Second type of criticality in the brain uncovers rich multiple-neuron dynamics

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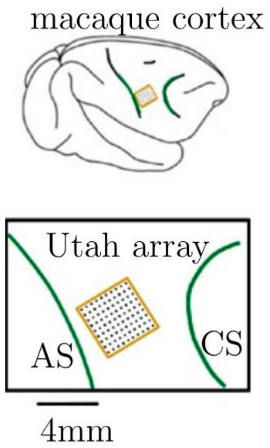
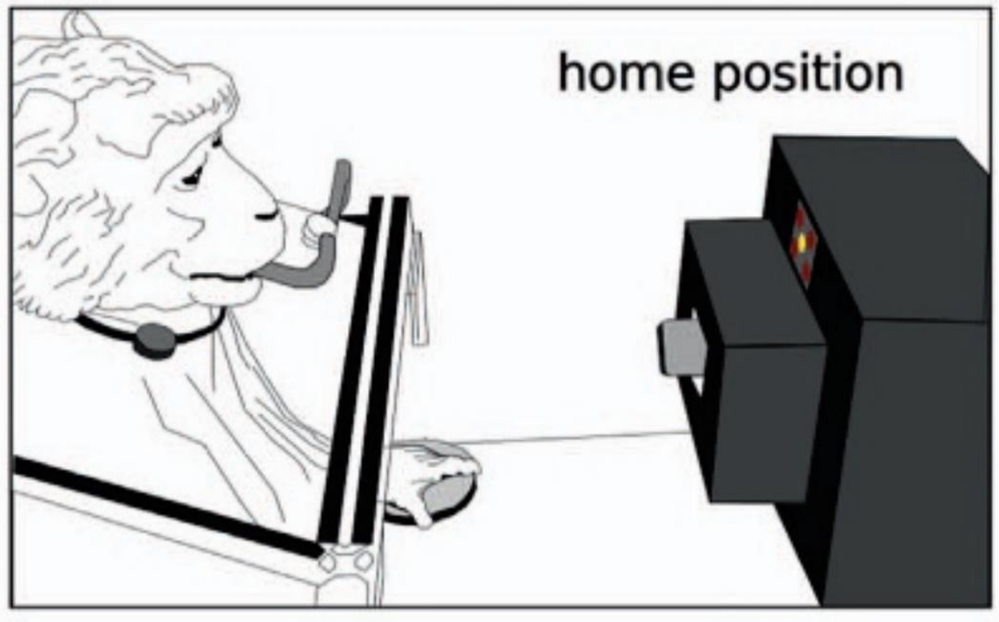
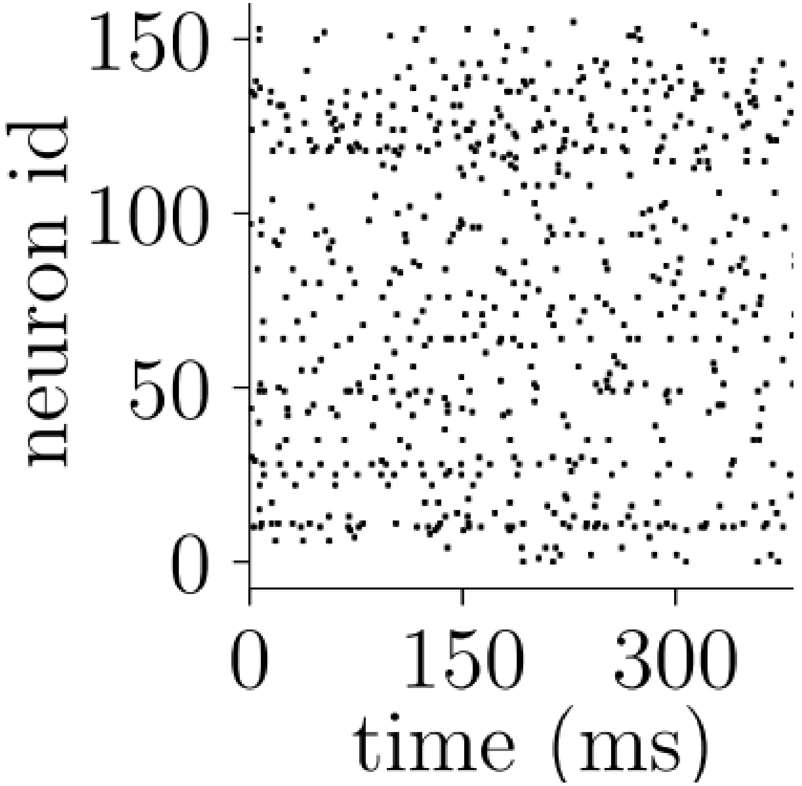
Spiking activity in macaque motor cortex



