Theory of correlation transfer and correlation structure in recurrent networks

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Part I: a Pair of Neurons

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Part II: Networks

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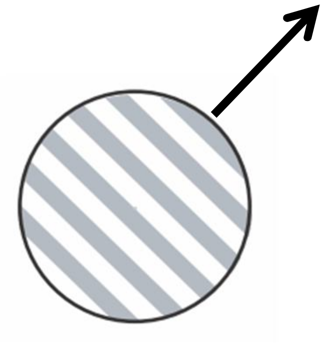
Cortical spiking variability



Cortical spiking variability

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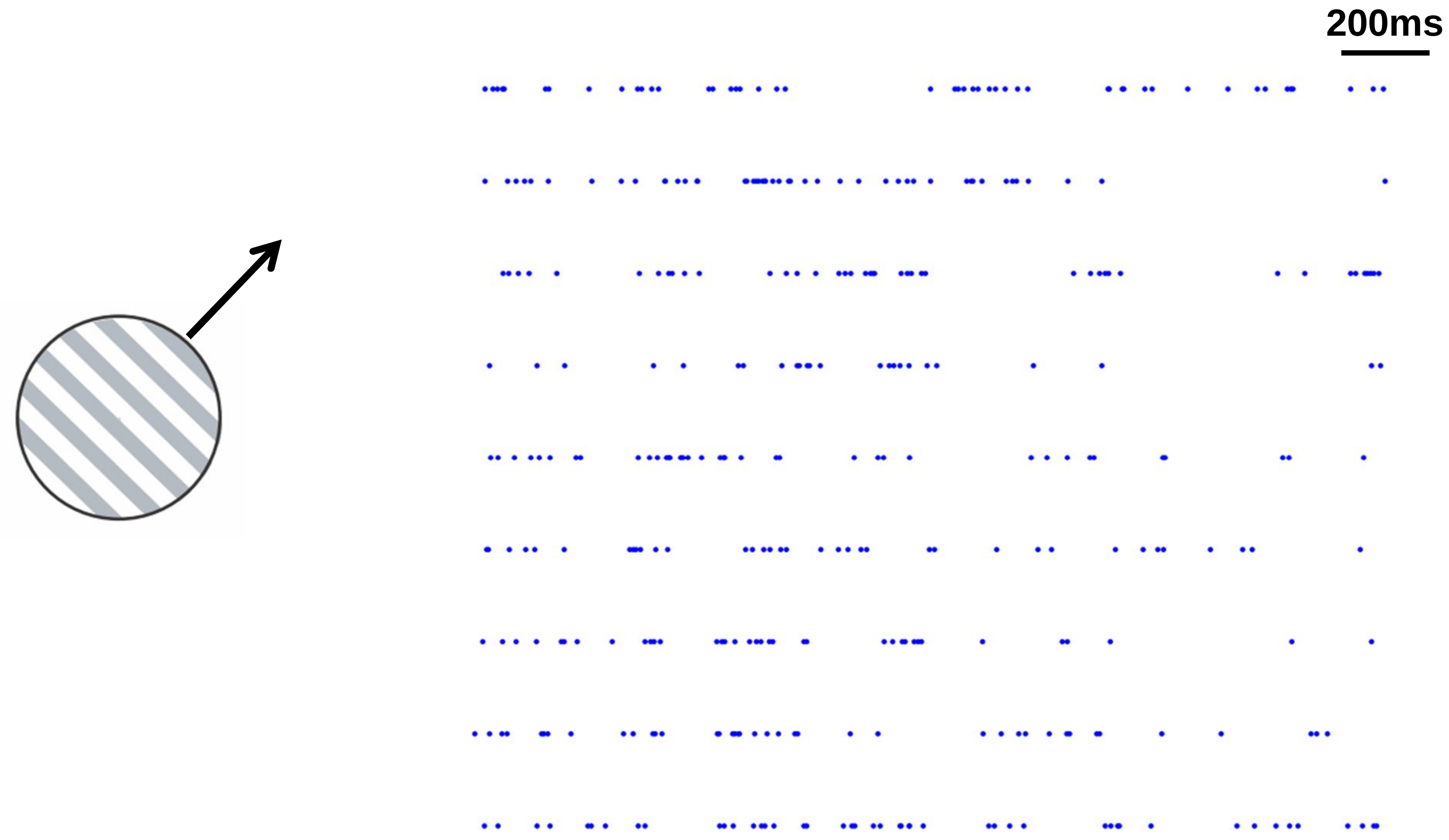
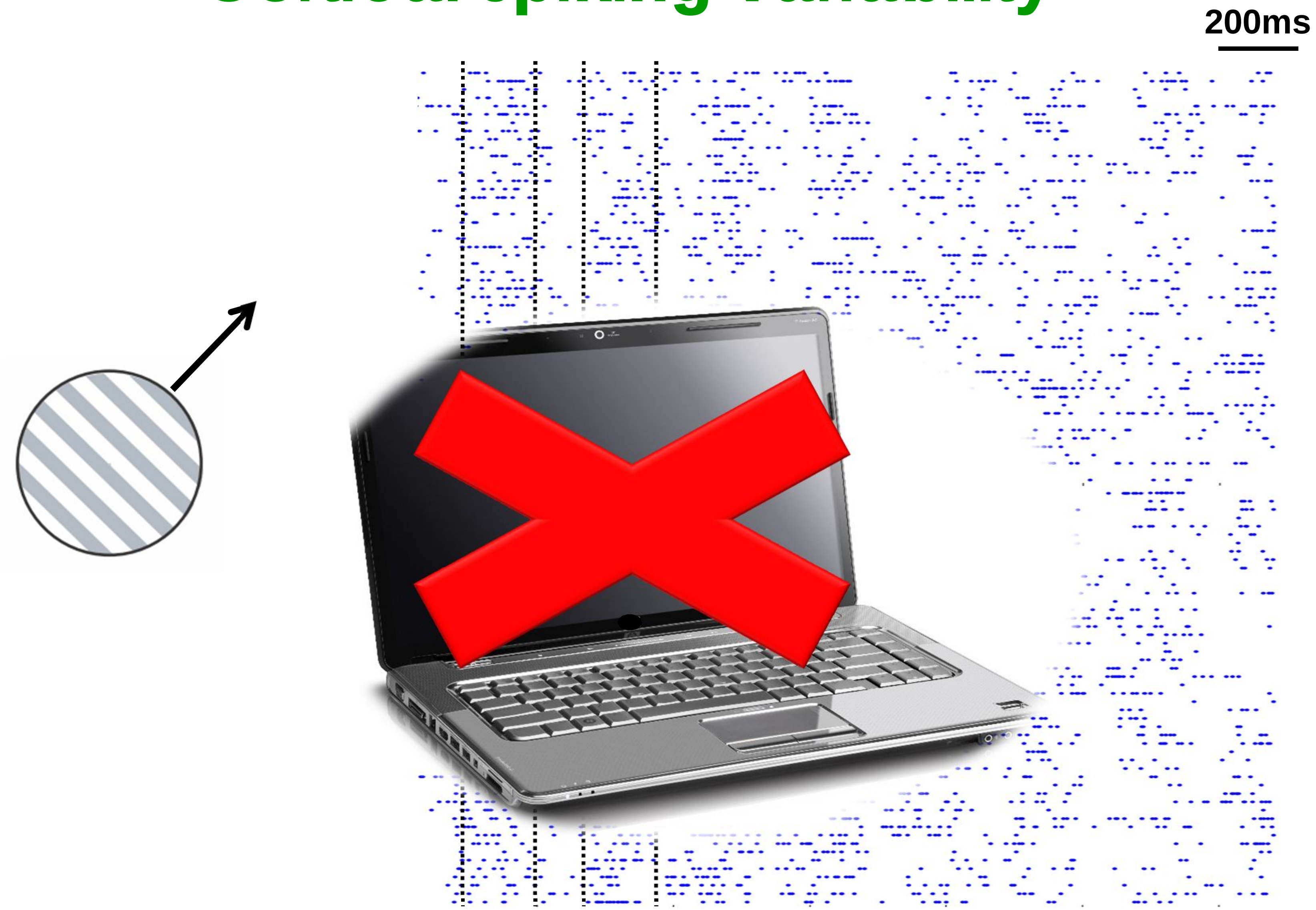
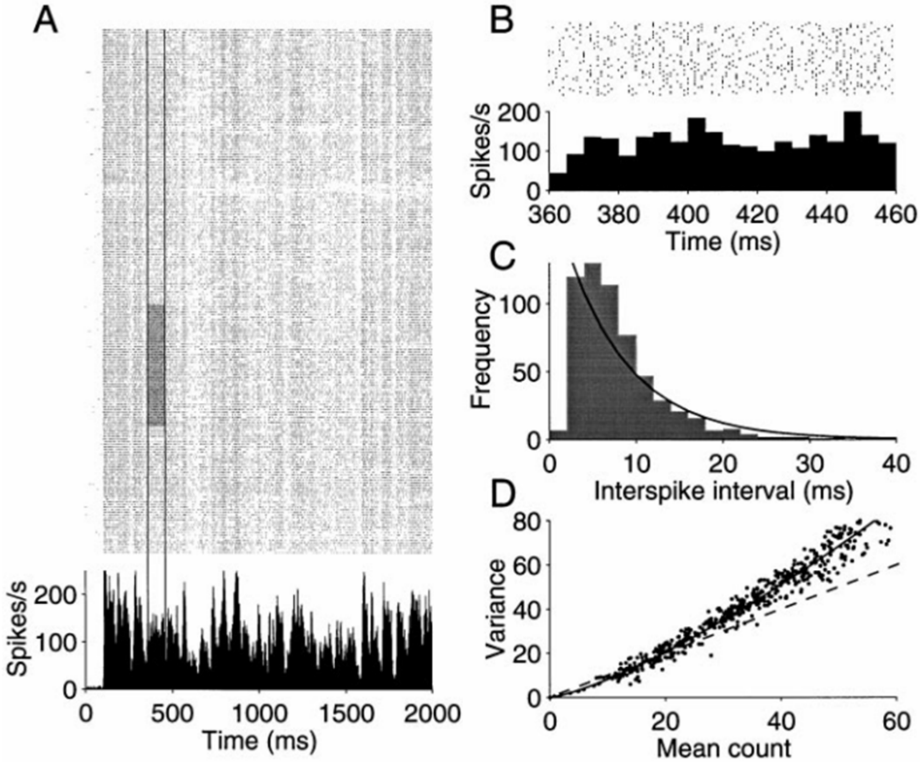


Cortical spiking variability



Cortical spiking variability

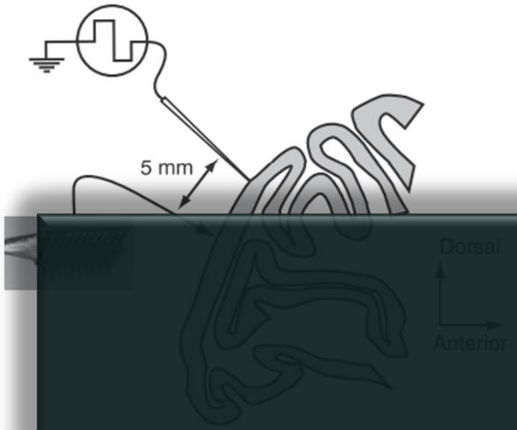


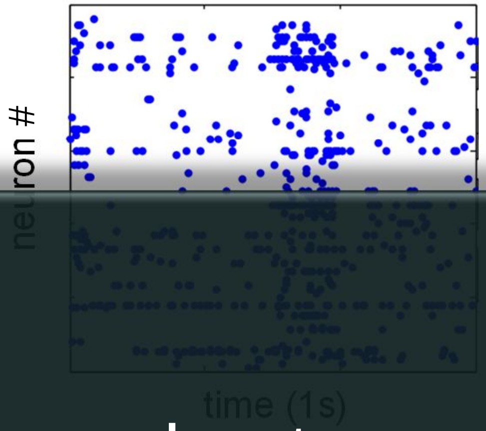
Shadlen and Newsome, 1998

Fano factor, F = Var(N) / <N> ~ constant
for at least two orders of magnitude in firing rate

‘Poisson-like’ firing

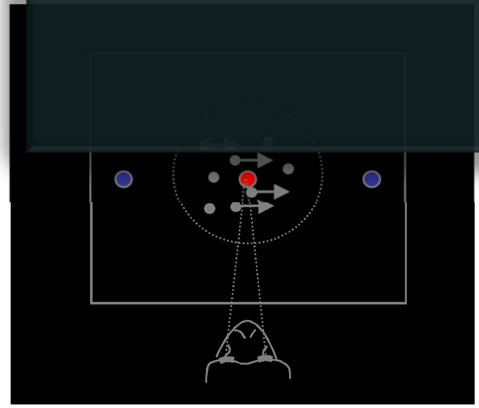
Correlated activity



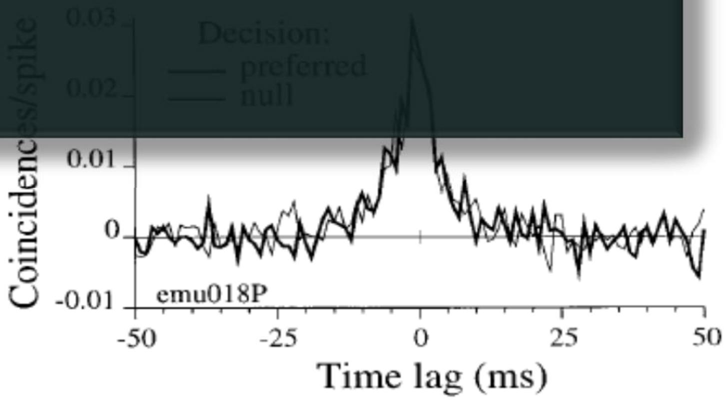


pair or multielectrode recordings **population activity**

Why should we care about variability and correlations?



animal behavior



peaks in CCFs: temporal coincidences

This is why you should care

- variability and correlations set fundamental limits on how much information can be extracted from the neuronal responses

Zohary et al, *Nature*, 1994
Shadlen and Newsome, *J. of Neurosci.*, 1998

- how the observed variability and correlations arise from the underlying neuronal dynamics is largely unknown

-pairs of cells:
Moreno-Bote and Parga, *Phys. Review Letters*, 2006
de la Rocha et al, *Nature*, 2007
Schultze-Kraft et al, *Plos Comp. Biol.*, 2013

-networks:
Ginzburg and Sompolinsky, *Phys. Review E*, 1994
Renart et al, *Science*, 2010
Hertz, *N. Computation*, 2010
Tetzlaff et al, *Plos Comp. Biol.*, 2012
Helias et al, *Plos Comp Biol*, 2014
Moreno-Bote et al, *Nat. Neurosc.*, In Press, 2014

This is why you should care

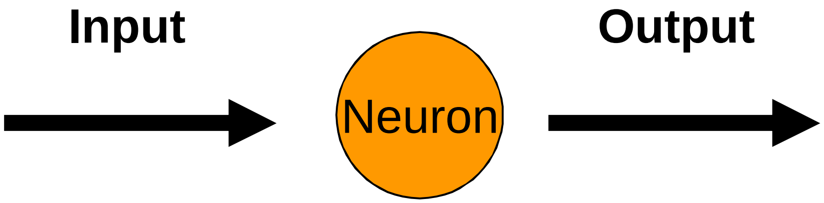
- correlations open the door to estimate functional connectivity between neurons

Aertsen et al, *J. Neurophys*, 1989
Schneidman et al, *Nature*, 2006
Pillow et al, *Nature*, 2008
Cocco et al, *PNAS*, 2009

- variability and correlations might indicate the type of neuronal computations carried out by neuronal circuits

Abeles, Book: Corticonics, 1991
Softky, *Current Opi. Neurobiology*, 1995
Shadlen and Newsome, *J. of Neurosci.*, 1998
Ma et al, *Nature Neurosci*., 2006
Moreno-Bote et al, *PNAS*, 2010
Moreno-Bote, *Plos Comp Biology*, 2014

This is why you should care: the input-output relationship is a Golden Problem

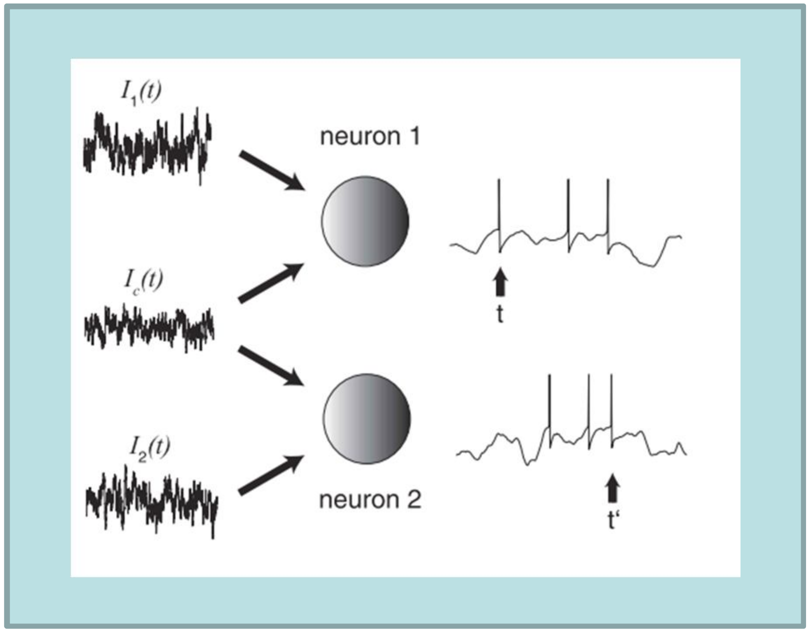


The problem can be faced in the **statistical sense** using average quantities

$$\nu_{in} \longrightarrow \nu_{out} \qquad \nu = \langle N(\mathrm{T}) \rangle / \mathrm{T}$$

$$F_{N,in} \longrightarrow F_{N,out} \qquad F_N = Var(N(\mathrm{T})) / \langle N(\mathrm{T}) \rangle$$

This is why you should care: the input-output relationship is a Golden Problem



$$\rho_{in} \longrightarrow \rho_{out}$$

$$\rho_{12} = \frac{\langle N_1(\mathrm{T}) N_2(\mathrm{T})\rangle - \langle N_1(\mathrm{T})\rangle\langle N_2(\mathrm{T})\rangle}{\sqrt{Var(N_1(\mathrm{T}))Var(N_2(\mathrm{T}))}}$$

Outline

- Information limits set by neuronal correlations (an example)
- Firing rate and variability in LIF neurons with fast and slow synapses (FPE formalism and solutions)
- Correlation transfer in LIF neurons with fast and slow synapses (FPE and approximate solutions)
- Review of literature & main results about correlation transfer:

1. Neurons are sensitive to input correlations (strength and correlation time; Salinas and Sejnowski, *J. of Neurosci.*, 2000; Moreno-Bote et al, *Phys. Review Letters*, 2002)
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3. Firing rate and correlation coefficients are not independent (de la Rocha et al, *Nature*, 2007)

- Open questions

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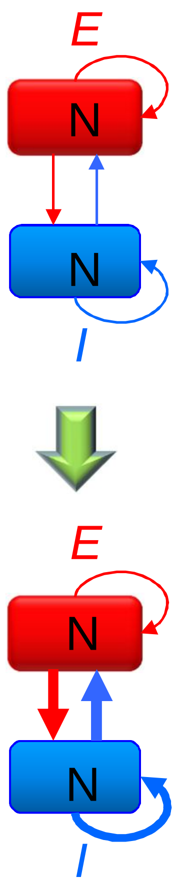
Signal/Noise limits induced by correlations

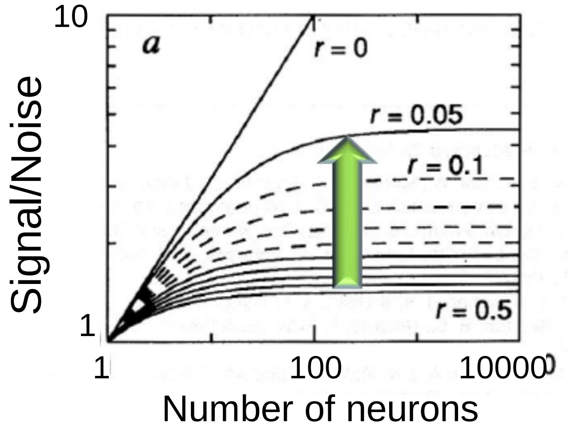


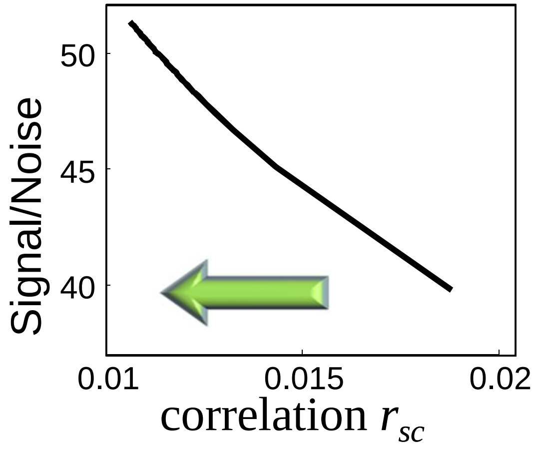
decorrelation

$r_{sc} \sim 0.1$

$r_{sc} \sim 0.01$

Zohary et al, 1994





- In homogenous neuronal populations, correlations are deleterious
- Whether decorrelation improves information is unknown (but await to the 2nd half of the tutorial!)

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- Open questions

Firing rate for a leaky integrate & fire (LIF) neuron with instantaneous synapses

$$\frac{dV(t)}{dt} = -\frac{V(t)}{\tau_m} + I(t),$$

$$I(t) = \sum_{j=1}^{C_E} J_{E_j}\, s_j(t) - \sum_{k=1}^{C_I} J_{I_k}\, s_k(t),$$

$$\nu^{-1} = \tau_{\mathrm{ref}} + \tau_m\sqrt{\pi}\int_{\frac{V_{\mathrm{res}}-\mu_V}{\sigma_V\sqrt{2}}}^{\frac{V_{\mathrm{th}}-\mu_V}{\sigma_V\sqrt{2}}} dx\, \mathrm{e}^{x^2}[1+\mathrm{erf}(x)]$$

$$\mathrm{CV}^2 = 2\pi\nu^2\int_{\frac{V_{\mathrm{res}}-\mu_V}{\sigma_V\sqrt{2}}}^{\frac{V_{\mathrm{th}}-\mu_V}{\sigma_V\sqrt{2}}} dx\, \mathrm{e}^{x^2}\int_{-\infty}^{x} dy\, \mathrm{e}^{y^2}[1+\mathrm{erf}(y)]^2$$

$$\mu_V = \tau_m\mu; \quad \sigma_V^2 = \frac{1}{2}\tau_m\sigma^2$$

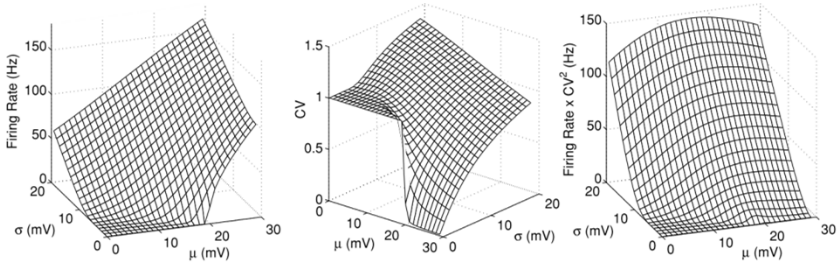


Figure 2: Mean firing rate ν (left), CV (middle), and product $\nu\mathrm{CV}^2$ (right) of the LIF neuron as a function of the mean and standard deviation of the depolarization. Parameters: $V_{\mathrm{th}} = 20$ mV, $V_{\mathrm{res}} = 10$ mV, $\tau_m = 10$ ms, and $\tau_{\mathrm{ref}} = 2$ ms.

