



1. [10 points] Please interpret, in full sentences, the circuit above as three coupled single compartment cells. (Each capacitance is  $C$ , each battery is  $E$ , the conductance in series with each battery is  $G$ , and the remaining resistors each have value  $R$ ).
2. [10] Carefully derive three coupled ordinary differential equations for  $V_1$ ,  $V_2$  and  $V_3$ .
3. [10] Define  $v_j = V_j - E$ ,  $j = 1, 2, 3$ , and  $v = [v_1 \ v_2 \ v_3]^T$  and show that  $v$  obeys

$$v'(t) = Bv(t) + f(t), \quad v(0) = 0. \quad (1)$$

Express the solution to this equation in terms of the (yet to be determined) eigenvalues and (normalized) eigenvectors of  $B$ .

4. [10] Consider  $B$  when  $C = R = G = 1$ . Show that  $-1$ ,  $-4$  and  $-4$  are the eigenvalues of  $B$ . and compute their associated eigenvectors. When normalizing please do not approximate any square roots. Hint: one eigenvector is

$$\frac{1}{\sqrt{3}} \begin{pmatrix} 1 \\ 1 \\ 1 \end{pmatrix}$$

and the other two may chosen so that one has a zero in its second component and the other has a zero in the third.

5. [10] Insert these into the general solution found in (3) and explicitly evaluate  $v(t)$  when

$$I_{stim}(t) = 18(\exp(-t) - \exp(-2t))$$

Hint:  $v_2(t) = v_3(t)$  and

$$v(t) = 6 \exp(-t)(t - 1 + \exp(-t)) \begin{pmatrix} 1 \\ 1 \\ 1 \end{pmatrix} + \dots$$

6. [10] If we now add a simple ion channel to each membrane compartment we find at node one that current balance requires (retaining  $C = R = G = 1$ )

$$V_1'(t) + (V_1(t) - E) + 2V_1(t) - V_2(t) - V_3(t) + g_m m_1(t)(V_1(t) - E_m) = I_{stim}(t)$$

where  $m_1$  is presumed to be governed by

$$m_1'(t) = m_\infty(v_1(t)) - m_1(t).$$

Please explain, in full sentences, the biological significance of  $g_m$ ,  $m_1$  and  $E_m$  and their role in these two equations.

7. [10] Please derive the current balance and gating equations at the other two nodes. What equation must the rest potential, call it  $\bar{V}$ , obey?

8. [10] Suppose that  $I_{stim} = \varepsilon I_0$  and assume that

$$V_j(t) = \bar{V} + \varepsilon \tilde{v}_j(t) + \dots \quad \text{and} \quad m_j(t) = m_\infty(\bar{V}) + \varepsilon \tilde{m}_j(t) + \dots$$

Show that

$$\tilde{v} = \begin{pmatrix} \tilde{v}_1 \\ \tilde{v}_2 \\ \tilde{v}_3 \end{pmatrix} \quad \text{and} \quad \tilde{m} = \begin{pmatrix} \tilde{m}_1 \\ \tilde{m}_2 \\ \tilde{m}_3 \end{pmatrix}$$

together are governed by a linear system of the form

$$\begin{pmatrix} \tilde{v}' \\ \tilde{m}' \end{pmatrix} = \begin{pmatrix} B - aI & bI \\ cI & -I \end{pmatrix} \begin{pmatrix} \tilde{v} \\ \tilde{m} \end{pmatrix} + \begin{pmatrix} I_0 \mathbf{e}_1 \\ 0 \end{pmatrix}$$

where  $B$  is the 3-by-3 matrix derived in questions 3 and 4 and  $I$  is the 3-by-3 identity matrix. Please carefully identify the scalars  $a$ ,  $b$  and  $c$ .

9. [10] Let us now study the eigenvalues and eigenvectors of

$$Q \equiv \begin{pmatrix} B - aI & bI \\ cI & -I \end{pmatrix}$$

In particular, from

$$\begin{pmatrix} B - aI & bI \\ cI & -I \end{pmatrix} \begin{pmatrix} p \\ q \end{pmatrix} = \lambda \begin{pmatrix} p \\ q \end{pmatrix}$$

deduce that  $q$  is an eigenvector of  $B$ , that  $p = (\lambda + 1)q/c$  and that  $\lambda$  is determined by

$$\lambda - \frac{bc}{\lambda + 1} + a = z$$

where  $z$  is an eigenvalue of  $B$ . Write down all 6 eigenvalues and their associated eigenvectors in the case that  $a = 2$ ,  $b = 4$  and  $c = 6$ .