Lesson 13
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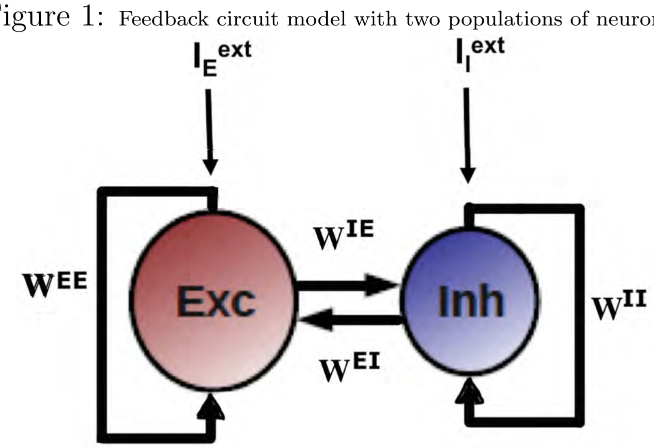
13 Noise, balanced feedback networks, synaptic scaling, and linear response. Part 2

13.1 Circuit model

So far we have only address noise and scaling at the level of noise in individual cells. Now we analyze a network of neurons with balanced inputs (Figure 1). We consider the consequences of the choice of connections in a network on the ability to maintain the balanced state.

Figure 1: Feedback circuit model with two populations of neurons



Consider a network of a population of interconnected excitatory (E) and inhibitory (I) cells.The full equations are

$$\tau_E \frac{dV_i^E(t)}{dt} + V_i^E(t) = \Big[\beta(\mu_i^E(t) - \theta_i^E)\Big]_+ \tag{13.1}$$

and

$$\tau_I \frac{dV_i^I(t)}{dt} + V_i^I(t) = \Big[\beta(\mu_i^I(t) - \theta_i^I)\Big]_+ , \tag{13.2}$$

where $[\cdots]_+$ is the Heavyside function, τ_E and τ_I are the cellular time constant, β is the conversion gain, and the θ_i^E and θ_i^I are thresholds. The inputs are

$$\mu_i^E(t) = \mu_{ext}^E(t) + \sum_{j=1}^{K} W_{i,j}^{EE} V_j^E(t) + \sum_{j=1}^{K} W_{i,j}^{EI} V_j^I(t) \tag{13.3}$$

and

$$\mu_i^I(t) = \mu_{ext}^I(t) + \sum_{j=1}^{K} W_{i,j}^{II} V_j^I(t) + \sum_{j=1}^{K} W_{i,j}^{IE} V_j^E(t). \tag{13.4}$$

As in the case of the model cell, we will scale the synaptic inputs by $1/\sqrt{K}$, as opposed to $1/K$, i.e.,

$$W_{ij}^{EE} \to \frac{W^{EE}}{\sqrt{K}}; \quad W_{ij}^{II} \to -\frac{W^{II}}{\sqrt{K}}; \quad W_{ij}^{EI} \to -\frac{W^{EI}}{\sqrt{K}}; \quad W_{ij}^{IE} \to \frac{W^{IE}}{\sqrt{K}} \tag{13.5}$$

where we explicitly put in the negative signs of inhibition. As will soon be clear, we need to scale the external inputs by

$$\mu_{ext}^E(t) \to \sqrt{K}\ E\ m_{ext}(t) \quad \text{and} \quad \mu_{ext}^I(t) \to \sqrt{K}\ I\ m_{ext}(t) \tag{13.6}$$

where E and I are inputs of strength of $O(1)$. The dependence on a common term is a statement that excitatory and inhibitory neurons share the same tuning curve. All together, we have

$$\mu_i^E(t) = \sqrt{K} E m_{ext}(t) + \frac{W^{EE}}{\sqrt{K}} \sum_{j=1}^{K} V_j^E(t) - \frac{W^{EI}}{\sqrt{K}} \sum_{j=1}^{K} V_j^I(t) \tag{13.7}$$

and

$$\mu_i^I(t) = \sqrt{K} I m_{ext}(t) + \frac{W^{IE}}{\sqrt{K}} \sum_{j=1}^{K} V_j^E(t) - \frac{W^{II}}{\sqrt{K}} \sum_{j=1}^{K} V_j^I(t). \tag{13.8}$$

