Biological Modeling of Neural Networks

EPFL

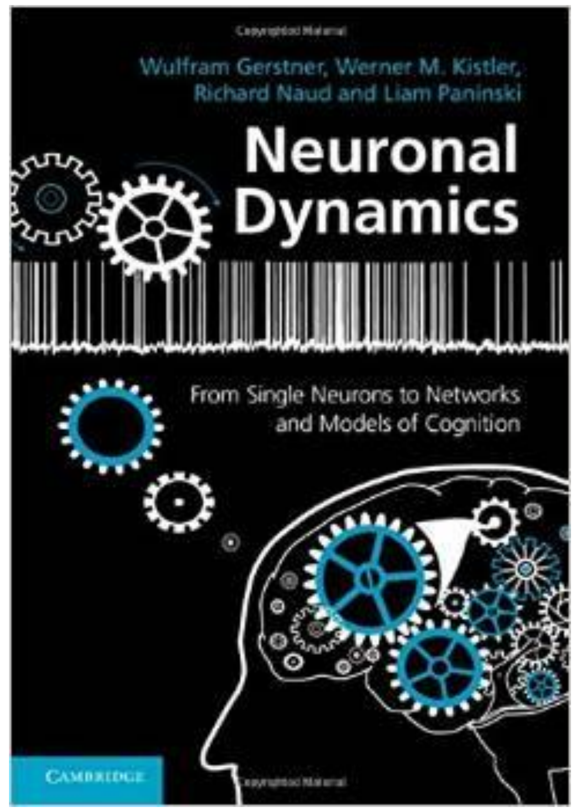
Week 13

Synaptic plasticity and Learning

Wulfram Gerstner

EPFL, Lausanne, Switzerland

Reading for plasticity:
NEURONAL DYNAMICS
- Ch. 19.1-19.3



Cambridge Univ. Press

1. Synaptic plasticity
motivation and aims

2. Classification of plasticity
short-term vs. long-term
unsupervised vs. reward modulated

3. Model of short-term plasticity

4. Models of long-term plasticity
- Hebbian learning rules
- Bienenstock-Cooper-Munro rule

5. Spiking Models of plasticity
- STDP as Hebbian learning
- Model of STDP: synaptic traces

6. From STDP to rate models

7. Triplet STDP model

8. Online learning of memories

1. Behavioral Learning – and Memory

Learning actions:

→ riding a bicycle

Remembering facts

→ previous president of the US

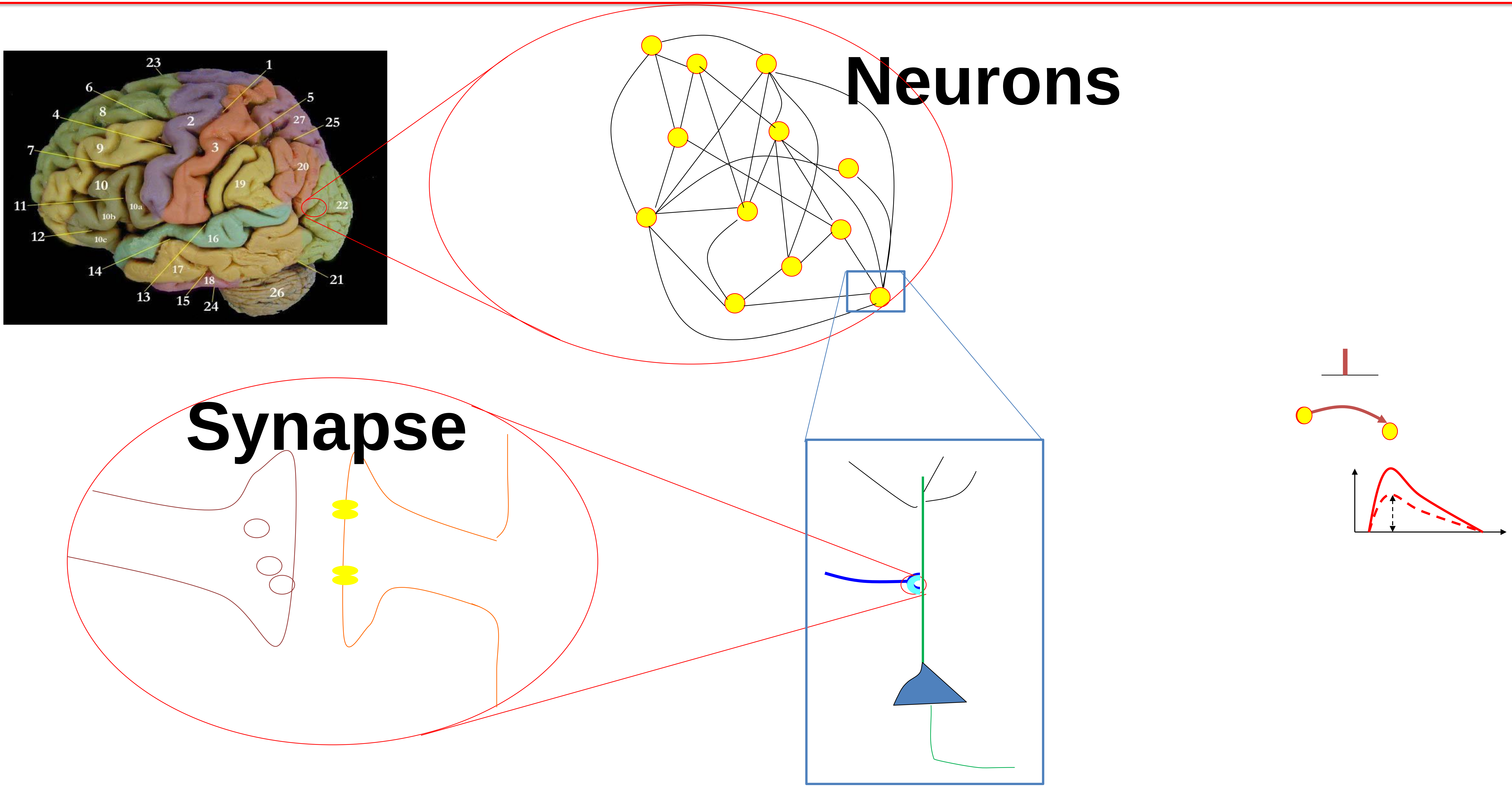
→ name of your mother

Remembering episodes

→ first day at EPFL

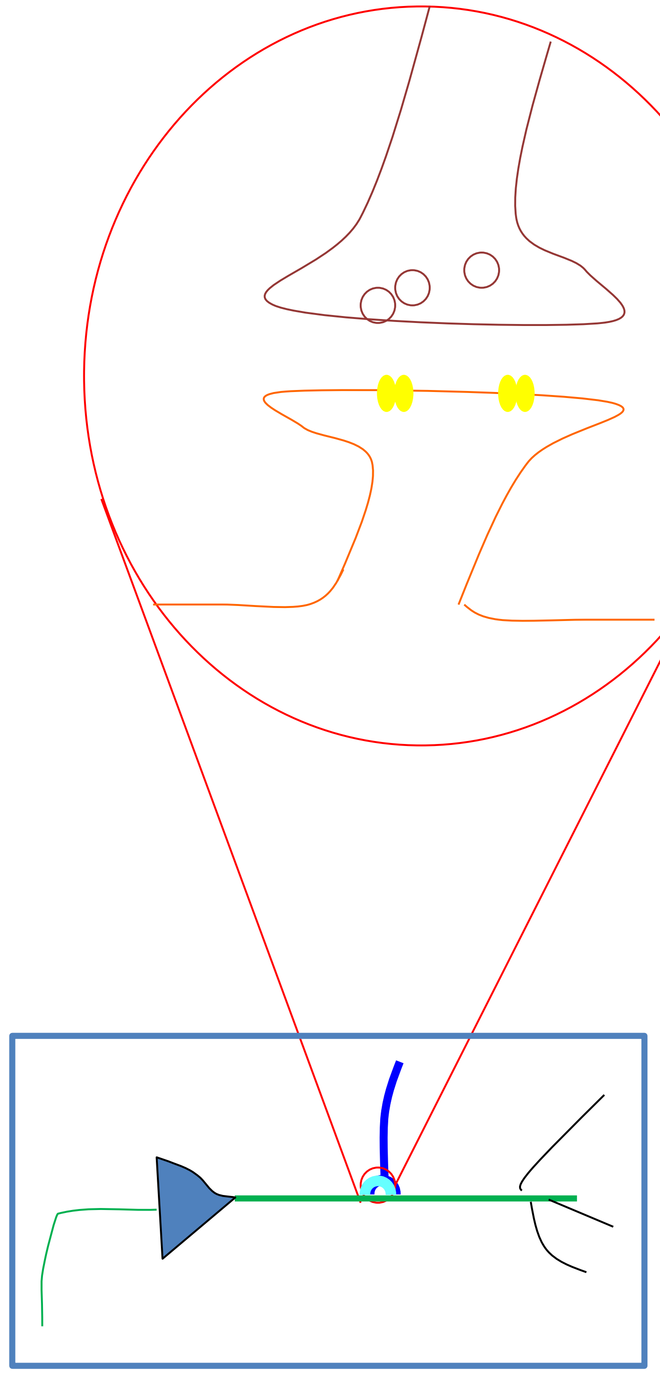
which parking spot?

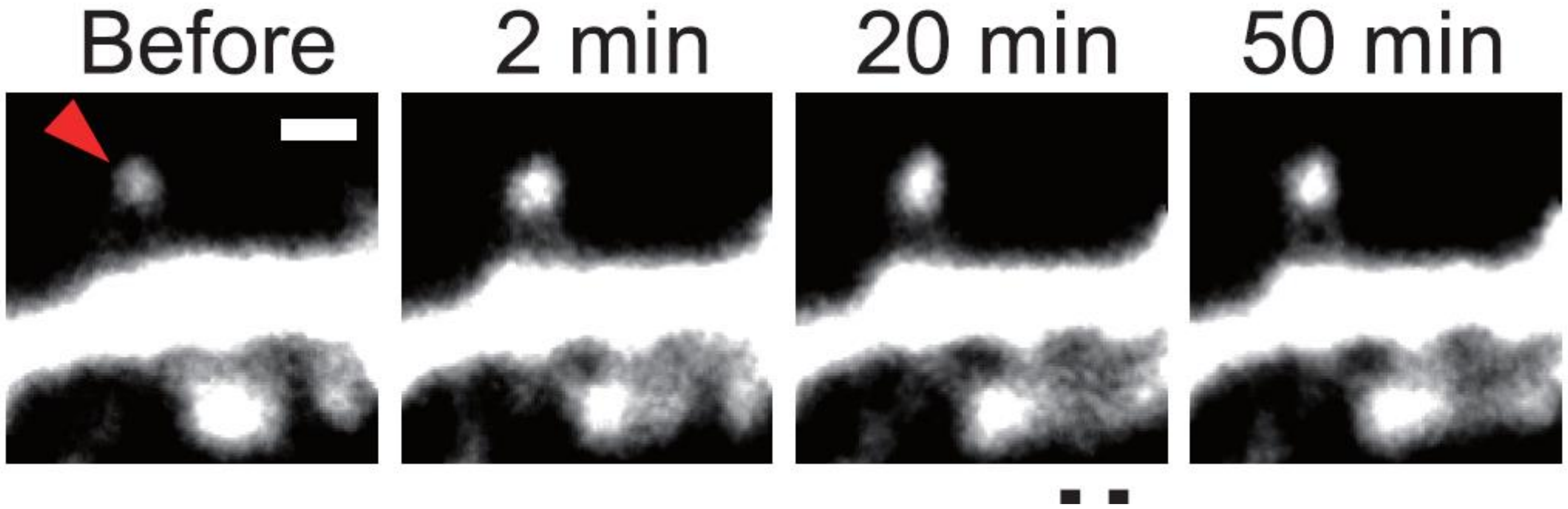
1. Behavioral Learning – and synaptic plasticity



Synaptic Plasticity =Change in Connection Strength

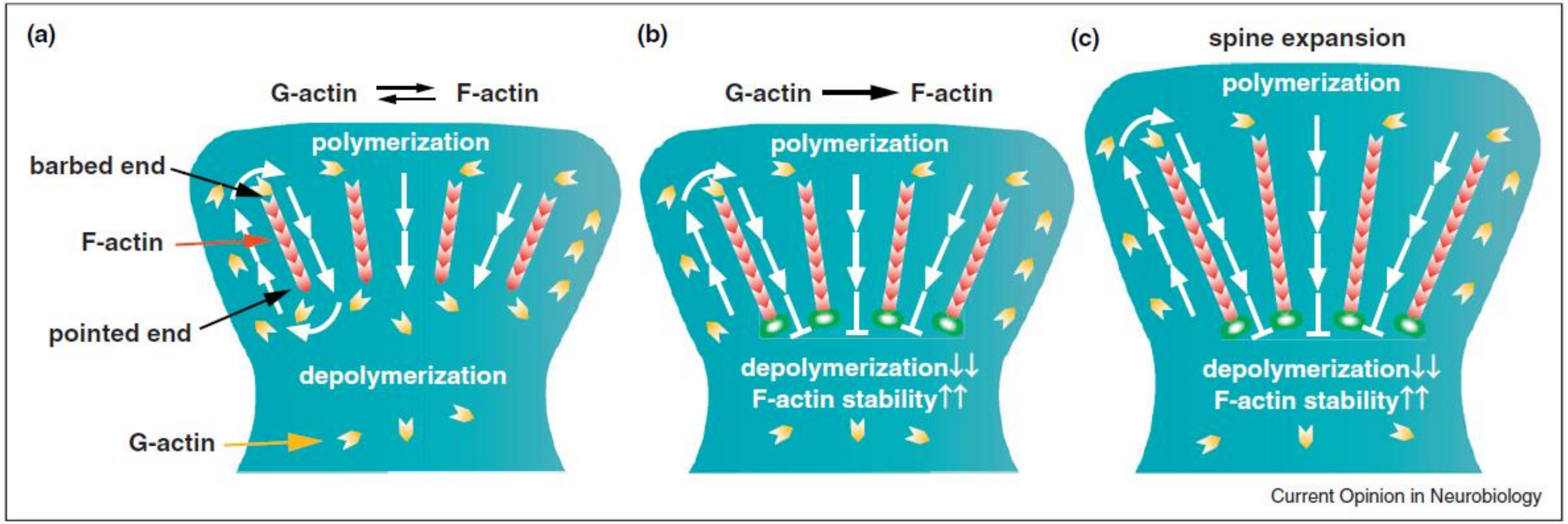
1. Synaptic plasticity – structural changes



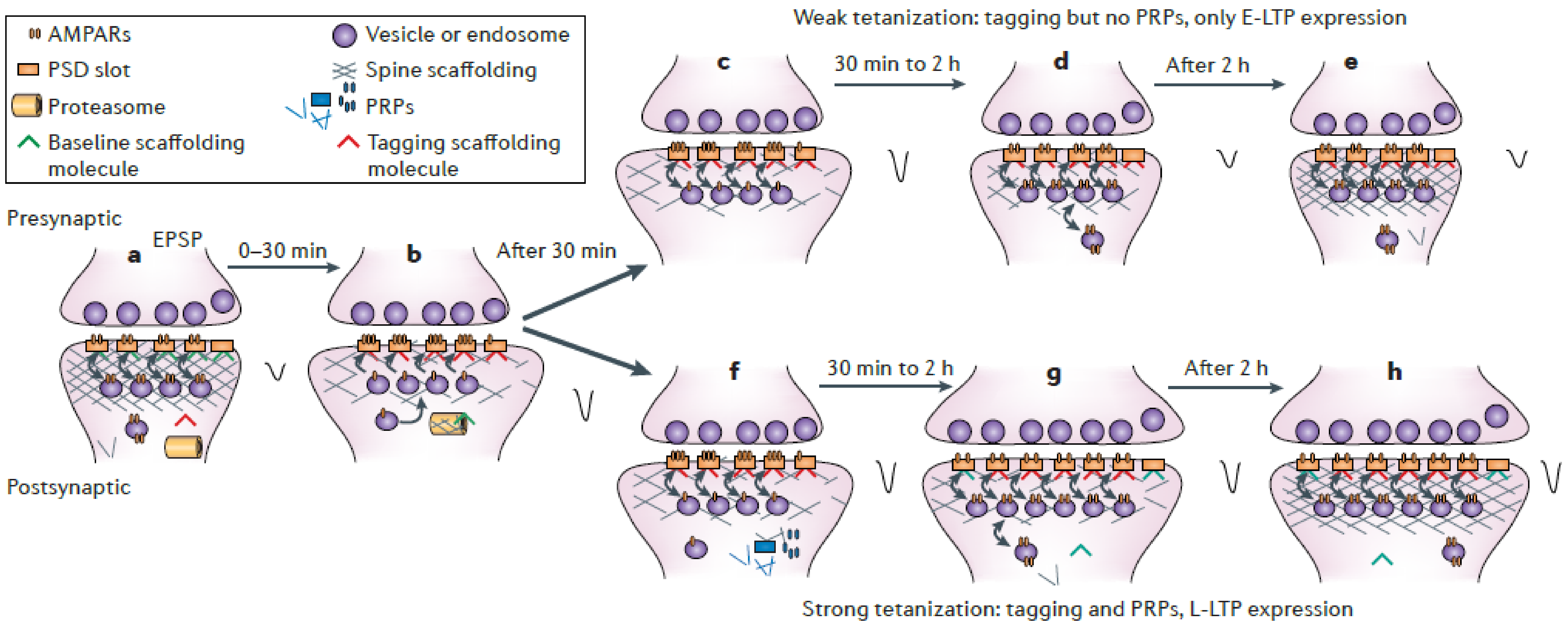


Yagishita et al.
Science, 2014

1. synaptic plasticity – molecular changes

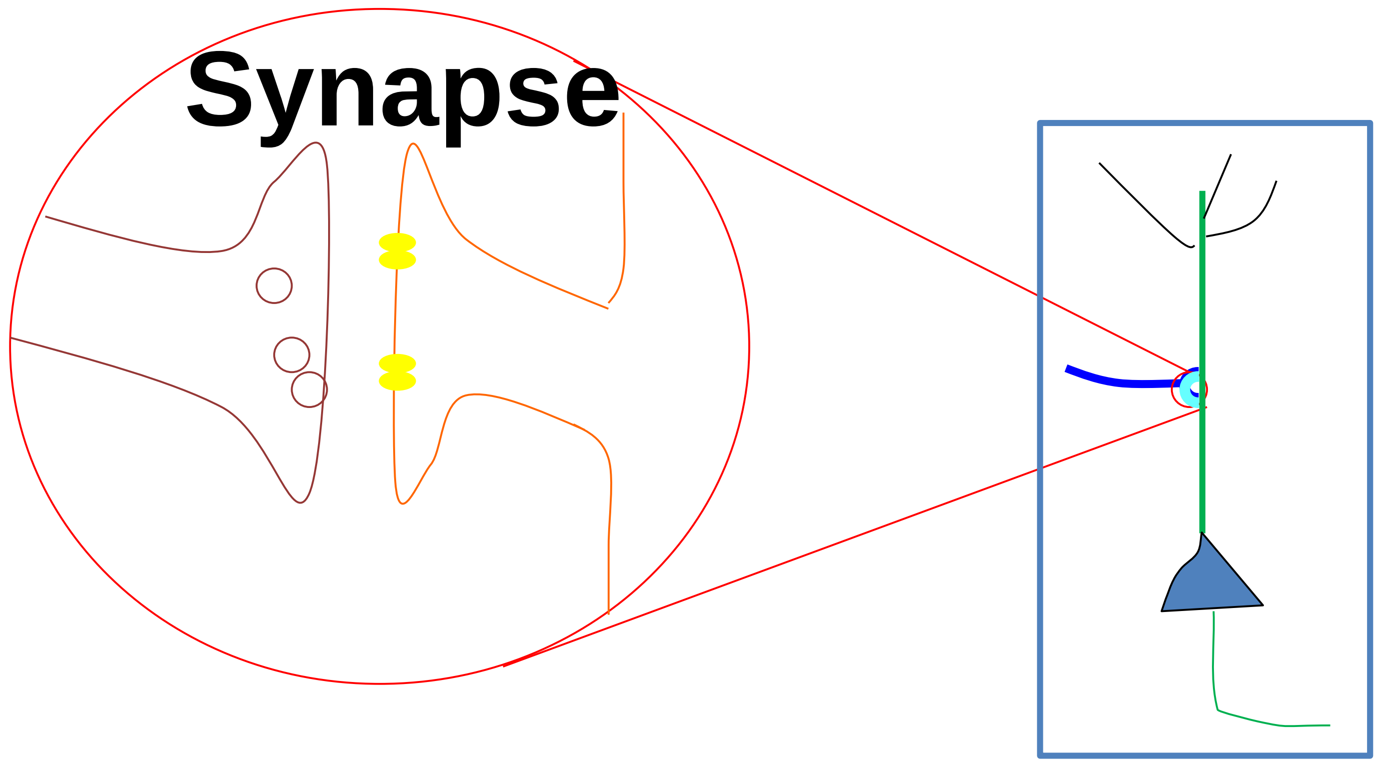


Bosch et al. 2012, Curr. Opinion Neurobiol.



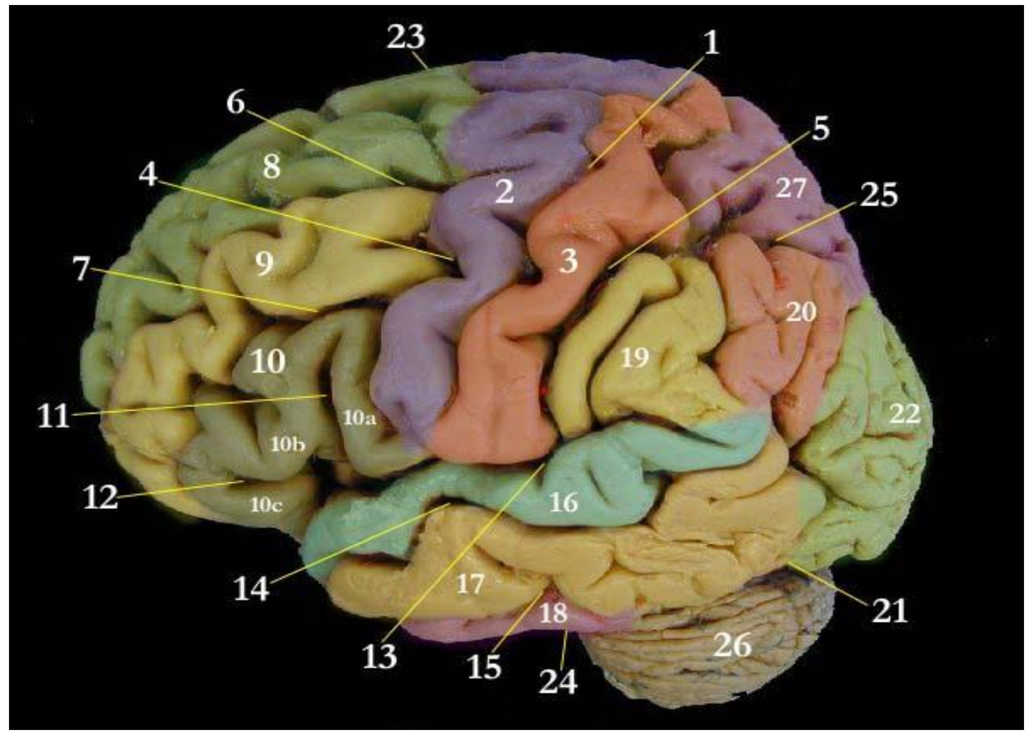
Redondo and Morris 2011, Nature Rev. Neurosci.

