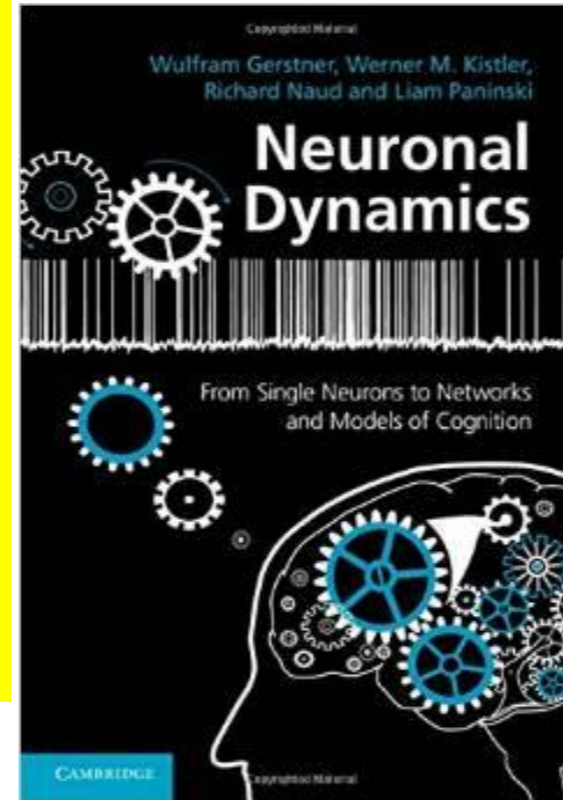


*Reading for this Lecture:*  
**NEURONAL DYNAMICS**  
Ch. 13.1-13.4

Cambridge Univ. Press



N. Brunel (2000) *Dynamics of sparsely connected networks of excitatory and inhibitory neurons*. J. Computational Neuroscience 8, pp. 183–208

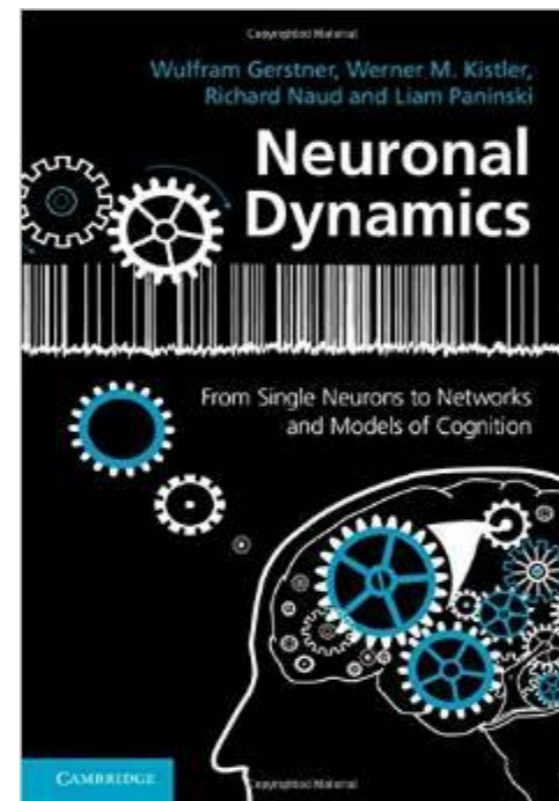
D. Nykamp and D. Tranchina (2000) *A population density approach that facilitates large-scale modeling of neural networks: analysis and application to orientation tuning*. J. Computational Neuroscience 8, pp. 19–50

## week 14 –Neural Manifolds and Low-dimensional dynamics

Wulfram Gerstner

EPFL, Lausanne, Switzerland

Cambridge Univ. Press



### 1. What are Neural Manifolds?

- experimental observations

### 2. Two views of Neural Activity

- computing (Hopfield model)
- neural circuits (field model)

### 3. Low-dimensional dynamics

- formalism and assumption
- dynamics

### 4. Examples of low-dim dynamics

- context-dependent decision making

**Lecture 15 of video series**

<https://lcnwww.epfl.ch/gerstner/NeuronalDynamics-MOOCall.html>

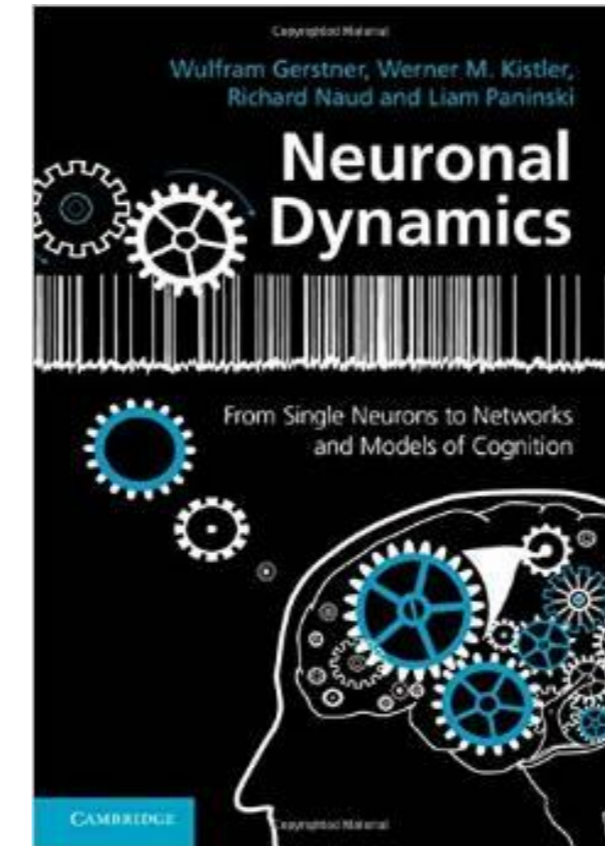
# Computational Neuroscience: Neuronal Dynamics

Written Exam (70%)  
+ miniproject (30%)  
→ 5 credits

- Select 1 Miniproject,  
(out of a list of 2)
- Perform task in teams of 2

Textbook:

<http://neurondynamics.epfl.ch/>



Video:

<https://lcnwww.epfl.ch/gerstner/NeuronalDynamics-MOOCall.html>

Miniproject in 2025: two variations of Hopfield model

# Computational Neuroscience: Neuronal Dynamics

## Written Exam (70%)

You can bring 1 sheet A5 (double-sided) of **handwritten** notes.  
(no calculator, no textbook, no phone)

Exam is orthogonal to miniproject.

- Look at written exercises
- Look at exams from previous years

## LEARNING OUTCOMES

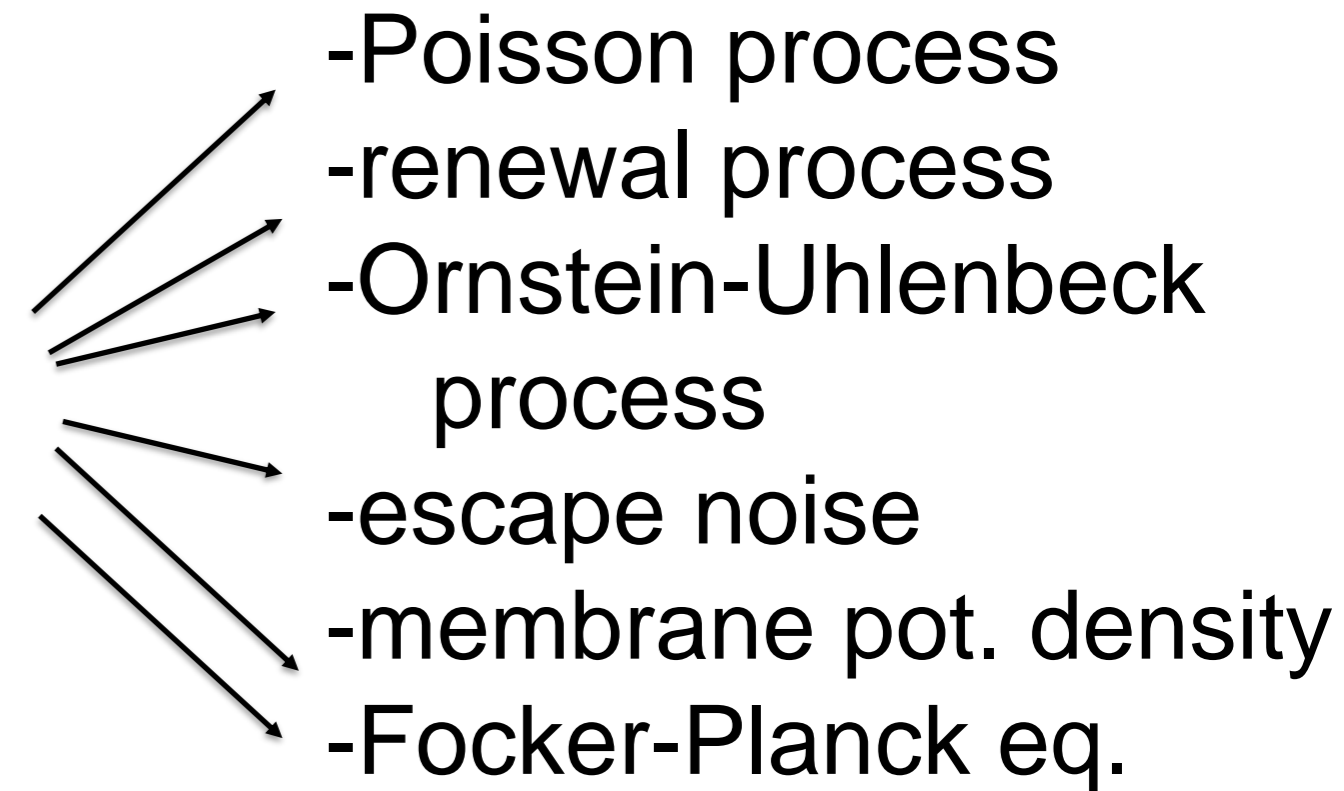
- Solve linear **one-dimensional differential equations**
- Analyze two-dimensional models in the **phase plane**
- Develop a simplified model by **separation of time scales**
- Analyze connected networks in the mean-field limit
- Formulate stochastic models of biological phenomena
- Formalize biological facts into mathematical models
- Prove **stability** and **convergence**
- Apply model concepts in simulations
- Predict outcome of dynamics
- Describe neuronal phenomena

## Transversal skills

- Plan and carry out activities in a way which makes optimal use of available time and other resources.
- Collect data.
- Write a scientific or technical report.

