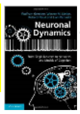
Biological Modeling of Neural Networks

Week 7: Neuronal Populations

Wulfram Gerstner

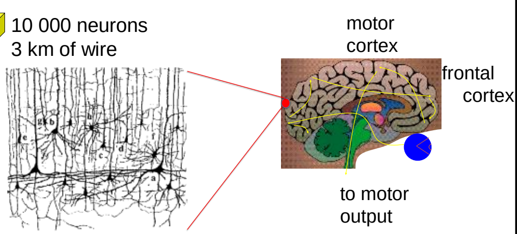
EPFL, Lausanne, Switzerland

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

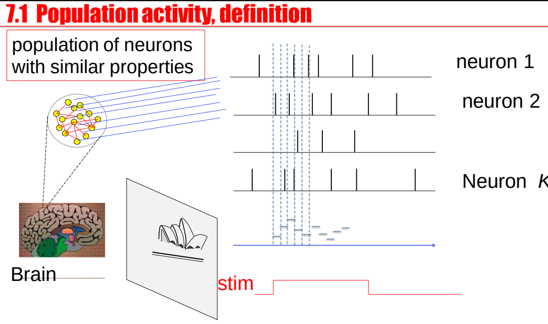


Biological Modeling of Neural Networks – Review from week 1

10 000 neurons
3 km of wire

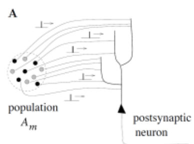


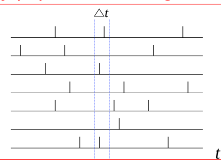
7.1 Population activity, definition



7.1 Population activity: definition

population activity - rate defined by population average





'natural readout'

population activity

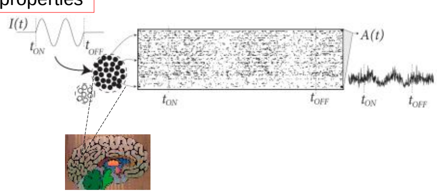
$$A(t) = \frac{n(t; t+\Delta t)}{N \Delta t}$$

Blackboard-1: definition $A(t)$

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

7.1 Population activity: example

population of neurons with similar properties



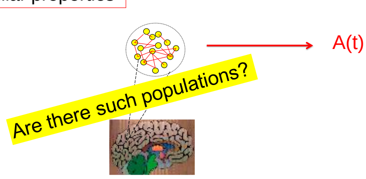
Brain

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

7.1 Population activity

population of neurons with similar properties

population activity



Brain

7.1: Scales of neuronal processes

population of neurons
with similar properties

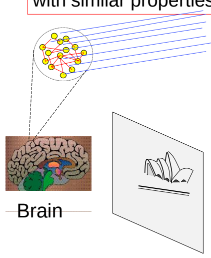
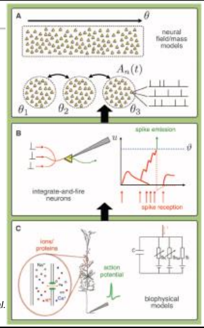


Image: Gerstner et al. Science (2012),



Week 7 – Quiz 1, now

The population activity
[ ] Is a firing rate
[ ] Is a fast variable on the time scale of milliseconds
[ ] Is proportional to the number of spikes
counted across a population in a short time window
[ ] Is defined as the number of spikes
counted across a population in a short time window

Biological Modeling of Neural Networks

Week 7: Neuronal Populations

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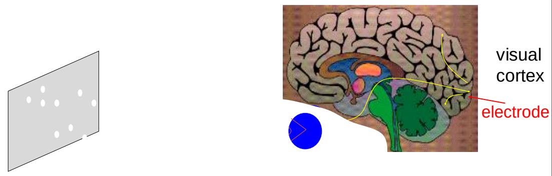
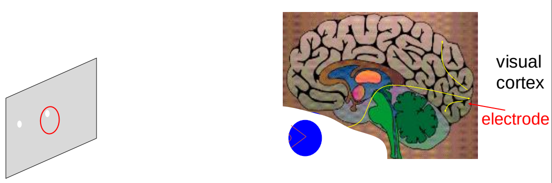
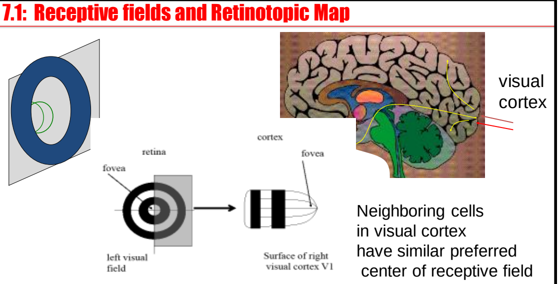
7.1: Receptive fields



