Network Correlations Tutorial

CAMP 2016, Bangalore
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Outline

- What are correlations?
- Mechanisms
- Effect on neural coding

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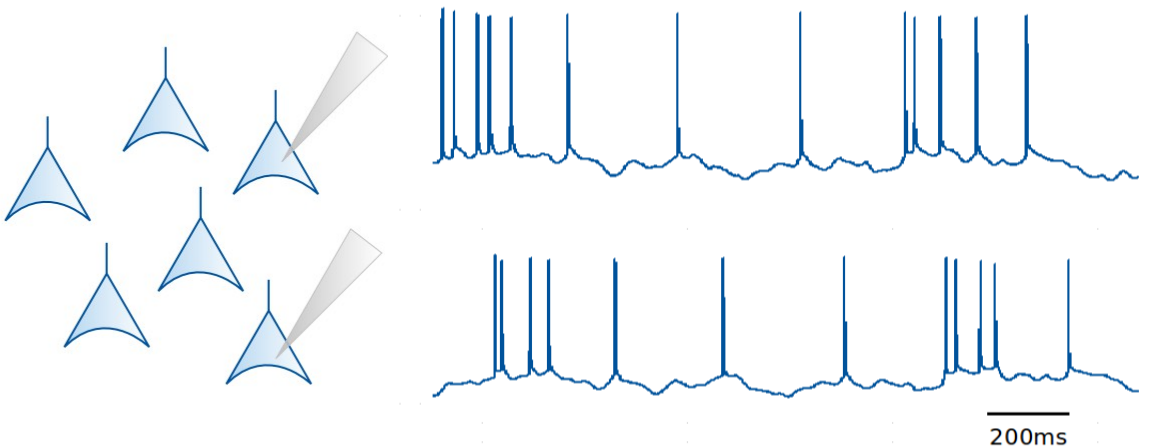
What are correlations?

- Correlation Coefficient:



$$\left\{t_1^{(1)}, t_2^{(1)}, t_3^{(1)} \ldots\right\}$$
$$S_1 = \sum \delta\left(t_i^{(1)}\right)$$

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- Spike recordings from a pair of neurons

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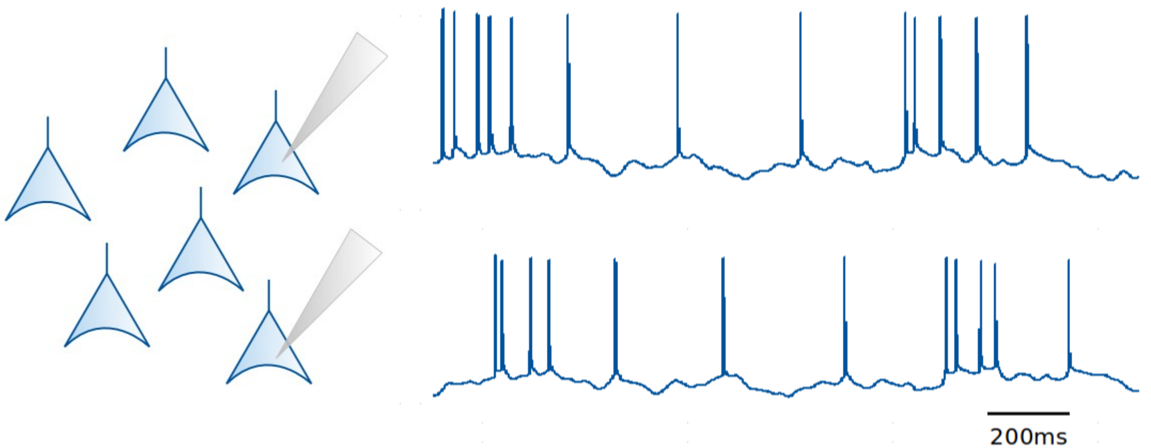

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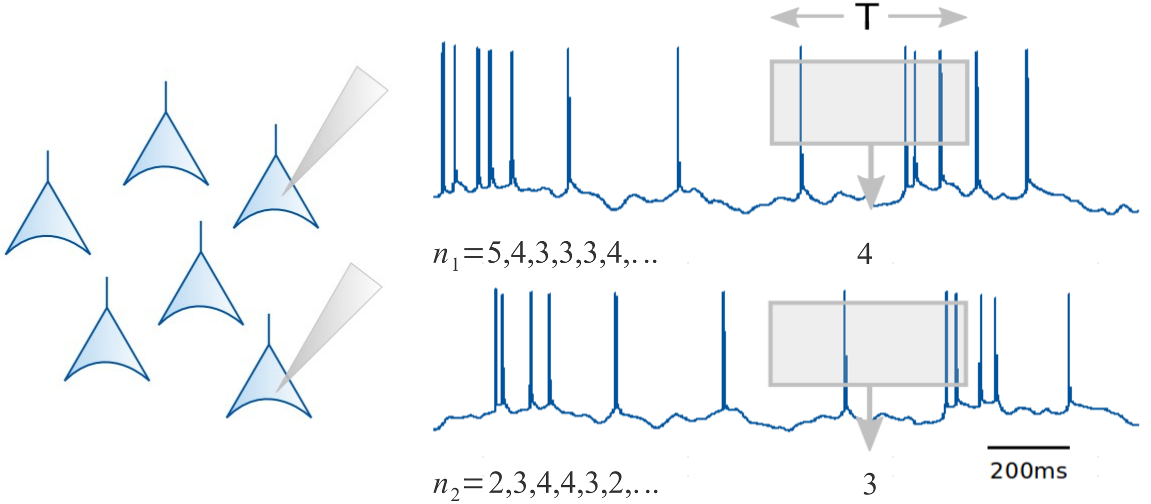

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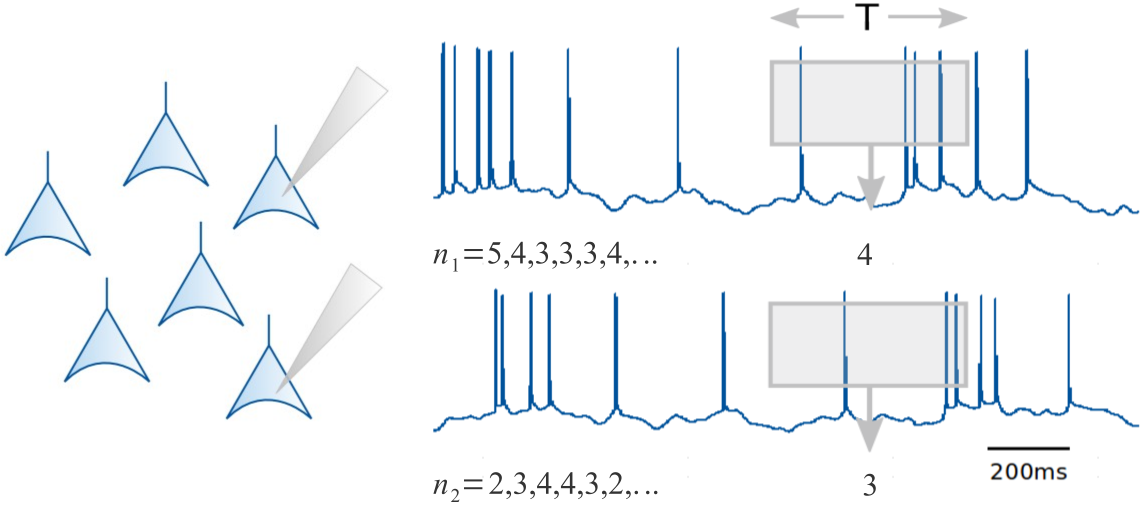

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- Spike recordings from a pair of neurons
- Slide window of size T and count events
- Compute correlation coefficient of the two series:

$$\rho_T = \frac{Cov[n_1, n_2]}{\sqrt{Var[n_1] Var[n_2]}}$$

$$Cov[n_1, n_2] = E[(n_1 - E[n_1])(n_2 - E[n_2])]$$

$$Var[n_1] = E[(n_1 - E[n_1])^2] = Cov[n_1, n_1]$$

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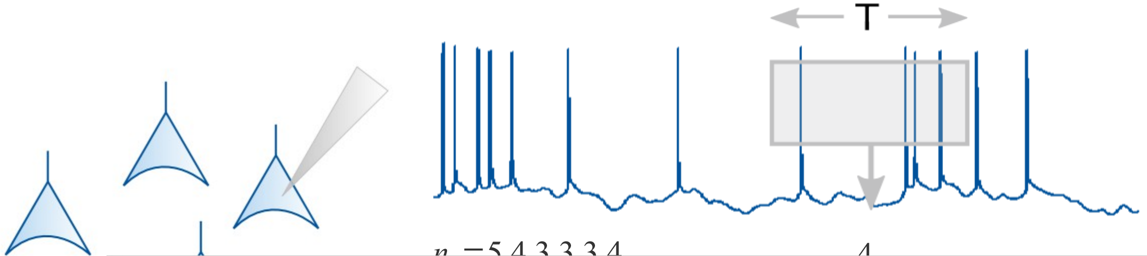

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- Spik
- Slid
- Con

Pairwise correlations are ubiquitous *in vivo!*

→ Retina: *Mastronade, 1983*

→ LGN: *Alonso et al 1996*

→ V1: *Kohn and Smith, 2005; Ecker et al, 2010*

→ PFC: *Constanidis & Goldman-Rakic, 2002*

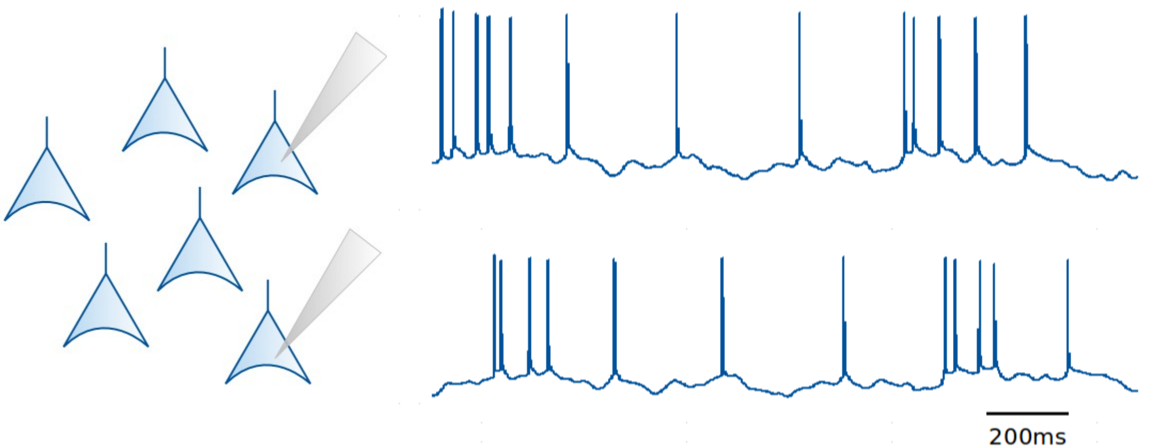
→ Motor Cortex: *Vaadiaet al, 1995*

→ S1: *Romo et al, 2003*

→ Somatosensory thal.: *Bruno & Sakmann, 2006*

What are correlations?

- Cross-Correlation-function:



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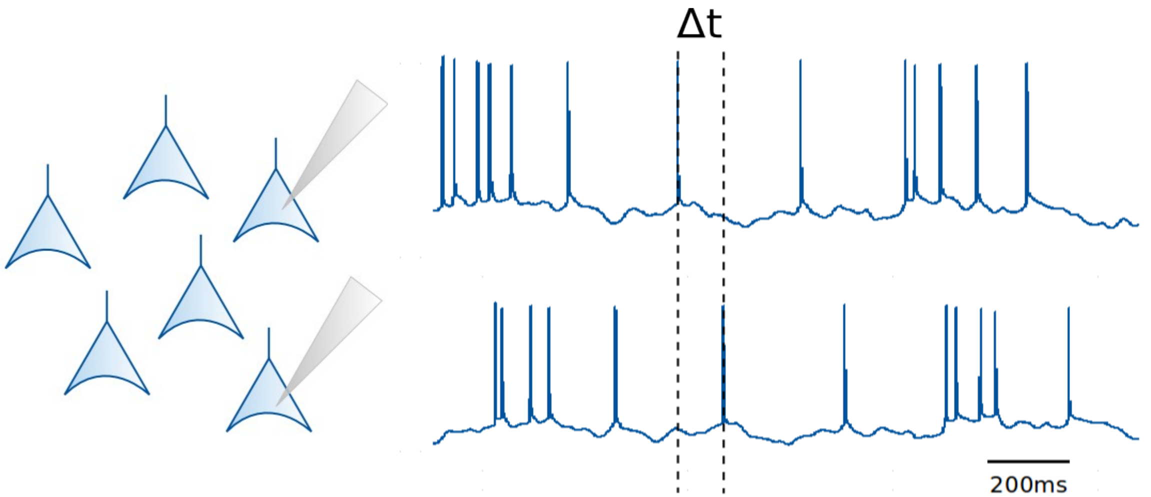

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- Take the time difference $t_j^{(2)} - t_i^{(1)}$ for all events of S_2 around each spike of S_1

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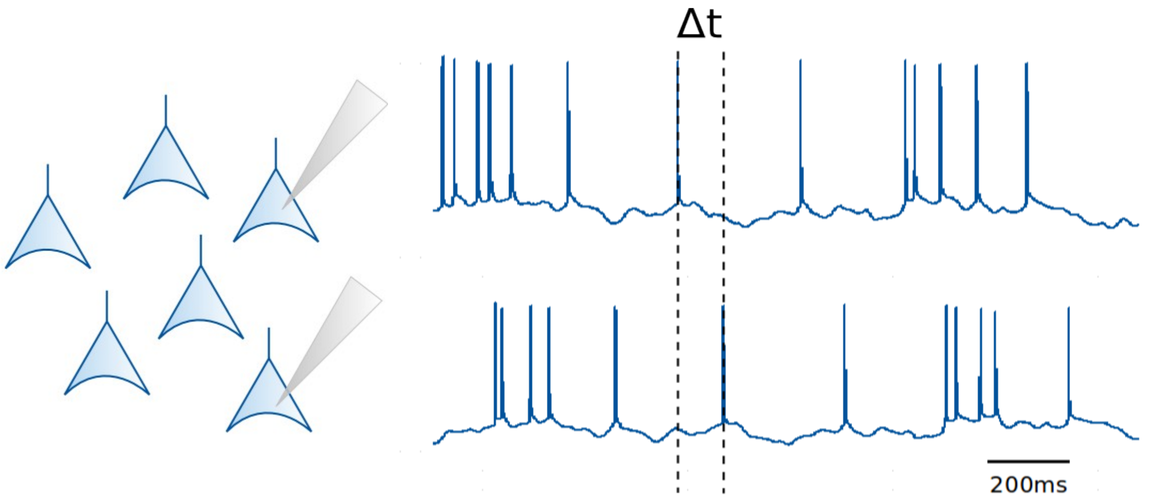

