Computational Neuroscience: Neuronal Dynamics

EPFL

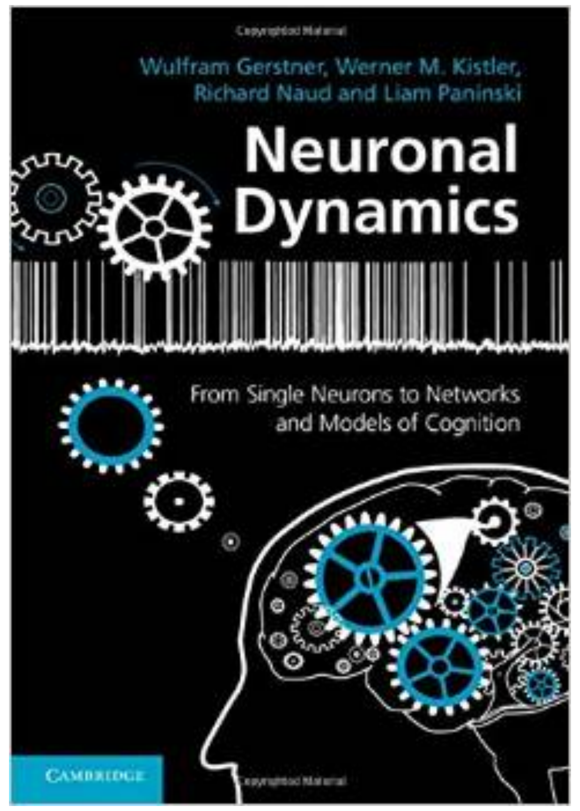
week 7: Neuronal Populations

Wulfram Gerstner

EPFL, Lausanne, Switzerland

Reading for week 7:
NEURONAL DYNAMICS
- Ch. 12.1 – 12.4.3
  (except Section 12.3.7)

Cambridge Univ. Press



7.1 Population Activity
- Definition

7.2 Detour: Cortical Populations

7.3 Detour: Connectivity
- cortical connectivity
- model connectivity schemes

7.4 Asynchronous State
- Definition

7.5 Mean-field Argument
- stationary solution

7.6 Random Networks
- Balanced state

Lecture 8 of video series

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

Miniproject

- Choice between 2 projects (both extension of Hopfiel-model)

- You must work in teams of 2

- See pdf on Moodle page for detailed instructions (also post on ed-Discussion)

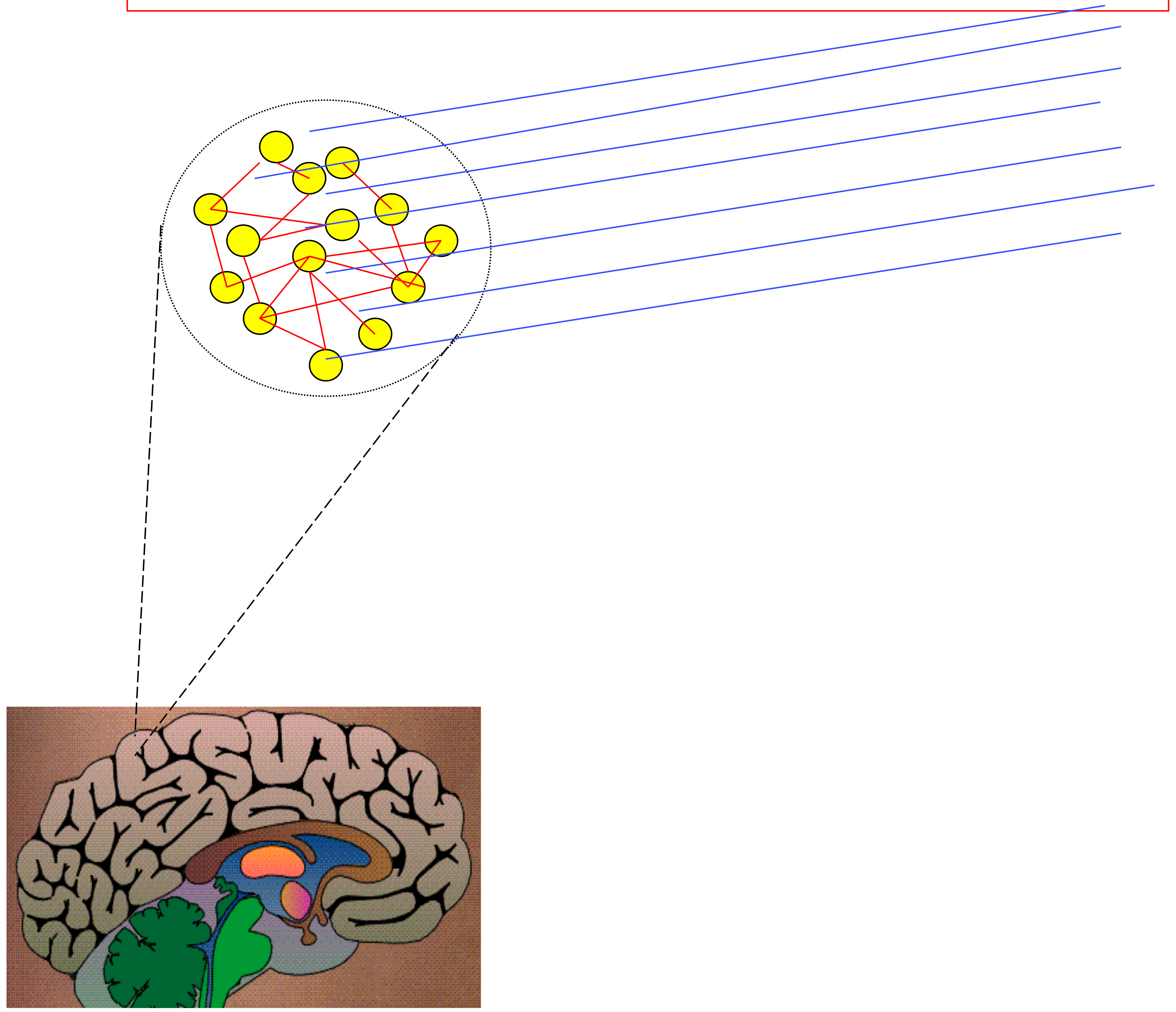
- 2 Deadline (your choice).
  - May 26th 2025, at 11.55 pm

    (→ fraud-detection slots: May 27th and 28th, 2025);
  - June 2nd 2025, at 11.55 pm

    (→ fraud-detection slots: June 5th and 6th, 2025).

1. Scales of neuronal processes

population of neurons
with similar properties



Brain

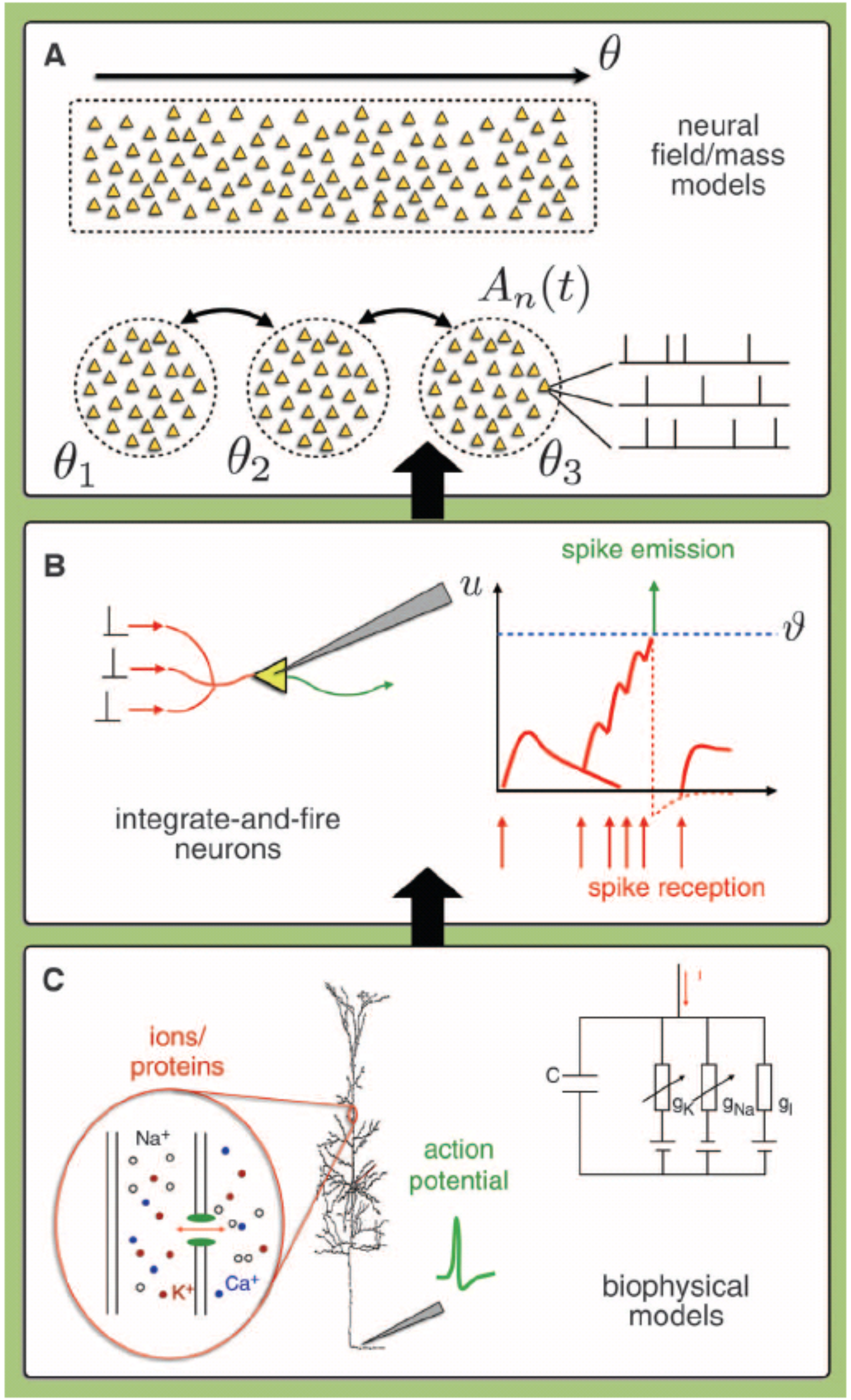
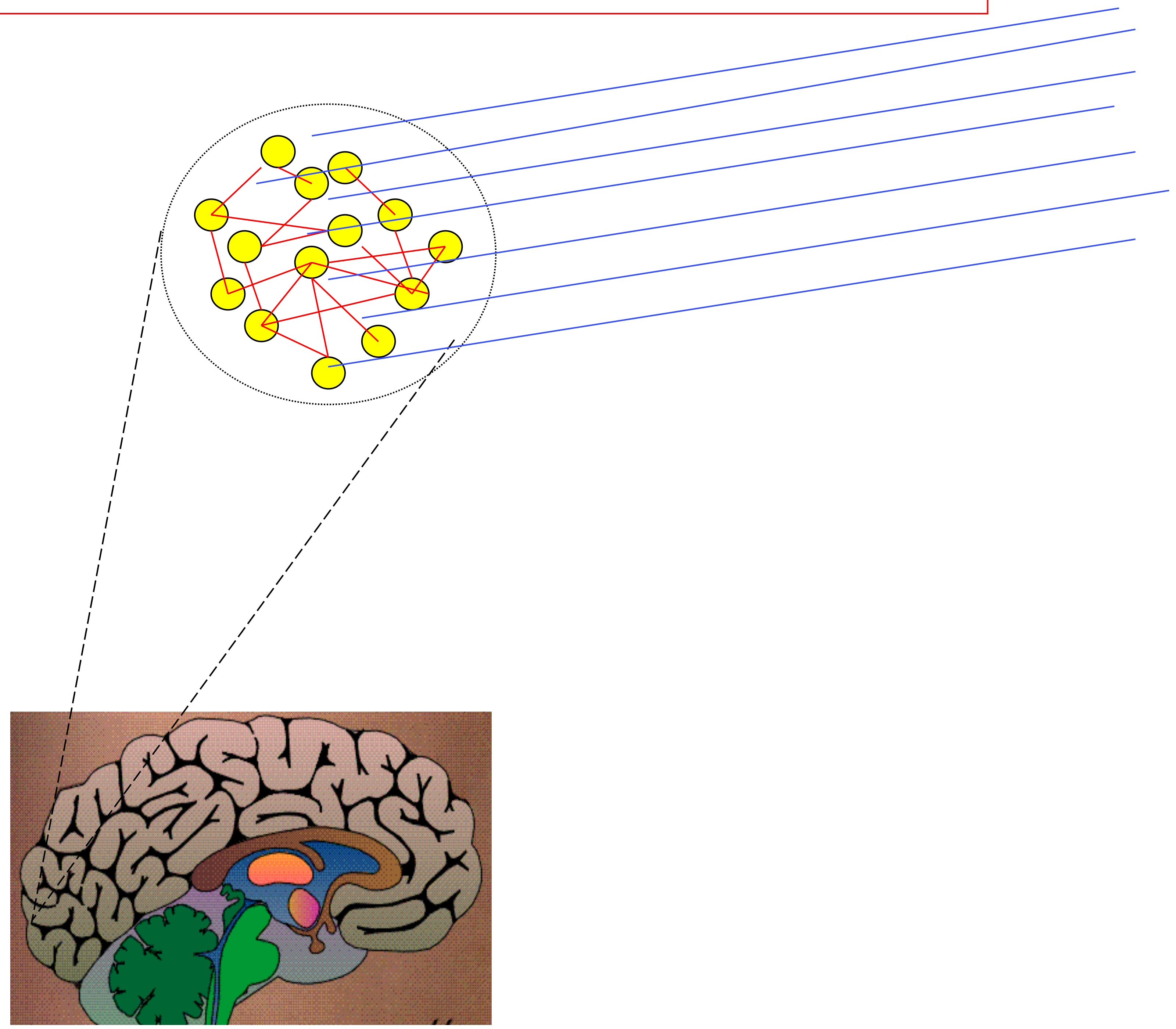


Image: Gerstner et al. Science (2012),

1. Population activity, definition

population of neurons
with similar properties

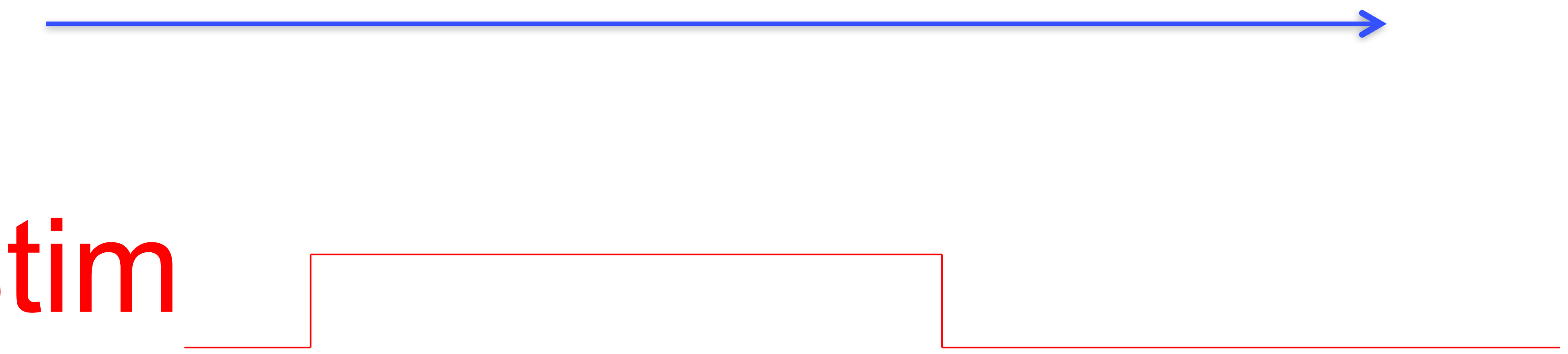


Brain

neuron 1

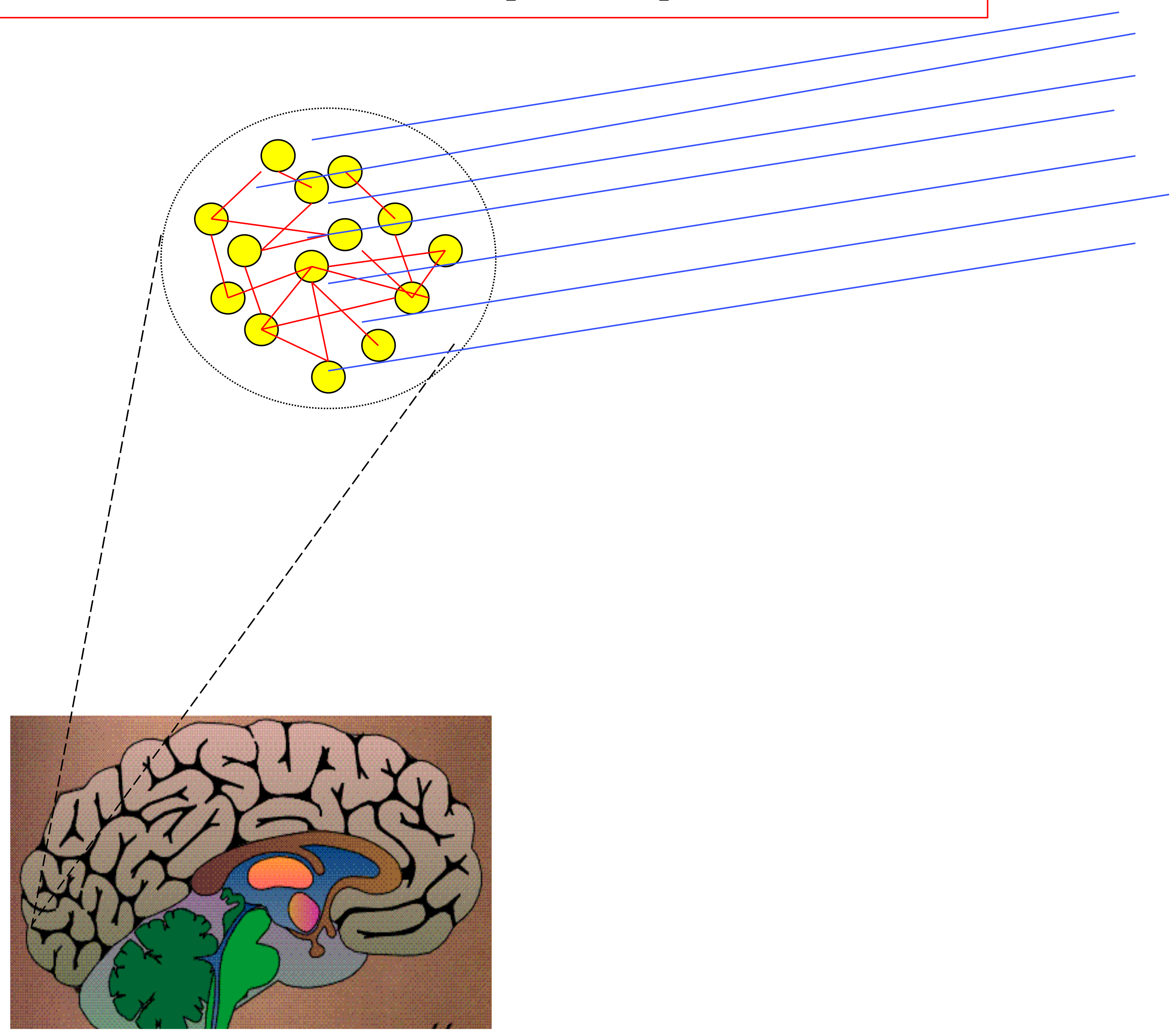
neuron 2

Neuron *K*

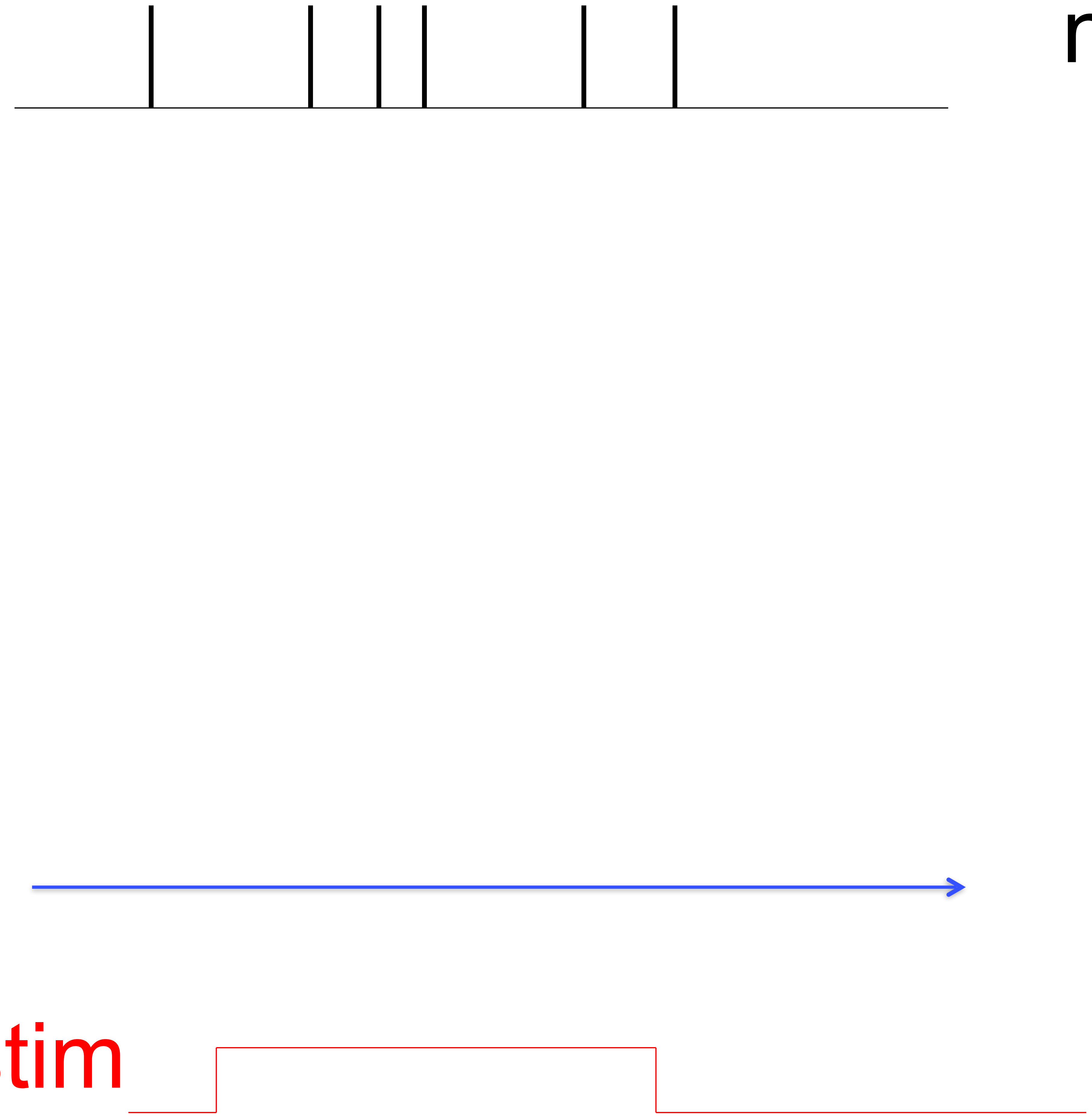


1. Population activity, definition

population of neurons
with similar properties



Brain



neuron 1

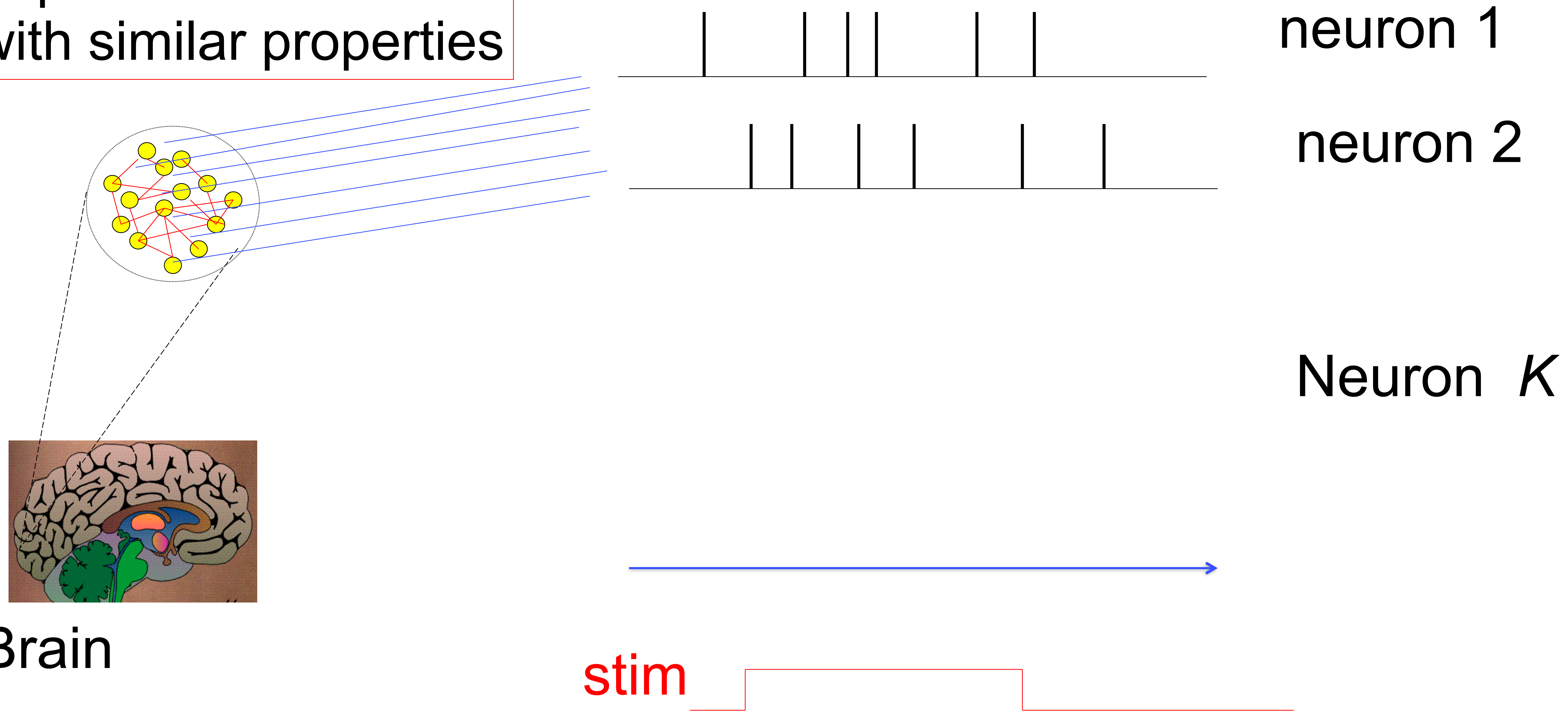
neuron 2

Neuron K

stim

1. Population activity, definition

population of neurons
with similar properties



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population of neurons
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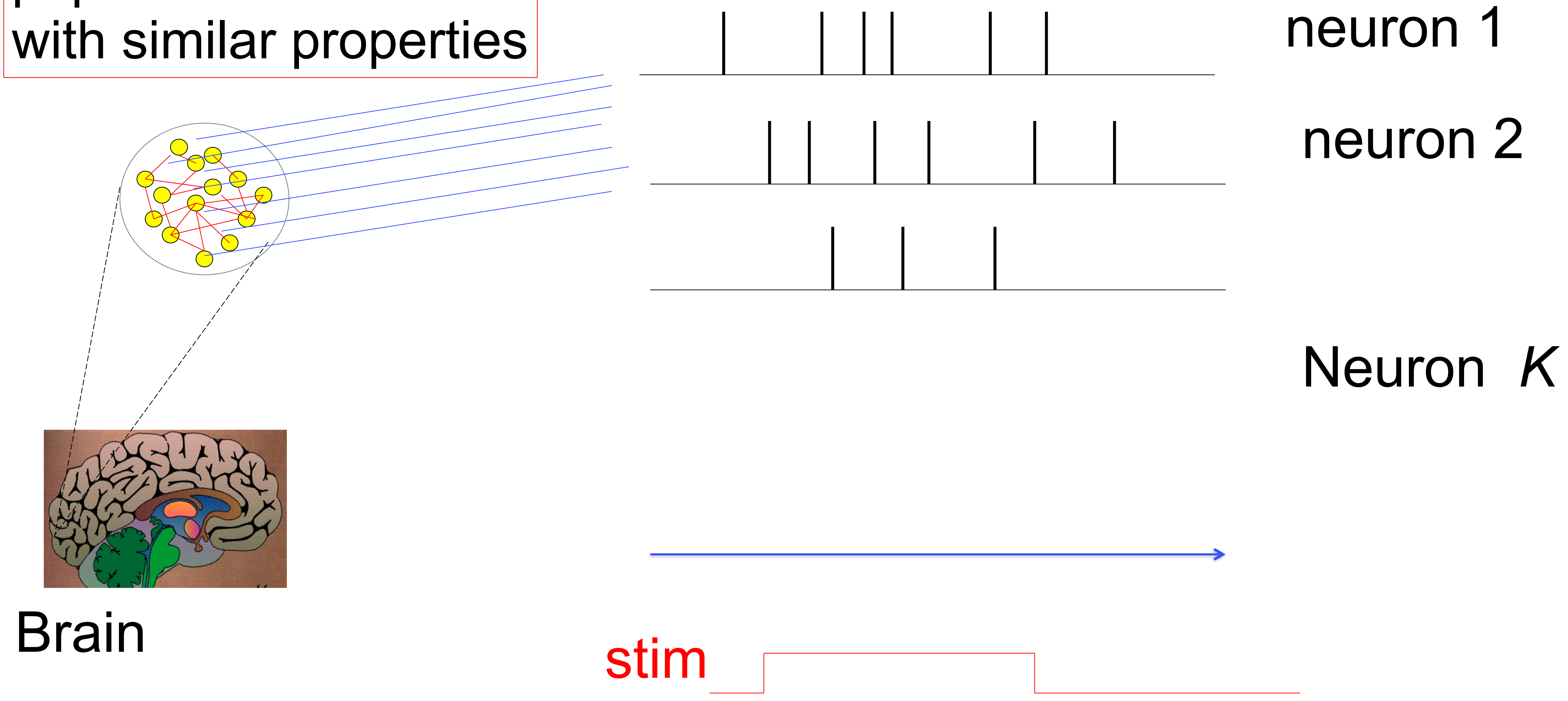

