Plasticity and Balance in Neuronal Networks

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Plasticity and Balance

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Outline

• Synaptic plasticity in balanced networks
• Homeostatic control of correlations in primate visual cortex
• Automated discovery of large scale organization in neuronal networks
Balanced Networks

van Vreeswijk and Sompolinsky, 1996
Balanced Networks - theory and experiments

The Mechanism of Orientation Selectivity in Primary Visual Cortex without a Functional Map
David Hansel and Carl van Vreeswijk

Published: 23 February 2016
Efficient codes and balanced networks
Sophie Denève & Christian K Machens
Nature Neuroscience 19, 375–382 (2016) | Cite this article

Published: 30 March 2008
Instantaneous correlation of excitation and inhibition during ongoing and sensory-evoked activities
Michael Oxn & Ilan Lampi
Nature Neuroscience 11, 535–537 (2008) | Cite this article

Nonlinear stimulus representations in neural circuits with approximate excitatory-inhibitory balance
Cody Baker, Vicky Zhu, Robert Rosenbaum
PLOS COMPUTATIONAL BIOLOGY
Version 2 | Published: September 18, 2020 • https://doi.org/10.1371/journal.pcbi.1008192

Synaptic scaling rule preserves excitatory-inhibitory balance and salient neuronal network dynamics
Jérémie Barra, Alex D Reyes
Uncorrelated and Correlated Balanced Networks

Renart, de la Rocha, et al 2010
Uncorrelated and Correlated Balanced Networks

Renart, de la Rocha, et al 2010
Uncorrelated and Correlated Balanced Networks

Rosenbaum, et al. 2017

Renart, de la Rocha, et al 2010
Uncorrelated and Correlated Balanced Networks

Renart, de la Rocha, et al. 2010
Baker, et al. 2019
Rosenbaum, et al. 2017
Uncorrelated and Correlated Balanced Networks

Renart, de la Rocha, et al. 2010

Rosenbaum, et al. 2017

Baker, et al. 2019
Spike Time Dependent Plasticity

Abbott and Nelson, 2000
Spike Time Dependent Plasticity

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Vogels, et al 2011
Hennequin, et al 2017
Can we extend the mean-field theory of balanced networks to include plasticity?

Can the theory predict when a balanced state is preserved?
Network Model

Akil, Rosenbaum and Josić, PLoS Comp Bio 2021
Network Model

\[ J_{jk}^{ab} = \frac{1}{\sqrt{N}} \begin{cases} j_{ab} & \text{with probability } p_{ab}, \\ 0 & \text{otherwise.} \end{cases} \]

Akil, Rosenbaum and Josić, PLoS Comp Bio 2021
Network Model

\[ J_{jk}^{ab} = \frac{1}{\sqrt{N}} \begin{cases} j_{ab} & \text{with probability } p_{ab}, \\ 0 & \text{otherwise.} \end{cases} \]

Akil, Rosenbaum and Josić, PLoS Comp Bio 2021
Network Model

Mean Recurrent Weights

$$\overline{W} = \begin{bmatrix} \overline{w_{ee}} & \overline{w_{ei}} \\ \overline{w_{ie}} & \overline{w_{ii}} \end{bmatrix}$$

Mean Feedforward Weights

$$\overline{W}_x = \begin{bmatrix} \overline{w_{ex}} \\ \overline{w_{ix}} \end{bmatrix}$$

Mean Firing Rates

$$\mathbf{r} = \begin{bmatrix} \overline{r_e} \\ \overline{r_i} \end{bmatrix}$$

Akil, Rosenbaum and Josić, PLoS Comp Bio 2021
Network Model

Mean Recurrent Weights

Mean Feedforward Weights

Mean Firing Rates

In balance the mean firing rates are:

$$
\lim_{N \to \infty} r = -W^{-1}W_x r_x
$$

Akil, Rosenbaum and Josić, PLoS Comp Bio 2021
Correlated Balanced State

Spike count covariance matrix in window $T_{\text{win}}$

$$C' = \begin{bmatrix} C_{ee} & C_{ei} \\ C_{ie} & C_{ii} \end{bmatrix}$$
Correlated Balanced State

Spike count covariance matrix in window $T_{\text{win}}$

$$C = \begin{bmatrix} C_{\text{ee}} & C_{\text{ei}} \\ C_{\text{ie}} & C_{\text{ii}} \end{bmatrix}$$