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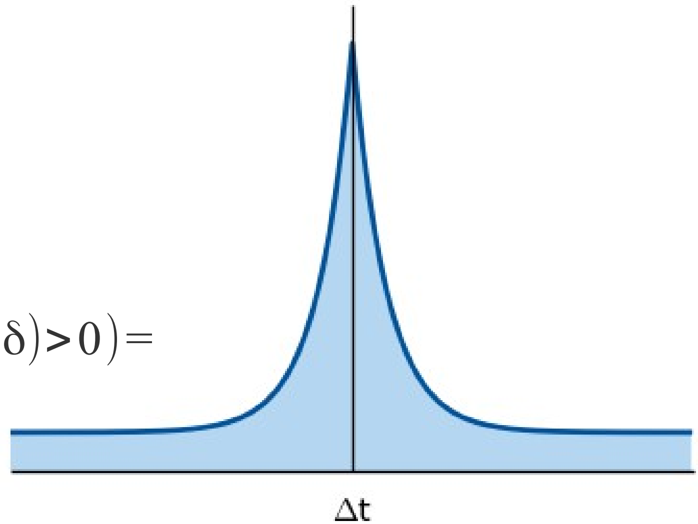
- Take the time difference $t_j^{(2)} - t_i^{(1)}$ for all events of S_2 around each spike of S_1
- Make a histogram of the time differences:



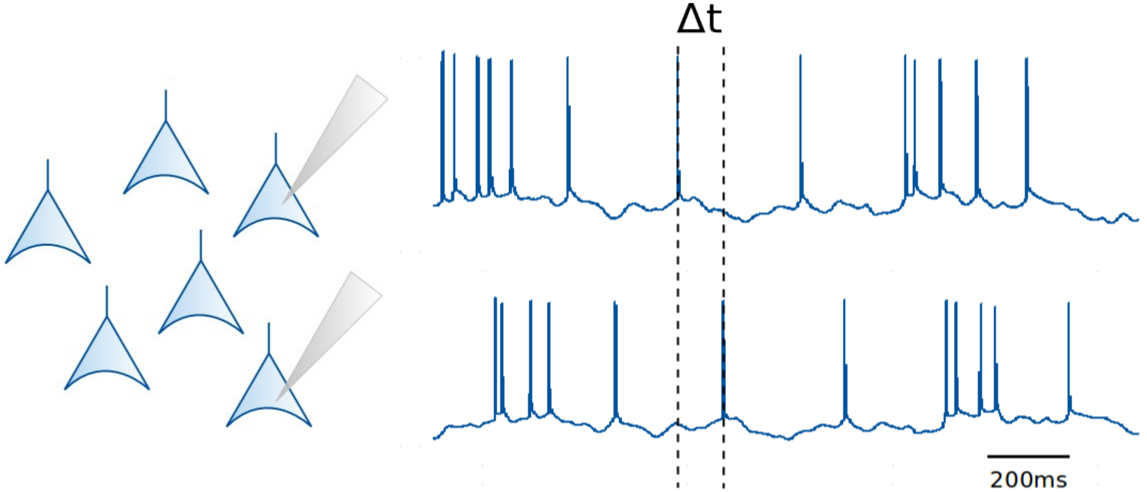
$$R_{12}(\Delta t) = E[S_1(t) S_2(t+\Delta t)] =$$

$$= \lim_{\delta \to 0} \frac{1}{\delta} Pr(N_2(t+\Delta t, t+\Delta t+\delta) > 0 \wedge N_1(t, t+\delta) > 0) =$$

$$= \lim_{\delta \to 0} \frac{1}{\delta} Pr(t_j^{(2)} - t_i^{(1)} \in [\Delta t, \Delta t + \delta])$$

What are correlations?

- Cross-Covariance-function:



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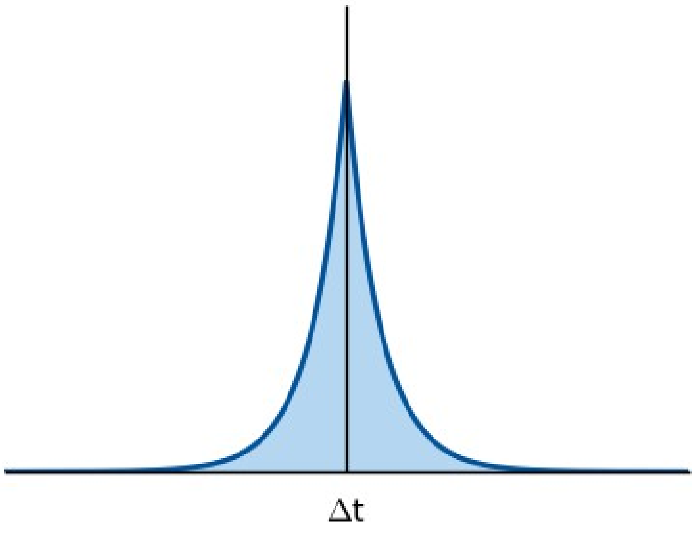
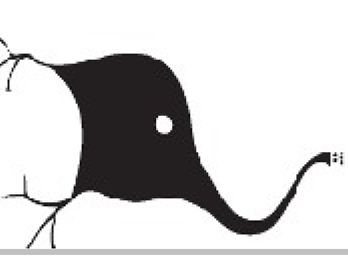
- Cross-Covariance-function:

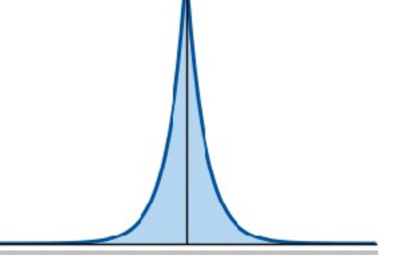
  → Subtract the mean rates

$$C_{12}(\Delta t) = E[S_1(t) S_2(t+\Delta t)] - E[S_1(t)] E[S_2(t+\Delta t)] =$$
$$= R_{12}(\Delta t) - \nu_1 \nu_2$$





Assignment 1: ρ_T and $C_{ij}(\Delta t)$



1) Compute the correlation coefficients and cross-correlation functions for the spiketrains provided. Interpret the data. Use simple_neuron to create new spiketrains and examine their correlations.

2) Try different time window sizes T. How does this change the measured correlation coefficient?

3)* Compare ρ_T to the integral of C(Δt) from -T to T. Verify the following identity numerically *(Shea-Brown, 2008)*:

$$\rho_T = \frac{\int_{-T}^{T} C_{12}(t)\,\frac{T-|t|}{T}\,dt}{\sqrt{\int_{-T}^{T} C_{11}(t)\,\frac{T-|t|}{T}\,dt \int_{-T}^{T} C_{22}(t)\,\frac{T-|t|}{T}\,dt}}$$

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- Effect on neural coding

Mechanisms

- Possible origins of correlations:

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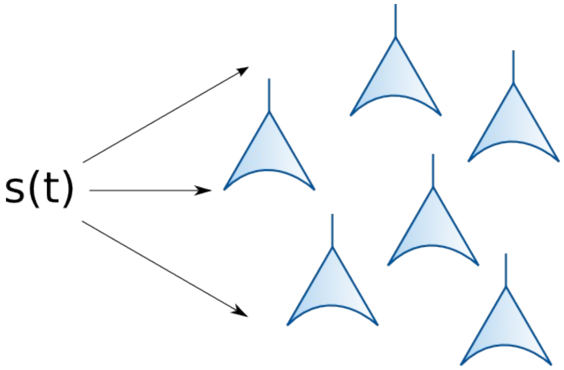
Common external input signal:

→ ***Signal correlations***



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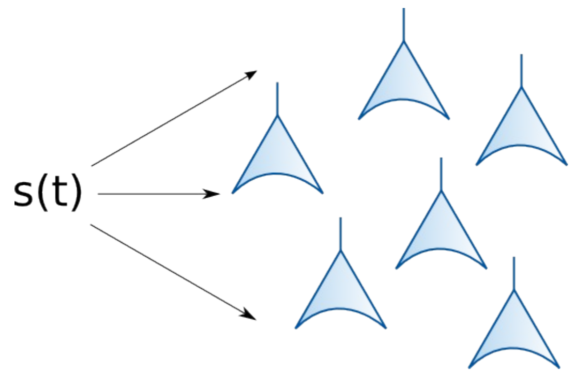
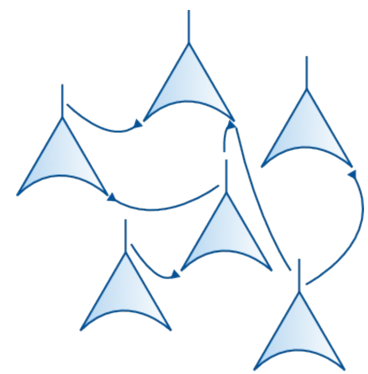


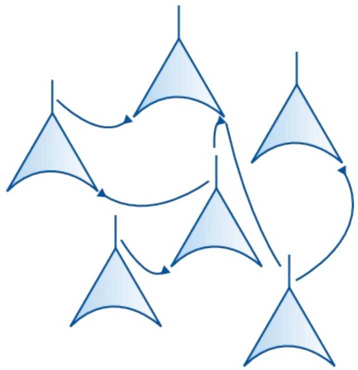
„Network driven“ correlations:
→ ***Noise correlations***



Origin and transfer

- Mechanisms for noise correlations:

  Direct connections:



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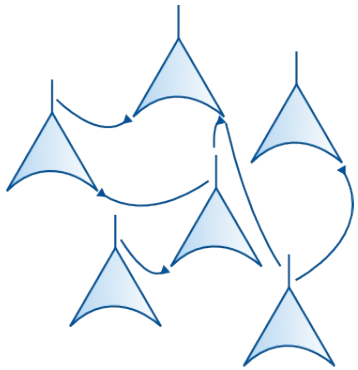
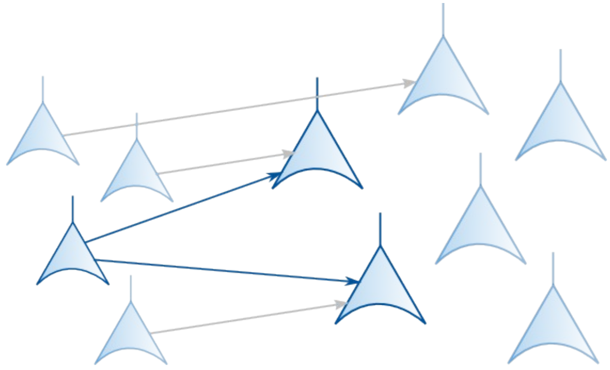


Common background input:



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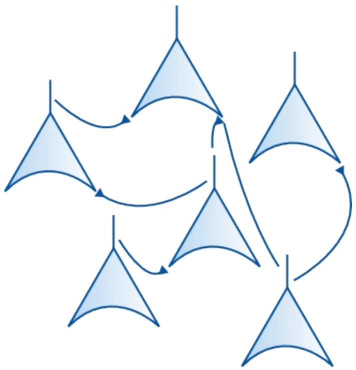

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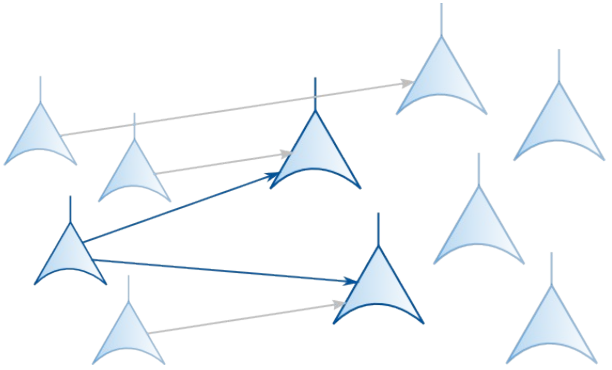
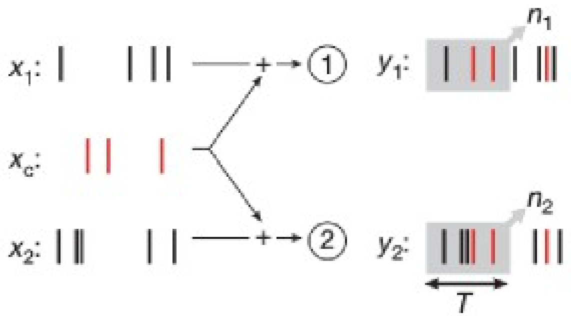


Assignment 2: Common Input

1) Create two correlated spiketrains:



2) Investigate the correlation coefficient of the output spiketrains, when you use y_1 and y_2 as inputs. Plot the correlation coefficient of the output spiketrains ρ_{out} for different correlation coefficients ρ_{in} between y_1 and y_2, the socalled correlation transfer function.

3) How does this correlation transfer function ρ_{out} *vs.* ρ_{in} change for different input rates and synaptic weights?

