

[1] (10 points) Our notes argue that

$$(V'(t) + a(t)V(t))e^{\int_0^t a(s) ds} = (V(t)e^{\int_0^t a(s) ds})' = b(t)e^{\int_0^t a(s) ds}$$

leads to

$$V(t) = V_{Cl}e^{-\int_0^t a(s) ds} + \int_0^t b(s)e^{-\int_s^t a(y) dy} ds.$$

Please carefully confirm this.

[2] Consider the isopotential cell with an h current and a synapse,

$$\begin{aligned} C_m V'(t) + g_{Cl}(V - V_{Cl}) + \bar{g}_h q^2(V - V_h) + g_{syn}(t)(V - V_{syn}) &= 0 \\ \tau_q(V(t))q'(t) &= q_\infty(V(t)) - q(t) \end{aligned}$$

[2.1] (10 points) At rest we suppose that $g_{syn} = 0$ and $V'(t) = q'(t) = 0$. We denote the resting voltage and gating variable by V_r and q_r . Argue that they obey $q_r = q_\infty(V_r)$ and

$$g_{Cl}(V_r - V_{Cl}) + \bar{g}_h q_\infty^2(V_r)(V_r - V_h) = 0. \quad (1)$$

To solve this by Newton's method we suppose that V_j is our current guess for V_r and we improve this guess via (recall Exercise 5.1)

$$V_{j+1} = V_j - X_j. \quad (2)$$

Express X_j in terms of the values and functions appearing in (1).

[2.2] (10 points) The denominator in X_j likely contains $q'_\infty(V_j)$. Given

$$q_\infty(V) = \frac{1}{1 + \exp((V + 68)/7)}$$

please check that $q'_\infty(V) = q_\infty(V)(q_\infty(V) - 1)/7$.

[2.3] (10 points) With $g_{Cl} = .75$ and $\bar{g}_h = 5$, $V_{Cl} = -68$ and $V_h = -40$, and $V_1 = V_{Cl}$ to be our first guess at V_r , show that equation (1) yields

$$V_2 = -63.$$

(This should not require a calculator).

[2.4] (20 points) Now suppose that $g_{syn}(t) = \varepsilon \tilde{g}(t)$ and $V(t) = V_r + \varepsilon \tilde{V}(t) + O(\varepsilon^2)$ and $q(t) = q_r + \varepsilon \tilde{q}(t) + O(\varepsilon^2)$ and derive a pair of differential equations for \tilde{V} and \tilde{q} . Express this in matrix form $\mathbf{y}' = \mathbf{B}\mathbf{y} + \mathbf{f}$ and carefully identify \mathbf{B} and \mathbf{f} .

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[3] Hodgkin and Huxley used a space clamp together with a voltage clamp to reveal the function of ion channels in the squid giant axon. Smaller structures, e.g., dendrites, have resisted the space clamp. Let us examine the cable equation for the ‘true’ membrane potential, V ,

$$\tau \frac{\partial V}{\partial t}(x, t) + V(x, t) - V_{Cl} = \lambda^2 \frac{\partial^2 V}{\partial x^2}(x, t)$$

subject to a seal at the right, $V_x(\ell, t) = 0$, and a voltage clamp at the left

$$V(0, t) = V_c.$$

[3.1] (15 points) As V_c is constant we may pass to the large time limit and derive an ordinary differential equation for the steady state value of $V(x, t)$. Derive this equation, and its boundary conditions.

[3.2] (15 points) Carefully solve this differential equation.

[3.3] (5 points) Graph your solution.

[3.4] (5 points) Interpret your graph.