Exam:

- written exam Wedn. 3.07.2019 from 8:15-11:00
- sample exams of previous years online
- miniproject counts 30 percent towards final grade

For written exam:

-bring 1 sheet A5 of own notes/summary

-HANDWRITTEN!

-no calculator, no textbook

LEARNING OUTCOMES

- Solve linear one-dimensional differential equations
- Analyze two-dimensional models in the phase plane
- Develop a simplified model by separation of time scales
- Analyze connected networks in the mean-field limit
- Formulate stochastic models of biological phenomena
- Formalize biological facts into mathematical models
- Prove stability and convergence
- Apply model concepts in simulations
- Predict outcome of dynamics
- Describe neuronal phenomena

Look at samples of past exams

Transversal skills

- Plan and carry out activities in a way which makes optimal use of available time and other resources.
- Collect data.
- Write a scientific or technical report.

Use a textbook,
(Use video lectures)
don't use slides (only)

miniproject

Biological Modeling of Neural Networks:

ÉCOLE POLYTECHNIQUE FÉDÉRALE DE LAUSANNE

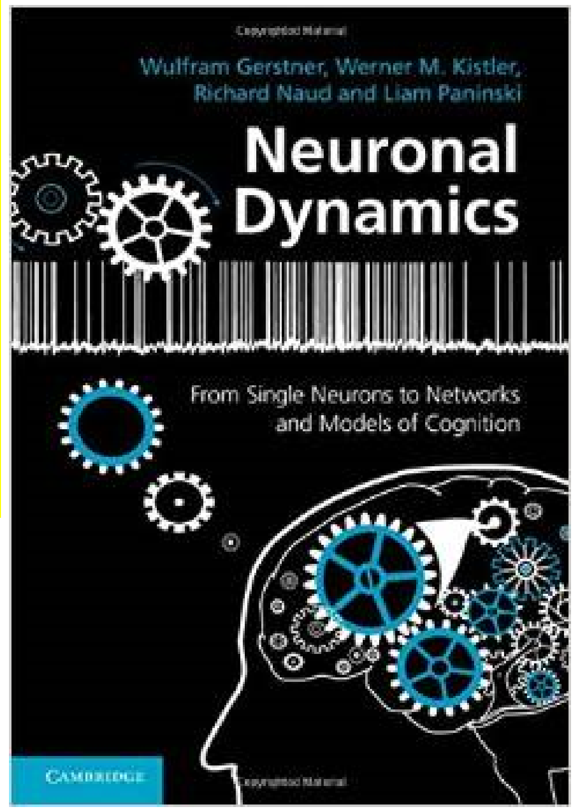
Week 9 – Decision models: Competitive dynamics

Wulfram Gerstner

EPFL, Lausanne, Switzerland

Reading for week 9:
NEURONAL DYNAMICS
Ch. 16 (except 16.4.2)

Cambridge Univ. Press



9.1 Introduction
- decision making

9.2 Perceptual decision making
- V5/MT
- Decision dynamics: Area LIP

9.3 Theory of decision dynamics
- competition via shared inhibition
- effective 2-dim model

9.4. Solutions
- symmetric case
- biased case

9.5. Simulations and Experiments
- simulations and theory
- simulations and experiments

9.6. Decisions, actions, volition
- the problem of free will

9.1. How do I decide?

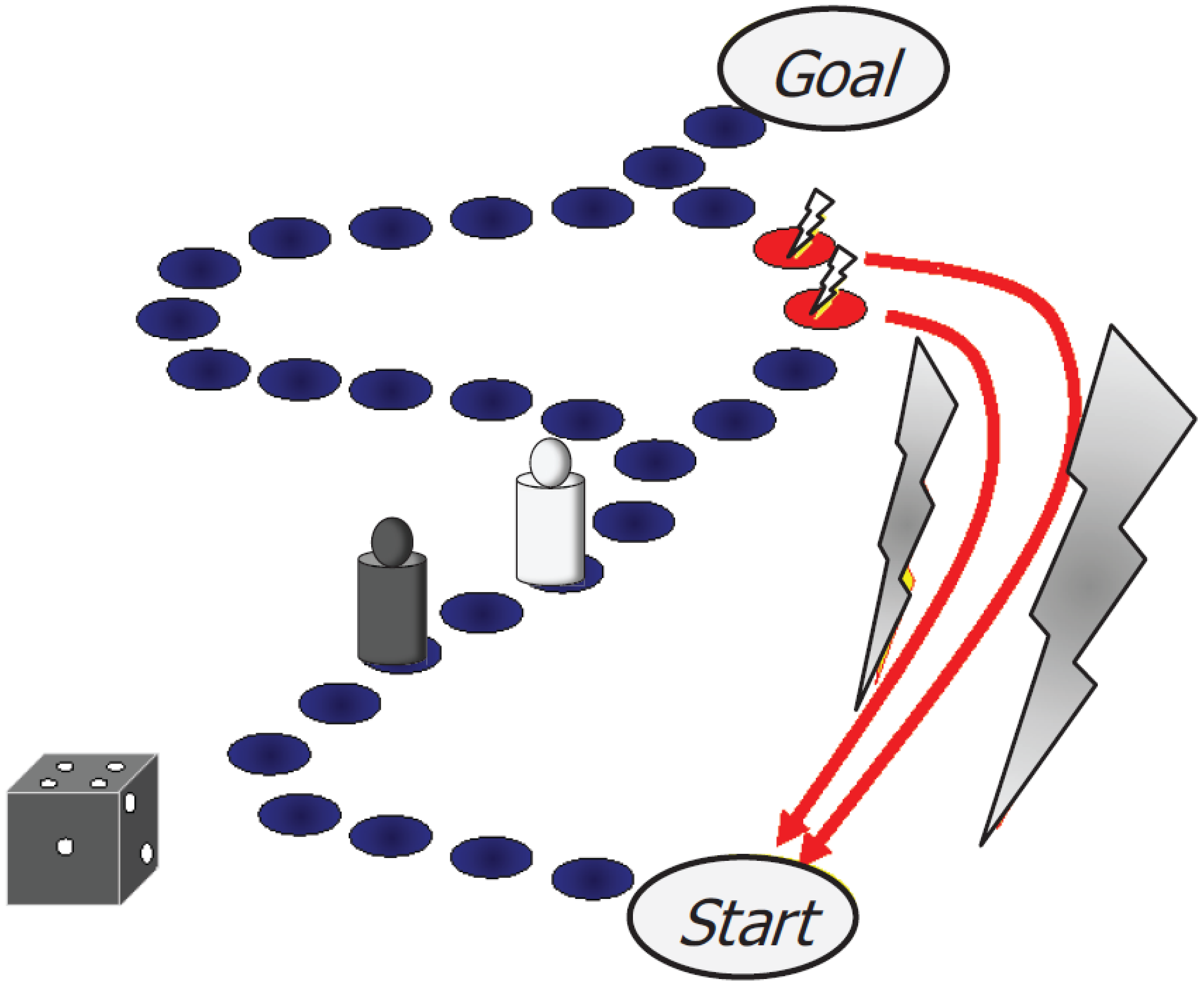
We take decisions all the time

- Coffee before class or not?

- Vote for candidate A or B?

- Turn left or right at the crossing?

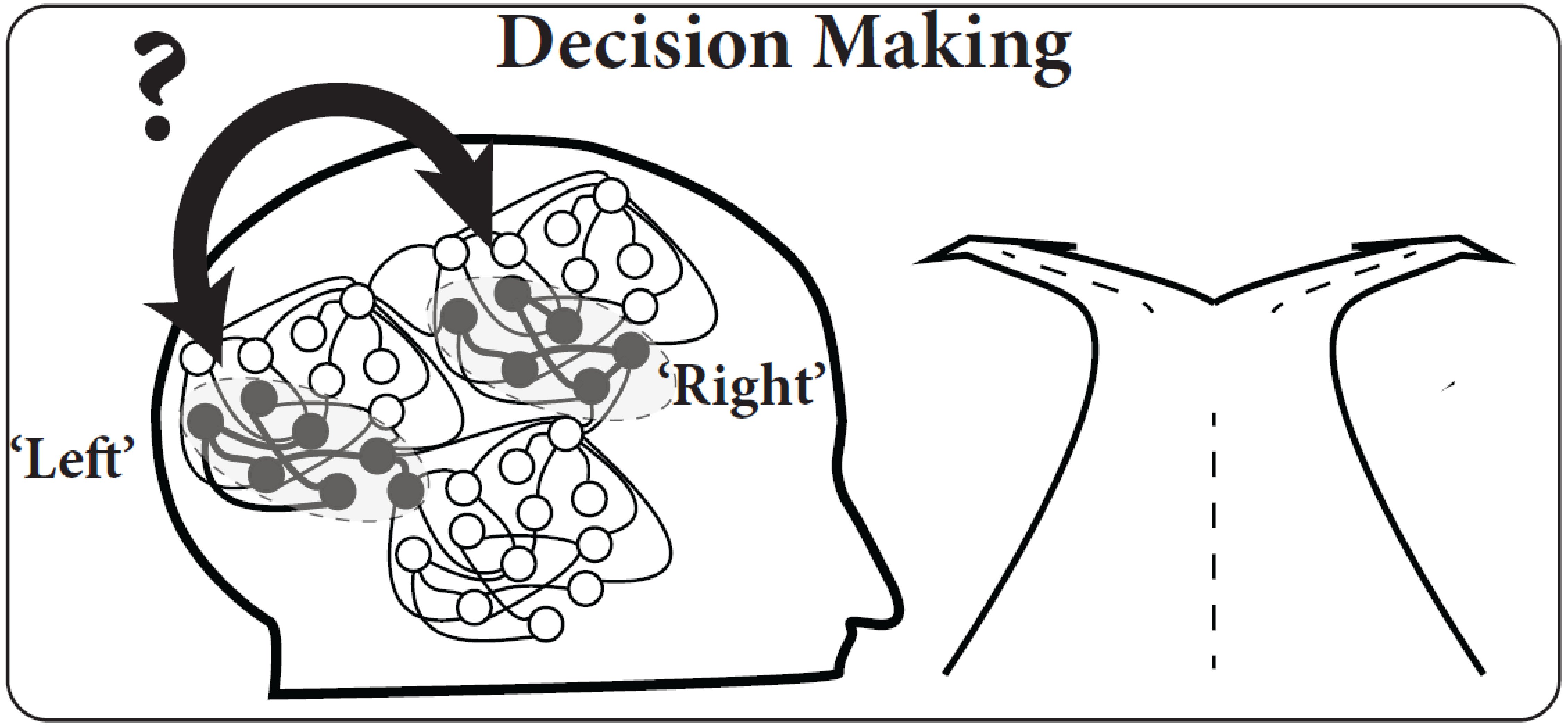
9.1. How do I decide?



9.1. Decision making

turn

Left? Right?



9.1. Review of week 8: High-noise activity equation

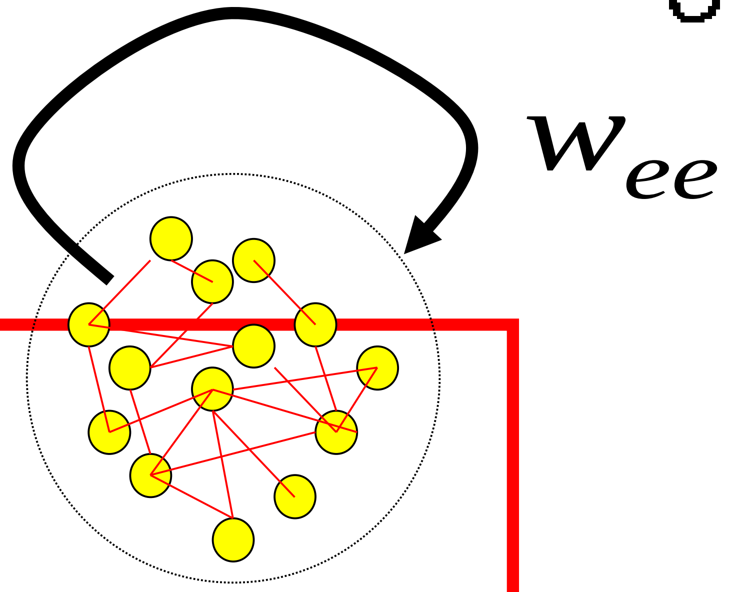
Population activity

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

Membrane potential caused by input

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

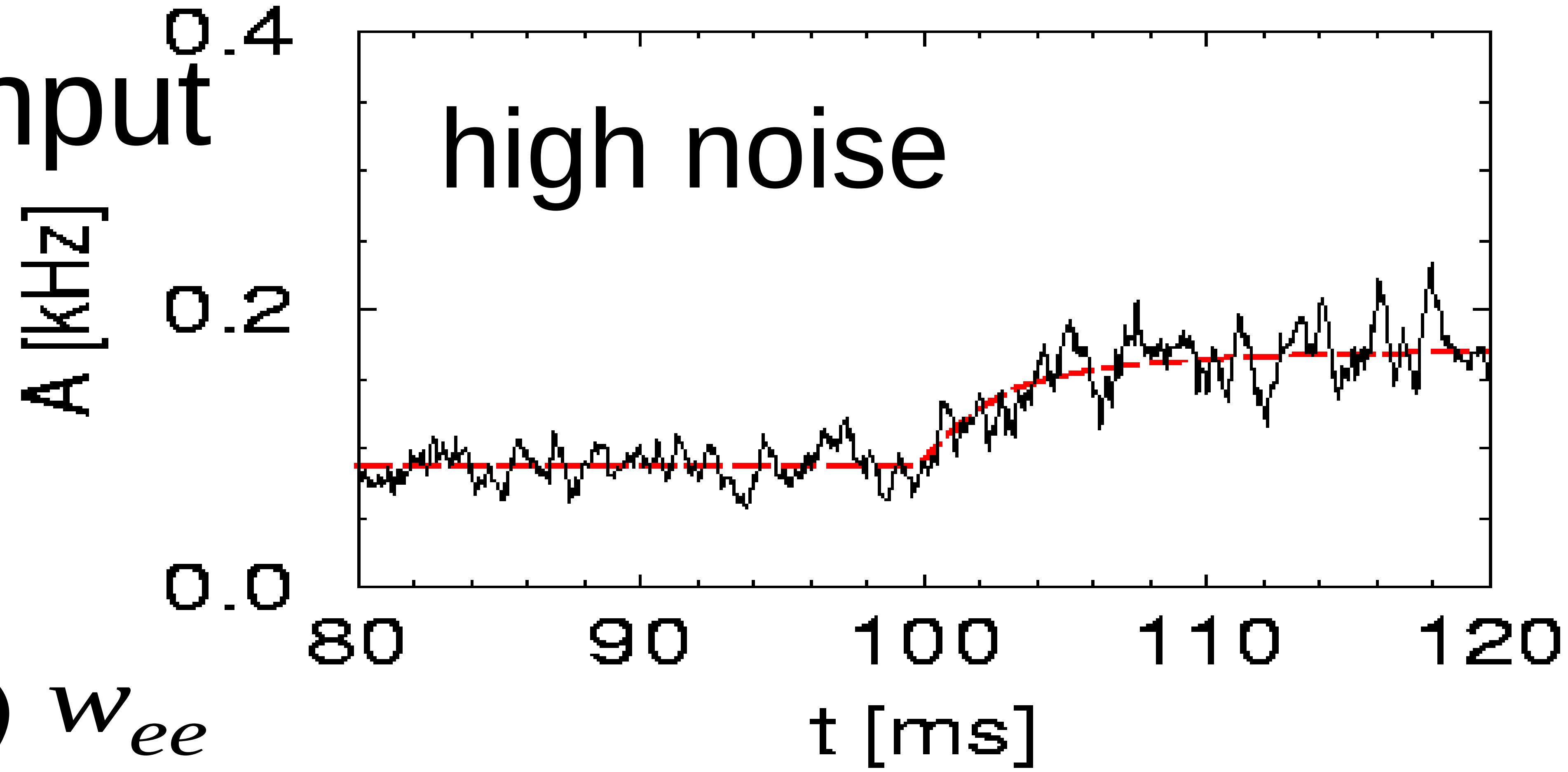
$$\boxed{\tau \frac{d}{dt} h(t) = -h(t) + R\, I^{ext}(t) + w_{ee}\, F(h(t))}$$

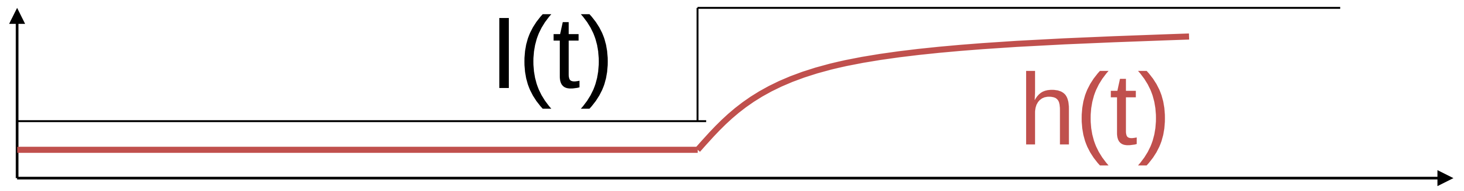


Attention:

- valid for high noise only, else transients might be wrong
- valid for high noise only, else spontaneous oscillations may arise

noise model A
(escape noise/fast noise)

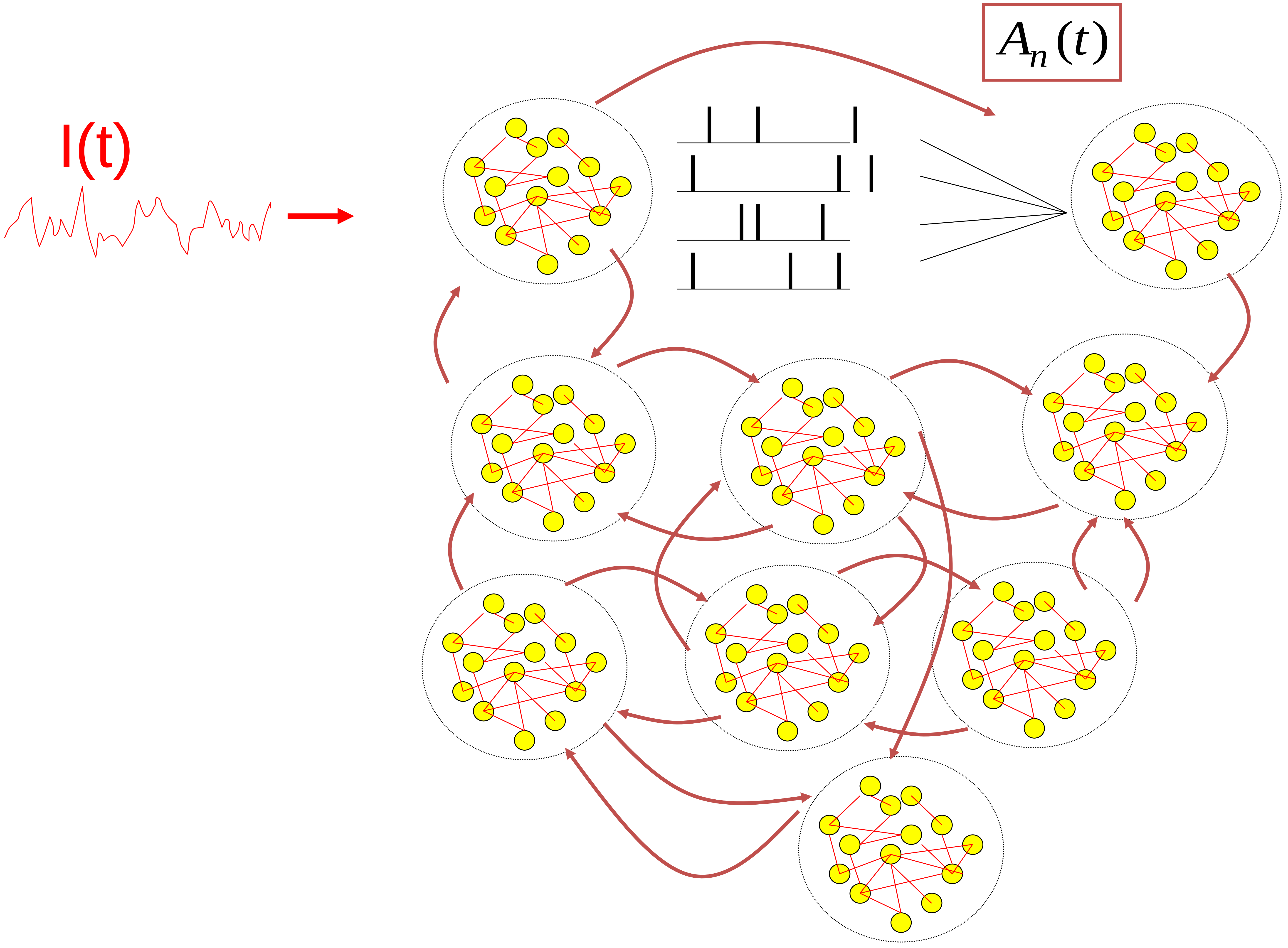




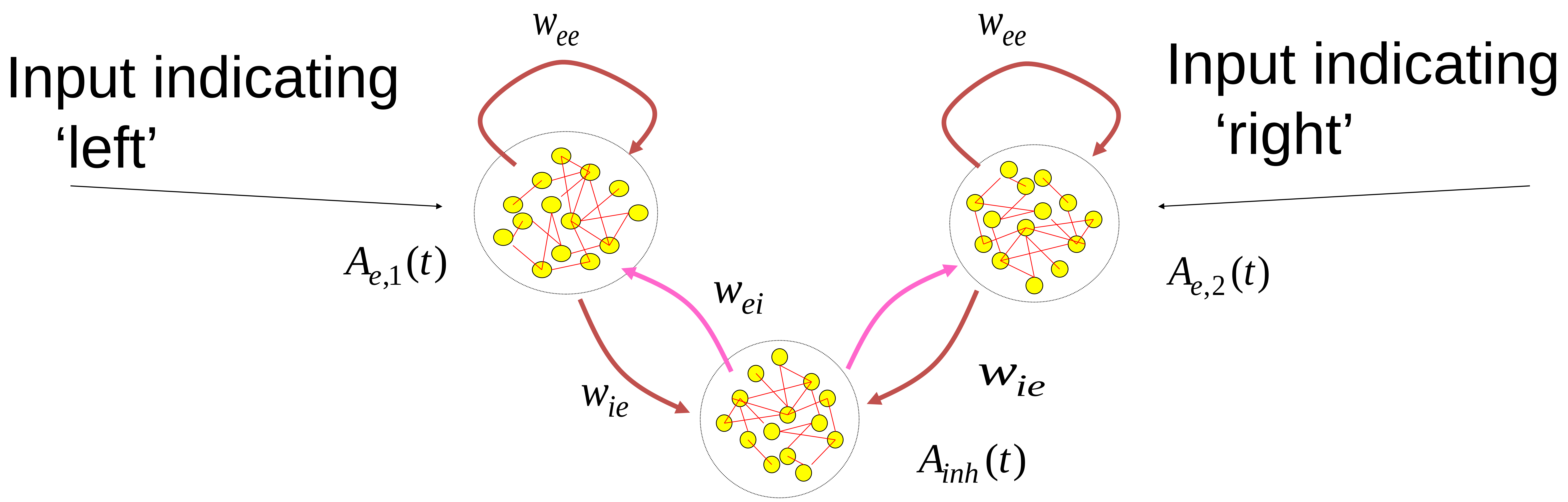
slow transient

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

9.1. Review: microscopic vs. macroscopic



9.1. Competition between two populations



9.1. How do YOU decide?

As selected EPFL student, pick your money at EPFL:

30CHF tomorrow / 100 CHF May first next year

90CHF tomorrow / 100 CHF May first next year

‘Neuro-economics’

Bisection task:

‘Is the middle bar shifted to the left or to the right?’