7.1: Receptive fields

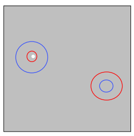


7.1: Receptive fields and Retinotopic Map

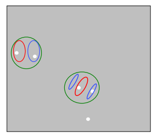


7.1: Receptive fields with Orientation Tuning

Receptive fields:
Retina, LGN



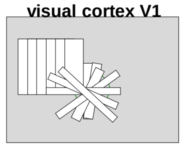
Receptive fields:
visual cortex V1



Orientation
selective

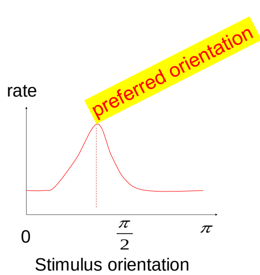
7.1: Receptive fields with Orientation Tuning

Receptive fields:
visual cortex V1

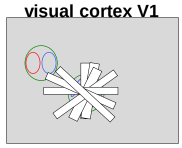


Orientation selective

7.1: Receptive fields with Orientation Tuning



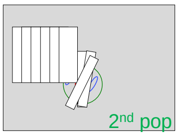
Receptive fields:
visual cortex V1

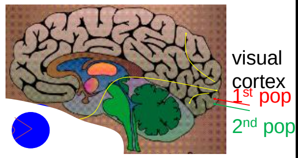


Orientation selective

7.1: Orientation Tuning and Orientation Maps

Receptive fields:
visual cortex V1

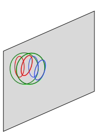


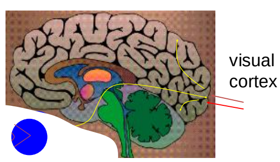


Orientation selective

Neighboring neurons have similar properties

7.1: Orientation Map





Neighboring cells in visual cortex
Have similar preferred orientation:
cortical orientation map

Hubel and Wiesel 1968; Bonhoeffer&Grinvald, 1991; Bressloff&Cowan, 2002; Kaschube et al. 2010

Week 7 – Quiz 2, now

The receptive field of a visual neuron refers to
[ ] The localized region of space to which it is sensitive
[ ] The orientation of a light bar to which it is sensitive
[ ] The set of all stimulus features to which it is sensitive

The receptive field of a auditory neuron refers to
[ ] The set of all stimulus features to which it is sensitive
[ ] The range of frequencies to which it is sensitive

The receptive field of a somatosensory neuron refers to
[ ] The set of all stimulus features to which it is sensitive
[ ] The region of body surface to which it is sensitive

Biological Modeling of Neural Networks

Week 7: Neuronal Populations

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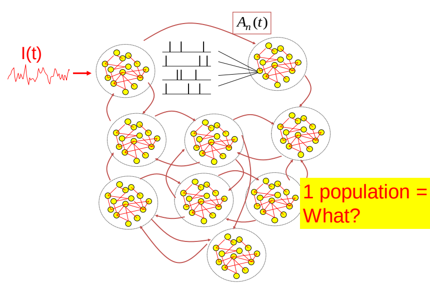
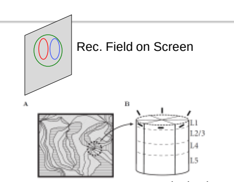
7.2: Interacting Populations in models



7.2: a single model population

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

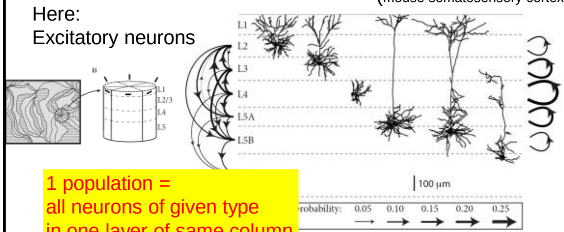


→ make this more precise

7.2: local cortical connectivity across layers

(mouse somatosensory cortex)

