Excitatory/inhibitory balance and eigenvector non-orthogonality of a synaptic connectivity matrix

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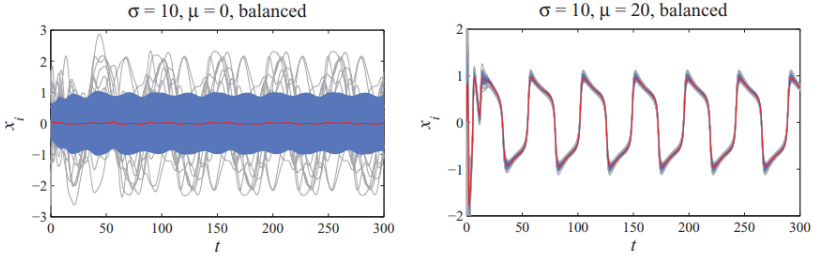
Simple model: random neural network

[Sompolinsky, Crisanti, Sommers, 1988]

$$\dot{x}_i = -x_i + \sum_{j=1}^{N} J_{ij}\phi(x_j)$$

All $\mathrm{Re}\lambda_j < 1$ trivial dynamics $x_i(t) \to 0$, $\mathrm{Re}\lambda_j > 1$ chaos.
[Rajan, Abbott, 2006]: $J = M + X\Lambda$ + balance condition
[del Molino, Pakdaman, Touboul, Weinrib, 2013] numerics



Eigenvalue analysis is not the end of the story!

Setting the stage: reminder from algebra

A matrix J is non-normal iff $JJ^T \neq J^T J$.
If a non-normal matrix can be diagonalized, it possesses two set of eigenvectors: right $\mathbf{r_k}$ (column) and left $\mathbf{l_k}$ (rows). They satisfy the eigenproblems

$$\mathbf{l}_k J = \mathbf{l}_k \lambda_k, \qquad J\mathbf{r}_k = \lambda_k \mathbf{r}_k$$

The diagonalization is via similarity transformation $J = S\Lambda S^{-1}$ with S and S^{-1} encoding eigenvectors. The eigenvectors are not orthogonal $\mathbf{r}_k \cdot \mathbf{r}_j \neq \delta_{kj}$ but biorthogonal $\mathbf{l}_k \cdot \mathbf{r}_j = \delta_{kj}$ ($S^{-1}S = \mathbf{1}$).
Resolution of identity $\sum_k \mathbf{r}_k \otimes \mathbf{l}_k = \mathbf{1}$ ($SS^{-1} = \mathbf{1}$).
They are not unique. Rescaling $\mathbf{r}_k \to c_k \mathbf{r}_k$, $\mathbf{l}_k \to c_k^{-1} \mathbf{l}_k$ gives equally good eigenvectors.
The simplest object invariant under rescaling [Chalker Mehlig 1999]

$$O_{ij} = (\mathbf{l}_i \cdot \mathbf{l}_j)(\mathbf{r}_j \cdot \mathbf{r}_i).$$

Readjusting synaptic strength seen as a perturbation

$$\overbrace{\begin{pmatrix} 0 & +1 \\ 0.5 & 1 \end{pmatrix}}^{J'} = \overbrace{\begin{pmatrix} 0 & -1 \\ 0.5 & 1 \end{pmatrix}}^{J} + \overbrace{\begin{pmatrix} 0 & 2 \\ 0 & 0 \end{pmatrix}}^{P}$$

Dynamics of learning is a complicated problem. Can we say anything about the dynamics of eigenvalues? Assuming that the change in weights is small → perturbation theory

$$\lambda_k' = \lambda_k + \mathbf{l}_k P \mathbf{r}_k + \mathcal{O}(P^2)$$

Upper bound $|\delta\lambda_k| \leqslant ||\mathbf{l}_k|| \cdot ||\mathbf{r}_k|| \cdot ||P|| = ||P|| \underbrace{\sqrt{(\mathbf{l}_k \cdot \mathbf{l}_k)(\mathbf{r}_k \cdot \mathbf{r}_k)}}_{\kappa(\lambda_k)=\sqrt{O_{kk}}}$.

Eigenvalue condition number [Wilkinson 1965]
O_{kk} controls stability of the spectrum, eigenvalues with larger condition number can move farther.