9.1. decision making - aims

Decisions are everywhere

Model: populations of neurons

Model feature Competition

Experimental data

Perceptual Decision task

Biological Modeling of Neural Networks:

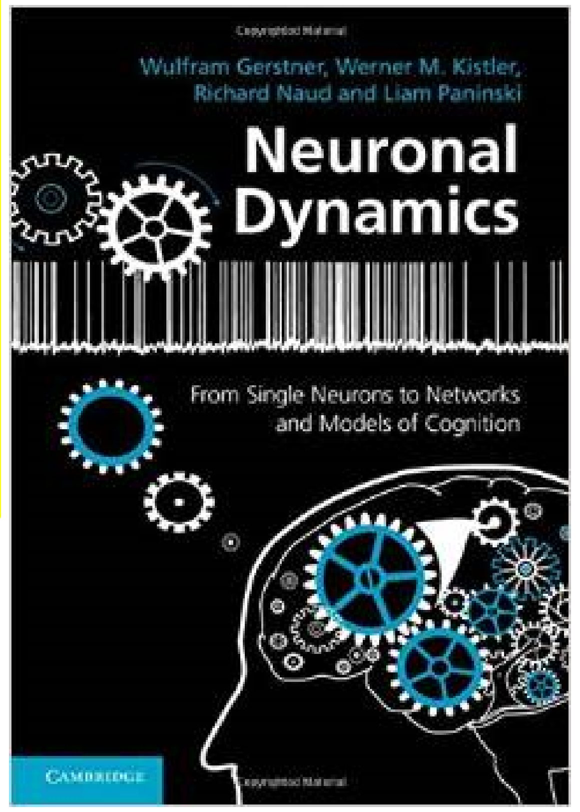
ÉCOLE POLYTECHNIQUE
FÉDÉRALE DE LAUSANNE

Week 9 – Decision models:
Competitive dynamics

Wulfram Gerstner

EPFL, Lausanne, Switzerland

Reading for week 9:
NEURONAL DYNAMICS
Ch. 16 (except 16.4.2)



Cambridge Univ. Press

9.1 Introduction
- decision making

9.2 Perceptual decision making
- V5/MT
- Decision dynamics: Area LIP

9.3 Theory of decision dynamics
- competition via shared inhibition
- effective 2-dim model

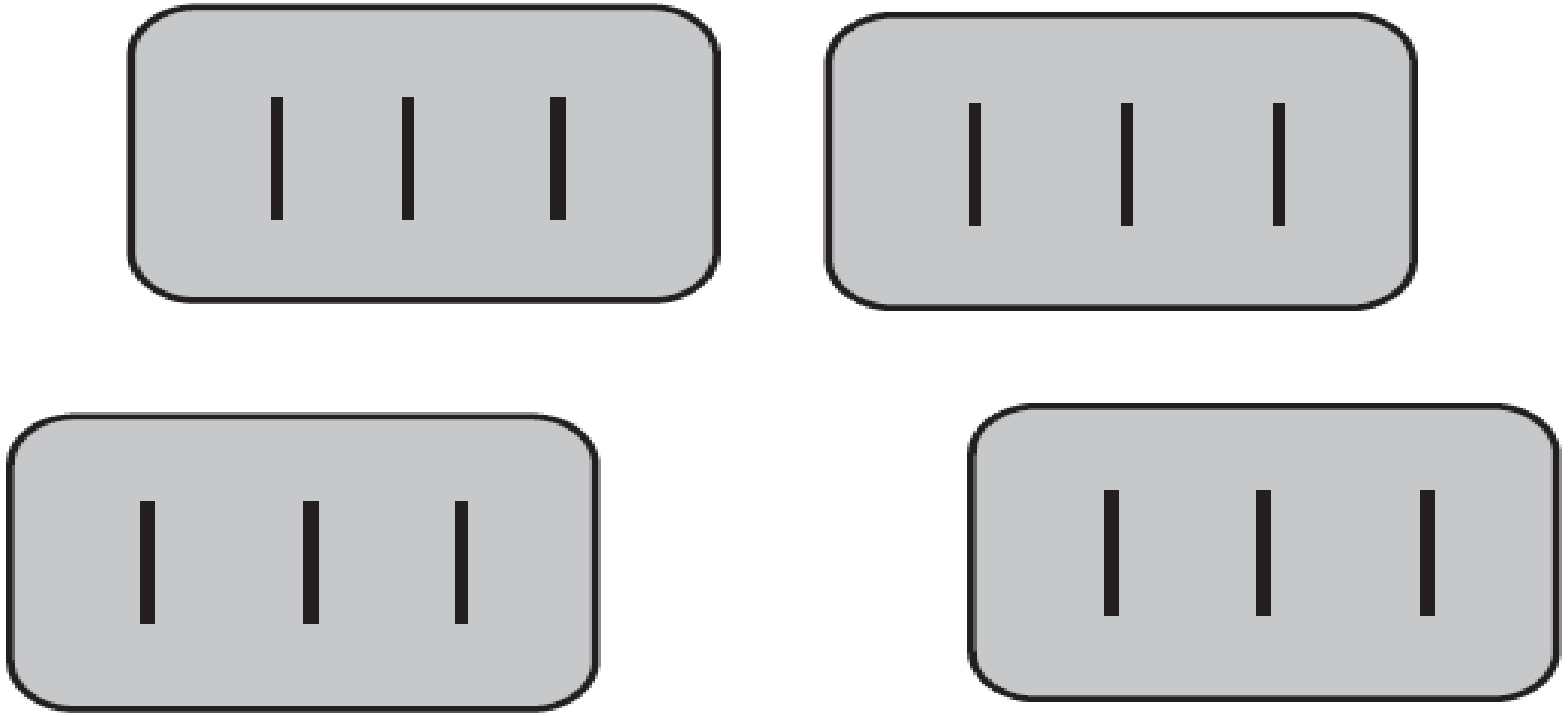
9.4. Solutions
- symmetric case
- biased case

9.5. Simulations and Experiments
- simulations and theory
- simulations and experiments

9.6. Decisions, actions, volition
- the problem of free will

Bisection task:

‘Is the middle bar shifted to the left or to the right?’



e.g., Herzog lab, EPFL

9.2. Detour: receptive fields in V5/MT

visual
cortex

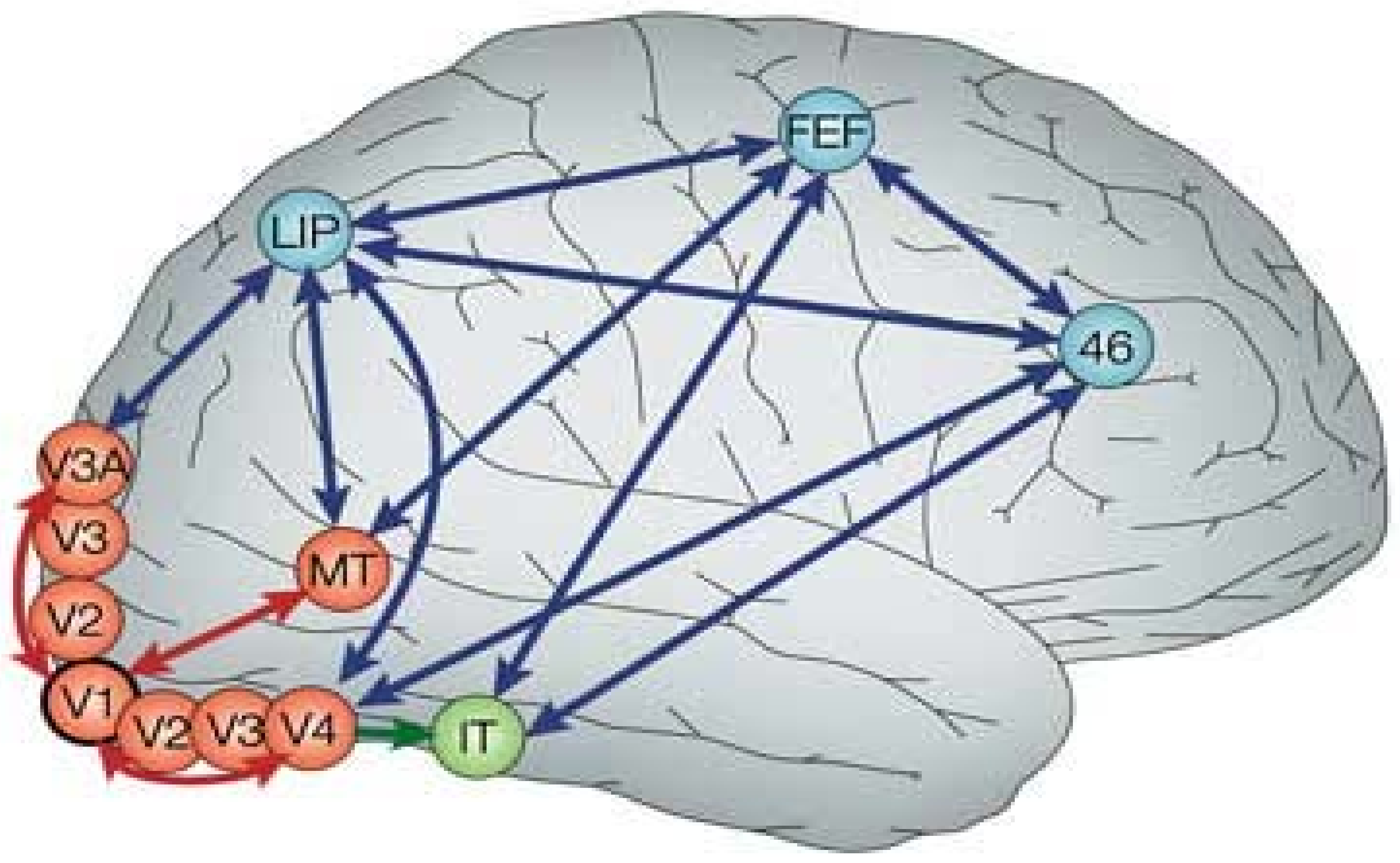
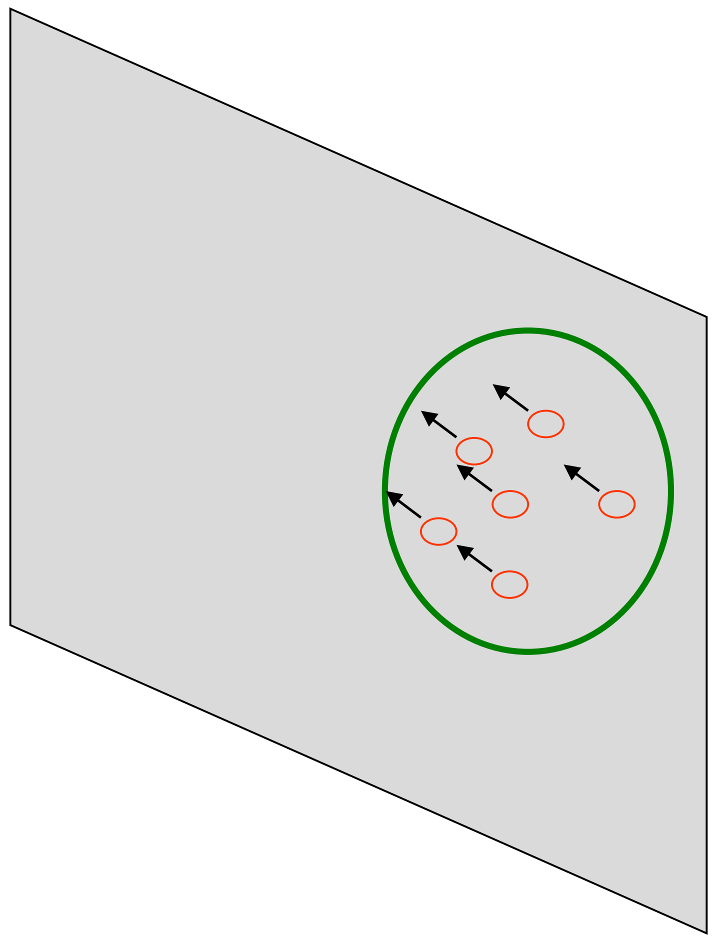


IMAGE Nature Reviews | Neuroscience



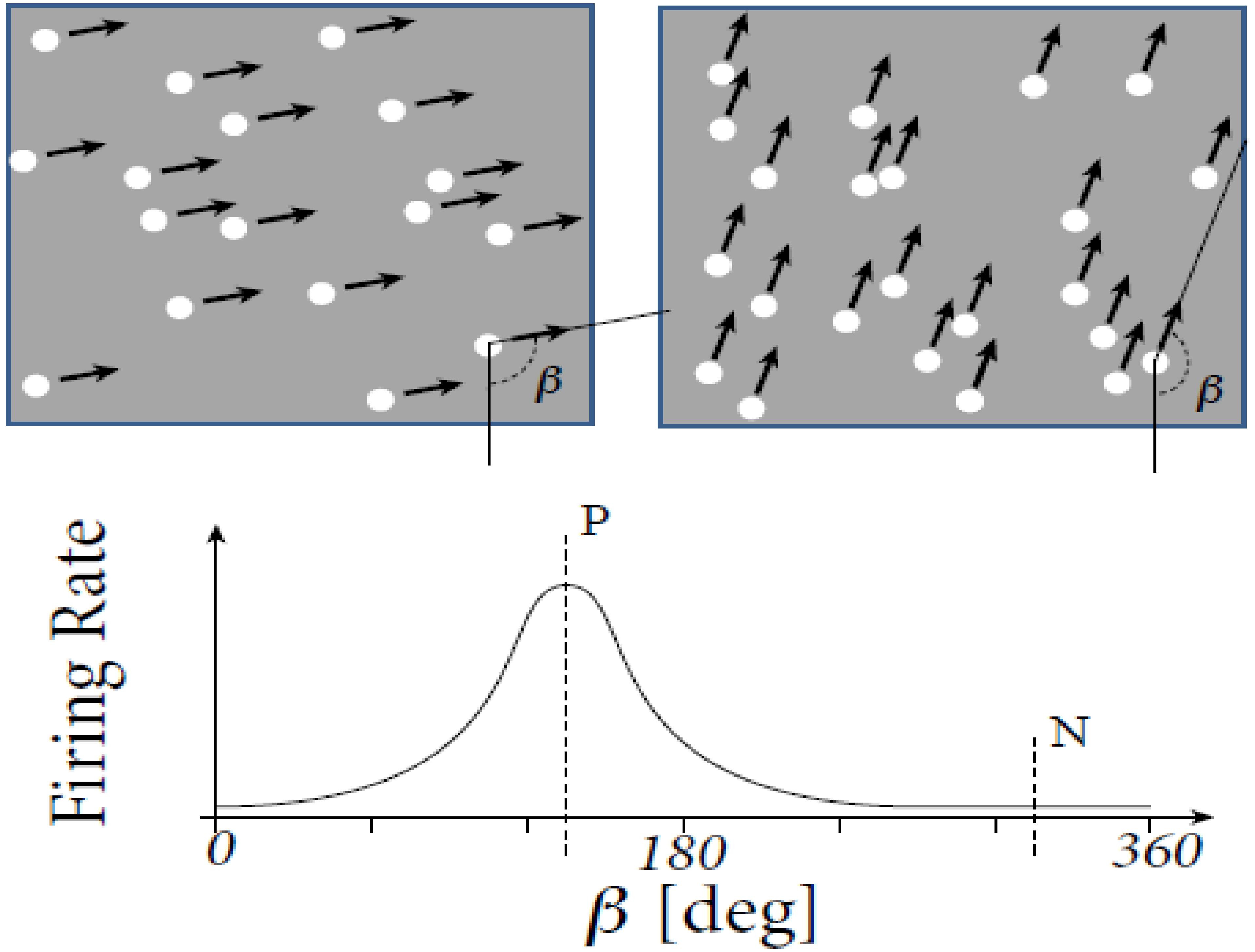
1) Cells in visual cortex MT/V5 respond
to motion stimuli

2) Neighboring cells in visual cortex MT/V5
respond to motion in similar direction
cortical columns

Albright, Desimone,Gross,
J. Neurophysiol, 1985

9. 2. Detour: receptive fields in V5/MT

Recordings from a single neuron in V5/MT

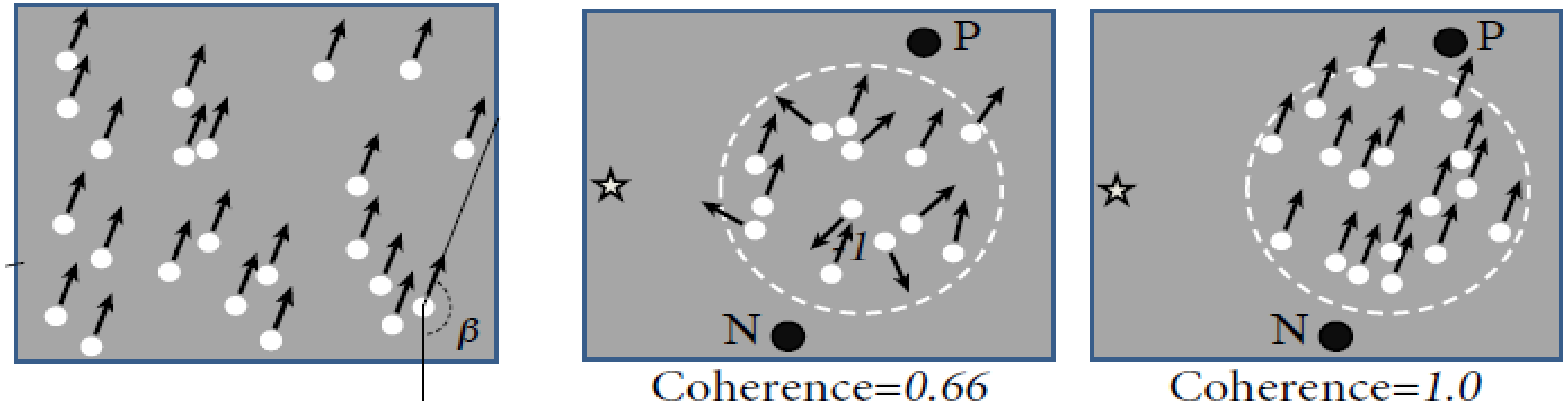


Receptive Fields depend on direction of motion

Random moving dot stimuli:

e.g.Salzman, Britten, Newsome, 1990
Roitman and Shadlen, 2002
Gold and Shadlen 2007

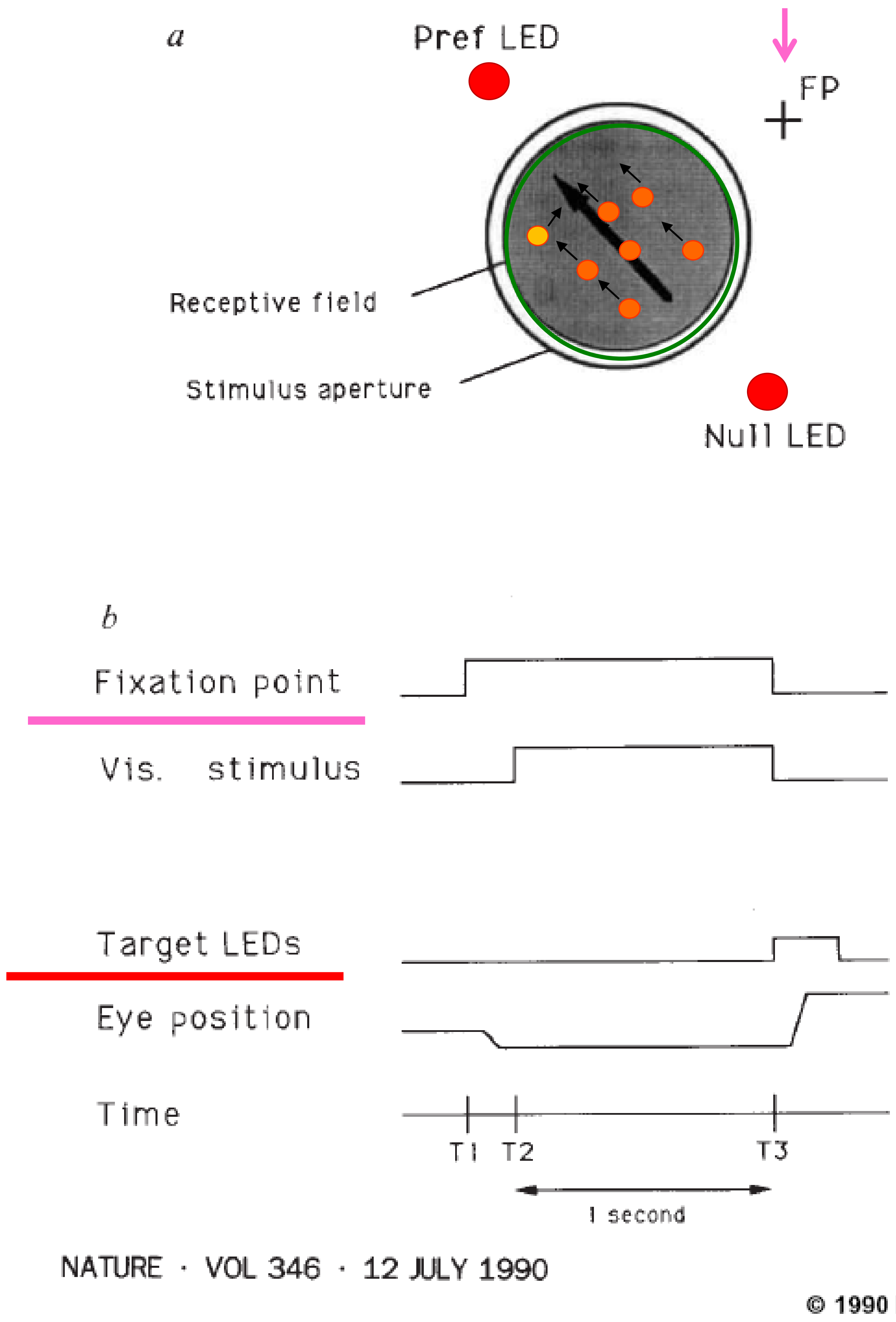
9.2. Detour: receptive fields in V5/MT



Receptive Fields depend
on direction of motion: β = preferred direction = P

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

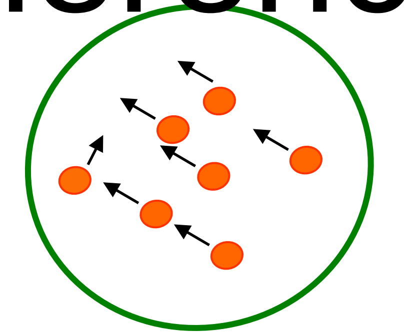
9.2. Experiment of Salzman et al. 1990



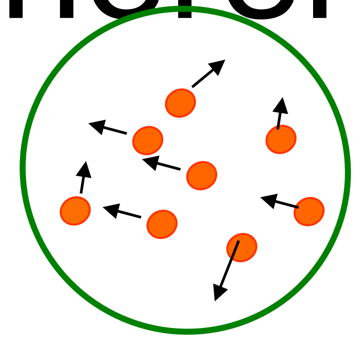
monkey indicates
decision by
eye movement