Here:
Excitatory neurons



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

Lefort et al. NEURON, 2009

7.2: Connectivity schemes (models)

full connectivity
all-to-all

Random connectivity
w. number K of inputs fixed

N=5000
neurons

N=10000
neurons

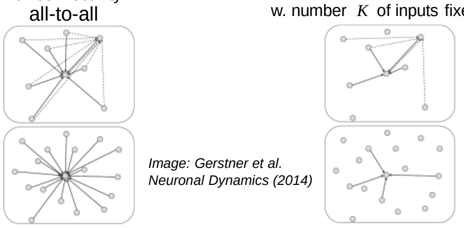


*Image: Gerstner et al.
Neuronal Dynamics (2014)*

Each neuron receives
N connections

Each neuron receives
K connections

7.2: Random connectivity – fixed number of inputs

random: number of inputs K=500, fixed

Network N=5 000

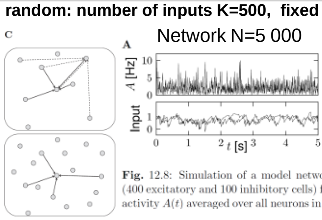


Fig. 12.8: Simulation of a model network with a fixed number of presynaptic partner
(400 excitatory and 100 inhibitory cells) for each postsynaptic neuron. A. Top: Populatio
activity $A(t)$ averaged over all neurons in a network of 4 000 excitatory and 1 000 inhibitor

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

7.2: Random connectivity – fixed number of inputs

random: number of inputs K=500, fixed

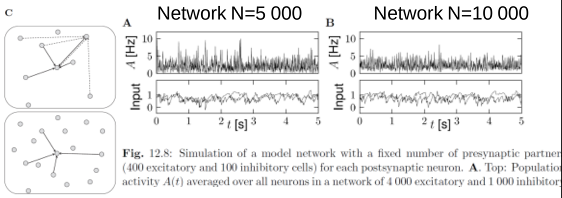


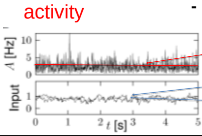
Image: Gerstner et al. Neuronal Dynamics (2014)

7.2: Random Connectivity: fixed p

Can we mathematically predict the population activity?

given
- **connection probability *p* and weight w_{ij}**
- **properties of individual neurons**
- **large population**

asynchronous activity



A(t) is nearly constant

Input is nearly identical for different neurons (and nearly constant)

Biological Modeling of Neural Networks

Week 7: Neuronal Populations

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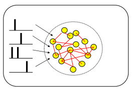
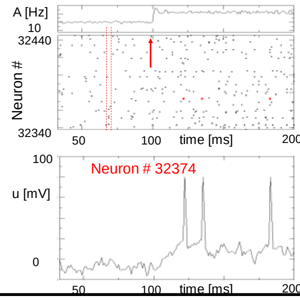
7.3: asynchronous firing / asynchronous state



input
low rate
high rate



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

7.3: asynchronous state

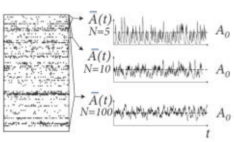


Image: Gerstner et al. Neuronal Dynamics (2014)

Next lecture: 10h15

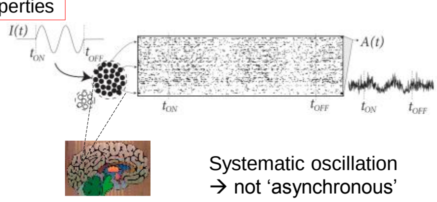
Blackboard-2:
-Definition of $A(t)$
- filtered $A(t)$
- $<A(t)>$
-convergence in weak sense

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

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

7.3: asynchronous state – counter examples, <A(t)> not constant

population of neurons with similar properties

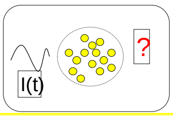


Systematic oscillation
→ not 'asynchronous'

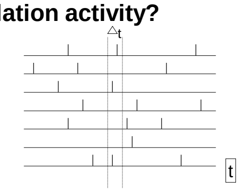
Brain

7.3: asynchronous state in a homogeneous network

population activity?



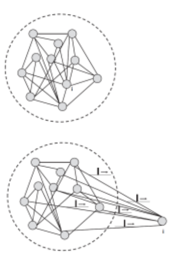
Homogeneous network:
- -all neurons are 'the same'
- -all synapses are 'the same'
- -each neuron receives input from k neurons in network
- -each neuron receives the same (mean) external input



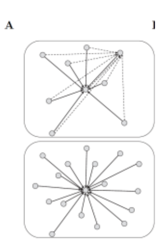
population activity $A(t) = \frac{n(t;t+\Delta t)}{N\Delta t}$

7.3: mean-field arguments (full connectivity)

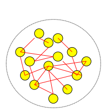
Blackboard-3: Input to neuron i



7.3: mean-field arguments (full connectivity)

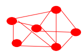


Full connectivity



7.3: mean-field arguments (full connectivity)

Fully connected network



fully connected
N >> 1

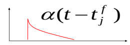
Synaptic coupling

$$w_{ij} = w_0$$

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

All spikes, all neurons

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

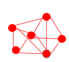


7.3: mean-field arguments (full connectivity)

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

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

Index i disappears



fully connected

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

All spikes, all neurons

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

7.3: mean-field arguments: asynchronous state

Assume all variables are constant in time:

Blackboard-4: Stationary state

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

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

Firing rate? Population rate?

