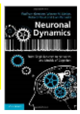
Biological Modeling of Neural Networks

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

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

8.3. Spatial continuum (cortex)
- orientation columns

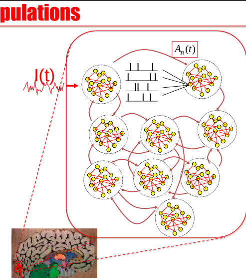
8.4. Spatial cotinuum (model)
- field equations

8.5. Solution types
- uniform solution
- bump solution

8.6. Perception

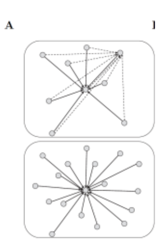
8.7. Head direction cells

Review from week 7: Interacting Populations

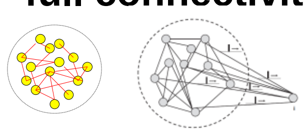


Visual cortex

review from Week 7: mean-field arguments



Single population full connectivity

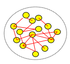


All neurons receive the same total input current ('mean field')

Review from Week 7: stationary state/asynchronous activity

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

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



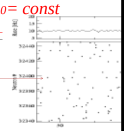
constant input

$$\boxed{I_0 = c}$$

Gain function at appropriate noise level

$A(t)= A_0= const$

Single neuron



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

Review from week7: mean-field arguments

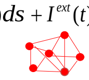
All neurons receive the same total input current ('mean field')

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

assume asynchronous state

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

Index i disappears



fully connected

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

All spikes, all neurons

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

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

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

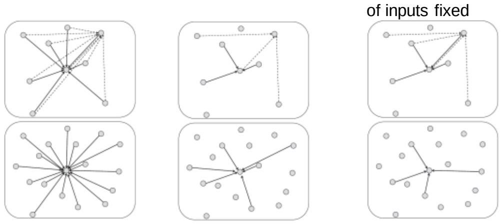


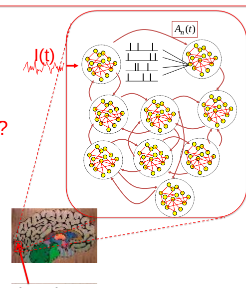
Image: Gerstner et al. Neuronal Dynamics (2014)

Review : 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

- beyond stationary states
  → transients?
- more than one population
  → how many? continuum?
- functional consequences
  → visual perception?



8.1. Aims and challenges: perception

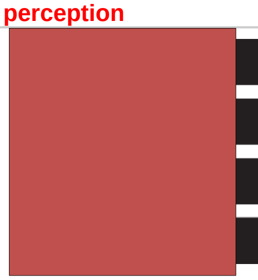


Image: Neuronal Dynamics, Gerstner et al., Cambridge Univ. Press (2014),

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Week 8 – Continuum models:

Cortical fields and perception

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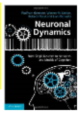
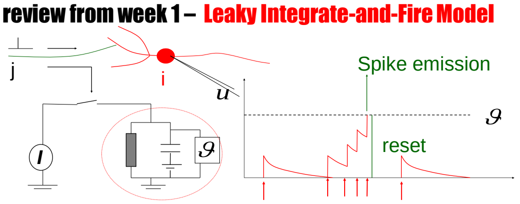


8.2. Aims and challenges

- beyond stationary states
  → transients?

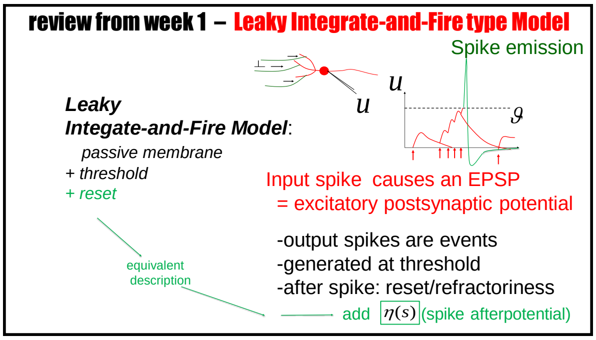
- but then neuron model matters!
  → introduce generalized integrate-and-fire models:
  - Spike Response Model (SRM)
  - Generalized Linear Model (GLM)

