APPM 4370/5370, Computational Neuroscience: Homework 4

Due Wed. Mar. 4, 2020
at 11am (in class)

PAGE 1-2: THREE MATH EXERCISES. PAGE 3: PYTHON EXERCISE.

Math exercises. Relevant Gerstner et al sections: 7.1-7.5, 8.1, 8.4, 10.1, 10.2; & probability primer

1. **Population codes.** In this problem, you will explore optimizing a downstream decoder 'neuron' to determine a stimulus value from two noisy neurons' firing rates. Note the mean of a zero-centered normal random variable $n \sim \mathcal{N}(0, \sigma^2)$ is $\langle n \rangle = 0$ and the variance $\text{Var}[n] = \langle n^2 \rangle - \langle n \rangle^2 = \sigma^2$, and means sum linearly and variances of independent random variables sum but have quadratic scaling:

$$\langle c_1 n_1 + c_2 n_2 \rangle = c_1 \langle n_1 \rangle + c_2 \langle n_2 \rangle,$$
$$\text{Var}[c_1 n_1 + c_2 n_2] = c_1^2 \text{Var}[n_1] + c_2^2 \text{Var}[n_2].$$

(a) *Scalar tuning curves.* Consider two neurons whose firing rates r_1 and r_2 encode a stimulus value x according to a linear function plus noise:

$$r_1 = a_1 x + b_1 + n_1, \quad r_2 = a_2 x + b_2 + n_2,$$

where $a_1, b_1, a_2, b_2 > 0$ are scalars and $n_1 \sim \mathcal{N}(0, \sigma^2)$ and $n_2 \sim \mathcal{N}(0, \sigma^2)$ are uncorrelated, zero-centered, normal random variables. Now consider a downstream 'neuron' whose output $\hat{x}$ linearly decodes the stimulus value x by weighing and shifting the rates r_1 and r_2:

$$\hat{x} = w_1 r_1 + w_2 r_2 - c.$$

- Determine relationships between w_1, w_2, and c that ensure the estimator is *unbiased* (that $\langle \hat{x} \rangle = x$, averaging over the noise). You should only have two equations but three unknowns, so your solution should be a line of points.
- Then, identify the specific w_1, w_2, and c values within this set that minimize the variance $\langle (\hat{x} - x)^2 \rangle$. Determine this minimal variance, and explain how it depends on a_1 and a_2.

(b) *High/low response functions.* Now consider neurons whose rates r_1 and r_2 encode a stimulus value according to some high or low response plus noise:

$$r_1 = H(x) + n_1, \quad r_2 = H(x) + n_2,$$

where $H(x)$ is the Heaviside step function ($H(x) = 1$ for $x \geq 0$, 0 otherwise) and $n_1 \sim \mathcal{N}(0, \sigma^2)$ and $n_2 \sim \mathcal{N}(0, \sigma^2)$. Consider again a shifted linearly decoding neuron response:

$$\hat{x} = w_1 r_1 + w_2 r_2 - c.$$

Assume $x = 1$ and $x = -1$ are the most common inputs, and find the relationship between w_1, w_2, and c that ensures an unbiased estimate at each of these x values. Then, find the specific values of w_1 and w_2 in this set that minimize the variance when $x = -1$. What is the mean squared error $\text{MSE} = \langle (\hat{x} - x)^2 \rangle$ for any $-1 \leq x \leq 1$? Of these values, for what x will the MSE be highest? Why might estimation be worse in this case than in part (a)?

2. **Competitive neural networks.** In this problem, you will analyze two-dimensional systems representing competitive neural networks, often used to model decision making and short term memory.

(a) Consider the following linear system of differential equations representing a competitive network:

$$u_1' = -u_1 - wu_2 + 1 + I_1(t),$$
$$u_2' = -u_2 - wu_1 + 1 + I_2(t),$$

where u_1 and u_2 represent the mean firing rate of each population, $w > 0$ is the strength of competitive inhibition between them and $I_1(t)$ and $I_2(t)$ are the inputs to each population. Consider the case in which $I_1(t) \equiv I_2(t) \equiv 0$ to start and find a formula for the equilibrium of this system as it depends on w and determine its linear stability. For what value of $w = w_c$ is there a line of fixed points (a line attractor)? What is its linear stability? Provide a neurobiological interpretation of your findings.

(b) Show that in the case of a line attractor, $w = w_c$ in (a), the network can remember past inputs. To do so, consider the case in which $u_1(0) = u_2(0) = 1/2$ initially and $I_1(t) = I_0$ for $0 < t < 1$ and then $I_1(t) = 0$ thereafter (while $I_2(t) \equiv 0$). Compute the long term value of neural population rates $\lim_{t\to\infty} u_1(t)$ and $\lim_{t\to\infty} u_2(t)$. How do these depend on I_0? Explain your result.