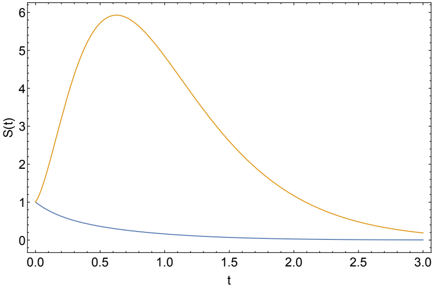
Transient amplification in the linearized dynamics

Linearization around the fixed point $x^* = 0$

$$\frac{d\mathbf{x}}{dt} = -\mathbf{x} + J\mathbf{x}$$

If $\mathrm{Re}(\lambda_k) < 1$ the system is asymptotically stable.

$$J_1 - \mathbf{1} = \begin{pmatrix} -1 & 1 \\ 0 & -2 \end{pmatrix} \quad J_2 - \mathbf{1} = \begin{pmatrix} -1 & 10 \\ 0 & -2 \end{pmatrix}$$



$S(t) = ||\mathbf{x}(t)||^2$ - squared Euclidean distance from the fixed point

Initial condition $x_0 = (\frac{1}{2}, \frac{\sqrt{3}}{2})^T$ [Caswell 2004]

Transient amplification in the linearized dynamics

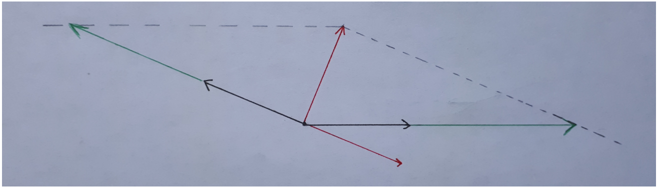
The problem is linear. Formal solution: $\mathbf{x}(t) = e^{(-1+J)t}\mathbf{x_0}$. Squared norm

$$S(t) = \mathbf{x}_0^T e^{(J^T-\mathbf{1})t} e^{(J-\mathbf{1})t}\mathbf{x_0} = \sum_{j,k=1}^{N} e^{-2t+\lambda_j+\lambda_k}(\mathbf{x}_0\cdot\mathbf{l}_k)(\mathbf{x}_0\cdot\mathbf{l}_j)(\mathbf{r}_k\cdot\mathbf{r}_j)$$

For normal matrices $\mathbf{r}_k \cdot \mathbf{r}_j = \delta_{jk}$:

$$S(t) = \sum_{k=1}^{N} e^{2(\lambda_k-1)t}(\mathbf{x}_0\cdot\mathbf{l}_k)^2$$

Averaging over initial conditions: $\langle S(t)\rangle = \sum_{j,k=1}^{N} e^{-2t+\lambda_j+\lambda_k} O_{jk}$.

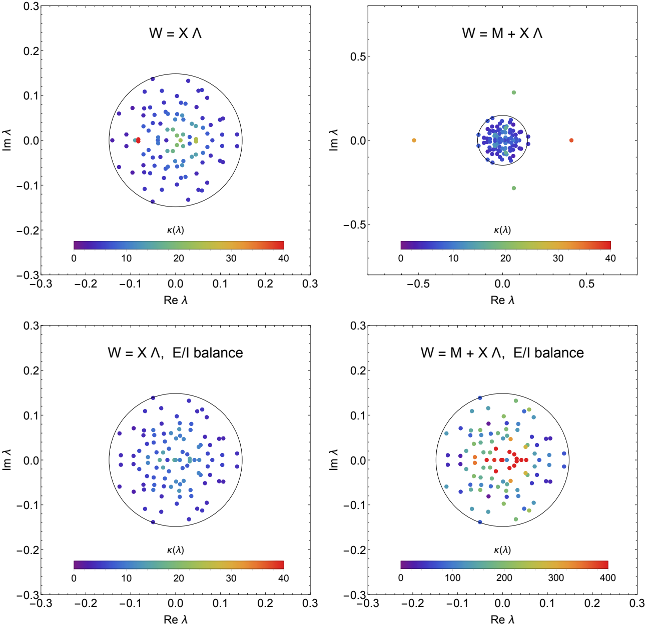


Rajan-Abbott model [PRL 97, 188104 (2006)]

