Biological Modeling of Neural Networks

ÉCOLE POLYTECHNIQUE FÉDÉRALE DE LAUSANNE

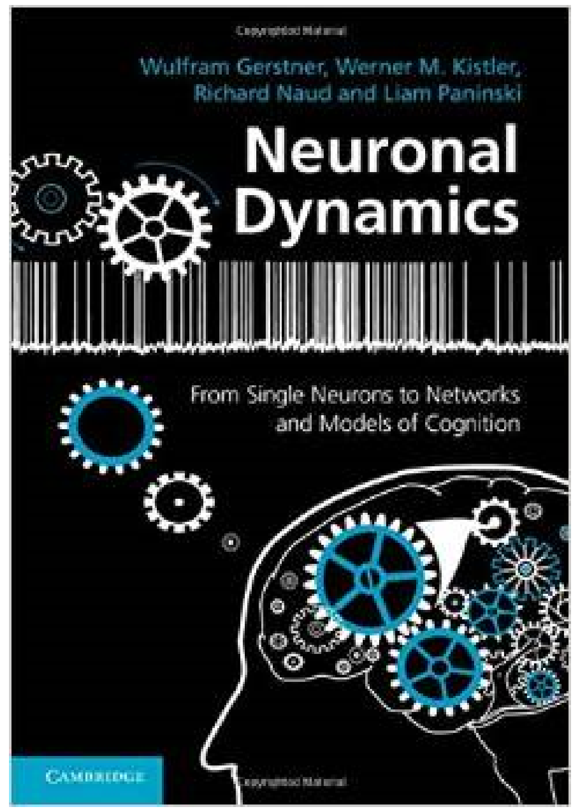
Week 8 – Continuum models: Cortical fields and perception

Wulfram Gerstner

EPFL, Lausanne, Switzerland

Reading for week 8:
NEURONAL DYNAMICS
Ch. 18 +
+Ch. 12.3.7+Ch 15.1-15.2.3

Cambridge Univ. Press



8.1. Aims and challenges
- review: mean-field arguments

8.2. Transients
- generalized integrate-and-fire model
- transients can be sharp or slow

8.3. Spatial continuum (cortex)
- orientation columns

8.4. Spatial cotinuum (model)
- field equations

8.5. Solution types
- uniform solution
- bump solution

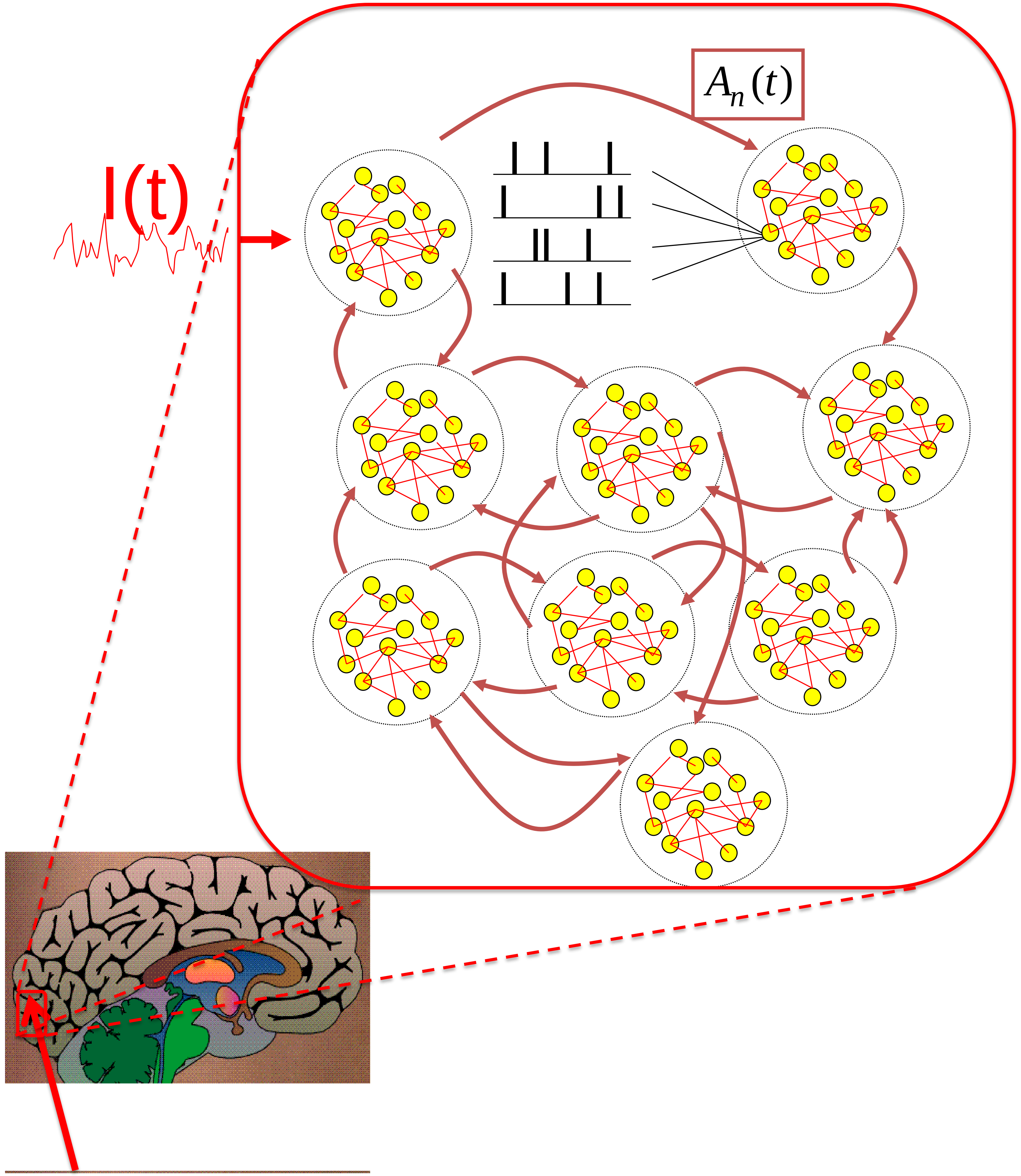
8.6. Perception

8.7. Head direction cells

8.1: Aims and Challenges; Interacting Populations

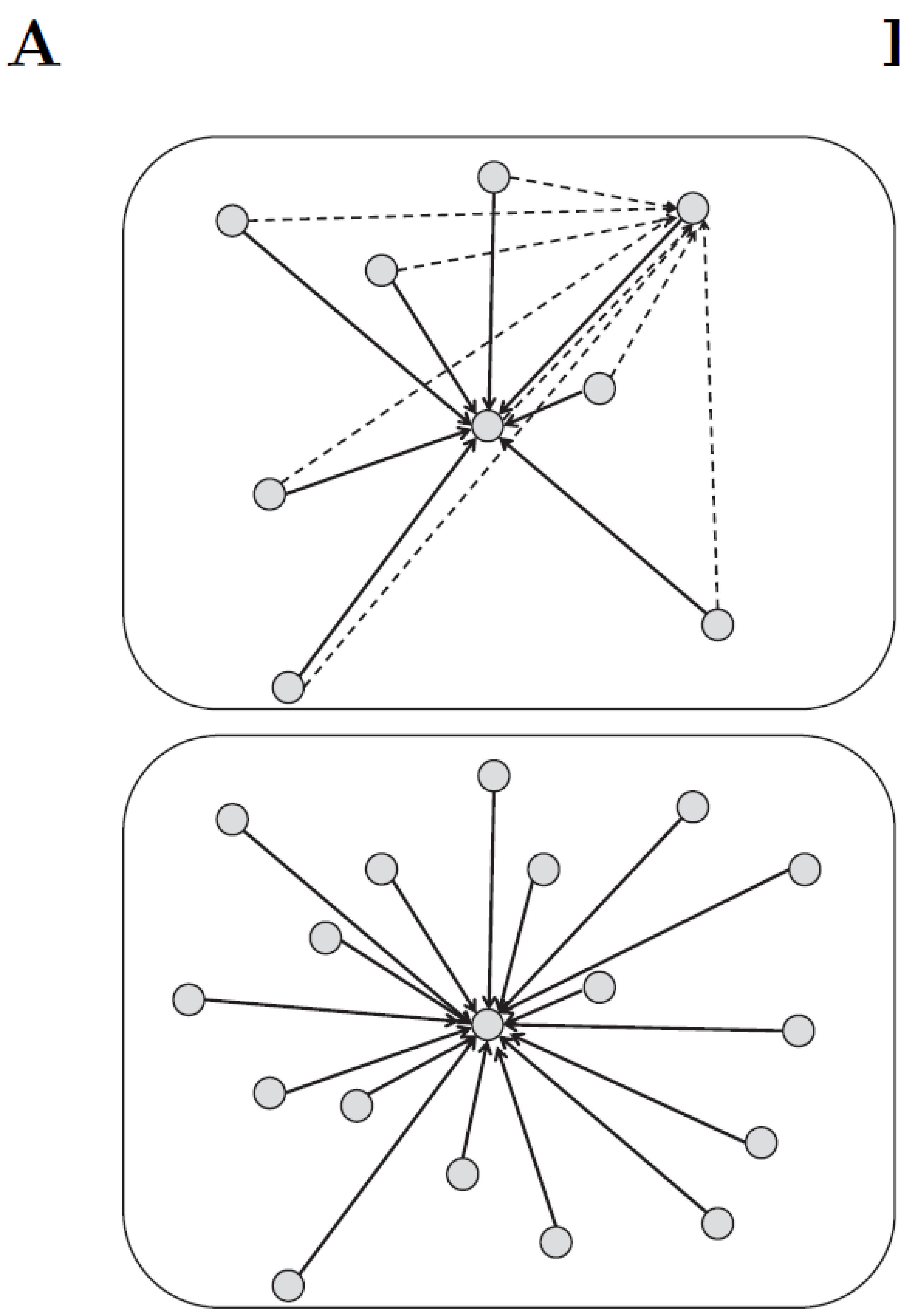
Sense of direction
→ internal compass

Perception
→weak contrasts
→world is continuous

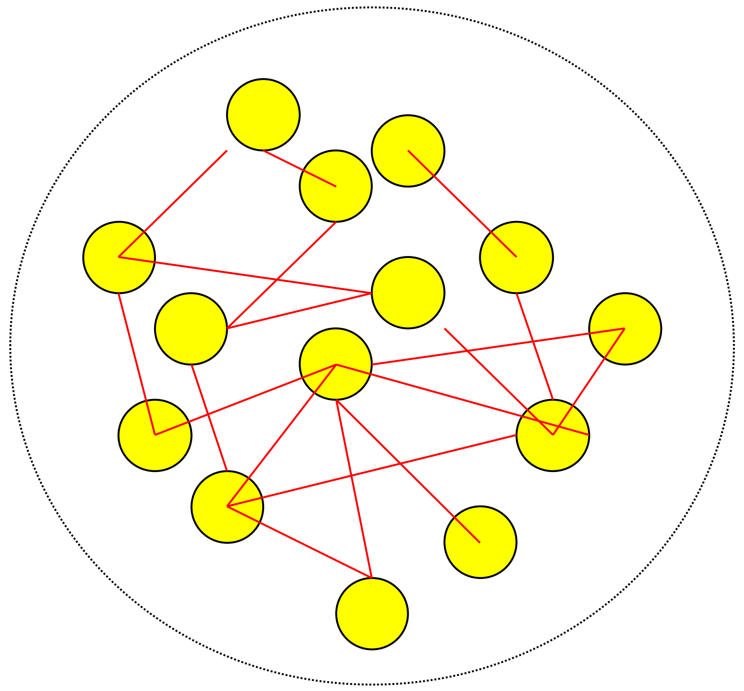


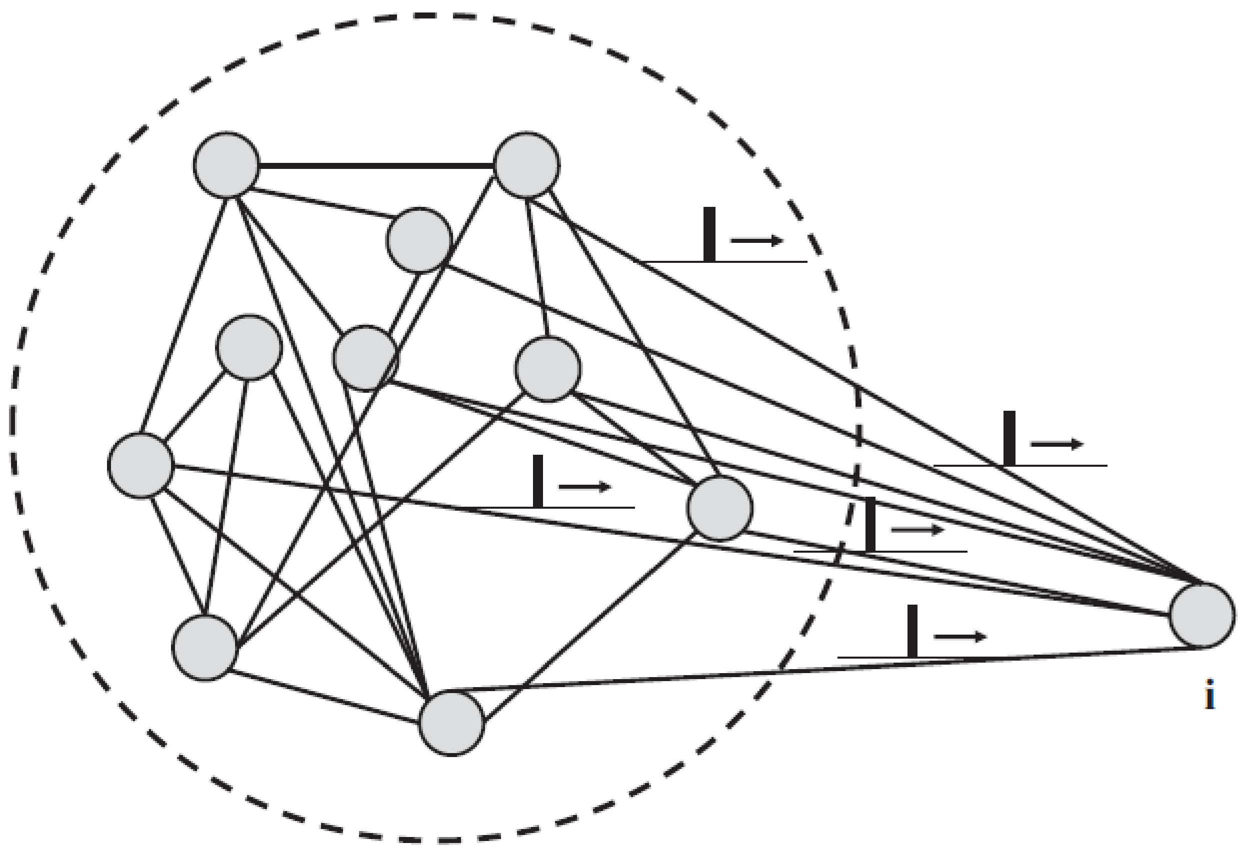
Visual cortex

review from Week 7: mean-field arguments



Single population full connectivity





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

Review from week7: mean-field arguments

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

$$I(t) = J_0 A(t) + I^{ext}(t)$$

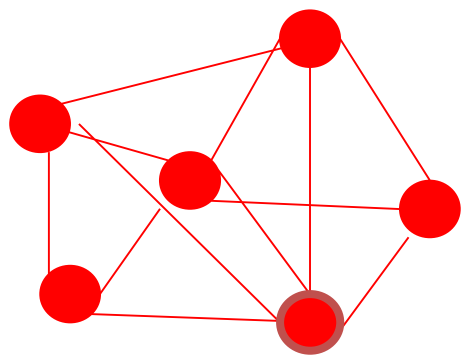
Ultra-short current pulse

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

Index i disappears

Blackboard 1: A(t)

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



fully connected

All spikes, all neurons

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

Review from week 7: mean-field also works for random coupling

full connectivity | random: prob p fixed | random: number K of inputs fixed

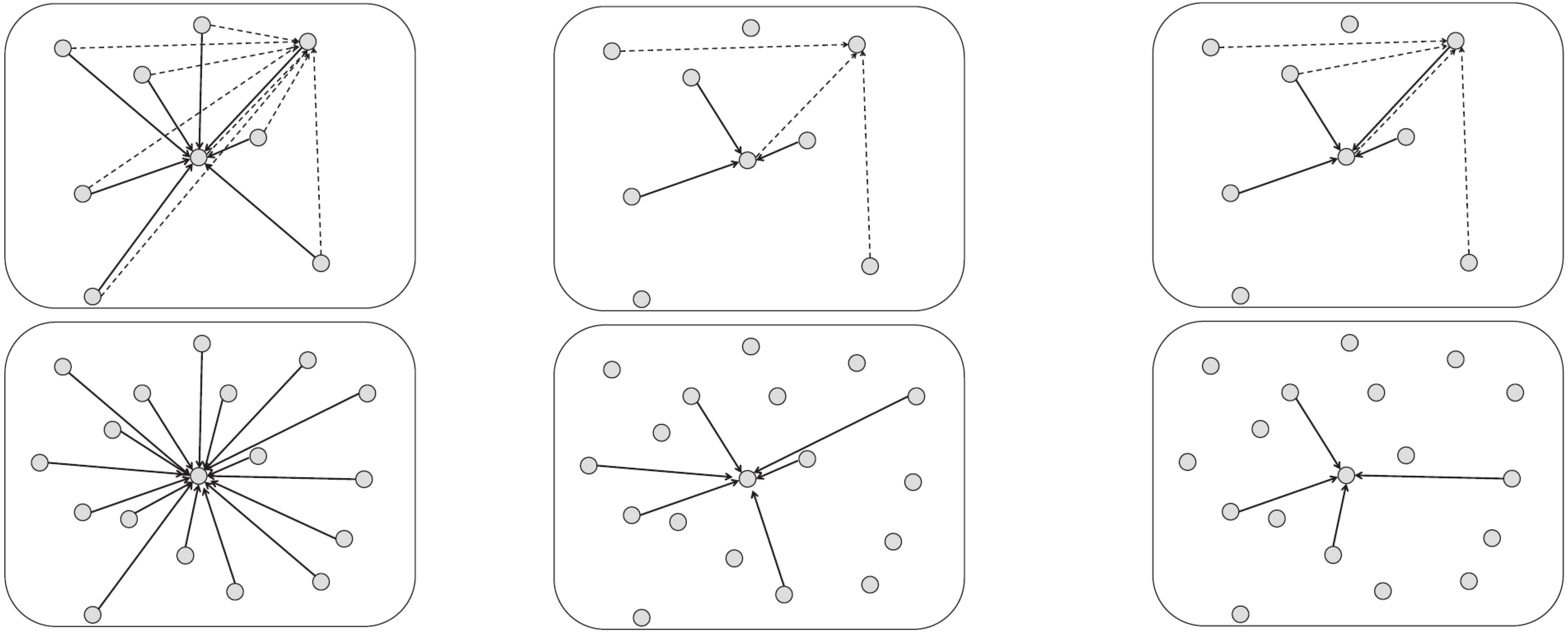
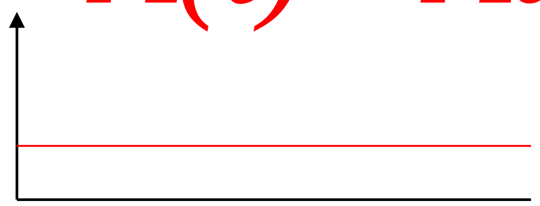


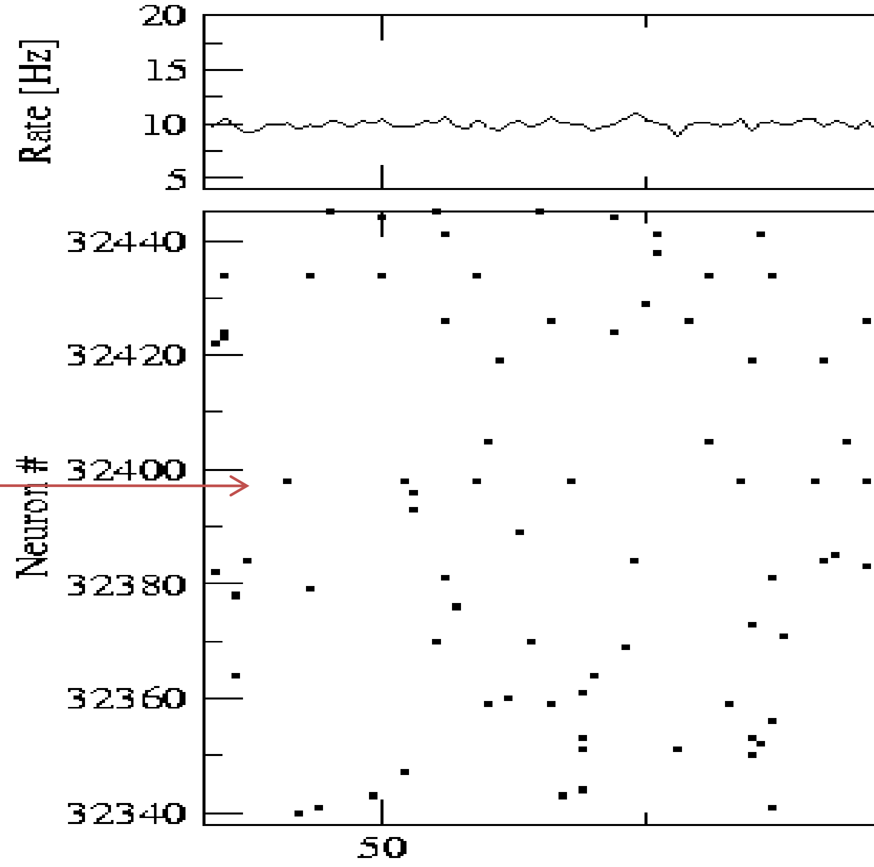
Image: Gerstner et al. Neuronal Dynamics (2014)

Review from Week 7: stationary state/asynchronous activity

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

A(t)= A₀= const



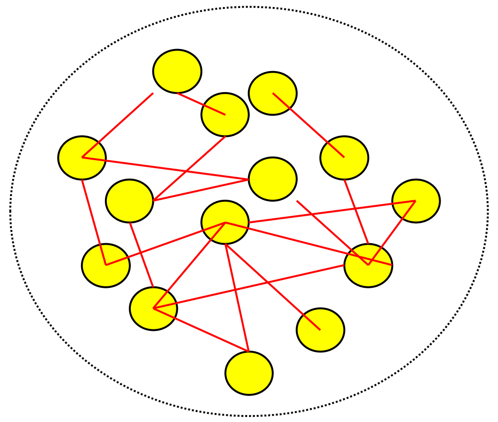


Single
neuron

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

constant input

$$I_0 = c$$



Gain function at appropriate noise level

frequency (single neuron) $\nu = 1/\langle s \rangle$ rate=1/(meanInterval)

Review : mean-field argument for homogeneous population

- single neuron is driven by the ‘population activity’ of all others
- all neurons in populations receive the same input
- mean-field argument work for fully connected and randomly connected populations
- in the **stationary** state, the single neuron firing rate is equal to the ‘population activity’ of a homogeneous population
- in the **stationary** state, ‘population activity’ can be predicted by
  (i) single neuron gain function (f-I curve)
  (ii) external input
  (iii) intra-population coupling strength
- in the **stationary** state, choice of neuron model irrelevant (apart from gain function/f-I curve)

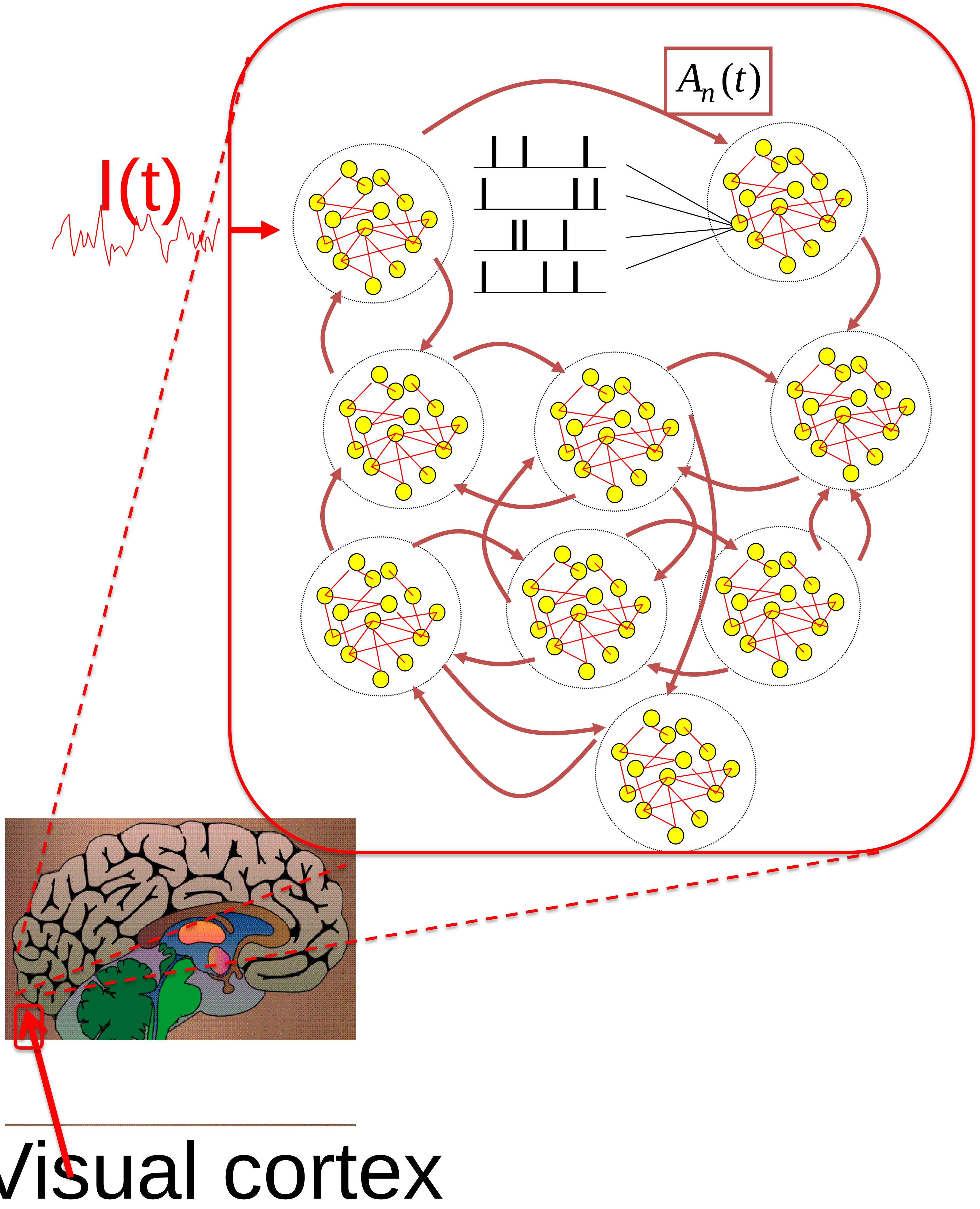
8.1. Aims and challenges

Mathematical aims:

- beyond stationary states
  → transients?
- more than one population
  → how many? continuum?

Cognitive Modeling aims:

- functional consequences
  → visual perception?
  → sense of direction?



8.1. Aims and challenges: compass and perception

sense of direction?

visual perception?

