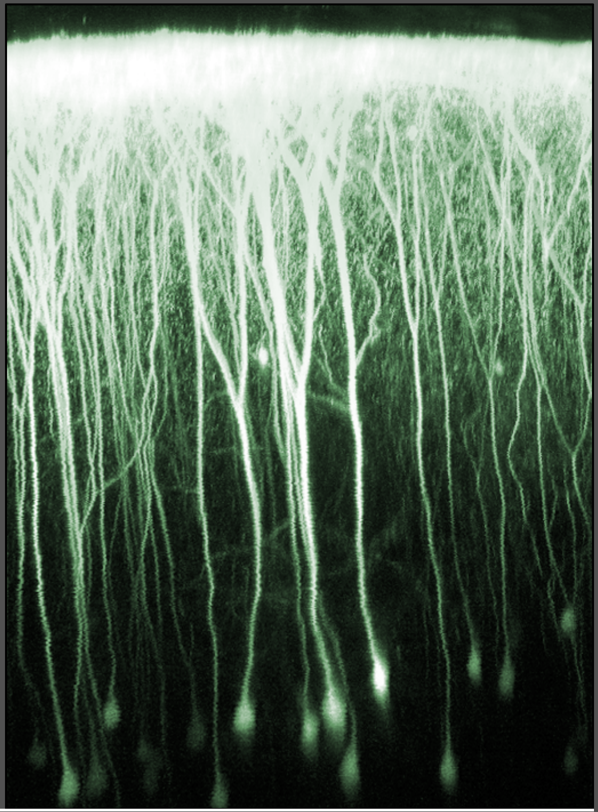

Alexander Ecker

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Baylor College of Medicine, Houston, TX

State dependence of noise correlations in monkey V1

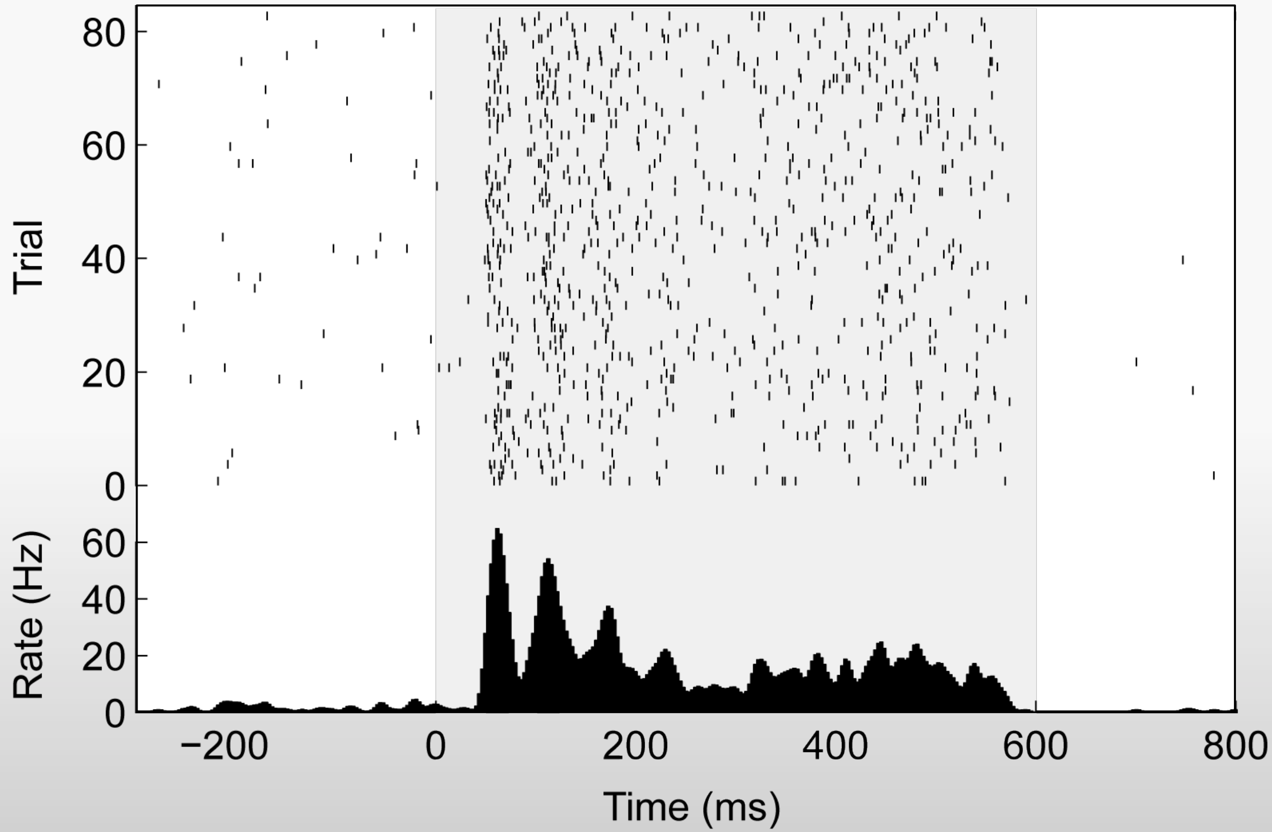
Outline

- Background: correlated variability
- Review: structure of noise correlations in awake monkey V1
- Noise correlations under anesthesia

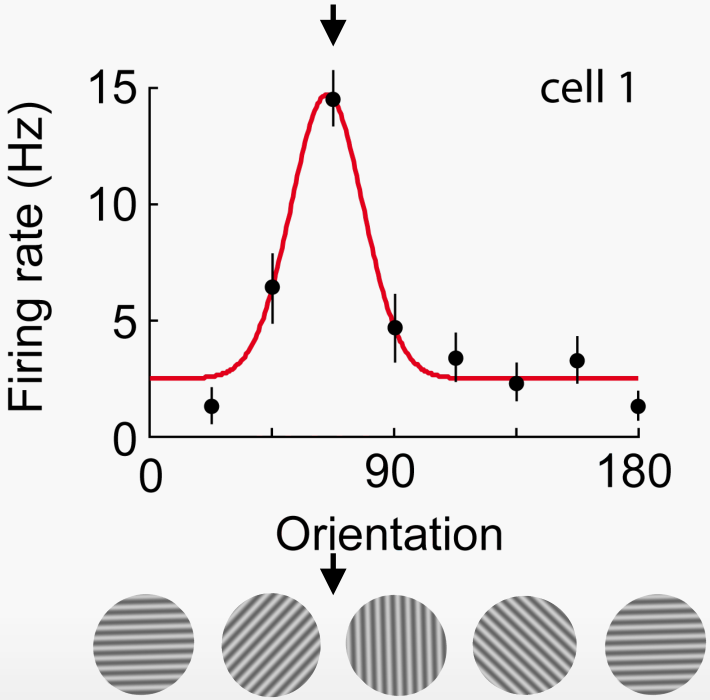
Background: what are noise correlations and why do we care?