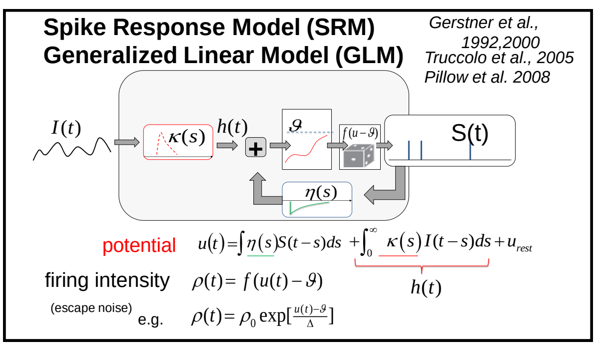
review from week 1 – Leaky Integrate-and-Fire Model

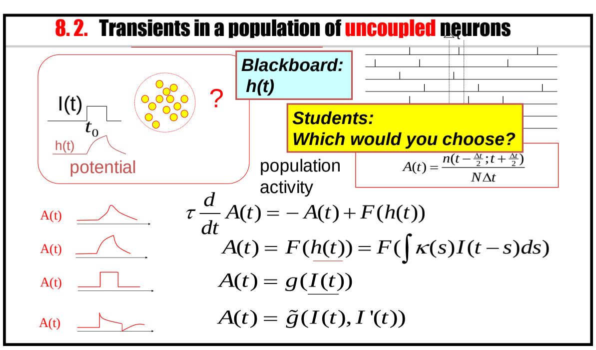


$$\tau \cdot \frac{d}{dt} u = -(u - u_{rest}) + RI(t)$$ linear

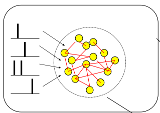
$u(t) = \vartheta \Rightarrow$ Fire+reset $u \to u_r$ threshold


review from week 1 – Leaky Integrate-and-Fire type Model
Spike emission
u
u
ϑ
Leaky
Integate-and-Fire Model:
passive membrane
+ threshold
+ reset
Input spike causes an EPSP
= excitatory postsynaptic potential
-output spikes are events
-generated at threshold
-after spike: reset/refractoriness
equivalent
description
add η(s) (spike afterpotential)


Spike Response Model (SRM)
Generalized Linear Model (GLM)
Gerstner et al., 1992,2000
Truccolo et al., 2005
Pillow et al. 2008
I(t)
κ(s)
h(t)
ϑ
f(u−ϑ)
S(t)
η(s)
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.
$\rho(t)=\rho_0 \exp[\frac{u(t)-\vartheta}{\Delta}]$

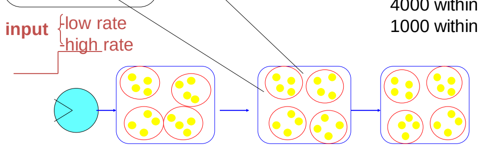

8.2. Transients in a population of uncoupled neurons
Blackboard:
h(t)
I(t)
t_0
h(t)
potential
?
Students:
Which would you choose?
population
activity
$A(t)=\frac{n(t-\frac{\Delta t}{2};t+\frac{\Delta t}{2})}{N\Delta t}$
A(t)
A(t)
A(t)
A(t)
$\tau \frac{d}{dt}A(t) = -A(t) + F(h(t))$
$A(t) = F(h(t)) = F(\int \kappa(s) I(t-s)ds)$
$A(t) = g(I(t))$
$A(t) = \tilde{g}(I(t), I'(t))$

8. 2. Transients in a population of neurons

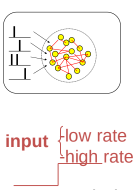


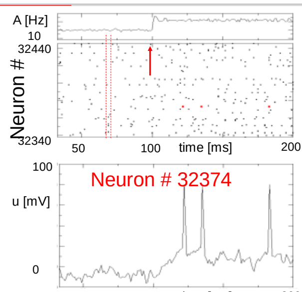
Population
- 50 000 neurons
- 20 percent inhibitory
- randomly connected

Connections
4000 external
4000 within excitatory
1000 within inhibitory



8.2. Transients in a population of neurons

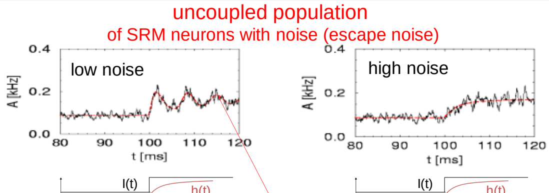




Population
- 50 000 neurons
- 20 percent inhibitory
- randomly connected

8. 2. Transients for populations of noisy neurons

uncoupled population
of SRM neurons with noise (escape noise)



fast transient

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

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

But transient oscillations

slow transient

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

8.2. High-noise activity equation

blackboard

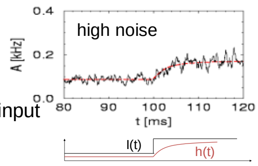
In the limit of **high noise**,
Population activity

