Spike train correlations derived from anatomical microstructure

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Workshop “Mean-field methods and multiscale analysis of neuronal populations”

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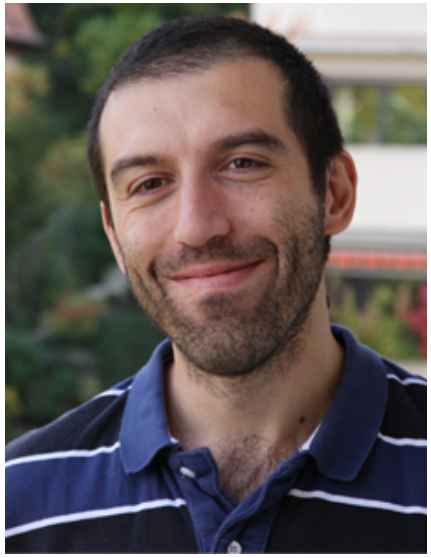
Volker Pernice



Stefano Cardanobile

Benjamin Staude

Pairwise correlations in recurrent networks

Disentangling multi-synaptic pathways

Impact of non-uniform connectivity

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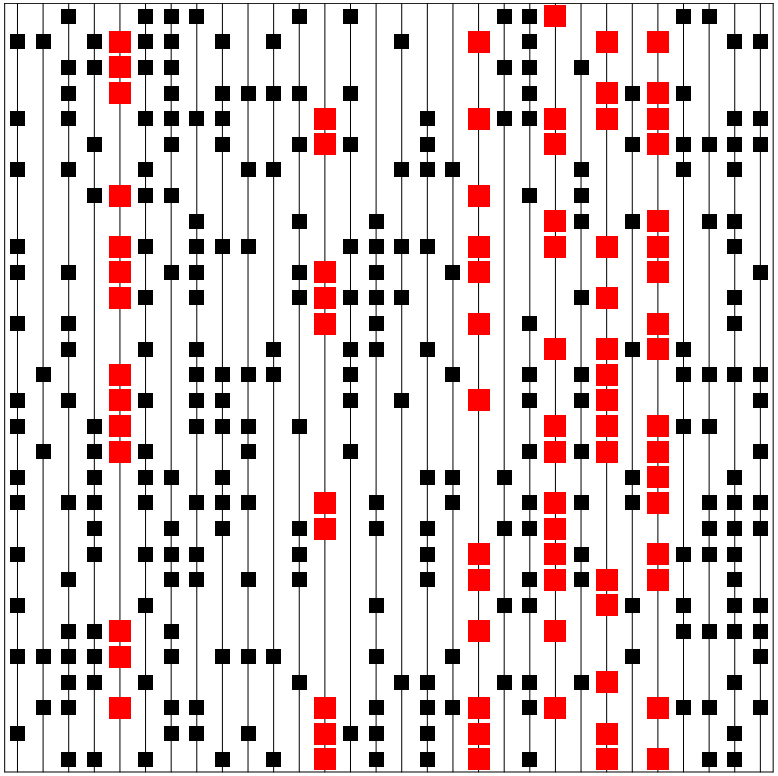
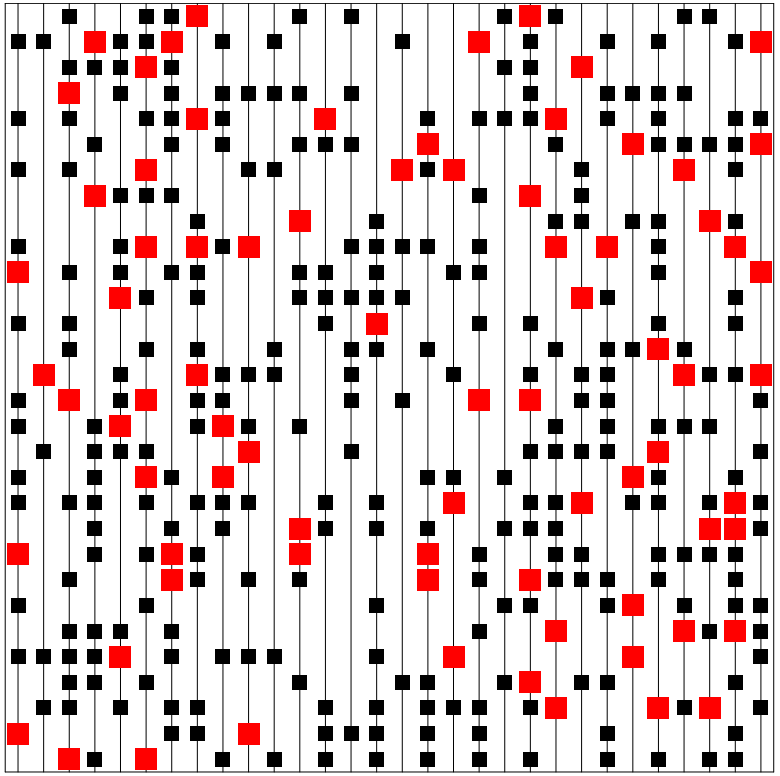
Impact of non-uniform connectivity