1. synaptic plasticity – connections change



More space in cortex allocated
- musicians vs. non-musicians

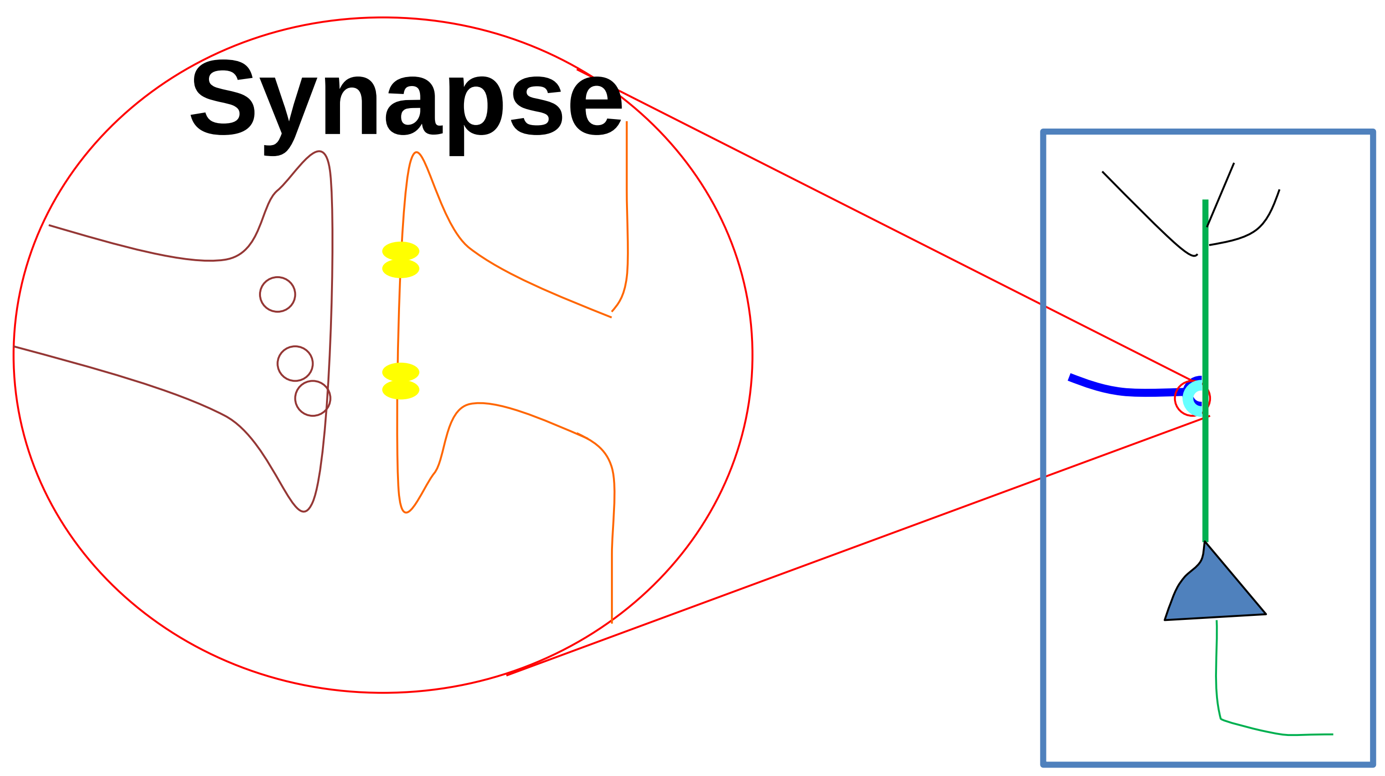
Amunts et al. Human Brain Map. 1997
Gaser and Schlaug, J. Neuosci. 2003

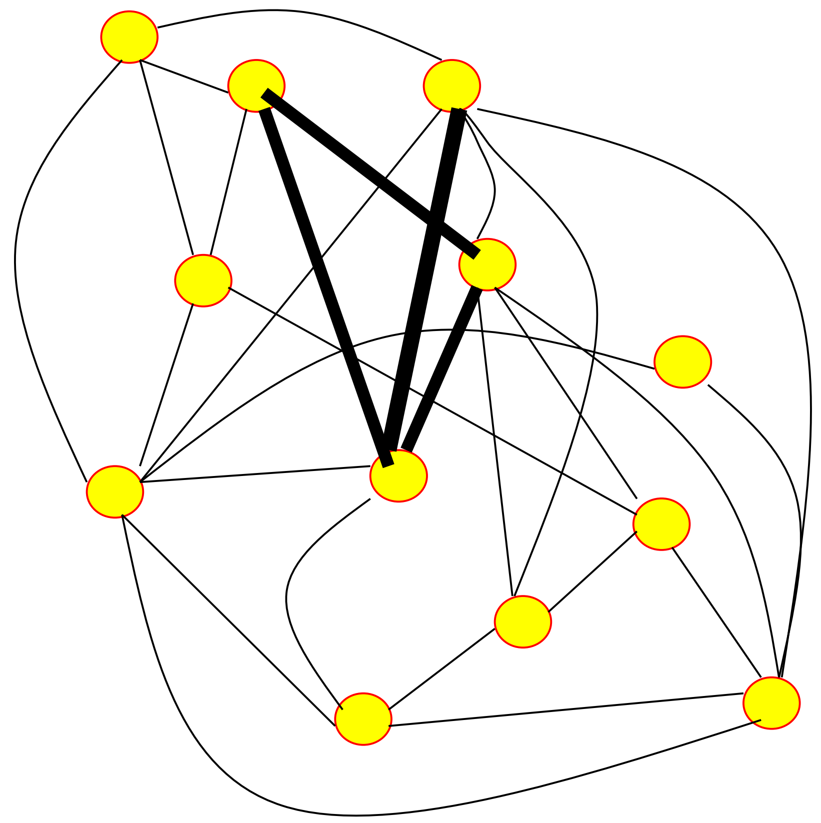


More space in hippocampus allocated
- London taxi driver vs bus driver

Macquire et al. Hippocampus 2006

1. Synaptic plasticity





Should enable Learning

- adapt to the statistics of task and environments (receptive fields, allocate space etc)
- memorize facts and episodes
- learn motor tasks

Should avoid:

- blow-up of activity
- unnecessary use of energy

homeostasis

Aim: models that capture the essence

1. Synaptic plasticity: program for this week

-**Hebbian Learning**

- Experiments on synaptic plasticity

- Mathematical Formulations of Hebbian Learning

- Back to Attractor Memory Models

1. Synaptic plasticity: summary

Synaptic plasticity (= changes of synaptic contact points) are the basis of learning.
Learning is necessary for a variety of different tasks.
Learning leads to measure changes in performance (you get better at a task) and to measurable changes in the brain.
As an example of a synaptic plasticity rule, we consider Hebbian learning first.
We start with some experimental data, before move on to the mathematical formulation.

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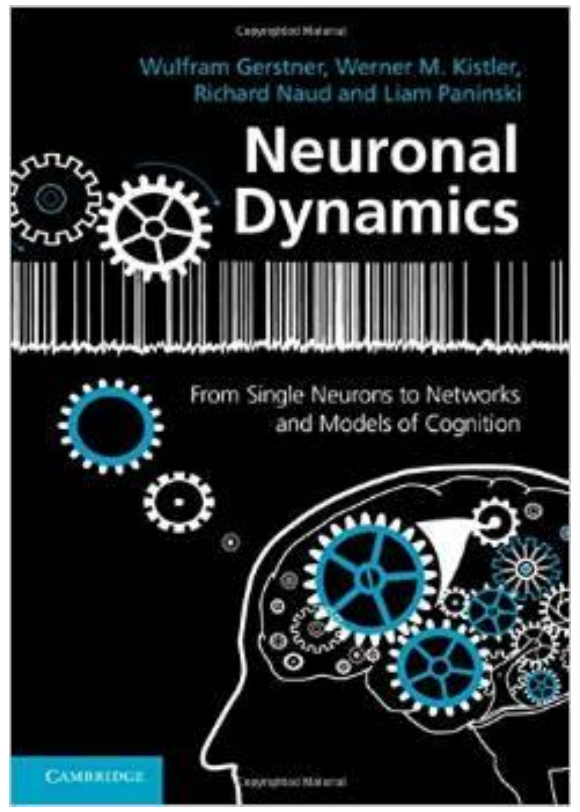

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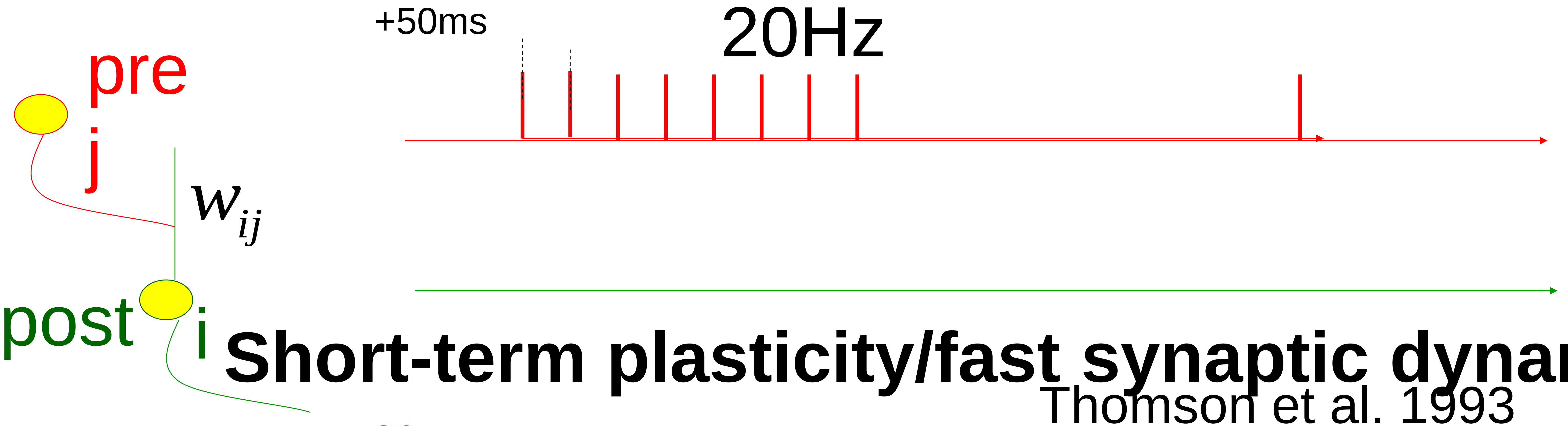
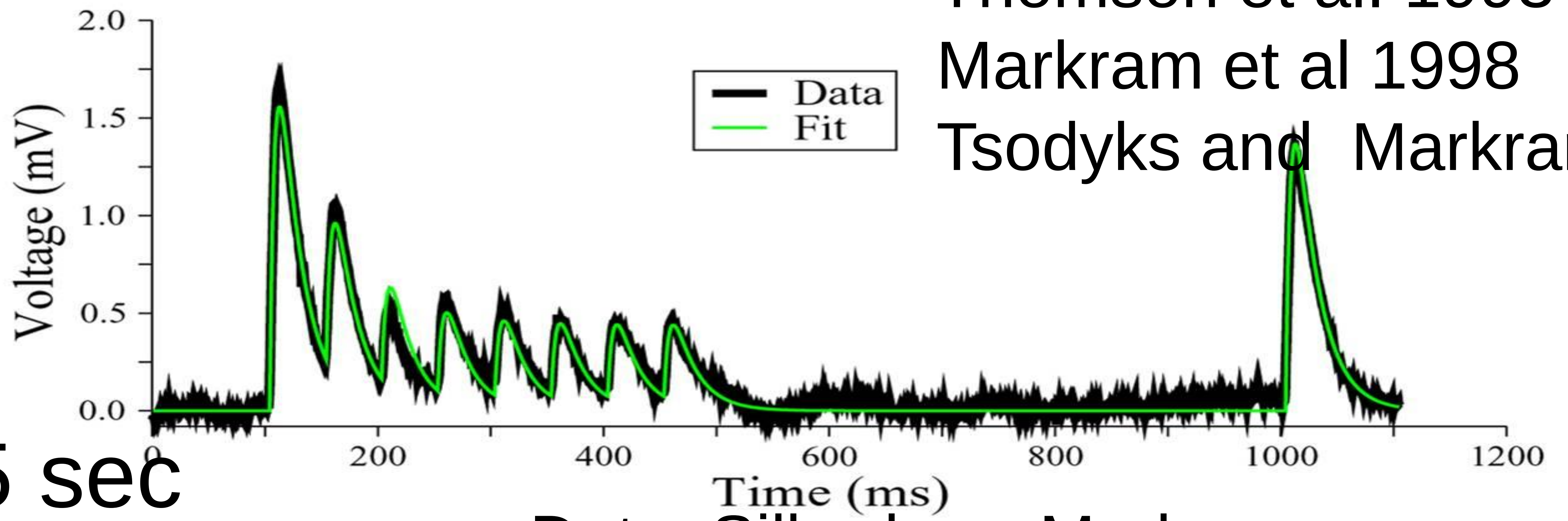
   motivation and aims
2. **Classification of plasticity**
   short-term vs. long-term
   unsupervised vs. reward modulated
3. **Model of short-term plasticity**
4. **Models of long-term plasticity**
   - Hebbian learning rules
   - Bienenstock-Cooper-Munro rule
5. **Spiking Models of plasticity**

2. Classification of synaptic changes: Short-term plasticity



Short-term plasticity/fast synaptic dynamics

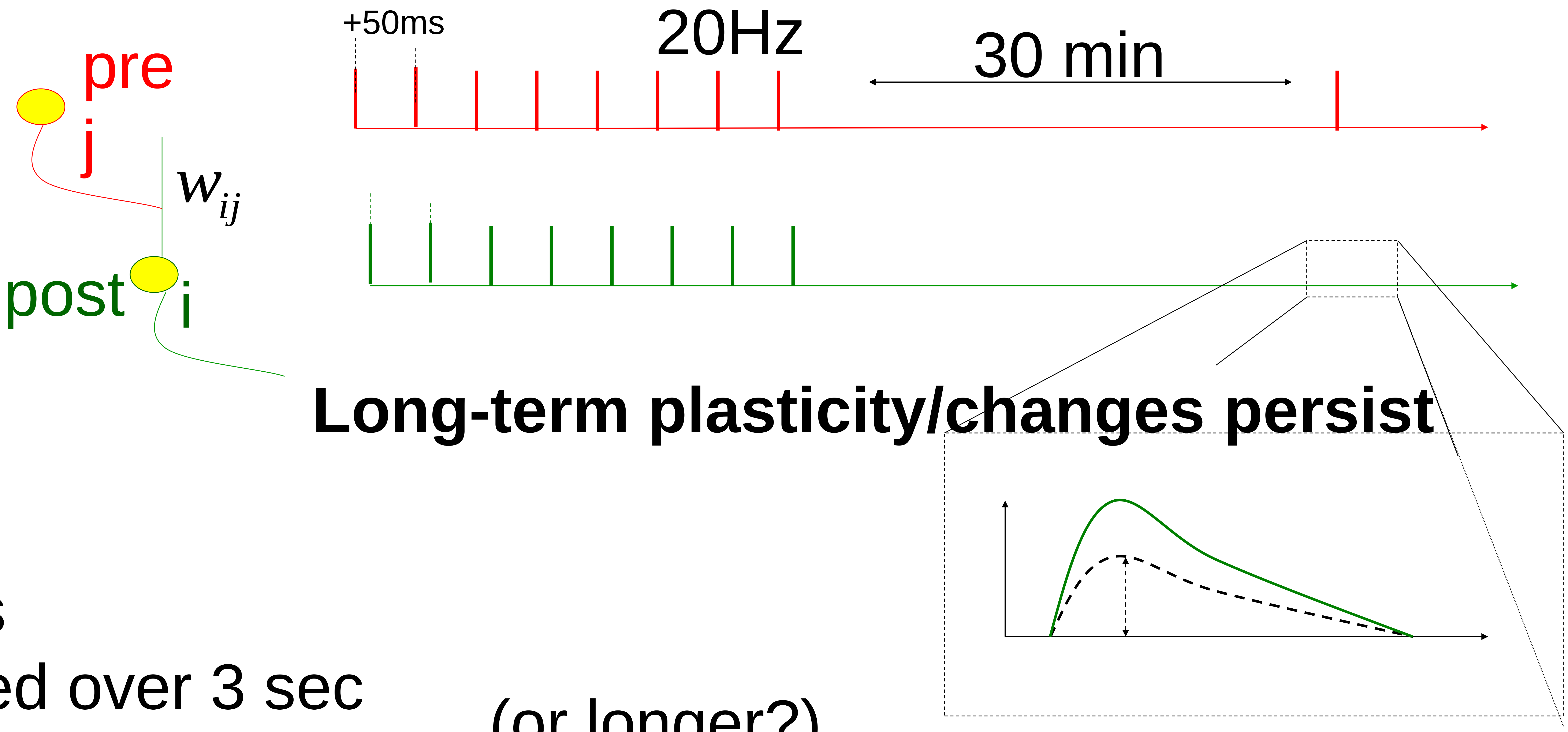
Thomson et al. 1993
Markram et al 1998
Tsodyks and Markram 1997



Changes
- induced over 0.5 sec
- recover over 1 sec

Data: Silberberg,Markram
Fit: Richardson (Tsodyks-Markram model)

2. Classification of synaptic changes: Long-term plasticity

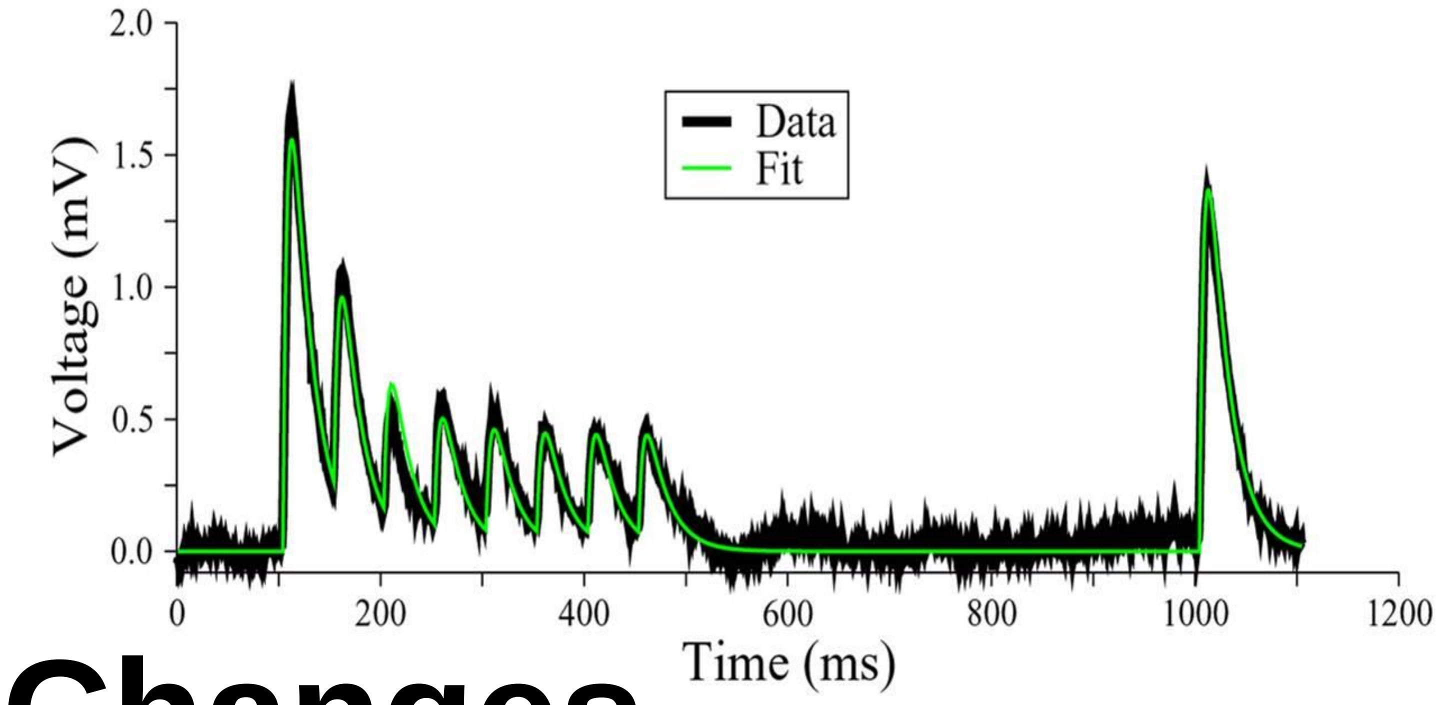


Long-term plasticity/changes persist

Changes
- induced over 3 sec
- persist over 1 – 10 hours (or longer?)