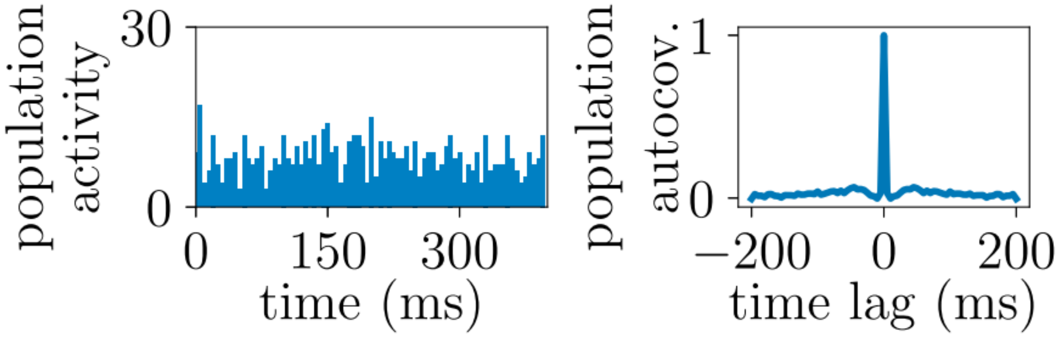




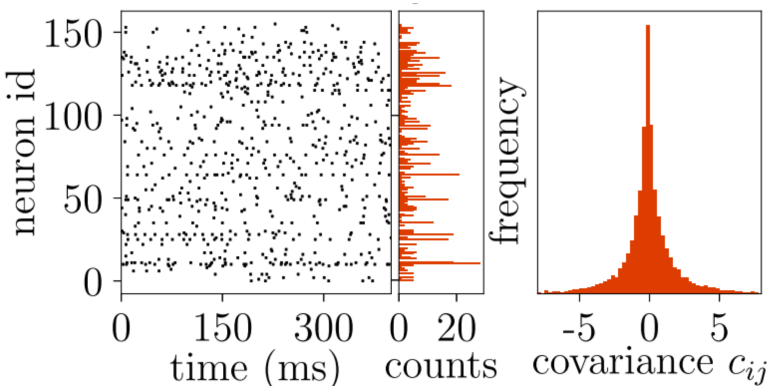
155 neurons

Statistics of motor cortex data

- **Fast decaying autocorrelation** of the population activity

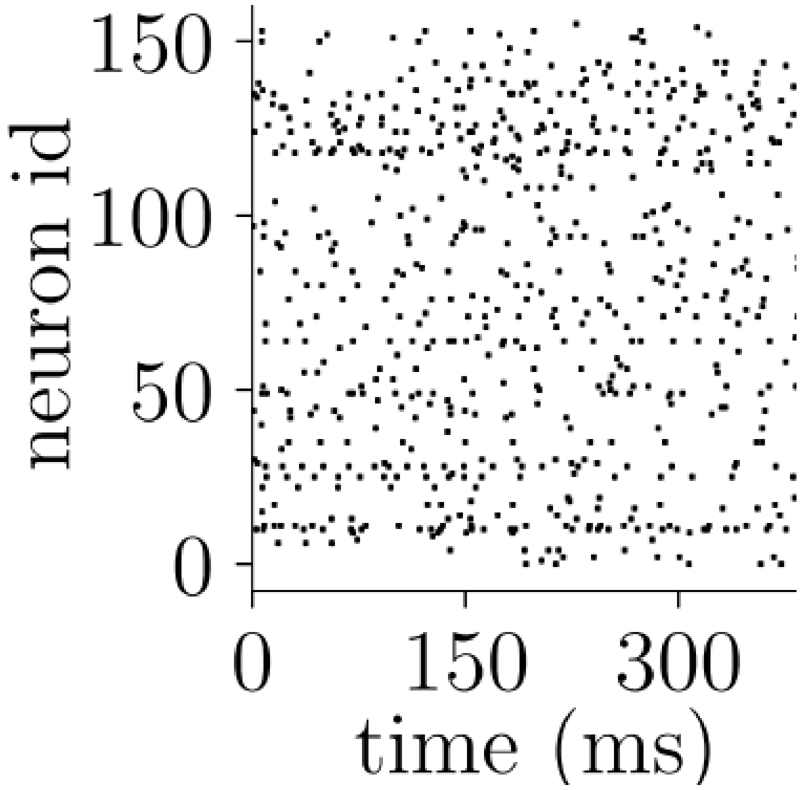


- **Weak** covariances on average



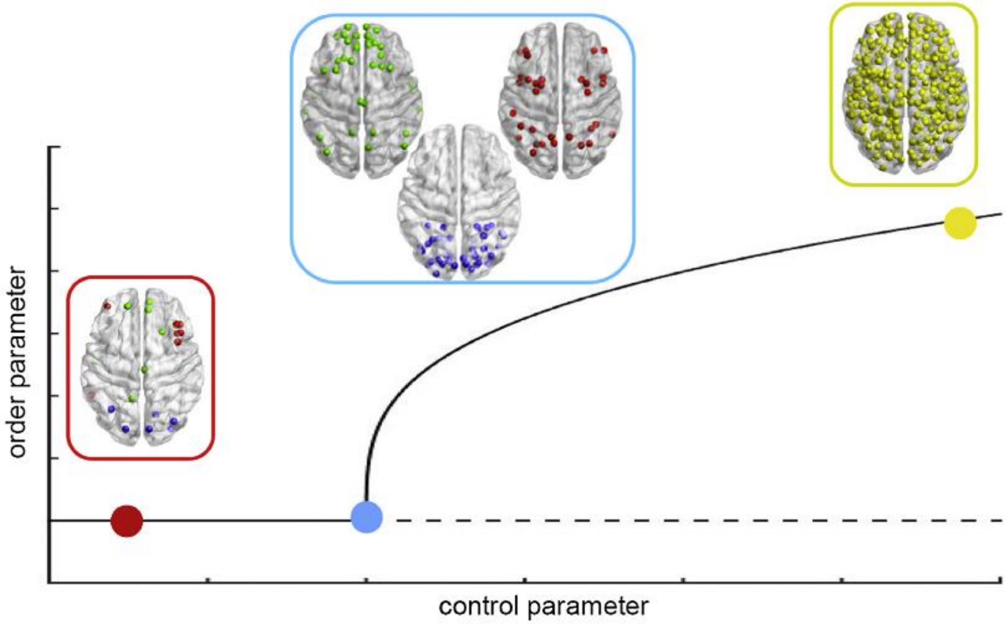
«Balanced» regime, inhibition dominated

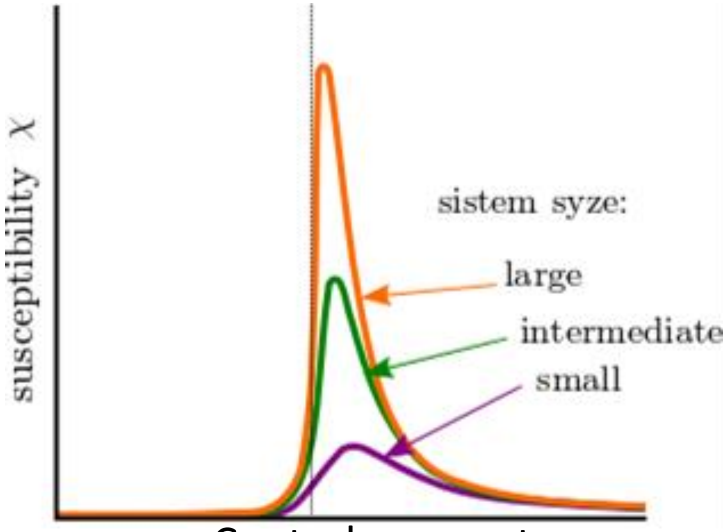
- ❑ Spiking activity of awake animals
- ❑ Excess of inhibitory feedback
- ❑ Weak correlations on average: **typically evidence against criticality**



