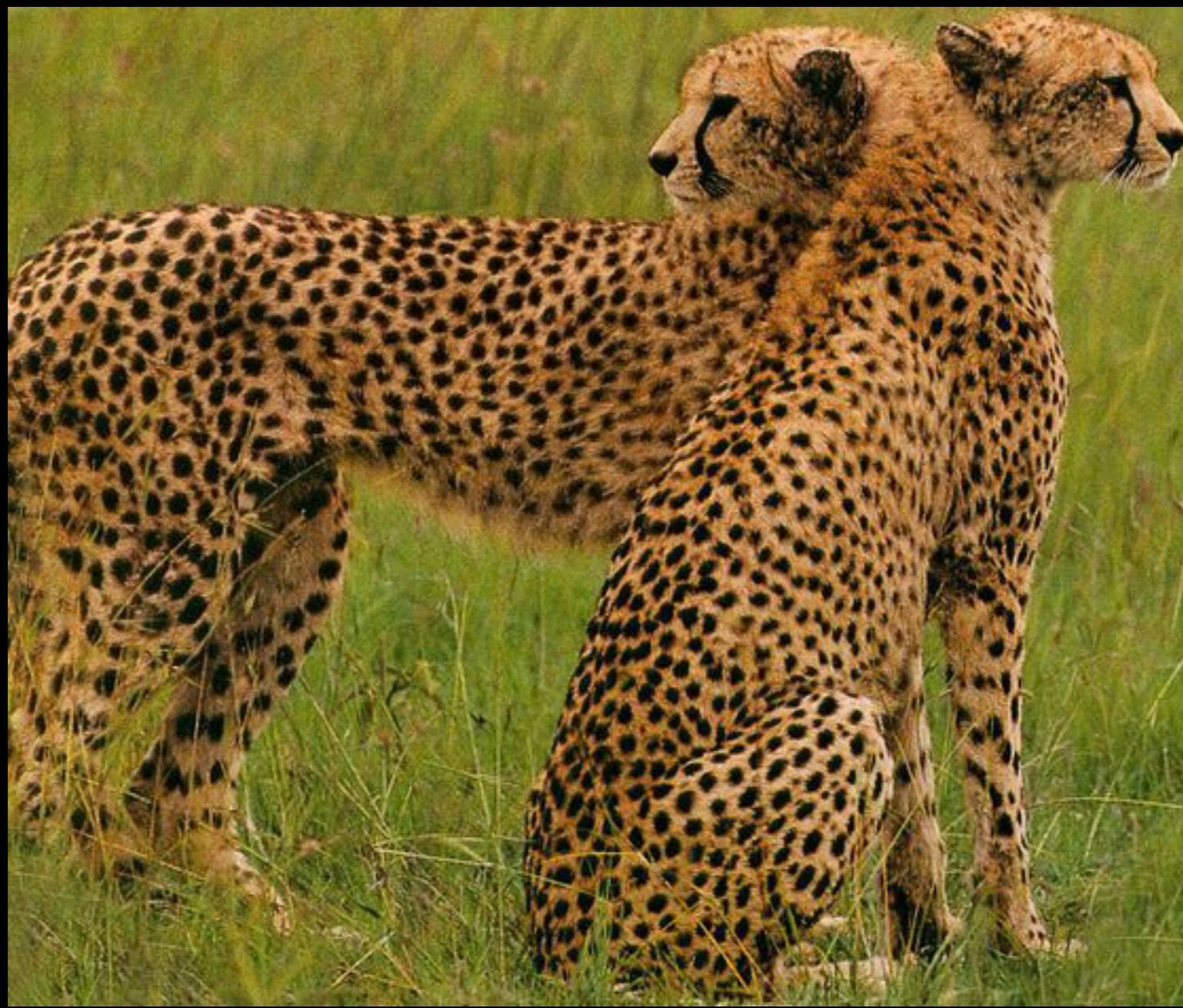


# Inference by Reparameterization in Neural Population Codes

Workshop on Theoretical Neuroscience  
Janelia Research Campus, Sep 2016

Rajkumar V  
Xaq Lab  
Rice University, BCM



# Probabilistic Inference

- Natural to perform tasks involving uncertainty using probabilistic computations
- Human behavior is highly consistent with probabilistic reasoning in sensory, motor and cognitive domains

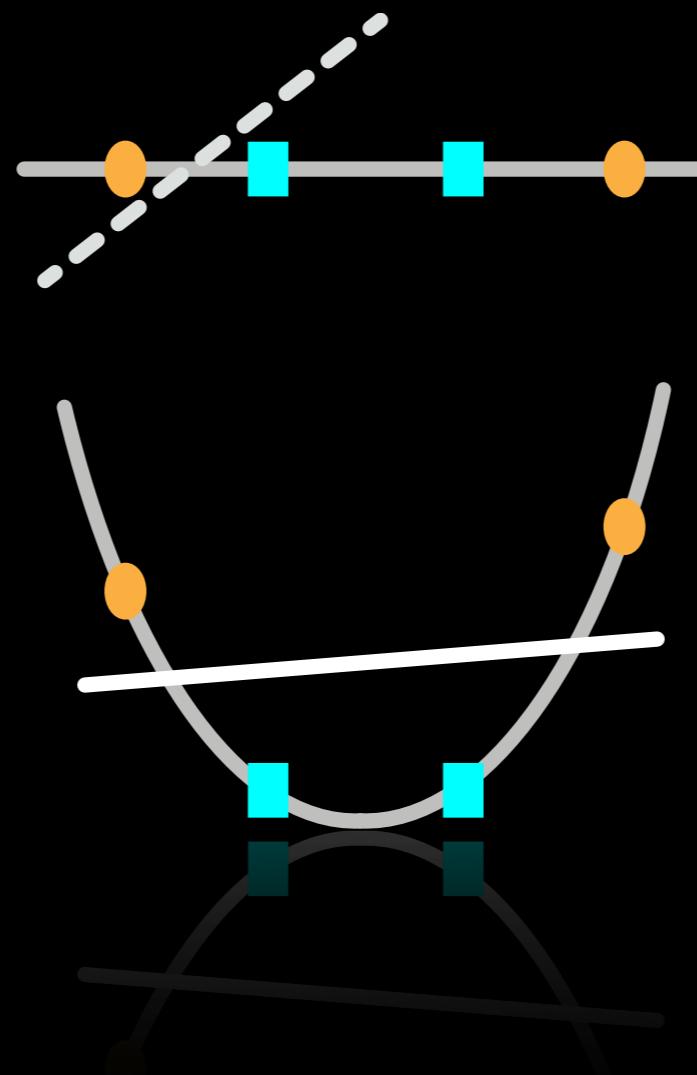


Inference!  
How?

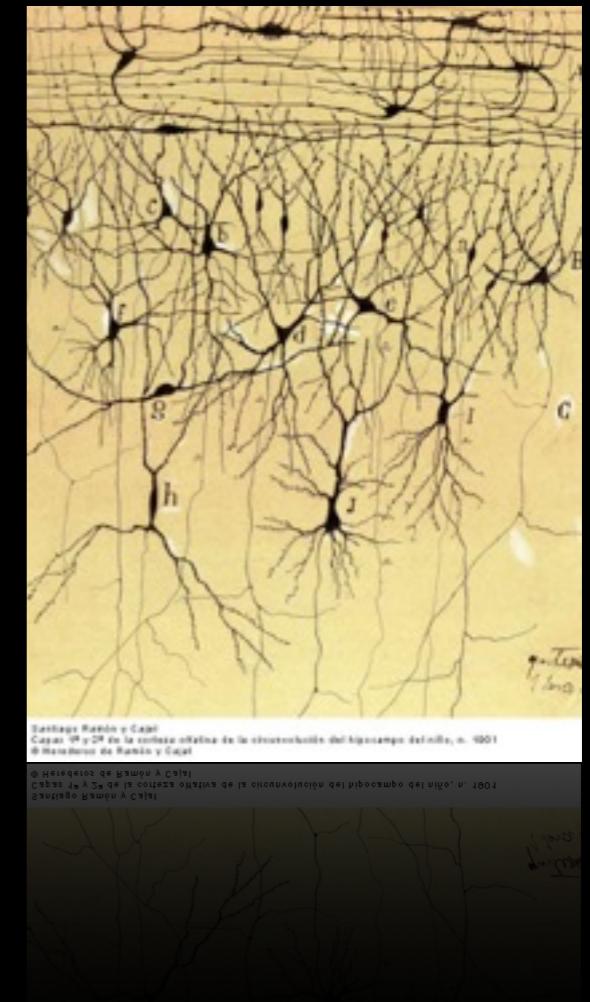
# Information is distributed

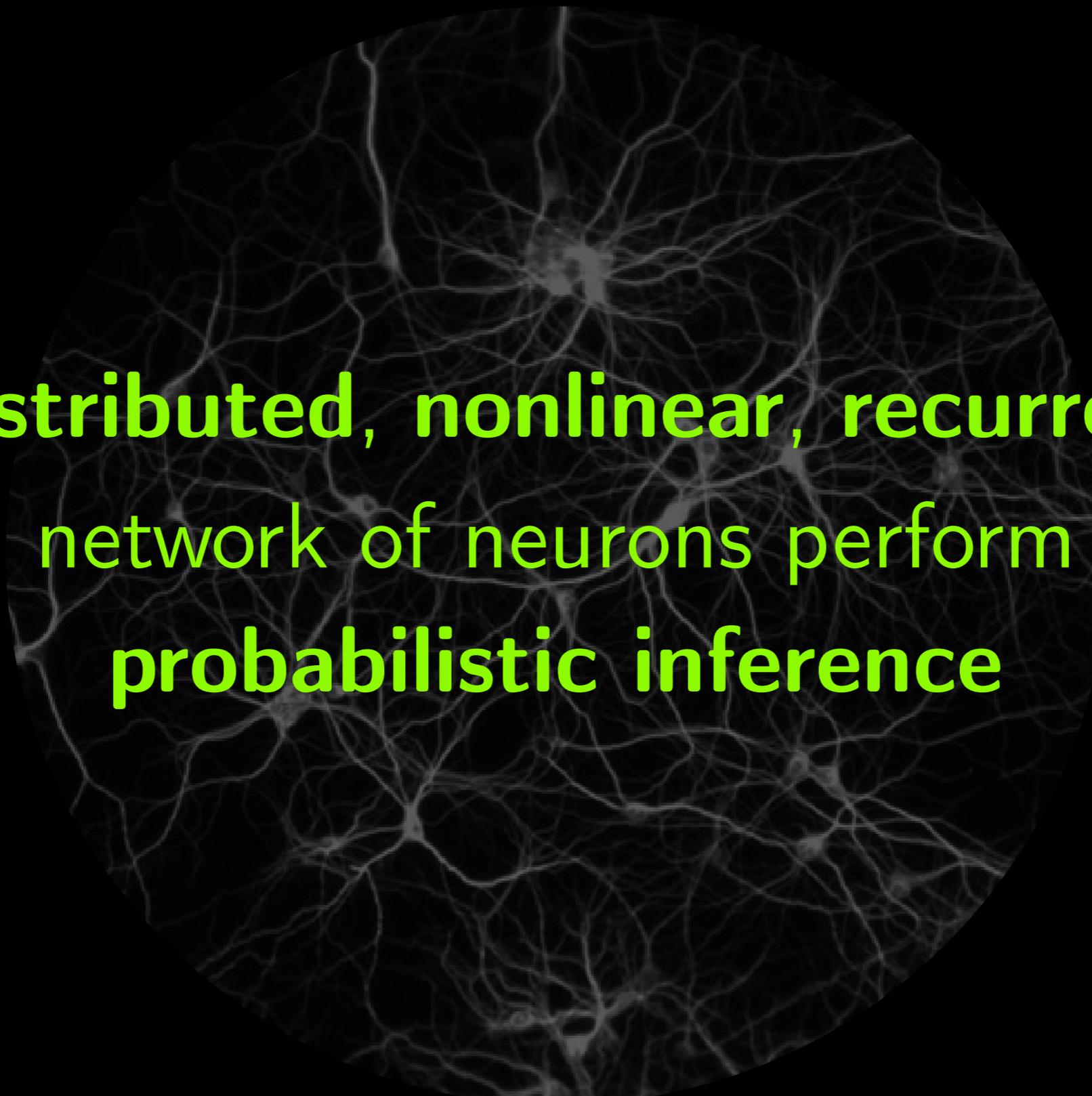


# Nonlinear transformations

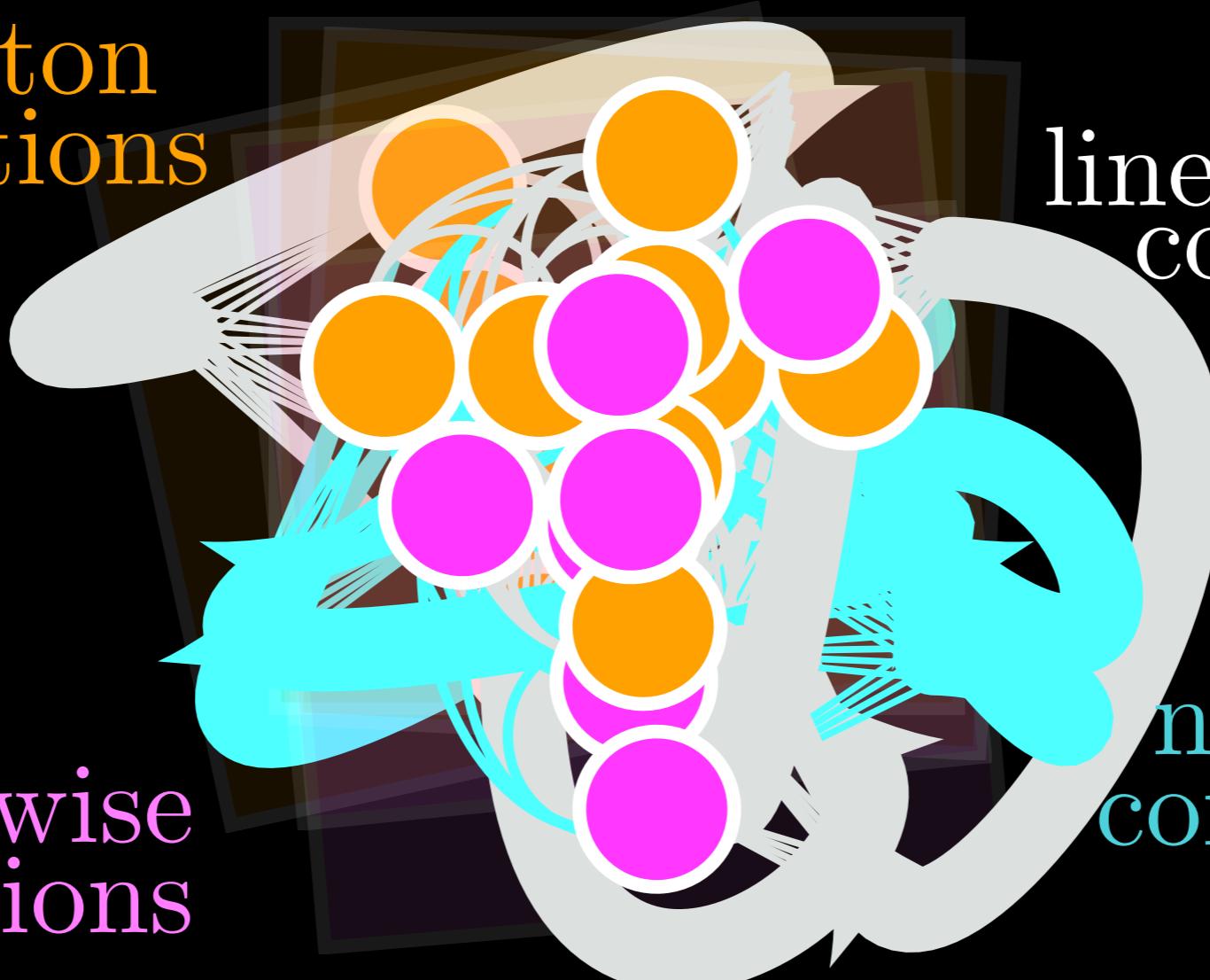


# Recurrent connections





**Distributed, nonlinear, recurrent**  
network of neurons perform  
**probabilistic inference**



A stylized brain diagram is shown in profile, facing right. It features several clusters of colored circles (nodes) in orange and pink, connected by various lines representing projections. The brain is set against a dark background with some translucent, overlapping rectangular shapes.

