Neuronal Variability and Co-variability in sensory cortices.

Jaime de la Rocha

Mean-field methods and multiscale analysis of neuronal populations
3-7 October 2011, CIRM, Marseille

Current work in collaboration with:

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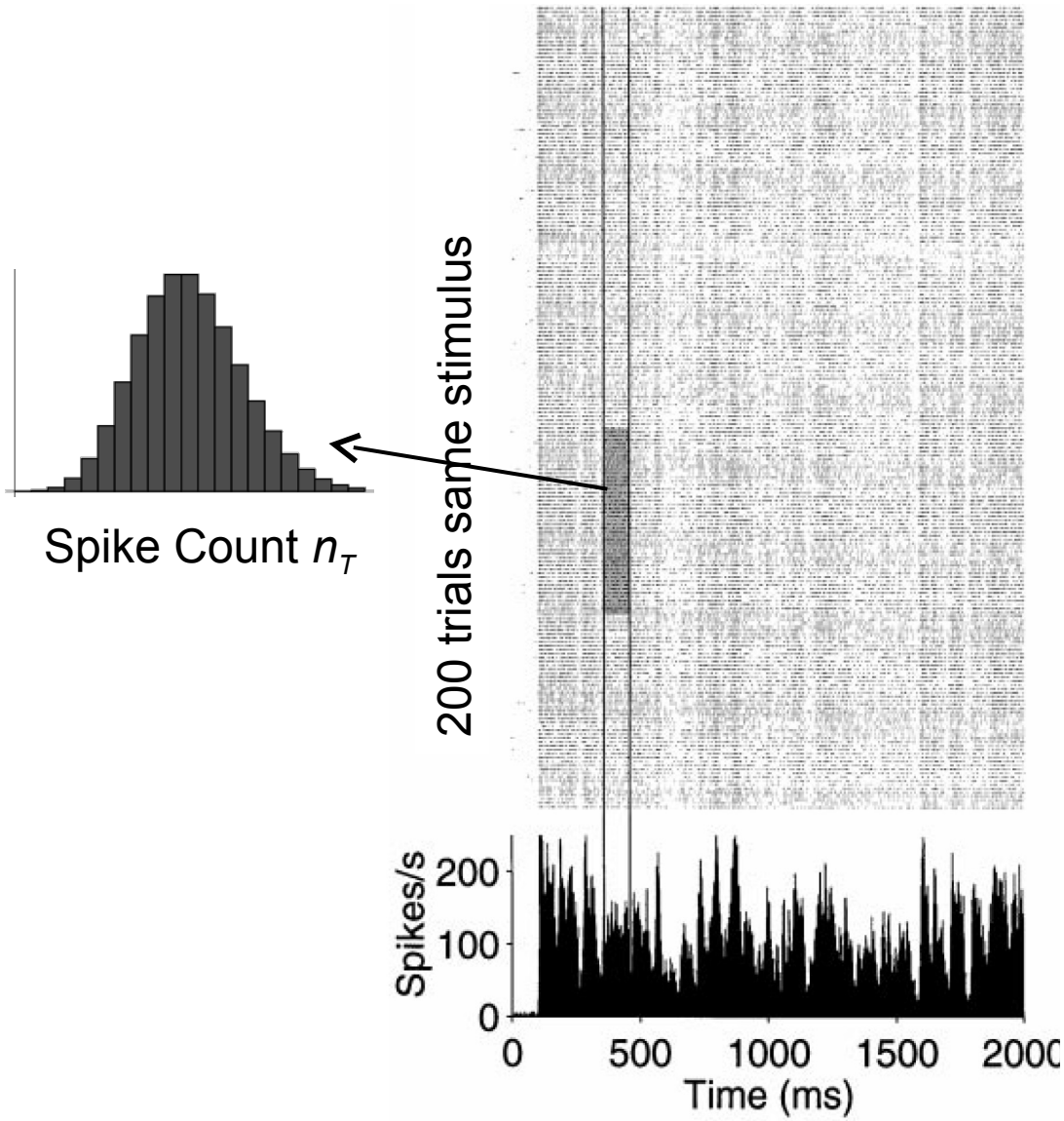
Raimundo Leong (Champalimaud Foundation, Lisbon).

Klaus Wimmer (IDIBAPS, Barcelona)
Albert Compte (IDIBAPS, Barcelona)
Alex Roxin (IDIBAPS/CRM, Barcelona).

Outline

- Intro: cortical variability and co-variability and the effect of sensory stimulation.
- Mechanisms producing single neuronal variability and pair-wise correlations.
- Asynchronous state in a recurrent randomly connected network.
- Mean field model of a competitive network.
- Spiking simulations.
- Conclusions.

Neural responses show trial-to-trial variability



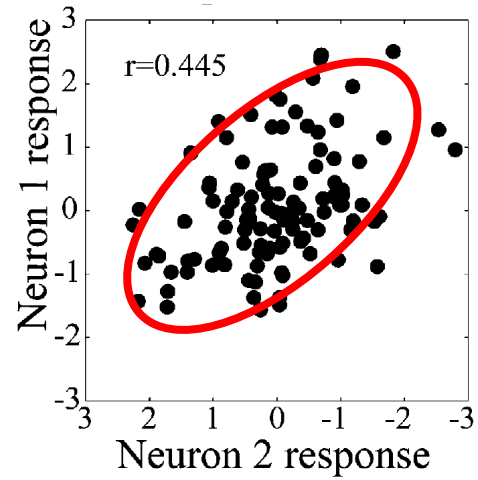
Shadlen & Newsome '98

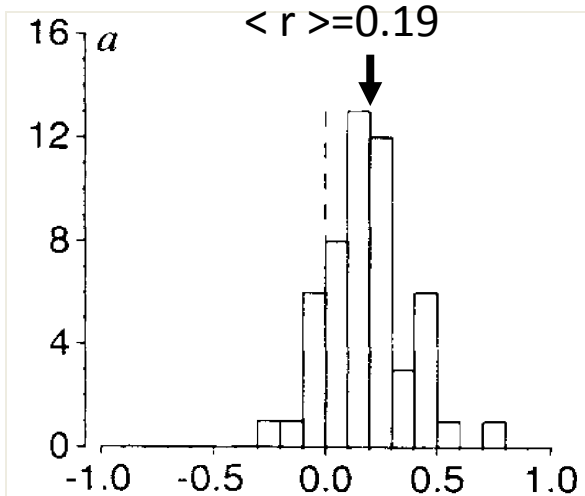
Neural responses are correlated

Correlation coefficient

spike count n_i:

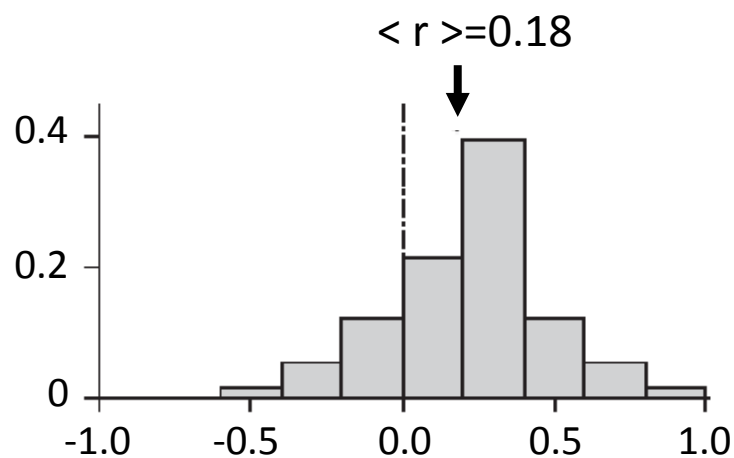
$$r_{12} = \frac{Cov(n_1 n_2)}{\sqrt{Var(n_1)Var(n_2)}}$$





Monkey MT awake

Zohari et al. '94



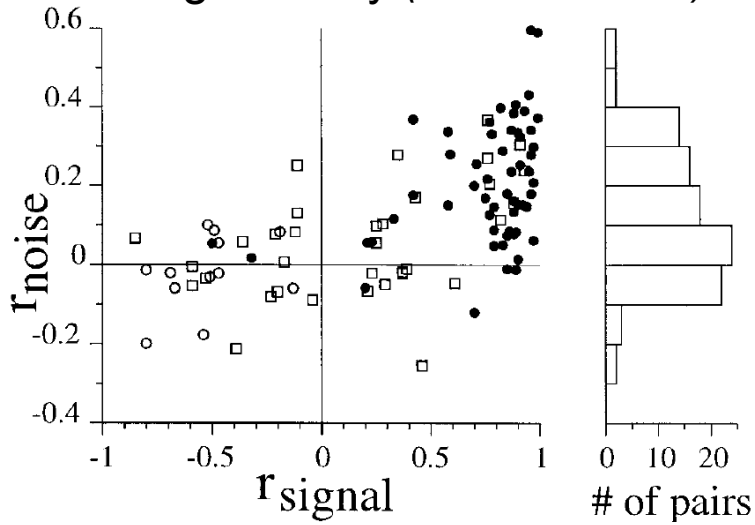
Monkey V1 anesthetized

Kohn & Smith, 2005

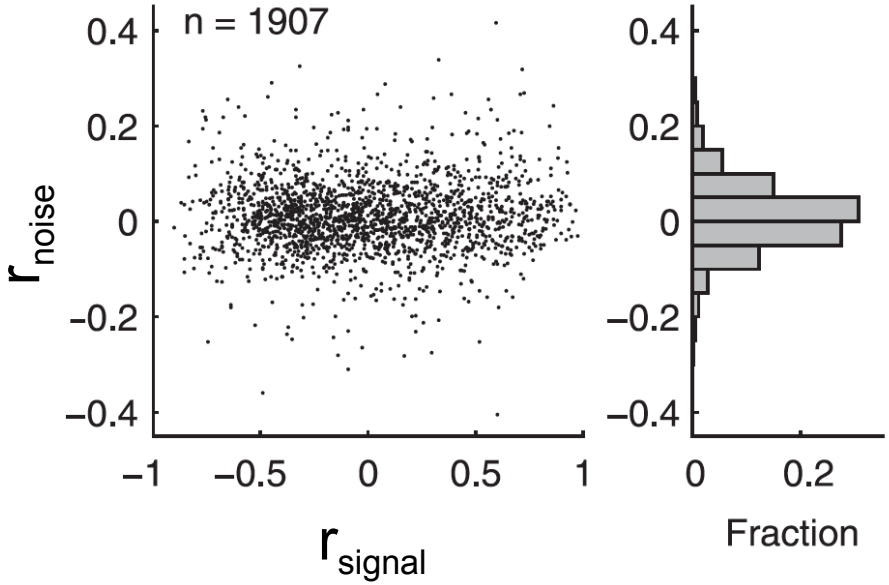
Correlation coefficient r_{ij}

Structure of correlations across the network

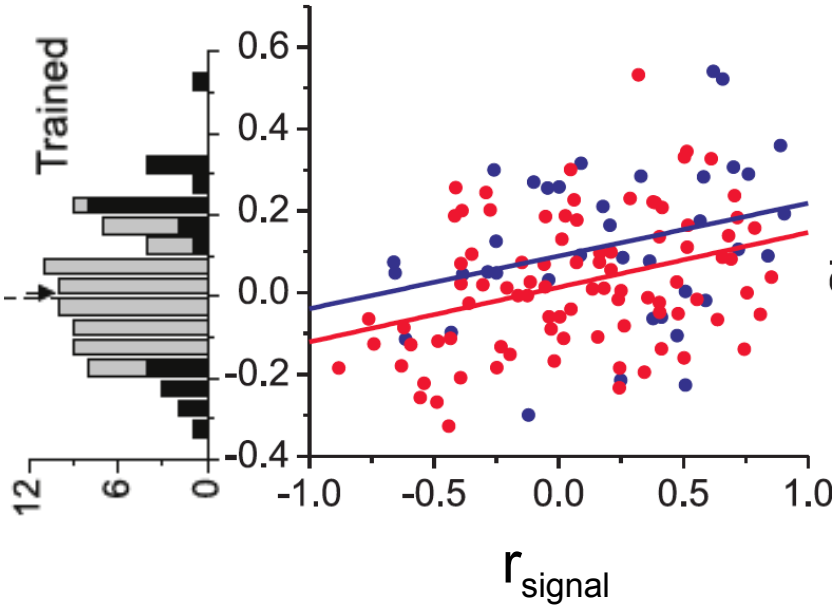
MT behaving monkey *(Bair et al 2001)*



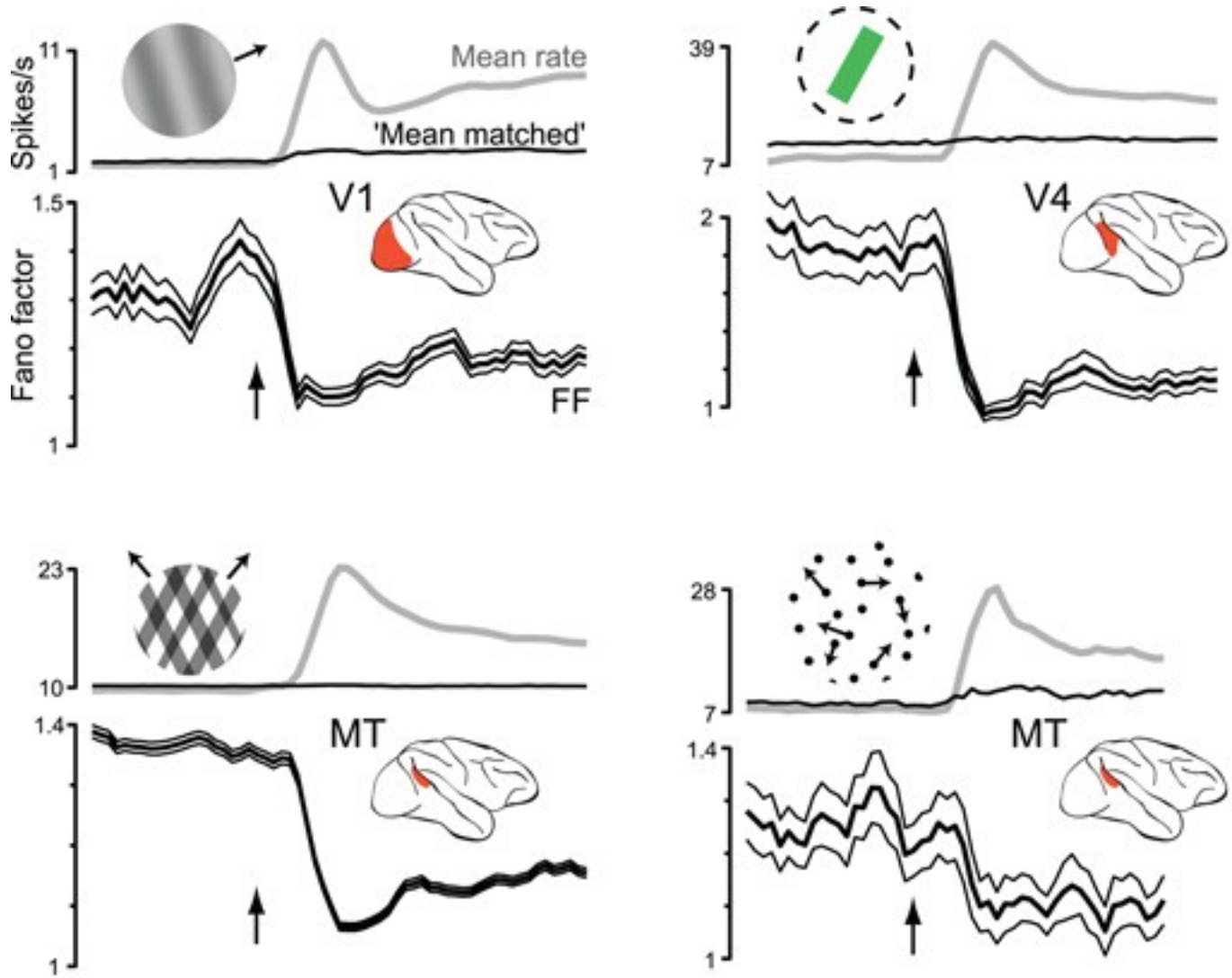
V1 awake monkey (*Ecker et al 2010*)



MSTd behaving monkey (*Gu et al 2011*)



