

Using artificial neural networks to uncover relationships between network structures and computations

Maturation and Plasticity in Biological and Artificial Neural Networks
Cargese, October 2024



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Outline

→ Introduction: cognitive modeling

Theory-based reverse-engineering of artificial neural networks

On the computational role of population structure

Modeling temporally structured behaviors

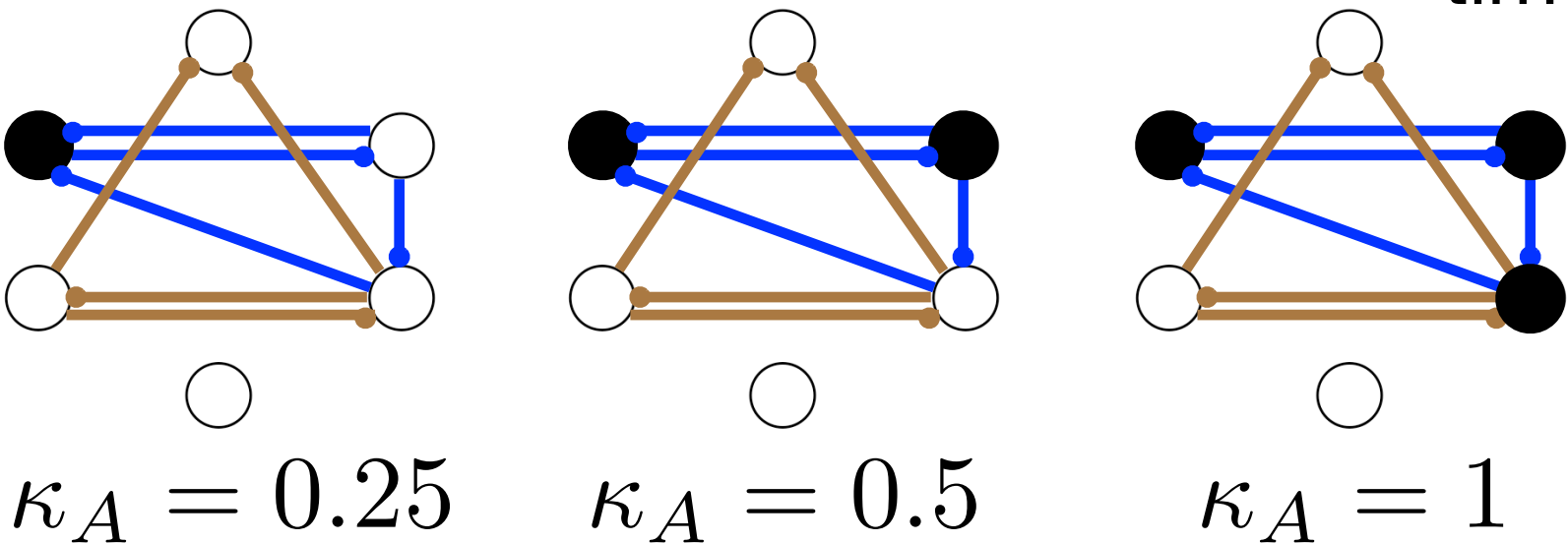
Neural implementation of working memory:

Associativity of working memory:



time

Neural implementation:
positive feed-back loops



○ silent neuron
● active neuron

Formalisation: synaptic structure

electrical activity

$$W_{rec,ij} = r_i^{\mu=1} r_j^{\mu=1} + r_i^{\mu=2} r_j^{\mu=2} + \dots$$

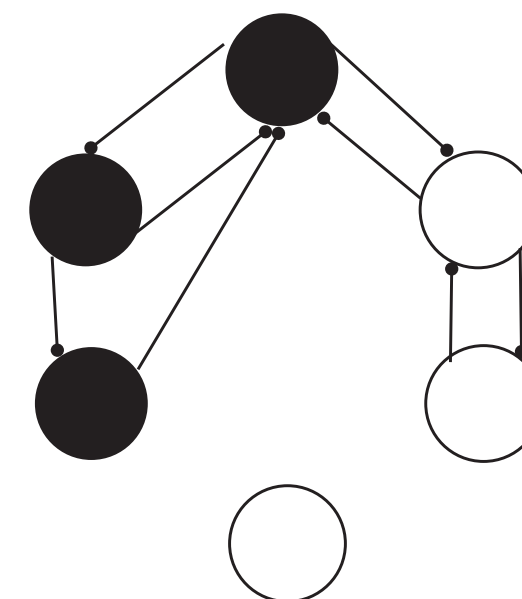
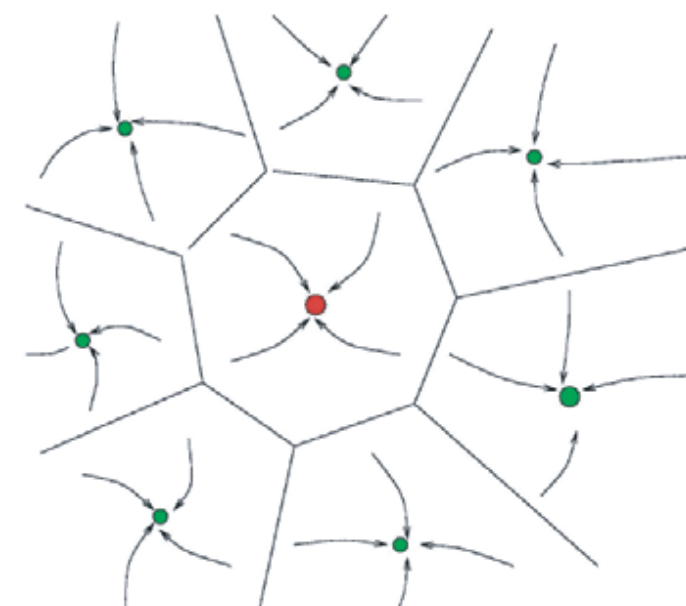
$$\frac{d\kappa_A}{dt} = F(\kappa_A(t))$$

Hopfield, 1982

Derrida, Gardner, Zippelius, 1987

Neural implementation of working memory:

Associativity of
working memory



cognitive
properties

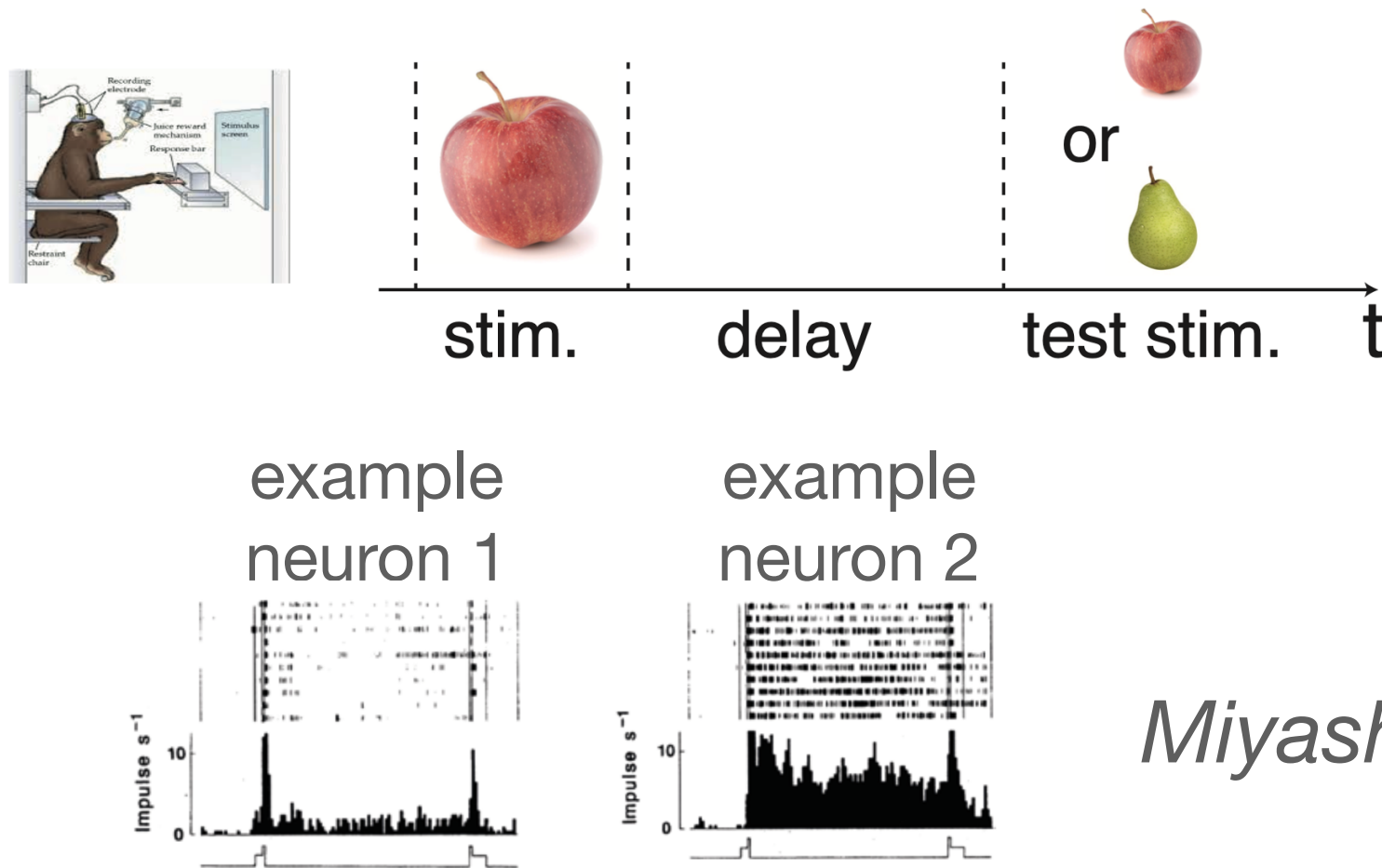
Trajectories of
network configurations

Synaptic
structure

$$\frac{d\kappa_A}{dt} = F(\kappa_A(t))$$

Relationship with properties of brain circuits

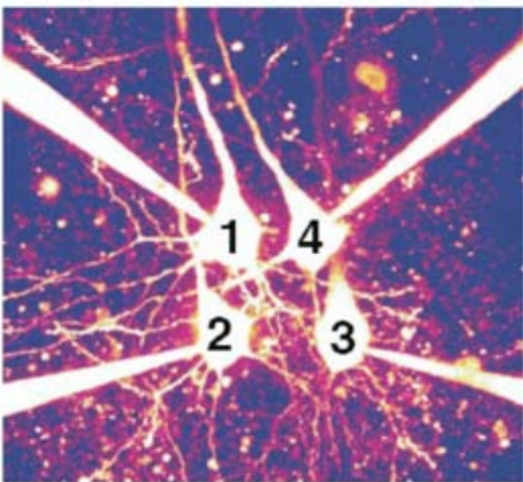
➔ Physiological correlates



Miyashita, 1988

➔ Anatomical correlates

PFC local connectivity



Proba. of connections = 0.1

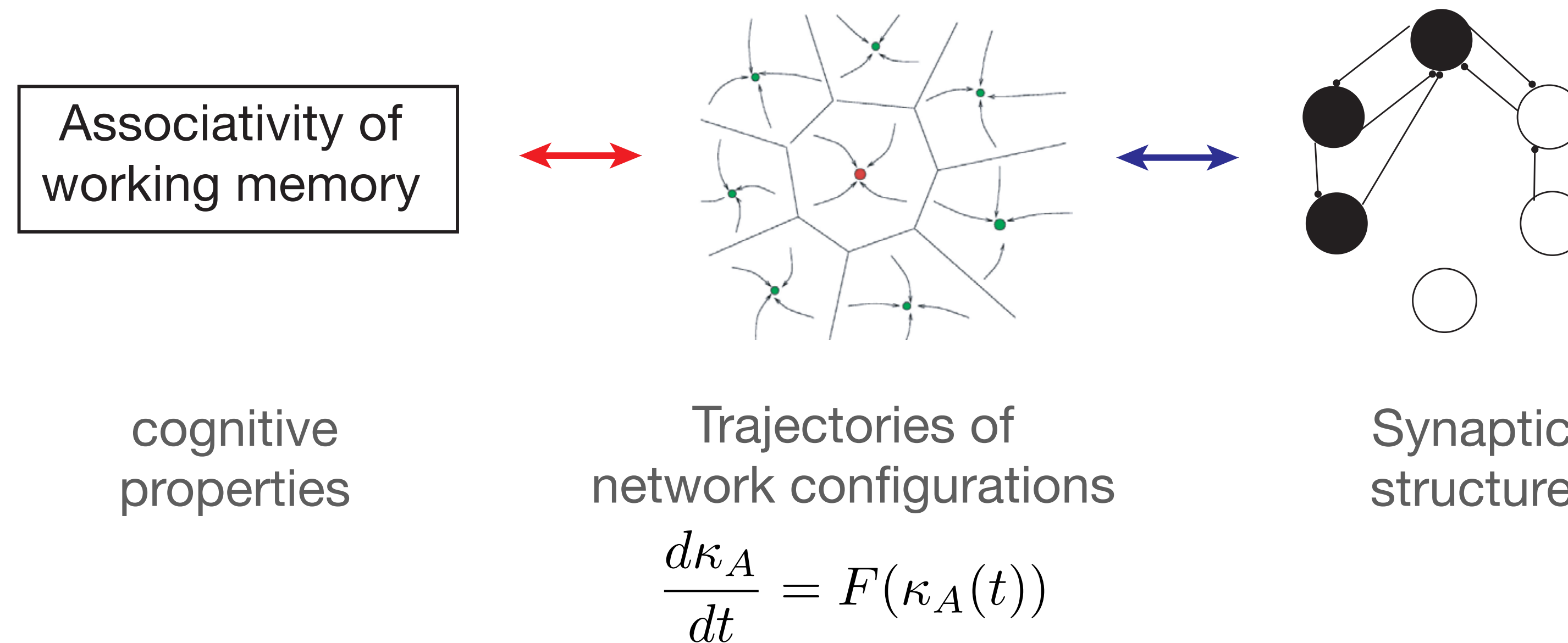
Proba. of reciprocal
connections = 0.04 > 0.01

Wang et al, 2006

Matches statistics of ANN
optimizing memory
storage

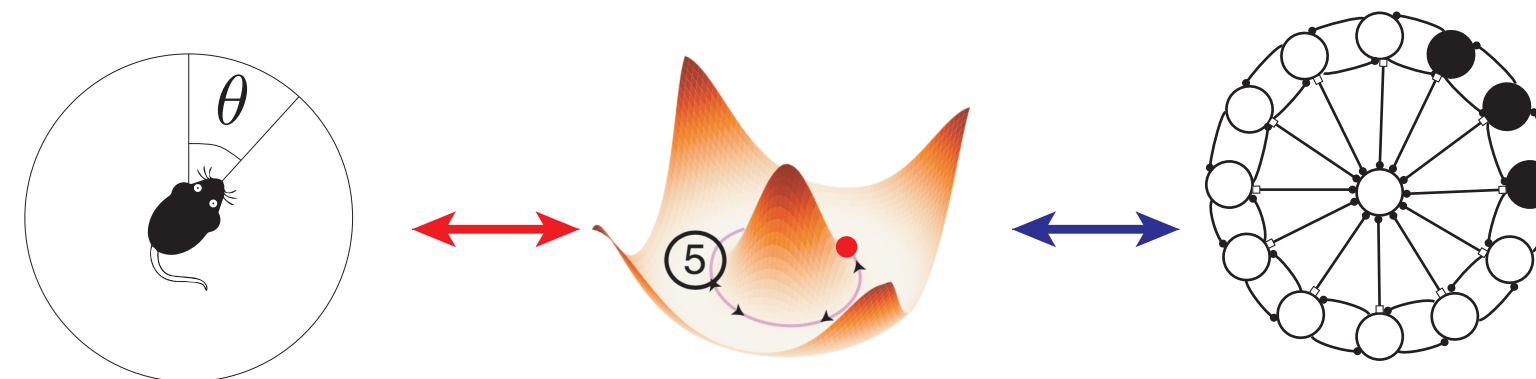
Brunel 2016

Neural implementation of working memory:



Modeling of other cognitive phenomena

➔ Sense of direction and ring model



Amari, 1979 ; Skaggs 1995
Kim, Rouault et al., 2017

➔ Sense of location and place cells or grid cells

Tsodyks & Sejnowski 1994
Burak & Fiete, 2009

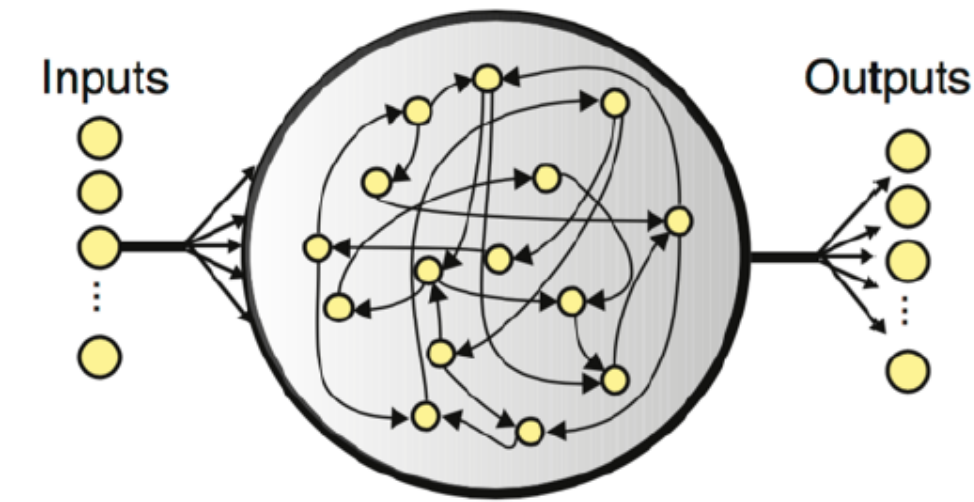
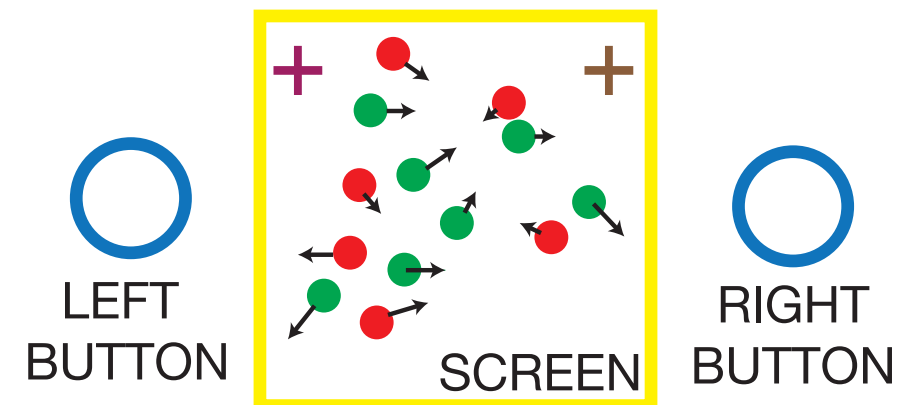
➔ Decision making

Wang, 2008

Modeling cognitive processes with artificial neural networks

Train artificial neural networks to perform neuroscience tasks

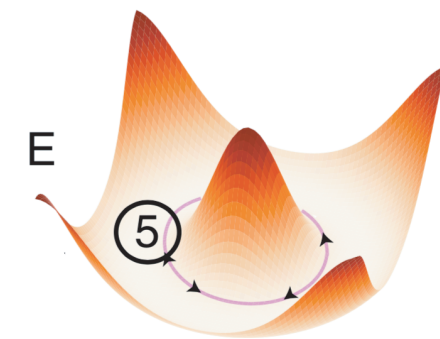
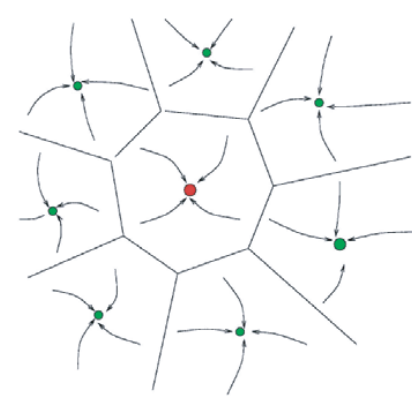
moving left or right ?
more green (left) or red (right) ?