2. Classification of synaptic changes

Short-Term vs/ Long-Term



Changes

- induced over 0.1-0.5 sec
- recover over 1 sec

Protocol

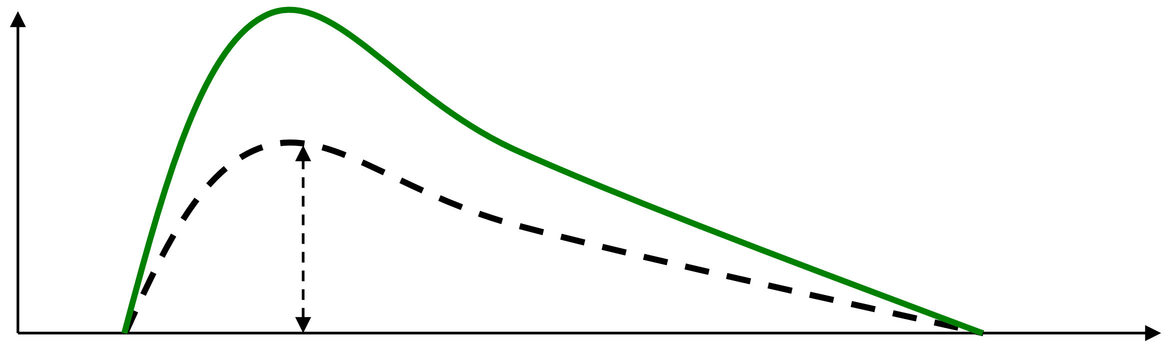
- presynaptic spikes

Model

- well established

(Tosdyks, Pawelzik, Markram Abbott-Dayan)

LTP/LTD/Hebb



Changes

- induced over 0.5-5sec
- remains over hours

Protocol

-presynaptic spikes + …

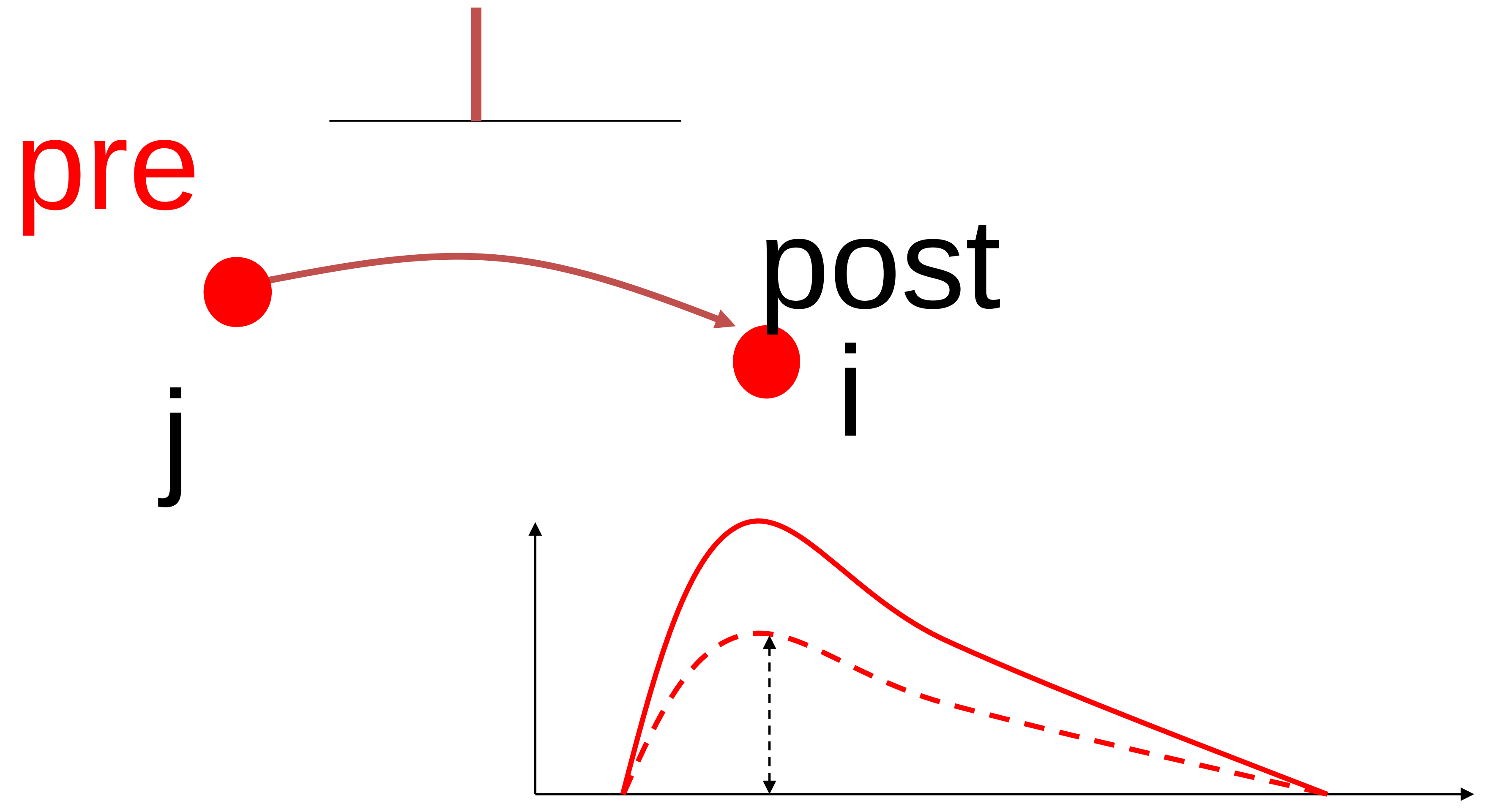
Model

- we will see

2. Classification of synaptic changes

Induction of changes

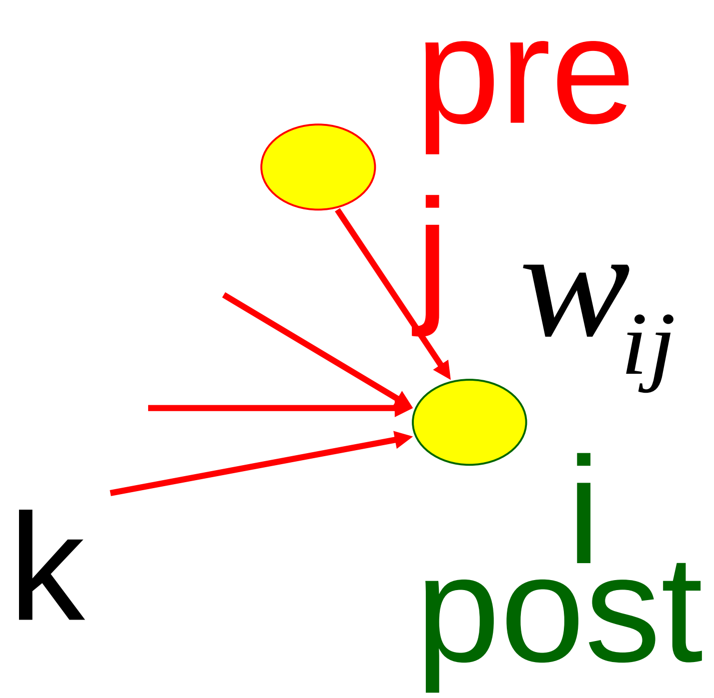
- fast (if stimulated appropriately)
- slow (homeostasis)

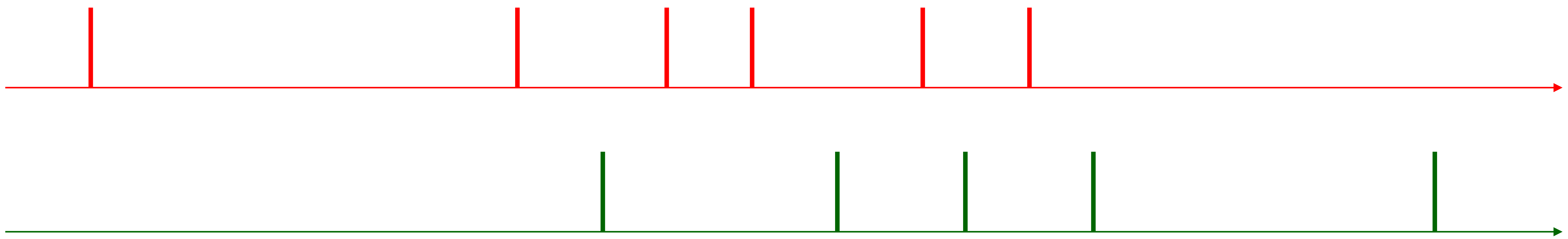


Persistence of changes

- long (LTP/LTD)
- short (short-term plasticity)

2. Review: Hebb rule





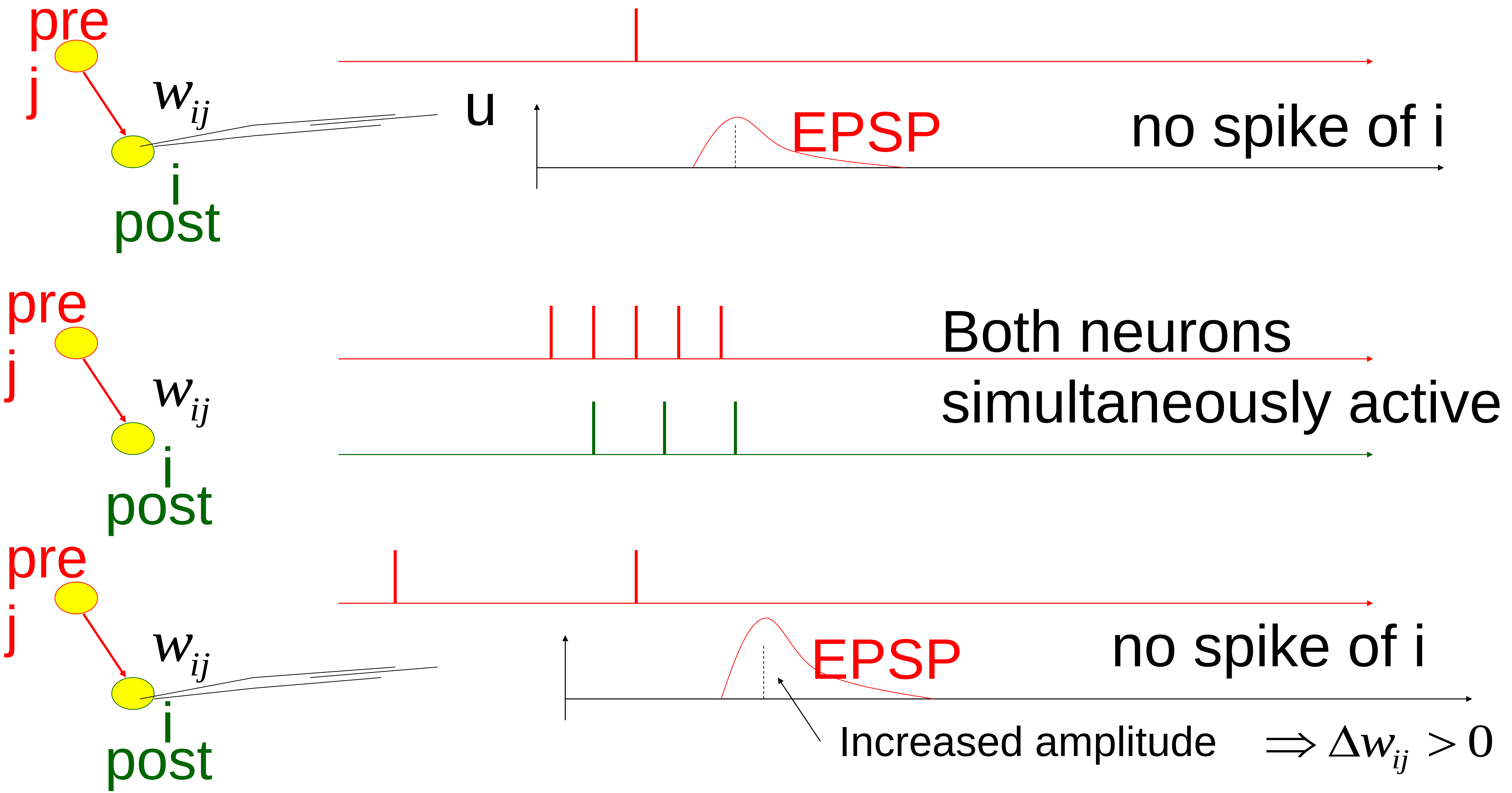
When an axon of cell **j** repeatedly or persistently takes part in firing cell **i**, then j's efficiency as one of the cells firing i is increased

Hebb, 1949

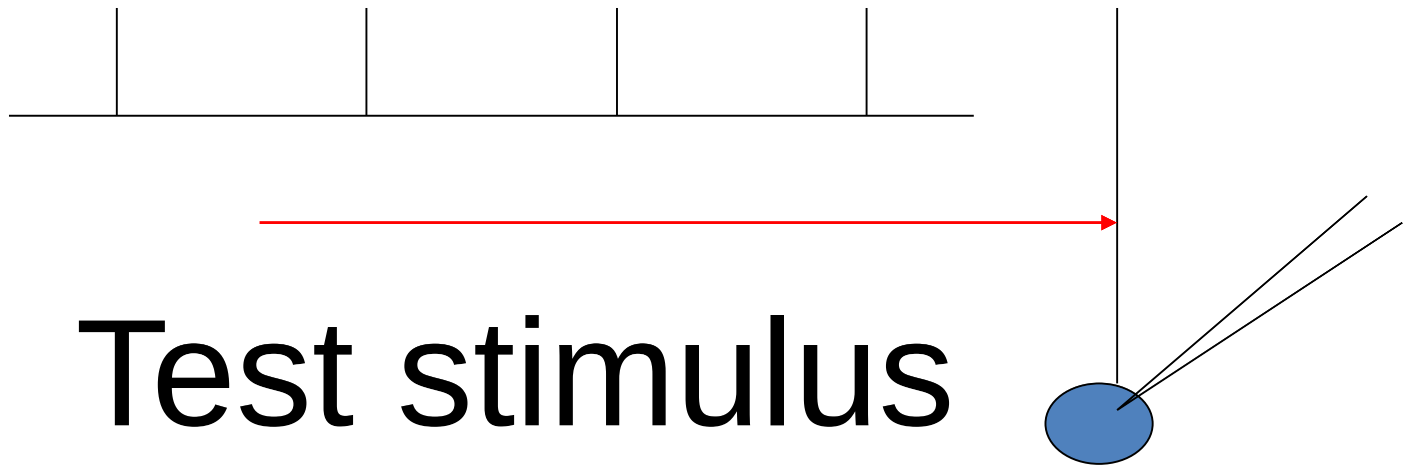
- local rule
- simultaneously active (correlations)

2. Synaptic plasticity: Long-Term Potentiation (LTP)

Hebbian Learning in experiments (schematic)



2. Classical paradigm of LTP induction – pairing



Test stimulus
At 0.1 Hz

neuron at -70mV

LTP induction:
tetanus at 100Hz

neuron depolarized to -40mV

Standard LTP
PAIRING experiment

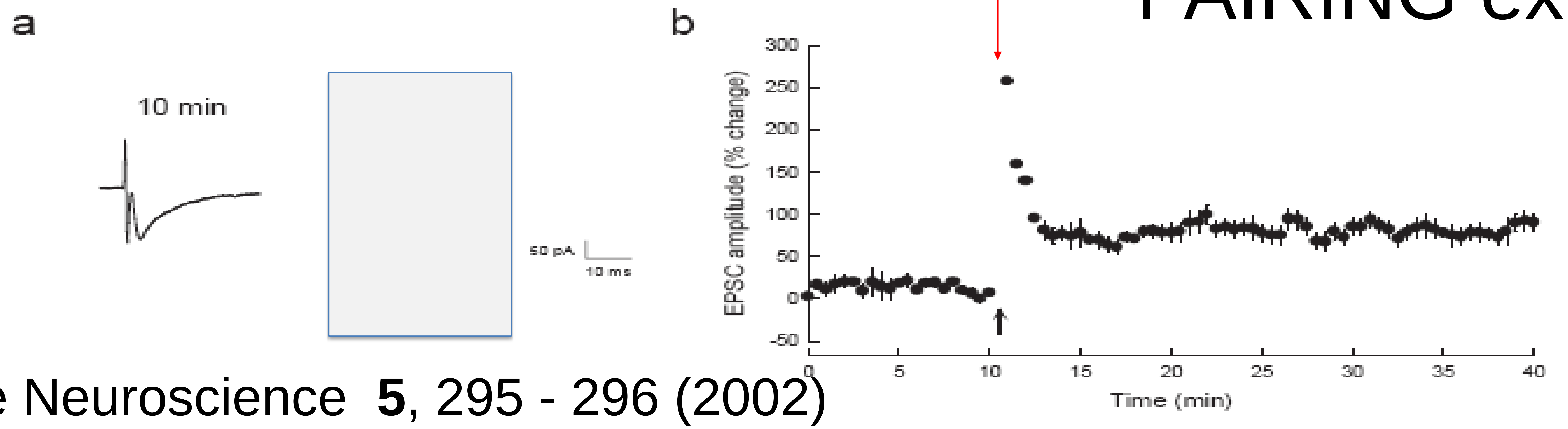
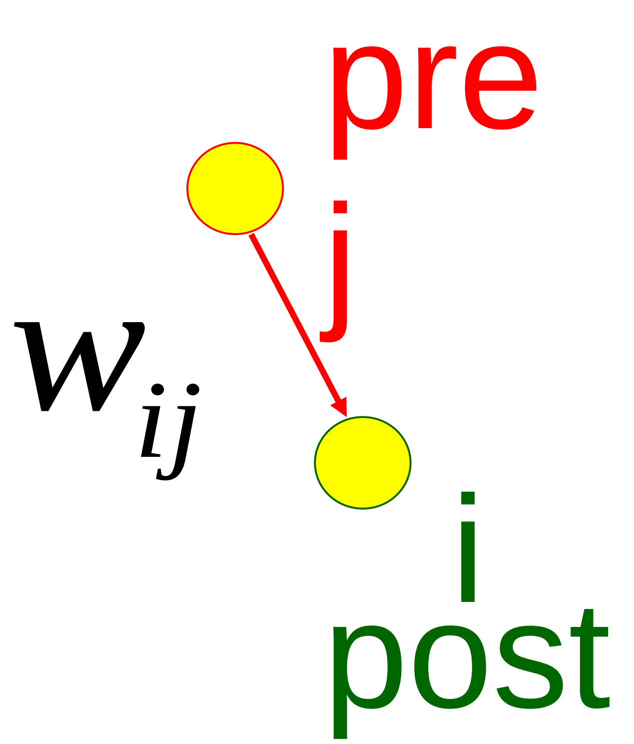


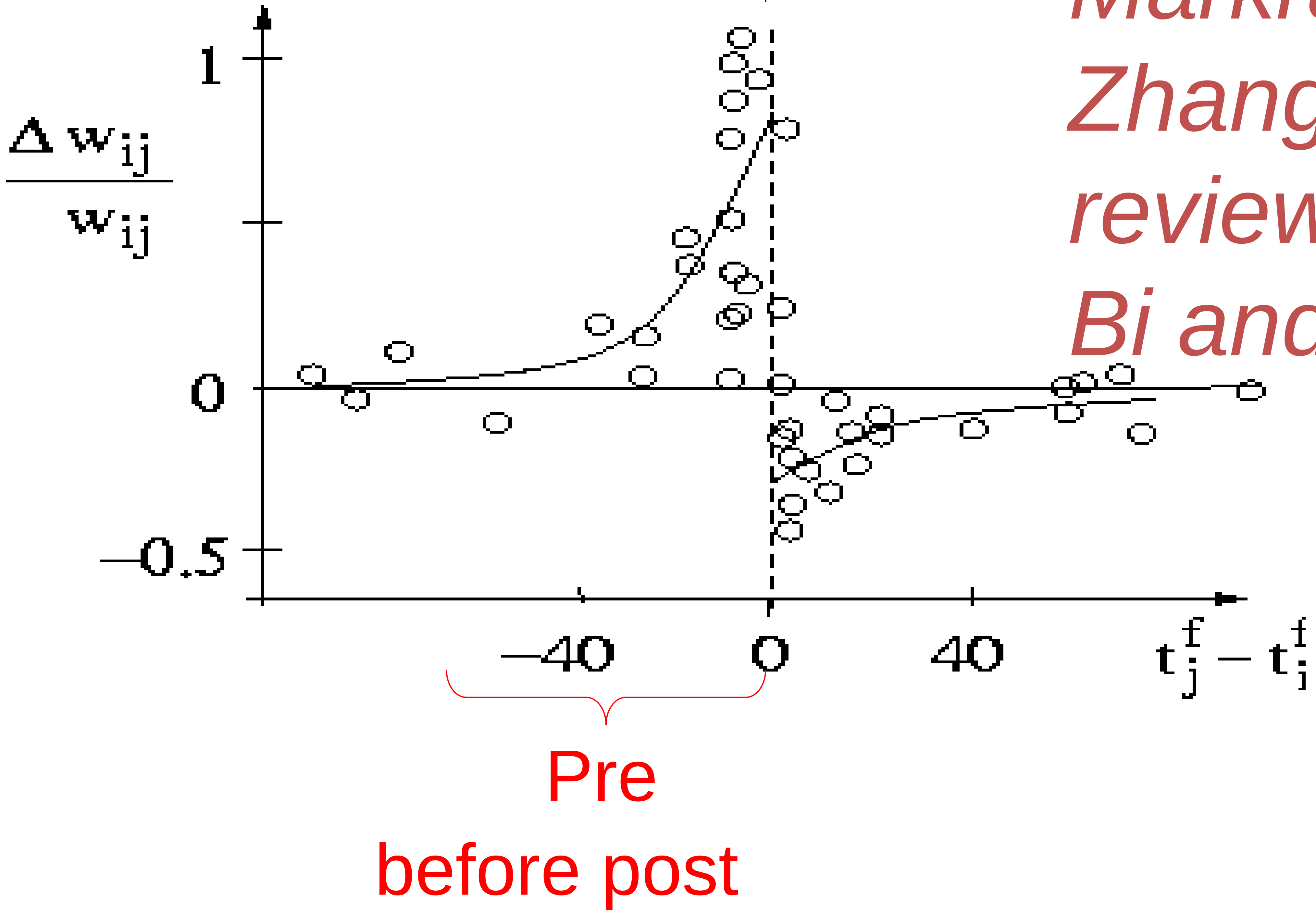
Fig. from Nature Neuroscience **5**, 295 - 296 (2002)
D. S.F. Ling, … & Todd C. Sacktor
See also: Bliss and Lomo (1973), Artola, Brocher, Singer (1990), Bliss and Collingridge (1993)

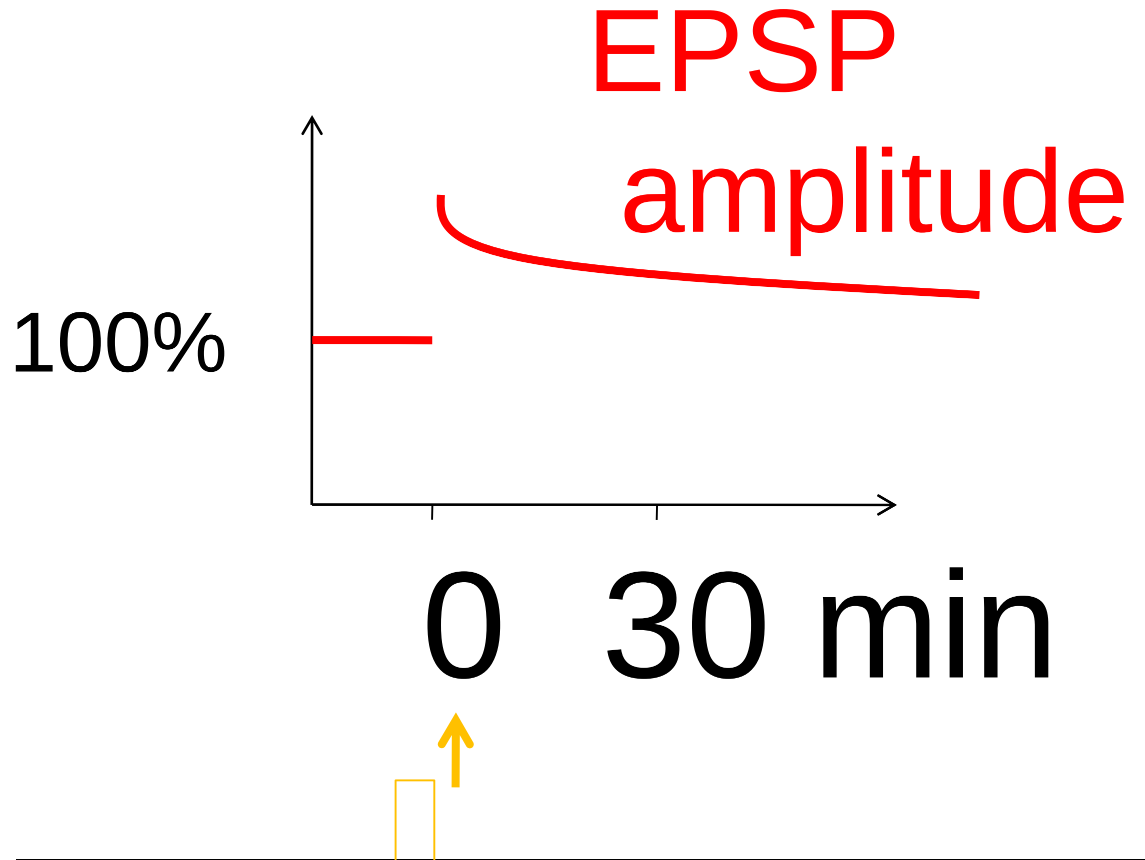
2. Spike-timing dependent plasticity (STDP)