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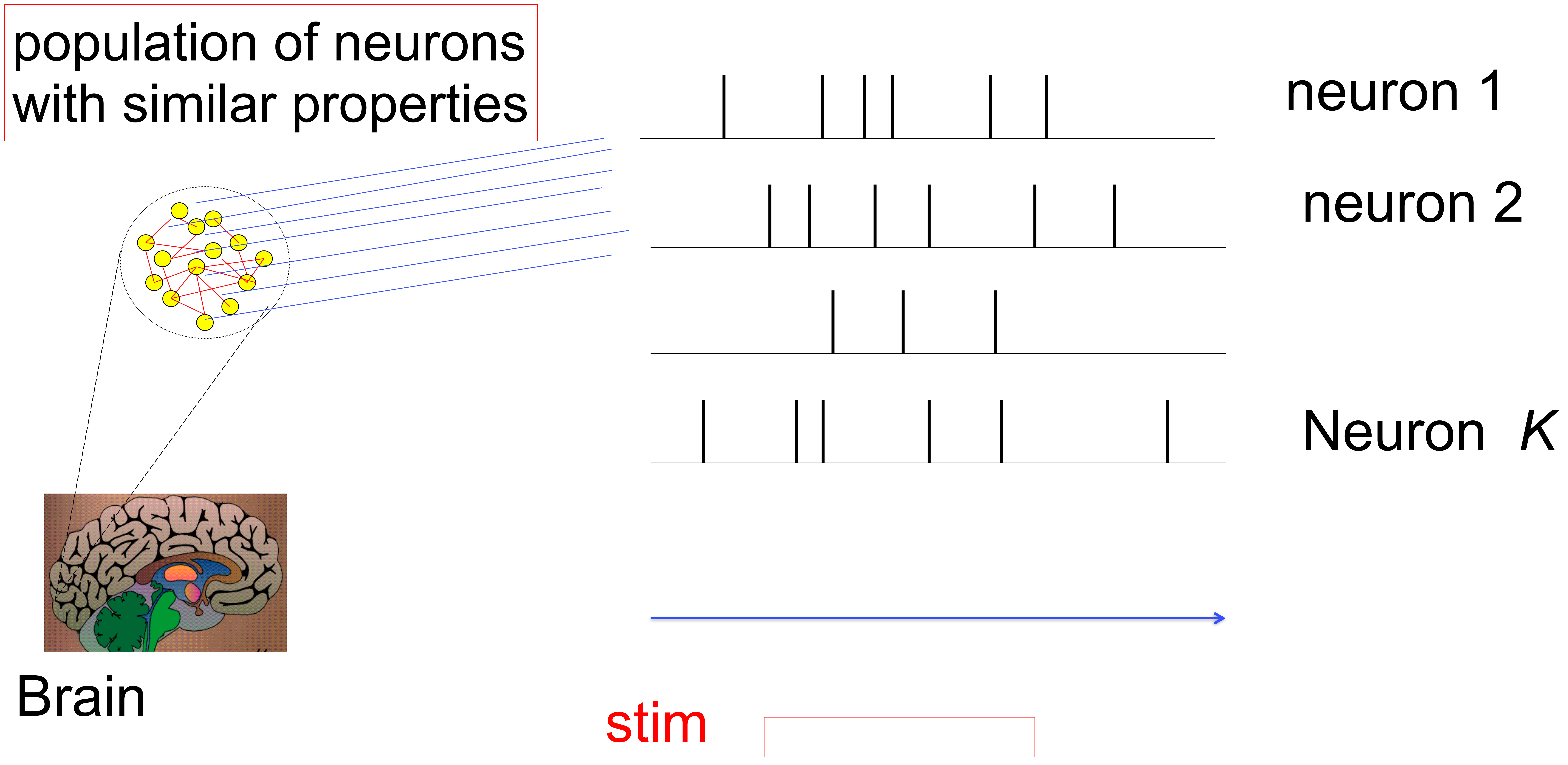

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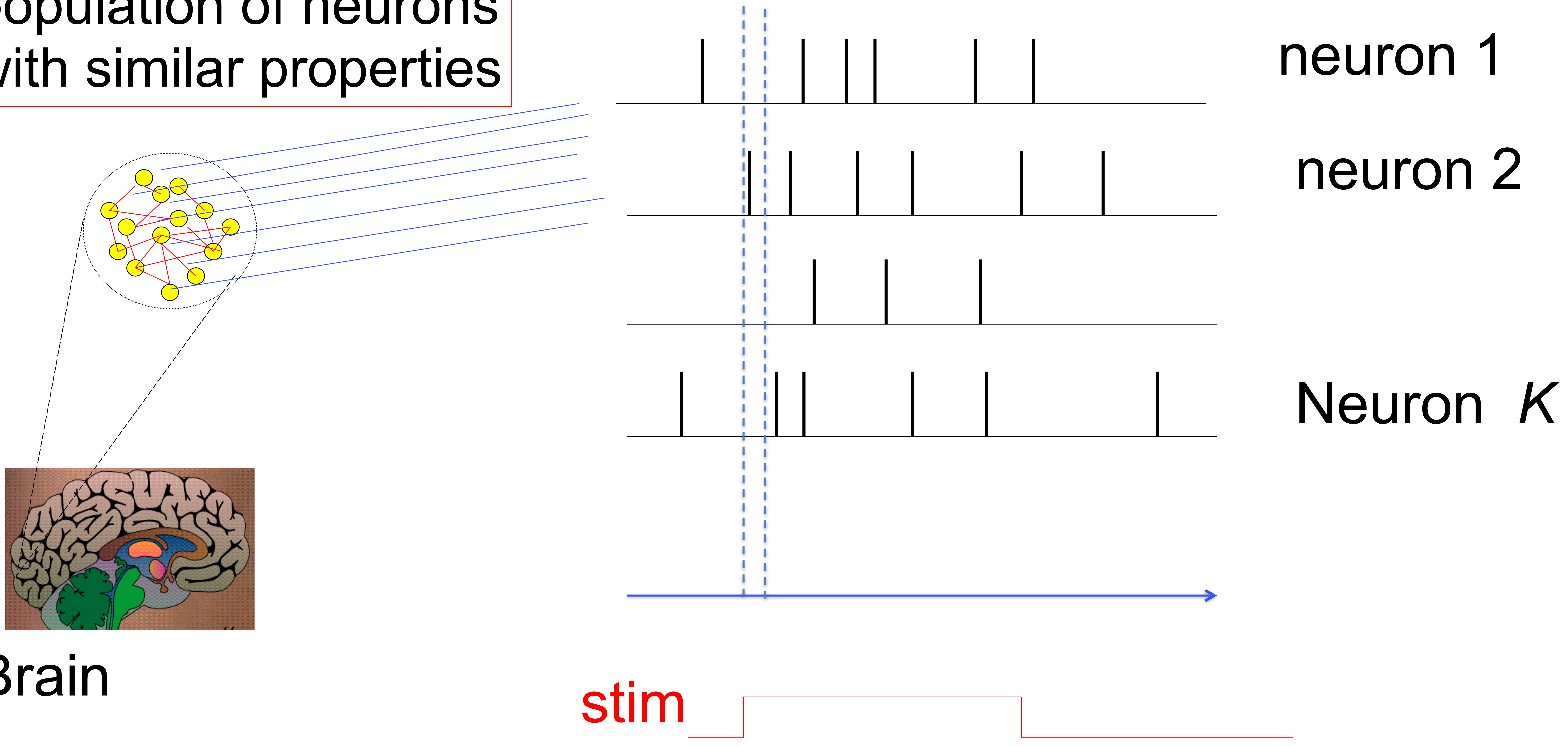
population of neurons
with similar properties



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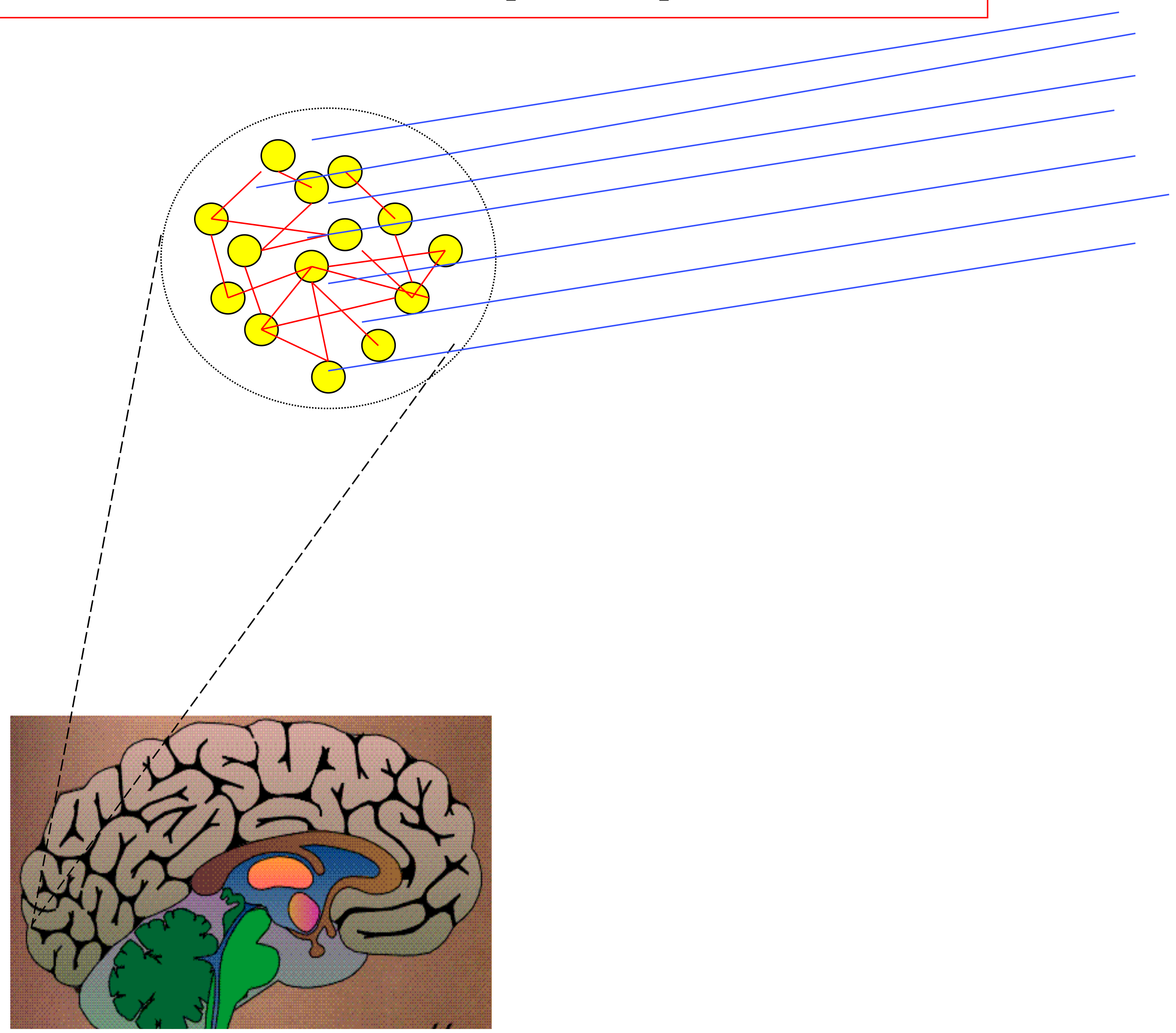
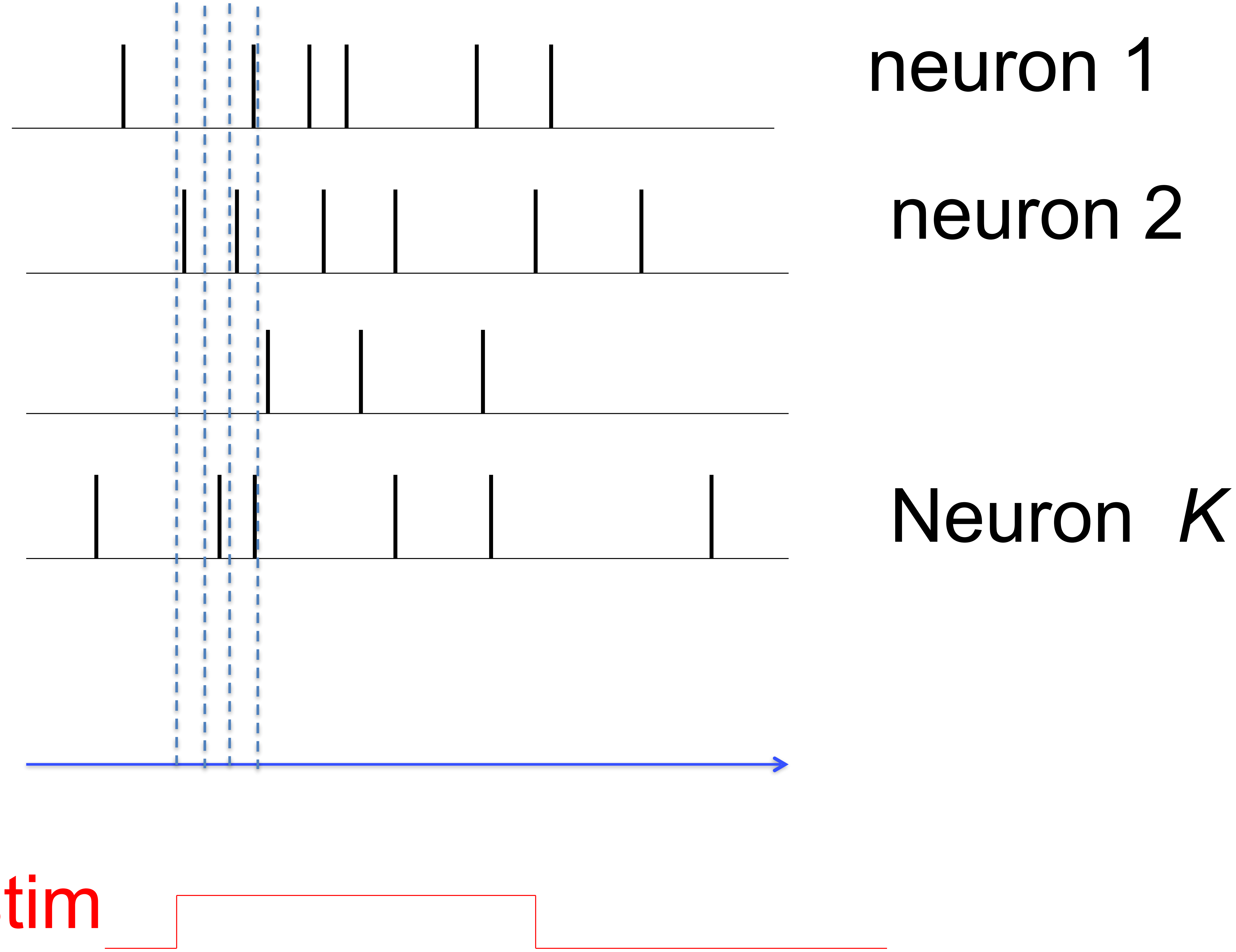
population of neurons
with similar properties





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population of neurons
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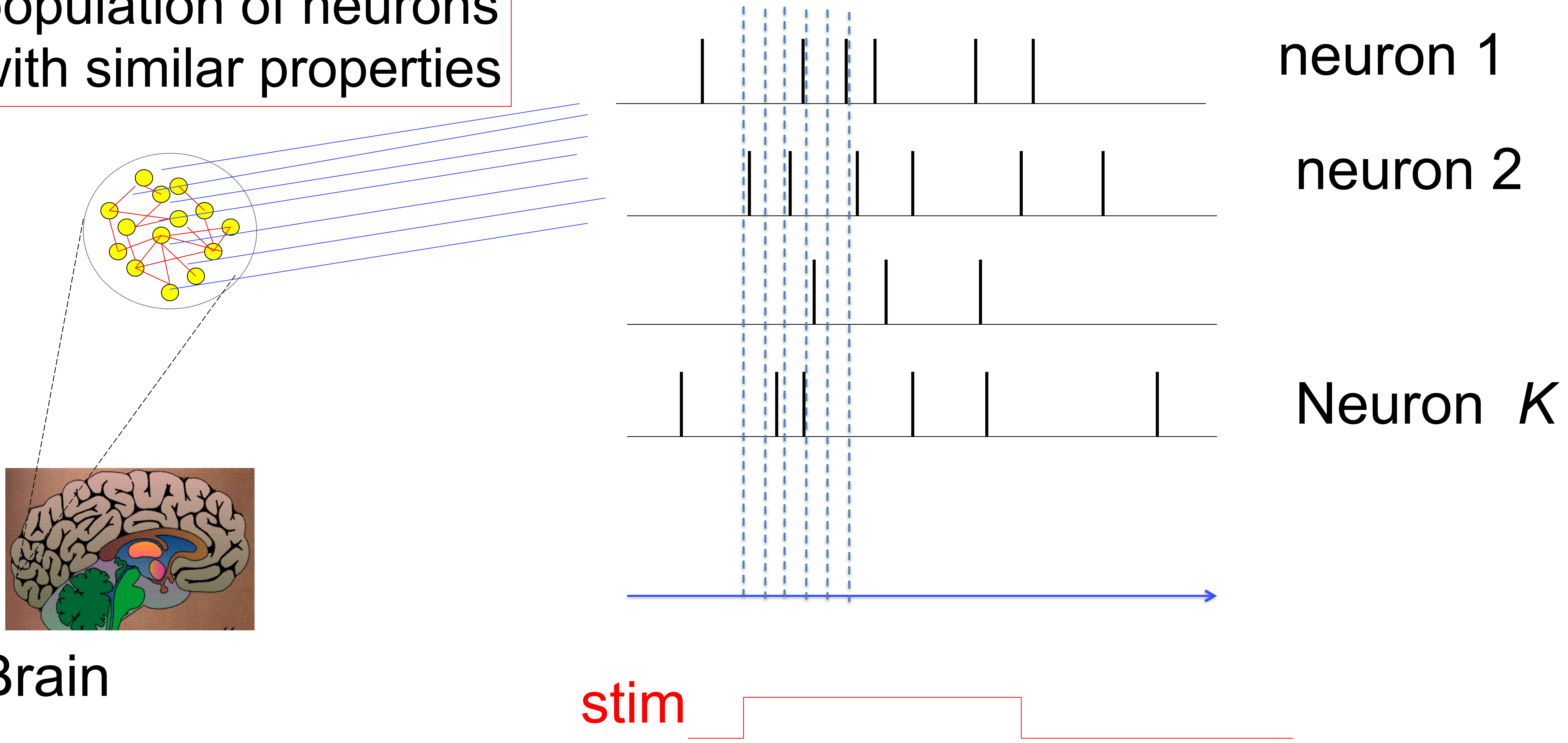