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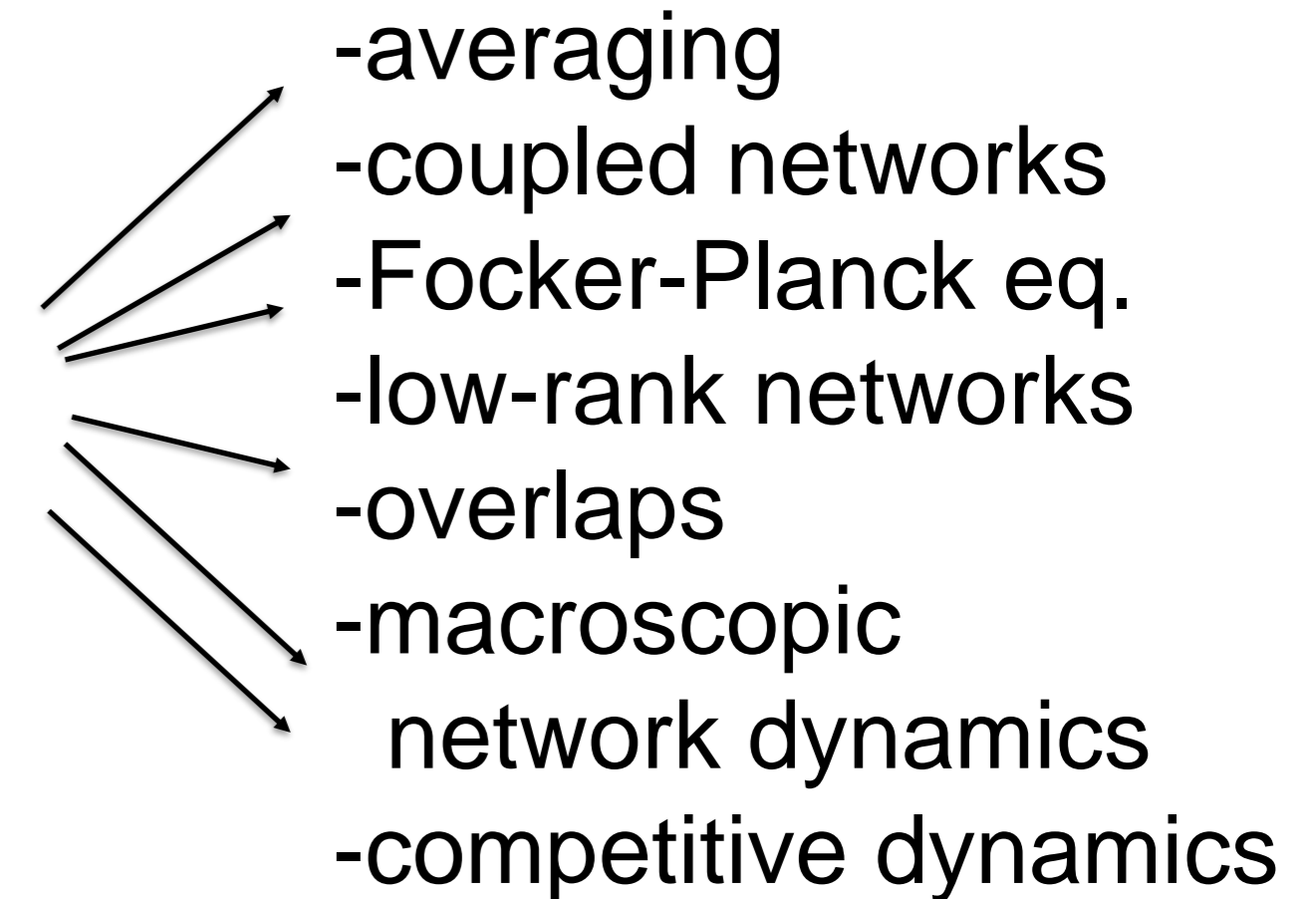
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## Neural Manifolds and Low-dimensional dynamics: **What are Neural Manifolds?**

### 1. What are Neural Manifolds?

- experimental observations

### 2. Two views of Neural Activity

- computing (Hopfield model)
- neural circuits (field model)

### 3. Low-dimensional dynamics

- formalism and assumption
- dynamics

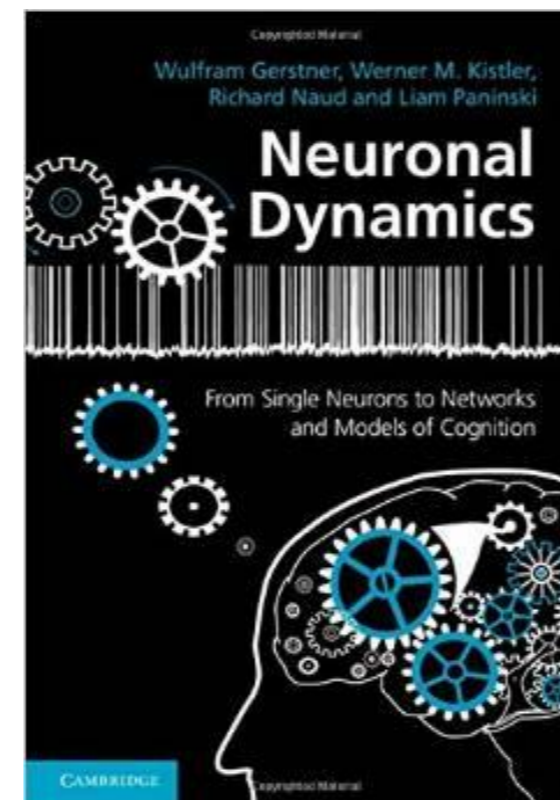
### 4. Examples of low-dim dynamics

- context-dependent decision making

Wulfram Gerstner

EPFL, Lausanne, Switzerland

Cambridge Univ. Press

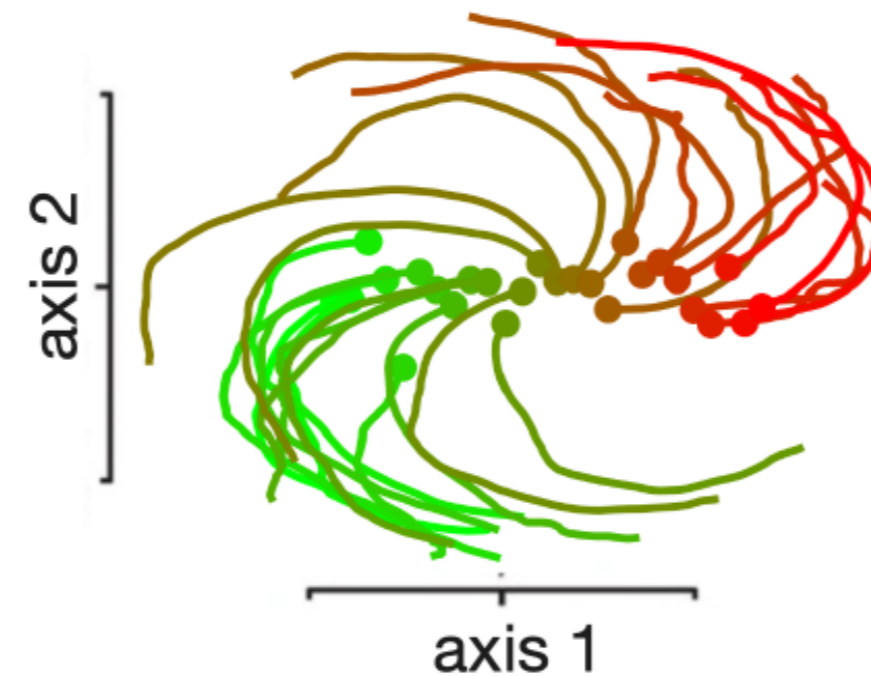


# Introduction: low-dimensional dynamics

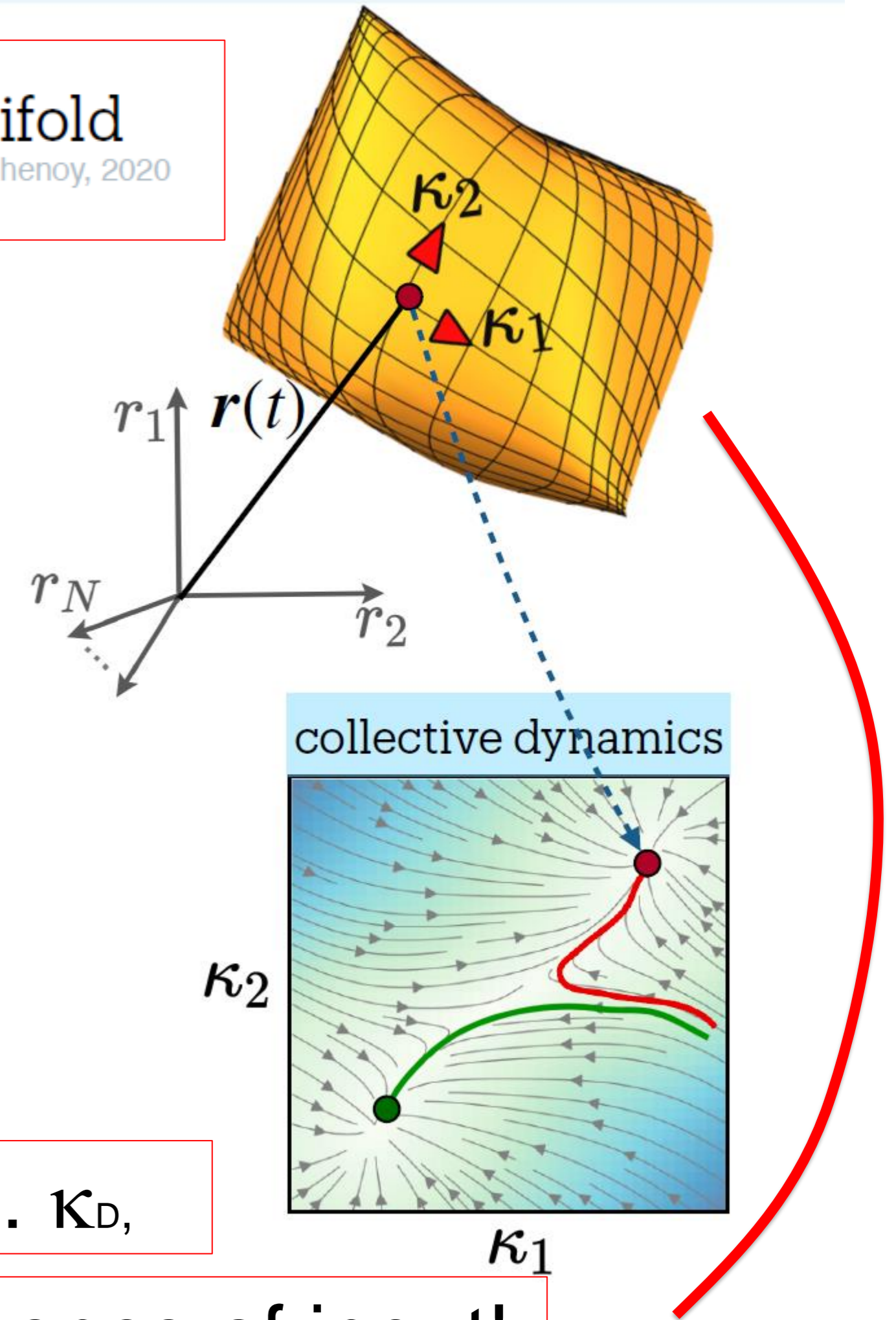
computations are described by **collective dynamics** in the manifold

Vyas, S., Golub, M.D., Sussillo, D., Shenoy, 2020

Ex: motor cortex (monkey)



adapted from Churchland, ..., Shenoy, 2012



Flow described by small number of variables  $\kappa_1, \dots, \kappa_D$ ,

Low-dimensional dynamics even during sleep/absence of input!

Chaudhuri et al, 2019

Image: Pezon et al. 2024

## Summary 1:

There are **two different perspectives** on how to interpret neuronal activity:

- The classic view since Hubel and Wiesel was to start with **receptive fields**. We can then define **functional similarity** between neurons as neurons with similar receptive fields. On the theory side, this view has led to **field models** where neurons are organized along one or several abstract axis. Functionally similar neurons have typically stronger (more positive) connections to each other than to functionally different neurons. Hence **wiring** reflects functional similarity.
- The modern view is that neurons perform computational and that these computations can be described by a **flow or dynamics in low-dimensional manifolds**: Even though modern experiment probe the activity of hundreds of neurons simultaneously, we do not need 100 variables to describe the activity but only a few. On the theory this is similar to mean-field models or the Hopfield model. In the Hopfield model, we have encountered **effective variables** ('overlap') that describe the **collective dynamics**.