60 repetitions

Markram et al, 1995,1997
Zhang et al, 1998
review:
Bi and Poo, 2001

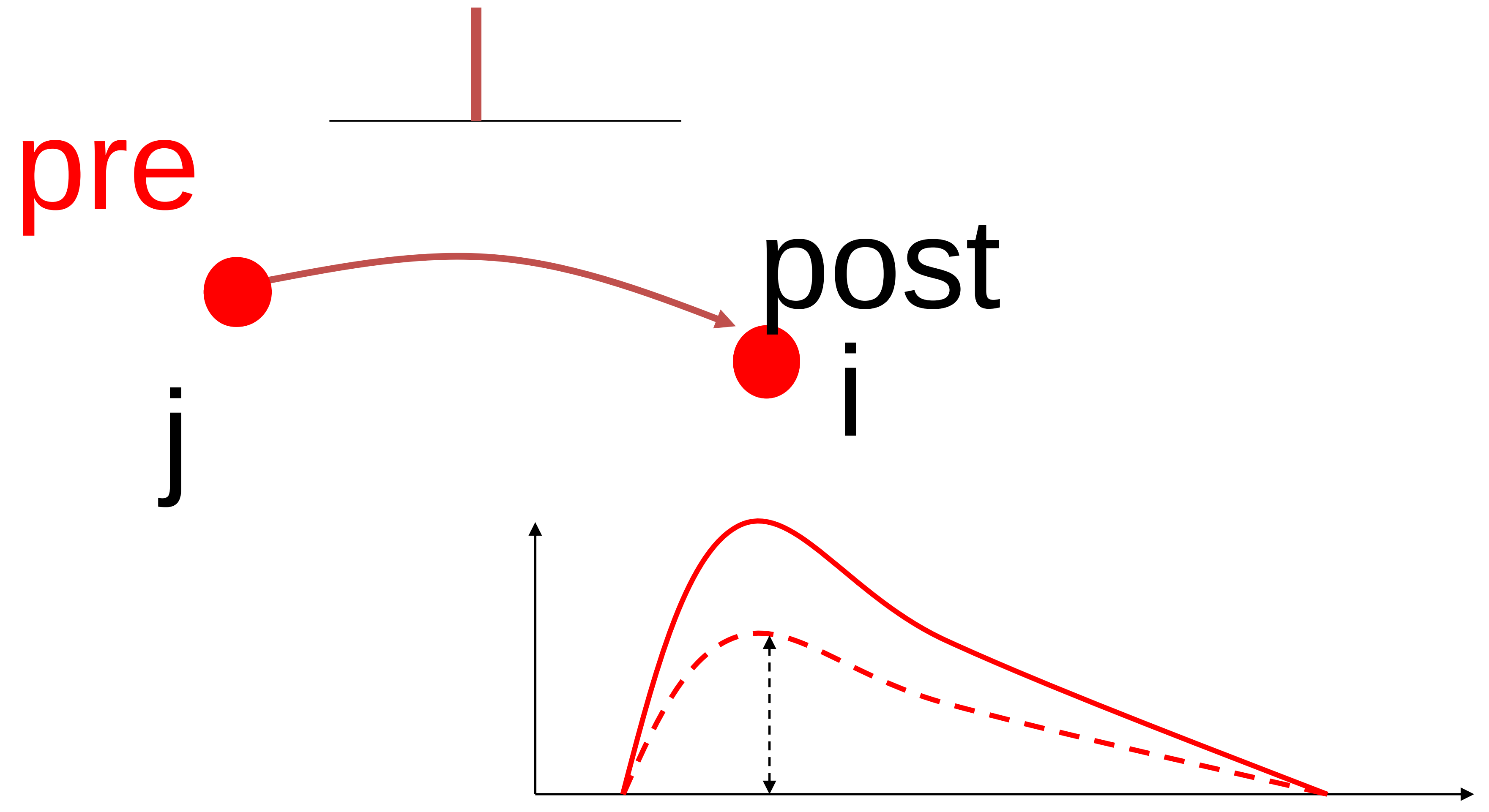




2. Classification of synaptic changes

Induction of changes

- fast (if stimulated appropriately)
- slow (homeostasis)



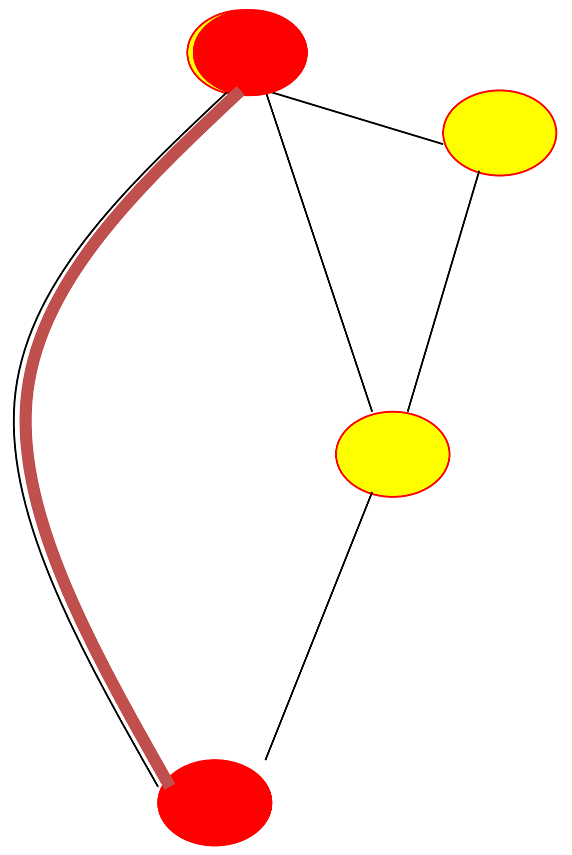
Persistence of changes

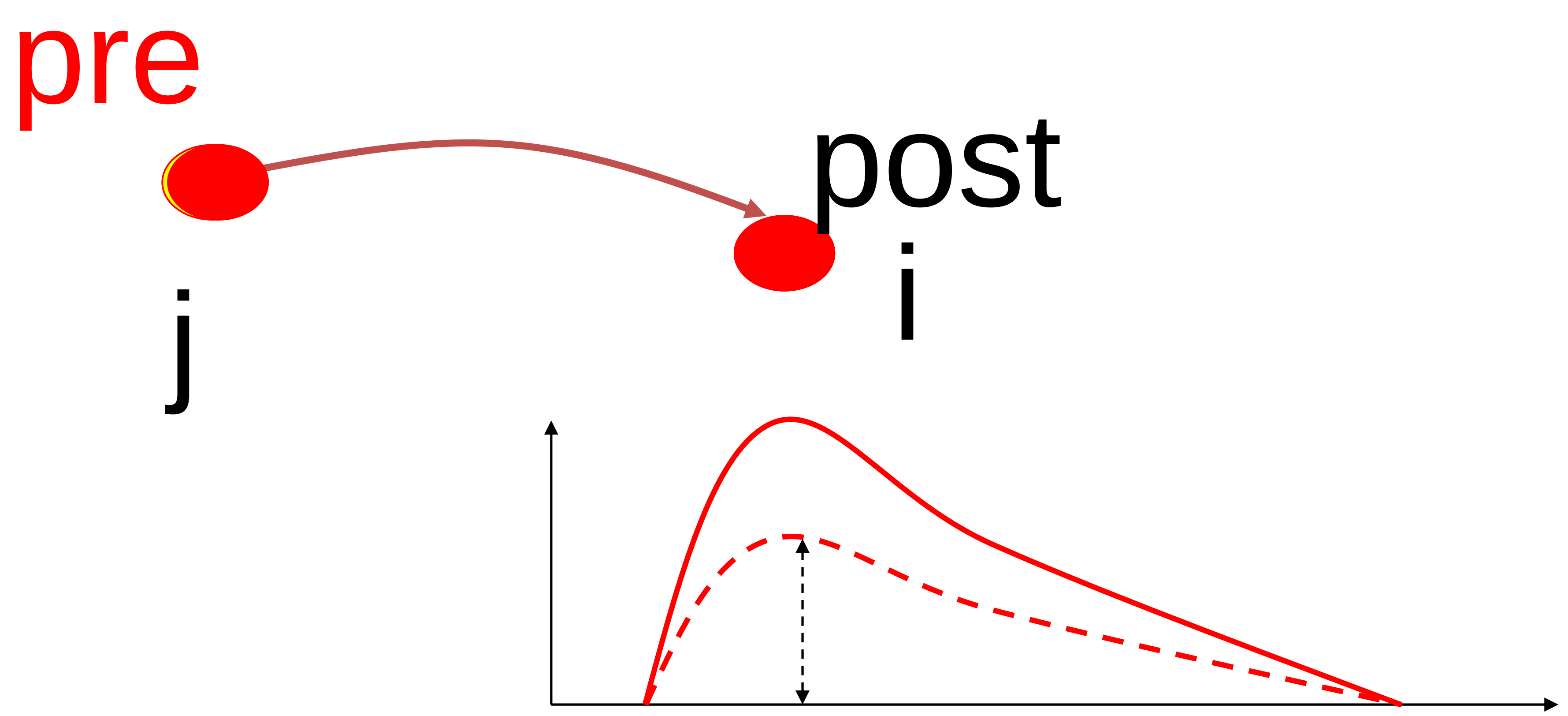
- long (LTP/LTD)
- short (short-term plasticity)

Functionality

- useful for learning a new behavior/forming new memories
- useful for development (wiring for receptive field development)
- useful for activity control in network: **homeostasis**
- useful for coding

Hebbian Learning
= unsupervised learning





$$w_{ij}\,\varepsilon\left(t - t_j^f\right)$$

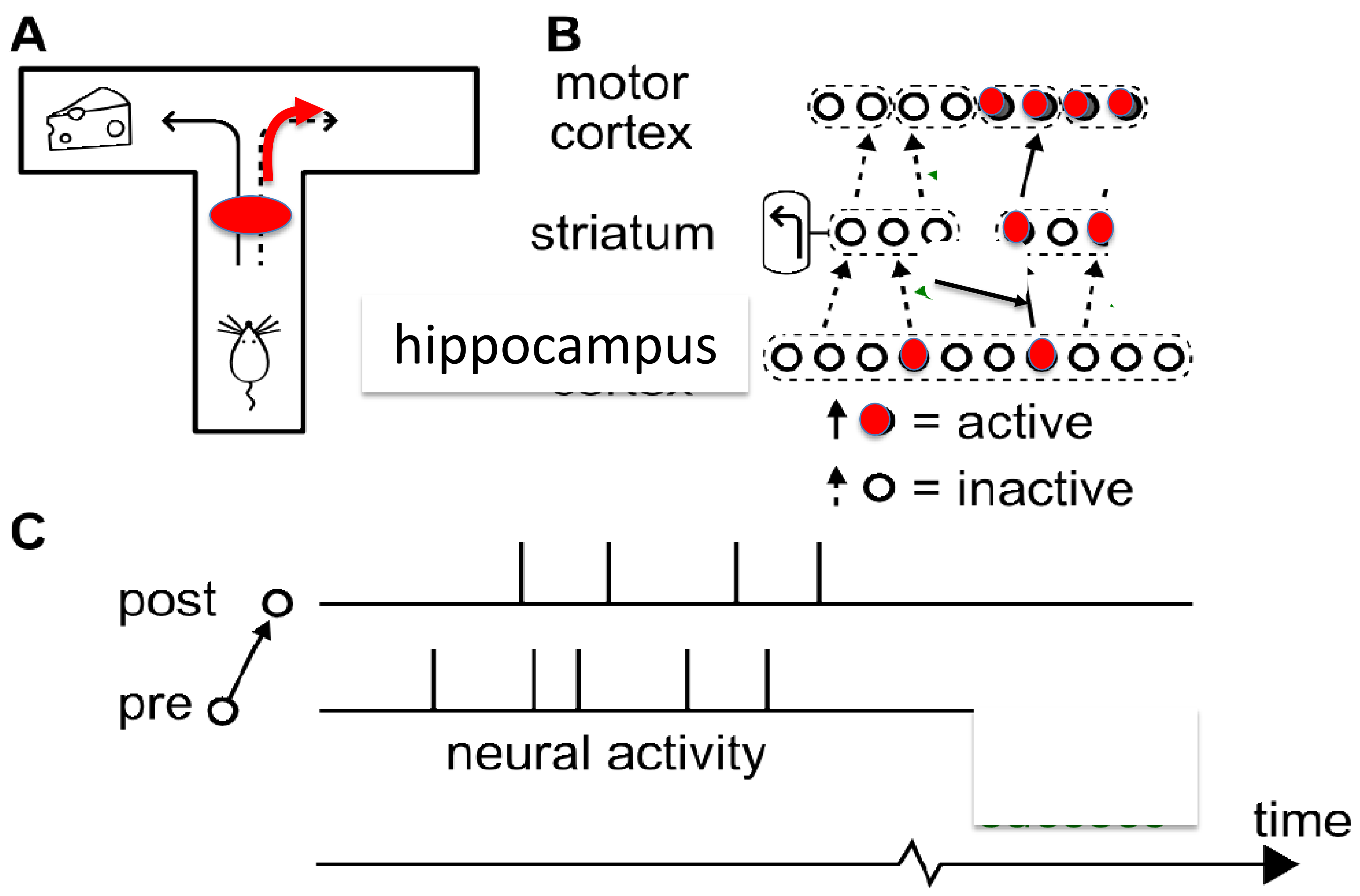
$$\Delta w_{ij} \propto F(pre, post)$$

2.Limits of unsupervised learning

Is Hebbian Learning sufficient?
No!

Image: Gerstner et al. NEURONAL DYNAMICS,

Eligibility trace:
Synapse keeps memory of pre-post Hebbian events



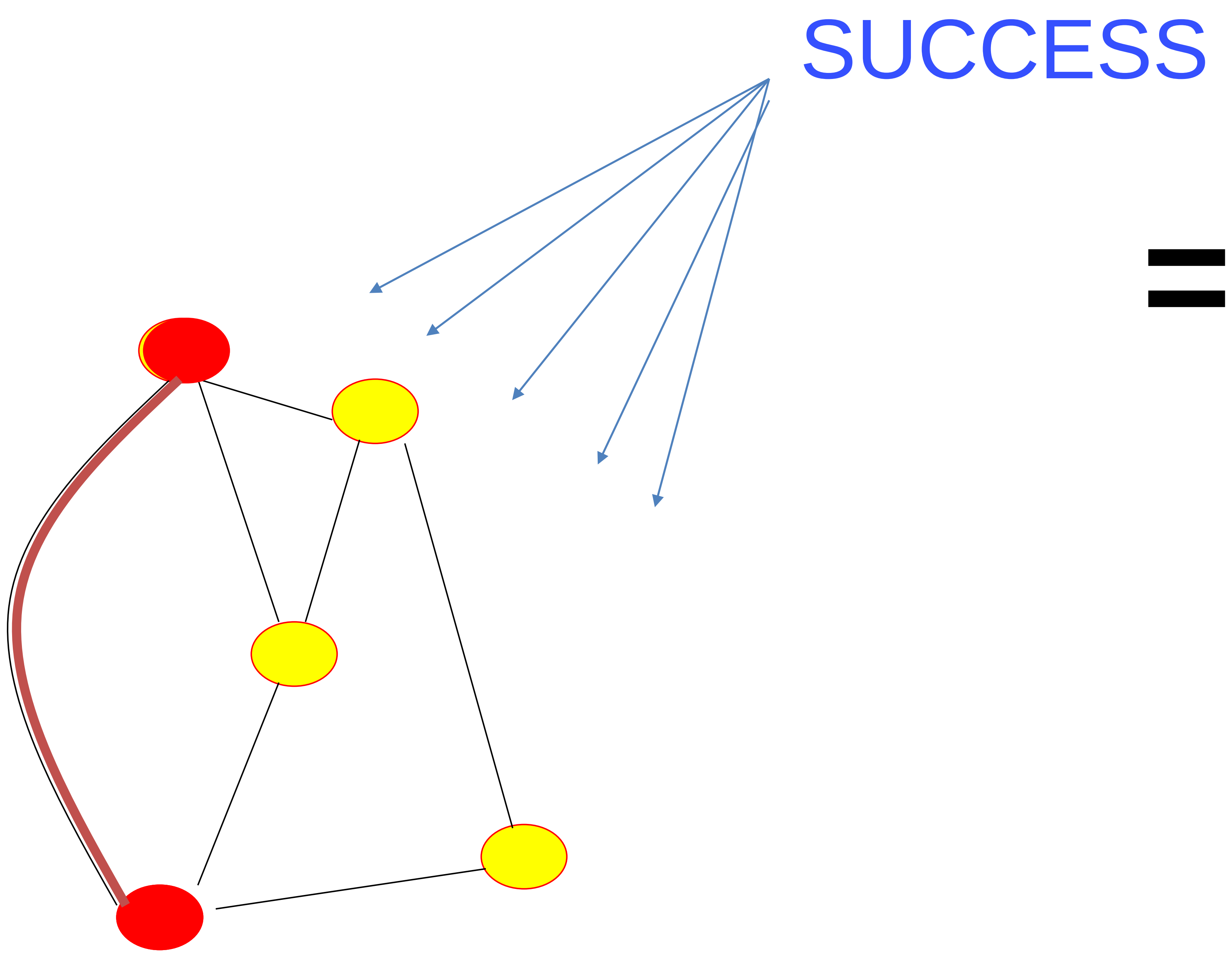
Dopamine: Reward/success

Schultz et al. 1997; Waelti et al., 2001;

→ Reinforcement learning: success = reward – (expected reward)

TD-learning, SARSA, Policy gradient (book: Sutton and Barto, 1997)

2. Classification of synaptic changes: Reinforcement Learning



Reinforcement Learning
= reward + Hebb

$$\Delta w_{ij} \propto F(pre, post, SUCCESS)$$

local global

broadly diffused signal:
neuromodulator

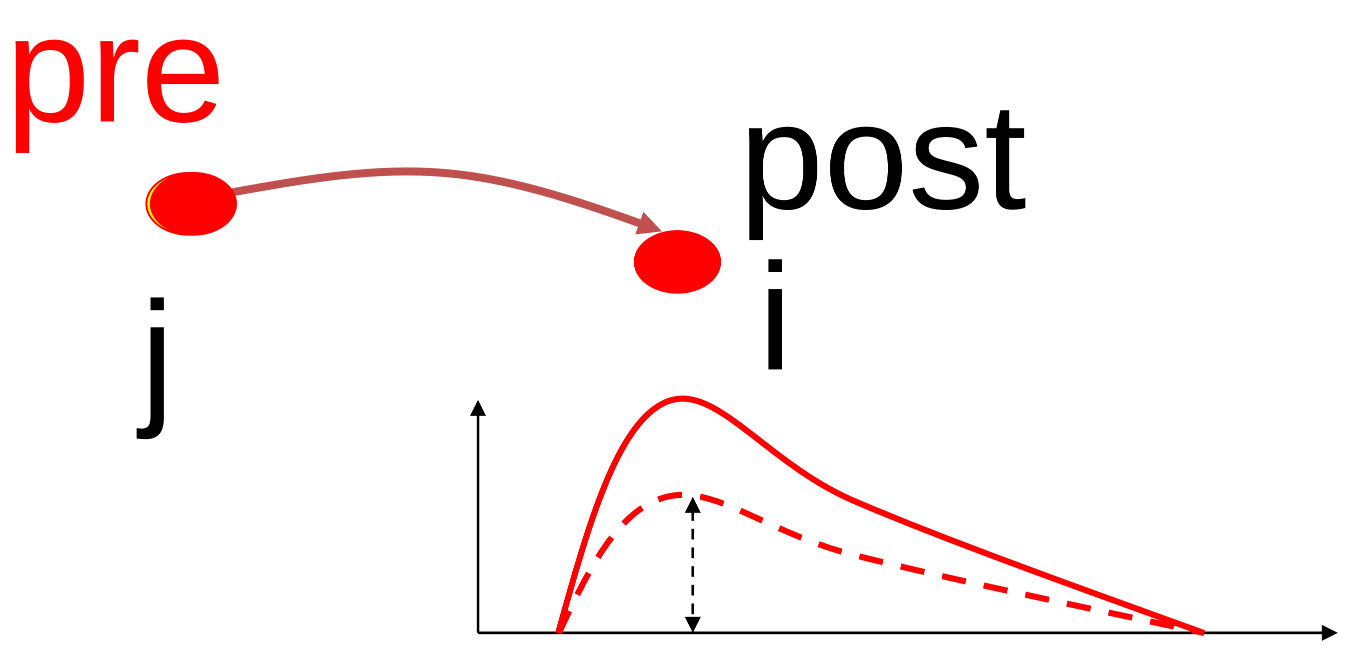
2. Classification of synaptic changes

unsupervised vs reinforcement

LTP/LTD/Hebb

Theoretical concept

- passive changes
- exploit statistical correlations



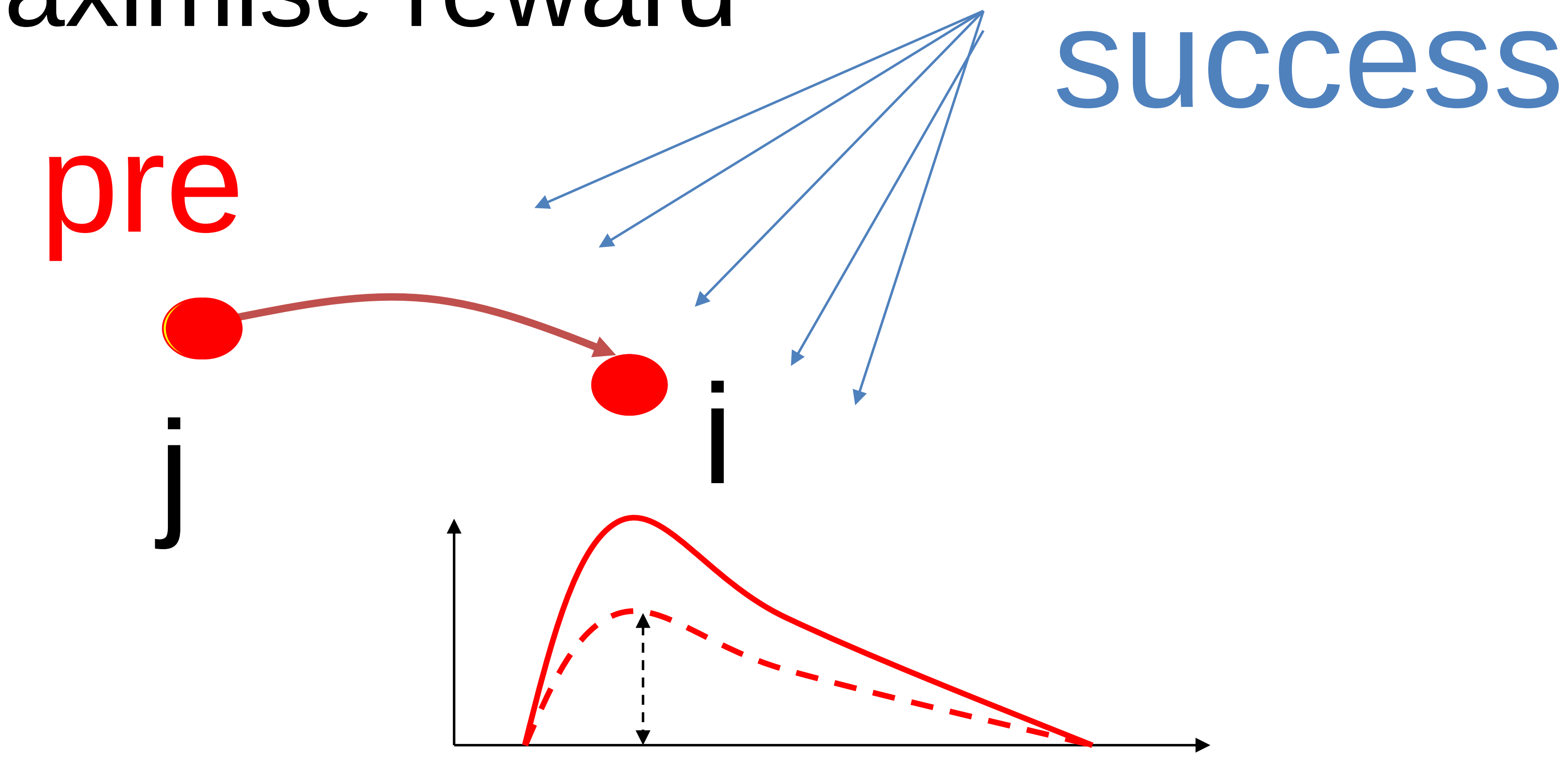
Functionality

-useful for development
(wiring for receptive field)

