Week 10 – part 1 : Neuronal Populations

ÉCOLE POLYTECHNIQUE
FÉDÉRALE DE LAUSANNE

Biological Modeling of Neural Networks:

Week 10 – Neuronal Populations

Wulfram Gerstner

EPFL, Lausanne, Switzerland

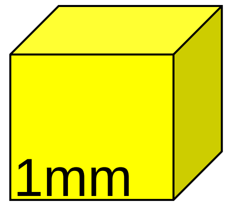
10.1 Cortical Populations
- columns and receptive fields

10.2 Connectivity
- cortical connectivity
- model connectivity schemes

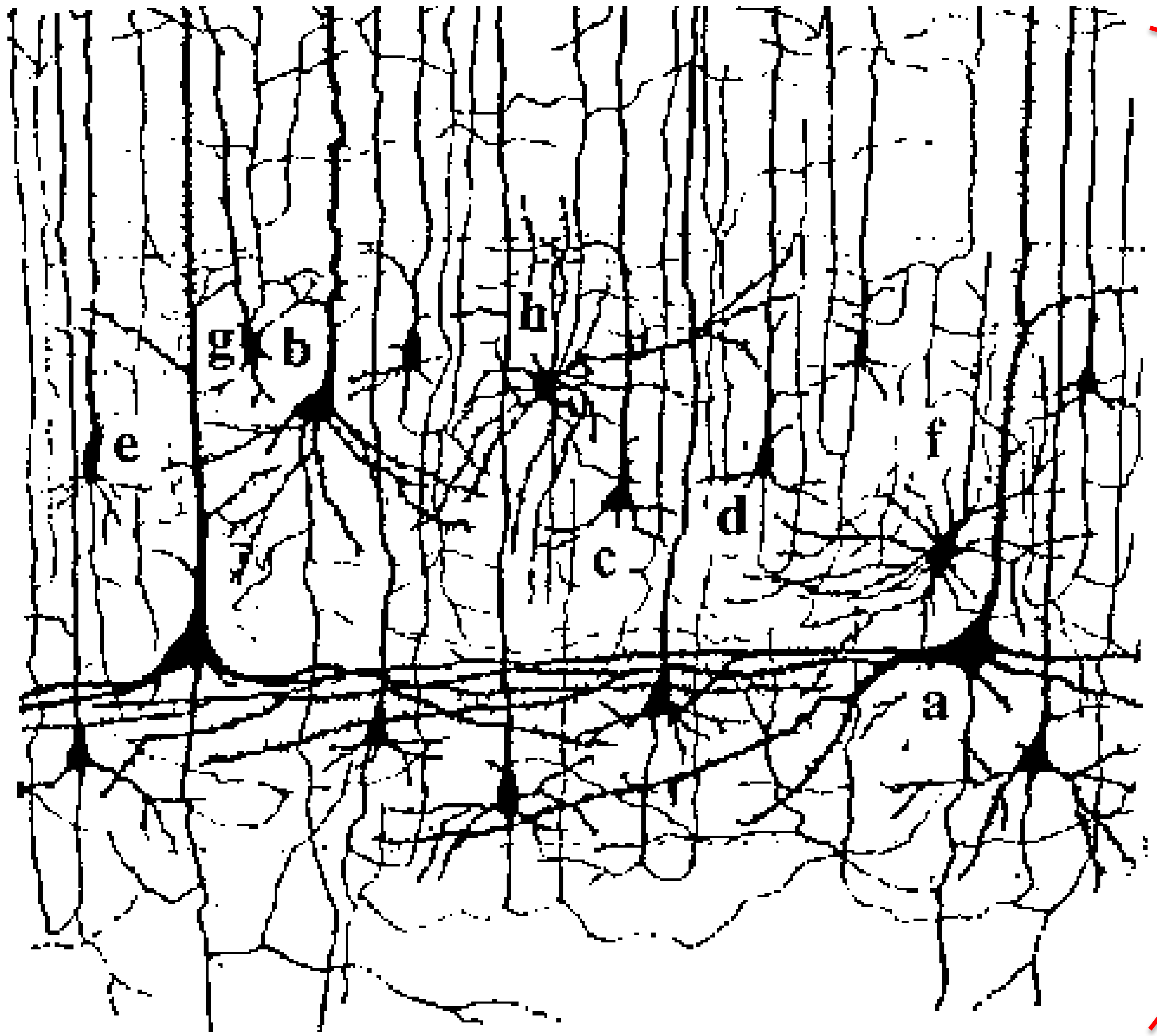
10.3 Mean-field argument
- asynchronous state

10.4 Random Networks
- Balanced state

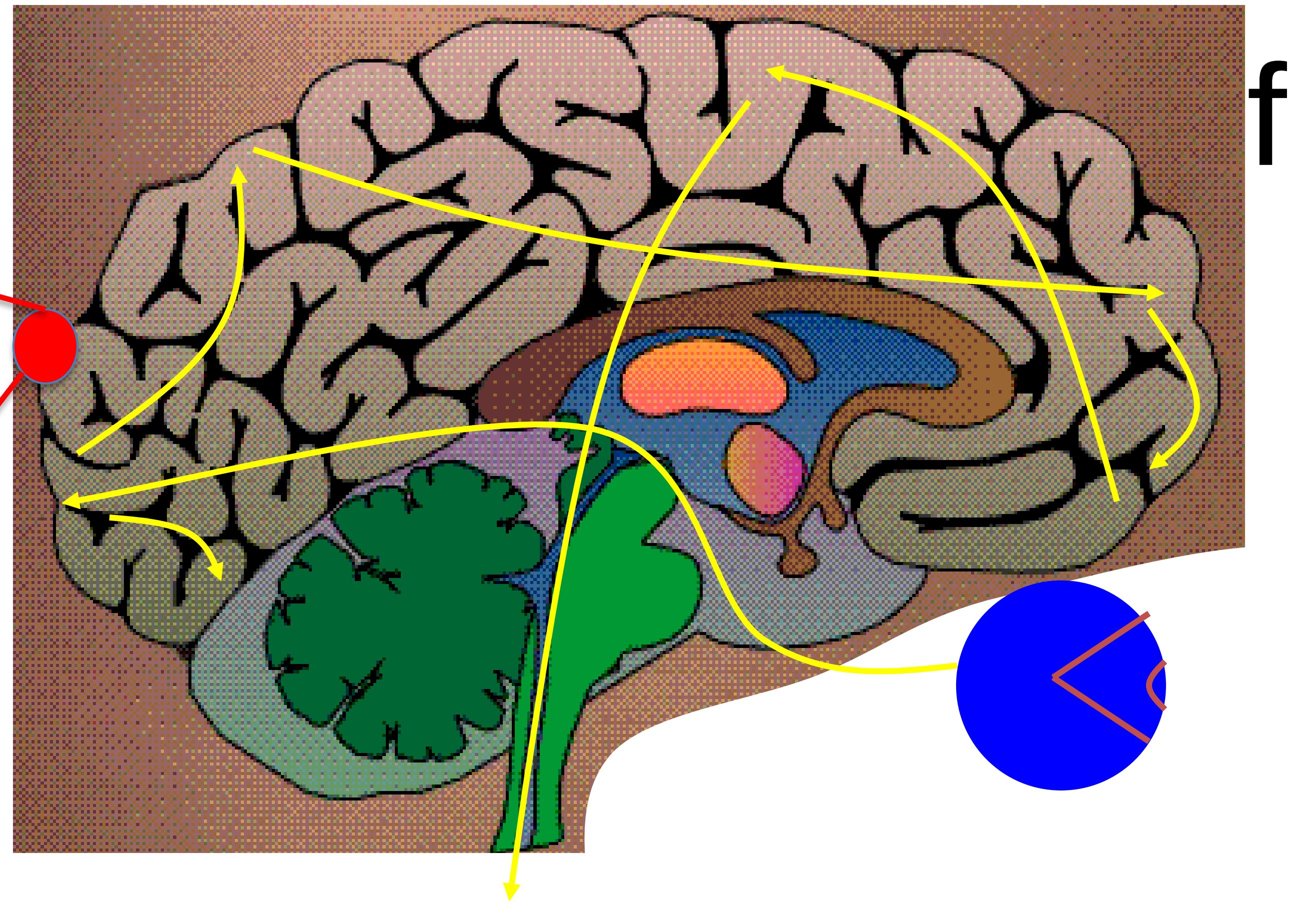
Biological Modeling of Neural Networks – Review from week 1



10 000 neurons
3 km wire



motor cortex

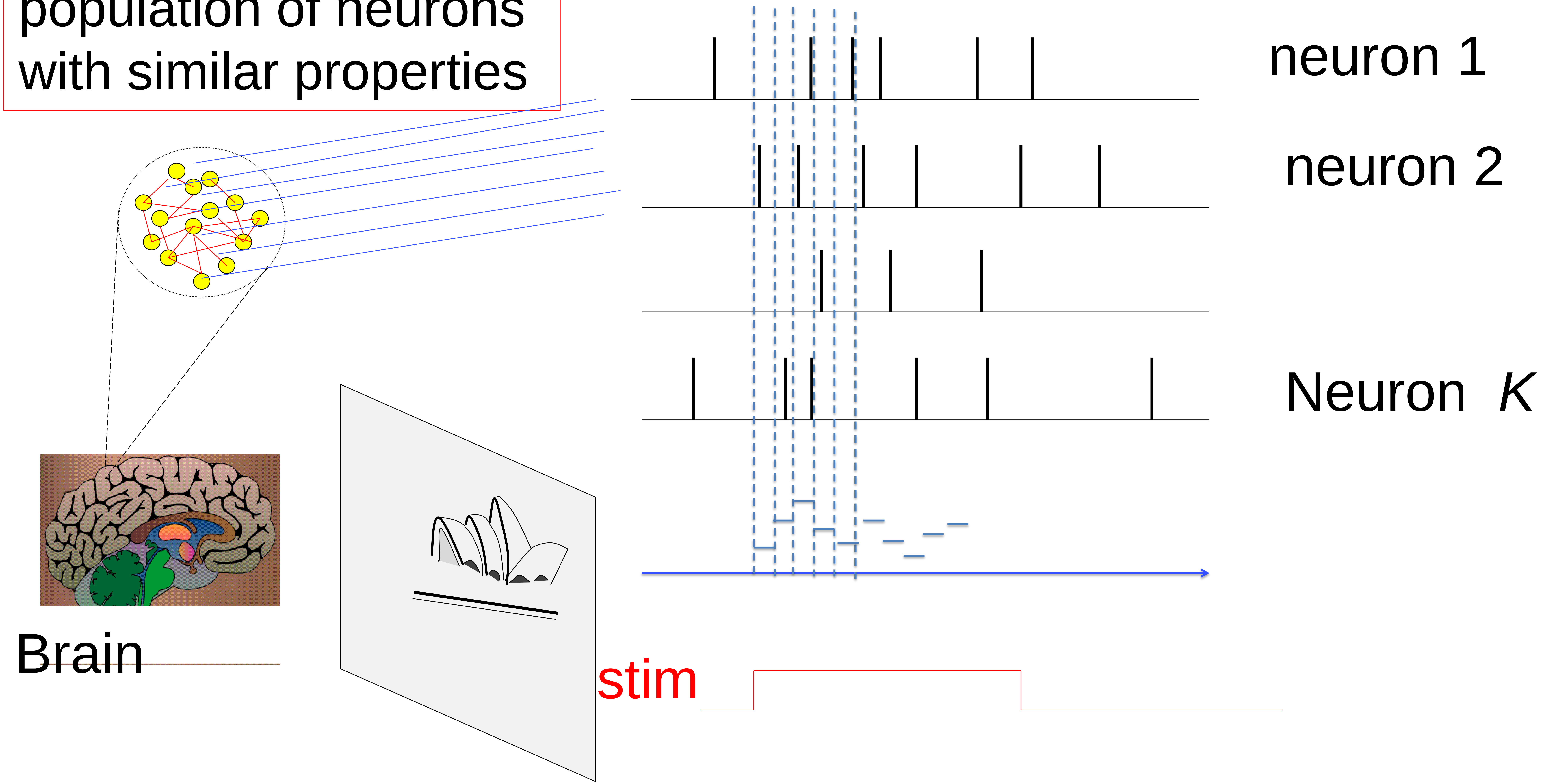


frontal cortex

to motor output

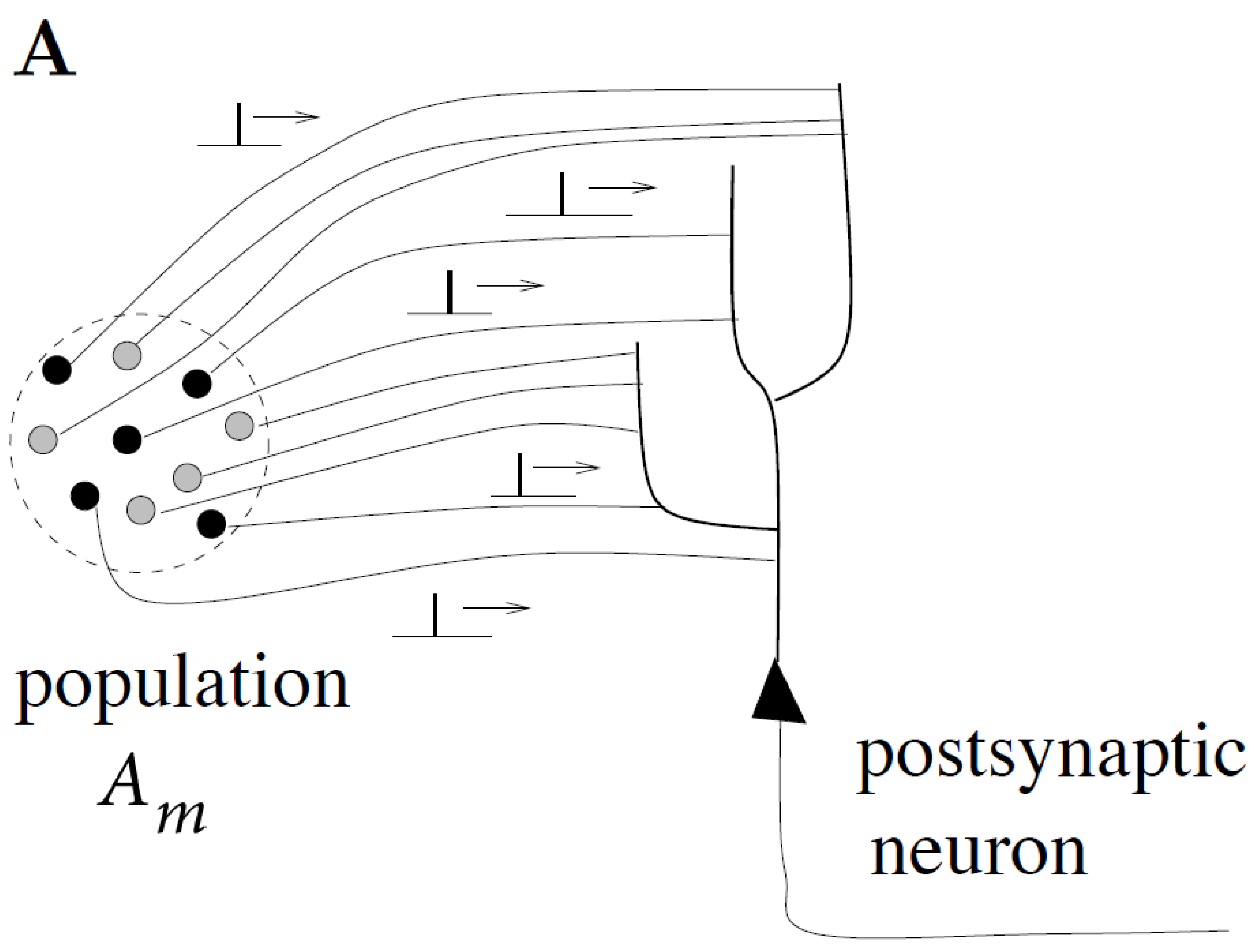
Biological Modeling of Neural Networks – Review from week 7

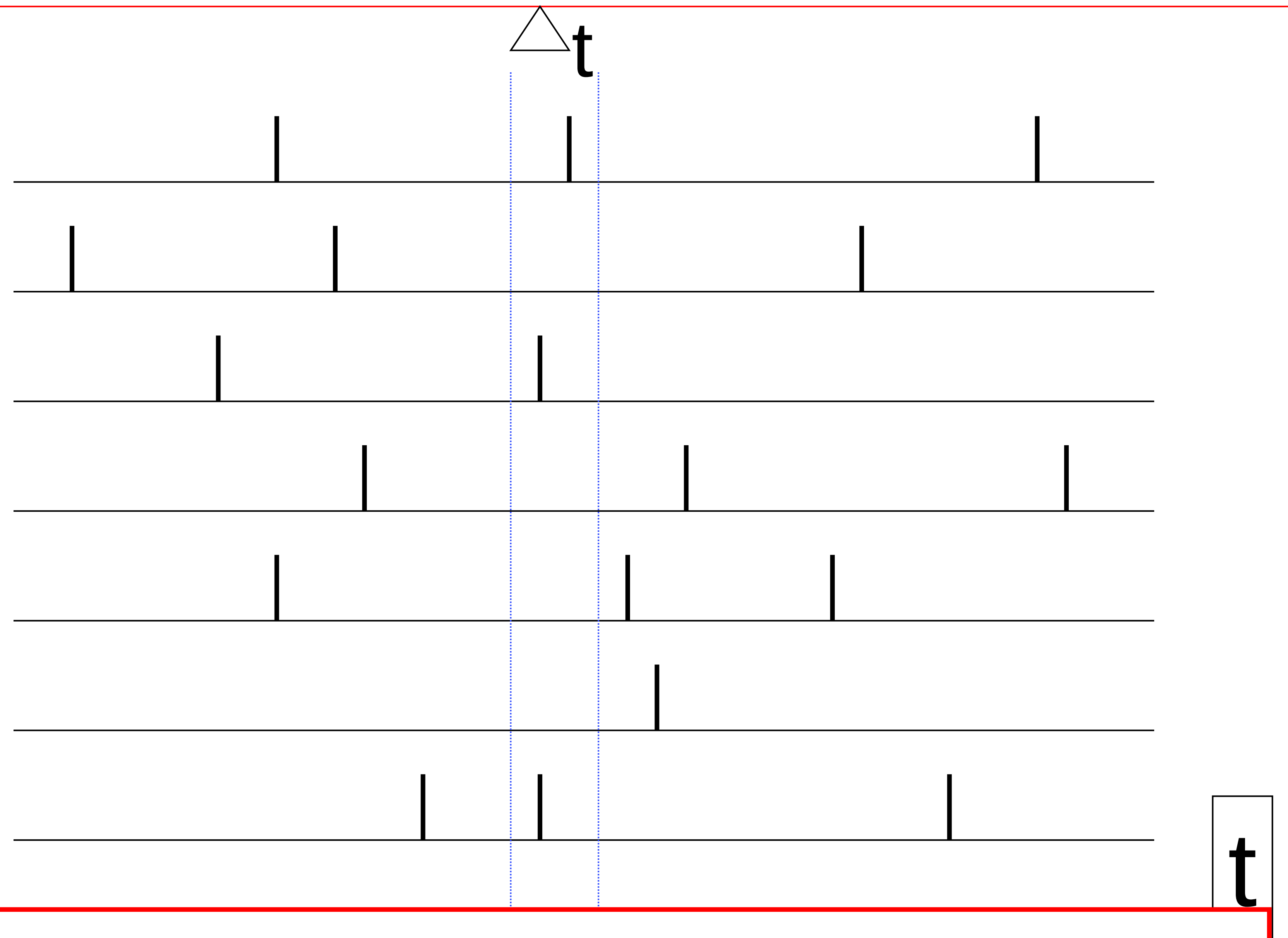
population of neurons
with similar properties



Biological Modeling of Neural Networks – Review from week 7

population activity - rate defined by population average





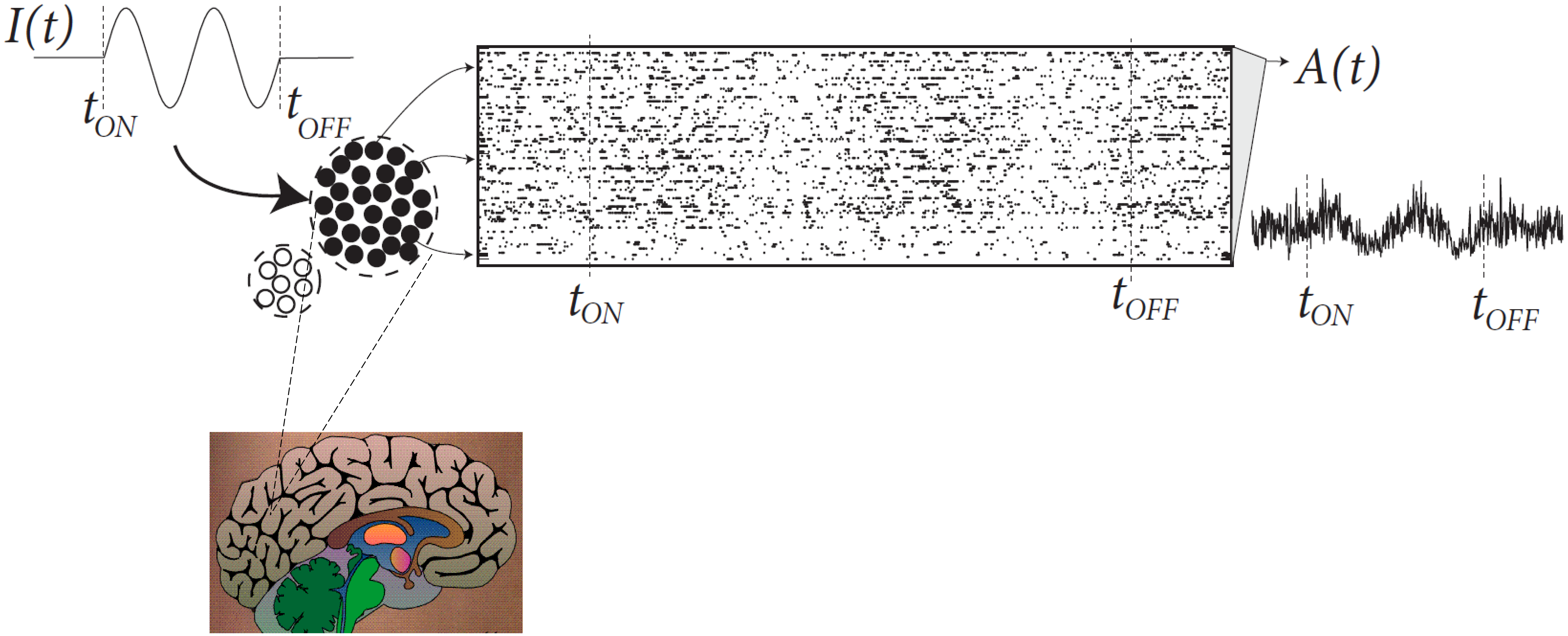
‘natural readout’

population activity

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

Week 10-part 1: Population activity

population of neurons
with similar properties

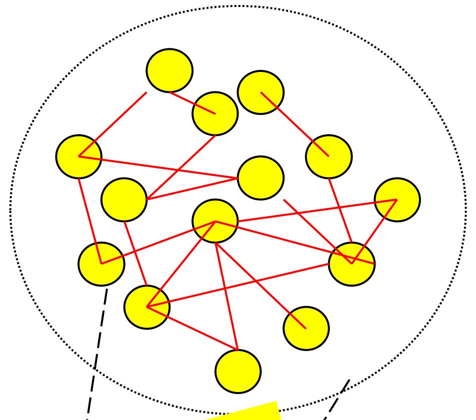


Brain

Week 10-part 1: Population activity

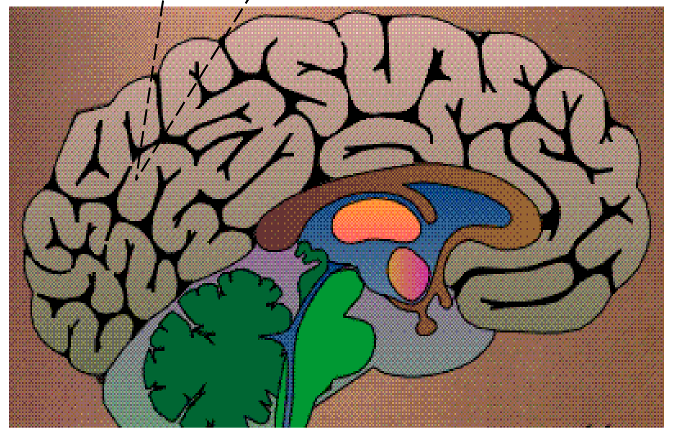
population of neurons
with similar properties

population activity



A(t)

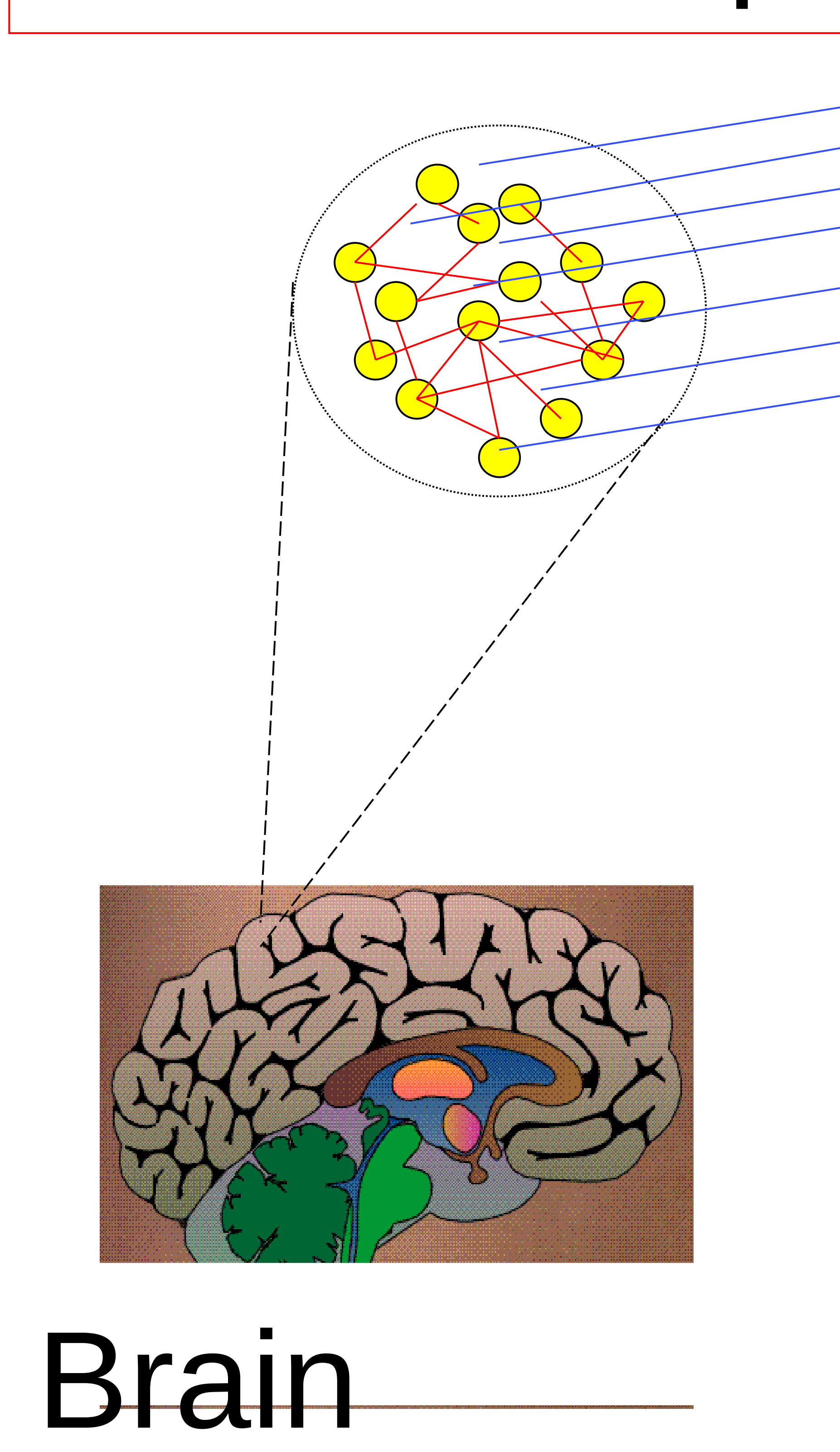
Are there such populations?

