Computational Neuroscience: Neuronal Dynamics of Cognition

ÉCOLE POLYTECHNIQUE
FÉDÉRALE DE LAUSANNE

Continuum models:

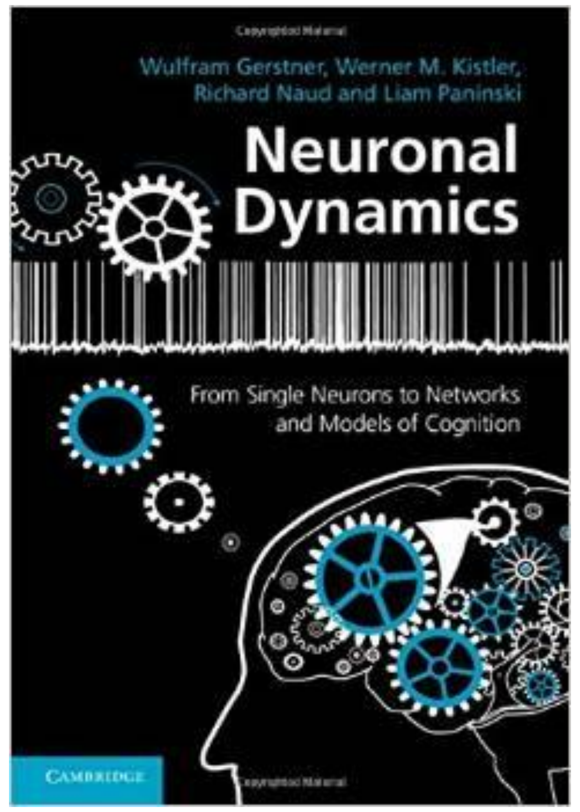
Cortical fields and perception

Wulfram Gerstner

EPFL, Lausanne, Switzerland

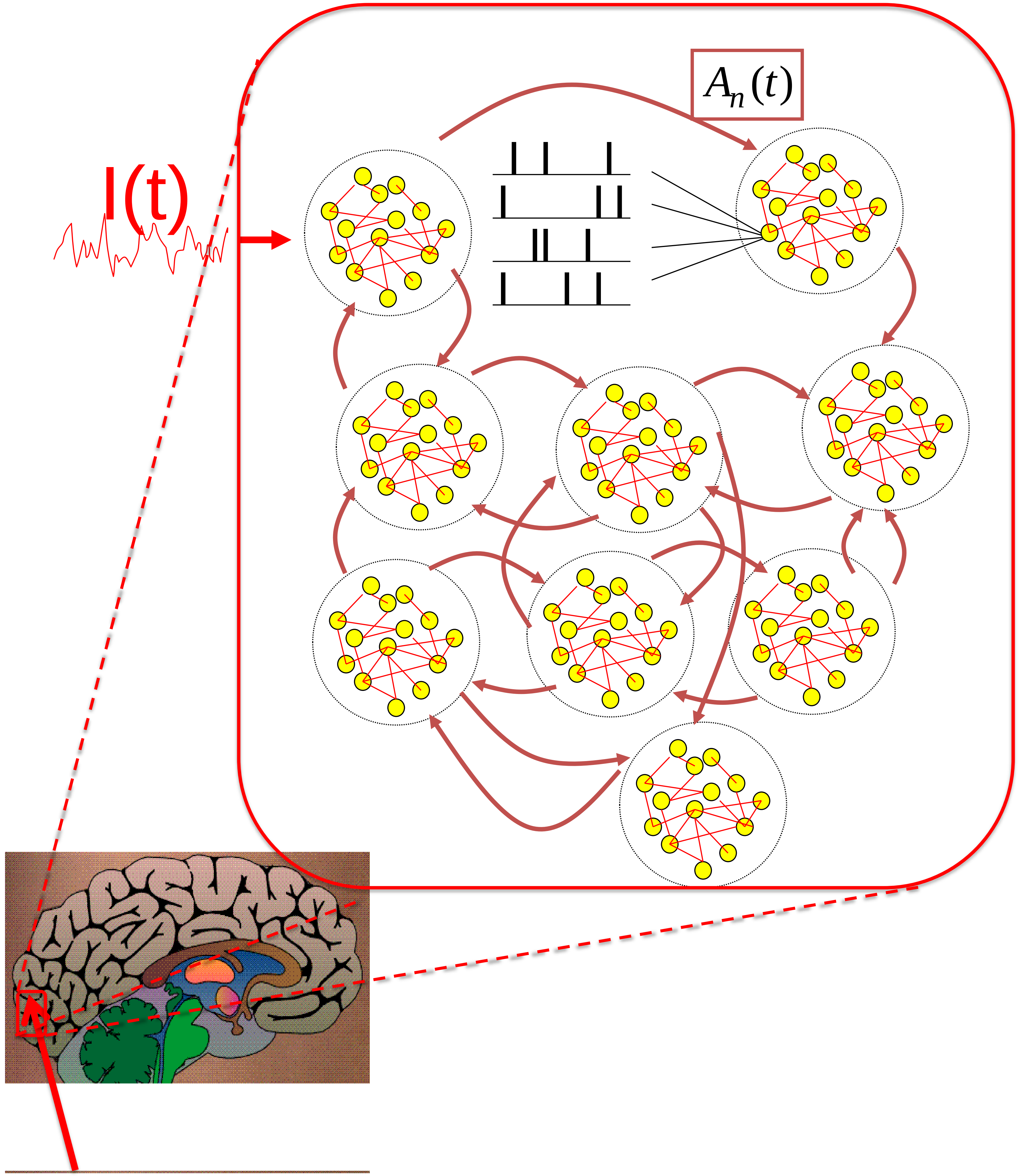
Reading:
NEURONAL DYNAMICS
Ch. 18 +
+Ch. 12.3.7+Ch 15.1-15.2.3

Cambridge Univ. Press



1. **Aims and challenges**
   - review: mean-field arguments
2. **Transients**
   - generalized integrate-and-fire model
   - transients can be sharp or slow
3. **Spatial continuum (cortex)**
   - orientation columns
4. **Spatial continuum (model)**
   - field equations
5. **Solution types**
   - uniform solution
   - bump solution
6. **Perception**
7. **Head direction cells**

1. Aims and Challenges



Visual cortex

1. Aims and Challenges: Visual Perception

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Visual Perception
→weak contrasts
→world is continuous

1. Aims and Challenges: sense of direction

Sense of direction
→ internal compass

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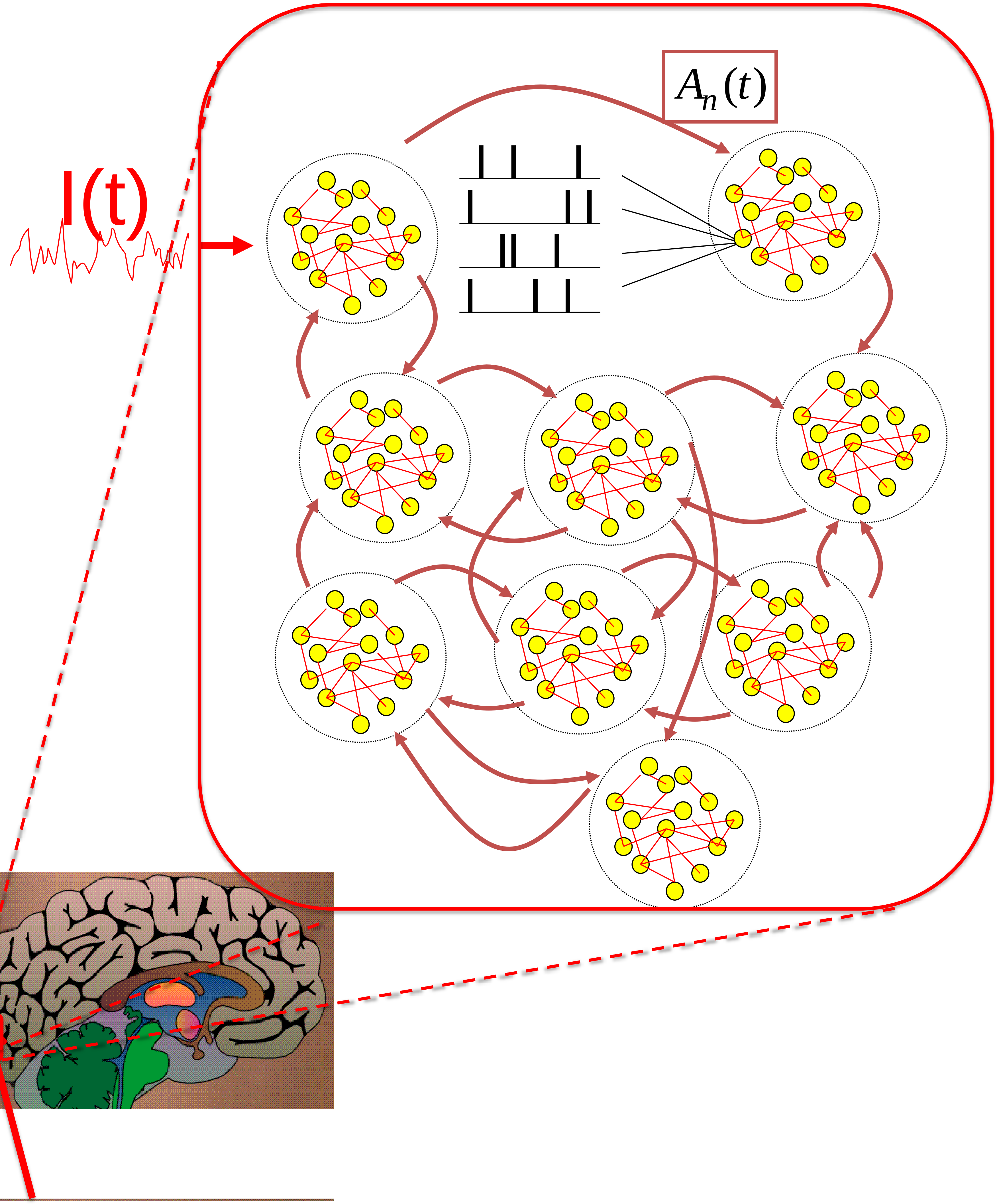
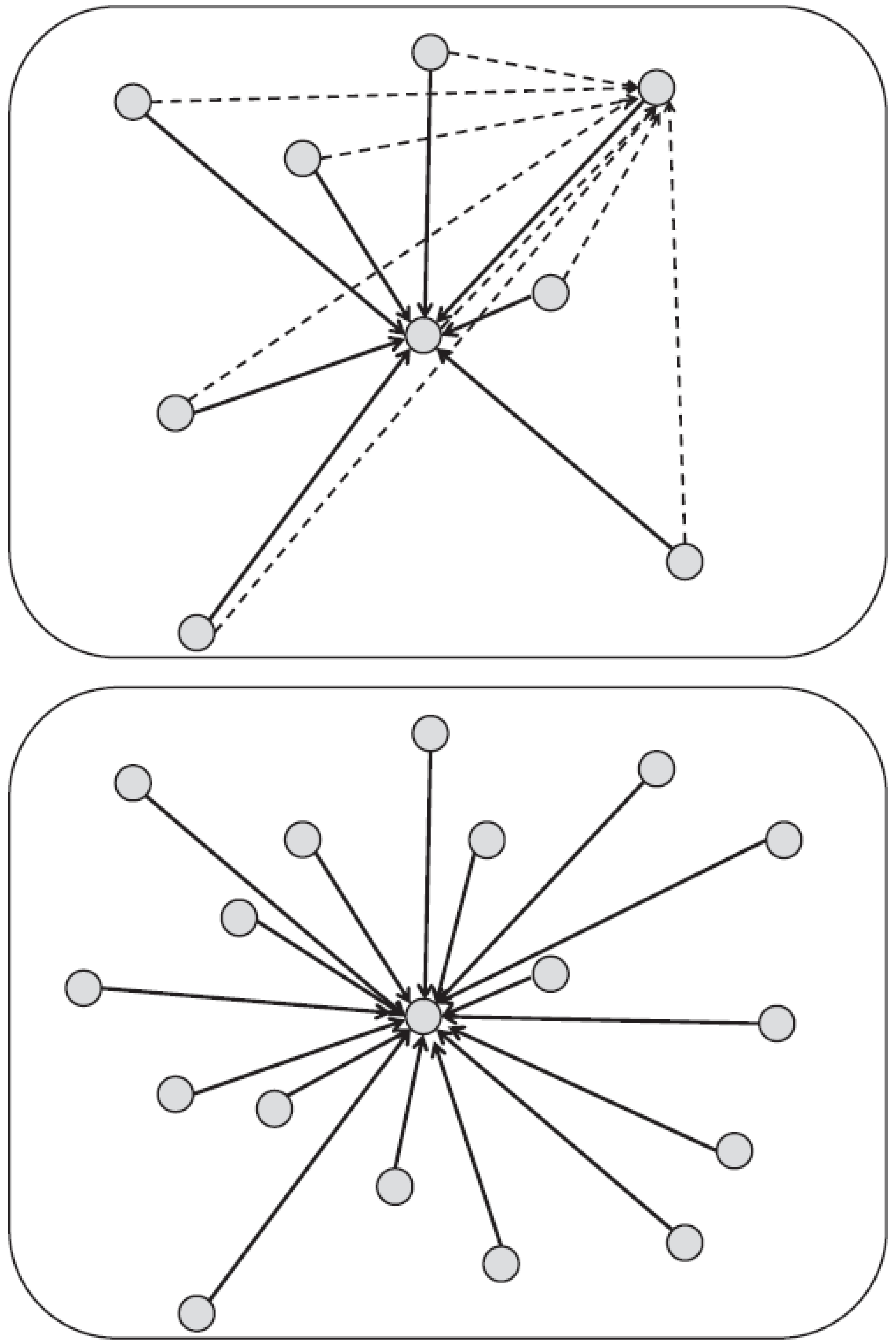
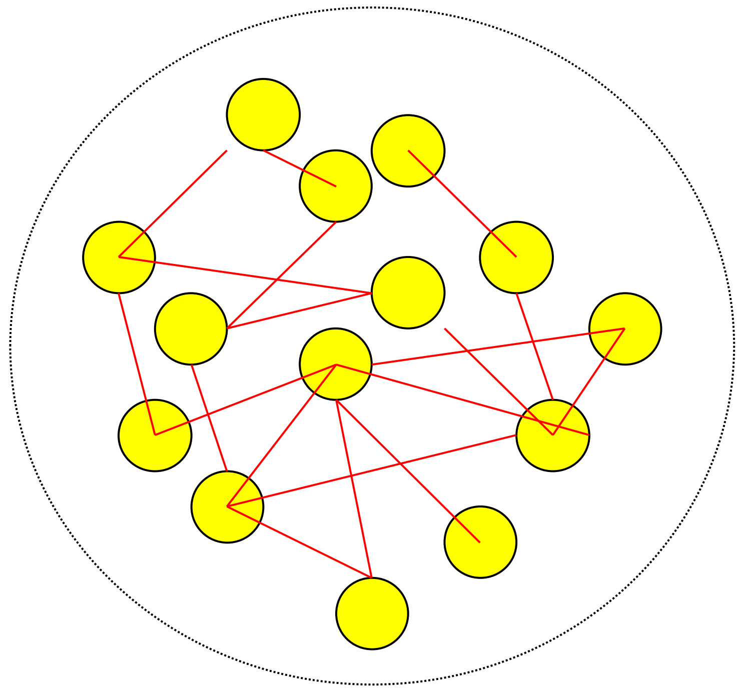


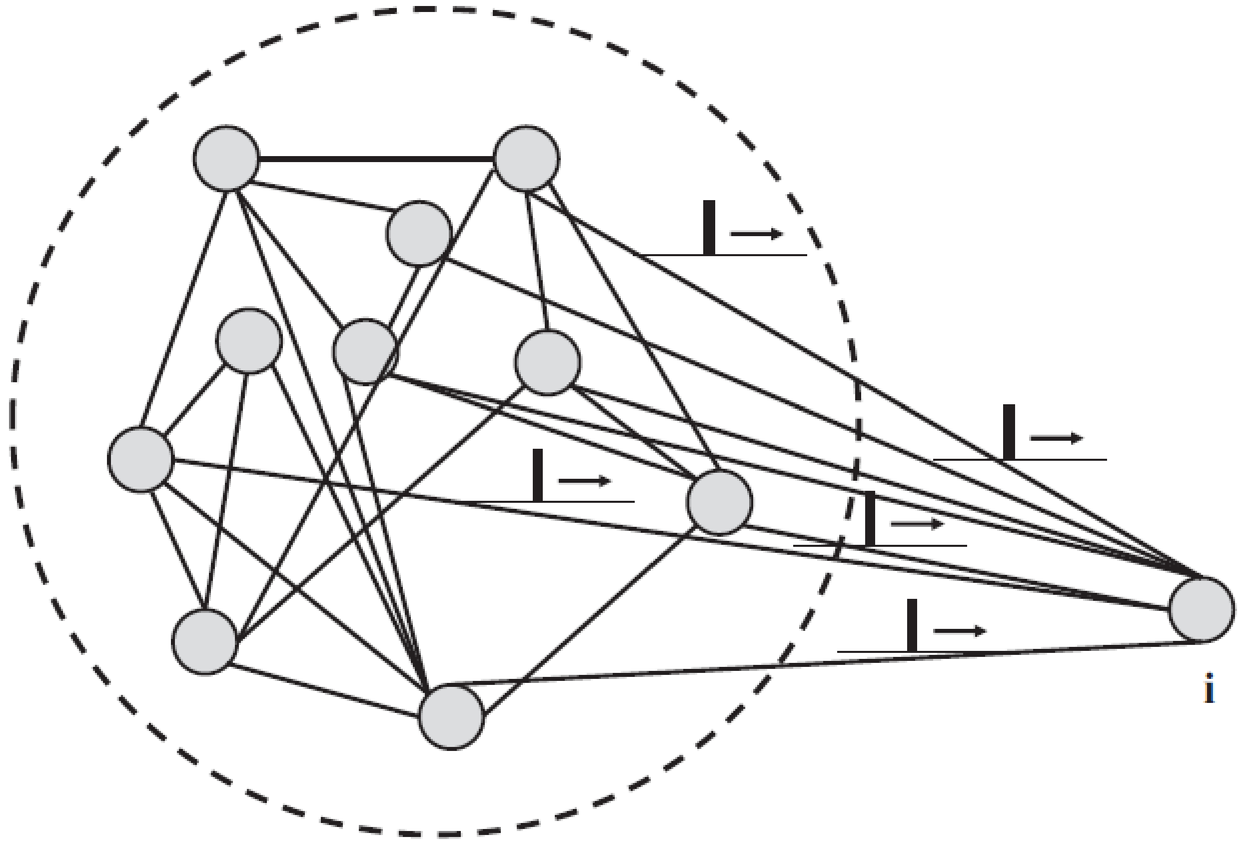
Visual cortex

1. review: mean-field arguments

Single population full connectivity







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

1. Review: mean-field arguments

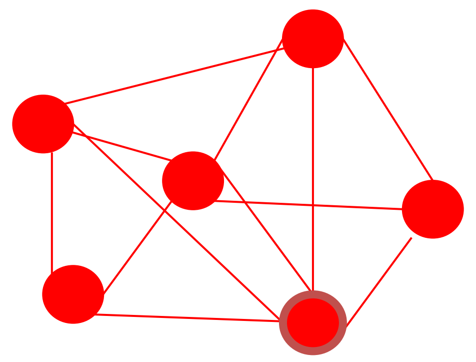
All neurons receive the same total input current ('mean field')

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

Ultra-short current pulse

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

index i disappears



fully connected

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

All spikes, all neurons

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

1. Review: mean-field also works for random coupling

full connectivity

random: prob *p* fixed

random: number K of inputs fixed

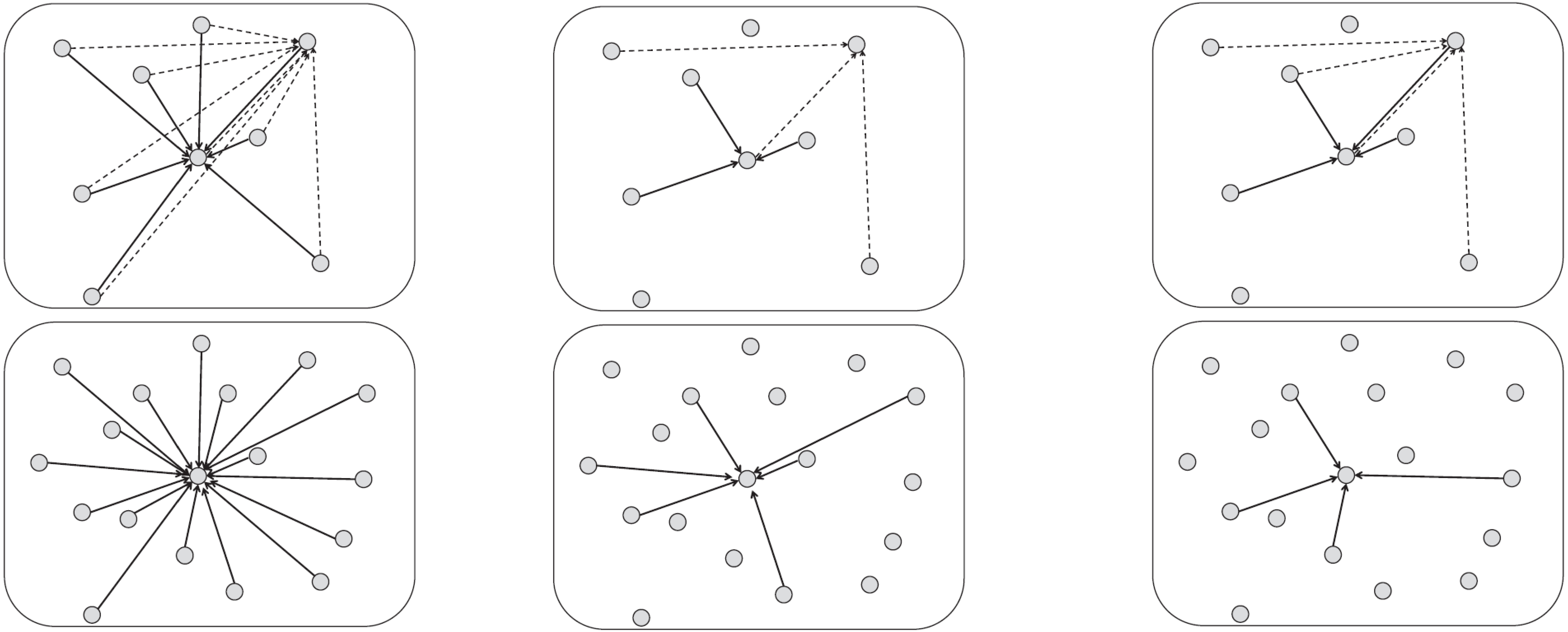


Image: Gerstner et al. Neuronal Dynamics (2014)

1. Review: stationary state/asynchronous activity

Homogeneous network

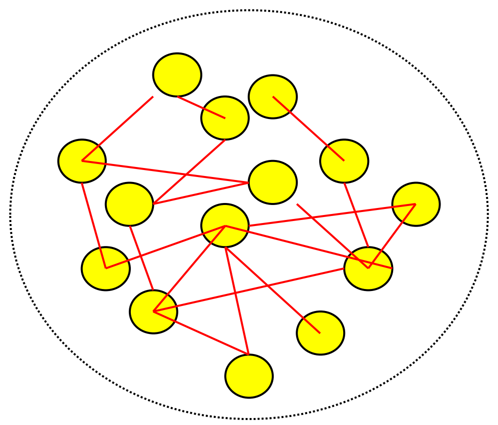
All neurons are identical,

Single neuron rate = population rate

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

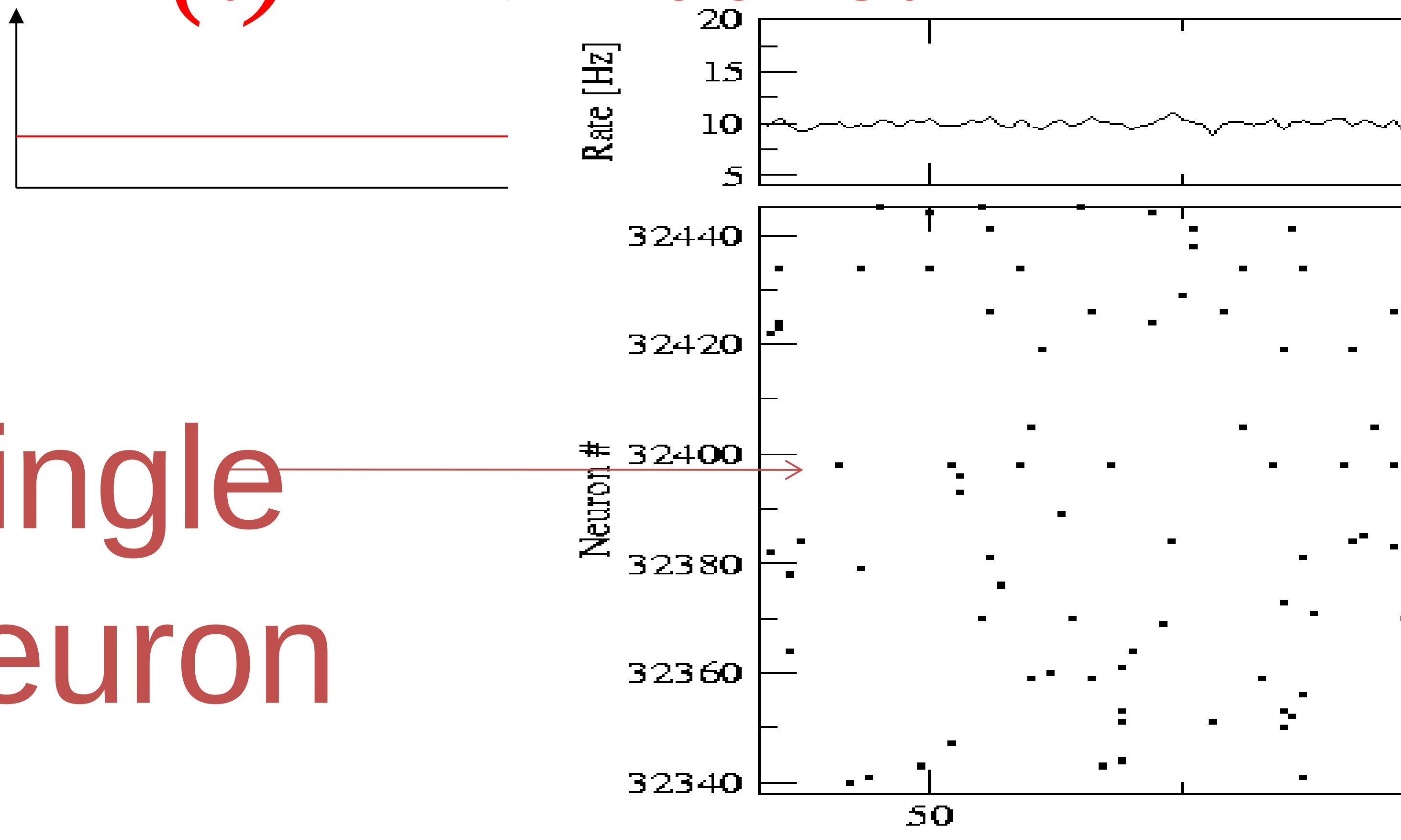
constant input

$$I_0 = c$$



Gain function at appropriate noise level

$A(t) = A_0 = const$



Single neuron

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

1. Review : mean-field arguments for homogeneous population

- single neuron is driven by the 'population activity' of all others
- all neurons in populations receive the same input
- mean-field arguments 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)

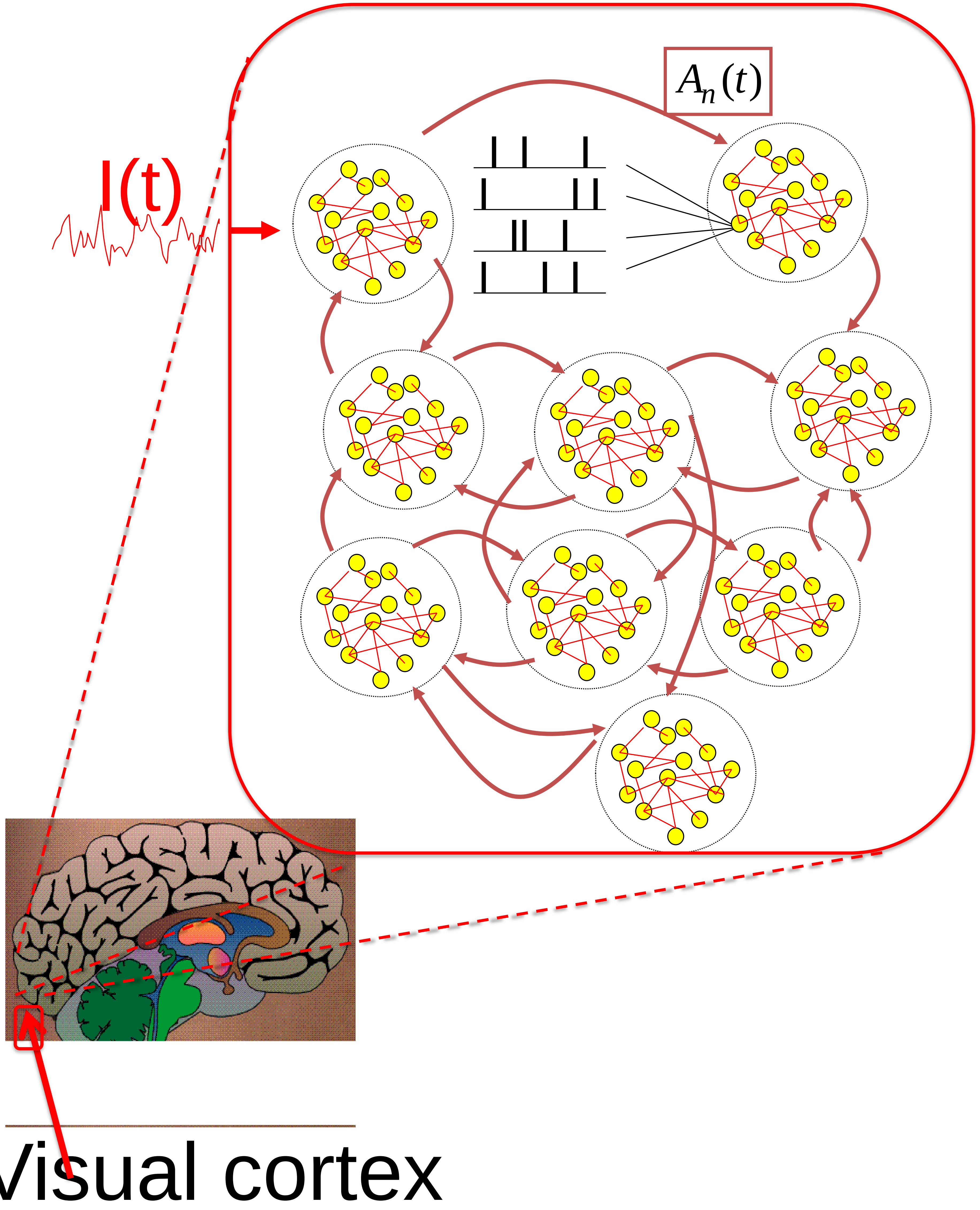
1. Aims and challenges

Mathematical aims:

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

Cognitive Modeling aims:

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



1. Aims and challenges: compass and perception

Sense of direction
→ internal compass

Visual Perception
→weak contrasts
→world is continuous

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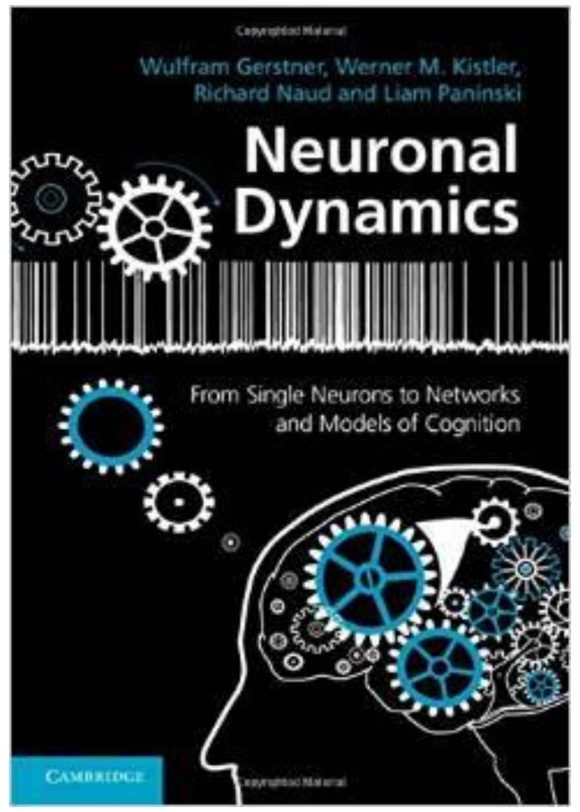

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2. Aims of this section: Transients

- beyond stationary states

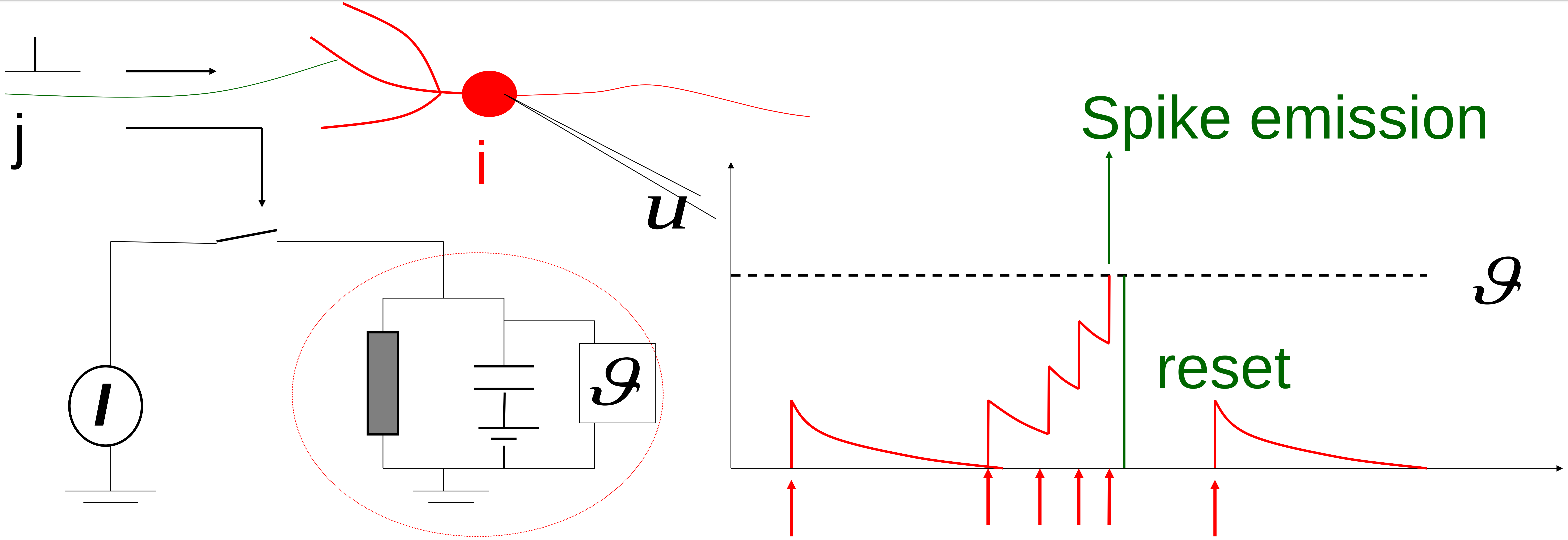
→ transients?

