Temporal Correlations in Recurrent Neural Networks with Balanced Excitation and Inhibition

Alfonso Renart

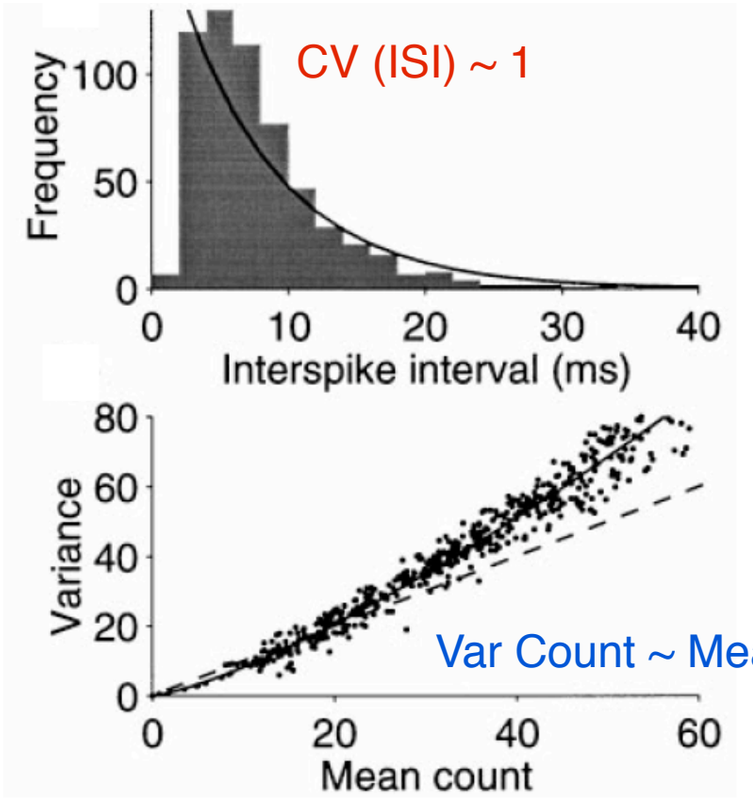
Champalimaud Neuroscience Programme, Lisbon, Portugal

Champalimaud Foundation

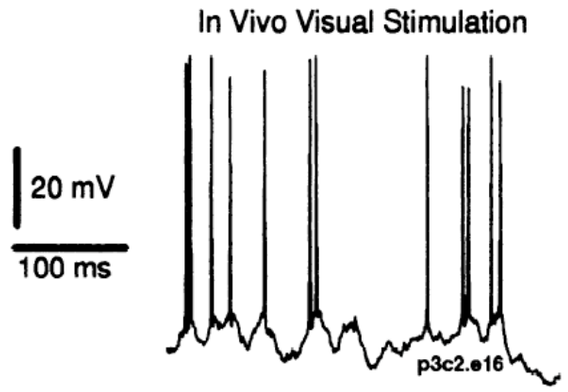
Banbury Center, April 2011

Variability in single neurons & in neuronal circuits

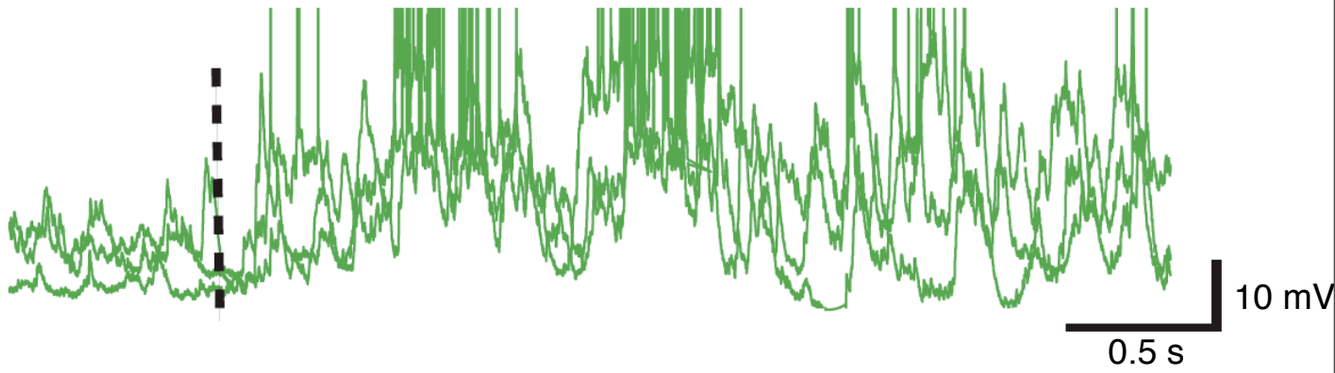
Shadlen et al., J. Neurosci. 1998



Holt et al., J. Neurophys. 1996



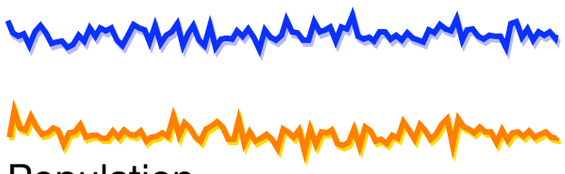
Anderson et al., Science, 2000

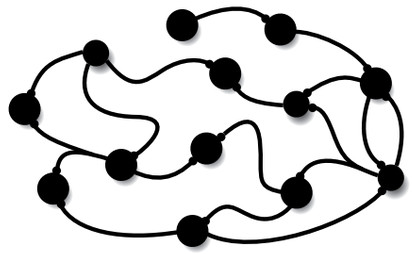


- Temporal variability in single neurons is inherited from their inputs
- Neurons do not 'generate' large amounts of noise

... in neuronal circuits the situation is less clear

Input





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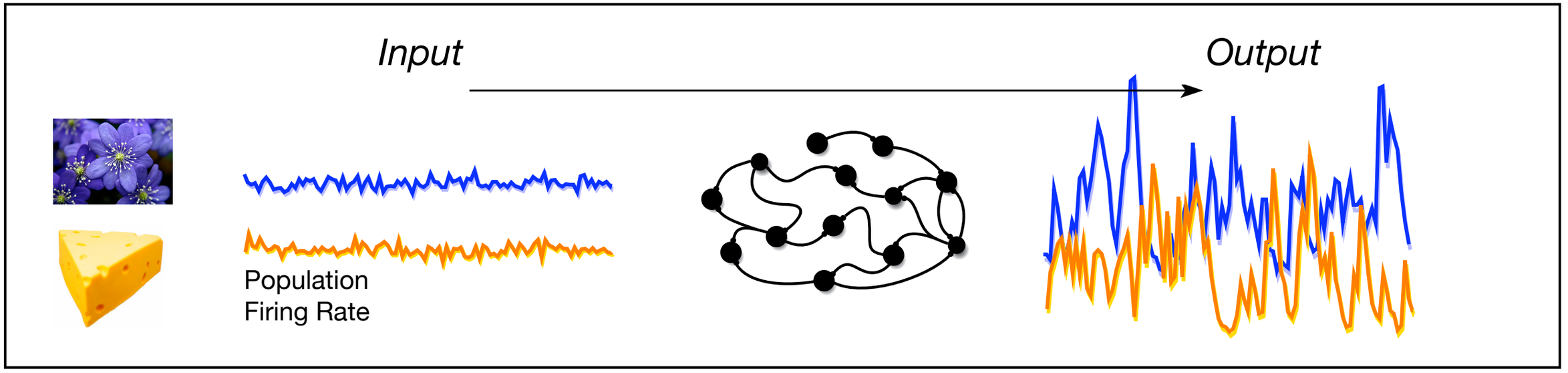

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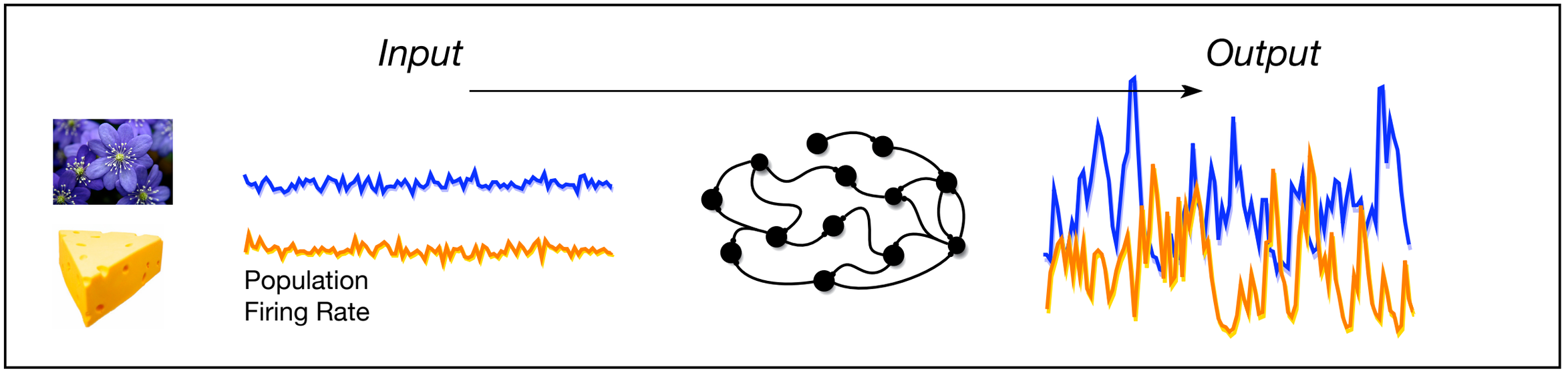
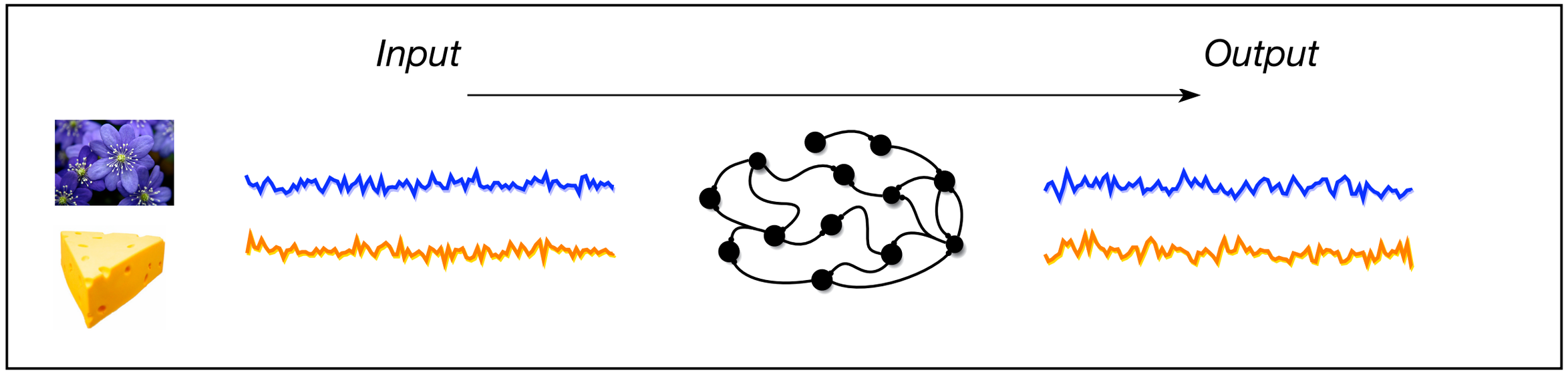
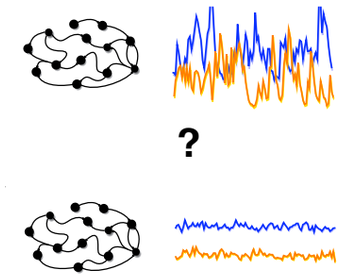
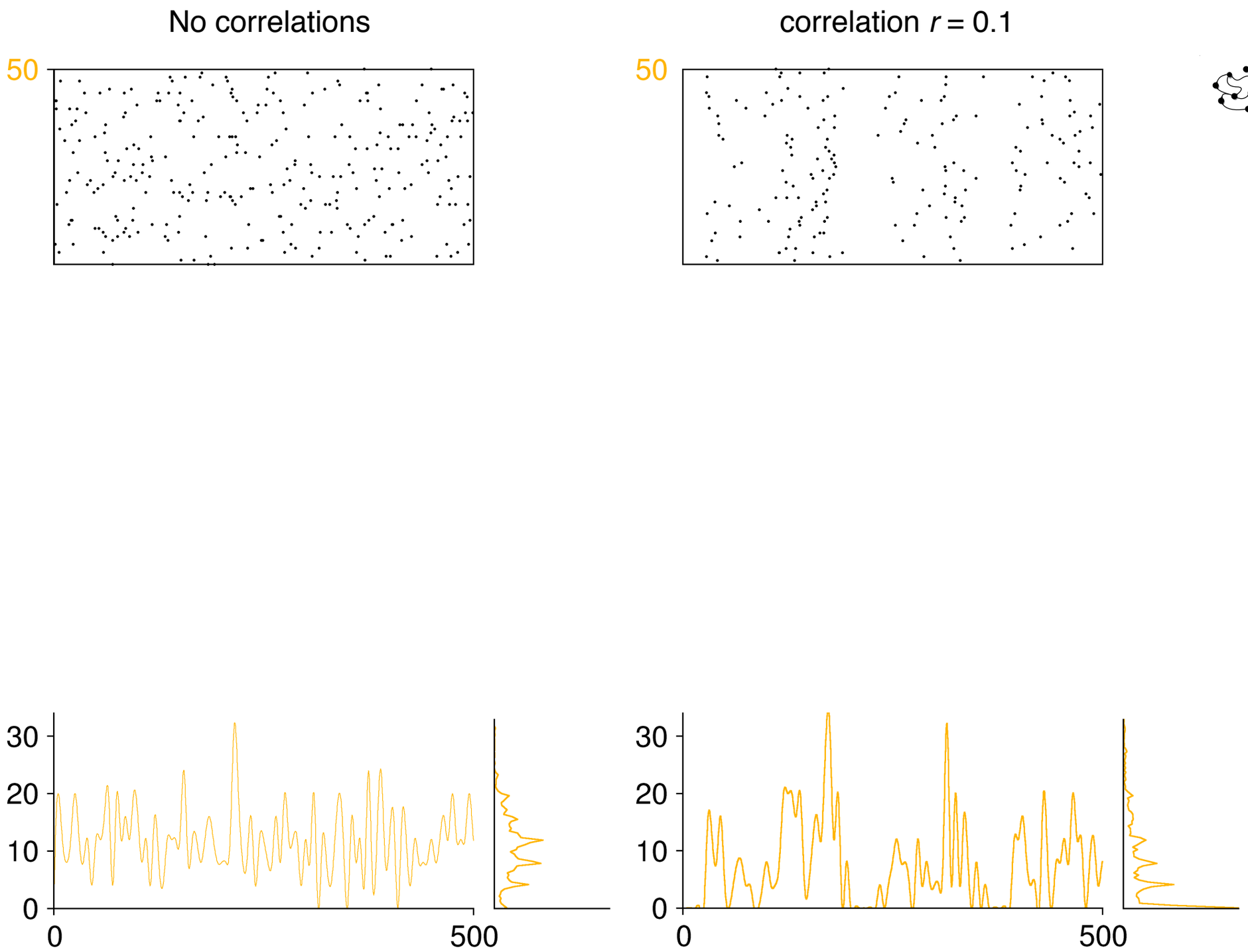


?



The population-averaged temporal correlation is related to the variance of the temporal fluctuations in global activity





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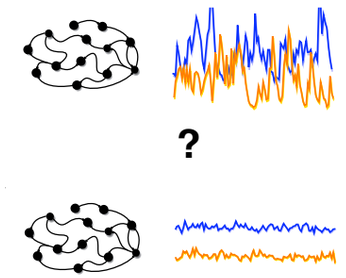
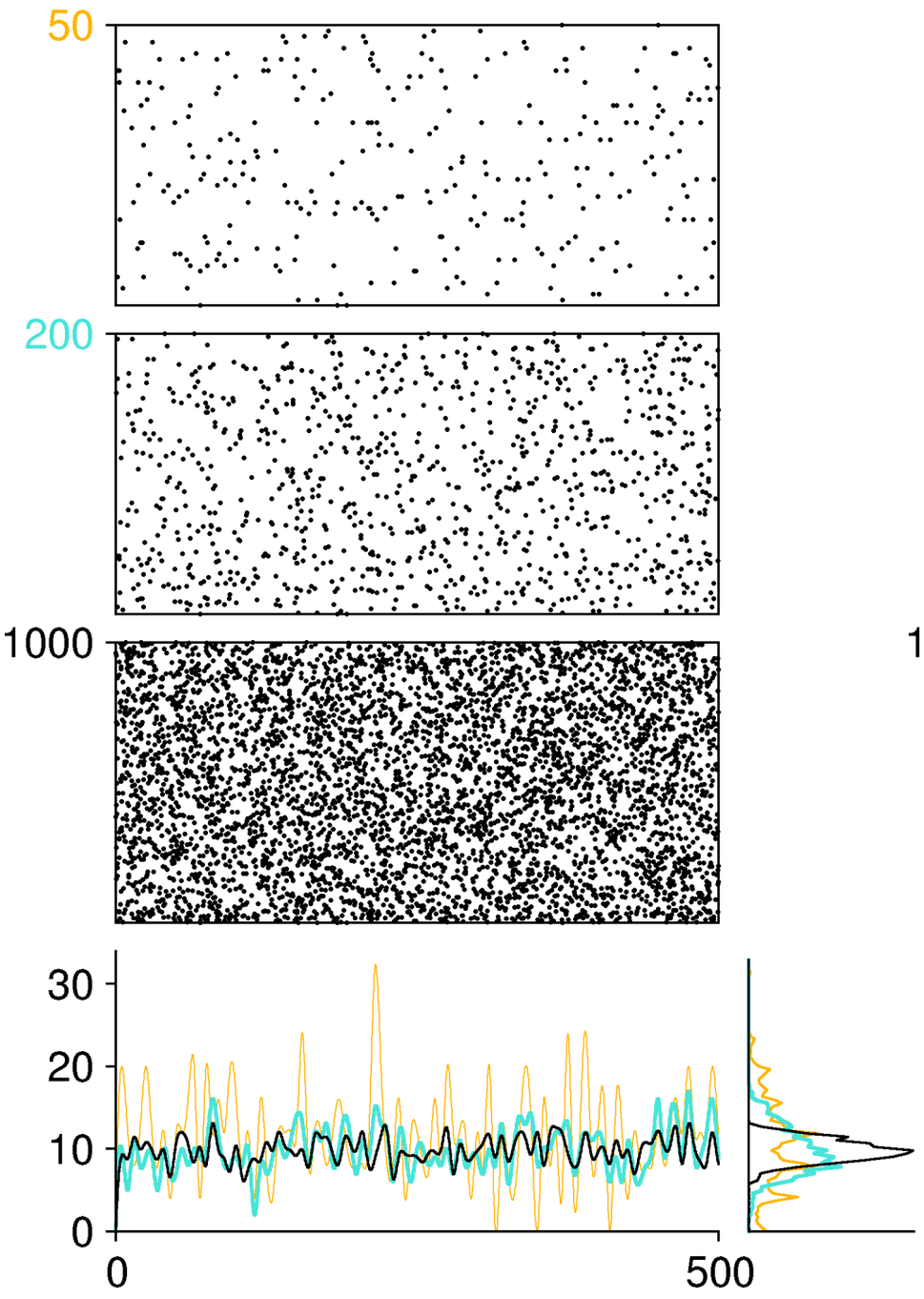
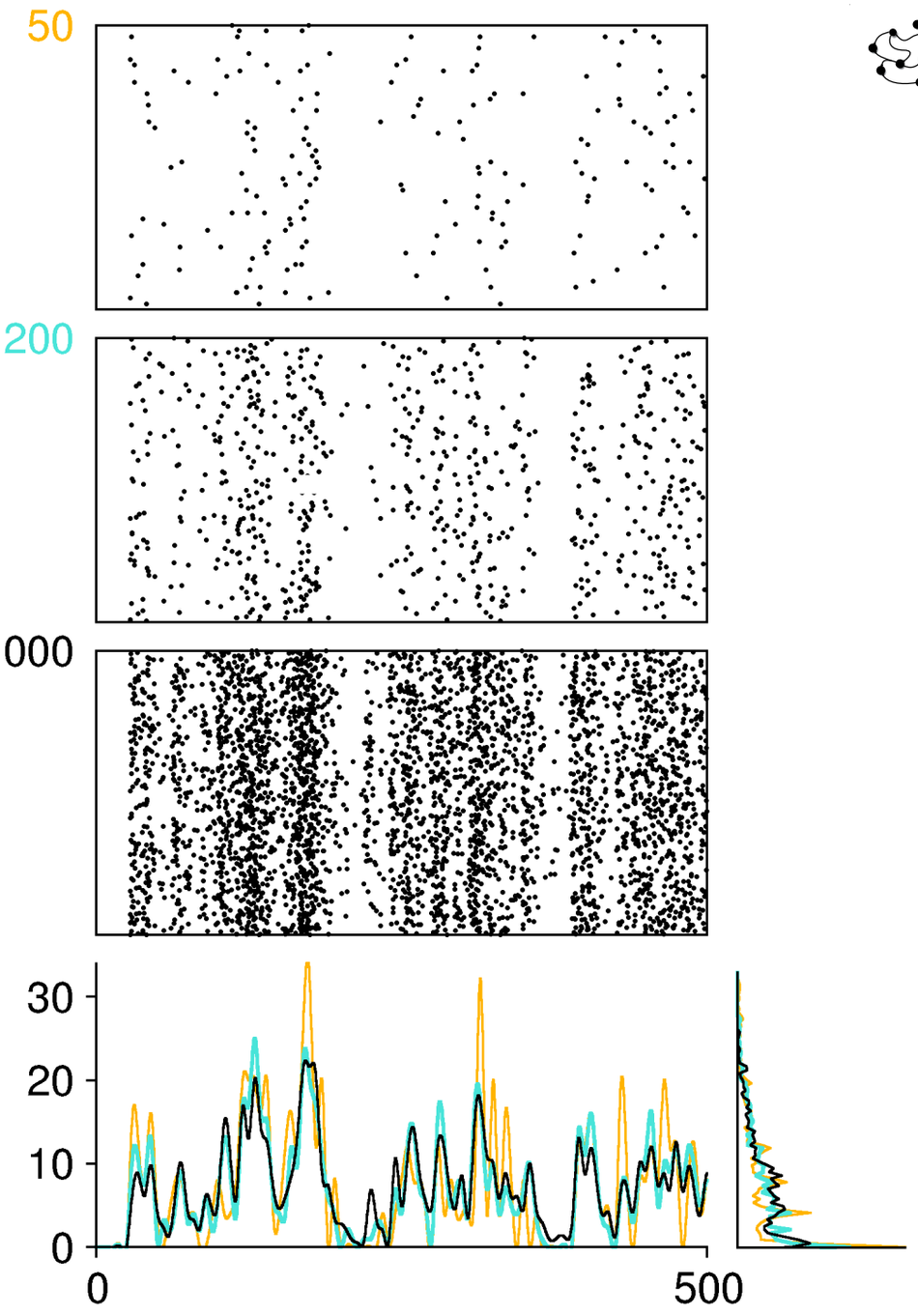


No correlations



correlation $r = 0.1$



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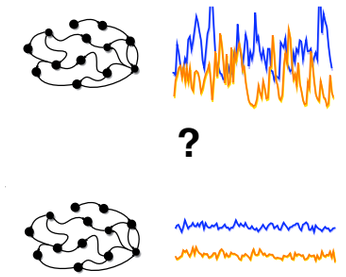


