Introduction to *correlated spiking* in neural coding and dynamics

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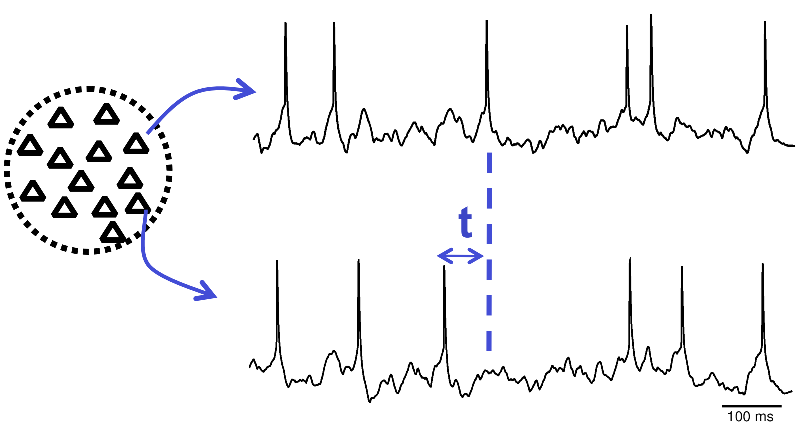
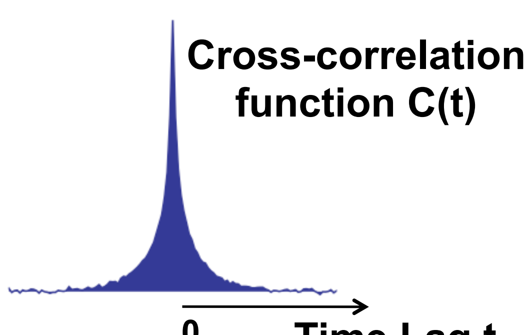
What do we mean by correlation?





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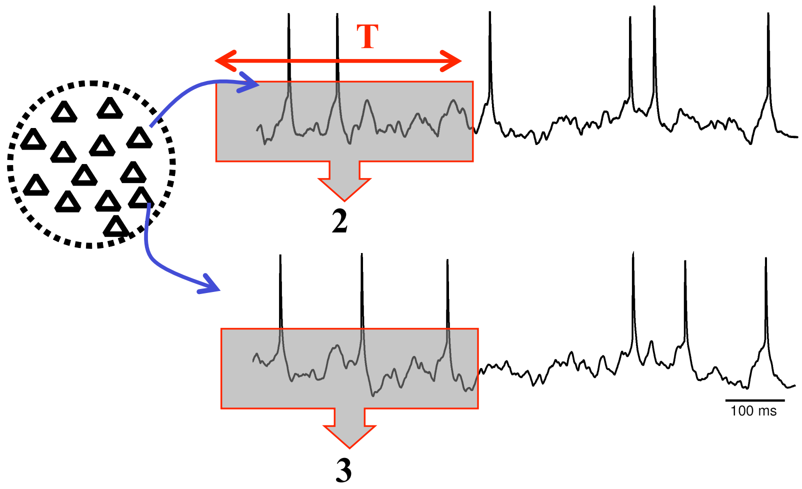

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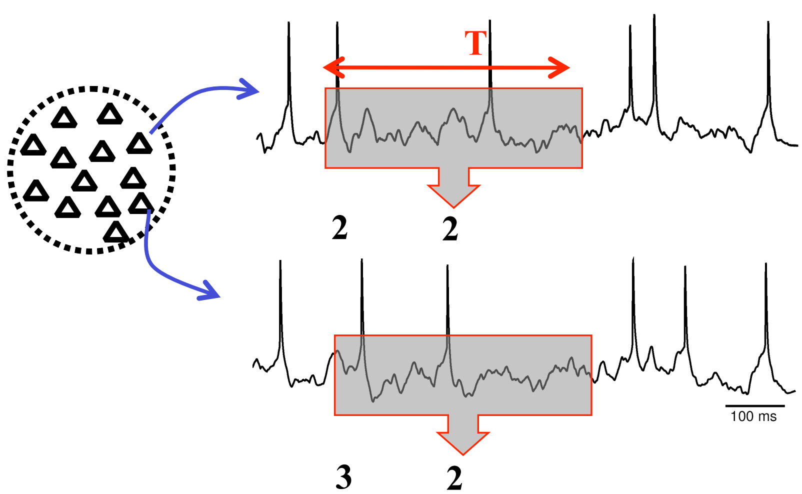

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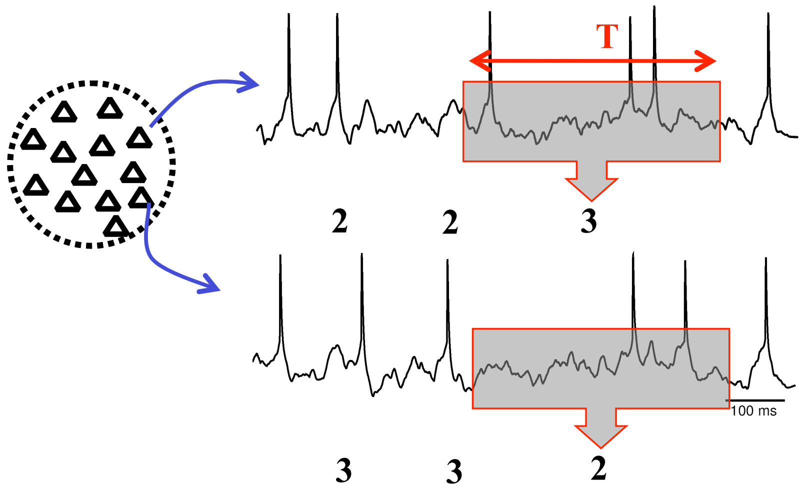

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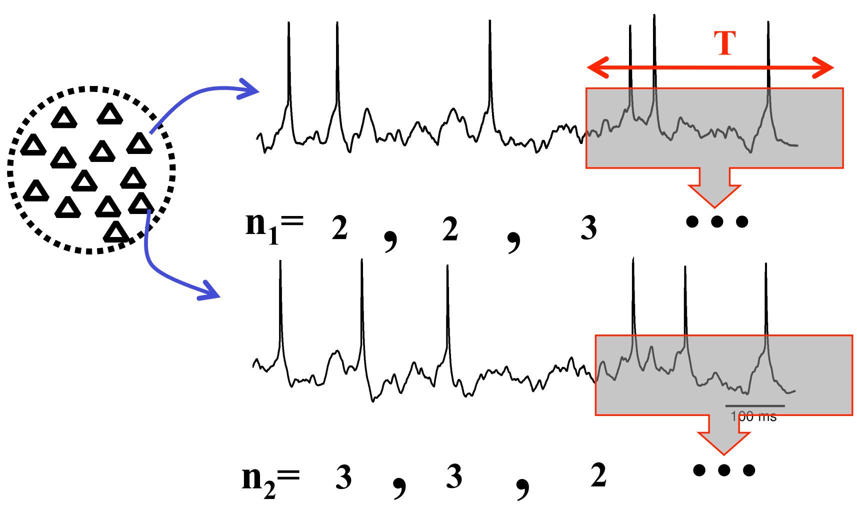
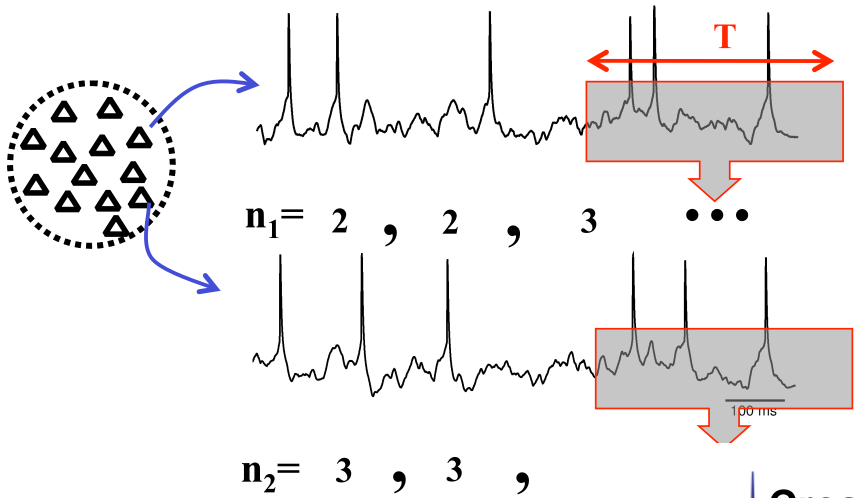
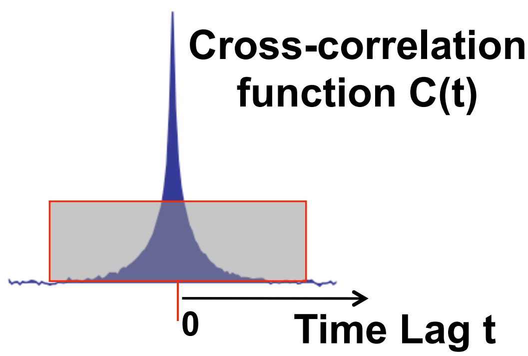


$$\rho_T = \frac{Cov(n_1 n_2)}{\sqrt{Var(n_1)Var(n_2)}}$$

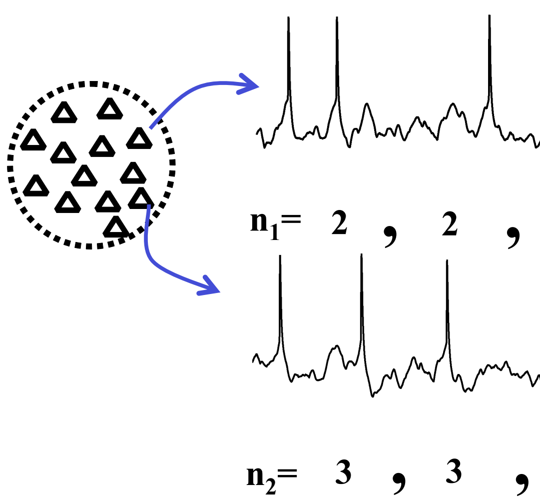
What do we mean by correlation?





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

T > ~50 ms (cf. Bair et al '01) …



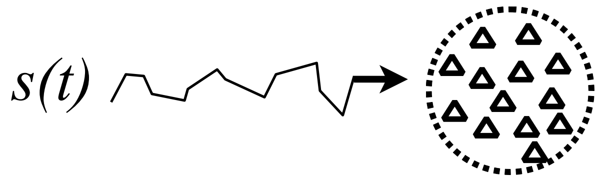
$$\rho = \frac{Cov(n_1 n_2)}{\sqrt{Var(n_1)Var(n_2)}}$$

Correlation $\rho \neq 0$ ubiquitous *in vivo*:

- **Retina:** ***Mastronade 1983*.**
- **LGN:** ***Alonso et al 1996***
- **V1:** ***Kohn and Smith 2005***
  see also Ecker et al 2010
- **IT:** ***Gawne & Richmond 1993***
- **PF:** ***Constanidis & Goldman-Rakic 2002.***
- **Motor cortex:** ***Vaadia et al 1995***
- **Parietal Cortex:** ***Lee et al 1998***
- **Somatosensory thal.:** ***Bruno & Sakmann 2006***
- **A1:** ***deCharms & Merzenich 1996***
- **SI:** ***Romo et al 2003*. …**

Why the correlations? $p(n_1, n_2) \neq p(n_1)p(n_2)$

Common signal input→Common spike response
→ SIGNAL CORRELATIONS



ADDITIONAL "NETWORK-DRIVEN" CORRELATIONS ARE ...
NOISE CORRELATIONS

$$p(n_1, n_2|s(t)) \neq p(n_1|s(t))p(n_2|s(t))$$

We'll focus on noise correlations.

OUTLINE

CONSEQUENCES OF CORRELATED SPIKING

Impact on coding
(a) Homogeneous populations
...