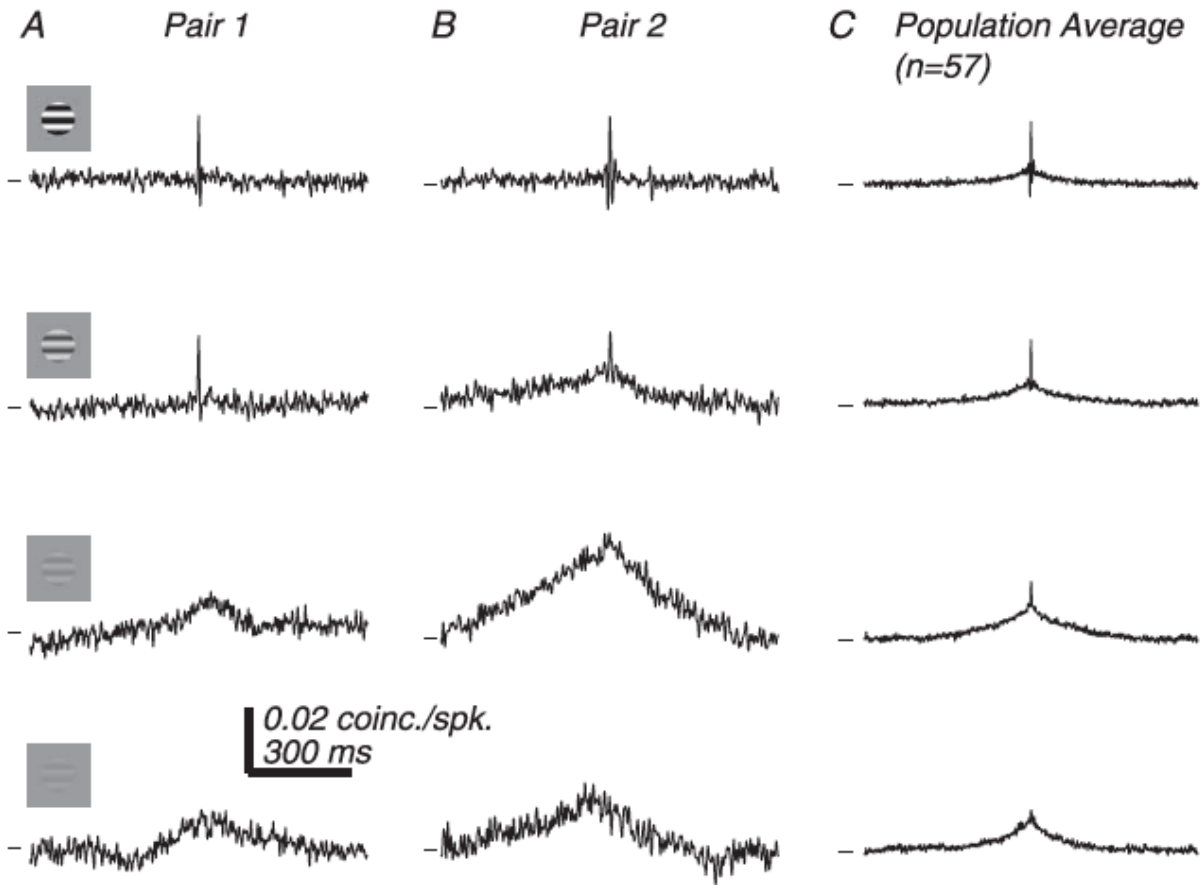
Impact of stimulus on single neuronal variability



Churchland et al 2010

Impact of stimulus on pair-wise correlations

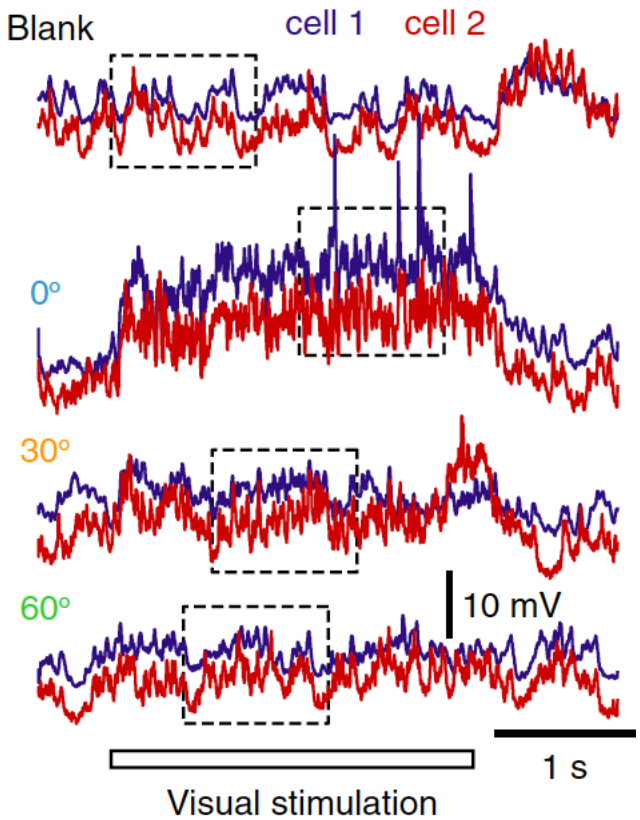
V1 anesthetized monkey.

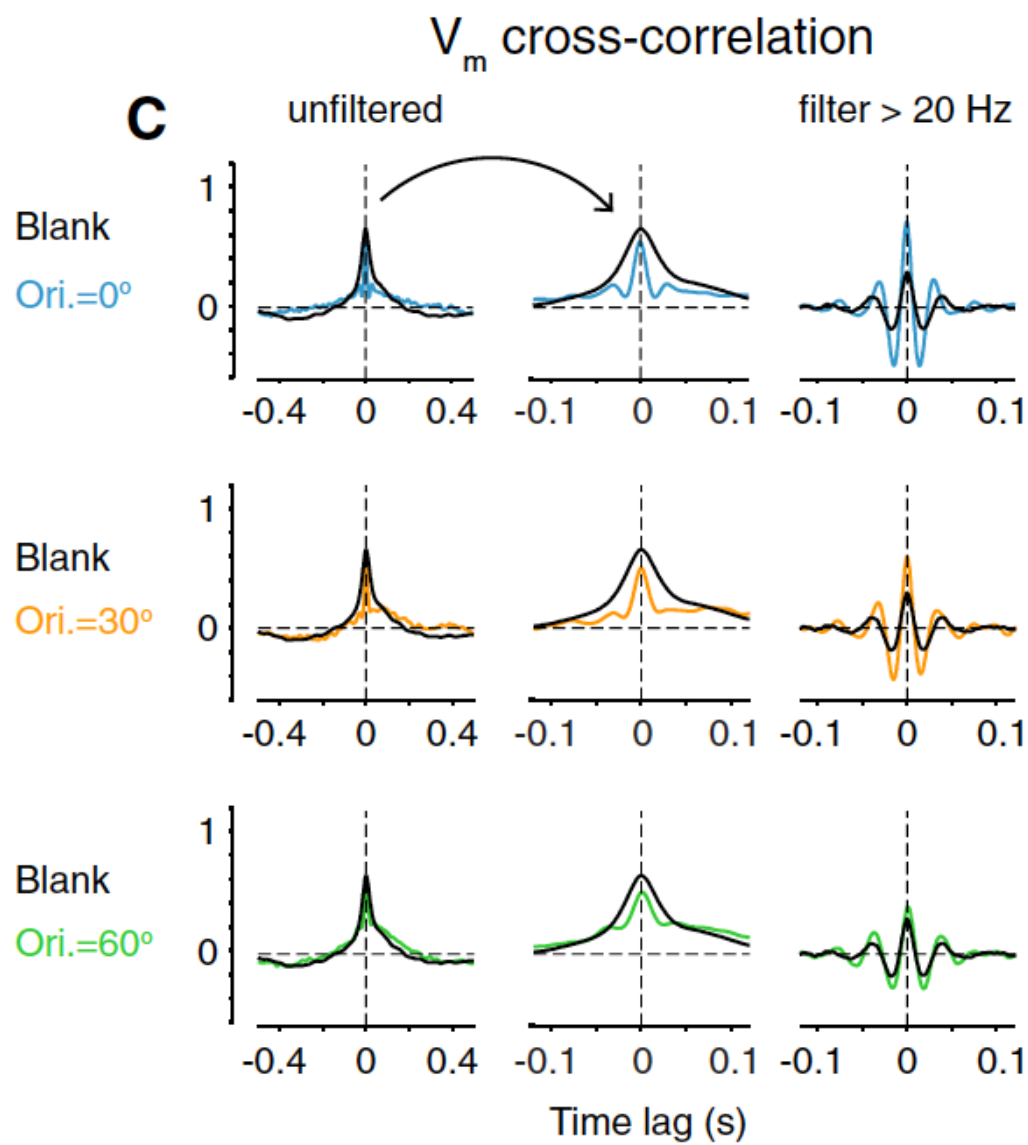


Kohn & Smith, 2005; Nahaus et al 2008.

Impact of stimulus on pair-wise correlations

V1 anesthetized cat.





Yu & Ferster, 2010.

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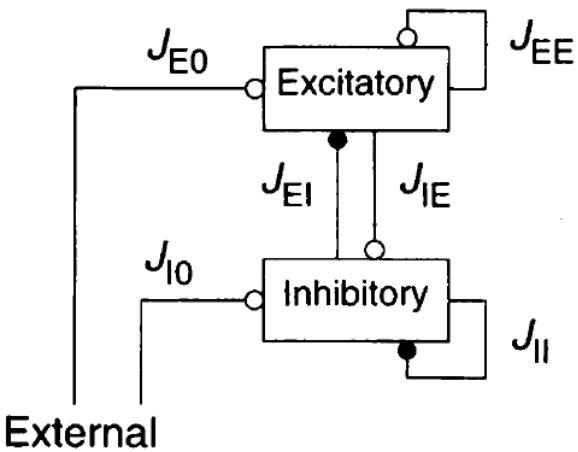
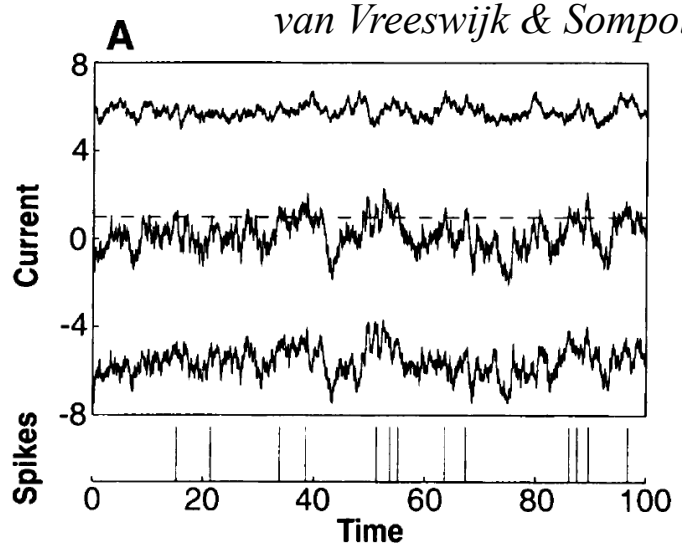
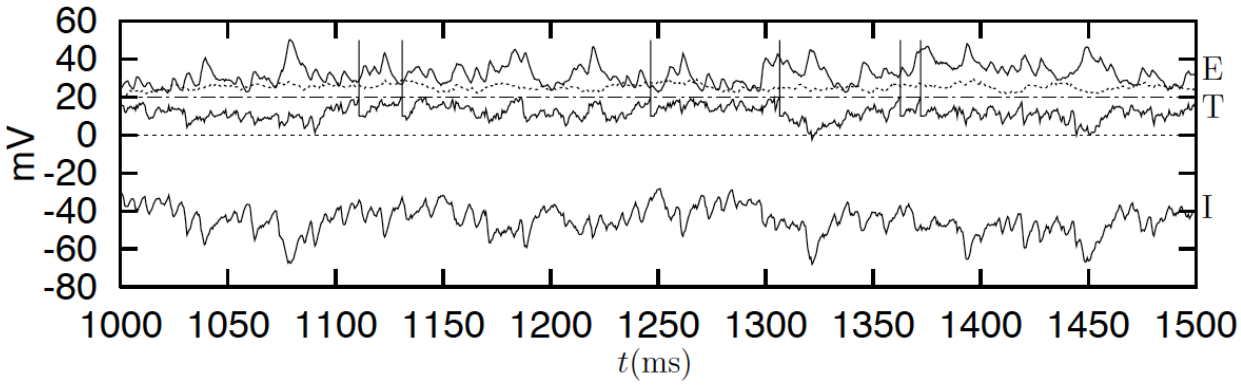
Mechanisms behind neuronal variability: balanced state



van Vreeswijk & Sompolinsky 1996



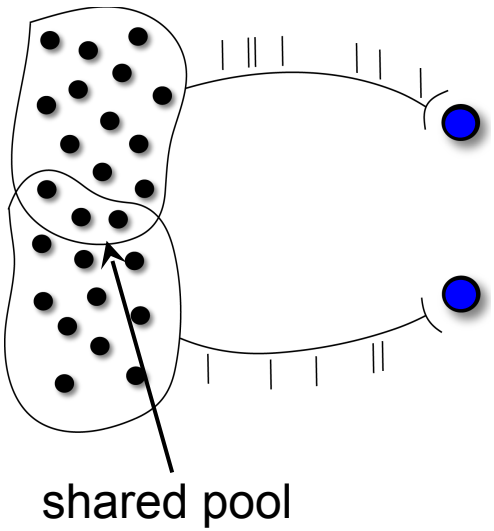
Amit & Brunel 1997

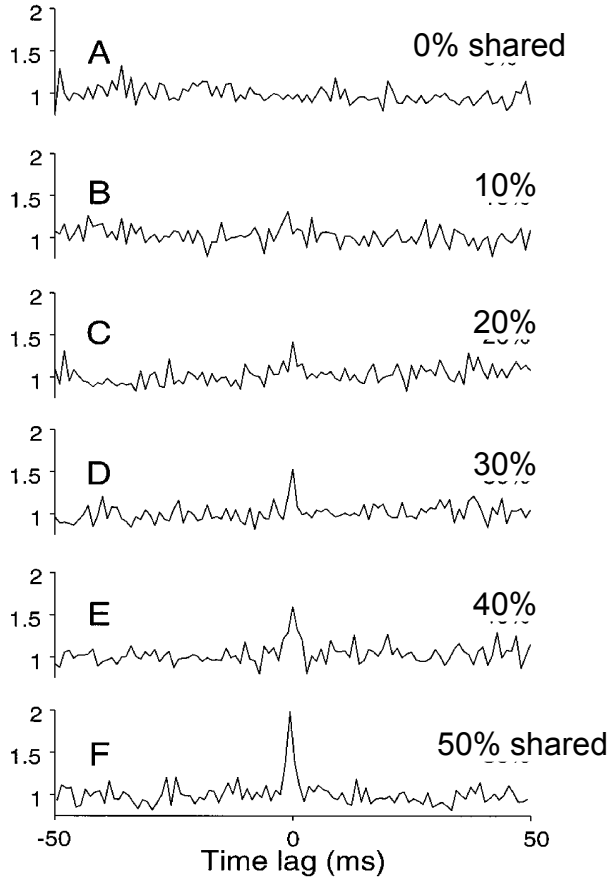


Banerjee 2007; Banerjee, Series & Pouget 2007; London et al 2010;

Shared input causes correlations.

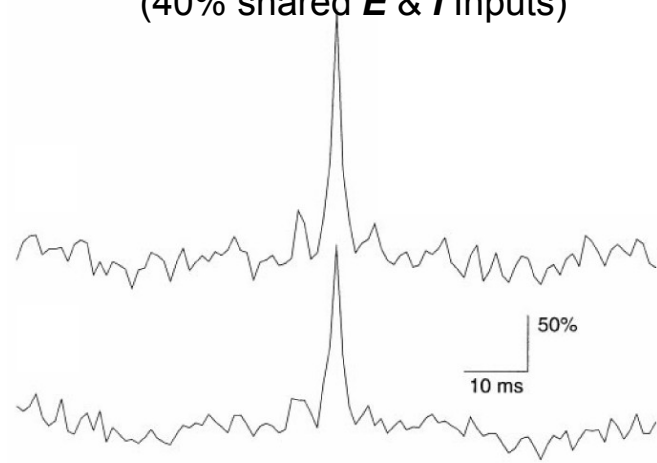
Feed-forward network:





Can correlations produced by shared inputs in a previous layer have an impact on output correlations?

Postsynaptic neurons
(40% shared ***E*** & ***I*** Inputs)



Pre-synaptic neurons

Shadlen & Newsome '98

Outline

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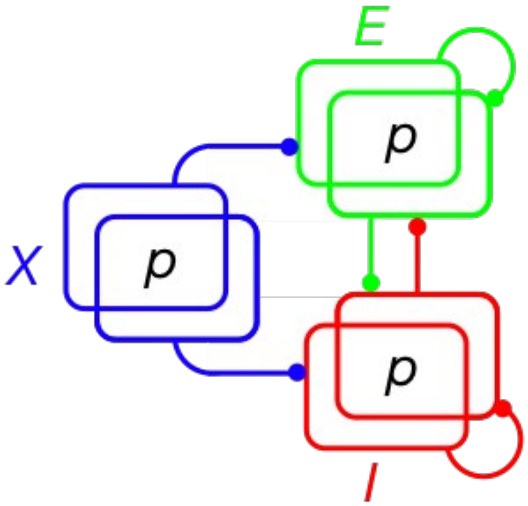
Model of a recurrent network.



1) Neurons are binary: σ_i=0 (inactive), 1 (active). Analytically tractable.

