Computational Neuroscience: Neuronal Dynamics

EPFL

week 9 – Decision models: Competitive dynamics

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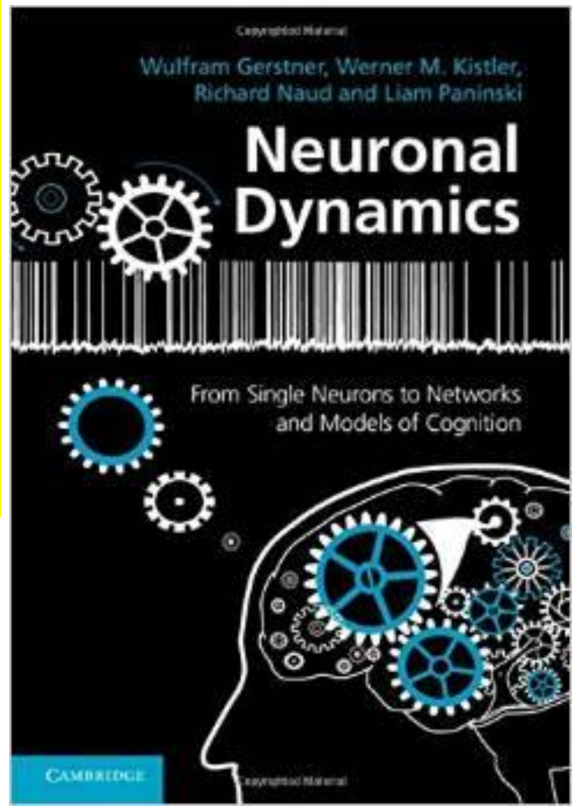
Reading for week 9:
NEURONAL DYNAMICS
Ch. 16 (except 16.4.2)



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

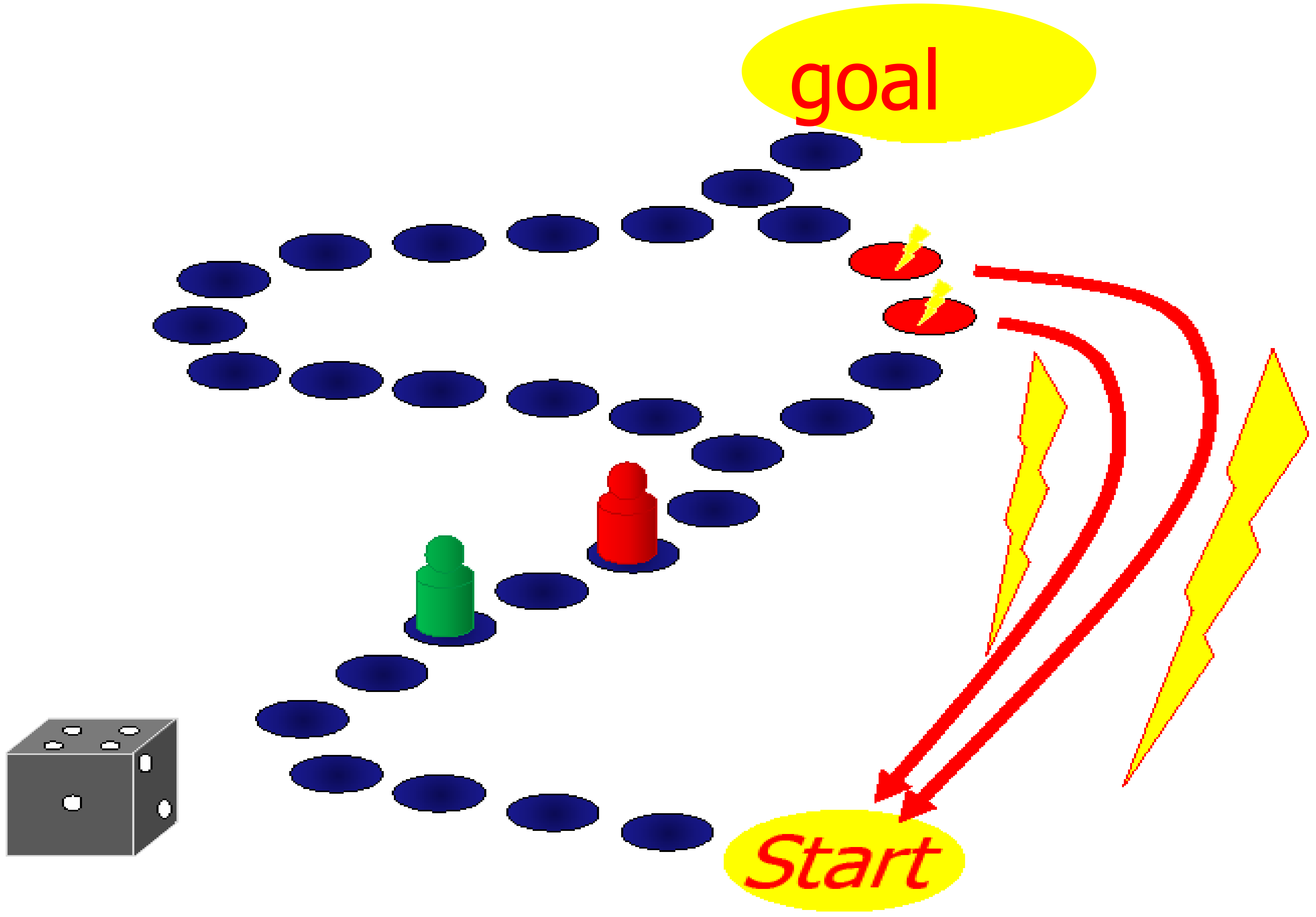
9.6. Decisions, actions, volition
- the problem of free will

Lecture 13 of video series

https://app.courseware.epfl.ch/learning/course/course-v1:EPFL+neuronal-dynamics-computational-neuroscience+2025/home

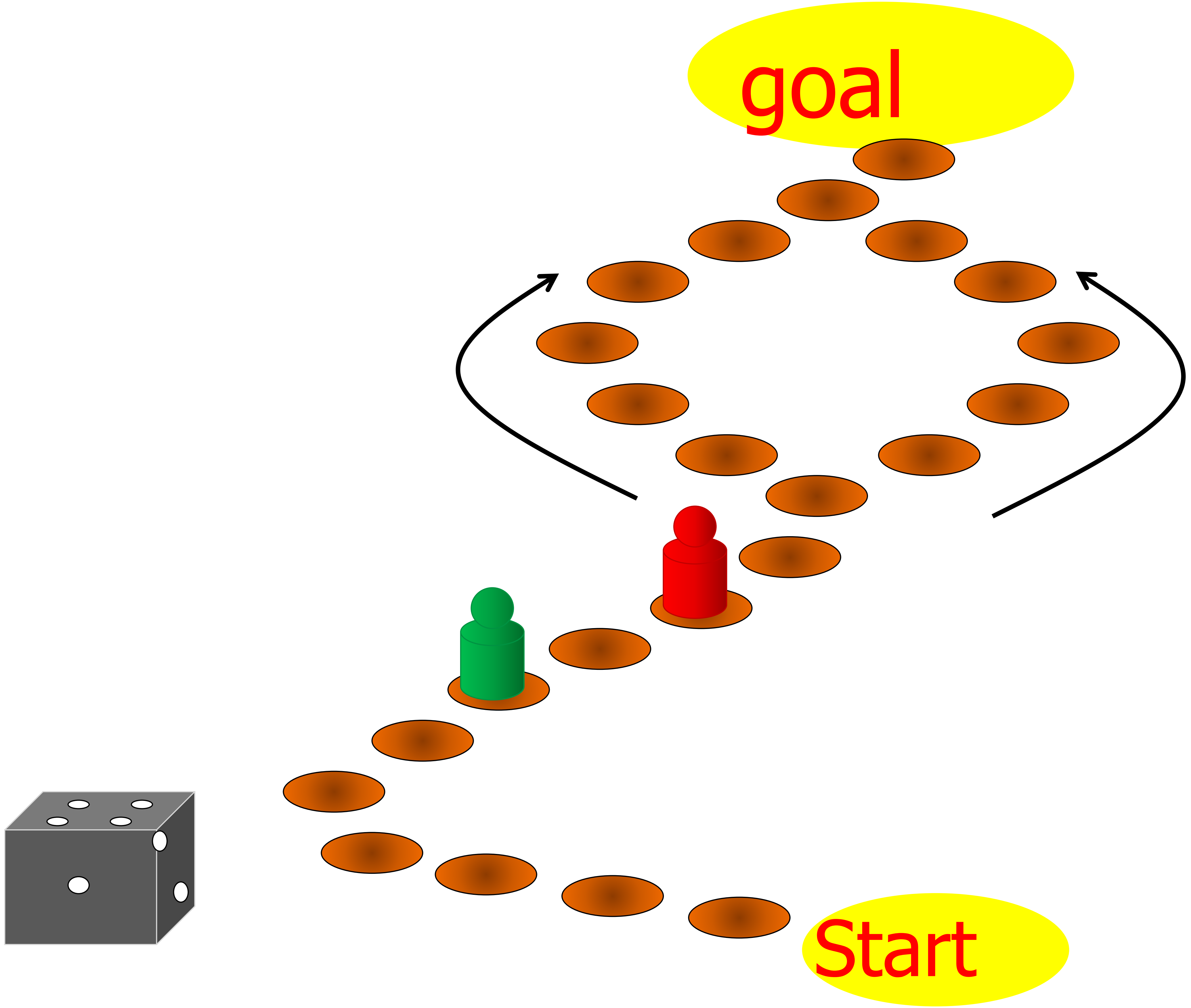
9.6. Decision: risky vs. safe

How would you decide?



9.6. Decision: risky vs. safe

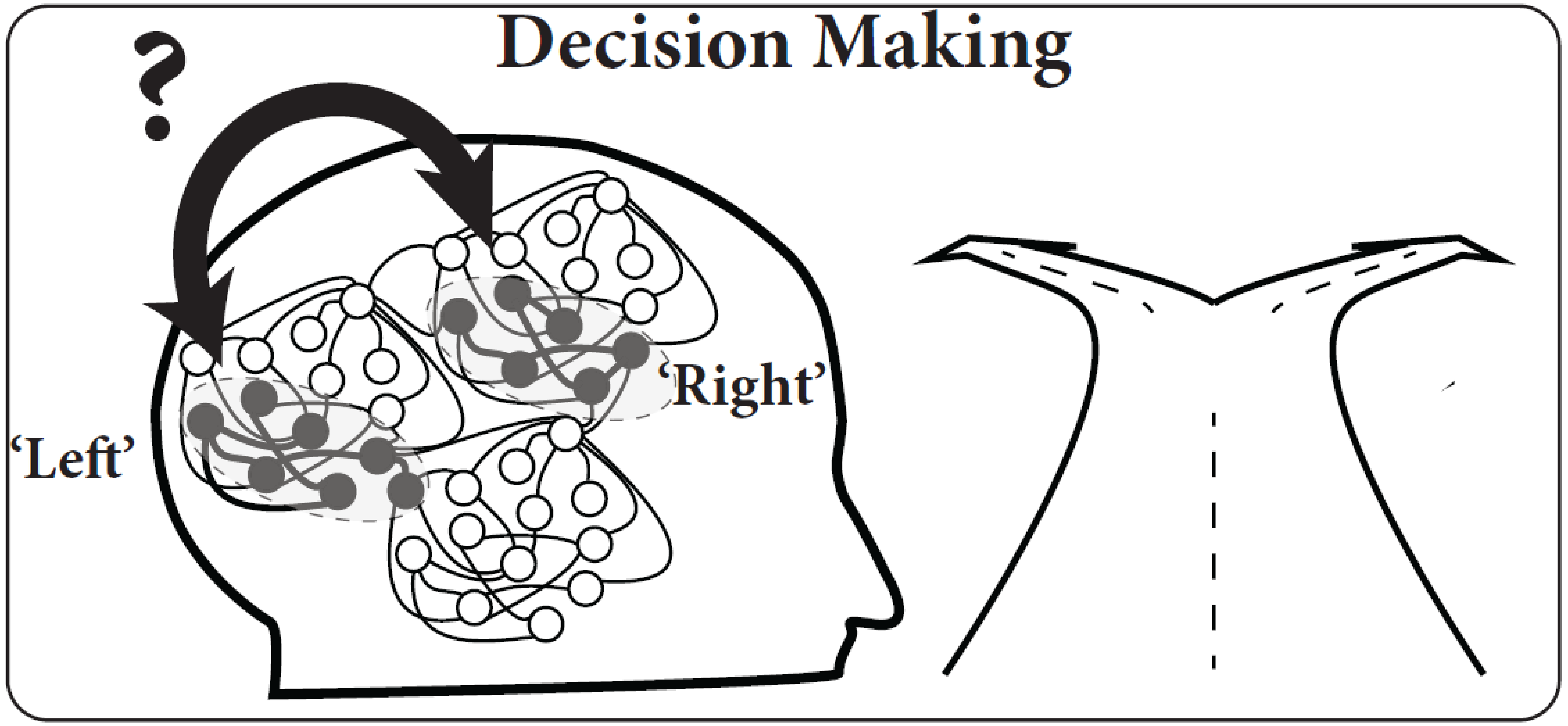
How would you decide?