Origin and transfer

- Correlations increase with output rate *(de la Rocha, Doiron et al, 2007; Shea-Brown et al, 2008)*

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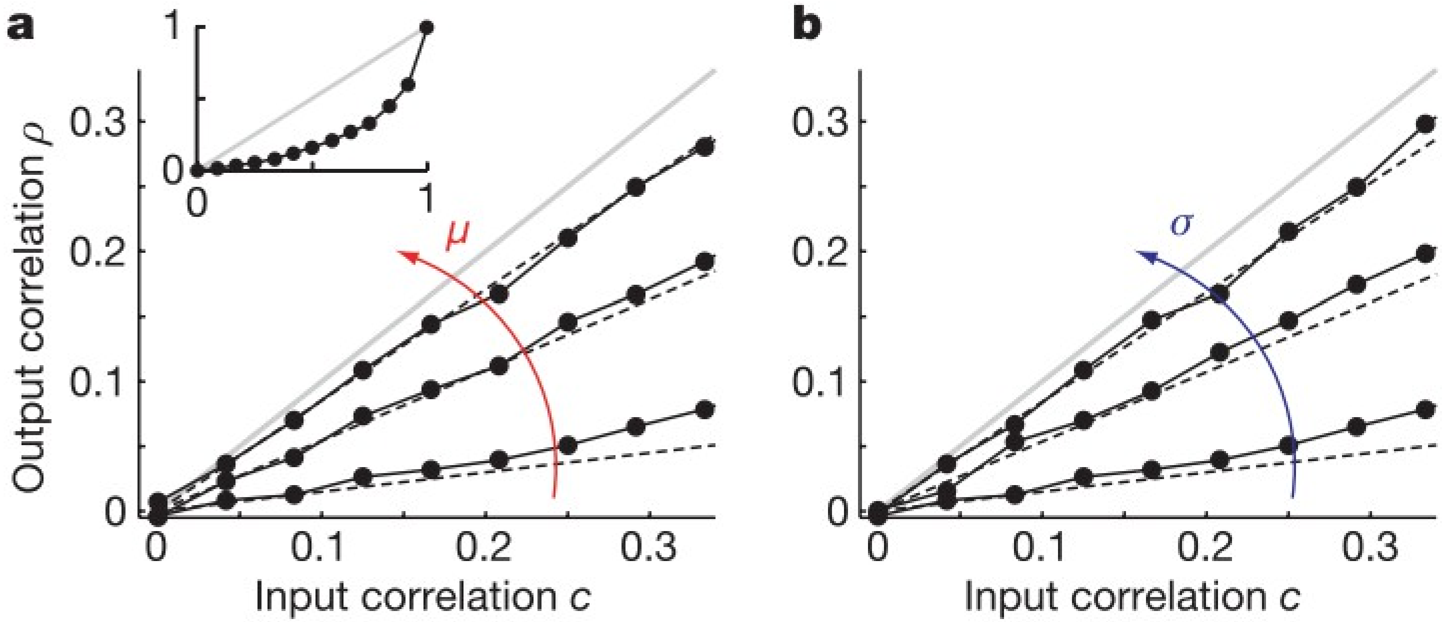

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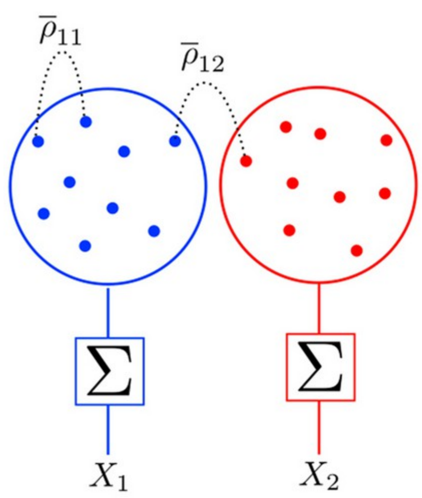

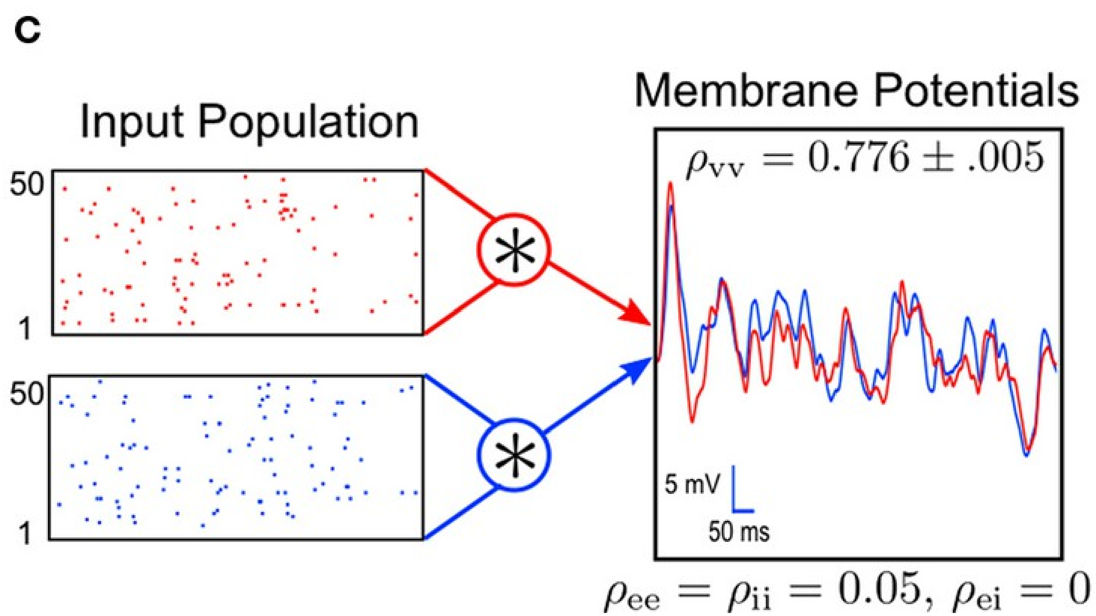

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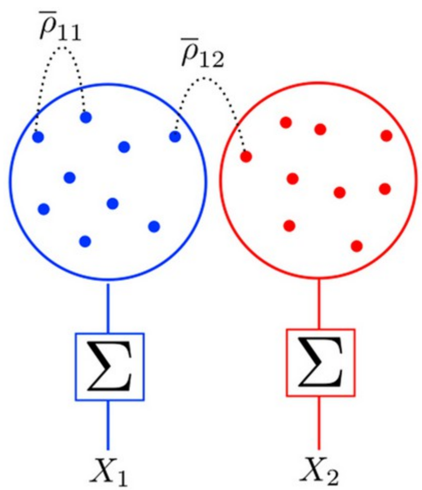

$$
\begin{aligned}
Var[X_1] &= Var\left[\sum_i x_i\right] = \\
&= \sum_i^N Var[x_i] + \sum_{i,j} Cov[x_i, x_j] = \\
&= N\, Var[x_i] + N(N-1)\rho_{11} Var[x_i] = \\
&= Var[x_i](N(\rho_{11} N - \rho_{11} + 1))
\end{aligned}
$$

$$
\begin{aligned}
Cov[X_1, X_2] &= Cov\left[\sum_i^N x_i, \sum_j^N x_j\right] = \\
&= \sum_i^N \sum_j^N Cov[x_i, x_j] = \\
&= N^2 Cov[x_i, x_j] = Var[x_i] N^2 \rho_{12}
\end{aligned}
$$

$$
c = \frac{Cov[X_1, X_2]}{\sqrt{Var[X_1] Var[X_2]}} \approx \frac{N \rho_{12}}{\rho_{11} N - \rho_{11} + 1}
$$

Origin and transfer

- Correlations increase with output rate *(de la Rocha, Doiron et al, 2007; Shea-Brown et al, 2008)*
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- Cancellation between E- and I-input decorrelates network activity *(Renart, de la Rocha, 2010)*

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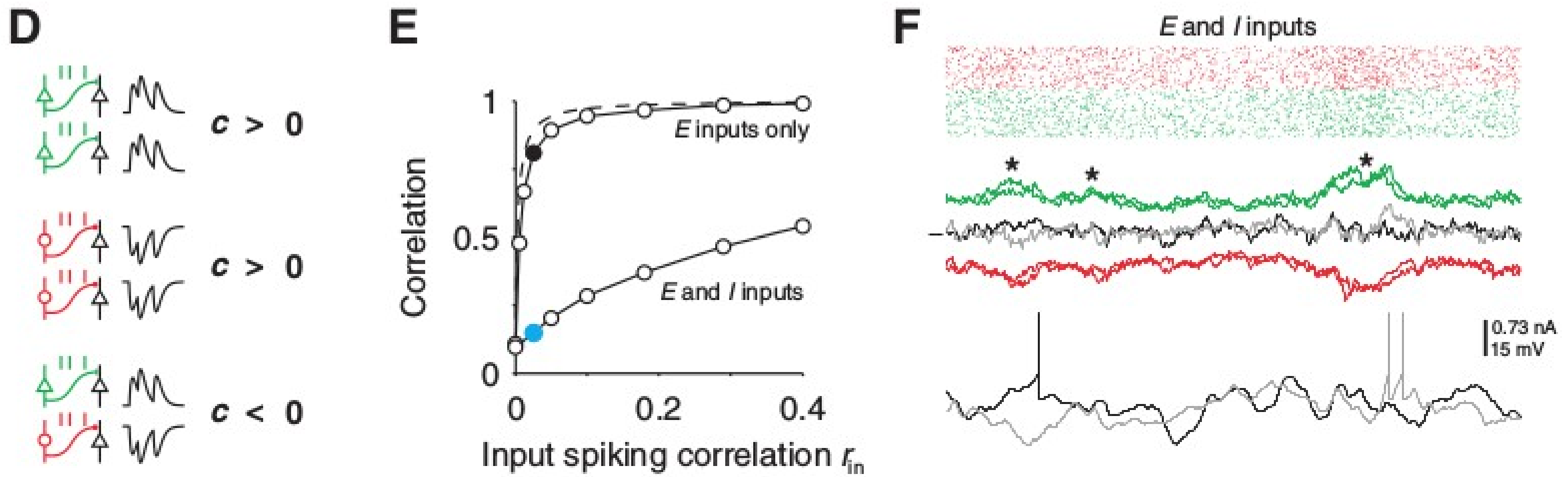

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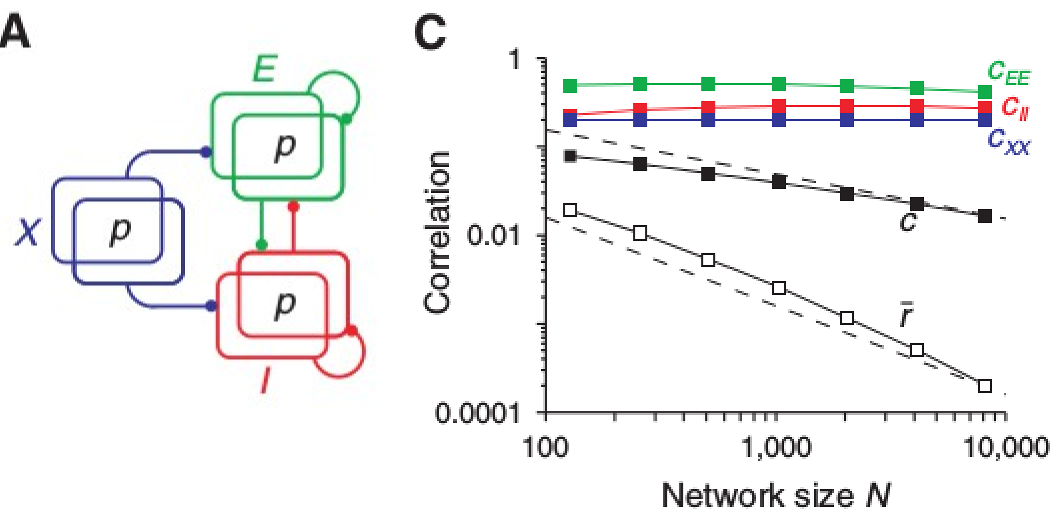

