Computational Neuroscience: Neuronal Dynamics of Cognition

ÉCOLE POLYTECHNIQUE
FÉDÉRALE DE LAUSANNE

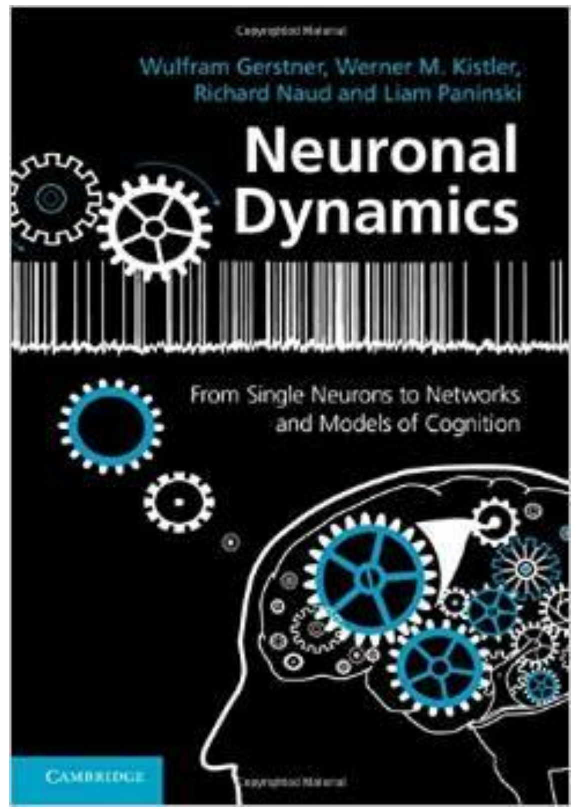
Neuronal Populations

Wulfram Gerstner

EPFL, Lausanne, Switzerland

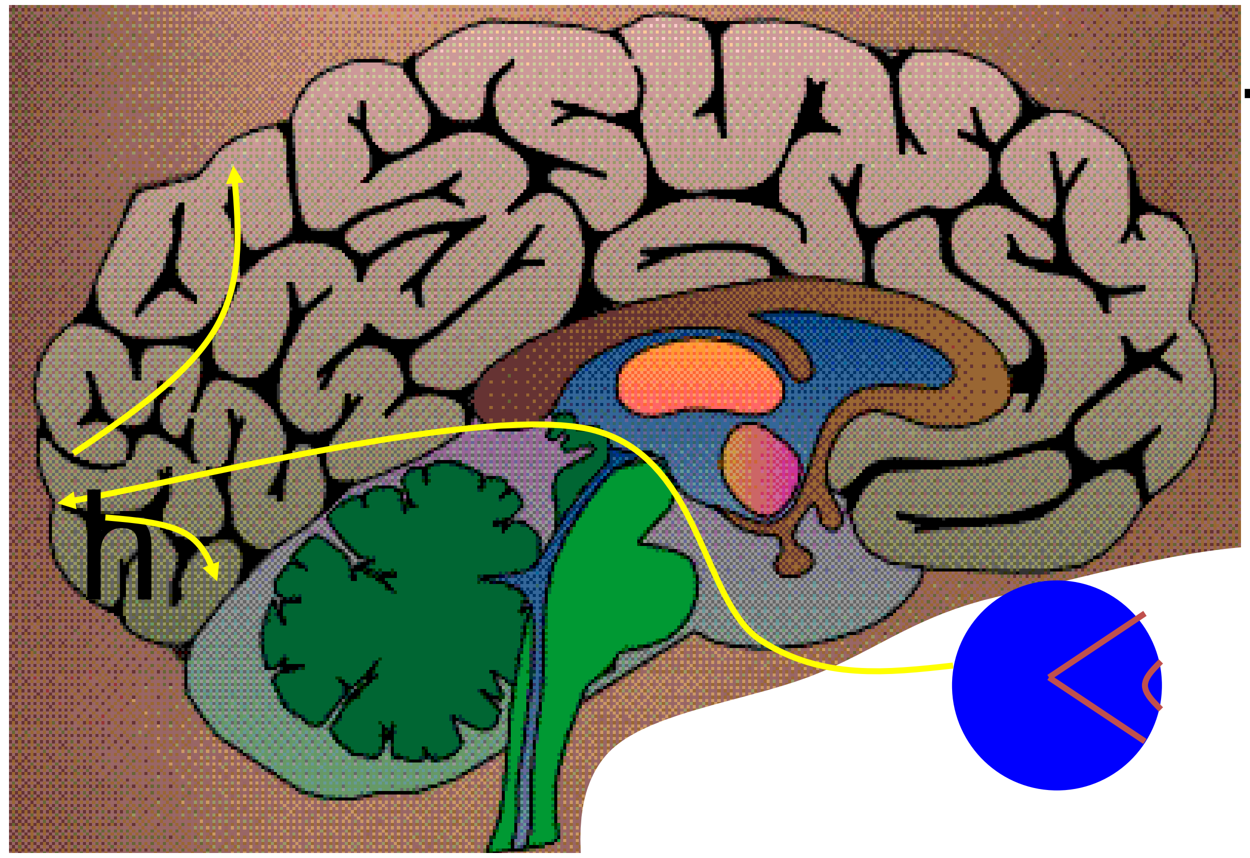
Reading:
NEURONAL DYNAMICS
- Ch. 12.1 – 12.4.3
(except Section 12.3.7)

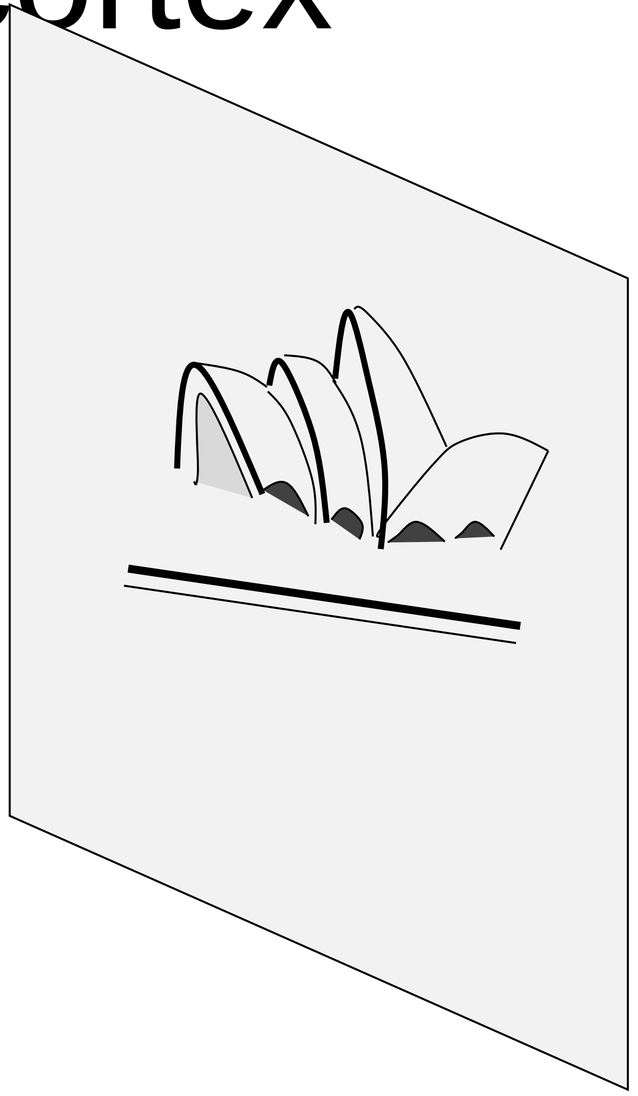
Cambridge Univ. Press



1. **Population activity**
   - definition and aims
2. **Cortical Populations**
   - columns and receptive fields
3. **Connectivity**
   - cortical connectivity
   - model connectivity schemes
4. **Mean-field argument**
   - input to one neuron
5. **Stationary mean-field**
   - asynchronous state: predict activity
6. **Random Networks**
   - Balanced state

1. review: the brain





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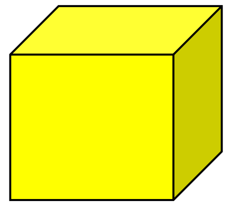
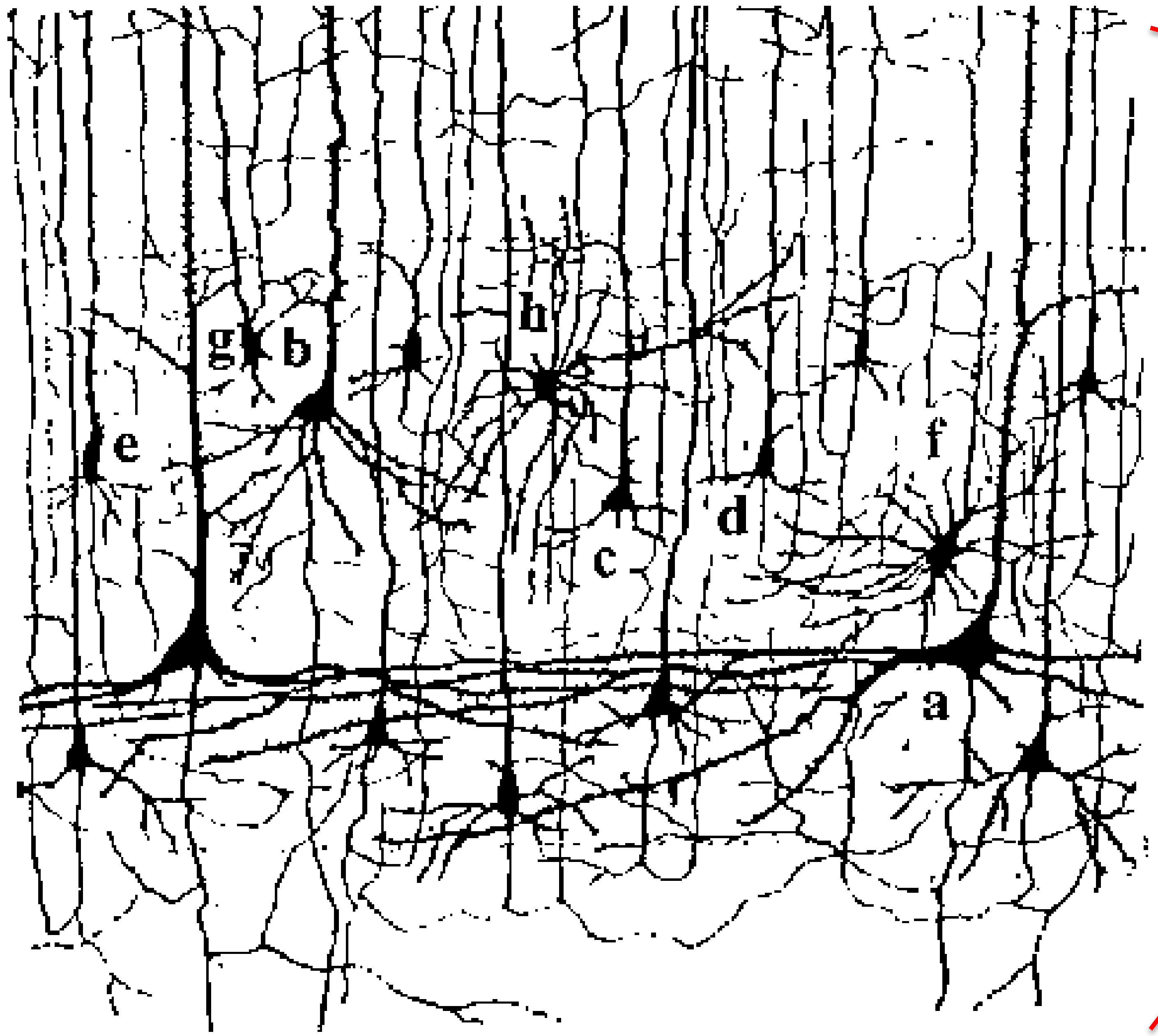
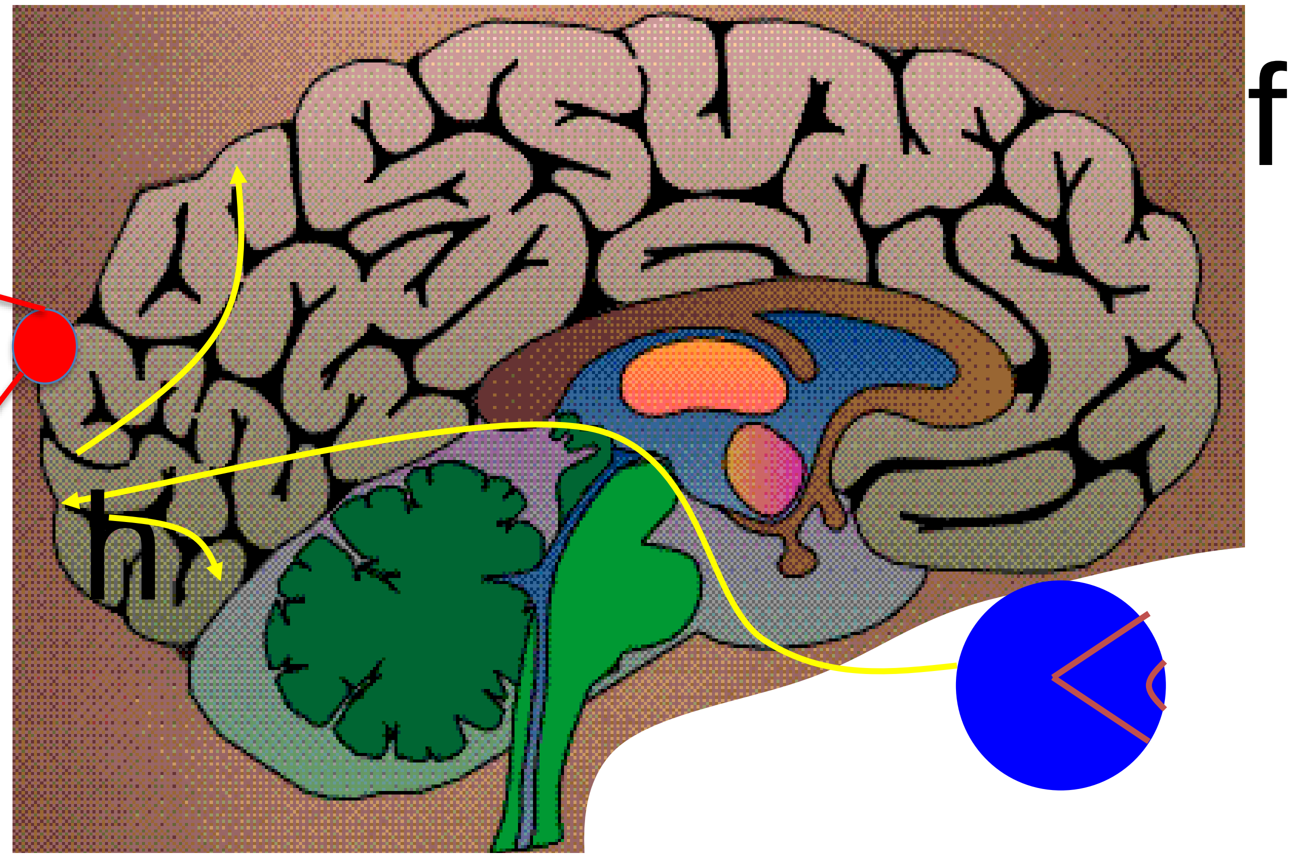


10 000 neurons
3 km of wire



motor
cortex

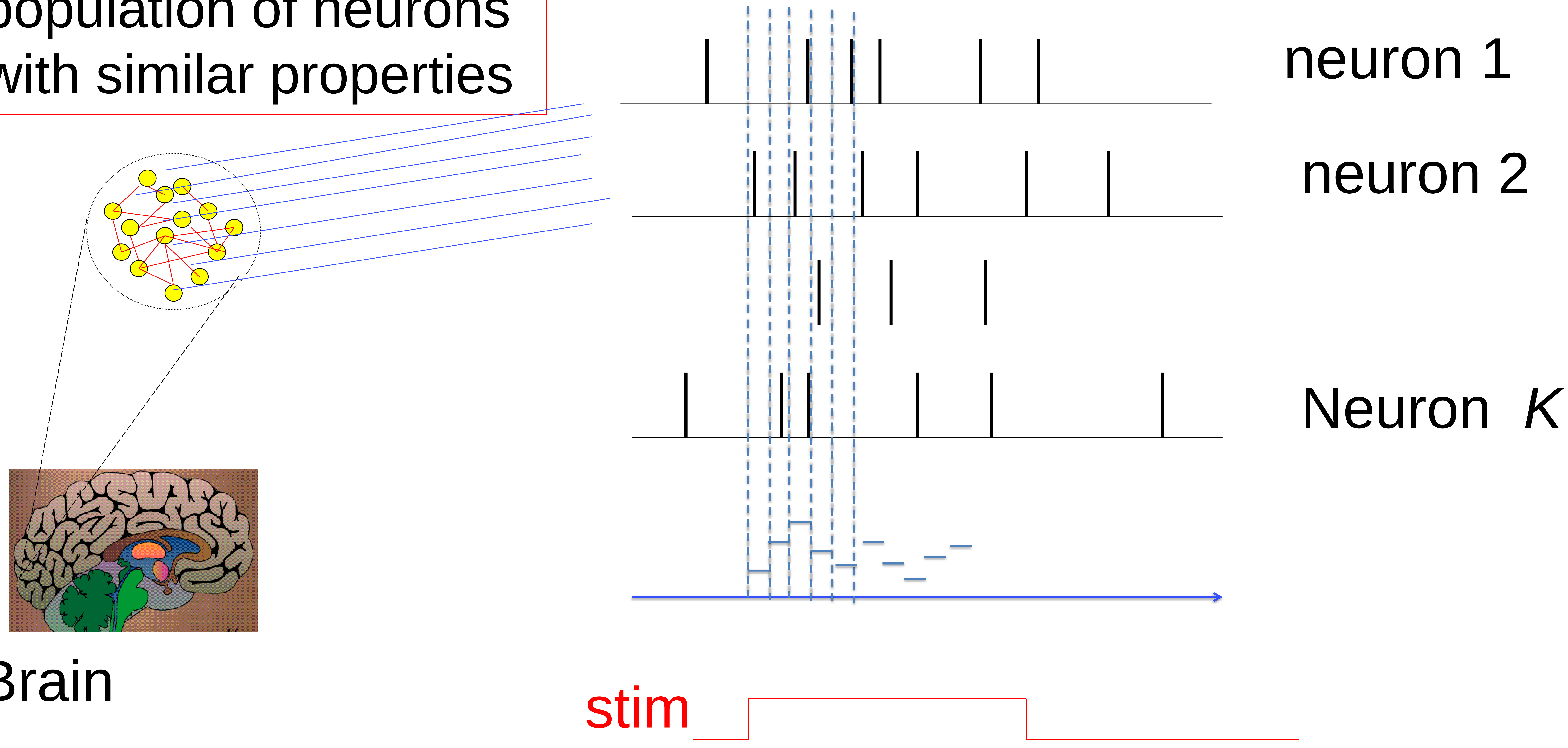


frontal
cortex

to motor
output

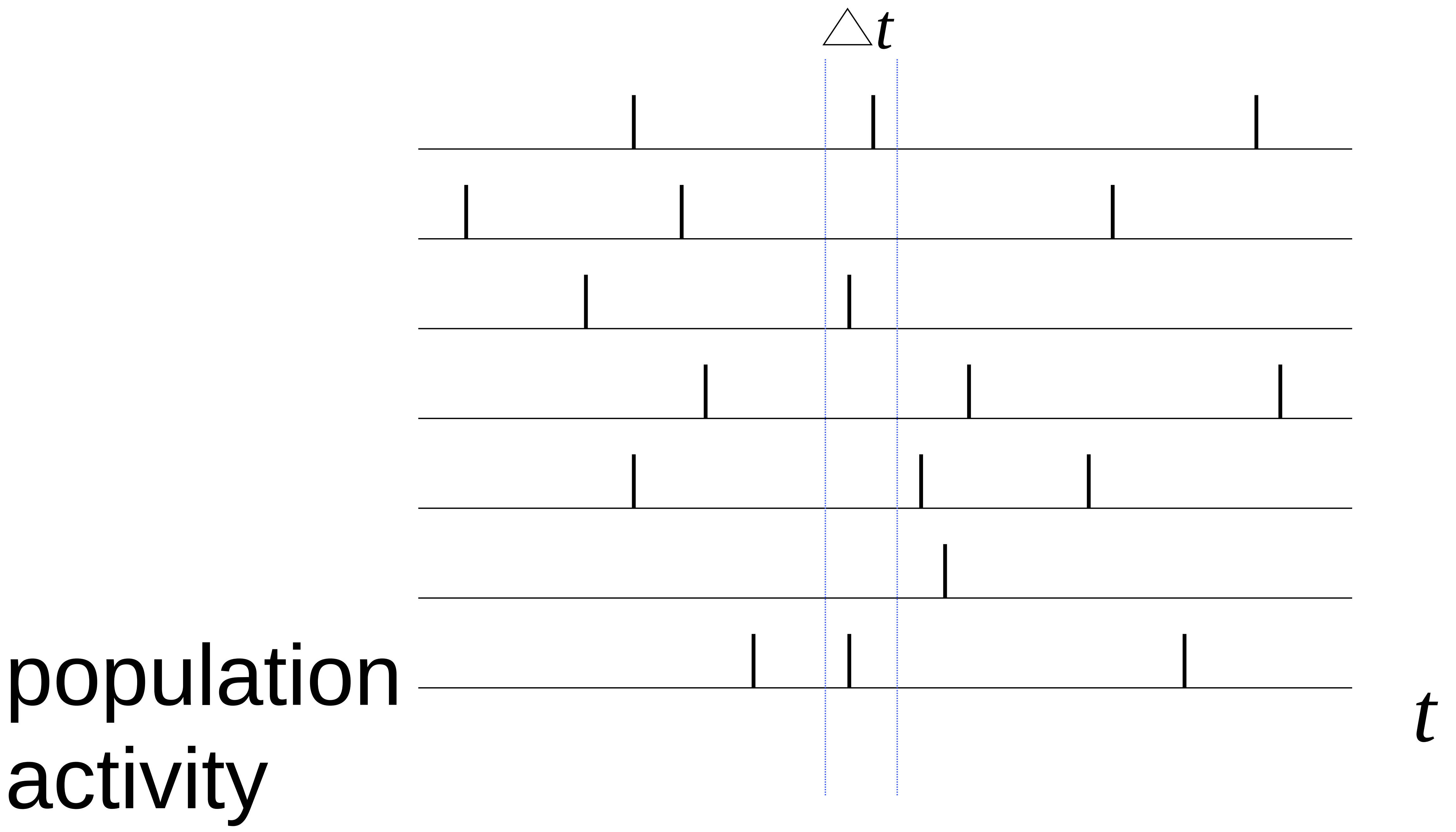
1. Population activity, definition

population of neurons
with similar properties



1. Population activity: definition

population activity - rate defined by population average



units?

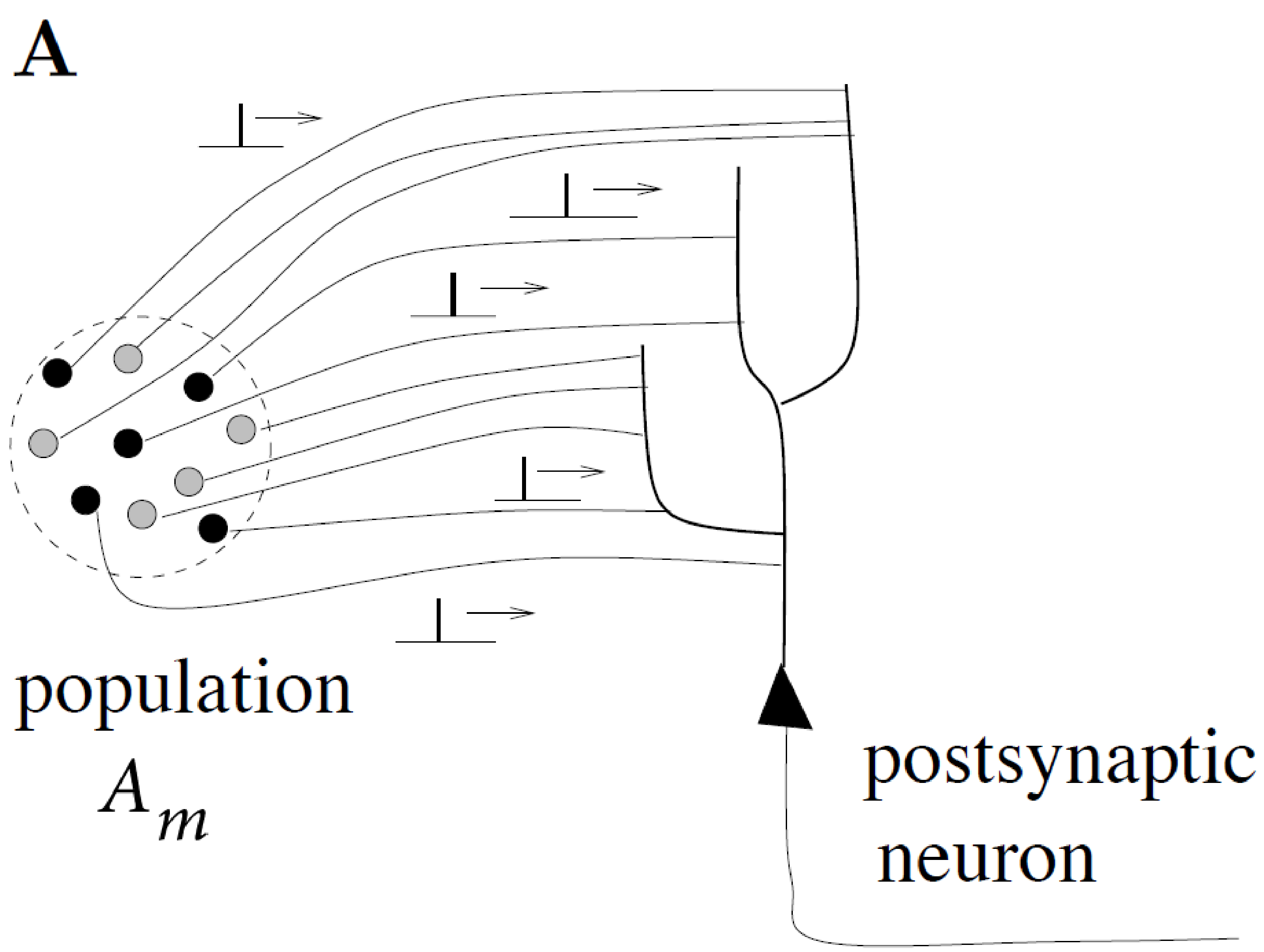
invariances?

$$A(t) =$$

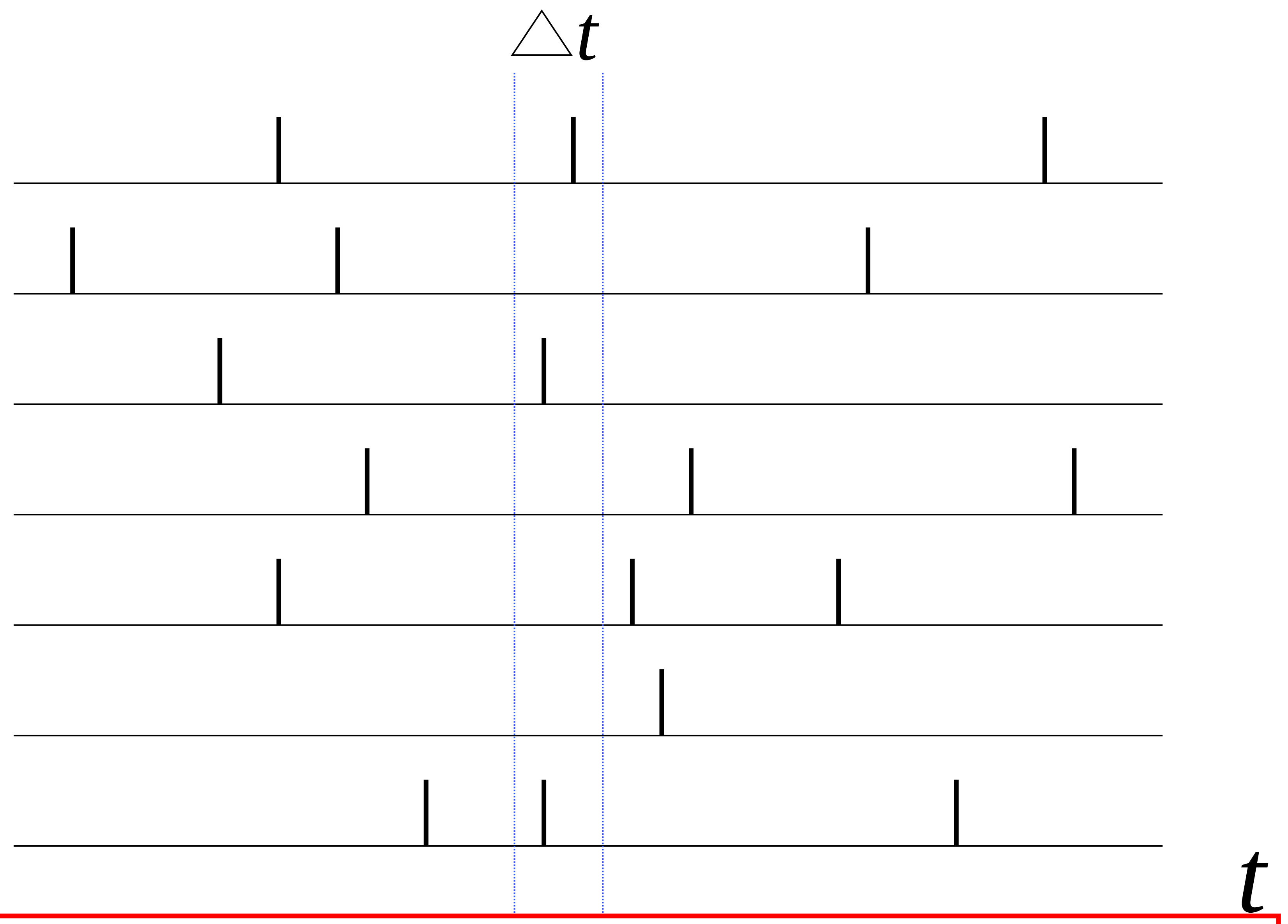
Time scale/averaging?