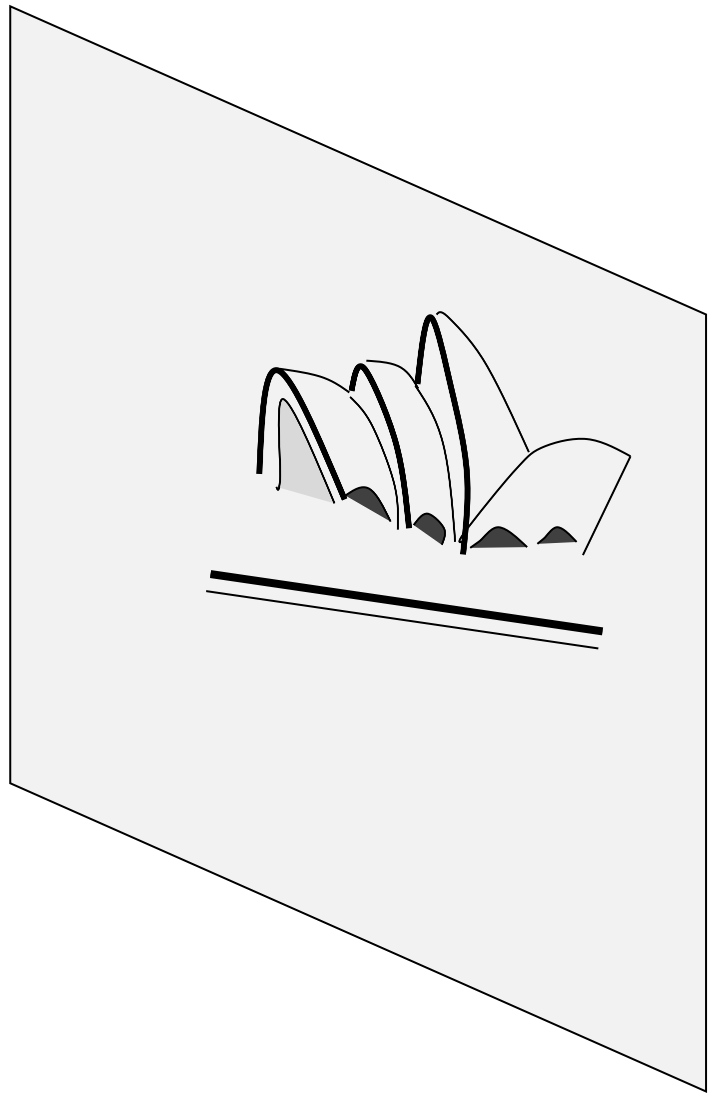


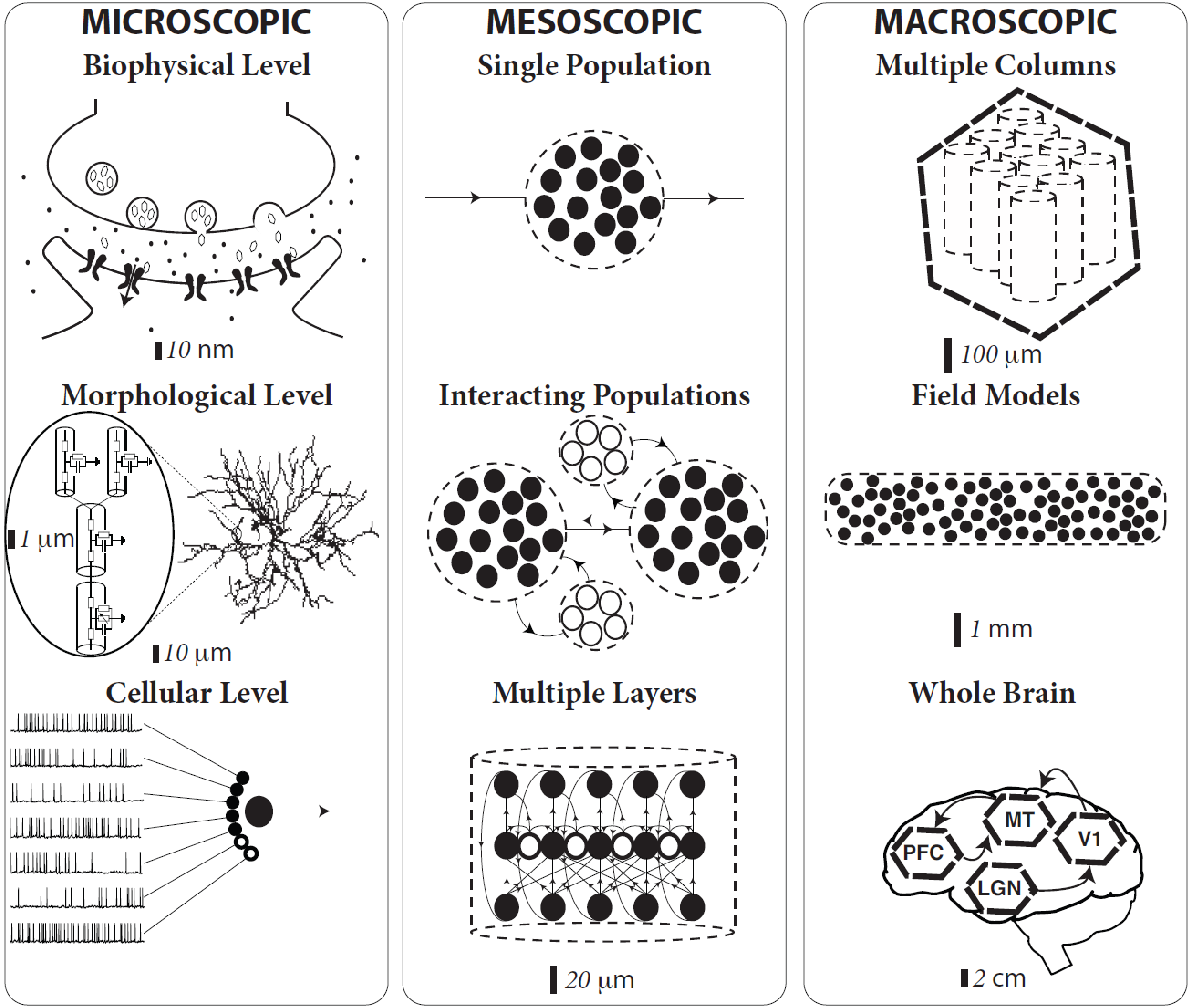
Brain

Week 10-part 1: Scales of neuronal processes

population of neurons
with similar properties







Week 10 – part 1b :Cortical Populations – columns and receptive fields

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Week 10 – Neuronal Populations

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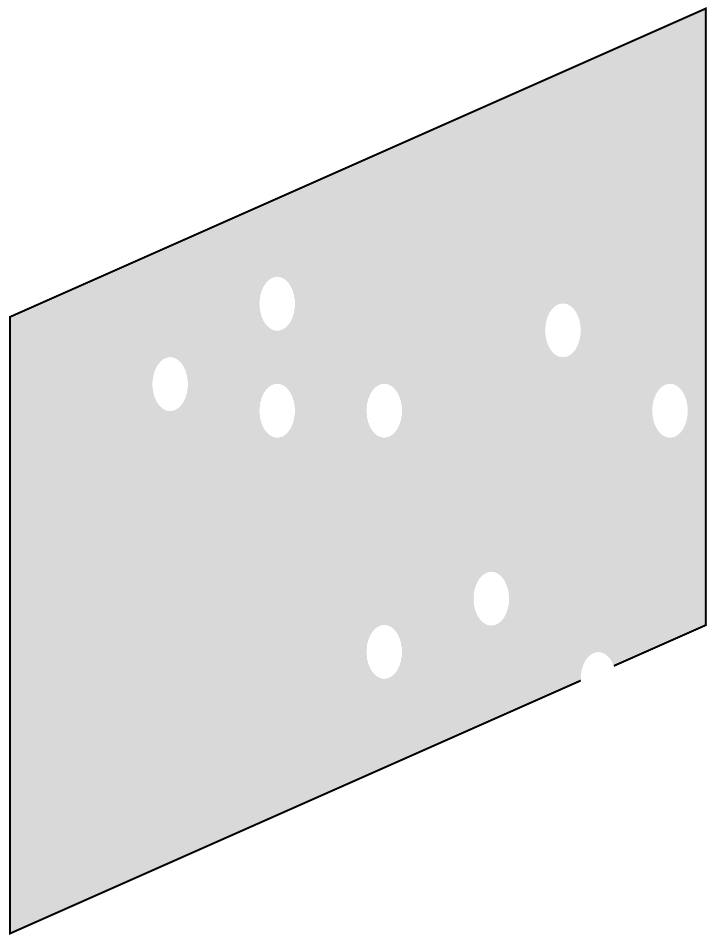
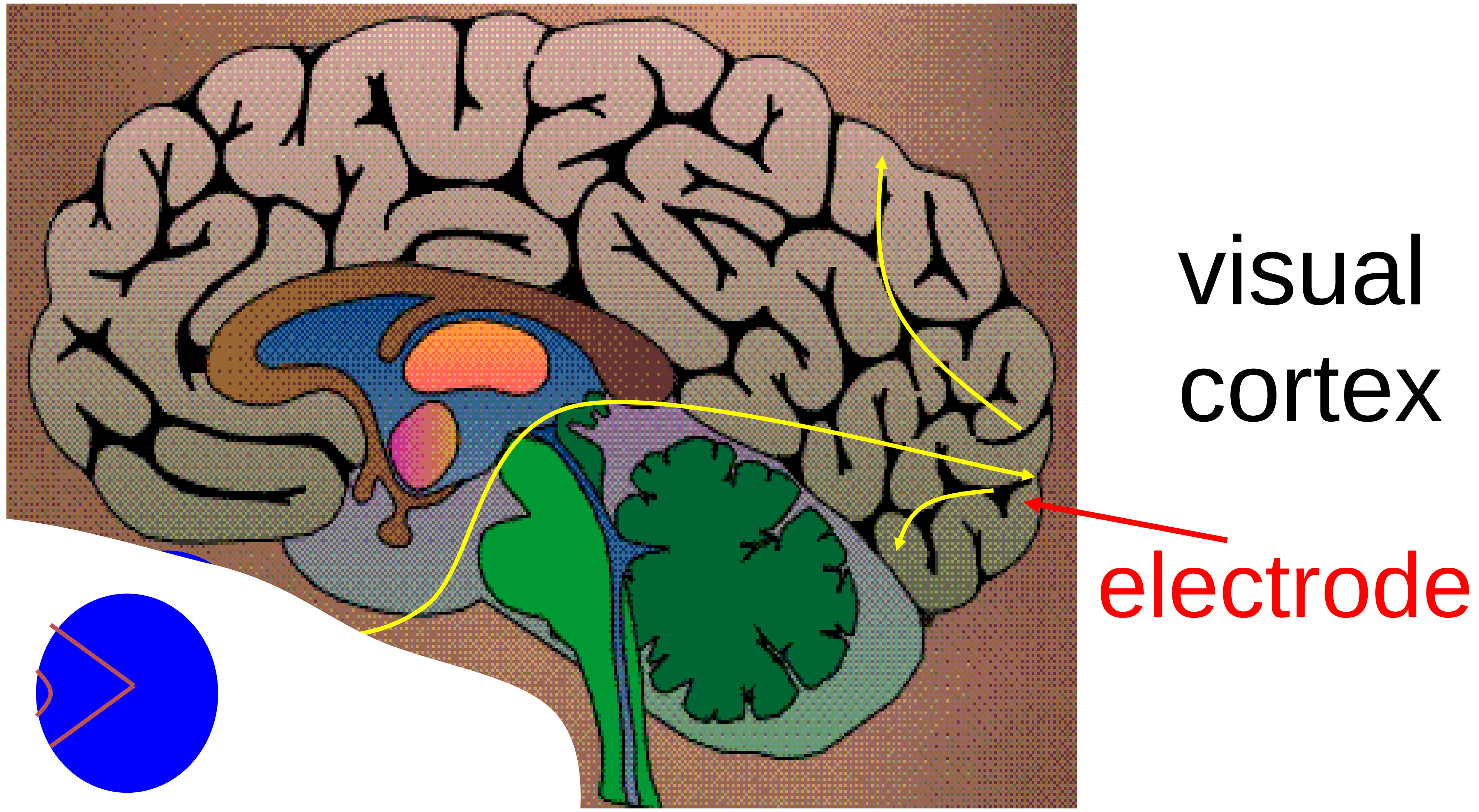
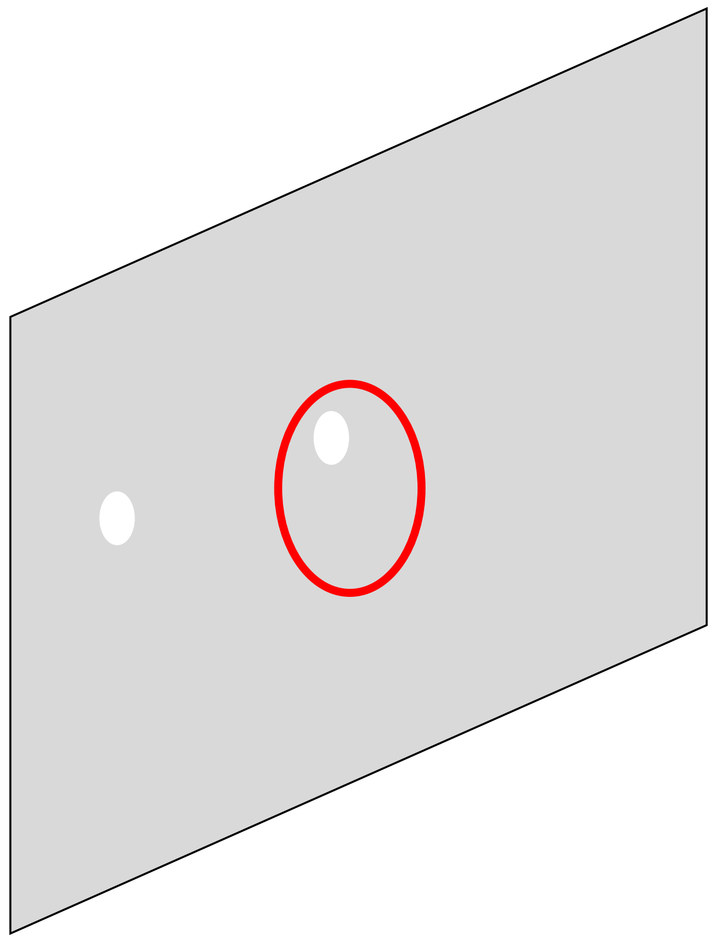
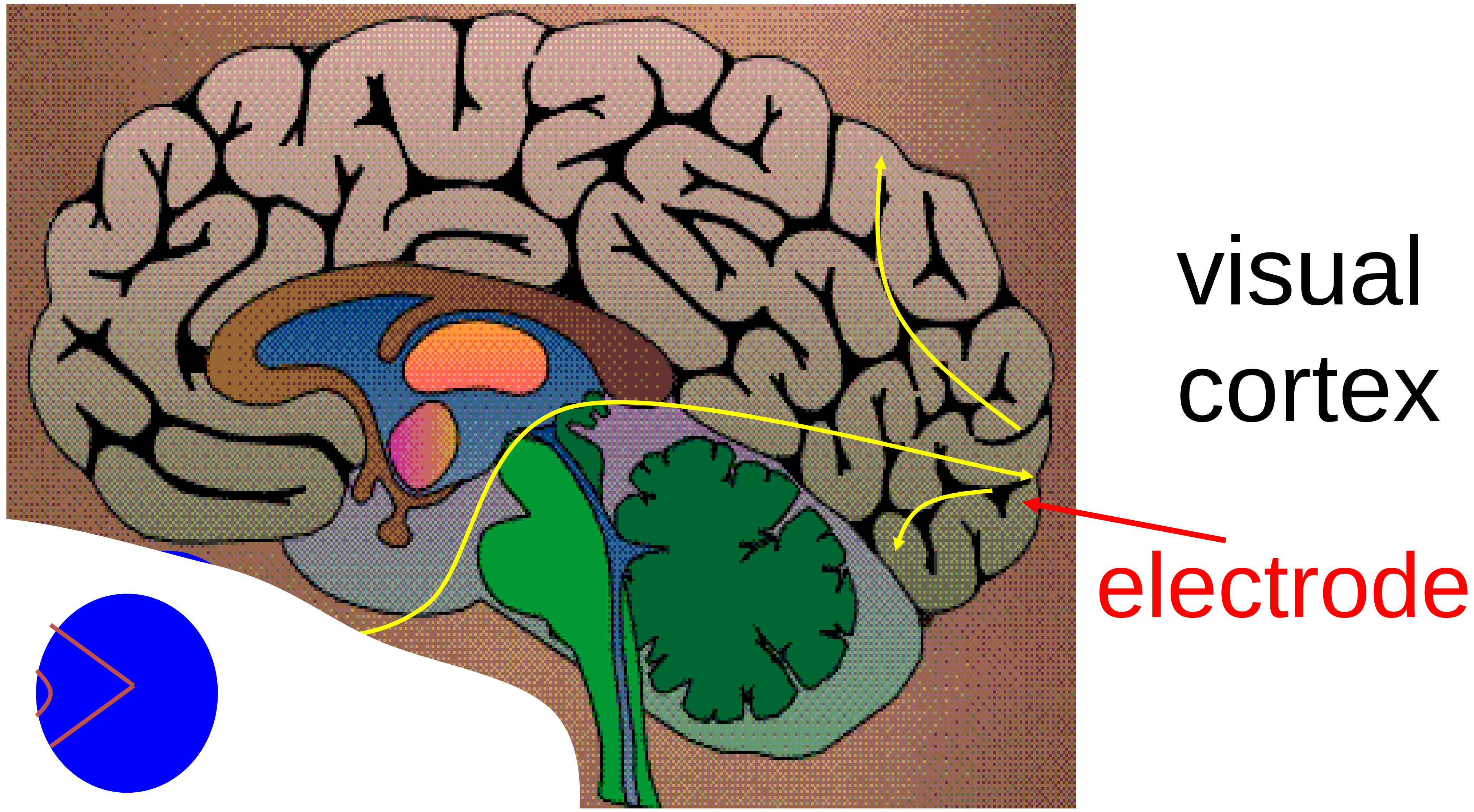
Week 10-part 1b: Receptive fields



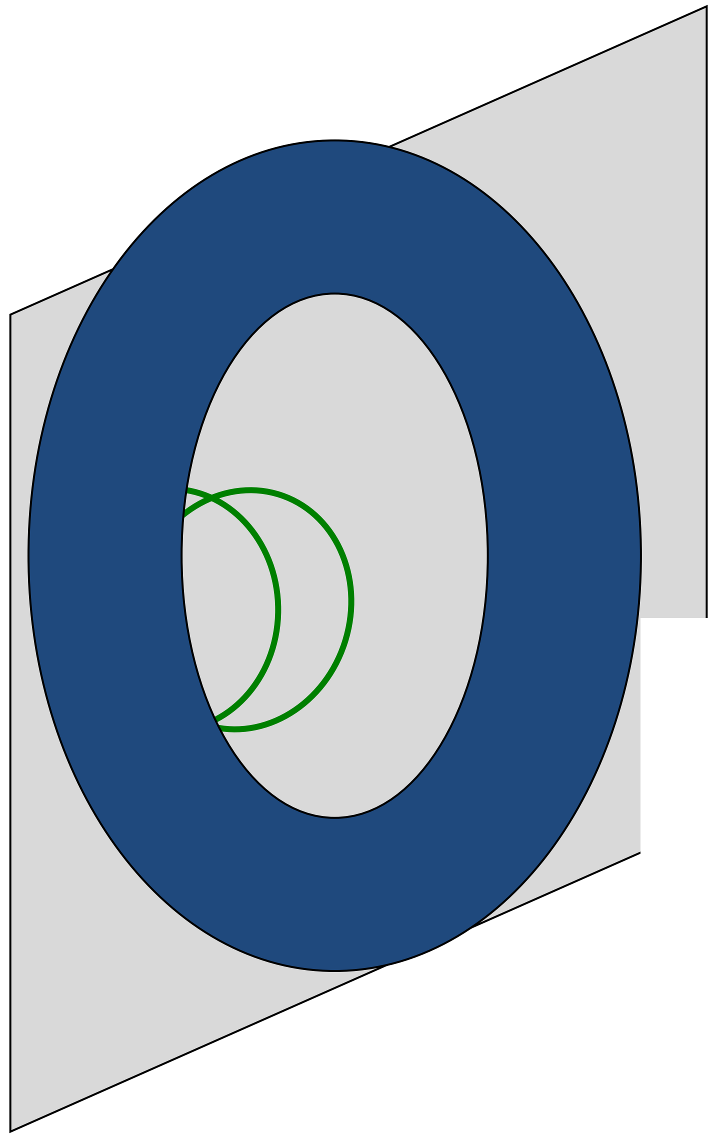


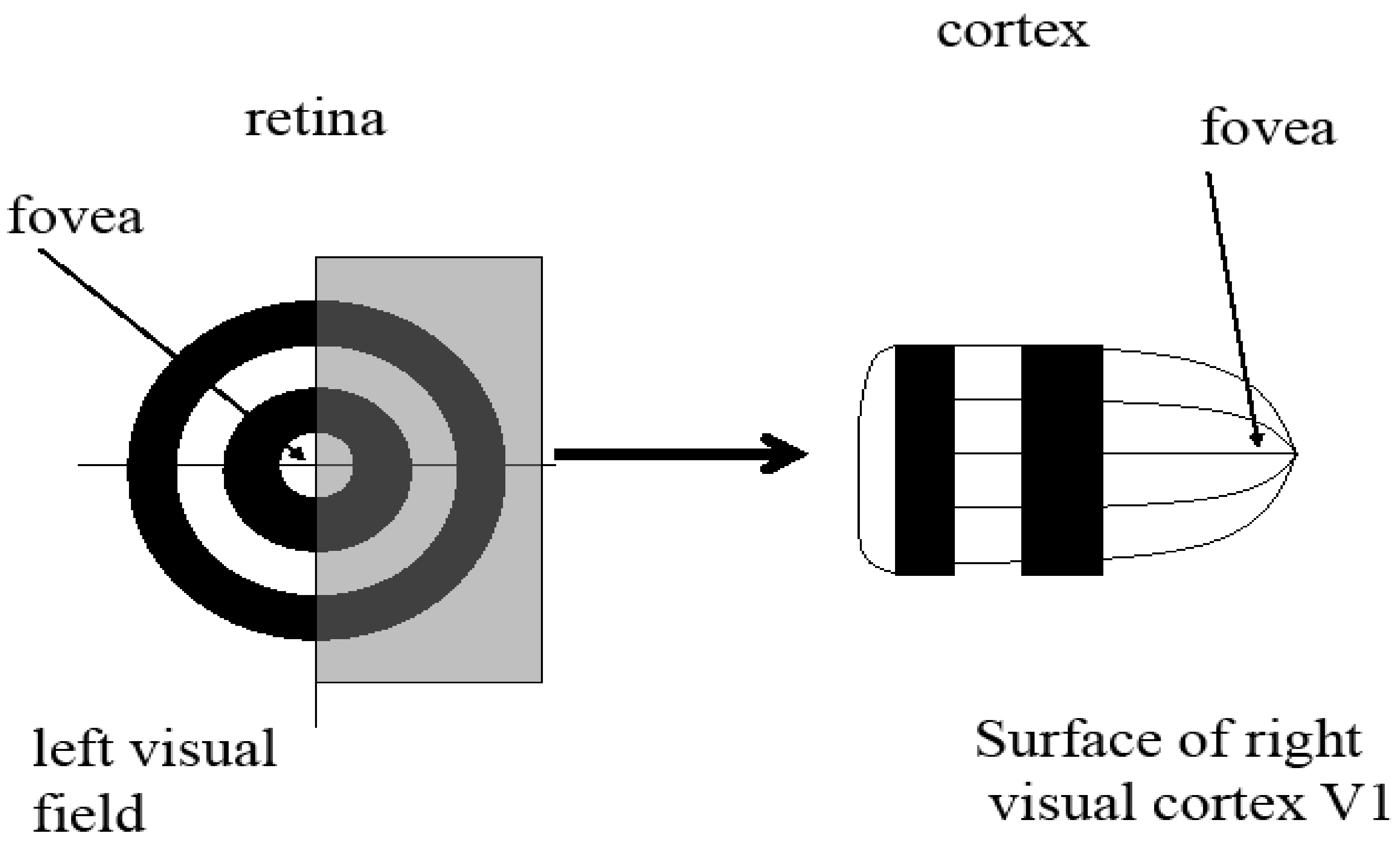
Week 10-part 1b: Receptive fields

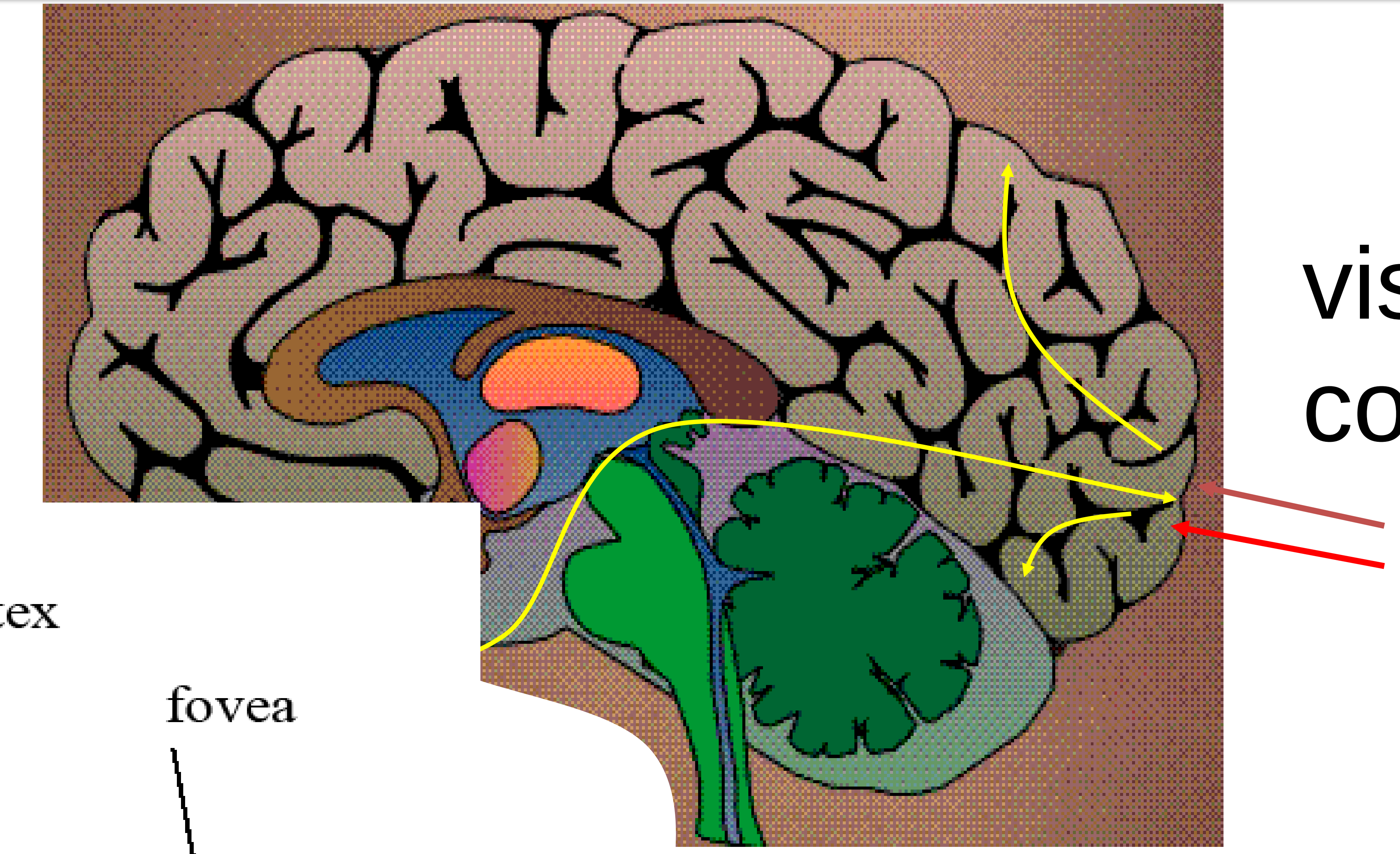




Week 10-part 1b: Receptive fields and retinotopic map





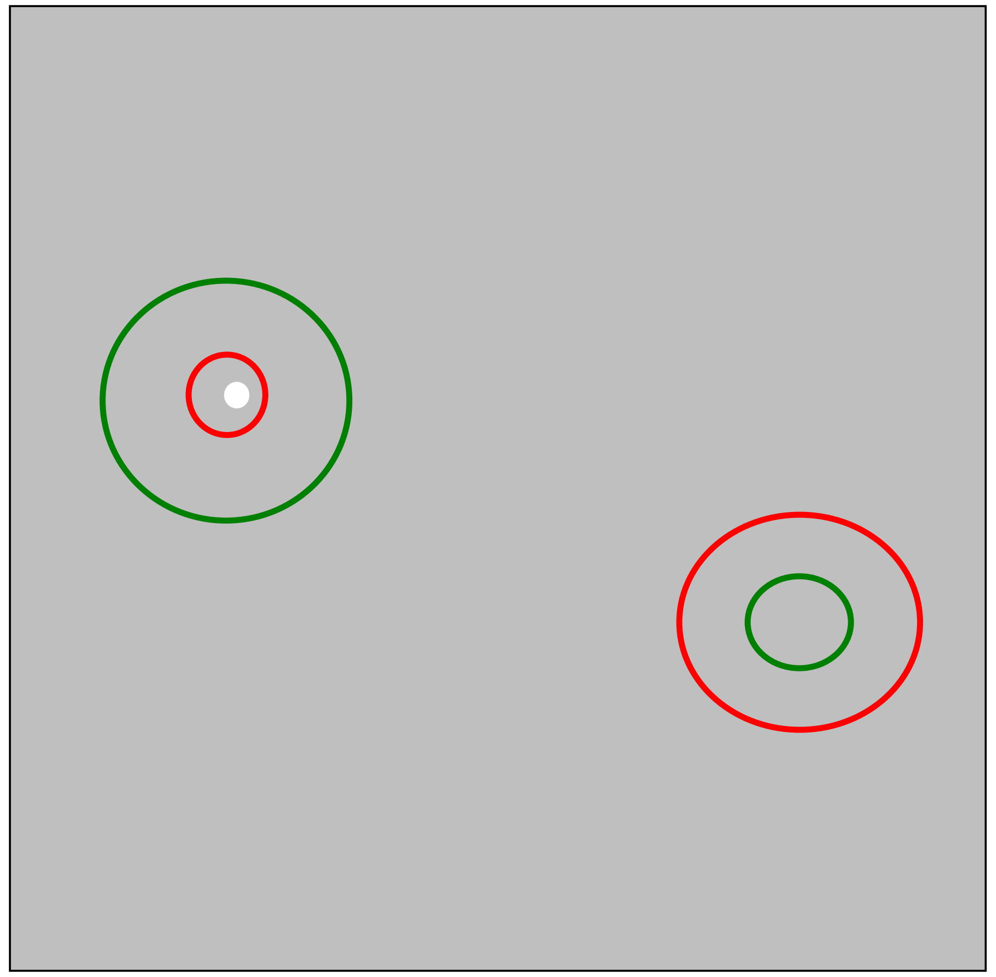


visual cortex

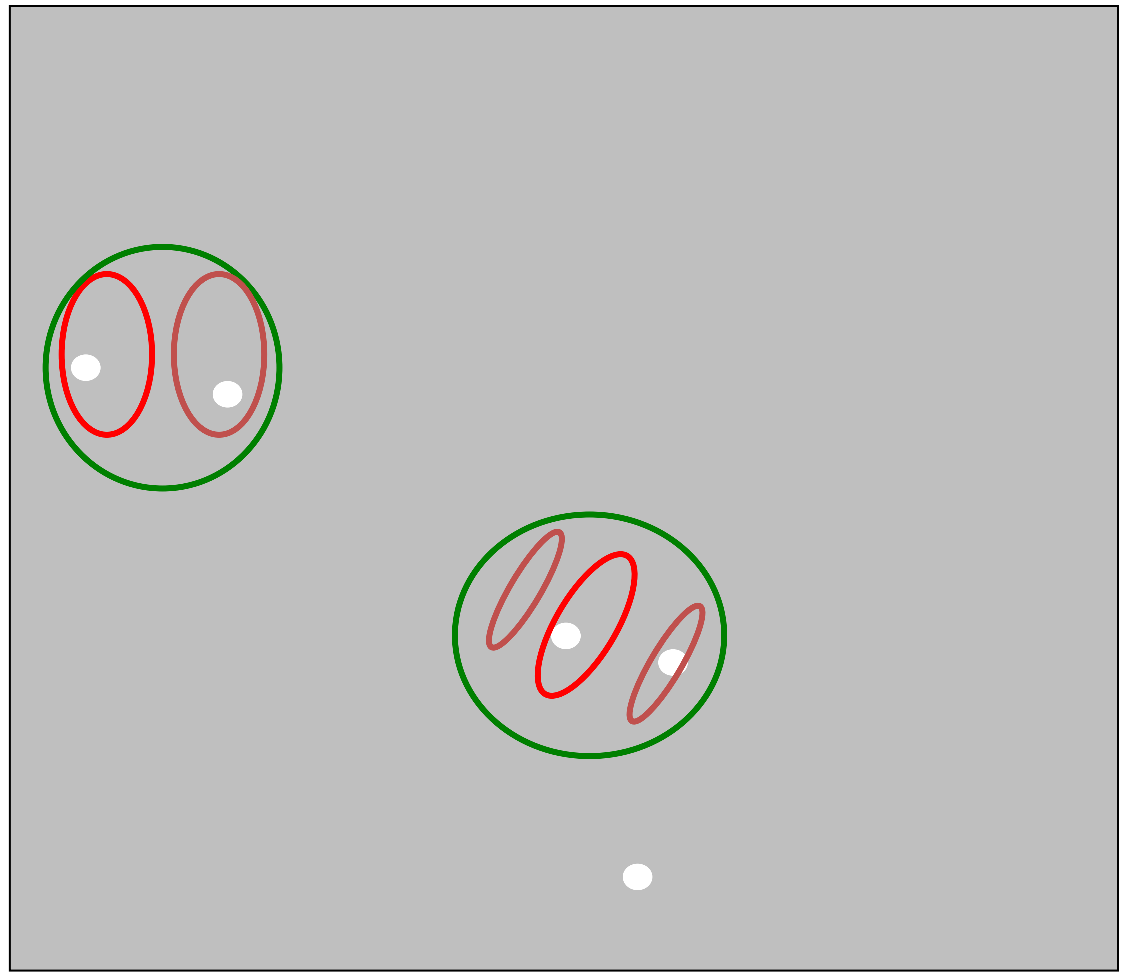
Neighboring cells
in visual cortex
have similar preferred
center of receptive field

