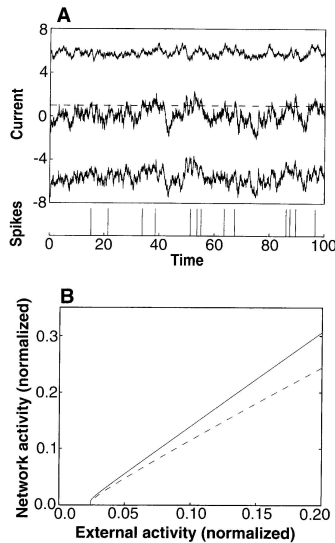


1 Balanced networks: Trading speed for noise

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, not inconsistent 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 others, 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.



(A) Temporal structure of the inputs and activity of a single excitatory unit. The upper panel shows the total excitatory input (consisting of external input and excitatory feedback) (upper trace) and the total inhibitory input (lower trace), as well as the net input (middle trace). The currents are shown in units of the threshold (dashed line). They were calculated by sampling from the Gaussian statistics of the currents predicted by the theory.

Below, the times when the cell switched to the active state are indicated. The cell is set to the active state when a suprathreshold net input coincides with the update time of the cell. (B) The mean activity of the excitatory neurons (solid line) and the inhibitory ones (dashed line) as functions of the activity of the external units. The activities shown here and in the following figures correspond to firing rates divided by their maximum value. Assuming a neuronal maximum rate of 1000 Hz, a mean activity of 0.1 corresponds to a firing rate of 100 Hz.

Let's start with a warm up on scaling of noise. The input to cell i is μ_i with $i = 1, 2, \dots, N$, while the output of the neuron is taken as V_i with $i = 1, 2, \dots, N$ where V 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 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, $V = 1$ with probability m and $V = 0$ with probability $1 - m$. The input to the

i – th neuron is:

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

Let's address the central issue, which is scaling of the synaptic inputs. The standard thermodynamic scaling is that each input scales as $1/K$. For simplicity, let's take all of the inputs to be equal, so

$$W_{ij} \rightarrow \frac{W}{K}. \quad (1.2)$$

Then

$$\mu_i = \frac{W}{K} \sum_{j=1}^K V_j. \quad (1.3)$$

The average value is

$$\begin{aligned} \langle \mu \rangle &= \frac{W}{K} \sum_{j=1}^K \langle V_j \rangle \\ &= \frac{W}{K} \sum_{j=1}^K m \\ &= Wm \end{aligned} \quad (1.4)$$

and the variance, under the assumption that the correlations in the neuronal outputs are zero, is

$$\begin{aligned} \langle \mu^2 \rangle &= \left(\frac{W}{K} \right)^2 \sum_{j=1}^K (V_j - \langle V_j \rangle)^2 \\ &= \left(\frac{W}{K} \right)^2 \left(\sum_{j=1}^K V_j^2 - K \langle V_j \rangle^2 \right) \\ &= \frac{W^2}{K} (m - m^2) \\ &= \frac{(Wm)^2}{Km} (1 - m) \end{aligned} \quad (1.5)$$

which is always positive and, crucially, diminishes as $mK \rightarrow \infty$.

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 come in to play. We need the input to be the sums of two terms, and we also need to noodle with the scaling so that the variance goes to a constant as $mK \rightarrow \infty$. Let W_{ij}^E be excitatory input and W_{ij}^I be inhibitory input, simplified as above but now scaled as $1/\sqrt{K}$, so that

$$W_{ij}^E \rightarrow \frac{W^E}{\sqrt{K}}, \quad W_{ij}^I \rightarrow -\frac{W^I}{\sqrt{K}} \quad (1.6)$$

where we implicitly fix the sign of the inhibition, and

$$\mu_i = \sum_{j=1}^K (W_{ij}^E V_j^E + W_{ij}^I V_j^I) \quad (1.7)$$

$$= \frac{W^E}{\sqrt{K}} \sum_{j=1}^K V_j^E - \frac{W^I}{\sqrt{K}} \sum_{j=1}^K V_j^I.$$

