#### Plasticity and Balance in Neuronal Networks

#### Krešimir Josić University of Houston



#### **Plasticity and Balance**

University of Houston Alan Akil

University of Notre Dame Robert Rosenbaum

UT, Houston Ariana Andrei Valentin Dragoi

#### Fly brain community detection

University of Houston

Kevin Bassler Jiahao Guo

**Baylor College of Medicine** Xaq Pitkow Alex Kunin

Janelia Brad Hulse **Romain Franconville** 

#### **Funding: NSF NeuroNex, NIH**

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

#### Outline

## **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

Journal of Neuroscience 21 March 2012, 32 (12) 4049-4064; DOI: https://doi.org/10.1523/JNEUROSCI.6284-11.2012

Published: 23 February 2016

#### **Efficient codes and balanced networks**

Sophie Denève 🖂 & Christian K Machens 🖂

Nature Neuroscience 19, 375–382 (2016) Cite this article

#### PLOS COMPUTATIONAL BIOLOGY

#### Nonlinear stimulus representations in neural circuits with approximate excitatory-inhibitory balance

Cody Baker, Vicky Zhu, Robert Rosenbaum 🖂

Version 2

Published: September 18, 2020 • https://doi.org/10.1371/journal.pcbi.1008192

Published: 31 October 2016

The spatial structure of correlated neuronal variability

Robert Rosenbaum 🖂, Matthew A Smith, Adam Kohn, Jonathan E Rubin & Brent Doiron 🖂

Nature Neuroscience 20, 107-114 (2017) Cite this article

#### Published: 30 March 2008

#### Instantaneous correlation of excitation and inhibition during ongoing and sensory-evoked activities

Michael Okun & Ilan Lampl 🖂

Nature Neuroscience 11, 535–537 (2008) Cite this article

> Nat Neurosci. 2016 Dec;19(12):1690-1696. doi: 10.1038/nn.4415. Epub 2016 Oct 17.

Synaptic scaling rule preserves excitatory-inhibitory balance and salient neuronal network dynamics

Jérémie Barral<sup>1</sup>, Alex D Reyes<sup>1</sup>





Renart, de la Rocha, et al 2010



Renart, de la Rocha, et al 2010



Renart, de la Rocha, et al 2010



Rosenbaum, et al. 2017



Renart, de la Rocha, et al 2010



Rosenbaum, et al. 2017



Baker, et al. 2019



Renart, de la Rocha, et al 2010

Baker, et al. 2019

## Spike Time Dependent Plasticity



Abbott and Nelson, 2000

## **Spike Time Dependent Plasticity**



Abbott and Nelson, 2000



# Can we extend the mean-field theory of balanced networks to include plasticity?

# Can the theory predict when a balanced state is preserved?



Akil, Rosenbaum and Josić, PLoS Comp Bio 2021



Akil, Rosenbaum and Josić, PLoS Comp Bio 2021









 $J_{jk}^{ab} = \frac{1}{\sqrt{N}} \begin{cases} j_{ab} & \text{with probability } p_{ab}, \\ 0 & \text{otherwise.} \end{cases}$  *Akil, Rosenbaum and Josić, PLoS Comp Bio 2021* 



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

Mean Recurrent Weights

$$\overline{W}_x = \begin{bmatrix} \overline{w}_{\text{ex}} \\ \overline{w}_{\text{ix}} \end{bmatrix}$$

Mean Feedforward Weights



Mean Firing Rates





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Mean Recurrent Weights

$$\overline{W}_x = \begin{bmatrix} \overline{w}_{\text{ex}} \\ \overline{w}_{\text{ix}} \end{bmatrix}$$

Mean Feedforward Weights



Mean Firing Rates

In balance the mean firing rates are:

$$\lim_{N \to \infty} \boldsymbol{r} = -\overline{W}^{-1}\overline{W}_{\mathbf{x}}r_{\mathbf{x}}$$



#### **Correlated Balanced State**



#### Spike count covariance matrix in window T<sub>win</sub>

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



#### **Correlated Balanced State**



#### Spike count covariance matrix in window T<sub>win</sub>

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

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

$$C \approx T_{\rm win} c_{\rm x} r_{\rm x} \overline{W}^{-1} \overline{W}_{\rm x} \overline{W}_{\rm x}^{T} \overline{W}^{-T}$$

