Final Exam of Biophysics I

Due Tuesday, January 14, 2020

Feedforward network with extreme convergence and divergence

In the class, we had discussed the synaptic organization of the cerebellum Figure 1. Mossy fibers, which are long range projections from various brain regions, make connections with granule cells , the most numerous ($\sim 10^{11}$) neurons in the whole brain. These granule cells have a very small convergence: each of which only receives inputs from a handful mossy fibers. The outputs of granule cells, called parallel fibers, travel along the cerebellar cortex for a few millimeters and synapse onto Purkinje dendrites. Purkinje cells have the highest convergence in the brain, each of which receives inputs from more than 10^5 synapses from parallel fibers. The granule-to-Purkinje projections are what we called Connecting dense array to sparse array with extreme convergence and divergence?.

Why do we need so many granule cells? What can we say about the number of granule cells N, the number of mossy fiber inputs M, and the convergence of a granule cell K? Perhaps each granule cell is sampling a different combination of mossy fiber inputs. The higher the functional diversity, the more powerful computation downstream circuits (e.g., Purkinje dendrites) could perform, such as classification.

Assume each granule cell can choose K inputs out of all M mossy fibers, the number of possibilities is simply a binomial coefficient $\binom{M}{K}$. Now we ask the following questions.

1. What is the probability p that granule cells all receive *different* combinations of inputs?
2. For given N and M, plot p as a function of K, and show when p reaches its maximum.
3. Using $N = 20000$, $M = 7000$, compute K when p approaches 95 percent of its maximum.
4. Discuss whether it is beneficial to have small K when M is very large.

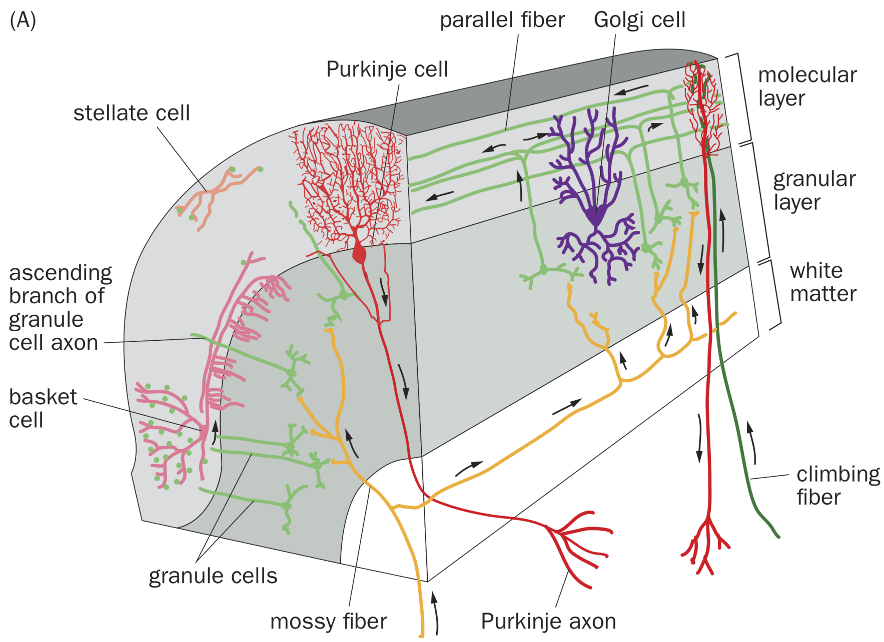

Figure 1: The synaptic organization of cerebellum

Sensory Neuron from an Electric Fish

Electric fish can generate and sense electric fields. The response of a electrosensory neuron $R(t)$ is characterized by the firing rate, which is the number of spikes (action potential)occurred within a time window divided by the time bin size Δt. Use the following equation