If $c_x \neq 0$, then $C$ remains $O(1)$, and the network is in a correlated state.

$$C \approx T_{\text{win}} c_x r_x W^{-1} W_x W_x^T W^{-T}$$

Baker, et al. 2019
Plasticity and Eligibility Traces

\[
\tau_{\text{STDP}} \frac{dx_j^a(t)}{dt} = -x_j^a(t) + S_j^a(t)
\]

\[
S_j^a(t) = \sum_n \delta(t - t_{n,j}^a)
\]
Example: Classical Hebbian plasticity
Example: Classical Hebbian plasticity

\[ \frac{dJ_{jk}^{ee}}{dt} = \]
Example: Classical Hebbian plasticity

\[
\frac{dJ_{jk}^{ee}}{dt} = C_{\text{pre-post}} x_k^e S_j^e
\]

Klopf 1982, many others
Example: Classical Hebbian plasticity

\[
\frac{dJ_{jk}^{ee}}{dt} = C_{\text{pre-post}} x_k^e S_j^e
\]

Klopf 1982, many others
Example: Classical Hebbian plasticity

\[
\frac{dJ_{jk}^{ee}}{dt} = C_{\text{pre-post}} x_k^e S_j^e - C_{\text{post-pre}} x_j^e S_k^e
\]

Klopf 1982, many others
Example: Classical Hebbian plasticity

\[ \frac{dJ_{jk}^{ee}}{dt} = \eta_{ee} \left( C_{\text{pre-post}} x_k^e S_j^e \right) - C_{\text{post-pre}} x_j^e S_k^e \]

Klopf 1982, many others
Example: Classical Hebbian plasticity

\[
\frac{dJ_{jk}^{ee}}{dt} = \eta_{ee} \left( C_{\text{pre-post}} x_k^e S_j^e - C_{\text{post-pre}} x_j^e S_k^e \right)
\]

Klopf 1982, many others
Plasticity Rules with up to Second Order Interactions

\[
\frac{dJ_{ab}^{jk}}{dt} = \eta_{ab} \left( A_0 + \sum_{\alpha = \{a,j\}, \{b,k\}} A_{\alpha} S_{\alpha} + \sum_{\alpha, \beta = \{a,j\}, \{b,k\}} B_{\alpha,\beta} x_{\alpha} S_{\beta} \right)
\]
Plasticity Rules with up to Second Order Interactions

\[
\frac{dJ_{jk}^{ab}}{dt} = \eta_{ab} \left( A_0 + \sum_{\alpha=\{a,j\},\{b,k\}} A_\alpha S_\alpha + \sum_{\alpha,\beta=\{a,j\},\{b,k\}} B_{\alpha,\beta} x_\alpha S_\beta \right)
\]

<table>
<thead>
<tr>
<th>STDP Rule</th>
<th>Coefficients</th>
<th>Equation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Classical EE Hebbian [22–24]</td>
<td>(B_{(e,j),(e,k)} = -J_{jk}^{ee}) (B_{(e,k),(e,j)} = J_{jk}^{ee}) (B_{(e,k),(e,j)} = J_{jk}^{ee})</td>
<td>(\frac{dJ_{jk}^{ee}}{dt} = \eta_{ee} (J_{jk}^{ee} x_k^e S_j^e - J_{jk}^{ee} x_j^e S_k^e))</td>
</tr>
<tr>
<td>Classical EE Anti–Hebbian [23, 24]</td>
<td>(B_{(e,j),(e,k)} = J_{jk}^{ee}) (B_{(e,k),(e,j)} = -J_{jk}^{ee})</td>
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</tr>
<tr>
<td>Homeostatic Inhibitory [26]</td>
<td>(A_{i,k} = \alpha_e J_{i,k}^{ei} / J_0^{ei}) (B_{(e,j),(i,k)} = -J_{jk}^{ei} / J_0^{ei}) (B_{(i,k),(e,j)} = -J_{jk}^{ei} / J_0^{ei})</td>
<td>(\frac{dJ_{jk}^{ei}}{dt} = -\eta_{ei} \frac{J_{jk}^{ei}}{J_0^{ei}} [(x_j^e - \alpha_e) S_k^i + x_k^i S_j^e])</td>
</tr>
<tr>
<td>Oja’s Rule [46]</td>
<td>(B_{(e,j),(e,k)} = -J_{jk}^{ee}) (B_{(e,j),(e,k)} = \beta)</td>
<td>(\frac{dJ_{jk}^{ee}}{dt} = \eta_{ee} (\beta x_j^e S_k^e - J_{jk}^{ee} x_j^e S_j^e))</td>
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<tr>
<td>Kohonen’s Rule [25]</td>
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</tr>
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</table>
Averaging synaptic weight dynamics

\[
\frac{dJ_{ab}^{\alpha \beta}}{dt} = \eta_{ab} \left( A_0 + \sum_{\alpha = \{a,j\}, \{b,k\}} A_{\alpha} S_{\alpha} + \sum_{\alpha, \beta = \{a,j\}, \{b,k\}} B_{\alpha, \beta} x_{\alpha} S_{\beta} \right)
\]