In terms of the order parameters,

$$\begin{aligned}
\mu_E(t) &= \sqrt{K} E m_{ext}(t) + \sqrt{K} W^{EE} \frac{1}{K} \sum_{j=1}^{K} V_j^E(t) - \sqrt{K} W^{EI} \frac{1}{K} \sum_{j=1}^{K} V_j^I(t) \\
&= \sqrt{K} E m_{ext}(t) + \sqrt{K} W^{EE} m_E(t) - \sqrt{K} W^{EI} m_I(t) \qquad (13.9) \\
&= \sqrt{K} \left[E m_{ext}(t) + W^{EE} m_E(t) - W^{EI} m_I(t) \right]
\end{aligned}$$

and

$$\begin{aligned}
\mu_I(t) &= \sqrt{K} I m_{ext}(t) + \sqrt{K} W^{IE} \frac{1}{K} \sum_{j=1}^{K} V_j^E(t) - \sqrt{K} W^{II} \frac{1}{K} \sum_{j=1}^{K} V_j^I(t) \\
&= \sqrt{K} \left[I m_{ext}(t) + W^{IE} m_E(t) - W^{II} m_I(t) \right]. \qquad (13.10)
\end{aligned}$$

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

$$0\left(\frac{1}{\sqrt{K}}\right) = Em_{ext}(t) + W^{EE}m_E(t) - W^{EI}m_I(t) \tag{13.11}$$

and

$$0\left(\frac{1}{\sqrt{K}}\right) = Im_{ext}(t) + W^{IE}m_E(t) - W^{II}m_I(t). \tag{13.12}$$

The implication of this equilibrium condition is that the average input remains finite as the fluctuations remain large (Figures 2 and 3). This is the balanced state.

Figure 2: Balanced networks have emergent variability. From Shadlen and Newsome, 1994.

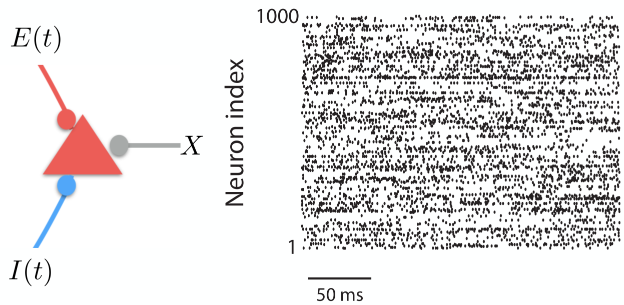
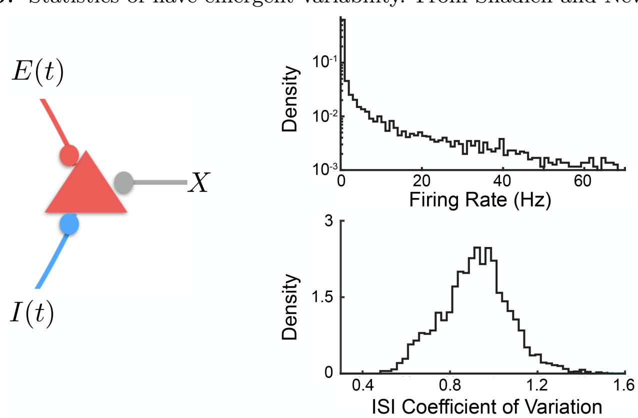


Figure 3: Statistics of have emergent variability. From Shadlen and Newsome, 1994.