Sussillo, 2014

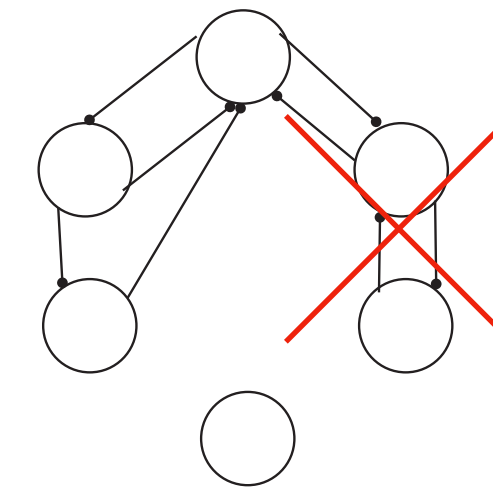
Barak, 2017

Reverse-engineering trained networks:



$$\frac{d\kappa_A}{dt} = F(\kappa_A(t))$$

Sussillo & Barak, 2013



Yang et al, 2019

➡ No unified framework to link macroscopic dynamics and network's structure

Outline

Introduction: cognitive modeling

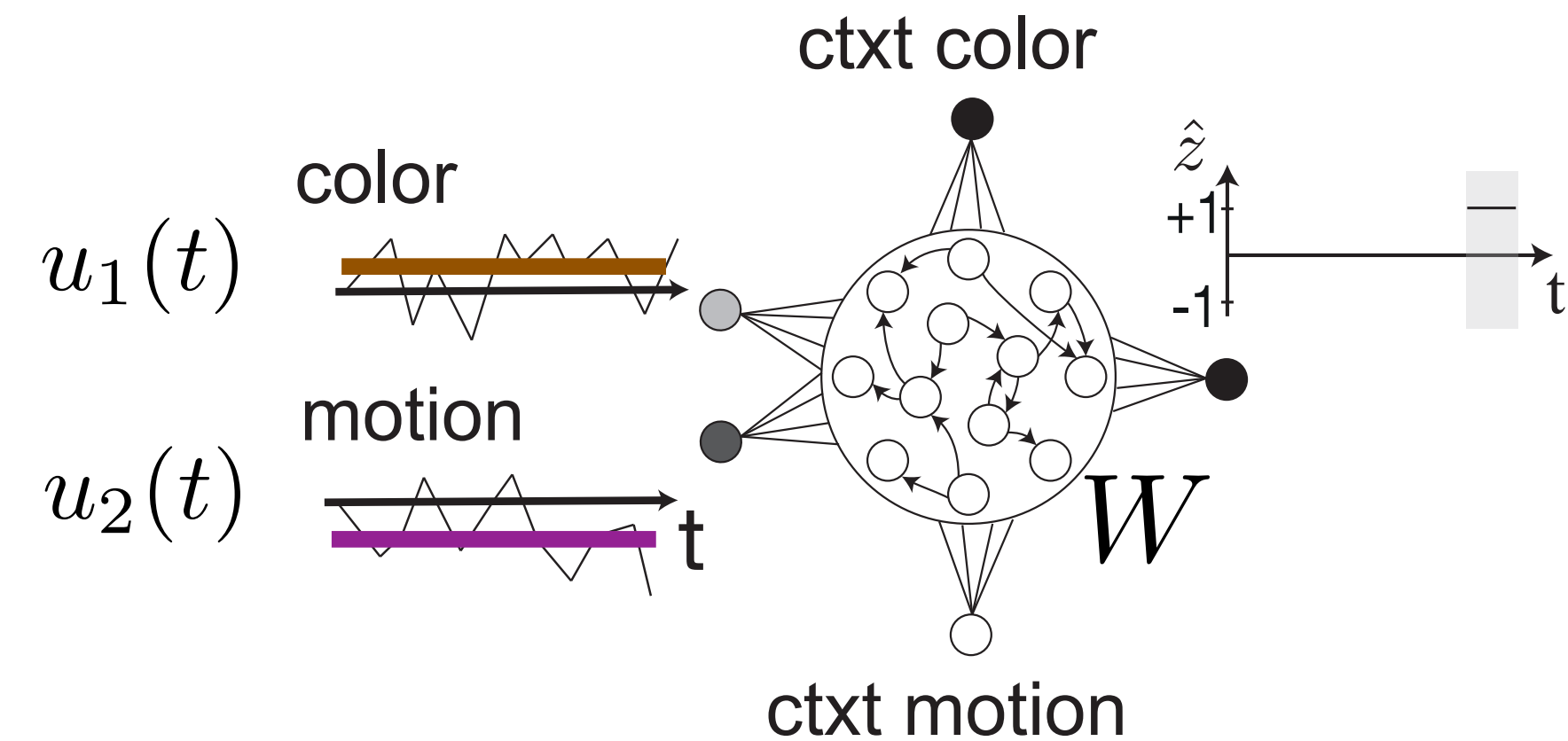
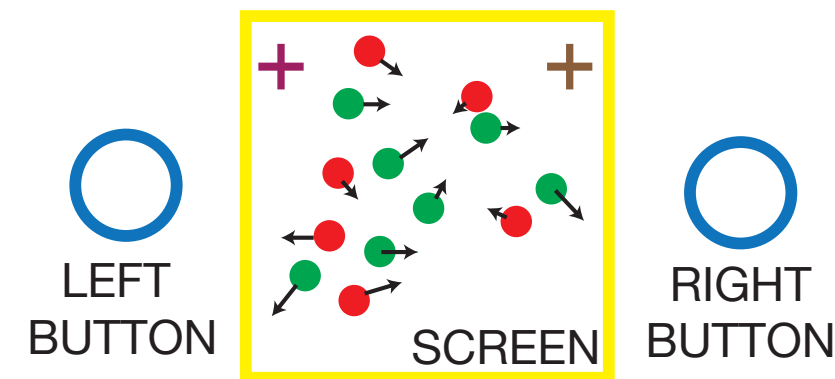
→ Theory-based reverse-engineering of artificial neural networks

On the computational role of population structure

Modeling temporally structured behaviors

Training artificial neural networks on neuroscience tasks

moving left or right ?
more green (left) or red (right) ?



→ Recurrent neural networks (amorphous connectivity structure): N neurons

→ Learning algorithms engineer artificial neural networks:

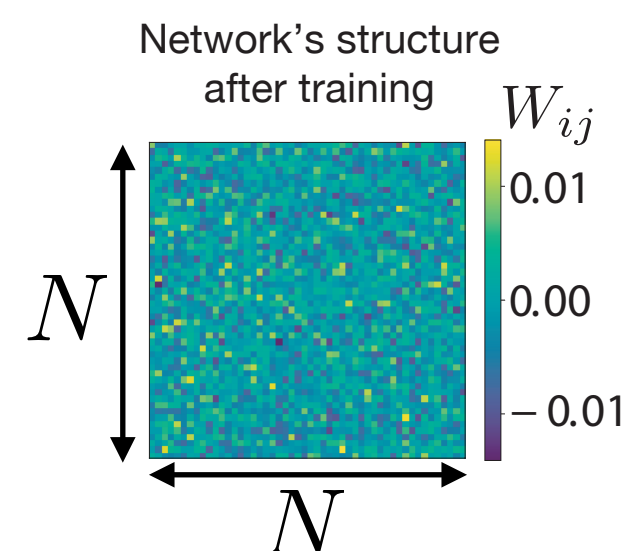
- training dataset + cost-function

$$\left\{ \left\{ \text{cat image}, +1 \right\}; \left\{ \text{dog image}, 0 \right\}; \dots \right\} = \left\{ \left\{ i^{\mu=1}, \hat{z}^{\mu=1} \right\}; \left\{ i^{\mu=2}, \hat{z}^{\mu=2} \right\}; \dots \right\} \quad \mathcal{L}_W = \sum_{\mu} (z_W^{\mu} - \hat{z}^{\mu})^2$$

- optimize cost-function over network parameters

compute $\nabla \mathcal{L}_W$; update W ; repeat...

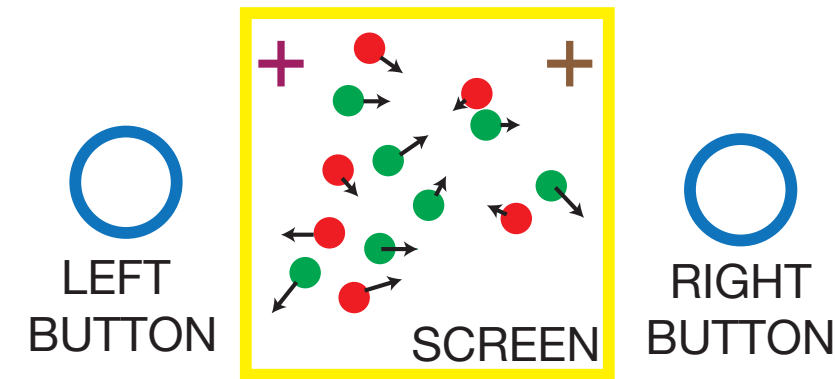
→ After training:



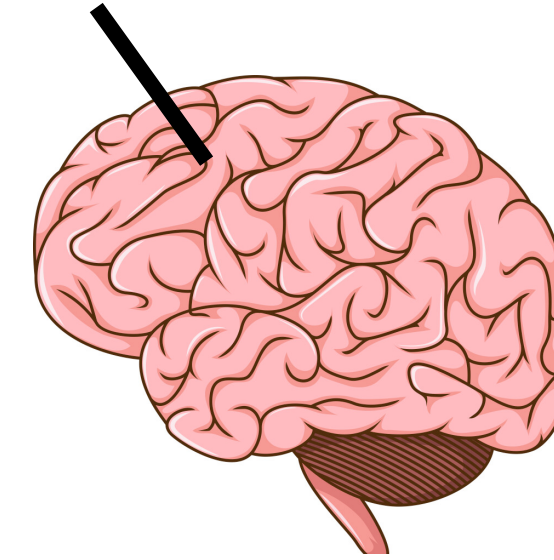
$$N^2 = 10^4 / 10^6$$

Reverse-engineering brain networks

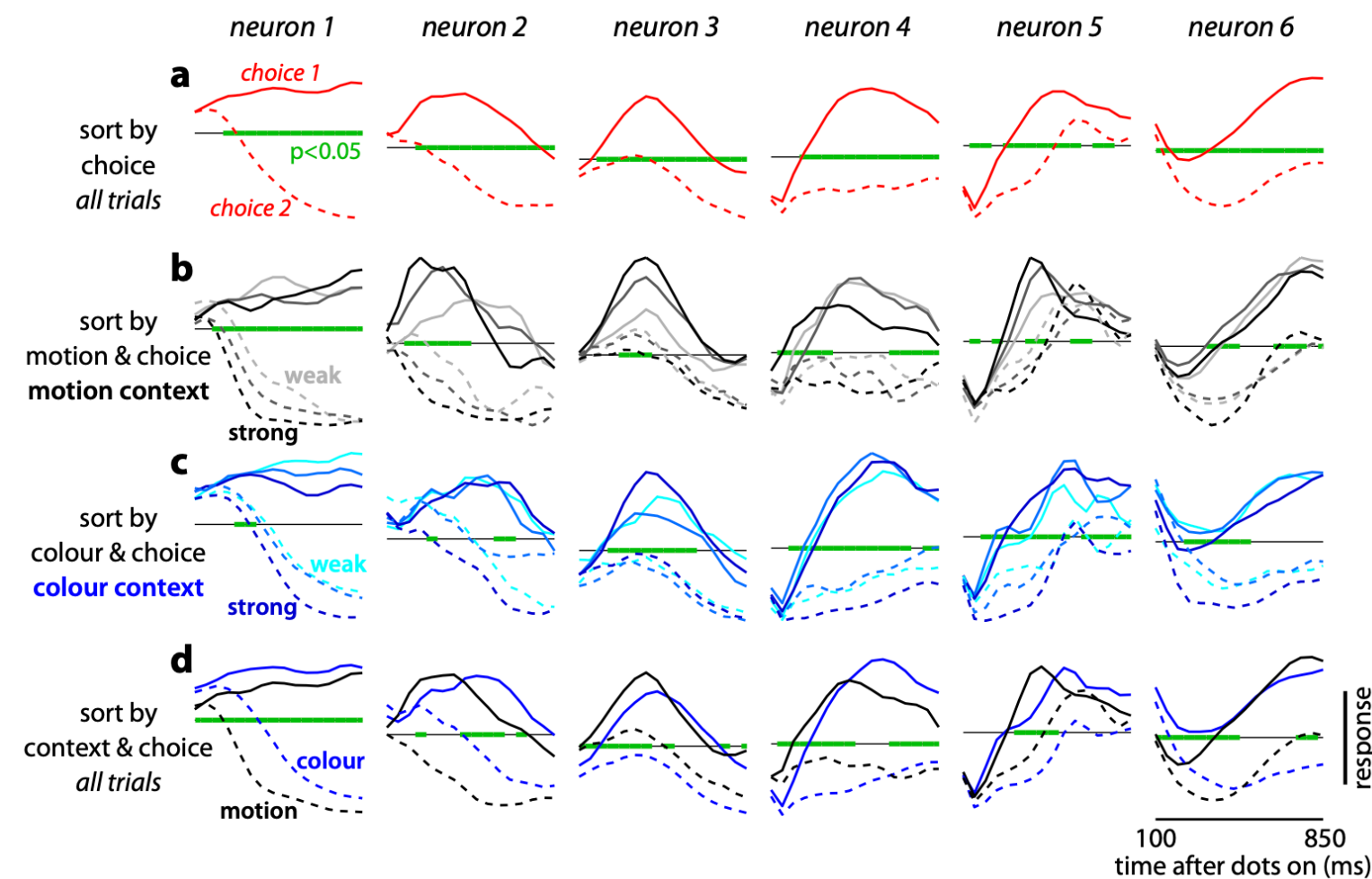
moving left or right ?
more green (left) or red (right) ?



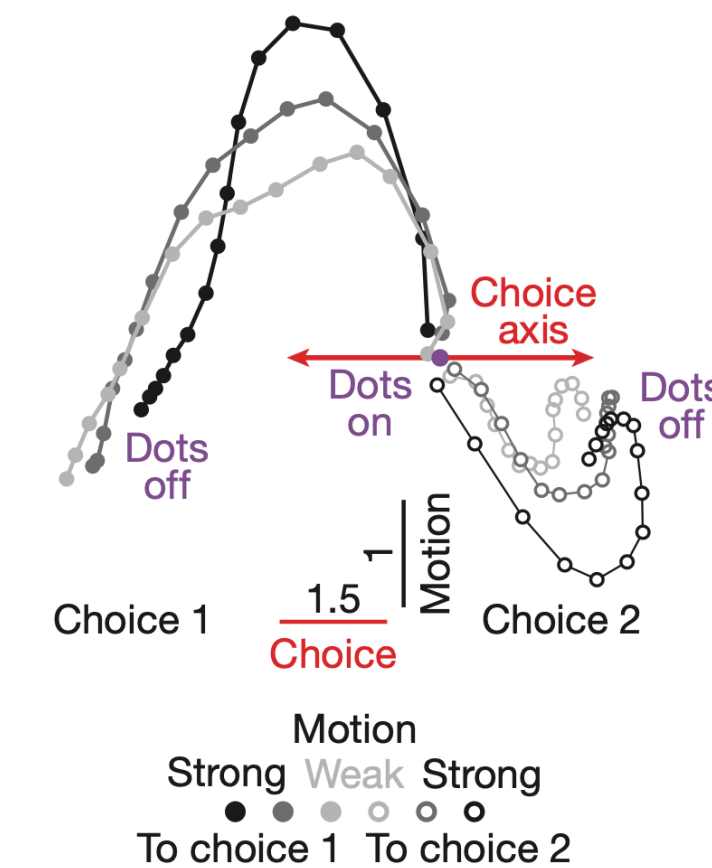
PFC recordings



→ Tuning of individual neurons

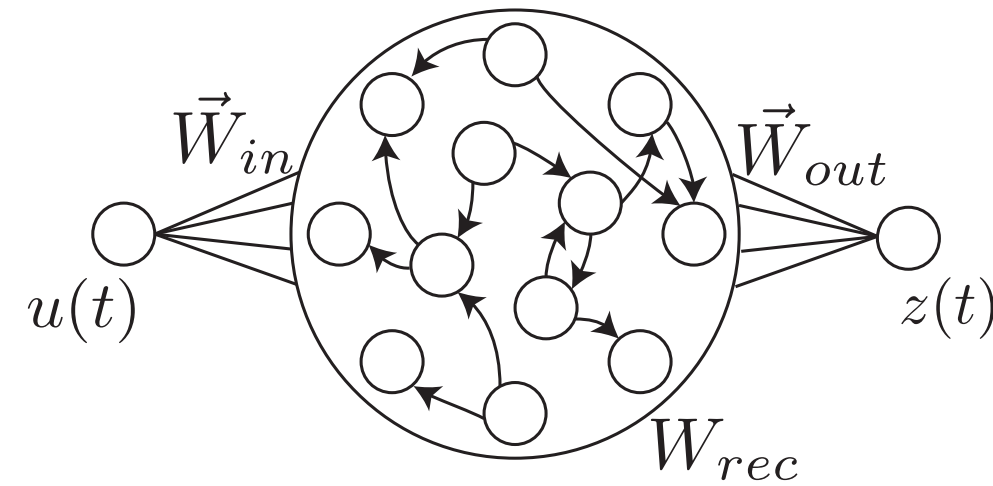


→ Population level analysis



$$r_{i,t}(k) = \beta_{i,t}(1) \text{ choice}(k) + \beta_{i,t}(2) \text{ motion}(k) + \beta_{i,t}(3) \text{ color}(k) + \beta_{i,t}(4) \text{ context}(k) + \beta_{i,t}(5)$$