Week 10-part 1b: Orientation tuning of receptive fields

Receptive fields:
Retina, LGN



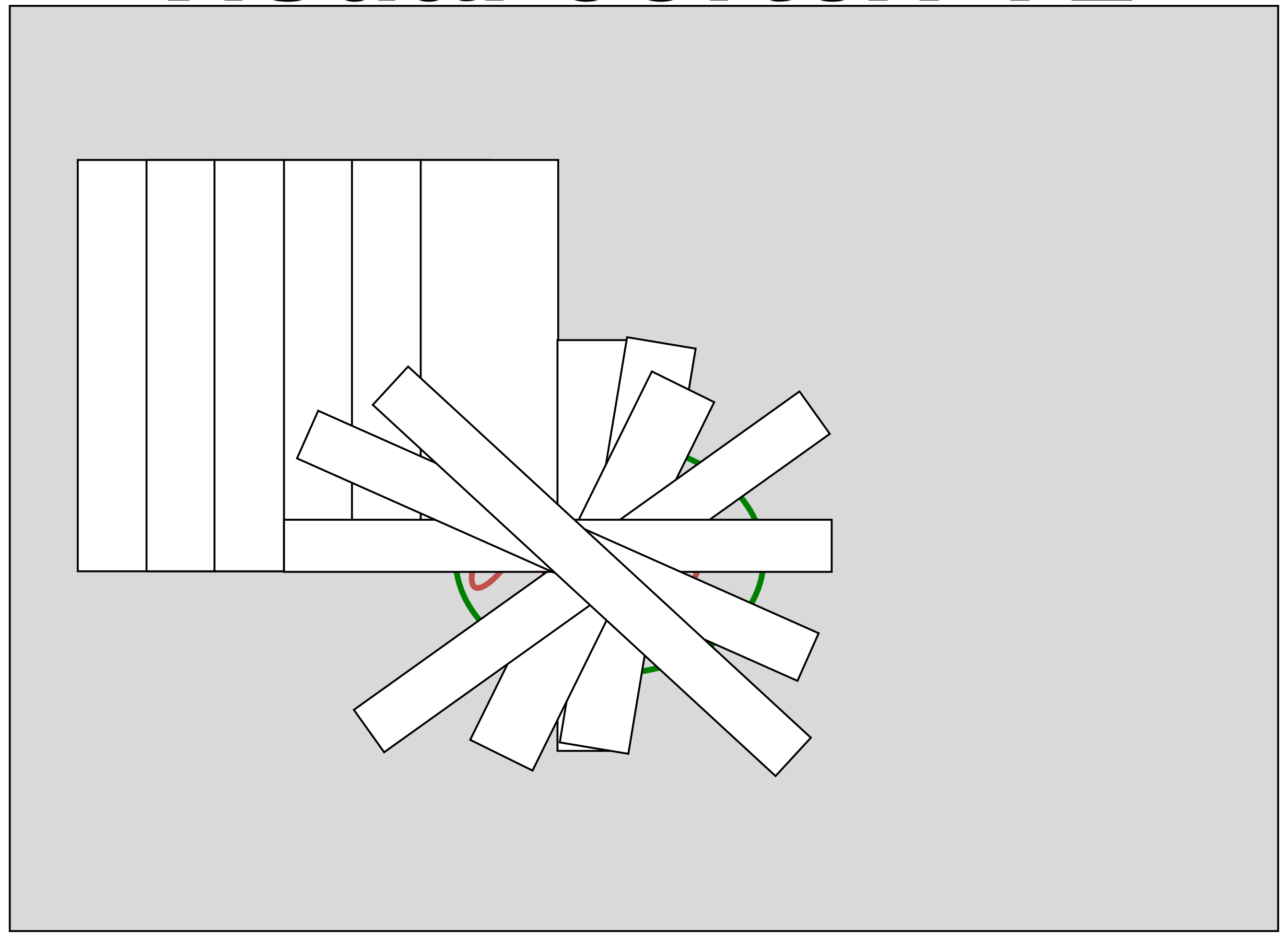
Receptive fields:
visual cortex V1



Orientation
selective

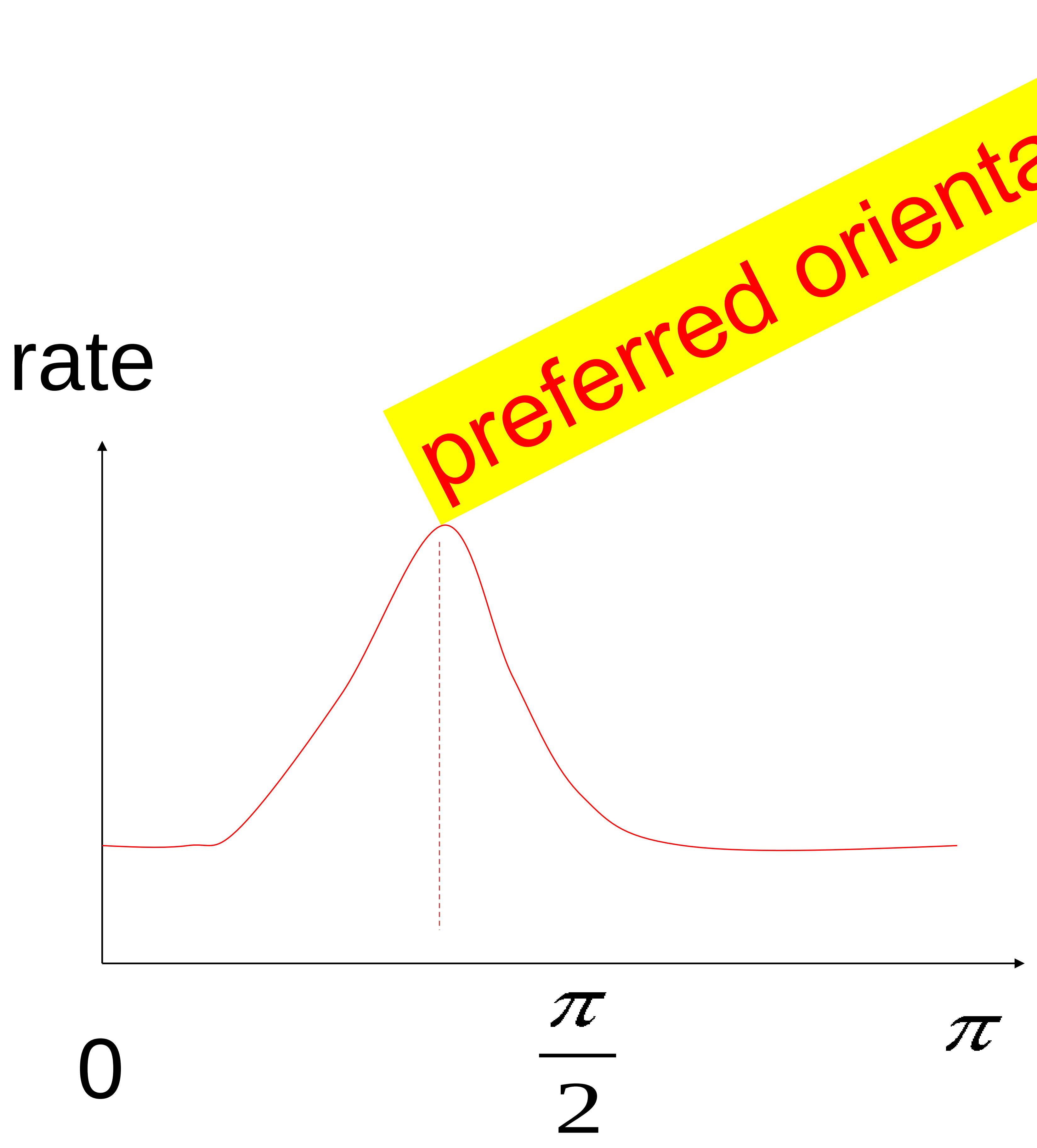
Week 10-part 1b: Orientation tuning of receptive fields

Receptive fields:
visual cortex V1



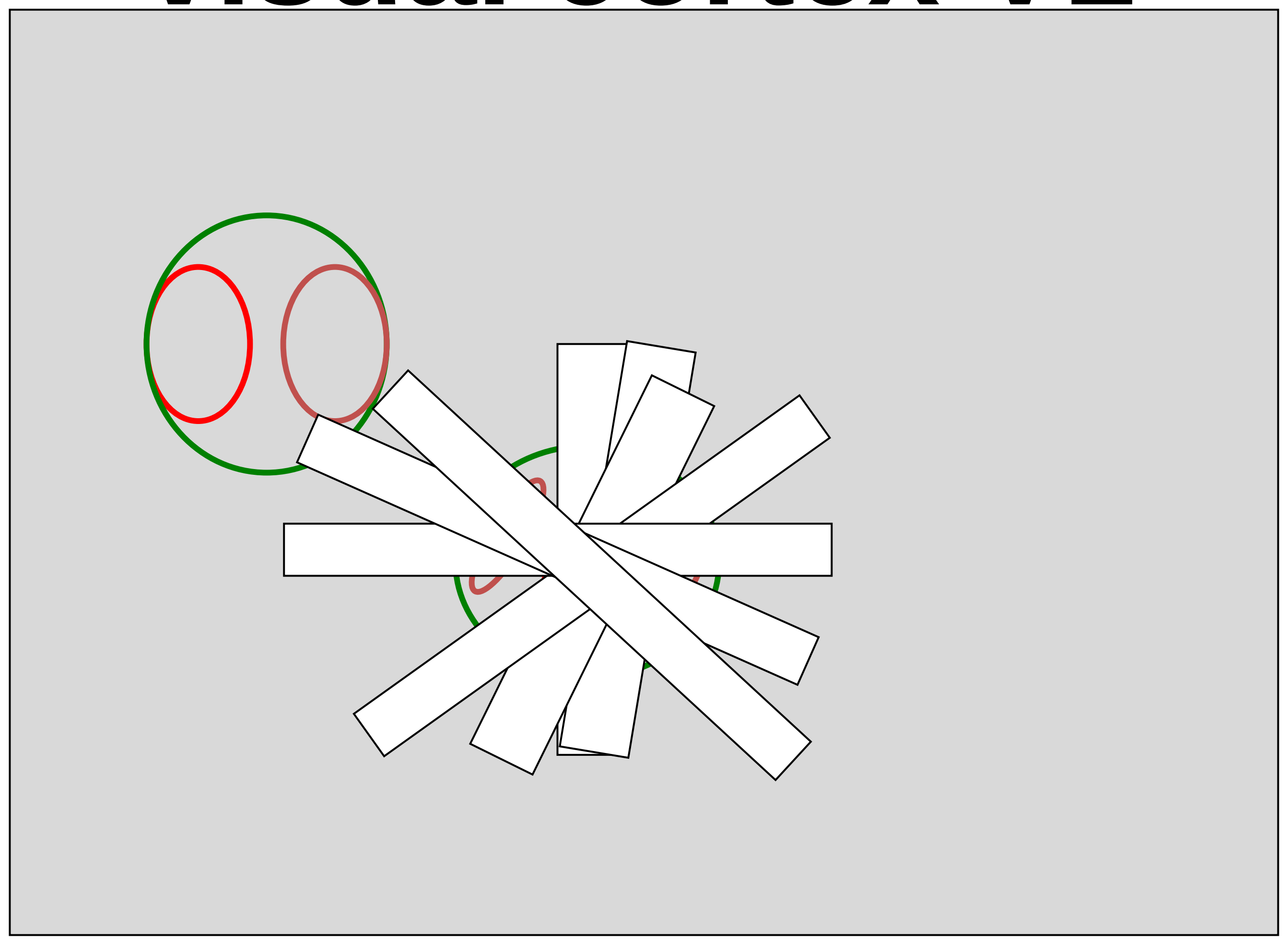
Orientation selective

Week 10-part 1b: Orientation tuning of receptive fields



Stimulus orientation

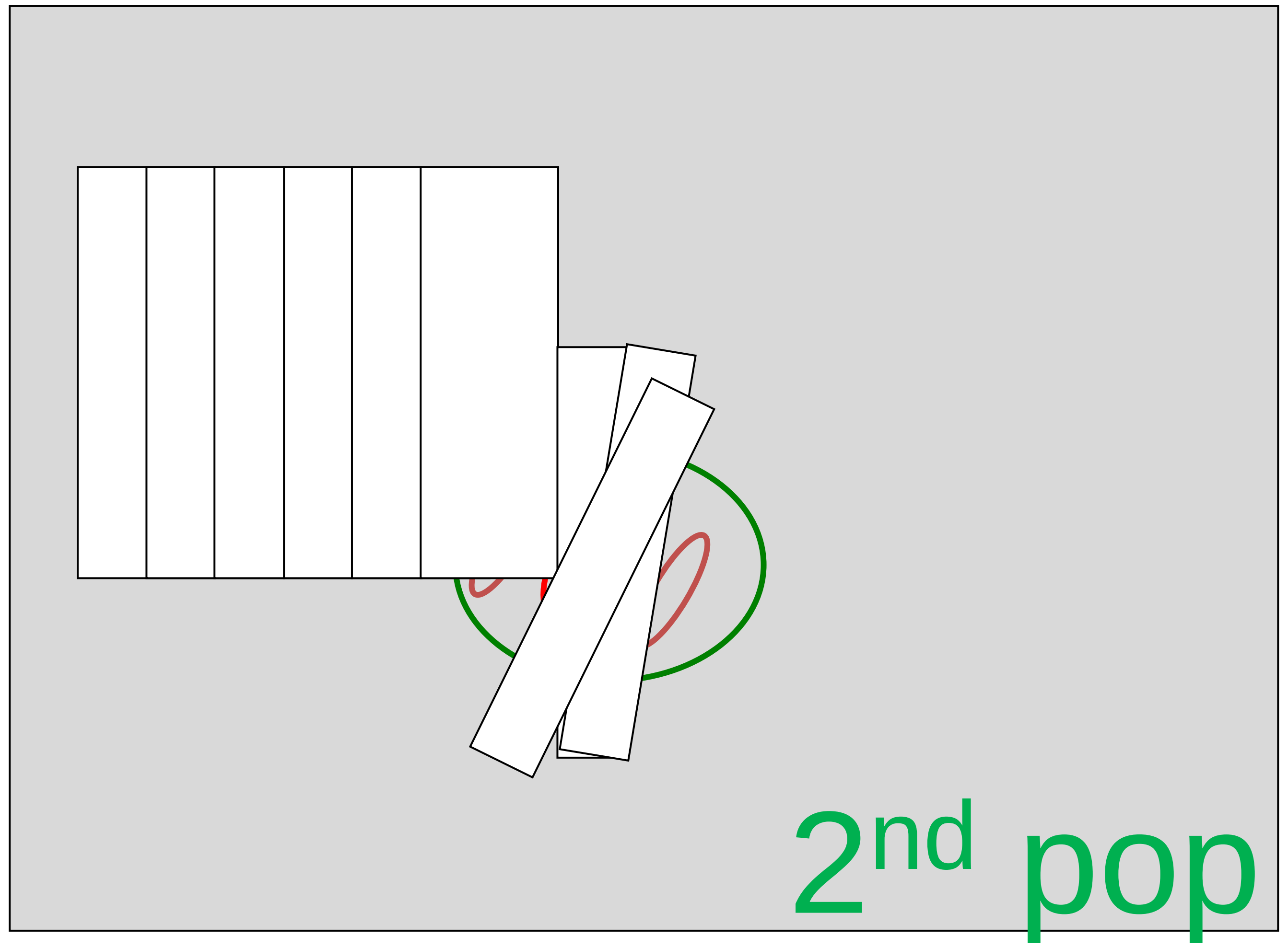
Receptive fields:
visual cortex V1



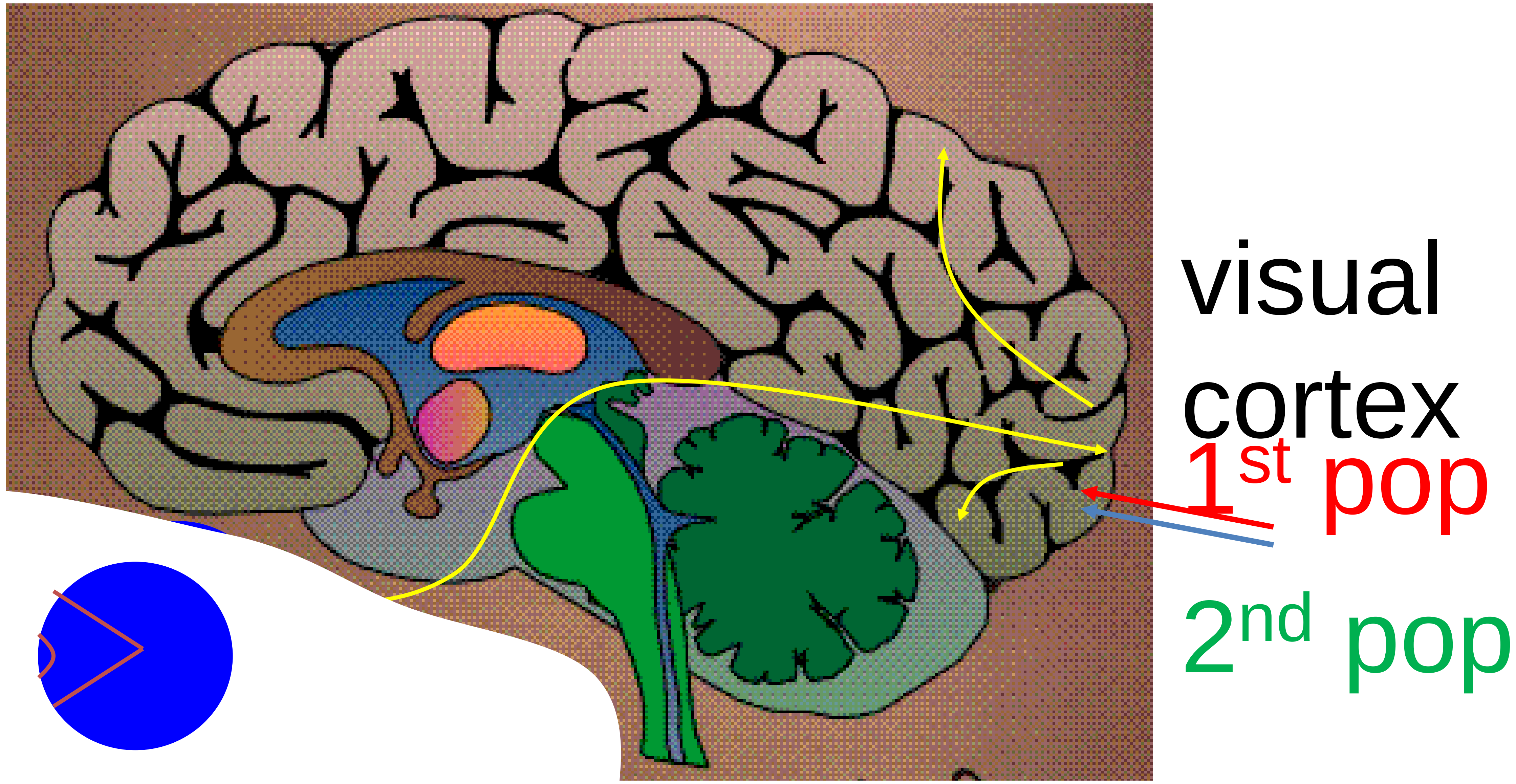
Orientation selective

Week 10-part 1b: Orientation columns/orientation maps

Receptive fields:
visual cortex V1

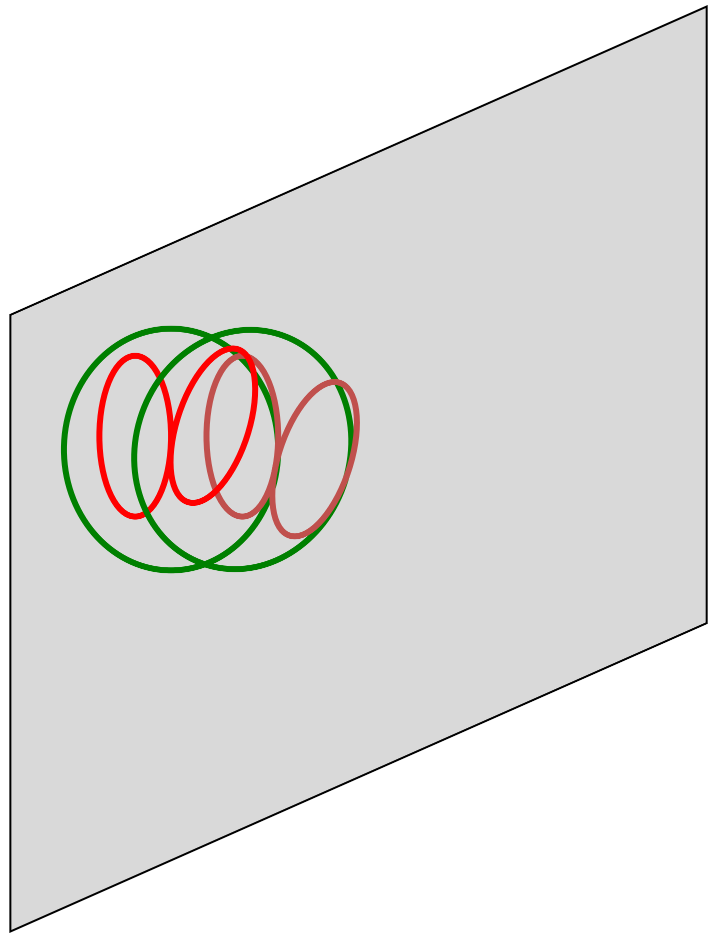


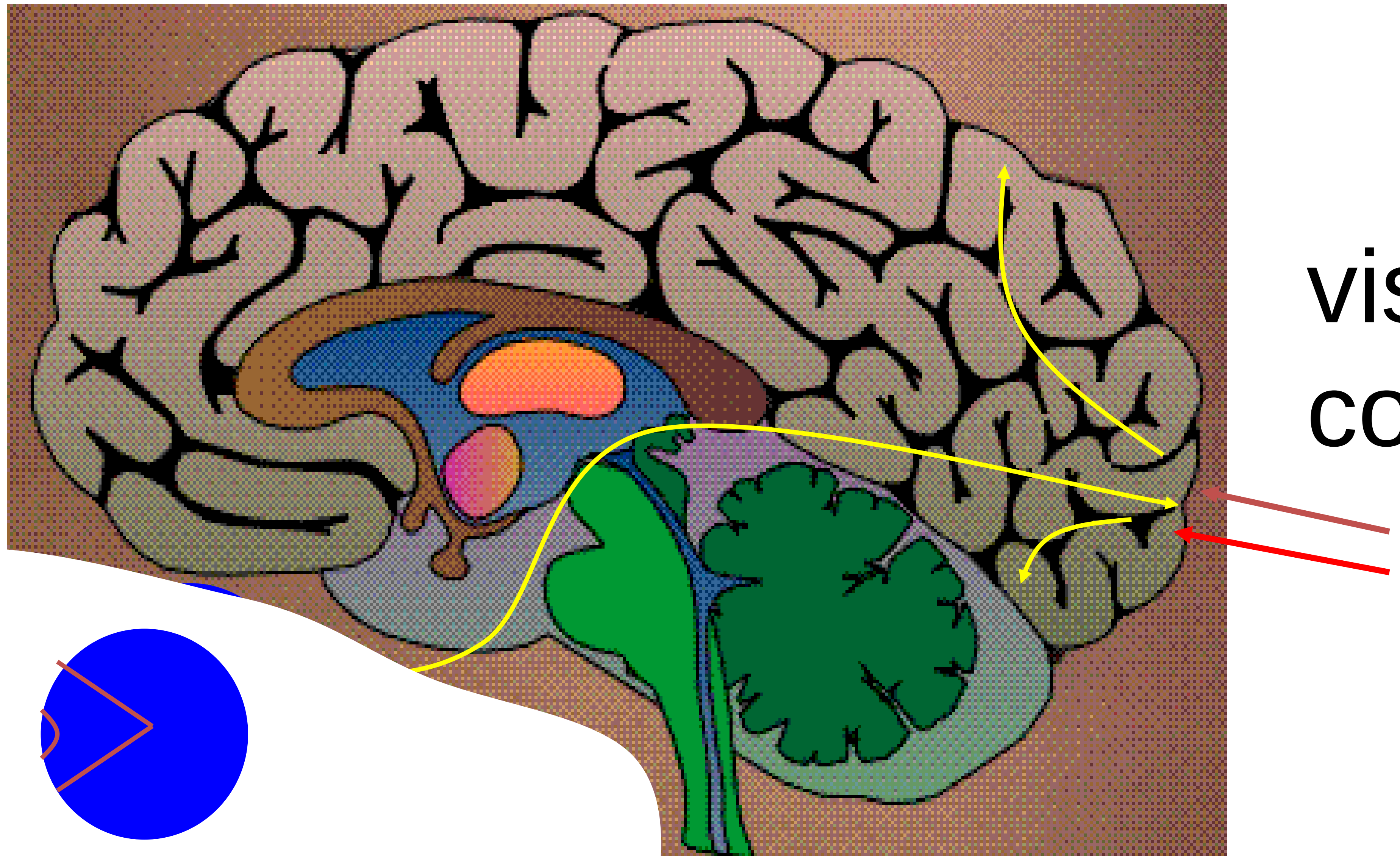
Orientation selective



Neighboring neurons have similar properties

Week 10-part 1b: Orientation map





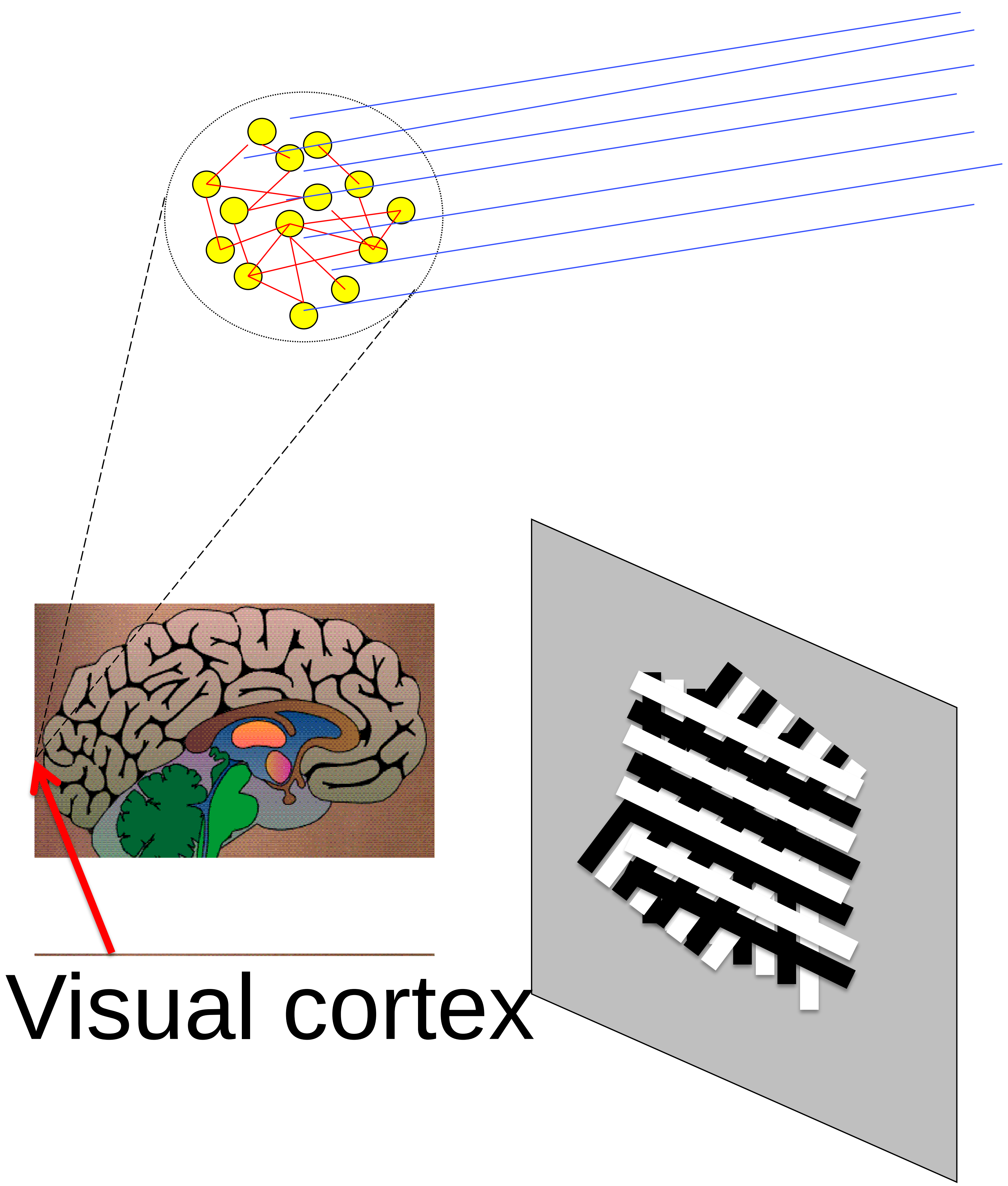
visual
cortex

Neighboring cells in visual cortex
Have similar preferred orientation:

cortical orientation map

Week 10-part 1b: Orientation columns/orientation maps

population of neighboring neurons: different orientations



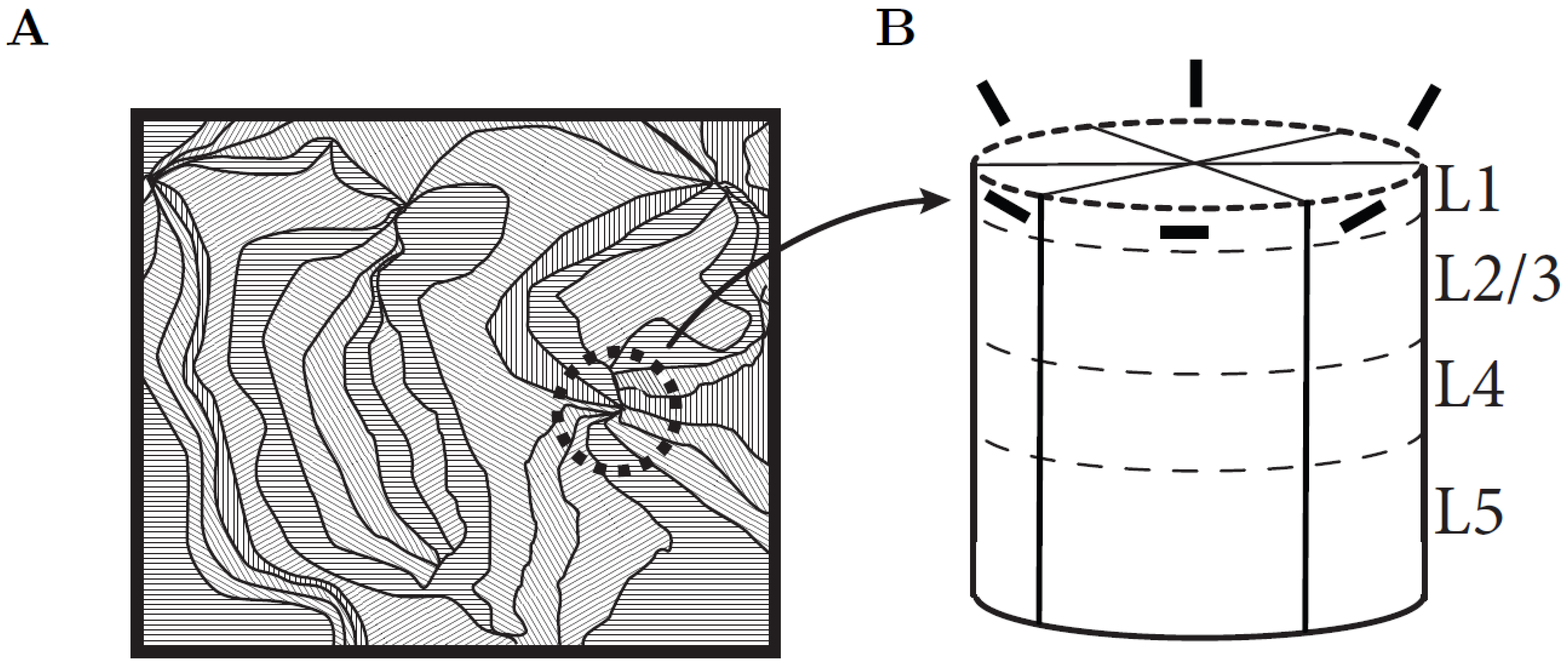
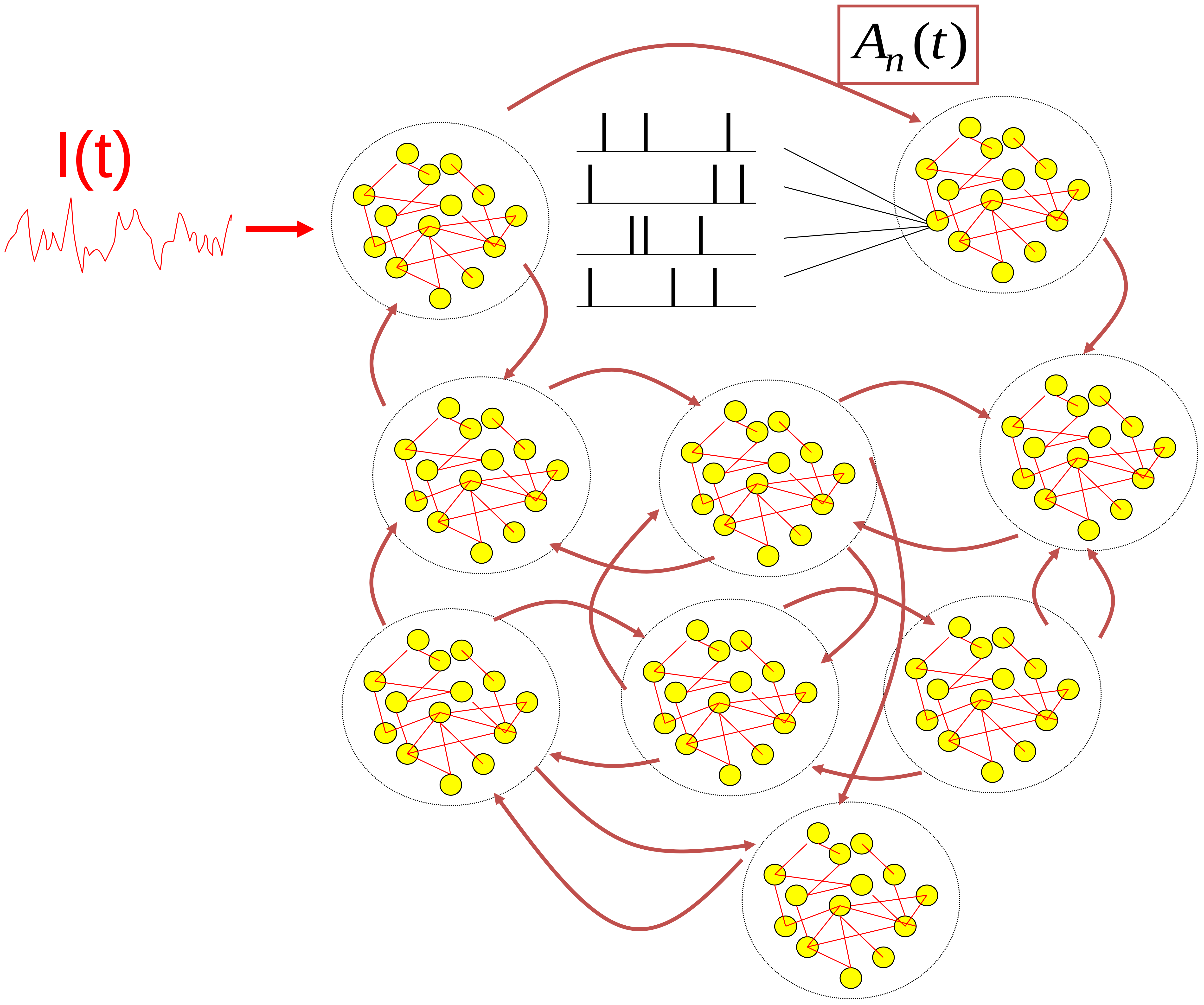
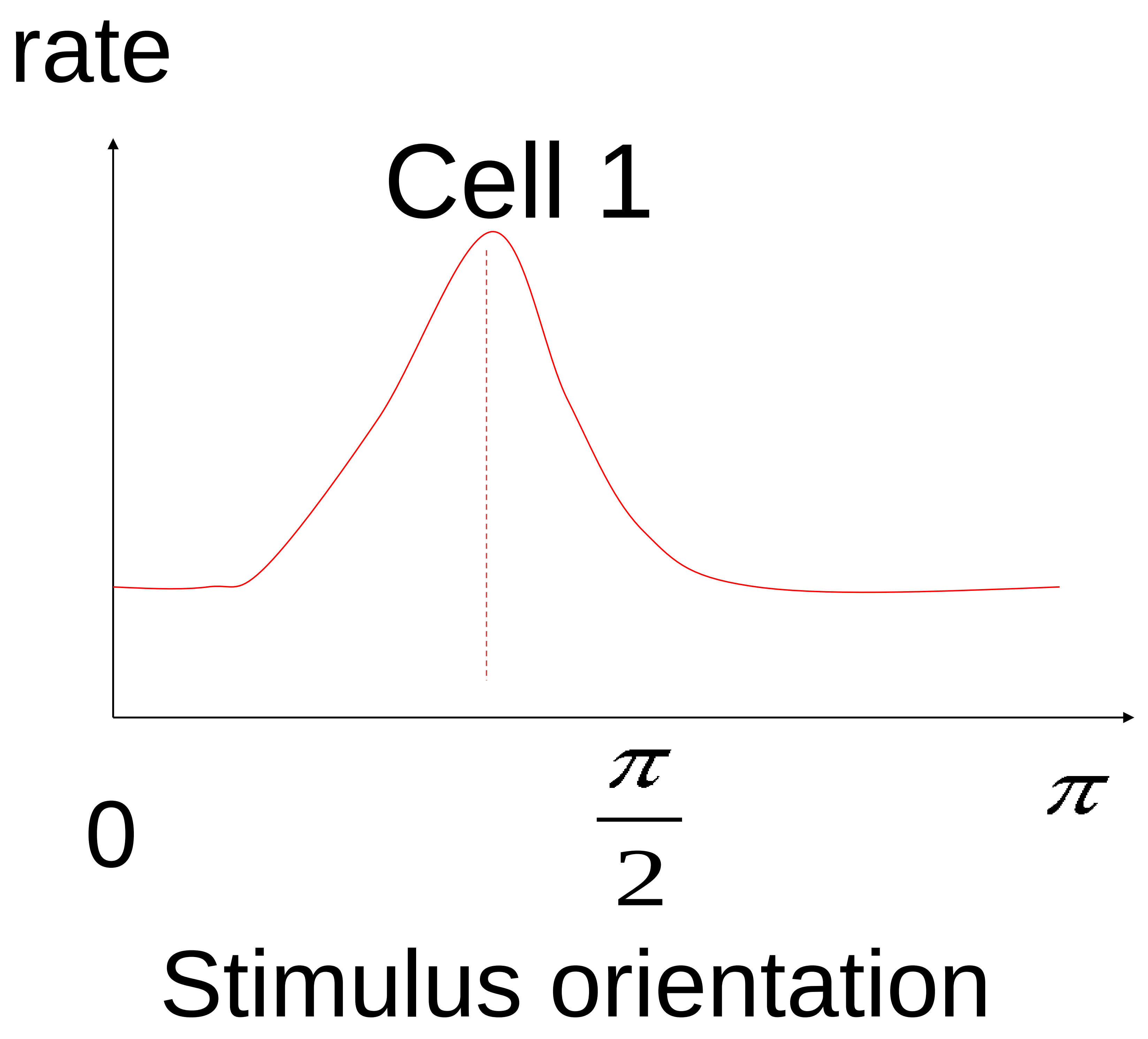


Image: Gerstner et al. Neuronal Dynamics (2014)

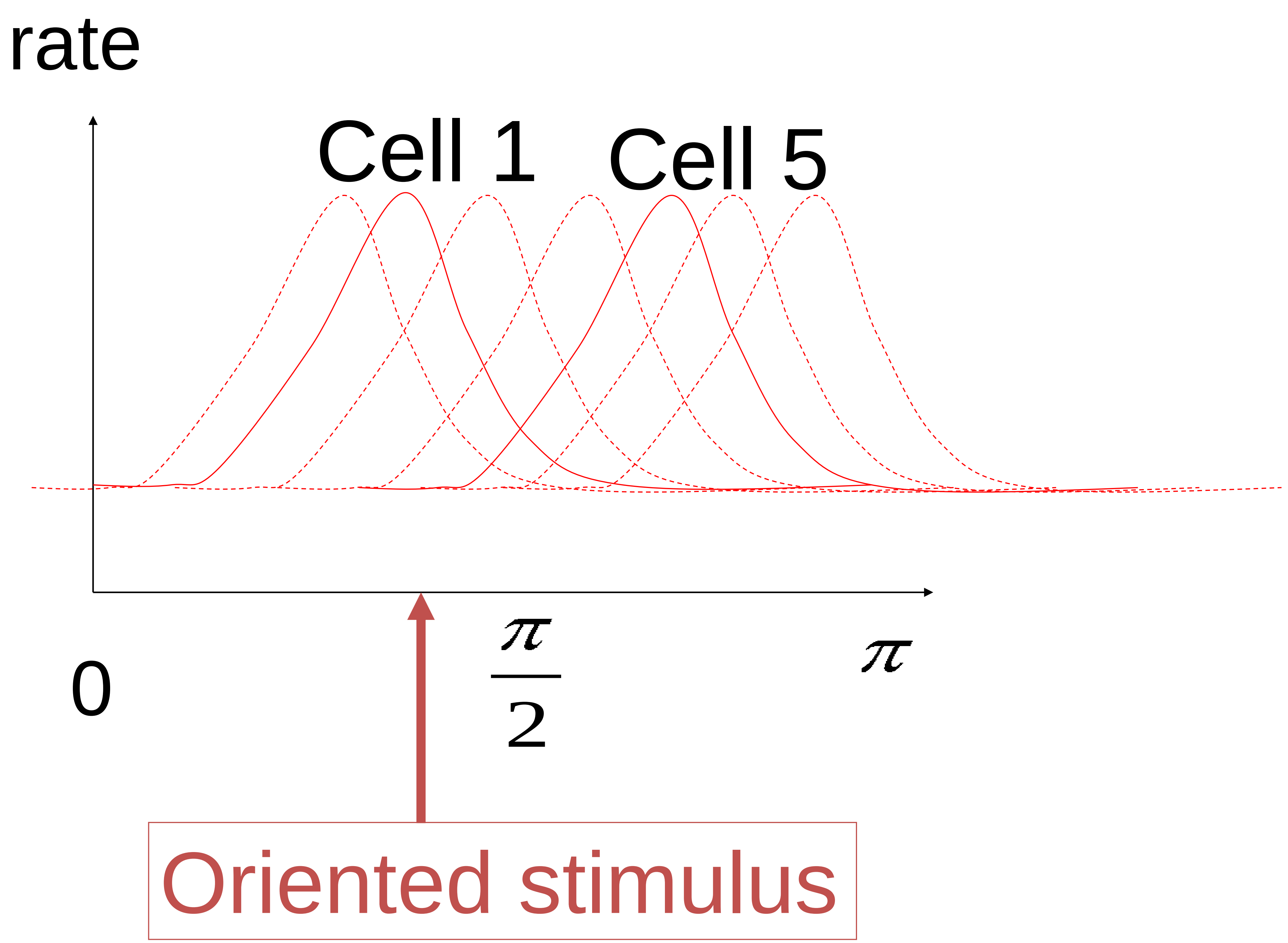
Week 10-part 1b: Interaction between populations / columns



Week 10-part 1b: Do populations / columns really exist?



Week 10-part 1b: Do populations / columns really exist?



Course coding

Many cells
(from different columns)
respond to a single
stimulus with different rate

Quiz 1, 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

Week 10 – part 2 : Connectivity

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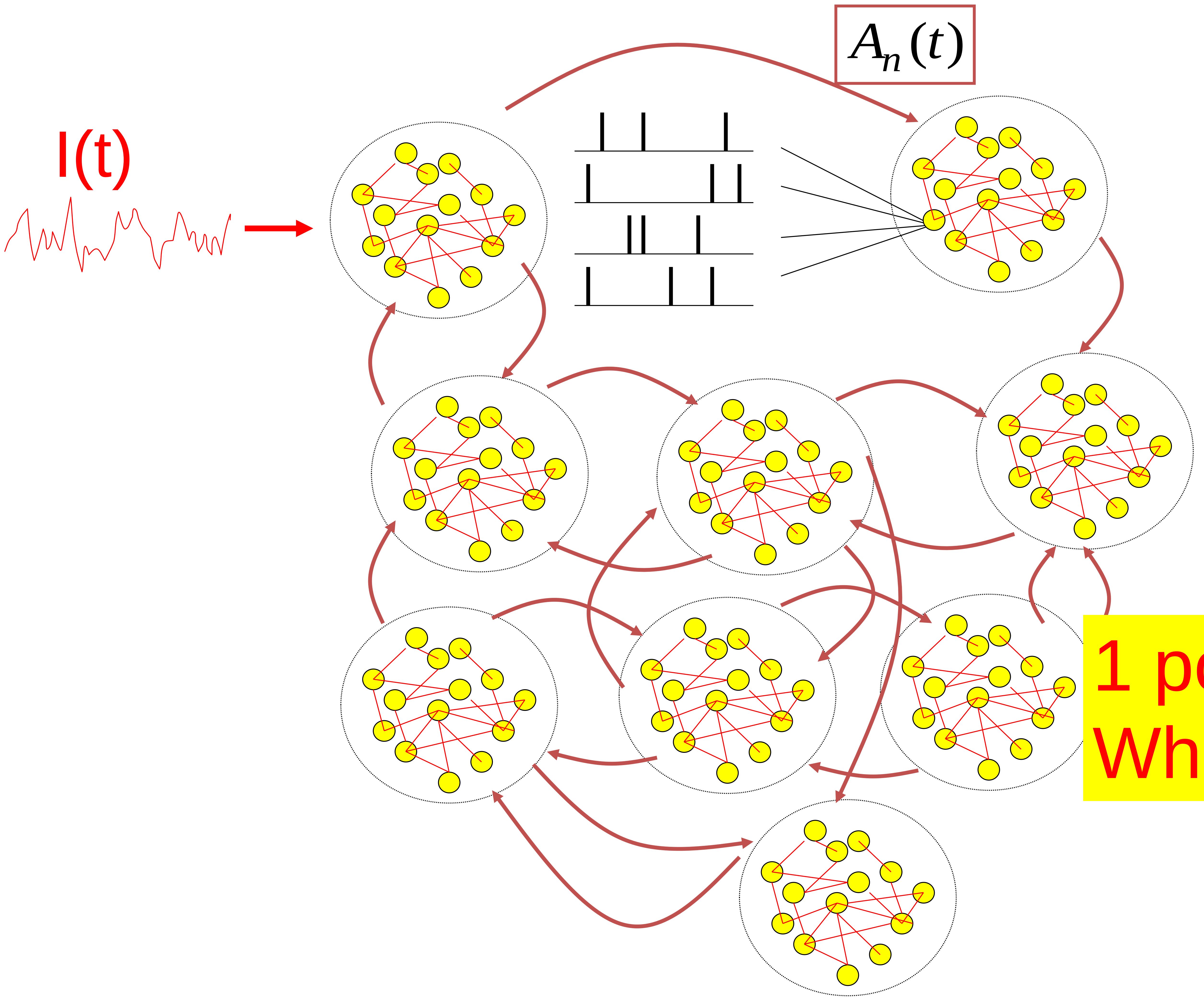
Biological Modeling of Neural Networks:

Week 10 – Neuronal Populations

Wulfram Gerstner

EPFL, Lausanne, Switzerland

Week 10-part 2: Connectivity schemes (models)



1 population = What?

Week 10-part 2: model population

population = group of neurons with

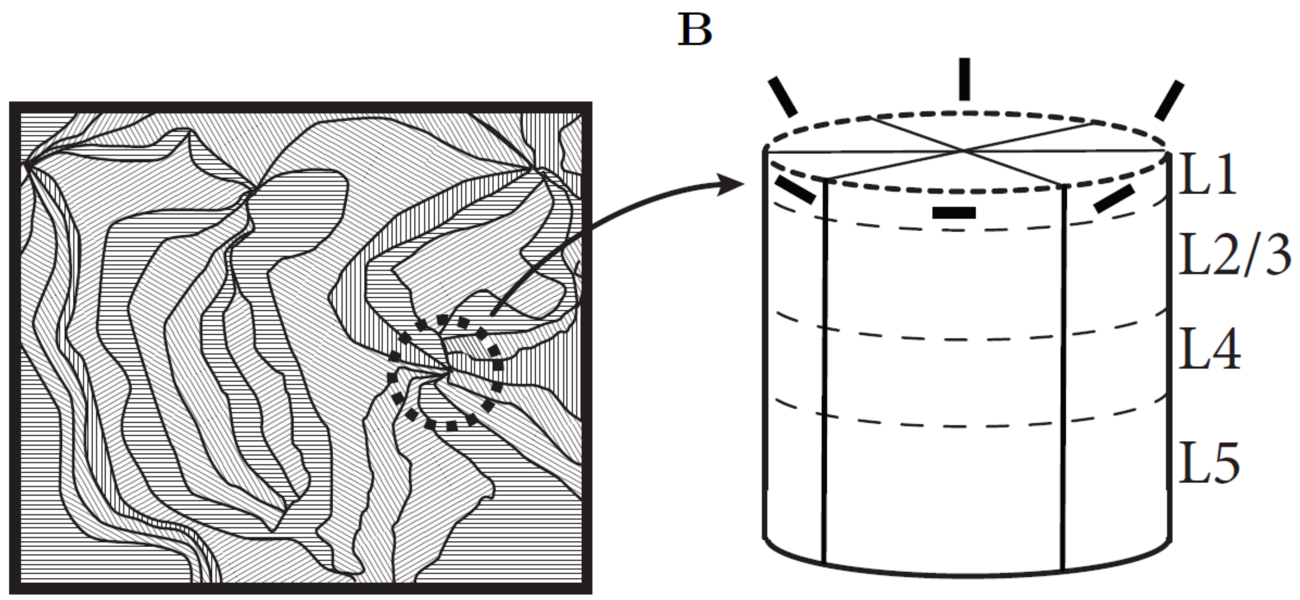
- similar neuronal properties
- similar input
- similar receptive field
- similar connectivity

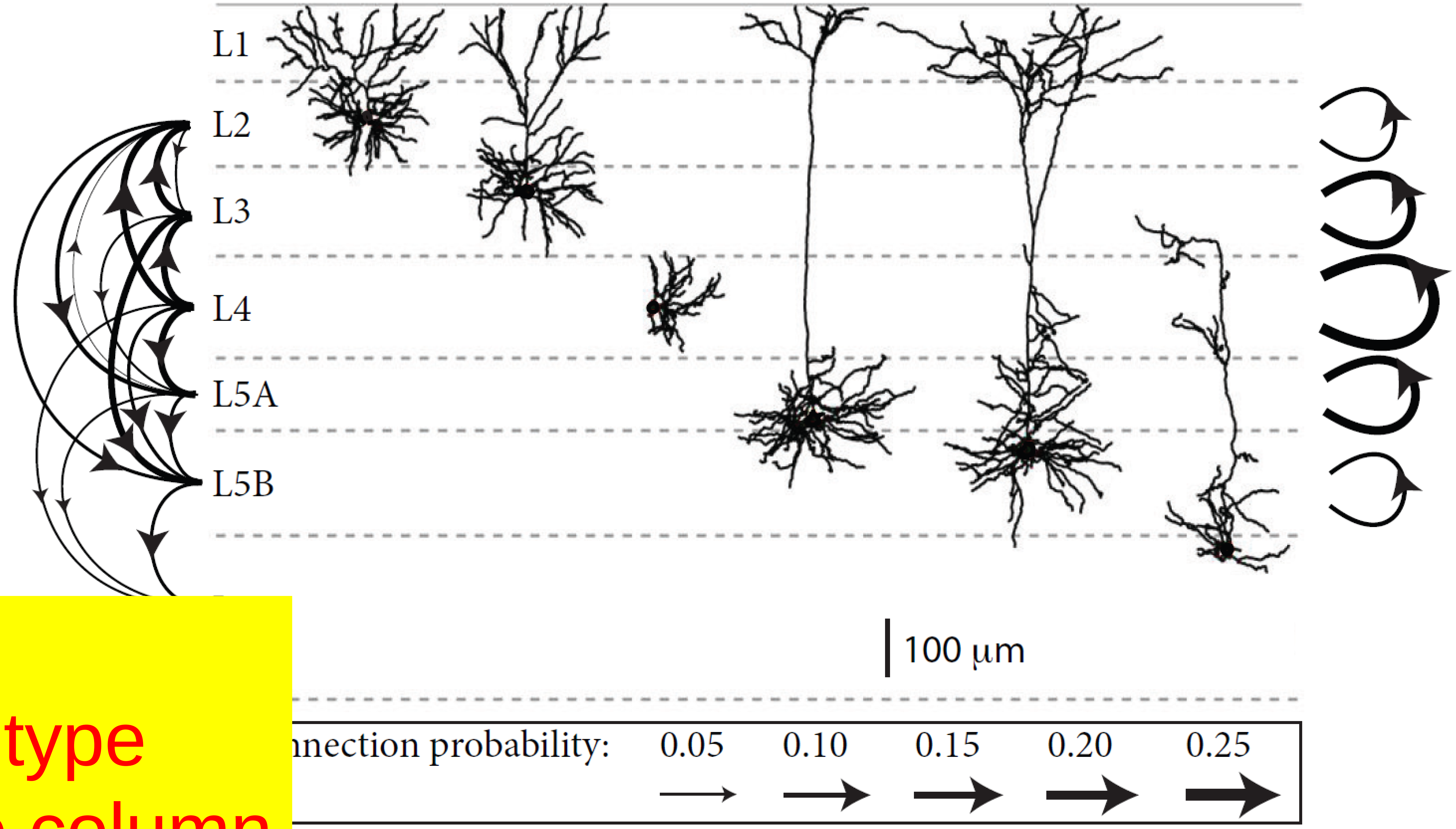
→ make this more precise

Week 10-part 2: local cortical connectivity across layers

(mouse somatosensory cortex)

Here:
Excitatory neurons



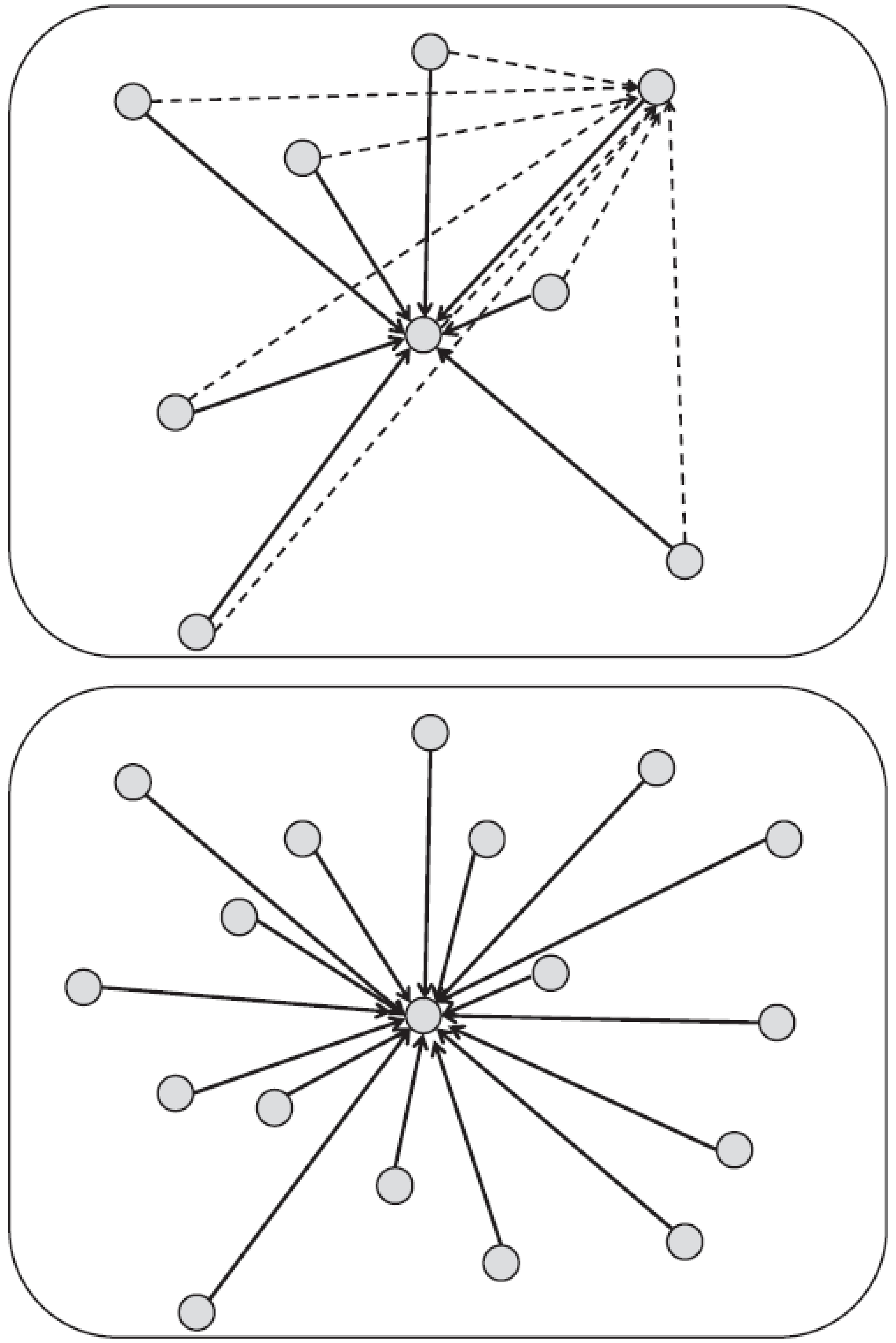


1 population =
all neurons of given type
in one layer of same column
(e.g. excitatory in layer 3)

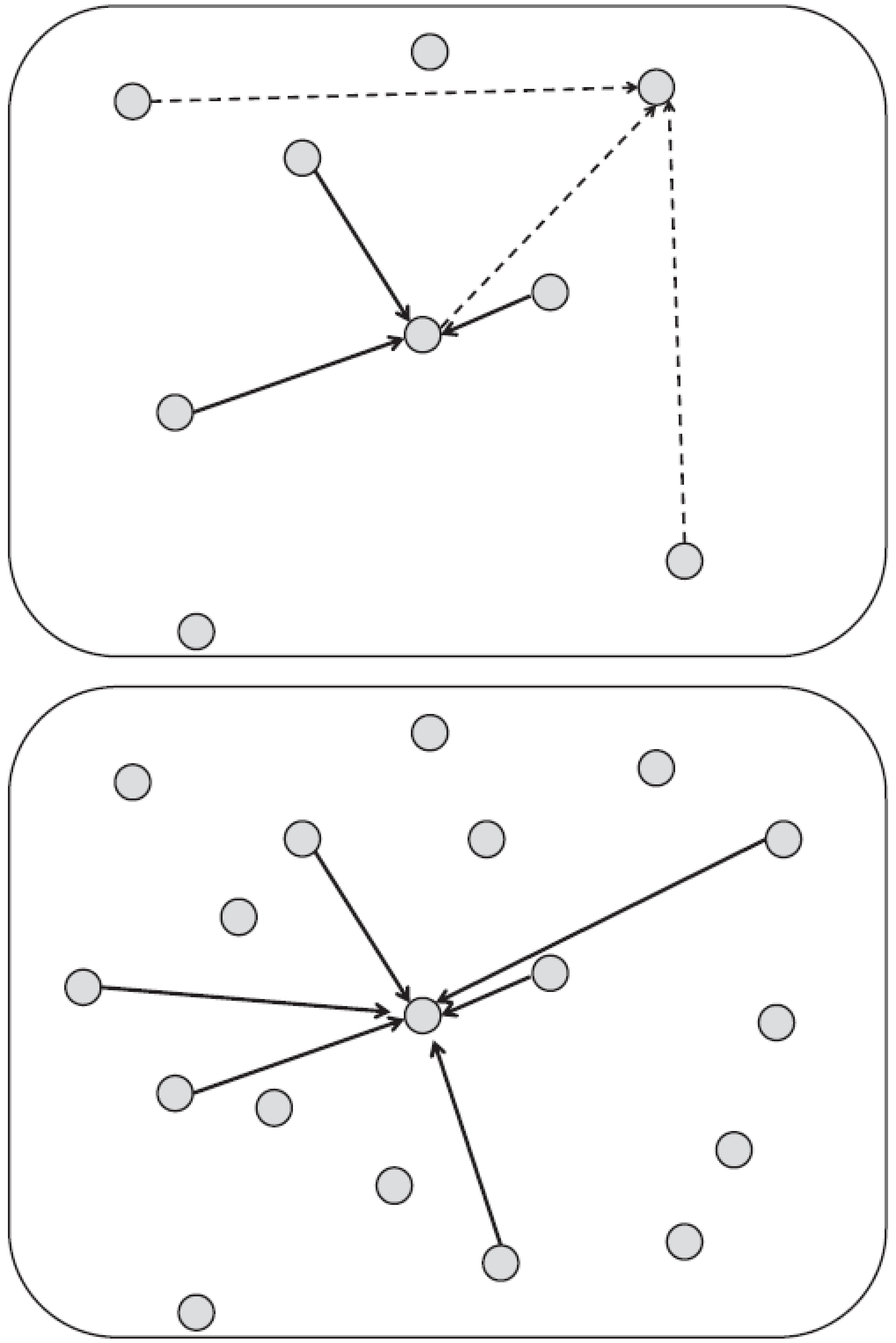
Lefort et al. NEURON, 2009

Week 10-part 2: Connectivity schemes (models)

full connectivity



random: prob p fixed



random: number K of inputs fixed

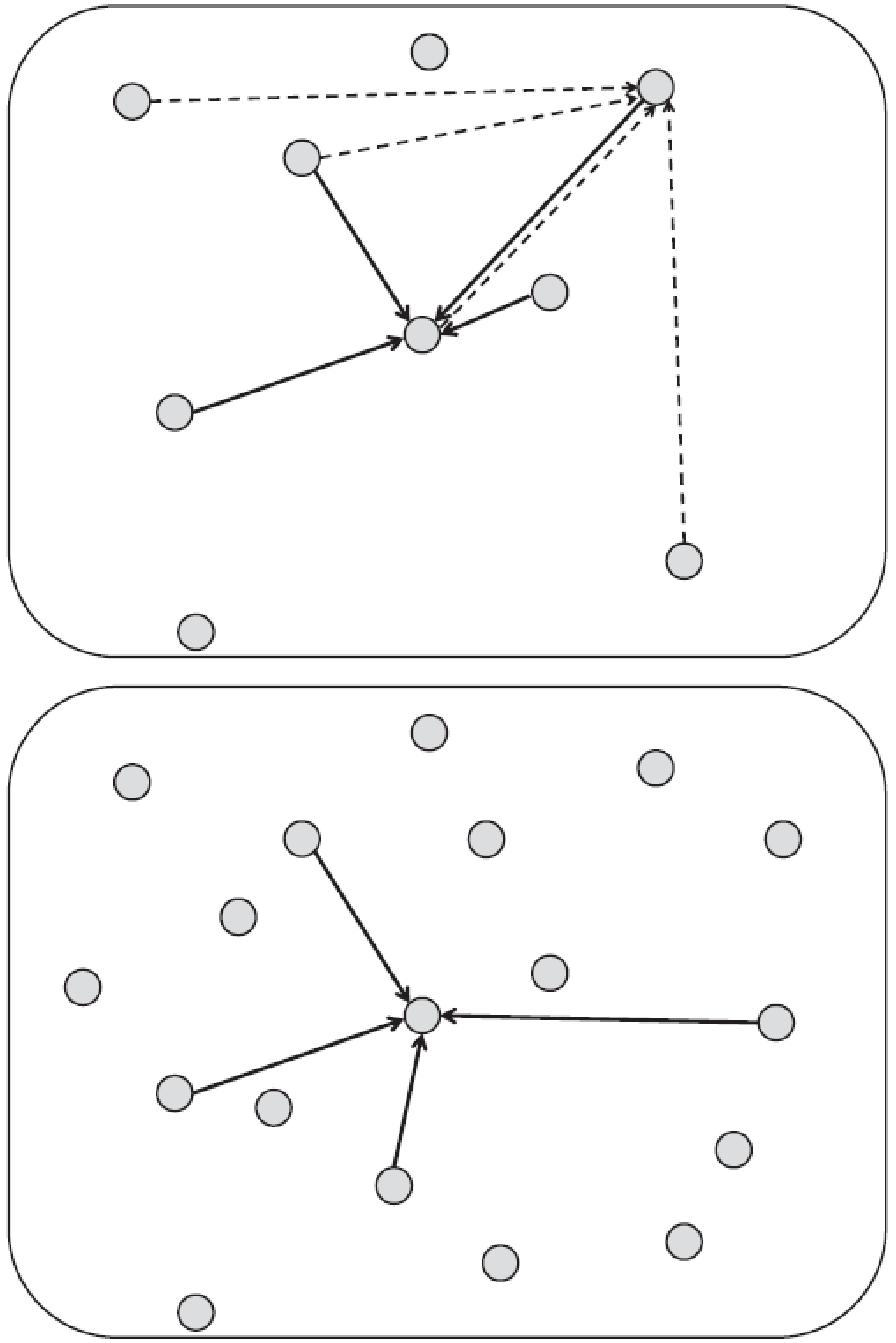
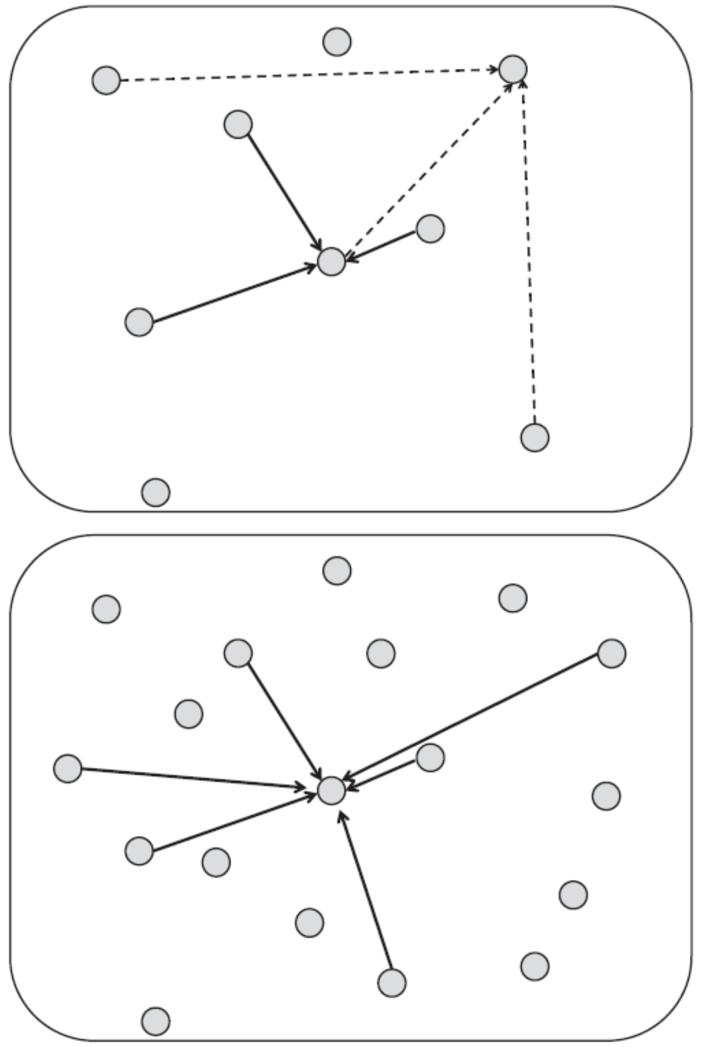