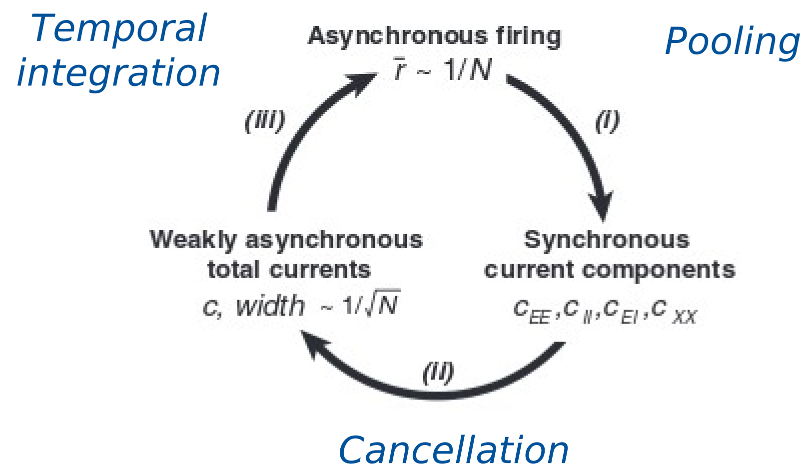

$$c = c_{EE} + c_{II} + 2c_{EI} \sim 1/\sqrt{N}$$

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Effect on neural coding

- Model system: Orientation tuning curves *(Hubel & Wiesel, 1962)*

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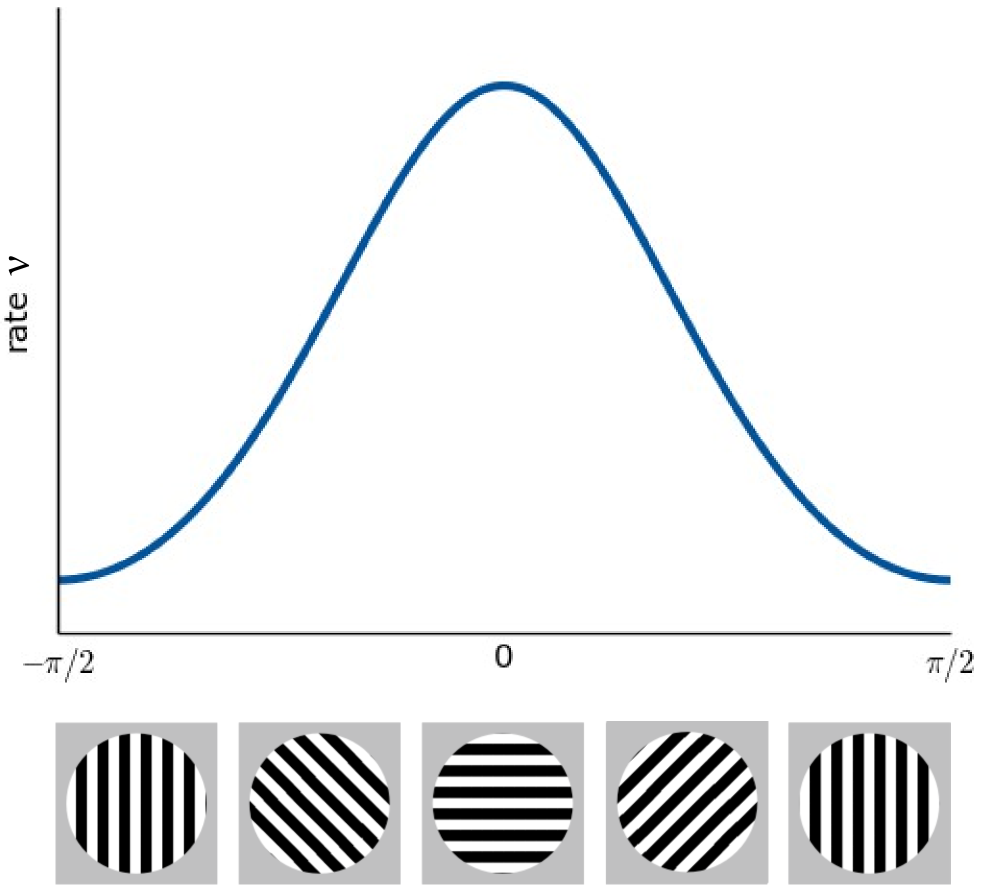
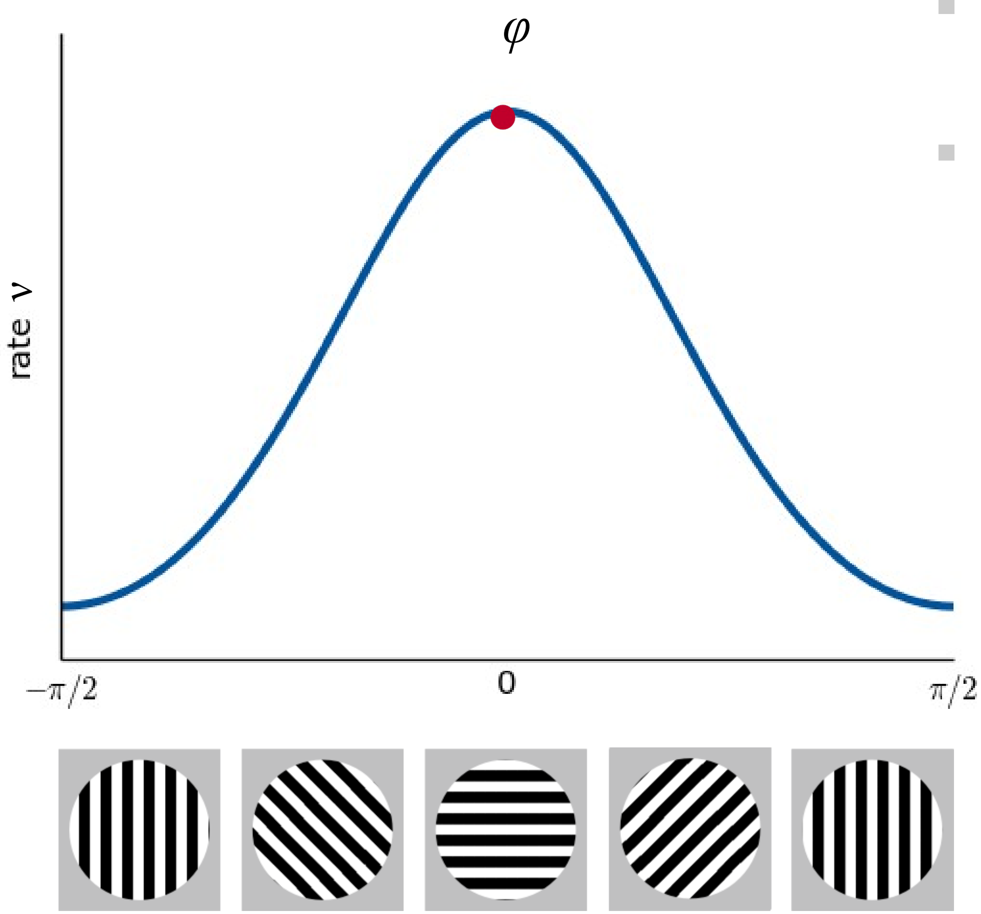


- Firing rate is orientation-dependent

Effect on neural coding

- Model system: Orientation tuning curves *(Hubel & Wiesel, 1962)*



- Firing rate is orientation-dependent
- Each neuron has a preferred orientation φ

Effect on neural coding

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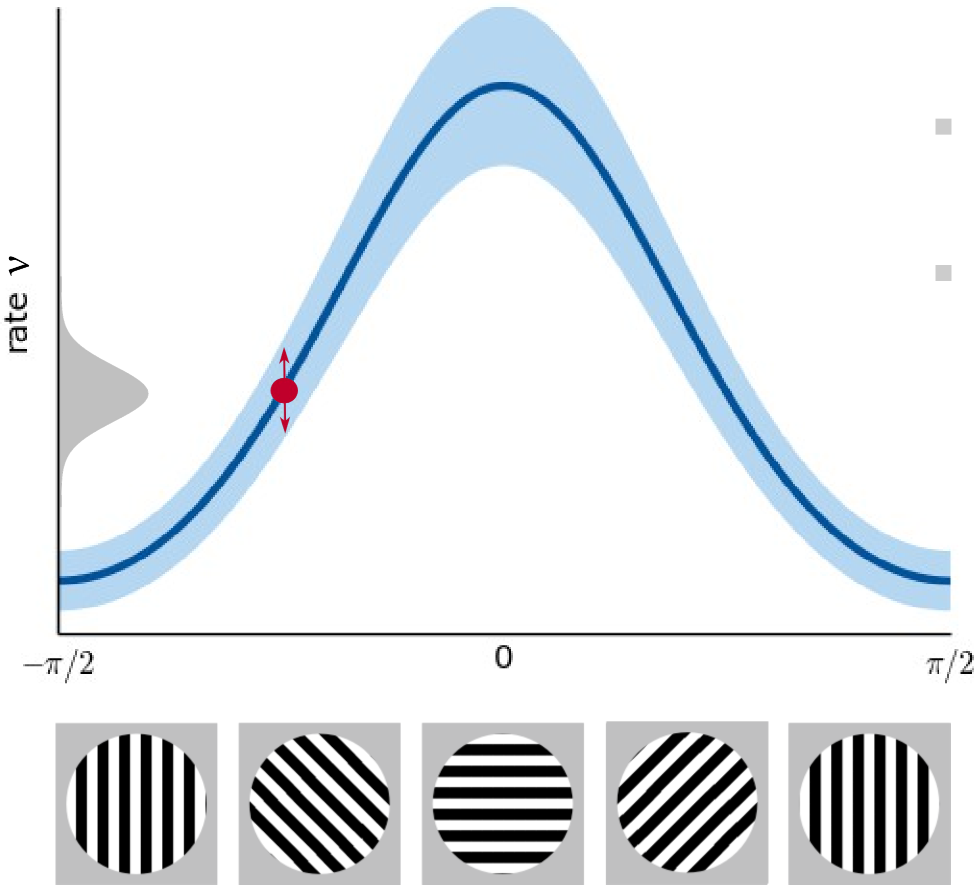

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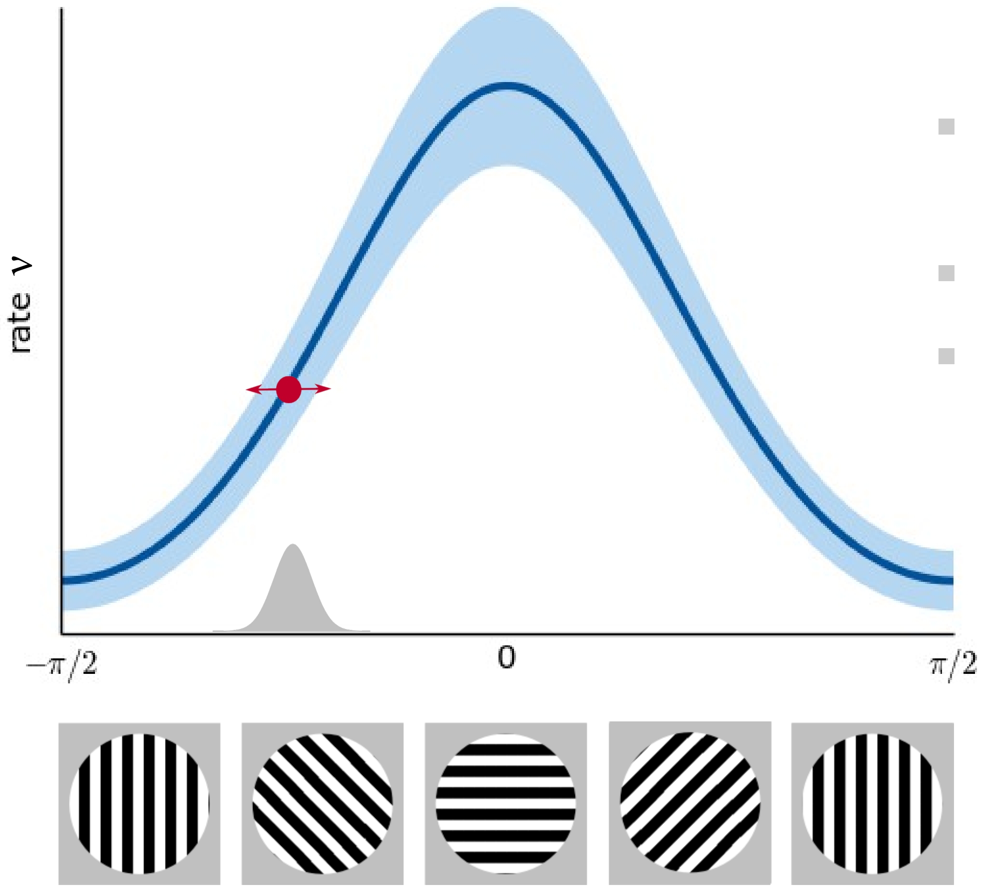
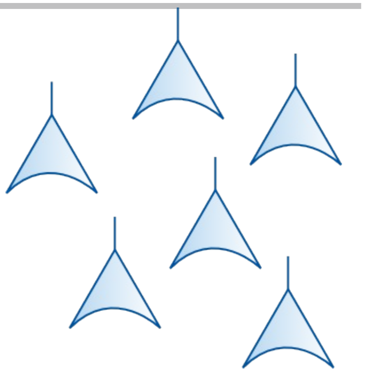
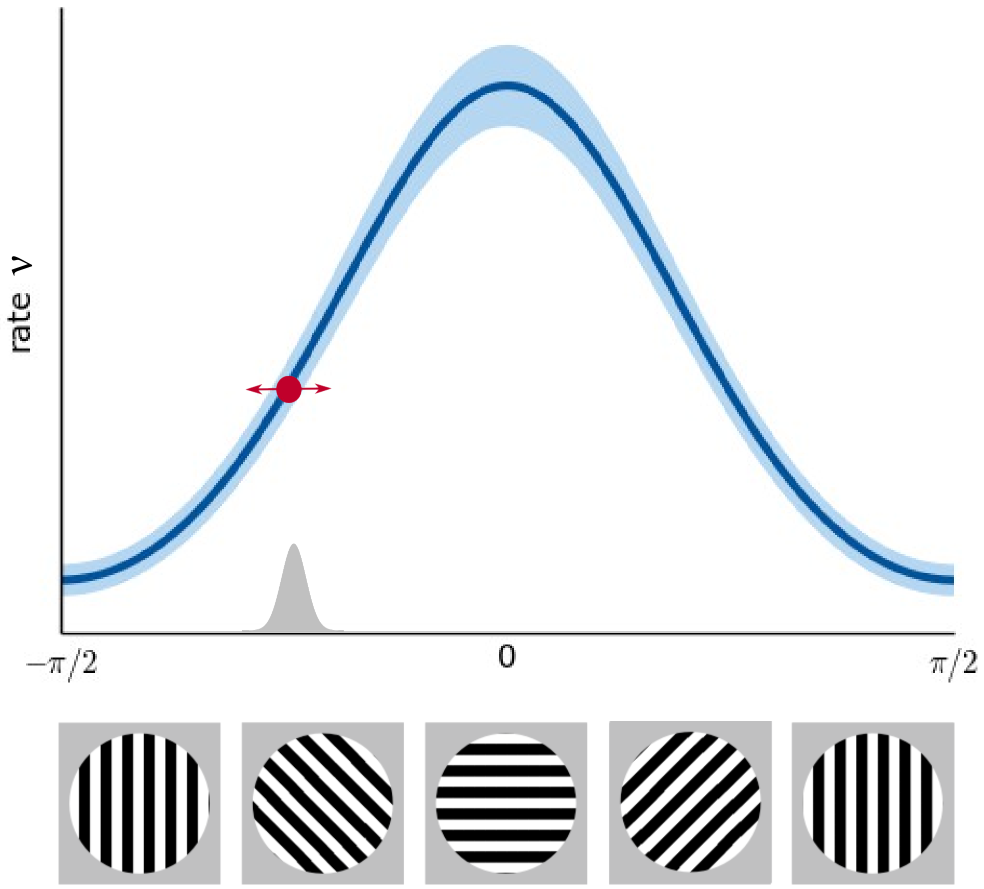


- Firing rate is orientation-dependent
- Each neuron has preferred orientation
- Neuron firing is variable
- This introduces ambiguity in decoding

