1 Balanced networks: Noise, synaptic scaling, and linear response

1.1 Scaling of neuronal inputs

An interesting observation is that the subthreshold neuronal voltage in cortical neurons is very noisy. Naively, one might expect that the subthreshold potential would be noisy if there were relatively few inputs, consistent with the notion of a few strong inputs that one sees in cortical slice experiments. But the other possibility is that the input is so noisy because large excitatory inputs are offset by large inhibitory inputs, so that their mean value just about cancels but the variances, of course, add. The notion of large offsetting currents comes from the intracellular recording experiments in cat V1 from the laboratories of Ferster, Fregnac, Douglas and more recently Scanziani, in which the excitatory and inhibitory inputs are found to be both large and have the same tuning curves, so that their inputs act to balance each other. The gain from offsetting currents is that a transient increase in excitatory input, as may occur with a large burst of input, will rapidly depolarize the cell. So balanced networks trade noise for speed.

Let’s start with a warm up on scaling of noise. The input to cell $i$ from cell $j$ is $W_{ij}$ with $j = 1, 2, \ldots, N$, while the output of the neuron is taken as $S_i$ with $i = 1, 2, \ldots, N$ where $S$ is a binary variable, 1 if the cell spikes and 0 if it does not. Let’s say that of the $N$ neurons in the network, only a smaller number $K$ make synaptic input to the $i$−th neuron. Let’s also say that the probability that a cell is spiking is $m$, that is, $S = 1$ with probability $m$ and $S = 0$ with probability $1 - m$. Later, when we get to balanced networks, the $m$’s will be associated with averages over all neurons, or ”order parameters”. The input to the $i$−th neuron is:

$$\mu_i \equiv \sum_{j=1}^{K} W_{ij} S_j.$$  \hspace{1cm} (1.1)

Let’s address the central issue, which is scaling of the synaptic inputs. The standard thermodynamic scaling, so that total synaptic currents are bounded as the size of the system increases, is that each input scales as $1/K$. For simplicity, let’s take all of the inputs to be equal, so

$$W_{ij} \rightarrow \frac{W}{K}.$$  \hspace{1cm} (1.2)

Then

$$\mu_i = \frac{W}{K} \sum_{j=1}^{K} S_j.$$  \hspace{1cm} (1.3)
The average value is

$$< \mu > = \frac{W}{K} \sum_{j=1}^{K} < S_j >$$

$$= W \frac{1}{K} \sum_{j=1}^{K} < S_j >$$

$$= Wm$$

and the variance, under the assumption of Poisson statistics for $S$ and that the correlations in the neuronal outputs are zero, is

$$< \sigma^2 > = \sum_{j=1}^{K} (\mu_j - < \mu >)^2$$

$$= \frac{W^2}{K} \frac{1}{K} \sum_{j=1}^{K} (S_j - < S >)^2$$

$$= \frac{W^2}{K} \left( \frac{1}{K} \sum_{j=1}^{K} S_j^2 - < S >^2 \right)$$

$$= \frac{W^2}{K} \left( m - m^2 \right)$$

$$= \frac{< \mu >^2}{K} \left( 1 - \frac{m}{m} \right)$$

which is always positive and, crucially, diminishes as $K \to \infty$.

The challenge is to recast the input so that the variance does not diminish as a function of $K$. This is where the idea of balanced excitation and inhibition comes in to play. We need the input to be the sums of two terms, and we also need to adjust the scaling so that the variance goes to a constant as $K \to \infty$. Let $W_{ij}^E$ be excitatory input and $W_{ij}^I$ be inhibitory input, simplified as above but now scaled as $1/\sqrt{K}$ rather than $1/K$, so that

$$W_{ij}^E \to \frac{W_{ij}^E}{\sqrt{K}}, \quad W_{ij}^I \to -\frac{W_{ij}^I}{\sqrt{K}}$$

(1.6)

where we implicitly fix the sign of the inhibition. The mean input to the $i$th neuron is now

$$\mu_i = \mu_i^E + \mu_i^I$$

$$= \sum_{j=1}^{K} W_{ij}^E S_j^E + \sum_{j=1}^{K} W_{ij}^I S_j^I$$

(1.7)

The average value under the assumed scaling is

$$< \mu > = \frac{W^E}{\sqrt{K}} \sum_{j=1}^{K} S_j^E - \frac{W^I}{\sqrt{K}} \sum_{j=1}^{K} S_j^I$$