Image: Gerstner et al. Neuronal Dynamics (2014)

Week 10-part 2: Random Connectivity: fixed p

random: probability p=0.1, fixed



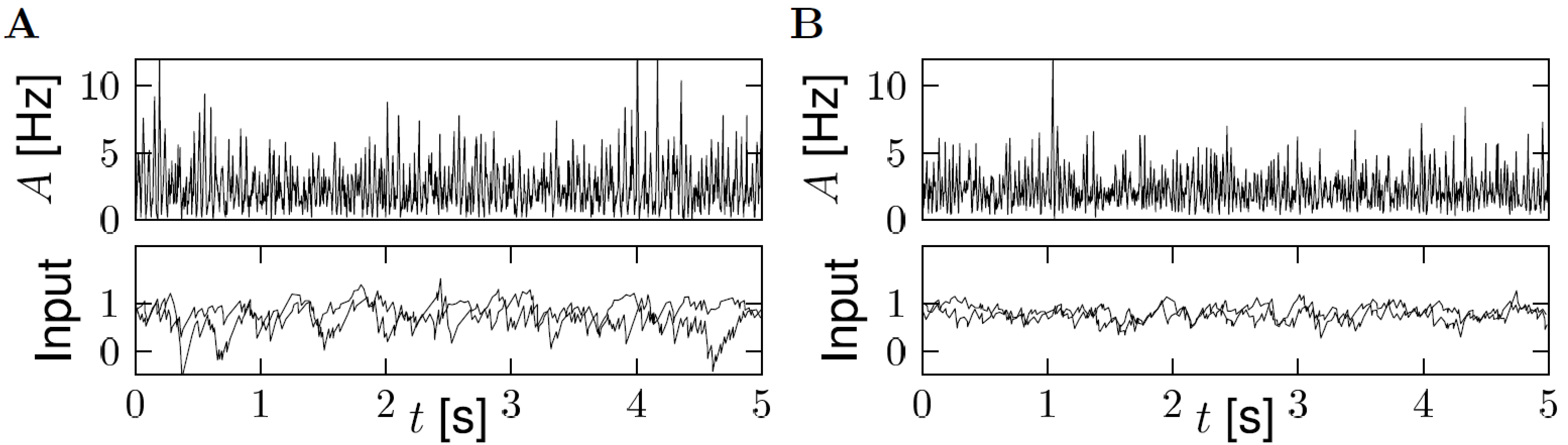


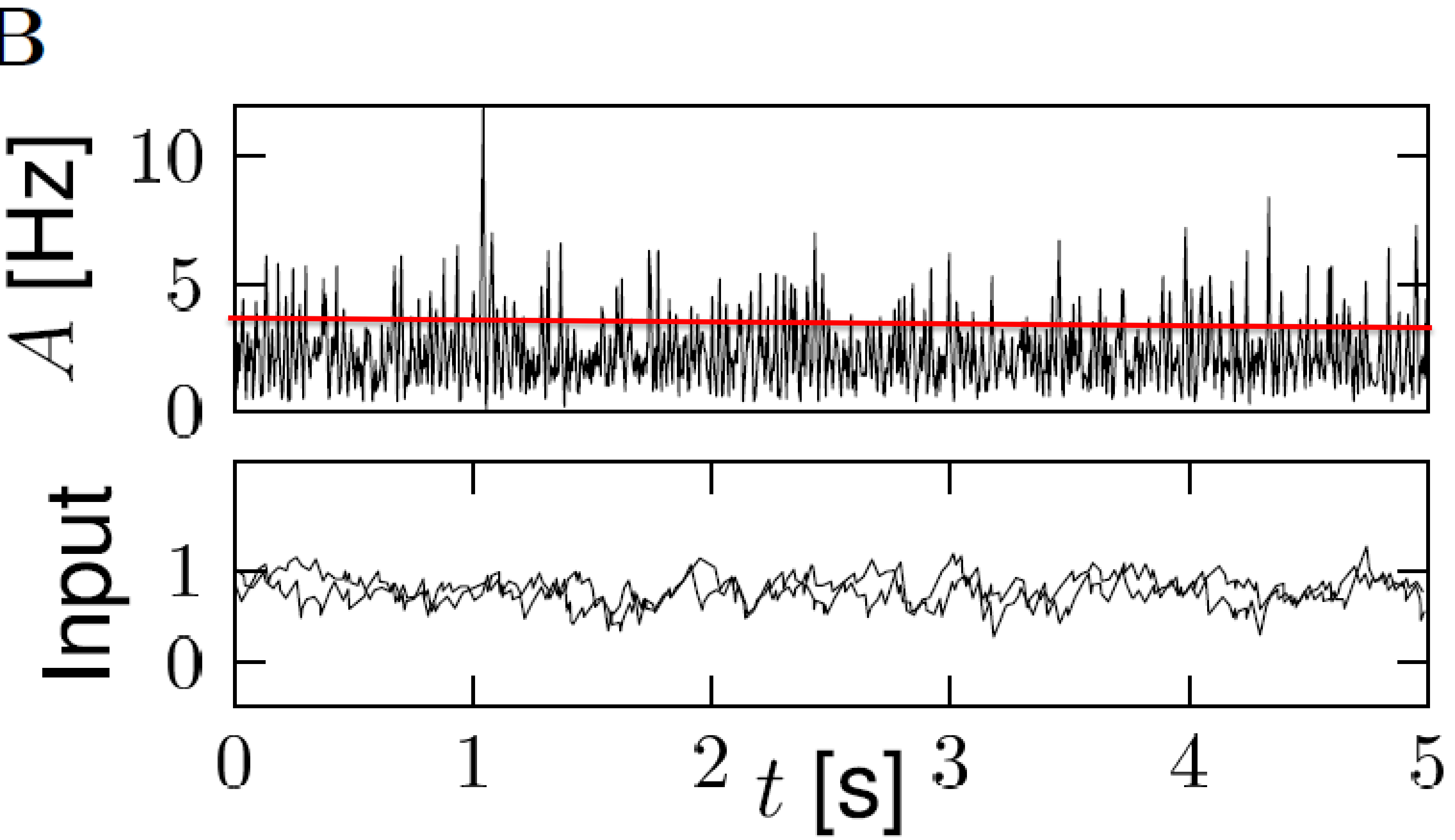
Fig. 12.7: Simulation of a model network with a fixed connection probability $p = 0.1$. **A.** Top: Population activity $A(t)$ averaged over all neurons in a network of 4 000 excitatory and 1 000 inhibitory neurons. Bottom: Total input current $I_i(t)$ into two randomly chosen

Image: Gerstner et al.
Neuronal Dynamics (2014)

Week 10-part 2: Random Connectivity: fixed p

Can we mathematically predict
the population activity?

given
- connection probability p
- properties of individual neurons
- large population



asynchronous
activity

Week 10 – part 2 : Connectivity

Biological Modeling of Neural Networks:

Week 10 – Neuronal Populations

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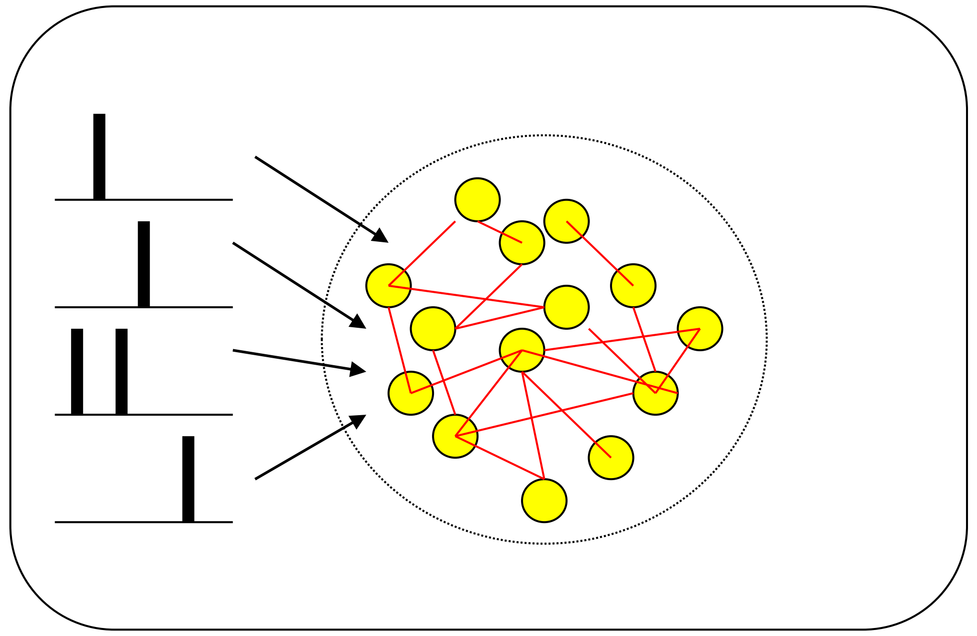
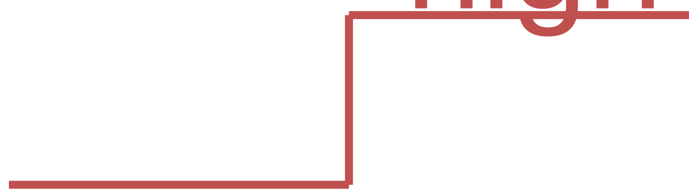
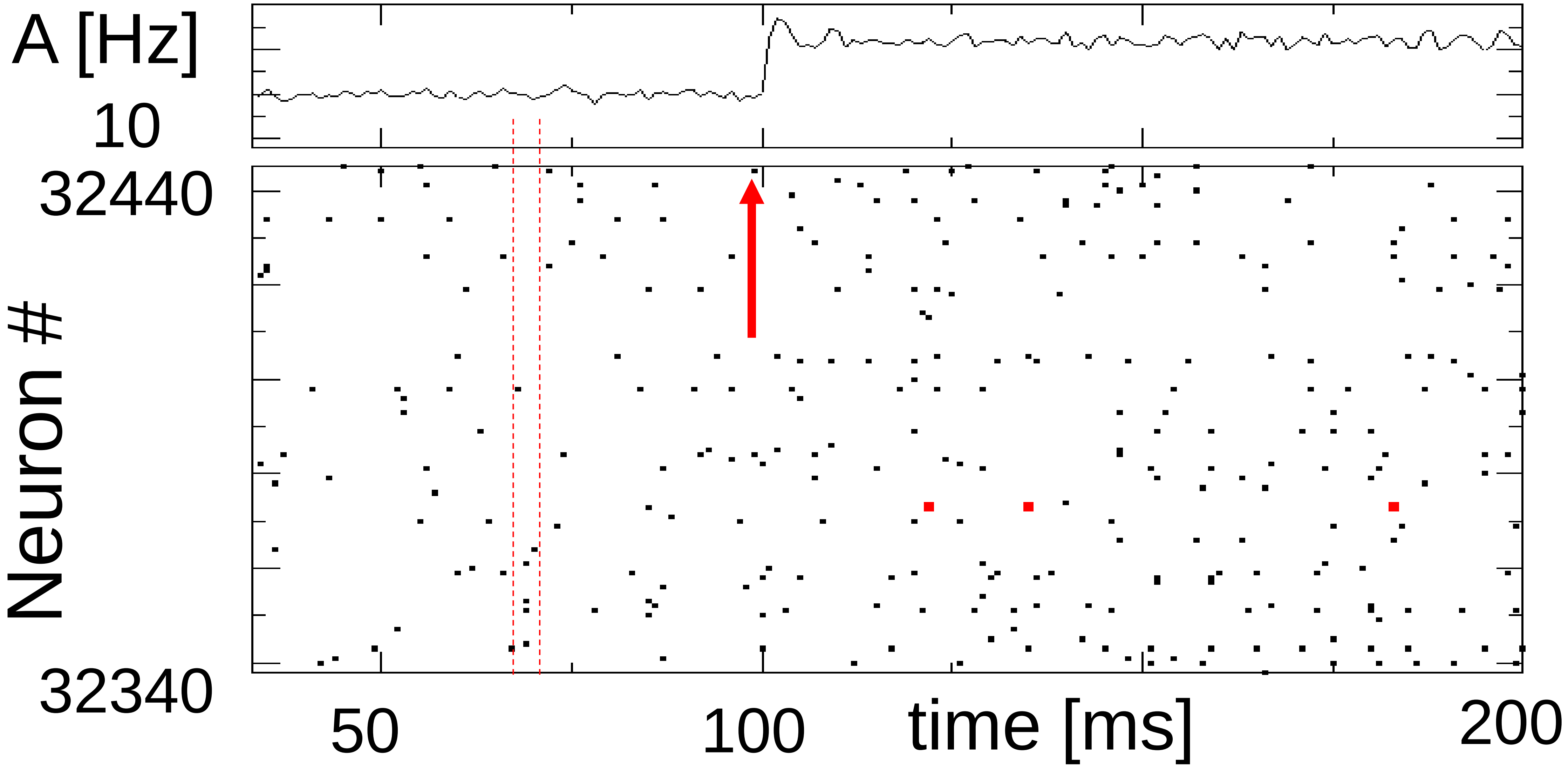
EPFL, Lausanne, Switzerland

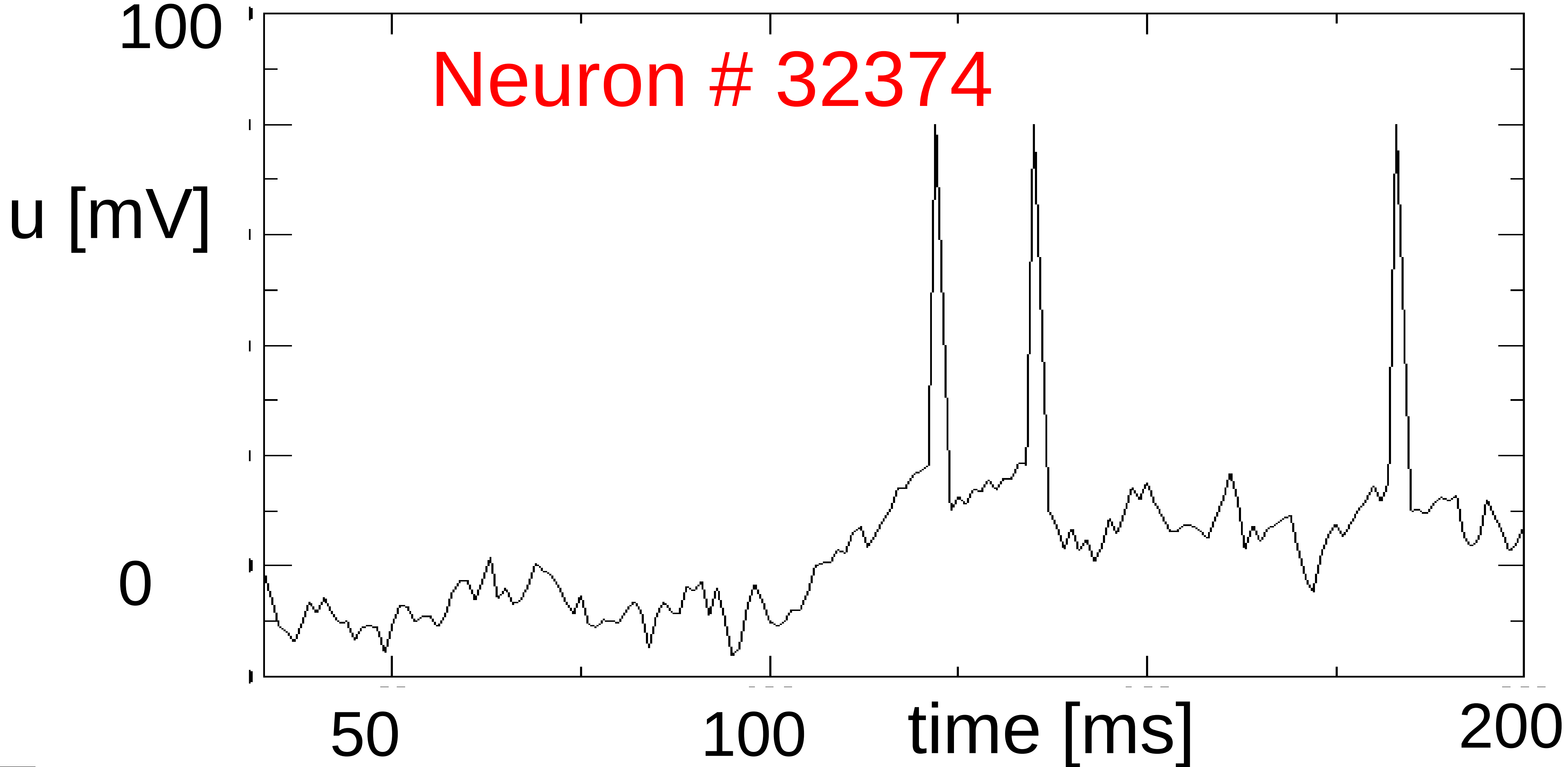
Random firing in a populations of neurons



input {low rate / high rate







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

Week 10-part 3: asynchronous firing

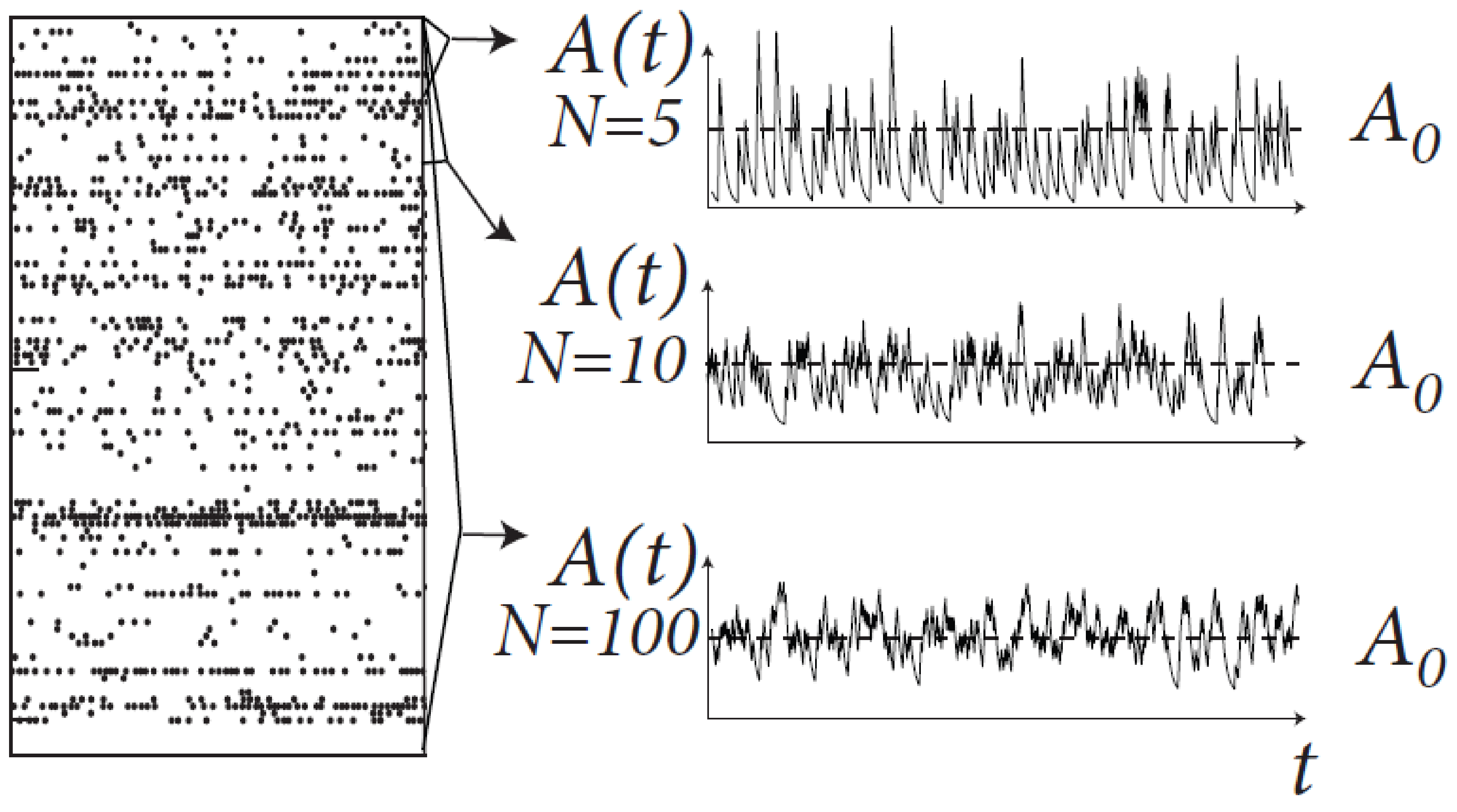


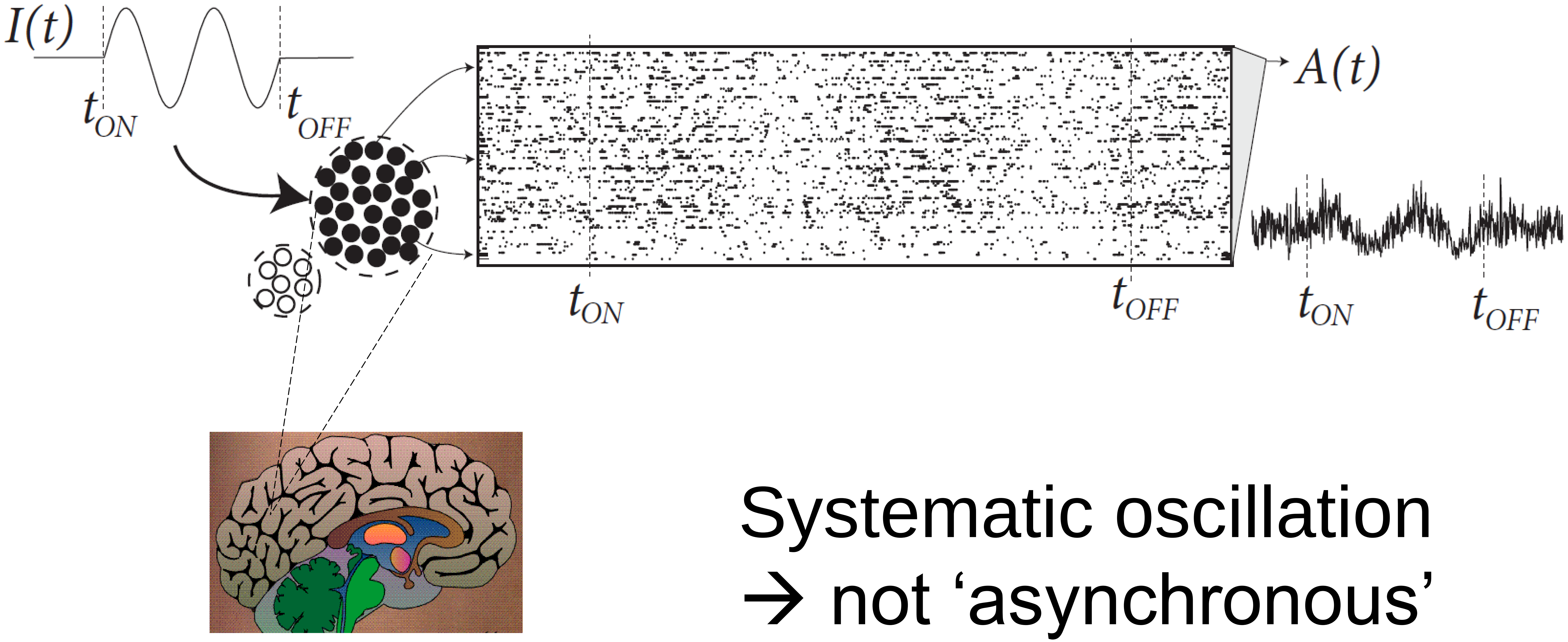
Image: Gerstner et al.
Neuronal Dynamics (2014)

Blackboard:
-Definition of A(t)
- filtered A(t)
- <A(t)>

Asynchronous state
$\langle A(t) \rangle = A_0 =$ *constant*

Week 10-part 3: counter-example: A(t) not constant

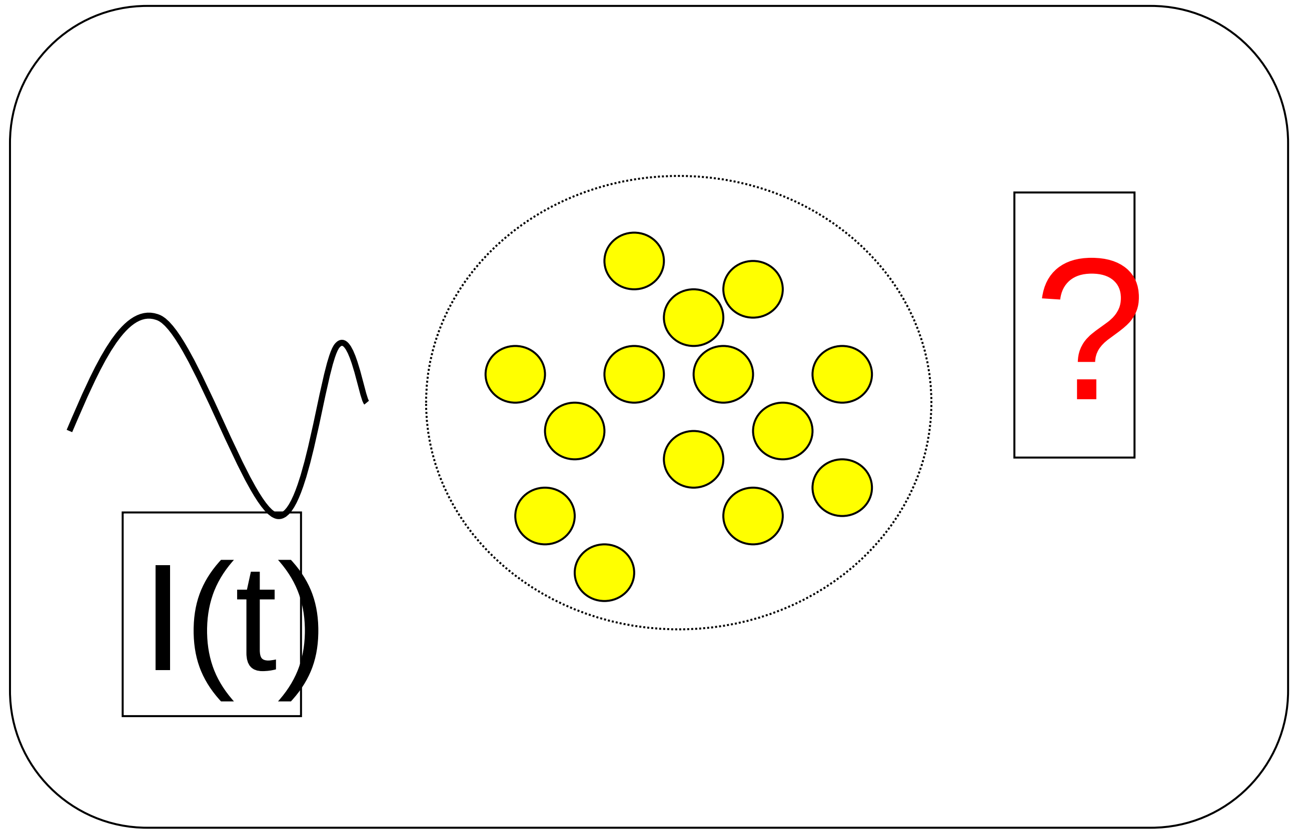
population of neurons
with similar properties



Systematic oscillation
→ not ‘asynchronous’

Brain

Populations of spiking neurons

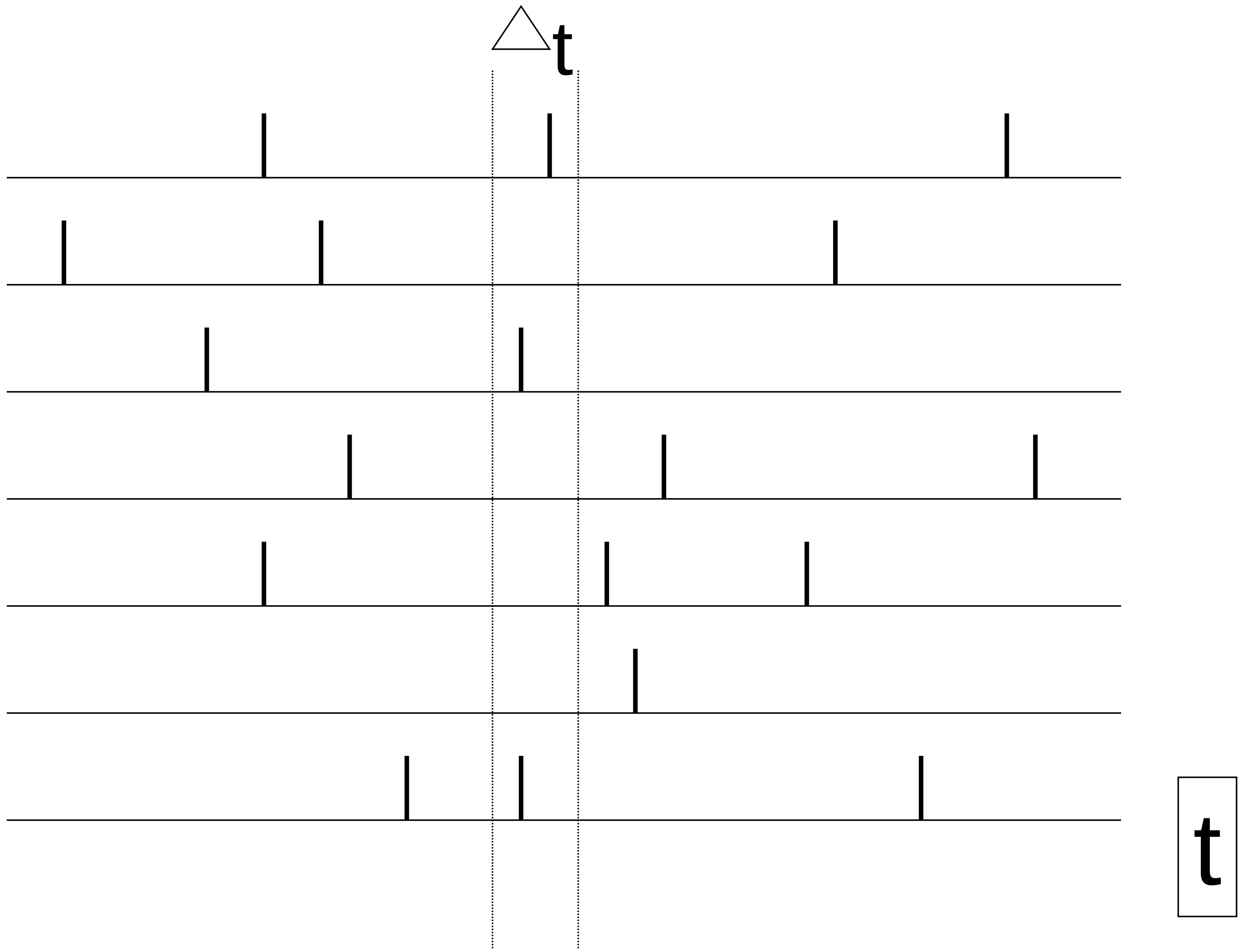


population activity?