- but then neuron model matters!

→ introduce **generalized integrate-and-fire models**:

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

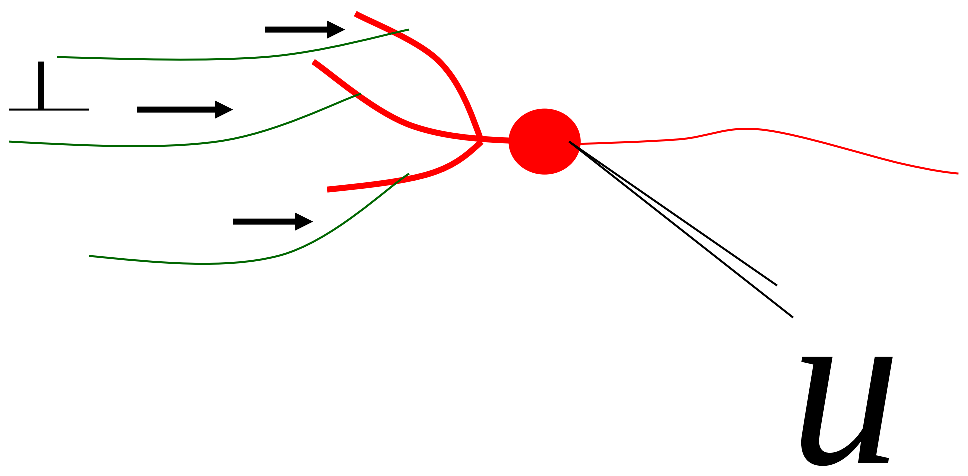
2. Leaky Integrate-and-Fire Model

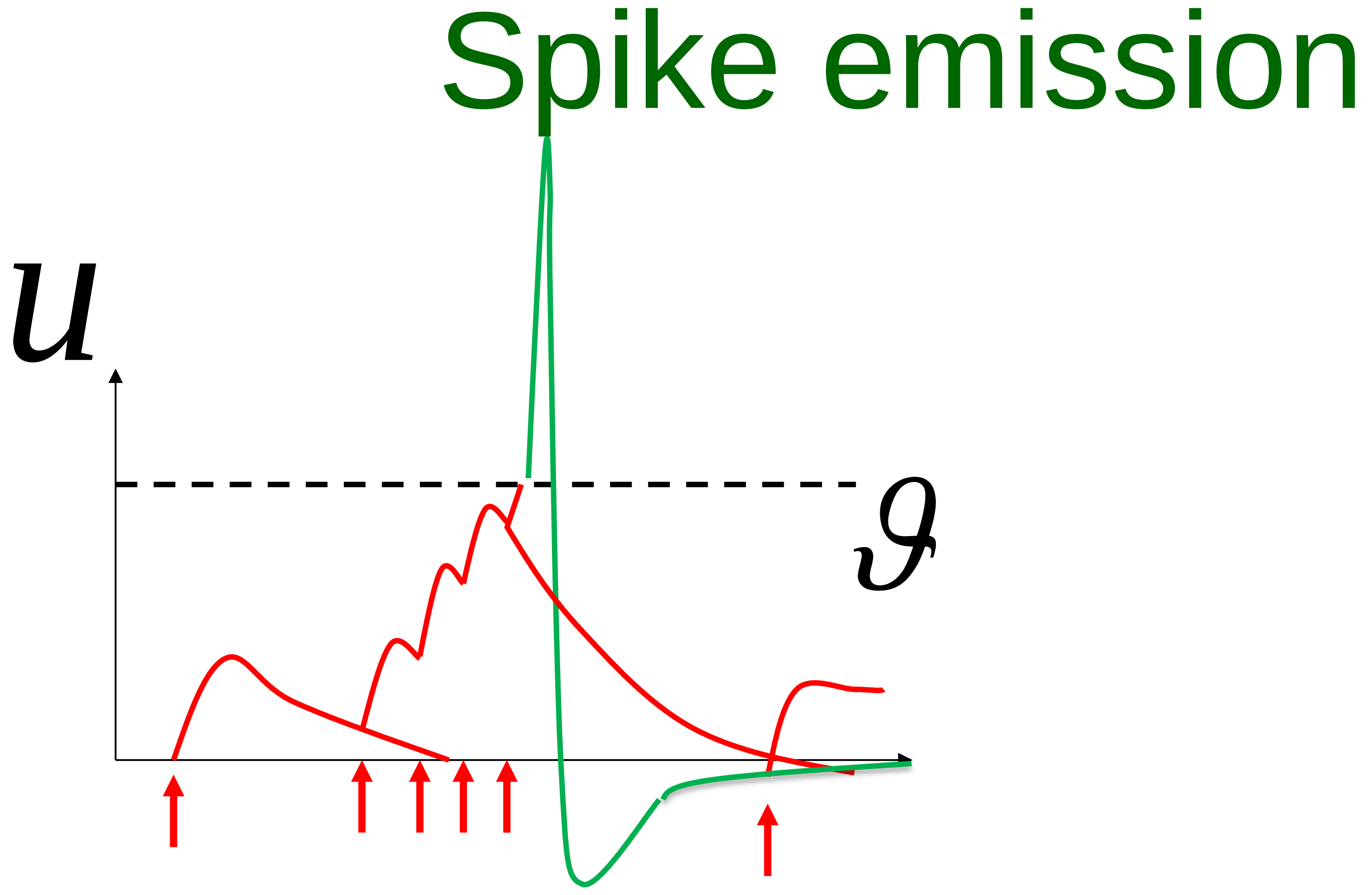


$$\tau \cdot \frac{d}{dt} u = -(u - u_{rest}) + RI(t)$$ linear

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

2. Generalized Integrate-and-Fire Model





***Leaky Integrate-and-Fire Model*:**

passive membrane

+ *threshold*

+ *reset*

Input spike causes an EPSP
= excitatory postsynaptic potential

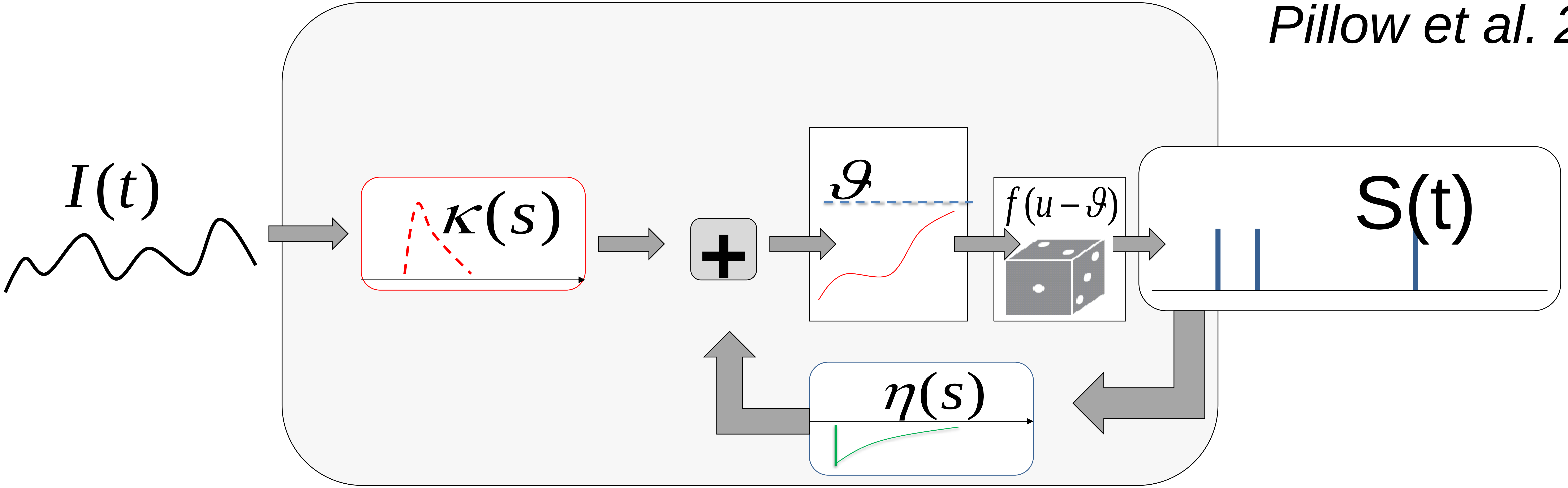
equivalent description

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

add $\boxed{\eta(s)}$ (spike afterpotential)

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

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



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

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

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

2. Leaky Integrate-and-Fire Model: input potential

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

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

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

Gerstner et al., 1992,2000
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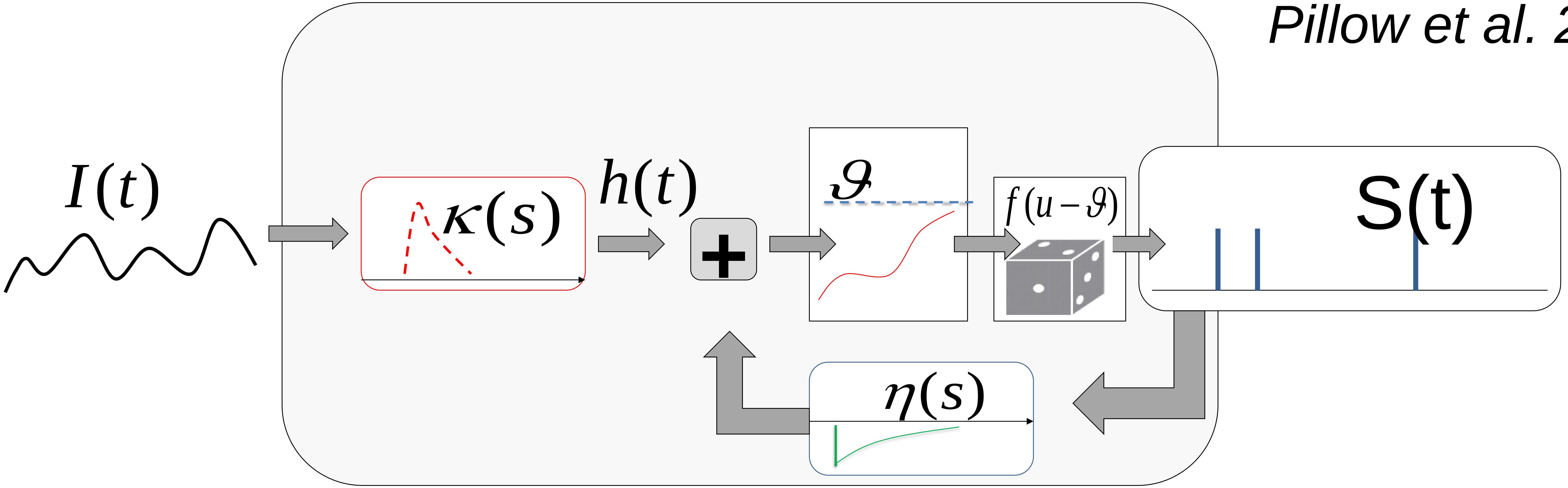
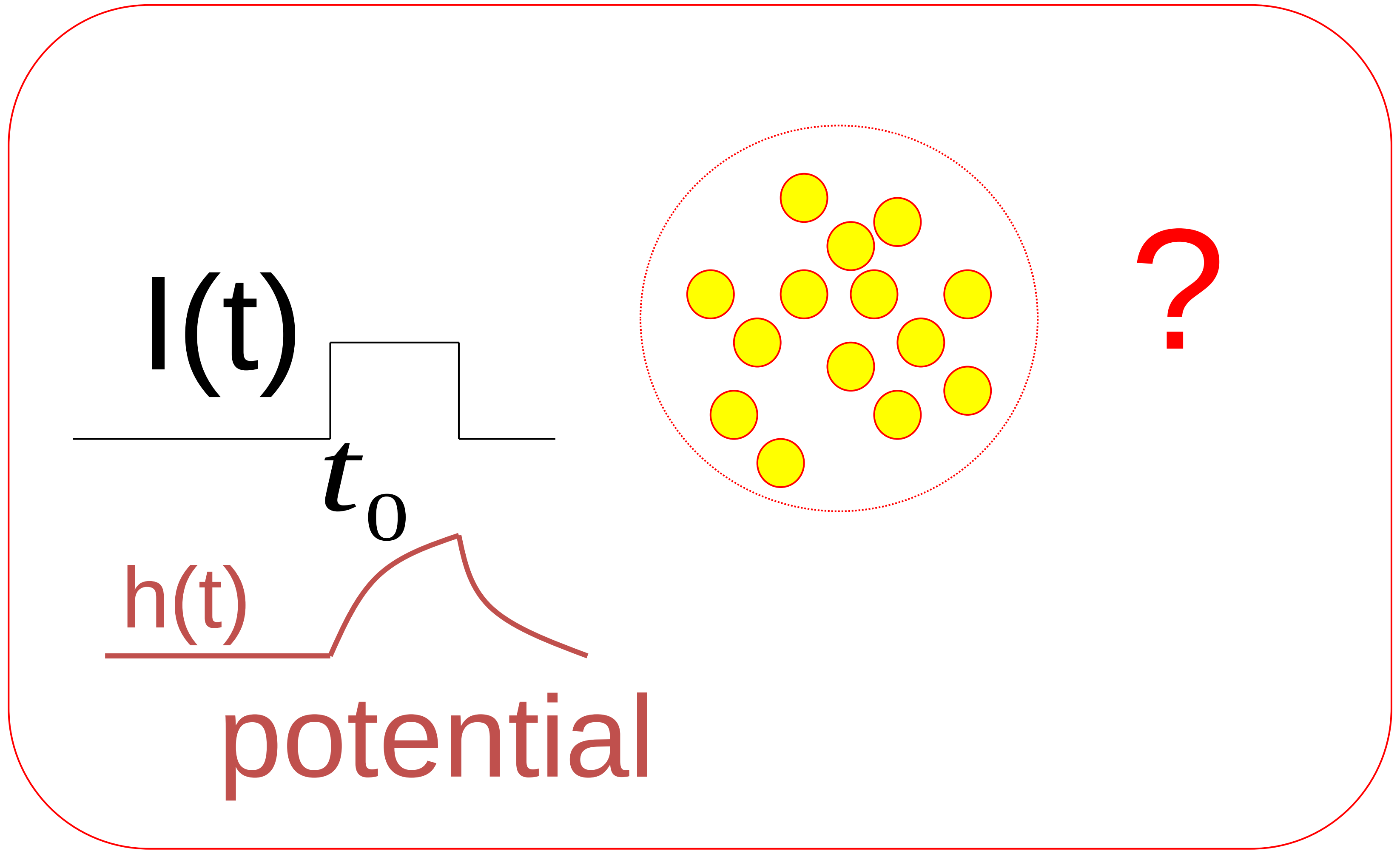
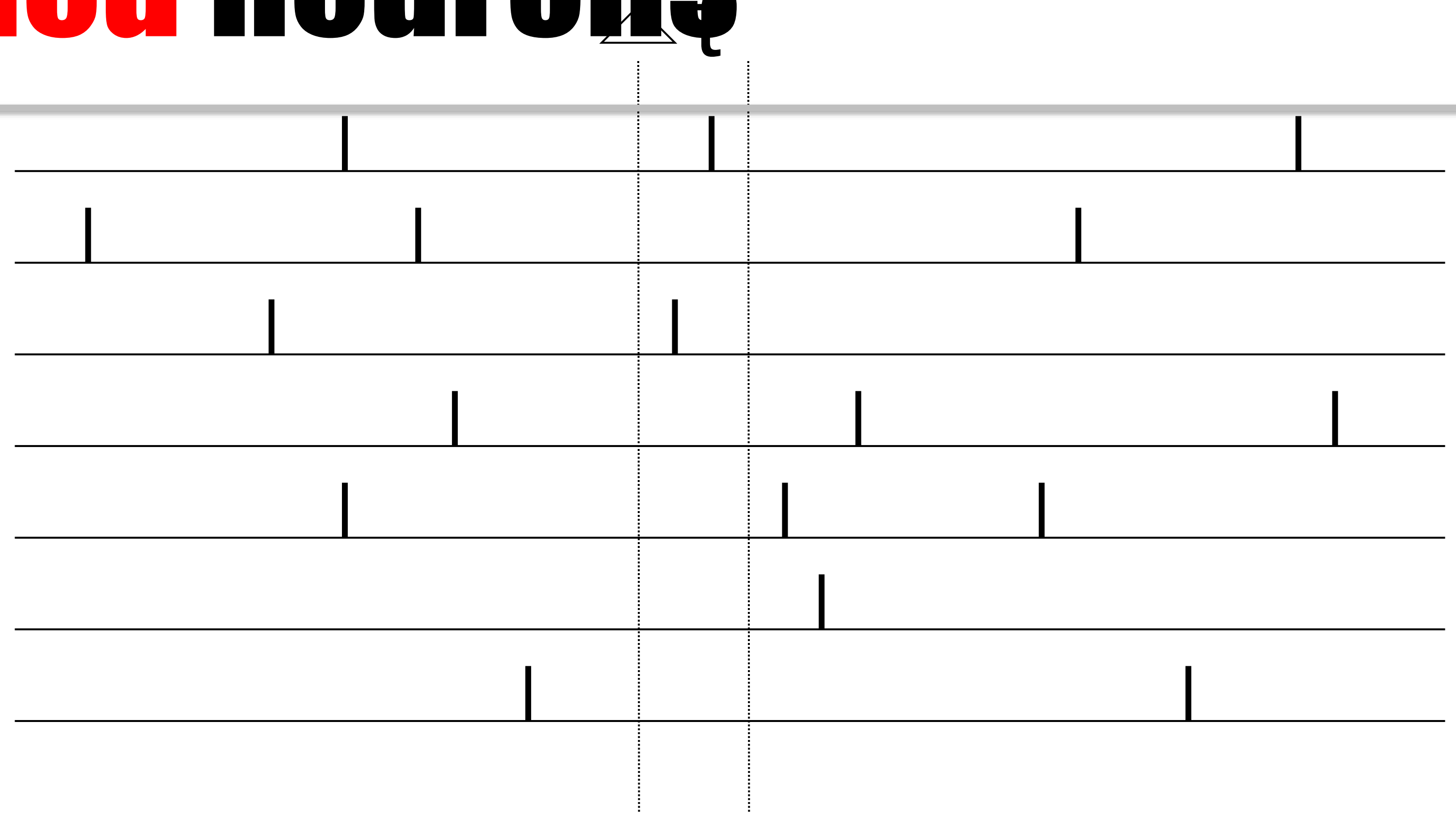


potential $u(t) = u_{rest} + \underbrace{\int_0^\infty \kappa(s) I(t-s) ds}_{h(t)} + \int \eta(s) S(t-s) ds$

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

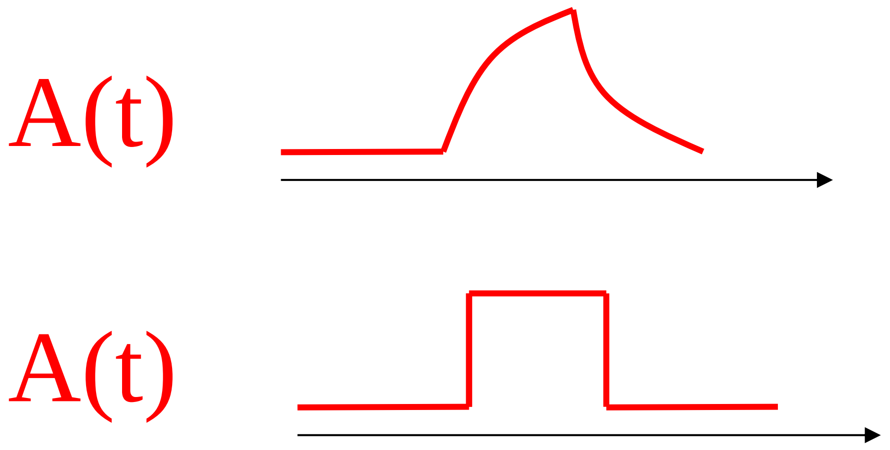
2. Transients in a population of uncoupled neurons





population activity

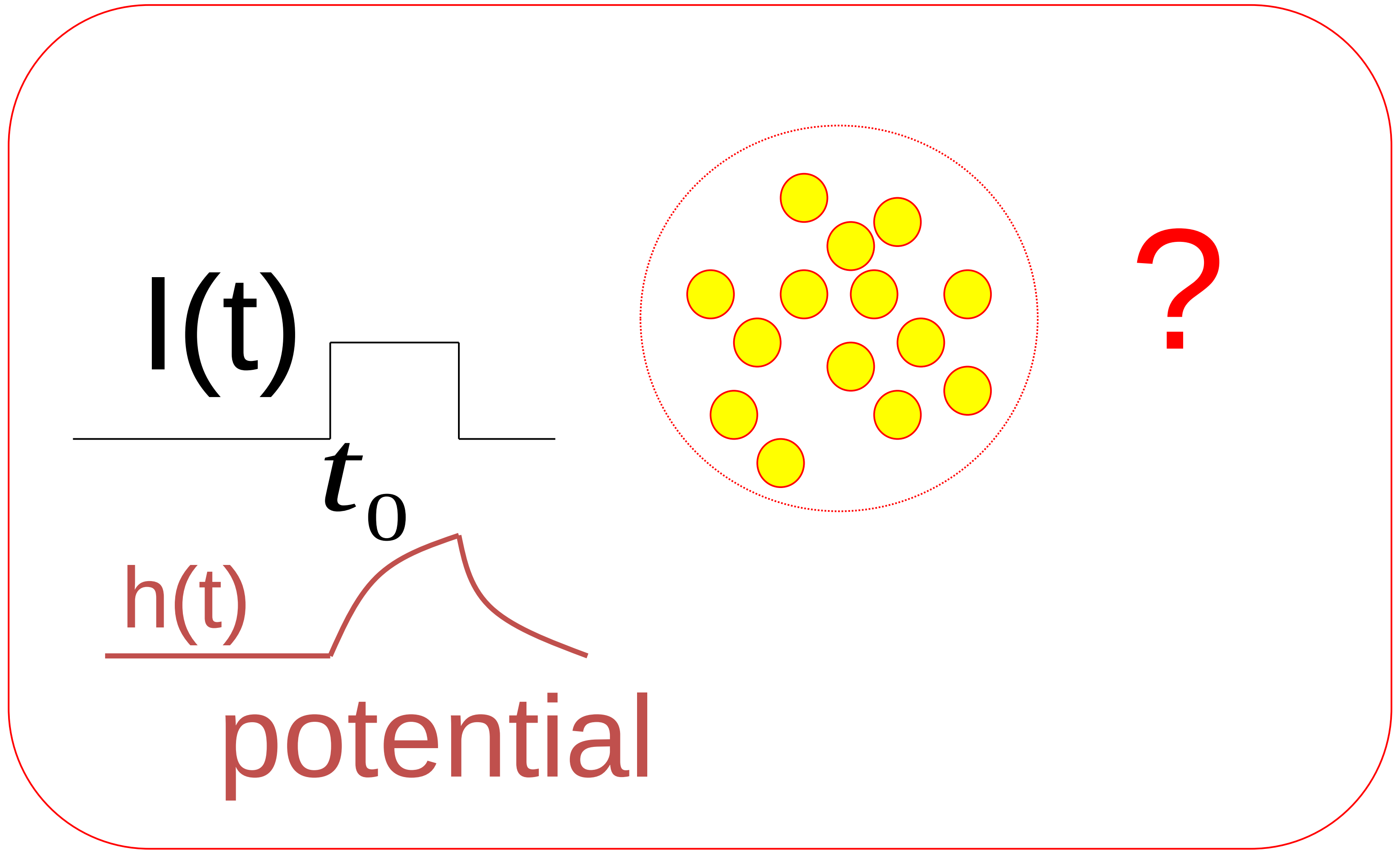
$$A(t) = \frac{n(t - \frac{\Delta t}{2}; t + \frac{\Delta t}{2})}{N \Delta t}$$

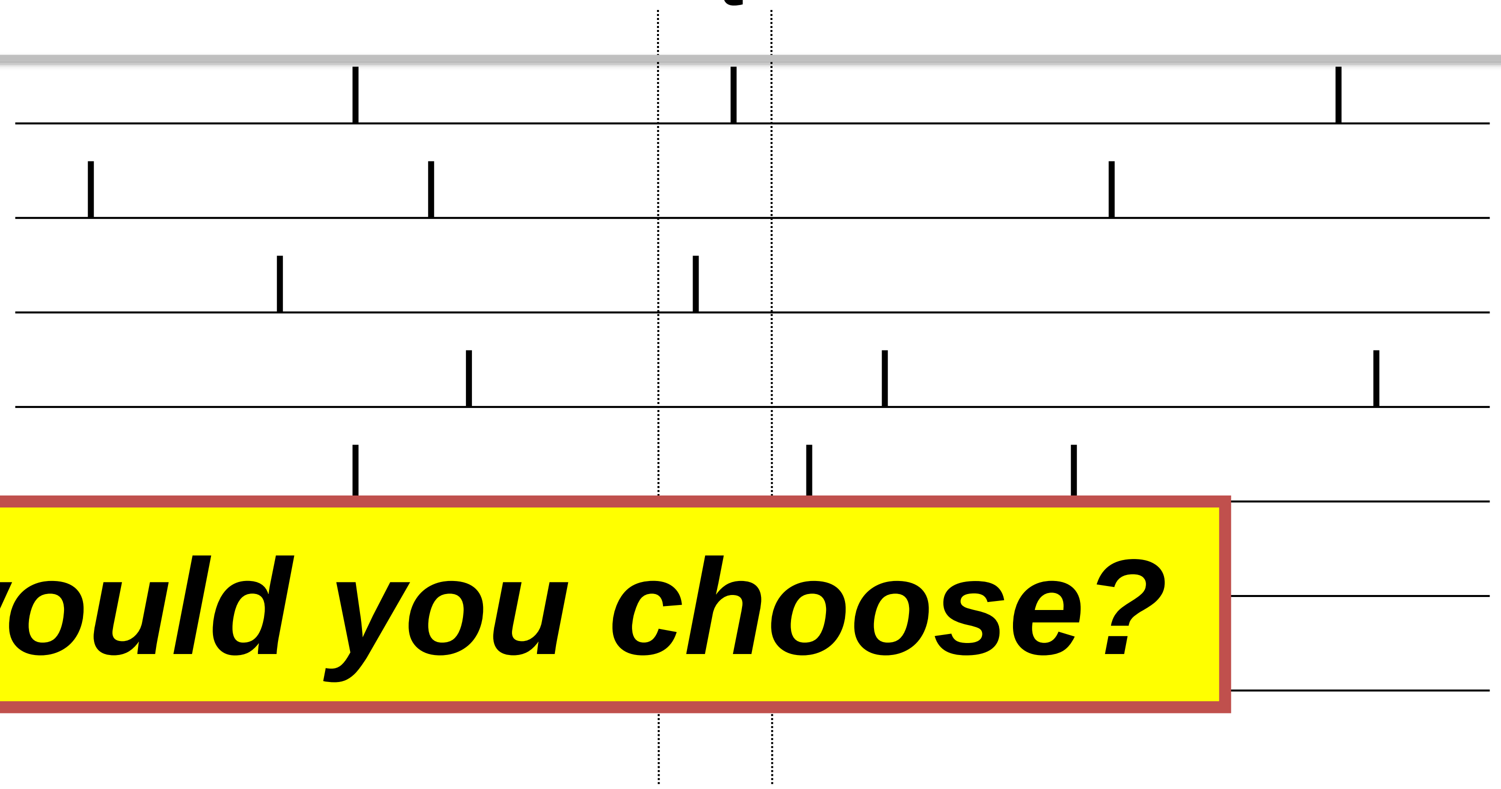


$$A(t) = F(h(t)) = F\left(\int \kappa(s) I(t-s) ds\right)$$

$$A(t) = g(I(t))$$

2. Transients in a population of uncoupled neurons

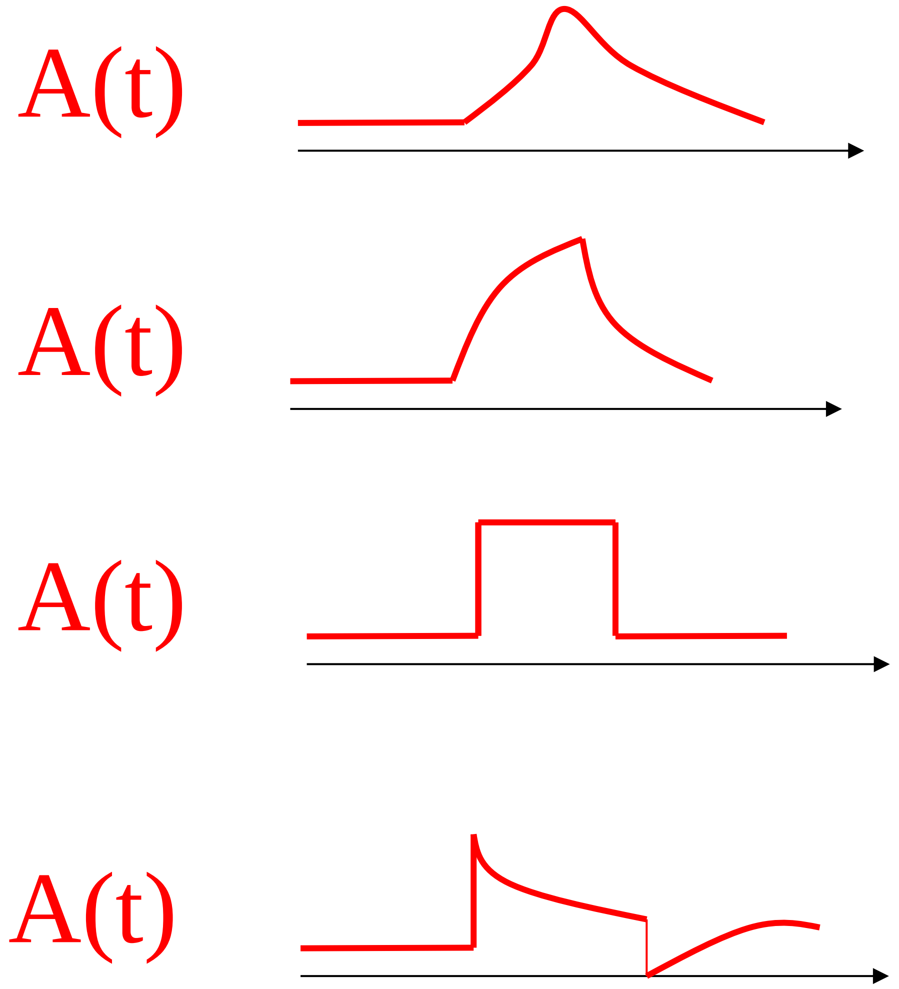




Which would you choose?

population activity

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



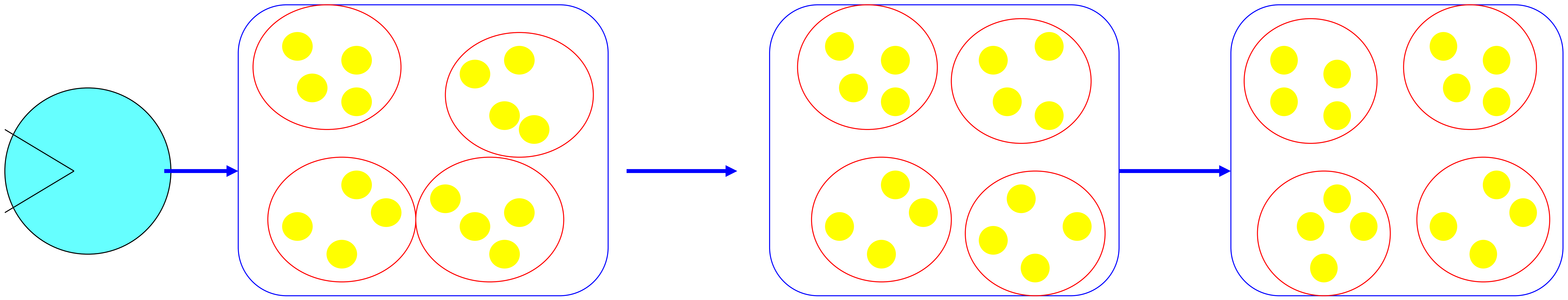
$$\tau \frac{d}{dt} A(t) = -A(t) + F(h(t))$$

