Problem Set 4

Due Thursday, Dec 22, 2022

A toy model of neural integrator

An animal moves on a one-dimensional track. In order to navigate properly (e.g., to find its way back home) the brain must compute the 'on line' position of the animal given sensory information about its velocity. We will assume that the position is computed by means of a network composed of two neurons, whose input is the animal's velocity. The network obeys the following equations:

$$\begin{aligned} \tau\frac{dx}{dt} &= -ax - 2y + \tau V(t); \\ \tau\frac{dy}{dt} &= -(3-a)x - y - \tau V(t) \end{aligned} \tag{1}$$

where the value of $x(t)$ represents the estimated position of the animal at time t.

(a) Study the dynamics of the network for constant velocity, i.e., $V(t) = V_0$ for all $t > 0$: First, find the fixed point of the network and the region of values of the parameter a for which this fixed point is stable. Next, write down the solution for $x(t)$ given that $(x(0), y(0)) = (0, 0)$ and explain what happens as time increases.

(b) Position Estimation. Assume that at $t = 0$, the animal starts out at the origin, and begins moving at a constant velocity $V(t) = 0.1$ m/s. Use $\tau = 100$ ms. If the system acted as a perfect integrator of the velocity, the expected position at $t = 10$ s would be 1 m. Is there a parameter choice (for parameter a) for which this system acts as a perfect integrator? (If so, take any appropriate limits to prove it.) For what range of parameters does the system act as a leaky integrator, i.e., the readout is within 1 cm error of the estimated position from a perfect integrator after 10 seconds? What happens to $x(t)$ when a is outside this range?

Ring network

Consider the ring network model we discussed in the class

$$\tau \frac{du_i}{dt} = -u_i + F\left(\sum_{j=1..N} w_{ij} u_j + I_i^0\right), \tag{2}$$

where $F(x) = [x]_+$ is a rectified linear function and the weights between the neurons are determined by their angular difference and thus are translational invariant.

$$w_{ij} = \frac{1}{N} J(\theta_i - \theta_j), \tag{3}$$

where $\theta_i = -\pi + \frac{2\pi i}{N}$ and J is a 2π periodic function, and I_i^0 is also a periodic 2π function. In the continuous limit, we have

$$\tau \frac{\partial u(\theta, t)}{\partial t} = -u(\theta, t) + \left[\frac{1}{2\pi} \int_{-\pi}^{\pi} J(\theta - \theta') u(\theta', t) d\theta' + I^0(\theta)\right]_+, \tag{4}$$

(a) If the connectivity matrix J is translational invariant and symmetric, prove that the eigenfunctions of J are Fourier basis, namely

$$\frac{1}{2\pi} \int_{-\pi}^{\pi} d\theta' J(\theta - \theta') e_\mu(\theta') = \lambda_\mu e_\mu(\theta) \tag{5}$$

$$e_\mu \sim \cos(\mu\theta) + \sin(\mu\theta), \tag{6}$$

where $\mu = 0, 1, 2, ...$ Find out the correct normalization factor for the eigenfunctions. The corresponding eigenvalues of the the connectivity matrix can be viewed as the Fourier transform $J(\theta)$, namely

$$\lambda_\mu = \frac{1}{2\pi} \int_{-\pi}^{\pi} J(\theta) \cos(\mu\theta) d\theta \tag{7}$$

(b) In the spirit of the linear recurrent network model we discussed in the class, derive the general solution of the *linear* ring network by assuming that $F(x) = x$ instead of a rectified linear network. In the class, we have considered a simple form of the connectivity matrix,

$$J(\theta) = J_0 + J_1 \cos\theta \tag{8}$$

$$I_i^0(\theta) = I_0 + I_1 \cos(\theta - \theta_0) \tag{9}$$

Discuss the stability of a linear ring network in this simple case.

(c) Consider the special case $I_1 = 0$, so that each neuron receives the same homogeneous inputs and $F(x) = [x]_+$. A naive solution is that the population neural activity is homogeneous : all neurons have the same activity. Show that this naive solution is unstable when $J_1 > 2$.

(d) We show in the class that a marginal stable solution is the emergence of a bump, namely, $u(\theta) = [u_1 \cos(\theta) + u_0]_+$. Please show that the bump can actually appear anywhere, namely $u(\theta) = [u_1 \cos(\theta - \phi) + u_0]_+$, where ϕ is arbitrary.

(e) Draw the phase diagram on the $J_0 - J_1$ plane. Discuss and plot in what region, the system is marginally stable? In what region, the system exhibits homogeneous activity? In what region, the system is unstable?