13.2 The balanced state

Solving the above equations for m_E^o and m_I^o gives relations for the equilibrium activity of the excitatory and inhibitory cells in terms of the external drive:

$$m_E^0 = \frac{W^{II}E - W^{EI}I}{W^{EE}W^{II} - W^{EI}W^{IE}} m_{ext}. \tag{13.13}$$

and

$$m_I^0 = \frac{W^{IE}E - W^{EE}I}{W^{EE}W^{II} - W^{EI}W^{IE}} m_{ext}. \tag{13.14}$$

Recall that the equilibrium values of activity m_E^o and m_I^o must be both positive and bounded by 1. This constrains the values of the synaptic weights.

13.2.1 Linear respopnse

A seemingly paradoxical effect is that increasing the external inhibitory input, i.e., increasing I, will lead to a net decreased spiking of inhibitory cells and lwill concurrently decrease both m_E and m_I (Figure 4). This is a feedback effect. Excitatory and inhibitory activity track each other until the excitatory cells are completely turned off; this behavior is seen across cortical regions (Figure 5).

Figure 4: Experimental set-up to study linear response of network as we drive inhibition. From Sanzeni, Akitake, Goldbach, Leedy, Brunel and Histed 2020.

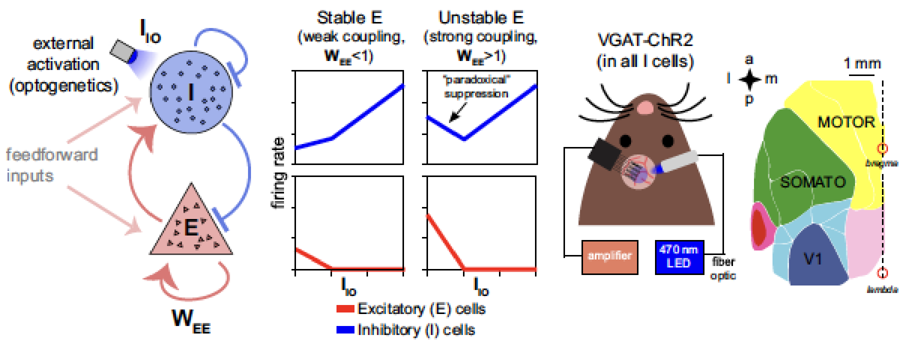
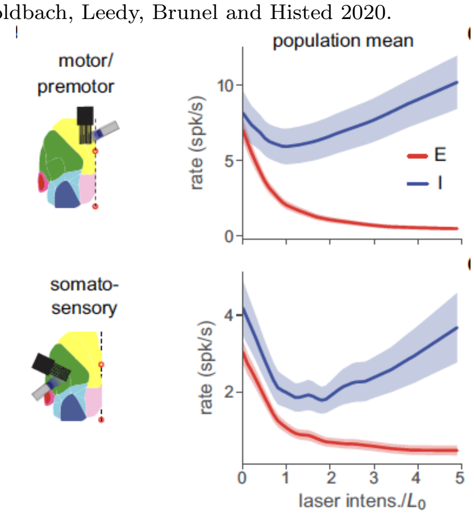


Figure 5: Linear response, until stauration, of network as we drive inhibition. From Sanzeni, Akitake, Goldbach, Leedy, Brunel and Histed 2020.



A second issue is that rapid feedback prevents the occurence of significant correlations. This depends of having faster inhibitory than excitatory synapses, as occurs for Gaba-A, but not Gaba-B (Figure **??**).