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

$$A(t) = g(I(t))$$

$$A(t) = g(I(t), I'(t))$$

2. Transients in a population of neurons: simulations



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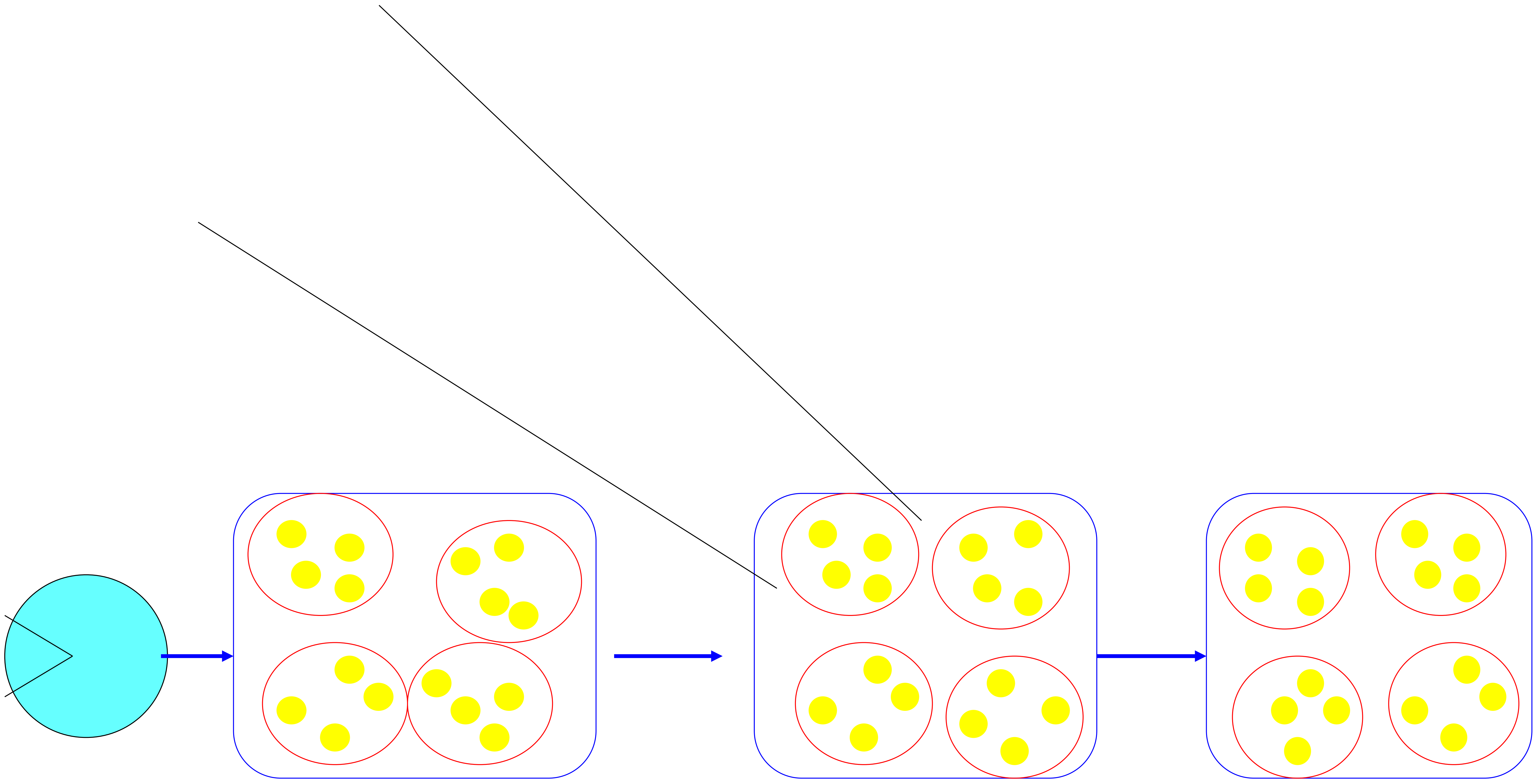

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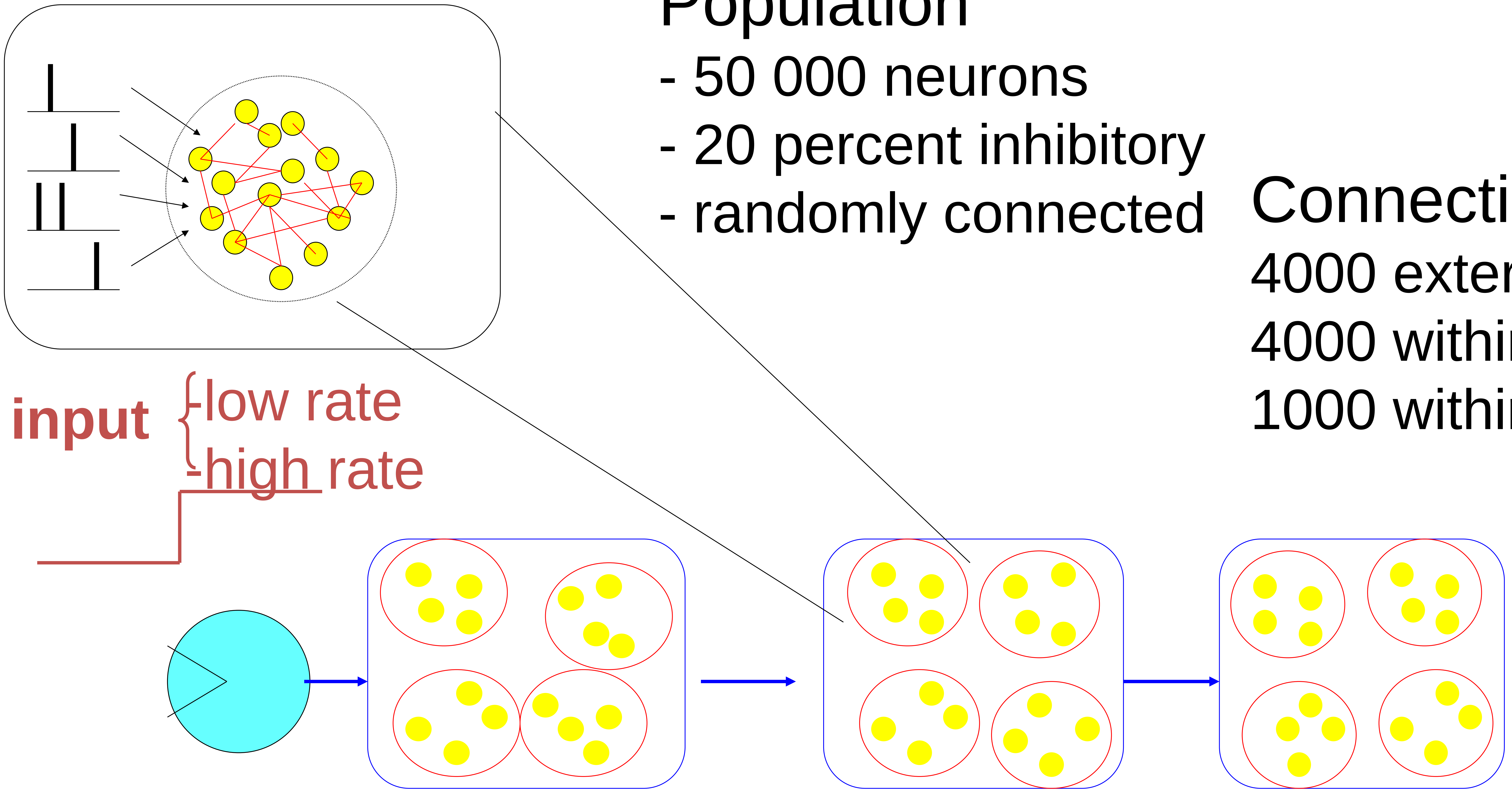
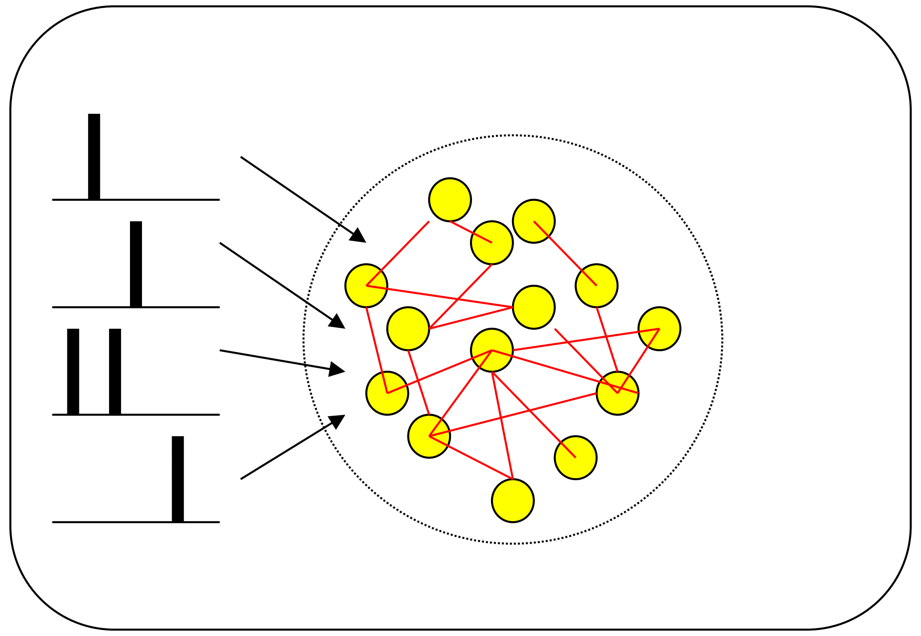


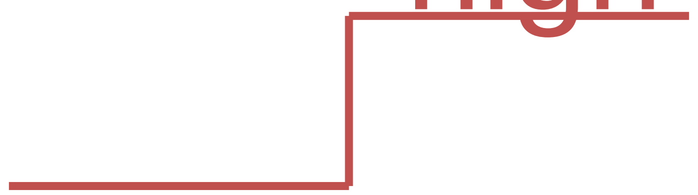
Population
- 50 000 neurons
- 20 percent inhibitory
- randomly connected

Connections
4000 external
4000 within excitatory
1000 within inhibitory

2. Transients in a population of neurons: simulations



input {low rate / high rate



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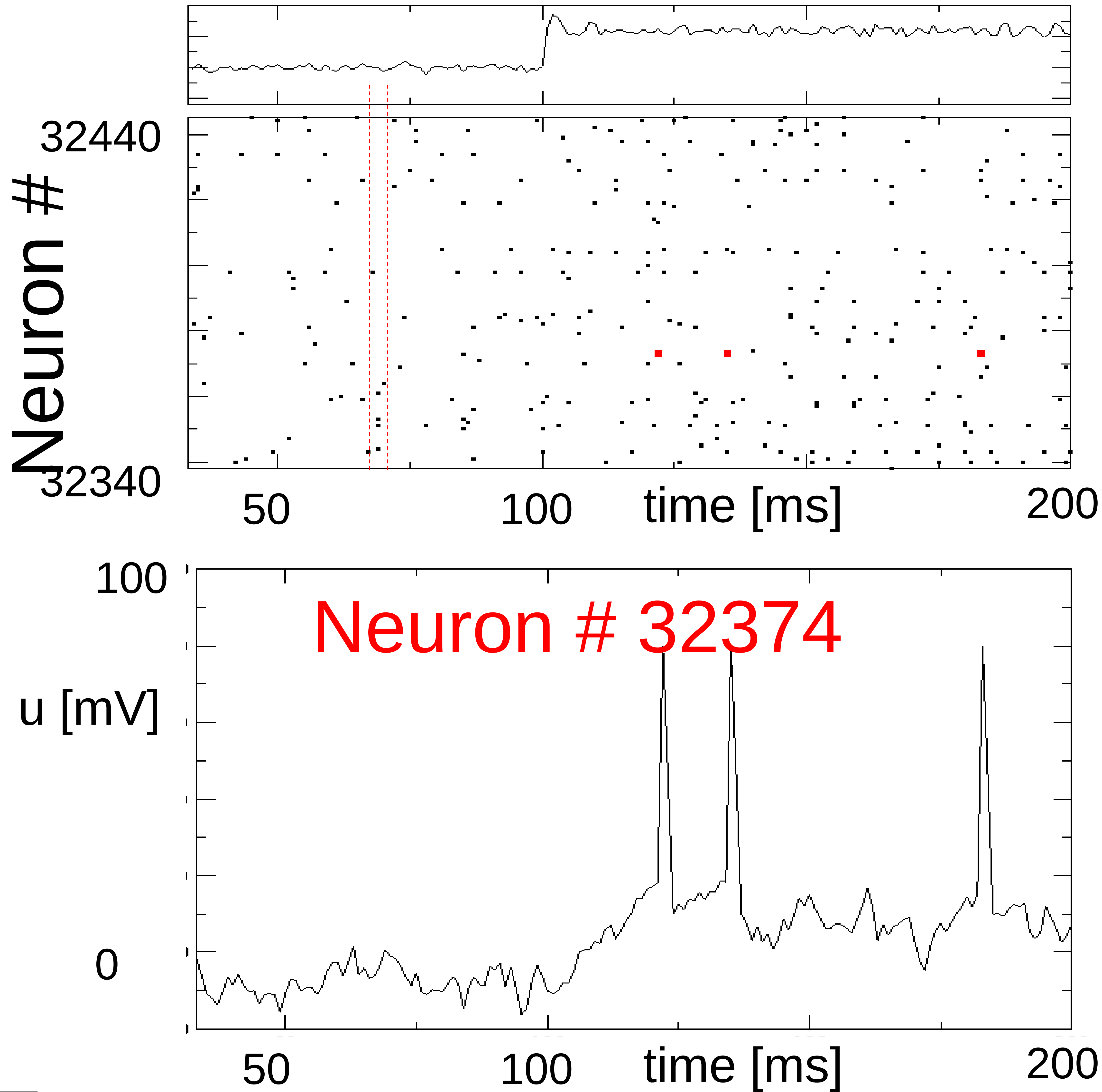
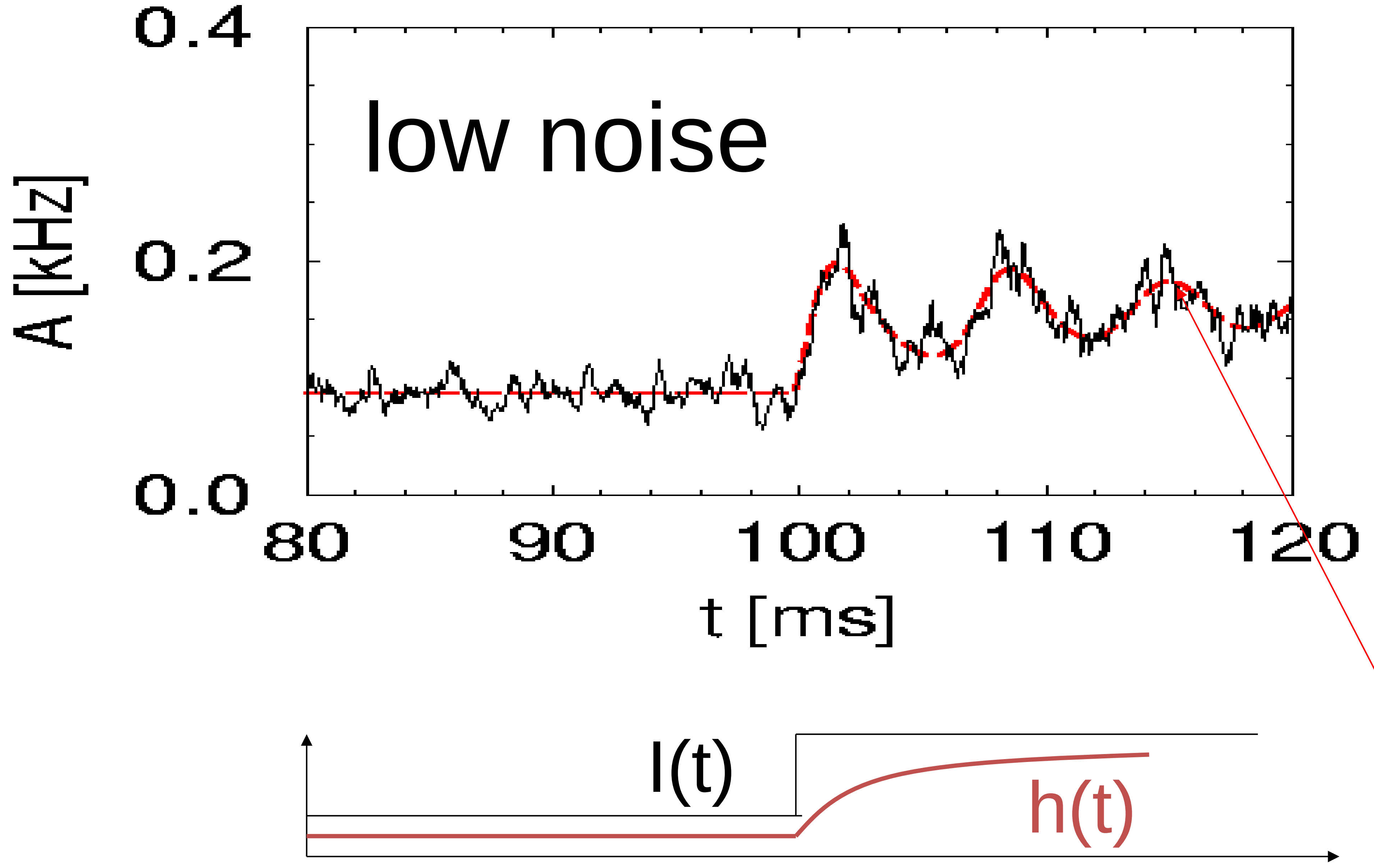
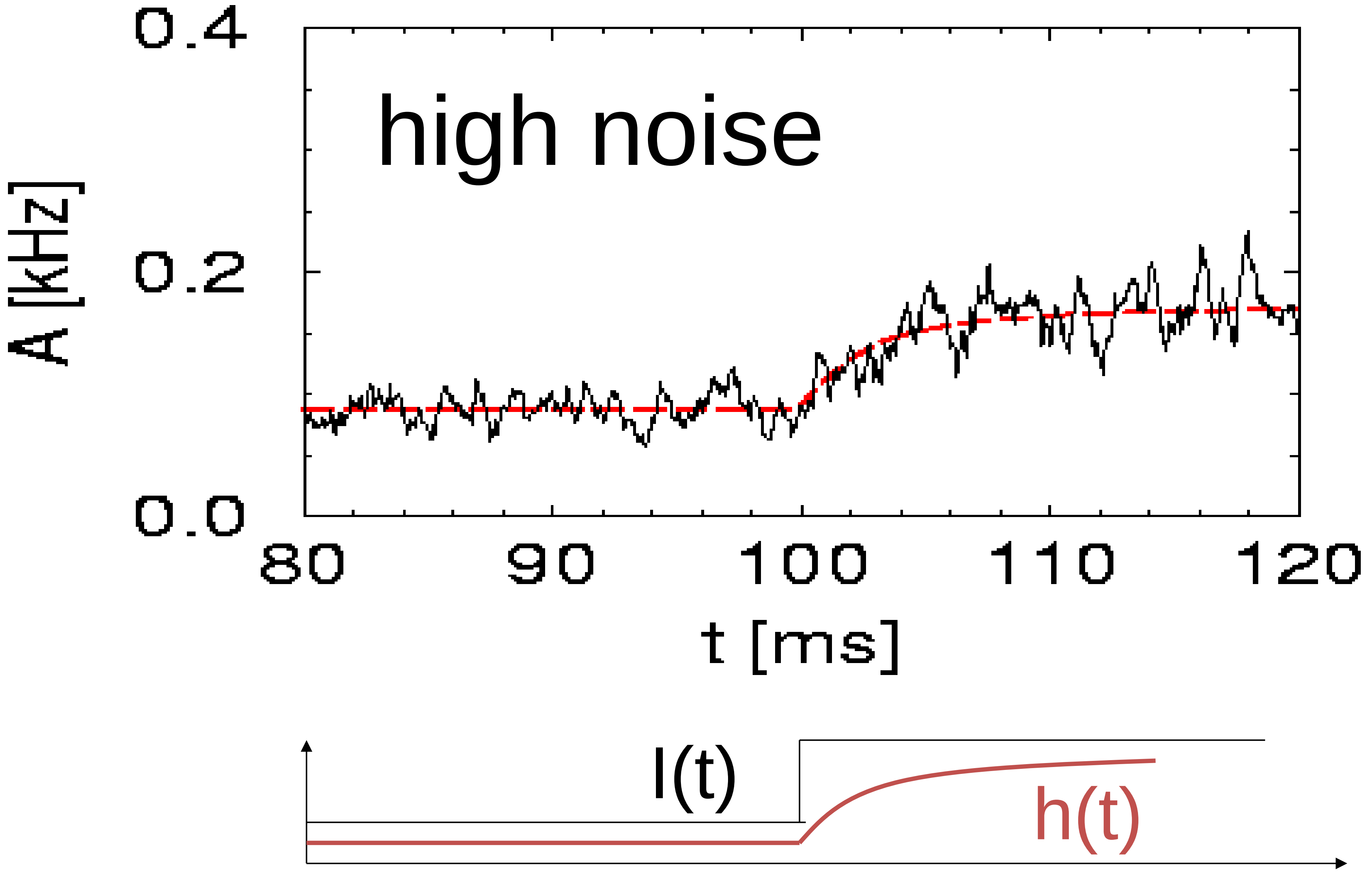


2. Transients for populations of noisy neurons

uncoupled population

of SRM neurons with noise (escape noise)





fast transient

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

slow transient

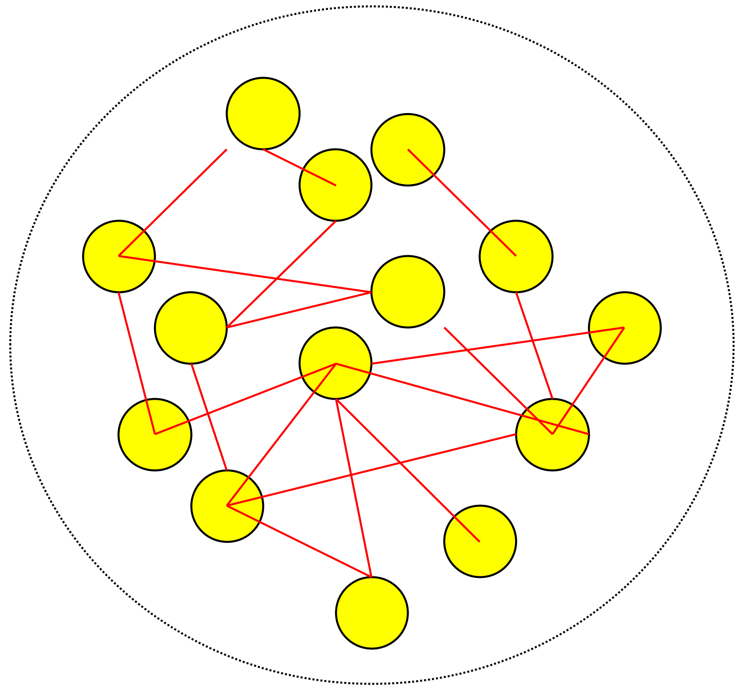
$$A(t) = F(h(t))$$

but transient oscillations

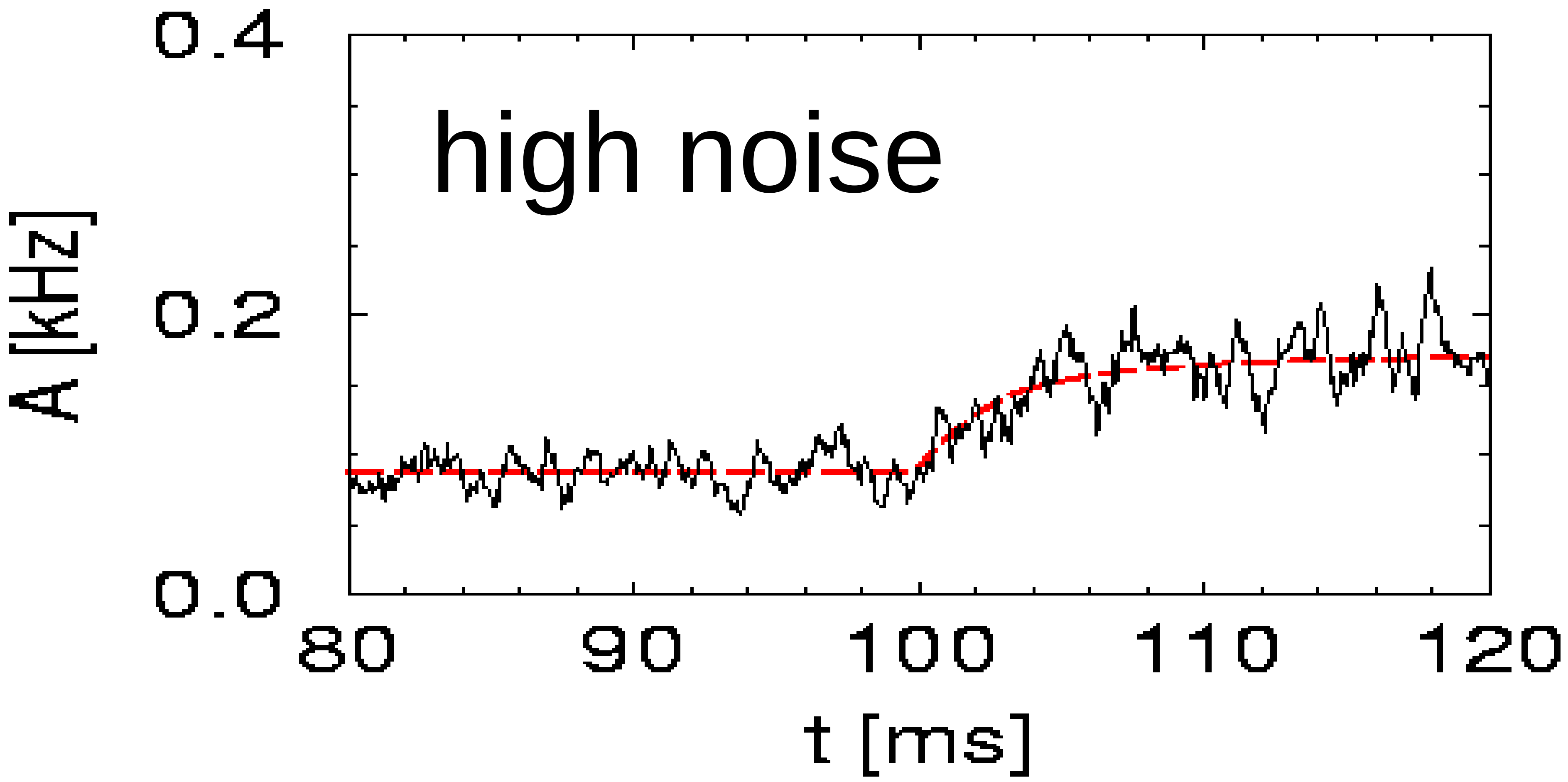
2. High-noise activity equation

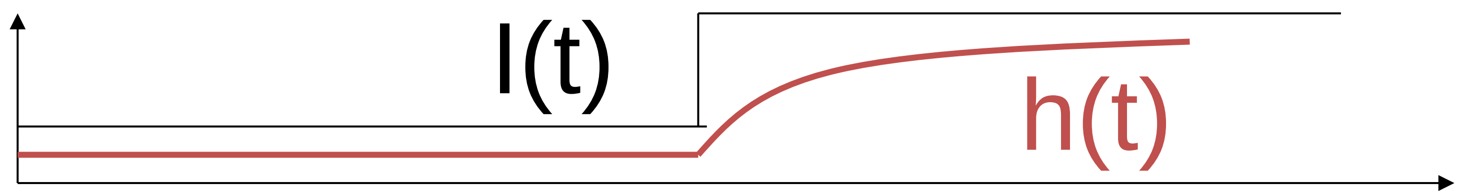
Membrane potential caused by input

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



(escape noise)





slow transient

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

In the limit of **high noise**,

2. High-noise activity equation

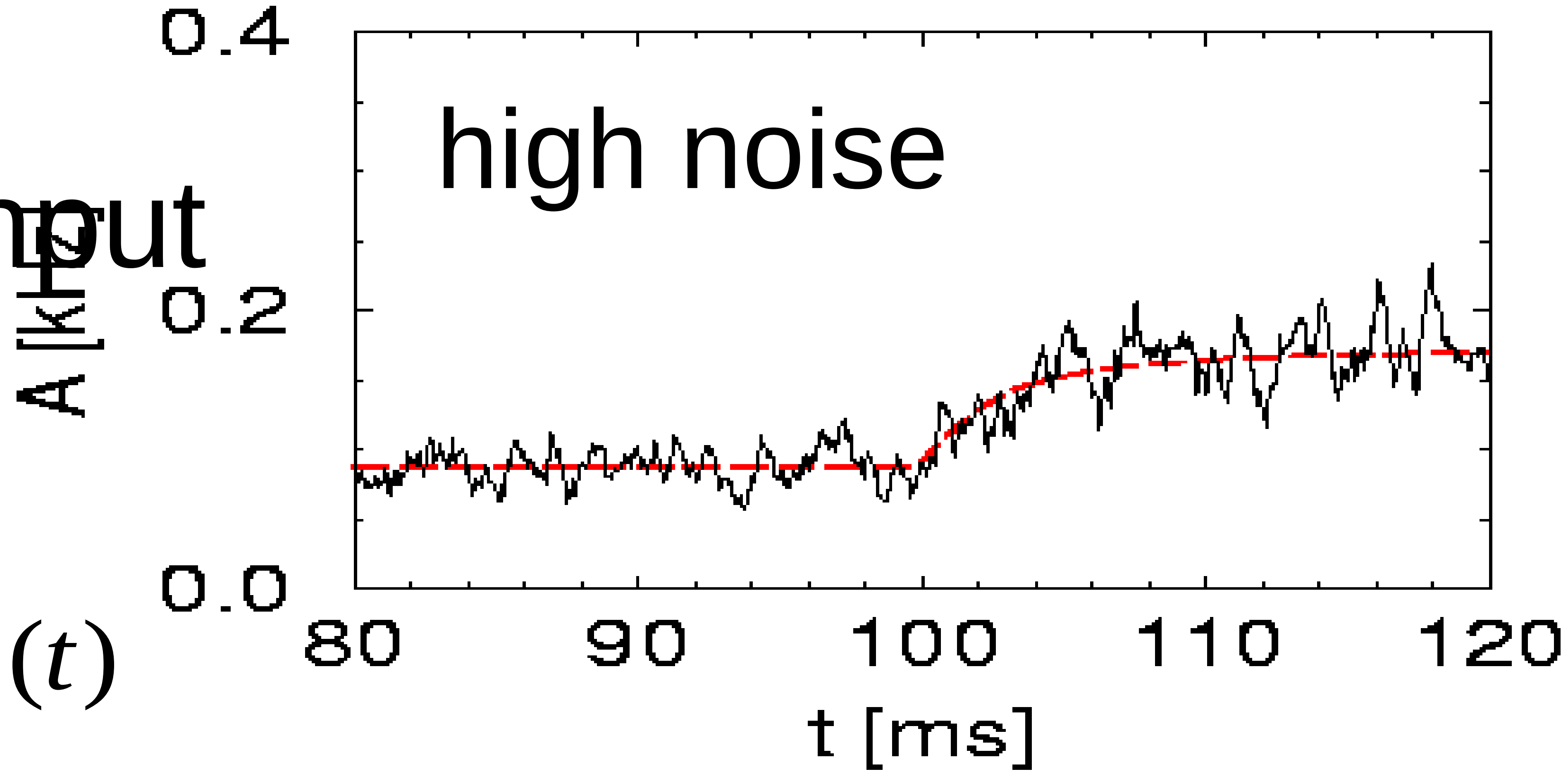
Population activity

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

Membrane potential caused by input

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

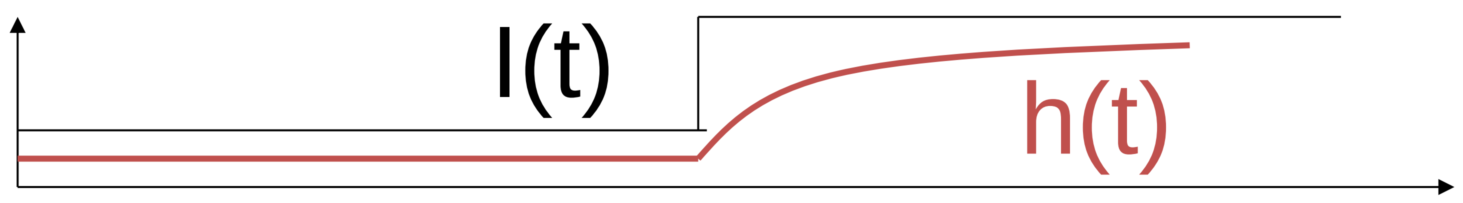
(escape noise)



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

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

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



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

2. Summary: Transients and population equations

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

- population activity equation
- smooth transient
- input potential determines activity

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

- valid in high-noise regime
- misses sharp transients
- misses transient oscillations

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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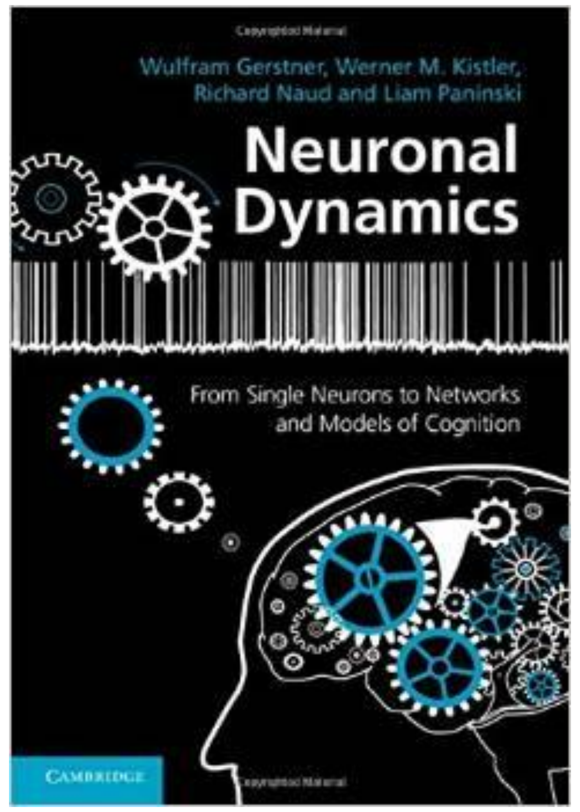