Impact on signal propagation

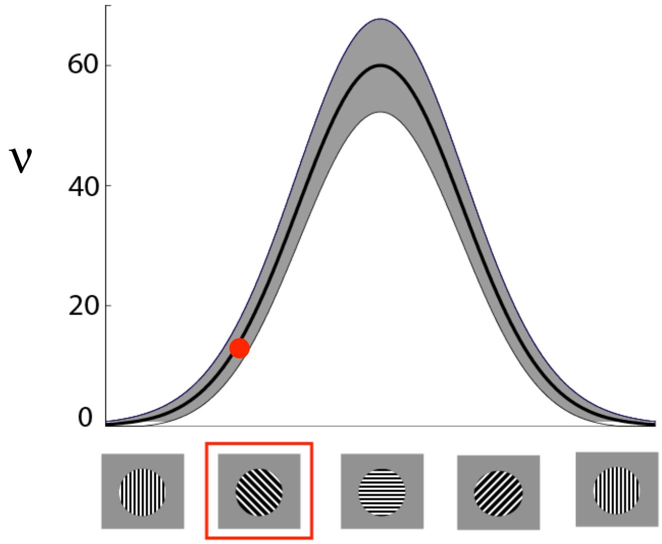
BASIC MECHANISMS FOR CORRELATED SPIKING
...

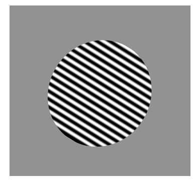
BEYOND CELL-PAIRS: HIGHER-ORDER CORRELATIONS

...

Rate coding

$$RATE: \nu = \frac{n}{T}$$





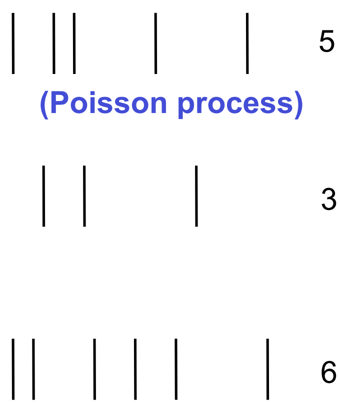
Hubel and Weisel. J. Physiol.,1962

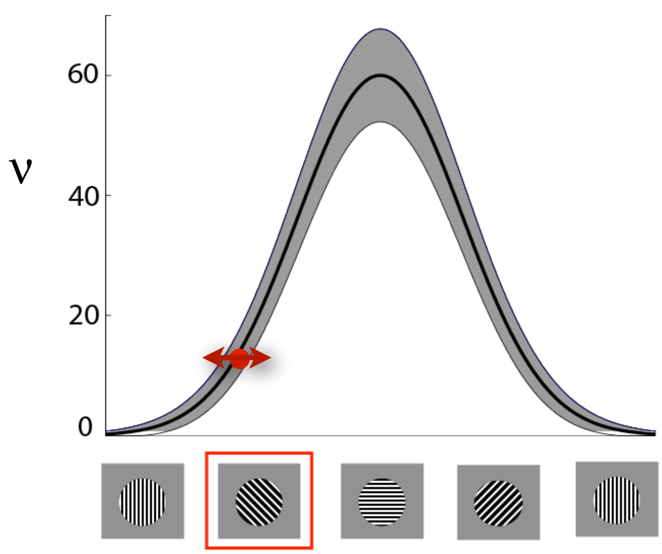
Reddy, Kreiman, Koch, and Fried (20

Response Variability

$$RATE: \nu = \frac{n}{T}$$

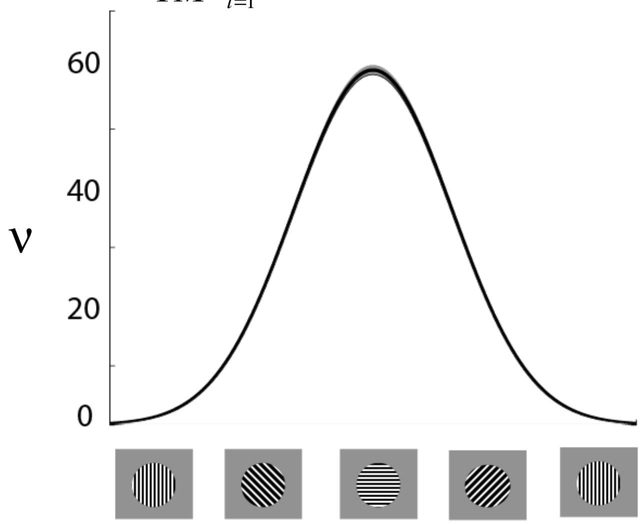
Variable spike count introduces ambiguity.

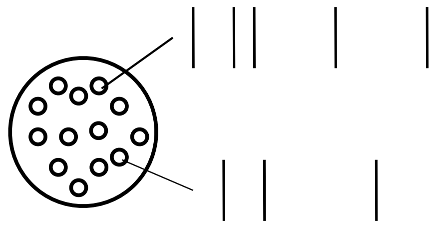




Population codes – average over *M* independent cells

$$RATE\ \nu = \frac{1}{TM}\sum_{i=1}^{M} n_i$$

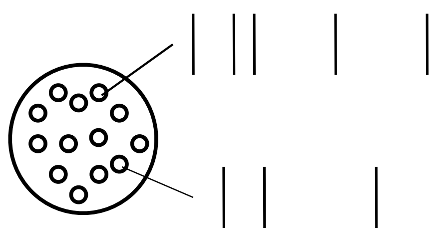




M **cells**
n_i **spikes each**
in time window T

Population codes – average over *M* independent cells

$$RATE\ \nu = \frac{1}{TM}\sum_{i=1}^{M} n_i$$



M **cells**
n_i **spikes each**
in time window T

$$\langle \nu \rangle = \frac{1}{TM}\sum_{i}^{M}\langle n_i \rangle$$
$$= \frac{1}{TM} MrT = r$$

$$var(\nu) = \frac{1}{T^2M^2}\sum_{i}^{M} var(n_i)$$
$$= \frac{1}{T^2M^2} MrT \sim \frac{1}{M} r$$

Population codes – average over *M* independent cells

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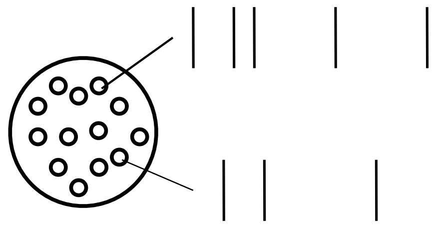


***M* cells**
n_i spikes each
in time window *T*

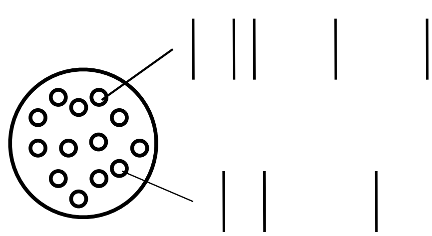
$$\langle \nu \rangle = \frac{1}{TM}\sum_{i}^{M}\langle n_i \rangle = \frac{1}{TM} MrT = r$$

$$var(\nu) = \frac{1}{T^2M^2}\sum_{i}^{M} var(n_i) = \frac{1}{T^2M^2} MrT \sim \frac{1}{M} r$$

$$\frac{\langle \nu \rangle}{var(\nu)} = SNR(\nu) \sim M$$

Population codes – average over *M* independent cells

$$RATE\ \nu = \frac{1}{TM}\sum_{i=1}^{M} n_i$$

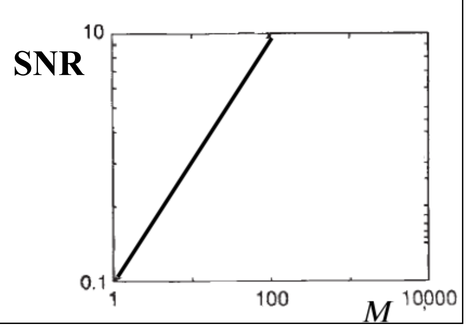


***M* cells**
n_i spikes each
in time window *T*

$$\langle \nu \rangle = \frac{1}{TM}\sum_{i}^{M}\langle n_i \rangle = \frac{1}{TM} MrT = r$$

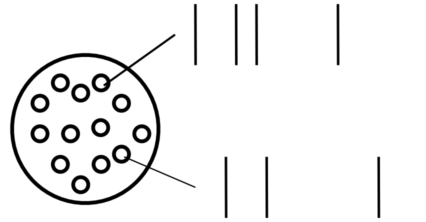
Population averaging improves SNR.

$$\frac{\langle \nu \rangle}{var(\nu)} = SNR(\nu) \sim M$$



Population codes – average over M correlated cells

$$RATE\ \nu = \frac{1}{TM}\sum_{i=1}^{M} n_i$$



M cells

n_i spikes each

in time window T

n_i have correlation coefficient ρ

$$\langle \nu \rangle = \frac{1}{TM}\sum_{i}^{M}\langle n_i \rangle$$

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Population codes – average over M correlated cells

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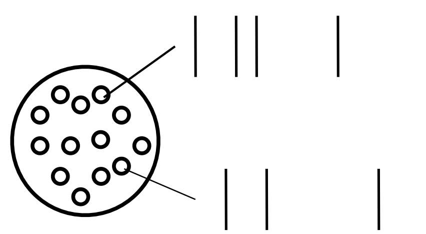

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n_i have correlation coefficient ρ

$$\langle \nu \rangle = \frac{1}{TM}\sum_{i}^{M}\langle n_i \rangle$$

$$= \frac{1}{TM} MrT = r$$

$$var(\nu) =$$

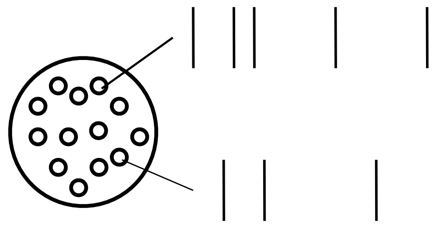
$$\frac{1}{T^2M^2}\left(\sum_{i}^{M} var(n_i) + \sum_{i \neq j} cov(n_i, n_j)\right)$$

$$\sim \frac{1}{T^2M^2} M^2 rT\rho \sim \rho$$

$$\boxed{\frac{\langle \nu \rangle}{var(\nu)} = SNR(\nu) \sim \frac{1}{\rho}}$$

Population codes – average over *M* correlated cells

$$RATE\ \nu = \frac{1}{TM}\sum_{i=1}^{M} n_i$$



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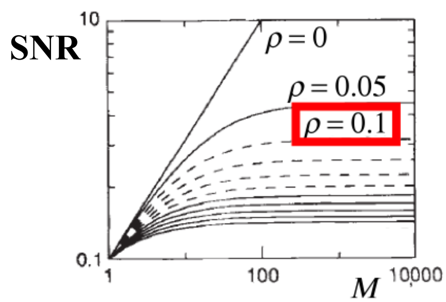
$$= \frac{1}{TM} MrT = r$$

M **cells**
n_i **spikes each**
in time window *T*
n_i **have correlation coefficient ρ**

Zohary, Shadlen and Newsome (1994)



$$\frac{\langle \nu \rangle}{var(\nu)} = SNR(\nu) \sim \frac{1}{\rho}$$

OUTLINE

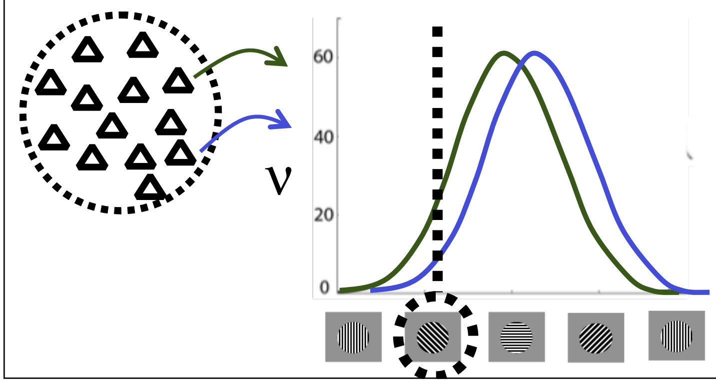
CONSEQUENCES OF CORRELATED SPIKING

Impact on coding

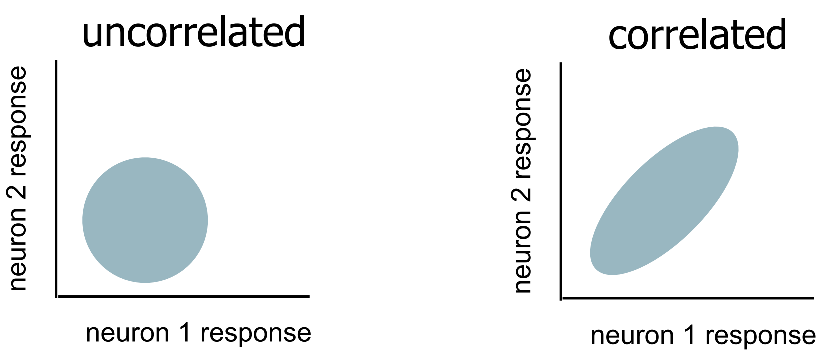
(a) Homogeneous populations: limits population averaging / degrades info

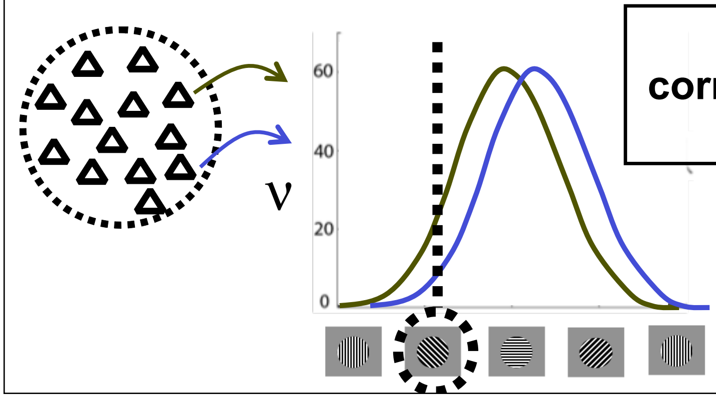
(b) Heterogeneous cell pairs ...