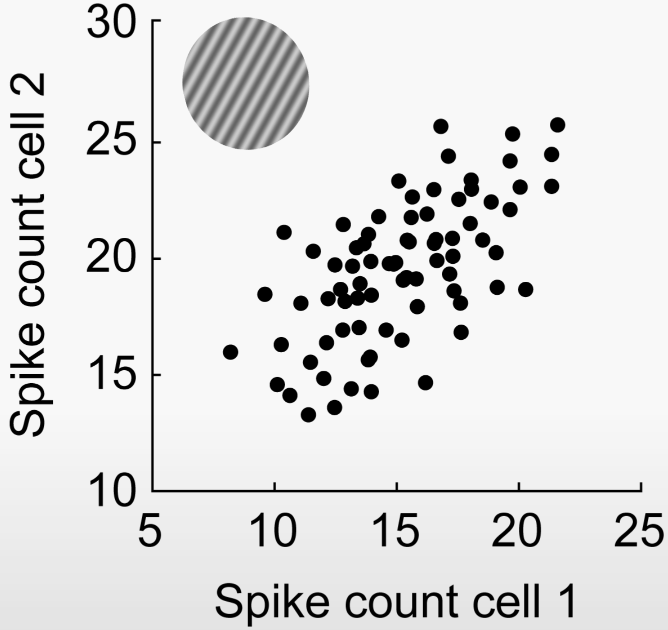
Response variability

Responses to the same stimulus are variable

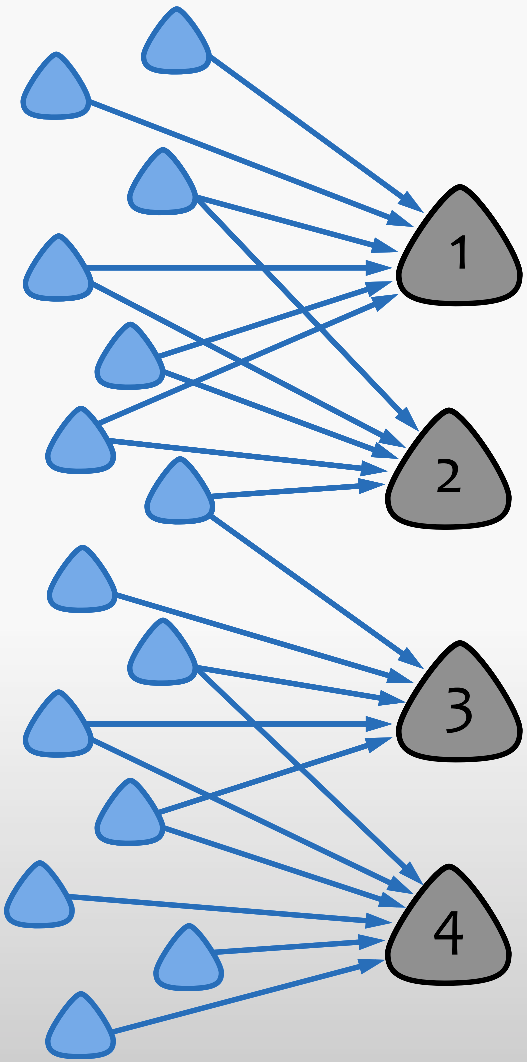


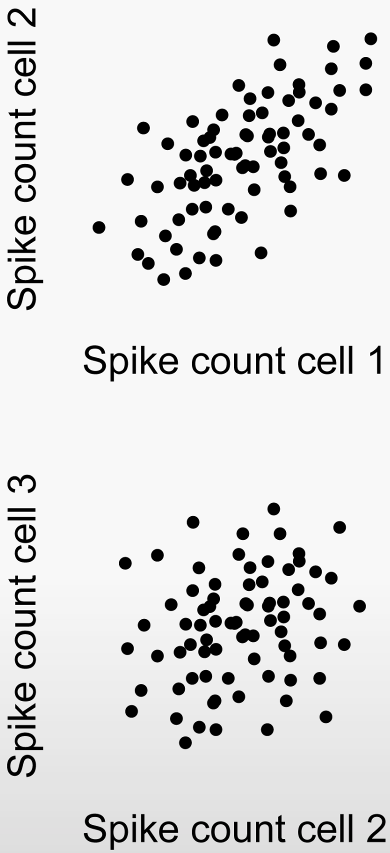
Signal versus noise correlations





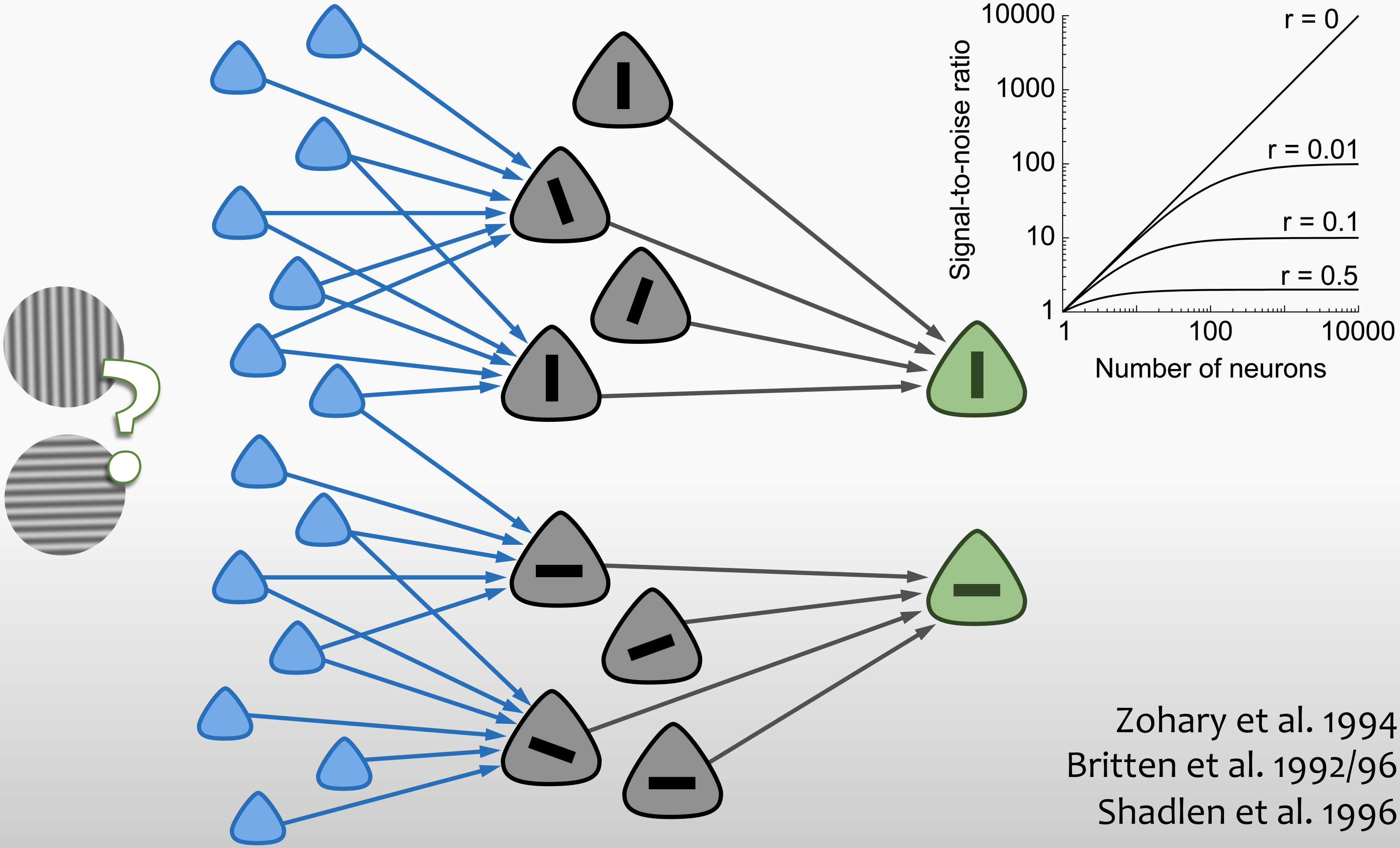
Common input leads to correlations





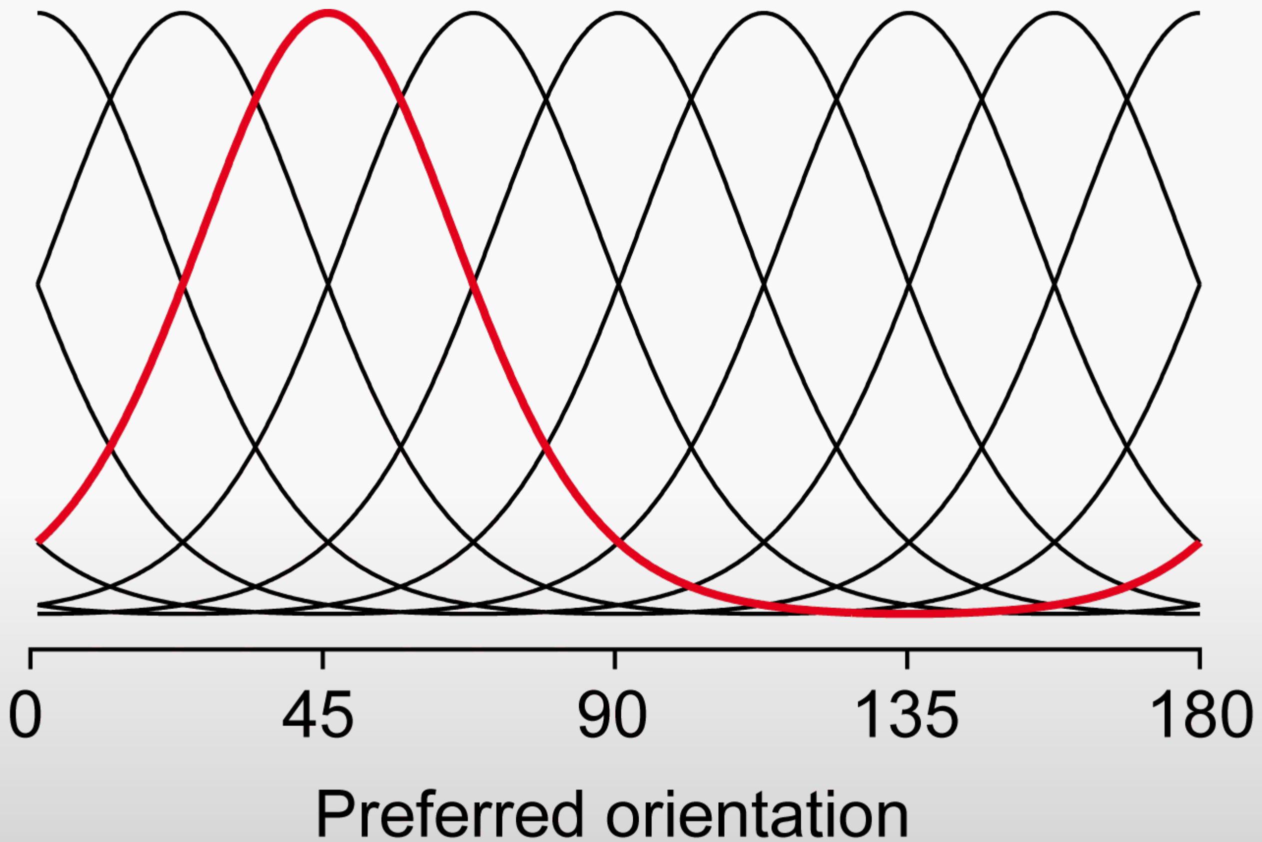
Shadlen & Newsome 1998

The pooling model and correlations

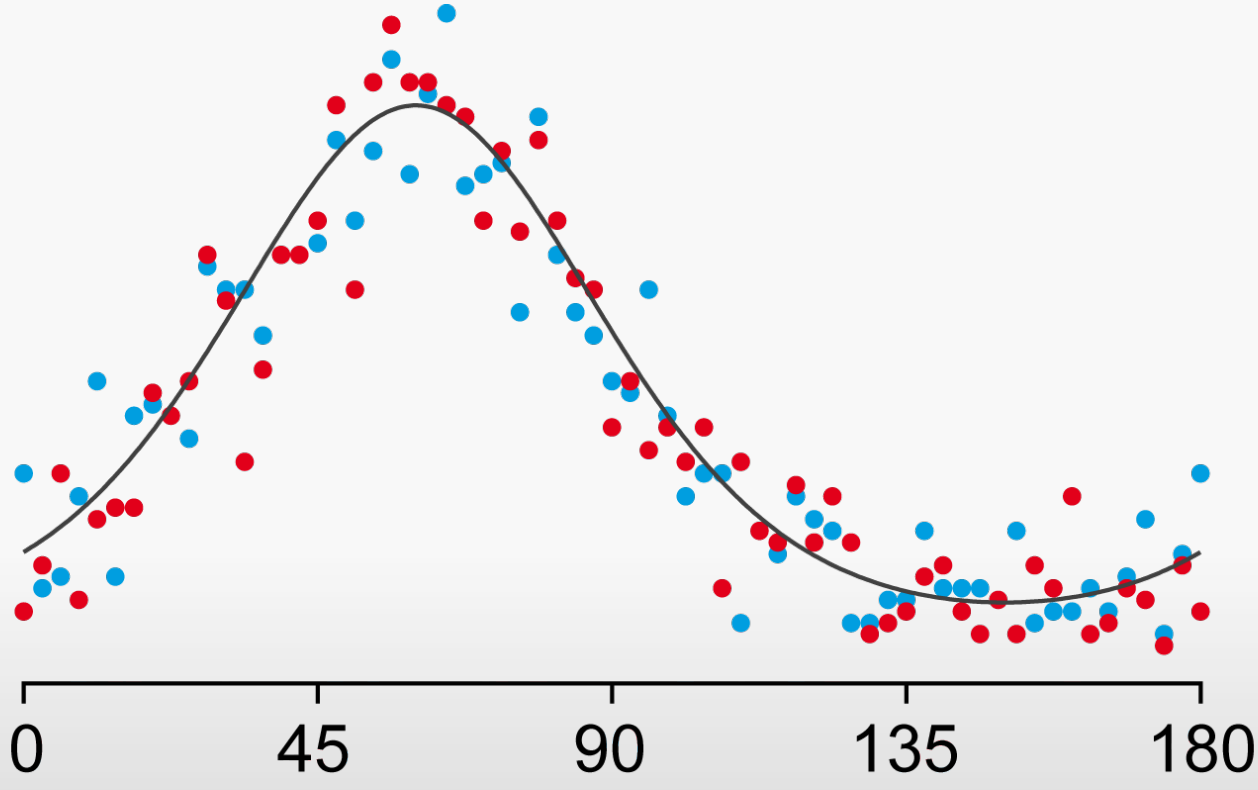


Zohary et al. 1994
Britten et al. 1992/96
Shadlen et al. 1996

Population coding

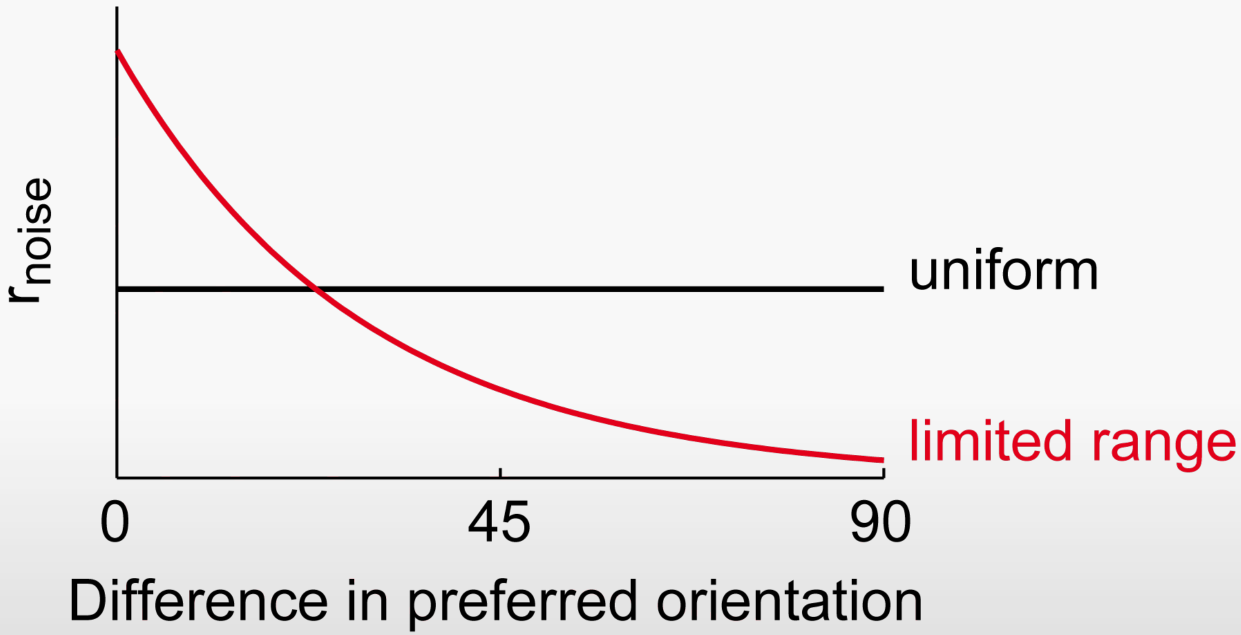


Uncorrelated populations

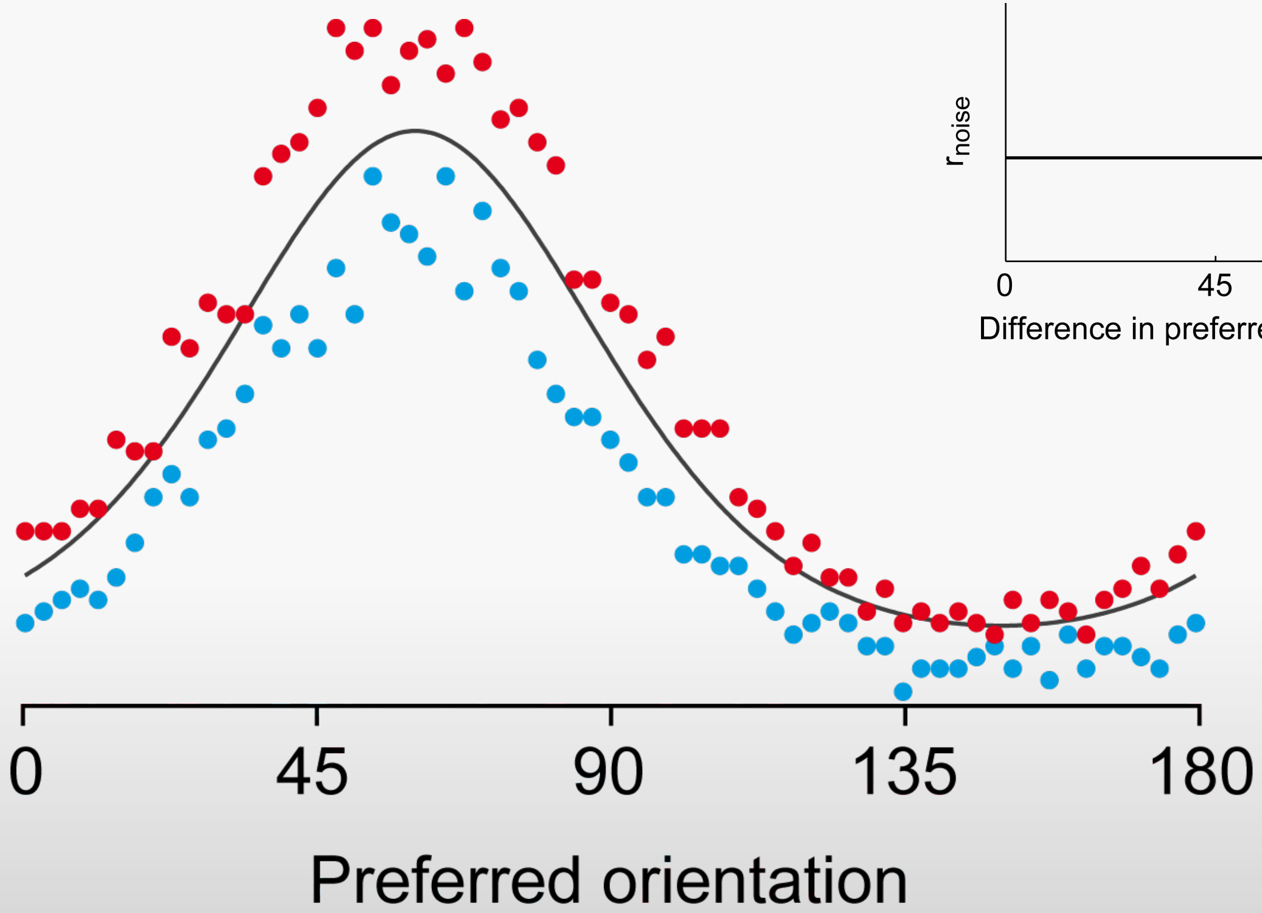


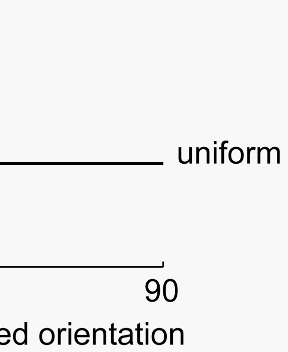