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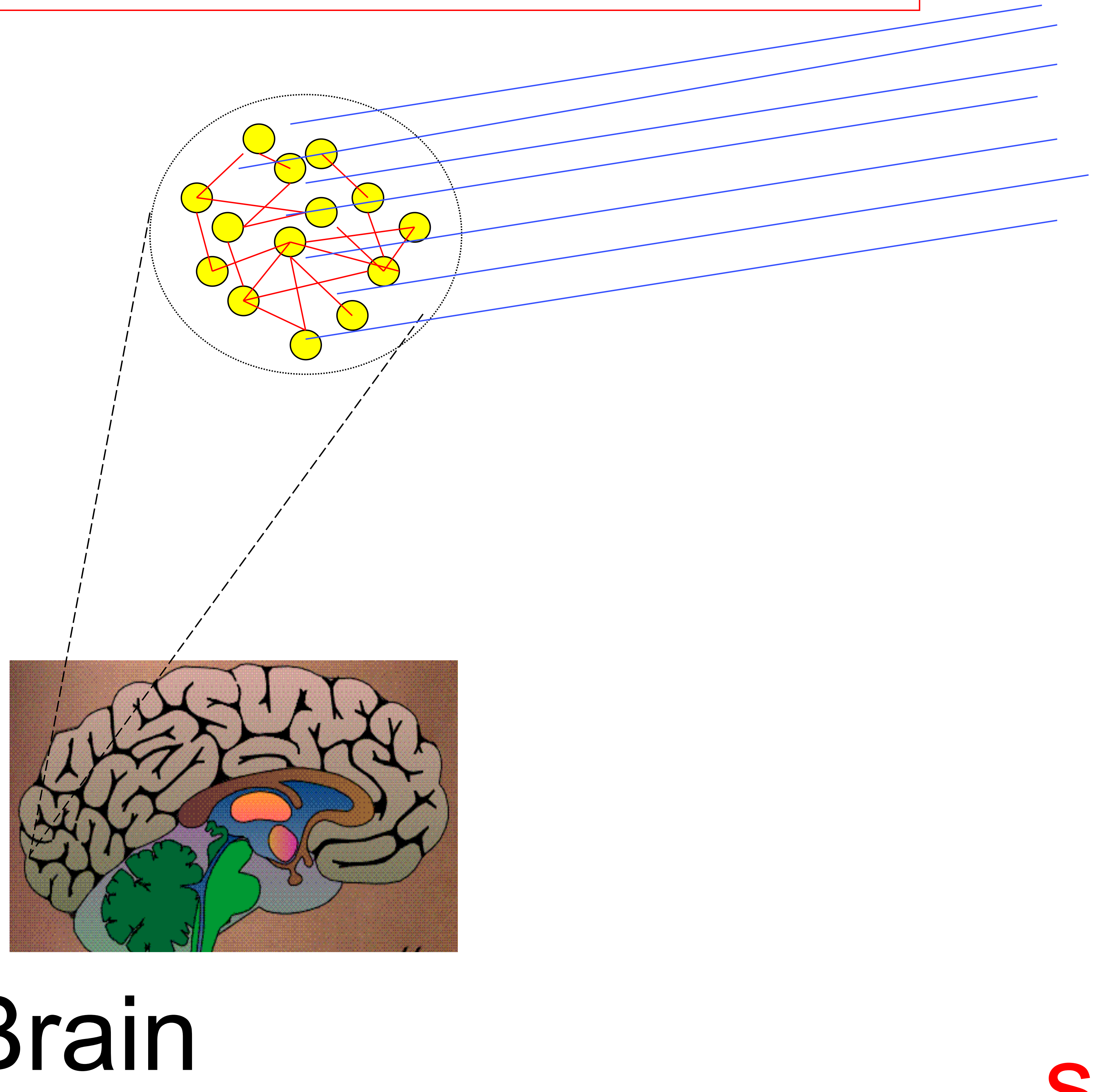
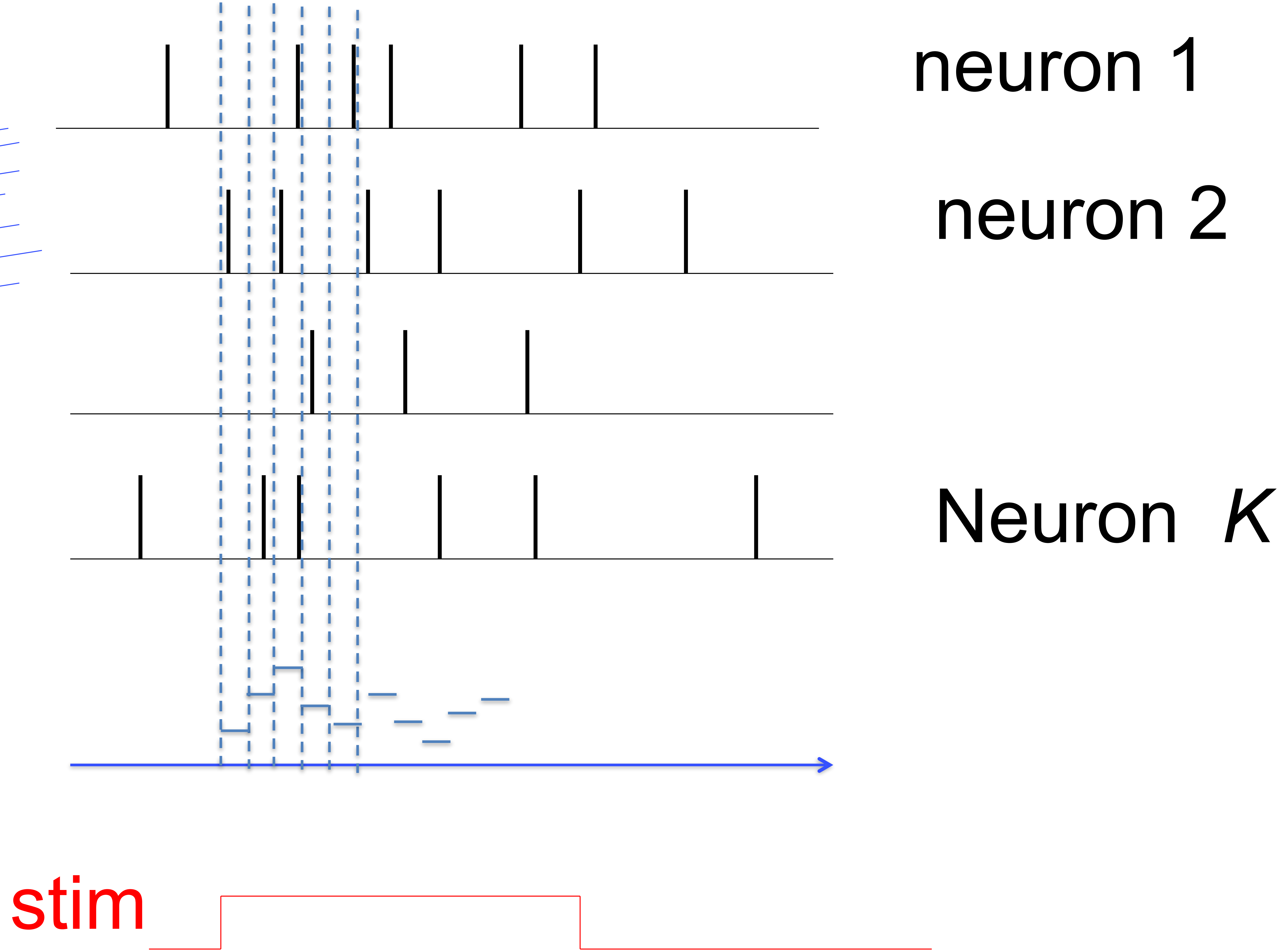
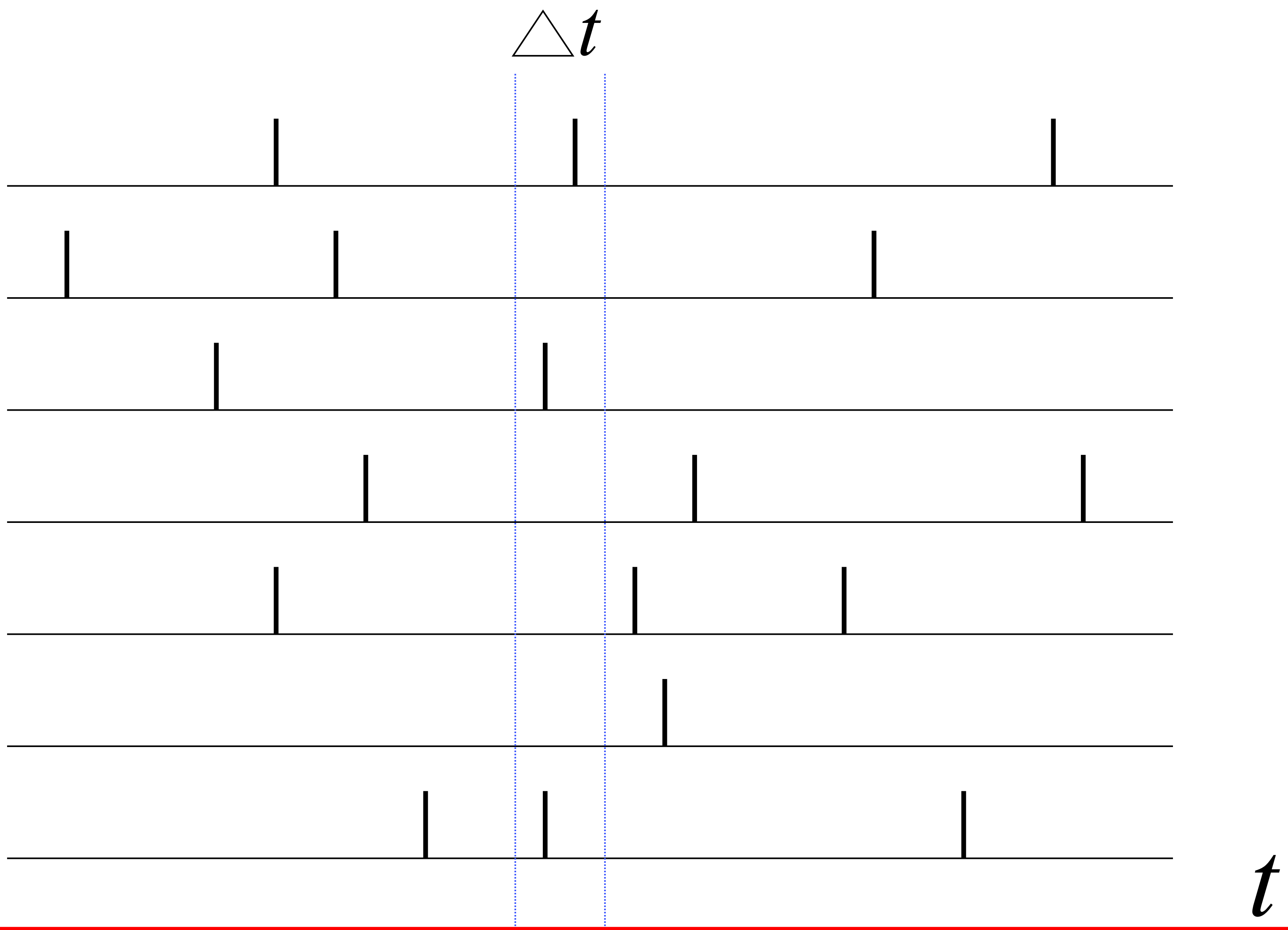




1. Population activity: definition

population activity - rate defined by population average



population activity

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

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

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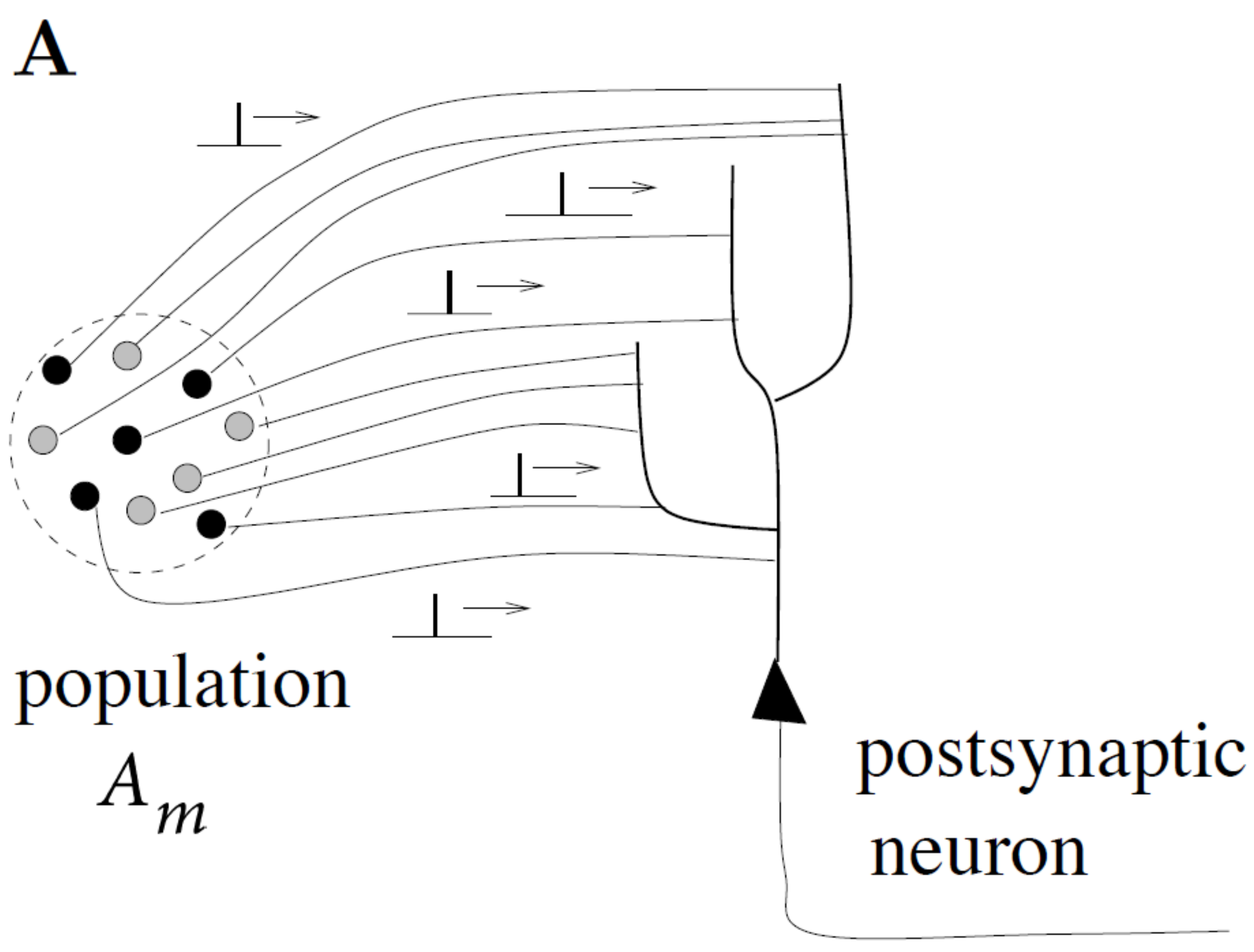

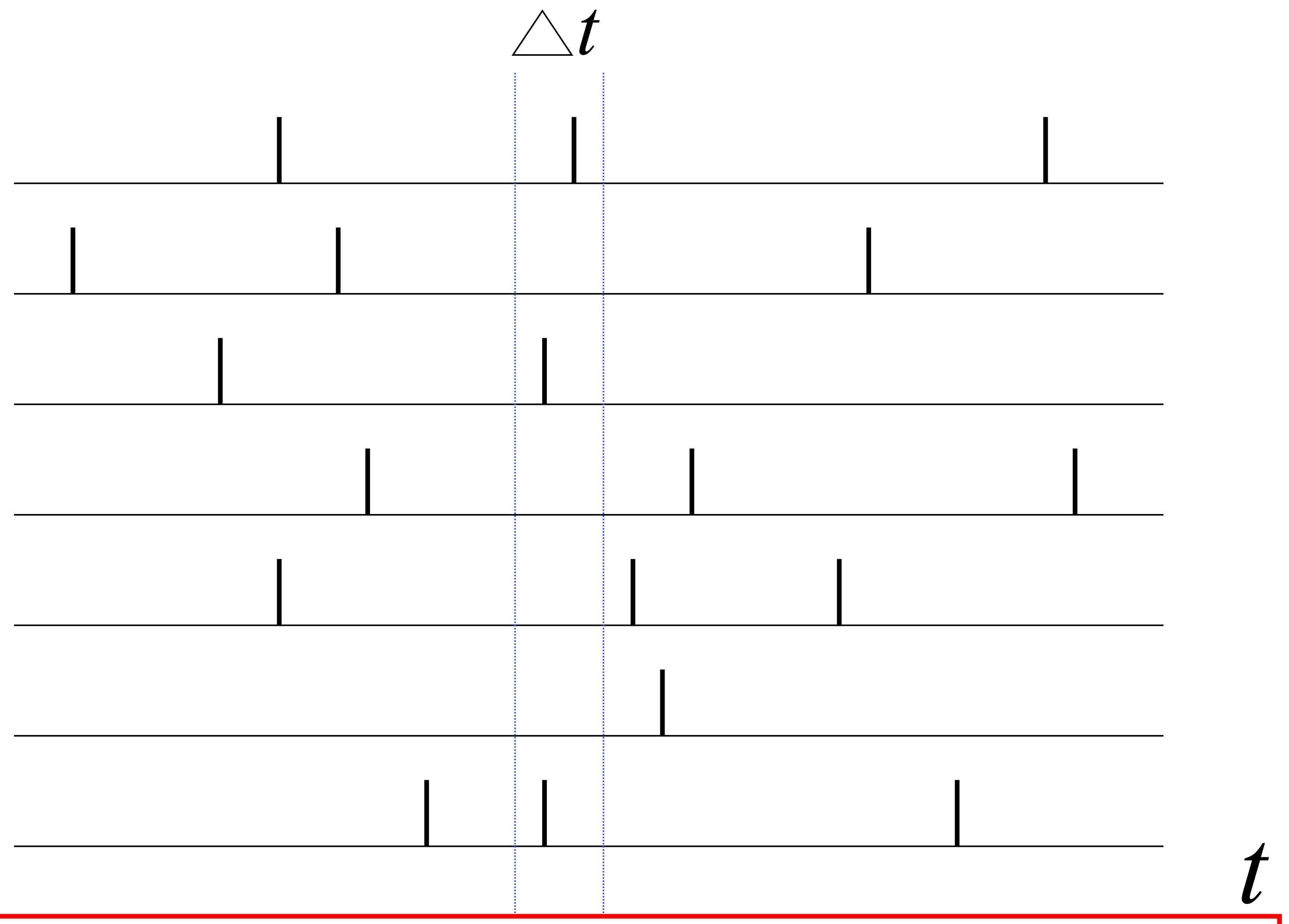

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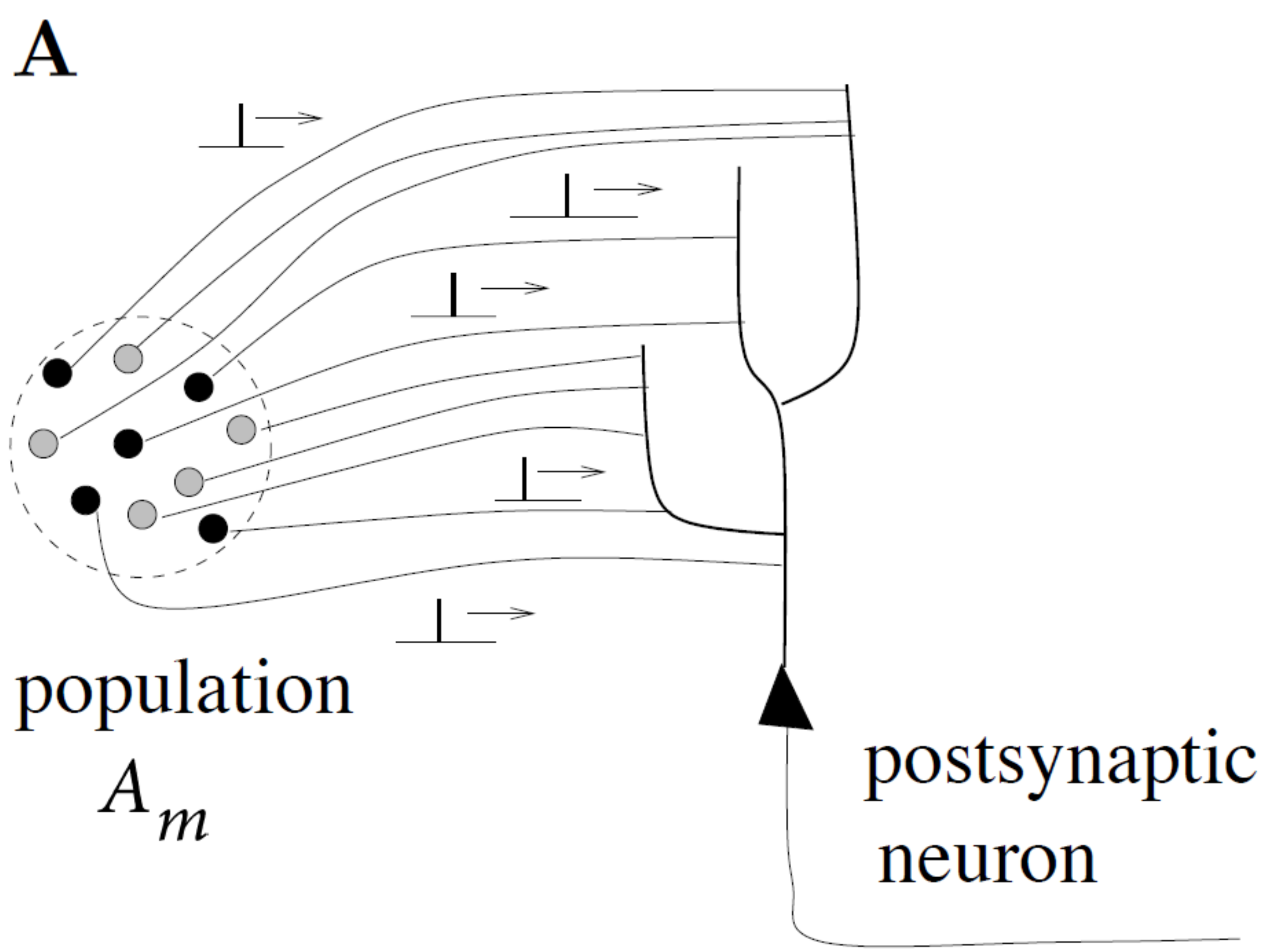
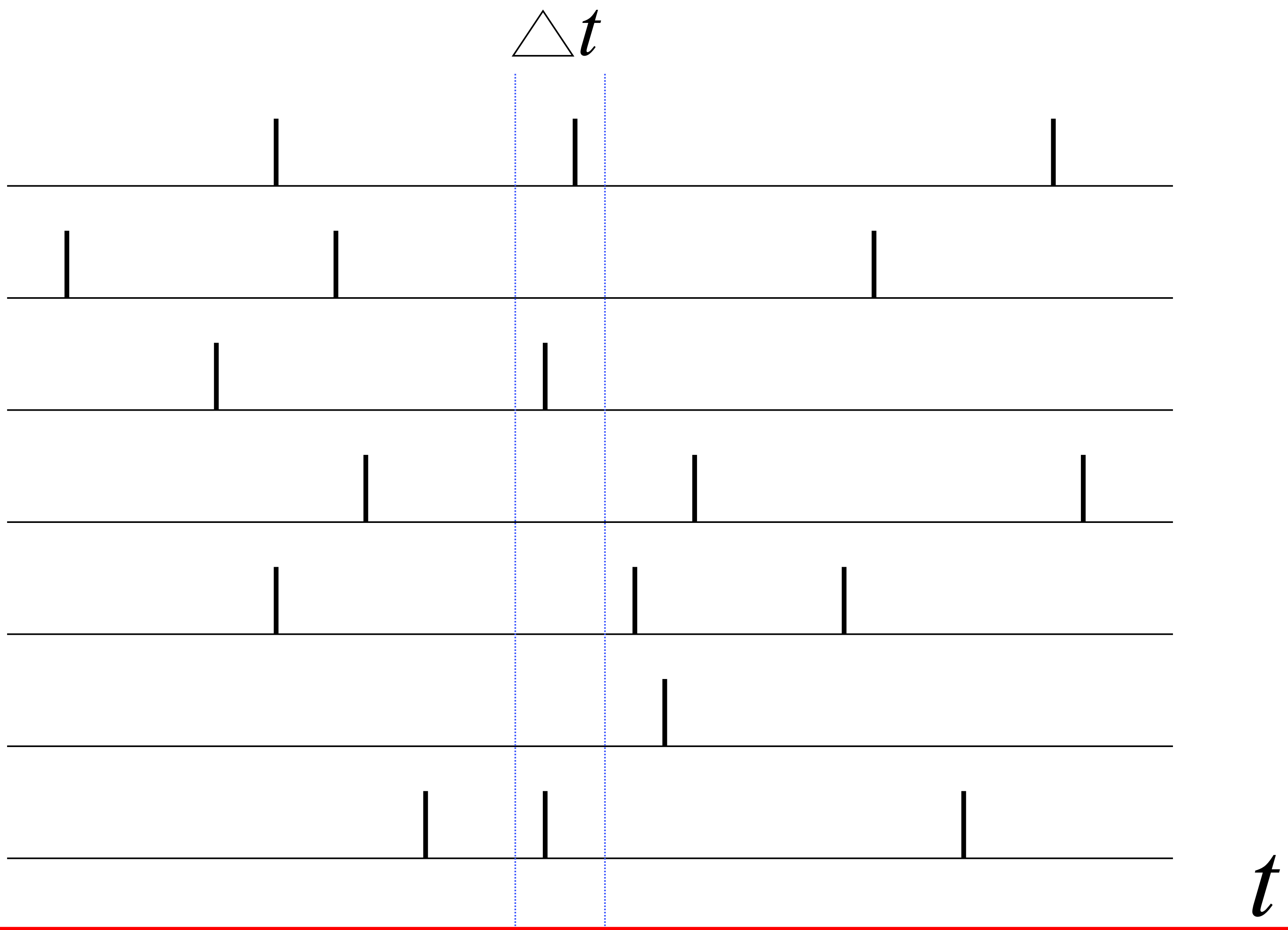


‘natural readout’



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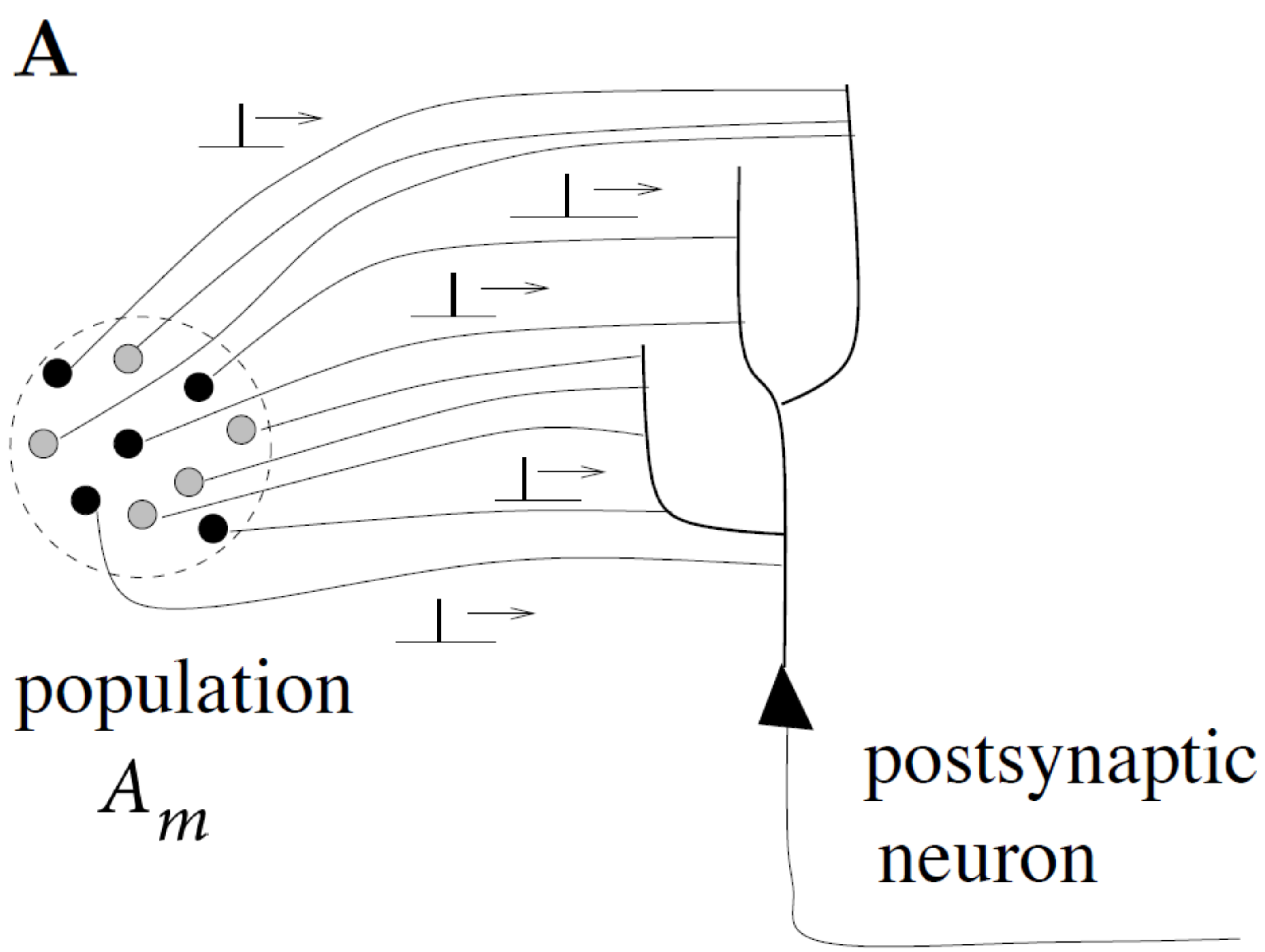
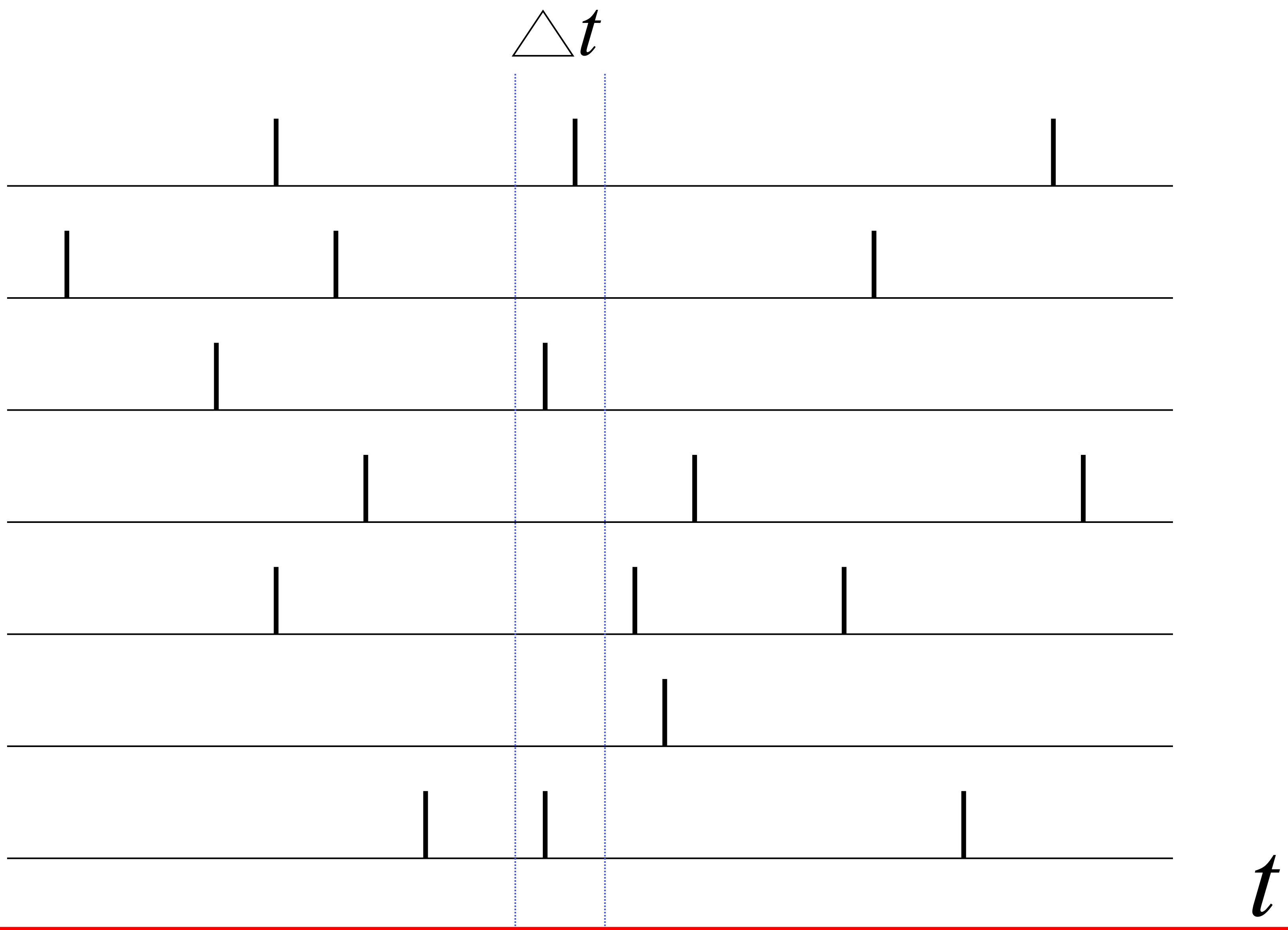