Eye movement

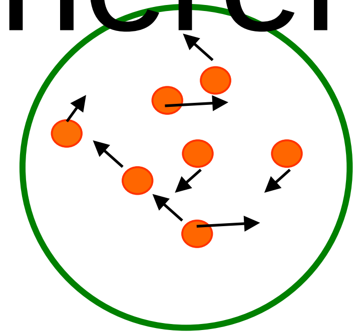
coherence 0.8=80%



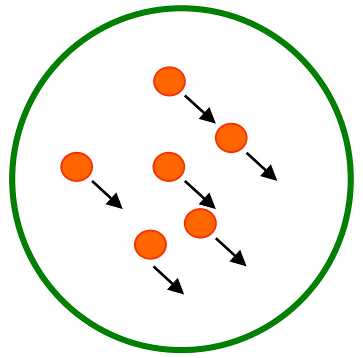
coherence 0.5 = 50%



coherence 0.0



coherence -1.0

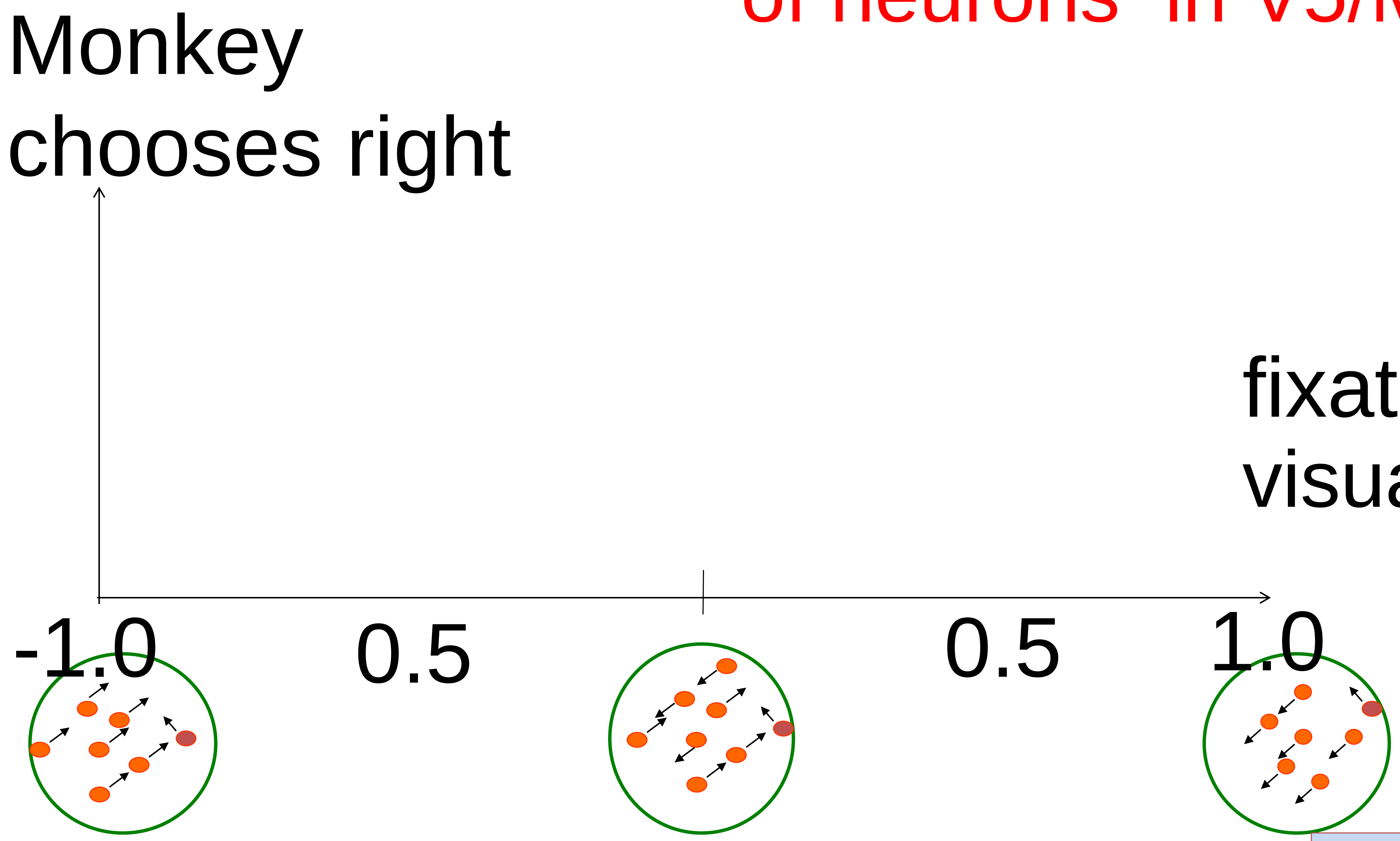


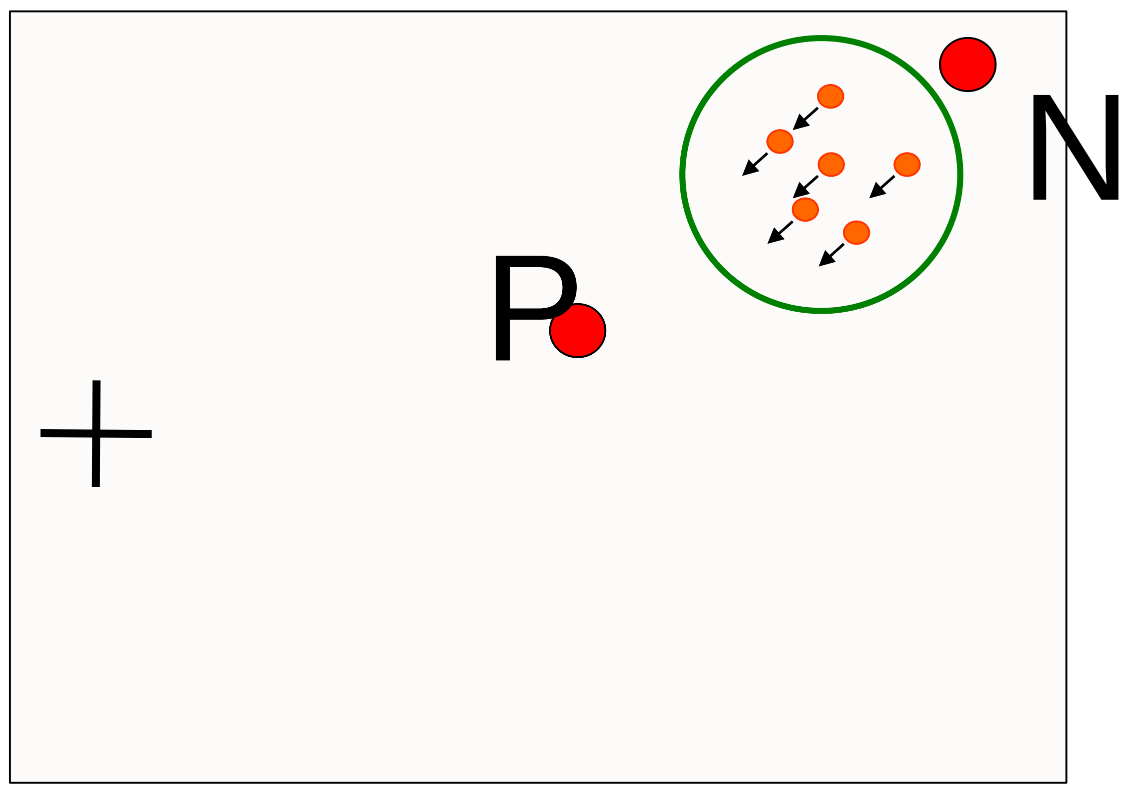
opposite
direction

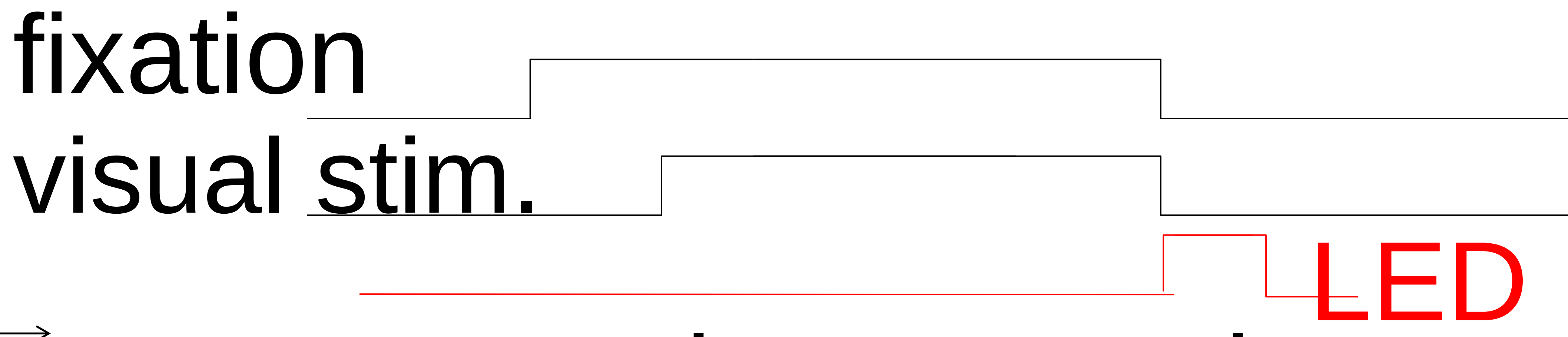
Image: Salzman, Britten, Newsome, 1990

9. 2: Experiment of Salzman et al. 1990

Monkey behavior w. or w/o Stimulation of neurons in V5/MT







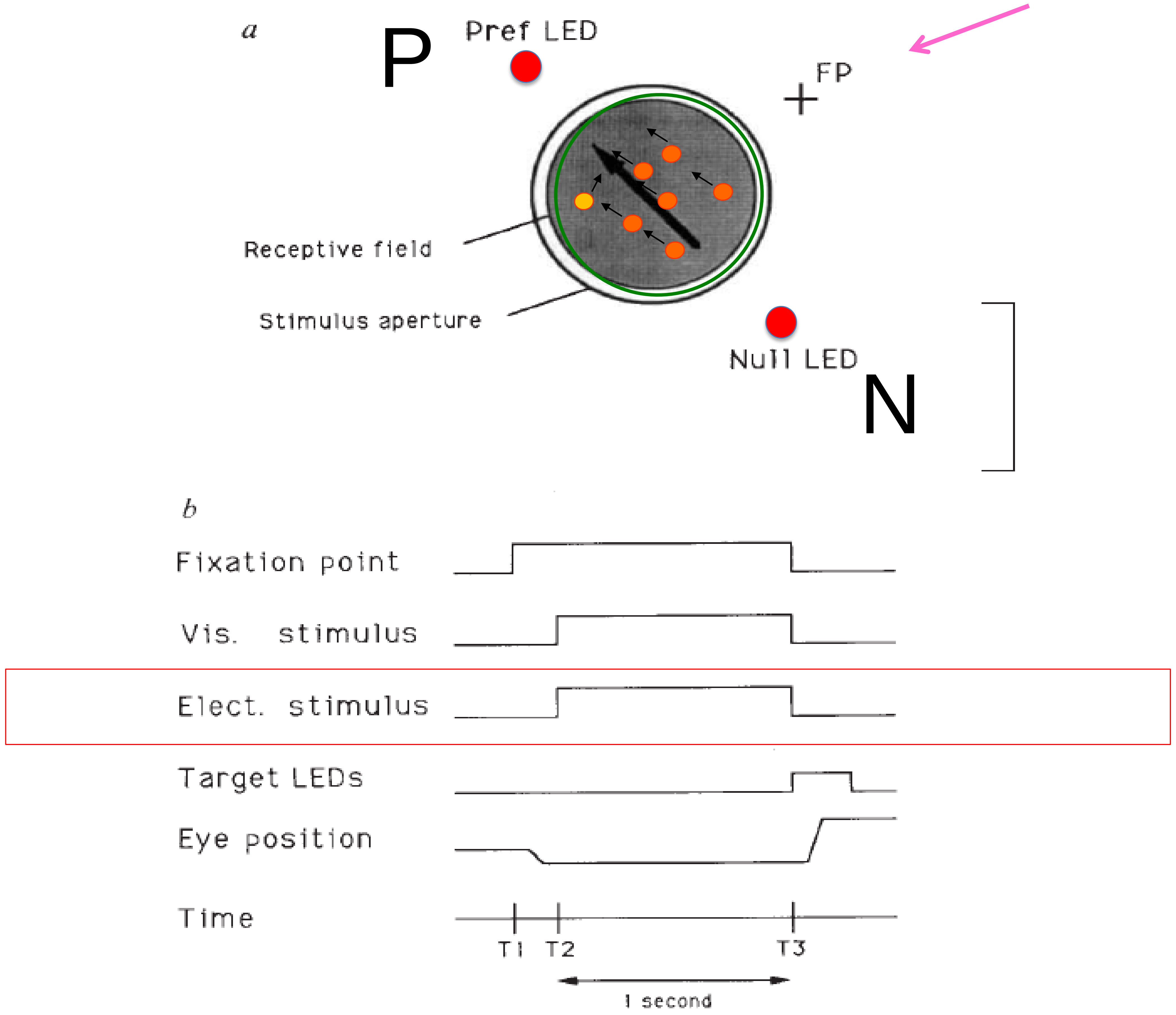
X = coherent motion to bottom right

No bias, each point moves in random direction

Salzman, Britten, Newsome, 1990

Blackboard:
Motion detection/stimulation

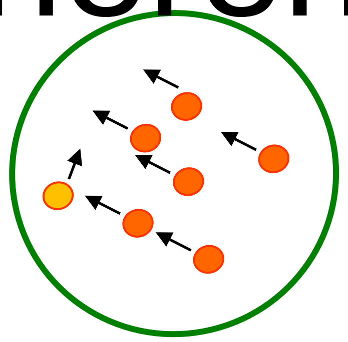
9.2: Experiment of Salzman et al. 1990



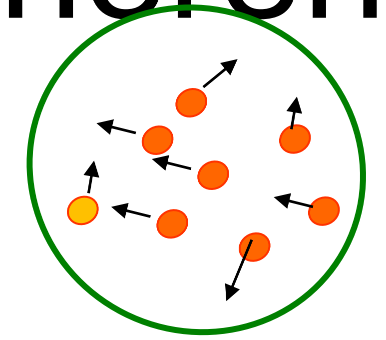
NATURE · VOL 346 · 12 JULY 1990

excites this group of neurons

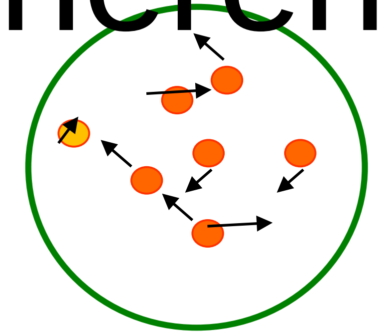
coherence 0.8=80%



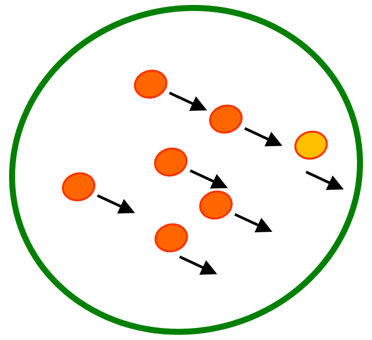
coherence 0.5 = 50%



coherence 0.0



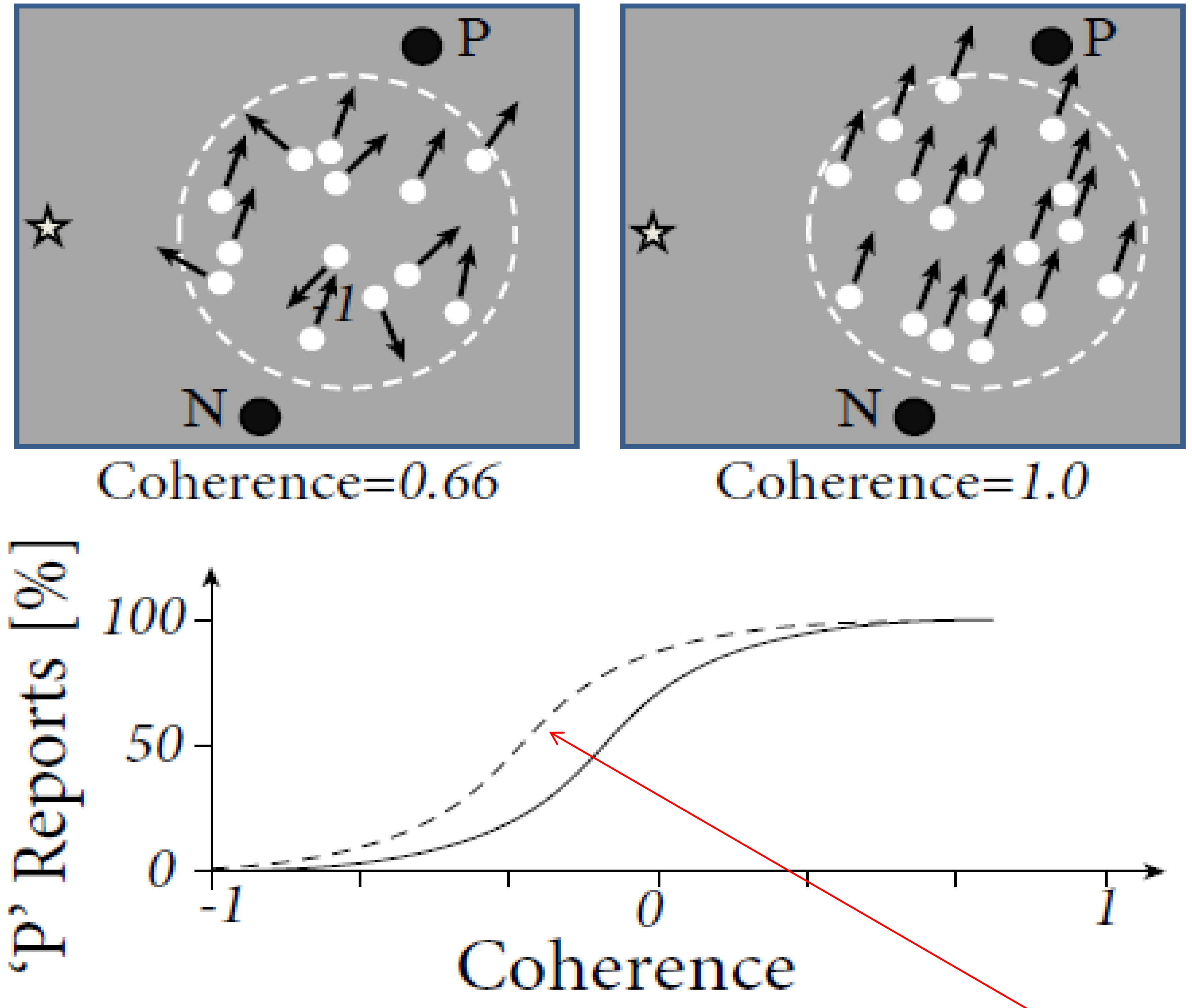
coherence -1.0



9. 2. Experiment of Salzman et al. 1990

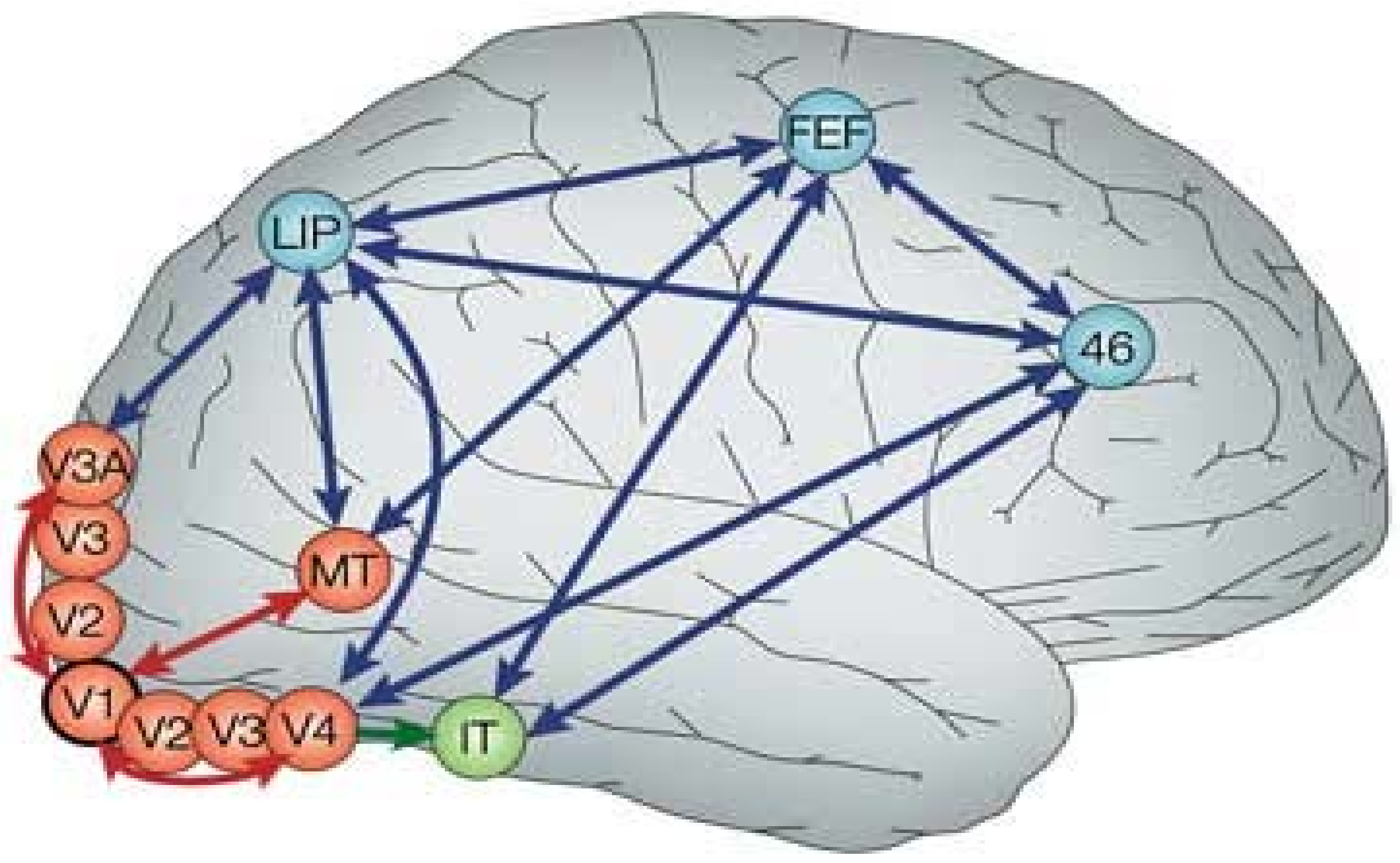
Behavior: psychophysics

Image:
Gerstner et al. (2014), Neuronal Dynamics; Redrawn after Salzman et al, 1990



