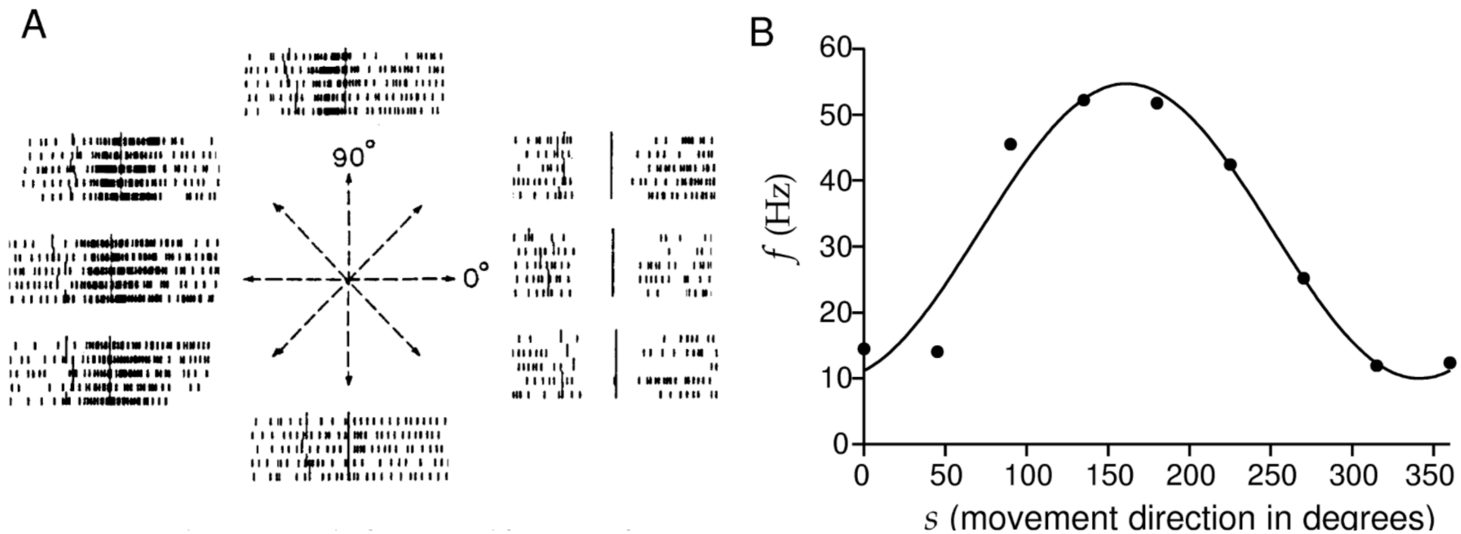
Correlations and coding in neural populations

Eric Shea-Brown
U. Washington

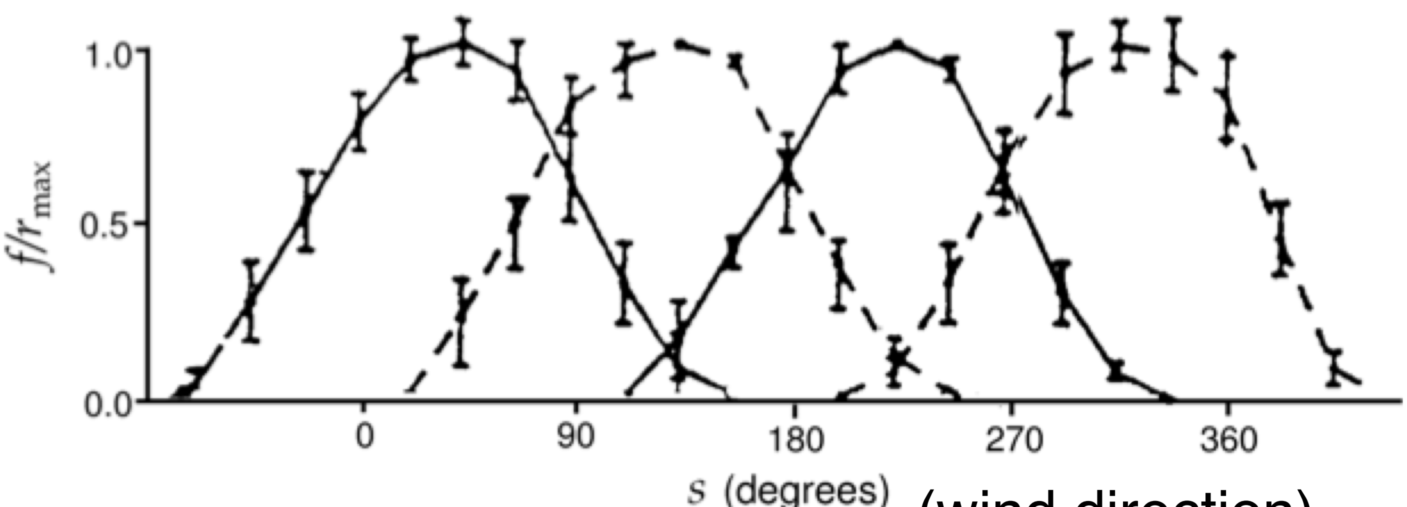
Neural firing rates are tuned with sensory and/or motor variables

Adrian, 1928 … Neural basis of sensation

Georgopoulis et al ’82
(Motor cortex)
[Fig: Abbott+Dayan ’99]



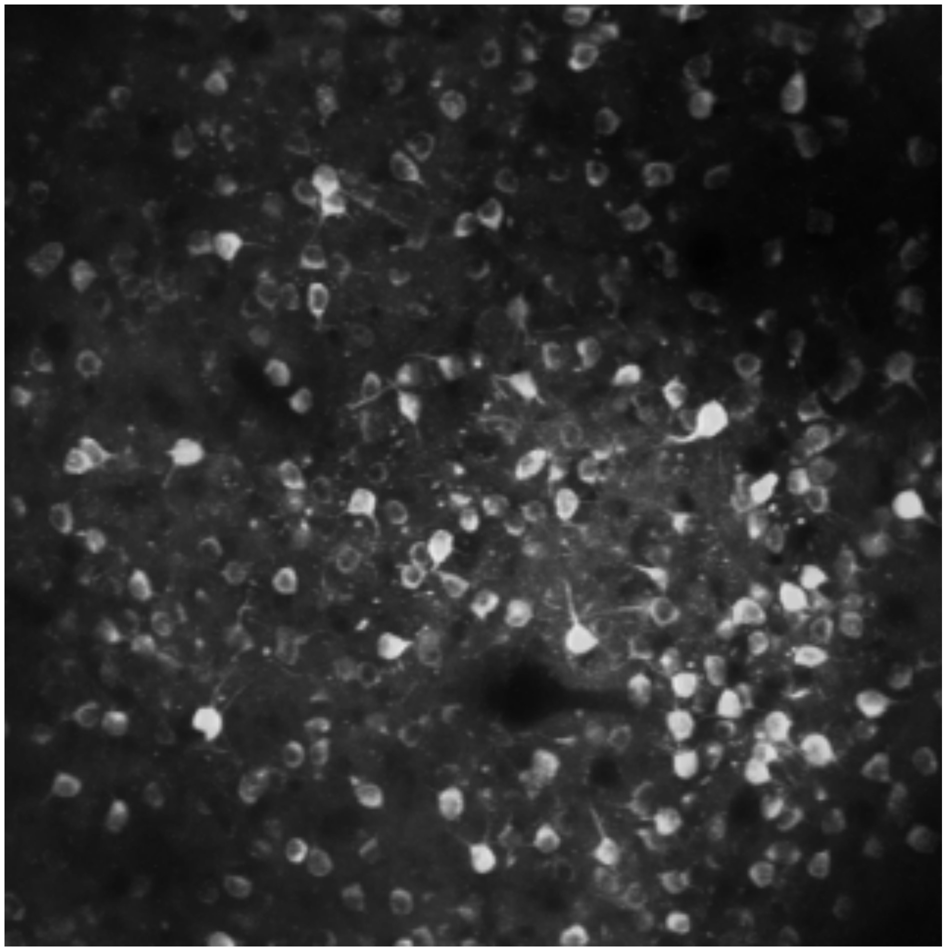
Theunissen and Miller, 1991
(Cricket circal ganglion)



(wind direction)

Today — Glorious mess: Heterogeneous, variable, simultaneous responses of large neural populations

2P data



Allen Brain Observatory

Population codes are cool and complex …

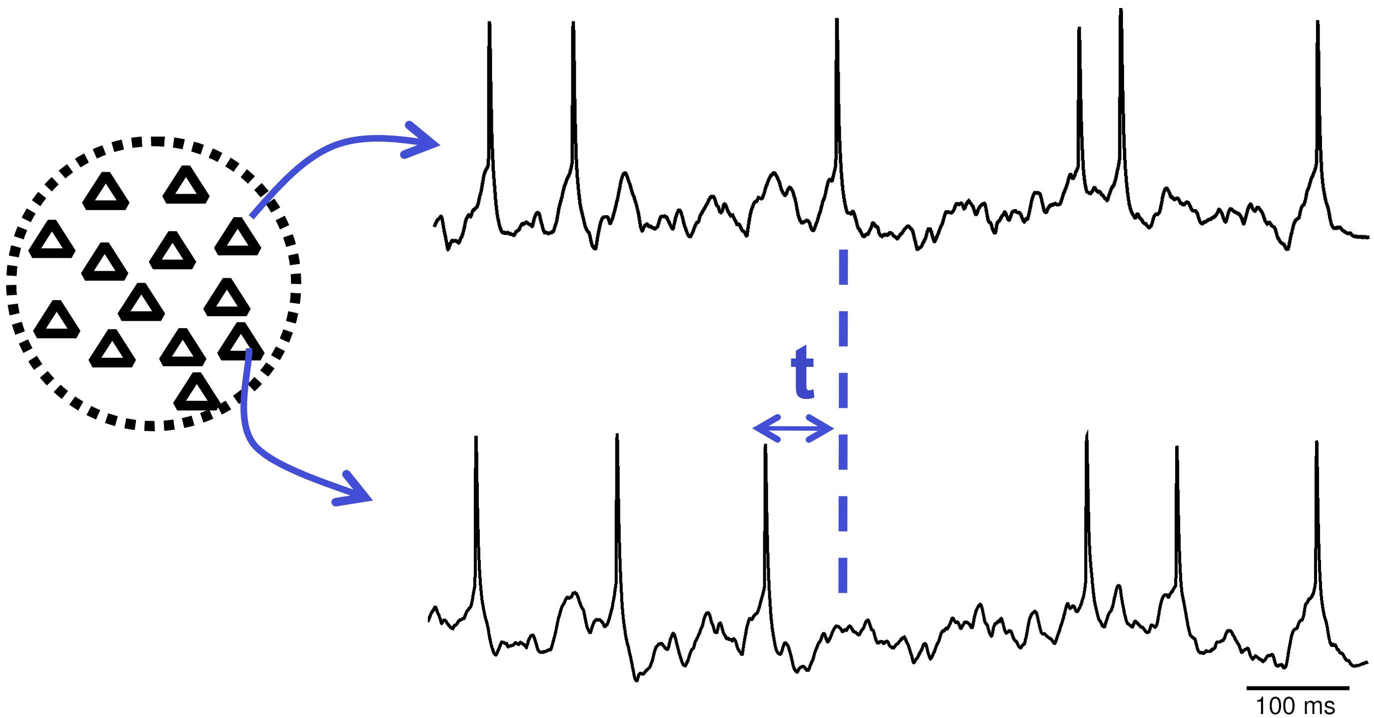
and pose rich conceptual and theoretical questions

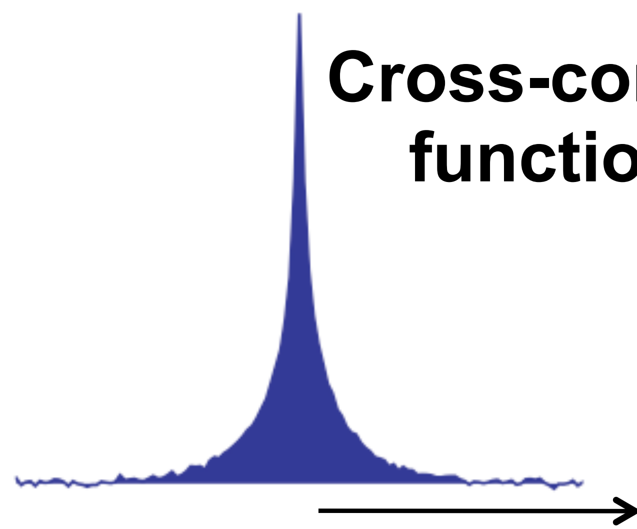
(1) Efficient encoding and decoding:

optimal tuning curves and receptive fields

(2) Collective (or *correlated*) neural activity:
What does it add (or subtract) from population codes defined by tuning of individual cells?

What do we mean by correlation?





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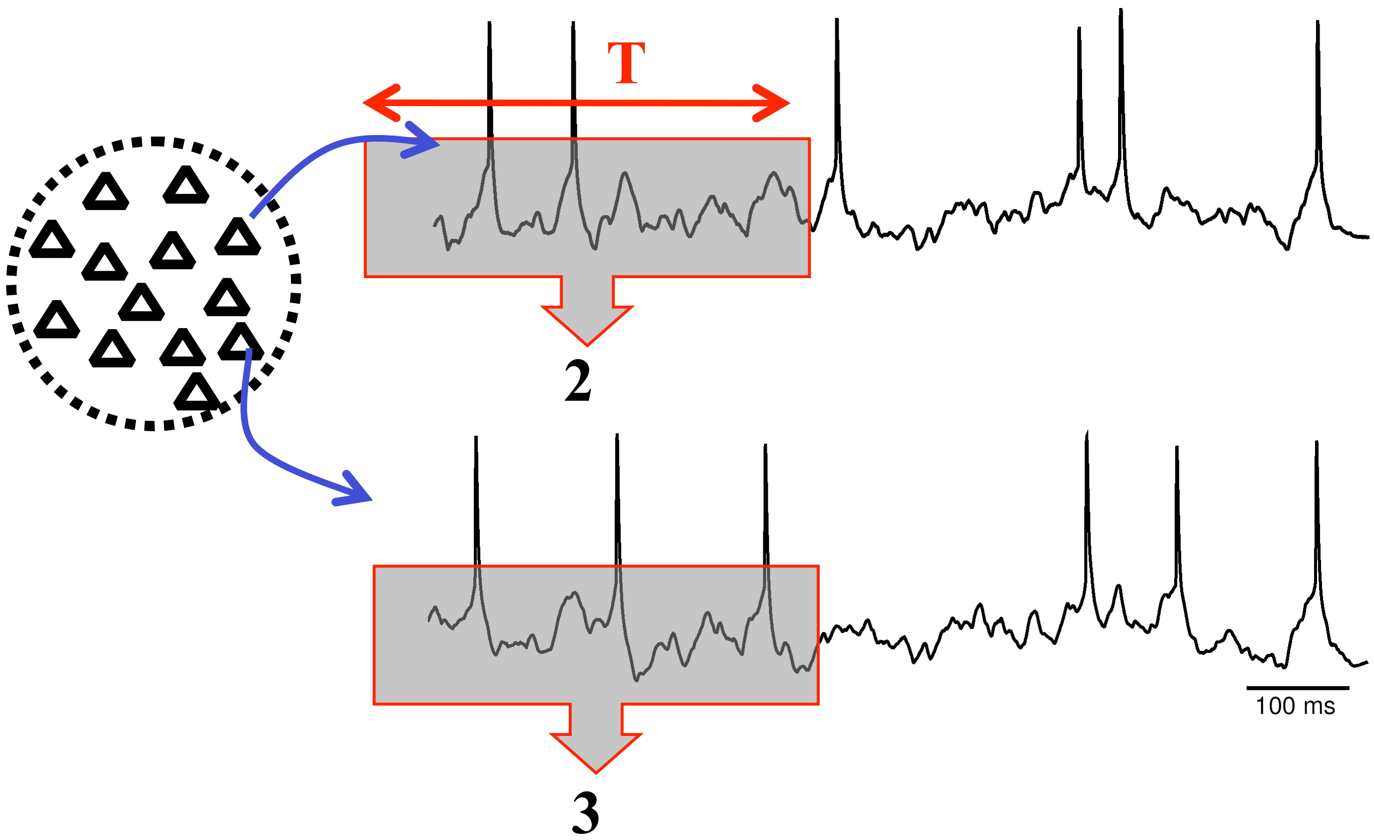

