2 of membrane.

The energy associated with ion fluxes crossing the membrane is given by the product between the ion flux and the difference in electrochemical potential across the membrane (ΔECP) for the respective ion. If V_M is the membrane potential (i.e. the electrical potential difference between axoplasm and external environment), $[Na^+_{in}]$, $[K^+_{in}]$ are the concentrations of sodium and potassium ions in the axoplasm and $[Na^+_{out}]$, $[K^+_{out}]$ are the extracellular sodium and potassium ions, respectively, then the electrochemical potential differences between axoplasm and external environment for Na^+ ($\Delta ECP_{Na(in\text{-}out)}$) and K^+ ($\Delta ECP_{K(in\text{-}out)}$) are described by the following expressions:

$$\Delta ECP_{Na(in\text{-}out)} = RT \ln ([Na^+_{in}]/[Na^+_{out}]) + F\,V_M$$

$$\Delta ECP_{K(in\text{-}out)} = RT \ln ([K^+_{in}]/[K^+_{out}]) + F\,V_M$$

where *R* is the gas constant, *T* is the absolute temperature, *F* is the Faraday number and *ln* is the natural logarithm. Using values for the squid axon from Sections 16.2.1 and 16.2.2 ($[Na_{in}] = 72$ mmol L^{-1}; $[Na_{out}] = 465$ mmol L^{-1}; $[K_{in}] = 345$ mmol L^{-1}; $[K_{out}] = 10$ mmol L^{-1}; $V_M = -60$ mV, T = 293 K), it follows that:

$$\begin{aligned}\Delta ECP_{Na(in\text{-}out)} &= 8.31\ \mathrm{J\ mol^{-1}K^{-1}} \times 293\ \mathrm{K} \times \ln(72\ \mathrm{mmol\ L^{-1}}/465\ \mathrm{mmol\ L^{-1}}) \\ &\quad + 96500\ \mathrm{C\ mol^{-1}} \times (-60\ \mathrm{mV}) \\ &= -4.5\ \mathrm{kJ\ mol^{-1}} - 5.8\ \mathrm{kJ\ mol^{-1}} \\ &= -10.3\ \mathrm{kJ\ mol^{-1}},\ \text{and}\end{aligned}$$

$$\begin{aligned}\Delta ECP_{K(in\text{-}out)} &= 8.31\ \mathrm{J\ mol^{-1}K^{-1}} \times 293\ \mathrm{K} \times \ln(345\ \mathrm{mmol\ L^{-1}}/10\ \mathrm{mmol\ L^{-1}}) \\ &\quad + 96500\ \mathrm{C\ mol^{-1}} \times (-60\ \mathrm{mV}) = 8.6\ \mathrm{kJ\ mol^{-1}} - 5.8\ \mathrm{kJ\ mol^{-1}} \\ &= 2.8\ \mathrm{kJ\ mol^{-1}}\end{aligned}$$

Thus, the amount of energy dissipated by 4×10^{-12} mol Na^+ entering the axoplasm across 1 cm^2 of membrane is 4×10^{-12} mol $cm^{-2} \times (-10.3 \times 10^3$ J $mol^{-1}) = -4.12 \times 10^{-8}$ J cm^{-2}. Similarly, the energy dissipated by 4×10^{-12} mol K^+ exiting the axoplasm across 1 cm^2 of membrane is -4×10^{-12} mol $cm^{-2} \times (2.8 \times 10^3$ J $mol^{-1}) = -1.12 \times 10^{-8}$ J cm^{-2}. If the surface area of a sensory neuron in contact with the extracellular fluid where action potentials are generated is about 50 μm^2, then the energy associated with the generation and propagation of one action potential in the sensory neuron is about 2.6×10^{-14}J (5.24×10^{-8} J $cm^{-2} \times 50 \times 10^{-8}$ $cm^{-2} = 2.6 \times 10^{-14}$ J).

Now, let us consider the energy associated with a stimulus that can elicit an action potential. For example, when one pheromone[1] molecule binds to a chemoreceptor and triggers an action potential, the free energy of binding the pheromone to the chemoreceptor is $-(RT \ln A)/N_A$, where A is the affinity constant in mol^{-1} L and N_A is Avogadro's number, representing the number of molecules in one mole (6.023×10^{23}). Thus, when the pheromone binds to the chemoreceptor with an affinity constant $A=10^7$ mol^{-1} L at 20°C (T = 293 K), it releases 7.4×10^{-20} J (-8.31 J $mol^{-1}K^{-1} \times 293$ K $\times \ln 10^7/(6.023 \times 10^{23}$ molecules $mol^{-1}) = -7.4 \times 10^{-20}$ J). The amplification factor for triggering an action potential that propagates in a sensory neuron that has 50 μm^2 of its surface in contact with the extracellular fluid is then 3.5×10^5 (2.6×10^{-14} J/7.4×10^{-20} J).

Alternatively, if one photon of green light ($\lambda = 500$ nm) is absorbed by a rhabdomeric photoreceptor and triggers one action potential in the sensory neuron, then the energy E of the photon is $E = h\,c/\lambda$, where h = Planck's constant[1] (6.626×10^{-34}J s), c = speed of light (3×10^8 m s^{-1}) and λ is the wavelength. For $\lambda = 500$ nm the photon has an energy of 4×10^{-19}J (6.626×10^{-34}J s $\times 3 \times 10^8$ m s^{-1}/500 nm $= 4 \times 10^{-19}$ J) and the amplification factor is 6.5×10^4 (2.6×10^{-14} J/4×10^{-19} J).

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[1] We discuss pheromones in Section 17.3.1.

[2] Max Planck was a German theoretical physicist who originated the quantum theory for which he received the Nobel Prize for Physics in 1918.