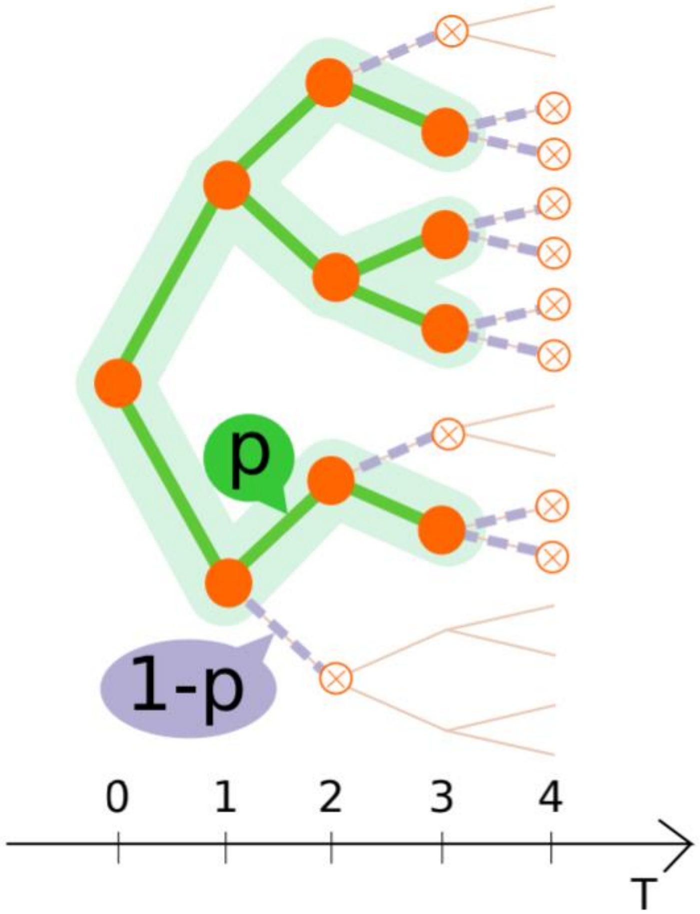
Critical brain hypothesis

- Hypothesis that brain operates at the critical point of a phase transition
- Optimal computational abilities from operating at a critical point
- e. g. optimal sensitivity to stimuli, optimal dynamic range

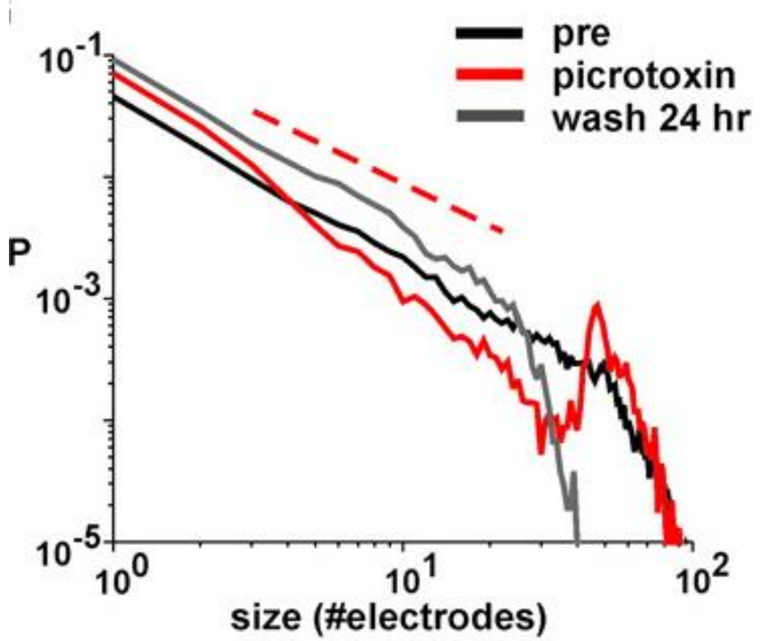




Which phase transition?



Neuronal avalanches criticality



Beggs and Plenz, 2003, Journal of Neuroscience

- ❑ Linked to balance between excitation and inhibition
- ❑ Slowly decaying population autocorrelation
- ❑ Positive correlations

Motor cortex data and criticality hypothesis

- Observations in line with the balanced state
  1. Does this contradict the criticality hypothesis?
- Another type of criticality: **EDGE OF CHAOS CRITICALITY**
- Known to be linked to the breakdown of the stability of fixed point of vanishing activity
- Study stability of the network

A measure of stability

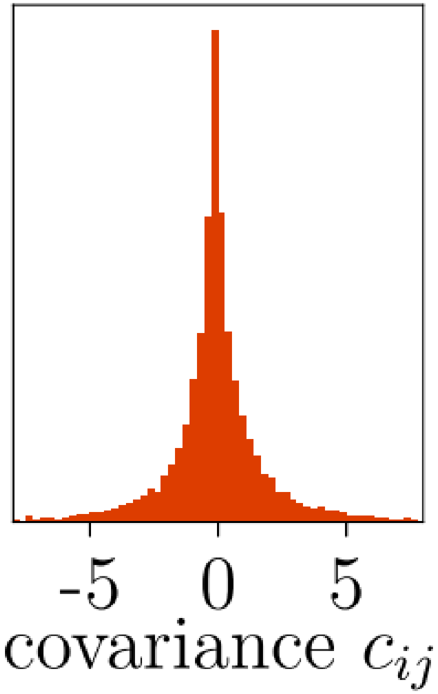
$$c(W) = \cancel{(I - W)^{-1} D (I - W^T)^{-1}}$$

- W determines the covariance and the **stability** of the dynamics
- If $Re(\lambda) \geq 1$ instability
- **Problem of sparse sampling**

2. Which is a reliable measure of stability with few neurons measured?

A measure of stability

- Low mean of covariances is known to relate to a single higly stable eigenvalue of W: $Re(\lambda) < 0$
- But what about the other eigenvalues?
- Get information on the **statistics of the connectivity** from the **statistics of covariances**
- We turn to ideas from disordered systems + dynamical mean field