'natural readout'

But presynaptic population is not homogeneous



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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

Quiz 1, now

[x]

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Quiz 1, now

[x]
[x]

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Quiz 1, now

[x]
[x]
[x]

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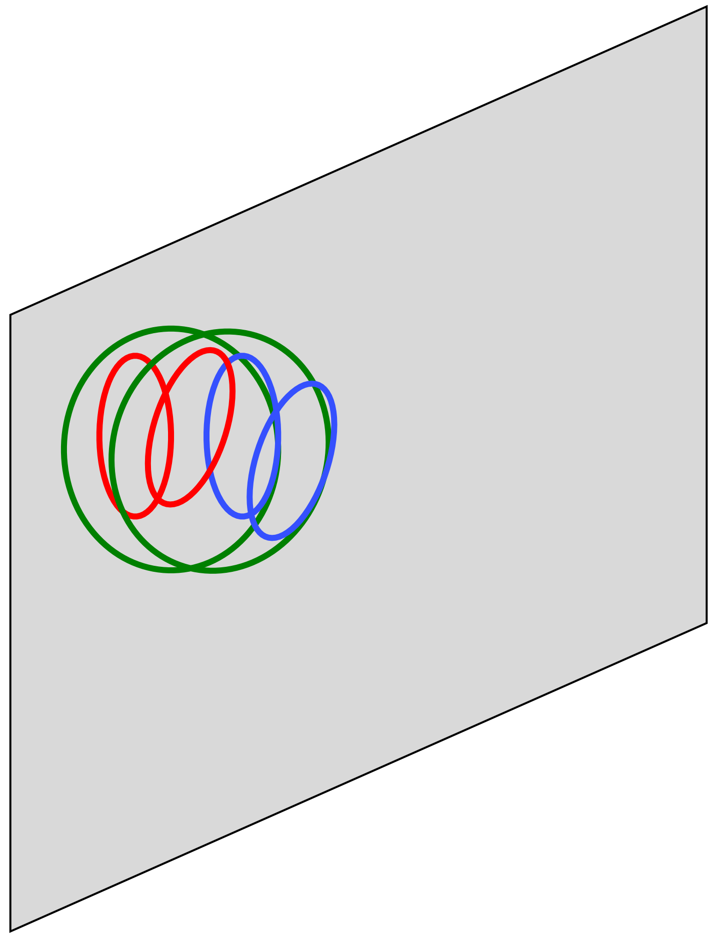
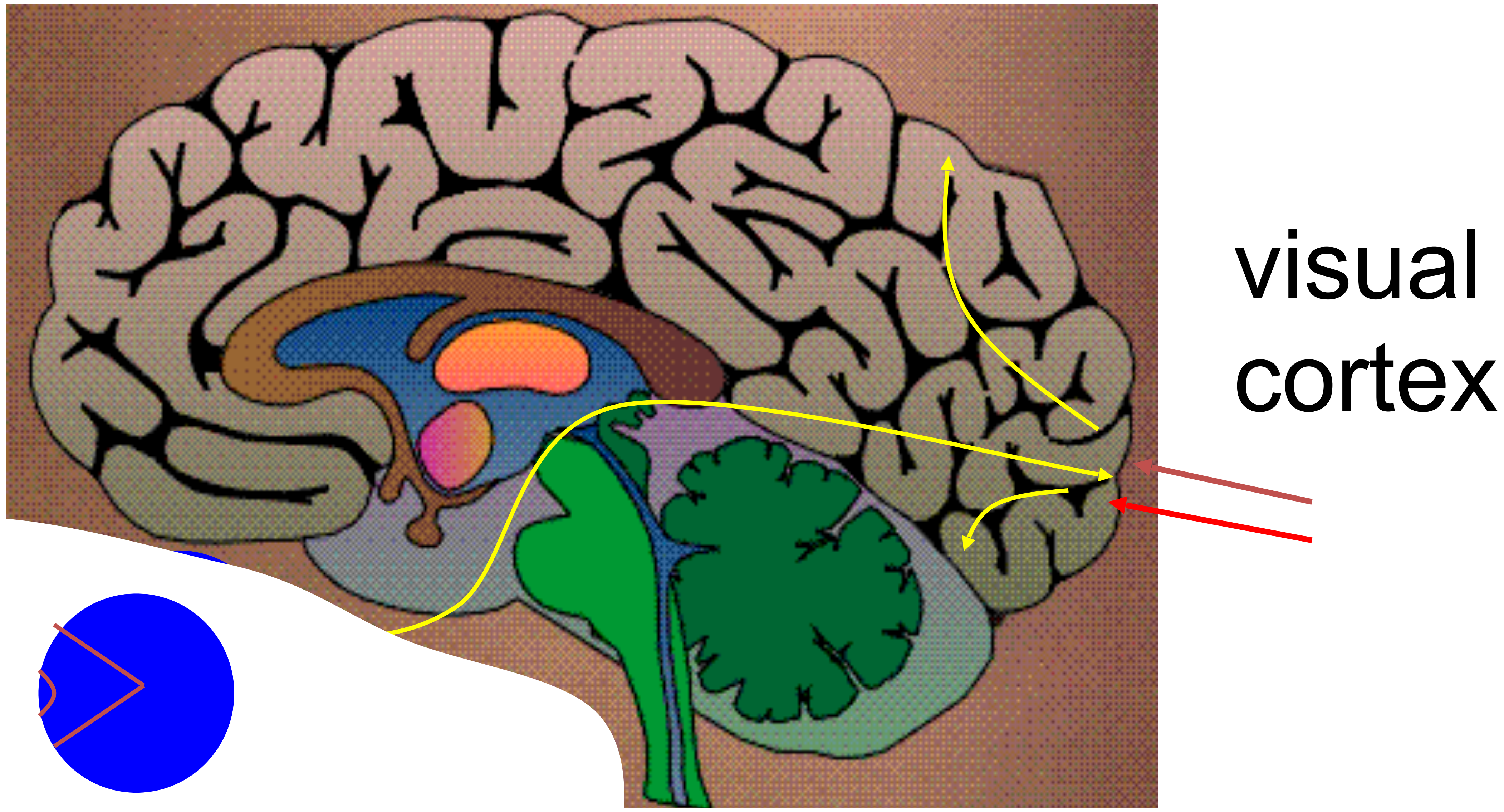
2. Orientation Map





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

Quiz 2, now

The receptive field of a visual neuron in V1 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 auditory frequencies to which it is sensitive

The receptive field of a somatosensory neuron refers to

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Summary 7.1 and 7.2:

- The population activity is a (spatial-like) average over an ensemble of neurons with similar properties and has units of a firing rate. The average does not have to be over a local group of neurons but could also be over a more distributed group (as long as they have similar properties).

- The population activity reflects the idea that each neuron gets input from a large number (= a population) of other neurons

- It is also consistent with the idea that concepts (compare Hopfield model) are represented by groups of neurons (and NOT in a single neuron).

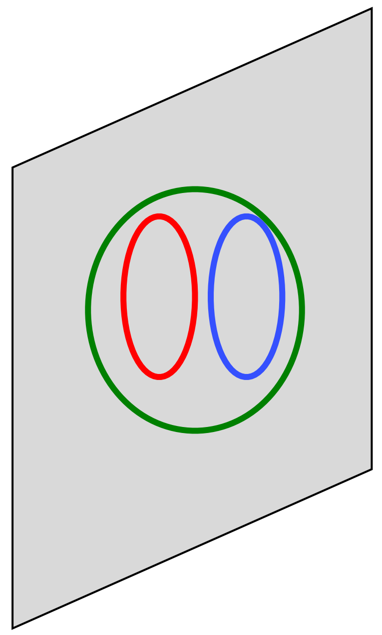
- In sensory areas of the cortex, neurons with similar properties are organized in columns, i.e., local groups of neurons with similar receptive fields.

- Receptive fields summarize the response profile of neurons in response to a stimulus

3. Cortical orientation map and cortical column

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

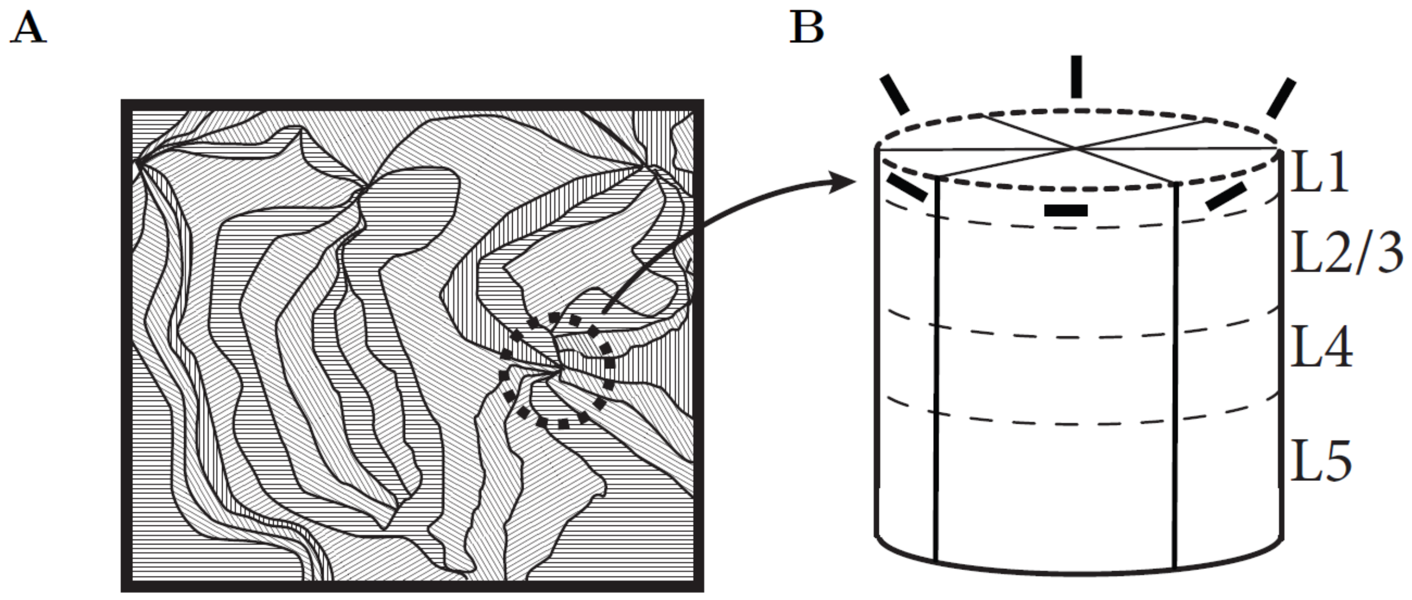
→ make this more precise



Rec. Field on Screen

cortical orientation map

Sheet of visual cortex   cortical column

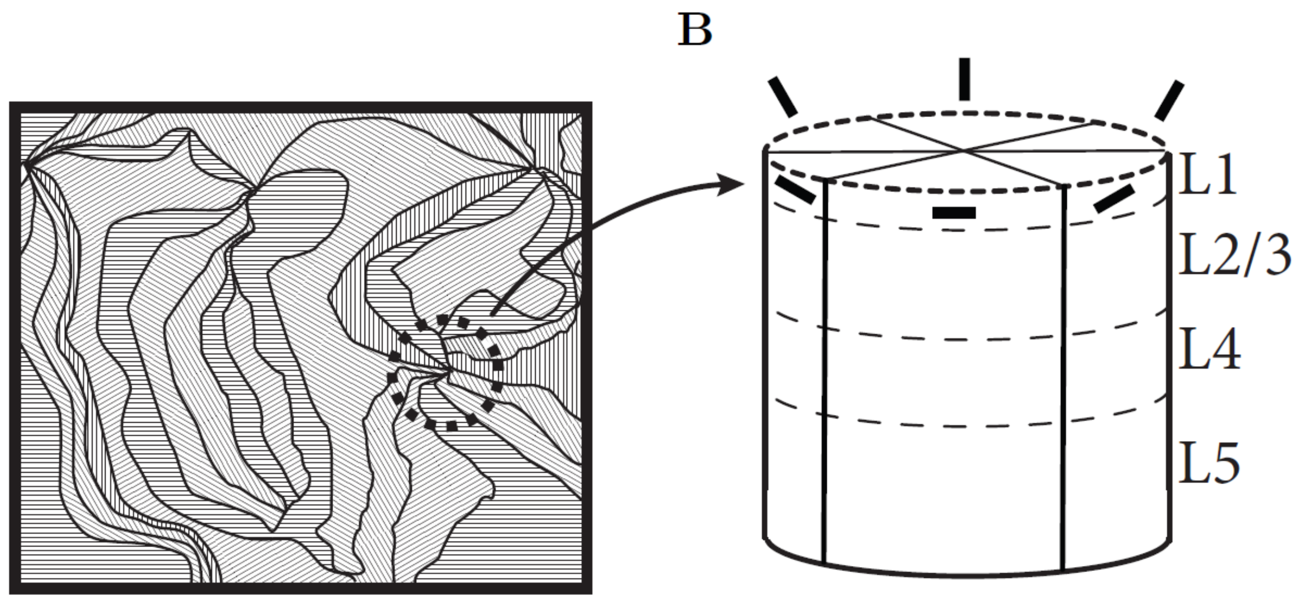


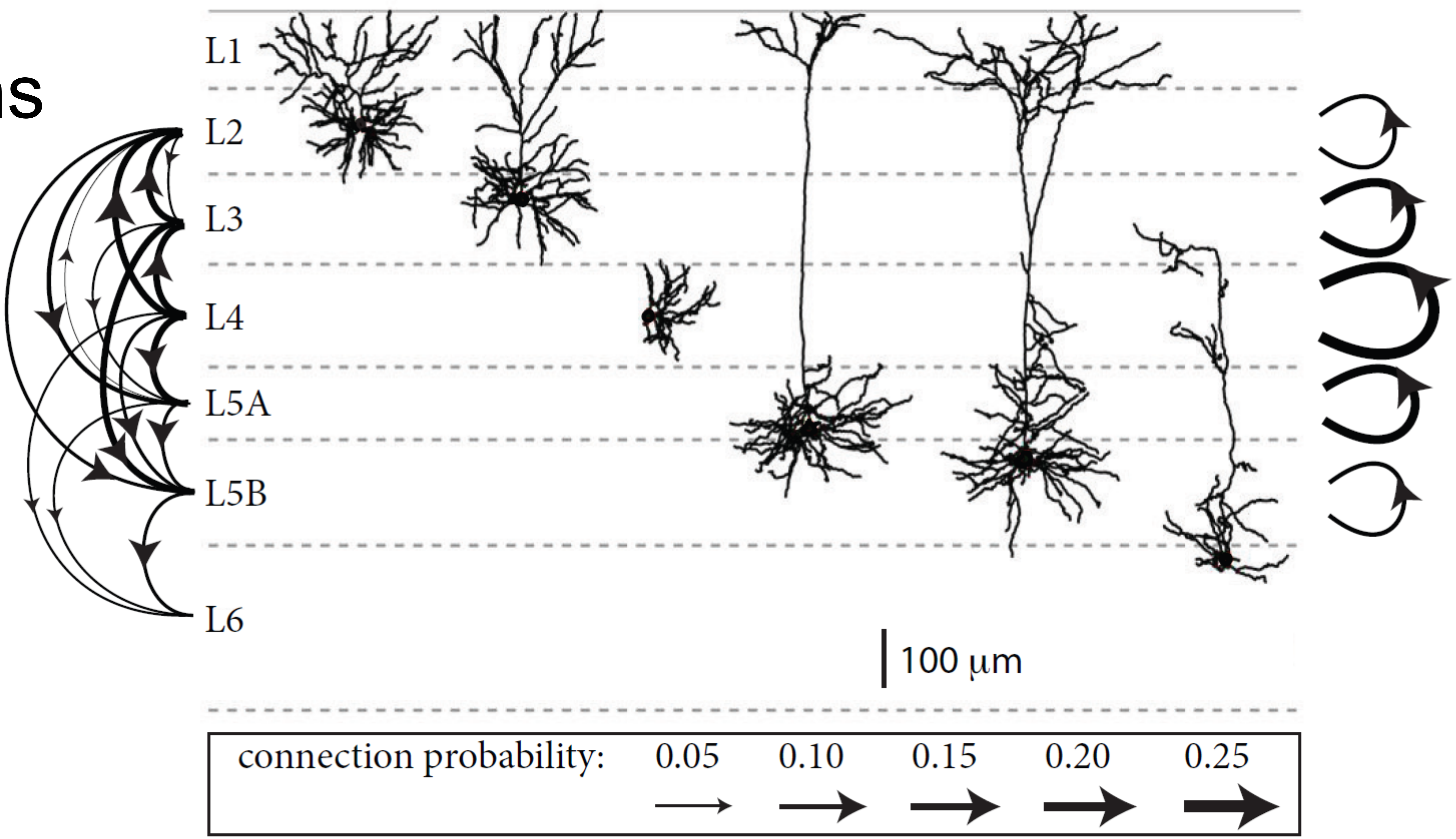
Hubel and Wiesel 1968; Bonhoeffer&Grinvald, 1991

3. local cortical connectivity across layers

(mouse somatosensory cortex)

Here:
Excitatory neurons





Lefort et al. NEURON, 2009

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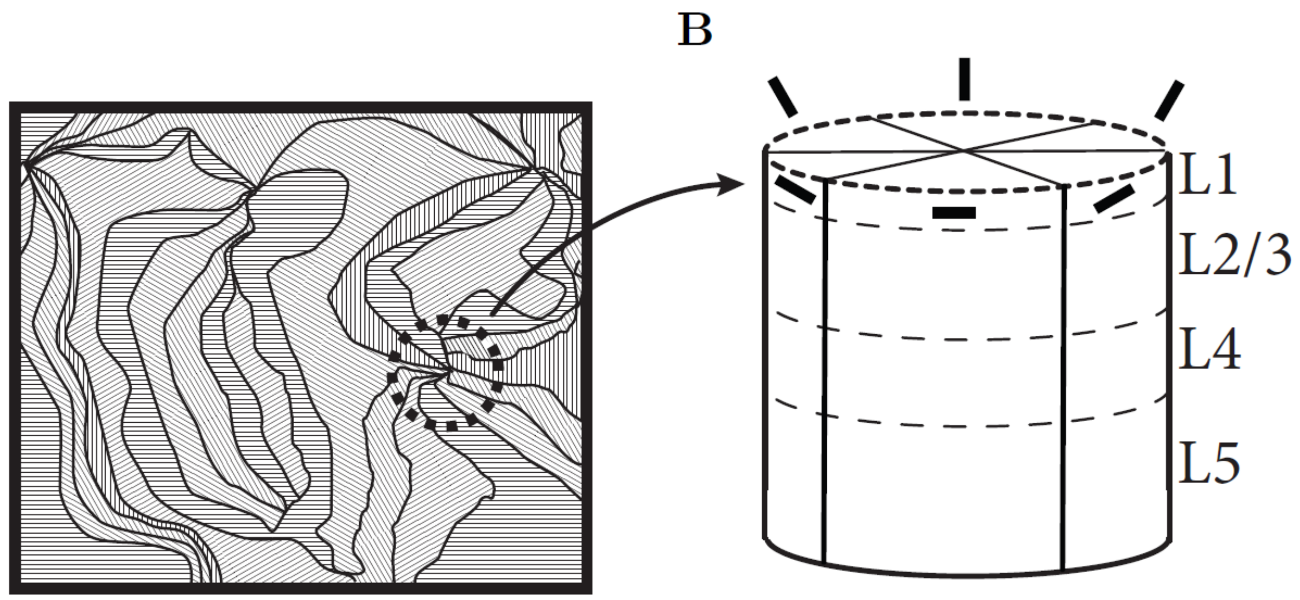

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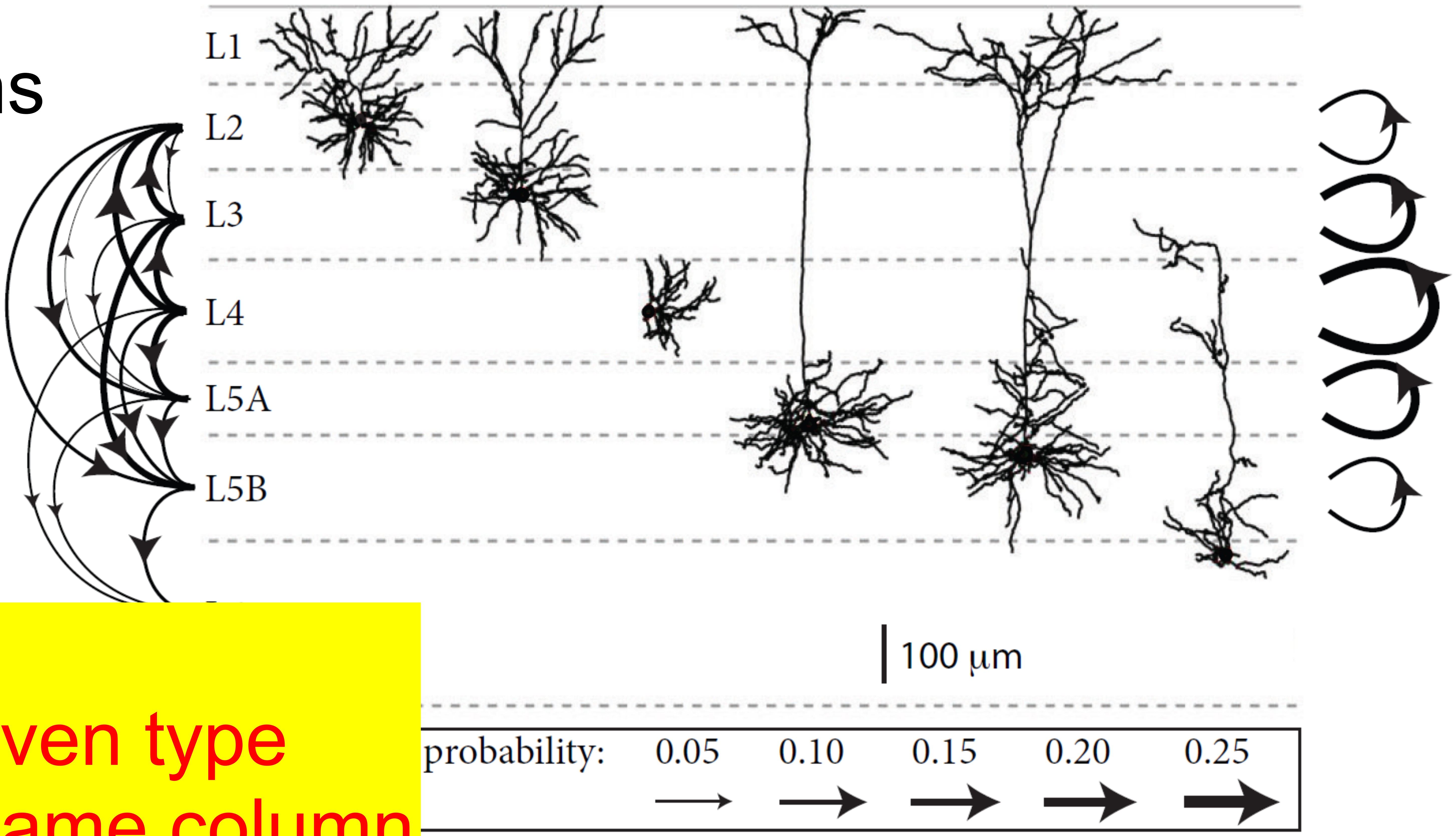


1 population =
all neurons of given type
in one layer of same column
(e.g. excitatory in layer 3)

Lefort et al. NEURON, 2009

Summary 7.3:

Theoreticians have taken an extreme view of neuronal populations. In their models a neuronal population consists of neurons with

- Identical parameters
- Identical input connectivity, in particular identical receptive field