No correlations

correlation $r = 0.1$

50

200

1000

30

20

10

0

0

500

$$\text{Variance} \sim \frac{1}{N} + r$$

100 %

10 %

Variance of inst. pop. rate

r=0.3

r=0.2

r=0.1

r=0

1

10

100

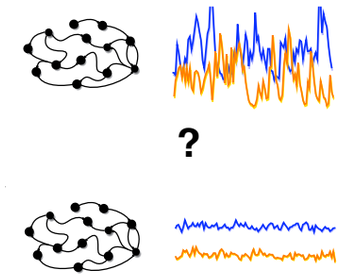
1000

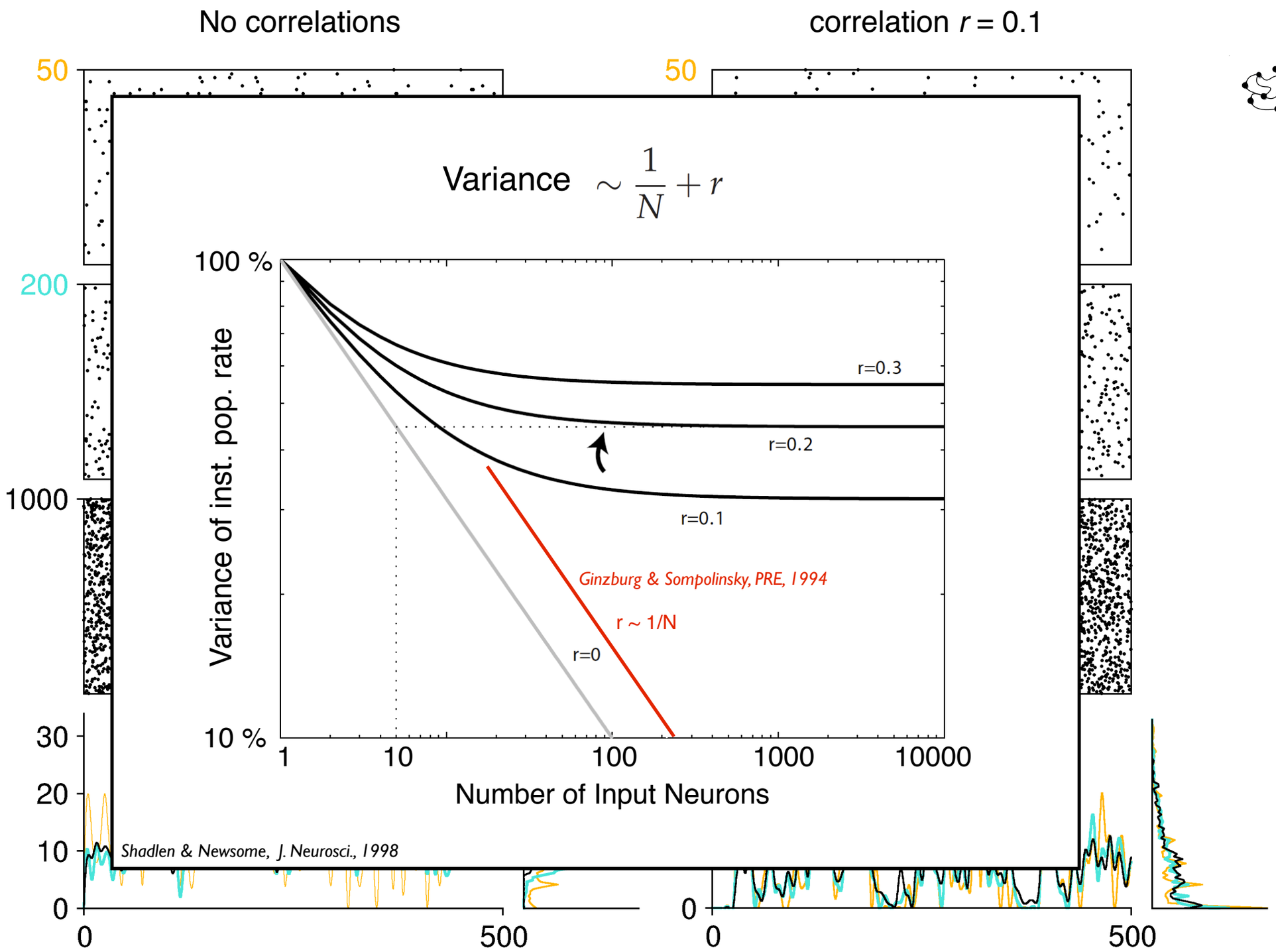
10000

Number of Input Neurons

Shadlen & Newsome, J. Neurosci., 1998

The population-averaged temporal correlation is related to the variance of the temporal fluctuations in global activity





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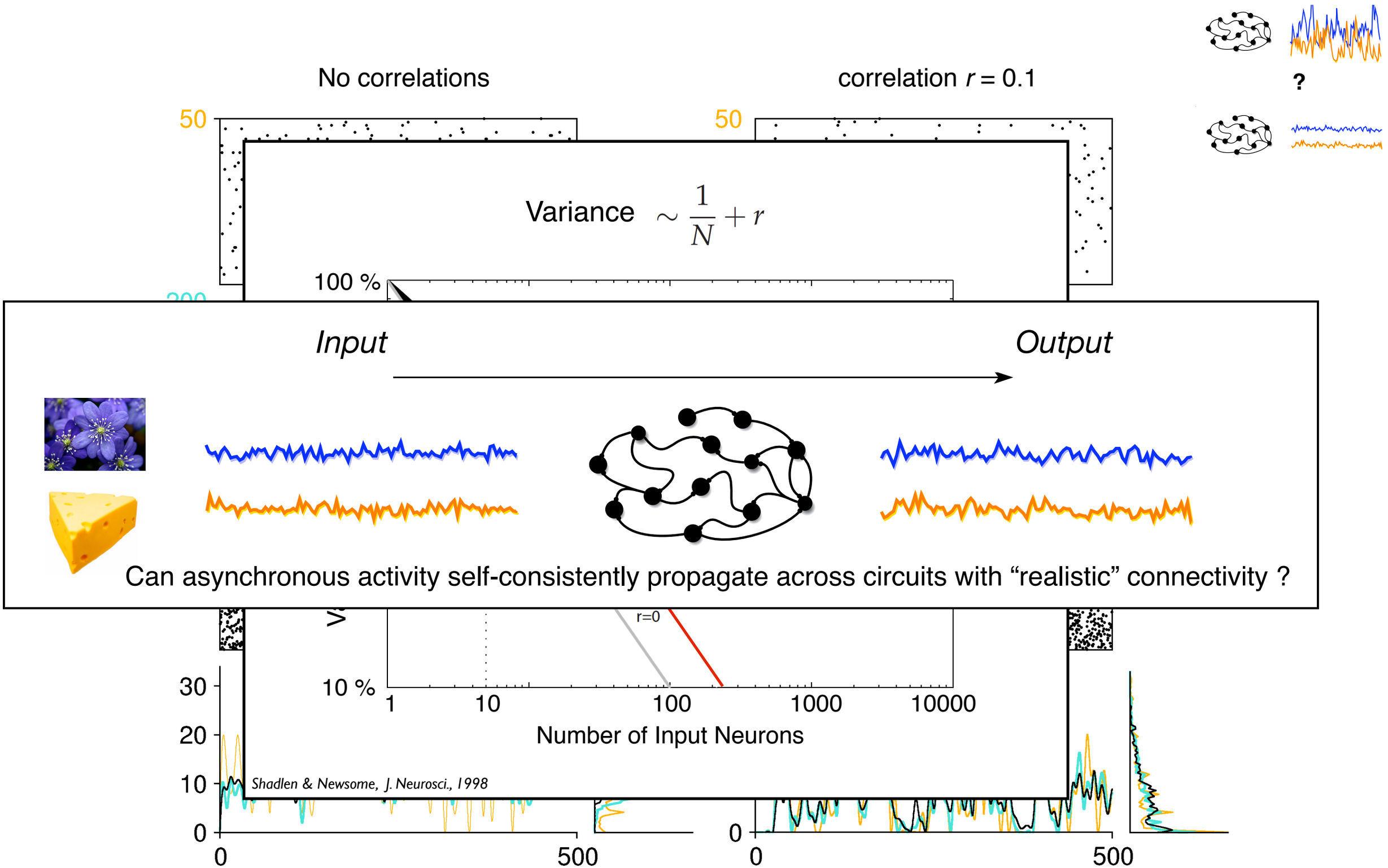

The Journal of Neuroscience, May 15, 1998, *18*(10):3870–3896

The Variable Discharge of Cortical Neurons: Implications for Connectivity, Computation, and Information Coding

Michael N. Shadlen[1] and William T. Newsome[2]

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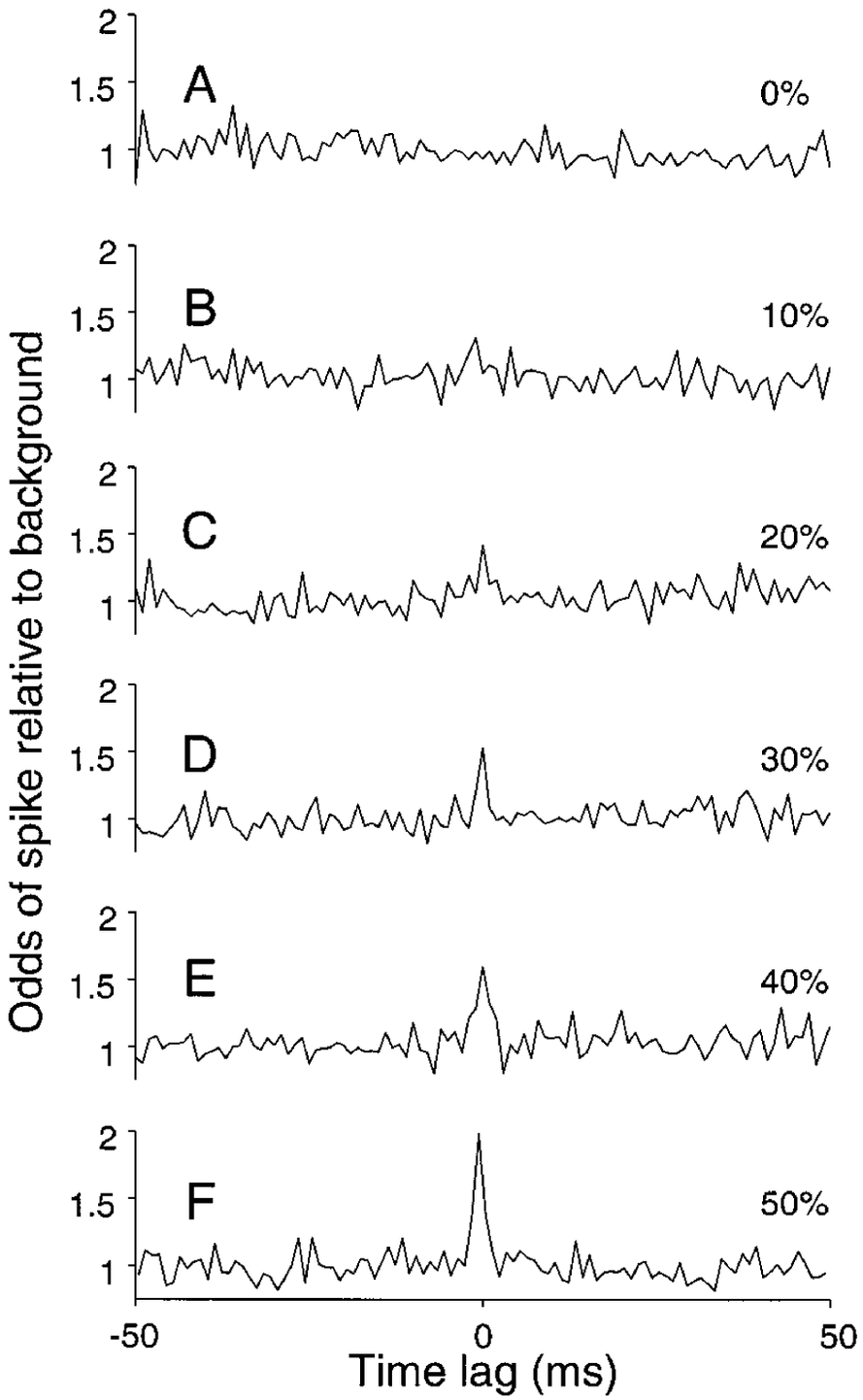

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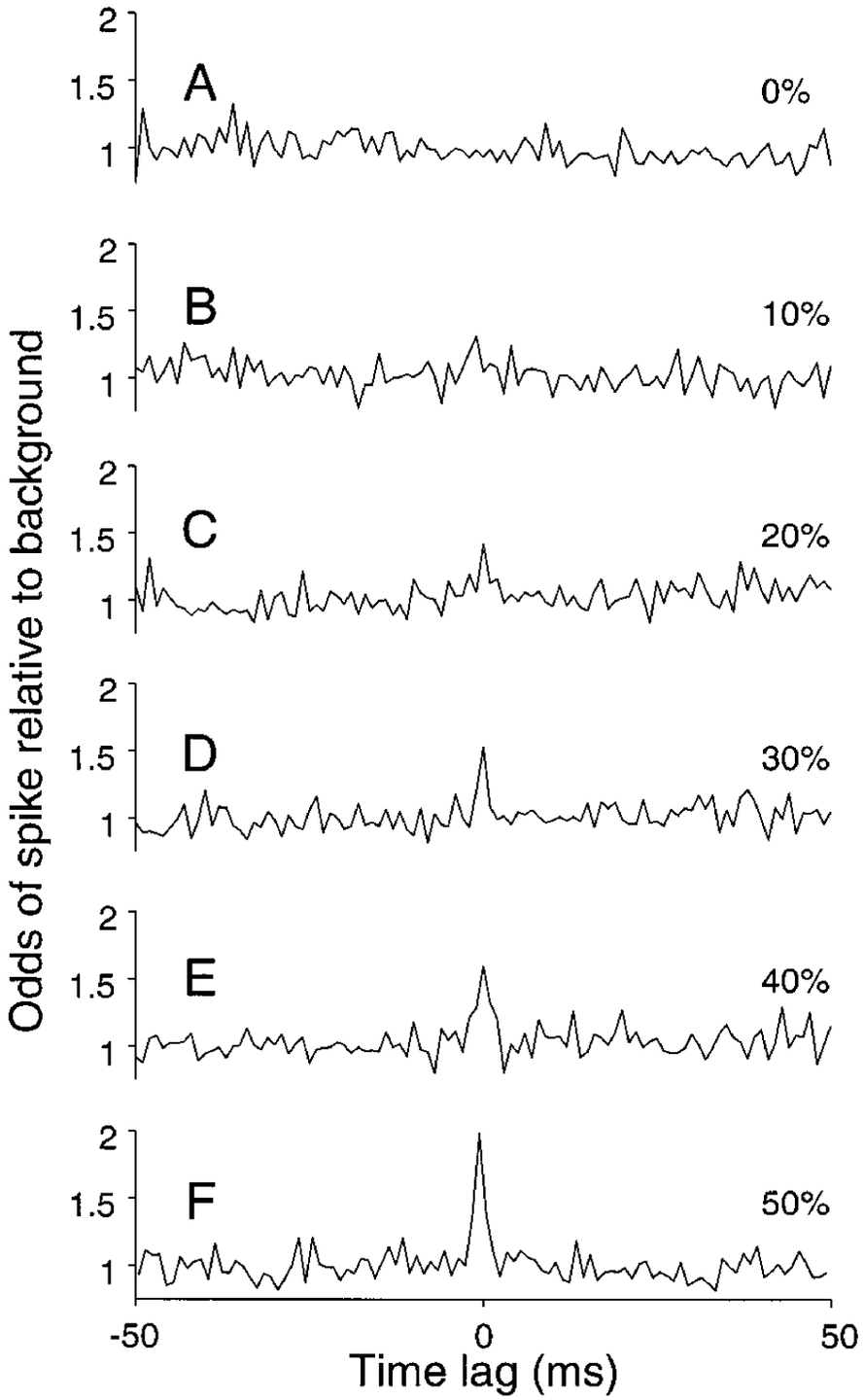

Are correlations due to shared input amplified by the connectivity ?

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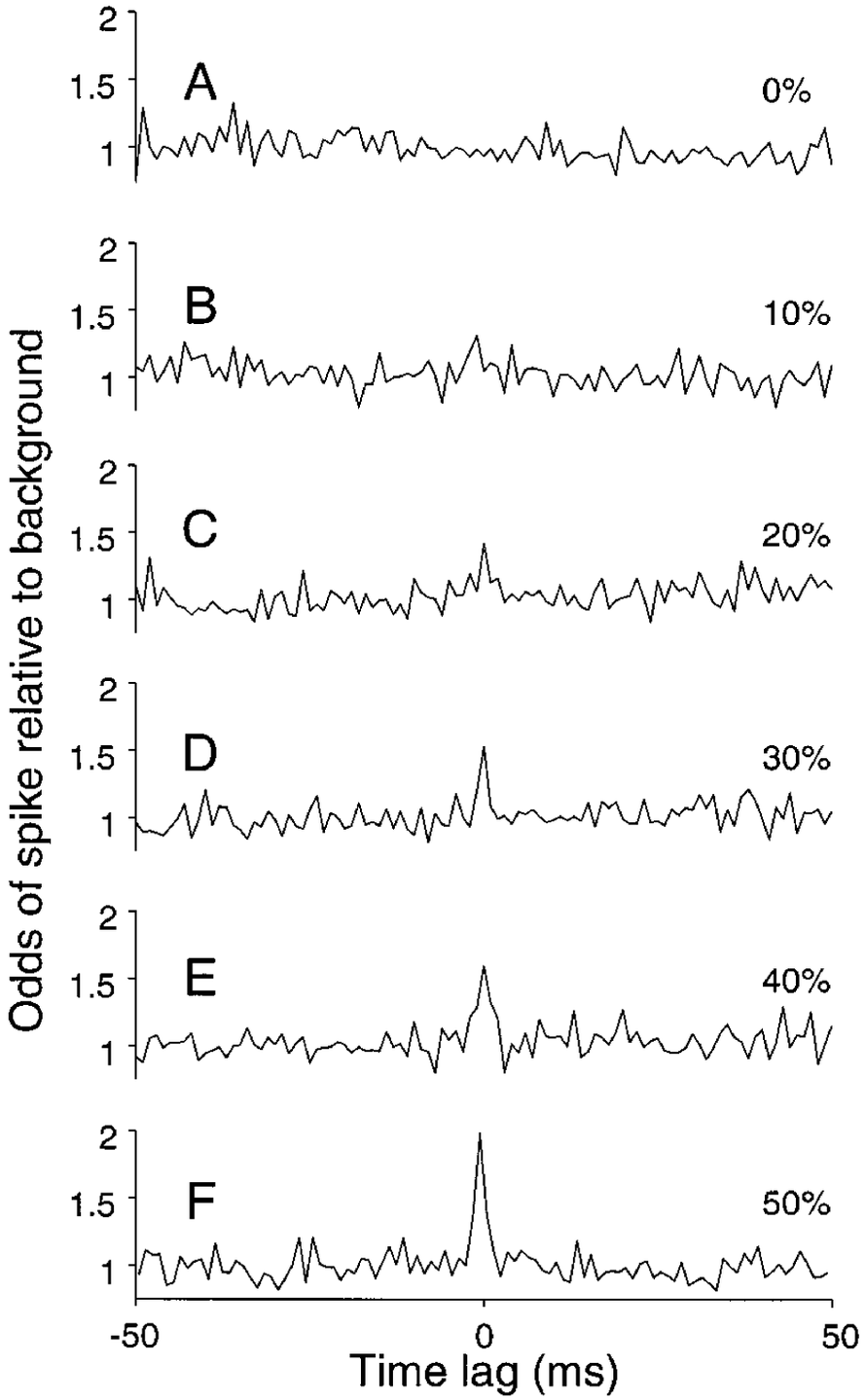

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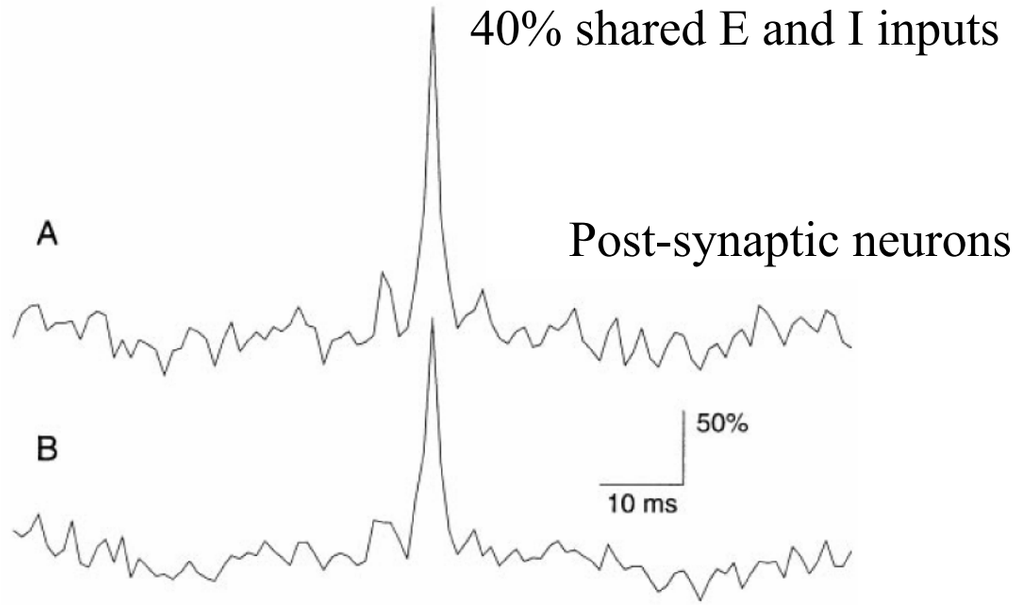

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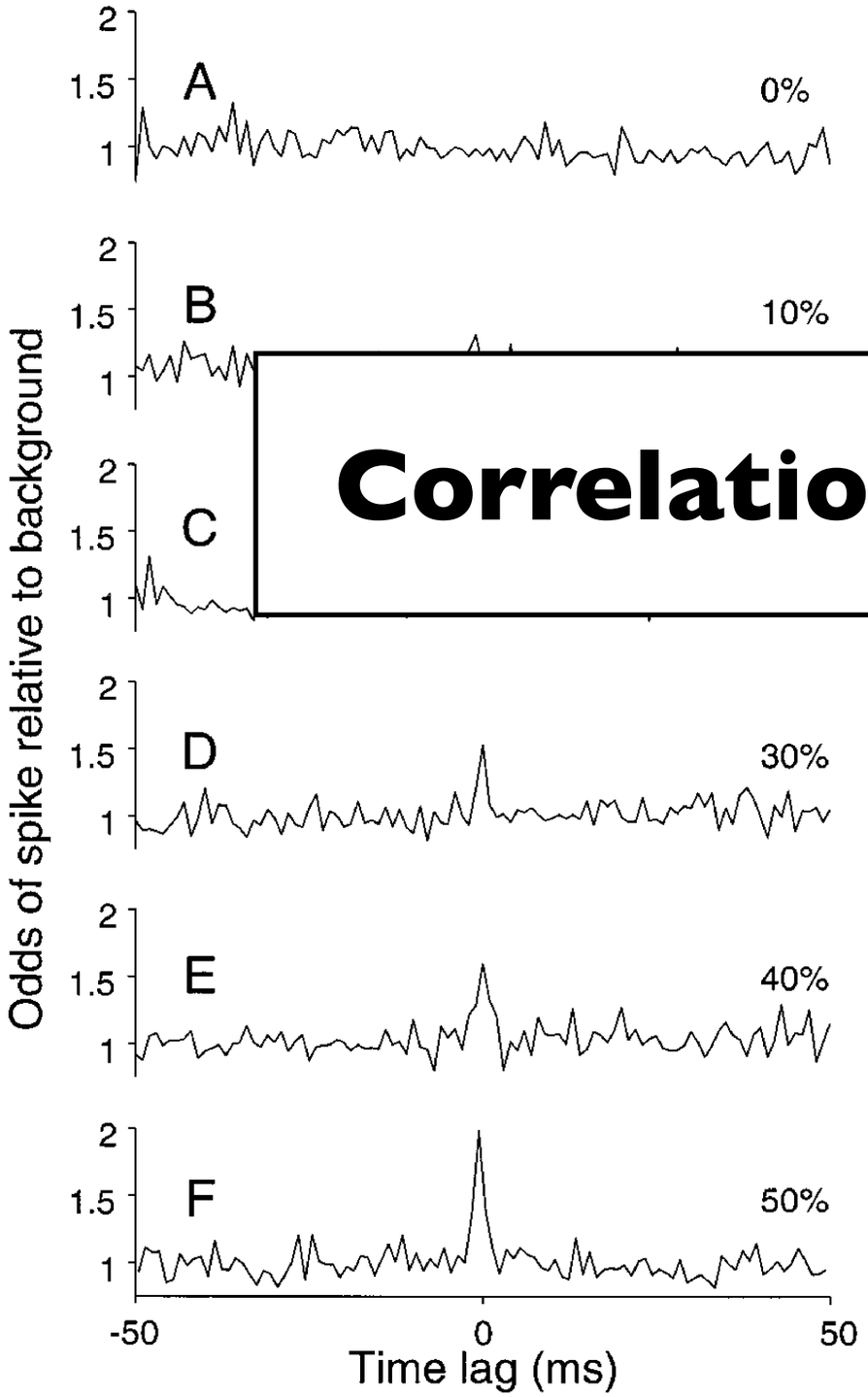
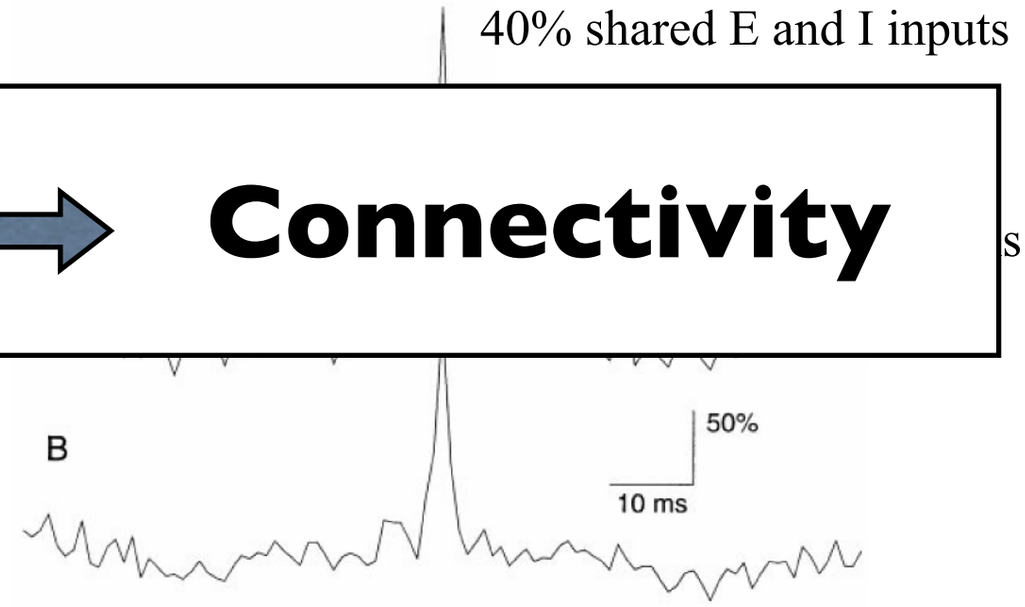
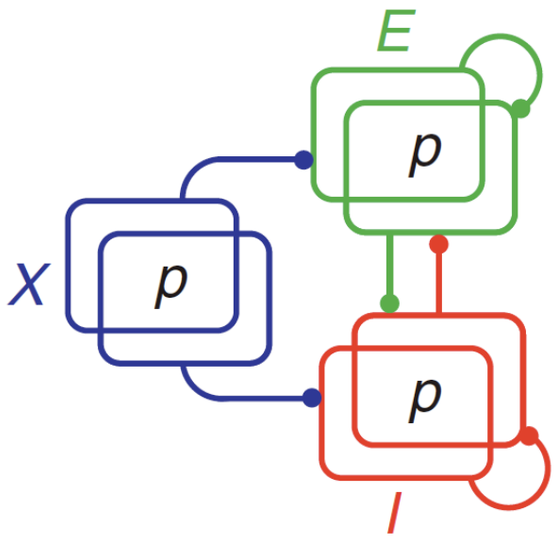
Correlations ⟺ Connectivity