**The question of today is how the two views are connected to each other and to topics that we have seen in this class.**

## week 14 –Neural Manifolds and Low-dimensional dynamics

### 1. What are Neural Manifolds?

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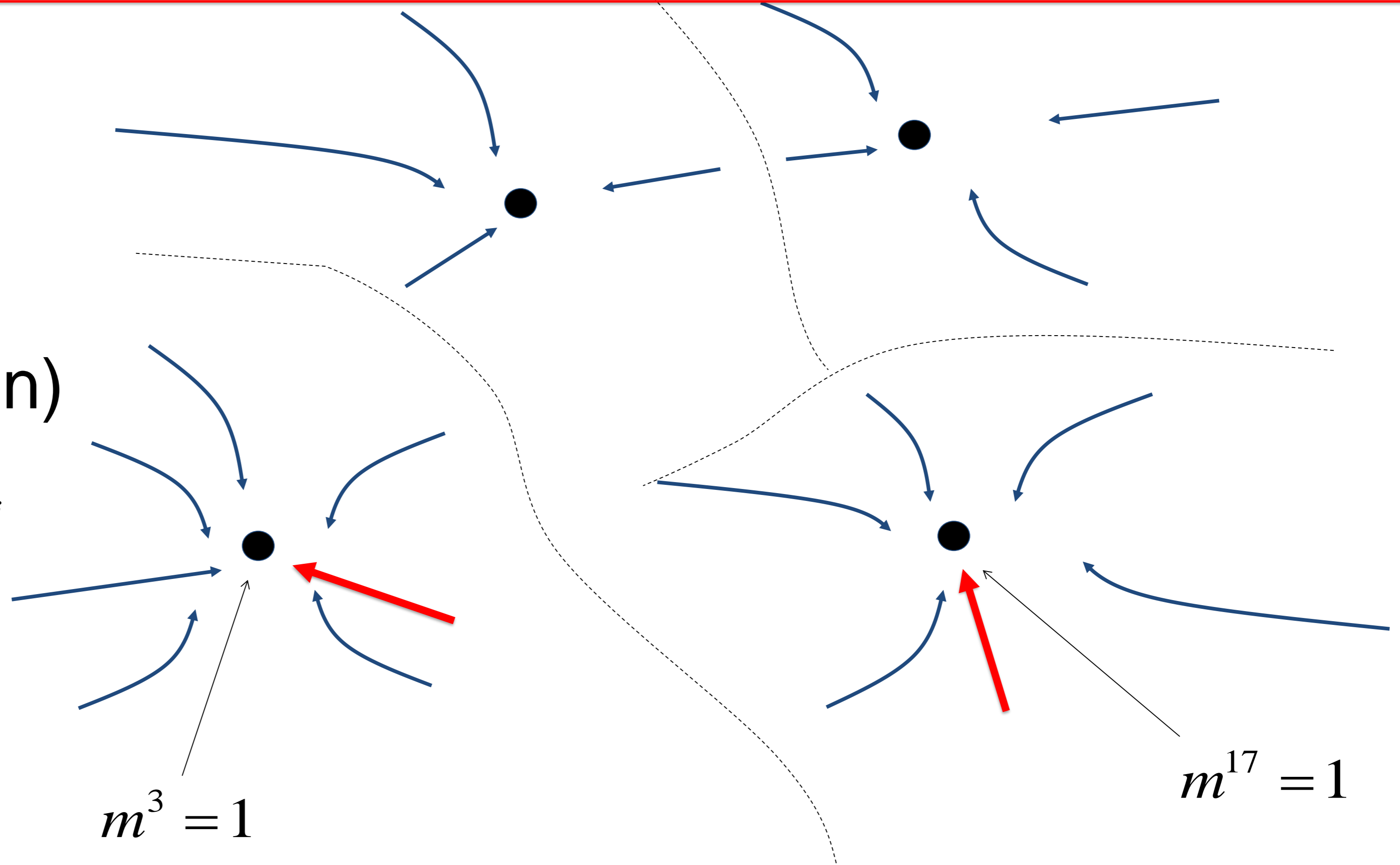
### 4. Examples of low-dim dynamics

- context-dependent decision making

# Review: Hopfield model: attractor dynamics

Overlap (definition)

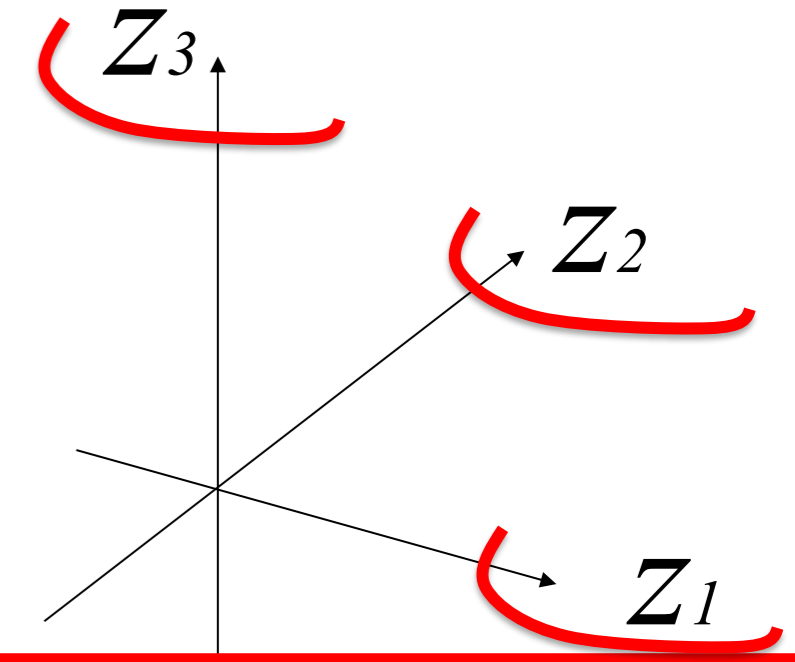
$$m^3(t+1) = \sum_j p_j^3 S_j$$



# Review: functional similarity of neurons

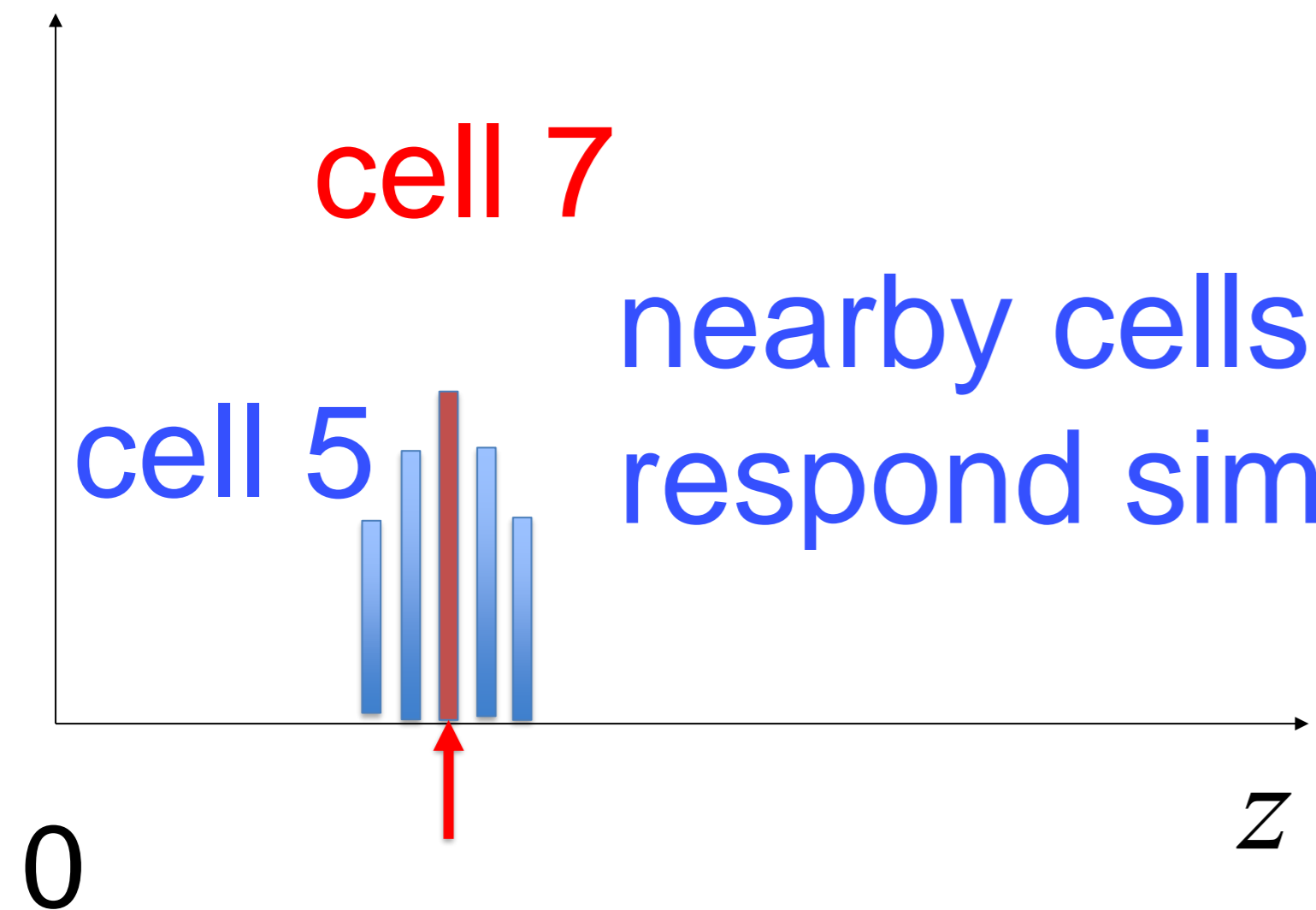
functional  
characterization  
of neuron

orientation of rec. field:  $z_1$   
horizontal placement of rec. field:  $z_2$   
vertical placement of rec. field:  $z_3$



rate (response to a stimulus)

**functional similarity =  
neighborhood in abstract space**



cell 7

nearby cells (along abstract axis)  
respond similarly

abstract axis: - a feature of receptive field

a stimulus that maximally  
excites cell 7

## Summary/review: Field equation

A population rate model in continuous space is sometimes called a field equation.

$$\tau \frac{d}{dt} h(x, t) = -h(x, t) + RI^{ext}(x, t) + d \int w(x - x') F(h(x', t)) dx'$$

Here the variable  $x$  can be interpreted as an **abstract quantity**, such as the **orientation and location** of the preferred visual stimulus: **Functional similarity**

In this case we may think of  $x$  as a three-dimensional vector

In the general model  $w(x, x')$  could be an arbitrary function; but in most field equations it is taken as a distance-dependent function  $w(x - x')$ . **Therefore connectivity is stronger between cells with similar ‘functional role’.**

A classic choice is the Mexican-Hat function with long-range inhibition and short-range excitation. Note that in real neural networks, inhibition involves a separated class of neurons.

# Summary: How can we interpret neural activity?

## How can we understand principles of neuronal activity?

*D. Barack and J. Krakauer, 2021*

*C. Langdon and T. Engel, 2023*

### Two different perspectives

- **low dimensional dynamics**

→ Hopfield model

(e.g., flow towards fixed point/attractor dynamics)

- **neurons and functional similarity**

→ continuum model

(functional similarity reflected in wiring,  
wiring causes dynamics)

→ Relation between the two views? Relation to known models?