Two different network topologies

Biological neurons

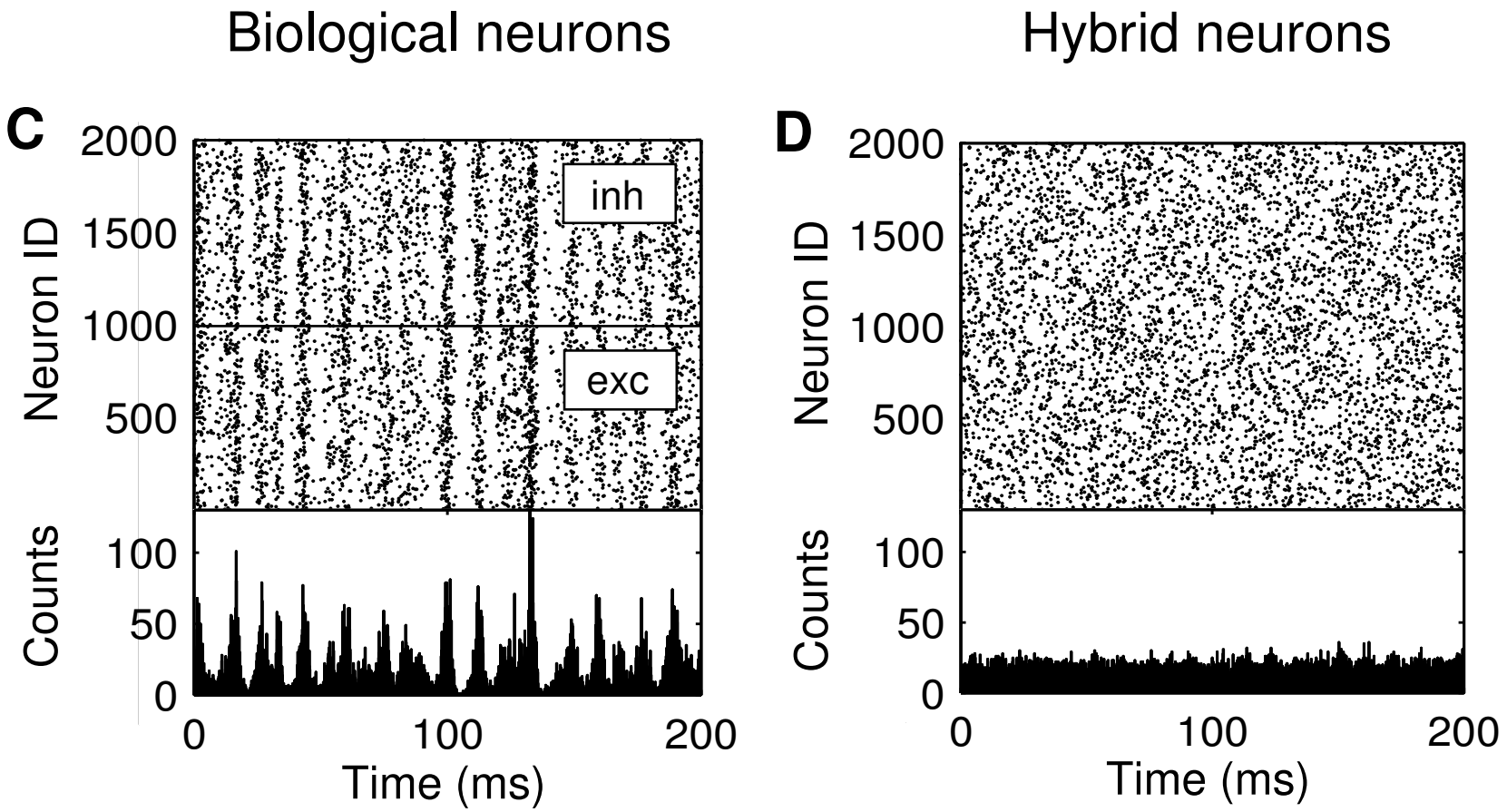


Hybrid neurons



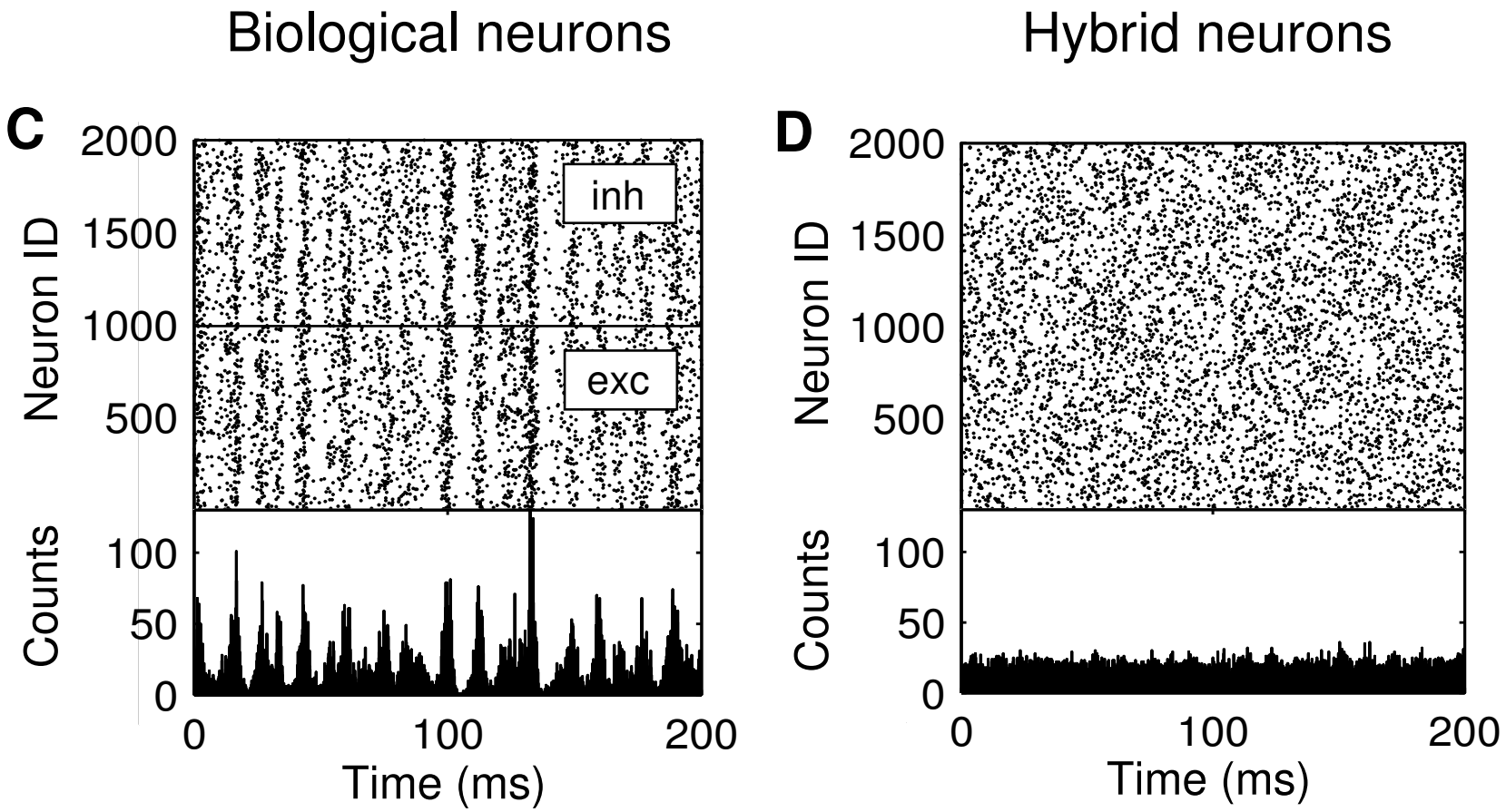
Mean input to individual neurons is identical in both cases!

Population fluctuations depend on correlations



Kriener et al., *Neural Computation*, 2008

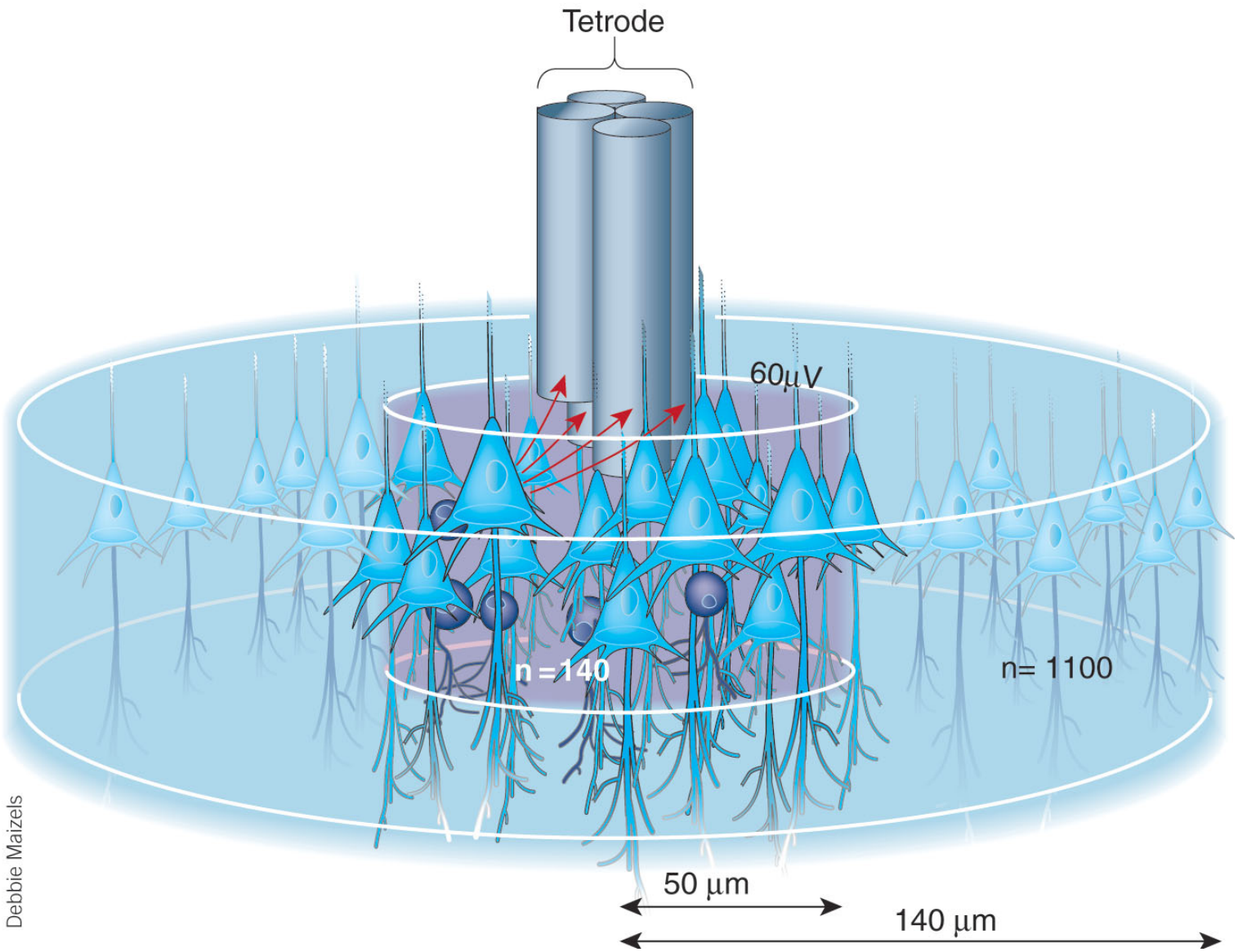
Population fluctuations depend on correlations



$$\mathbb{V}\mathrm{ar}\left[\sum_i X_i\right] = \sum_i \mathbb{V}\mathrm{ar}\left[X_i\right] + \sum_{i \neq j} \mathbb{C}\mathrm{ov}\left[X_i, X_j\right]$$

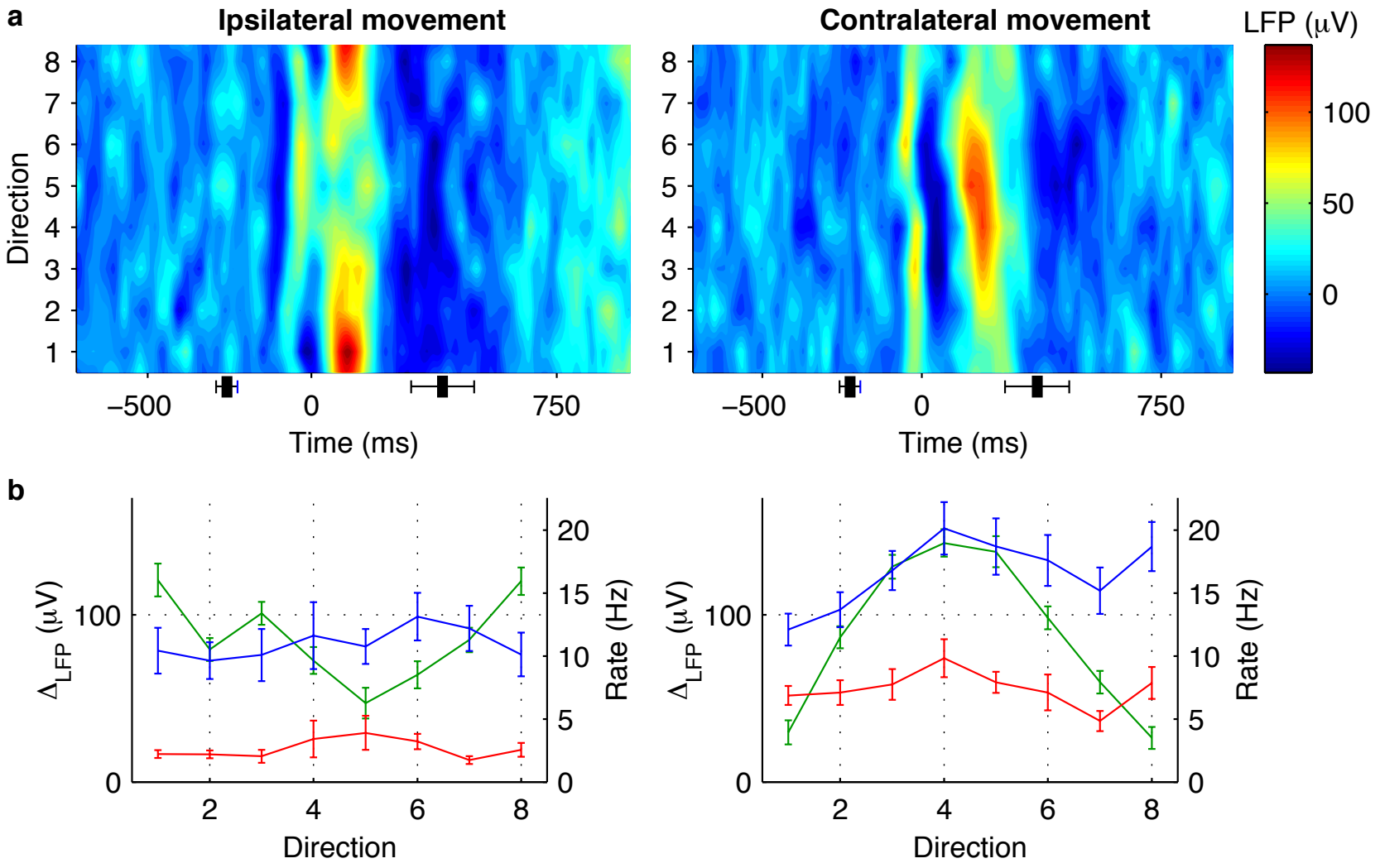
Kriener et al., *Neural Computation*, 2008