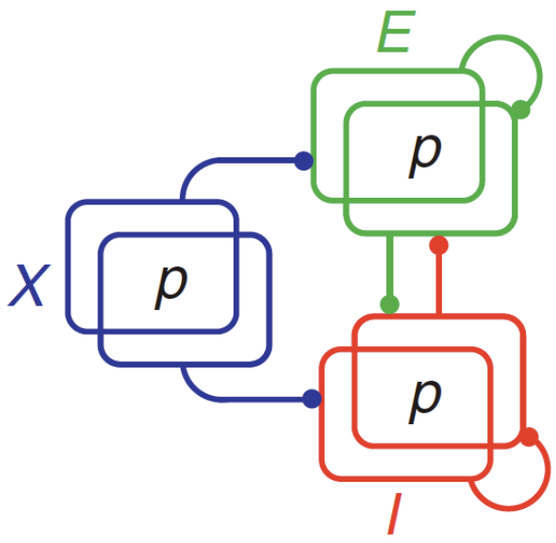


A "densely" connected network



- Neurons are randomly connected with probability *p*
  Pairs of neurons share a fraction *p* of their inputs (on average)

A "densely" connected balanced network



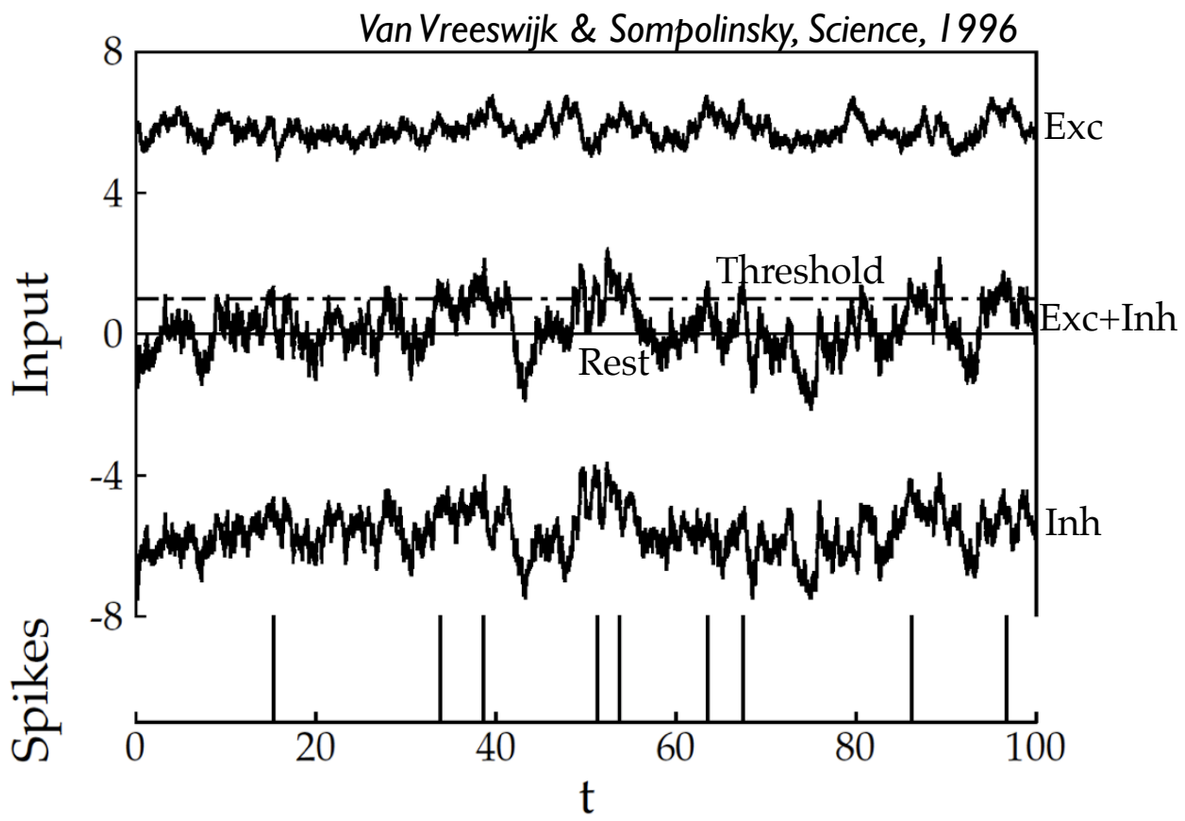
- Neurons are randomly connected with probability *p*

  Pairs of neurons share a fraction *p* of their inputs (on average)

- Neurons are "strongly" coupled, i.e., PSP ~ O(1/√N)

Chaos in Neuronal Networks with Balanced Excitatory and Inhibitory Activity

C. van Vreeswijk and H. Sompolinsky



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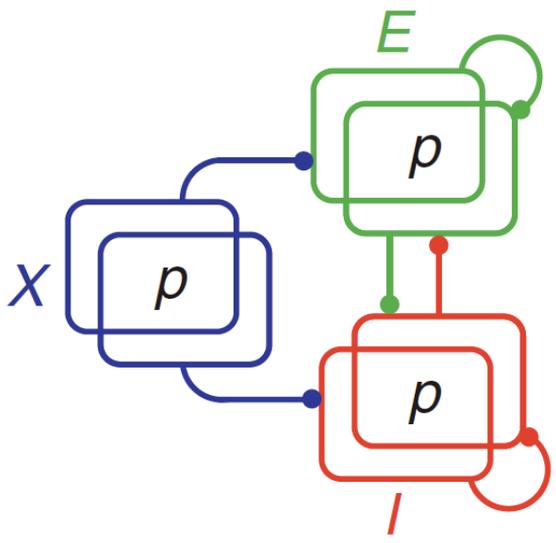

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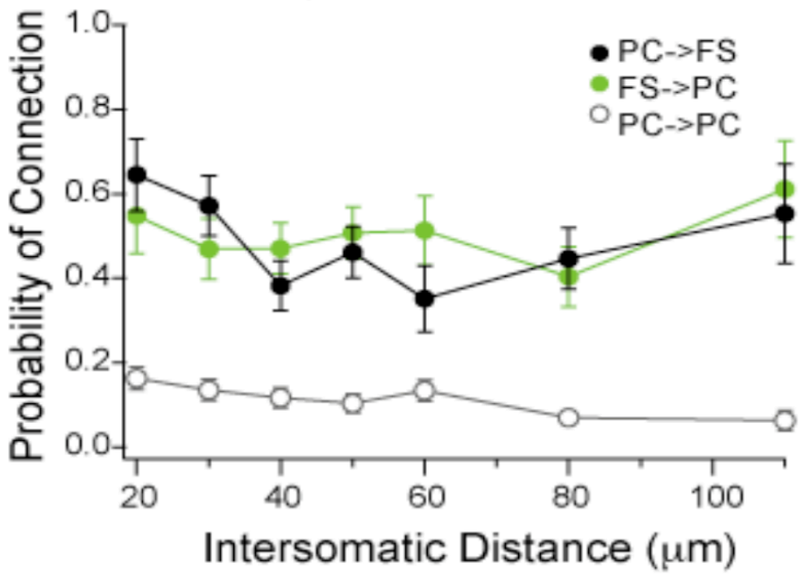
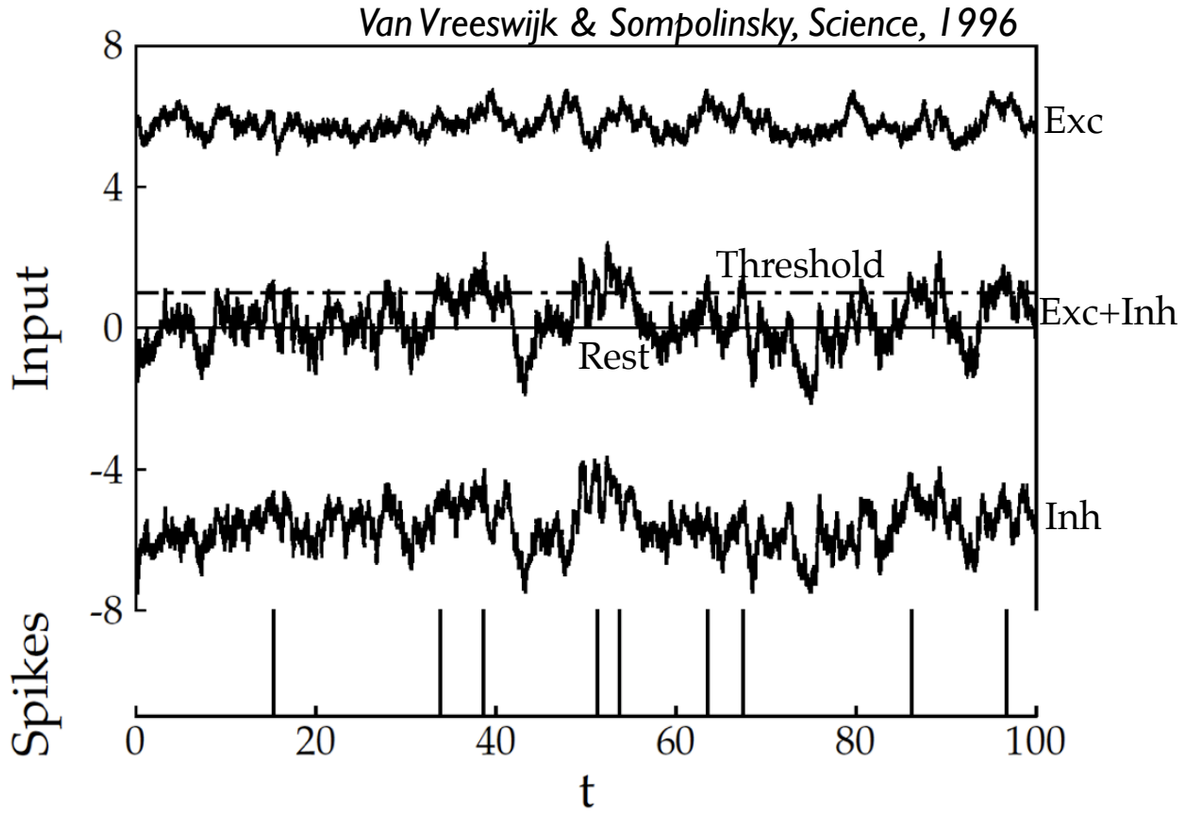


Van Vreeswijk & Sompolinsky, Science, 1996



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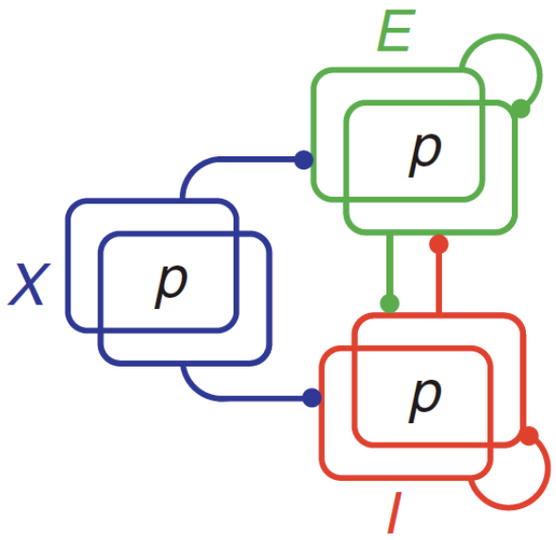

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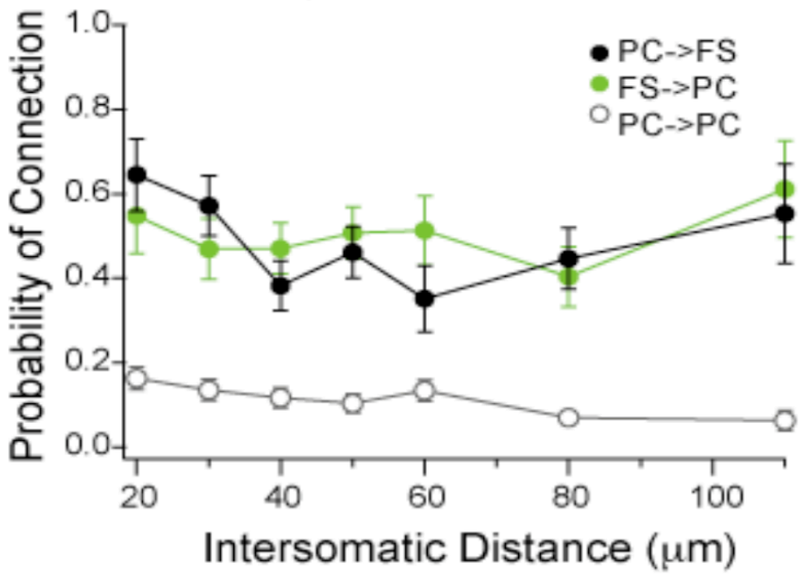
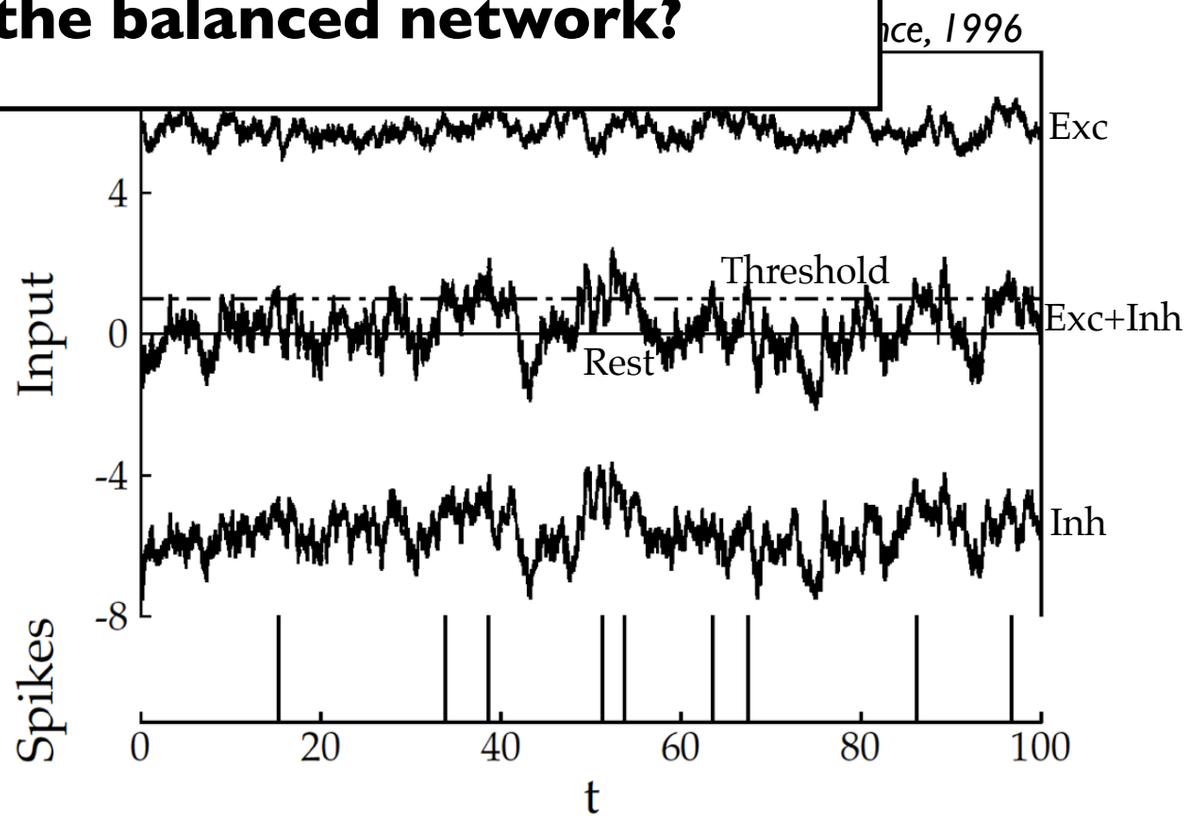
Chaos in Neuronal Networks with Balanced Excitatory and Inhibitory Activity

What is the effect of shared input on the dynamics of the balanced network?