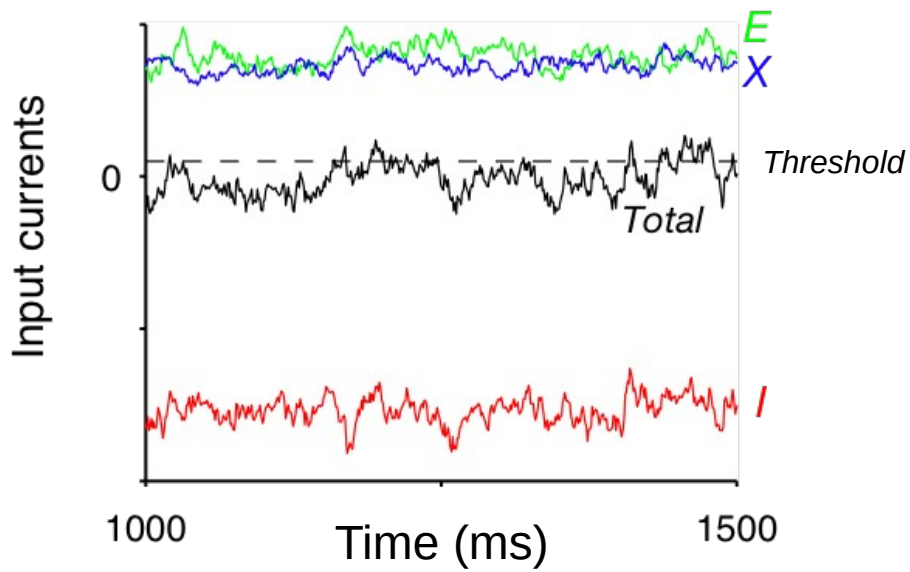
2) Network is randomly and ***densely*** connected (connection probability does not decrease with N).

3) Neurons are **strongly coupled**: only a small fraction of a neuron's inputs are enough to make it fire: synaptic couplings scale as 1/sqrt(N).

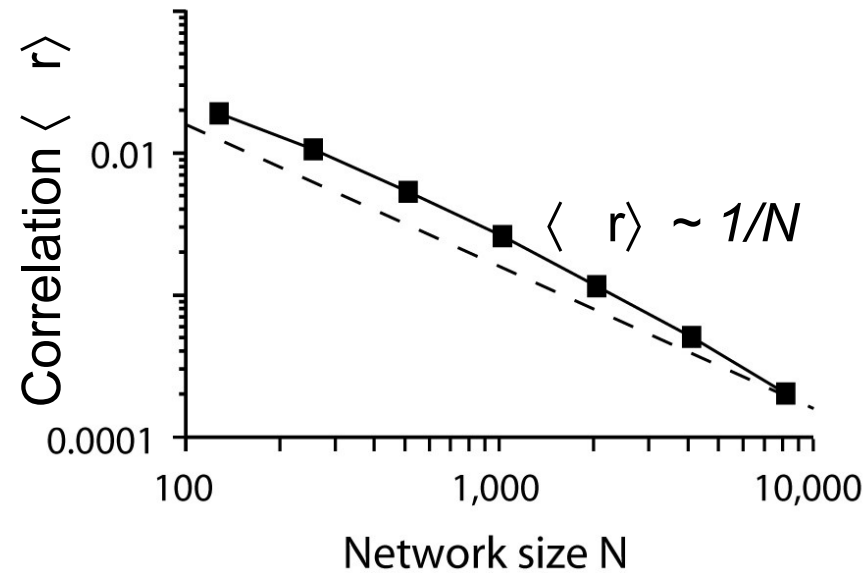
Recurrent balanced network is asynchronous

If inhibition is not too weak or slow,...

1. the network is **BALANCED**



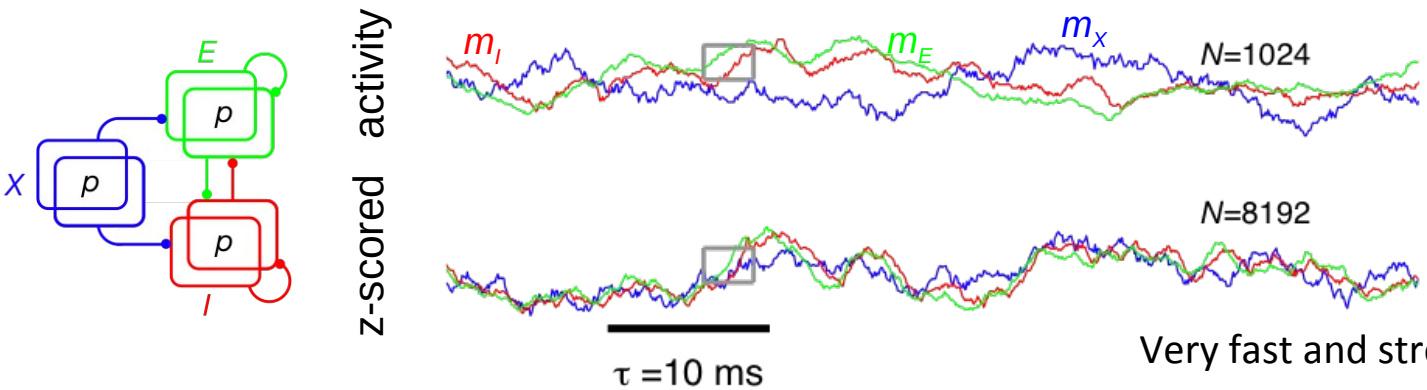
2. the network is **ASYNCHRONOUS**:



Correlation decreases at fixed *p* (avg. shared fraction).

Renart et al '10

Tracking of spontaneous E and I activity fluctuations generates strong EI correlations

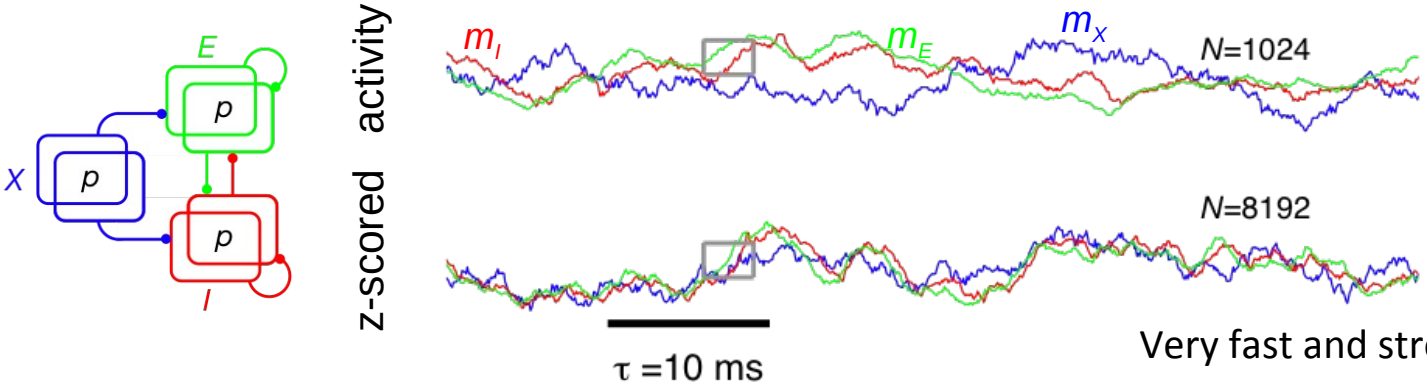


$m_E(t) = A_E\, m_X(t)$

$m_I(t) = A_I\, m_X(t)$

Very fast and strong negative feedback!

Tracking of spontaneous E and I activity fluctuations generates strong EI correlations



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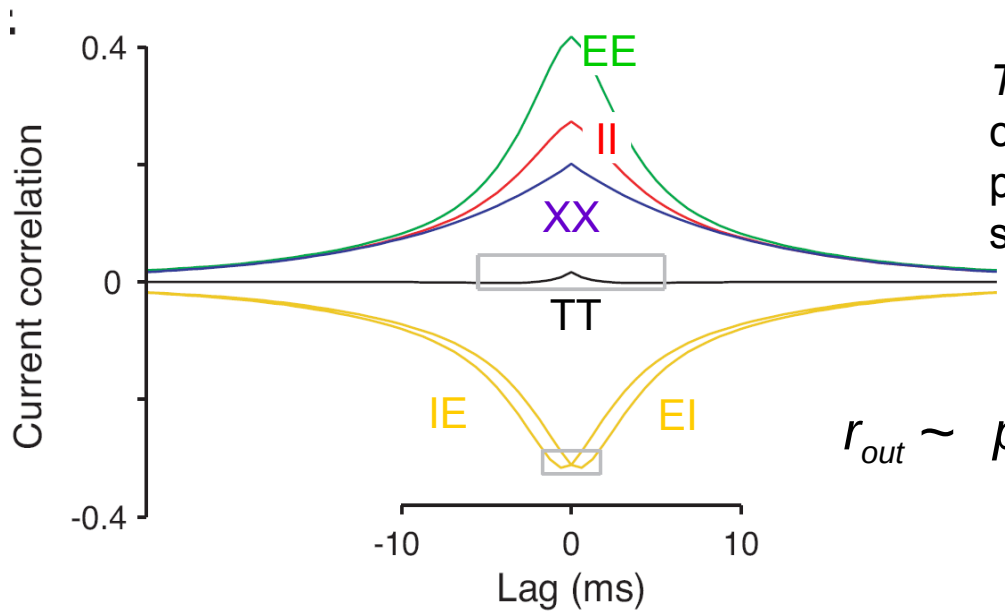


Tracking generates negative current correlations which cancel all sources of positive current correlations, including shared inputs.

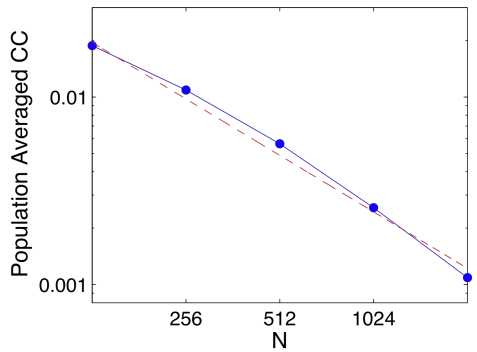
Dominates!!

$$r_{out} \sim p + N(J_E^2 r_{EE} + J_I^2 r_{II} - 2J_E J_I\, r_{EI} + \ldots)$$

Becomes ~ -p

Self-consistent Asynchronous state

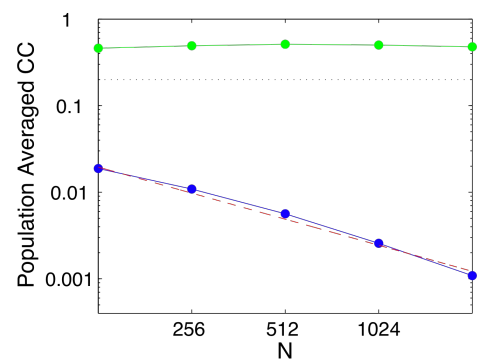
Asynchronous firing: r ~ O(1/N)



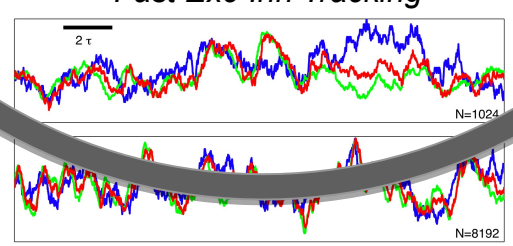
Common input (Recurrent & Exernal)

Amplification due to strong coupling

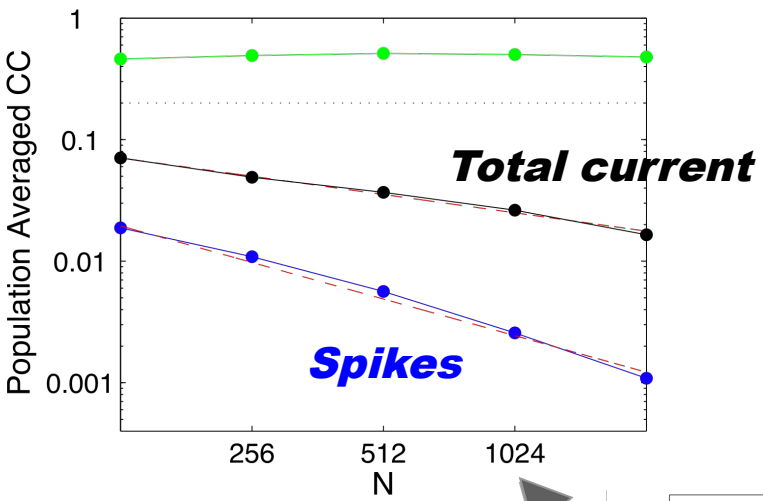
Synchronous Currents: c_{EE} ~ O(1)



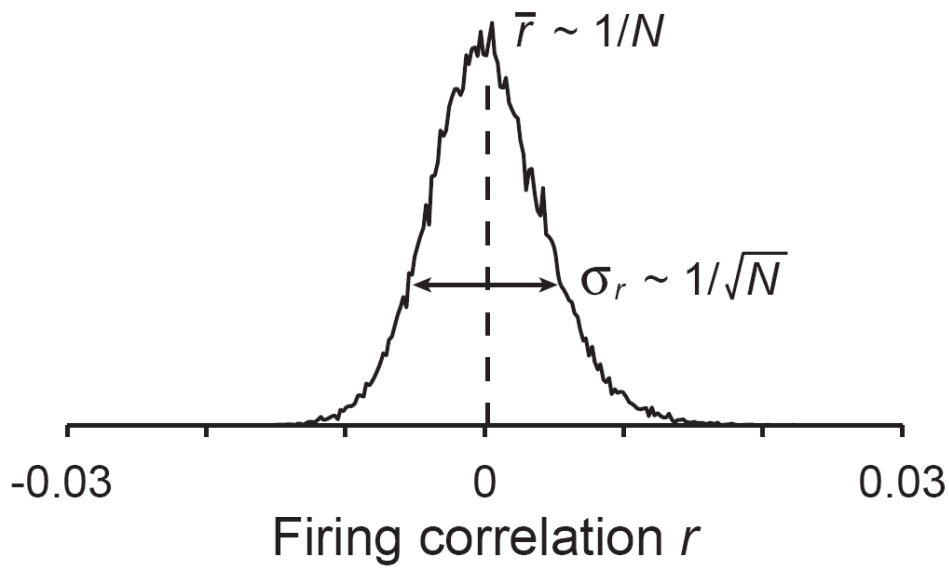
Fast Exc-Inh Tracking



Weakly Synchronous Total Current
c ~ O(1/√N)



The sources of heterogeneity in the correlation are larger than the mean



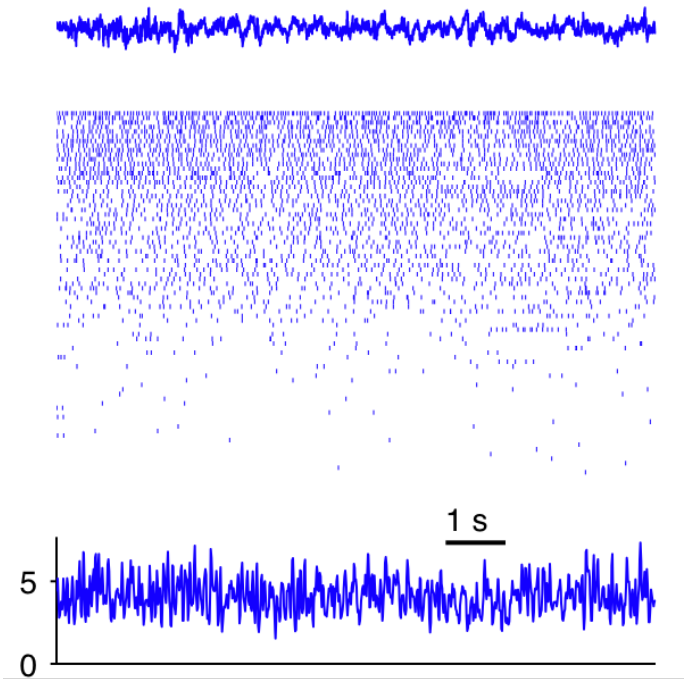
The distribution of *r* is '*wide*', meaning $\frac{\sigma_r}{\bar{r}} >> 1$

This implies that around half of the pairs have $r < 0$

Correlations in spontaneous activity during *Activated* states.