9.1. Decision making

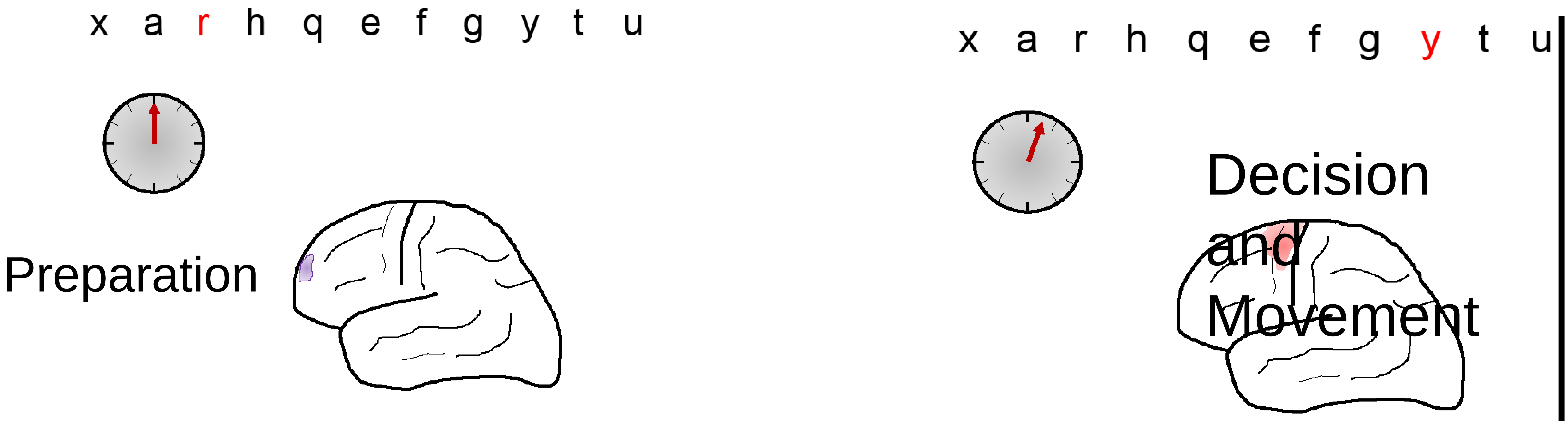
turn

Left? Right?



Do you agree with the assumption that decisions are taken in the brain?
[ ] yes
[ ] no

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 *'urge to move'*

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 … ’

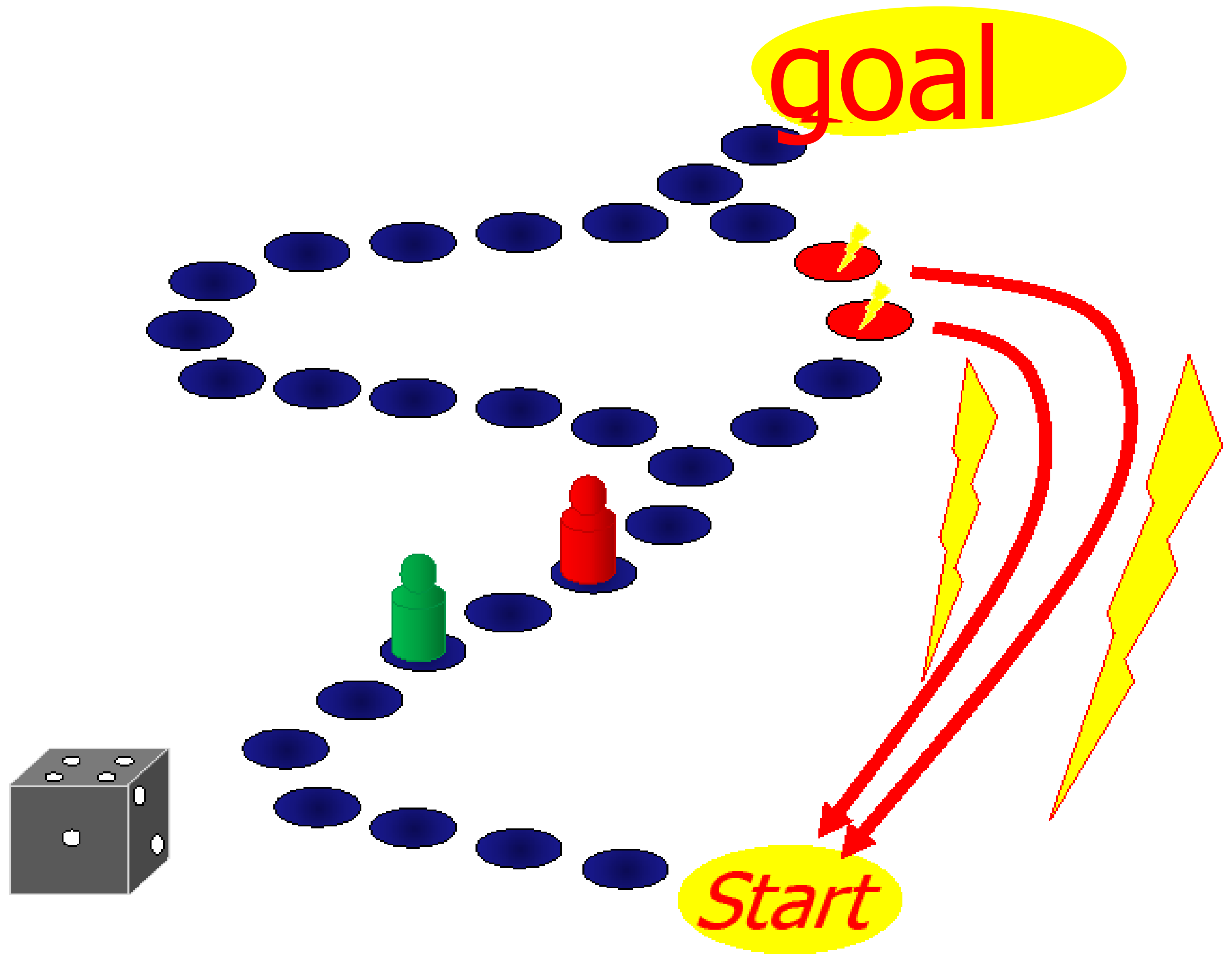
‘ … but your brain – this is you!!!’

-Your experiences are memorized in your brain

-Your values are memorized in your brain

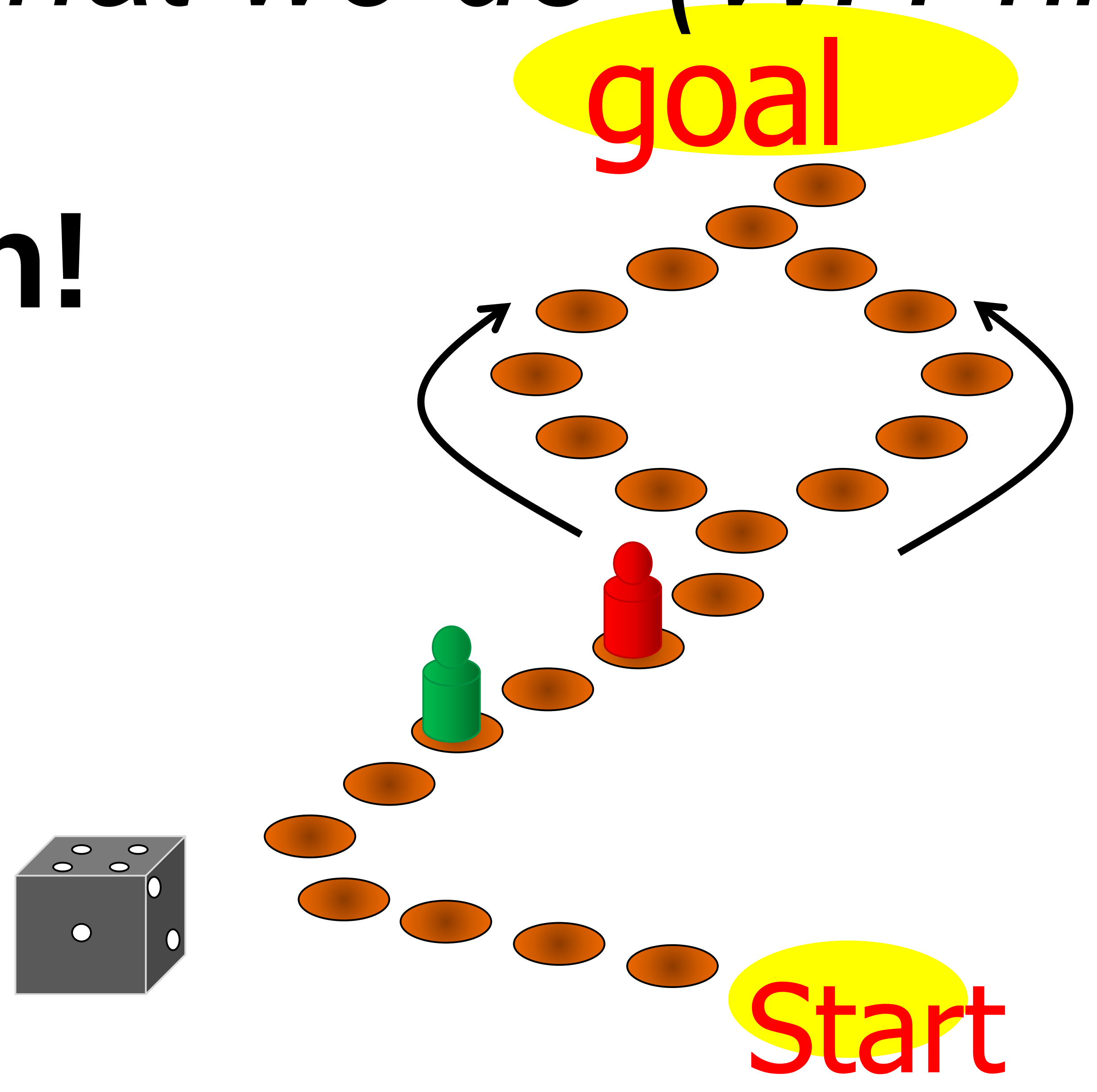
-Your decisions are reflected in brain activities

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



Irrelevant decision!

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



9.6. Decisions: fast decision vs slow decision

React to red light

Respond to service

Vote for candidate A or B?

Choose Princeton or Harvard?