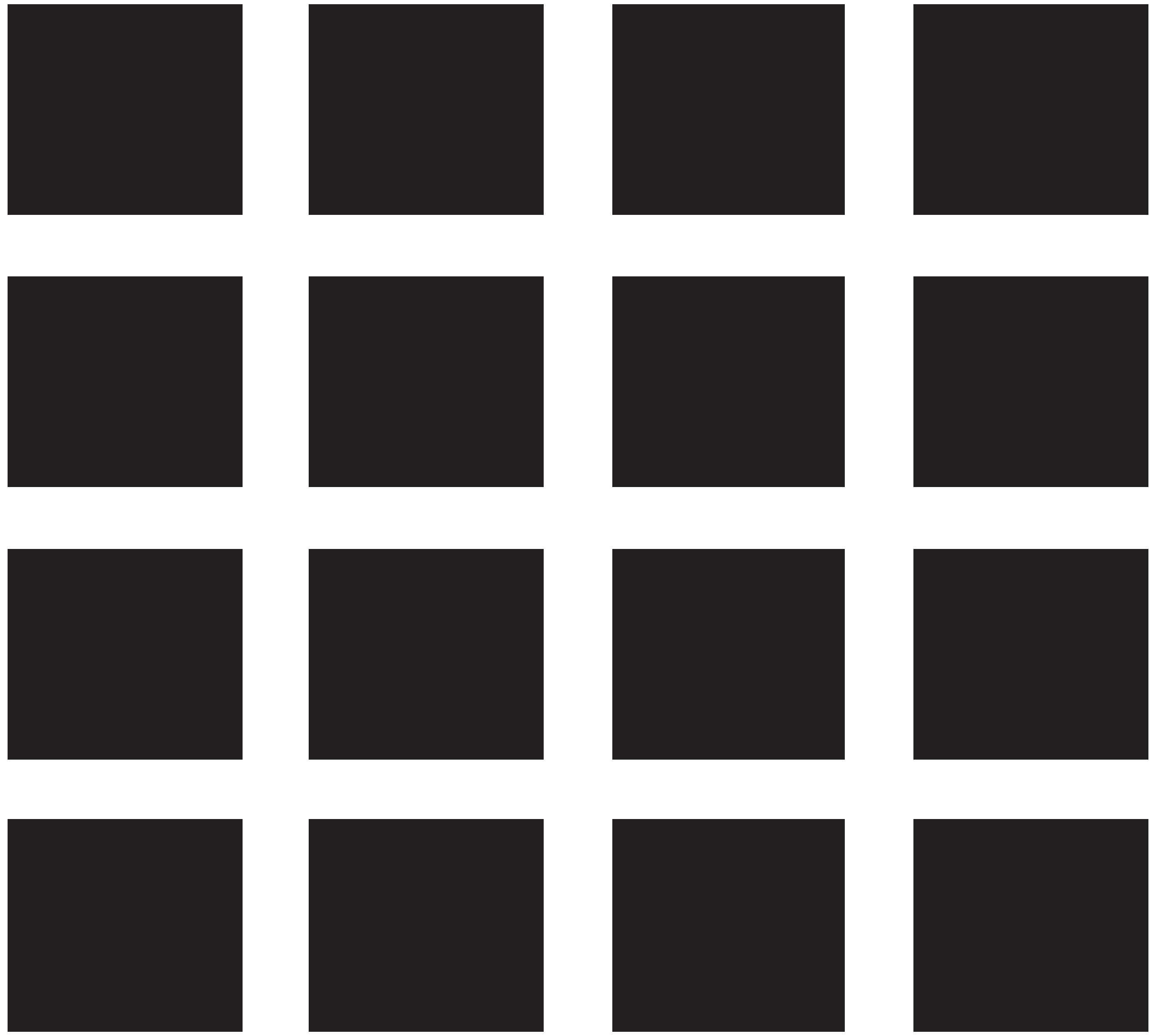


Image: Neuronal Dynamics, Gerstner et al., Cambridge Univ. Press (2014),

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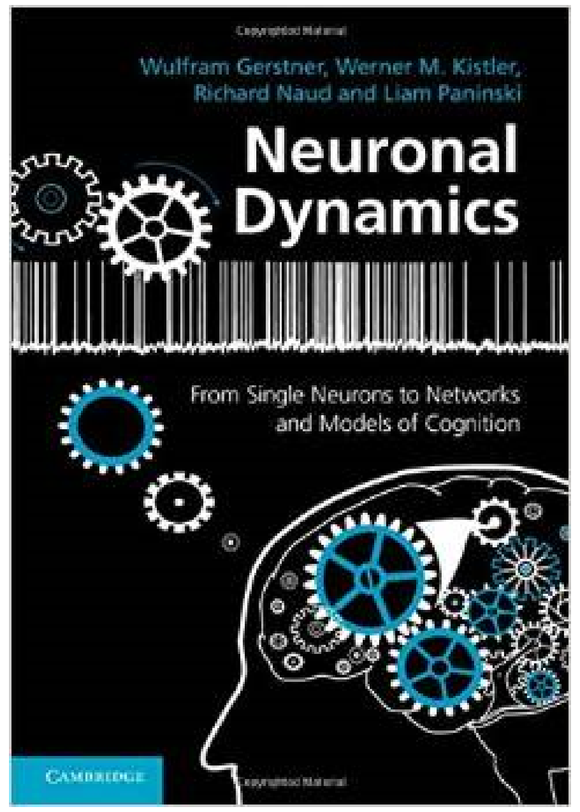

8.1. Mean-field argument (review)
- aims and challenges for this week

8.2. Transients
- generalized integrate-and-fire model
- transients can be sharp or slow

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- orientation columns

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8.5. Solution types
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8.7. Head direction cells

8.2. Aims and challenges

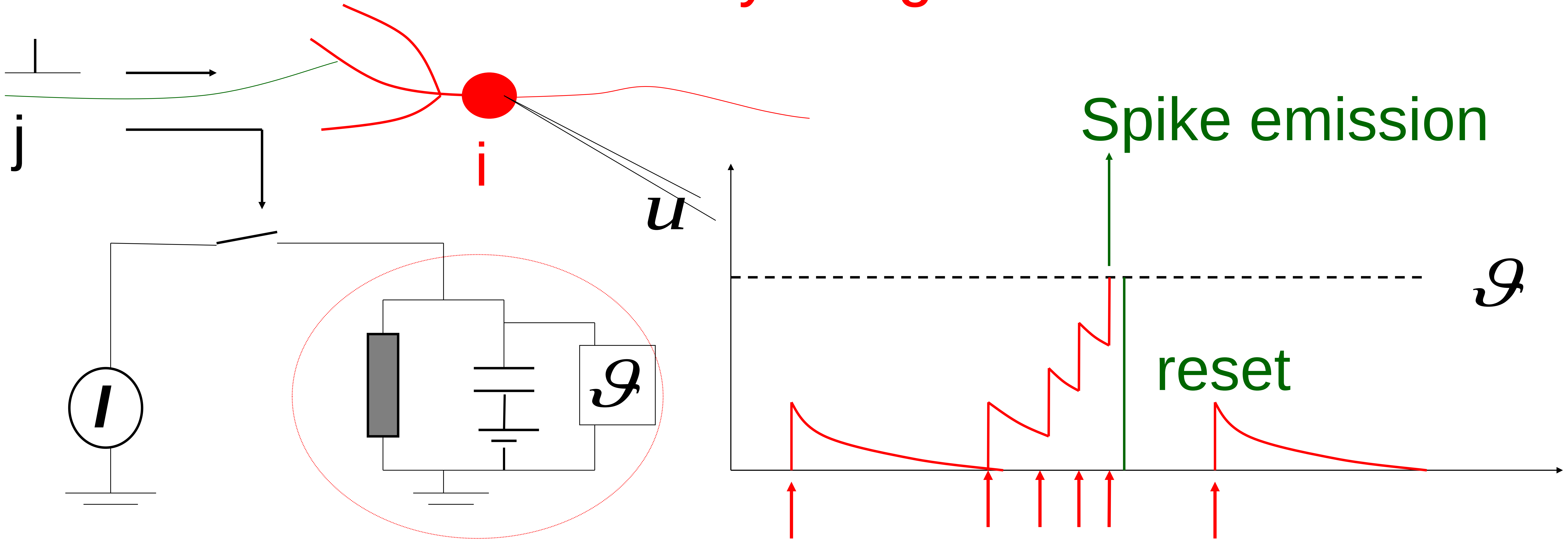
- beyond stationary states

→ transients?

- but then neuron model matters!

→ introduce generalized integrate-and-fire models:
  - Spike Response Model (SRM)
  - Generalized Linear Model (GLM)

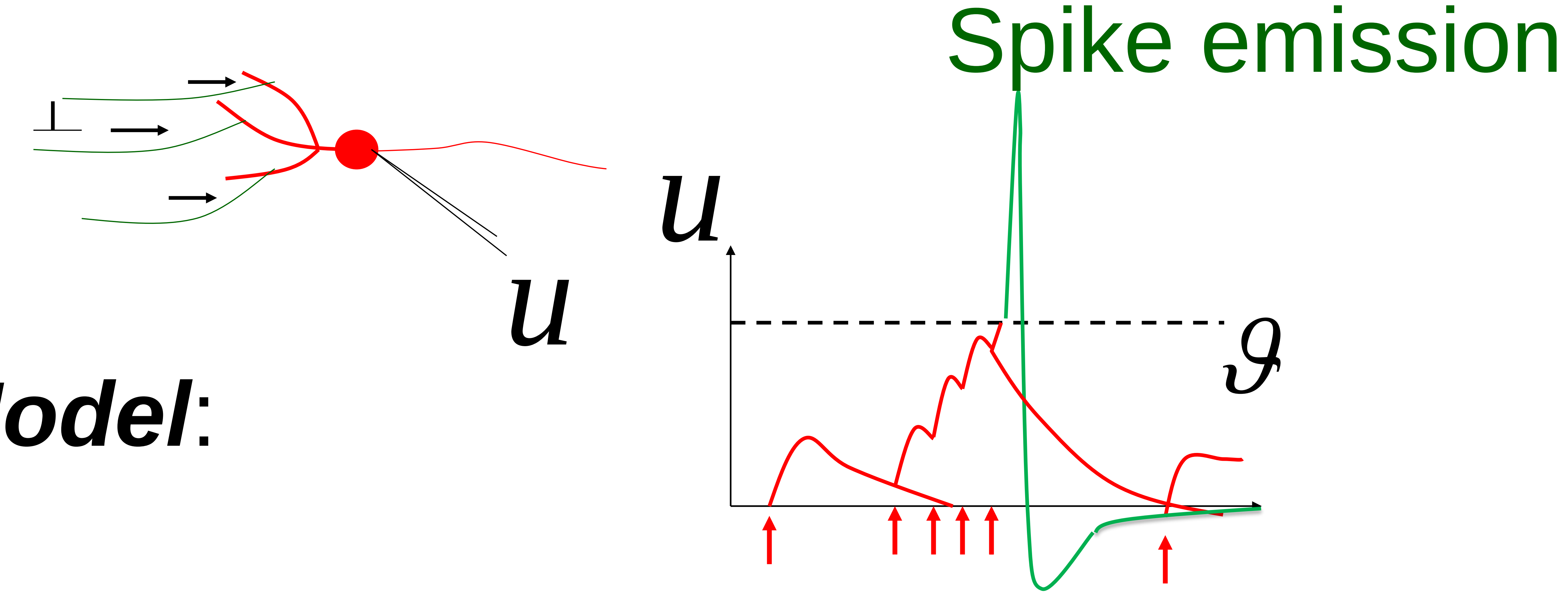
review from week 1 – Leaky Integrate-and-Fire Model



$$\tau \cdot \frac{d}{dt} u = -(u - u_{rest}) + RI(t)$$ linear

$$u(t) = \vartheta \Rightarrow \text{Fire+reset } u \rightarrow u_r$$ threshold

review from week 1 – Leaky Integrate-and-Fire type Model



Leaky
***Integate-and-Fire Model*:**

passive membrane
\+ *threshold*
\+ *reset*

equivalent description

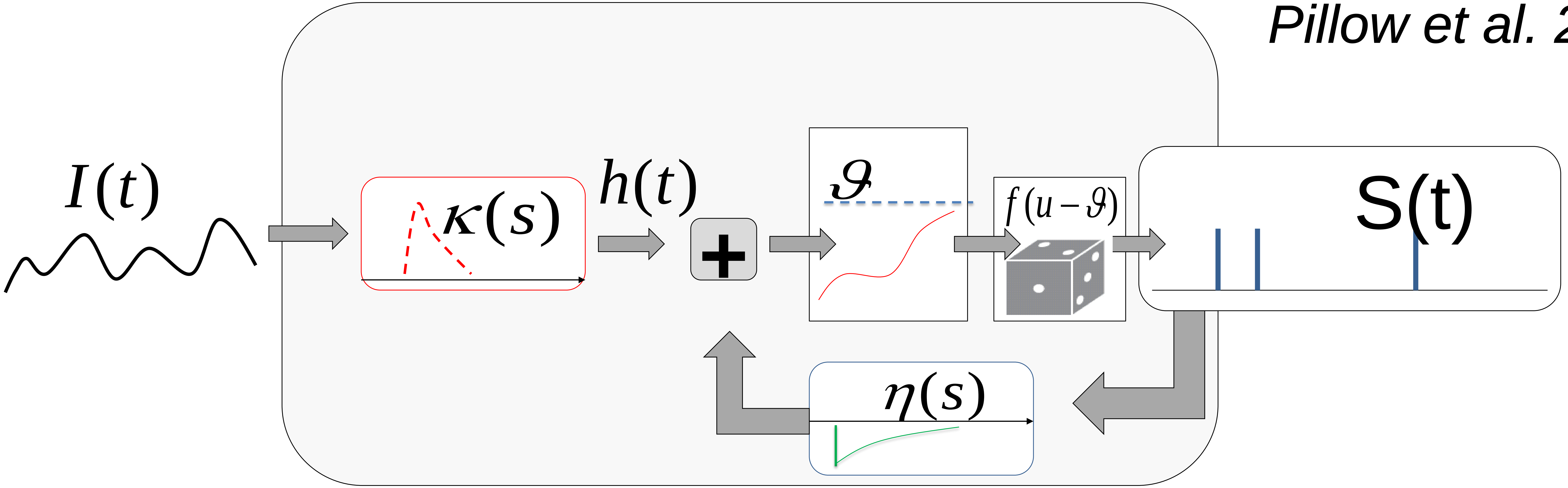
Input spike causes an EPSP
= excitatory postsynaptic potential

-output spikes are events
-generated at threshold
-after spike: reset/refractoriness

add $\eta(s)$ (spike afterpotential)

Spike Response Model (SRM)
Generalized Linear Model (GLM)

Gerstner et al., 1992,2000
Truccolo et al., 2005
Pillow et al. 2008



potential $u(t) = \int \eta(s) S(t-s)ds + \int_0^\infty \kappa(s) I(t-s)ds + u_{rest}$

$h(t)$

firing intensity $\rho(t) = f(u(t) - \vartheta)$

(escape noise) e.g. $\rho(t) = \rho_0 \exp[\frac{u(t)-\vartheta}{\Delta}]$

Blackboard 2: h(t)

Spike Response Model (SRM)
Generalized Linear Model (GLM)

Gerstner et al., 1992,2000
Truccolo et al., 2005
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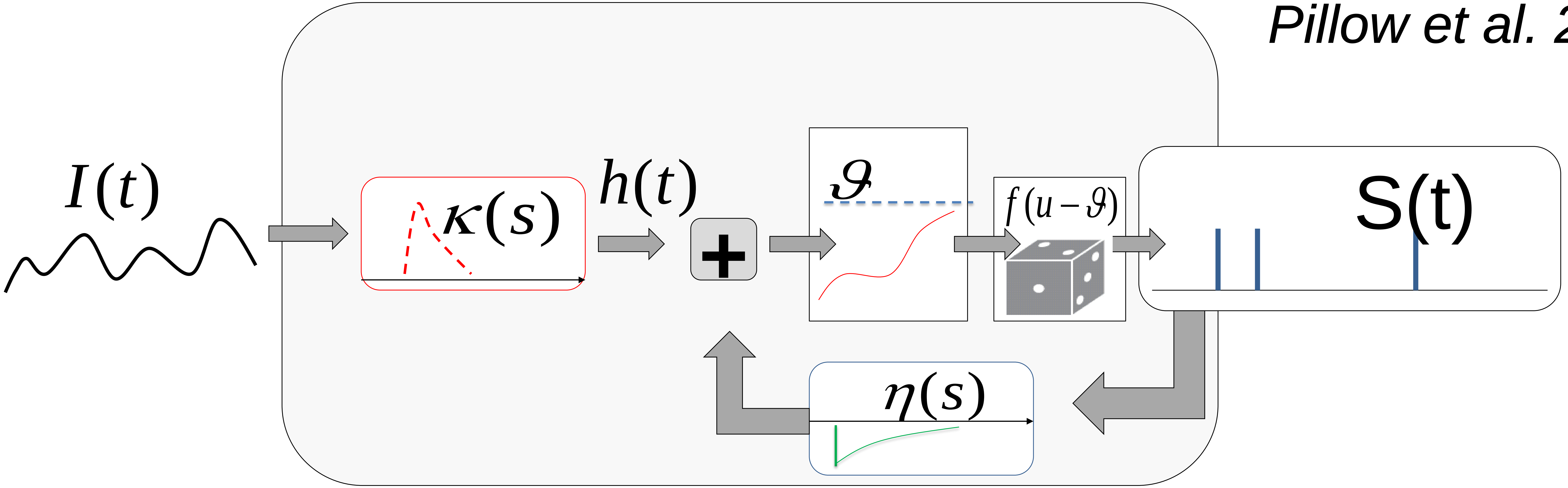
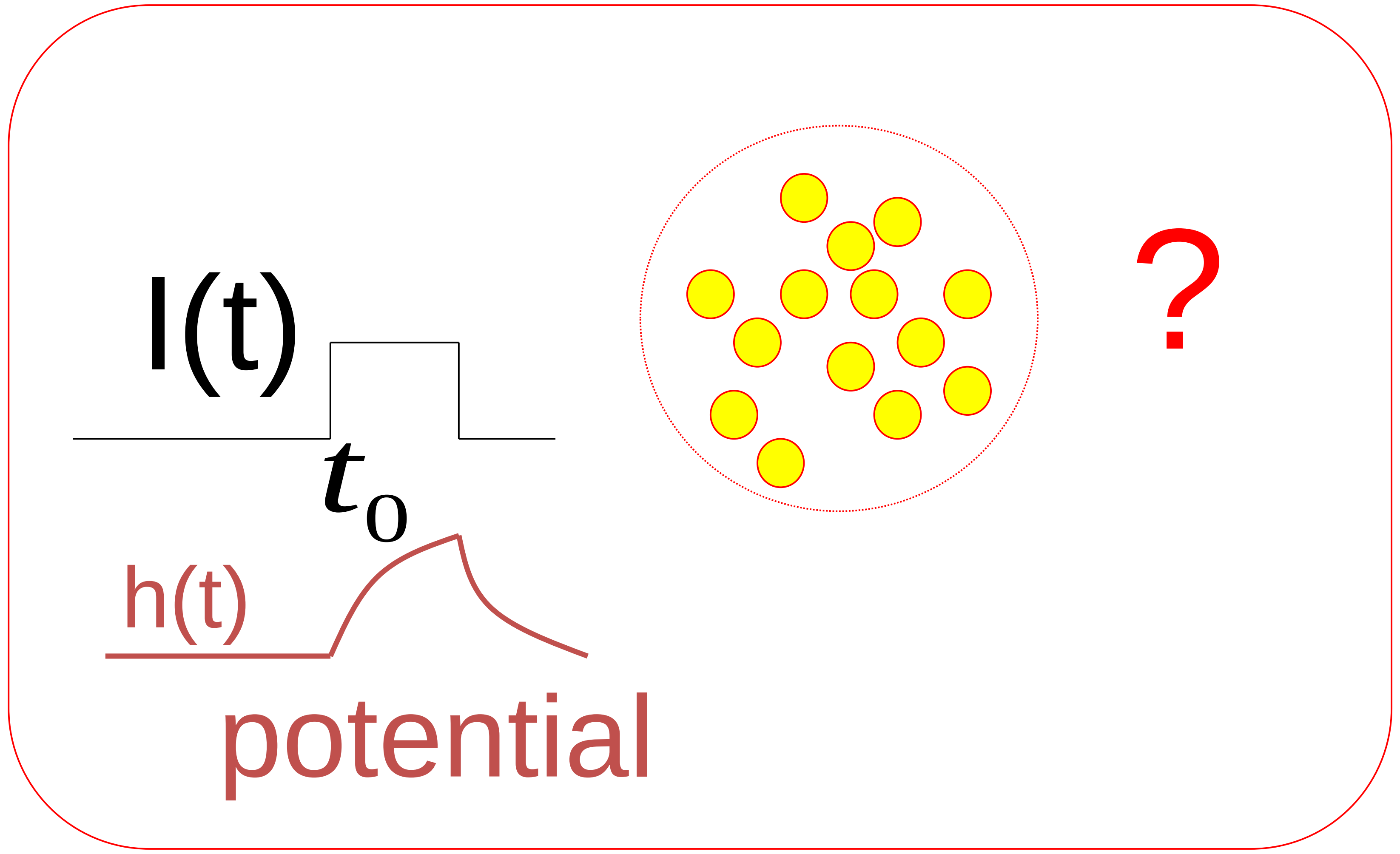
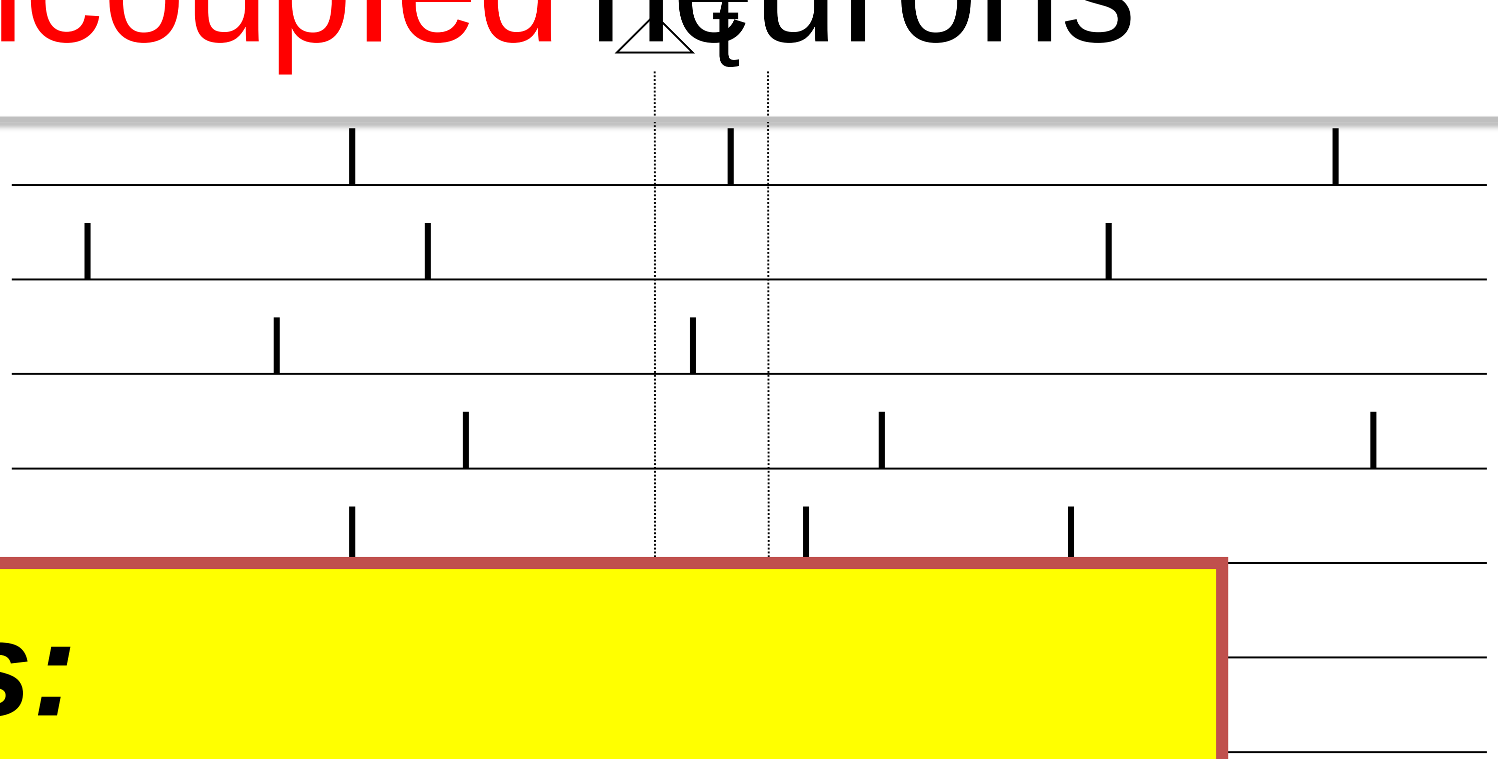


potential $u(t) = u_{rest} + \underbrace{\int_0^\infty \kappa(s) I(t-s)\,ds}_{h(t)} + \int \eta(s) S(t-s)\,ds$

$u(t) = u_{rest}$ + *input potential* + *reset potential*

8. 2. Transients in a population of uncoupled neurons

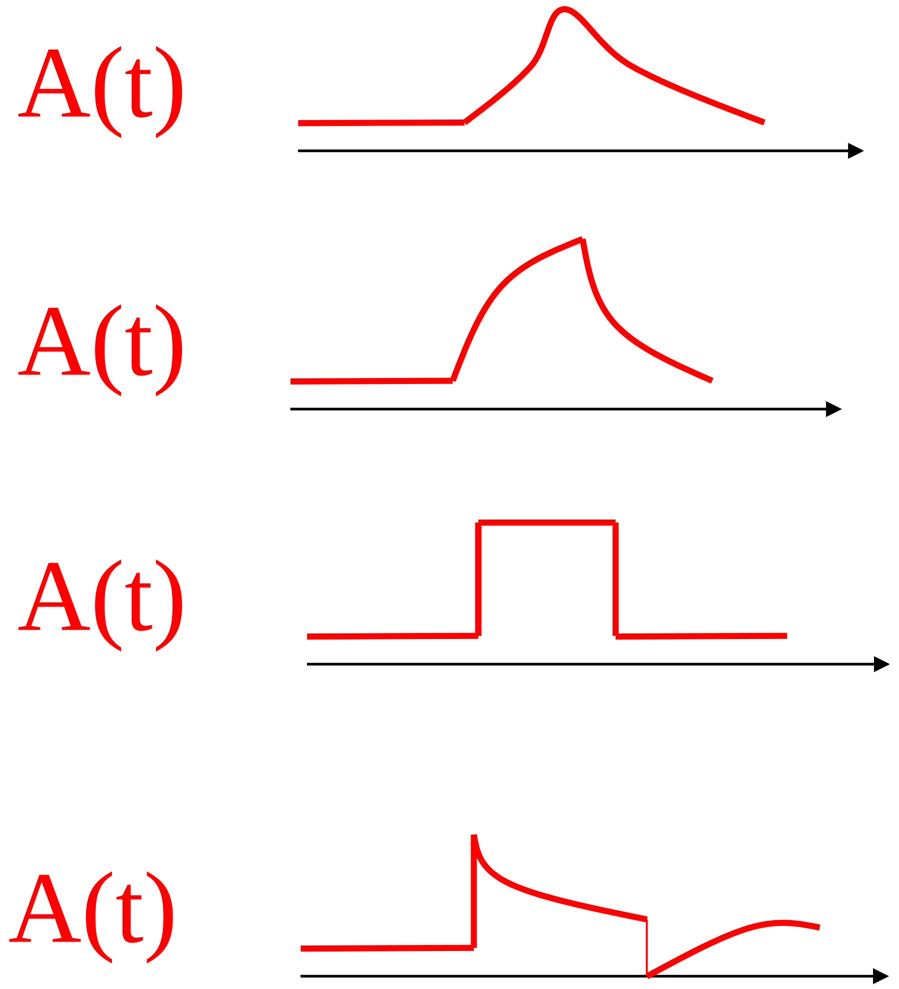




Students:
Which would you choose?

population activity

$$A(t) = \frac{n(t-\frac{\Delta t}{2};t+\frac{\Delta t}{2})}{N\Delta t}$$



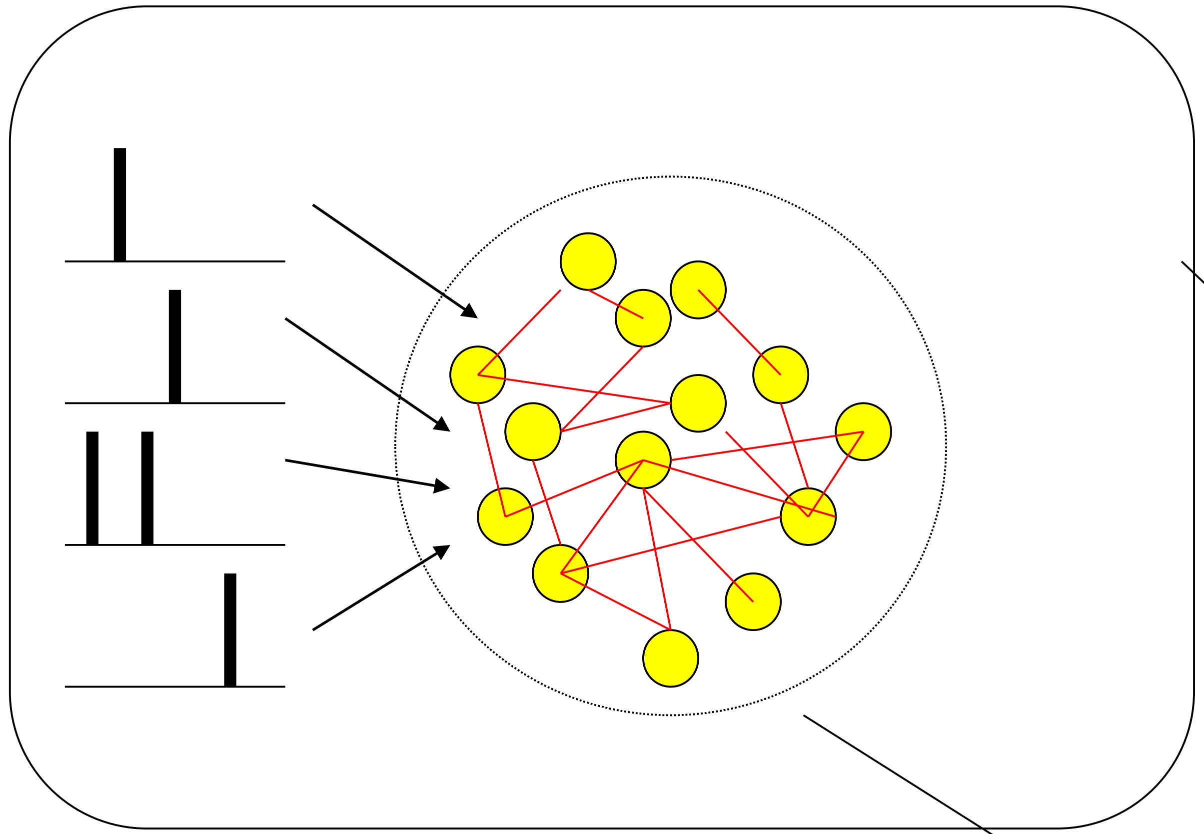
$$\tau \frac{d}{dt} A(t) = -A(t) + F(h(t))$$

$$A(t) = F(\underline{h(t)}) = F(\int \kappa(s) I(t-s) ds)$$

$$A(t) = g(\underline{I(t)})$$

$$A(t) = \tilde{g}(I(t), I'(t))$$

8. 2. Transients in a population of neurons



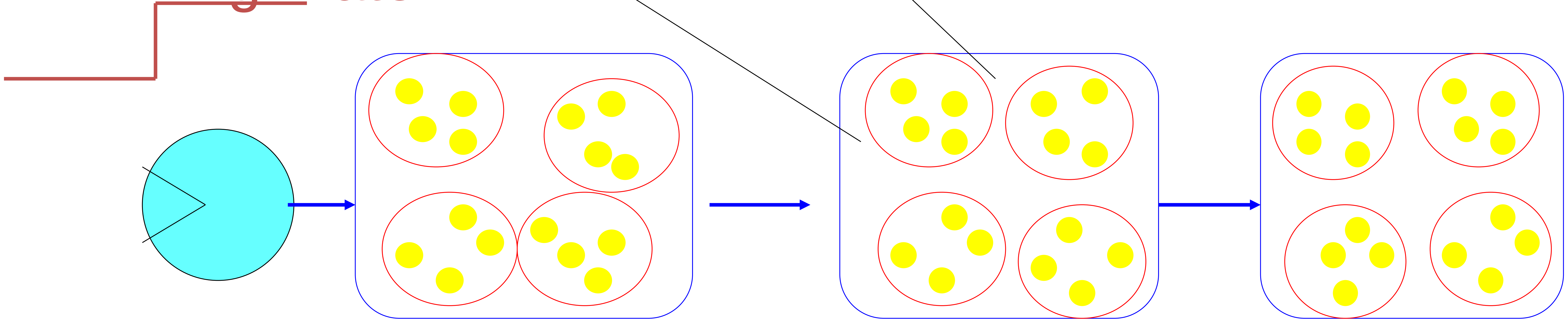
Population
- 50 000 neurons
- 20 percent inhibitory
- randomly connected

