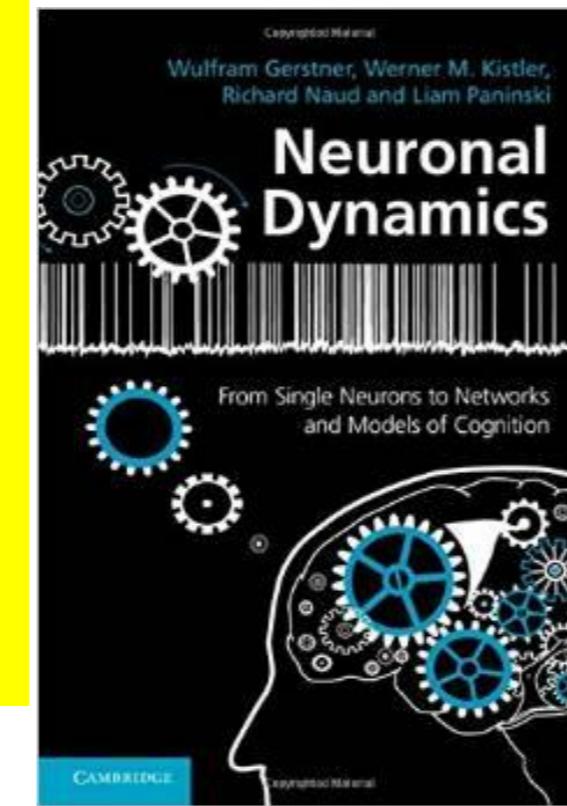


Reading for this Lecture: NEURONAL DYNAMICS Ch. 13.1-13.4

Cambridge Univ. Press



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

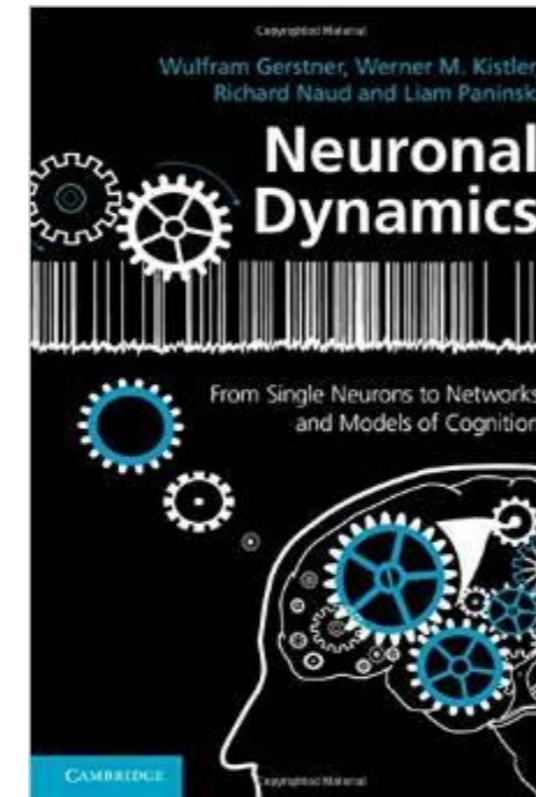
D. Nykamp and D. Tranchina (2000) *A population density approach that facilitates large-scale modeling of neural networks: analysis and application to orientation tuning*. J. Computational Neuroscience 8, pp. 19–50

week 14 –Neural Manifolds and Low-dimensional dynamics

Wulfram Gerstner

EPFL, Lausanne, Switzerland

Cambridge Univ. Press



Lecture 15 of video series

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

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

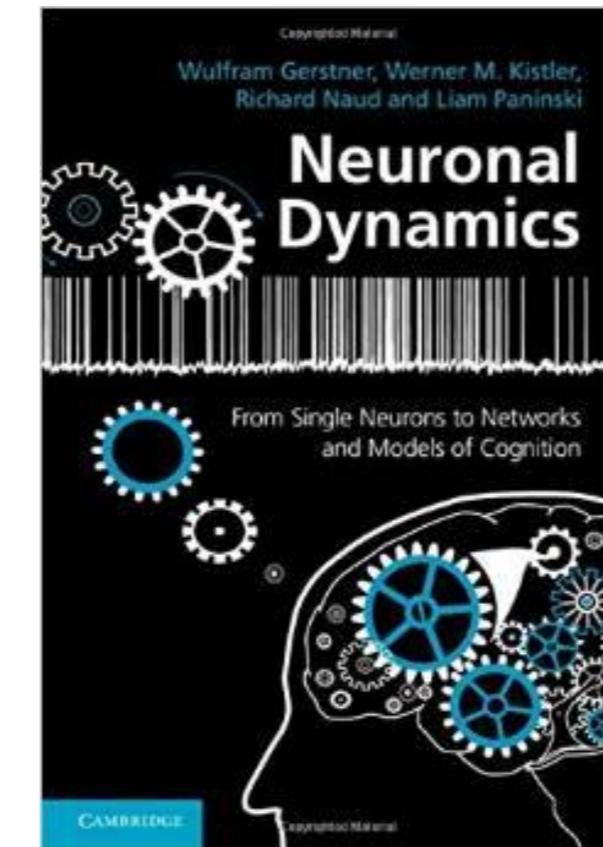
4. Examples of low-dim dynamics

- context-dependent decision making

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://neuronal-dynamics.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.

LEARNING OUTCOMES

- Solve linear one-dimensional differential equations
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Transversal skills

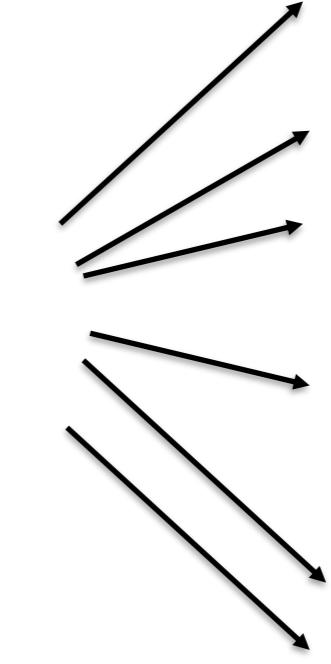
- Plan and carry out activities in a way which makes optimal use of available time and other resources.
- Collect data.
- Write a scientific or technical report.



- Poisson process
- renewal process
- Ornstein-Uhlenbeck process
- escape noise
- membrane pot. density
- Focker-Planck eq.

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
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- Describe neuronal phenomena



- averaging
- coupled networks
- Focker-Planck eq.
- low-rank networks
- overlaps
- macroscopic network dynamics
- competitive dynamics

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.

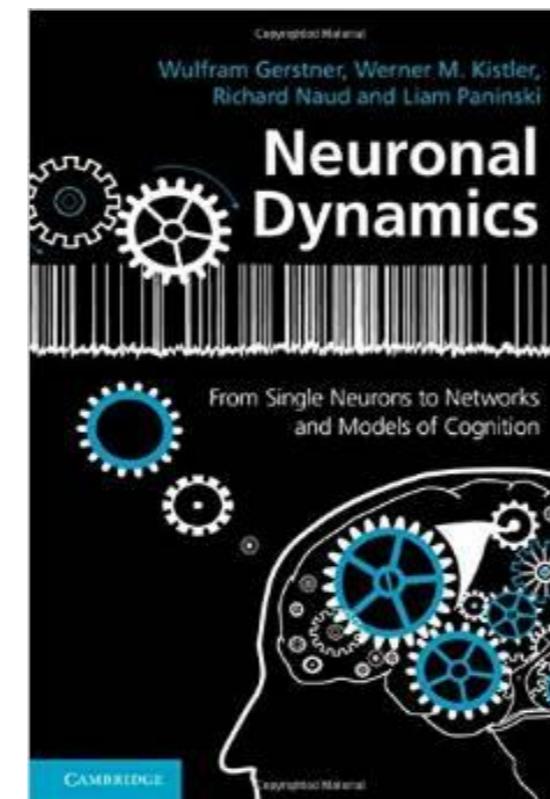
Neural Manifolds and Low-dimensional dynamics:

What are Neural Manifolds?