Conditions on ‘identical connectivity’ can be loosened a little bit

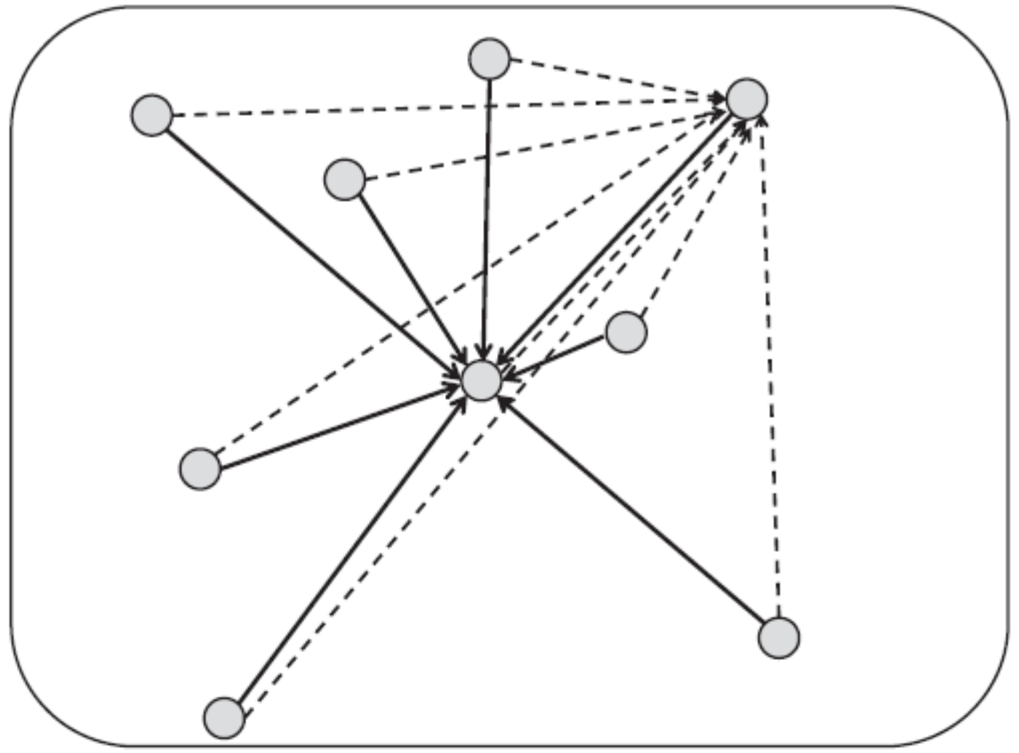
- The reference model is full connectivity
- The weaker assumption is that connectivity is random
- There are several variants of random connectivity
    - for a given population, we fix the total number of input connections per neuron (examples given earlier)
    - or, for a given population, we fixe the connection probability (examples will come next)

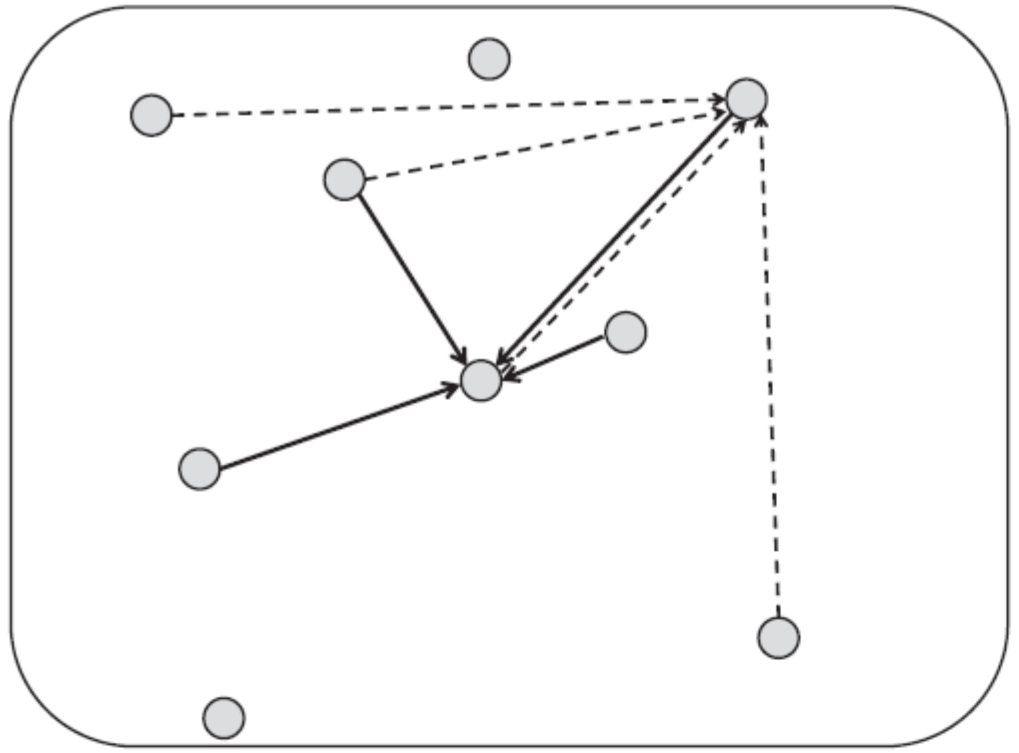
3. Connectivity schemes (models)

full connectivity
all-to-all

Random connectivity
w. number K of inputs fixed

N=5000
neurons





N=10000
neurons

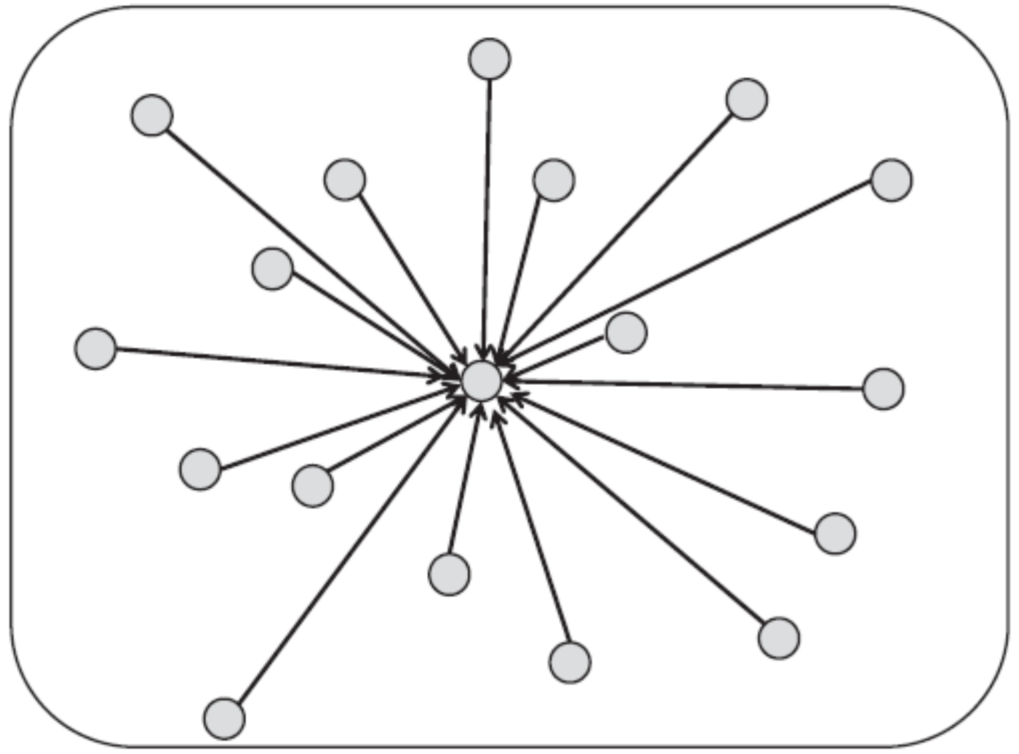
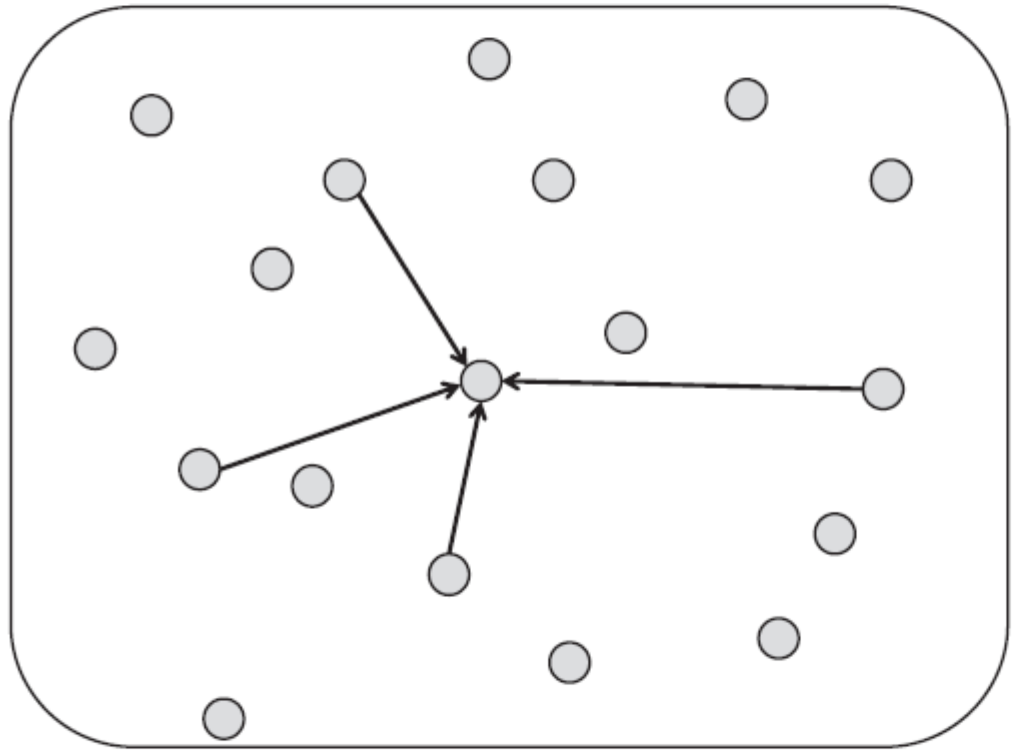


Image: Gerstner et al.
Neuronal Dynamics (2014)



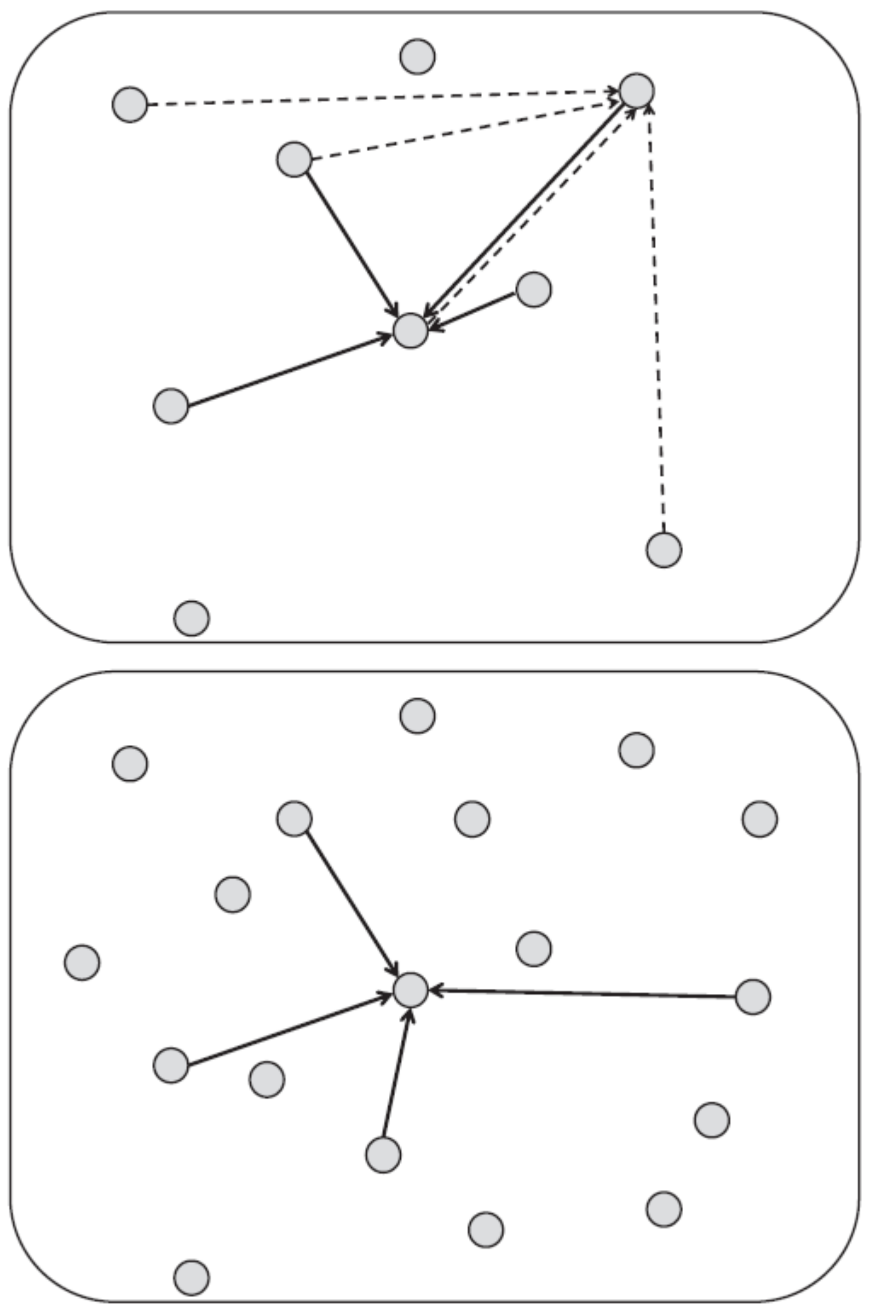
Each neuron receives
N connections

Each neuron receives
K connections

3. Random connectivity – fixed number of inputs

random: number of inputs K=500, fixed

C



Network N=5 000 Network N=10 000

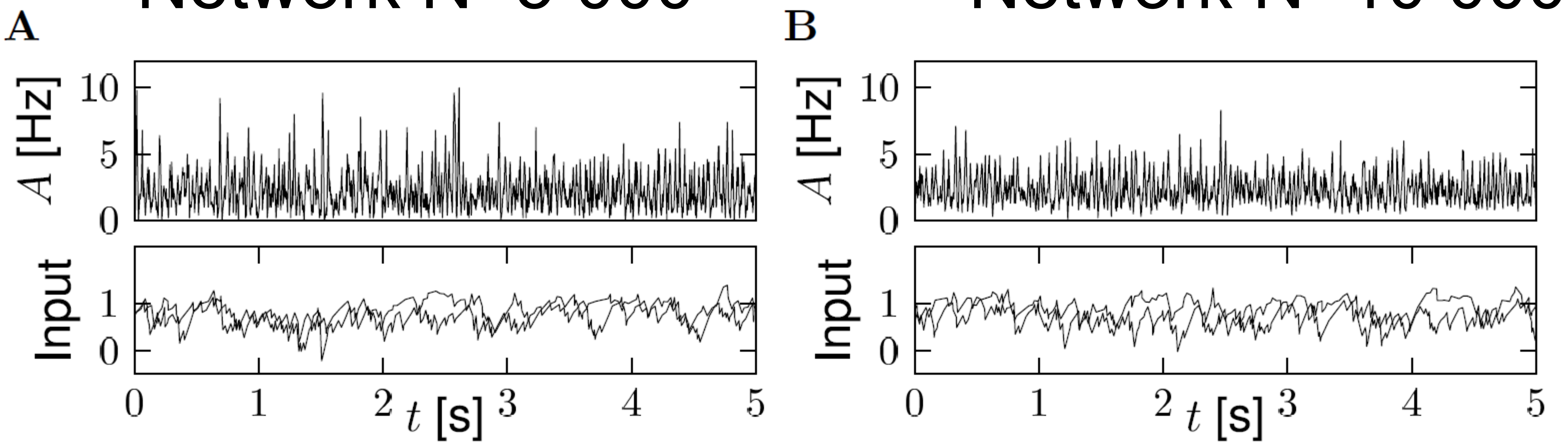


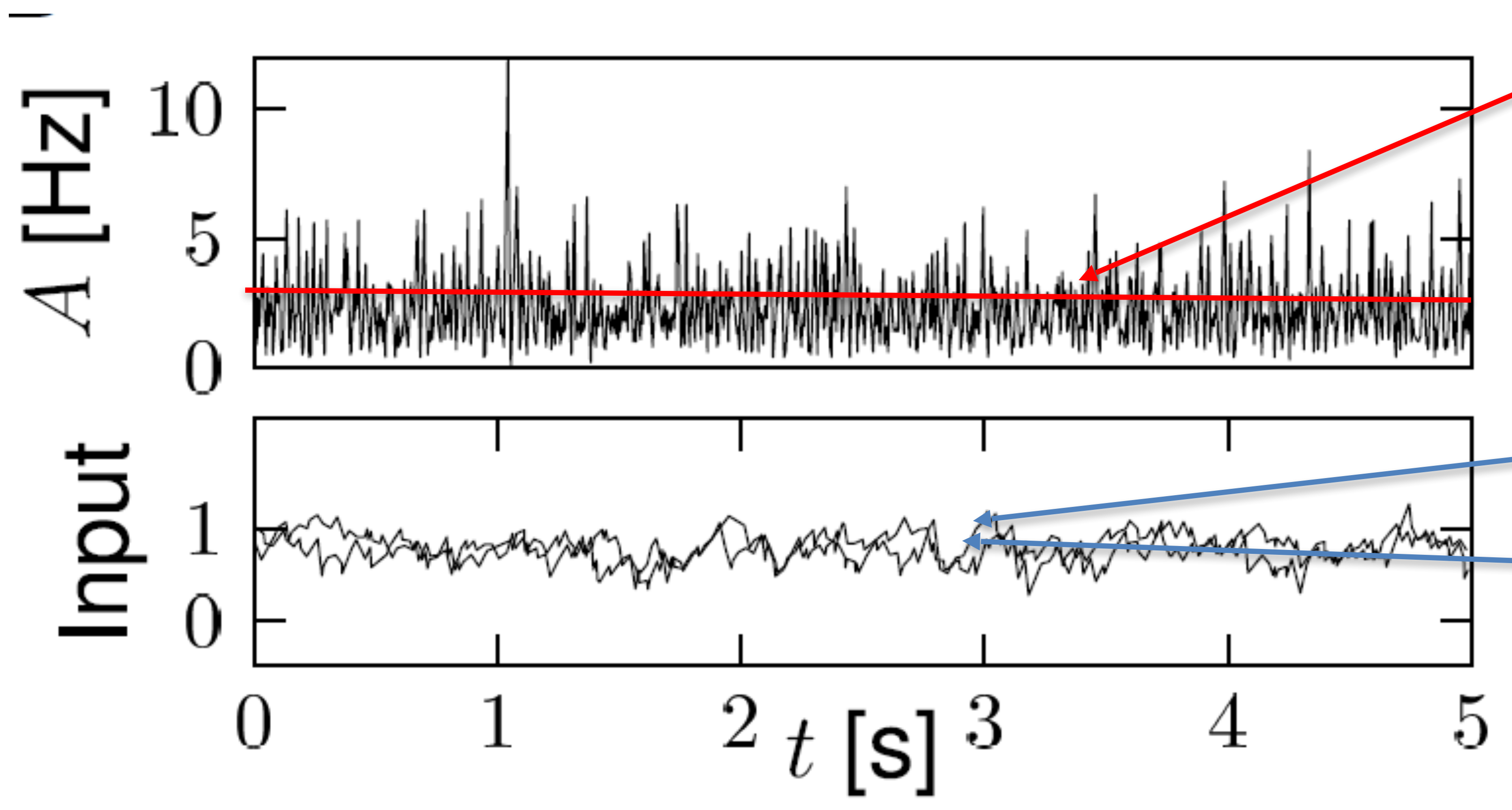
Fig. 12.8: Simulation of a model network with a fixed number of presynaptic partners (400 excitatory and 100 inhibitory cells) for each postsynaptic neuron. **A**. Top: Population activity $A(t)$ averaged over all neurons in a network of 4 000 excitatory and 1 000 inhibitory

Image: Gerstner et al. Neuronal Dynamics (2014)

3. Random Connectivity: 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?

4. asynchronous state

Asynchronous state

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

- filtered $A(t)$

-convergence in weak sense

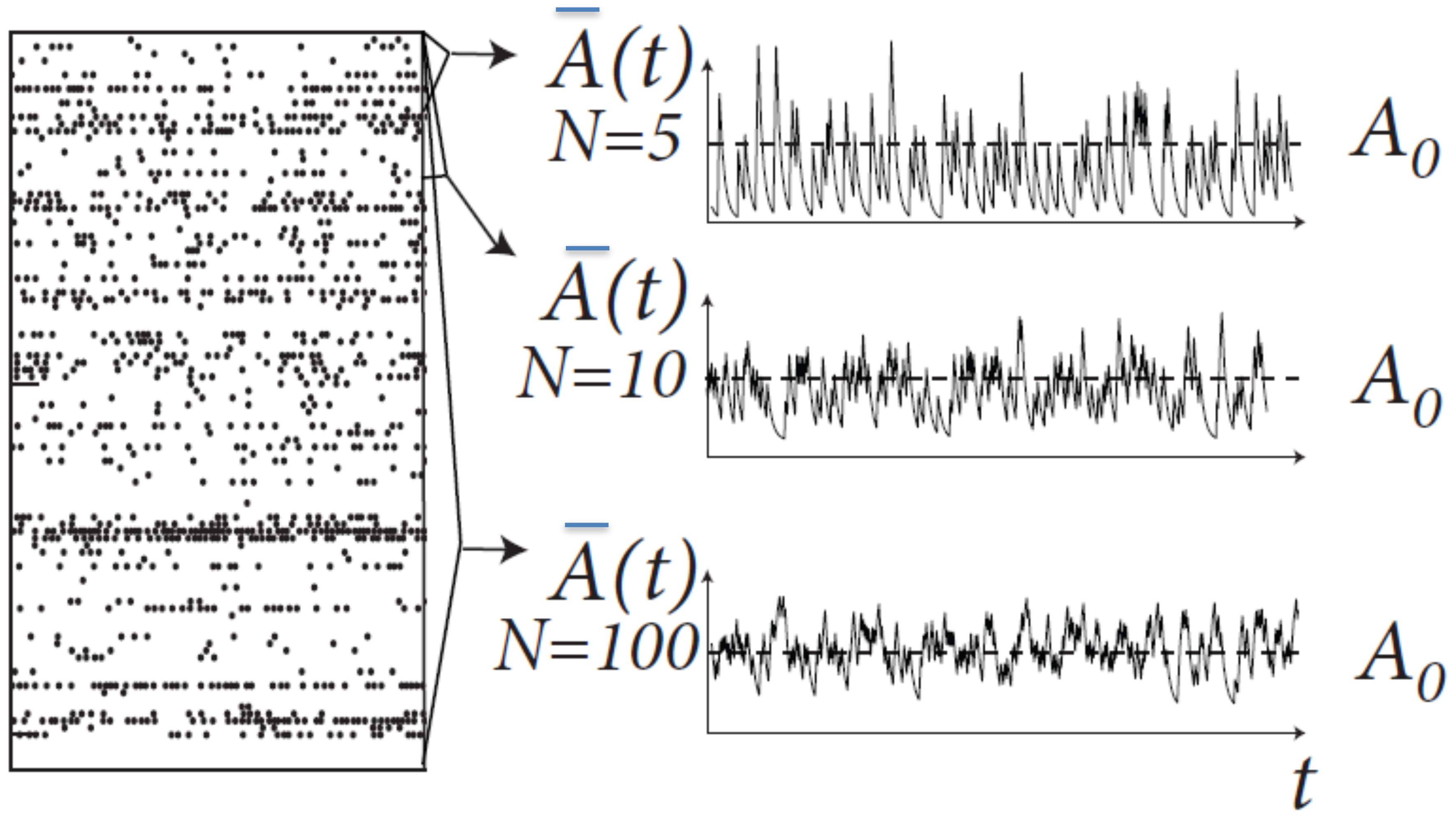
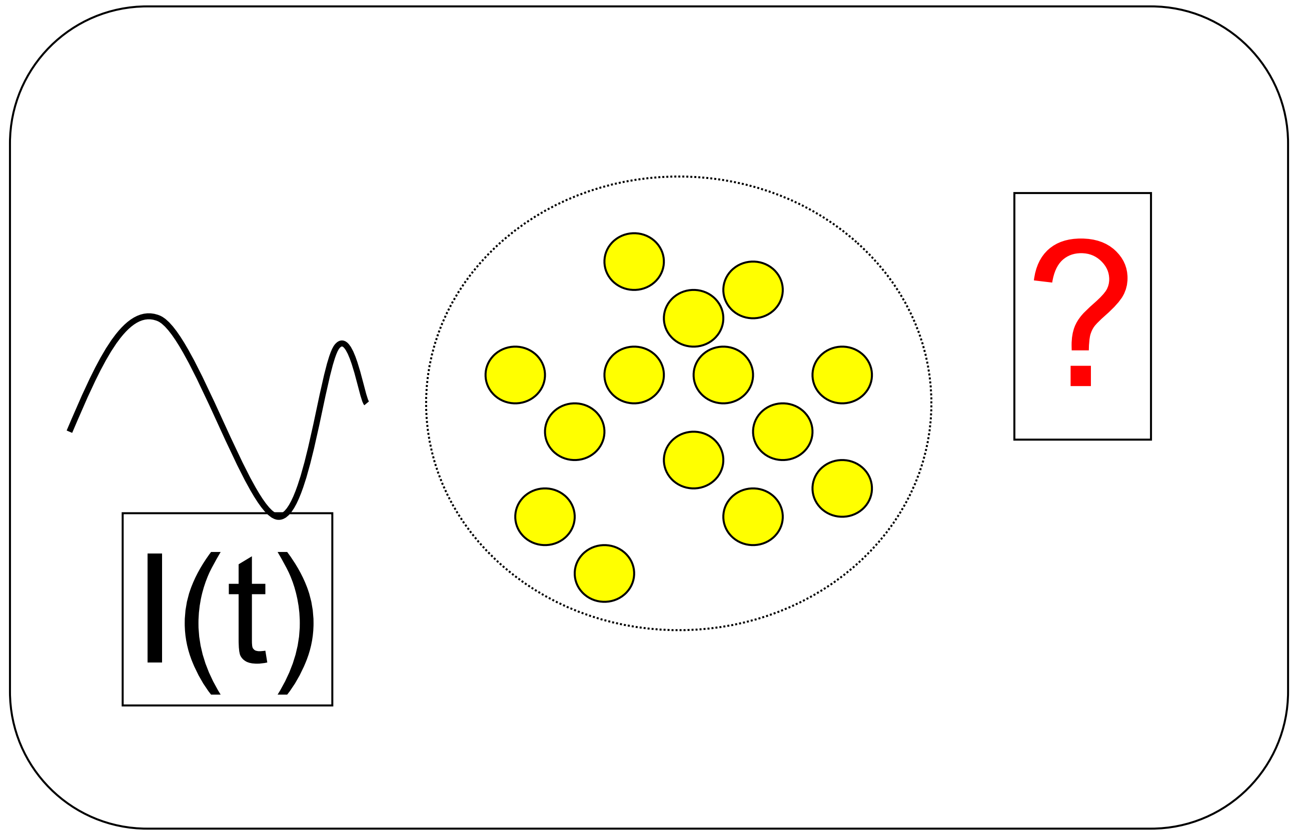