Sompolinsky et al., Phys Rev. E., 2001
Averbeck et al., Nat Rev Nsci 2006



Abbott+Dayan, N. Comp. 99; Sompolinsky et al., PRE 01; Averbeck et al., Nat Rev Nsci 06





What are effects of correlations on information content in cell pair?

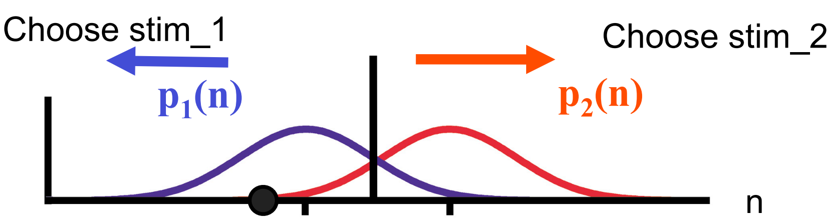
Consider discriminating two nearby stimuli

For one neuron:

$p_1(n)$: response n under stimulus 1

$p_2(n)$: response n under stimulus 2

Decode … via (optimal) maximum likelihood discrimination



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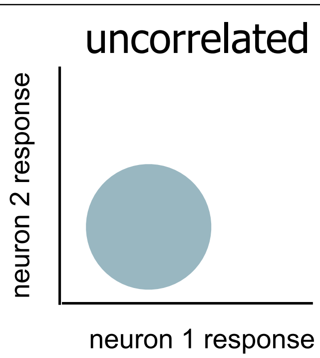

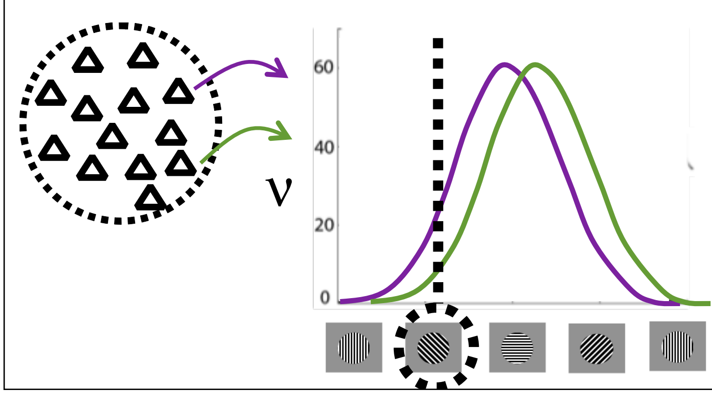

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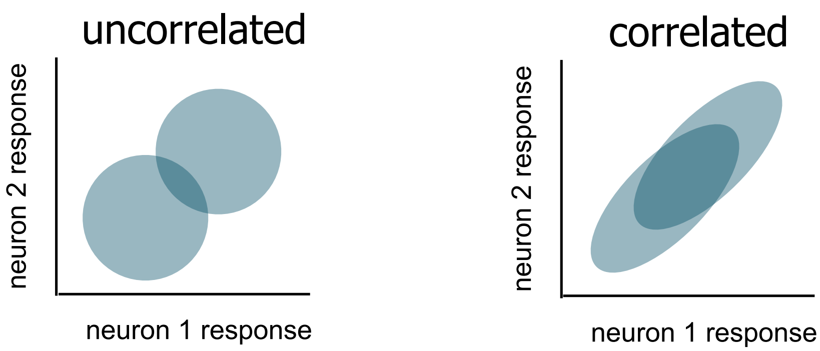
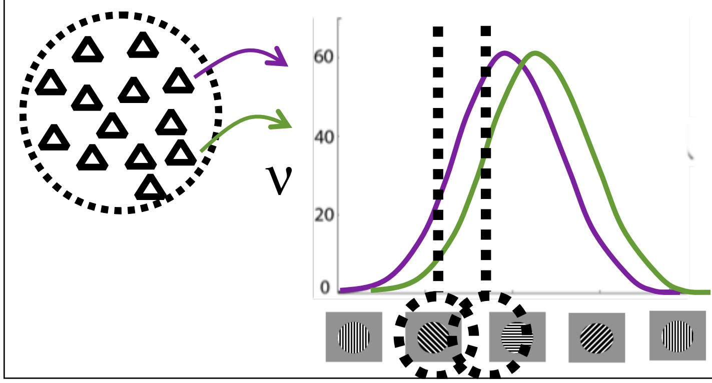


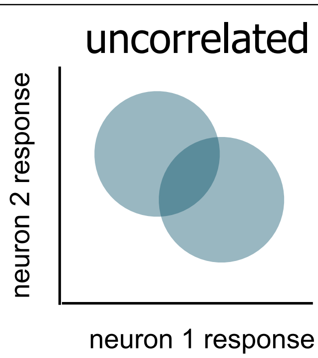


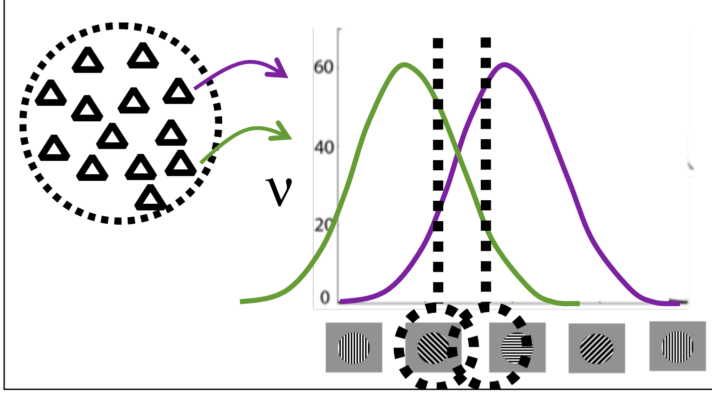
Positive **noise correlation** degrades signal encoding.

...

when also have positive signal correlation.

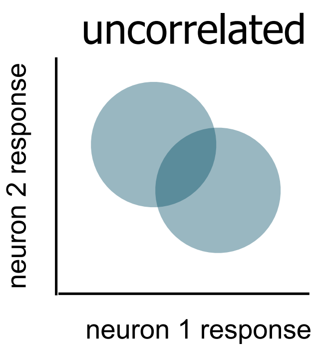
Abbott+Dayan, N. Comp. 99, Sompolinsky et al., PRE 01, Averbeck et al., Nat Rev Nsci 06

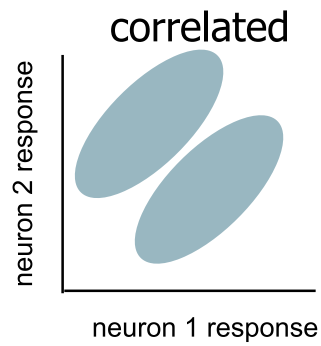


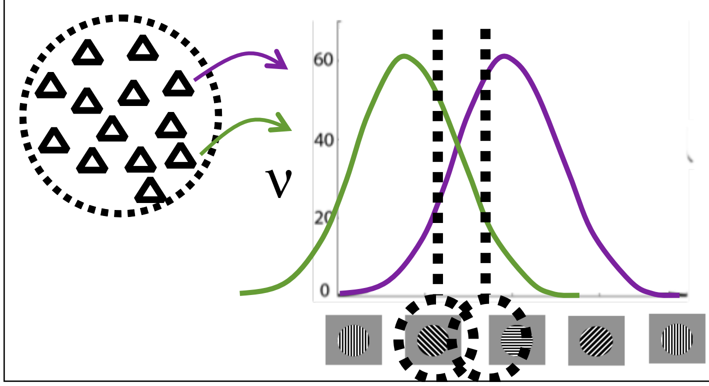


when also have **negative signal correlation.**

Abbott+Dayan, N. Comp. 99, Sompolinsky et al., PRE 01, Averbeck et al., Nat Rev Nsci 06







Positive **noise correlation** ENHANCES signal encoding.

...

when also have **negative signal correlation.**

Neuron, Vol. 38, 649–657, May 22, 2003, Copyright ©2003 by Cell Press

Correlated Neuronal Discharges that Increase Coding Efficiency during Perceptual Discrimination

Ranulfo Romo,[1,*] Adrián Hernández,[1] Antonio Zainos,[1] and Emilio Salinas[2]

rate increases similar to those observed in S1, but for other units the firing rate decreases monotonically as a

OUTLINE

CONSEQUENCES OF CORRELATED SPIKING

Impact on coding

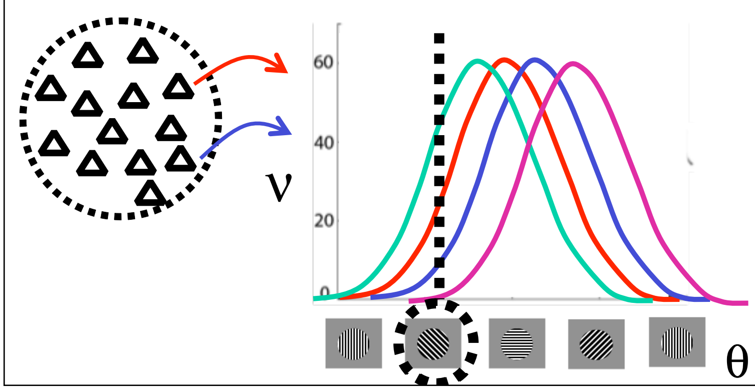
(a) Homogeneous populations: limits population averaging / degrades info

(b) Heterogeneous cell pairs ...