Wulfram Gerstner

EPFL, Lausanne, Switzerland

Cambridge Univ. Press



1. What are Neural Manifolds?

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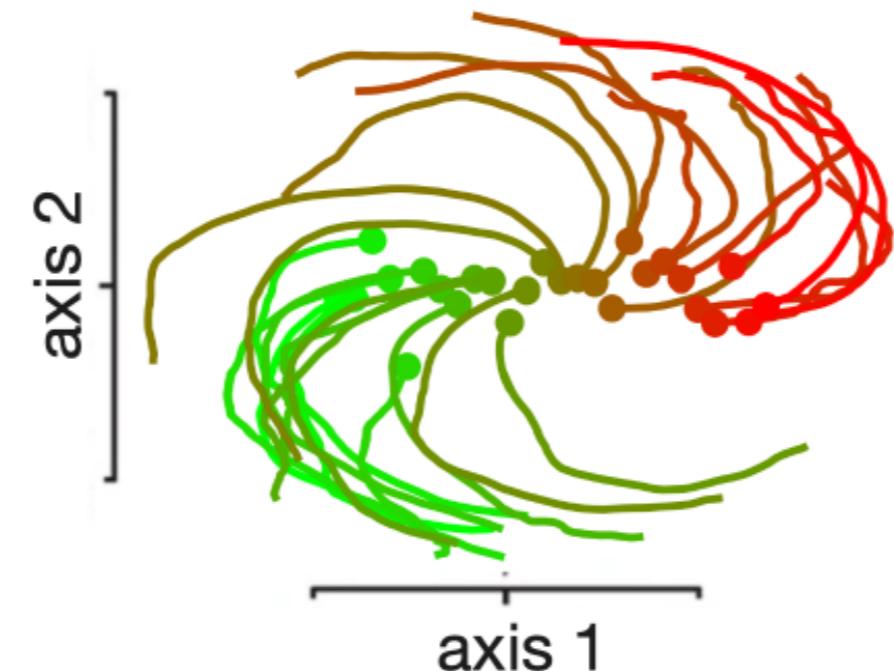
- context-dependent decision making

Introduction: low-dimensional dynamics

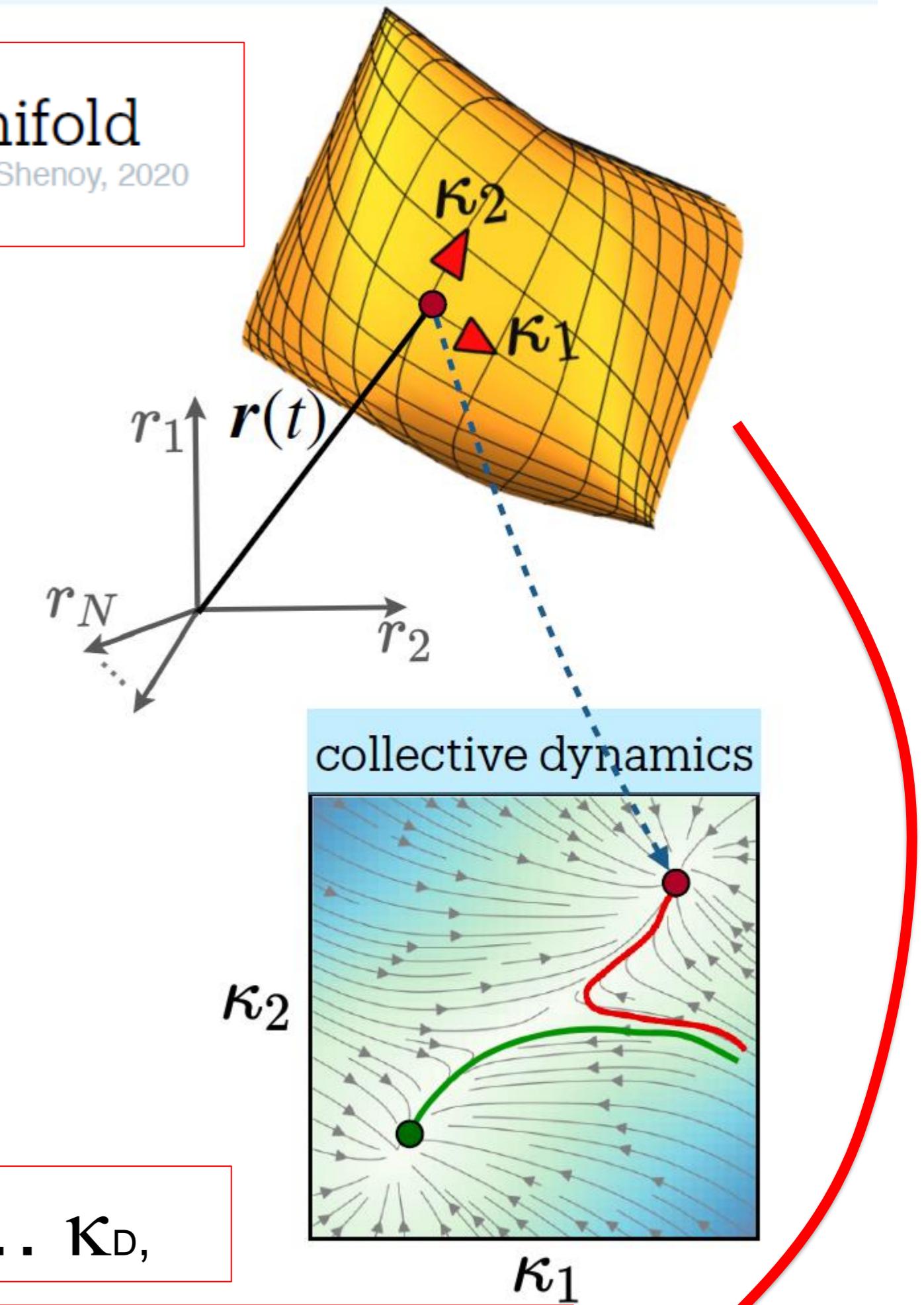
computations are described by **collective dynamics** in the manifold

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!

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

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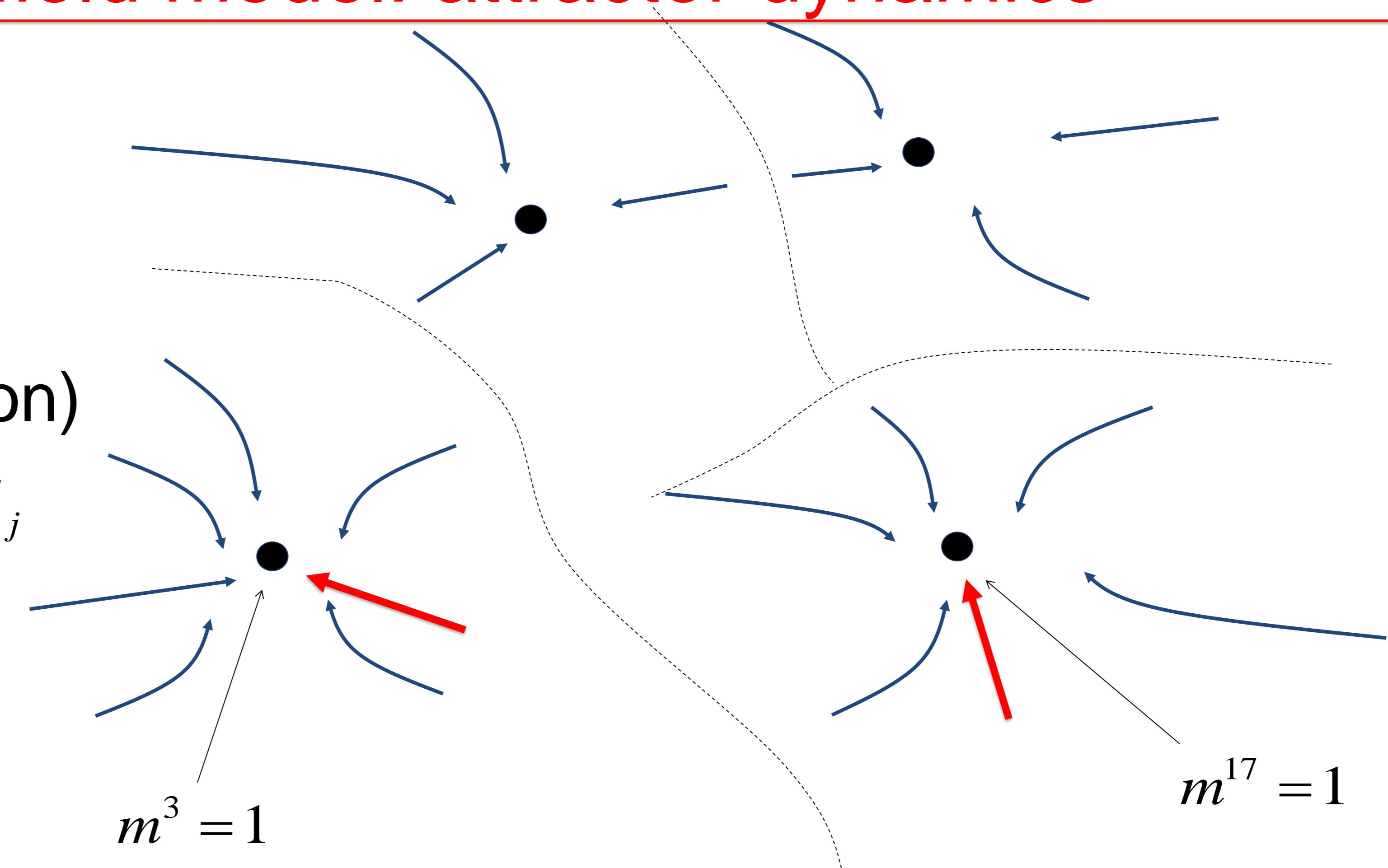
4. Examples of low-dim dynamics