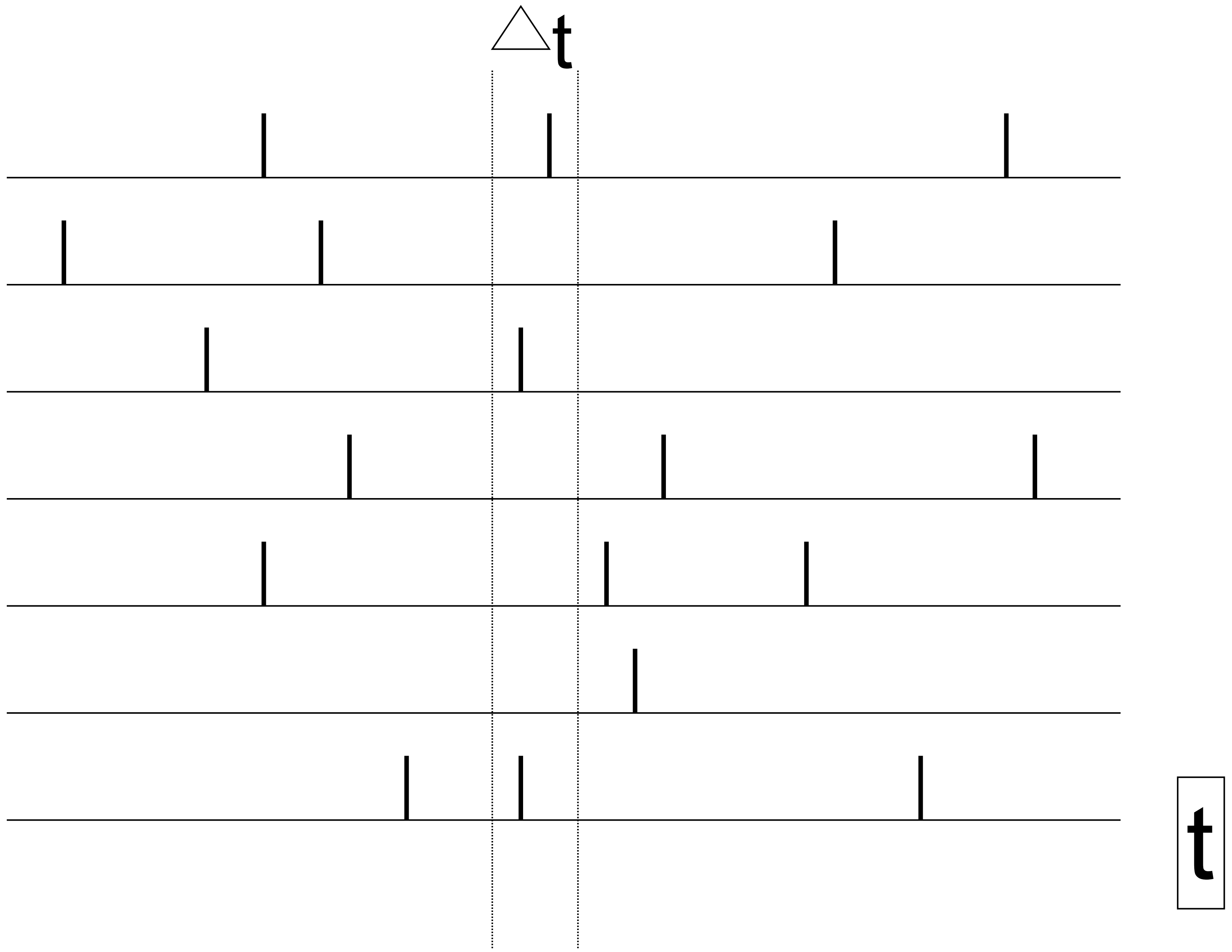
Image: Gerstner et al.
Neuronal Dynamics (2014)

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

4. asynchronous state in a homogeneous network



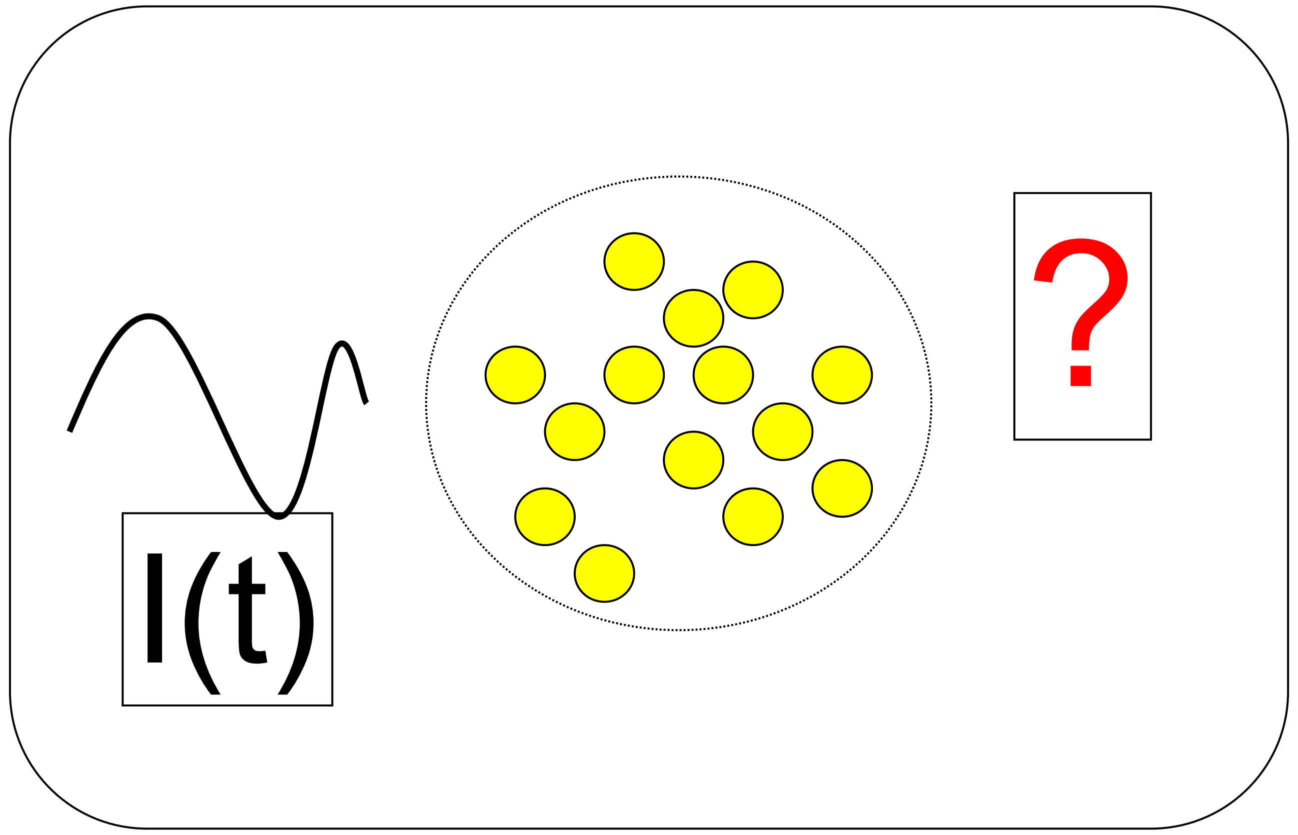
population activity?



population activity

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

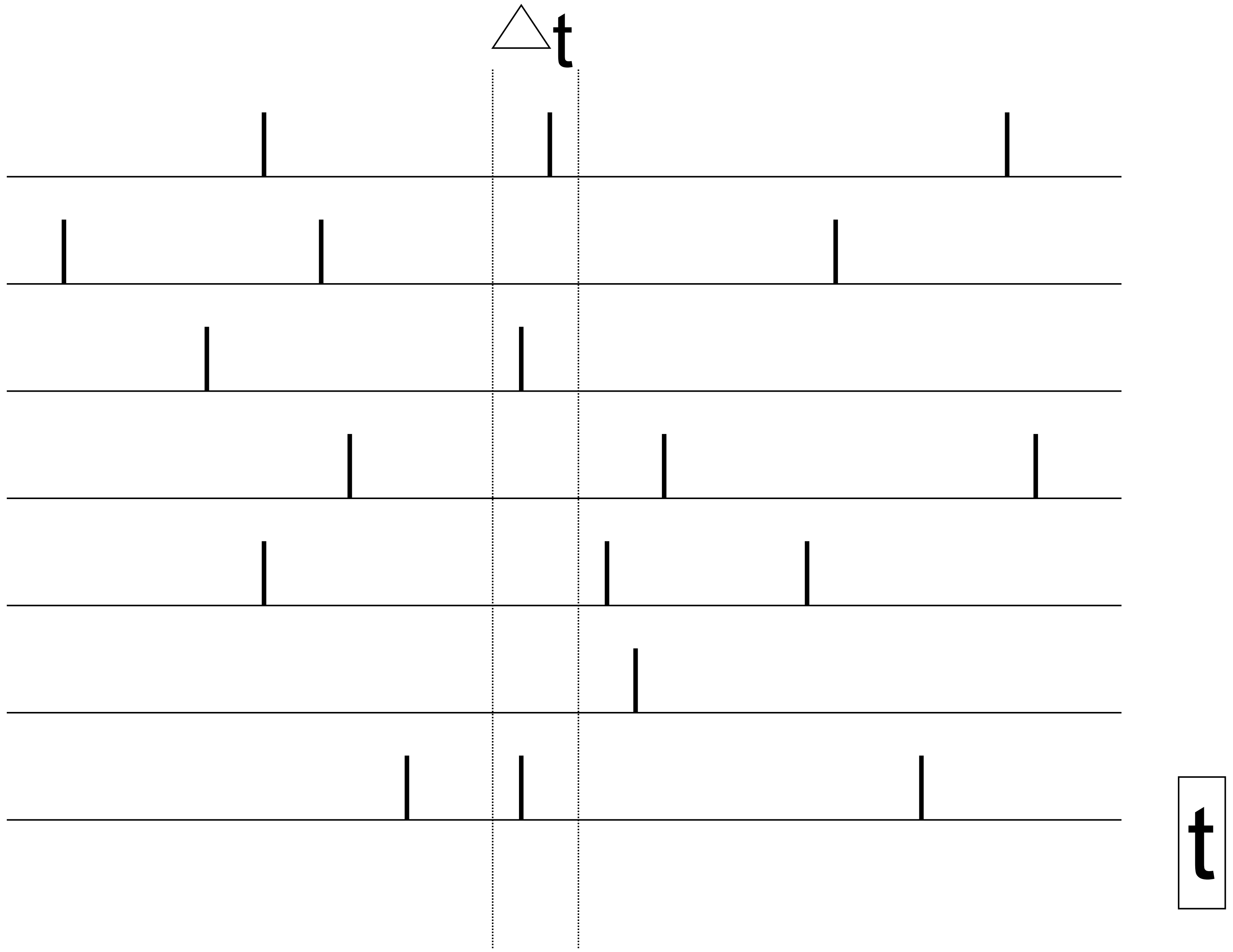
4. asynchronous state in a homogeneous network



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?

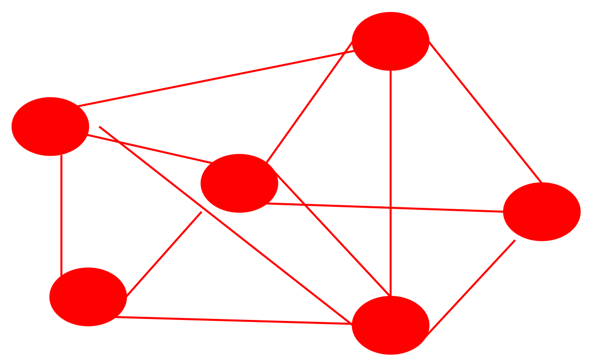


population activity

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

4. mean-field arguments (full connectivity)

Fully connected network



fully connected
N >> 1

Synaptic coupling

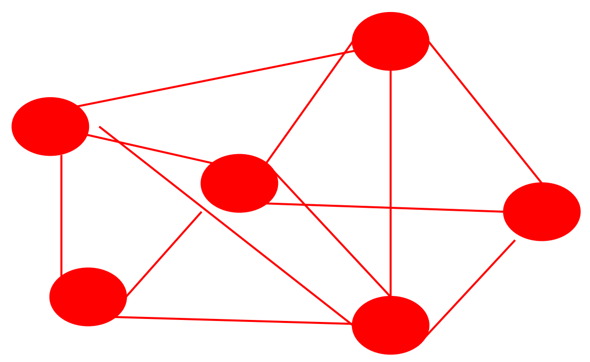
$$w_{ij} = w_0$$

Input current to neuron i

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

4. mean-field arguments (full connectivity)

Fully connected network



fully connected
N >> 1

Synaptic coupling

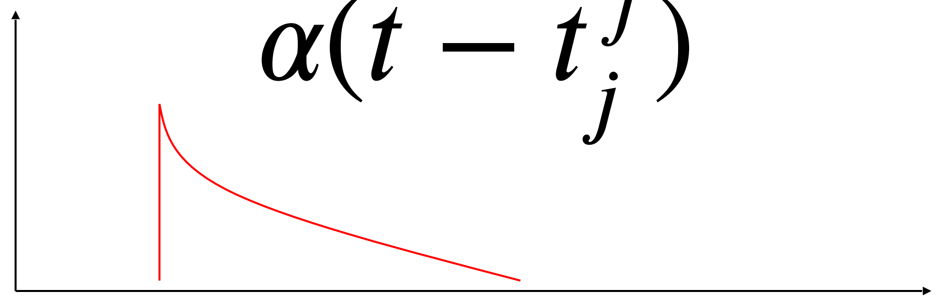
$$w_{ij} = w_0$$

Input current to neuron i

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

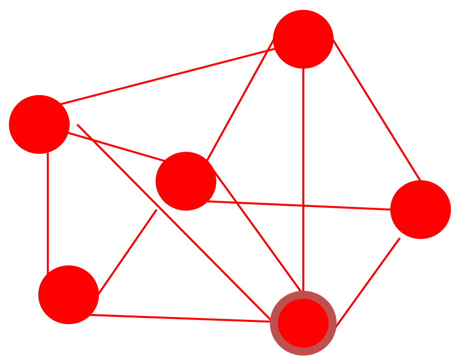
Sum over all spikes, all neurons

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



4. mean-field arguments (full connectivity)

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



fully connected

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

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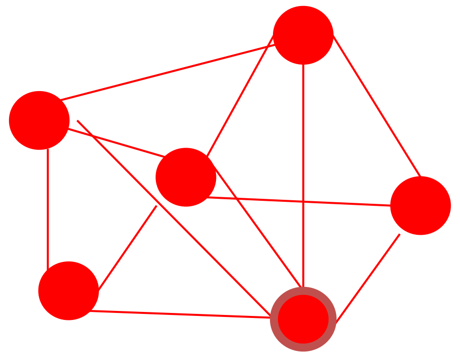

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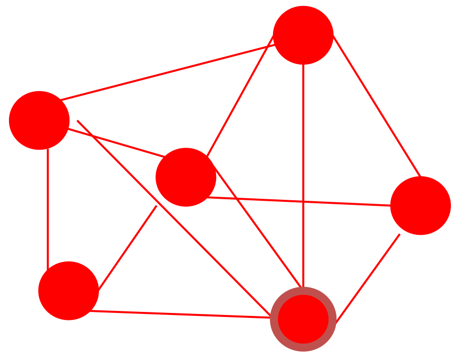
$$I_i^{net}(t) = J_0 \int \alpha(s) A(t-s) ds + I^{ext}(t)$$



fully connected

All spikes, all neurons

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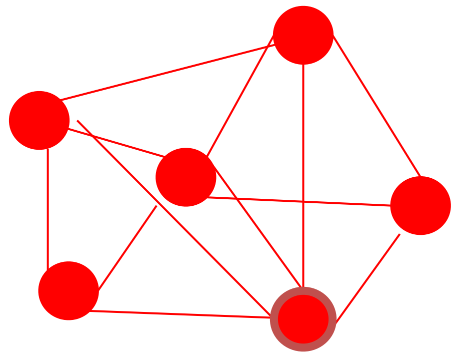
Index i disappears

All spikes, all neurons

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



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

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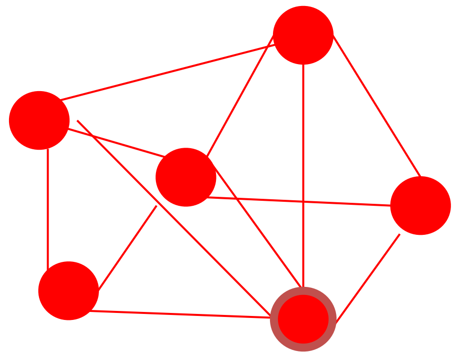

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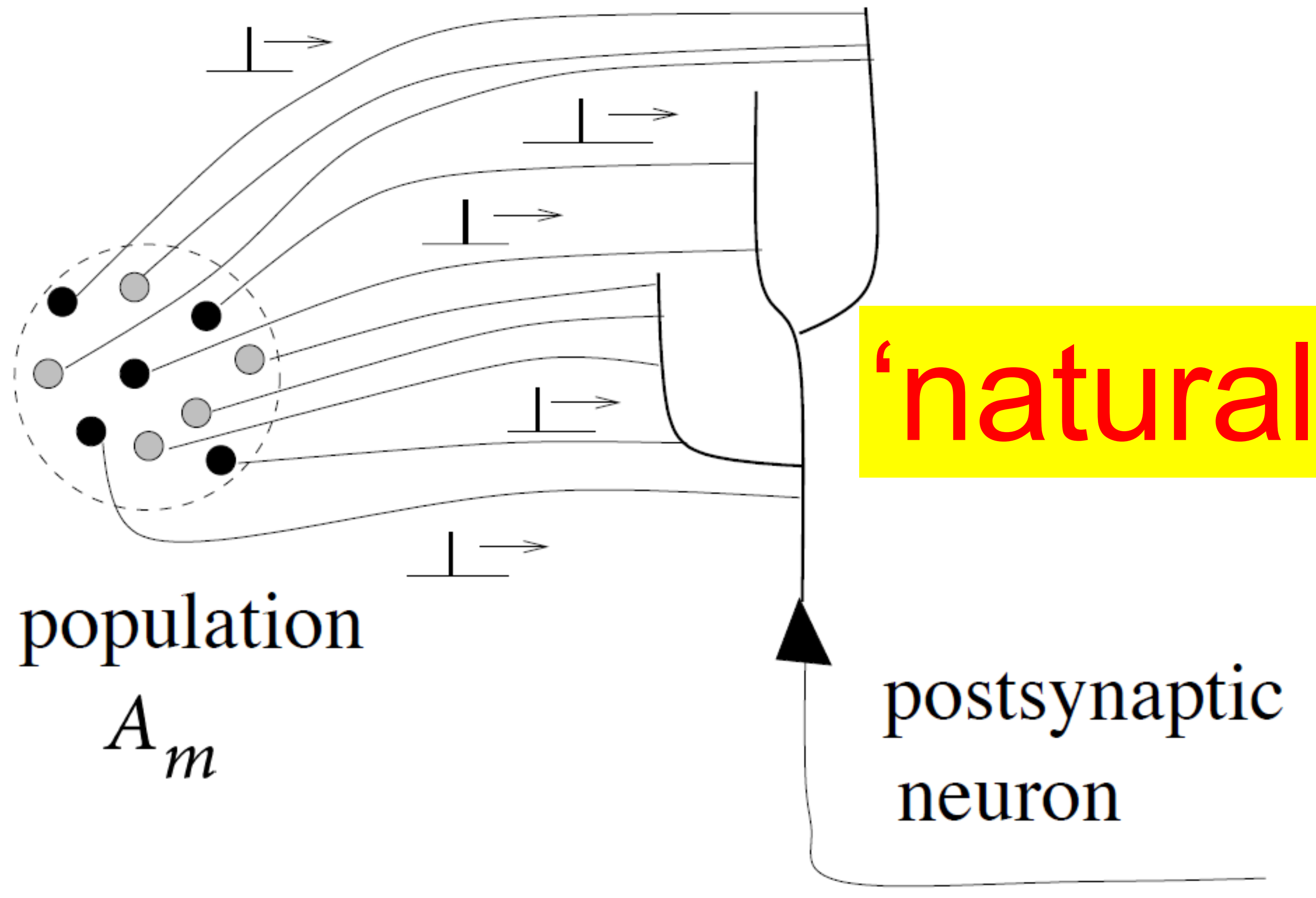


'natural readout'

5. mean-field arguments: asynchronous state

Stationary state

Assume all variables are constant in time:

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

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

Firing rate? Population rate?

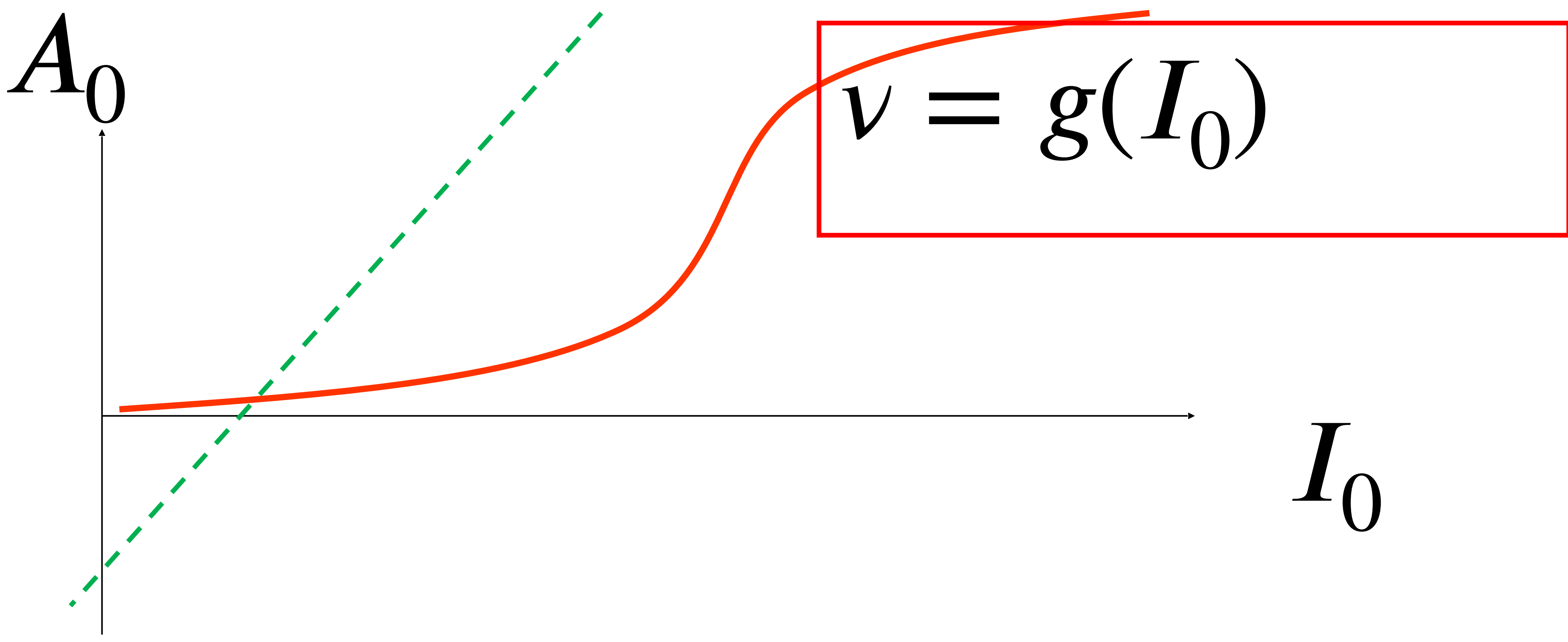
5. stationary solution: population activity (asynchr. state)

Stationary solution
=asynchronous state

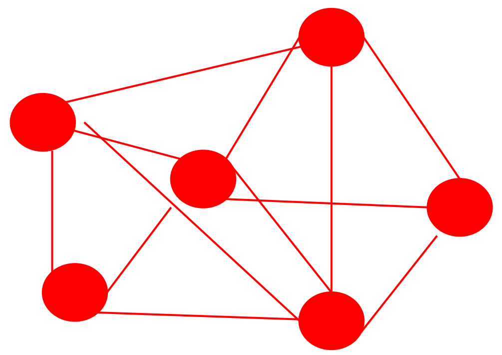
(1) $I_0 = [J_0 q A_0 + I_0^{ext}]$

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

(3) $\nu = A_0$



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)

Stationary solution
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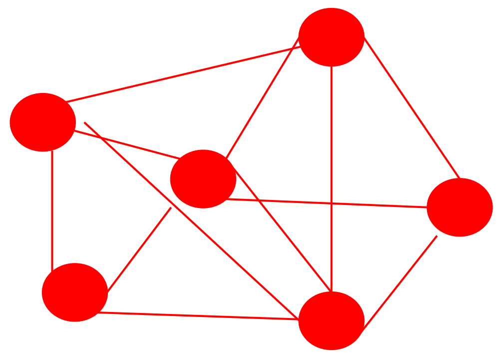

fully connected
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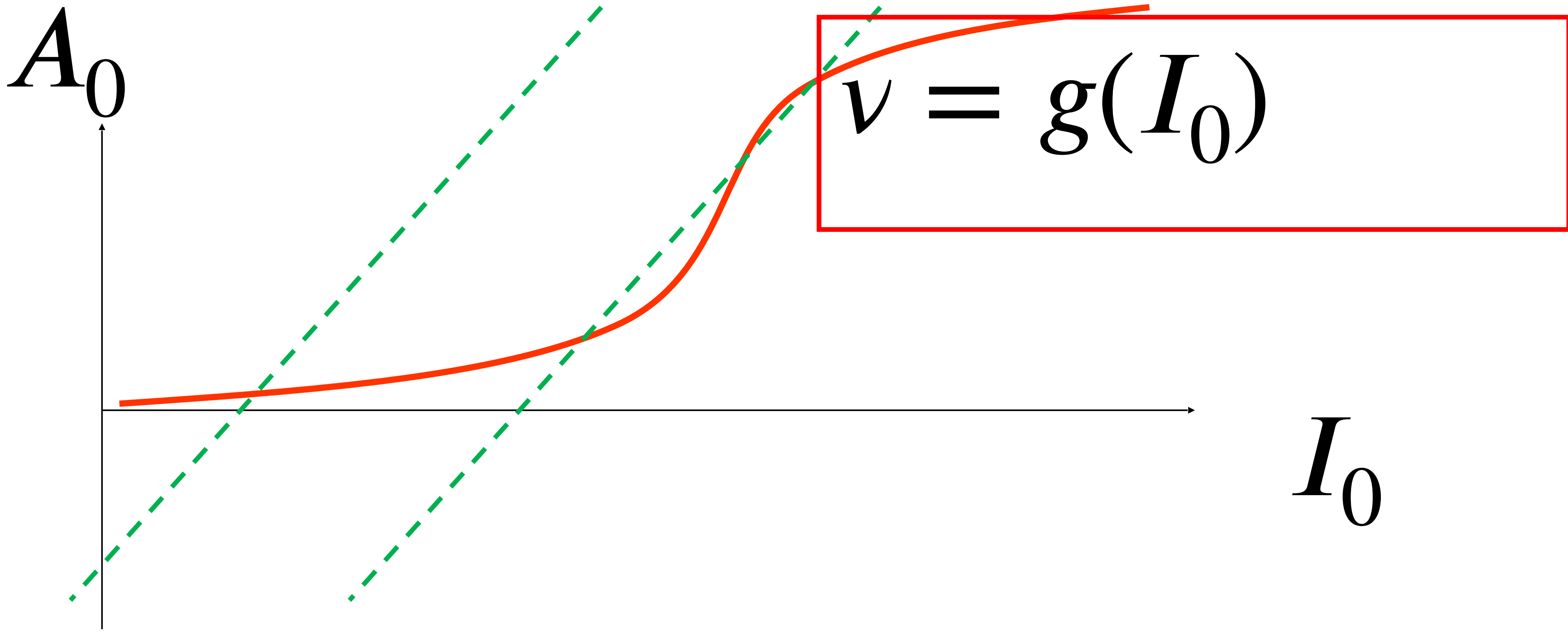