Theory-based reverse-engineering of artificial neural networks

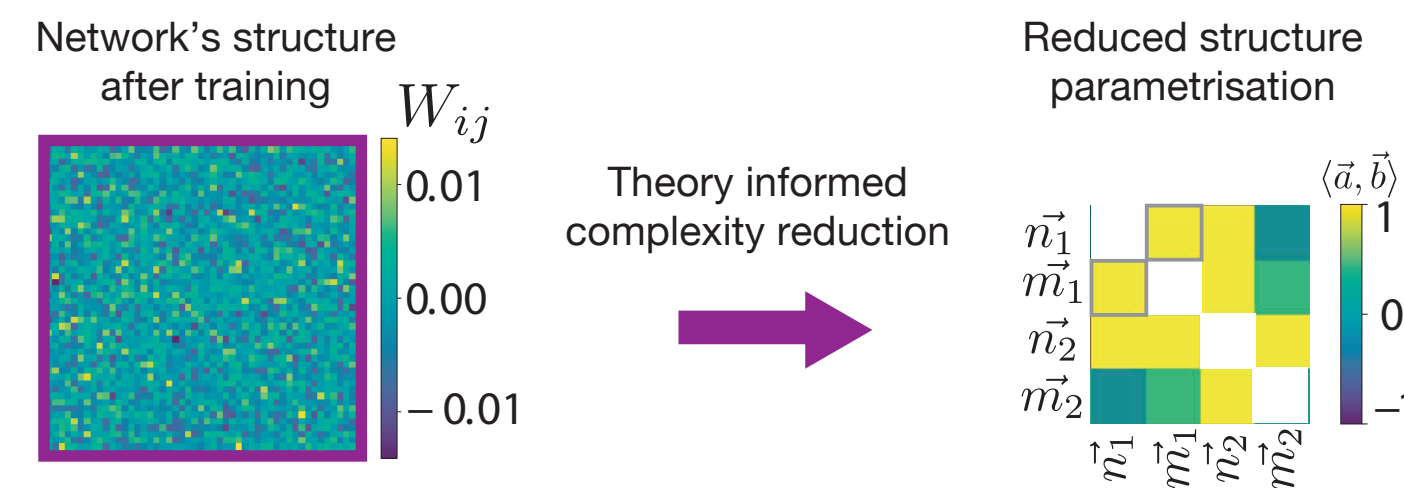


$$\tau \frac{d\vec{x}}{dt} = -\vec{x} + W_{rec} \vec{\Phi}(\vec{x}) + u(t) \vec{W}_{in}$$

$$z(t) = \vec{W}_{out}^T \vec{\Phi}(\vec{x}) \text{ with } \Phi(x) = \tanh(x)$$

- ➔ Goal: understand how these networks solve a task
- ➔ Difficulty: lots of parameters, non-linear systems
- ➔ Solution: leverage theoretical results on rate models

Connectivity



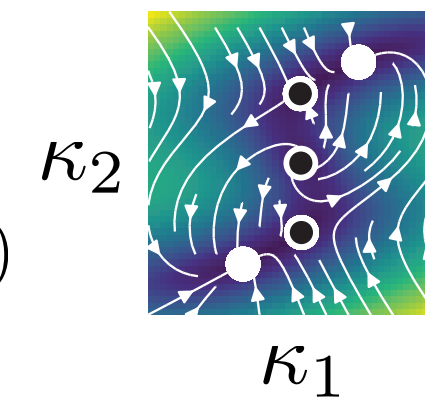
Dynamics

$$\tau \frac{d\vec{x}}{dt} = -\vec{x} + W_{rec} \vec{\Phi}(\vec{x}) + u(t) \vec{W}_{in}$$

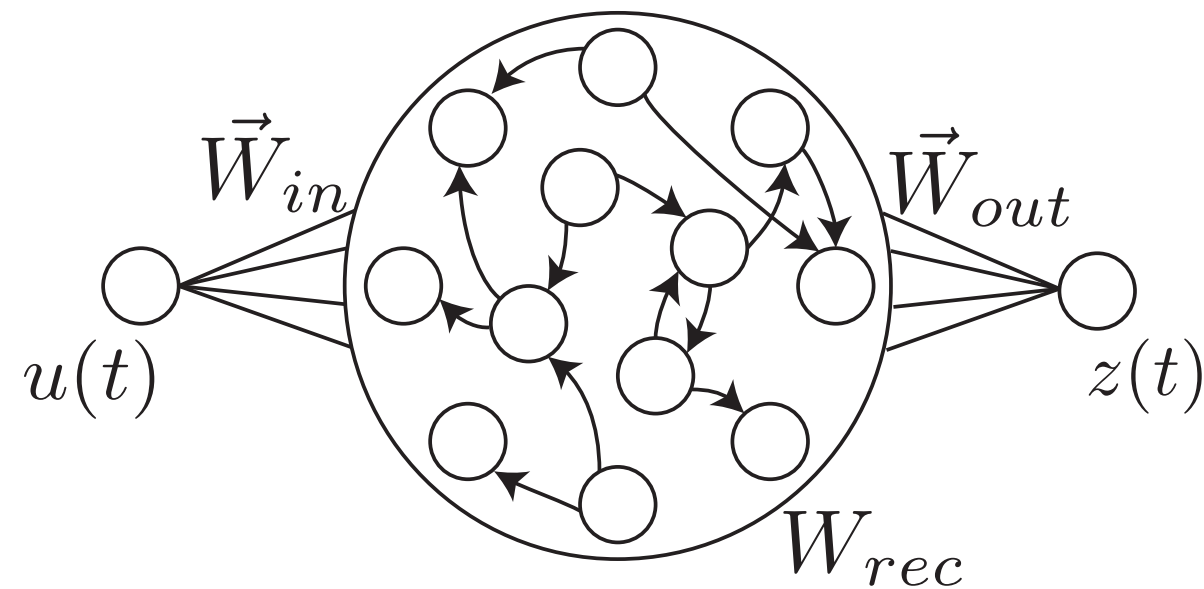
$$\vec{x} \in \mathbb{R}^N \text{ . } N \gg 1$$

$$\frac{d\vec{\kappa}}{dt} = F(\vec{\kappa})$$

$$\vec{\kappa} \in \mathbb{R}^D \text{ . } D = O(1)$$



Low-rank connectivity matrices



$$\tau \frac{d\vec{x}}{dt} = -\vec{x} + W_{rec} \vec{\Phi}(\vec{x}) + u(t) \vec{W}_{in}$$

$$z(t) = \vec{W}_{out}^T \vec{\Phi}(\vec{x}) \text{ with } \Phi(x) = \tanh(x)$$

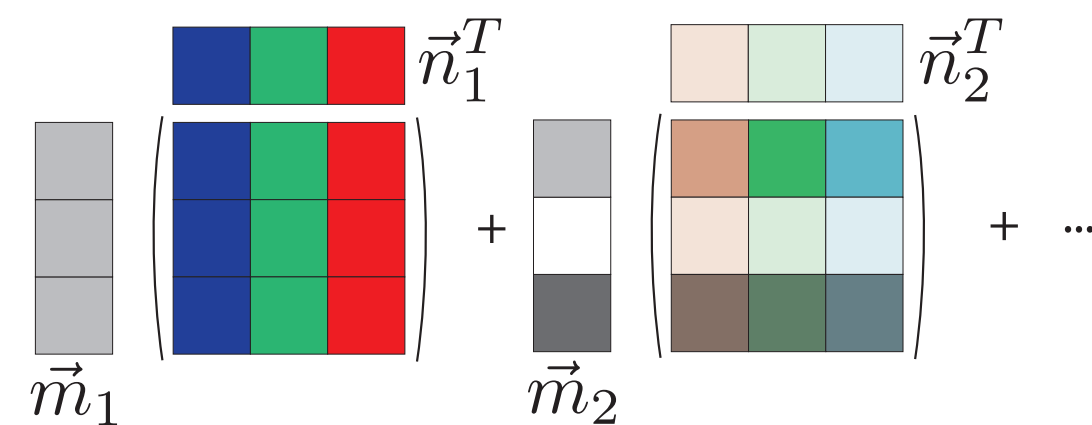
Low-rank recurrent matrix:

$$W_{rec} = \vec{m}_1 \vec{n}_1^T + \vec{m}_2 \vec{n}_2^T + \dots$$

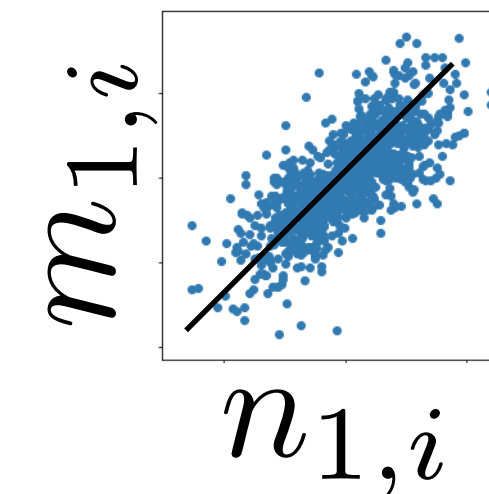
Seung, 1996

Landau & Sompolinsky, 2018

Mastrogiuseppe & Ostojic, 2018

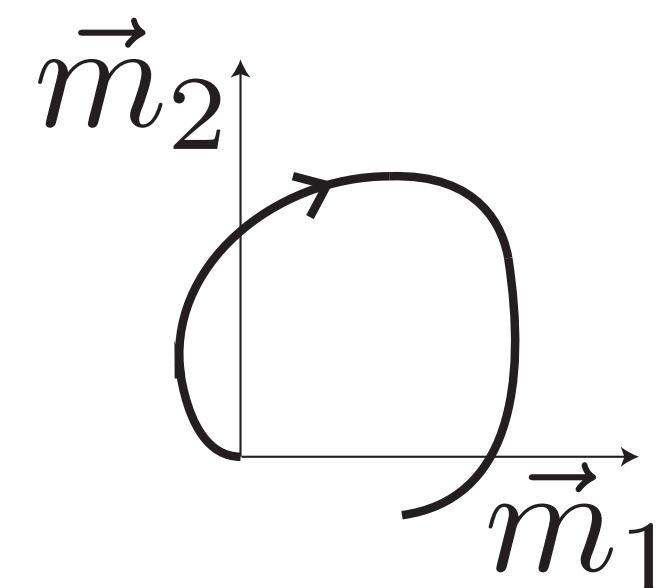


Gaussian connectivity vectors:



Rank controls dimensionality:

$$W_{rec} \vec{\Phi}(\vec{x}) = \vec{m}_1 \underbrace{\vec{n}_1^T \vec{\Phi}(\vec{x})}_{\kappa_1} + \vec{m}_2 \underbrace{\vec{n}_2^T \vec{\Phi}(\vec{x})}_{\kappa_2} + \dots$$



κ_1 κ_2

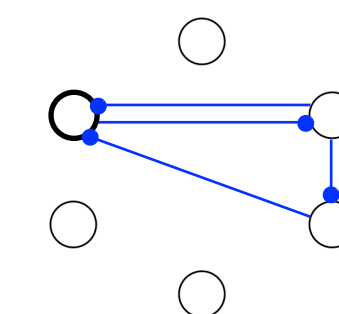
macroscopic variables

Relate connectivity parameters and dynamical features of RNN.

$$\sigma_{mn} < 1$$



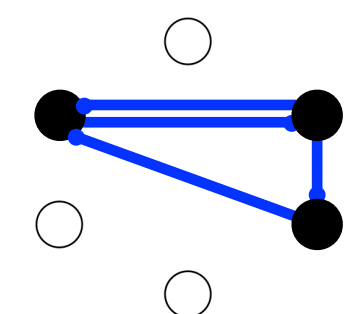
$$\kappa^* = 0$$



$$\sigma_{mn} > 1$$

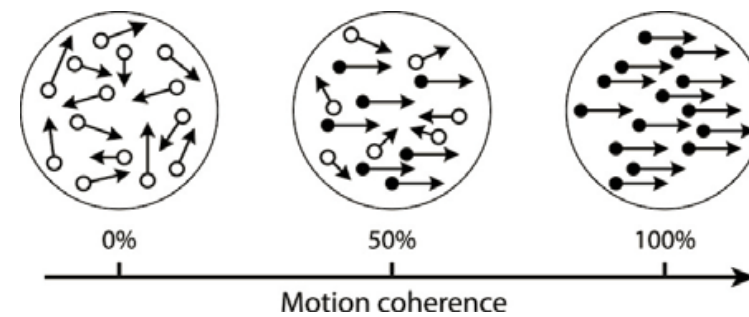


$$\kappa^* = \pm \kappa_0$$



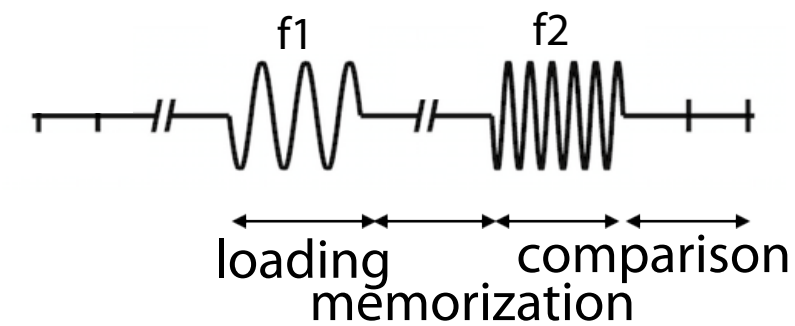
Training low-rank networks to perform various tasks

Decision making



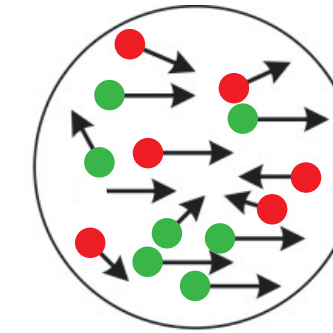
Salzman, Britten, Newsome, 1990

Parametric working memory



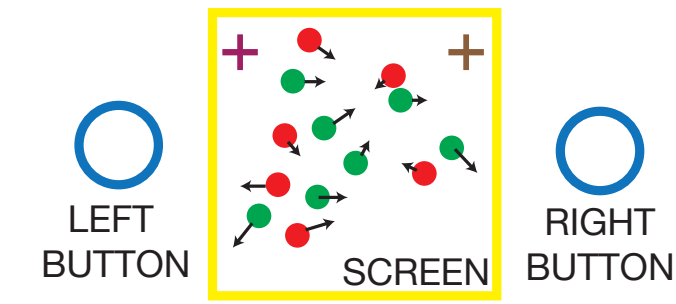
Romo et al, 1999

Multi-sensory decision making



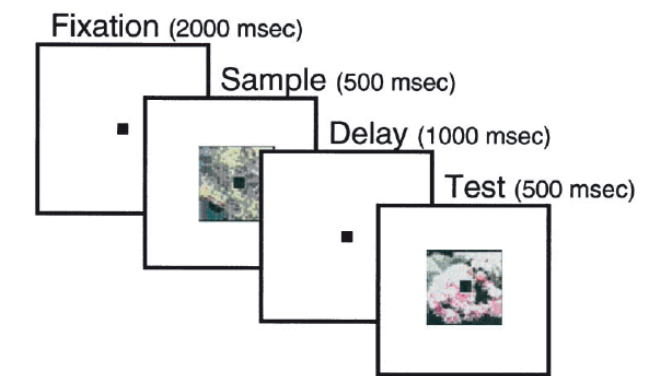
Raposo et al, 2014

Context dependent decision making



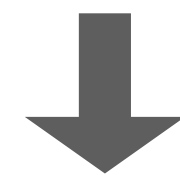
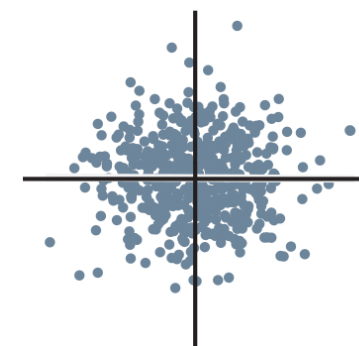
Mante et al, 2013

Object working memory

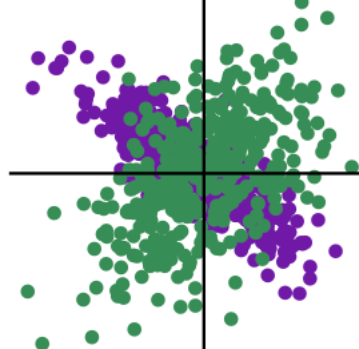
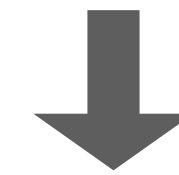
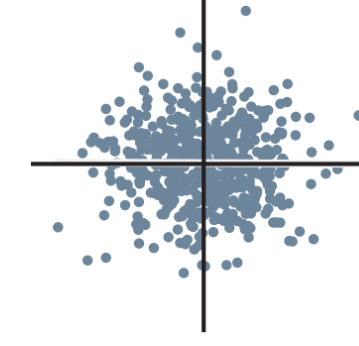
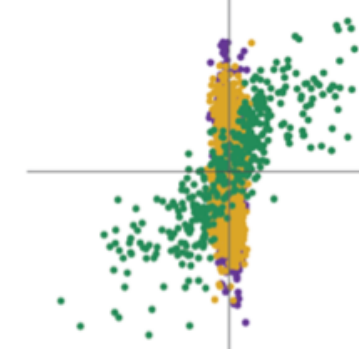
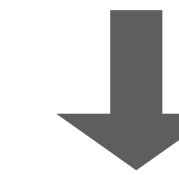
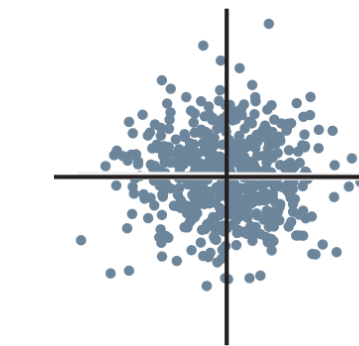
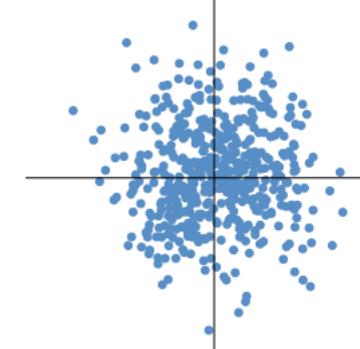
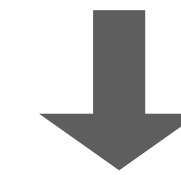
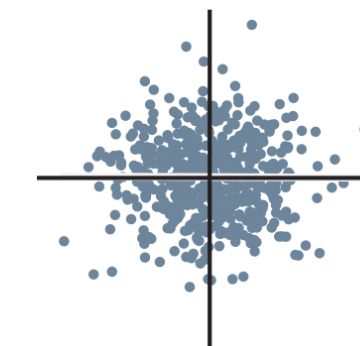
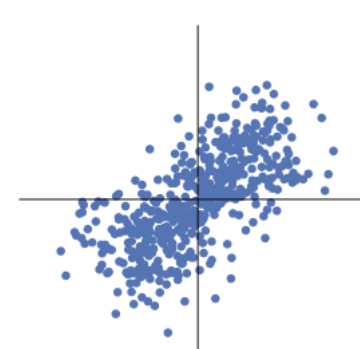
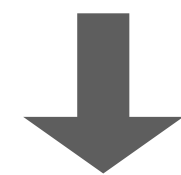
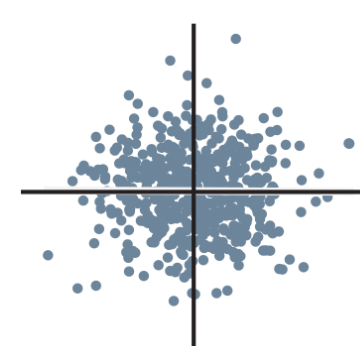
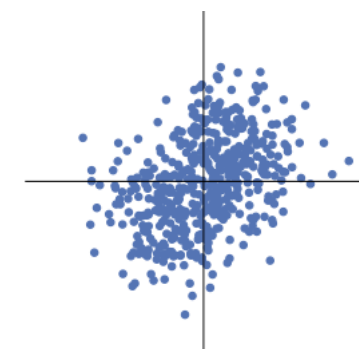