Reinforcement Learning

Theoretical concept

- conditioned changes
- maximise reward

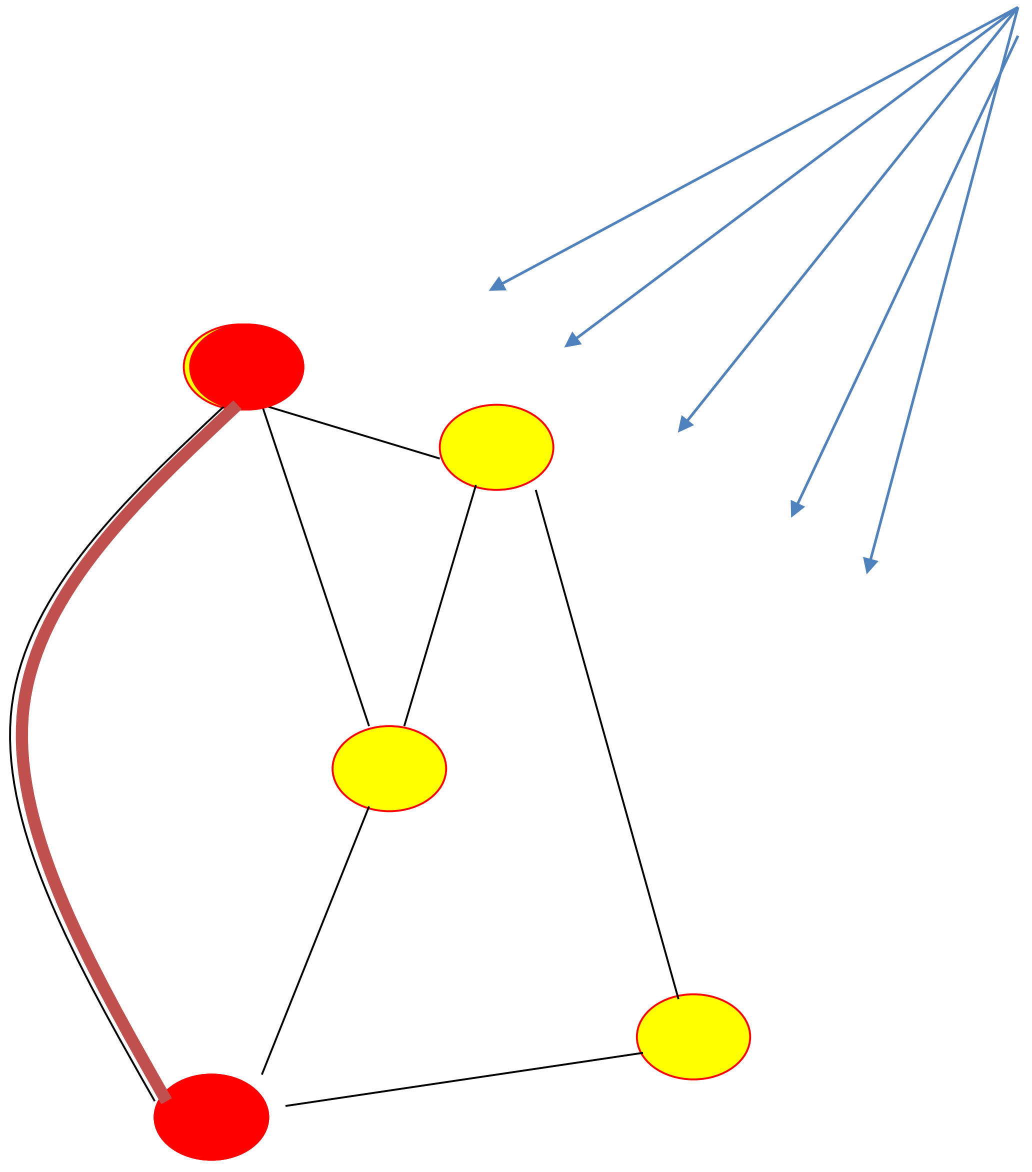


Functionality

- useful for learning
a new behavior

2. Three-factor rule of Hebbian Learning

= Hebb-rule gated by a neuromodulator



Neuromodulators: Interestingness, surprise; attention; novelty

$$\Delta w_{ij} \propto F(pre, post, MOD)$$

local global

Neuromodulator projections

- 4 or 5 neuromodulators
- near-global action

Dopamine/reward/TD:
Schultz et al., 1997,
Schultz, 2002

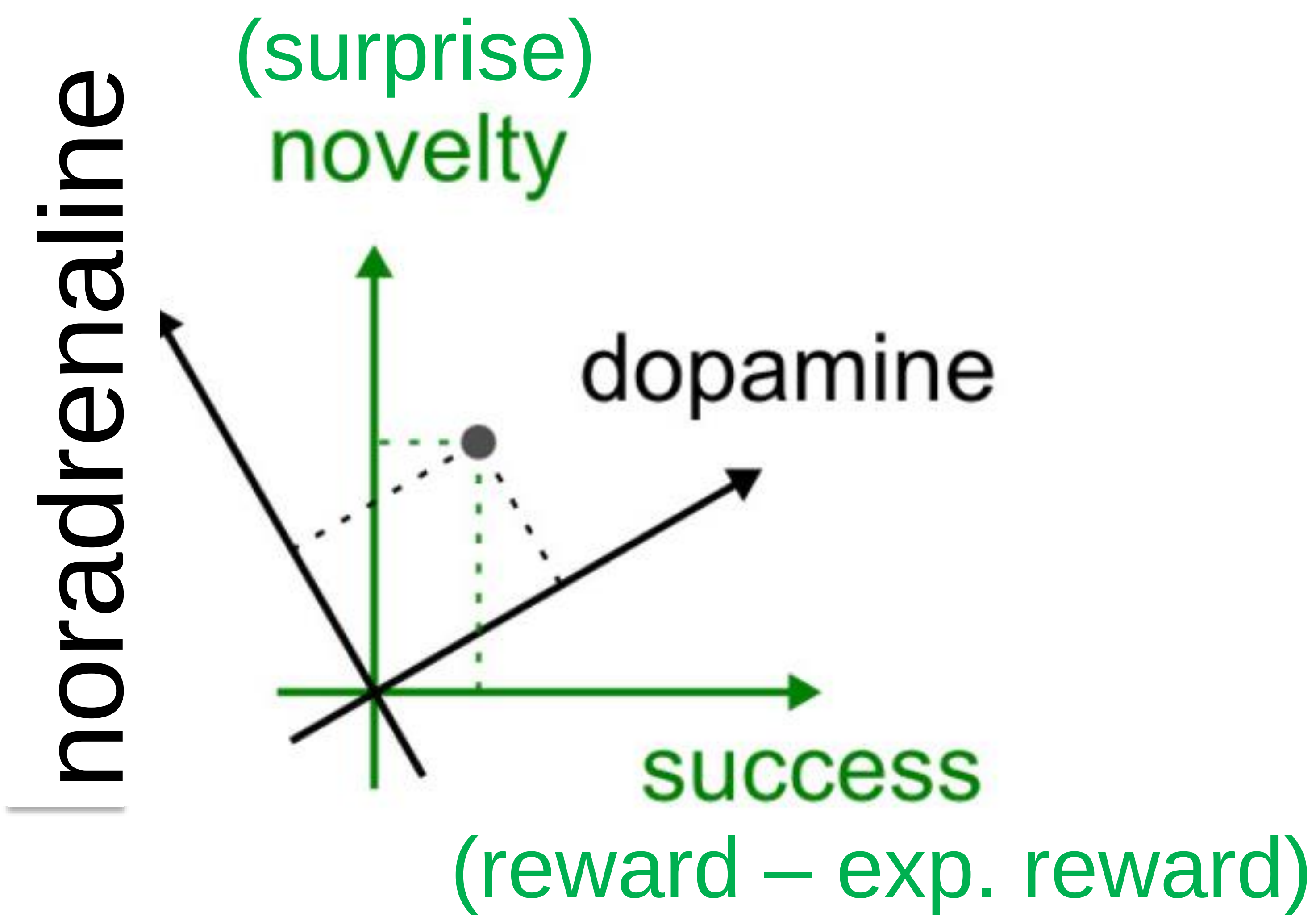
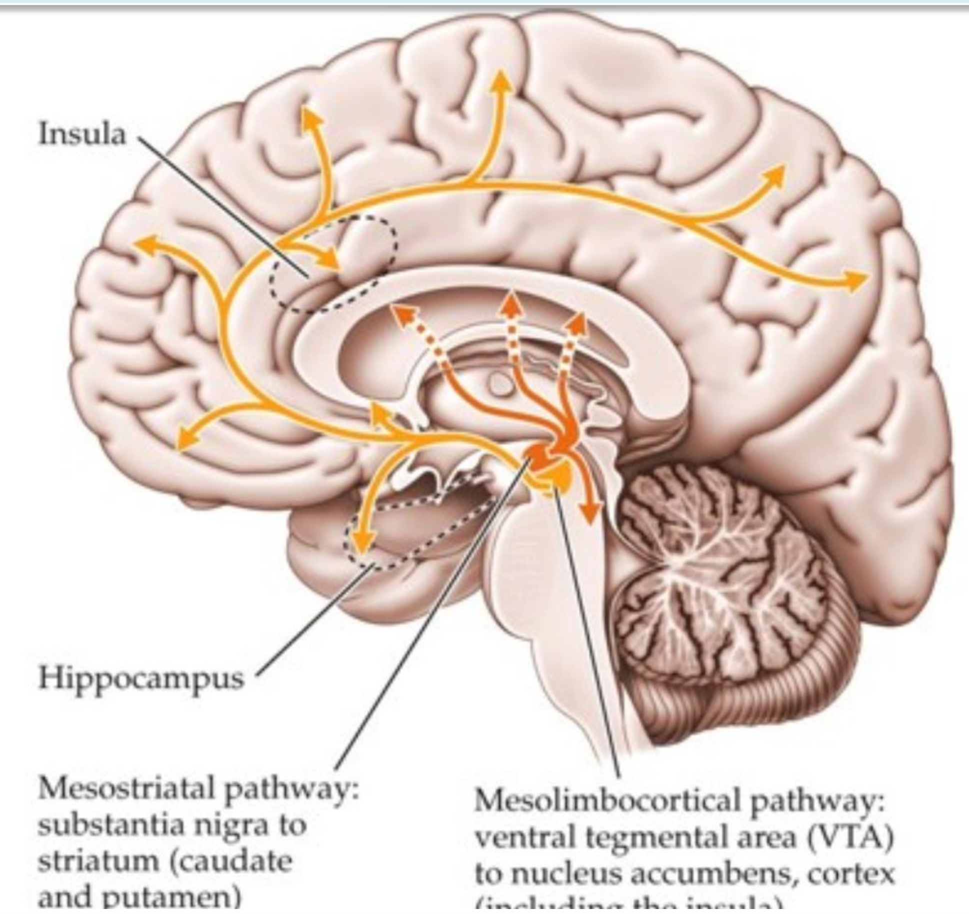


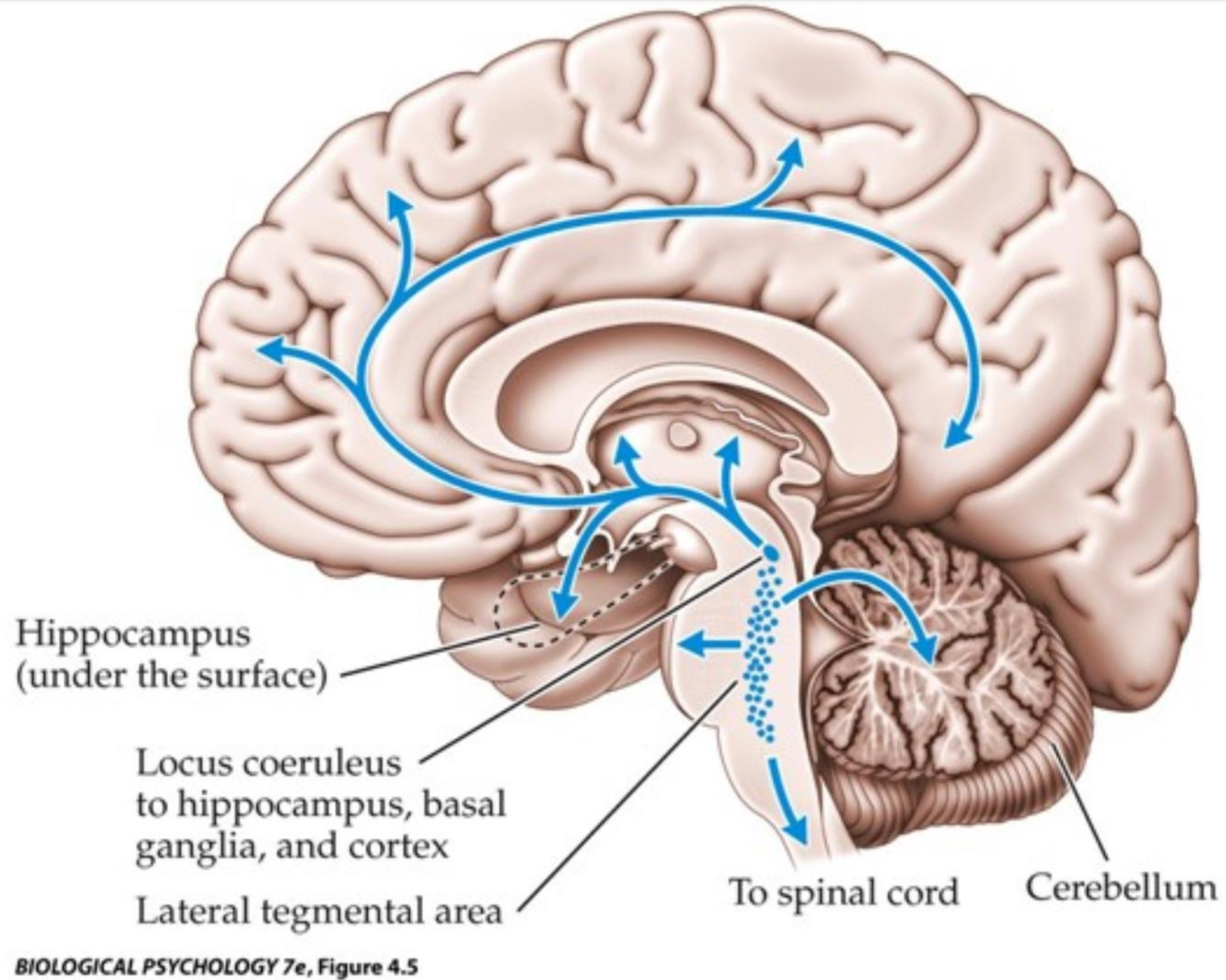
Image:
Fremaux and Gerstner, Frontiers (2016)

Image: Biological Psychology, Sinauer

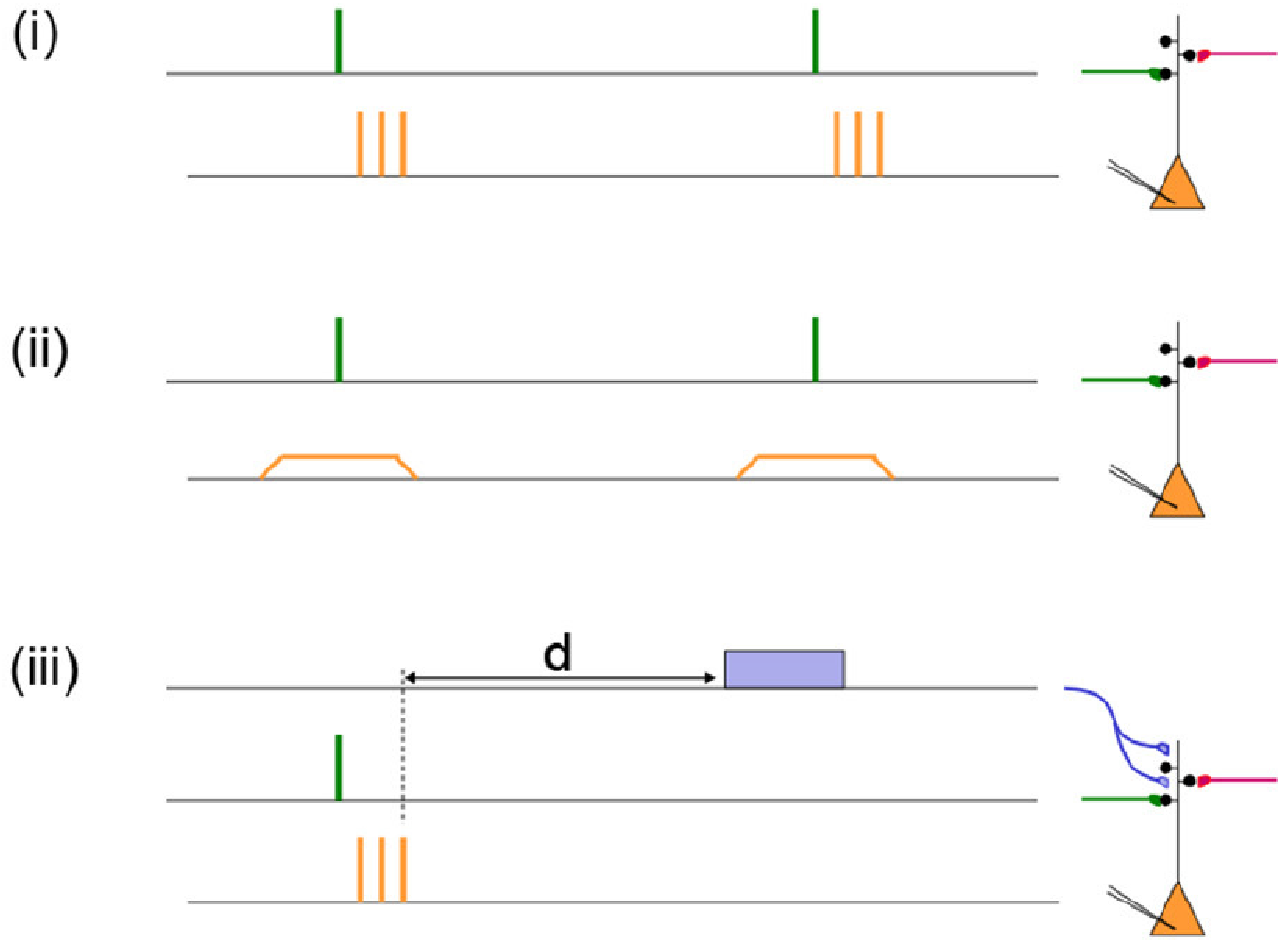
Dopamine



Noradrenaline



2-factor versus 3-factor rules



Hebbian:
 'post' = spikes

Hebbian:
 'post' = voltage

3-factor

3-factor = Hebbian combined with
(potentiall delayed) Neuromodulator:

Image: Gerstner et al. (2018, review paper in Frontiers)

2. Summary: Classification of synaptic changes

Several categories can be used to classify synaptic changes:

1) Do changes last for a long time (hours: Long-Term Potentiation) or do they decay rapidly back to baseline (around a second: Short-Term Potentiation).
2) Do changes depend mainly on presynaptic and postsynaptic activity (Hebbian learning/2-factor rule), or also on the presence of a neuromodulator (three-factor rule).
3) Learning paradigm: is the learning scenario just exploiting input statistics (unsupervised learning/no teacher, no reward); or does it also involve notions of ‘reward’ or ‘success (reinforcement learning)

Quiz 1. Synaptic Plasticity and Learning Rules

Long-term potentiation

[ ] has an acronym LTP

[ ] takes more than 10 minutes to induce

[ ] lasts more than 30 minutes

[ ] depends on presynaptic activity, but not on state of postsynaptic neuron

Short-term potentiation

[ ] has an acronym STP

[ ] takes more than 10 minutes to induce

[ ] lasts more than 30 minutes

[ ] depends on presynaptic activity, but not on state of postsynaptic neuron

Learning rules

[ ] Hebbian learning depends on presynaptic activity and on state of postsynaptic neuron

[ ] Reinforcement learning depends on neuromodulators such as dopamine indicating reward

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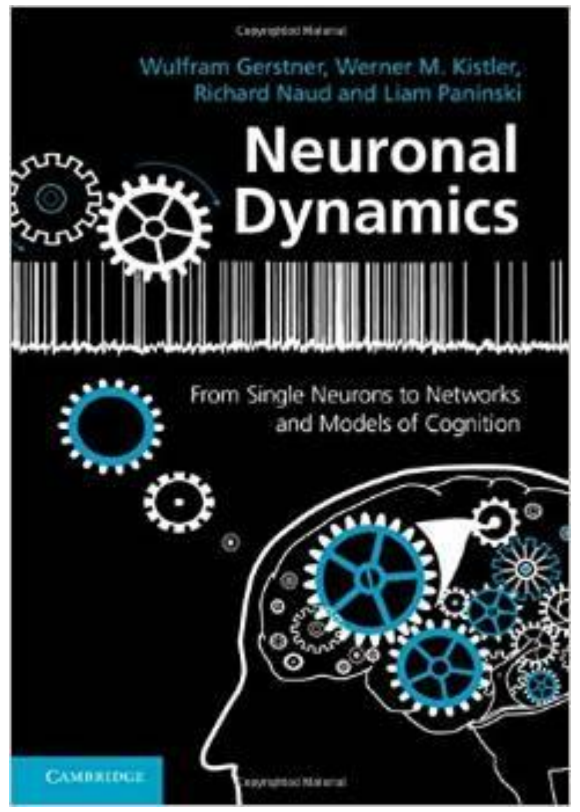

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4. Models of long-term plasticity

- Hebbian learning rules
- Bienenstock-Cooper-Munro rule

5. Spiking Models of plasticity

3. Model of short-term plasticity

See Week X on MOODLE or See week 3 on:

http://lcn.epfl.ch/~gerstner/NeuronalDynamics-MOOC1.html

Synapses, dendrites and the cable equation

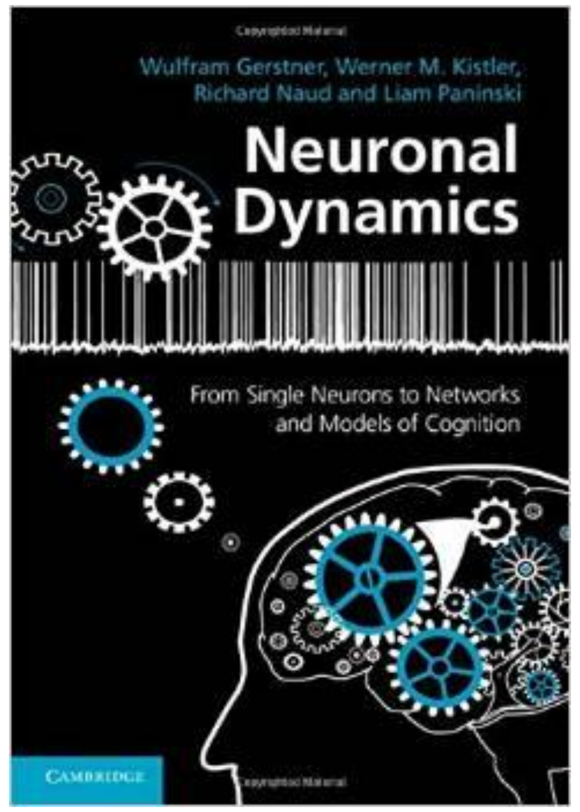
Part 1 - Synapses (15 min)

Part 2 - Synaptic short term plasticity (9 min)

https://www.youtube.com/watch?v=iEz_SUsJMJ8

Reading for STP:
NEURONAL DYNAMICS
- Ch 3.1.3.