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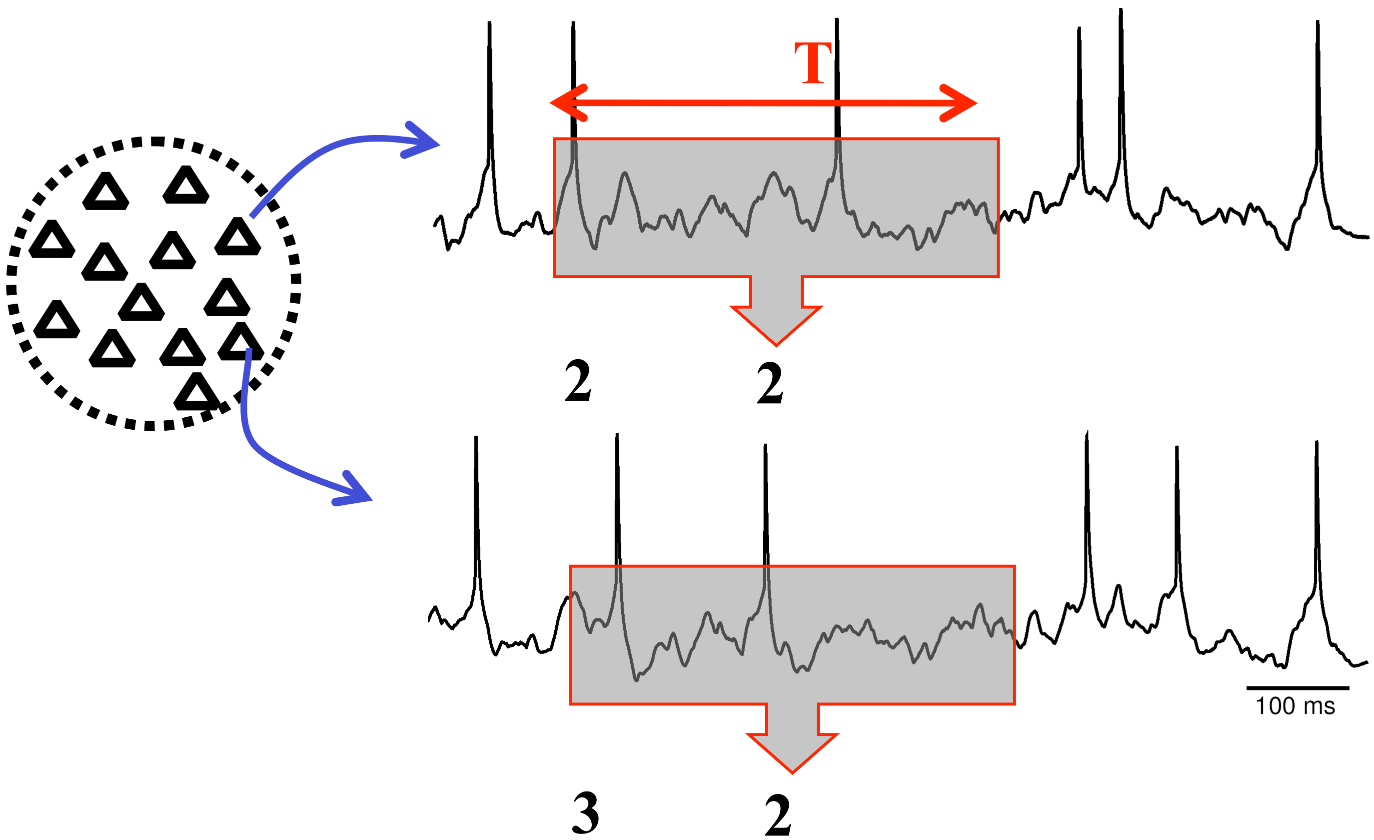

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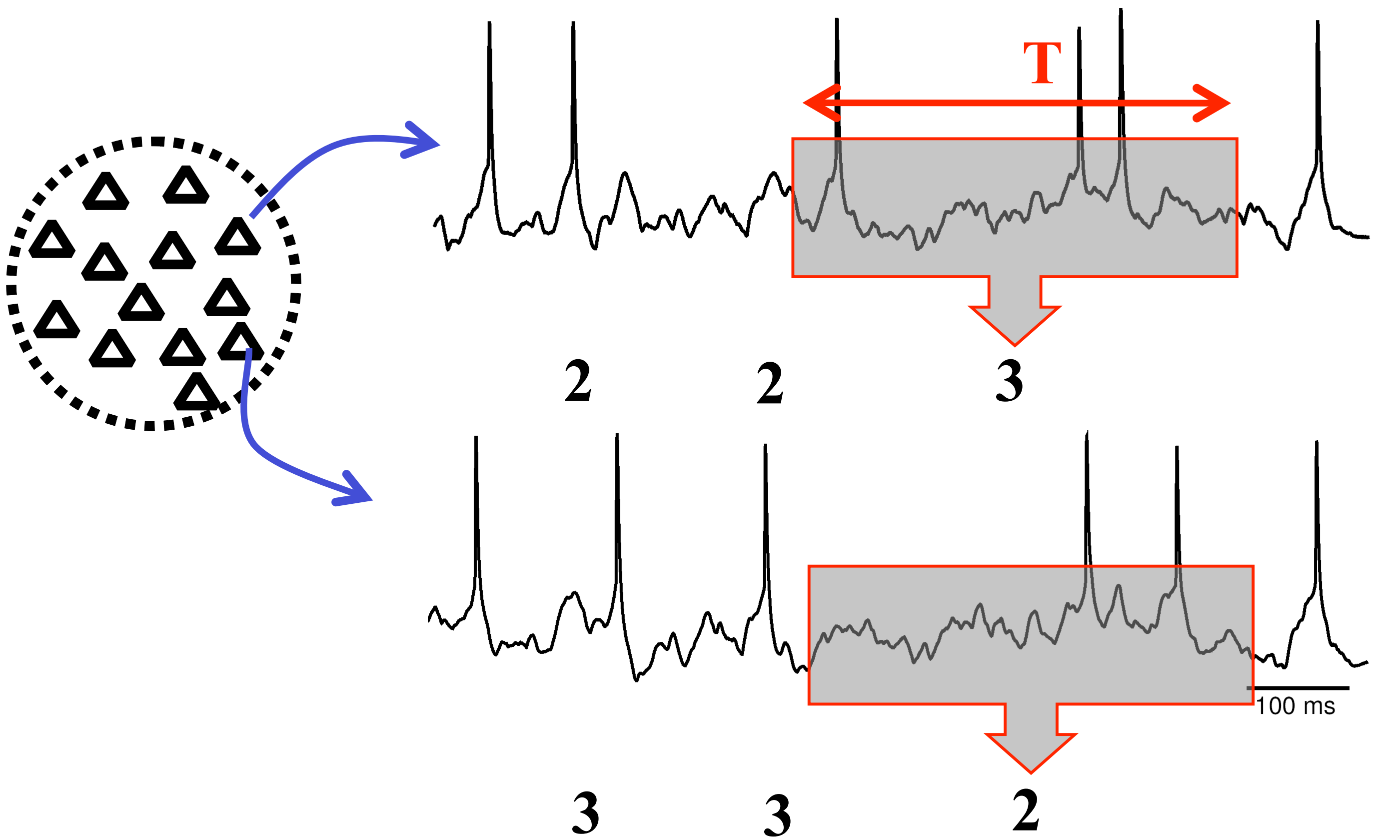

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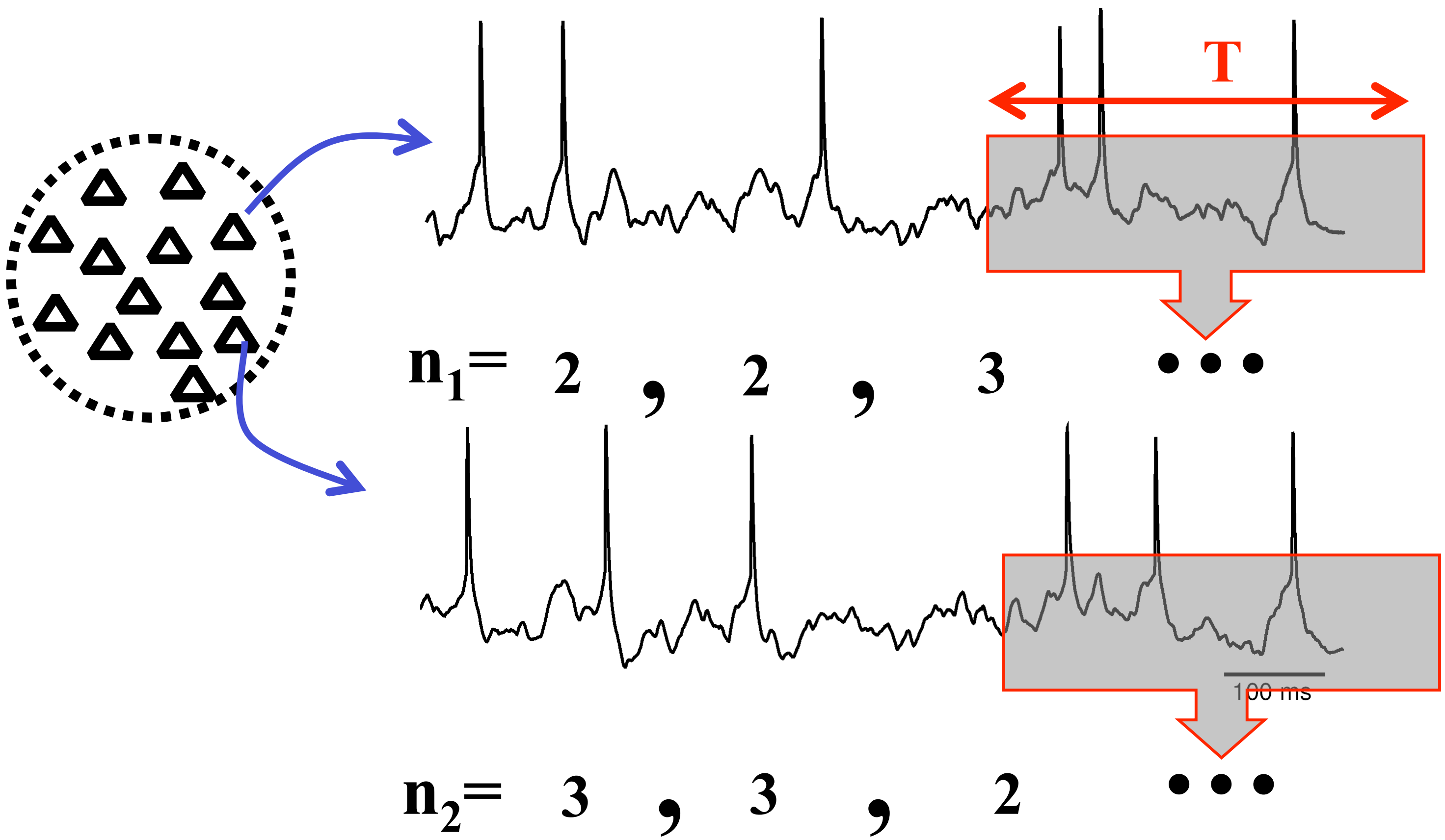
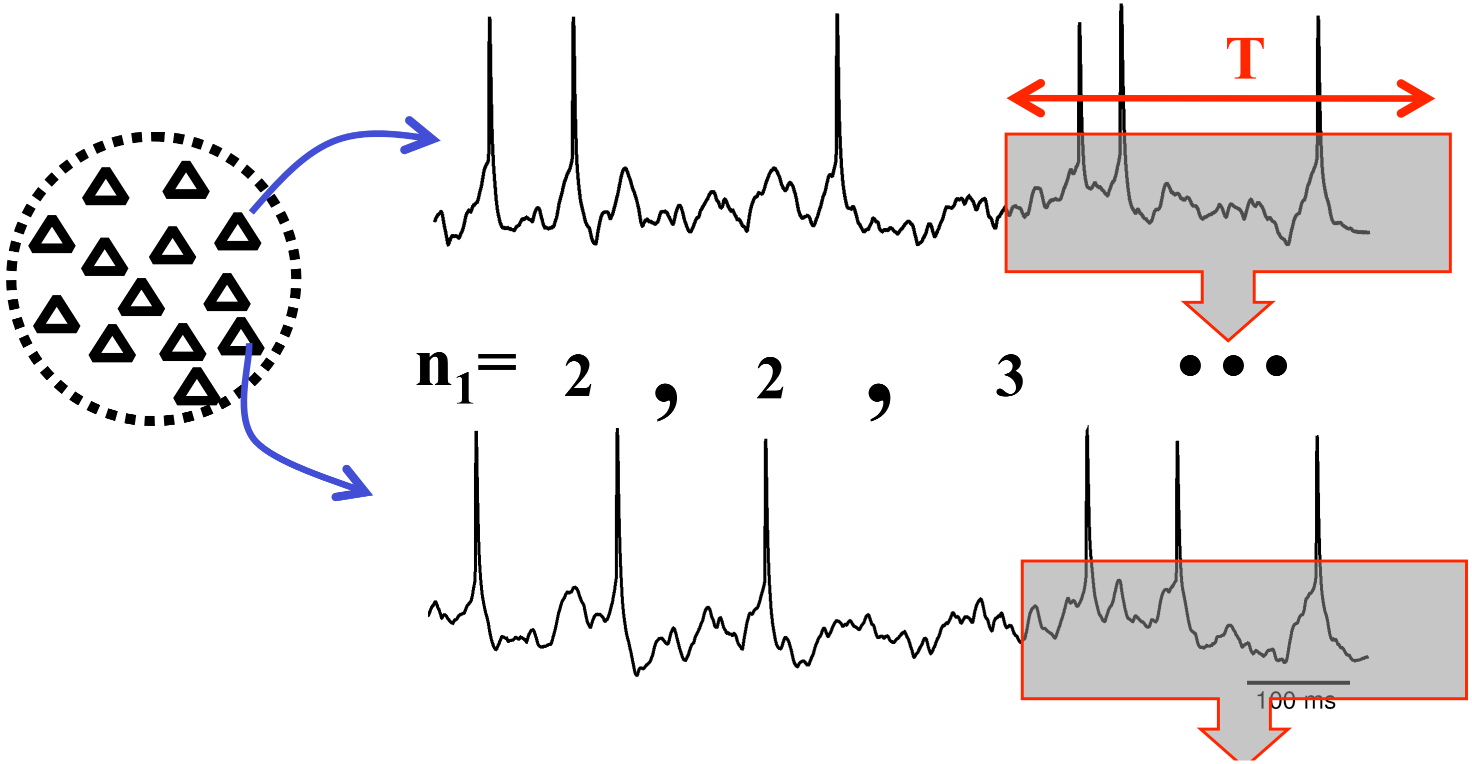