Burkitt, Biol Cybern, 2006

Rate with non-instantaneous synapses
Fast neuronal dynamics

$$\dot{V} = -\frac{V}{\tau_m} + \mu + \frac{\sigma}{\sqrt{2\tau_s}} z(t)$$

$$\dot{z} = -\frac{z}{\tau_s} + \sqrt{\frac{2}{\tau_s}}\,\eta(t)$$

$$\longrightarrow \quad V = \mu\tau_m + x\,\sigma\sqrt{\tau_m/2}:$$

$$\left[\frac{\partial}{\partial x}(x - \epsilon z) + \epsilon^2 L_z\right] P = 0$$

$$\epsilon = \sqrt{\tau_m/\tau_s}$$

stationary FPE

$$L_z = \frac{\partial}{\partial z} z + \frac{\partial^2}{\partial^2 z}$$

In the long synaptic time scale limit $\tau_s \geq \tau_m$
we treat $\epsilon = \sqrt{\tau_m/\tau_s}$ as a small parameter

This limit is useful in the high conductance regime
(Destexhe et al.,Nat.Rev.Neurosc. 2003)
or when slow filters (NMDA, GABA$_B$, etc) are important

firing rate $\nu = \int_{\hat{\Theta}/\epsilon}^{\infty} \frac{dz}{\sqrt{2\pi}}\, e^{-z^2/2}\, \nu_0(z).$

$$\nu_0{}^{-1}(z) = \tau_m \ln\left(\frac{\hat{H} - \epsilon z}{\hat{\Theta} - \epsilon z}\right)$$

$$\hat{\Theta} = \sqrt{2}(\Theta - \mu\tau_m)/\sigma\sqrt{\tau_m} \text{ and } \hat{H} = \sqrt{2}(H - \mu\tau_m)/\sigma\sqrt{\tau_m}$$

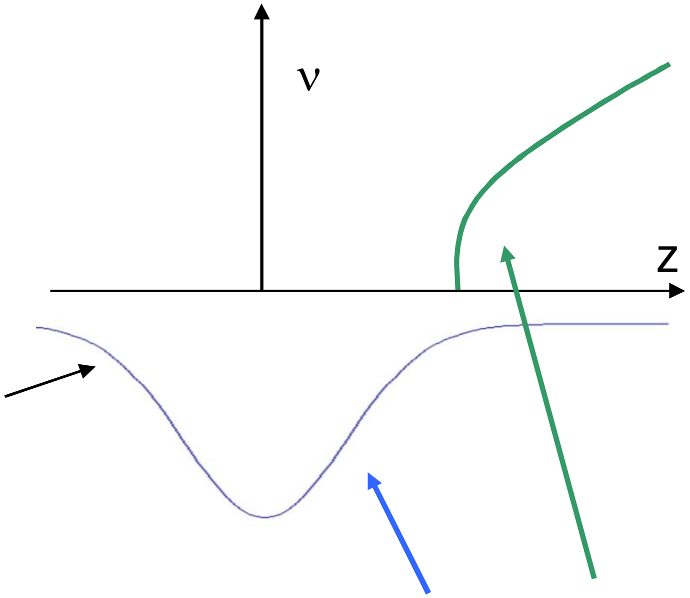
Moreno-Bote and Parga, Phys Rev. Lett, 2004
Moreno-Bote and Parga, Neural Computation, 2010

Rate with non-instantaneous synapses

At first order $$\frac{\partial}{\partial x}(x - \epsilon z)P_0 = 0 \longrightarrow \nu(z) = \frac{1}{\tau_m log\left(\frac{\hat{H}-\epsilon z}{\hat{\Theta}-\epsilon z}\right)}$$

leak

constant drift

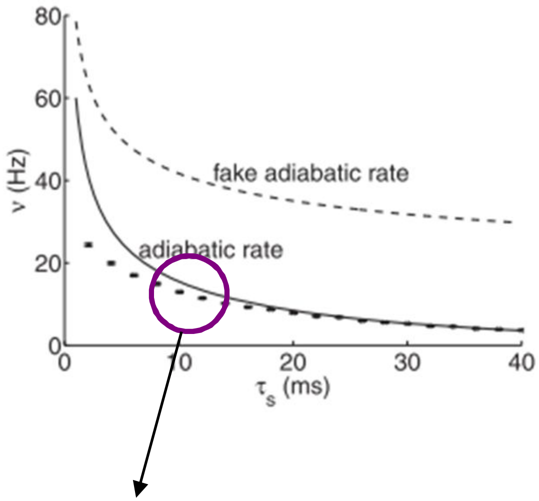


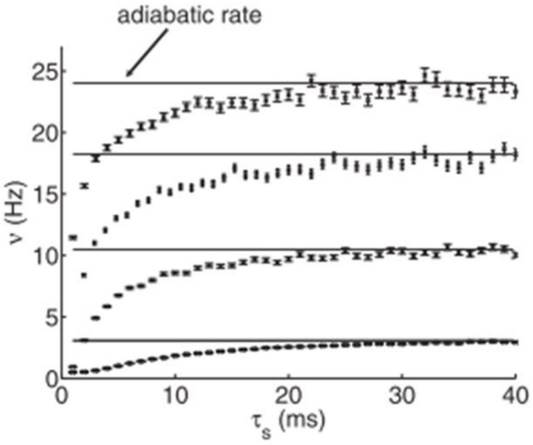
$$P(z) = \frac{e^{-z^2/2}}{\sqrt{2\pi}}$$

Firing rate → $$\nu = \int dz P(z) \nu(z)$$

The only approx. is $\tau_s \geq \tau_m$

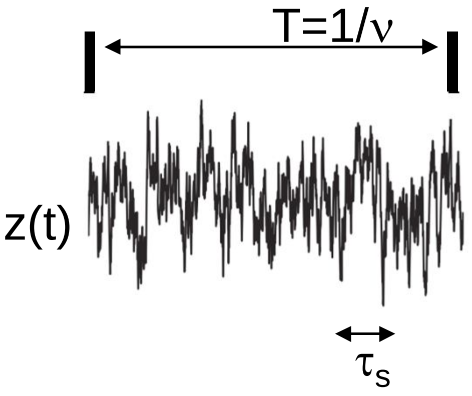
Rate with non-instantaneous synapses



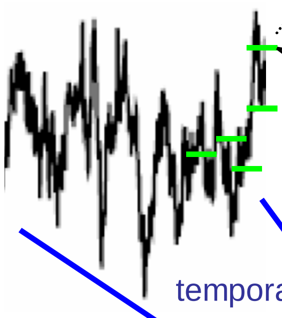


here $\tau_s = \tau_m = 10$ms

This is surprising because here z(t) is not constant during an ISI of typical duration T = 100-200 ms.



Rate with non-instantaneous synapses



z, constant

temporal average

$$\tau_m \dot{x} = -x + \epsilon z$$

$$\nu(z) = \frac{1}{\tau_m log\left(\frac{\hat{H}-\epsilon z}{\hat{\Theta}-\epsilon z}\right)}$$

instantaneous firing rate

$$\boxed{\nu = \int dz P(z)\, \nu(z)}$$

firing rate

Why not $T = \int dz P(z)\, T(z)$?

ISI for fixed z

It does not do a very good job

Rate with non-instantaneous synapses
Fast synapses

In the short synaptic time scale limit $\tau_s \leq \tau_m$
we treat the inverse of $\epsilon = \sqrt{\tau_m/\tau_s}$ as a small parameter

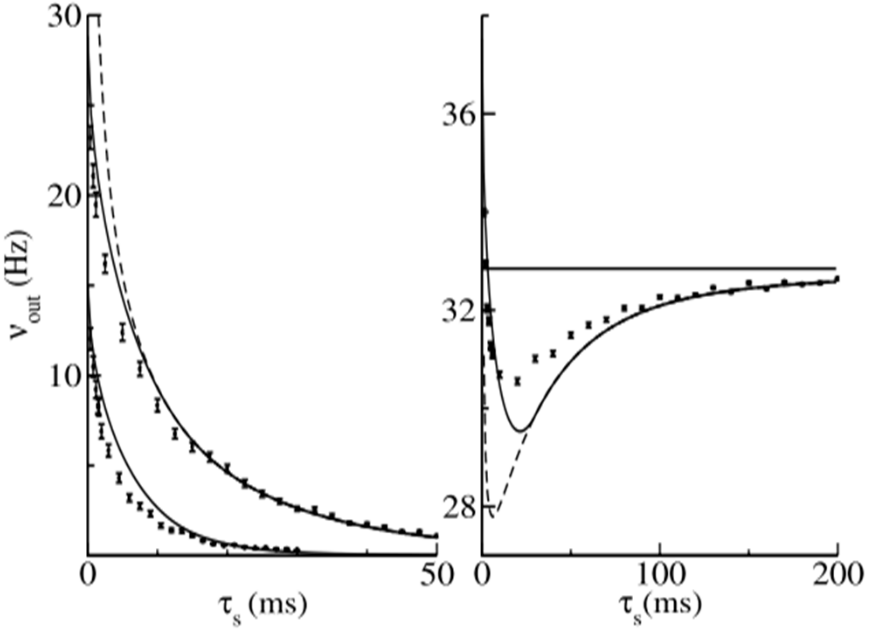
This limit is useful when AMPA receptors are abundant

firing rate

$$\frac{1}{\nu} = \tau_m\sqrt{\pi}\int_{\frac{V_r-\mu}{\sigma}+\frac{\alpha}{2}\sqrt{\frac{\tau_s}{\tau_m}}}^{\frac{\theta-\mu}{\sigma}+\frac{\alpha}{2}\sqrt{\frac{\tau_s}{\tau_m}}} \Psi(s)\,ds$$

$$\Psi(s) = e^{s^2}\left(1+\mathrm{erf}(s)\right)$$

$$\alpha = \sqrt{2}\left|\zeta\left(\frac{1}{2}\right)\right| \simeq \sqrt{2}\ 1.46\ldots$$



Brunel and Sergi, J theor Biol, 1998
Fourcaud and Brunel, Neural Comput., 2002
Moreno-Bote and Parga, Phys Rev Lett, 2004

Interpolating the fast and slow synaptic time scale limits

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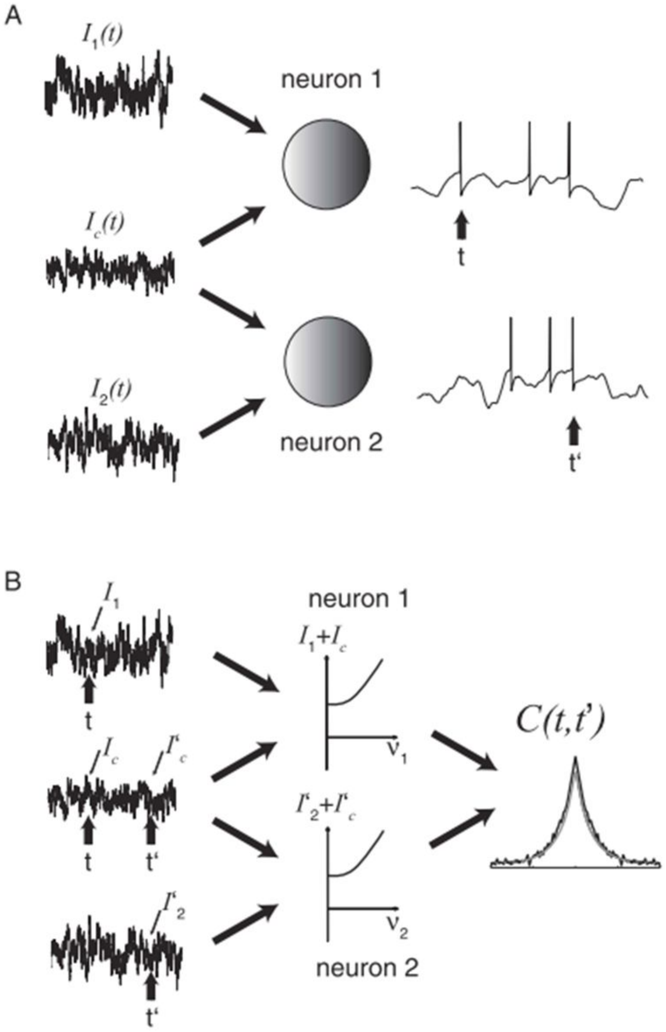
- Open questions

Correlations with non-instantaneous synapses



$$\tau_m \dot{V}_1 = -V_1 + \tau_m(I_1(t) + I_c(t)),$$
$$\tau_m \dot{V}_2 = -V_2 + \tau_m(I_2(t) + I_c(t)).$$

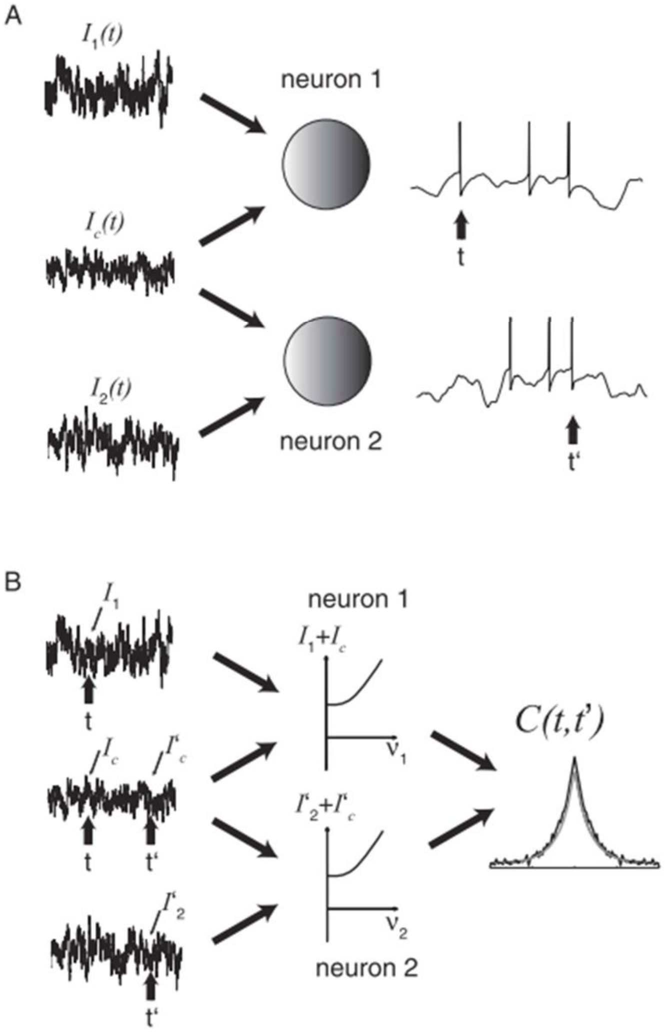
$$\tau_s \dot{I}_i(t) = -I_i(t) + \mu_{ind} + \sigma_{ind}\,\eta_i(t),$$
$$\tau_s \dot{I}_c(t) = -I_c(t) + \mu_c + \sigma_c \eta_c(t),$$

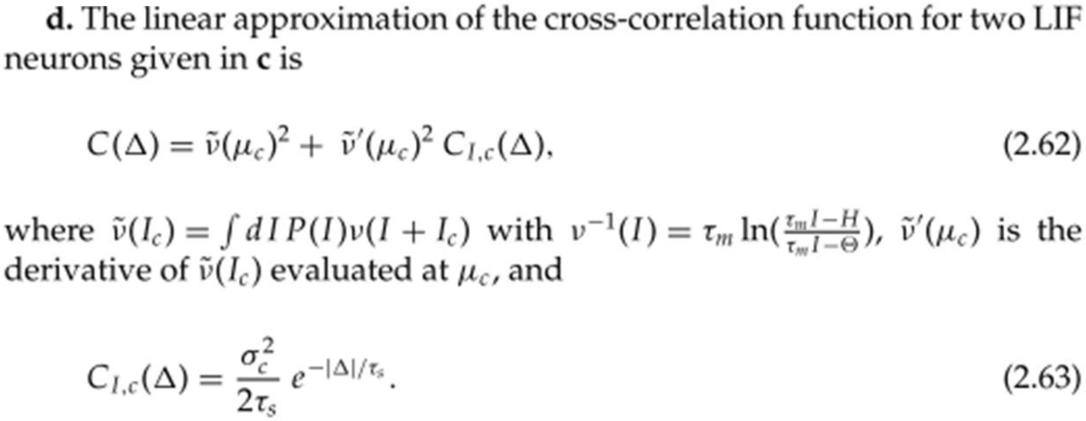
$$C_{pq}(t,t') \equiv \left\langle \left(\sum_{k_p} \delta(t - t_i^{k_p}) - \nu_p \right) \left(\sum_{k_q} \delta(t' - t_j^{k_p}) - \nu_q \right) \right\rangle$$

$$C(t,t') \simeq \int dI_1\, dI'_2\, dI_c\, dI'_c\; P(I_c, t; I'_c, t')\; P(I_1)\; P(I'_2)$$
$$\times\, \nu_1(I_1 + I_c)\, \nu_2(I'_2 + I'_c).$$

Moreno-Bote and Parga, Phys Rew Lett, 2006
Moreno-Bote and Parga, Neural Comput, 2010

Correlations with non-instantaneous synapses





d. The linear approximation of the cross-correlation function for two LIF neurons given in **c** is

$$C(\Delta) = \tilde{\nu}(\mu_c)^2 + \tilde{\nu}'(\mu_c)^2\, C_{I,c}(\Delta), \tag{2.62}$$

where $\tilde{\nu}(I_c) = \int dI\, P(I)\nu(I + I_c)$ with $\nu^{-1}(I) = \tau_m \ln(\frac{\tau_m I - H}{\tau_m I - \Theta})$, $\tilde{\nu}'(\mu_c)$ is the derivative of $\tilde{\nu}(I_c)$ evaluated at μ_c, and

$$C_{I,c}(\Delta) = \frac{\sigma_c^2}{2\tau_s}\, e^{-|\Delta|/\tau_s}. \tag{2.63}$$

Moreno-Bote and Parga, Phys Rew Lett, 2006
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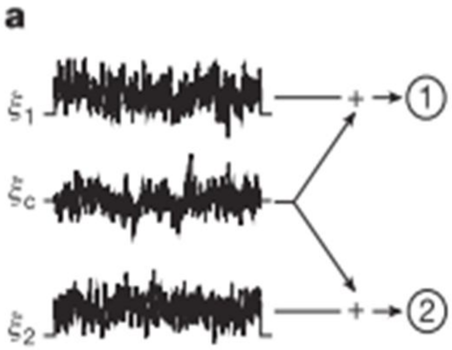
Correlations with instantaneous synapses



$$\tau_\mathrm{m}\frac{\mathrm{d}V_i}{\mathrm{d}t} = -V_i + \mu + \sigma\sqrt{\tau_\mathrm{m}}\left(\sqrt{1-c}\,\xi_i(t) + \sqrt{c}\,\xi_\mathrm{c}(t)\right)$$

$$I_i = \mu_i + \sigma_i\left(\sqrt{1-c}\,\xi_i(t) + \sqrt{c}\,\xi_\mathrm{c}(t)\right)$$

$$\rho \approx S(\mu,\sigma)c = \frac{\sigma^2\left(\frac{\mathrm{d}\nu}{\mathrm{d}\mu}\right)^2}{\mathrm{CV}^2\nu}c$$

de la Rocha et al, Nature, 2007

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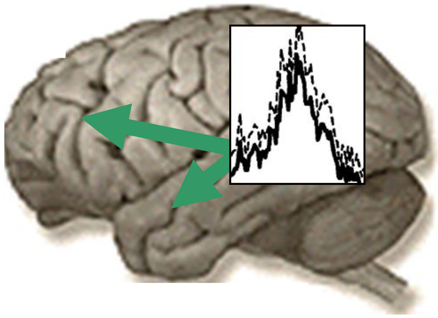
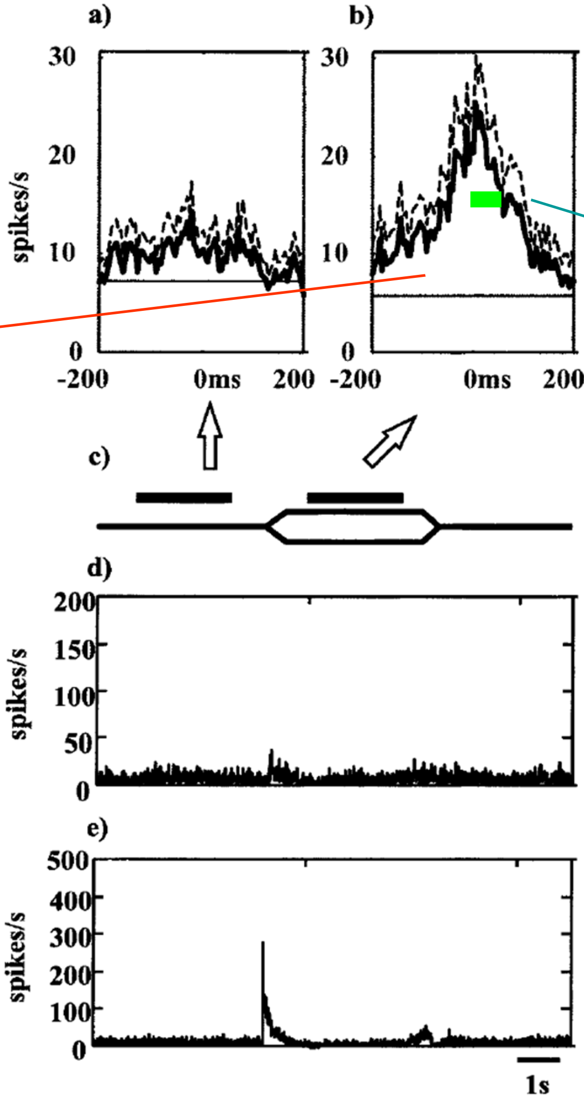
Correlated activity in primary auditory cortex



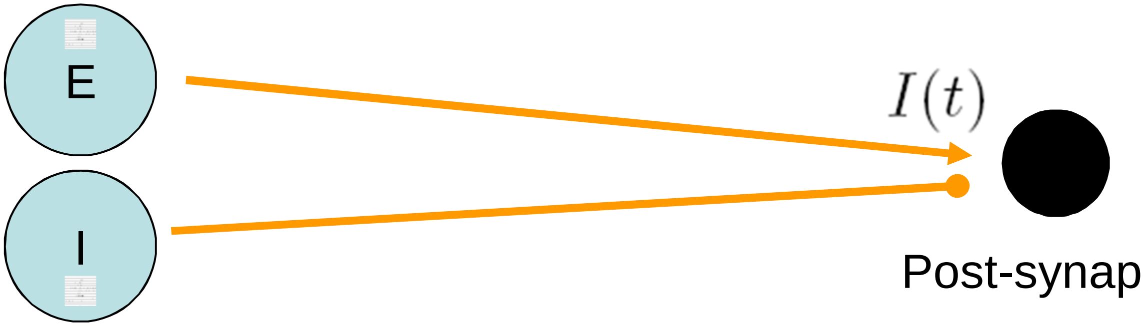


Exponential-like correlations

50 ms

deCharms and Merzenich, 1996

Model. The total presynaptic current



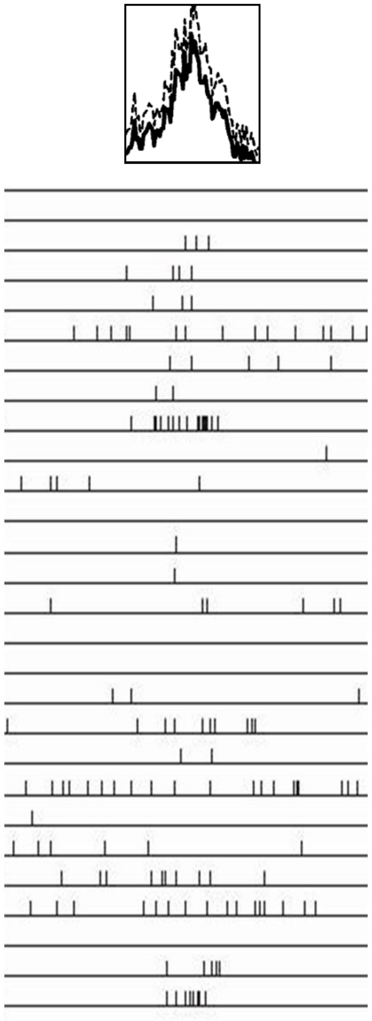
Post-synaptic Neuron

$$\dot{V}(t) = -\frac{V(t)}{\tau_m} + I(t)$$

Leaky Integrate-and-Fire neuron

$$I(t) = J_E \sum_{i=1}^{N_E} \sum_k \delta(t - t_i^k) - J_I \sum_{j=1}^{N_I} \sum_l \delta(t - t_j^l)$$

Model. Temporal Correlations



Auto-correlations:

$$C_p(t,t') \equiv \left\langle \left(\sum_k \delta(t - t_i^k) - \nu_p \right) \left(\sum_{k'} \delta(t' - t_i^{k'}) - \nu_p \right) \right\rangle$$

$$= \nu_p \delta(t - t') + \nu_p \left(\frac{F_p - 1}{2\tau_c} \right) e^{-\frac{|t-t'|}{\tau_c}}$$

rate

Fano factor

Cross-correlations:

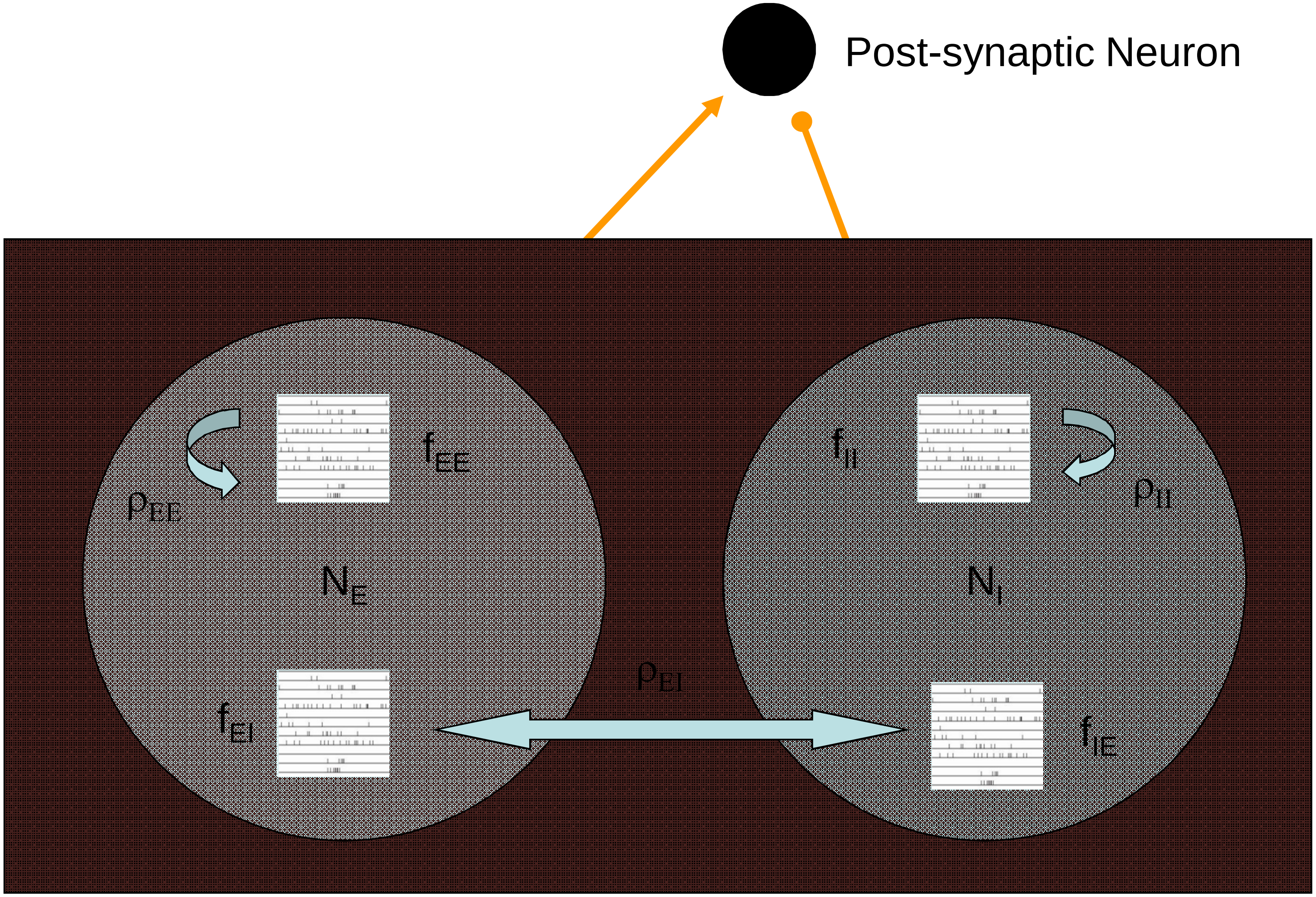
$$C_{pq}(t,t') \equiv \left\langle \left(\sum_{k_p} \delta(t - t_i^{k_p}) - \nu_p \right) \left(\sum_{k_q} \delta(t' - t_j^{k_p}) - \nu_q \right) \right\rangle$$

corr. time

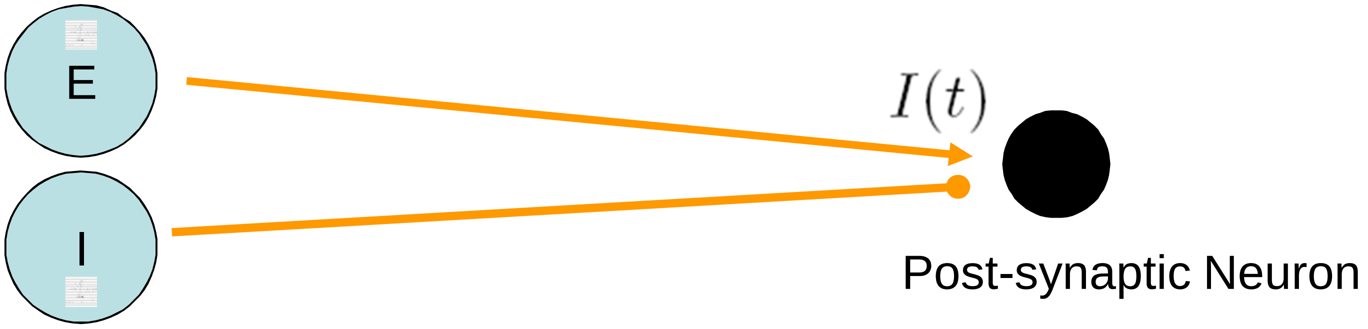
$$= \sqrt{\nu_p \nu_q} \left(\frac{\rho_{pq} \sqrt{F_p\, F_q}}{2\tau_c} \right) e^{-\frac{|t-t'|}{\tau_c}}$$

correlation coefficient

Model. Spatial Correlations



Results. Properties of the syn. current



$$I(t) = J_E \sum_{i=1}^{N_E} \sum_{k} \delta(t - t_i^k) - J_I \sum_{j=1}^{N_I} \sum_{l} \delta(t - t_j^l)$$

$$\mu = J_E N_E \nu_E - J_I N_I \nu_I$$

mean current

correlation magnitude

$$C_{current}(t,t') = \sigma_w^2 \left[\delta(t-t') + \frac{\alpha}{2\tau_c} e^{-\frac{|t-t'|}{\tau_c}} \right]$$

white noise variance

correlation time

Results. α and τ_c

$$C_{current}(t,t') = \sigma_w^2 \left[\delta(t-t') + \frac{\alpha}{2\tau_c} \, e^{-\frac{|t-t'|}{\tau_c}} \right]$$

correlation magnitude

correlation time

$$\begin{aligned}
\sigma_w^2 &= J_E^2 N_E \nu_E + J_I^2 N_I \nu_I \\
\alpha \; \sigma_w^2 &= J_E^2 N_E \nu_E [(F_E - 1) + f_{EE}(f_{EE} N_E - 1) F_E \; \rho_{EE}] \\
&\quad + J_I^2 N_I \nu_I [(F_I - 1) + f_{II}(f_{II} N_I - 1) F_I \; \rho_{II}] \\
&\quad - 2 \; J_E J_I \; f_{EI} f_{IE} N_E N_I \; \sqrt{\nu_E \nu_I} \; \sqrt{F_E \; F_I} \rho_{EI} \; .
\end{aligned}$$

How to generate such a current?

$$I(t) = J_E \sum_{i=1}^{N_E} \sum_{k} \delta(t - t_i^k) - J_I \sum_{j=1}^{N_I} \sum_{l} \delta(t - t_j^l)$$

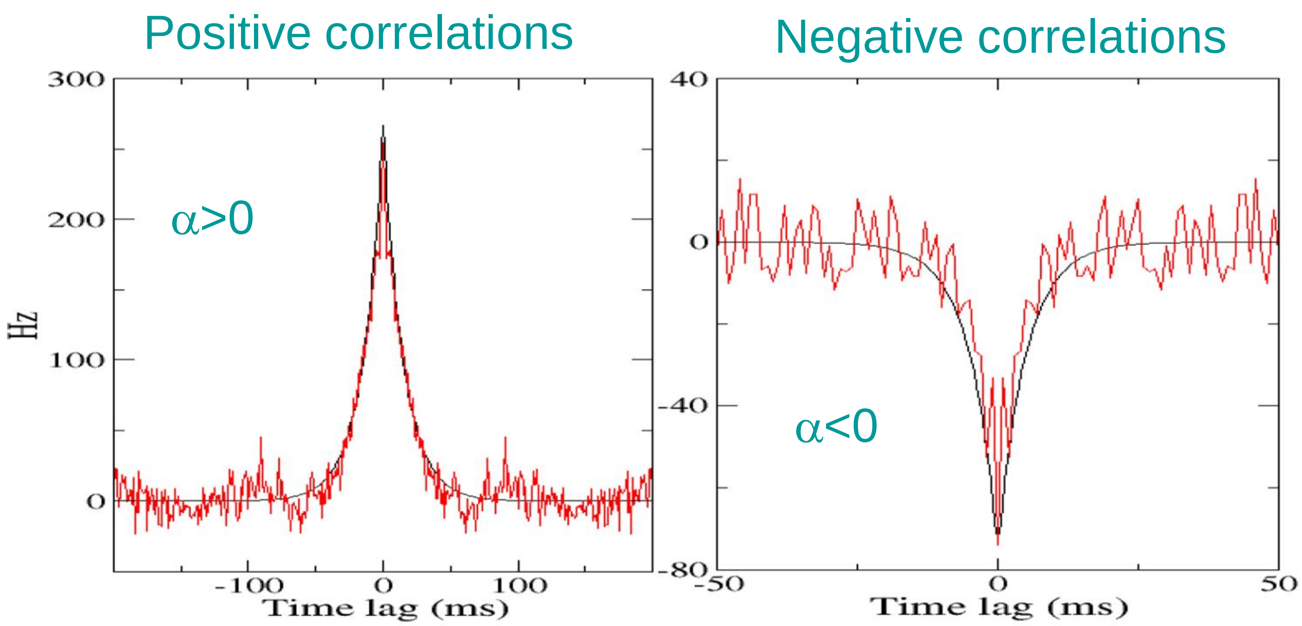
$$\mu = J_E N_E \nu_E - J_I N_I \nu_I$$

$$C_{current}(t, t') = \sigma_w^2 \left[\delta(t - t') + \frac{\alpha}{2\tau_c} e^{-\frac{|t-t'|}{\tau_c}} \right]$$

Why a simple representation of the current is required?

1. Generating the current in the way defined above is complex.
2. If the representation of the current is simple enough, it can allow us to find an analytical solution in some limits.
3. It can be used to simulate neurons receiving correlated inputs.
4. It can be used to stimulate real neurons with current waves mimicking correlated inputs.

Results. Generating I(t) using an auxiliar OUP



Positive correlations

Negative correlations

$$I(t) = \mu + \sigma_w \eta(t) + \sigma_w \frac{\beta}{\sqrt{2\tau_c}} z(t)$$

$$\dot{z}(t) = -\frac{z}{\tau_c} + \sqrt{\frac{2}{\tau_c}}\eta(t) \; ,$$

$$\beta = \pm\sqrt{1+\alpha} - 1$$

$$\longrightarrow \quad C_{current}(t,t') = \sigma_w^2 \left[\delta(t-t') + \frac{\alpha}{2\tau_c} e^{-\frac{|t-t'|}{\tau_c}}\right]$$

Moreno et al, PRL, 2002

Results. The FPE and the firing rate

The **FPE** associated to the equation for V and the current is

$$[L_x + \frac{L_z}{k^2} + \frac{2}{k}\frac{\partial}{\partial x}(\frac{\partial}{\partial z} - \frac{\beta z}{2})]P_\beta(x, z) = -\tau_m \delta(x - \sqrt{2}\hat{H}) J_\beta(z)$$

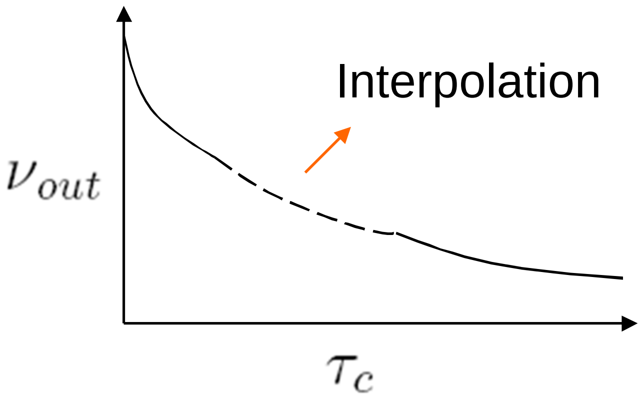
It can be solved in the **long correlation time limit**

$$\nu_{out} = \nu_0 + \frac{C}{\tau_c}$$

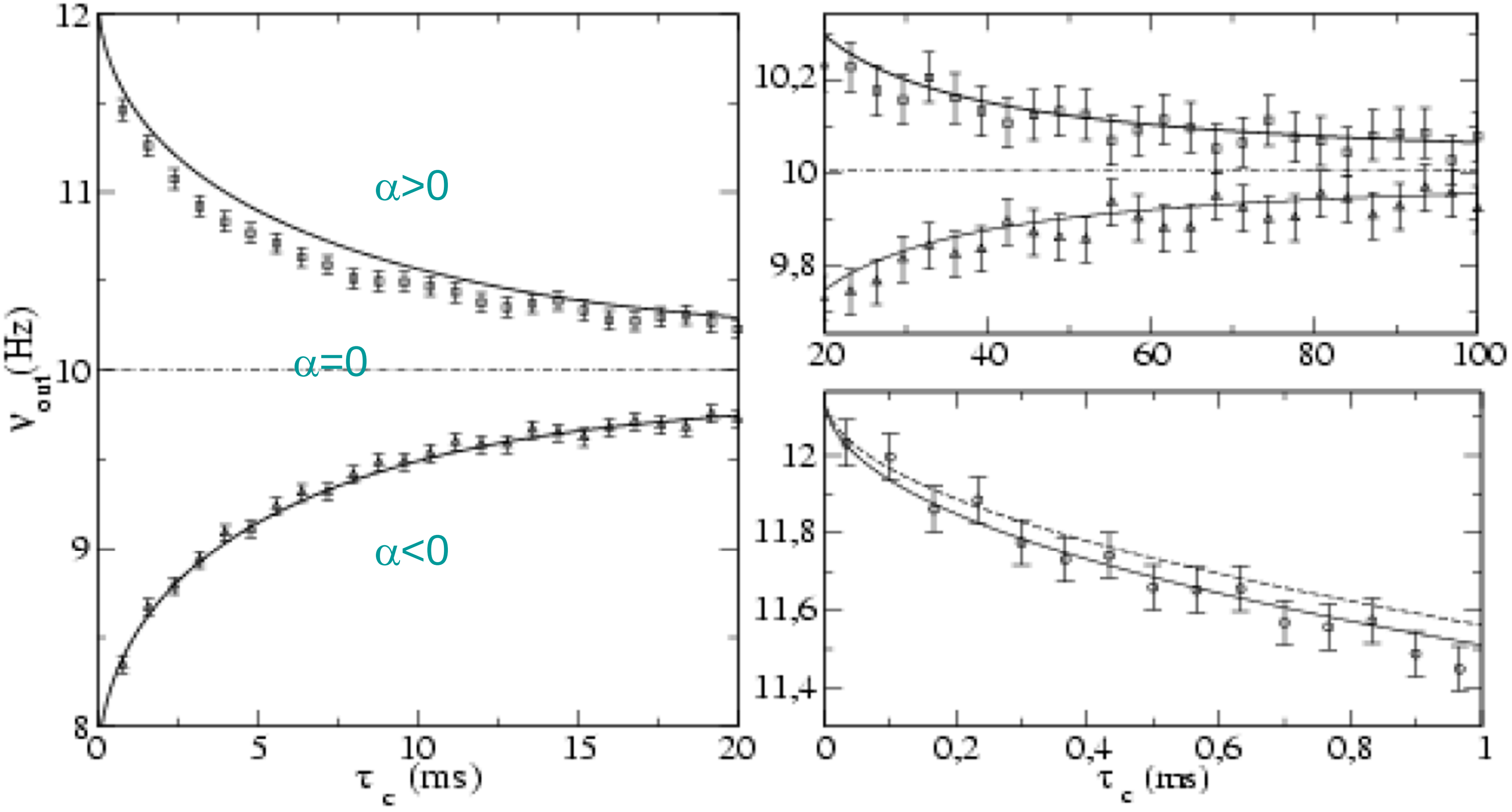
The FPE is also solved in the **short correlation time limit**

$$\nu_{out} = \nu_{eff} - \alpha\sqrt{\tau_c \tau_m}\nu_0^2 R(\hat{\Theta})$$

$$\sigma_{eff}^2 = \sigma_w^2(1 + \alpha)$$



Results. Stationary rate as a function of τ_c



Results. Non-stationary response.
Fast responses predicted by the FPE

The **instantaneous firing rate** of the neuron is exactly

$$\nu_{out}(t) = -\frac{\sigma_w^2(t)}{2}\frac{\partial}{\partial V}\int_{-\infty}^{\infty} dw P(V,w,t)|_{V=\Theta}$$

Changing $\sigma_w^2(t)$ will procude an instantaneous change in the rate

When the **correlation time** becomes **zero**, it can be expressed as

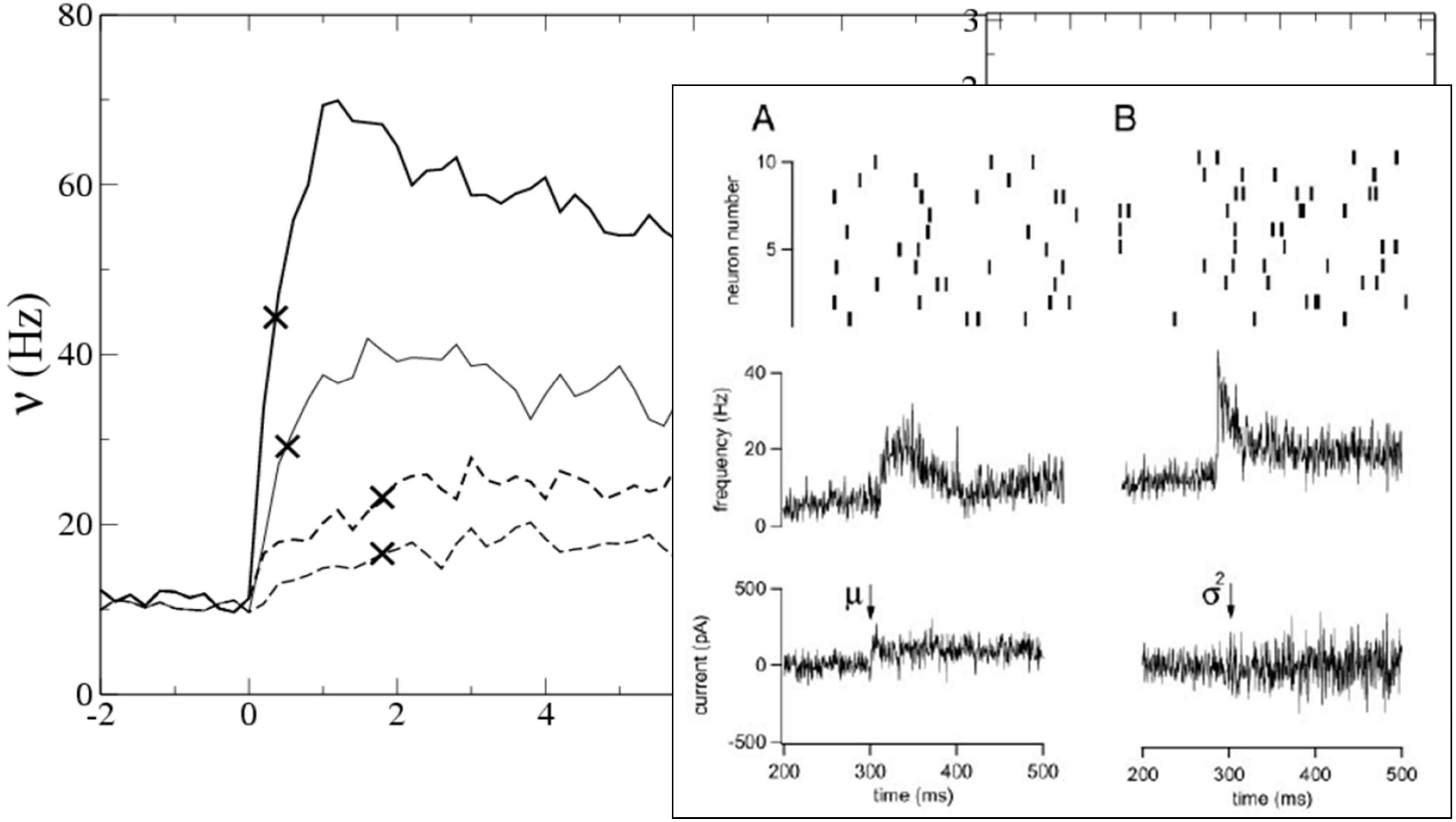
$$\nu_{out}(t) = -\frac{\sigma_{eff}^2(t)}{2}\frac{\partial}{\partial V}\int dw P(V,w,t)|_{V=\Theta}$$

$$\sigma_{eff}^2 = \sigma_w^2(1+\alpha)$$

Changing it will procude an instantaneous change in the rate

For short enough correlation times, the response has also to be very fast!

Results. Rapid response to instantaneous changes of α



Silberberg et al, 2004

… in conclusion

1. We have described the statistical properties of a current that considers the acitivity of many correlated neurons.

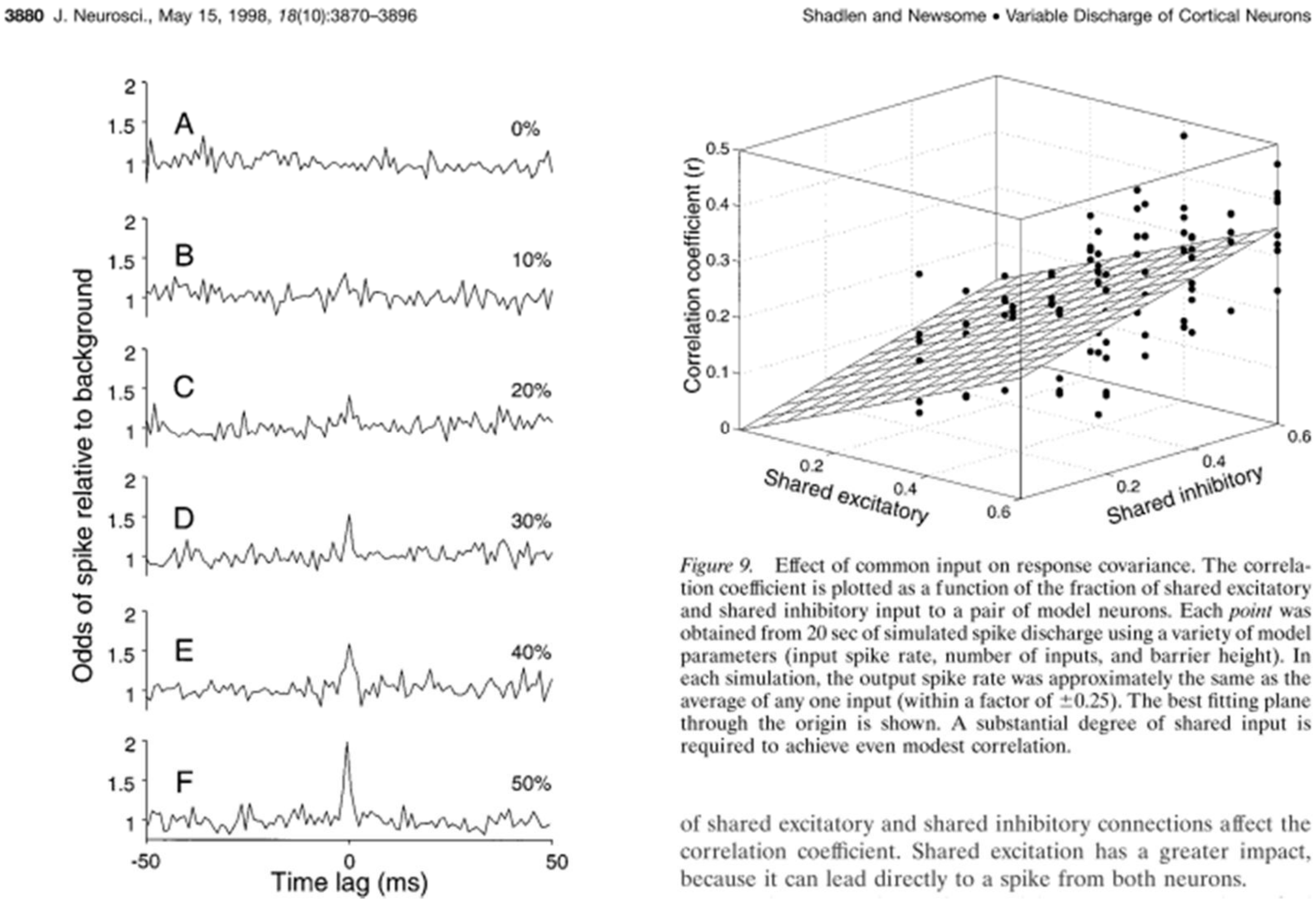
2. This current has been generated using an auxiliary OU process.

3. The associated FPE to this current and to an IF neuron has been solved in the limits of short and long correlation times.

4. These solutions predict the modulation of neuronal resposes to variations of the parameters defining the correlated activity.

5. Changing the correlation magnitude of pre-synaptic populations produces a very fast increase of the output firng rate.

Weak effects of correlations on firing rate?