(Beyond) mean-field theory for metastatistics of activity

$$\boxed{\tau \frac{dx(t)}{dt} = -x(t) + W \cdot x(t) + \xi(t)}$$

Linear response approximation

$$Z(J) = \det(1-W) \int \mathcal{D}X \int \mathcal{D}\tilde{X}\, e^{S_0(X,\tilde{X}) + J^{\mathrm{T}} X}$$

$$= \exp\left(\frac{1}{2} J^{\mathrm{T}} \underbrace{\boxed{(\mathcal{I}-W)^{-1} D \left(\mathcal{I}-W^{\mathrm{T}}\right)^{-1}}}_{c(W)} J\right)$$

$$S_0(X,\tilde{X}) = \tilde{X}^{\mathrm{T}} (\mathcal{I}-W)\, X + \frac{D}{2} \tilde{X}^{\mathrm{T}} \tilde{X},$$

(Beyond) mean-field theory for metastatistics of activity

i. i. d. weights

Disordered averaged generating function

$$\left\langle e^{\tilde{X}^{\mathrm{T}} W X} \right\rangle = \prod_{i,j} \left\langle e^{W_{ij} \tilde{X}_i X_j} \right\rangle = \prod_{i,j} e^{\sum_{k=1}^{\infty} \frac{\kappa_k}{k!} (\tilde{X}_i X_j)^k} .$$

Homogeneous random network approximation

Truncation at the second moment

$$\langle Z(J) \rangle \sim \int \mathcal{D}X \int \mathcal{D}\tilde{X}\, e^{S_0(X,\tilde{X}) + \frac{\lambda_{\max}^2}{2N} V(X,\tilde{X}) + J^{\mathrm{T}} X},$$

$$S_0(X,\tilde{X}) = \tilde{X}^{\mathrm{T}} (\mathcal{I} - \mu \mathcal{J})\, X + \frac{D}{2} \tilde{X}^{\mathrm{T}} \tilde{X},$$

$$V(X,\tilde{X}) = \tilde{X}^{\mathrm{T}} \tilde{X}\, X^{\mathrm{T}} X$$

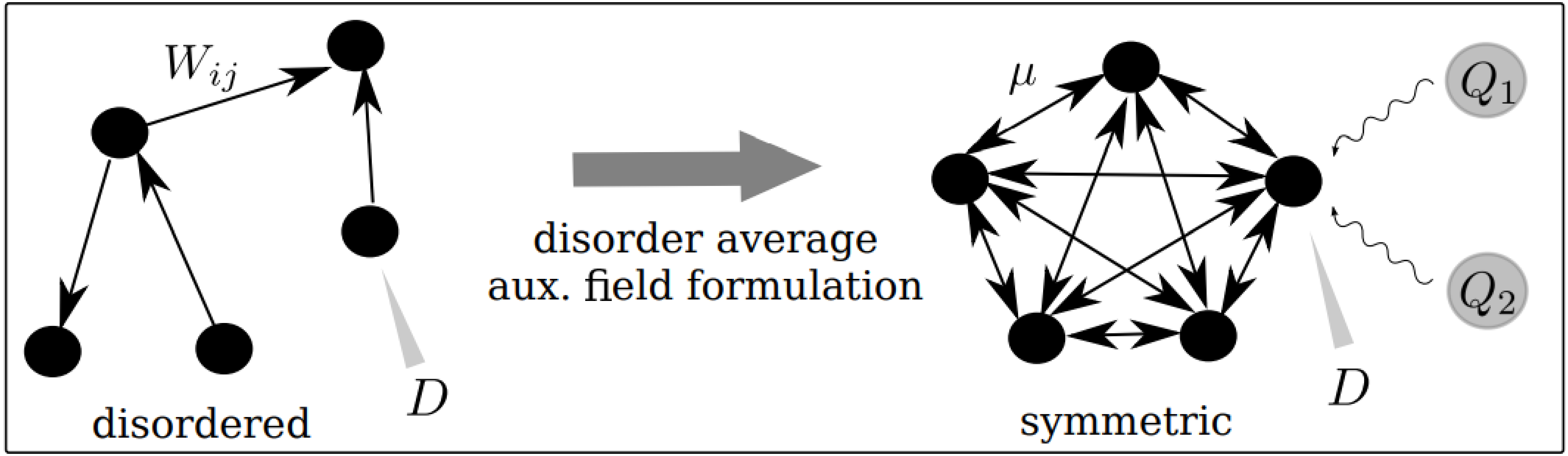
Statistics of the connectivity

Auxiliary field formalism

$$Q_1 = \frac{\lambda_{\max}^2}{N} X^{\mathrm{T}} X$$

Beyond mean-field theory

- Standard mean field: neuron to neuron variability is lost
- Take into account also the fluctuations of the auxiliary fields (dependencies on the sources *j*)


W_{ij}
D
disordered
disorder average
aux. field formulation
μ
Q_1
Q_2
D
symmetric

Beyond mean-field theory

$$\overline{c_{ij}} = \left[(\mathcal{I} - \mu\mathcal{J})^{-1} D_\lambda (\mathcal{I} - \mu\mathcal{J})^{-1}\right]_{ij} = D_\lambda \gamma_{ij} \qquad \sim \frac{1}{N}$$

$$\overline{\delta c_{ij}^2} = \lambda_{\max}^2 \left[\frac{1}{(1-\lambda_{\max}^2)^2} + \frac{1}{1-\lambda_{\max}^2}\right] D_\lambda^2 \chi_{ij}. \qquad \delta c_{ij} \sim \frac{1}{\sqrt{N}}$$

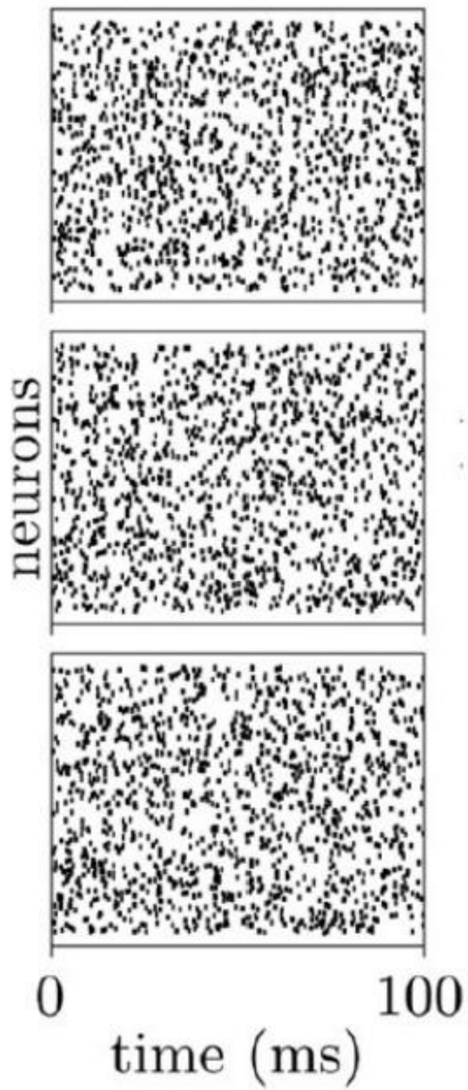
$\gamma_{ij} = \delta_{ij} + \gamma$ $\quad \gamma = \frac{\mu}{1-\mu N}$ setting $\gamma \approx 0$ balanced state, $\mu < 0$ $\quad D_\lambda = \frac{D}{(1 - \lambda_{max}^2)}$