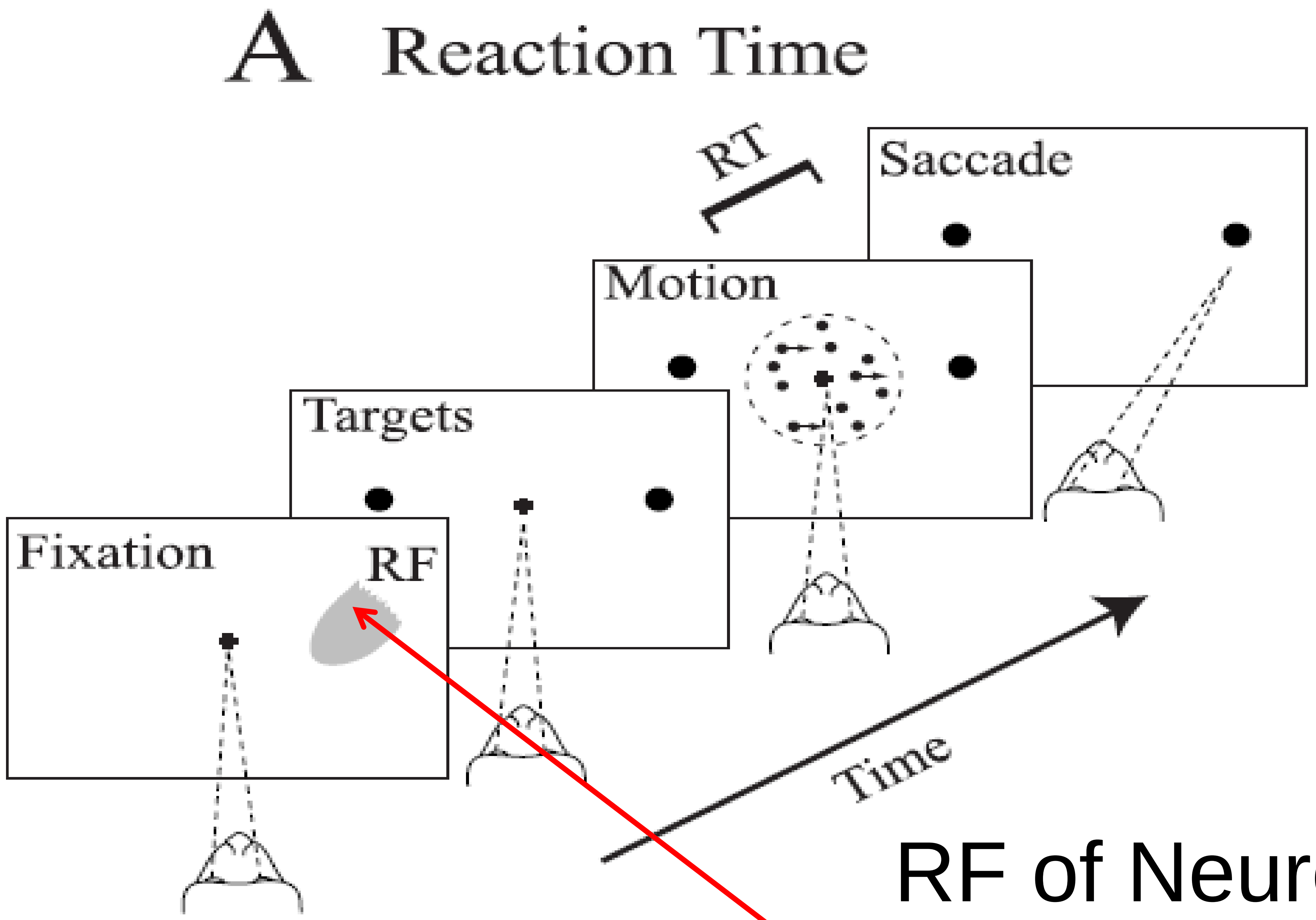
With stimulation

9.2. Perceptual Decision Making

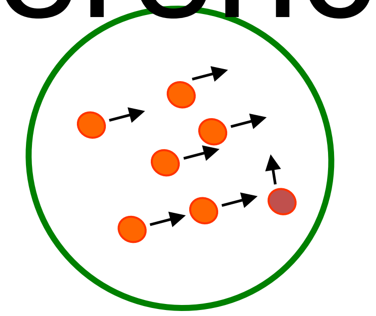


Nature Reviews | Neuroscience

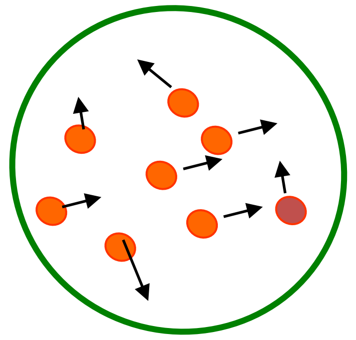
9.2. Experiment of Roitman and Shadlen in LIP (2002)



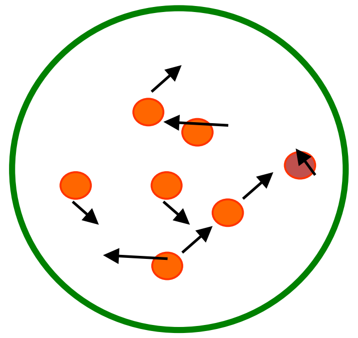
coherence 85%



coherence 50%



coherence 0%



RF of Neuron in LIP:
-selective to target of saccade
- response increases faster if signal is stronger
- activity is noisy

LIP is somewhere between MT (movement detection) and Frontal Eye Field (saccade control)

Roitman and Shadlen 2002

9.2: Experiment of Roitman and Shadlen in LIP (2002)

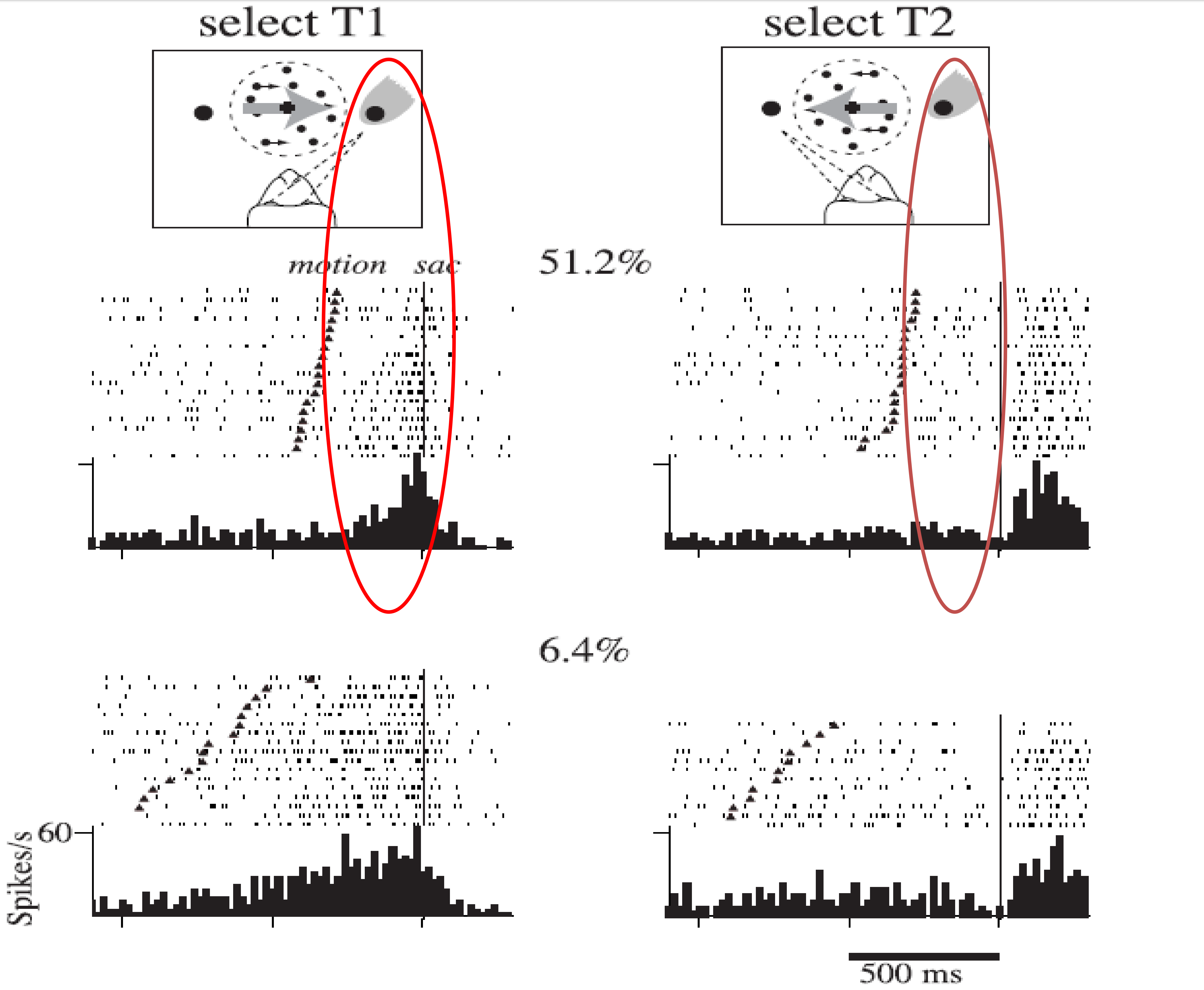


Figure 4. Response of an LIP neuron during the RT-direction-

Neurons in LIP:
- -selective to target of saccade
- -increases faster if signal is stronger
- - activity is noisy

LIP is somewhere between MT (movement detection) and Frontal Eye Field (saccade control)

2. Experiment of Roitman and Shadlen in LIP (2002)

Neurons in LIP:

- Selective to target of saccade
- Activity increases faster if signal is stronger
- Activity is noisy
- Located in the signal processing stream between sensory areas and saccade control
- I do not claim that these neurons ‘take the decision’
- Interesting correlations with decision outcome

Quiz 1, now

Receptive field in LIP

[ ] related to the target of a saccade

[ ] depends on movement of random dots

Biological Modeling of Neural Networks:

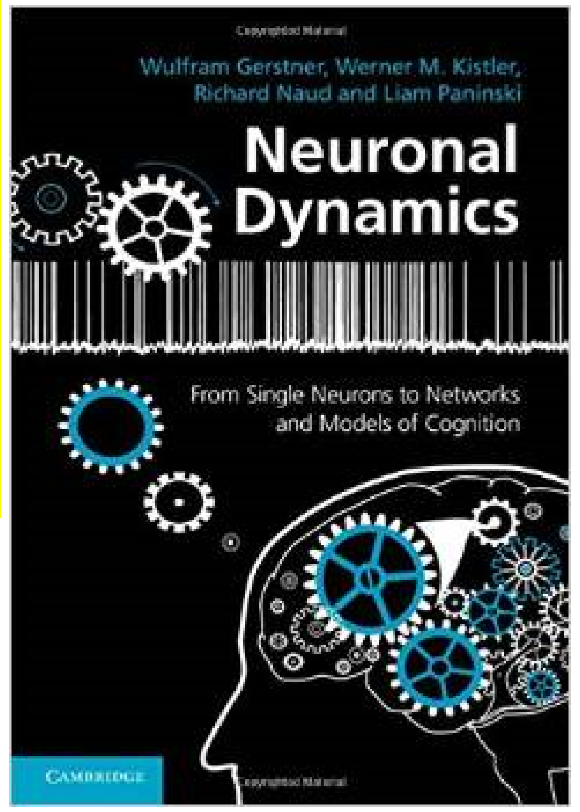
ÉCOLE POLYTECHNIQUE
FÉDÉRALE DE LAUSANNE

Week 9 – Decision models: Competitive dynamics

Wulfram Gerstner

EPFL, Lausanne, Switzerland

Reading for week 9:
NEURONAL DYNAMICS
Ch. 16 (except 16.4.2)



Cambridge Univ. Press

9.1 Introduction
- decision making

9.2 Perceptual decision making
- V5/MT
- Decision dynamics: Area LIP

9.3 Theory of decision dynamics
- competition via shared inhibition
- effective 2-dim model

9.4. Solutions
- symmetric case
- biased case

9.5. Simulations and Experiments
- simulations and theory
- simulations and experiments

9.6. Decisions, actions, volition
- the problem of free will

9.3. Theory of decision dynamics

$$A_n(t) = F(h_n(t))$$

activity equations

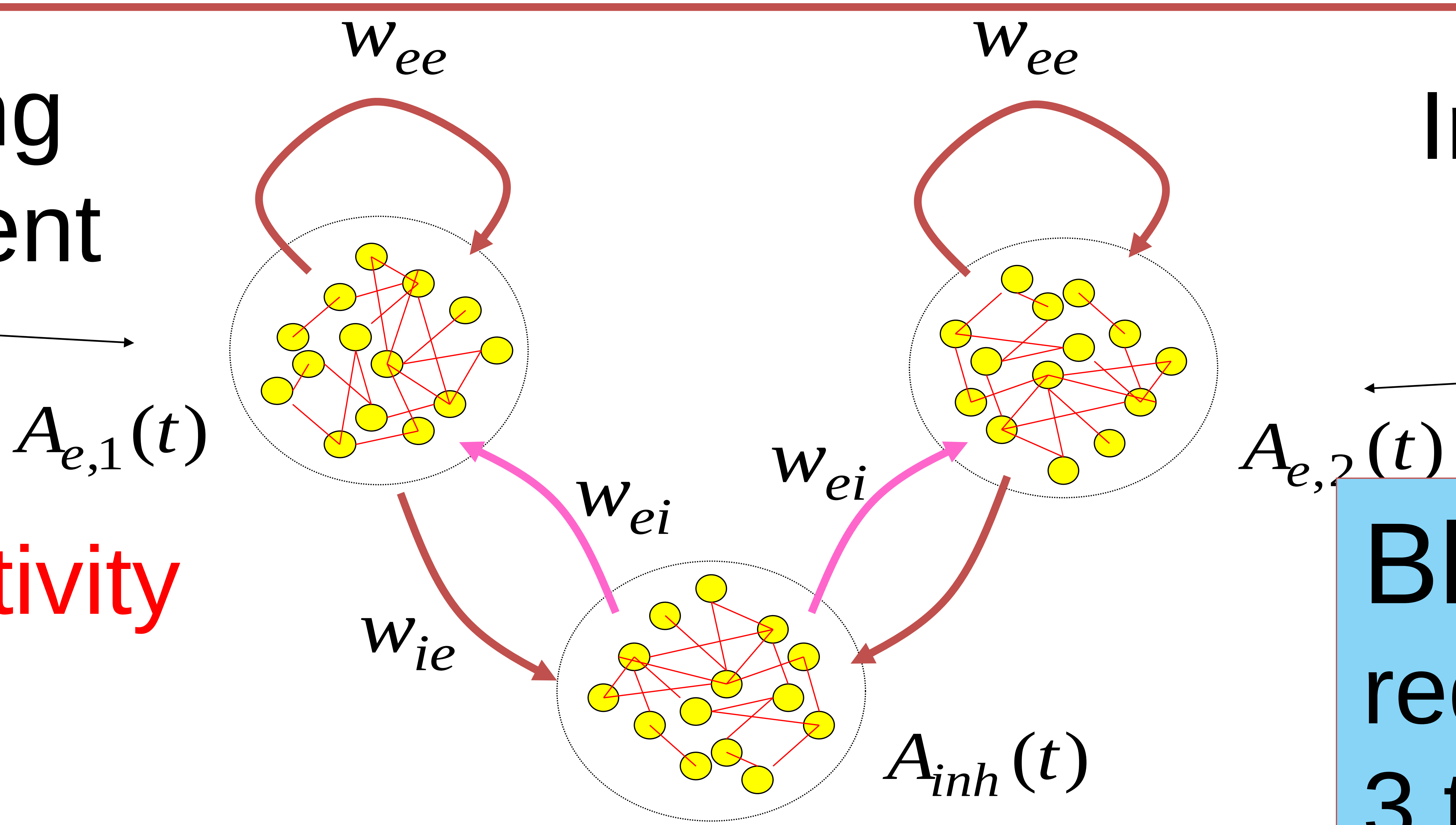
Membrane potential caused by input

$$\tau \frac{d}{dt} h_1(t) = -h_1(t) + R\, I_1^{ext}(t) + w_{ee}\, F(h_1(t)) + w_{ei}\, F(h_{inh}(t))$$

$$\tau \frac{d}{dt} h_2(t) = -h_2(t) + R\, I_2^{ext}(t) + w_{ee}\, F(h_2(t)) + w_{ei}\, F(h_{inh}(t))$$

Input indicating left movement

Input indicating right moveme



population activity

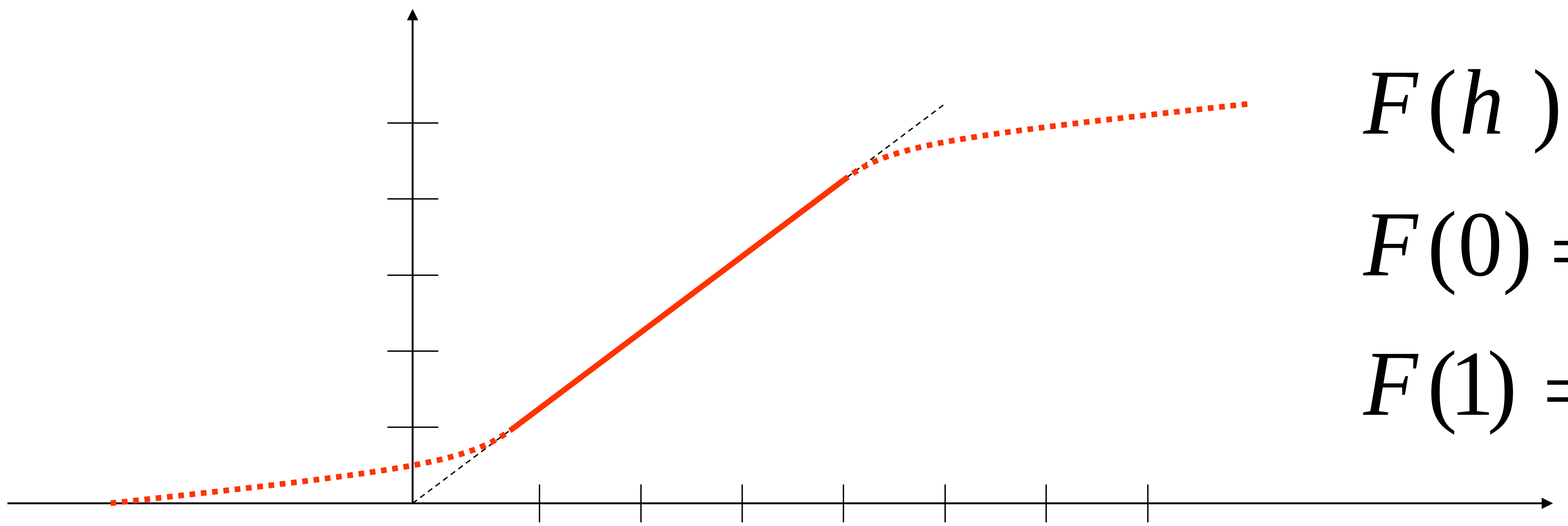
Blackboard:
reduction from
3 to 2 equations

9.3. Theory of decision dynamics

Population activity

activity equations

$$A_n(t) = F(h_n(t))$$



$$F(h) = h \quad for \quad 0.2 < h < 0.8$$

$$F(0) = 0.1$$

$$F(1) = 0.9$$

Blackboard:
Linearized inhibition

Inhibitory Population

$$A_{inh}(t) = F(h_{inh}(t)) = h_{inh}(t) = w_{ie}(A_{e,1}(t) + A_{e,2}(t))$$

9.3. Effective 2-dim. model

$$A_n(t) = F(h_n(t))$$

activity equations

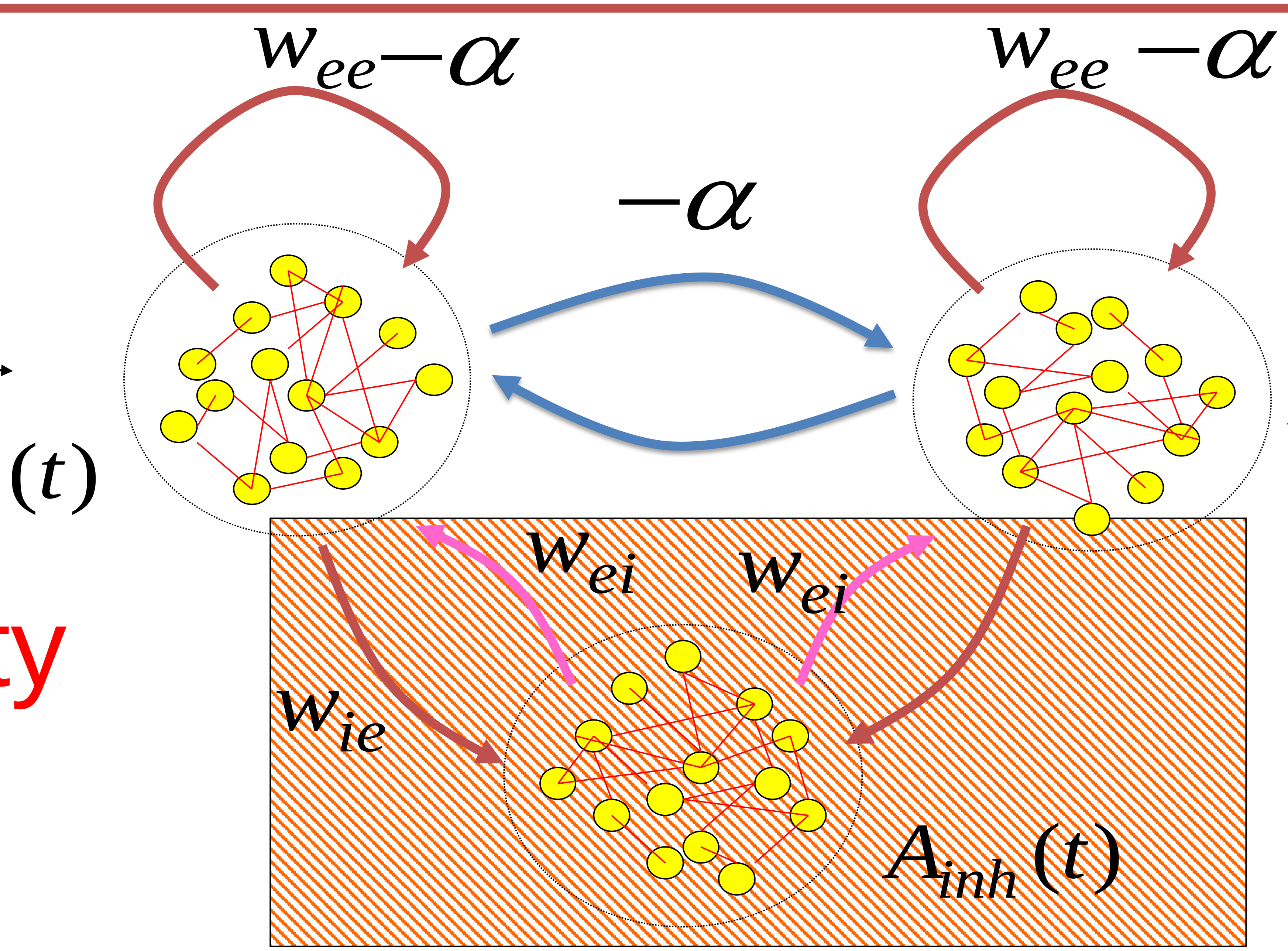
Membrane potential caused by input

$$\boxed{\tau \frac{d}{dt} h_1(t) = -h_1(t) + h_1^{ext}(t) + (w_{ee} - \alpha) F(h_1(t)) - \alpha F(h_2(t))}$$

$$\boxed{\tau \frac{d}{dt} h_2(t) = -h_2(t) + h_2^{ext}(t) + (w_{ee} - \alpha) F(h_2(t)) - \alpha F(h_1(t))}$$