Baker, et al. 2019



$$\tau_{\rm STDP} \frac{dx_j^a(t)}{dt} = -x_j^a(t) + S_j^a(t)$$

$$S_j^a(t) = \sum_n \delta(t - t_n^{a,j})$$

#### **Plasticity and Eligibility Traces**





t



 $dJ_{jk}^{\rm ee}$ dt



t



 $dJ_{jk}^{\rm ee}$ dt

 $C_{\text{pre-post}} x_k^{\text{e}} S_j^{\text{e}}$ 





 $dJ_{jk}^{\mathrm{ee}}$ dt

 $C_{\text{pre-post}} x_k^{\text{e}} S_j^{\text{e}}$ 





 $dJ_{jk}^{\rm ee}$ dt

 $C_{\text{pre-post}} x_k^{\text{e}} S_j^{\text{e}}$ 

$$- C_{\text{post-pre}} x_j^{\text{e}} S_k^{\text{e}}$$





 $\frac{dJ_{jk}^{\text{ee}}}{dt} = \eta_{\text{ee}} (C_{\text{pre-post}} x_k^{\text{e}} S_j^{\text{e}})$ 

$$- C_{\text{post-pre}} x_j^{\text{e}} S_k^{\text{e}}$$
)





 $\frac{dJ_{jk}^{\text{ee}}}{dt} = \eta_{\text{ee}} (C_{\text{pre-post}} x_k^{\text{e}} S_k^{\text{e}})$ 

$$C_j^{\mathrm{e}} - C_{\mathrm{post-pre}} x_j^{\mathrm{e}} S_k^{\mathrm{e}} )$$



#### Plasticity Rules with up to Second Order Interactions

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

#### Plasticity Rules with up to Second Order Interactions

$$\frac{dJ_{jk}^{ab}}{dt} = \eta_{ab} \left( A_0 + \sum_{\alpha = \{a,j\},\{b,k\}} \right)$$

STDP Rule	Coefficients
Classical $EE$	$B_{(e,j),(e,k)} = -J_{jk}^{ee}$
Hebbian $[22-$	$B_{(e,k),(e,j)} = J_{\max}$
24]	
Classical $EE$	$B_{(e,j),(e,k)} = J_{jk}^{ee}$
Anti–	$B_{(e,k),(e,j)} = -J_{\max}$
Hebbian $[23,$	
24]	
Homeostatic	$A_{\mathrm{i},k} = \alpha_{\mathrm{e}} J_{jk}^{\mathrm{ei}} / J_0^{\mathrm{ei}}$
Inhibitory	$B_{({ m e},j),({ m i},k)} = -J_{jk}^{ m ei}/J$
$\lfloor 26 \rfloor$	$B_{(i,k),(e,j)} = -J_{jk}^{ei}/J$
Oja's	$B_{(e,j),(e,j)} = -J_{jk}^{ee}$
Rule $[46]$	$B_{(\mathrm{e},j),(\mathrm{e},k)} = \beta$
	Λ ΤΡΡ
Kononen's	$A_{\mathrm{e},j} = -J_{jk}^{\mathrm{e}}$
Rule $[25]$	$B_{(e,j),(e,k)} = \beta$

$$A_{\alpha}S_{\alpha} + \sum_{\alpha,\beta=\{a,j\},\{b,k\}} B_{\alpha,\beta}x_{\alpha}S_{\beta}$$

Equation  $\frac{dJ_{jk}^{\mathrm{ee}}}{dt} = \eta_{\mathrm{ee}} \left( J_{\mathrm{max}} x_k^{\mathrm{e}} S_j^{\mathrm{e}} - J_{jk}^{\mathrm{ee}} x_j^{\mathrm{e}} S_k^{\mathrm{e}} \right)$  $\frac{dJ_{jk}^{\mathrm{ee}}}{dt} = \eta_{\mathrm{ee}} \left( -J_{\mathrm{max}} x_k^{\mathrm{e}} S_j^{\mathrm{e}} + J_{jk}^{\mathrm{ee}} x_j^{\mathrm{e}} S_k^{\mathrm{e}} \right)$  $\frac{dJ_{jk}^{\mathrm{ei}}}{dt} = -\eta_{\mathrm{ei}} \frac{J_{jk}^{\mathrm{ei}}}{J_{0}^{\mathrm{ei}}} \left[ (x_{j}^{\mathrm{e}} - \alpha_{\mathrm{e}}) S_{k}^{\mathrm{i}} + x_{k}^{\mathrm{i}} S_{j}^{\mathrm{e}} \right]$ rei 0 ei  $\frac{dJ_{jk}^{\text{ee}}}{dt} = \eta_{\text{ee}} \left(\beta x_j^{\text{e}} S_k^{\text{e}} - J_{jk}^{\text{ee}} x_j^{\text{e}} S_j^{\text{e}}\right)$  $\frac{dJ_{jk}^{\text{ee}}}{dt} = \eta_{\text{ee}} \left(\beta x_j^{\text{e}} S_k^{\text{e}} - J_{jk}^{\text{ee}} S_j^{\text{e}}\right)$ 