Average in time, and over different network realizations

\[
\frac{dJ_{ab}}{dt} = \eta_{ab} \left( A_0 + A_a r_a + \text{Rate}_{a,b} + \text{Cov}_{a,b} \right)
\]
Closing Equations using Quasi Steady State Assumption

Firing rates:

$$\lim_{N \to \infty} r = -W^{-1}_x W_x r_x$$

Spike count covariances:

$$C \approx \frac{1}{N} T_{\text{win}} W^{-1} \Gamma W^{-T}$$

Mean synaptic weights:

$$\tau J_{ab} \frac{dJ_{ab}}{dt} = A_0 + \sum_{\alpha, \beta = \{a,b\}} \text{Rate}_{\alpha, \beta} + \text{Cov}_{\alpha, \beta}$$
Closing Equations using Quasi Steady State Assumption

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Closing Equations using Quasi Steady State Assumption

\[ \lim_{N \to \infty} r = -\bar{W}^{-1}\bar{W}_x r_x \]

\[ C \approx \frac{1}{N} T_{\text{win}} \bar{W}^{-1} \Gamma \bar{W}^{-T} \]

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\]
Theory predicts stable asynchronous and correlated states
The theory predicts stable asynchronous and correlated states. Theory predicts stable asynchronous and correlated states.

Asynchronous

Correlated

Table 1. Examples of STDP rules.

Appendix.

The difference in timescales allows us to assume that the firing rates and covariances are weights using Eqs. (1–2). The following is an outline, and details can be found in S2.

To understand how the dynamics of the network, and synaptic weights co-evolve we mean-field equation for the weights:

\[ \tau \frac{d J_{jk}^{ee}}{dt} = \eta_{ee}(J_{jk}^{ee} S_k e - J_{jk}^{ec} S_j e) \]

where \( J_{jk}^{ee} \) is the effective spike count covariance, \( J_{jk}^{ec} \) is the effective spike count covariances, and \( S_k e \) is the effective spike count covariance.

Kohonen’s Rule

Inhibitory

Homeostatic

Hebbian [22

Classical

STDP

Hebbian [23,

Kohonen’s Rule

Anti–STDP

[25

Oja’s

[26

In the following, we introduce a number of different plasticity rules can be derived effective equations for the firing rates, spike count covariances, and synaptic weights using Eqs. (1–2). The following is an outline, and details can be found in S2.

To understand how the dynamics of the network, and synaptic weights co-evolve we mean-field equation for the weights:

\[ \tau \frac{d J_{jk}^{ee}}{dt} = \eta_{ee}(J_{jk}^{ee} S_k e - J_{jk}^{ec} S_j e) \]

where \( J_{jk}^{ee} \) is the effective spike count covariance, \( J_{jk}^{ec} \) is the effective spike count covariances, and \( S_k e \) is the effective spike count covariance.

Kohonen’s Rule

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In the following, we introduce a number of different plasticity rules can be derived effective equations for the firing rates, spike count covariances, and synaptic weights using Eqs. (1–2). The following is an outline, and details can be found in S2.

To understand how the dynamics of the network, and synaptic weights co-evolve we mean-field equation for the weights:
Asynchronous and correlated states

Theory predicts stable asynchronous and correlated states

Table 1. Examples of STDP rules.

Appendix.

The difference in timescales allows us to assume that the firing rates and covariances are averages over time, and over different network subpopulations, we obtain the following mean-field equation for the weights:

\[ \frac{dJ_{jk}}{dt} = \eta_{x}(\beta \alpha_{j} S_{k}^{e} - J_{jk}^{ee} S_{j}^{e}) \]

Kohonen’s Rule
Theory predicts stable asynchronous and correlated states.
Theory predicts stable asynchronous and correlated states

Asynchronous

Correlated

Table 1. Examples of STDP rules.