## week 14 –Neural Manifolds and Low-dimensional dynamics

### 1. What are Neural Manifolds?

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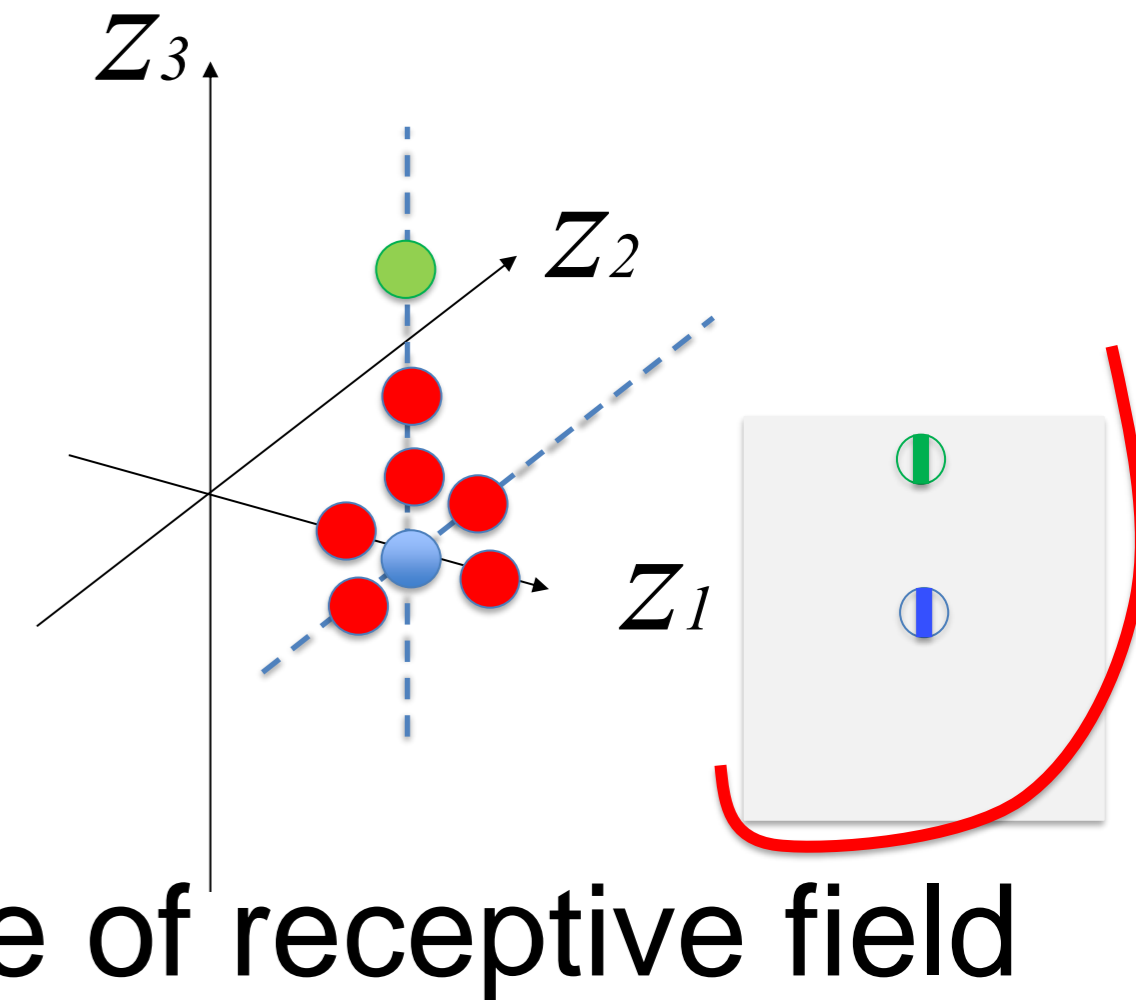
- context-dependent decision making

# Three assumptions

Assumption 1: neurons are functionally characterized by features

functional  
characterization  
of neuron

orientation of rec. field:  $z_1$   
horizontal placement of rec. field:  $z_2$   
vertical placement of rec. field:  $z_3$



Each abstract axis: a feature of receptive field

**functional similarity = neighborhood in abstract space**

# Functional similarities and 'wiring'

**functional similarity = neighborhood in abstract space**

Assumption 1:

Position of neuron  $i$  in abstract space:  $\mathbf{z}_i = (z_1, z_2, z_3, \dots)$  ( $i$ )

Assumption 2:

Weight of connection from  $j$  to  $i$  depends on the positions  $\mathbf{z}_i, \mathbf{z}_j$ :

$$W_{ij} = w(\mathbf{z}_i, \mathbf{z}_j)$$

Assumption 3:

Specific choice of weight from  $j$  to  $i$ :

$$W_{ij} = \sum_{\mu}^D F_i^{\mu} G_j^{\mu} = \sum_{\mu}^D f_{\mu}(\mathbf{z}_i) g_{\mu}(\mathbf{z}_j)$$

$$f_{\mu}(\mathbf{z}_i) = F_i^{\mu}$$

$$g_{\mu}(\mathbf{z}_j) = G_j^{\mu}$$

# Field equation in functional similarity space

$$\frac{d}{dt}h_i(t) = -\frac{1}{\tau}h_i(t) + \sum_j W_{ij} \phi(h_j(t))$$

use weights:

$$W_{ij} = \sum_{\mu}^D f_{\mu}(\mathbf{z}_i) g_{\mu}(\mathbf{z}_j)$$

with neuron  $i$  at position  $\mathbf{z}_i$

$$\frac{d}{dt}h(\mathbf{z}_i, t) = -\frac{1}{\tau}h(\mathbf{z}_i, t) + \sum_j \sum_{\mu}^D f_{\mu}(\mathbf{z}_i) g_{\mu}(\mathbf{z}_j) \phi(h(\mathbf{z}_j, t))$$

$$\frac{d}{dt}h(\mathbf{z}, t) = -\frac{1}{\tau}h(\mathbf{z}, t) + \int d\mathbf{z}' \rho(\mathbf{z}') \sum_{\mu}^D f_{\mu}(\mathbf{z}) g_{\mu}(\mathbf{z}') \phi(h(\mathbf{z}', t))$$

generalized field equation (large number of neurons)

# Field equation and low-dimensional dynamics

$$\frac{d}{dt}h(\mathbf{z}, t) = -\frac{1}{\tau}h(\mathbf{z}, t) + \underbrace{\int d\mathbf{z}' \rho(\mathbf{z}')}_{\text{weight}} \sum_{\mu}^D \underbrace{f_{\mu}(\mathbf{z}) g_{\mu}(\mathbf{z}') \phi(h(\mathbf{z}', t))}_{\alpha_{\mu}(t)}$$

$$\frac{d}{dt}h(\mathbf{z}, t) = -\frac{1}{\tau}h(\mathbf{z}, t) + \sum_{\mu}^D \underbrace{f_{\mu}(\mathbf{z})}_{\text{basis function}} \underbrace{\alpha_{\mu}(t)}_{\text{coefficient}}$$

$D$  'basis functions'

Idea: write

$$h(\mathbf{z}, t) = \sum_{\mu}^D \underbrace{f_{\mu}(\mathbf{z})}_{\text{basis function}} \underbrace{\kappa_{\mu}(t)}_{\text{projection onto basis f.}}$$

# Field equation and low-dimensional dynamics

Idea: write

$$h(\mathbf{z}, t) = \sum_{\mu}^D f_{\mu}(\mathbf{z}) \kappa_{\mu}(t)$$

→ yields D coupled equations

$$\frac{d}{dt} \kappa_{\mu}(t) = -\frac{1}{\tau} \kappa_{\mu}(t) + \int d\mathbf{z} \rho(\mathbf{z}) g_{\mu}(\mathbf{z}) \underbrace{\phi\left(\sum_{\nu}^D f_{\nu}(\mathbf{z}) \kappa_{\nu}(t)\right)}_{\phi(h(\mathbf{z}, t))}$$

→ activity of all N neurons ( $N \gg 1$ ) is described by D equations in recurrent network (without external input)

## Summary 3: low-dimensional dynamics

---

To generate **low-dimensional dynamics** in **heterogeneous** networks of neurons, three ingredients are important:

- (i) neurons characterized by abstract positions  $z$  representing functional similarity
- (ii) Weight matrix depends on  $z$  and  $z'$
- (iii) Weight matrix is of low rank: outer-product of rank  $D$

**Result:** - field model for  $N$  to infinity  
- small number  $D \ll N$  of variables describe dynamics

# Exercise at 11h15

$$\frac{d}{dt}h(t, z) = -\frac{1}{\tau}h(t, z) + J \int_V \sum_{\mu=1}^D f_{\mu}(z)g_{\mu}(z')\phi(h(t, z'))\rho(z')dz' \quad (3)$$

As a field model, this is an infinite-dimensional dynamical system. Yet, due to the particular form of the connectivity in Eq.(2), it can be reduced to a  $D$ -dimensional description. The goal of this exercise is to derive the hidden  $D$ -dimensional dynamics.

In this exercise, we assume that the functions  $f_{\mu}$  are orthonormal:

$$\int_V f_{\mu}(z)f_{\nu}(z)\rho(z)dz = \delta_{\mu\nu} = \{1 \text{ if } \mu = \nu, \text{ and } 0 \text{ otherwise}\} \quad (4)$$

**1.1** Assume that the field  $h(t, z)$  is given by a linear combination of the functions  $f_{\mu}$ , with time-dependent coefficients  $\kappa_{\mu}(t)$  ( $\mu = 1, \dots, D$ ); that is:

$$h(t, z) = \sum_{\mu=1}^D f_{\mu}(z)\kappa_{\mu}(t) \quad (5)$$

What is the expression of each coefficient  $\kappa_{\mu}$  in terms of the field  $h(t, z)$ ?

*Hint:* compute the projection of the field on the function  $f_{\mu}$ :  $\int_V f_{\mu}(z)h(t, z)\rho(z)dz$ .

**1.2** We are now interested in the fixed points of Eq.(3). Find a closed-form expression solved by the coefficients  $\kappa_{\mu}$  in the steady-state.

*Hint:* use Eq.(5) to replace the field with the variables  $\kappa_{\mu}$ .

**1.3** Starting from the field dynamics of Eq.(3), derive a closed-form expression for the dynamics of the coefficients  $\kappa_{\mu}$ .

*Hint:* use Eq.(5) to compute the time derivative of the variables  $\kappa_{\mu}(t)$ .

**1.4** Consider that, at initial time  $t = 0$ , the field is a linear combination of the functions  $f_{\mu}$ , *plus* an additional term:

$$h(t = 0, z) = \sum_{\mu} f_{\mu}(z)\kappa_{\mu}(0) + \Delta h(z)$$

where  $\int_V \Delta h(z)f_{\mu}(z)\rho(z)dz = 0$ , for all  $\mu$ . What are the dynamics of  $\Delta h$ ? Why is Eq.(5) a good assumption?