Recording from localized neuronal populations



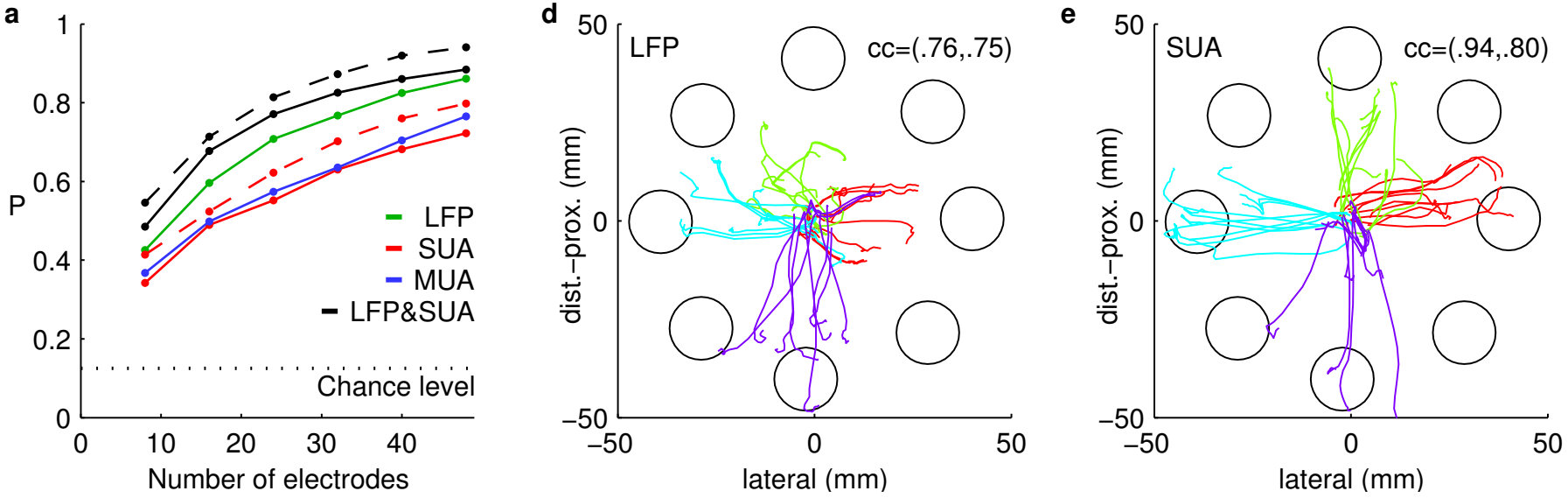
Buzsáki, *Nature Neuroscience*, 2004

Tuning of mass signals for hand movements



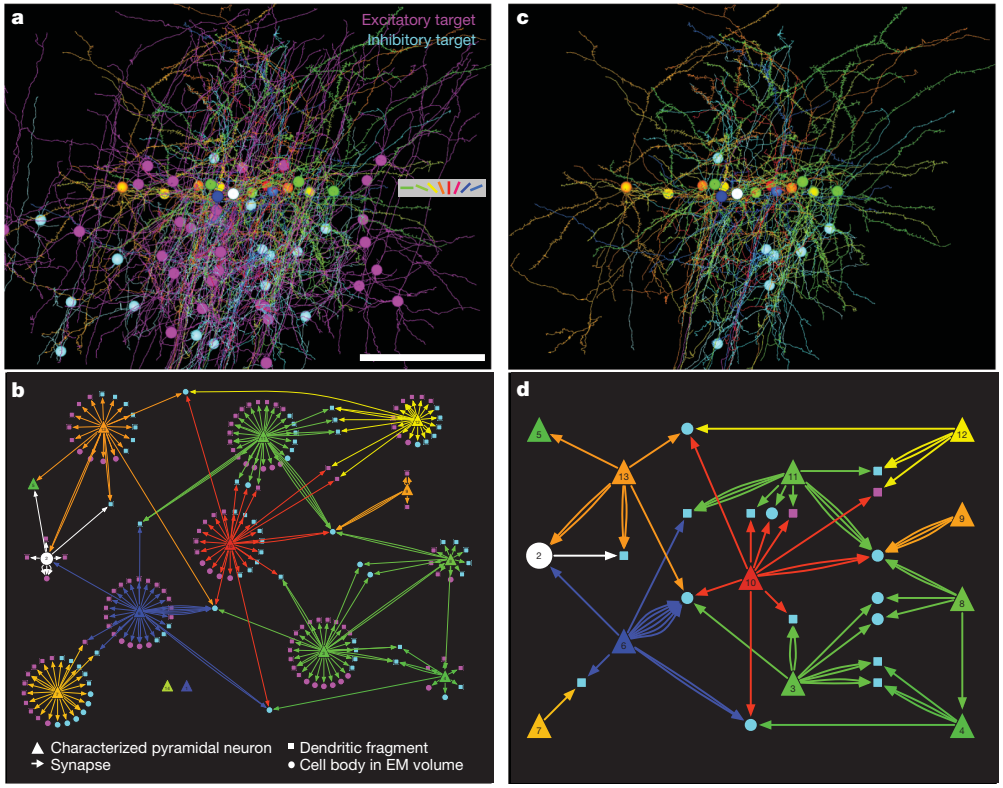
Mehring et al., *Nature Neuroscience*, 2003