Input indicating left movement

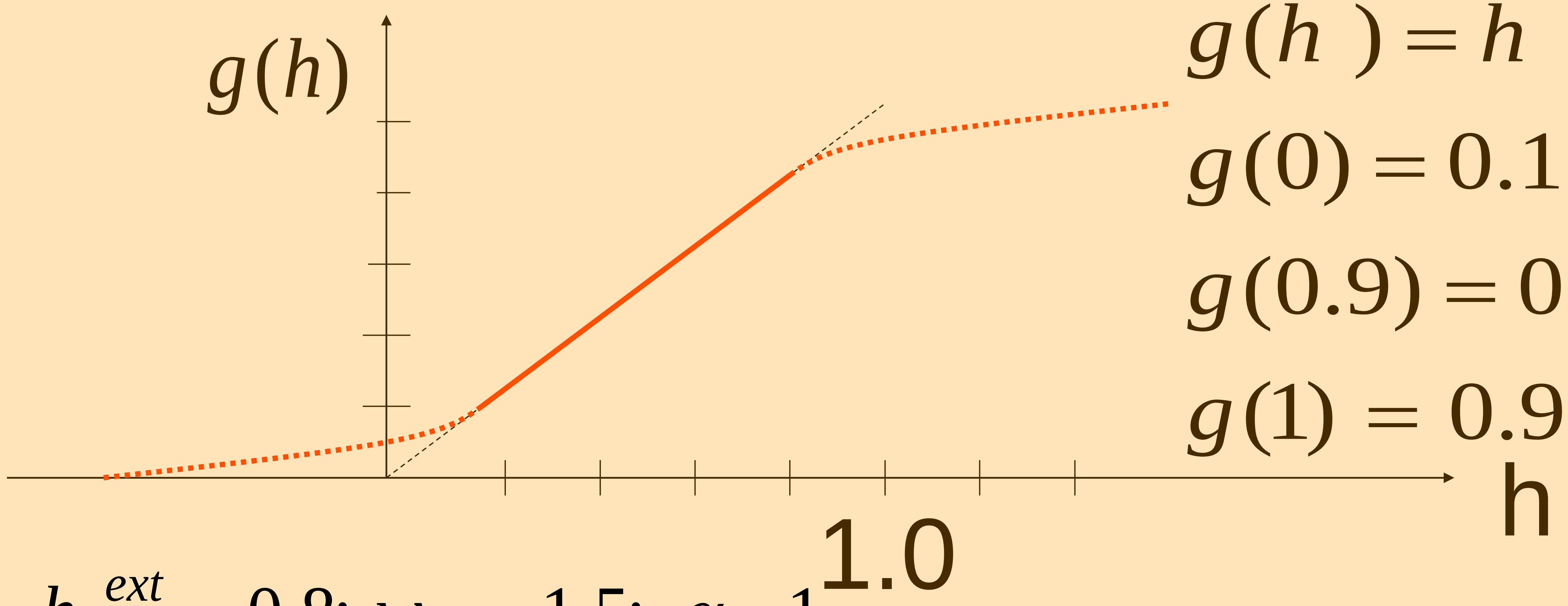
Input indicating right movement



population activity

Exercise 1 now: draw nullclines and flow arrows

$$\tau \frac{d}{dt} h_1(t) = -h_1(t) + h_1^{ext}(t) + (w_{ee} - \alpha) g(h_1(t)) - \alpha\, g(h_2(t))$$



$$g(h\ ) = h \quad for \quad 0.2 < h < 0.8$$

$$g(0) = 0.1$$

$$g(0.9) = 0.85$$

$$g(1) = 0.9$$

$$h_1^{ext} = h_2^{ext} = 0.8;\ w_{ee} = 1.5;\ \alpha = 1$$

$\boxed{\frac{d}{dt} h_1 = 0}$

h_1	$g(h_2)$	h_2
1.0		
0.8		
0.2		
0.0		

$\boxed{\frac{d}{dt} h_2 = 0}$

h_2	$g(h_1)$	h_1
1.0		
0.8		
0.2		
0.0		

Next Lecture at 10:45

Biological Modeling of Neural Networks:

ÉCOLE POLYTECHNIQUE FÉDÉRALE DE LAUSANNE

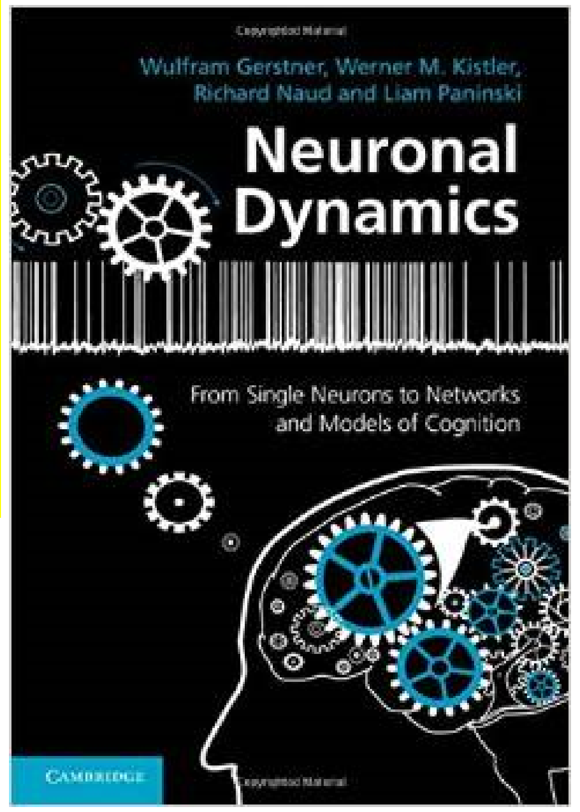
Week 9 – Decision models: Competitive dynamics

Wulfram Gerstner

EPFL, Lausanne, Switzerland

Reading for week 9:
NEURONAL DYNAMICS
Ch. 16 (except 16.4.2)

Cambridge Univ. Press



9.1 Introduction
- decision making

9.2 Perceptual decision making
- V5/MT
- Decision dynamics: Area LIP

9.3 Theory of decision dynamics
- competition via shared inhibition
- effective 2-dim model

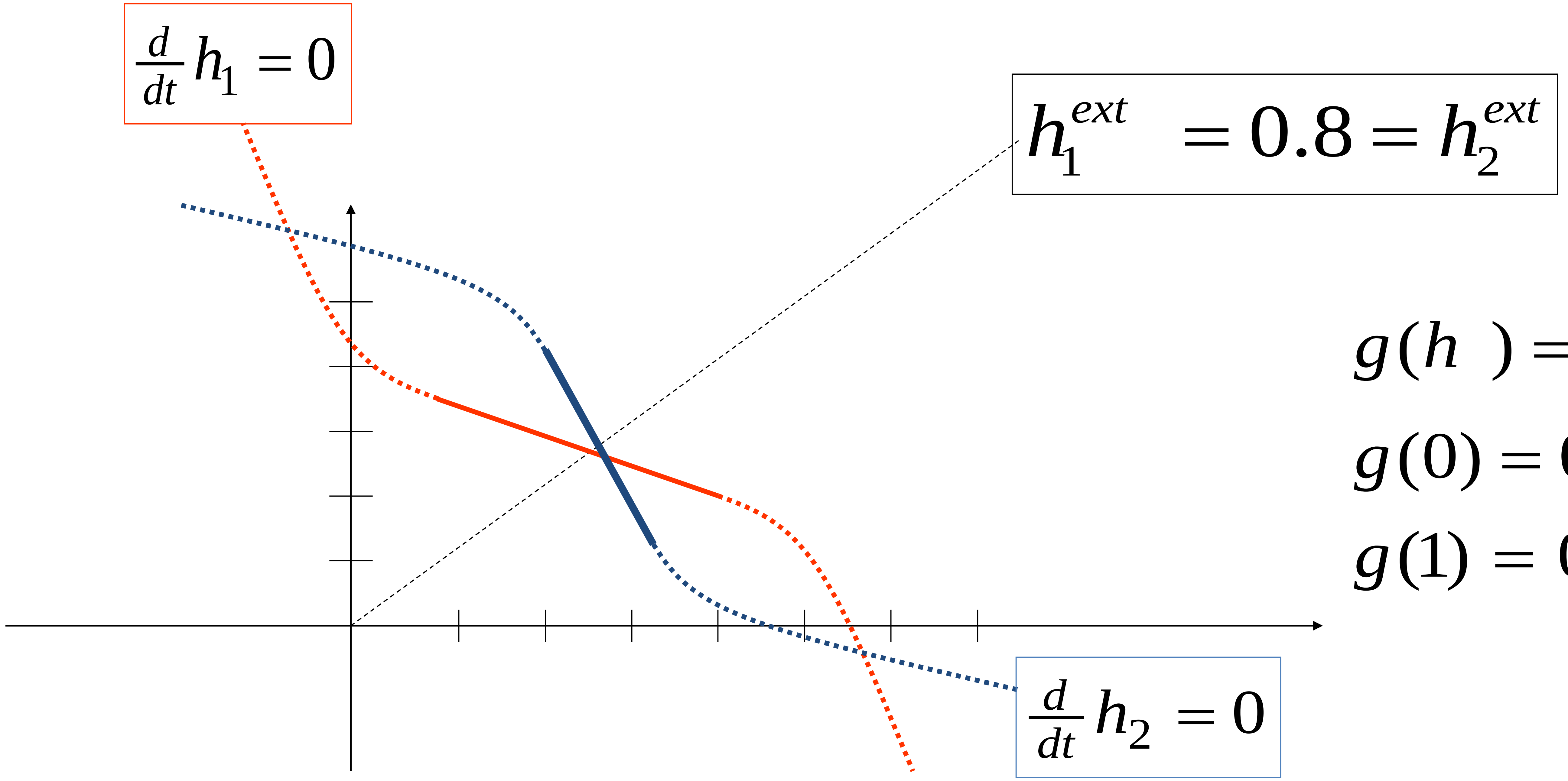
9.4. Solutions
- symmetric case
- biased case

9.5. Simulations and Experiments
- simulations and theory
- simulations and experiments

9.6. Decisions, actions, volition
- the problem of free will

9.4. Theory of decision dynamics

Phase plane, strong external input



$$g(h) = h \quad for \quad 0.2 < h < 0.8$$

$$g(0) = 0.1$$

$$g(1) = 0.9$$

Quiz 2, take 5 minutes now

Continue with Exercise 1, but change the external inputs.

A Keep the input to population 1,
 but reduce the input to population 2 from 0.8 to 0.2

[ ] The nullcline for dh_2/dt shifts vertically downward

[ ] The nullcline for dh_2/dt shifts horizontally leftward

[ ] The nullcline for dh_1/dt shifts vertically downward

[ ] The number of fixed points changes

B In addition, you now also reduce the input to population 1,
 0.8 to 0.2

[ ] The nullcline for dh_2/dt shifts vertically downward

[ ] The nullcline for dh_2/dt shifts horizontally leftward

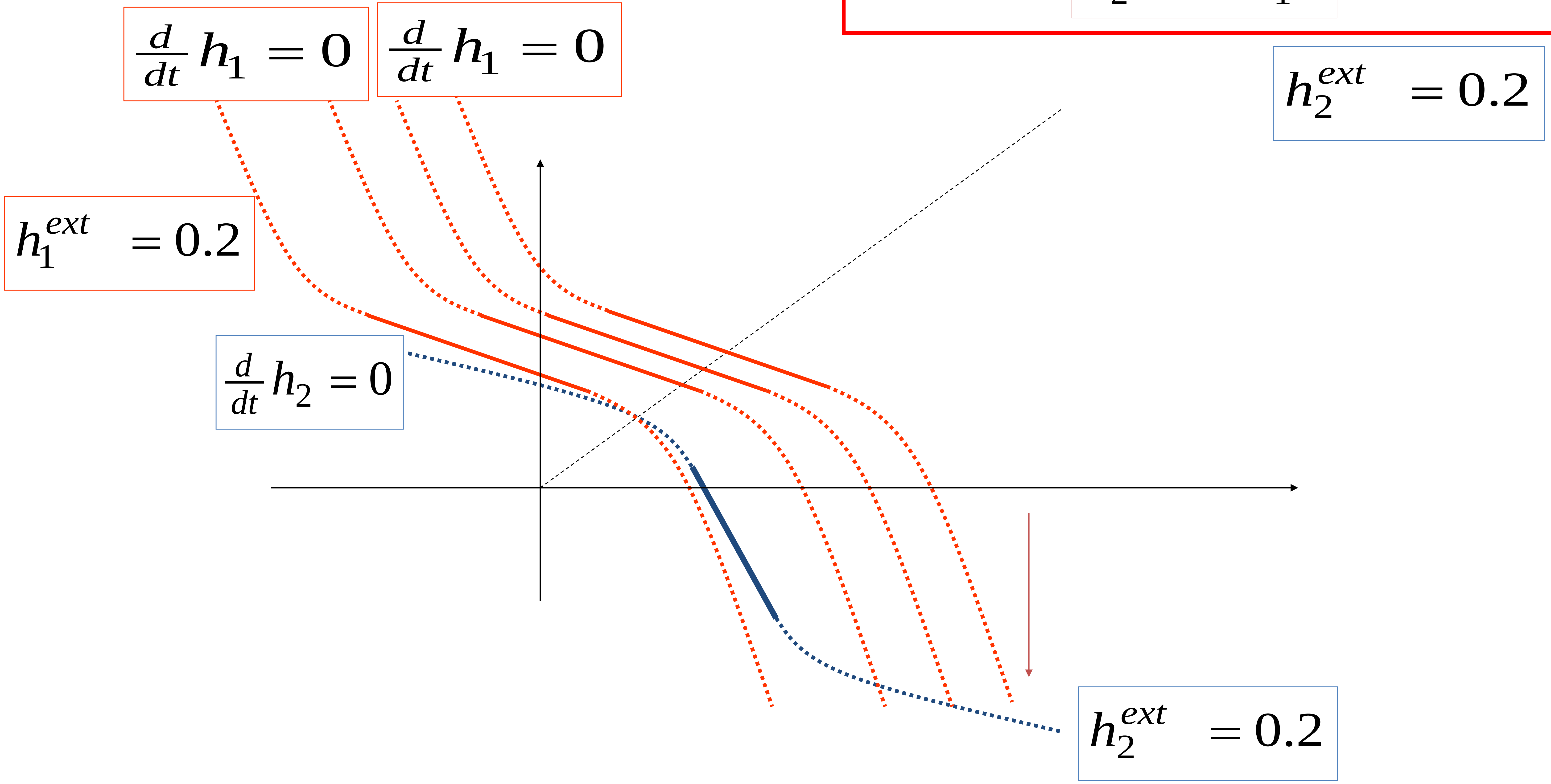
[ ] The nullcline for dh_1/dt shifts vertically downward

9.4. Theory of decision dynamics: biased input

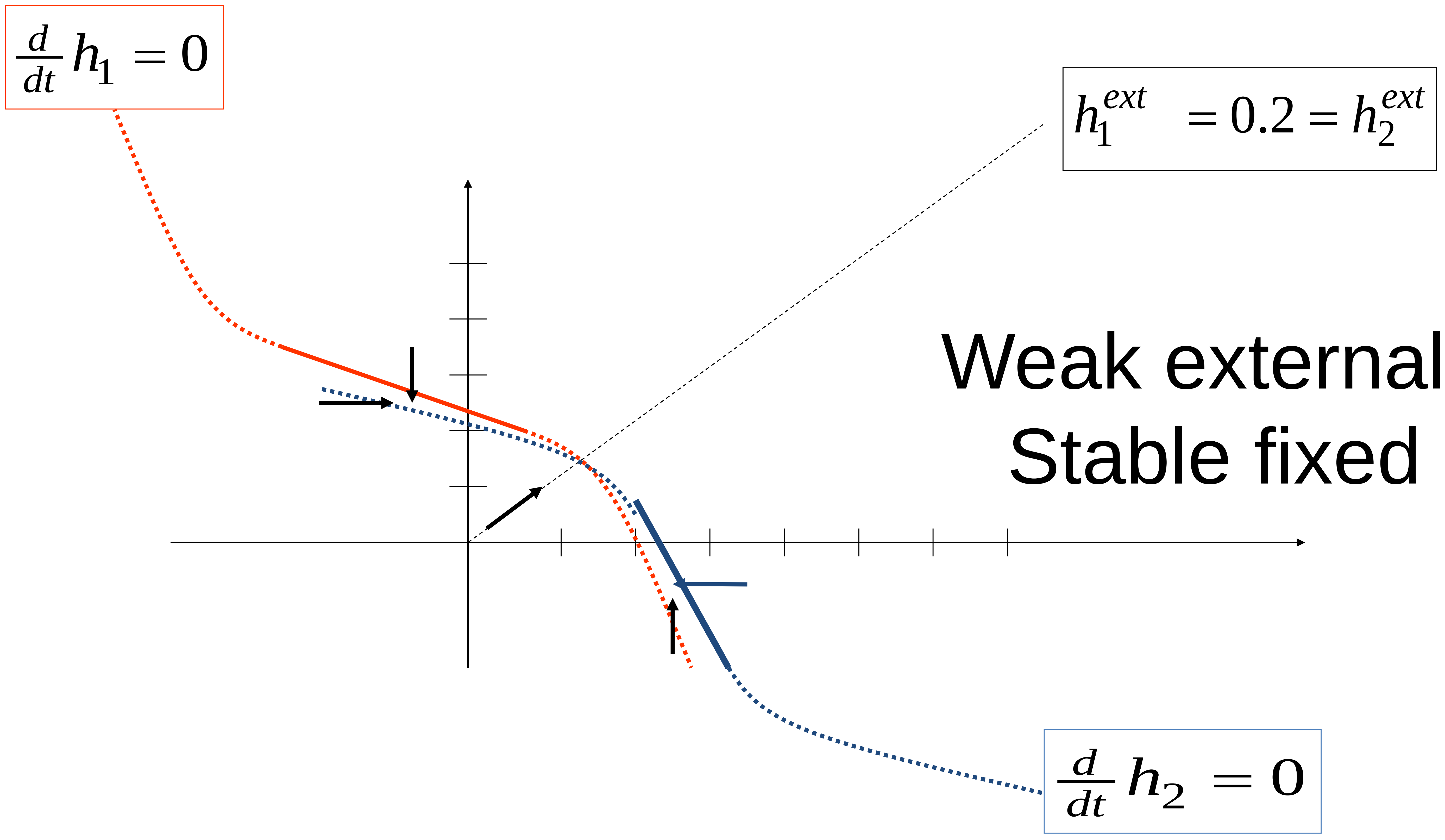
Population activity

Phase plane – biased input:

$h_2^{ext} < h_1^{ext}$



Phase plane – symmetric but small input



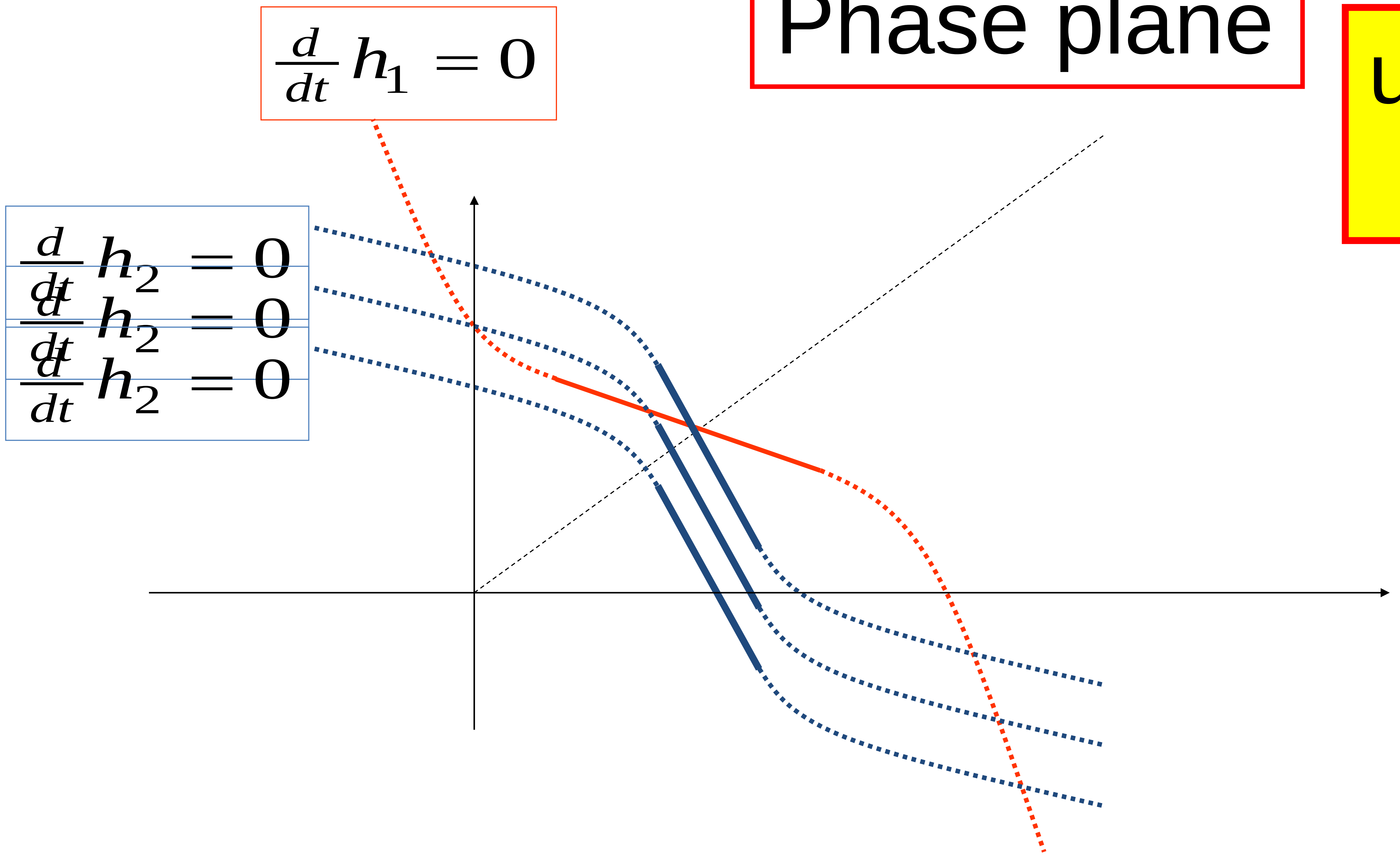
Weak external input:
Stable fixed point

9.4. decision dynamics: unbiased strong to biased

Symmetric, but strong input

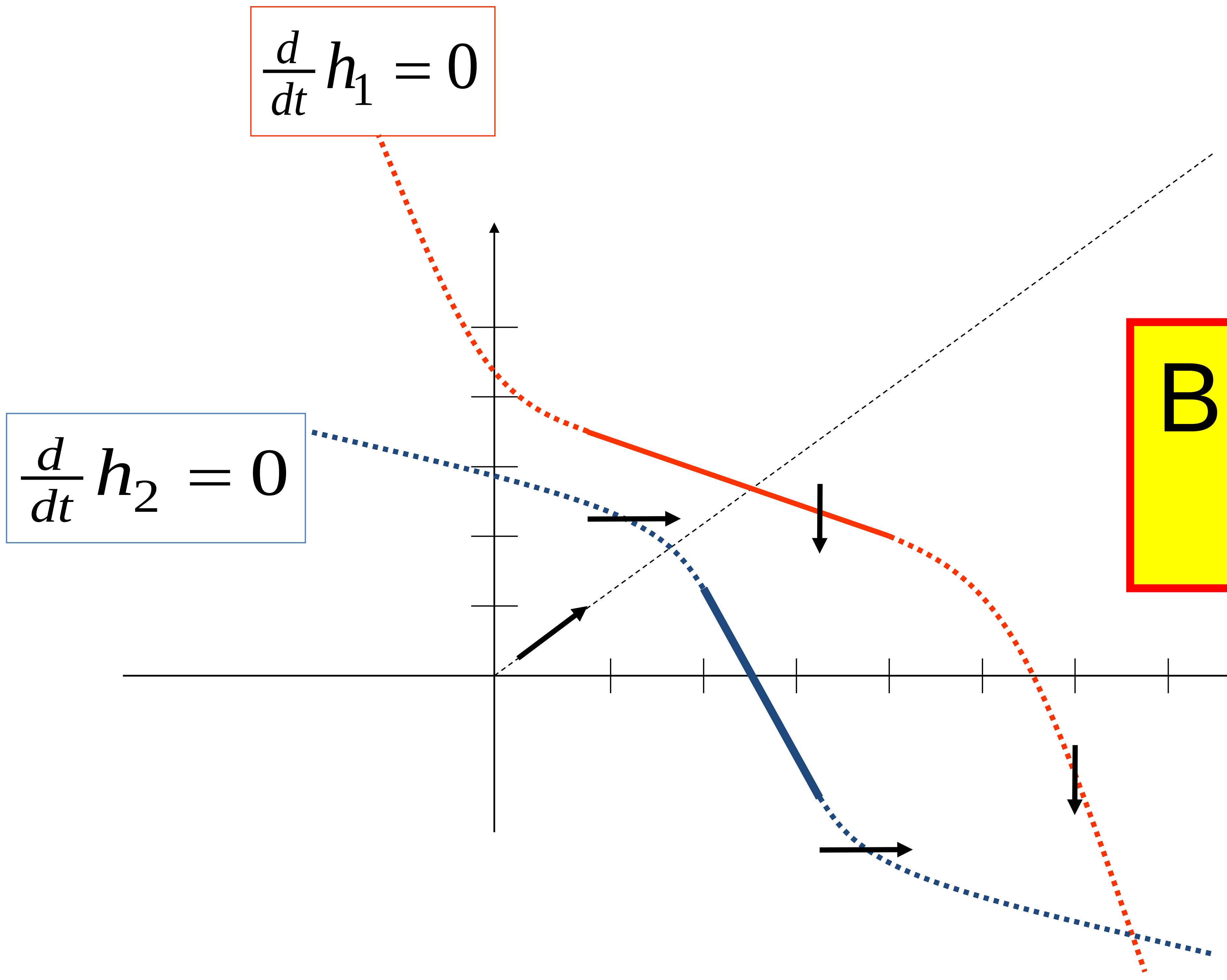
Phase plane

unbiased strong input
= 2 stable fixed points



Phase plane

Population activity



$h_1^{ext} = 0.8;$

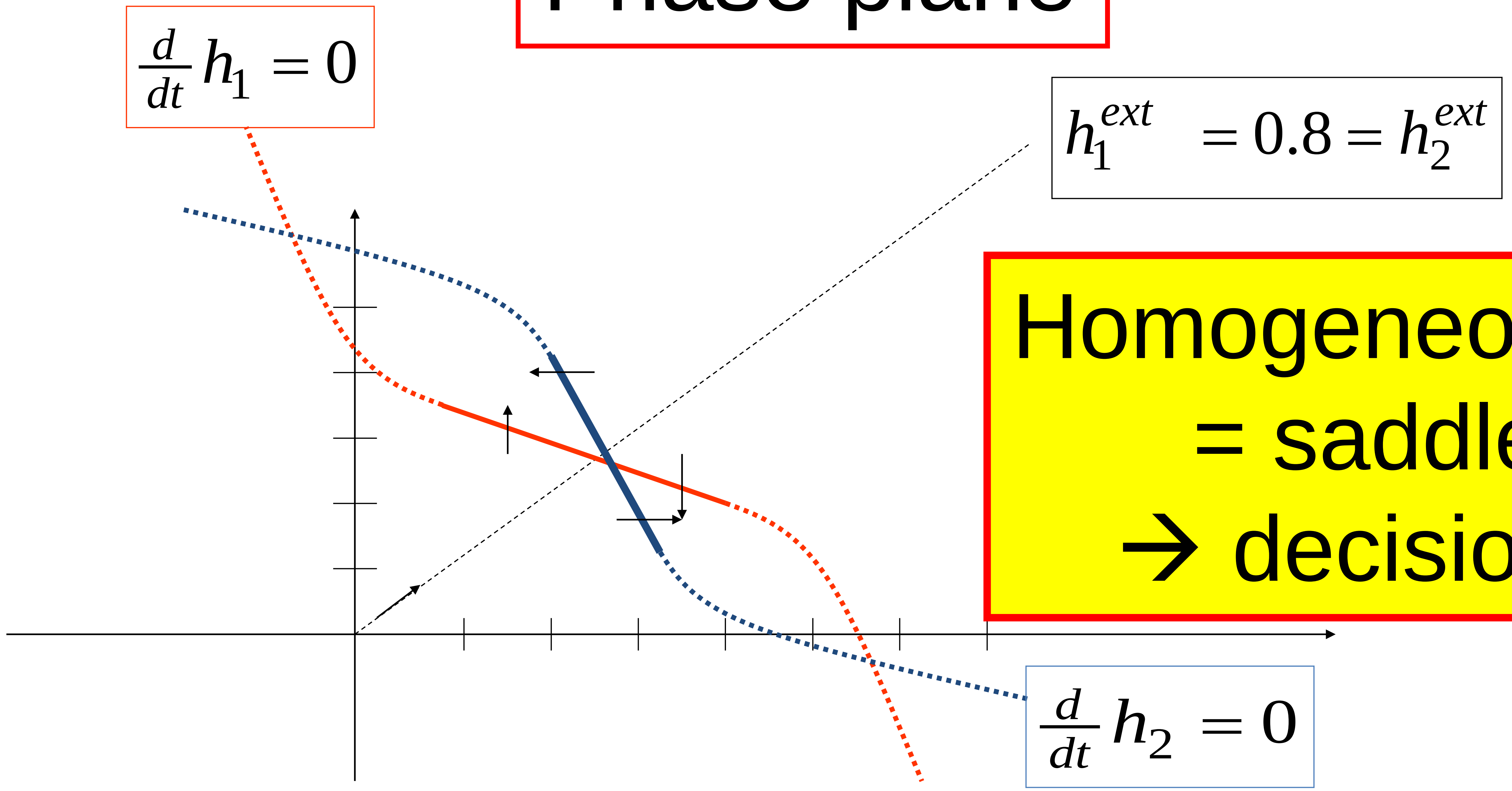
$h_2^{ext} = 0.2$

Biased input = stable fixed point

→ decision reflects bias

9.4. Theory of decision dynamics: unbiased strong

Phase plane



Homogeneous solution
= saddle point
→ decision must be taken

Biological Modeling of Neural Networks:

ÉCOLE POLYTECHNIQUE
FÉDÉRALE DE LAUSANNE

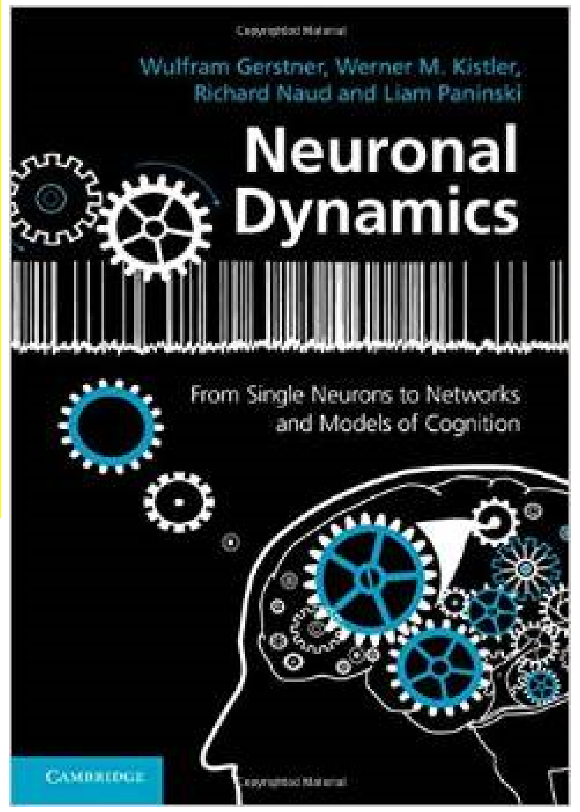
Week 9 – Decision models:

Competitive dynamics

Wulfram Gerstner

EPFL, Lausanne, Switzerland

Reading for week 9:
NEURONAL DYNAMICS
Ch. 16 (except 16.4.2)



Cambridge Univ. Press

9.1 Introduction
- decision making

9.2 Perceptual decision making
- V5/MT
- Decision dynamics: Area LIP

9.3 Theory of decision dynamics
- competition via shared inhibition
- effective 2-dim model

9.4. Solutions
- symmetric case
- biased case

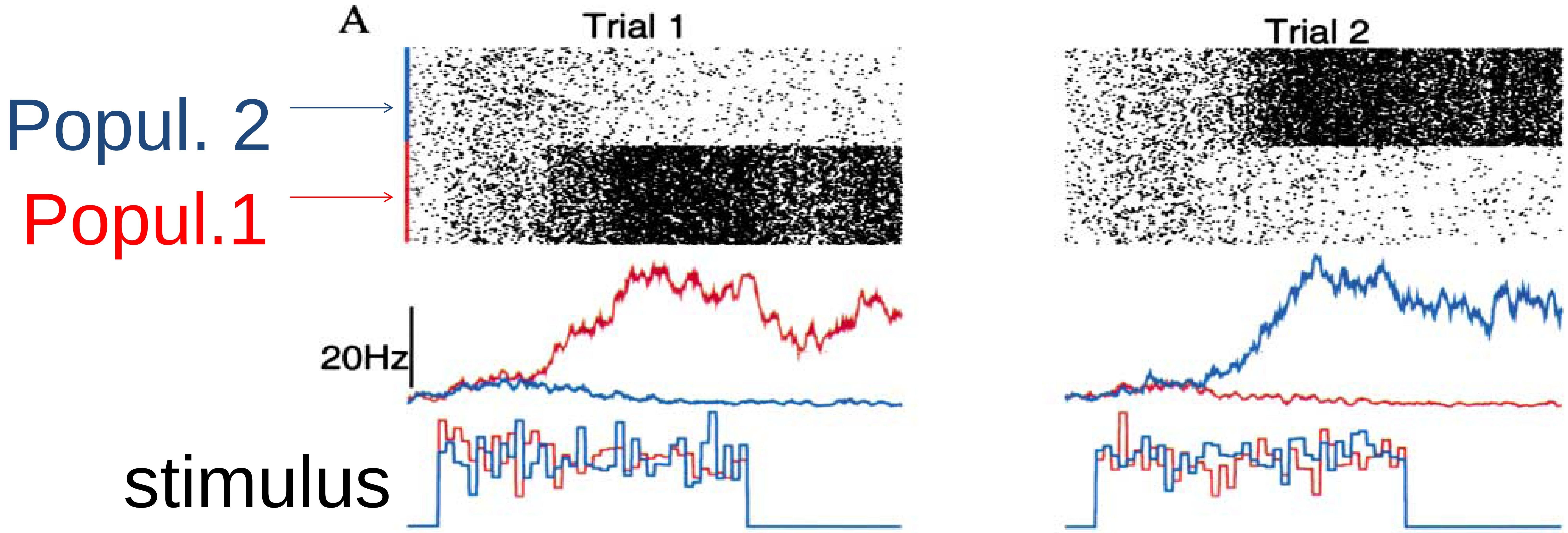
9.5. Simulations and Experiments
- simulations and theory
- simulations and experiments

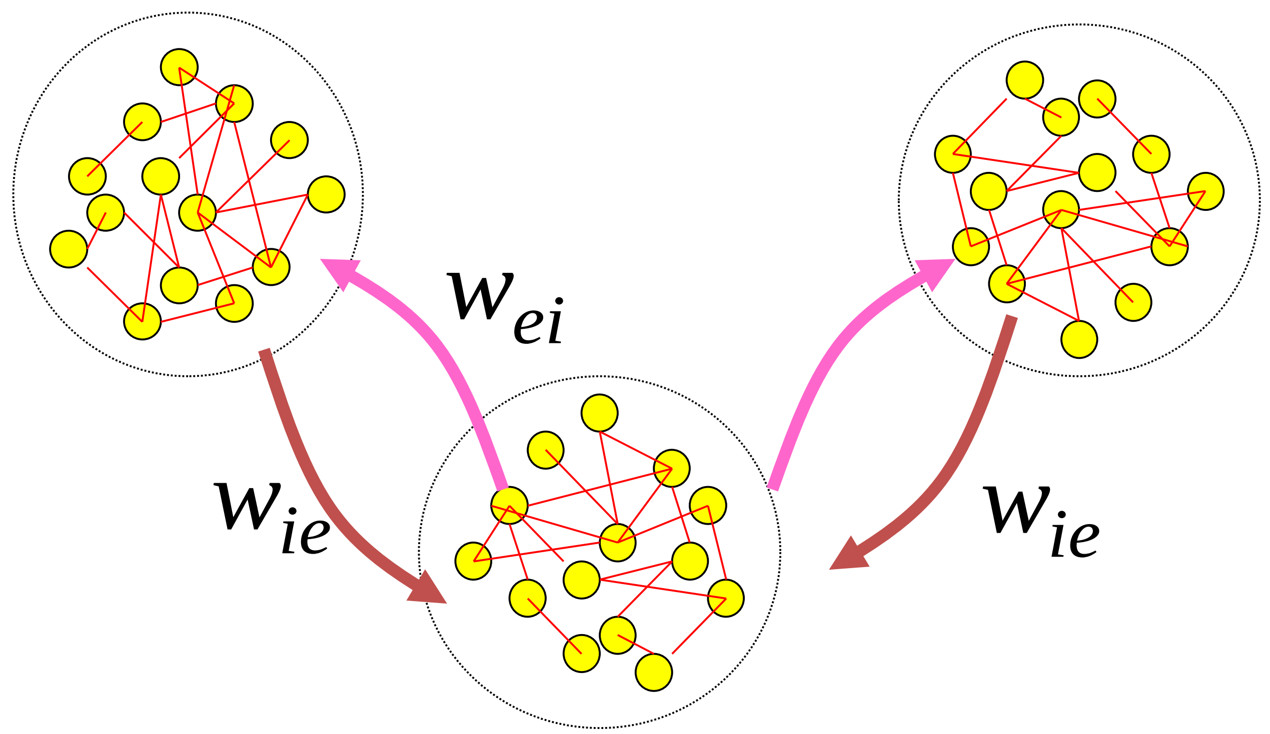
9.6. Decisions, actions, volition
- the problem of free will

9.5. Decisions in populations of neurons: simulation

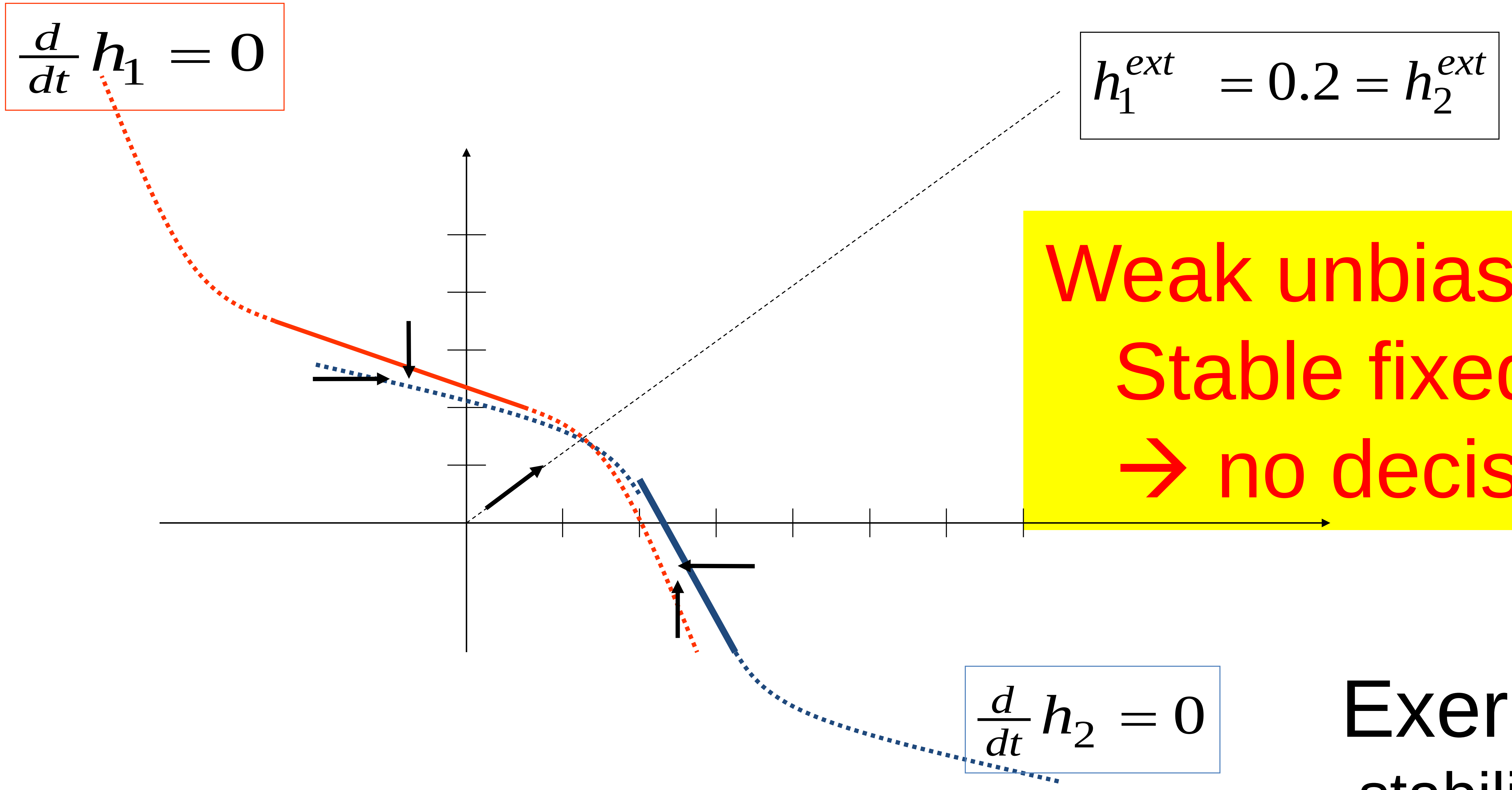
Simulation of 3 populations of spiking neurons, unbiased strong input

X.J. Wang, 2002
NEURON





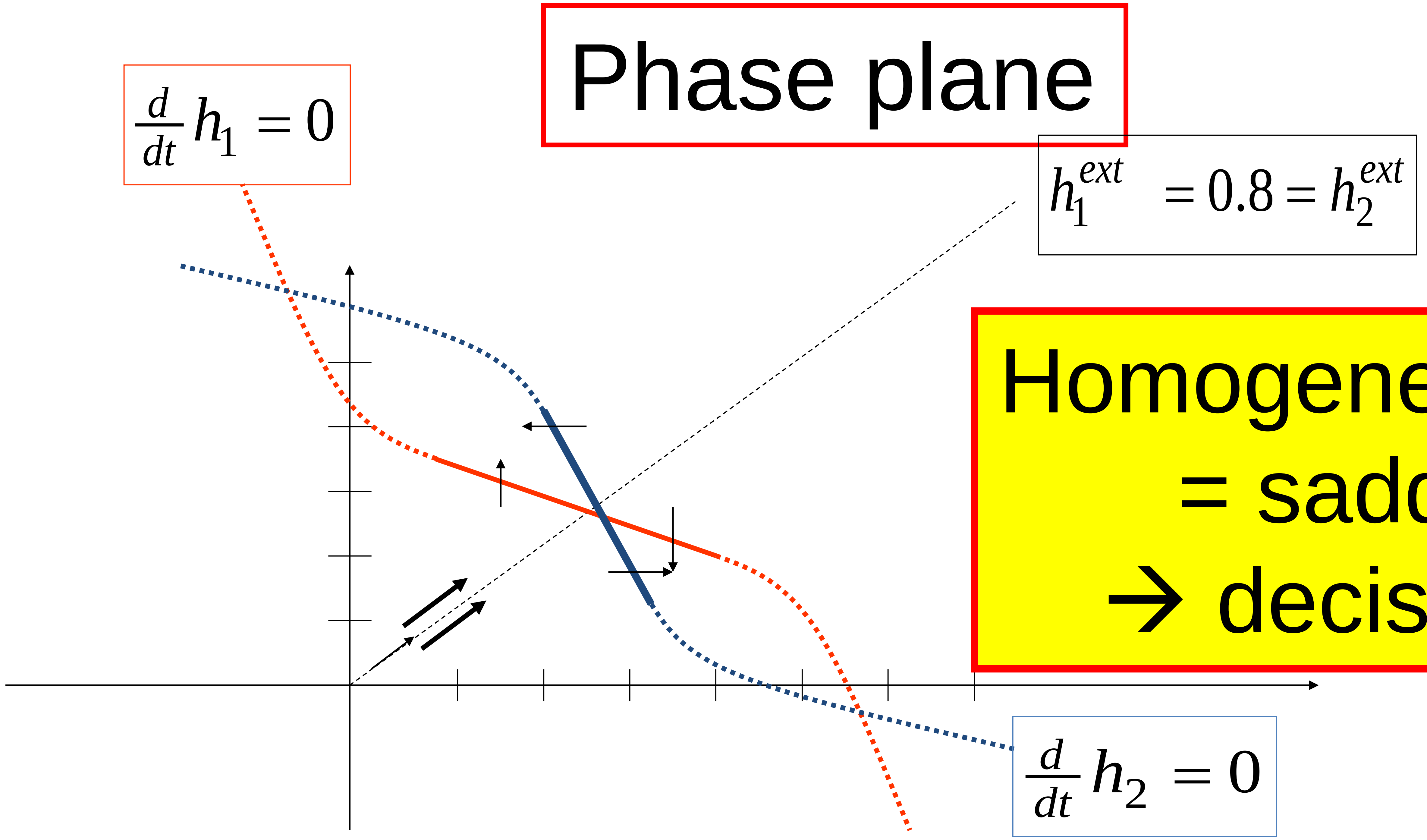
1) Before stimulus is given: symmetric but small input