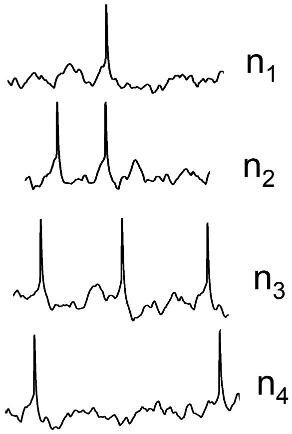
similar stimulus tuning: DEGRADE CODING

different stimulus tuning: ENHANCE CODING

- **Now, generalize to populations of more than two cells …**



Tuning curves [e.g Hubel+Wiesel, '60s]



$$\mathbf{n} = (n_1, n_2, n_3, \ldots).$$

Stimulus x

Task: given $\mathbf{n}$, estimate x

Usually, but not always saturated! (Berens et al COSYNE '11)

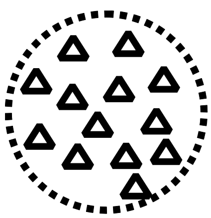
Cramér-Rao Bound:

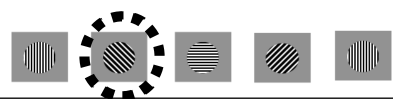
$$(Estimation\ error)^2 \geq \frac{1}{I_{FISHER}}$$

Each neuron i fires spike count $n_i = f_i(x) + \eta_i(x)$

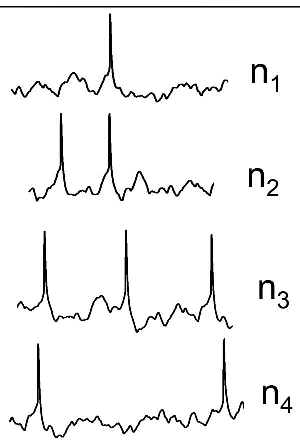
Fisher Information

$$I_F(x) = \left\langle \frac{d^2}{dx^2} \log P[\mathbf{n}|x] \right\rangle$$





Implications: Tuning curves [e.g Hubel+Wiesel, '60s]



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Each neuron i fires spike count $n_i = f_i(x) + \eta_i(x)$

Fisher Information

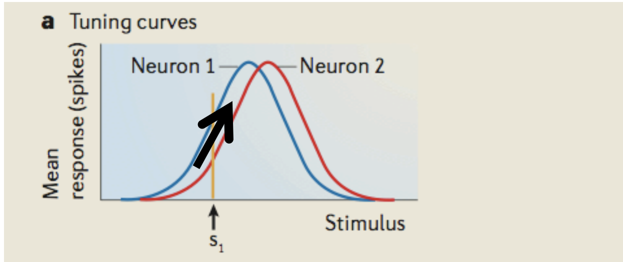
$$I_F = \left\langle \left(\frac{d}{dx} \log P(n|x) \right)^2 \right\rangle$$

[Somplinsky et al

Take η_i gaussian with: $Q_{i,j} = \delta_{i,j} v + (1 - \delta_{i,j}) c \exp(-\alpha |i - j|) v$

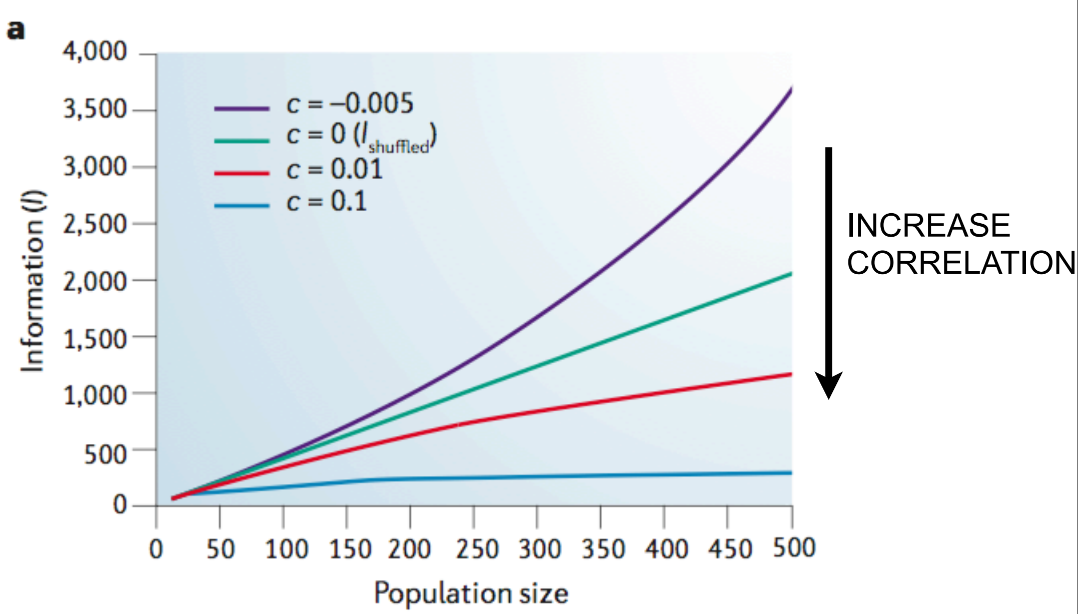
Interpret: positive correlations for "nearby" cells

… and nearby cells have positive signal correlations



… so, expect presence of correlations to DECREASE information

Averbeck et al 2006:



CONCLUDE: Here, correlations *degrade* coding.

In general, *degrade* OR *enhance* effect could dominate -- must examine case by case.

OUTLINE

CONSEQUENCES OF CORRELATED SPIKING

Impact on coding

(a) Homogeneous populations: limits population averaging / degrades info

(b) Heterogeneous cell pairs ...

similar stimulus tuning: DEGRADE CODING

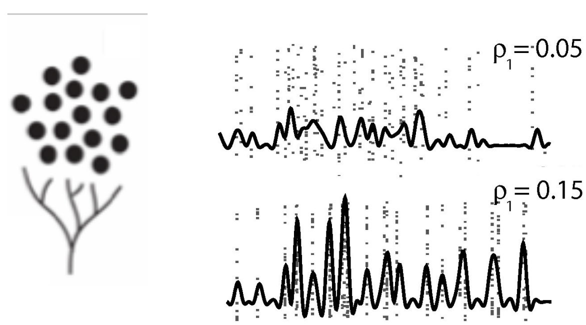
different stimulus tuning: ENHANCE CODING

(c) Heterogeneous population ... mixed effects

Impact on signal propagation

Correlated variability modulates downstream rates

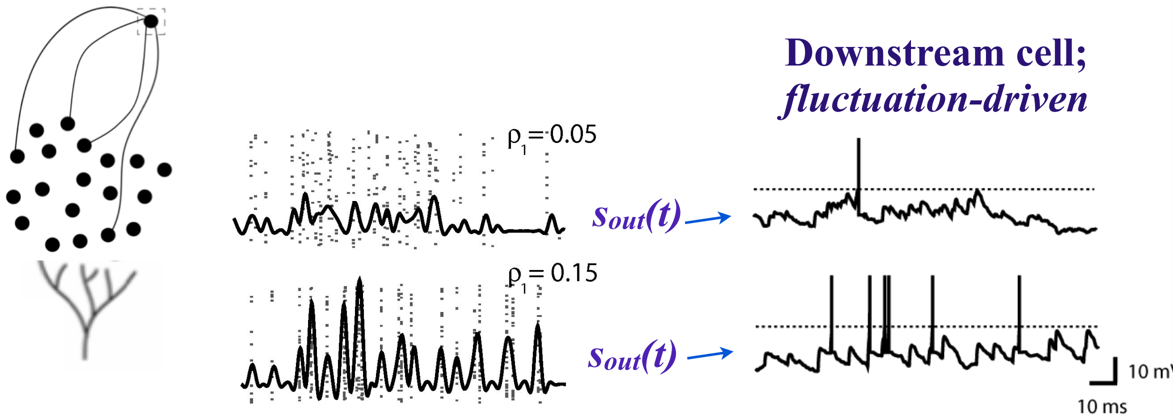
Salinas and Sejnowski, 2000



$$\text{std. dev.} \sim (\text{ rate} \times \text{corr })^{1/2}$$

Correlated variability modulates downstream rates

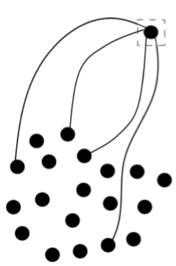
Salinas and Sejnowski, 2000



$$\text{std. dev.} \sim (\text{ rate} \times \text{corr })^{1/2}$$

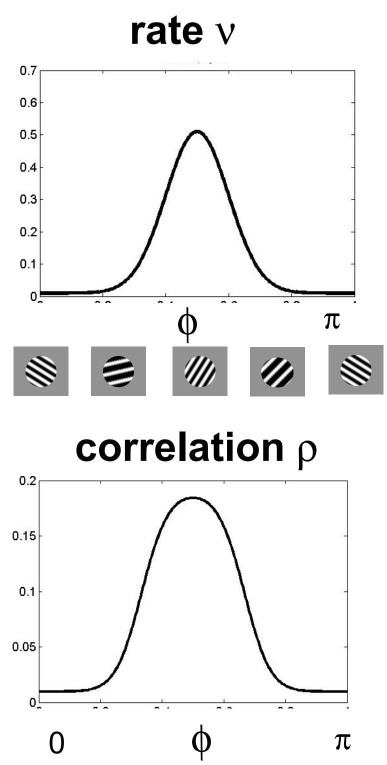
rate = f (std dev)

What if correlations are *stimulus-dependent?*



$$I_{FISHER}(\phi) \sim k + \frac{1}{2}\left[\frac{v'(\phi)}{v(\phi)} + \frac{\rho'(\phi)}{\rho(\phi}\right]^2$$

Here, co-tuning of correlations typically INCREASES information for SUMMED outputs!



Stimulus-dependent correlations - an example

LETTER

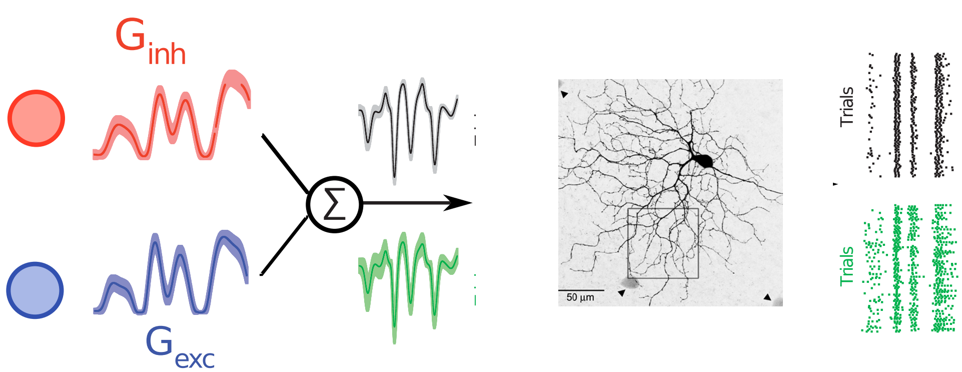
doi:10.1038/nature09570

Noise correlations improve response fidelity and stimulus encoding

Jon Cafaro[2] & Fred Rieke[1,2]

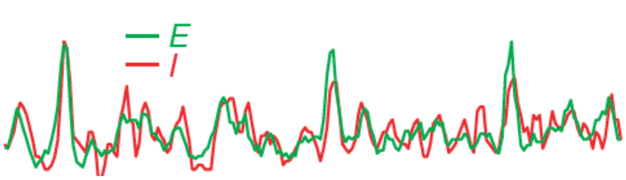
Stimulus-dependent correlations - an example

Cafaro and Rieke, Nature, 2010



Chen et al., J Phys, 2009

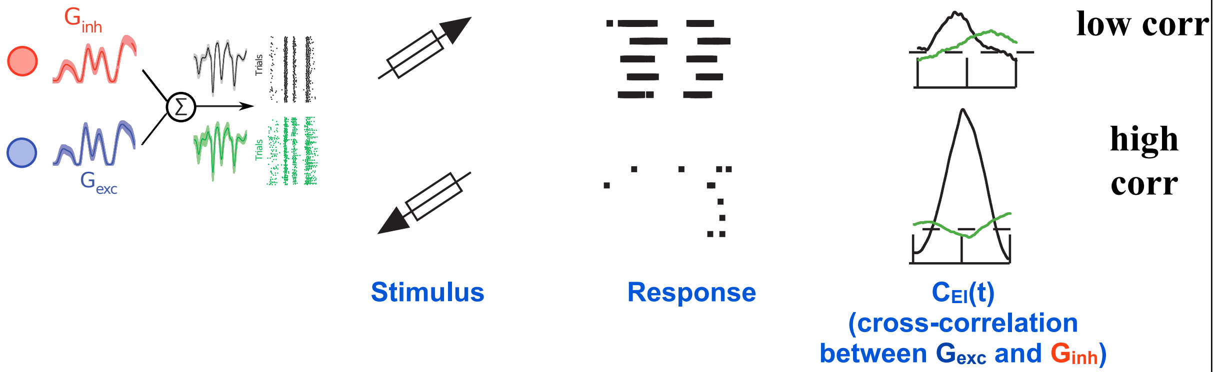
POSITIVE correlations b/w incoming conductances

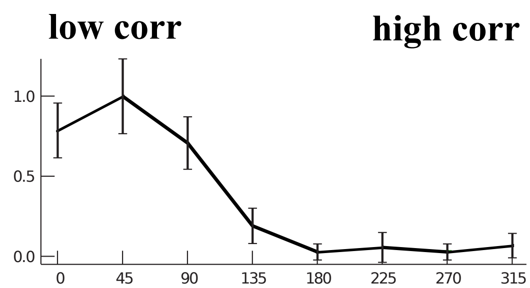


→ NEGATIVE correlations b/w incoming currents.