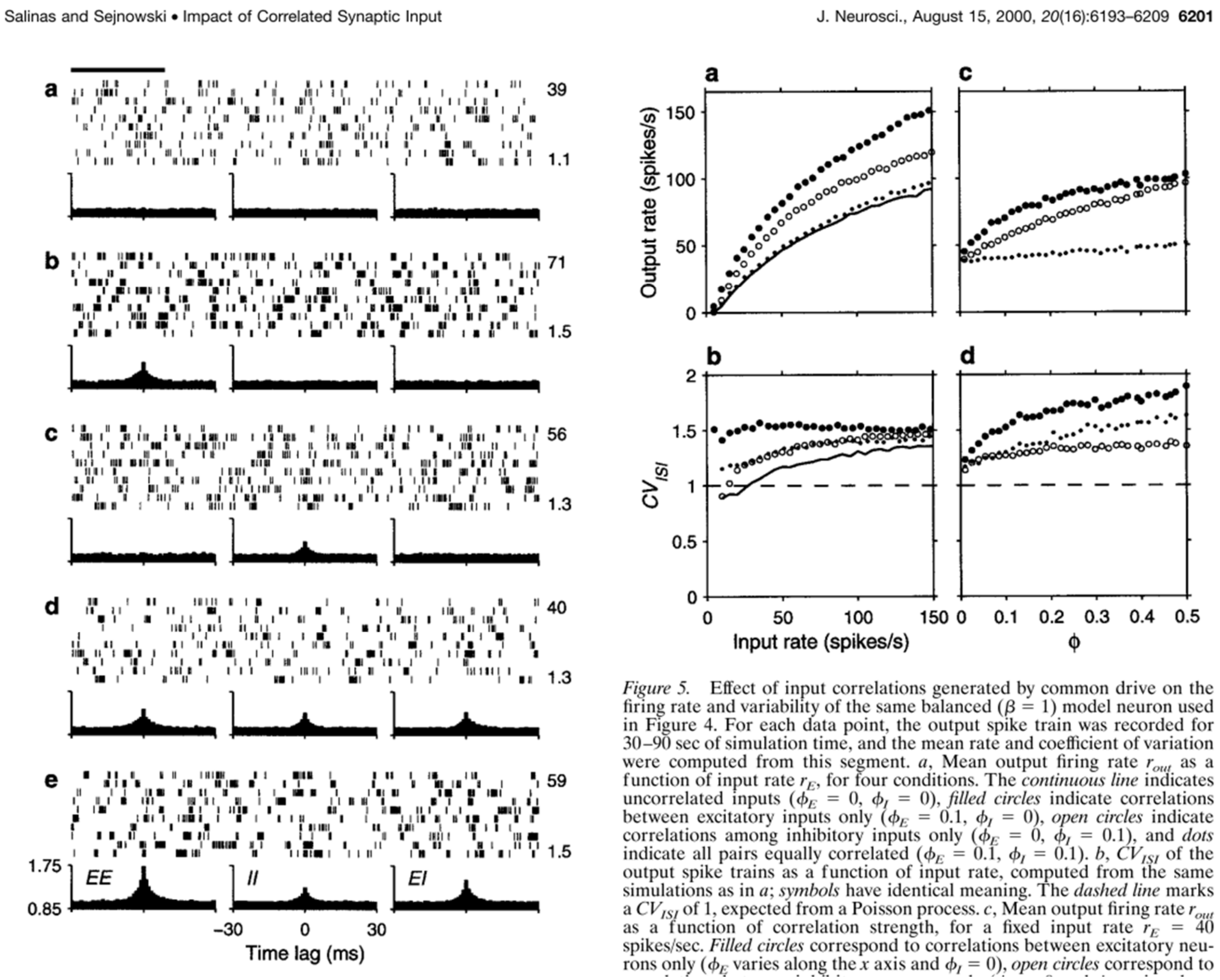
3880 J. Neurosci., May 15, 1998, *18*(10):3870–3896

Shadlen and Newsome • Variable Discharge of Cortical Neurons

Figure 9. Effect of common input on response covariance. The correlation coefficient is plotted as a function of the fraction of shared excitatory and shared inhibitory input to a pair of model neurons. Each *point* was obtained from 20 sec of simulated spike discharge using a variety of model parameters (input spike rate, number of inputs, and barrier height). In each simulation, the output spike rate was approximately the same as the average of any one input (within a factor of ±0.25). The best fitting plane through the origin is shown. A substantial degree of shared input is required to achieve even modest correlation.

of shared excitatory and shared inhibitory connections affect the correlation coefficient. Shared excitation has a greater impact, because it can lead directly to a spike from both neurons.

Strong effects correlations on rate and CV

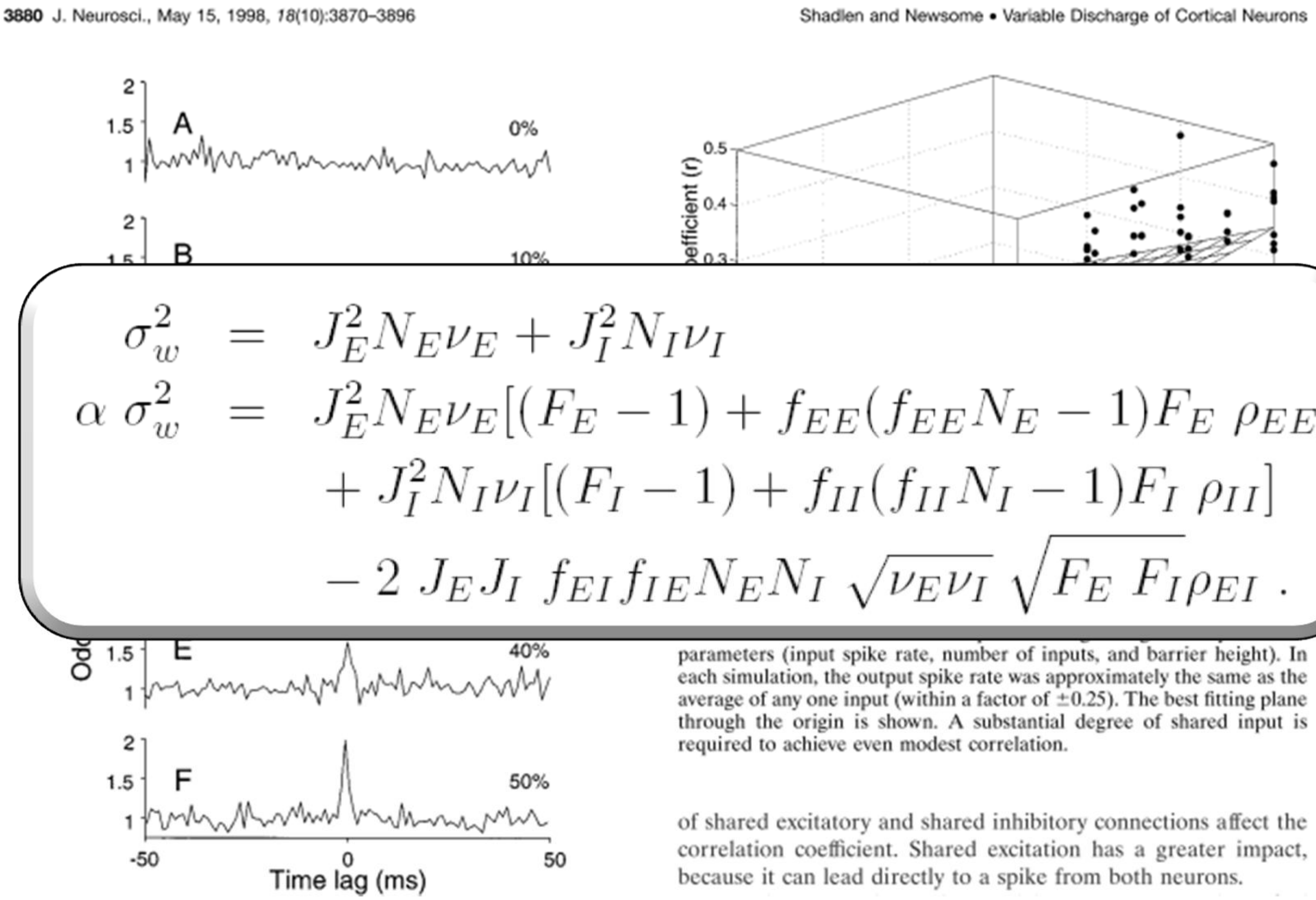


Salinas and Sejnowski • Impact of Correlated Synaptic Input

J. Neurosci., August 15, 2000, *20*(16):6193–6209 **6201**

Figure 5. Effect of input correlations generated by common drive on the firing rate and variability of the same balanced ($\beta = 1$) model neuron used in Figure 4. For each data point, the output spike train was recorded for 30–90 sec of simulation time, and the mean rate and coefficient of variation were computed from this segment. *a*, Mean output firing rate r_{out} as a function of input rate r_E, for four conditions. The *continuous line* indicates uncorrelated inputs ($\phi_E = 0$, $\phi_I = 0$), *filled circles* indicate correlations between excitatory inputs only ($\phi_E = 0.1$, $\phi_I = 0$), *open circles* indicate correlations among inhibitory inputs only ($\phi_E = 0$, $\phi_I = 0.1$), and *dots* indicate all pairs equally correlated ($\phi_E = 0.1$, $\phi_I = 0.1$). *b*, CV_{ISI} of the output spike trains as a function of input rate, computed from the same simulations as in *a*; *symbols* have identical meaning. The *dashed line* marks a CV_{ISI} of 1, expected from a Poisson process. *c*, Mean output firing rate r_{out} as a function of correlation strength, for a fixed input rate $r_E = 40$ spikes/sec. *Filled circles* correspond to correlations between excitatory neurons only (ϕ_E varies along the *x* axis and $\phi_I = 0$), *open circles* correspond to

Weak effects of correlations on firing rate?



3880 J. Neurosci., May 15, 1998, 18(10):3870–3896

Shadlen and Newsome • Variable Discharge of Cortical Neurons

$$
\begin{aligned}
\sigma_w^2 &= J_E^2 N_E \nu_E + J_I^2 N_I \nu_I \\
\alpha\, \sigma_w^2 &= J_E^2 N_E \nu_E [(F_E - 1) + f_{EE}(f_{EE} N_E - 1) F_E\, \rho_{EE}] \\
&\quad + J_I^2 N_I \nu_I [(F_I - 1) + f_{II}(f_{II} N_I - 1) F_I\, \rho_{II}] \\
&\quad - 2\, J_E J_I\, f_{EI} f_{IE} N_E N_I\, \sqrt{\nu_E \nu_I}\, \sqrt{F_E\, F_I}\rho_{EI}\ .
\end{aligned}
$$

parameters (input spike rate, number of inputs, and barrier height). In each simulation, the output spike rate was approximately the same as the average of any one input (within a factor of ±0.25). The best fitting plane through the origin is shown. A substantial degree of shared input is required to achieve even modest correlation.

of shared excitatory and shared inhibitory connections affect the correlation coefficient. Shared excitation has a greater impact, because it can lead directly to a spike from both neurons.

Outline

- Information limits set by neuronal correlations (an example)
- Firing rate and variability in LIF neurons with fast and slow synapses (FPE formalism and solutions)
- Correlation transfer in LIF neurons with fast and slow synapses (FPE and approximate solutions)
- Review of literature & main results about correlation transfer:

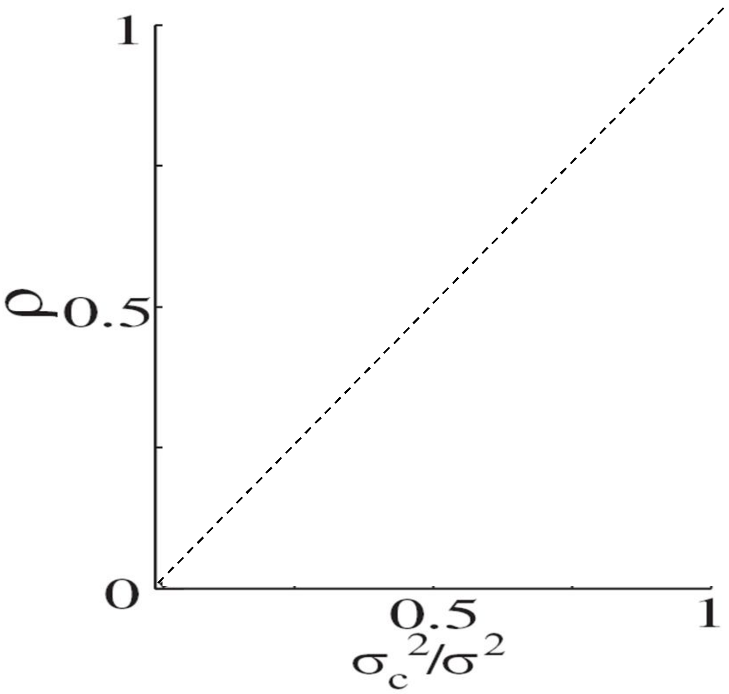
1. Neurons are sensitive to input correlations (strength and correlation time; Salinas and Sejnowski, *J. of Neurosci.*, 2000; Moreno-Bote et al, *Phys. Review Letters*, 2002)
2. Output correlation is lower than input correlation in spiking neurons (Moreno-Bote and Parga, *Phys. Review Letters*, 2006)
3. Firing rate and correlation coefficients are not independent (de la Rocha et al, *Nature*, 2007)

- Open questions

Lower output correlations than in the inputs

Correlation coefficient: $\rho = \dfrac{2\int C(s)ds}{F_N \nu}$

correlation



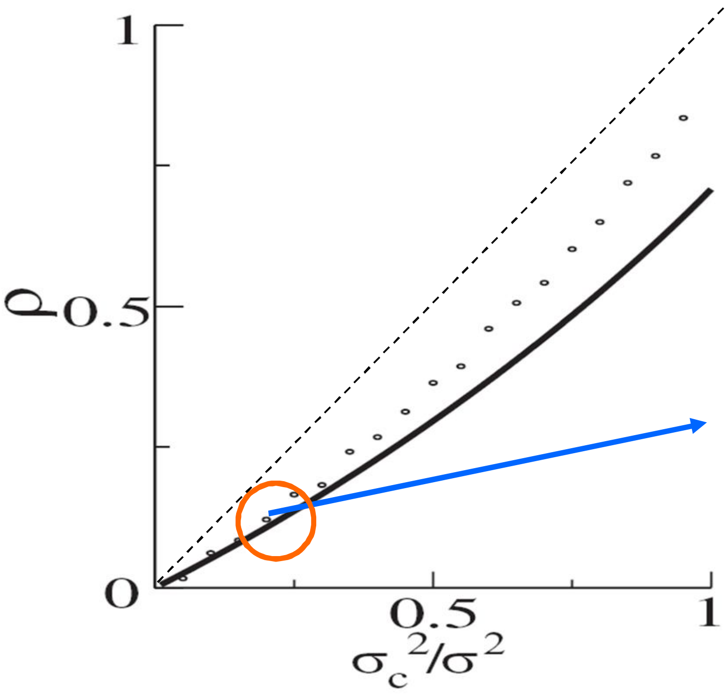
input correlation, or
fraction of common noise

$$\sigma^2 = \sigma_{ind}^2 + \sigma_c^2$$

Lower output correlations than in the inputs

Correlation coefficient: $\rho = \frac{2\int C(s)ds}{F_N \nu}$

correlation



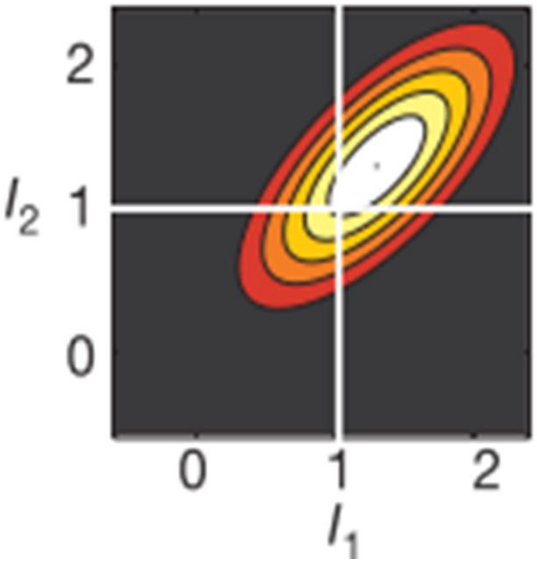
Slow rise with slope smaller than 1

To get **ρ=0.1**, neurons need to share around **20%** of their input variability

input correlation, or
fraction of common noise

$$\sigma^2 = \sigma_{ind}^2 + \sigma_c^2$$

Lower output correlations than in the inputs: intuition and generality of the result



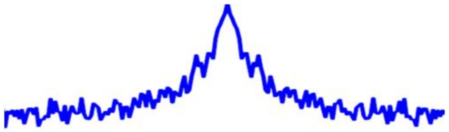
The correlation coefficient of the output of a pair of non-linear rate neurons receiving correlated Gaussian noise is bounded by the correlation in the input: in the picture, the blob surviving in the first quadrant is less elongated that the original Gaussian distribution, leading to lower correlation in the output than in the input

Lancaster, Biometrika, 1957

The shape of the cross-correlation function

Low fraction of common noise

$$\frac{\sigma_c^{\,2}}{\sigma^{\,2}} \ll 1$$

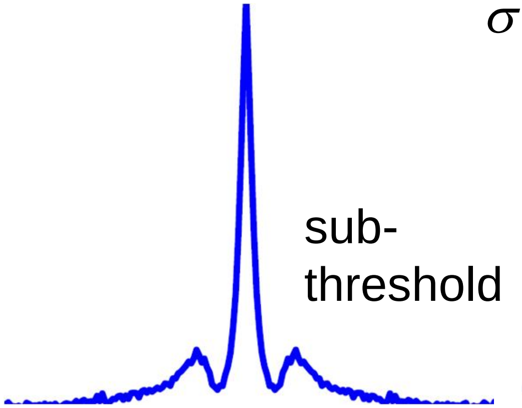


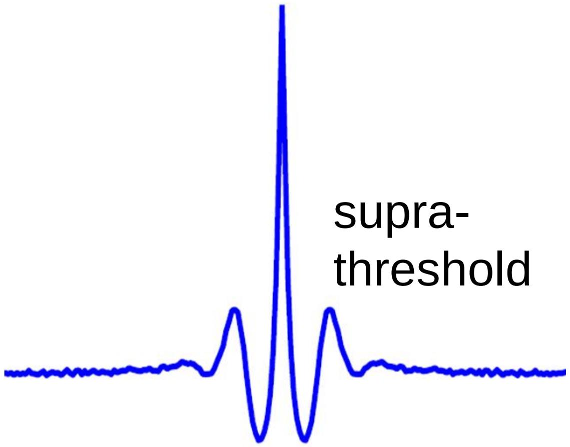
-A **single peak** in both sub- and supra-threshold regimes

-**Width** of the **peak** is approx. τ_s

Large fraction of common noise

$$\frac{\sigma_c^{\,2}}{\sigma^{\,2}} \approx 1$$





-**Damped oscillatory profile** in both regimes

-**Width** is not simply related to τ_s

Outline

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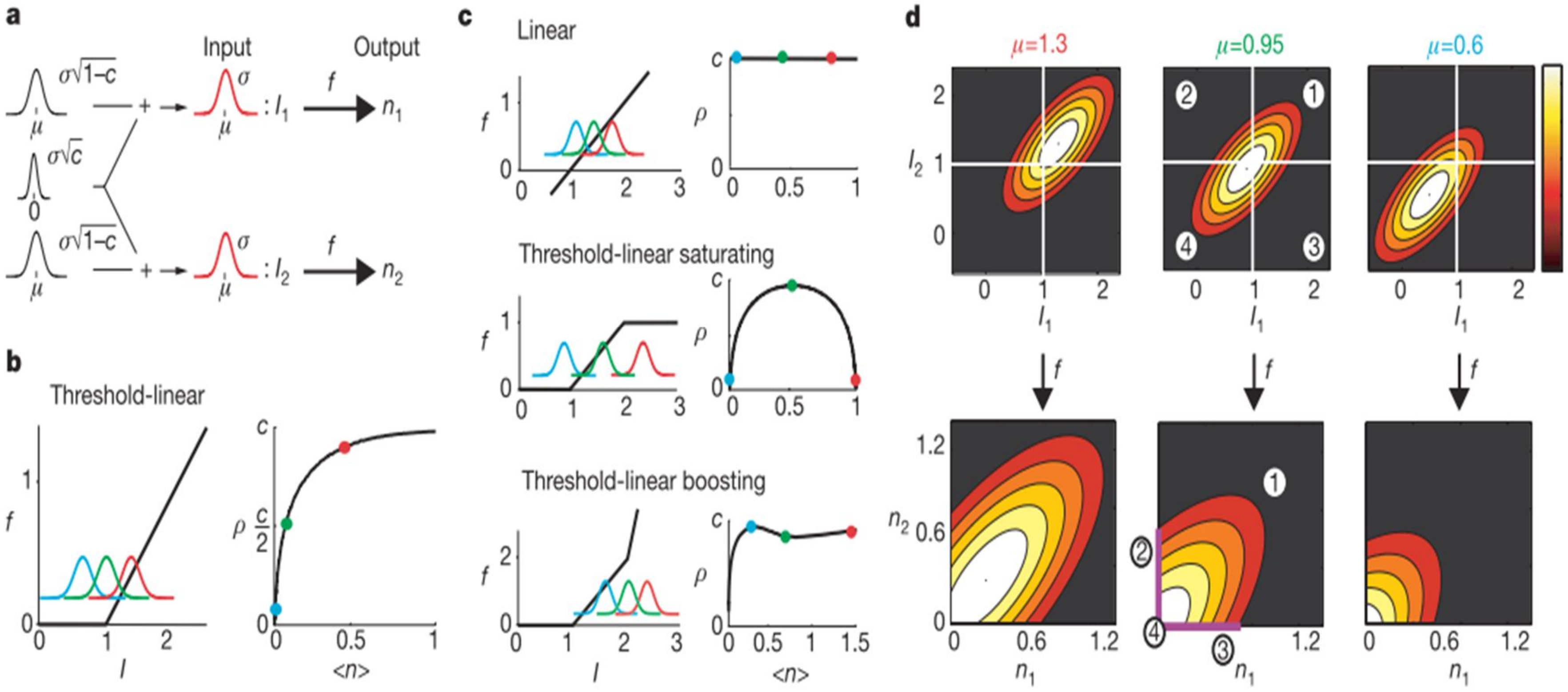
2. Output correlation is lower than input correlation in spiking neurons (Moreno-Bote and Parga, *Phys. Review Letters*, 2006)
3. Firing rate and correlation coefficients are not independent (de la Rocha et al, *Nature*, 2007)

- Open questions

Correlations increase with firing rate



Output correlation increases with output firing rate

Outline

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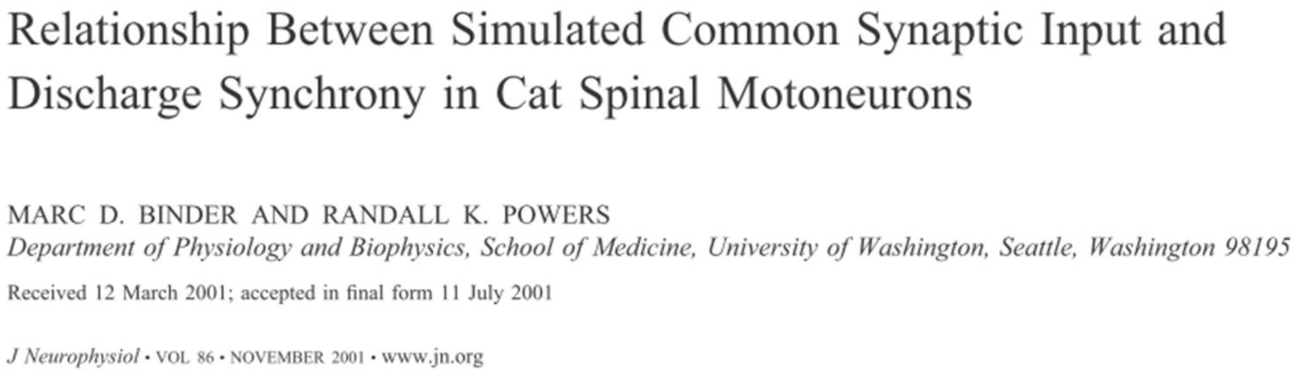
- Open questions



Relationship Between Simulated Common Synaptic Input and Discharge Synchrony in Cat Spinal Motoneurons

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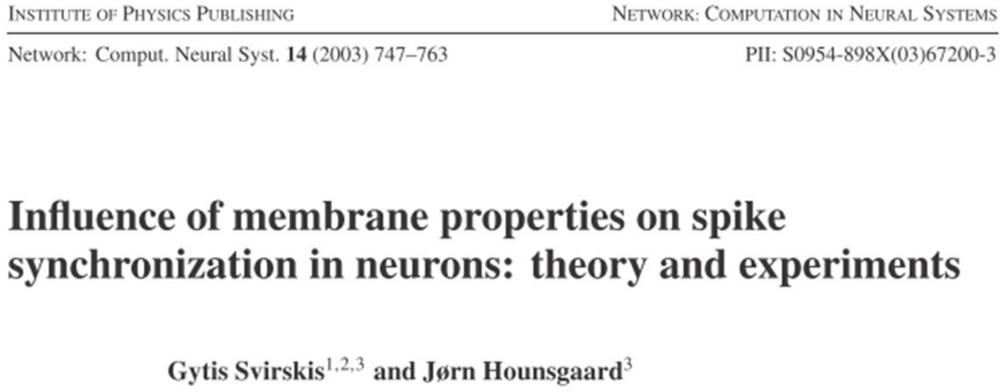
J Neurophysiol • VOL 86 • NOVEMBER 2001 • www.jn.org