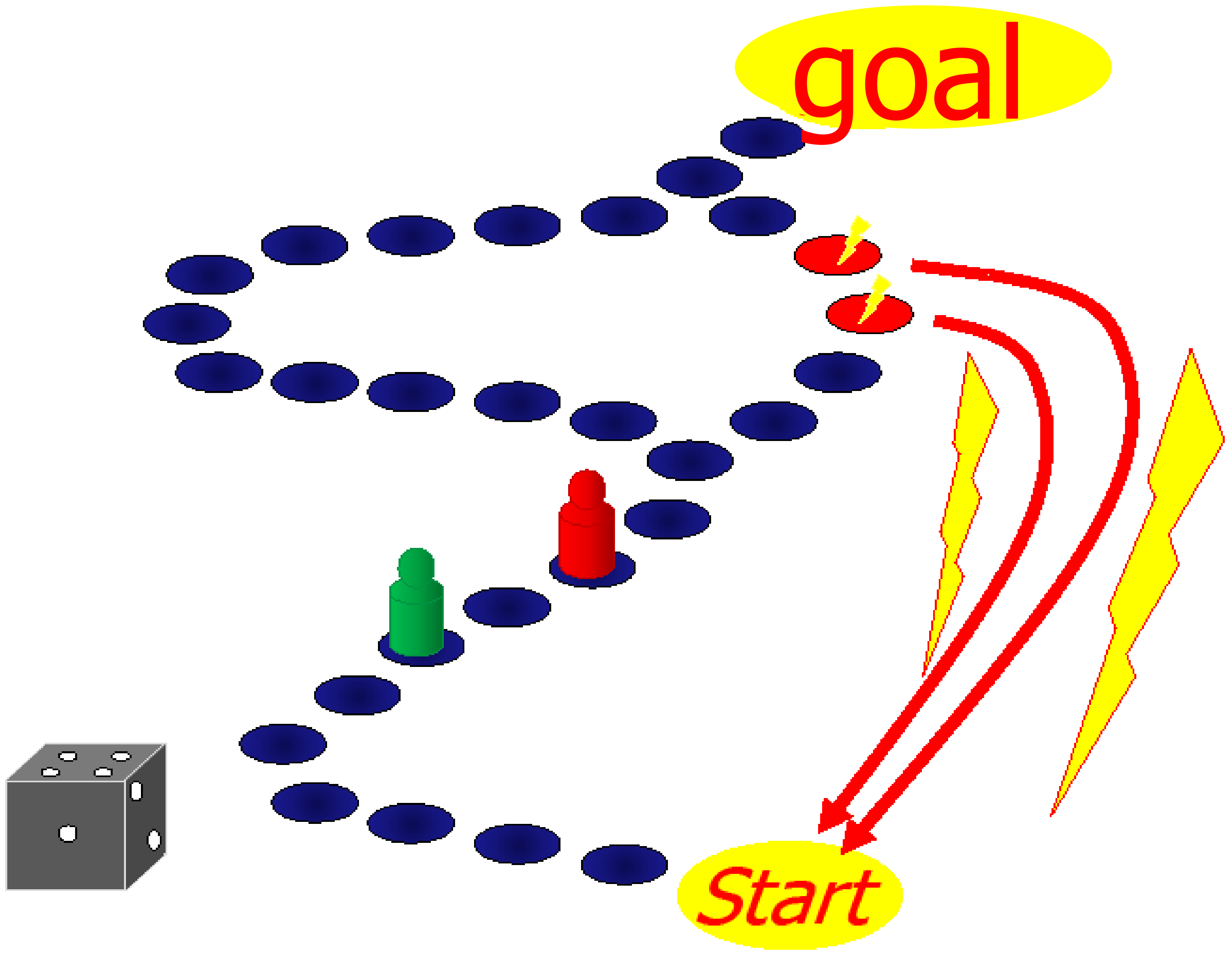
9.6. Decision: summary

Decisions are taken in the brain

- fast (unreflected) decisions can be the outcome of years of training
  (that sets brain dynamics in appropriate regime)

- relevant slow decisions involve personal values and experiences
  (that are stored in the brain)

-competition between populations is a transparent model



9.1. Summary: decision making

We have to take many decisions every day, from simple decisions such as ‘should I order coffee or cappuccino’ to bigger decisions such as turning left or right, or voting for candidate A or B.

Decisions can be studied experimentally at several levels. In the field of Neuroeconomics, human participants have to make choices in game-like situtations, with money as reward. In visual psychophysics, participants are asked to judge a visual stimulus, etc. Similar tasks have also been developed for animal studies.

This week we are interested in building models of decision making using the formalism of population activity. The basic model consists of two populations of excitatory neurons that compete with each other via a shared population of inhibitory neurons.

9.6. Summary: Neurophilosphy of decision making and free will

Decision making tasks are fascinating since we humans feel that decisions are our own private choices. Yet brain activity is related to our decisions. This points to several philosophical questions. We cannot answer these questions here. A few pointers are the indicated Wikipedia pages which link to further reading.

A few comments:

1. Obviously, our decisions are linked to the activity of the brain (and not to activity of the feet).
2. A correlation in a specific experiment is only a correlation, and not more. Decisions that are prepared early on can be 'interrupted/stopped/overwritten' if later information suggests that this is better. Hence the correlations detected in one specific experimental task do not imply that the decisions have been 'really taken'.
3. In experiments, the links between early activity and later decision outcome are only stochastic.
4. In typical experiments on free decisions/free will, the task is absolutely irrelevant, i.e., we do not care about the outcome. In these cases there is no philosophical problem if we rely on a noise source.
5. In cases where we care about the outcome (voting in an election), we have reflected beforehand and vote according to our preferences.
6. These preferences in turn are the result of our experiences and education – and these experiences, concepts, and insights are stored in the brain (where else?).
7. Rapid decisions (Roger Federer's reaction to the flying ball) are automatically taken before reflecting about them.

9.2. Detour: receptive fields in V5/MT

visual
cortex

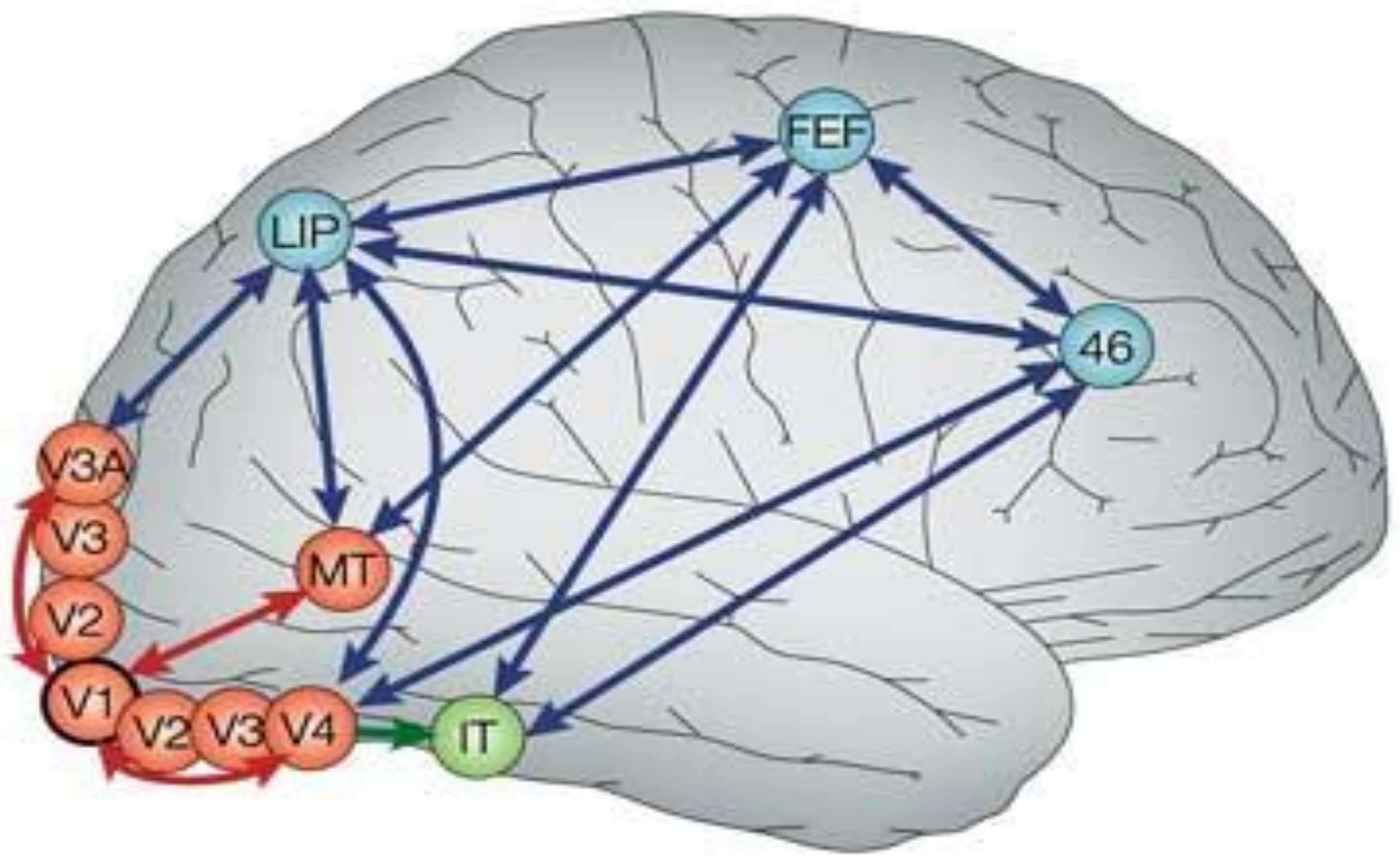
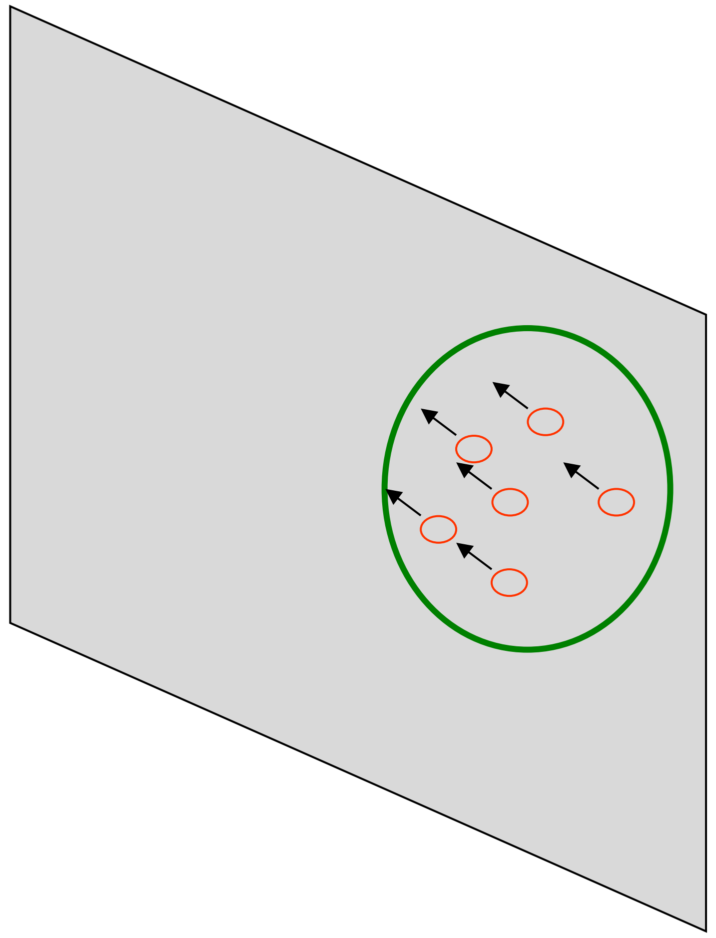


IMAGE Nature Reviews | Neuroscience



1) Cells in visual cortex MT/V5 respond
to motion stimuli (inside their receptive fields)