Stationary solution

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

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

→ **where g is the f-I curve!**

Examples: - leaky integrate-and-fire (with noise or without noise)
- Spike Response Model (with noise or without noise)
- Hodgkin-Huxley model

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

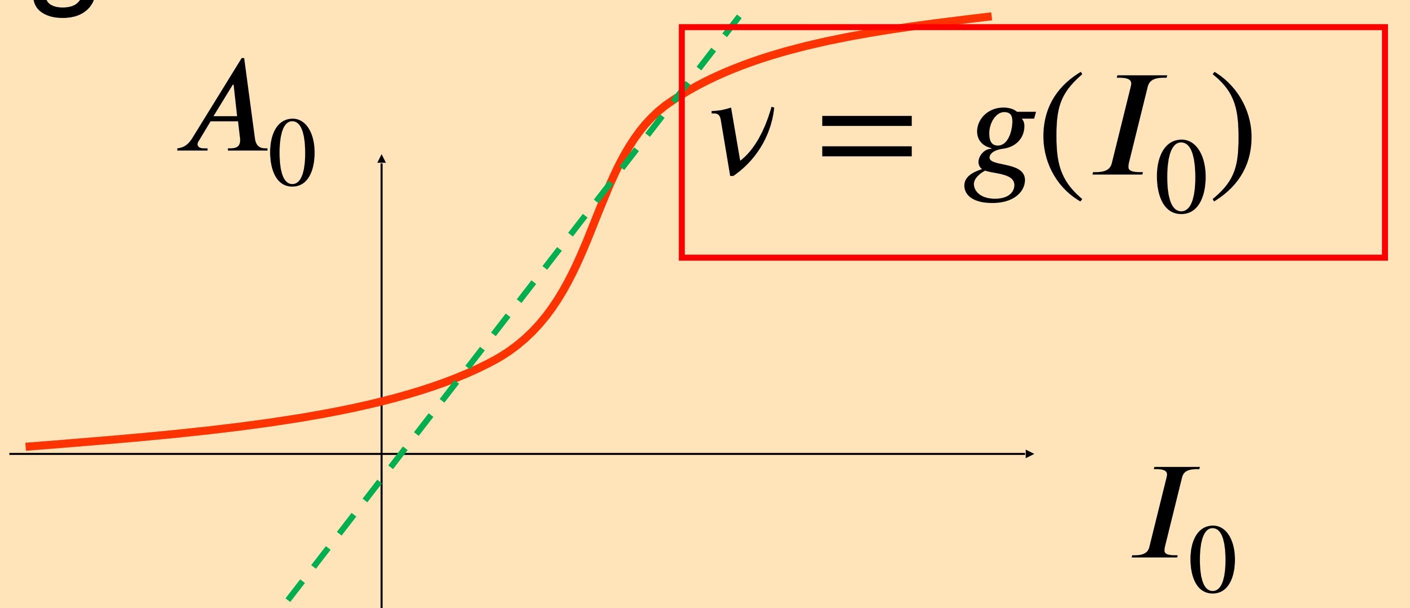
Quiz 4, now

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

In a large fully connected homogeneous network, we find the stationary state by a graphical construction. If the interaction weights INCREASE, the green line

[ ] does not change
[ ] becomes less steep
[ ] moves horizontally



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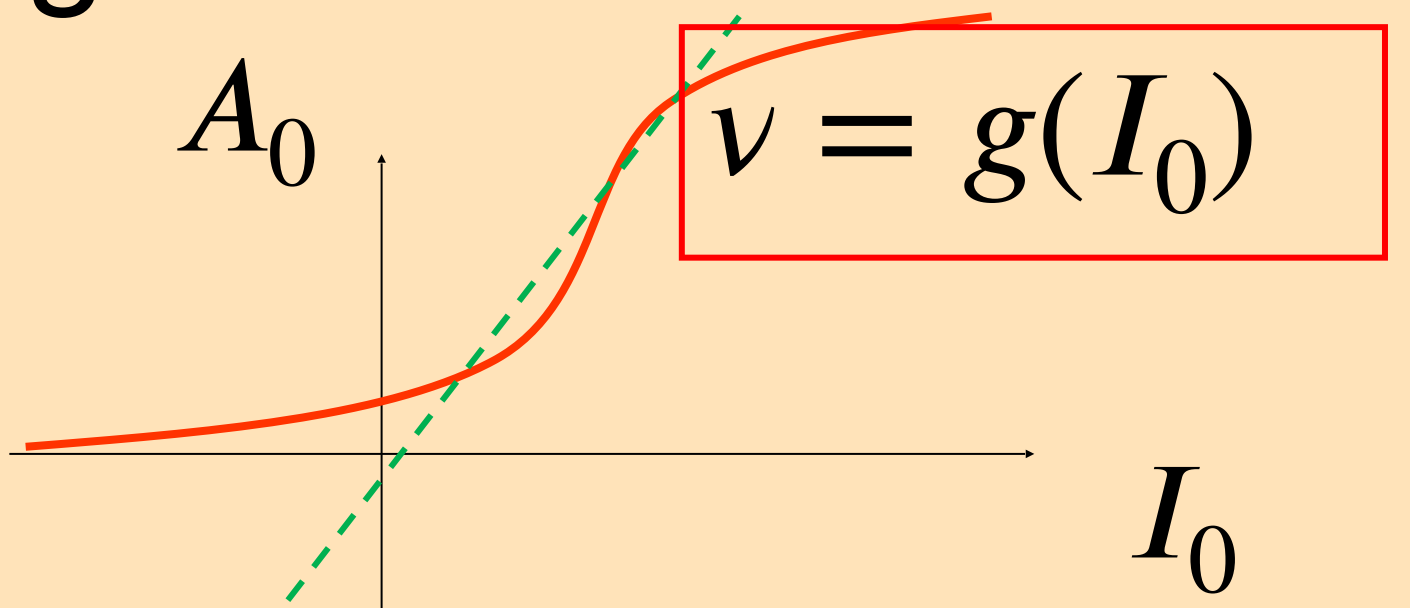

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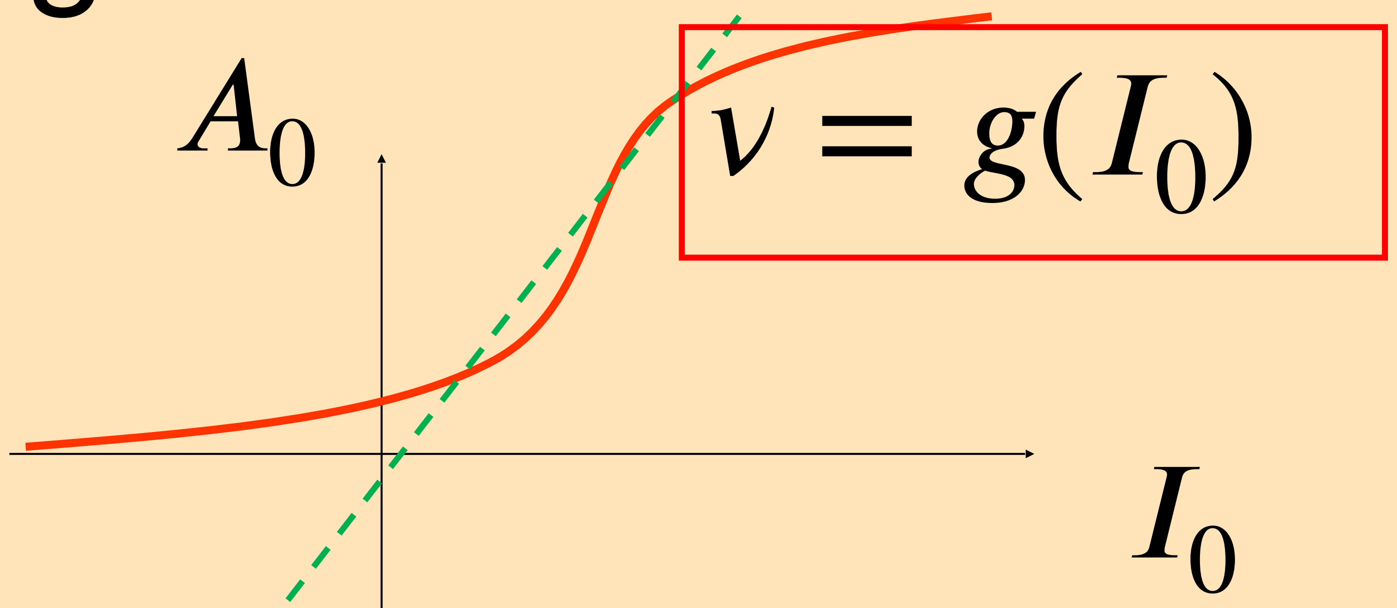

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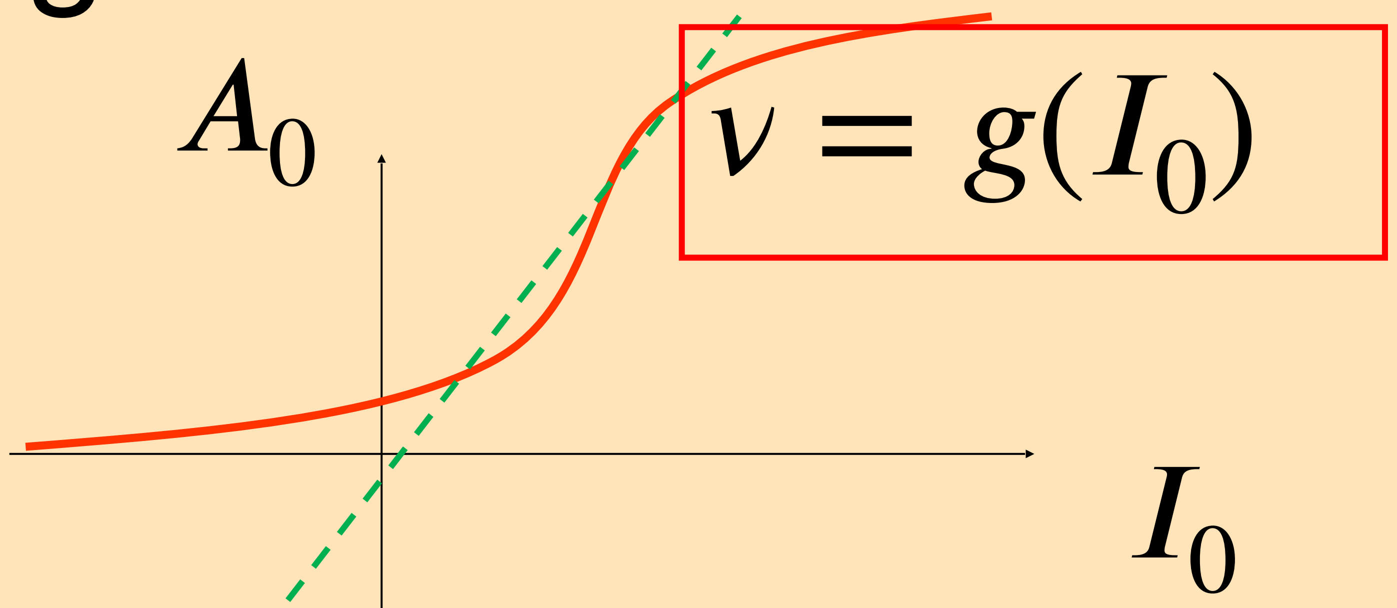

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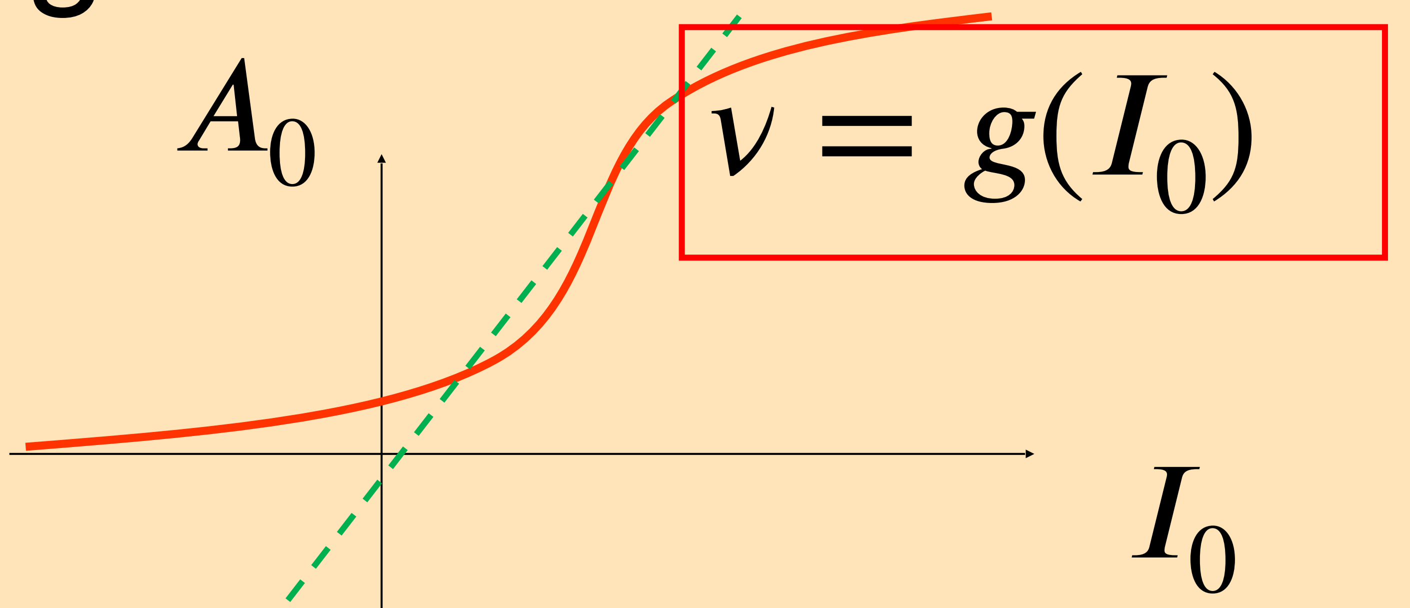

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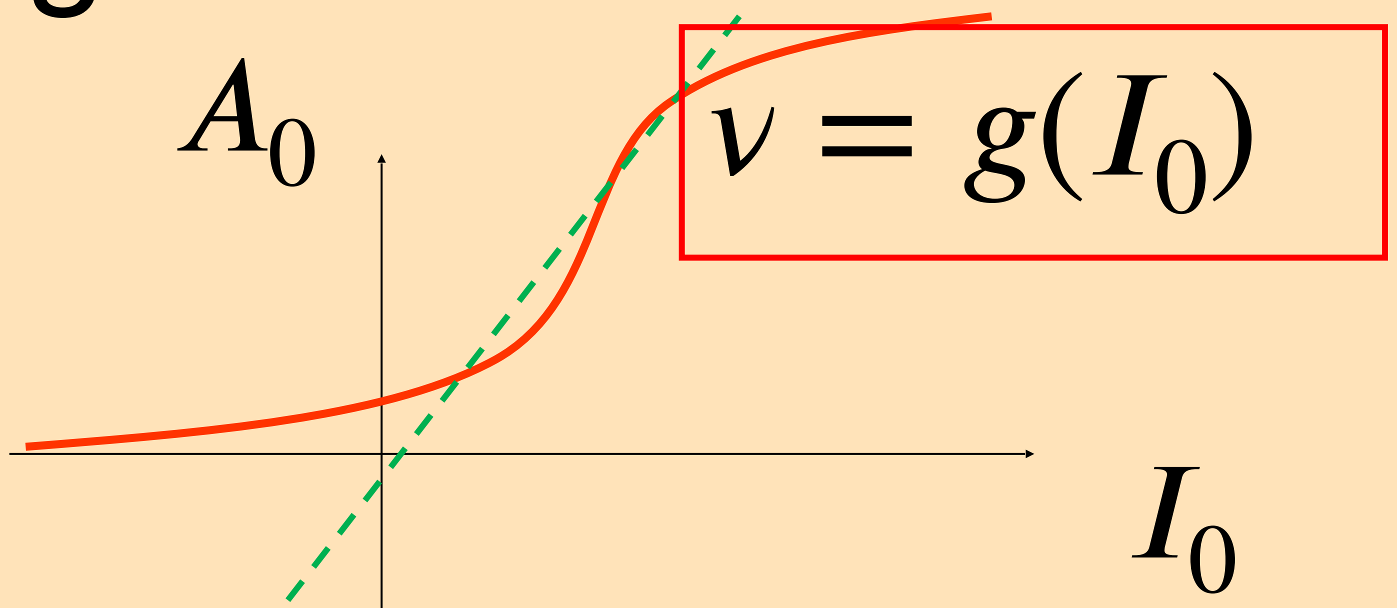

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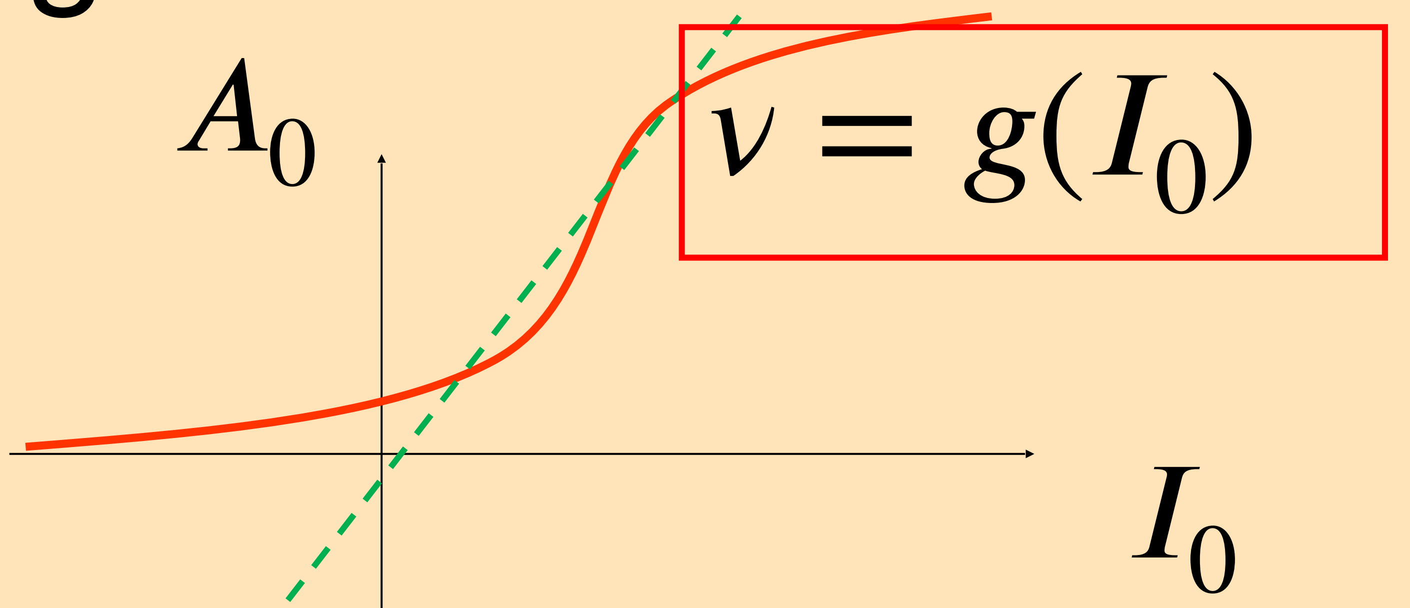

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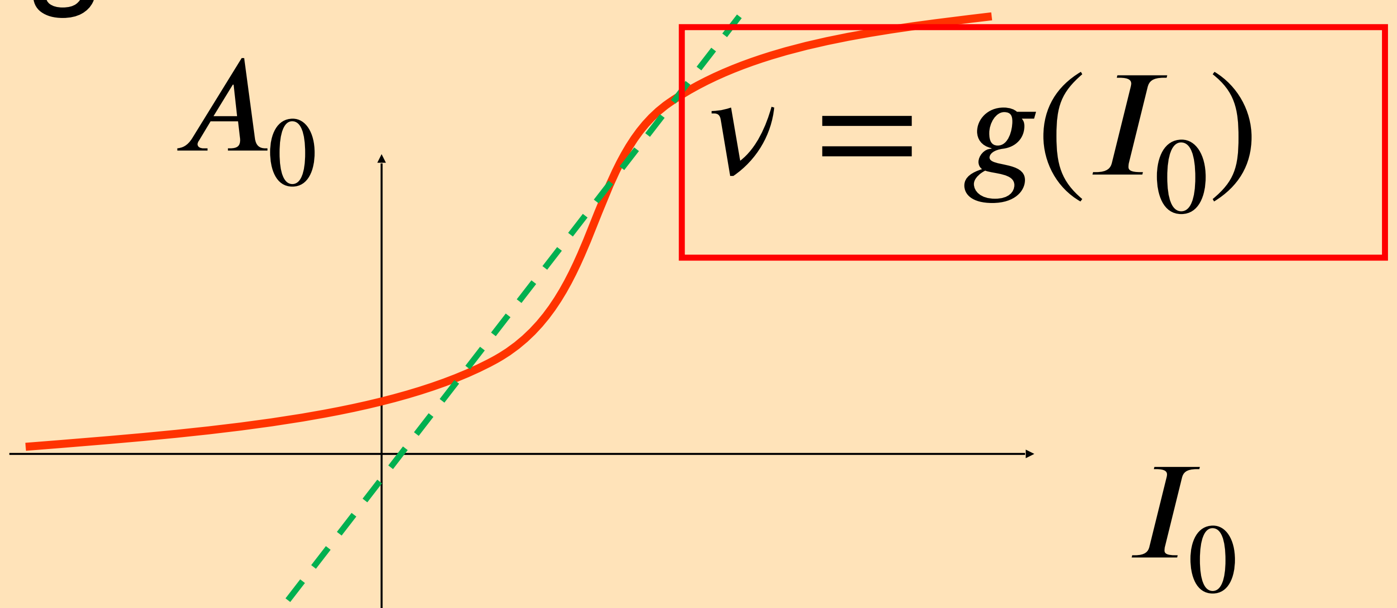
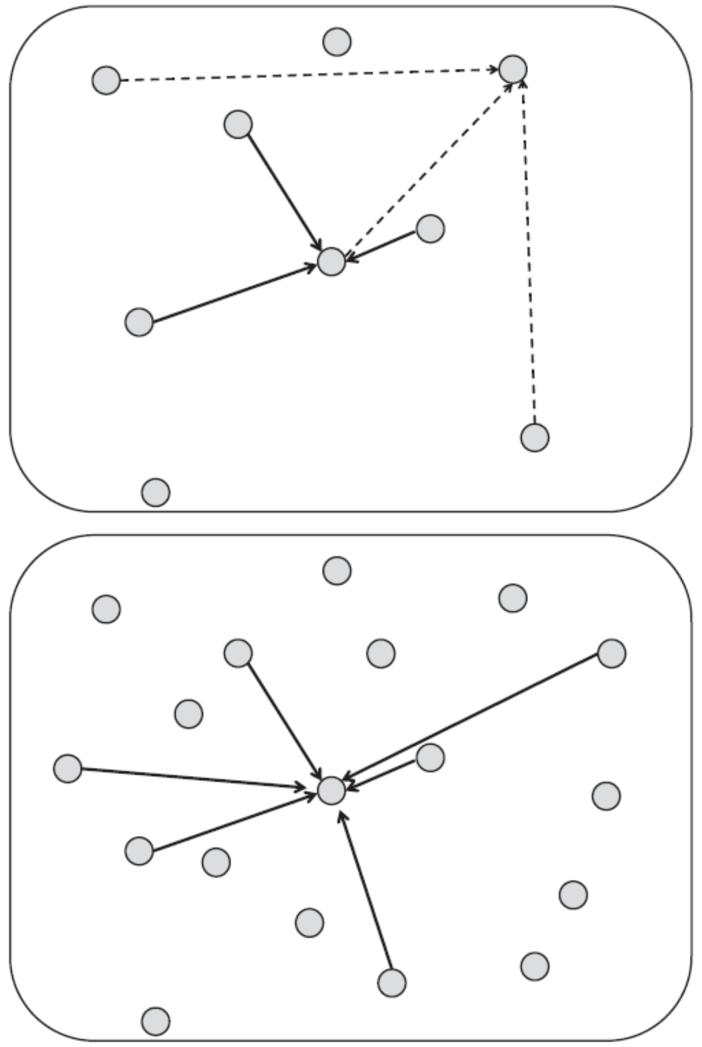


6. mean-field arguments (random connectivity)