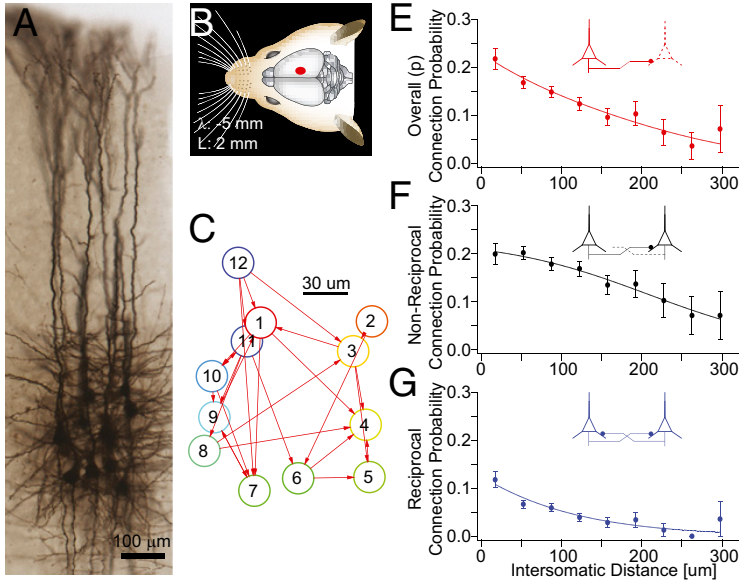
Decoding movements from mass signals

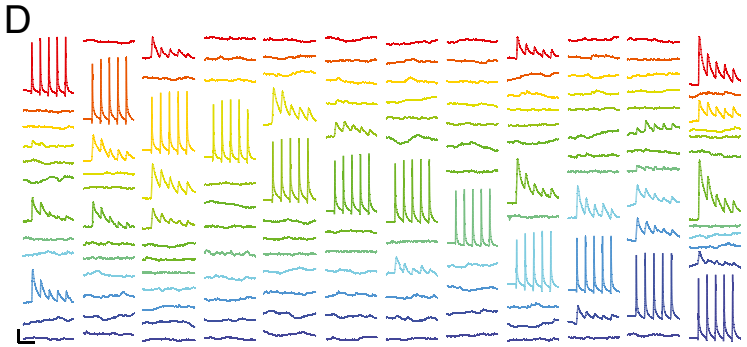


Mehring et al., *Nature Neuroscience*, 2003

Toward the connectome







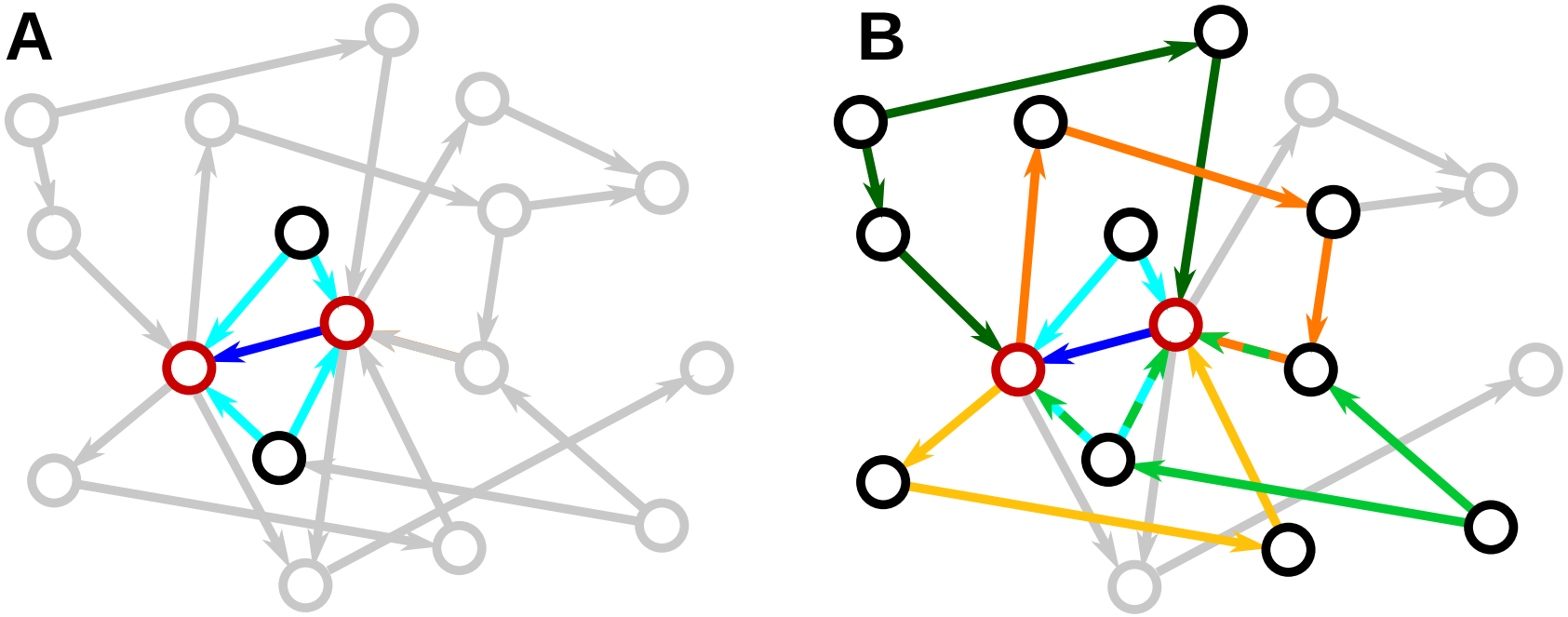
Mouse visual cortex
Calcium imaging *in vivo* + electron microscopy *in vitro*
Bock et al., *Nature*, 2011

Rat somatosensory cortex
12-fold patch recording *in vitro*
Perin et al., *PNAS*, 2011

Questions

- What is the relation between structure and dynamics in strongly recurrent networks of spiking neurons?
- What are the consequences for biological function of these networks?
- Specifically, what is the impact of detailed synaptic network topology on pairwise correlations?
- What is a minimal/suitable mathematical framework to study structure-dynamics relations?
- To which degree is a self-consistent description of correlations in recurrent networks possible?

Connectivity induces correlations



Pernice, Staude, Cardanobile, Rotter, *PLoS Computational Biology* 7(5): e1002059, 2011

Pairwise correlations in recurrent networks

Disentangling multi-synaptic pathways

Impact of non-uniform connectivity

The Hawkes process

A network of N nodes (neurons) is described in terms of

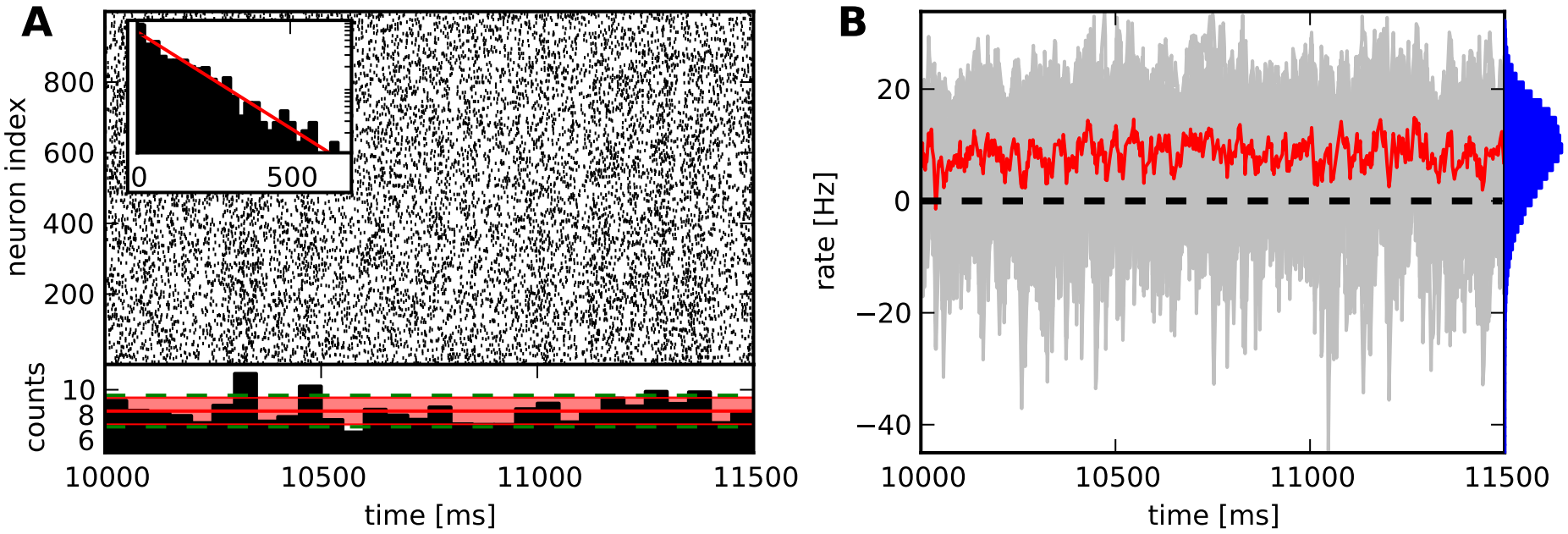
spike trains	$s_i(t) = \sum_k \delta(t - t_k^i)$
firing rates	$y_i(t) = \langle s_i(t) \rangle$
external inputs	$y_0 \geq 0$
interaction kernels	$G(t) = \big(g_{ij}(t)\big).$

Its dynamics is defined in terms of the linear integral equation

$$y(t) = y_0 + \int_{-\infty}^{\infty} G(\tau) s(t - \tau)\, d\tau = y_0 + (G * s)(t).$$

Hawkes, 1971

Example: Balanced random networks



Pernice et al., 2011

Stationary firing rates

Assuming stationarity $y(t) = y$, one has

$$y = y_0 + \int_{-\infty}^{\infty} G(\tau) y \, d\tau = y_0 + Gy$$

with

$$G = \int_{-\infty}^{\infty} G(\tau) \, d\tau.$$

If the matrix $\mathbb{1} - G$ is invertible we have

$$y = [\mathbb{1} - G]^{-1} y_0.$$

If, in addition, $|\lambda| < 1$ for all eigenvalues λ of G, the geometric series expansion suggests a decomposition into contributions of recurrent pathways of all orders

$$y = [\mathbb{1} - G]^{-1} y_0 = [\sum_{n=0}^{\infty} G^n] y_0 = \sum_{n=0}^{\infty} G^n y_0.$$

Regular networks

Assume that

$$\int_{-\infty}^{\infty} G_{ij}(t)\,dt = \begin{cases} g_E > 0 & \text{for an excitatory synapse} \\ 0 & \text{if there is no synapse} \\ g_I < 0 & \text{for an inhibitory synapse.} \end{cases}$$

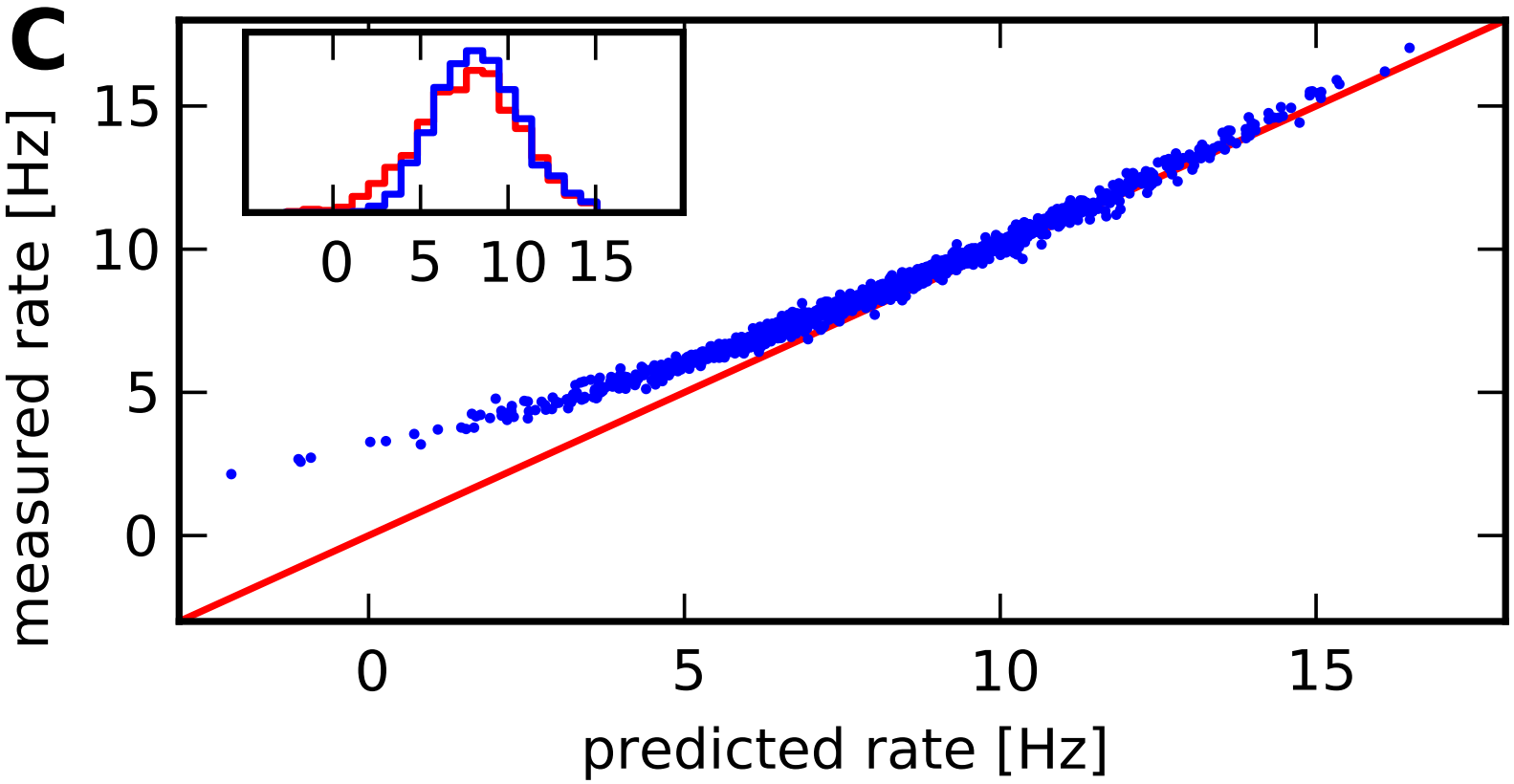
Assume that each neuron receives k_E excitatory inputs and k_I inhibitory inputs. We then obtain for $g = k_E g_E + k_I g_I$