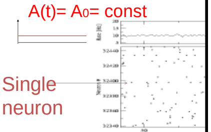
7.3: mean-field arguments: population activity (asynchr. state)

Input is constant and identical for all neurons

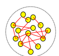
(1) $I_0 = [J_0 q A_0 + I_0^{ext}]$ $q = \int \alpha(s) ds$

frequency (single-neuron gain function)

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



Homogeneous network
All neurons are identical,



Single neuron rate = population rate

(3) $\nu = A_0$

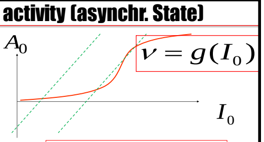
7.3: stationary solution: population activity (asynchr. State)

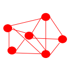
Stationary solution
=asynchronous state

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

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

(3) $\nu = A_0$





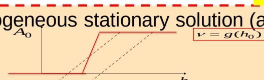
Homogeneous network, stationary,
All neurons are identical,
Single neuron rate = population rate

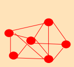
$\nu = g(I_0) = A_0$

Exercise 1, now

Next lecture: 11h15

Exercise 1: homogeneous stationary solution (asynchronous)





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

$\nu = A_0$

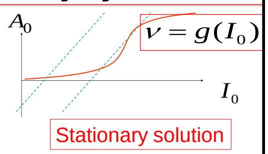
7.3: stationary solution: population activity (asynchr. state)

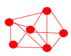
Stationary solution
=asynchronous state

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

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

(3) $\nu = A_0$





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

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

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

Single Population

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

Single neuron rate = population rate

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

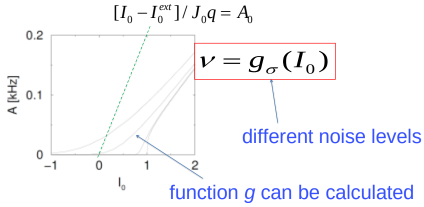
→ **What is this function g?**

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

7.3: stationary solution: integrate-and-fire neurons

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

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



7.3: gain function is noise-dependent

Gain-function g =frequency-current relation

function g can be calculated analytically or measured in **single-neuron simulations/single-neuron experiments**

$$\nu = g_\sigma(I_0)$$

different noise levels

Biological Modeling of Neural Networks

EPFL

Week 7: Neuronal Populations

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7.1 Cortical Populations
- population activity
- columns and receptive fields

7.2 Connectivity
- cortical connectivity
- model connectivity schemes

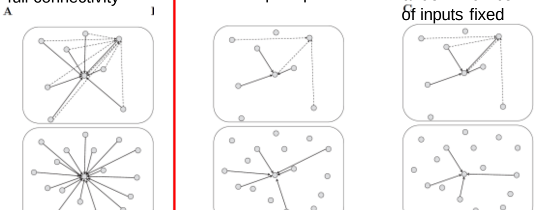
7.3 Mean-field argument
- asynchronous state

7.4 Random Networks
- Changing network size
- Balanced state

7.4: mean-field arguments (random connectivity)

random connectivity

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

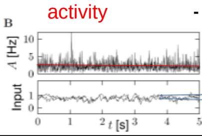


7.4: Review from 7.2 - Random Connectivity: fixed p

Can we mathematically predict the population activity?

given
- **connection probability *p* and weight w_{ij}**
- **properties of individual neurons**
- **large population**

asynchronous activity



Input is nearly identical for different neurons

7.4: mean-field arguments (random connectivity)

I&F with stochastic spike arrival

Blackboard: Excitatory input

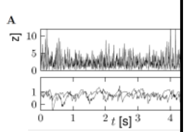
For any arbitrary neuron in the population

$$\tau \frac{d}{dt} u_i = -u + I_i$$

$$I_i = \sum_{k,f} w_{ik} \alpha(t - t_k^f)$$

EPSC

excitatory input spikes



Can we predict the mean current?
- and its fluctuations?