Adapted from Sompolinsky et al., 2001

Correlation structure



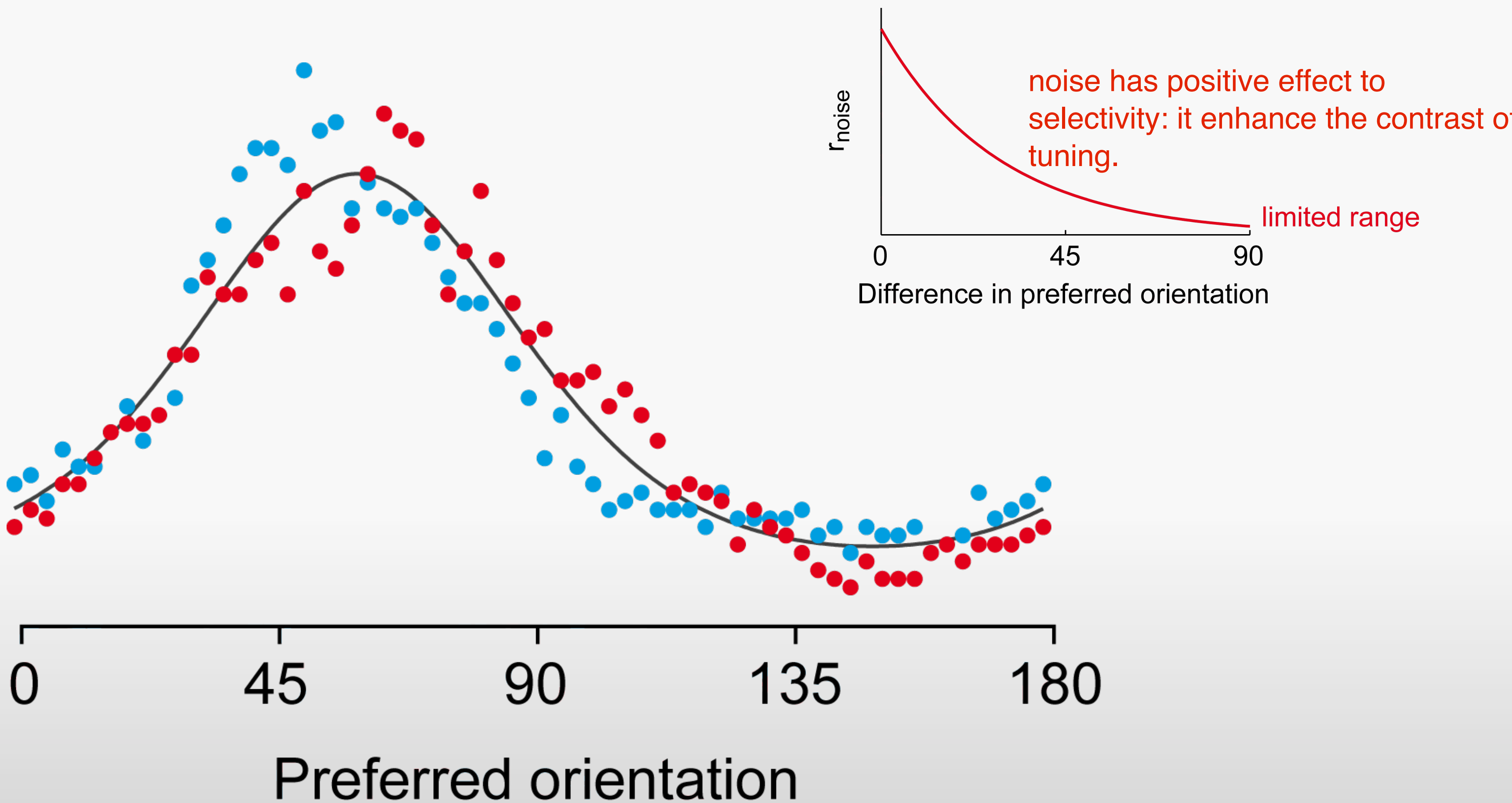
Uniform correlations





Adapted from Sompolinsky et al., 2001

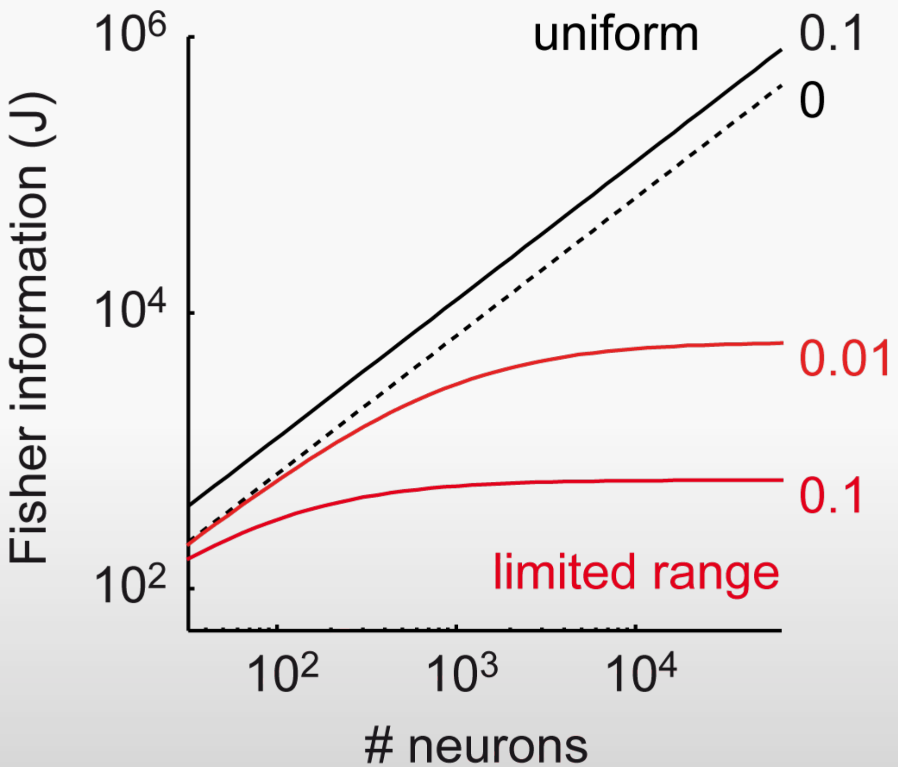
Limited range correlations

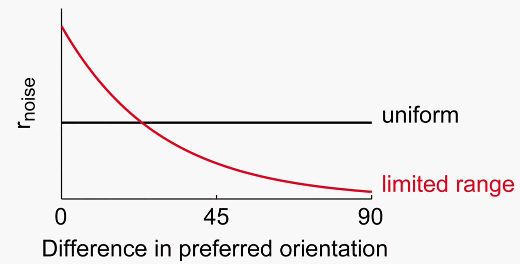


Adapted from Sompolinsky et al., 2001

Optimal readout

Assuming additive noise





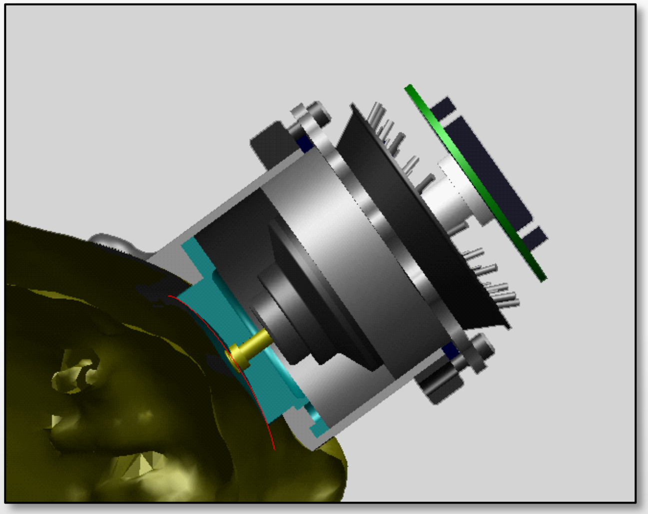
Sompolinsky et al. 2001

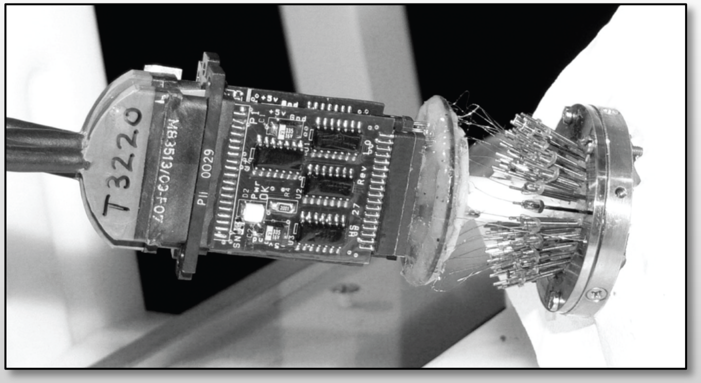
Conclusion

Structure and level of noise correlations strongly affect the population code

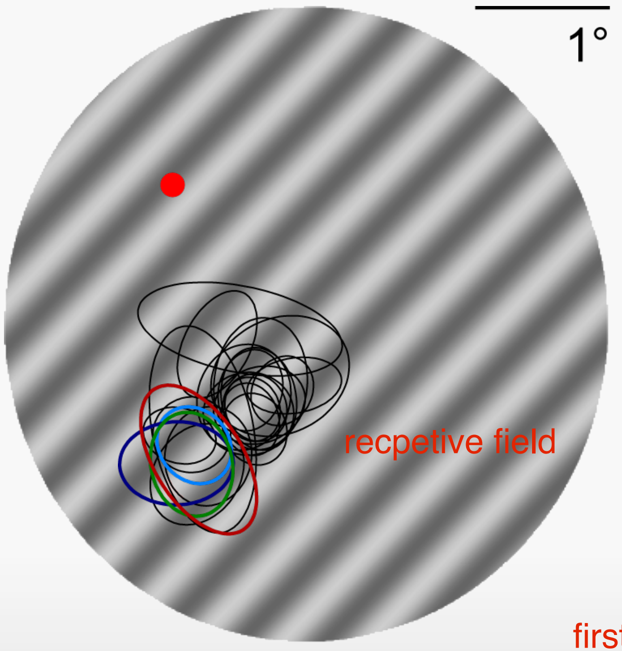
Structure of noise correlations in awake monkey V1