(c) Lastly, we consider a nonlinear competitive network given by the system

$$u_1' = -u_1 + \frac{1}{1 + \mathrm{e}^{-\gamma(1-2u_2)}}, \tag{1a}$$
$$u_2' = -u_2 + \frac{1}{1 + \mathrm{e}^{-\gamma(1-2u_1)}}, \tag{1b}$$

where $\gamma > 0$ is the *gain* of the firing rate function. Show there is a symmetric fixed point at $\bar{u}_1 = \bar{u}_2 = 1/2$. Show it is the only one by demonstrating the functions $f(u) = u$ and $g(u) = \frac{1}{1+\mathrm{e}^{-\gamma(1-2u)}}$ can only intersect once. Then, determine the linear stability of this fixed point. For $\gamma > 0$ small enough, show the fixed point is stable. Determine the critical value γ_c at which the fixed point becomes unstable and the network becomes competitive.

3. **Winner-take-all model of working memory.** An extension of the competitive neural network in Ex. 2c is a model of N competitive neural populations where only a single population can remain active. To study this in some detail, we consider a model with firing rate functions in the high gain limit ($\gamma \to \infty$), so the sigmoids become Heaviside step functions:

$$u_j' = -u_j + H\left[I_j(t) + u_j - w \sum_{k=1,k\neq j}^{N} u_k\right], \quad j = 1, ..., N,$$

where $H[x] = 1$ for $x \geq 0$ and zero otherwise, $w > 0$ is the strength of competitive inhibition, and the sum is over $k = 1, 2, ..., j-1, j+1, ..., N$ (all neural populations except j).

(a) Consider the $N = 3$ case where $I_1(t) \equiv I_2(t) \equiv I_3(t) \equiv 0$ and $w = 0$, show $u_1 \equiv u_2 \equiv u_3 \equiv 1$ is the only fixed point. Call this the *fully active* state.

(b) Now, show if $w > 0$, there is a critical value w_c above which ($w > w_c$) the only fixed points are of the form $u_a = 1$ (for some $a = 1, 2, 3$) and $u_j = 0$ for all $j \neq a$. Call this the *winner-take-all* state. Why is this a better regime for storing information than the case $w = 0$?

(c) Lastly, if $w = 2 > w_c$ (from (b)), show that if $u_1(0) = 1$ and $u_2(0) = u_3(0) = 0$, and $I_2(t) = 3$ while $I_1(t) \equiv I_3(t) \equiv 0$ for all $t > 0$, then as $t \to \infty$, $u_1 \to 0$, $u_2 \to 1$, and $u_3 \to 0$. Then find a finite time t_1 at which $I_2(t)$ could be switched back to $I_2(t) \equiv 0$ and still have this occur. Hint: This will be the time at which $u_1(t) < u_2(t)$ (u_2 becomes the *winner*). Interpret this finding in terms of the winner-take-all network being a computational model of memory.

python exercise. You will write your own code for the following problem.

4. **Visualizing attractors in competitive neural networks.** Here you will test the theory developed in Ex. 2.

(a) You showed in Ex. 2b that the system

$$u_1' = 1 - u_1 - u_2 + I_1(t), \tag{2a}$$

$$u_2' = 1 - u_1 - u_2 + I_2(t), \tag{2b}$$

contains a line attractor, so we expect it to integrate and store inputs $I_1(t)$ and $I_2(t)$. Validate your result from 2b by writing a code to solve Eq. (2) when $u_1(0) = u_2(0) = 1/2$, $I_1(t) = 1 - H(t-1)$, and $I_2(t) = 0$ for all t. Use Euler's method (or your favorite numerical ODE solving scheme). It will be helpful to use the function np.heaviside(). Plot the trajectories $u_1(t)$ and $u_2(t)$ in the phase plane along with the line attractor $u_2 = 1 - u_1$ to show that the trajectory relaxes to the line. What is the long term value of $(u_1(t), u_2(t))$? Does it match your prediction from 2b?

(b) Now consider the case in which $I_1(t) = 1 - H(t-1)$ and $I_2(t) = 1 - H(t-1)$. Again plot the result in the phase plane. What happens in the long time limit? Why do you get such qualitatively different behavior than the case studied in (a).

(c) Finally, consider the system, Eq. (1), you studied in 2c. First, numerically simulate the case where $\gamma = 1$ and $u_1(0) = 1$ and $u_2(0) = 0$ and plot the result in the phase plane. Then simulate the case where $\gamma = 3$ and $u_1(0) = 3/5$ and $u_2(0) = 2/5$. Finally, simulate the case where $\gamma = 3$ and $u_1(0) = 2/5$ and $u_2(0) = 3/5$. Explain your findings in the context of your analysis in 2c. Is this consistent with what you predicted in terms of having a competitive neural network for γ sufficiently large?