Cambridge Univ. Press



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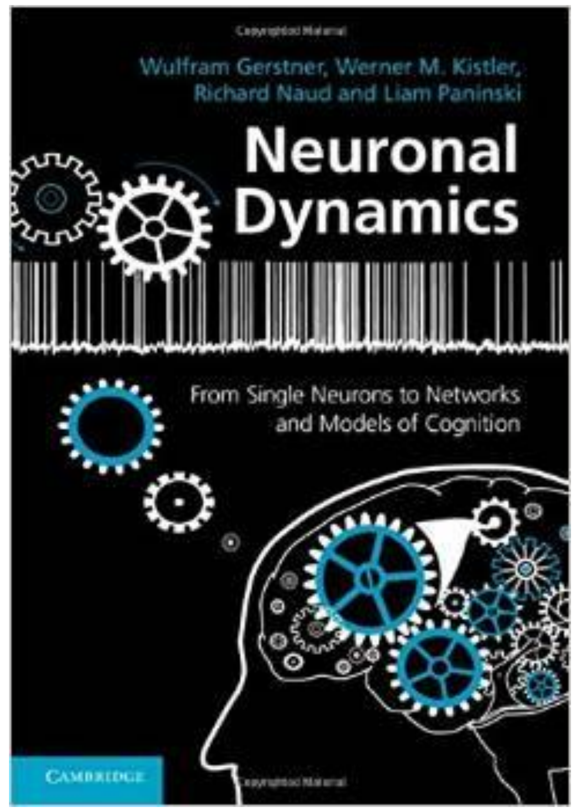

Cambridge Univ. Press

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7. Triplet STDP model

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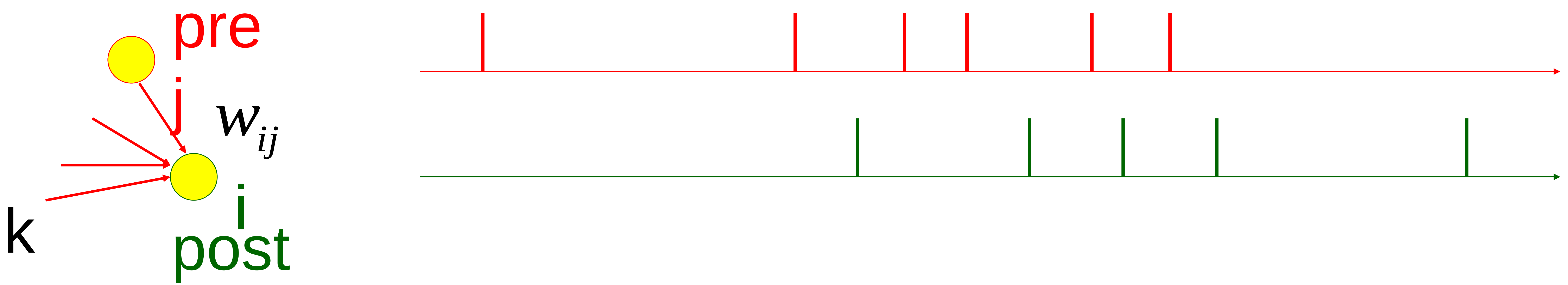
4. Hebbian Learning (rate models)



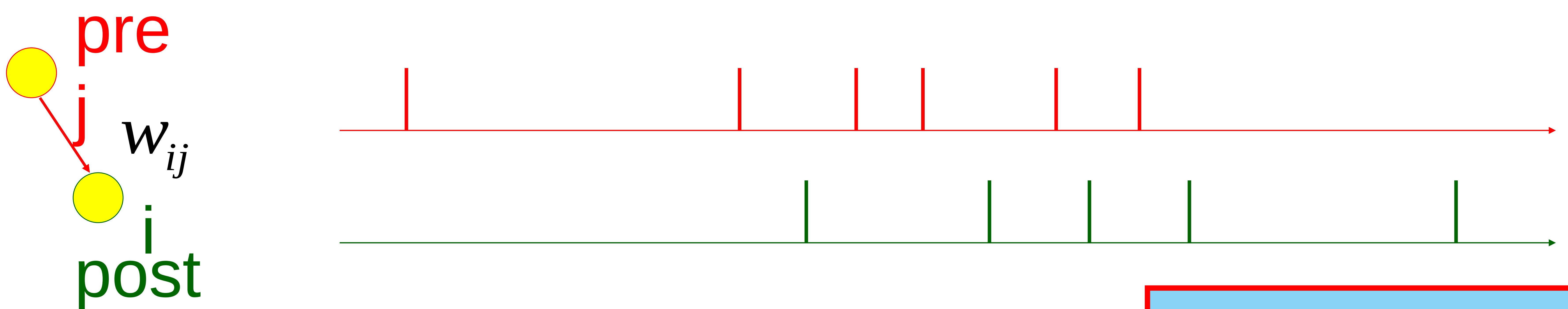
When an axon of cell **j** repeatedly or persistently takes part in firing cell **i**, then j's efficiency as one of the cells firing i is increased

Hebb, 1949

- local rule
- simultaneously active (correlations)

Rate model:
active = high rate = many spikes per second

4. Rate-based Hebbian Learning



Blackboard1

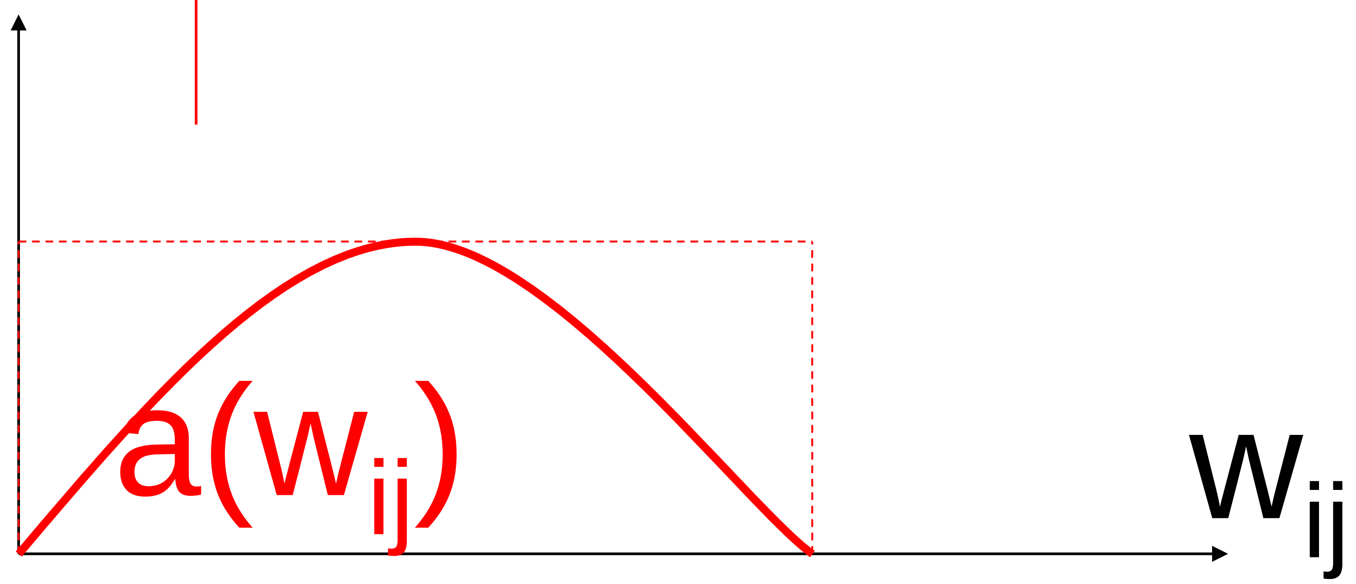
Local rule:

$$\frac{d}{dt} w_{ij} = F(w_{ij}, MOD; \nu_j^{pre}, \nu_i^{post})$$

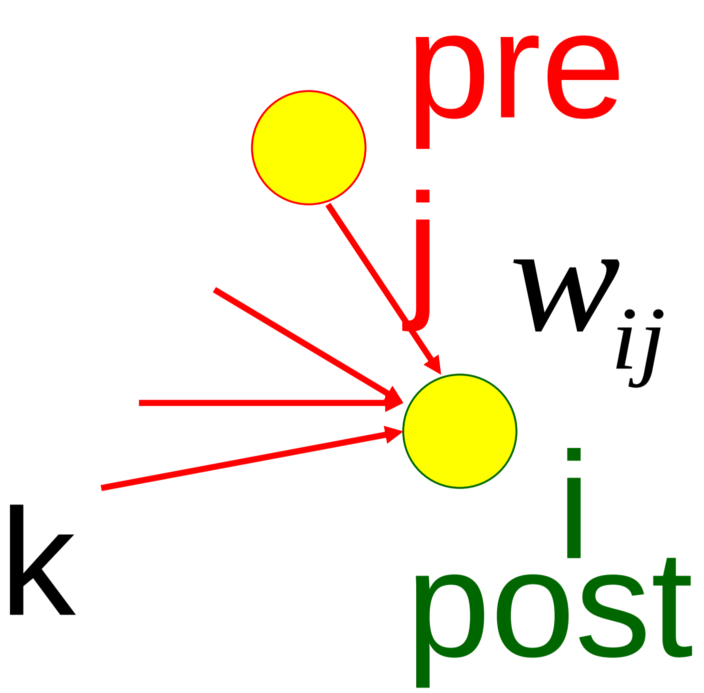
Taylor expansion:

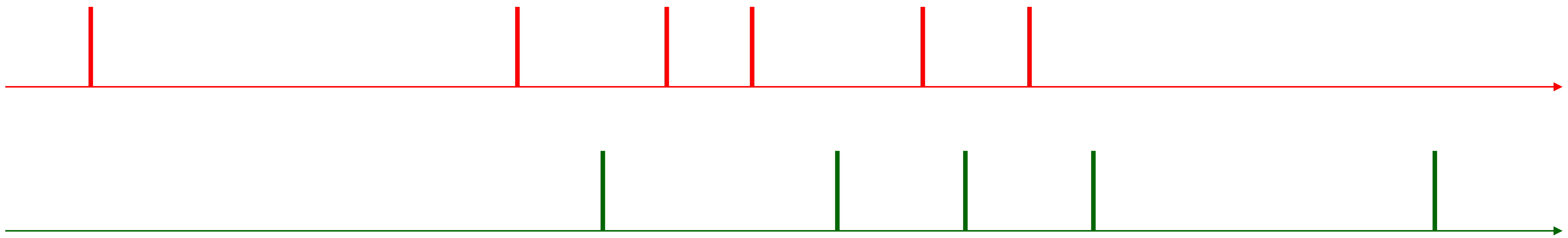
$$\frac{d}{dt} w_{ij} = a_0 + a_1^{pre} \nu_j^{pre} + a_1^{post} \nu_i^{post} + a_2^{corr} \nu_j^{pre} \nu_i^{post} + \ldots$$

$a = a(w_{ij})$



4. Rate-based Hebbian Learning

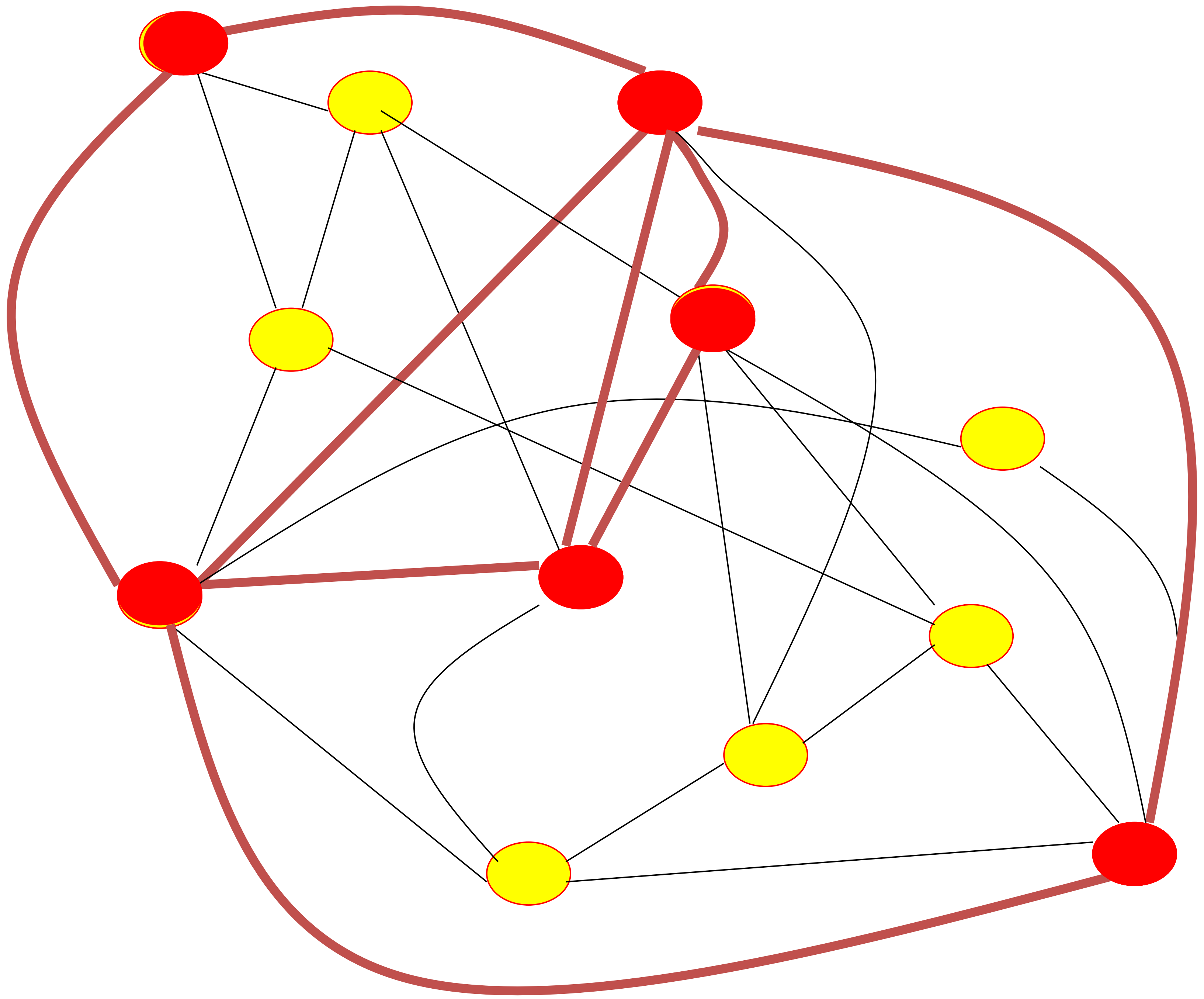




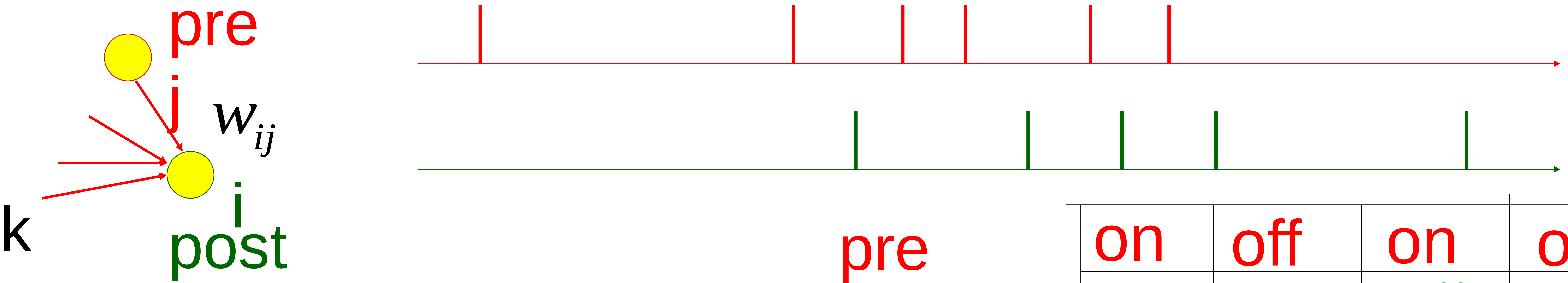
$$\frac{d}{dt} w_{ij} = a_2^{corr} \nu_j^{pre} \nu_i^{post}$$

pre	on	off	on	off
post	on	on	off	off
	+	**0**	**0**	**0**

Review from week 5: Hebbian Learning

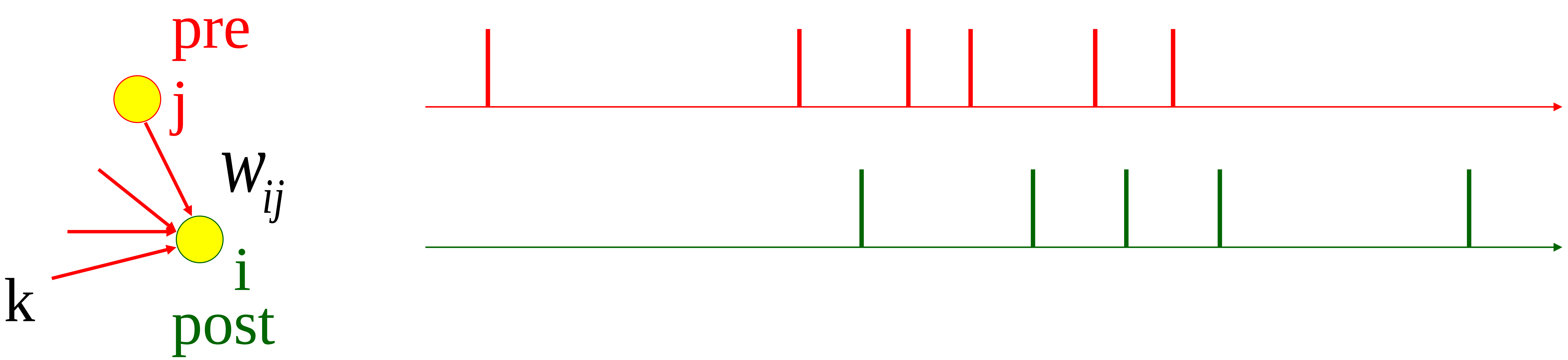


4. Rate-based Hebbian Learning



	pre: on post: on	pre: off post: on	pre: on post: off	pre: off post: off
$\frac{d}{dt}w_{ij} = a_2^{corr}\nu_j^{pre}\nu_i^{post}$	+	0	0	0
$\frac{d}{dt}w_{ij} = a_2^{corr}\nu_j^{pre}\nu_i^{post} - c$	+	-	-	-
$\frac{d}{dt}w_{ij} = a_2^{corr}\nu_j^{pre}(\nu_i^{post} - \vartheta)$	+	0	-	0
$\frac{d}{dt}w_{ij} = a_2^{corr}(\nu_j^{pre} - \vartheta)(\nu_i^{post} - \vartheta)$	+	-	-	+