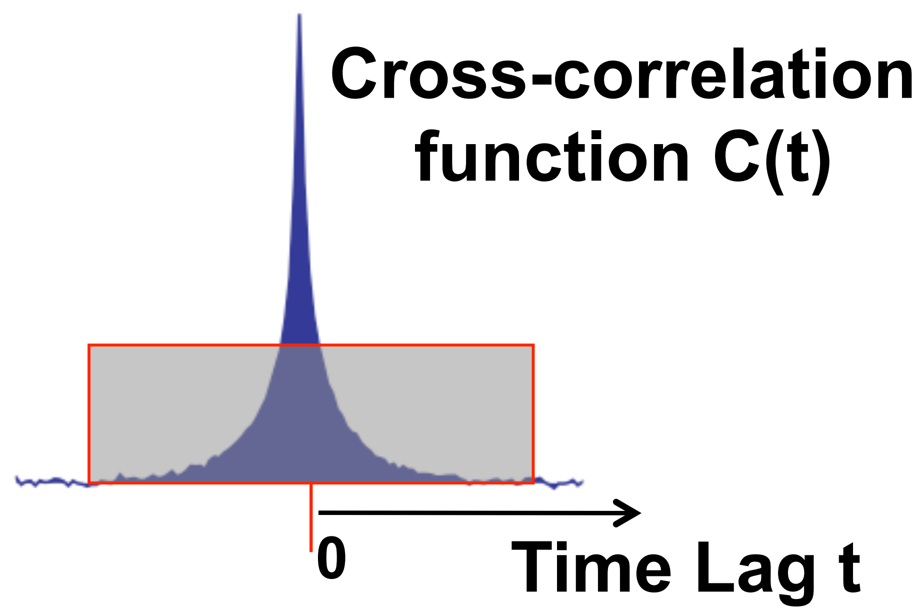
$$\rho_T = \frac{Cov(n_1 n_2)}{\sqrt{Var(n_1)Var(n_2)}}$$

What do we mean by correlation?



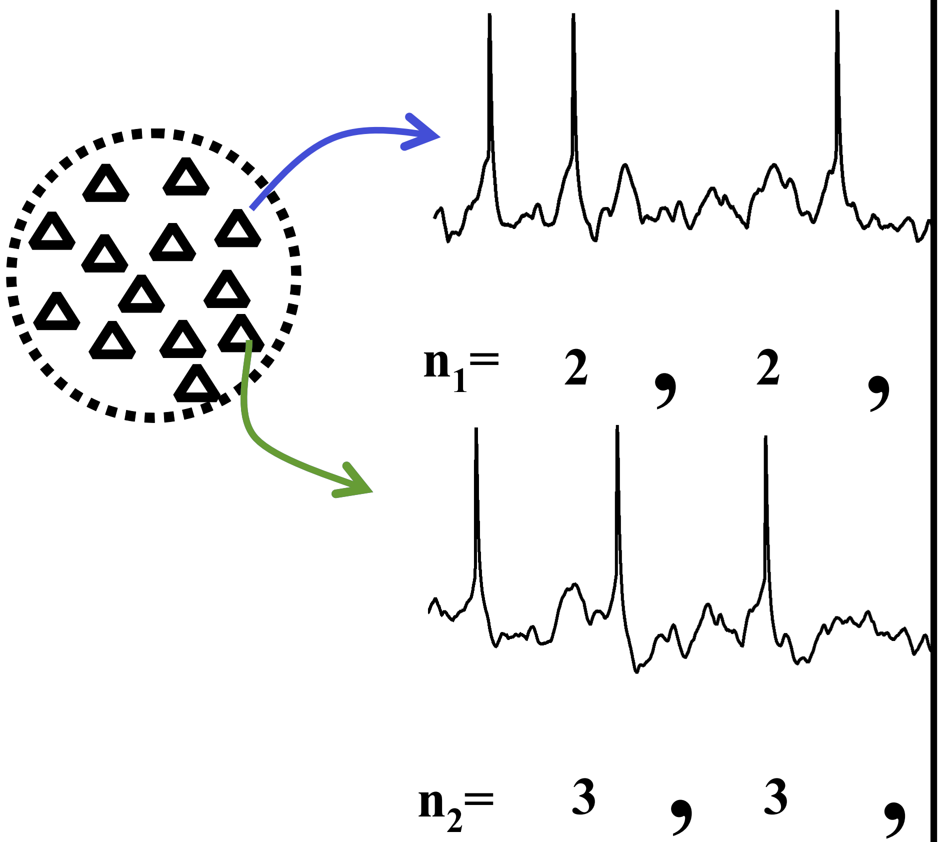
$n_1 = 2, 2, 3 \dots$

$n_2 = 3, 3,$



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

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:

- **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.*
- **Parietal Cortex:** *Lee et al 1998*
- **Somatosensory thal.:** *Bruno & Sakmann 2006*
- **A1:** *deCharms & Merzenich 1996*
- **SI:** *Romo et al 2003*. …

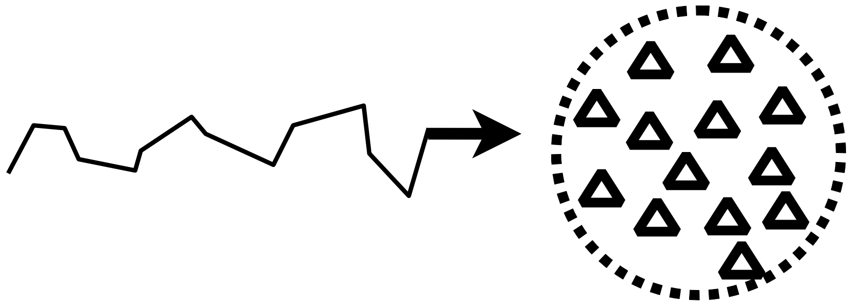
Motor cortex: *Vaadia et al 1995*

Motor neurons: *Binder and Powers 2001*

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

Common signal input→Common spike response
→ SIGNAL CORRELATIONS

$s(t)$



ADDITIONAL CORRELATIONS ARE ...
NOISE CORRELATIONS

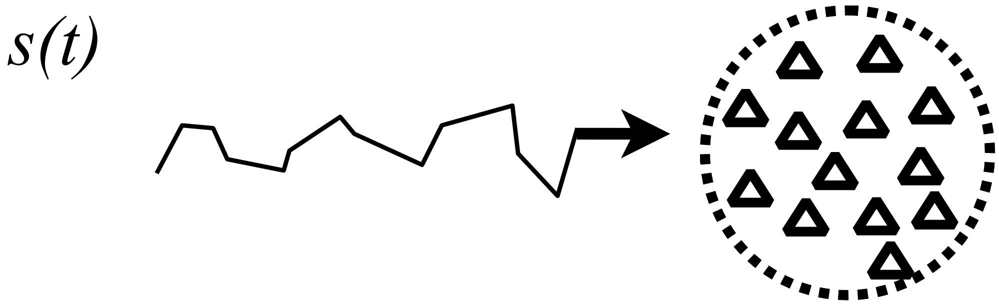
$$p(n_1, n_2|s(t)) \neq p(n_1|s(t))p(n_2|s(t))$$

These describe the population response beyond tuning "curves" of mean stimulus response.

Our focus today.

Why the NOISE correlations?

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

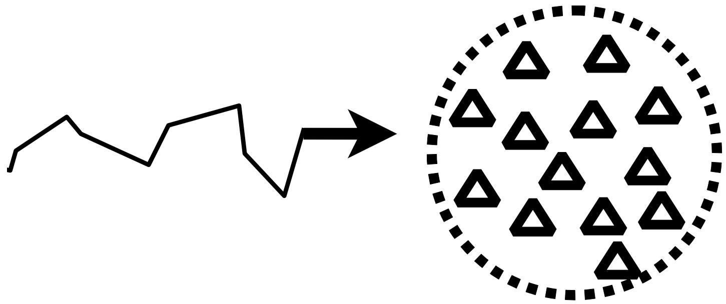


Why the NOISE correlations?

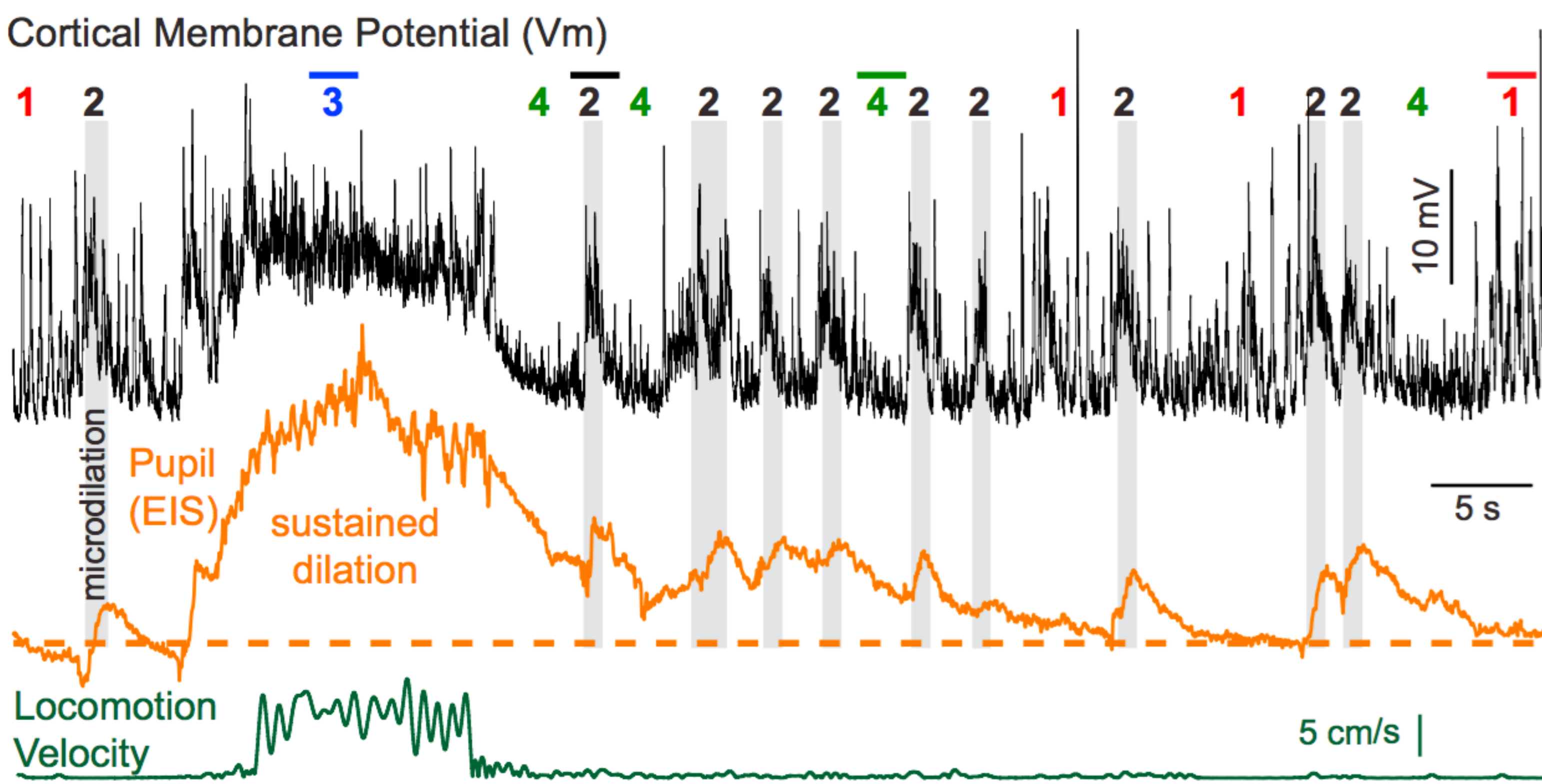
$$p(n_1, n_2 | s(t)) \neq p(n_1 | s(t)) p(n_2 | s(t))$$

s(t)

running speed(t)
pupil size(t)
vigilance(t)



More sources of common modulation!



McGinley, Vinck, Reimer, …, Tolias, Cardin, McCormick, Neuron 2015

Why the NOISE correlations?

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

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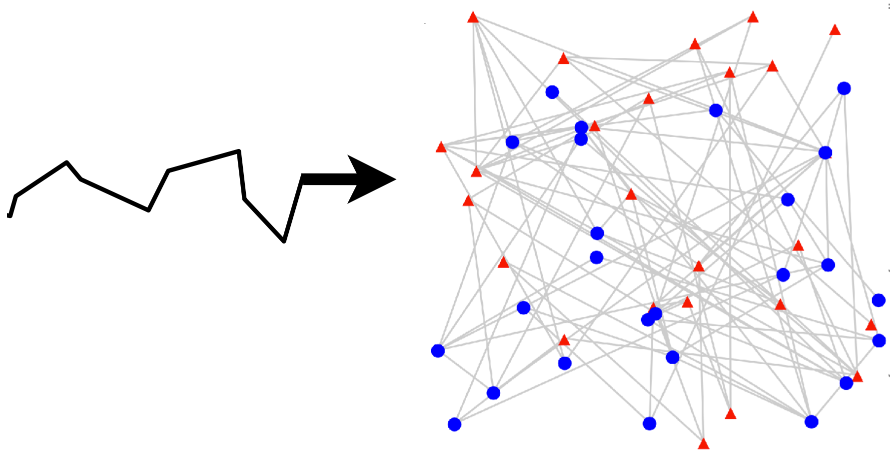


(1) Corrs from comodulation by behavioral or internal state

(2) Corrs from network interactions

These can be separated from comodulation:

(a) regress out known variable (here, running speed)

(b) regress out unknown "latent variables" [Ecker '14, Yatsenko '15]

These pose algorithmic questions:

Signatures of computation?

sparse auto encoders (Olshausen/Field, …)

spike-based predictive coding: (Deneve, cf. Rozell, …)

These pose population coding questions: Our focus today.