13.2.2 Stability and response speed

We return to the full network equations and look at the variation around the equilibrium value of m_E and m_I. Taking the time constants, τ, conversion gains, β, and thresholds to be the same for the E and I populations, and denoting

$$\delta m_E(t) = m_E(t) - m_E^o \tag{13.15}$$

and

$$\delta m_I(t) = m_I(t) - m_I^o \tag{13.16}$$

leads to

$$\tau \frac{d\ \delta m_E(t)}{dt} + \delta m_E(t) = \left[\beta\sqrt{K}\left(W^{EE}\delta m_E(t) - W^{EI}\delta m_I(t)\right)\right]_+ \tag{13.17}$$

and

$$\tau \frac{d\ \delta m_I(t)}{dt} + \delta m_I(t) = \left[\beta\sqrt{K}\left(W^{IE}\delta m_E(t) - W^{II}\delta m_I(t)\right)\right]_+ . \tag{13.18}$$

When the neurons are active, this reduces to the linear equations

$$\tau \frac{d\ \delta m_E(t)}{dt} + \delta m_E(t) = \beta\sqrt{K}\left(W^{EE}\delta m_E(t) - W^{EI}\delta m_I(t)\right) \tag{13.19}$$

and

$$\tau \frac{d\ \delta m_I(t)}{dt} + \delta m_I(t) = \beta\sqrt{K}\left(W^{IE}\delta m_E(t) - W^{II}\delta m_I(t)\right) . \tag{13.20}$$

These linear equations are solved by taking $\delta m_E(t) \propto e^{\lambda t}$, so that

$$(\lambda\tau + 1)\,\delta m_E(t) = \beta\sqrt{K}\left(W^{EE}\delta m_E(t) - W^{EI}\delta m_I(t)\right) \tag{13.21}$$

and

$$(\lambda\tau + 1)\,\delta m_I(t) = \beta\sqrt{K}\left(W^{IE}\delta m_E(t) - W^{II}\delta m_I(t)\right) , \tag{13.22}$$

which requires that

$$\begin{vmatrix} \beta\sqrt{K}W^{EE} - 1 - \lambda\tau & -\beta\sqrt{K}W^{EI} \\ \beta\sqrt{K}W^{IE} & -\beta\sqrt{K}W^{II} - 1 - \lambda\tau \end{vmatrix} = 0 \tag{13.23}$$

and leads to

$$
\begin{aligned}
\lambda_{1,2} \quad &= \quad \frac{\beta\sqrt{K}\left(W^{EE}-W^{II}\right)-2}{2\tau} \\
&\pm \quad \frac{1}{\tau}\sqrt{\left(\frac{\beta\sqrt{K}\,(W^{EE}-W^{II})-2}{2}\right)^2-\beta^2 K\, W^{IE}W^{EI}} \\
\xrightarrow{K\to\infty} \quad & \frac{\beta\sqrt{K}}{\tau}\left[\frac{W^{EE}-W^{II}}{2}\pm\sqrt{\left(\frac{W^{EE}-W^{II}}{2}\right)^2-\ W^{IE}W^{EI}}\ \right] \\
&= \quad \frac{\beta\sqrt{K}}{\tau}\left[\frac{W^{EE}-W^{II}}{2}\right]\left[1\pm\sqrt{\left(1-4\frac{W^{IE}W^{EI}}{(W^{EE}-W^{II})^2}\right)}\right].
\end{aligned}
\tag{13.24}
$$

The system is stable only if the real part of $\lambda_{1,2} < 0$. This implies

$$W^{II} > W^{EE}, \tag{13.25}$$

which is a prediction for connectomic analysis. We note that, by construction, $W^{IE}W^{EI} > 0$. The response time of the system is shortened by a factor of $\sqrt{K}$, i.e.,

$$\frac{\tau}{\beta} \rightarrow \frac{\tau}{\beta\sqrt{K}}O(1). \tag{13.26}$$

The change in recovery speed of the network has not been properly measured. But a sudden jump in the excitation of cortical input leads to an observed time-constant of about 10 ms (Figure 6). Unfortunately this is not very different from estimates for isolated neurons and thus the dynamics of the balanced still is a topic under analysis.

Figure 6: Relaxation of the signal in V1 cortical neurons after shut-down of thalamus. From Reinhold, Lien and Scanziani 2015