$$\chi_{ij} = \frac{1}{N}(1 + \delta_{ij} + O(N))$$

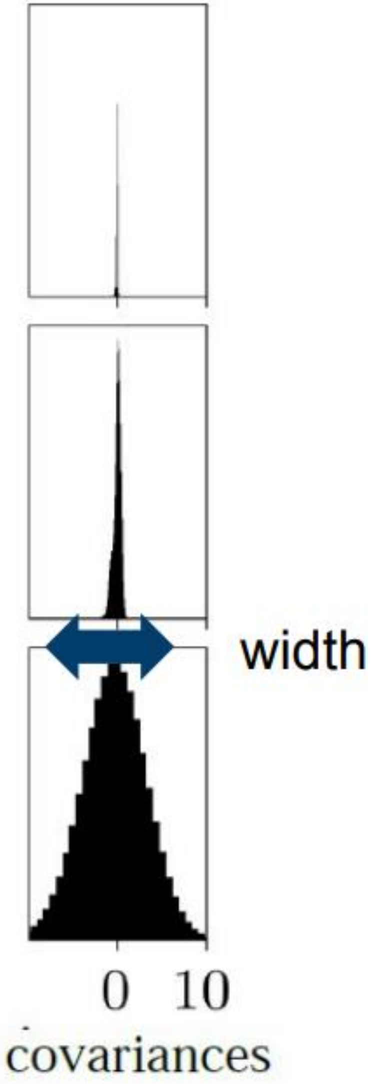
$$\lambda_{\max} = \sqrt{1 - \sqrt{\frac{1}{1 + N\Delta^2}}}. \qquad \Delta = \frac{\delta c_{ij}}{c_{ii}}$$

Sparse inhibition dominated networks

Weights: i. i. d. from a Bernoulli distribution with p = 0.1



What’s different in these networks ?

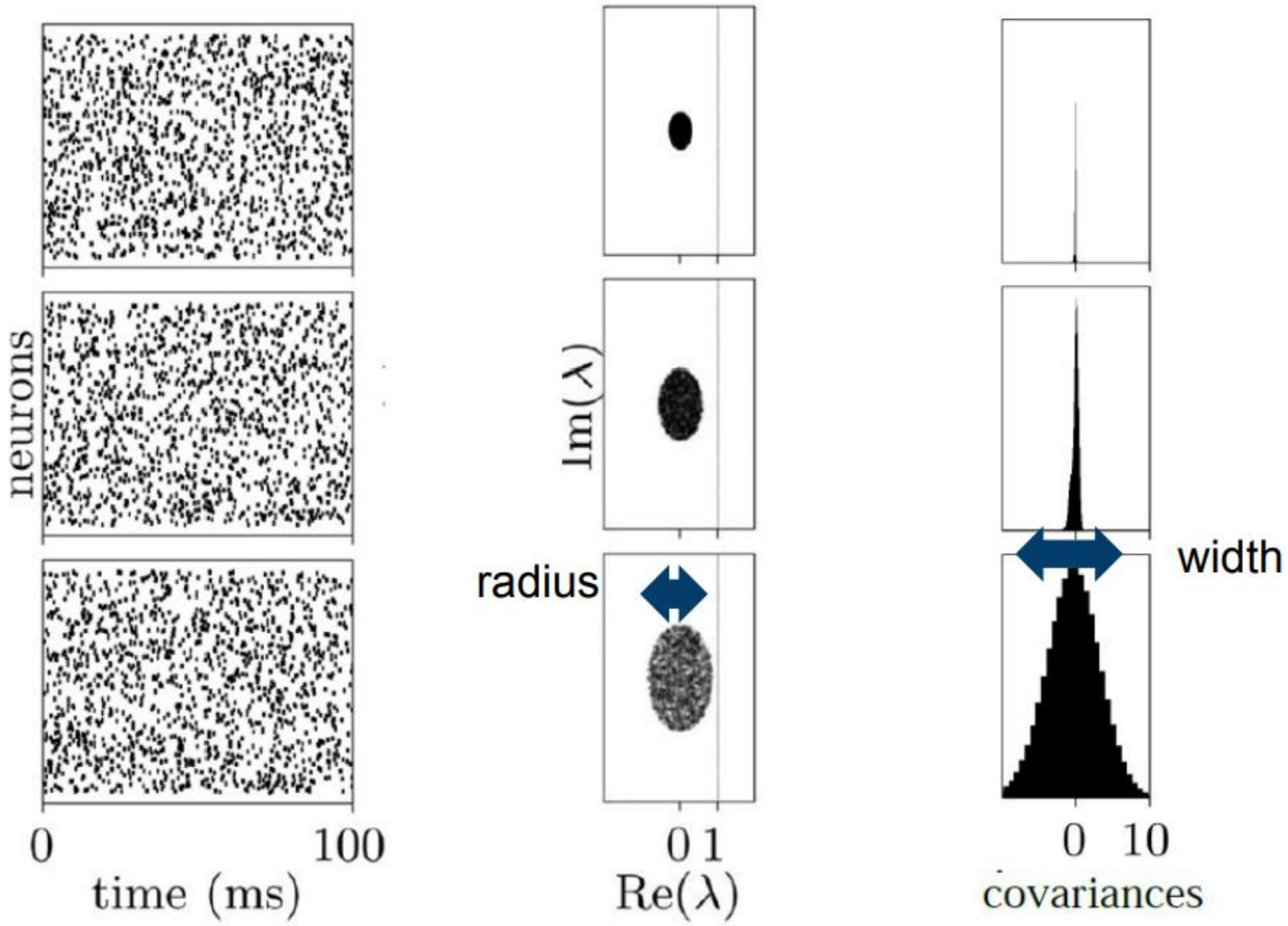


Sparse inhibition dominated networks
Weights: i. i. d. from a Bernoulli distribution with p = 0.1