Kohonen’s Rule

\[
\frac{dJ_{jk}^{ee}}{dt} = \eta_{ee}(\beta a_j^e S_k^e - J_{jk}^{ee} S_j^e)
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**Asynchronous**

- Correlated
Theory predicts stable asynchronous and correlated states
Theory predicts stable asynchronous and correlated states

Table 1. Examples of STDP rules.

<table>
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<tr>
<th>Rule</th>
<th>Description</th>
</tr>
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<tbody>
<tr>
<td>Hebbian</td>
<td>Positive correlation, weight increase</td>
</tr>
<tr>
<td>Anti-Hebbian</td>
<td>Negative correlation, weight decrease</td>
</tr>
<tr>
<td>STDP</td>
<td>Spike timing-dependent plasticity</td>
</tr>
<tr>
<td>Kohonen's</td>
<td>Neuron-specific plasticity</td>
</tr>
<tr>
<td>Oja's</td>
<td>Principal component analysis</td>
</tr>
</tbody>
</table>

Equation 1:
\[ \frac{dJ_{jk}}{dt} = \eta_{\text{ee}}(\beta_{jk}S_{jk} - J_{jk}S_{jk}) \]

Coefficients:
- \( J_{jk} \)
- \( S_{jk} \)
- \( \beta_{jk} \)
- \( \eta_{\text{ee}} \)

Diagram showing network size vs. exc weight, rates, and covariance for asynchronous and correlated states. Kohonen's Rule diagram with time delay function.
Loss of Stability with Kohonen’s Rule

\[ \frac{dJ^{ee}_{jk}}{dt} = \eta_{ee}(\beta x_j^e s_k^e - J^{ee}_{jk} S_j^e) \]
Correlations have a small impact

\[
\frac{dJ_{ab}}{dt} = \eta_{ab} \left( A_0 + A_a r_a + \text{Rate}_{a,b} + \text{Cov}_{a,b} \right)
\]

See also Graupner, et al, 2016, Ocker and Doiron, 2015
Can we extend the mean-field theory of balanced networks to include plasticity?

Can the theory predict when the balanced state is preserved?
Can we extend the mean-field theory of balanced networks to include plasticity?

Can the theory predict when the balanced state is preserved?

Yes - We can get a closed set of equations that describe the evolving dynamics of the network

Multiple forms of plasticity acting together
Homeostatic Plasticity and Optogenetic Stimulation?

Homeostatic Plasticity and Optogenetic Stimulation?

Correlation changes are heterogeneous
No changes during rest
Model with Homeostatic Inhibitory Plasticity

\[ \tau_{J_{ei}} \frac{dJ_{jk}^{ei}}{dt} = -\frac{J_{jk}^{ei}}{J_{0_{ei}}} \left[ (x_j^e - \alpha_e)S_k^i + x_k^iS_j^e \right] \]

\[ \Delta \text{Rate (Laser - Control)} \text{ (Hz)} \]

\[ \Delta \text{Correlations (Laser - Control)} \]

Excitatory
Inhibitory
ChR2-expressing

- \( r_s = 10 \text{Hz} \)
- \( c_s = 0.1 \)
- \( P_{\text{connect}} = 10\% \)

Narrow spiking units
Broad spiking units

Narrow
Cell
Broad
Cell
Broad pairs

Potentiation index

Correlations (baseline sub.)
Correlations (L-C)

\[ \Delta \text{Correlations (L-C)} \]

Trial block

"Awake" network
"Resting" network

ISTDP
Model Shows Small Effect During Rest

Vyazovkiy, et al 2008,
Johansen, et al 2010
Putative IE Synapses are Potentiated

\[ \text{Potentiation index (PI)} = \frac{\text{AUC late trials}}{\text{AUC early trials}} \]

Narrow spiking units
Broad spiking units
Putative IE Synapses are Potentiated

Potentiation index ("PI") = \frac{AUC \text{ late trials}}{AUC \text{ early trials}}

Early control trials

Late control trials

Depressed \leftrightarrow Potentiated

Pair count

Potentiation index

Early control trials

Late control trials

PI = 1.55

0.996

1.677 *

Correlations (Laser - Control)

Correlations (baseline sub.)