Effect on neural coding

- Population code: N independent cells with the same preferred orientation





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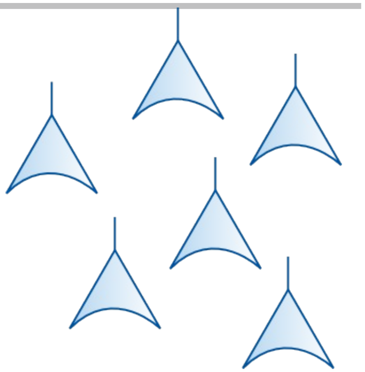
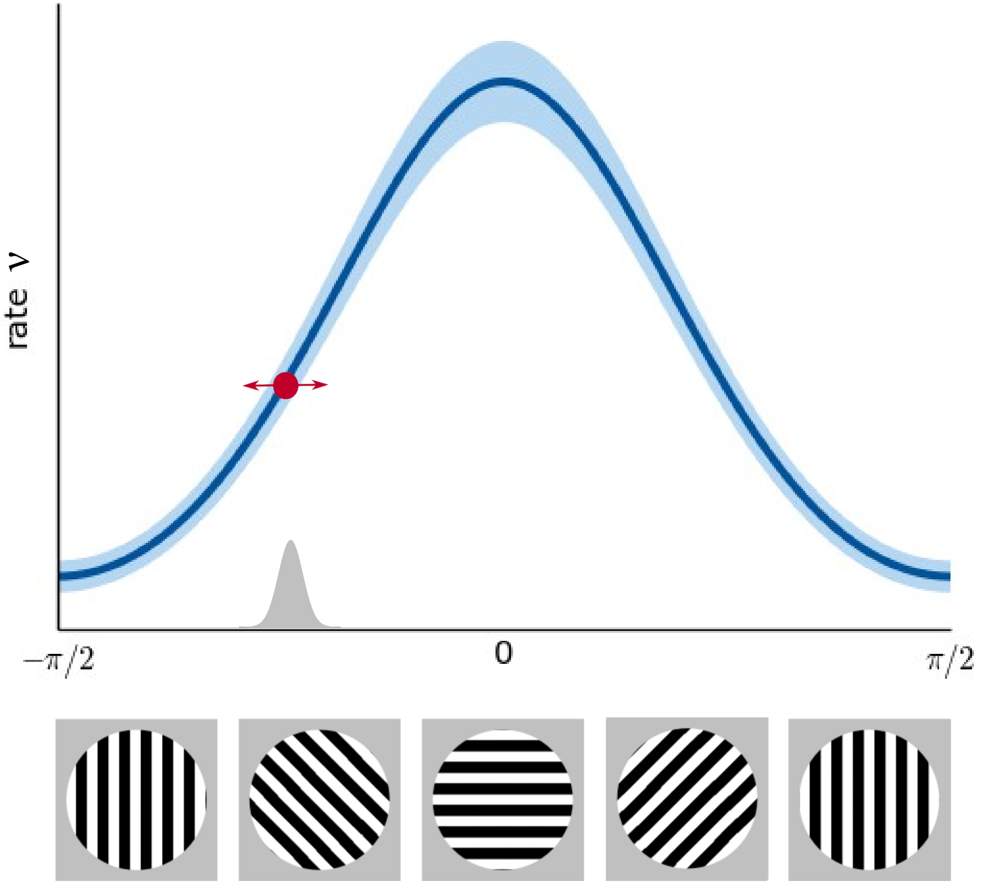




- Variance decreases:

$$\nu = \frac{1}{N} \sum_i^N \nu_i$$

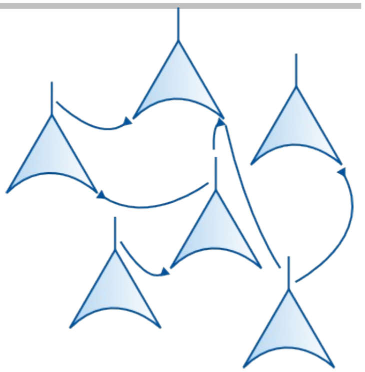
$$E[\nu] = \frac{1}{N} \sum_i^N \nu_i = \frac{1}{N} N\, E[\nu_i] = E[\nu_i]$$

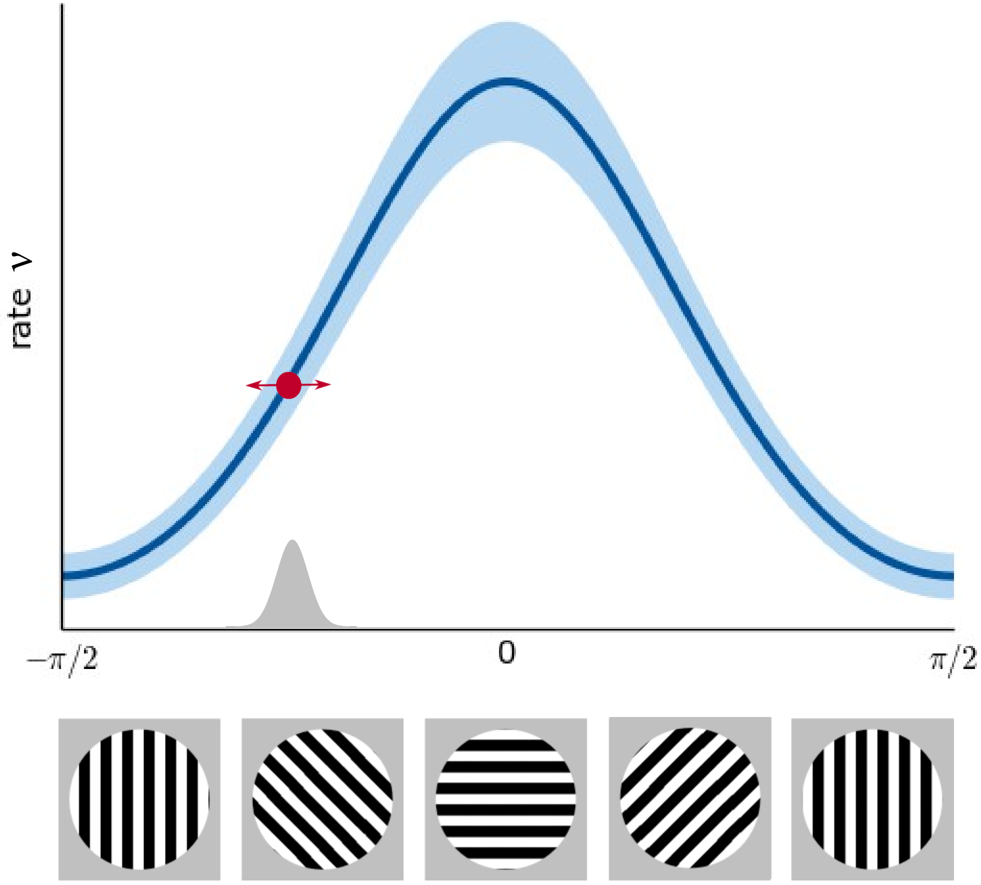
$$Var[\nu] = \frac{1}{N^2} \sum_i^N Var[\nu_i] = \frac{1}{N} Var[\nu_i]$$

- Improved precision!

Effect on neural coding

- Population code: N *correlated* cells with the same preferred orientation





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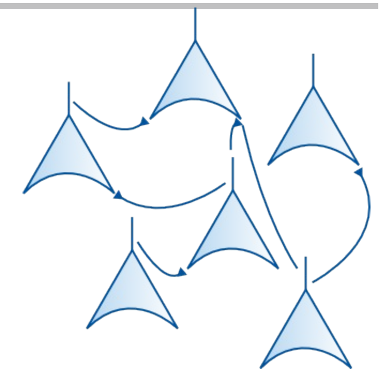

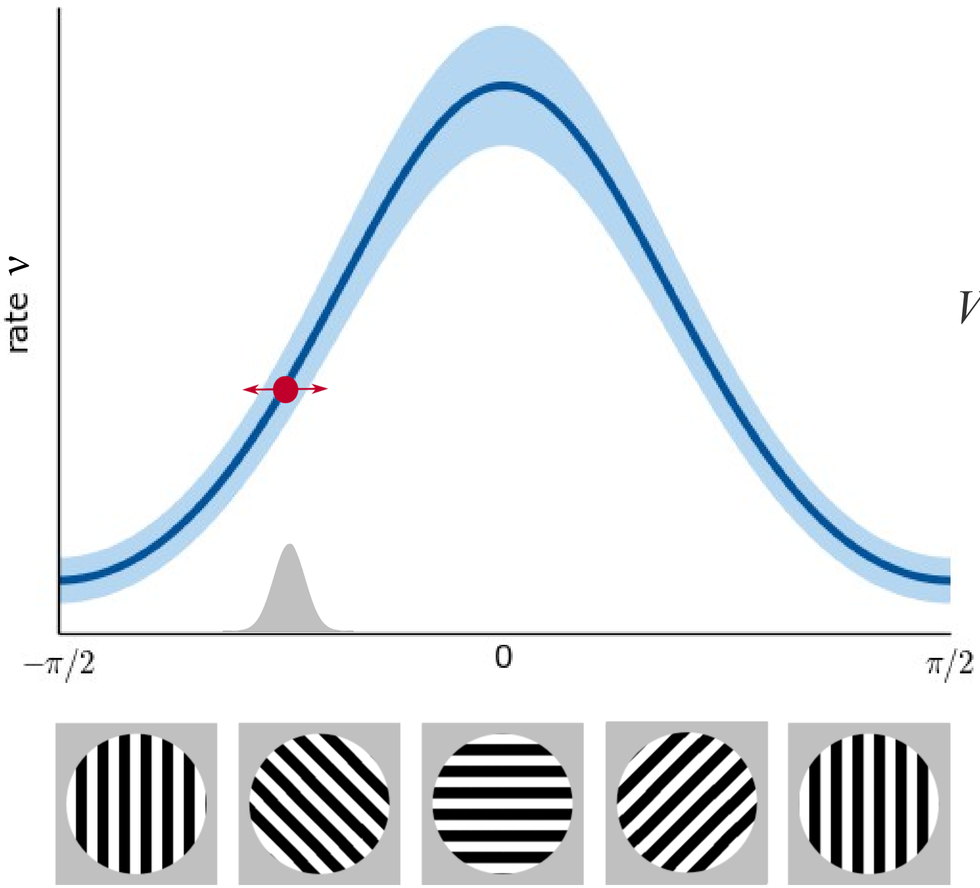

- Variance increases with ρ:

$$Var[\nu] = \frac{1}{N^2}\left(\sum_i^N Var[\nu_i] + \sum_{i \neq j} Cov[\nu_i \nu_j]\right)$$
$$= \frac{1}{N^2} Var[\nu_i]\left(N + N(N-1)\rho\right)$$
$$\approx \rho\, Var[\nu_i]$$

Effect on neural coding

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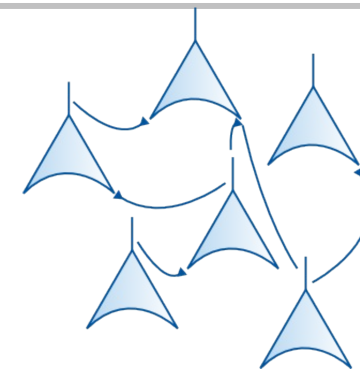

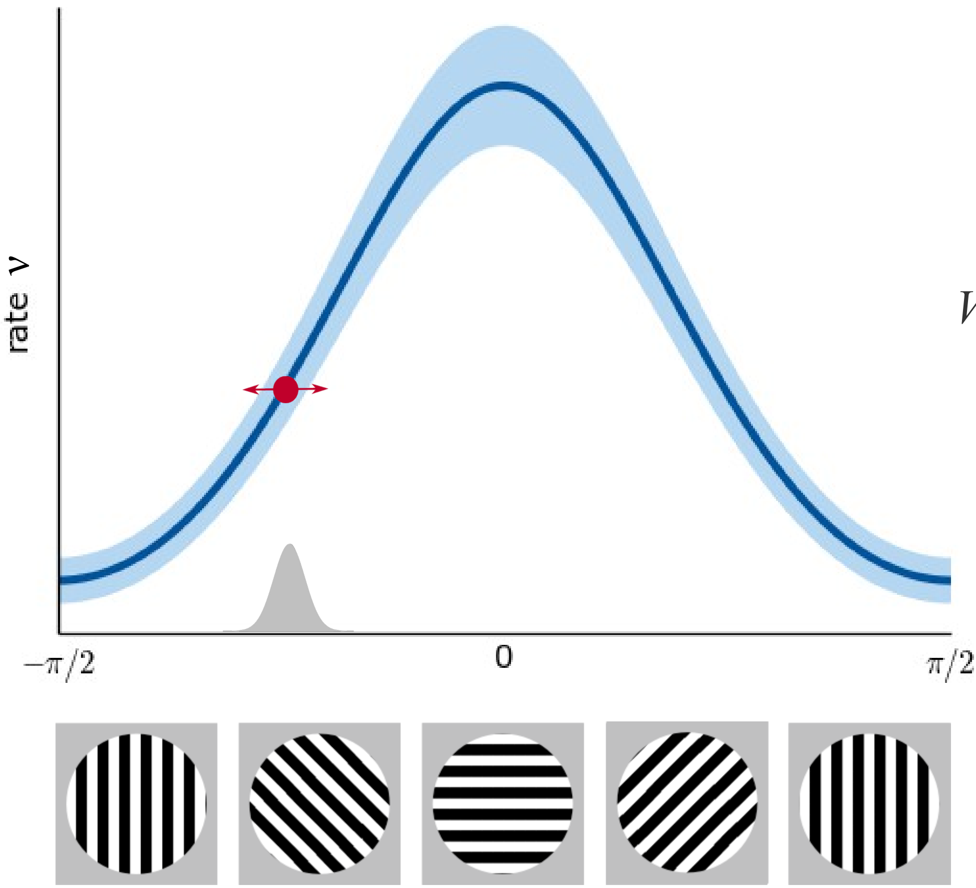

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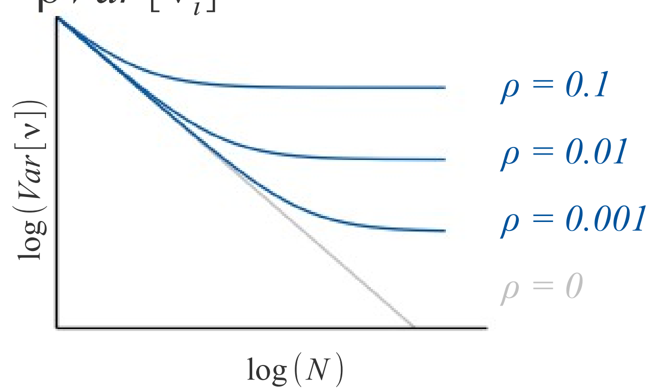
$$Var[\nu]=\frac{1}{N^2}\left(\sum_i^N Var[\nu_i]+\sum_{i\neq j} Cov[\nu_i\nu_j]\right)$$

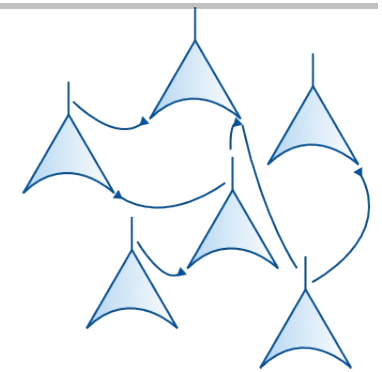
$$=\frac{1}{N^2}Var[\nu_i](N+N(N-1)\rho)$$