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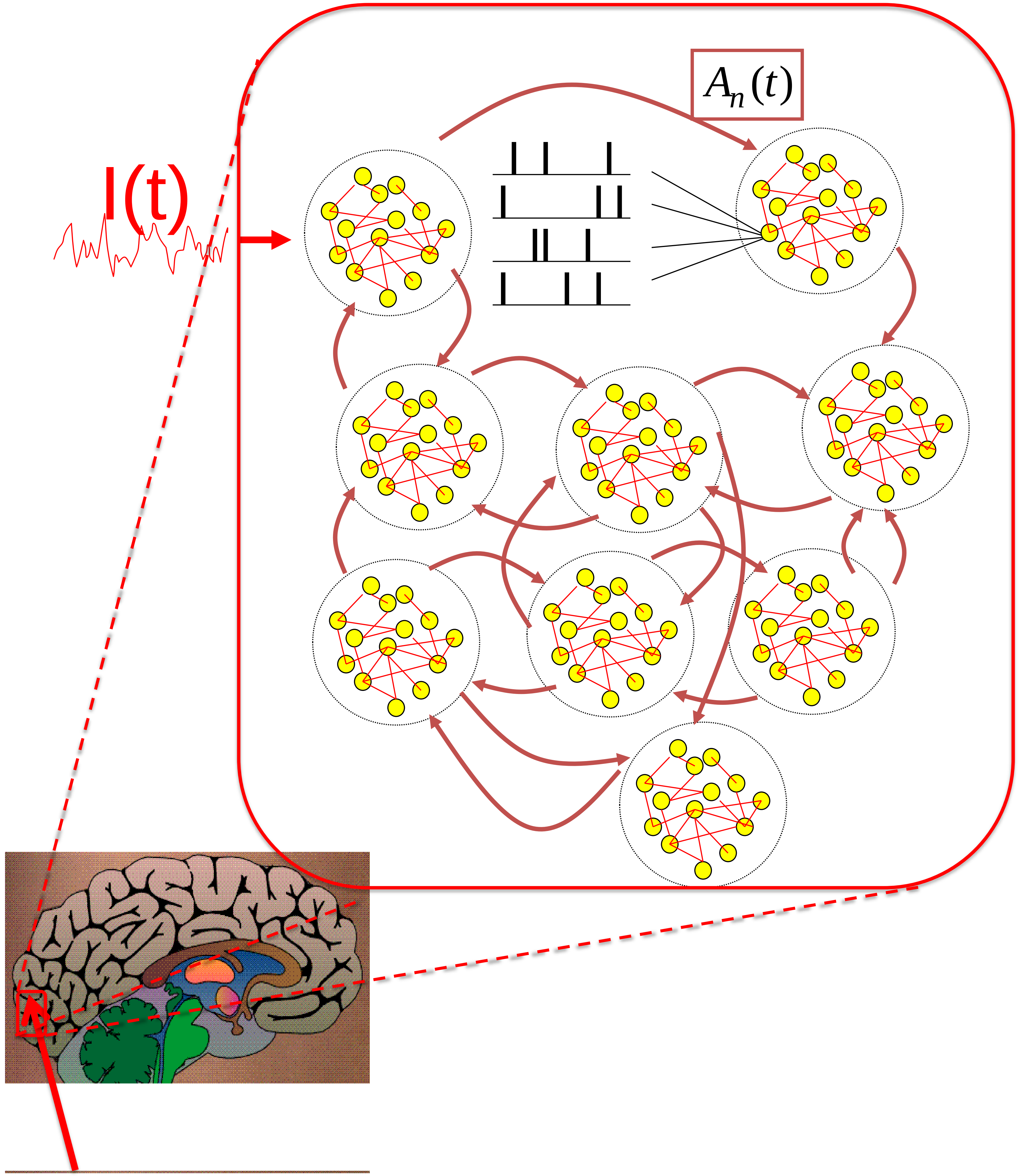
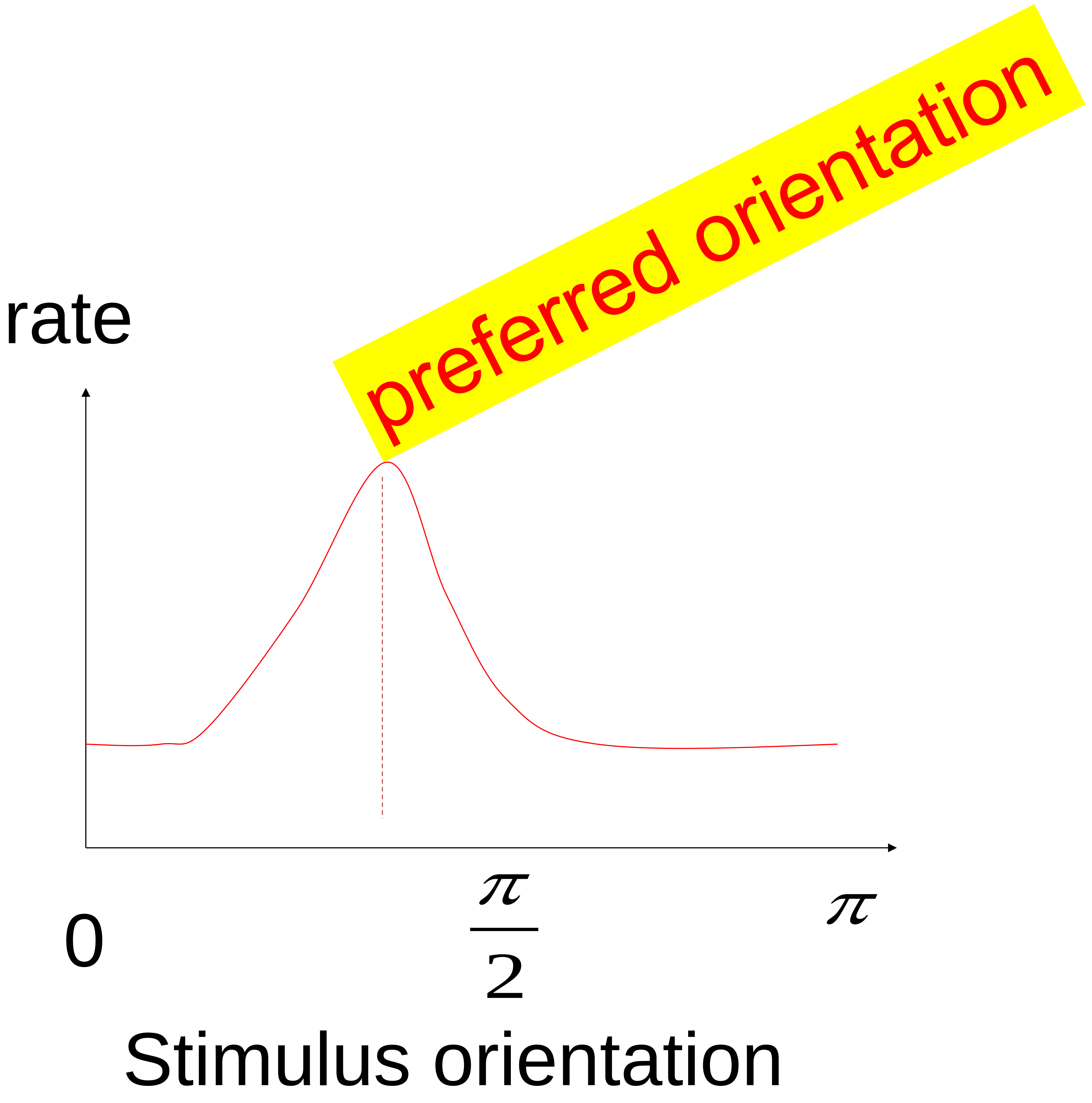
3. Interacting Populations: how many populations?



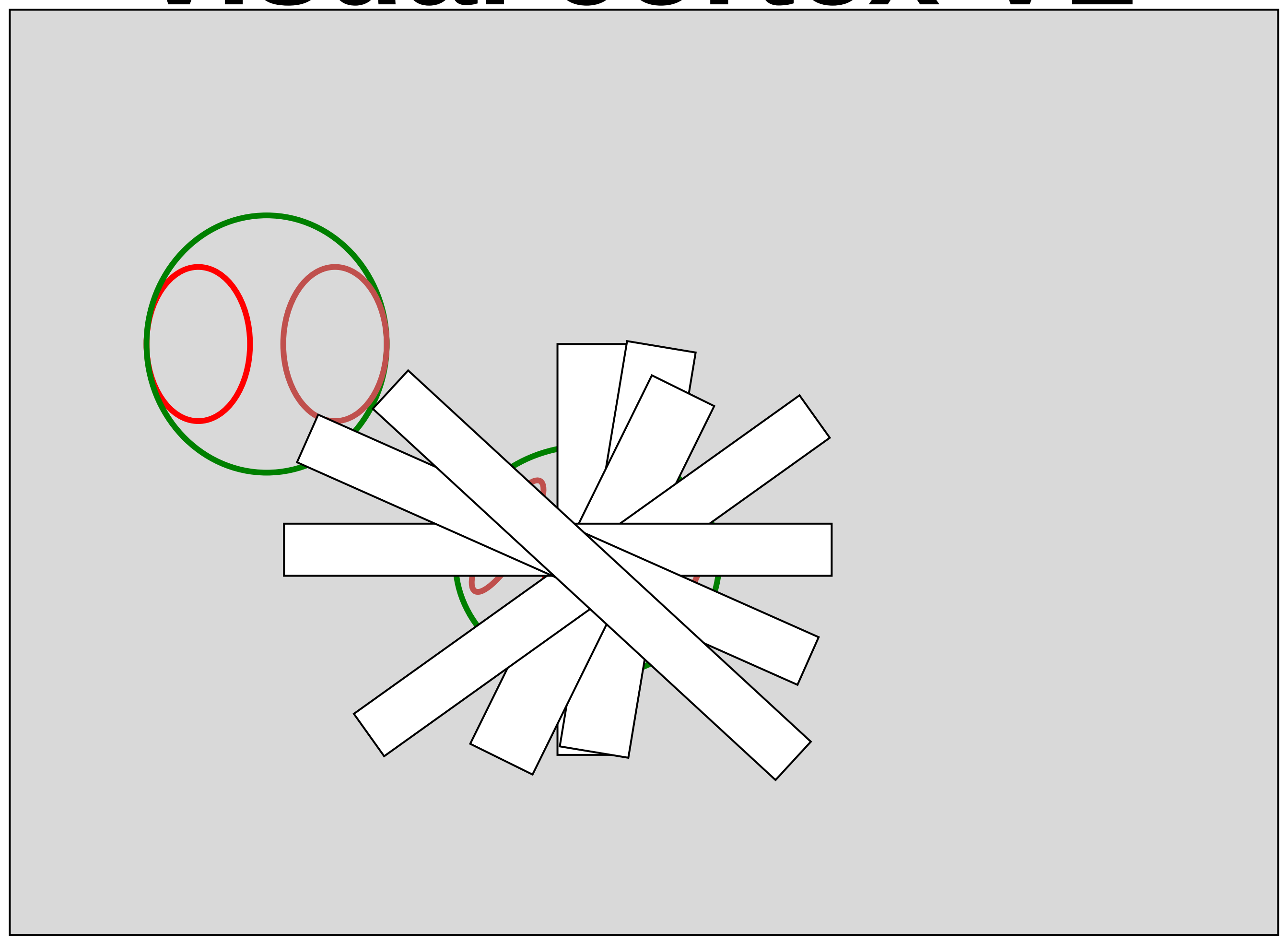
Visual cortex

3. Review: Receptive fields with Orientation Tuning



Receptive fields:

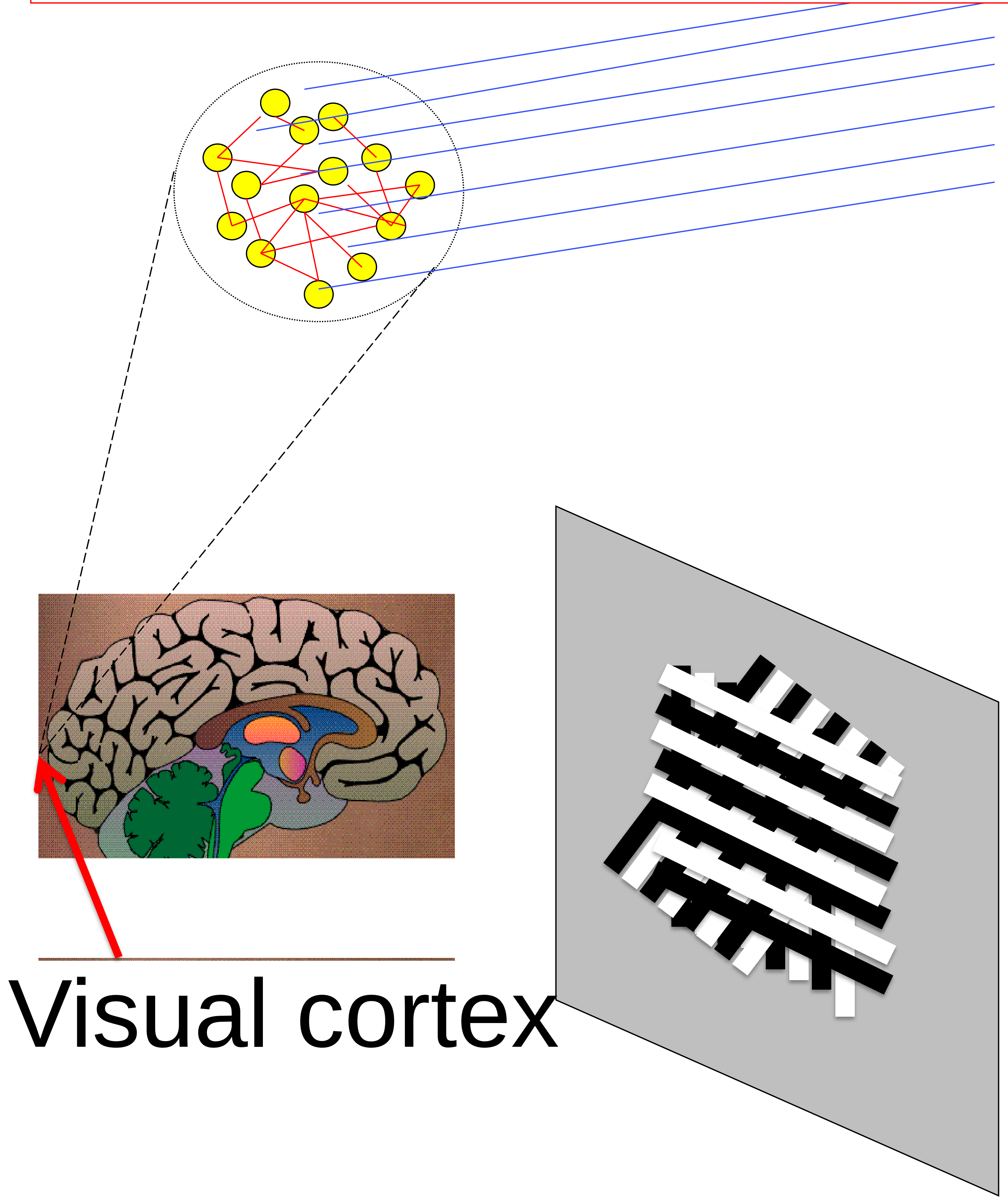
visual cortex V1



Orientation selective

3. Orientation Map

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



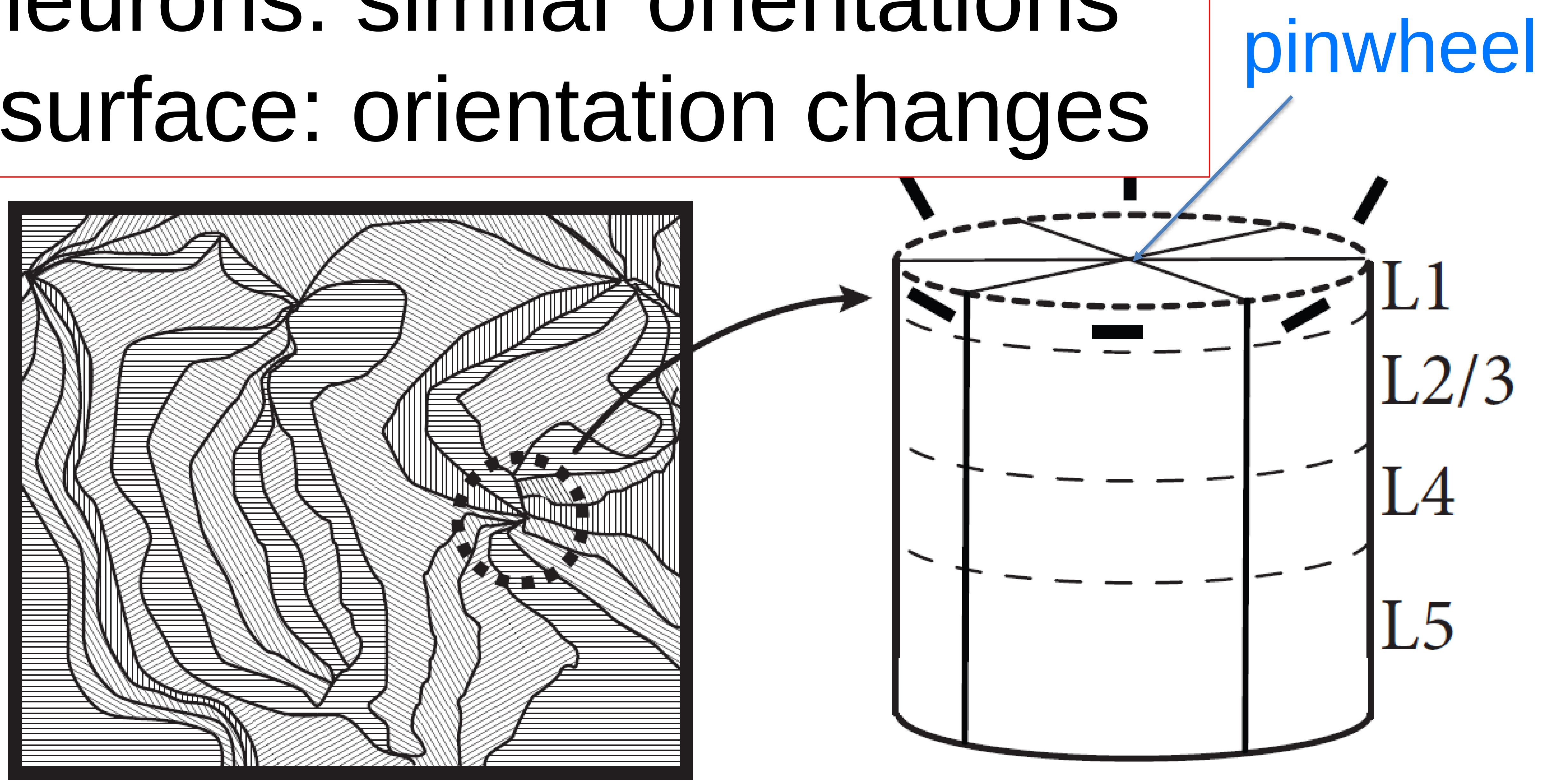
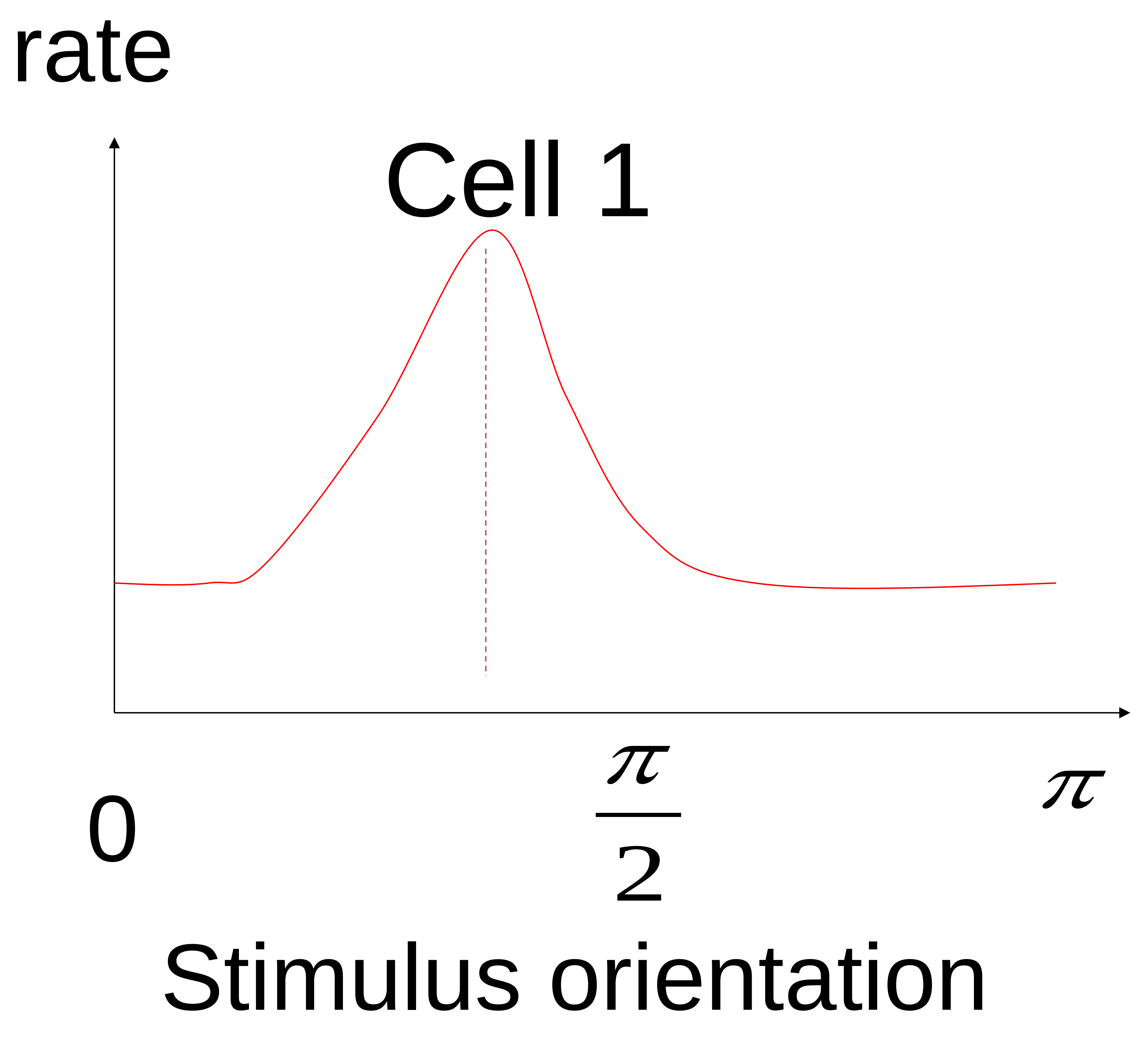


Image: Gerstner et al.
Neuronal Dynamics (2014)

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

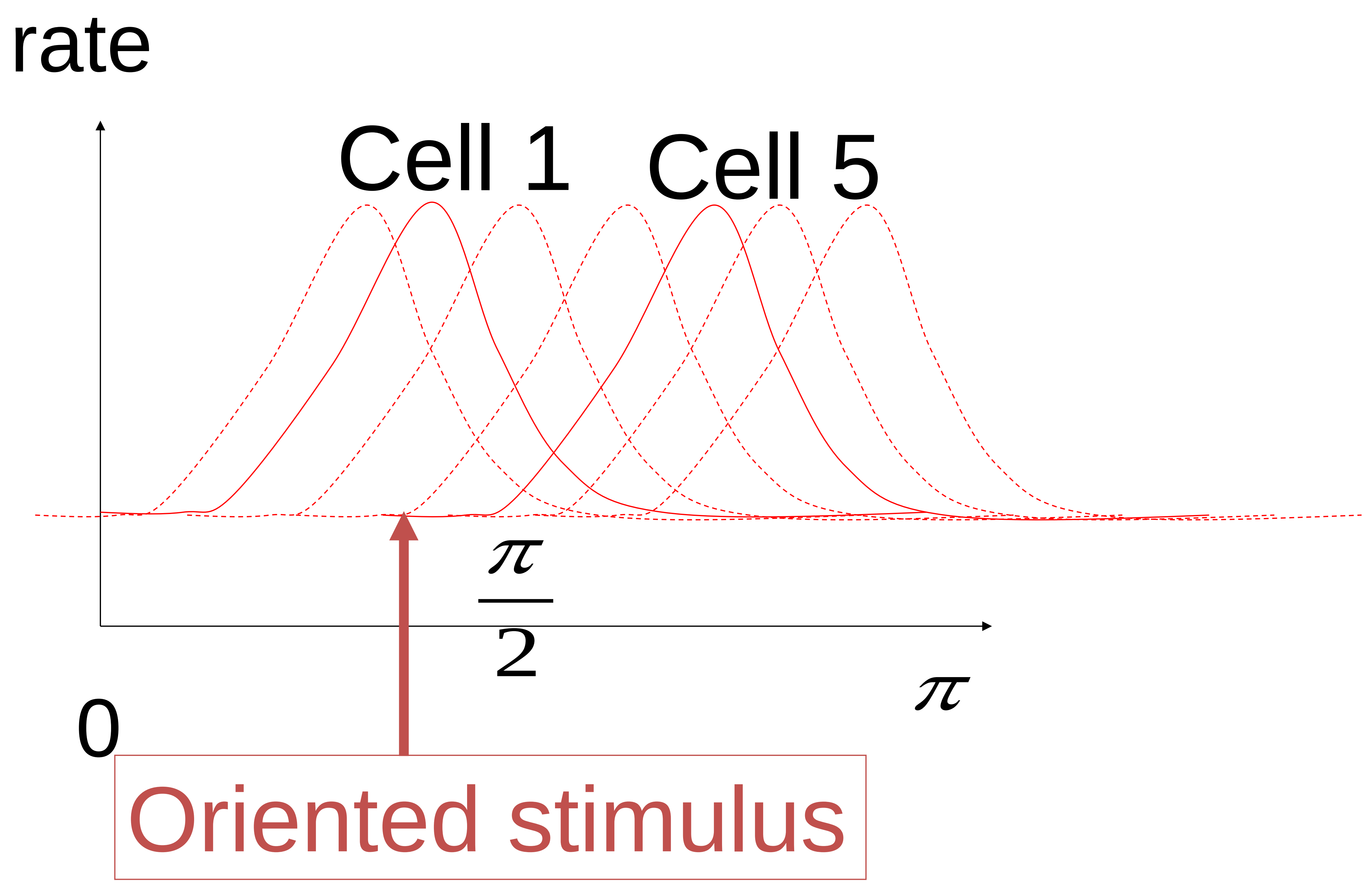
3. Do Orientation Columns exist? Do identical cells exist?



3. Do Orienation colums exist? Do identical cells exist?

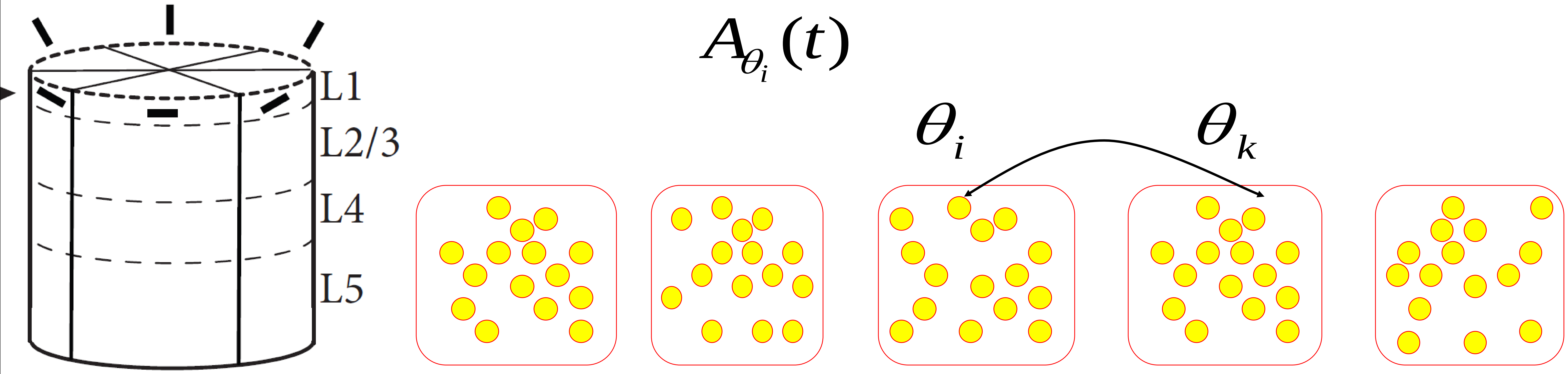
Coarse coding

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

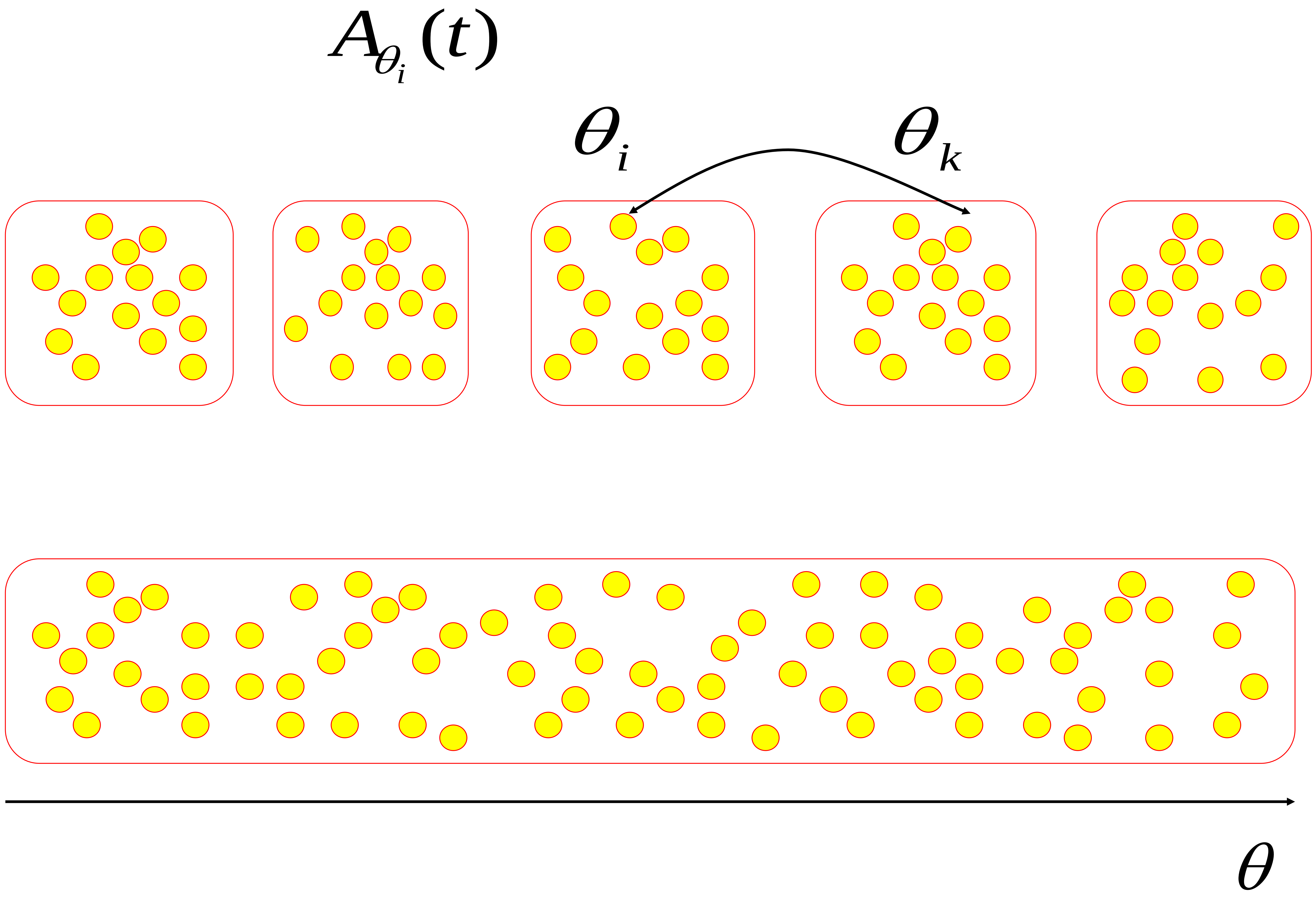


→ no discrete columns

3. multiple populations → continuum



3. multiple populations → continuum



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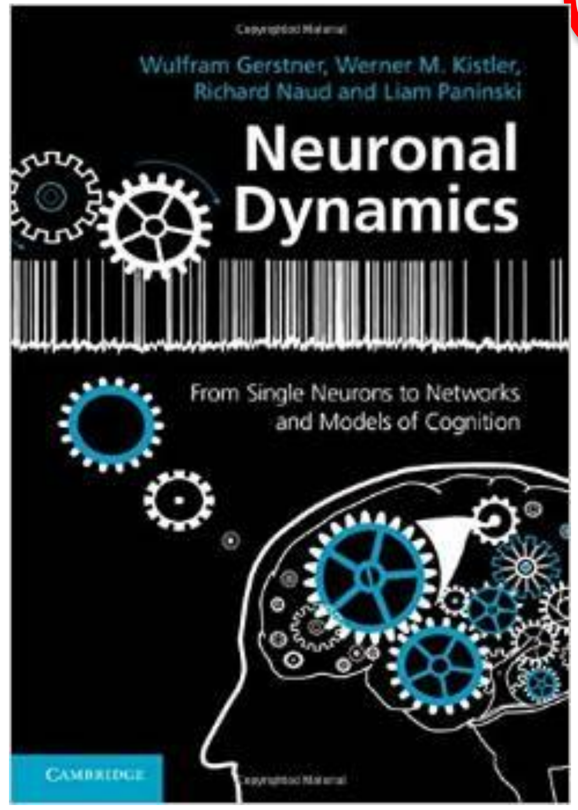