(f) Now consider some tiny modulatory input with $0 < I_1 \ll I_0$ and $J_1 > 2$. Show that in this case, the location of the peak of the stationary activity is not arbitrary, but aligned to the stimulus angle θ_0.

(g) Add to the connectivity matrix a term $\frac{J_1}{N}\gamma \sin(\theta_i - \theta_j)$, where $|\gamma| \ll 1$. Show that there is a solution with the form

$$u(\theta, t) = f(\theta - \omega t), \tag{10}$$

where $f(\theta)$ is the steady state activity profile calculated in the class for $\gamma = 0$ and the angular velocity satisfies

$$\omega = \frac{\gamma}{\tau} \tag{11}$$

Here is some specific guide for the last question:
A. Assume a traveling profile of the form of **??** (for now just use an arbitrary profile $f(\theta)$) and insert it into the two sides of **??**. Express the RHS in terms of the order parameters as was done in the class. Expand the RHS in powers of γ and keep only terms up to linear in γ.
B. Show that if $f(\theta)$ is the profile for $\gamma = 0$ the dynamic equations **??** are satisfied.

Balanced Excitation and Inhibition

Consider an Integrate-and-Fire model. The timing of a spike is defined as the time where the membrane potential V reaches the firing threshold value, V_{th}, from below. Whenever a spike occurs the voltage is reset immediately to a lower value, which for simplicity will be taken as $V_{res} = E_L$. In other words, $V(t^-_{spike}) = V_{th}$, and $V(t^+_{spike}) = V_{res}$.

$$\begin{aligned} C_m \frac{dV}{dt} &= -g_L(V - E_L) + I_e(t) \\ V(t^-_{spike}) &= V_{th} \\ V(t^+_{spike}) &= V_{res} = E_L \end{aligned} \tag{12}$$

Here $I_e(t)$ is an external input to mimic synaptic inputs. Follow my lecture notes, if we define a new variable

$$\tilde{V} = (V - V_{res})/(V_{th} - V_{res}),$$

and denote

$$I_c = g_L(V_{th} - V_{res}),$$

the RC equation together with the resetting event can be rewritten as

$$\begin{aligned} \tau \frac{d\tilde{V}}{dt} &= -\tilde{V} + \frac{I_e}{I_c} \\ \tilde{V}(t^-_{spike}) &= 1 \\ \tilde{V}(t^+_{spike}) &= 0 \end{aligned} \tag{13}$$

1. Let us first consider that $\tilde{I}_e = \frac{I_e}{I_c}$ is a constant, namely time-independent. Derive the condition by which the system will fire action potentials.

2. Consider the case that the model neuron now receives N excitatory synaptic inputs, and each input can be modeled as Gaussian white noise, namely,

$$\tilde{I}_e = \sum_{i=1}^{N} w\xi_i(t),$$

   Here $\xi_i(t)$ can be viewed as the activity of a presynaptic neuron, say proportional to firing rate. Each neuron's activity has the same mean and variance $\langle \xi(t) \rangle = u_0$, $\langle \xi(t)\xi(t') \rangle = \sigma^2 \delta(t - t')$; and the synaptic weight $w = \frac{J_0}{N}$, $J_0 > 0$. Adjust u_0, J_0 so that the neuron would fire action potentials. Now explore the firing pattern of the neuron as you increase the number of inputs N. Ask how would the neuron behave if N is large, say a few thousands. Note that in practice, you should consider noisy inputs as a discrete random time sequence satisfying $\langle \xi(t_k)^2 \rangle = \frac{1}{N} \frac{\sigma^2}{\Delta t}$, and $\langle \xi(t_k)\xi(t'_k) \rangle = 0$, if $t_k \neq t'_k$. Here Δt is the time step in your simulation. $\sigma^2 \sim O(1)$ is the variance of neural activity and is assumed to be of the order of 1.

3. Now consider the neuron receives 20% inhibitory synaptic inputs and 80% excitatory inputs, as well as a constant external input I_0. The synaptic weights for excitatory inputs are given by $w_+ > 0$, and those from inhibitory inputs are given by $w_- < 0$. Derive the condition (look at my lecture note) by which the total synaptic inputs have a finite variance that is independent of the total number of inputs N. Find the condition that the neuron can exhibit irregular spiking patterns as N becomes large, and perform a simulation and compute the Fano factor of the spike statistics. **Hint**: the mean total synaptic current $\langle \tilde{I}_e \rangle$ cannot be too small. It should drive the membrane potential close to the threshold, and it is the fluctuation of the input current that drives neurons above threshold