Homogeneous network:

-each neuron receives input from k neurons in network

-each neuron receives the same (mean) external input

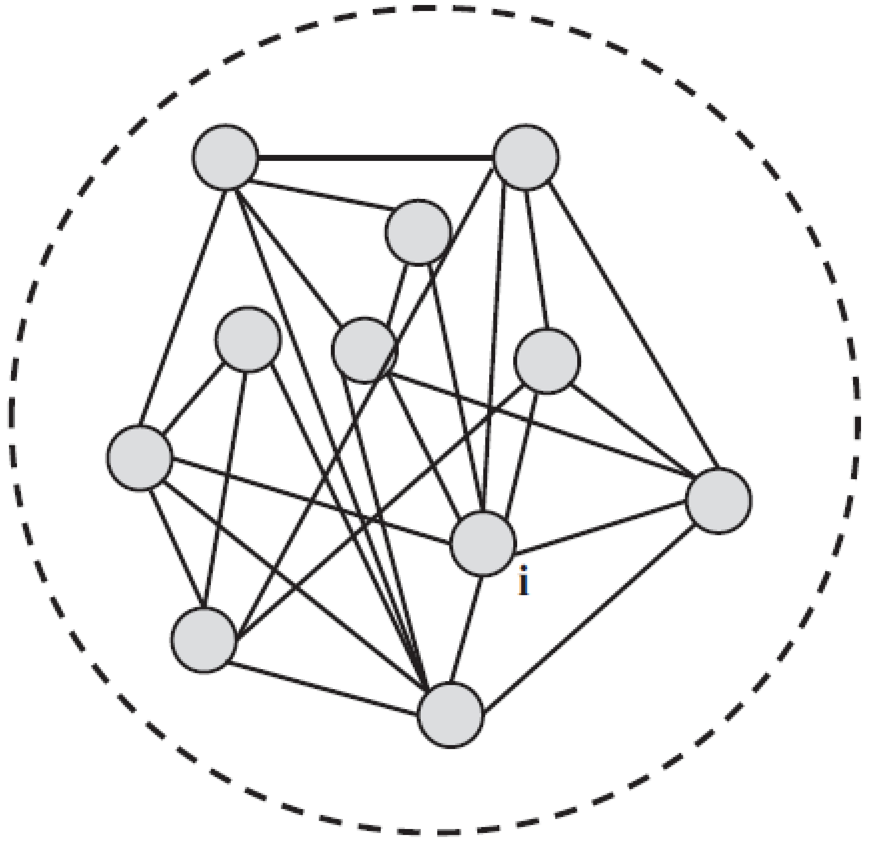


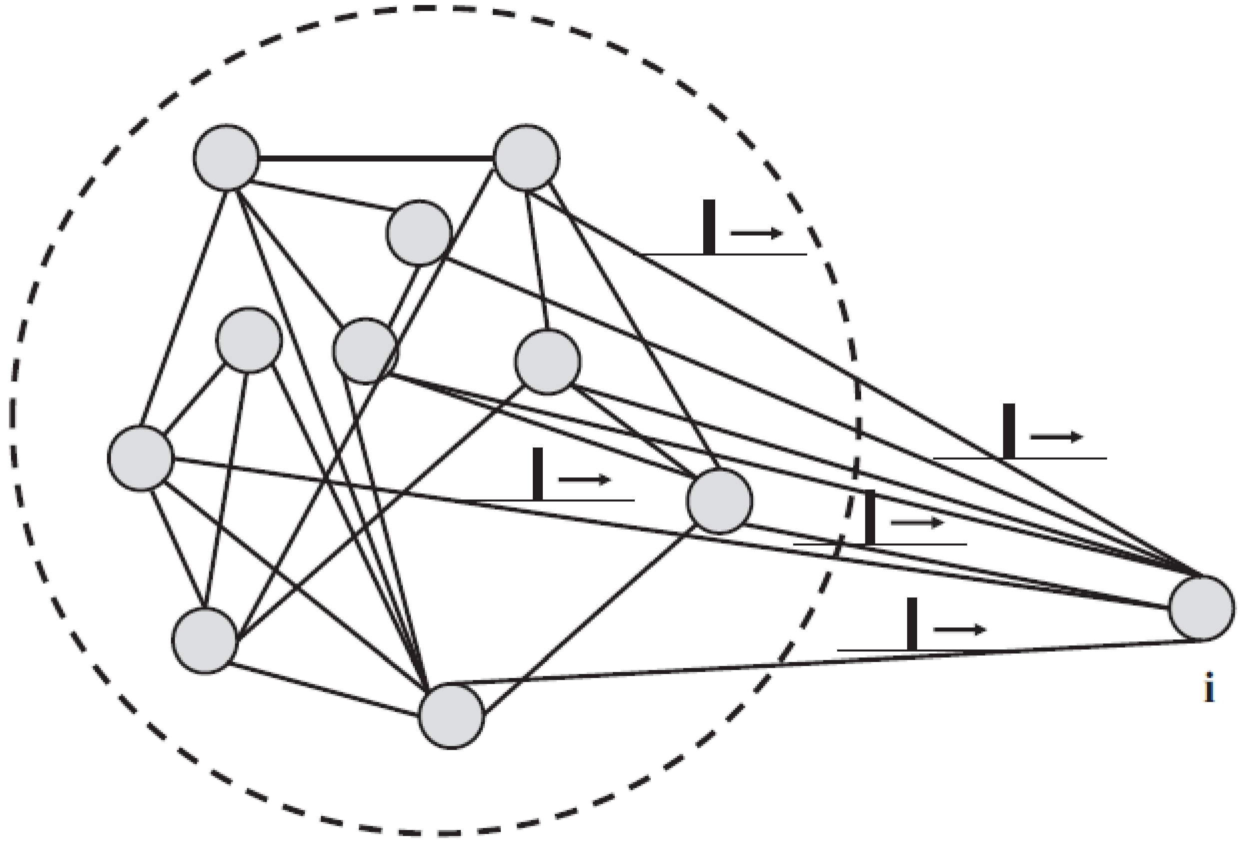
population activity

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

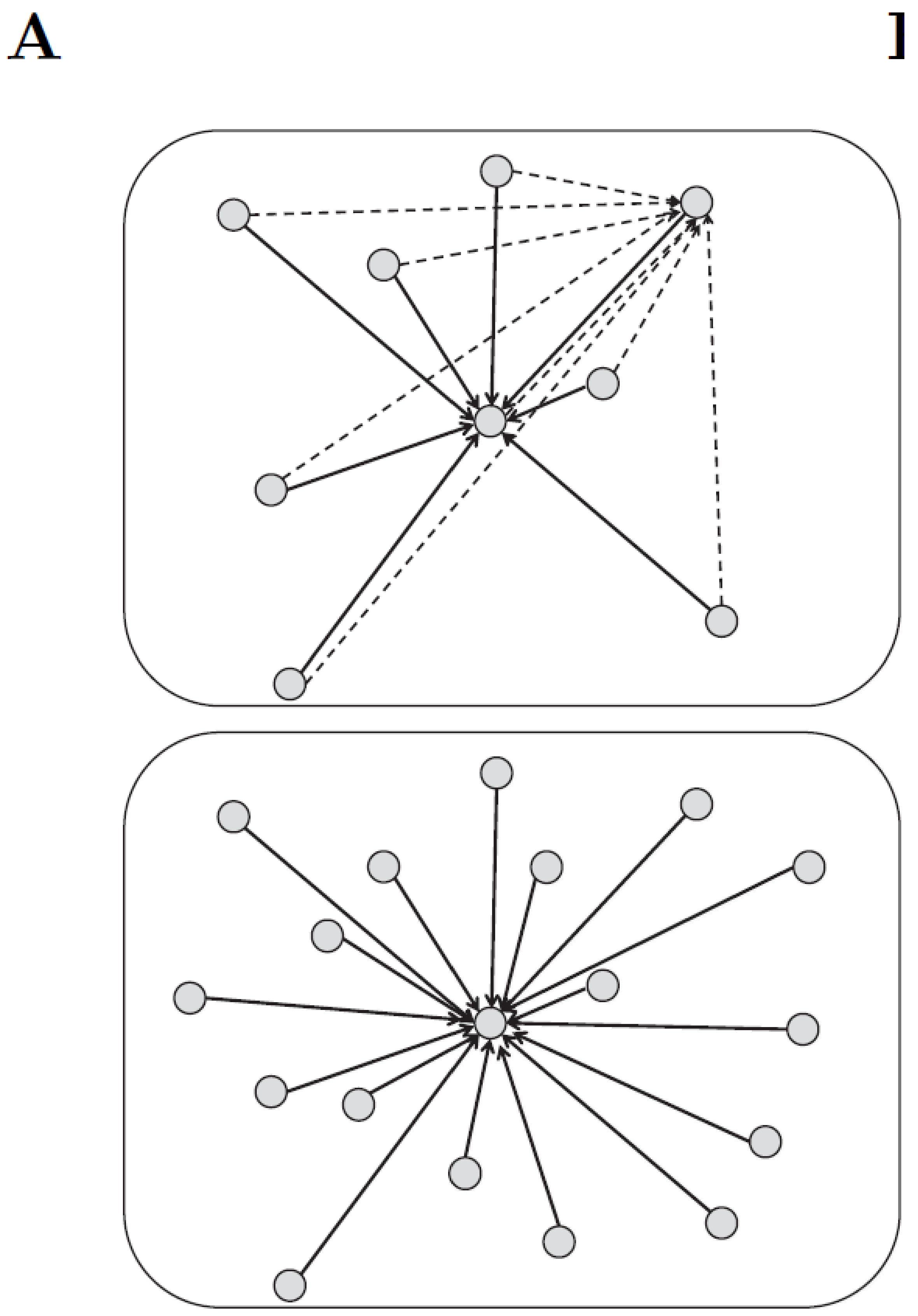
Week 10-part 3: mean-field arguments

Blackboard:
Input to neuron i

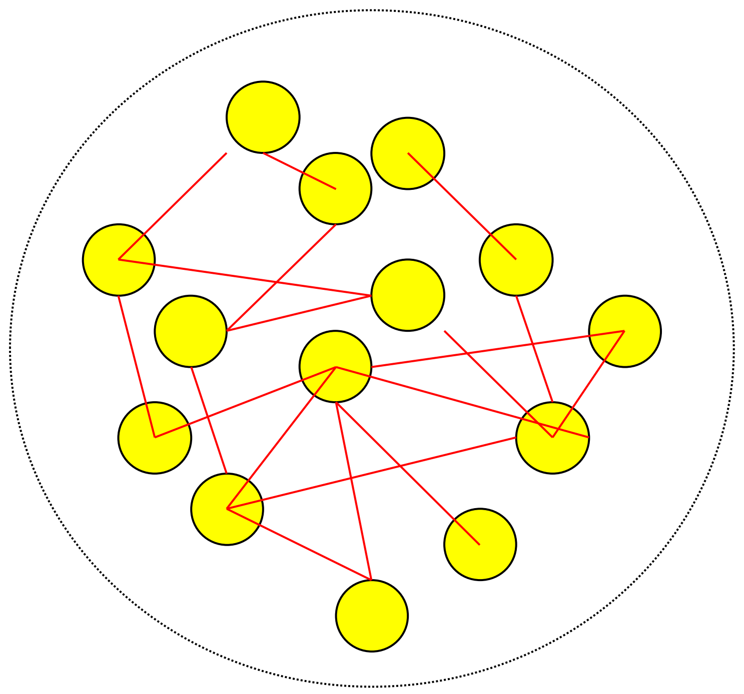




Week 10-part 3: mean-field arguments



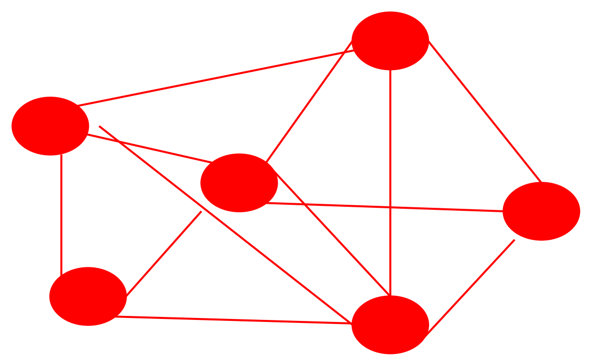
Full connectivity



Week 10-part 3: mean-field arguments

Fully connected network

blackboard



fully connected

N >> 1

Synaptic coupling

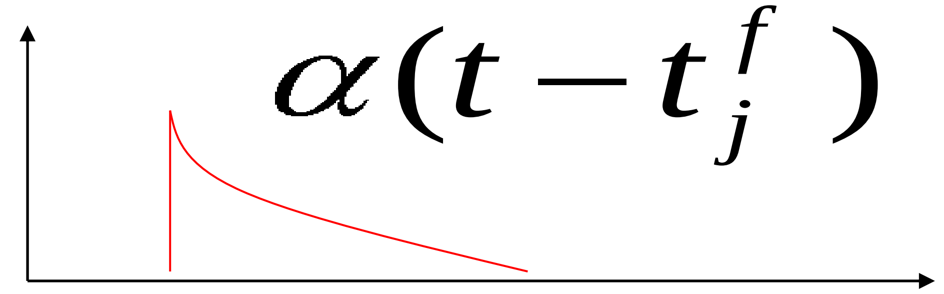
$$w_{ij} = w_0$$

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

All spikes, all neurons

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

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



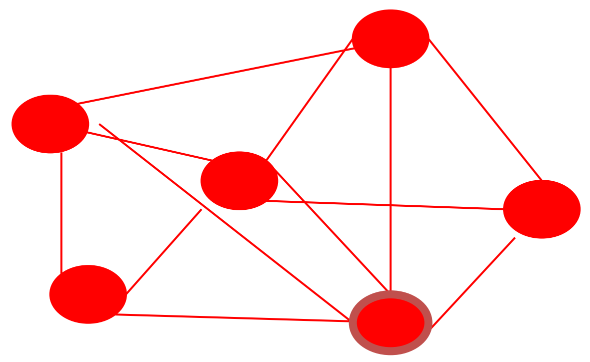
Week 10-part 3: mean-field arguments

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

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

Index i disappears

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



All spikes, all neurons

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

Week 10-part 3: stationary state/asynchronous activity

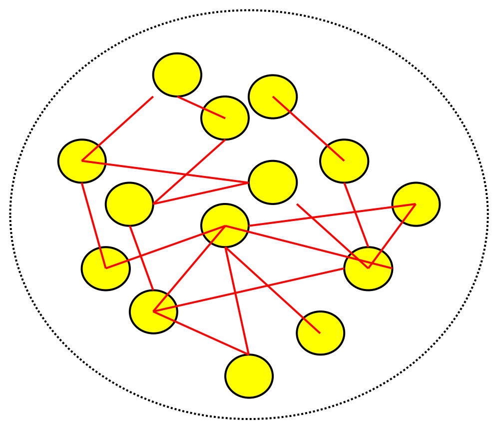
$$I_0 = [J_0 q A_0 + I_0^{ext}]$$

Homogeneous network

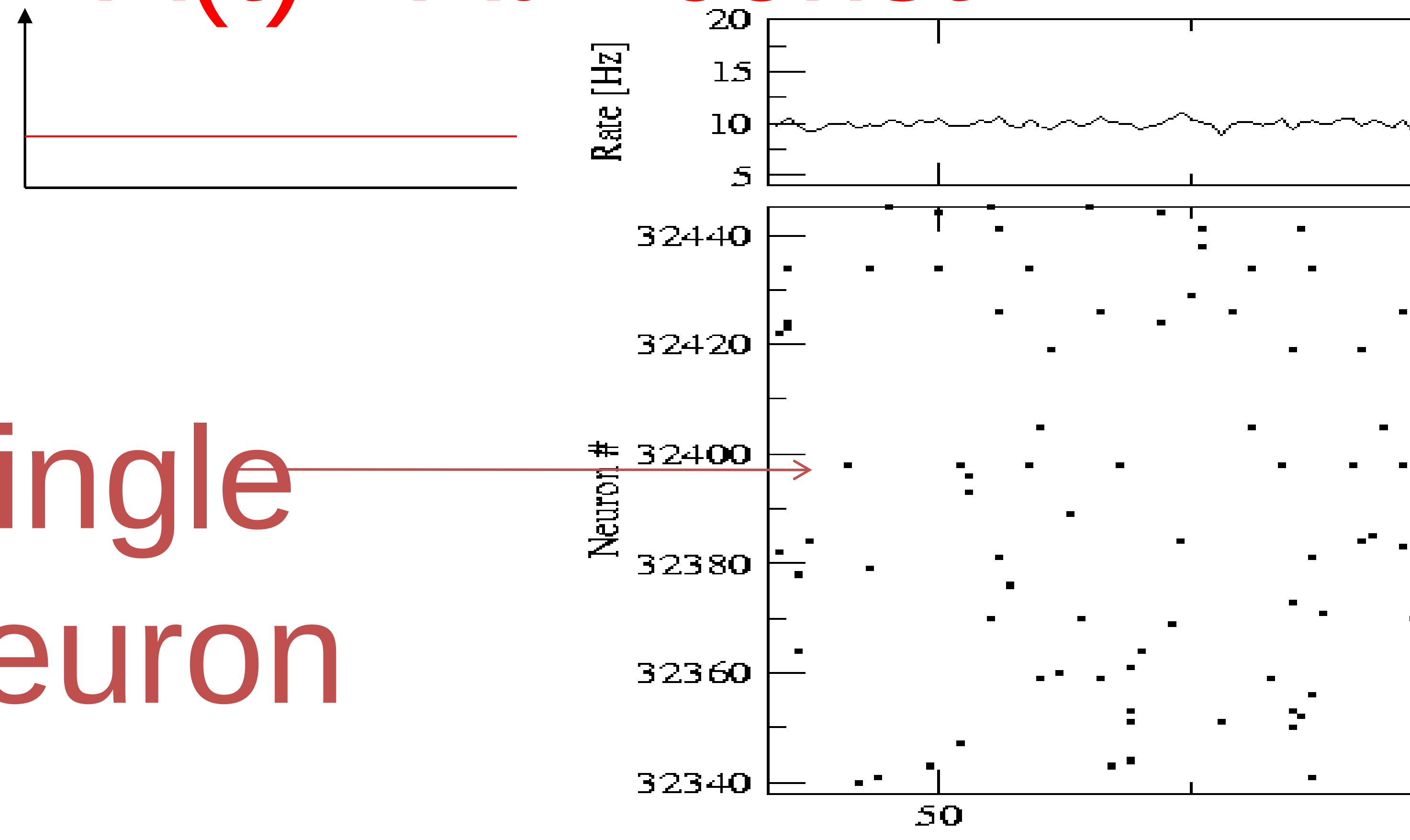
All neurons are identical,

Single neuron rate = population rate

$$\boxed{\nu = g(I_0) = A_0}$$



A(t)= A_0= const



Single neuron

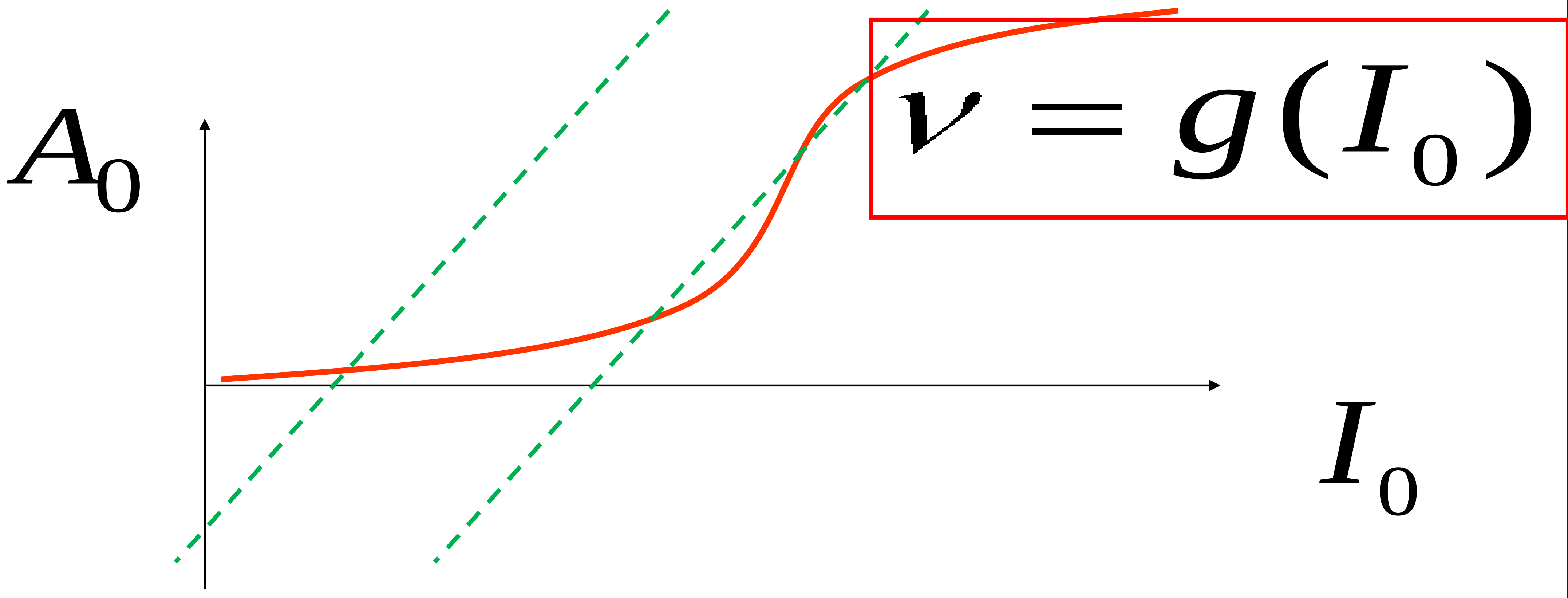
blackboard

frequency (single neuron) $\nu = \langle s \rangle^{-1} = \left[\int_0^\infty s \, P_I(\hat{t} + s \,|\, \hat{t}) \, ds \right]^{-1} = g(h_0)$

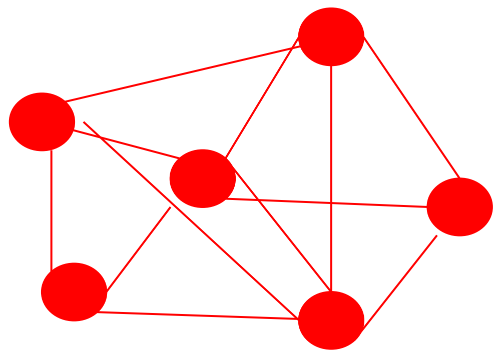
Stationary solution

$$\boxed{\nu = g(I_0)}$$

$$\boxed{\nu = A_0}$$



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



fully connected

N >> 1

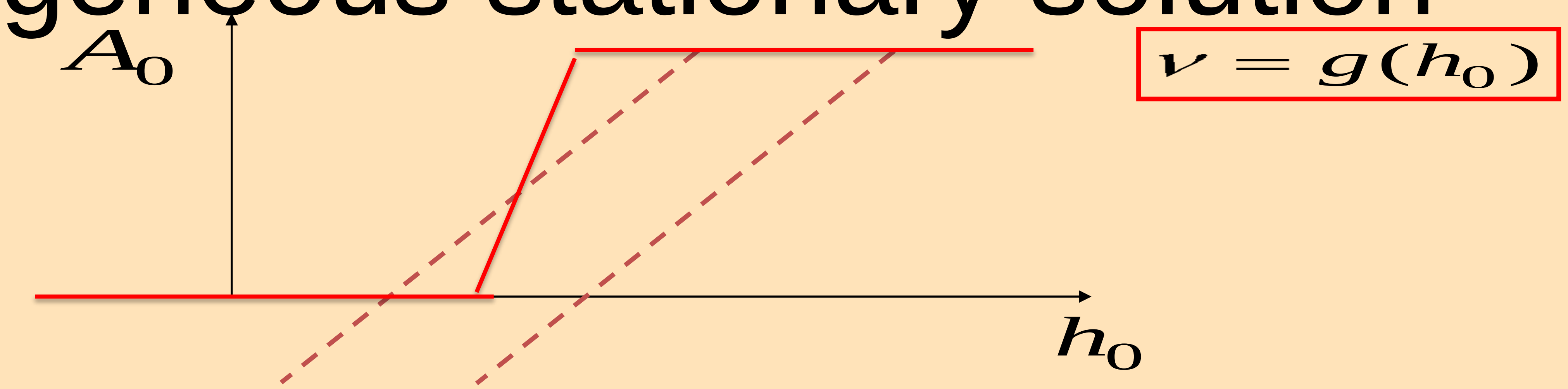
Homogeneous network, stationary,
All neurons are identical,
Single neuron rate = population rate

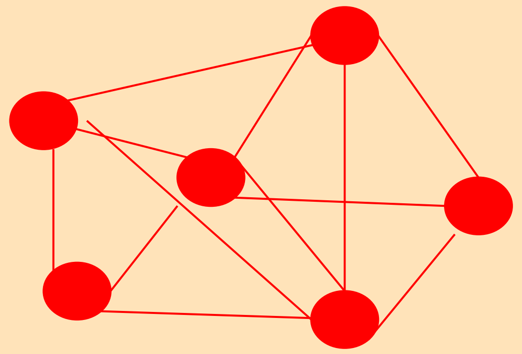
$$\boxed{\nu = g(I_0) = A_0}$$

Exercise 1, now

Next lecture: 11h15

Exercise 1: homogeneous stationary solution





fully connected

N >> 1

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

$$\boxed{\nu = A_0}$$

Single Population

- population activity, definition
- full connectivity
- stationary state/asynchronous state

Single neuron rate = population rate

$$\boxed{\nu = g(I_0) = A_0}$$

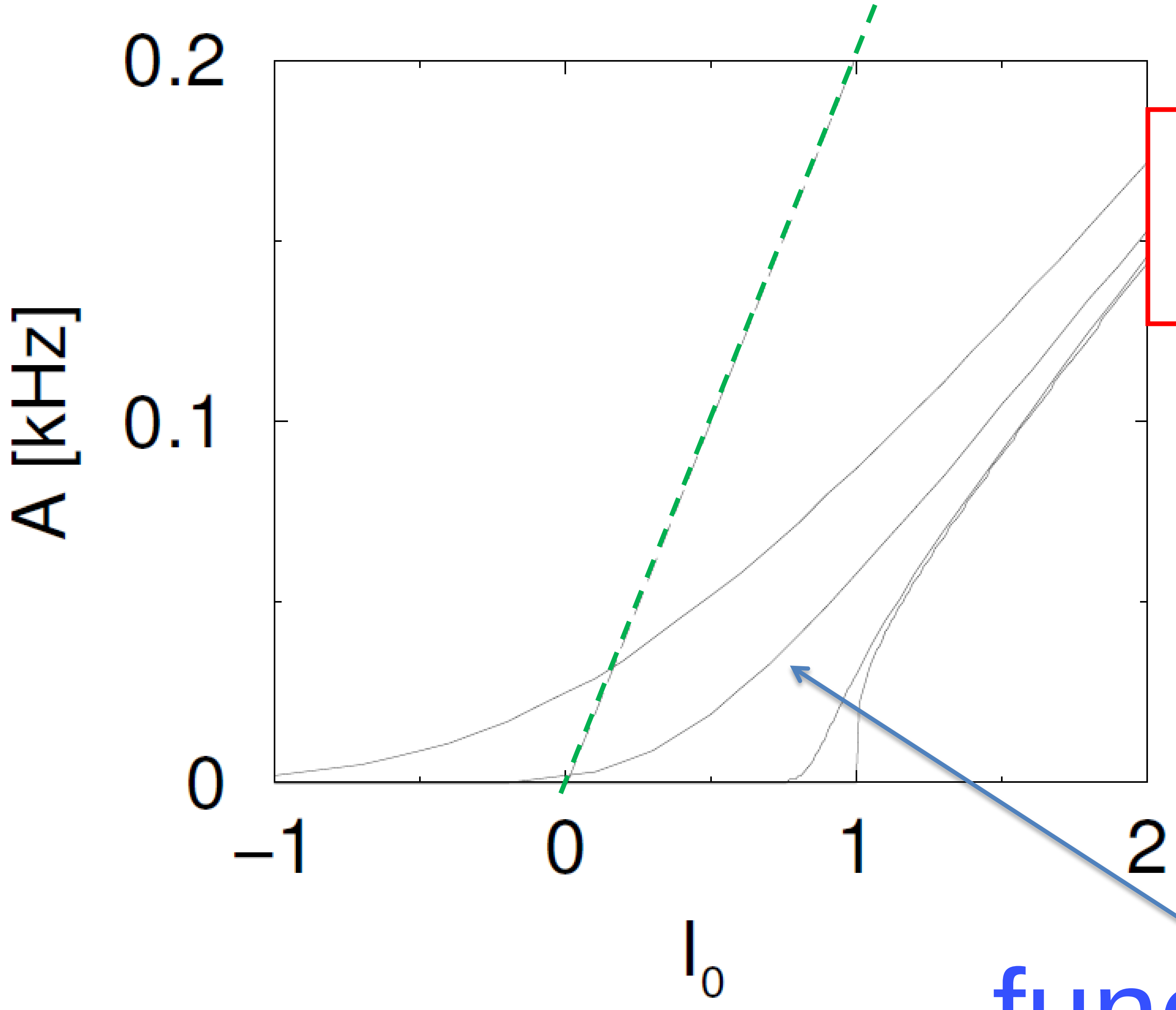
What is this function g?