7.4: mean-field arguments (random connectivity)

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

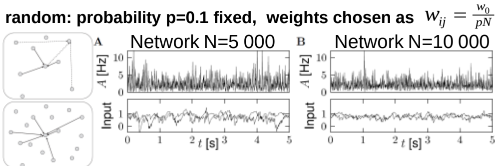


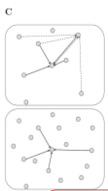
Fig. 12.7: Simulation of a model network with a fixed connection probability $p = 0.1$. **A.** Top: Population activity $A(t)$ averaged over all neurons in a network of 4 000 excitatory and 1 000 inhibitory neurons. Bottom: Total input current $I_i(t)$ into two randomly chosen

Image: Gerstner et al. Neuronal Dynamics (2014)

fluctations of *A* decrease → fluctuations of *I* decrease

7.4: Random connectivity – fixed number of inputs

random: input connections K=500 fixed, weights chosen as $w_{ij} = \frac{w_0}{K}$



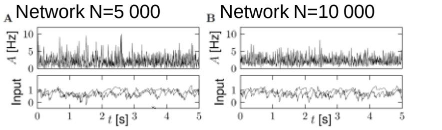


Fig. 12.8: Simulation of a model network with a fixed number of presynaptic partners (400 excitatory and 100 inhibitory cells) for each postsynaptic neuron. A. Top: Population activity $A(t)$ averaged over all neurons in a network of 4 000 excitatory and 1 000 inhibitory

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

Image: Gerstner et al. Neuronal Dynamics (2014)

Exercise 2.: Random network, K inputs per neuron

Randomly connected network
N =8000 neurons, each has
K=1000 presynaptic neurons,
Whenever a spike arrives it generates a
Current pulse $\alpha(t-t_k^f)$
The current to neuron i is therefore

$$I_i = \sum_{k,f} w_{ik}\alpha(t-t_k^f)$$

*Assume that * the weights are* $w_{ij} = \frac{w_0}{K}$
** activity is constant* $A(t) = A_0$

Give an intuitive or a mathematical argument why

$$I_i \approx w_0 A_0 \int \alpha(s)ds$$

What happens if we increase N? What is the
Current I_j *to another neuron j in the network?*

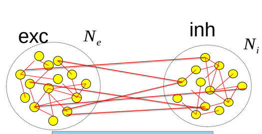
random: number of inputs K fixed

Next lecture: 11h42

7.4: Connectivity schemes – random, fixed p, but balanced

$$\tau \frac{d}{dt} u_i = -u + I_i$$

$$I_i = \sum_{k,f} w_{ik}\alpha^{exc}(t-t_k^f) - \sum_{k,f} w_{ik}\alpha^{inh}(t-t_k^f)$$



Blackboard: Exc. + Inh. input

make network bigger, but
-keep mean input close to zero $\quad w_{ij} = \frac{J_e}{\sqrt{pN}}$

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

-keep variance of input $\quad w_{ij} = \frac{J_i}{\sqrt{pN}}$

7.4: Connectivity schemes – random, fixed p, but balanced

Image: Gerstner et al. Neuronal Dynamics (2014)

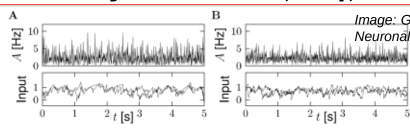


Fig. 12.9: Simulation of a model network with balanced excitation and inhibition and fixed connectivity $p = 0.1$ **A**. Top: Population activity $A(t)$ averaged over all neurons in a network of 4 000 excitatory and 1 000 inhibitory neurons. Bottom: Total input current $I_i(t)$ into two randomly chosen neurons. **B**. Same as A, but for a network with 8 000 excitatory and 2 000 inhibitory neurons. The synaptic weights have been rescaled by a factor $1/\sqrt{2}$ and the common constant input has been adjusted. All neurons are leaky integrate-and-fire units with identical parameters coupled interacting by short current pulses.

→ fluctations of *A* decrease
fluctations of *I* become 'smooth'

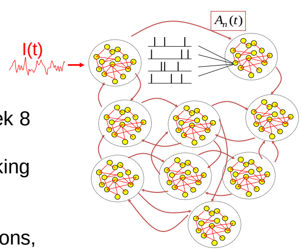
7.4: Connectivity schemes – random, fixed p, but balanced

One population
→ multiple populations

Application to visual cortex
→ visual processing, week 8

Application to decision making
→ week9

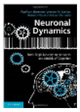
Understanding the fluctuations,
→ noise and the neural code, week 10-12



Biological Modeling of Neural Networks

The END

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



7.1 Cortical Populations
- population activity
- columns and receptive fields

7.2 Connectivity
- cortical connectivity
- model connectivity schemes

7.3 Mean-field argument
- asynchronous state

7.4 Random Networks
- Changing network size
- Balanced state