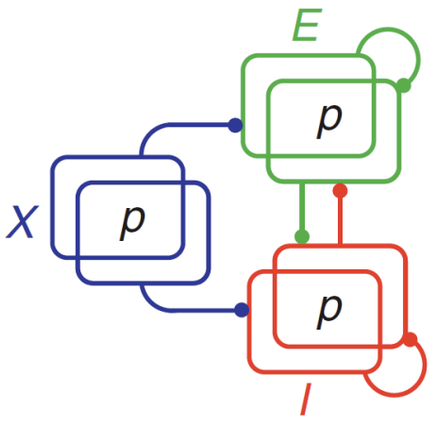
Oswald et al., J. Neurosci., 2009

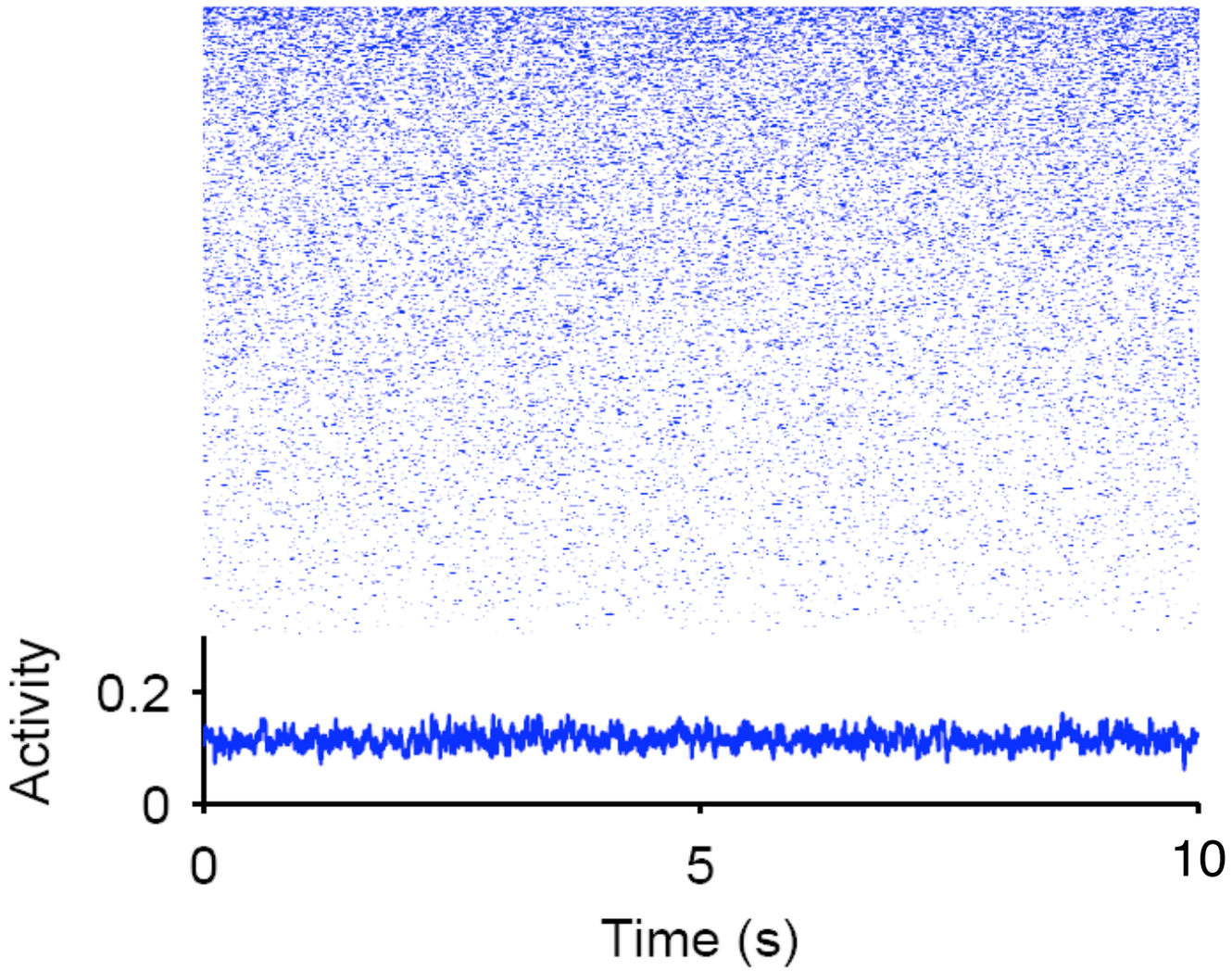


nce, 1996



Temporal correlations are very weak in the balanced network





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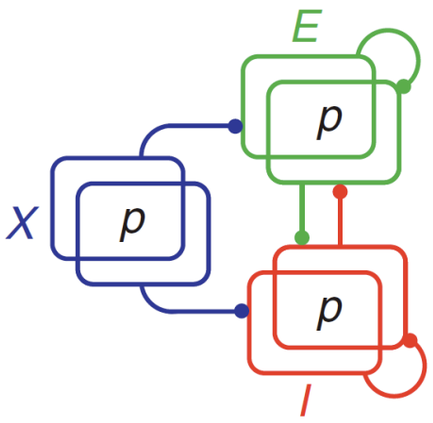
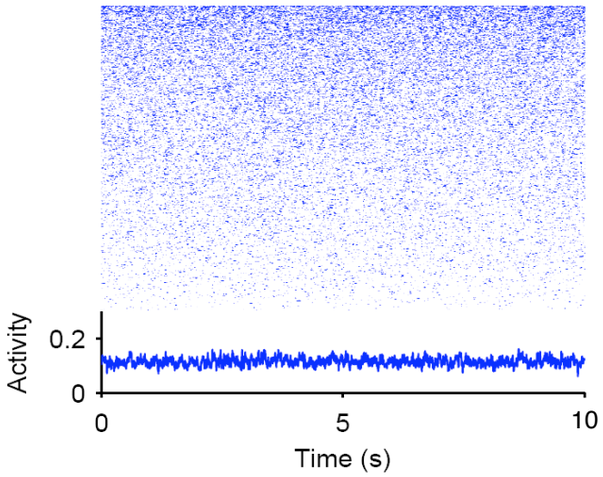
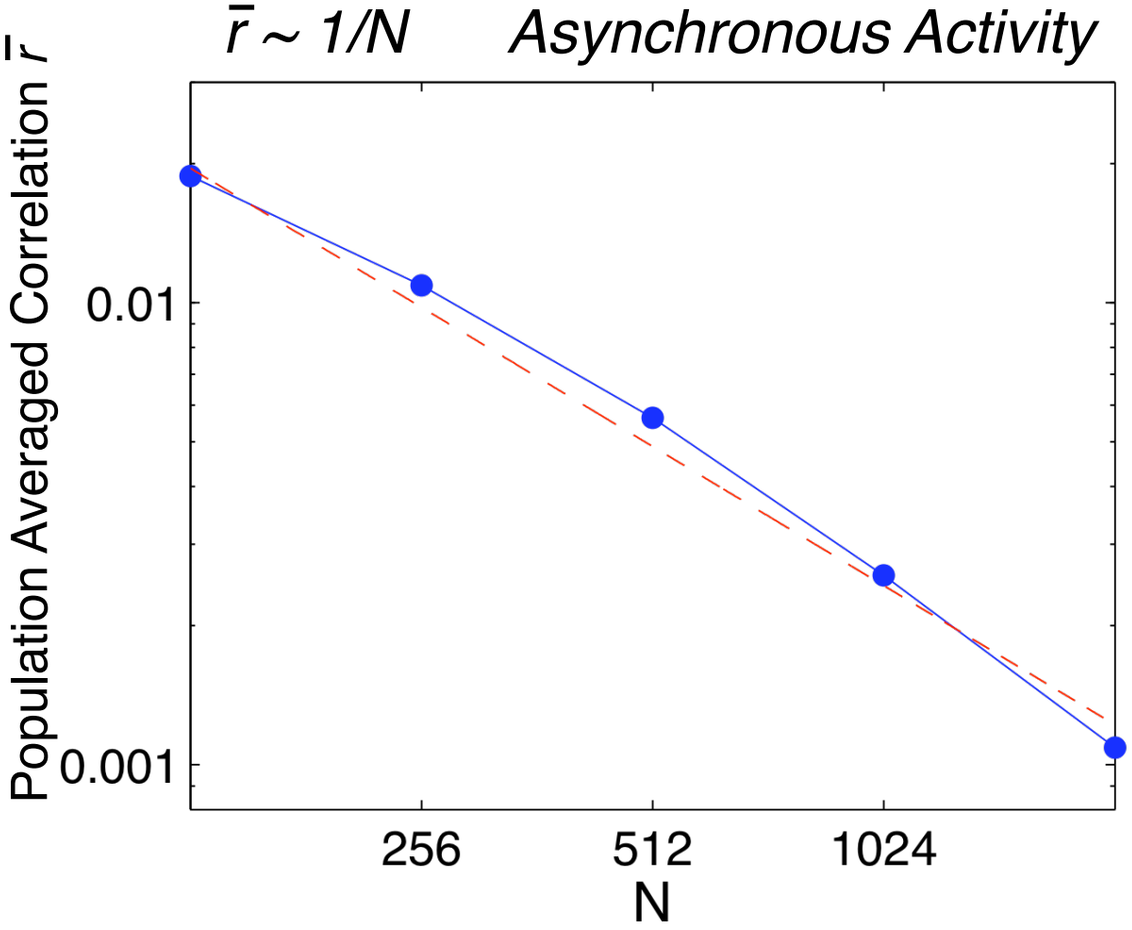
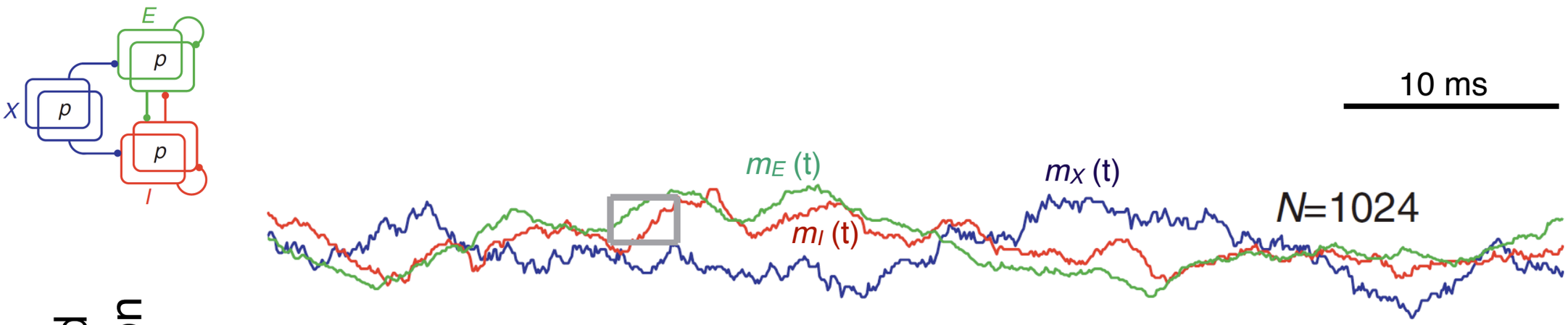
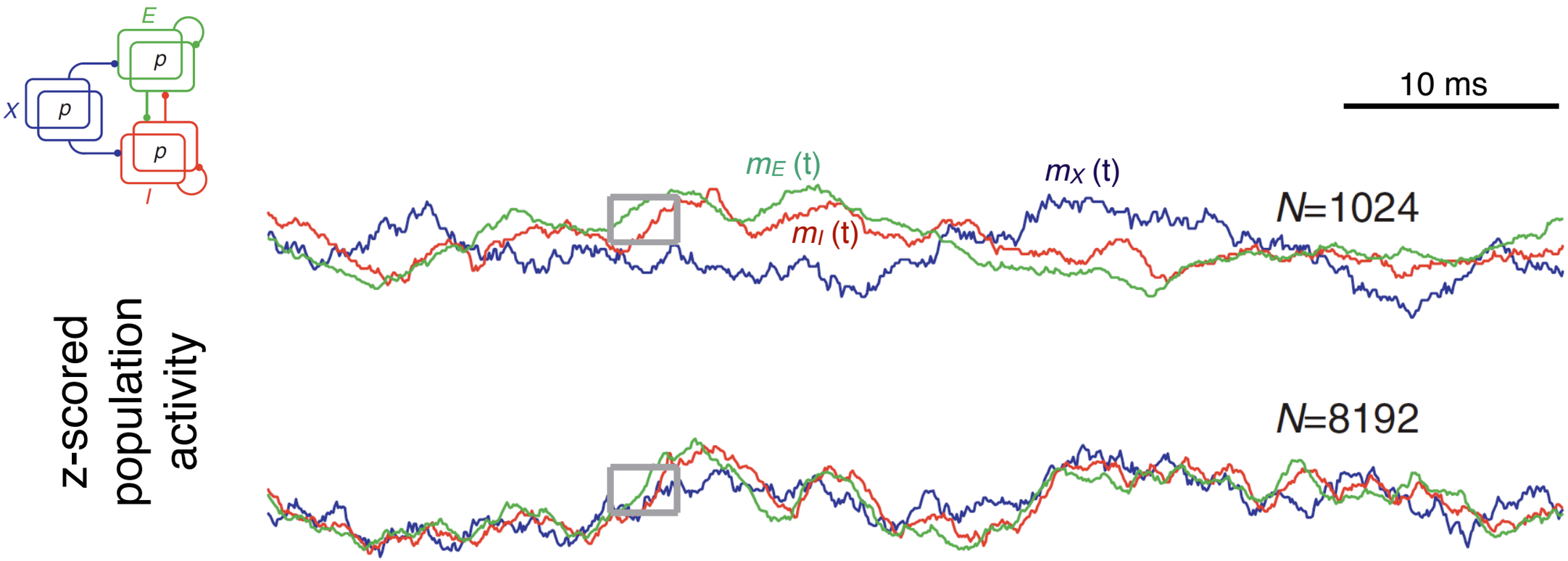
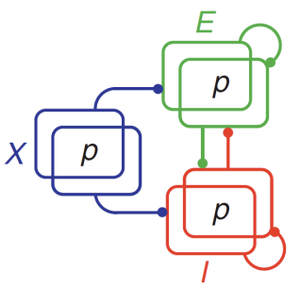


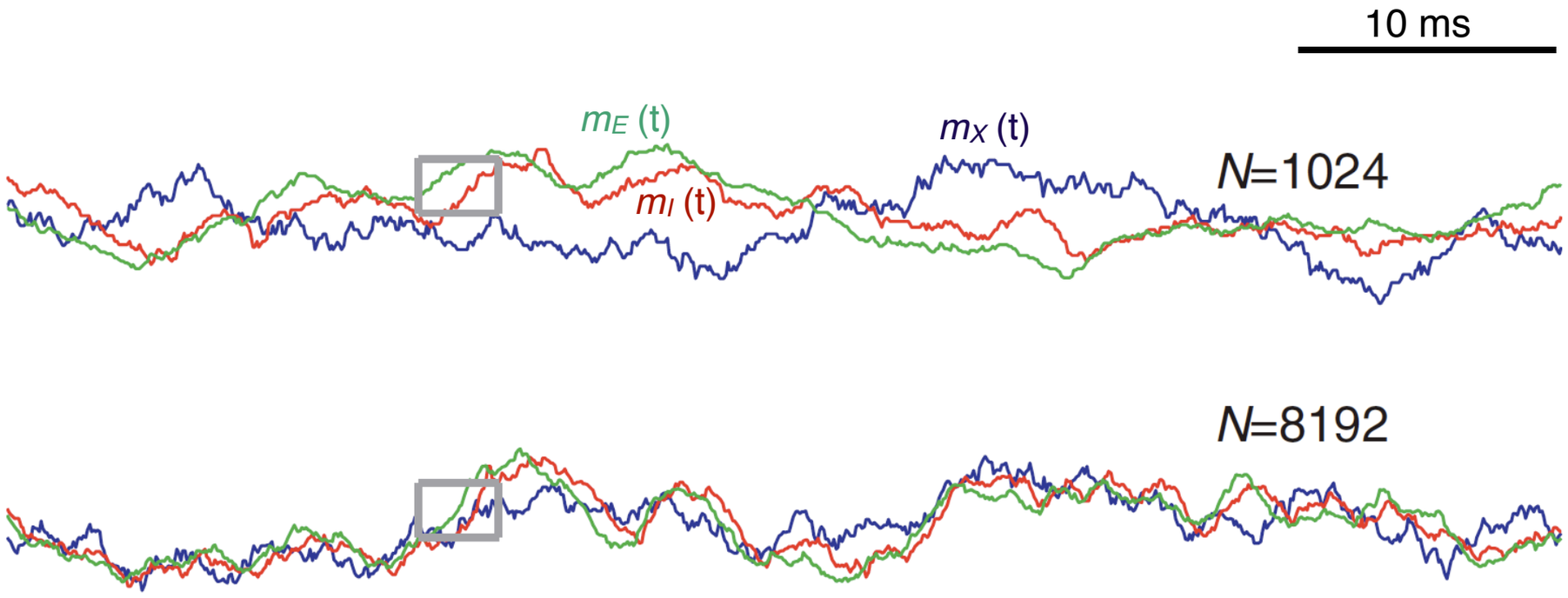





E
p
X
p
p
I
10 ms
m_E (t)
m_X (t)
m_I (t)
N=1024
z-scored
population
activity

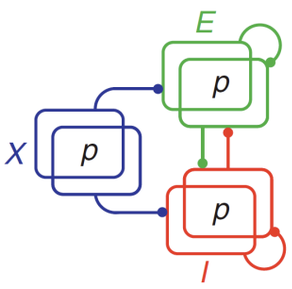

E
p
X
p
p
I
10 ms
m_E (t)
m_X (t)
m_I (t)
N=1024
N=8192
z-scored
population
activity

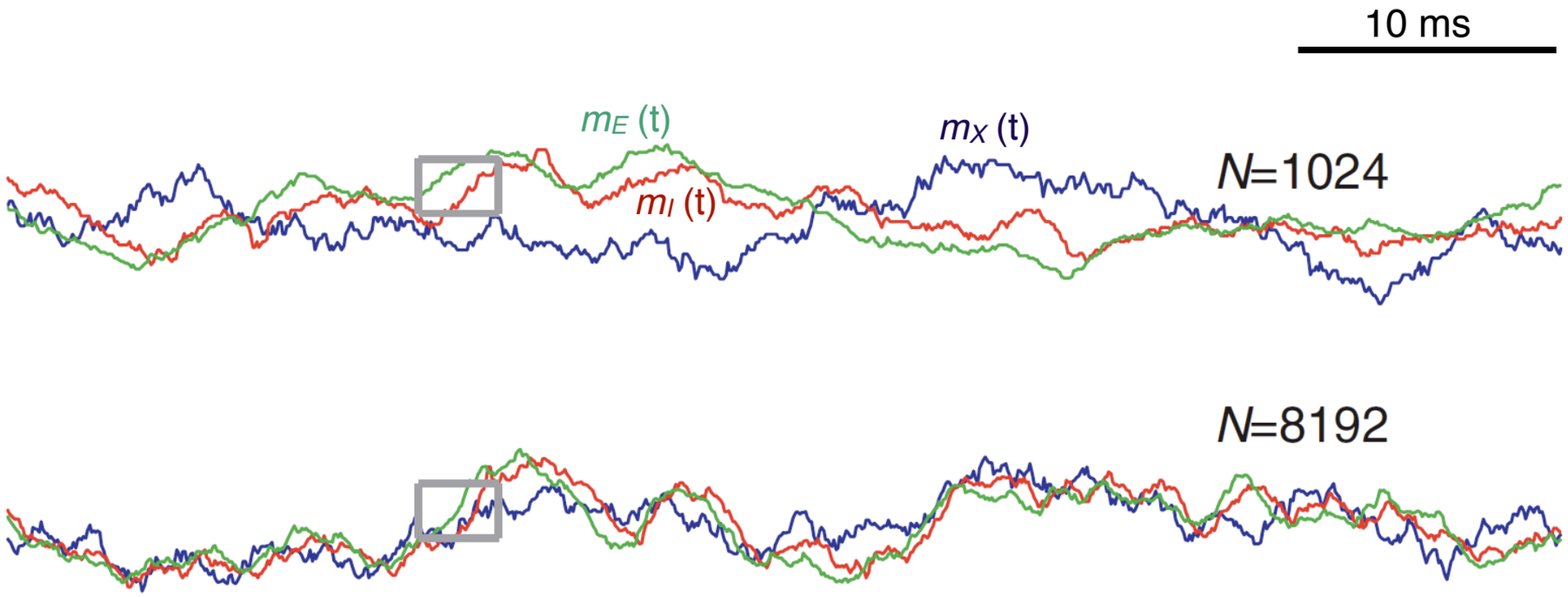




... asymptotically tracking becomes perfect !!

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





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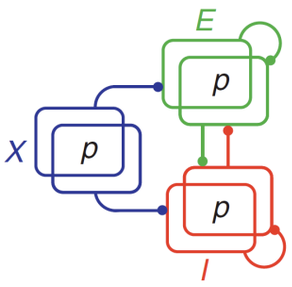
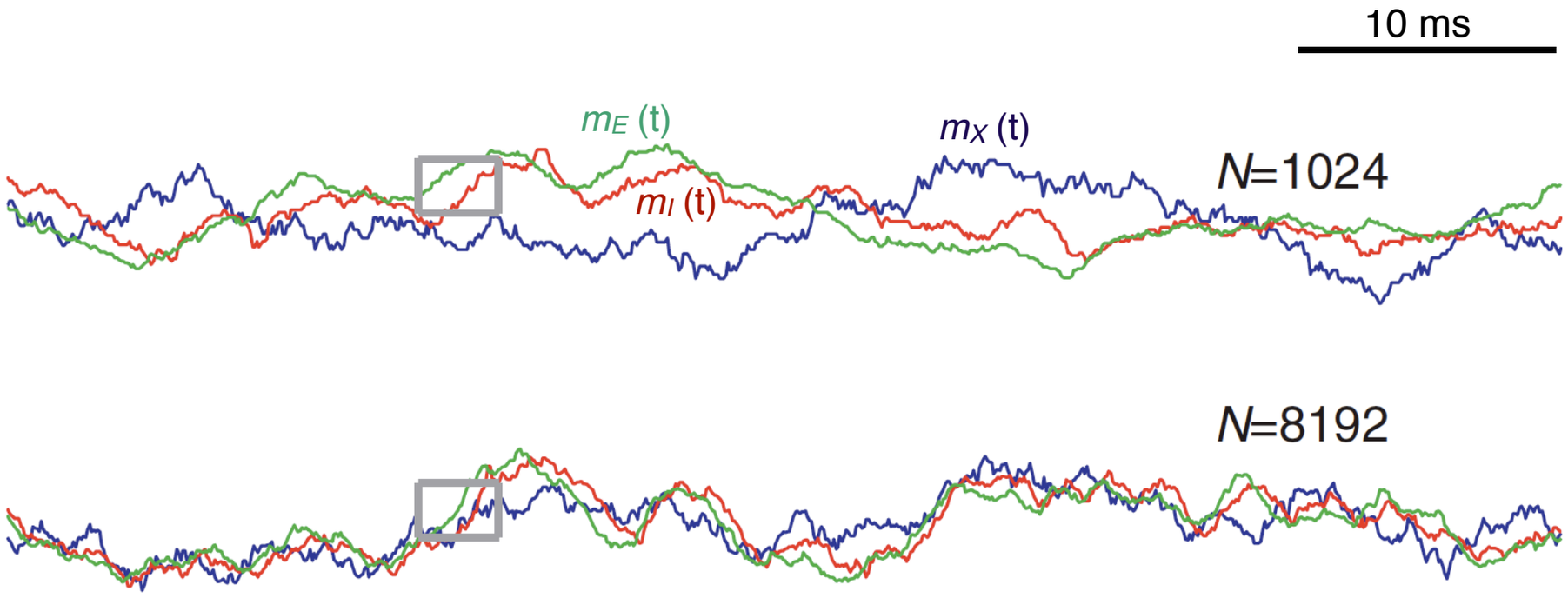
PSP ~ O(1/√N)

...even small “random” fluctuations in activity are big enough to recruit inhibitory feedback





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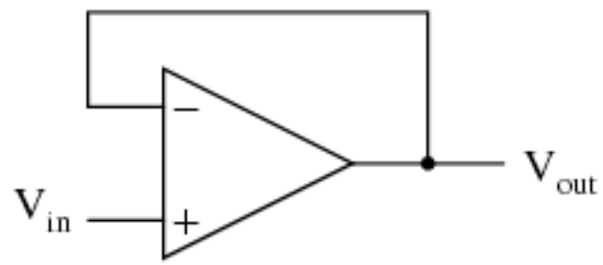
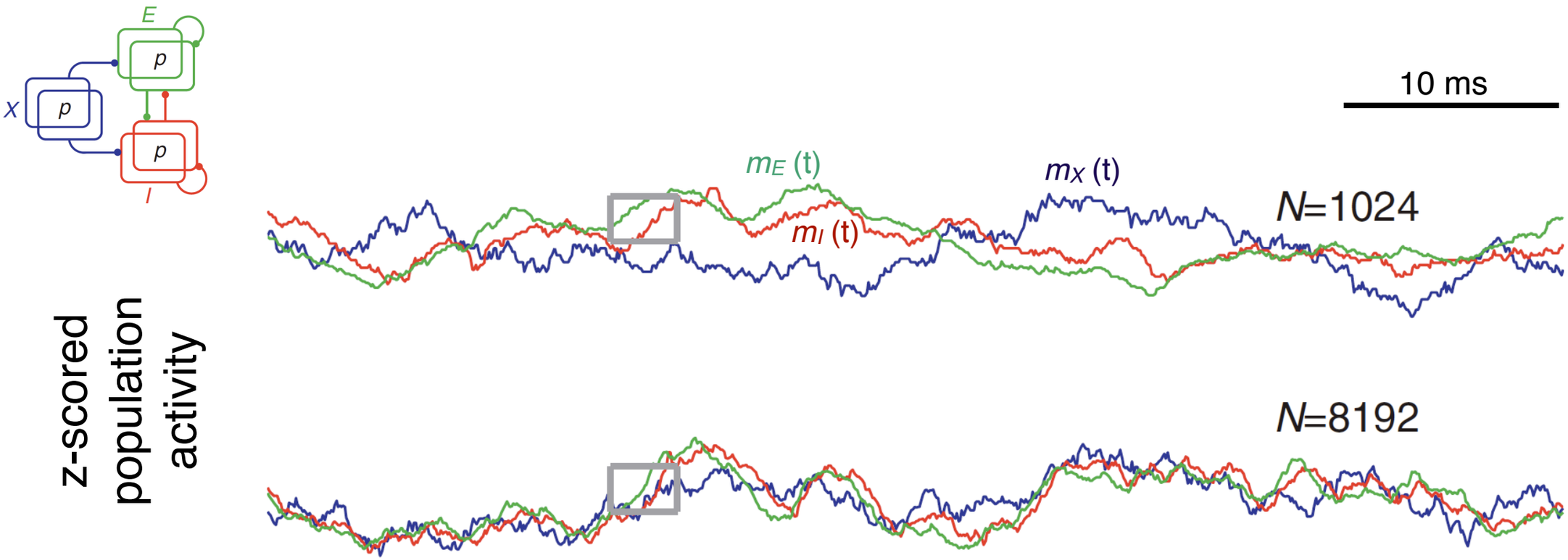
The densely connected balanced network implements an extremely efficient negative feedback loop (~ an Op. Amp.) ... so efficient that it tracks the noise!!





... but what about shared input ?

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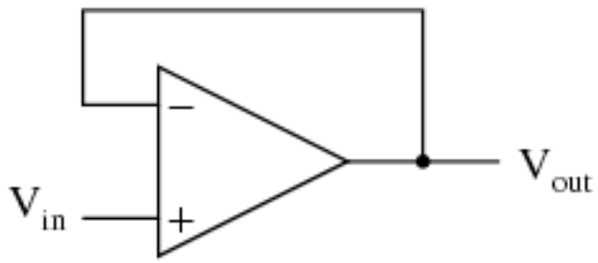
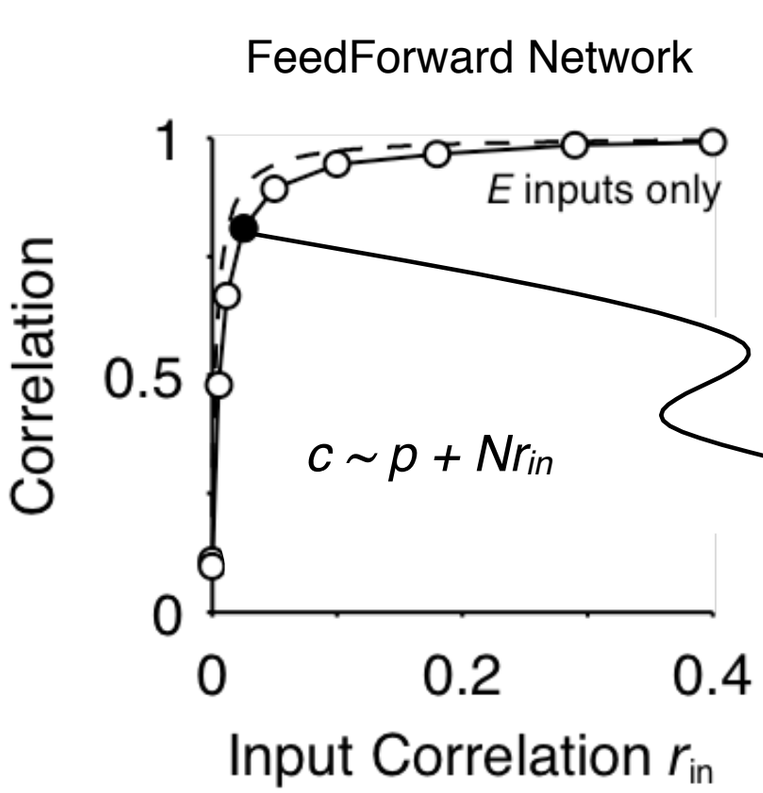
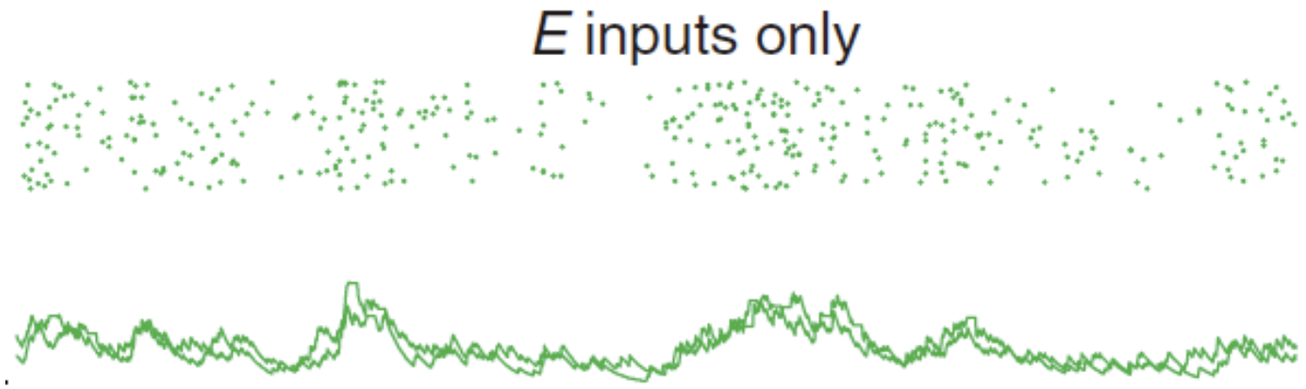
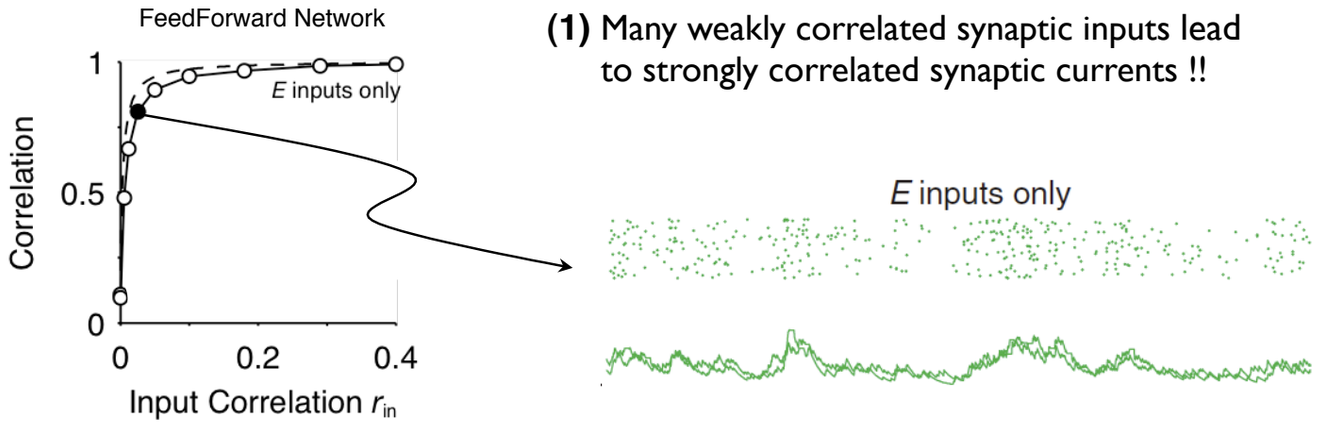




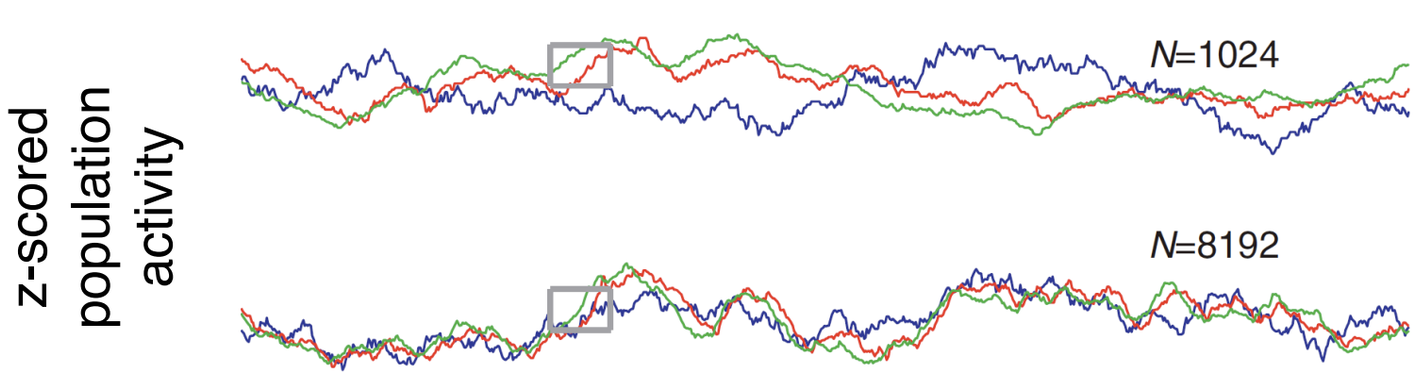
(1) Many weakly correlated synaptic inputs lead to strongly correlated synaptic currents !!