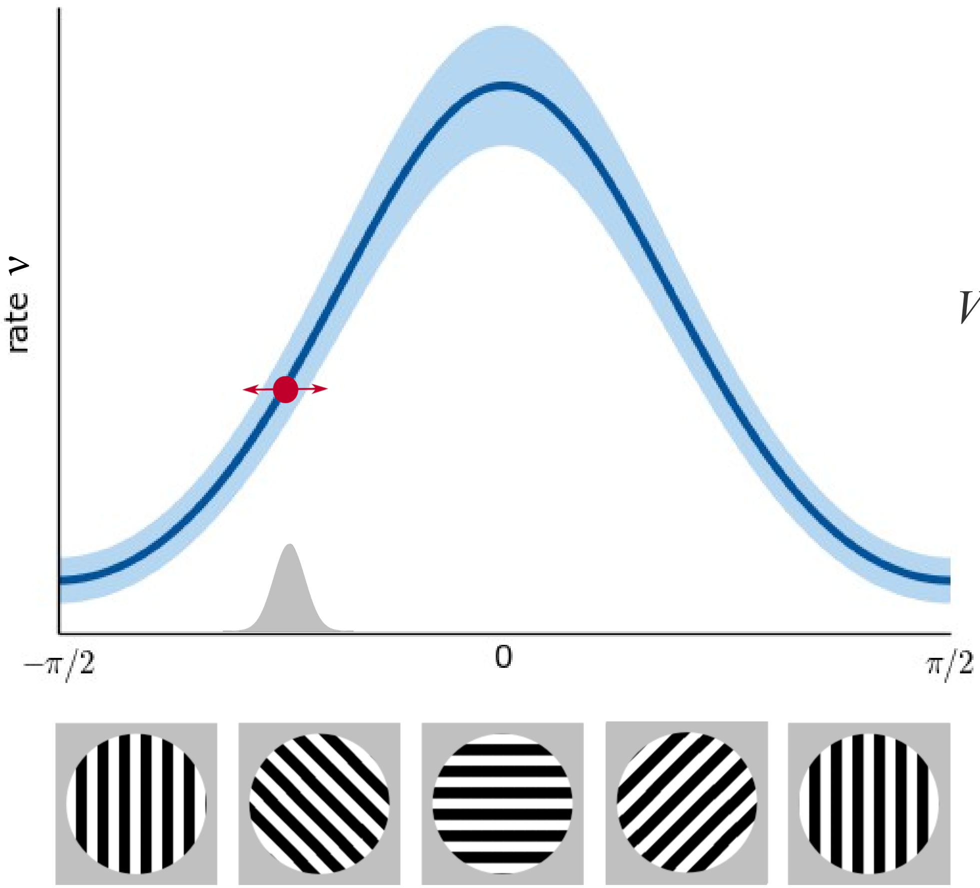
$$\approx\rho\, Var[\nu_i]$$



Effect on neural coding

- Population code: N *correlated* cells with the same preferred orientation





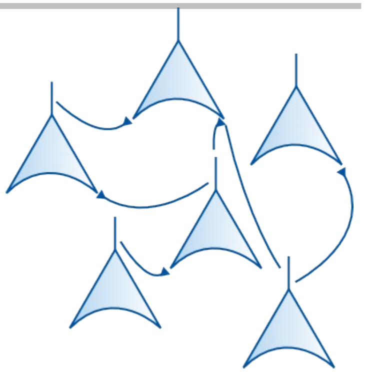
- Variance increases with ρ:

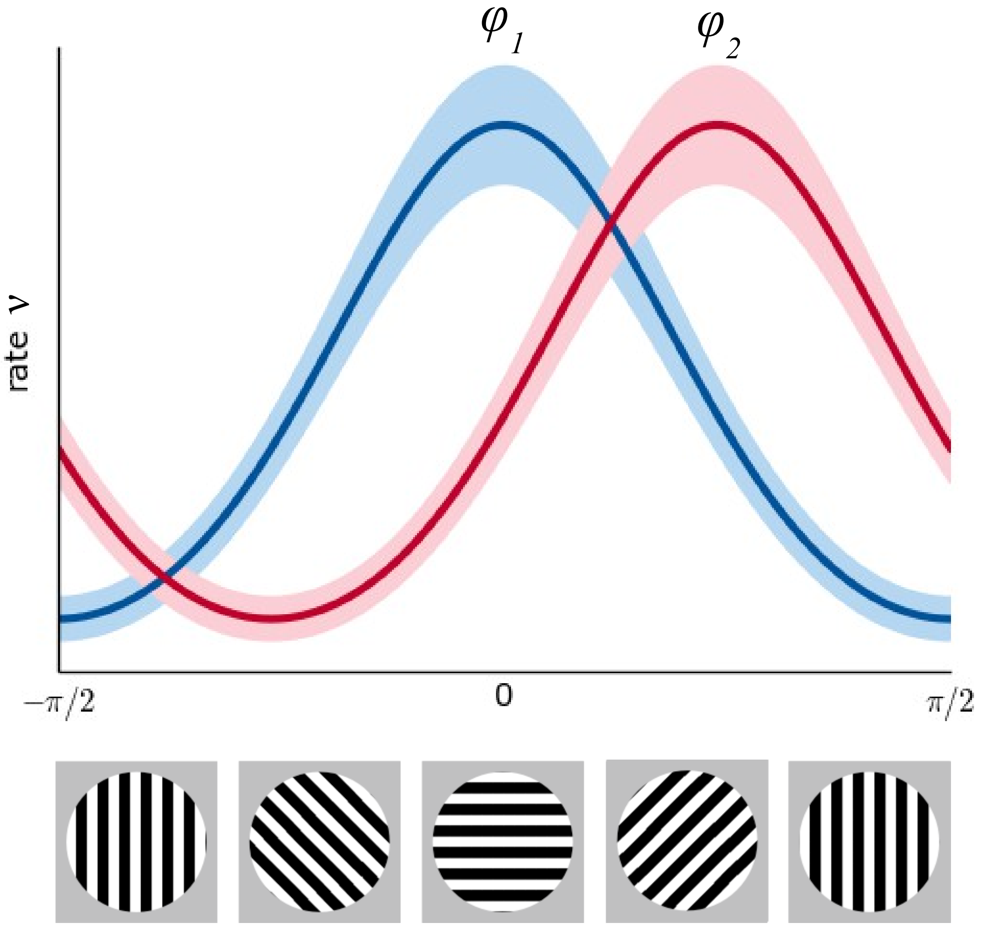
$$Var[\nu] = \frac{1}{N^2}\left(\sum_i^N Var[\nu_i] + \sum_{i\neq j} Cov[\nu_i \nu_j]\right)$$
$$= \frac{1}{N^2} Var[\nu_i]\left(N + N(N-1)\rho\right)$$
$$\approx \rho\, Var[\nu_i]$$

- Correlations degrade signal encoding!

Effect on neural coding

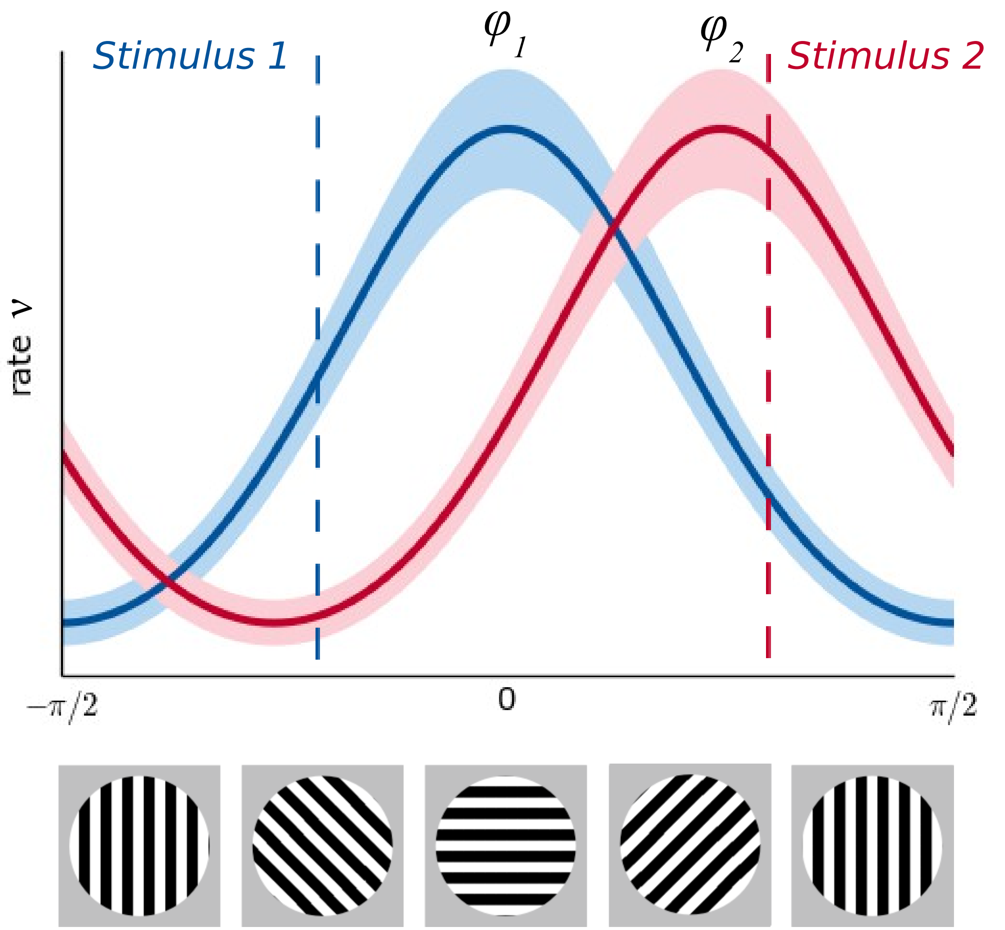
- Population code: 2 cells with *different* preferred orientations

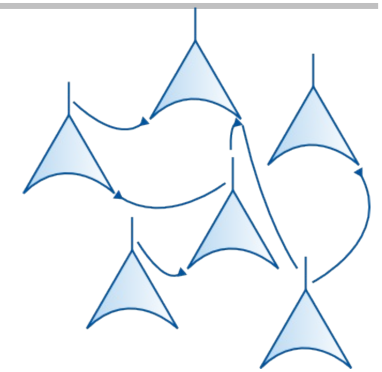




Effect on neural coding

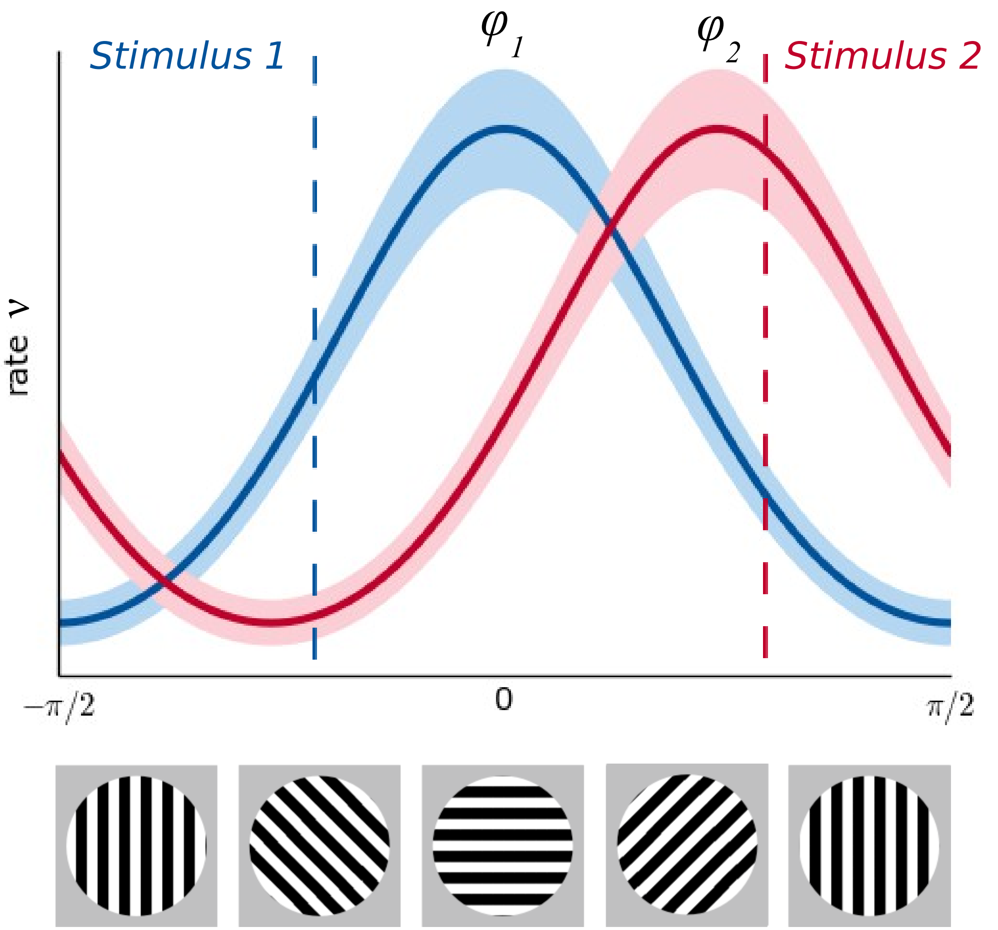
- Population code: 2 cells with *different* preferred orientations