Examples:
- leaky integrate-and-fire with diffusive noise
- Spike Response Model with escape noise
- Hodgkin-Huxley model (see week 2)

Week 10-part 3: mean-field, leaky integrate-and-fire

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

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

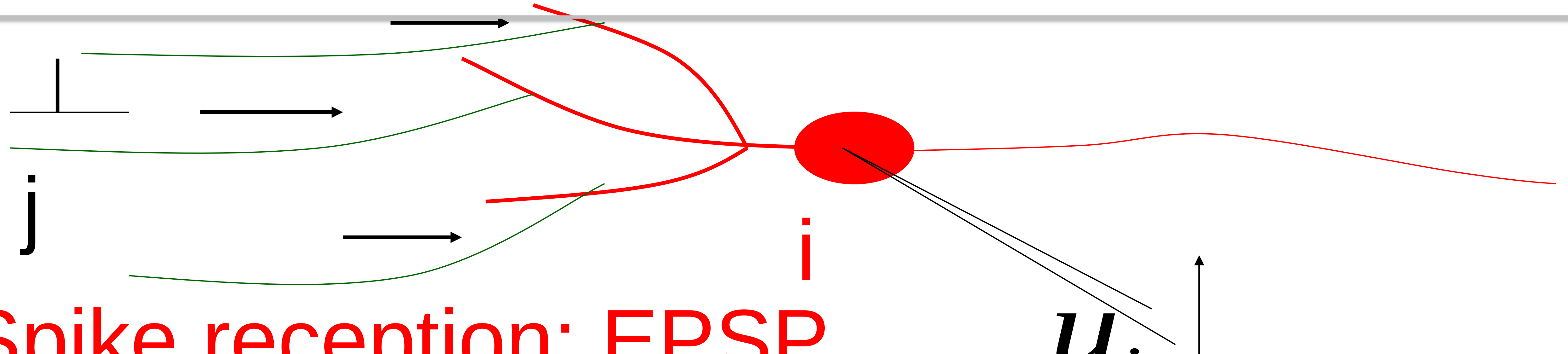


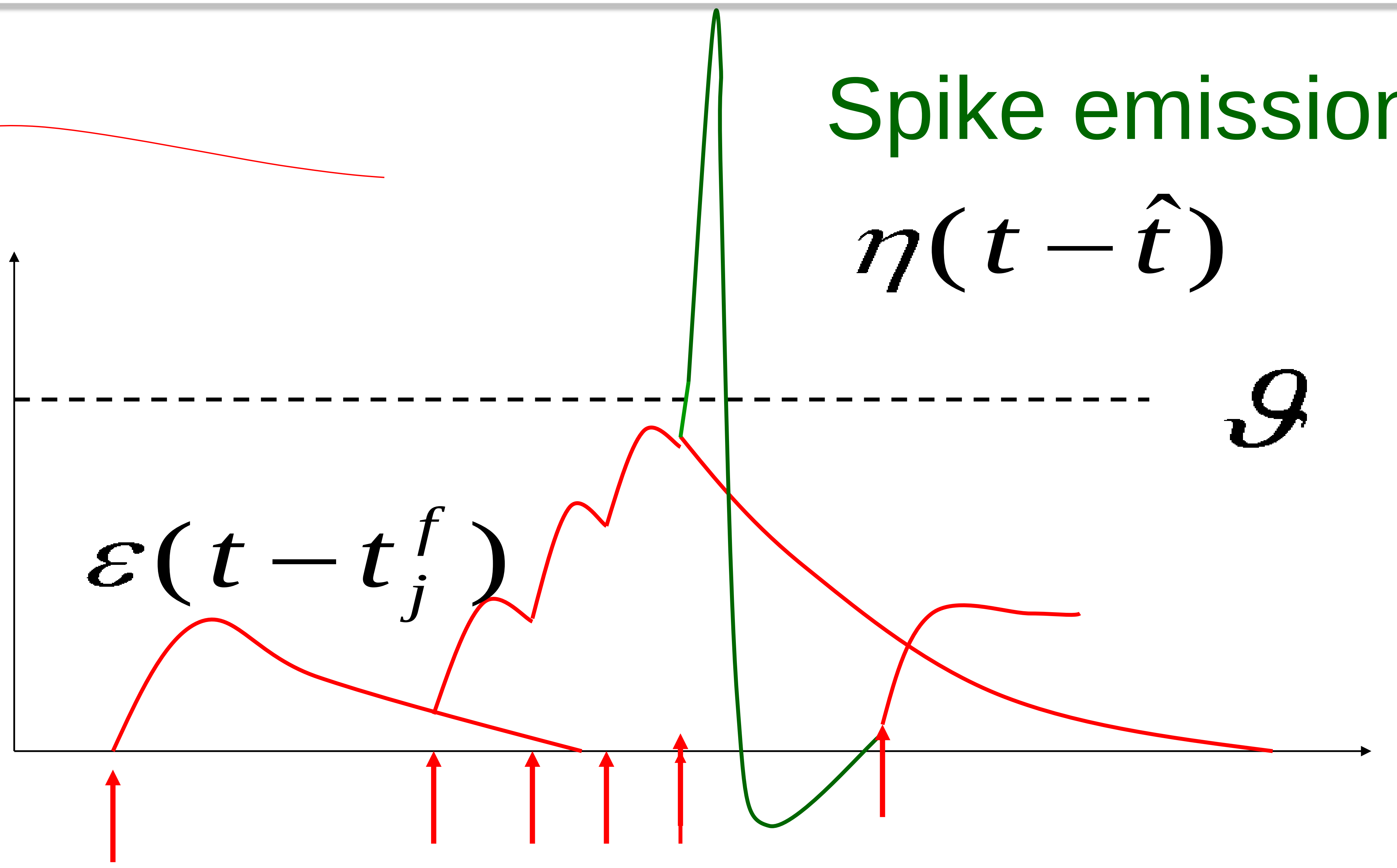
$$\boxed{\nu = g_\sigma(I_0)}$$

different noise levels

function *g* can be calculated

Review: Spike Response Model with Escape Noise

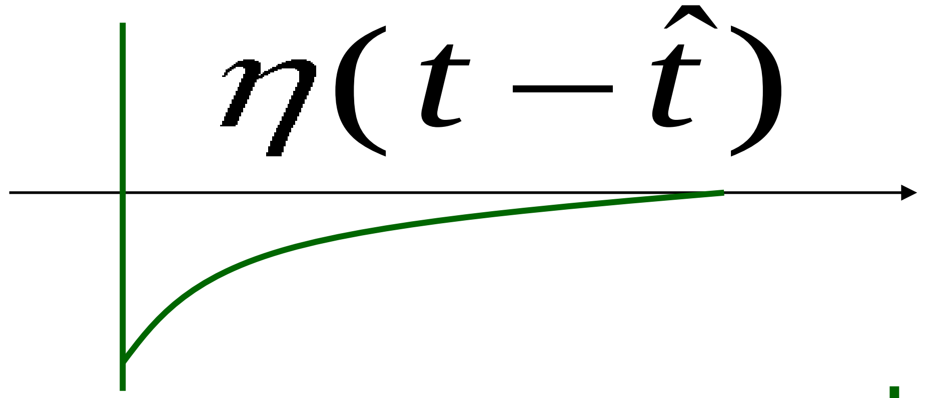




Spike reception: EPSP

$$\varepsilon(t-t_j^f) = \exp[-\frac{t-t_j^f}{\tau}]$$

Spike emission: AP



Last spike of i

All spikes, all neurons

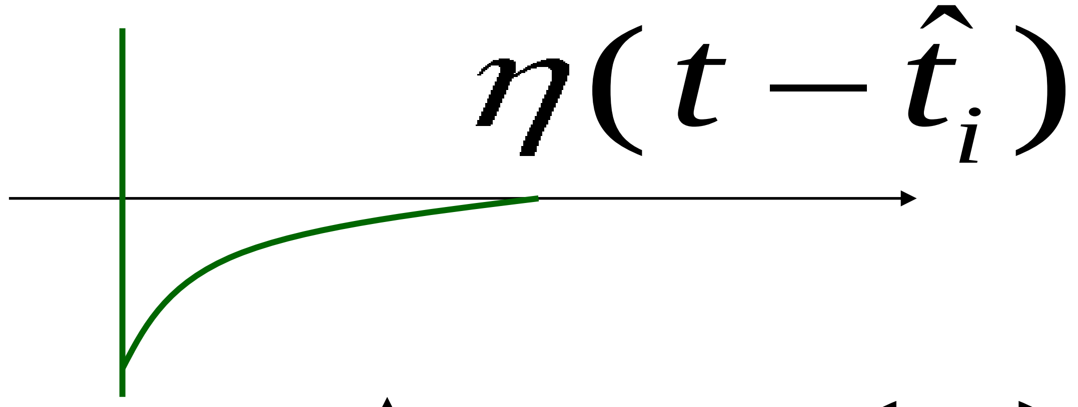
$$u_i(t) = \underline{\eta(t-\hat{t}_i)} + \sum_j \sum_f w_{ij}\, \underline{\varepsilon(t-t_j^f)}$$

Firing intensity

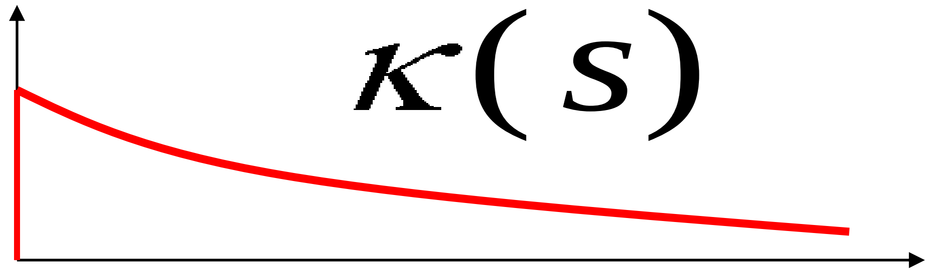
$$\rho(t\,|\,u) = f(u-\vartheta)$$

Review: Spike Response Model with Escape Noise

Spike emission: AP



Response to current pulse



Blackboard
-Renewal model
-Interval distrib.

potential Last spike of i external input

$$u_i(t|\hat{t}_i) = \underline{\eta(t-\hat{t}_i)} + \int \underline{\kappa(s)}\, I(t-s)\,ds$$

potential Last spike of i input potential

$$u_i(t|\hat{t}_i) = \underline{\eta(t-\hat{t}_i)} + \underline{h(t)}$$

instantaneous rate

$$\rho(t) = f(h(t)) = \rho_0 \exp\left(\frac{h(t)-\vartheta}{\Delta}\right)$$

Week 10-part 3: Example - Asynchronous state in SRM0

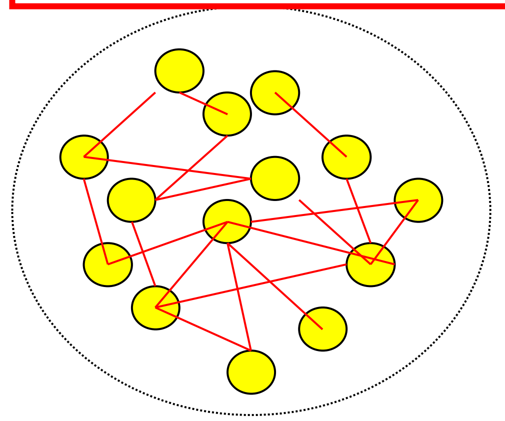
$$h_0 = RI_0 = R\,[J_0 q\, A_0 + I_0^{ext}\ ]$$

Homogeneous network

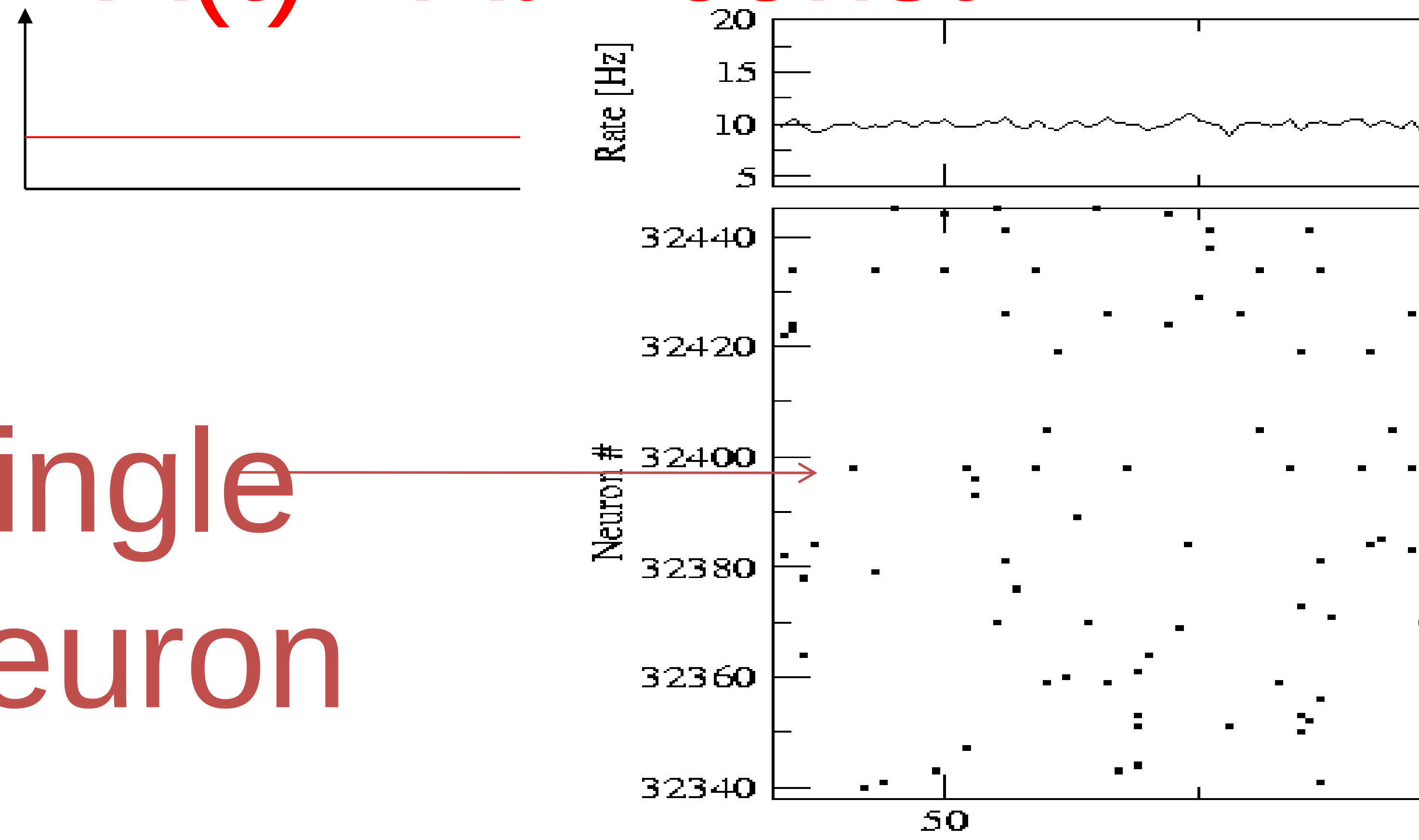
All neurons are identical,

Single neuron rate = population rate

$$\boxed{\nu = g(I_0) = A_0}$$



A(t)= A_0= const



Single neuron

frequency (single neuron)

$$\nu = \langle s \rangle^{-1} = \left[\int_0^\infty s\, P_I(\hat{t}+s \,|\, \hat{t})\, ds\right]^{-1} = g(I_0)$$

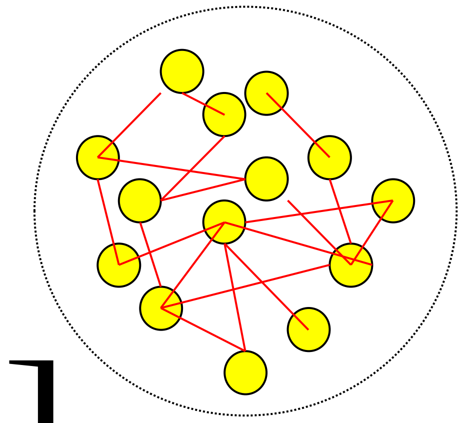
Week 10-part 3: Example - Asynchronous state in SRM0

input potential

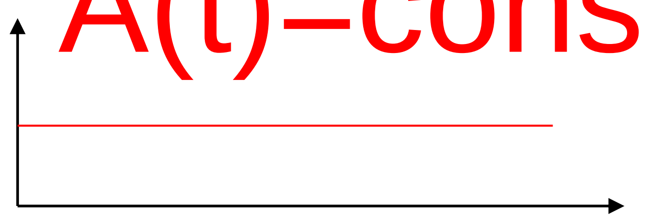
$$u(t\,|\hat{t}\,) = \eta(t-\hat{t}) + h_0$$

$$h_0 = RI_0 = R\,[J_0 q\, A_0 + I_0^{ext}\,]$$

$$\boxed{A_0 = \frac{1}{J_0 qR}[h_0 - RI_0^{ext}\,]}$$



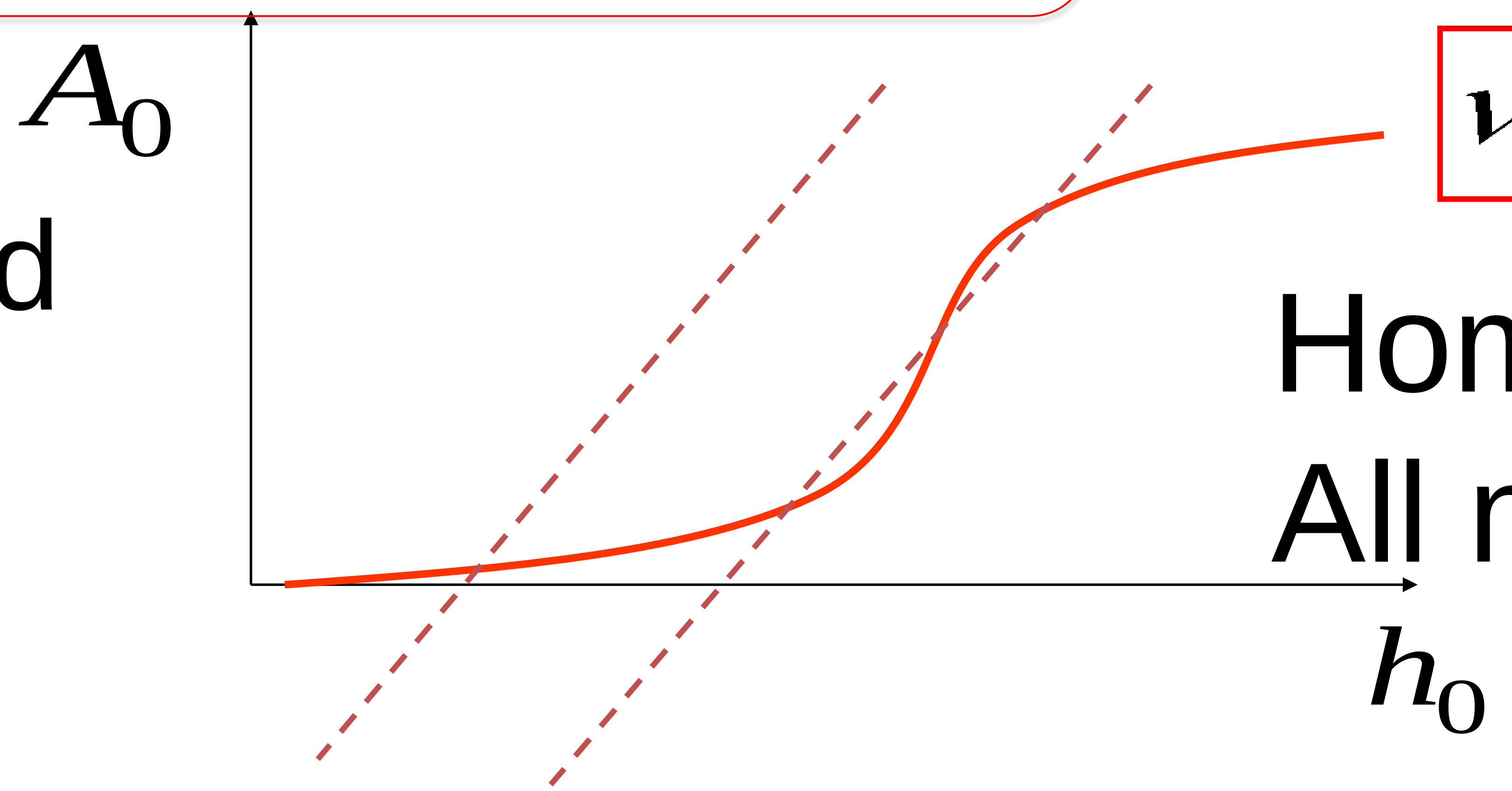
fully connected



$$\int \alpha(s)ds = q$$

$$\boxed{\nu = \tilde{g}(h_0)}$$

typical mean field
(Curie Weiss)



Homogeneous network
All neurons are identical,

frequency (single neuron)

$$\nu = \langle s\rangle^{-1} = \left[\int_0^\infty s\,P_I\ \hat{t}+s\,|\,\hat{t}\ \ ds\right]^{-1} = \tilde{g}(h_0)$$

Week 10 – part 4 : Random networks

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Biological Modeling of Neural Networks:

Week 10 – Neuronal Populations

Wulfram Gerstner

EPFL, Lausanne, Switzerland

10.1 Cortical Populations
- columns and receptive fields

10.2 Connectivity
- cortical connectivity
- model connectivity schemes

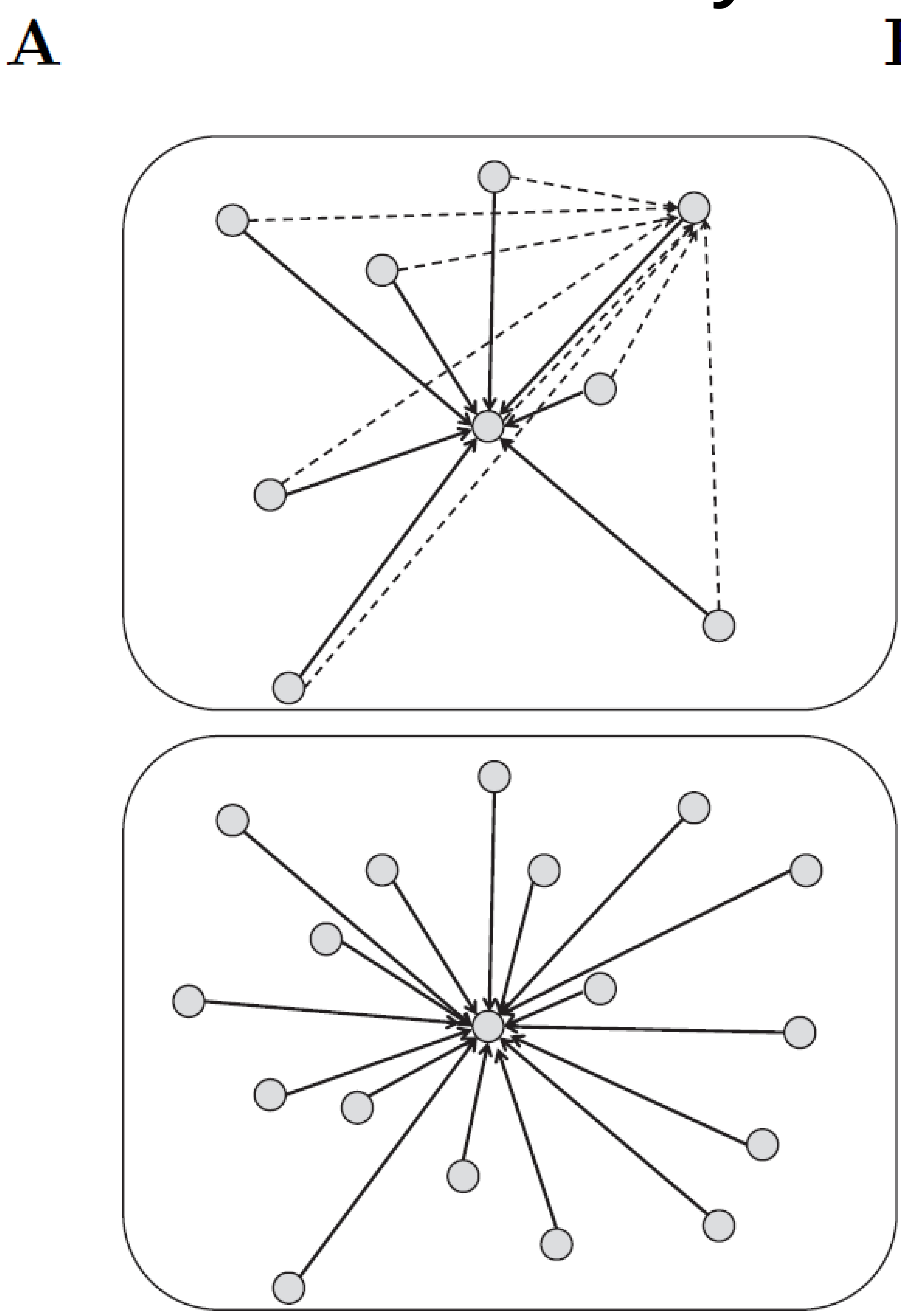
10.3 Mean-field argument
- asynchronous state

10.4 Random networks
- balanced state

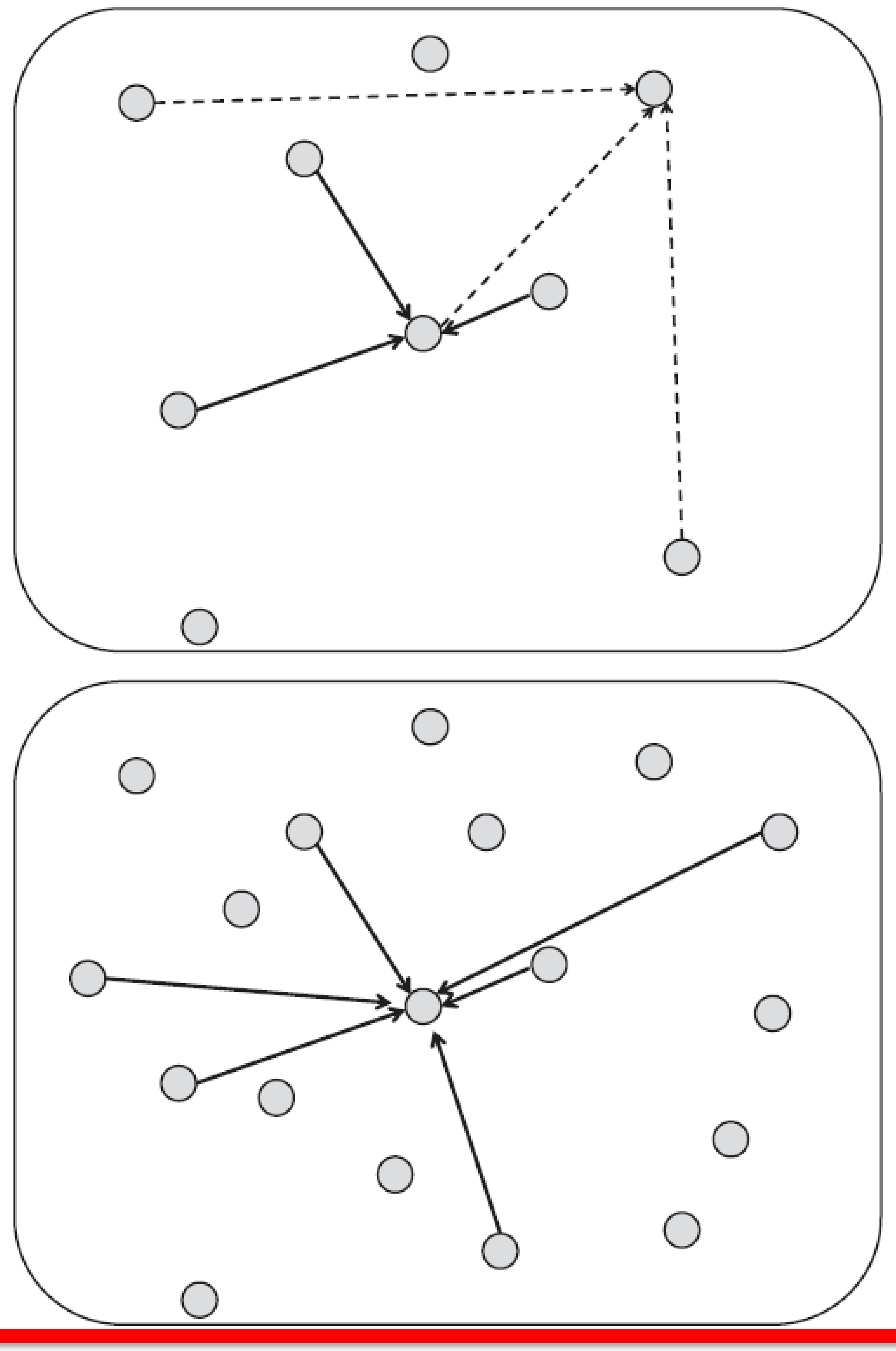
Week 10-part 4: mean-field arguments – random connectivity

random connectivity

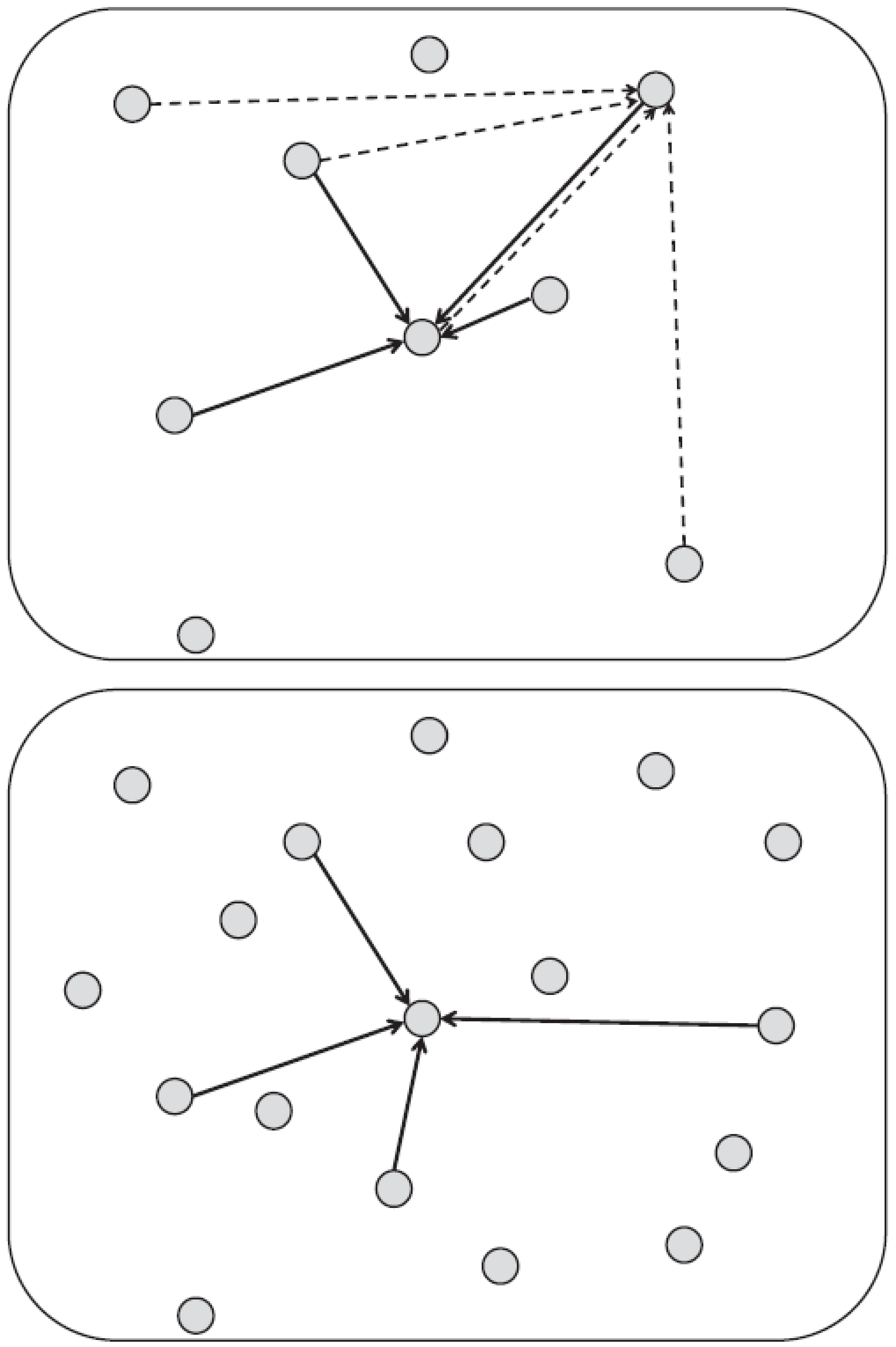
full connectivity



random: prob p fixed



random: number K of inputs fixed



Week 10-part 4: mean-field arguments – random connectivity

I&F with diffusive noise
(stochastic spike arrival)

Blackboard:
excit. – inhib.