$$\sum_j [\delta_{ij} + g_{ij} + g_{ij}^2 + \ldots] = 1 + \sum_j g_{ij} + \sum_k g_{ik} \sum_j g_{kj} + \ldots = \sum_{n=0}^{\infty} g^n.$$

If $|g| < 1$ and all neurons receive the same external input y_0, they all respond with the same rate

$$\bar{y} = \frac{y_0}{1-g}.$$

Firing rates in balanced random networks



Eigenvalue spectrum of a random network

The complex eigenvalue spectrum of a random matrix with columns that are either non-negative or non-positive typically has two components

1. a single real eigenvalue

$$g = k_E g_E + k_I g_I$$

   that corresponds to the mean input into each neuron. It can be positive or negative;

2. a circular bulk of complex eigenvalues centered at the origin, and asymptotically bounded by the radius

$$\rho^2 = [k_E g_E^2 + k_I g_I^2]\Big[1 - \frac{k_E + k_I}{N}\Big]$$

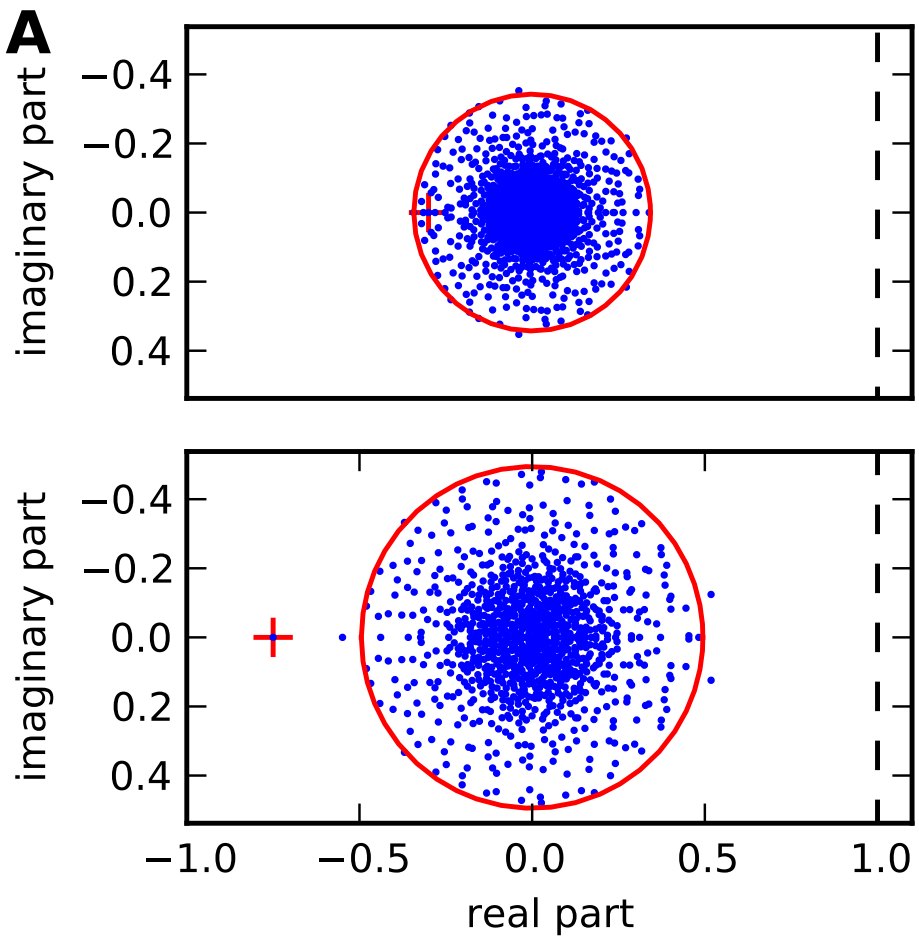
   It corresponds to the input variance induced by the connectivity matrix.

Rajan & Abbott, 2006

Stability of balanced random networks

A Hawkes process with integrated kernel matrix G is dynamically stable, if $|\lambda| < 1$ for all eigenvalues λ of G.

Shown are the eigenvalue spectra for two different stable random networks with connection probabilities $p = \frac{k_E + k_I}{N} = 0.1$ and $p = 0.25$.



Stationary correlations

Assuming joint stationarity, the pulse-coded interactions are best quantified by the covariance functions

$$c_{ij}(\tau) = \mathbb{C}\mathrm{ov}\big[s_i(t+\tau), s_j(t)\big] = \big\langle s_i(t) s_j(t+\tau)\big\rangle - \big\langle s_i(t)\big\rangle\big\langle s_j(t)\big\rangle.$$

Using Fourier transforms

$$\hat{f}(\omega) = \int_{-\infty}^{\infty} f(t) e^{-i\omega t}\, dt \qquad \text{and} \qquad \hat{f}(0) = \int_{-\infty}^{\infty} f(t)\, dt.$$

one obtains the expression

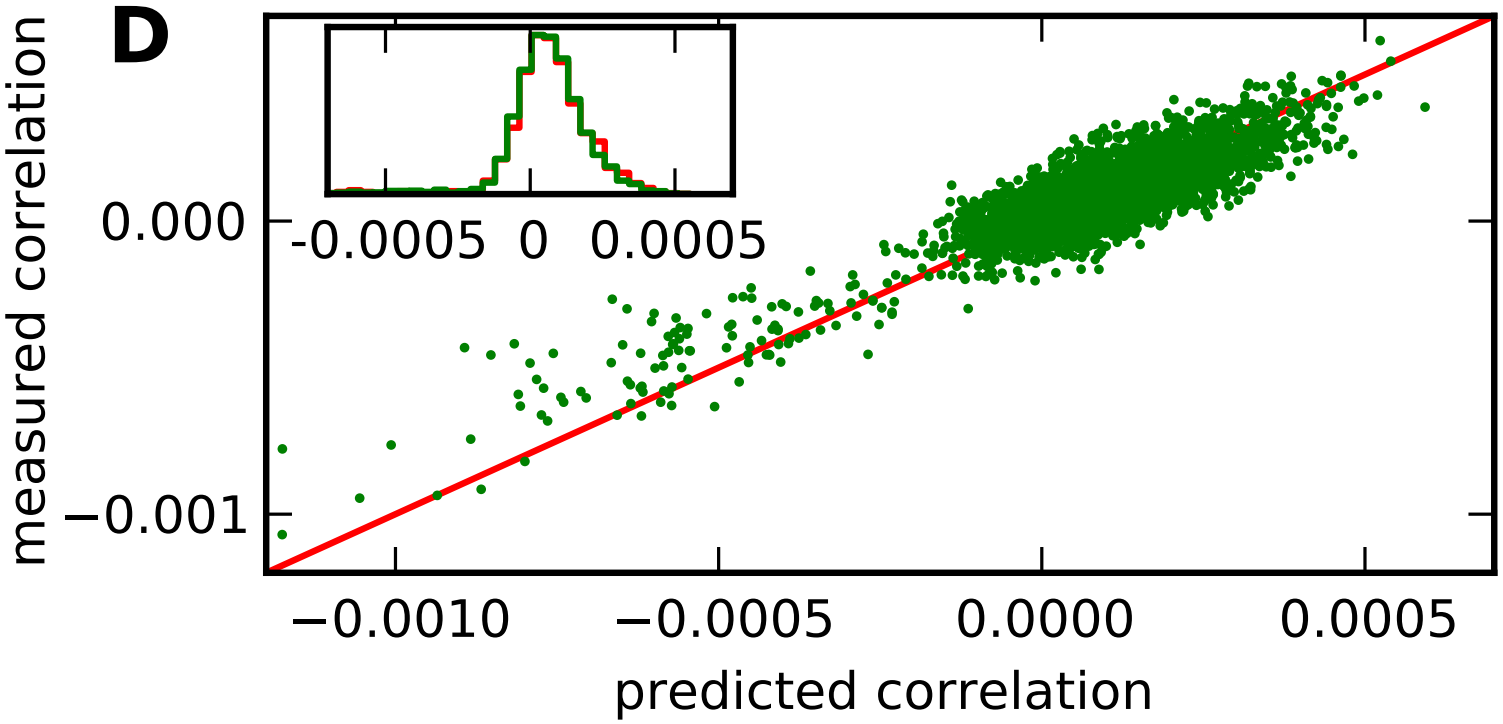
$$\hat{C}(\omega) = \big[\mathbb{1} - \hat{G}(\omega)\big]^{-1} Y \big[\mathbb{1} - \hat{G}^T(\omega)\big]^{-1}.$$

where $Y = \mathrm{diag}(y)$. For the integrated covariances, one gets

$$C = \hat{C}(0) = [\mathbb{1} - G]^{-1} Y [\mathbb{1} - G^T]^{-1}.$$

Hawkes, 1971

Example: Balanced random networks



Expanding correlations

Assuming $|\lambda| < 1$ for all eigenvalues λ of G, the expansion

$$[\mathbb{1} - G]^{-1} = \sum_{n=0}^{\infty} G^n$$

can be exploited to re-write the covariance matrix

$$C = [\mathbb{1} - G]^{-1} Y [\mathbb{1} - G^T]^{-1} = [\sum_{n=0}^{\infty} G^n] Y [\sum_{m=0}^{\infty} (G^T)^m]$$
$$= \sum_{nm} G^n Y (G^T)^m = \sum_{nm} G^{(n,m)}$$