Fluctuations cancel.

Stimulus-dependent correlations - an example

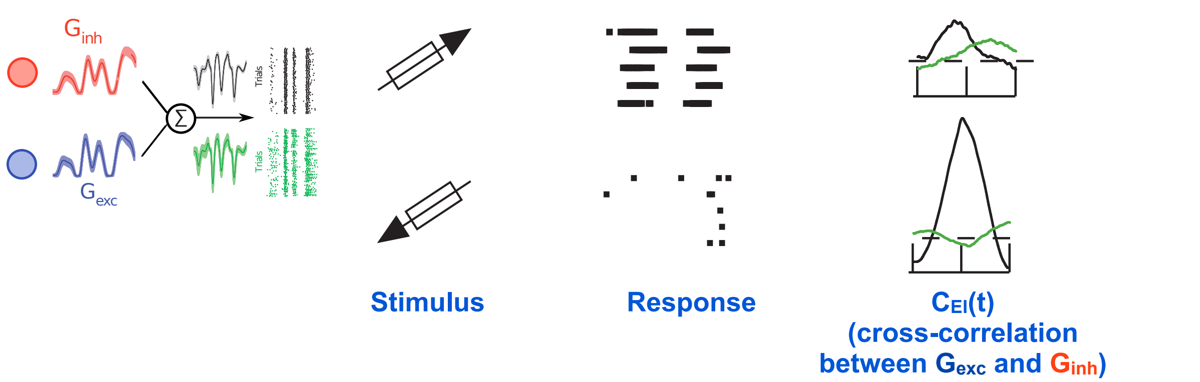


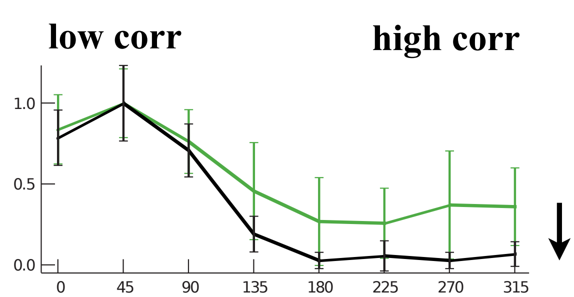


Correlated

adapted from
Cafaro and Rieke, Nature, 2010

Stimulus-dependent correlations - an example





Uncorrelated (trial shuffled)

Correlated

adapted from
Cafaro and Rieke, Nature, 2010

More neg. corr
→ lower rates / variance

OUTLINE

CONSEQUENCES OF CORRELATED SPIKING

Impact on coding

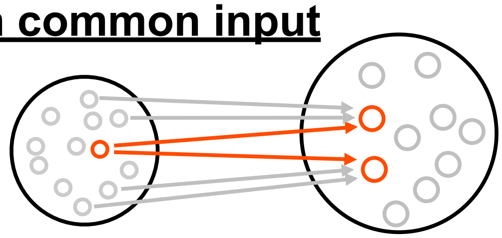
Impact on signal propagation

Positive correlation sets *gain*:

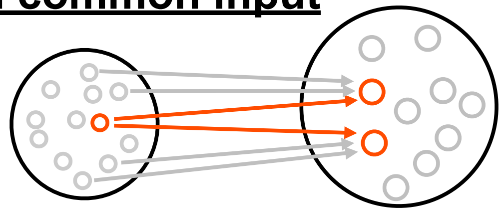
Downstream rate ~ upstream rate X upstream correlation

BASIC MECHANISMS FOR CORRELATED SPIKING

Correlations from common input



Correlations from common input



As in:
Shadlen and Newsome, *J. Nsci.* '98
Binder and Powers, *J. Neurophys.* '01
Tetzlaff, Geisel, and Diesmann, *Neurocomp.* '02
Moreno-Bote et al, *Phys. Rev. Lett.* '06
Galan et al, *J. Nsci.* '06
… and others

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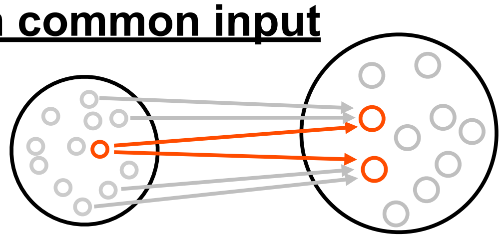

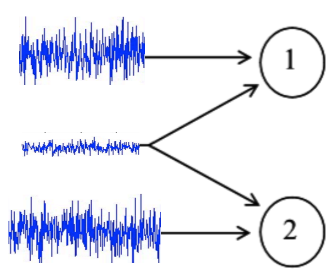

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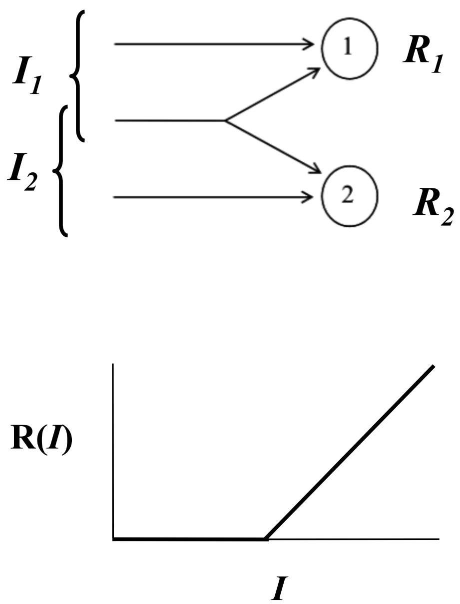
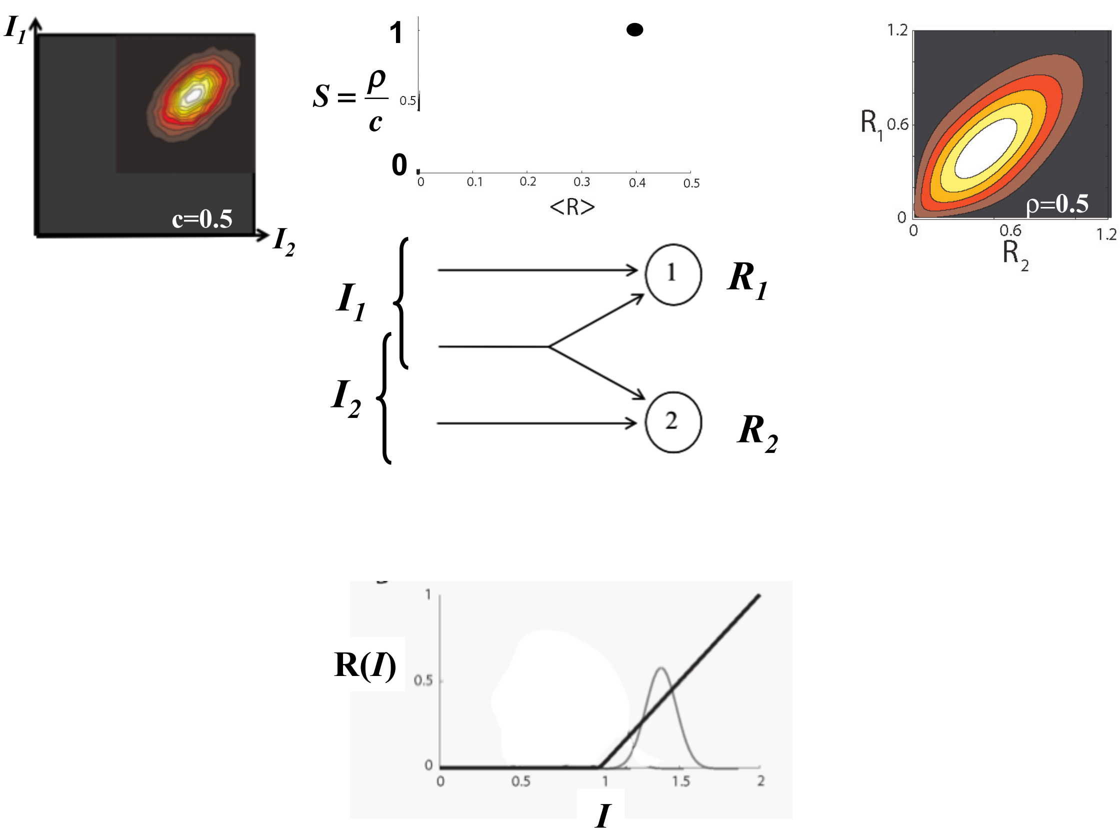
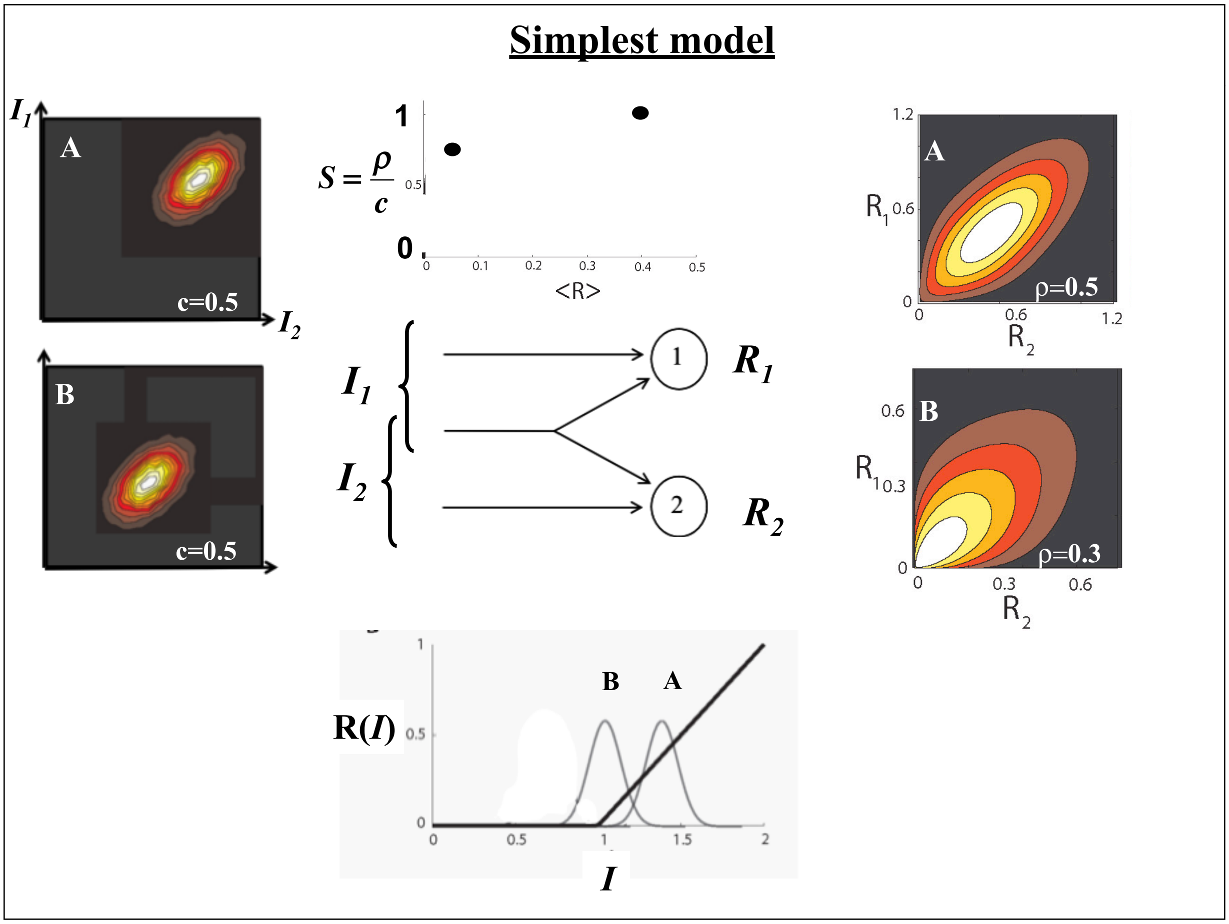
… and others