Connections
4000 external

4000 within excitatory

1000 within inhibitory

input {low rate / high rate}



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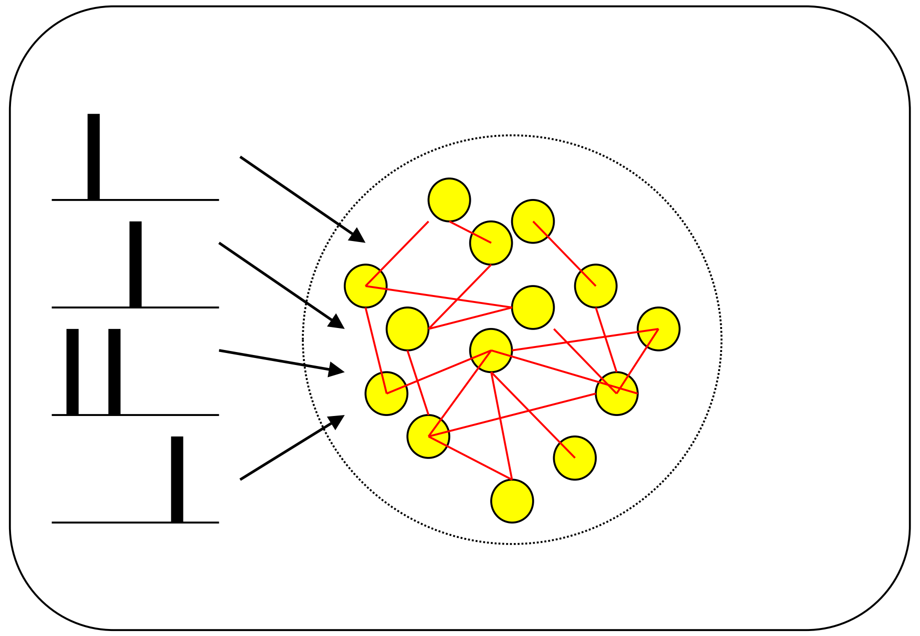
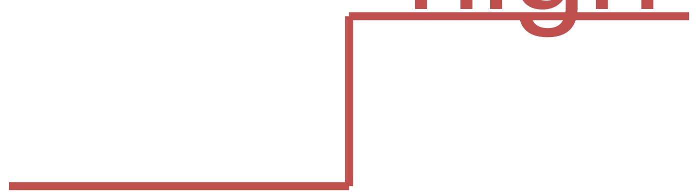


input {low rate / high rate



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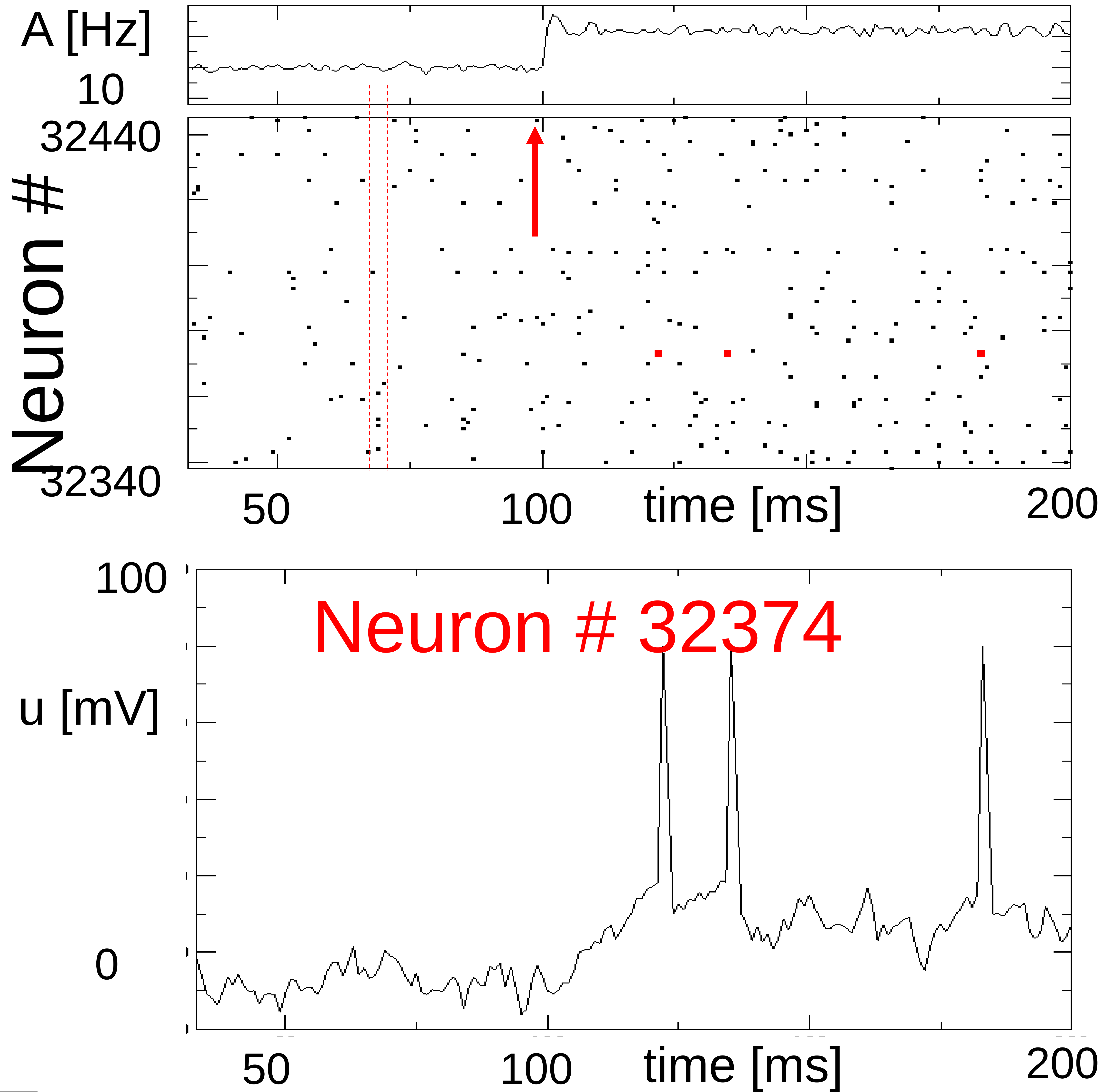
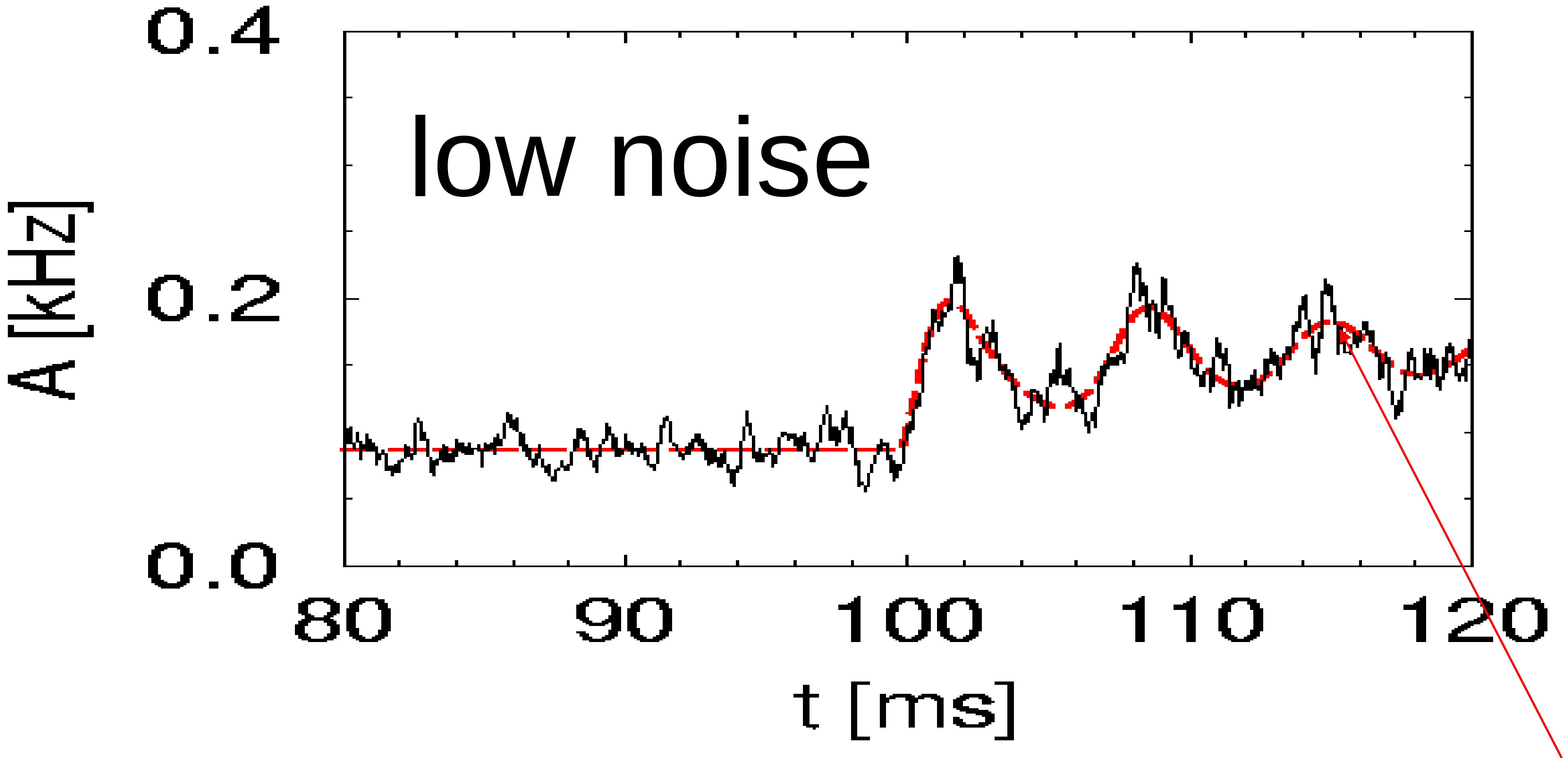
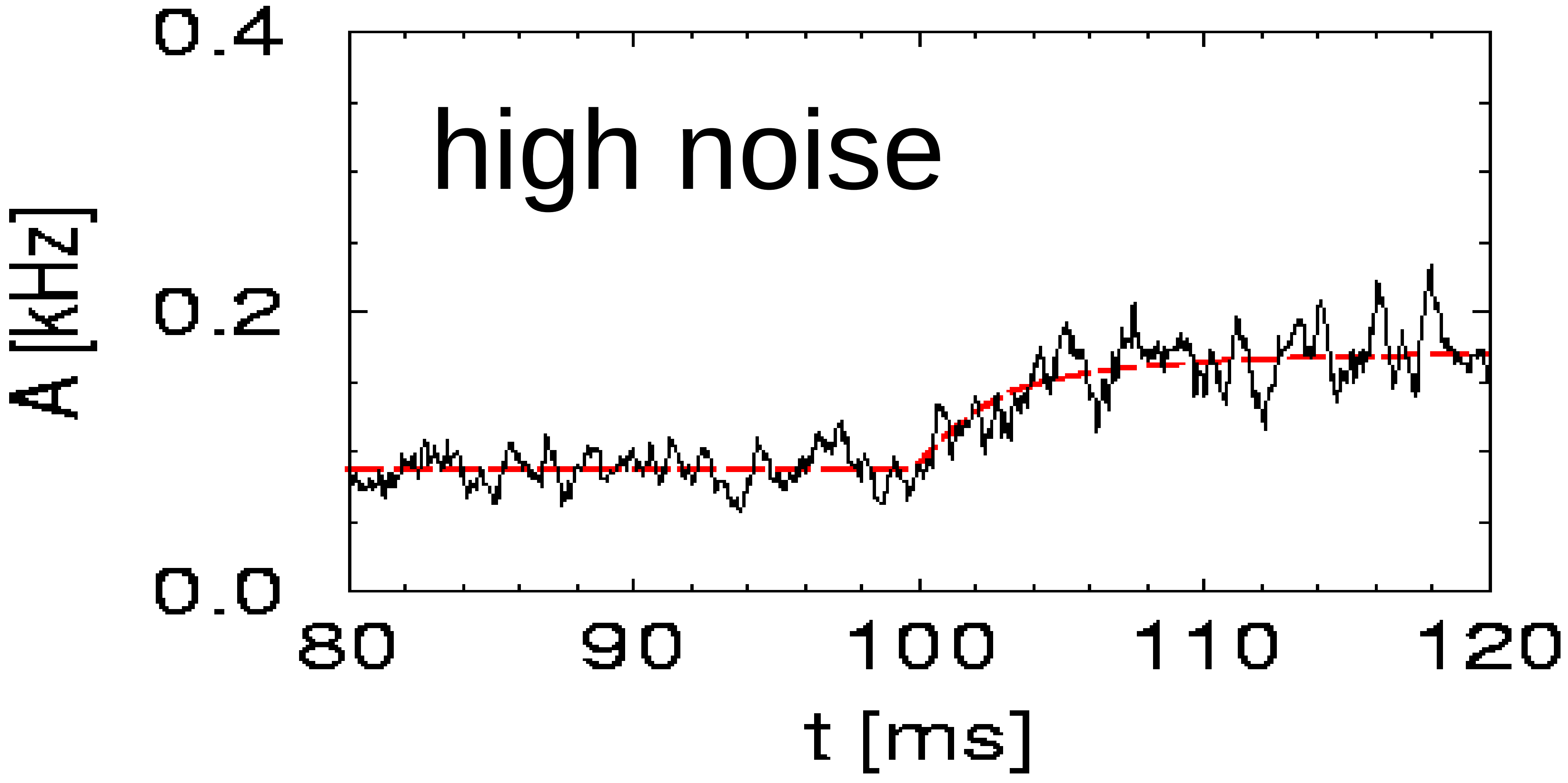
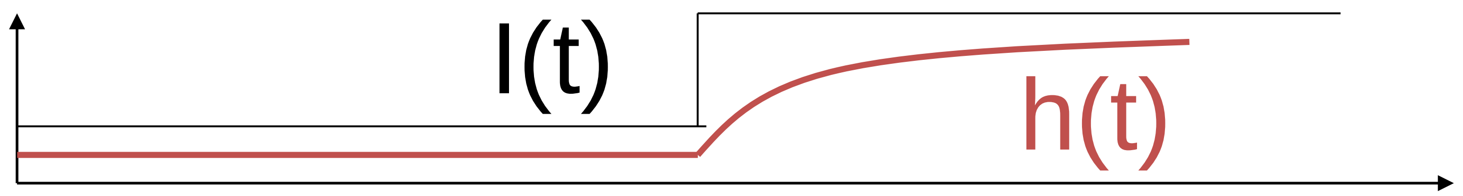


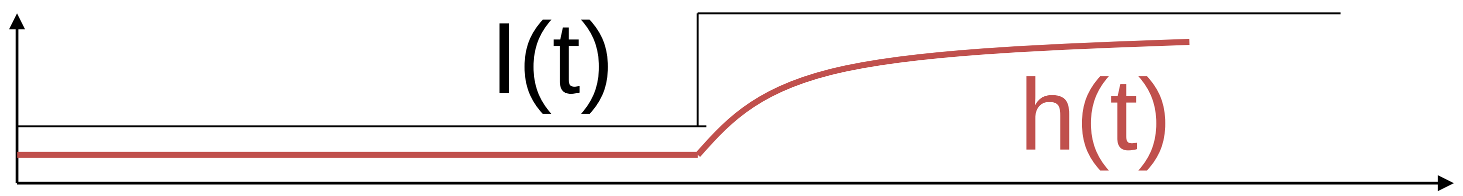
8. 2. Transients for populations of noisy neurons

uncoupled population
of SRM neurons with noise (escape noise)









fast transient

$$A(t) \approx g(I(t))$$

$$A(t) \approx \tilde{g}(I(t), I'(t))$$

slow transient

$$A(t) = F(h(t))$$

But transient oscillations

8.2. High-noise activity equation

blackboard

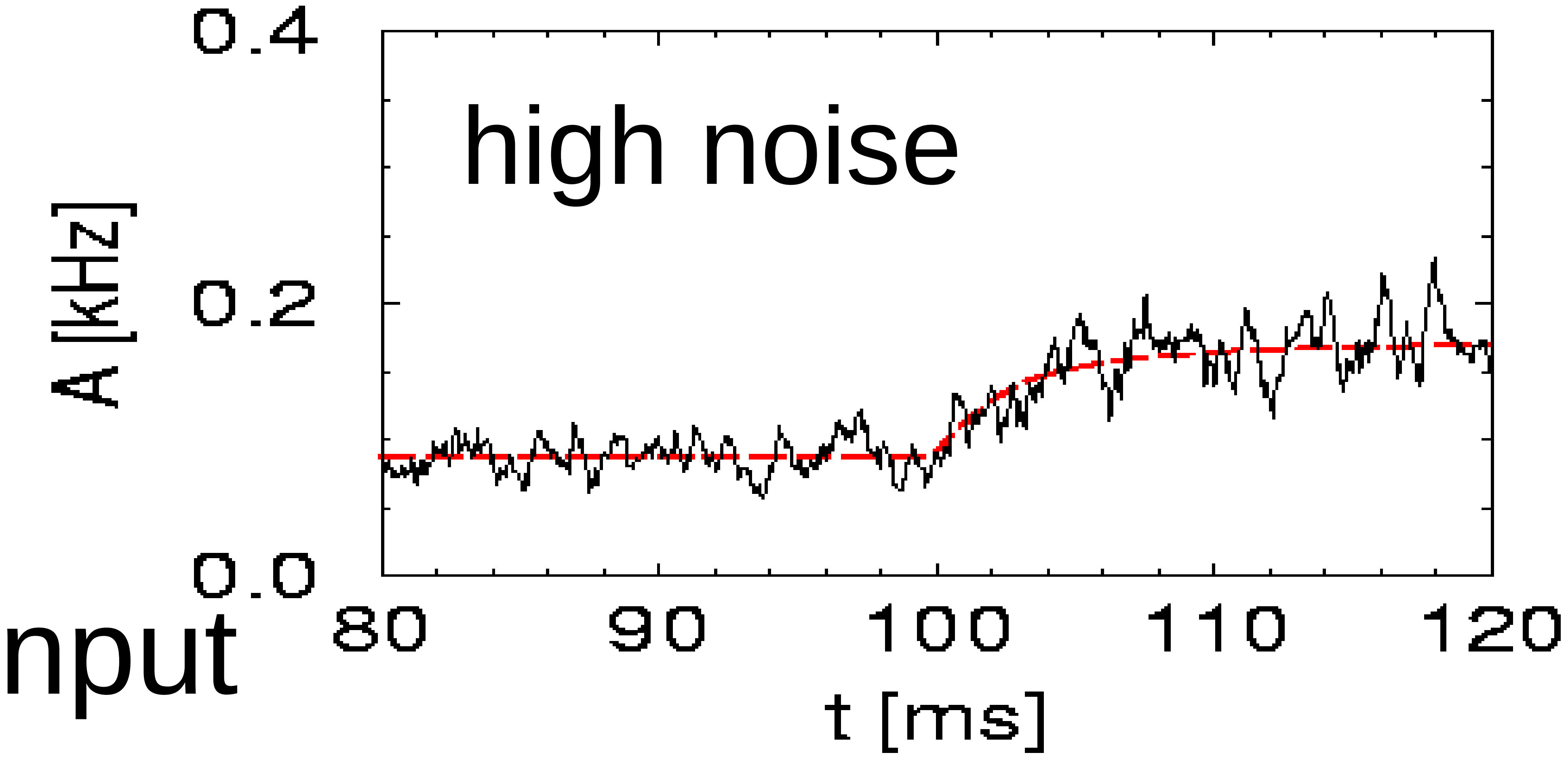
In the limit of **high noise**,
Population activity

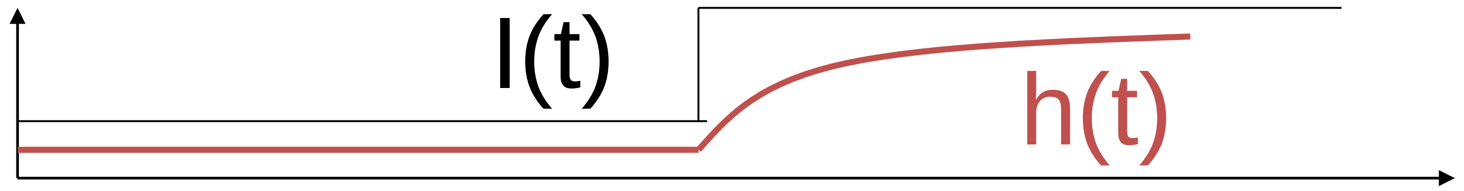
$$A(t) = F(h(t))$$

Membrane potential caused by input

$$\tau \frac{d}{dt} h(t) = -h(t) + R\, I(t)$$

(escape noise)





slow transient

$$A(t) = F(h(t))$$

8. 2. High-noise activity equation

Population activity

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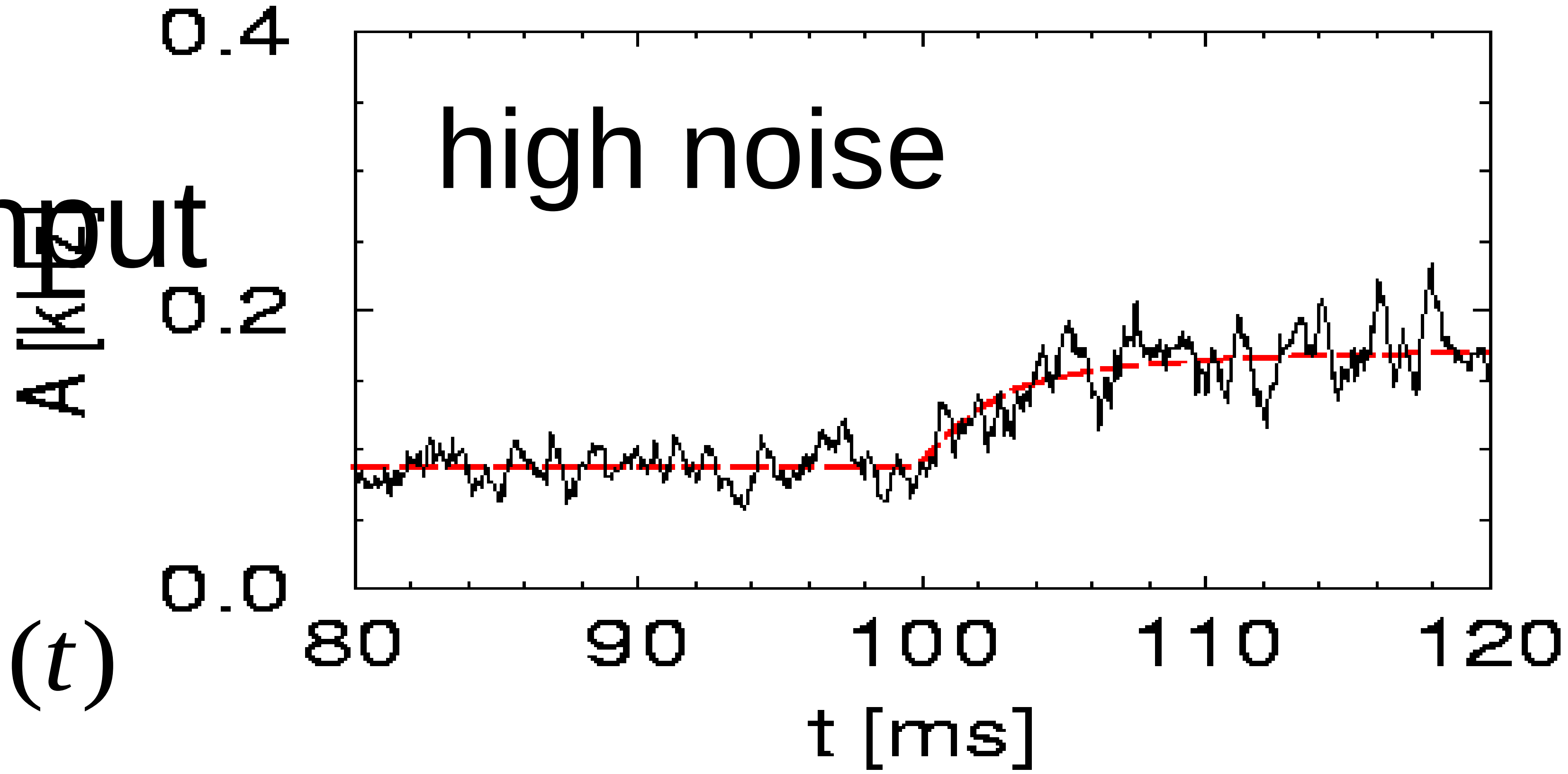
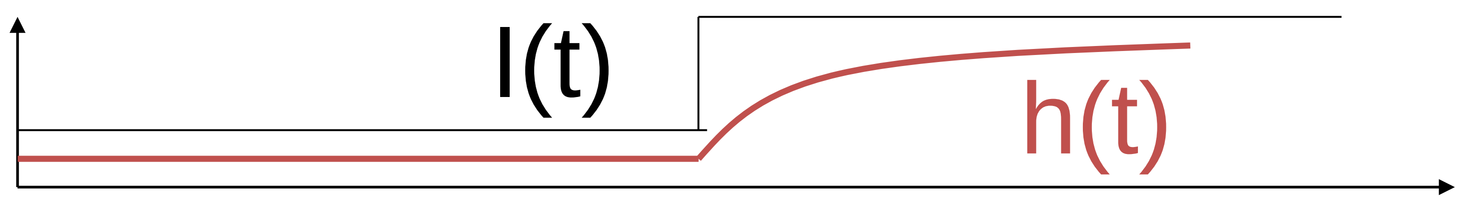
(escape noise)



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

$$I(t) = I^{ext}(t) + J_0\, q\, A(t)$$

$$I(t) = I^{ext}(t) + J_0\, q\, F(h(t))$$



slow transient

$$\tau \frac{d}{dt} h(t) = -h(t) + R\, I^{ext}(t) + \gamma\, F(h(t))$$

$$A(t) = F(h(t))$$

1 population = 1 differential equation

Quiz 1, now

Population equations

A single homogeneous population of neurons is driven by a step current causing a transient response of the population activity.

[ ] A single cortical model population can exhibit transient oscillations

[ ] Transients are always sharp

[ ] Transients are always slow

[ ] in a certain limit transients can be slow

[ ] An escape noise model in the high-noise limit has transients which are always slow

[ ] A single population described by a single first-order differential equation (no integrals/no delays) can exhibit transient oscillations

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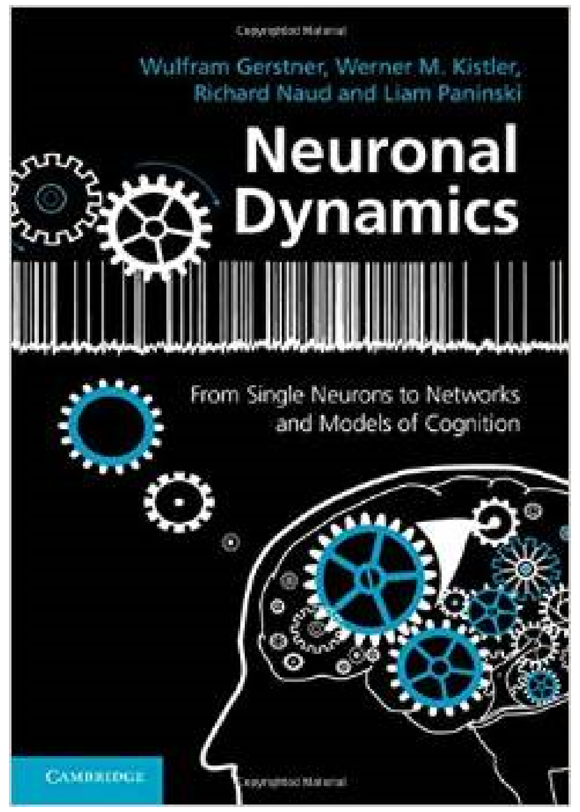