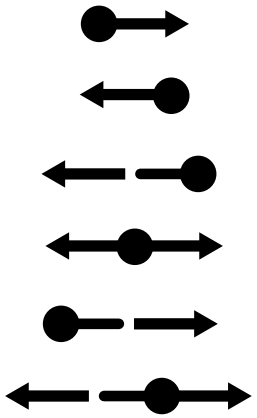
with matrix elements $g_{ij}^{(n,m)}$. The parts of the sum correspond to shared input mediated by various multi-synaptic pathways.

Pernice et al., 2011

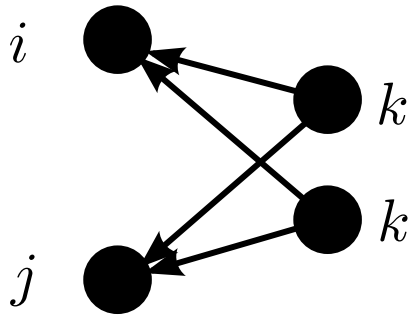
Shared input motifs contributing to correlations

A

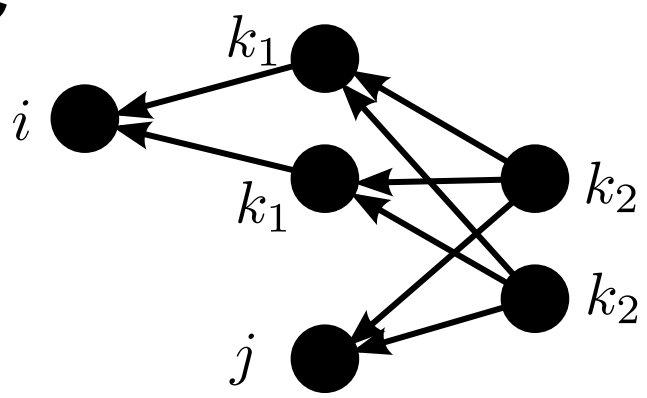
Matrix $G^{(n,m)}$	Elements $g_{ij}^{(n,m)}$	Symbol for $g^{(n,m)}$
GY	$g_{ij}y_{jj}$	
YG^T	$y_{ii}g_{ji}$	
G^2Y	$\sum_k g_{ik}g_{kj}y_{jj}$	
GYG^T	$\sum_k g_{ik}y_{kk}g_{jk}$	
$Y(G^T)^2$	$\sum_k y_{ii}g_{ki}g_{jk}$	
G^2YG^T	$\sum_{k_1,k_2} g_{ik_1}g_{k_1k_2}y_{k_2k_2}g_{jk_2}$	



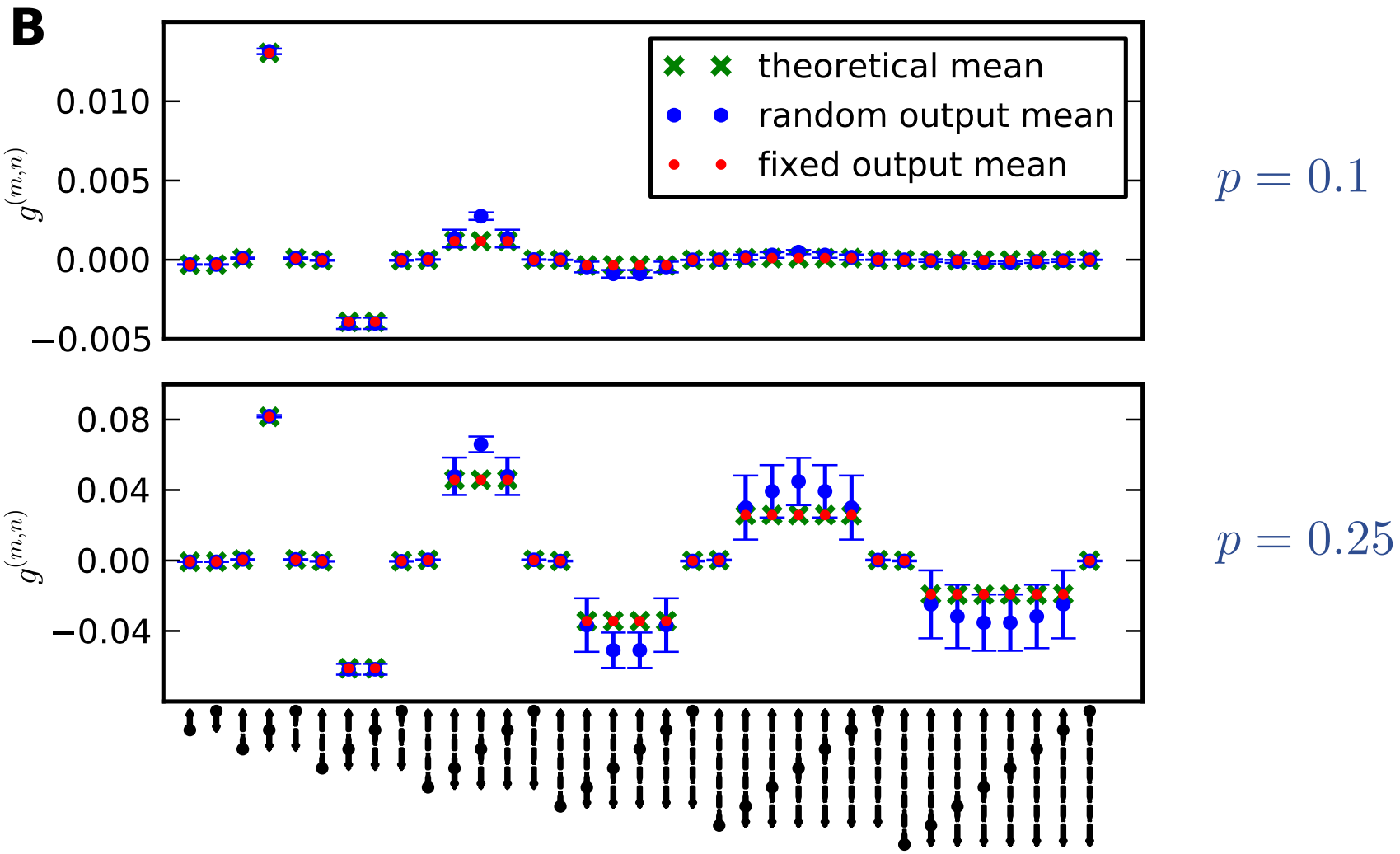
B



C



Negative feedback decorrelates activity



In networks with dominant recurrent inhibition, motifs of uneven order $m + n$ contribute negatively.

Fluctuations of population activity

Fluctuations of stationary population activity

$$S(t) = \sum_i s_i(t)$$

can be expanded into contributions from all auto- and cross-covariances

$$\mathbb{C}\mathrm{ov}\big[S(t+\tau), S(t)\big] = \sum_{ij} \mathbb{C}\mathrm{ov}\big[s_i(t+\tau), s_j(t)\big].$$

For a Hawkes process, we can exploit the power series expansion for the matrix of integrated covariances

$$\sum_{ij} C_{ij} = \sum_{ij} \sum_{nm} g_{ij}^{(n,m)} = \sum_{nm} \sum_{ij} g_{ij}^{(n,m)}.$$

Example: Balanced random network

Let again $g = k_E g_E + k_I g_I$ with $|g| < 1$ be the total input to a neuron which is part of a balanced random network. Writing $\eta = (k_E g_E^2 + k_I g_I^2)(k_E + k_I)/N$, we obtain

$$\sum_{ij} g_{ij}^{(n,m)} = \eta \bar{y} g^{n+m-2}$$

and, therefore

$$\sum_{ij} C_{ij} = \sum_{nm} \eta \bar{y} g^{n+m-2} = \sum_{k} \eta \bar{y} (k+1) g^{k-2} = \frac{\eta \bar{y}}{[g(1-g)]^2}.$$

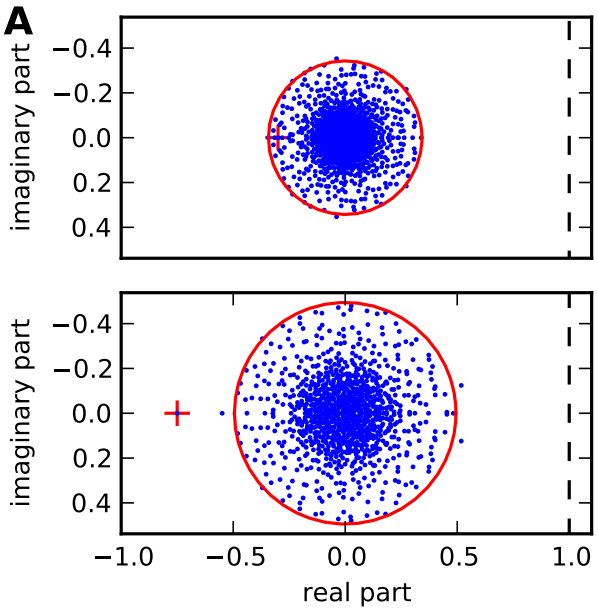
For networks with $g < 0$, motifs of uneven order $m + n$ always contribute negatively to the total correlation. In this case, the denominator $[g(1-g)]^2$ accounts for the strong decorrelation typically observed in such networks.