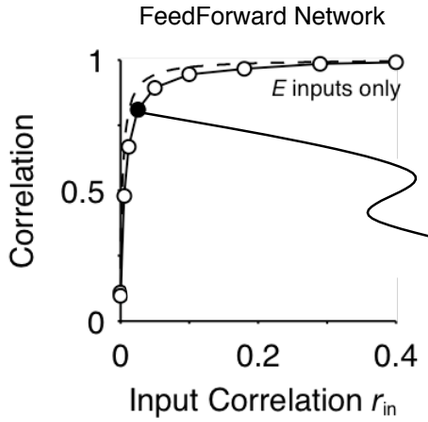




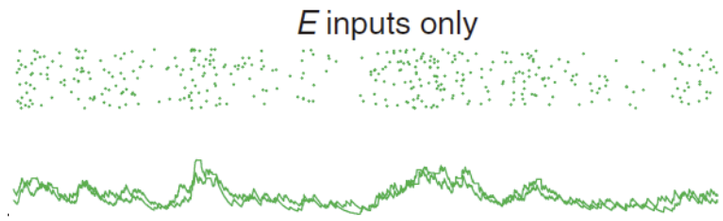
(1) Many weakly correlated synaptic inputs lead to strongly correlated synaptic currents !!

(2) *E-I* tracking generates (very weak) positive correlations between *E* and *I* neurons

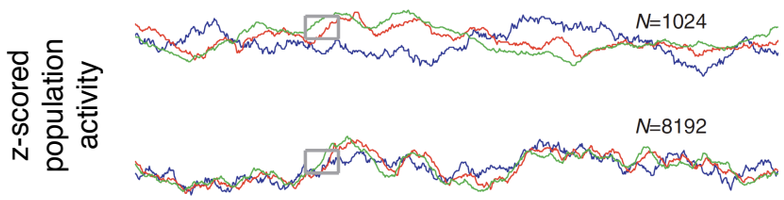




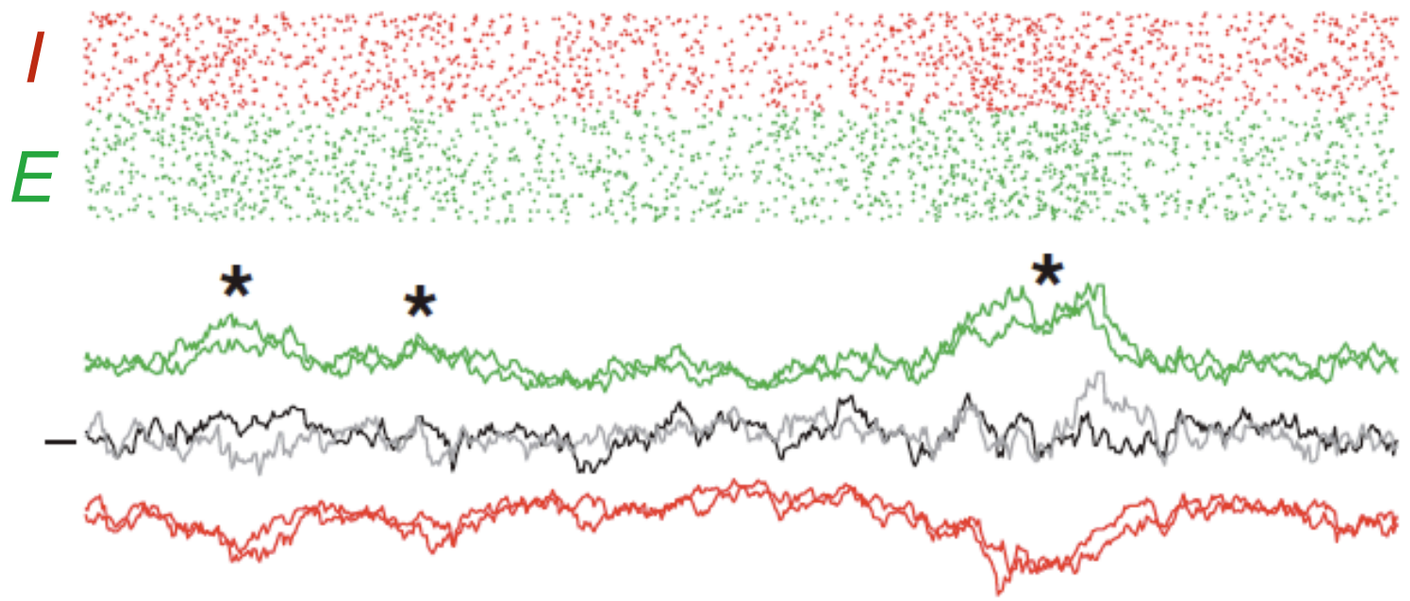
(1) Many weakly correlated synaptic inputs lead to strongly correlated synaptic currents !!



(2) *E-I* tracking generates (very weak) positive correlations between *E* and *I* neurons



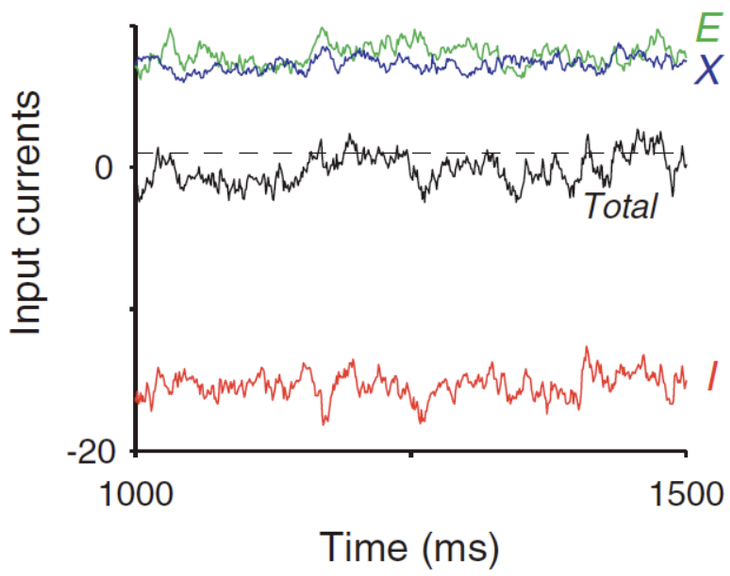
(3) Weak positive correlations between *E* and *I* neurons generate strong **negative** correlations in synaptic currents which cancel positive correlations due to shared input



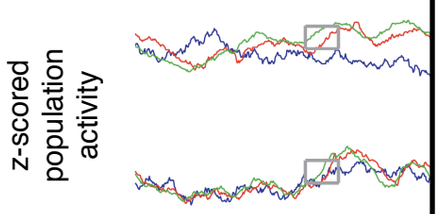
FeedForward Network

1

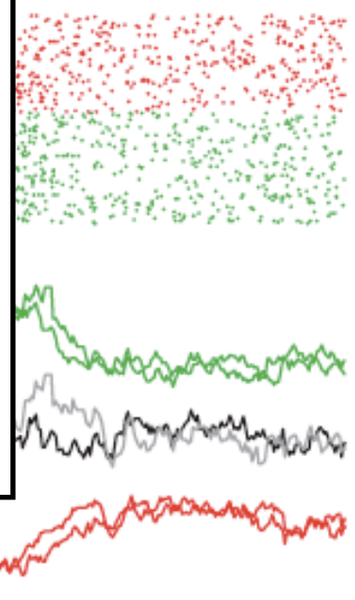
(1) Many weakly correlated synaptic inputs lead to strongly correlated synaptic currents !!



(2) *E-I* tracking genera
correlations betw



E and *I* neurons
synaptic currents
o shared input



FeedForward Network

1

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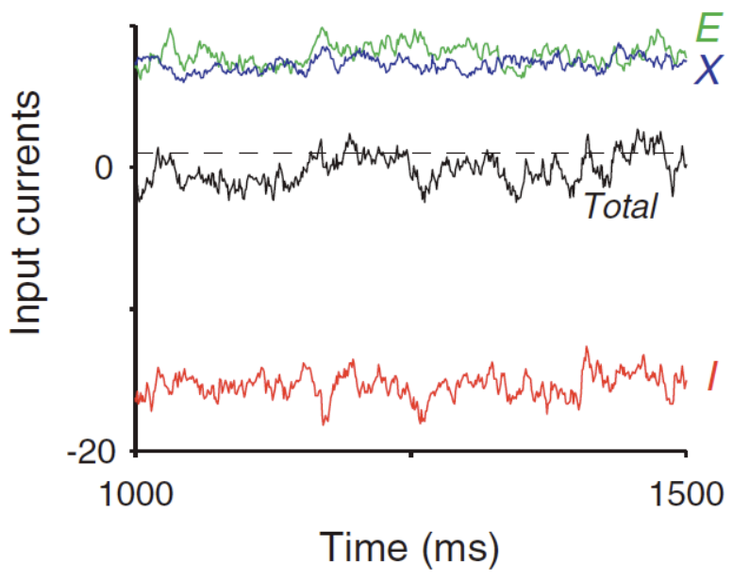
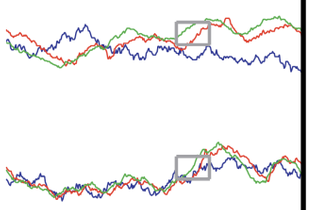
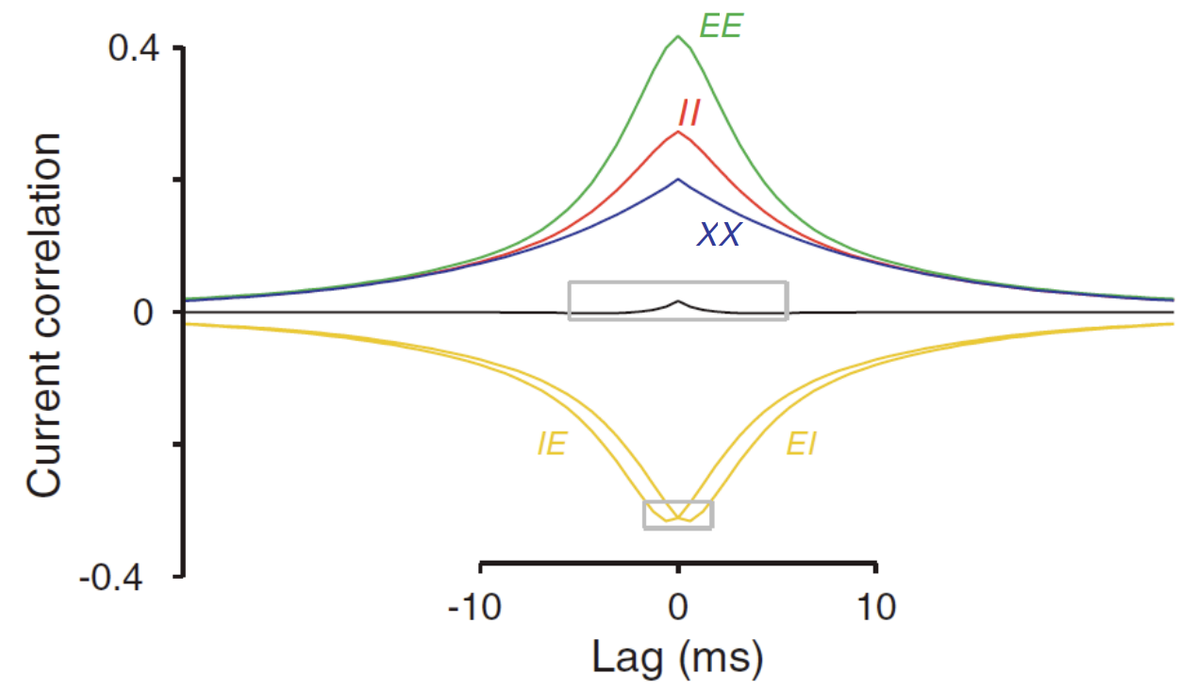


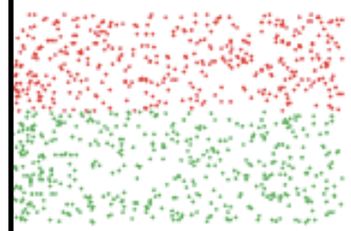
(2) *E-I* tracking genera
correlations betw

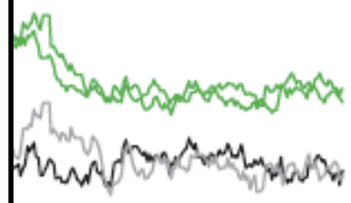
z-scored population activity

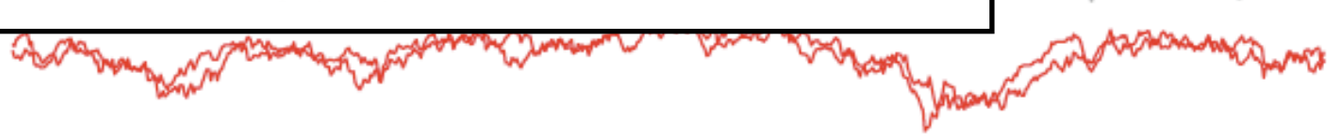


E and *I* neurons
synaptic currents
o shared input









FeedForward Network

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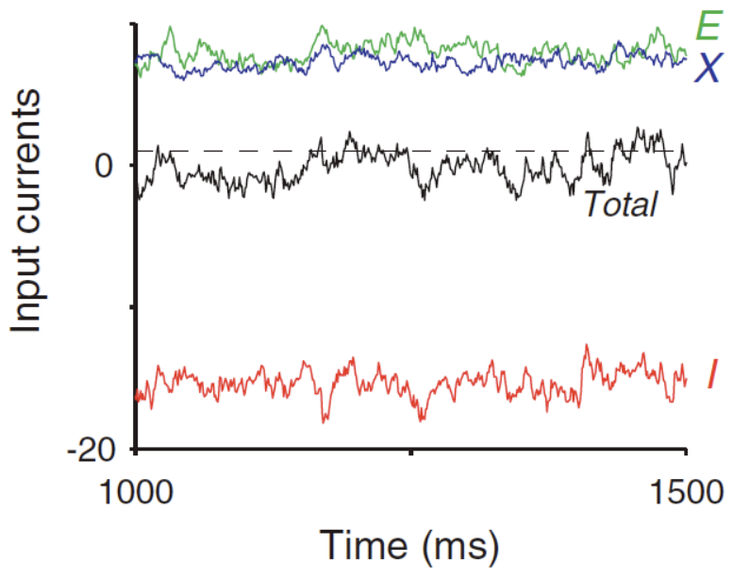
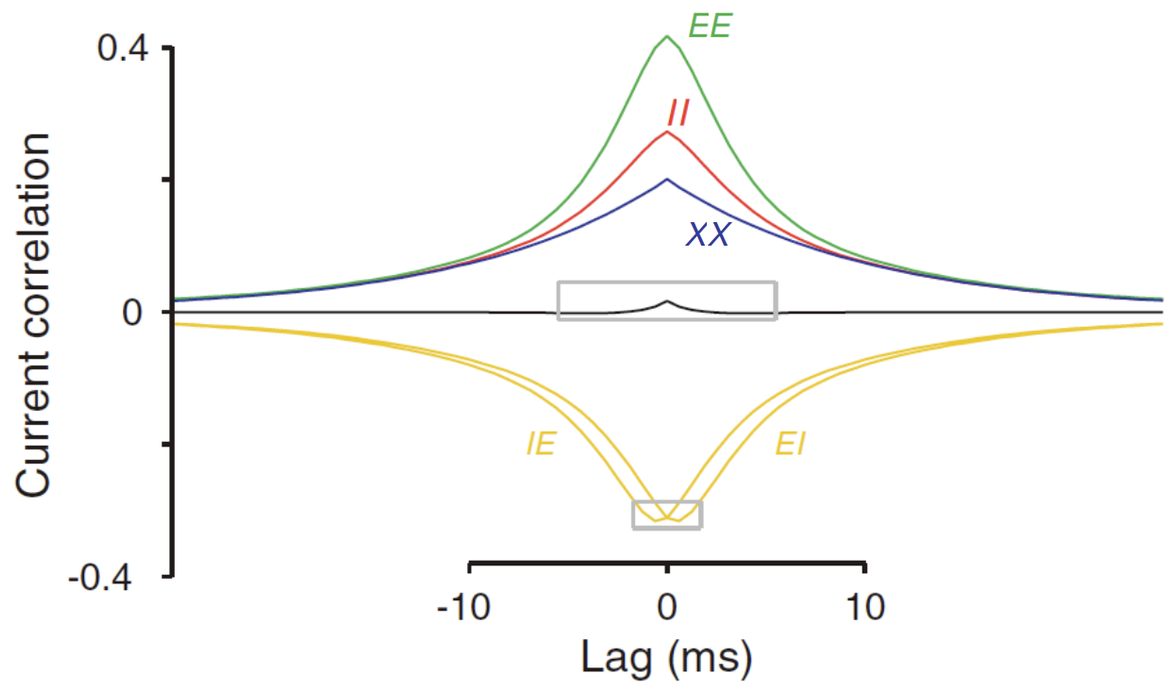


(2) *E-I* tracking genera
correlations betw

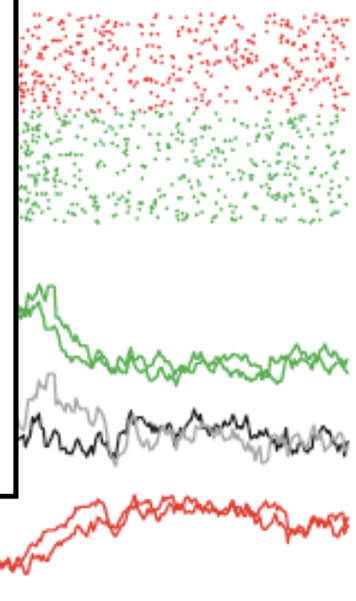
z-scored population activity

Shared Input

$$c \sim p + N(J_{EE}^2 r_{EE} + J_{II}^2 r_{II} - 2J_{EI} J_{IE} r_{EI})$$



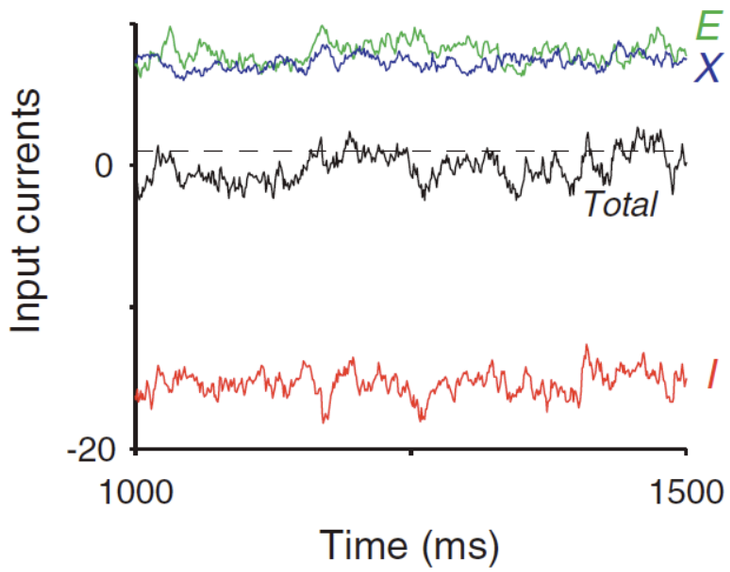
E and *I* neurons
synaptic currents
to shared input



FeedForward Network

1

(1) Many weakly correlated synaptic inputs lead to strongly correlated synaptic currents !!



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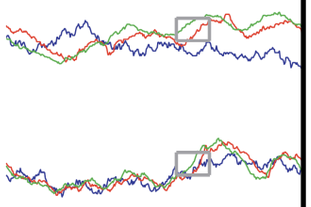
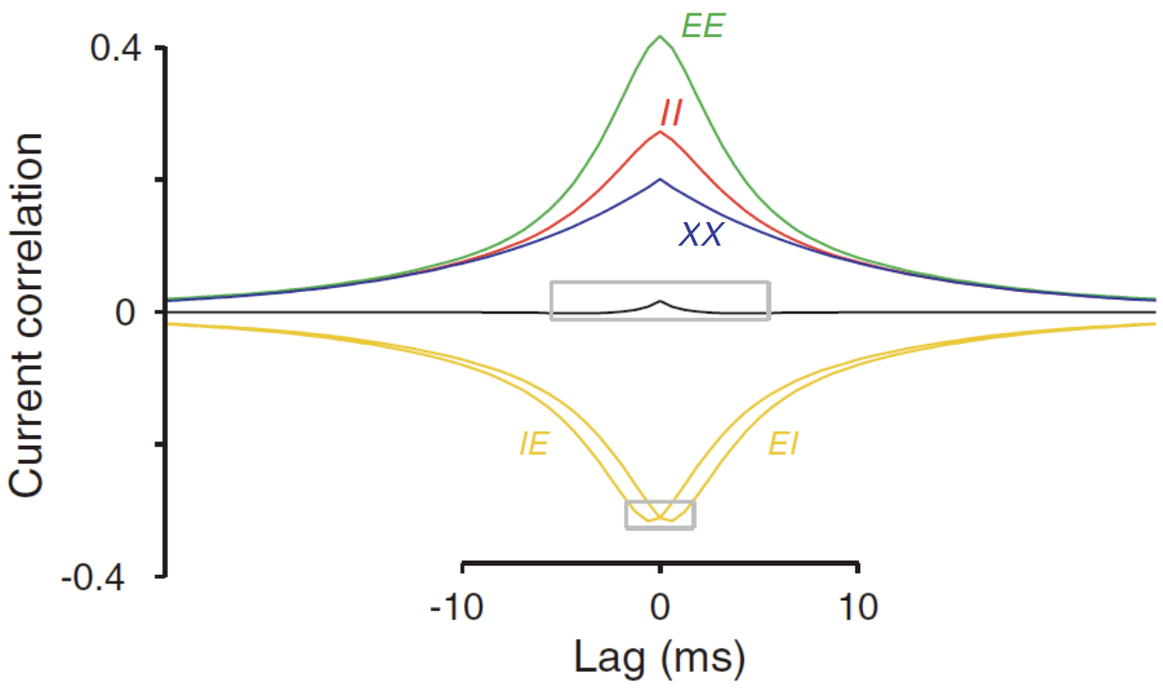
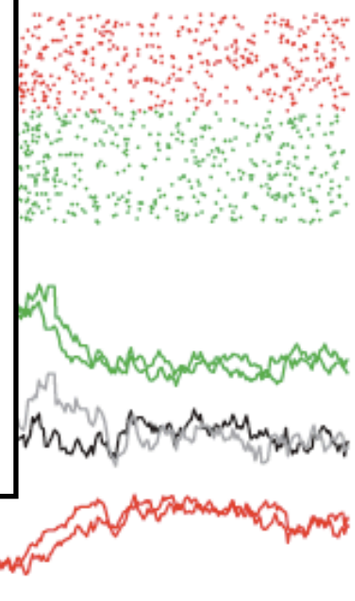


E and *I* neurons
synaptic currents
o shared input





FeedForward Network

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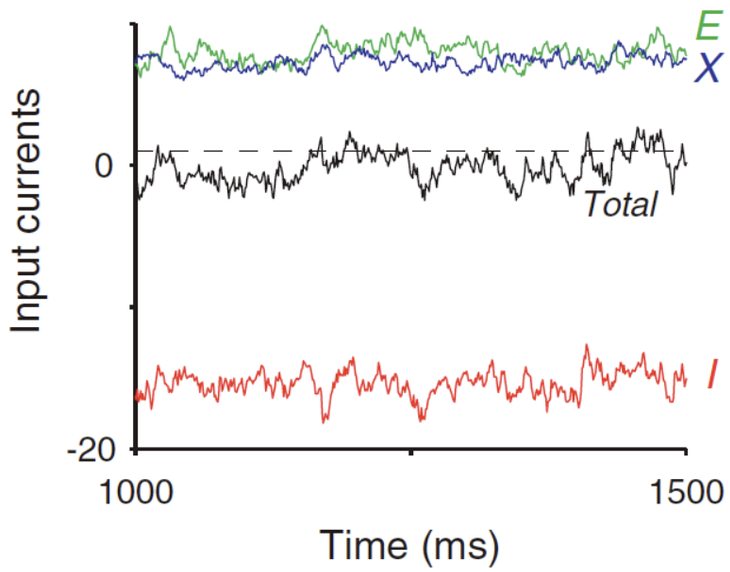
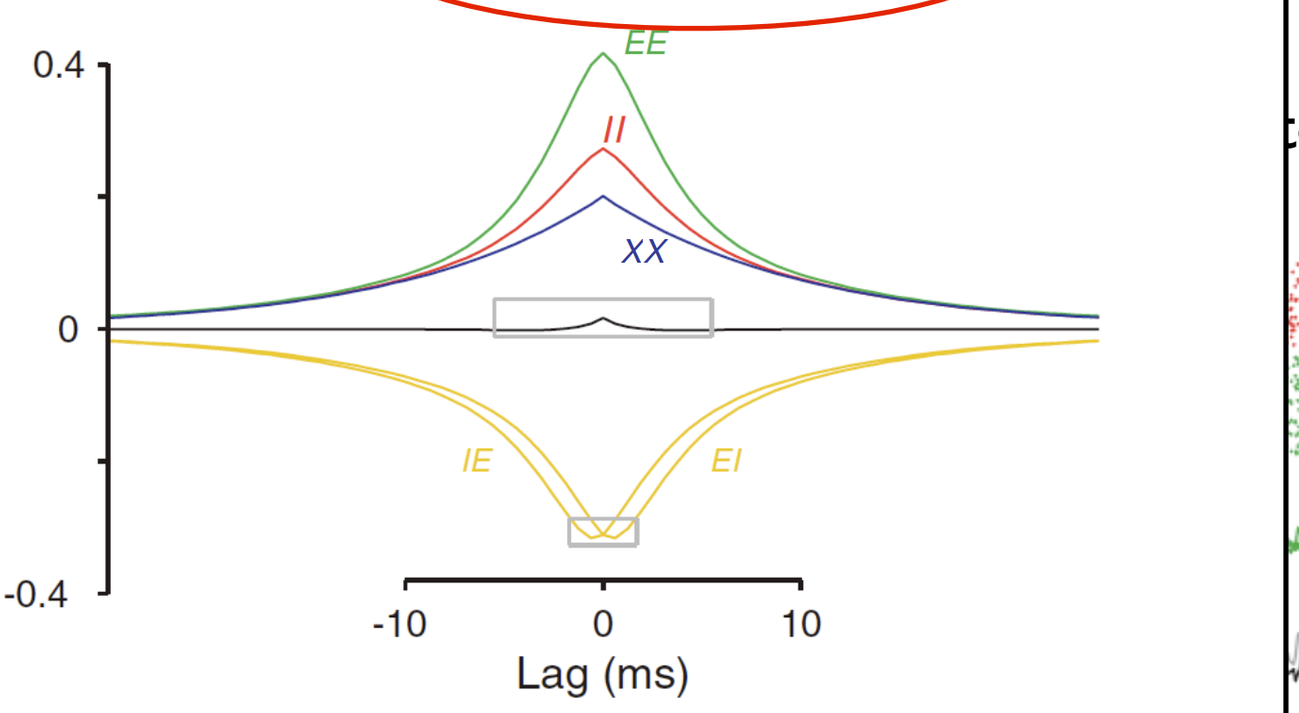


Shared Input

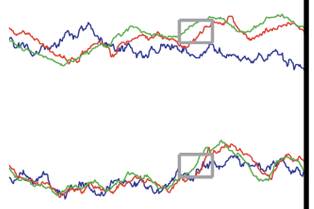
$$c \sim p + N(J_{EE}^2 r_{EE} + J_{II}^2 r_{II} - 2J_{EI} J_{IE} r_{EI})$$

$\sim -p$!!