$$R(t) = R_0 + \int_0^{\infty} D(\tau) s(t-\tau) dt, \tag{1}$$

with $R_0 = 50$ Hz, and

$$D(\tau) = -\cos\left(\frac{2\pi(\tau - 20\text{ms})}{140\text{ms}}\right) \exp\left(-\frac{\tau}{60\text{ms}}\right) \text{Hz/ms}, \tag{2}$$

to predict the response of a neuron of the electrosensory lateral-line lobe to a stimulus. Use an approximate Gaussian white noise stimulus constructed by choosing a stimulus value every 10 ms ($\Delta t = 10$ ms) from a Gaussian distribution with zero mean and variance $\sigma^2/\Delta t$, with $\sigma^2 = 10$. A detailed description of white noise can be found on page 21 of the theoretical neuroscience textbook.

1. Compute the firing rate over a 10 s period.
2. From the results, compute the firing rate-stimulus correlation function $Q_{rs}(\tau)$.

3. Compare $Q_{rs}(-\tau)/\sigma^2$ with the kernel $D(\tau)$ given above.

Winner Take All Circuit

Consider the following recurrent network dynamics of N neurons:

$$\begin{aligned} \frac{dx_i}{dt} &= -x_i + \left[b_i + \alpha x_i - \beta \sum_{j=1, j\neq i}^{N} x_j \right]_+ & (3) \\ &= -x_i + [b_i + (Wx)_i]_+ & (4) \end{aligned}$$

where we have denoted $W = (\alpha + \beta)I - \beta \underline{1}_N$ ($\underline{1}_N$ is an $N \times N$ matrix of ones) and $[x]_+ \equiv max(x, 0)$. $\alpha > 0$ is self-excitation and $\beta > 0$ represents a global inhibition.

The external inputs ($b_i > 0$) are fixed in time and we assume that they are all different from each other. Prove the following:

*A. If $\alpha < 1$, then the network will converge asympotatically to a fixed point from almost all initial conditions.

B. If $\alpha < 1$ and $\beta > 1 - \alpha$ then the only possible stable states of the network are fixed points in which only a single neuron is active.

C. Given B, the neurons that can remain active at long time are those for which:

$$b_i \geq \frac{1-\alpha}{\beta} b_{\max} \tag{5}$$

(where $b_{\max} = \max_i b_i$). From this result, derive the conditions which guarantee that, independent of the initial conditions, the network evolves into a state where only the neuron with the largest b_i is active (i.e., the network picks the "winner" neuron).

Instructions for *A: Prove that

$$\begin{aligned} E(x) &= -\sum_i b_i x_i + \frac{1}{2}(1-\alpha)\sum_i x_i^2 + \frac{\beta}{2}\sum_{i\neq j} x_i x_j & (6) \\ &= \frac{1}{2}x^T x - b^T x - \frac{1}{2}x^T W x & (7) \end{aligned}$$

is a Lyapunov function of the system. When calculating $\frac{dE}{dt}$ it is useful to consider separately the contributions from neurons such that $b_i + (Wx)_i > 0$ and those for which $b_i + (Wx)_i < 0$.

Instructions for B: Assume there exists a fixed point with K active neurons.

We can arrange the order of the neurons in the system so that: $x_1^*, ...x_K^* > 0$, $x_{K+1}^*, ...x_N^* = 0$ where K denotes the number of active neurons in the fixed point. By linearizing around such a fixed point, prove that if $\alpha < 1$ and $\beta > 1-\alpha$, then the fixed point is stable iff $K = 1$. Note: stability of the inactive neurons is quite straightforward to show. For the active neurons you need to diagonalize a matrix of the form $\underline{1}_K$. If you have difficulty in this part, try at least to analyze the stability of the state with $K = 1$.

Instructions for C: Assume a fixed point with a single active neuron as claimed by **B** and show that consistency requires that the active neuron obey the property Equation 5.

Note: If you have difficulty with proving A, you can assume A and proceed to prove B and C. Likewise, if you have difficulties proving B, assume that B holds and proceed to prove C.