Pairwise correlations in recurrent networks

Disentangling multi-synaptic pathways

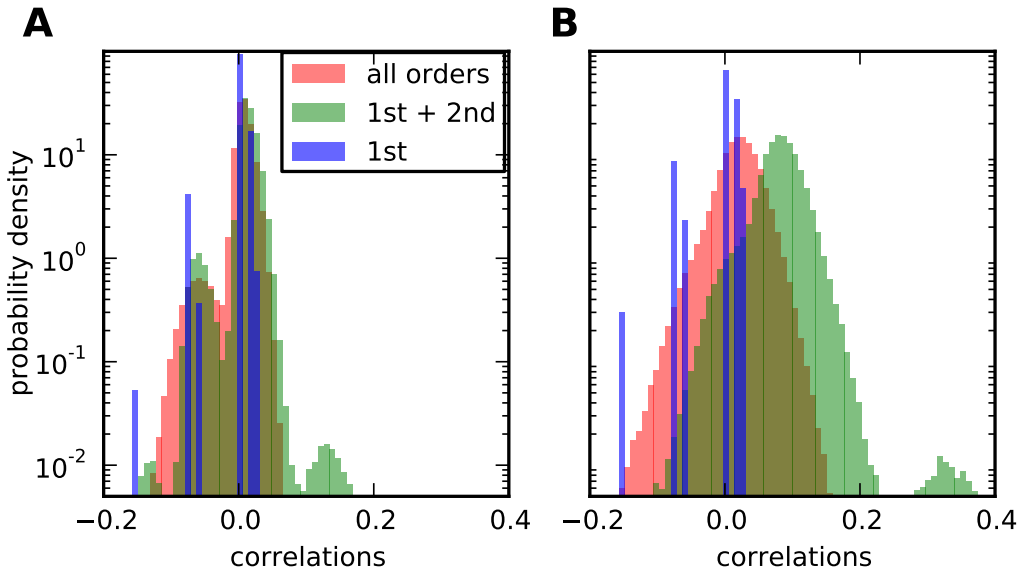
Impact of non-uniform connectivity

Some effects of increased recurrence



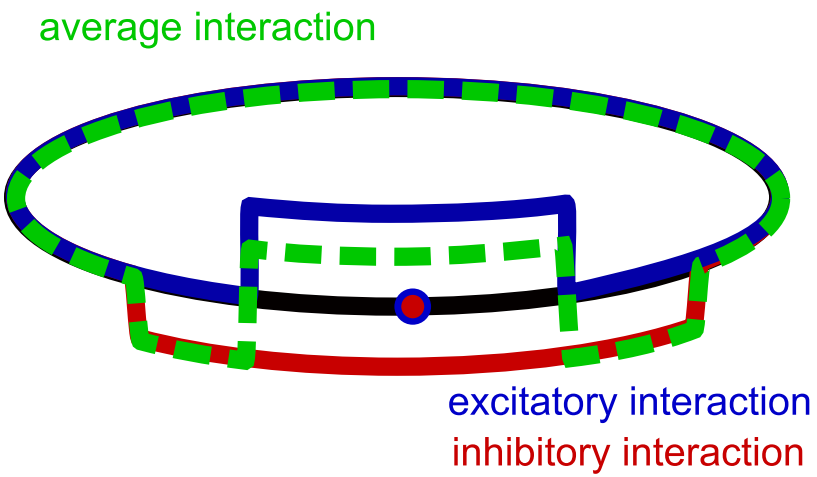
eigenvalues of G

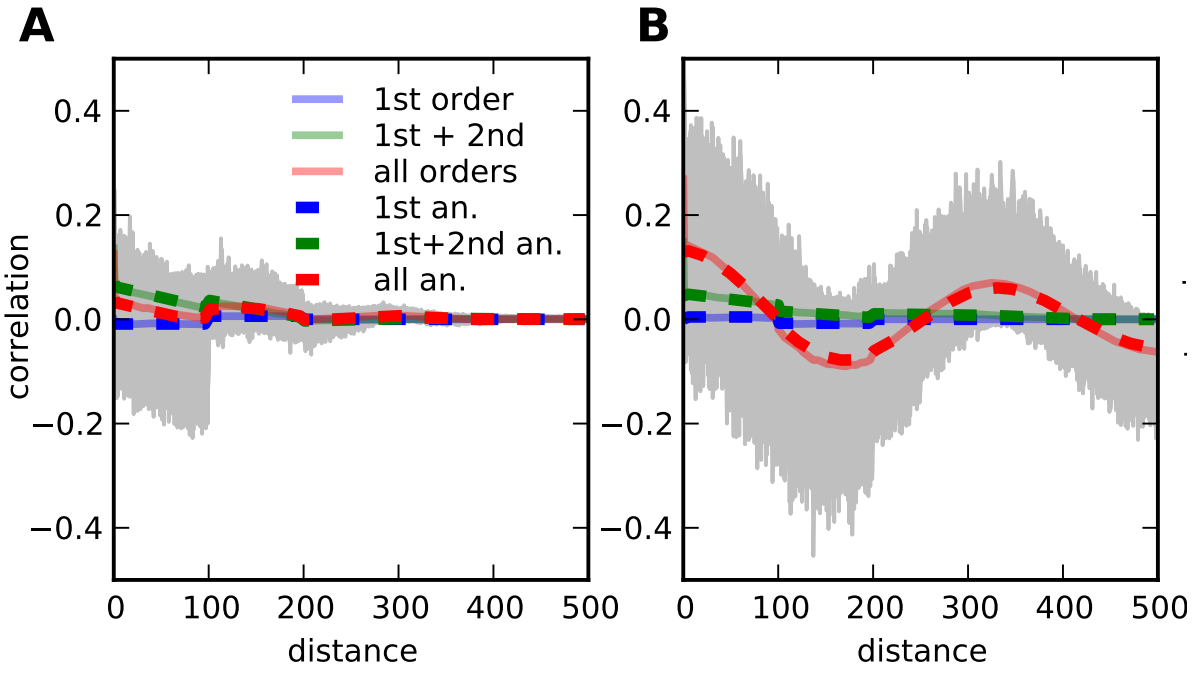
$p = 0.1$ $p = 0.25$



distribution of correlations

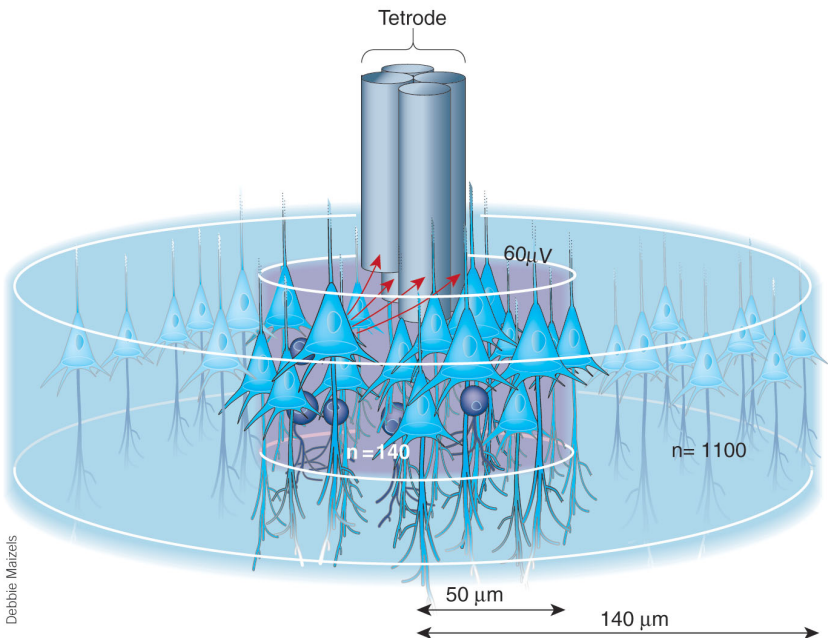
Local inhibition vs. local excitation

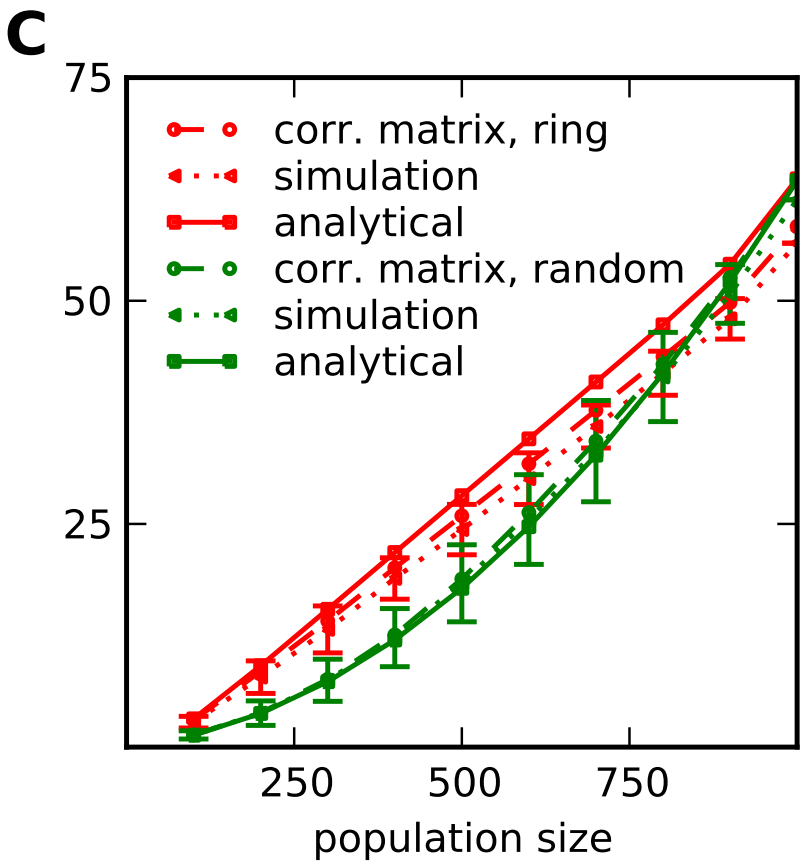




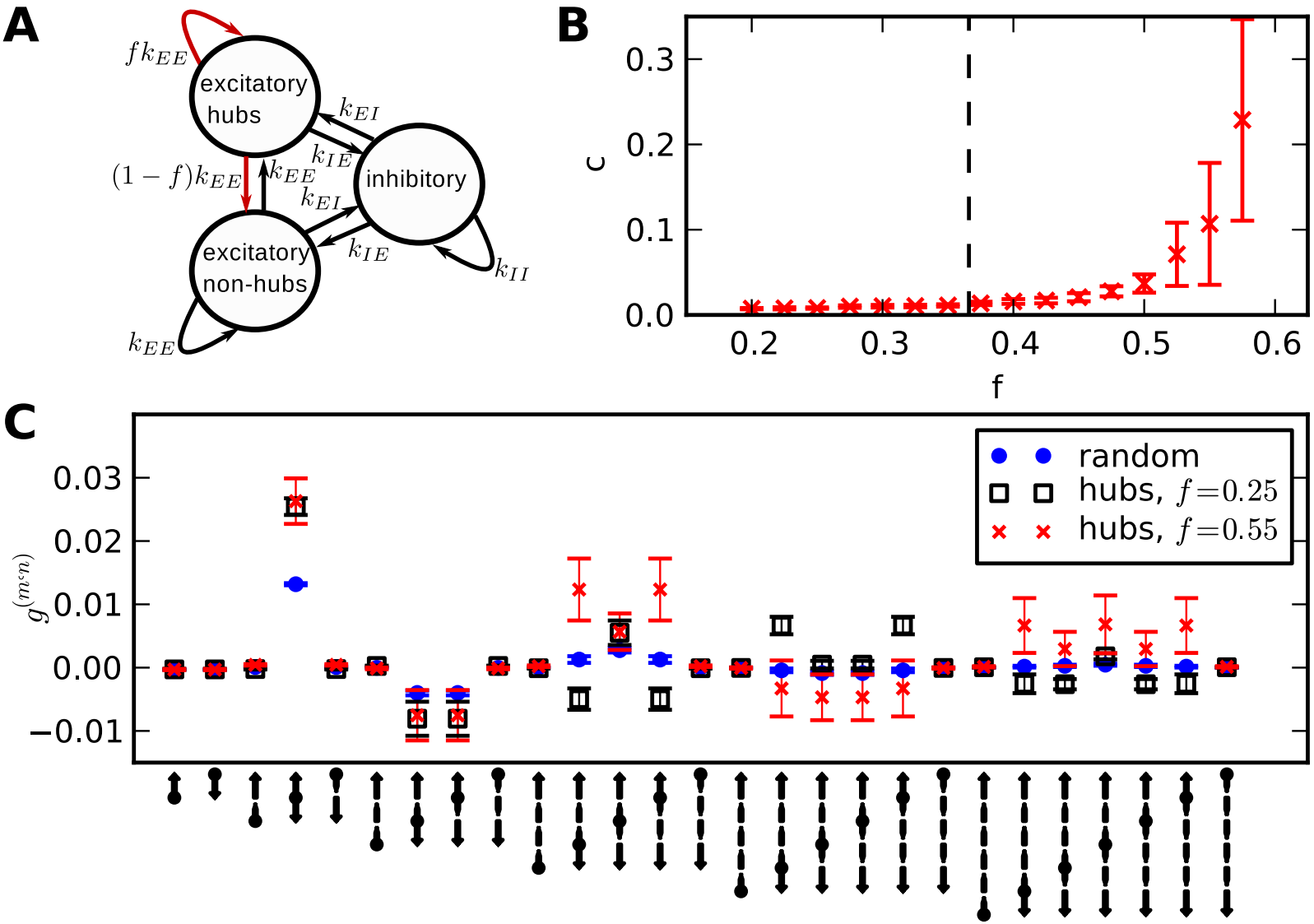
$\sigma_I = 100, \sigma_E = 200$ $\sigma_I = 200, \sigma_E = 100$

Fluctuations of local populations

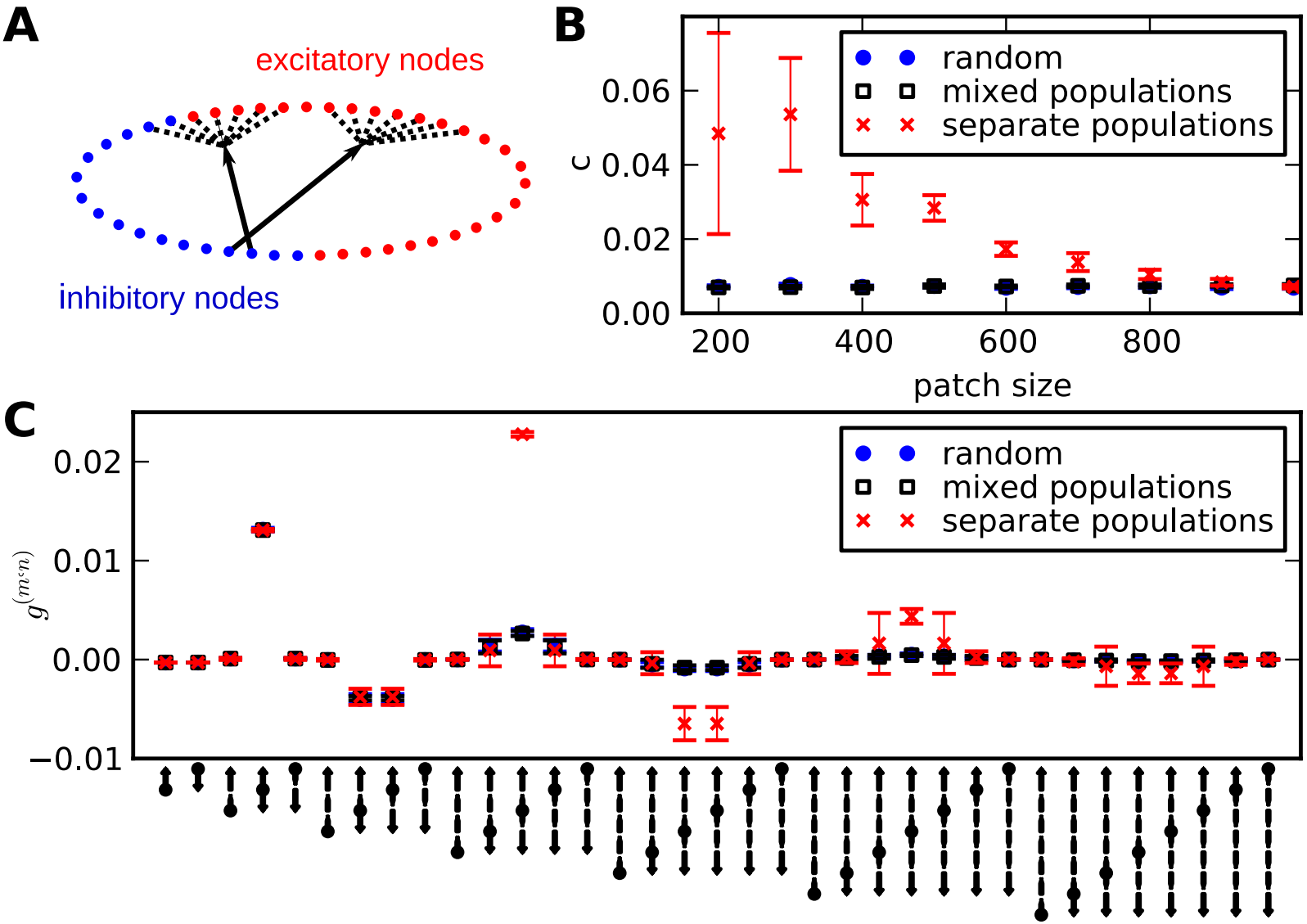




Non-regular networks: cliques of excitatory hubs



Patchy and/or cell-type specific connectivity



Discussion

- Pairwise correlations have a large impact on the fluctuations of population signals like LFP, ECoG, EEG.
- Linear Hawkes processes are good models for networks of irregularly spiking neurons.
- Dynamic properties of networks with arbitrary topology can be inferred by matrix algebra.
- The contributions of individual multi-synaptic pathways (network motifs) to correlations can be computed in a self-consistent manner.
- In general, many details of the connectivity matrix have an impact on the covariance matrix.
- By measuring the interaction kernels, nonlinear neuronal networks can be approximated by Hawkes processes.

Ad	Aertsen
Stefano	Cardanobile
Simone	Cardoso de Oliveira
Moritz	Deger
Markus	Diesmann
Moritz	Helias
Birgit	Kriener
Arvind	Kumar
Carsten	Mehring
Volker	Pernice
Jörn	Rickert
Benjamin	Staude
Tom	Tetzlaff
Eilon	Vaadia

Thanks!