Correlations (L-C)

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Enormous Efforts to Reconstruct the Brain

Synapse-level dense reconstructions

C. Elegans ~300 neurons (1986)
Larval MB ~300 neurons (2020)
Drosophila Hemibrain, ~22,000 neurons (2020)
Platinum Mouse ~80,000 neurons (2022)
Human brain by Lichtman’s lab (2021…)
Drosophila Brain, ~130,000 neurons (2023)
Enormous Efforts to Reconstruct the Brain

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Analysis requires new tools and methods
Neuroscience's Existential Crisis

We're mapping the brain in amazing detail—but our brain can't understand the picture.

BY GRIGORI GUICHOUTS
OCTOBER 27, 2021
The Fly Hemibrain
The Fly Hemibrain
The Fly Hemibrain

janelia.org/project-team/flyem/hemibrain
The Fly Hemibrain

Gives us a graph of 21,733 nodes (neurons)
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3,521,163 connected pairs (one or more synapses)
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(in version 1.1)
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3,521,163 connected pairs (one or more synapses)

(in version 1.1)
Community Detection

\[ Q_g = \frac{1}{2m} \sum_c \left( 2m_c - \frac{K_c^2}{2m} \right) \]

- \( K_c \) is total degree of nodes in \( c \)
- \( m, m_c \) are number of edges in graph or in \( c \) respectively

Number of edges in \( c \)
Expected number of edges in \( c \) if randomly assigned.

Guo et al, 2019
Community Detection

$K_c$ is total degree of nodes in $c$

$m, m_c$ are number of edges in graph or in $c$ respectively

$$Q_g = \frac{1}{2m} \sum_c \left( 2m_c - \frac{K_c^2}{2m} \right)$$

Guo et al, 2019
Community Detection

\[ K_c \] is total degree of nodes in \( c \)
\[ m, m_c \] are number of edges in graph or in \( c \) respectively

\[
Q_g = \frac{1}{2m} \sum_c \left( 2m_c - \frac{K_c^2}{2m} \right) \rho_c^\chi 
\]

\[
\rho_c = \frac{2m_c}{n_c(n_c - 1)} \quad -\text{Link density in community } c
\]

Guo et al, 2019
Community Detection

\[ Q_g = \frac{1}{2m} \sum_c \left( 2m_c - \frac{K_c^2}{2m} \right) \rho_c^x \]
Community Detection

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Community Detection

\[ Q_g = \frac{1}{2m} \sum_c \left( 2m_c - \frac{K_c^2}{2m} \right) \rho_c^\chi \]
Community Detection

RenEEL algorithm (Guo et al 2019)

Input: weighted undirected graph, control parameter $\chi$

Output: list of communities $c$ maximizing $Q_g$

$$Q_g = \frac{1}{2m} \sum_c \left( 2m_c - \frac{K_c^2}{2m} \right) \rho_c^\chi$$
Why apply community detection to the connectome?

1. Complement what fly physiologists have discovered about the anatomy of the Drosophila brain.

2. Discover potentially meaningful structures that fly physiologists may not know about yet.
8 clusters

\[ \chi = 0 \]
$\chi = 0$

8 clusters
8 clusters

$\chi = 0$

Mushroom body
$\chi = 0$

8 clusters

Mushroom body

chi = 0.0
8 clusters

\[ \chi = 0 \]

Mushroom body

chi = 0.05
8 clusters

\( \chi = 0 \)

Mushroom body

chi = 0.1
8 clusters

\[ \chi = 0 \]

Mushroom body

\[ \chi = 0.25 \]
8 clusters

\[ \chi = 0 \]

Mushroom body

\[ \text{chi} = 0.5 \]
8 clusters

\[ \chi = 0 \]
χ = 0

8 clusters

Mushroom body

chi = 1.0
Clonal Units

Clonal Units

Clonal Units

Clonal Units

Clonal Units

Clonal Units

Clonal Units

Clonal Units

To visualize clonal units, we labeled the progeny of single neurons in the anterior or posterior brain, respectively. Images of the entire set of the identified clones are shown in Figure 1. Examples of Clonal Units in the Adult.

Results

We identified 80 groups of neuroblast clones with a single companion study by Yu et al. in this issue of Current Biology, 23(8), 644–655.