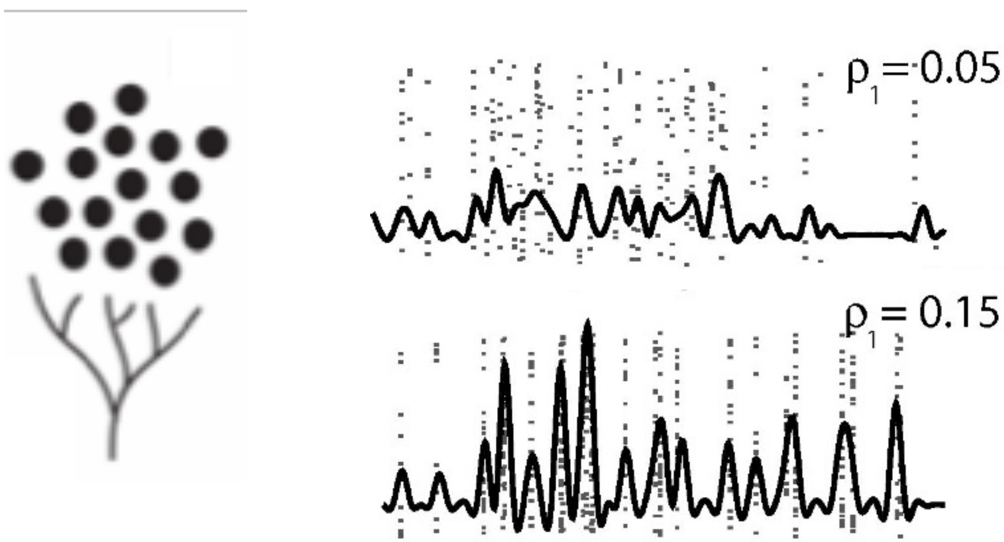
CODING IMPACT OF CORRELATED SPIKING

(a) Signal propagation

Correlated spiking modulates signal propagation

[Abeles ’92; Salinas and Sejnowski,’00; Reid et al ’01;
Bruno ’11; Jia, Tanabe, and Kohn, ’13;
but see Histed, Maunsell et al ‘14]

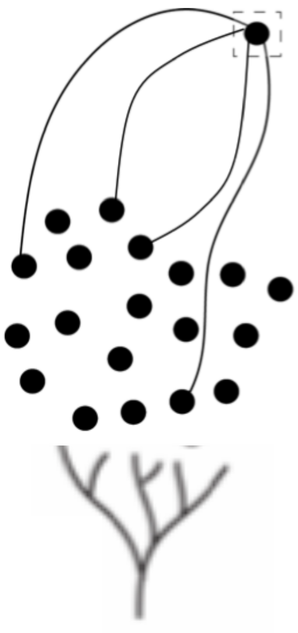
Positive correlations



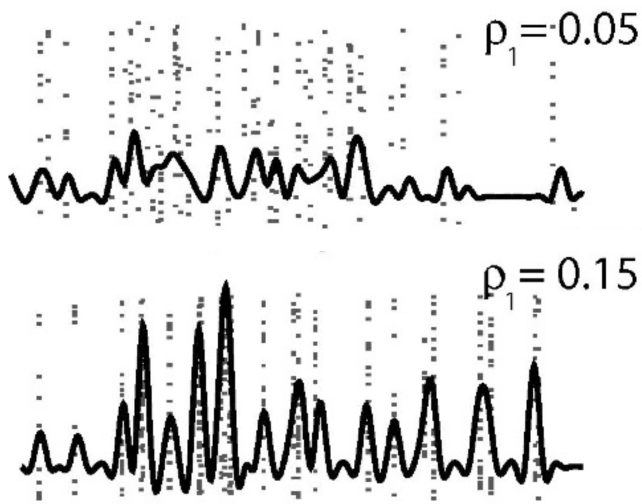
$$\text{std. dev.} \sim (\ \text{rate} \times \text{corr}\ )^{1/2}$$

Correlated spiking modulates signal propagation

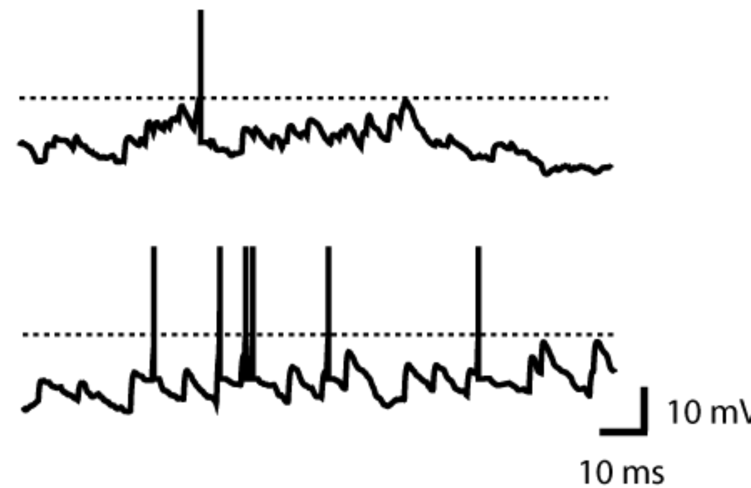
[Abeles '92; Salinas and Sejnowski,'00; Reid et al '01; Bruno '11; Jia, Tanabe, and Kohn, '13; but see Histed, Maunsell et al '14]



Positive correlations



Downstream cell;
fluctuation-driven



gain

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

rate = f (std dev)

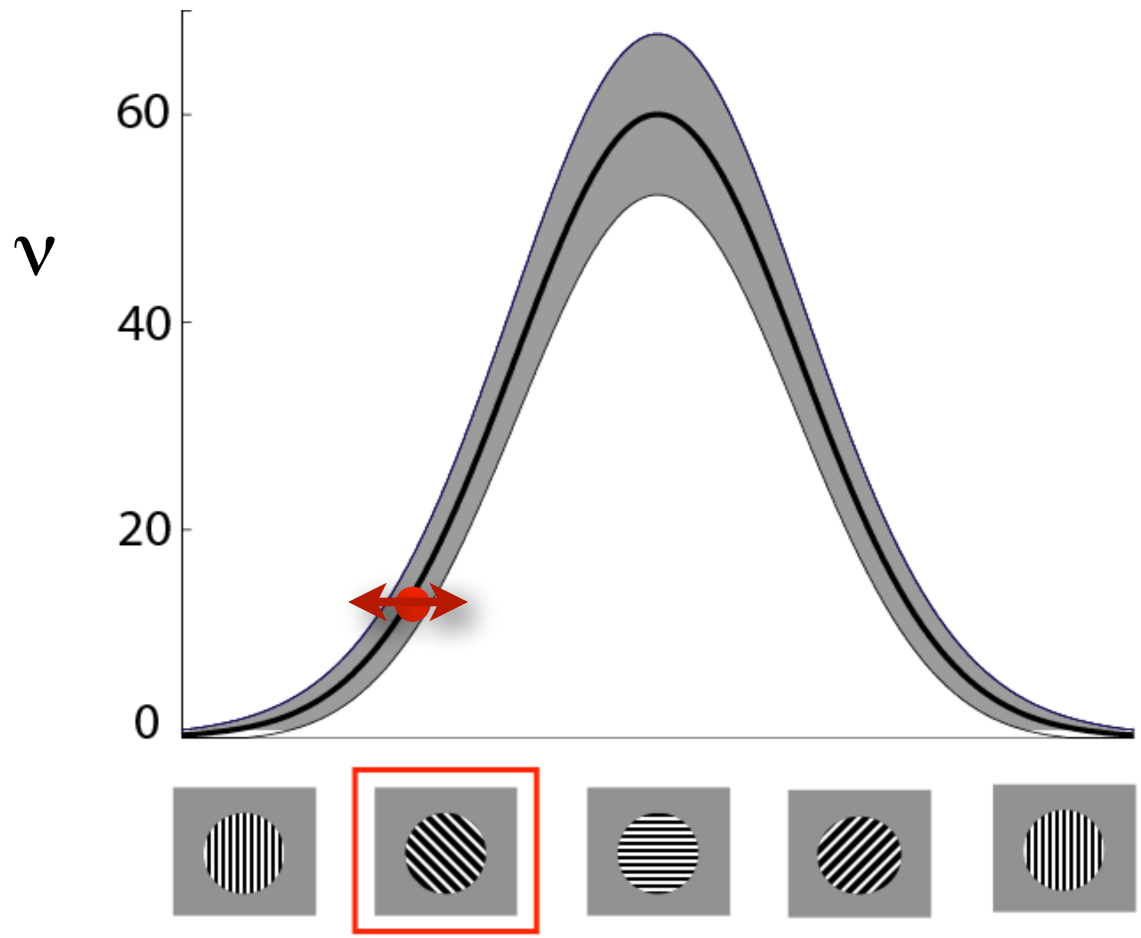
CODING IMPACT OF CORRELATED SPIKING

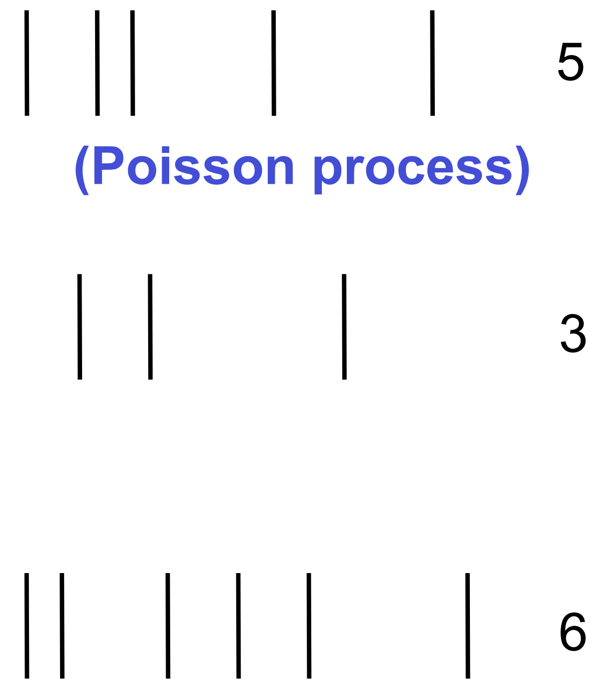
(a) Modulates signal propagation

(b) Information in homogeneous populations

Response Variability

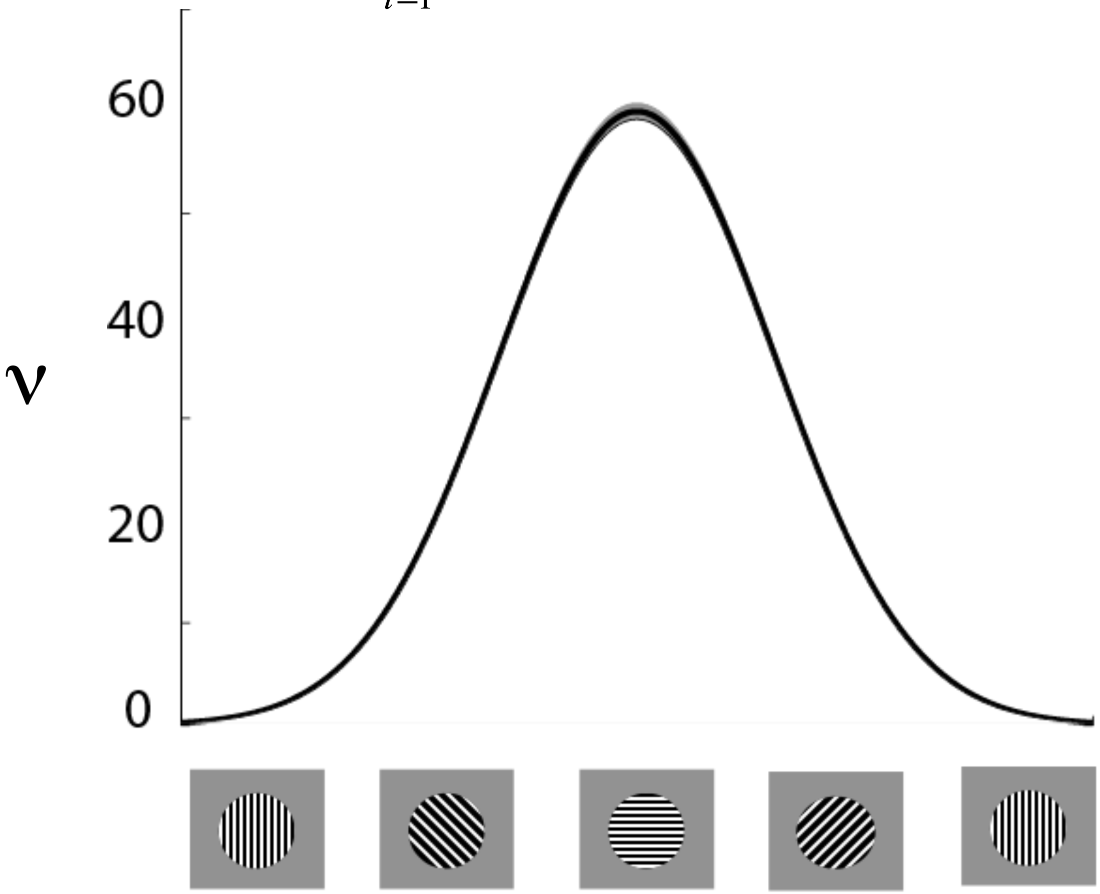
$$RATE : \nu = \frac{n}{T}$$

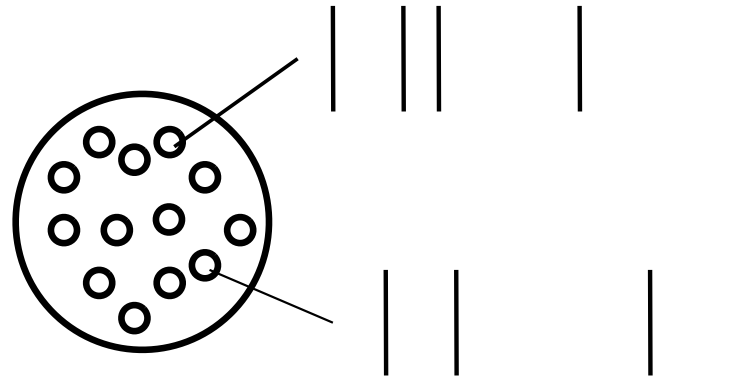




Population codes – average over *M* independent cells

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

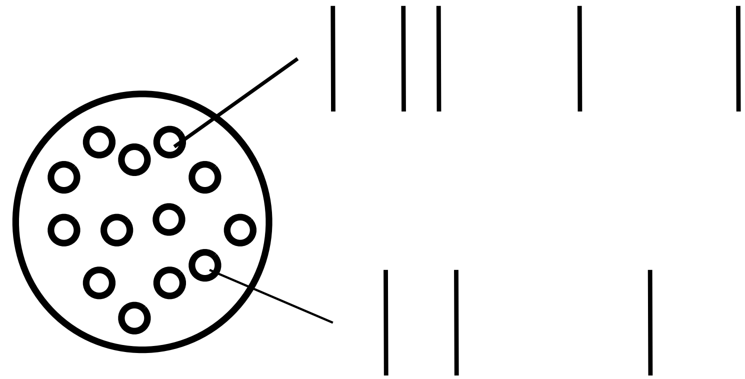




M **cells**
n_i spikes each
in time window *T*

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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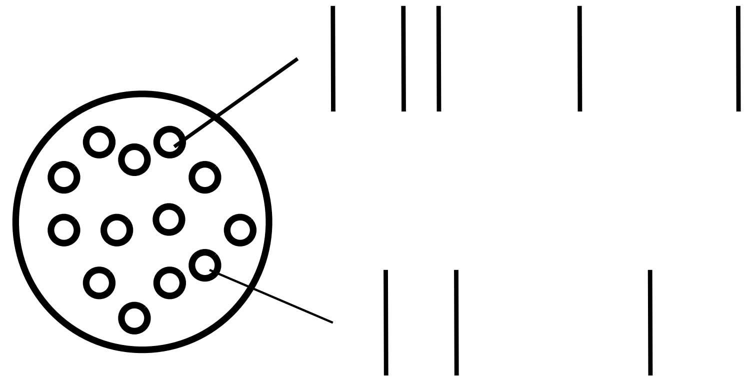