- 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

rate (response to a stimulus)

cell 7

cell 5

0

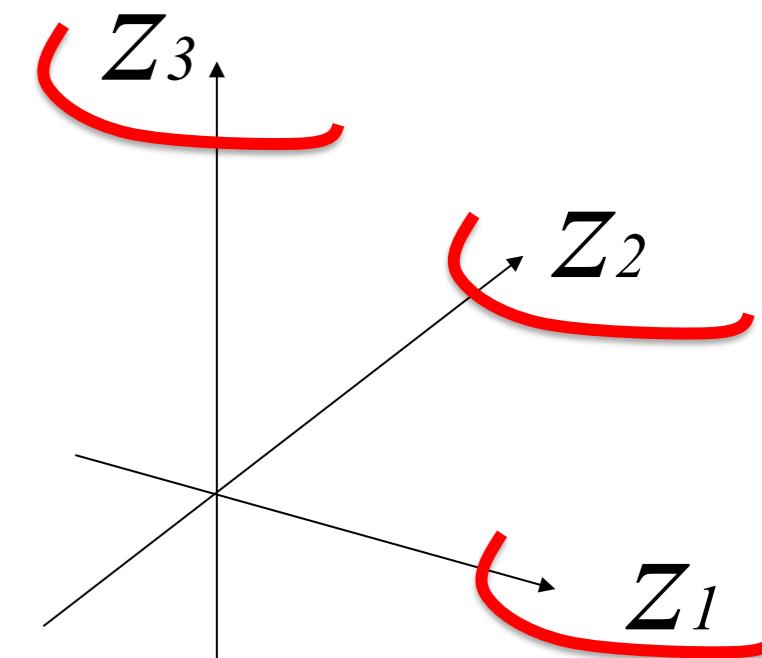
a stimulus that maximally excites cell 7

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

functional similarity = neighborhood in abstract space

abstract axis: - a feature of receptive field

z



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?

Two different perspectives

D. Barack and J. Krakauer, 2021

C. Langdon and T. Engel, 2023

- **low dimensional dynamics**

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

→ Hopfield model

- **neurons and functional similarity**

(functional similarity reflected in wiring,
wiring causes dynamics)

→ continuum model

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

week 14 –Neural Manifolds and Low-dimensional dynamics

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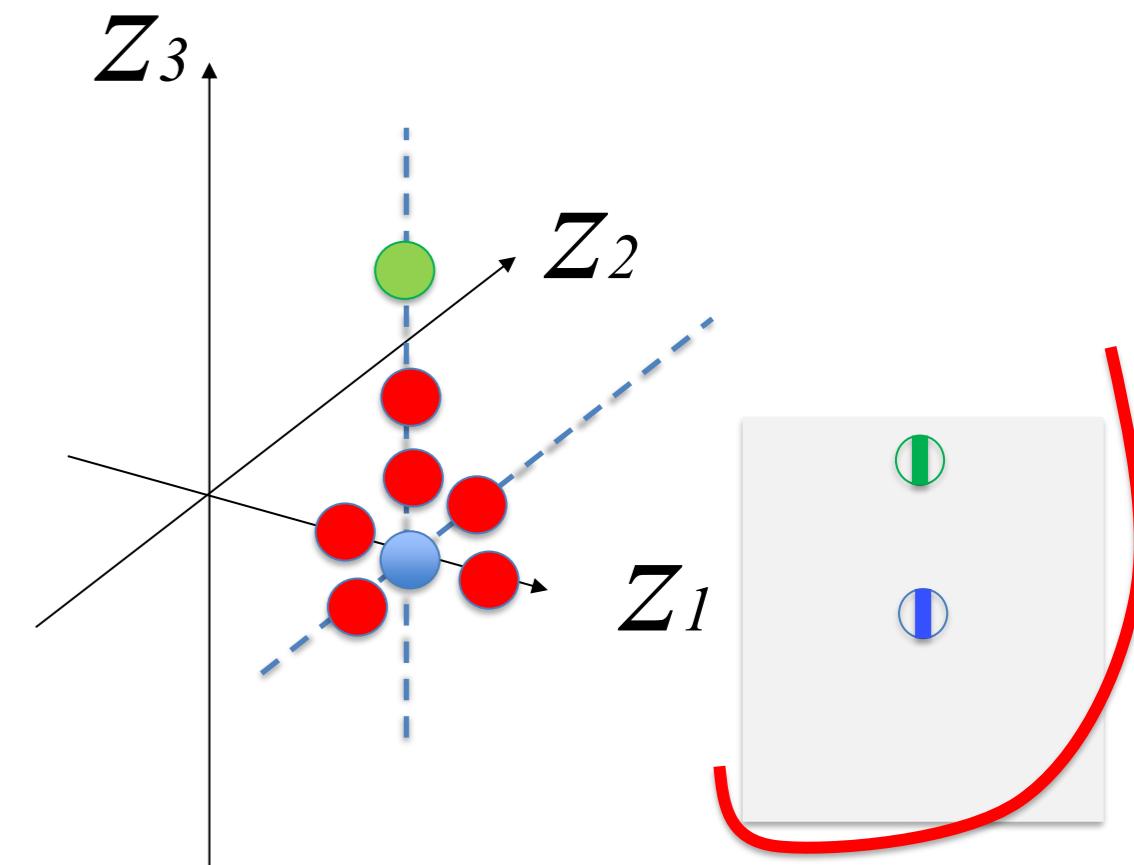
Three assumptions

Assumption 1: neurons are functionally characterized by features

functional
characterization
of neuron

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:

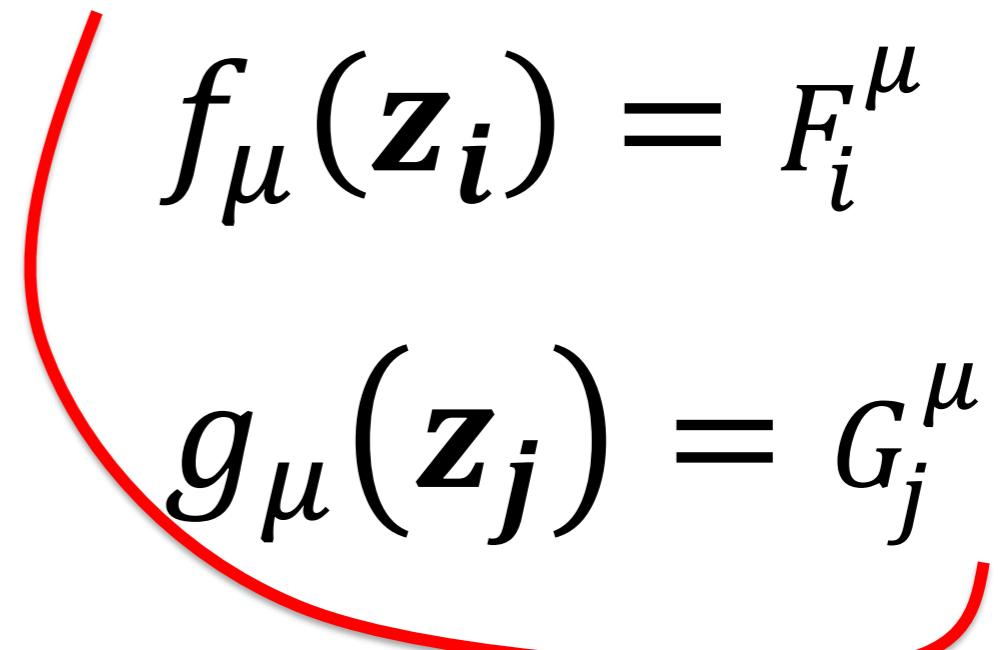
Weight of connection from j to i depends on the positions \mathbf{z}_i , \mathbf{z}_j :