1. Population activity: definition

population activity - rate defined by population average



‘natural readout’



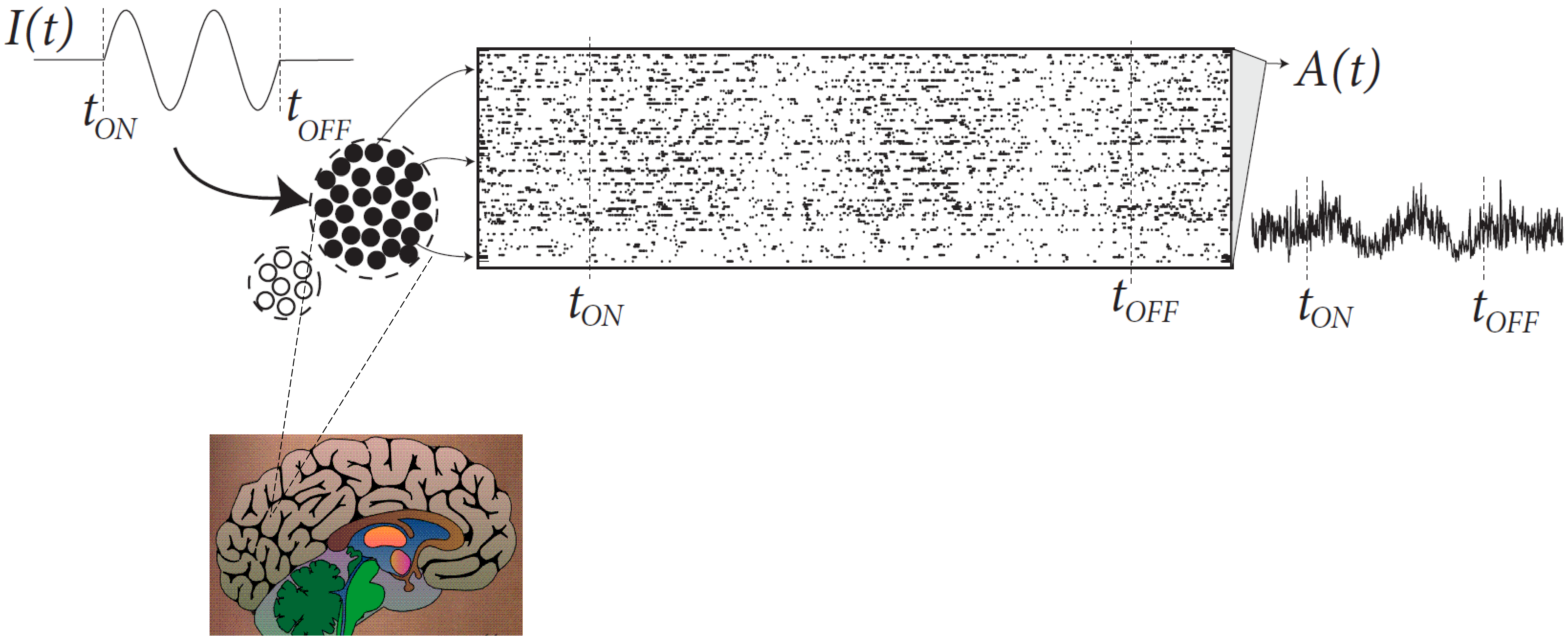
population activity

$$A(t) = \frac{n(t;t+\Delta t)}{N\Delta t}$$

Image: Neuronal Dynamics, Gerstner et al., Cambridge Univ. Press (2014),

1. Population activity: example

population of neurons
with similar properties

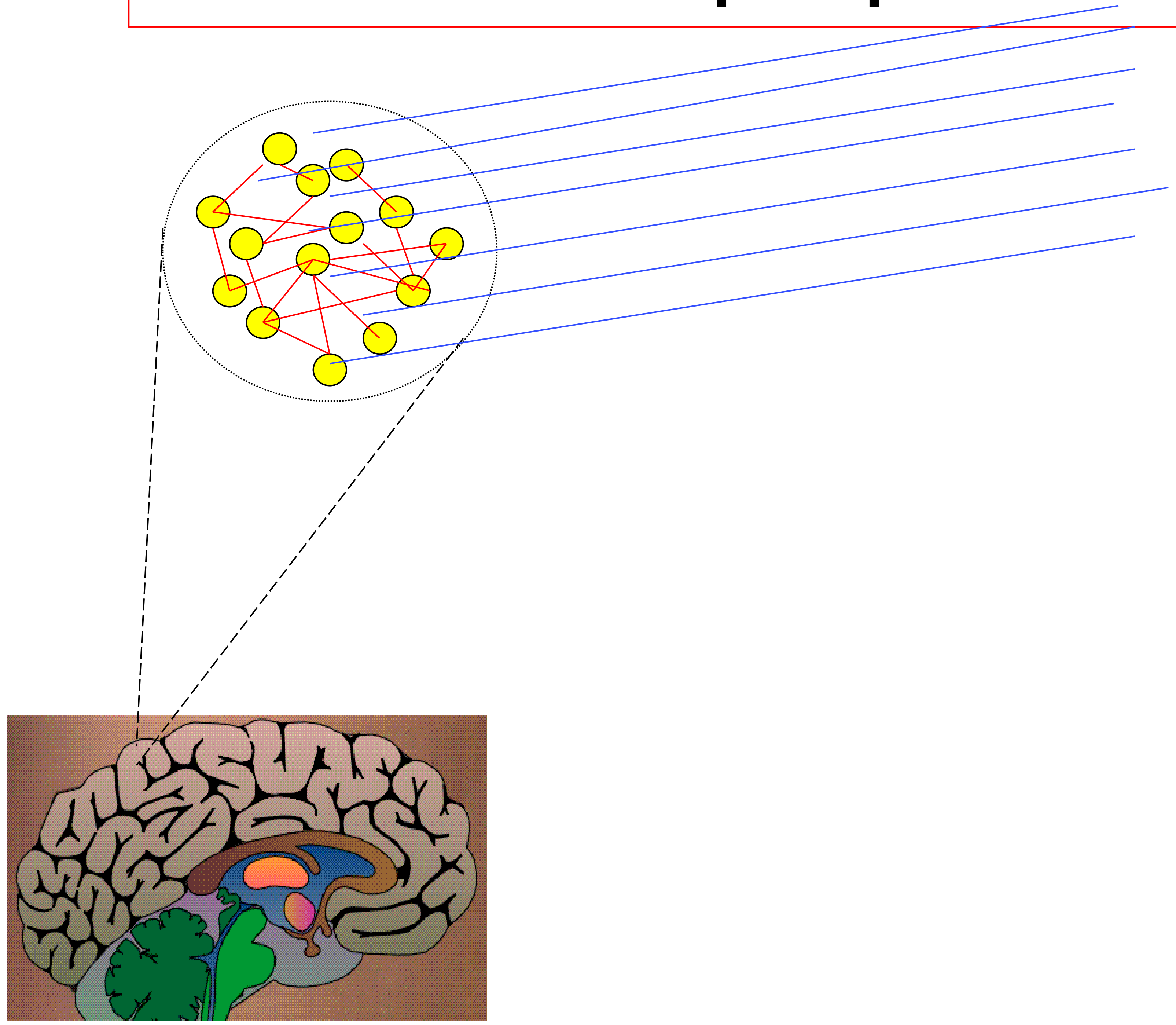


Brain

Image: Neuronal Dynamics,
Gerstner et al.,
Cambridge Univ. Press (2014),

1. Scales of neuronal processes

population of neurons
with similar properties



Brain

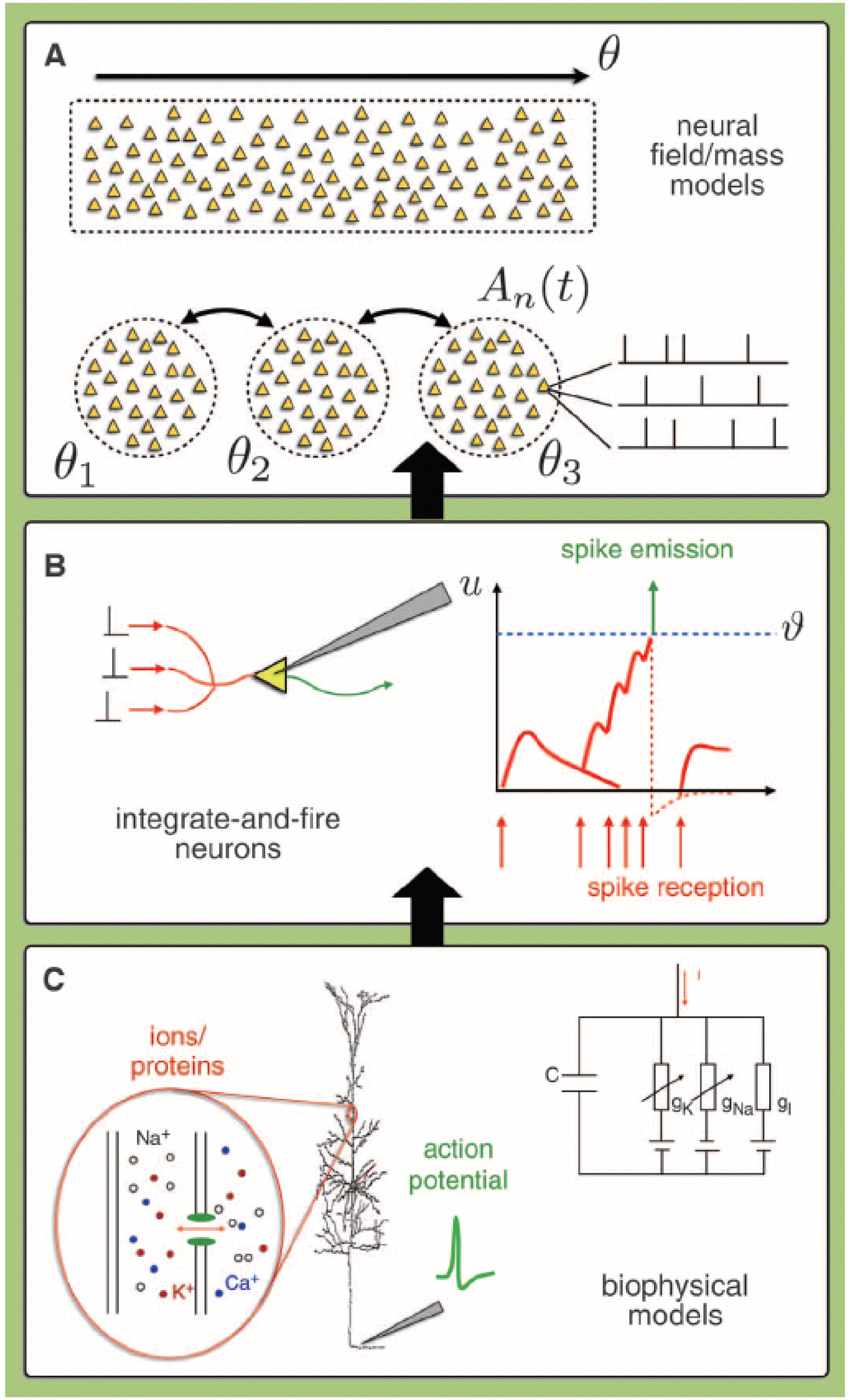


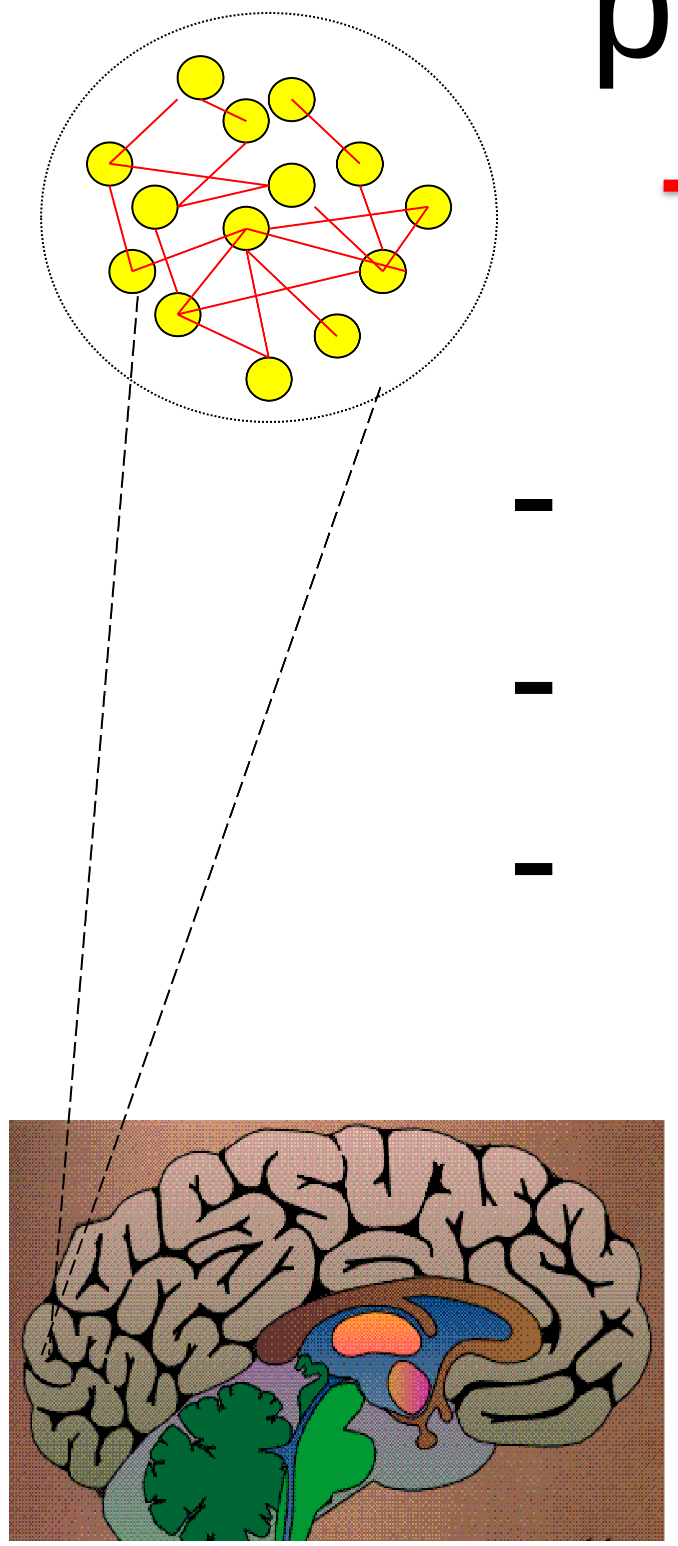
Image: Gerstner et al. Science (2012),

1. Population activity

population of neurons
with similar properties

population activity

$A(t)$



- do populations exist?
- how do they interact?
- can we predict $A(t)$?

Quiz 1, now

The population activity

[ ] Is a firing rate

[ ] Is a fast variable on the time scale of milliseconds

[ ] Is proportional to the number of spikes
counted across a population in a short time window

[ ] Is defined as the number of spikes
counted across a population in a short time window

Additional information: Computational Neuroscience

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EPFL, Lausanne,

Switzerland

Additional links to short MOOC - videos

http://lcn.epfl.ch/~gerstner/NeuronalDynamics-MOOC1.html

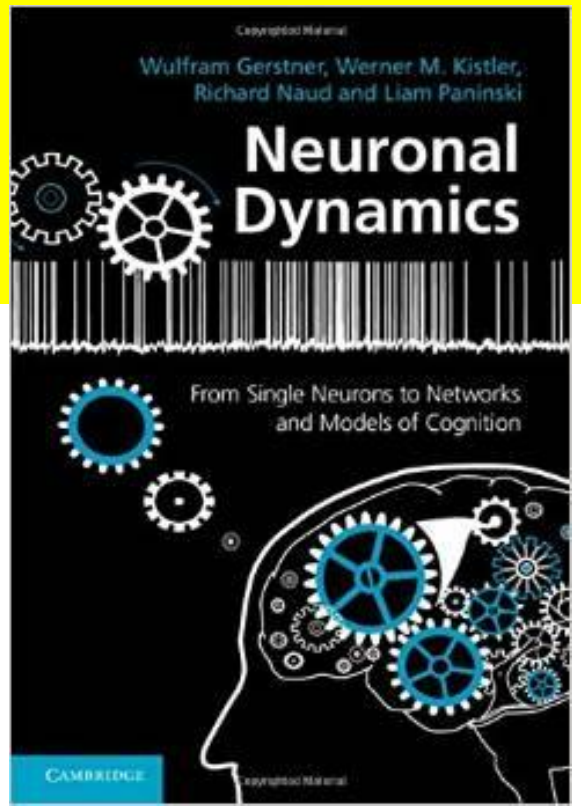
- Dirac delta-function in computational neuroscience

https://www.youtube.com/watch?v=l3hvrx33lZc

- Integrate-and-fire model, a first introduction

https://www.youtube.com/watch?v=gU9UzFeg8f4

Background Reading:
NEURONAL DYNAMICS
- Ch. 1.3.
- Ch. 12.1



Cambridge Univ. Press

Textbook also online:

http://neuronaldynamics.epfl.ch/

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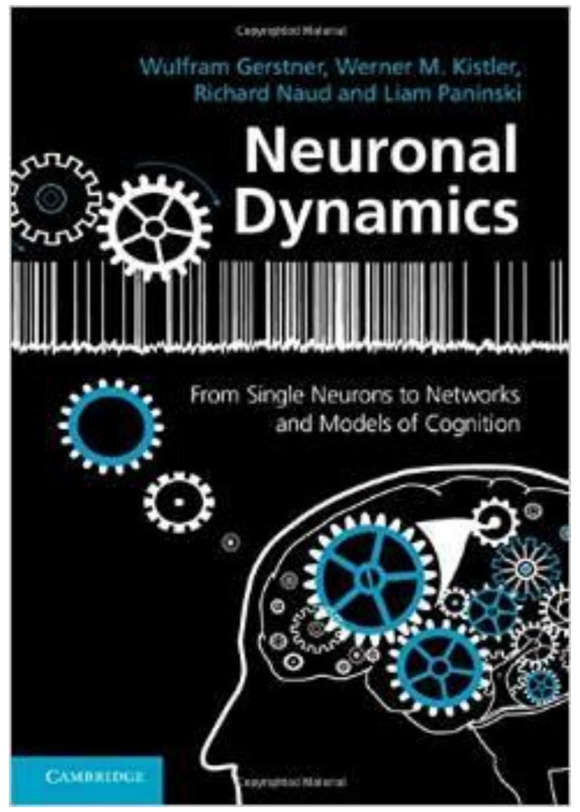

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- columns and receptive fields

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- cortical connectivity
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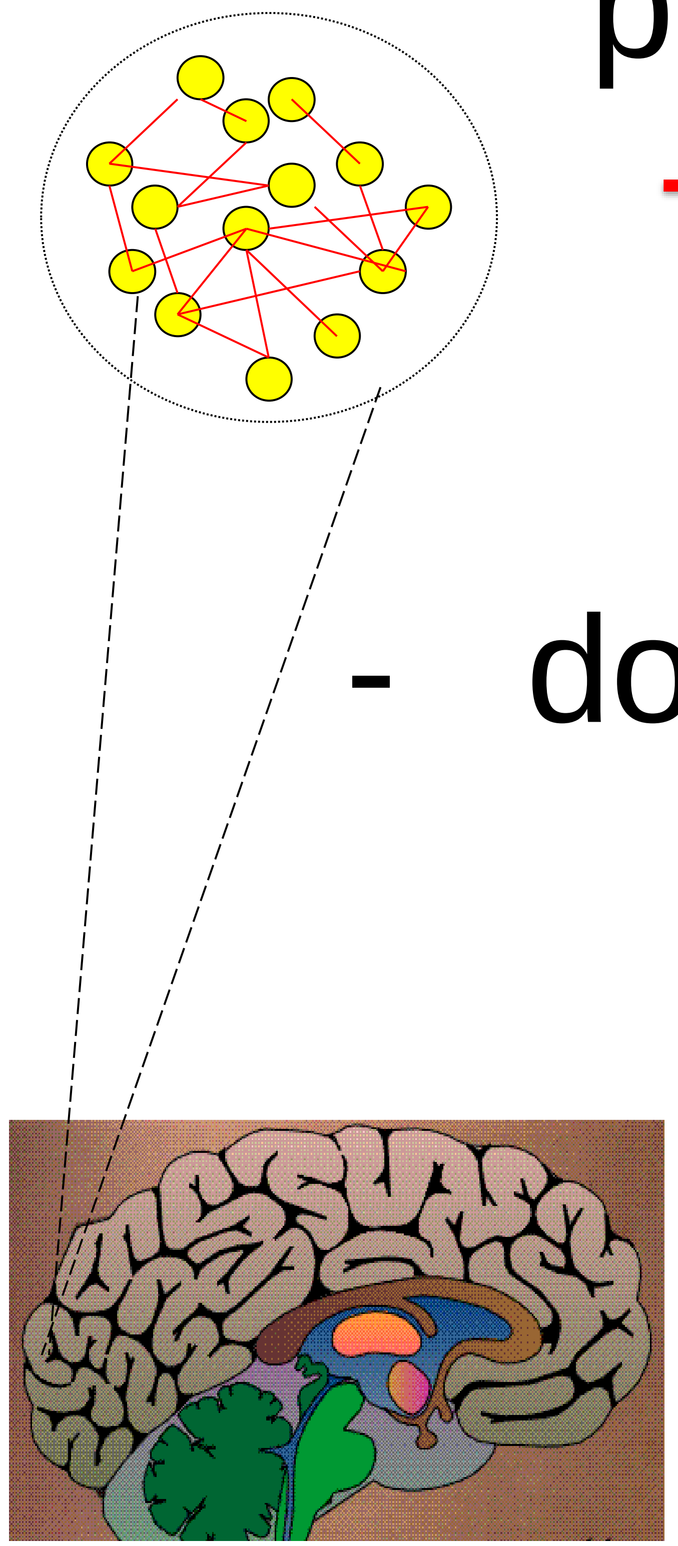
2. Population activity and cortical populations

population of neurons
with similar properties

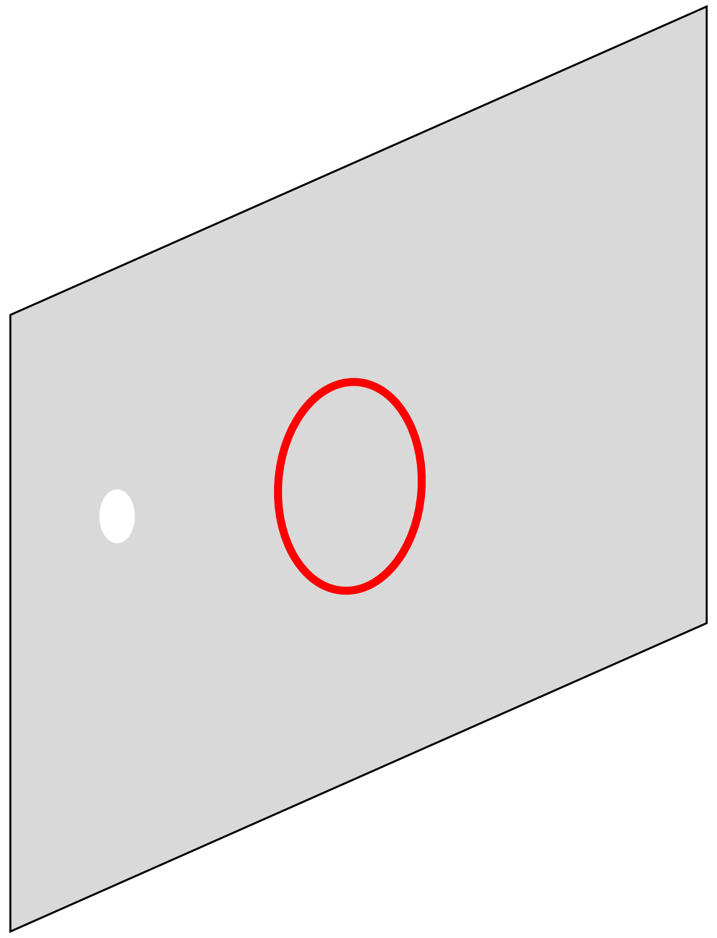
population activity

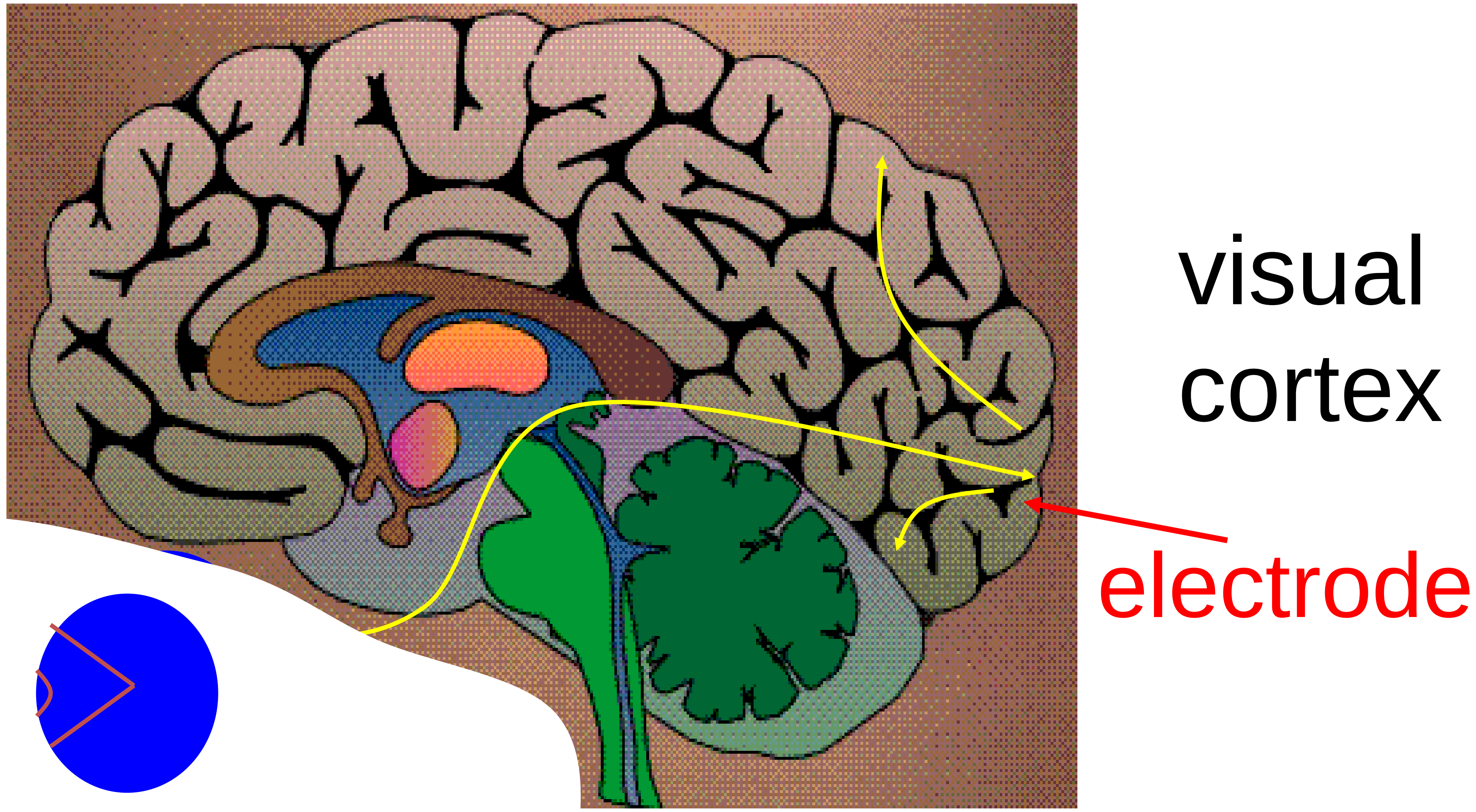
→ $A(t)$



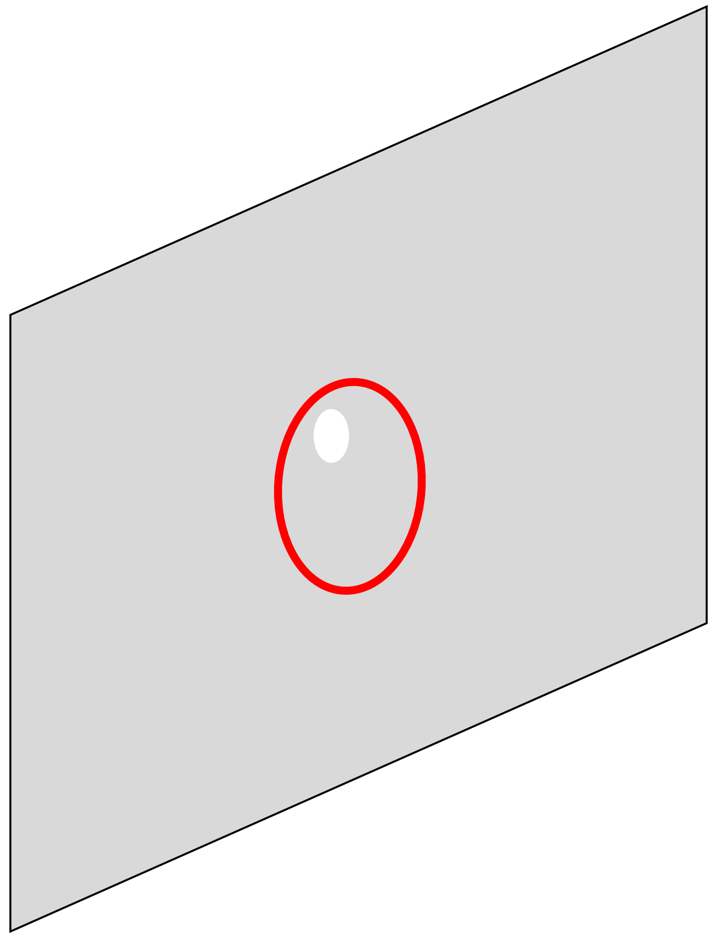
- do populations exist?