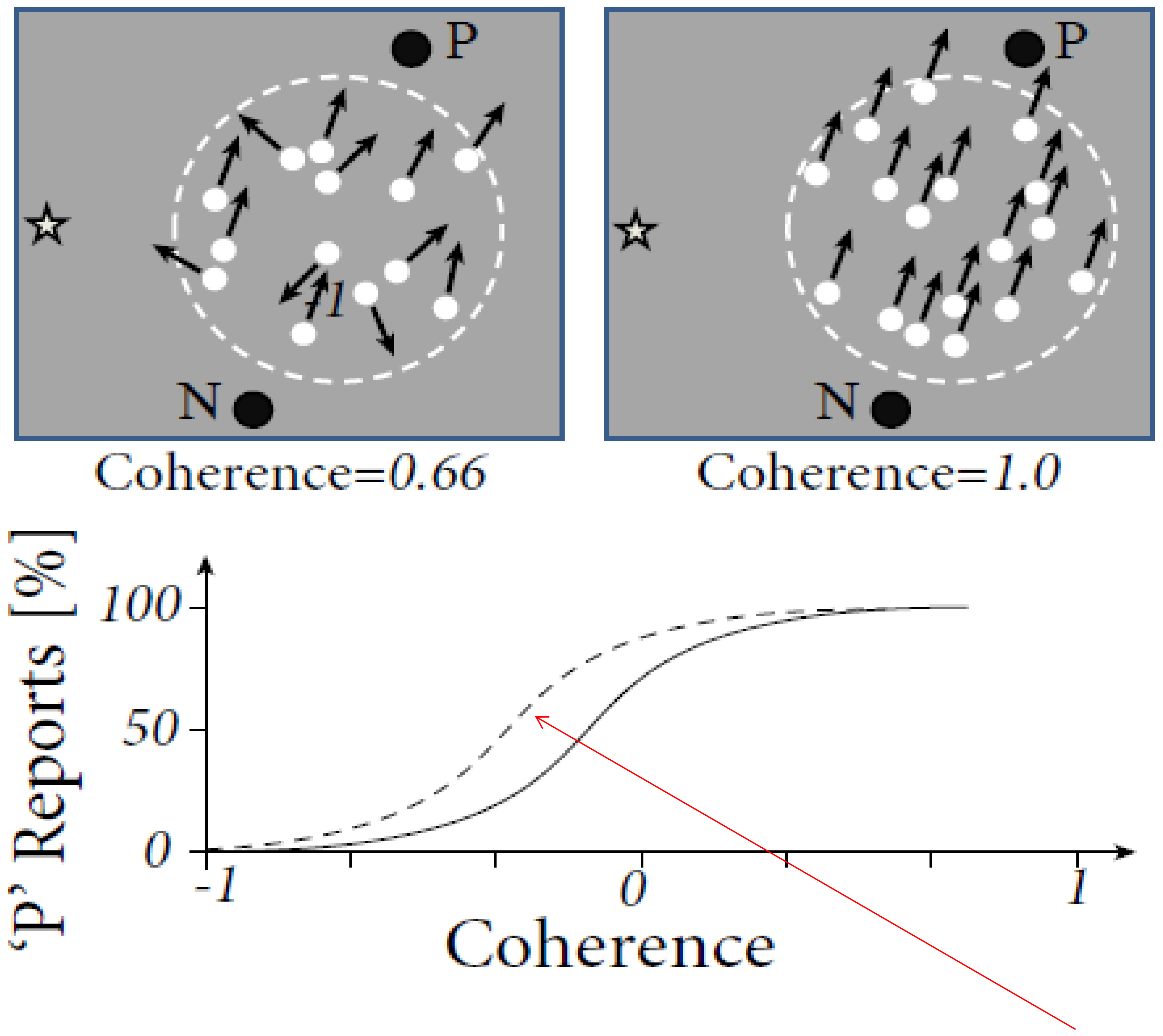
2) Neighboring cells in visual cortex MT/V5
respond to motion in similar direction:
cortical columns

Albright, Desimone,Gross,
J. Neurophysiol, 1985

9. 2. Experiment of Salzman et al. 1990

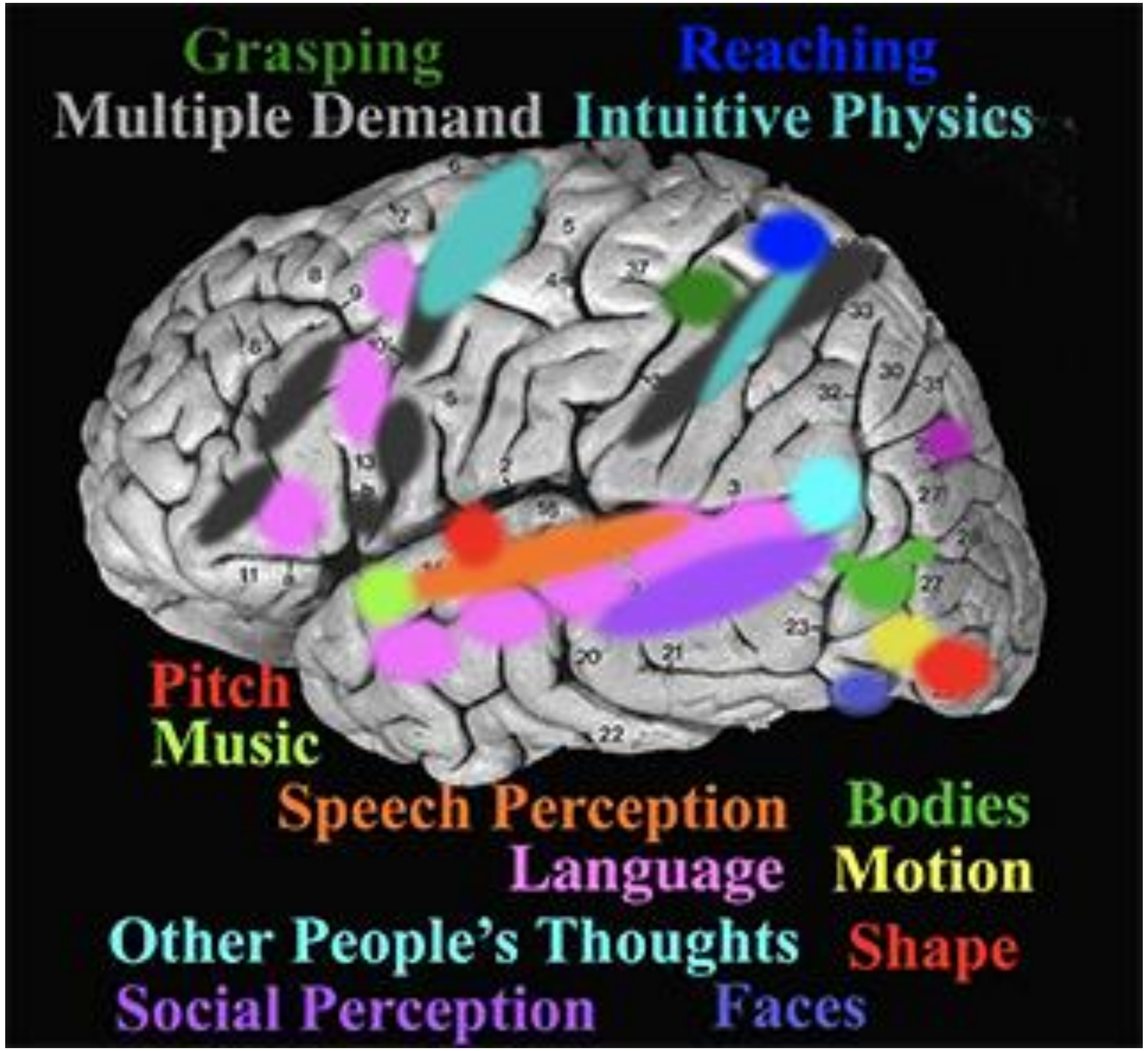
Behavior: monkey psychophysics, many trials

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



With stimulation

Extra. Human brain regions (web page of Kanwisher course)



https://ocw.mit.edu/courses/9-13-the-human-brain-spring-2019/

Extra. Experiment of Kanwisher (Schalk et al. 2017)

Behavior: human patient, psychophysics, single trial, conscious reporting

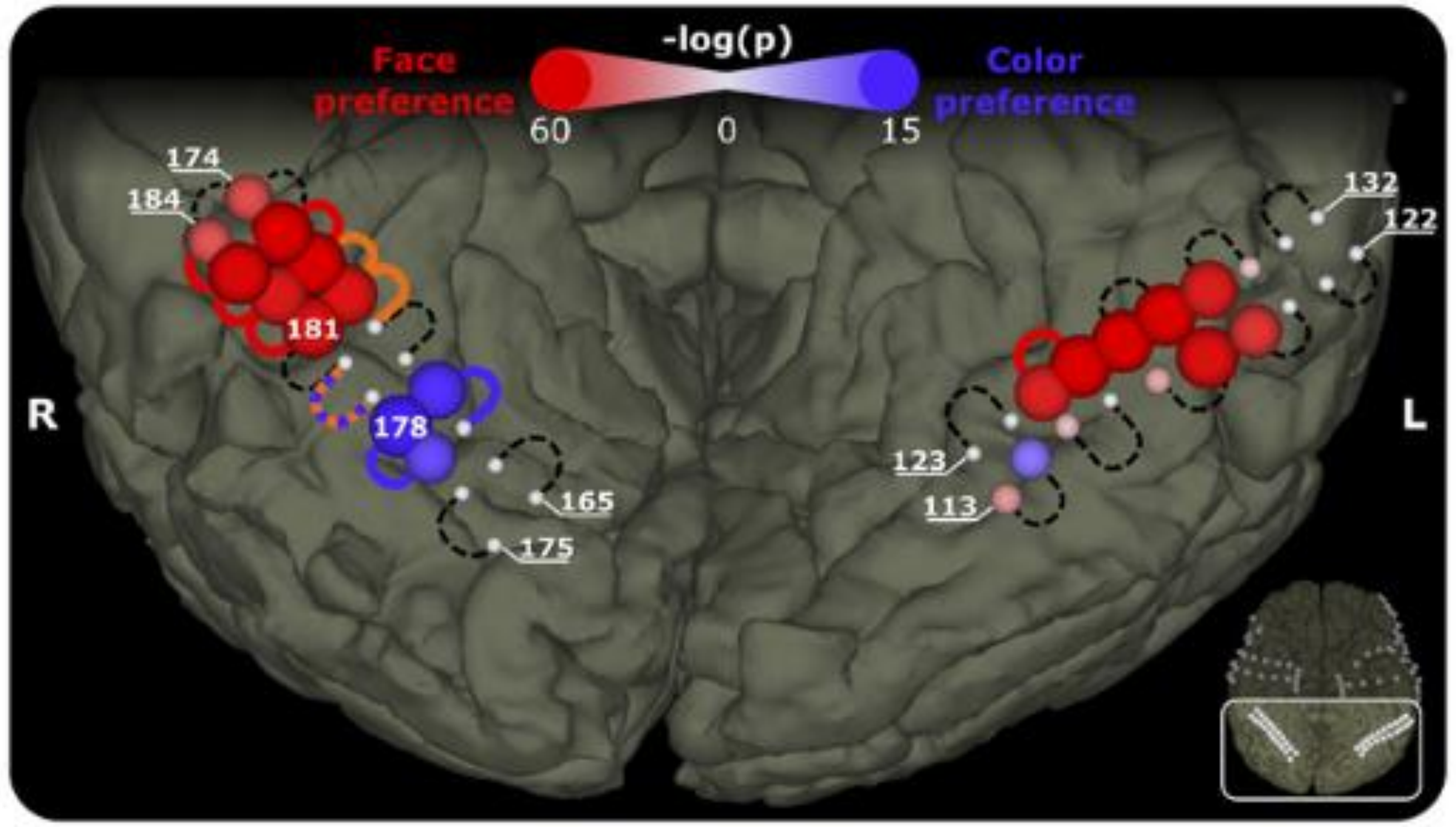


Fig. 1. Location and significance [in −log(p)] of preference for faces > objects (red) and color > grayscale (blue) of ventral electrodes. Arcs show electrode pairs that were stimulated, with arc color indicating resulting percepts: red for faces, orange for eyes, blue for colors, and dashed black for no consistent change in color or shape (see *Supporting Information* for details). The effects (or lack thereof) from electrical stimulation shown here are based on the main experiment (see *Transcript of Entire Stimulation Session*) and clinical mapping conducted on the previous day.