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

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:

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

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

generalized field equation (large number of neurons)

with neuron i at position z_i

Field equation and low-dimensional dynamics

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

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

D 'basis functions'

Idea: write

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

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

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

$\phi(h(\mathbf{z}, t))$

→ 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

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

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_μ are orthonormal:

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

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

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

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

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

1.2 We are now interested in the fixed points of Eq.(3). Find a closed-form expression solved by the coefficients κ_μ in the steady-state.

Hint: use Eq.(5) to replace the field with the variables κ_μ .

1.3 Starting from the field dynamics of Eq.(3), derive a closed-form expression for the dynamics of the coefficients κ_μ .

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_μ , *plus* an additional term:

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

where $\int_V \Delta h(\mathbf{z})f_\mu(\mathbf{z})\rho(\mathbf{z})d\mathbf{z} = 0$, for all μ . What are the dynamics of Δh ? 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):

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

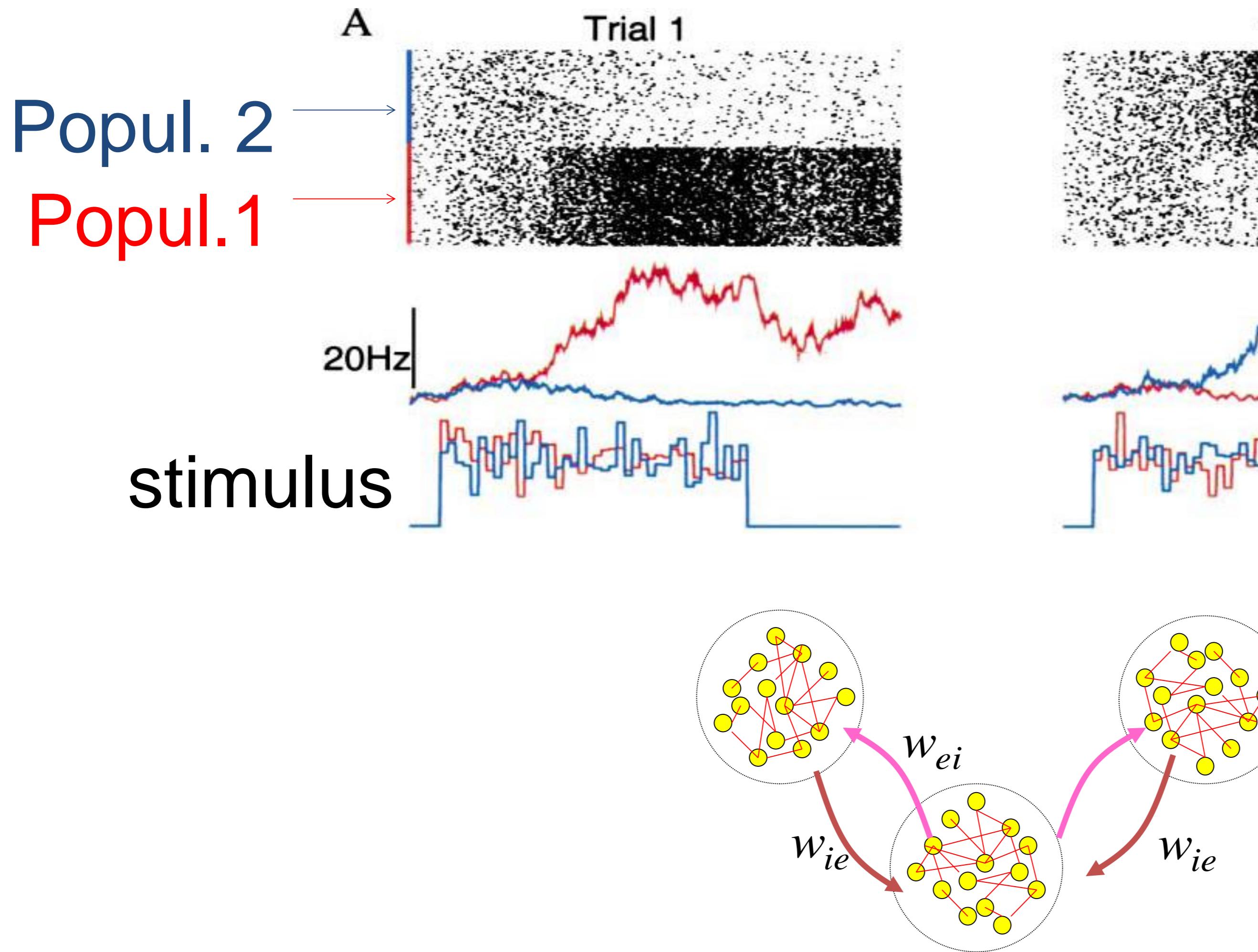
What are the dynamics of the coefficients κ_μ now? Can the external input affect the fixed points?

Examples of low-dimensional dynamics:

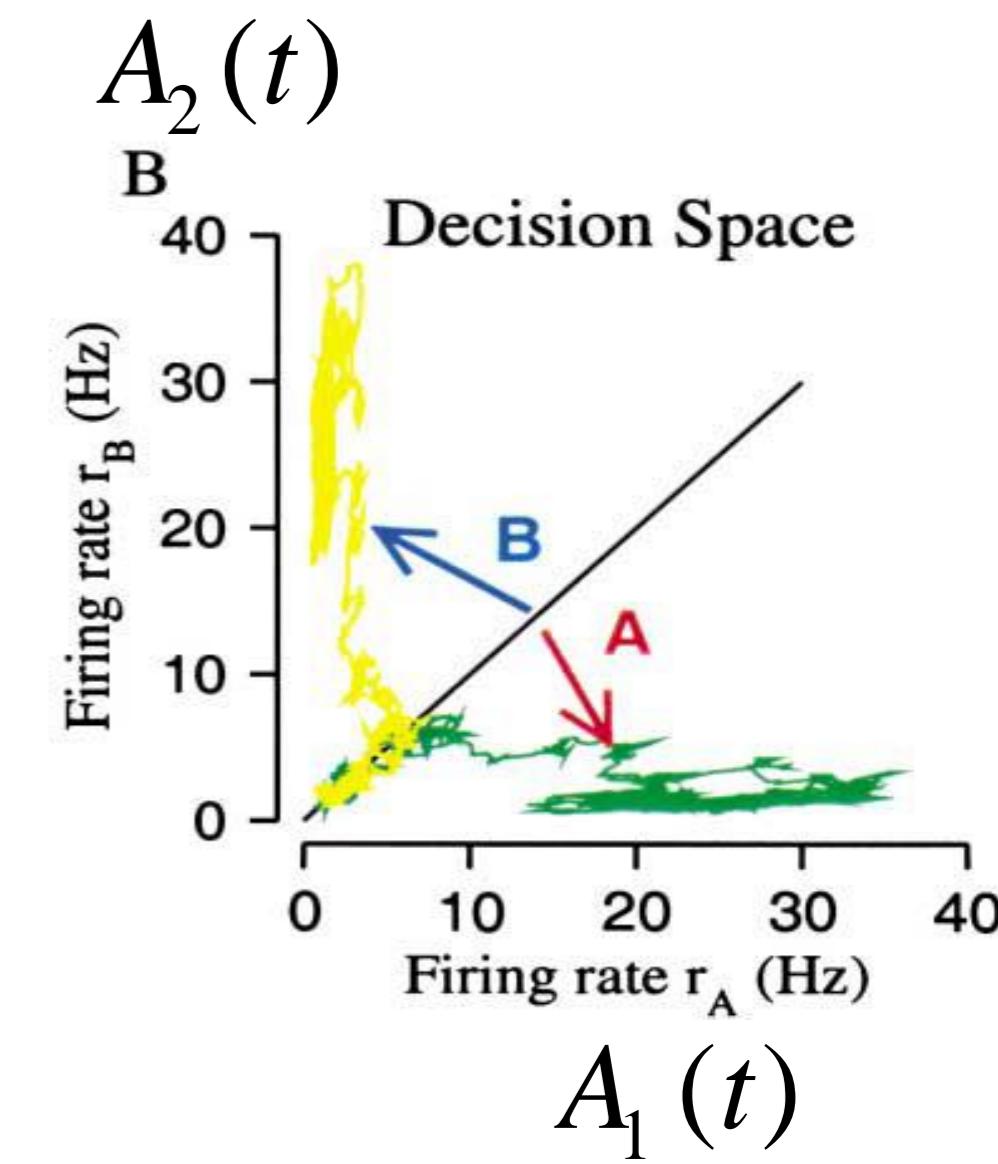
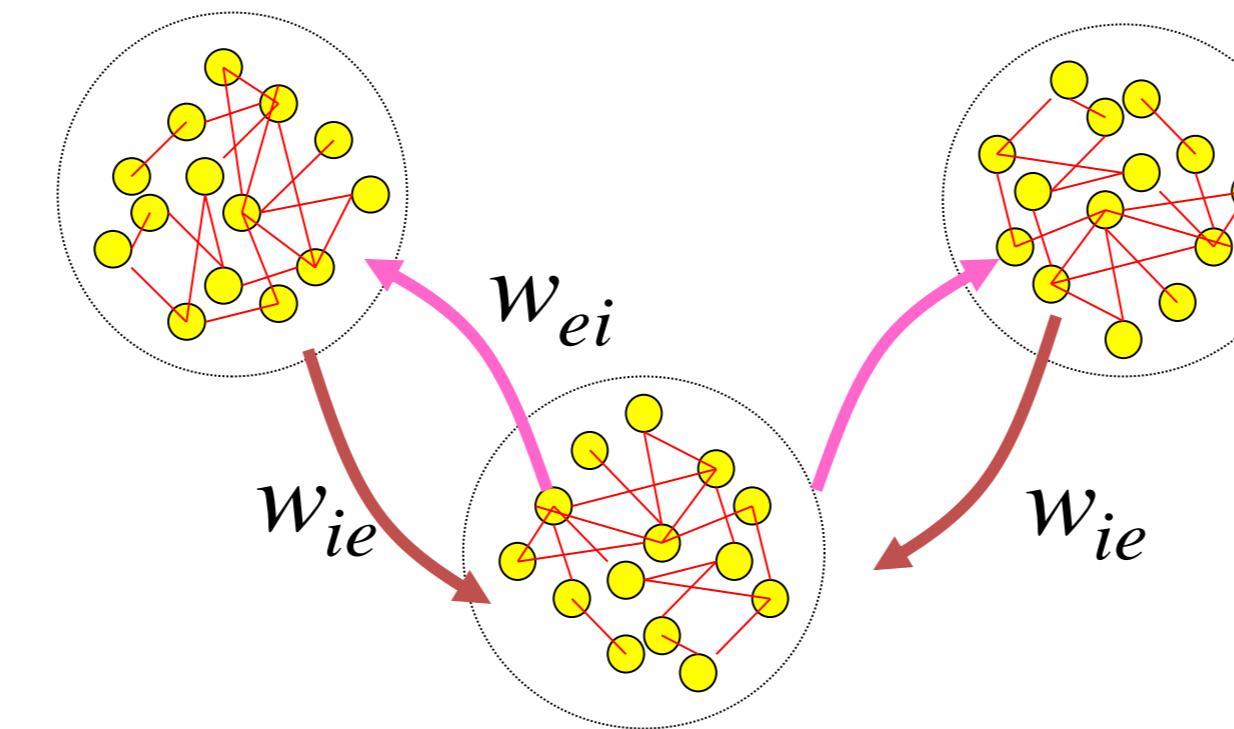
- Visual Cortex Model
- Ring model (with sinusoidal coupling)
- Hopfield model
- **Decision making**

Review: Decisions in populations of neurons: simulation

Simulation of 3 populations of spiking neurons, unbiased strong input



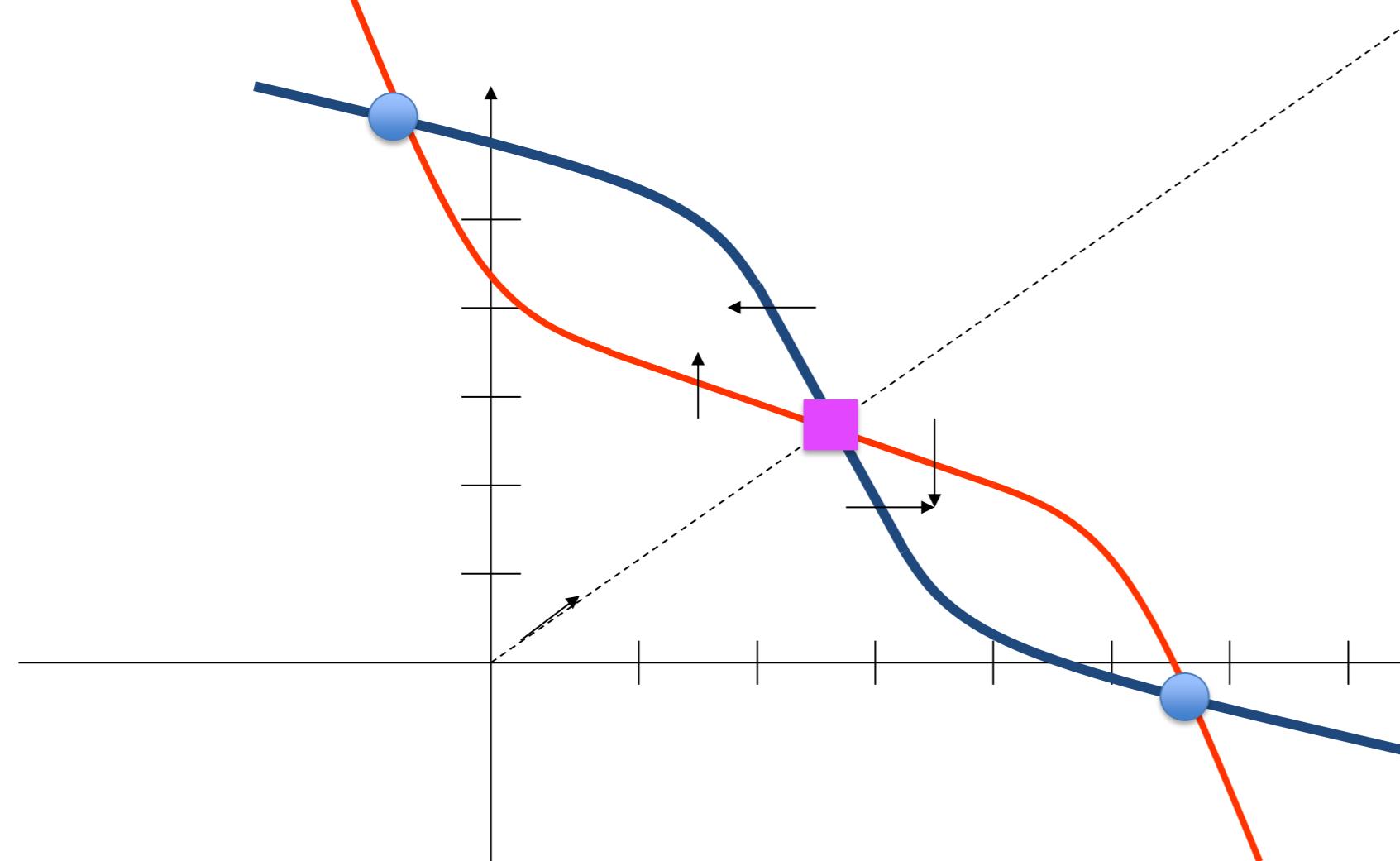
X.J. Wang, 2002
NEURON



Review. Theory of decision dynamics: unbiased strong

Phase plane

$$\frac{d}{dt} h_1 = 0$$



$$h_1^{ext} = 0.8 = h_2^{ext}$$

symmetric solution exists, but
→ saddle point ■
→ decision must be taken
2 asymmetric stable solutions