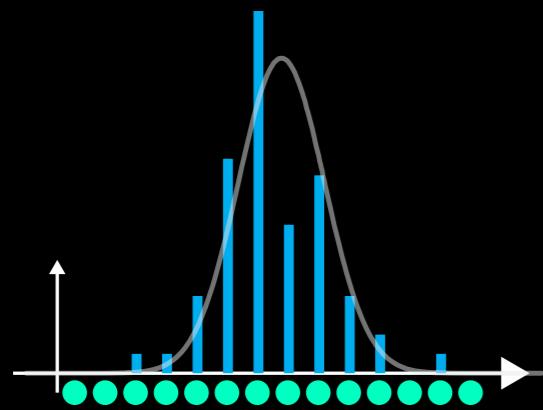
singleton  
projections

linear  
connections

pairwise  
projections

nonlinear  
connections

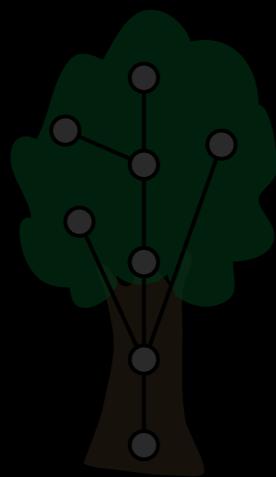
# Probabilistic Population Codes



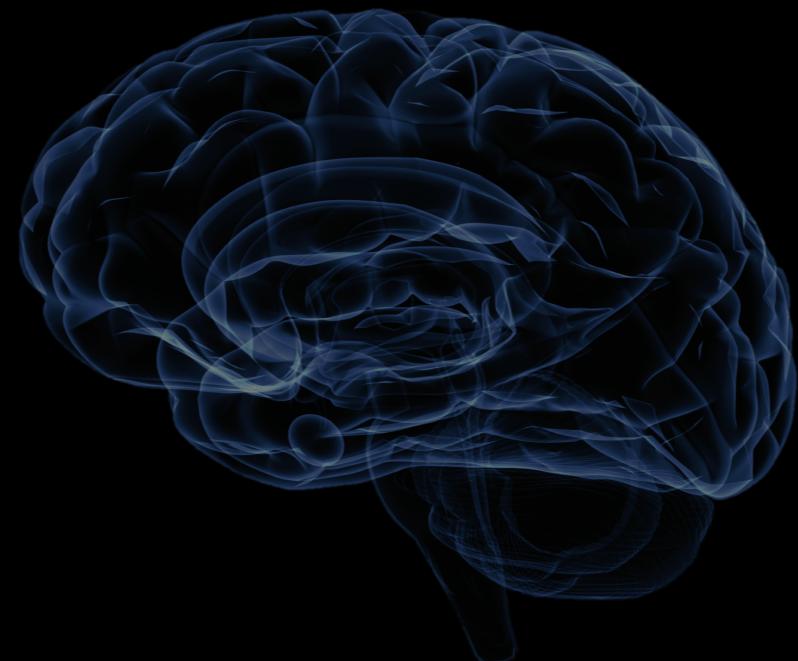
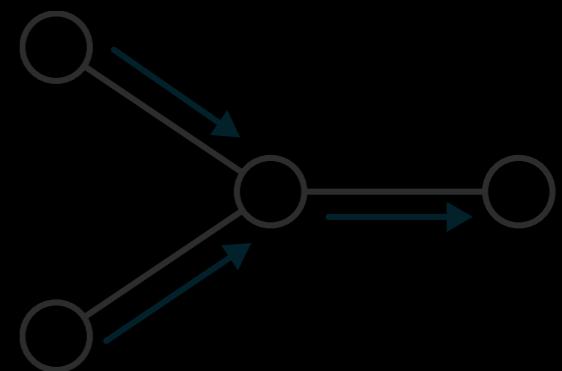
# Graphical Models



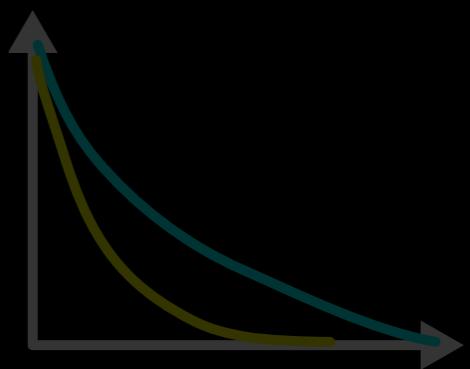
# Tree-based Re-parameterization



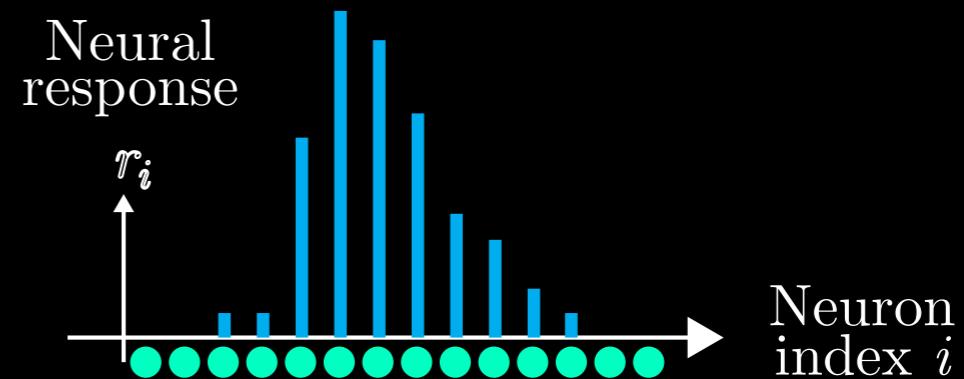
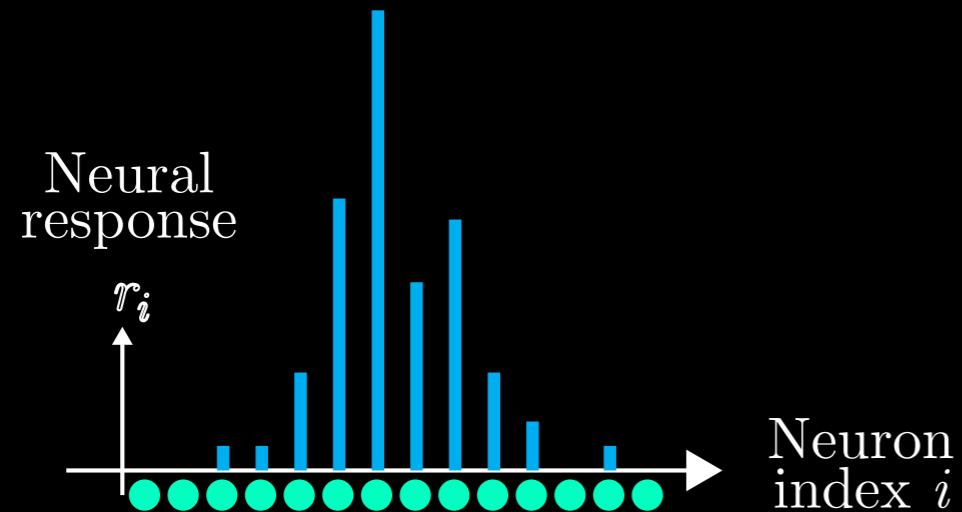
# Belief Propagation



# Dynamical Systems



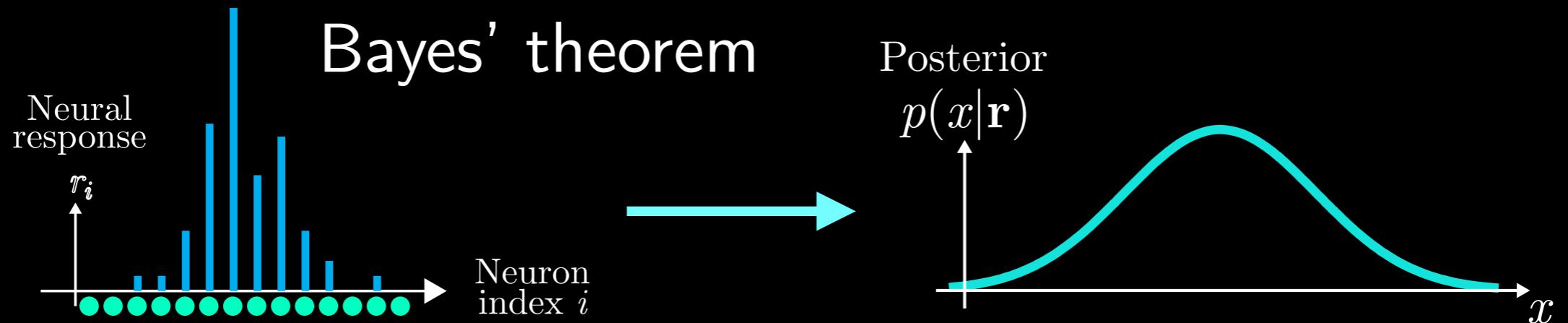
# Probabilistic Population Codes



Variability can be captured as  $p(\mathbf{r}|x)$

$x$  : stimulus

# Using Bayes' theorem



## Linear PPC

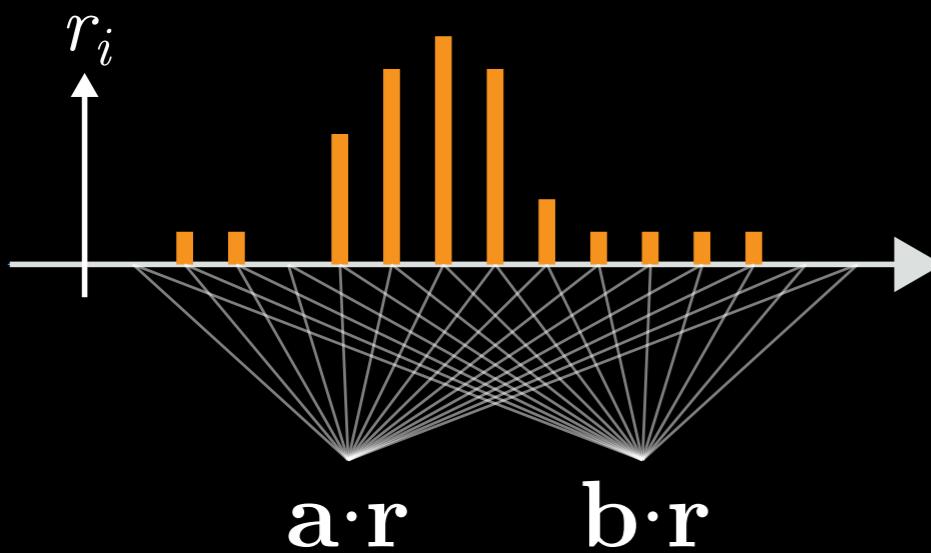
$$p(\mathbf{r}|x) = \phi(\mathbf{r}) \exp(\mathbf{h}(x) \cdot \mathbf{r})$$

Log probability is linear in  $\mathbf{r}$

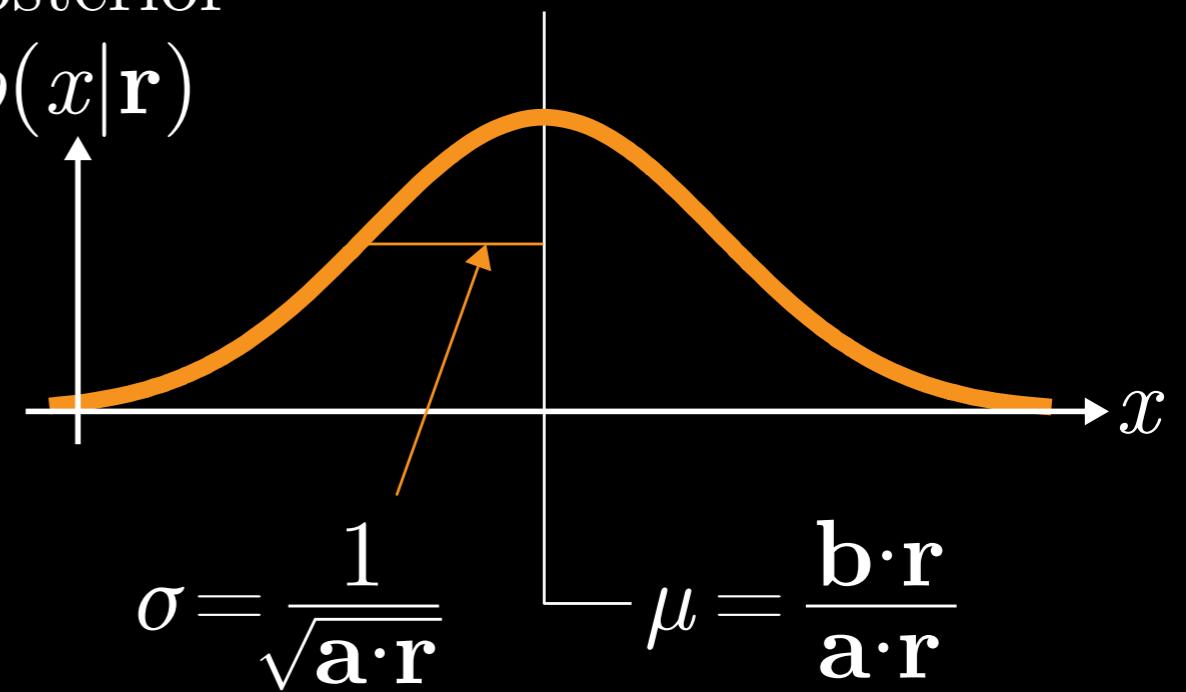
Posterior distribution will also have this general form:

$$p(x|\mathbf{r}) \propto \exp(\mathbf{h}(x) \cdot \mathbf{r})$$

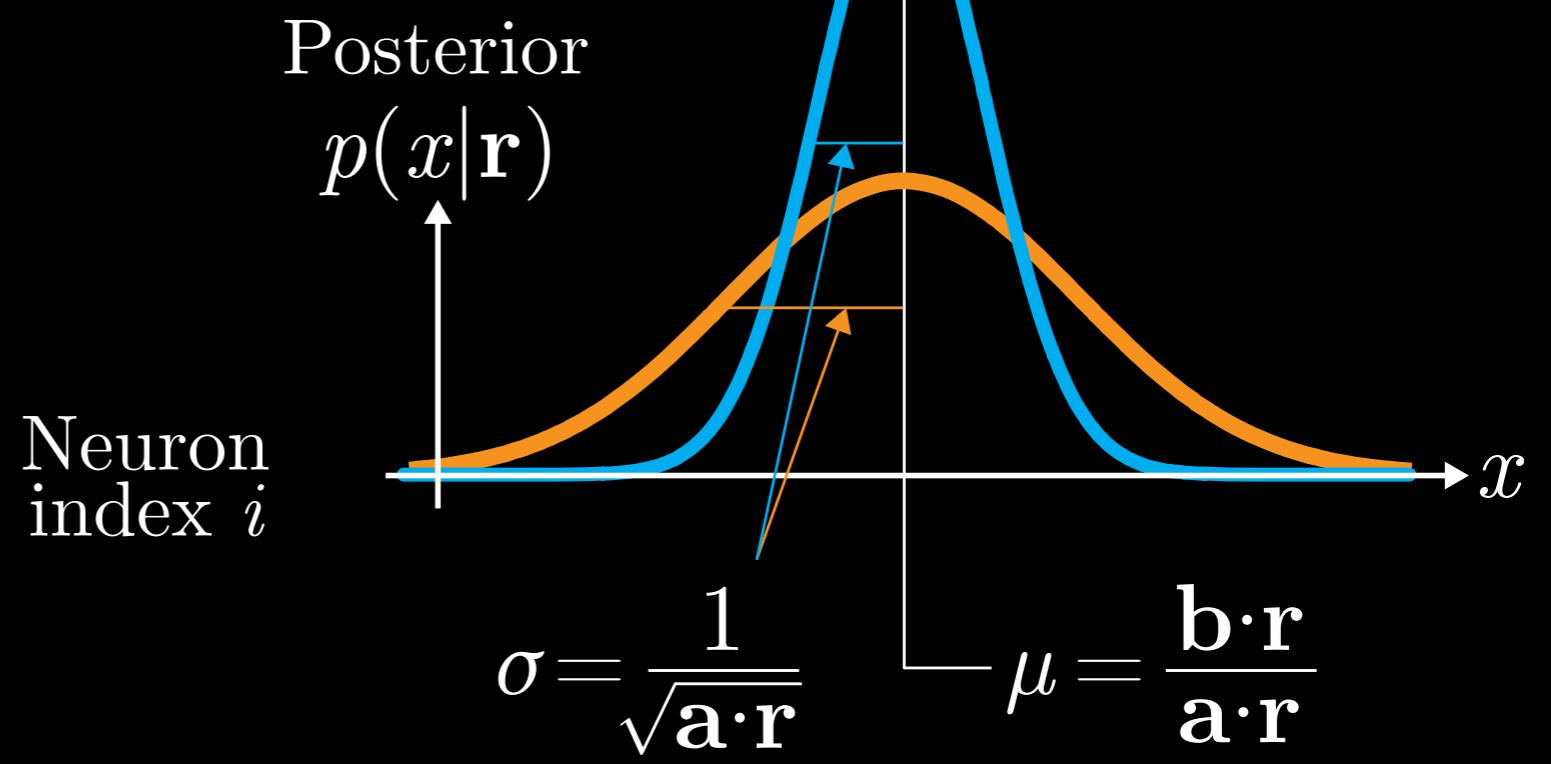
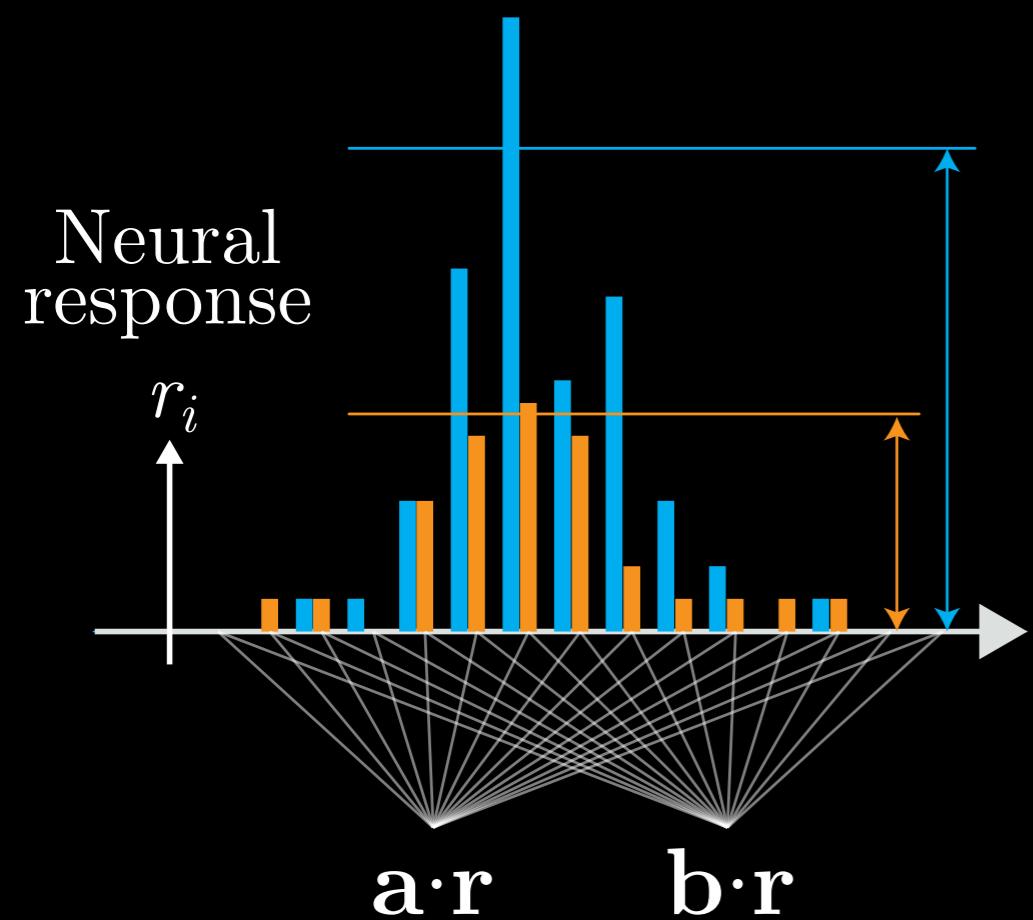
Neural response



Posterior  
 $p(x|\mathbf{r})$



Different projections of  $\mathbf{r}$  encode natural parameters of the underlying distribution



More spikes means more certainty

# Probabilistic operations with PPCs

Cue integration

$$p(x|c_1, c_2) \propto p(x|c_1)p(x|c_2)p(x)$$

Linear transformation of  $\mathbf{r}$

Marginalization

$$p(x_1) = \int p(x_1, x_2) dx_2$$

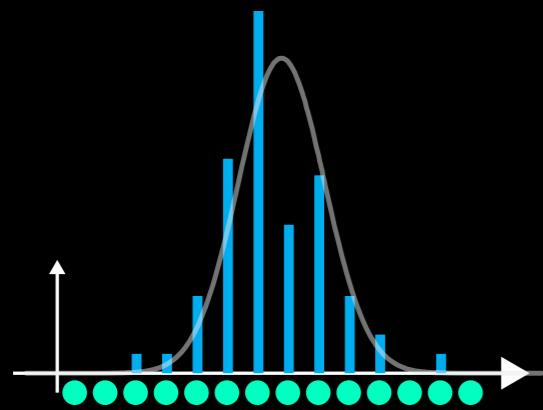
Nonlinear

# Marginalization

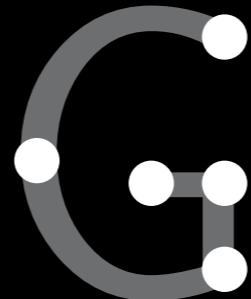
$$p(x_i) = \int p(\mathbf{x}) d\mathbf{x}_{\setminus i}$$

Arises in a wide range of computations in the brain:  
causal reasoning, visual tracking, motor control,  
olfaction, object recognition, decision making ...

