8.581 Entropy, information and the brain

Problems for Lecture 2.

Consider a neuron that has one type of ion channel that is sensitive to voltage, and a 'leak' conductance.[1] Let the channel have just states, open and closed, and a conductance g when it is open. Assume that the number of open channels $n(t)$ relaxes to its equilibrium value $n_{\rm eq}(V)$ with a time constant $\tau(V)$. In addition assume that the gated channel is (perfectly) selective for ions that have a chemical potential difference of $V_{\rm ion}$ across the membrane, while the leak conductance $G_{\rm leak}$ pulls the membrane potential back to its resting level $V_{\rm rest}$. Finally, assume that the cell has a capacitance C, and allow for the possibility of injecting a current I across the membrane. Then the equations of motion for the coupled dynamics of channels and voltage are

$$C\frac{dV}{dt} = -gn(V - V_{\rm ion}) - G_{\rm leak}(V - V_{\rm rest}) + I, \quad (1)$$

$$\frac{dn}{dt} = -\frac{1}{\tau(V)}[n - n_{\rm eq}(V)]. \quad (2)$$

1. **Effective impedances.** These equations have (at least one!) stationary solution for reasonable forms of $n_{\rm eq}(V)$ and $\tau(V)$. Assume that, for $I = 0$, there is a stationary solution with $V = V_0$. Linearize the equations around this steady state and find the linear response of the voltage to small injected currents. You should write the result in the form

$$V(t) - V_0 = \int dt' Z(t-t')I(t') + \cdots, \quad (3)$$

$$Z(t-t') = \int \frac{d\omega}{2\pi} \exp[-i\omega(t-t')]\tilde{Z}(\omega), \quad (4)$$

which identifies the frequency dependent impedance $\tilde{Z}(\omega)$. You can assume that $\partial n_{\rm eq}(V)/\partial V > 0$, but otherwise you should keep your analysis general.

2. **Instabilities.** The impedance $\tilde{Z}(\omega)$ describes the response of the voltage to injected currents. It should be causal, and it should be stable. Unless you did something wrong in the calculation, causality is guaranteed. What are the conditions for stability? What is the nature of the instability?

[1] Note that this problem amplifies the discussion in the lecture. You should be careful to fill in all the steps.

3. **Equivalent circuits.** For parameter values where the system is stable near V_0, sketch an equivalent electrical circuit that describes the effective impedance $\tilde{Z}(\omega)$. Is the relationship between $V_{\rm ion}$ and $V_{\rm rest}$ important in determining the form of this circuit?

4. **Phase portraits.** Look at the whole phase space of V and n and sketch the possible trajectories (phase portrait). In principle you should be able to do this without assuming precise forms for $n_{\rm eq}(V)$ and $\tau(V)$, just taking some general ideas (e.g., $n_{\rm eq}(V)$ increases monotonically and saturates). It is particularly interesting to see what happens in a regime where the calculation of the impedance indicates that the fixed point at V_0 is unstable.

5. **Propagating fronts.** Imagine that the 'spherical cell' with a single voltage V is replaced by a long tube, or axon. Then the voltage need not be the same at every point, and the dynamics above apply locally, but there is also coupling of neighboring points by diffusion of current in the fluid. Phenomenologically this means that the time derivative of the voltage is replaced by a mixed time and space derivative,

$$C\frac{dV}{dt} \rightarrow C\frac{\partial V}{\partial t} + D\frac{\partial^2 V}{\partial x^2}, \tag{5}$$

while there is no such diffusion of the channel populations. We also need to reinterpret all the parameters; rather than the capacitance of the cell C should be the capacitance per unit length of axon, and so on. Find an approximation (some limiting case) for these spatially extended equations so it becomes clear that there are solutions that propagate at constant velocity. In fact, you should be able to see that not all velocities are allowed. See how much analytic progress you can make toward showing that the equations admit a stereotyped 'action potential' that propagates at fixed velocity.