1. Aims and challenges
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- transients can be sharp or slow

3. Spatial continuum (cortex)
- orientation columns

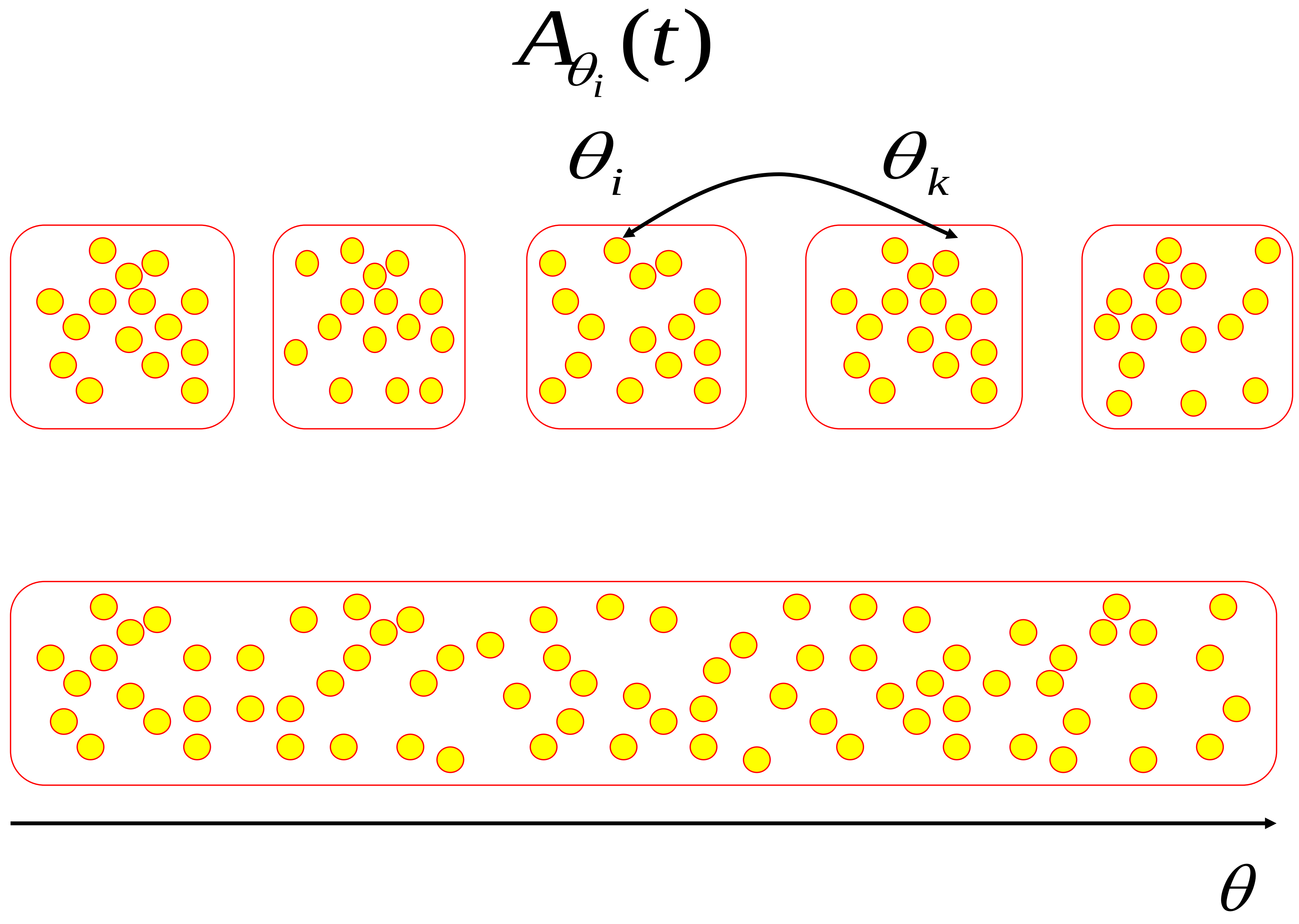
4. Spatial continuum (model)
- field equations

5. Solution types
- uniform solution
- bump solution

6. Perception

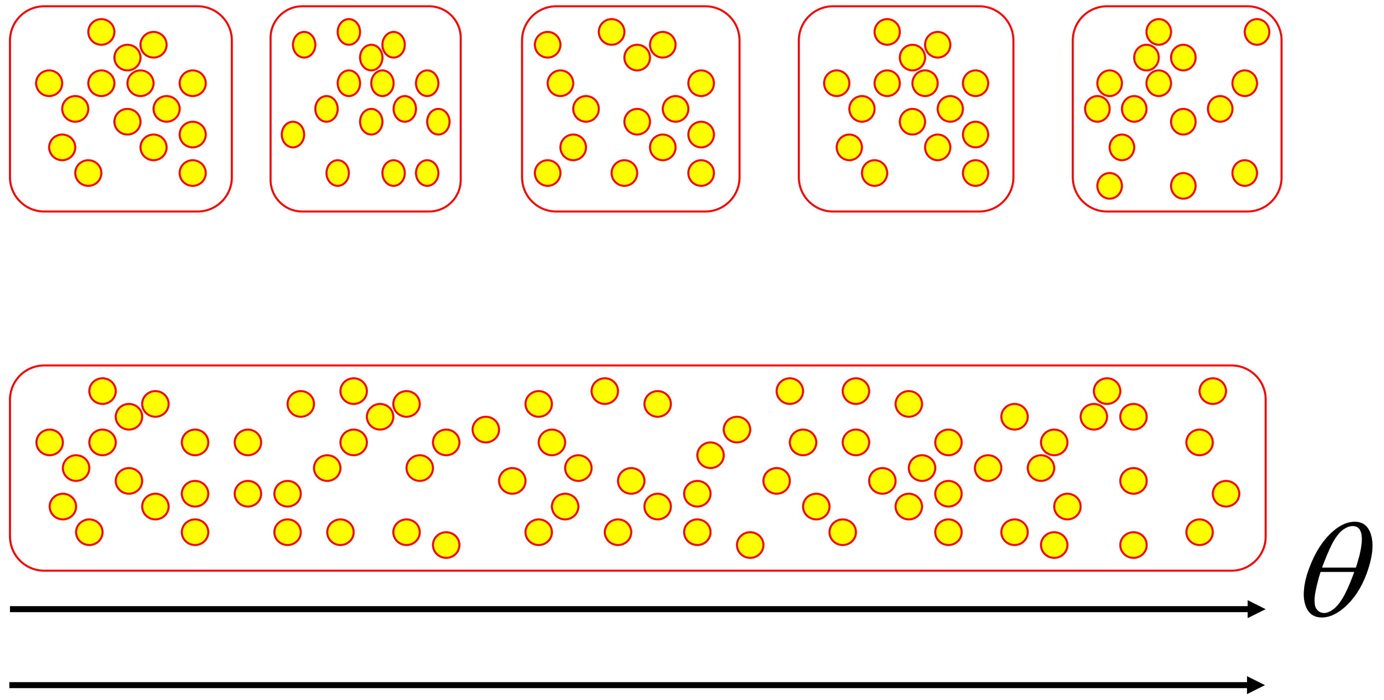
7. Head direction cells

4. multiple populations → continuum



Mathematical aim:
perform continuum limit

4. multiple populations → continuum



4. Field equation (continuum model)

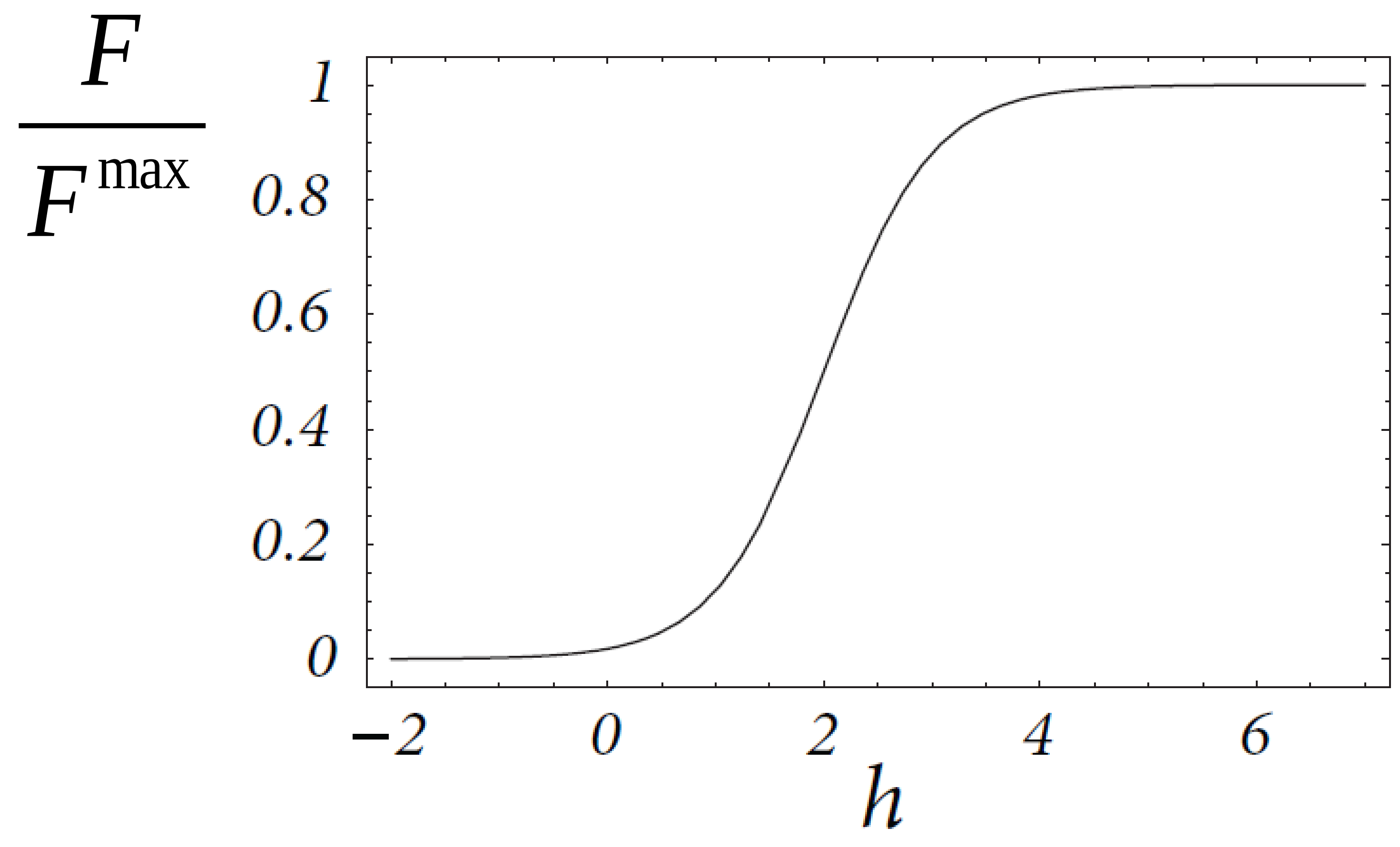
Wilson and Cowan, 1973

Population activity

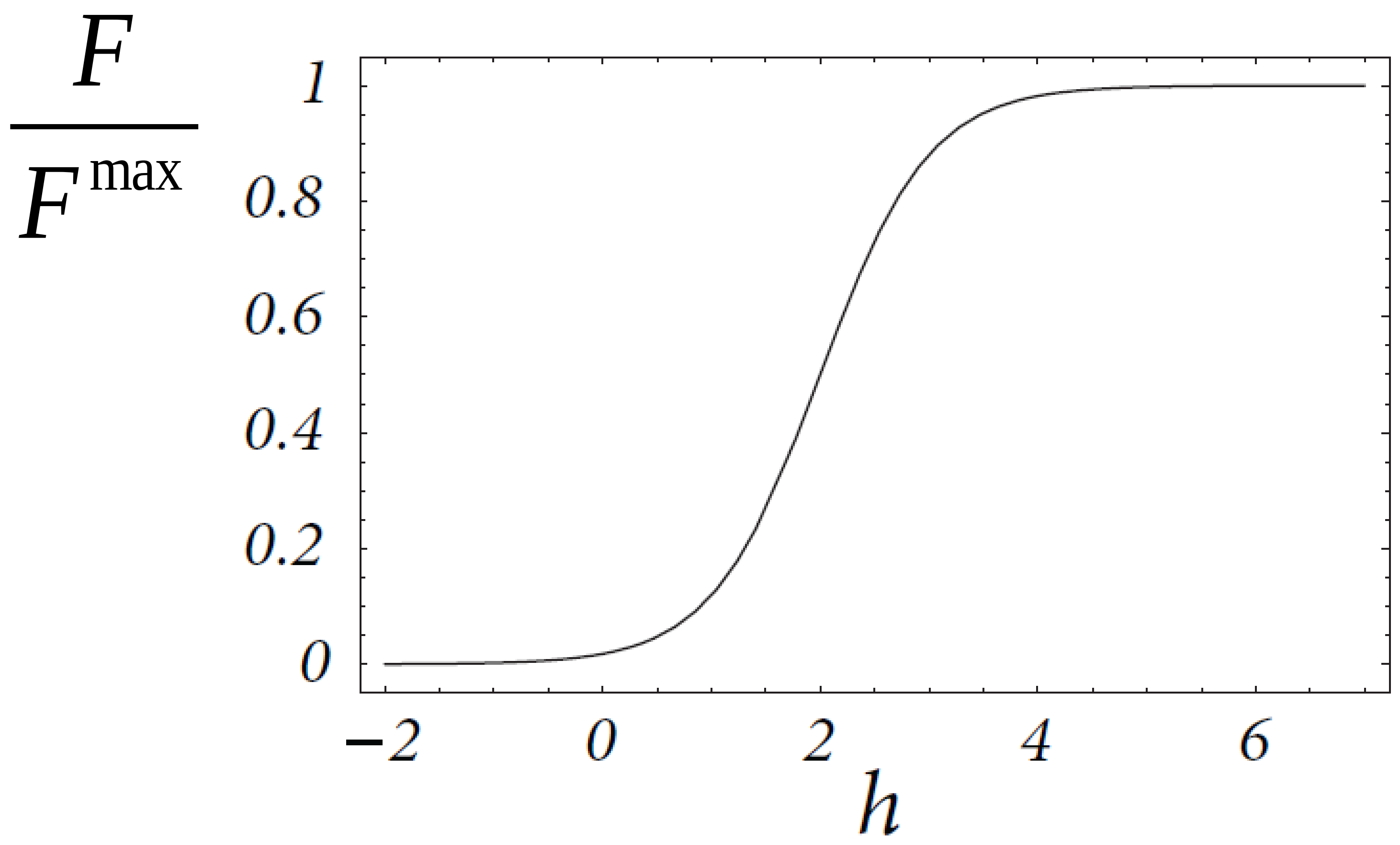
$$A(x,t) = F(h(x,t))$$

Membrane potential caused by input

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



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



Population activity

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

Membrane potential caused by input

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

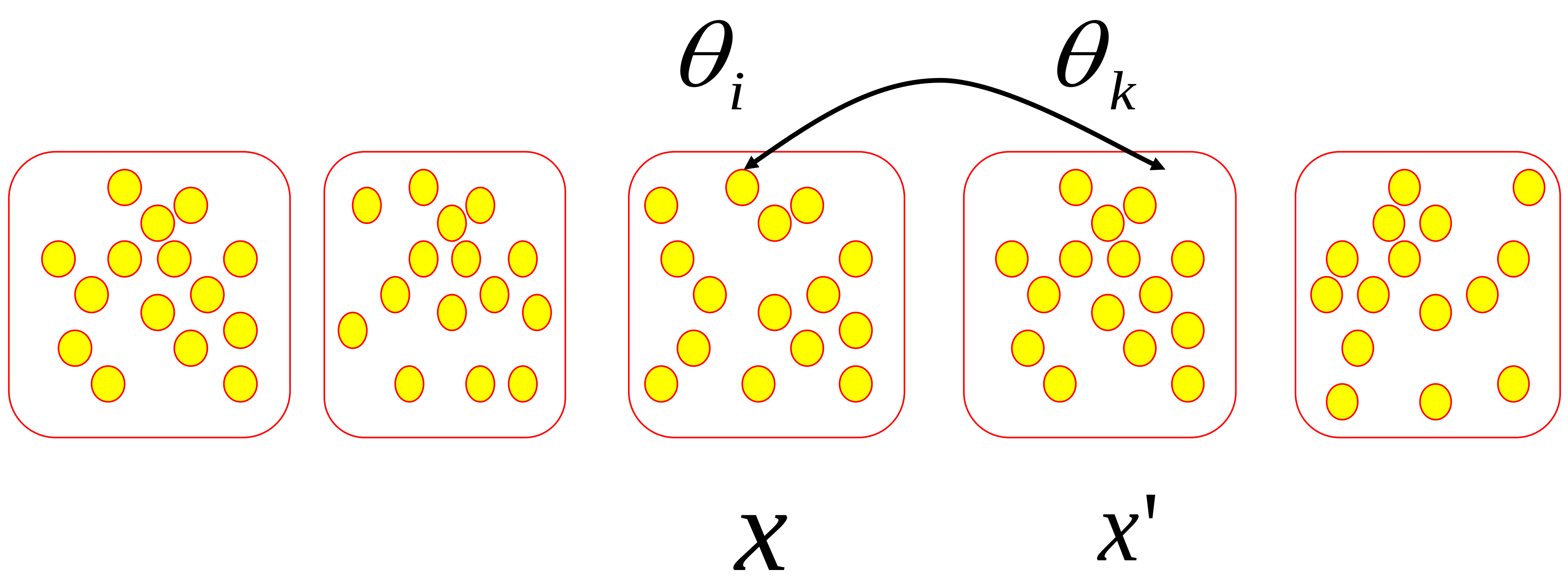
$$I(x,t) = I^{ext}(x,t) + I^{netw}(x,t)$$

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

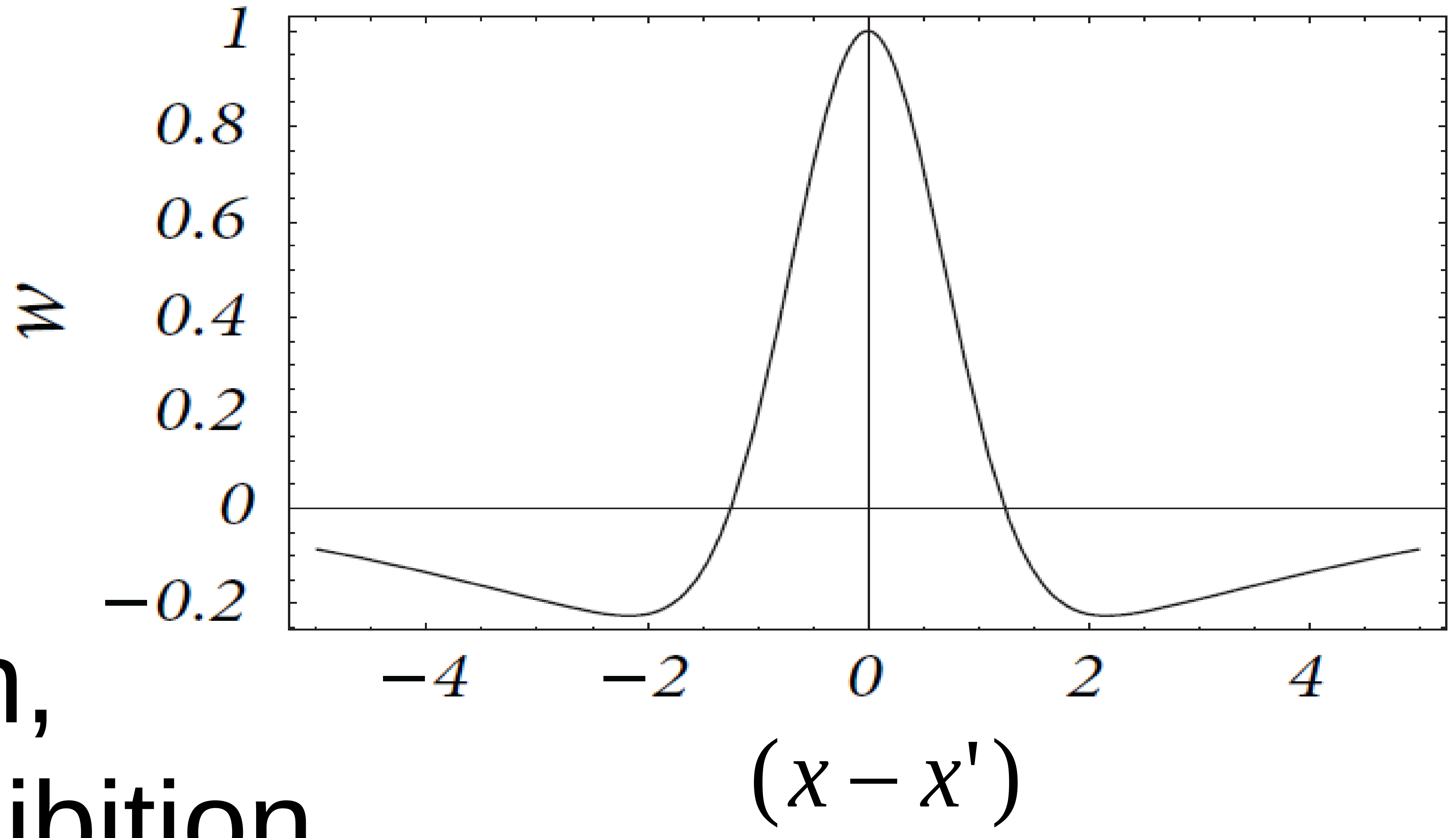
$$\tau \frac{d}{dt} h(x,t) = -h(x,t) + R\, I^{ext}(x,t) + d \int w(x-x') F(h(x',t))\, dx'$$

1 field = 1 integro-differential equation

4. coupling across continuum: Mexican hat



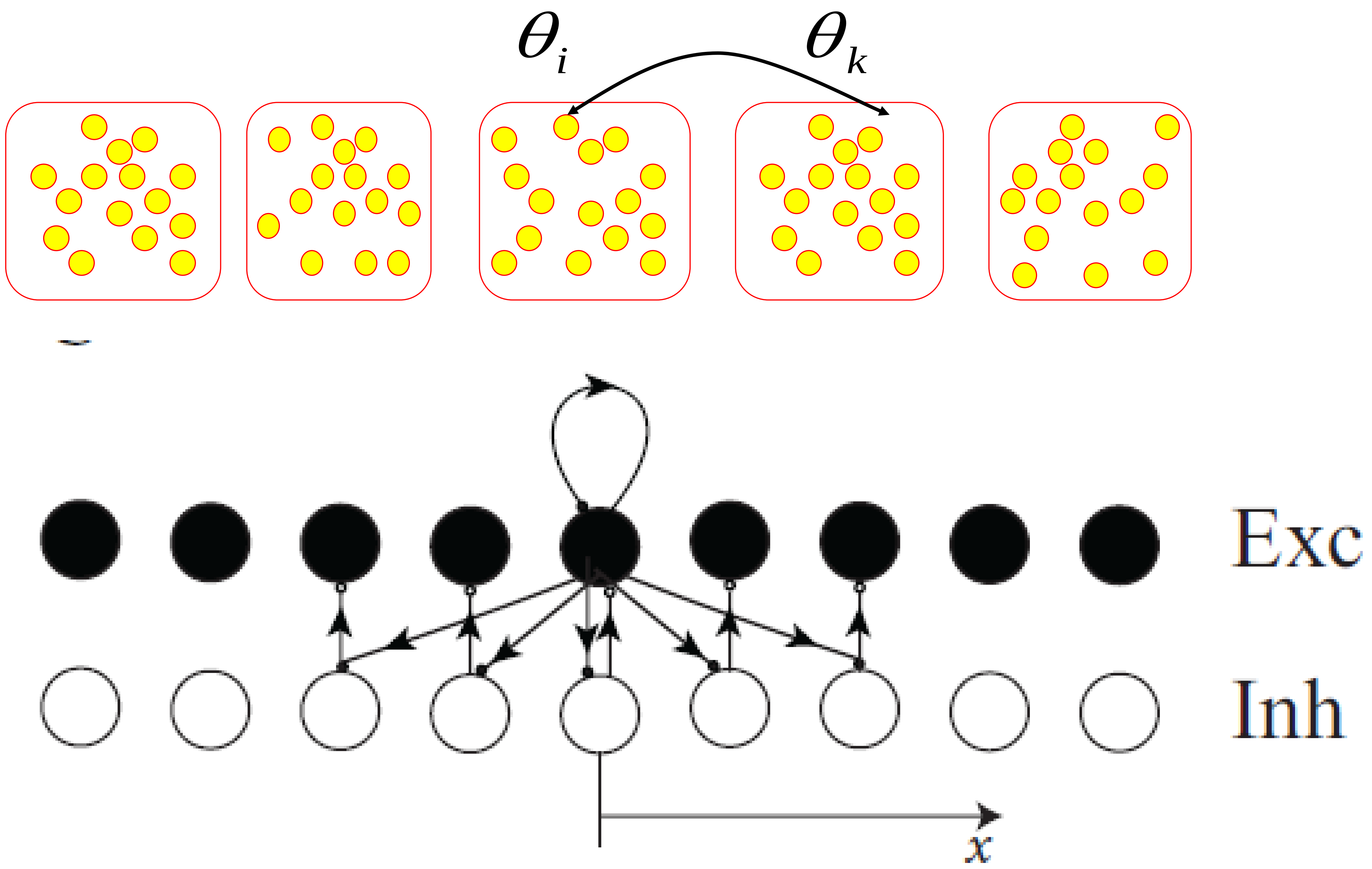
Mexican hat



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

local excitation,
long-range inhibition

4. more realistic cortical coupling



Effective long-range negative interaction with local inhibition

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)

Computational Neuroscience: Neuronal Dynamics of Cognition

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Continuum models:

Cortical fields and perception

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EPFL, Lausanne, Switzerland

Reading:
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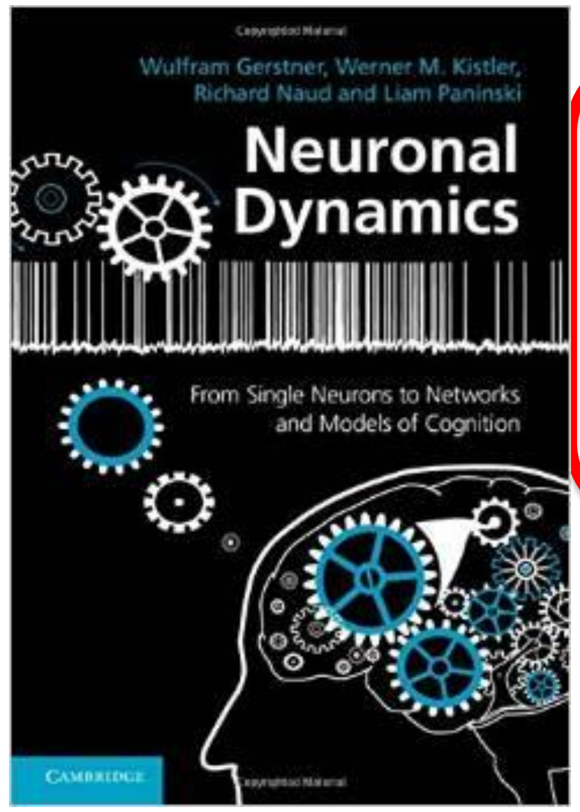

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   - uniform solution
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7. **Head direction cells**

5. Two Solution Types (ring model)

Coupling:

Input-driven regime

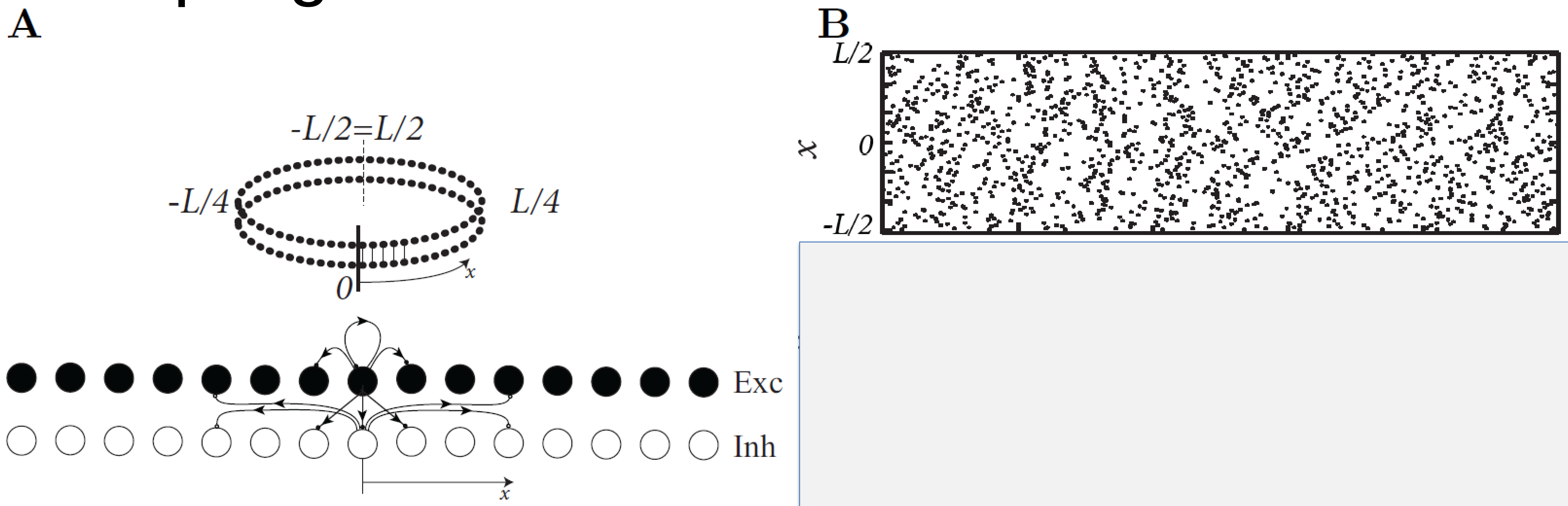
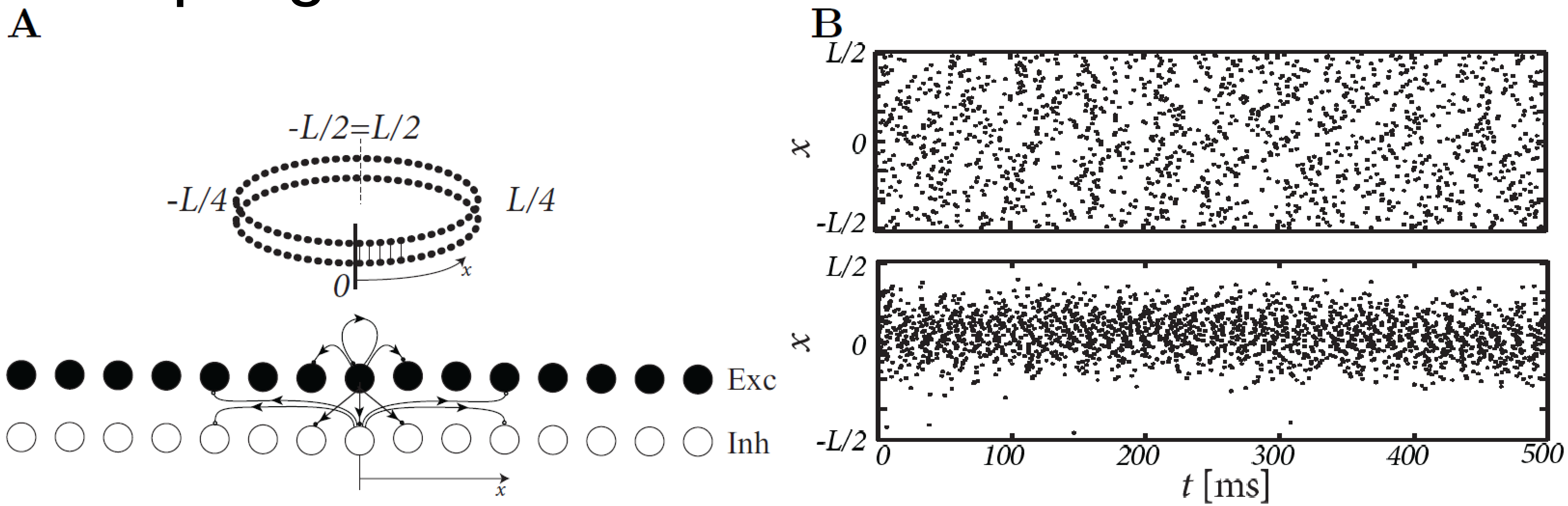


Image: Neuronal Dynamics, Gerstner et al., Cambridge Univ. Press (2014),

5. Two Solution Types (ring model)

Coupling:

Input-driven regime



Bump attractor regime

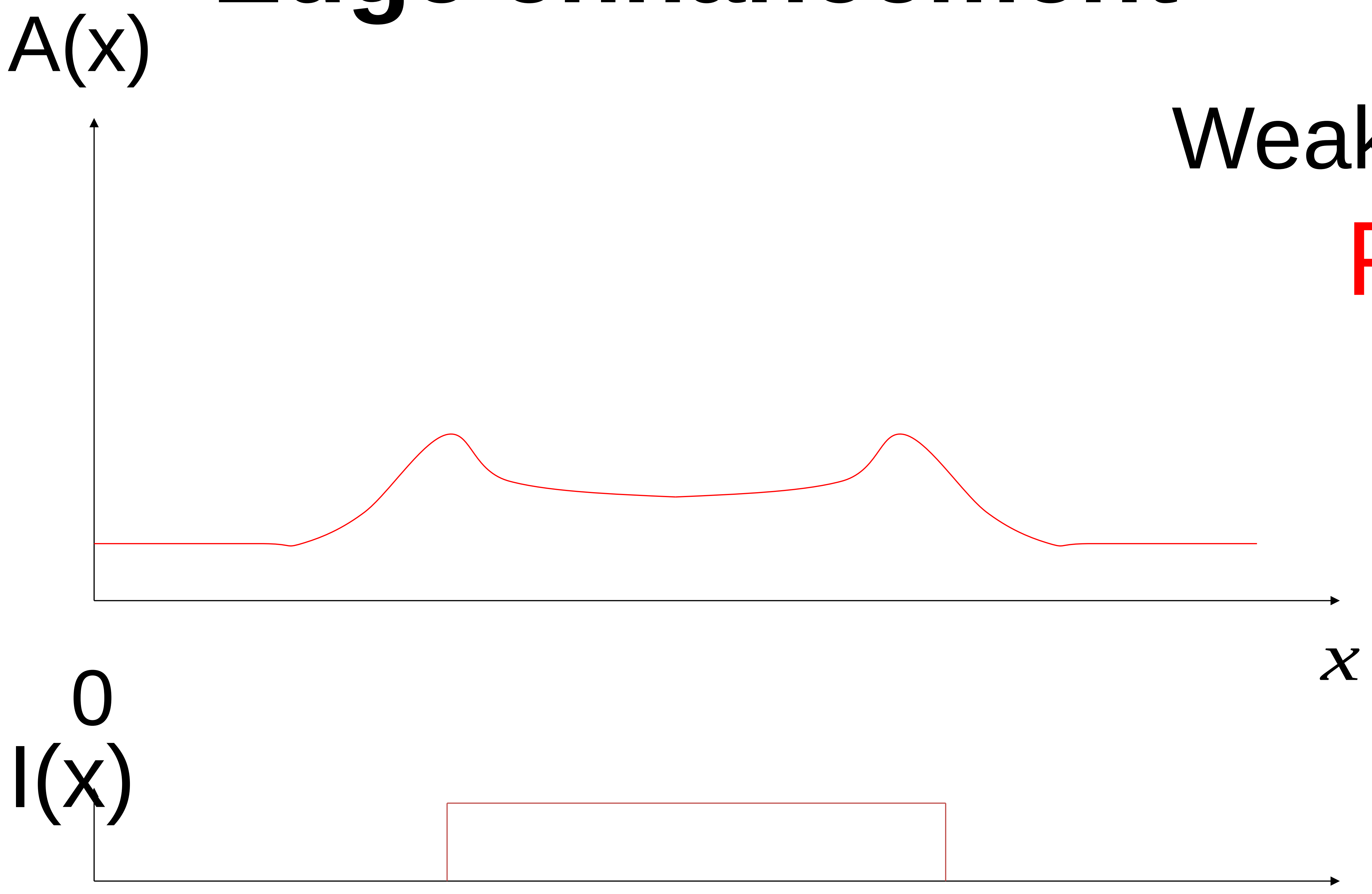
Image: Neuronal Dynamics, Gerstner et al., Cambridge Univ. Press (2014),