	
Stim. Elec. 181-182	*…just for the very first second… I saw an eye, an eye, and a mouth.*
Stim. Elec. 177-178	*The left side of the box looks like a rainbow.*

Fig. 3. Transcript excerpts from patient's report during electrical stimulation of electrodes 181–182 (FFA) and 177–178 (color-preferring site) while viewing a box, a ball, the experimenter's face, or a kanji character. For full transcript see *Transcript of Entire Stimulation Session*; for excerpted videos see Movies S1 and S2.

Facephenes and rainbows: Causal evidence for functional and anatomical specificity of face and color processing in the human brain

Gerwin Schalk[a], Christoph Kapeller[b,c], Christoph Guger[b], Hiroshi Ogawa[d], Satoru Hiroshima[d], Rosa Lafer-Sousa[e], Zeynep M. Saygin[e,f,1], Kyousuke Kamada[d], and Nancy Kanwisher[e,f,2]

www.pnas.org/cgi/doi/10.1073/pnas.1713447114

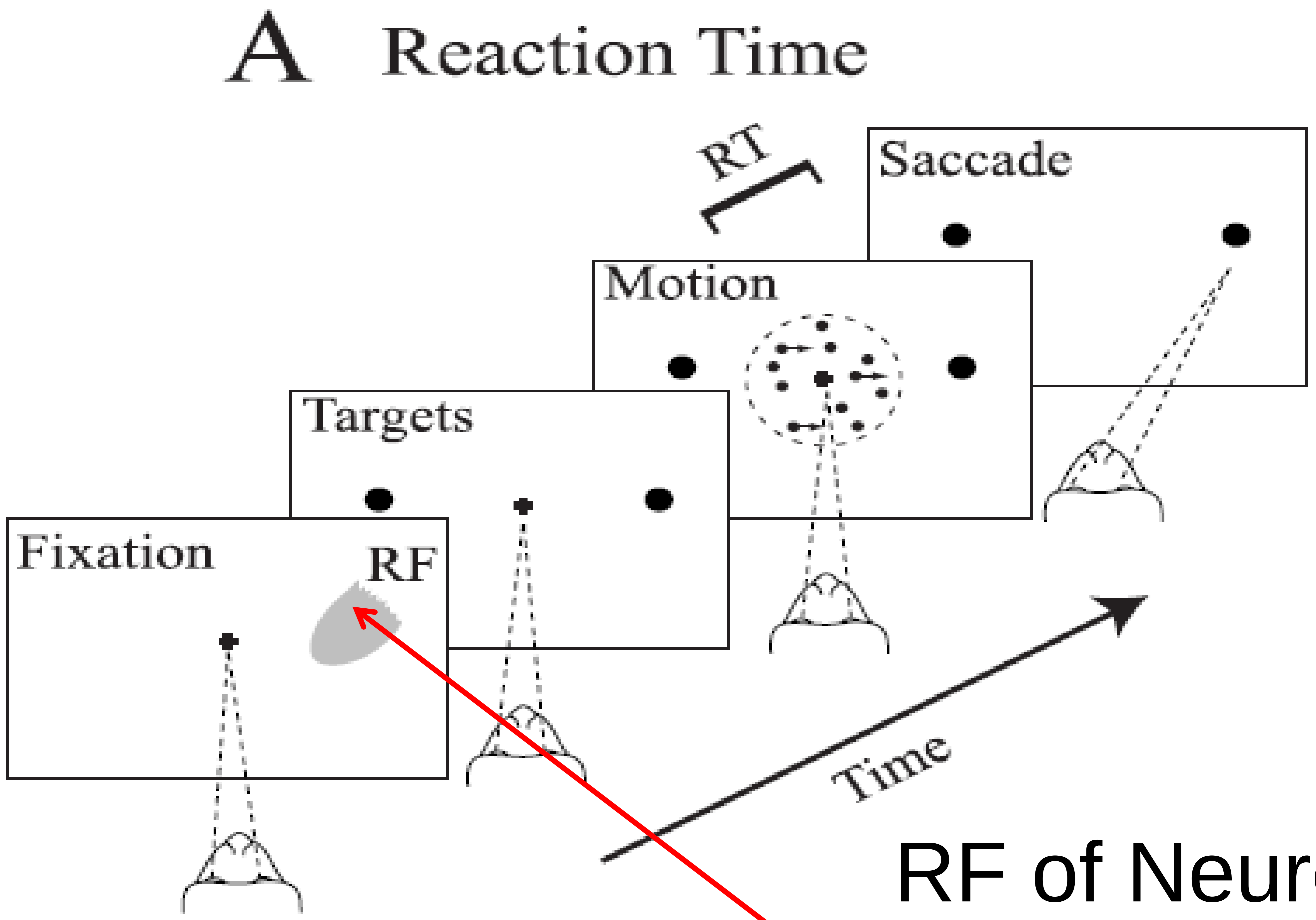
9.2a. Summary: Decision making in V5/MT and LIP

Neurons in V5/MT (two names for the same area) are sensitive to motion. A widely used stimulus is a random dot pattern with coherent motion. The response of neurons depends on the direction of motion: each neuron has its ‘preferred direction’ within a spatially localized receptive field.

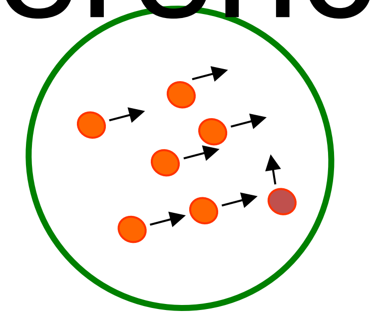
A stimulus with coherence of 100% implies that all dots move in the same direction (often chosen to be the preferred direction of the recorded neuron). Coherence of 60% implies that 60 percent of the dots move in the same direction and 40 percent in a random direction. Coherence -100% is defined as all dots moving coherently in the null-direction (opposite to the preferred direction).

Monkeys can be trained to report by eye movements (saccades) what they perceive. In experiments with monkeys it was found that stimulating a localized group of V5/MT neurons during the random-dot task shifts the response curve of the perceived movement stimulus. Hence, the experimenter can influence the decision of the monkey at the level of the perception.

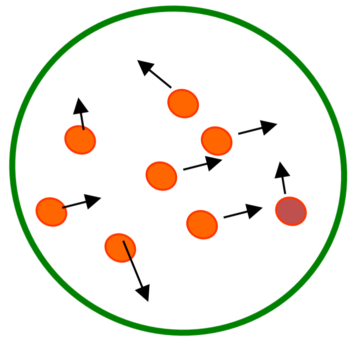
9.2. Experiment of Roitman and Shadlen in LIP (2002)



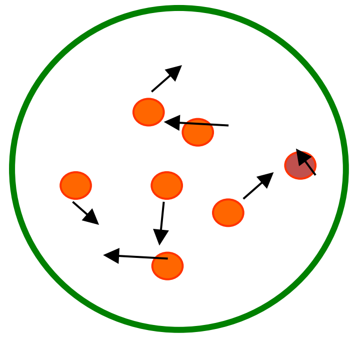
coherence 85%



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)

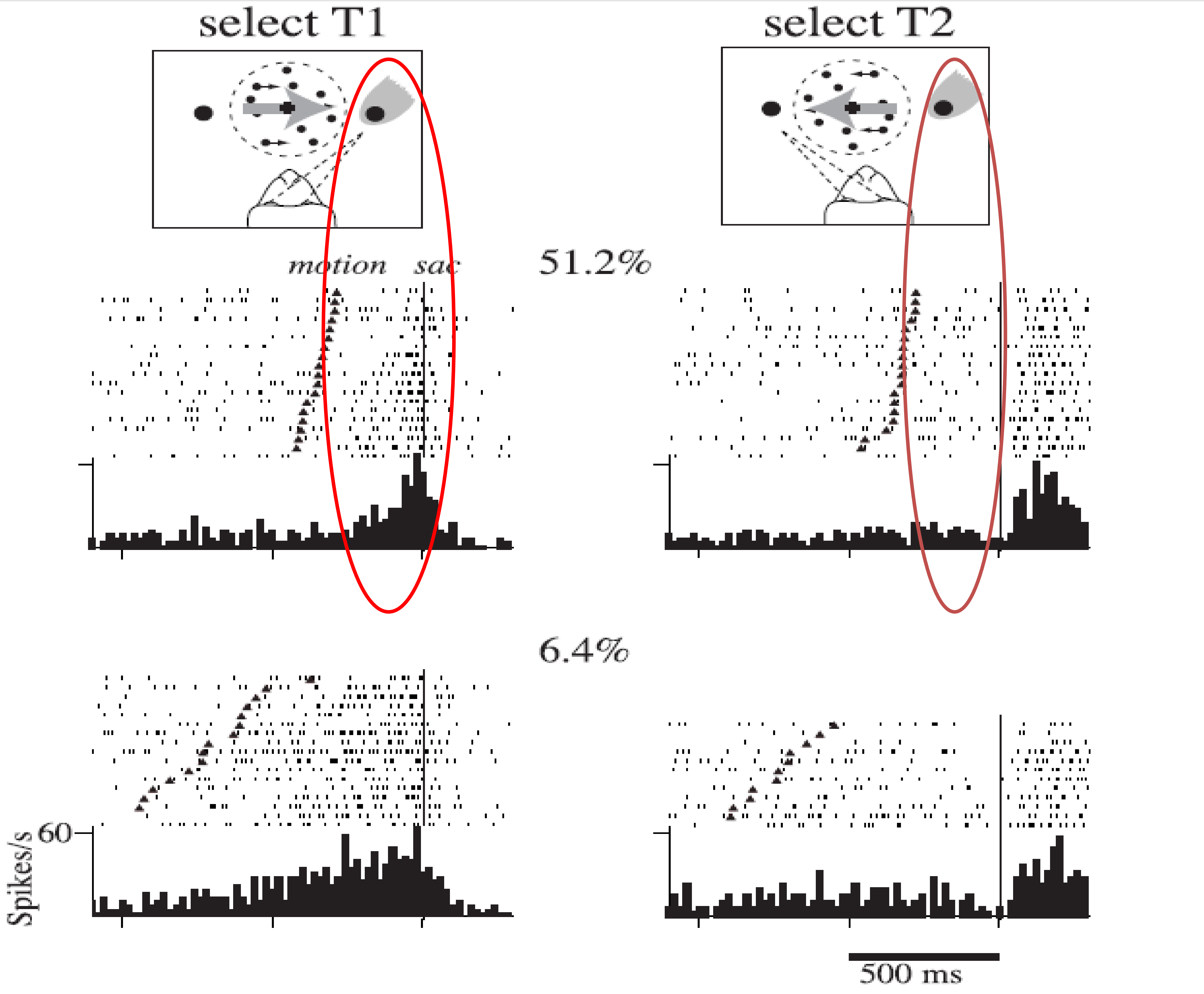
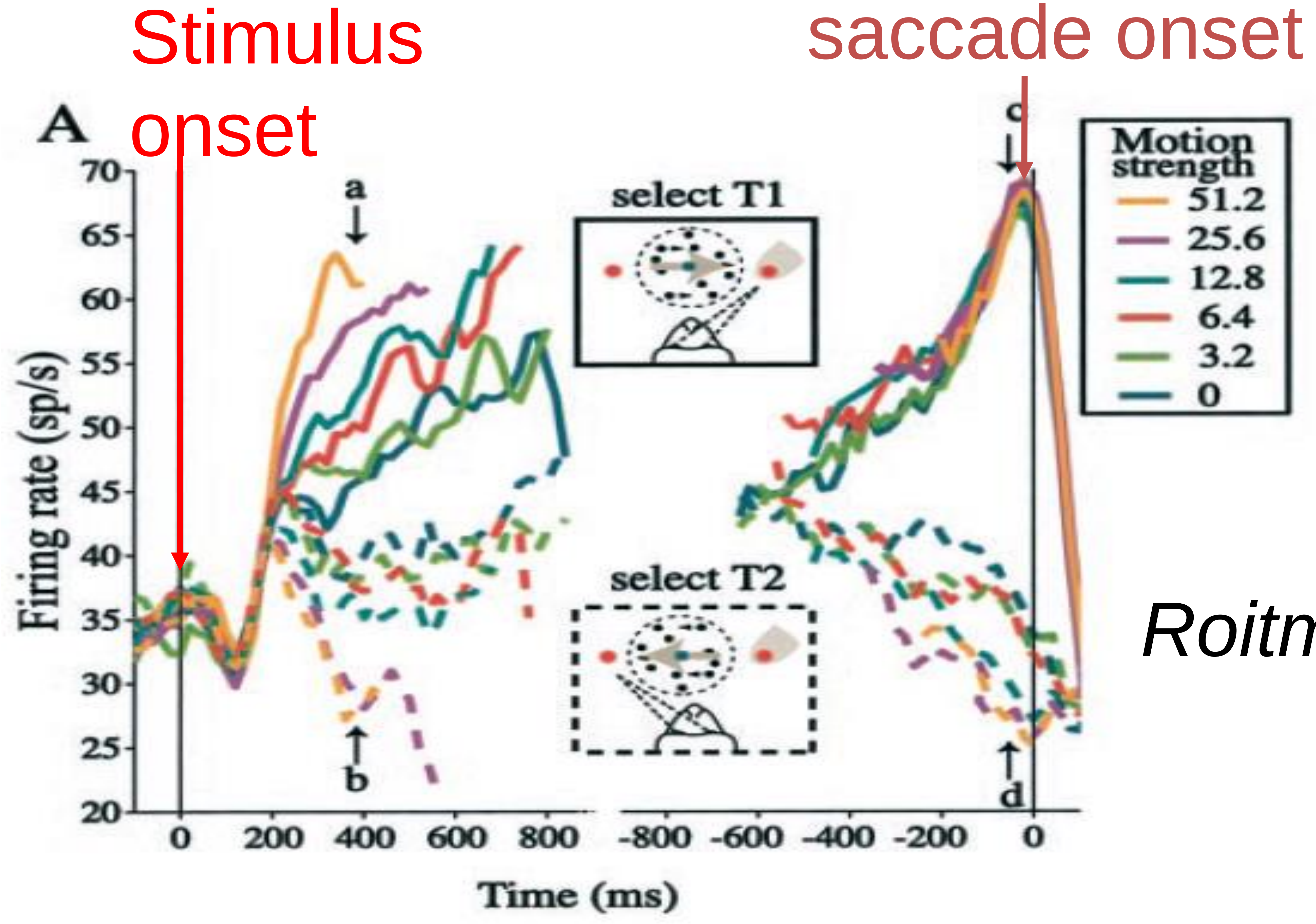