Clonal Units

175 clusters

\[ \chi = 0.1 \]
$\chi = 0.1$

175 clusters
\chi = 0.25

440 clusters
$\chi = 0.25$

440 clusters
Partitioning is Largely Hierarchical
Partitioning is Largely Hierarchical

Chi = 0.0. n = 8, m = 26
Partitioning is Largely Hierarchical

Chi = 0.0. n = 8, m = 26

Chi = 0.05. n = 68 (22 shown), m = 307
Partitioning is Largely Hierarchical

Chi = 0.0. n = 8, m = 26

Chi = 0.05. n = 68 (22 shown), m = 307

Chi = 0.1. n = 175 (50 shown), m = 1,266
Partitioning is Largely Hierarchical

Majority of clusters identified at resolutions $\chi > 0$ were at least 85% contained in one of the 8 clusters found with $\chi = 0$. 
The central complex

Hulse et al, 2021
Nine anatomically-identified layers

**Our clustering is meaningful:**
Clusters identify layers

**New finding:**
Ventral layers form a separate module at low values of $\chi$
Nine anatomically-identified layers

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**Our clustering is meaningful:**
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**New finding:**
Ventral layers form a separate module at low values of $\chi$
Including cell type
Including cell type

MC61 cells
Conclusion and Outlook

- A general framework to model the effects of STDP on network dynamics. It predicts the state of the network, and average quantities.

- Does not capture higher order interactions (e.g., triplets) which are important in some rules.

- Homeostatic processes observed in waking and resting state can be explained using fast changes in inhibitory synapses.

- Automated detection of the large scale organization of neuronal networks can provide experimentally testable hypotheses.

- The reconstructed connectome is noisy. We need new statistical methods to make inferences about structures, both small and large.
Plasticity and Balance

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University of Notre Dame
Robert Rosenbaum

UT, Houston
Ariana Andrei
Valentin Dragoi

Fly brain community detection

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Funding: NSF NeuroNex, NIH
Plasticity and Balance

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Valentin Dragoi

Funding: NSF NeuroNex, NIH
Mean Field Theory

\[
\overline{W} = \begin{bmatrix}
\overline{w}_{ee} & \overline{w}_{ei} \\
\overline{w}_{ie} & \overline{w}_{ii}
\end{bmatrix} \quad \overline{W}_x = \begin{bmatrix}
\overline{w}_{ex} \\
\overline{w}_{ix}
\end{bmatrix} \quad \mathbf{r} = \begin{bmatrix}
\overline{r}_e \\
\overline{r}_i
\end{bmatrix}
\]
Mean Field Theory

The average input to the two cell types

\[ \bar{I} = \sqrt{N} \left[ \bar{W} \bar{r} + \bar{W}_x \bar{r}_x \right] \]

\[
\begin{align*}
\bar{W} &= \begin{bmatrix}
\bar{w}_{ee} & \bar{w}_{ei} \\
\bar{w}_{ie} & \bar{w}_{ii}
\end{bmatrix} & \bar{W}_x &= \begin{bmatrix}
\bar{w}_{ex} \\
\bar{w}_{ix}
\end{bmatrix} & \bar{r} &= \begin{bmatrix}
\bar{r}_e \\
\bar{r}_i
\end{bmatrix}
\end{align*}
\]
Correlated Balanced State

Spike count covariance matrix in window $T_{\text{win}}$

\[ C' = \begin{bmatrix} C_{\text{ee}} & C_{\text{ei}} \\ C_{\text{ie}} & C_{\text{ii}} \end{bmatrix} \]
Correlated Balanced State

Spike count covariance matrix in window $T_{\text{win}}$

$$C' = \begin{bmatrix} C_{ee} & C_{ei} \\ C_{ie} & C_{ii} \end{bmatrix}$$

If $c_x \neq 0$, then $C$ remains $O(1)$, and the network is in a correlated state.

$$C \approx T_{\text{win}} c_x r_x \overline{W}^{-1} \overline{W}_x \overline{W}_x^T \overline{W}^{-T}$$

Baker, et al. 2019
Correlated Balanced State

Spike count covariance matrix in window $T_{\text{win}}$

$$C = \begin{bmatrix} C_{ee} & C_{ei} \\ C_{ie} & C_{ii} \end{bmatrix}$$
Correlated Balanced State

Spike count covariance matrix in window $T_{\text{win}}$

$$C = \begin{bmatrix} C_{ee} & C_{ei} \\ C_{ie} & C_{ii} \end{bmatrix}$$

Covariance in the balanced state

$$C \approx \frac{1}{N} T_{\text{win}} W^{-1} \Gamma W^{-T}$$

If $c_x \neq 0$, then the network is in a correlated state

$$\Gamma = N \overline{W}_x \overline{W}_x^T c_x r_x$$

Baker, et al. 2019