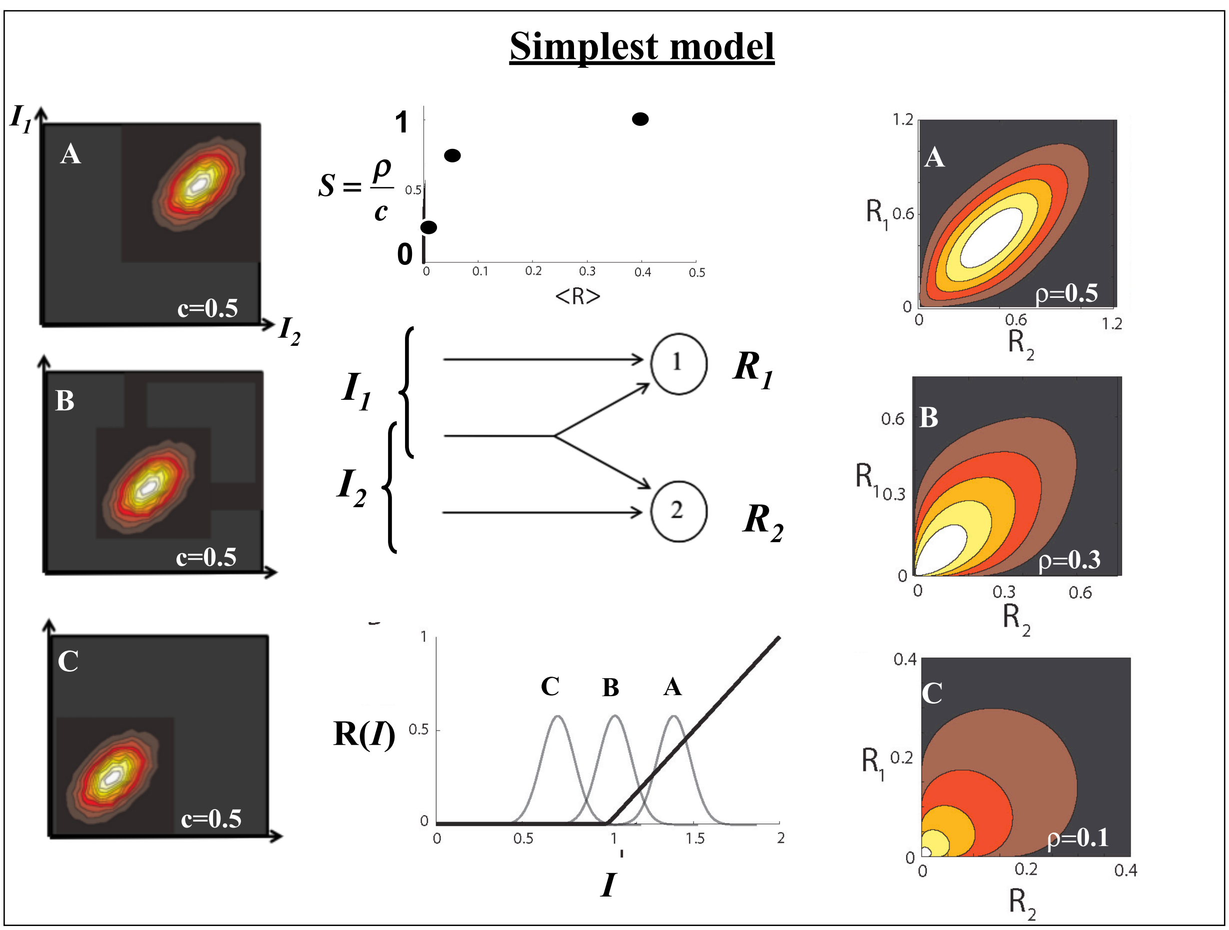
Simplest model



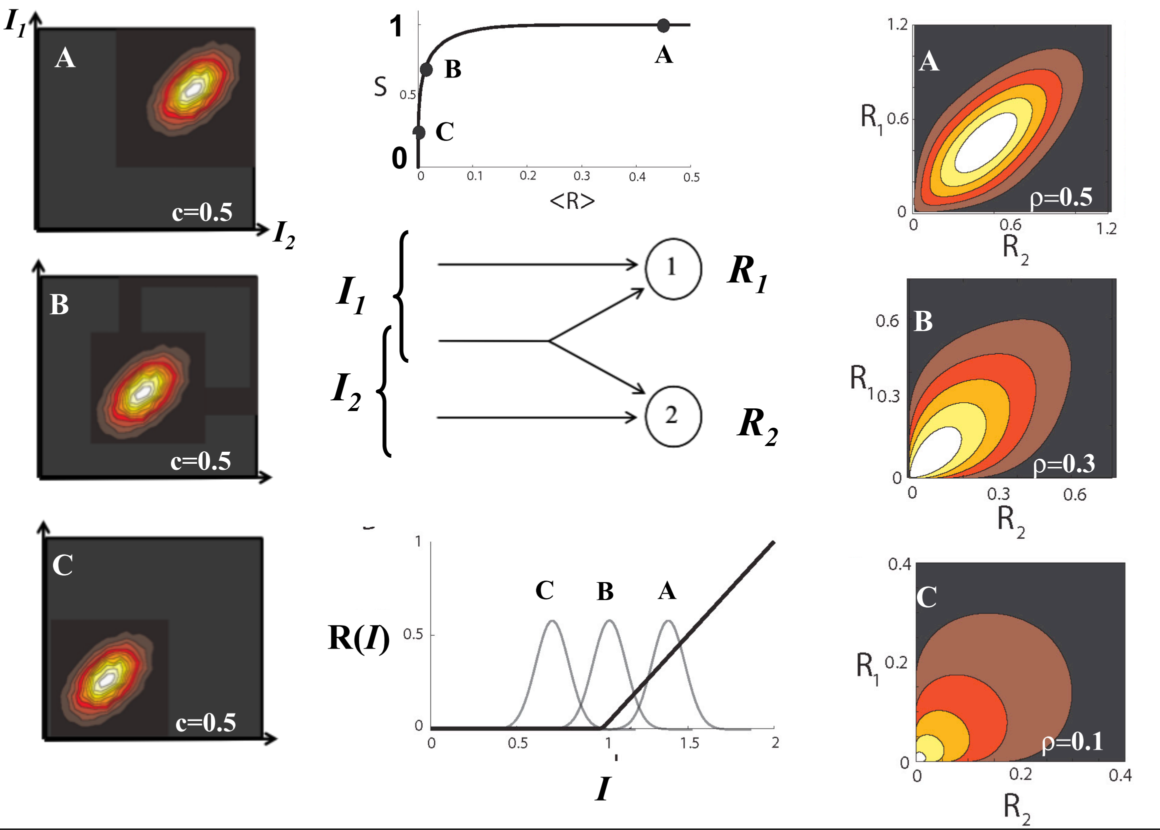
Simplest model




Simplest model
A
c=0.5
B
c=0.5
$S = \frac{\rho}{c}$
<R>
I_1
I_2
R_1
R_2
R(I)
I
ρ=0.5
ρ=0.3

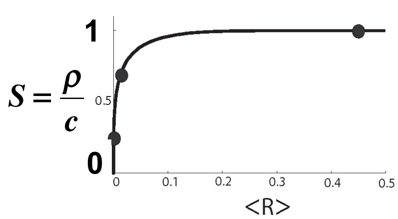

Simplest model
A
c=0.5
B
c=0.5
C
c=0.5
$S = \frac{\rho}{c}$
<R>
I_1
I_2
R_1
R_2
R(I)
I
ρ=0.5
ρ=0.3
ρ=0.1

Simplest model



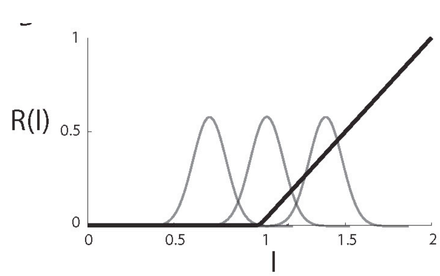
Simplest model

Integrate-and-fire model

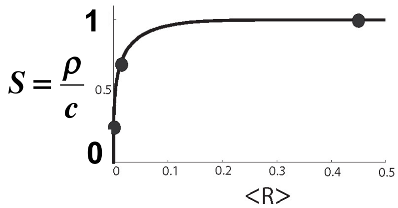


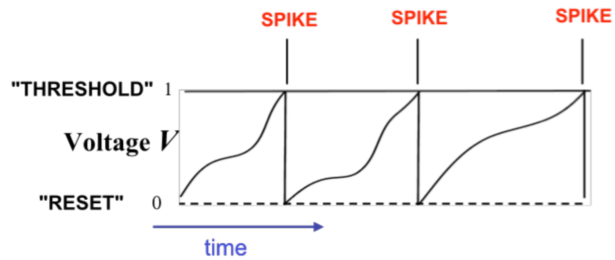
Correlations increase with rate

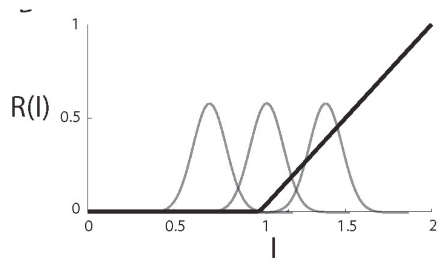
[de la Rocha, Doiron et al ’07; Shea-Brown et al ’08; Rosenbaum+Josic, ’10]



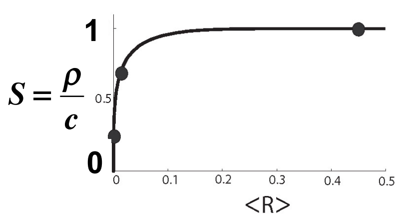
Simplest model **Integrate-and-fire model**

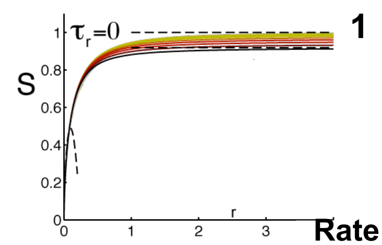


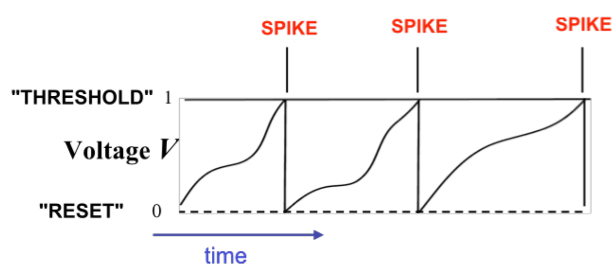




Simplest model **Integrate-and-fire model**





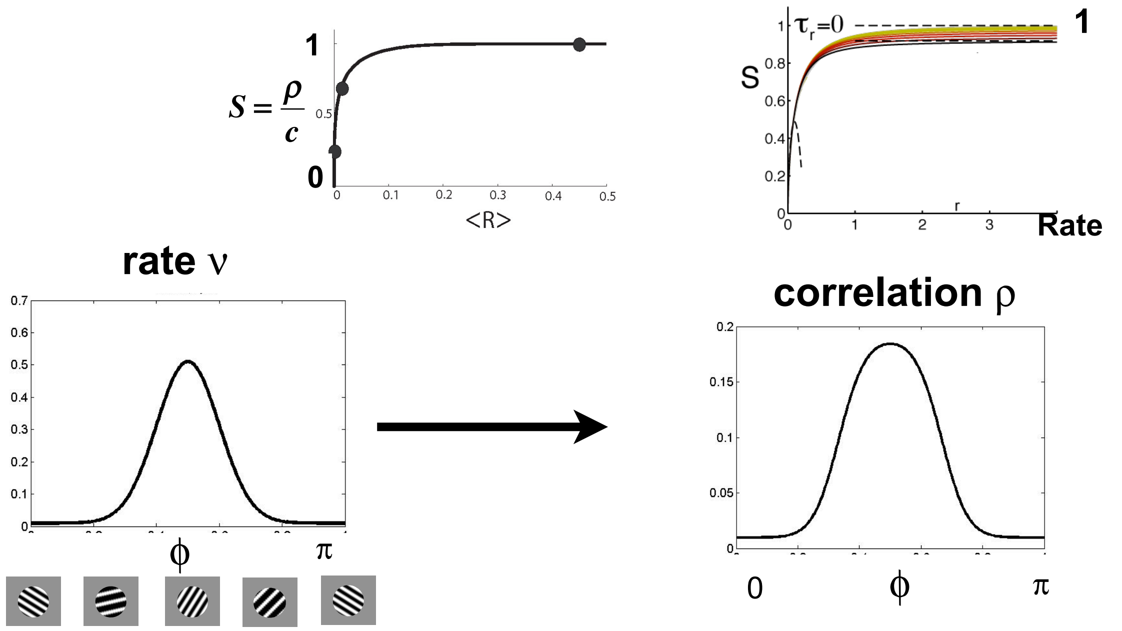


de la Rocha, Doiron et al, Nature ’07
Shea-Brown et al, PRL ’08

Spike generation and myriad other *nonlinearities* shape correlated spiking ...