Weight strength = $\frac{-1}{\sqrt{N}}$

Weight strength = $\frac{-2}{\sqrt{N}}$

Weight strength = $\frac{-3}{\sqrt{N}}$



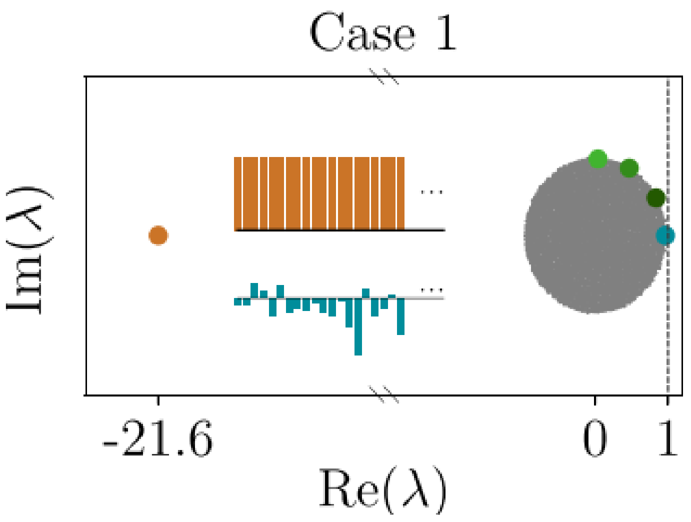
How robust this result is wrt more biologically realistic networks? And beyond linear response approximation?

$$\lambda_{\max} = \sqrt{1 - \sqrt{\frac{1}{1 + N\Delta^2}}}.$$

$$\Delta = \frac{\delta c_{ij}}{c_{ii}}$$

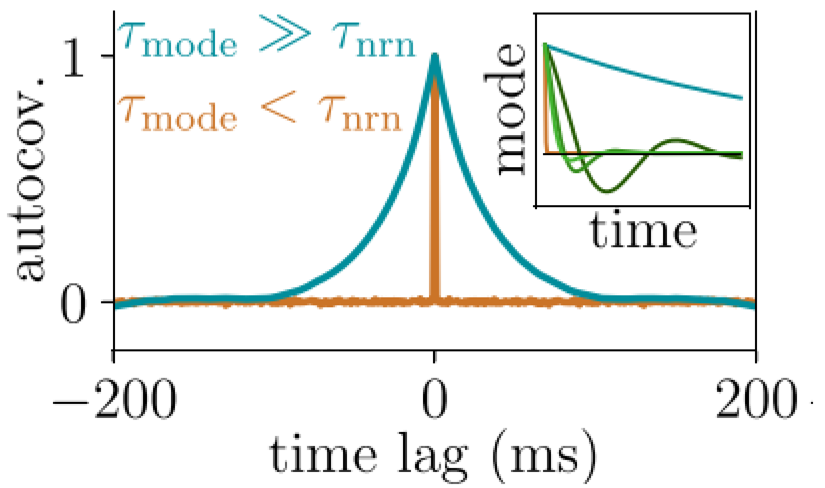
- Checked with simulations with more complex topologies
- Checked in simulations on Leaky Integrate and Fire model
- Δ is still well predicted by the theory
- $\lambda_{max} \lesssim 1$ in motor cortex data ($N = 10^4, \Delta = 0.15$): **dynamically balanced critical regime**

Functional and dynamical consequences of dynamically balanced criticality

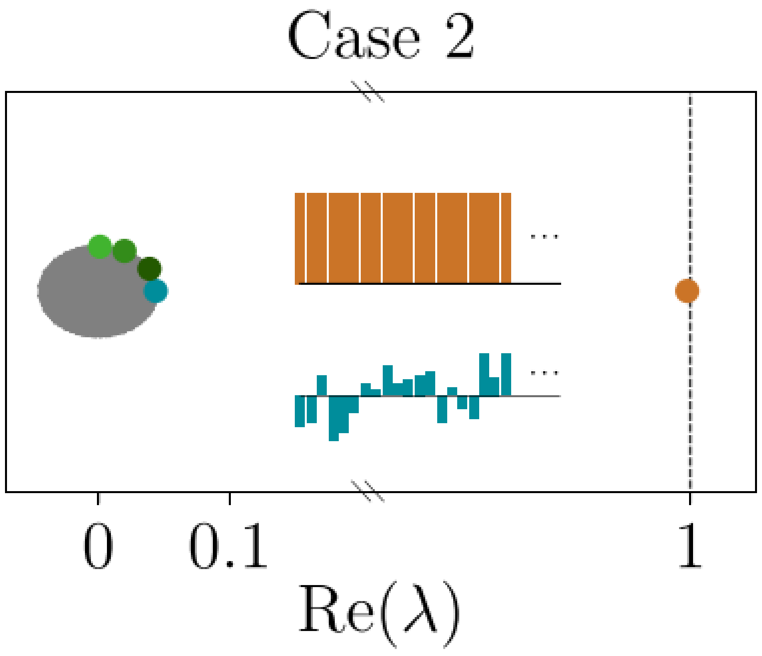


- One stable eigenvalue, then **many eigenvalues** close to the critical line
- Many modes with **slow dynamics**
- **Multiple neurons** and **heterogeneous** dynamics