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

Membrane potential caused by input

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

noise model A
(escape noise)



slow transient

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

8.2. High-noise activity equation

Population activity

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

Membrane potential caused by input

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

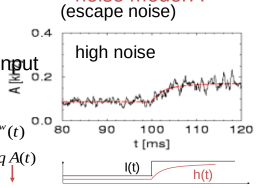
$$I(t) = I^{ext}(t) + I^{netw}(t)$$

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

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

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

noise model A
(escape noise)



slow transient

$$\boxed{A(t) = F(h(t))}$$

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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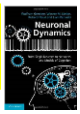

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- orientation columns

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- uniform solution
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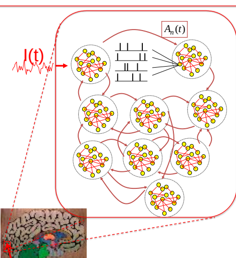
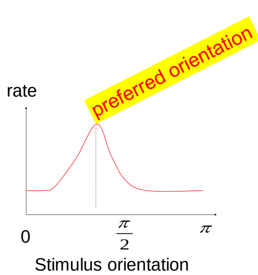
8.7. Head direction cells

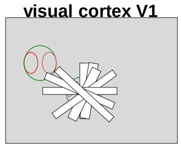
Review: Interacting Populations



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

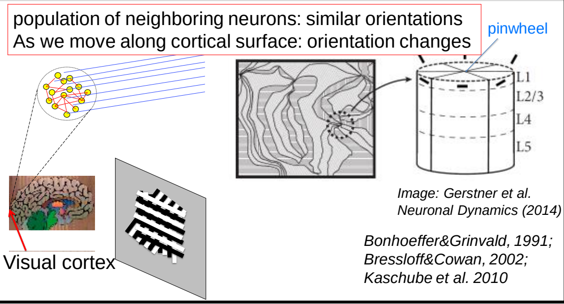
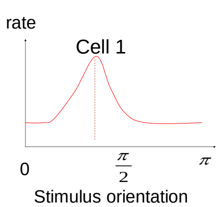


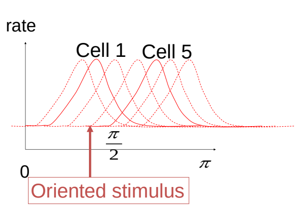
Image: Gerstner et al. Neuronal Dynamics (2014)

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

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



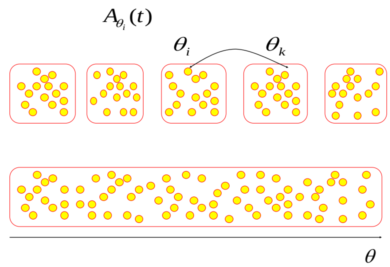
8.3. Do Orienation colums exist? Do identical cells exist?



Coarse coding

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

8.3. multiple populations → continuum



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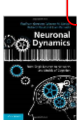

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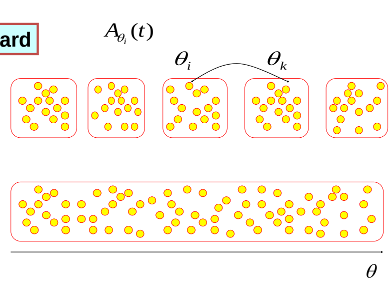
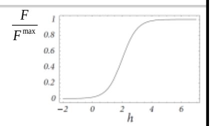
8.4. multiple populations → continuum

Blackboard



8.4: Field equation (continuum model)



Population activity

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

Membrane potential caused by input

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

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

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

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

1 field = 1 integro-differential equation

Exercise 1.1 now (stationary solution)

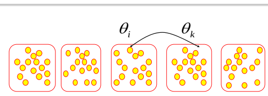
Consider a continuum model,
Find analytical solutions:

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

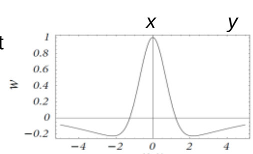
Next lecture at 11:15

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

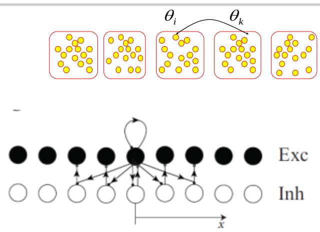
8.4: coupling across continuum



Mexican hat



8.4: more realistic cortical coupling



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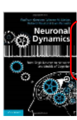

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8.5. Solution types (ring model)

Coupling:

Input-driven regime

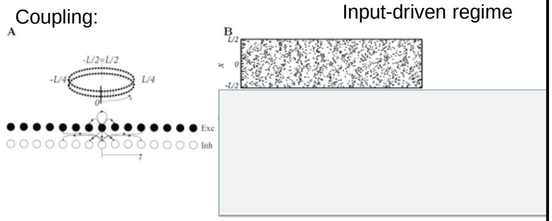
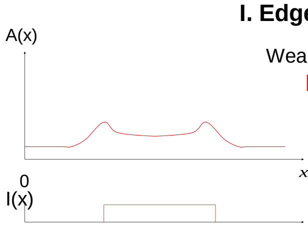


Image: Neuronal Dynamics, Gerstner et al., Cambridge Univ. Press (2014),

8.5. Solution types: input driven regime

Field Equations:
Wilson and Cowan, 1972

I. Edge enhancement



Weaker lateral connectivity

Possible interpretation of visual cortex cells:

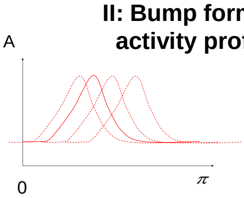
(see later this week)

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

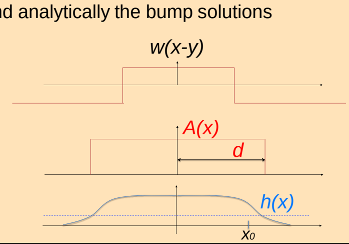


Possible interpretation of head direction cells:

→ (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

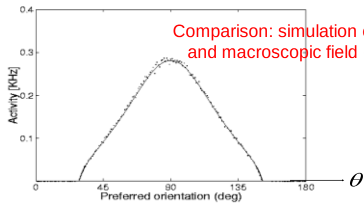
calculate input potential at location x_0

8.5. Solution types: bump solution

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

Spiridon&Gerstn

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 (continuum model)

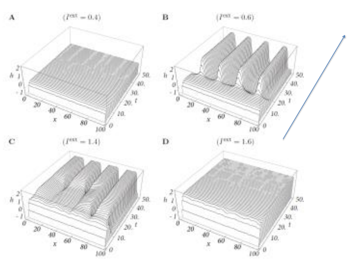


Image: Neuronal Dynamics, Gerstner et al., Cambridge Univ. Press (2014),

Biological Modeling of Neural Networks

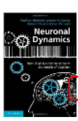
EPFL

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

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

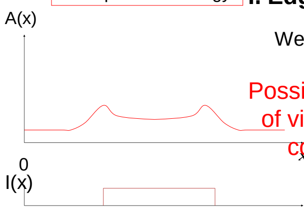
8.7. Head direction cells

8.6. uniform/input driven solution

Field Equations:
Wilson and Cowan, 1972

Basic phenomenology

I. Edge enhancement



Weaker lateral connectivity

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

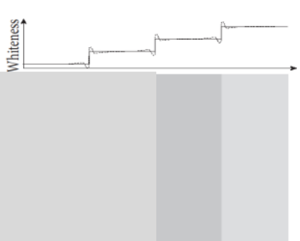
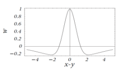
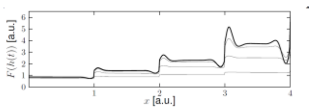


Image: Neuronal Dynamics, Gerstner et al., Cambridge Univ. Press (2014),

8.6. **Mach bands in a continuum model**

Mexican-hat coupling

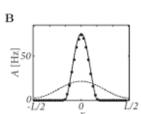


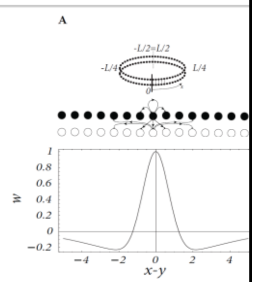


ig. 18.9: **A**. Mach bands in a field model with mexican hat

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

8.6: Field models and Perception





8.6: Field models and Perception

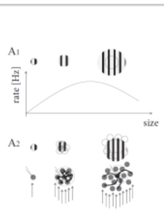


Fig. 18.12: Surround suppression.