**1.5** Consider now that the network receives an external input, given by an additional term in Eq.(3):

$$I^{\text{ext}}(z) = \sum_{\mu=1}^D f_{\mu}(z)I_{\mu}(t)$$

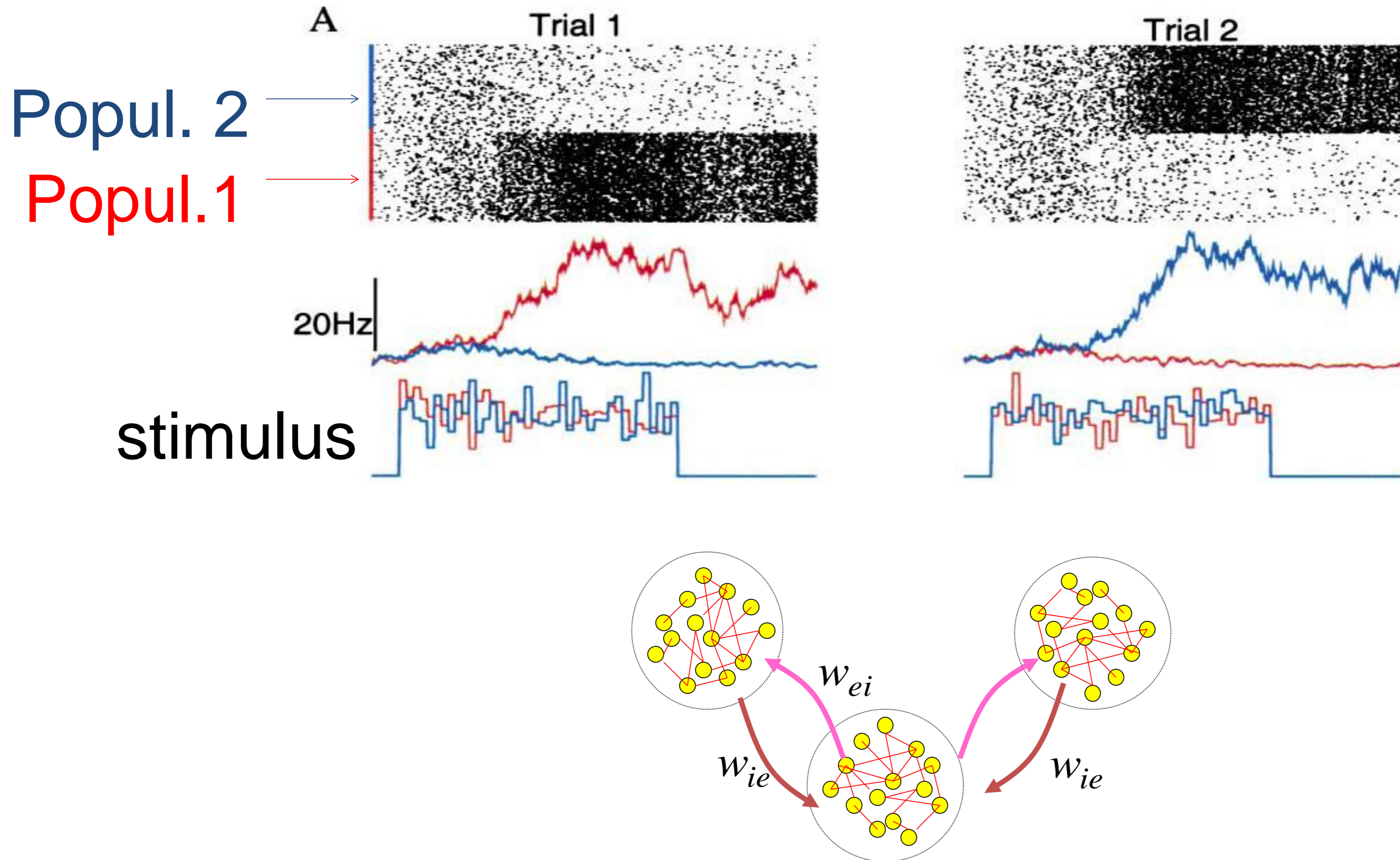
What are the dynamics of the coefficients  $\kappa_{\mu}$  now? Can the external input affect the fixed points?

# Examples of low-dimensional dynamics:

- Visual Cortex Model
- Ring model (with sinusoidal coupling)
- Hopfield model
- **Decision making**

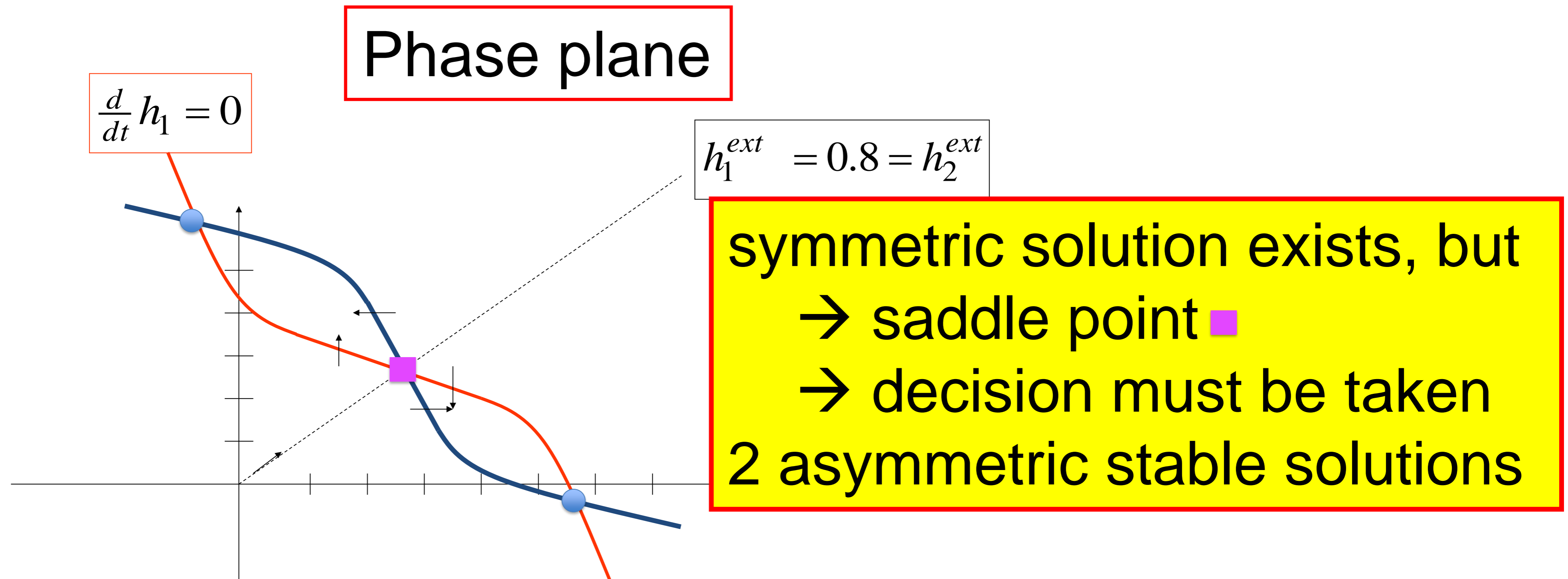
# Review: Decisions in populations of neurons: simulation

Simulation of 3 populations of spiking neurons, unbiased strong input



*X.J. Wang, 2002*  
*NEURON*

# Review. Theory of decision dynamics: unbiased strong



With unbiased input, there is a minimal input strength where the (single) stable solution turns into a saddle

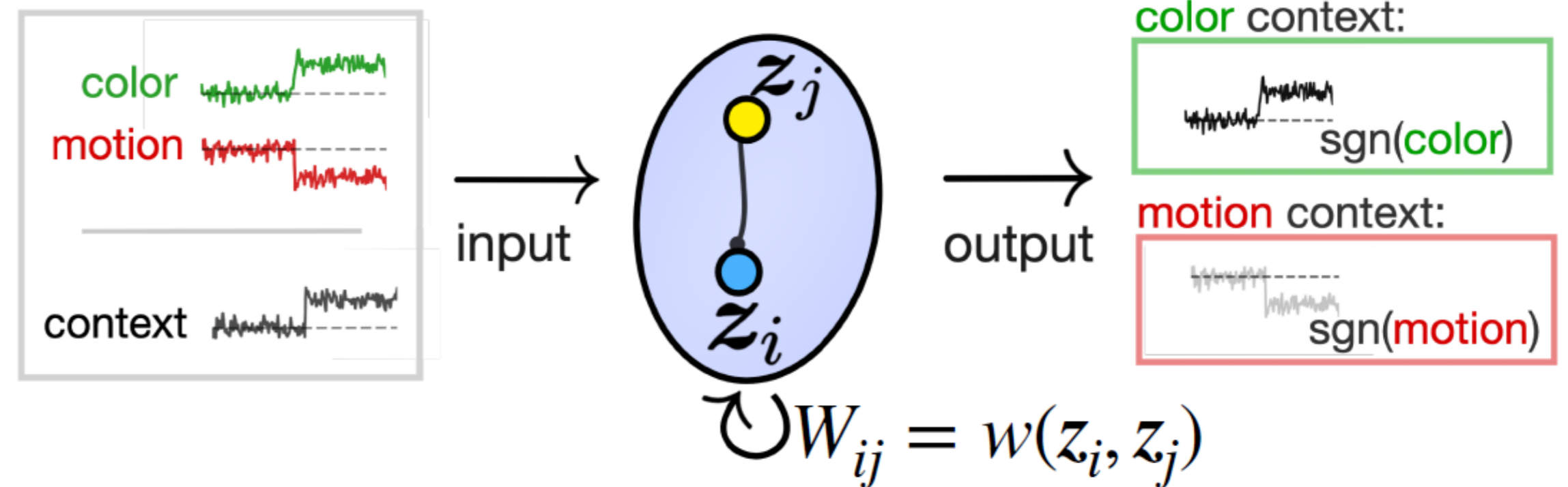
# Example : low-dimensional dynamics in decision making

## Context-dependent decision making

Task setup:

- 2 sensory inputs (color & motion)
- binary context input
- the network must output the sign of the specified sensory feature

Mante,...,Newsome. 2014



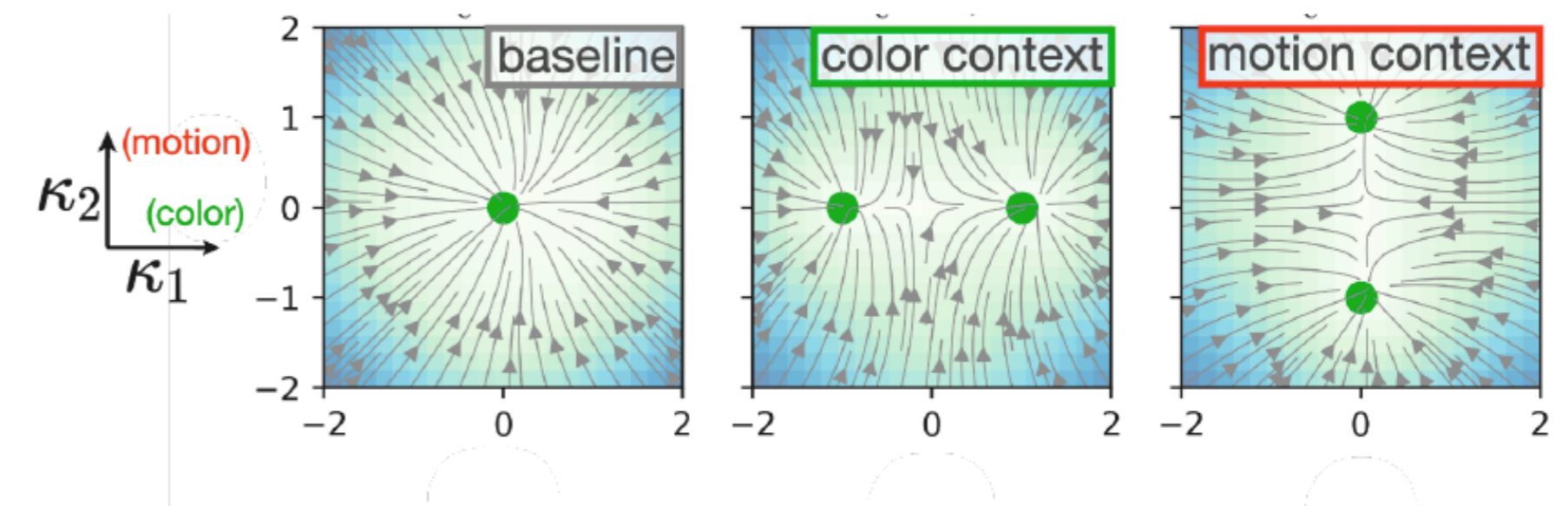
Task: Mante, ... Newsome 2014

... solved by 2-dimensional collective dynamics.