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



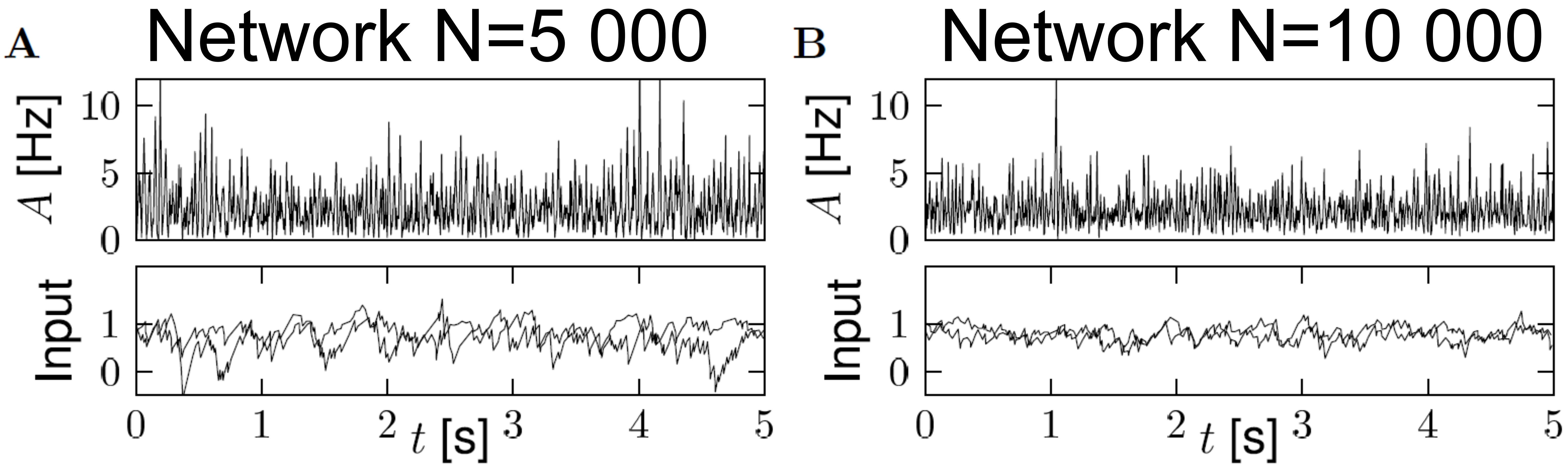


Fig. 12.7: Simulation of a model network with a fixed connection probability $p = 0.1$. **A.** Top: Population activity $A(t)$ averaged over all neurons in a network of 4 000 excitatory and 1 000 inhibitory neurons. Bottom: Total input current $I_i(t)$ into two randomly chosen

Image: Gerstner et al. Neuronal Dynamics (2014)

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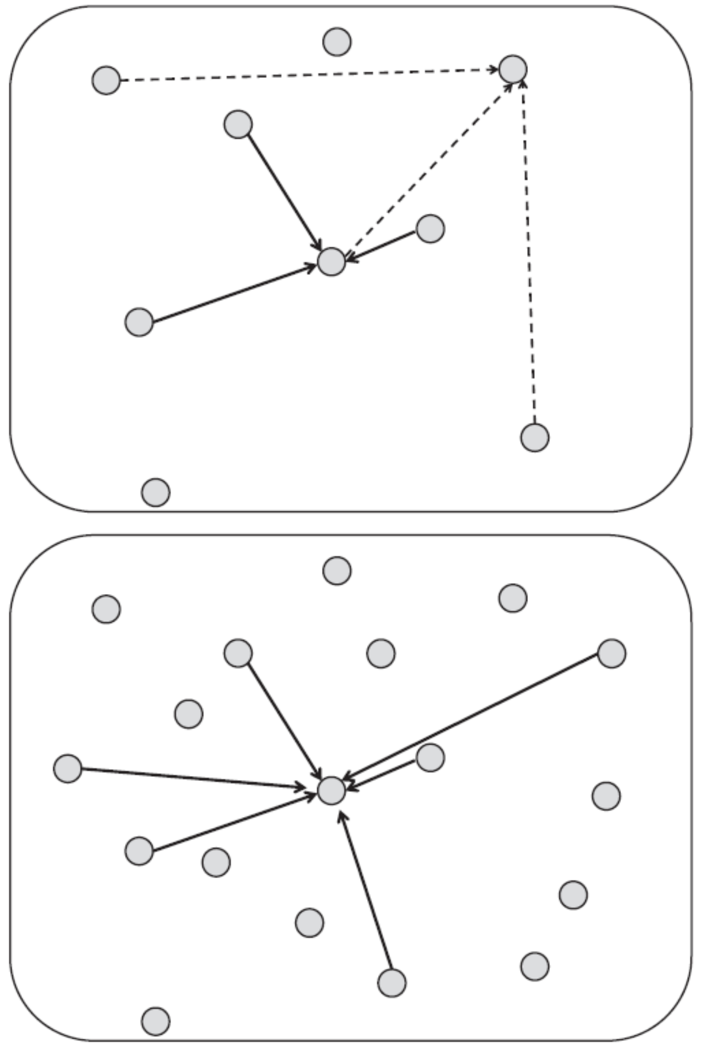

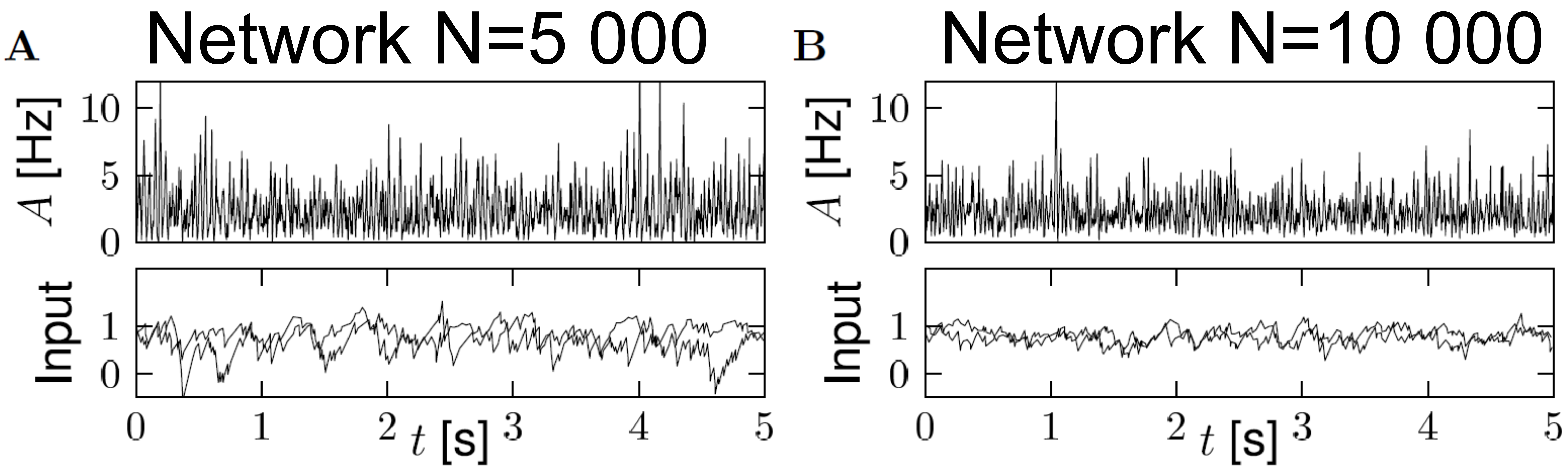

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fluctations of *A* decrease

→ 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 $w_{ij} = \frac{w_0}{K}$

Network N=5 000 | Network N=10 000

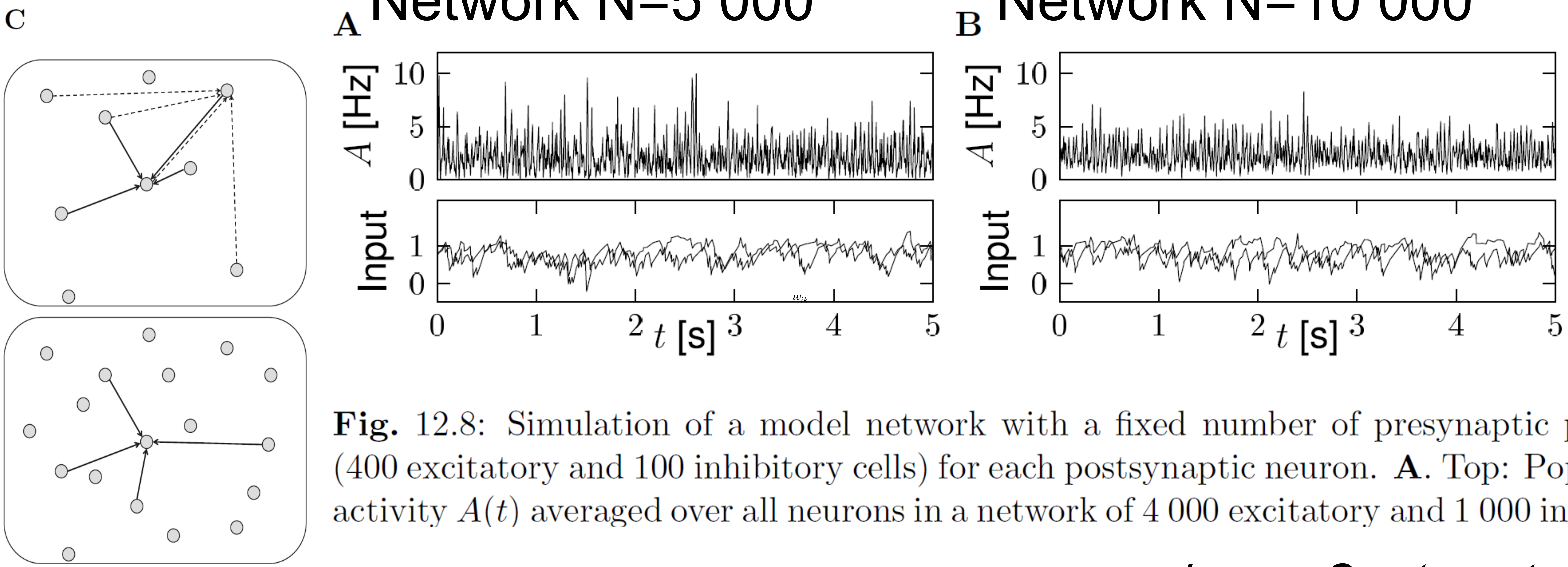

Fig. 12.8: Simulation of a model network with a fixed number of presynaptic partners (400 excitatory and 100 inhibitory cells) for each postsynaptic neuron. **A**. Top: Population activity $A(t)$ averaged over all neurons in a network of 4 000 excitatory and 1 000 inhibitory

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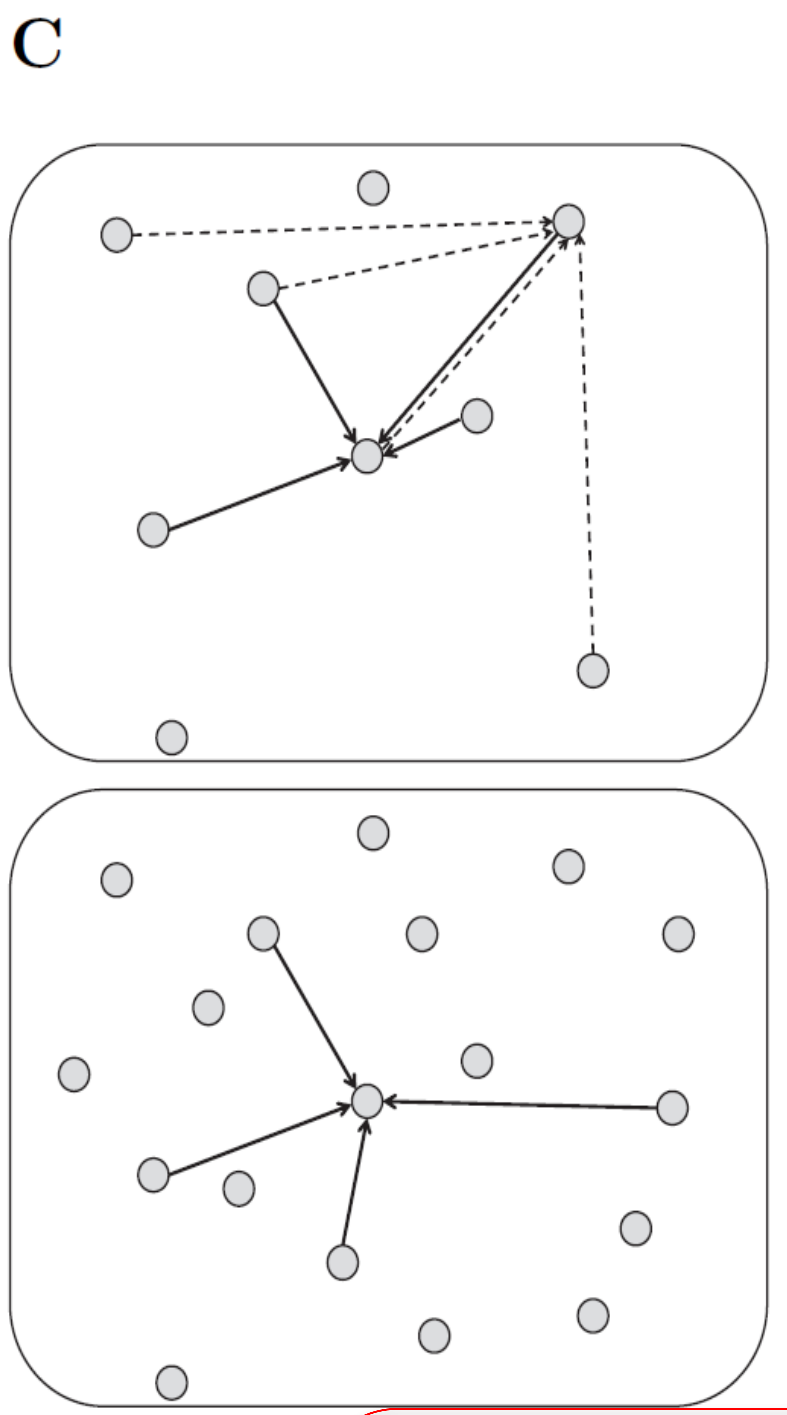

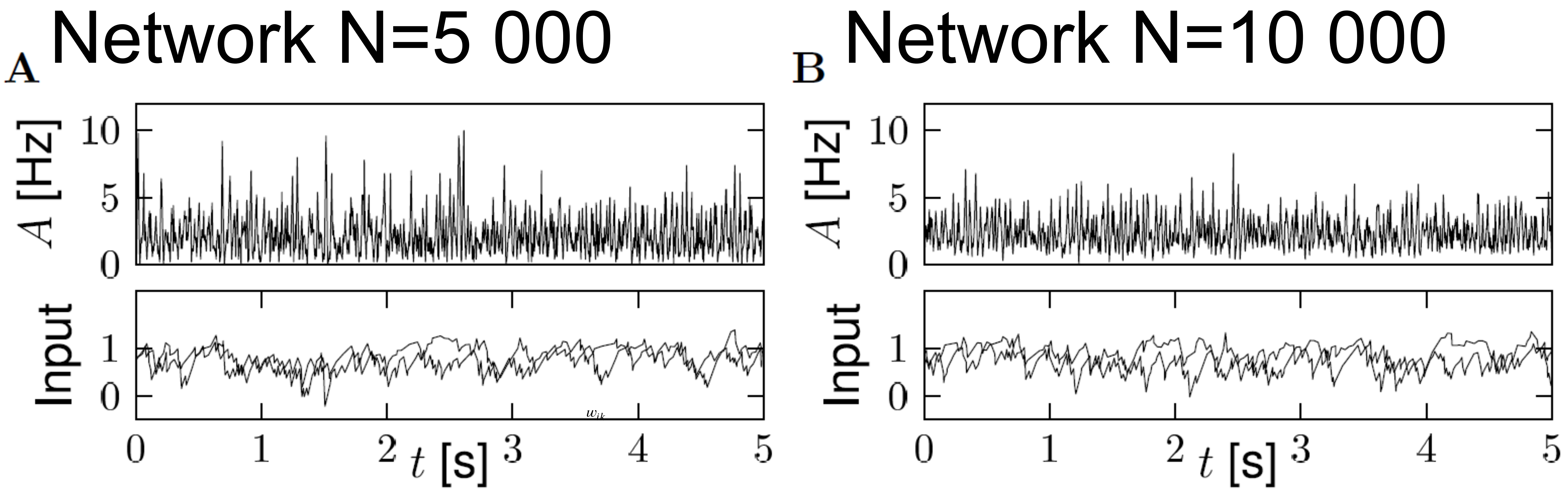

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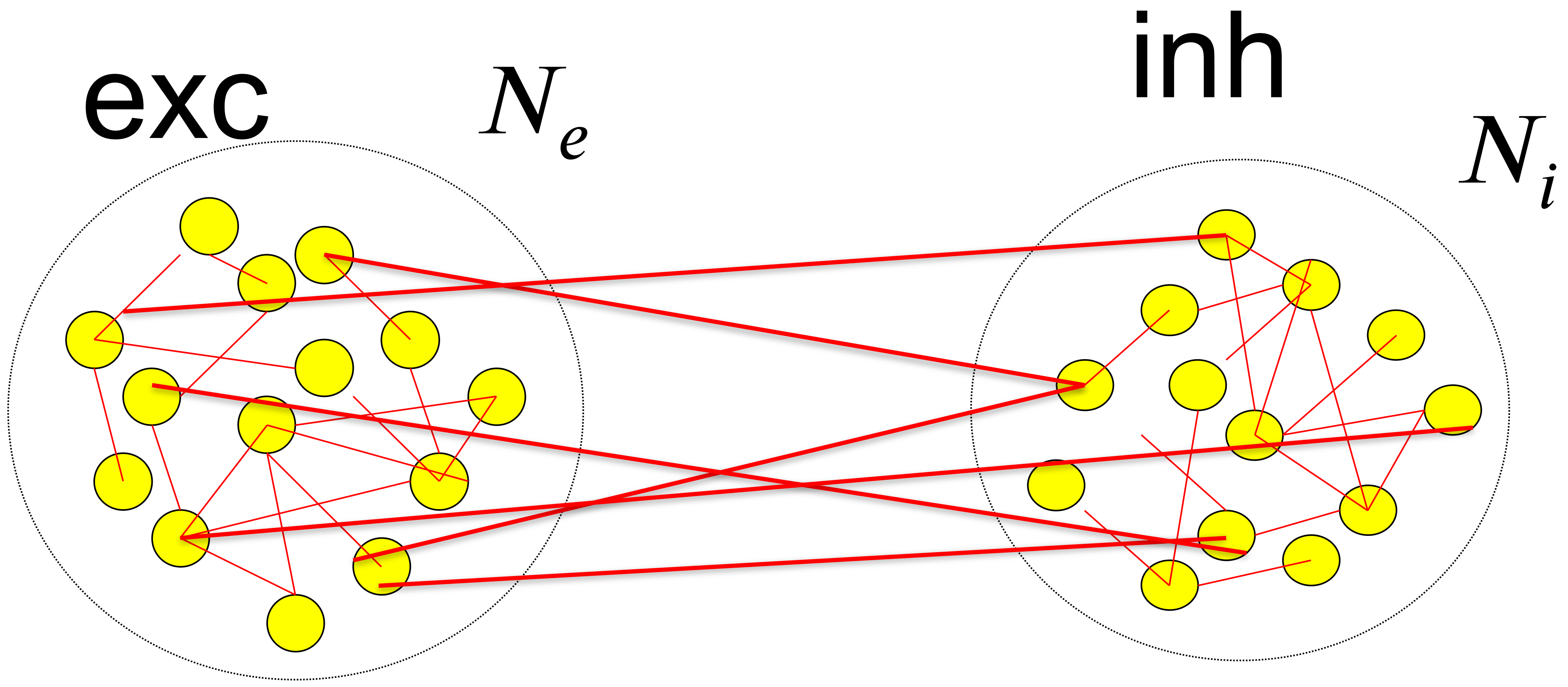
→ fluctations of *A* decrease
fluctations of *I* remain

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

$$pN_eJ_e = -pN_iJ_i$$

-keep variance of input

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

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

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

Quiz 5, now

In a **randomly** connected homogeneous network of 5000 neurons, we have several choices of connectivity.
We suppose that the network is in a state of asynchronous firing.

A Suppose that each neuron receives exactly 500 inputs. Then the total input into neuron i=10

[ ] is, after temporal averaging, the same as the input into neuron i=3564.
[ ] fluctuates nearly independently from fluctuations in neuron i=3564.
[ ] depends on the population activity of the network

B Suppose that connections are drawn randomly with prob 10 percent. Then the total input into neuron i=10

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Quiz 6, now

In a **randomly** connected homogeneous network of 5000 neurons, we have several choices of connectivity. We suppose that the network is in a state of asynchronous firing.

A Suppose that each neuron receives exactly 500 inputs and $w_{ij} = w_0/K$

[ ] Then the typical fluctuations of the input into neuron i=10 decrease when we double the network size.

[ ] Then the fluctuations of the input into neuron i=10 do not change when we double the network size.

B Suppose connections are drawn randomly with prob 10% and $w_{ij} = \frac{w_0}{pN}$

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Quiz 6B, now (continuation

C In a **randomly** connected homogeneous network of 8000 neurons, we have 10% connectivity across all neuron types (excitatory/inhibitory).
Excitatory neurons have weights $w_{ij} = \ w/\sqrt{pN}$
Inhibitory neurons have weights $w_{ij} = \ -w/\sqrt{pN}$
All neurons have the same parameters.
We suppose that the network is in a state of asynchronous firing.

[ ] Then the typical fluctuations of the input into neuron i=10 decrease when we double the network size.

[ ] Then the fluctuations of the input into neuron i=10 do not change when we double the network size.

[ ] The expected input to each neuron remains the same when we double the network size

[ ] The expected population activity has the same value when we double the network size

[ ] the fluctuations of the population activity decrease with network size

Quiz 6B, now (continuation

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

Image: Gerstner et al. Neuronal Dynamics (2014)

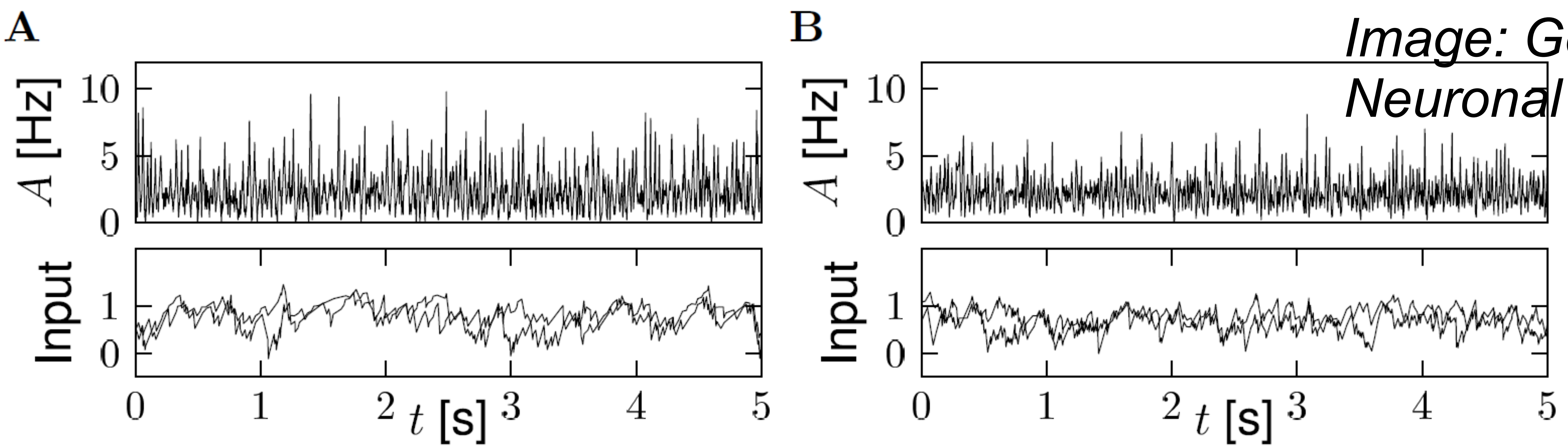

Fig. 12.9: Simulation of a model network with balanced excitation and inhibition and fixed connectivity $p = 0.1$ **A**. Top: Population activity $A(t)$ averaged over all neurons in a network of 4 000 excitatory and 1 000 inhibitory neurons. Bottom: Total input current $I_i(t)$ into two randomly chosen 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.

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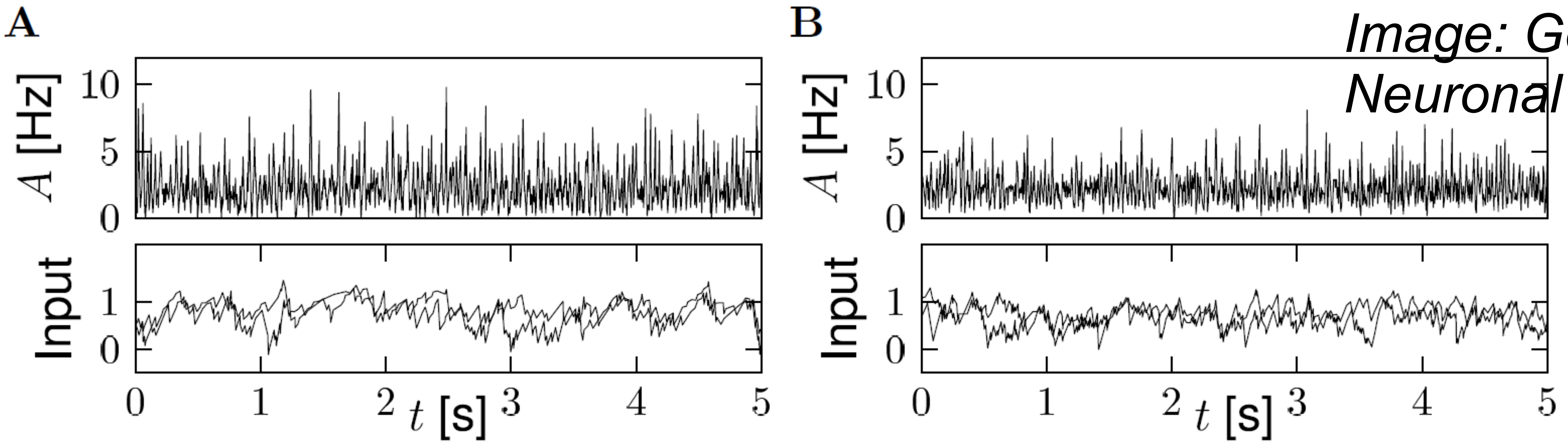

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→ fluctations of *A* decrease

fluctations of *I* become 'smoother'

Summary 7.4 and 7.5: Mean-field argument

Mean-field arguments enable us to calculate (or at least estimate) the input to a given neuron. The neuron receives the ‘mean activity/population activity’ as input.

If all neurons in a population are ‘the same’ then the input calculated with mean-field theory is the same for all neurons.

Furthermore, if the input is constant, we can predict the output firing rate, and hence the population activity in the stationary state.

Applications of this idea to cognition/brain processes will come in the next few lectures.

Summary 7.1-7.6: Connectivity schemes and Mean-field theory

Mean-field arguments enable us to calculate (or at least estimate) the input to a given neuron – and this is possible for different random connectivity schemes.

In mean-field theory, a useful question to ask is whether the mean and the standard deviation of the input change, if we assume that the number of neurons increases from N to 5 N or even to infinity.

To achieve convergence of the mean input in the N-to-infinity limit, we need some assumption about how synaptic weights in the model should be rescaled with N.

However, we should always keep in mind that the brain is finite and that each neuron in the brain only receives a FINITE number of connections (in the range of a few thousand). Hence, scaling is first-of-all of interest for understanding the theory. But, it is also of interest if one wonders during a simulation whether the model gives the same result when I simulate 5000 neurons instead of 10000.

Mean-field arguments are the basis of many ‘rate models’ of the brain (also called neural mass models). We will see some of these in the next weeks.