Figure 4. Response of an LIP neuron during the RT-direction-

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)

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

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

Neurons in LIP:

- Selective to target of saccade
- 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', but:
- Interesting correlations with decision outcome
- Activity increases "faster" if signal is stronger

but: single-neuron data, other interpretations possible

9.2b. Summary: Decision making in V5/MT and LIP

Neurons in the area LIP are selective to the target of planned saccade and show an increase of activity BEFORE the saccade is initiated. In the decision making task with random dots, the activity of LIP neurons increases faster if the random-dot pattern is more coherent, and hence easier to detect. However, the activity looks ‘noisy’, i.e., it is different in different trials. A simple interpretation is that the saccade is initiated if LIP neurons reach a threshold value for the activity.

The area LIP is located in the signal processing stream somewhere between sensory areas and the area (frontal eye field) that controls the saccade. Neurons in LIP show interesting correlations with the decision outcome, but this does not prove that the decision is taken by this group of neurons.

9.3. Effective 2-dim. model

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

activity equations

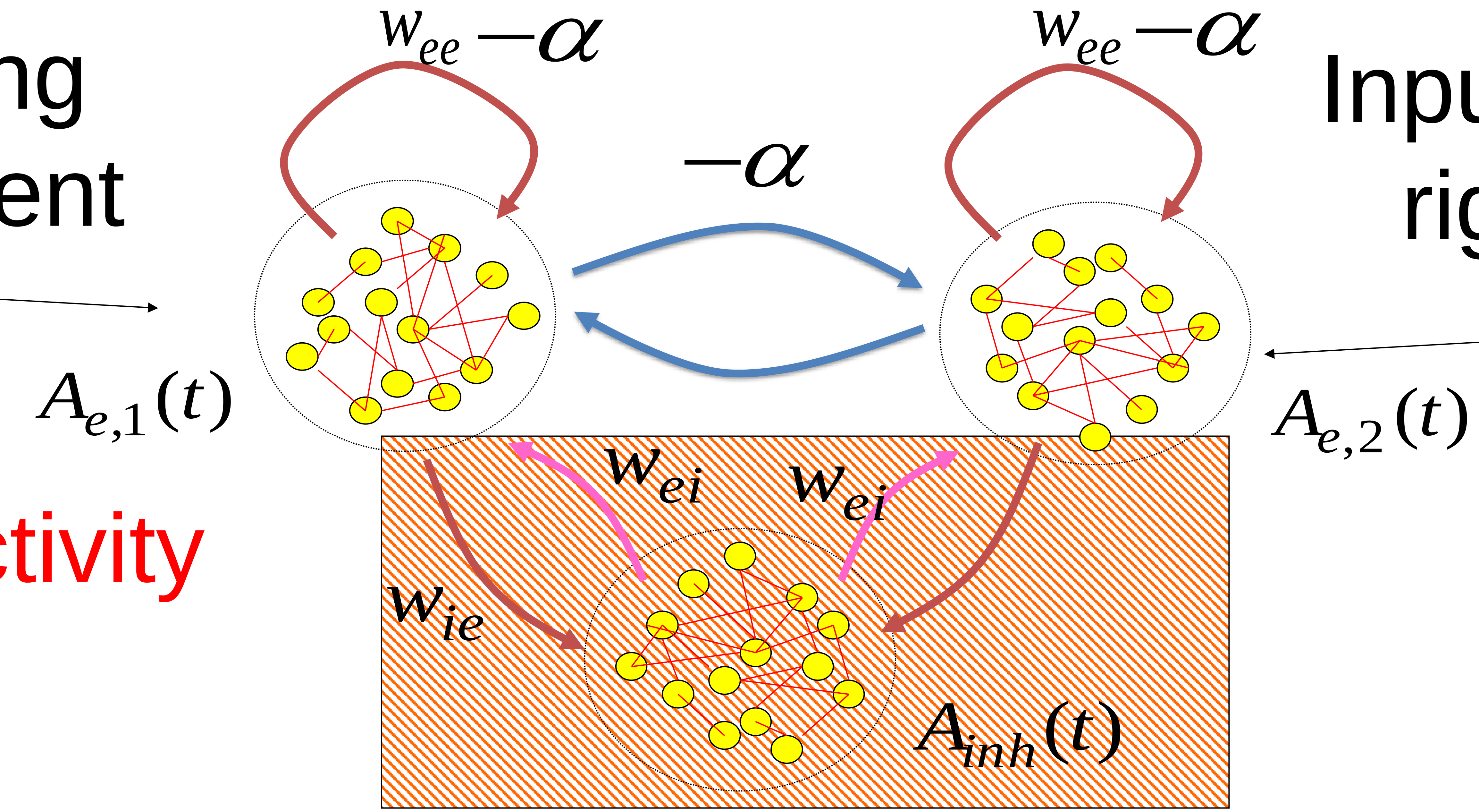
Membrane potential caused by input

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

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

Input indicating left movement

Input indicating right movement



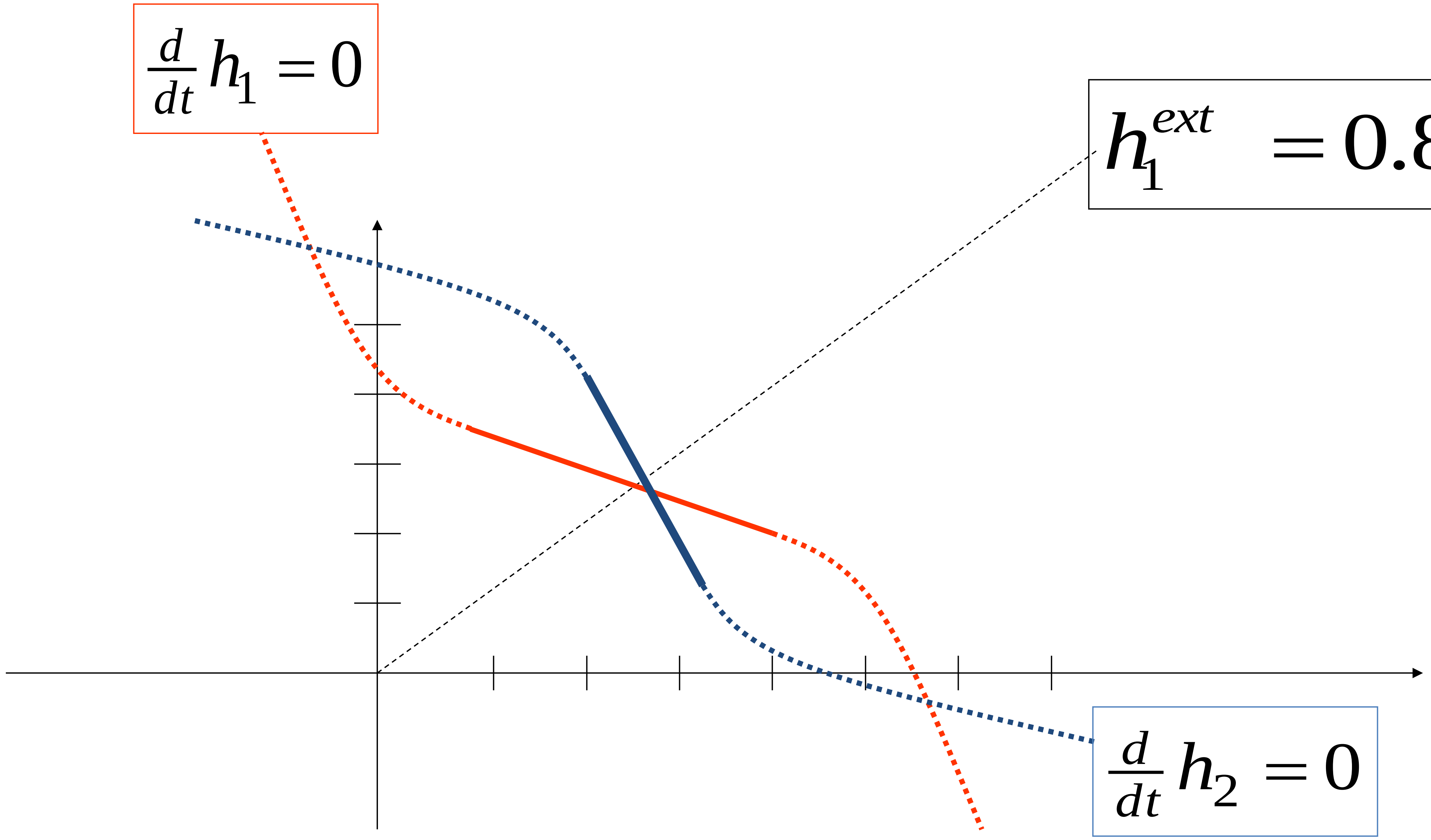
population activity

9.3. Phase plane analysis for effective model

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

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

Phase plane, strong external input



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

$$g(0) = 0.1$$

$$g(1) = 0.9$$

Quiz:

Start with Exercise 1. Once finished, imagine that you change the external inputs.