Mastrogiuseppe, Ostojic. 2018  
Mante,...,Newsome. 2014

Model of 2-dim dynamics

- Mante, ... Newsome 2014
- Mastrogiuseppe, Ostojic, 2018

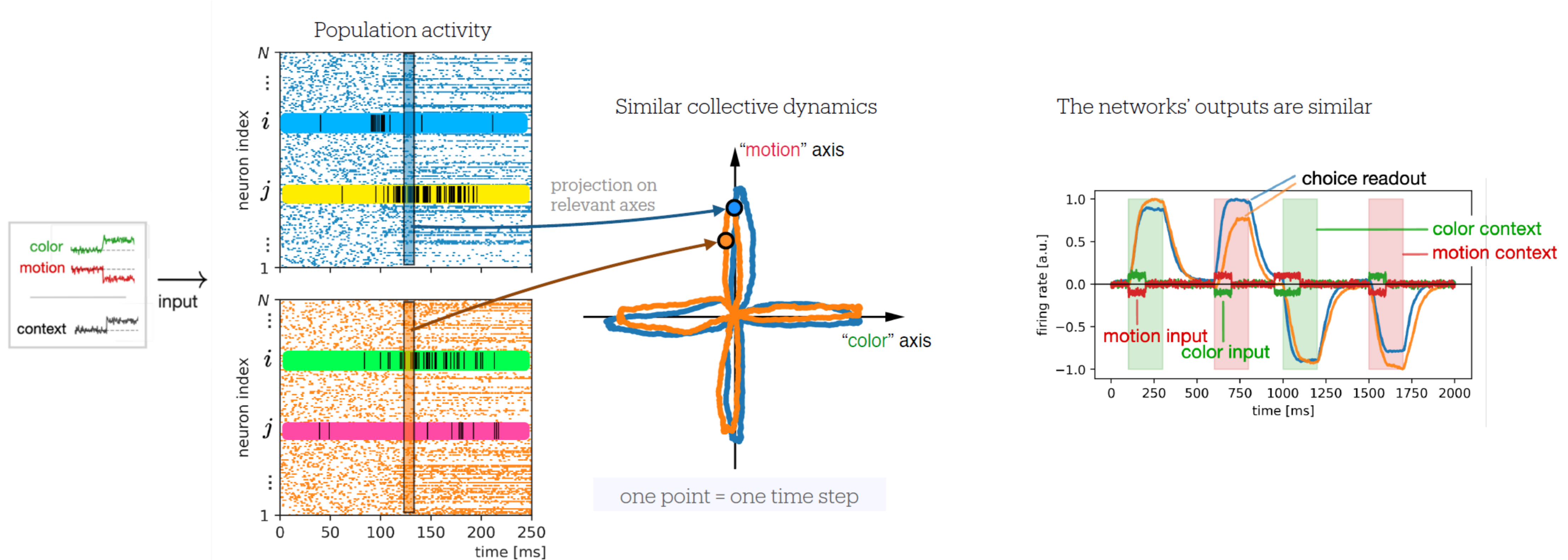


Idea: - design fixed-point structure in D-dim. decision space  
- embedded in N-dimensional neuronal space

# Example: low-dimensional dynamics in decision making

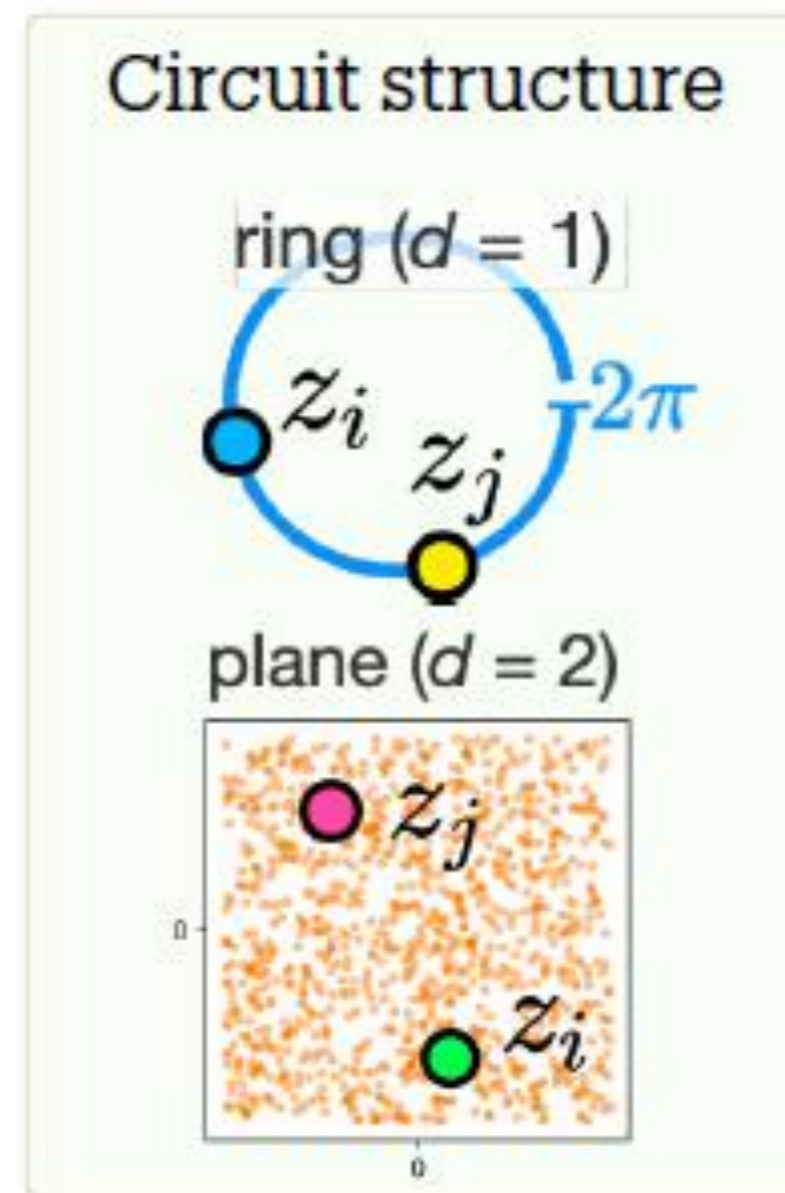
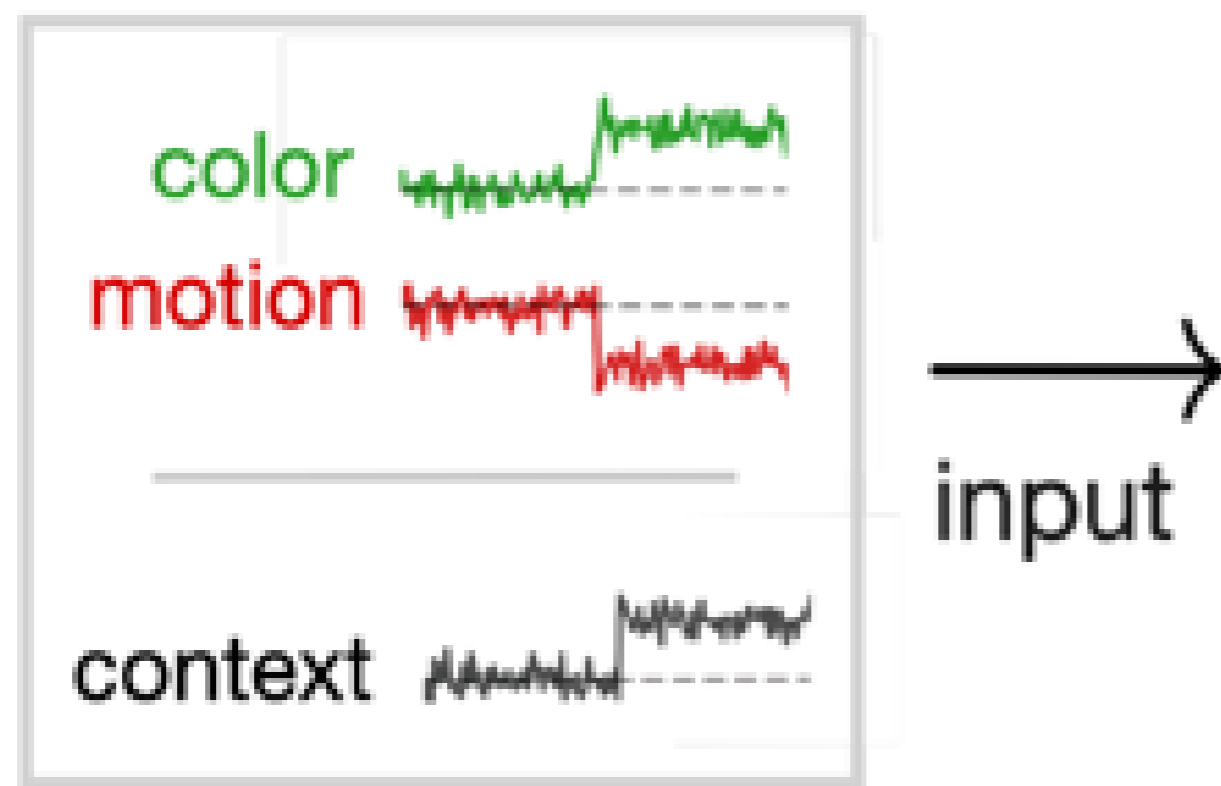
## Two different spiking neuron models, similar dynamics

model of context-dependent decision-making



# Example 2: low-dimensional dynamics in decision making

Two different spiking neuron models, similar dynamics



uniform in 1d, ring

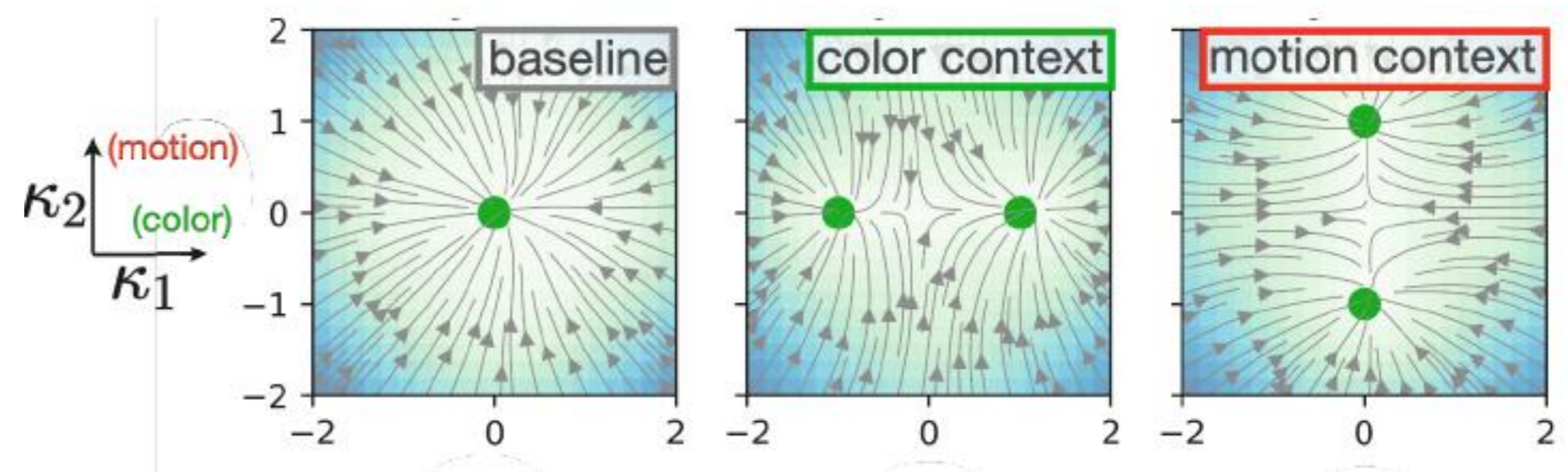
uniform in 2d, square

Flow in 2 dimensions:

1<sup>st</sup> axis: color

2<sup>nd</sup> axis: motion

Flow pattern depends  
on context input



#### Summary 4: **Task of context-dependent decision making (Mante et al.)**

Patterns of dots move on a screen. Dots have two characteristic features, i.e. color (green or magenta) and motion (movement up or down). A monkey watches the dot pattern. An additional context input tells the monkey which of the two features he should consider, color or motion.

