

Balanced Network, Mean Field Arguments

Basic mean field argument: N E and I neurons. Assume random connectivity: prob. connection = K/N , connected neurons have strength (abs value) J^{XY} . Input to neuron is

$$I_i^X = \sum_j J_{ij}^{XE} r_E - J_{ij}^{XI} r_I + h_X^i \quad (1)$$

(h_x^i can incorporate threshold, $h - \theta$; so it is negative for subthreshold external input).

Then assuming inputs fire independently and as Poisson processes at given rates, with rates uncorrelated with weights $\langle Jr \rangle = \langle J \rangle \langle r \rangle$ (all true in large- N limit). Consider updates in time bins of size 1, input is integrated over time bin. Letting mean rates per time bin be m_E, m_I , mean external input h_X , get mean input

$$\mu_X \equiv \langle I^X \rangle = K (J^{XE} m_E - J^{XI} m_I) + h_X \quad (2)$$

Spikes of type X received in timebin is Poisson process with mean Km_x , variance Km_x , so

$$\sigma_X^2 \equiv (\delta I^x)^2 = K (J^{XE})^2 m_E + K (J^{XI})^2 m_I \quad (3)$$

For simplicity we've ignored (1) variance in nonzero weights (2) time variance in external inputs.

(Given equation for rates in terms of inputs, and Gaussian assumption on I 's, get equation for m_E, m_I in terms of μ 's, σ 's)

Basic conundrum: we believe neural noise indicates neurons fire on fluctuations. How to get mean and variance to both be $O(1)$ given $K \gg 1$? (think: distance rest to threshold = 1). If J 's scale as $1/K$, mean is order 1 but variance is order $1/K$; if J 's scale as $1/\sqrt{K}$, variance is order 1 but mean is order \sqrt{K} .

Some ways out:

1. Neurons not really uncorrelated; can enhance variance for given mean.
2. K is not really big: real factor is $Km\tau$. If PSP's have time constant τ , $V(t) = J e^{-(t-t_{sp})/\tau}$, mean voltage is $\bar{V} = JKm\tau$, variance is $J^2 Km\tau/2$, standard deviation is $\frac{J}{\sqrt{2}} \sqrt{Km\tau} = \bar{V}/\sqrt{2Km\tau}$. Say $\tau = 10\text{ms}$, so denominator is $\sqrt{Km/50\text{Hz}}$. For $Km = 1000 - 2000\text{Hz}$, this is $\sqrt{20 - 40}$, i.e. 4.5 - 6.3. Significant but not an order of magnitude.

E.g. if assume $J = 0.5\text{mV}$, find what's in table below. And we've neglected additional sources of variance (temporal variance of inputs; variance of nonzero weights; neuronal correlations).

| Km | mean | stdev |
|------|-------|--------|
| 1000 | 5 mV | 1.1 mV |
| 2000 | 10 mV | 1.6 mV |
| 4000 | 20 mV | 2.2 mV |

Nonetheless suppose we take dilemma seriously: balanced network. Discovery (VV and Somp, 1996/1998): if $J \sim 1/\sqrt{K} \rightarrow KJ \sim \sqrt{K}$ and $h \sim \sqrt{K}$, then under simple conditions network will find “balanced” solution: mean of order 1 (and variance automatically of order 1 with this scaling).

Write J as J/\sqrt{K} , h as $h\sqrt{K}$ with new J 's, h 's of order 1. To lowest order in K : solution requires

$$\boldsymbol{\mu} = \sqrt{K}(\mathbf{J}\mathbf{m} + \mathbf{h}) = O(1) \quad (4)$$

To lowest order in K ,

$$\mathbf{J}\mathbf{m} + \mathbf{h} = 0 \rightarrow \mathbf{m} = -\mathbf{J}^{-1}\mathbf{h} = \frac{1}{\det J} \begin{pmatrix} J_{II} & -J_{EI} \\ J_{IE} & -J_{EE} \end{pmatrix} \begin{pmatrix} h_E \\ h_I \end{pmatrix} \equiv \frac{1}{\det J} \begin{pmatrix} \Omega_E \\ \Omega_I \end{pmatrix} \quad (5)$$

where $\Omega_E = J_{II}h_E - J_{EE}h_I$, $\Omega_I = J_{EI}h_E - J_{IE}h_I$. Rates \mathbf{m} are linear in inputs and are $O(1)$ (h/J). Then residual corrections to \mathbf{m} of order $1/\sqrt{K}$ give $O(1)$ contribution to input which accounts for this $O(1)$ response.

