TNI, 2011

Long Questions

There are four questions, one from each main section of the course. Please answer three out of the four, starting the answers for each new question on a new page. Don't forget to write your name at the top of the answer to each question.

You have a maximum of 7 hours for this exam.

Good luck!

1 Biophysics

Consider a simple model of a single neuron with an H-current,

$$\begin{aligned}\tau \frac{dV}{dt} &= f(V) - gxV \\ \tau_x \frac{dx}{dt} &= x_\infty(V) - x\,.\end{aligned}$$

Here V is voltage and x is the gating variable for the H-current. The H-current is a depolarizing current (its reversal potential in this example is 0 mV) which is activated at hyperpolarizing voltages, so $x_\infty(V)$ has the form

$$x_\infty(V) = \frac{1}{1+\exp[(V-V_0)/\Delta V]}\,.$$

Typically V_0 is around -60 mV. Note that x lies between 0 and 1.

Spiking is governed by $f(V)$, and it can be just about anything; common examples are linear integrate and fire, for which $f(V) \sim -(V-V_r)$, and quadratic integrate and fire, for which $f(V) \sim (V-V_r)^2 + C_0$. Here, though, we will use the rather strange form (chosen mainly to reduce the amount of algebra you have to do)

$$f(V) = -\frac{V[(V-V_r)^2 - \mu^2]}{2\mu(\mu - V_r)}\,,$$

with μ = 10 mV and V_r = -60 mV. A spike is generated when V = -30 mV, at which point the voltage is reset to -90 mV. During reset, x does not change.

1. For $x = 0$, plot $\tau dV/dt$ versus V. You should get three fixed points. Write down the linearized the dynamics around each of them, and show explicitly that two are stable and one is unstable. (10 marks)
2. Consider the full set of equations, set g to 1/7, and draw the V-nullcline. Plot the x-nullcline when V_0 = -59 mV and ΔV = 5 mV. (10 marks)
3. Use the nullclines you found above (V_0 = -59 mV and ΔV = 5 mV). Assume $\tau_x \ll \tau$ and sketch two trajectories: one starting at V = -90 mV, x = 0.2; the other at V = -90 mV, x = 0.8. Show that both result in repetitive spiking. (10 marks) Screwed up: it should have been $\tau \ll \tau_x$.
4. Show that if τ_x is sufficiently large compared to τ, then this system of equations will exhibit repetitive spiking if $V_0 > V_r$ and will eventually stop spiking if $V_0 < V_r$. (10 marks)

2 Networks

Consider a network of coupled linear integrate and fire neurons. The voltage of neuron i, V_i, evolves according to

$$
\begin{aligned}
C\frac{dV_i}{dt} &= -g_L(V_i - V_L) - \sum_j c_{ij} g_j(t)(V_i - \mathcal{E}_j) \\
\frac{dg_j}{dt} &= -\frac{g_j}{\tau_g} + g_0 \sum_j \delta(t - t_j^k)\,.
\end{aligned}
$$

Here V_L is the leak potential, c_{ij} specifies whether or not there is a connection (it is 1 if there is a connection and 0 otherwise), $\mathcal{E}_j$ is the reversal potential associated with neuron j, t_j^k is the time of the k^{th} spike on neuron j, $\delta(\cdot)$ is the Dirac delta function, and C, g_L, τ_g and g_0 are parameters. When the voltage crosses threshold, denoted V_{th}, a spike is emitted and the voltage is reset to V_L.

The answers to all questions will depend on the parameters of the model. They are essentially arbitrary, except for the set of conditions $\mathcal{E}_I < V_L < V_{th} < \mathcal{E}_E$ where $\mathcal{E}_I$ and $\mathcal{E}_E$ are the inhibitory and excitatory reversal potentials, respectively. In addition, the fraction of inhibitory neurons stays fixed at about 20%.

1. If neuron j emits a spike at time $t = 0$, and there are no spikes after that, show that

$$g_j(t) = (g_j(0_-) + g_0)e^{-t/\tau_g}$$

   where $g_j(0_-)$ is the value of g_j immediately before the spike. (3 marks)

2. Assume that no spikes have been emitted for a long time, so that neuron i is at rest ($V_i = V_L$), and all the g_j are zero. A single action potential occurs on neuron j (with $j \neq i$ and $c_{ij} = 1$). Write down an expression for $V_i(t)$ in the limit that g_0 is very small. (7 marks) Note: this is not used in any other part of this question.