Fuster, Miyashita, etc

Network connectivity
before training

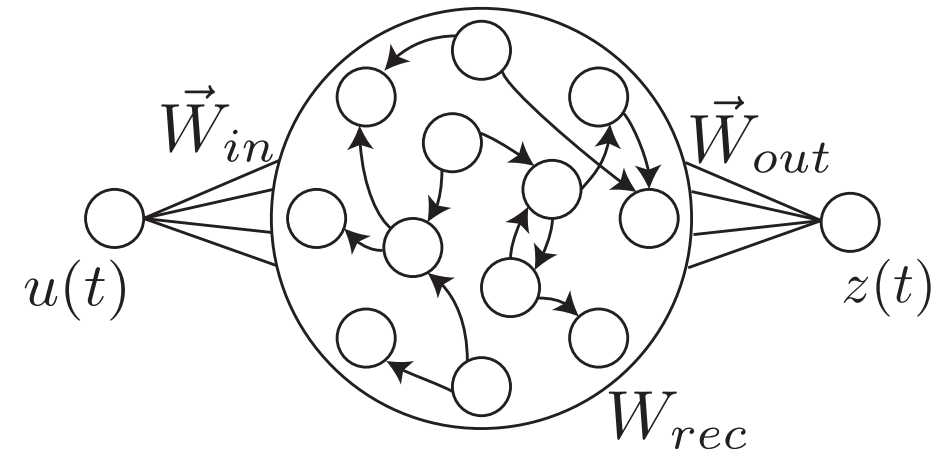


Network connectivity
after training



➔ A priori amorphous networks, for some tasks, segregate into populations

Theory: cognitive variables and inputs interact through functional couplings



$$\tau \frac{d\vec{x}}{dt} = -\vec{x} + W_{rec} \vec{\Phi}(\vec{x}) + u(t) \vec{W}_{in}$$

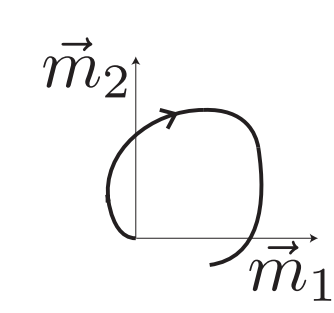
$$z(t) = \vec{W}_{out}^T \vec{\Phi}(\vec{x}) \text{ with } \Phi(x) = \tanh(x)$$

$$W_{rec} = \vec{m}_1 \vec{n}_1^T + \vec{m}_2 \vec{n}_2^T + \dots$$

$$\kappa_1 = \langle \vec{x}, \vec{m}_1 \rangle$$

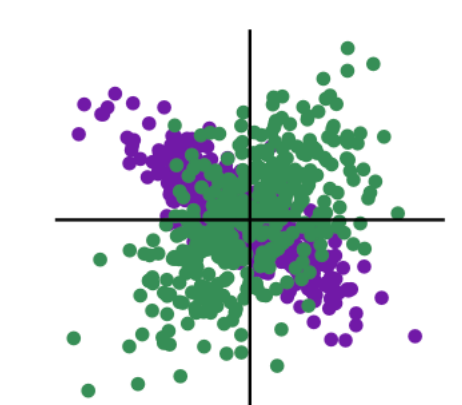
$$\kappa_2 = \langle \vec{x}, \vec{m}_2 \rangle$$

Functional dynamics (e.g. K=2):

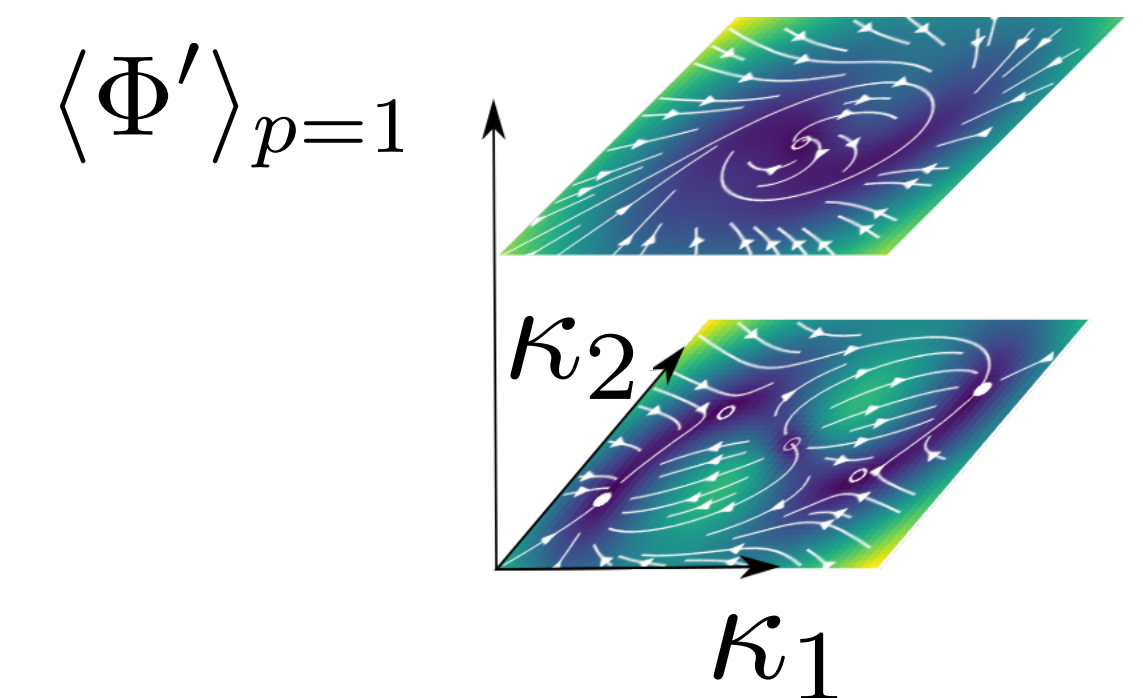
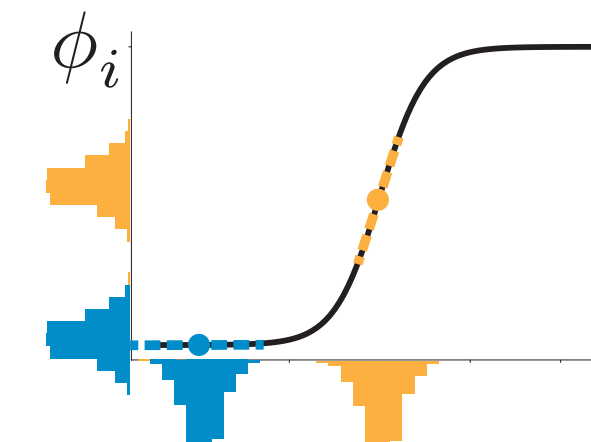


$$\begin{aligned} \tau \dot{\kappa}_1 &= -\kappa_1 + \tilde{\sigma}_{n_1 m_1} \kappa_1 + \tilde{\sigma}_{n_1 m_2} \kappa_2 + \tilde{\sigma}_{n_1} W_{in} u(t) \\ \tau \dot{\kappa}_2 &= -\kappa_2 + \tilde{\sigma}_{n_2 m_1} \kappa_1 + \tilde{\sigma}_{n_2 m_2} \kappa_2 + \tilde{\sigma}_{n_2} W_{in} u(t) \end{aligned} \quad \left| \frac{du}{dt} \right| \gg \tau$$

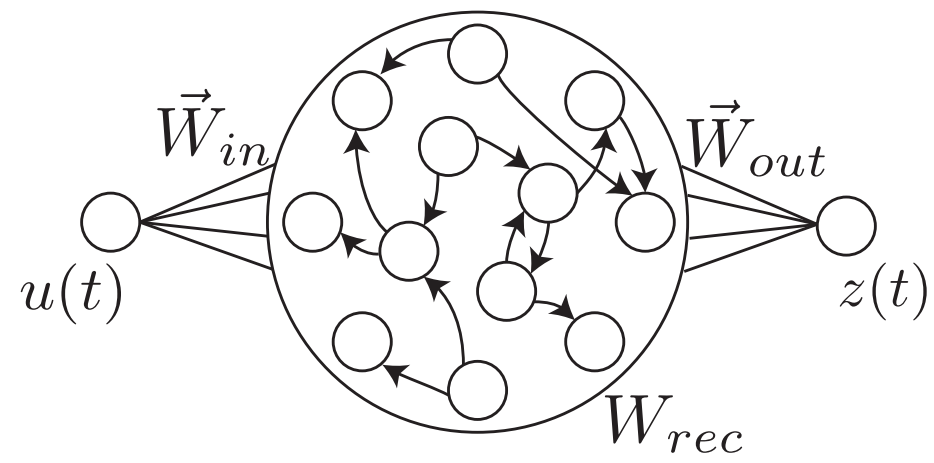
Functional couplings: $\tilde{\sigma}_{ab} = \sum_{p=1}^P \sigma_{ab}^p \langle \phi' \rangle_p$



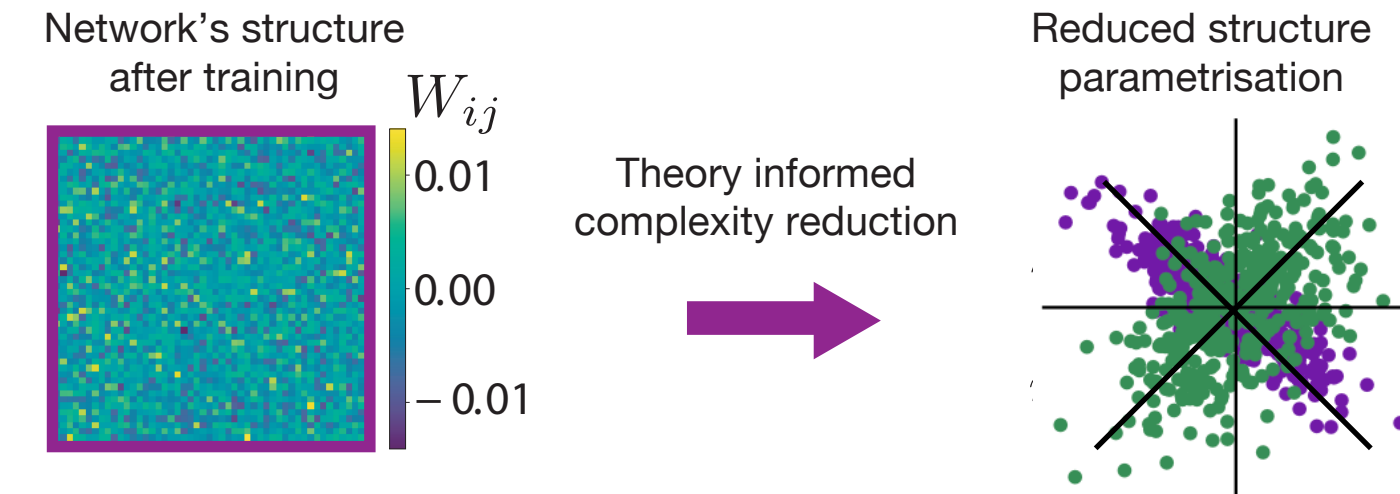
↑ structural ↑ activity dependent



Summary: leveraging theory for reverse-engineering ANN



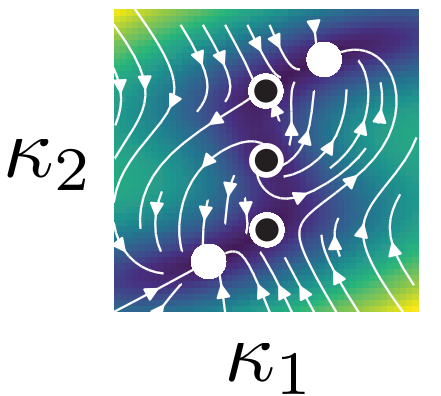
➔ Picking-up dynamically relevant summary statistics of the connectivity matrix



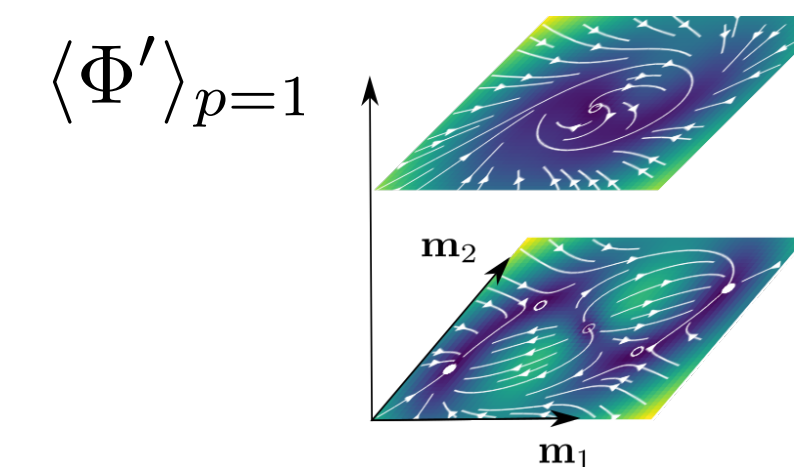
➔ Reduce dimensionality of the dynamics

$$\tau \frac{d\vec{x}}{dt} = -\vec{x} + W_{rec} \vec{\Phi}(\vec{x}) + u(t) \vec{W}_{in} \quad \dot{\kappa}_1 = -\kappa_1 + \tilde{\sigma}_{n_1 m_1} \kappa_1 + \tilde{\sigma}_{n_1 m_2} \kappa_2 + \tilde{\sigma}_{n_1} W_{in} u(t)$$

$$\vec{x} \in \mathbb{R}^N : N \gg 1 \quad \dot{\kappa}_2 = -\kappa_2 + \tilde{\sigma}_{n_2 m_1} \kappa_1 + \tilde{\sigma}_{n_2 m_2} \kappa_2 + \tilde{\sigma}_{n_2} W_{in} u(t)$$



➔ Reconfiguration of dynamics through gain modulation of specific populations



Outline

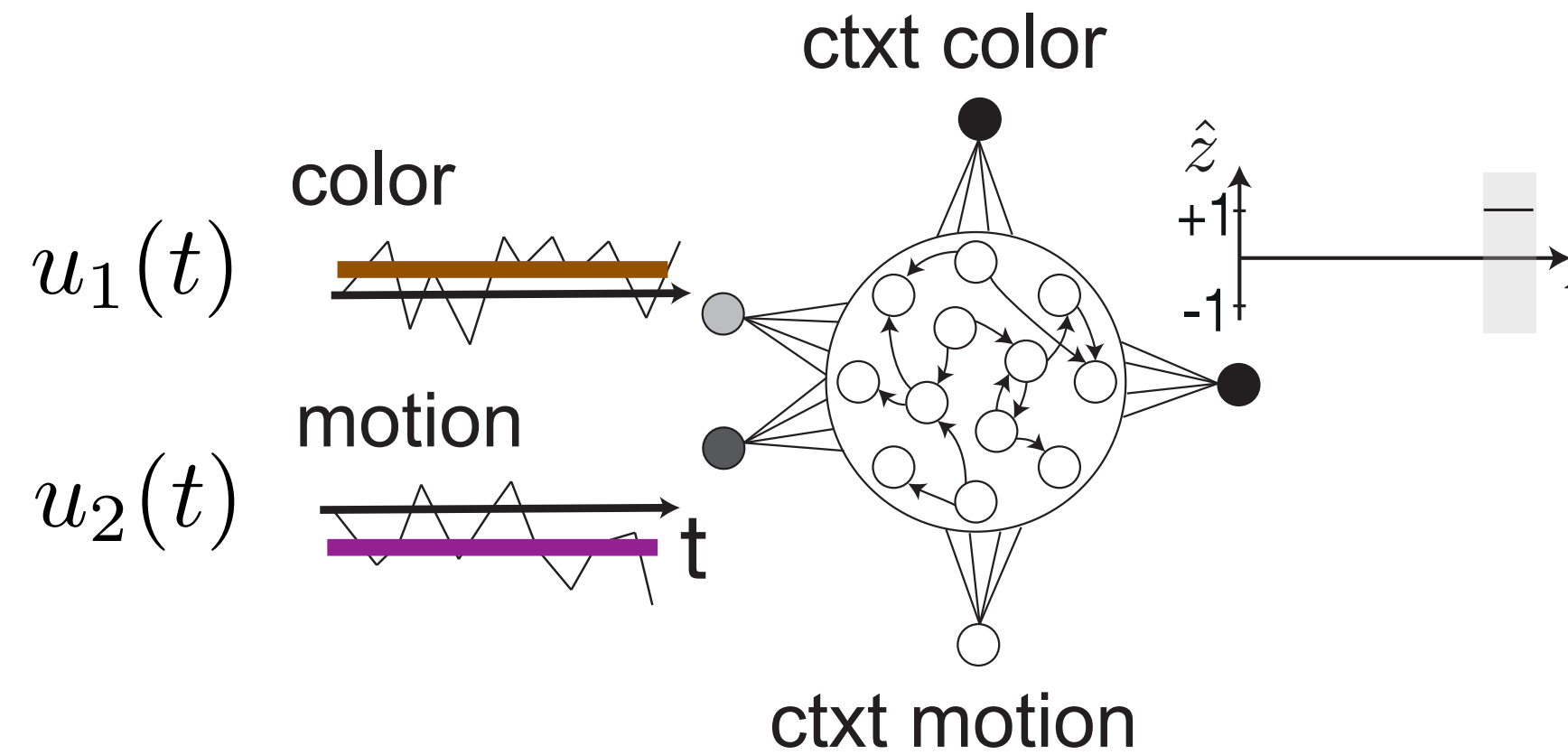
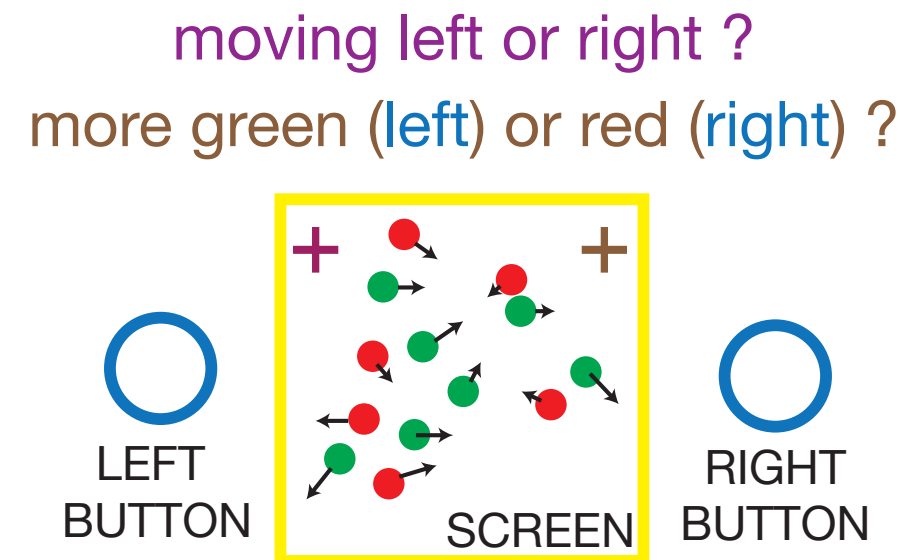
Introduction: cognitive modeling

Theory-based reverse-engineering of artificial neural networks

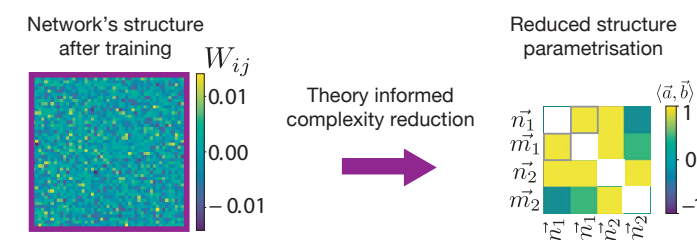
→ On the computational role of population structure

Modeling temporally structured behaviors

Example: context-dependent decision making



Assess relationship between connectivity vectors
(4 input vectors, 2 recurrent vectors, 1 output vector)