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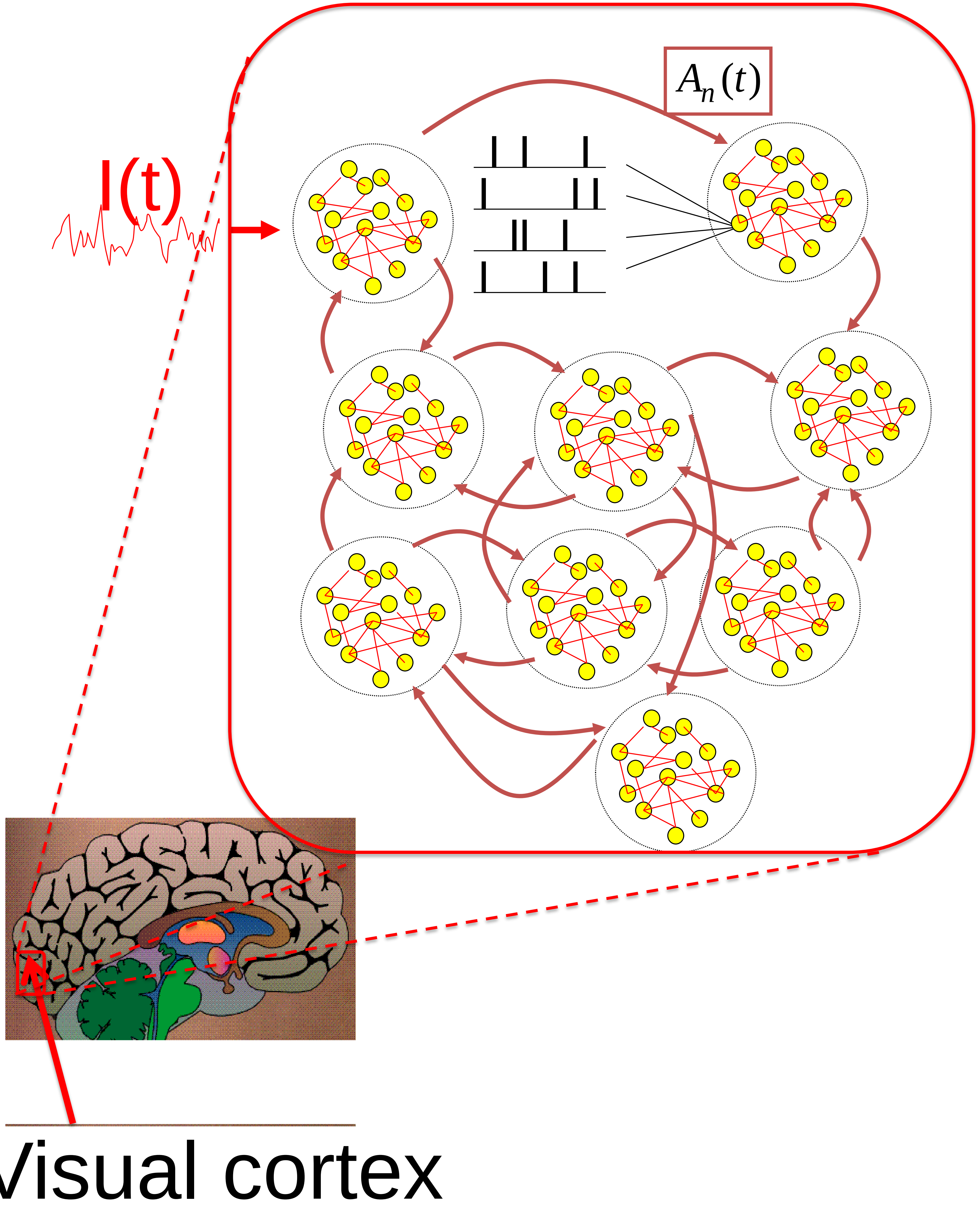
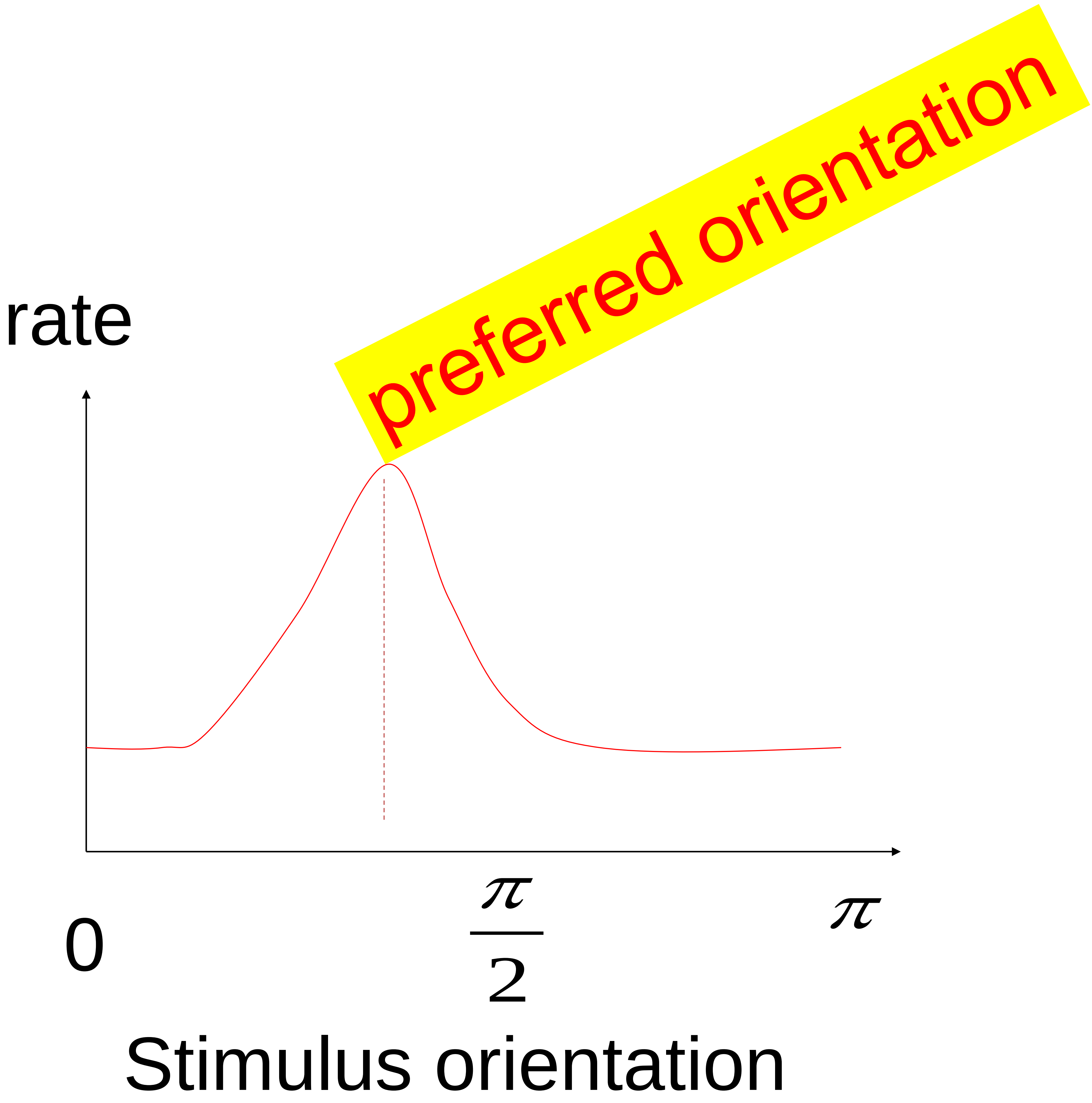
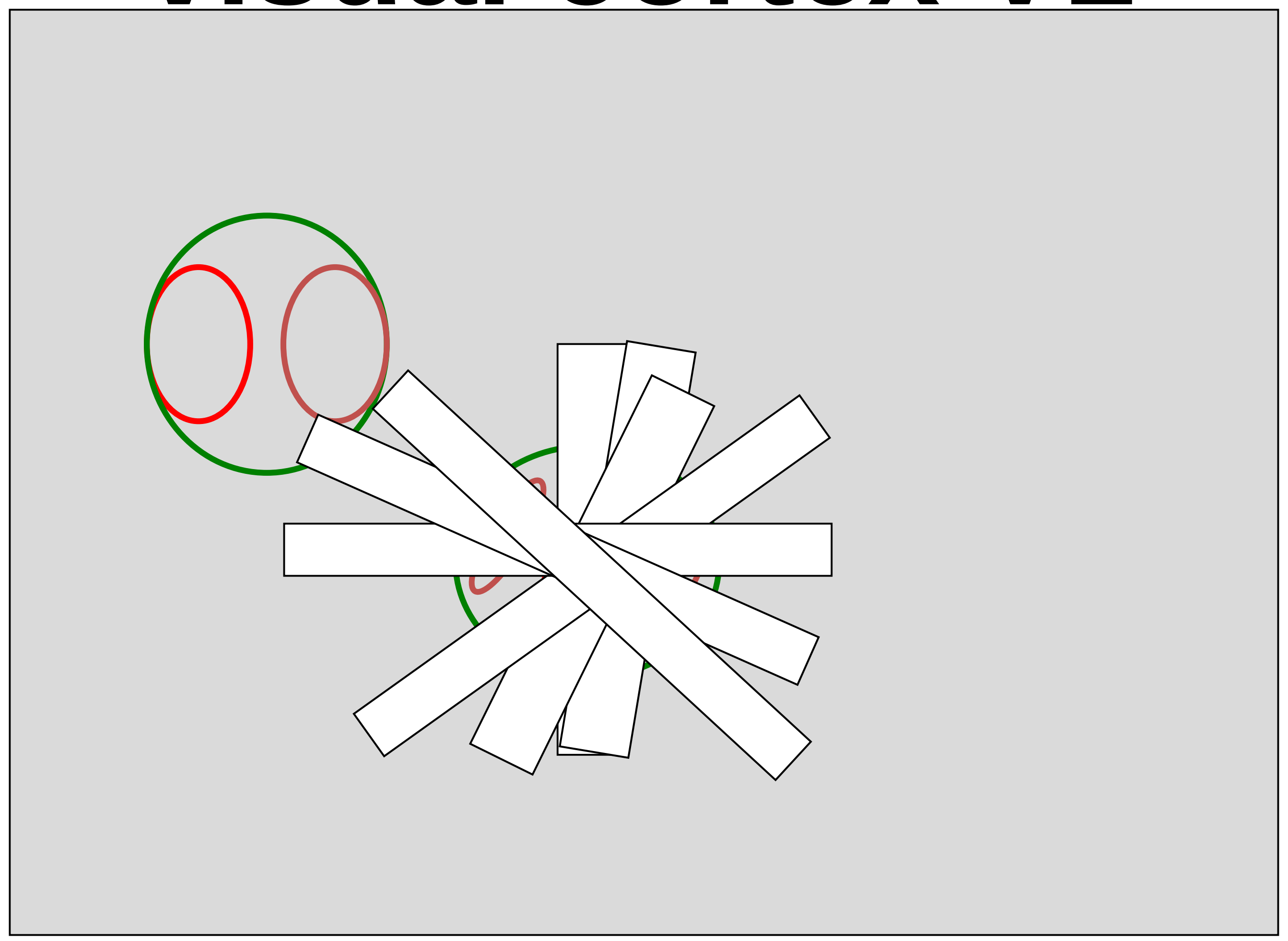
Review: Interacting Populations



Review: Receptive fields with Orientation Tuning



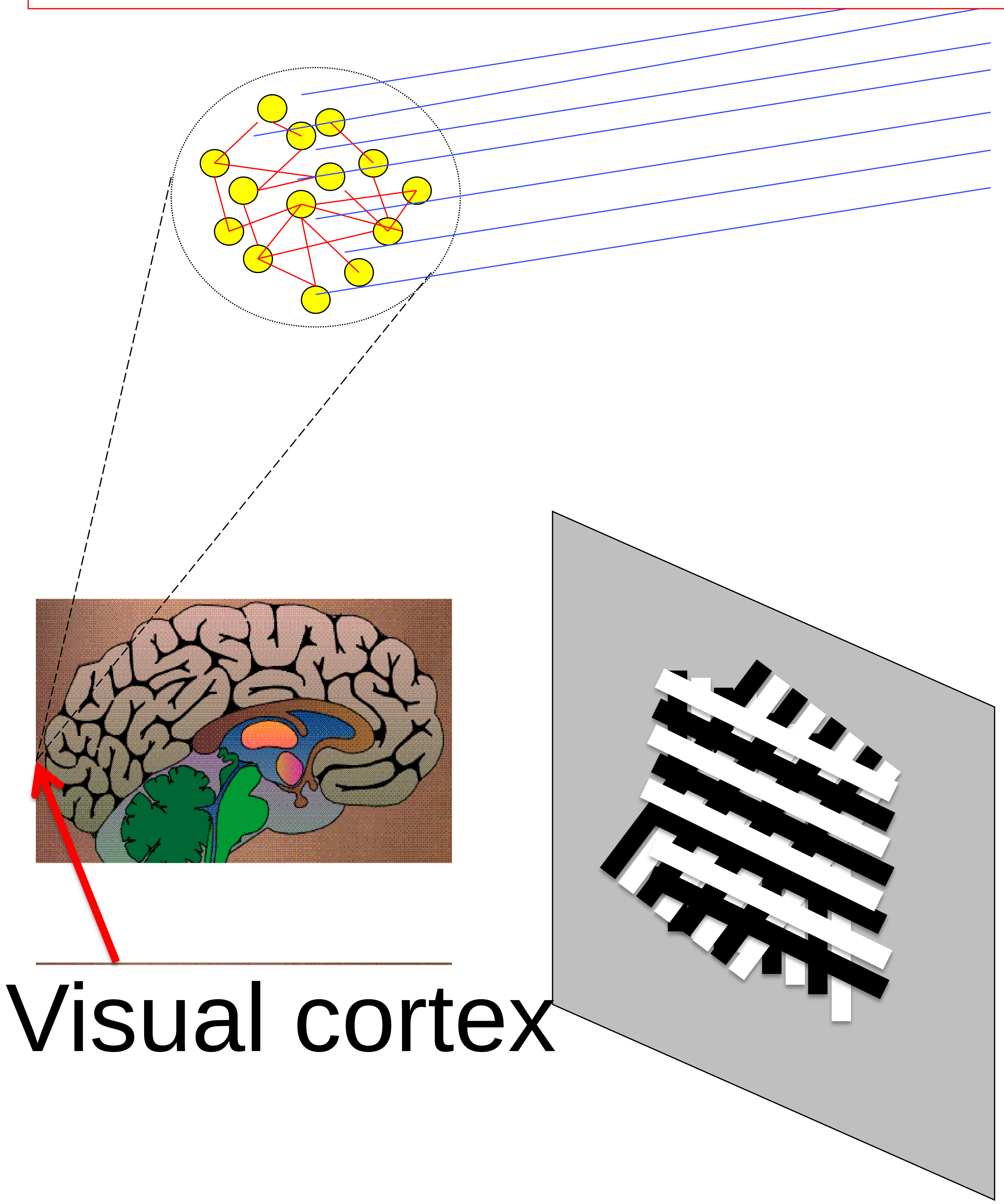
Receptive fields:
visual cortex V1

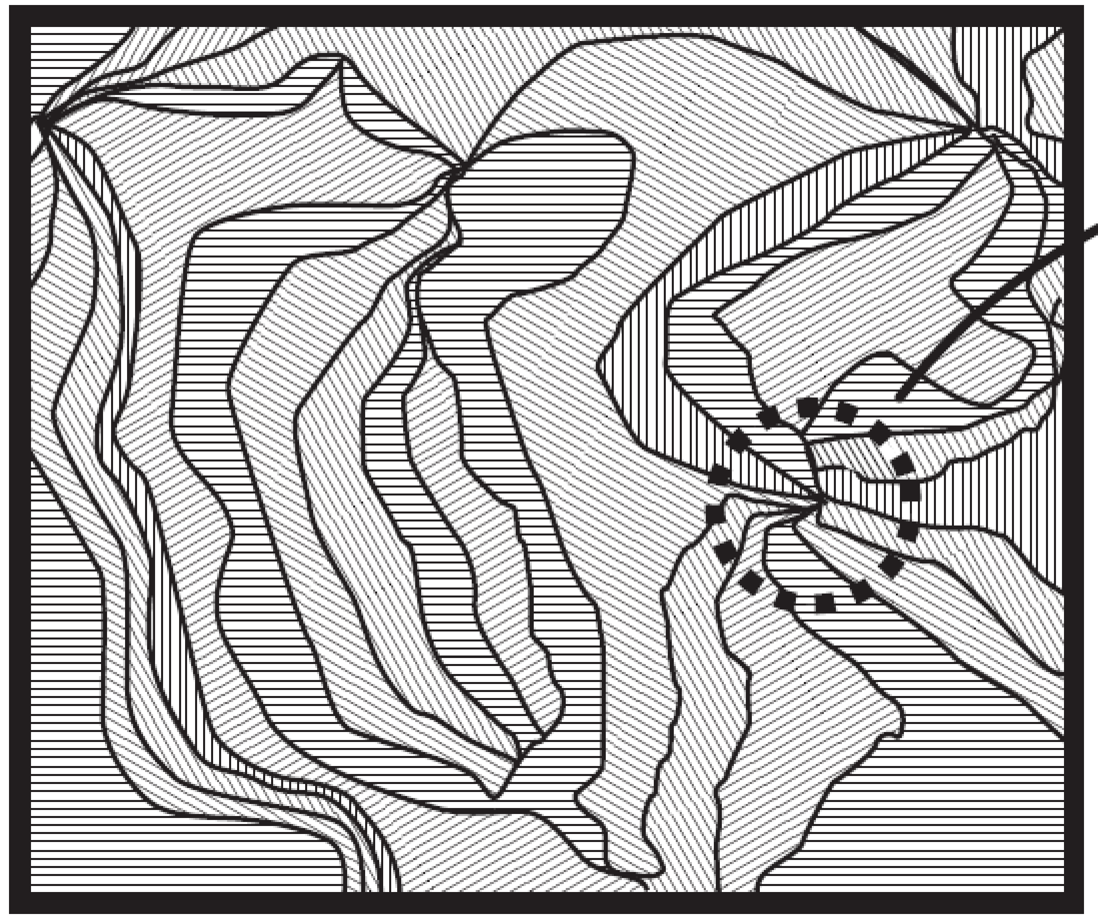


Orientation selective

8.3. Orientation Map

population of neighboring neurons: similar orientations
As we move along cortical surface: orientation changes





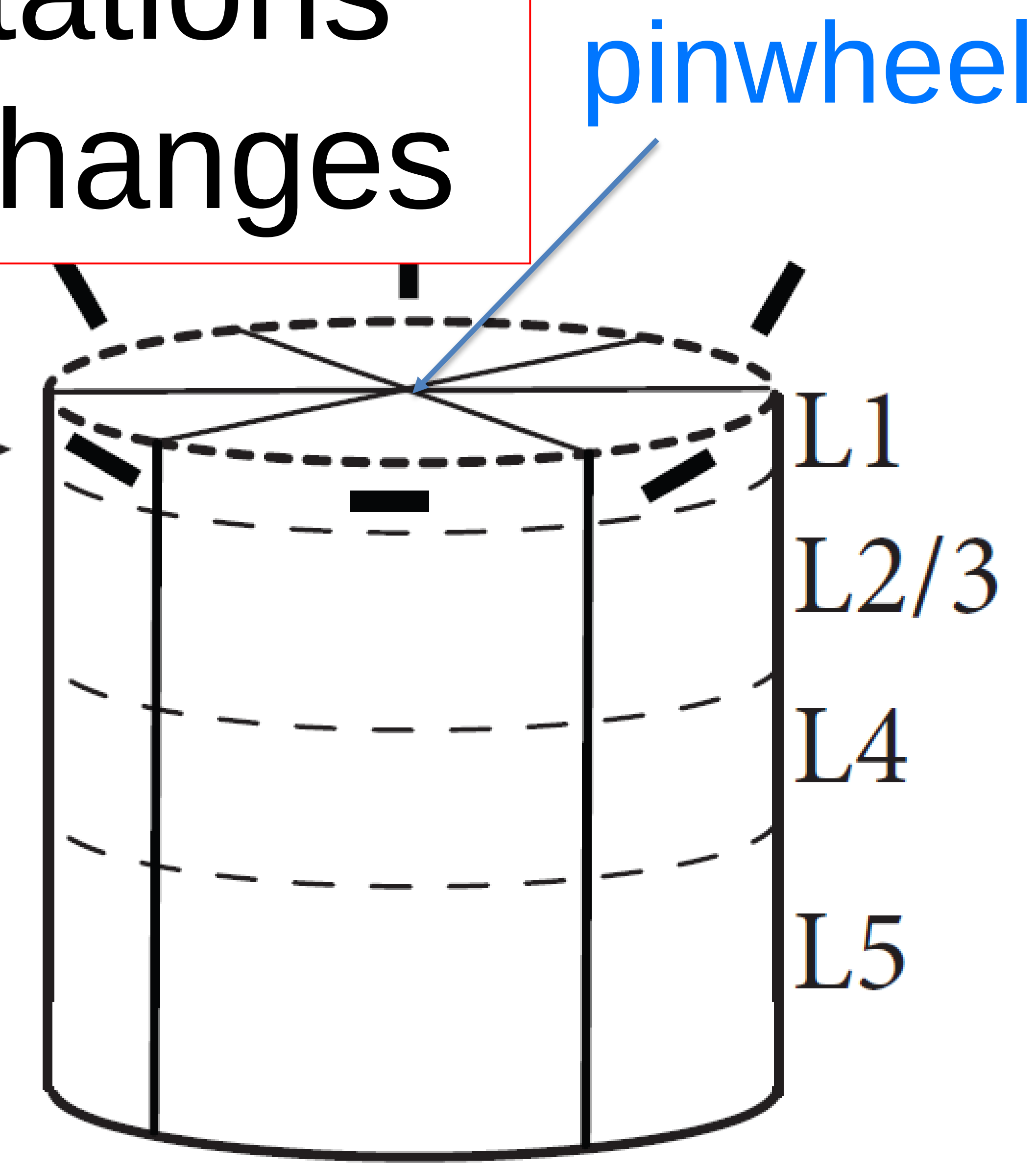
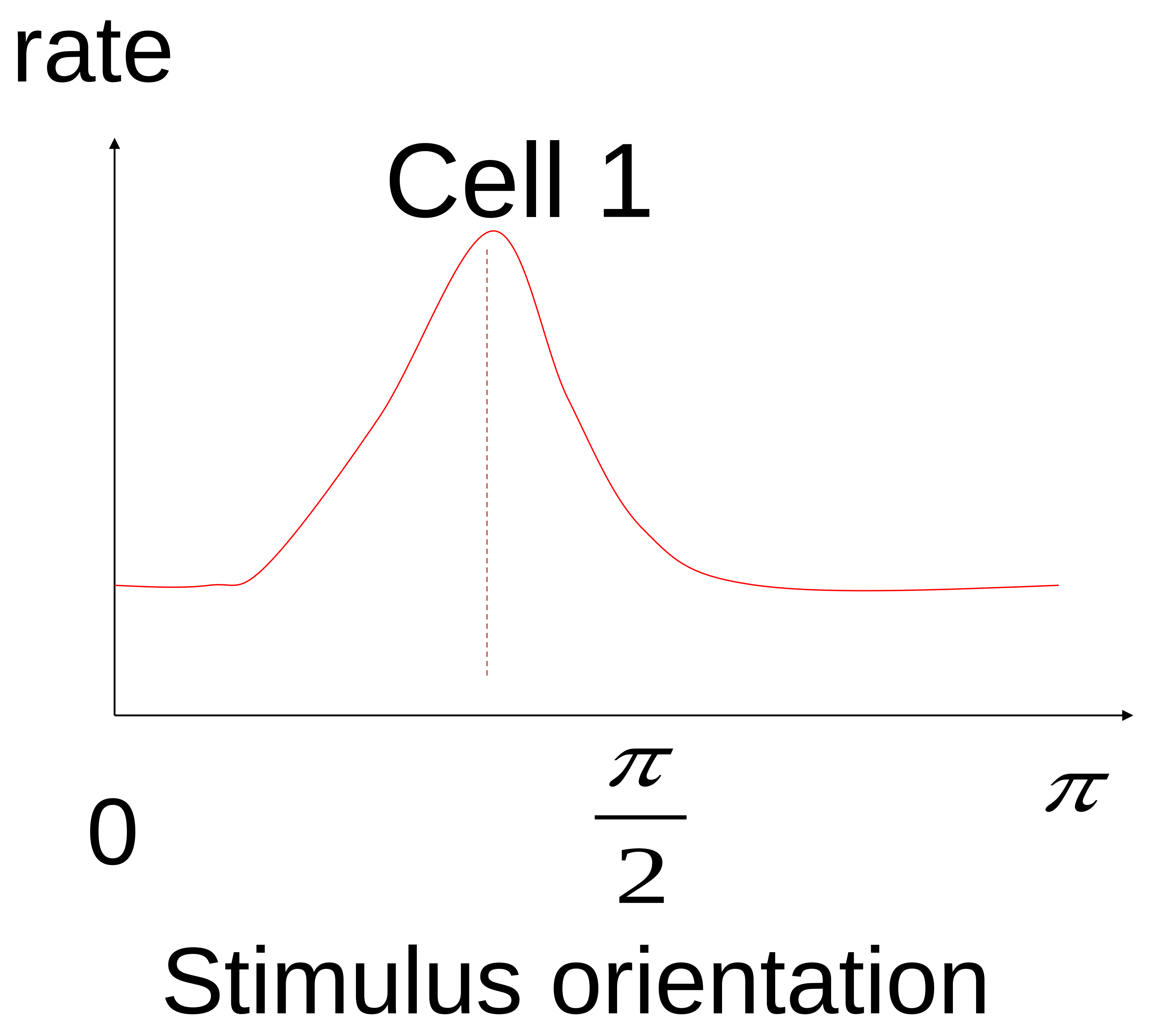


Image: Gerstner et al. Neuronal Dynamics (2014)

Bonhoeffer&Grinvald, 1991; Bressloff&Cowan, 2002; Kaschube et al. 2010

8.3. Do Orientation Columns exist? Do identical cells exist?



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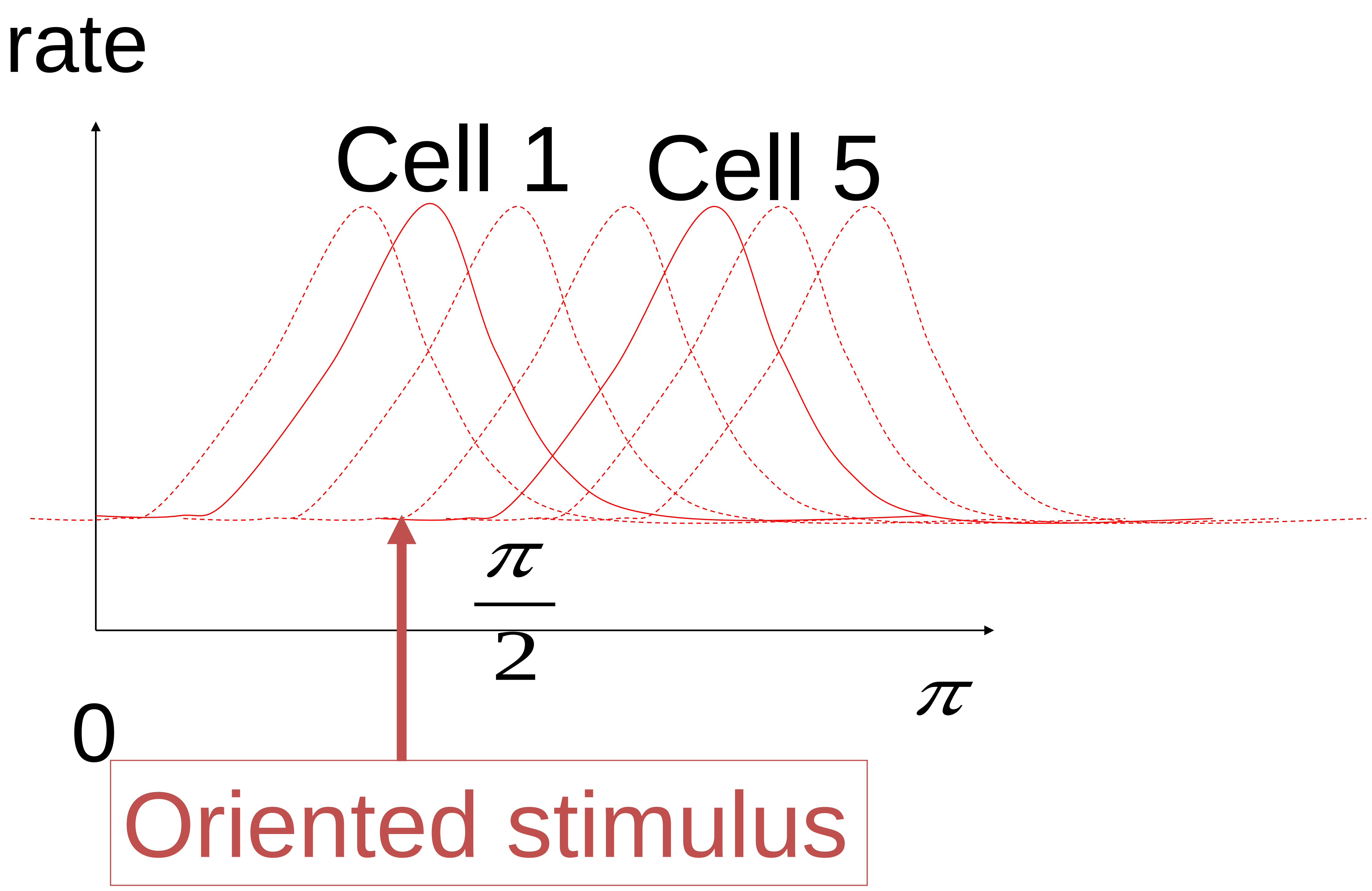
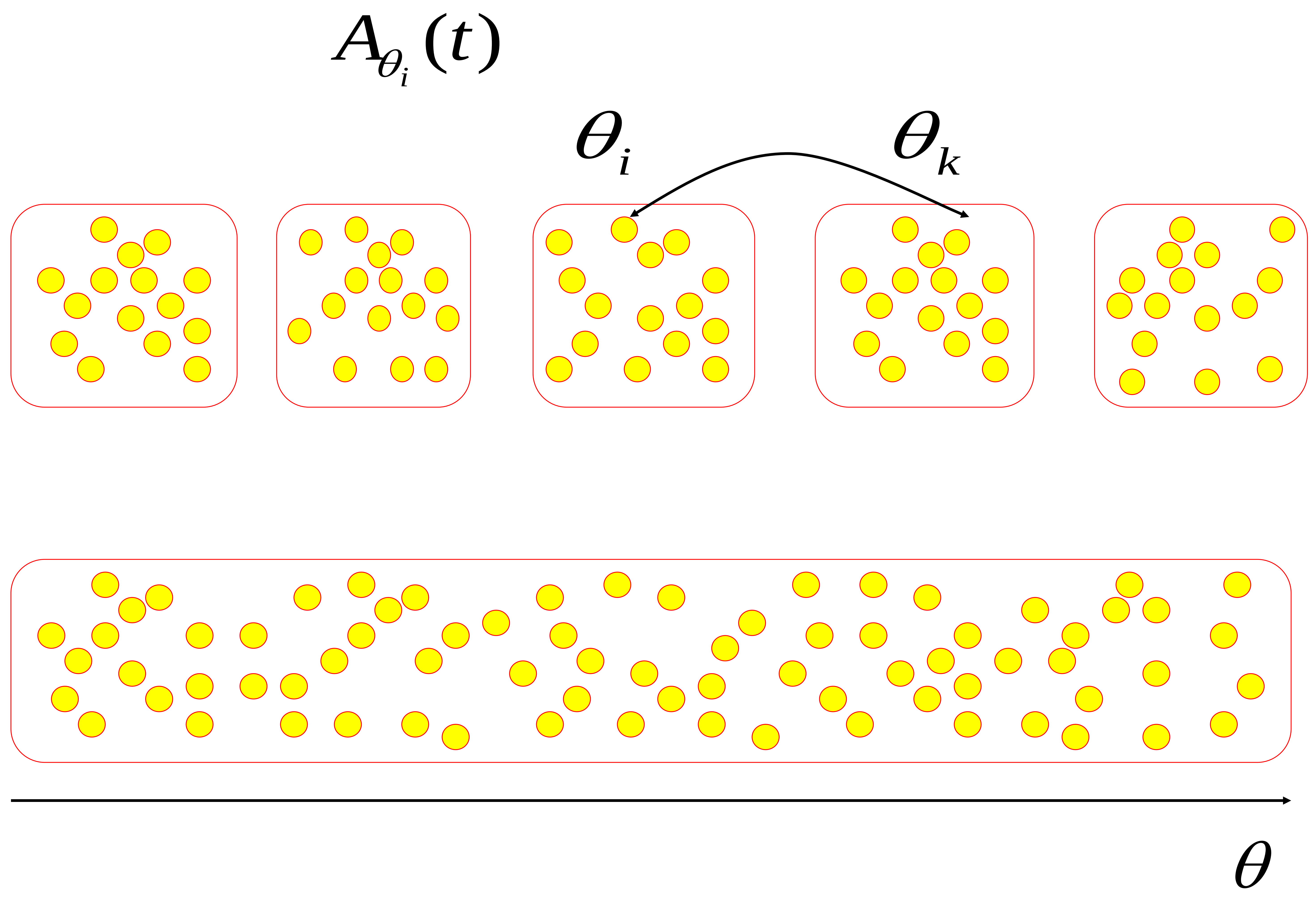


Coarse coding

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

8.3. multiple populations → continuum



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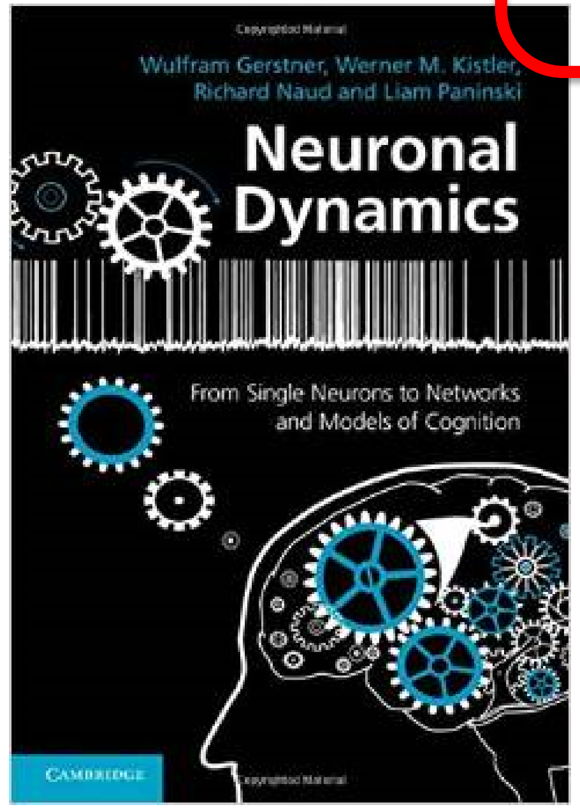