5. Solution type A: homogeneous solution=input driven regime

Field Equations:

Wilson and Cowan, 1973

Edge enhancement



Weak lateral connectivity

Possible application

visual cortex cells:

(see next part)

5. Solution type B: bump solution

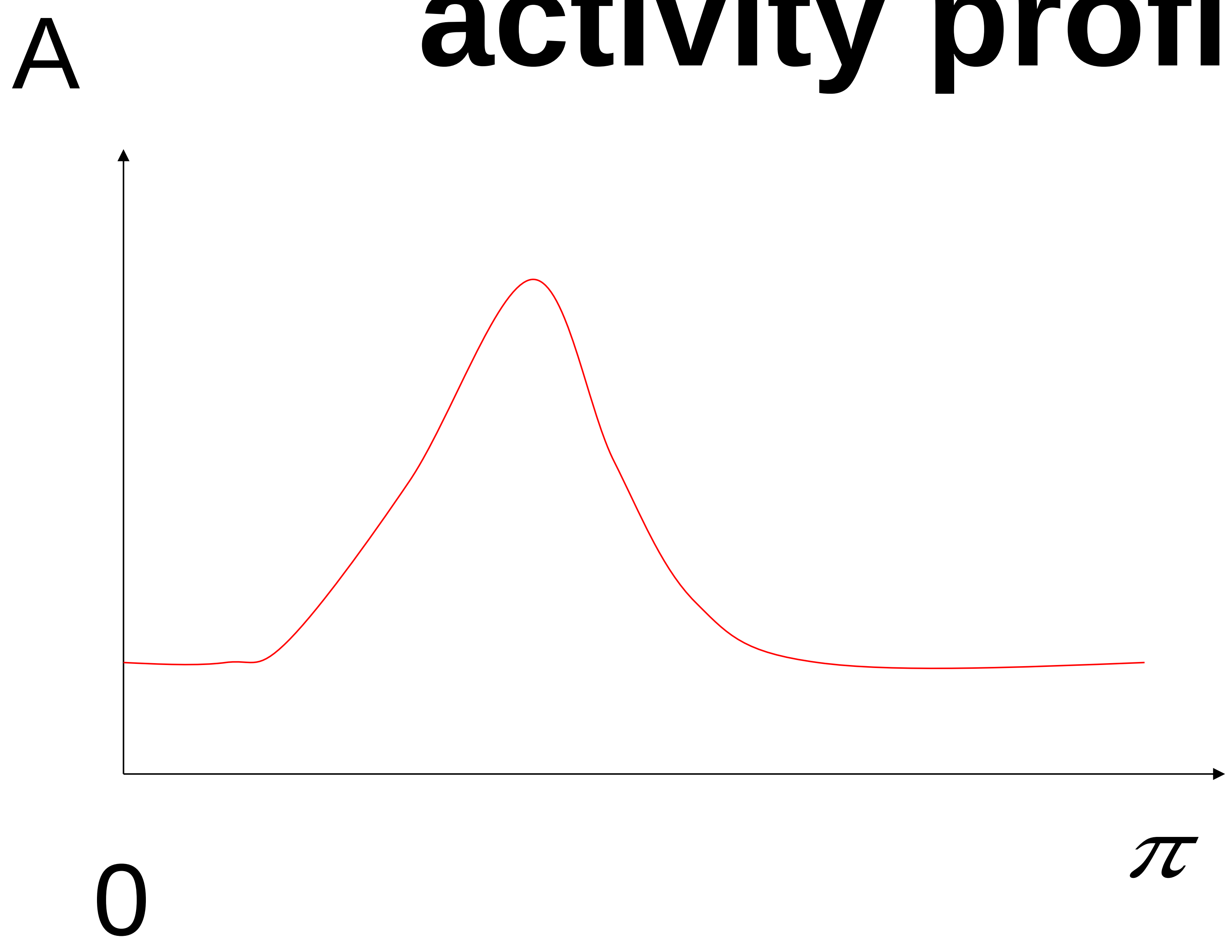
Field Equations:

Wilson and Cowan, 1973

Bump formation:

activity profile in the absence of input

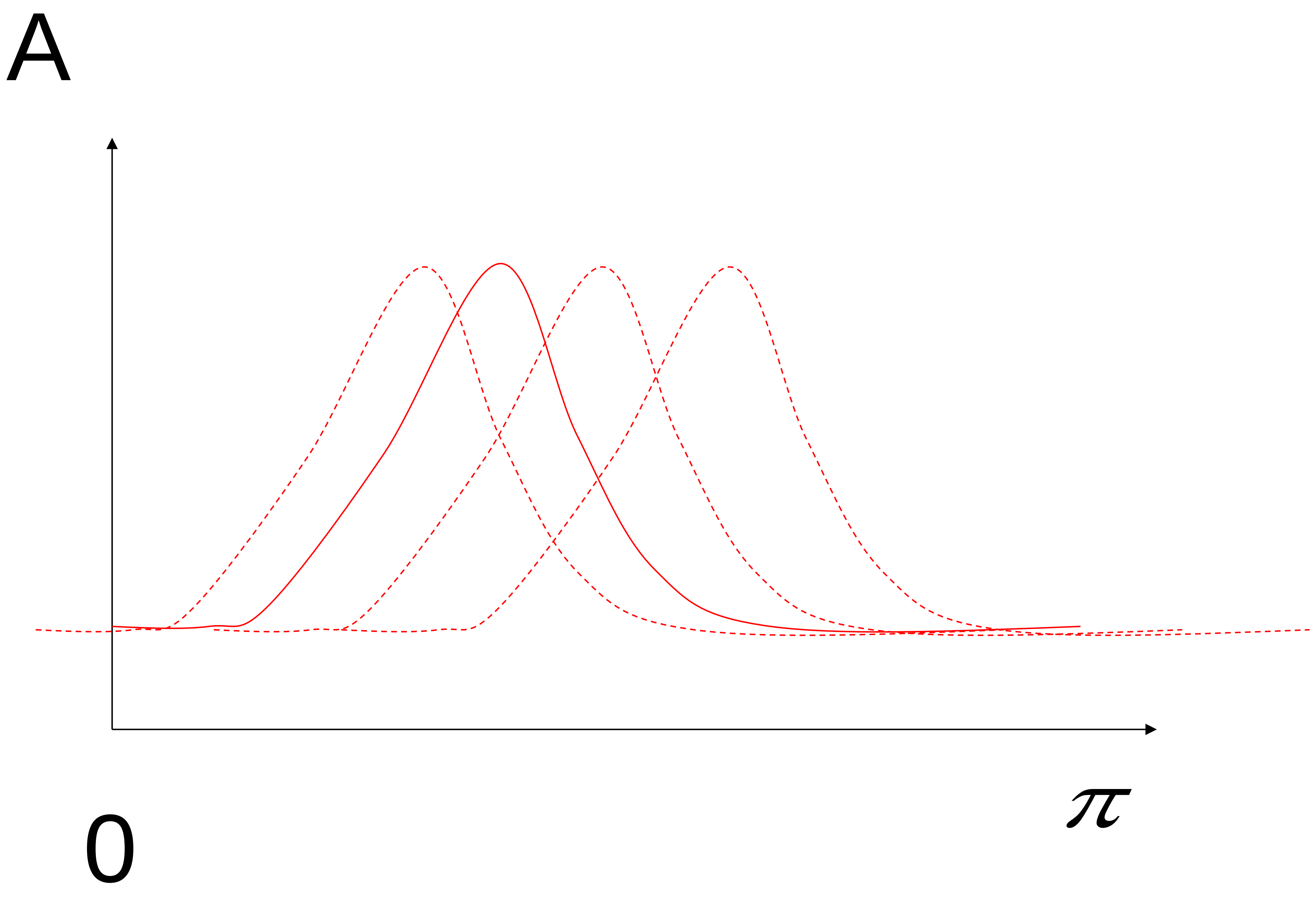
strong lateral connectivity



5. Solution type B: bump solution

Field Equations:
Wilson and Cowan, 1973

Bump formation:
activity profile in the absence of input



- strong lateral connectivity;
- long-range inhibition

Possible application
- head direction cells
  → (see part 7)
- spatial working memory

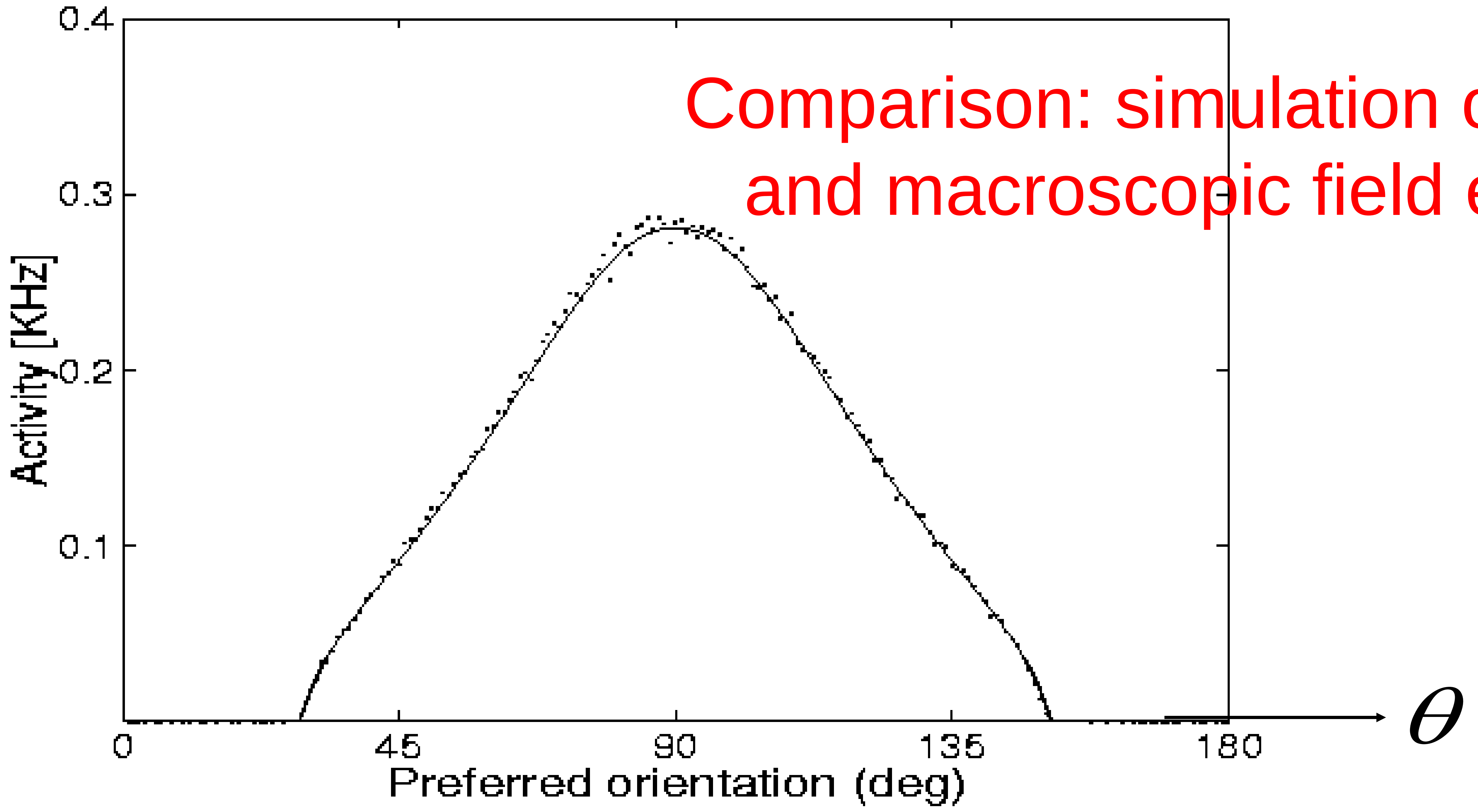
A Compte, N Brunel, PS Goldman-Rakic, XJ Wang (2000) Synaptic mechanisms and network dynamics underlying spatial working memory, Cerebral Cortex 10 (9), 910-923

5. Solution type B: bump solution

Spiridon&Gerstner

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

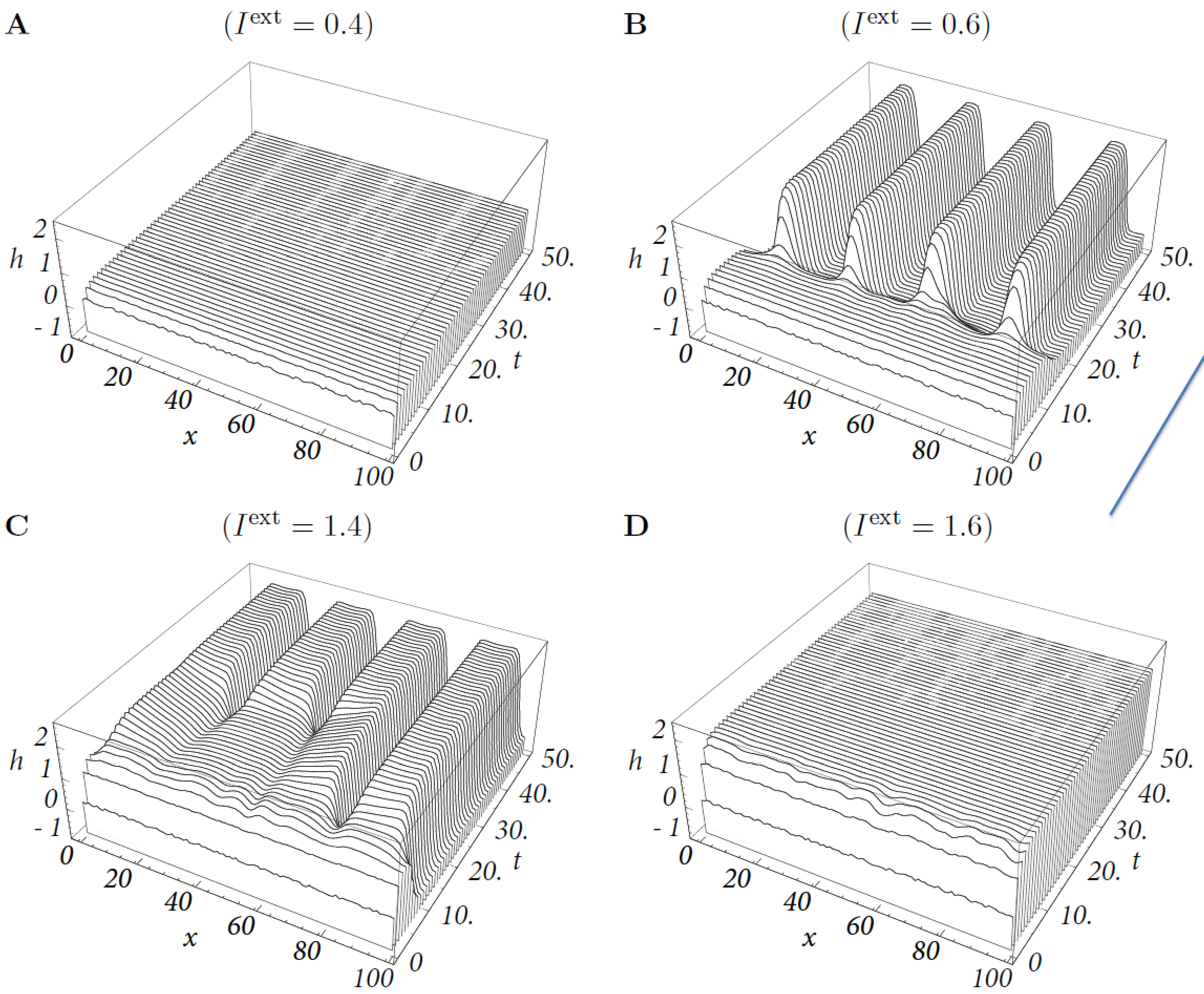
Comparison: simulation of neurons and macroscopic field equation



Continuum: stationary profile

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

5. Solution types: multiple bump solutions with local interaction



time

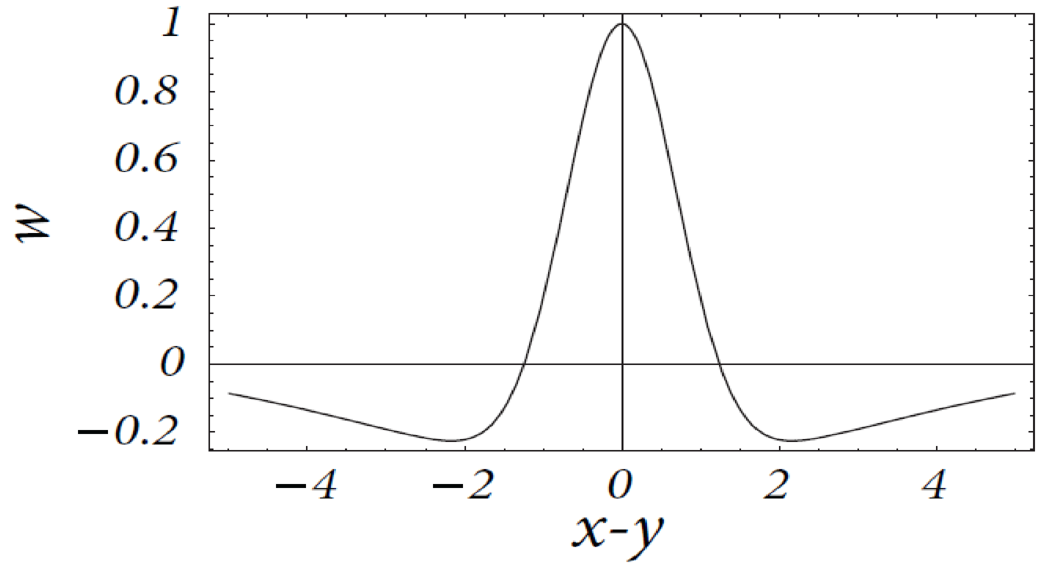


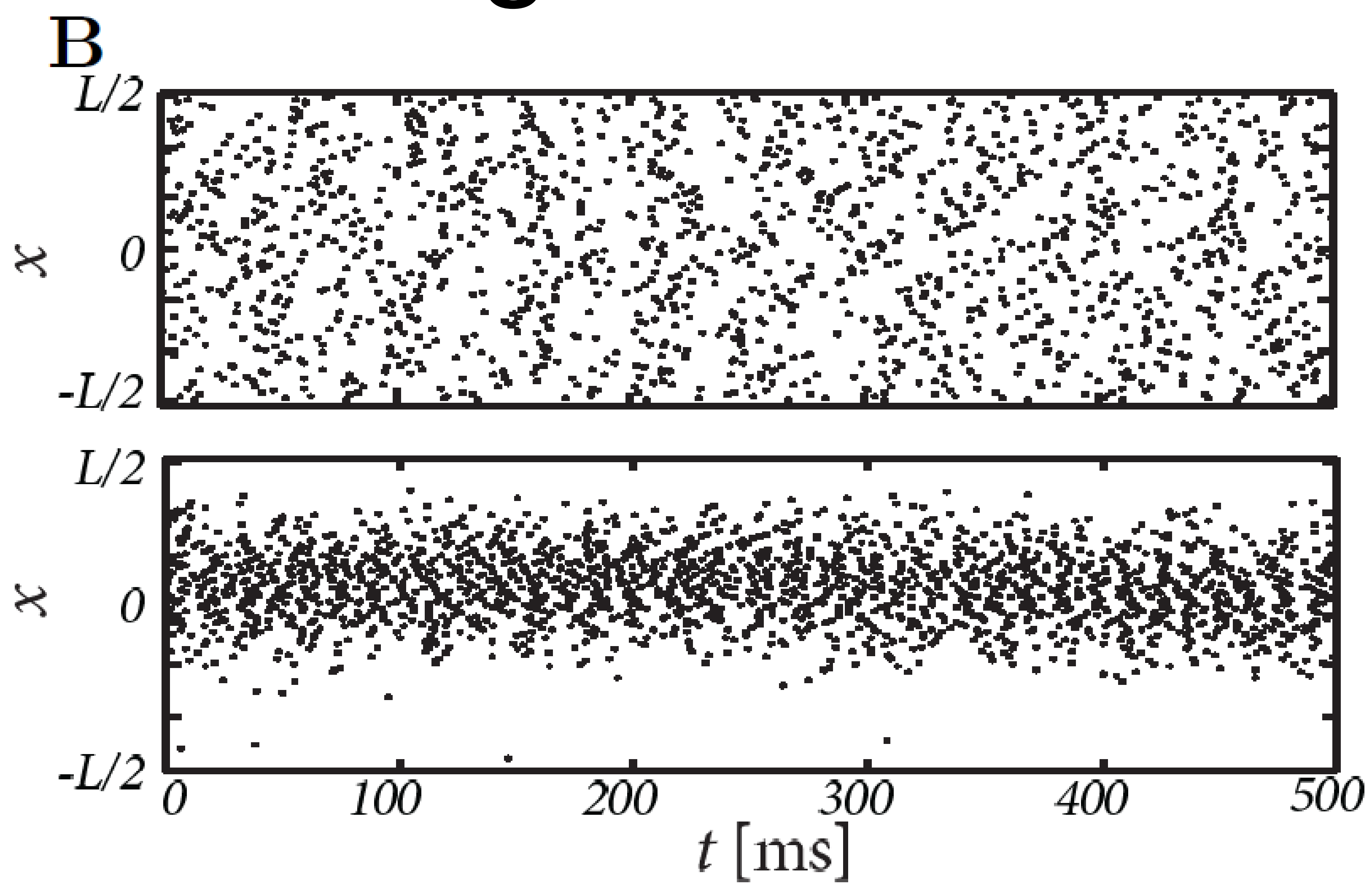
Image: Neuronal Dynamics, Gerstner et al.,
Cambridge Univ. Press (2014),

5. Two Solution Types (ring model)

Input-driven regime:
homogeneous solution

Two stationary solution types:

- homogeneous for flat input
  → responds to input
- bump attractor for flat input
  → moves to location of input



Bump attractor regime

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

Quiz

Solution of Field equations (1-dimensional ring model)

[ ] If a solution exists with a single bump localized around x_0, there are also bump solutions 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 likeliy to exist

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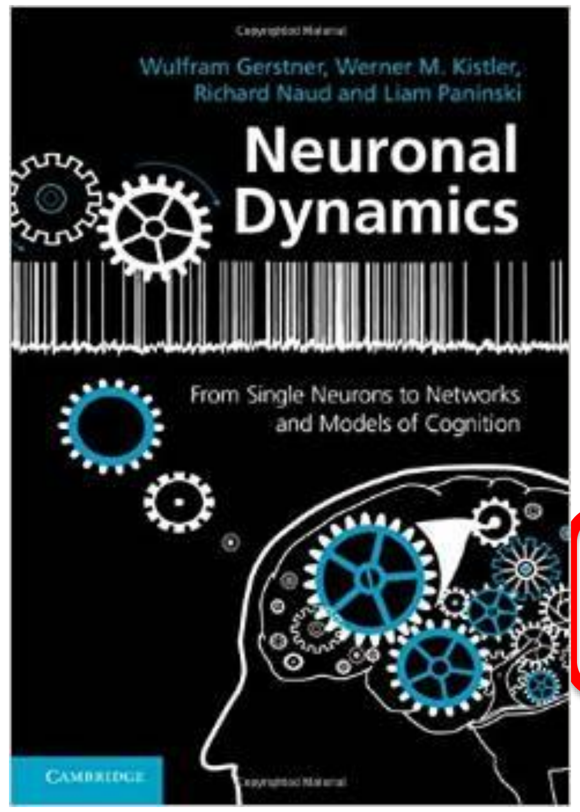

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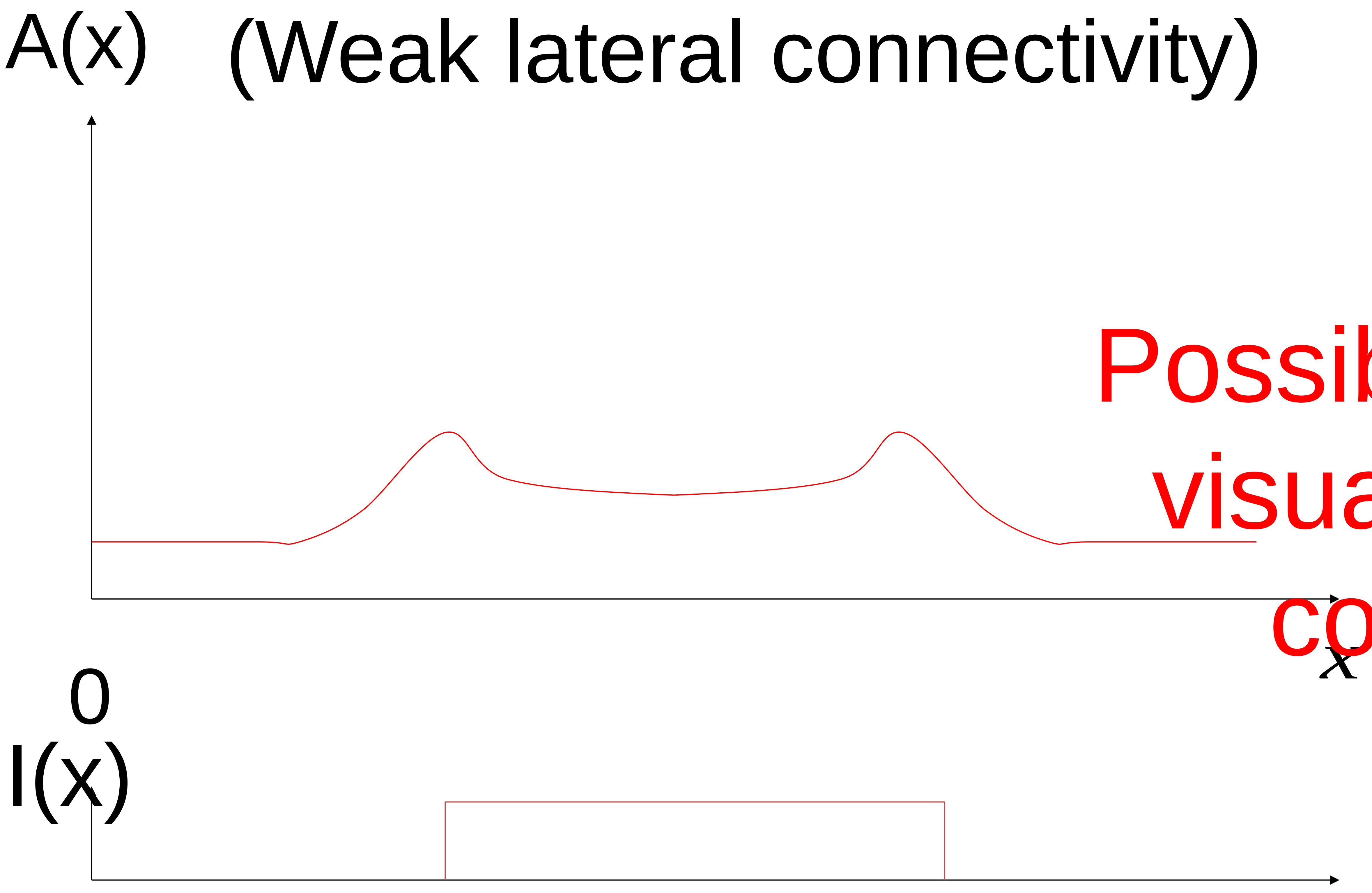
6. homogeneous/input driven solution

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

Edge enhancement

(Weak lateral connectivity)



Possible application to visual cortex cells:
contrast enhancement in
- orientation
- location

6. **Perception - grid illusion**

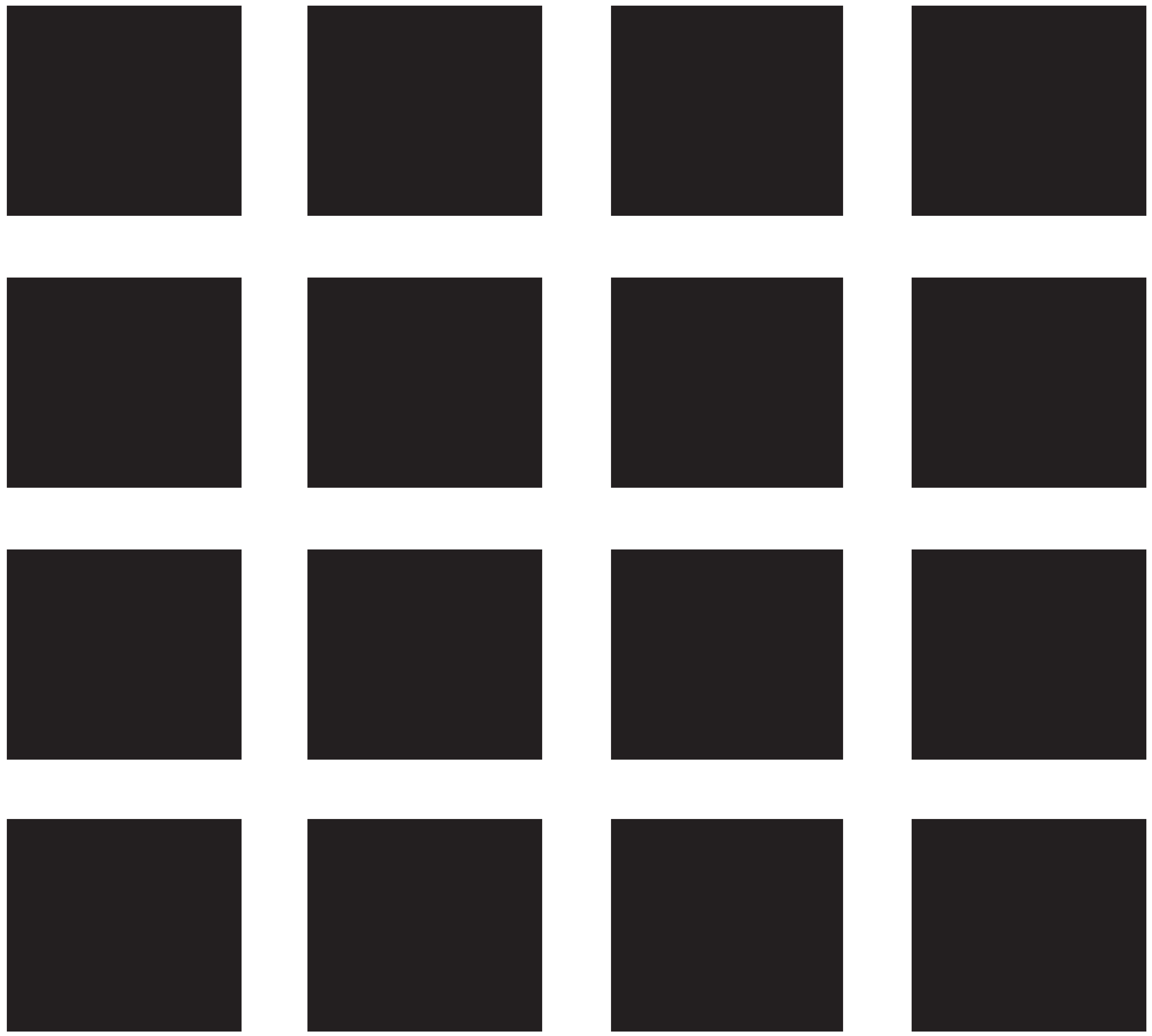


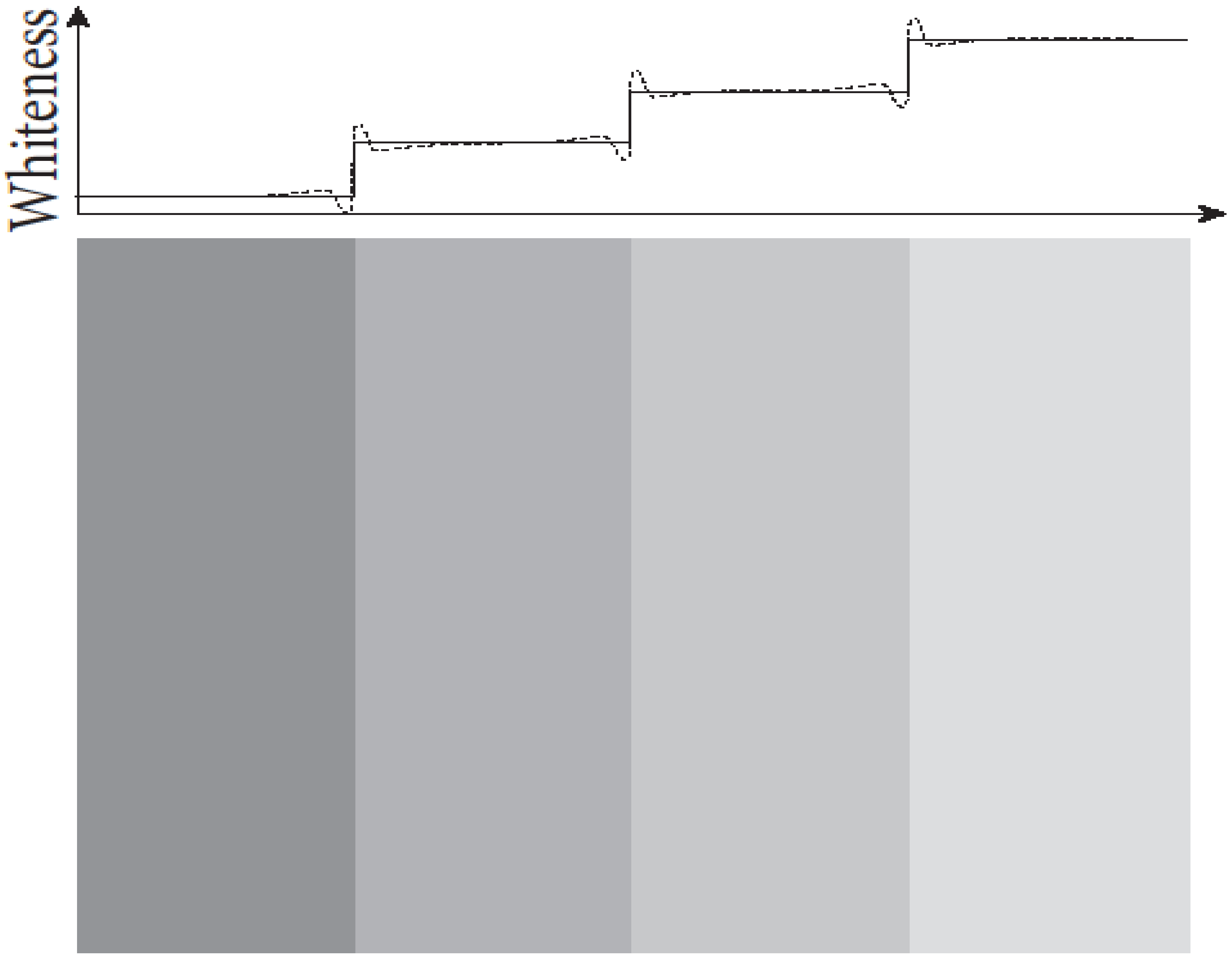
Image: Neuronal Dynamics, Gerstner et al., Cambridge Univ. Press (2014),