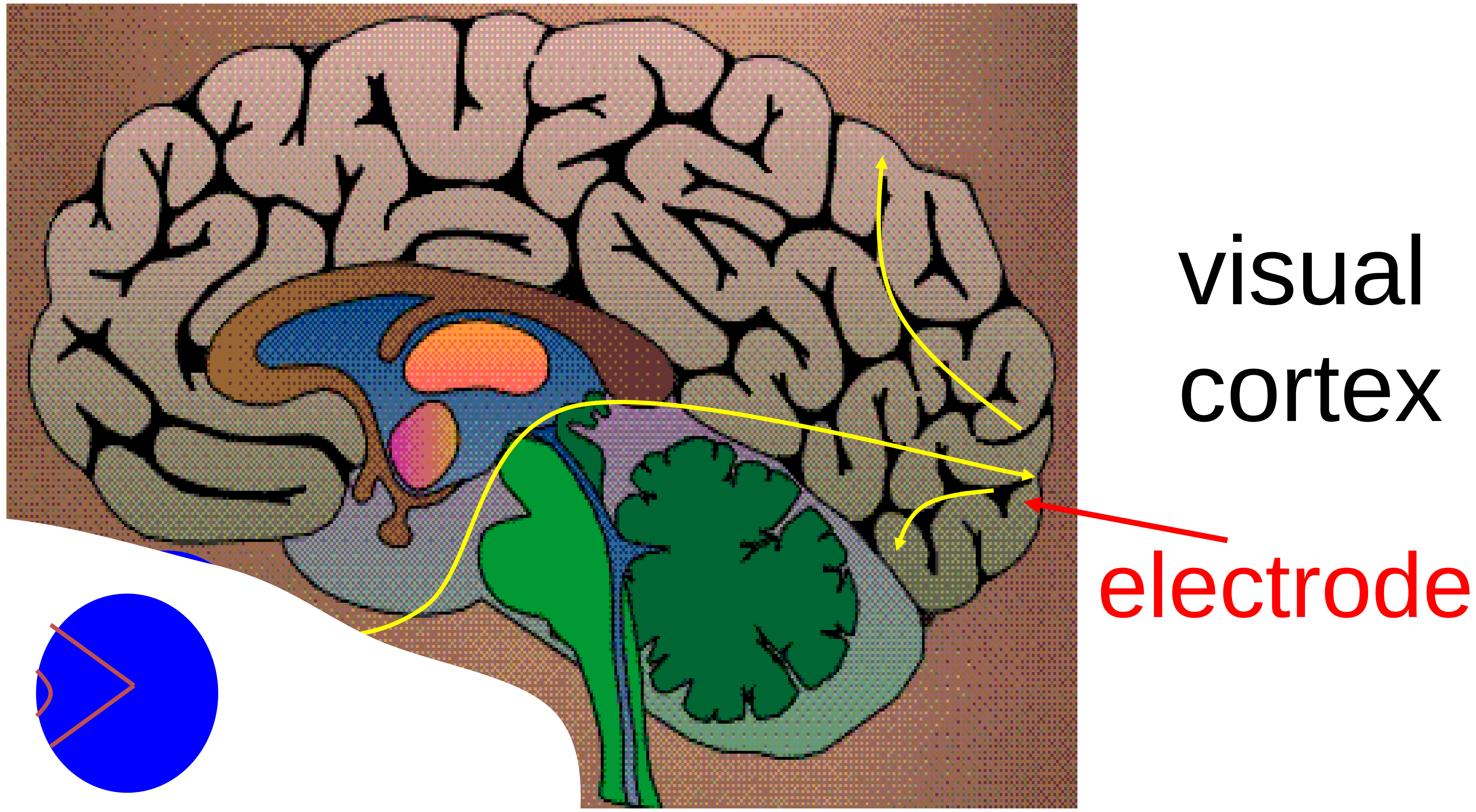
2. Receptive fields



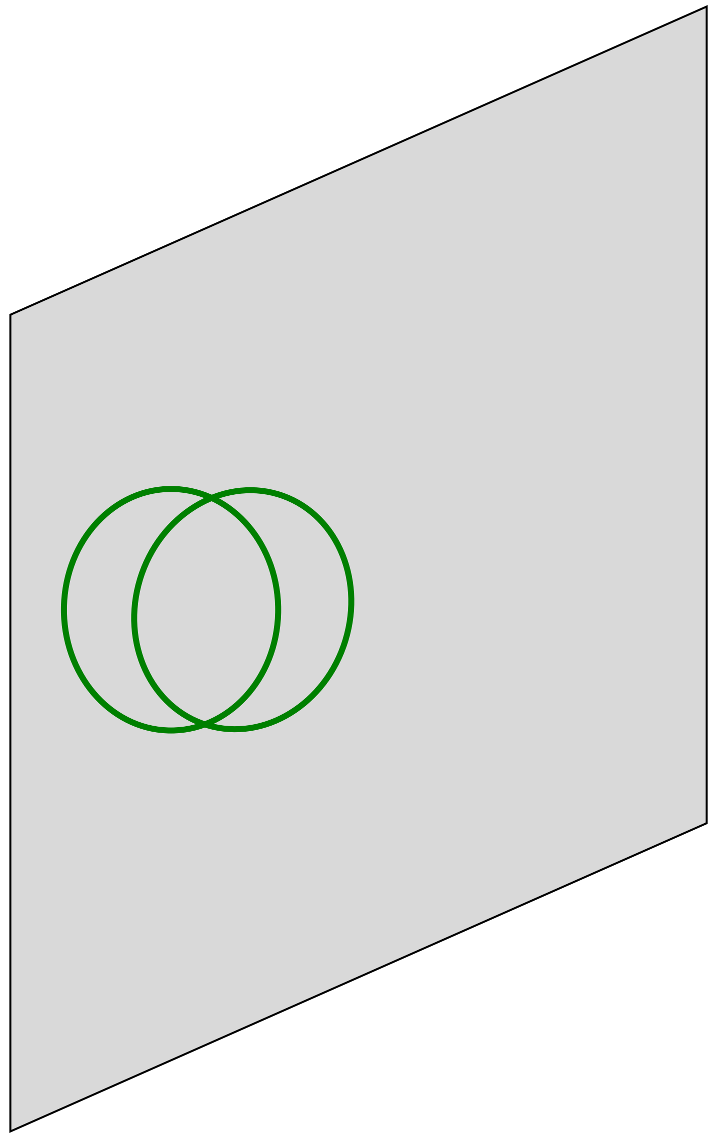


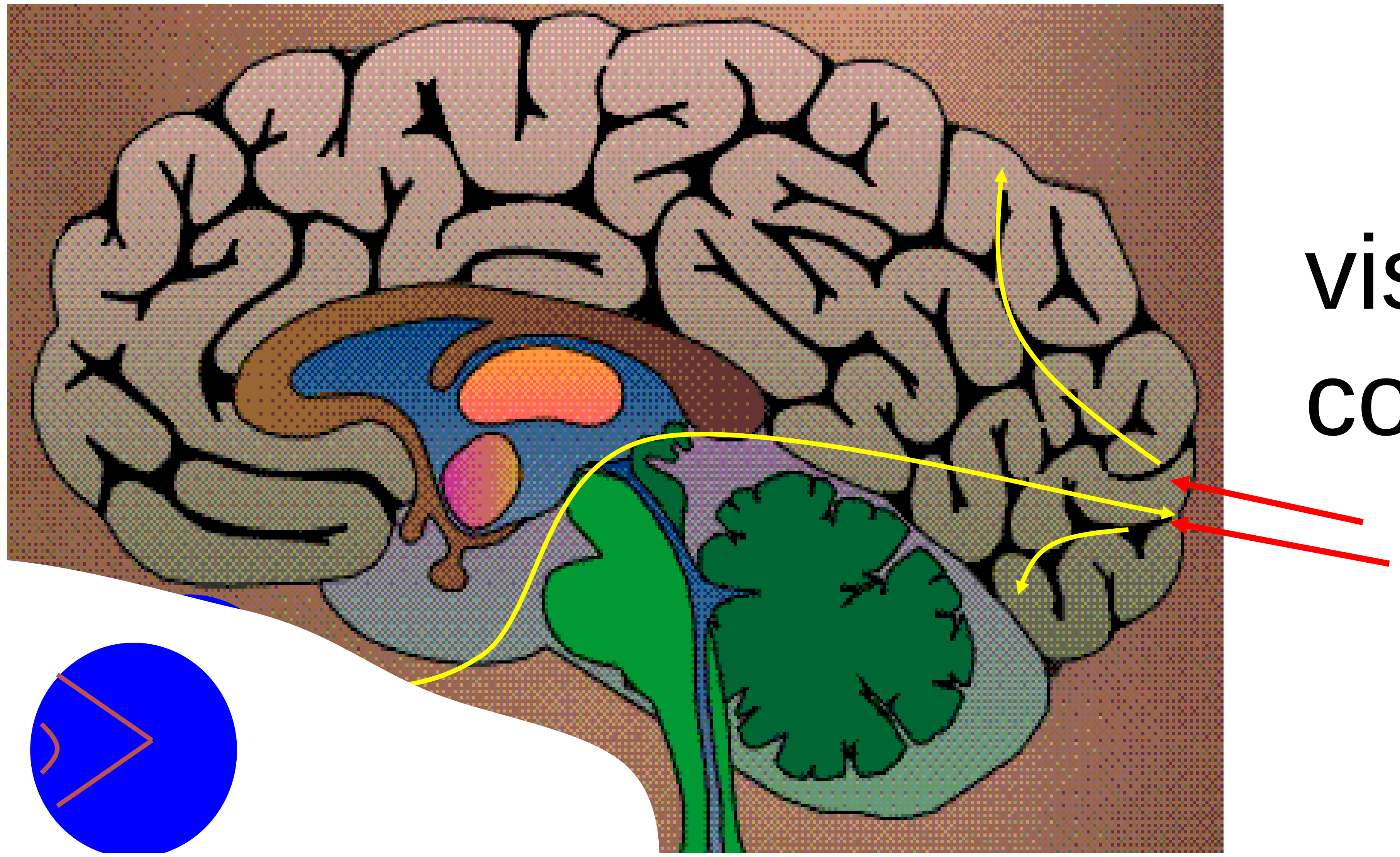
2. Receptive fields





2. Receptive fields and Retinotopic Map

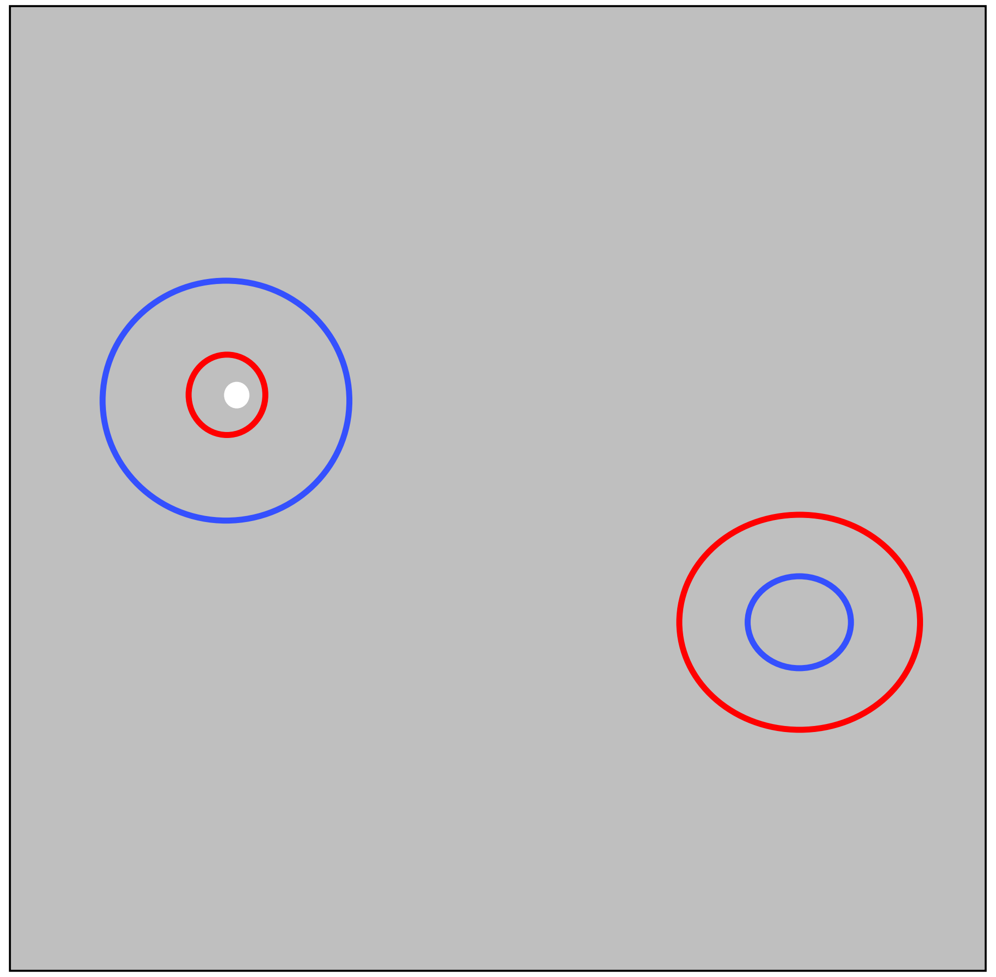




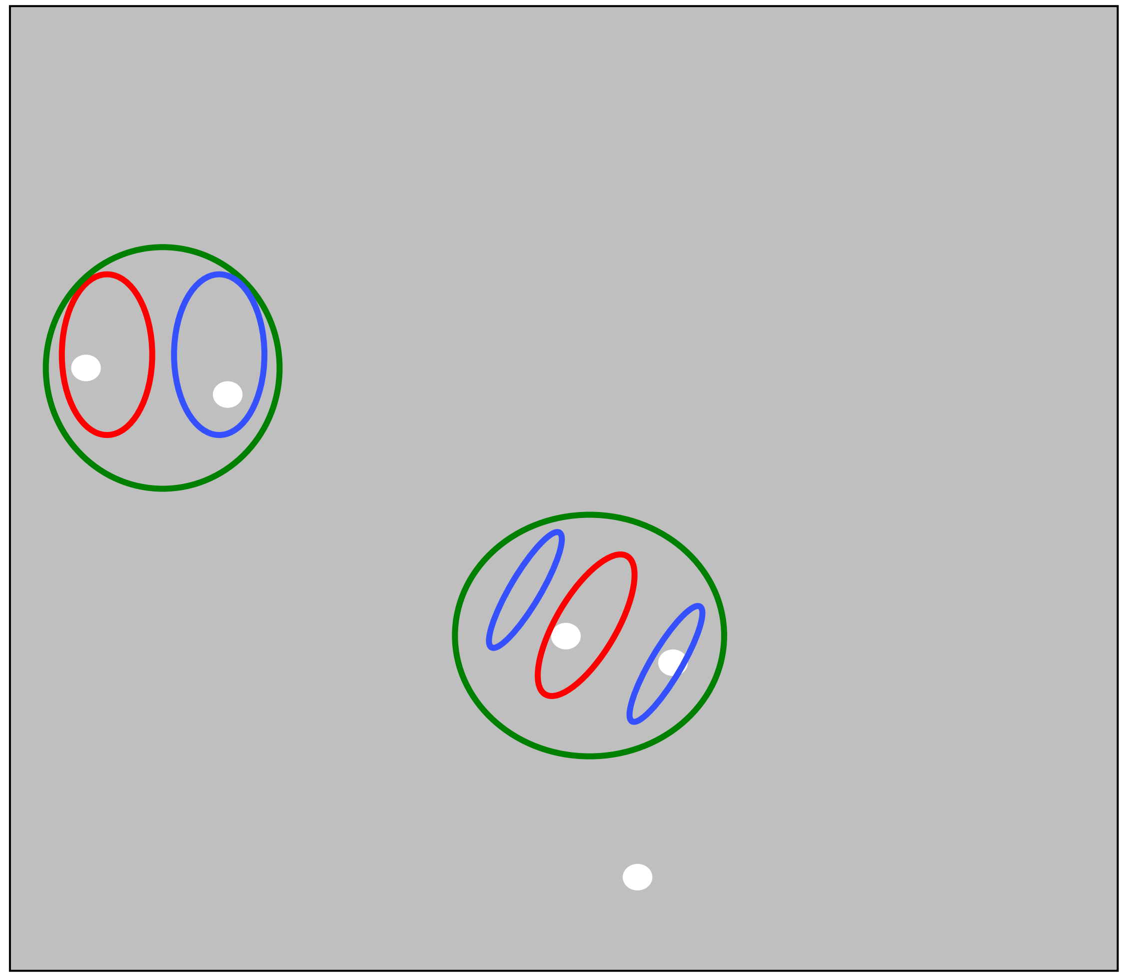
Neighboring cells
in visual cortex
have similar preferred
center of receptive field

2. Receptive fields with Orientation Tuning

Receptive fields:
Retina, LGN



Receptive fields:
visual cortex V1



Orientation
selective

2. Receptive fields with Orientation Tuning

Receptive fields:
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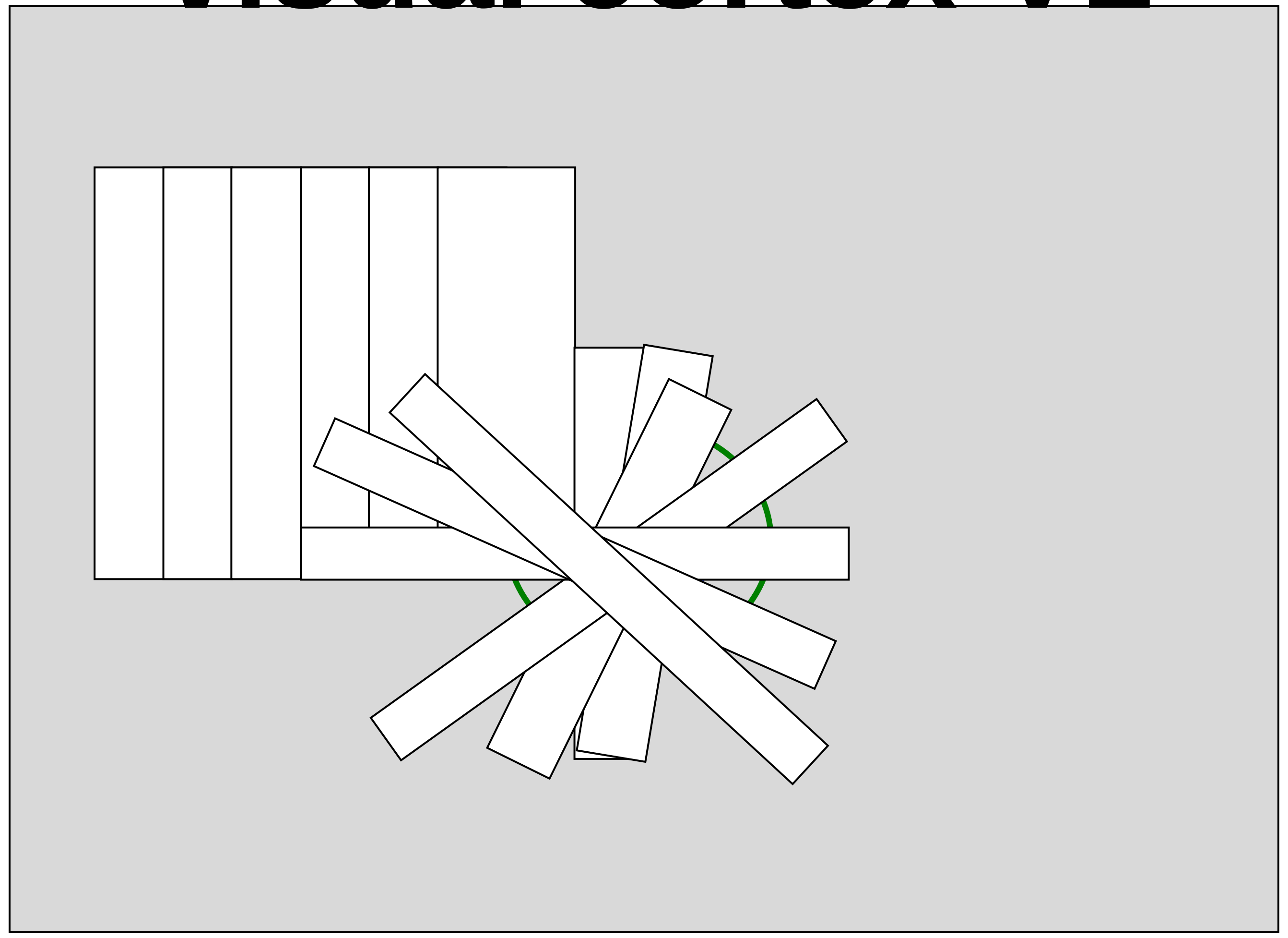
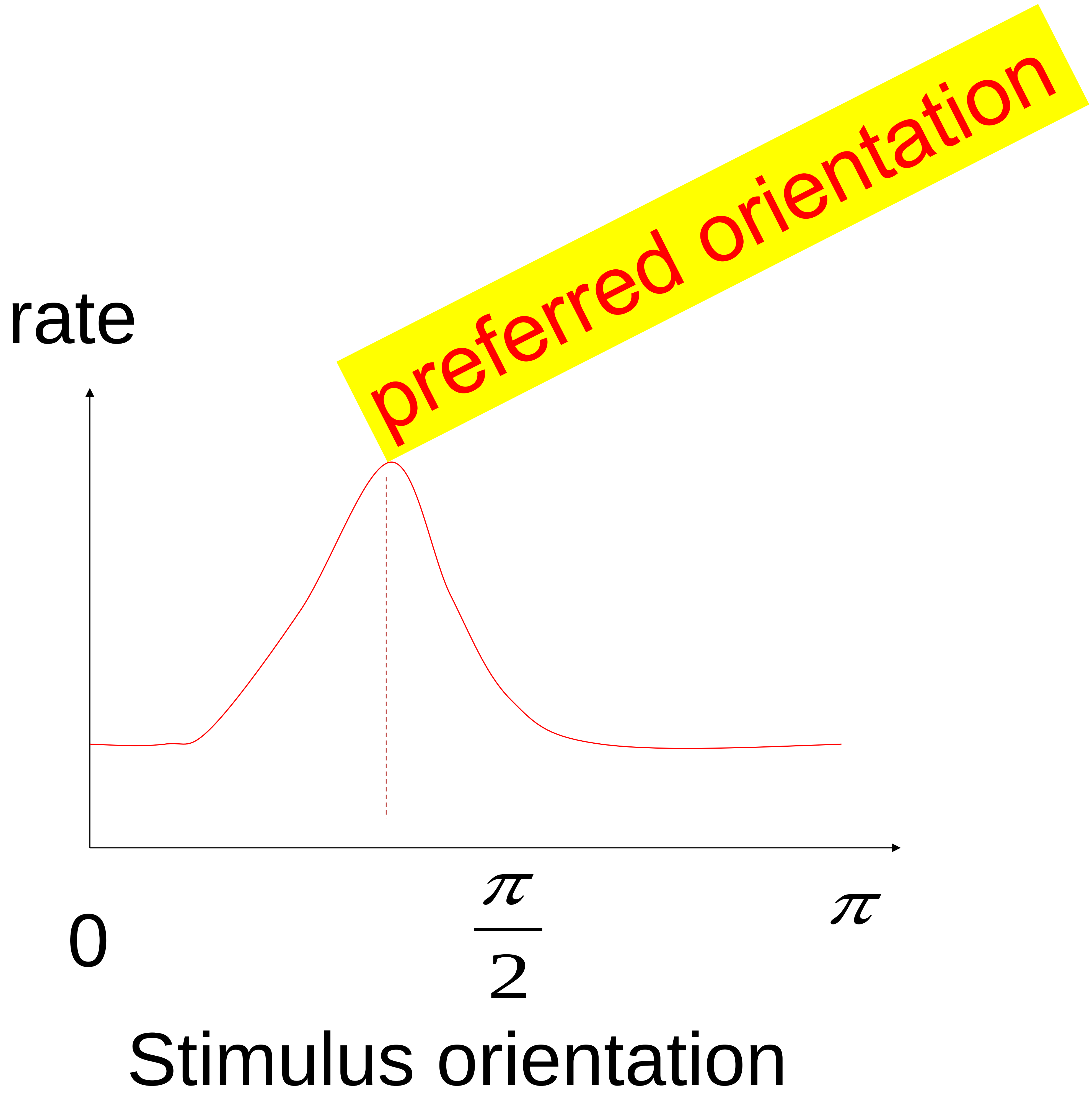


Orientation selective

2. Receptive fields with Orientation Tuning



Receptive fields:
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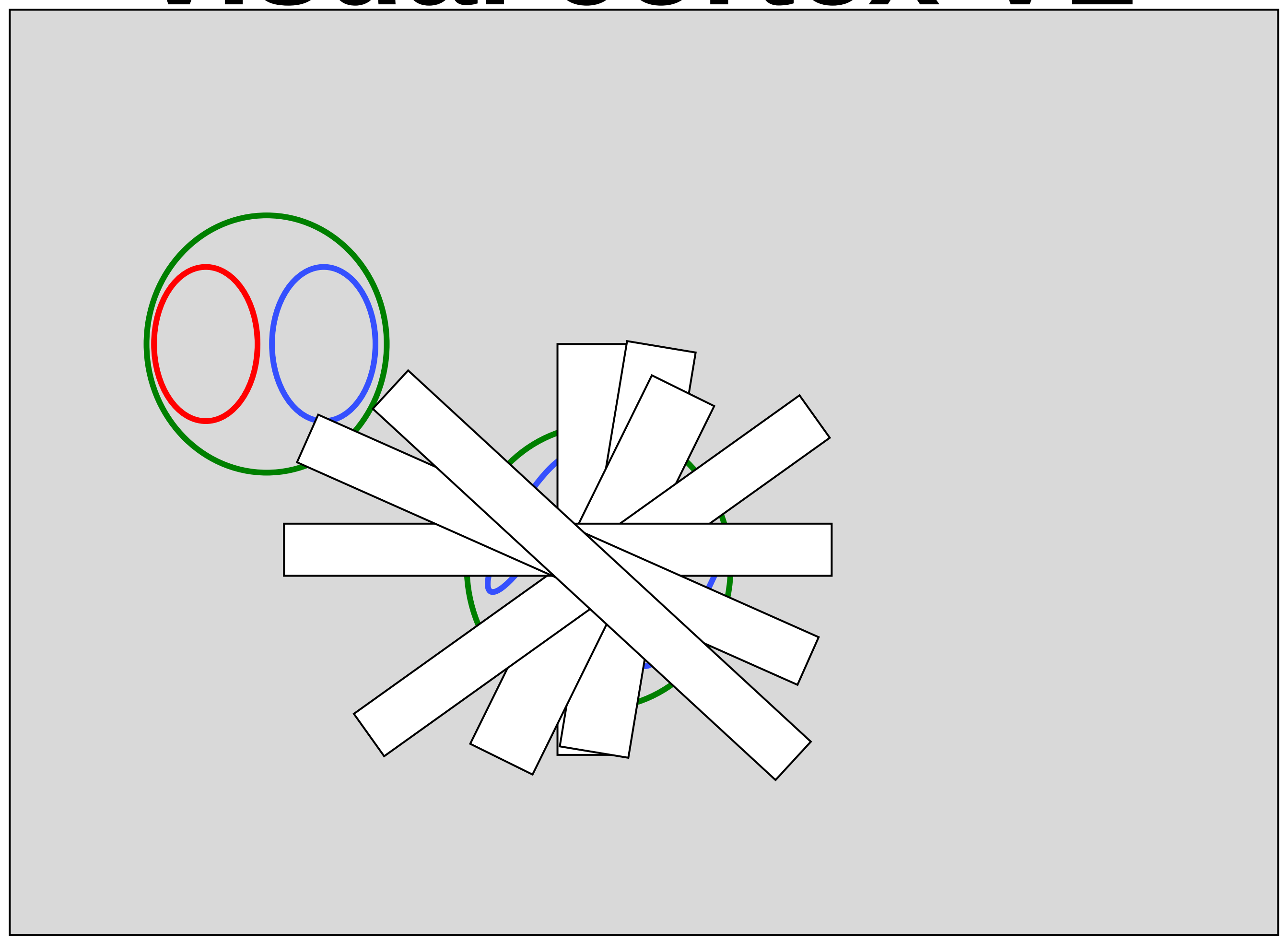
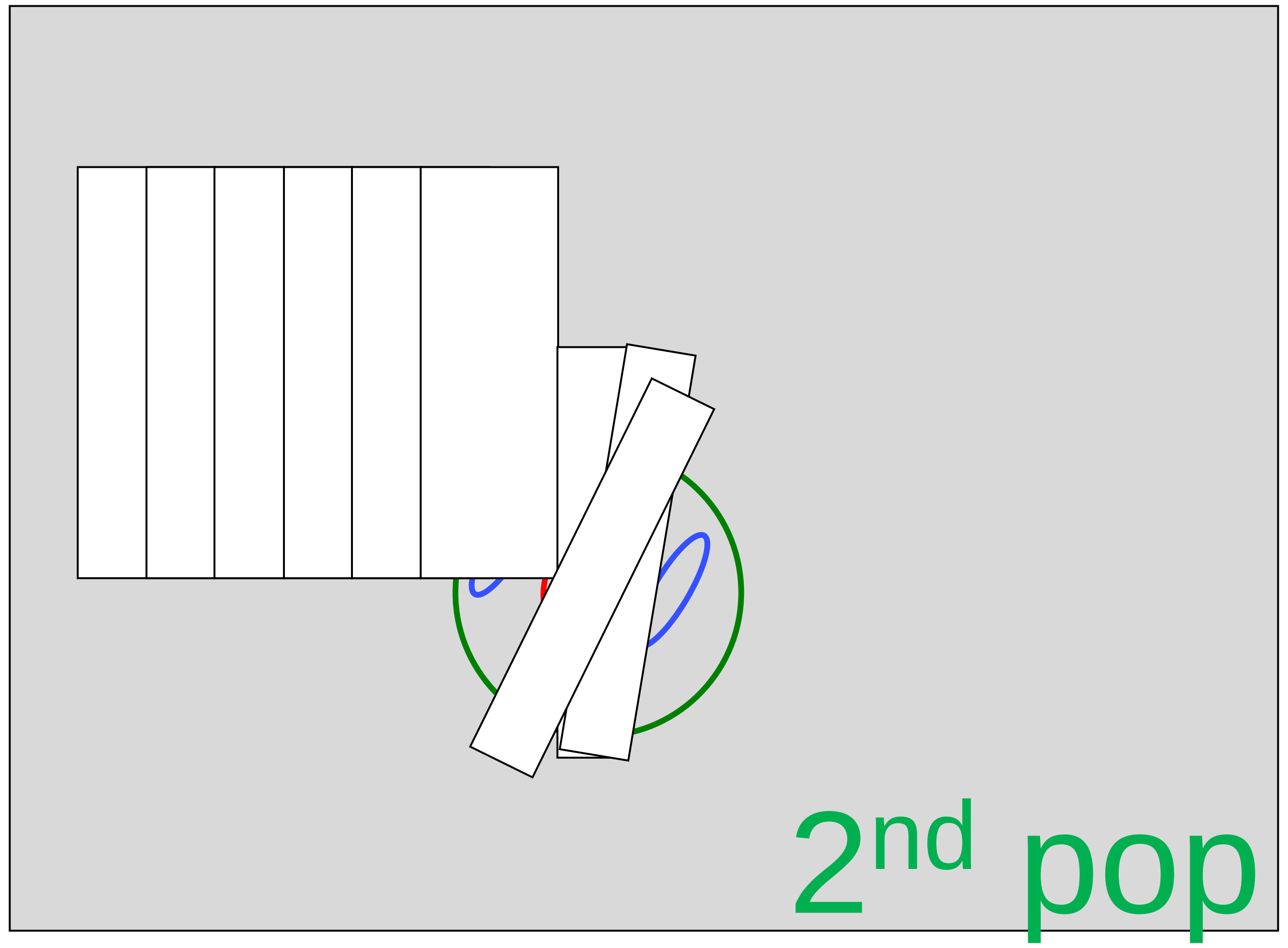
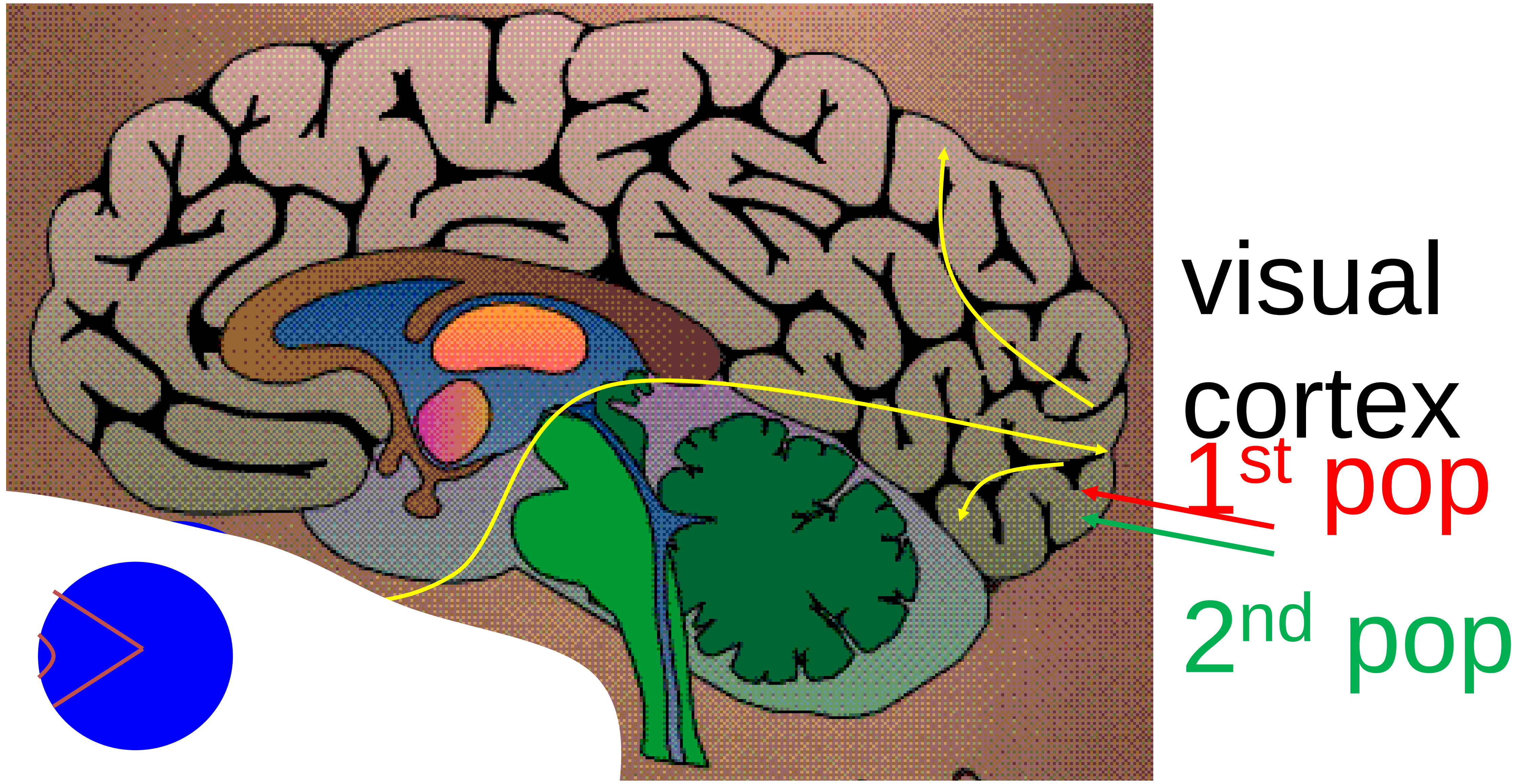


Orientation selective

2. Orientation Tuning and Orientation Maps

Receptive fields:
visual cortex V1

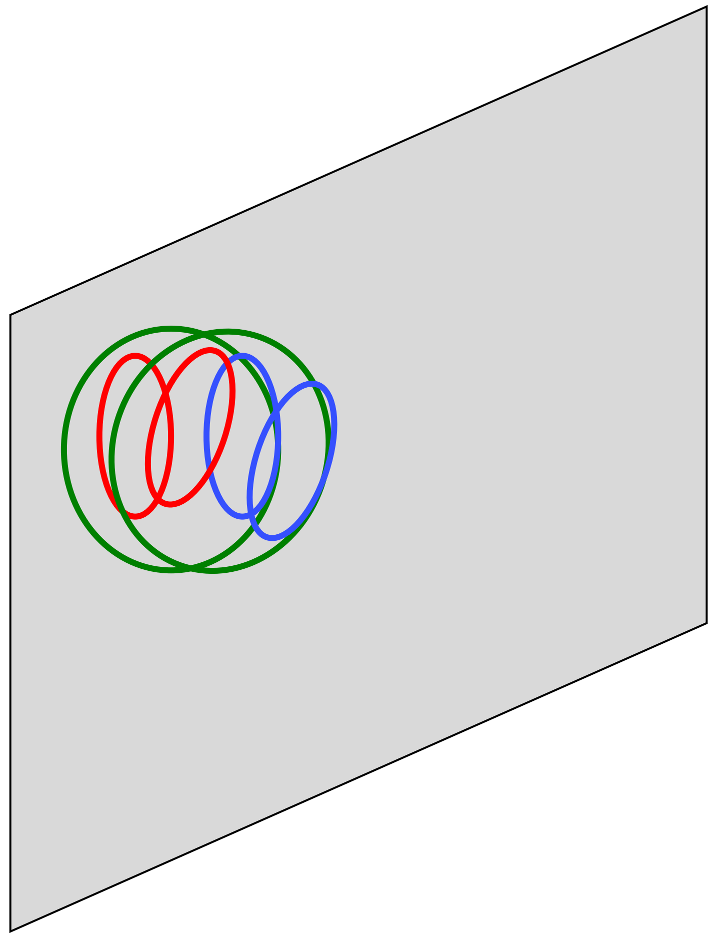


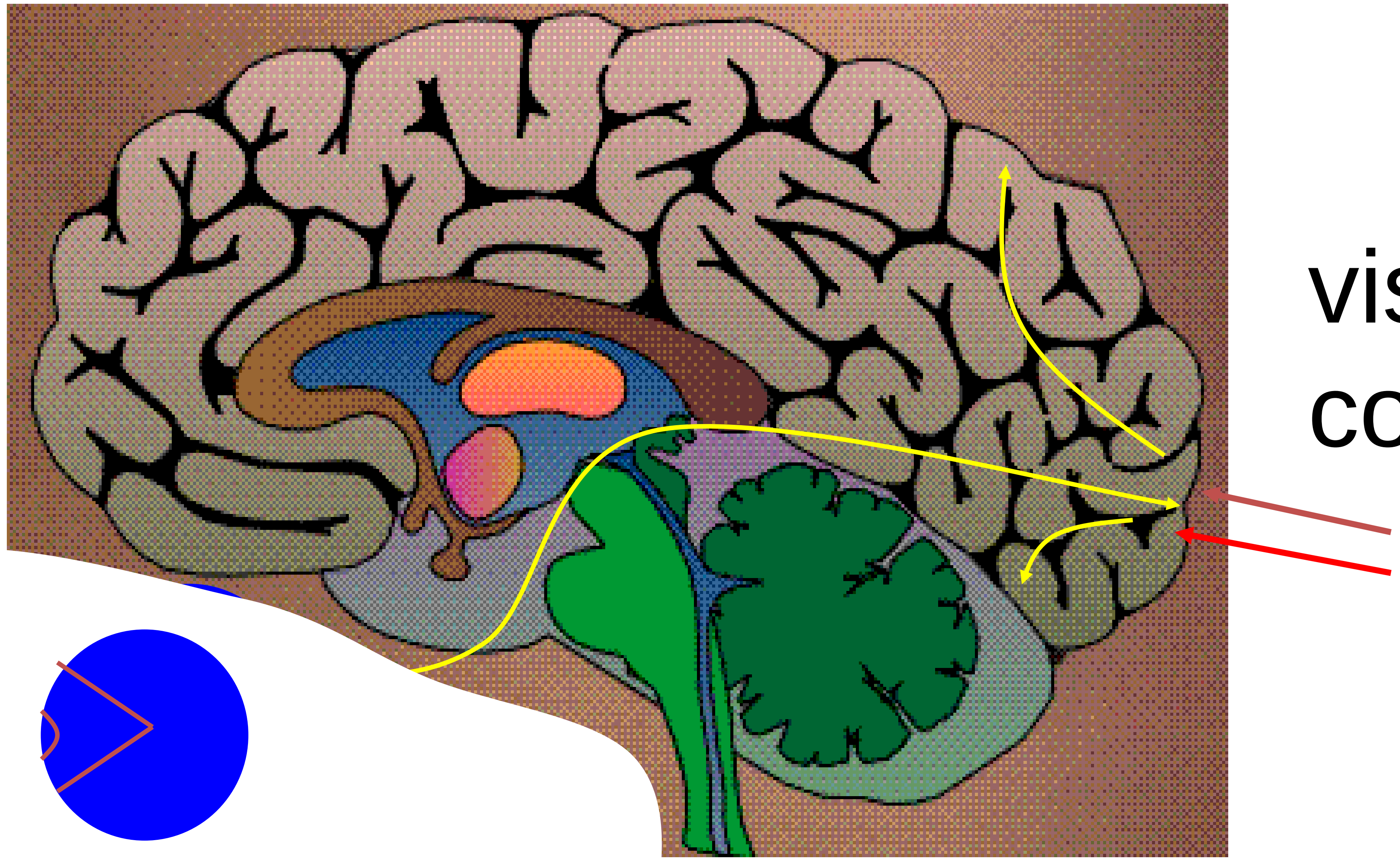


Orientation selective

Neighboring neurons have similar properties

2. Orientation Map





Neighboring cells in visual cortex
Have similar preferred orientation:

cortical orientation map

Hubel and Wiesel 1968; Bonhoeffer&Grinvald, 1991; Bressloff&Cowan, 2002; Kaschube et al. 2010

2. Orientation Map

Receptive field

- set of stimulus features to which a neuron responds
- for visual neurons: location, orientation, color, …

Neighboring cells in visual cortex

- similar preferred orientation
- similar location of receptive field

→ **candidate of ‘neuronal population’**

Quiz 2, now

The receptive field of a visual neuron refers to
[ ] The localized region of space to which it is sensitive
[ ] The orientation of a light bar to which it is sensitive
[ ] The set of all stimulus features to which it is sensitive

The receptive field of a auditory neuron refers to
[ ] The set of all stimulus features to which it is sensitive
[ ] The range of frequencies to which it is sensitive

The receptive field of a somatosensory neuron refers to
[ ] The set of all stimulus features to which it is sensitive
[ ] The region of body surface to which it is sensitive

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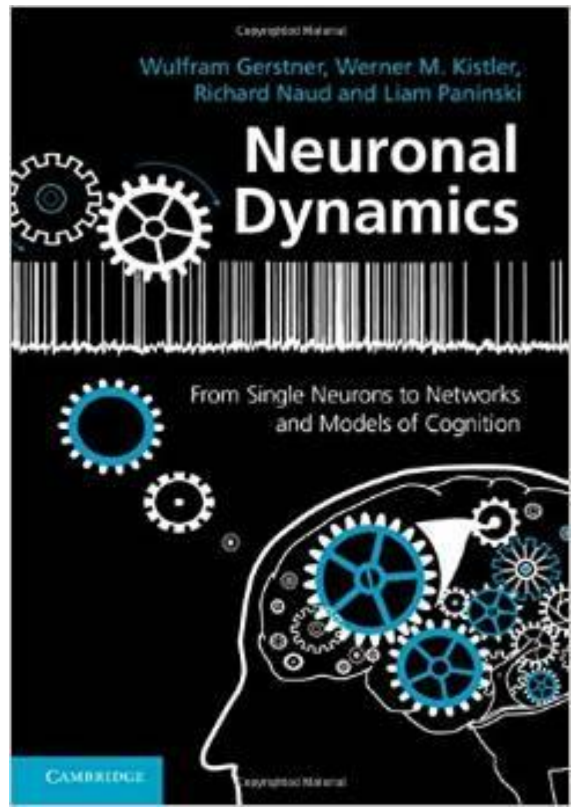

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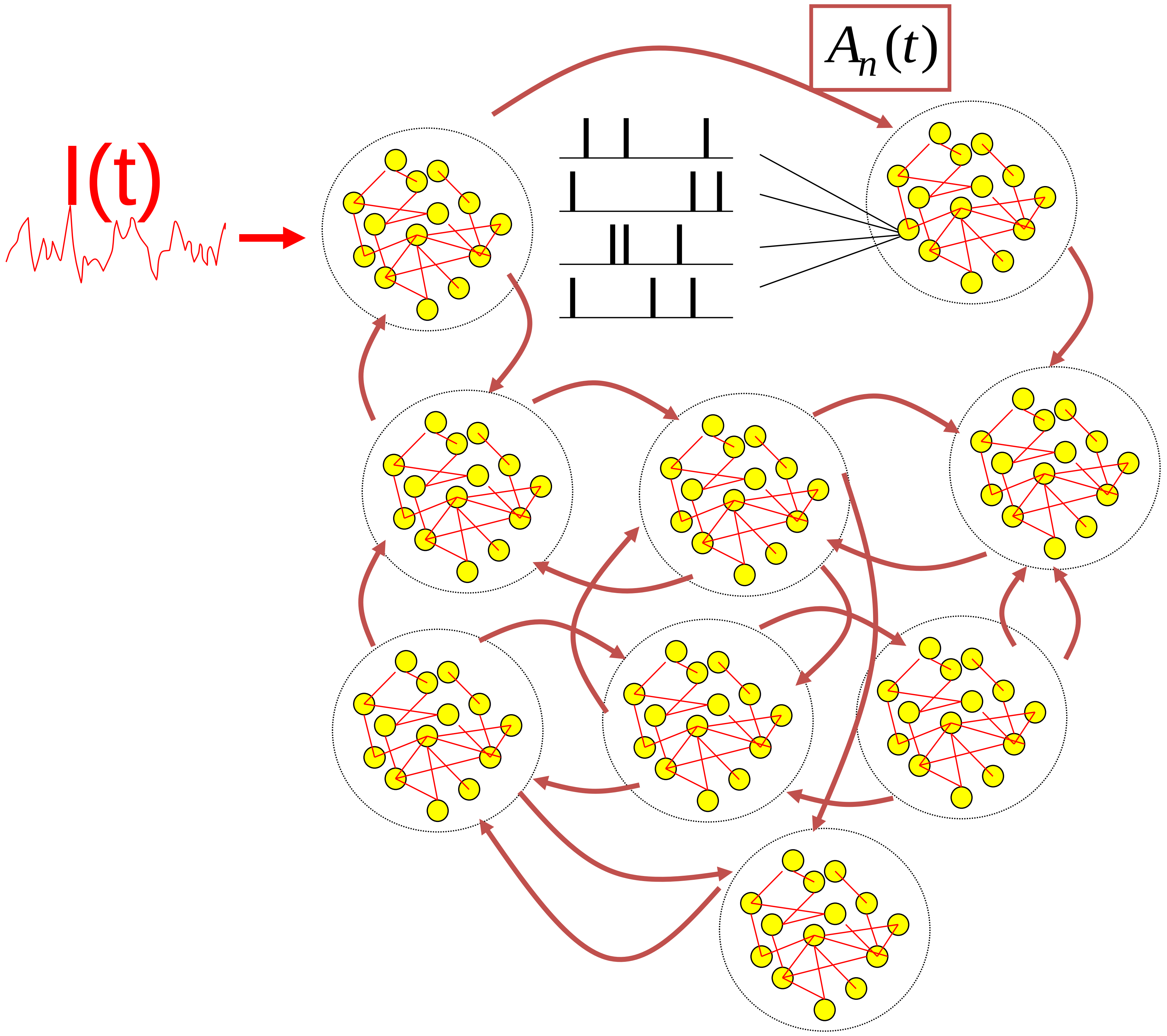
   - Balanced state

3. Interacting Populations in models



What are these population?
How are they connected?