After a go-cue, the monkey has to respond positively if the majority of the dots move upwards (for motion context) or if the majority of dots is green (color context).

Simulations of a model with thousands of neurons can reproduce this behavior. A theoretical model implements a low-dimensional manifold as follows.

- (i) If no context cue is given, then there is a single fixed point. The monkey does not move.
- (ii) If color context is given, then there are two fixed points at two different horizontal positions.  
The one to the left corresponds to color=green.
- (iii) If motion context is given, then there are two fixed points at two different vertical positions.  
The one on top corresponds to motion=upward.

The model can be implemented with the formalism of outer-product matrix as described starting from two different layouts of functional similarity in the z-space: either a one-dimensional ring model (blue model), or a two-dimensional square (orange model). Both models generate the same trajectories in the manifold and both lead to a valid choice readout.

Summary 4, Mante task, continued.

To extract the similarity space (embeddings of neurons in the z-space), one can use the fact that functionally similar neurons generate very similar time-dependent signals  $r(t)$ .

Therefore the similarity becomes visible if we plot the time-series  $r(t)$  of each neuron (= one row of the experimental data matrix) in some high-dimensional space: similar neurons will be neighbors.

The simplest way of doing this would be to cut the time series in  $K$  distinct intervals, and plot neurons as point in  $K$ -dimensional space. However, any other preprocessing tool that takes the time series and transforms it into  $K$  values can be used as well.

Hence:

if you plot the columns (rate vector) of the data matrix in the  $N$ -dimension space as a function of time , you can extract the low-dimensional manifold.

If you plot the rows (time series for each neuron) in the  $K$ -dimensional space as a function of neurons (1 neuron = 1 point), then you can extract the similarity of neurons in the z-space.

Importantly, different implementations in z-space can give rise to qualitatively identical low-dimension trajectories in the manifold: trajectory  $(\kappa_1(t), \kappa_2(t) | \text{context})$

**Barack, D.L., Krakauer, J.W.: Two views on the cognitive brain. Nature Reviews Neuroscience 22(6), 359–371 (2021)**

**Langdon, C., Genkin, M., Engel, T.A.: A unifying perspective on neural manifolds and circuits for cognition. Nature Reviews Neuroscience 24(6), 363–377 (2023)**

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Churchland, M.M., Cunningham, J.P., Kaufman, M.T., Foster, J.D., Nuyujukian, P., Ryu, S.I., Shenoy, K.V.: Neural population dynamics during reaching. Nature 487(7405), 51–56 (2012)

Vyas, S., Golub, M.D., Sussillo, D., Shenoy, K.V.: Computation through neural population dynamics. Annual Review of Neuroscience 43(1), 249–275 (2020)

Mante, V., Sussillo, D., Shenoy, K.V., Newsome, W.T.: Context-dependent computation by recurrent dynamics in prefrontal cortex. Nature 503(7474), 78–84 (2013)

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**THE END**

## Neural Manifolds and Low-dimensional dynamics:

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- experimental observations

### 2. Two views of Neural Activity

- computing (Hopfield model)
- neural circuits (field model)

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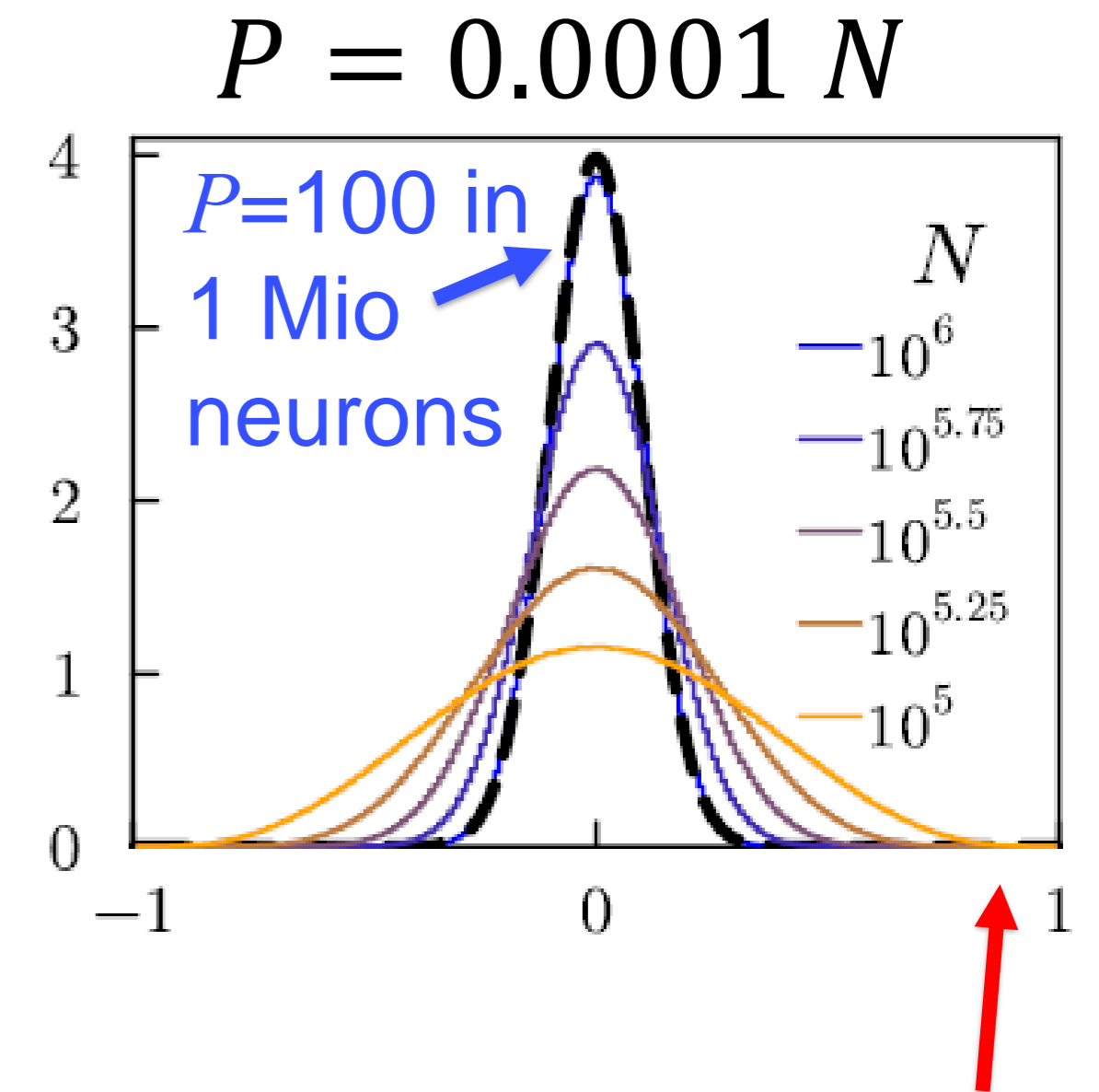
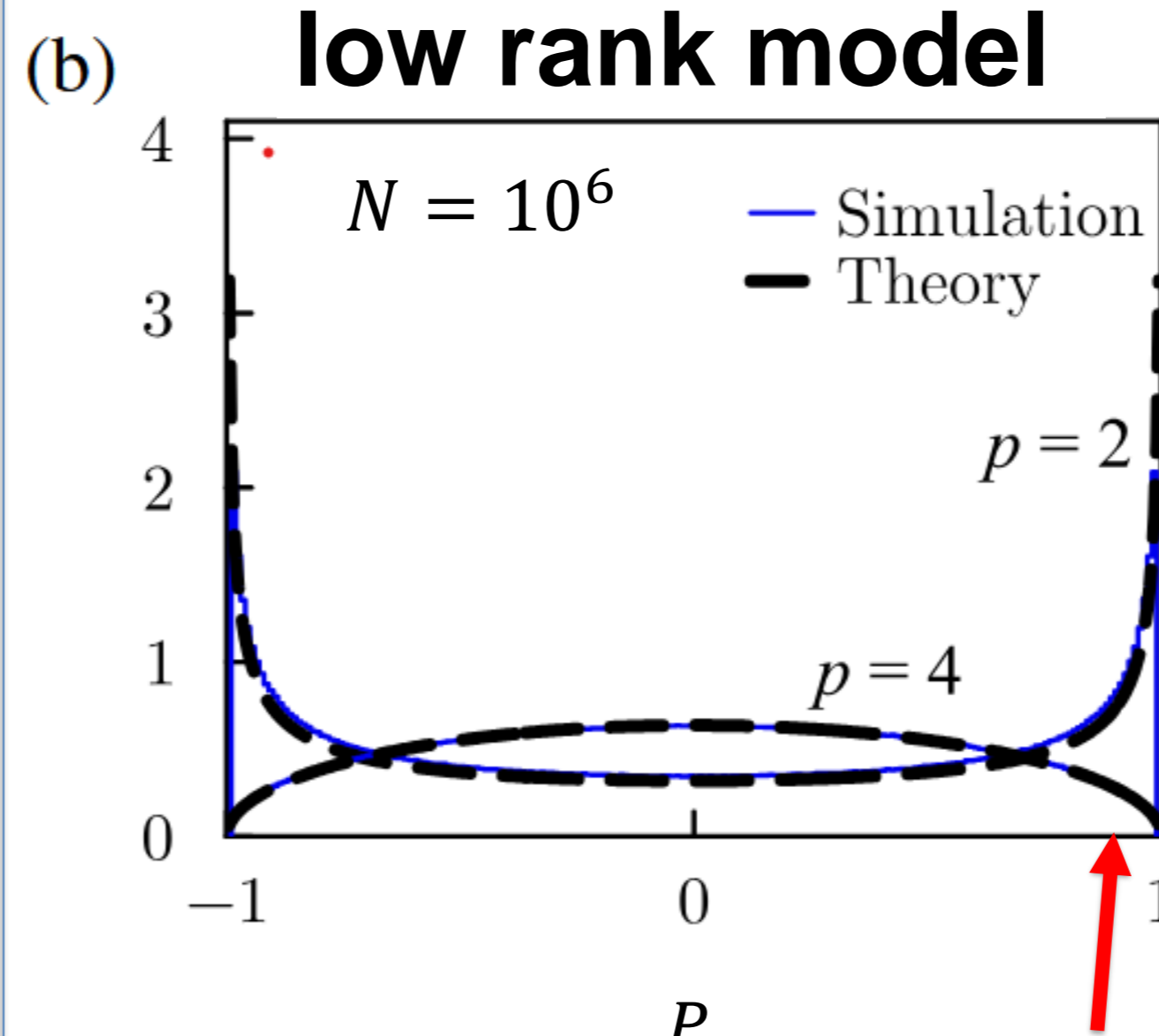
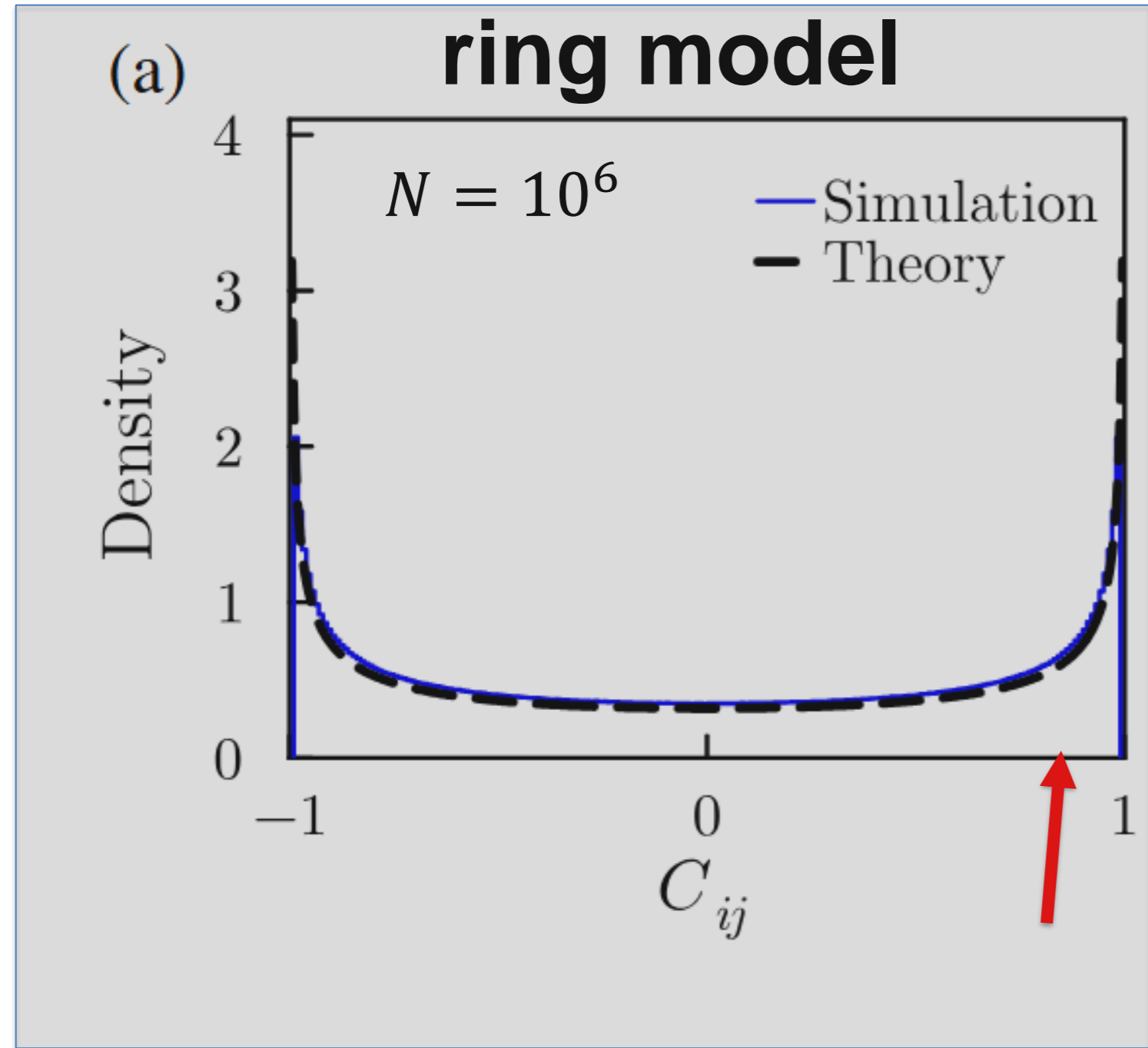
- formalism and assumption
- dynamics