6. **Perception - grid illusion**

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

6. Perception – Mach bands

Mach, 1865, 1906



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Mach, 1865, 1906

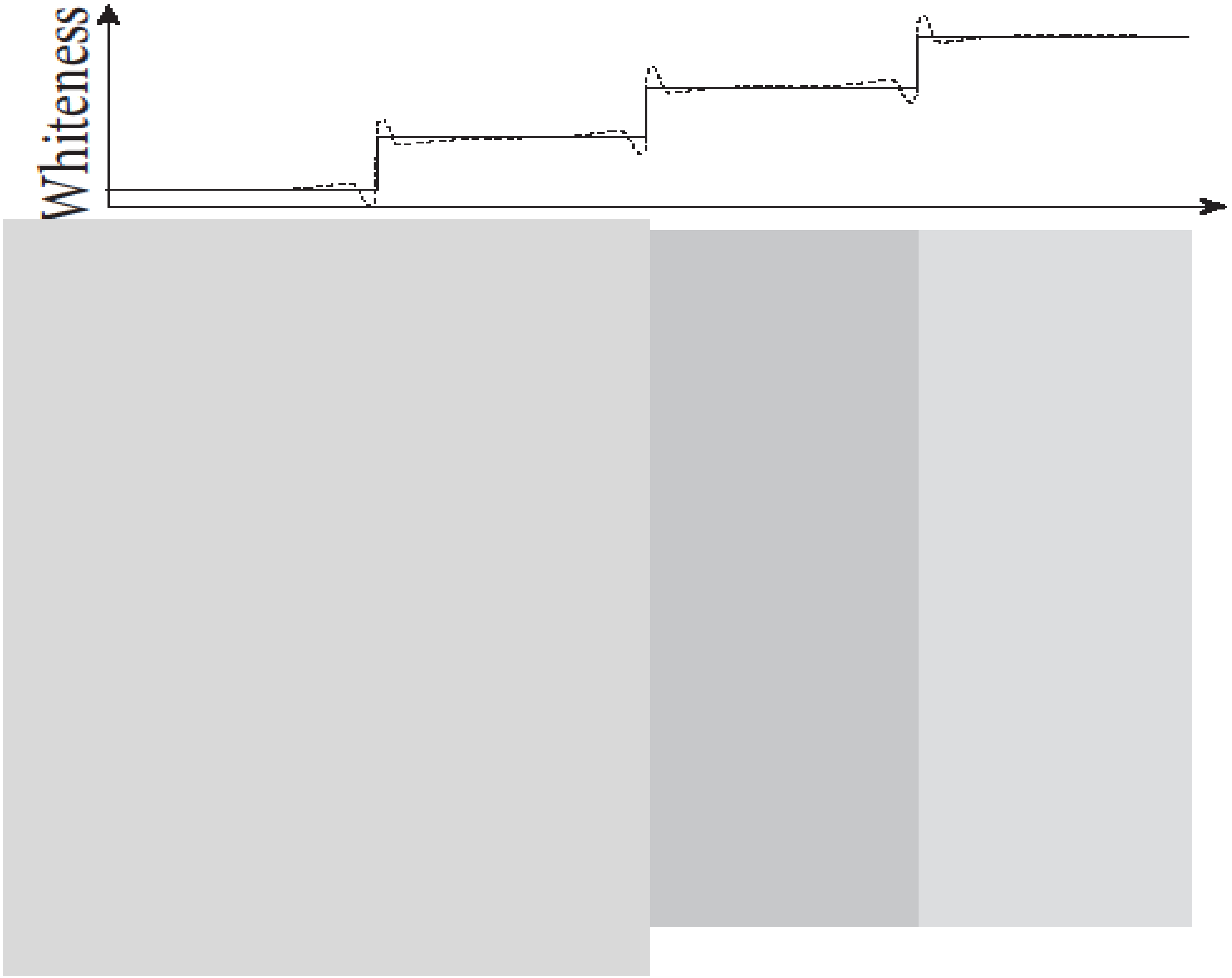
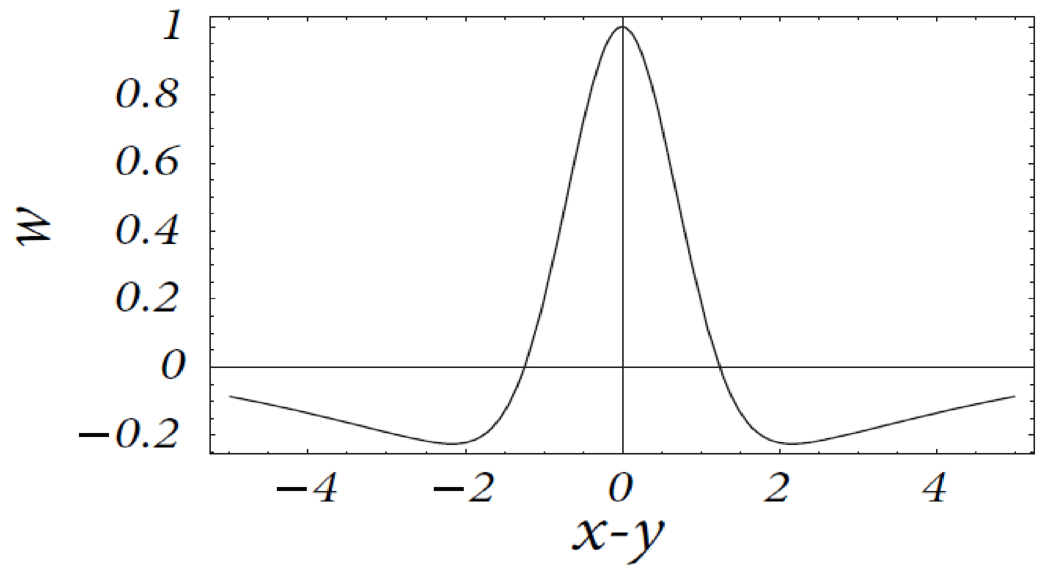
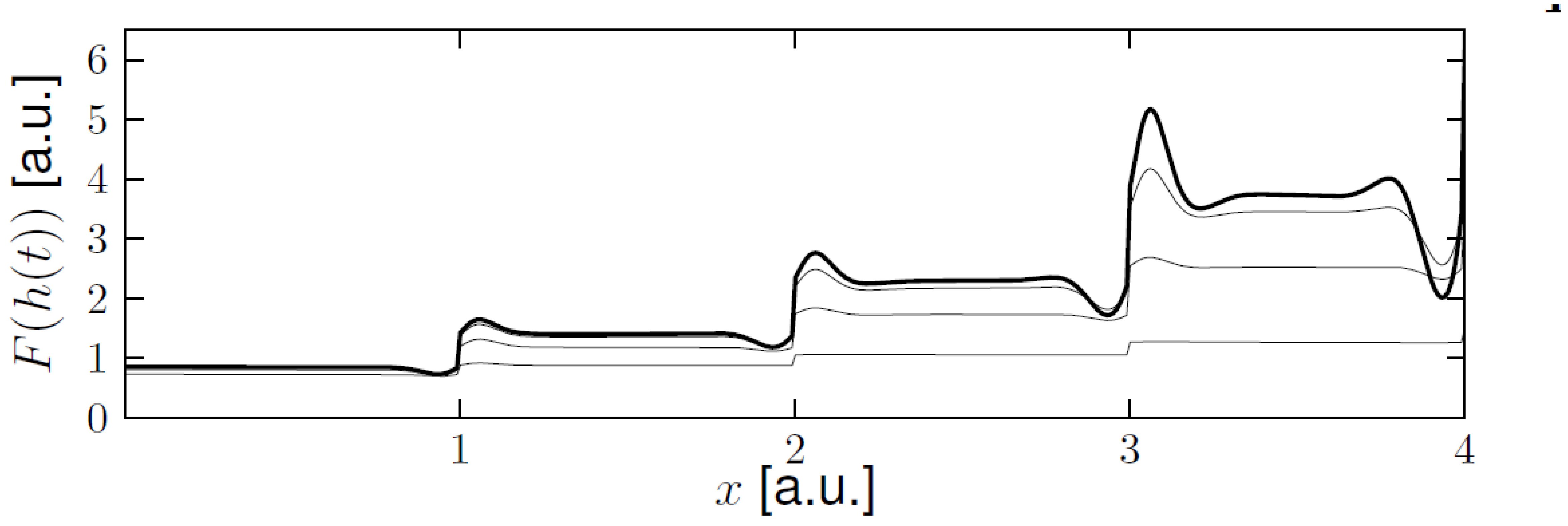


Image: Neuronal Dynamics, Gerstner et al., Cambridge Univ. Press (2014),

6. Mach bands in a continuum model

Mexican-hat coupling

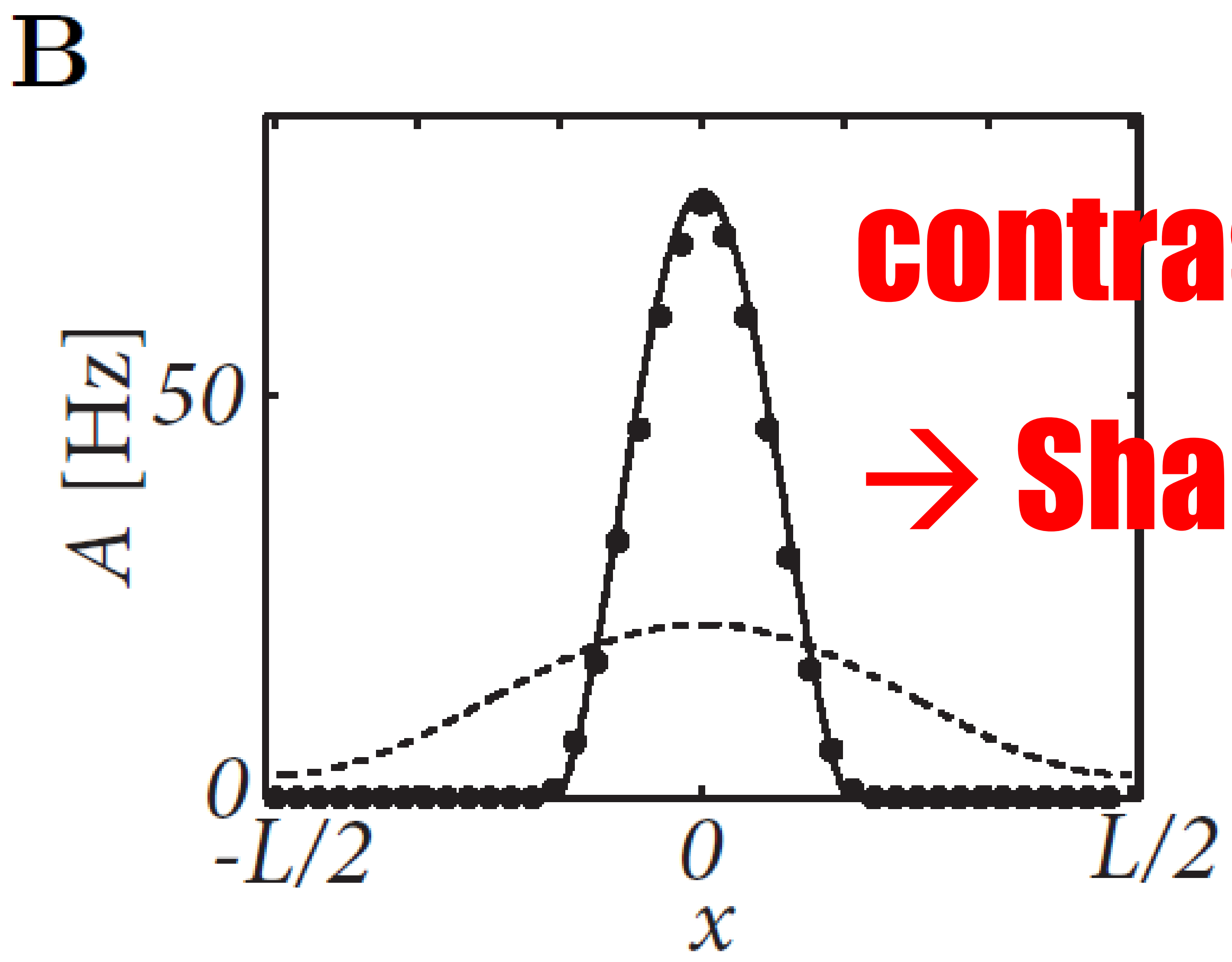




ig. 18.9: **A**. Mach bands in a field model with mexican hat

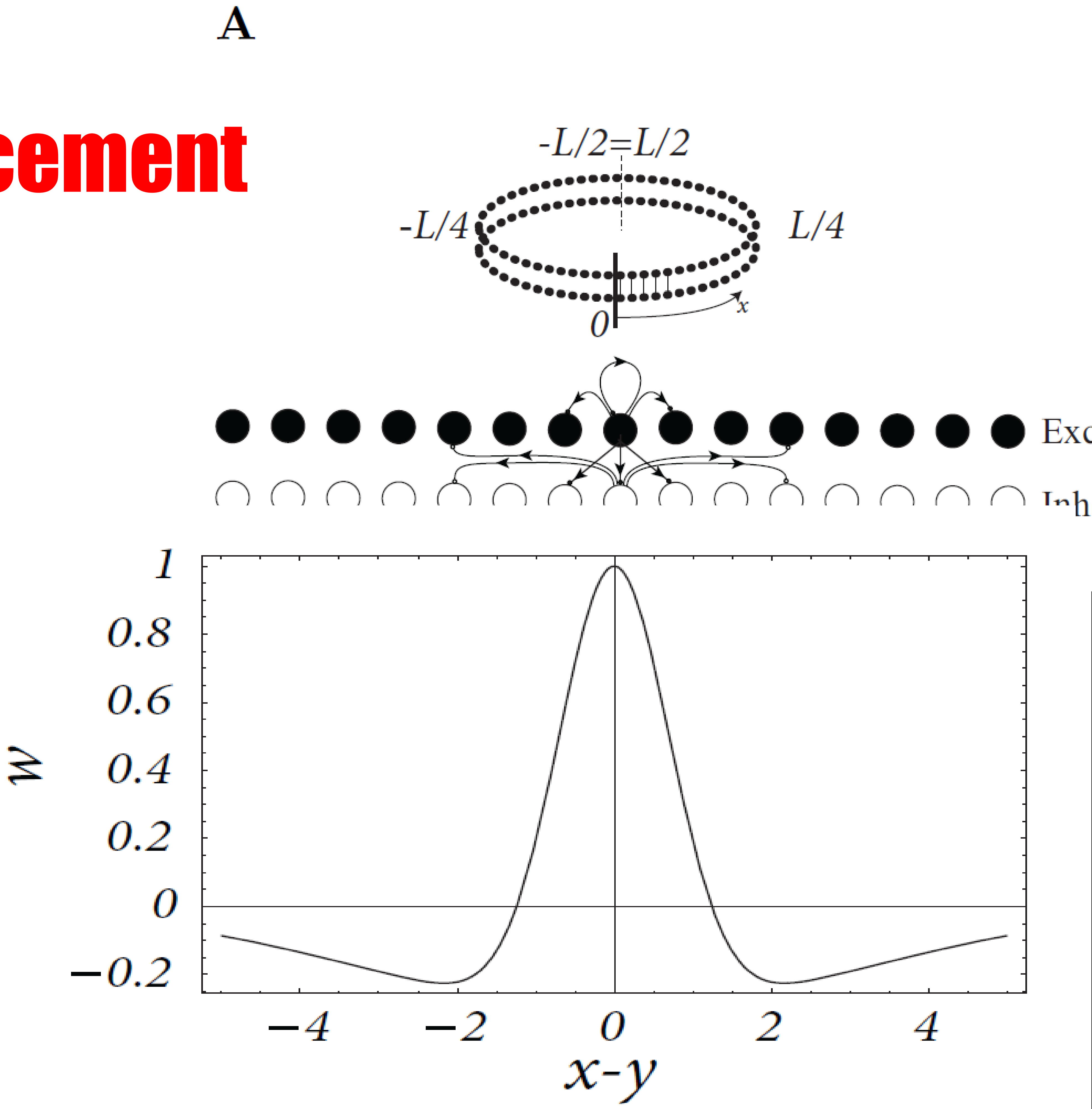
Image: Neuronal Dynamics, Gerstner et al., Cambridge Univ. Press (2014),

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

6: Field models and Perception: surround suppresion

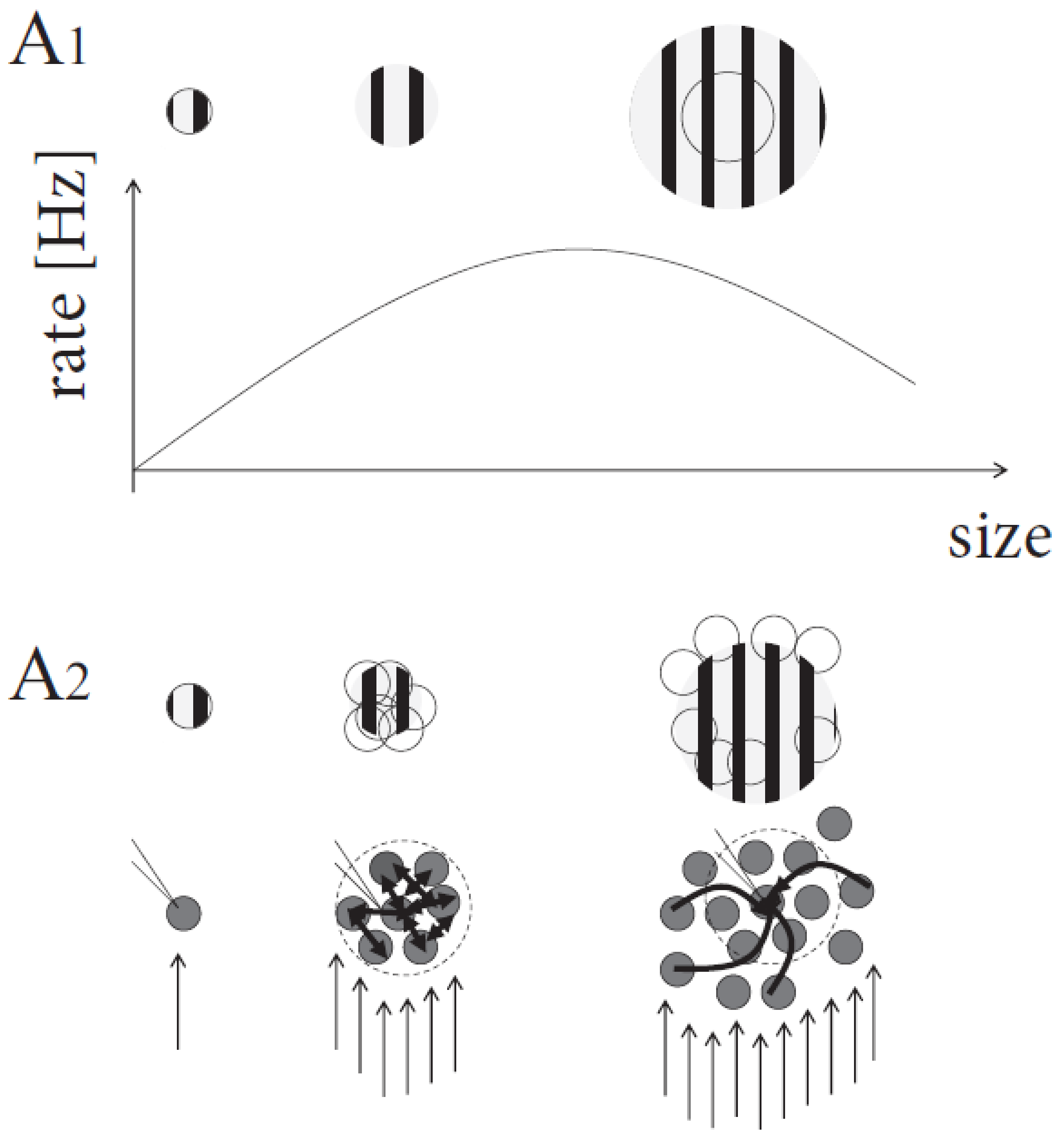


Fig. 18.12: Surround suppression.

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

Ozeki et al. (2009):

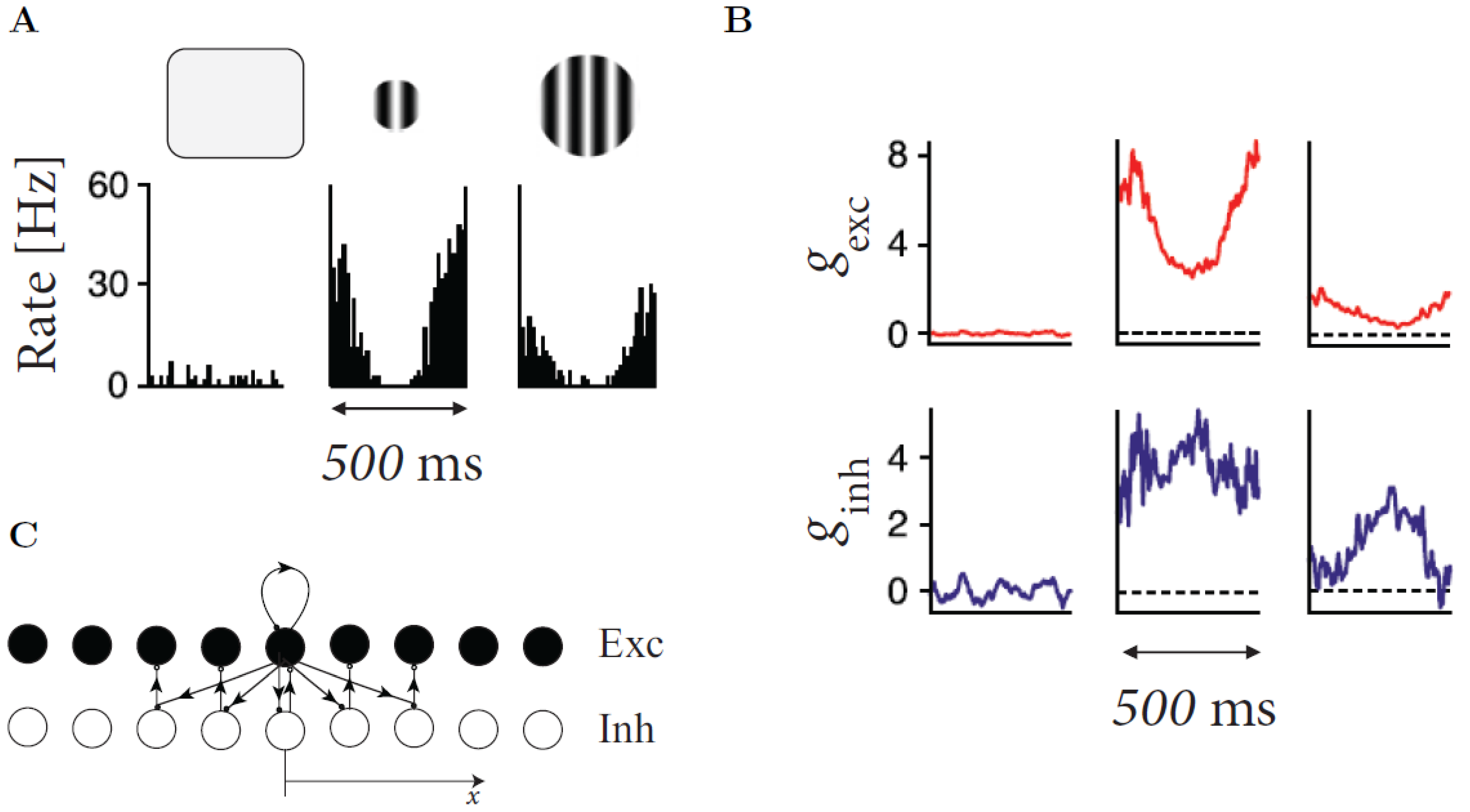


Fig. 18.13: Network stabilized by local inhibition. The schematic model could potentially explain why larger gratings lead not only to less excitatory input g_{exc}, but also to less inhibitory input g_{inh}. **A**. The firing rate as a function of the phase of the moving grating for the three stimulus 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.

6. Field models and Perception

Psychophysics:

-contrast enhancement is a stable psychophysical phenomenon

-Mach bands are but one example

Neuronal:

-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

Modeling

-continuum model with Mexican-hat interaction in the input-driven regime for Mach bands

- Receptive Field tuning: contrast enhancement = ‘sharpening’

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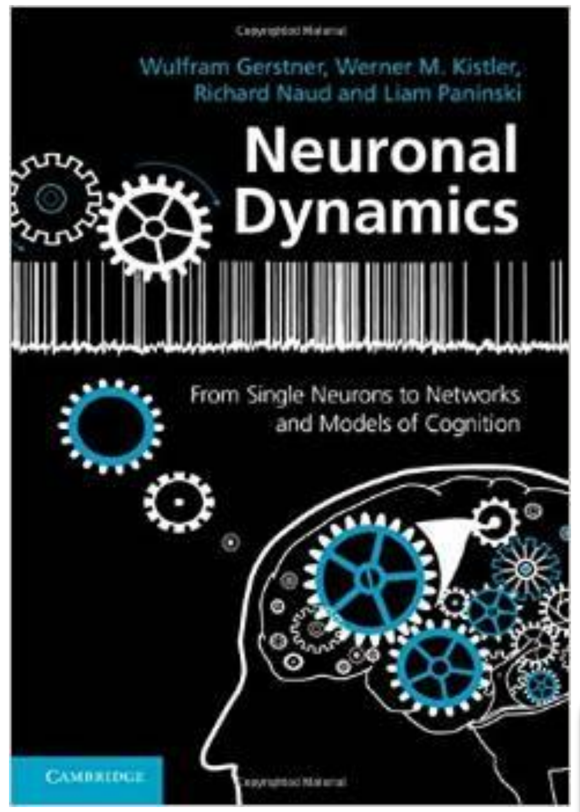

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7. Head direction cells: aims

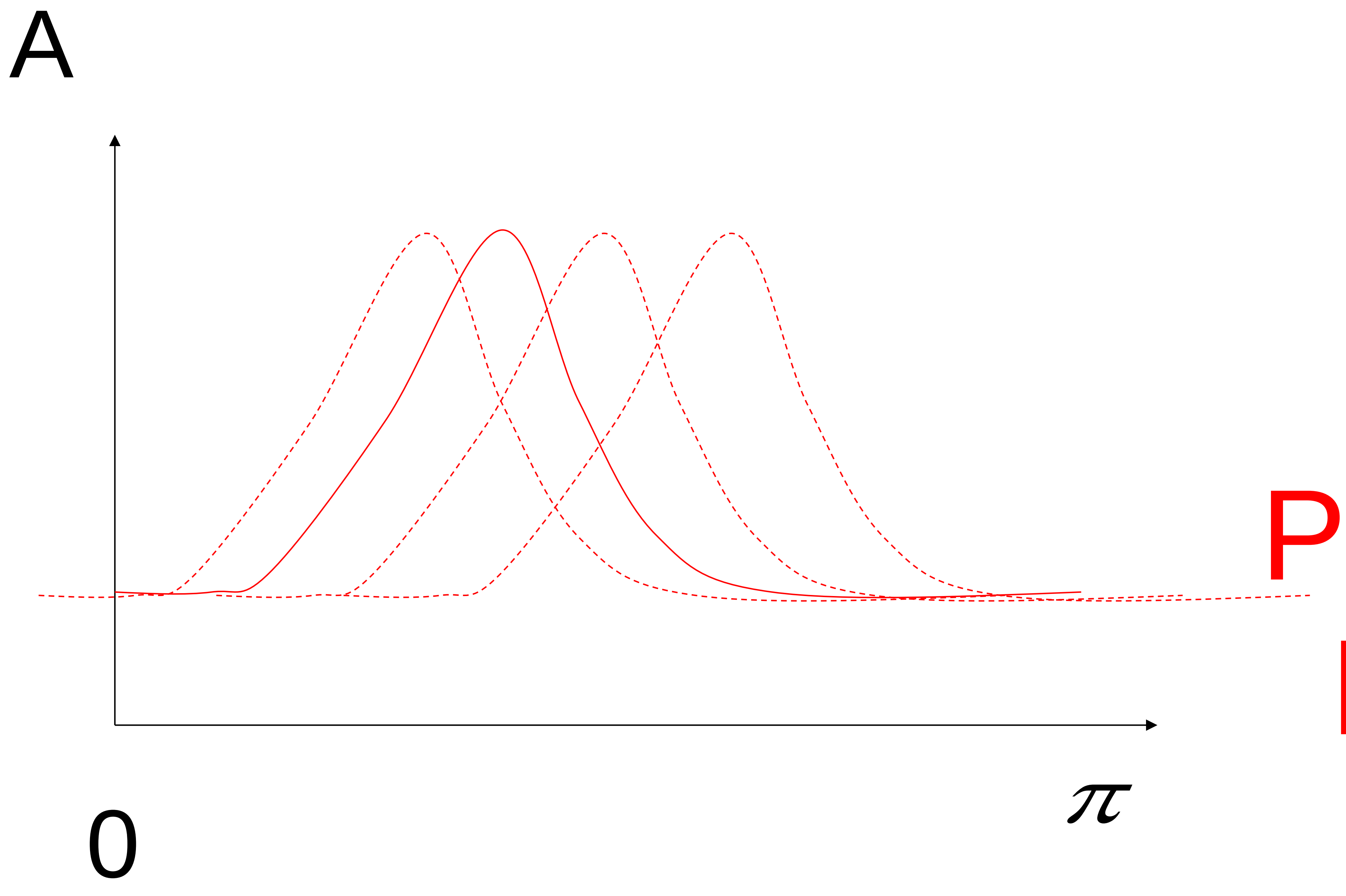
sense of direction

Model

memory of direction related
to bump solution of ring model

7. Bump solution

Basic phenomenology

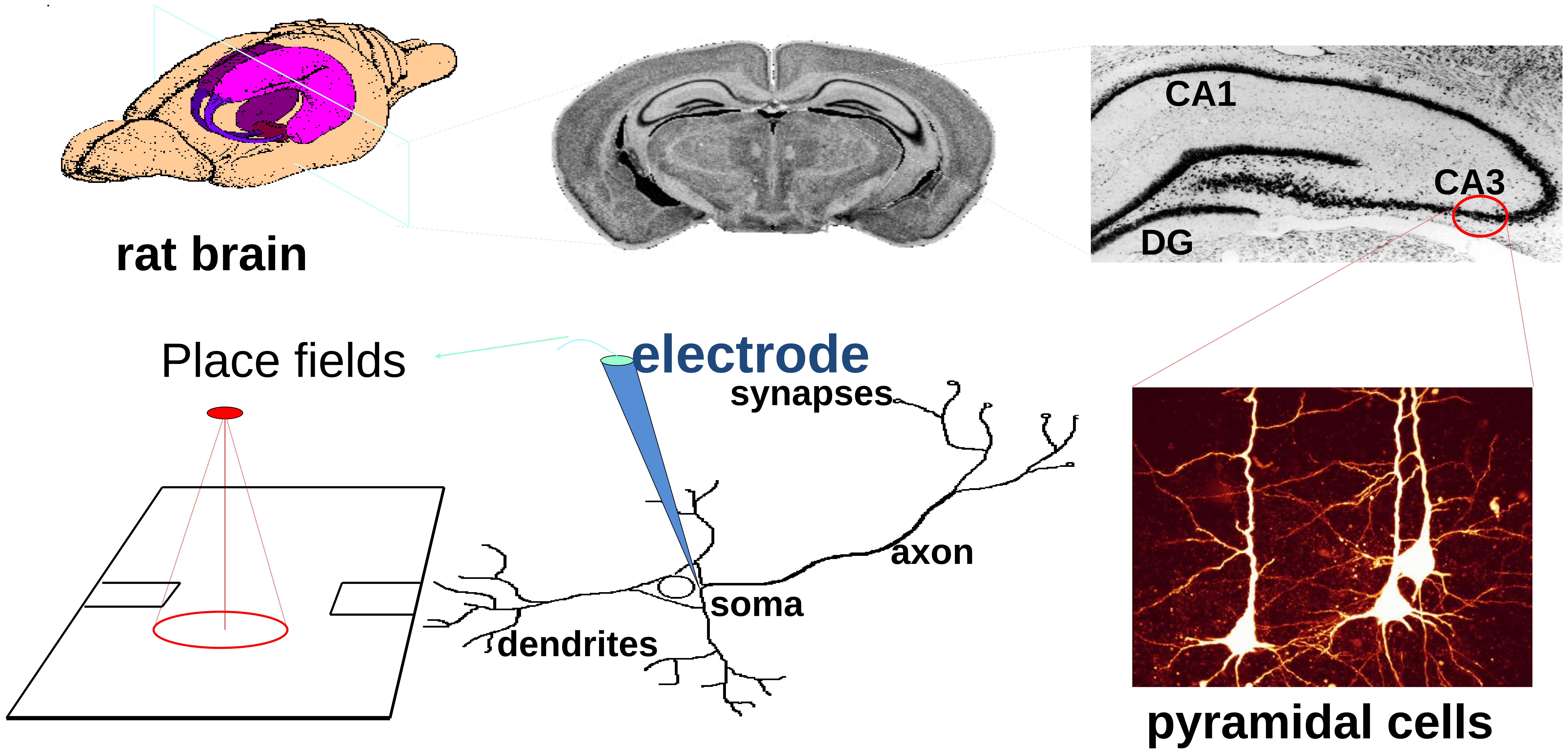


Bump formation

strong lateral connectivity

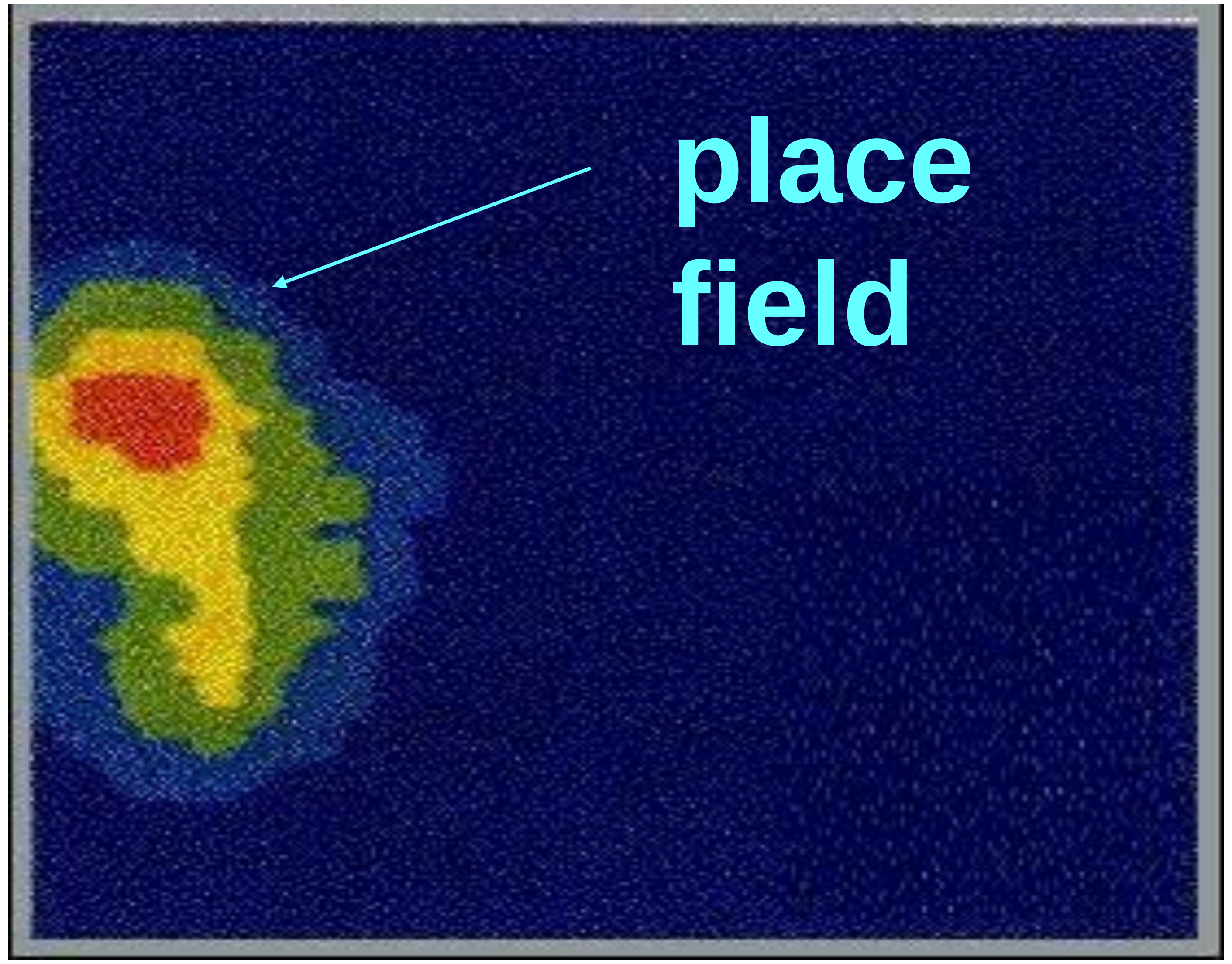
Possible application:
head direction cells -
bump of active cells
→ indicate current orientation