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

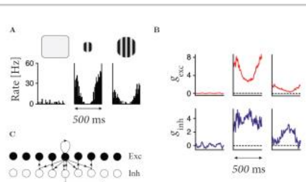


Fig. 18.13: Network stabilized by local inhibition. The schematic model could potentially explain why larger gratings lead not only to less excitatory input g_{exc}, but also to less inhibitory input g_{inh}. **A**. The firing rate as a function of the phase of the moving grating for the three stimulus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

Biological Modeling of Neural Networks

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EPFL, Lausanne, Switzerland

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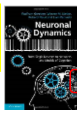
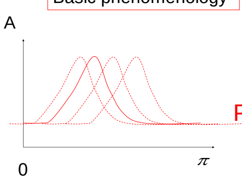


Cambridge Univ. Press

8.7. Bump solution

Basic phenomenology

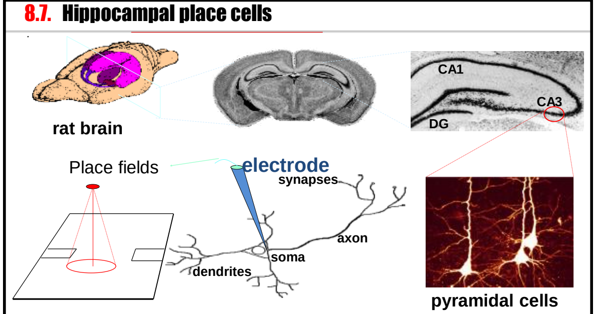
II: Bump formation



strong lateral connectivity

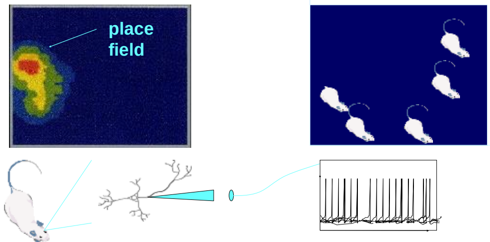
Possible interpretation
of head direction cells:
always some cells active
→ indicate current orientation

8.7. Hippocampal place cells



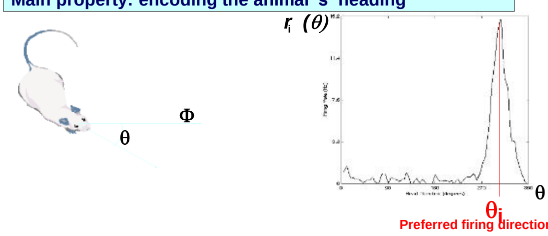
8.7. Hippocampal place cells

Main property: encoding the animal's location



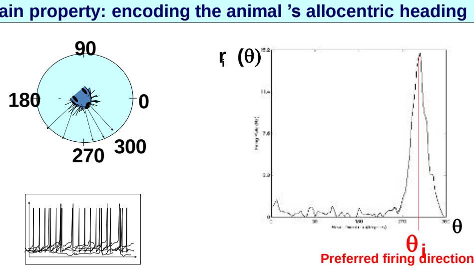
8.7. Head direction cells

Main property: encoding the animal 's heading



8.7. Head direction cells

Main property: encoding the animal 's allocentric heading



8.7. Head direction cells

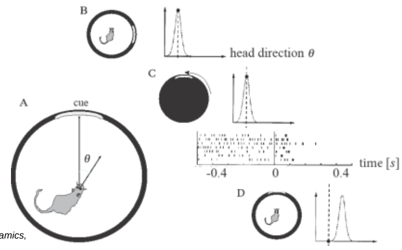


Image: Neuronal Dynamics, Gerstner et al., Cambridge Univ. Press (2014), Adapted from Zugaro et al. (2003), J. Neurosci. 23:3478-3482

8.7. Summary

Continuum model provides understanding for:

- head direction cell – bumps of activity
- contrast enhancement and some visual illusions

Biological Modeling of Neural Networks

Week 8 – Continuum models: Cortical fields and perception

Wulfram Gerstner
EPFL, Lausanne, Switzerland

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

THE END