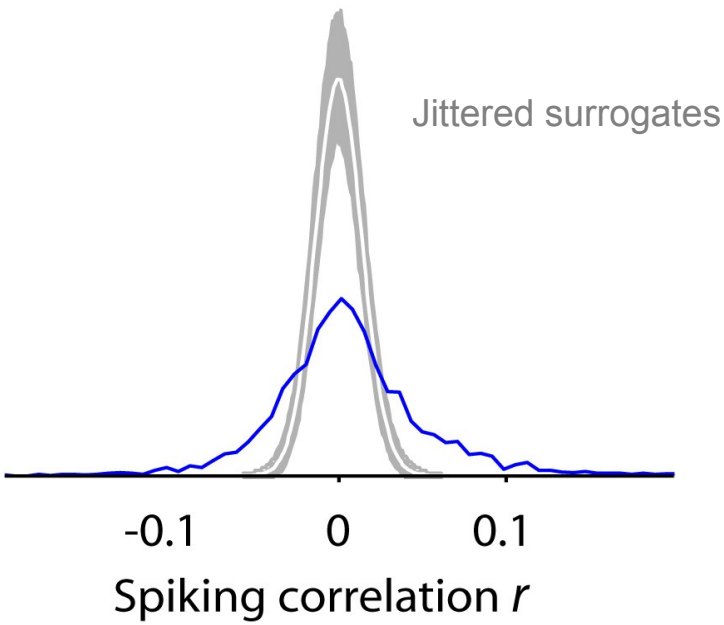
Cortical Activation:

anesthetized rats; auditory and somatosensory cortices

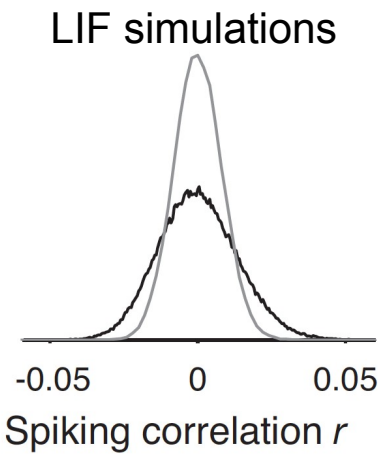


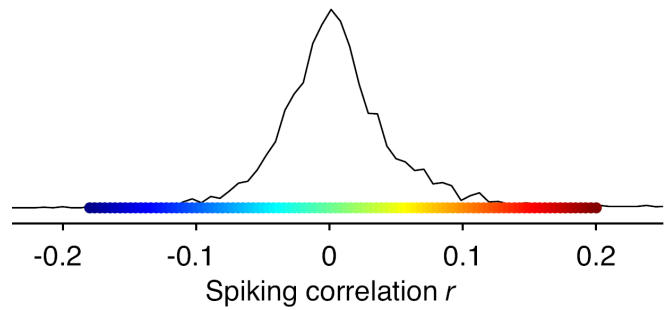
As predicted, *r* distribution is ***wide***:

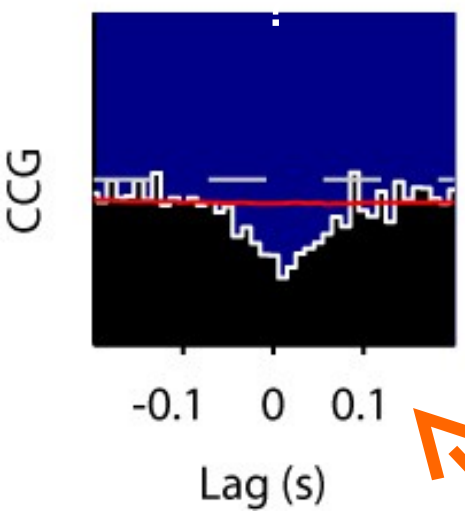
$\sigma_r >> \langle r \rangle$

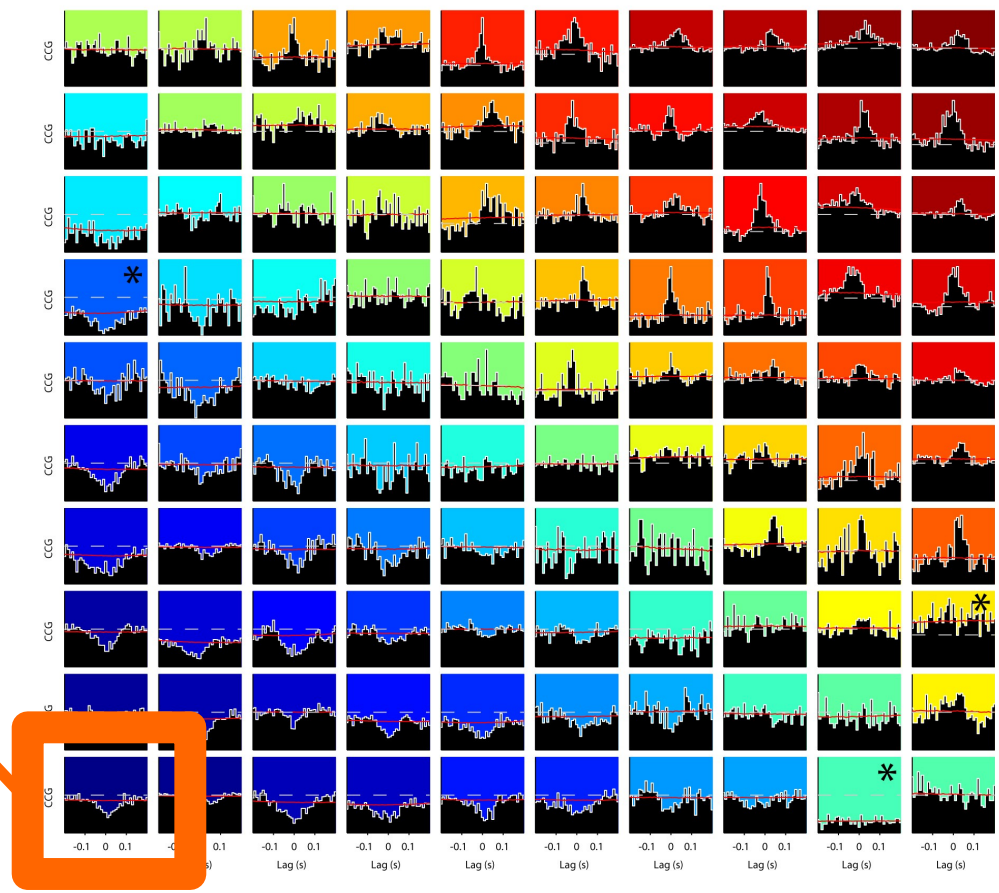


Correlations during the Activated state.









Question:

- What kind of network mechanisms can generates **large positive** and **negative slow** correlations with a **near-zero** average?

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Theory of correlations in stochastic neural networks

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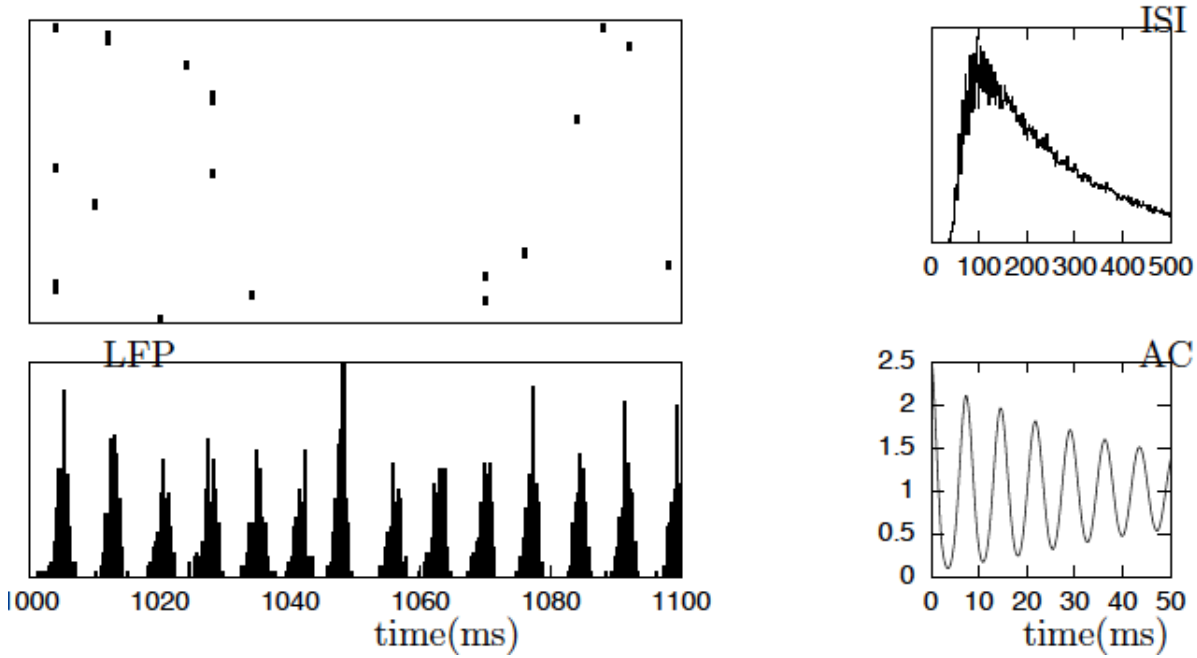
(Received 21 March 1994)

VII. AMPLIFICATION OF FLUCTUATIONS NEAR A BIFURCATION POINT

One of the main consequences of the above results is concerned with the behavior of the correlations near a bifurcation point. This occurs when the parameters of the system are such that the real part of one of the eigenvalues of $\tilde{J}$ becomes close to 1. Our analysis shows that in this case, the system will exhibit anomalously large fluctuations about the (stable) fixed point and the fluctuations will have an anomalously long correlation time.

Correlations via Hopf Bifurcations



This **fast** oscillatory states have a small impact on individual and pair wise statistics over large window sizes.

Brunel & Hakim 1999; Hansel & Mato 2002; Brunel & Wang 2003; Mazzoni et al, 2008

Shaddle-node bifurcations and correlations:

see Mr. Roxin tomorrow

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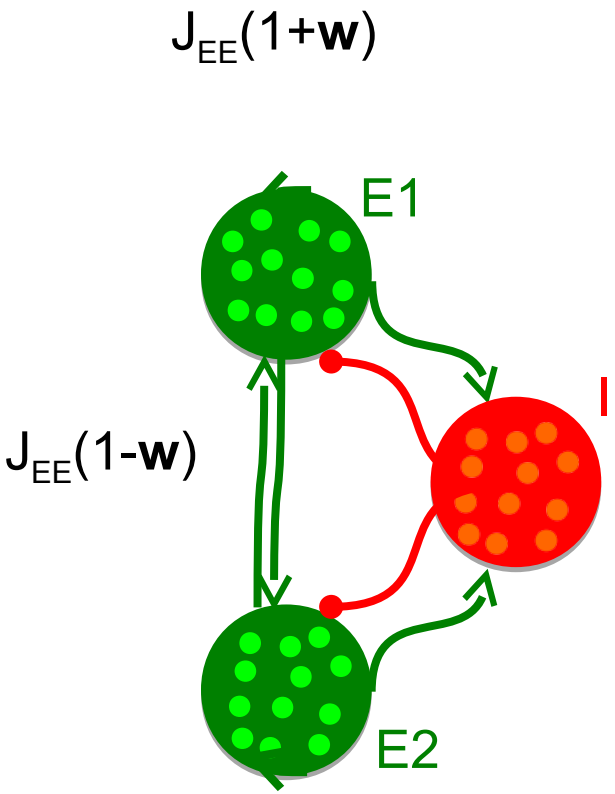
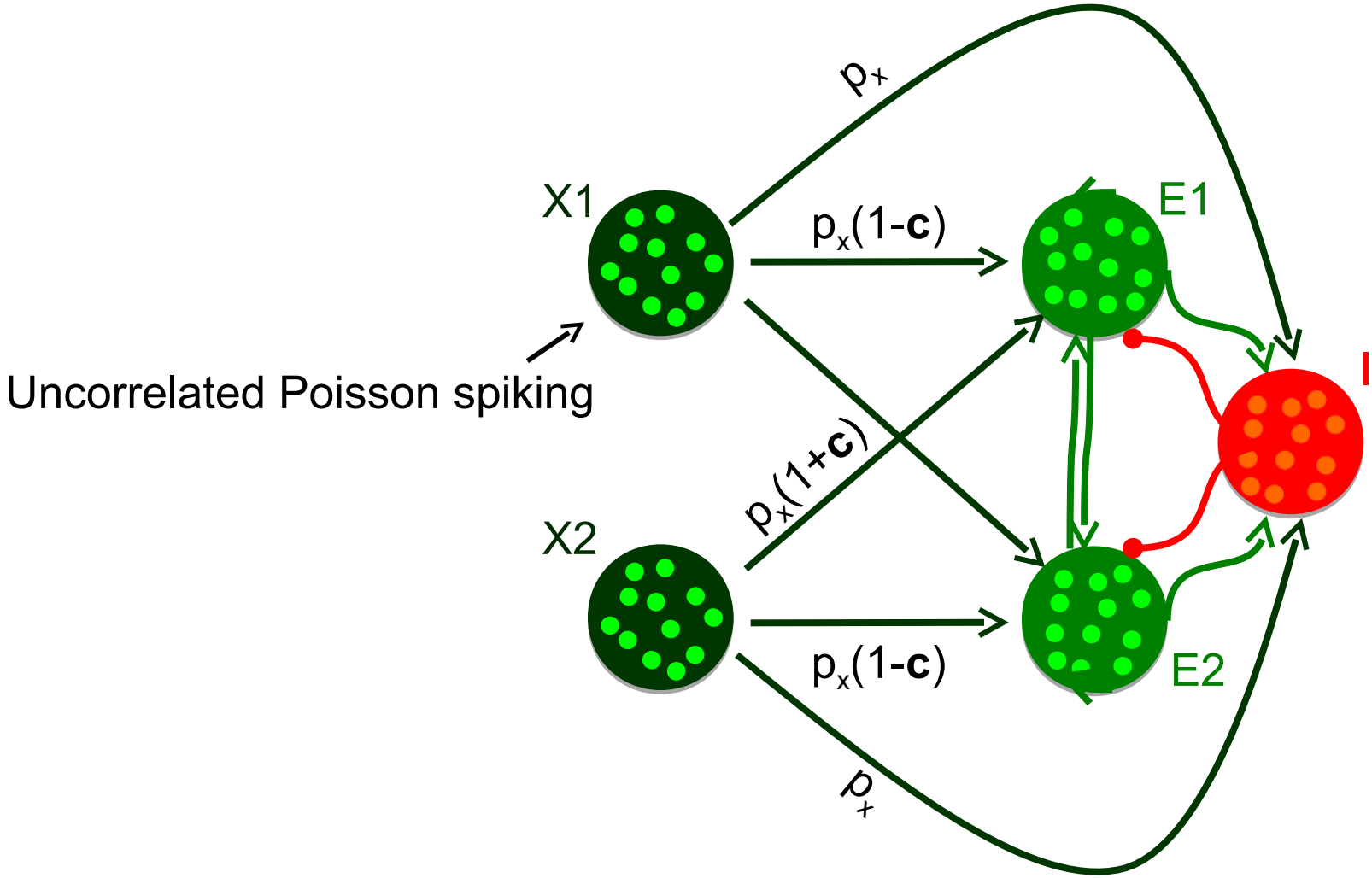
Competitive networks

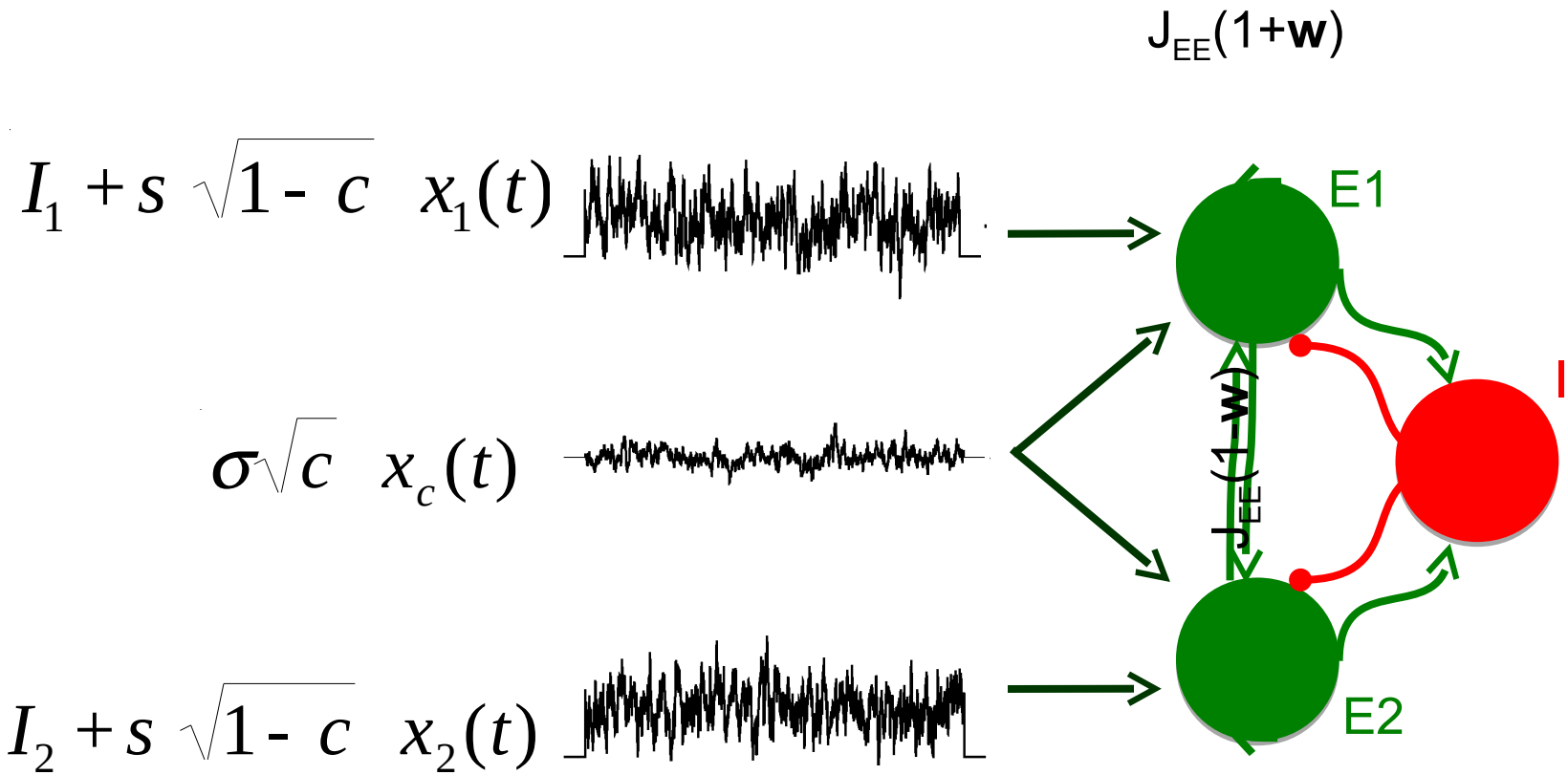


Dynamics in competitive networks



Work in progress

- Reduce the spiking network to Wilson-Cowan equations with additive noise.
- The magnitude and time-scale of the fluctuations of the rate variables is a proxy of the correlations across pairs within spiking network.
- Assumption: the asynchronous state is not perturbed by the addition of the competitive structure (needs to be proven).