3. A single model population

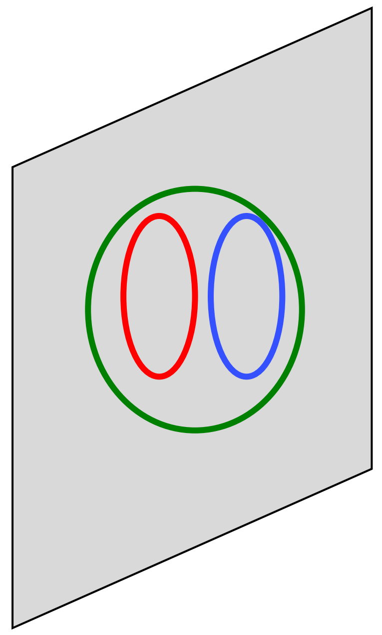
population = group of neurons
with
- similar neuronal properties
- similar input
- similar receptive field
- similar connectivity

→ make this more precise

3. Cortical orientation map and cortical column

population = group of neurons with
- similar neuronal properties
- similar input
- similar receptive field
- similar connectivity

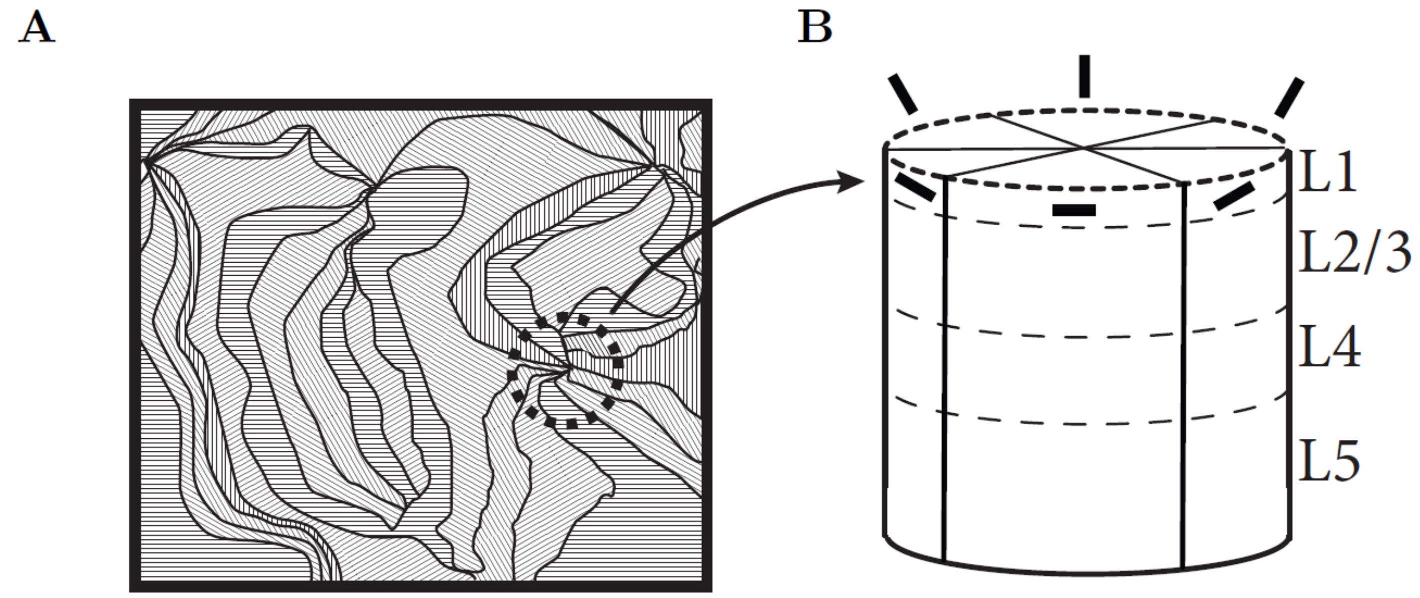
⟶ make this more precise



Rec. Field on Screen

cortical orientation map

Sheet of visual cortex   cortical column

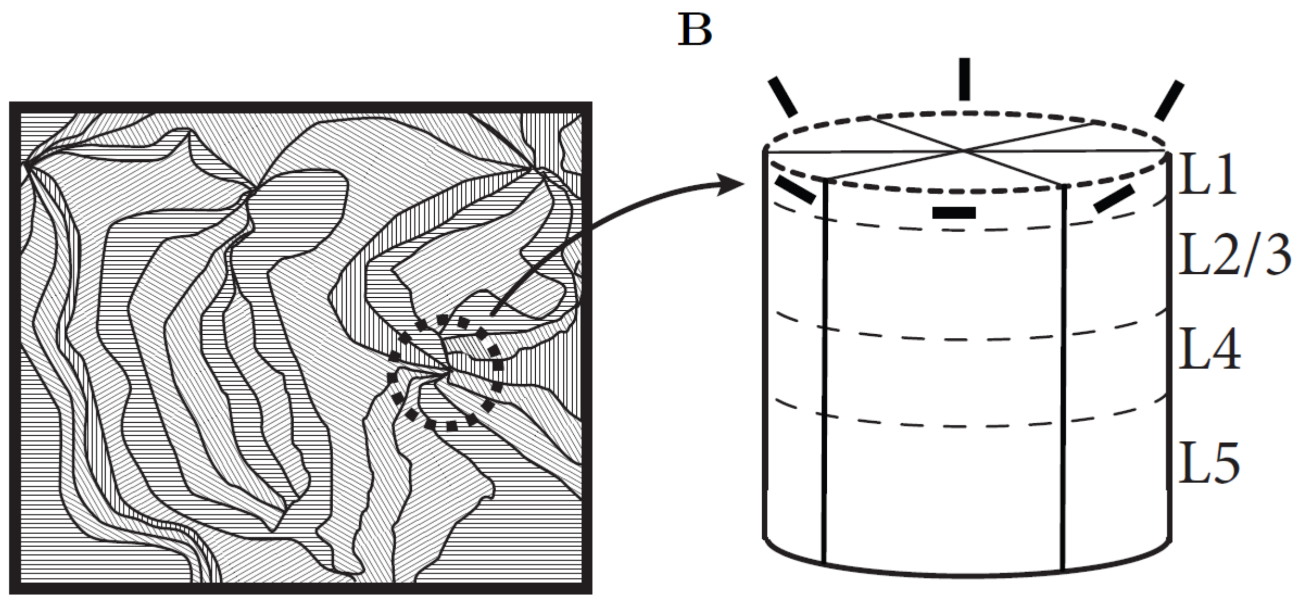


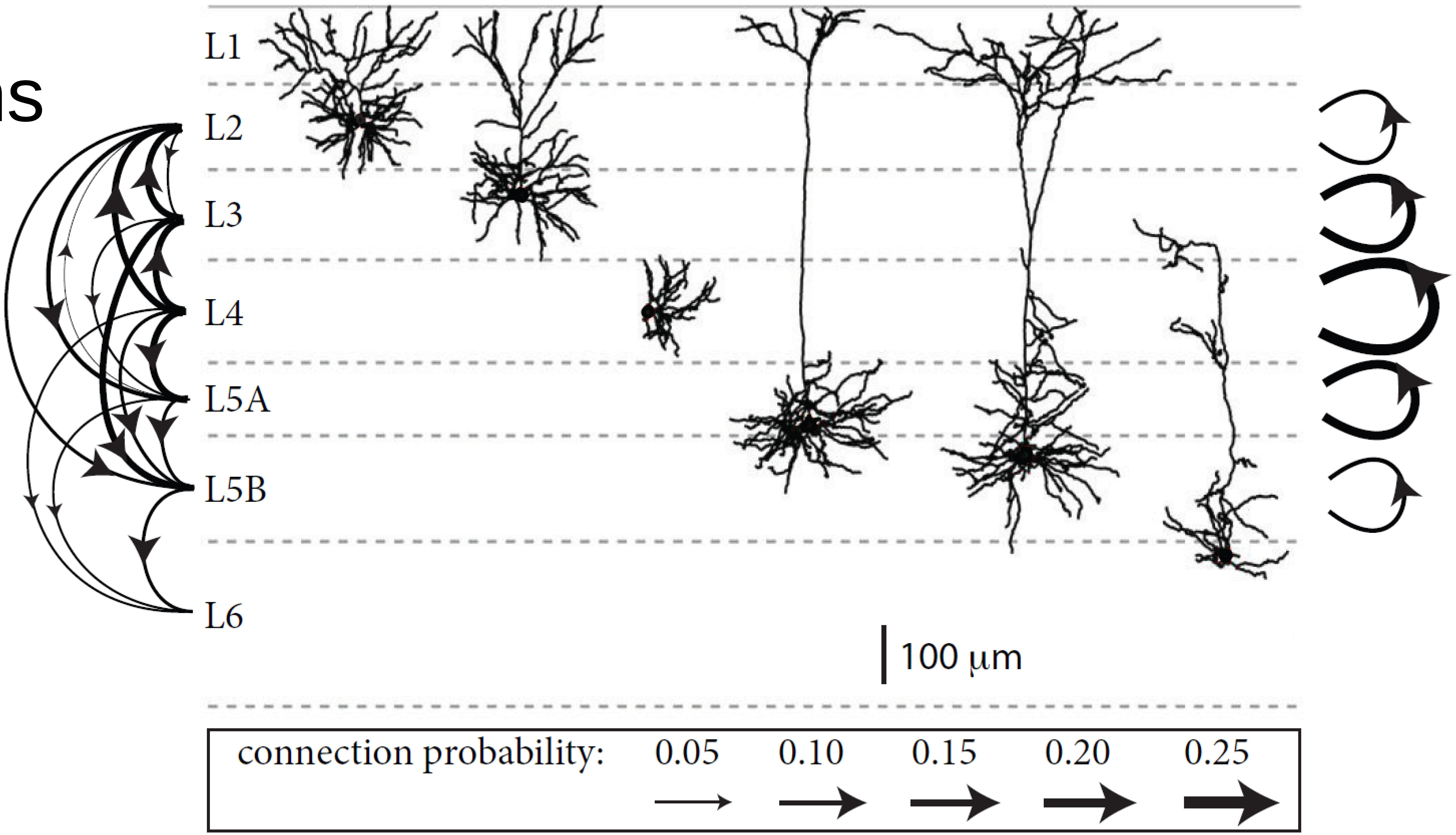
Hubel and Wiesel 1968; Bonhoeffer&Grinvald, 1991

3. local cortical connectivity across layers

(mouse somatosensory cortex)

Here:
Excitatory neurons





Lefort et al. NEURON, 2009

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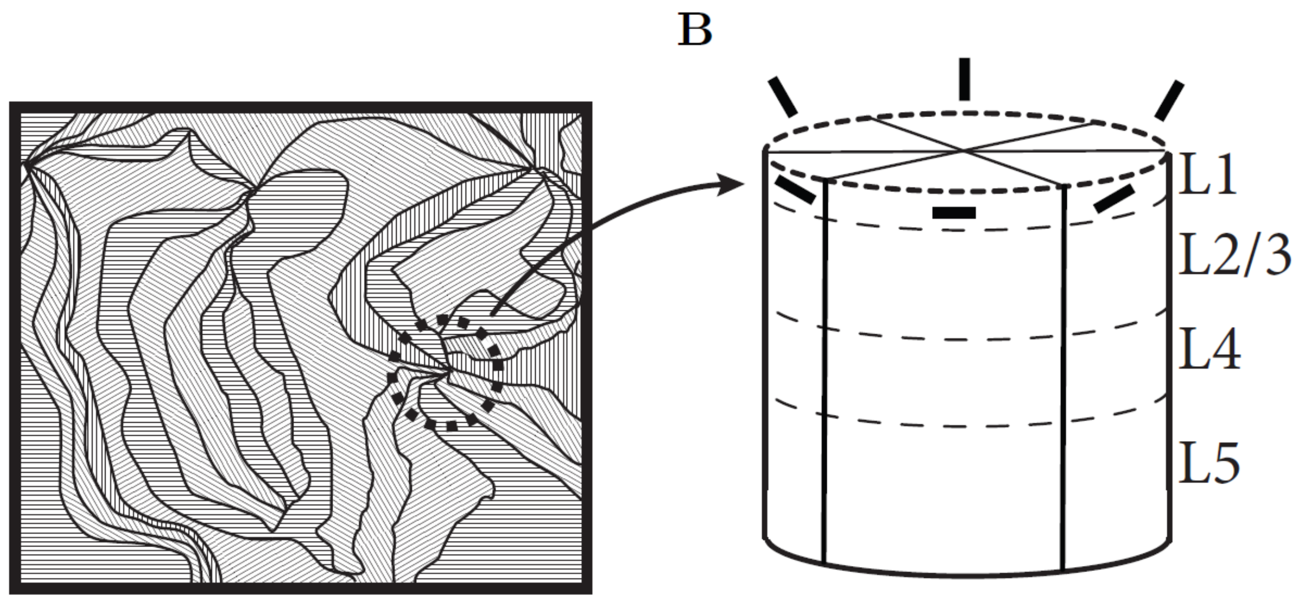
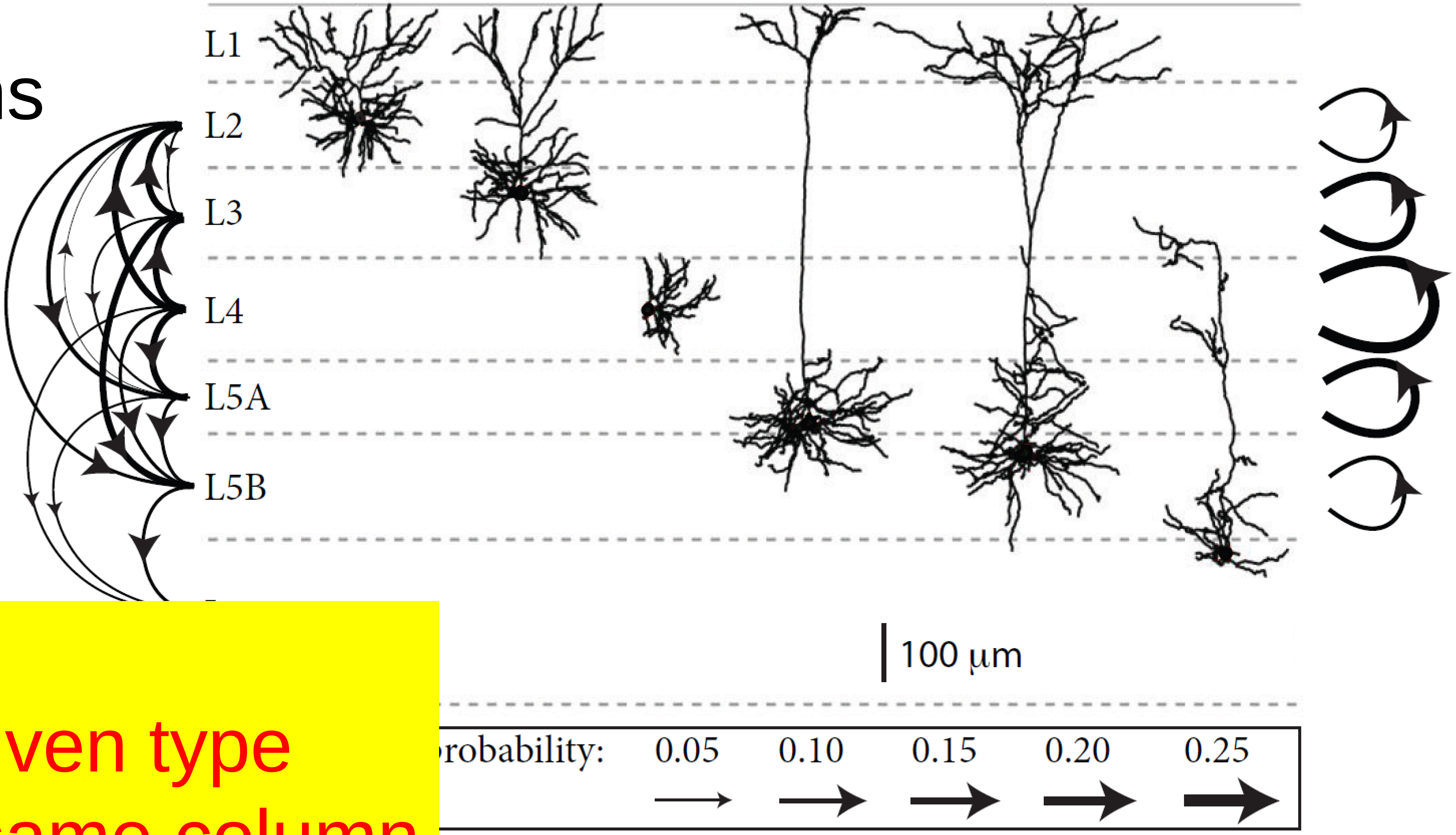


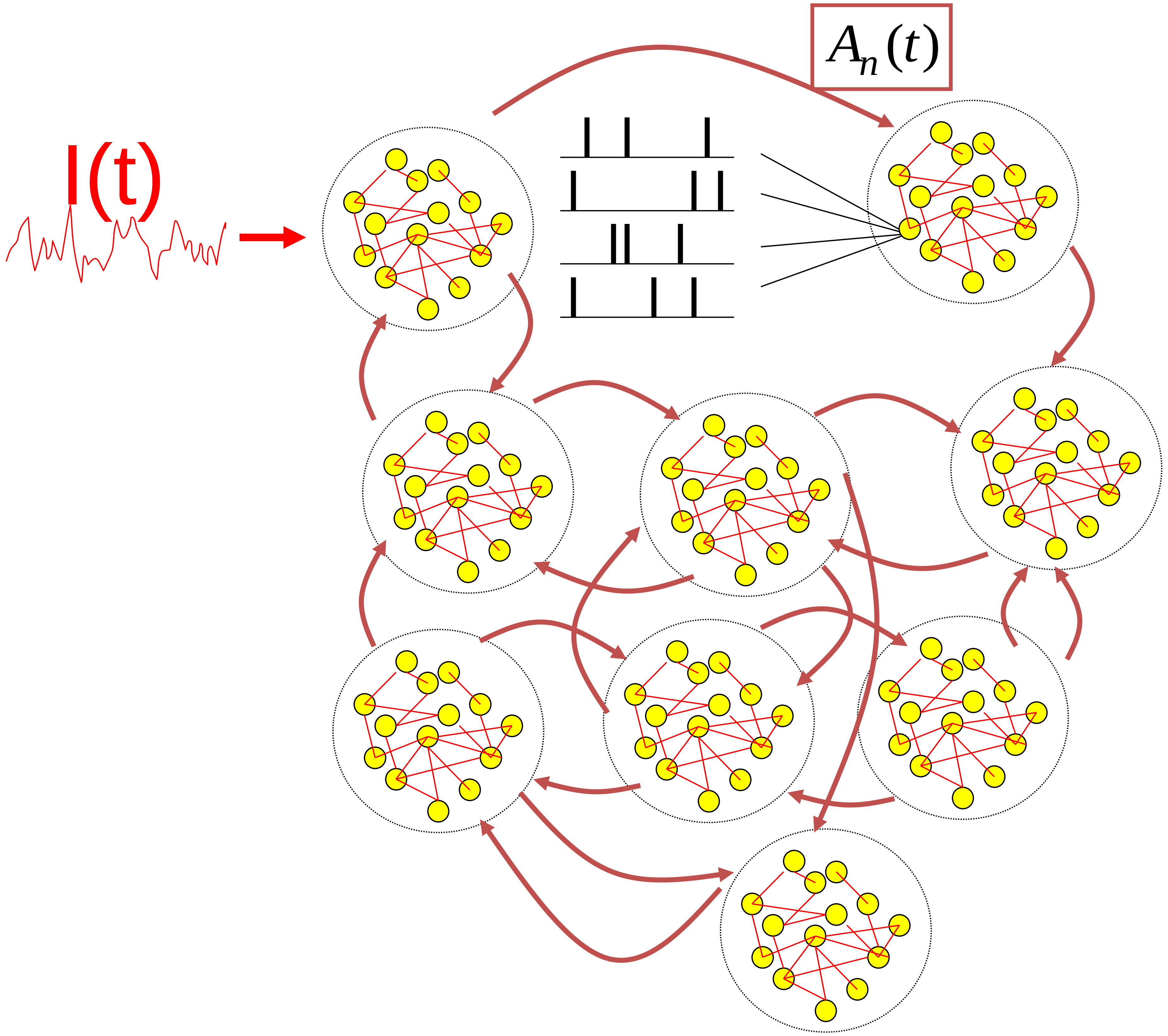


1 population =
all neurons of given type
in one layer of same column
(e.g. excitatory in layer 3)

Lefort et al. NEURON, 2009

3. Interacting Populations in models

Connection probability:
- within population
- across population

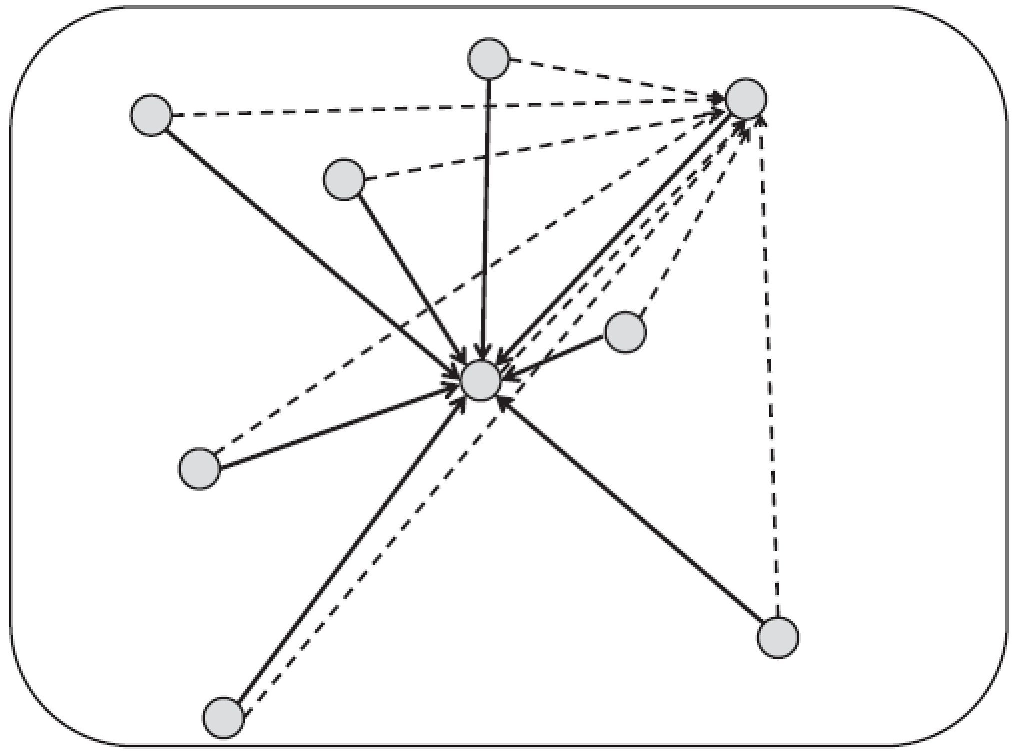


1 population =
all neurons of given type
in one layer of same column
(e.g. excitatory in layer 3)

3. Connectivity schemes (models)

full connectivity
all-to-all

N=5000
neurons



N=10000
neurons

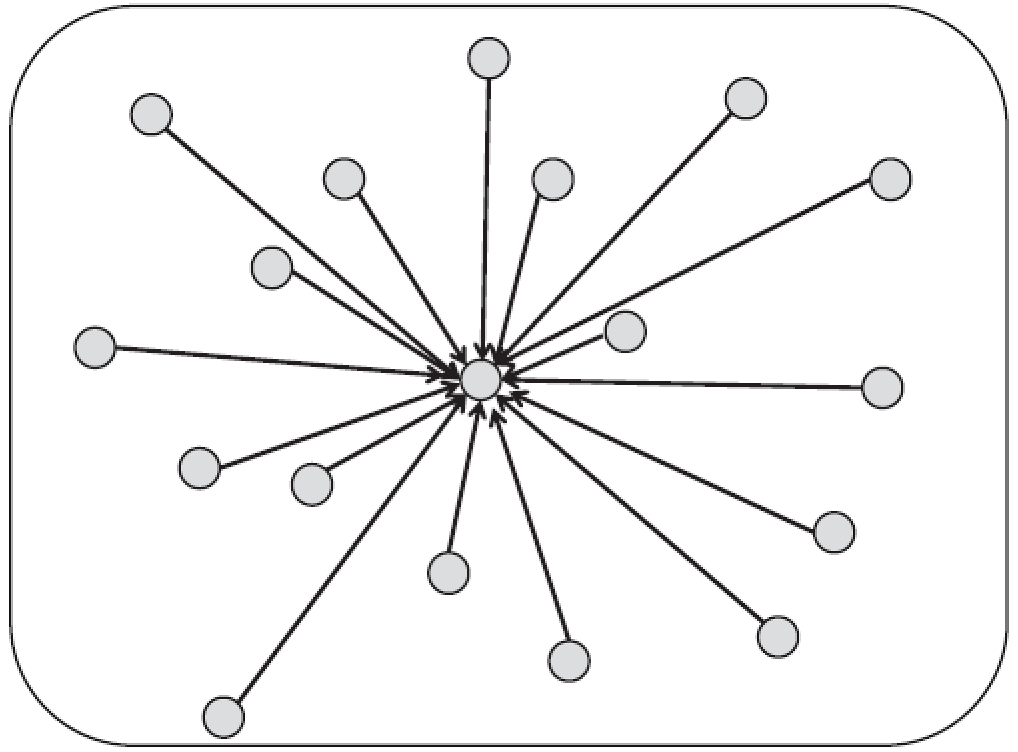


Image: Gerstner et al.
Neuronal Dynamics (2014)

Each neuron receives
N connections

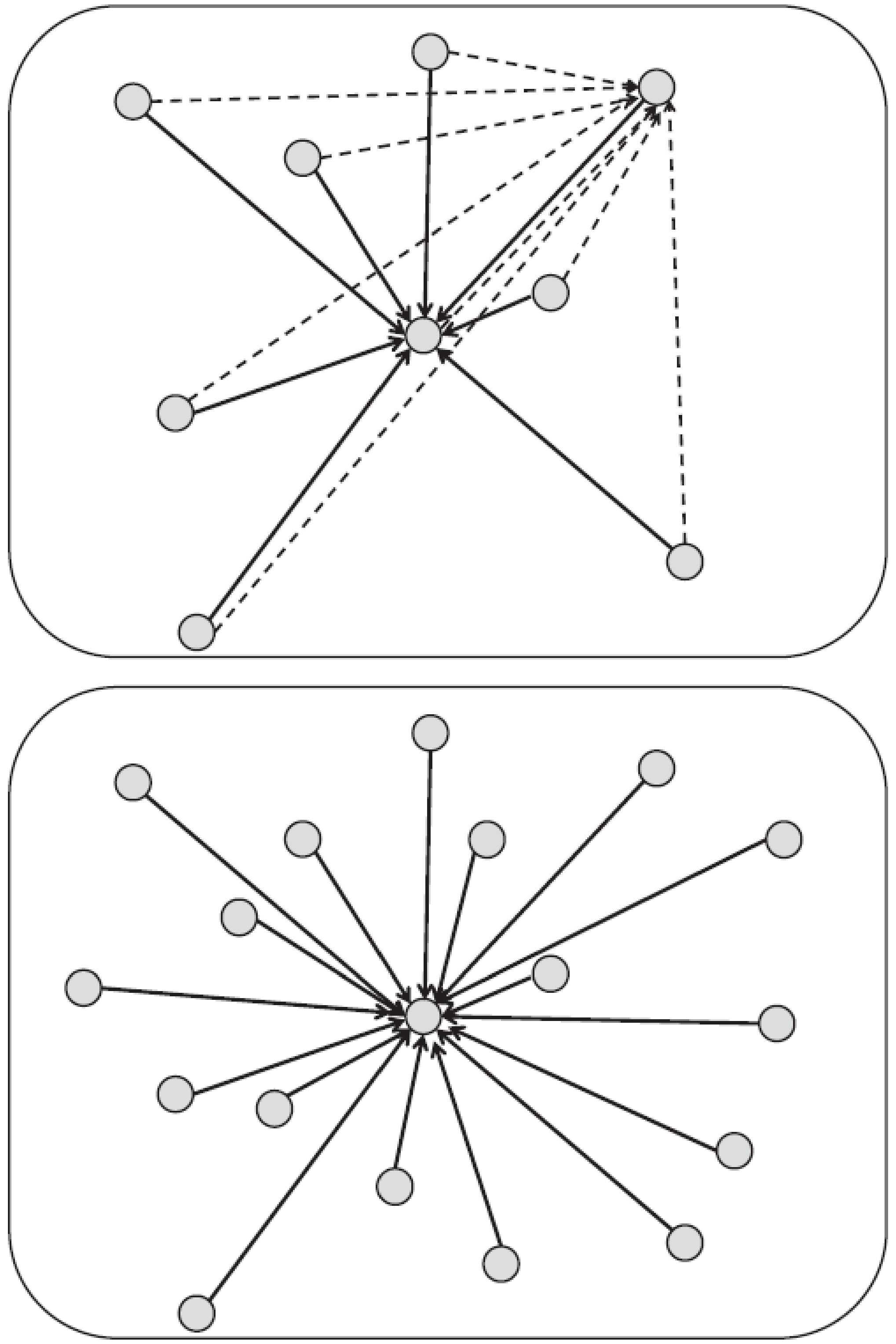
3. Connectivity schemes (models)

full connectivity
all-to-all

Random connectivity
w. number K of inputs fixed

N=5000
neurons

N=10000
neurons



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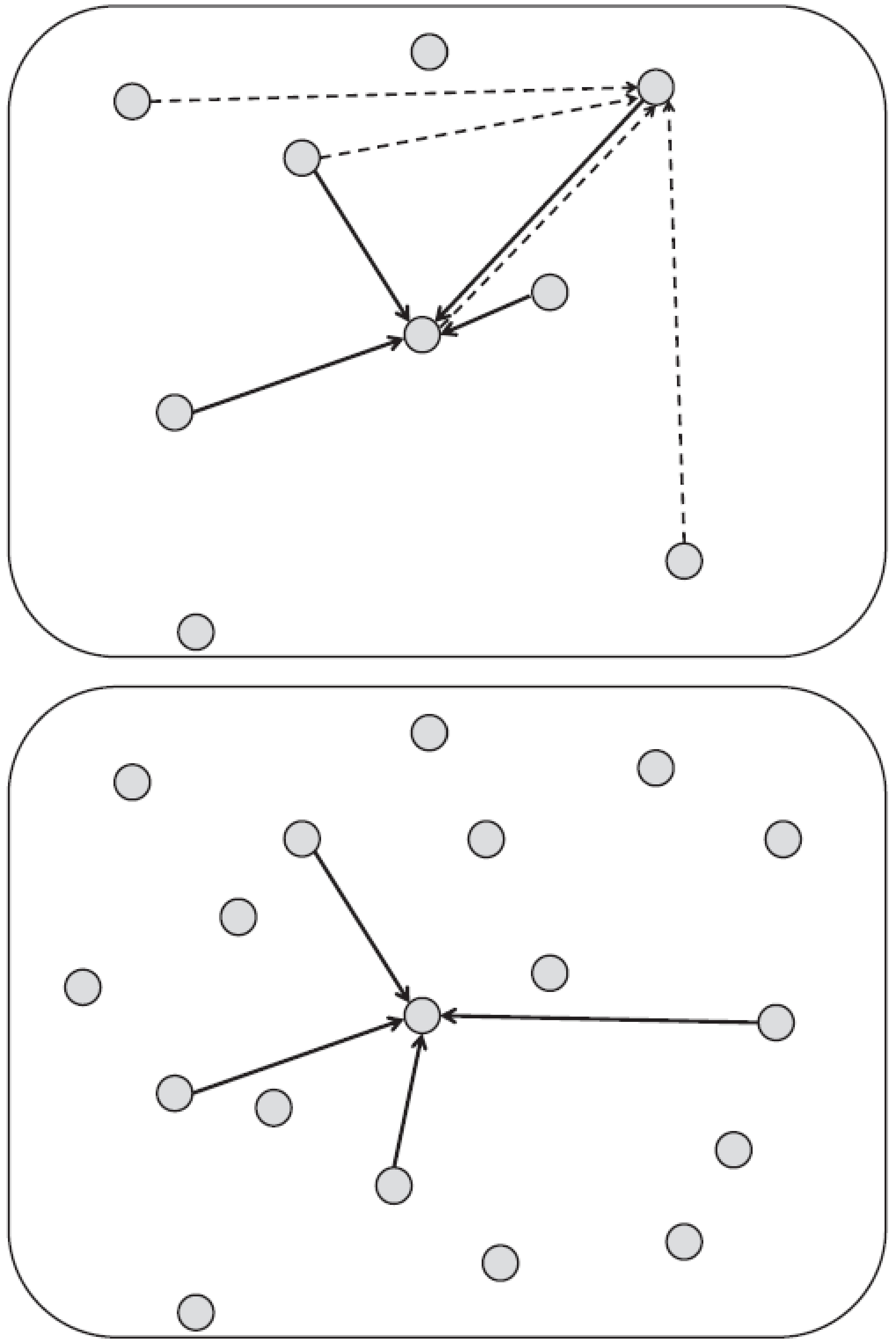