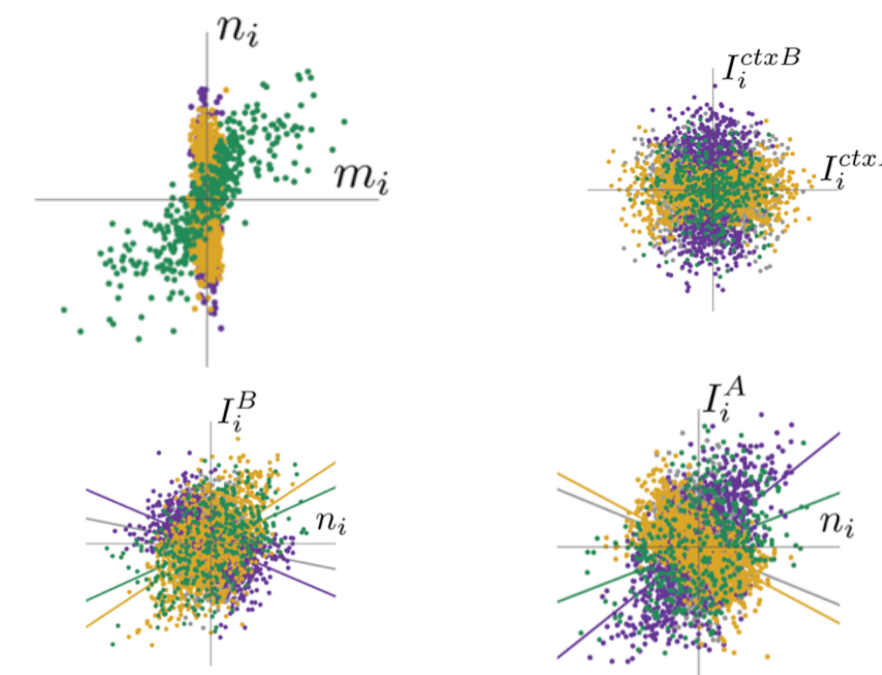
Reduced dynamical system

$$\dot{\kappa} = -\kappa + \tilde{\sigma}_{nm}\kappa + \tilde{\sigma}_n W_{in1} u_1(t) + \tilde{\sigma}_n W_{in2} u_2(t)$$

$$\kappa = \langle \vec{x}, \vec{m} \rangle$$

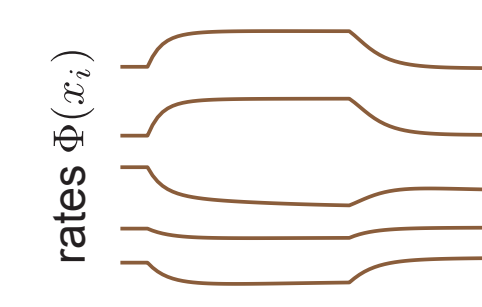
Cognitive variable temporally integrates the relevant sensory input

cf recordings in LIP, *Steinemann et al. 2024*

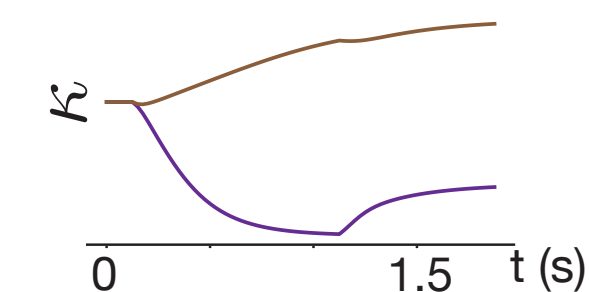
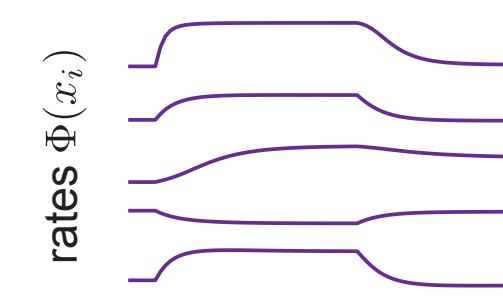


color = +10%
motion = -20%

Color context

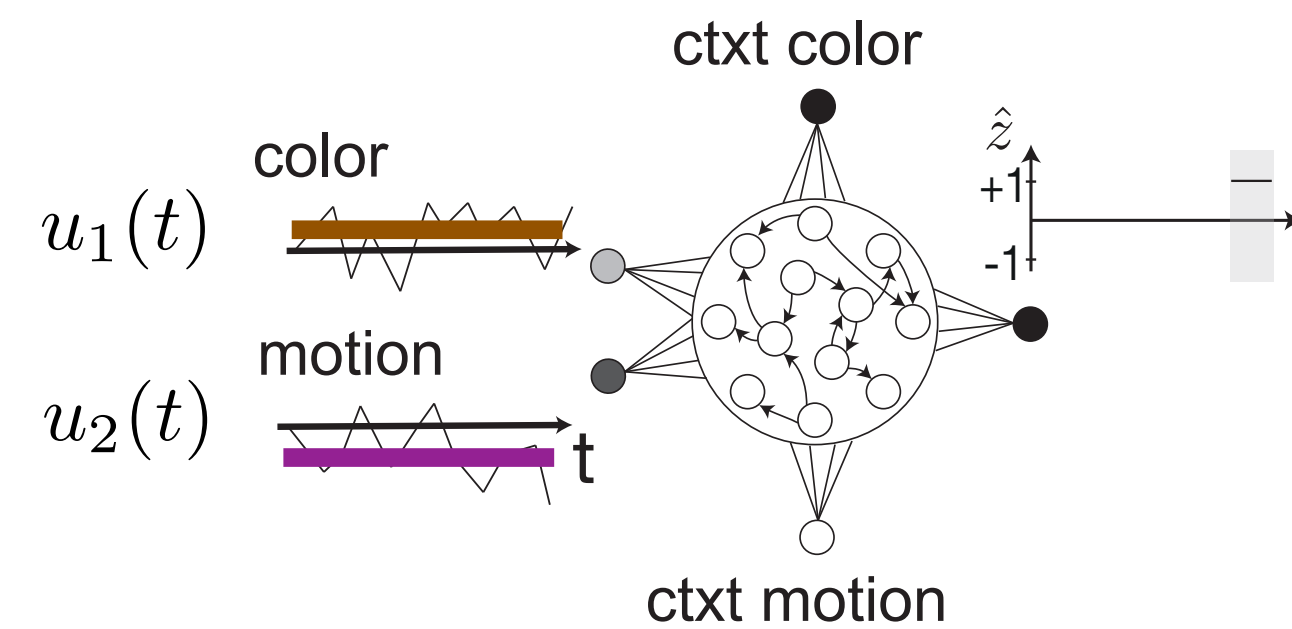
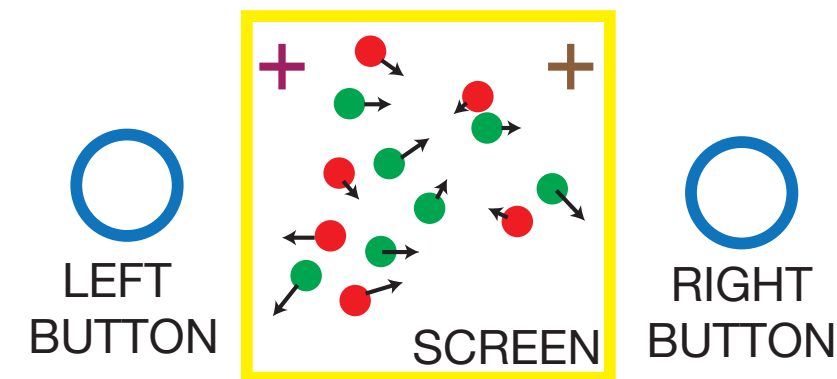


Motion context



Example: context-dependent decision making

moving left or right ?
more green (left) or red (right) ?

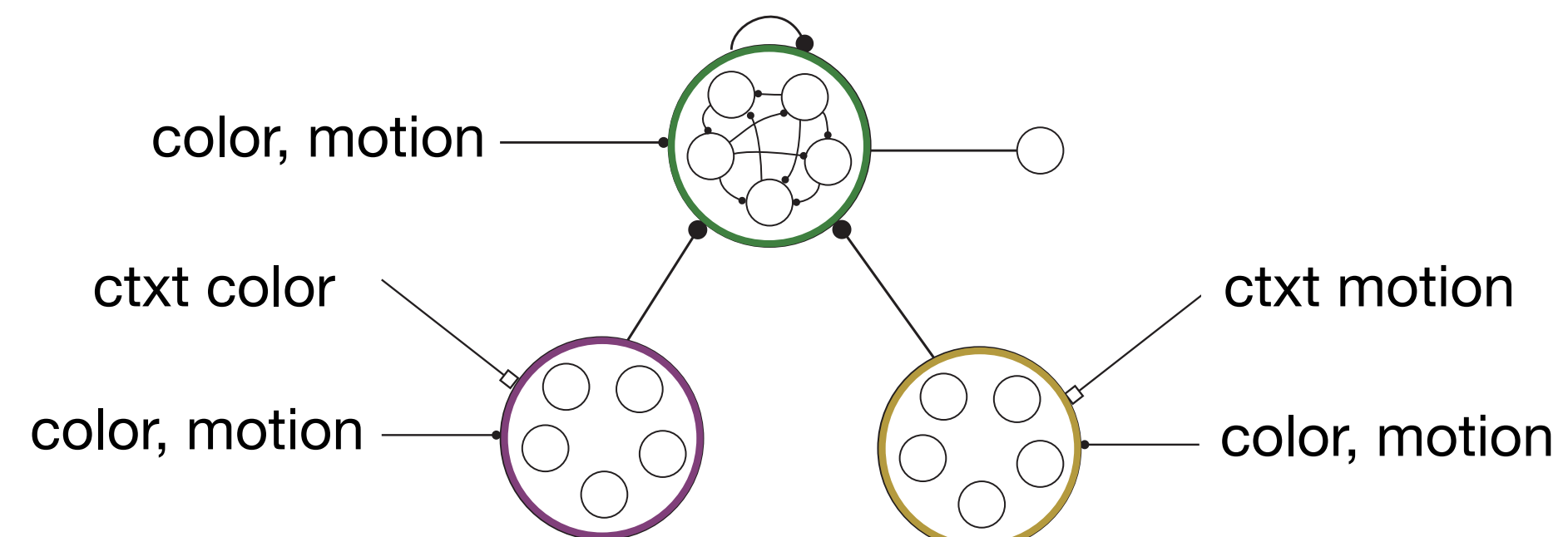
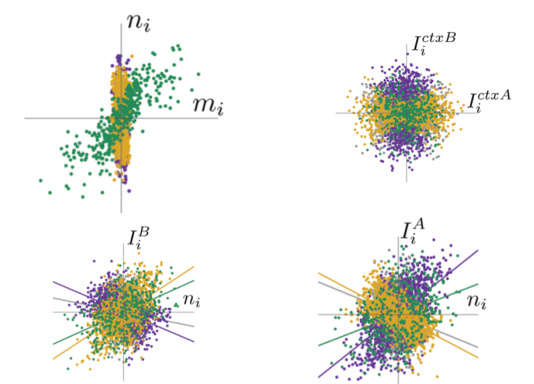
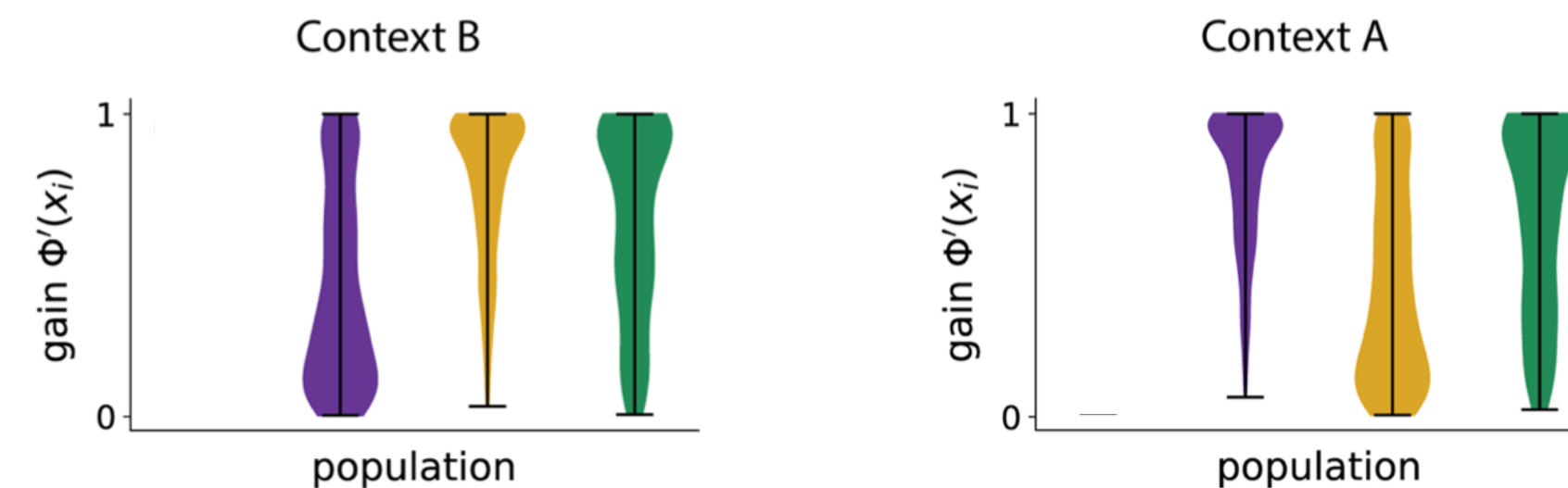


→ Reduced dynamical system $\dot{\kappa} = -\kappa + \tilde{\sigma}_{nm}\kappa + \tilde{\sigma}_n W_{in1} u_1(t) + \tilde{\sigma}_n W_{in2} u_2(t)$



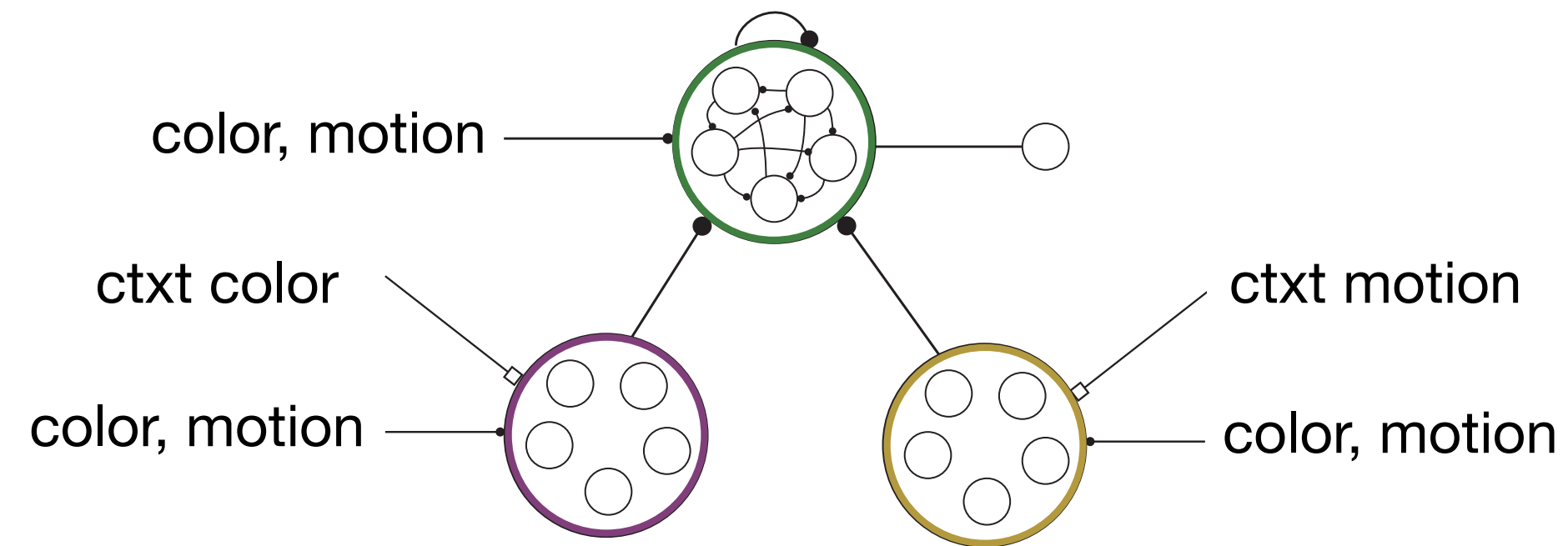
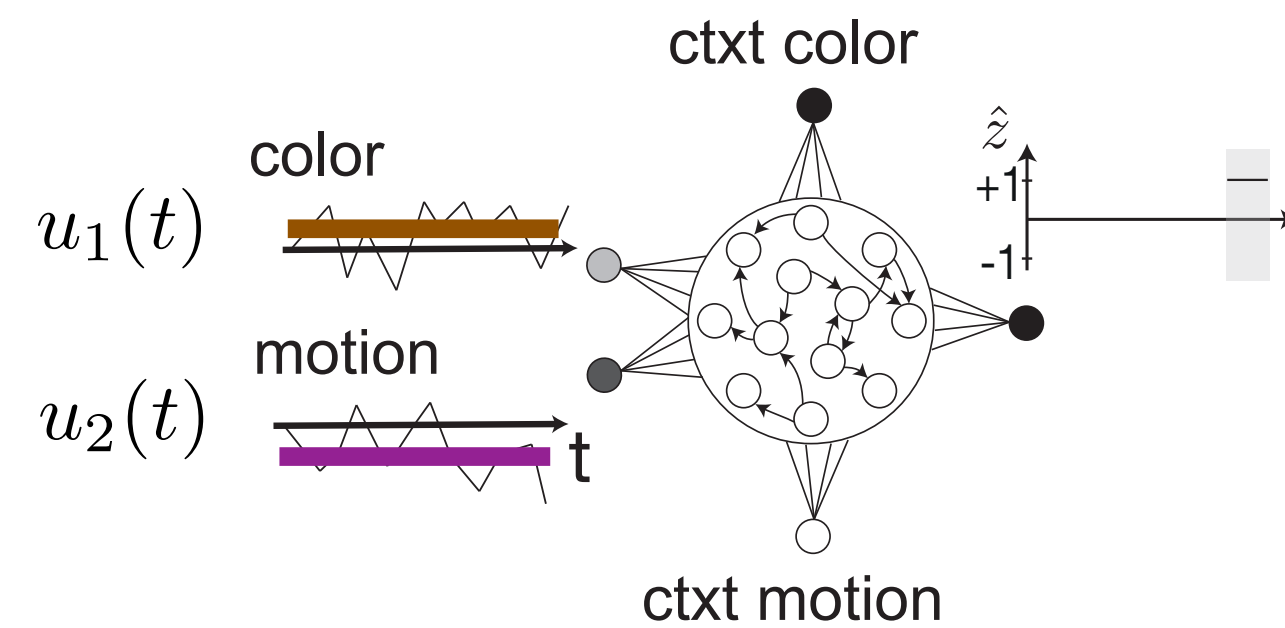
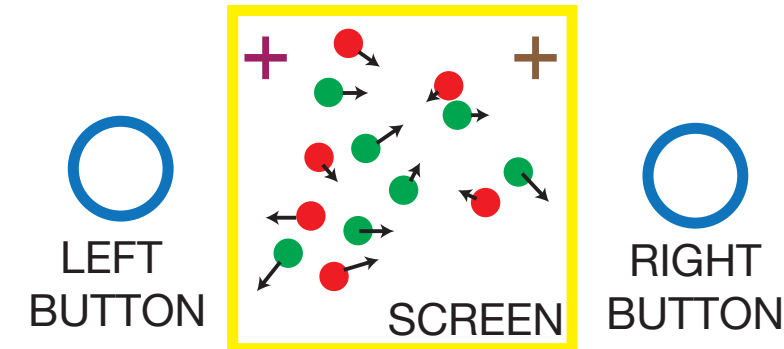
→ Functional couplings controlled via gain modulation of specific populations