... and can introduce *stimulus-dependent correlations.*

Simplest model **Integrate-and-fire model**

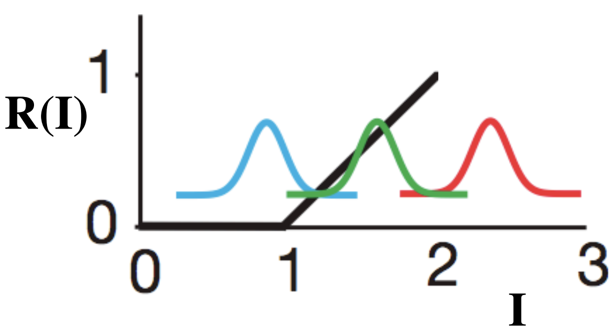


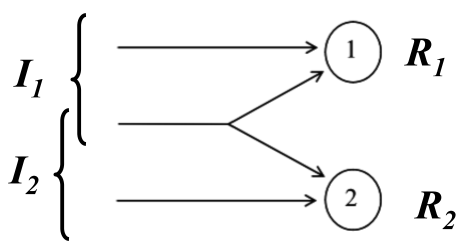
Spike generation and myriad other *nonlinearities* shape correlated spiking ...

de la Rocha, Doiron et al, Nature '07
Shea-Brown et al, PRL '08

... and can introduce *stimulus-dependent correlations.*

Another simple (nonlinear) mechanism





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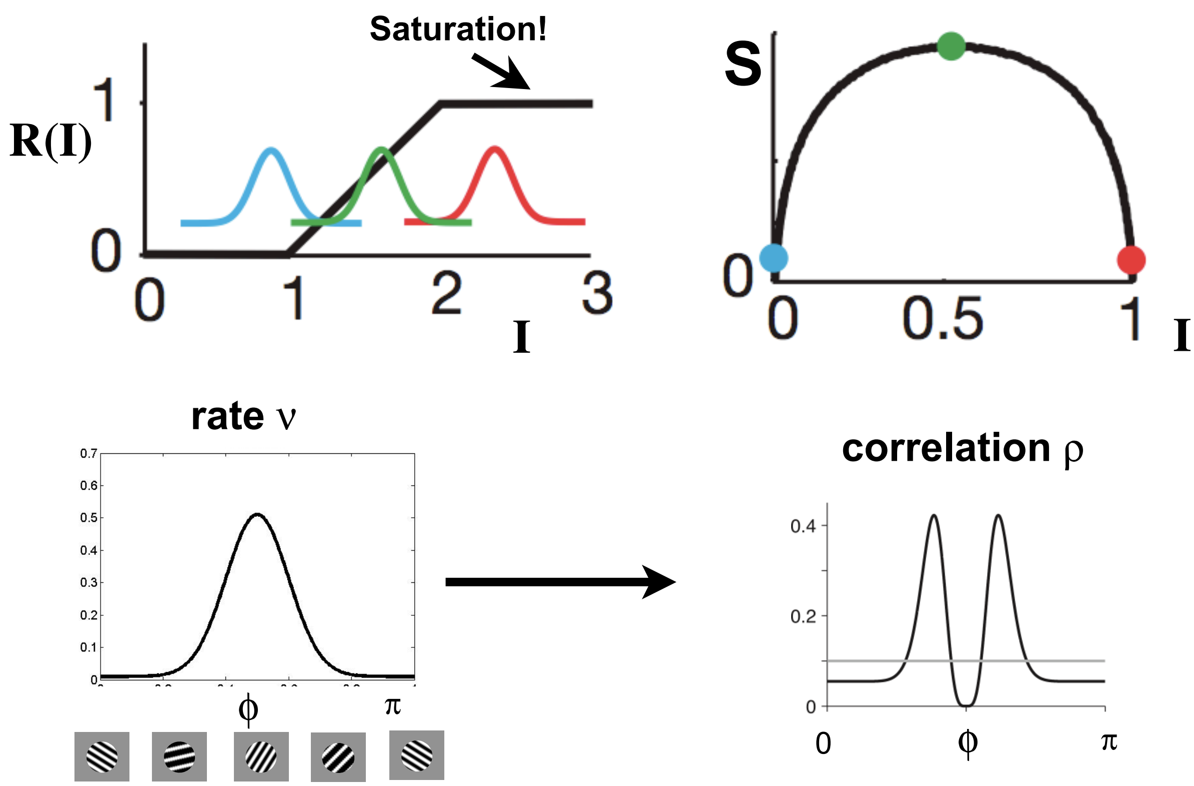


Pooling amplifies input correlations!

Renart, de la Rocha, Science '10;
Rosenbaum et al, Frontiers '10

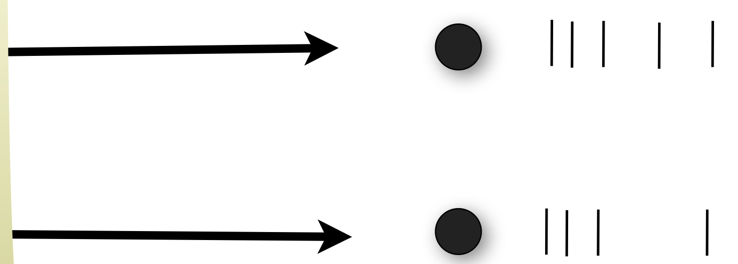
Fraction p of EPSPs is *common*, *+ correlated w/ r_{in}* ⇒ Input Currents, correlation c ⇒ SPIKES, correlation ρ

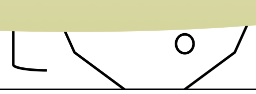
$$c = \frac{cov(\Sigma)}{var(\Sigma)}$$

$$c \gtrsim \frac{r_{in}N(N-1)}{N + r_{in}N(N-1)} \rightarrow 1$$

Denom in formula comes from # of correlated pairs ... UNDEREST correlation if ignore p

Numer is variance: variances sum plus cross terms, p makes not diff here ...



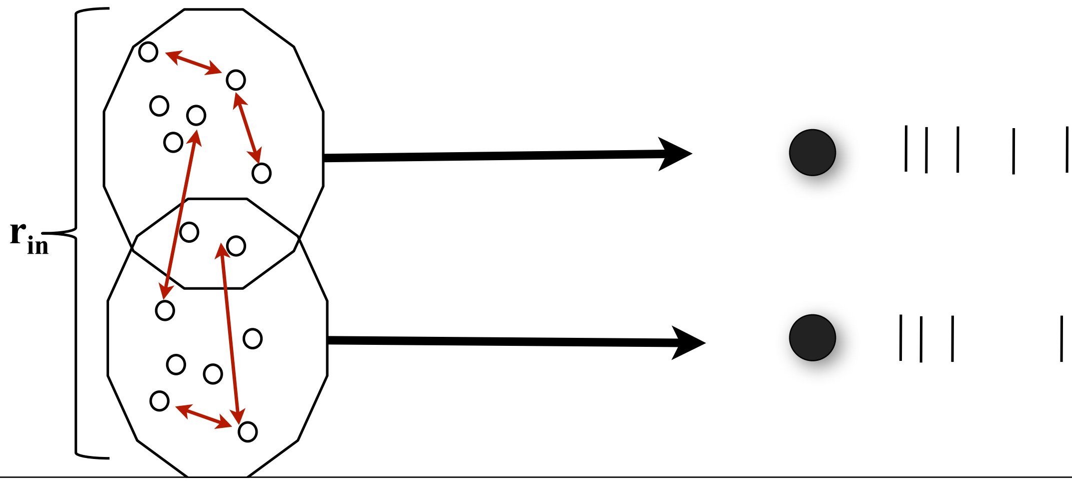


Recurrent connections: story gets surprising fast ...

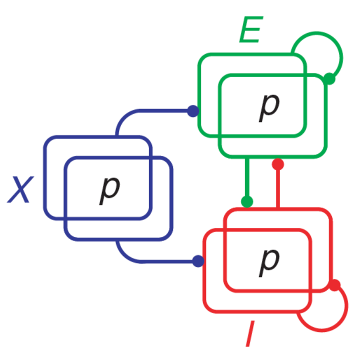
e.g.

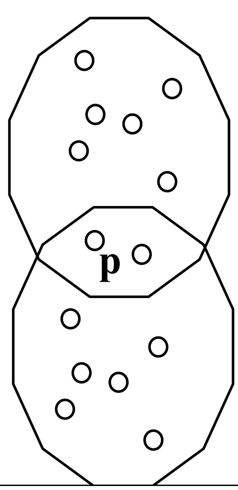
The Asynchronous State in Cortical Circuits

Alfonso Renart,[1*‡] Jaime de la Rocha,[1,2*] Peter Bartho,[1,3] Liad Hollender,[1] Néstor Parga,[4] Alex Reyes,[2] Kenneth D. Harris[1,5†]



Suggests big network → big correlations?





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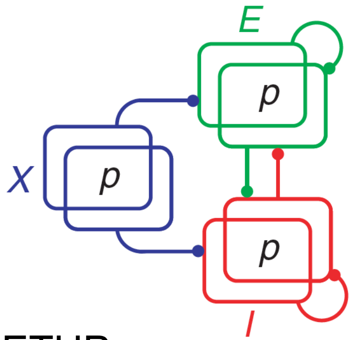
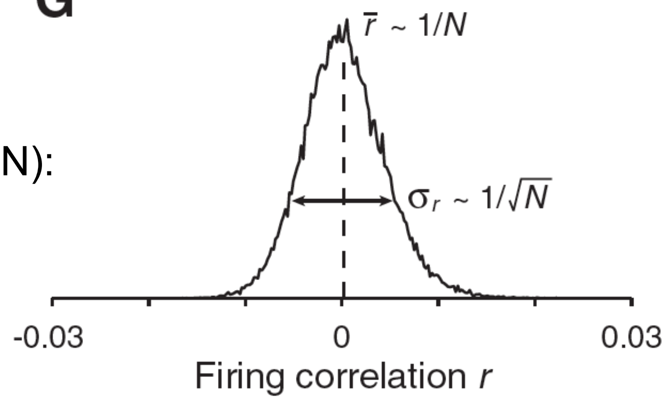
Renart, de la Rocha, Science '10



Main result: no.
Big network → <u>small correlations</u>

G



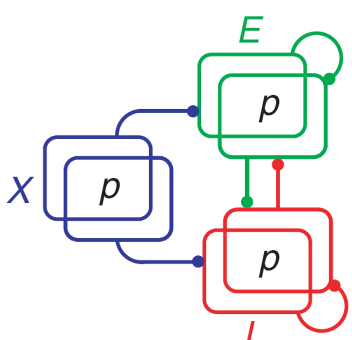
SETUP:
N cells / pop.
Connection proba p=0.2:
DENSE
Connection strength ~1/sqrt(N):
STRONG

Mechanism: cancellation

$$c = c_{EE} + c_{II} + 2c_{EI}$$

Suggests big network → big correlations?