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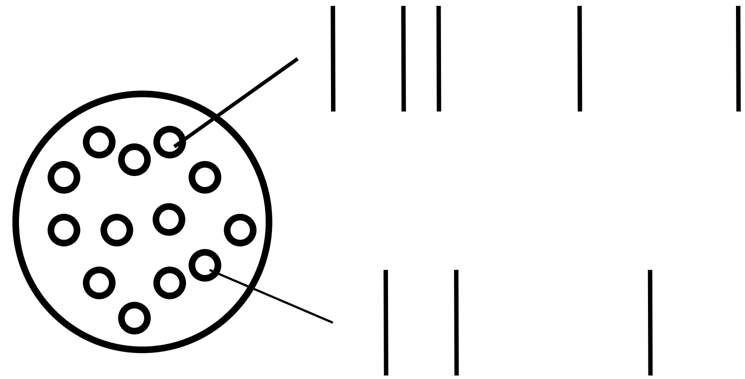
$$\boxed{\frac{\langle \nu \rangle}{var(\nu)} = SNR(\nu) \sim M}$$

Population codes – average over *M* independent cells

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



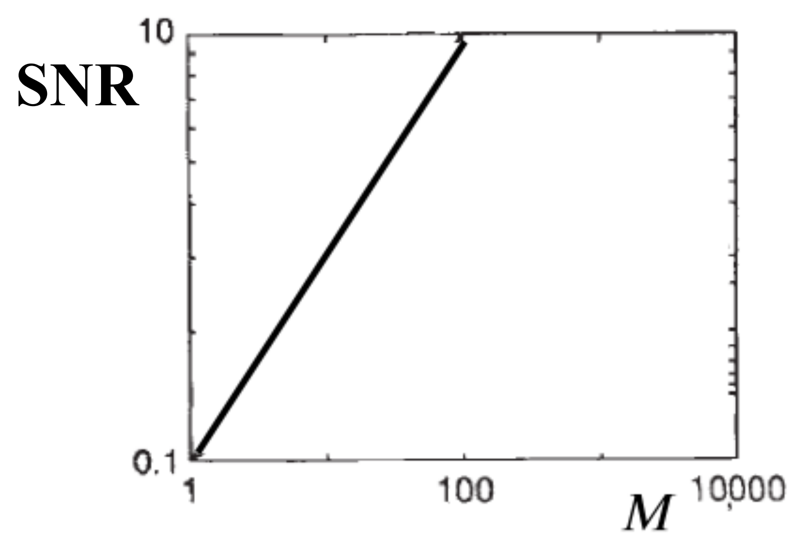
M cells
n_i spikes each
in time window *T*

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

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

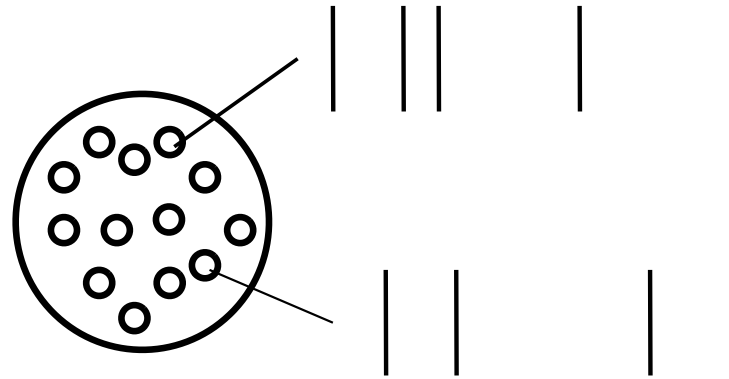
Population averaging improves SNR.

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



Population codes – average over M correlated cells

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



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

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

M **cells**

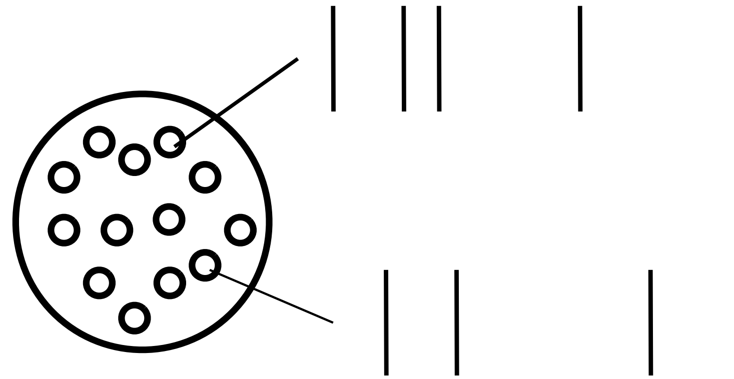
n_i spikes each

in time window *T*

n_i have correlation coefficient ρ

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

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

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

$$var(\nu) =$$

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

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

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

Population codes – average over *M* correlated cells

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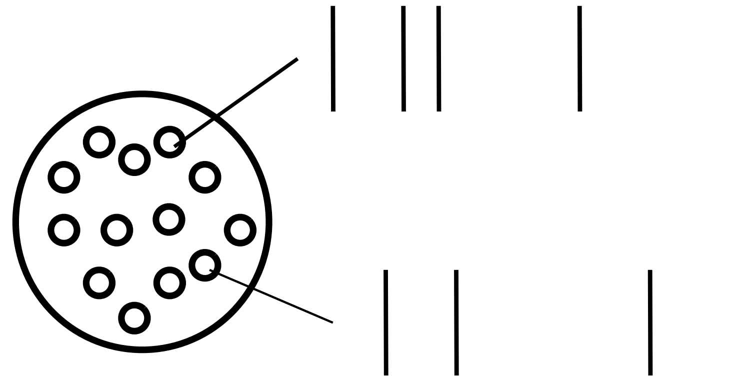

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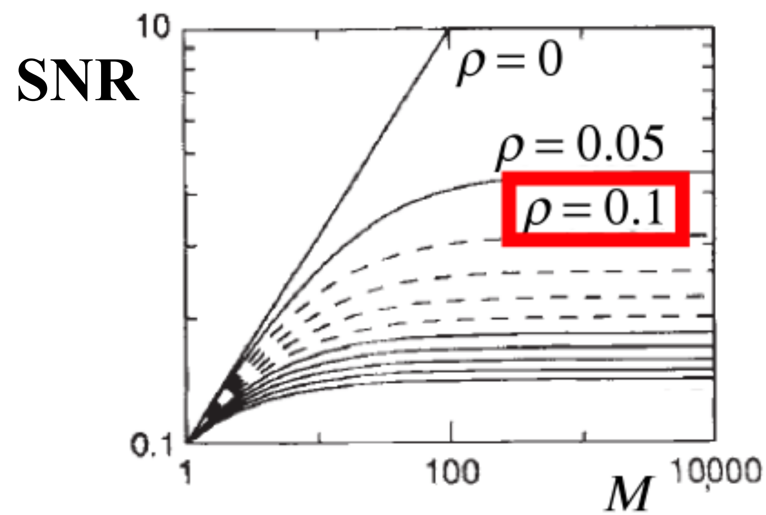
$$= \frac{1}{TM} MrT = r$$

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

Zohary, Shadlen and Newsome (1994)

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



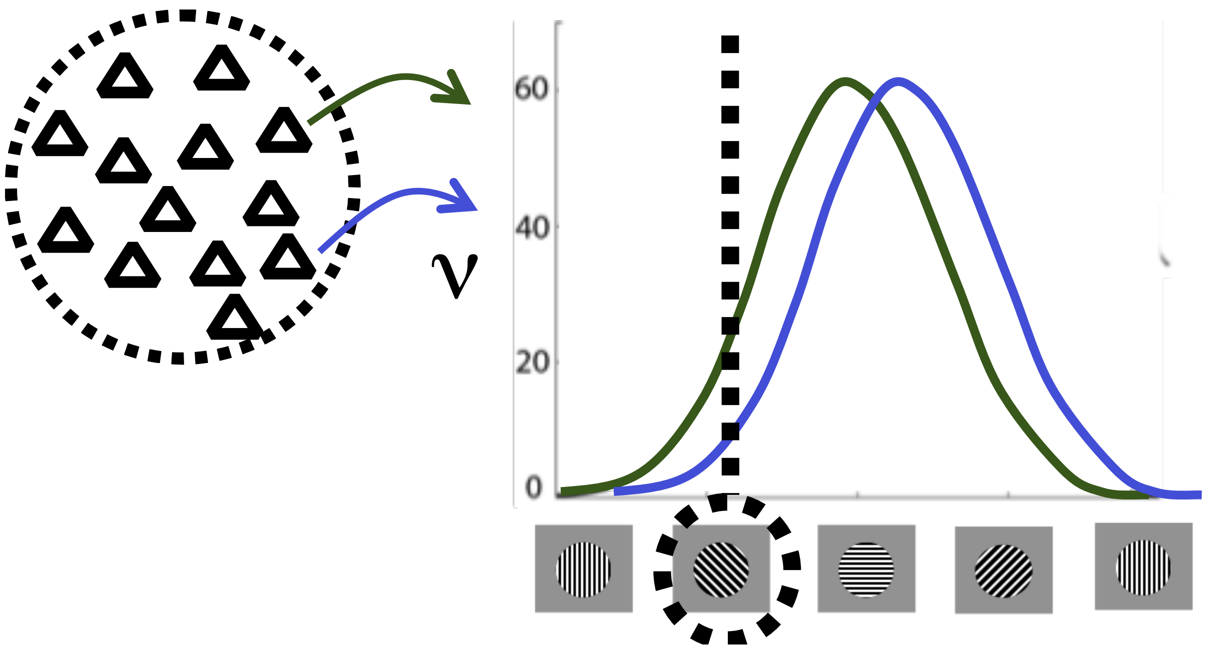
CODING IMPACT OF CORRELATED SPIKING

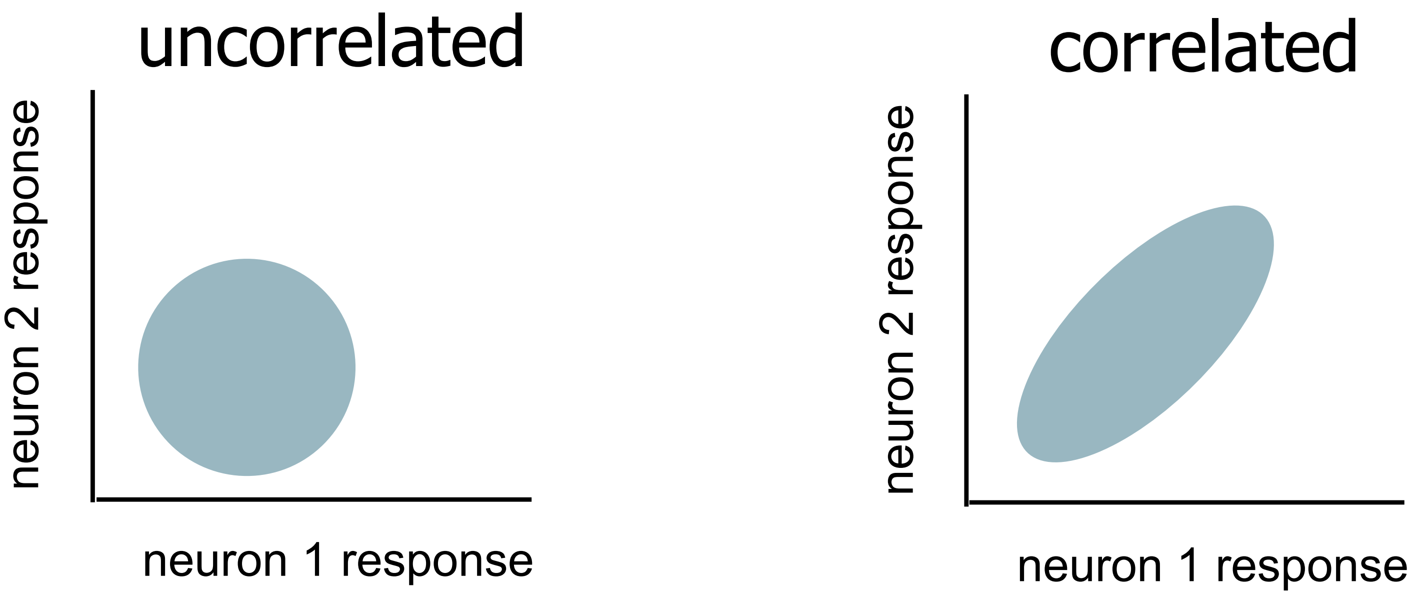
(a) Modulates signal propagation

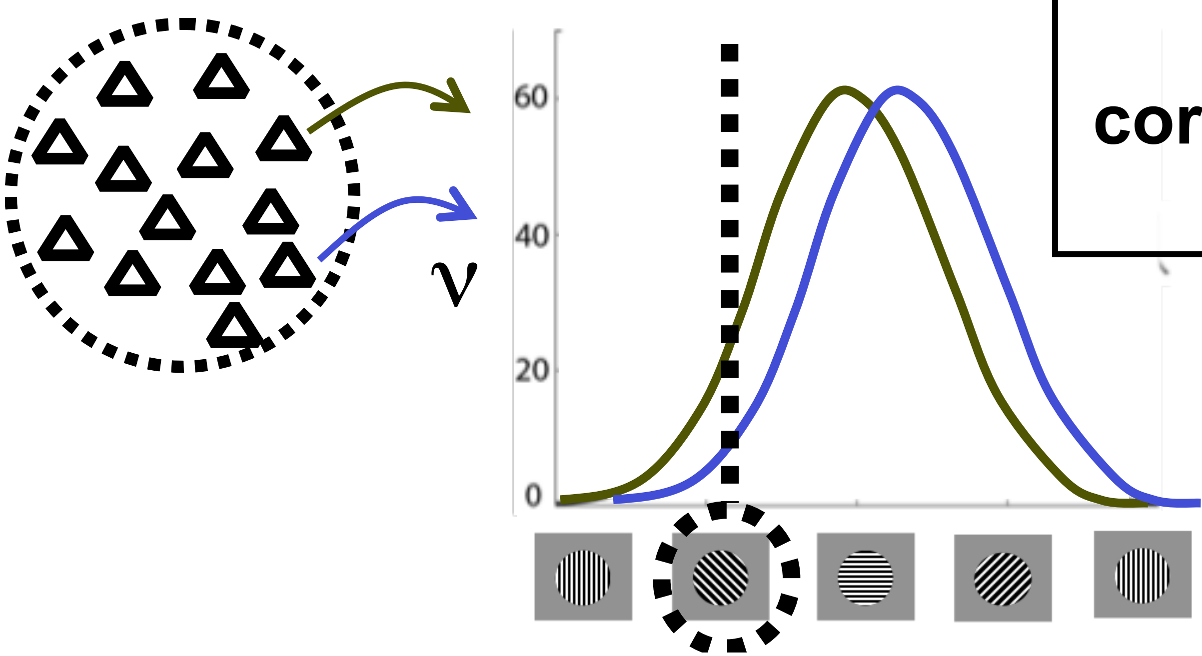
(b) Homogeneous populations: impedes pop. averaging/ decreases SNR

(c) Heterogeneous populations ...