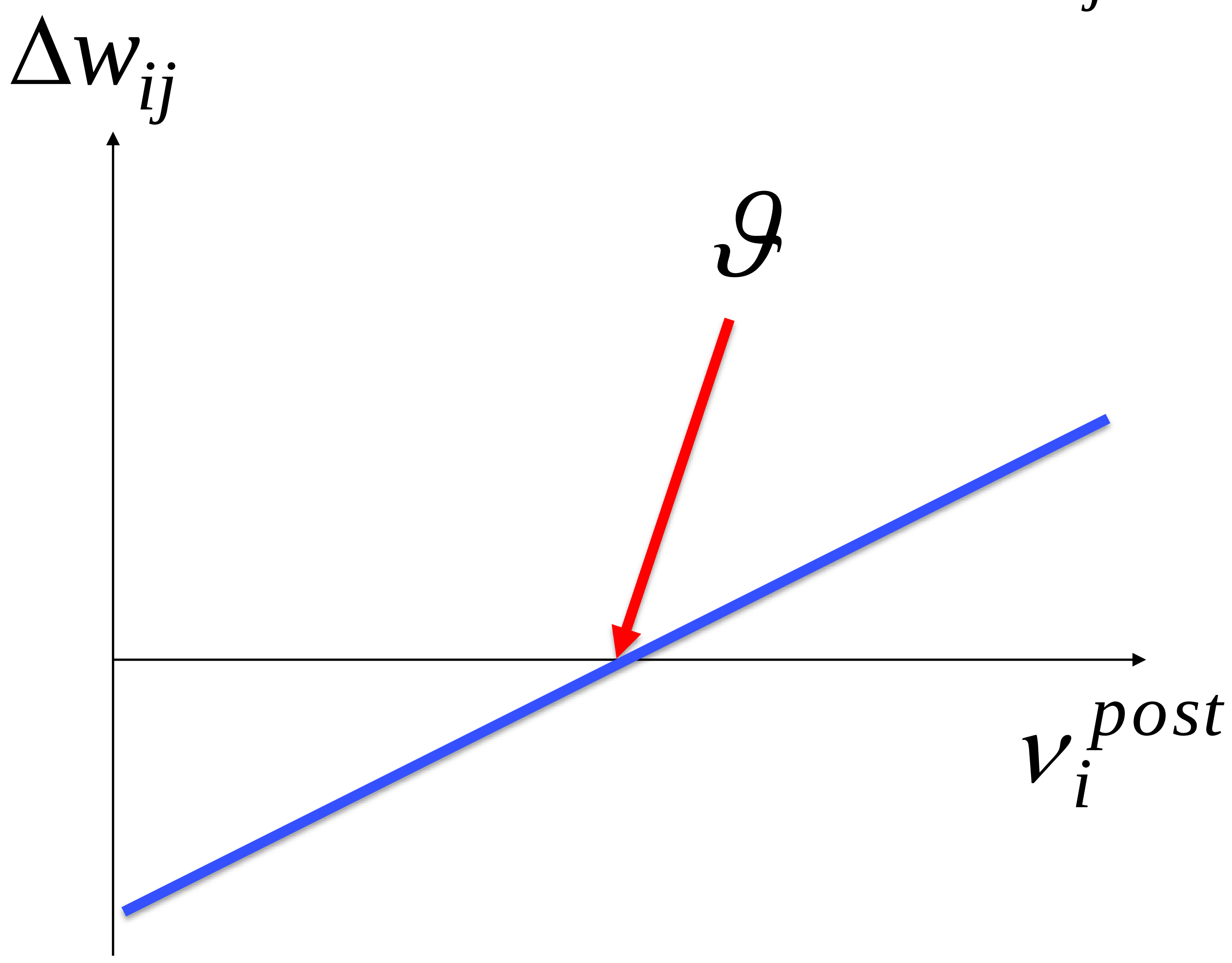
4. Presynaptically gated plasticity rule



presynaptically gated

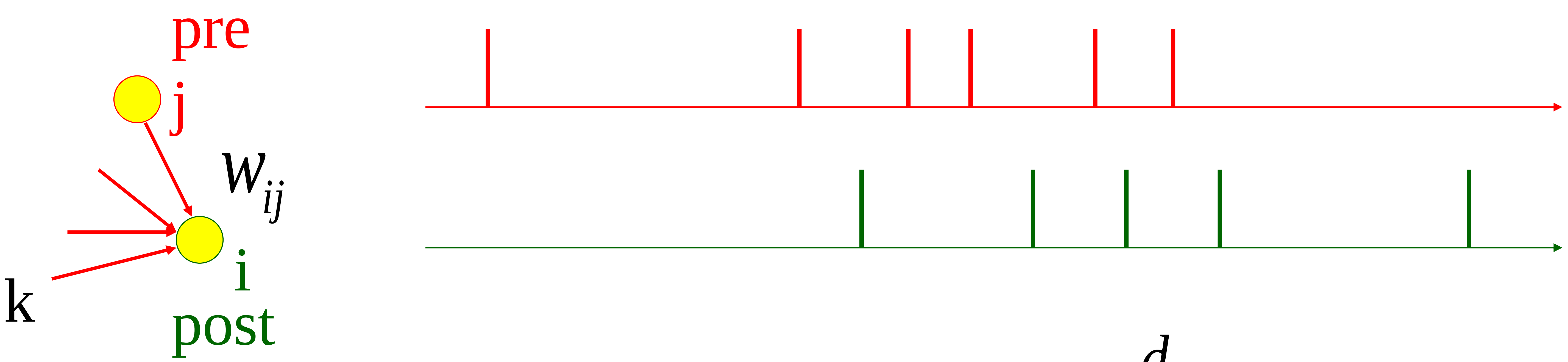
$$\frac{d}{dt} w_{ij} = a_2^{corr} (\nu_i^{post} - \vartheta) \nu_j^{pre}$$

Assume activity $\nu_j^{pre} > 0$



4. Bienenstock-Cooper-Munro rule

Bienenstock, Cooper Munro, 1982



presynaptically gated

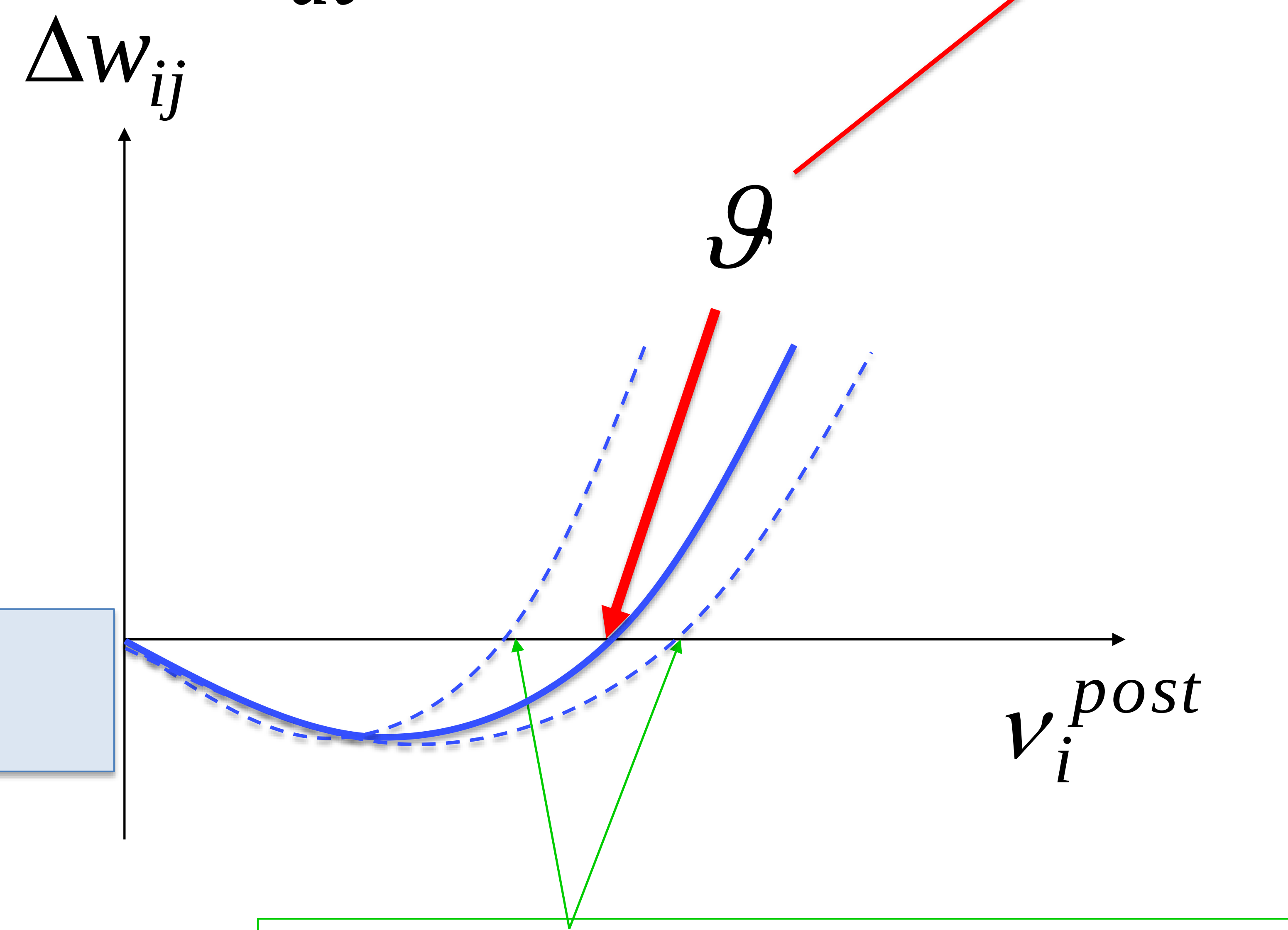
$$\frac{d}{dt} w_{ij} = a_2^{corr} (v_i^{post} - \vartheta) v_j^{pre}$$

BCM: 3rd order ('triplet')

$$\frac{d}{dt} w_{ij} = \underbrace{b\, v_i^{post} (v_i^{post}}_{\text{triplet}} - \underbrace{\vartheta) v_j^{pre}}_{\text{pair}}$$

Map to
Taylor expansion?

$$\frac{d}{dt} w_{ij} = b\, v_i^{post} (v_i^{post} - \vartheta) v_j^{pre}$$



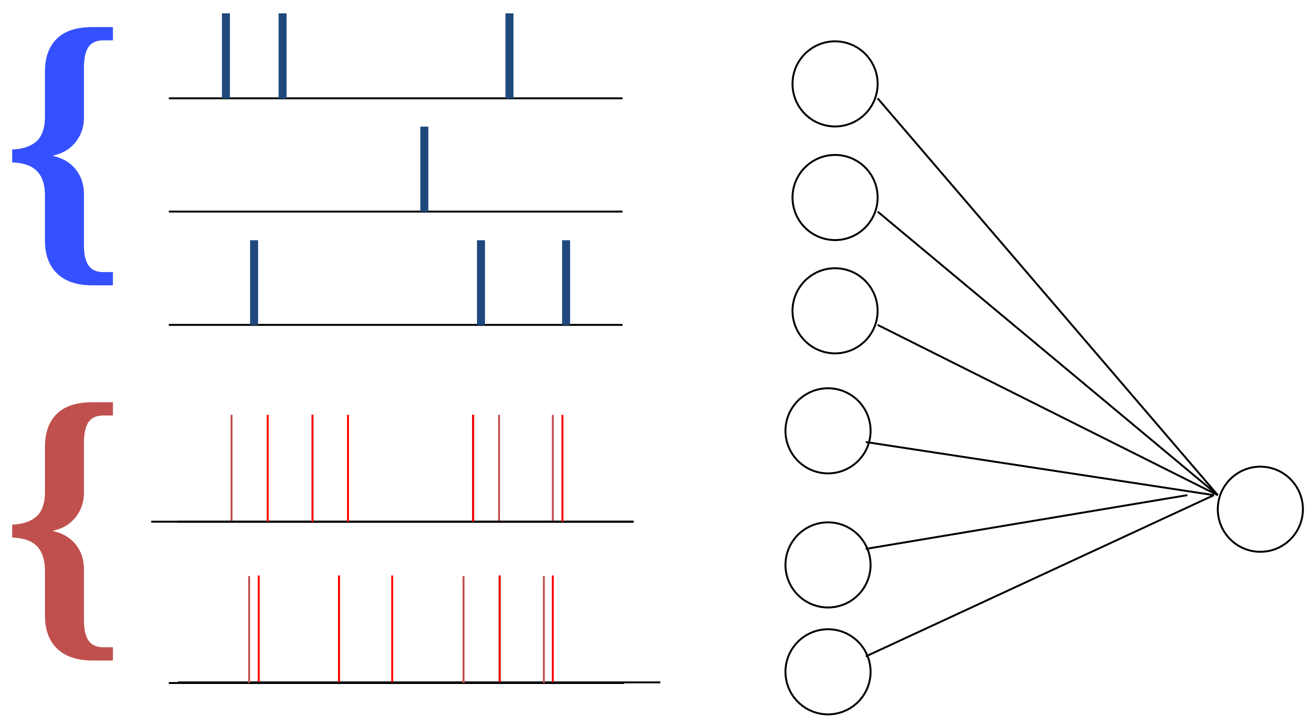
assume
$v_j^{pre} > 0$

Homeostasis $\vartheta = f(\overline{v}_i^{post})$

4. Functional Consequence of Hebbian Learning

Fixed rate

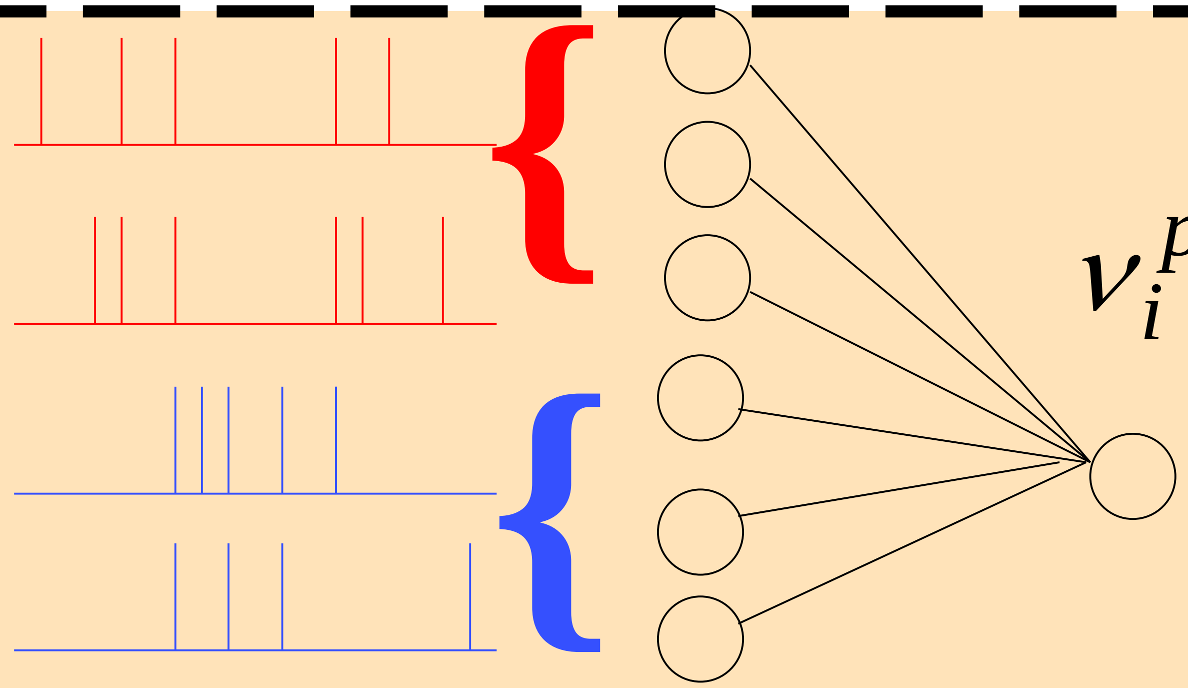
Jointly variing rate



Hebbian Learning detects correlations in the input

Development of Receptive Fields
(see also course:
Unsupervised and Reinforcement Learning)

Exercise 1 now: Bienenstock-Cooper-Munro



$$\nu_i^{post} = g(I_i) = \sum_j w_{ij}\, \nu_j^{pre}$$

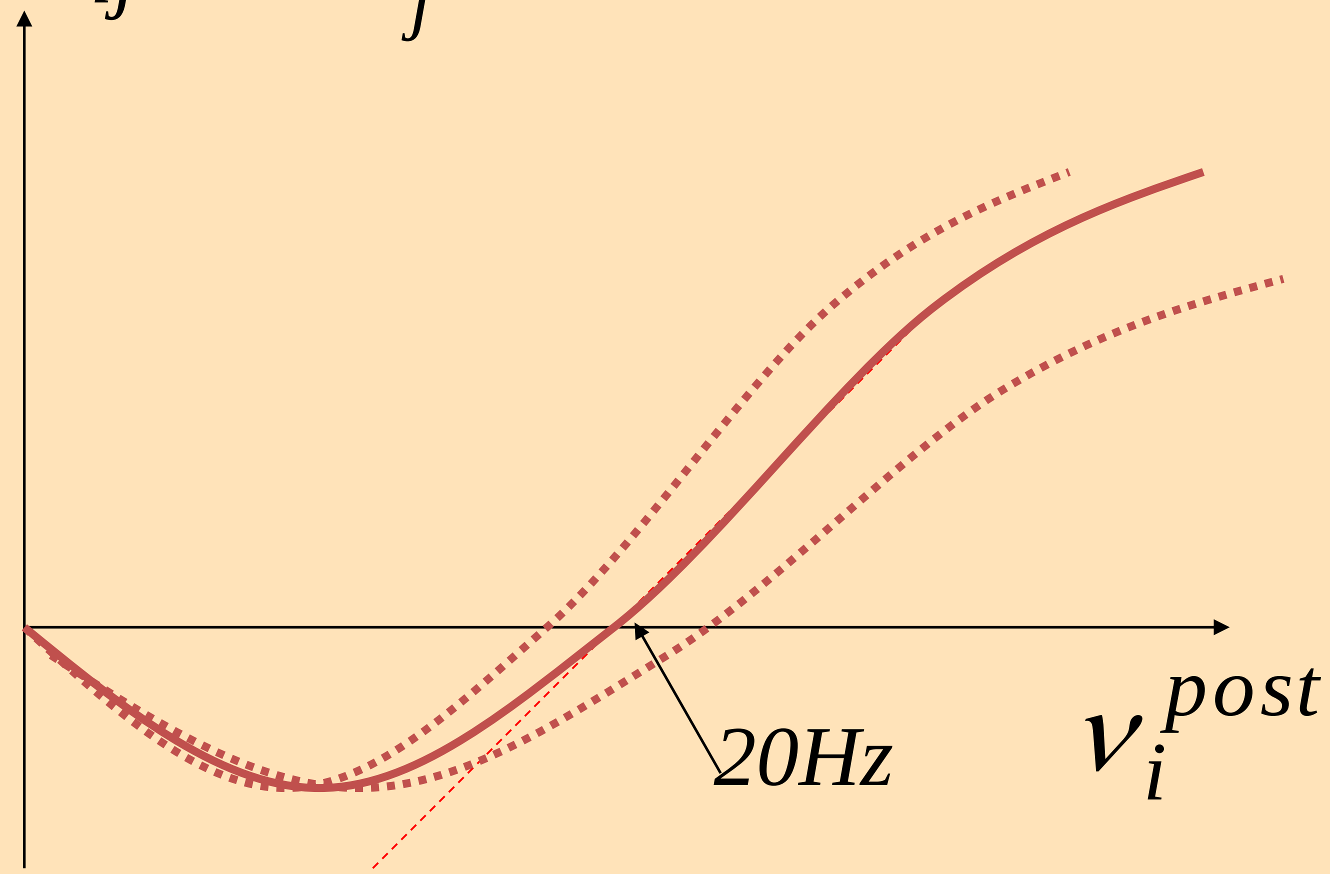
Take 8 minutes =
Discussion of ex
At 10:20

BCM rule

$$\frac{d}{dt} w_{ij} = a_2^{corr}\, \Phi(\nu_i^{post} - \vartheta)\, \nu_j^{pre}$$

20Hz

$$\frac{d}{dt} w_{ij} \text{ if } \nu_j^{pre} > 0$$



Assume 2 groups of 10 neurons each. All weights equal 1.

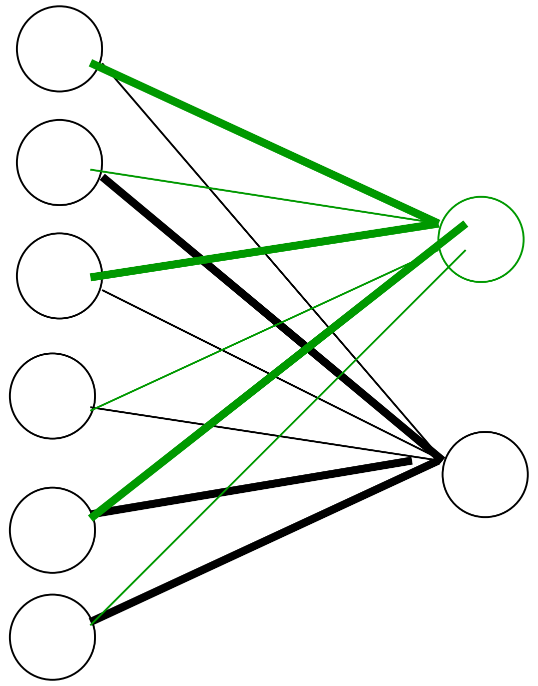
a)Group 1 fires at 3 Hz, then group 2 at 1 Hz. What happens?

b)Group 1 fires at 3 Hz, then group 2 at 2.5 Hz. What happens?

c) As in b, but make theta a function of the averaged rate. What happens?

