MODELS OF SPIKING NEURONS: QUESTIONS

• Q1. THRESHOLD AND SPIKES IN AN EXCITABLE MODEL

A simple model of a type I neuron, driven by a current $I < 0$ and with a voltage V is

$$\frac{dV}{dt} = qV^2 + I \tag{1}$$

where $q < 0$. By a suitable rescaling this equation can be written in terms of a dimensionless voltage x and time s

$$\frac{dx}{ds} = x^2 - 1 \tag{2}$$

[Q] What are the rescaled x and s in terms of the original voltage and time? Where are the stable and unstable fixed points?
[A]

$$x = \sqrt{\frac{q}{-I}}V \qquad s = t\sqrt{-Iq}. \tag{3}$$

The fixed points are at -1 (stable) and 1 (unstable).
Solve equation (2) with initial conditions (at $t = 0$) of (i) $x_0 > 1$ or $x_0 < -1$, and (ii) when $-1 < x_0 < 1$ and show that the solutions for these two cases may be written

$$x = -\coth(s - \text{arccoth}(x_0)), \quad x = -\tanh(s - \text{arctanh}(x_0)), \tag{4}$$

respectively.
[A] Divide by $x^2 - 1$ and separate into partial fractions and then integrate

$$dx\left(\frac{1}{x-1} - \frac{1}{x+1}\right) = 2ds \quad \text{so that} \quad \log\left|\frac{x-1}{x+1}\right| = 2(s - \kappa) \tag{5}$$

where κ is a constant. For $x > 1$ or $x < -1$ the mod signs are not required. For $-1 < x < 1$ the mod signs can be replaced with a minus sign. On solving for x the results given can be found.
[Q] Confirm that for case (i) there is a spike at $s = \text{arccoth}(x_0)$.
[A] When the argument of coth vanishes there is a divergence - a "spike".
[Q] Sketch $x(s)$ for cases (i) and (ii) You may choose x_0 so that the equations are antisymmetric around the origin.

• Q2. EFFECTS OF MYELINATION

(The following analysis is taken from the book of Dayan and Abbott, P173, but try to do the question without looking it up in the book!). Myelinated axons are covered with an "insulating" cell that effectively thickens the membrane. There are periodic gaps in the insulation which have a high density of sodium channels. Hence the signal along a myelinated axon propagates by diffusion of voltage along the insulated region and re-triggering of the spike at the gaps. We will now calculate the ratio of the internal and external radii of the membrane and insulation in the myelinated regions that maximises the signal velocity.

Let C_m be the capacitance per unit area of an uninsulated bit of membrane of thickness d_m. We will assume that the effect of the insulation is just to wrap the membrane in more sheets of membranous material. We will first calculate the capacitance of an insulated membrane of internal radius a_1 and external radius a_2. The total capacitance of a small cylindrical element of width Δ_a and length L is

$$C_m \frac{d_m}{\Delta a} 2\pi a L. \tag{6}$$

Capacitance in series adds by reciprocals, i.e. two capacitors C_1 and C_2 in series have a capacitance $C = 1/(1/C_1 + 1/C_2)$.
[Q] Use this to show that the total capacitance of the insulated membrane is given by

$$C = \frac{C_m d_m 2\pi L}{\log(a_2/a_2)} \tag{7}$$

[A] The insulation runs from a radius a_1 to a_2, so the total capacitance for a length of insulation L is given by the integral

$$\frac{1}{C} = \frac{1}{c_m d_m 2\pi L} \int_{a_1}^{a_2} \frac{da}{a} \tag{8}$$

In the insulated stretch of cable there are no transmembrane channels - the membrane is not leaky.
[Q] Use basic cable theory to show that the voltage inside the myelinated stretch of axon obeys:

$$\frac{C}{L}\frac{dV}{dt} = \frac{\pi a_1^2}{r_a}\frac{\partial^2 V}{\partial x^2}. \tag{9}$$

where r_a is the axial resistance.
[A] The axial current as a function of voltage is

$$I = -\frac{\pi a^2}{r_a}\frac{dV}{dx} \tag{10}$$

A small cylindrical element of myelinated cable of thickness Δ_x has a capacitance $C\Delta_x/L$. On considering the currents flowing in and out of this element and the internal capacitive current, the required result is found.
The diffusion constant for the voltage is found by the prefactor of the double derivative multiplied by L/C.

$$D = \frac{\pi a_1^2 L}{C r_a} \tag{11}$$

The larger the diffusion constant the faster the signal velocity in the myelinated sections of axon. In nature it is seen that $a_1 \simeq 0.6 a_2$.
[Q] Substitute in the form for C into the definition of the diffusion constant and find the internal radius a_1 that maximises the diffusion of the voltage at fixed a_2. Show that this is consistent with the experimental ratio.
[A]

$$\frac{\partial D}{\partial a_1} = 0 \quad \text{requires} \quad 2\log(a_2/a_1) = 1 \quad \text{so } a_2 = a_1 e^{1/2} \tag{12}$$

which is close to $a_1 \simeq 0.6 a_2$.