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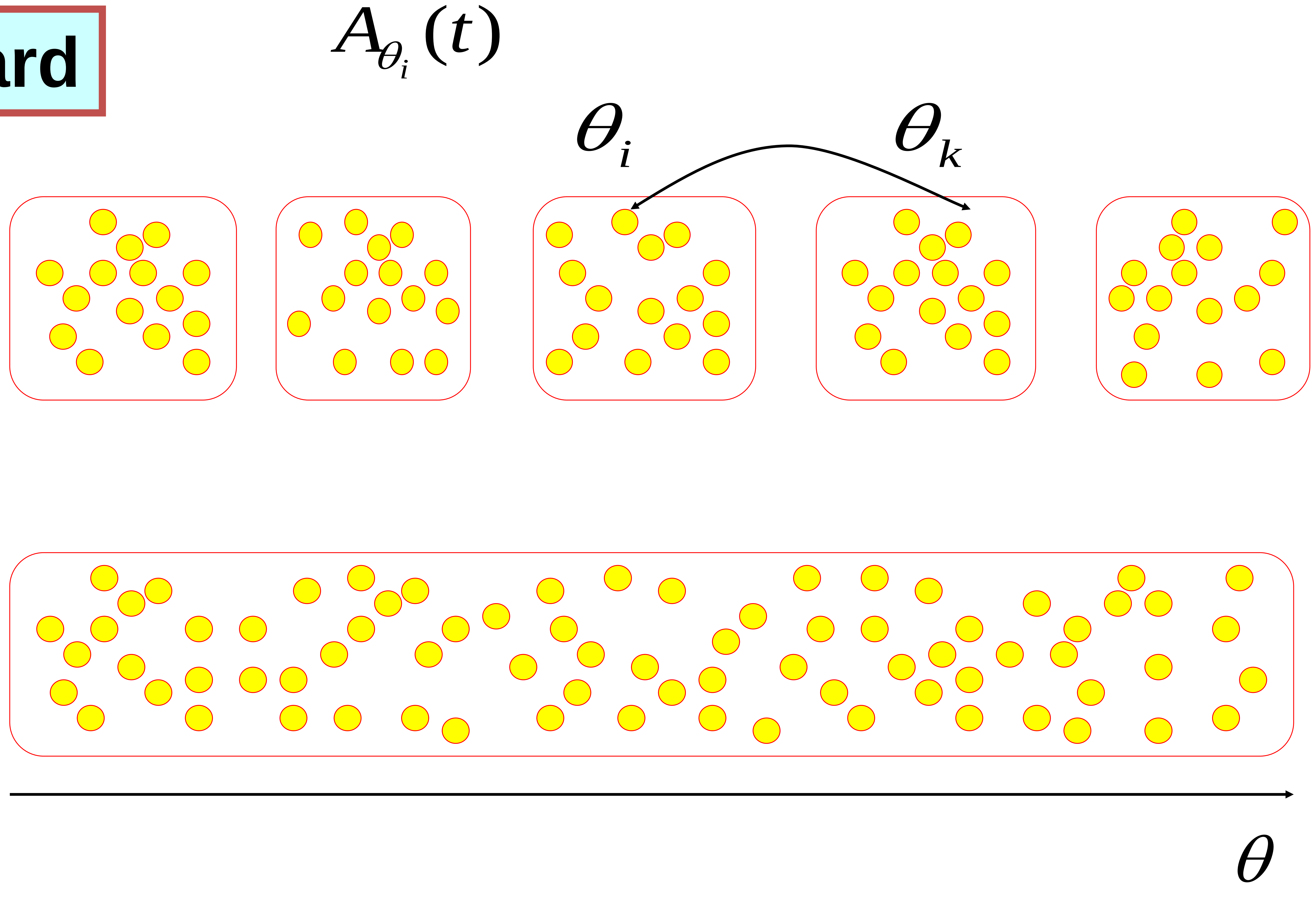
8.4. multiple populations → continuum

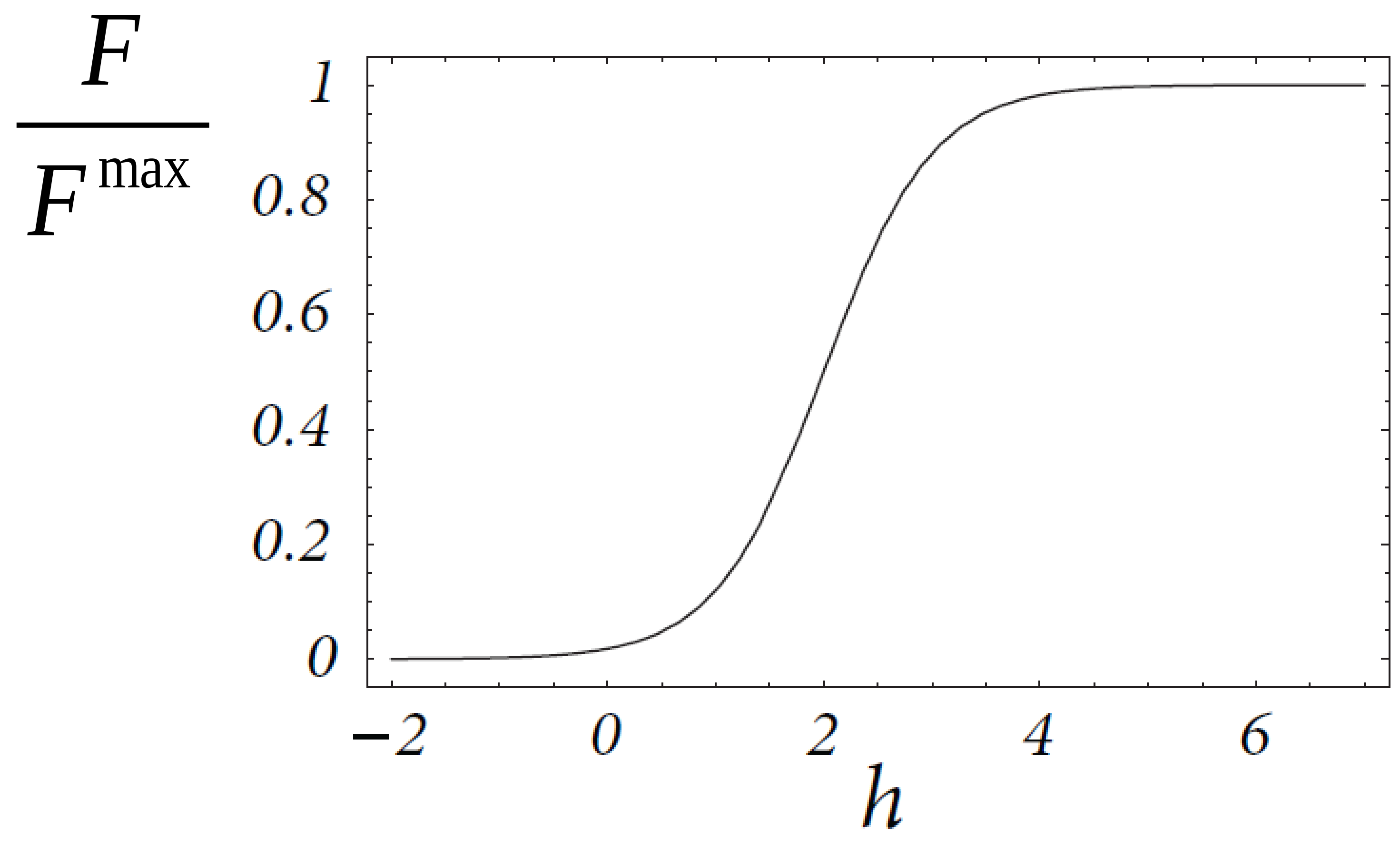
Blackboard



8. 4: Field equation (continuum model) *Wilson and Cowan, 1973*

Population activity

$$A(x,t) = F(h(x,t))$$



Membrane potential caused by input

$$\tau \frac{d}{dt} h(x,t) = -h(x,t) + R\, I(x,t)$$

$$I(x,t) = I^{ext}(x,t) + I^{netw}(x,t)$$

$$I^{netw}(x,t) = d \int w(x-x',t)\, A(x',t)\, dx'$$

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

1 field = 1 integro-differential equation

Exercise 1.1 now (stationary solution)

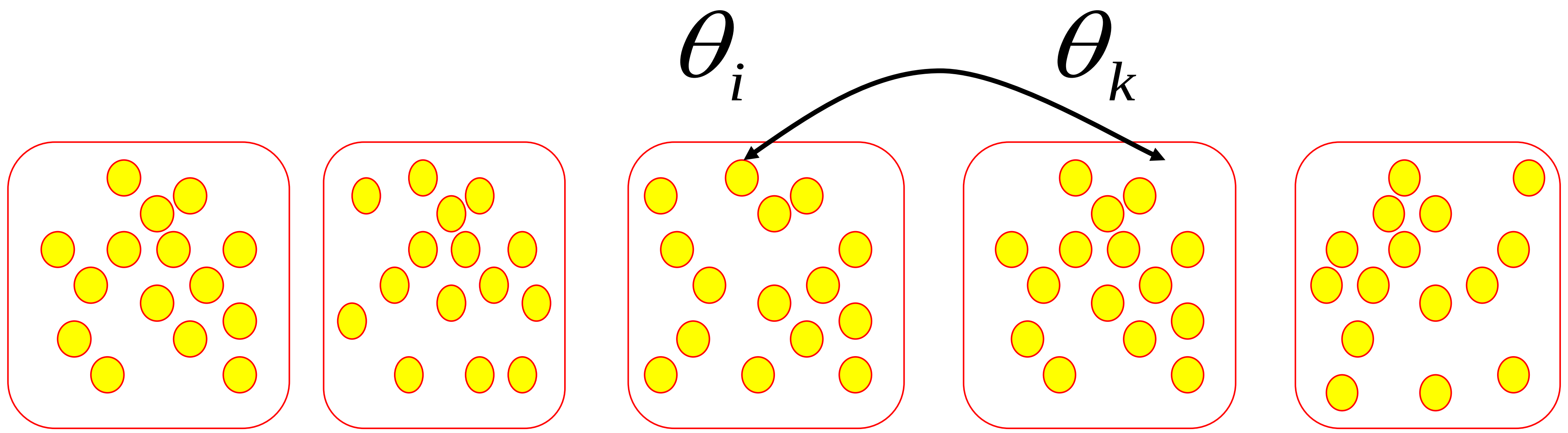
Consider a continuum model,
Find analytical solutions:

- spatially uniform solution $A(x,t) = A_0$

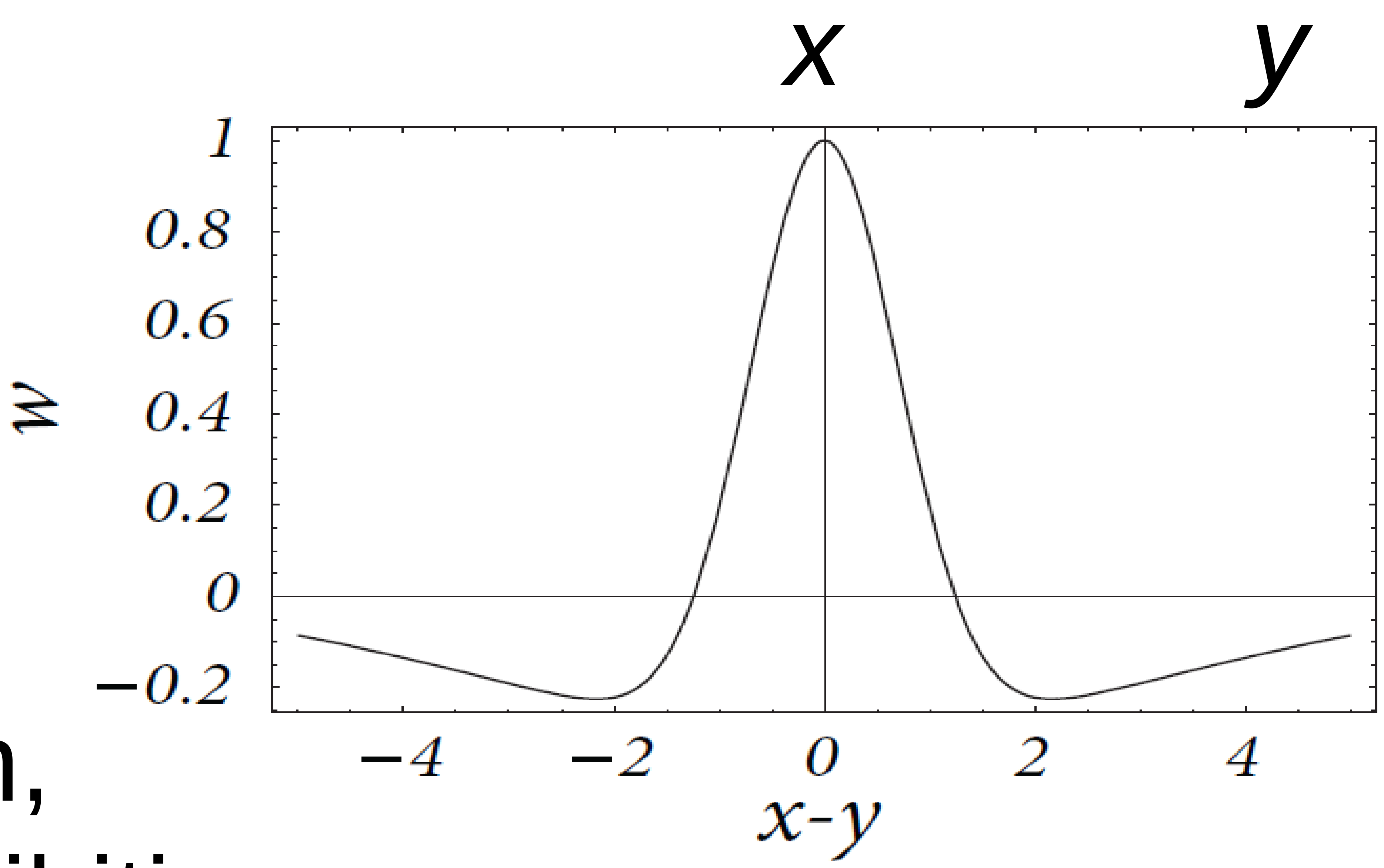
Next lecture at 11:15

If done: start with Exercise 1.2 now (spatial stability)

8.4: coupling across continuum

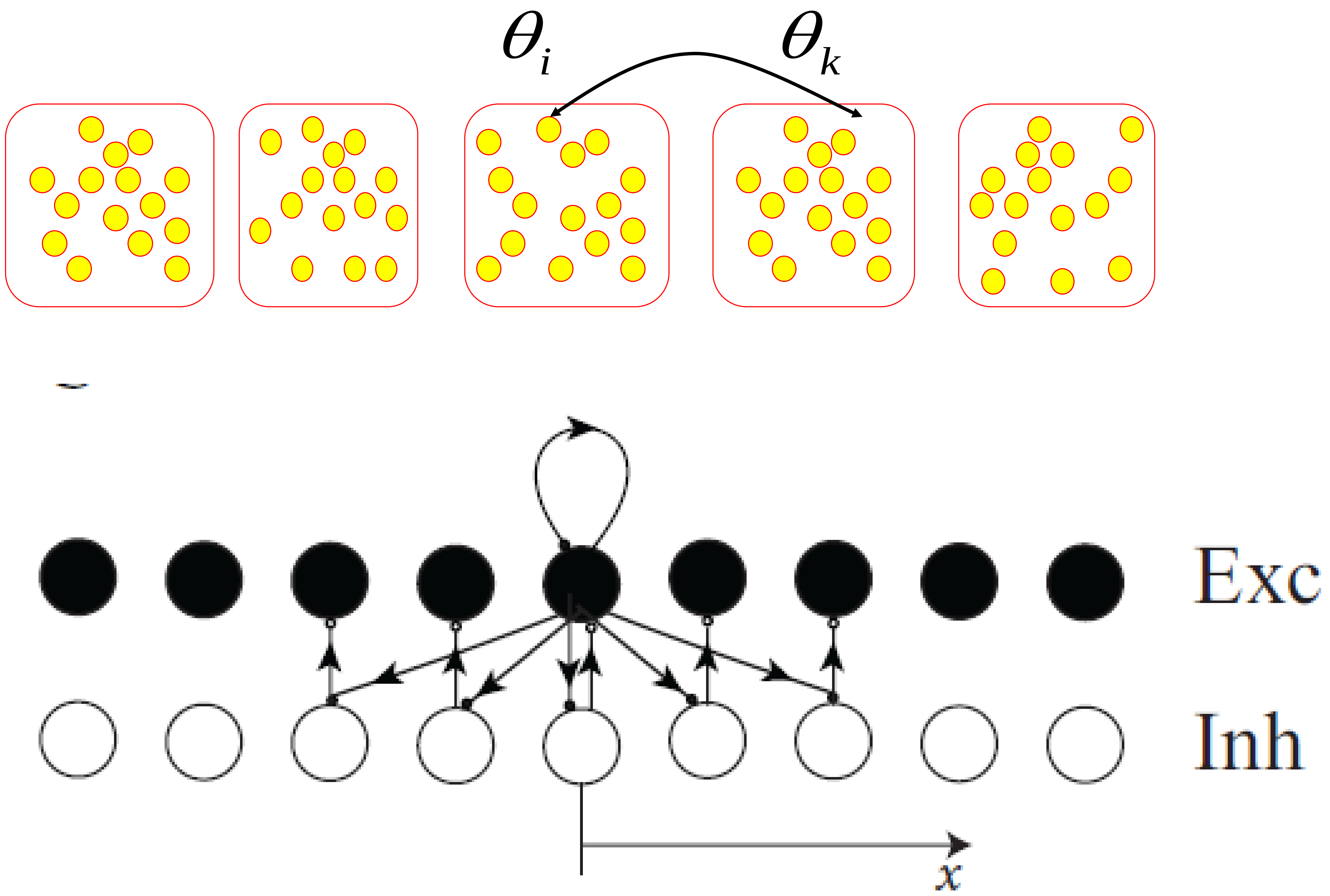


Mexican hat



local excitation,
long-range inhibition

8.4: more realistic cortical coupling



Effective long-range negative interaction with local inhibition

8. 4: Summary: Field equations and coupling

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

-field equations = population activity models in the spatial continuum

-coupling often distance-dependent

$$w(x,x') = w(x-x')$$

-activity $A = F(h(t))$

-effective long-range inhibition instead of local inhibitory neurons

-variable x can represent space or abstract quantity (e.g., orientation)

Biological Modeling of Neural Networks

ÉCOLE POLYTECHNIQUE
FÉDÉRALE DE LAUSANNE

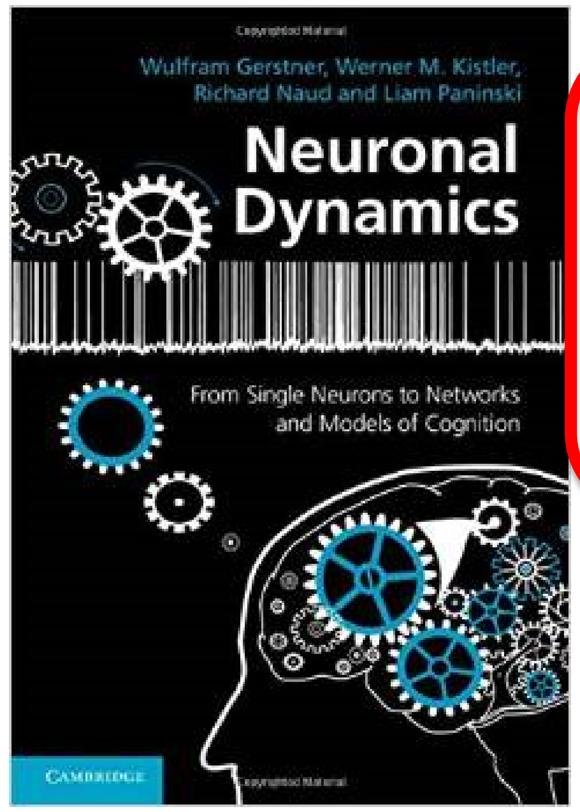
Week 8 – Continuum models: Cortical fields and perception

Wulfram Gerstner

EPFL, Lausanne, Switzerland

Reading for week 8:
NEURONAL DYNAMICS
Ch. 18

Cambridge Univ. Press



8.1. Aims and challenges
- review: mean-field arguments

8.2. Transients
- generalized integrate-and-fire model
- transients can be sharp or slow

8.3. Spatial continuum (cortex)
- orientation columns

8.4. Spatial continuum (model)
- field equations

8.5. Solution types
- uniform solution
- bump solution

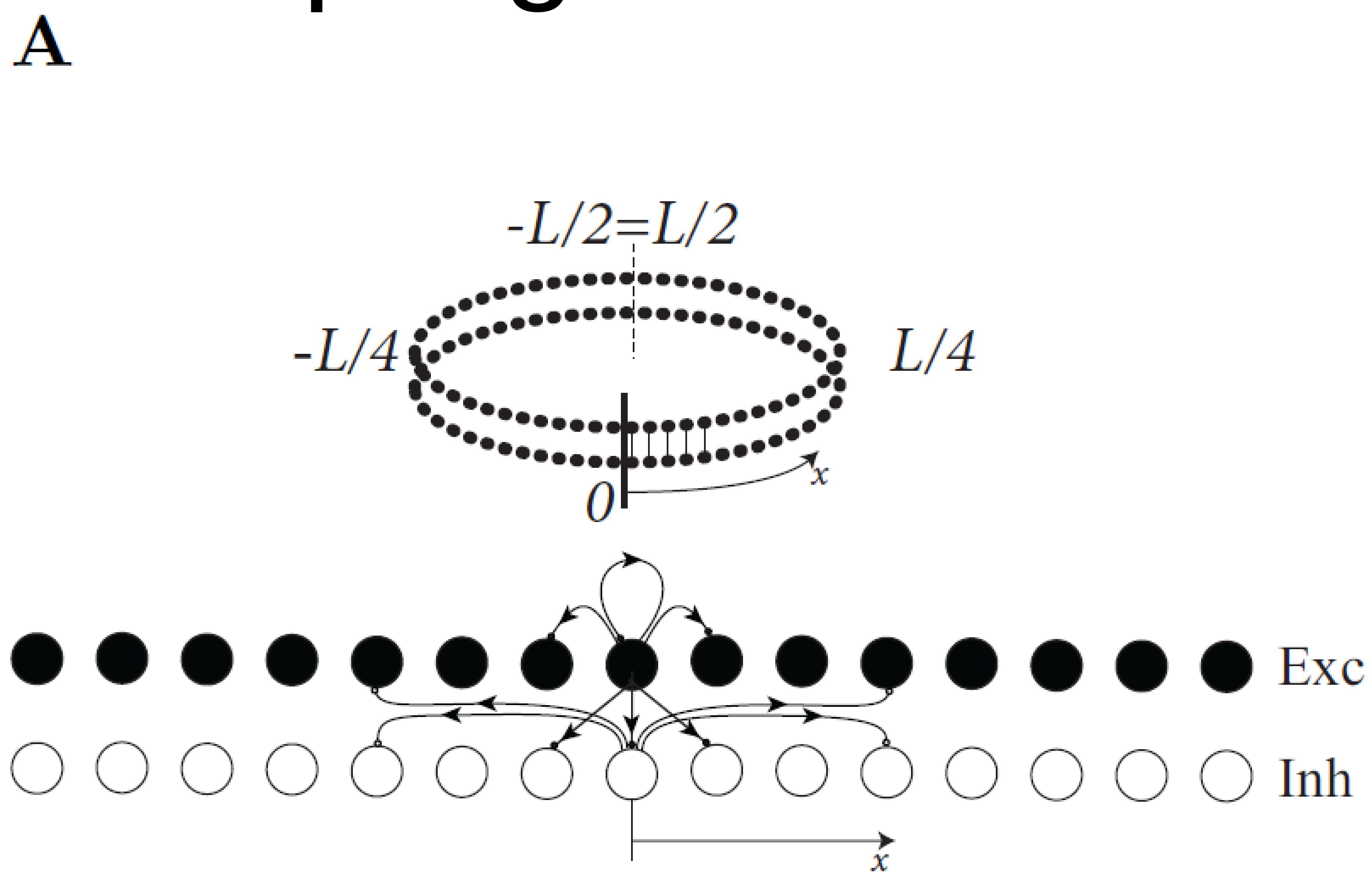
8.6. Perception

8.7. Head direction cells

8.5. Two Solution Types (ring model)

Coupling:

Input-driven regime



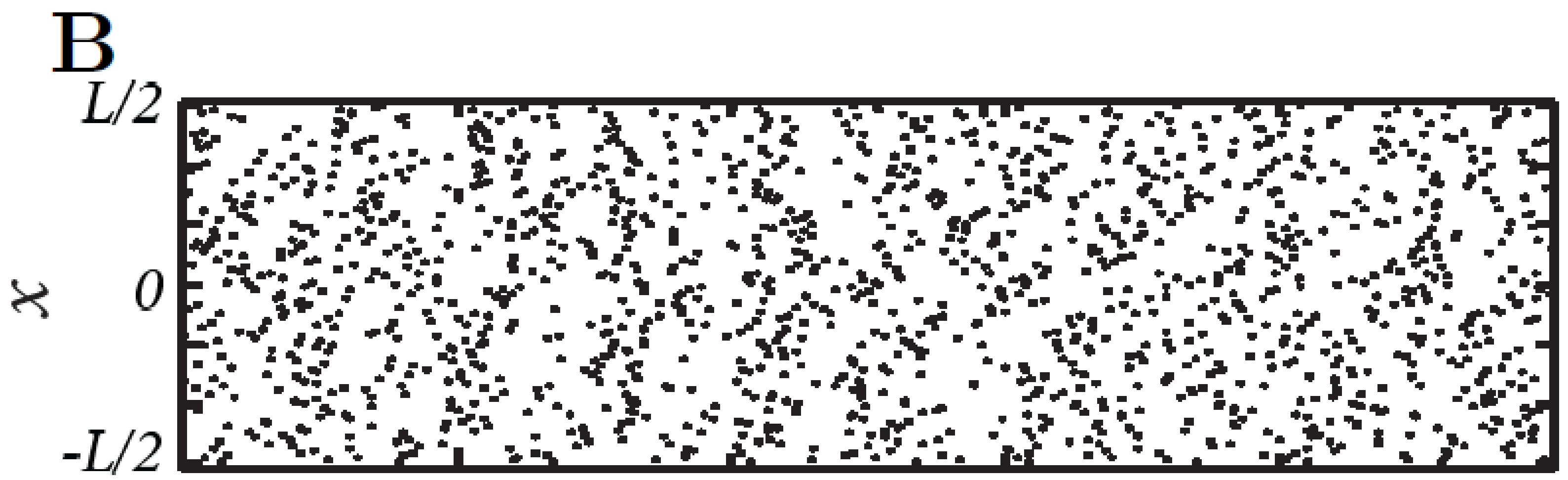
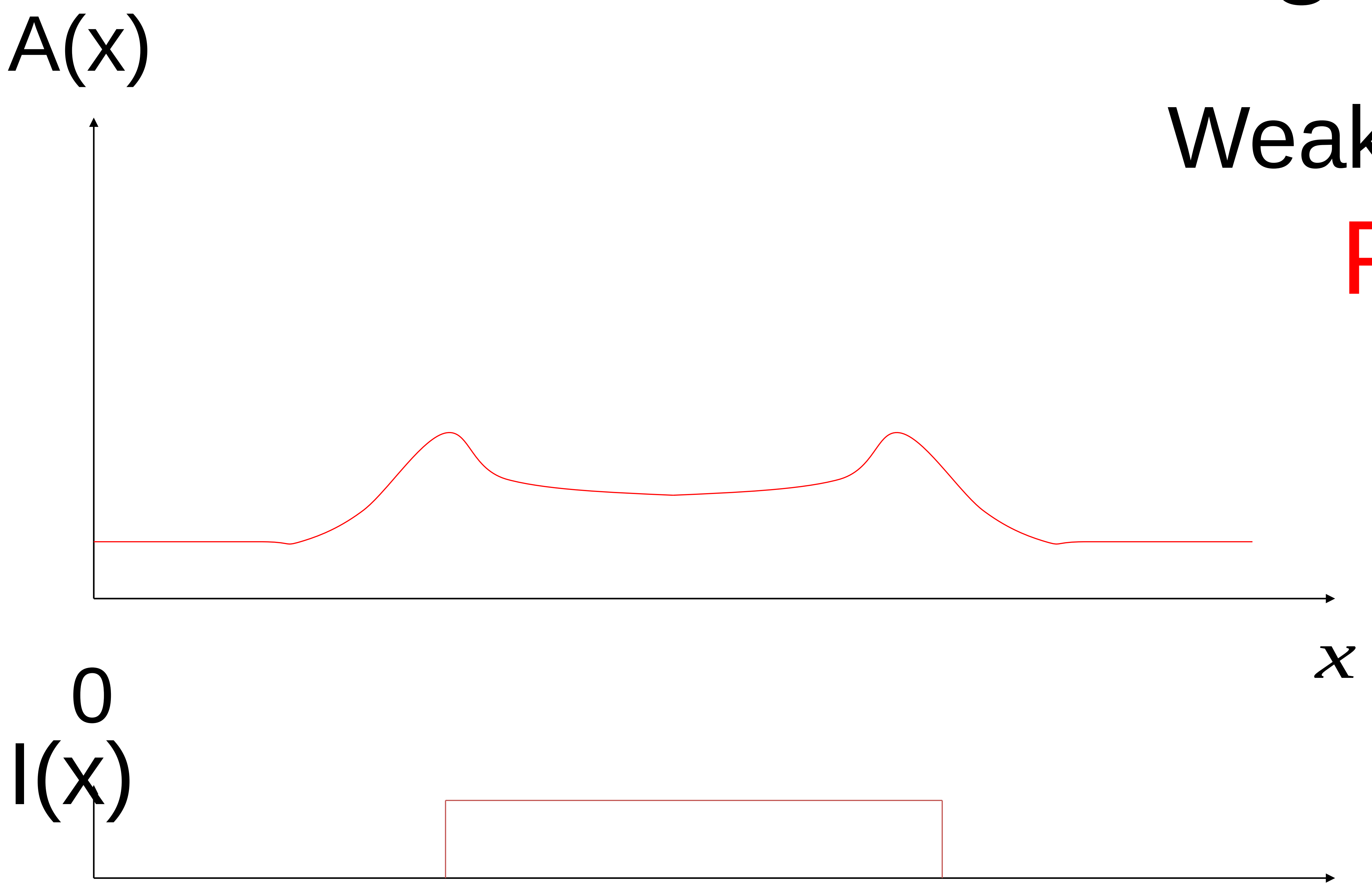


Image: Neuronal Dynamics, Gerstner et al., Cambridge Univ. Press (2014),

8.5. Solution types: input driven regime

Field Equations:
Wilson and Cowan, 1973

I. Edge enhancement



Weaker lateral connectivity

Possible interpretation of visual cortex cells:

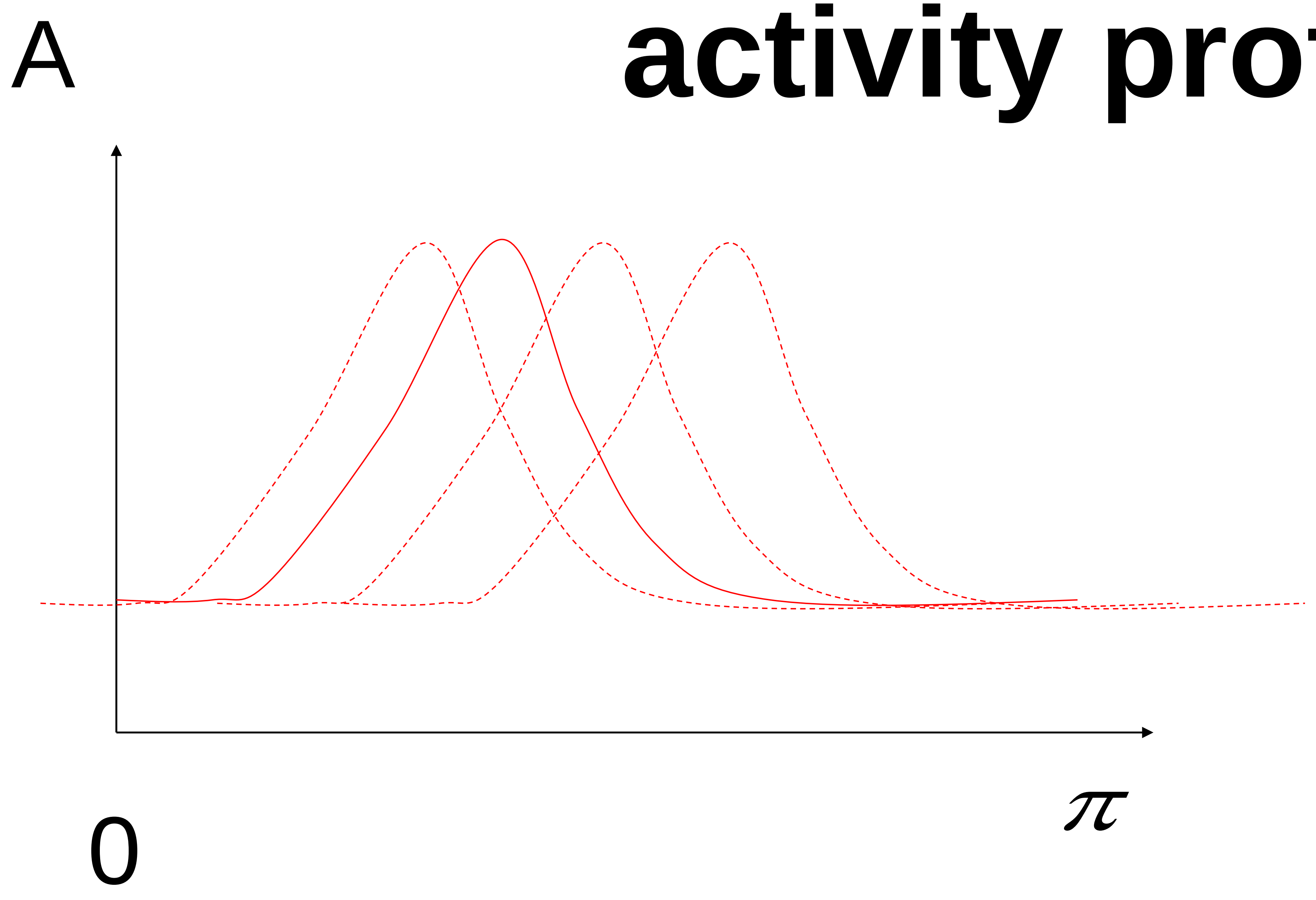
(see later today)

8.5. Solution types: bump solution

Field Equations:
Wilson and Cowan, 1972

II: Bump formation:
activity profile in the absence of input

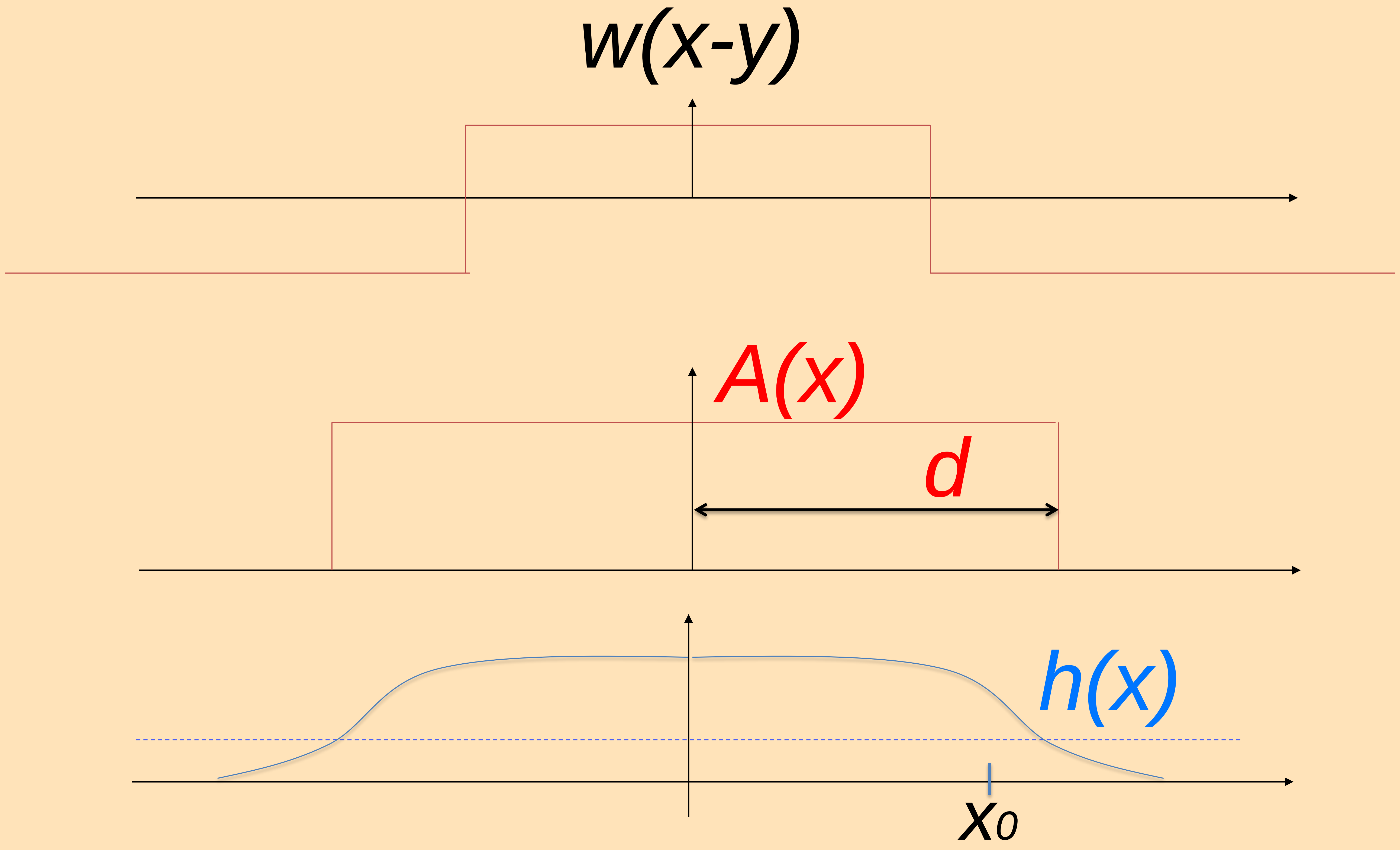
strong lateral connectivity



Possible interpretation
of head direction cells:
→ (see later today)

Exercise 2.1+2.2 now (stationary bump solution)

Consider a continuum model with step gain-fuctnion,
Find analytically the bump solutions



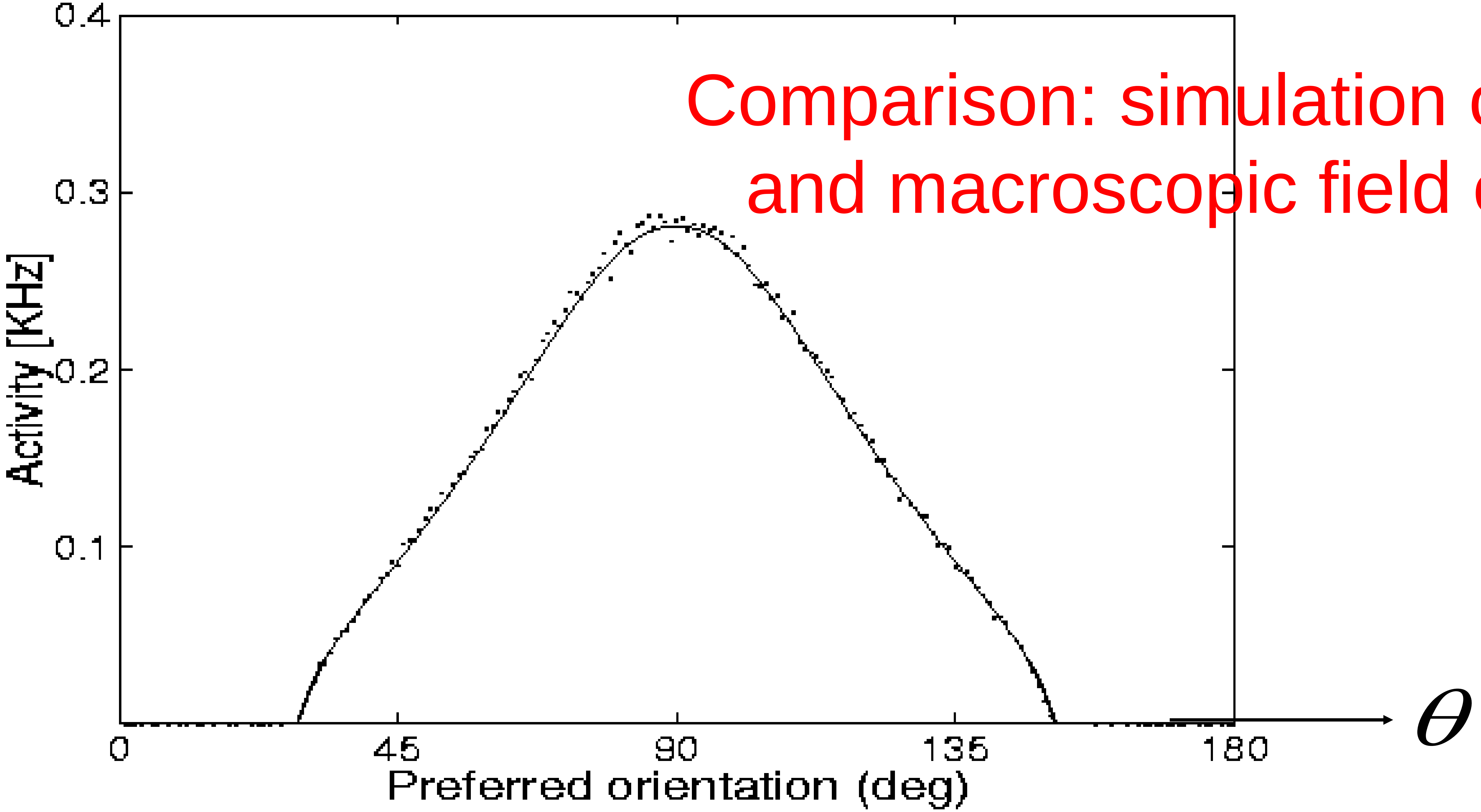
Next lecture at 11:40

calculate input potential at location x_0

8.5. Solution types: bump solution

Spiridon&Gerstner

$$A(\theta,t) = A(\theta)$$



Comparison: simulation of neurons and macroscopic field equation

Continuum: stationary profile

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

8.5. Solution types: multiple bump solutions with local interaction

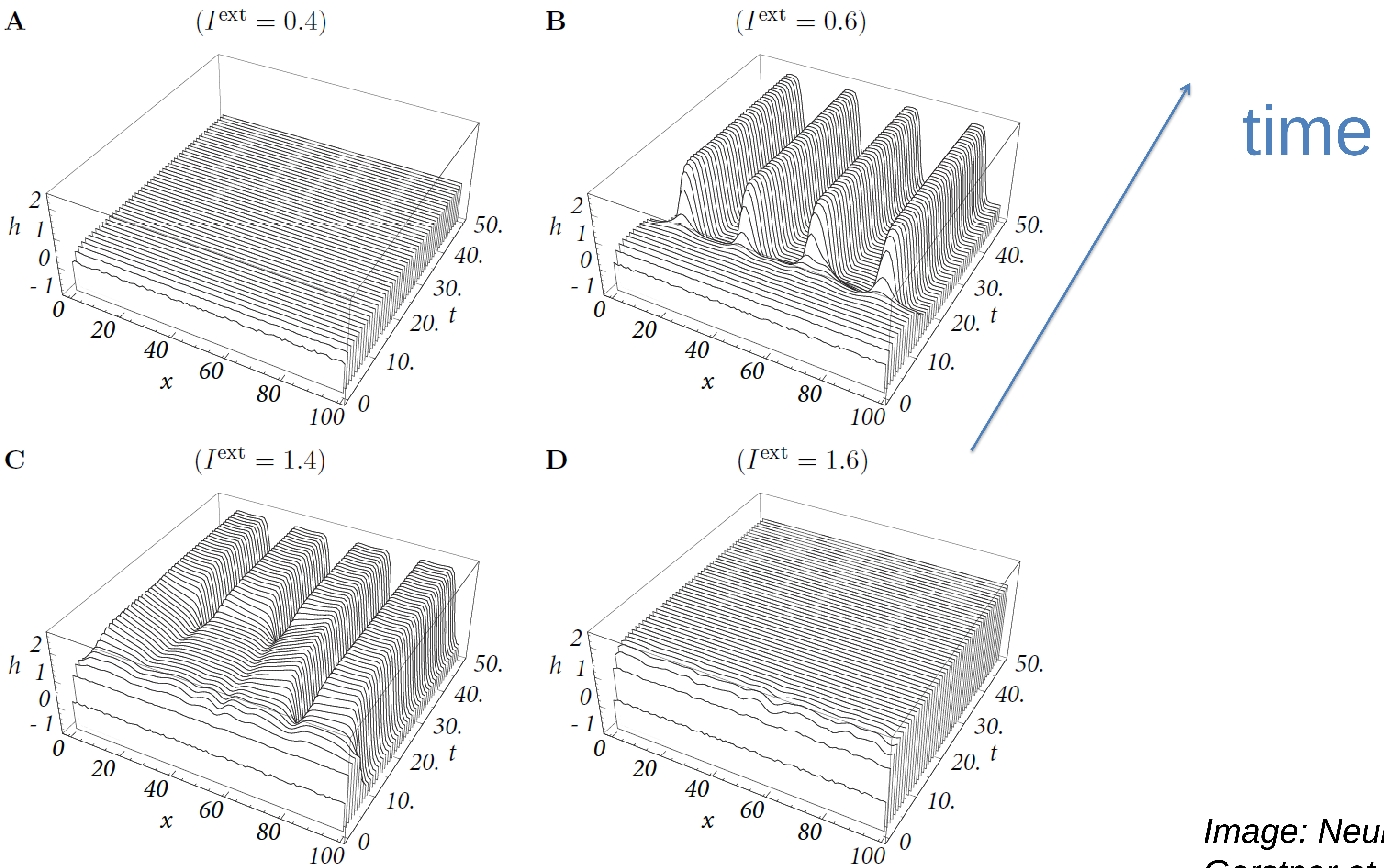


Image: Neuronal Dynamics, Gerstner et al., Cambridge Univ. Press (2014),

Quiz → see exercises 1 and 2

Solution of Field equations (1-dimensional ring model)

[ ] If a solution exists with a single bump localized around x_0, equivalent solutions exist at other locations.

[ ] If the interaction is Mexican hat, a stationary solution can have at most a single bump

[ ] A homogeneous solution (constant in time and space) always exists

[ ] A homogeneous solution (constant in time and space) is always stable

[ ] If I increase in a model the spatial scale of inhibition, the activity profile of an existing bump solution becomes broader

[ ] If I increase in a model the amplitude of excitation and the spatial scale of inhibition, a bump solution is more likely to exist

Biological Modeling of Neural Networks

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Week 8 – Continuum models: Cortical fields and perception

Wulfram Gerstner

EPFL, Lausanne, Switzerland

Reading for week 8:
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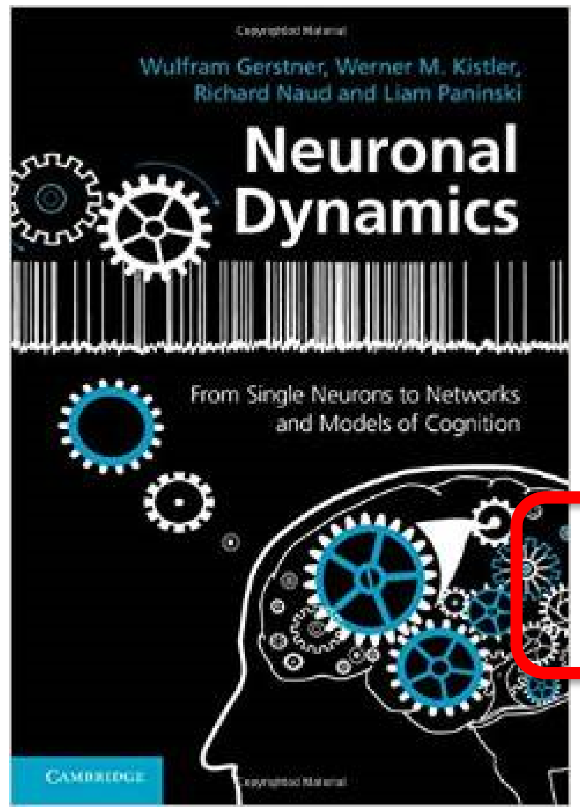

8.1. Aims and challenges
- review: mean-field arguments

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- transients can be sharp or slow

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- orientation columns

8.4. Spatial continuum (model)
- field equations

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- uniform solution
- bump solution

8.6. Perception

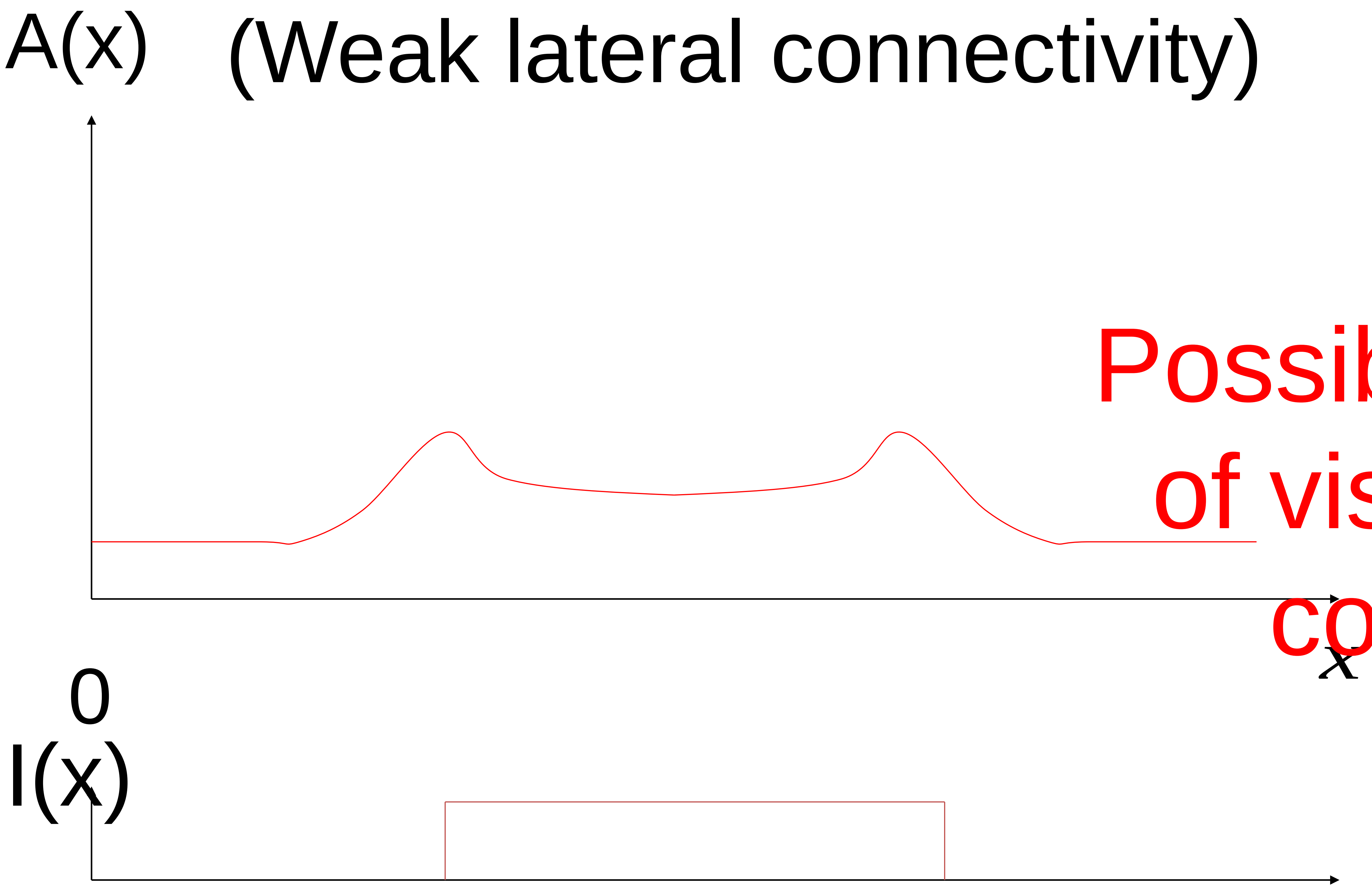
8.7. Head direction cells

8.6. uniform/input driven solution

Basic phenomenology

I. Edge enhancement

(Weak lateral connectivity)



Field Equations
for edge enhancement
Wilson and Cowan, 1973
Grossberg, 1973

Possible interpretation
of visual cortex cells:
contrast enhancement in
- orientation
- location

8.6. **Perception -grid illusion**

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

8.6. **Perception – Mach bands**

Mach, 1865, 1906

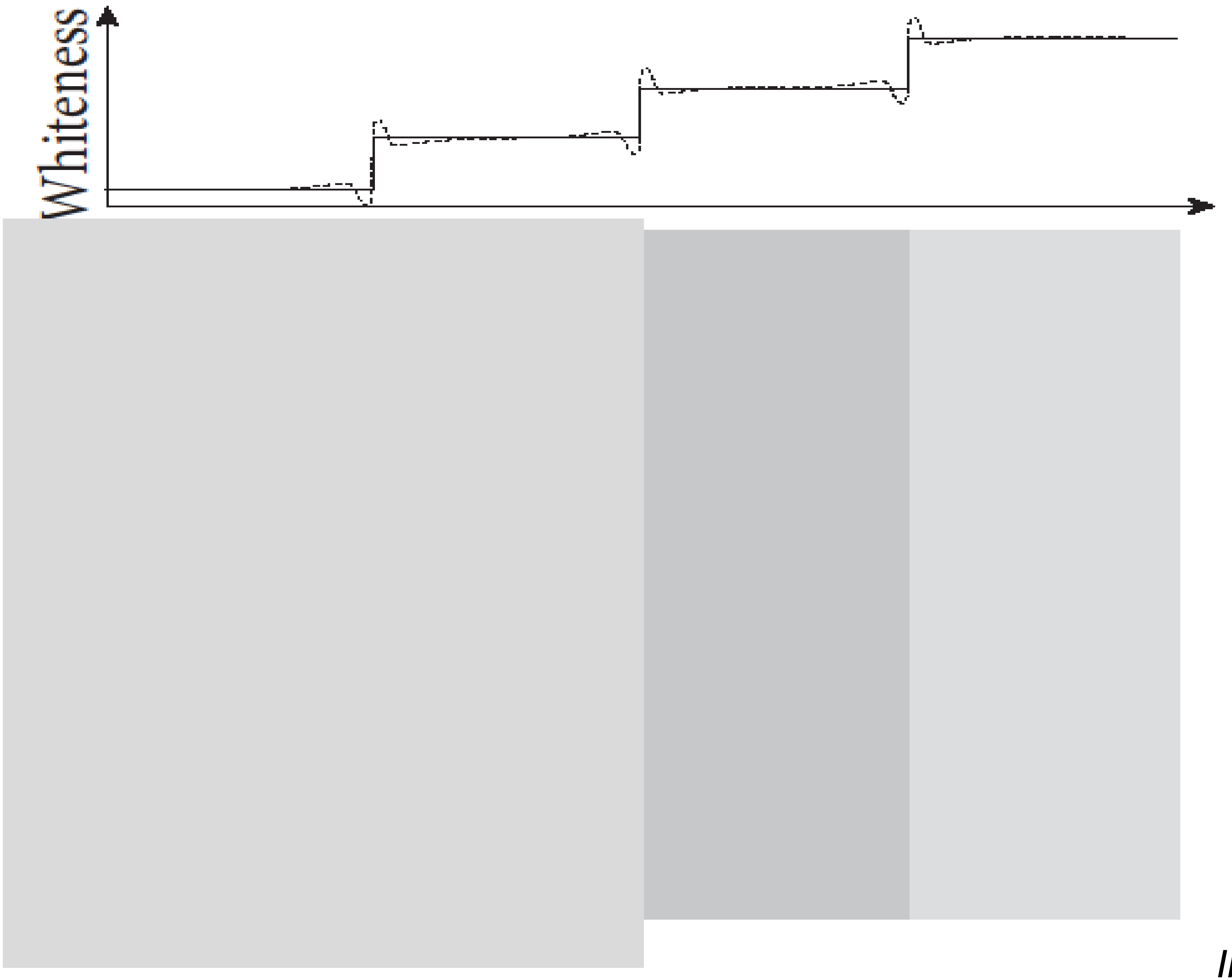
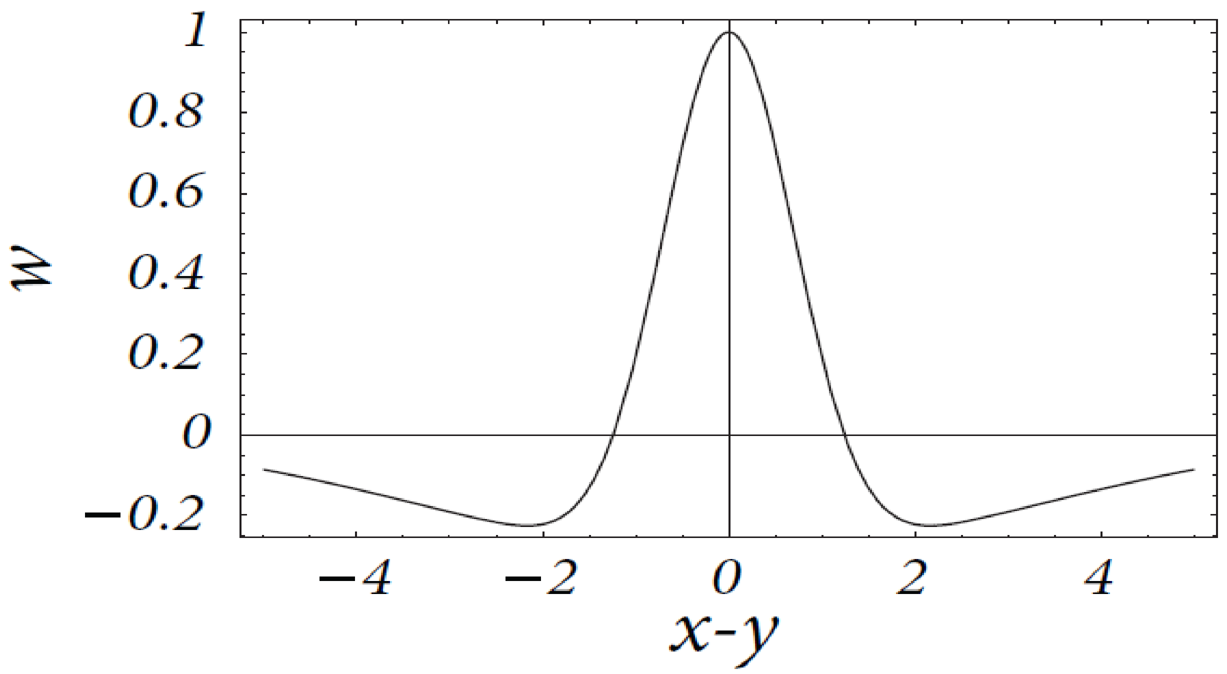
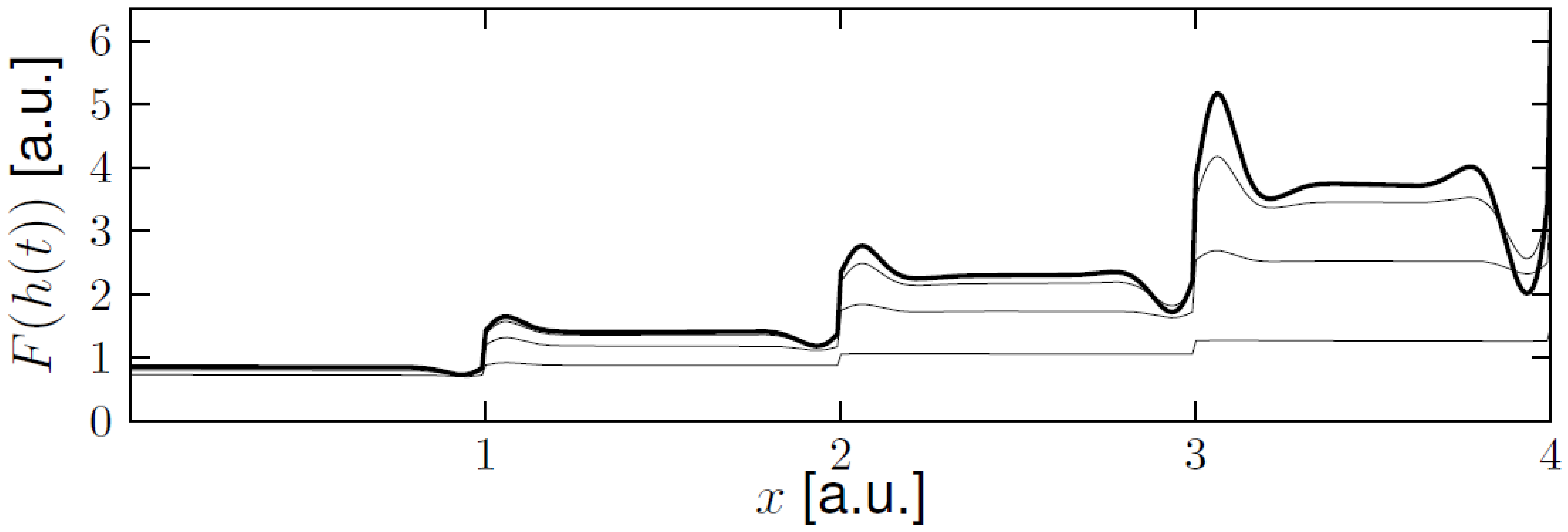