For any arbitrary neuron in the population

$$\tau \frac{d}{dt} I_i = -I_i + \sum_{k,f} w_{ik} q_e \delta(t - t_k^f) - \sum_{k',f'} w_{ik'} q_i \delta(t - t_{k'}^{f'})$$

EPSC

IPSC

excitatory input spikes

Week 10-Exercise 2.1/2.2 now: Poisson/random ne

Next lecture: 11h40

random: prob p fixed

Exercises

2. **1. Fully connected network.** *Assume a fully connected network of N Poisson neurons with firing rate $\nu_i(t) = g(I_i(t)) > 0$. Each neuron sends its output spikes to all other neurons as well as back to itself. When a spike arrives at the synapse from a presynaptic neuron j to a postsynaptic neuron i is, it generates a postsynaptic current*

$$I_i^{\text{syn}} = w_{ij} \exp[-(t - t_j^{(f)})/\tau_s] \quad \text{for} \quad t > t_j^{(f)}, \tag{12.39}$$

where $t_j^{(f)}$ is the moment when the presynaptic neuron j fired a spike and τ_s is the synaptic time constant.

a) Assume that each neuron in the network fires at the same rate ν. Calculate the mean and the variance of the input current to neuron i.

Hint: Use the methods of Chapter 8

b) Assume that all weights of equal weight $w_{ij} = J_0/N$. Show that the mean input to neuron i is independent of N and that the variance decreases with N.

c) Evaluate mean and variance and the assumption that the neuron receives 4 000 inputs at a rate of 5Hz. The synaptic time constant is 5ms and $J_0 = 1\mu A$.

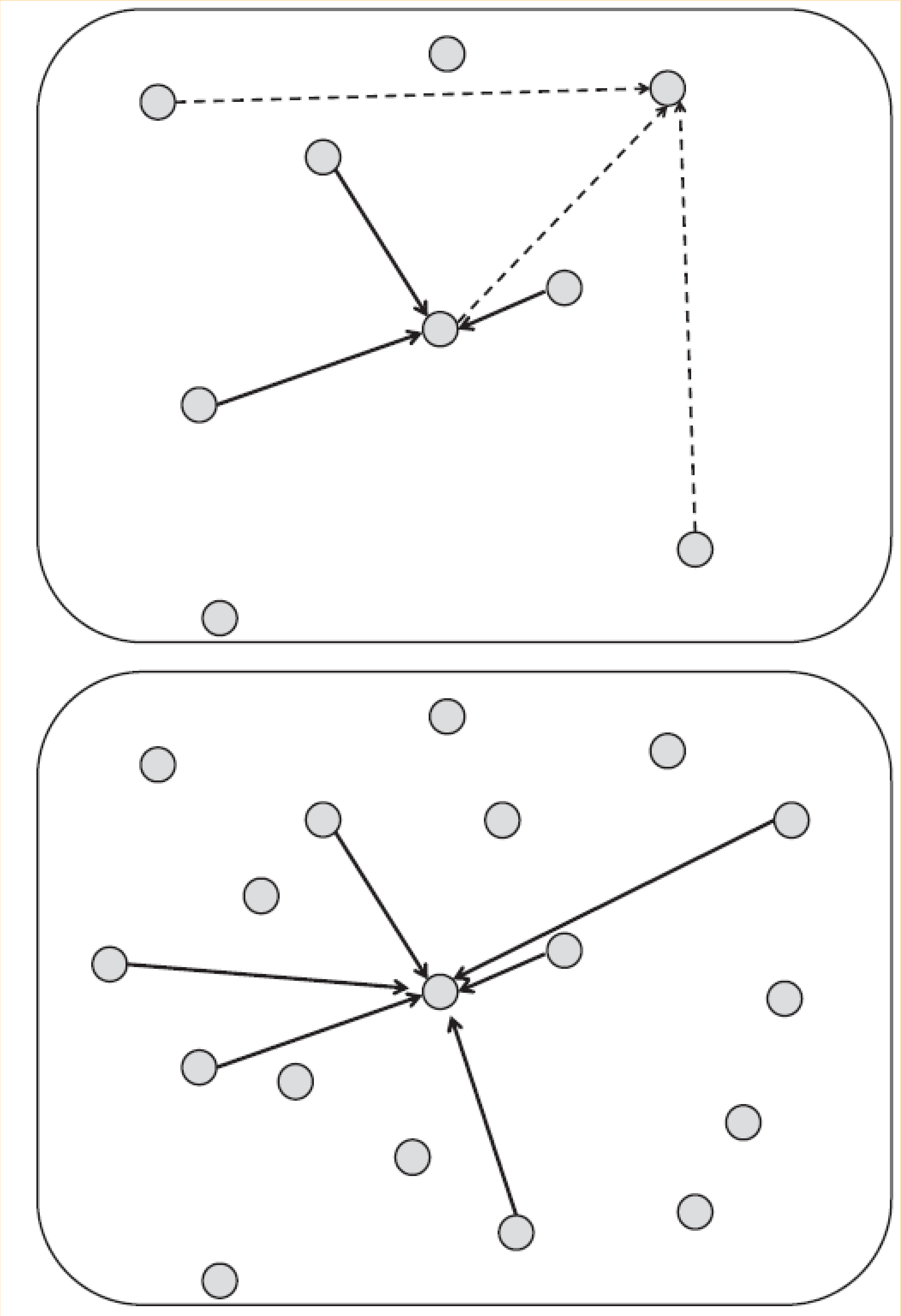
3. **2. Stochastically connected network.** *Consider a network analogous to that discussed in the previous exercise, but with a synaptic coupling current*

$$I_i^{\text{syn}} = w_{ij} \left\{ \left(\frac{1}{\tau_1}\right) \exp[-(t - t_j^{(f)})/\tau_1] - \left(\frac{1}{\tau_2}\right) \exp[-(t - t_j^{(f)})/\tau_2] \right\} \quad \text{for} \quad t > t_j^{(f)}, \tag{12.40}$$

which contains both an excitatory and an inhibitory component.

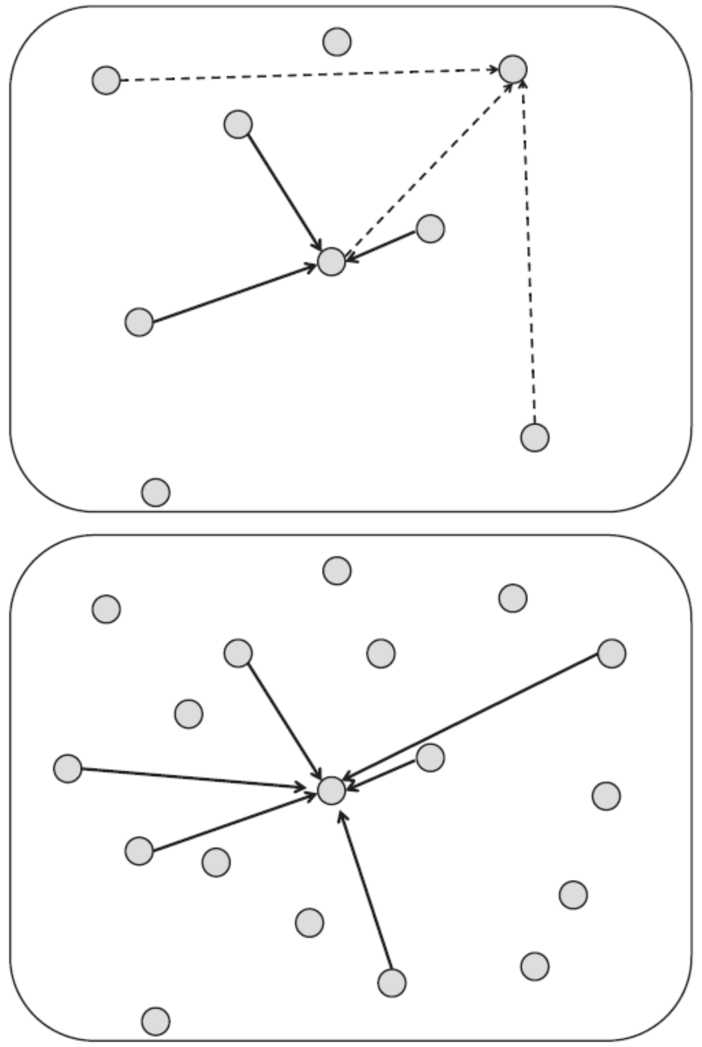
a) Calculate the mean synaptic current and its variance assuming arbitrary coupling weights w_{ij}. How do mean and variance depend upon the number of neurons N?

b) Assume that the weights have a value $J_0/\sqrt{N}$. How do the mean and variance of the synaptic input current scale as a function of N?



Week 10-part 4: Random Connectivity: fixed p

random: probability p=0.1, fixed $w_{ik} \sim \frac{J}{pN}$



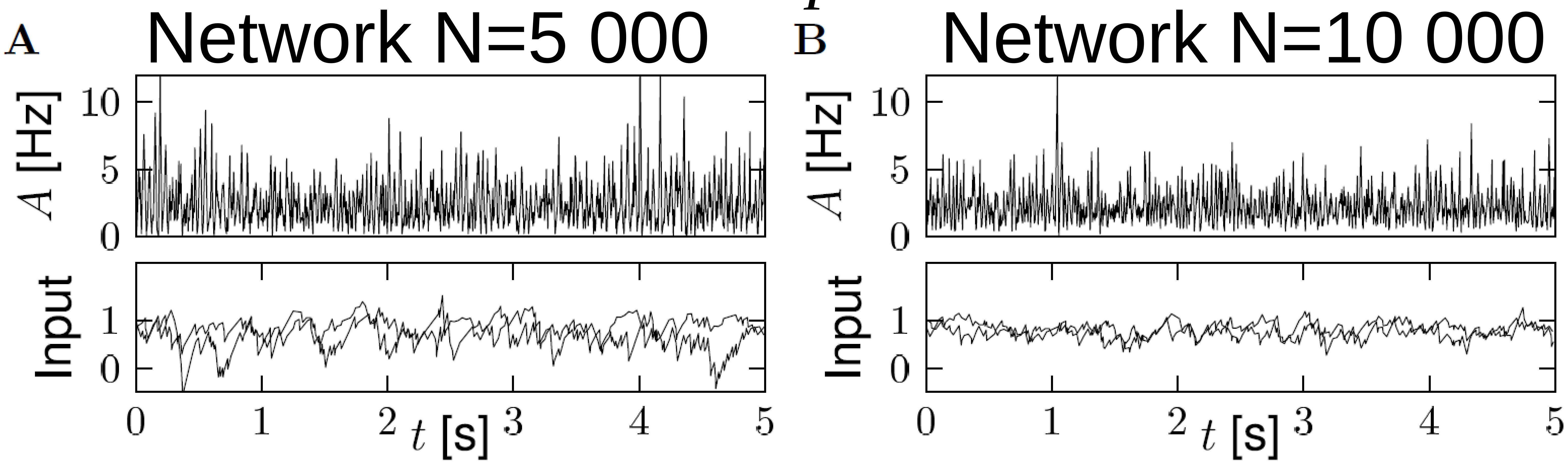


Fig. 12.7: Simulation of a model network with a fixed connection probability $p = 0.1$. **A.** Top: Population activity $A(t)$ averaged over all neurons in a network of 4 000 excitatory and 1 000 inhibitory neurons. Bottom: Total input current $I_i(t)$ into two randomly chosen

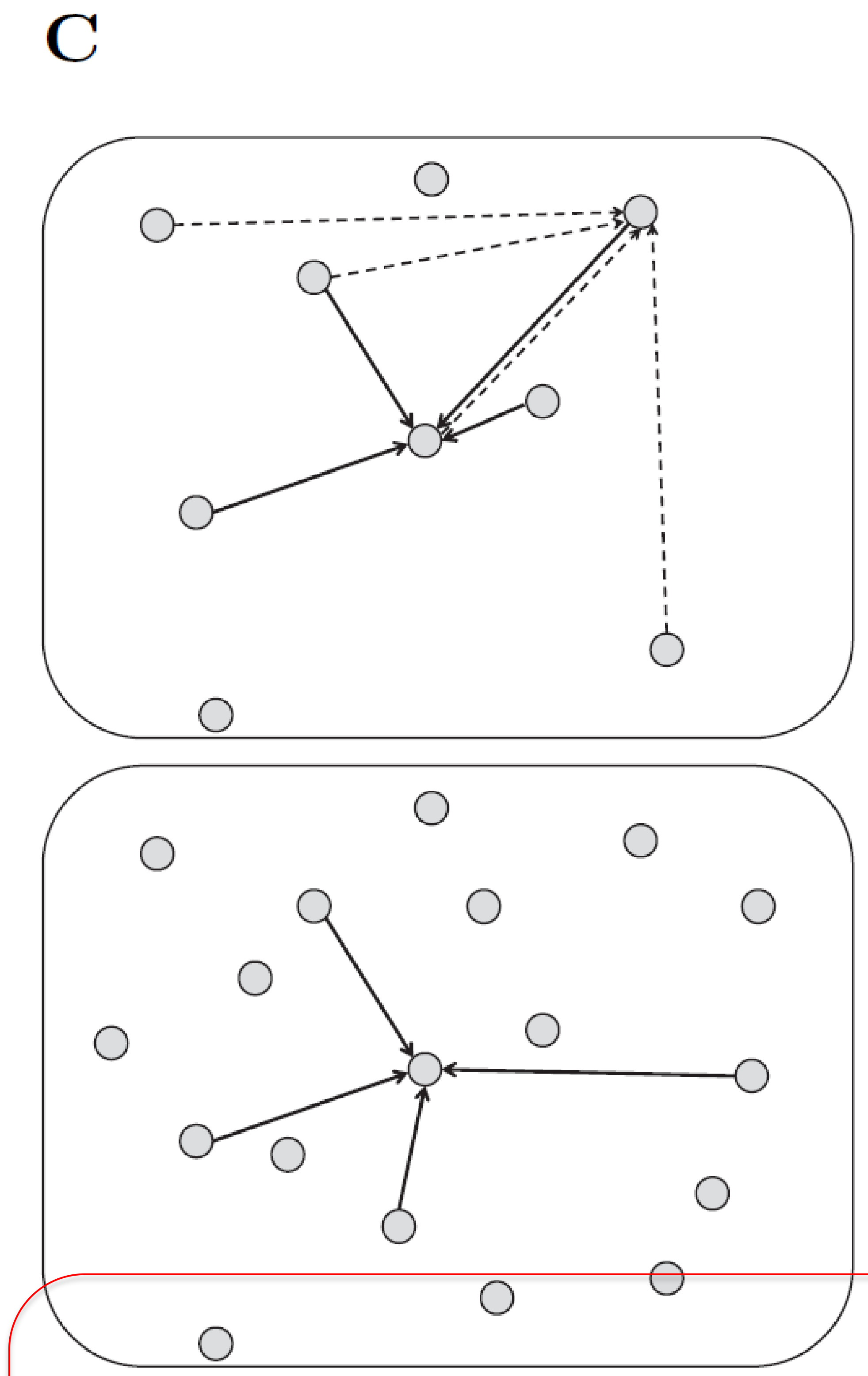
→ fluctations of *A* decrease

fluctations of *I* decrease

Image: Gerstner et al. Neuronal Dynamics (2014)

Week 10-part 4: Random connectivity – fixed number of inputs

random: number of inputs K=500, fixed $w_{ik} \sim \frac{J}{K}$



Network N=5 000

Network N=10 000

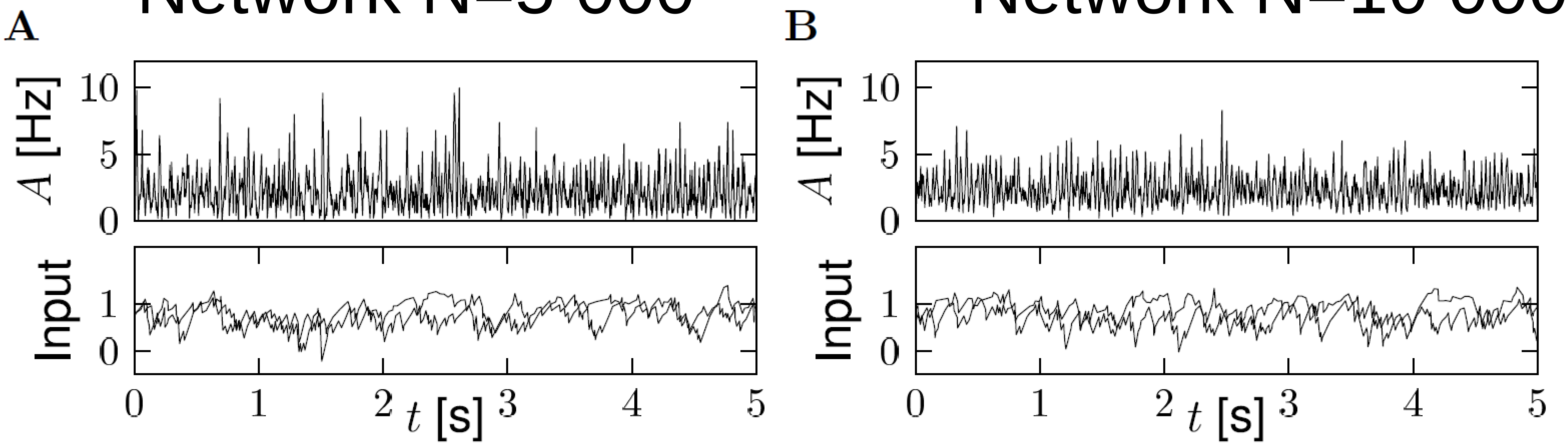


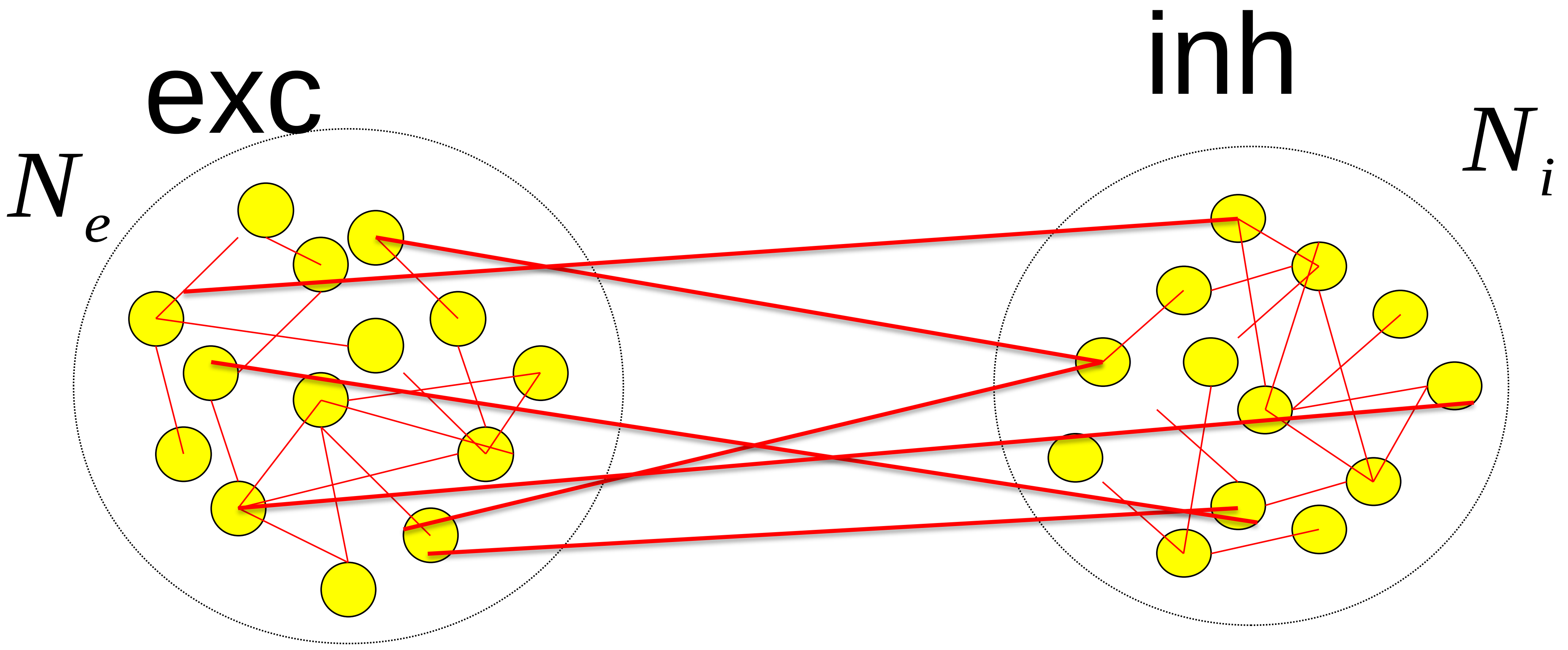
Fig. 12.8: Simulation of a model network with a fixed number of presynaptic partners (400 excitatory and 100 inhibitory cells) for each postsynaptic neuron. **A**. Top: Population activity $A(t)$ averaged over all neurons in a network of 4 000 excitatory and 1 000 inhibitory

Image: *Gerstner et al. Neuronal Dynamics (2014)*

→ fluctations of *A* decrease

fluctations of *I* remain

Week 10-part 4: Connectivity schemes – fixed p, but balanced



$$\tau \frac{d}{dt} u_i = -u_i + R\Big(\sum_{k,f} w_{ik} q_e \delta(t - t_k^f) - \sum_{k',f'} w_{ik'} q_i \delta(t - t_{k'}^{f'})\Big) + I^{ext}$$

make network bigger, but

-keep mean input close to zero

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

-keep variance of input

$$w_{ik} \sim \frac{J_e}{\sqrt{pN_e}} \qquad J_e = 'random'$$

$$w_{ik} \sim \frac{J_i}{\sqrt{pN_i}} \qquad J_i = 'random'$$

Week 10-part 4: Connectivity schemes - balanced

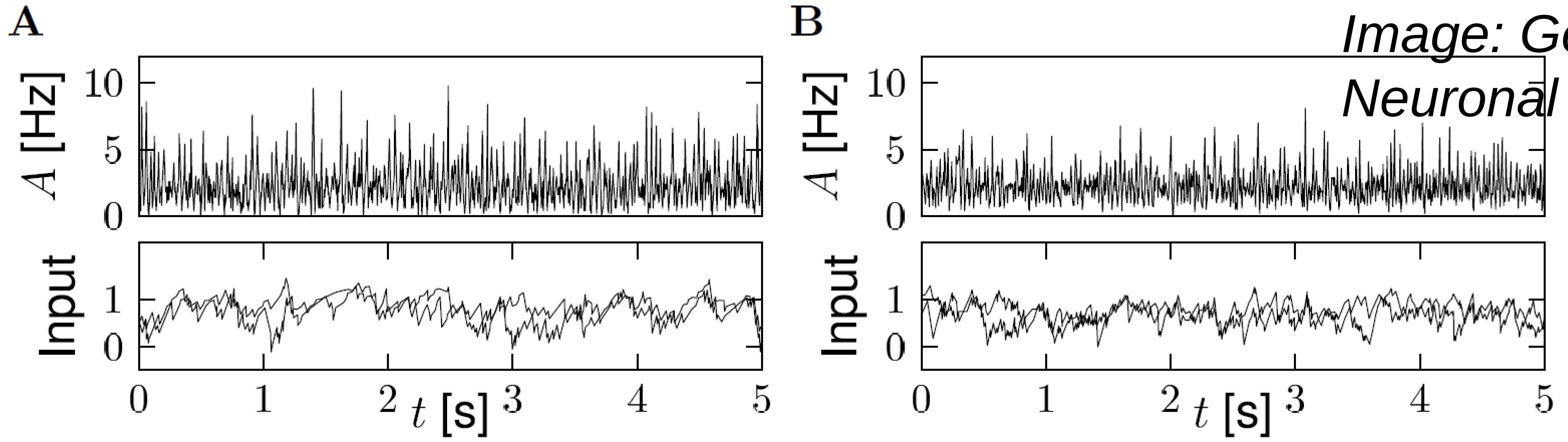


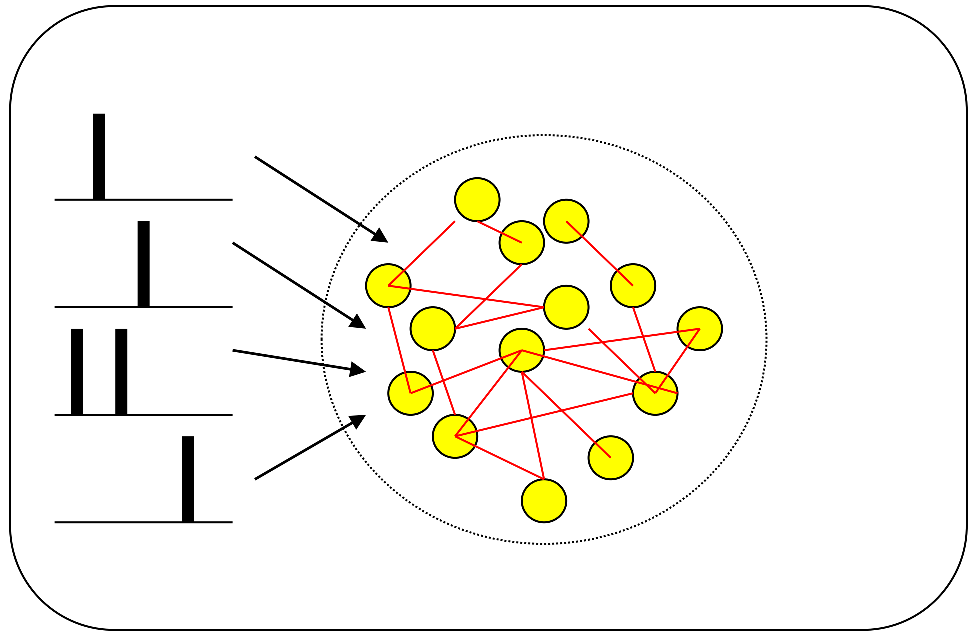
Image: Gerstner et al. Neuronal Dynamics (2014)

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* decrease, but 'smooth'

Week 10-part 4: leaky integrate-and-fire, balanced random network



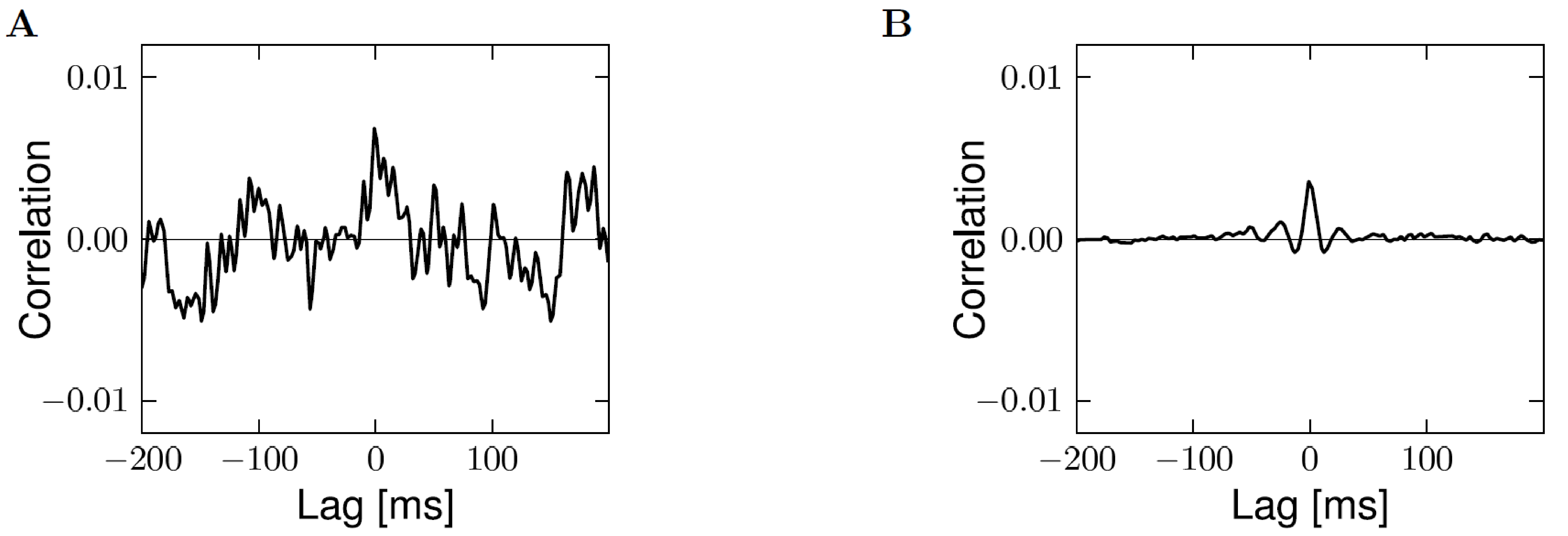


Fig. 12.18: Pairwise correlation of neurons in the Vogels-Abbott network. **A**. Excess

Network with balanced excitation-inhibition
- 10 000 neurons
- 20 percent inhibitory
- **randomly connected**

Image: Gerstner et al. Neuronal Dynamics (2014)

Week 10-part 4: leaky integrate-and-fire, balanced random network

Image: Gerstner et al.
Neuronal Dynamics (2014)

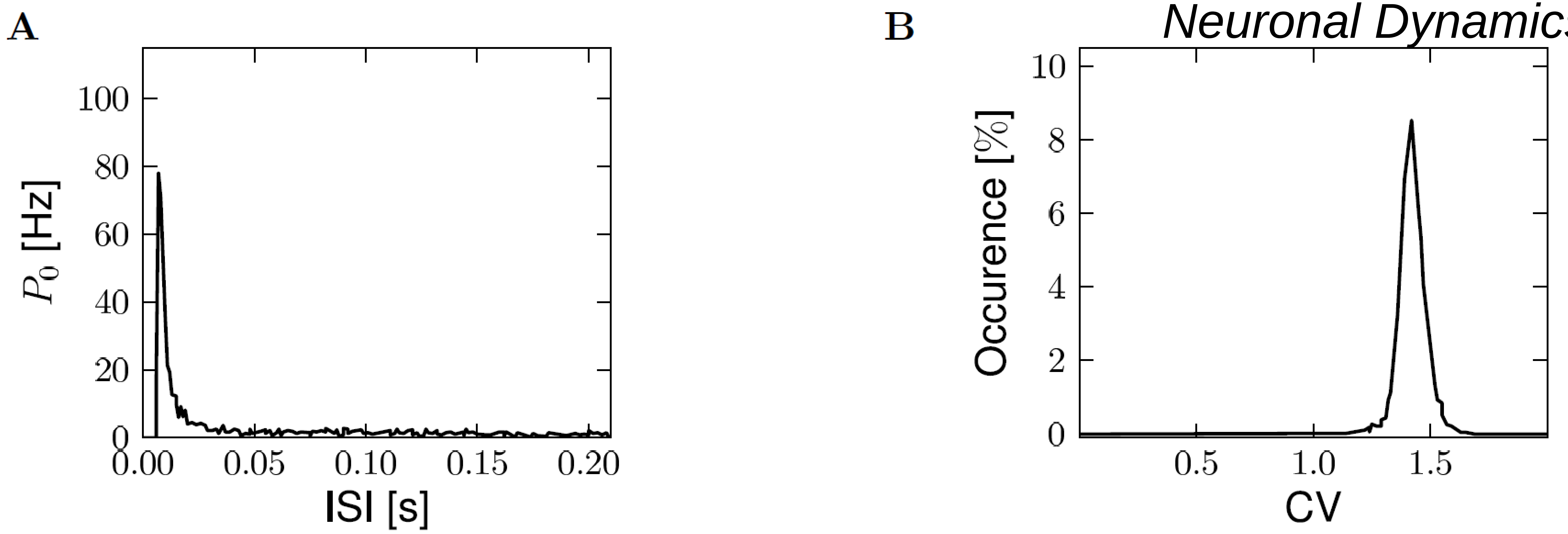


Fig. 12.19: Interspike interval distributions in the Vogels-Abbott network. **A**. Interspike interval distribution of a randomly chosen neuron. Note the long tail of the distribution. The width of the distribution can be characterized by a coefficient of variation of $CV = 1.9$. **B**. Distribution of the CV index across all 10 000 neurons of the network. Bin width of

Week 10 – Introduction to Neuronal Populations

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The END

Course evaluations

10.1 Cortical Populations
- columns and receptive fields

10.2 Connectivity
- cortical connectivity
- model connectivity schemes

10.3 Mean-field argument
- asynchronous state

10.4 Random Networks
- Balanced state