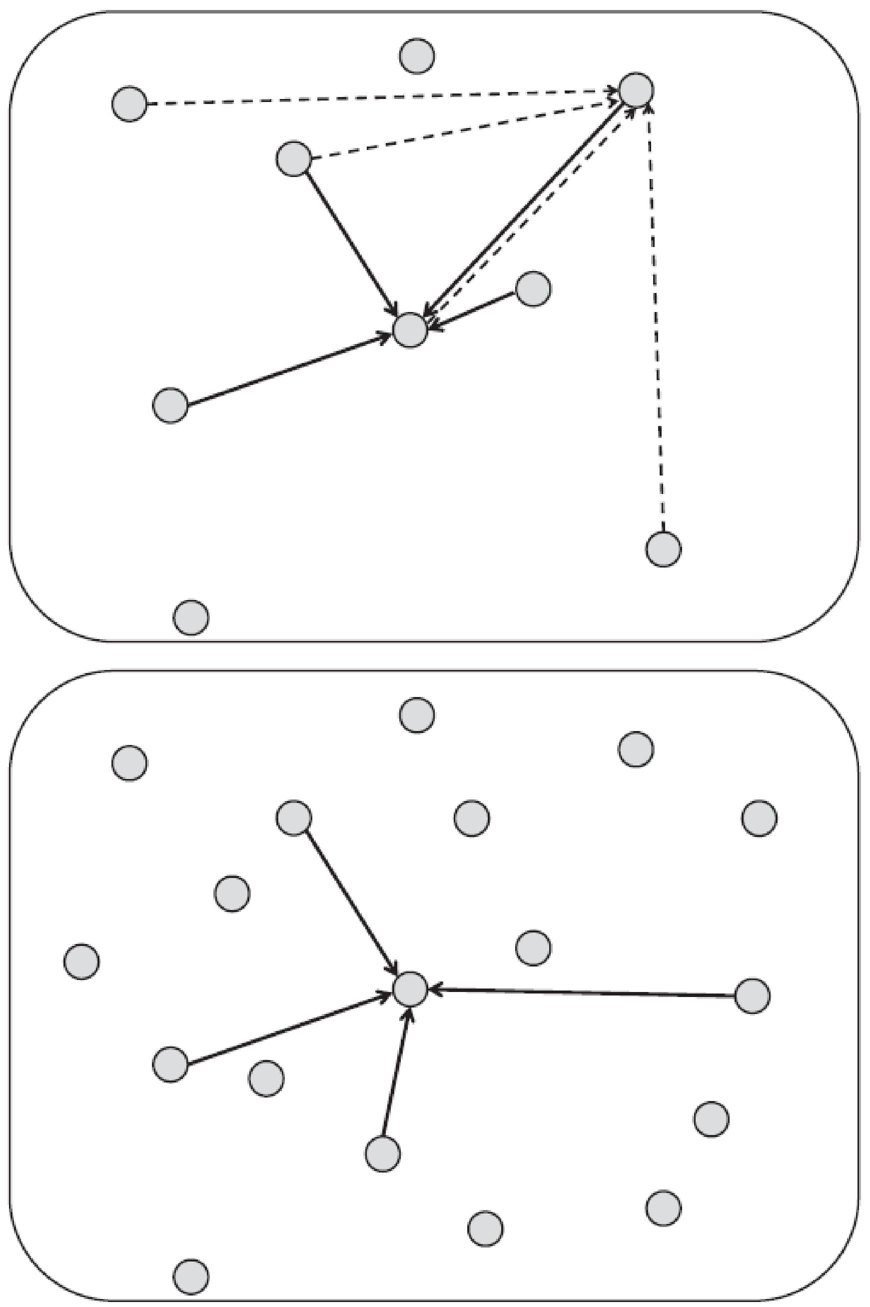
Each neuron receives
N connections

Each neuron receives
K connections

3. Random connectivity – fixed number of inputs

random: number of inputs K=500, fixed

Network N=5 000



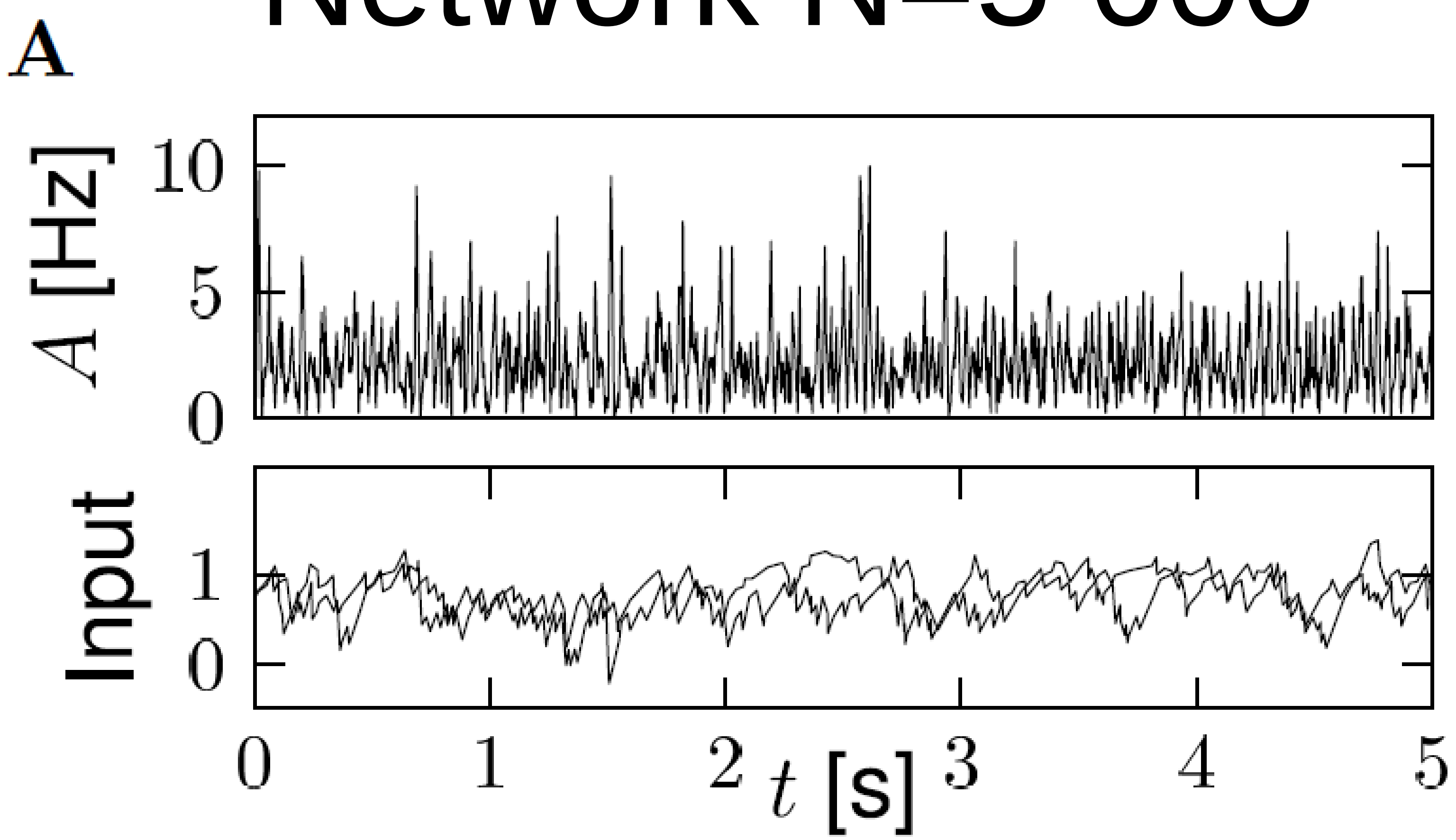


Fig. 12.8: Simulation of a model network with a fixed number of presynaptic partners (400 excitatory and 100 inhibitory cells) for each postsynaptic neuron. **A**. Top: Population activity $A(t)$ averaged over all neurons in a network of 4 000 excitatory and 1 000 inhibitory

Image: Gerstner et al. Neuronal Dynamics (2014)

3. Random connectivity – fixed number of inputs

random: number of inputs K=500, fixed

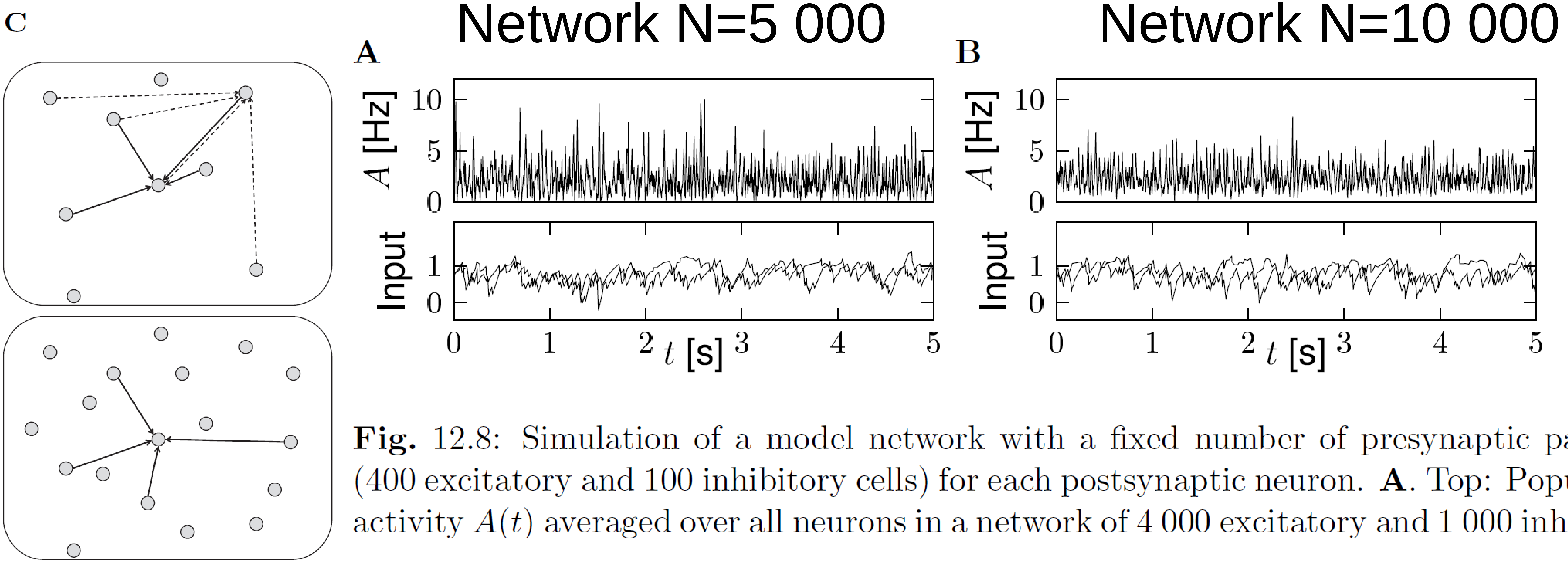


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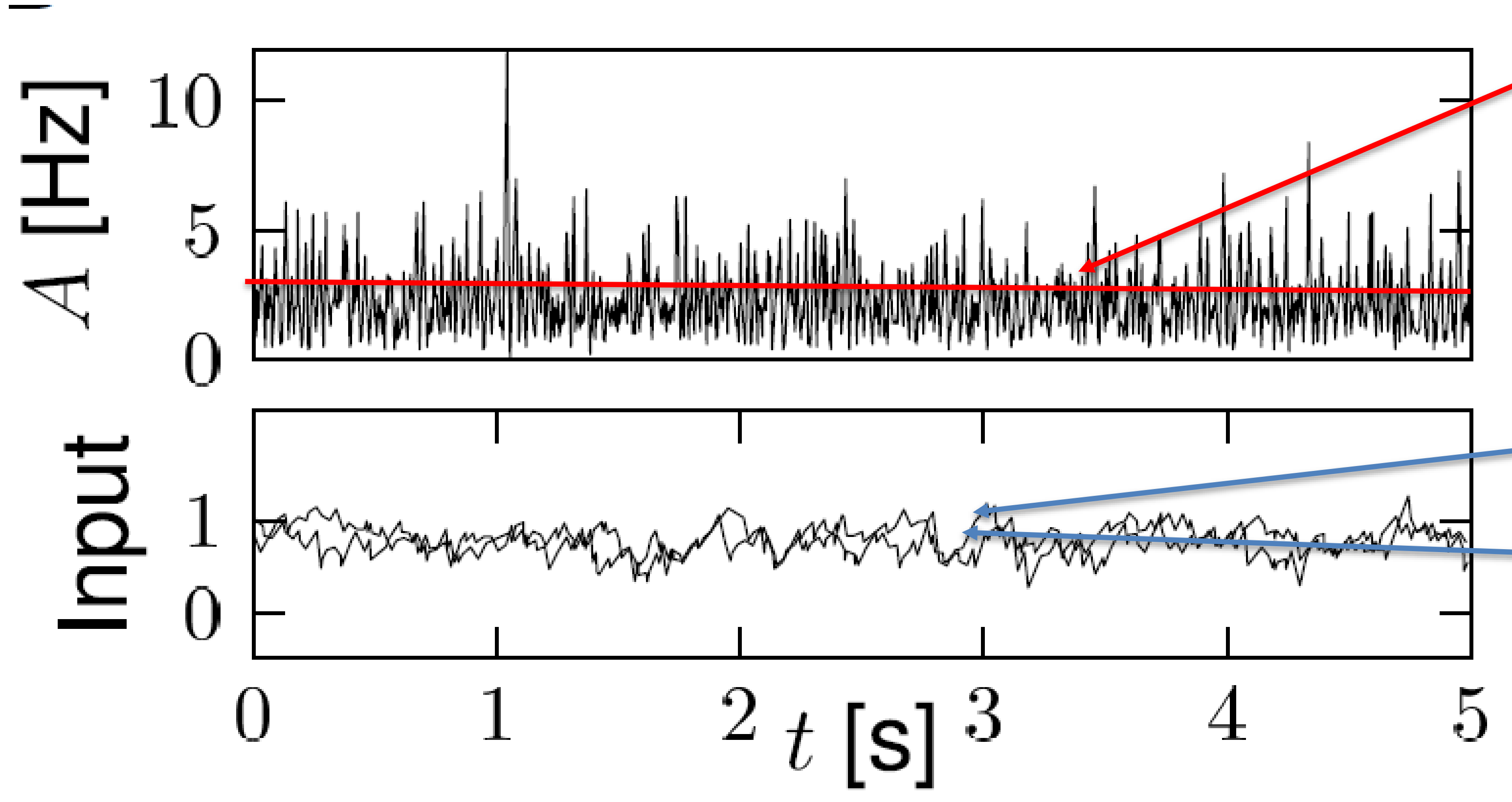
Image: Gerstner et al. Neuronal Dynamics (2014)

3. Random Connectivity: stationary asynchronous activity

Observations:

stationary asynchronous activity

- $A(t)$ is nearly constant
- $A(t)=A_0$ independent of N



Input is nearly identical for different neurons (and nearly constant)

3. Random Connectivity network: population activity

Can we mathematically predict the population activity?

given

- connection probability p and
- weight w_{ij}
- properties of individual neurons
- large population

Can we mathematically define stationary asynchronous activity?

Quiz 3, now

You simulate a network of 5000 neurons or 10000 neurons. In both networks you have randomly selected 500 input connections for each neuron. You observe that the population activity fluctuations around a stationary value.

[ ] The connectivity in the first network is 10 percent.

[ ] The connectivity in the second network is 10 percent.

[ ] Since there are twice as many neurons, the value of the stationary population activity increases by a factor of 2 when you compare the network of 10000 neurons with that of 5000 neuron.

[ ] The value of the average input into one neuron increases by a factor of 2 when you compare the network of 10000 neurons with that of 5000 neuron.

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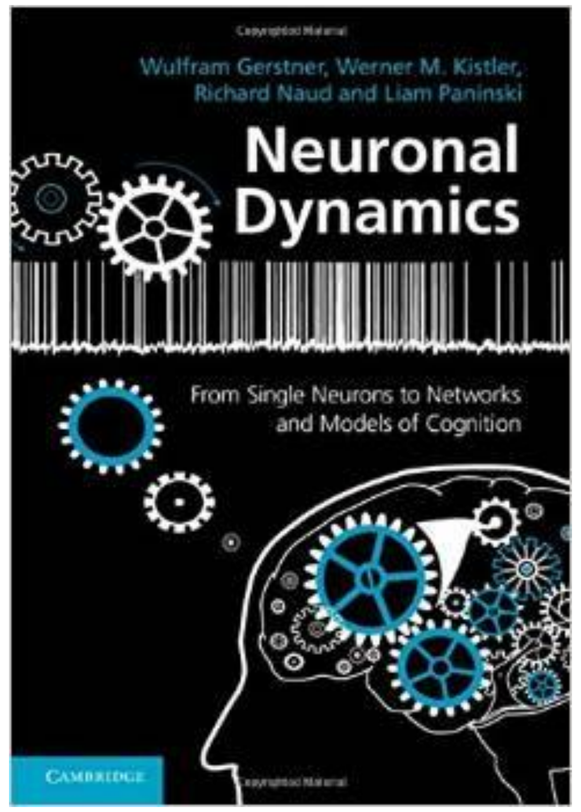

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4. Review and aims

Can we mathematically predict the population activity?

given
- **connection probability *p* and**
- **weight w_{ij}**
- **properties of individual neurons**
- **large population**

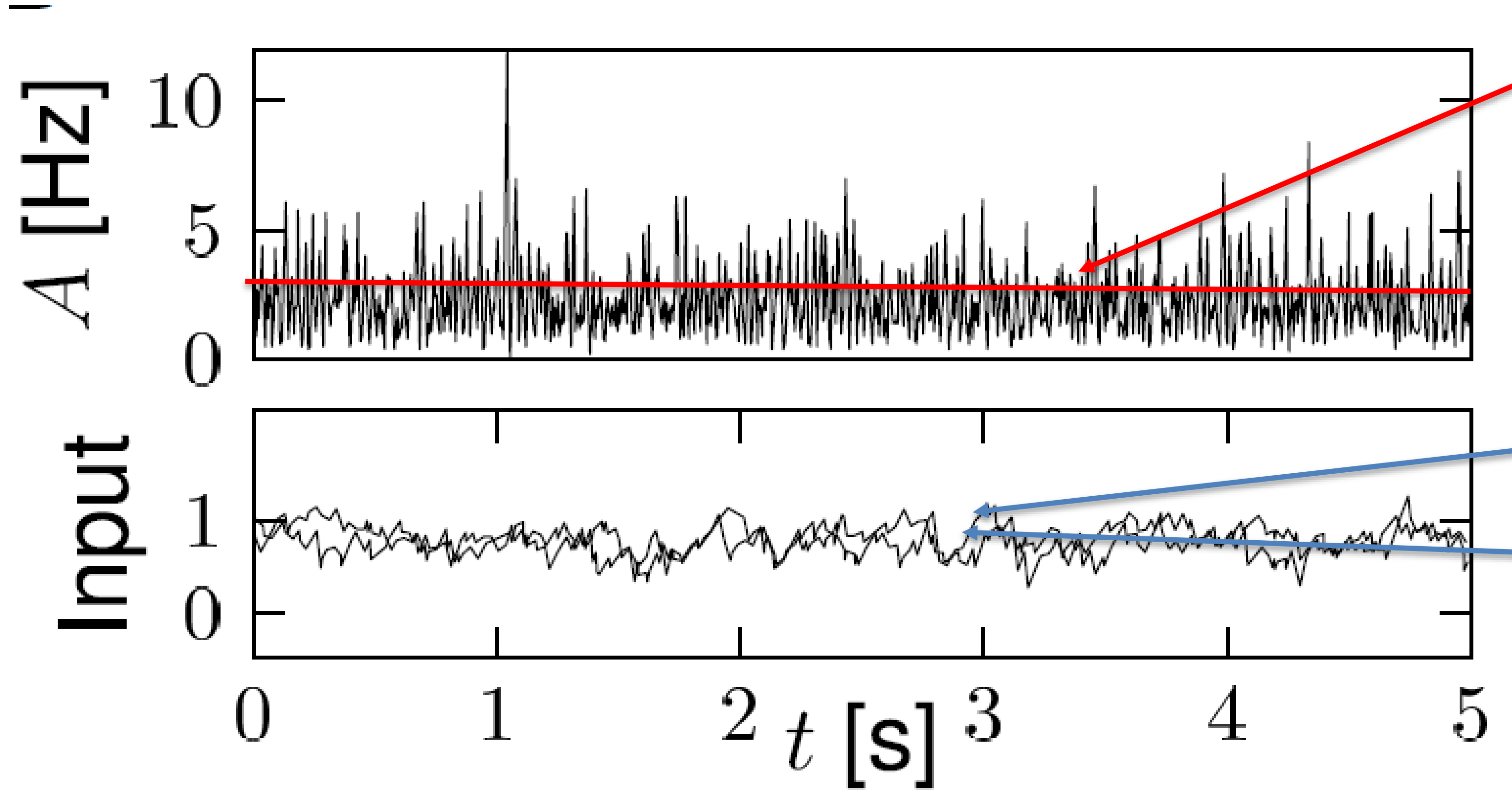
Can we mathematically define stationary asynchronous activity?

4. Review: stationary asynchronous activity

Observations:

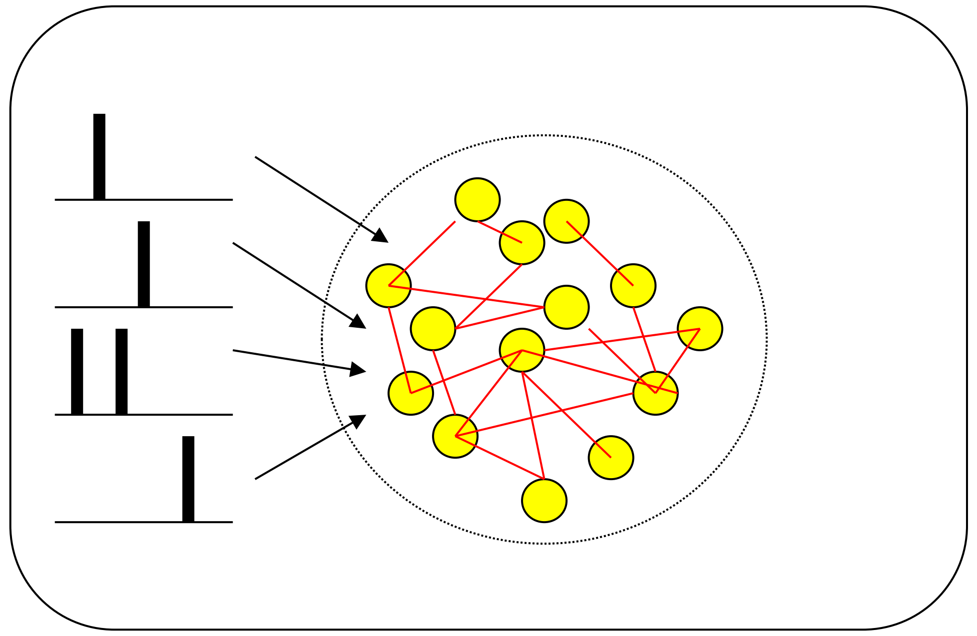
stationary asynchronous activity

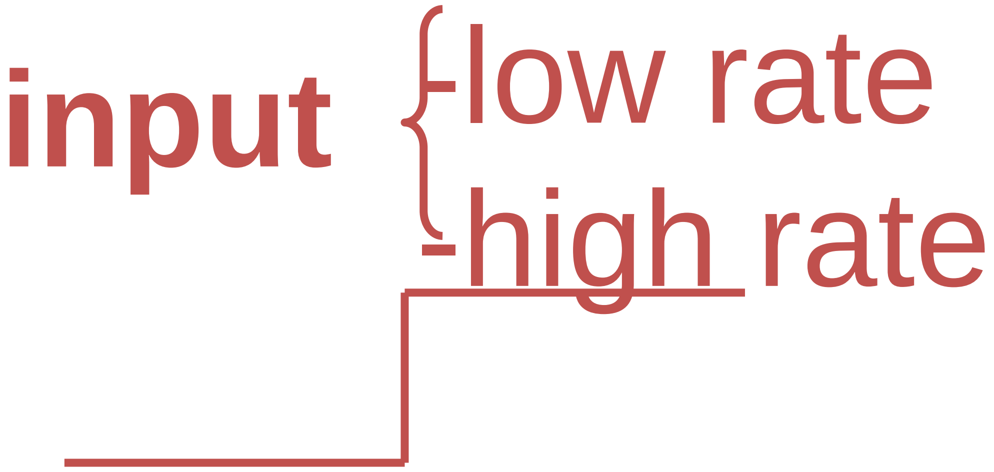
- $A(t)$ is nearly constant
- $A(t)=A_0$ independent of N



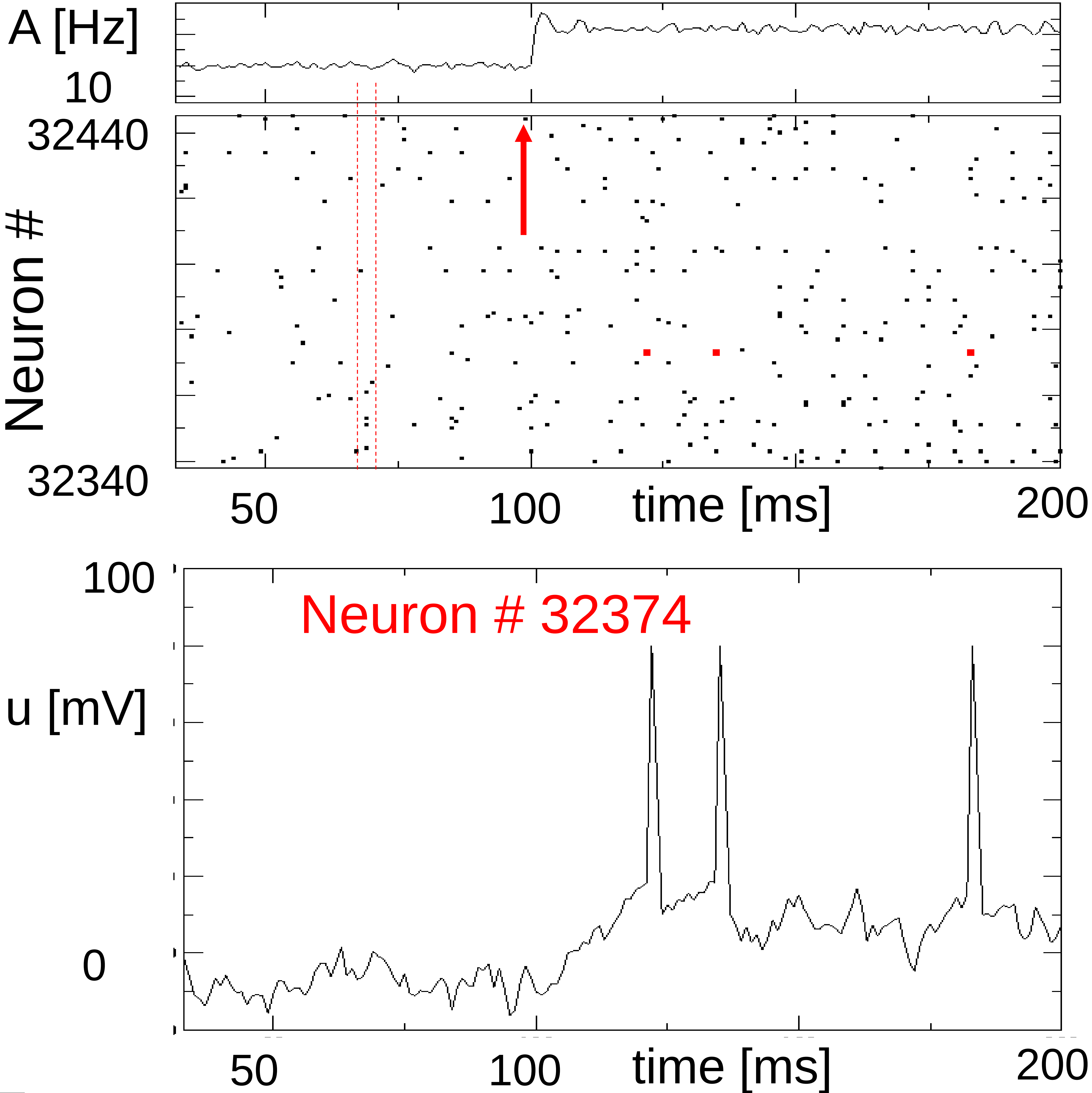
Input is nearly identical for different neurons (and nearly constant)

4. asynchronous firing / asynchronous state





Population
- 50 000 neurons
- 20 percent inhibitory
- **randomly connected**



4. asynchronous state

- Definition of $A(t)$
- filtered $A(t)$
- $<A(t)>$

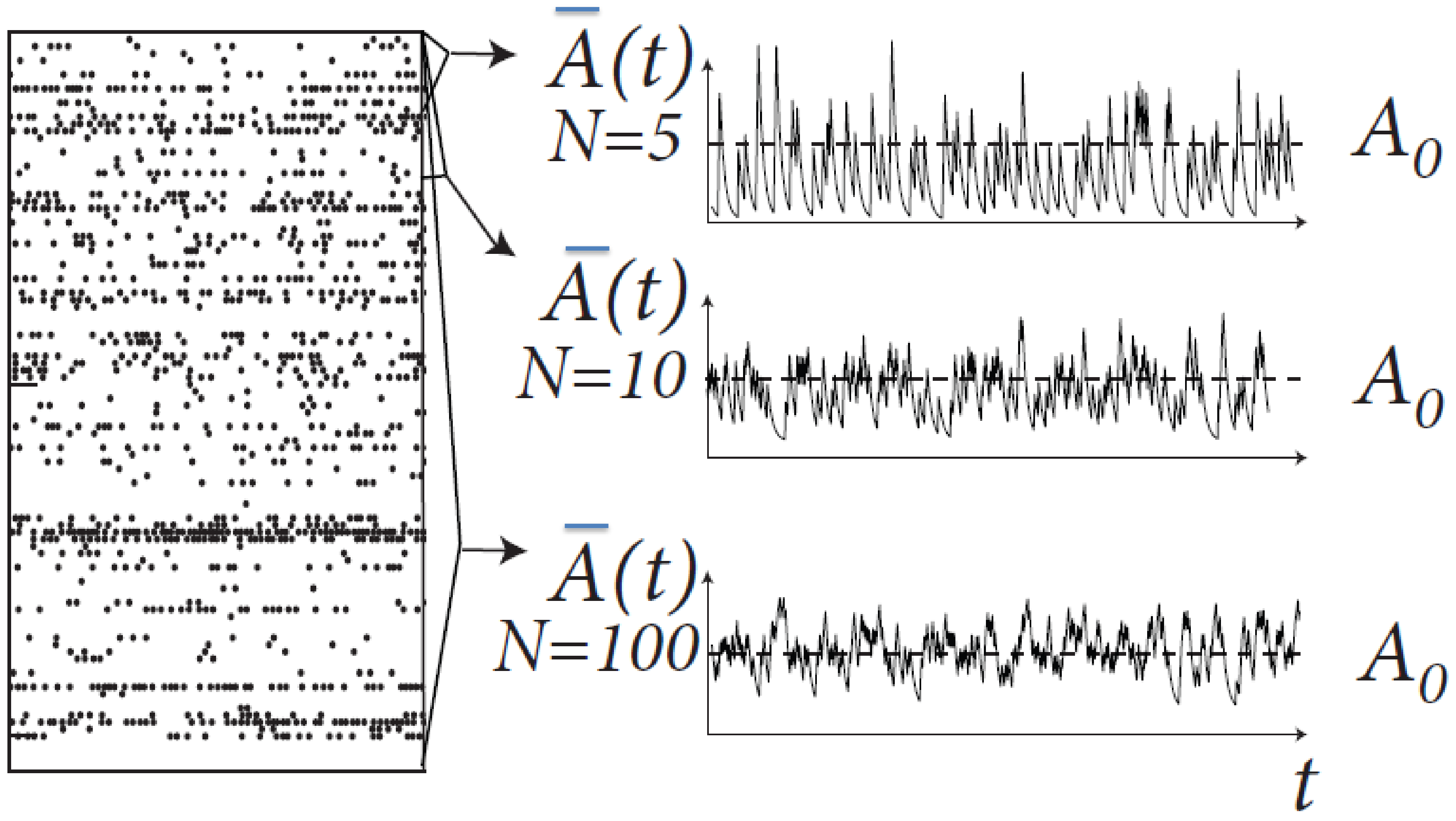


Image: Gerstner et al.
Neuronal Dynamics (2014)