$$\dot{x}_i = -x_i + \sum_k J_{ik}\phi(x_k)$$

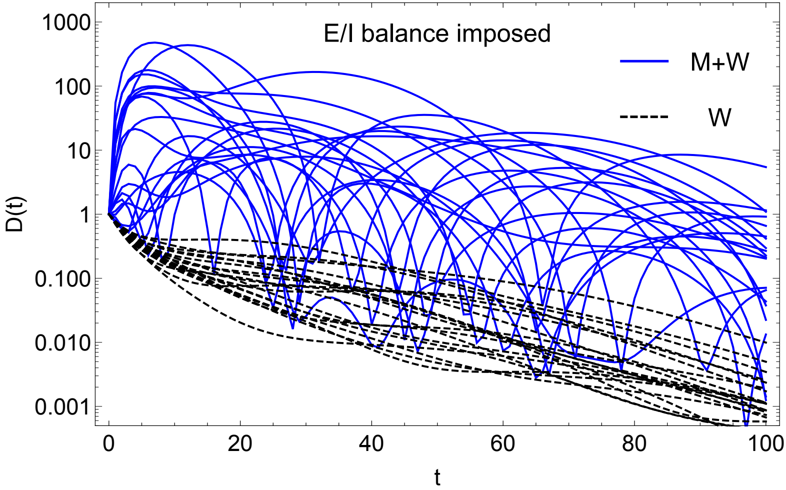
Two types of neurons: $f_E N$ excitatory (E) and $f_I N$ inhibitory (I). Modelling populational variability: couplings distributed according to $\mathcal{N}(\mu_E, \frac{\sigma_E}{\sqrt{N}})$ and $\mathcal{N}(\mu_I, \frac{\sigma_I}{\sqrt{N}})$. Mathematically, $J = M + X\Lambda$. Addition of M to the model causes few outliers $\rightarrow$ instability of the fixed point $\rightarrow$ chaotic dynamics in the full nonlinear model.

Balance condition: For each neuron
$\sum(excitations) + \sum(inhibition) = 0 \quad (\sum_{k=1}^{N} J_{ik} = 0)$
Eigenvalues of balanced $M + X\Lambda$ are exactly the same as of balanced $X\Lambda$. Spectral radius $r^2 = f_E\sigma_E^2 + f_I\sigma_I^2$

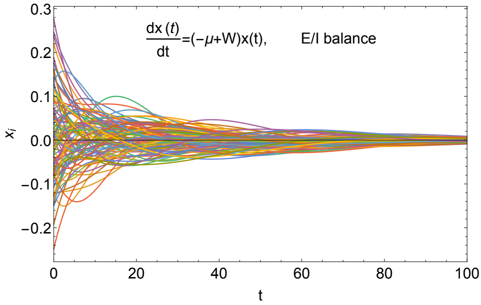

W = X Λ
W = M + X Λ
W = X Λ, E/I balance
W = M + X Λ, E/I balance
κ(λ)
0 10 20 30 40
0 100 200 300 400
Re λ
Im λ

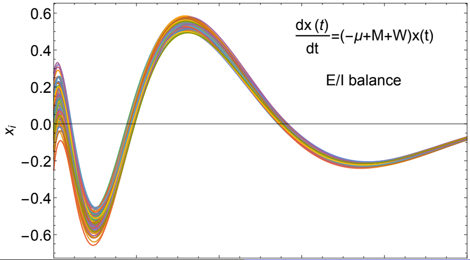
Transient dynamics

$$S(t) = \mathbf{x}_0 e^{(-\mathbf{1}-J^T)t} e^{(-\mathbf{1}+J)t} \mathbf{x}_0$$



Onset of synchronization





Can we have more quantitative description than just numerics?

YES!

Random matrix theory + free probability
More in ArXiv: [1805.03592]

Conclusions

- There is much more beyond the eigenvalue analysis
- Inclusion of E/I balance leads to high sensitivity to perturbations and is responsible for the transient amplification
- Stability - plasticity dilemma
- Random matrix theory allows for quantitative results

Work in progress, more results soon