Renart, de la Rocha, Science '10



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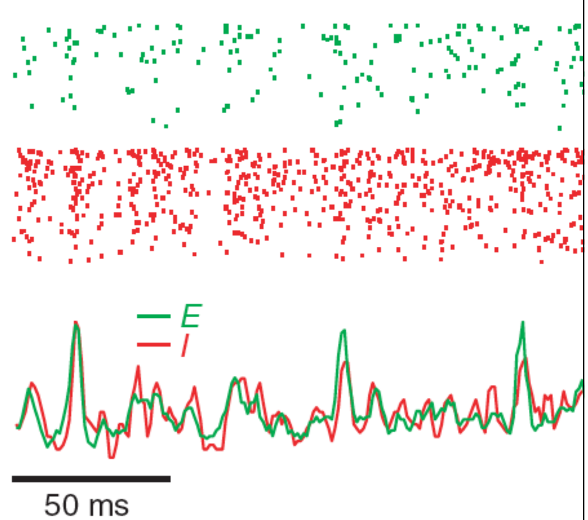

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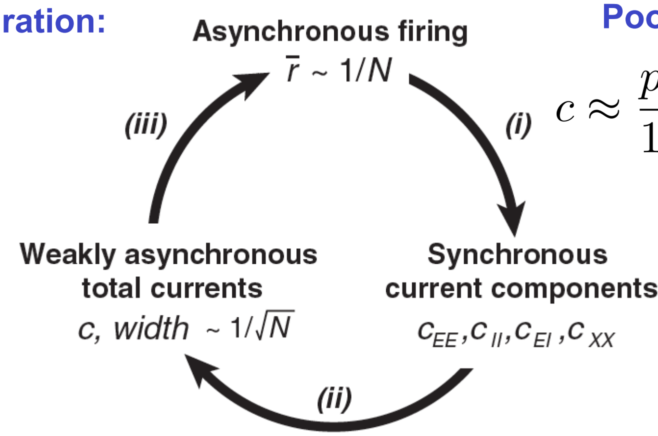
Suggests big network → big correlations?

Renart, de la Rocha, Science '10

Time-integration:

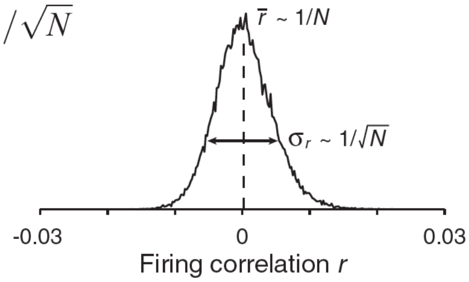


Pooling:

$$c \approx \frac{p + r_{in}(N-p)}{1 + r_{in}(N-1)} \approx 1$$

Cancellation:

$$c = c_{EE} + c_{II} + 2c_{EI} \sim 1/\sqrt{N}$$



Mechanism: cancellation

$$c = c_{EE} + c_{II} + 2c_{EI}$$

OUTLINE

CONSEQUENCES OF CORRELATED SPIKING

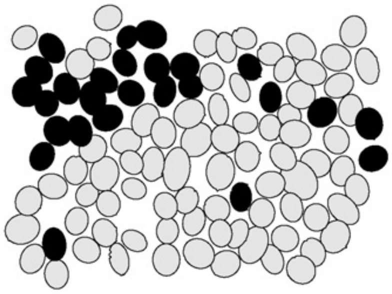
- **Impact on coding**
- **Impact on signal propagation**

BASIC MECHANISMS FOR CORRELATED SPIKING

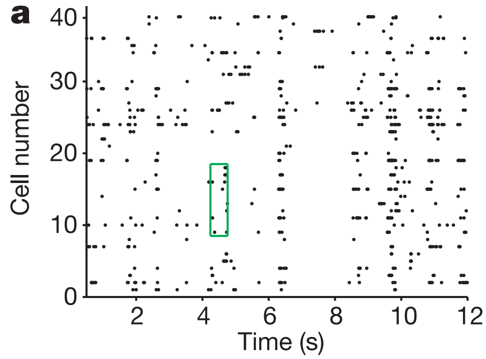
- **Common input → rate-dependent correlations**
- **Pooling over correlated population → amplification of correlations**
- **Recurrent balanced networks → cancellation of correlations**

BEYOND CELL-PAIRS: HIGHER-ORDER CORRELATIONS

Population-wide spiking dynamics



Graphic:
Shlens, Rieke and Chichilnisky, 2008



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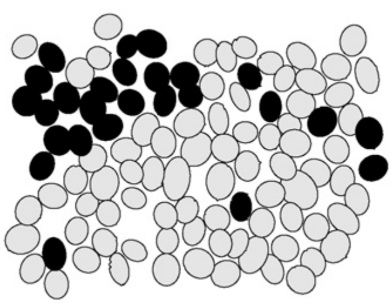
Schneidman et al. 2006

Population-wide spiking dynamics



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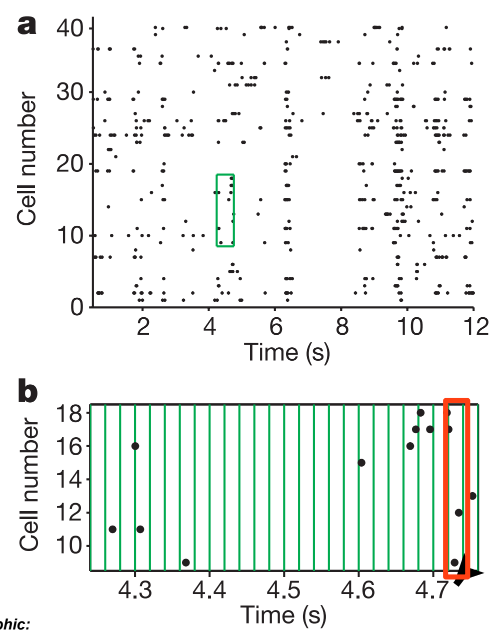

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1001000010

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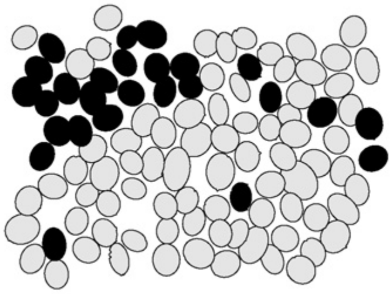

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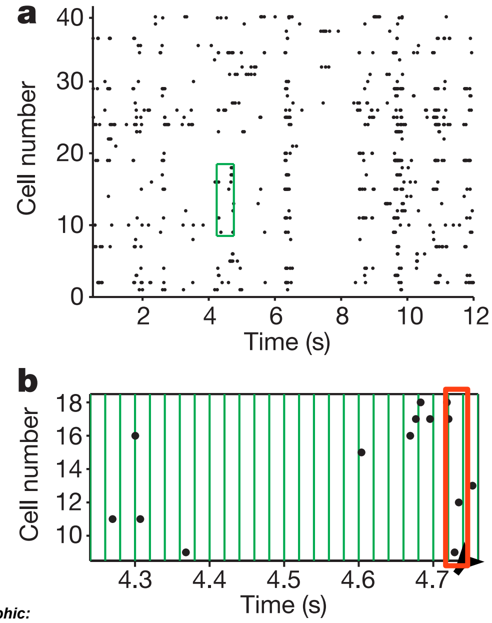
$$x_j = \{0,1\}$$

$$P(x_1, x_2, \cdots, x_N)$$



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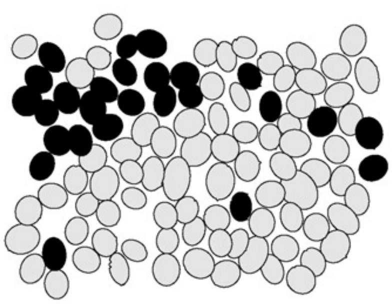
Population-wide spiking dynamics



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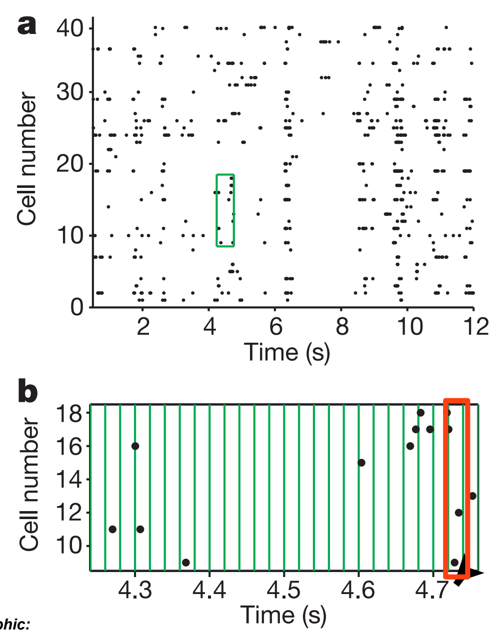

Graphic:
Schneidman et al. 2006

1001000010

Log-linear probability distribution

[Martignon et al, ’95; Amari et al, ’01; Schneidman et al, ’06, Shlens et al, ’06, ’09, ...]

$$x_j = \{0,1\}$$

$$P(x_1, x_2, \cdots, x_N) = \frac{1}{Z}\exp\left(\sum_i \lambda_i x_i + \sum_{i,j} \lambda_{ij} x_i x_j + \sum_{i,j,k} \lambda_{ijk} x_i x_j x_k + \ldots\right)$$

2^N parameters (one for each state) → complete description

N=100 → 10^30 parameters / impossibly complex

Maximum entropy approach:

Choose observables. $f_n(x_1, x_2, \cdots, x_N)$.

Measure their averages: $\langle f_n \rangle$.

max:

$$H(P) = -\sum_{\{\vec{x} \in S\}} P(\vec{x}) \log P(\vec{x})$$

Fit λ parameters so $\langle f_n \rangle$ hold but mimimal further assumptions.

Get $P(x_1, x_2, \cdots, x_N) = \frac{1}{Z}\exp\left(\sum_n \lambda_n f_n(x_1, x_2, \cdots, x_N)\right)$

Maximum entropy approach:

[Jaynes et al, ’57; Shlens et al, ’06, ’09, Schneidman et al, ’06, ...]

Choose observables. $f_n(x_1, x_2, \cdots, x_N)$.

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Get $P(x_1, x_2, \cdots, x_N) = \frac{1}{Z}\exp\left(\sum_n \lambda_n f_n(x_1, x_2, \cdots, x_N)\right)$

Choose $\{f_n(x_1, x_2, \cdots, x_N)\} = \{x_1, x_2, \cdots, x_1 x_2, \cdots\}$.

Measure means + second-order moments $\langle x_1 \rangle, \cdots, \langle x_1 x_2 \rangle, \cdots$.

Get $P(x_1, x_2, \cdots, x_N) = \frac{1}{Z}\exp\left(\sum_i \lambda_i x_i + \sum_{i,j} \lambda_{ij} x_i x_j\right)$

PAIRWISE MAXIMUM-ENTROPY MODEL P_2
Minimal-assumptions model that fits means + pairwise correlations
If accurate, declare: no “extra” beyond-pairwise correlations

“Accurate” means small Kullback-Leibler distance from true distribution P

$$D_{KL}(P,P_2) \equiv \sum_{\{\vec{x}\in S\}} P(\vec{x}) \log\left(\frac{P(\vec{x})}{P_2(\vec{x})}\right)$$
$$= H(P_2) - H(P)$$

Choose $\{f_n(x_1,x_2,\cdots,x_N)\} = \{x_1,x_2,\cdots,x_1x_2,\cdots\}$.

Measure means + second-order moments $\langle x_1\rangle,\cdots,\langle x_1x_2\rangle,\cdots$.

Get $P_2(x_1,x_2,\cdots,x_N) = \frac{1}{Z}\exp\left(\sum_i \lambda_i x_i + \sum_{i,j}\lambda_{ij}x_i x_j\right)$

PAIRWISE MAXIMUM-ENTROPY MODEL P_2
Minimal-assumptions model that fits means + pairwise correlations
If accurate, declare: no “extra” beyond-pairwise correlations

SUMMARY

CONSEQUENCES OF CORRELATED SPIKING

Impact on coding

(a) Homogeneous populations: limits population averaging / degrades info

(b) Heterogeneous cell pairs ...

similar stimulus tuning: DEGRADE CODING

different stimulus tuning: ENHANCE CODING

(c) Heterogeneous populations: competing effects

Impact on signal propagation

Correlation sets *gain*: Downstream rate ~ upstream rate X upstream correlation

Review: Averbeck et al, Nature Rev. Nsci. ’06

BASIC MECHANISMS FOR CORRELATED SPIKING

Common input → rate-dependent correlations

Pooling over correlated population → amplification of correlations

Recurrent balanced networks → cancellation of correlations

BEYOND CELL-PAIRS: HIGHER-ORDER CORRELATIONS

Maximum-entropy methods measure via log-linear model

Mixed results for presence and impact on coding