Wong & Wang '06; Wong et al '07; Roxin & Ledberg '08; Martí et al 2008; Albantakis & Deco 2011.

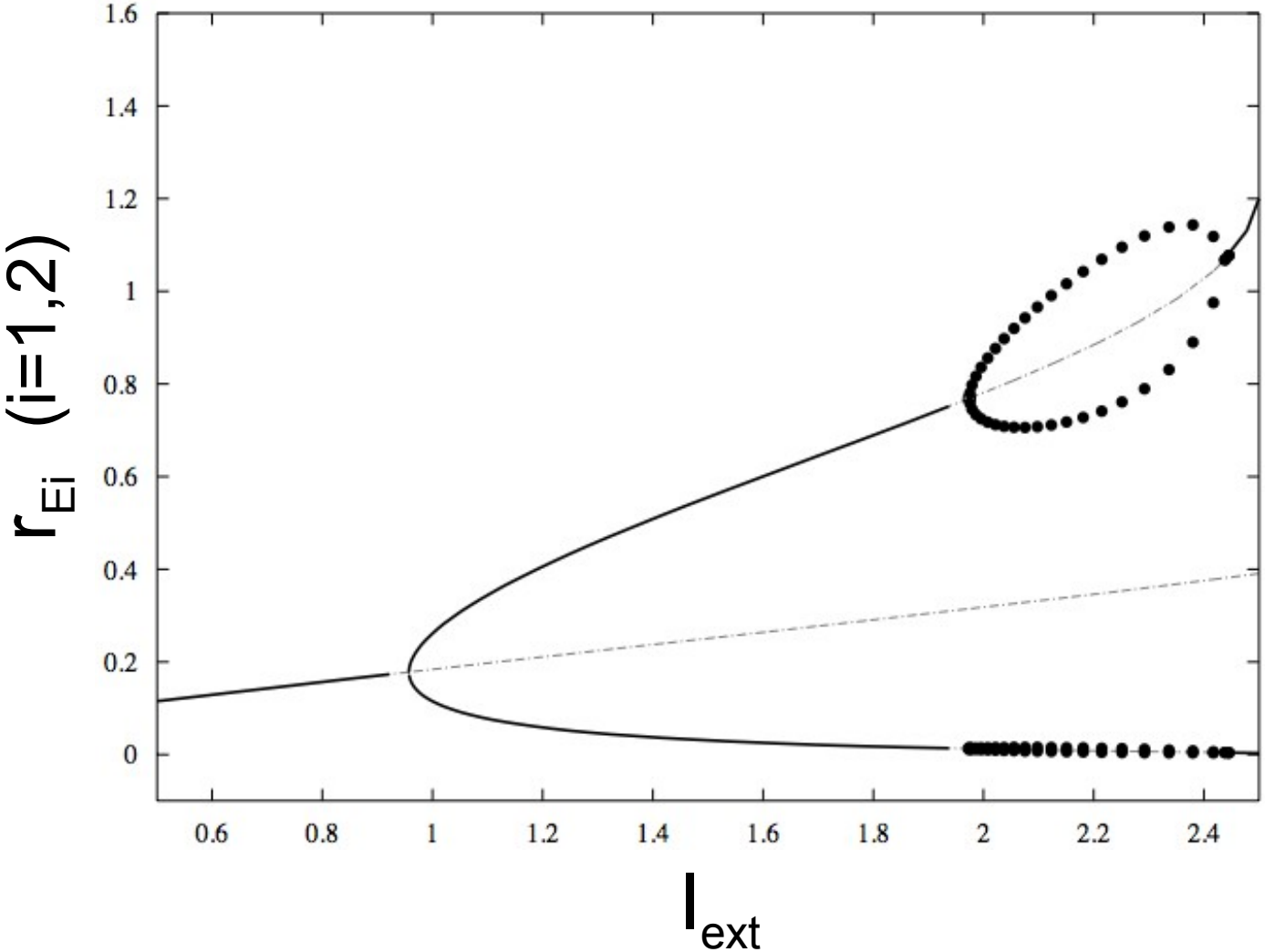
Mean-field equations.

$$\tau_E \frac{dr_1(t)}{dt} = -r_1(t) + \Phi(h_1(t))$$
$$\tau_E \frac{dr_2(t)}{dt} = -r_2(t) + \Phi(h_2(t))$$
$$\tau_I \frac{dr_I(t)}{dt} = -r_I(t) + \Phi_I(h_I(t))$$

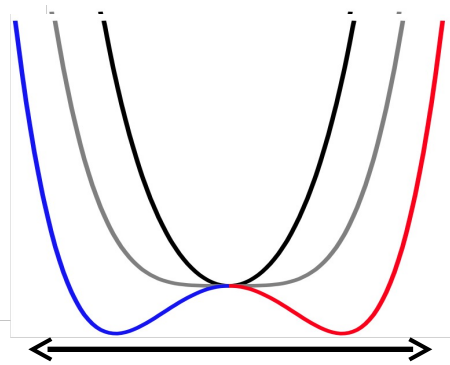
$$\Phi(x) = \frac{\alpha}{1 + e^{-\beta(x - x_0)}}$$

$$h_1 = J_{EE}[(1+w)r_1 + (1-w)r_2] - J_{EI} r_I + I_1 + \sigma_E(\sqrt{1-c}\xi_1 + \sqrt{c}\xi_c)$$
$$h_2 = J_{EE}[(1-w)r_1 + (1+w)r_2] - J_{EI} r_I + I_2 + \sigma_E(\sqrt{1-c}\xi_2 + \sqrt{c}\xi_c)$$
$$h_3 = J_{IE}(r_1 + r_2) - J_{II} r_I + I_I$$

Supercritical Pitchfork Bifurcation

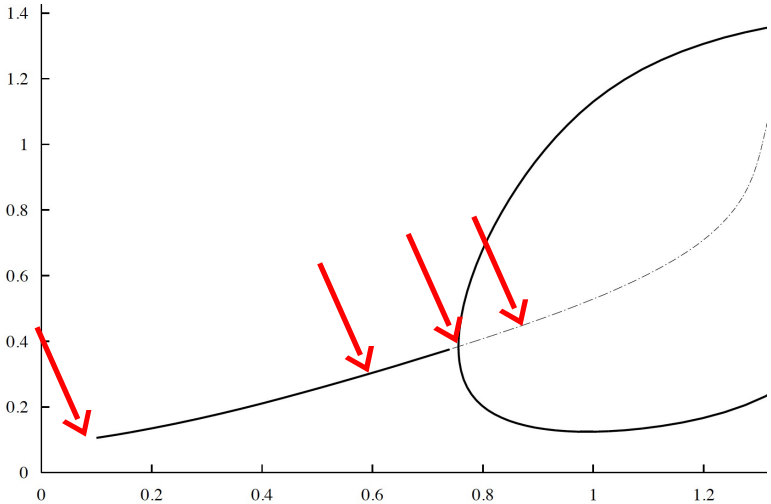


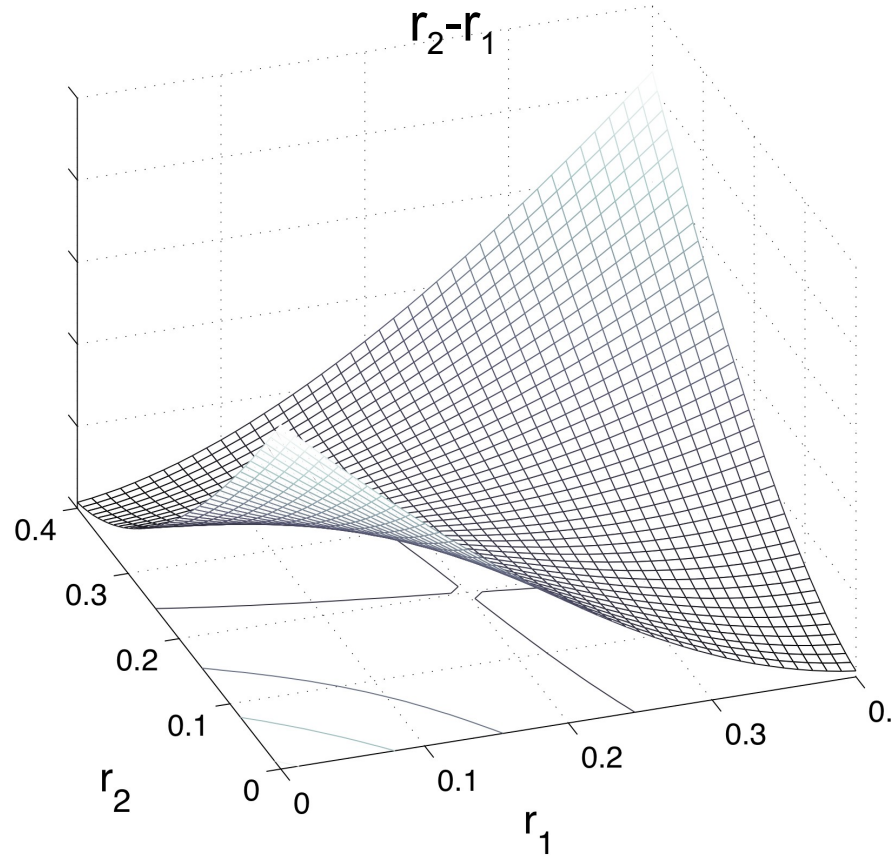
Supercritical Pitchfork Bifurcation



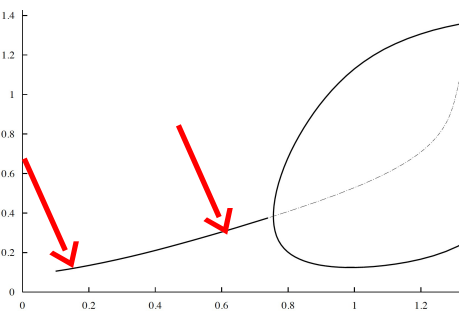
Roxin & Ledberg ’08:

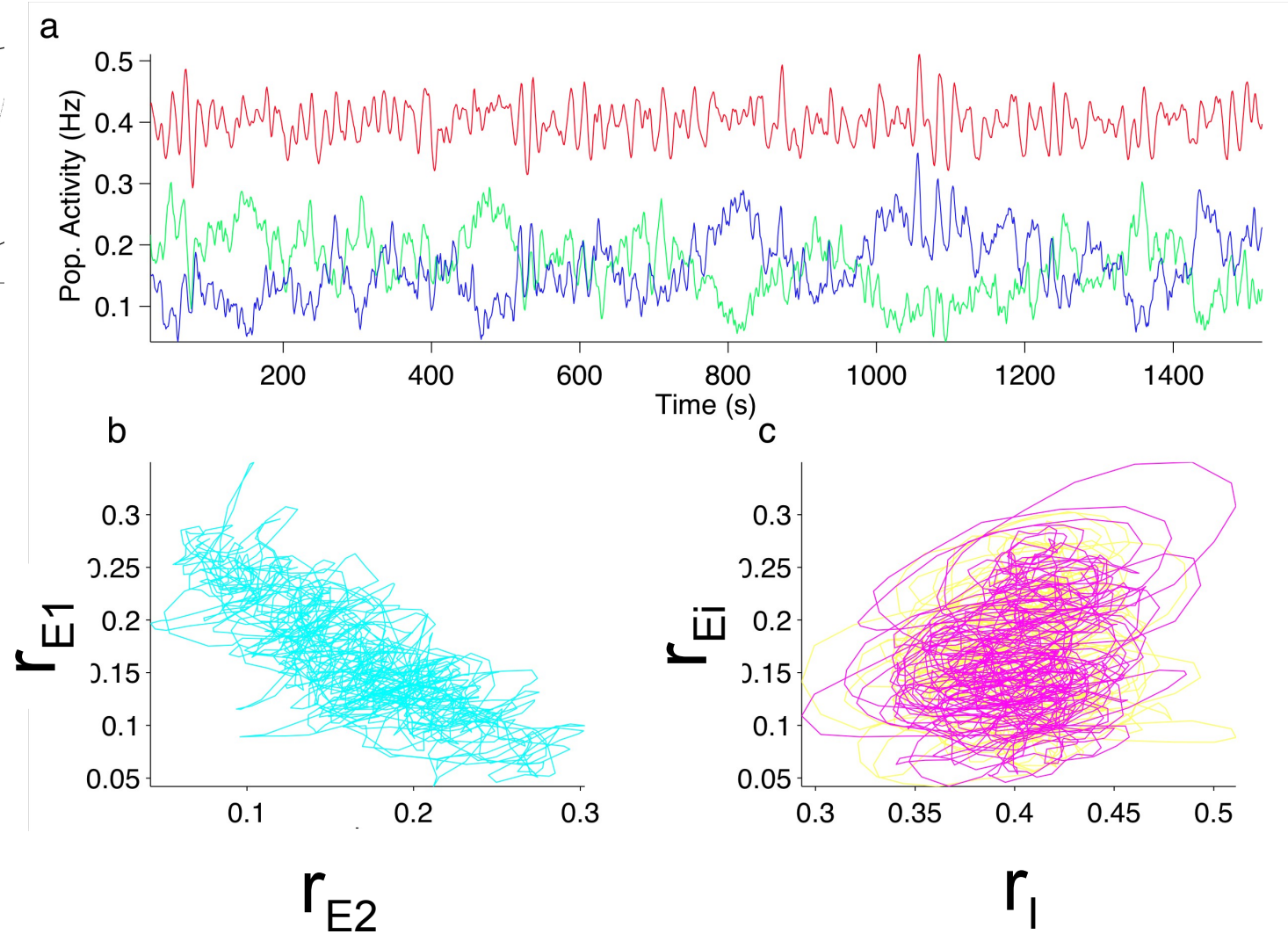
$$E(X) = a(I_1 - I_2)X - b(I - I_{bif})X^2 + X^4$$



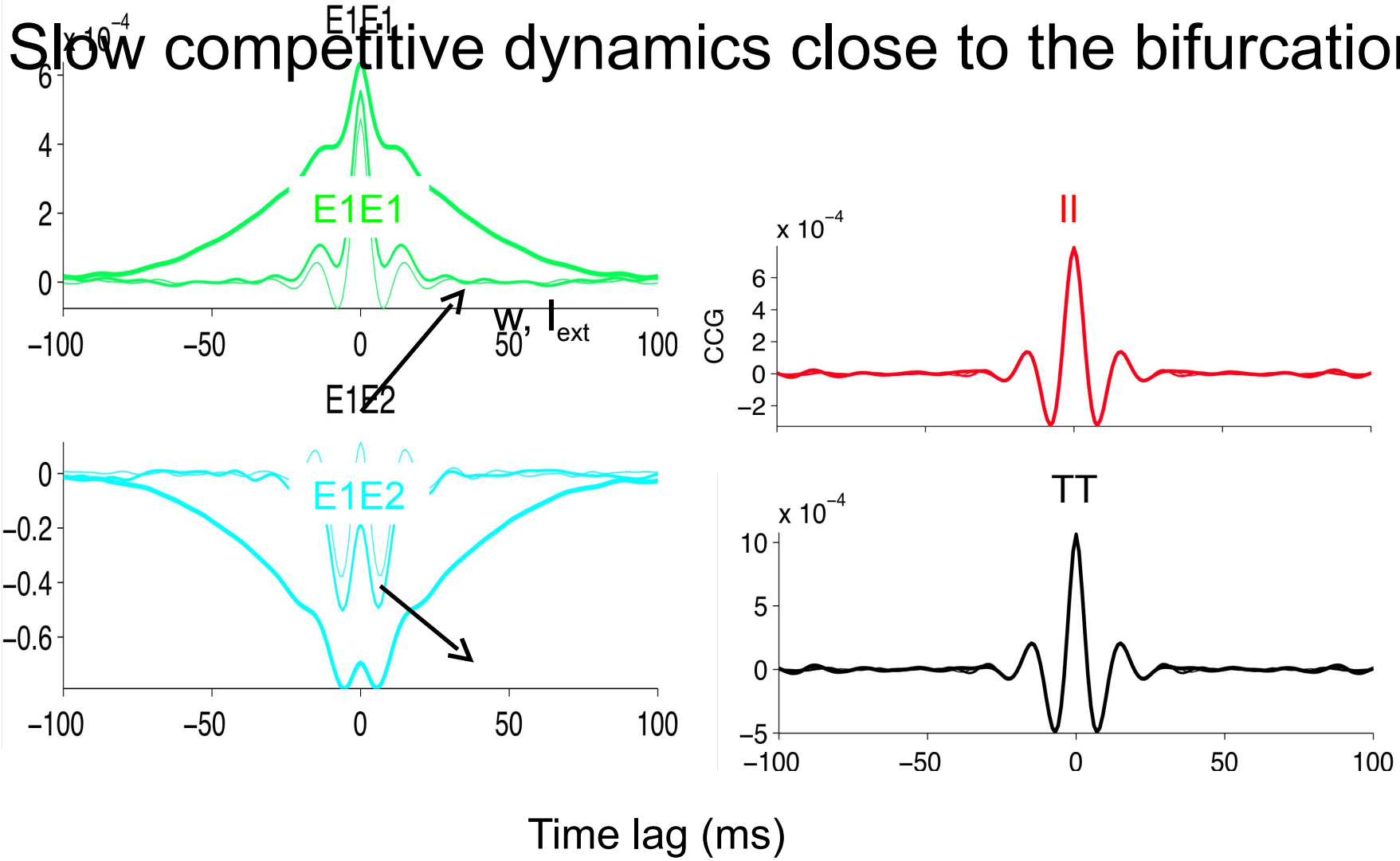


Slow competitive dynamics close to the bifurcation.