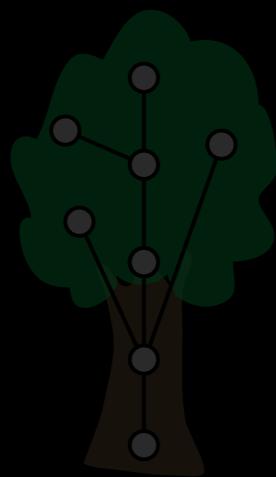
# Probabilistic Population Codes



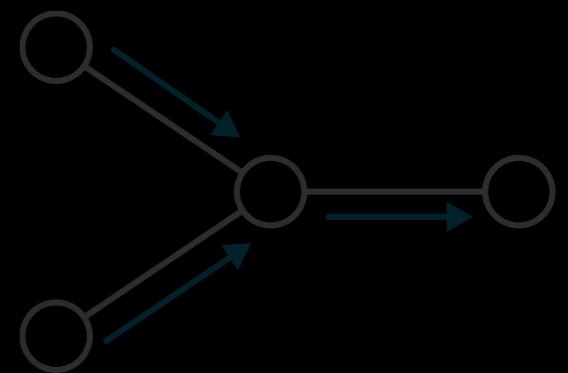
# Graphical Models



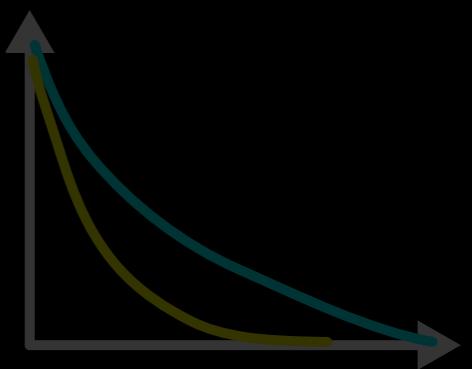
# Tree-based Re-parameterization



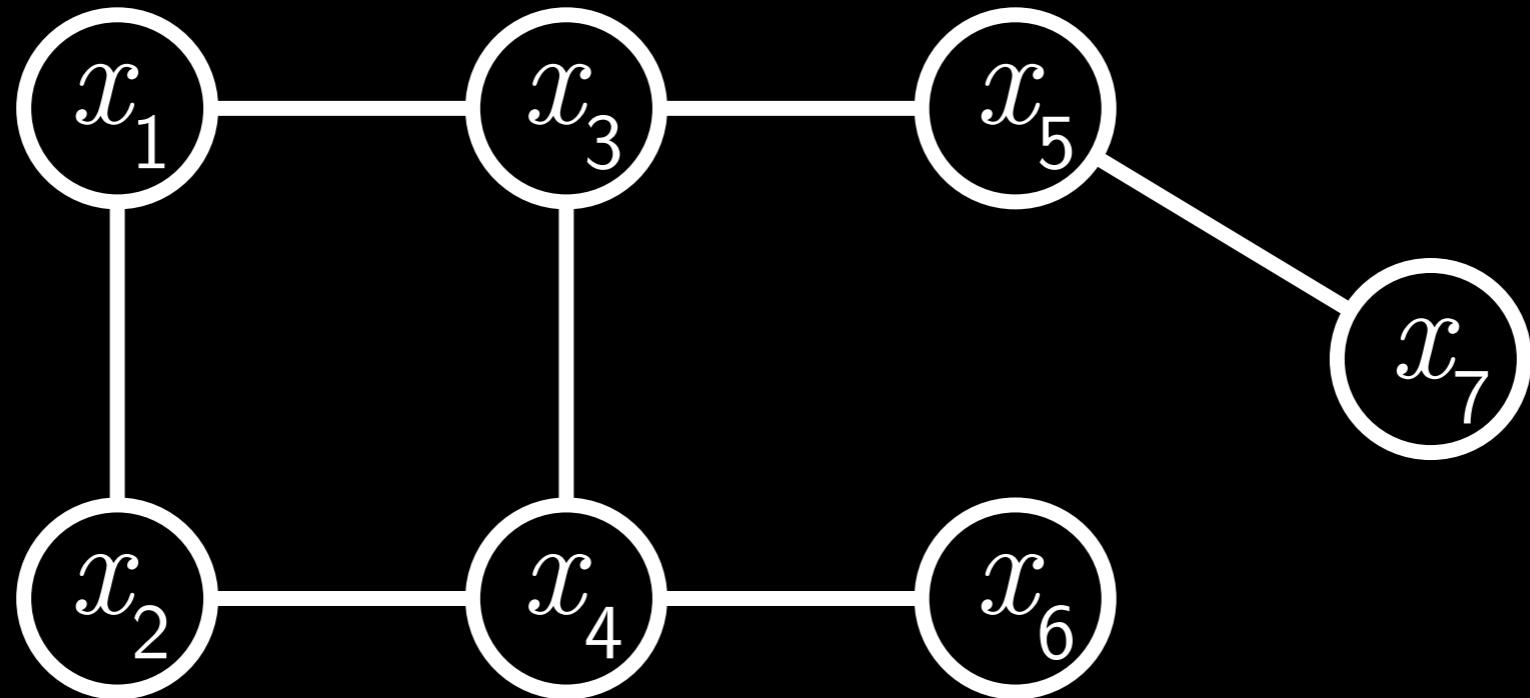
# Belief Propagation



# Dynamical Systems



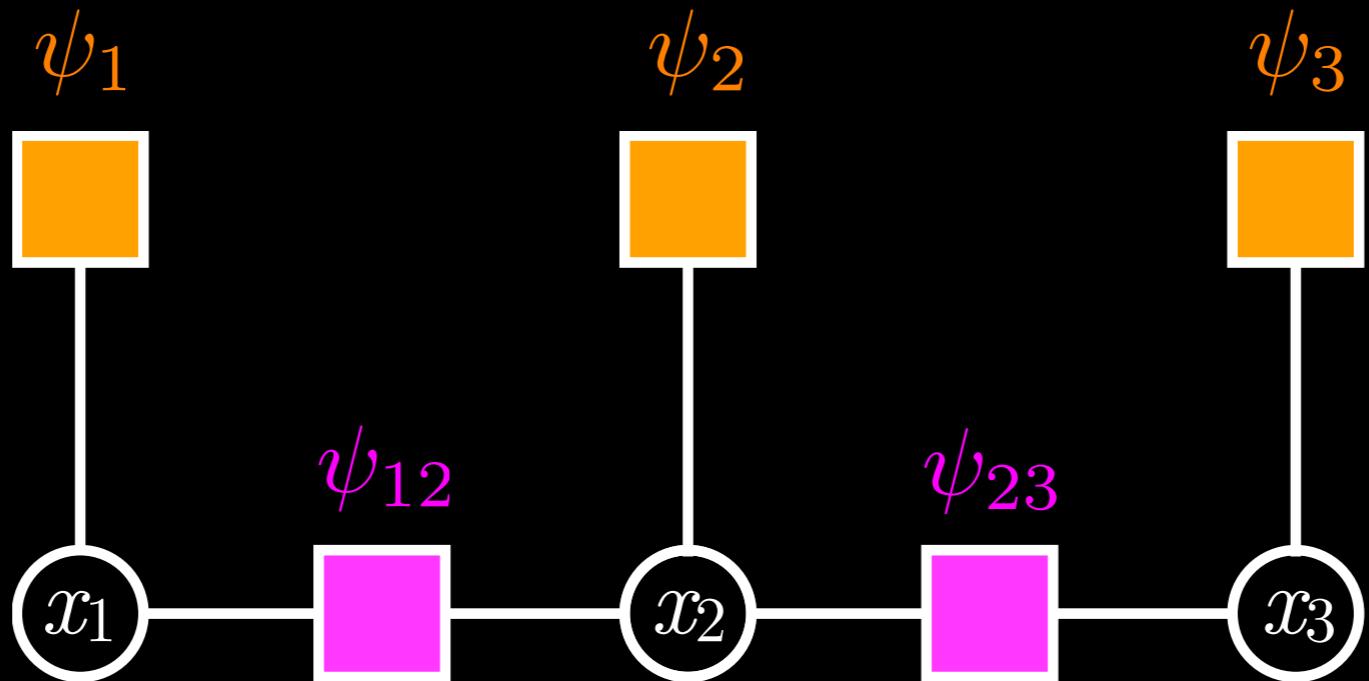
# Probabilistic Graphical Models



Graph expresses conditional dependencies between random variables

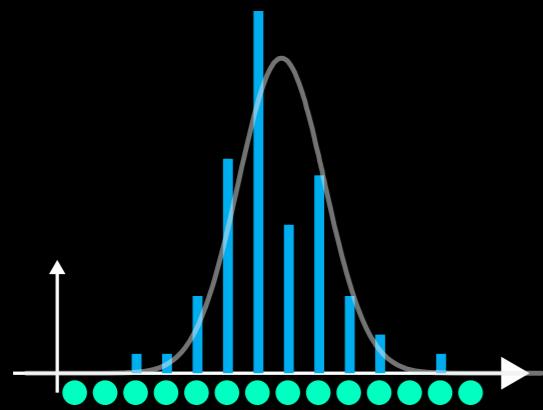
Factorization property:  $p(\mathbf{x}) = \frac{1}{Z} \prod_{C \in \mathbf{C}} \psi_C(\mathbf{x}_C)$

# Pairwise Markov Random Field

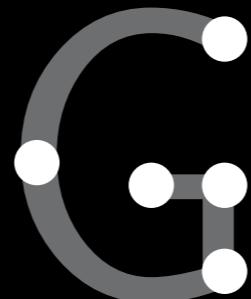


$$p(\mathbf{x}) = \frac{1}{Z} \prod_{s \in V} \psi_s(x_s) \prod_{(s,t) \in E} \psi_{st}(x_s, x_t)$$

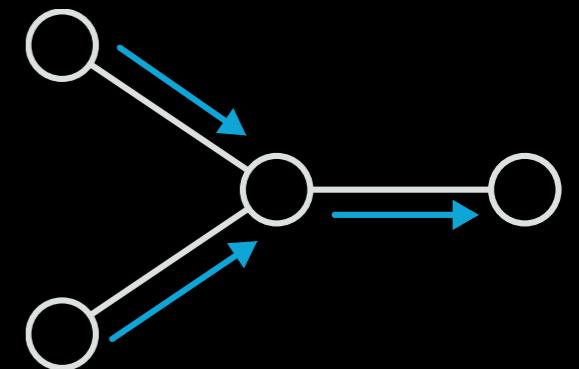
# Probabilistic Population Codes



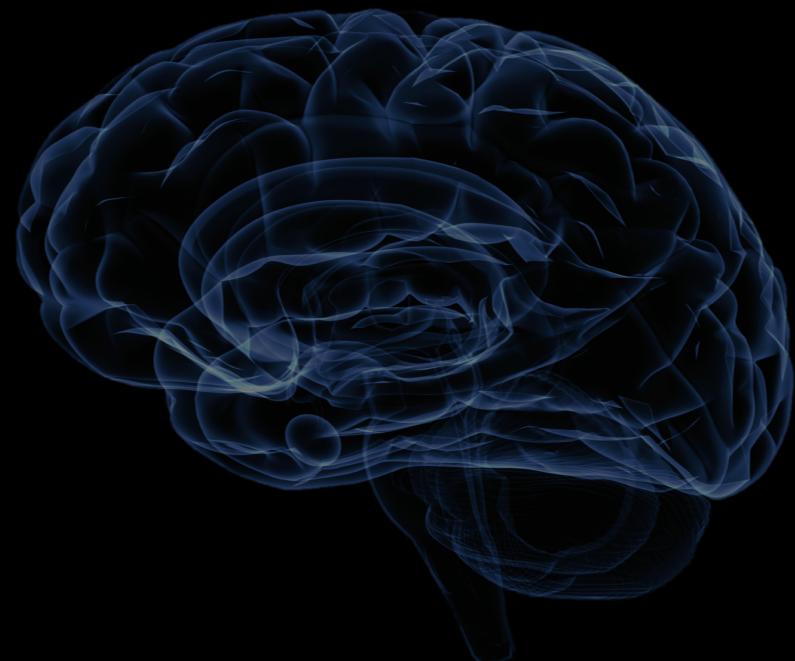
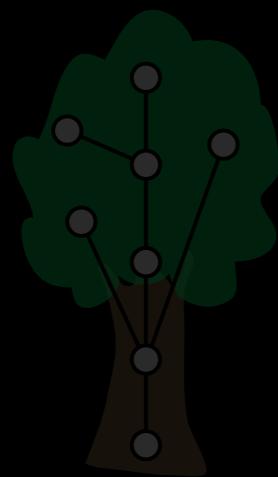
# Graphical Models



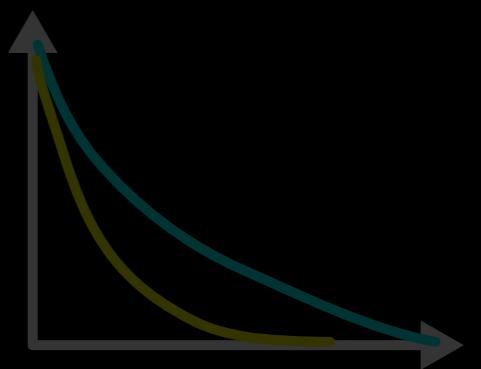
# Belief Propagation



# Tree-based Re-parameterization



# Dynamical Systems

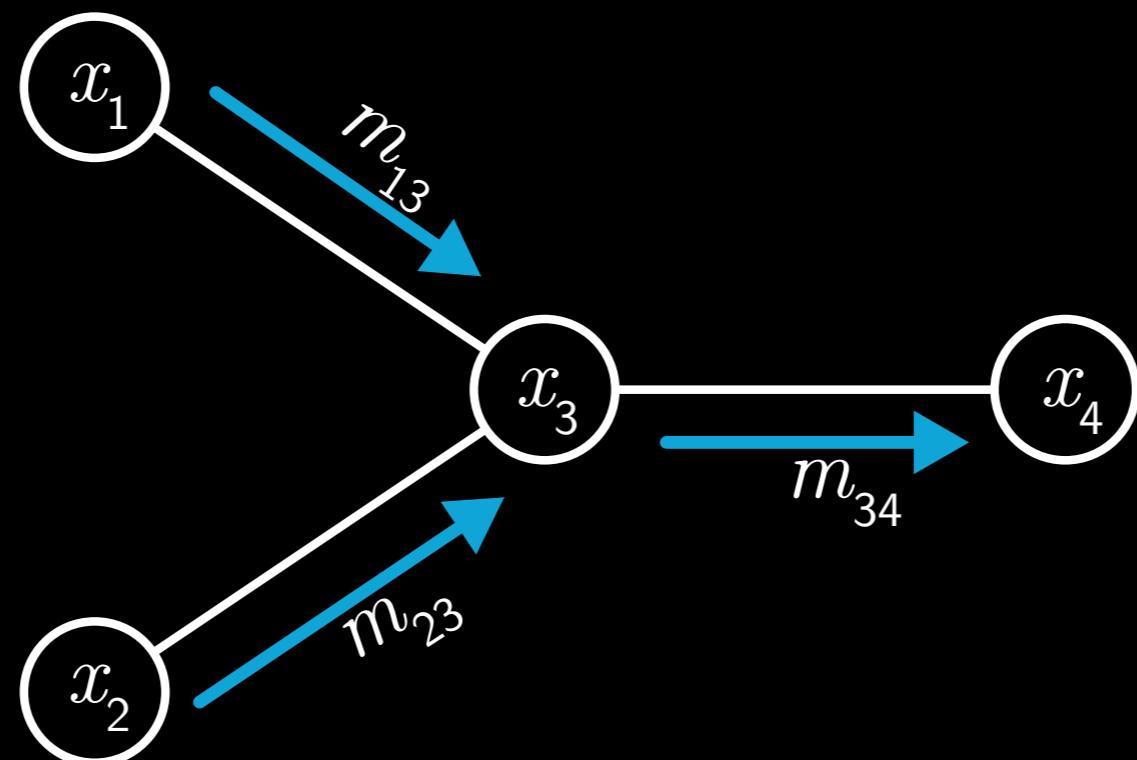


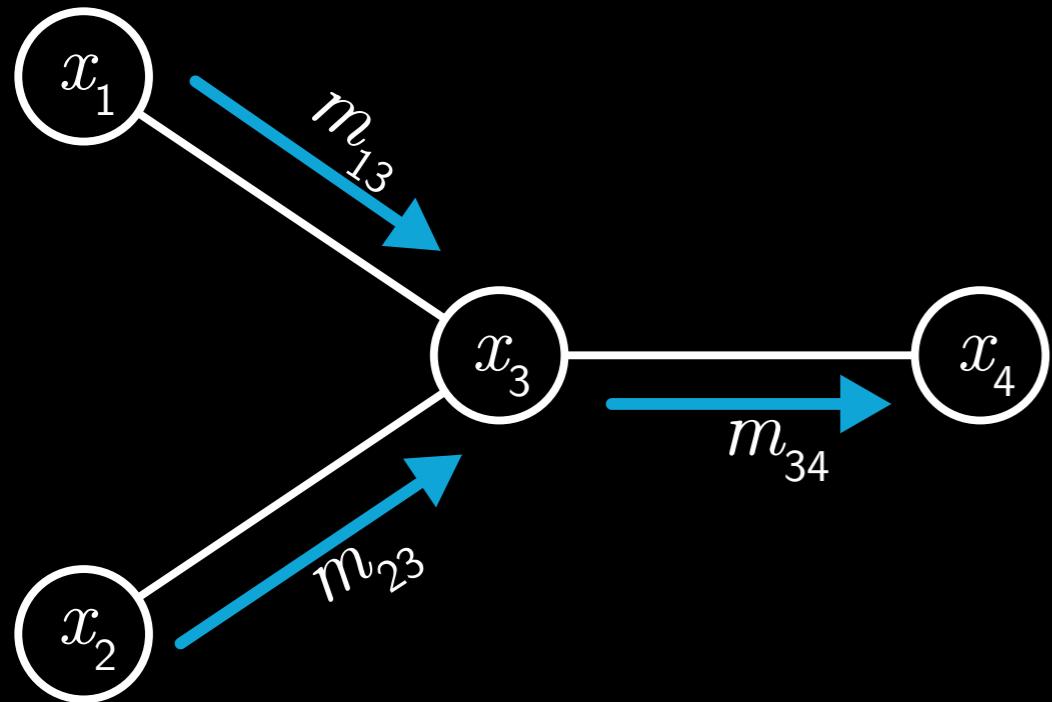
# Belief Propagation

Compute marginals:

$$p(x_i) = \int p(\mathbf{x}) d\mathbf{x}_{\setminus i}$$

Standard, efficient inference algorithm which uses  
**localized computations** and **message passing**





Belief at node  $s$  :

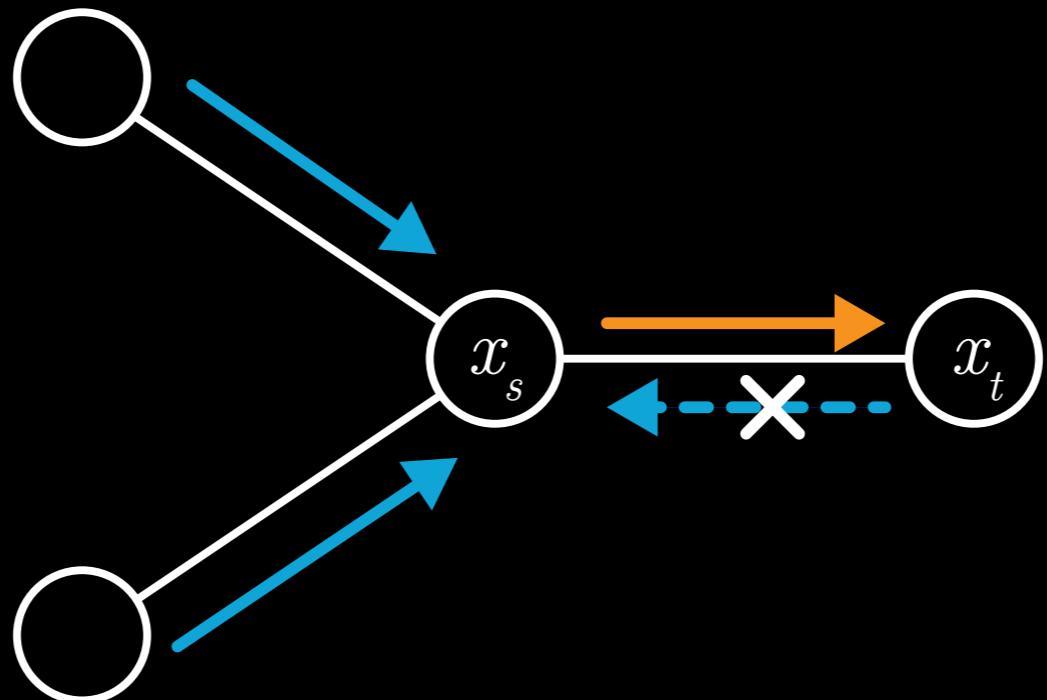
$$b_s(x_s) = \kappa \psi_s(x_s) \prod_{u \in N(s)} m_{us}(x_s)$$