Asynchronous state

$<A(t)> = A_0 = \text{constant}$

4. asynchronous state

Asynchronous state

$<A(t)> = A_0 = constant$

- filtered $A(t)$
- convergence in weak sense

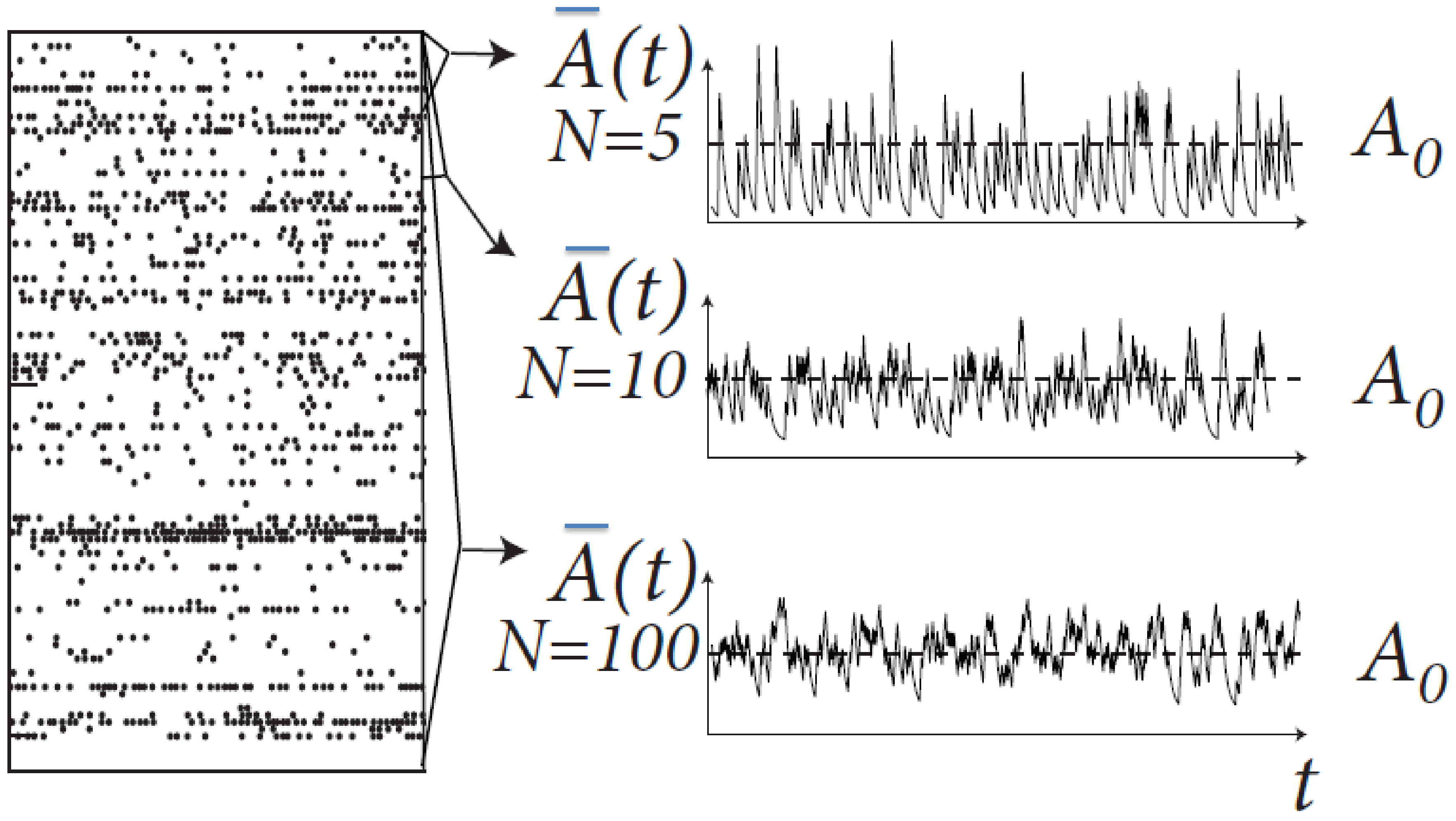
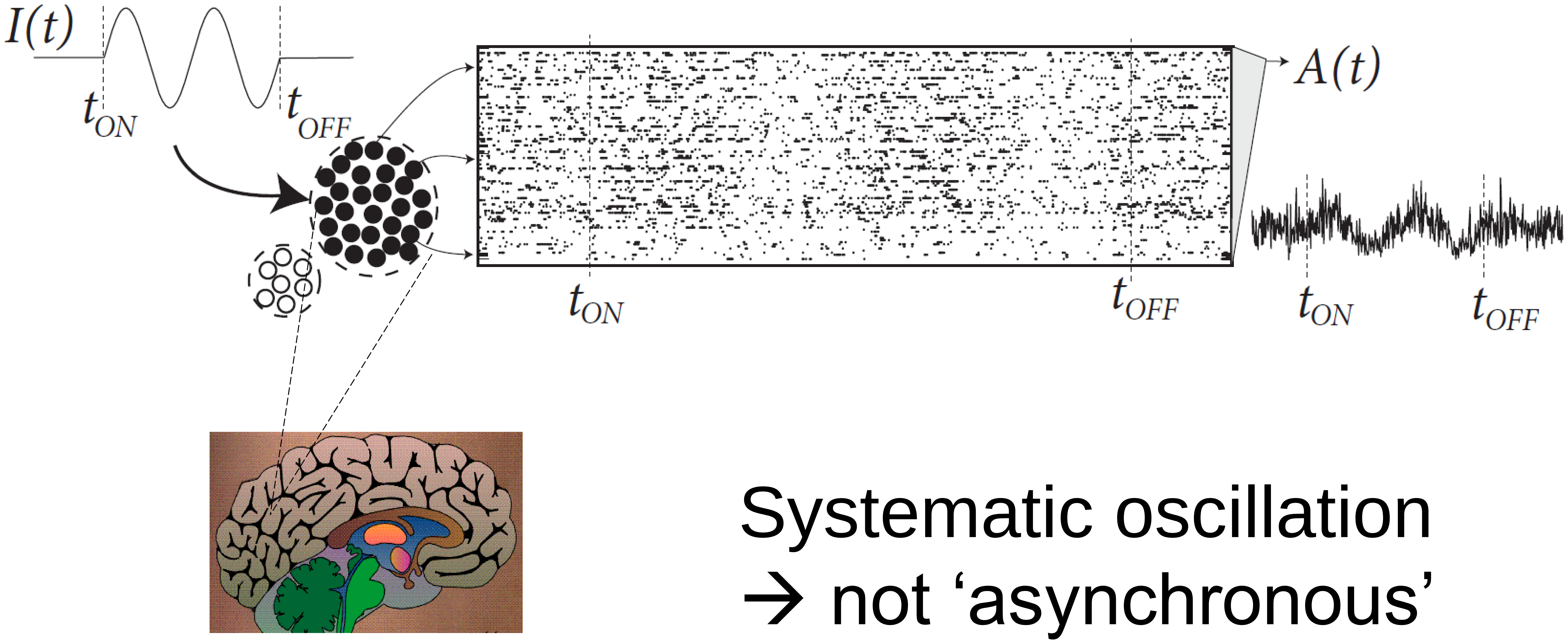


Image: Gerstner et al.
Neuronal Dynamics (2014)

Weak convergence in Hilbert space:
https://en.wikipedia.org/wiki/Weak_convergence_(Hilbert_space)

4. asynchronous state – counter examples, <A(t)> not constant

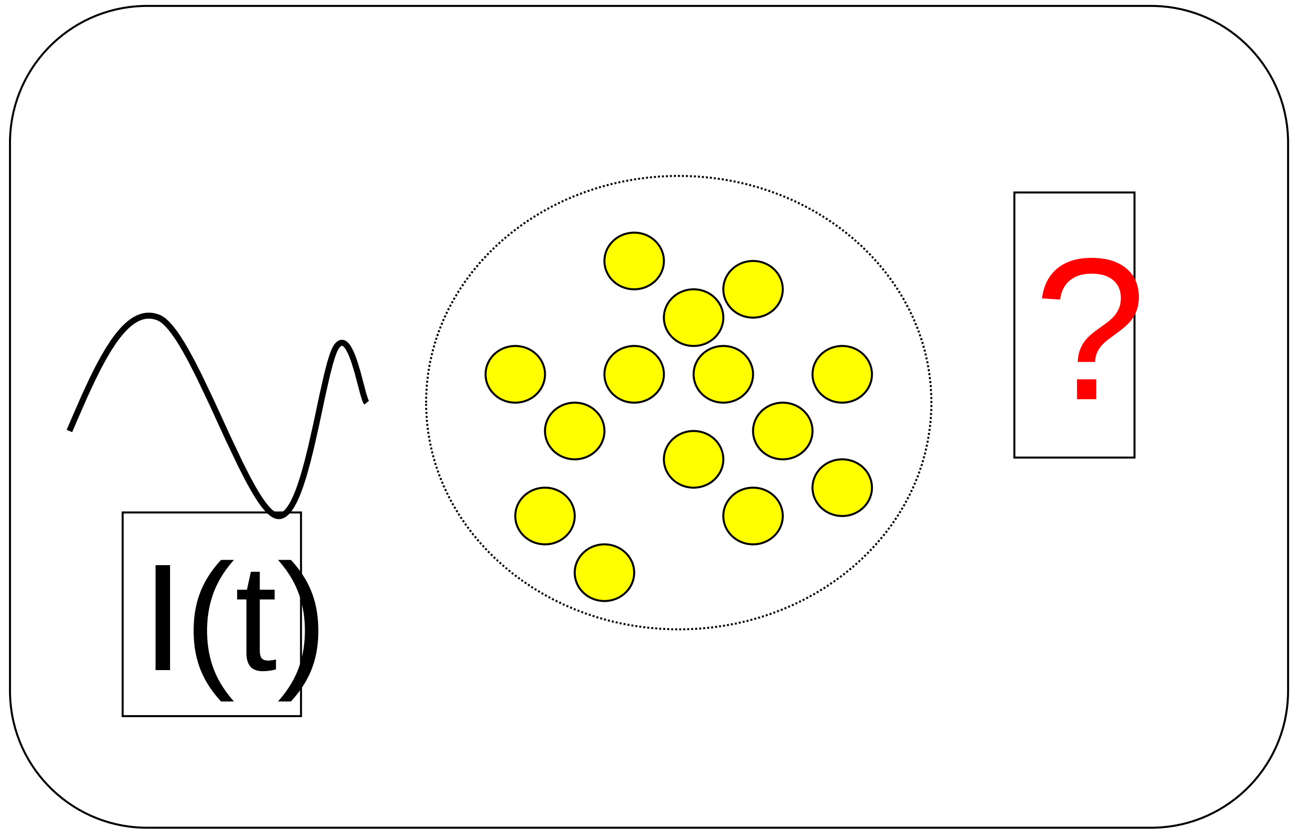
population of neurons
with similar properties



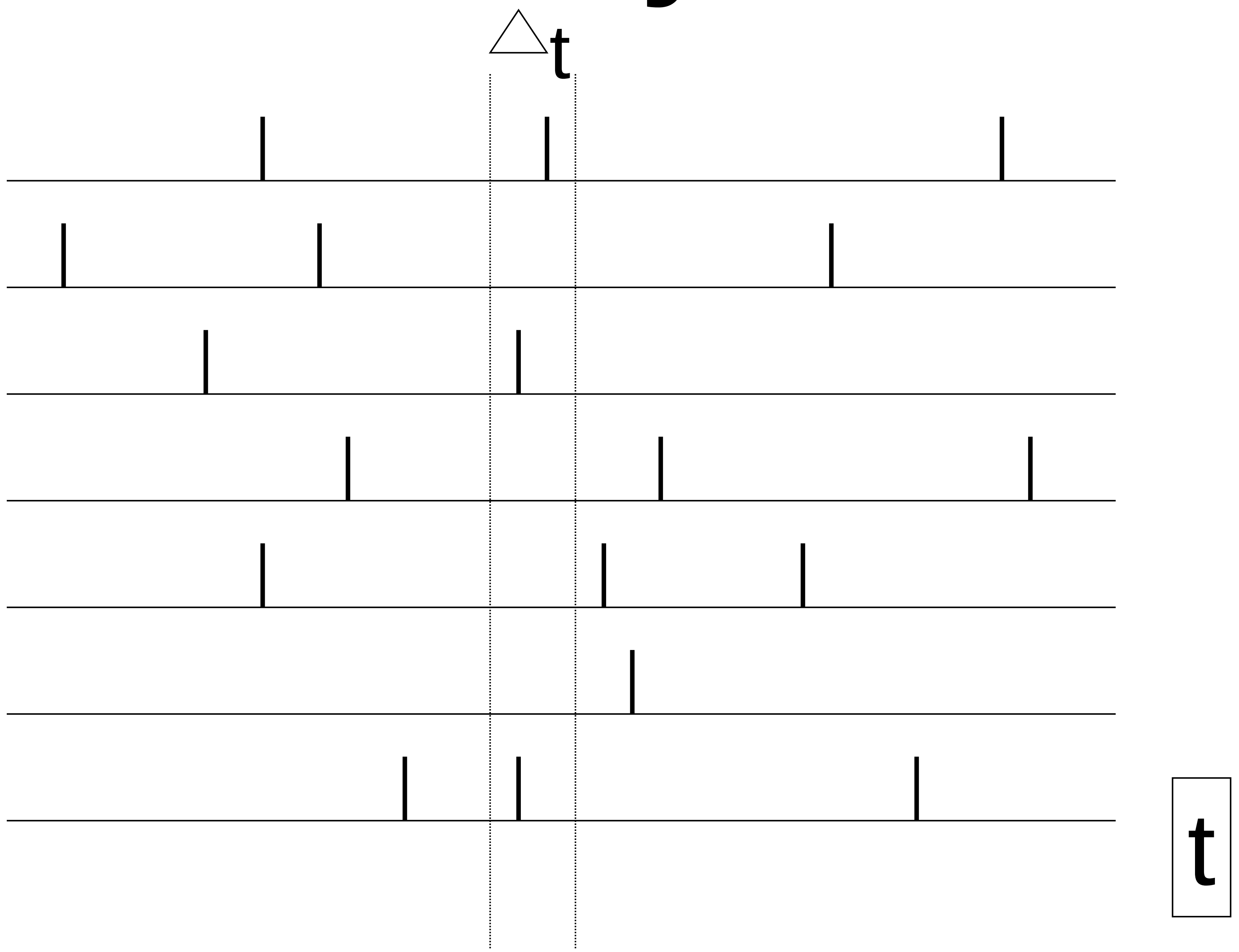
Systematic oscillation
→ not ‘asynchronous’

Brain

4. asynchronous state in a homogeneous network



population activity?



Homogeneous network:

-all neurons are ‘the same’
-all synapses are ‘the same’
-each neuron receives input from k neurons in network
-each neuron receives the same (mean) external input

population activity

$$A(t) = \frac{n(t;t+\Delta t)}{N\Delta t}$$

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Wulfram Gerstner

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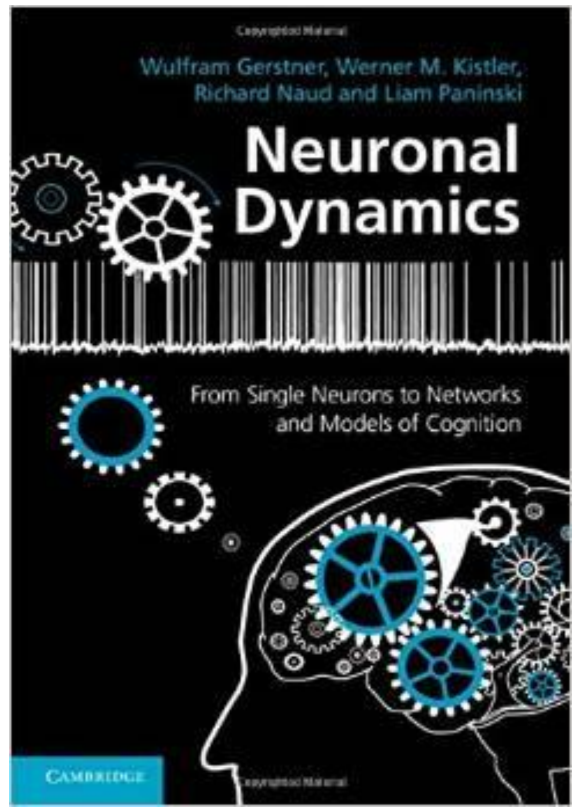

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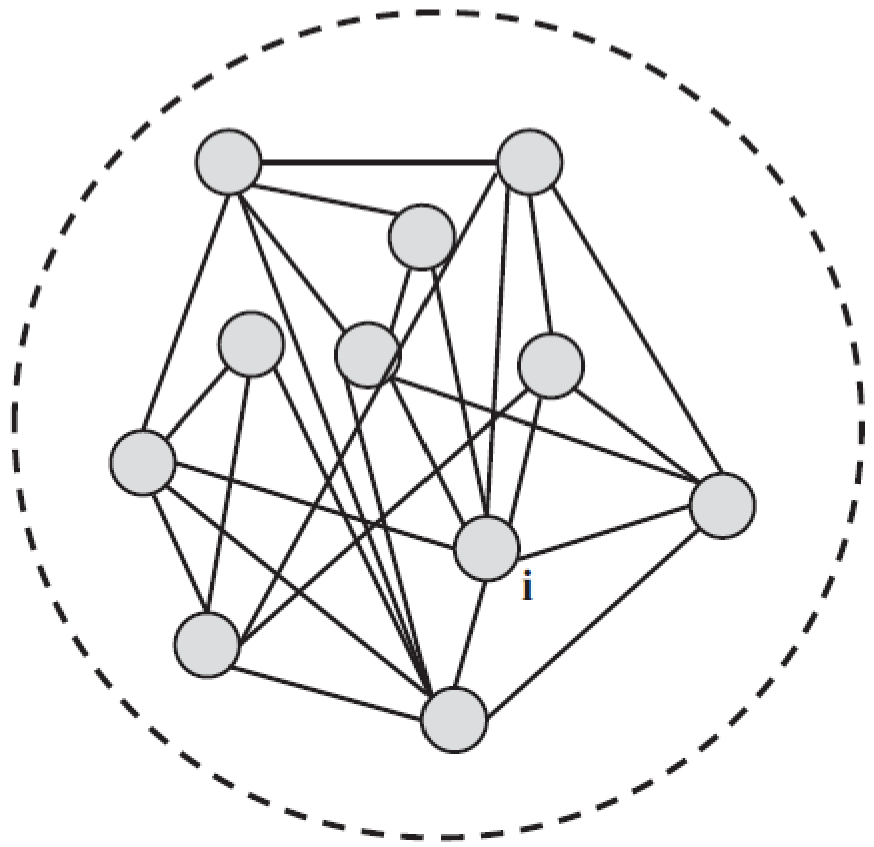
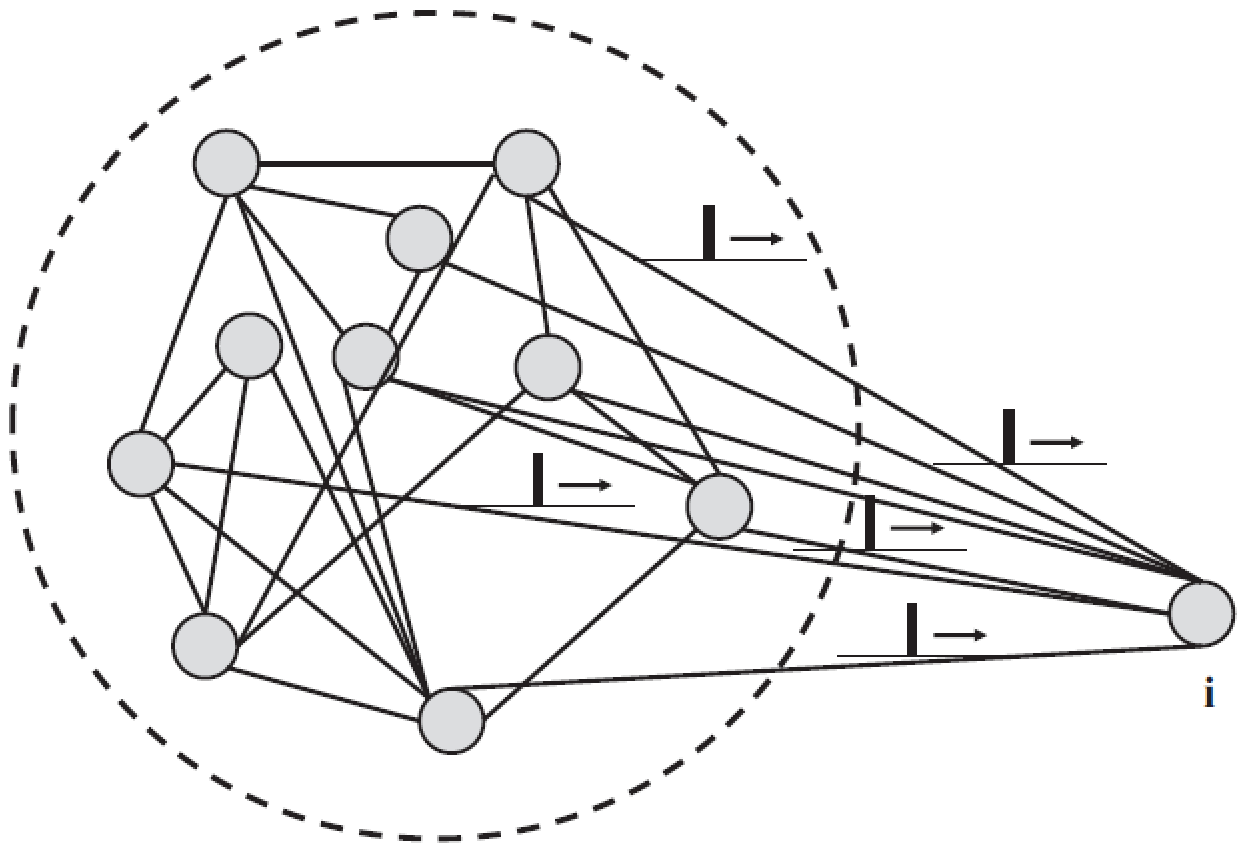
   - Balanced state

4. mean-field arguments (full connectivity)

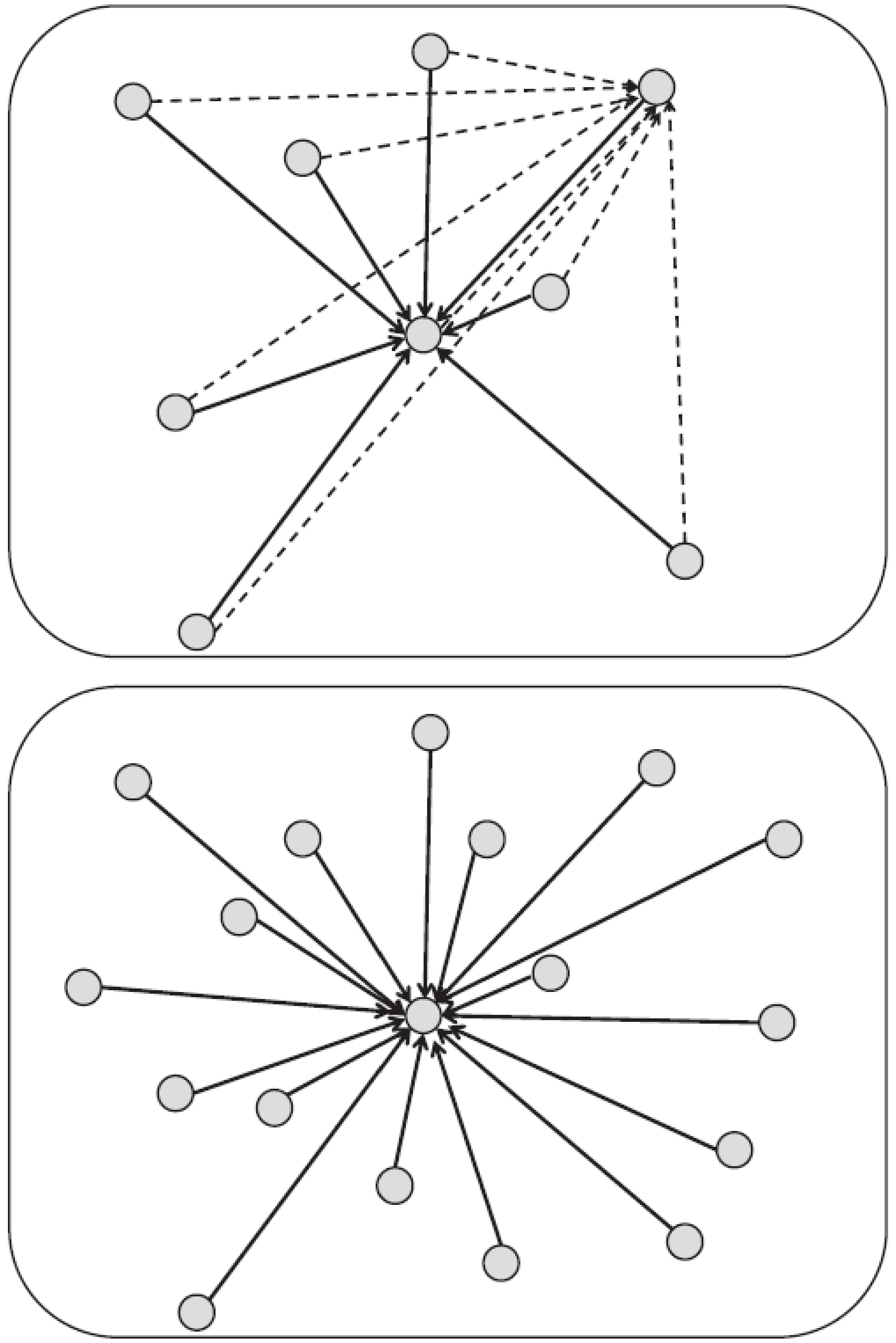
Input to neuron i



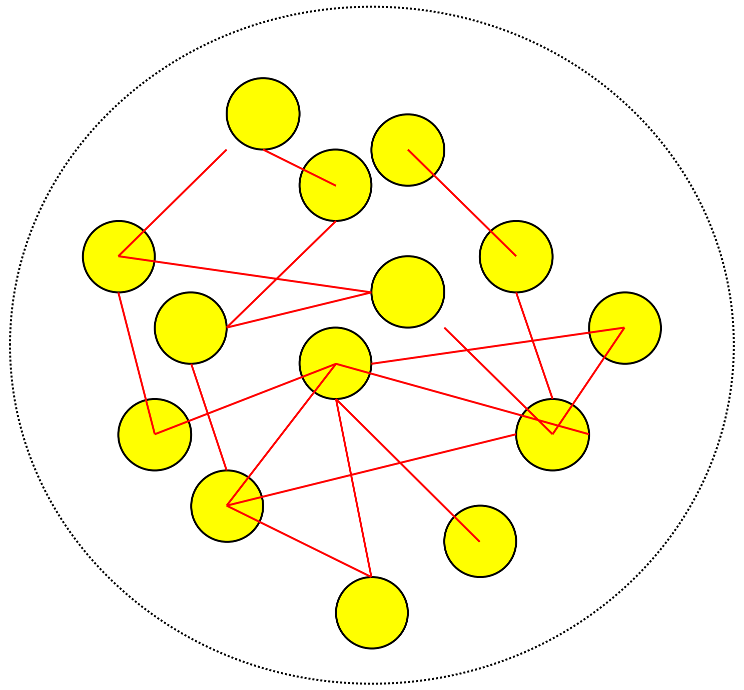


4. mean-field arguments (full connectivity)

A

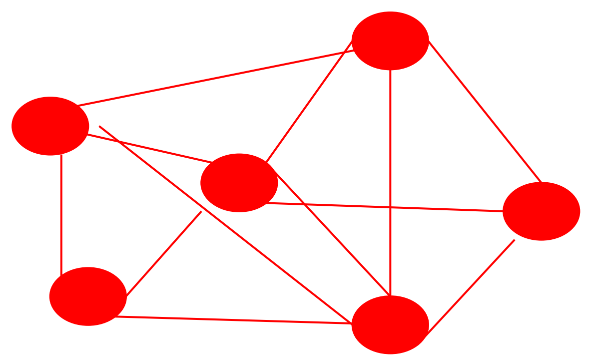


Full connectivity



4. mean-field arguments (full connectivity)

Fully connected network



fully connected

N >> 1

$$I(t) = I^{ext}(t) + I^{net}(t)$$

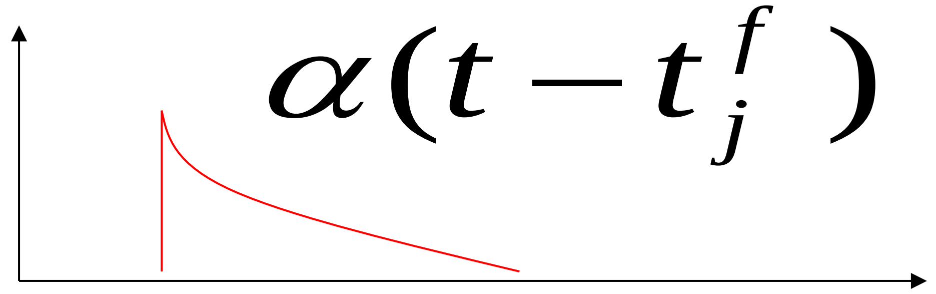
All spikes, all neurons

$$I^{net}(t) = \sum_j \sum_f w_{ij} \, \alpha(t - t_j^f)$$

Synaptic coupling

$$w_{ij} = w_0$$

$$\alpha(t - t_j^f)$$

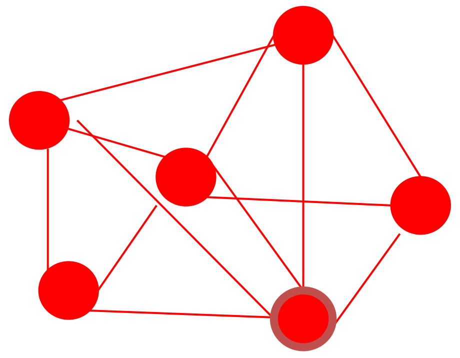


4. mean-field arguments (full connectivity)

All neurons receive the same total input current ('mean field')

$$I_{i}(t) = J_0 \int \alpha(s)\, A(t-s)\, ds + I^{ext}(t)$$

Index i disappears



$$w_{ij} = \frac{J_0}{N}$$

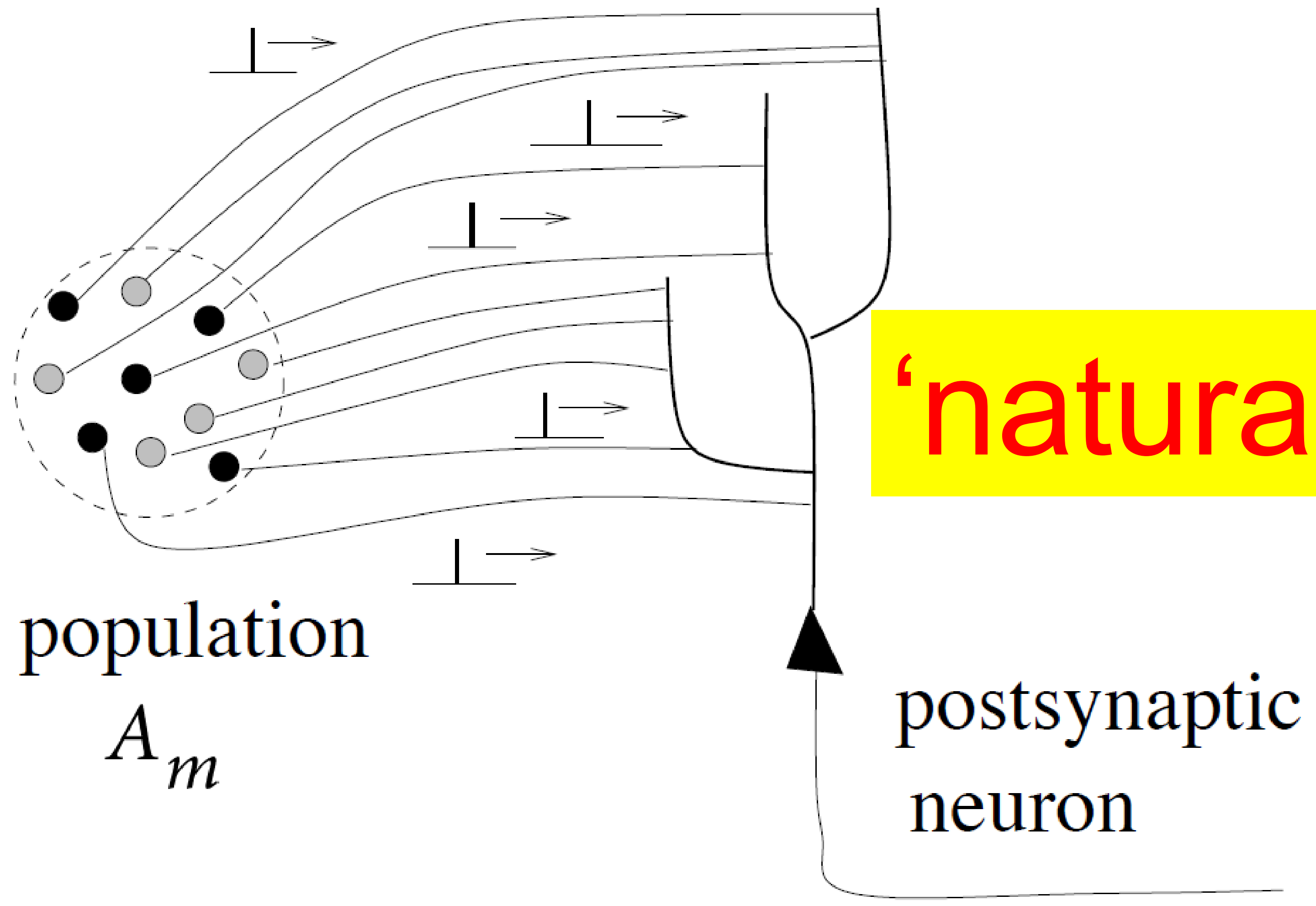
All spikes, all neurons

$$I^{net}(t) = \sum_j \sum_f w_{ij}\, \alpha(t - t_j^f) + I^{ext}(t)$$

4. mean-field arguments (full connectivity)

All neurons receive the same total input current ('mean field')

$$I_i(t) = J_0 \int \alpha(s)\, A(t-s)\,ds + I^{ext}(t)$$



'natural readout'

Quiz 4, now

In a fully connected homogeneous network of 5000 neurons, the total input into neuron i=10

[ ] is the same as the input into its neighbors (i=9 and i=11)
[ ] is the same as the input into the neuron i=3564
[ ] depends on the population activity of the network
[ ] is always constant

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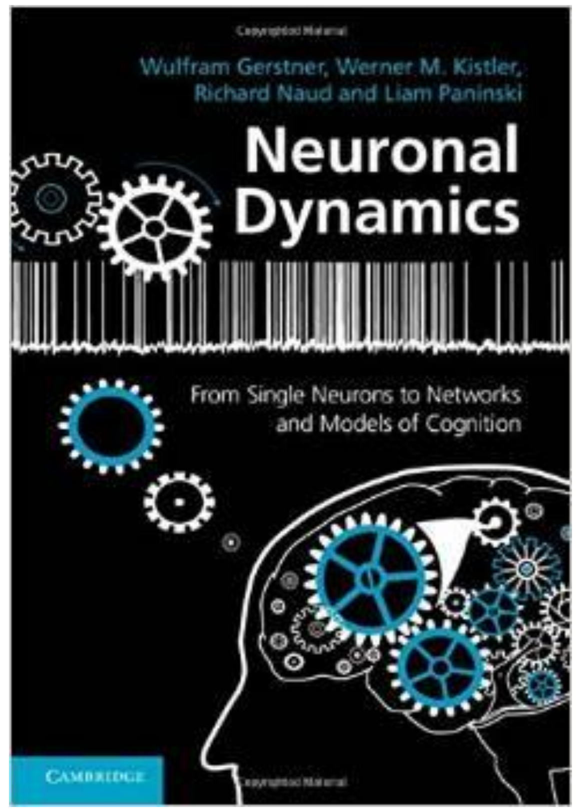

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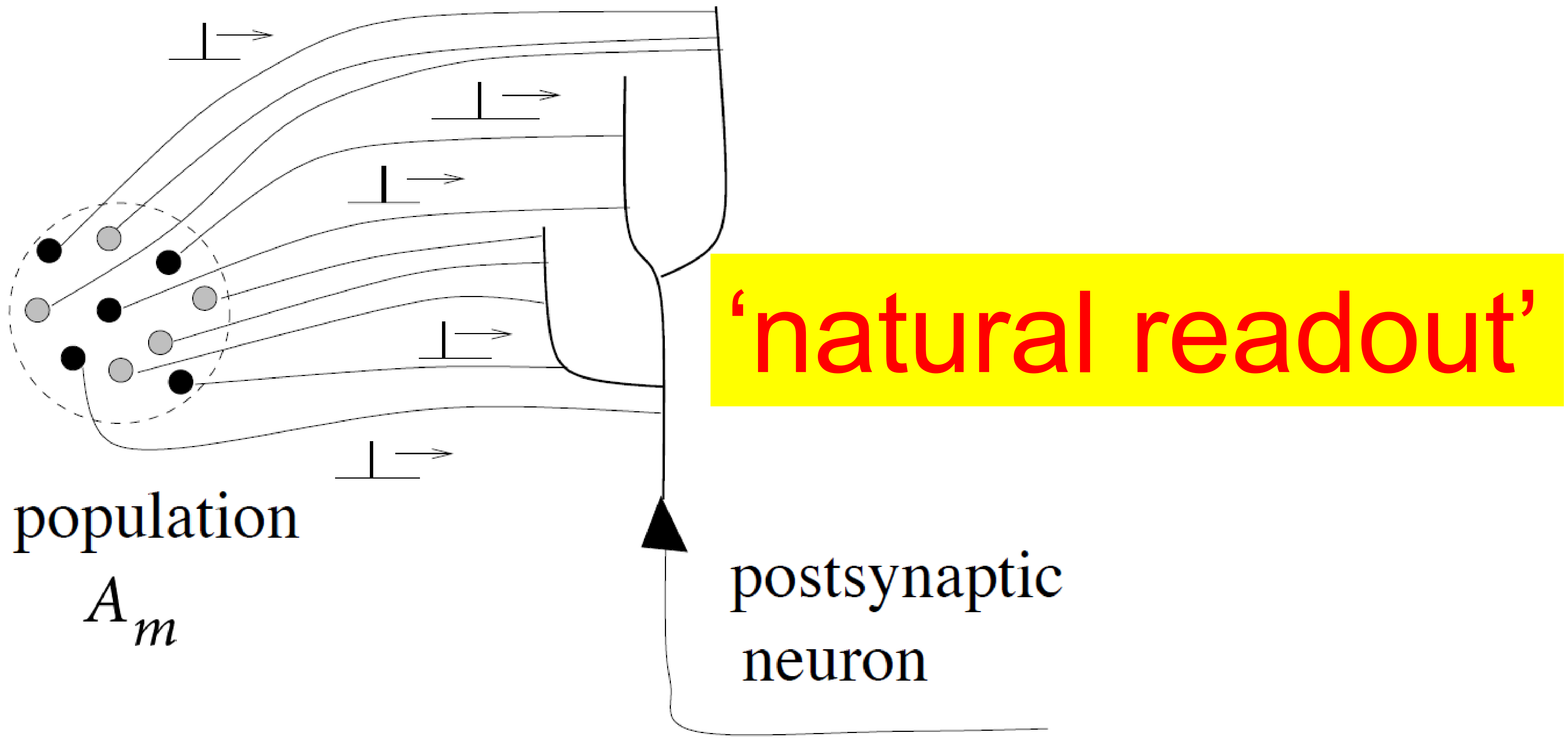
   - Balanced state

5. Review and aims: predict activity

- all neurons receive the same input current
- population activity drives input

→ Predict population activity?