The average value is

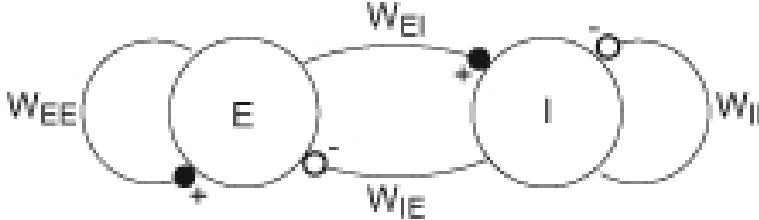
$$\begin{aligned} \langle \mu \rangle &= \frac{W^E}{\sqrt{K}} K m^E - \frac{W^I}{\sqrt{K}} K m^I \\ &= \sqrt{K} (W^E m^E - W^I m^I) \end{aligned} \quad (1.8)$$

which can be large if the excitatory and inhibitory terms do not balance. The variance, again under the assumption that the correlations in the neuronal outputs are zero, is

$$\begin{aligned} \langle \mu_i^2 \rangle &= \frac{(W^E)^2}{K} (m^E - (m^E)^2) K + \frac{(W^I)^2}{K} (m^I - (m^I)^2) K \\ &= (W^E m^E)^2 \frac{1 - m^E}{m^E} + (W^I m^I)^2 \frac{1 - m^I}{m^I}. \end{aligned} \quad (1.9)$$

The important point is that there is no decrement as $m^E K \rightarrow \infty$ or $m^I K \rightarrow \infty$. Further, the variance remains nonzero for the special case of $W^E m^E = W^I m^I$ where the network is in perfect balance.

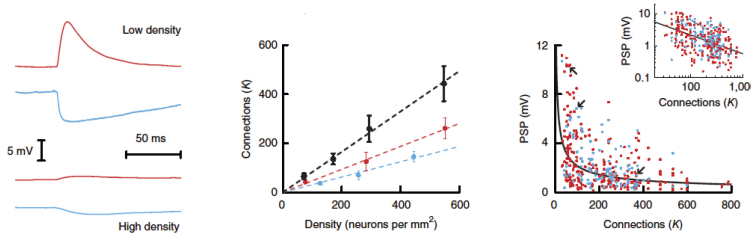
Before we go further, it is fair to ask if there is evidence to support this scaling, which would depend on a homeostatic mechanism. Barres and Reyes built networks in cell culture of different size and find scaling of the synaptic weights $W \propto K^{-0.6}$ as opposed to the predicted value of $W \propto K^{-0.5}$ for this model. Not bad!



1.2 Circuit model

We now consider the consequences on the choice of connections in a network to maintain the balanced state. Consider a network of a population of excitatory (E) and inhibitory (I) cells:

$$\begin{aligned} \mu_i^E(t) &= \mu_o^E + \sum_{j=1}^K W_{i,j}^{EE} V_j^E(t) + \sum_{j=1}^K W_{i,j}^{EI} V_j^I(t) \\ \mu_i^I(t) &= \mu_o^I + \sum_{j=1}^K W_{i,j}^{II} V_j^I(t) + \sum_{j=1}^K W_{i,j}^{IE} V_j^E(t) \end{aligned} \quad (1.10)$$