Require positive rates, so need $\det J > 0$ and $\Omega_E, \Omega_I > 0$ or all < 0 .¹

Assume m 's saturate at 0, maximal value for large negative or positive inputs. Want to avoid such unbalanced solutions. Look for solutions with $m_E = 0 \rightarrow m_I = h_I/J_{II}$ to leading order, so $\mu_E = \sqrt{K}(h_E - J_{EI}h_I/J_{II}) < 0$ or $\sqrt{K}\Omega_E/J_{II} < 0$, *i.e.* this requires $\Omega_E < 0$. (Can't have $m_I < 0$ if $m_E \neq 0$, unless $\mathbf{h}_I < 0$; but threshold is order 1, \mathbf{h} of order \sqrt{K} , so h 's are > 0 .)

What about solution with $m_E = m_I = m_{\max}$? Then $\mu_X = \sqrt{K}m_{\max}(J_{EX} - J_{IX} + h_X/m_{\max})$ must be > 0 and $O(\sqrt{K})$. This requires $J_{IE} < J_{EE} + h_X/m_{\max}$, $J_{II} < J_{EI} + h_X/m_{\max}$. Can

¹Note meaning of Ω 's: can rewrite net input as

$$\mu_E = \sqrt{K}h_E \left(\frac{J_{EE}}{h_E}m_E - \frac{J_{EI}}{h_E}m_I + 1 \right) \quad (6)$$

$$\mu_I = \sqrt{K}h_I \left(\frac{J_{IE}}{h_I}m_E - \frac{J_{II}}{h_I}m_I + 1 \right) \quad (7)$$

$$= \sqrt{K}h_I \left(\left(\frac{\Omega_I}{h_E h_I} + \frac{J_{EE}}{h_E} \right) m_E - \left(\frac{\Omega_E}{h_E h_I} + \frac{J_{EI}}{h_E} \right) m_I + 1 \right) \quad (8)$$

$$(9)$$

So $\Omega_E > 0$ means, relative to FF input, inhibition is stronger to I than to E, while $\Omega_I > 0$ means the same for excitation.

eliminate this solution at $\mathbf{h} = 0$ if $J_{IE} > J_{EE}$. Then if $m_I = m_{\max}$, $m_E = (J_{EI}m_{\max})/J_{EE}$, so

$$\mu_I = \sqrt{K} \left(\frac{J_{IE}J_{EI}}{J_{EE}} m_{\max} - J_{II}m_{\max} \right) \quad (10)$$

$$= \sqrt{K} \frac{\det \mathbf{J}}{J_{EE}} m_{\max} \quad (11)$$

which is consistent, so doesn't seem to eliminate possibility of I saturating. Also not clear unbalanced solutions are eliminated for $\mathbf{h} > 0$. They claim $J_{IE} > J_{EE}$ eliminates all unbalanced solutions, but not clear to me.

At any rate, they claim only solution is balanced solution for $\det J > 0$, $\Omega_E > 0$, $\Omega_I > 0$, $J_{IE} > J_{EE}$.

Stability

Suppose equation of form

$$\tau_X \frac{d}{dt} m_X(t) = -m_x(t) + f(\mu_k) \quad (12)$$

Then local stability given by

$$\tau_X \frac{d}{dt} \delta m_X = -\delta m_x + \sqrt{K} f'(\mu_k) \mathbf{J} \delta m_X \quad (13)$$