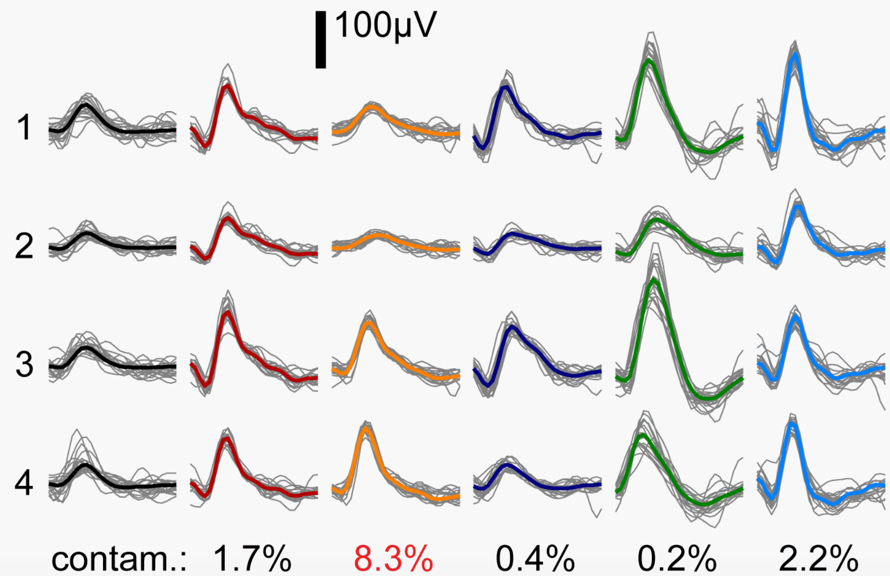
Chronically Implanted Tetrodes



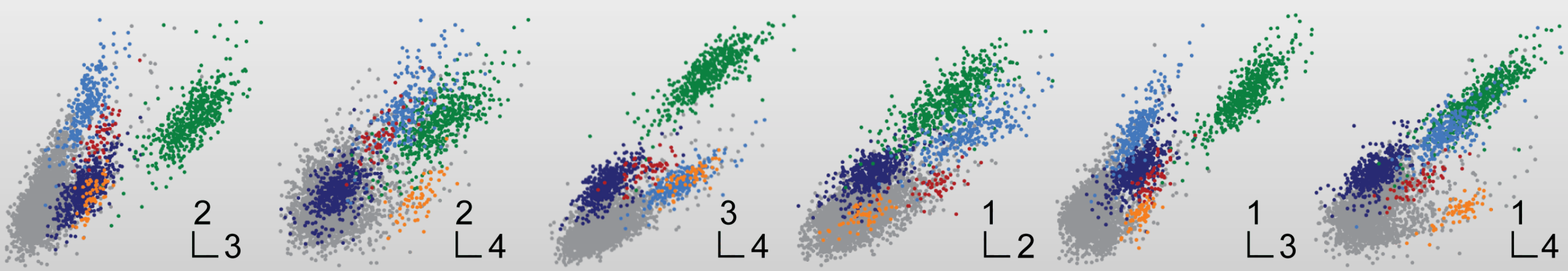


Experimental Paradigm

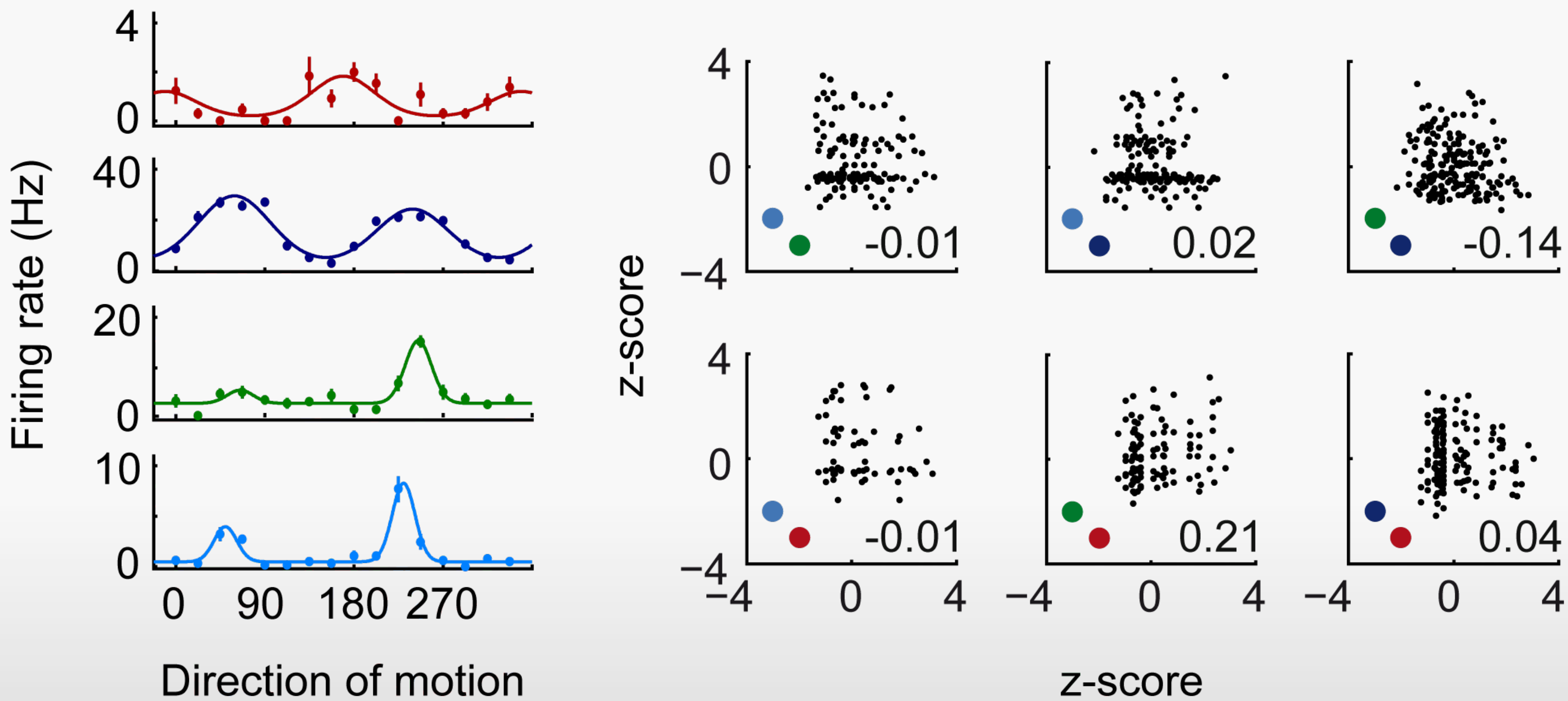




first component of PCA of each pair of 4 channels



Noise correlation of adjacent cells

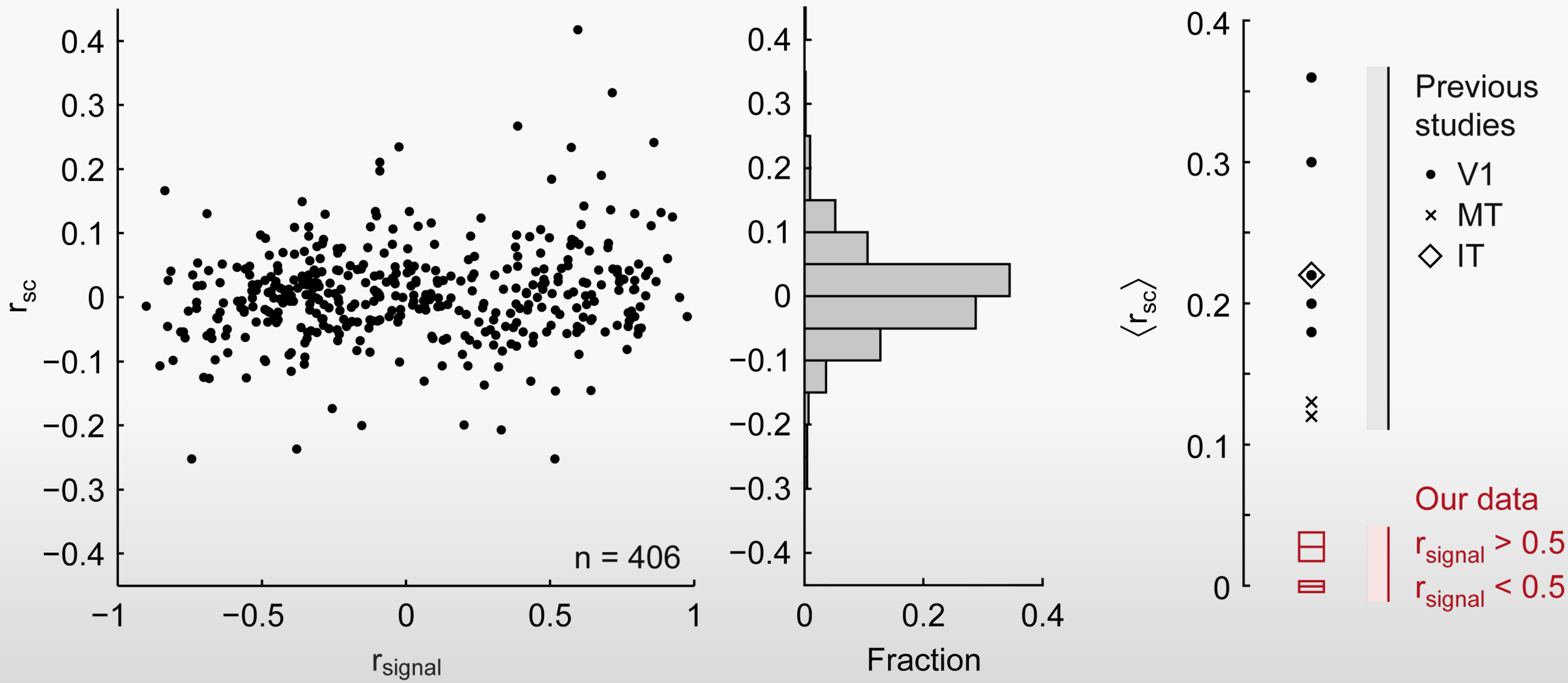


Average correlations on this tetrode: 0.02

to conclude. we can regard electrodes as independent.

Population data

Pairs recorded from same tetrode

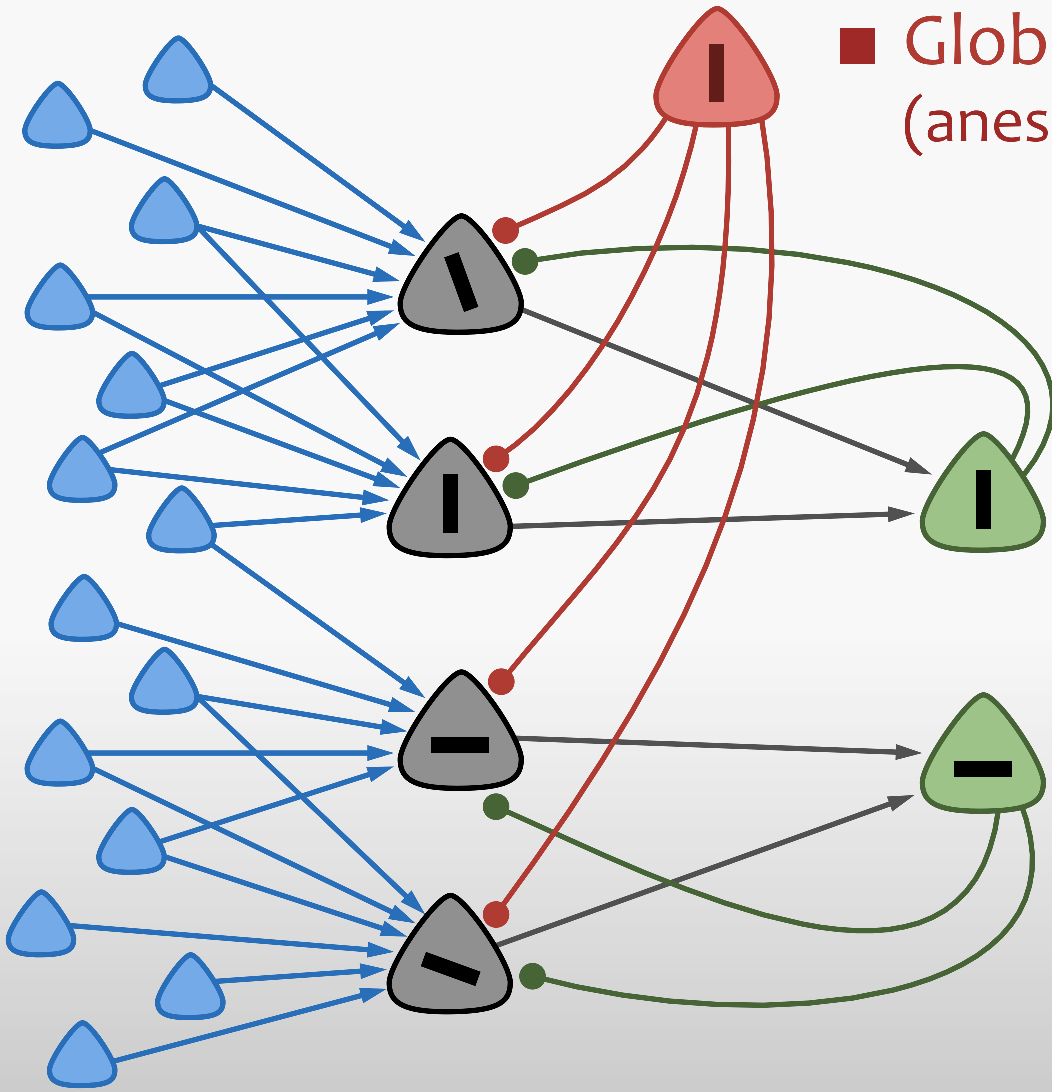


Ecker et al. 2010, Science

Results in awake monkeys

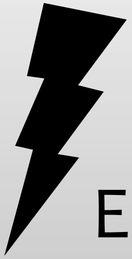
- Noise correlations in awake monkey V1
  - are on average are extremely low (~0.01)
  - depend on difference in preferred orientations (limited range)
- Noise correlations do not depend on the type of stimulus (not shown)
  - static/moving gratings
  - natural images
  - moving bars

Factors affecting correlations



- Global brain states (anesthesia)

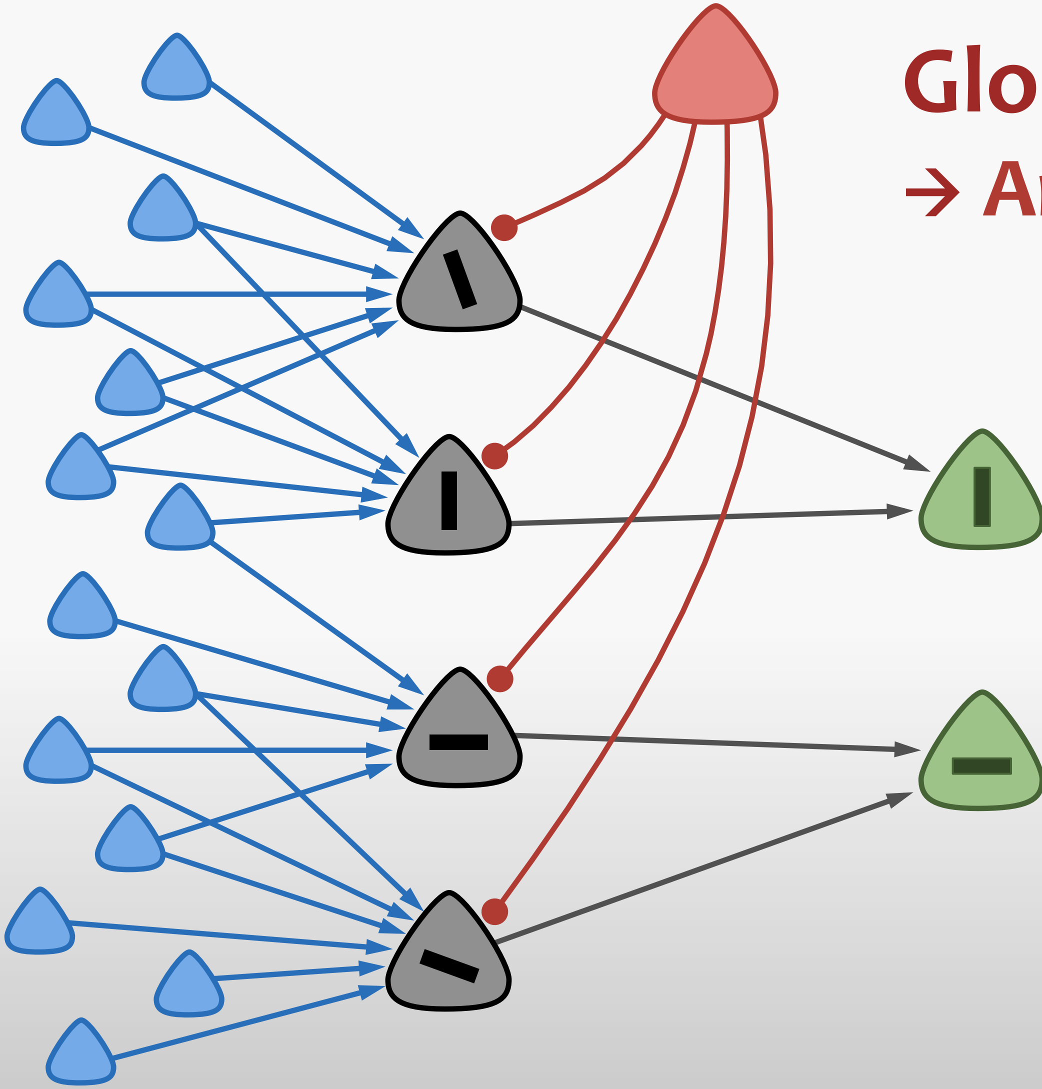
Decision-making
- Attention
- Priors
- Strategies