5. mean-field arguments: asynchronous state

Stationary state

Assume all variables are constant in time:

$$I_i(t) = J_0 \int \alpha(s)\, A(t-s)\, ds \quad + I^{ext}(t)$$

(1) $I_0 = [J_0 q A_0 + I_0^{ext}]$

Firing rate? Population rate?

5. mean-field argument: f-I curve of single neuron

$$I_0 = [J_0 q A_0 + I_0^{ext}]$$

Firing rate?

5. mean-field argument: population rate = single neuron rate

5. mean-field arguments: population activity (asynchr. state)

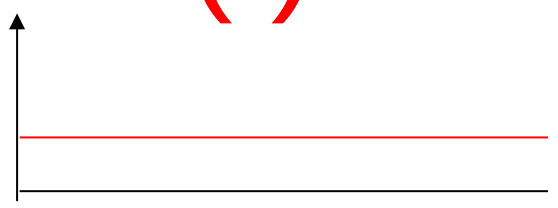
Input is constant and identical for all neurons

(1) $$I_0 = [J_0 q A_0 + I_0^{ext}]$$ $$q = \int \alpha(s)ds$$

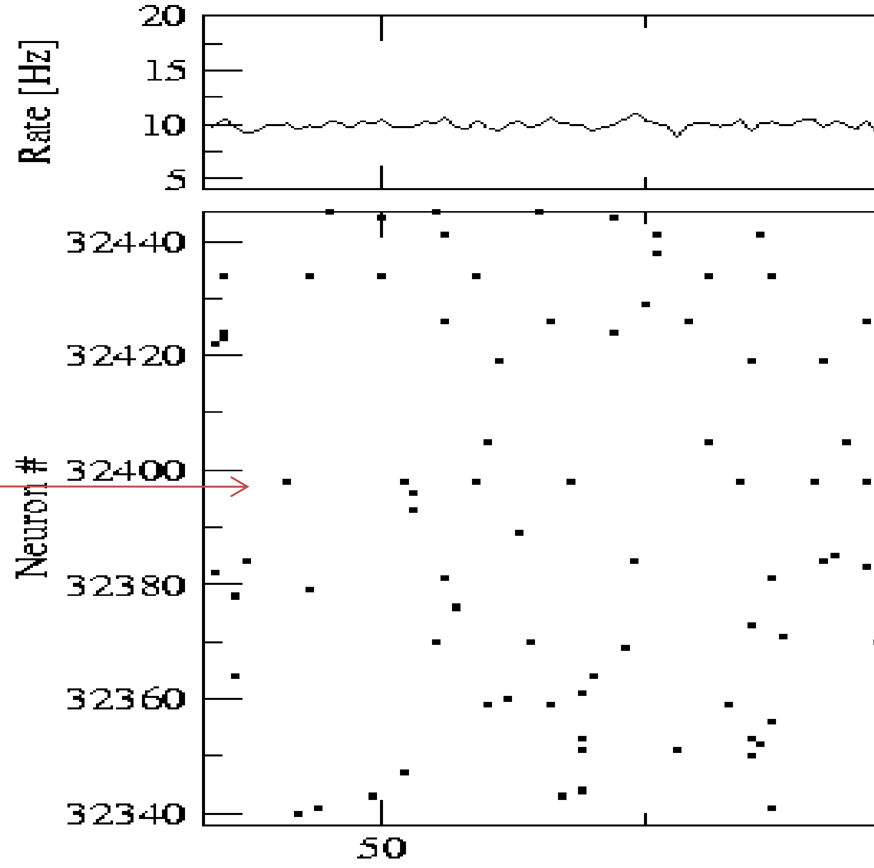
frequency (single-neuron gain function)

(2) $$\nu = g(I_0)$$

A(t)= A_0= const



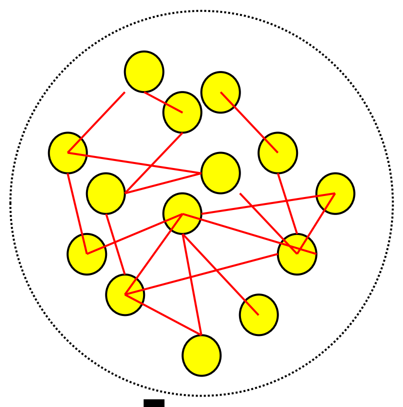
Single neuron



Homogeneous network

All neurons are identical,

Single neuron rate = population rate



(3) $$\nu = A_0$$

5. stationary solution: population activity (asynchr. State)

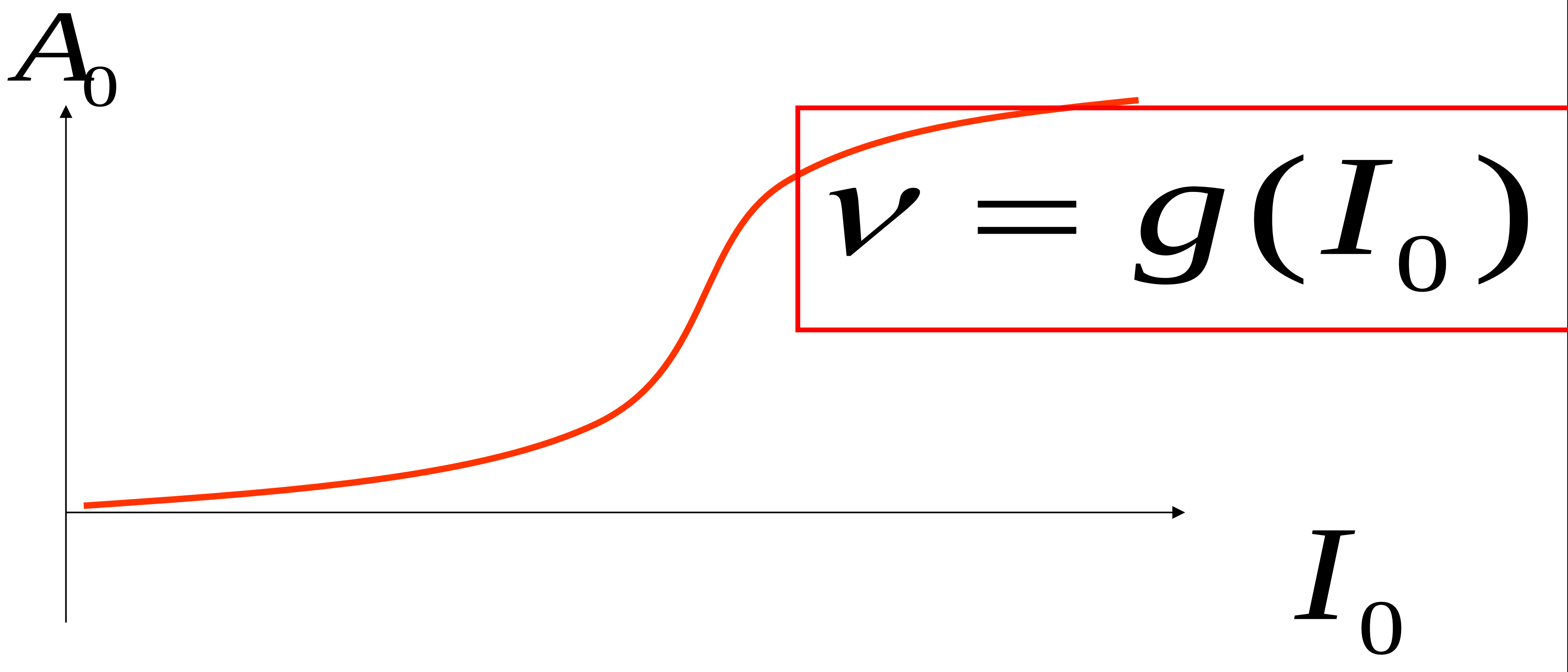
Stationary solution

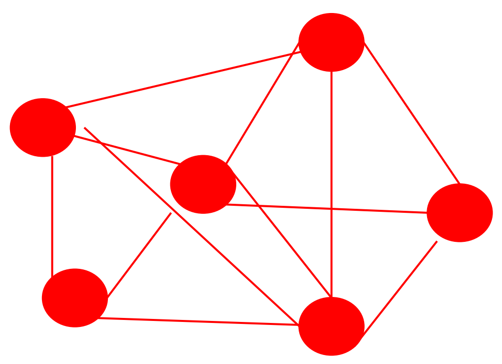
=asynchronous state

(1) $I_0 = [J_0 q A_0 + I_0^{ext}]$

(2) $\nu = g(I_0)$

(3) $\nu = A_0$





fully connected

N >> 1

$$\nu = g(I_0) = A_0$$

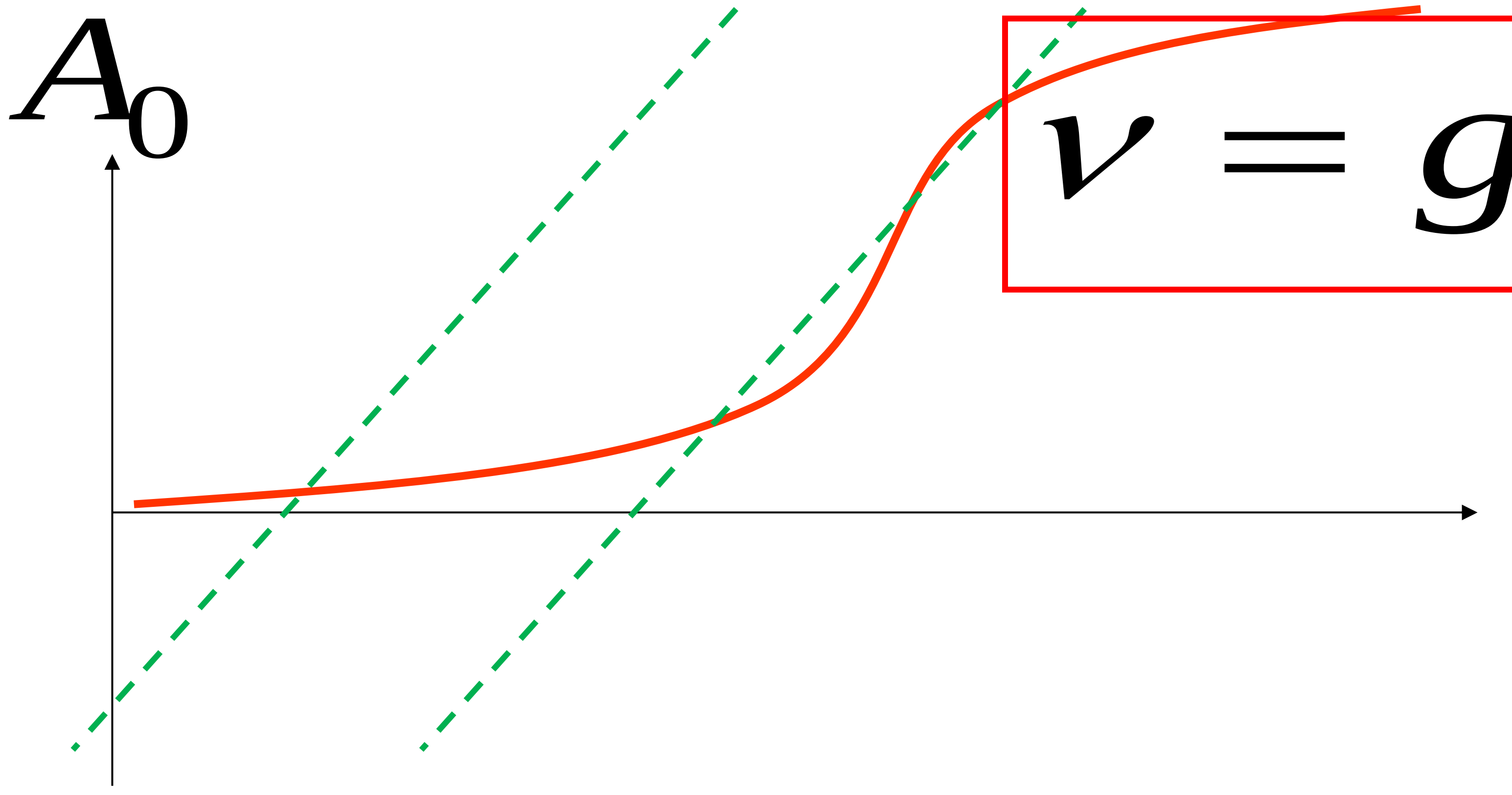
5. stationary solution: population activity (asynchr. state)

Stationary solution
=asynchronous state

(1) $I_0 = [J_0 q A_0 + I_0^{ext}]$

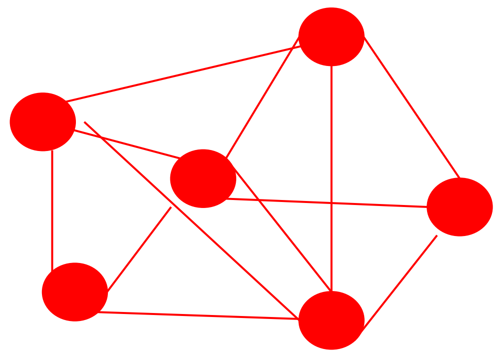
(2) $\nu = g(I_0)$

(3) $\nu = A_0$



$\nu = g(I_0)$

Stationary solution



fully
connected
N >> 1

Homogeneous network, stationary,
All neurons are identical,
Single neuron rate = population rate

5. stationary solution: population activity (asynchr. state)

Single Population

- homogeneous
- full connectivity
- stationary state/asynchronous state

Single neuron rate = population rate

$$A_0 = \nu = g(I_0) = g(J_0 q A_0 + I_0^{ext})$$

5. stationary solution: population activity (asynchr. state)

Single Population

- homogeneous
- full connectivity
- stationary state/asynchronous state

Single neuron rate = population rate

$$A_0 = \nu = g(I_0) = g(J_0 q A_0 + I_0^{ext})$$

→ **What is this function g?**

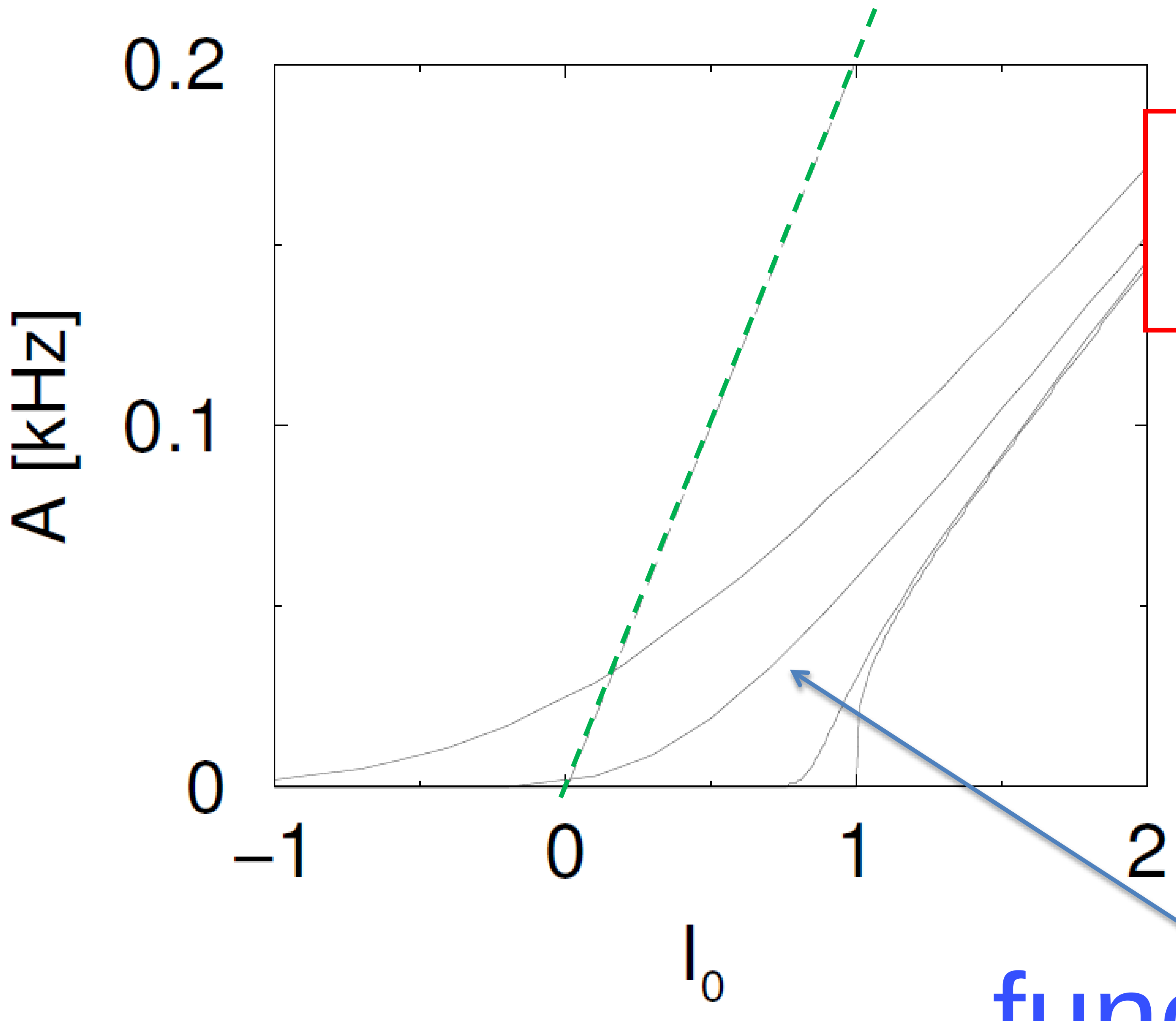
Examples:
- leaky integrate-and-fire (with noise)
- Spike Response Model (with noise)
- Hodgkin-Huxley model

http://lcn.epfl.ch/~gerstner/NeuronalDynamics-MOOC1.html

5. stationary solution: integrate-and-fire neurons

$$I_0 = J_0 q A_0 + I_0^{ext}$$

$$[I_0 - I_0^{ext}] / J_0 q = A_0$$



$$\nu = g_\sigma(I_0)$$

different noise levels

function *g* can be calculated

5. gain function is noise-dependent

Gain-function *g* =frequency-current relation = f-I curve

function *g* can be calculated analytically or measured in **single-neuron simulations/single-neuron experiments**

$$\nu = g_\sigma(I_0)$$

different noise levels

http://lcn.epfl.ch/~gerstner/NeuronalDynamics-MOOC1.html

5. stationary solution: population activity (asynchr. state)

Single Population

- homogeneous
- full connectivity
- stationary state of asynchronous firing

Single neuron rate = population rate

$$A_0 = \nu = g(I_0) = g(J_0 q A_0 + I_0^{ext})$$

Gain function for constant input

- available for many neurons
- available for many neuron models

Limited to stationary state.

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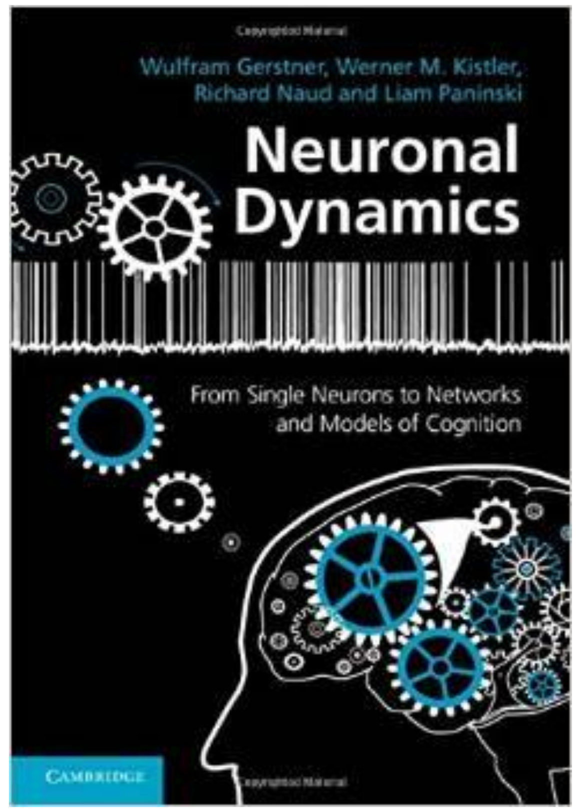

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6. mean-field arguments (random connectivity)

So far:
Full connectivity

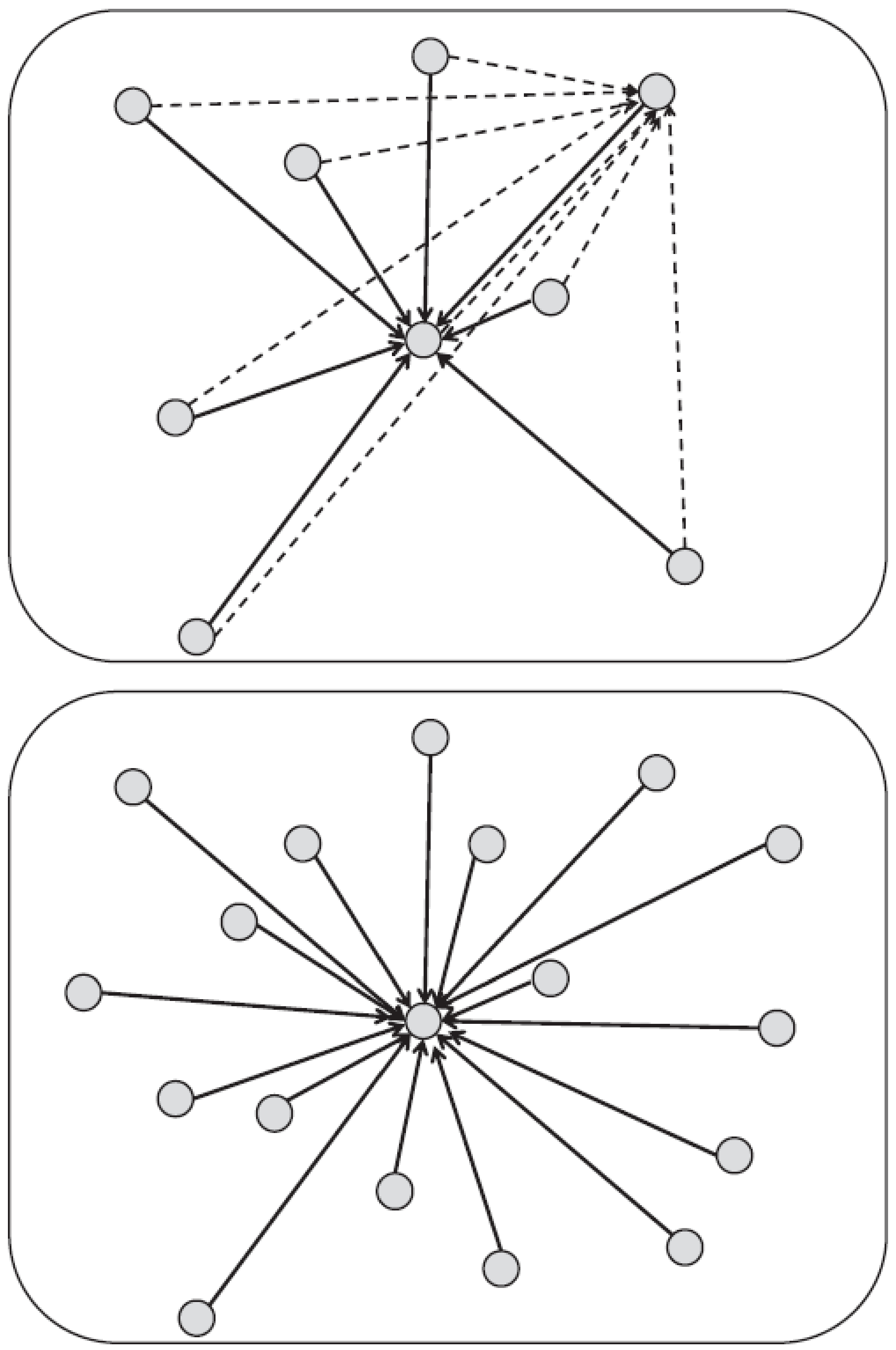
More realistic:
random connectivity

Can we repeat the
mean-field arguments?

6. mean-field arguments (random connectivity)

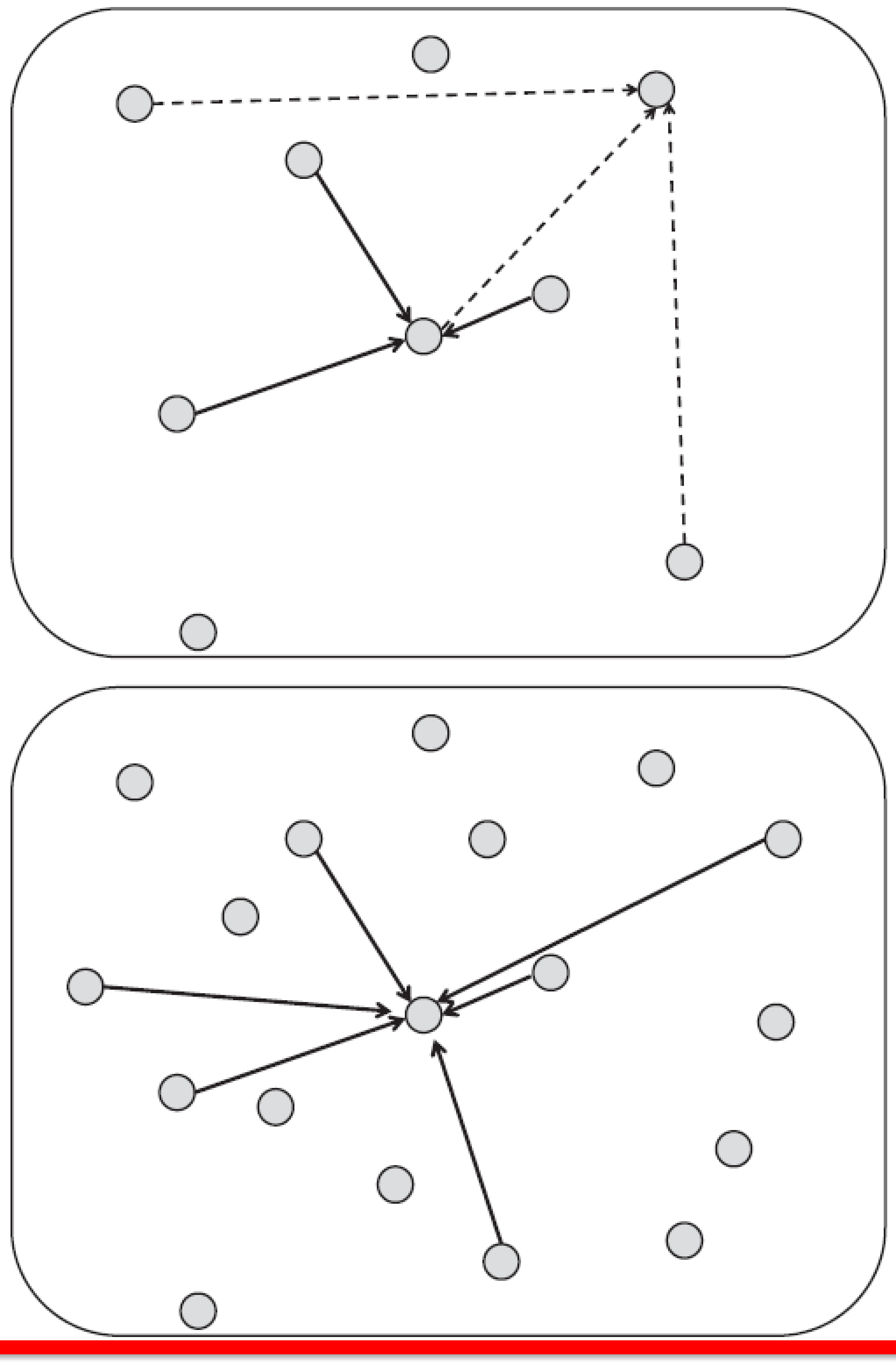
full connectivity

A

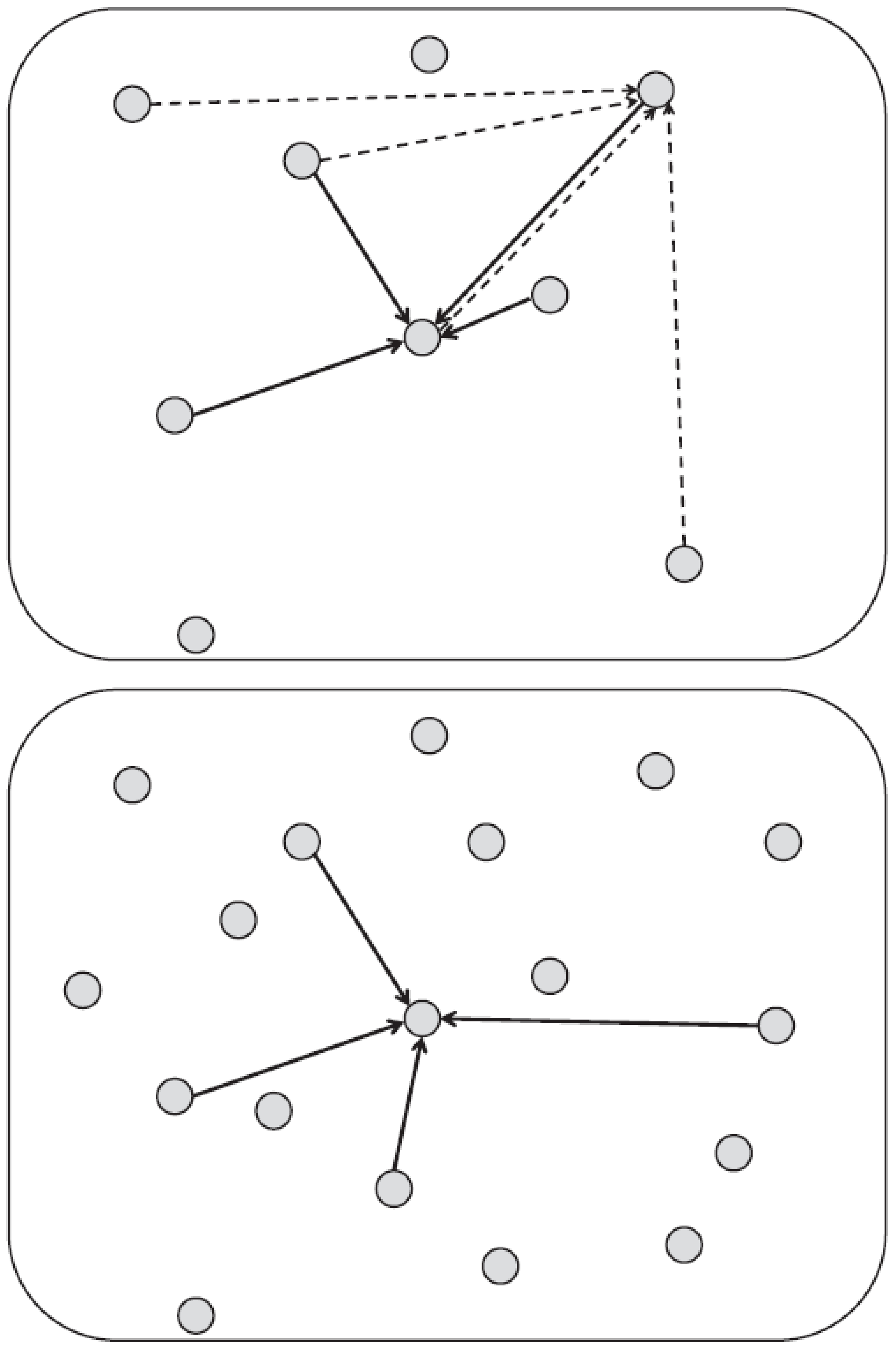


random connectivity

random: prob p fixed



random: number K of inputs fixed

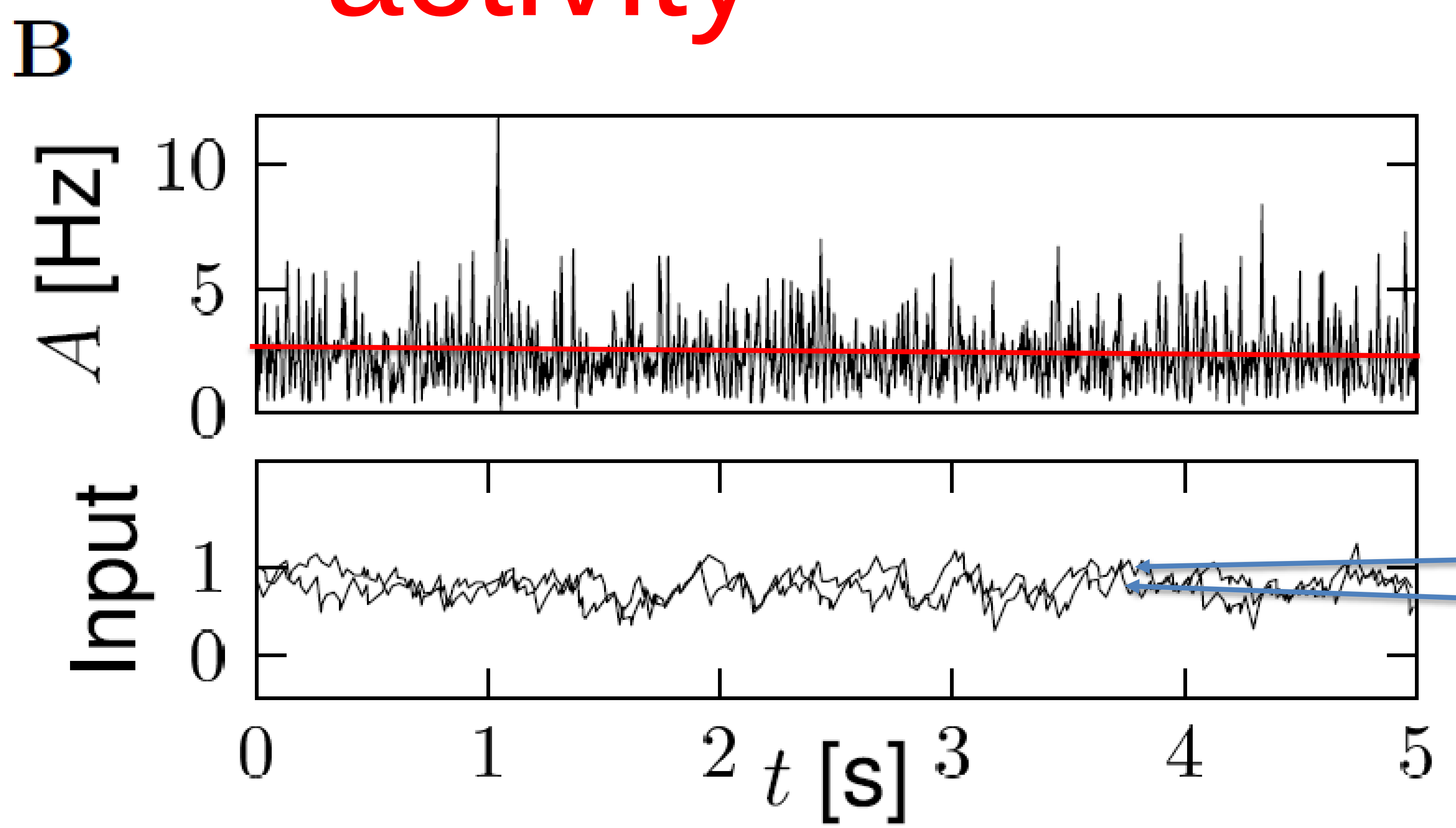


6. Review - Random Connectivity: fixed p

Can we mathematically predict the population activity?