Abbott+Dayan, `99; Panzeri et al, `99; Oram et al, '98; Averbeck et al., Nat Rev Nsci 06

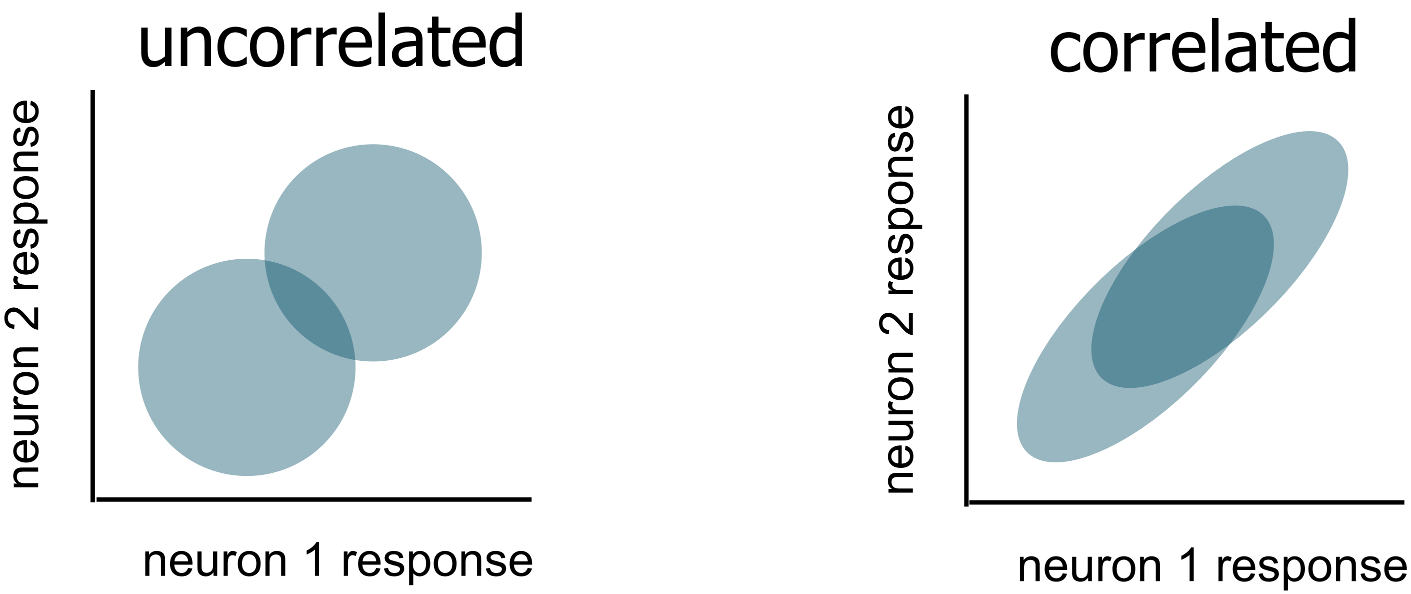


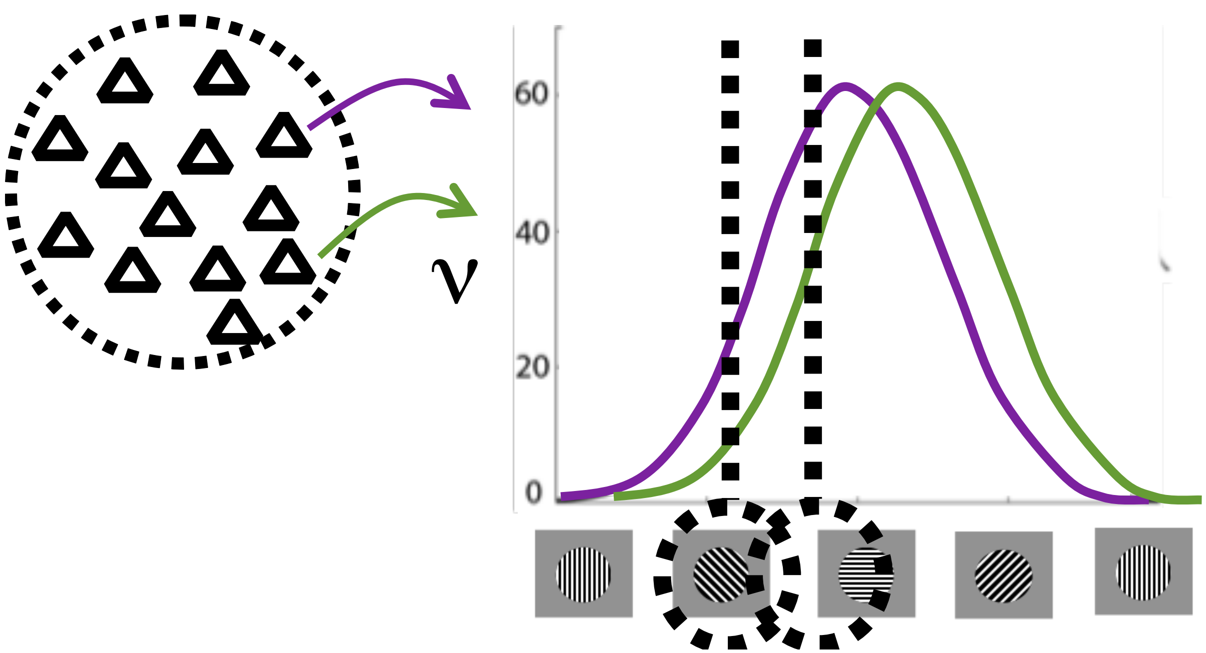




What are effects of correlations on information content in cell pair?

Abbott+Dayan, `99; Panzeri et al, `99; Oram et al, ‘98; Averbeck et al., Nat Rev Nsci 06

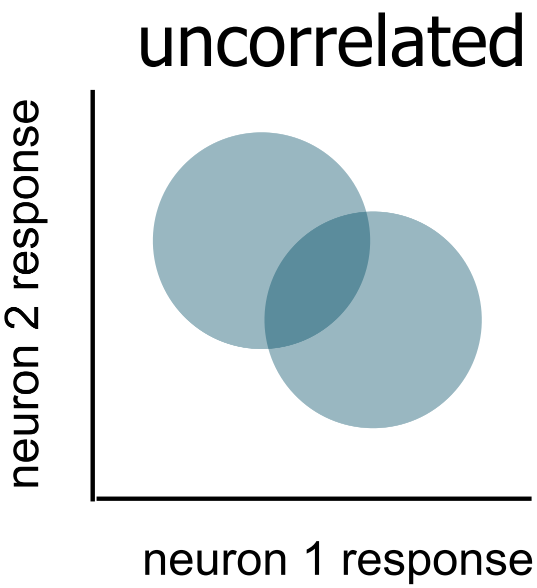


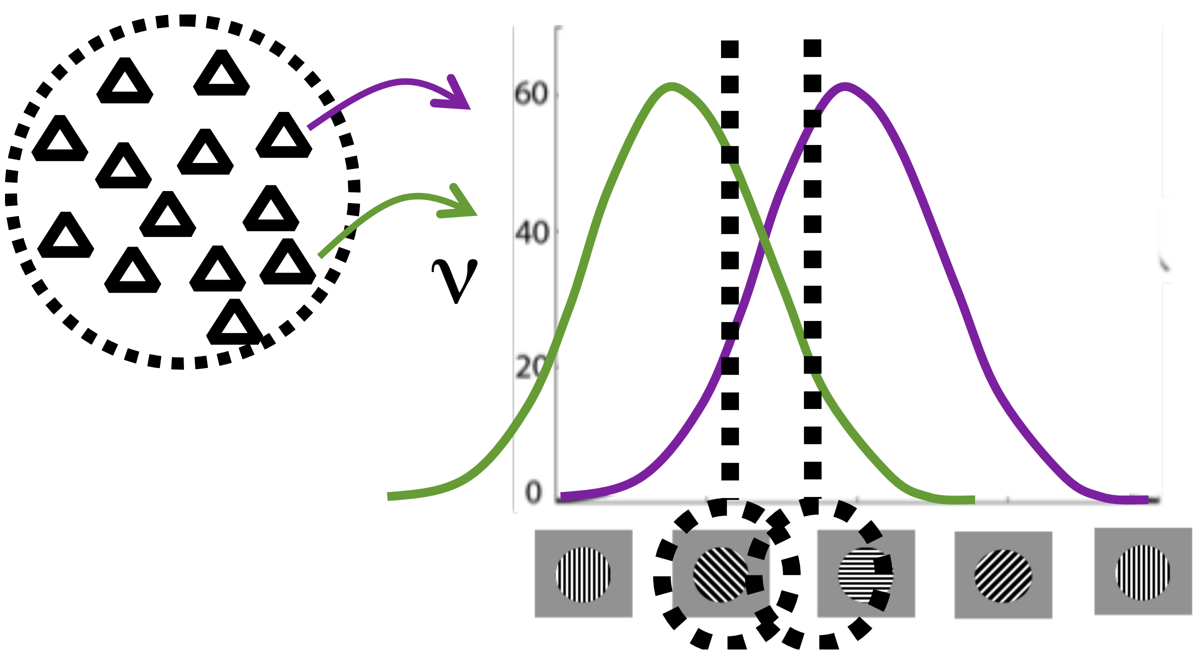


Positive **noise correlation** DEGRADES signal encoding.

...

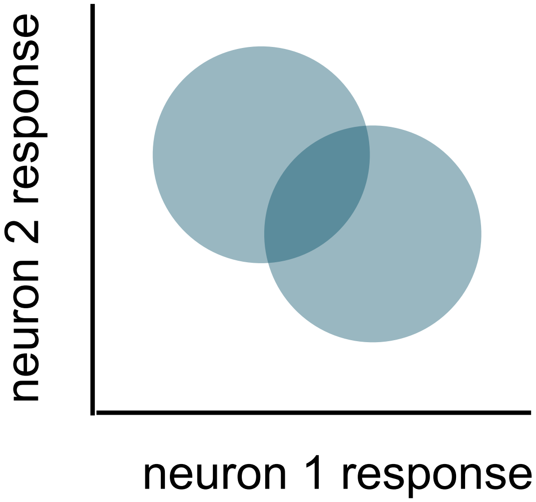
when also have positive signal correlation.


uncorrelated
neuron 2 response
neuron 1 response

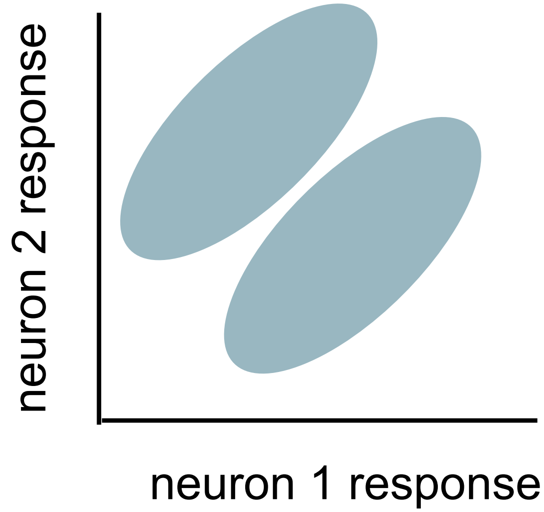

60
40
20
0
ν

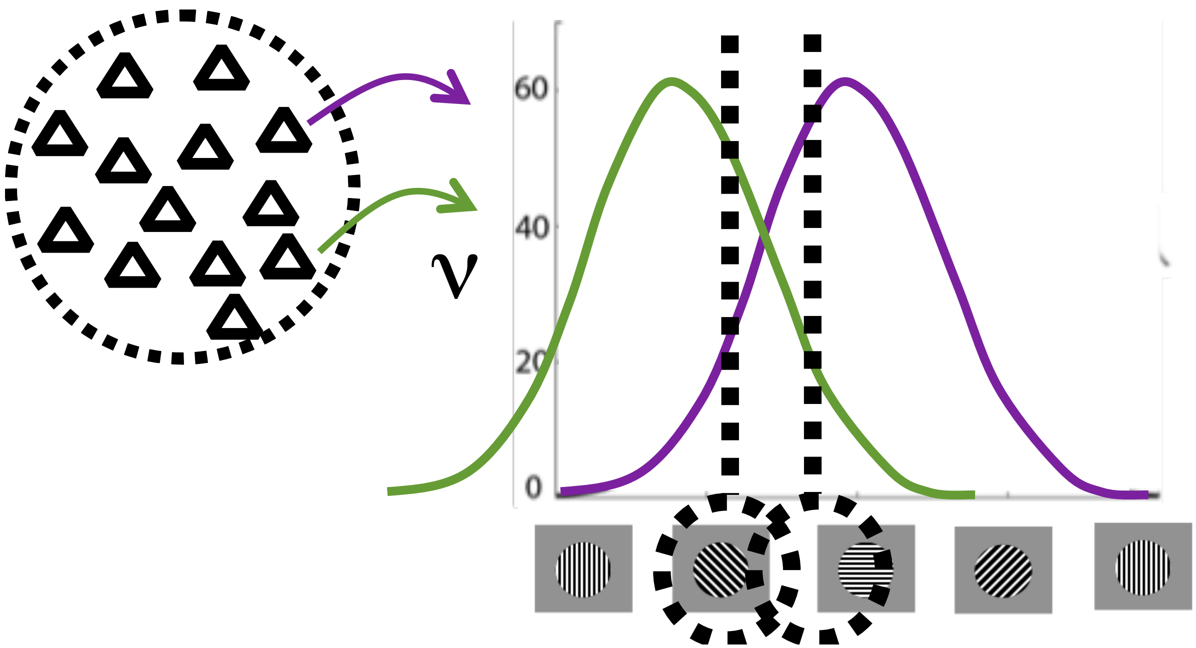
Abbott+Dayan, `99; Panzeri et al, `99; Oram et al, ‘98; Averbeck et al., Nat Rev Nsci 06

uncorrelated



correlated





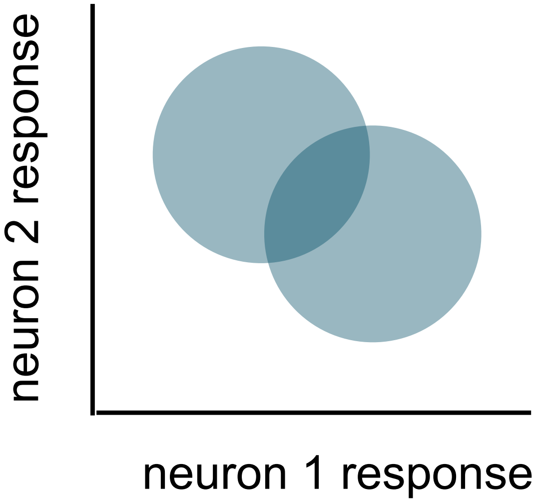
Positive **noise correlation** ENHANCES signal encoding.

...