Message update rule:

$$m_{st}^{n+1}(x_t) = \int_{x_s} dx_s \psi_s \psi_{st} \prod_{u \in N(s) \setminus t} m_{us}^n(x_s)$$

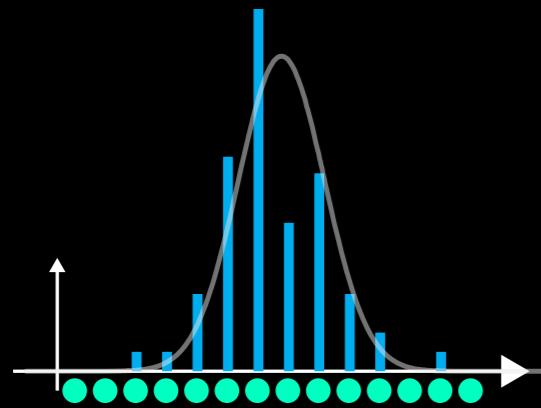
- Exact for trees, approximate for loopy graphs
- E.g. satellite communications

$$m_{st}^{n+1}(x_t) = \int_{x_s} dx_s \psi_s \psi_{st} \prod_{u \in N(s) \setminus t} m_{us}^n(x_s)$$



**Neurons cannot readily send many different signals  
to many different target neurons**

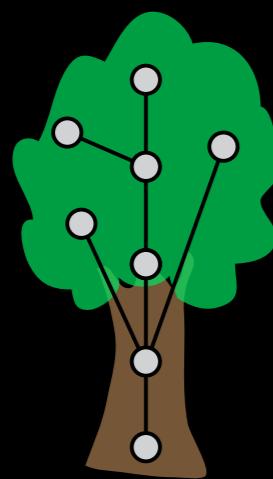
# Probabilistic Population Codes



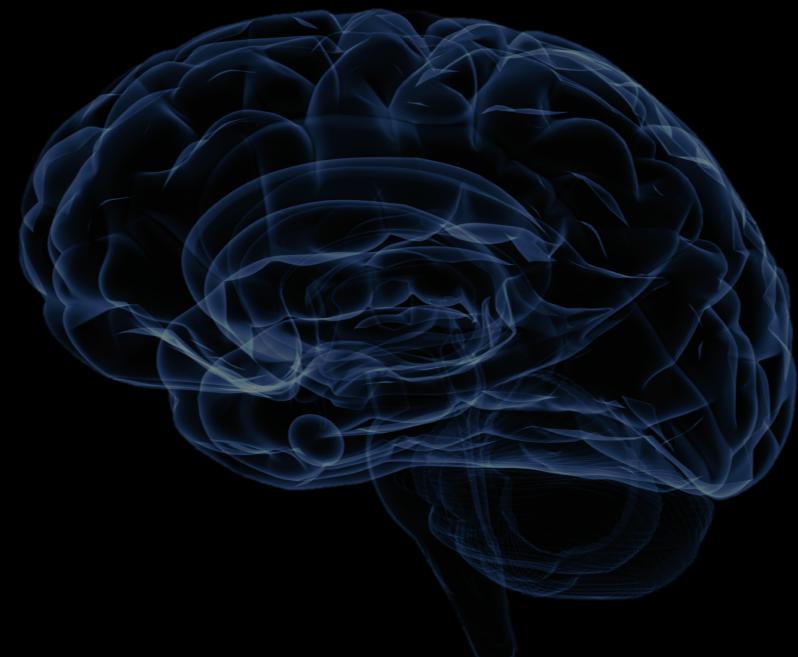
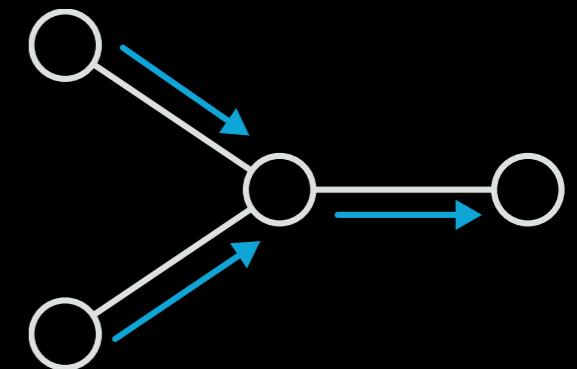
# Graphical Models



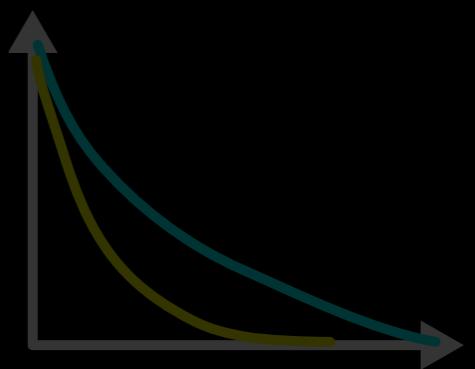
# Tree-based Re-parameterization



# Belief Propagation

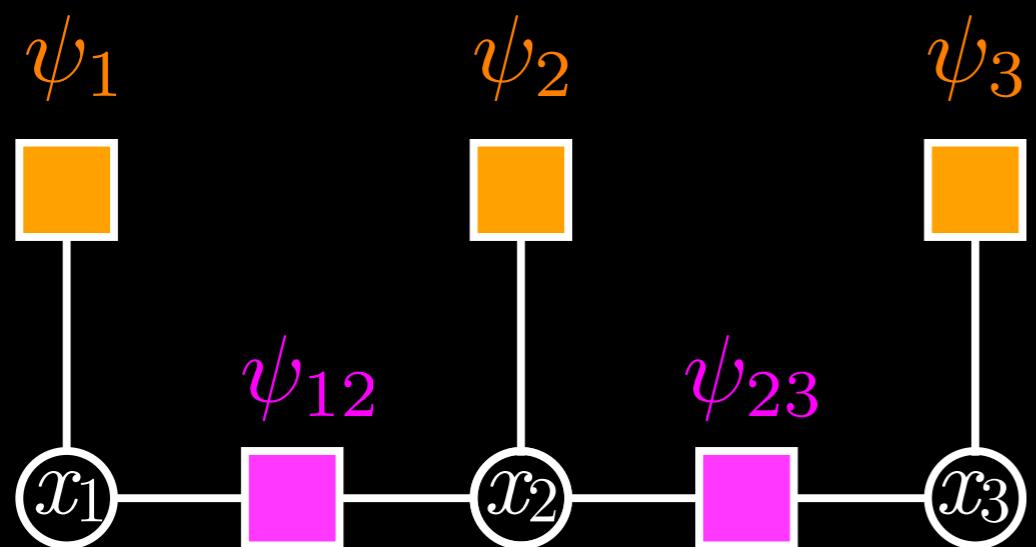


# Dynamical Systems



# Tree-based Re-parameterization

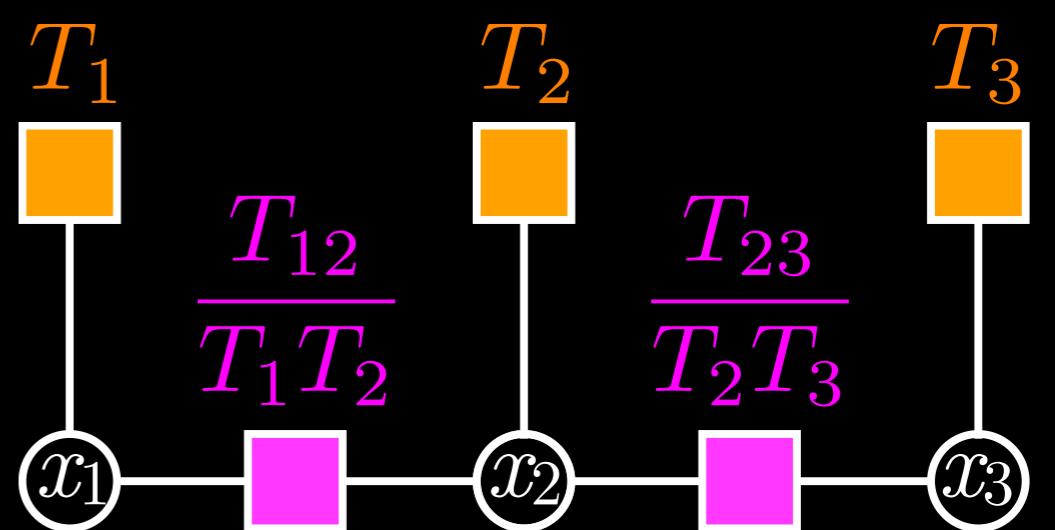
Original



$\psi_s(x_s), \psi_{st}(x_s, x_t)$

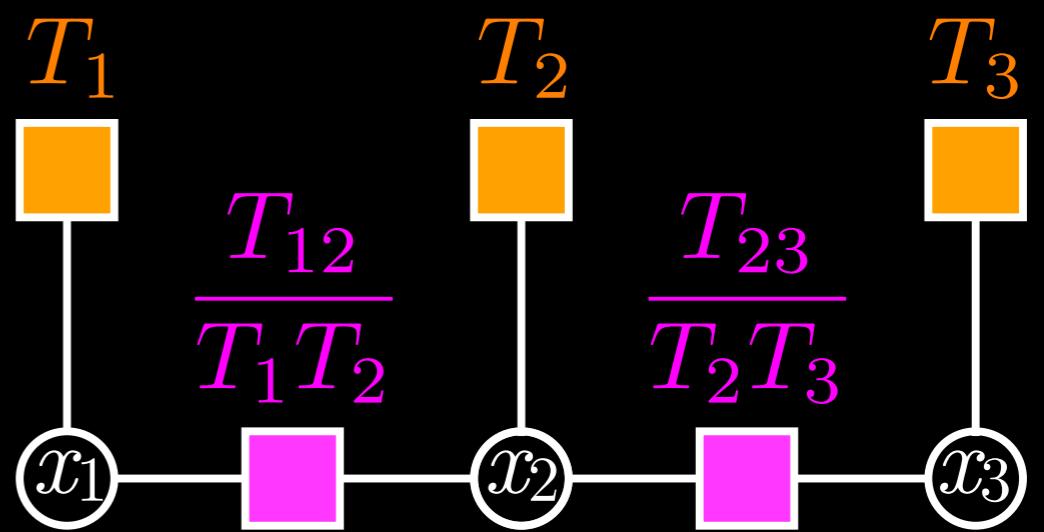
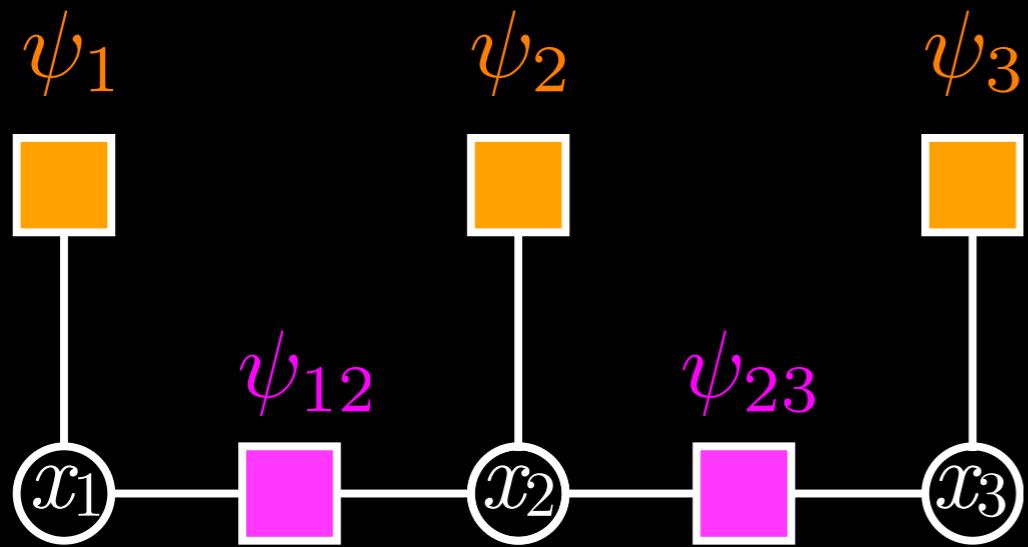
$\psi$  :Factors

Re-parameterized



$T_s(x_s), T_{st}(x_s, x_t)$

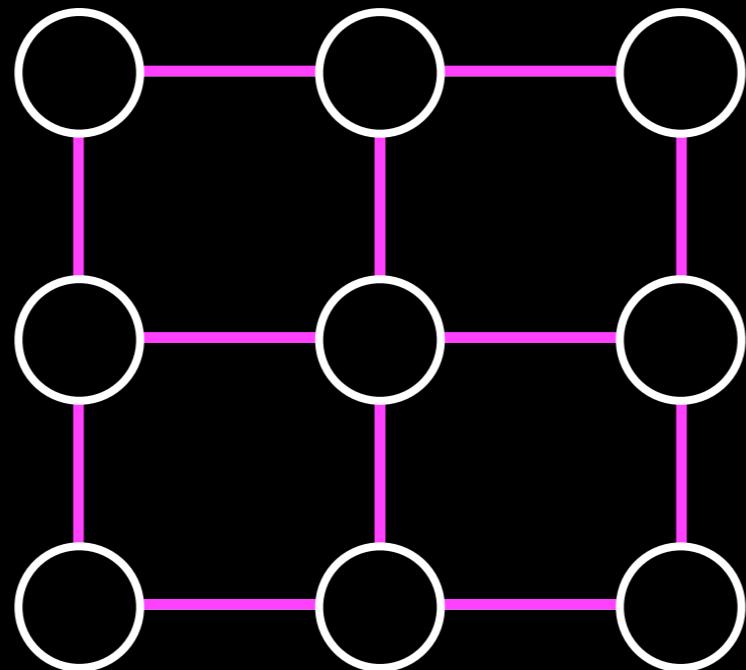
$T$  :Marginals



$$p(\mathbf{x}) = \frac{1}{Z} \prod_{s \in V} \psi_s(x_s) \prod_{(s,t) \in E} \psi_{st}(x_s, x_t)$$

$$p(\mathbf{x}) = \prod_{s \in V} T_s(x_s) \prod_{(s,t) \in E} \frac{T_{st}(x_s, x_t)}{T_s(x_s)T_t(x_t)}$$

For loopy graphs, re-factorize acyclic subgraphs iteratively



$$p(\mathbf{x}) = p^\tau(\mathbf{x})r^\tau(\mathbf{x})$$

- Refactor tree in terms of *pseudomarginals* ( $T_s, T_{st}$ )
- Pick a different tree and repeat