As in the case of the model cell, we will scale the synaptic inputs by $1/\sqrt{K}$

$$W_{ij}^{EE} \rightarrow \frac{W^{EE}}{\sqrt{K}}, \quad W_{ij}^{II} \rightarrow -\frac{W^{II}}{\sqrt{K}}, \quad W_{ij}^{EI} \rightarrow -\frac{W^{EI}}{\sqrt{K}}; \quad W_{ij}^{IE} \rightarrow \frac{W^{IE}}{\sqrt{K}}. \quad (1.11)$$

and as will be clear soon, we need to scale the external inputs by

$$\mu_o^E \rightarrow \sqrt{K}Em_o; \quad \mu_o^I \rightarrow \sqrt{K}Im_o \quad (1.12)$$

where E and I are scales of $O(1)$, so that

$$\begin{aligned} \mu_i^E(t) &= \sqrt{K}Em_o + \frac{W^{EE}}{\sqrt{K}} \sum_{j=1}^K V_j^E(t) - \frac{W^{EI}}{\sqrt{K}} \sum_{j=1}^K V_j^I(t) \\ \mu_i^I(t) &= \sqrt{K}Im_o + \frac{W^{IE}}{\sqrt{K}} \sum_{j=1}^K V_j^E(t) - \frac{W^{II}}{\sqrt{K}} \sum_{j=1}^K V_j^I(t). \end{aligned} \quad (1.13)$$

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

$$m_E(t) = \frac{1}{N_E} \sum_{i=1}^{N_E} V_i^E(t) \quad (1.14)$$

$$m_I(t) = \frac{1}{N_I} \sum_{i=1}^{N_I} V_i^I(t)$$

where the inputs are connected by

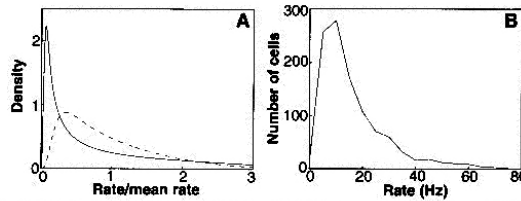
$$V_i^E(t) = H(\mu_i^E(t) - \theta_i^E) \quad (1.15)$$

$$V_i^I(t) = H(\mu_i^I(t) - \theta_i^I) \quad (1.16)$$

$$(1.17)$$

$H(\cdot)$ is the Heavyside function, and the θ_i^E and θ_i^I are threshold functions. Note that the order parameters are small,

(A) The distribution of the rates of neurons in the excitatory population for different population-averaged rates: (solid line) $m_E = 0.01$ and (dashed line) $m_E = 0.03$. The rate distribution is shown in terms of the local rates divided by the mean rate. (B) The distribution



of firing rates of neurons in the right prefrontal cortex of a monkey attending to a variety of stimuli (light source and sound) and executing simple reaching movements. The rates were averaged over the duration of events (stimuli or movements) that showed a significant response. The average rate was 15.8 Hz. Most cells fire at a lower rate, whereas a small fraction of the cells fire at much higher rates.

The order parameters allows us to write equations for the average input, i.e.,

$$\begin{aligned} \langle \mu_E(t) \rangle &= \sqrt{K} E m_o + \frac{W^{EE}}{\sqrt{K}} \sum_{j=1}^K \langle V_j^E(t) \rangle - \frac{W^{EI}}{\sqrt{K}} \sum_{j=1}^K \langle V_j^I(t) \rangle \quad (1.18) \\ &= \sqrt{K} E m_o + \sqrt{K} W^{EE} m_E(t) - \sqrt{K} W^{EI} m_I(t) \end{aligned}$$

and

$$\begin{aligned} \langle \mu_I(t) \rangle &= \sqrt{K} I m_o + \frac{W^{IE}}{\sqrt{K}} \sum_{j=1}^K \langle V_j^E(t) \rangle - \frac{W^{II}}{\sqrt{K}} \sum_{j=1}^K \langle V_j^I(t) \rangle \quad (1.19) \\ &= \sqrt{K} I m_o + \sqrt{K} W^{IE} m_E(t) - \sqrt{K} W^{II} m_I(t) \end{aligned}$$

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

$$\begin{aligned} 0 \left(\frac{1}{\sqrt{K}} \right) &= E m_o + W^{EE} m_E - W^{EI} m_I \quad (1.20) \\ &= I m_o + W^{IE} m_E - W^{II} m_I \end{aligned}$$