Spike sorting
Electrode drift

State dependence of noise correlations under anesthesia

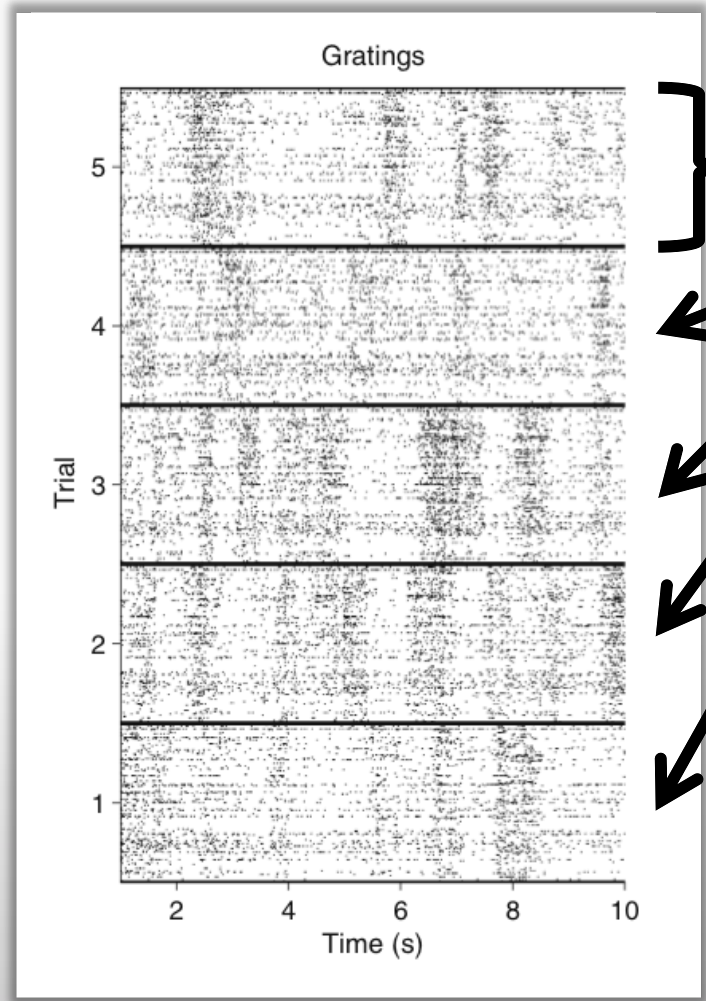
Noise correlations under anesthesia



Global brain states
→ Anesthesia

Compare to:
Smith & Kohn (2008)
Journal of Neuroscience

Variability in anesthetized data

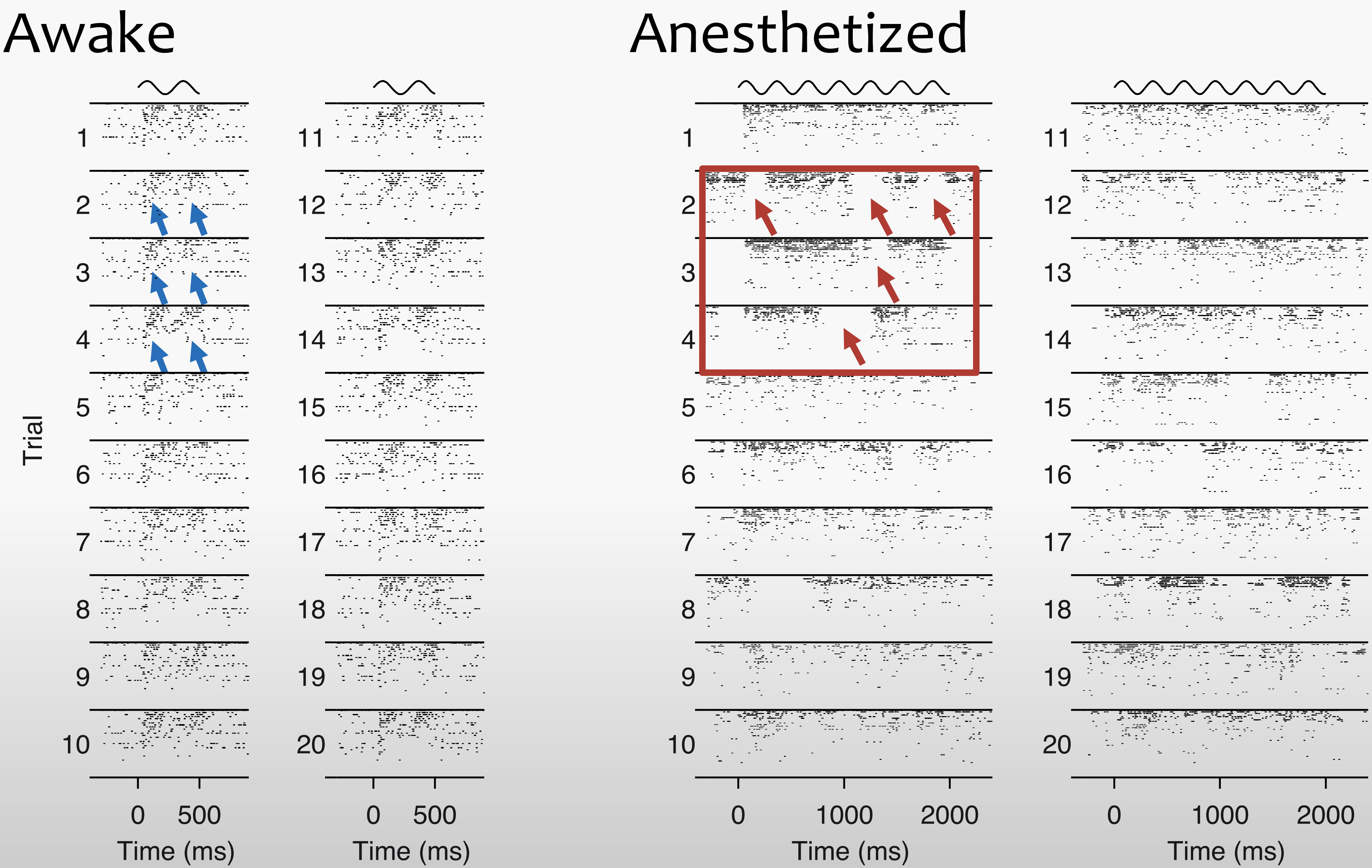


1 trial, 120 neurons

- different trial
- **same** stimulus
- **same** neurons

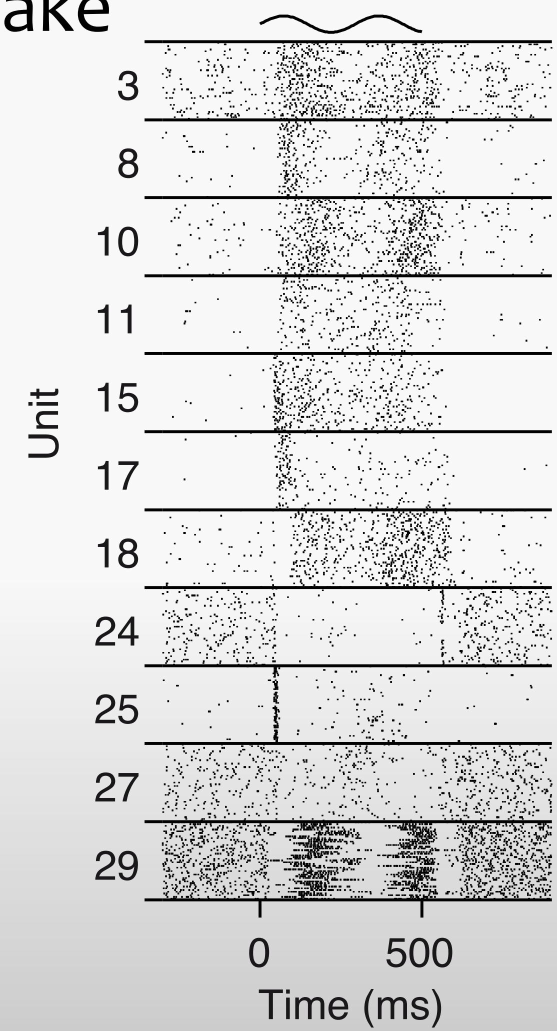
Kelly et al. (2010), *Journal of Computational Neuroscience*