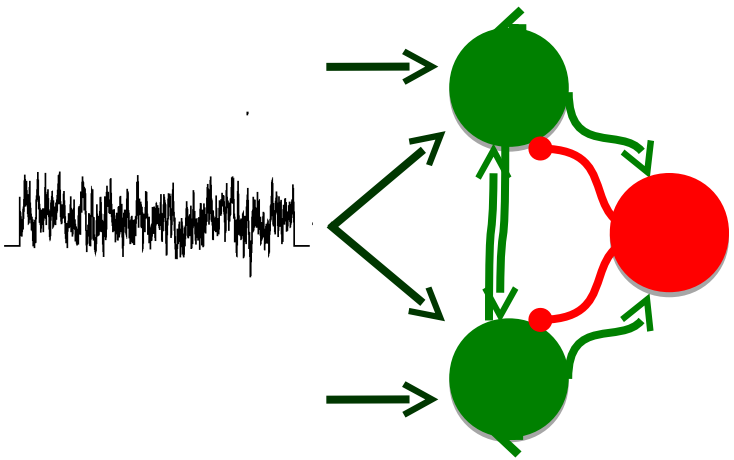


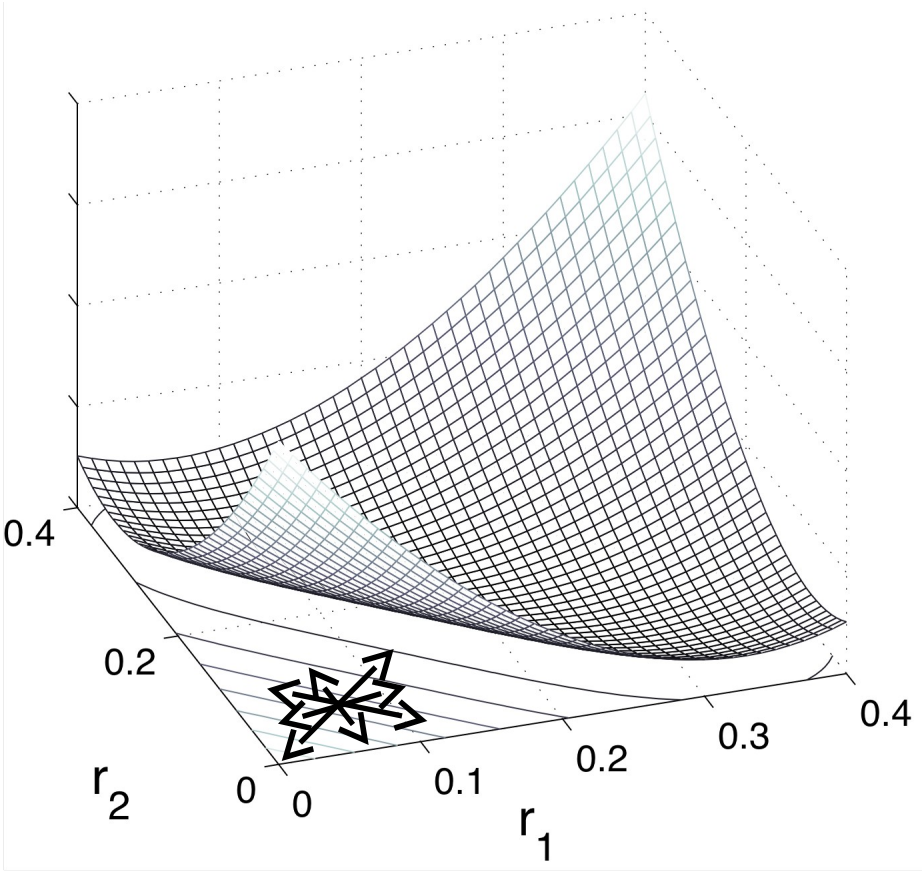


Slow competitive dynamics close to the bifurcation.



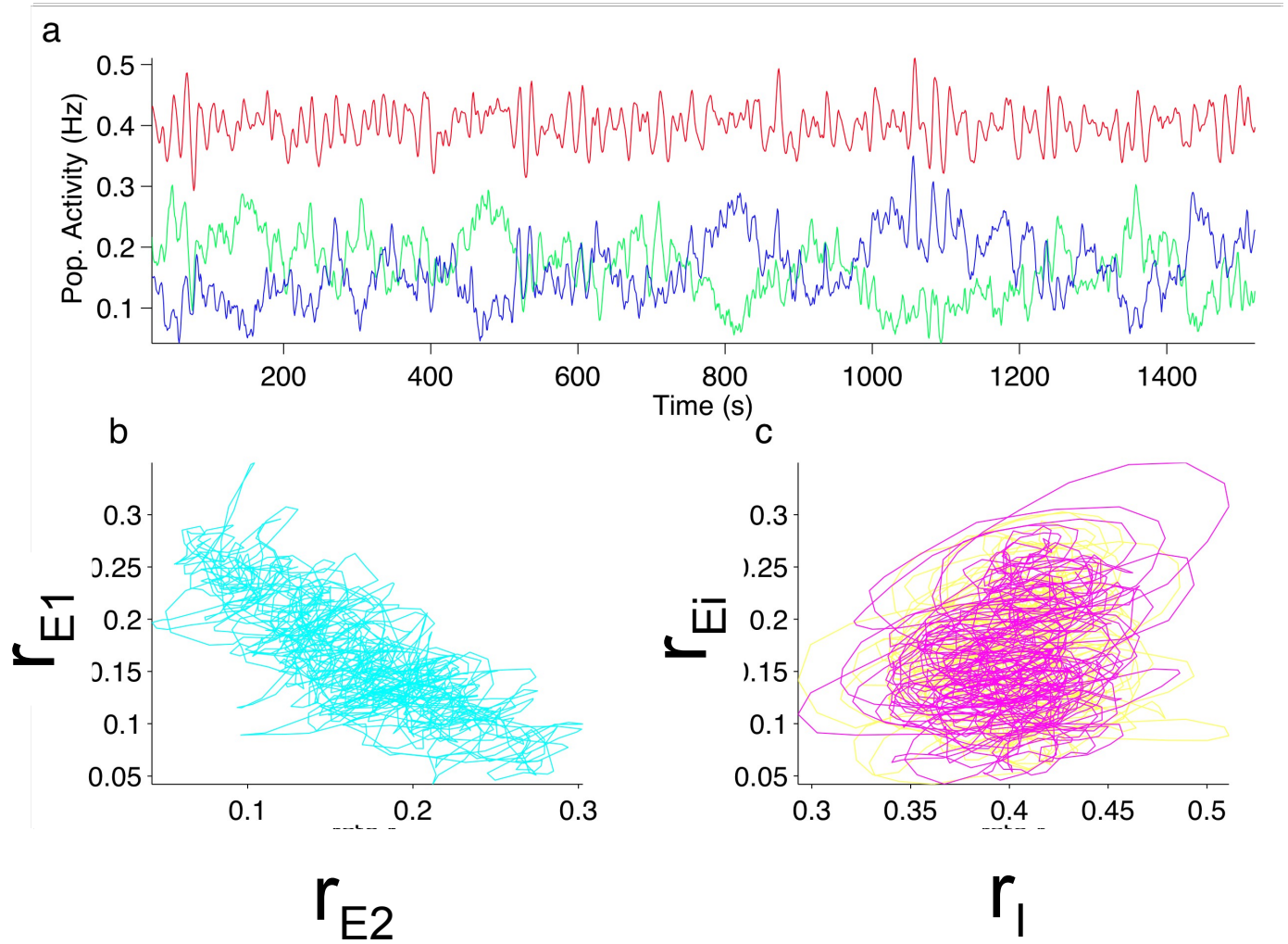
Impact of common noise on global fluctuations.



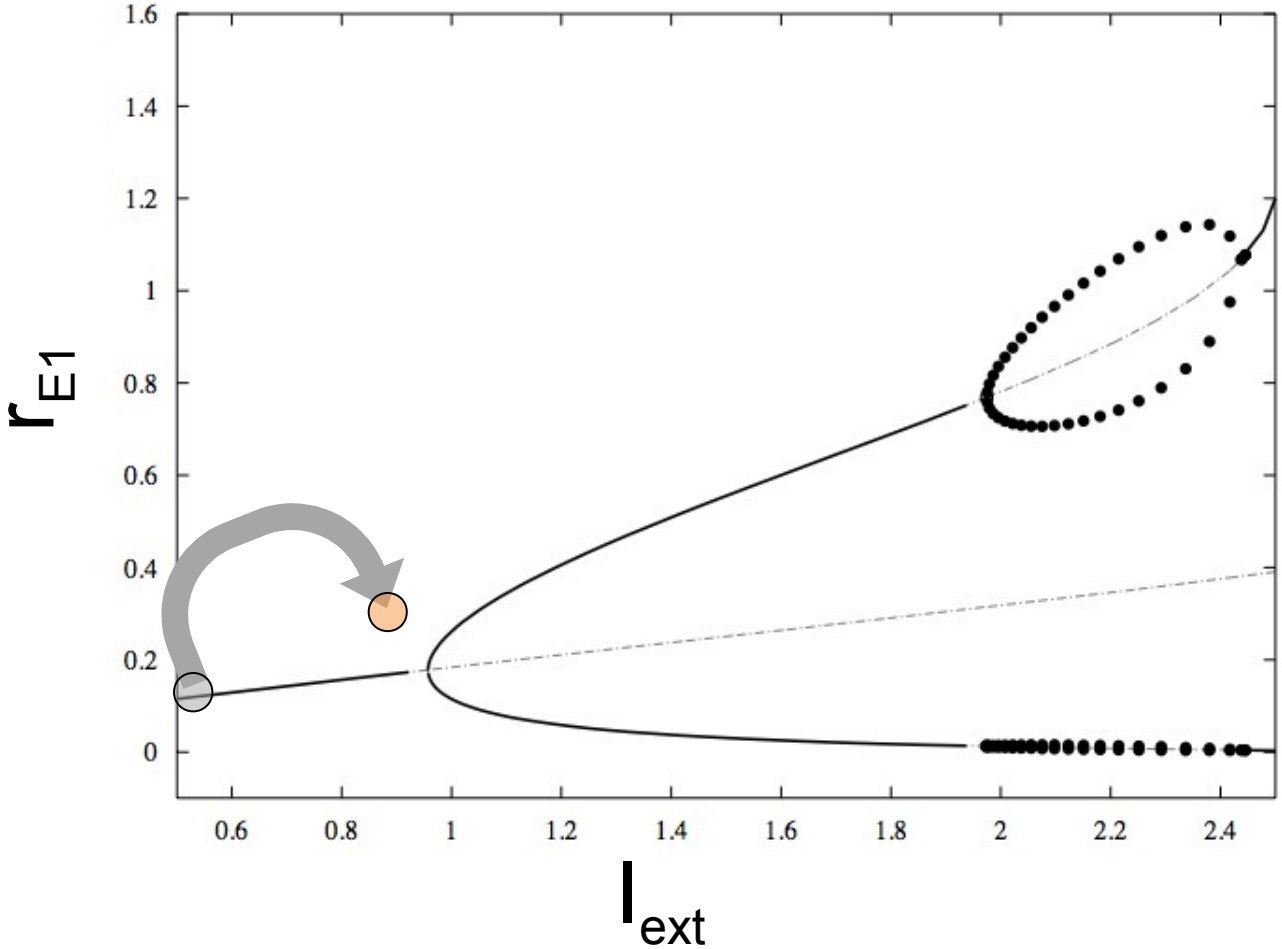


Impact of common noise on global fluctuations.

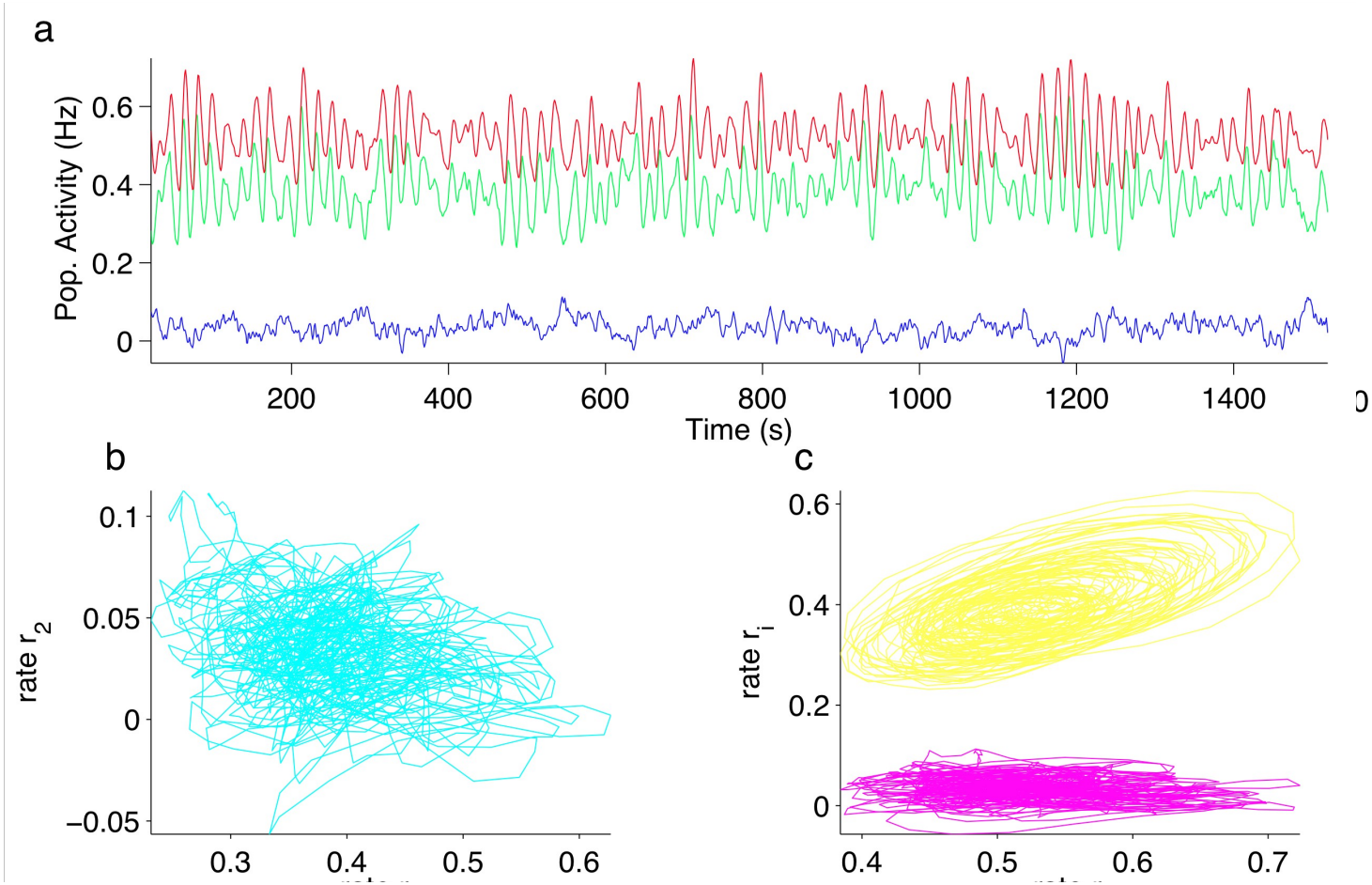
c=0



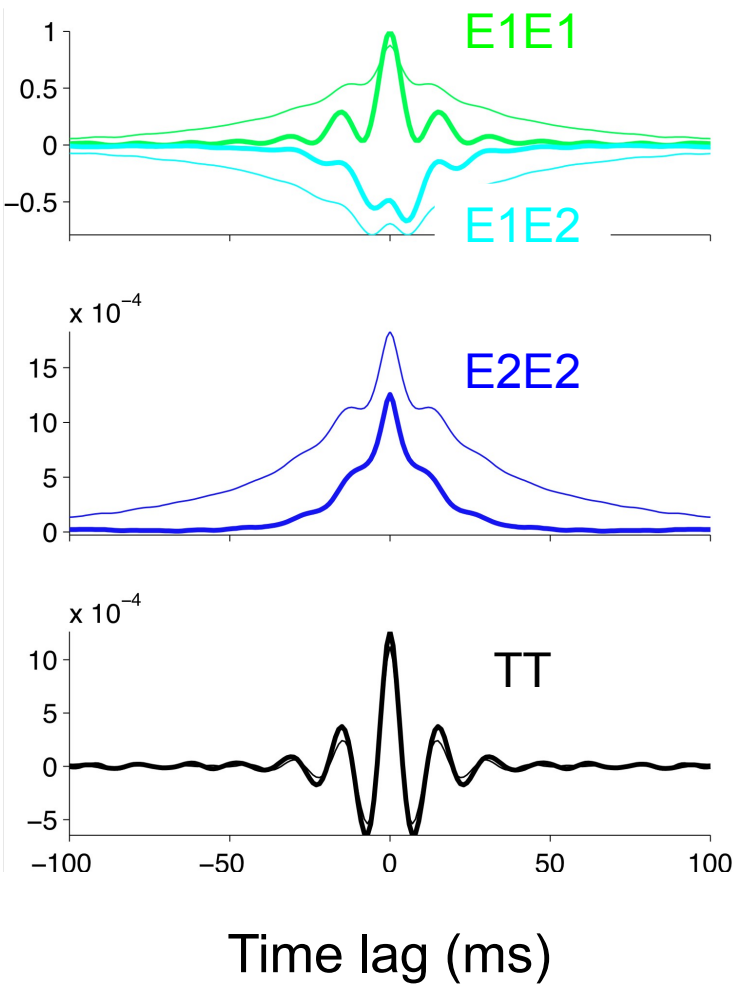
Impact of an *asymmetric* stimulus: $I_1 > I_2$



