Spring College on the Physics of Complex Systems
Theoretical Neuroscience: Final Exam
July 20, 2104

Question 1: Integrate-and-fire neuron

Suppose that a neuron has a membrane resistance of $R_m = 50\text{M}\Omega$ and a membrane capacitance of $C_m = 200\text{pF}$. The neuron is at rest at $t = 0$, so that $V(t = 0) = V_R = -65\text{mV}$. Starting at $t = 0$, a constant current of $I_e = 300\text{pA}$ is injected into the cell. The subsequent depolarization of the cell is described by the equation

$$C_m \frac{dV}{dt} = -\frac{V}{R_m} + I_e$$

1.1 Write the equation such that all terms have units of voltage. What is the value of the membrane time constant τ?

1.2 What steady-state voltage does the neuron asymptotically approach for long times? Remember to take into account that at $t = 0$, $V(t = 0) = V_R = -65\text{mV}$.

1.3 Sketch the solution for $V(t)$. Indicate the starting value and the asymptotic value for V on the vertical axis, and the role of τ. The plot only needs to be a sketch, but try to capture the proper scale for the various quantities

1.4 The firing threshold for this neuron is $V_T = -50\text{mV}$. Will this neuron fire? Now assume that the injected current is $I_e = 400\text{pA}$. Will the neuron fire?

1.5 In the case when the neuron does fire, how would you calculate how long will it take for the neuron to emit its first spike after current injection begins at $t = 0$? What about the time interval between the first spike and the second spike?

Question 2: Hodgkin-Huxley equation

Consider the Hodgkin-Huxley equation for a unit area of membrane:

$$c_m \frac{dV}{dt} = -\bar{g}_K n^4 (V - E_K) - \bar{g}_{Na} m^3 h\,(V - E_{Na}) - \bar{g}_L (V - E_L) + \frac{I_e}{A}$$

and the resulting action potential shown at the end of this question. Look at this plot before your start answering the questions.

2.1 Consider the term $\bar{g}_K n^4 (V - E_K)$. To which ionic current does it correspond? What is the meaning of $\bar{g}_K$? What is the meaning of the reversal potential E_K? Is E_K positive or negative? Do you remember the approximate value of E_K? What is the role of gating variable n? What range of values can n take? What determines the value of n?

2.2 Consider the term $\bar{g}_{Na} m^3 h\,(V - E_{Na})$. To which ionic current does it correspond? What is the meaning of $\bar{g}_{Na}$? What is the meaning of the reversal potential E_{Na}? Is E_{Na} positive or negative? Do you remember the approximate value of E_{Na}? What is the role of gating variable h? What is the role of gating variable m? What range of values can h and m take? What determines the value of h and m?

2.3 Are *Na* channels open at the rest potential V_R? What is needed to open *Na* channels? What happens when *Na* channels start to open? Is the *Na* current inwards or outwards? Use these facts to explain the rising part of the action potential shown below. Why is this rise so steep? What is the role of the gating variable h?

2.4 Are *K* channels open at the rest potential V_R? What is needed to open more *K* channels? What happens when *K* channels start to open? Is the *K* current inwards or outwards? Use these facts to explain the falling part of the action potential shown below. Why is this process slower than the rise? Why does the action potential overshoot at the end?

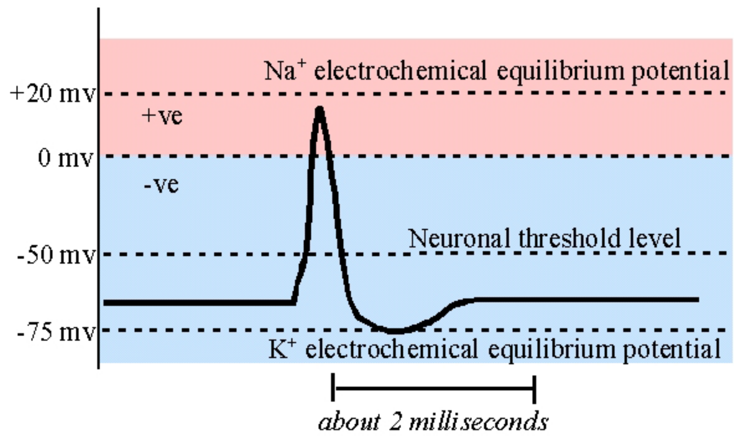
2.5 Let's go back to the gating variable m. What does $m = 0$ mean? What does $m = 1$ mean? The equation that controls this dynamical variable is

$$\frac{dm}{dt} = \alpha(1 - m) - \beta m$$

where both α and β are rates that depend on the membrane potential V. Justify this equation. Show how to transform the above equation for m into

