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 $\text{Re}\lambda_j < 1$ trivial dynamics, $x_i(t) \to 0$, $\text{Re}\lambda_j > 1$ chaos.

[Rajan, Abbott, 2006]: $J = M + X\Lambda + \text{balance condition}$

[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 $r_k$ (column) and left $l_k$ (rows). They satisfy the eigenproblems
\[ l_k J = l_k \lambda_k, \quad J r_k = \lambda_k r_k \]

The diagonalization is via similarity transformation $J = S \Lambda S^{-1}$ with $S$ and $S^{-1}$ encoding eigenvectors. The eigenvectors are not orthogonal $r_k \cdot r_j \neq \delta_{kj}$ but biorthogonal $l_k \cdot r_j = \delta_{kj}$ ($S^{-1} S = 1$).

Resolution of identity $\sum_k r_k \otimes l_k = 1$ ($SS^{-1} = 1$).

They are not unique. Rescaling $r_k \rightarrow c_k r_k$, $l_k \rightarrow c_k^{-1} l_k$ gives equally good eigenvectors.

The simplest object invariant under rescaling [Chalker Mehlig 1999]
\[ O_{ij} = (l_i \cdot l_j)(r_j \cdot r_i). \]
Readjusting synaptic strength seen as a perturbation

\[
\begin{pmatrix}
0 & +1 \\
0.5 & 1
\end{pmatrix}
= \begin{pmatrix}
0 & -1 \\
0.5 & 1
\end{pmatrix} + \begin{pmatrix}
0 & 2 \\
0 & 0
\end{pmatrix}
\]

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

\[\lambda'_k = \lambda_k + l_k P r_k + O(P^2)\]

Upper bound \( |\delta \lambda_k| \leq ||l_k|| \cdot ||r_k|| \cdot ||P|| = ||P|| \sqrt{(l_k \cdot l_k)(r_k \cdot r_k)} \cdot \kappa(\lambda_k) = \sqrt{O_{kk}} \)

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

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E/I balance and non-orthogonality
Transient amplification in the linearized dynamics

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

$$\frac{dx}{dt} = -x + Jx$$

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

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

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

Initial condition

$$x_0 = \left( \frac{1}{2}, \frac{\sqrt{3}}{2} \right)^T$$

[Caswell 2004]
Transient amplification in the linearized dynamics

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

\[
S(t) = x_0^T e^{(J^T-1)t} e^{(J-1)t} x_0 = \sum_{j,k=1}^{N} e^{-2t+\lambda_j+\lambda_k} (x_0 \cdot l_k)(x_0 \cdot l_j)(r_k \cdot r_j)
\]

For normal matrices \( r_k \cdot r_j = \delta_{jk} \):

\[
S(t) = \sum_{k=1}^{N} e^{2(\lambda_k-1)t} (x_0 \cdot l_k)^2
\]

Averaging over initial conditions: \( \langle S(t) \rangle = \sum_{j,k=1}^{N} e^{-2t+\lambda_j+\lambda_k} O_{jk} \).
\[ \dot{x}_i = -x_i + \sum_k J_{ik} \phi(x_k) \]

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

$W = M + X \Lambda$

$W = X \Lambda, \ E/I \ balance$

$W = M + X \Lambda, \ E/I \ balance$

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Transient dynamics

\[ S(t) = x_0 e^{(-1-J^T)t} e^{(-1+J)t} x_0 \]
Onset of synchronization

\[ \frac{d x(t)}{d t} = (-\mu + W)x(t), \quad E/I \text{ balance} \]

\[ \frac{d x(t)}{d t} = (-\mu + M + W)x(t), \quad E/I \text{ balance} \]

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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