$$\tilde{\sigma}_{ab} = \sum_{p=1}^P \sigma_{ab}^p \langle \phi' \rangle_p$$

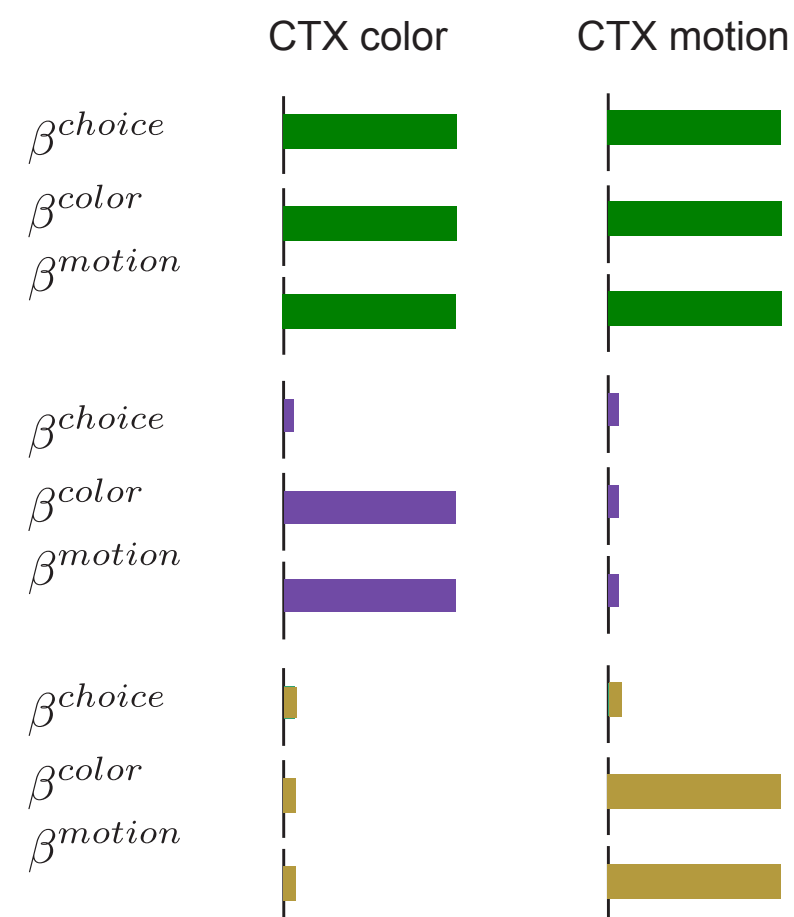
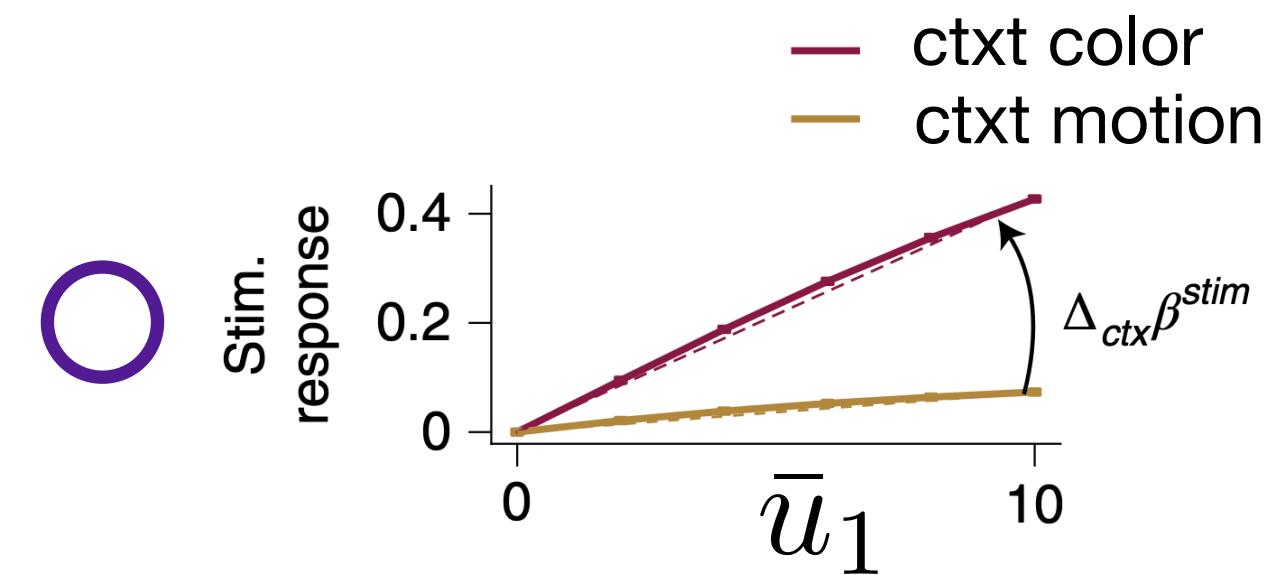


Selectivity profiles of populations: non-linear mixed-selectivity

moving left or right ?
more green (left) or red (right) ?



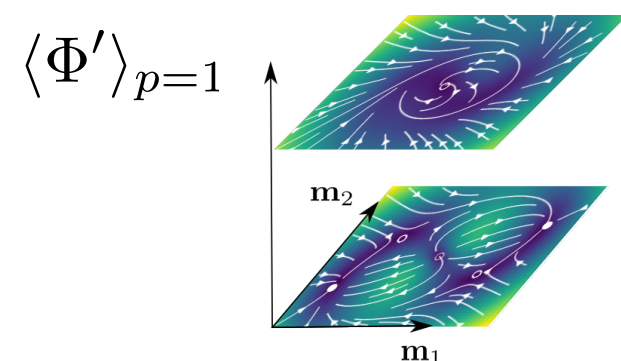
Context-dependent tuning curves



$$r_i = \phi(x_i)$$

$$= \phi(u_1(t)W_{in1,i} + u_2(t)W_{in2,i} + c_{col}.W_{c.col.,i})$$

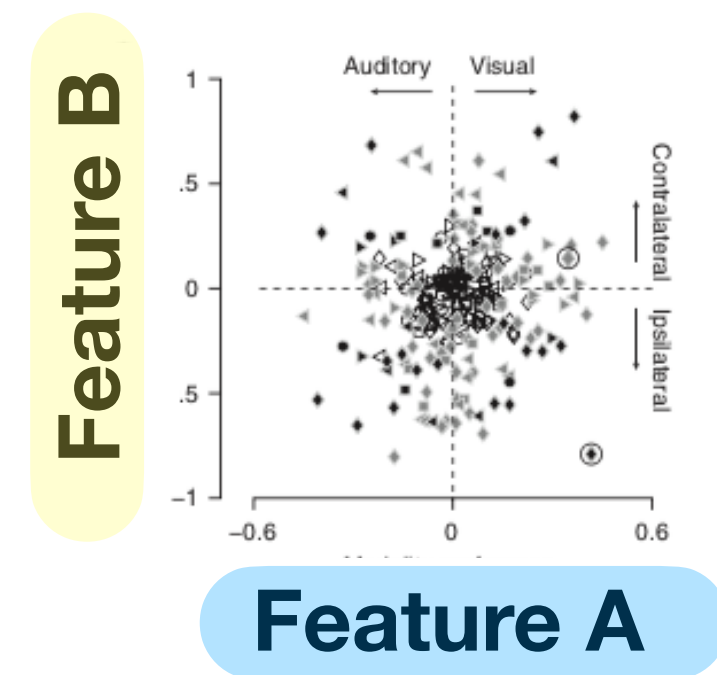
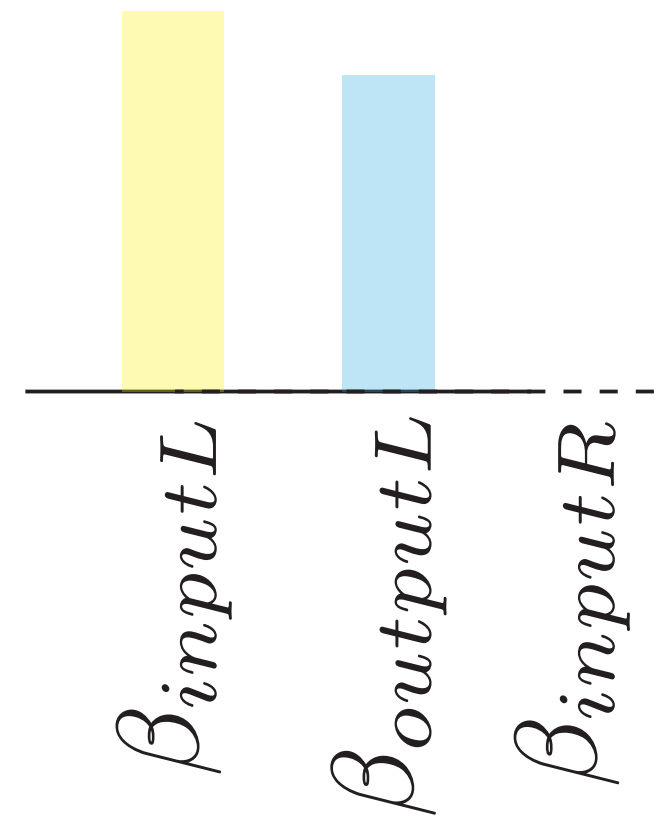
→ Non-linear mixed selectivity can reflect reconfiguration of network's dynamics



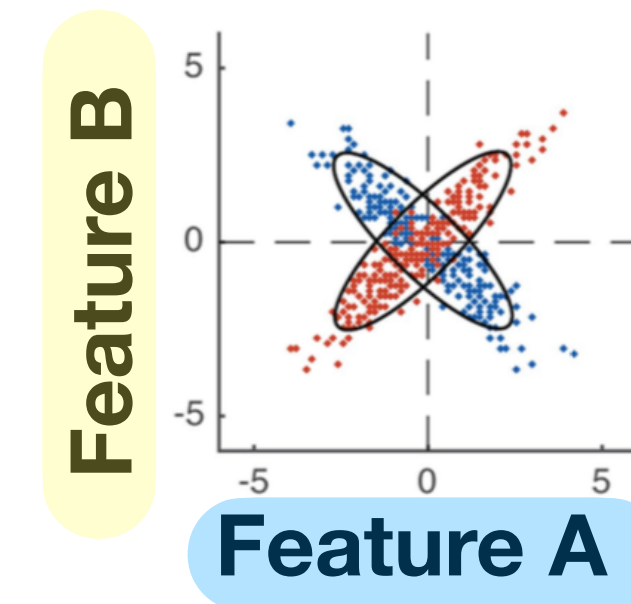
Selectivity profiles of populations: random mixed selectivity

→ Structure of population-level selectivity profiles

Selectivity profiles

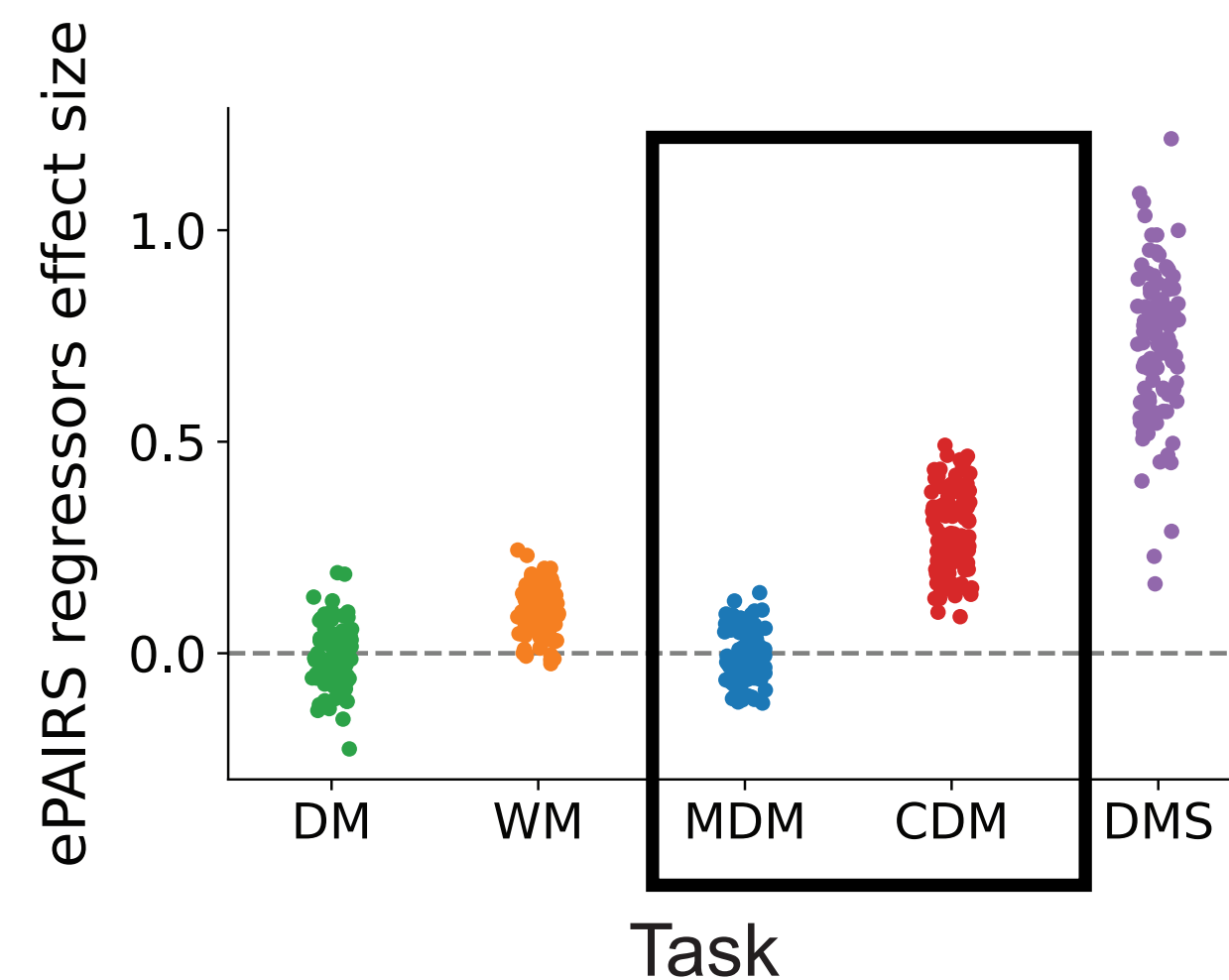
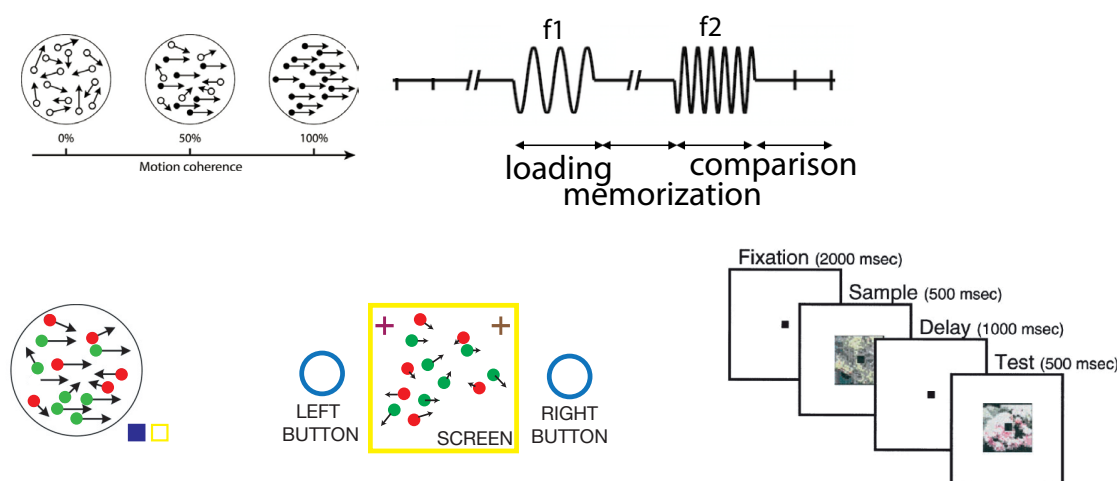


Unstructured selectivity
Raposo et al, 2014



Structured selectivity
Hirokawa et al, 2019

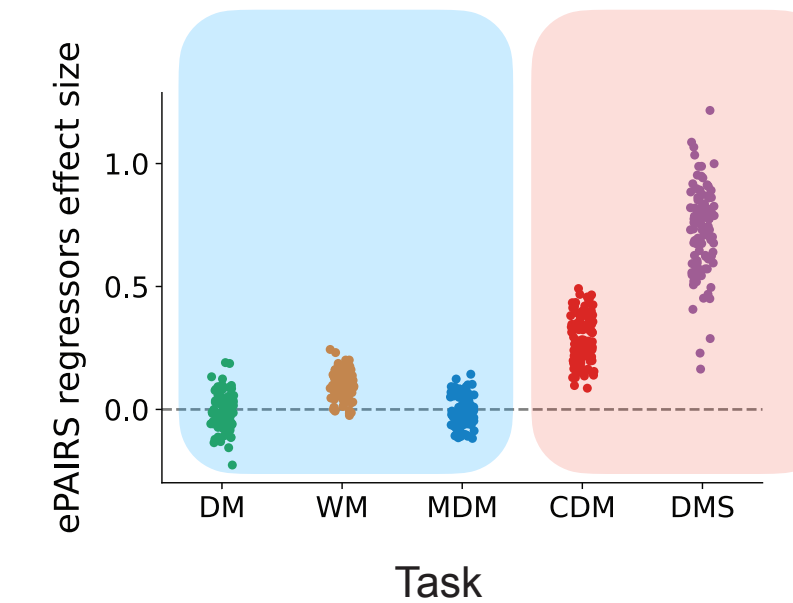
→ Statistical test for population structure in selectivity



