and the leakage current, $V_i$ are the equilibrium potentials for each of the currents, and $\alpha_j$ and $\beta_j$ are nonlinear functions of $V$. We use the notation $n$, $m$, and $h$ for the gate functions because the notation is universally used in the literature. These gate functions are empirical attempts to describe how the membrane controls the flow of ions into and out of the nerve cell. Hodgkin and Huxley found the following empirical forms for $\alpha_j$ and $\beta_j$:

$$\alpha_n = 0.01(V + 10)/[e^{(1+V/10)} - 1] \tag{4.31a}$$

$$\beta_n = 0.125\, e^{V/80} \tag{4.31b}$$

$$\alpha_m = 0.01(V + 25)/[e^{(2.5+V/10)} - 1] \tag{4.31c}$$

$$\beta_m = 4\, e^{V/18} \tag{4.31d}$$

$$\alpha_h = 0.07\, e^{V/20} \tag{4.31e}$$

$$\beta_m = 1/[e^{(3+V/10)} + 1]. \tag{4.31f}$$

The parameter values are $C = 1.0\,\mu\text{F/cm}^2$, $g_K = 36\,\text{mmho/cm}^2$, $g_{Na} = 120\,\text{mmho/cm}^2$, $g_L = 0.3\,\text{mmho/cm}^2$, $V_K = 12\,\text{mV}$, $V_{Na} = -115\,\text{mV}$, and $V_L = 10.6\,\text{mV}$. The unit mho represents ohm$^{-1}$, and the unit of time is milliseconds (ms). These parameters assume that the resting potential of the nerve cell is zero; however, we now know that the resting potential is about $-70\,\text{mV}$.

We can use the ODE solver to solve (4.30) with the state vector $\{V, n, m, h, t\}$; the rates are given by the right-hand side of (4.30). The following questions ask you to explore the properties of the model.

(a) Write a program to plot $n$, $m$, and $h$ as a function of $V$ in the steady state (for which $\dot{n} = \dot{m} = \dot{h} = 0$). Describe how these gates are operating.

(b) Write a program to simulate the nerve cell membrane potential and plot $V(t)$. You can use a simple Euler algorithm with a time step of 0.01 ms. Describe the behavior of the potential when the external current is 0.

(c) Consider a current that is zero except for a one millisecond interval. Try a current spike amplitude of $7\,\mu$A (that is, the external current equals 7 in our units). Describe the resulting nerve impulse $V(t)$. Is there a threshold value for the current below which there is no large spike but only a broad peak?

(d) A constant current should produce a train of spikes. Try different amplitudes for the current and determine if there is a threshold current and how the spacing between spikes depends on the amplitude of the external current.

(e) Consider a situation where there is a steady external current $I_1$ for 20 ms and then the current increases to $I_2 = I_1 + \Delta I$. There are three types of behavior depending on $I_2$ and $\Delta I$. Describe the behavior for the following four situations: (1) $I_1 = 2.0\,\mu$A, $\Delta I = 1.5\,\mu$A; (2) $I_1 = 2.0\,\mu$A, $\Delta I = 5.0\,\mu$A; (3) $I_1 = 7.0\,\mu$A, $\Delta I = 1.0\,\mu$A; and (4) $I_1 = 7.0\,\mu$A, $\Delta I = 4.0\,\mu$A. Try other values of $I_1$ and $\Delta I$ as well. In which cases do you obtain a steady spike train? Which cases produce a single spike? What other behavior do you find?

(f) Once a spike is triggered, it is frequently difficult to trigger another spike. Consider a current pulse at $t = 20$ ms of $7\,\mu$A that lasts for one millisecond. Then give a second current pulse of the same amplitude and duration at $t = 25$ ms. What happens? What happens if you add a third pulse at 30 ms? ∎



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