## Averaging synaptic weight dynamics

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

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

#### Average in time, and over different network realizations

Firing rates:

Spike count covariances:

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

 $N \rightarrow \infty$ 

Mean synaptic weights:

$$\tau_{J_{ab}} \frac{dJ_{ab}}{dt} = A_0 + \sum_{\alpha,\beta = \{a,b\}} \text{Rate}_{\alpha,\beta} + \text{Cov}_{\alpha,\beta}$$

$$\lim_{W \to \infty} \boldsymbol{r} = -\overline{W}^{-1}\overline{W}_{\mathbf{x}}r_{\mathbf{x}}$$



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

$$\tau_{J_{ab}} \frac{dJ_{ab}}{dt} = A_0 + \sum_{\alpha,\beta = \{a,b\}} \text{Rate}_{\alpha,\beta} + \text{Cov}_{\alpha,\beta}$$

$$= -\overline{W}^{-1}\overline{W}_{\mathbf{x}}r_{\mathbf{x}}$$

$$\lim_{N \to \infty} \boldsymbol{r} = -\overline{W}^{-1}\overline{W}_{\mathbf{x}}r_{\mathbf{x}}$$

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

$$\tau_{J_{ab}} \frac{dJ_{ab}}{dt} = A_0 + \sum_{\alpha,\beta = \{a,b\}} \text{Rate}_{\alpha,\beta} + \text{Cov}_{\alpha,\beta}$$

$$\lim_{N\to\infty} \boldsymbol{r} = -\overline{W}^{-1}\overline{W}_{\mathbf{x}}r_{\mathbf{x}}$$

$$\tau_{J_{ab}} \frac{dJ_{ab}}{dt} = A_0 + \alpha$$

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

 $\operatorname{Rate}_{\alpha,\beta} + \operatorname{Cov}_{\alpha,\beta}$  $\alpha,\beta = \{a,b\}$ 

 $\left| C \approx \frac{1}{N} T_{\text{win}} \overline{W}^{-1} \Gamma \overline{W}^{-T} \right|$  $g(J_{ab})$  $\operatorname{Rate}_{\alpha,\beta} + \operatorname{Cov}_{\alpha,\beta}$  $a,\beta = \{a,b\}$
# Closing Equations using Quasi Steady State Assumption

 $C \approx \frac{1}{N} T_{\rm win} \overline{W}^{-1} \Gamma \overline{W}^{-T}$  $g(J_{ab})$  $_{\beta} + \mathrm{Cov}_{\alpha,\beta}$ 

















### **Asynchronous**







**Asynchronous** 







**Asynchronous** 

Correlated





**Asynchronous** 

**Correlated** 

### Kohonen's Rule







### Correlated







### Loss of Stability with Kohonen's Rule



 $\frac{dJ_{jk}^{\rm ee}}{dt} = \eta_{\rm ee} \left(\beta x_j^{\rm e} S_k^{\rm e} - J_{jk}^{\rm ee} S_j^{\rm e}\right)$ 

### **Correlations have a small impact**

$$\frac{dJ_{ab}}{dt} = \eta_{ab} \left( A_0 + \right.$$



See also Graupner, et al, 2016, Ocker and Doiron, 2015

 $A_a r_a + \mathbf{Rate}_{a,b} + \mathbf{Cov}_{a,b}$ 

### 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

Can we extend the mean-field theory of balanced networks to include plasticity?