A **Keep the input to population 2 at 0.8,**
but reduce the input to population 1 from 0.8 to 0.2 or 0.0

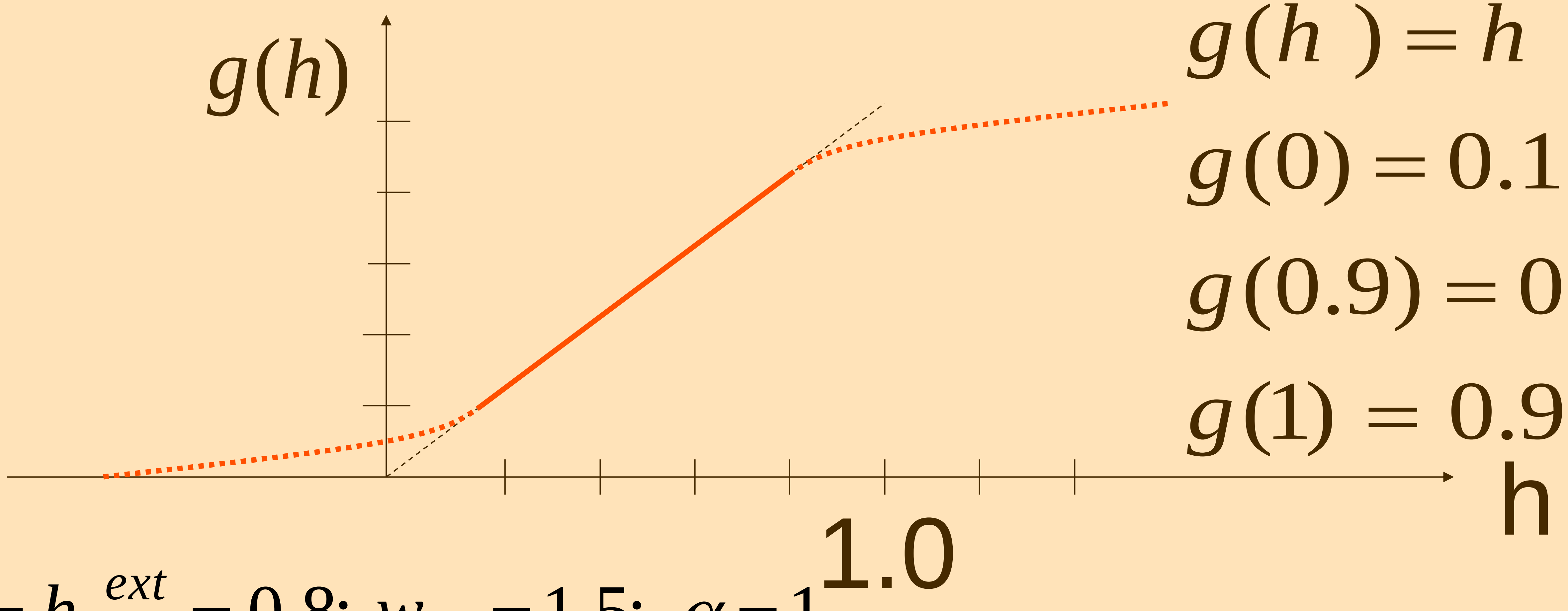
[ ] The (linear section of the) h_2-nullcline shifts vertically downward
[ ] The (linear section of the) h_2-nullcline shifts horizontally leftward
[ ] The (linear section of the) h_1-nullcline shifts vertically downward
[ ] The number of fixed points may changes

B **In addition, you now also reduce the input to population 2,**
0.8 to 0.2 or 0.0

[ ] The (linear section of the) h_2-nullcline shifts vertically downward
[ ] The (linear section of the) h_2-nullcline shifts horizontally leftward
[ ] The (linear section of the) h_1-nullcline shifts vertically downward

Exercise 1: draw nullclines, flow arrows, trajectories

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



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

$$g(0) = 0.1$$

$$g(0.9) = 0.85$$

$$g(1) = 0.9$$

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

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

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

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

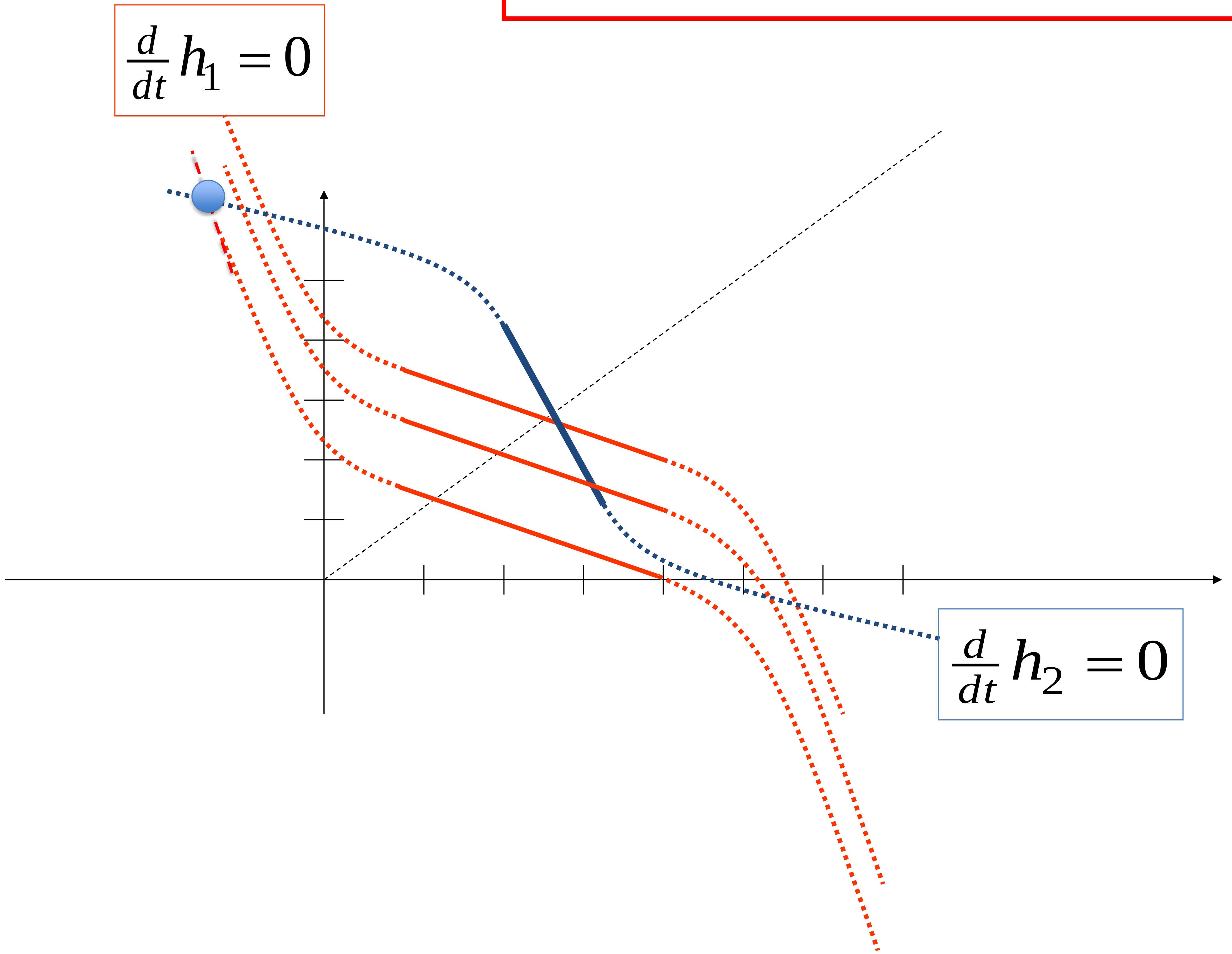
h_2	$g(h_1)$	h_1
1.0		
0.8		
0.2		
0.0		

9.3. Summary: Competition and Model of Decision making

A simple model of decision making consists of two populations of excitatory and one population of inhibitory neurons. Excitatory neurons send recurrent inputs inside their own population and also excite the population of inhibitory neurons. Each population is modeled by a population rate equation (model of population activity A). We think of the two excitatory populations as groups of neurons representing the choice ‘left’ (e.g., initiating movement to the left/pressing the left button) or ‘right’ – an appropriate stimulus can therefore excite one or the other; or even both groups if we think of an ambiguous stimulus. An example would be a stimulus where 50 percent of dots move to the left and 50 percent to the right and the task is to find out whether more dots move left or right.

The mathematical model has three coupled differential equations. However, under the assumption that (i) inhibitory neurons are more rapid than excitatory ones and (ii) the output of inhibitory neurons is a linear function we can eliminate one of the three equations so as to arrive at a system of two coupled equations.

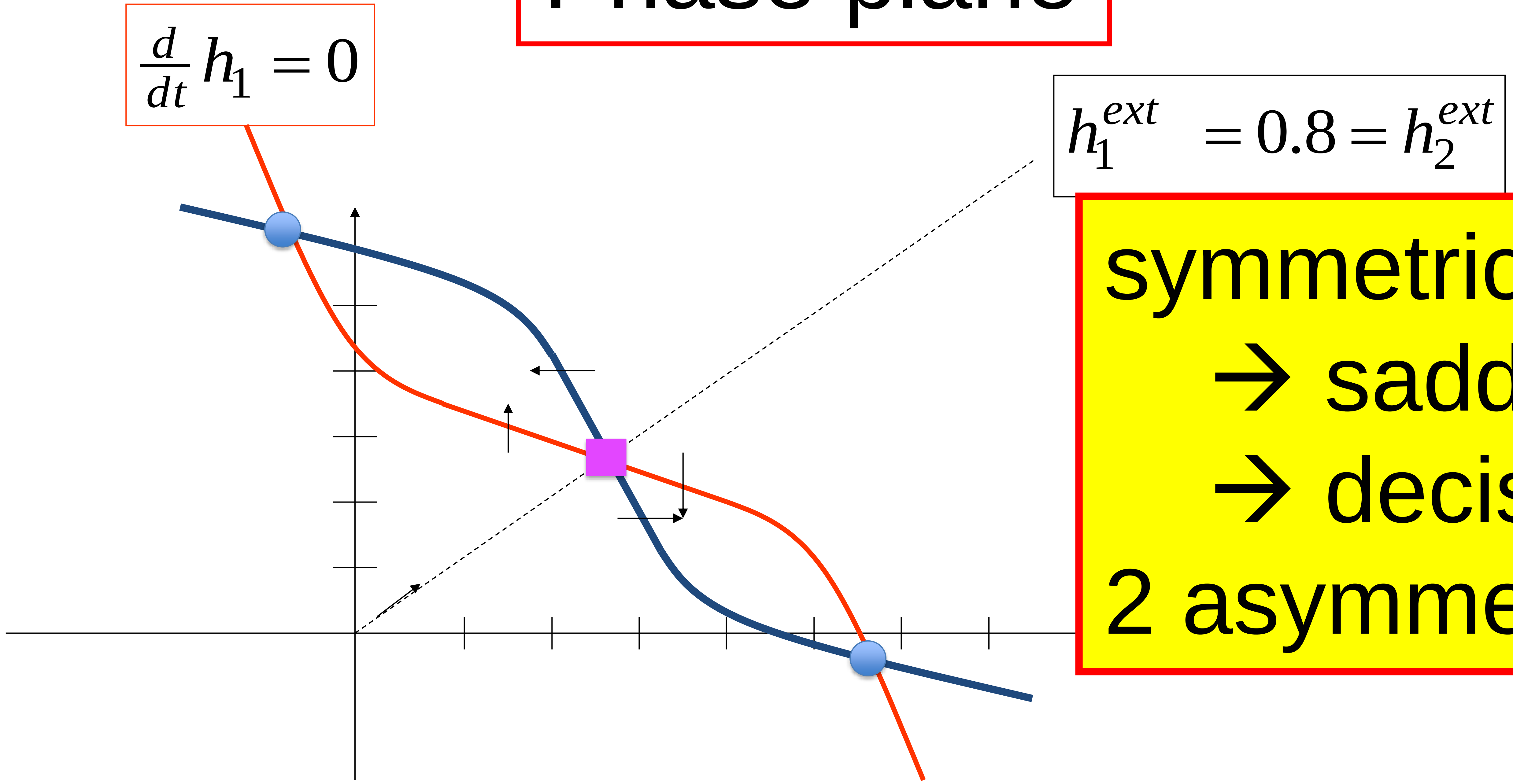
Phase plane, strong input to population 2
weak input to population 1



9.4. Theory of decision dynamics: unbiased strong

Next Lecture at 11h15.