given
- **connection probability *p* and weight w_{ij}**
- **properties of individual neurons**
- **large population**

asynchronous activity



Input is nearly identical for different neurons

6. Integrate-and-Fire neurons

Integrate-and-fire with stochastic spike arrival

For any arbitrary neuron in the population

$$\tau \frac{d}{dt} u_i = -u + I_i$$

$$if \quad u_i = \vartheta : "reset"$$

$$I_i = \sum_{k,f} w_{ik} \underline{\alpha(t - t_k^f)}$$

EPSC

excitatory input spikes

6. Network of integrate-and-fire neurons (random connectivity)

Integrate-and-fire neurons with stochastic spike arrival

For any arbitrary neuron in the population

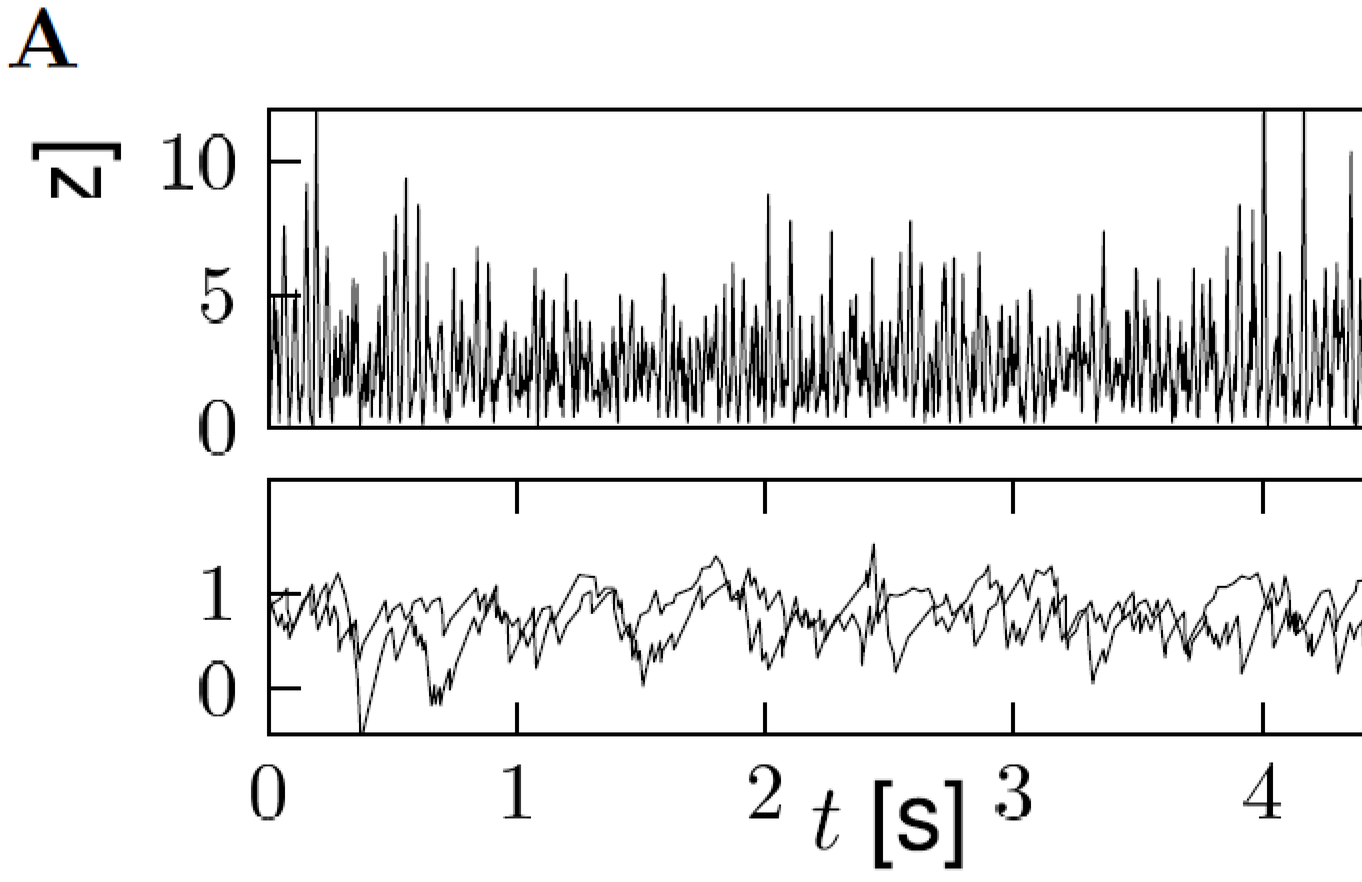
$$\tau \frac{d}{dt} u_i = -u + I_i$$

$$if \quad u_i = \vartheta : "reset"$$

$$I_i = \sum_{k,f} w_{ik} \underline{\alpha(t - t_k^f)}$$

EPSC

excitatory input spikes



Can we predict the mean current?

6. mean-field argument: random connectivity

$$w_{ij} = \frac{w_0}{pN}$$

$$A_0 = \nu = g(I_0) = g(J_0 w_0 A_0 + I_0^{ext})$$

6. mean-field arguments (random connectivity)

random: probability p=0.1 fixed, weights chosen as $w_{ij} = \frac{w_0}{pN}$

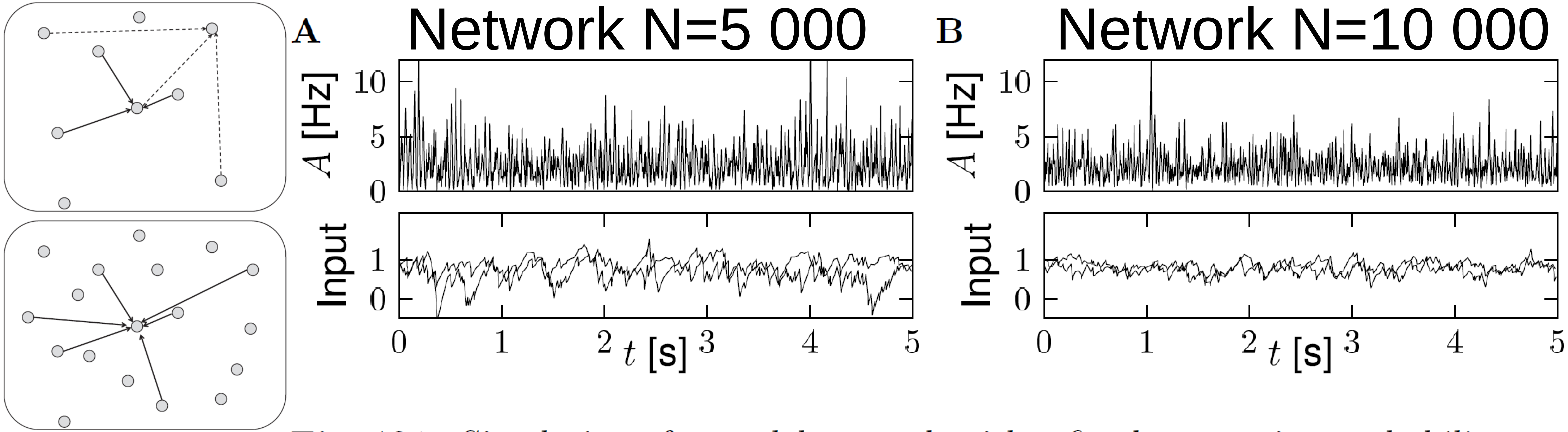


Fig. 12.7: Simulation of a model network with a fixed connection probability $p = 0.1$. **A**. Top: Population activity $A(t)$ averaged over all neurons in a network of 4 000 excitatory and 1 000 inhibitory neurons. Bottom: Total input current $I_i(t)$ into two randomly chosen

→ fluctations of *A* decrease

fluctations of *I* decrease

Image: Gerstner et al. Neuronal Dynamics (2014)

6. Random connectivity – fixed number of inputs

random: input connections K=500 fixed, weights chosen as $w_{ij} = \frac{w_0}{K}$

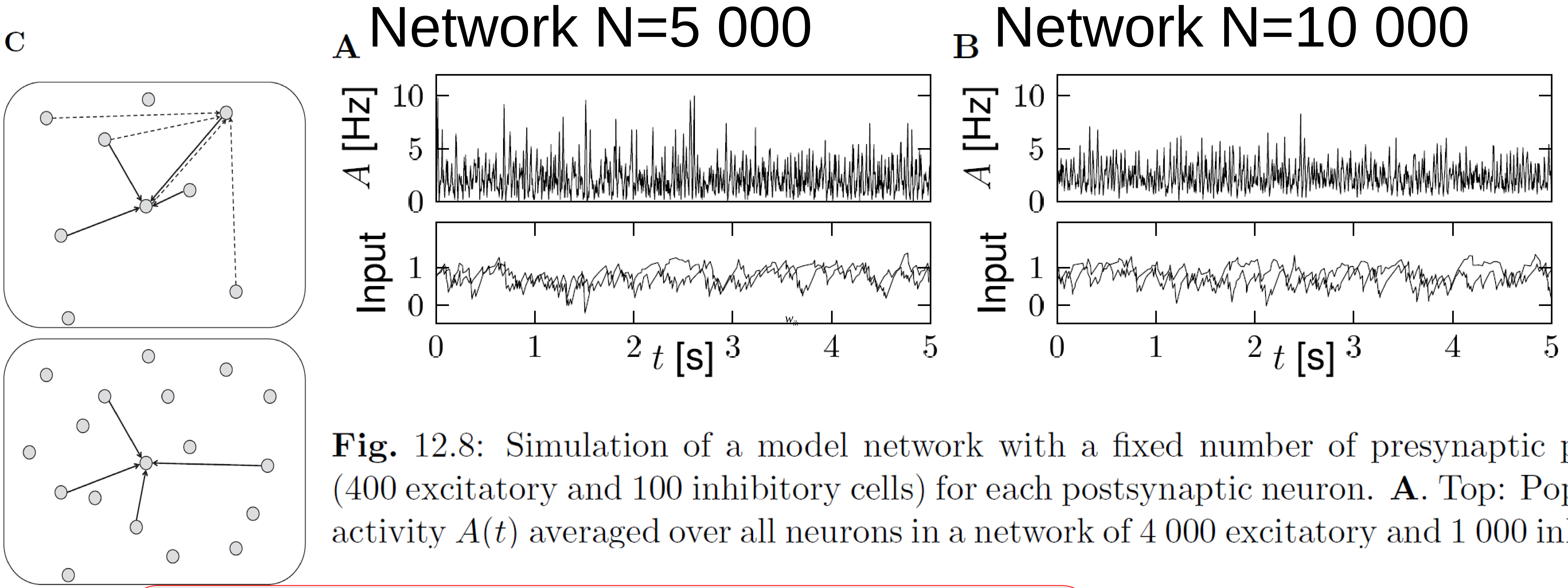


Fig. 12.8: Simulation of a model network with a fixed number of presynaptic partners (400 excitatory and 100 inhibitory cells) for each postsynaptic neuron. **A**. Top: Population activity $A(t)$ averaged over all neurons in a network of 4 000 excitatory and 1 000 inhibitory

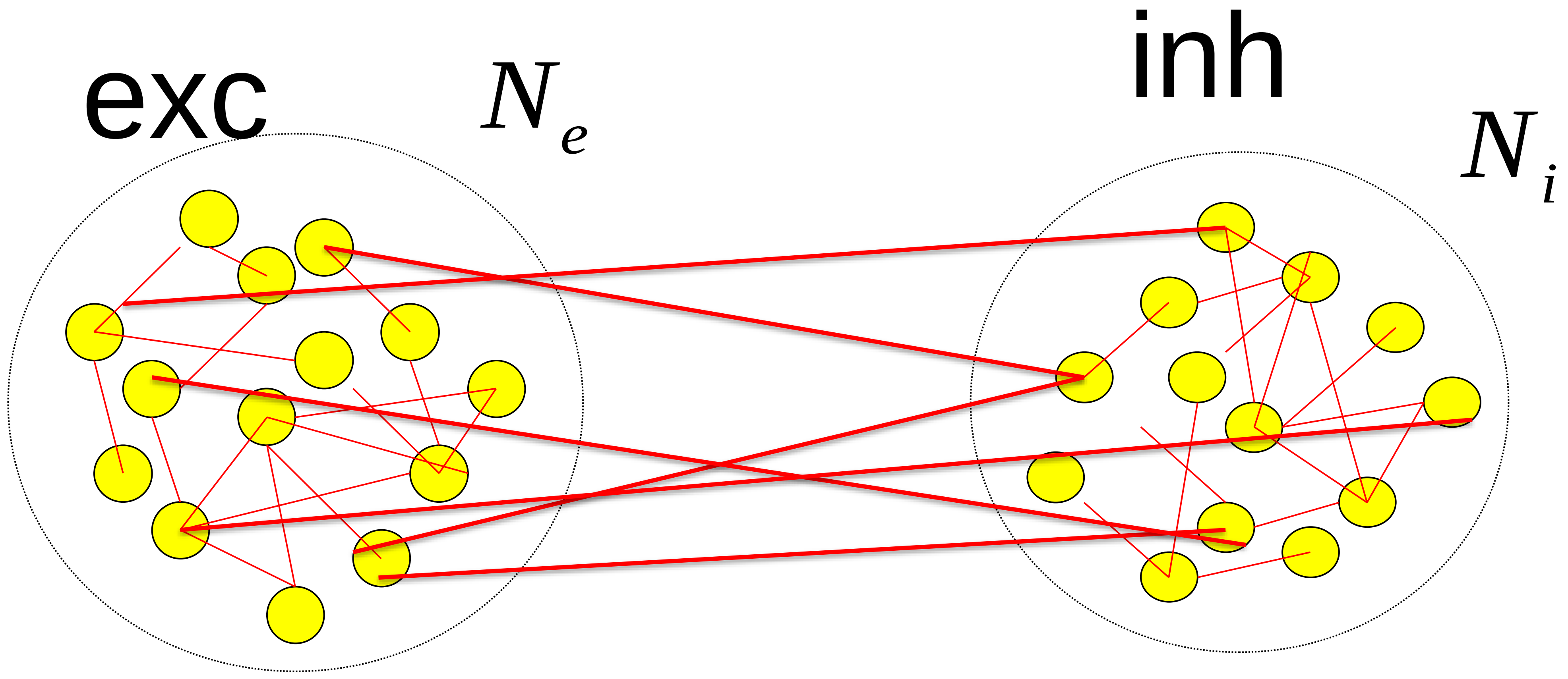
→ fluctations of *A* decrease

fluctations of *I* remain

Image: Gerstner et al. Neuronal Dynamics (2014)

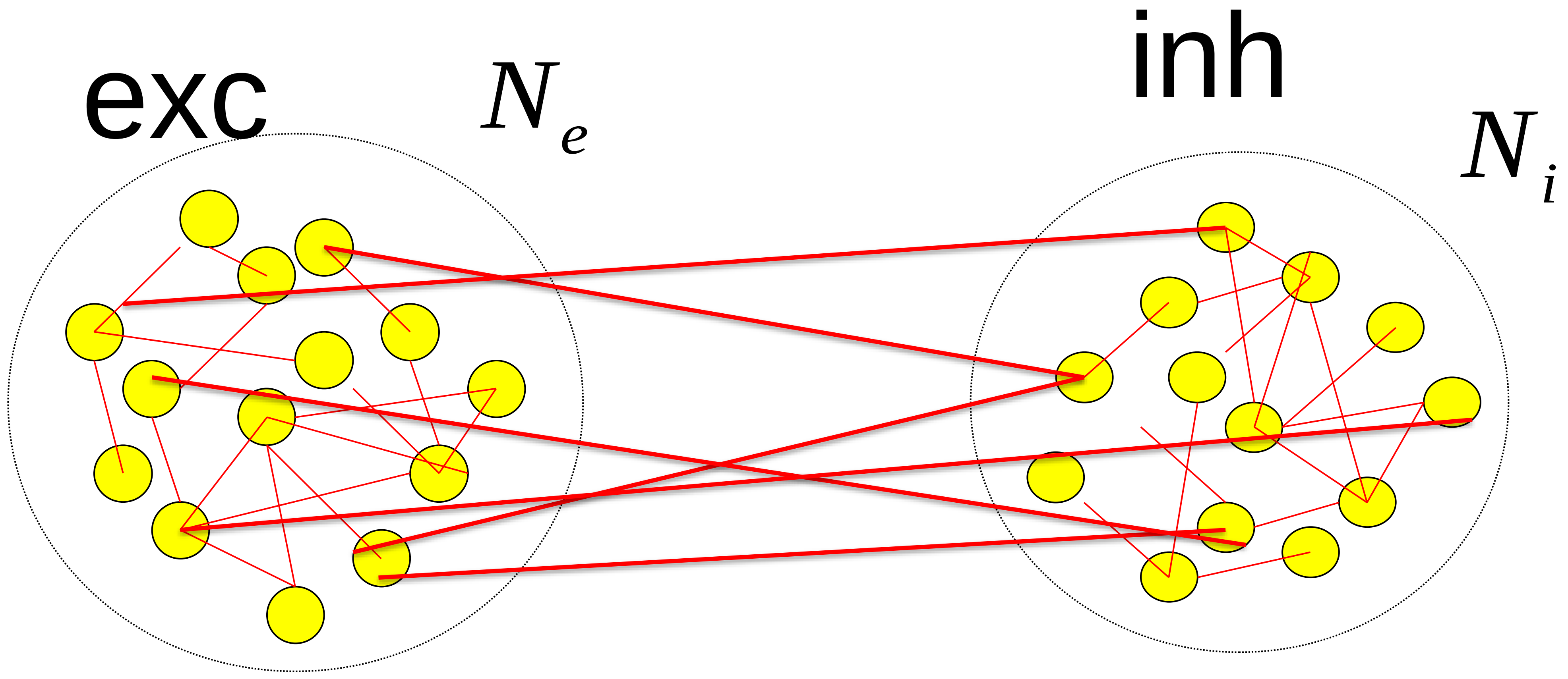
6. Connectivity schemes – random, fixed p, but balanced

$$I_i = \sum_{k,f} w_{ik} \alpha^{exc}(t - t_k^f) - \sum_{k,f} w_{ik} \alpha^{inh}(t - t_k^f)$$



6. Connectivity schemes – random, fixed p, but balanced

$$I_i = \sum_{k,f} w_{ik} \alpha^{exc}(t - t_k^f) - \sum_{k,f} w_{ik} \alpha^{inh}(t - t_k^f)$$



make network bigger, but

-keep mean input close to zero

$$p\, N_e J_e = -p\, N_i J_i$$

-keep variance of input

$$w_{ij} = \frac{J_e}{\sqrt{pN}}$$

$$w_{ij} = \frac{J_i}{\sqrt{pN}}$$

C. van Vreeswijk and H. Sompolinsky (1996) Science

6. Connectivity schemes – random, fixed p, but balanced

Image: Gerstner et al. Neuronal Dynamics (2014)

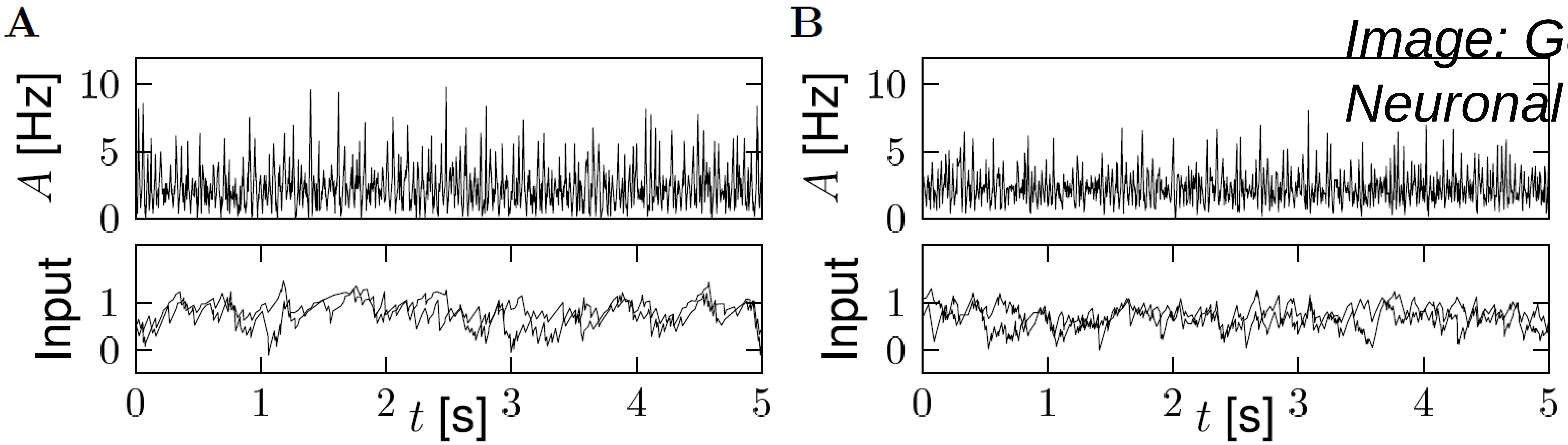


Fig. 12.9: Simulation of a model network with balanced excitation and inhibition and fixed connectivity $p = 0.1$ **A**. Top: Population activity $A(t)$ averaged over all neurons in a network of 4 000 excitatory and 1 000 inhibitory neurons. Bottom: Total input current $I_i(t)$ into two randomly chosen neurons. **B**. Same as A, but for a network with 8 000 excitatory and 2 000 inhibitory neurons. The synaptic weights have been rescaled by a factor $1/\sqrt{2}$ and the common constant input has been adjusted. All neurons are leaky integrate-and-fire units with identical parameters coupled interacting by short current pulses.

fluctations of *A* decrease

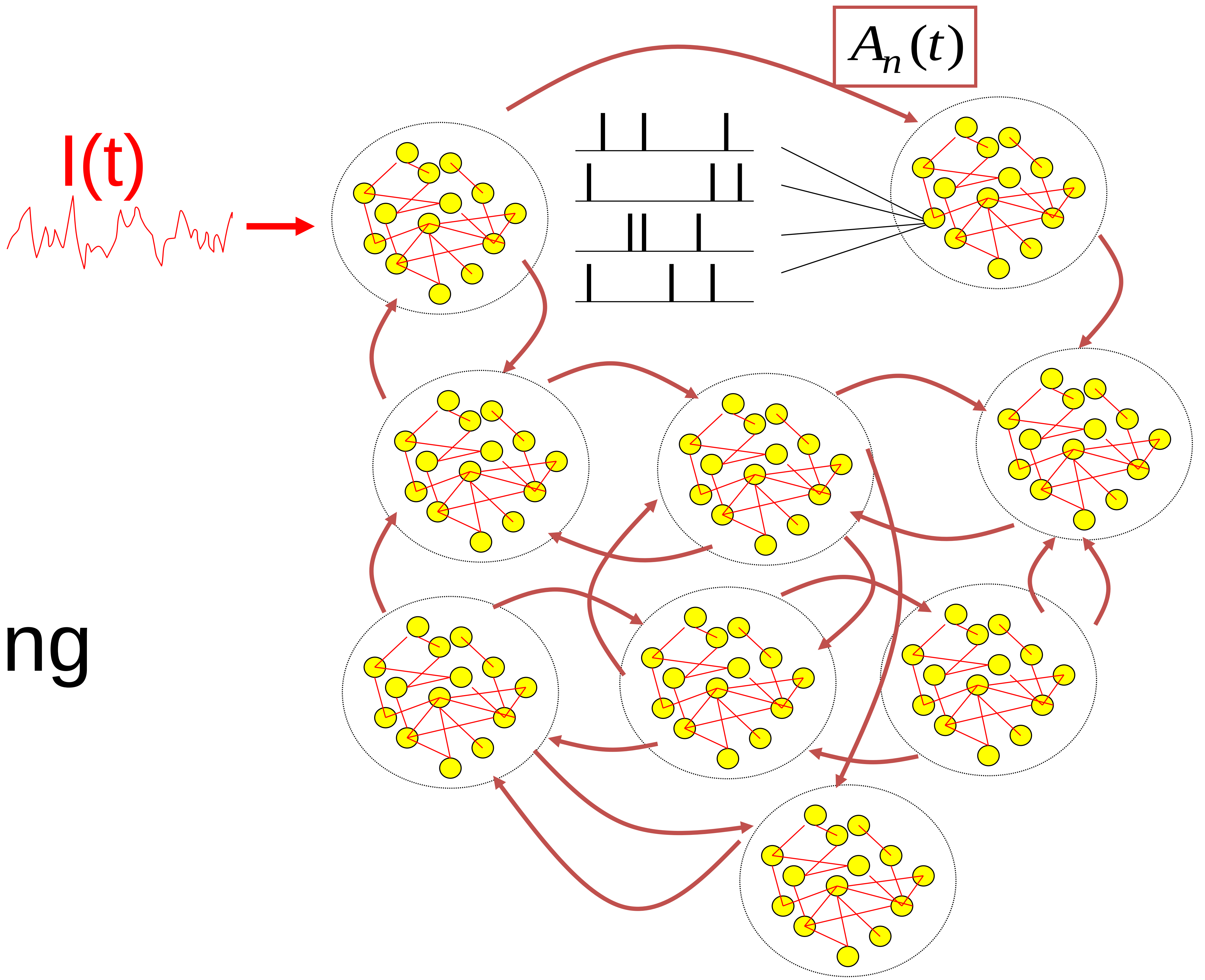
→ fluctations of *I* become 'smoother'

6. Neuronal populations: outlook

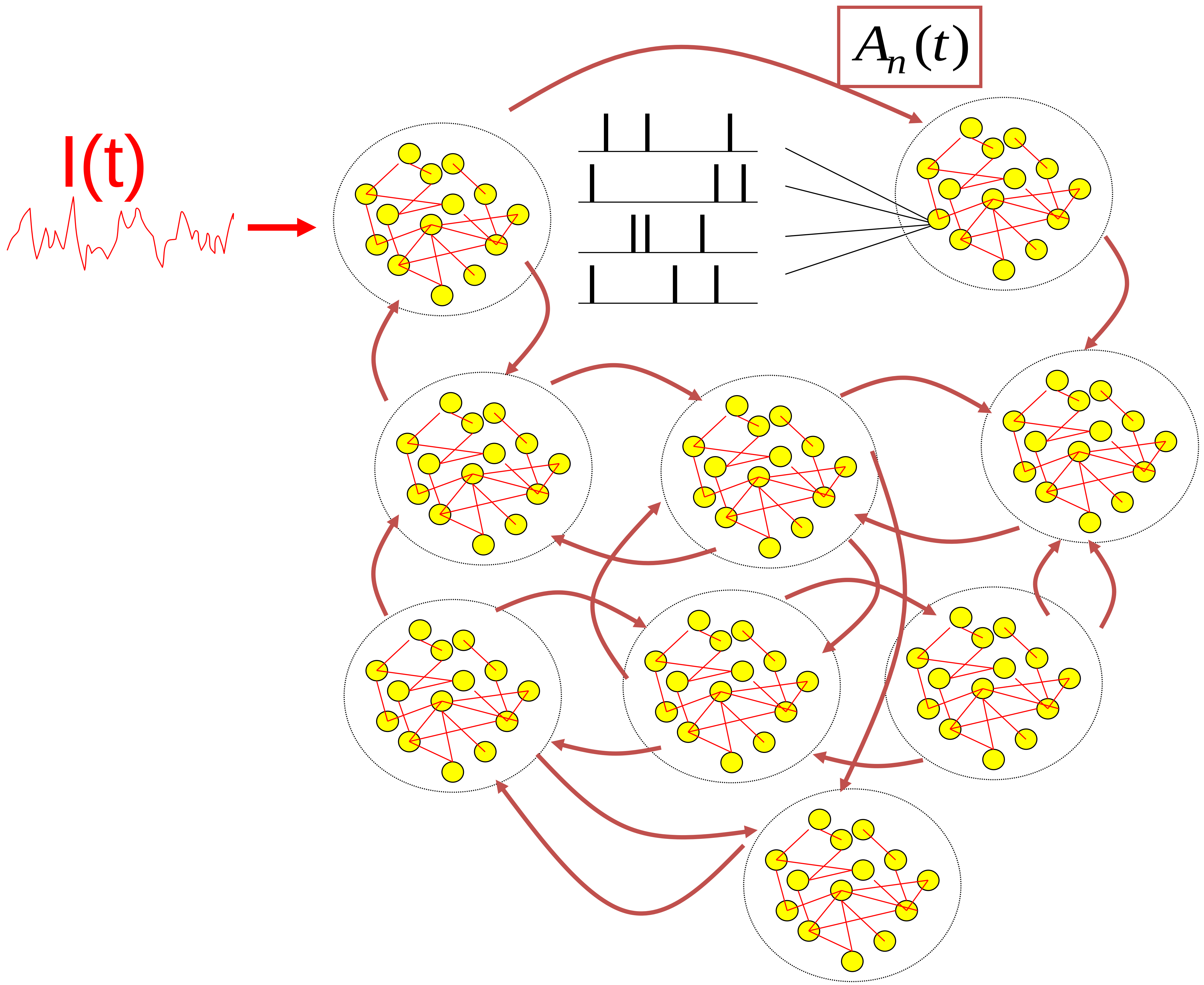
One population
→ multiple populations

Application to visual cortex
→ visual processing

Application to decision making
→ competitive networks



6. Summary: Neuronal Populations



6. Selected References: Neuronal Populations

Receptive fields, columns, and cortical connectivity

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S. Lefort, C. Tomm, J.C.F. Sarria and C.C.H. Petersen (2009) The excitatory neuronal network of the c2 barrel column in mouse primary somatosensory cortex. neuron 61: 301-316.. Neuron 61, pp. 301–316.

Modeling populations

H. R. Wilson and J. D. Cowan (1972) Excitatory and inhibitory interactions in localized populations of model neurons.. Biophys. J. 12, pp. 1–24.
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W. Gerstner (2000) Population dynamics of spiking neurons: fast transients, asynchronous states and locking. Neural Computation 12, pp. 43–89.

For those not familiar with the Dirac delta: https://www.youtube.com/watch?v=l3hvrx33lZc

More info on neuron models: http://lcn.epfl.ch/~gerstner/NeuronalDynamics-MOOC1.html

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Neuronal Populations

The end

Documentation:
http://neuronaldynamics.epfl.ch/

Online html version available

Reading:
NEURONAL DYNAMICS
- Ch. 12.1 – 12.4.3
  (except Section 12.3.7)

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