### **Homeostatic Plasticity and Optogenetic Stimulation?**



Andrei, et al. Nature Neuroscience, 2023



### Homeostatic Plasticity and Optogenetic Stimulation?



Andrei, et al. Nature Neuroscience, 2023



### Homeostatic Plasticity and Optogenetic Stimulation?



Andrei, et al. Nature Neuroscience, 2023



### Correlation changes are heterogeneous





# No changes during rest



# Model with Homeostatic Inhibitory Plasticity







### Model Shows Small Effect During Rest



Vyazovkiy, et al 2008, Johansen, et al 2010



50

0

Time lag (ms)

100

-100 -50

Broad spiking units

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











### **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, ~130,00 neurons (2023)

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### Neuroscience's Existential Crisis

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

BIOLOGY NEUROSCIENCE

BY GRIGORI GUITCHOUNTS OCTOBER 27, 2021









### 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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Guo et al, 2019





Guo et al, 2019

 $K_c$  is total degree of nodes in c

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

$$=\frac{1}{2m}\sum_{c}\left(2m_{c}-\frac{K_{c}^{2}}{2m}\right)$$





Guo et al, 2019

 $K_c$  is total degree of nodes in c

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

$$=\frac{1}{2m}\sum_{c}\left(2m_{c}-\frac{K_{c}^{2}}{2m}\right)\rho_{c}^{\chi}$$

$$\frac{2m_c}{n_c(n_c-1)}$$

- Link density in community c





 $Q_g = \frac{1}{2m} \sum_{c} \left( 2m_c - \frac{K_c^2}{2m} \right) \rho_c^{\chi}$


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Increase  $\chi$ 



 $Q_g = \frac{1}{2m} \sum_{c} \left( 2m_c - \frac{K_c^2}{2m} \right) \rho_c^{\chi}$ 



Increase  $\chi$ 





RenEEL algorithm (Guo et al 2019) *Output:* list of communities c maximizing  $Q_g$ 



Increase  $\chi$ 

$$\left(2m_c - \frac{K_c^2}{2m}\right)\rho_c^{\chi}$$

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

# 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.







# $\chi = 0$





# $\chi = 0$





# $\chi = 0$





# $\chi = 0$











### $\chi = 0$











# $\chi = 0$











### $\chi = \mathbf{0}$











# $\chi = 0$











# $\chi = 0$











# $\chi = \mathbf{0}$









































#### **Clonal Units** ALH SIP Β VL CA PED SEG MBp1 ALv1 Η ΑΟΤυ **PVLP** LO LO VPNd2 VPNv2 Ν SMP SPS ICL LO AVLP VES FLA SEG AMMC CREa1 PSp3 S PVLP ICL CRE LAL FLA FLAa1 ME PSa1



























Chi = 0.1. n = 175 (50 shown), m = 1,266





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  $\chi$ 



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Chi = 0.25

Nine anatomically-identified layers

Our clustering is meaningful: Clusters identify layers

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

Chi = 0.5

Nine anatomically-identified layers

Our clustering is meaningful: Clusters identify layers

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

Chi = 0.75

Nine anatomically-identified layers

Our clustering is meaningful: Clusters identify layers

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

Chi = 10

# Including cell type

# Including cell type



## **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 (eg 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.



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### Mean Field Theory



$$\mathbf{r} = \left[ egin{array}{c} \overline{r}_{\mathrm{e}} \ \overline{r}_{\mathrm{i}} \end{array} 
ight]$$

### Mean Field Theory



The average input to the two cell types

$$\overline{\boldsymbol{I}} = \sqrt{N} \left[ \overline{W} \boldsymbol{r} + \overline{W}_{\mathbf{x}} r_{\mathbf{x}} \right]$$







### Spike count covariance matrix in window T<sub>win</sub>

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





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$$C \approx T_{\rm win} c_{\rm x} r_{\rm x} \overline{W}^{-1} \overline{W}_{\rm x} \overline{W}_{\rm x}^{T} \overline{W}^{-T}$$

Baker, et al. 2019





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

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

Baker, et al. 2019





Spike count covariance matrix in window T<sub>win</sub>

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

Covariance in the balanced state

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

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

$$\Gamma = N \overline{W}_{\mathbf{x}} \overline{W}_{\mathbf{x}}^T c_{\mathbf{x}} r_{\mathbf{x}}$$

Baker, et al. 2019