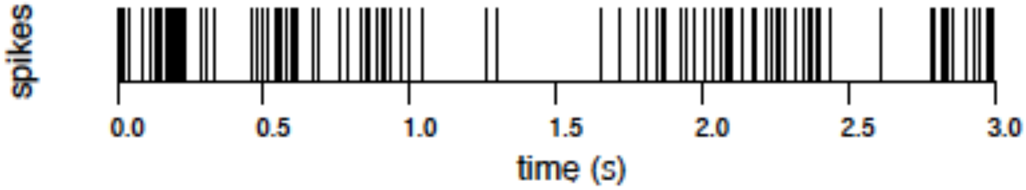
$$\tau_m \frac{dm}{dt} = -m + m_\infty$$

Express τ_m and m_∞ in terms of α and β.



Question 3: Rate models

3.1 Given a spike train such as the one shown here, how would you go about smoothing it into a time-dependent rate? Describe the procedure and sketch what you expect to obtain.



3.2 How would you choose the time window used for this smoothing process? What are the advantages and disadvantages of a very short time window versus a very long time window?

3.3 Consider a postsynaptic neuron that emits spikes at a rate $v(t)$ in response to the activation provided by N presynaptic neurons that spike with rates $\vec{u} = (u_1, u_2, \cdots, u_N)$. The firing rate of the postsynaptic neuron is controlled by the equation

$$\tau_v \frac{dv}{dt} = -v + g(\vec{w} \cdot \vec{u})$$

Consider the driving term $g(\vec{w} \cdot \vec{u})$: sketch a possible shape for the nonlinear function g and interpret its argument $\vec{w} \cdot \vec{u}$.

3.4 How would you incorporate a threshold for firing into this description?

3.5 Assume that the postsynaptic firing rate tracks the driving force, that is to say $v(t) = g(\vec{w} \cdot \vec{u}\,(t))$. If the nonlinear function g is a step function, give an example of this model neuron implementing a Boolean function from *N=2* binary inputs into *1* binary output.

Question 4: Hopfield model

Consider a fully connected system of N neurons, such that their rates $\vec{r} = (r_1, r_2, \cdots, r_N)$ follow the system of equations

$$r_i(t + \tau) = g(\vec{w}_i \cdot \vec{r}(t))$$

4.1 Assume that the firing rates are normalized to their maximum value, so that they all range between 0 and 1. Describe the space in which the dynamical evolution of this N-dimensional system will take place.

4.2 Explain the concept of a fixed point of the dynamics, and sketch the flow around a fully stable fixed point.

4.3 Why do we think that the fixed points of the dynamics of the Hopfield model correspond to memories? How is the process of memory retrieval associated with the concept of the basin of attraction of the corresponding fixed point?

4.4 Given a list of m \`memories', or special patterns of activity $\{\vec{\xi}^{\mu}\}$, $1 \leq \mu \leq m$, Hopfield proposed that we connect the N neurons as follows

$$W_{ij} = \sum_{\mu=1}^{m} \xi_i^{\mu}\, \xi_j^{\mu}$$

to ensure that the \`memories' would be fixed points of the network dynamics. Discuss this form for obtaining the connectivity parameters $\{W_{ij}\}$ in the context of the Hebbian postulate

4.5 Hopfield then proposed that we assign to every possible state $\vec{r} = (r_1, r_2, \cdots, r_N)$ of the system a scalar \`energy' given by

$$E(\vec{r}) = -\frac{1}{2} \sum_{i,j} W_{ij}\, r_i\, r_j$$

Describe in words how the this energy landscape helps us understand the idea of attractive fixed points, basins of attraction, and memory retrieval.