(2) *E-I* tracking genera
correlations betw

z-scored population activity

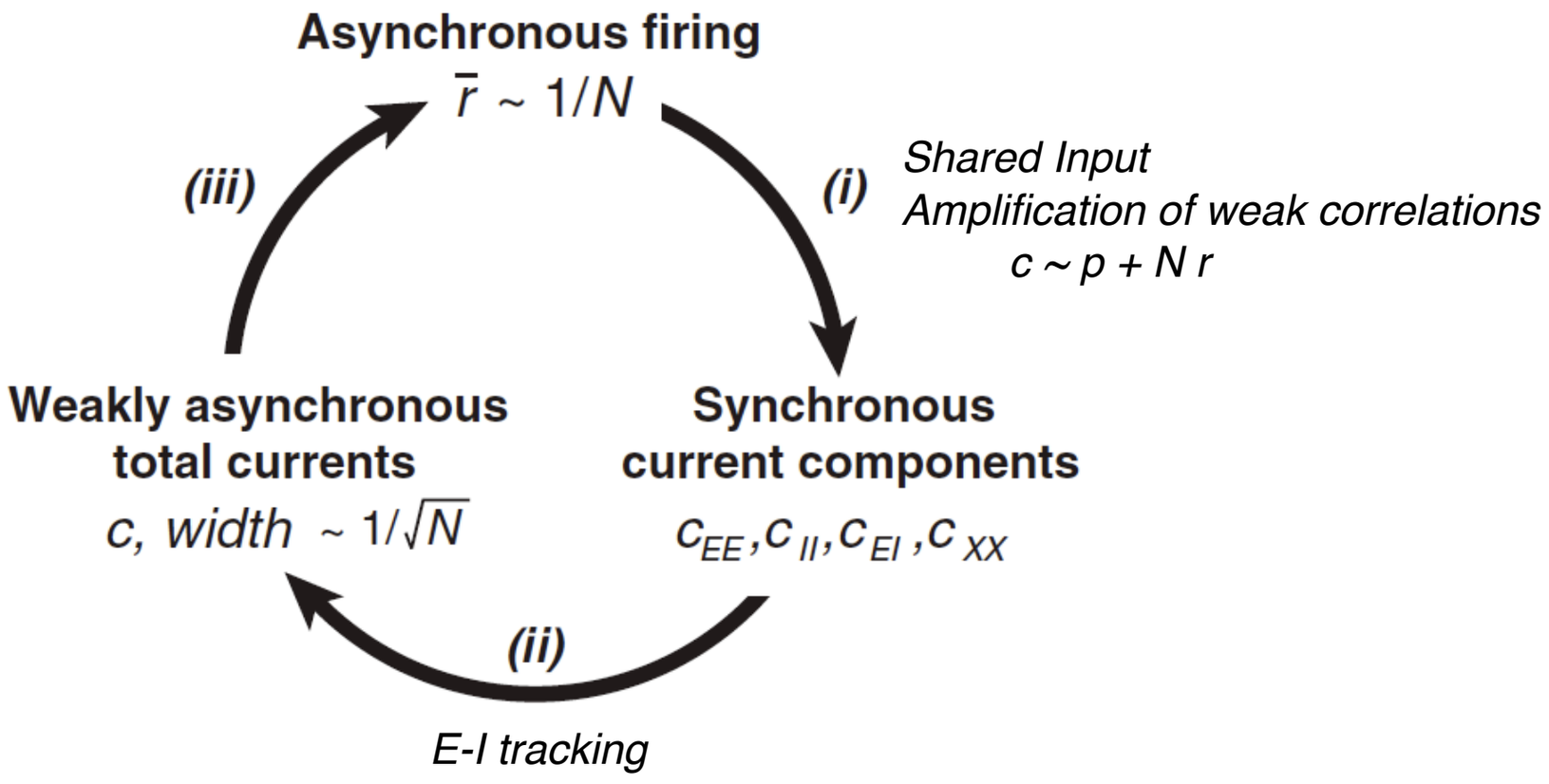


E and *I* neurons synaptic currents to shared input

FeedForward Network

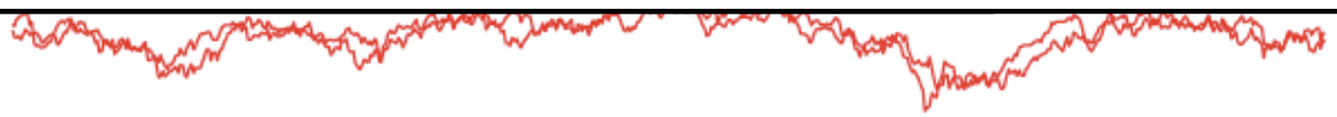
1

(1) Many weakly correlated synaptic inputs lead to strongly correlated synaptic currents !!



Self-consistent description of irregular and weakly correlated states in recurrent networks with "realistic" connectivity

z-scored population activity



Summary

- Balanced networks of *E* and *I* neurons display extremely low global correlations in the steady-state, even when the shared input fraction is large, unless inhibition is too slow or too weak.

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- Balanced networks of *E* and *I* neurons display extremely low global correlations in the steady-state, even when the shared input fraction is large, unless inhibition is too slow or too weak.

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Summary

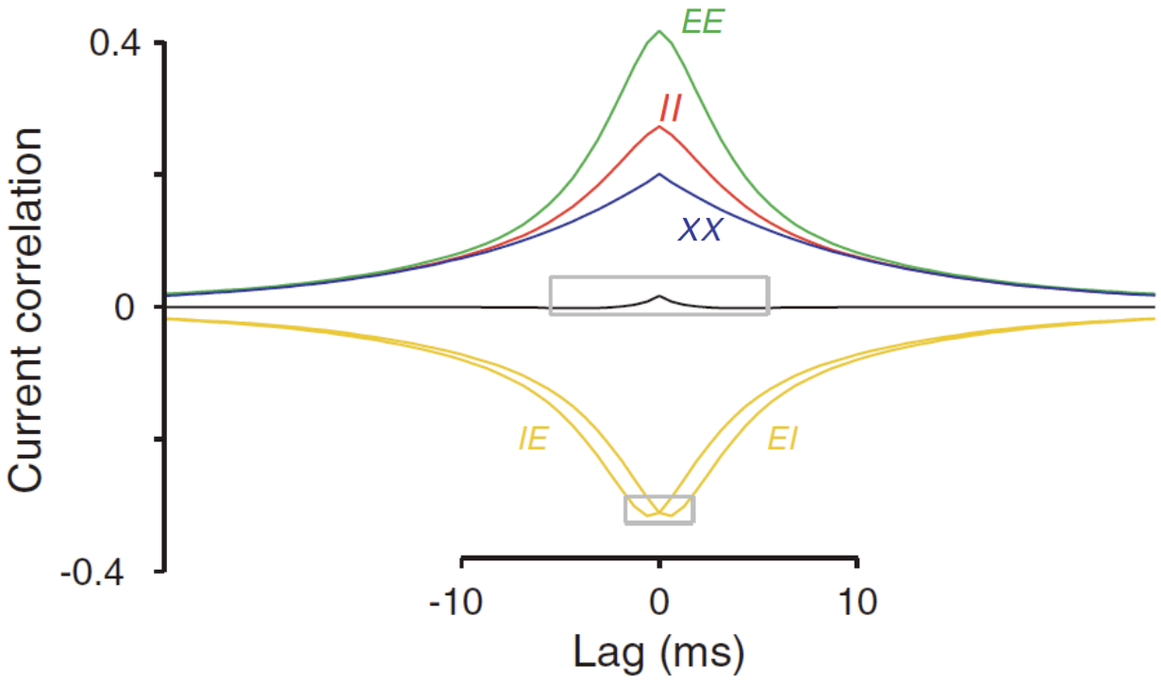
- Balanced networks of *E* and *I* neurons display extremely low global correlations in the steady-state, even when the shared input fraction is large, unless inhibition is too slow or too weak.

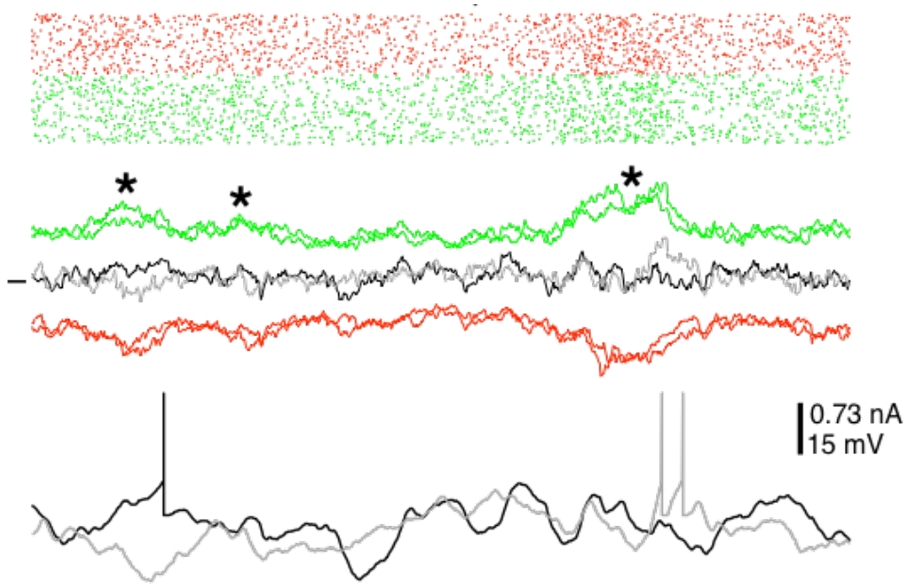
- We believe a **qualitatively** similar phenomenon takes place for spiking (not binary) neurons.

- Temporal correlations produced when the asynchronous state breaks down (when inhibitory feedback is weak) have an oscillatory character and are fast compared with those measured in many primate experiments.

  It is unlikely that the typically observed slow, non-oscillatory spike-count correlations are the result of the interplay between synaptic excitation and inhibition in simple circuits. We currently don't have a mechanistic understanding of how they are generated.

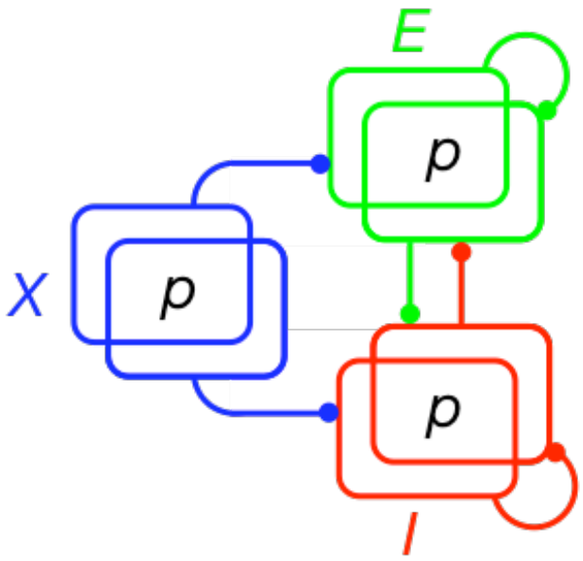
Experimental Prediction 1

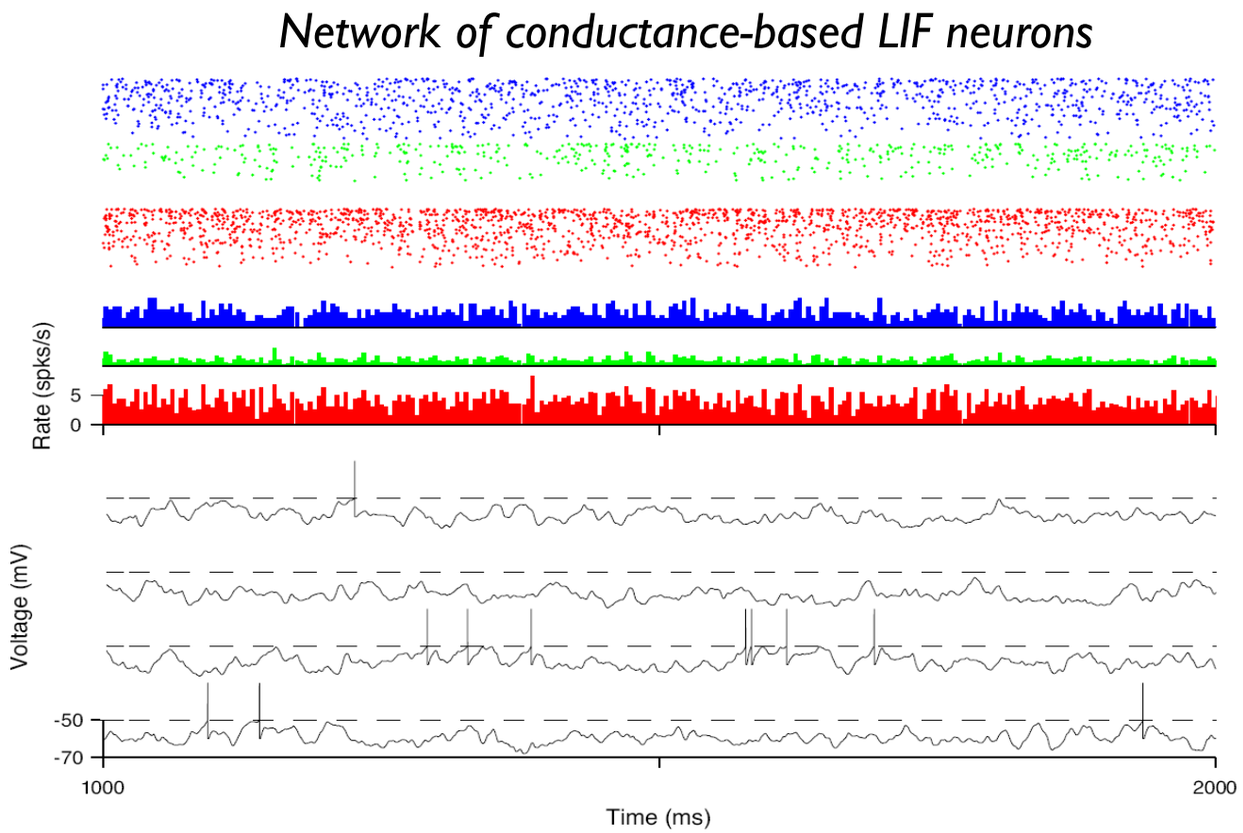




Strong correlations within and between *E* and *I* currents should coexist with weak correlations in the total synaptic current to the neurons