BP as TRP using extremely simple trees: **edges**

At iteration  $n+1$ , the pseudomarginals are computed as:

$$T_s^{n+1} \propto T_s^n \prod_{u \in N(s)} \frac{1}{T_s^n} \int T_{su}^n dx_u$$

$$T_{st}^{n+1} \propto \frac{T_{st}^n}{\left( \int T_{st}^n dx_t \right) \left( \int T_{st}^n dx_s \right)} T_s^{n+1} T_t^{n+1}$$

Operations on neighbors **do not differentiate between targets**

# TRP for Exponential Family

Exponential  
family of distributions:

$$p(\mathbf{x}; \boldsymbol{\theta}) = \exp(\boldsymbol{\theta}) \cdot \phi(\mathbf{x}) - A(\boldsymbol{\theta}) + B(\mathbf{x})$$

$\boldsymbol{\theta}$  : natural parameters

$\phi(\mathbf{x})$  : sufficient statistics

Pseudomarginal for a  
clique, at iteration  $n$  :

$$T_c^n(\mathbf{x}_c) = \exp (\boldsymbol{\theta}_c^n \cdot \phi_c(\mathbf{x}_c))$$

Updates in terms of the natural parameters:

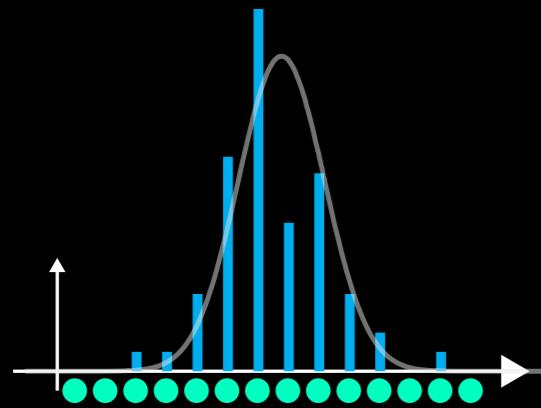
$$T_s^{n+1} \propto T_s^n \prod_{u \in N(s)} \frac{1}{T_s^n} \int T_{su}^n dx_u$$

$$\theta_s^{n+1} = (1 - d_s) \theta_s^n + \sum_{u \in N(s)} \mathbf{g}_V(\theta_{su}^n)$$

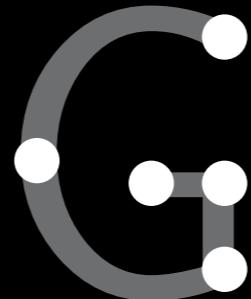
$$T_{st}^{n+1} \propto \frac{T_{st}^n}{\left( \int T_{st}^n dx_t \right) \left( \int T_{st}^n dx_s \right)} T_s^{n+1} T_t^{n+1}$$

$$\theta_{st}^{n+1} = \theta_{st}^n + Q_s \theta_s^{n+1} + Q_t \theta_t^{n+1} + \mathbf{g}_E(\theta_{st}^n)$$

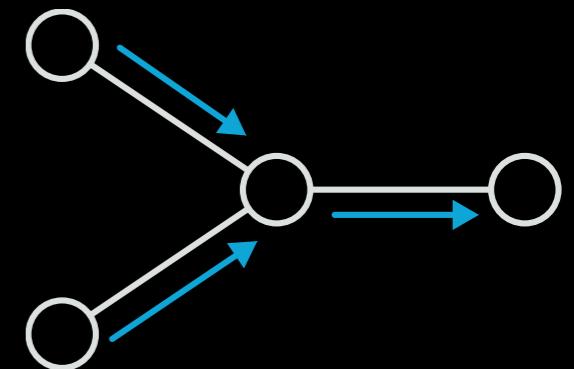
# Probabilistic Population Codes



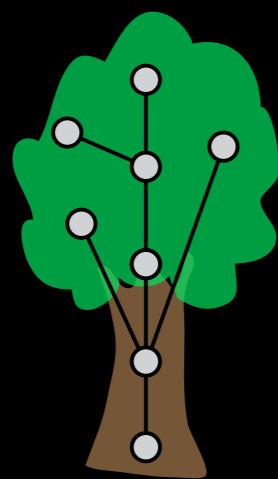
# Graphical Models



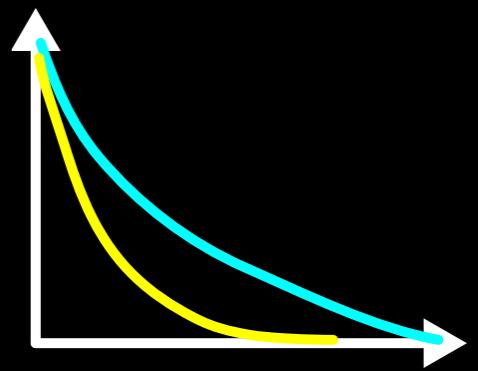
# Belief Propagation



# Tree-based Re-parameterization



# Dynamical Systems



# Separation of Time Scales for TRP updates

TRP updates circumvent the ‘message exclusion’ problem

$$\theta_s^{n+1} = (1 - d_s) \theta_s^n + \sum_{u \in N(s)} \mathbf{g}_V(\theta_{su}^n)$$

$$\theta_{st}^{n+1} = \theta_{st}^n + Q_s \theta_s^{n+1} + Q_t \theta_t^{n+1} + \mathbf{g}_E(\theta_{st}^n)$$

No free lunch: update for pairwise term is instantaneous

The brain can use **fast and slow timescales**  
instead of instant and delayed signals

Introduce auxiliary variables  $\tilde{\theta}$ ,  
convert updates to continuous time

$$\tau_{\text{slow}} \dot{\tilde{\theta}} = -\tilde{\theta} + \theta$$

Nonlinear dynamics are updated on a faster timescale:

$$\tau_{\text{fast}} \dot{\theta}_s = -d_s \tilde{\theta}_s + \sum_{u \in N(s)} \mathbf{g}_V(\tilde{\theta}_{su})$$

$$\tau_{\text{fast}} \dot{\theta}_{st} = Q_s \theta_s + Q_t \theta_t + \mathbf{g}_E(\tilde{\theta}_{st})$$

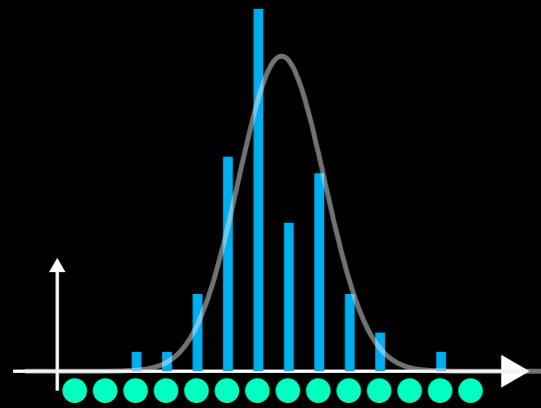
Concatenate the two sets of parameters:  $\Theta = (\theta, \tilde{\theta})$

Dynamical system which represents the approximation to the TRP iterations:

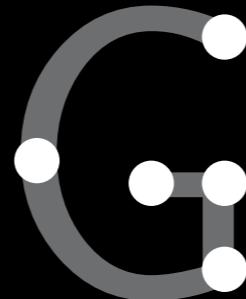
$$\dot{\Theta} = W\Theta + \mathbf{G}(\Theta)$$

$W$  and  $\mathbf{G}$  inherit their structure from the discrete time updates and the filtering at different timescales

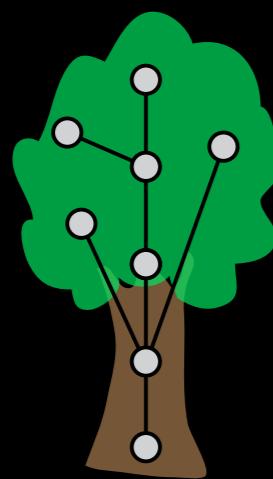
# Probabilistic Population Codes



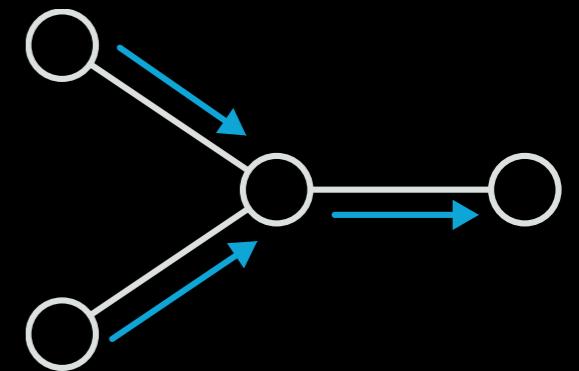
# Graphical Models



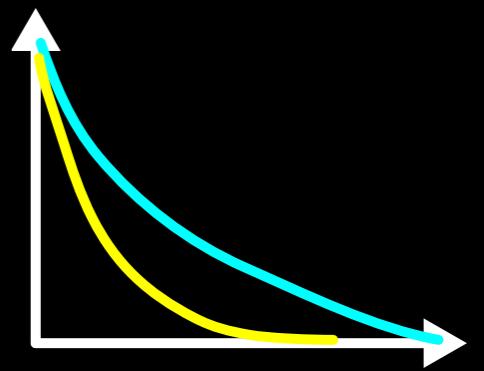
# Tree-based Re-parameterization



# Belief Propagation



# Dynamical Systems



# Network Architecture

Map neural activity onto  
natural parameters:

$$\mathbf{r} = U\Theta$$

$U$  is a rectangular embedding  
matrix of size:

$$N_{\mathbf{r}} \times N_{\Theta}$$

Parameters can be decoded  
from neural activity:

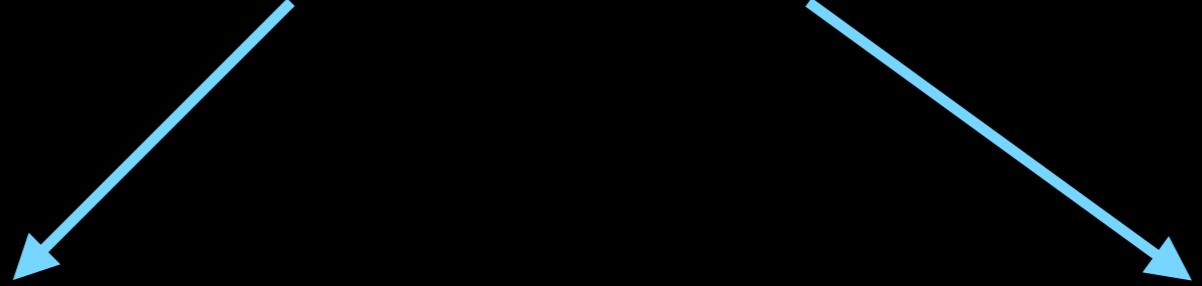
$$\Theta = U^+ \mathbf{r}$$

$U^+$  is the pseudoinverse of  $U$

Applying this basis transformation to  $\dot{\Theta} = W\Theta + \mathbf{G}(\Theta)$   
we obtain

$$\dot{\mathbf{r}} = U\dot{\Theta} = U(W\Theta + \mathbf{G}(\Theta)) = UWU^+\mathbf{r} + U\mathbf{G}(U^+\mathbf{r})$$

$$\dot{\mathbf{r}} = W_L\mathbf{r} + \mathbf{G}_{NL}(\mathbf{r})$$



Linear computation  
Integrate evidence

Nonlinear computation  
Marginalize evidence

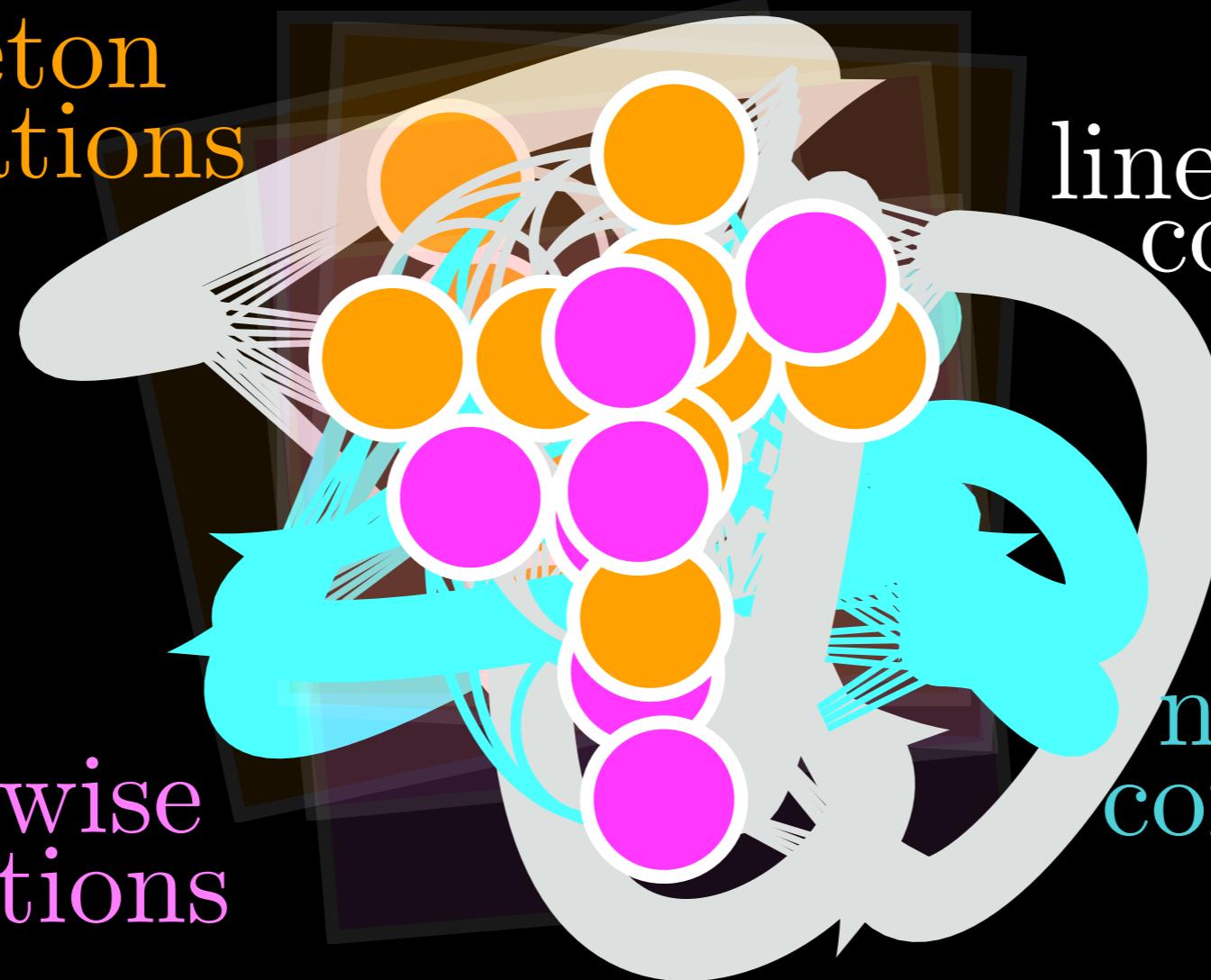
$$\dot{\mathbf{r}} = W_L \mathbf{r} + \mathbf{G}_{NL}(\mathbf{r})$$