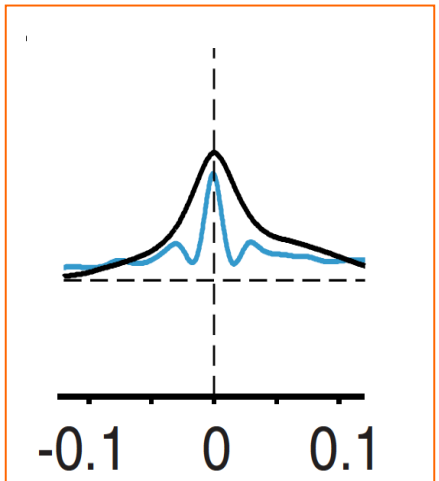
Impact of an *asymmetric* stimulus: $I_1 > I_2$



Impact of an *asymmetric* stimulus: $I_1 > I_2$



i. Slow fluctuations decreased.
ii. E1 population couples more strongly with I and shows a more oscillatory behavior.
iii. Total correlations are largely unaffected.

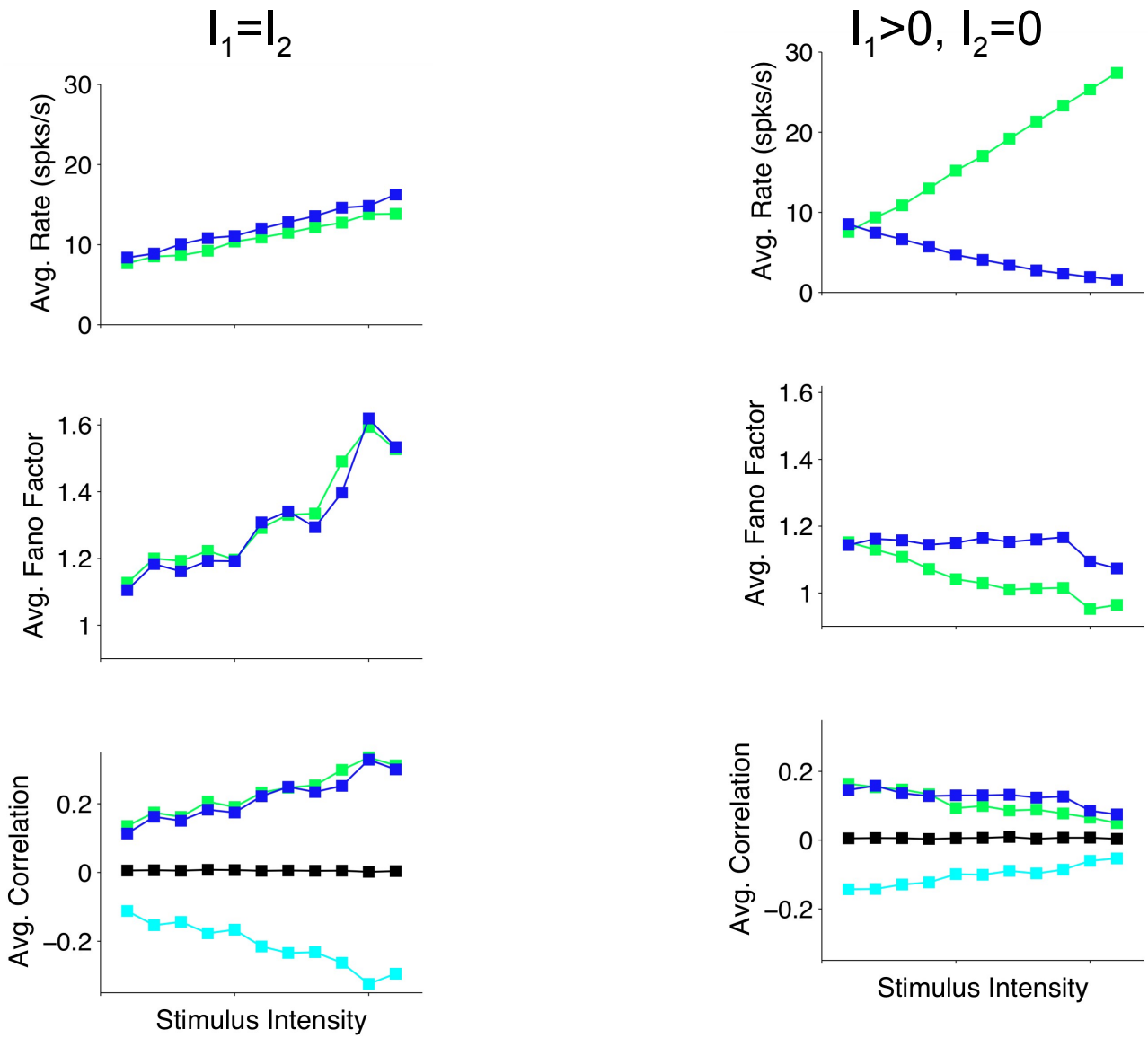


Yu & Ferster, 2010.

Outline

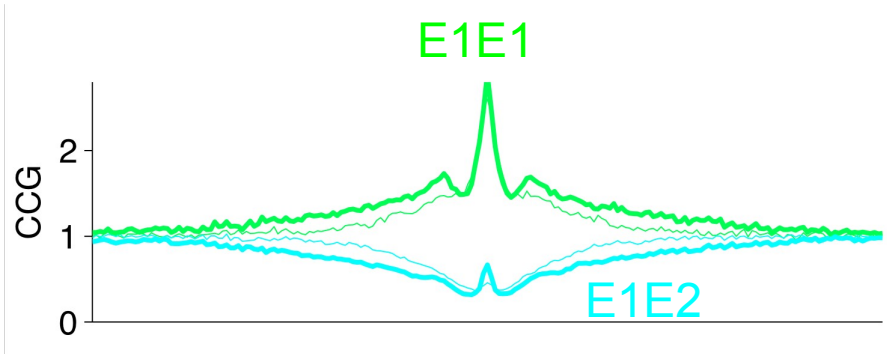
- Mechanisms producing single neuronal variability and pair-wise correlations.
- Asynchronous state in a recurrent randomly connected network.
- Mean field model of a competitive network.
- Spiking simulations.
- Conclusions.

Impact of an stimulus on correlations

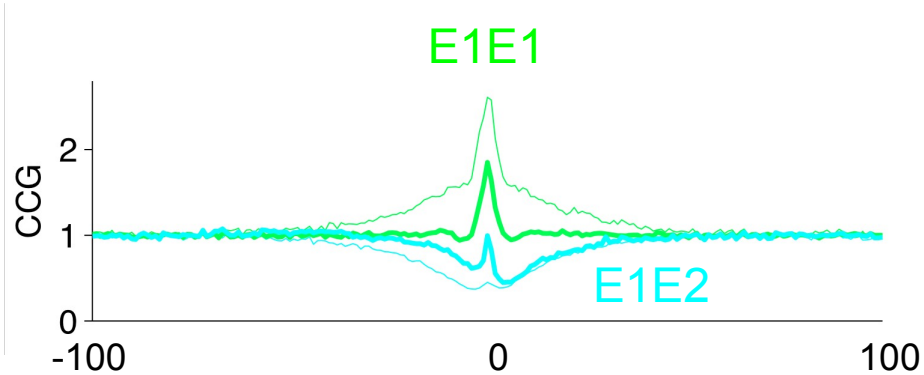


Impact of an stimulus on correlations

Symmetric: $I_1=I_2$

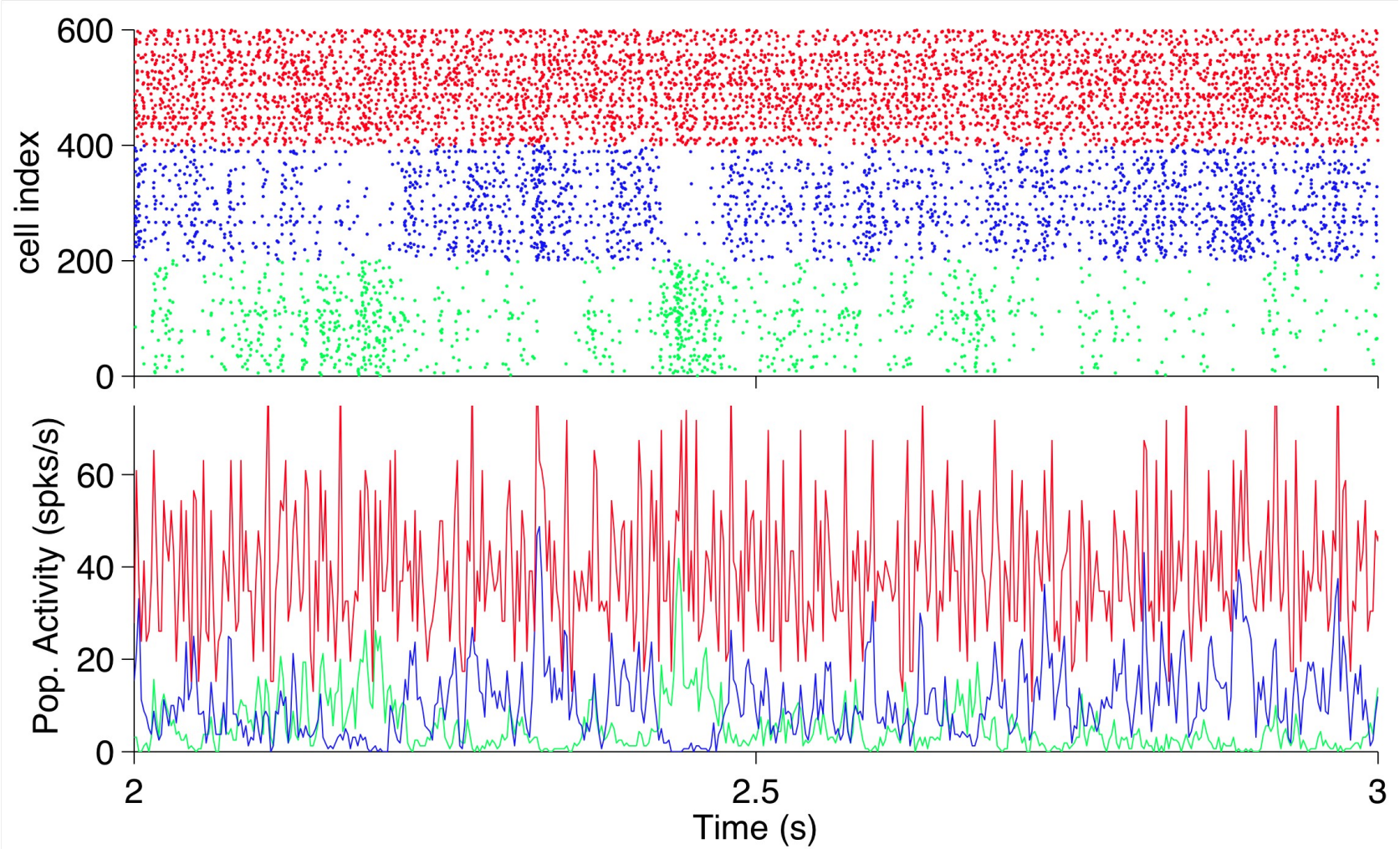


Asymmetric: $I_1>0$, $I_2=0$

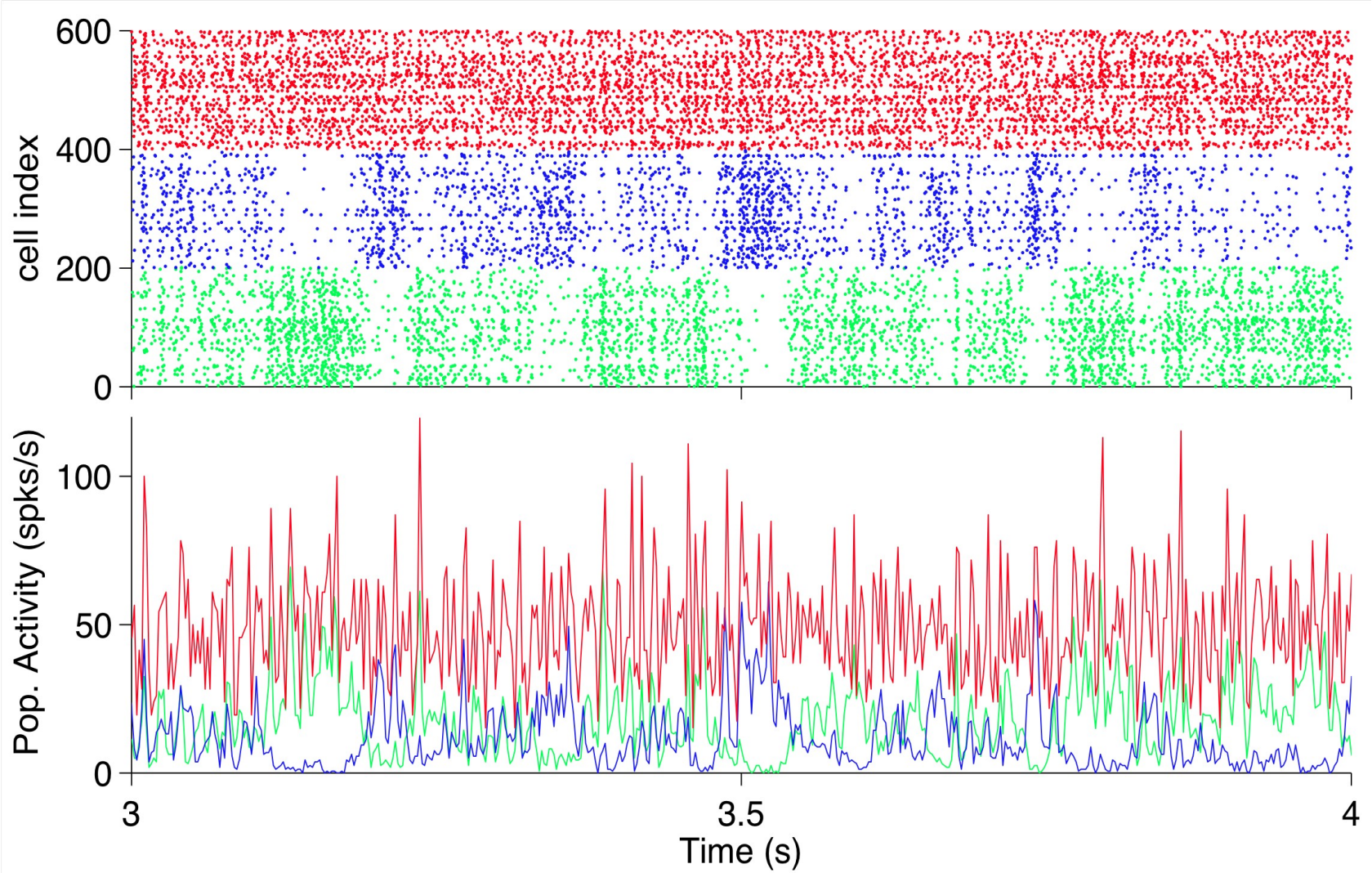


Time lag (ms)