INSTITUTE OF PHYSICS PUBLISHING — NETWORK: COMPUTATION IN NEURAL SYSTEMS
Network: Comput. Neural Syst. **14** (2003) 747–763 — PII: S0954-898X(03)67200-3

Influence of membrane properties on spike synchronization in neurons: theory and experiments

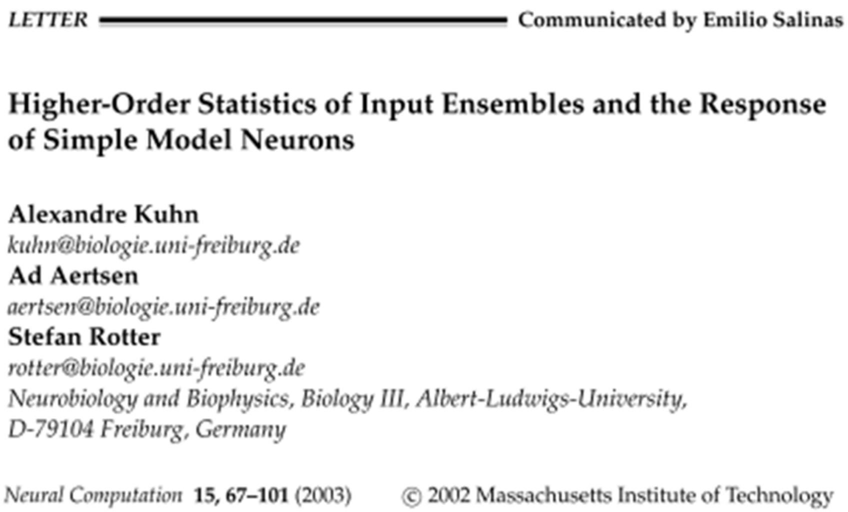
Gytis Svirskis[1,2,3] and Jørn Hounsgaard[3]

3646 • The Journal of Neuroscience, April 5, 2006 • 26(14):3646–3655

Behavioral/Systems/Cognitive

Correlation-Induced Synchronization of Oscillations in Olfactory Bulb Neurons

Roberto F. Galán,[1,3]* Nicolas Fourcaud-Trocmé,[2,3]* G. Bard Ermentrout,[2,3] and Nathaniel N. Urban[1,3]
[1]Department of Biological Sciences, Carnegie Mellon University, Pittsburgh, Pennsylvania 15213, [2]Department of Mathematics, University of Pittsburgh, Pittsburgh, Pennsylvania 15260, and [3]Center for the Neural Basis of Cognition, Pittsburgh, Pennsylvania 15213



LETTER **Communicated by Emilio Salinas**

Higher-Order Statistics of Input Ensembles and the Response of Simple Model Neurons

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Neural Computation **15, 67–101** (2003) © 2002 Massachusetts Institute of Technology

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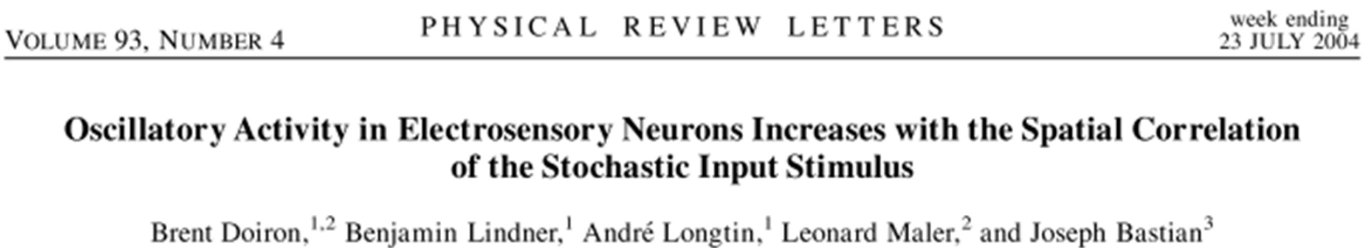
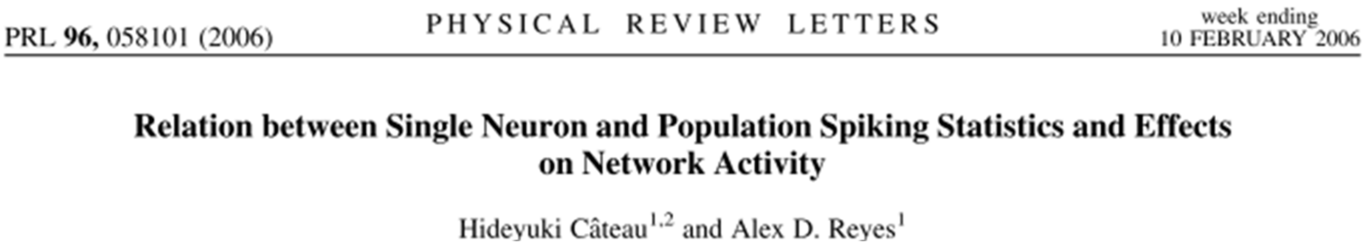


VOLUME 93, NUMBER 4 PHYSICAL REVIEW LETTERS week ending 23 JULY 2004

Oscillatory Activity in Electrosensory Neurons Increases with the Spatial Correlation of the Stochastic Input Stimulus

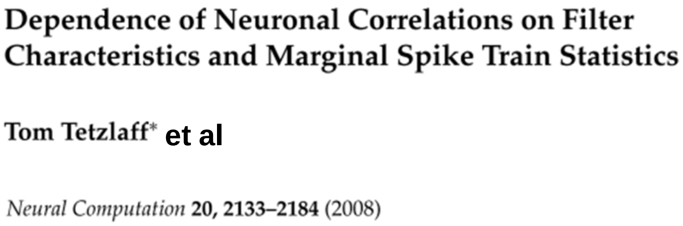
Brent Doiron,[1,2] Benjamin Lindner,[1] André Longtin,[1] Leonard Maler,[2] and Joseph Bastian[3]



PRL **96,** 058101 (2006) PHYSICAL REVIEW LETTERS week ending 10 FEBRUARY 2006

Relation between Single Neuron and Population Spiking Statistics and Effects on Network Activity

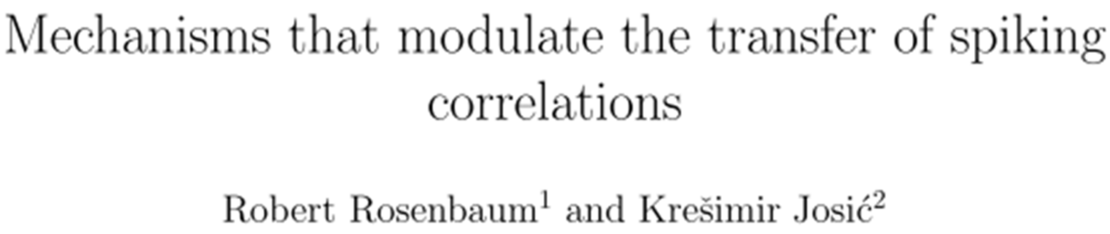
Hideyuki Câteau[1,2] and Alex D. Reyes[1]



Dependence of Neuronal Correlations on Filter Characteristics and Marginal Spike Train Statistics

Tom Tetzlaff* **et al**

Neural Computation **20, 2133–2184** (2008)



Mechanisms that modulate the transfer of spiking correlations

Robert Rosenbaum[1] and Krešimir Josić[2]

NEURAL COMPUTATION

May 2011, Vol. 23, N. 5, Pages 1261-1305

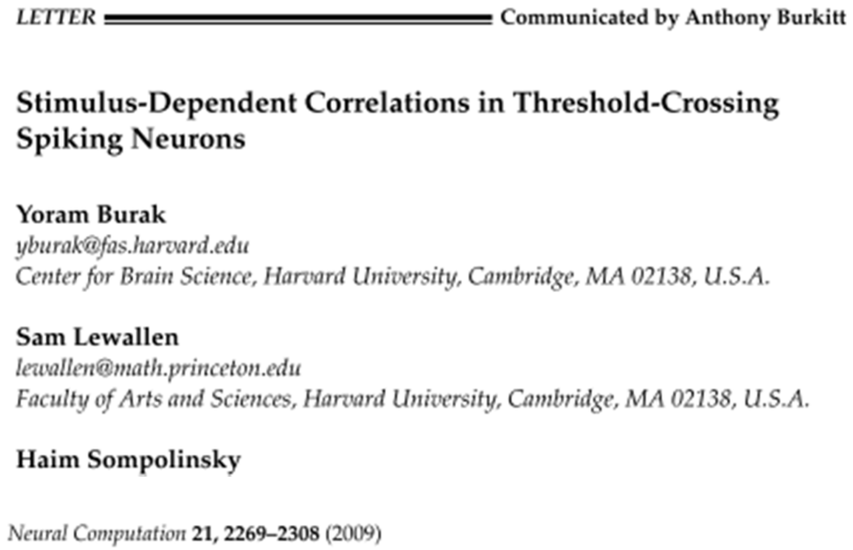
OPEN ACCESS Freely available online

April 2013 | Volume 9 | Issue 4 | e1002904

PLOS | COMPUTATIONAL BIOLOGY

Noise Suppression and Surplus Synchrony by Coincidence Detection

Matthias Schultze-Kraft[1,2,3*], Markus Diesmann[4,5,6], Sonja Grün[4,6,7], Moritz Helias[4]



LETTER **Communicated by Anthony Burkitt**

Stimulus-Dependent Correlations in Threshold-Crossing Spiking Neurons

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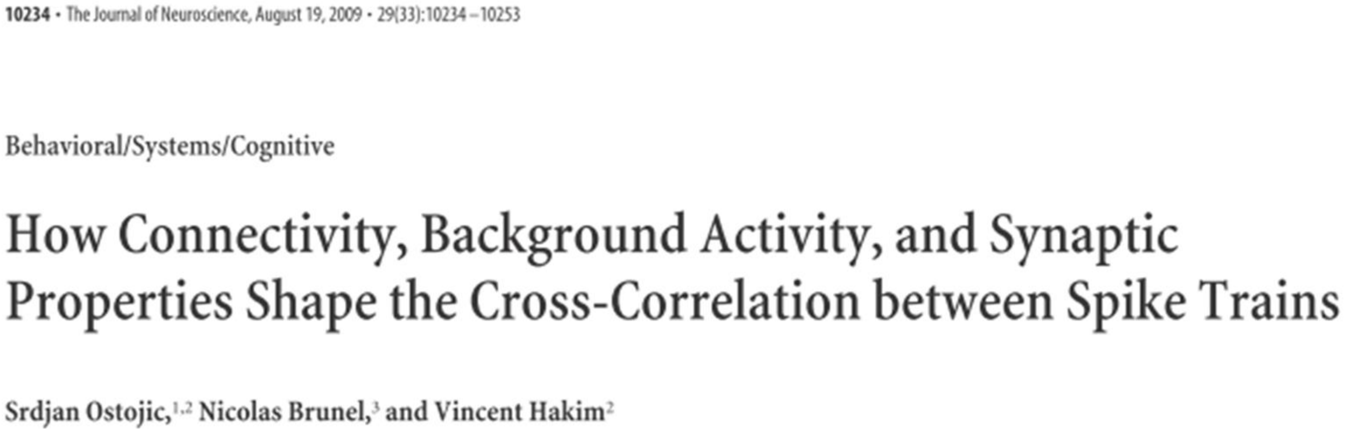
Haim Sompolinsky

Neural Computation **21, 2269–2308** (2009)

PRL **104,** 058102 (2010) PHYSICAL REVIEW LETTERS week ending 5 FEBRUARY 2010

Correlations and Synchrony in Threshold Neuron Models

Tatjana Tchumatchenko,[1,2] Aleksey Malyshev,[3,4] Theo Geisel,[1] Maxim Volgushev,[3,4,5] and Fred Wolf[1]

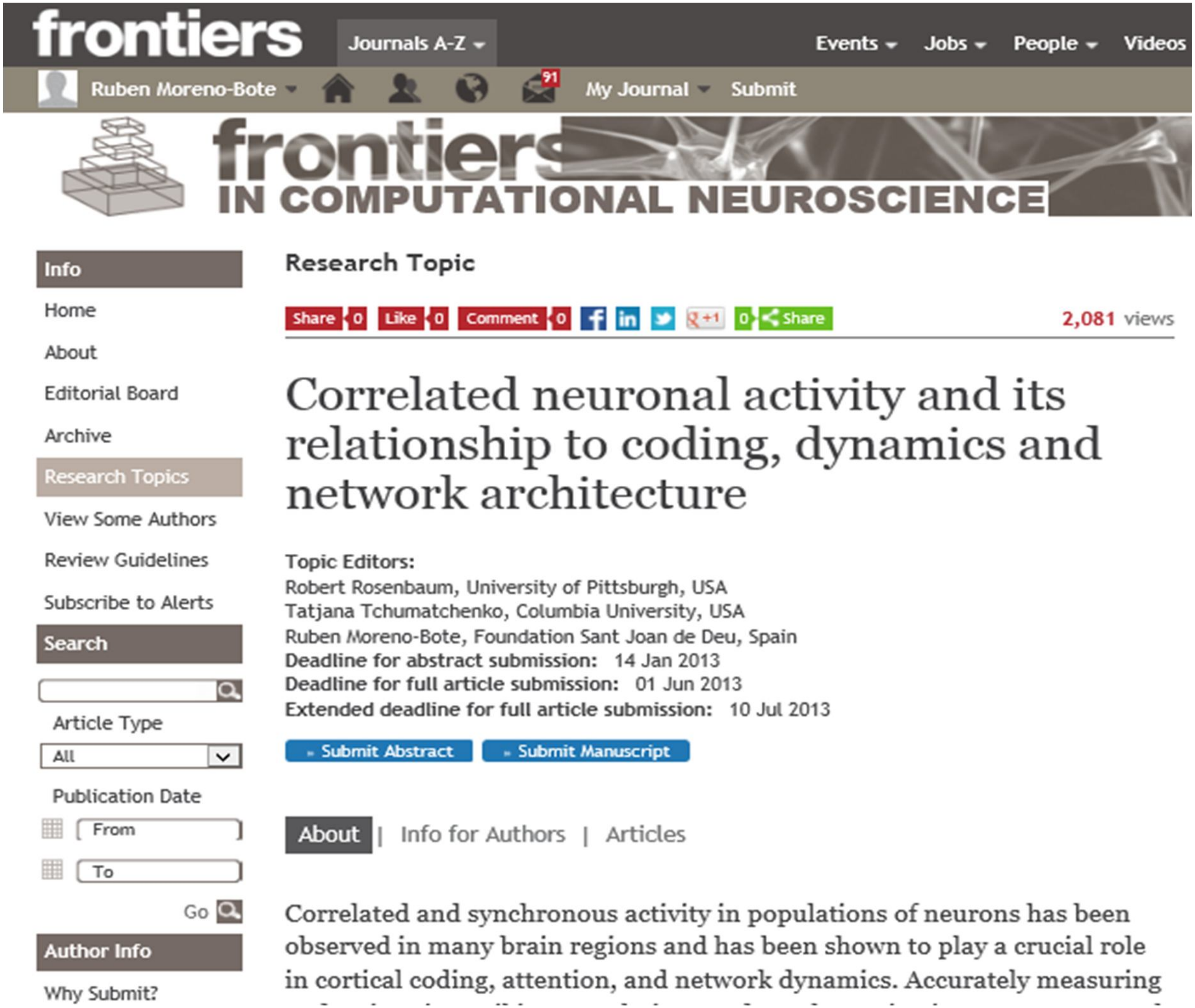


10234 • The Journal of Neuroscience, August 19, 2009 • 29(33):10234–10253

Behavioral/Systems/Cognitive

How Connectivity, Background Activity, and Synaptic Properties Shape the Cross-Correlation between Spike Trains

Srdjan Ostojic,[1,2] Nicolas Brunel,[3] and Vincent Hakim[2]



Research Topic

Correlated neuronal activity and its relationship to coding, dynamics and network architecture

Topic Editors:
Robert Rosenbaum, University of Pittsburgh, USA
Tatjana Tchumatchenko, Columbia University, USA
Ruben Moreno-Bote, Foundation Sant Joan de Deu, Spain
Deadline for abstract submission: 14 Jan 2013
Deadline for full article submission: 01 Jun 2013
Extended deadline for full article submission: 10 Jul 2013

Correlated and synchronous activity in populations of neurons has been observed in many brain regions and has been shown to play a crucial role in cortical coding, attention, and network dynamics. Accurately measuring

frontiers in
COMPUTATIONAL NEUROSCIENCE

ORIGINAL RESEARCH ARTICLE
published: 14 August 2013
doi: 10.3389/fncom.2013.00108

Direct connections assist neurons to detect correlation in small amplitude noises

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We address a question on the effect of common stochastic inputs on the correlation of the spike trains of two neurons when they are coupled through direct connections. We show that the change in the correlation of small amplitude stochastic inputs can be better detected when the neurons are connected by direct excitatory couplings. Depending on whether intrinsic firing rate of the neurons is identical or slightly different, symmetric or asymmetric connections can increase the sensitivity of the system to the input correlation by changing the mean slope of the correlation transfer function over a given range of input correlation. In either case, there is also an optimum value for synaptic strength which maximizes the sensitivity of the system to the changes in input correlation.

Keywords: correlation, correlation transfer, coupling, inhomogeneity, synchrony

Outline

- Information limits set by neuronal correlations (an example)
- Firing rate and variability in LIF neurons with fast and slow synapses (FPE formalism and solutions)
- Correlation transfer in LIF neurons with fast and slow synapses (FPE and approximate solutions)
- Review of literature & main results about correlation transfer:
  1. Neurons are sensitive to input correlations (strength and correlation time; Salinas and Sejnowski, *J. of Neurosci.*, 2000; Moreno-Bote et al, *Phys. Review Letters*, 2002)
  2. Output correlation is lower than input correlation in spiking neurons (Moreno-Bote and Parga, *Phys. Review Letters*, 2006)
  3. Firing rate and correlation coefficients are not independent (de la Rocha et al, *Nature*, 2007)
- Open questions

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- Information limits set by neuronal correlations (an example)

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- Open questions

Open questions

- The Fokker-Planck equation (FPE) for a pair of correlated neurons remains unsolved exactly for any limit
  (however, very good approximations are available in some limits, as described in this tutorial)

- How correlation transfer operates in more complex neuronal models (e.g., Hodgkin & Huxley) is not known

- How correlation transfer depends on reciprocal connections deserves further research (but await to the 2nd part of the tutorial)

- The role of (active) dendrites in synchronization is largely unknown

- The relationship between correlations and information in neuronal networks remains unexplored

Theory of correlation transfer and correlation structure in recurrent networks

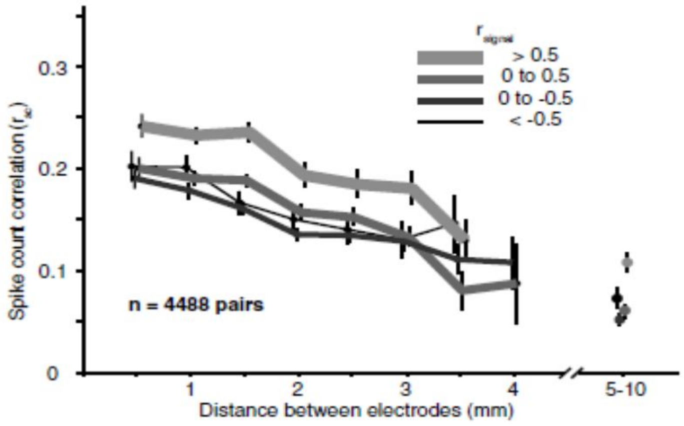
Part II: Networks

Rubén Moreno-Bote

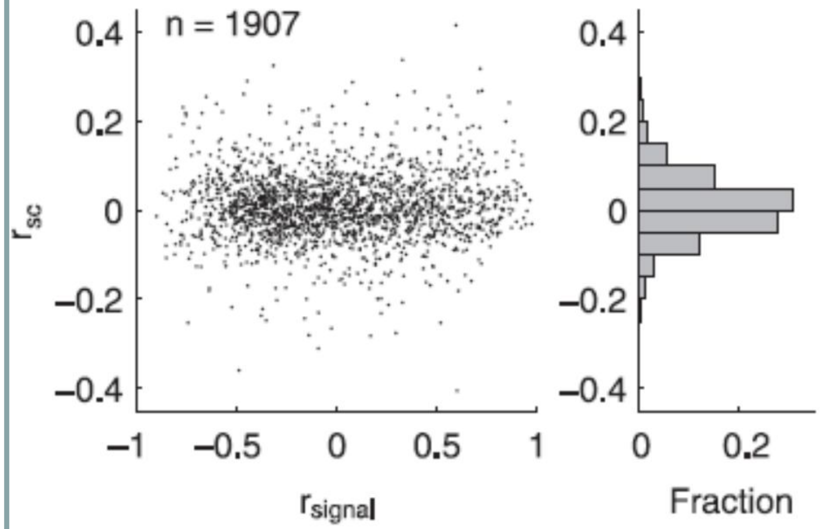
Foundation Sant Joan de Déu, Barcelona

Ramón y Cajal Researcher

How strong are correlations in cortex?



Smith and Kohn, 2008

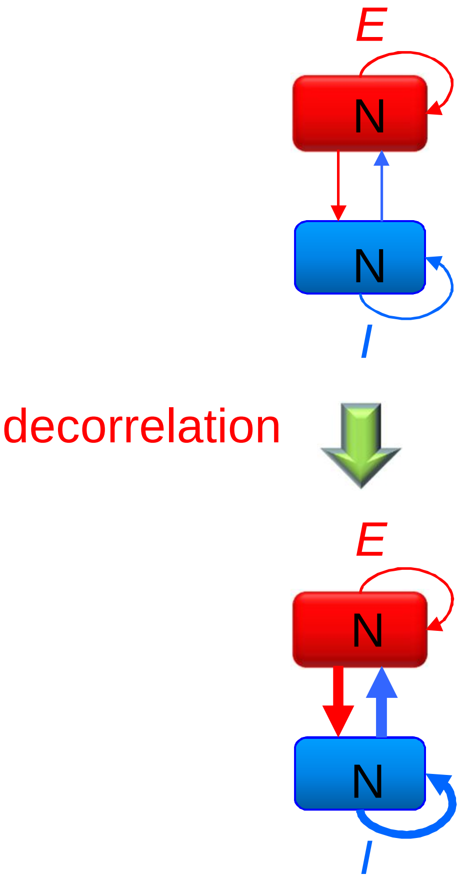


Ecker et al, 2010

$r_{sc} \sim 0.1$

$r_{sc} \sim 0.01$

Signal/Noise limits induced by correlations

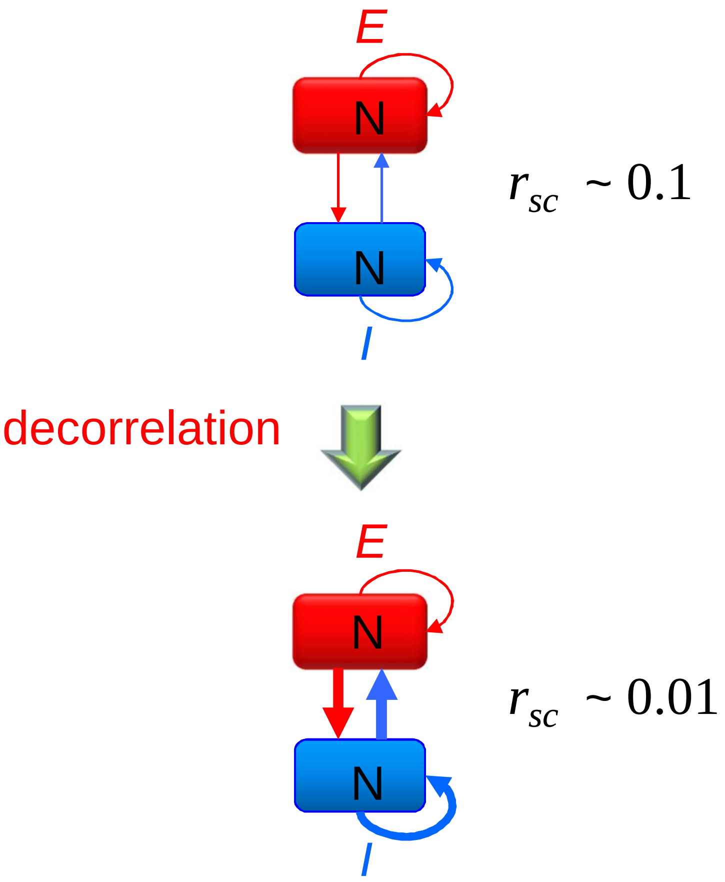


$r_{sc} \sim 0.1$

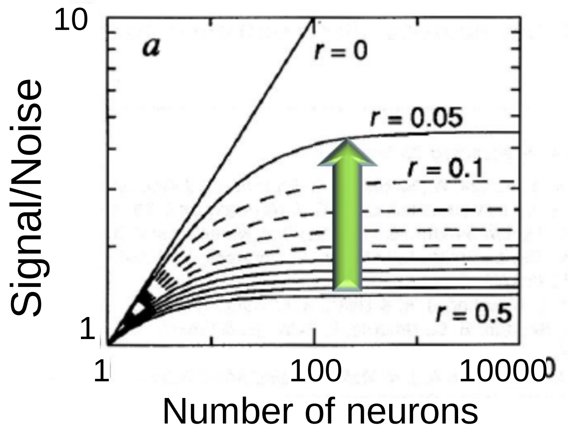
$r_{sc} \sim 0.01$

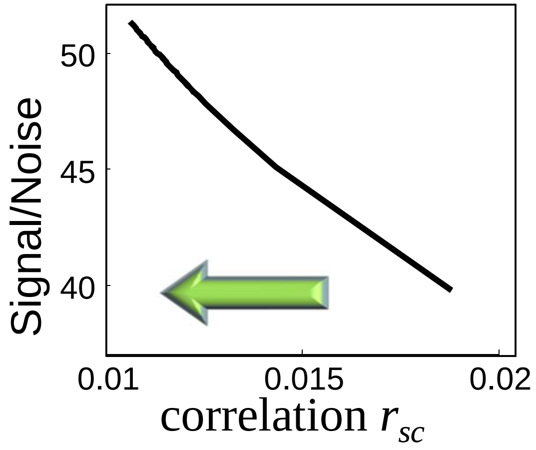
Does this improve information?