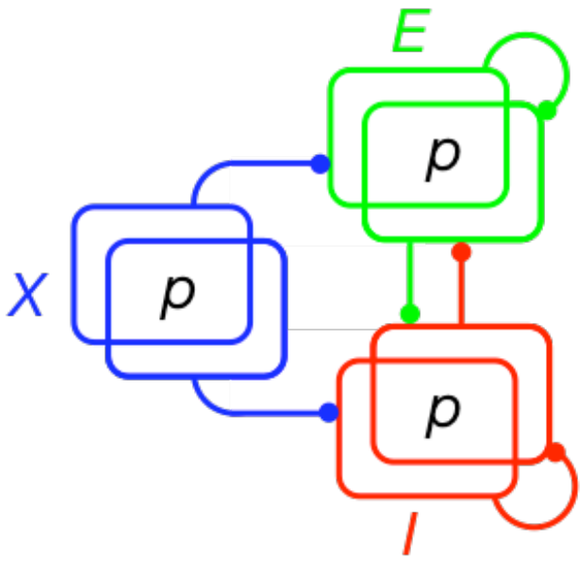
Experimental Prediction 1

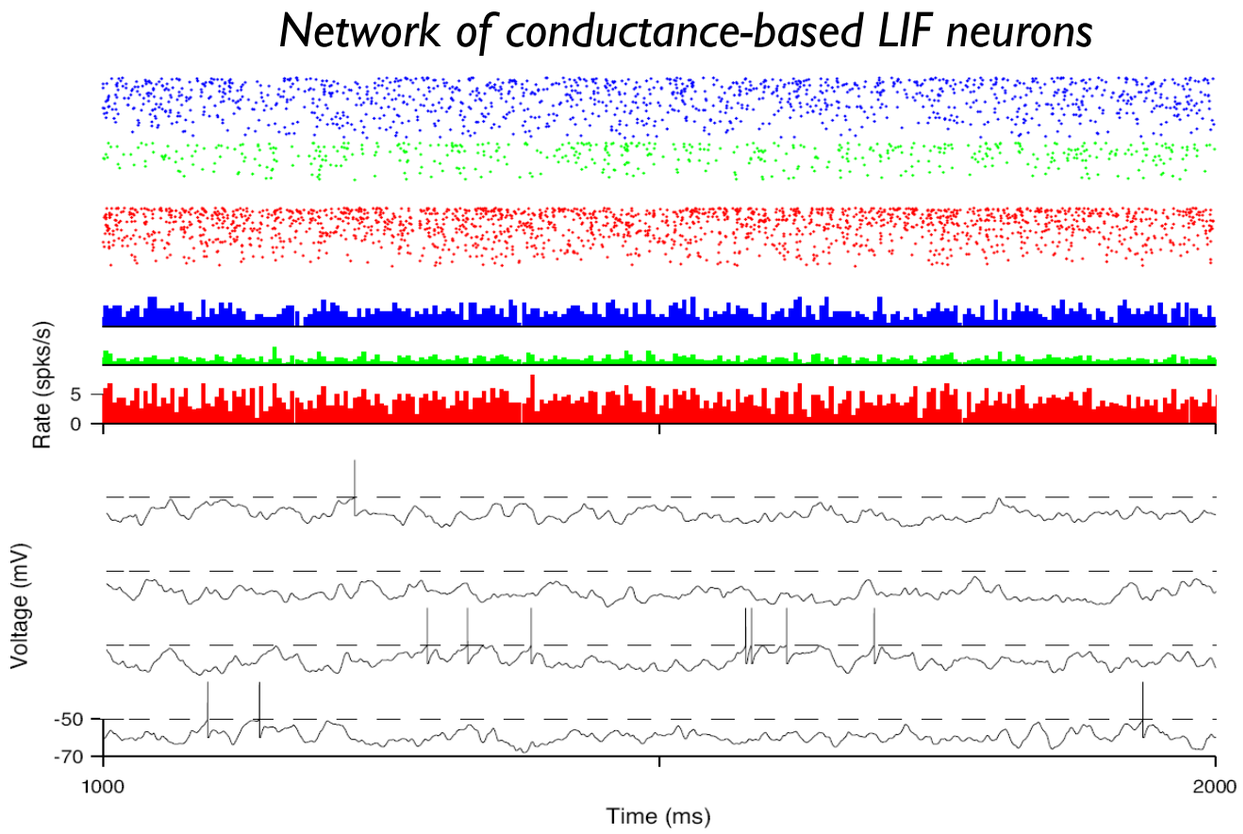


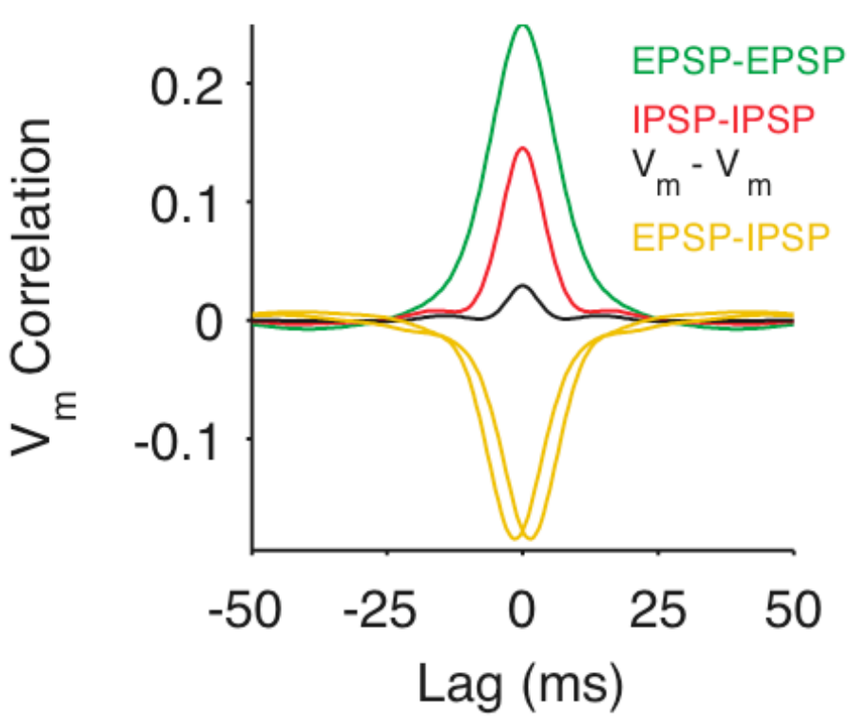


Renart et al., Science, 2010

Experimental Prediction 1







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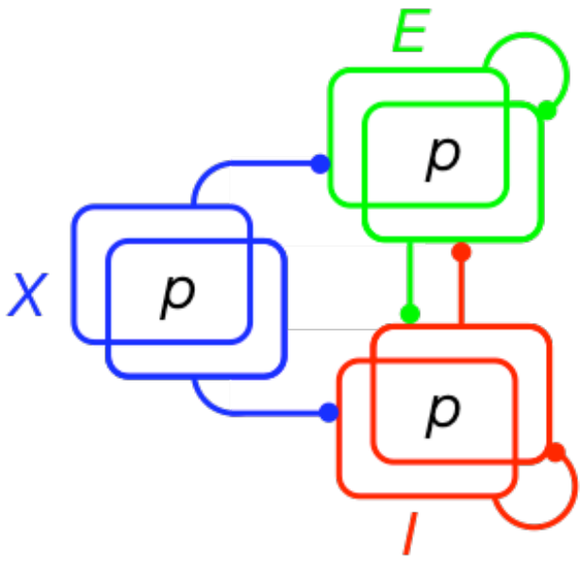
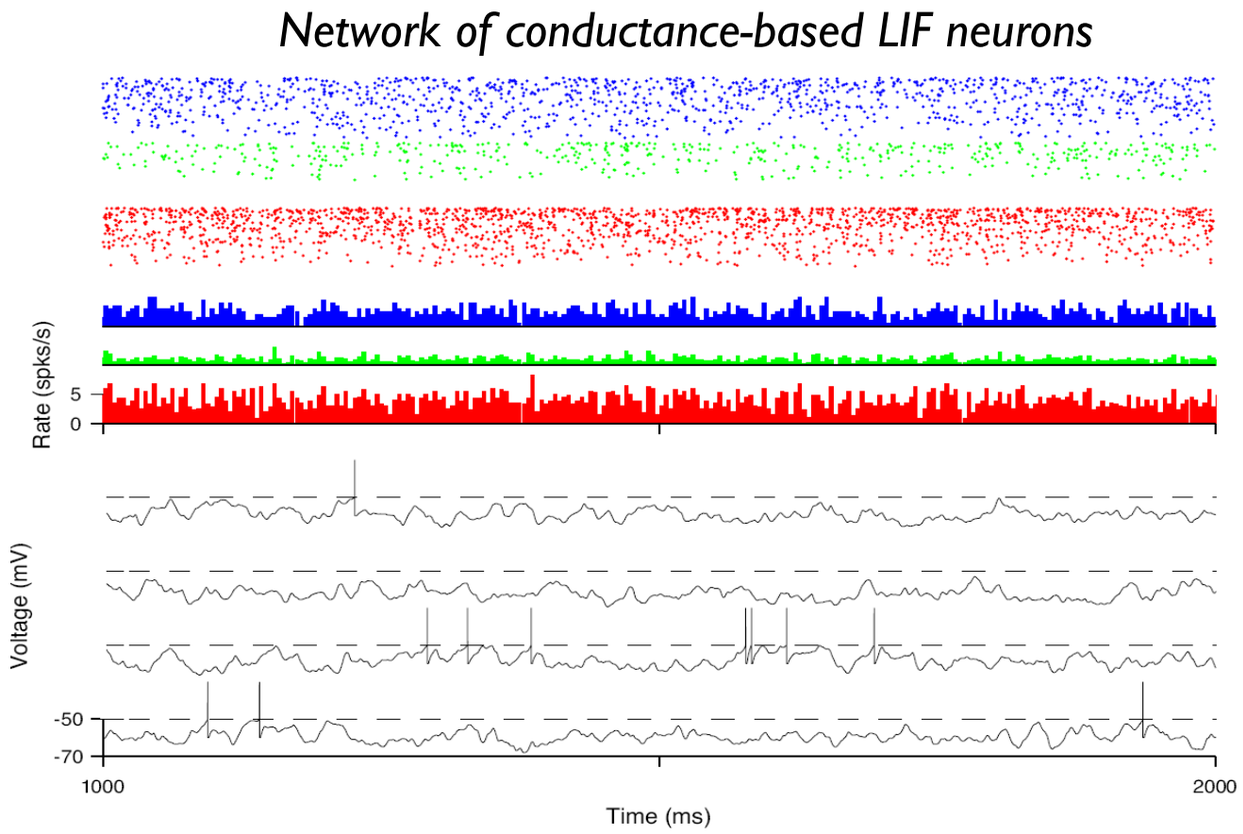
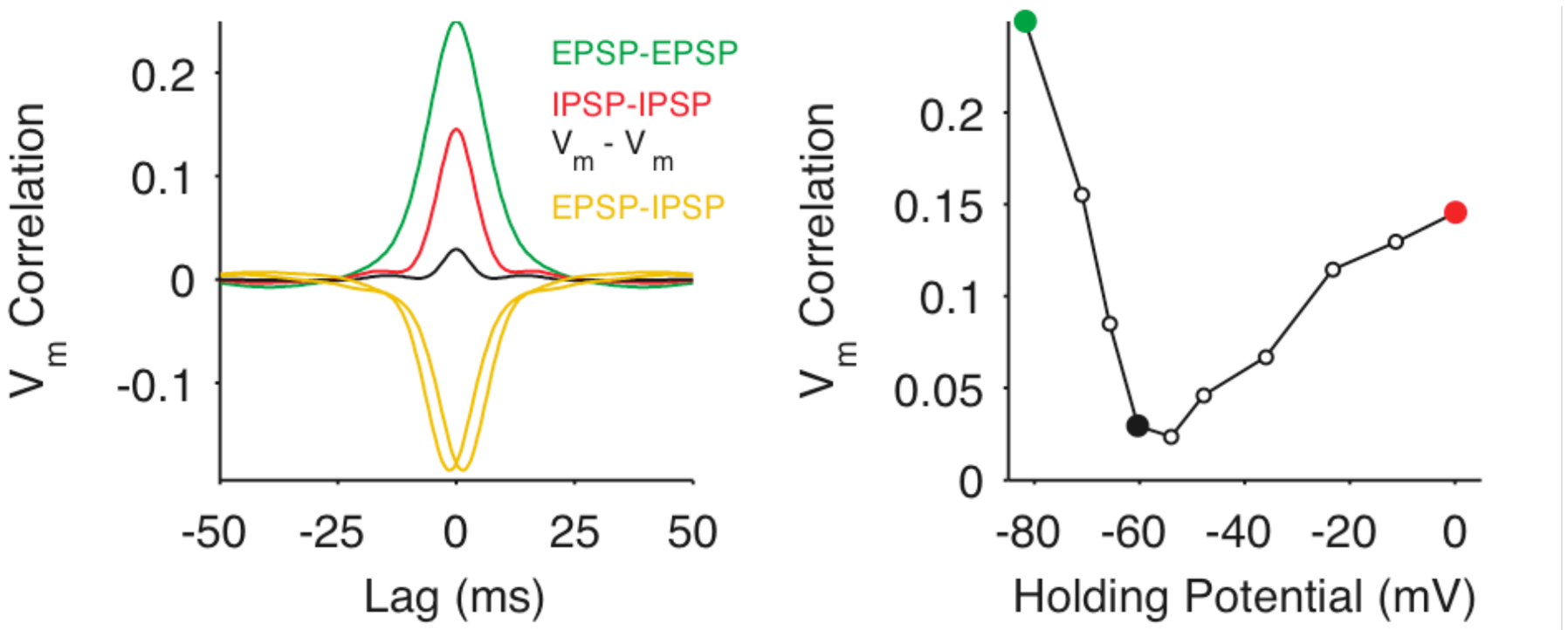
Experimental Prediction 1

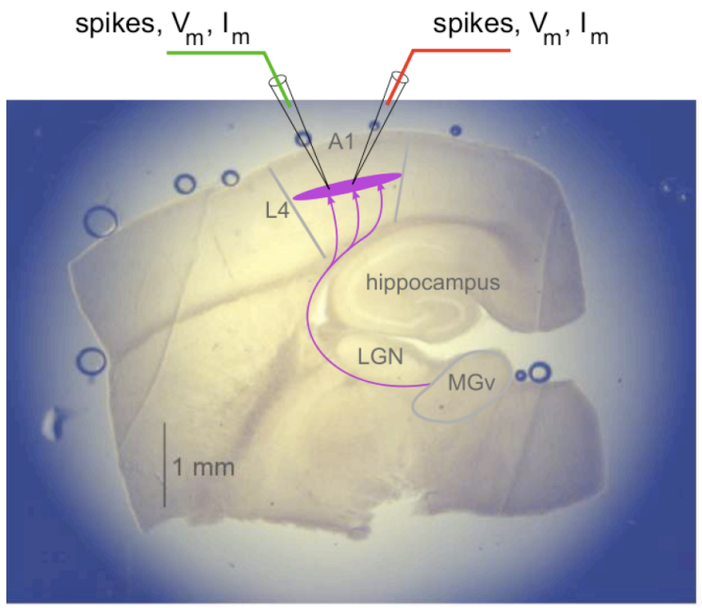


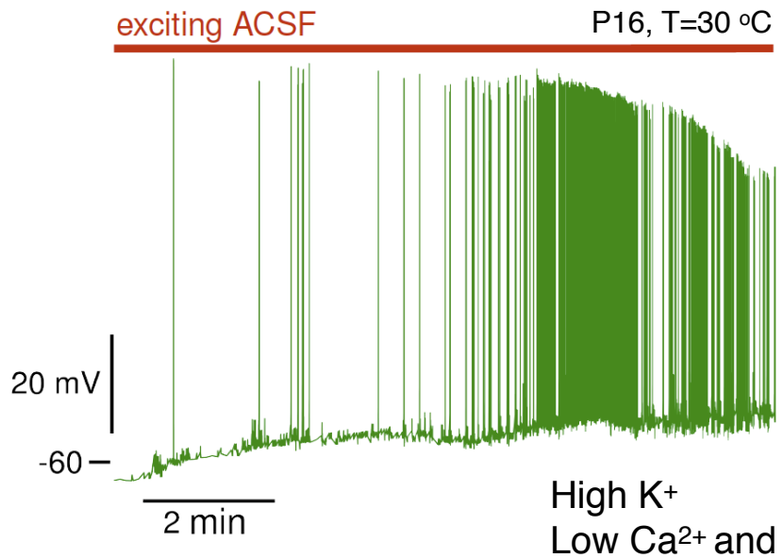




Renart et al., Science, 2010

Testing Experimental Prediction 1 *in vitro*

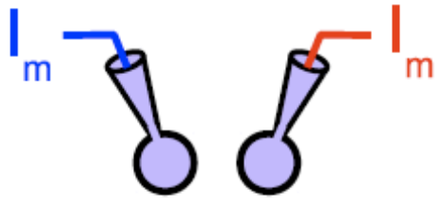




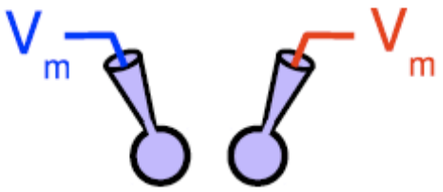
High K^+
Low Ca^{2+} and Mg^{2+}
(Silberberg et al., J. Physiol. 2004)

Michael Graupner
(Reyes Lab)

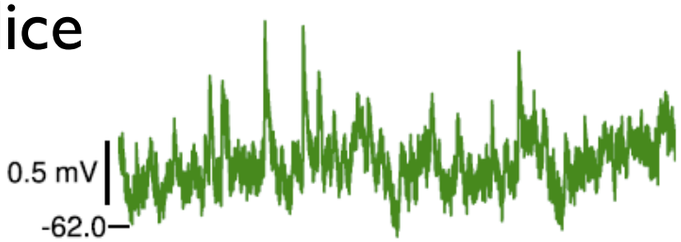
1. voltage clamp



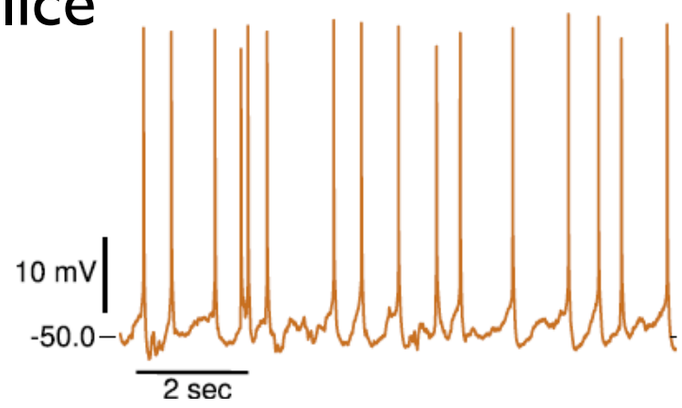
2. current clamp

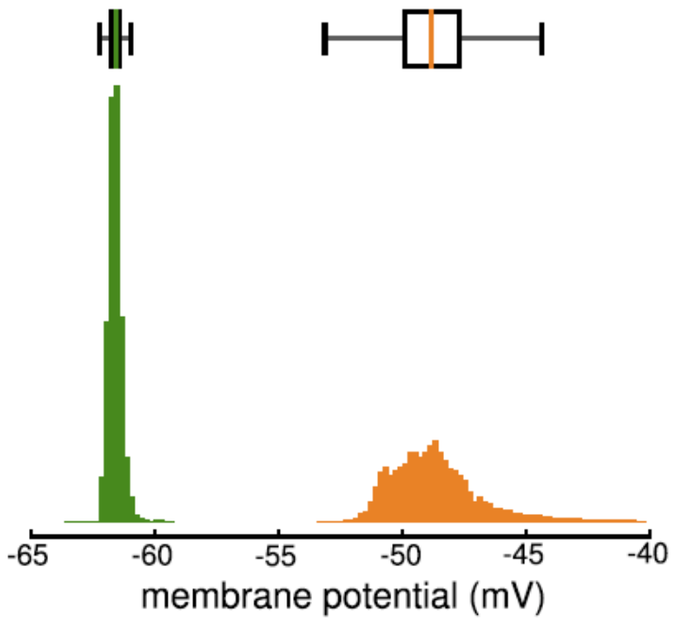


‘silent’ slice



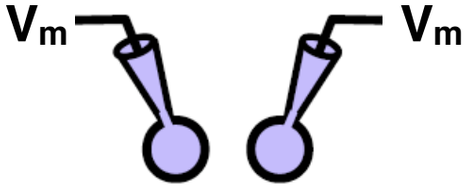
‘activated’ slice



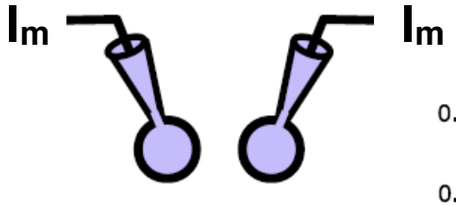


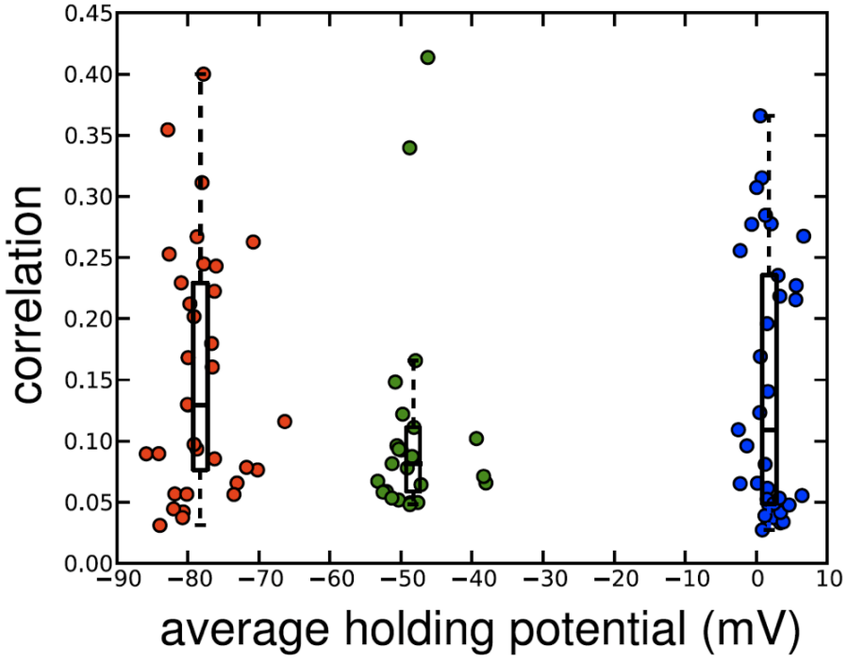
Testing Experimental Prediction 1 *in vitro*

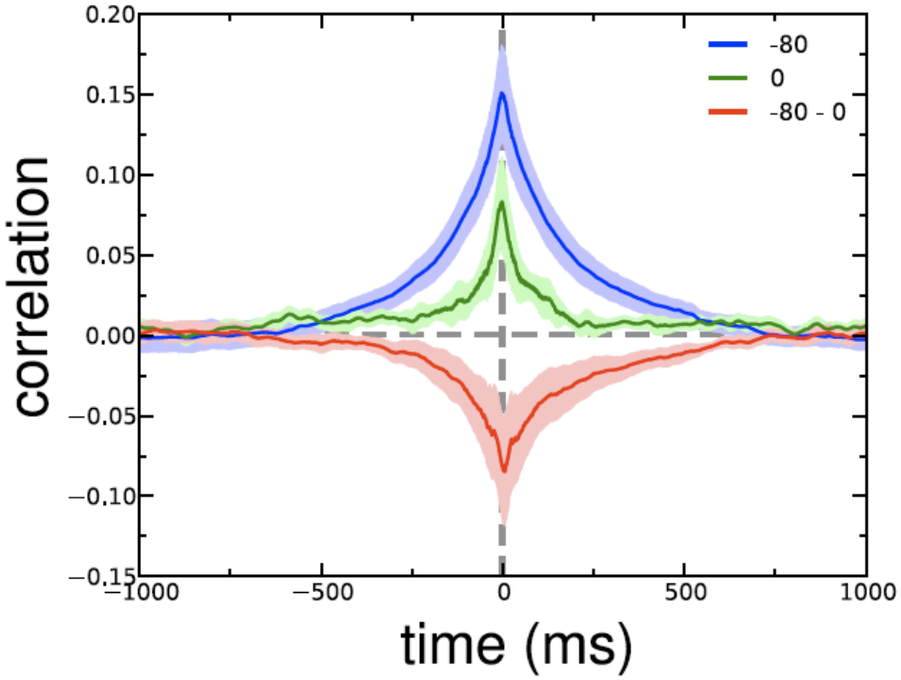
Current Clamp

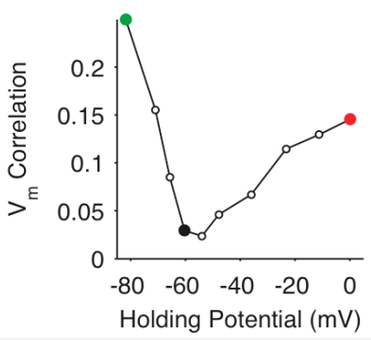


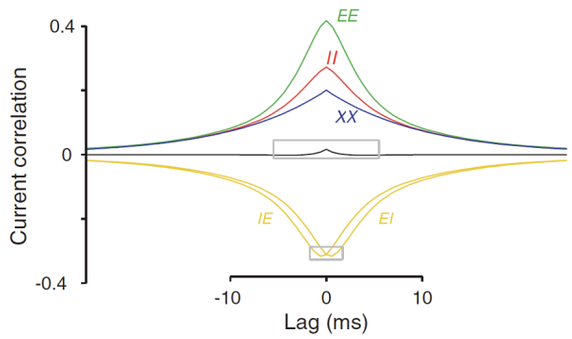
Voltage Clamp

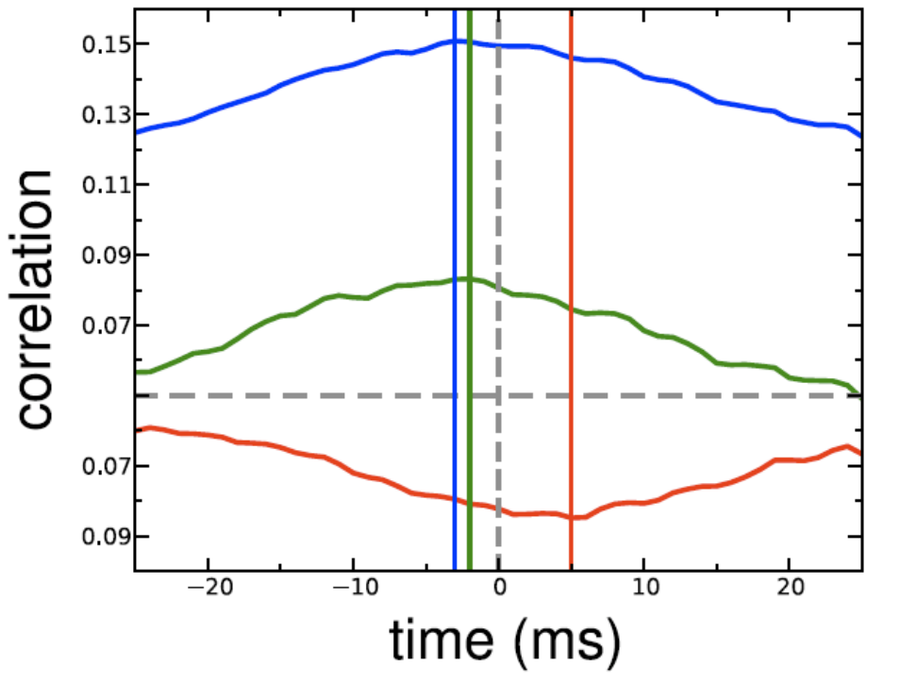








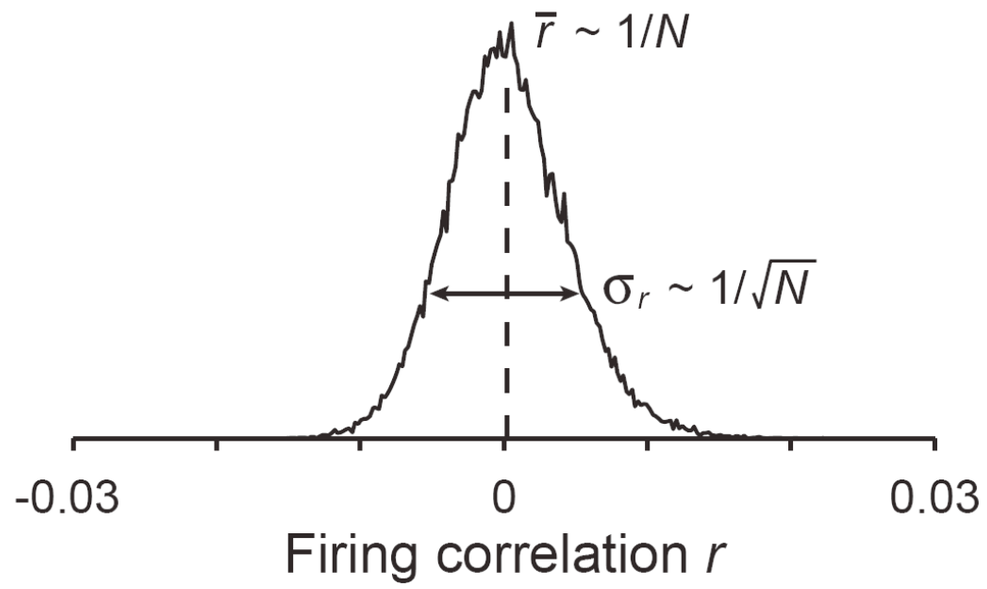




Experimental Prediction 2

The distribution of spiking correlations in the asynchronous state is "**wide**"

$$\text{STD}(r_{ij}) >> \text{Mean}(r_{ij})$$



The sources of variability in the level of correlation:

- Fraction of shared input
- Presence/absence of mono-synaptic connection
- Variability in the level of correlation of inputs

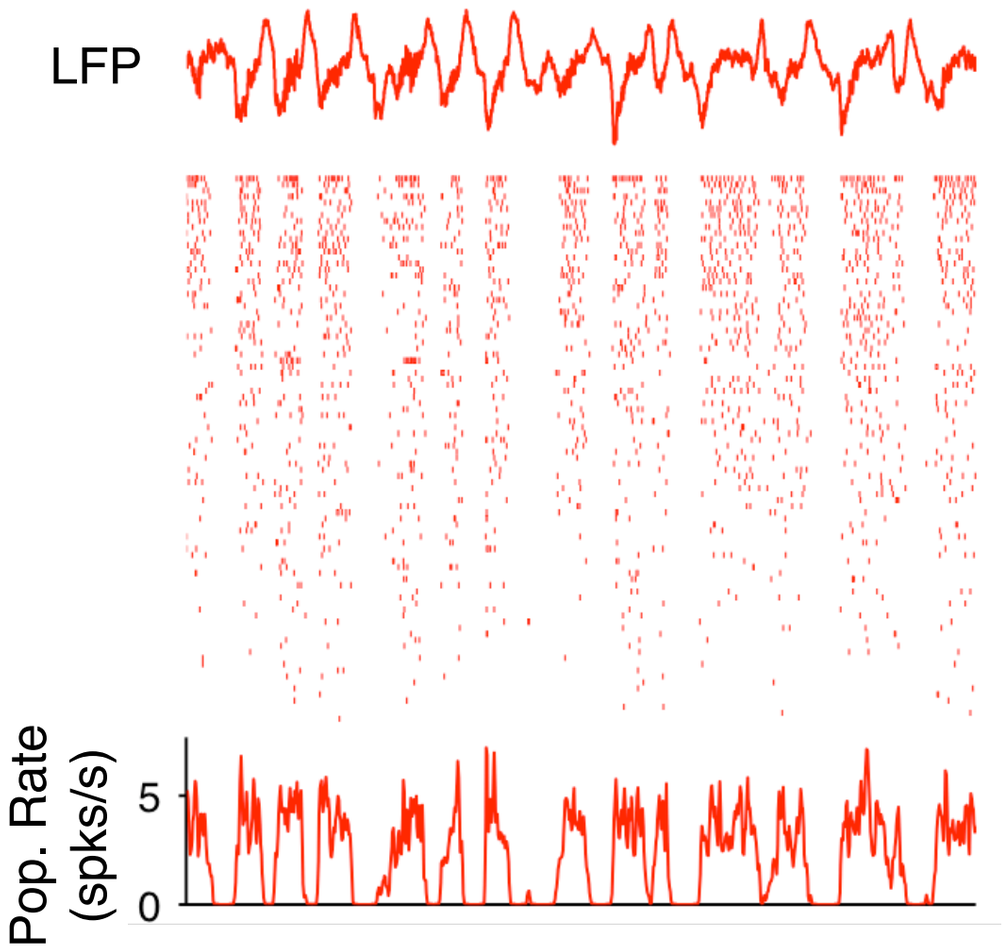
are all ~ O(1/√N)

whereas the mean correlation is ~ O(1/N) in the asynchronous state

Brain State changes under Urethane anesthesia

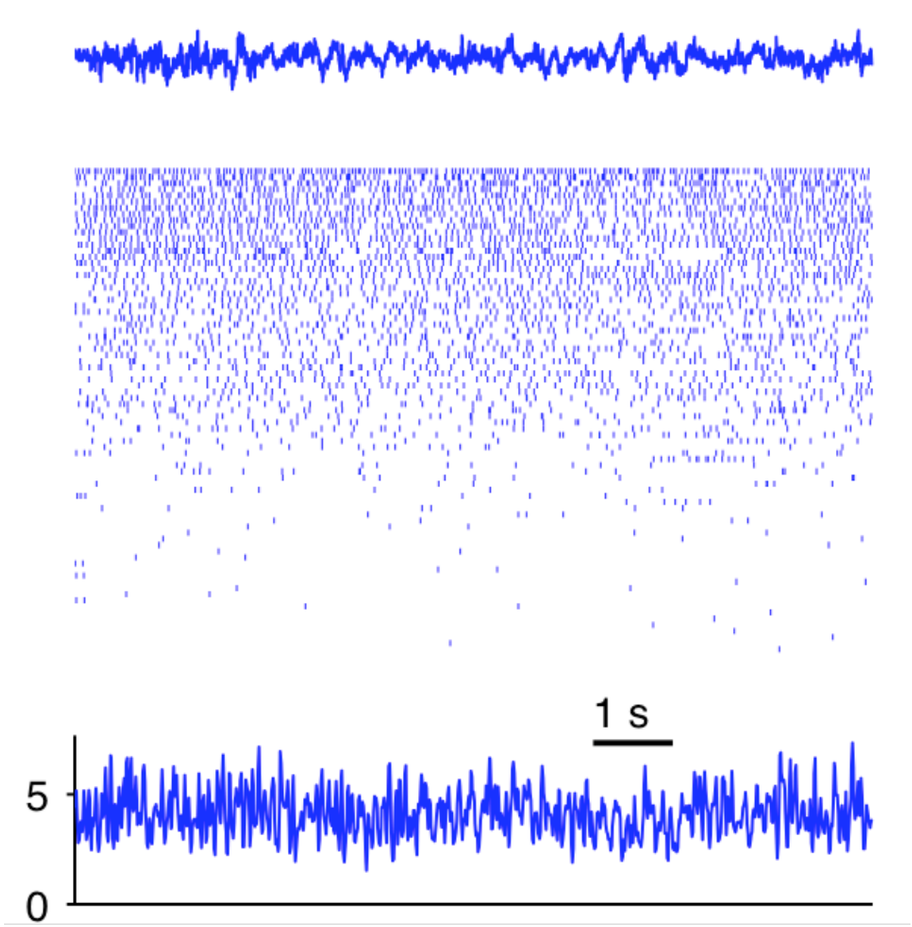
Cortical INACTIVATION

SWS; Drowsiness...