Image: Neuronal Dynamics, Gerstner et al., Cambridge Univ. Press (2014),

8.6. Mach bands in a continuum model

Mexican-hat coupling

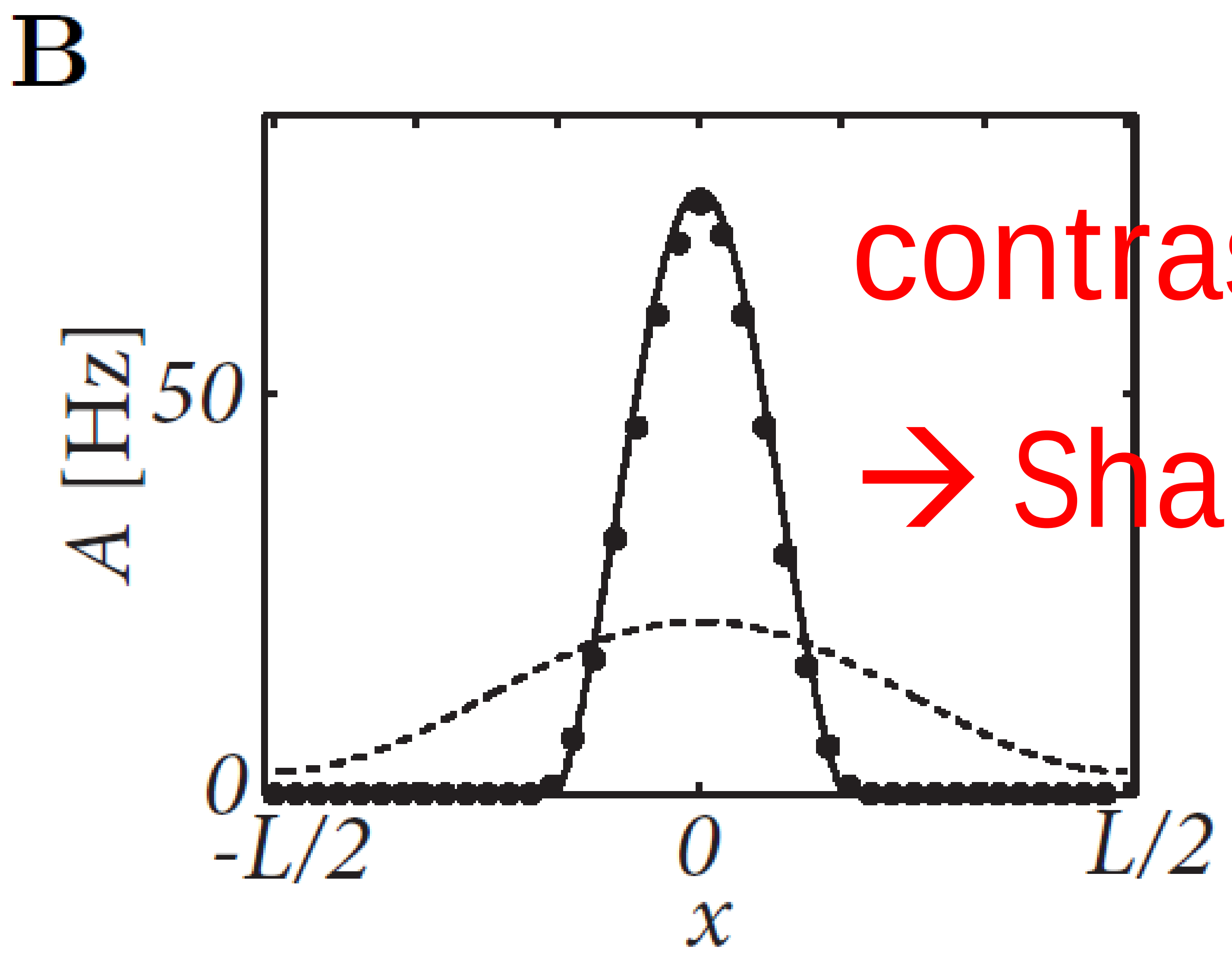




ig. 18.9: **A**. Mach bands in a field model with mexican hat

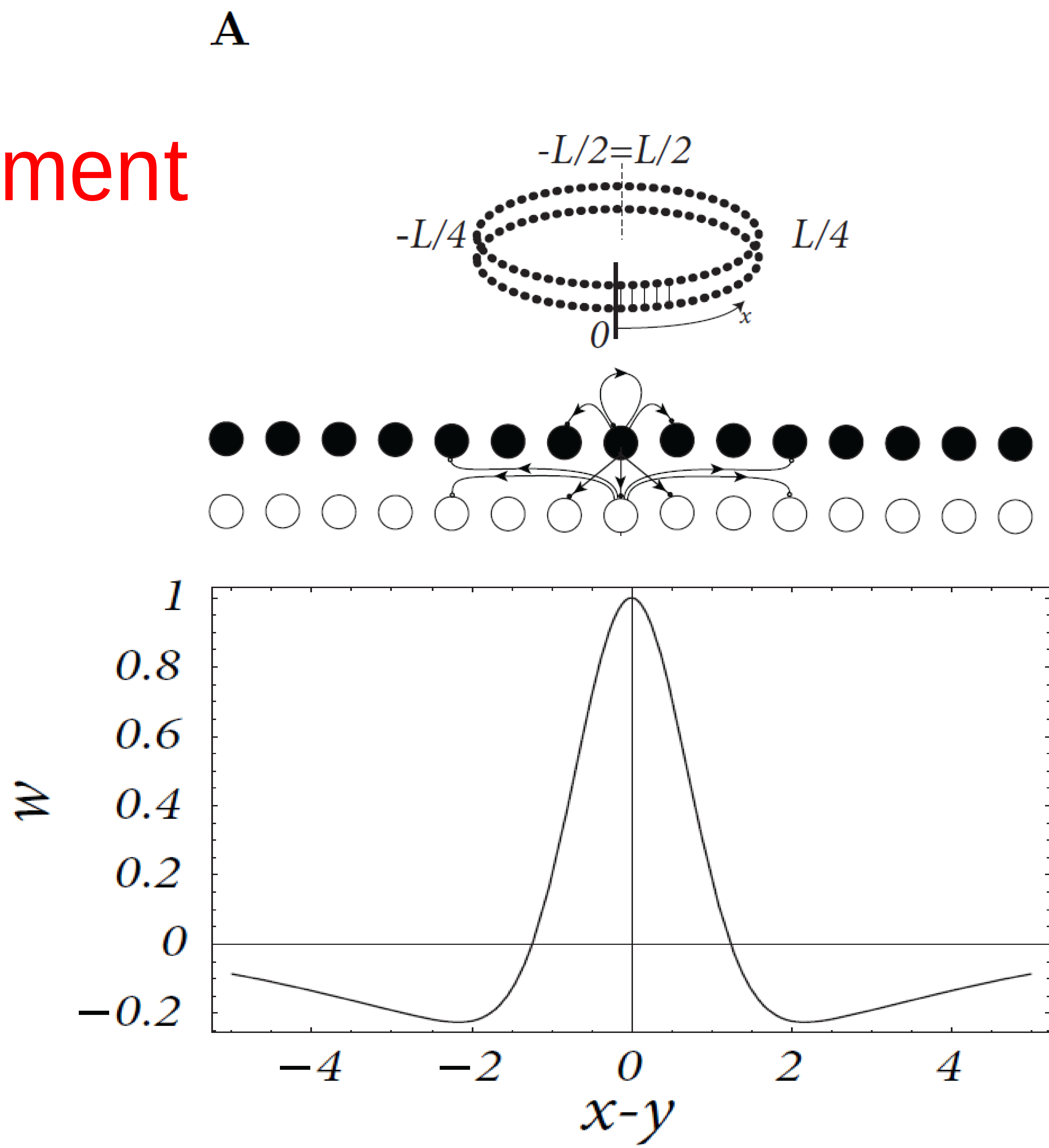
Image: Neuronal Dynamics, Gerstner et al., Cambridge Univ. Press (2014),

8.6: Field models and Perception: contrast enhancement



contrast enhancement

→ Sharpening



Shriki et al. (2003):
Ring model in input-driven regime, driven by broad input (dashed line), causes sharp activity bump;
See also: Ben-Yishai et al. 1995; Hansel and Sompolinsky, 1998

8.6: Field models and Perception: surround suppresion

Ozeki et al. (2009):

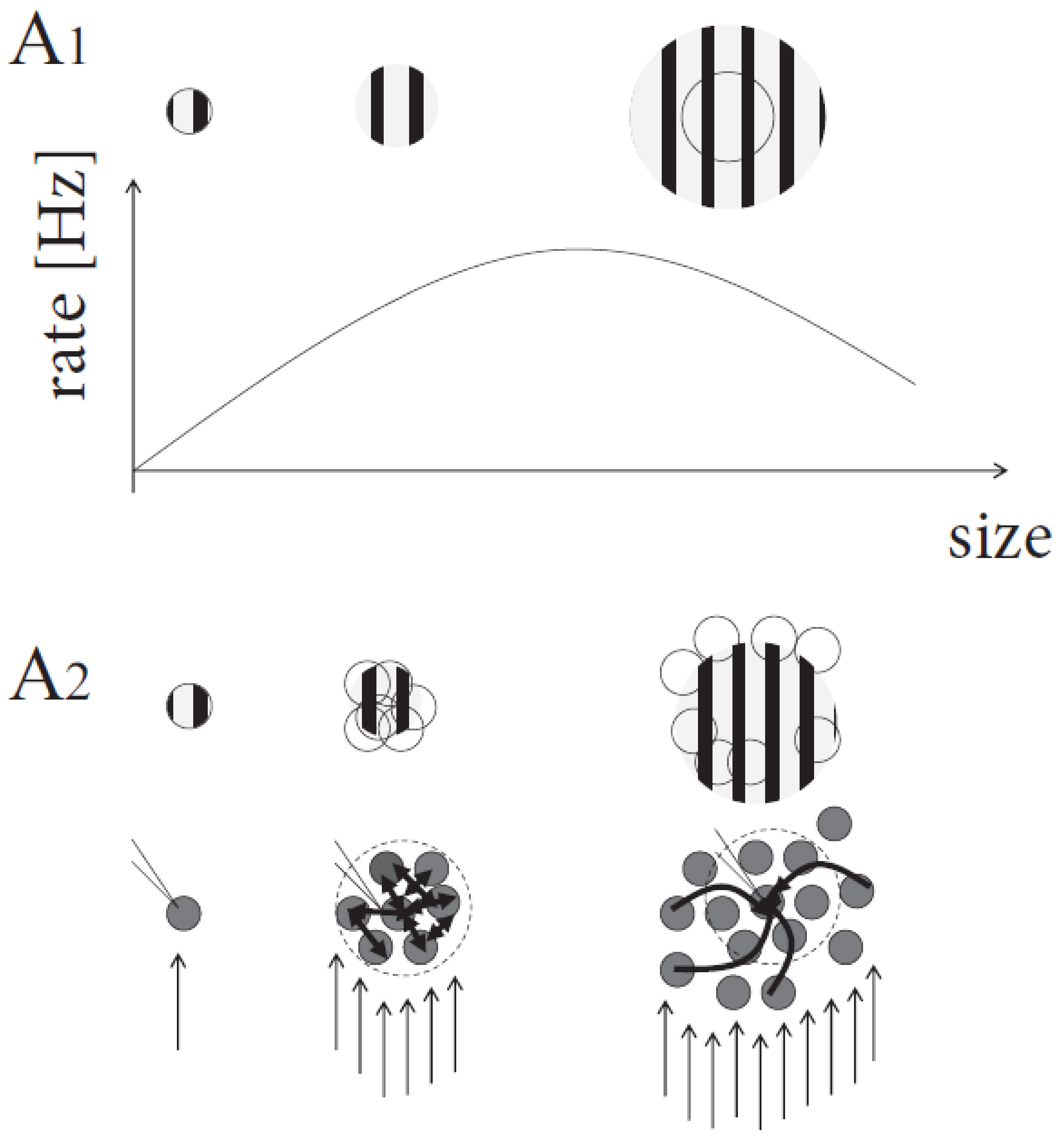


Fig. 18.12: Surround suppression.

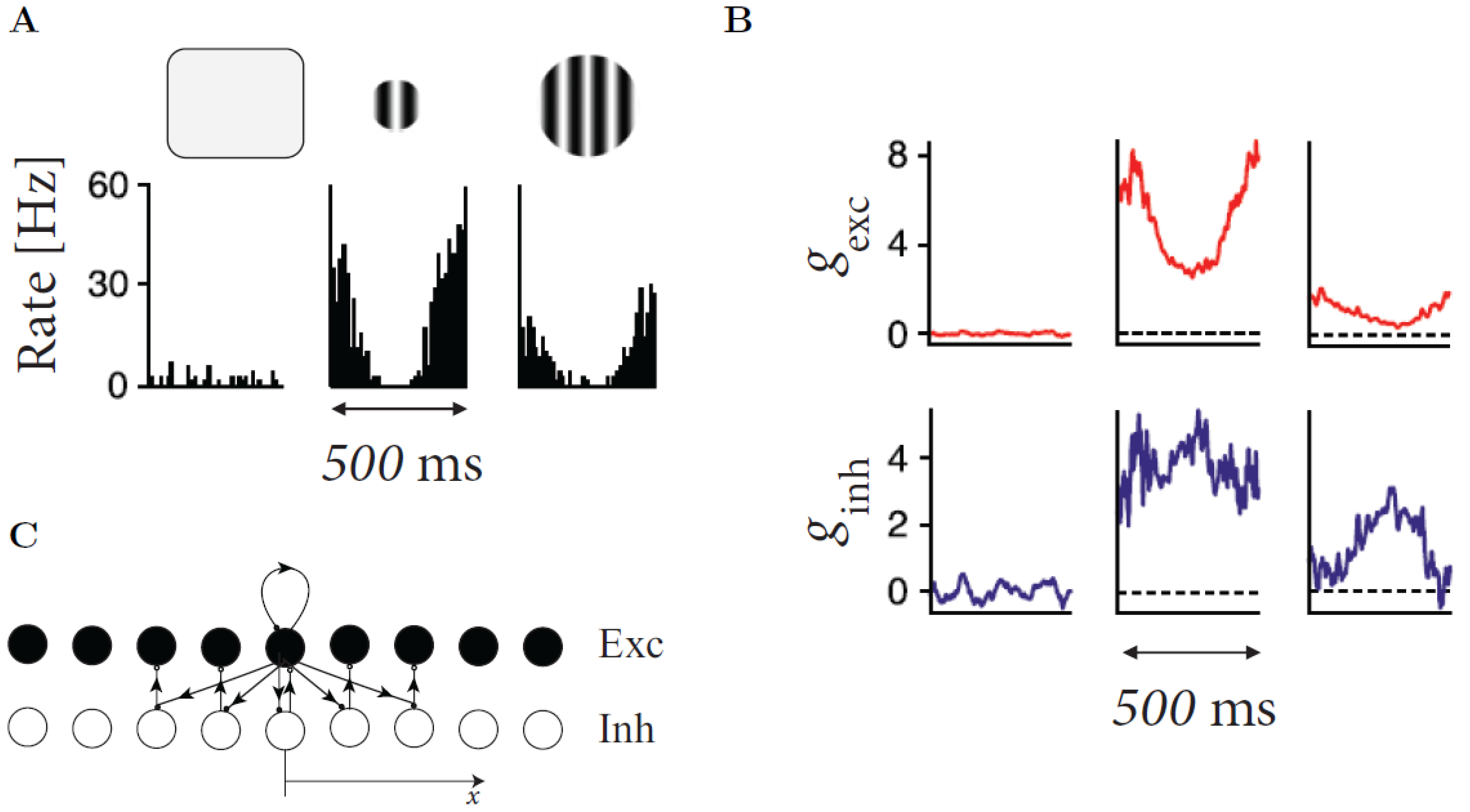


Fig. 18.13: Network stabilized by local inhibition. The schematic model could potentially explain why larger gratings lead not only to less excitatory input g_{exc}, but also to less inhibitory input g_{inh}. **A**. The firing rate as a function of the phase of the moving grating for the three stimulus conditions (blank screen, small and large grating). **B**.Top: Excitatory input into the cell. Bottom: Inhibitory input into the same cell. As in A, left, middle and right correspond to a blank screen, a small grating and or a large grating. Note that the larger grating leads to a reduction of both excitation and inhibition; adapted from (Ozeki et al., 2009). **C**. Network model with long range excitation and local inhibition. Excitatory neurons within a local population excite themselves (feedback arrow), and also send excitatory input to inhibitory cells (downward arrows). Inhibitory neurons project to local excitatory neurons.

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

8.6: Field models and Perception

-contrast enhancement is a stable psychophysical phenomenon

-Mach bands are one example

-the activity of V1 cell first increases and then decreases with size of stimulus

-both excitatory and inhibitory input into a cell show similar changes

-Mach bands can be explained by a continuum model with Mexican-hat interaction in the input-driven regime

-contrast enhancement = ‘sharpening’

Biological Modeling of Neural Networks

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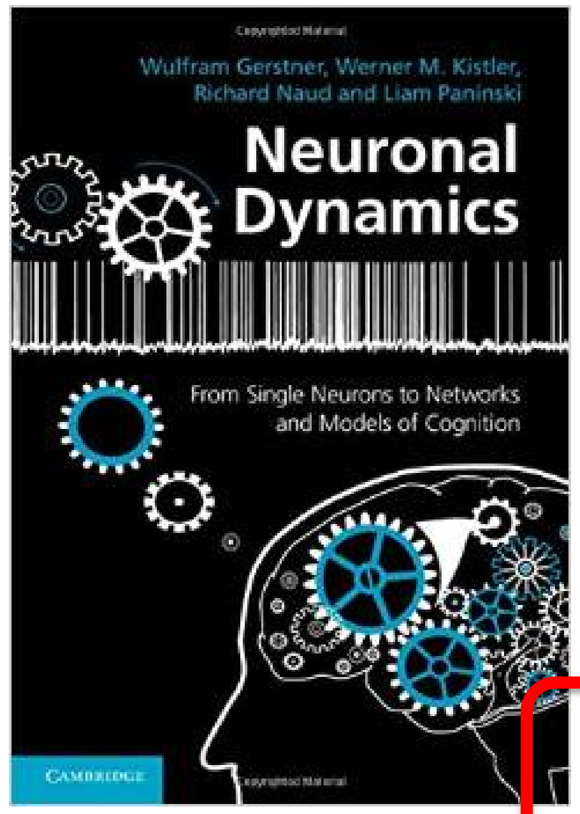

Cambridge Univ. Press

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- field equations

8.5. Solution types
- uniform solution
- bump solution

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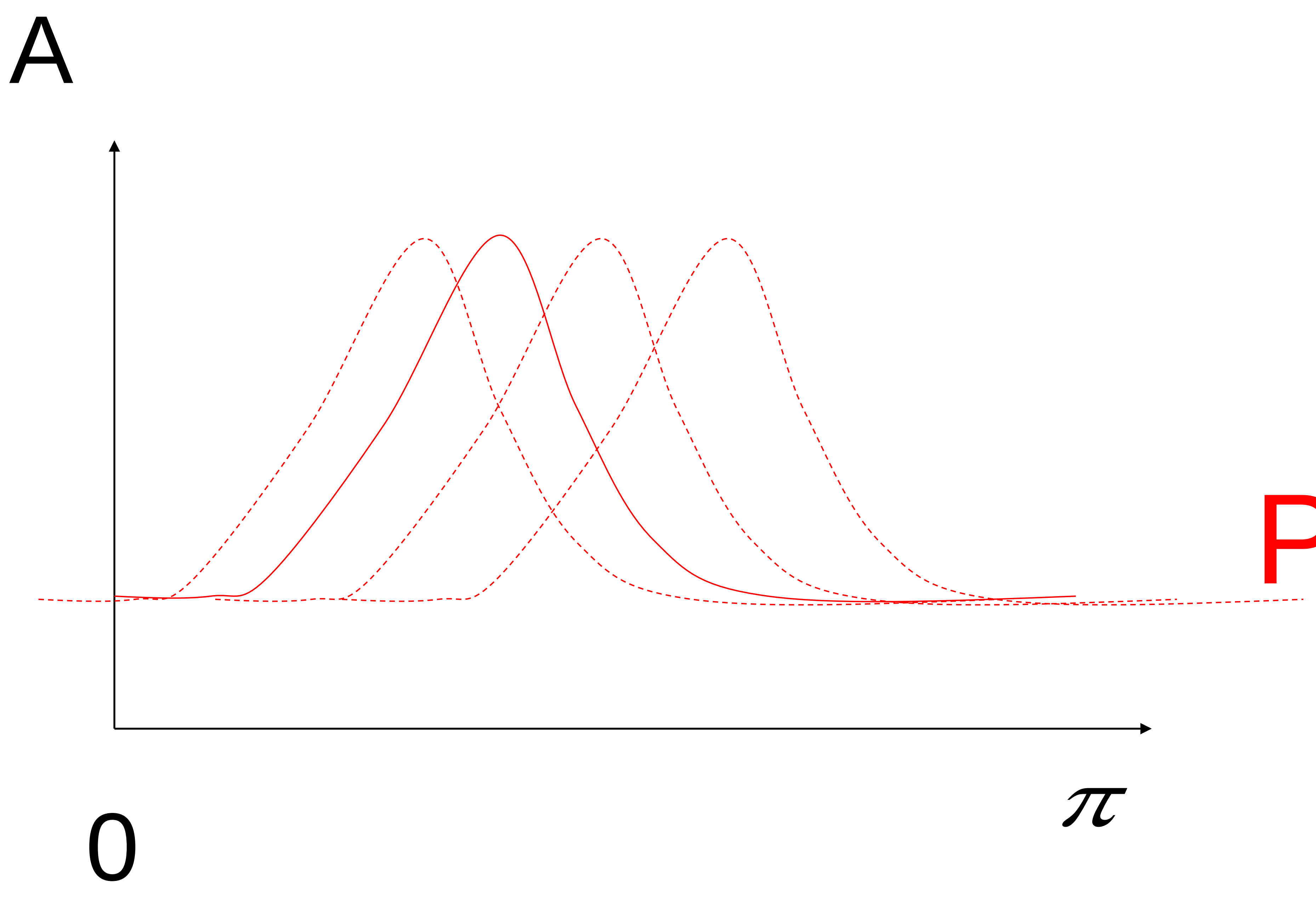
8.7. Head direction cells

Basic phenomenology

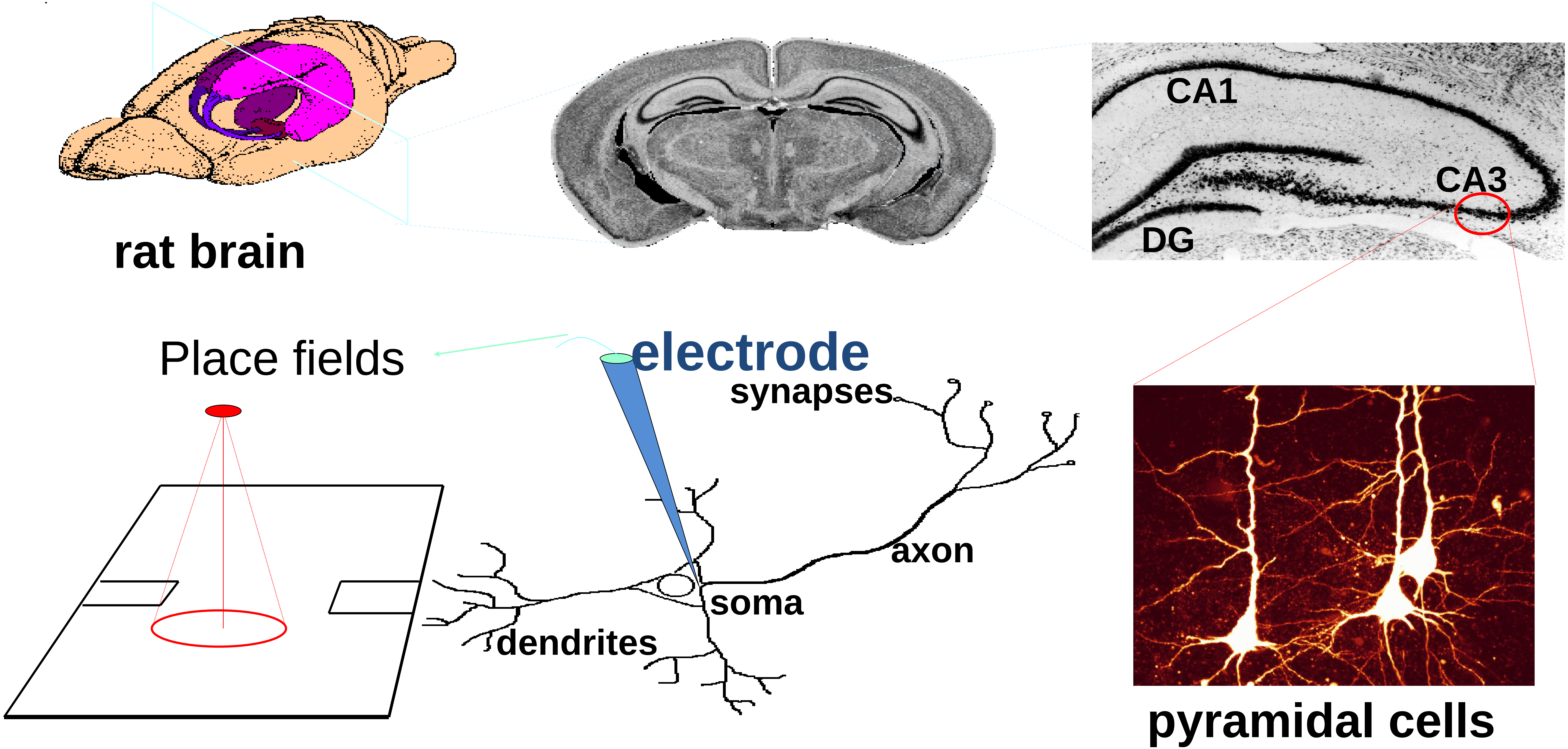


Bump formation

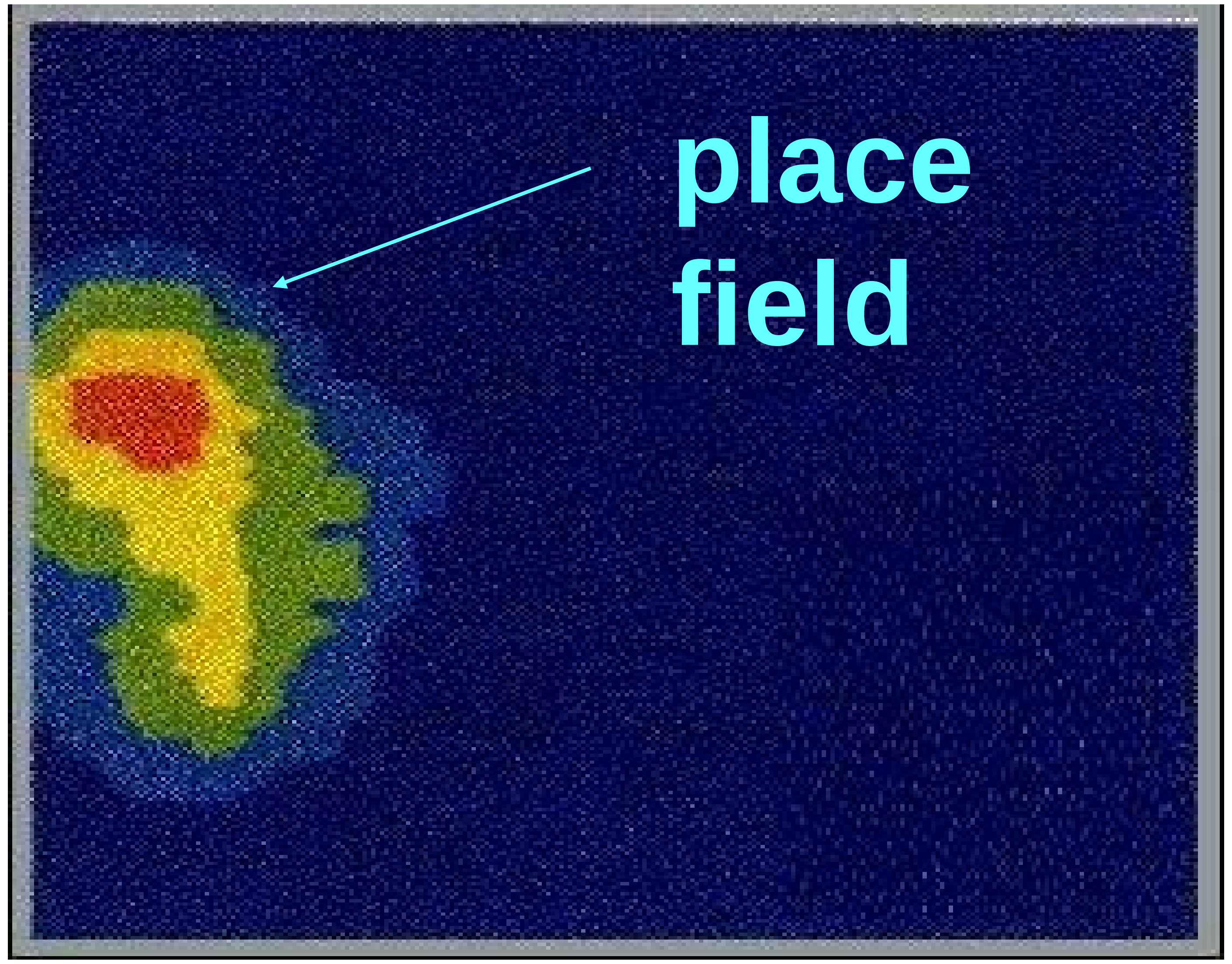
strong lateral connectivity

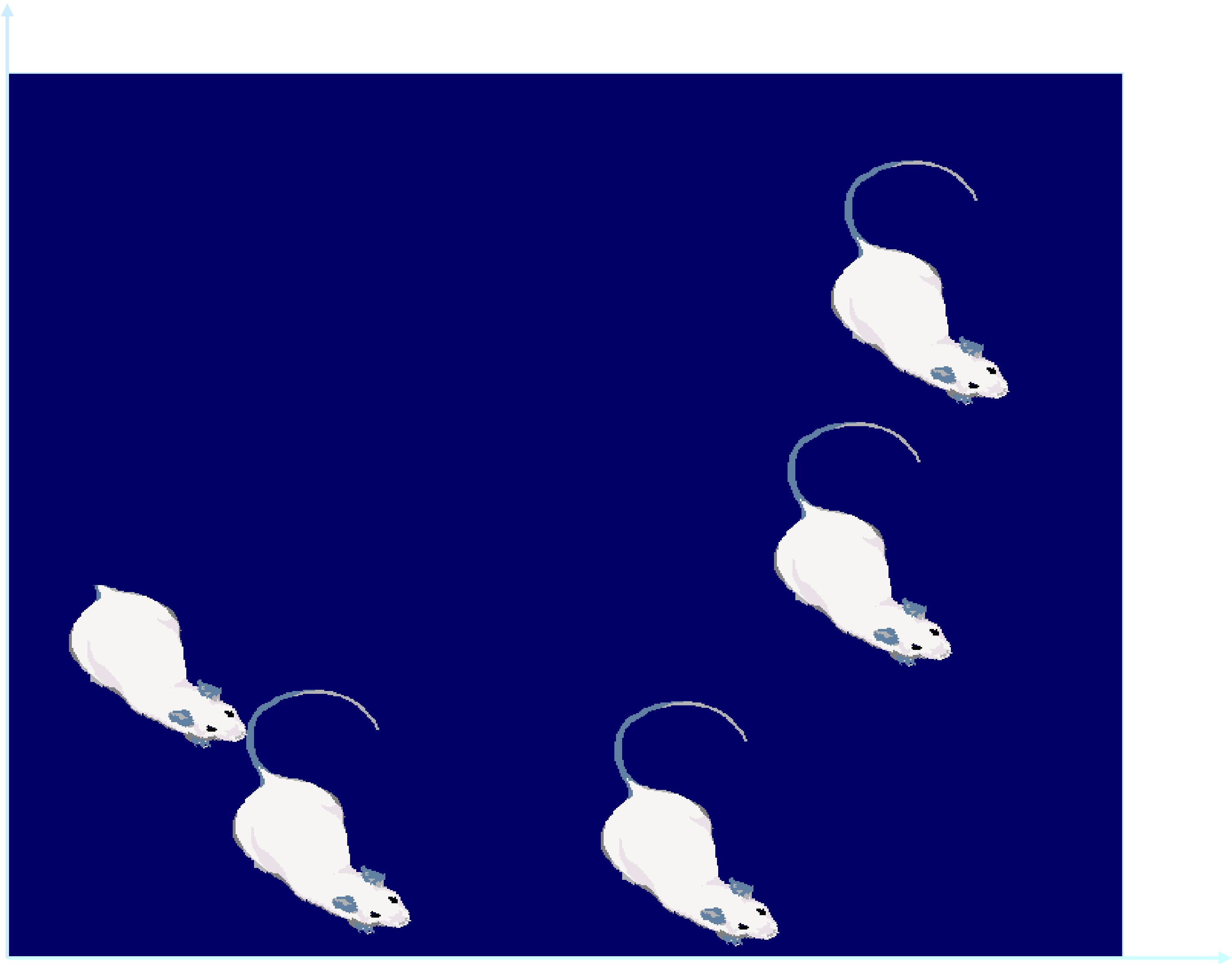
Possible interpretation
of head direction cells:
always some cells active
→ indicate current orientation