Signal/Noise limits induced by correlations



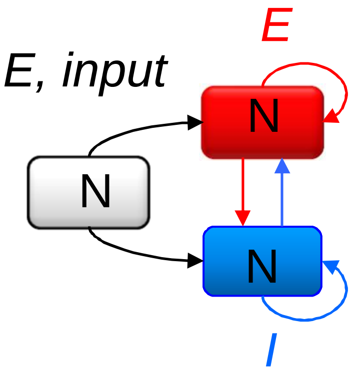
Zohary et al, 1994





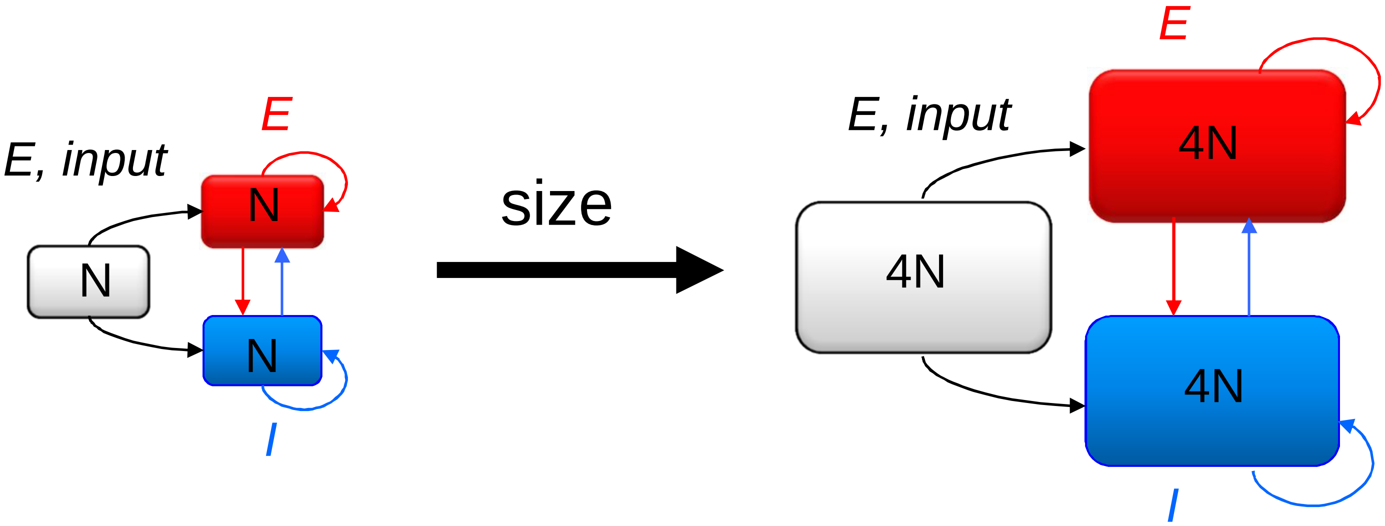
- Decorrelation appears to be an universal recipe for increasing information
- But is it really so?

Correlations in neuronal networks



Ginzburg and Sompolinsky, 1994
Kriener et al, 2008
Kumar et al, 2008
Renart et al, 2010
Hertz, 2010
Helias et al, 2014

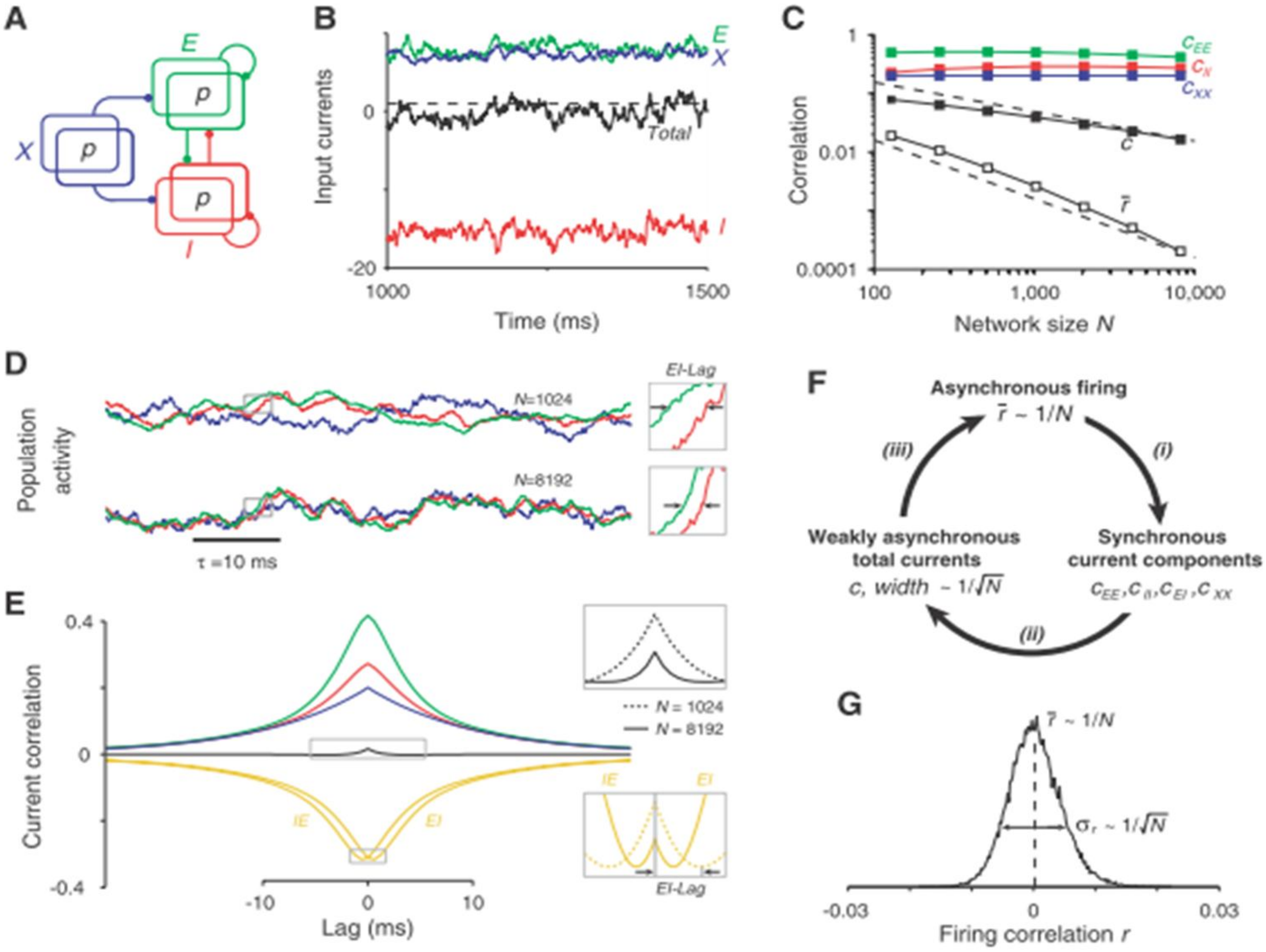
Correlations in neuronal networks



$$\text{Correlation} = r_{sc} \sim \frac{1}{N}$$

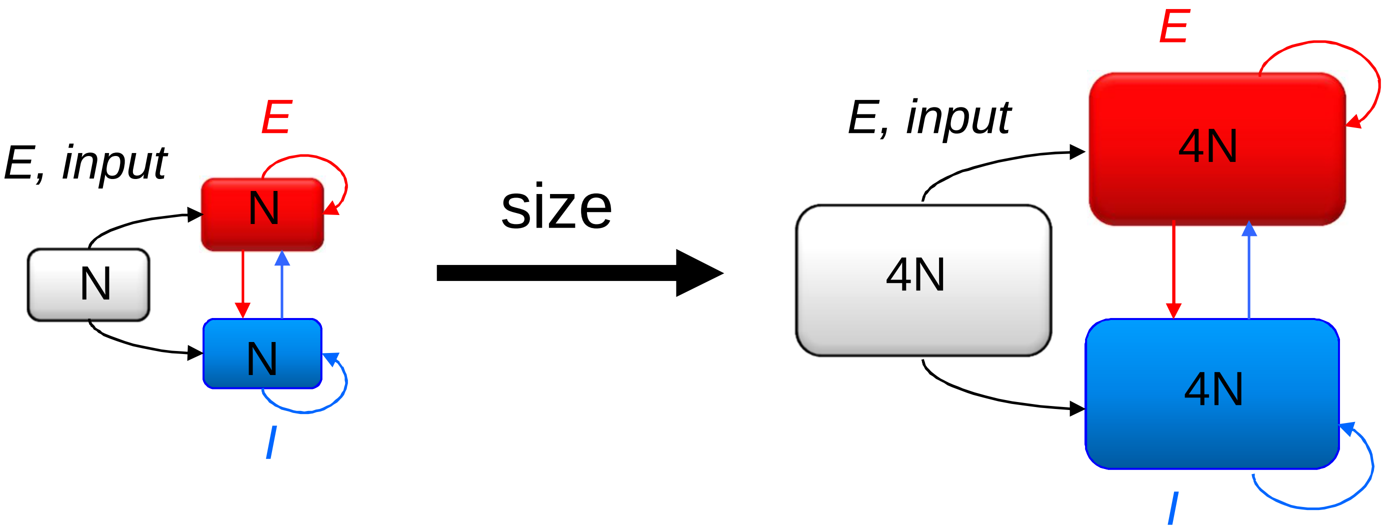
asynchronous regime

Correlations in binary networks in the thermodynamic limit



Renart et al, 2010 (see also Hertz 2010 and Helias et al, 2014)

Correlations in neuronal networks

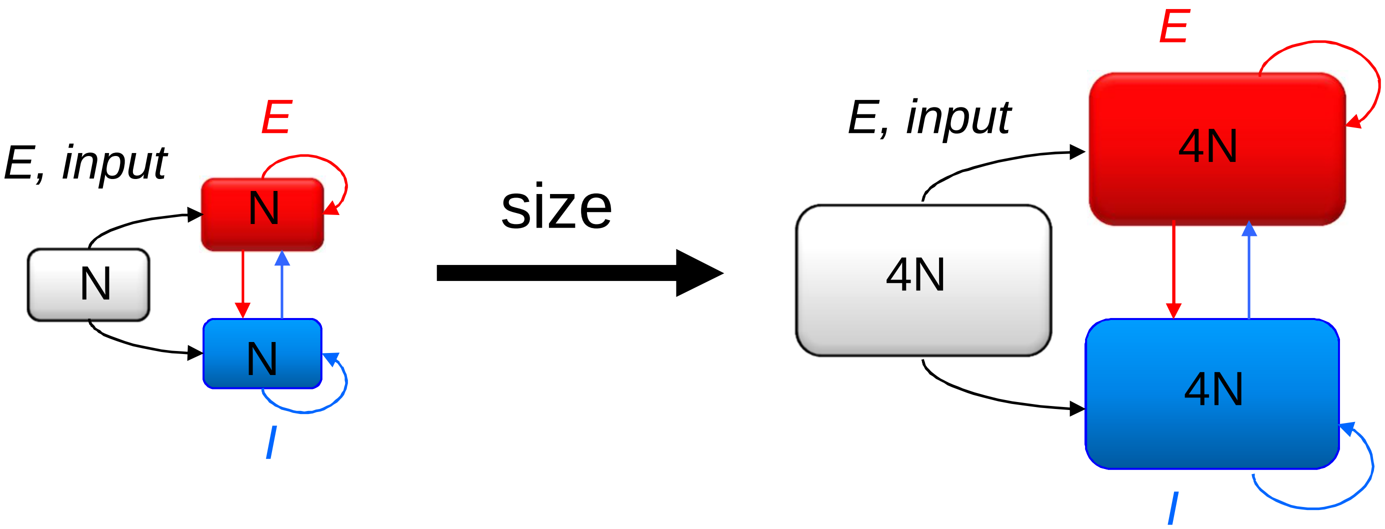


$$\boxed{\text{Correlation} = r_{sc} \sim \frac{1}{N}}$$

asynchronous regime

However…

Correlations in neuronal networks



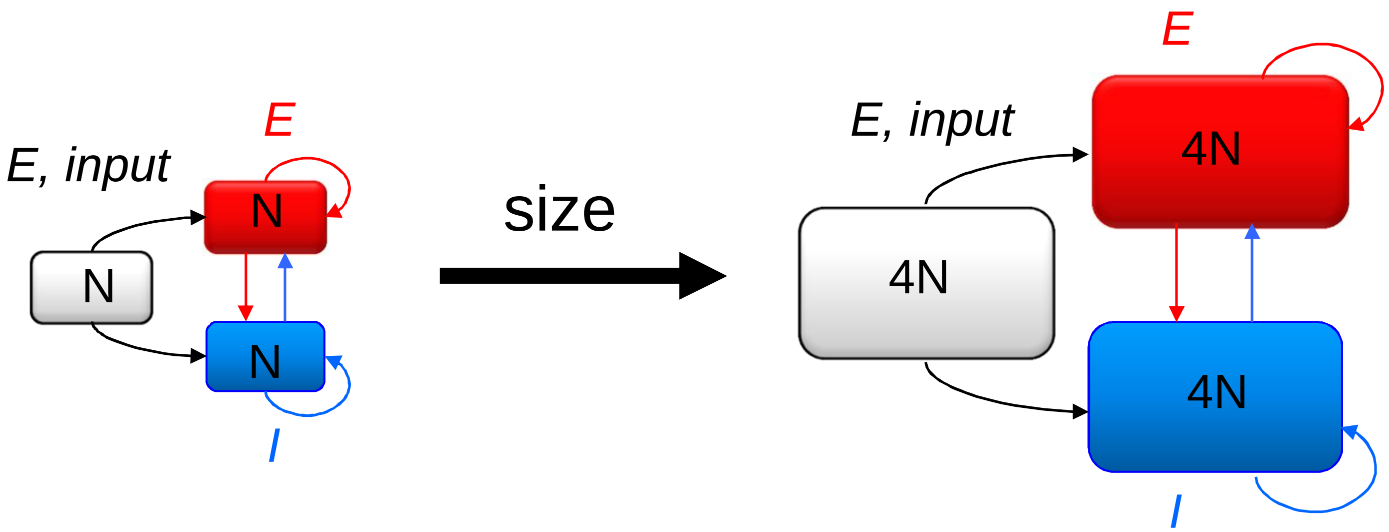
$$\text{Correlation} = r_{sc} \sim \frac{1}{N}$$

asynchronous regime

However…

this decorrelation mechanism has been shown to work only when input information increases without bound as the size *N* increases.

Correlations in neuronal networks

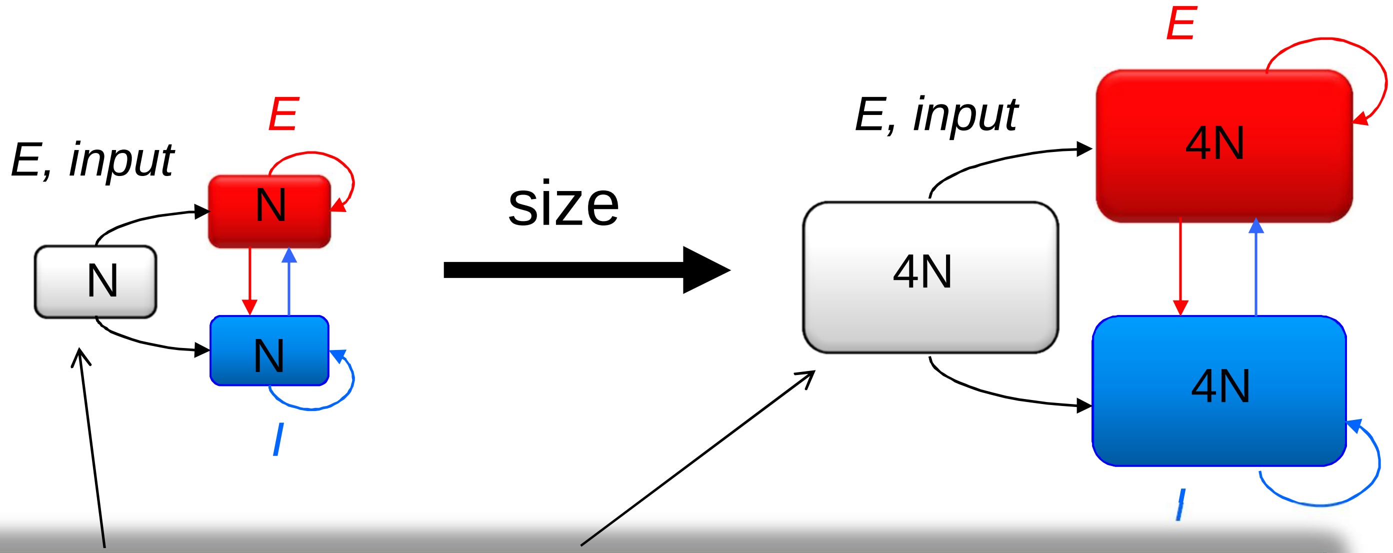


$$\left\langle \sum n_{i,input} \right\rangle = N \left\langle n_{input} \right\rangle$$

$$Var\left(\sum n_{i,input}\right) = N Var\left(n_{input}\right)$$

$$SNR_{input} \propto \frac{N}{\sqrt{N}} = \sqrt{N}$$

Correlations in neuronal networks

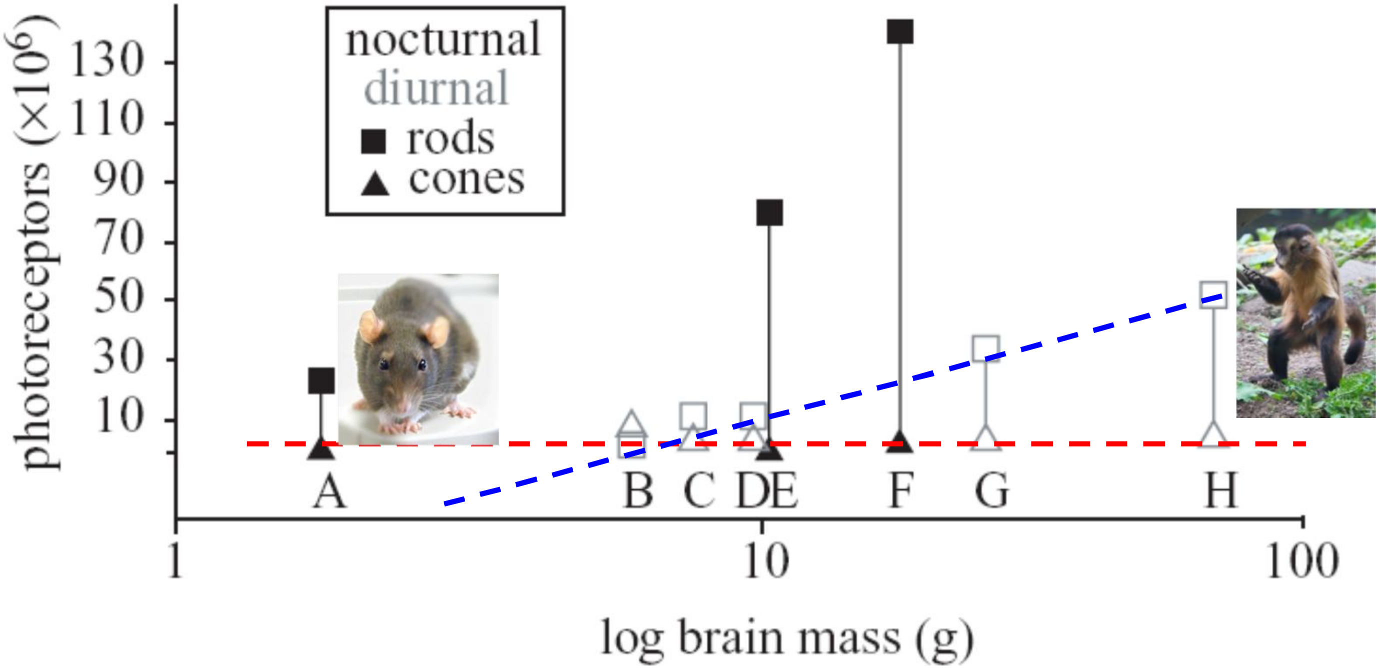


input information increases without bound

Networks with finite input information

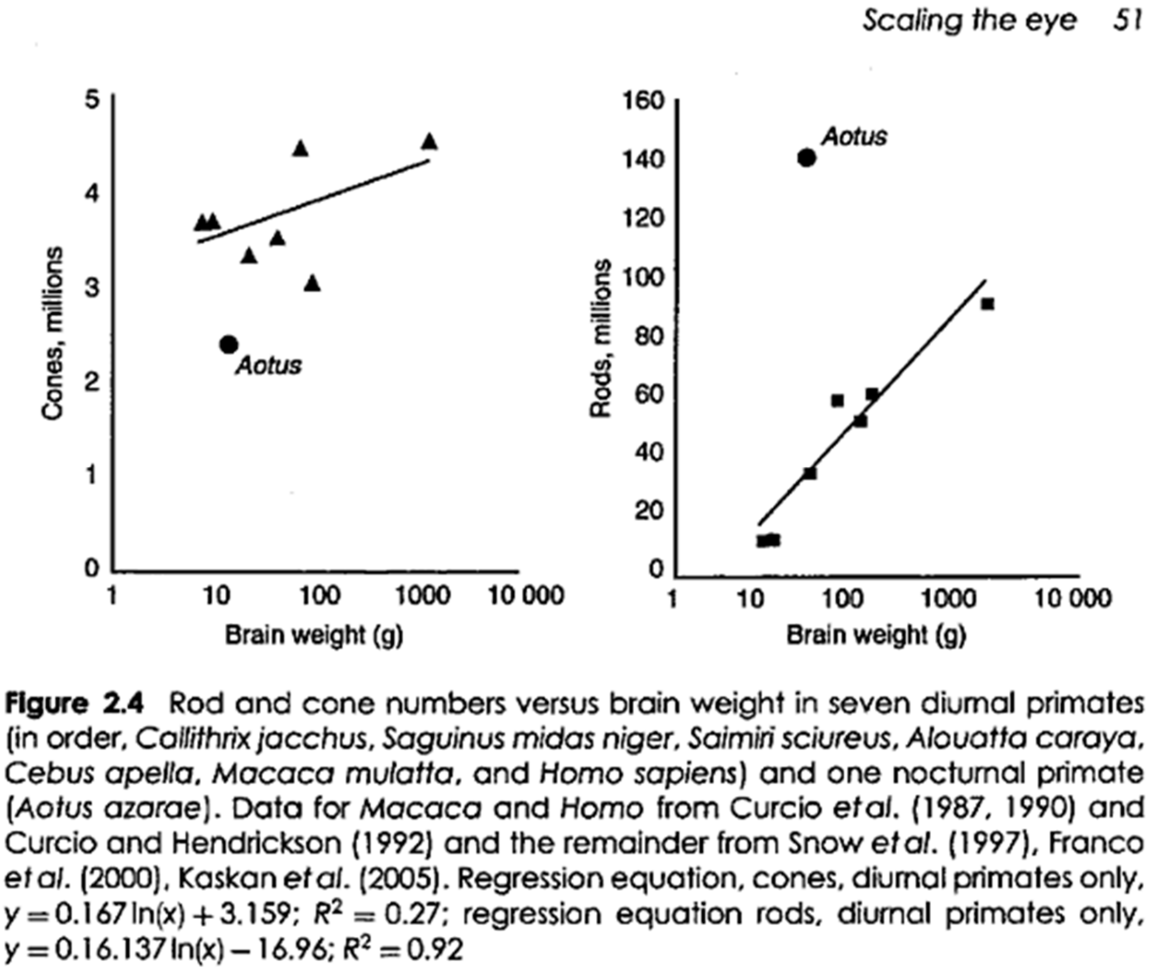
In real world situations, input information is fixed