Cortical ACTIVATION

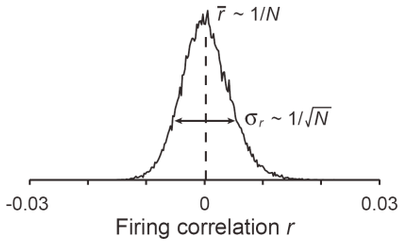
REM; attentive wakefulness...



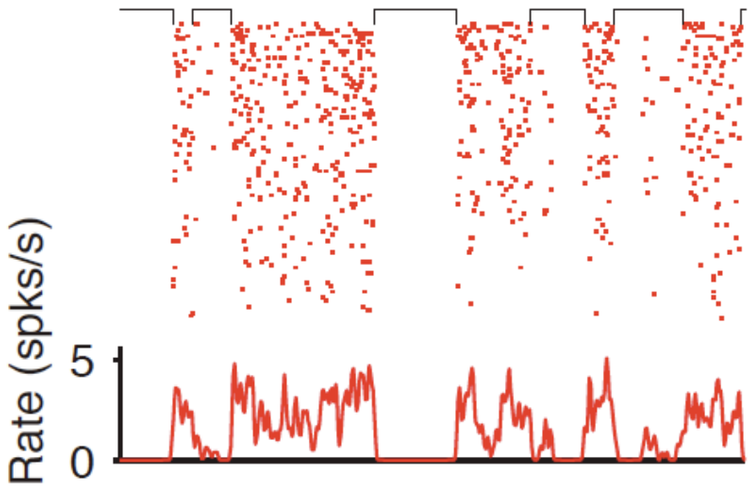
- Spontaneous Activity in Rat Auditory and Somatosensory Cortex
- Urethane Anesthesia
- 64 Ch. Silicon Probes

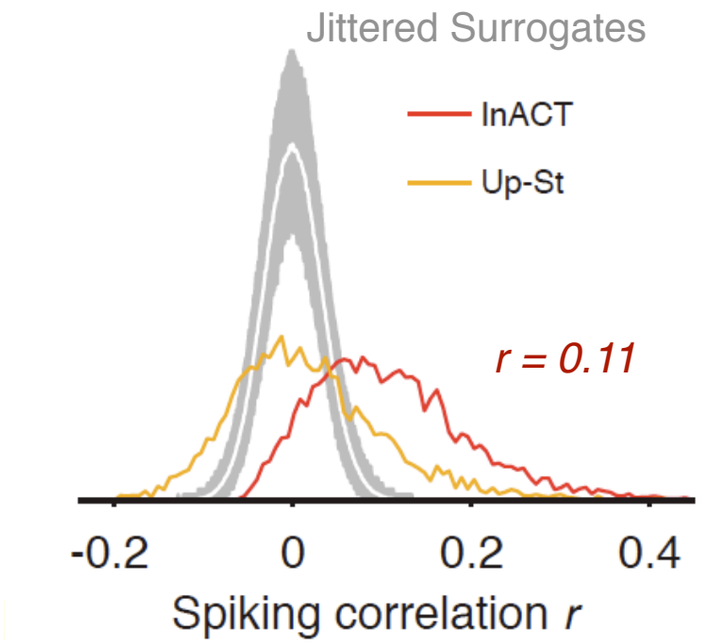
Renart et al., Science, 2010

Experimental Prediction 2



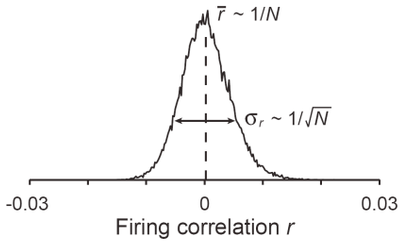
Cortical INACTIVATION



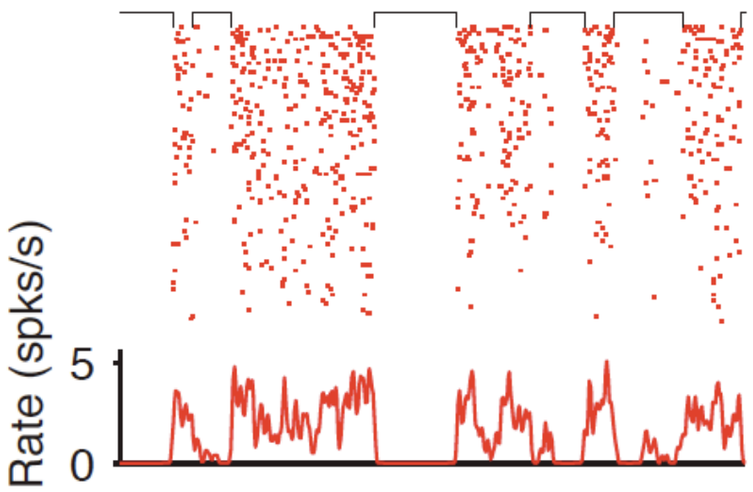


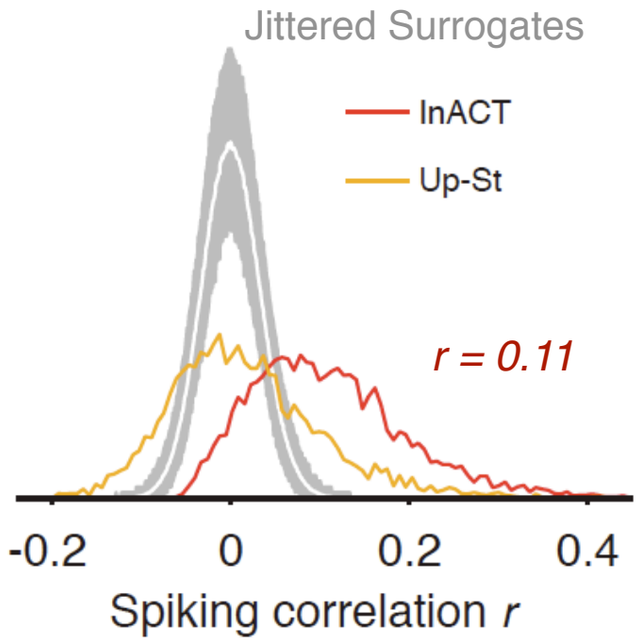
Renart et al., Science, 2010

Experimental Prediction 2

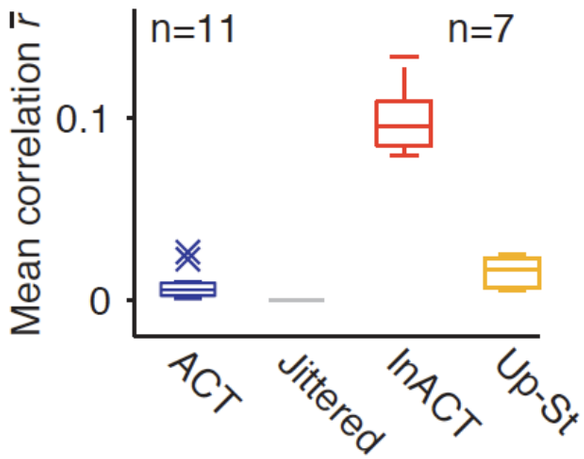


Cortical INACTIVATION

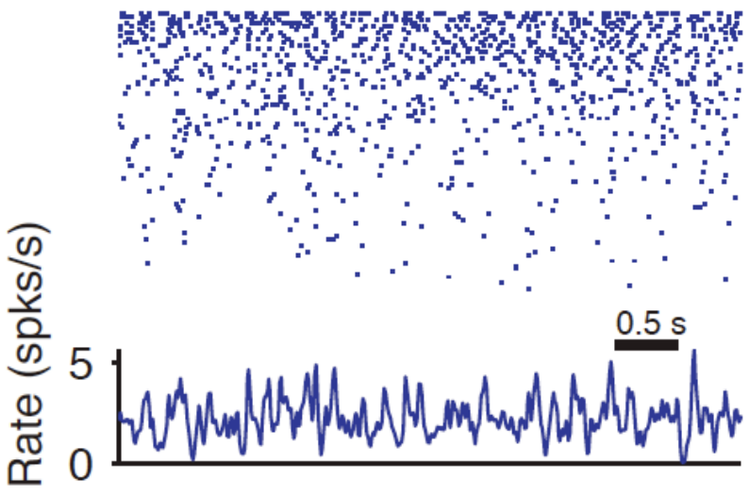


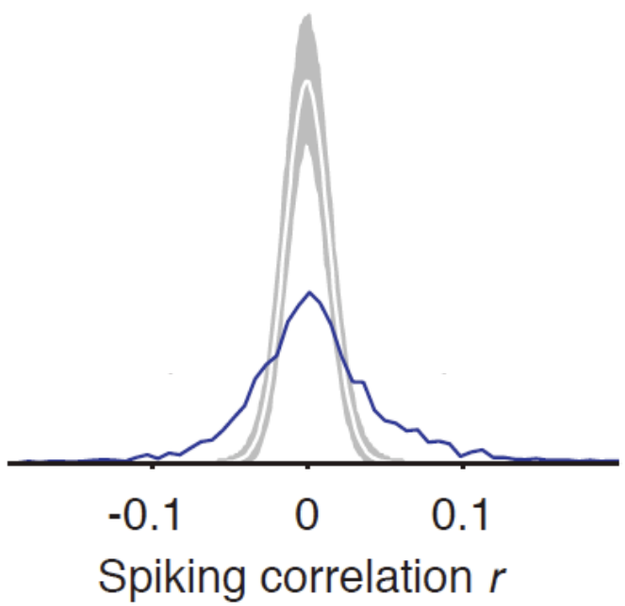


Summary Statistics



Cortical ACTIVATION

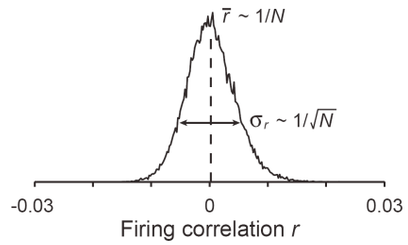




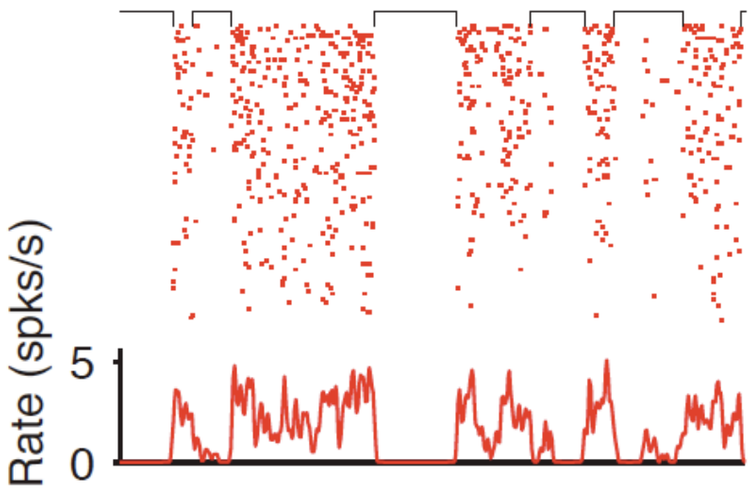
The histogram of correlations during cortical activation is **wide**

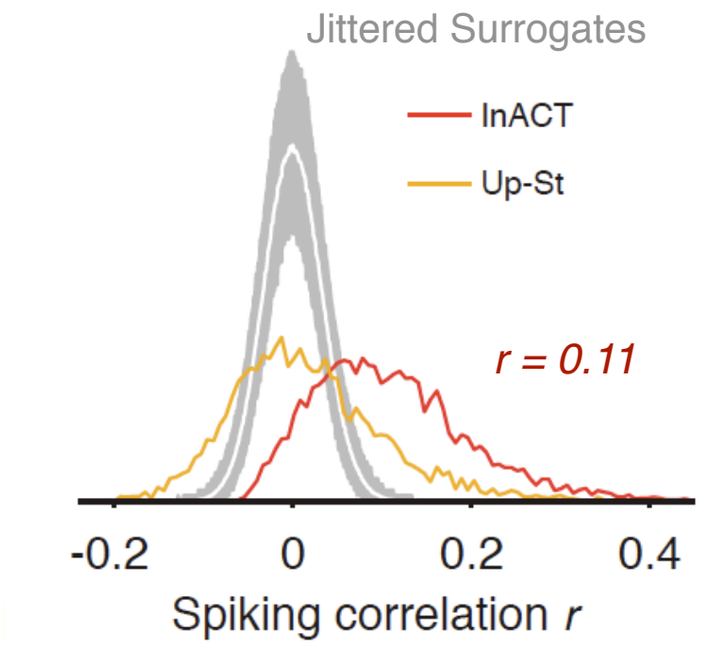
Renart et al., Science, 2010

Experimental Prediction 2

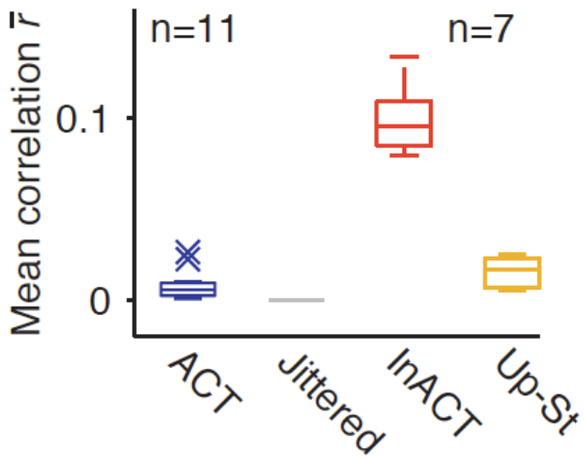


Cortical INACTIVATION

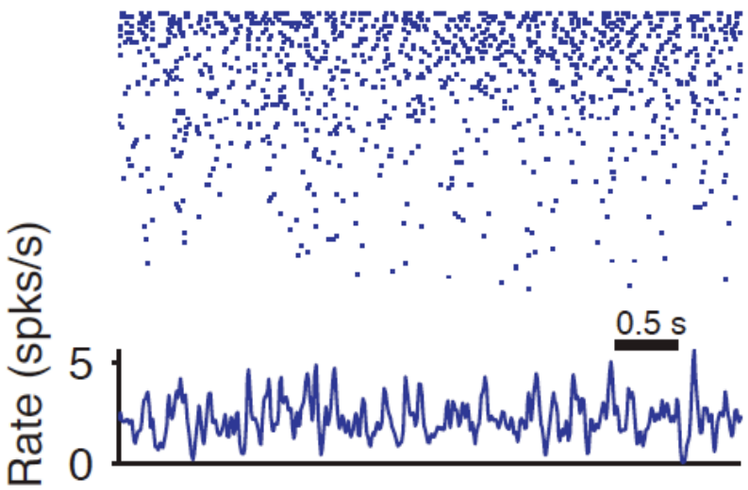


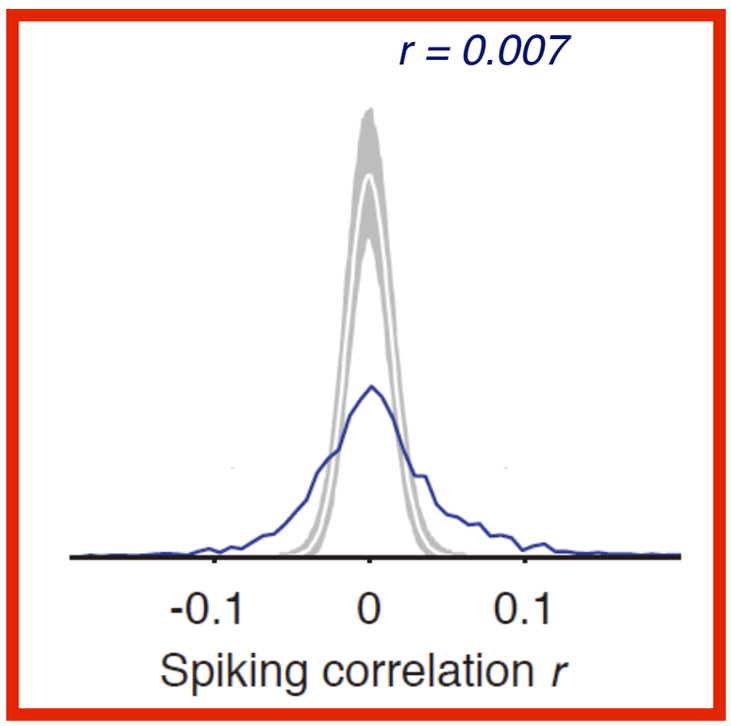


Summary Statistics



Cortical ACTIVATION

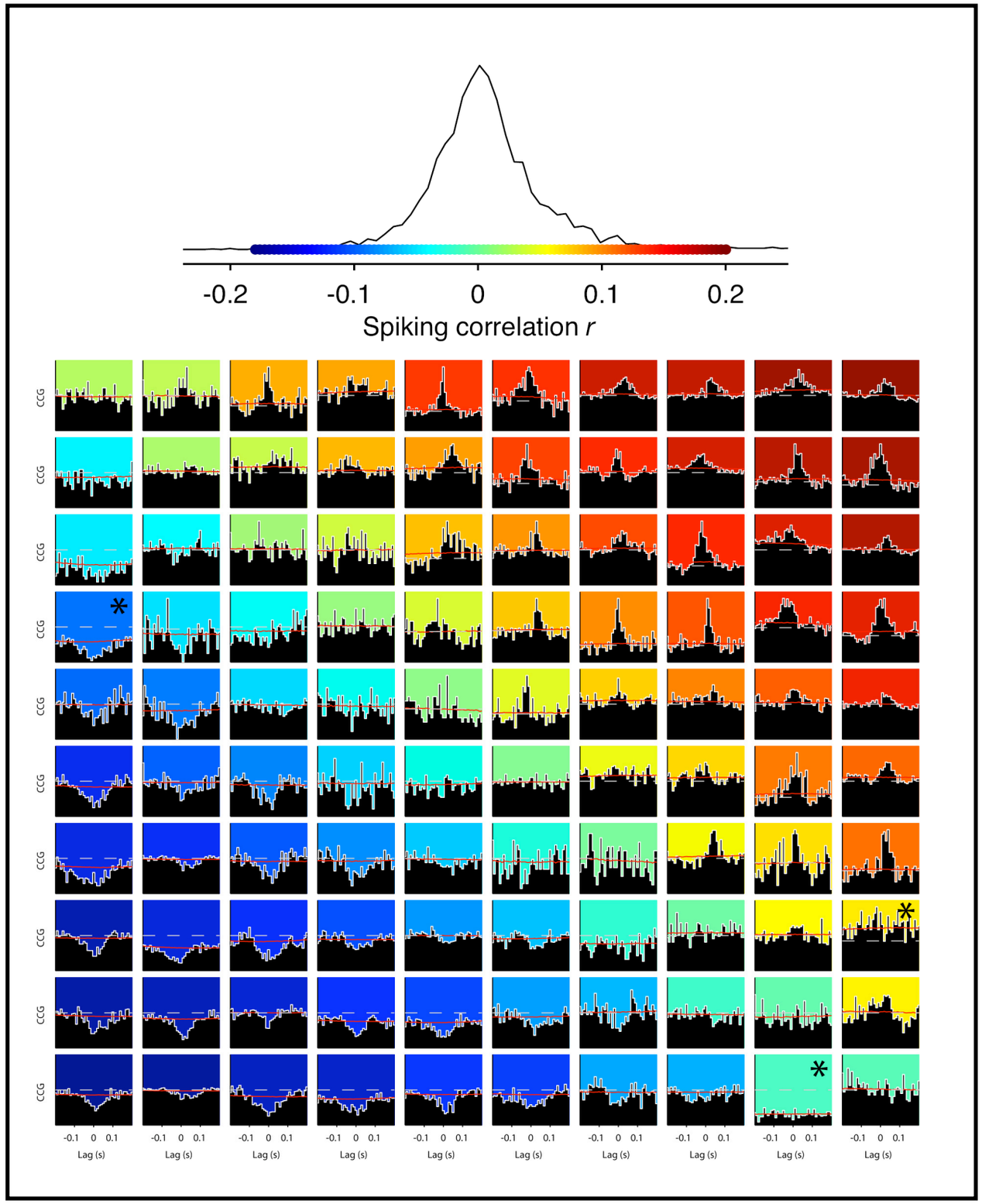


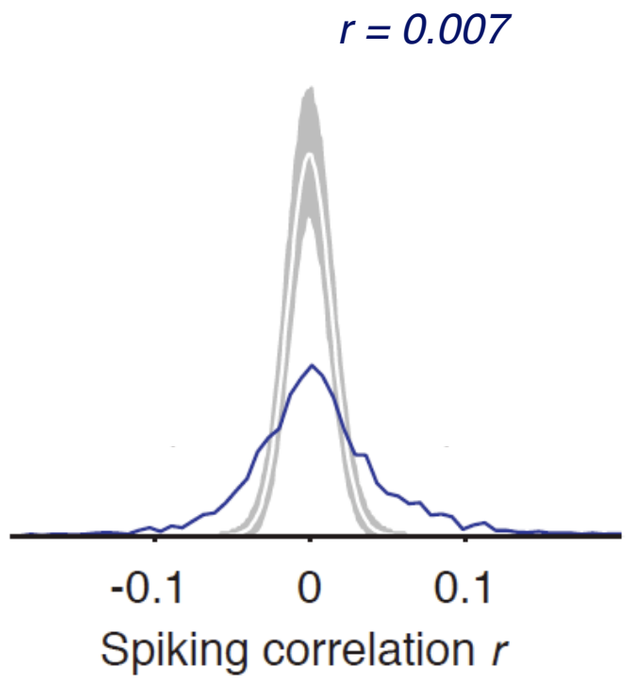


The histogram of correlations during cortical activation is **wide**

Renart et al., Science, 2010

Weak correlations on average occur together with significant positive and negative correlations between some pairs



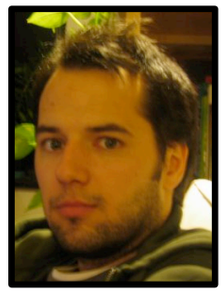


- A nearly zero population averaged correlation is indicative of an approximately constant global population activity

- Long tails appear to be the result of competitive interactions between two mutually inhibitory neuronal populations

Collaborators

Jaime de la Rocha



Peter Bartho

Liad Hollender

Michael Graupner

Nestor Parga

Alex Reyes

Kenneth. D. Harris

Champalimaud Foundation