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

$$m_E = \frac{W^{II} E - W^{EI} I}{W^{EE} W^{II} - W^{EI} W^{IE}} m_o. \quad (1.21)$$

and

$$m_I = \frac{W^{IE} E - W^{EE} I}{W^{EE} W^{II} - W^{EI} W^{IE}} m_o. \quad (1.22)$$

The equilibrium values of activity m_E and m_I must be positive. If we wish to avoid saturated solutions This requires:

$$\frac{E}{I} > \frac{W^{EI}}{W^{II}} > \frac{W^{EE}}{W^{IE}} < 1 \quad (1.23)$$

The final point concerns dynamics. The dynamic of the order parameters, defined above, follow Glauber dynamics - a formalism for binary variables. Thus, without derivation, the equation for the i -th excitatory neuron is

$$\tau_E \frac{dm_{E,i}(t)}{dt} = -m_{E,i}(t) + H \left(\mu_i^E(t) - \theta_i^E \right). \quad (1.24)$$

If we look at the entire network, we can replace the thresholded inputs from the neighbors by the probability that neighboring cells are firing. This will depend on the mean input and on the variance in the input. The mean inputs at equilibrium, from above, are

$$\begin{aligned} \mu_E &= \sqrt{K} E m_o + \sqrt{K} W^{EE} m_E - \sqrt{K} W^{EI} m_I - \theta_E \quad (1.25) \\ \mu_I &= \sqrt{K} I m_o + \sqrt{K} W^{IE} m_E - \sqrt{K} W^{II} m_I - \theta_I. \end{aligned}$$

The variance to excitatory cells, $\sigma_E^2(t)$, is given by

$$\sigma_E^2(t) = (W^{EE})^2 m_E(t) + (W^{EI})^2 m_I(t) \quad (1.26)$$

with a similar expression for the inhibitory cells, i.e.,

$$\sigma_I^2(t) = (W^{IE})^2 m_E(t) + (W^{II})^2 m_I(t) \quad (1.27)$$

so that

$$m_E(t) = \frac{(W^{EE})^2 \sigma_I^2(t) - (W^{IE})^2 \sigma_E^2(t)}{(W^{EI})^2 (W^{IE})^2 - (W^{EE})^2 (W^{II})^2}. \quad (1.28)$$

We approximate the noise by a Gaussians so that we can estimate when the input exceeds the threshold level θ^E , i.e.,

$$\tau_E \frac{dm_E(t)}{dt} = -m_E(t) + \frac{1}{\sqrt{2\pi} \sigma} \int_{\theta^E}^{\infty} e^{-(x-\mu^E)^2/2\sigma^2} dx \quad (1.29)$$

$$= -m_E(t) + \frac{1}{\sqrt{\pi}} \int_{\sqrt{2}(\mu^E - \theta^E)/\sigma_E}^{\infty} e^{-x^2} dx \quad (1.30)$$

$$\equiv -m_E(t) + \frac{\sigma_E}{\sqrt{2}} \operatorname{erfc} \left(\frac{\mu^E - \theta^E}{\sqrt{2}\sigma_E} \right)$$

For a small ratio of mean input to standard deviation, the erfc can be expanded as

$$\operatorname{erfc}(x) \approx \frac{e^{-x^2}}{\sqrt{2\pi}x}. \quad (1.31)$$

In equilibrium, $\frac{dm_E(t)}{dt} = 0$ so so we have a nonlinear relation between the average input, $\langle \mu_E \rangle$ and the variances σ_E^2 and σ_I^2 at equilibrium. This leads to a leading term:

$$\mu^E \approx \theta^E + \sigma_E \sqrt{2|\log m_E|} \quad (1.32)$$

(CHECK SIGN OF θ^E). We see that the average activity is driven, almost linearly, by the standard deviation of the input. There is ample evidence from Fairhall that variance with drive spikes from a neuron, although a gain curve for spike rate versus the standard deviation is not to be found in the literature.