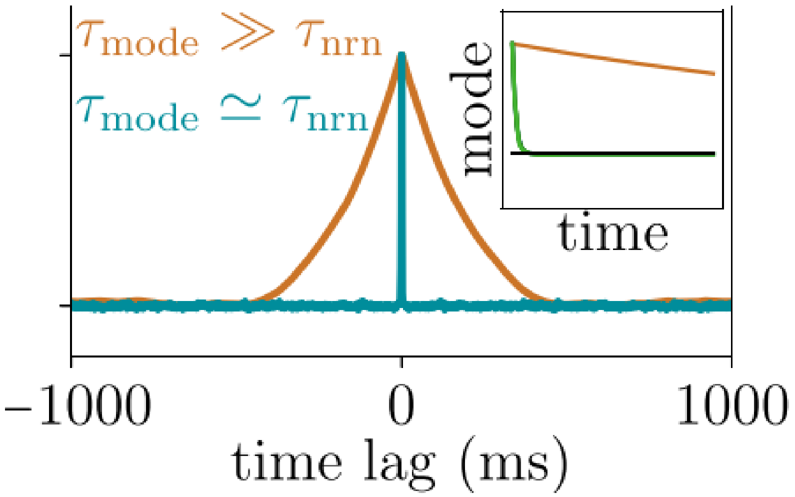
$$v_\alpha(t) \sim e^{\frac{t(1-\lambda_\alpha)}{\tau}}$$



Avalanches criticality



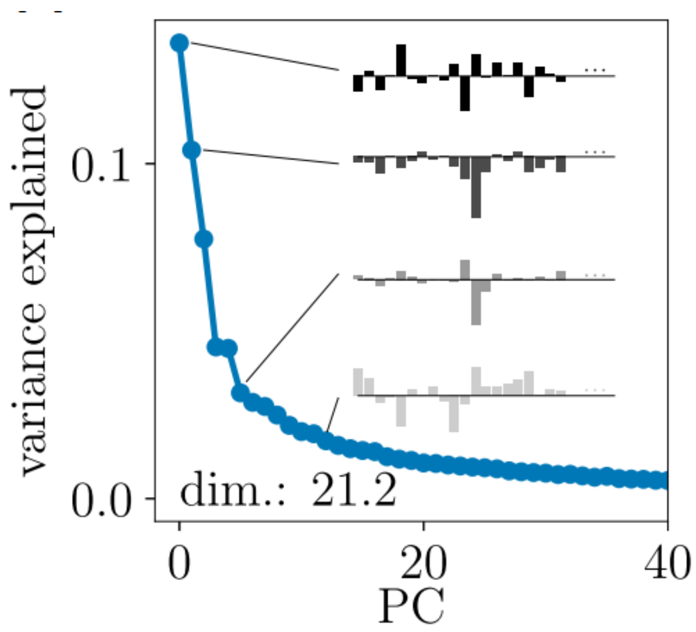
- One dominating eigenvalue close to edge of stability, that is **population eigenvalue**
- **Dynamics is effectively one dimensional**

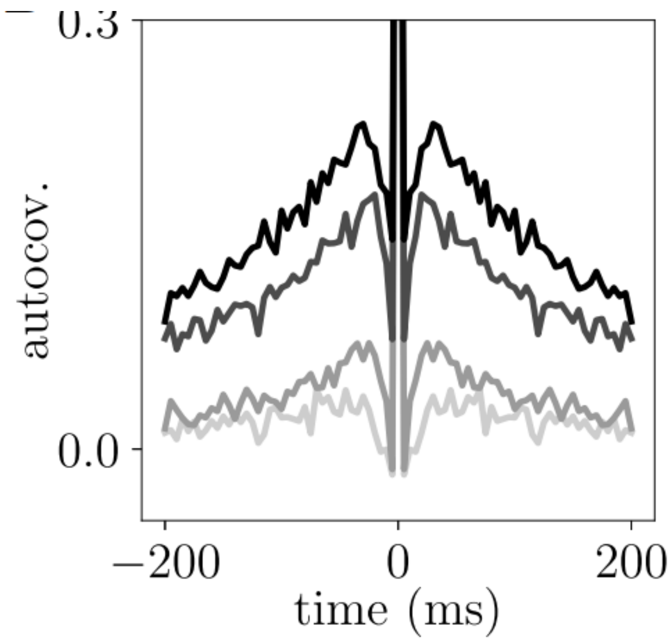


Other signatures of balanced critical regime from data

- The eigenvectors and eigenvalues of the W of the data are not know.
- PCA **detects modes with longer timescales**
- Motor cortex data: continuum of PCs **with hetereogeneous loadings**
- Many modes with **long time scales**

$$v_\alpha(t) \sim e^{\frac{t(1-\lambda_\alpha)}{\tau}}$$





Dynamically balanced criticality vs avalanches criticality

	DYNAMICALLY BALANCED CRITICALITY	*AVALANCHES CRITICALITY*
Feature	Case 1	Case 2
Population activity		
Fluctuations	Fast and weak	Slow and strong
Spike count covariance		
Mean	Low	High
Width	Large	Small
Stimulation		
Whole population	Fast and small response	Slow and strong response
Specific direction (mode)	Various timescales and amplitudes	Stereotypic timescale and amplitude
PCs		
Eigenvalues	Gradual decline	Single dominant eigenvalue
Dominant eigenvectors	Heterogenous loadings	Homogeneous loadings
Dimensionality	$1 < \mathrm{dim} \ll N$	$1 \lesssim \mathrm{dim}$

Summary and conclusions

- Going beyond mean field, analytical expression that links covariance statistics to statistics of connectivity, and solves for sampling problem
- No more contradiction between asynchronous irregular regime and criticality: another kind of criticality linked to spectral radius of connections
- Macaque motor cortex is **dynamically critically balanced, rich multiple neuron dynamics**
- The typically considered population activity is only one particular mode that weights all neurons equally!
- Critical modes are hidden if one just looks at population activity

Quasi-universal scaling in mouse-brain neuronal activity stems from edge-of-instability critical dynamics, Nov 2021, arXiv:2111.12067

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Thank you!
Questions?