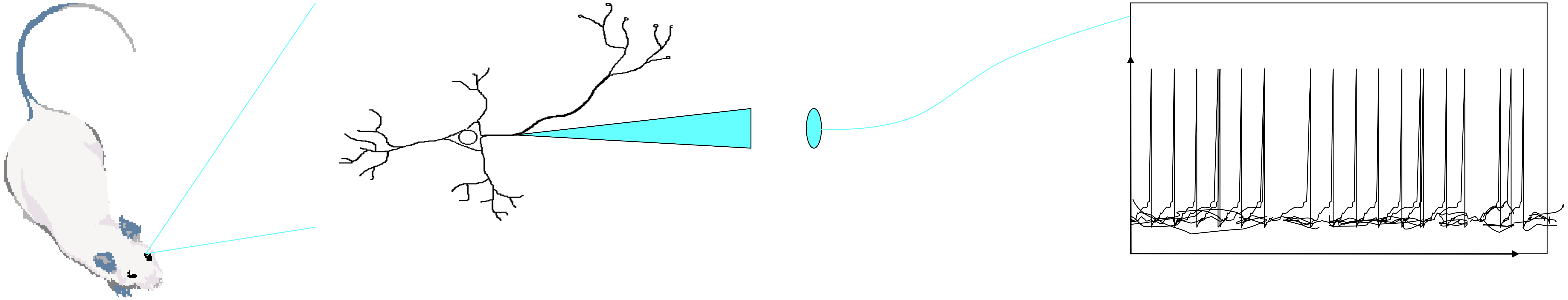
8.7. Hippocampal place cells



Main property: encoding the animal's location

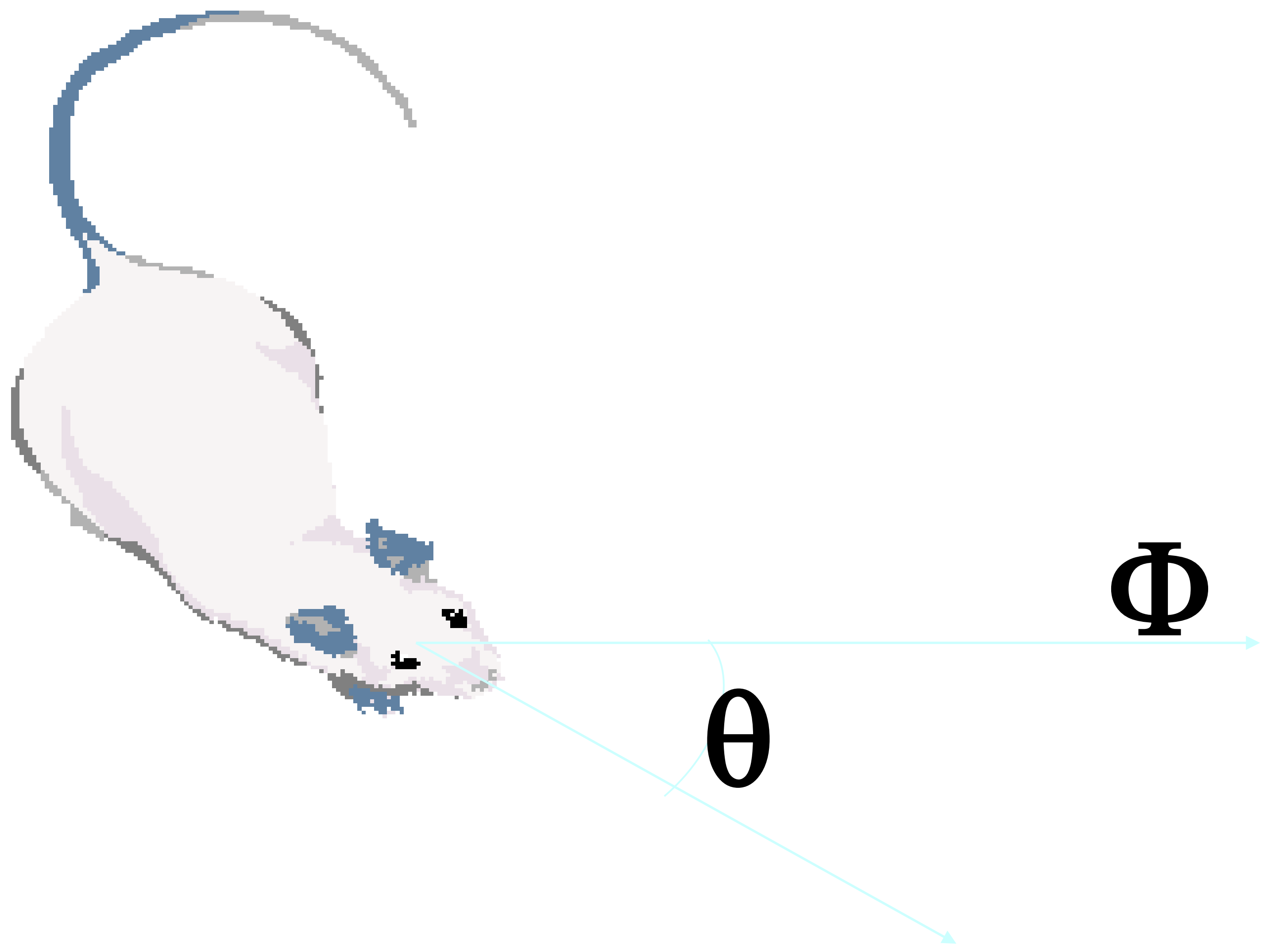


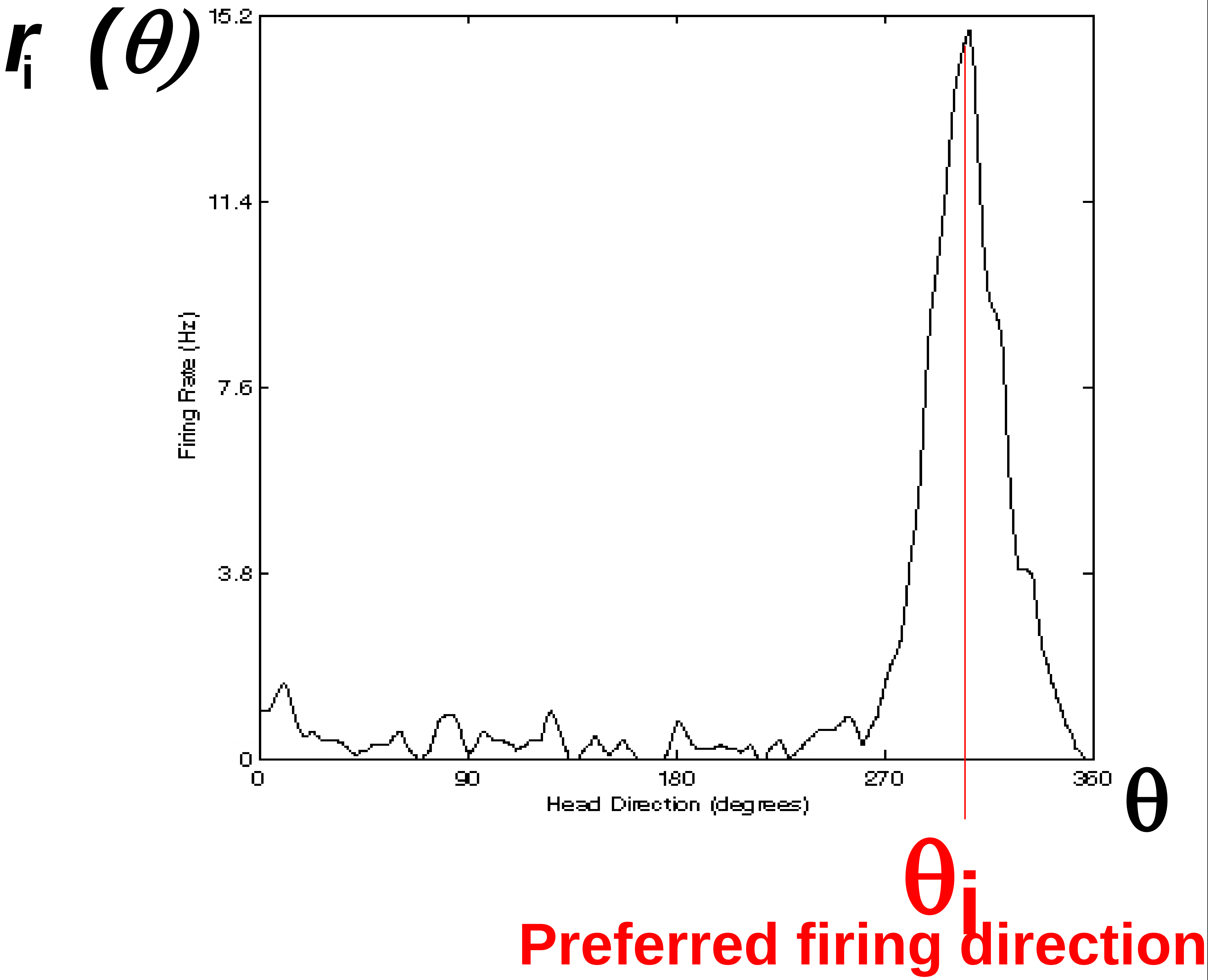




8.7. Head direction cells

Main property: encoding the animal 's heading

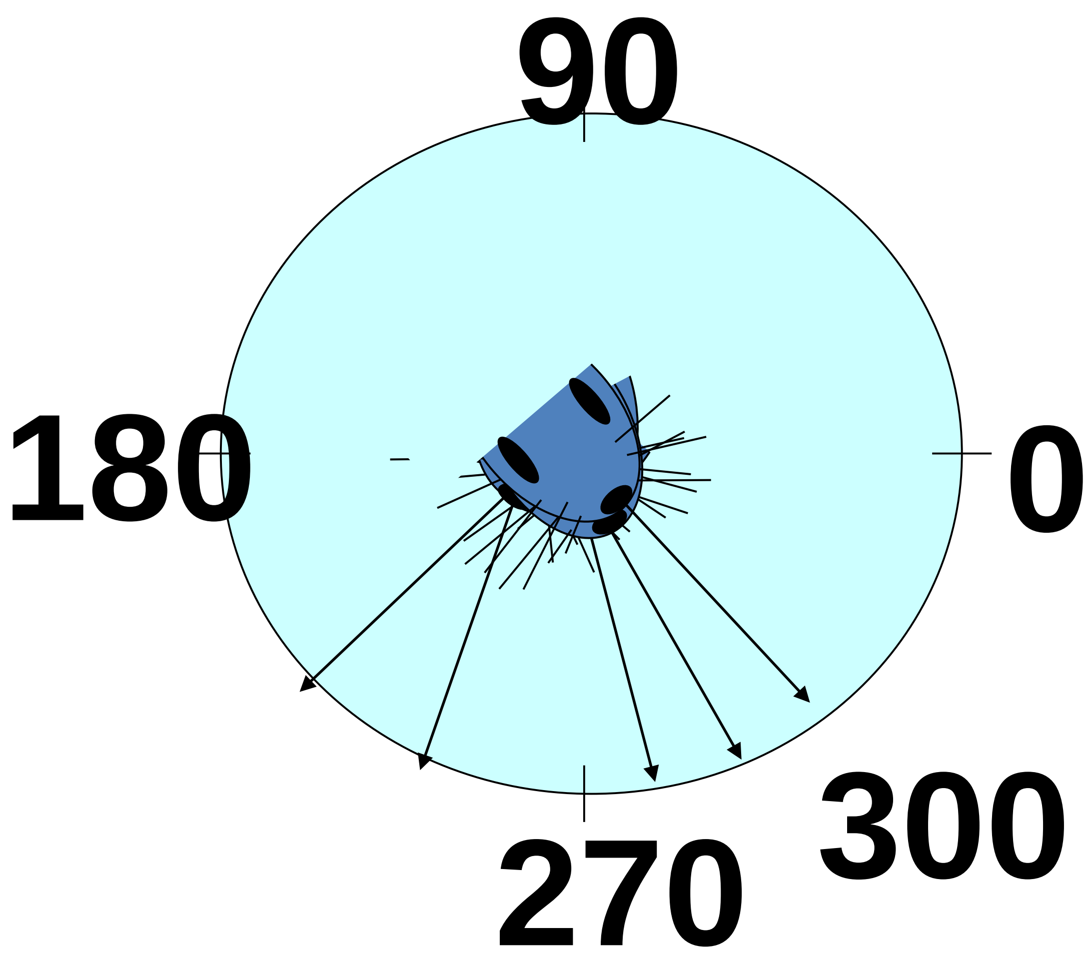


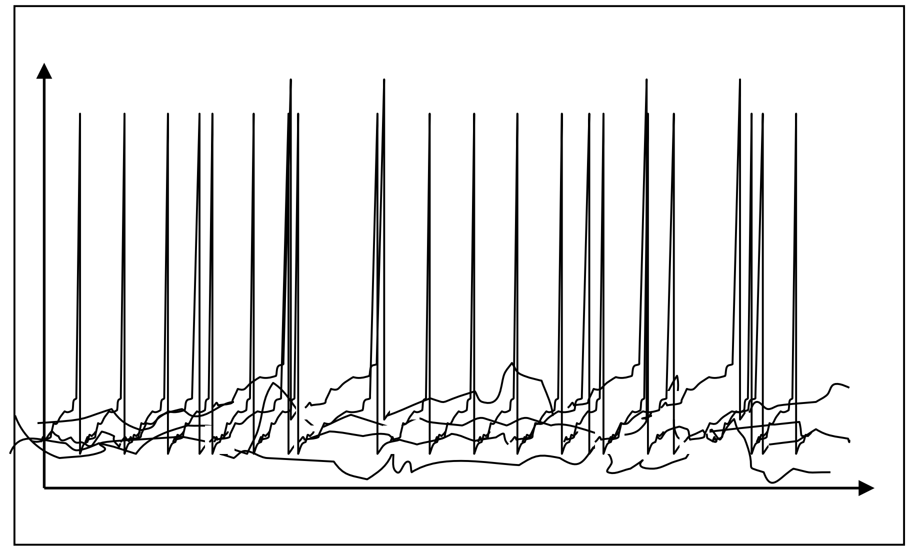


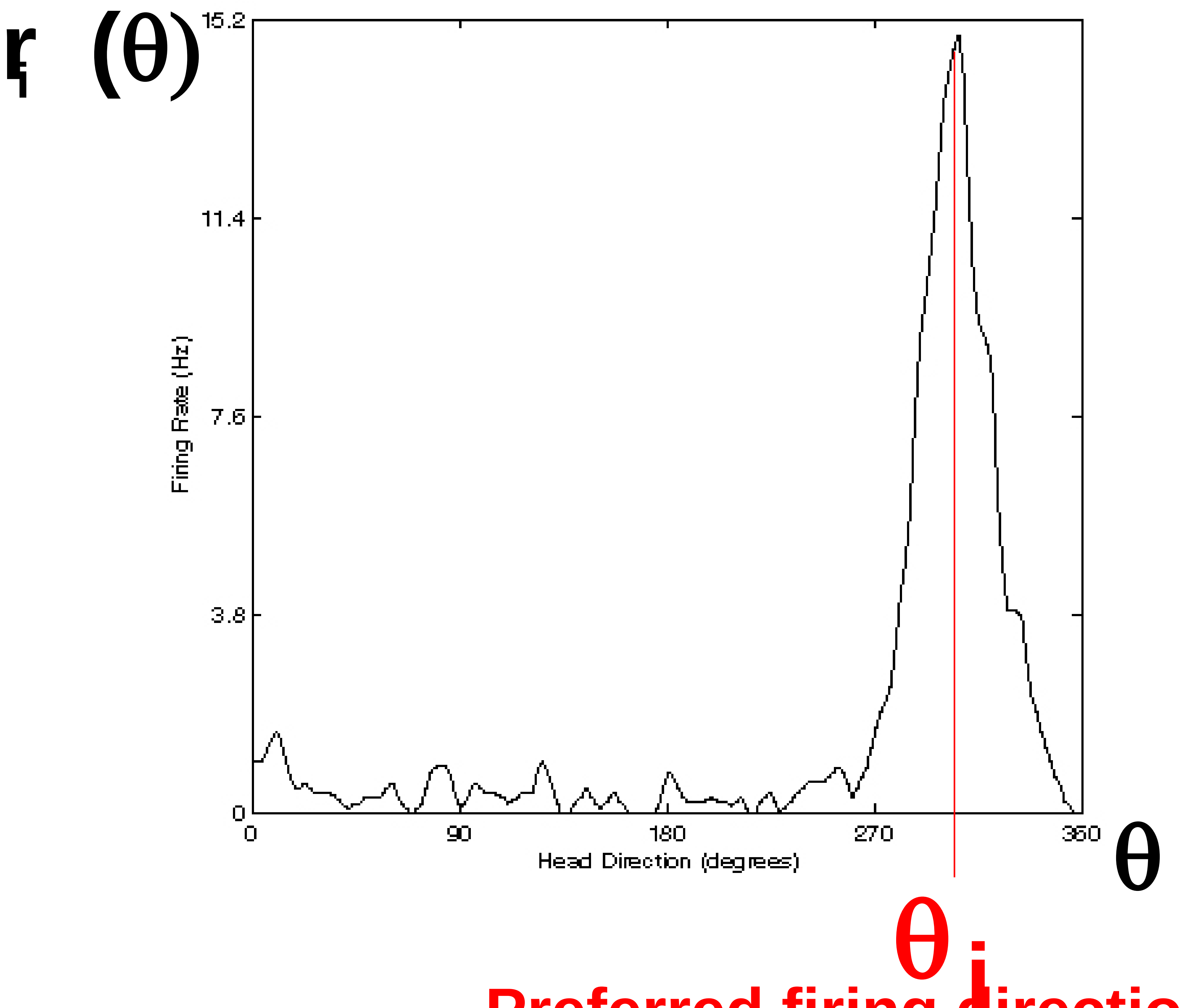
Taube and Muller,
Hippocampus 1998,

8.7. Head direction cells

Main property: encoding the animal 's allocentric heading







Preferred firing direction

8.7. Head direction cells

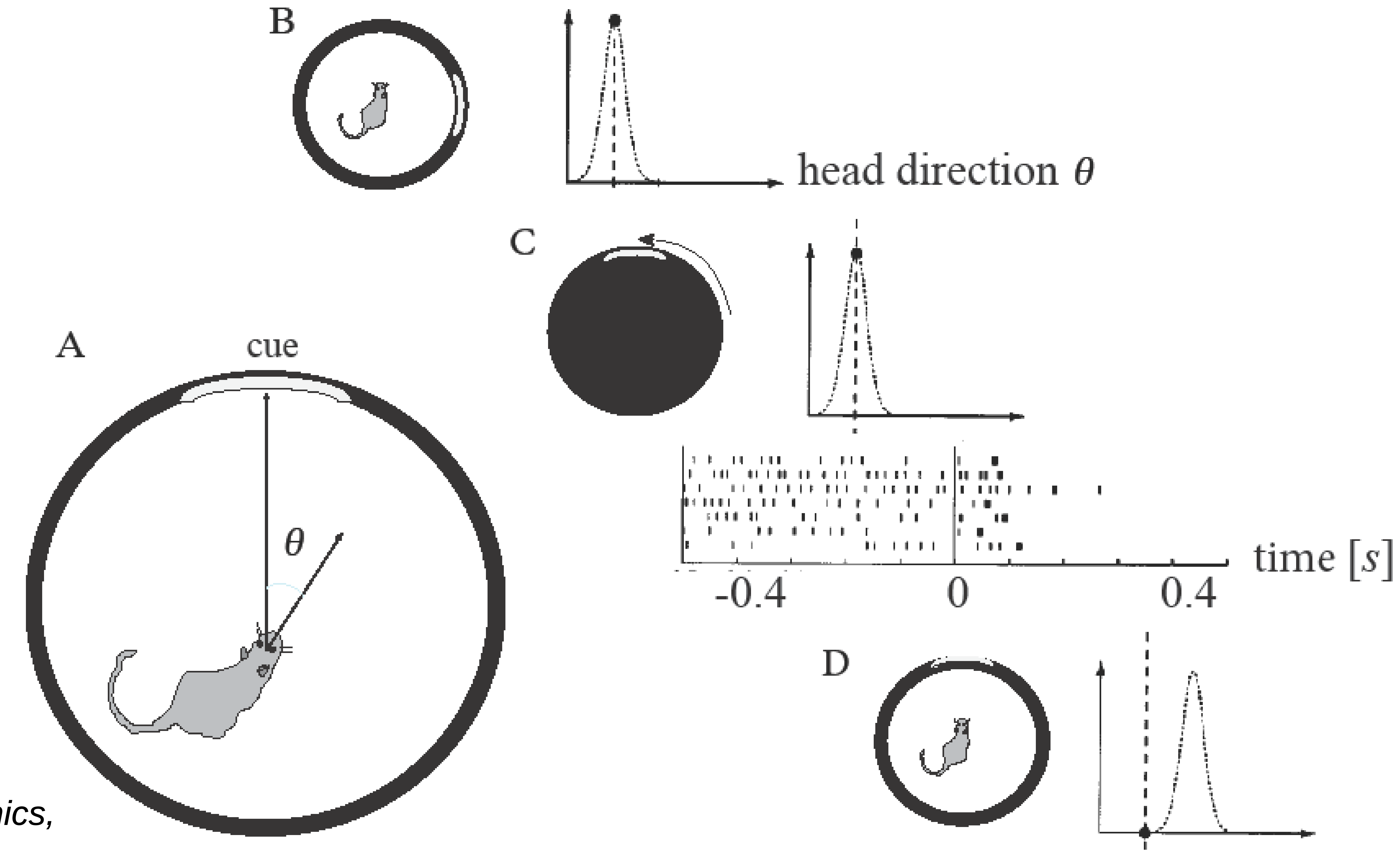
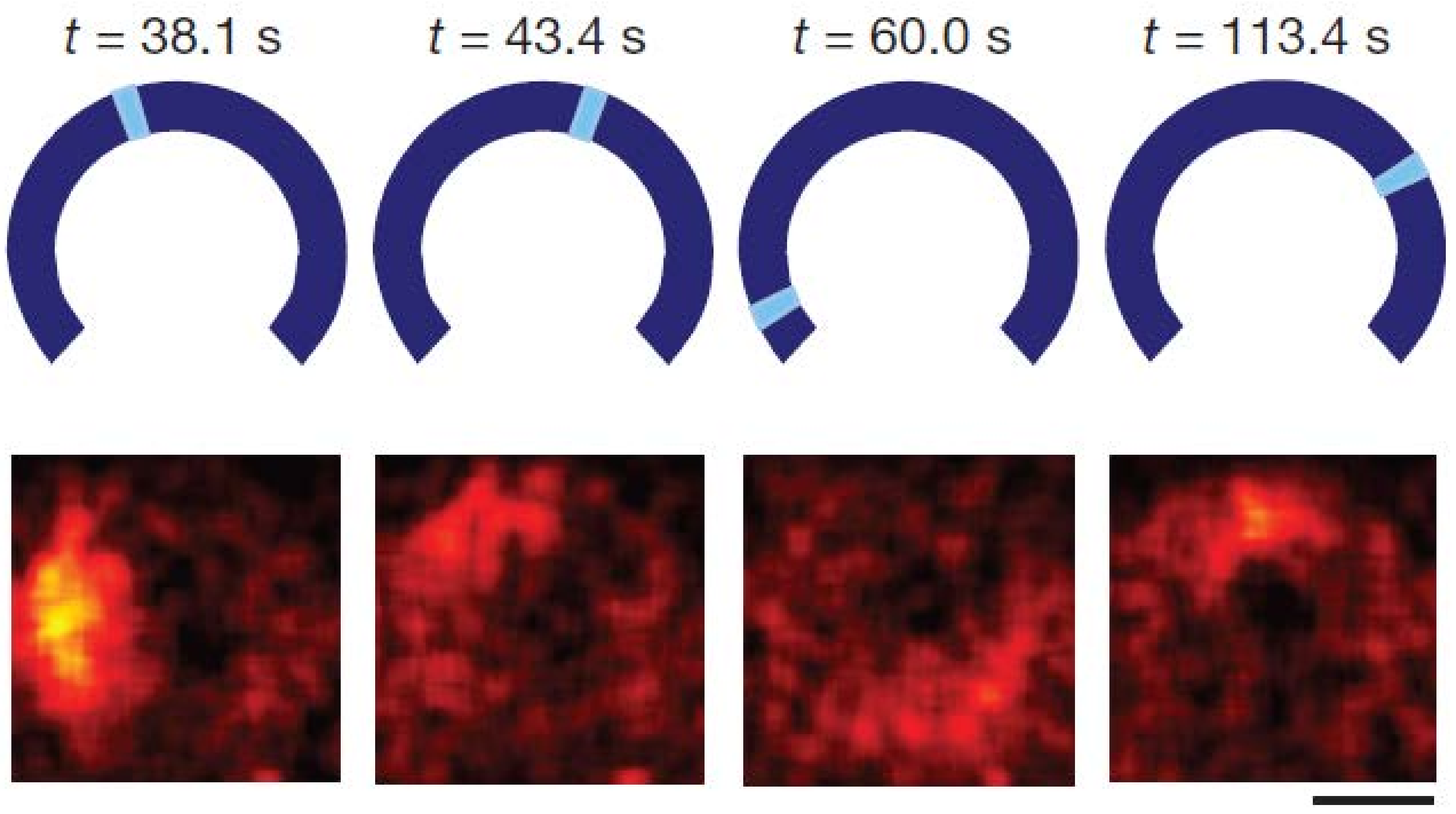


Image: Neuronal Dynamics, Gerstner et al., Cambridge Univ. Press (2014), Adapted from Zugaro et al. (2003), J. Neurosci. 23:3478-3482

Similar to the rat: head direction cells in fly brain (ellipsoid body)

stimulus on screen:

activity in
ellipsoid body



- bump activity persists in the dark
- cue is landmark configuration

Seelig and Jarayaman, Nature, 2015,

Neural dynamics for landmark orientation and angular path integration

8.7. Head direction cells: summary

head direction cells

- are sensitive to direction of head
  with respect to visual cues
- keep their activity if light is switched off
- exist in rodents and in flies
- can be explained by bump solution in ring model

Taube and Muller, Hippocampus 1998,
Zugaro et al., J. Neurosci. 2003
Seelig and Jarayaman, Nature, 2015
Redish et al., Network, 1996, Zhang, J. Neurosci. 1996

8.7. Summary: field models

Continuum model provides understanding for:

- head direction cell
  → bumps of activity
- contrast enhancement and some visual illusions
  → input driven regime

6. Selected References: Field Models

Field Models

H. R. Wilson and J. D. Cowan (1973) A mathematical theory of the functional dynamics of cortical and thalamic nervous tissue. Kybernetik 13, pp. 55–80

S. Grossberg (1973) Contour enhancement, short term memory and constancies in reverberating neural networks. Studies in Applied Mathematics 52:217-257.

Mach bands and Field Models for Visual Cortex and contrast Enhancement

E. Mach (1865) Über die Wirkung der räumlichen vertheilung des Lichtreizes auf die Netzhaut. Sitzungsberichte der mathematisch-naturwissenschaftlichen Classe kaiserl. Akademie der Wissenschaften 52, pp. 303–322.

E. Mach (1906) Die Analyse der Ampfindungen. 5th edition, Gustav Fischer, Jena.

R. Ben-Yishai, R.L. Bar-Or and H. Sompolinsky (1995) Theory of orientation tuning in visual cortex. Proc. Natl. Acad. Sci. USA 92, pp. 3844–3848.

O. Shriki, D. Hansel and H. Sompolinsky (2003) Rate models for conductance-based cortical neuronal networks. Neural Computation 15, pp. 1809–1841

Head Direction Cells and Field Models for Head direction and Spatial Working Memory

J. S. Taube and R. U. Muller (1998) Comparisons of head direction cell activity in the postsubiculum and anterior thalamus of freely moving rats. Hippocampus 8, pp. 87–108.

A.D. Redish, A.N. Elga and D.S. Touretzky (1996) A coupled attractor model of the rodent head direction system. Network 7, pp. 671–685.

K. Zhang (1996) Representaton of spatial orientation by the intrinsic dynamics of the head-direction ensemble: a theory. J. Neurosci. 16, pp. 2112–2126.

A Compte, N Brunel, PS Goldman-Rakic, XJ Wang (2000) Synaptic mechanisms and network dynamics underlying spatial working memory, Cerebral Cortex 10 (9), 910-923

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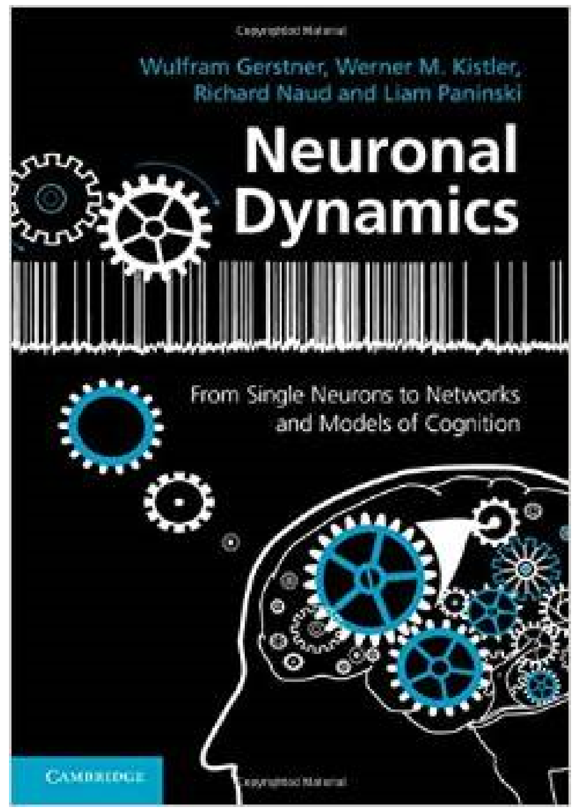
Ch. 18 +
+Ch. 12.3.7+Ch 15.1-15.2.3



THE END