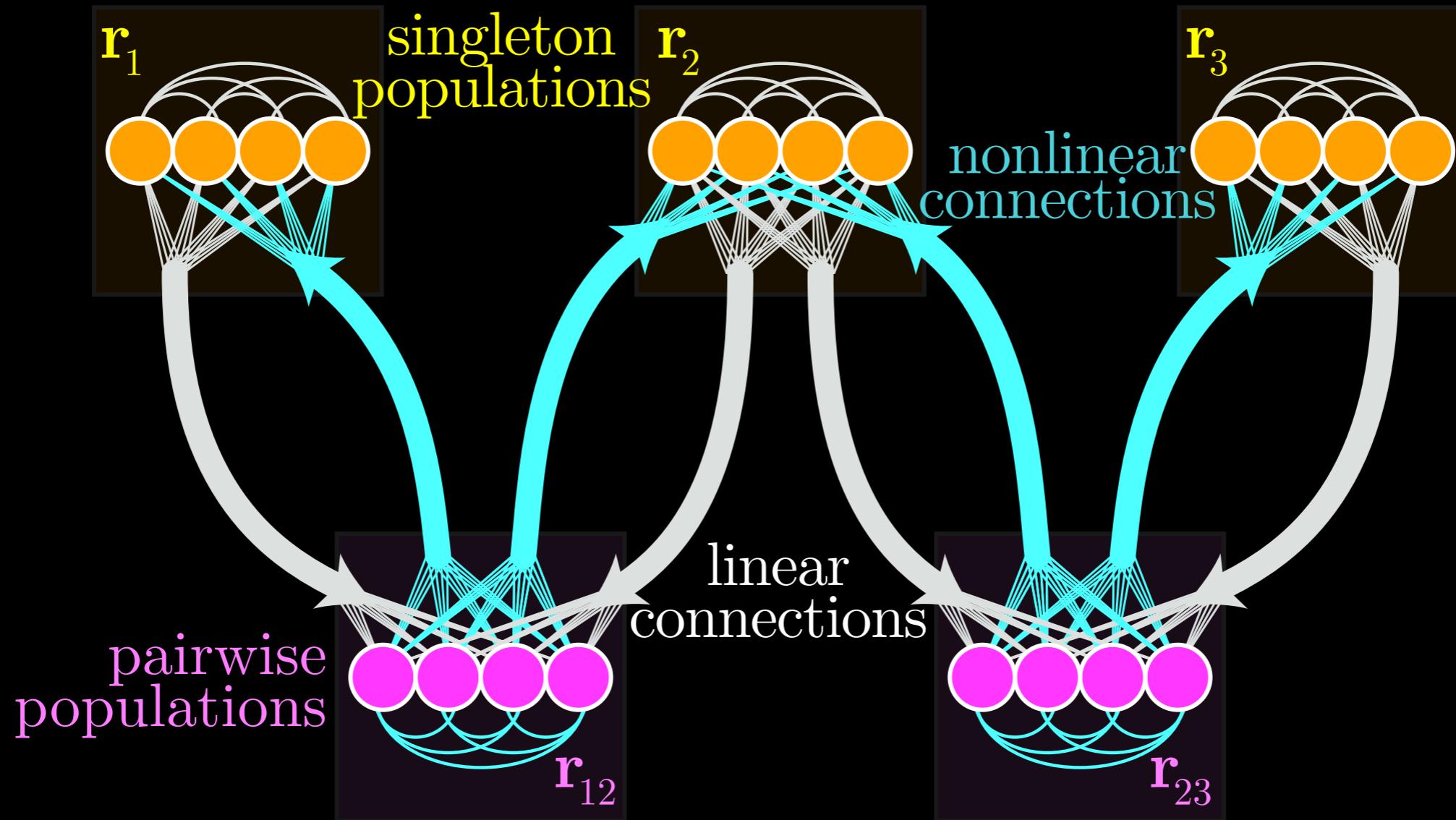
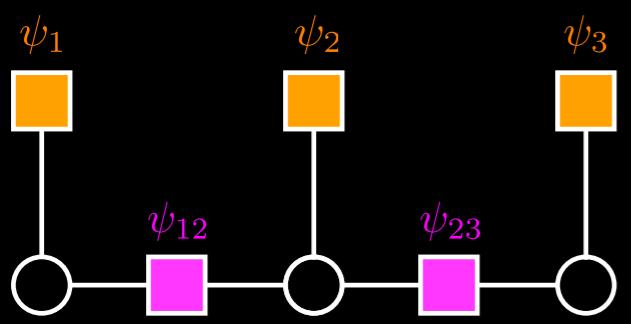
singleton  
populations

linear  
connections

pairwise  
populations

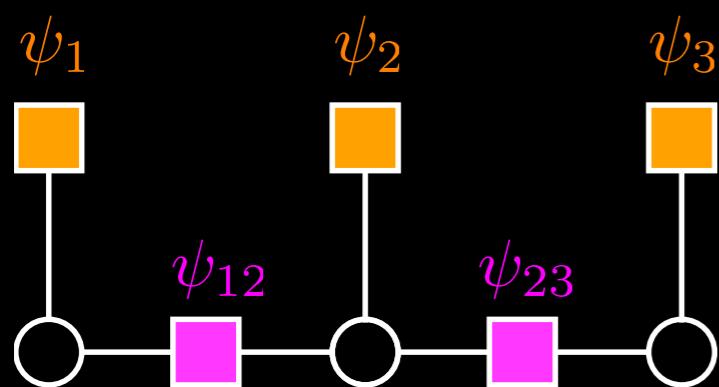
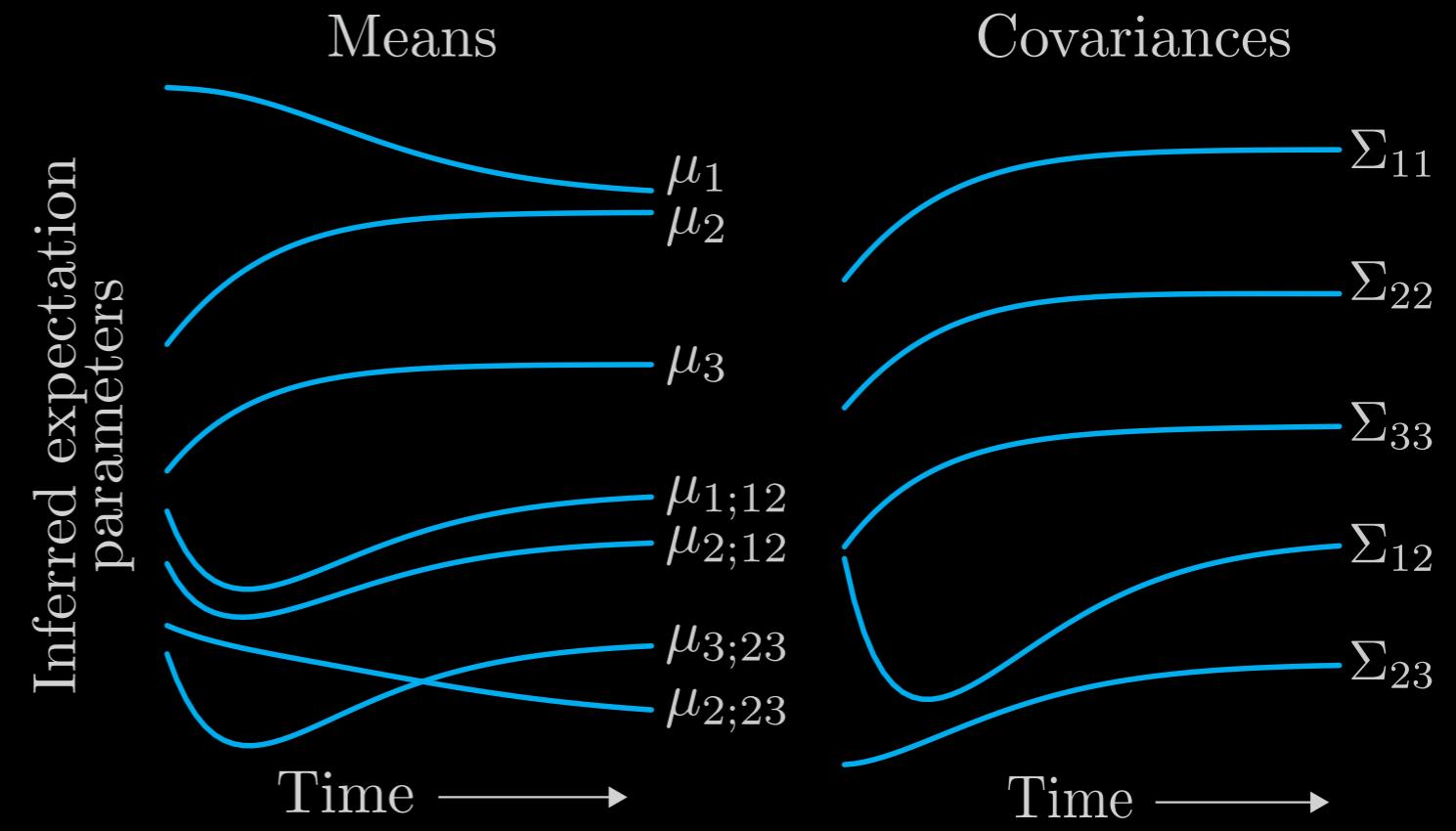
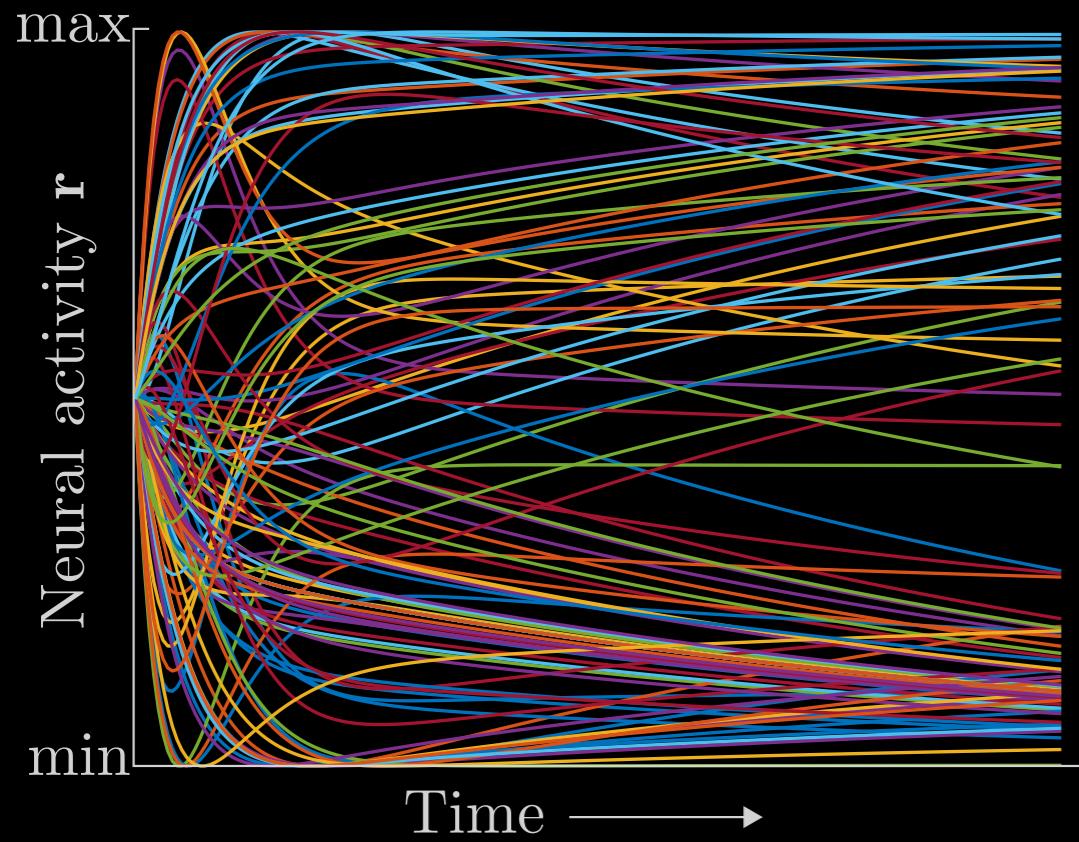
nonlinear  
connections