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

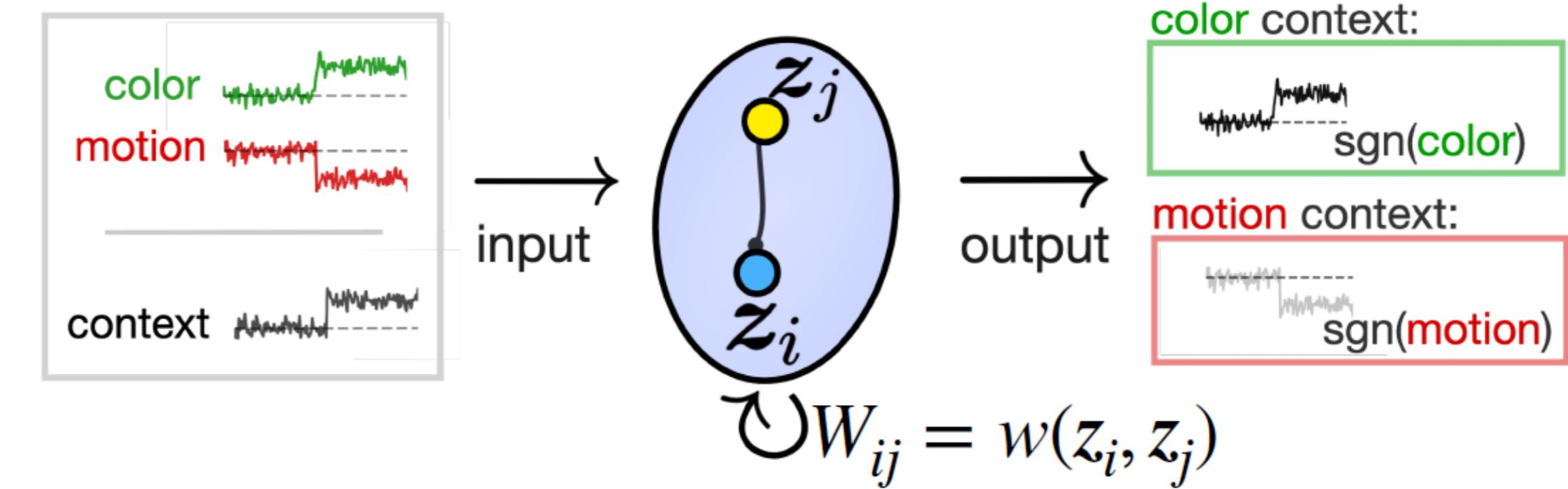
Example : low-dimensional dynamics in decision making

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



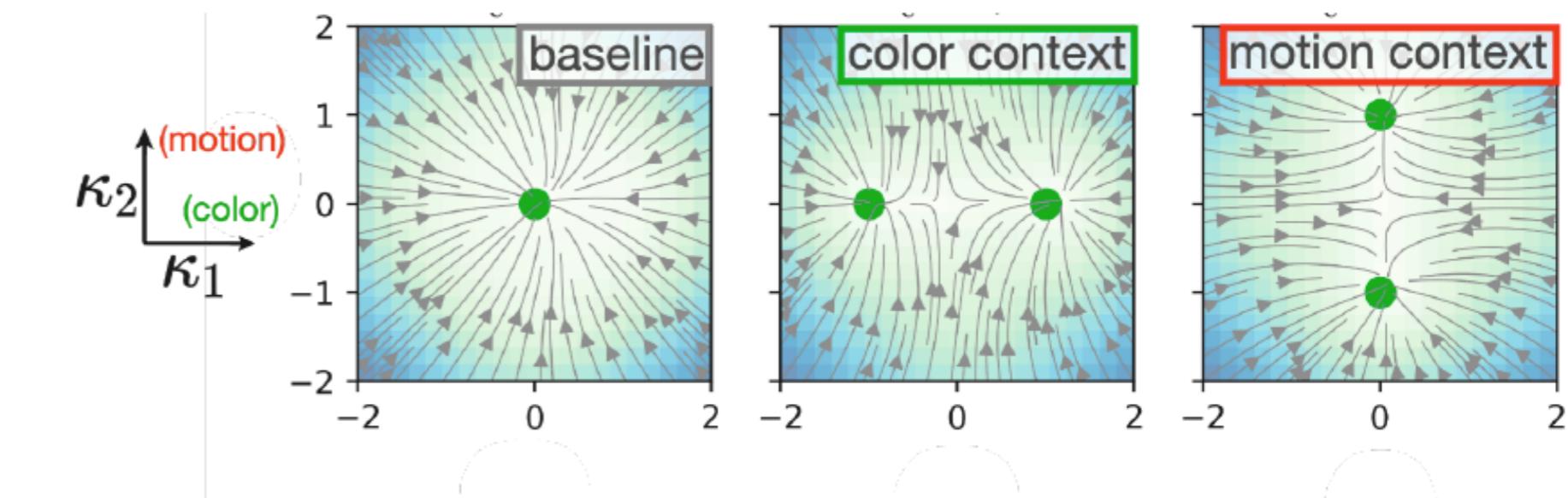
Task: Mante, ... Newsome 2014

... solved by 2-dimensional collective dynamics.

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

Model of 2-dim dynamics

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

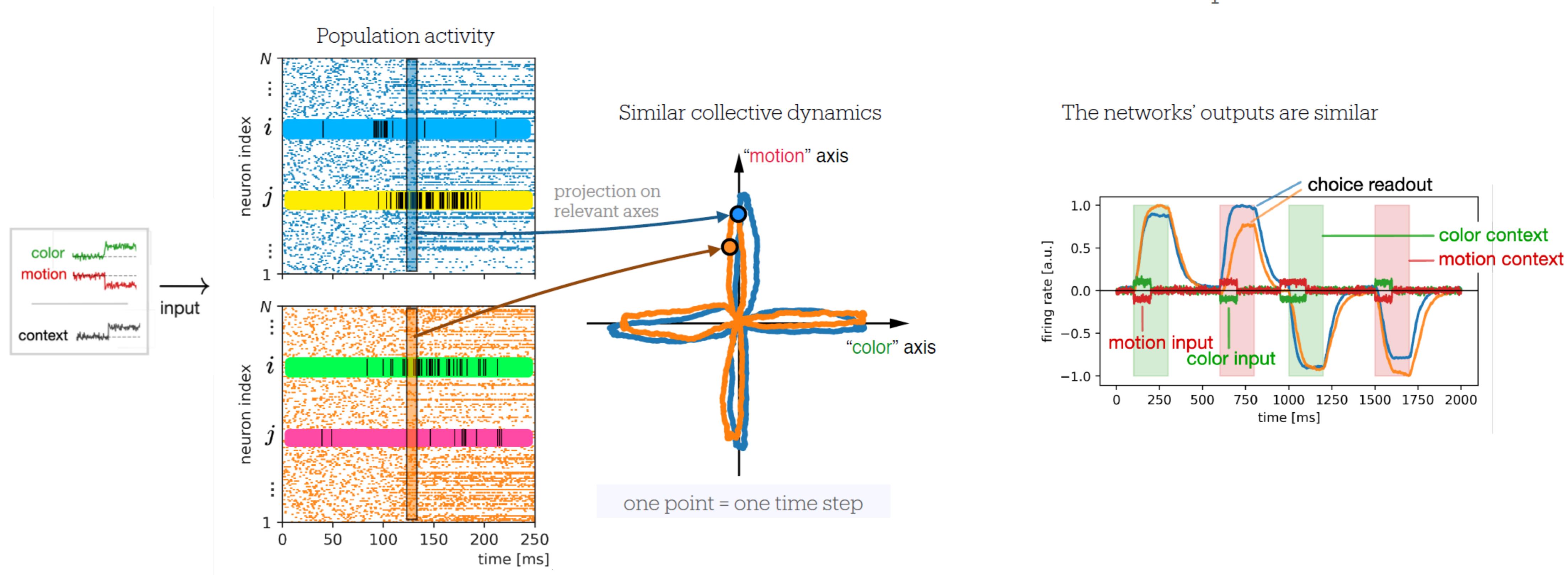


Idea: - design fixed-point structure in D-dim. decision space
- embedded in N-dimensional neuronal space

