Exercises

Chapter 6

1. Build a Connor-Stevens model neuron by numerically integrating the equations for V, m, h, n, a, and b given in chapter 6 (see, in particular, equations 6.1, 6.4, and appendix A). Use $c_m = 10$ nF/mm^2, and as initial values take: $V = -68$ mV, $m = 0.0101$, $h = 0.9659$, $n = 0.1559$, $a = 0.5404$, and $b = 0.2887$. Use an integration time step of 0.1 ms. Use an external current with $I_e/A = 200$ nA/mm^2 and plot V, m, h, n, a, and b as functions of time over a suitable interval. Plot the firing rate of the model as a function of I_e/A over the range from 0 to 500 nA/mm^2. How does this differ from what you got for the Hodgkin-Huxley model in exercise 8 of chapter 5. Finally, apply a pulse of negative current with $I_e/A = -500$ nA/mm^2 for 5 ms followed by $I_e/A = 200$ nA/mm^{2}and show what happens.

2. Construct a Morris-Lecar model neuron (Morris, C & Lecar, H (1981) Voltage oscillations in the barnacle giant muscle fiber. *Biophysical Journal* **35**:193–213). Instead of simulating the fast sodium spikes of an action potential, this model describes slower calcium spikes. The model has just two active currents, an instantaneous voltage-dependent Ca^{2+} current and a persistent K^+ current, described by a single dynamical gating variable N:

$$i_m = \overline{g}_L(V - E_L) + \overline{g}_{Ca} M_\infty(V)(V - E_{Ca}) + \overline{g}_K N(V - E_K)$$

with $\overline{g}_L = 0.005$ mS/mm^2, $\overline{g}_{Ca} = 0.01$ mS/mm^2 and $\overline{g}_K = 0.02$ mS/mm^2, $E_L = -50$ mV, $E_{Ca} = 100$ mV and $E_K = -70$ mV. Use $c_m = 10$ nF/mm^2. The function $M_\infty(V)$ is given by

$$M_\infty(V) = \frac{1}{1 + \exp[-.133(V + 1)]}$$

and the gating variable N is given by

$$\tau_N(V)\frac{dN}{dt} = N_\infty(V) - N$$

with

$$\tau_N(V) = \frac{3}{\cosh[.0345(V - 10)]}$$

and

$$N_\infty(V) = \frac{1}{1 + \exp[-.138(V - 10)]} .$$

Here, V is understood to be in mV units, and τ_N is expressed in ms units. Determine the firing rate as a function of injected current and plot the membrane potential and N as a functions of time. Also, show a phase-plane trajectory, which is a plot of that path taken by these variables in the two-dimensional space described by the points (V,

N), while the model is firing. In the phase plane, plot the nullclines for the V and N equations. These are lines in the V-N plane along which either $dV/dt = 0$ or $dN/dt = 0$. (Phase-plane descriptions and nullclines are described in chapter 7.)

3. The FitzHugh-Nagumo equations (see FitzHugh, R (1961) Impulses and physiological states in models of nerve membrane. *Biophysical Journal* **1**:445–466) are given by

$$\frac{dv}{dt} = v(1 - v^2) - u + I_e \quad \text{and} \quad \frac{du}{dt} = \epsilon(v - 0.5u)$$

   Draw the nullclines for these equations for $I_e = 0$ and $I_e = -1$. These are the lines in the v-u plane where the right side of one or the other of these two equations is zero. In which case or cases do you think the model will produce oscillations? Next simulate the model to see what happens when these equations are integrated over time. Determine what happens for $I_e = 0$ with $\epsilon = 0.3$, 0.1, and 1 and for $I_e = -1$ with $\epsilon = 0.3$. (Phase-plane descriptions and nullclines are described in chapter 7.)

4. Show that solution of equation 6.19 satisfies the cable equation along an infinite cable in response to the injected current $i_e = I_e \tau_m \delta(x)\delta(t)/(2\pi a)$.

5. Verify that the solution for an isolated junction given by equations 6.21 and 6.22 satisfies the correct boundary conditions at the junction point: $v_1(0) = v_2(0) = v_3(0)$ and

$$\sum_{i=1}^{3} a_i^2 \left. \frac{\partial v_i}{\partial x} \right|_{x=0} = 0\,.$$

6. Generalize the solution for an isolated junction of equation 6.21 to the time-dependent case when the injected current on segment 2 is $i_e = I_e \tau_m \delta(x_2 - y)\delta(t)/(2\pi a)$.

7. Show that the expression for $v(x)$ given in figure 6.10, with R_1 and R_2 given by equations 6.23 and 6.24, satisfies the cable equation and the boundary conditions, $v(0) = v_{\text{soma}}$ and $\partial v/\partial x = 0$ when $x = L$.

8. Show that the expression for $v(x)$ given in figure 6.12, with R_3 and R_4 given by equations 6.26 and 6.27, satisfies the cable equation and the boundary conditions, $v(0) = 0$ and $\partial v/\partial x = 0$ when $x = L$.

9. Construct a non-branching axonal cable with conductances in each compartment described by the Connor-Stevens model (as in exercise 1). Solve for the membrane potential using the methods of appendix B of chapter 6. Initiate action potential propagation at one end of the cable by injecting current into the terminal compartment of the cable. Plot the action potential propagation velocity as a function of the axon radius. Inject current into the middle of the cable to generate two, opposite-moving action potentials. Generate action

potentials from each end of the cable and show that they annihilate each other when they collide.

10. Determine the numerical solution for a multi-compartment cable with a single branching node (where a single cable splits into two branches) analogous to the solution for a non-branching cable (equations 6.53–6.56) given in appendix B of chapter 6.