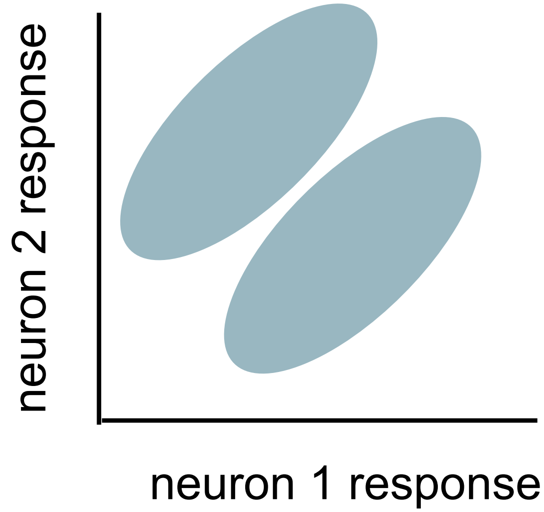
when also have **negative signal correlation.**

Abbott+Dayan, `99; Panzeri et al, `99; Oram et al, '98; Averbeck et al., Nat Rev Nsci 06

uncorrelated



correlated



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Correlated Neuronal Discharges that Increase Coding Efficiency during Perceptual Discrimination

(S2 cells)

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

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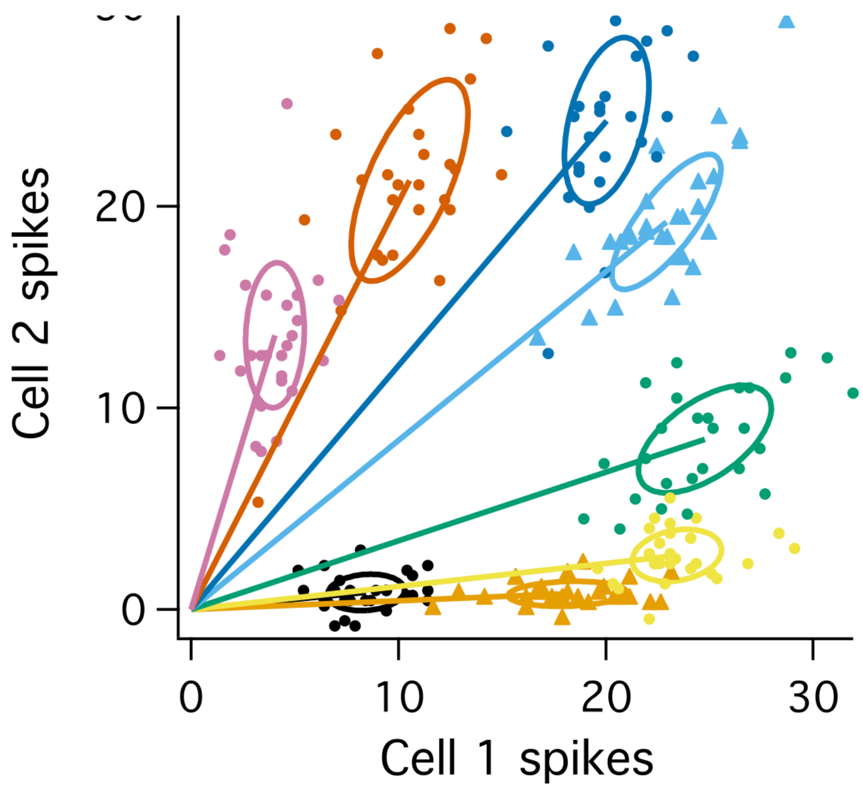
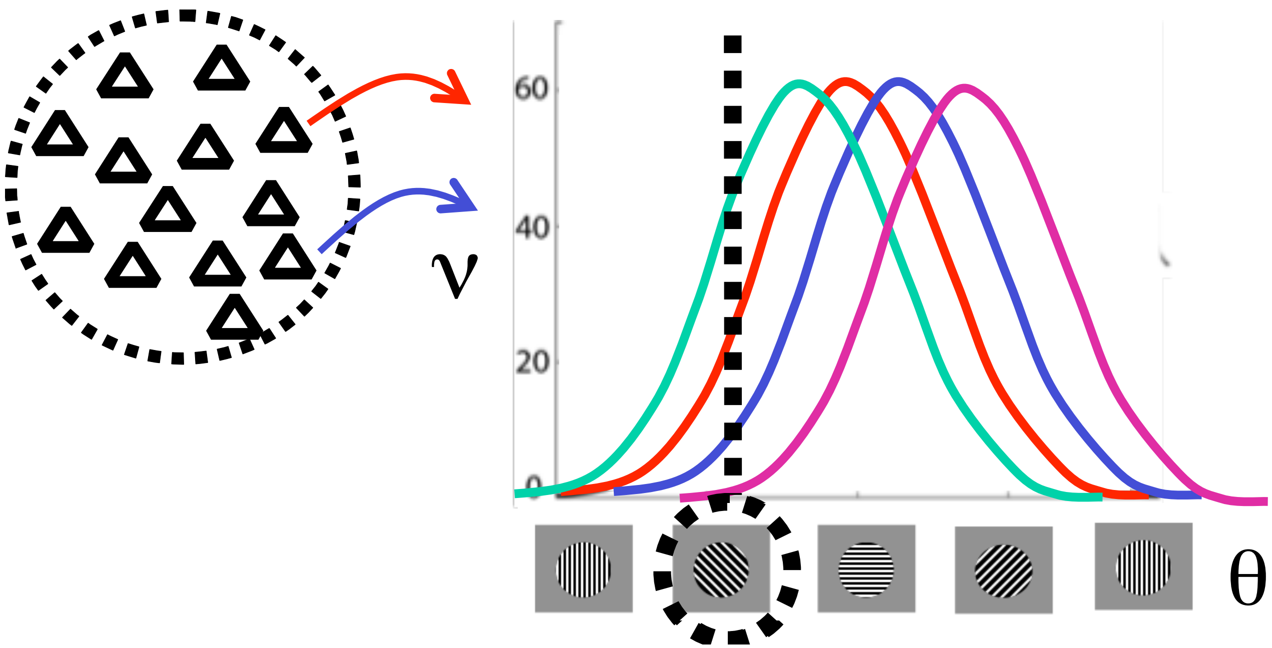
Direction-Selective Circuits Shape Noise to Ensure a Precise Population Code

(RGC cells)

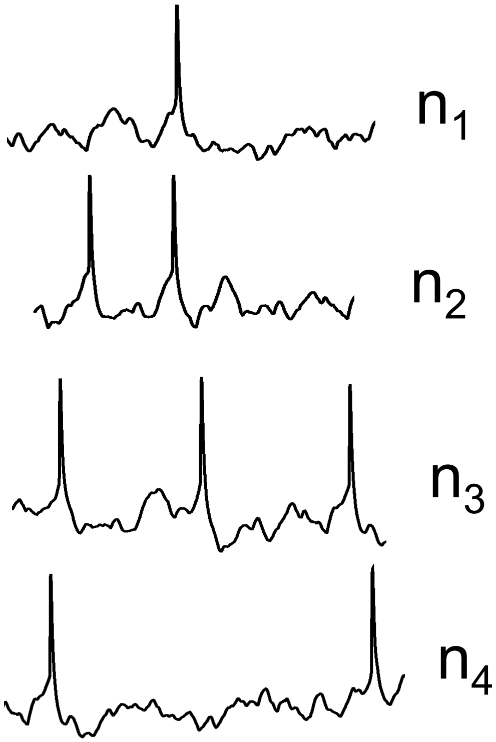


Zylberberg, Cafaro, Turner et al.
Neuron 2016

Correlations and coding in larger cell populations



Correlations and coding in larger cell populations



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

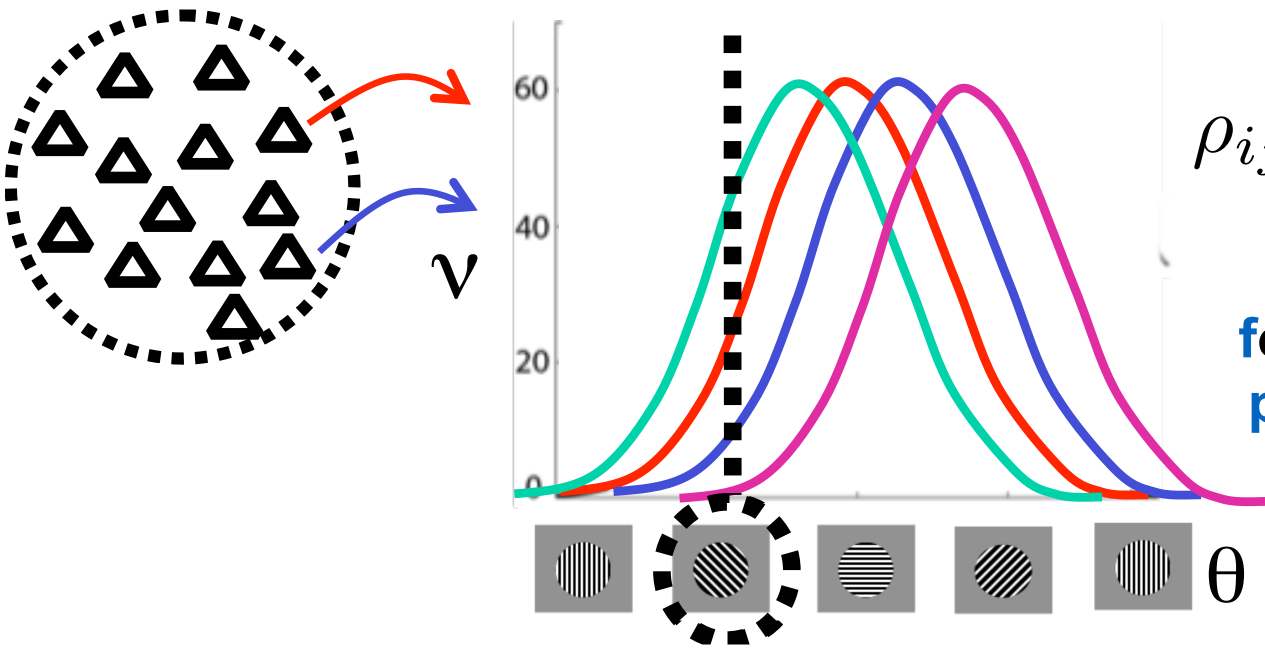
Stimulus x

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

Cramér-Rao Bound:

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

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



$\theta \sim \mathbf{x}$

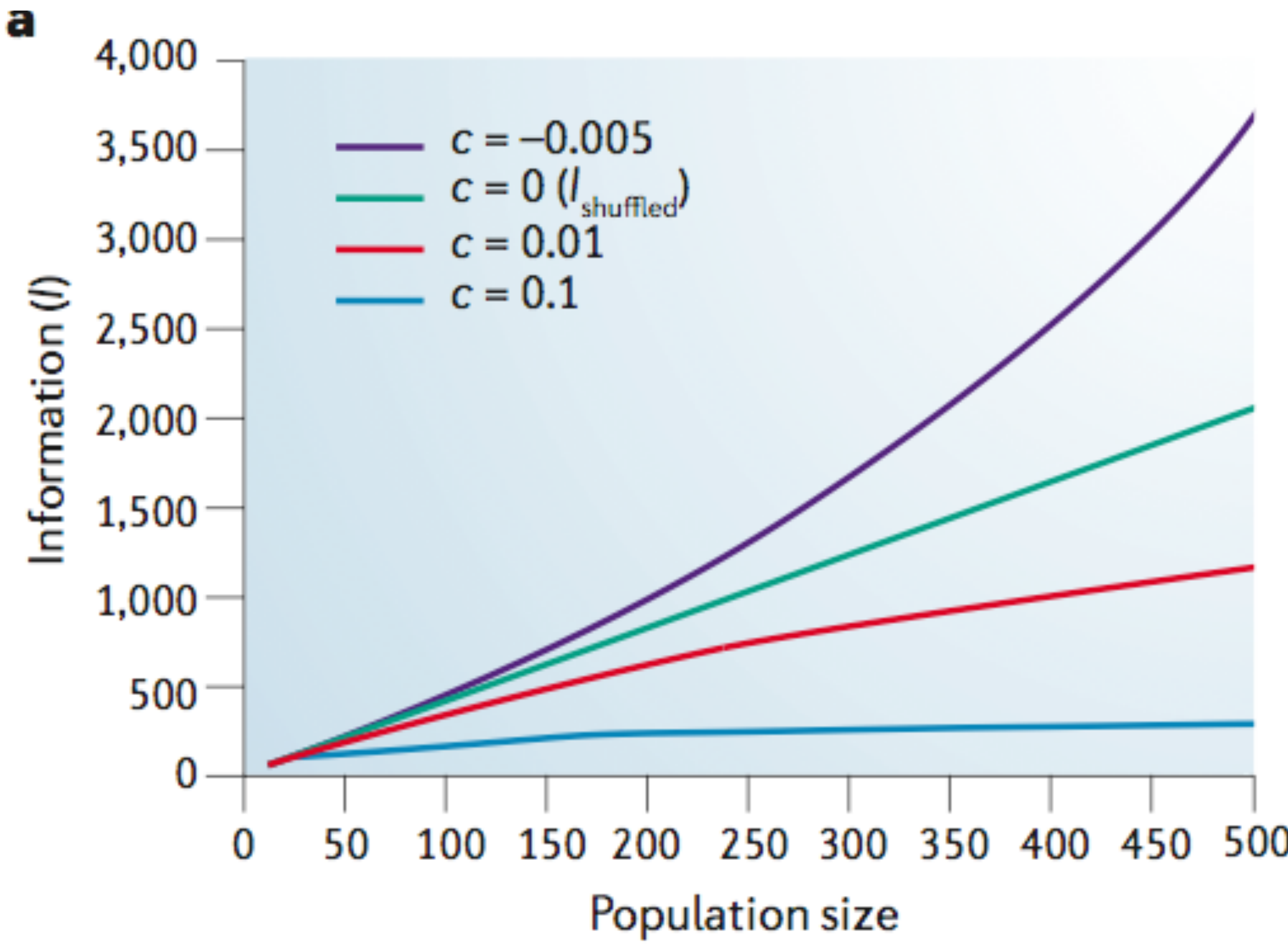
$$\rho_{ij} \sim \exp\left(-|\bar{\theta}(i) - \bar{\theta}(j)|\right)$$

Positive noise correlations for "nearby" cells, which have positive stimulus correlations

Should DEGRADE CODING

Sompolinsky et al, 2001

Correlations and coding in larger cell populations



INCREASE CORRELATION, **DEGRADE CODING**

[Averbeck et al Nat. Nsci. `06]

MANTRA (*SIGN RULE*): IF NOISE + SIGNAL CORRELATIONS HAVE ...

SAME "SIGN", BAD **(At least for "small" correlations w.r.t. population size N.)**

DIFFERENT SIGN, GOOD.

FORMALIZE: Hu et al '14 , Ecker et al '11; Shamir, '14; da Silvera+Berry'14

CODING IMPACT OF CORRELATED SPIKING:

(a) Modulates signal propagation

(b) Homogeneous populations: DEGRADES CODING

(c) Heterogeneous populations:

SIGN RULE MANTRA:

correlate cells w/ similar stimulus tuning: DEGRADE*

correlate cells w/different stimulus tuning: ENHANCE

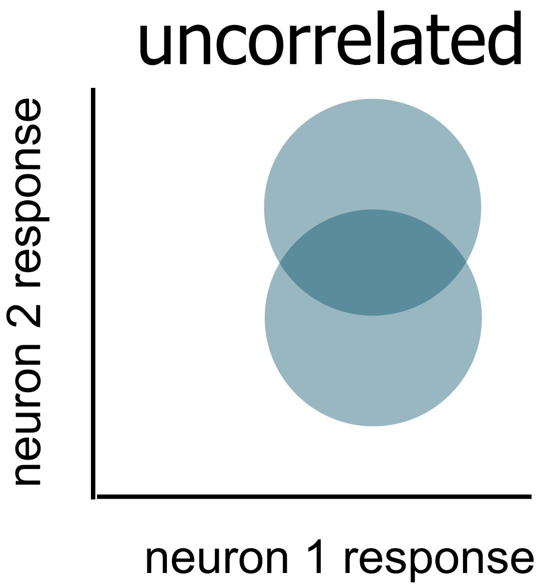
*(only guaranteed if correlations small w.r.t. # cells in pop.)