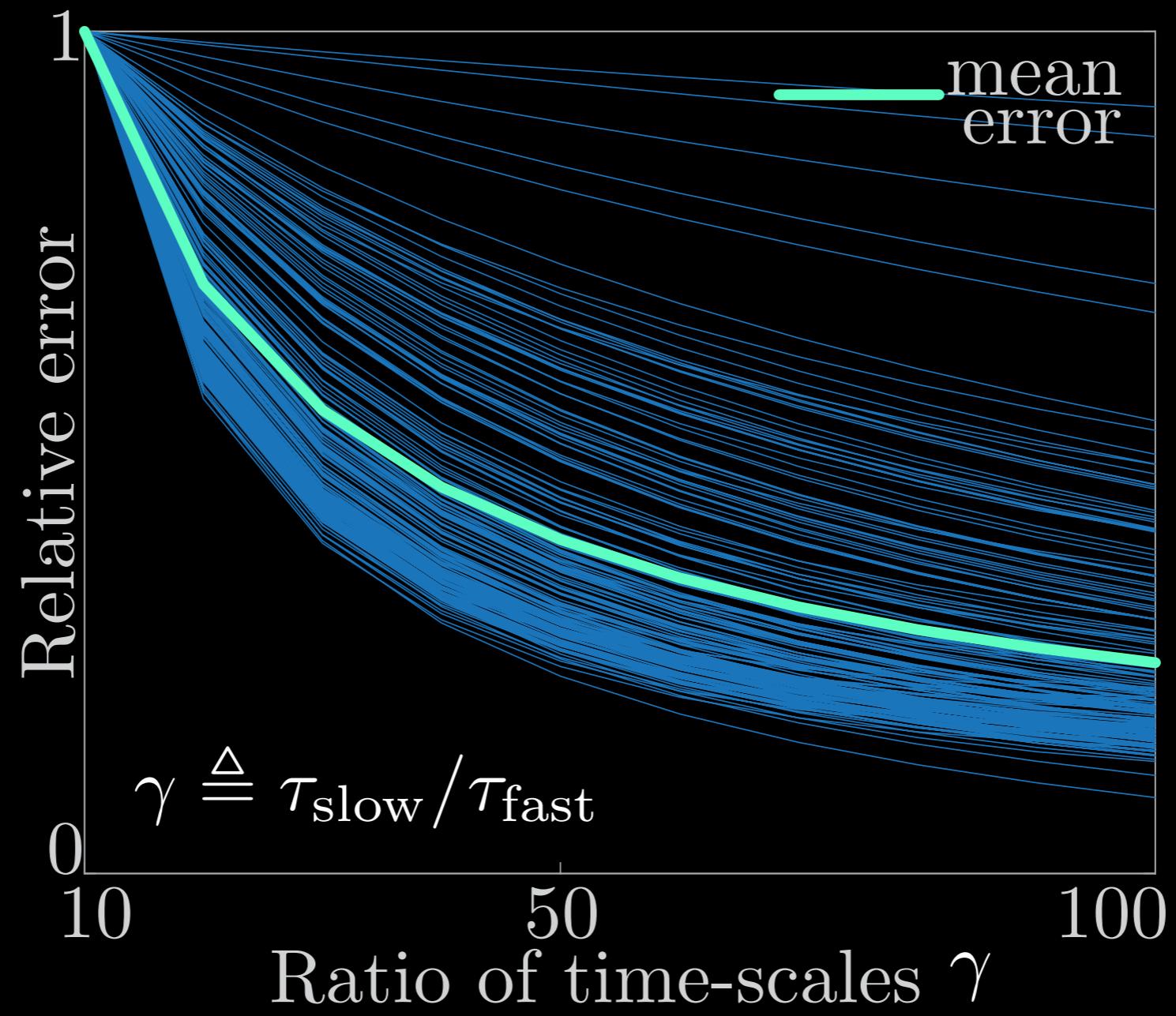


# Experiments

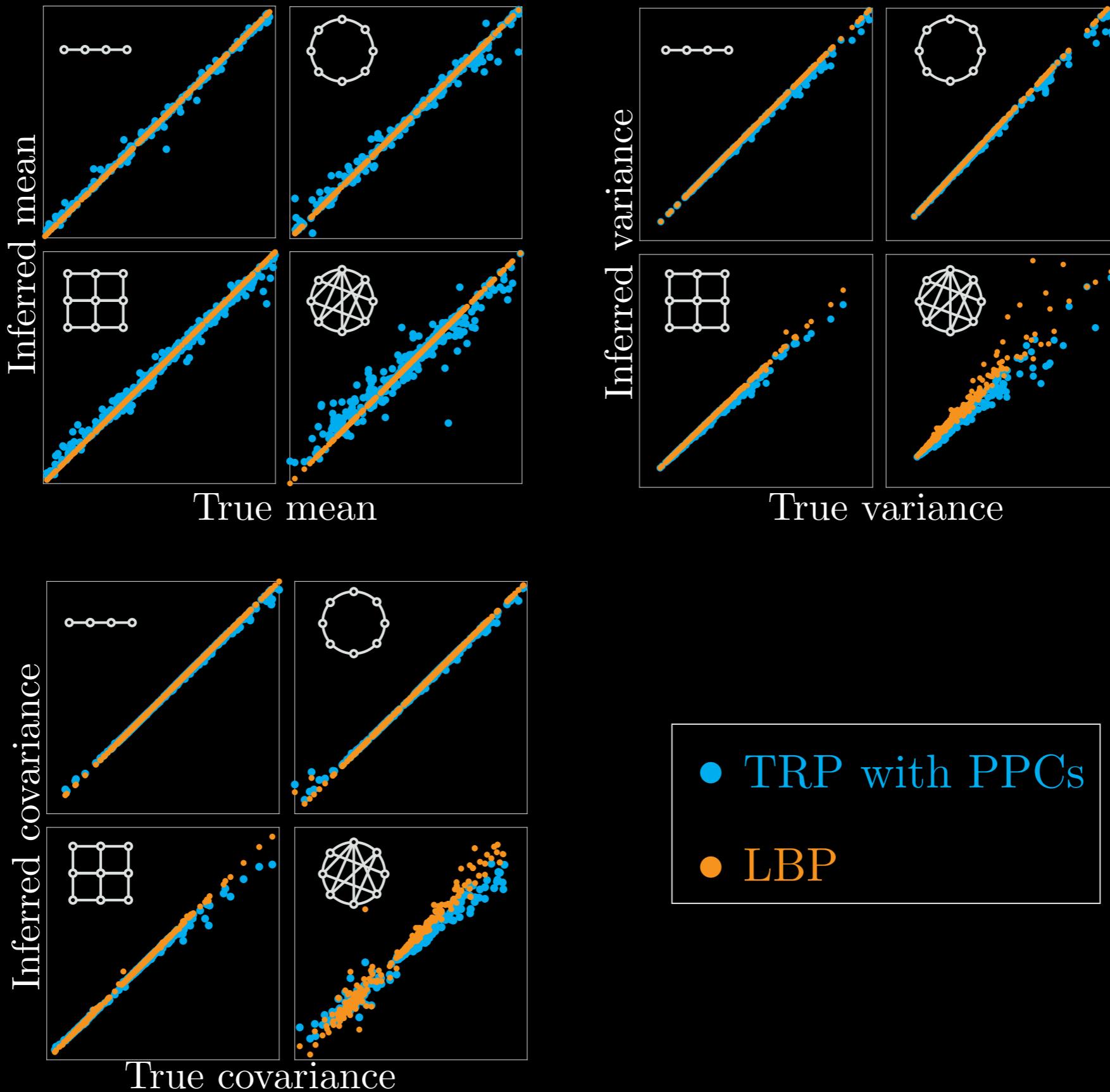
- Performance of the network evaluated on Gaussian graphical models
  - ★ of different topologies - chains, loops, grids, dense
  - ★ up to 400 variables
- Network time constants were set to have a ratio of  $\tau_{\text{slow}}/\tau_{\text{fast}} = 20$



Dynamics of neural population activity and expectation parameters of the underlying distribution for an example graph

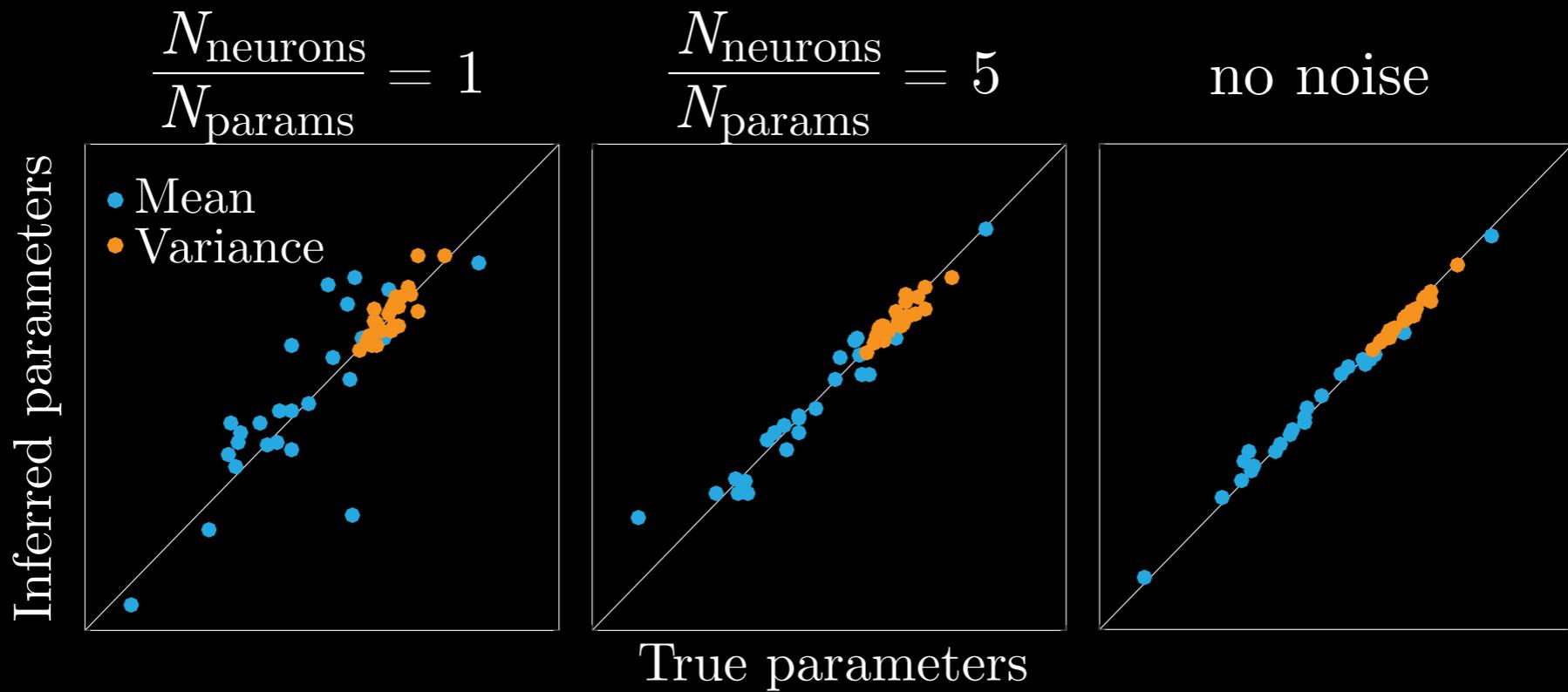
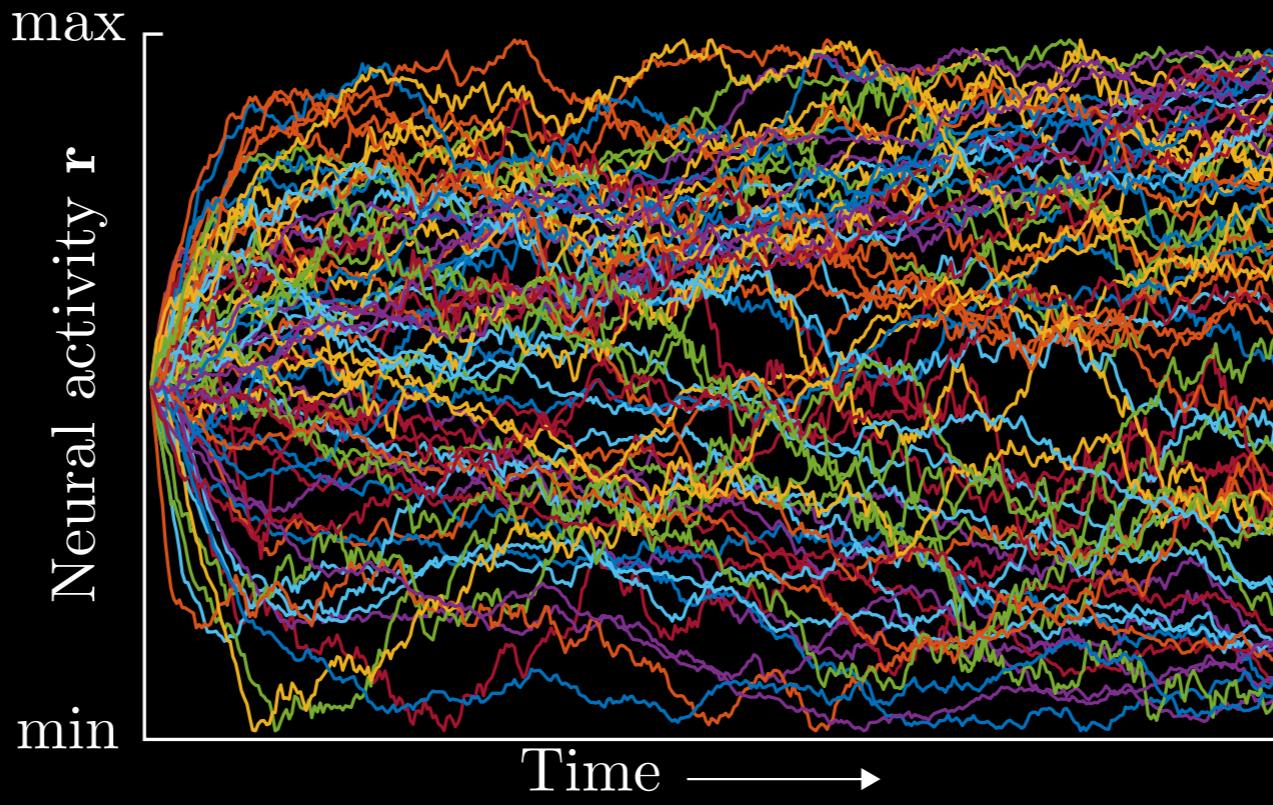


Performance is quantified by the mean squared error in inferred parameters for a given  $\gamma$  divided by the error for a reference  $\gamma_0 = 10$



- TRP with PPCs
- LBP

Inference performance of our model vs. LBP for various graph topologies



Network performance is robust to noise and improves with more neurons

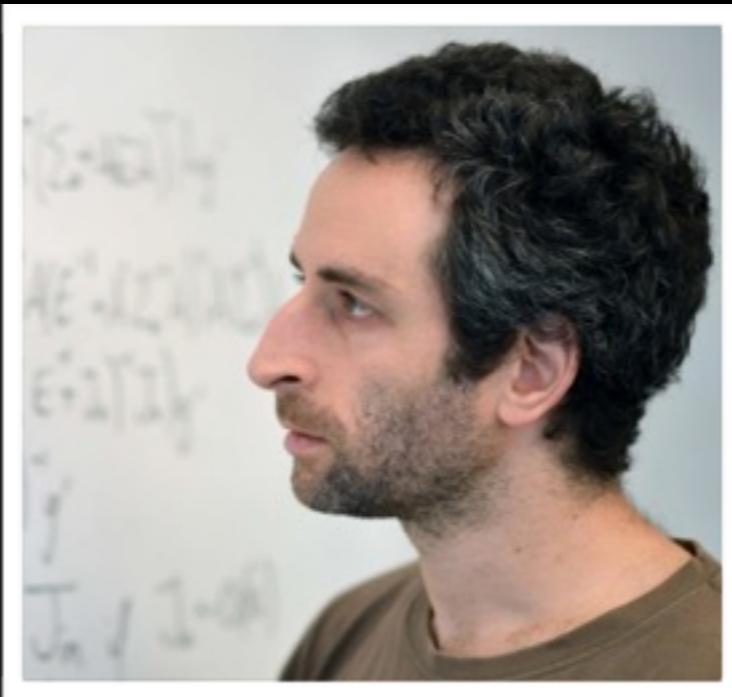
# Conclusion

**Distributed, nonlinear, recurrent network of neurons  
perform probabilistic inference**

- Neural activity encodes parameters of the distribution
- Nonlinear interactions implement marginalization
- Multiple time scales compensate for message exclusion

# Future directions

- Testing detailed biological validity of the model
- Inferring network from data
- Limited to static graphical models
- How can the network learn?



[xaqlab.com](http://xaqlab.com)