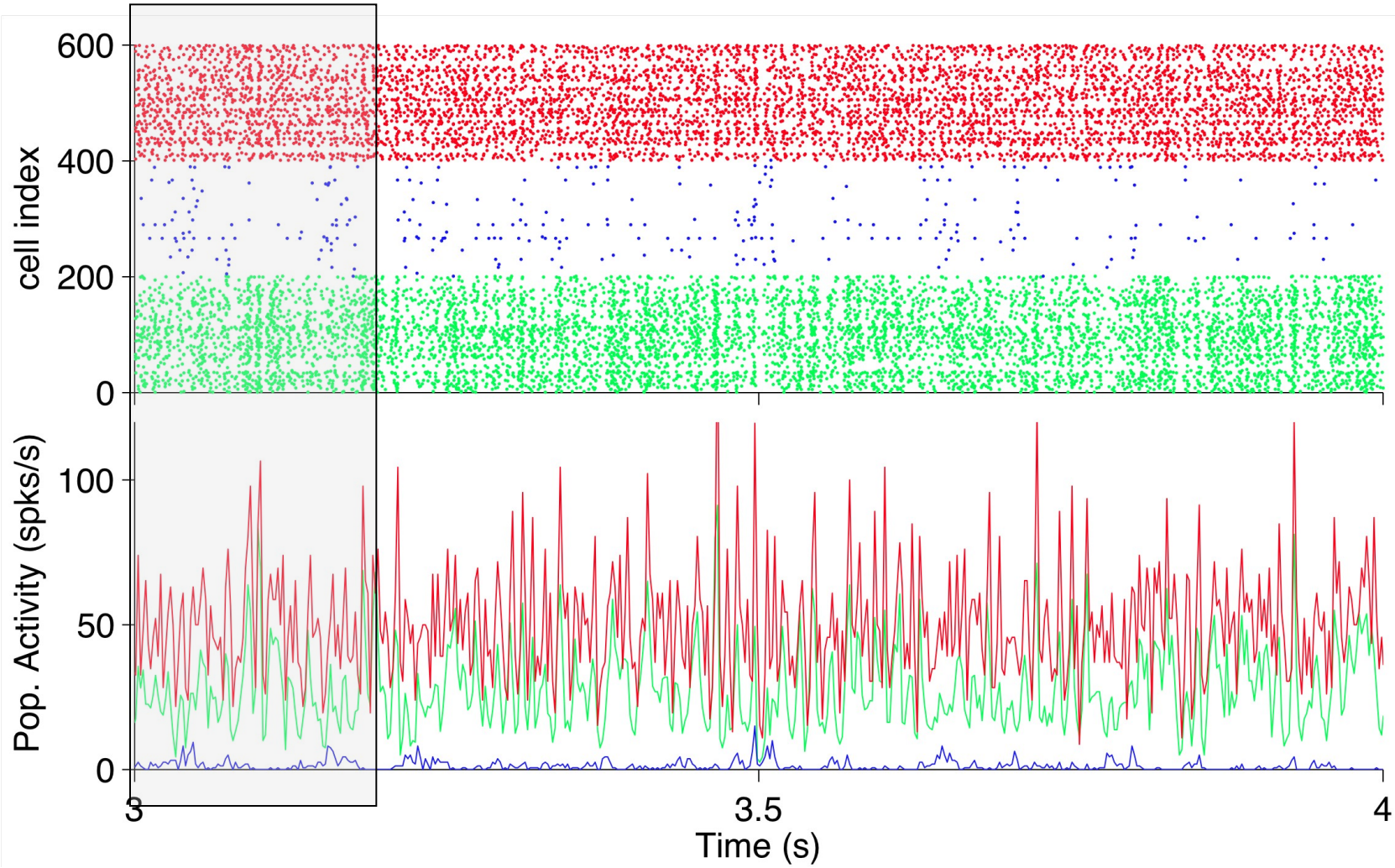
Spontaneous activity near the bifurcation.



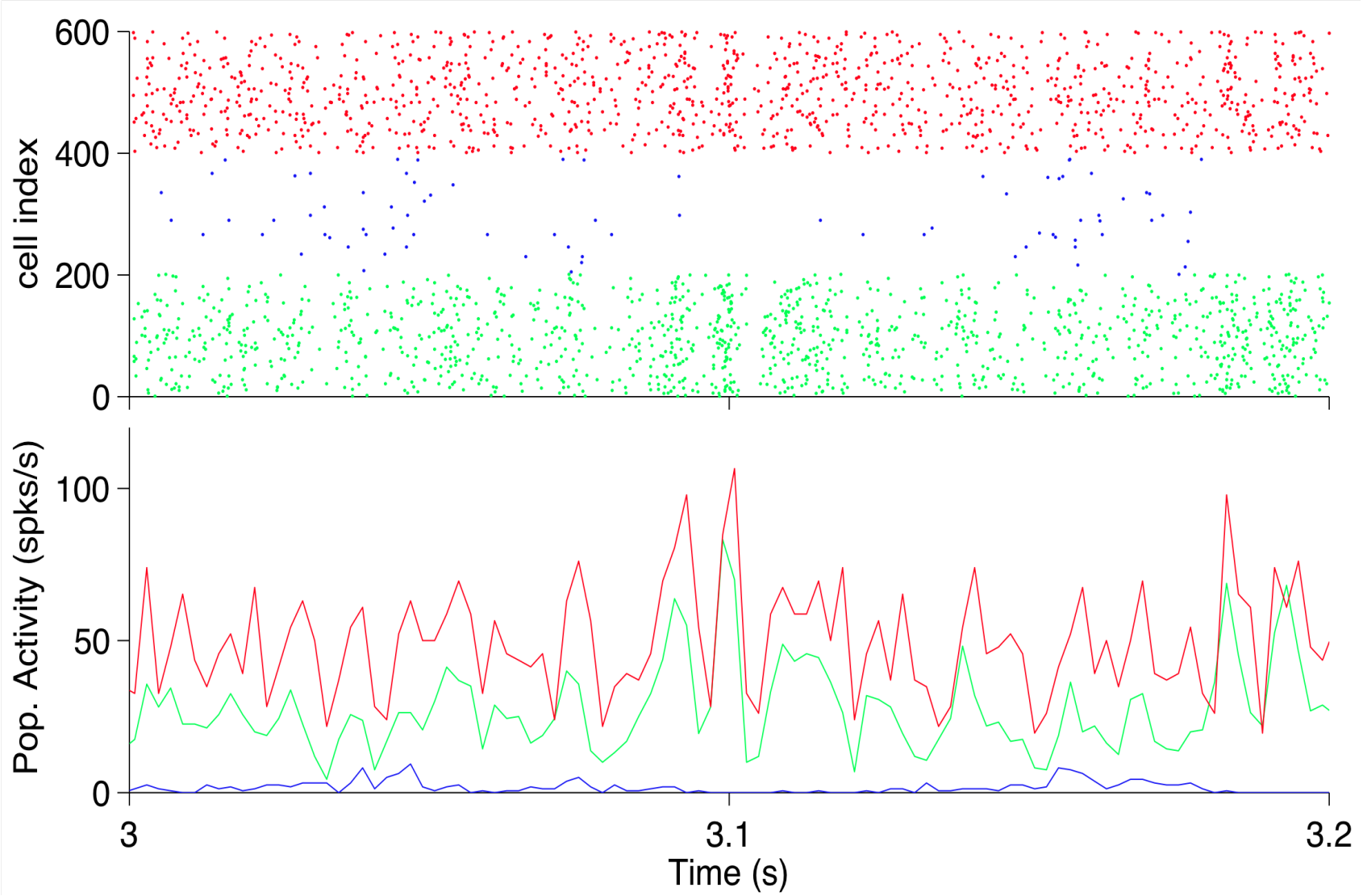
Unbiased stimuli increase competition.



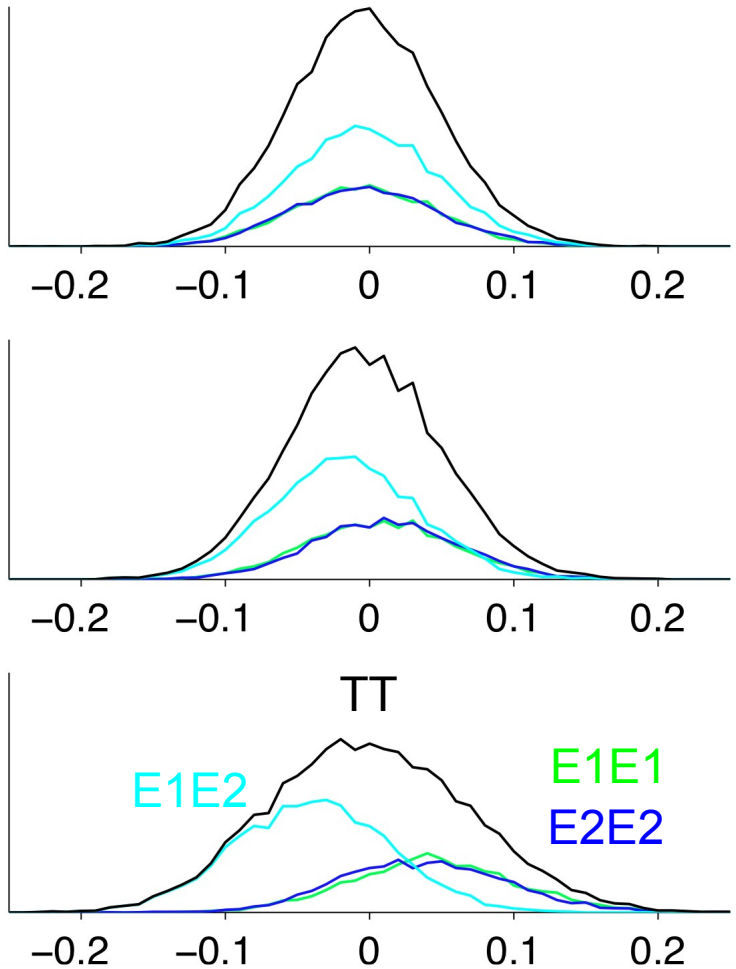
Asymmetric stimuli decrease competition…



…and an “asynchronous” state, like in the EI network, is recovered.



Competitive interactions broaden the distribution of Spike Count Corr. Coefs. r_{ij} without affecting the mean.



i. increase E1E2-shared inputs

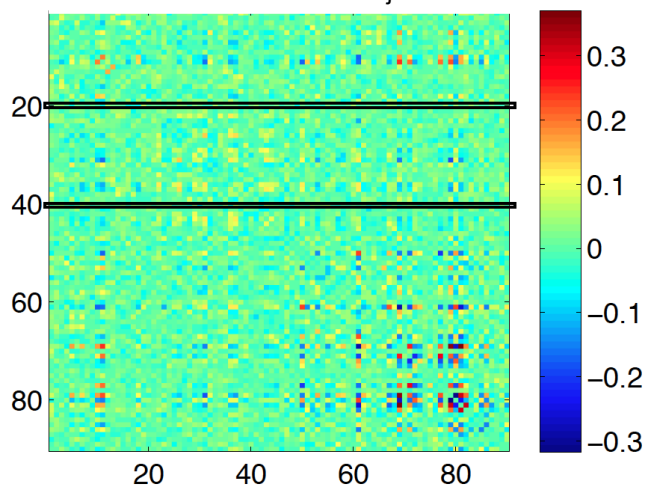
ii. Asymmetric stimuli.

i. decrease E1E2-shared inputs

ii. Symmetric stimuli.

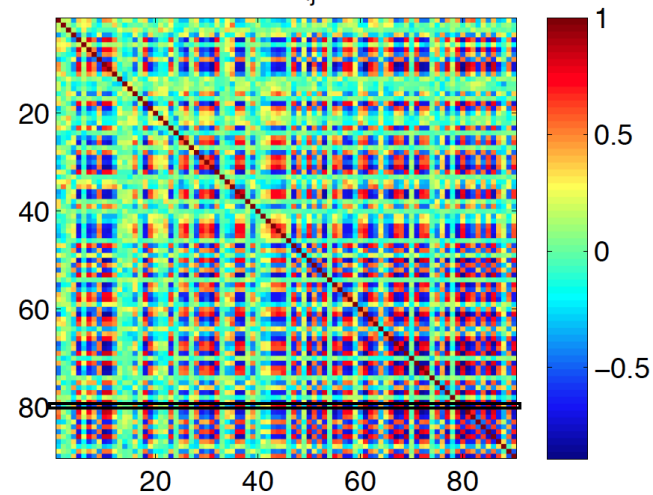
Competitive interactions in sensory cortex during spontaneous activity.

matrix of spike count corr. coef. r_{ij}

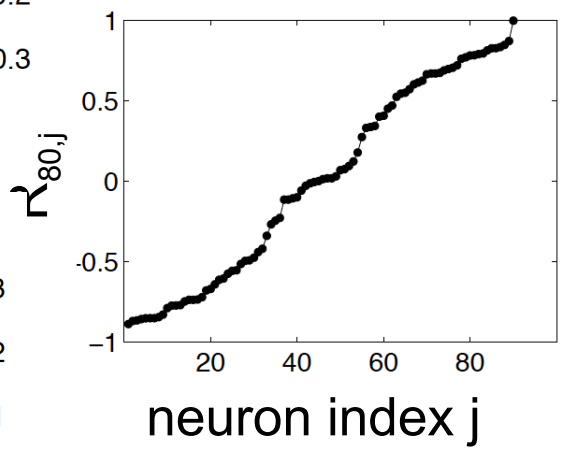


$R_{ij} = \mathrm{CorrCoef}(r_{ik}, r_{jk})$

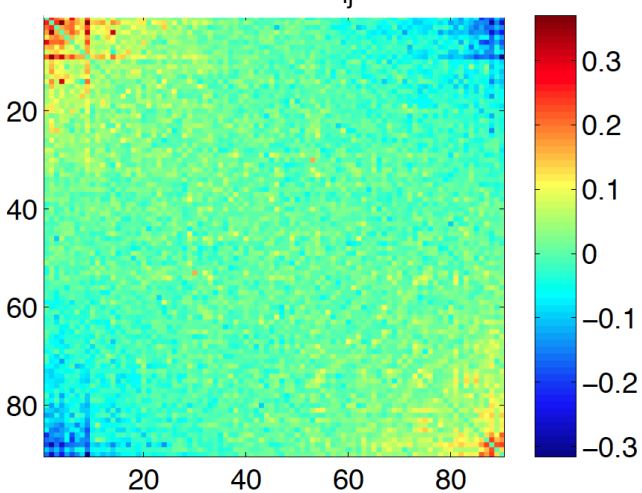
R_{ij}



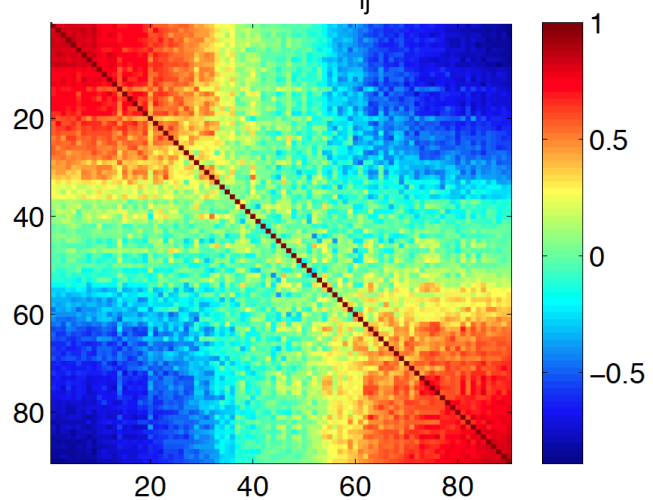
maximally varying neuron i=80



sorted r_{ij}



sorted R_{ij}



Conclusions

•Recurrent balanced network dynamics generate near-zero average correlations despite large amounts of shared input. This is caused by an active decorrelation of synaptic inputs arising from tracking of *E* and *I* fluctuations which occurs in the balance state.

•Noise correlations in sensory cortices could be reflecting competitive dynamics between similarly ‘tuned’ populations which interact via inhibition. This explains why signal and noise correlations are positively correlated.

•Stimuli can impact the competition and therefore modulate the magnitude and time-scale of correlations.

•The correlations observed in the cortex are most likely **not** about shared-inputs, but reflect the the dynamics of intrinsic cortical states and their interaction with external stimuli.

Collaborators

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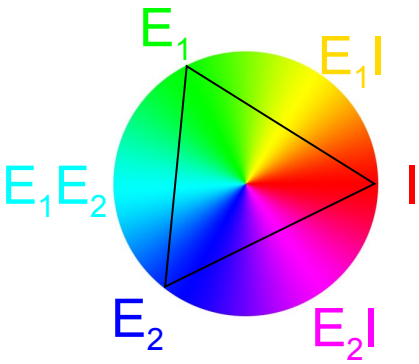
Thanks