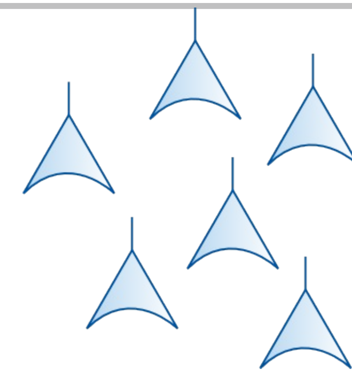




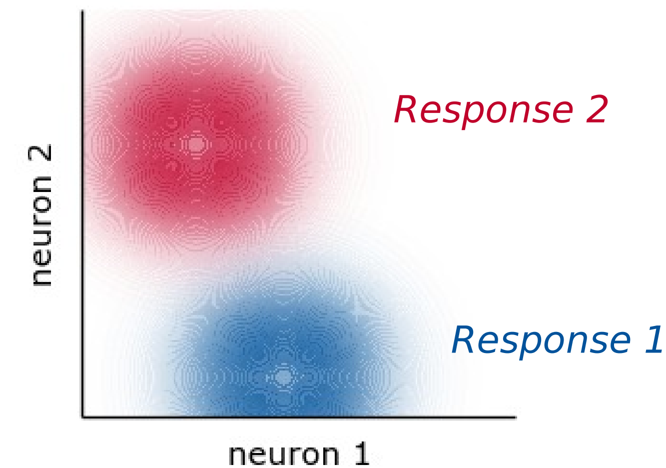
Effect on neural coding

- Population code: 2 cells with *different* preferred orientations



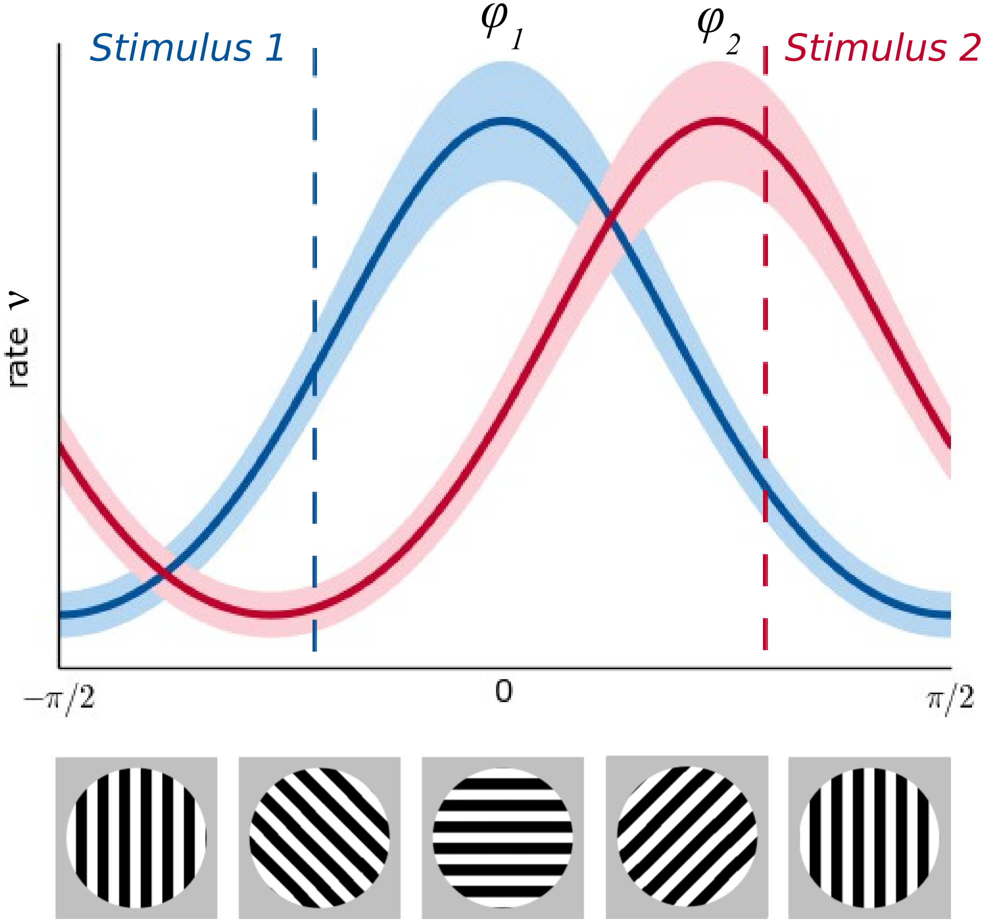


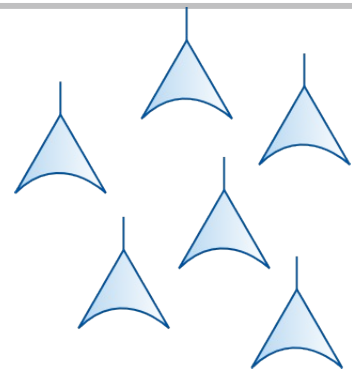
- Readout: Rates ν_1 and ν_2



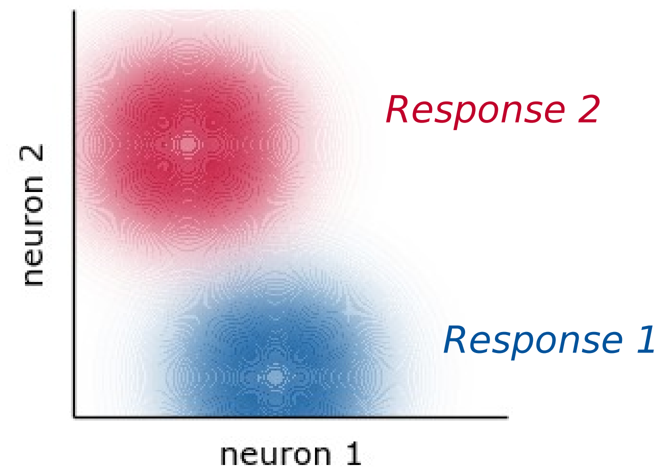
Effect on neural coding

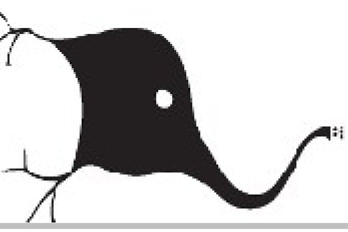
- Population code: 2 cells with *different* preferred orientations



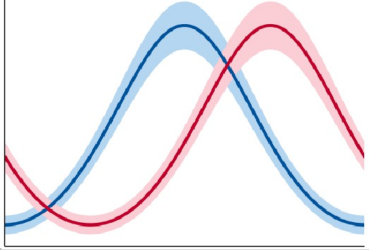


1) ν_1 and ν_2 independent:





Assignment 3: Rate coding



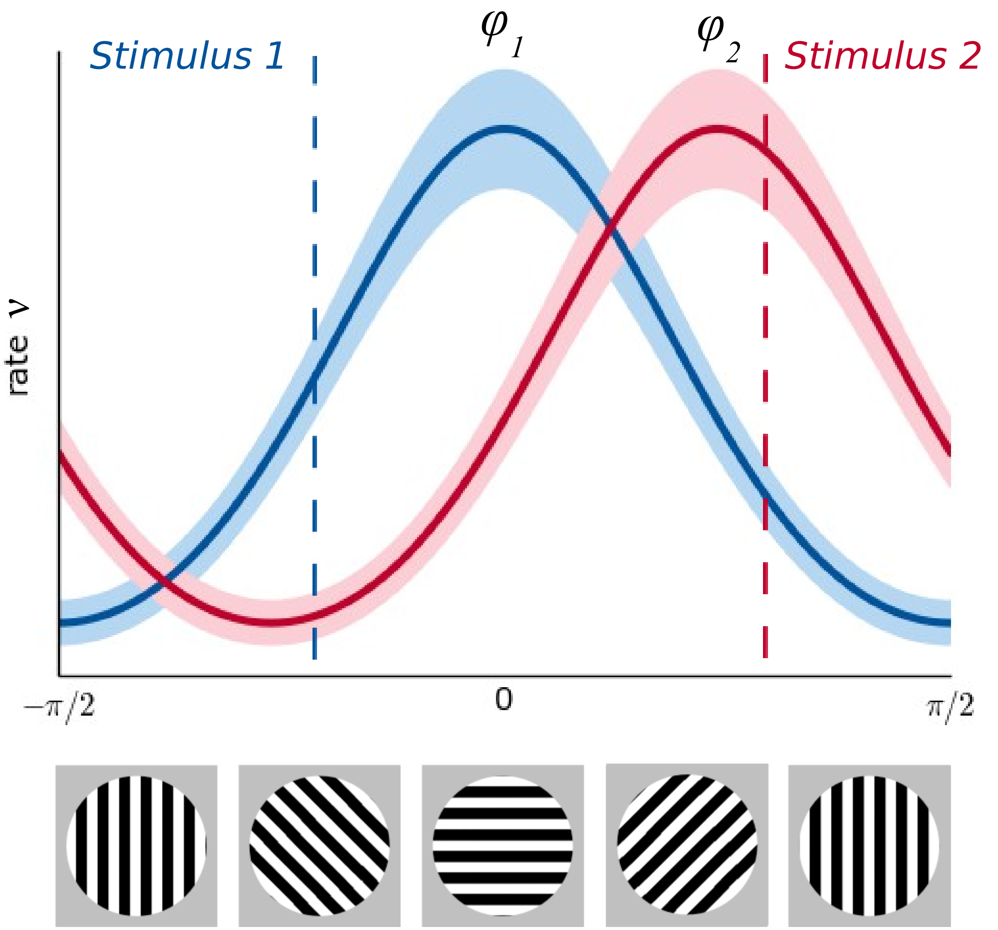
1) Plot the rates of neuron 1 and neuron 2 together using the provided code. What happens when you induce correlations?

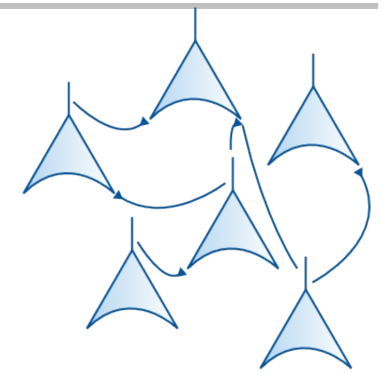
2) Try different combinations of stimuli and preferred orientation and check how noise correlations affect the separability of the output firing rates.

3) How does the difference between prefered orientations relate to signal correlations?

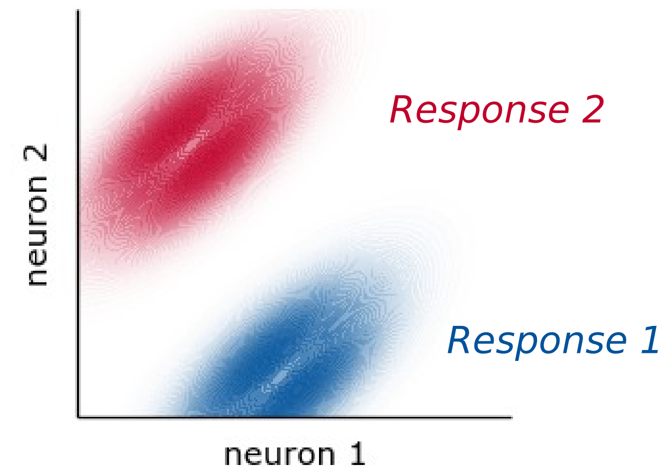
Effect on neural coding

- Population code: 2 cells with *different* preferred orientations



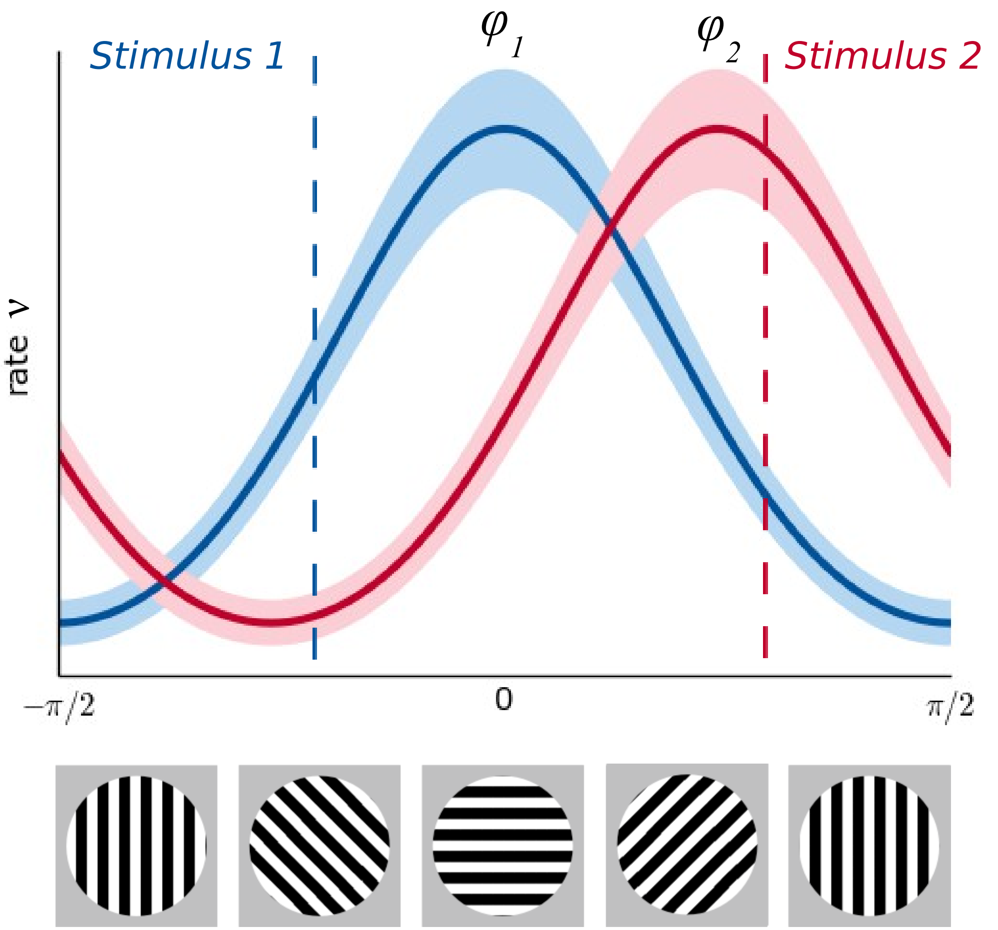


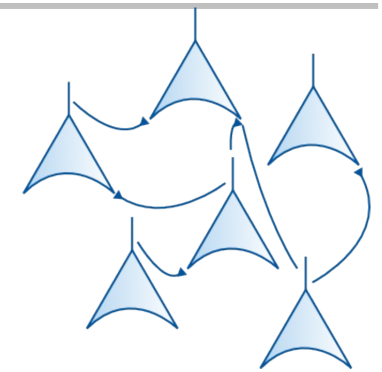
2) ν_1 and ν_2 correlated:



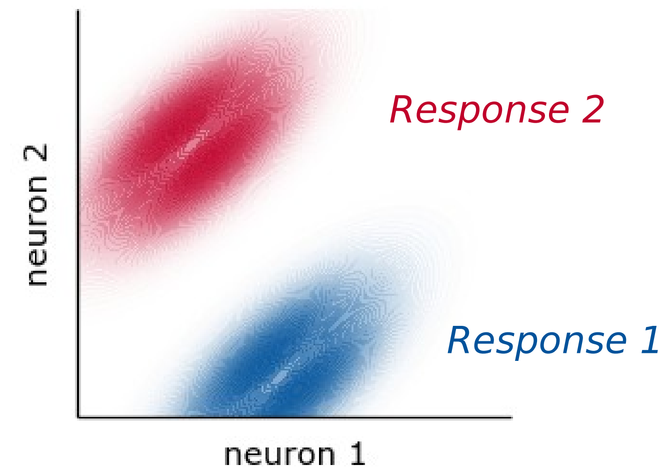
Effect on neural coding

- Population code: 2 cells with *different* preferred orientations





2) ν_1 and ν_2 correlated:

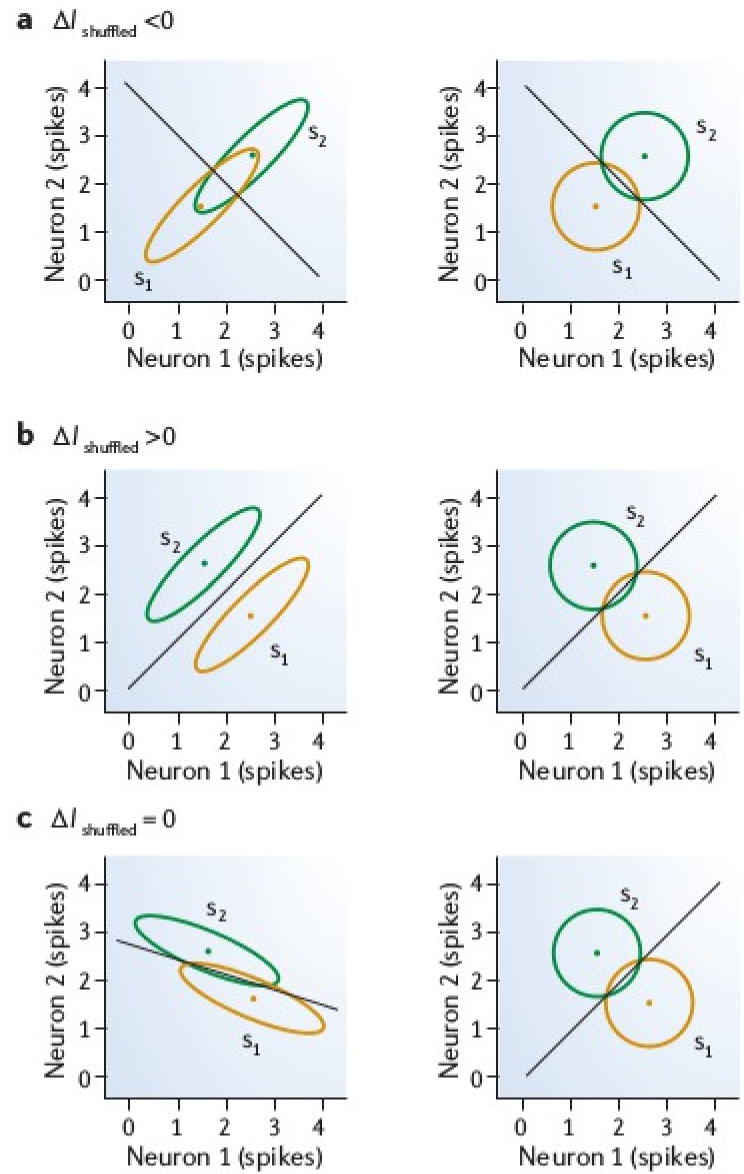


- Effect depends on φ

(Averbeck et al, 2006)

Effect on neural coding

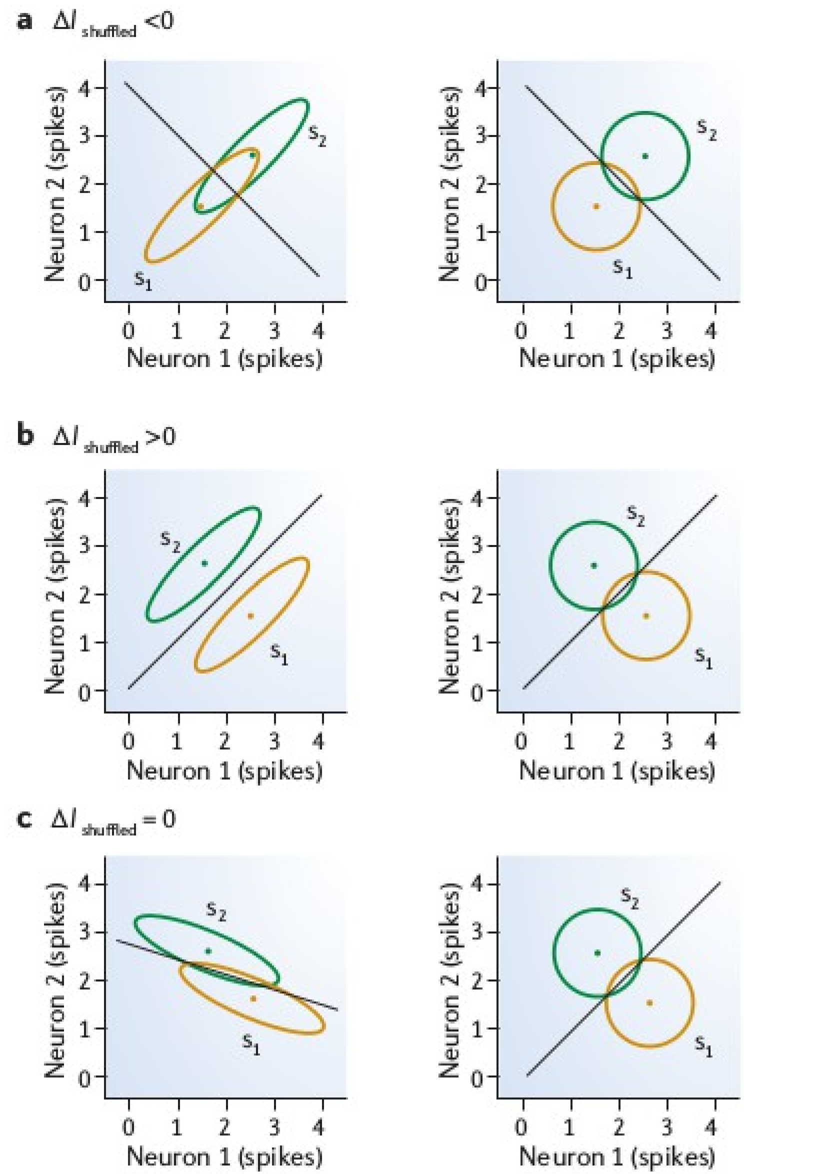
- Effect of noise correlations depends on signal correlations *(Averbeck et al, 2006; Abbott & Dayan, 1999)*



Effect on neural coding

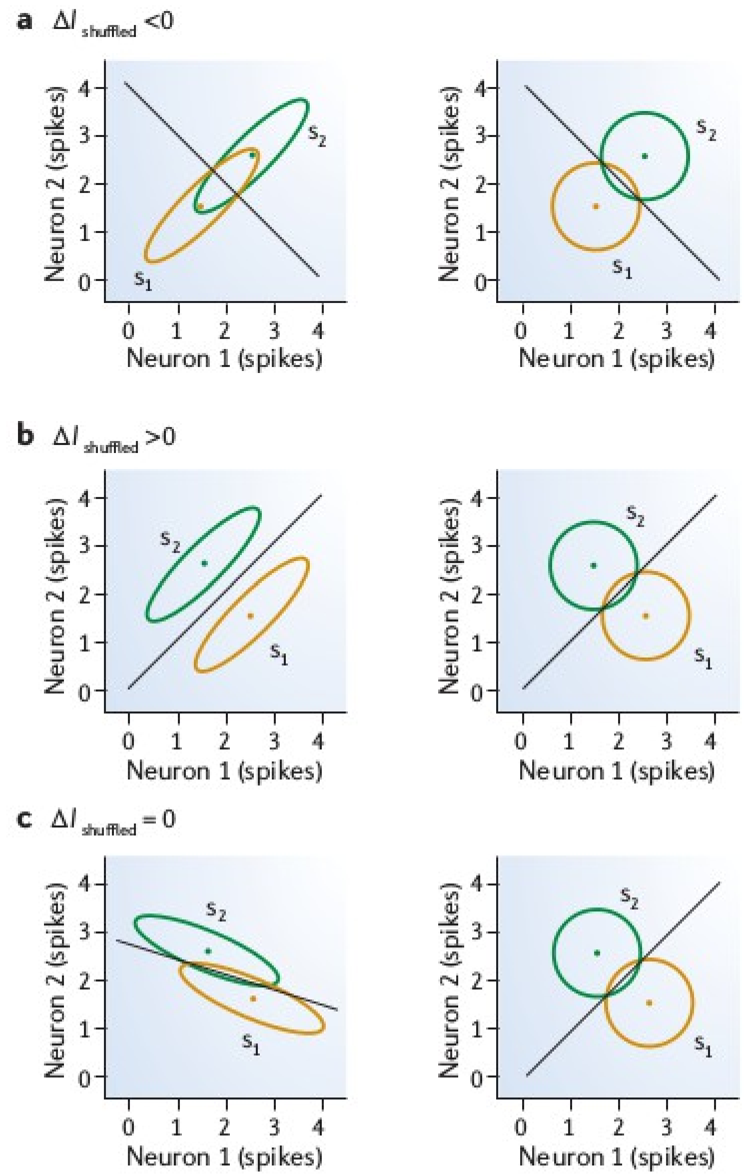
- Effect of noise correlations depends on signal correlations *(Averbeck et al, 2006; Abbott & Dayan, 1999)*

- Details matter in studying the effect of correlations on coding!



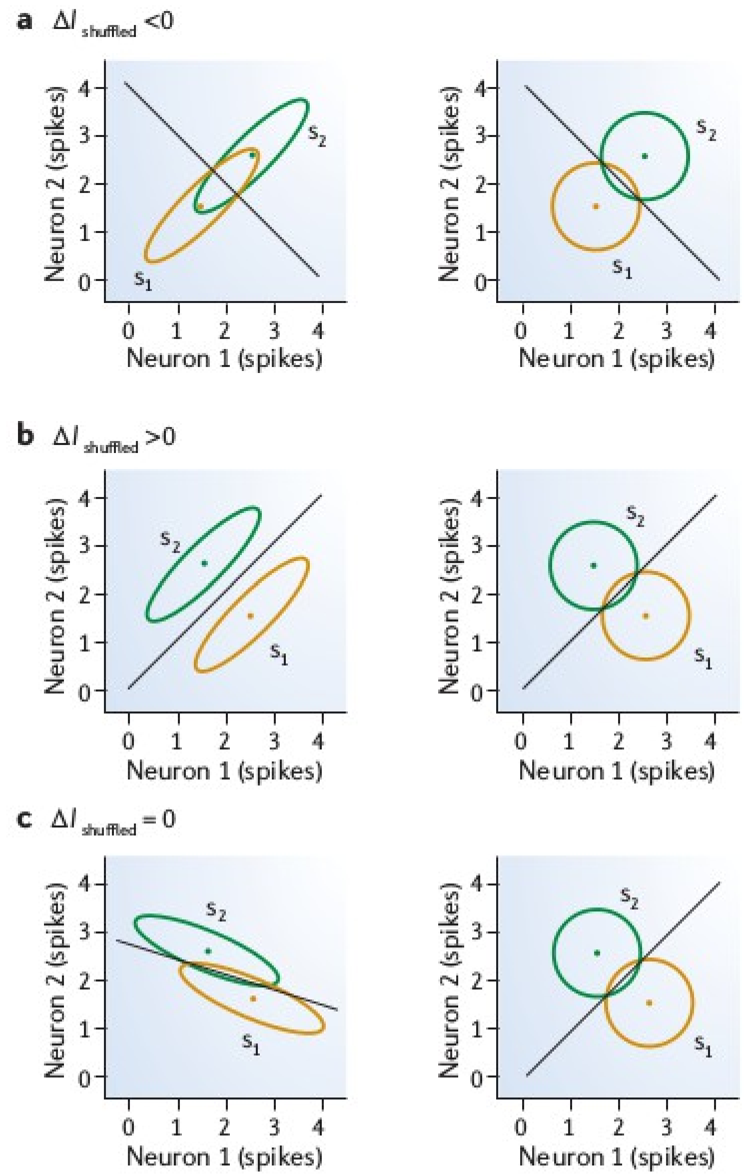
Effect on neural coding

- Effect of noise correlations depends on signal correlations *(Averbeck et al, 2006; Abbott & Dayan, 1999)*
- Details matter in studying the effect of correlations on coding!
- Active role of correlations in coding also possible! *(Gray & Singer 1989; Riehle & Grun, 1997)*



Effect on neural coding

- Effect of noise correlations depends on signal correlations *(Averbeck et al, 2006; Abbott & Dayan, 1999)*
- Details matter in studying the effect of correlations on coding!
- Active role of correlations in coding also possible! *(Gray & Singer 1989; Riehle & Grun, 1997)*
- Still many open questions: higher order correlations...



References and further reading

- These slides are based on lecture slides titled 'Introduction to correlated spiking in neural coding and dynamics' by Eric Shea-Brown, available online.

- Mechanisms:

de la Rocha, Doiron et al., Correlation between neural spike trains increaseswith firing rate, Nature, 2007

Shea-Brown et al., Correlation and Synchrony Transfer in Integrate-and-Fire Neurons: Basic Properties and Consequences for Coding, PRL, 2008

Rosenbaum et al., Pooling and correlated neural activity, Front Comput Neurosci, 2010

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- Effects on coding:

Averbeck et al., Neural correlations, population coding and computation, Nat Neurosci Reviews, 2006

Abbot & Dayan, The effect of correlated variability on the accuracy of a population code, Neural Computation, 1999

Gray & Singer, Stimulus-specific neuronal oscillations in orientation columns of cat visual cortex, Proc Natl Acad Sci, 1989

Riehle, Grun et al, Spike synchronization and rate modulation differentially involved in motor cortical function, Science, 1997

- Spiketrains & point processes:

Nawrot et al, Measurement of variability dynamics in cortical spike trains, Jneurosci Methods, 2008