Time lagged integrated covariances

$$c_{ij} = \frac{1}{T}\left(\langle n_i n_j \rangle - \langle n_i \rangle \langle n_j \rangle\right) = \int_{-T}^{T} \frac{T - |\tau|}{T} c_{ij}(\tau)\, d\tau$$

$$\underset{T \to \infty}{\to} \int_{-\infty}^{\infty} c_{ij}(\tau)\, d\tau,$$

Possible future perspectives

- The equal time covariance C of the Ornstein Uhlenbeck process is linked to the effective connectivity matrix. And it is nothing but the Controllability Gramian C

$$(1 - W)C + C(1 - W)^T = DD^T$$

Controllability is linked to spectral properties of C

- Being at the edge of instability might have effects on the controllability
- But experimentally we face sampling problem

Going beyond mean-field

$$c_{ij} = \int c_{ij}(\tau) d\tau = \int \int \langle x_i(t+\tau) x_j(t) \rangle_x \, dt \, d\tau$$
$$= \langle X_i(0) X_j(0) \rangle_x$$

$$\tau \frac{dx(t)}{dt} = -x(t) + W \cdot x(t) + \xi(t)$$

Linear response approximation

$$Z[j] = \int \mathcal{D}x \int \mathcal{D}\tilde{x} \, \exp\left(S_0[x, \tilde{x}] + j^{\mathrm{T}} x \right)$$

with $\quad S_0[x, \tilde{x}] = \tilde{x}^{\mathrm{T}} \left((\partial_t + 1)\mathcal{I} - W \right) x + \frac{D}{2} \tilde{x}^{\mathrm{T}} \tilde{x}.$

$$Z[J] = \int \mathcal{D}X \int \mathcal{D}\tilde{X} \, \exp\left(S_0[X, \tilde{X}] + J^{\mathrm{T}} X \right)$$

with $S_0[X, \tilde{X}] = \tilde{X}^{\mathrm{T}} \left((i\omega + 1)\mathcal{I} - W \right) X + \frac{D}{2} \tilde{X}^{\mathrm{T}} \tilde{X},$

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$$= \exp\left(\frac{1}{2} J^{\mathrm{T}} \boxed{\left(\mathcal{I} - W\right)^{-1} D \left(\mathcal{I} - W^{\mathrm{T}}\right)^{-1}} J \right)$$

$$S_0(X, \tilde{X}) = \tilde{X}^{\mathrm{T}} \left(\mathcal{I} - W\right) X + \frac{D}{2} \tilde{X}^{\mathrm{T}} \tilde{X},$$

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Disordered averaged generating function

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$$S_0(X,\tilde{X}) = \tilde{X}^{\mathrm{T}}\,(\mathcal{I}-\mu\mathcal{J})\,X + \frac{D}{2}\tilde{X}^{\mathrm{T}}\tilde{X},$$

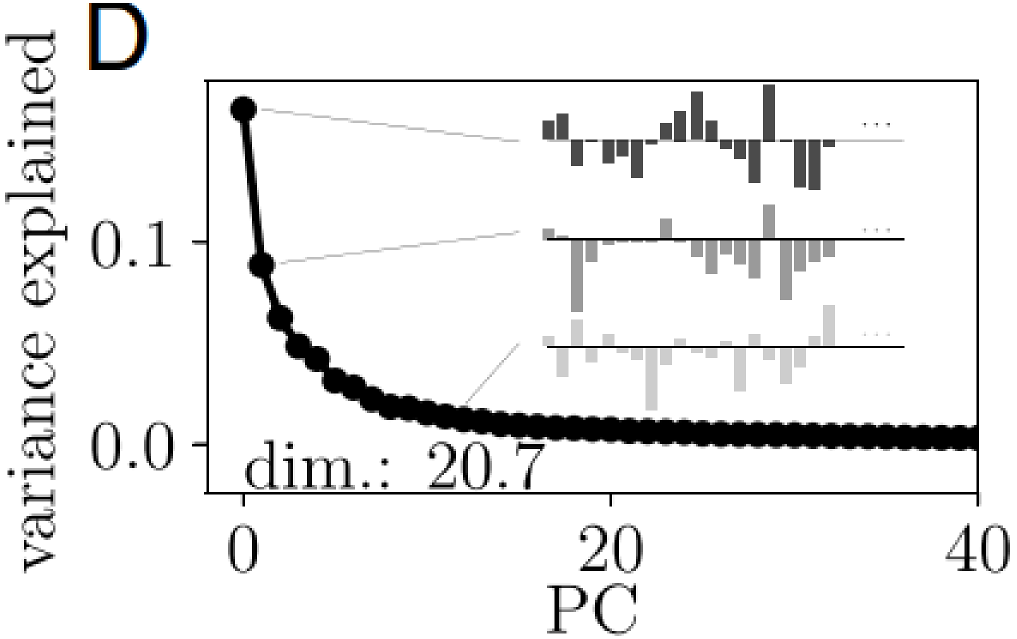
$$V(X,\tilde{X}) = \tilde{X}^{\mathrm{T}}\tilde{X}\,X^{\mathrm{T}}X$$

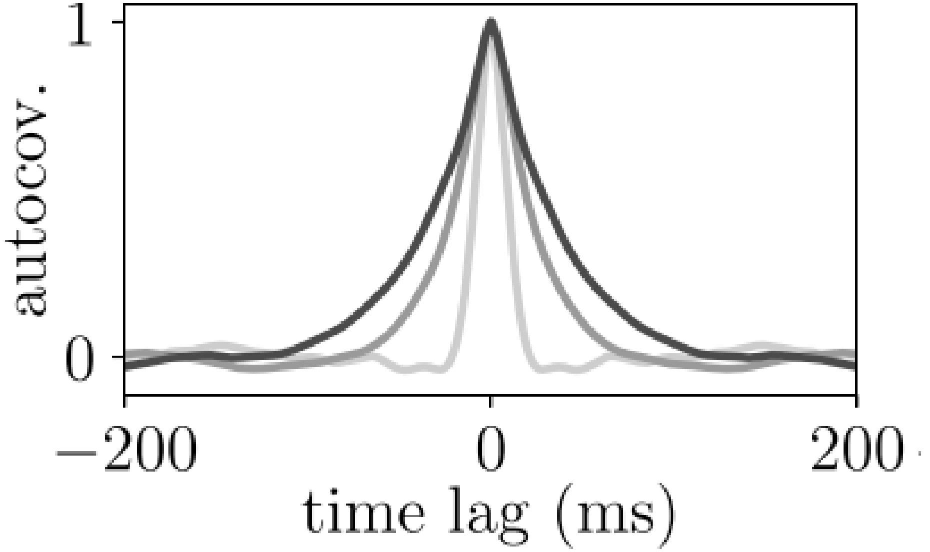
Auxiliary field formalism

$$Q_1 = \frac{\lambda_{\max}^2}{N}X^{\mathrm{T}}X$$

The auxiliary field formalism translates the high-dimensional ensemble average over W to a low-dimensional average over Q; it maps the local disorder in the connections to fluctuations of global fields Q interacting with a highly symmetric all-to-all connected network.

PCs and modes in a dynamically balanced network





PCs and modes in avalanches criticality