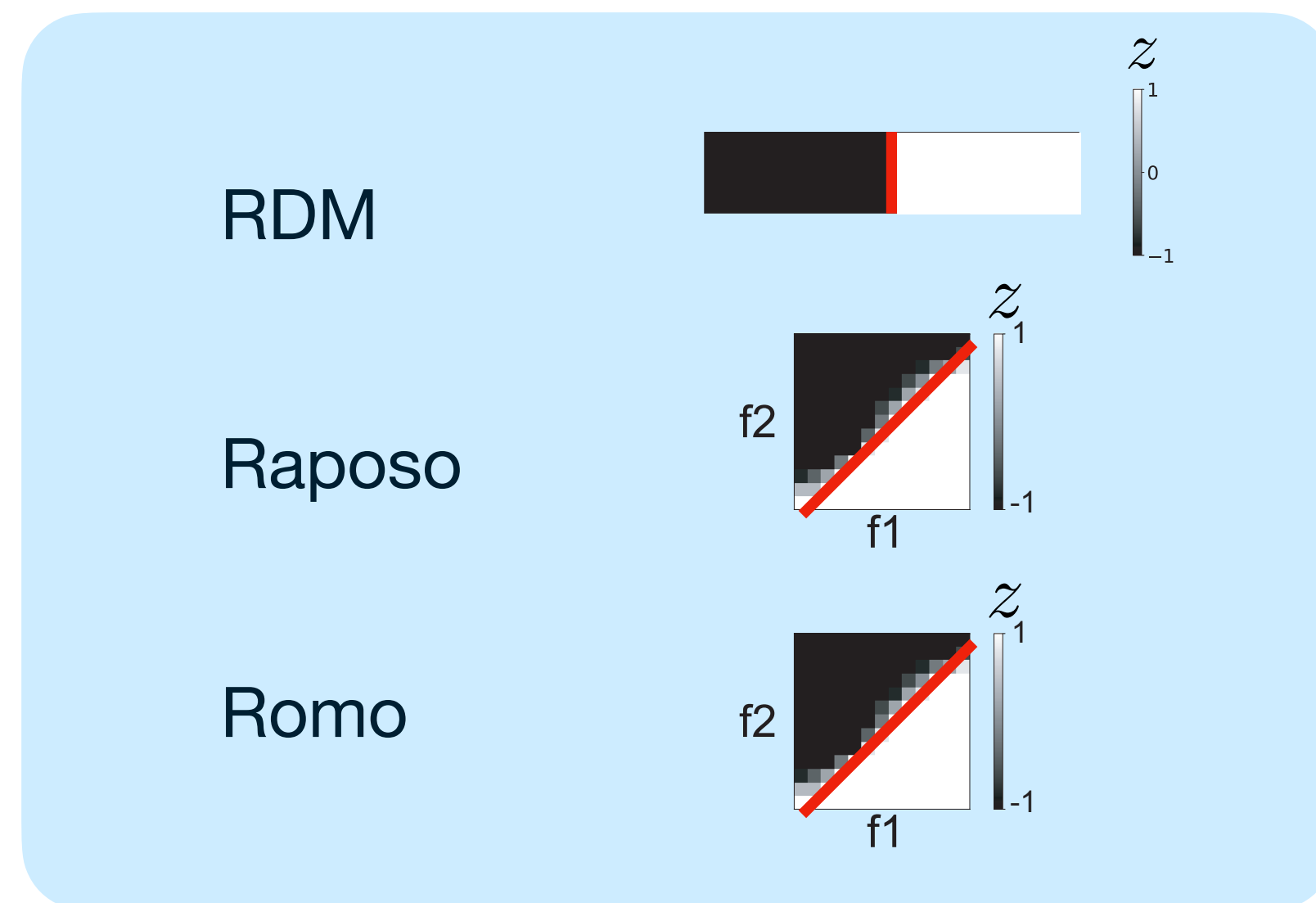
Tasks shape selectivity
profiles of populations

Selectivity profiles of populations: random mixed selectivity

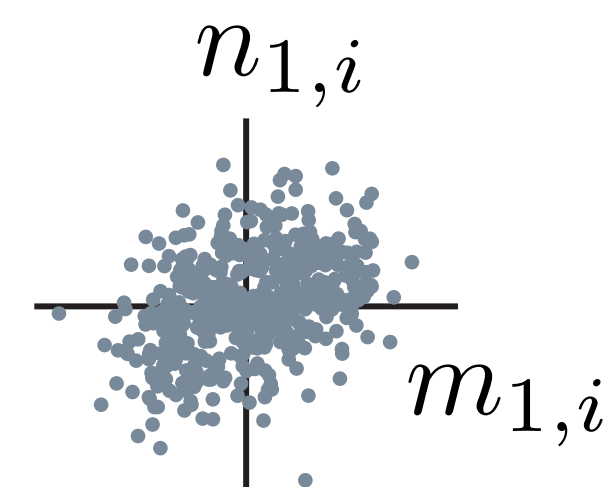
- ➔ Statistical test for population structure in selectivity
- ➔ Training/Reverse-engineering on multiple tasks



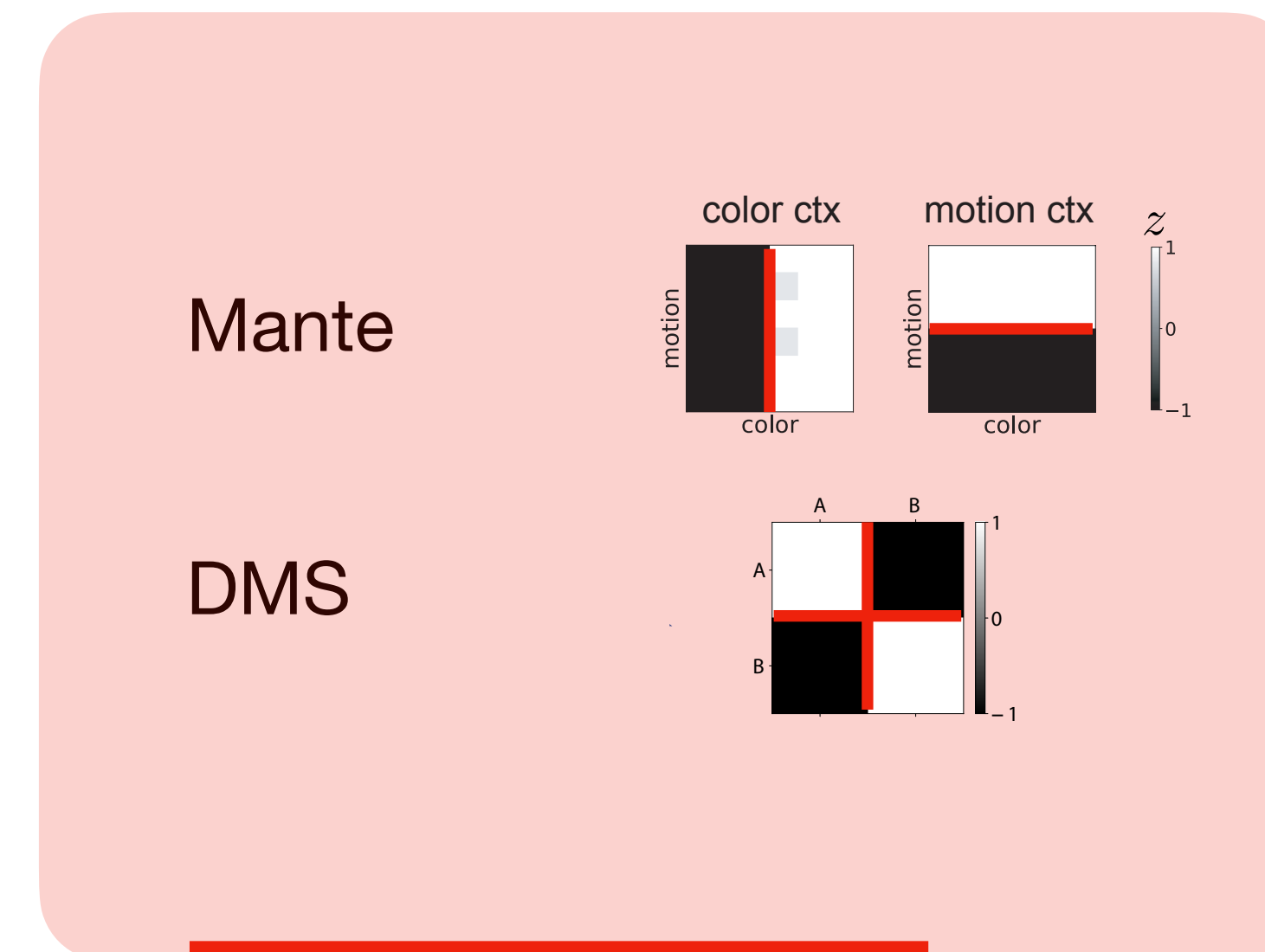
stereotyped tasks



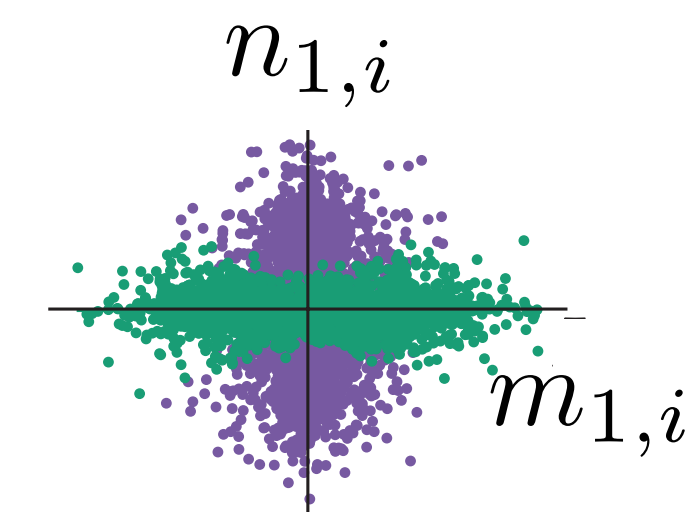
no population structure



flexible tasks

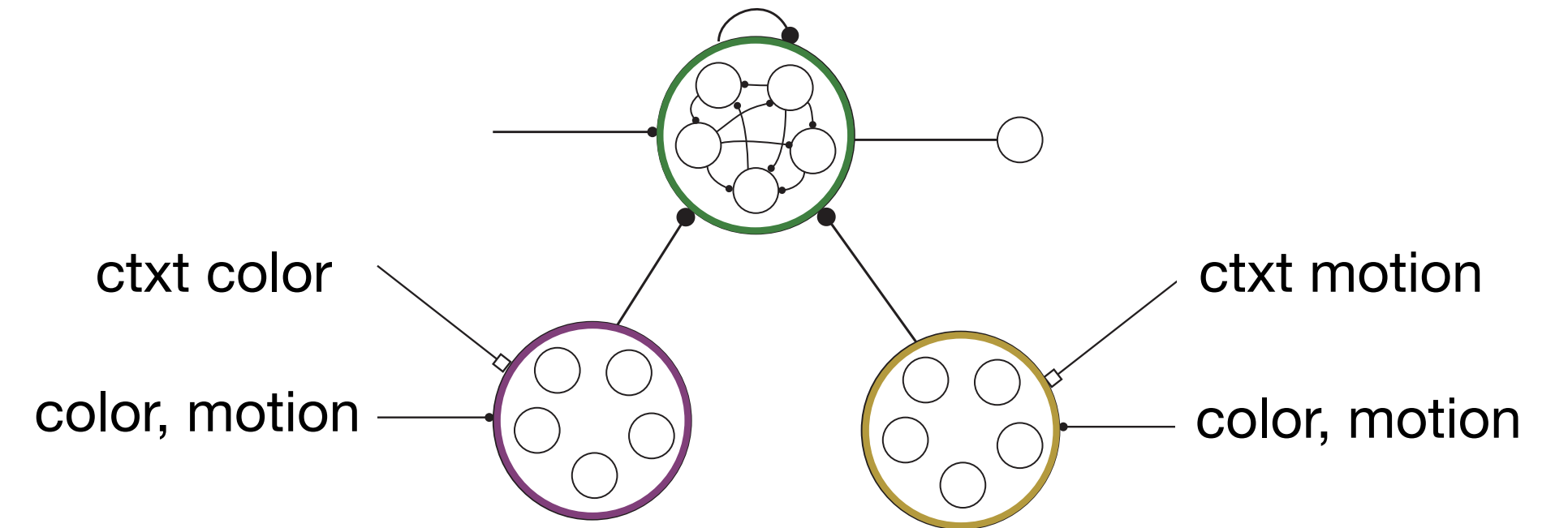


population structure



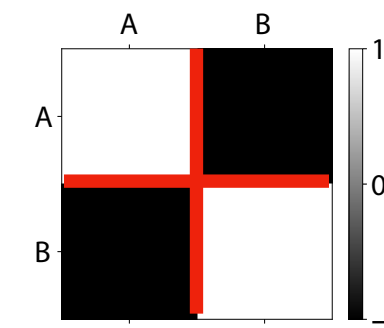
Summary: leveraging theory for reverse-engineering ANN

- Reconfiguration of dynamics through gain modulation



$$\dot{\kappa} = -\kappa + \tilde{\sigma}_{nm}\kappa + \tilde{\sigma}_n W_{in1} u_1(t) + \tilde{\sigma}_n W_{in2} u_2(t)$$

- Population structure was task dependent and required for flexible tasks



- Population structure can be detected in data
Non-linear mixed selectivity of the purple and gold populations ?

Outline

Introduction: cognitive modeling

Theory-based reverse-engineering of artificial neural networks

→ On the computational role of population structure

Modeling temporally structured behaviors

Outline

Introduction: cognitive modeling

Theory-based reverse-engineering of artificial neural networks

On the computational role of population structure

→ Modeling temporally structured behaviors

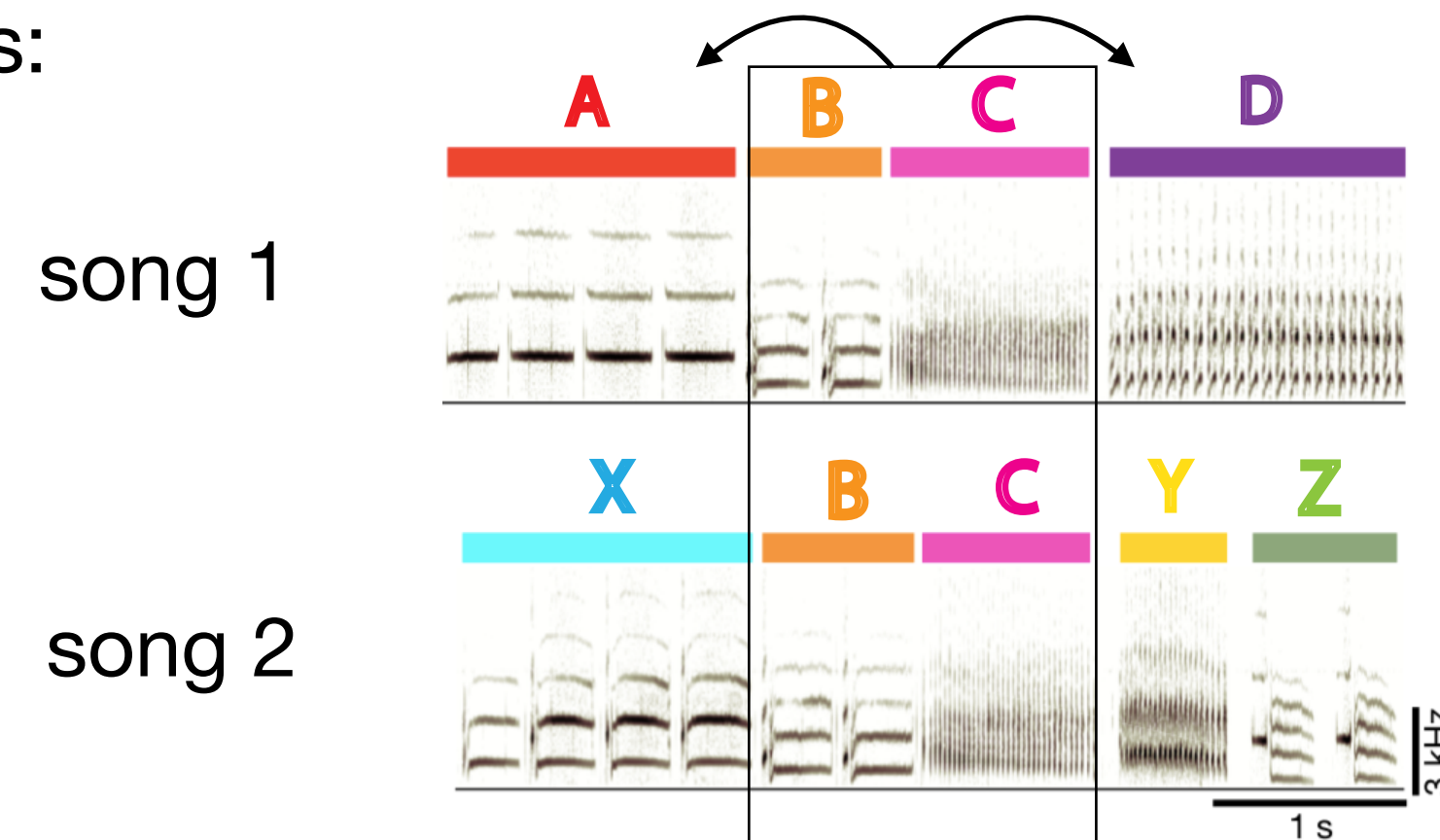
Long-distance dependencies in behavior

→ Natural language processing:

The cat near the trees catches the mouse

The cats near the trees catch the mouse

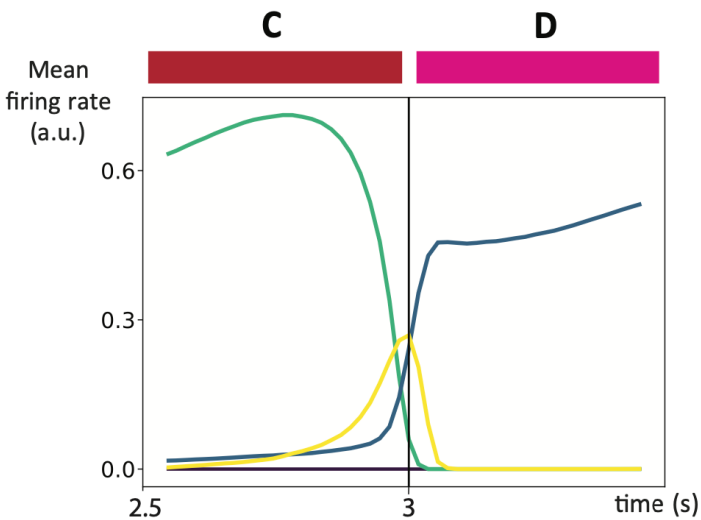
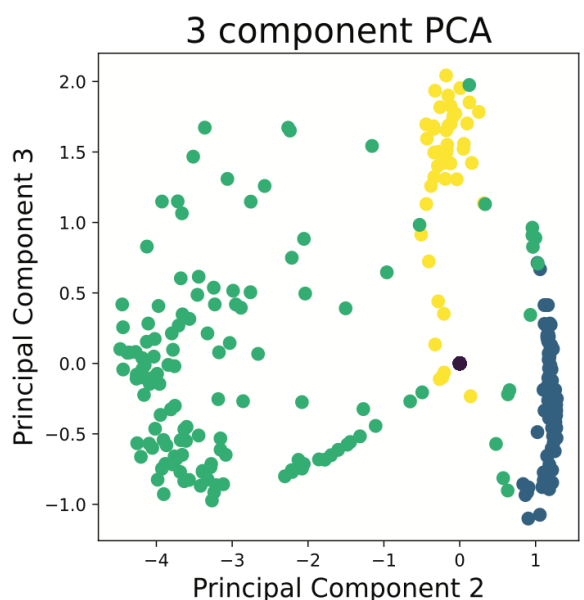
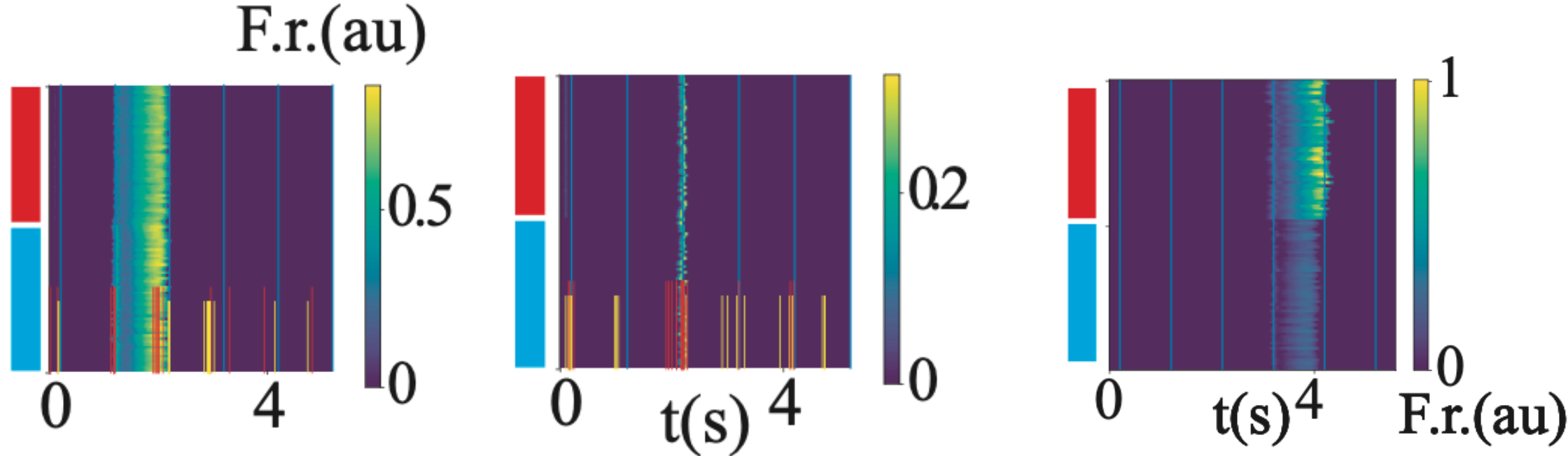
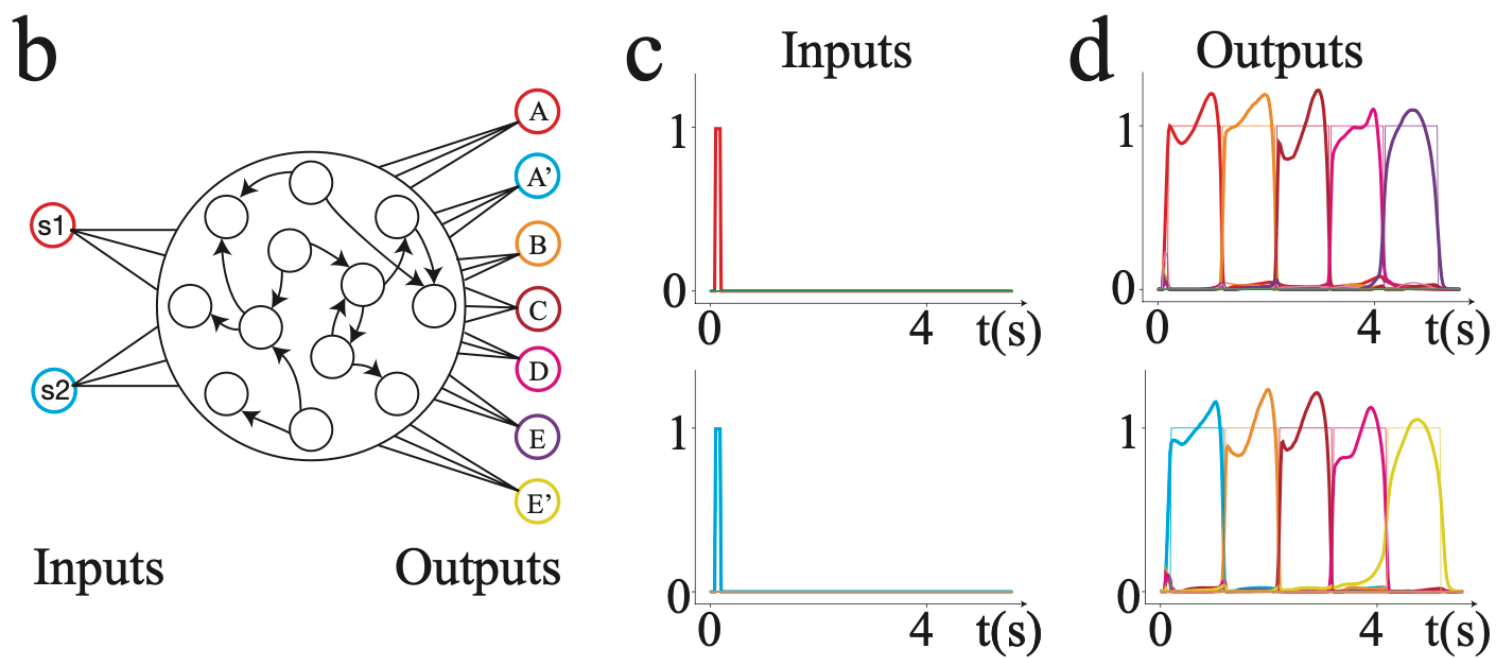
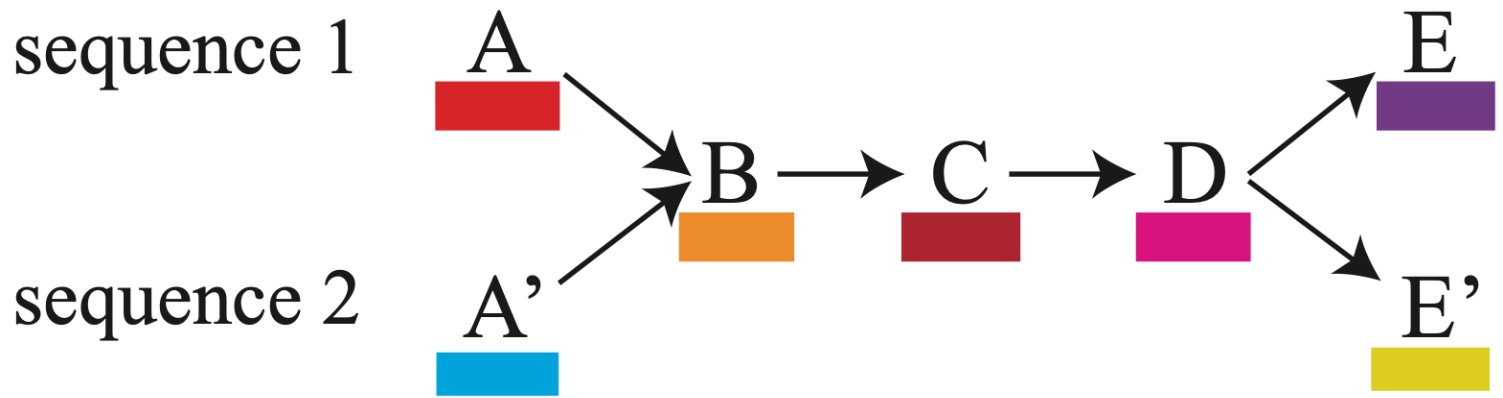
→ Bird songs:



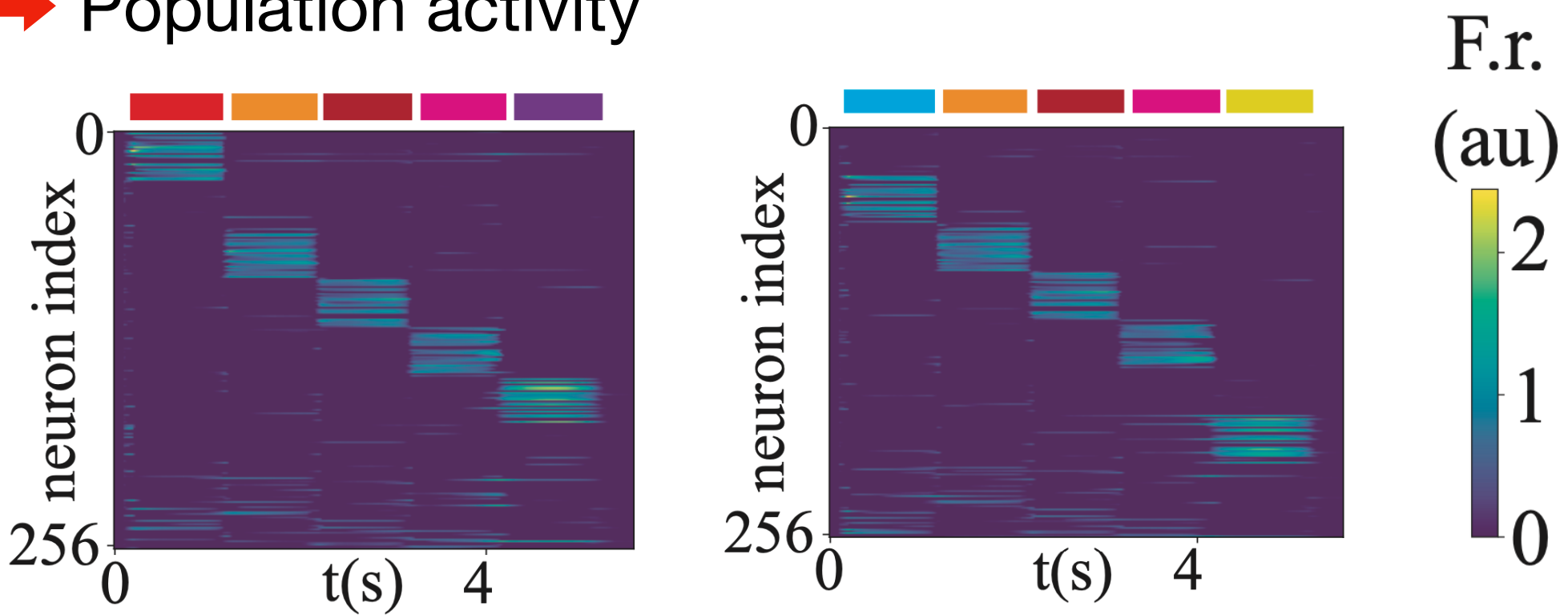
Markovitz et al, 2013

Long-distance dependencies in neural networks

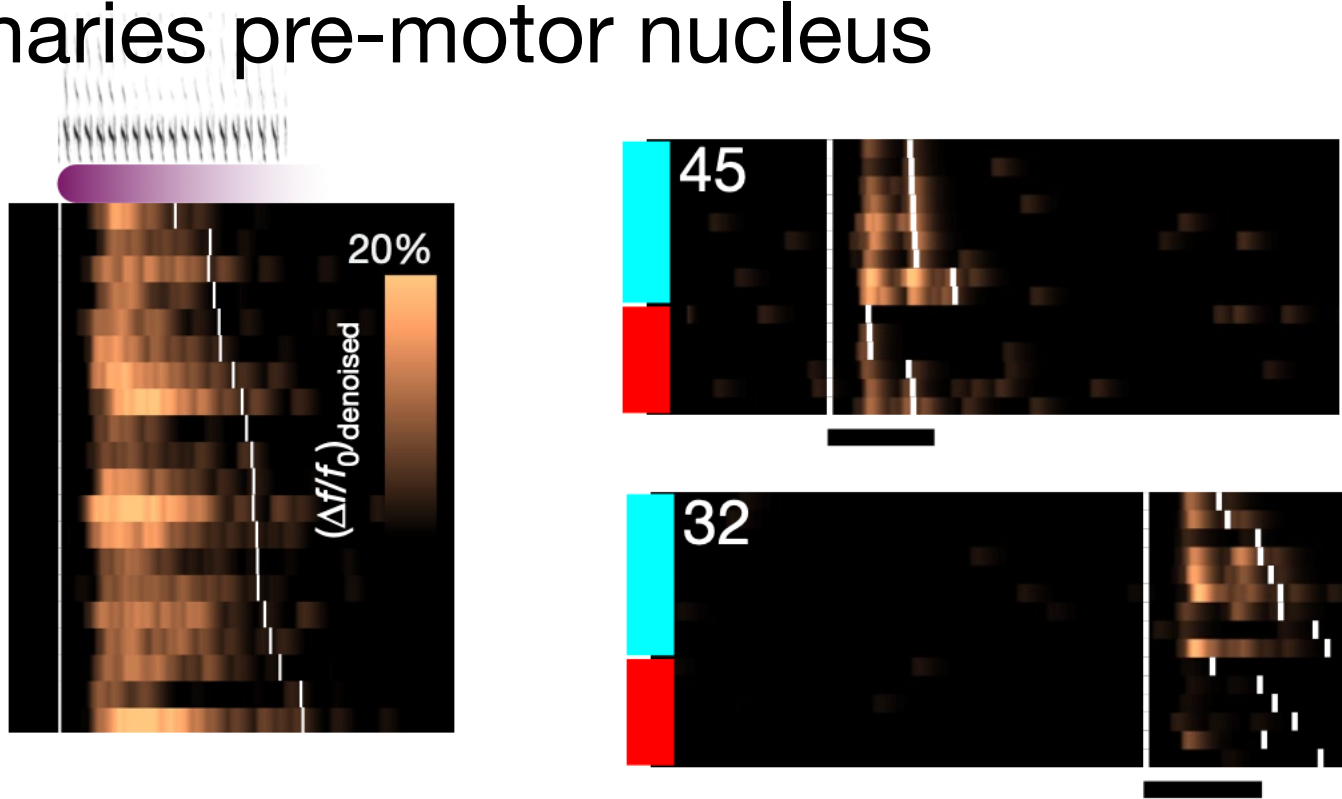
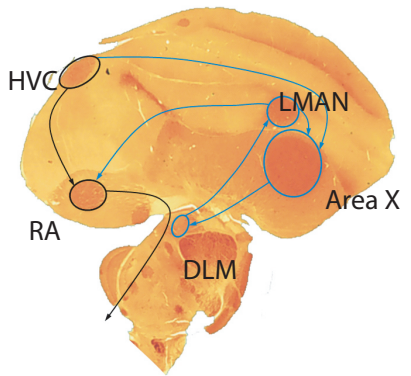
→ Single neuron activity



→ Population activity



→ Brain recordings in canaries pre-motor nucleus



Dubreuil & Leblois, 2021

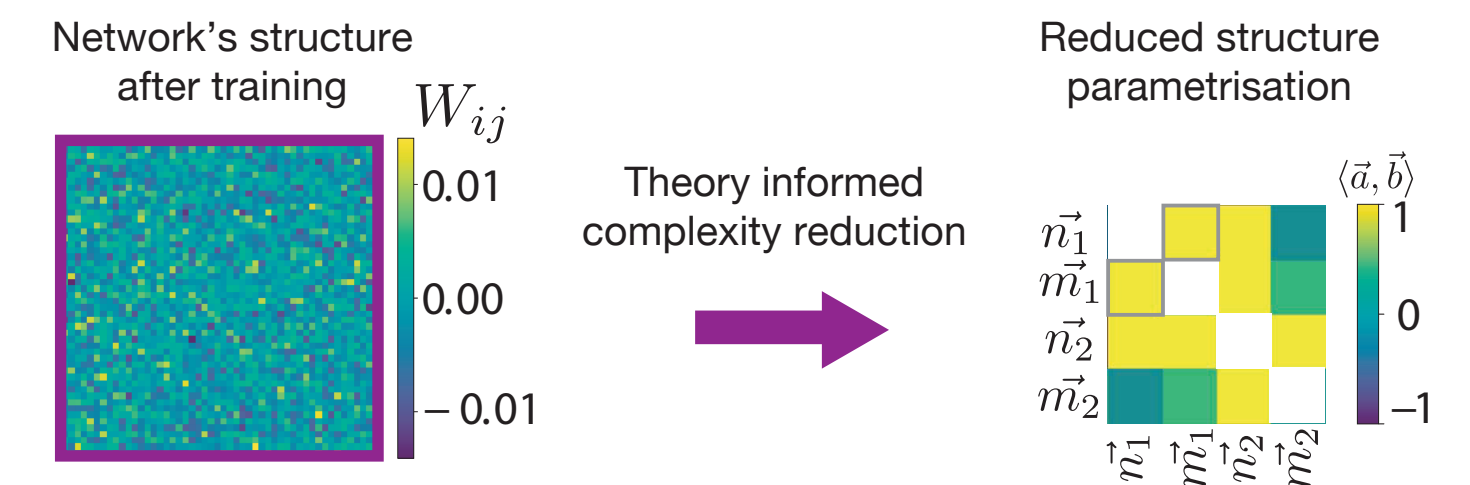
Cohen et al, 2020

Conclusion

➔ Dynamics of rate networks with low-rank connectivity can be reduced to dynamics on cognitive variables

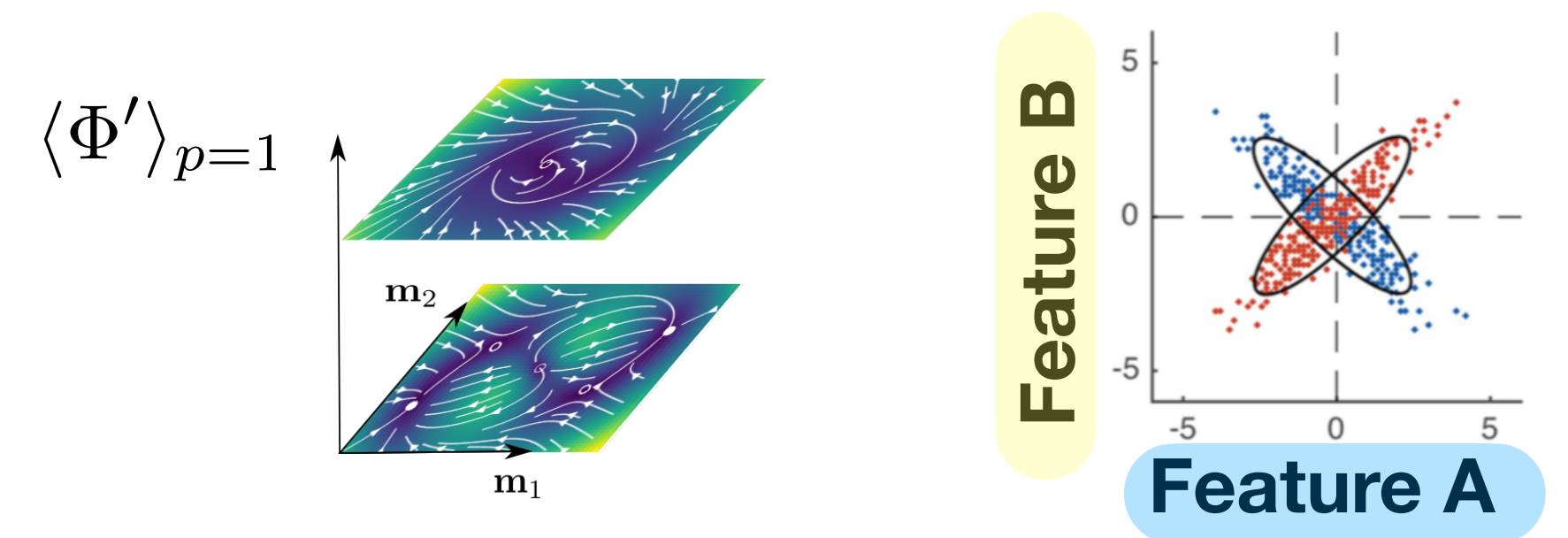
$$\begin{aligned}\dot{\kappa}_1 &= -\kappa_1 + \tilde{\sigma}_{n_1 m_1} \kappa_1 + \tilde{\sigma}_{n_1 m_2} \kappa_2 + \tilde{\sigma}_{n_1} W_{in} u(t) \\ \dot{\kappa}_2 &= -\kappa_2 + \tilde{\sigma}_{n_2 m_1} \kappa_1 + \tilde{\sigma}_{n_2 m_2} \kappa_2 + \tilde{\sigma}_{n_2} W_{in} u(t)\end{aligned}$$

➔ Use of theory to reverse-engineer artificial neural networks



➔ Gain modulation of specific populations can reconfigure network's dynamics

Neural correlates: specific connectivity profiles



Thanks

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