Population activity: grouped by **trial**

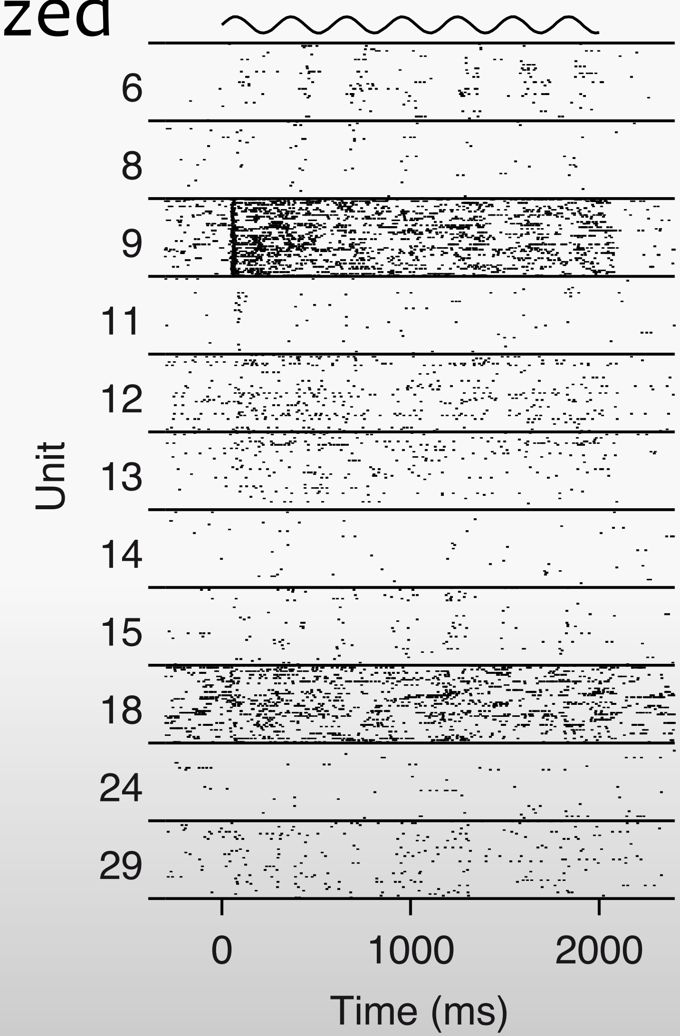


Population activity: grouped by **neuron**

Awake

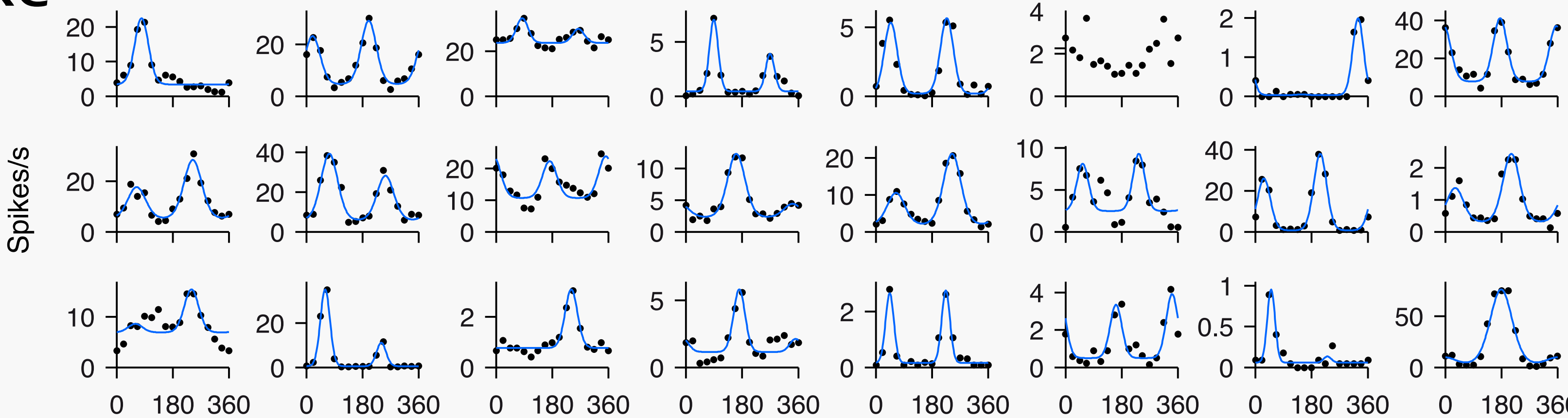


Anesthetized

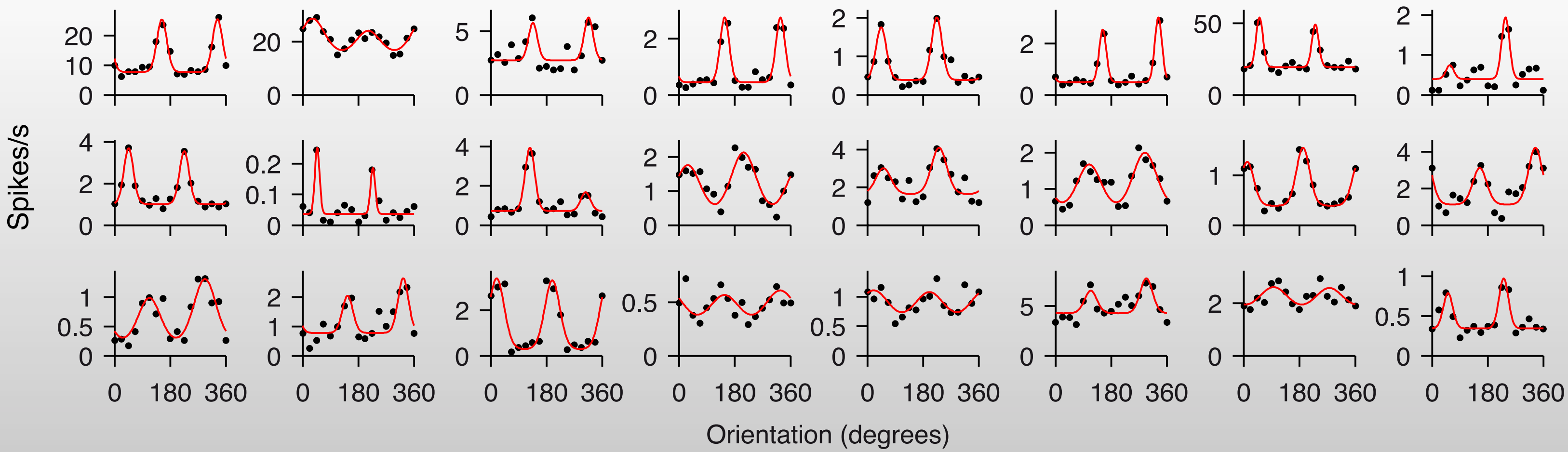


Tuning curves

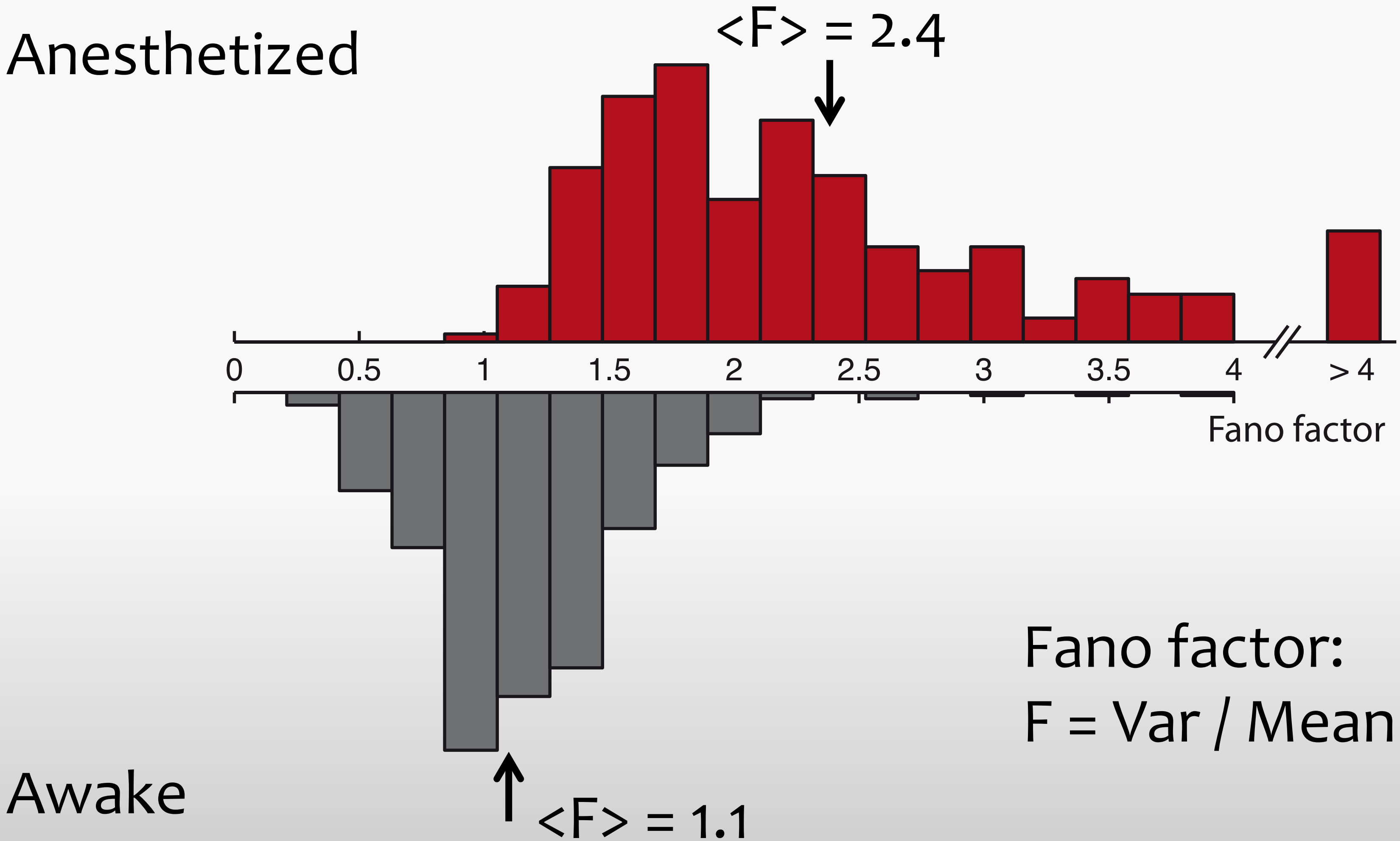
Awake



Anesthetized



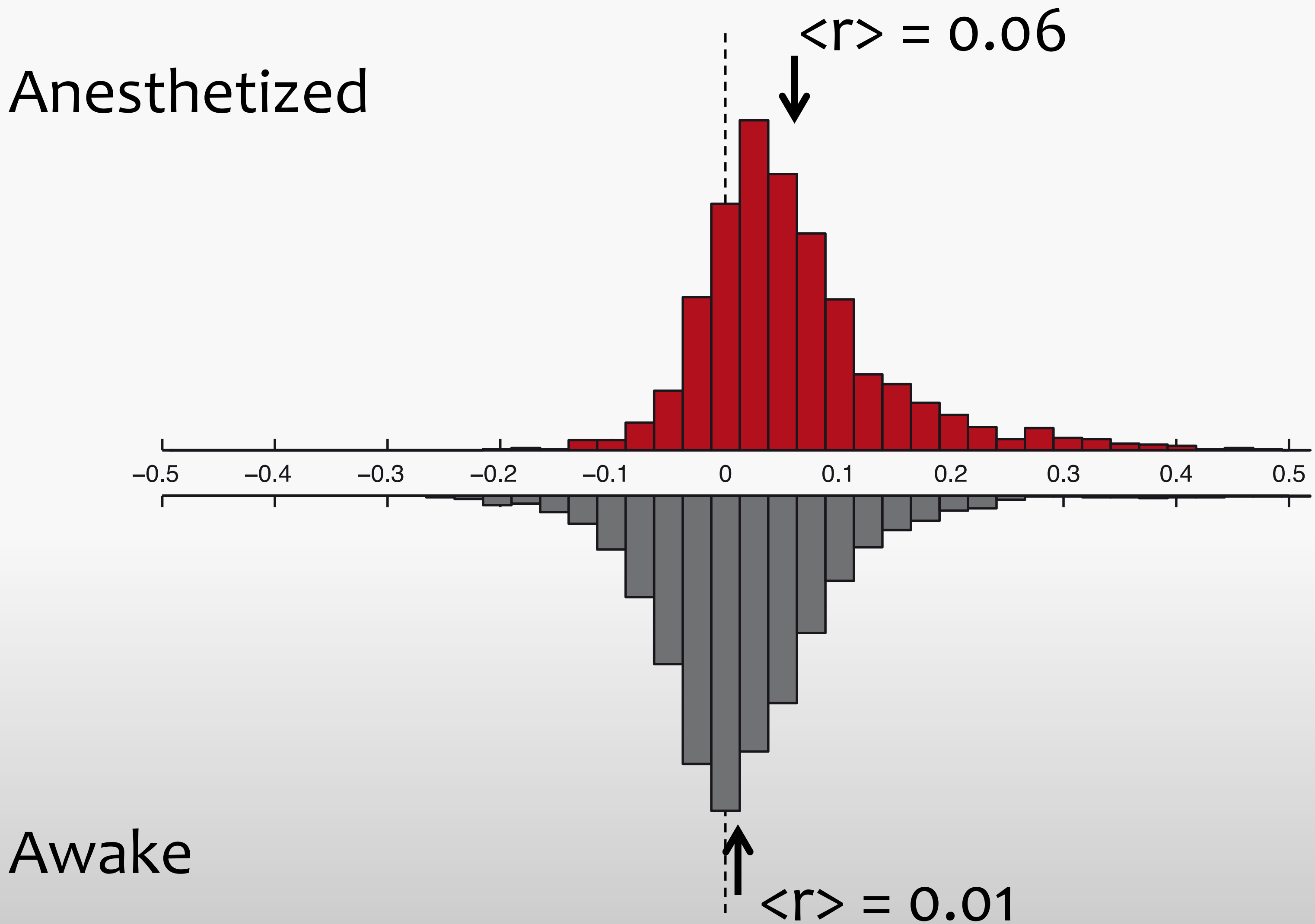
Variability: Fano factor



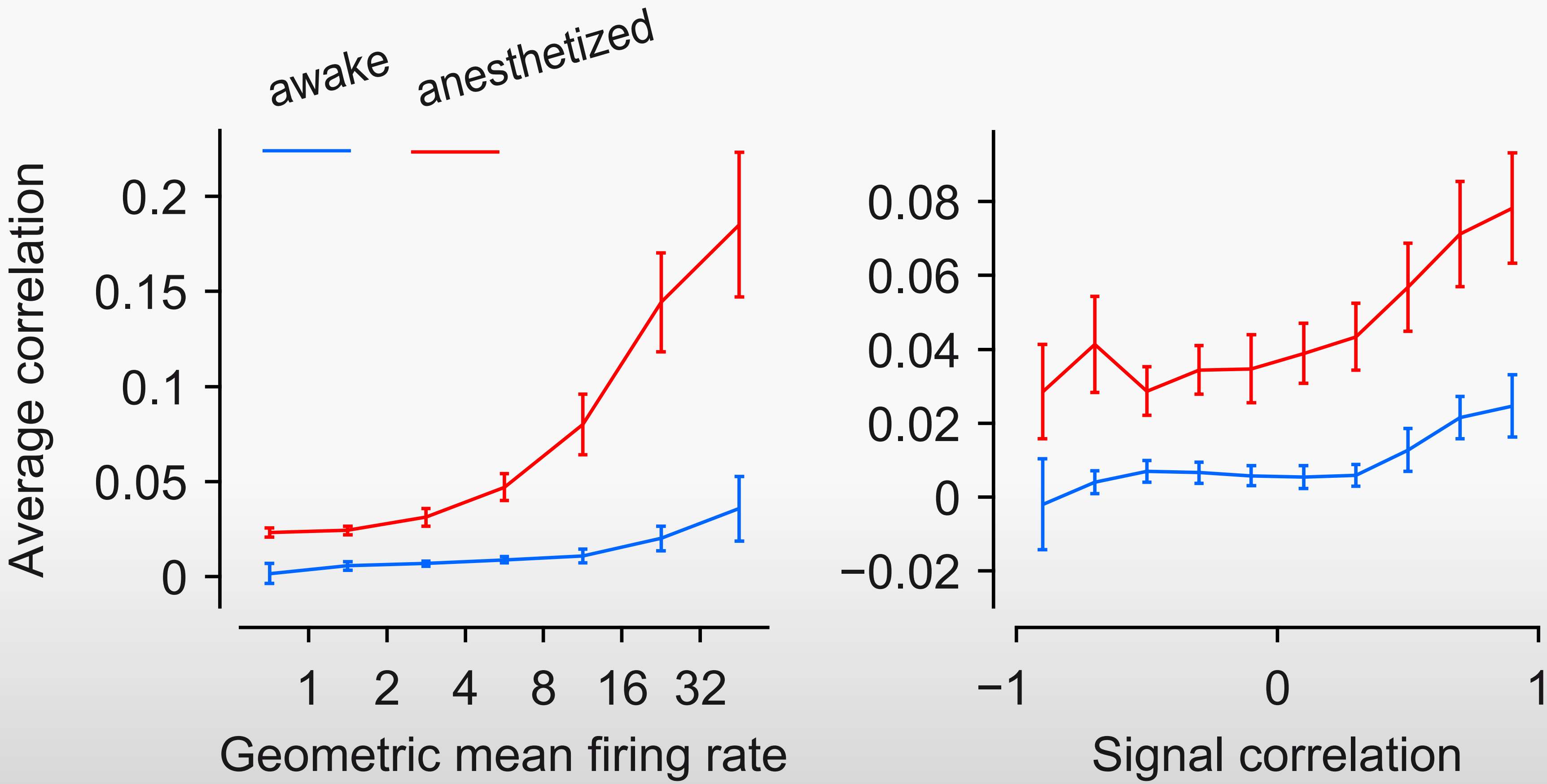
Fano factor:

F = Var / Mean

Noise correlations under anesthesia



Correlation structure

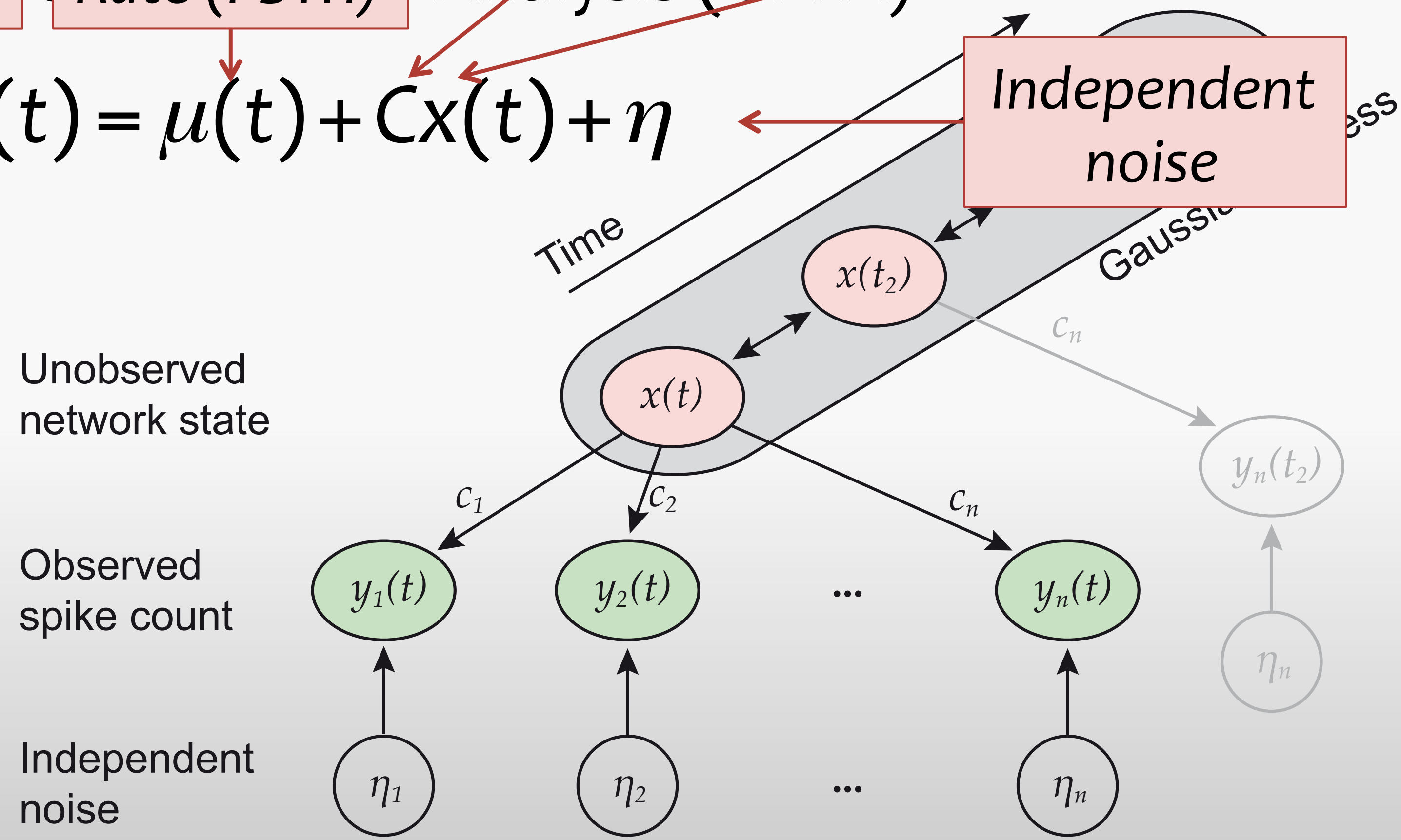


Source of correlations?