(1.8)
\[
W^E \rightarrow \frac{W^{EE}}{\sqrt{K}}, \quad W^{II} \rightarrow -\frac{W^{II}}{\sqrt{K}}, \quad W^{EI} \rightarrow -\frac{W^{EI}}{\sqrt{K}}, \quad W^{IE} \rightarrow \frac{W^{IE}}{\sqrt{K}}.
\]

and as will be clear soon, we need to scale the external inputs by
\[
\mu^E_o \rightarrow \sqrt{K} E m_o; \quad \mu^I_o \rightarrow \sqrt{K} I m_o
\]
where $E$ and $I$ are inputs of strength of $O(1)$. All together, we have

$$
\mu^E_i(t) = \sqrt{K} E m_o + \frac{W^{EE}}{\sqrt{K}} \sum_{j=1}^{K} S^E_j(t) - \frac{W^{EI}}{\sqrt{K}} \sum_{j=1}^{K} S^I_j(t) \quad (1.15)
$$

$$
\mu^I_i(t) = \sqrt{K} I m_o + \frac{W^{IE}}{\sqrt{K}} \sum_{j=1}^{K} S^E_j(t) - \frac{W^{II}}{\sqrt{K}} \sum_{j=1}^{K} S^I_j(t).
$$

Let’s write the average activities, the so-called order parameters, as

$$
m^E_i(t) = \frac{1}{K} \sum_{i=1}^{K} S^E_i(t) \quad (1.16)
$$

$$
m^I_i(t) = \frac{1}{K} \sum_{i=1}^{K} S^I_i(t)
$$

where for simplicity we assumed equal number of excitatory and inhibitory cells. The inputs and outputs are connected by

$$
S^E_i(t) = H \left( \mu^E_i(t) - \theta^E_i \right) \quad (1.17)
$$

$$
S^I_i(t) = H \left( \mu^I_i(t) - \theta^I_i \right),
$$

$H(\cdot)$ is the Heavyside function, and the $\theta^E_i$ and $\theta^I_i$ are threshold functions. The so-called ”order parameters” allows us to write equations for the average input, i.e.,

$$
<\mu^E(t)> = \sqrt{K} E m_o + \frac{W^{EE}}{\sqrt{K}} \sum_{j=1}^{K} <S^E_j(t)> - \frac{W^{EI}}{\sqrt{K}} \sum_{j=1}^{K} <S^I_j(t)> \quad (1.18)
$$

$$
= \sqrt{K} E m_o + \sqrt{K} W^{EE} m^E(t) - \sqrt{K} W^{EI} m^I(t)
$$

$$
= \sqrt{K} \left( E m_o + W^{EE} m^E(t) - W^{EI} m^I(t) \right)
$$

and

$$
<\mu^I(t)> = \sqrt{K} I m_o + \frac{W^{IE}}{\sqrt{K}} \sum_{j=1}^{K} <S^E_j(t)> - \frac{W^{II}}{\sqrt{K}} \sum_{j=1}^{K} <S^I_j(t)> \quad (1.19)
$$

$$
= \sqrt{K} \left( I m_o + W^{IE} m^E(t) - W^{II} m^I(t) \right)
$$

As $\sqrt{K} \to \infty$ the left hand side goes to zero and the equilibrium state will satisfy

$$
0 \left( \frac{1}{\sqrt{K}} \right) = E m_o + W^{EE} m^E - W^{EI} m^I \quad (1.20)
$$

and

$$
0 \left( \frac{1}{\sqrt{K}} \right) = I m_o + W^{IE} m^E - W^{II} m^I. \quad (1.21)
$$

The implication of this equilibrium condition is that the average input remains finite as the fluctuations remain large. This is the balanced state.
Solving the above gives relations for the equilibrium activity of the excitatory and inhibitory cells in terms of the external drive:

\[ m_E = \frac{W^{II}E - W^{EI}I}{W^{EE}W^{II} - W^{EI}W^{IE}}m_0. \]  

(1.22)

and

\[ m_I = \frac{W^{IE}E - W^{EE}I}{W^{EE}W^{II} - W^{EI}W^{IE}}m_0. \]  

(1.23)

The equilibrium values of activity \( m_E \) and \( m_I \) must be positive. This implies

\[ \frac{E}{I} > \frac{W^{EI}}{W^{II}} < 1 \]  

(1.24)

and

\[ \frac{E}{I} > \frac{W^{EE}}{W^{IE}}. \]  

(1.25)

For the solution must remain finite

\[ \frac{E}{I} > \frac{W^{EE}}{W^{IE}} > \frac{W^{EI}}{W^{II}} < 1. \]  

(1.26)