Example: low-dimensional dynamics in decision making

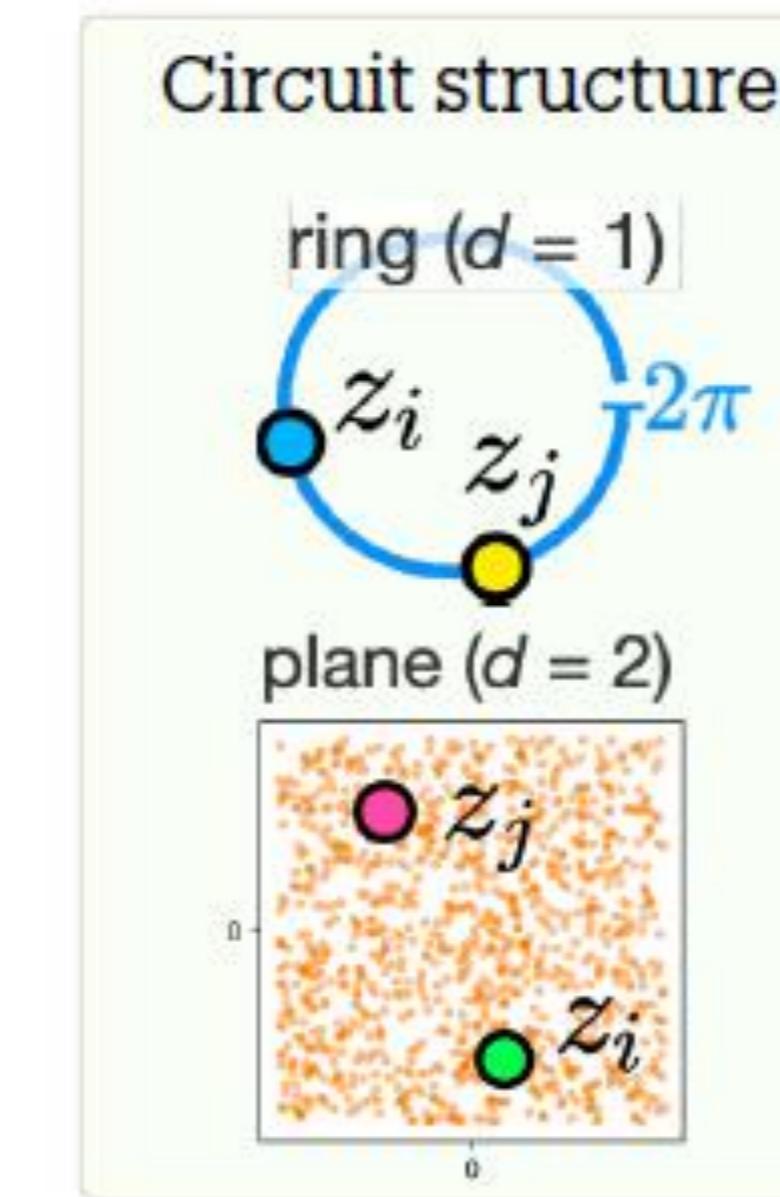
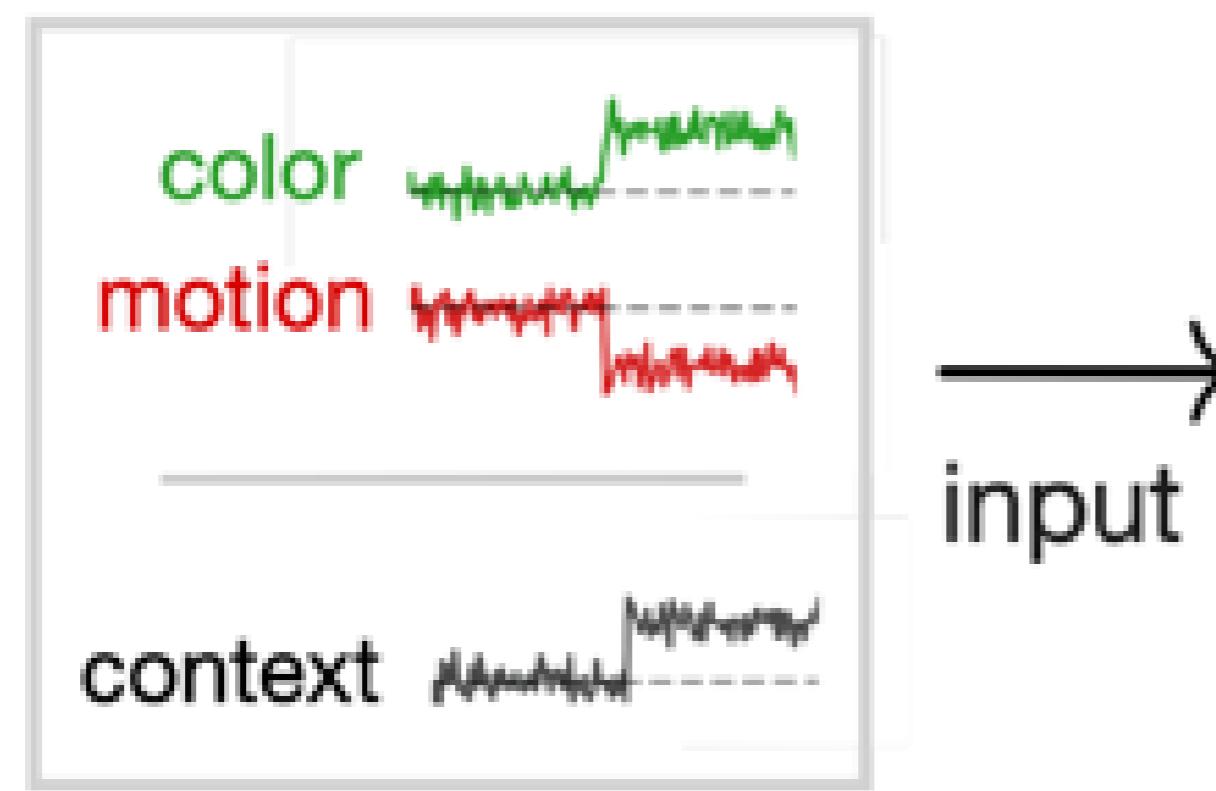
Two different spiking neuron models, similar dynamics

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

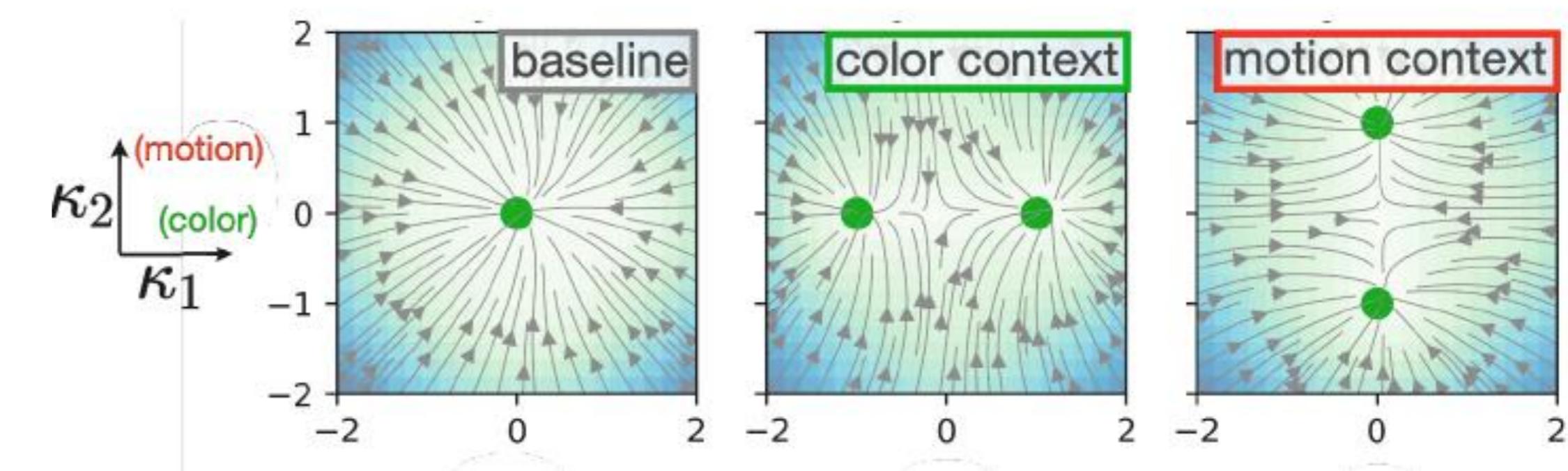
uniform in 2d, square

Flow in 2 dimensions:

1st axis: color

2nd 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 $(\kappa_1(t), \kappa_2(t) | \text{context})$

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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)

Shenoy, K.V., Sahani, M., Churchland, M.M.: Cortical control of arm movements: A dynamical systems perspective. *Annual Review of Neuroscience* 36(1), 337–359 (2013) <https://doi.org/10.1146/annurev-neuro-062111-150509> . PMID: 23725001

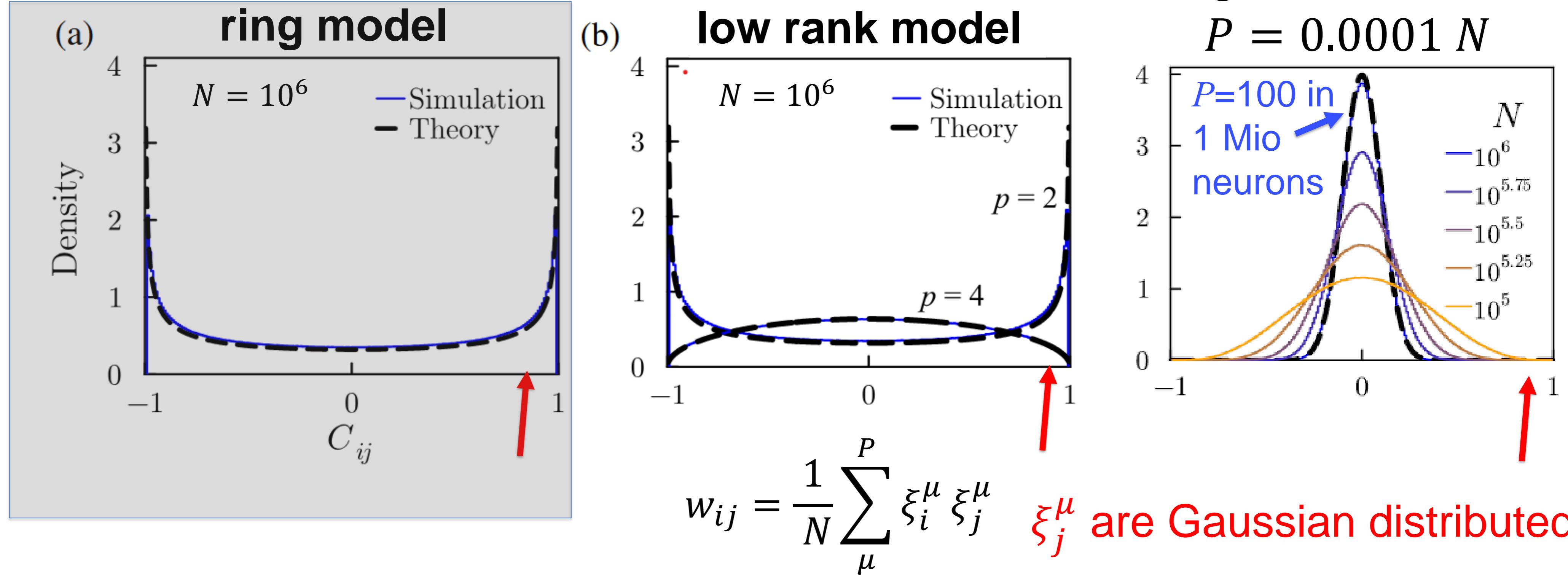
Gallego, J.A., Perich, M.G., Miller, L.E., Solla, S.A.: Neural manifolds for the control of movement. *Neuron* 94(5), 978–984 (2017)

THE END

Neural Manifolds and Low-dimensional dynamics:

- 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
- 5. From Spikes to Rates**

Correlations between two neurons: low-rank weight matrix



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

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

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

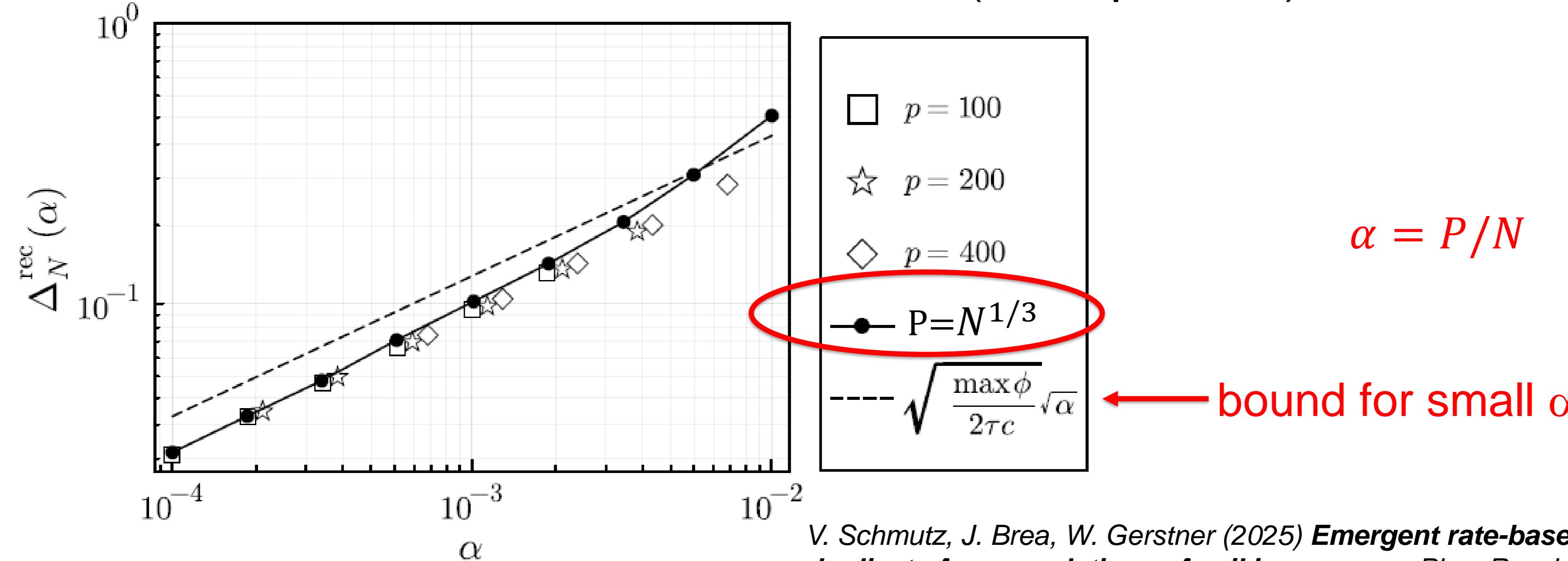
- [] There are at most P different ‘types of neuron’ so that if $N > P$ neurons can become correlated.
- [] There are at most P^3 different ‘types of neuron’ so that if $N > P^3$ neurons can become correlated.
- [] There are at most 2^P different ‘types of neuron’ so that if $N > 2^P$ neurons can become 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 $\Delta_N^{\text{rec}} \propto \sqrt{\alpha}$ finite!

$\text{SNN} \neq \text{RNN}$

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

$\text{SNN} \rightarrow \text{RNN}$

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), 609–62329 (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