Observed spike count | *Mean firing Rate (PSTH)* | *Weights* | *Latent variable* | *Independent noise*

r Analysis (GPFA)

Model: $y(t) = \mu(t) + Cx(t) + \eta$

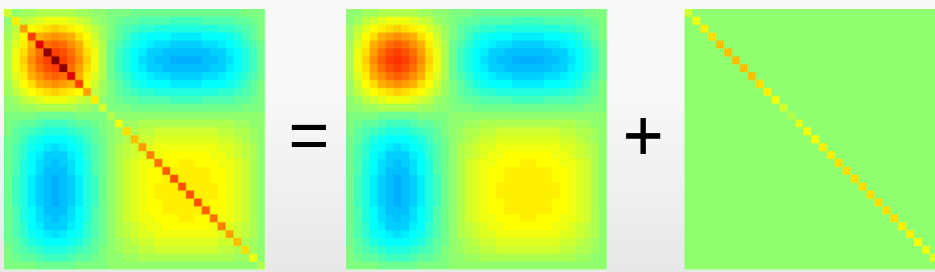


Gaussian Process Factor Analysis

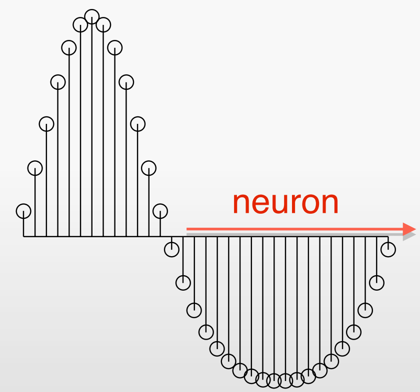
Observed spike count — *Mean firing Rate (PSTH)* — *Weights* — *Latent variable* — *Independent noise*

Model: $y(t) = \mu(t) + Cx(t) + \eta$

$\mathrm{Cov}[y] = CC^{\mathrm{T}} + R$



$C =$

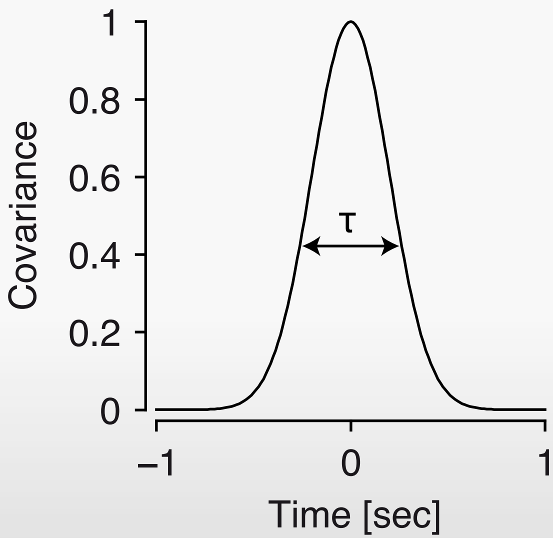


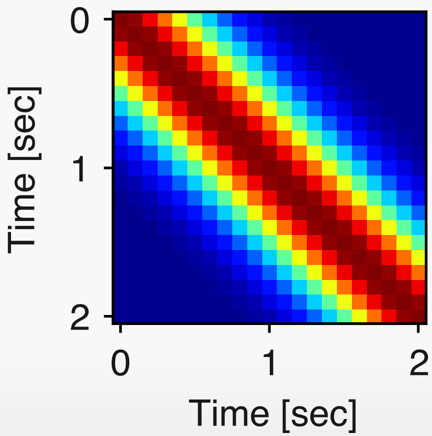
C and R are learned from the data

Yu et al. 2009, Journal of Neurophysiology

GPFA: latent dynamics

Latent variable $x(t)$ is assumed to be smooth in time
→ Gaussian process





$$K_{ij} = \exp\left(-\frac{(t_i - t_j)^2}{2\tau^2}\right)$$

τ is learned from the data

stationary. autocorrelation depends entirely on time difference.

GPFA: inference of latent state

Model is jointly Gaussian:

$$\begin{bmatrix} \bar{\mathbf{x}} \\ \bar{\mathbf{y}} \end{bmatrix} \sim N\left(0, \begin{bmatrix} \bar{K} & \bar{K}\bar{C}^{\mathrm{T}} \\ \bar{C}\bar{K} & \bar{C}\bar{K}\bar{C}^{\mathrm{T}} + \bar{R} \end{bmatrix}\right) \qquad \bar{\mathbf{x}} = \begin{bmatrix} \mathbf{x}(t_1) \\ \vdots \\ \mathbf{x}(t_T) \end{bmatrix}$$

Distribution of $\bar{\mathbf{x}} \mid \bar{\mathbf{y}}$ is known in closed form:

posterior

$$\mathrm{E}[\bar{\mathbf{x}}] = \bar{K}\bar{C}^{\mathrm{T}}(\bar{C}\bar{K}\bar{C}^{\mathrm{T}} + \bar{R})^{-1}\bar{\mathbf{y}}$$

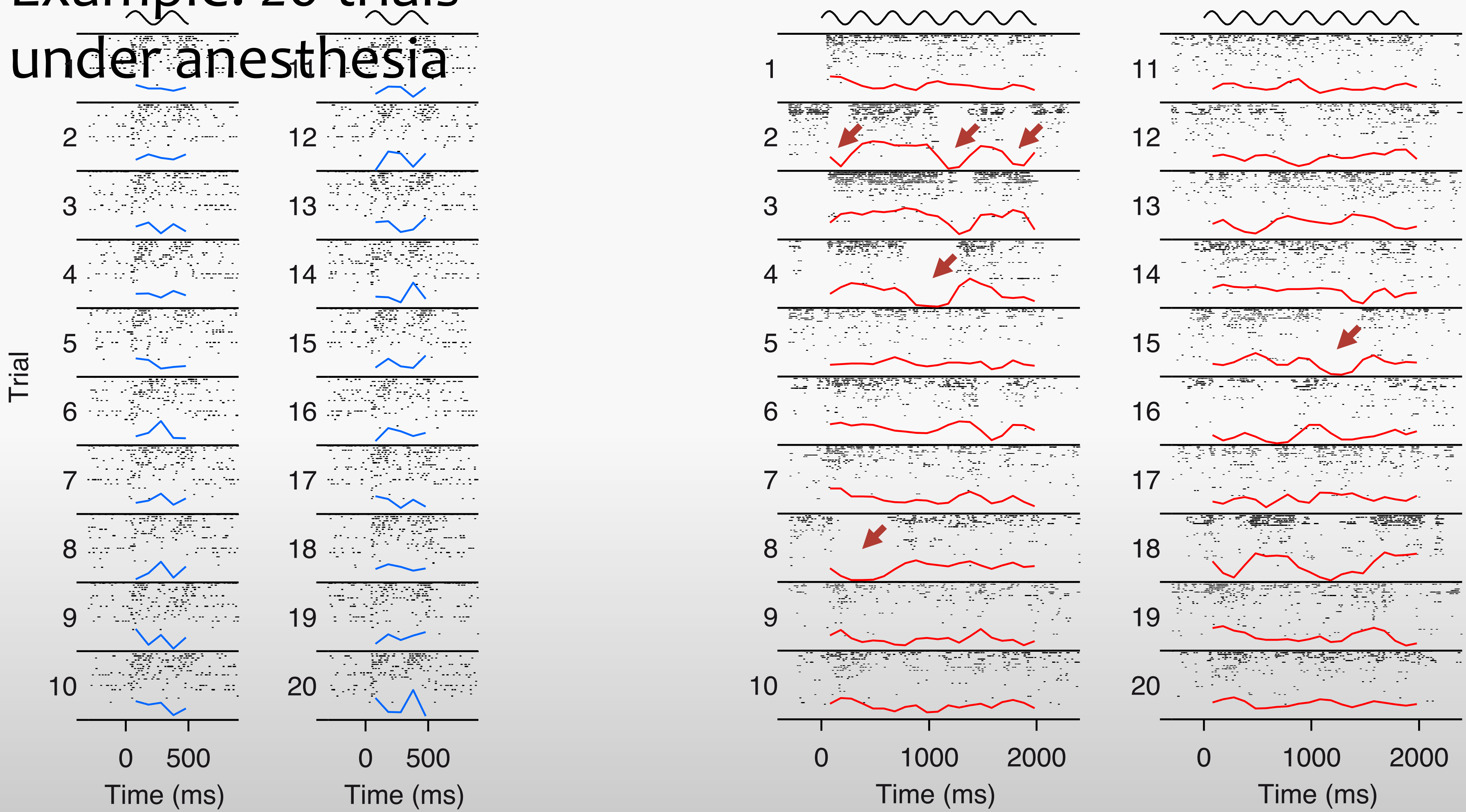
$$\mathrm{Cov}[\bar{\mathbf{x}}] = \bar{K} - \bar{K}\bar{C}^{\mathrm{T}}(\bar{C}\bar{K}\bar{C}^{\mathrm{T}} + \bar{R})^{-1}\bar{C}\bar{K}$$

GPFA: estimate latent state

Awake

Example: 20 trials under anesthesia

Anesthetized



GPFA: learning

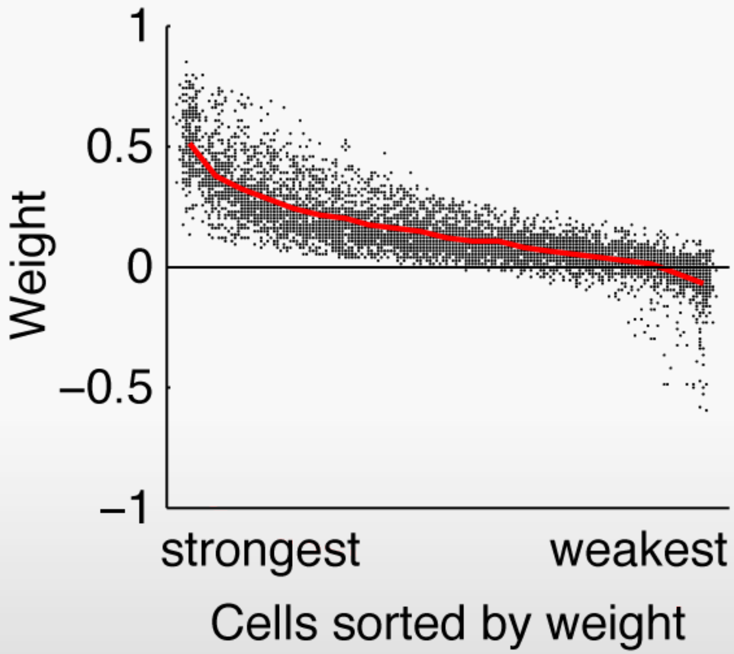
Expectation maximization (EM) algorithm

Alternate between:

- **E step**
  maximum likelihood. using x l y
  Computing best estimate of ***x*** under the current model
- **M step**
  Update model parameters (C, R, τ) given the current estimate of ***x***

Code: https://github.com/aecker/gpfa
See also: Yu et al. 2009, Journal of Neurophysiology

Anesthesia: structure of weights



Variance explained

Variance can be separated into two independent contributors:

$$\mathrm{Cov}[\mathbf{y}] = CC^{\mathrm{T}} + R \qquad \Rightarrow \qquad \mathrm{Var}[y_k] = C_k^2 + R_k$$

Fraction of variance explained by C:

$$\mathrm{VE}[y_k] = \frac{C_k^2}{\mathrm{Var}[y_k]} = 1 - \frac{R_k}{\mathrm{Var}[y_k]} > 0$$

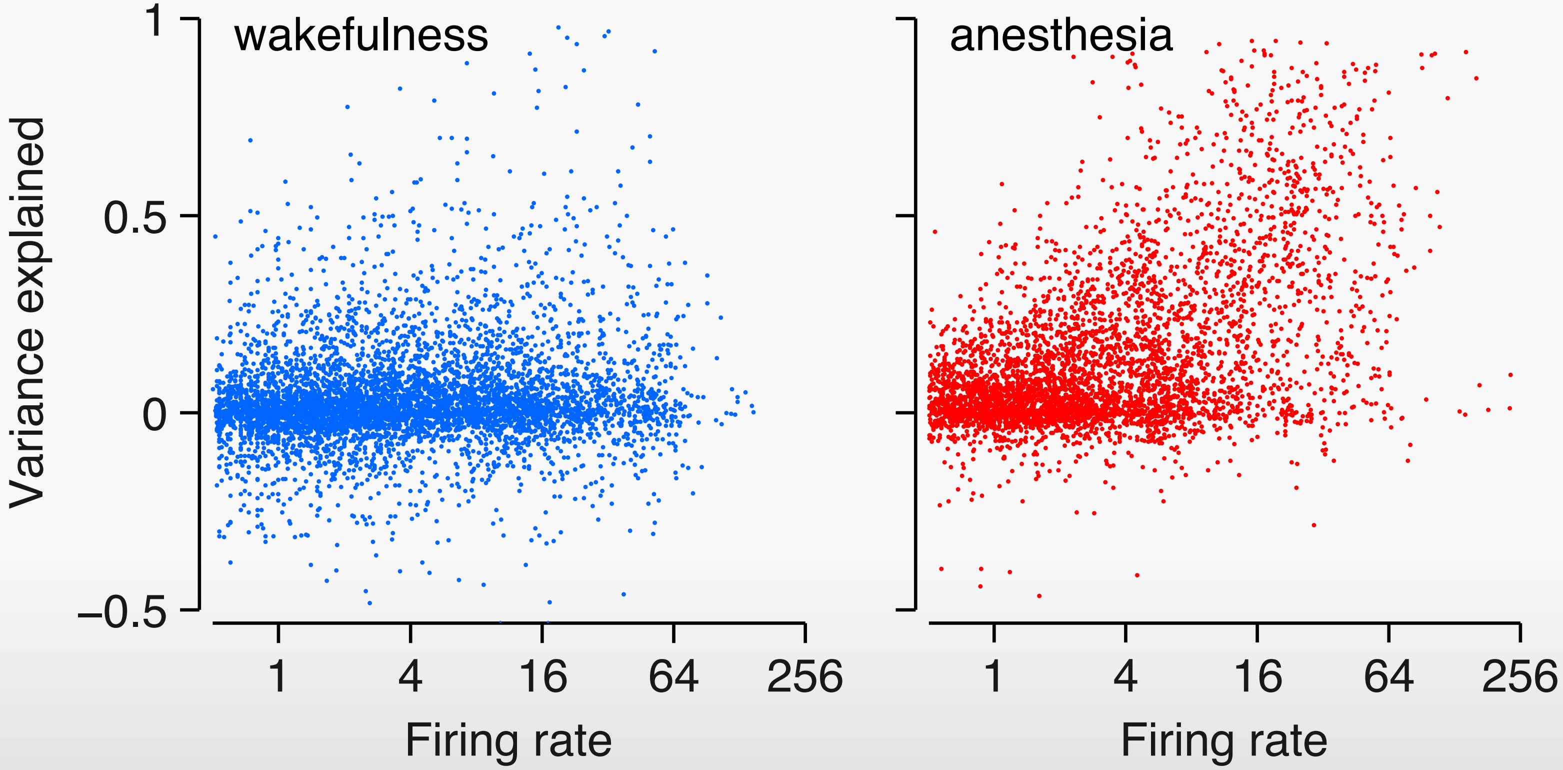
Problem: overfitting!