### 4. Examples of low-dim dynamics

- context-dependent decision making

### 5. From Spikes to Rates

# Correlations between two neurons: low-rank weight matrix



$$w_{ij} = \frac{1}{N} \sum_{\mu}^P \xi_i^{\mu} \xi_j^{\mu} \quad \xi_j^{\mu} \text{ are Gaussian distributed}$$

Neurons become uncorrelated for  $P \rightarrow \infty$ ;  $N \rightarrow \infty$ ;  $\frac{P}{N} \rightarrow 0$   
*e.g.*  $P = N^{1/3}$

→ **no duplicate neurons**

V. Schmutz, J. Brea, W. Gerstner (2025) *Emergent rate-based dynamics in duplicate-free populations of spiking neurons*  
 Physical Review Letters, 134:018401

Quiz: Hopfield model –  
Are neurons correlated or uncorrelated for large N?

We have stored P binary patterns in a networks of N neurons using  
The standard weight matrix

$$w_{ij} = \frac{1}{N} \sum_{\mu} \xi_i^{\mu} \xi_j^{\mu}$$

The number of neurons N is (much) larger than the number P.

[ ] There are at most P different ‘types of neuron’ so that if  
N > P neurons can become correlated.

[ ] There are at most  $P^3$  different ‘types of neuron’ so that if  
 $N > P^3$  neurons can become correlated.

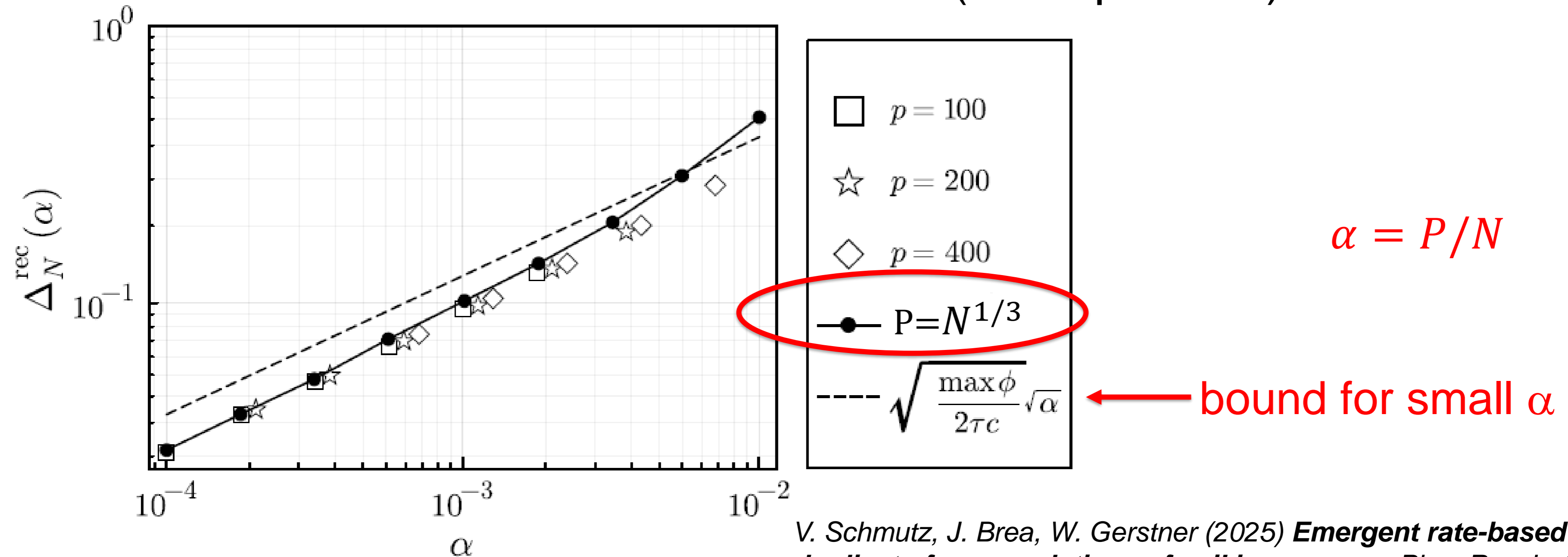
[ ] There are at most  $2^P$  different ‘types of neuron’ so that if  
 $N > 2^P$  neurons can become correlated.

# Distance between potential in SNN (spikes) and RNN (rates)

fixed  $P$  while  $N \rightarrow \infty$ : correlated neurons (duplicates, e.g. ring model)

$P = \alpha N$  while  $N \rightarrow \infty$ : uncorrelated neurons (no duplicates)

$P = N^{1/3}$  while  $N \rightarrow \infty$ : uncorrelated neurons (no duplicates)



$P = \alpha N$  while  $N \rightarrow \infty$ : distance  $\Delta_N^{rec} \propto \sqrt{\alpha}$  finite!

**SNN  $\neq$  RNN**

$P = N^{1/3}$  while  $N \rightarrow \infty$ : distance  $\Delta_N^{rec} \propto \sqrt{\alpha} = 1/N^{1/3}$

**SNN  $\rightarrow$  RNN**

**Summary** Rate coding with **instantaneous time-dependent rates** is possible in network of spiking neurons even though not a single pair of neurons is correlated (**no duplicates**)

- completely heterogeneous population
- no spatial averaging
- no temporal averaging

SNN → RNN

Rather: low-rank weight matrix

- **low-dimensional** network-input to each neuron
- neural activity lives in a ***P*-dimensional manifold**
- *e.g.*  $P = N^{1/3}$
- $P=100$ -dimensional activity in 1 Mio neurons

# Conclusions

- SNN  $\rightarrow$  RNN without averaging!
- rather 'loose' conditions
- rank  $P$  can be 'relatively large'

*V. Schmutz, J. Brea, W. Gerstner (2025) **Emergent rate-based dynamics in duplicate-free populations of spiking neurons**  
Phys.Rev. Lett. 134:018401*

# Is low-rank connectivity a strange assumption?

1) *“Neurons have receptive fields and wiring patterns: is a low-rank model realistic AT ALL?”*

Barack, D.L., Krakauer, J.W.: Two views on the cognitive brain. Nat. Rev. Neurosc. (2021)

Langdon, C., Genkin, M., Engel, T.A.: A unifying perspective on neural manifolds and circuits for cognition. Nat. Rev. Neurosci. (2023)

**Answer: All standard models of cortex are dominated by a low-rank connectivity matrix**

Pezon, L., Schmutz, V, Gerstner, W. (2024), Linking Neural Manifolds to Principles of Circuit Structure in Recurrent Networks bioRxiv doi: <https://doi.org/10.1101/2024.02.28.582565>

2) *“How are low-rank networks related to low-dim. dynamics?”*

**Answer: rank  $P$  weight matrix (outer product matrix) always generate  $P$ -dimensional dynamics ( $\rightarrow$ neural manifolds)**

Mastrogiuseppe, F., Ostojic, S.: Linking connectivity, dynamics, and computations in low-rank recurrent neural networks. Neuron 99(3), 609–623 (2018)

# Computational Neuroscience: Neuronal Dynamics

## Written Exam (70%)

You can bring 1 sheet A5 (double-sided) of **handwritten** notes.  
(no calculator, no textbook, no phone)

Exam is orthogonal to miniproject.

- Look at written exercises
- Look at exams from previous years

I wish you Good Luck and Great Success  
for the Written Exam