Weak unbiased input:
Stable fixed point
→ no decision

Exercise 2 at home:
stability of symmetric solution

2) When stimulus is given: symmetric but strong input



Homogeneous solution
= saddle point
→ decision must be taken

9.5: Decisions in populations of neurons: simulation

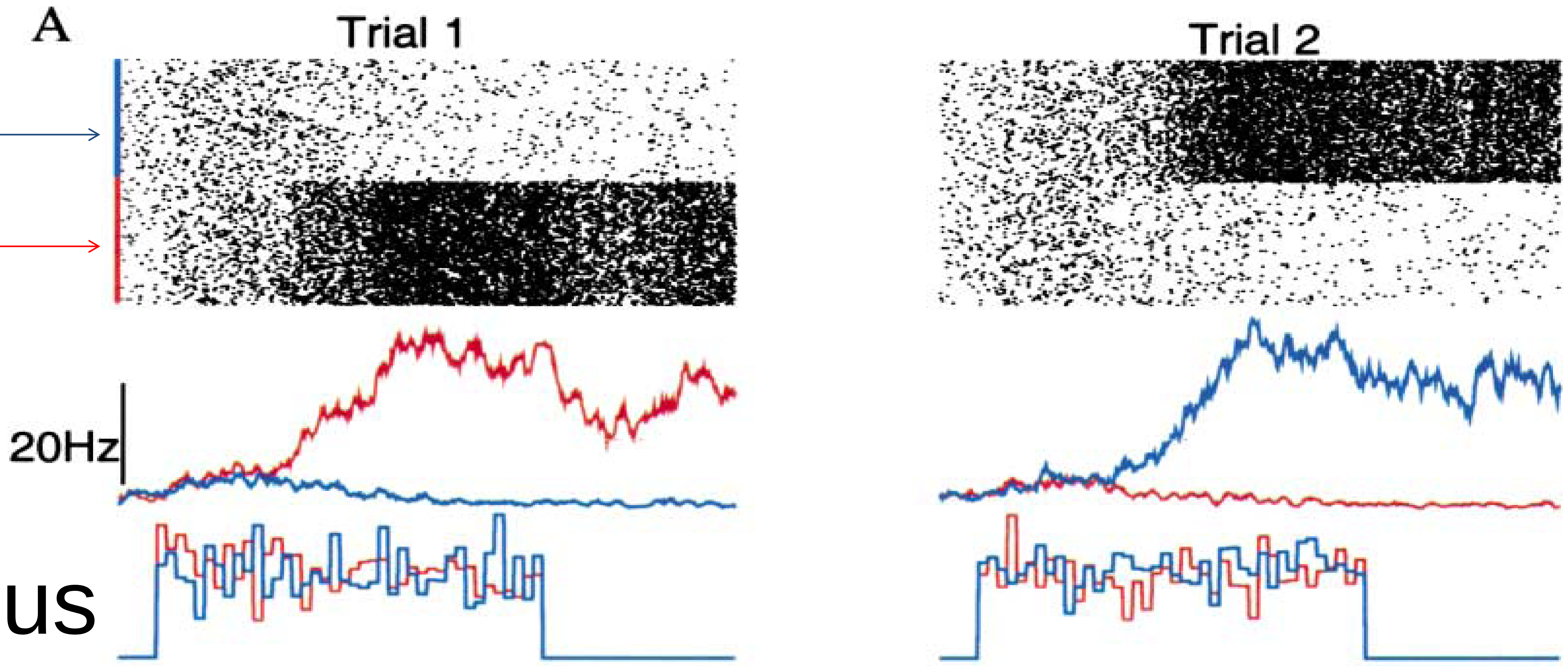
Simulation of 3 populations of spiking neurons, unbiased strong input

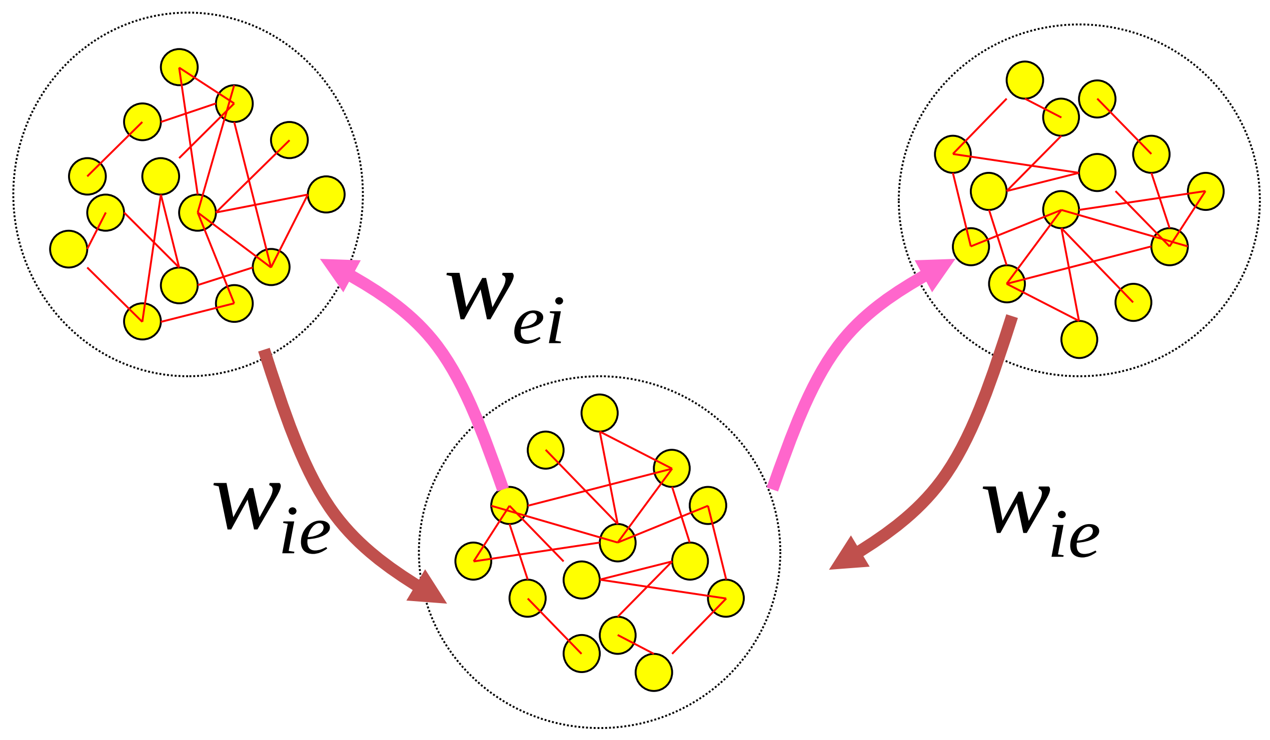
X.J. Wang, 2002
NEURON

Popul. 2

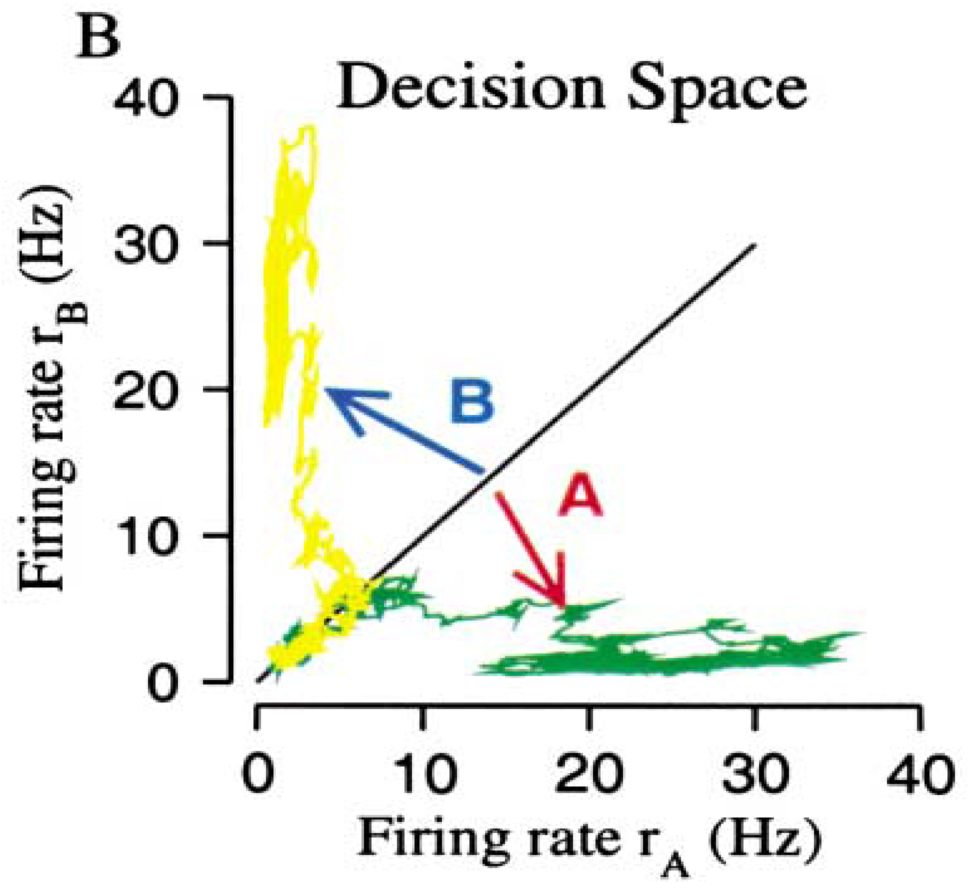
Popul.1

stimulus





$A_2(t)$

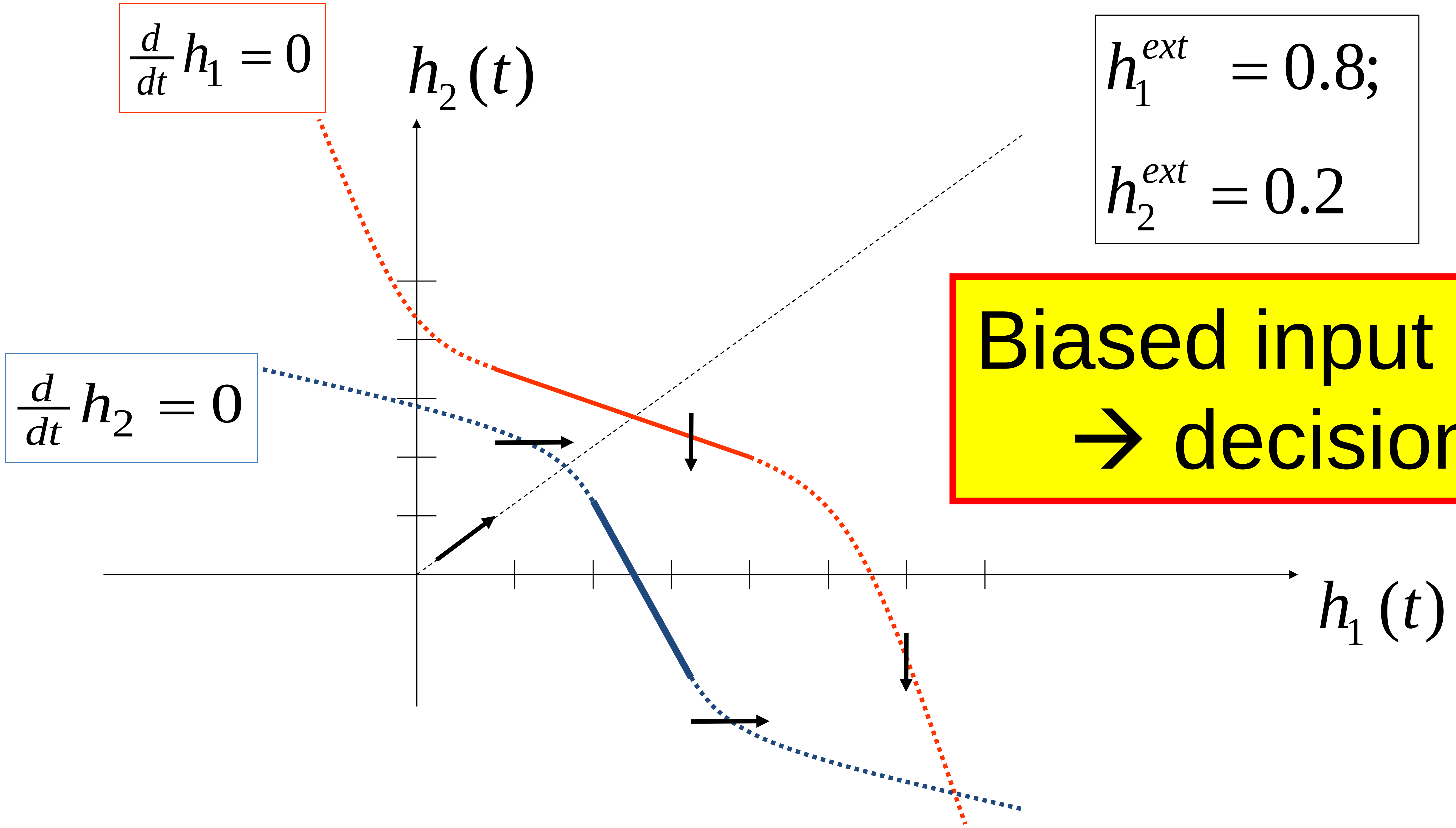


$A_1(t)$

9.5. Comparison with experiment: biased strong input

Prediction by theory - for input potential $h_1(t)$

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

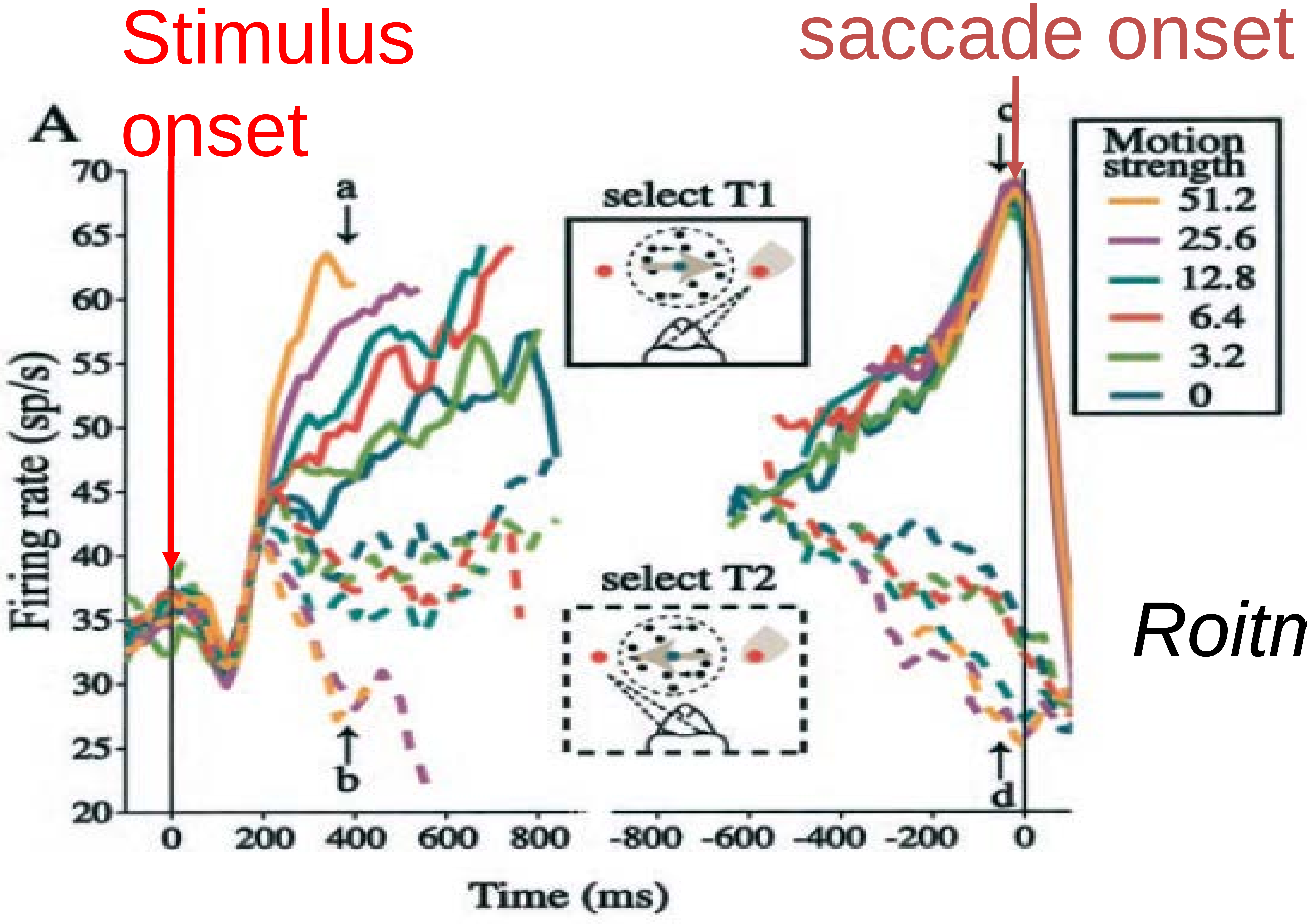


$h_1^{ext} = 0.8;$

$h_2^{ext} = 0.2$

Biased input = stable fixed point
→ decision reflects bias

9.5. Decisions in populations of neurons: LIP data



Roitman and Shadlen 2002

Figure 7. Time course of LIP activity in the RT-direction-discrimination task. *A*, Average response from 54 LIP neurons. Responses are grouped by motion strength and choice as indicated by *color* and *line type*. The responses are aligned to two events in the trial. On the *left*, responses are aligned to the onset of stimulus motion. Response averages in this portion of the graph are drawn to the median RT for each motion strength and exclude any activity within 100 msec of eye movement initiation. On the *right*, responses are aligned to initiation of the eye movement response. Response averages in this portion of the graph show the buildup and decline in activity at the end of the decision process. They exclude any activity within 200 msec of motion onset. The average firing rate was smoothed using a 60 msec running mean. *Arrows* indicate the epochs used to compare spike rate as a function

9.5. Decisions in populations of neurons: simulations and data

simulation of competing populations
shares properties with LIP data:
- faster increase for strong bias
- suppression for opposite saccade

BUT: there is no claim that
decision is taken in LIP

LIP is somewhere in the processing
stream from input to saccades

Biological Modeling of Neural Networks:

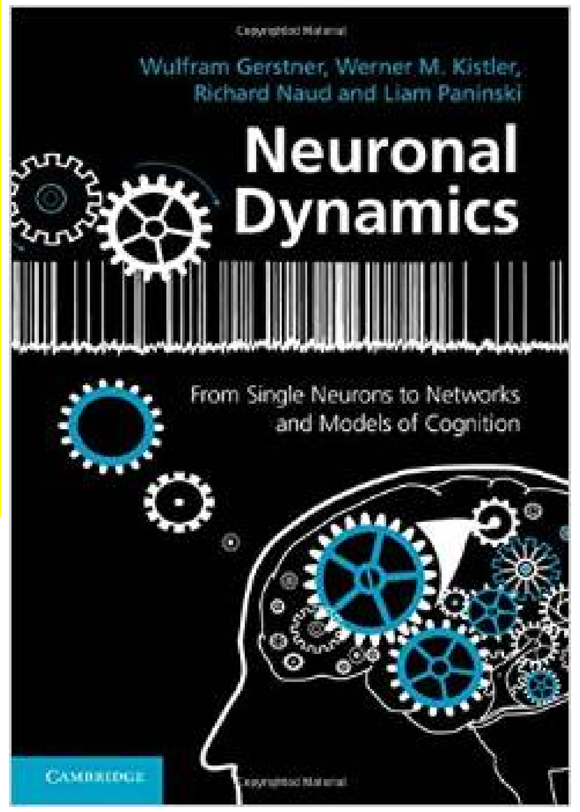
Week 9 – Decision models:
Competitive dynamics

Wulfram Gerstner

EPFL, Lausanne, Switzerland

Reading for week 9:
NEURONAL DYNAMICS
Ch. 16 (except 16.4.2)