Phase plane



symmetric solution exists, but
→ saddle point
→ decision must be taken
2 asymmetric stable solutions

With unbiased input, there is a minimal input strength where the (single) stable solution turns into a saddle

9.4. Summary: Phase plane analysis of decision model

Symmetric case: In the absence of an external stimulus, the only solution is the one where both populations have the same level of low or vanishing activity.

However, if both populations receive a strong stimulus of equal amplitude (e.g., an ambiguous stimulus where 50 percent of points move coherently to the left and 50 percent coherently to the right with decision task to find out whether more dots move left or right), then there are two equivalent stable solutions: either the first population is highly active and the second one silent or vice versa. Hence, a decision in favor of one of the two options is enforced (necessarily taken) despite the fact that the stimulus is completely symmetric. Physicists call this a case of 'spontaneous symmetry breaking'. The two stable solutions are separated by a saddle point.

Biased case: In the presence of a strong stimulus favoring one of the two populations (and no stimulus for the other one), there is only one fixed point which reflects the favored input. Hence the decision (= the population which is highly activated) is in agreement with the input.

9.5: Decisions in populations of neurons: simulation

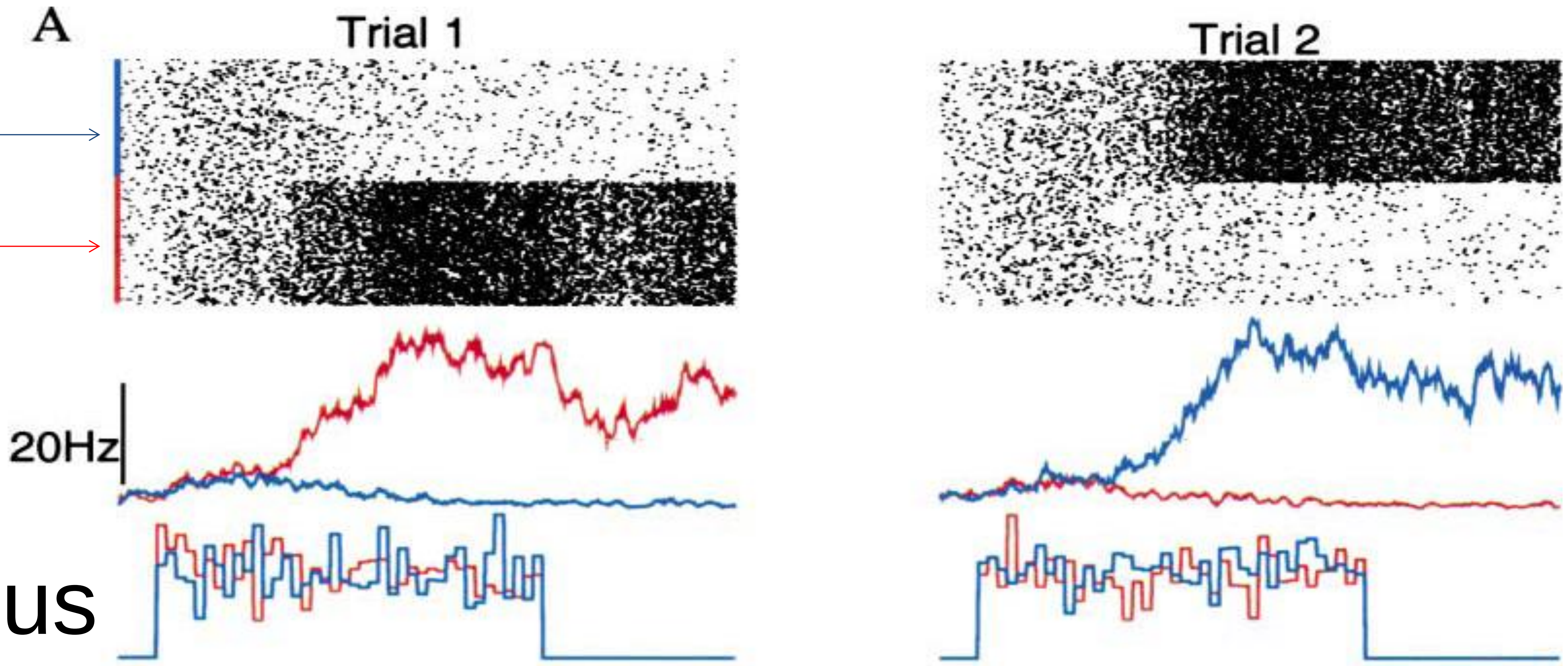
Simulation of 3 populations of spiking neurons, unbiased strong input

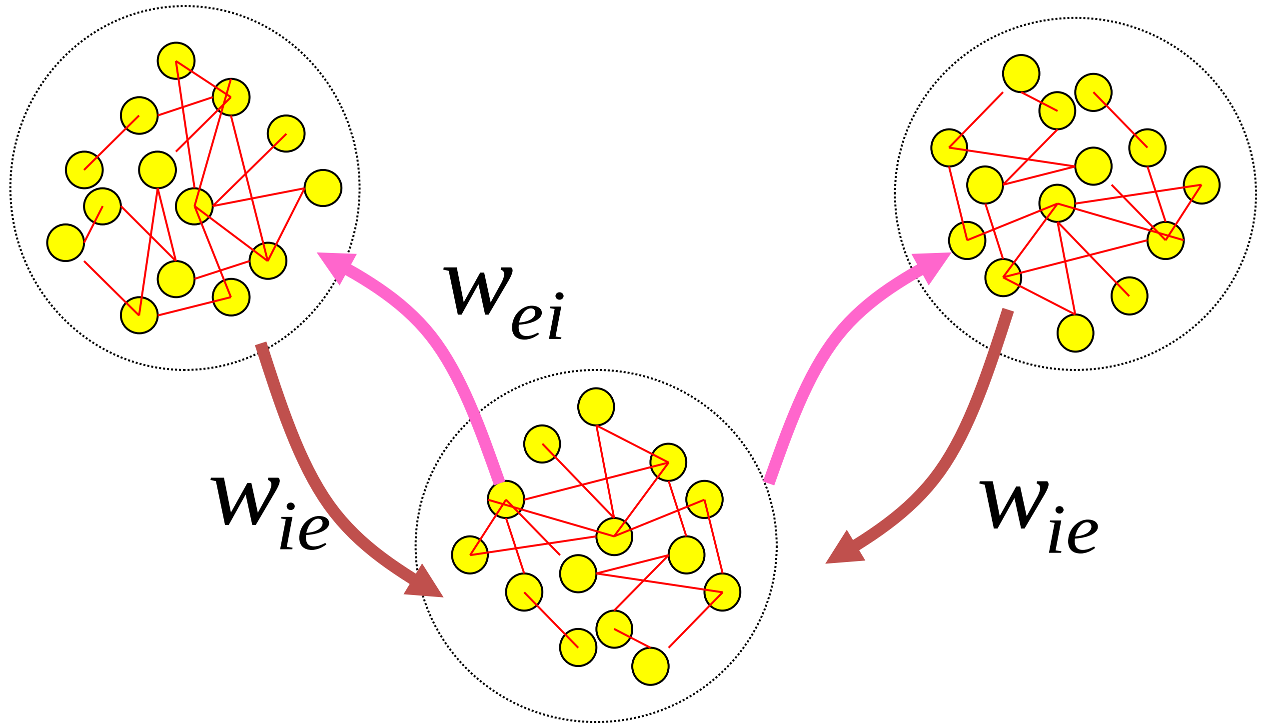
X.J. Wang, 2002
NEURON

Popul. 2

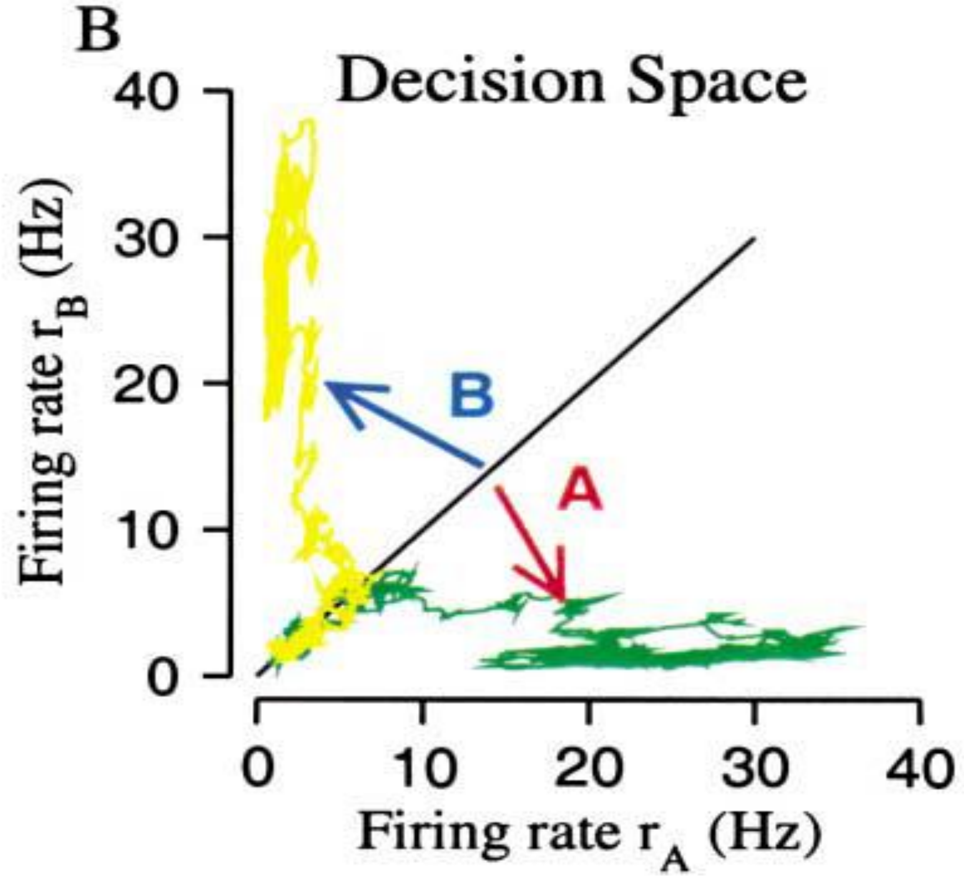
Popul.1

stimulus





$A_2(t)$



$A_1(t)$

9.5. Summary: Spiking Models and data

As we have seen in Lecture 7, the population rate model is an abstraction and simplification of a population of spiking neurons. If we directly simulate three populations of spiking neurons, we find the same qualitative behavior that we have derived mathematically using phase plane analysis for the population activity model (reduced to two interacting populations).

The spiking model shares many features with the experimental data. In particular the fact that activity of the non-preferred population DECREASES while the activity of the preferred population (i.e., that of the more strongly stimulated population) increases (‘ramp-up’ or ‘integration phase’)

Again a warning: this is a model of decision making which shares features with experimental data of LIP neurons during a decision making task, but this correlation does neither imply that decisions (for such a saccadic task) are taken in area LIP nor that the model is a correct description of these experiments. For example, the ramp-up/integration could be an artifact of the PSTH (averaging of trials) while in single trials, the transition could be more discrete.

9.6. Summary: Neurophilosphy of decision making and free will

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3. In experiments, the links between early activity and later decision outcome are only stochastic.
4. In typical experiments on free decisions/free will, the task is absolutely irrelevant, i.e., we do not care about the outcome. In these cases there is no philosophical problem if we rely on a noise source.
5. In cases where we care about the outcome (voting in an election), we have reflected beforehand and vote according to our preferences.
6. These preferences in turn are the result of our experiences and education – and these experiences, concepts, and insights are stored in the brain (where else?).
7. Rapid decisions (Roger Federers reaction to the flying ball) are automatically taken before reflecting about them.

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