3. Assume that the neurons are firing asynchronously, their firing times are uncorrelated, and neuron i fires at rate ν_i. In addition, the c_{ij} are chosen independently, and Prob($c_{ij} = 1) = p_c$. Show that if p_c is set to some nonzero value, in the limit of a large number of neurons the network equations reduce to the following equation. (15 marks)

$$C\frac{dV_i}{dt} = -g_L(V_i - V_L) - \tau_g g_0 \sum_j c_{ij}\nu_j(V_i - \mathcal{E}_j)\,.$$

4. In the limit of a large number of neurons, are the firing patterns regular (meaning nearly constant interspike intervals), or irregular (meaning approximately Poisson)? Justify your answer. (5 marks)

5. How should g_0 scale with the number of neurons, N, to ensure that the firing rates stay at reasonable values (around a few Hz) as N goes to infinity? (10 marks)

3 Coding

Consider a population of neurons which encode the orientation θ of a bar. The population can be broken down into A subpopulations of cells, each of size N_a and each tuned to a common orientation θ_a. Suppose that each cell fires n_{ai} spikes with a probability distribution given by $P(n_{ai}|f(\theta - \theta_a))$ where f is a common tuning curve shape.

Assuming that all values of θ are equally likely *a priori* and that the population tuning is dense enough (that is, A is large enough) to encode all values of θ equally well, derive an asymptotic relationship between the mutual information $I(\theta; \{n_{ia}\})$ and the Fisher information in the population.

Specifically, show that:

1. as the population size for each a grows, the posterior distribution on θ approaches
$$P(\theta|\{n_{ia}\}) \to \mathcal{N}(\theta^*, 1/\sum_a N_a J_a(\theta^*)),$$
where θ^* is the maximum-likelihood orientation and $J_a(\theta^*)$ is the Fisher information conveyed by the sub-population tuned to θ_a;
2. and thus that
$$I(\theta; \{n_{ia}\}) \to \log \pi - \tfrac{1}{2} \log 2\pi e/J$$
where J is the population Fisher information.

Now assume that $f = [f_{max} - \rho|\theta - \theta_a|]^+$ (where $[x]^+ = \max(x, 0)$), and that $P(n|f)$ is Poisson with mean f.

3. Using the result above, detemine the value of ρ that would maximize the mutual information.

Finally,

4. discuss two circumstances in which the above relationship might break down, even for very large populations.

4 Learning

Consider a synapse w between pre-synaptic (x) and post-synaptic (y) neurons. $x, y \in \{0, 1\}$ are binary, each with probability p of being 1 for each pattern.

Consider first the case that $w \in \{0, 1\}$ is also binary (figure A). We define the storage operation by a set of Markov transition matrices $M(x, y)_{ss'}$, one for each combination of inputs and outputs x, y, defining the probability that w goes from state s to state s' (one example is shown).

1. Write down and justify a set of M consistent with the intent of standard Hebbian learning. (7 marks)
2. Write down an expression for the expected transition operator T, averaging over input patterns. (5 marks)
3. Using matlab notation, define matrix $\mathcal{I}_q = [q\ 1-q; 1-q\ q]$ and $\mathcal{J}_q = [q\ 1-q; q\ 1-q]$. Consider the case that

$$M(0,0) = \mathcal{J}_q \qquad M(0,1) = \mathcal{J}_{1-q} \qquad M(1,0) = \mathcal{I}_q \qquad M(1,1) = \mathcal{I}_q$$

   What is T in this case? (5 marks)

4. What is the stationary distribution of the weight w assuming that weight changes only happen when patterns are presented? (7 marks)
5. Write down an expression for the mutual information

$$\mathrm{MI}((x, y)_{t-k}, w_t)$$

   between the input at time $t - k$ and the weight at time t. In terms of T, what governs the longevity of the influence of a pair (x, y)? (12 marks)

6. Fusi has suggested that making the weight have hidden metastates as in the figure (B) (hidden since each node in the cascade has an output of either 0 or 1), longevity can be increased. Very briefly explain the intuition underlying this suggestion. (4 marks)