Cambridge Univ. Press



9.1 Introduction
- decision making

9.2 Perceptual decision making
- V5/MT
- Decision dynamics: Area LIP

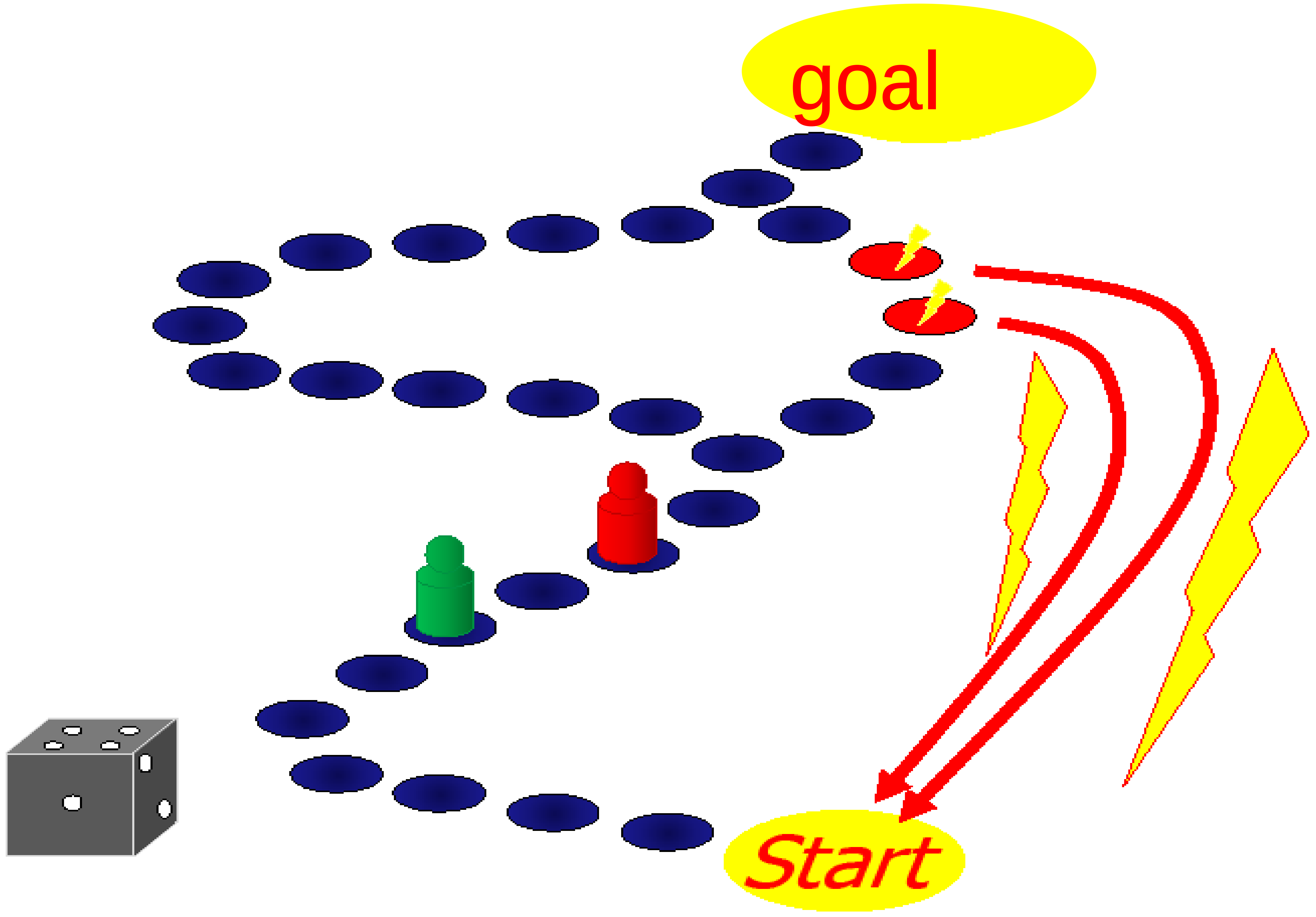
9.3 Theory of decision dynamics
- competition via shared inhibition
- effective 2-dim model

9.4. Solutions
- symmetric case
- biased case

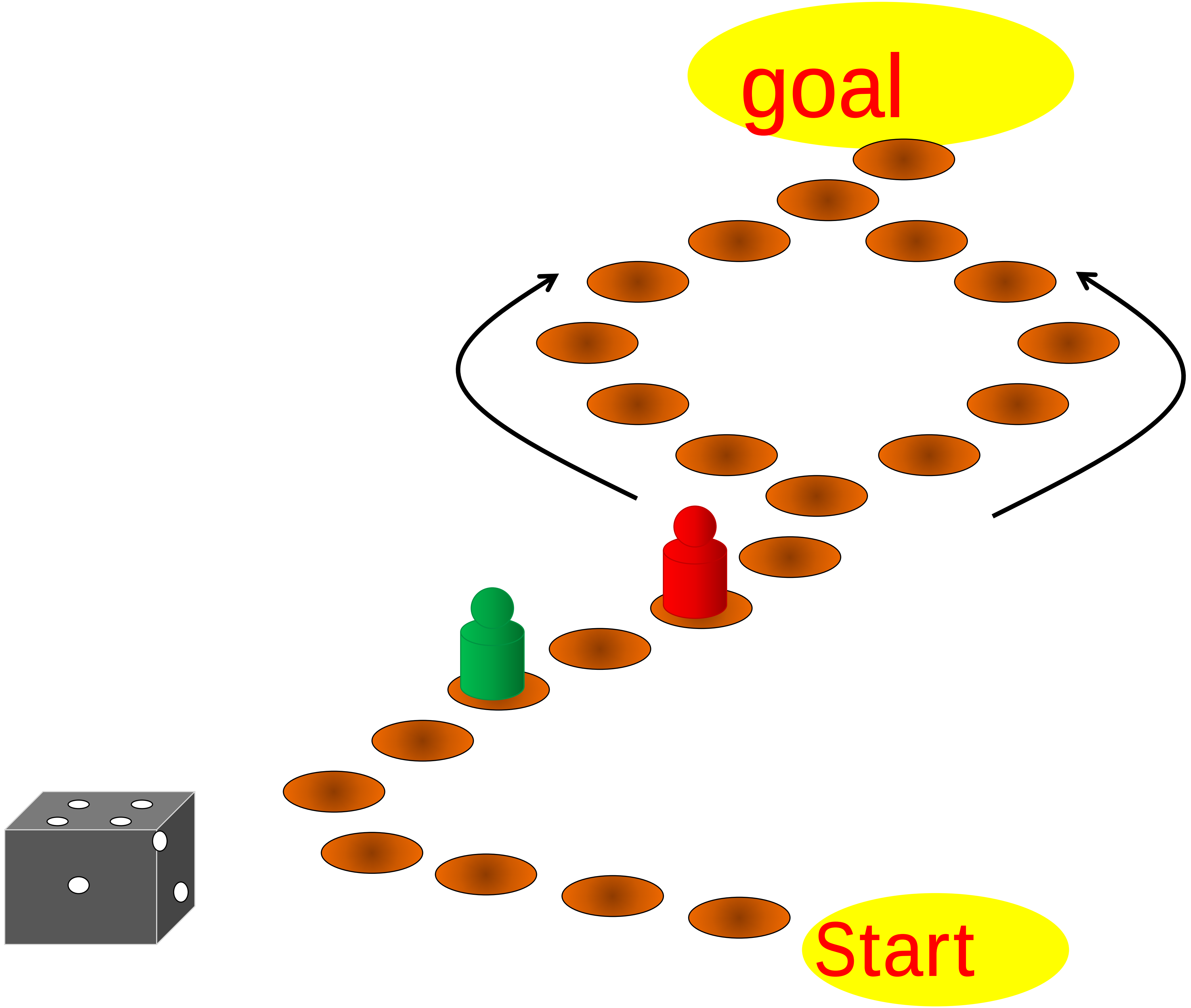
9.5. Simulations and Experiments
- simulations and theory
- simulations and experiments

9.6. Decisions, actions, volition
- the problem of free will

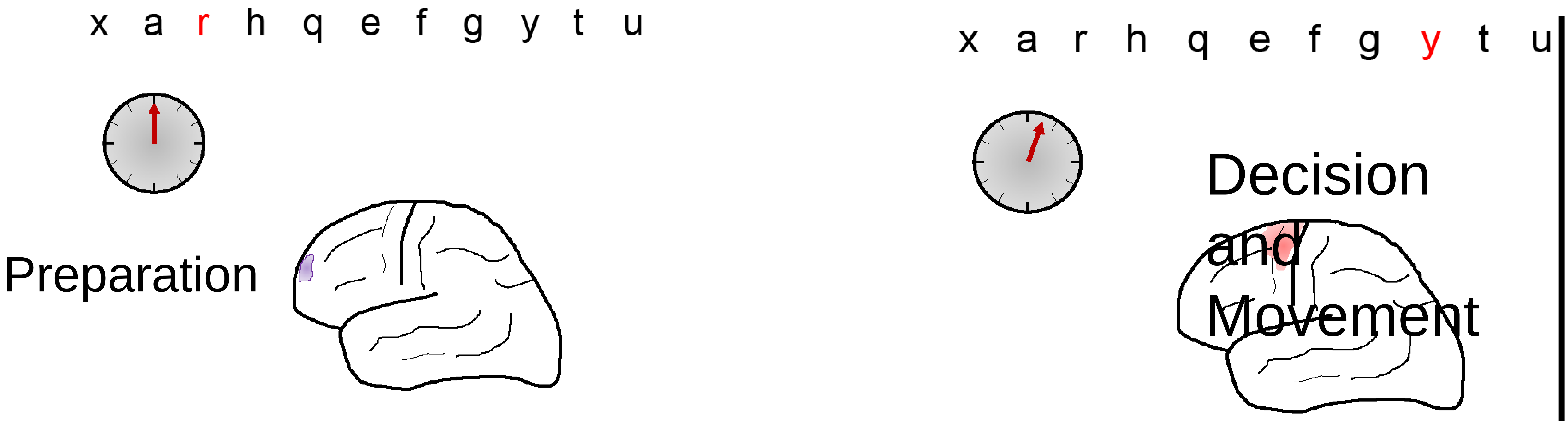
How would you decide?



How would you decide?



9.6. fMRI variant of Libet experiment: volition and free will



-Subject decides spontaneously
to move left or right hand

- report when they made their decision

Libet, Behav. Brain Sci., 1985
Soon et al., Nat. Neurosci., 2008

What decides? Who decides?

'Your brain decides what you want or what you prefer … '

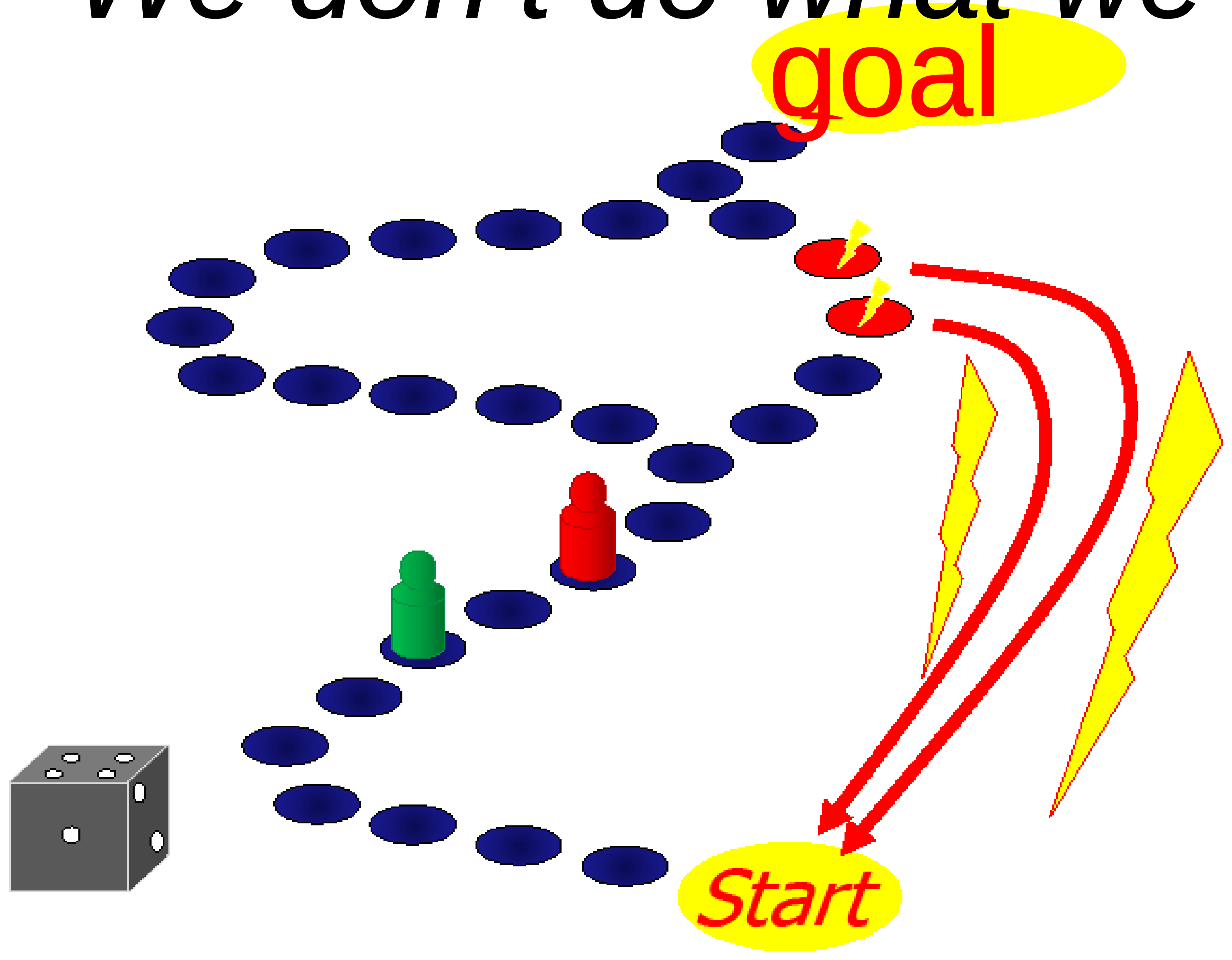
' … but your brain – this is you!!!'

-Your experiences are memorized in your brain

-Your values are memorized in your brain

-Your decisions are reflected in brain activities

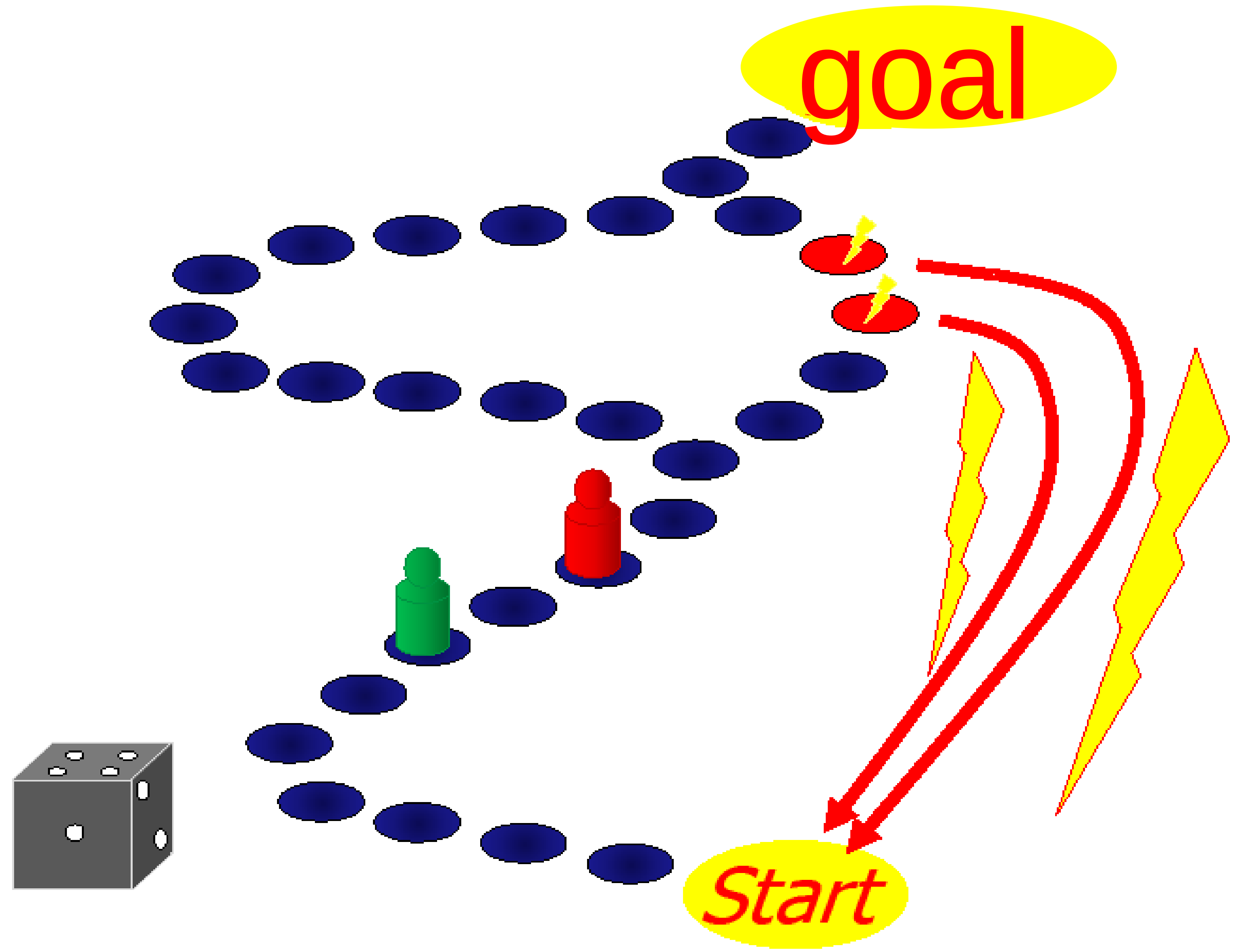
'We don't do what we want, but we want what we do' (W. Prinz)



The problem of Free Will (see e.g. Wikipedia article)

9.6. Decision: risky vs. safe

- decisions are taken in the brain
- competition between populations is a transparent model
- relevant decisions involve personal values and experiences



9.6. Selected References: Decision Making

Suggested Reading:
- *Salzman et al. Nature 1990*
- *Roitman and Shadlen, J. Neurosci. 2002*
- *Abbott, Fusi, Miller: Theoretical Approaches to Neurosci.*
- *X.-J. Wang, Neuron 2002*
- *Libet, Behav. Brain Sci., 1985*
- *Soon et al., Nat. Neurosci., 2008*
- *free will, Wikipedia*

Chapter 16, *Neuronal Dynamics*, Gerstner et al. Cambridge 2014

Exercise 2.1 now: stability of homogeneous solution

$$A_n(t) = g(h_n(t))$$

Membrane potential caused by input

$$\boxed{\tau \frac{d}{dt} h_1(t) = -h_1(t) + b + (w_{ee} - \alpha) g(h_1(t)) - \alpha\, g(h_2(t))}$$

$$\boxed{\tau \frac{d}{dt} h_2(t) = -h_2(t) + b + (w_{ee} - \alpha) g(h_2(t)) - \alpha\, g(h_1(t))}$$

Assume: $\boxed{h_1^{ext} = h_2^{ext} = b}$

a) Calculate homogeneous fixed point $h_1 = h_2 = h^*(b)$

b) Analyze stability of the fixed point h(b) as a function of b

Quick feedback on course:

"What can I do better and differently next year?"

- support: link to book chapter, video, slides
  not sufficient, sufficient, good, excellent
- integrated exercises?
  repeat next year, do not repeat next year
- workload for a 4 credit course (=6 h p. week, for 18 weeks)
  In addition to class 9-12: 2h or less, 3h, 4h or more
- difficulty?
  easier than other theory classes,
  same, harder than other theory classes
- other points?

Biological Modeling of Neural Networks

Wulfram Gerstner

EPFL, Lausanne, Switzerland

Week 1: **A first simple neuron model/ neurons and mathematics**

Week 2: **Hodgkin-Huxley models and biophysical modeling**

Week 3: **Two-dimensional models and phase plane analysis**

Week 4: **Two-dimensional models, type I and type II models**

Week 5,6: **Associative Memory, Hebb rule, Hopfield**

Week 7-9: **Perception, Cognition, Decision**

Week 10-12: **Noise models, noisy neurons and coding**

Week 13: **Learning in Networks**

Week x: **Online video: Dendrites/Biophysics**

Week xx: **Online video: GLM/ estimating neuron models**

LEARNING OUTCOMES

- Solve linear one-dimensional differential equations
- Analyze two-dimensional models in the phase plane
- Develop a simplified model by separation of time scales
- Analyze connected networks in the mean-field limit
- Formulate stochastic models of biological phenomena
- Formalize biological facts into mathematical models
- Prove stability and convergence
- Apply model concepts in simulations
- Predict outcome of dynamics
- Describe neuronal phenomena

Look at samples of past exams

Transversal skills

- Plan and carry out activities in a way which makes optimal use of available time and other resources.
- Collect data.
- Write a scientific or technical report.

Use a textbook,
(Use video lectures)
don't use slides (only)

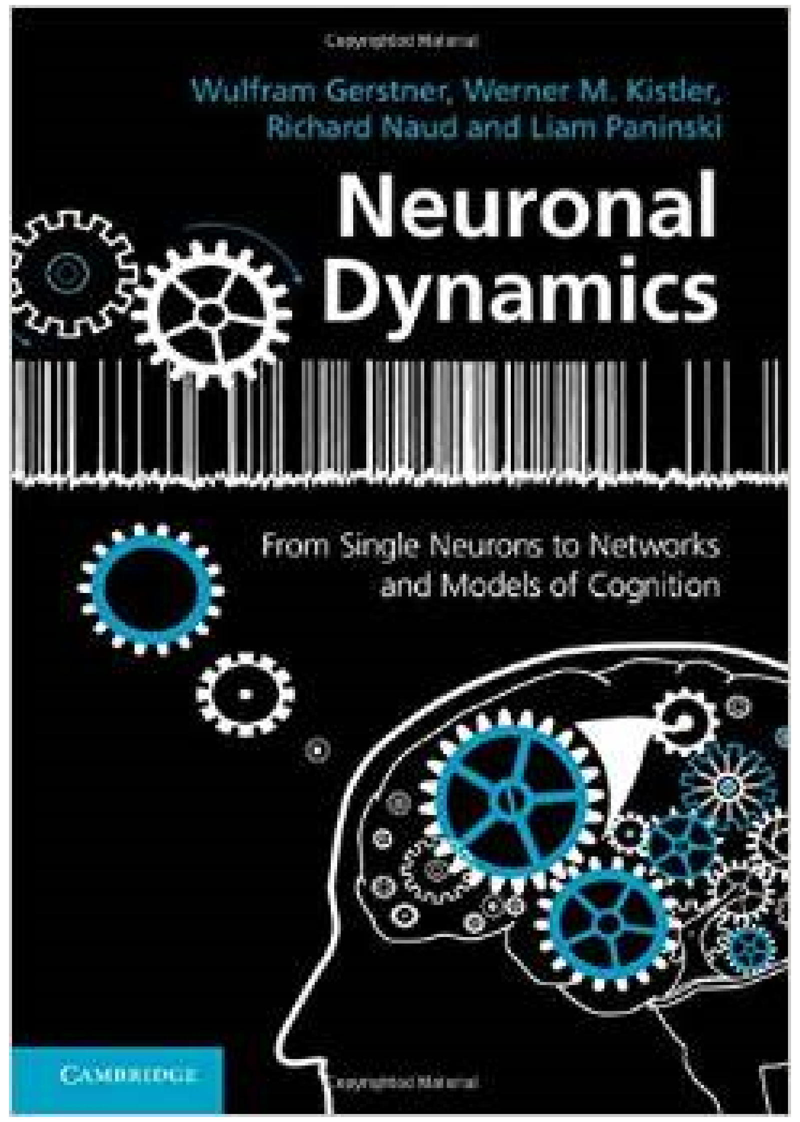
miniproject

Biological Modeling of Neural Networks

Written Exam (70%)
+ miniproject (30%)

http://neuronaldynamics.epfl.ch/

Textbook:



Written exam:
- checks 'Learning Outcomes'
- no calculator, no textbook
- bring **A5** sheet of ***handwritten*** notes

Videos:

https://lcnwww.epfl.ch/gerstner/NeuronalDynamics-MOOCall.html

The end:

good luck with your exams!