Variance explained (not overfitted)

- Train model on subset of the data (e.g. 80%)
- Keep weights (C) and timescale (τ) fixed
- Use remaining data as test set:
  - **E step** to estimate trajectory of latent variable x
  - **M step** to re-estimate residual noise R_{test}
- Calculate Variance Explained as:

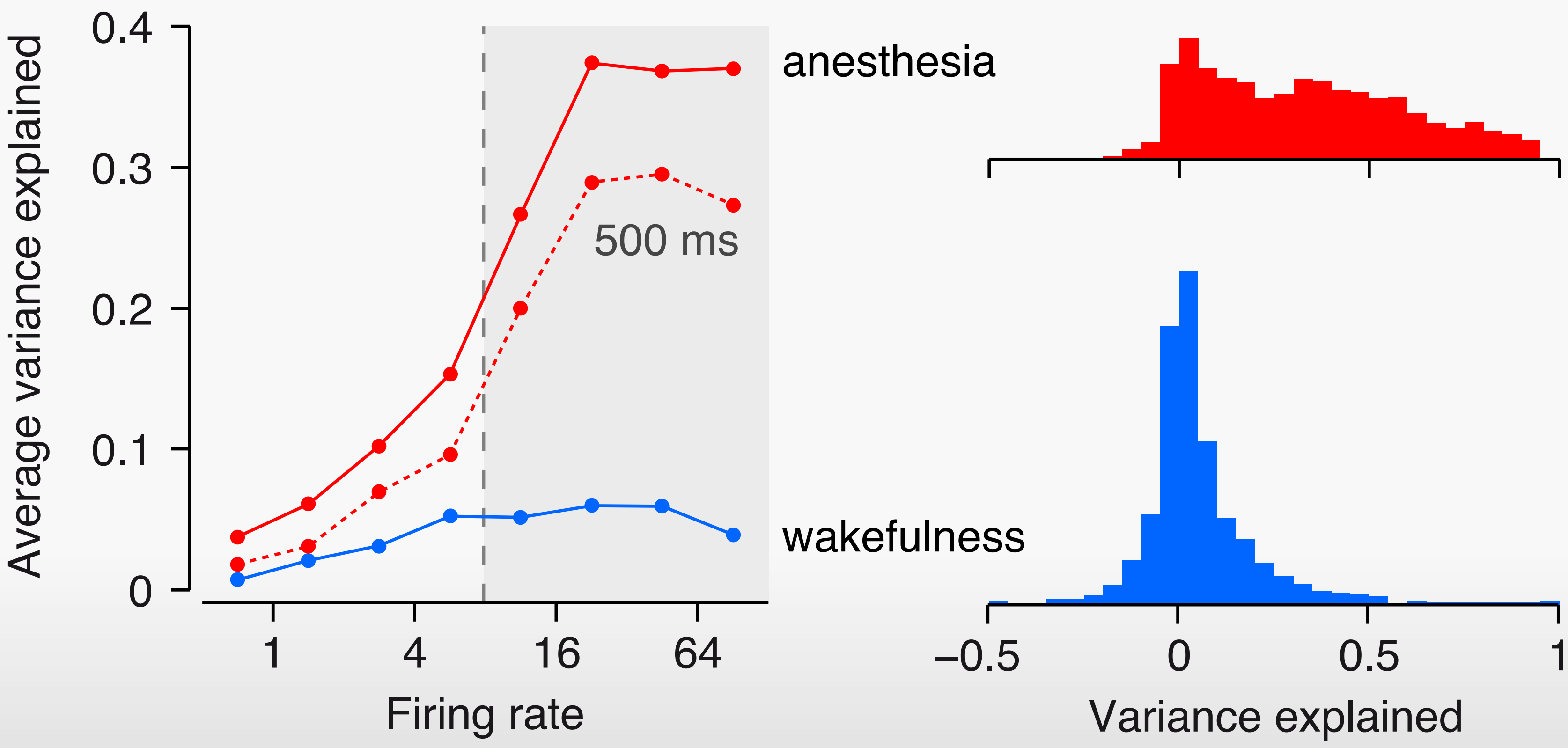
$$\mathrm{VE} = 1 - \frac{R_{\text{test}}}{\mathrm{Var}[y_{\text{test}}]}$$

Variance explained by latent state



VE evaluated on separate test set

Variance explained by latent state



Anesthesia: up to 40% of the variance explained by a single state

Residual noise correlations

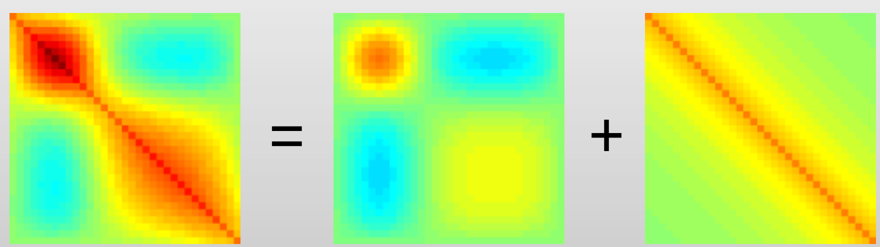
What is the (residual) correlation structure not captured by the model?

As before

- Estimate C and τ on training set and keep them fixed
- Estimate $\mathbf{x}$ on test set by E step
- Obtain residual covariance on test set by M step

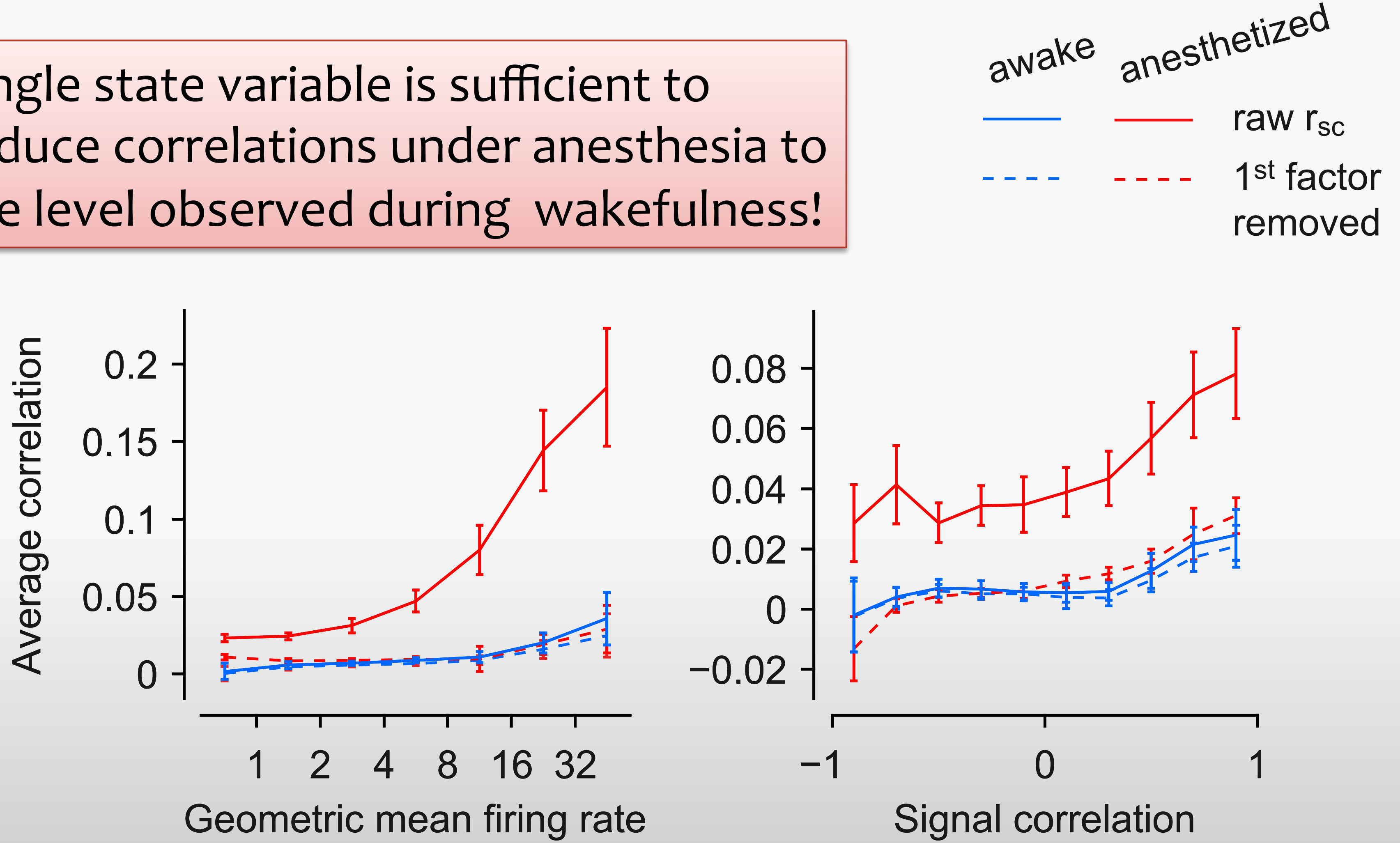
On test set, replace diagonal R by full matrix Q

$$\mathrm{Cov}[\mathbf{y}] = CC^{\mathrm{T}} + Q$$

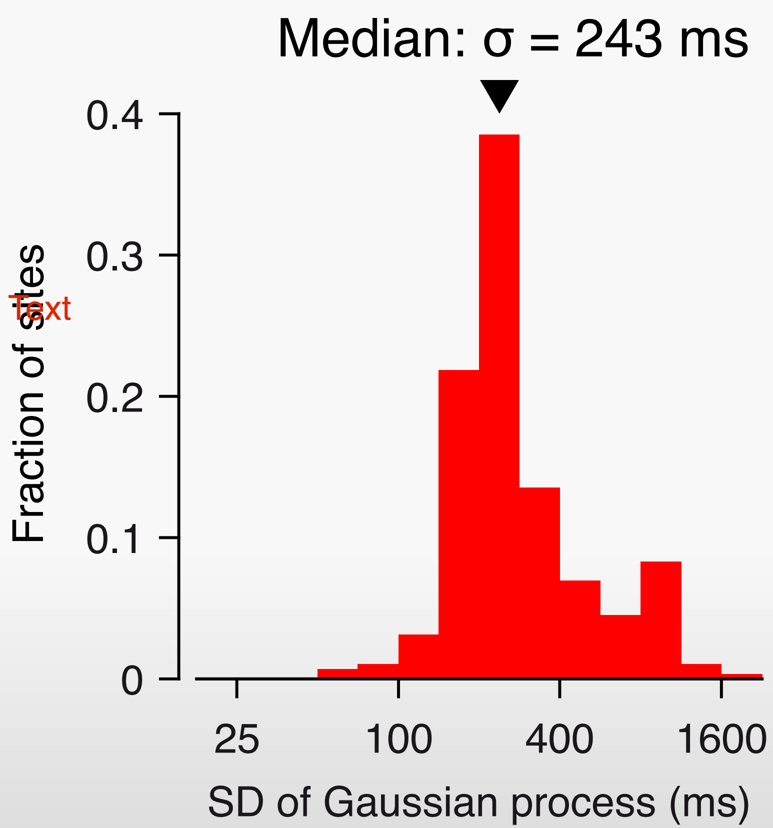


Residual noise correlations

Single state variable is sufficient to reduce correlations under anesthesia to the level observed during wakefulness!



Timescale of latent state

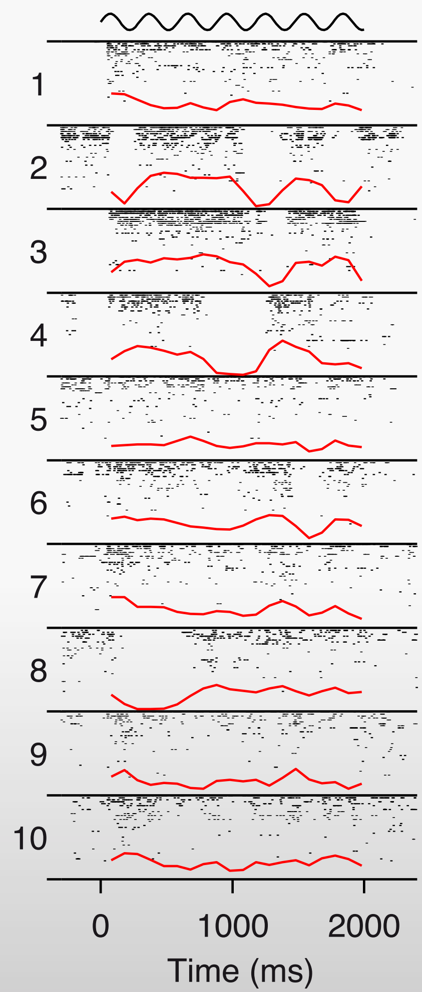


→ ca. 1–2 Hz

Summary (scientific)

Neural activity under anesthesia is dominated by state fluctuations (‘up’/’down’)

- Increased Fano factors and noise correlations
- Can be accounted for by a single latent variable (GPFA model)
  → Explains up to 40% of the variance
- Timescale: 1–2 Hz



Summary (data analysis)

Latent variable models are powerful tools to study population dynamics

- Low-dimensional state space + mapping to neural response space
- Timescale + smoothness in time

Limitations of GPFA

- **Additivity** → pre-transform data / more general graphical models
- **Gaussian** → Poisson linear dynamical systems (PLDS)
  Macke et al. 2011, Büsing et al. 2012