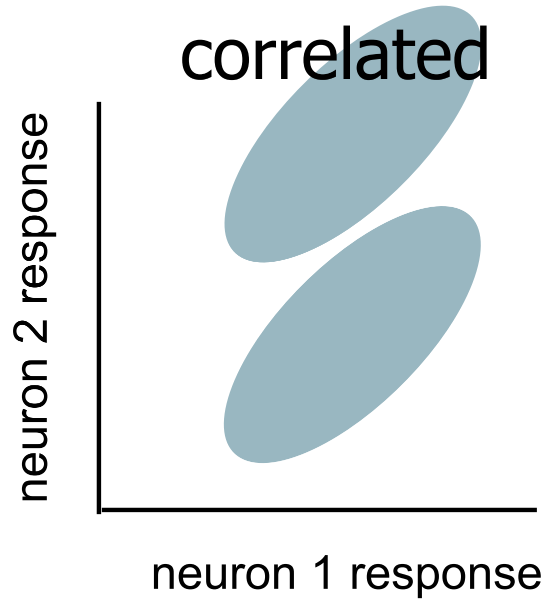
BEYOND THE MANTRA:

many possibilities for correlations that ENHANCE coding in large populations

[Shamir and Sompolinsky Neural Comp 2006,
Hu, Zylberberg et al PLOS CB 2014
Shamir Current Opinion Neurobio 2014]

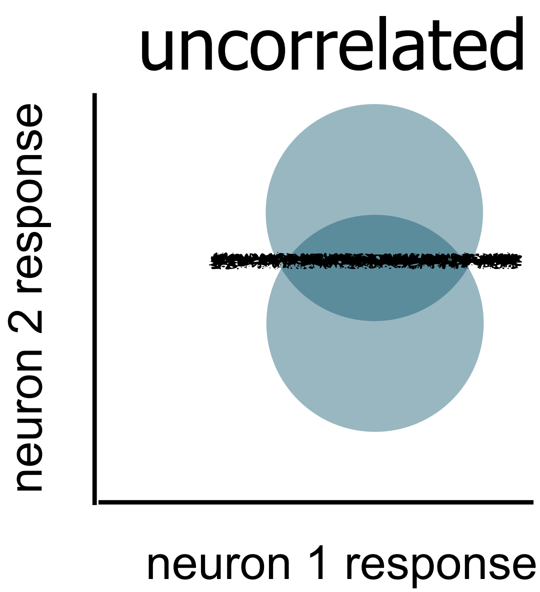
That was the encoding perspective on correlations

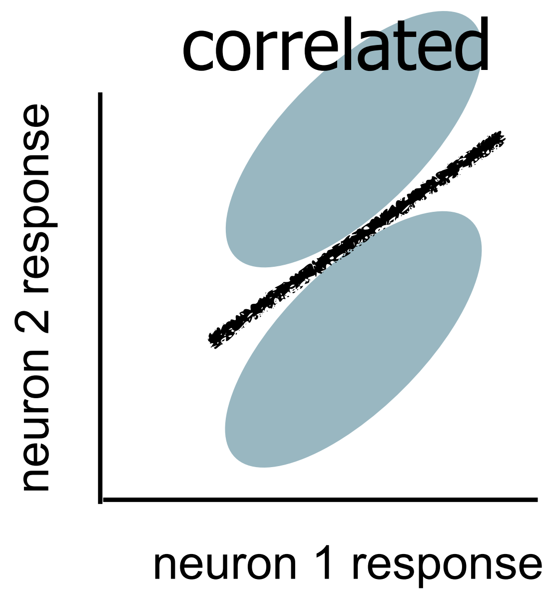




- **Am I glad they are there?**
  - **Yes**

There is also a decoding perspective

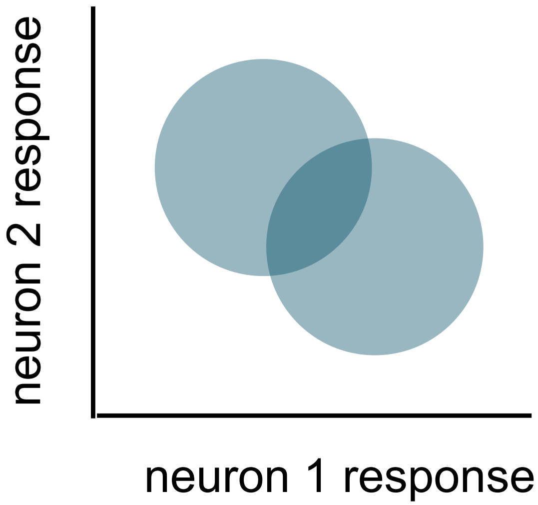




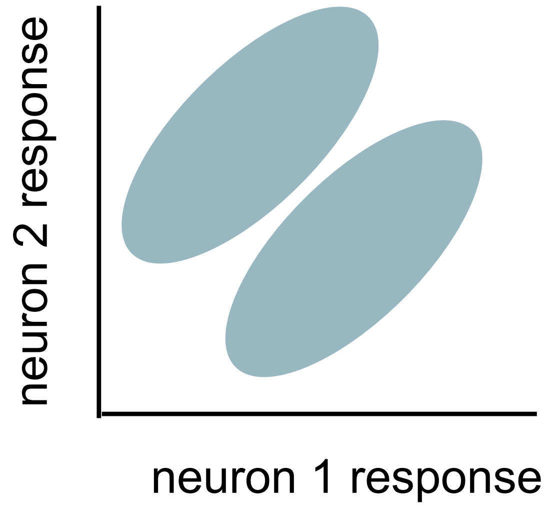
- **Do I have to know they are there to decode the signal?**
  - **Yes**

That was the encoding perspective on correlations

uncorrelated



correlated



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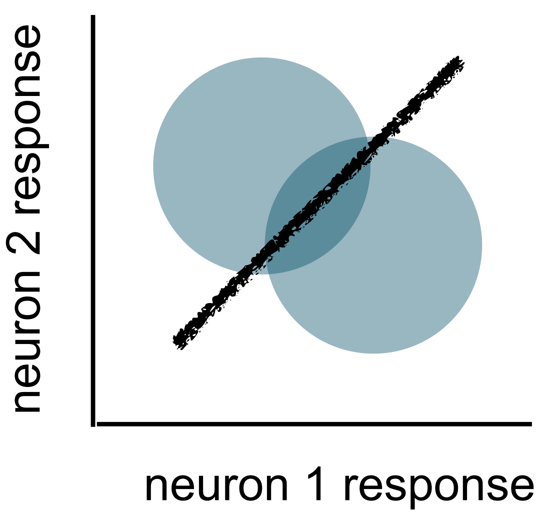
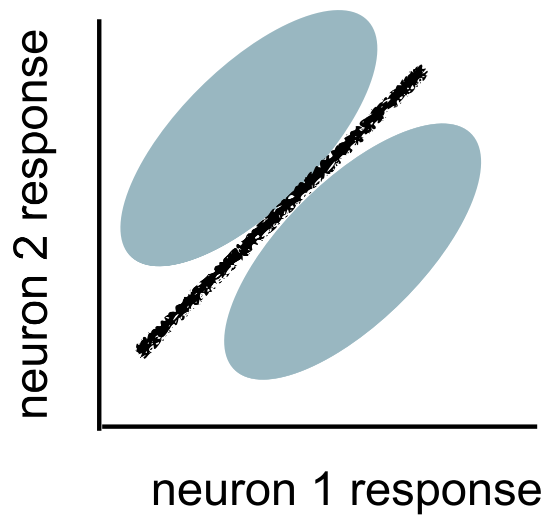
There is also a decoding perspective

uncorrelated



correlated



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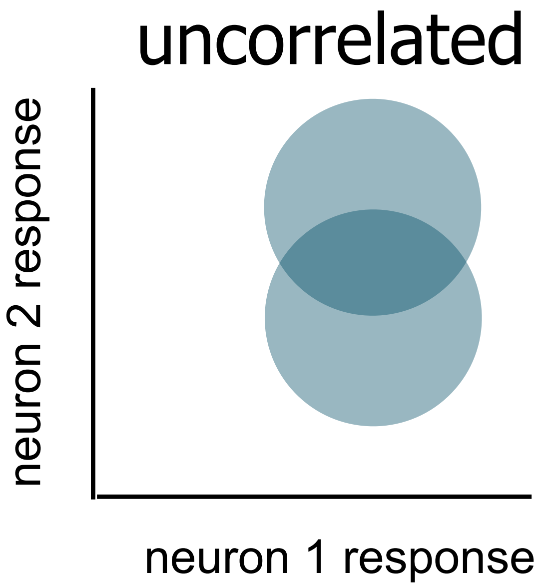
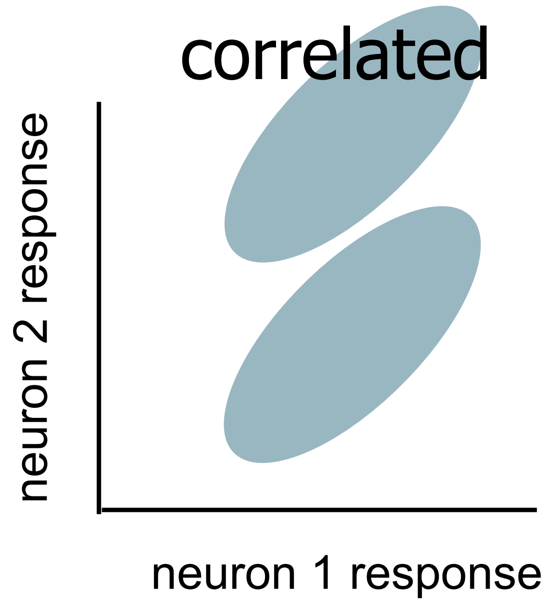
That was the encoding perspective on correlations





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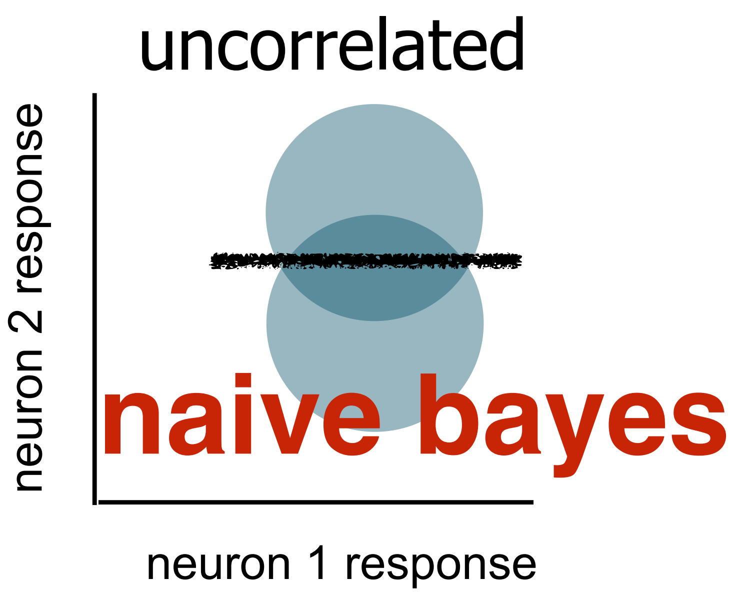
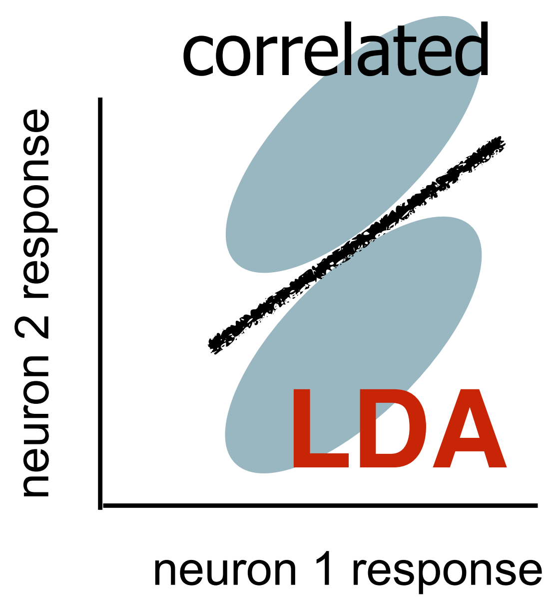
There is also a decoding perspective





- **Do I have to know they are there to decode the signal?**
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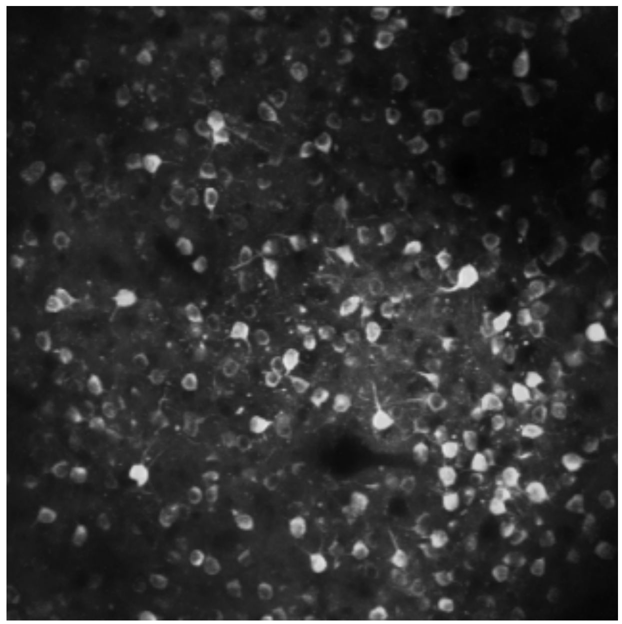
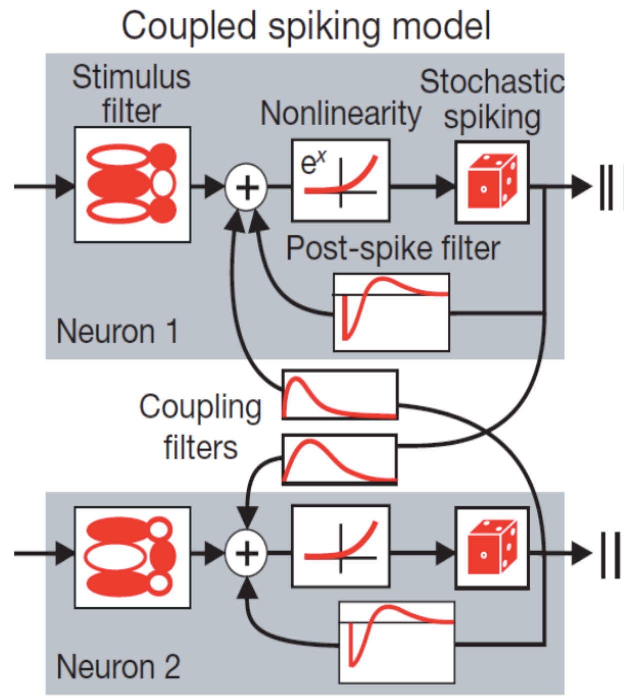
Projects galore…

What does collective activity contribute to *decoding* stimuli in different visual areas (and Cre lines)?





Pillow et al, 2008

Can ask via other decoders, e.g. GLM with vs. without coupling filters

Collective (or *correlated*) neural activity and population codes

Algorithmic: Evidence for signatures (or exhaust fumes) of computation?

Propagation: Do correlations modulate signal transmission?

Encoding: How do correlations impact info?

Decoding: Are readouts sensitive to correlations?

Geometry of signal and noise:

sign rule mantra (and beyond)

Collective (or *correlated*) neural activity and population codes

Algorithmic: Signatures (or exhaust fumes) of computation?

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