Retina vs. brain evolution across mammals



Kaskan et al, 2005

Retina and brain evolution in primates

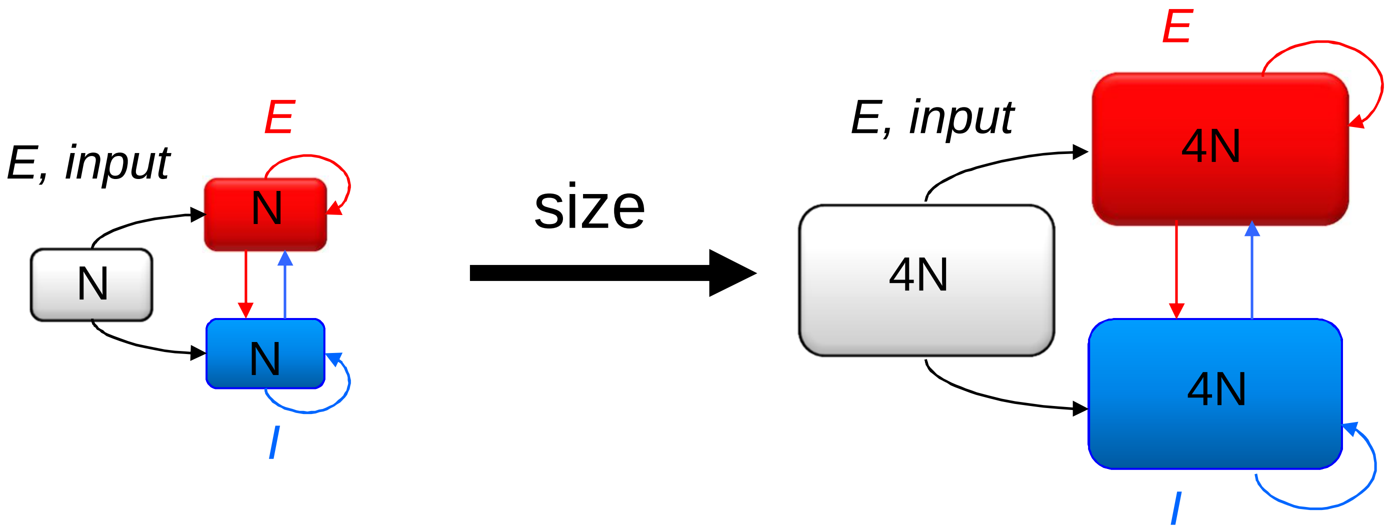


Scaling the eye 51

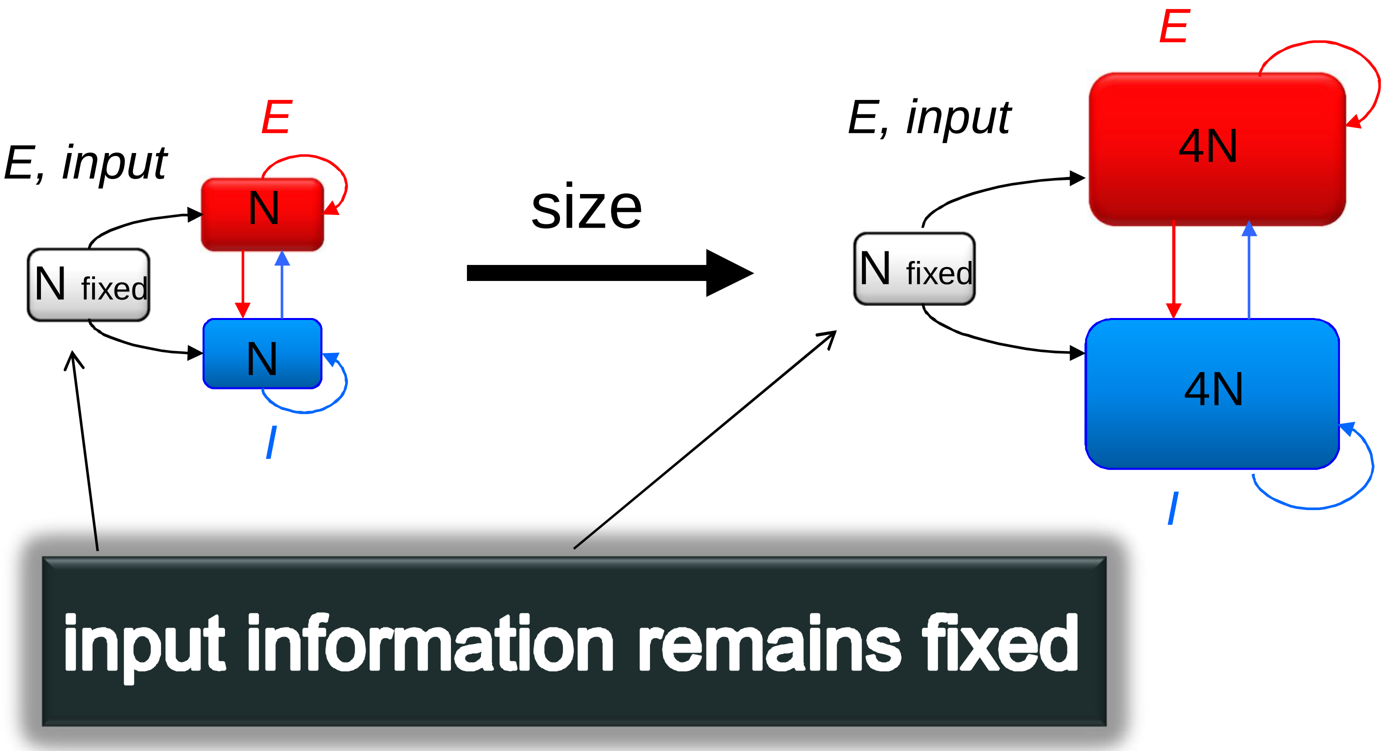
Figure 2.4 Rod and cone numbers versus brain weight in seven diurnal primates (in order, *Callithrix jacchus*, *Saguinus midas niger*, *Saimiri sciureus*, *Alouatta caraya*, *Cebus apella*, *Macaca mulatta*, and *Homo sapiens*) and one nocturnal primate (*Aotus azarae*). Data for *Macaca* and *Homo* from Curcio *et al.* (1987, 1990) and Curcio and Hendrickson (1992) and the remainder from Snow *et al.* (1997), Franco *et al.* (2000), Kaskan *et al.* (2005). Regression equation, cones, diurnal primates only, $y = 0.167\ln(x) + 3.159$; $R^2 = 0.27$; regression equation rods, diurnal primates only, $y = 0.16.137\ln(x) - 16.96$; $R^2 = 0.92$

Kremers, *The primate visual system: a comparative approach*

Networks with finite input information



Networks with finite input information



input information remains fixed

Questions:

- does decorrelation improve information?
- what type of correlations limit information?

Outline

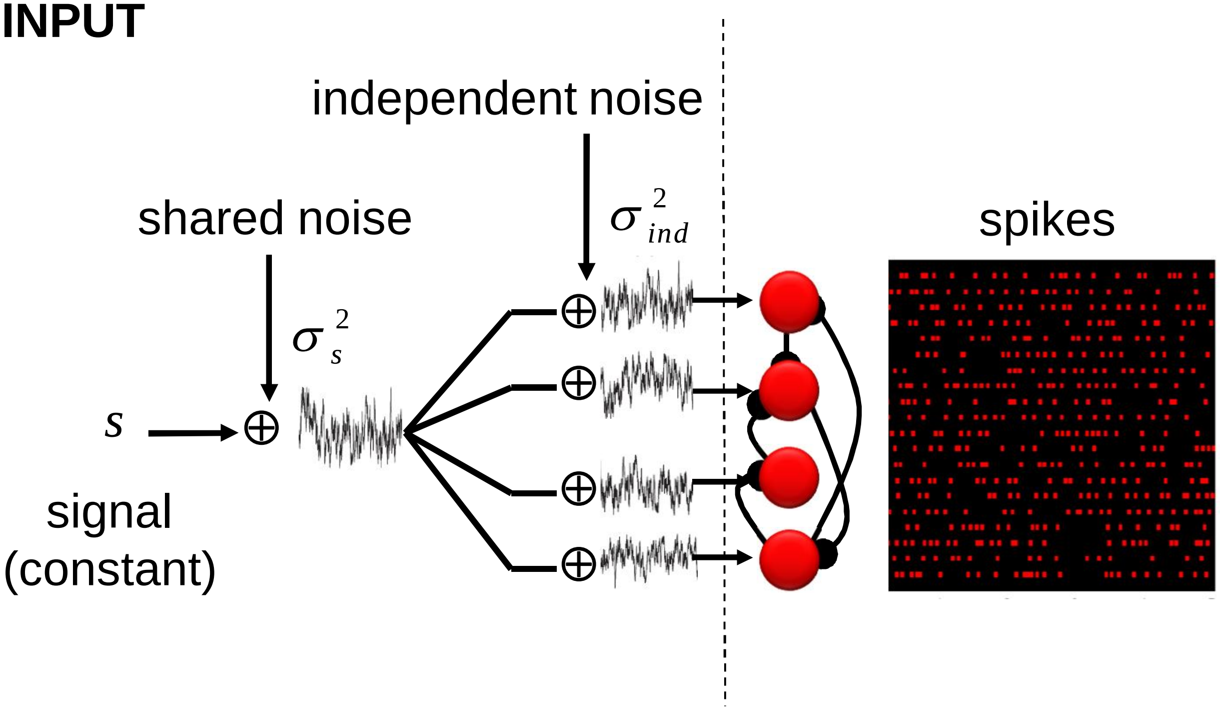
- Spiking neuronal networks transmit virtually all input information
- Noise decorrelation does not imply information improvement
- Shared connectivity does not limit information
- The only information-limiting correlations are differential correlations, proportional to the product of the derivatives of the tuning curves: $\mathbf{f}'\mathbf{f}'^{\mathrm{T}}$
- Correlations in any other direction does not affect information for large neuronal populations

Moreno-Bote et al, *Nature Neuroscience*, In Press, 2014

Coding and decoding in a spiking network

INPUT

OUTPUT



independent noise

σ_{ind}^2

shared noise

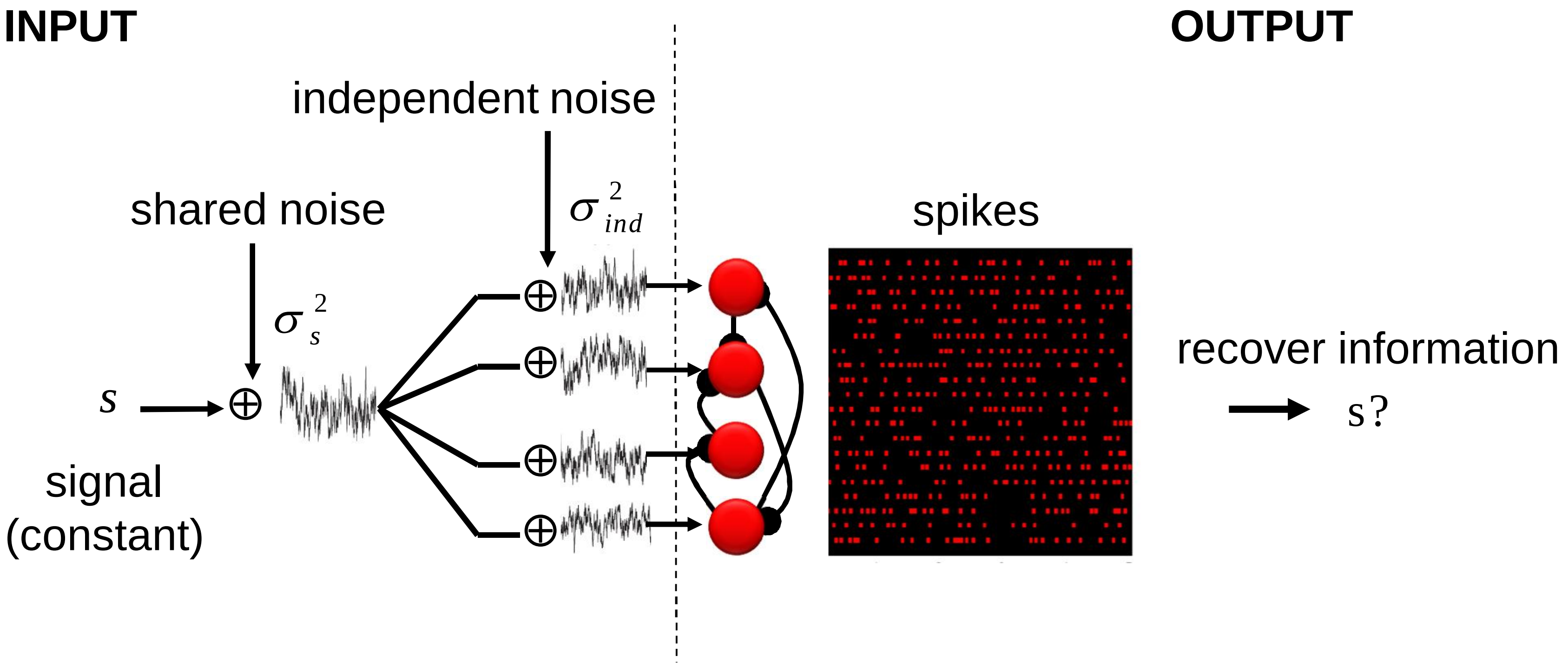
σ_s^2

s

signal
(constant)

spikes

Coding and decoding in a spiking network



INPUT

OUTPUT

independent noise

σ_{ind}^2

shared noise

σ_s^2

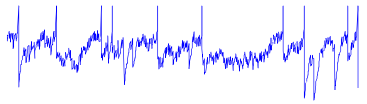
s

signal
(constant)

spikes

recover information

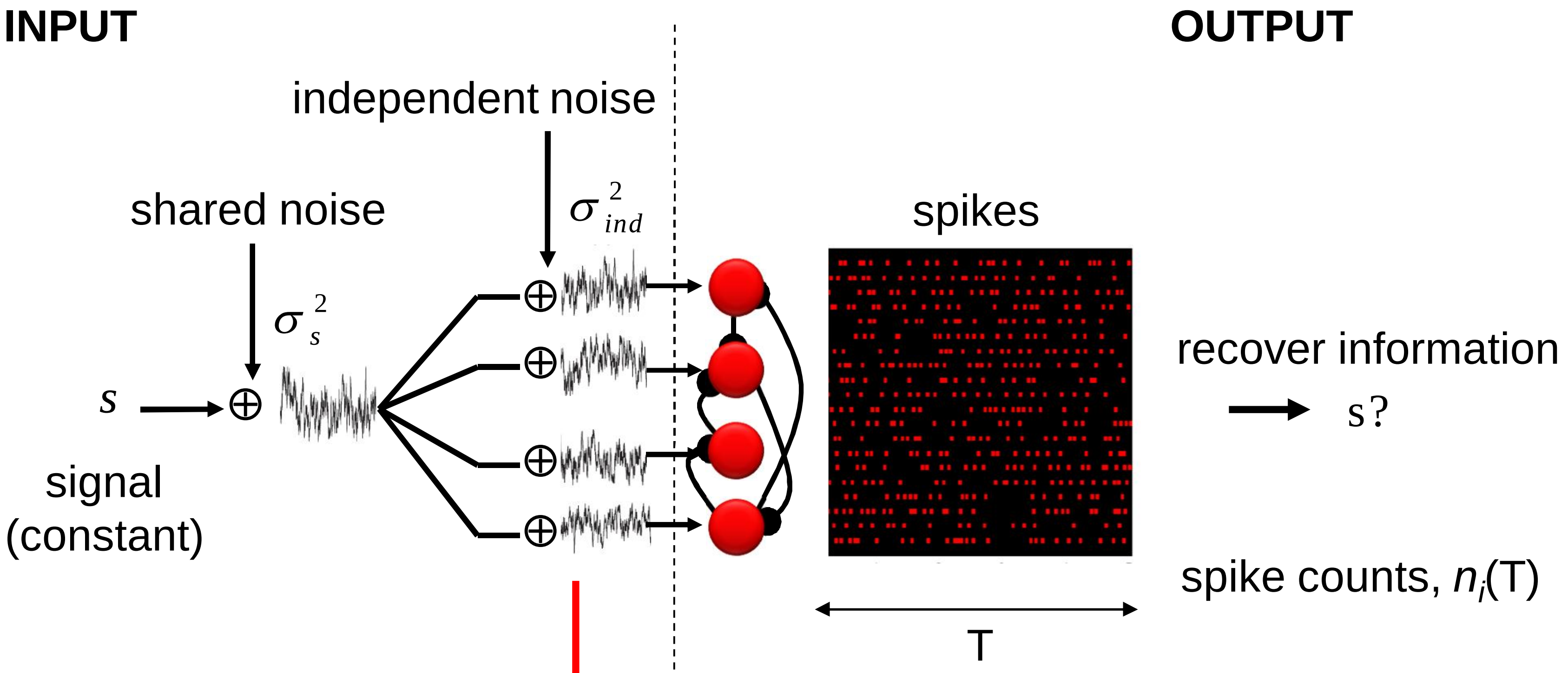
→ s?



$$\dot{V}_i = I_i(t)$$

$$I_i(t) = \underbrace{\sum_{j,k} J_{ij}\delta(t-t_j^k)}_{\text{recurrent inputs}} + \overbrace{\mu}^{\text{signal}} + \underbrace{\sigma_c\eta_c(t) + \sigma_{ind}\eta_i(t)}_{\text{external noise}}$$

Coding and decoding in a spiking network



INPUT

OUTPUT

independent noise

σ^2_{ind}

shared noise

σ^2_s

s

signal (constant)

spikes

recover information

→ s?

spike counts, n_i(T)

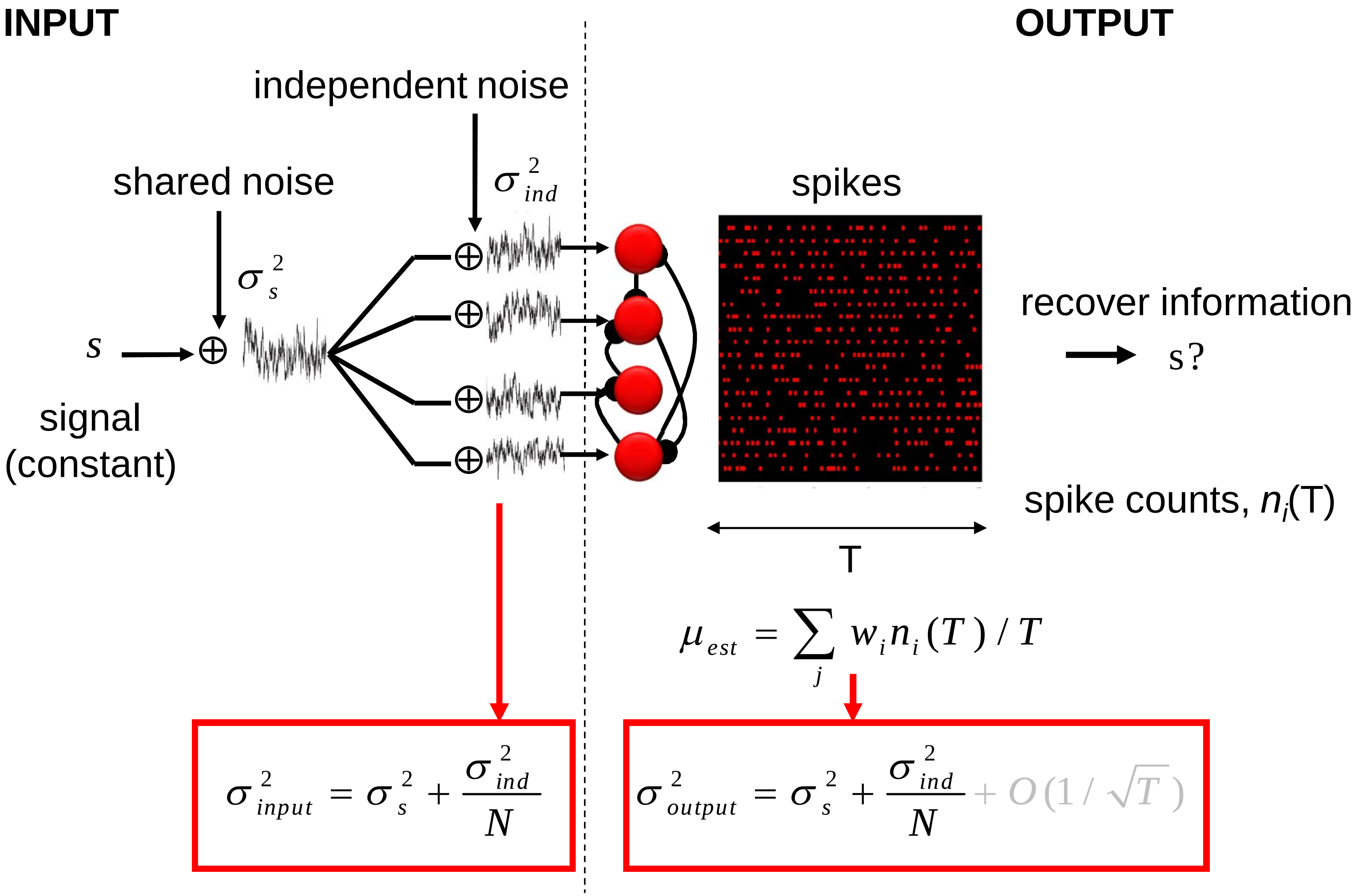
T

$$\mu_{est} = \sum_j w_i n_i(T)/T$$

$$\sigma^2_{input} = \sigma^2_s + \frac{\sigma^2_{ind}}{N}$$

$$\sigma^2_{output} = ?$$

Coding and decoding in a spiking network



INPUT

OUTPUT

independent noise

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signal (constant)

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recover information

→ s?

spike counts, n_i(T)

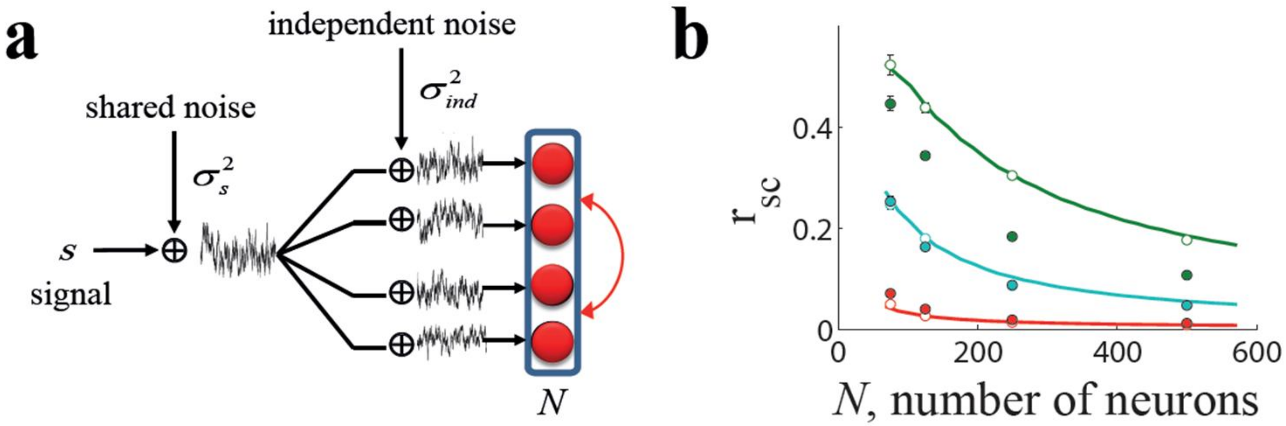
T

$$\mu_{est} = \sum_j w_i n_i(T)/T$$

$$\sigma^2_{input} = \sigma^2_s + \frac{\sigma^2_{ind}}{N}$$

$$\sigma^2_{output} = \sigma^2_s + \frac{\sigma^2_{ind}}{N} + O(1/\sqrt{T})$$

The size of correlations does not matter



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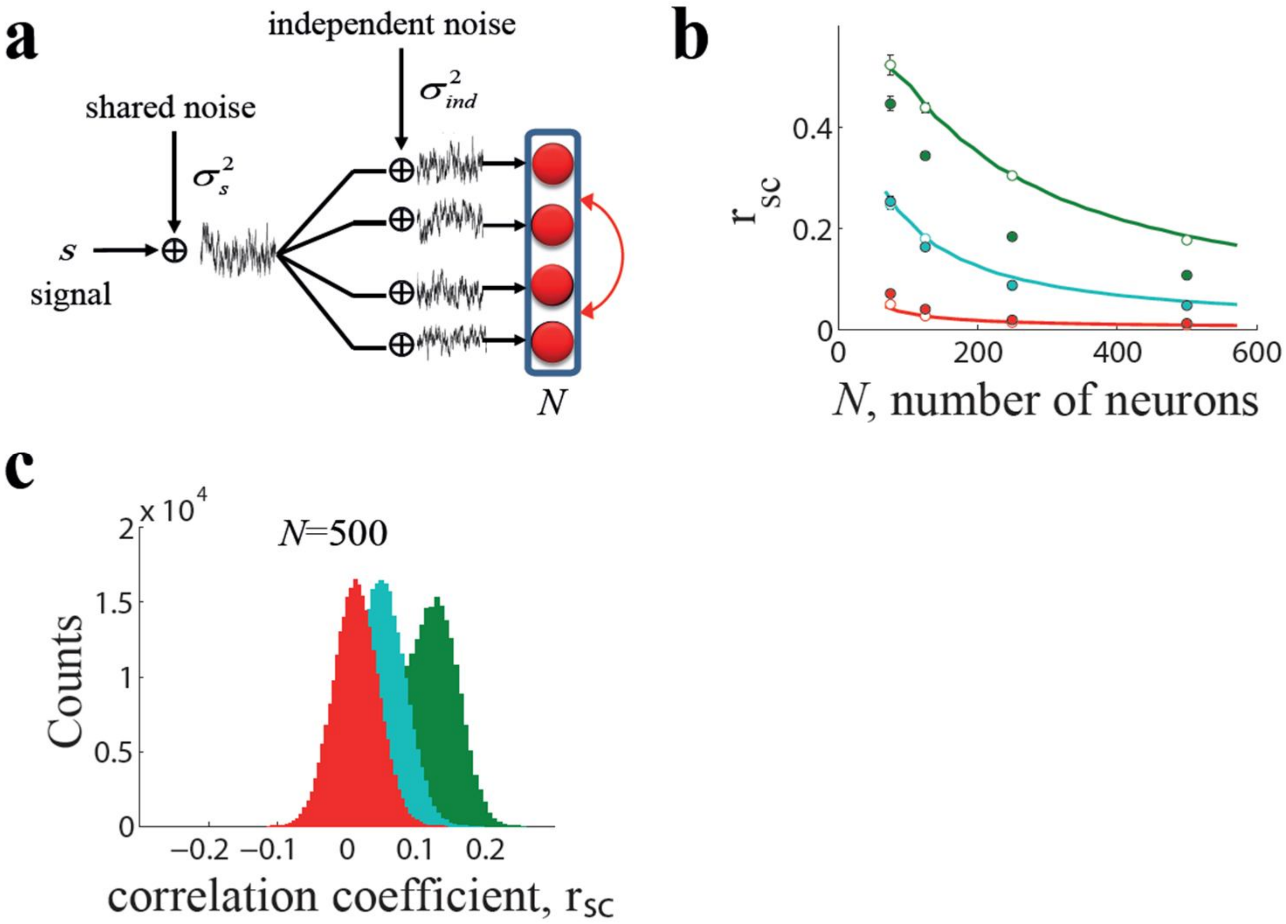