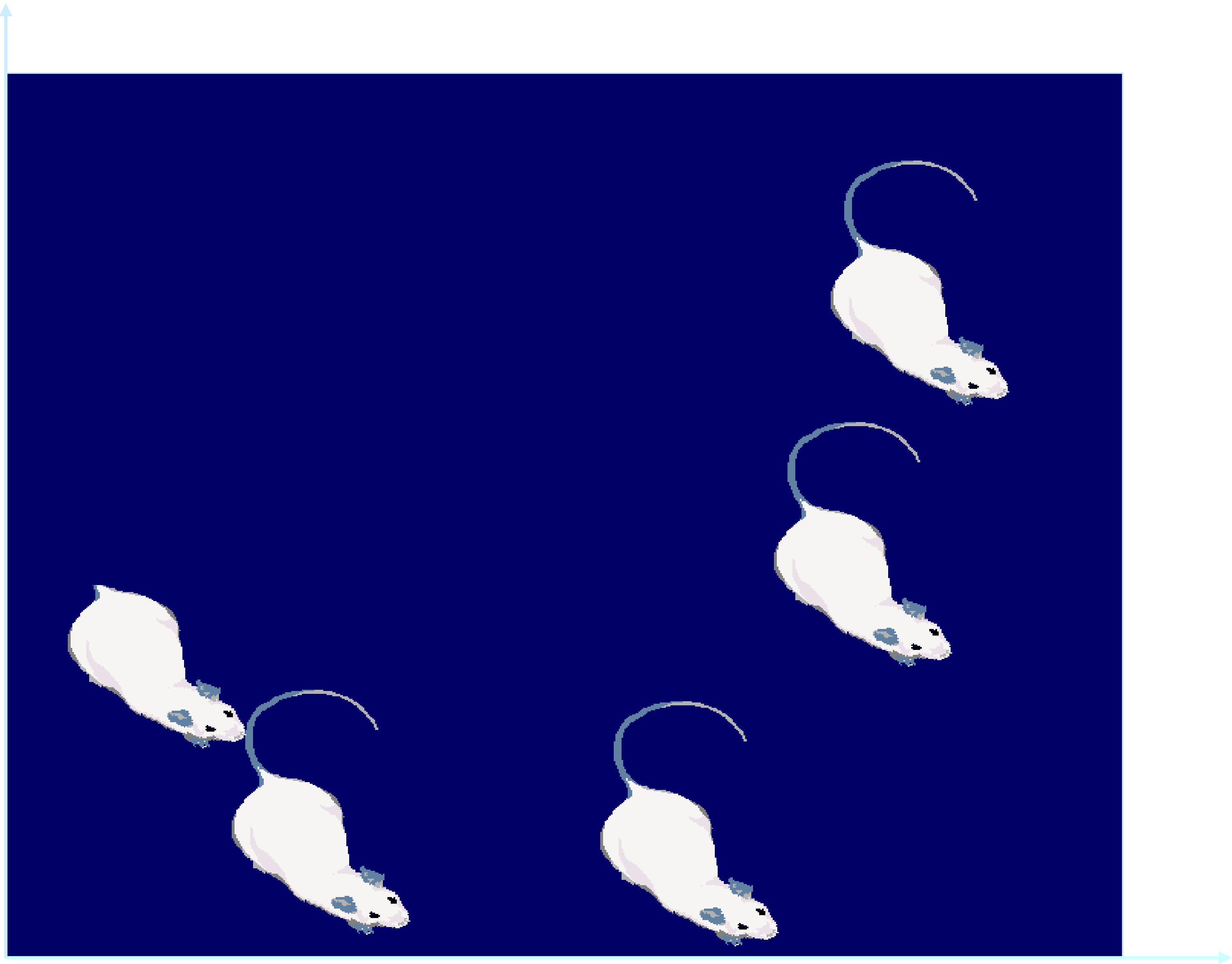
7. Hippocampal place cells

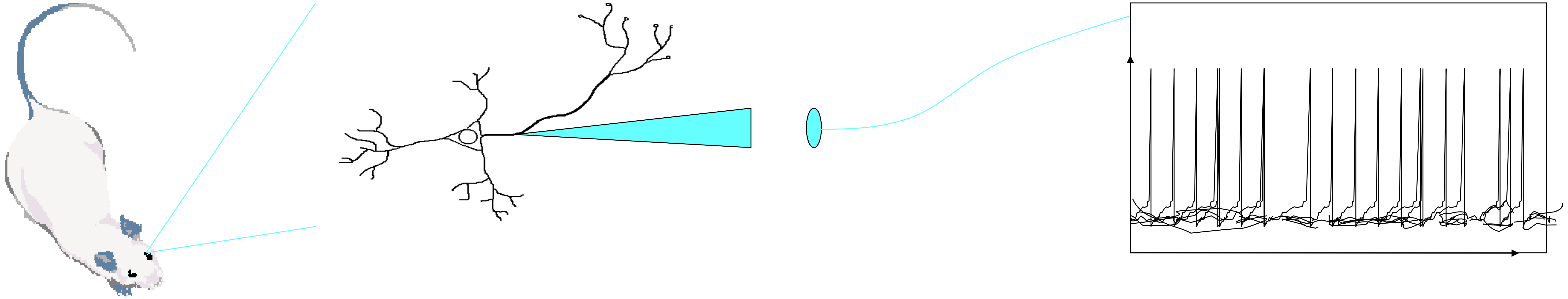


.7. Hippocampal place cells

Main property: encoding the animal's location

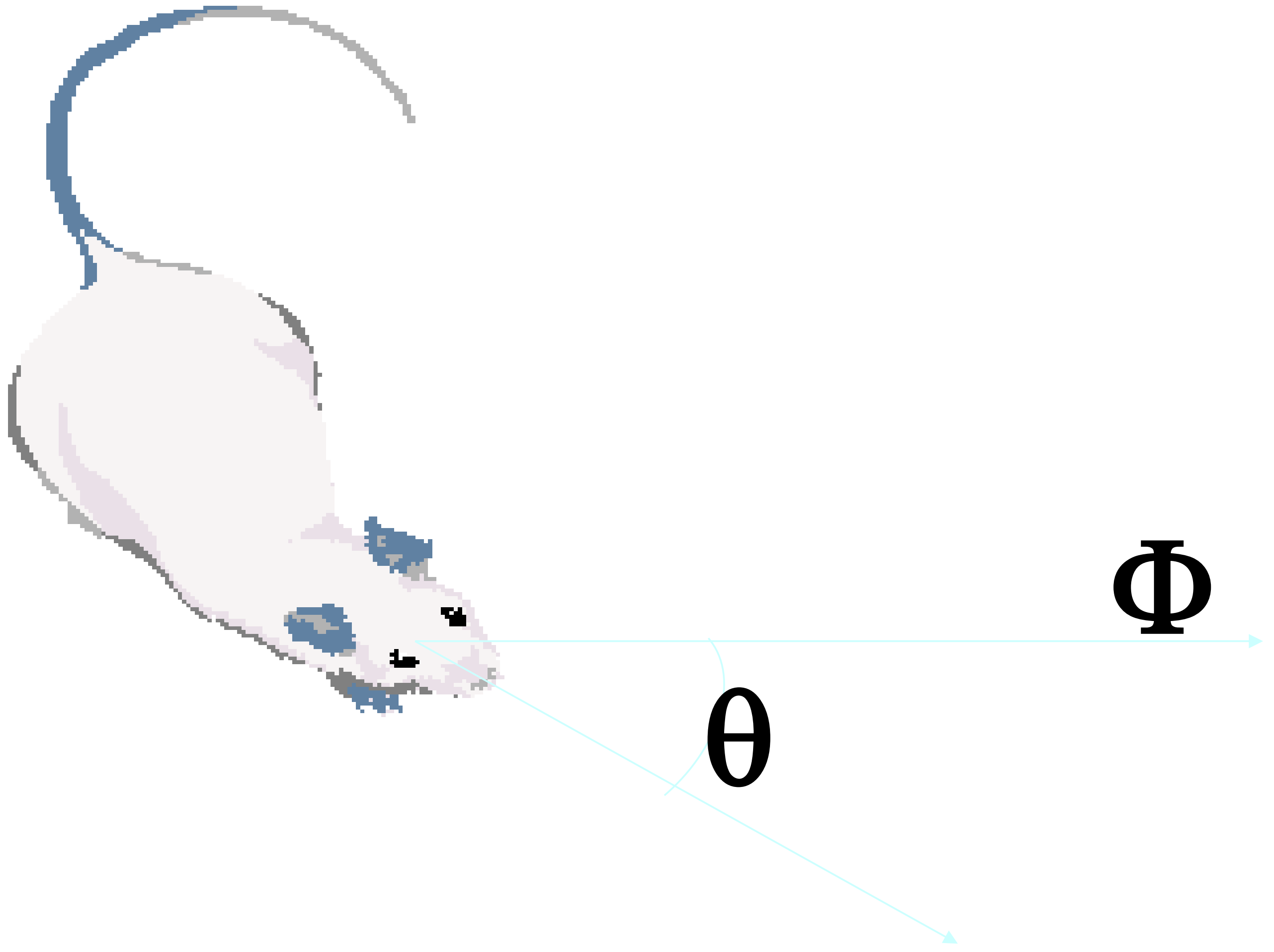


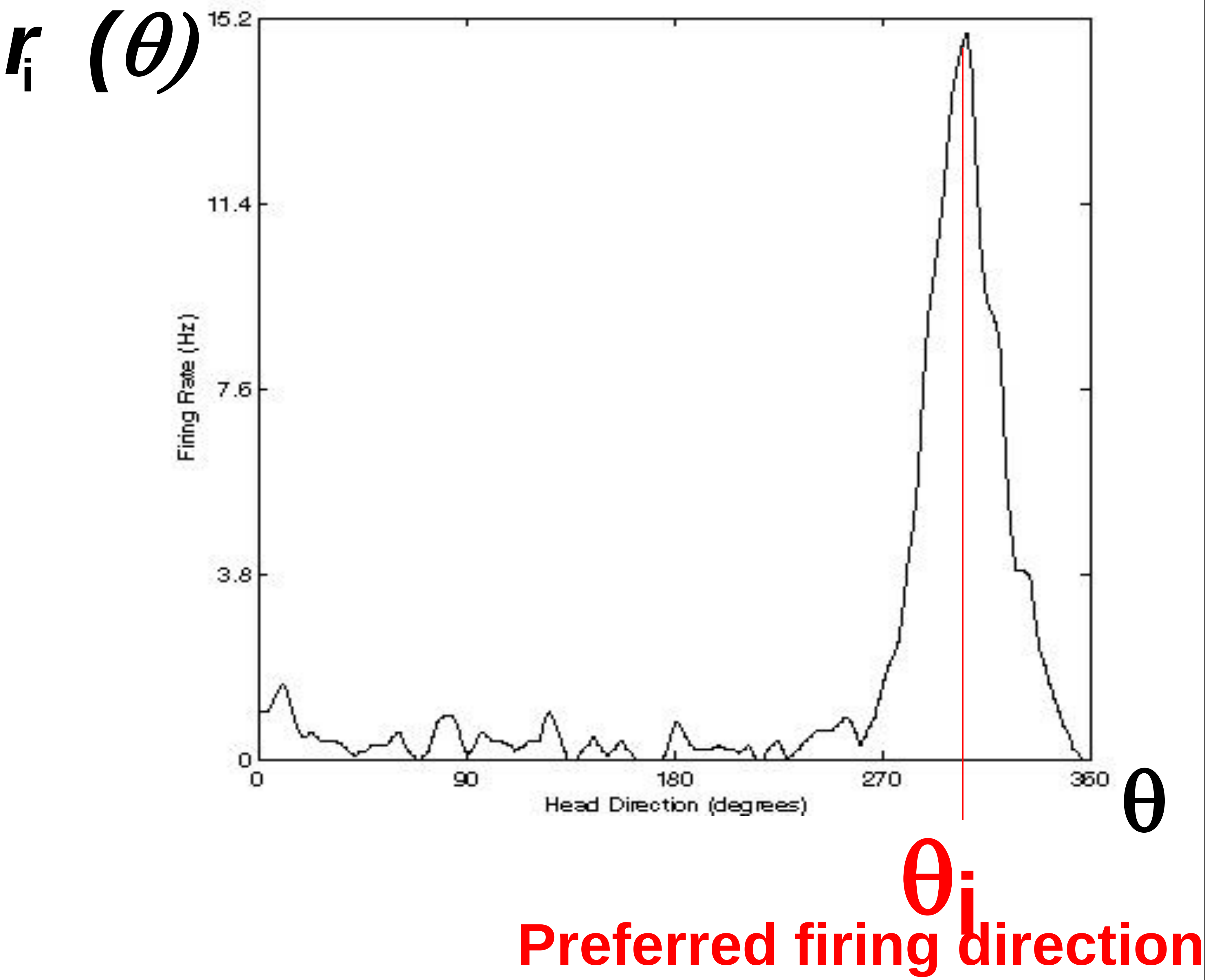




7. Head direction cells

Main property: encoding the animal 's heading

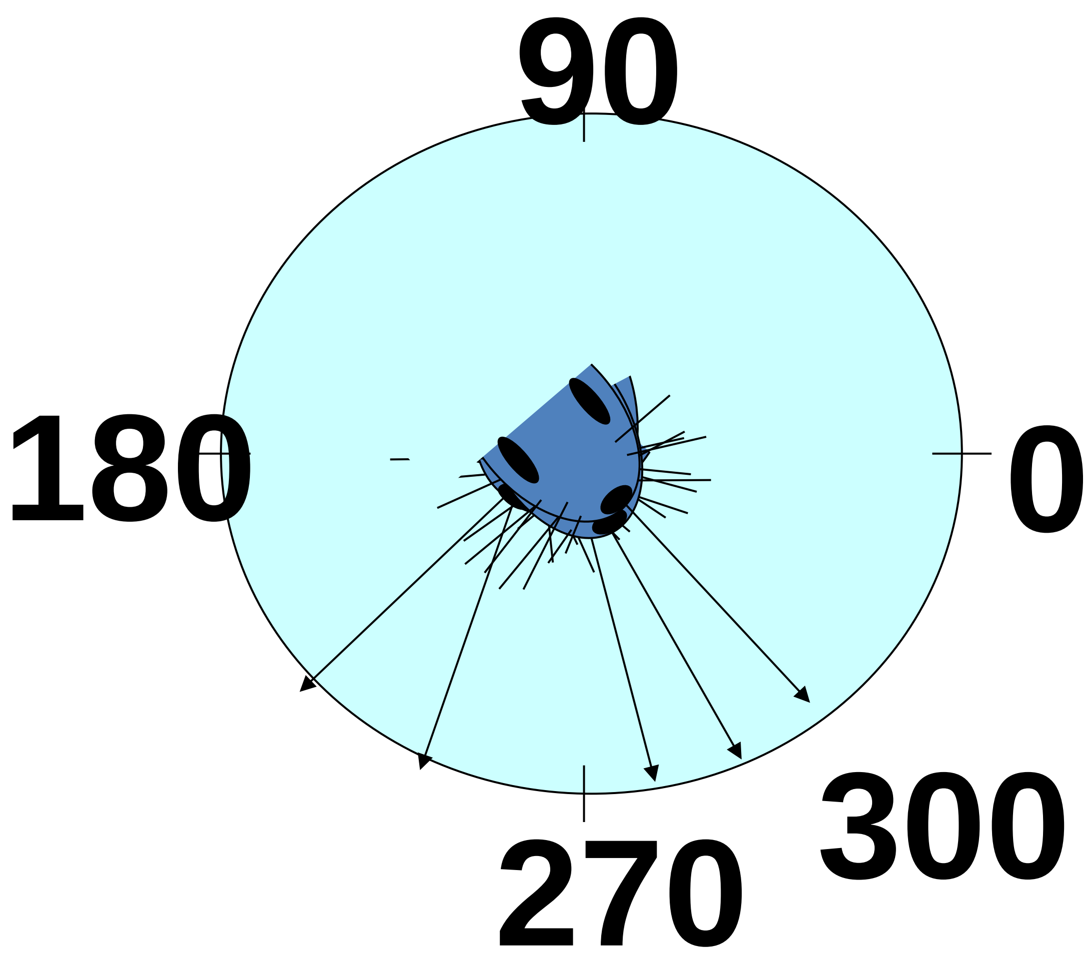


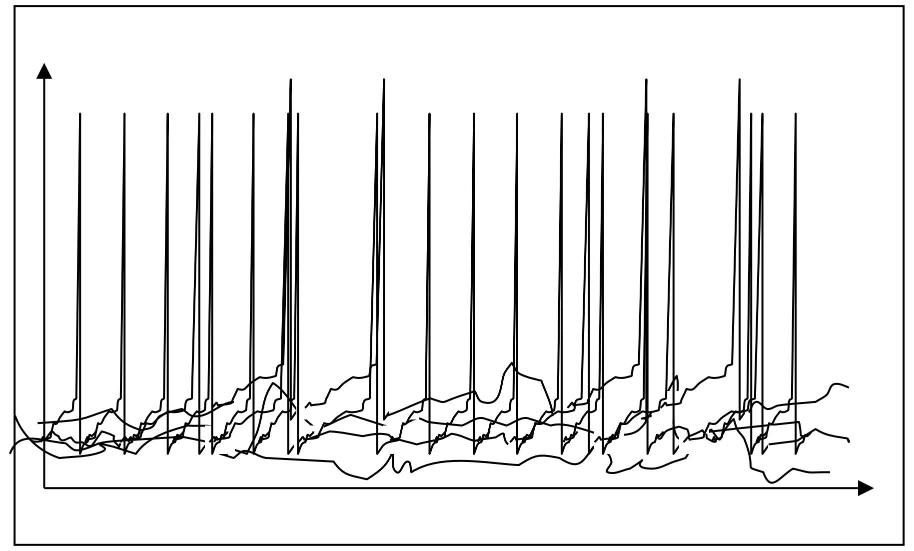


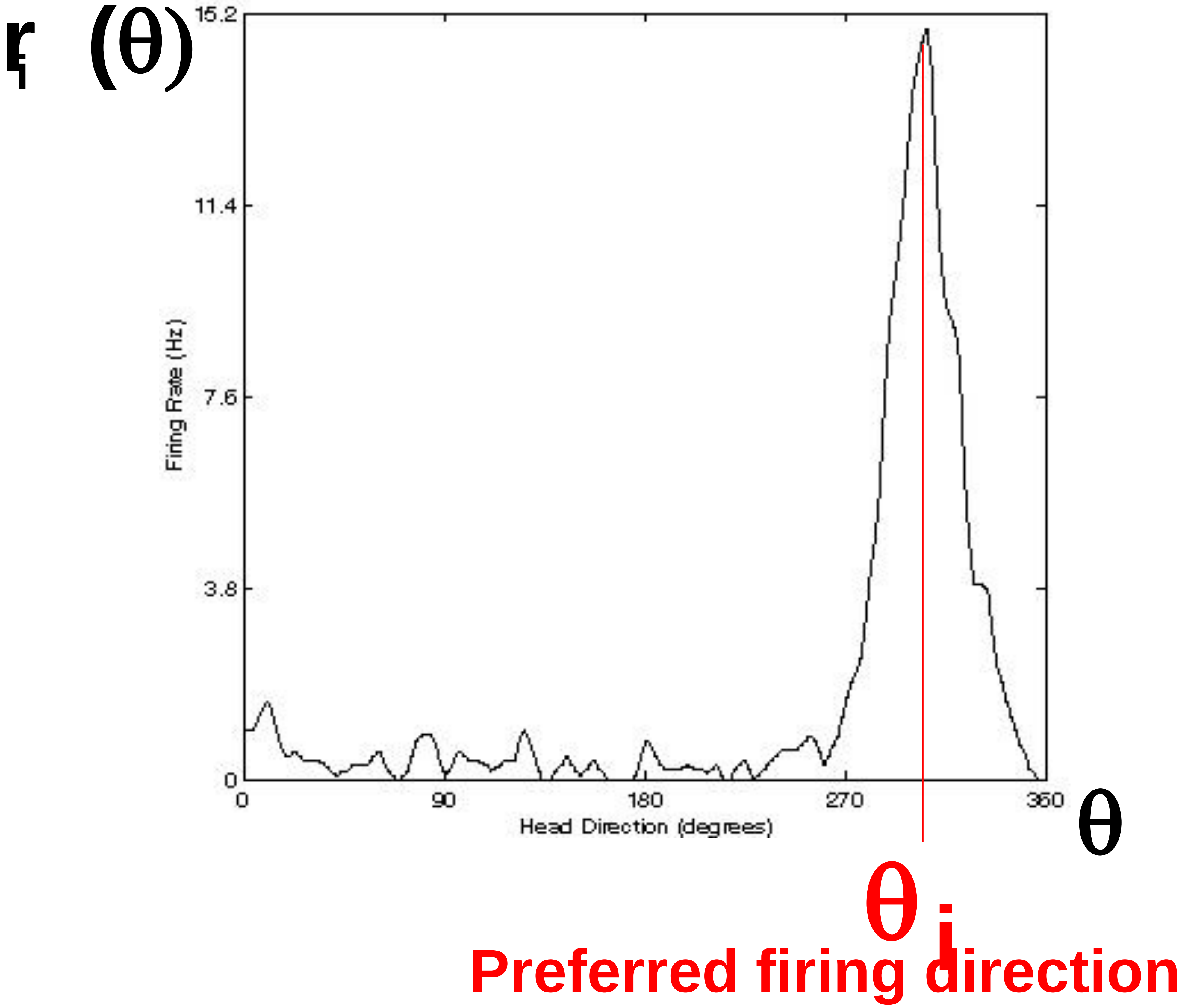
Taube and Muller,
Hippocampus 1998,

7. Head direction cells

Main property: encoding the animal ’s allocentric heading







7. Head direction cells

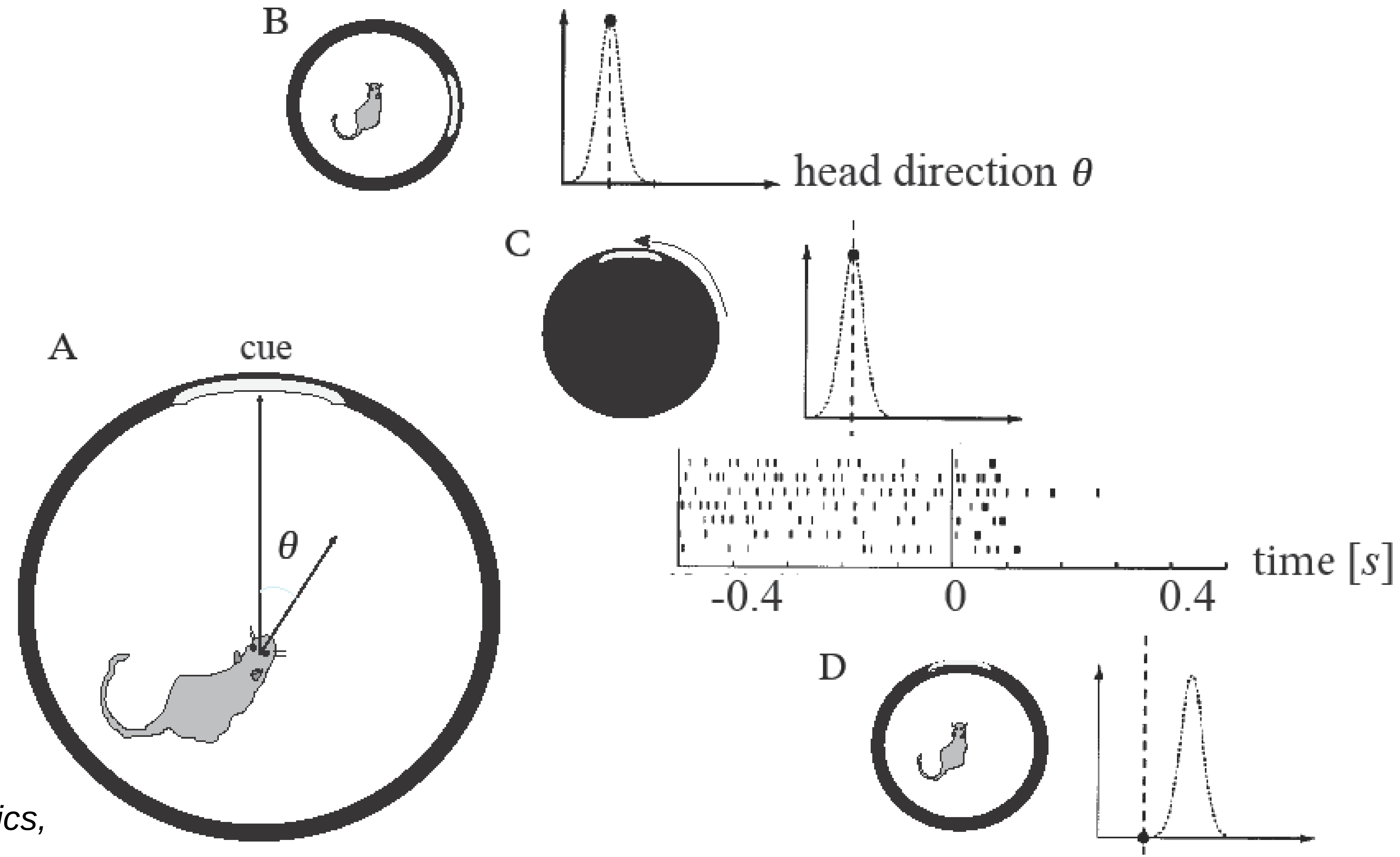


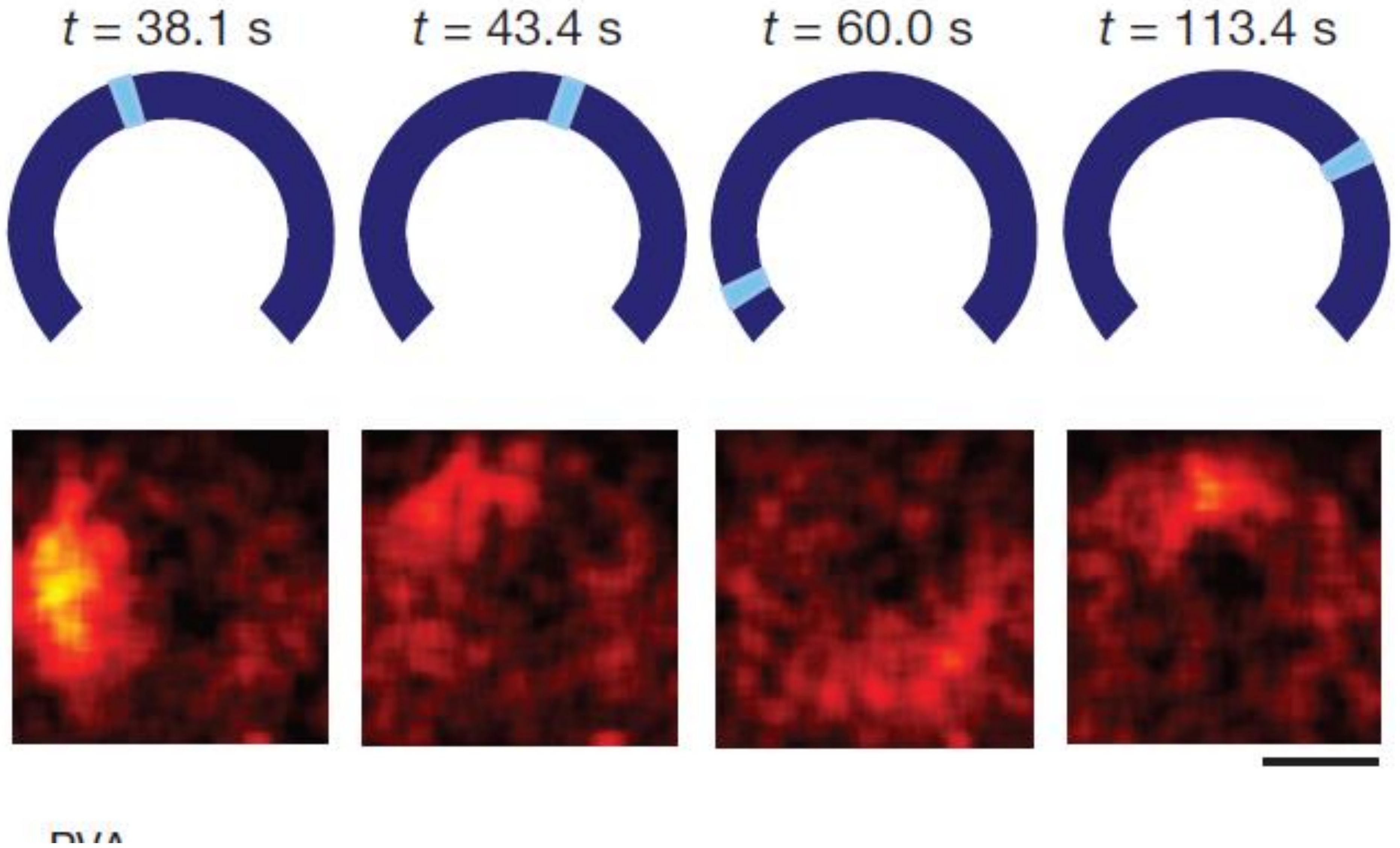
Image: Neuronal Dynamics,
Gerstner et al.,
Cambridge Univ. Press (2014),
Adapted from Zugaro et al. (2003), J. Neurosci. 23:3478-3482

7. Head direction cells in the fly brain

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

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

7. Summary: field models

Continuum model provides understanding for:

- head direction cell
  → bumps of activity
- spatial working memory
  → bumps of activity
- place cells
  → bumps of activity
- contrast enhancement and some visual illusions
  → input driven regime
- receptive field properties
  → input driven regime

7. 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

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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.

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