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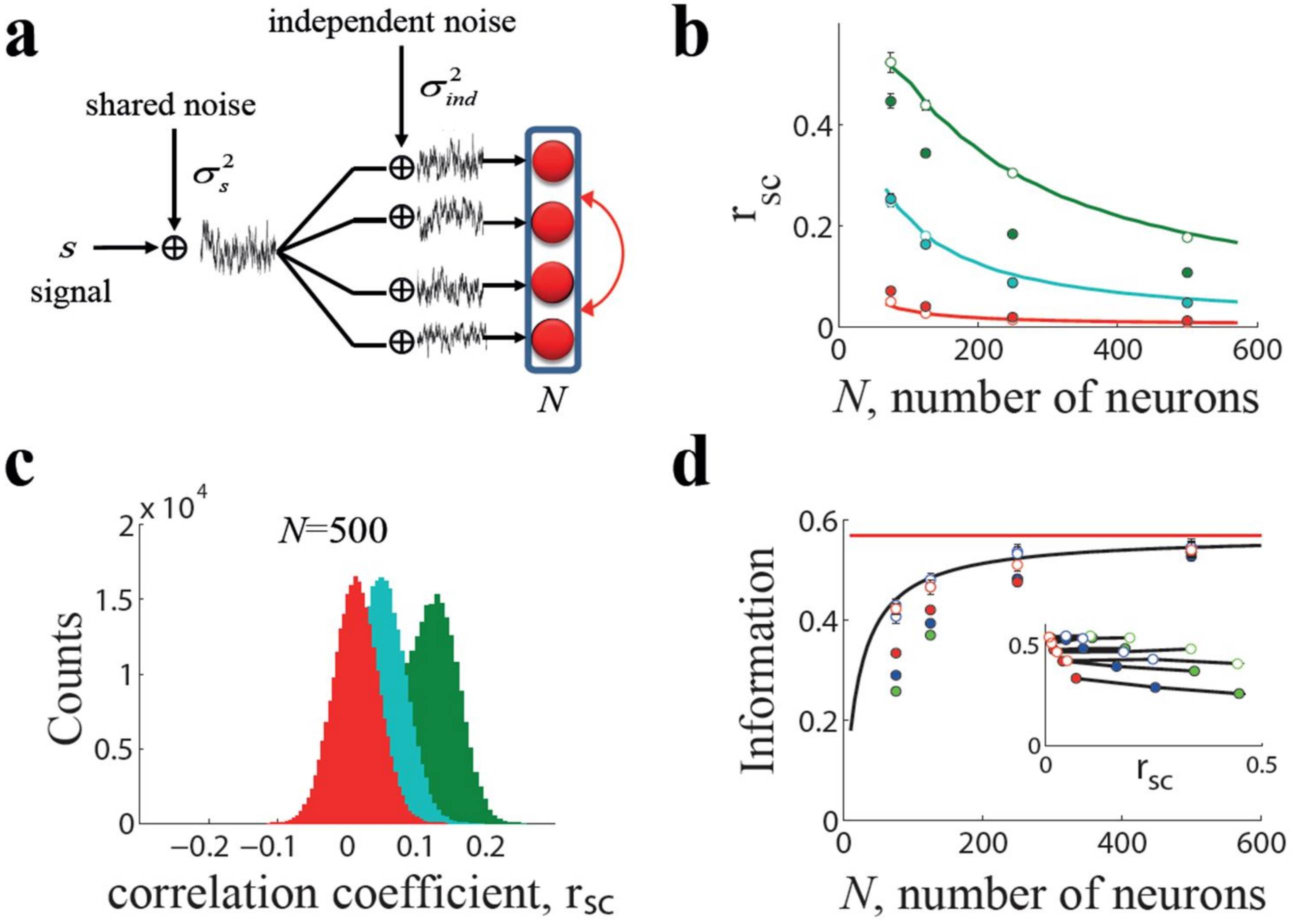
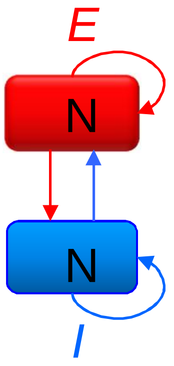
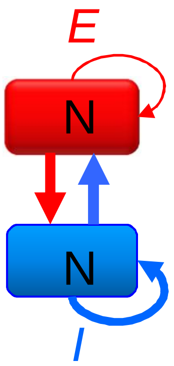


Signal/Noise limits induced by correlations



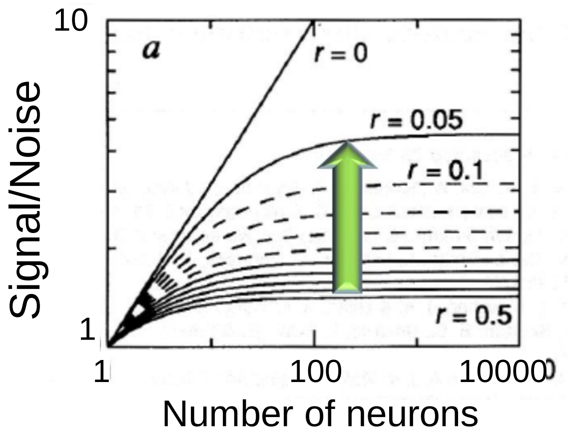
$r_{sc} \sim 0.1$

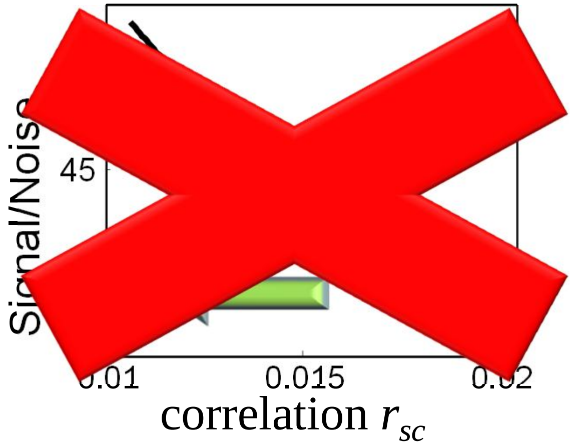
decorrelation



$r_{sc} \sim 0.01$

Zohary et al, 1994





Outline

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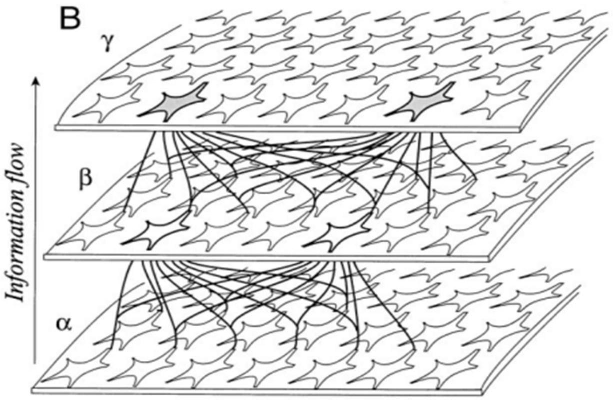
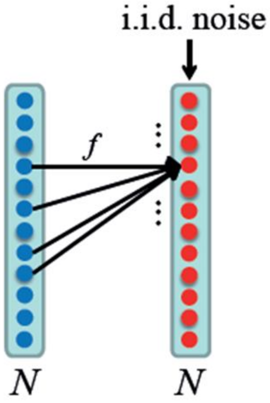
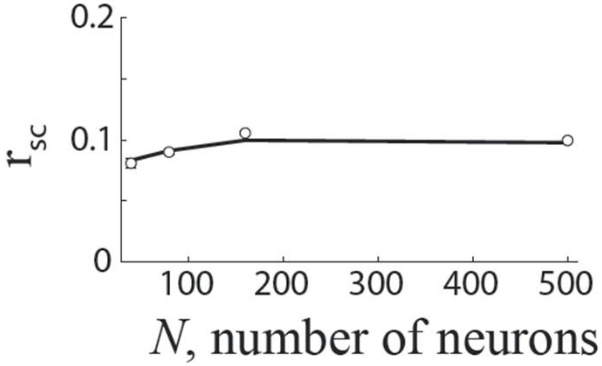
Moreno-Bote et al, *Nature Neuroscience*, In Press, 2014

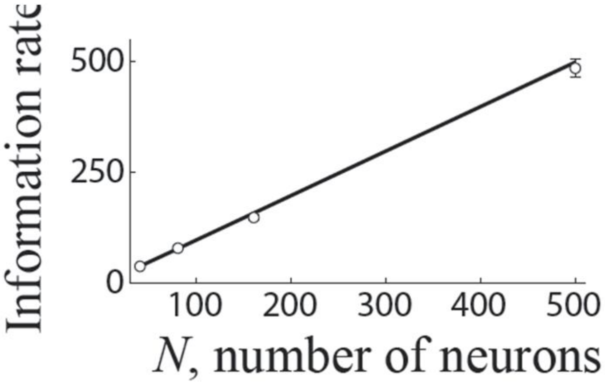
Shared connectivity does not limit information



Shadlen and Newsome, 1998







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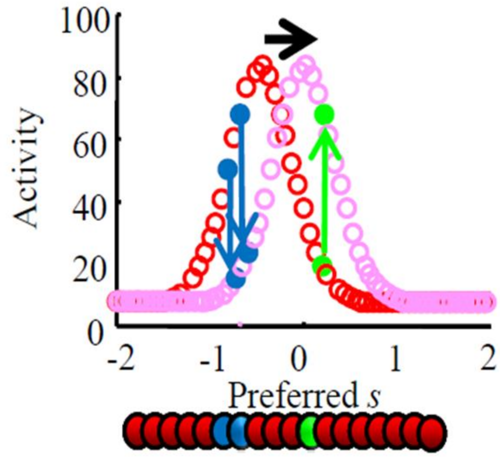
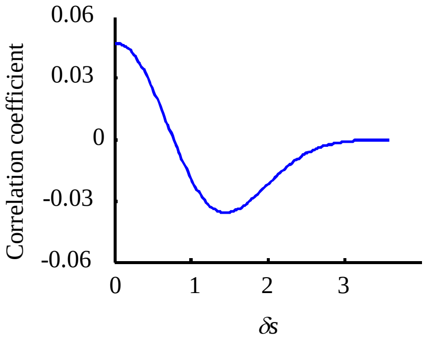
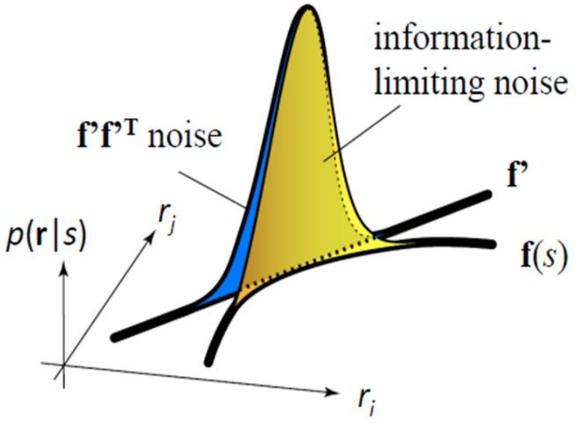
Moreno-Bote et al, *Nature Neuroscience*, In Press, 2014

Limiting-information correlations: $\mathbf{f}'\mathbf{f}'^{T}$

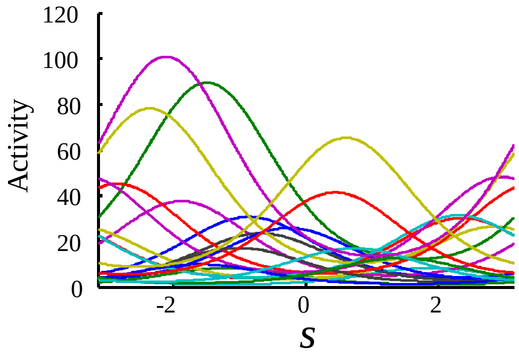


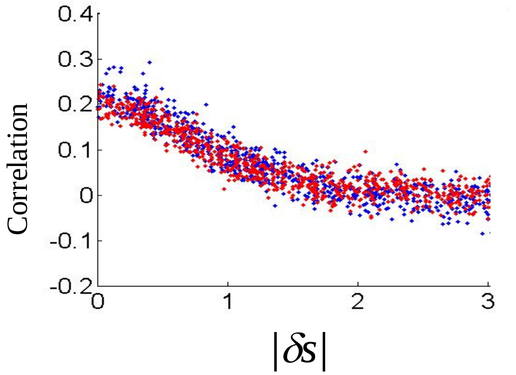


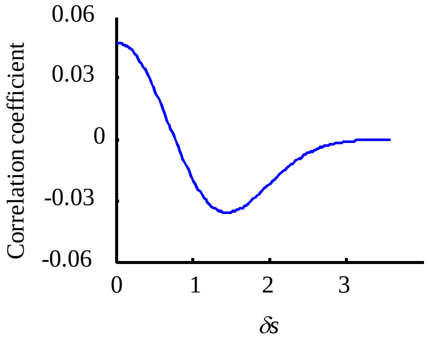


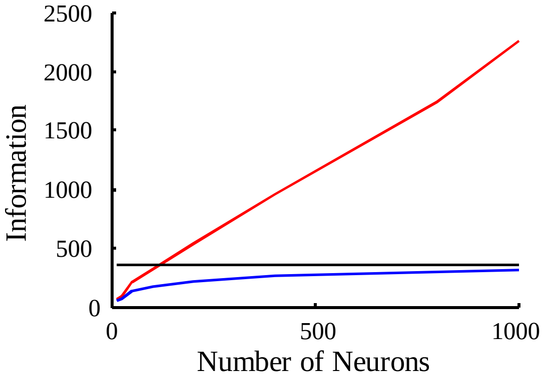
$$\boxed{\Sigma_\epsilon(s) = \Sigma_0(s) + \epsilon\mathbf{f}'(s)\mathbf{f}'^T(s)}$$

Limiting-information correlations can be very weak but important









Conclusions

- Spiking neuronal networks transmit virtually all input information
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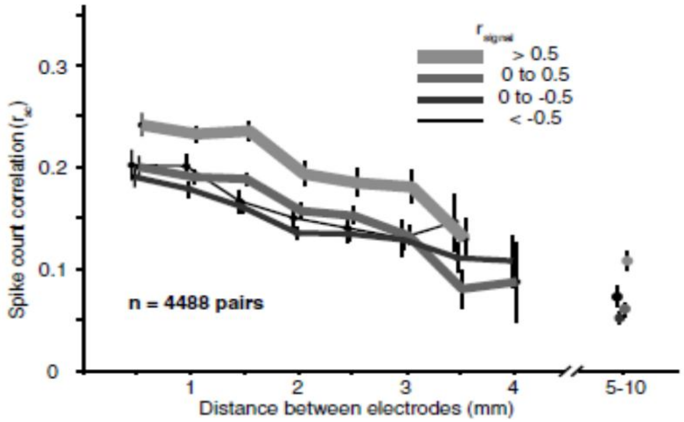
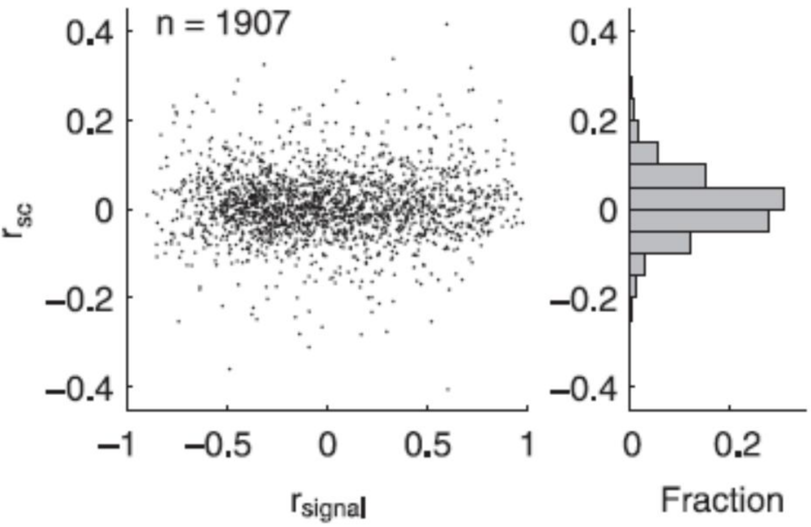
Moreno-Bote et al, *Nature Neuroscience*, In Press, 2014

How strong are correlations in cortex?



Smith and Kohn, 2008



Ecker et al, 2010

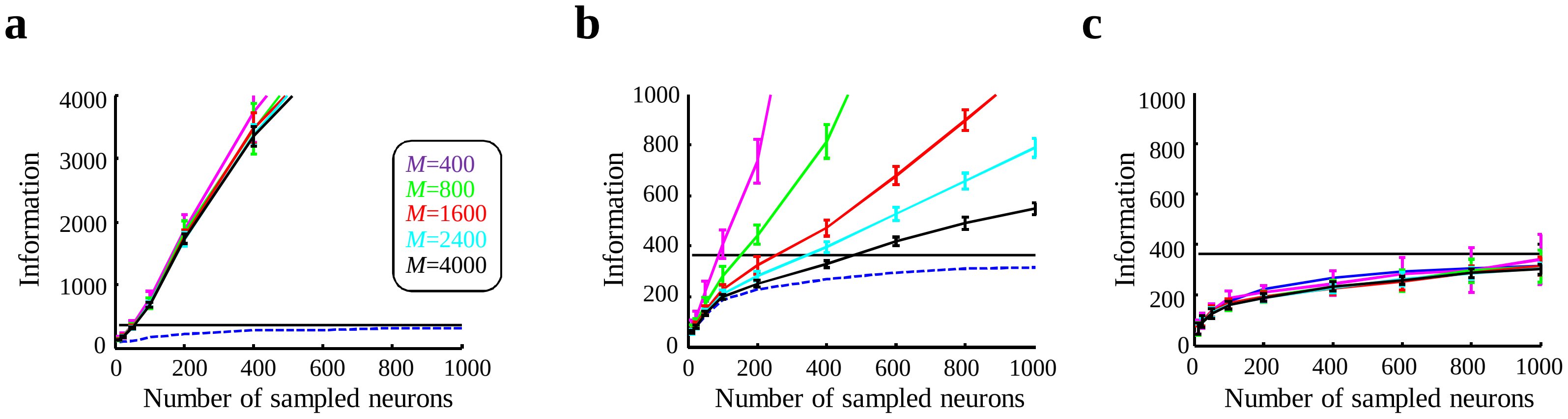
$r_{sc} \sim 0.1$

$r_{sc} \sim 0.01$

$$<\mathbf{f}'\mathbf{f}'^{T}>=0$$

differential correlations cannot be seen in average correlations

Detecting differential correlations



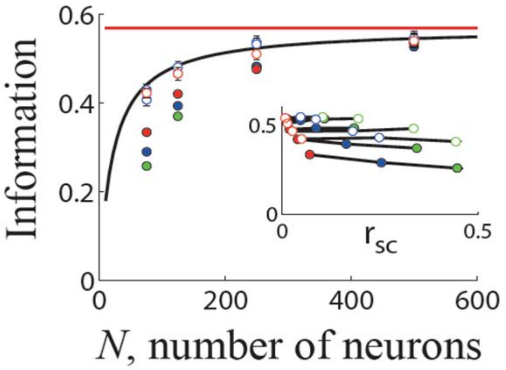
differential correlations can be detected by their effects on information

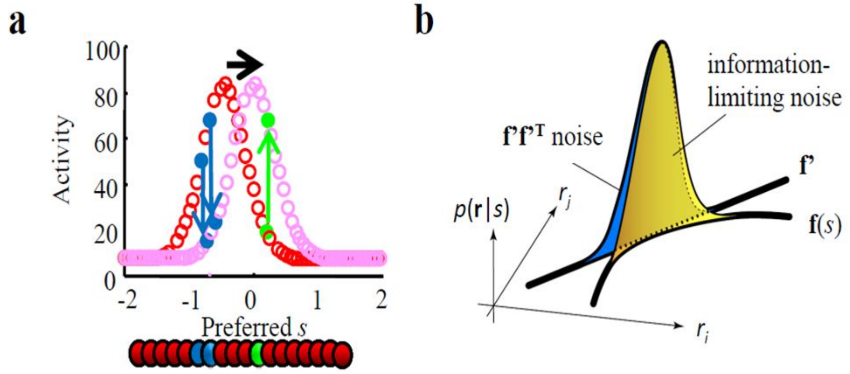
Conclusions

- Spiking neuronal networks transmit virtually all input information
- **Noise decorrelation does not improve information**
- Shared connectivity does not limit information
- **The only information-limiting correlations are differential correlations, proportional to the product of the derivatives of the tuning curves**: $\mathbf{f'f'^T}$
- Correlations in any other direction does not affect information for large neuronal populations
- Differential correlations can be very weak, almost unnoticeable at the correlation level, but their effect can be seen at the information level

Moreno-Bote et al, *Nature Neuroscience*, In Press, 2014

Conclusions





the size of correlations does not limit information

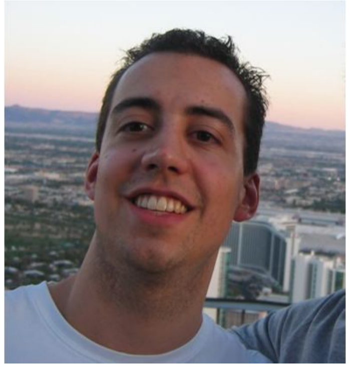
information-limiting correlations: $f'f'^T$ correlations

Acknowledgments

PhD students


Iñigo Arandia


Ramon Nogueira


Philipp Schustek

Post-doc


Alexandre Hyafil

Rat & Monkey


Mavi Sanchez-Vives


Adam Kohn

Drosophila larvae


Matthieu Louis

Theory

Alex Pouget

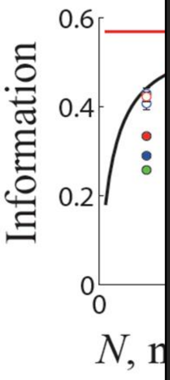
Jan Drugowitsch

Peter Latham

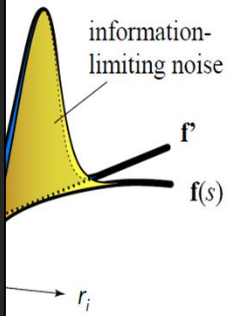
Jeff Beck

Xaq Pitkow

Conclusions



MERCI !



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