4. Synaptic Changes for Development of Cortex

Initial:
random
connections

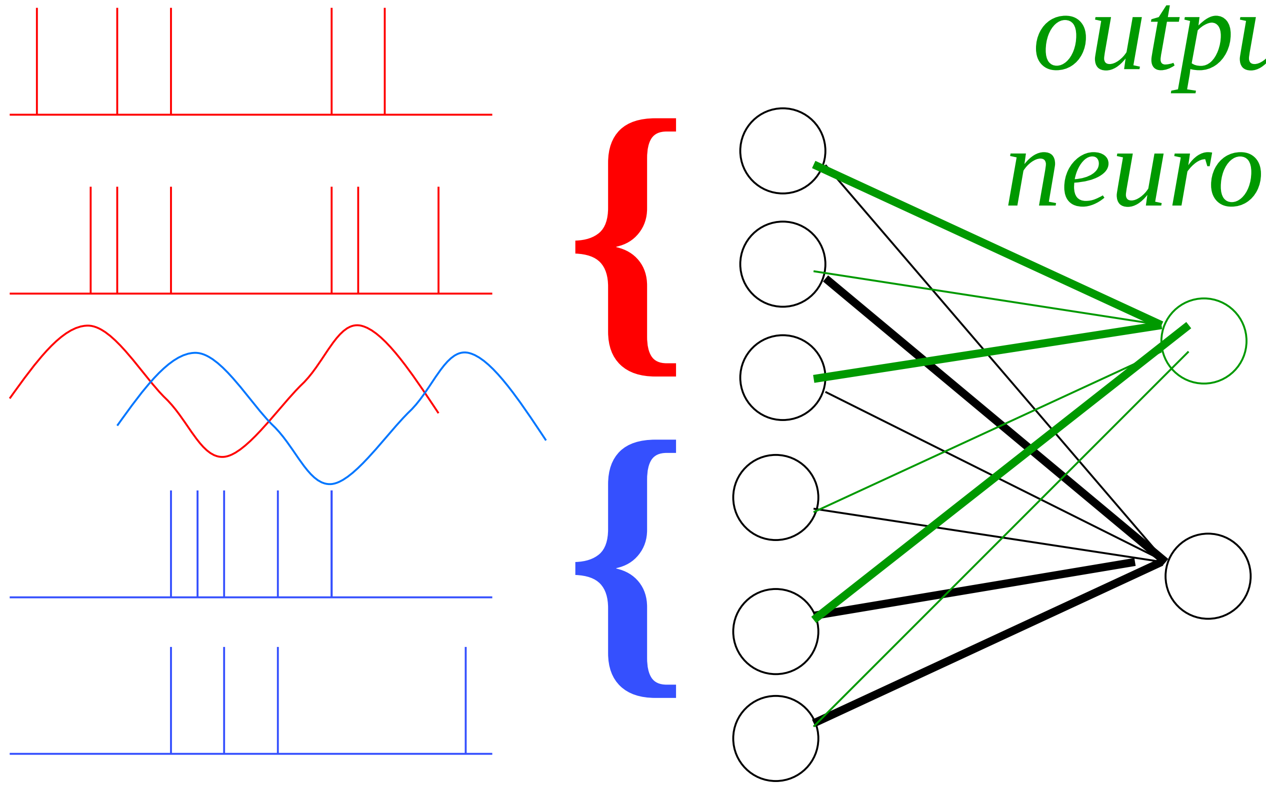


unselective
neurons

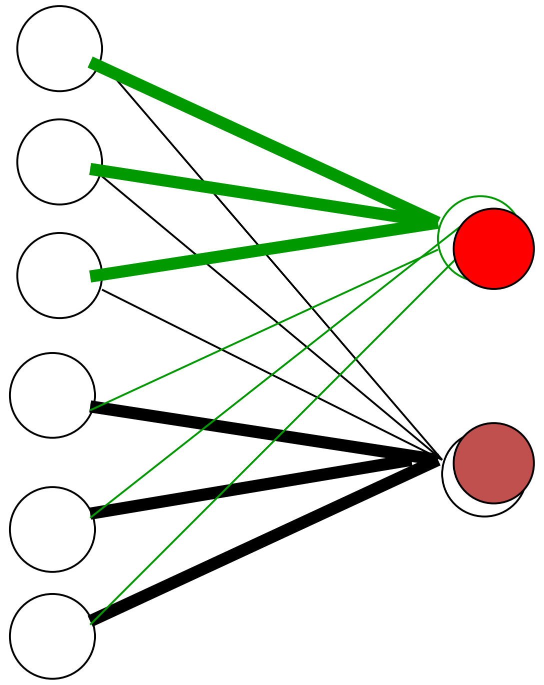
BCM leads to specialized
Neurons (developmental learning);
Bienenstock et al. 1982

Development and learning rules:
Willshaw&Malsburg, 1976
Linsker, 1986
K.D. Miller et al., 1989

output
neurons



Correlated input



output neurons specialize:
Receptive fields

4. Models for Hebbian Long-Term-Plasticity

- Many ‘Hebbian’ rules
- LTP and LTD
- Can describe RF development
- BCM is a well-known example
- Competition: some synapses grow at the expense of others

4. Summary: Models for Hebbian Learning

- Hebbian learning refers to a family of learning rules, rather than one specific rule.
- Rules can be classified by mapping them to a Taylor explansion.
- Terms with a negative coefficient induce long-term depression (LTD).
- A clever combination of LTP and LTD can explain the development of receptive fields (RF).
- A clever combination of LTP and LTD leads to competition: some synapses grow at the expense of others. A well-known example of a Hebbian rule is the Bienenstock-Cooper-Munro (BCM) rule

Biological Modeling of Neural Networks

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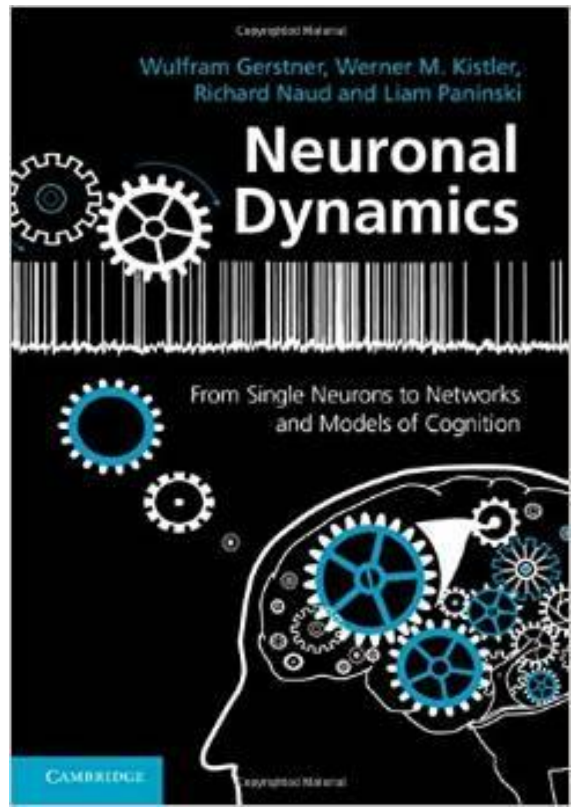
Week 13

Synaptic plasticity and Learning

Wulfram Gerstner

EPFL, Lausanne, Switzerland

Reading for plasticity:
NEURONAL DYNAMICS
- Ch. 19.1-19.3



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   motivation and aims
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   short-term vs. long-term
   unsupervised vs. reward modulated
3. **Model of short-term plasticity**
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   - Hebbian learning rules
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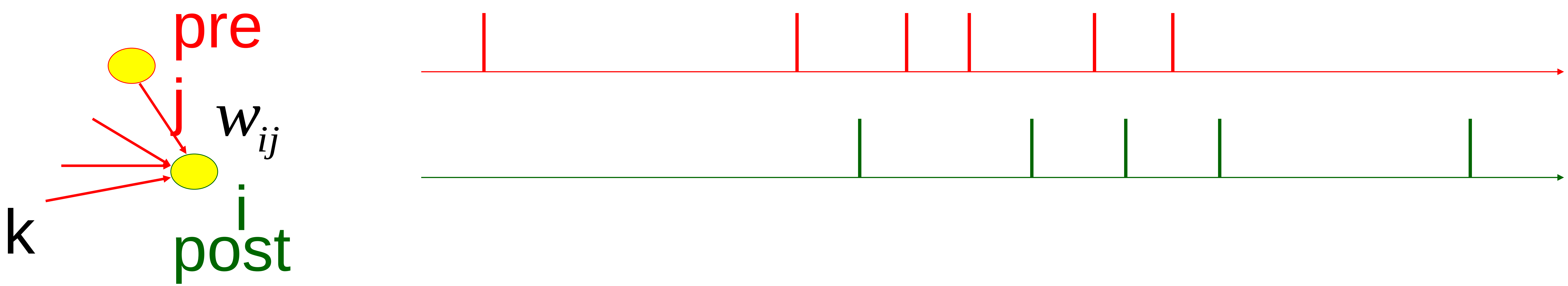
5. **Spiking Models of plasticity**
   - STDP as Hebbian learning
   - Model of STDP: synaptic traces
6. **From STDP to rate models**
7. **Triplet STDP model**
8. **Online learning of memories**

5. Hebbian Learning

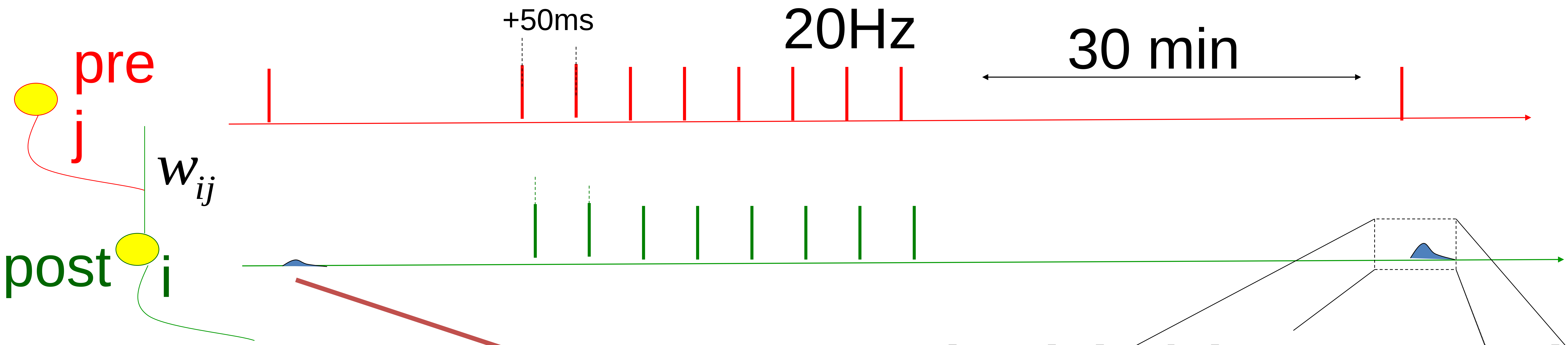


When an axon of cell **j** repeatedly or persistently takes part in firing cell **i**, then j's efficiency as one of the cells firing **i** is increased **Hebb, 1949**

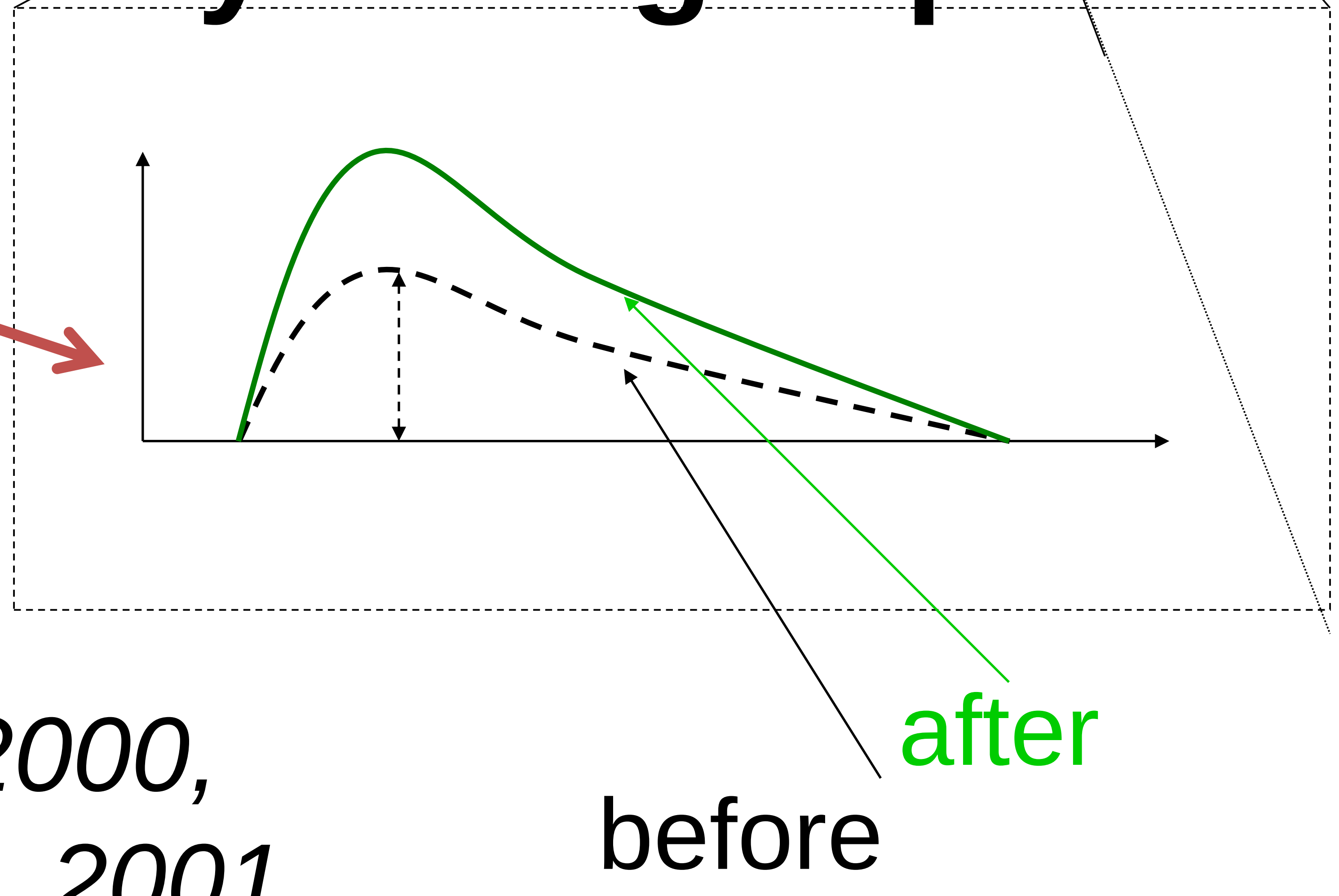
Experiments: Bliss and Lomo 1973, Levy and Stewart, 1983, …
Markram et al. 1997, Bi and Poo, 1998, …

Reviews: Bliss and Collingridge, 1993, Sjostrom et al. 2008...
Markram et al. 2011, ...

5. STDP as Hebbian Learning



Long-term plasticity/changes persist



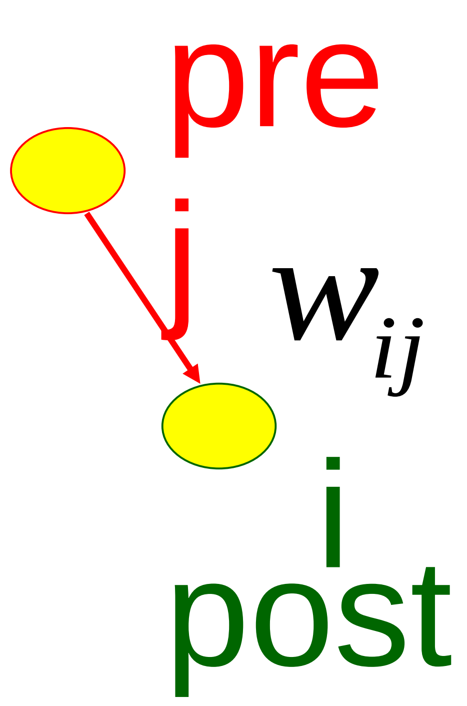
Changes

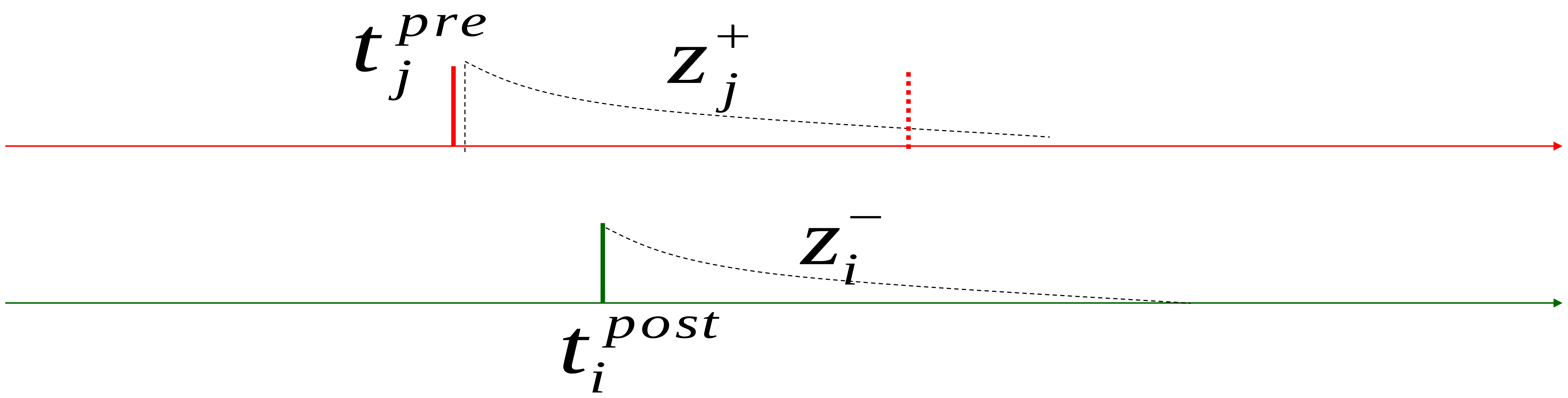
- induced over 3 sec
- persist over hours and days

Models of STDP

Gerstner et al. 1996, Kempter et al., 1999, Song et al. 2000, Senn et al. (2001), van Rossum et al. 2000, Rubin et al. 2001 Shouval et al. (2002), Clopath et al. (2010)

5. Spike-timing dependent plasticity: 'traces' for STDP





$$\tau_+ \frac{d}{dt} z_j^+ = -z_j^+ + \delta(t - t_j^{pre})$$ jump at presyn. spike

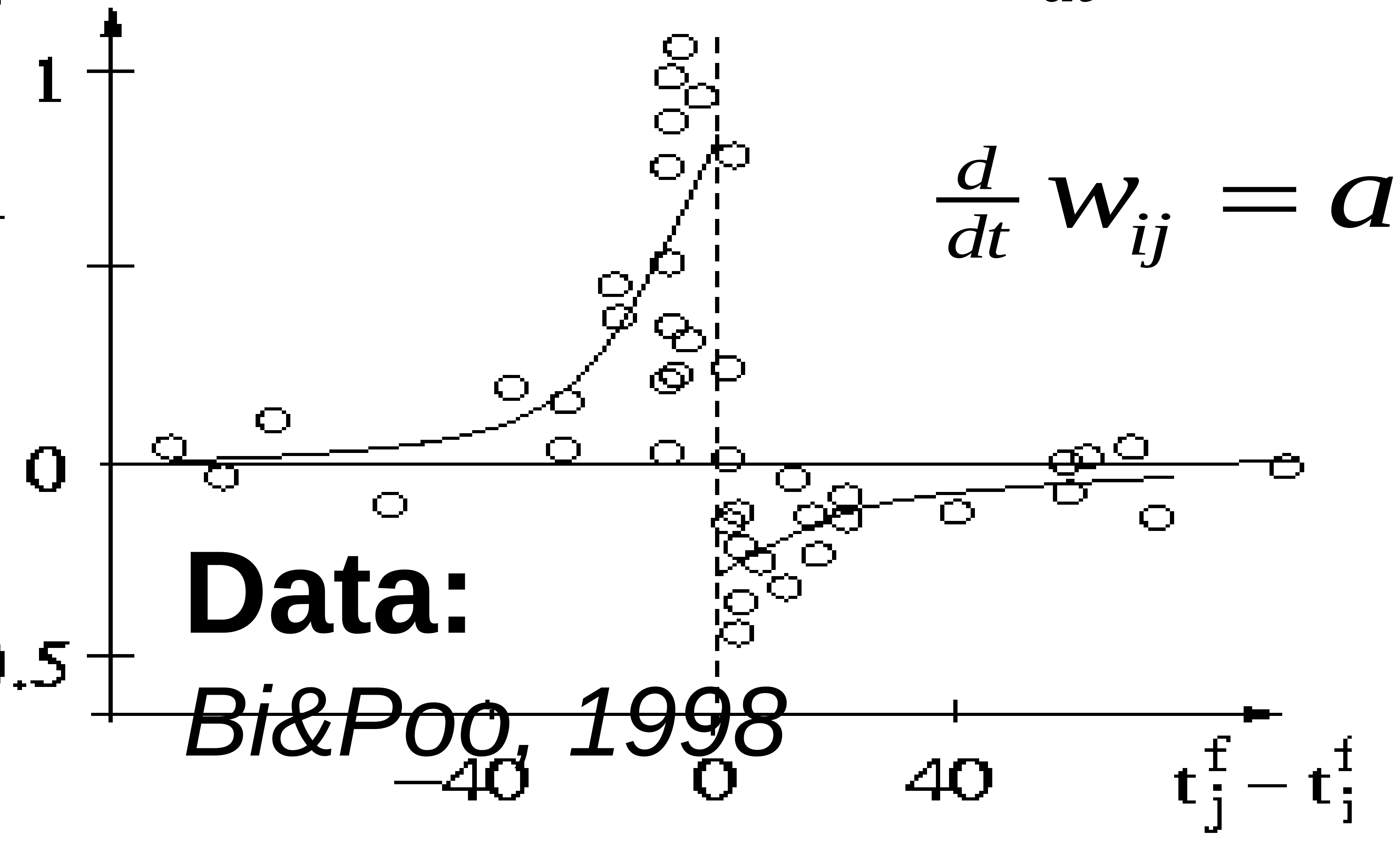
$$\tau_- \frac{d}{dt} z_i^- = -z_i^- + \delta(t - t_i^{post})$$ jump at postsyn. spike

pair

$$\frac{d}{dt} w_{ij} = a(w_{ij}) z_j^+ \delta(t - t_i^{post}) - b(w_{ij}) z_i^- \delta(t - t_j^{pre})$$

pre-before-post

post-before-pre



Data:

Bi&Poo, 1998

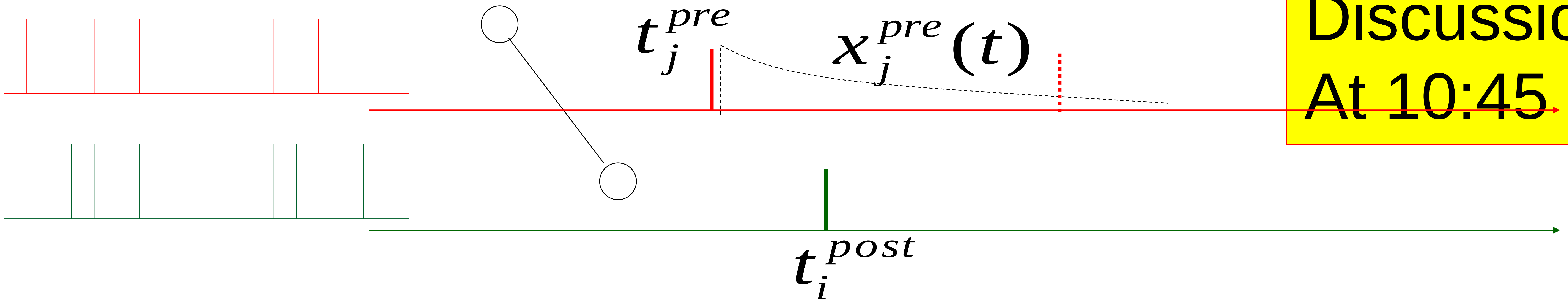
→ **Simple STDP model**

(Gerstner et al. 1996,

Song-Miller-Abbott 2000, etc)

Exercise STDP now:

Take 8 minutes =
Discussion of ex
At 10:45



-What is the shape of the STDP window?

-calculate the effect of one pair of spikes

-calculate the effect of many pairs of spikes

5. Summary: Spike-timing dependent plasticity (STDP)

STDP is a form of Hebbian learning induced by spikes.
For a phenomenological model, we can take the view that each spike arriving at the presynaptic terminal leaves a trace at the synapse (e.g., amount of glutamate in the synaptic cleft, or bound to the postsynaptic receptor).
If a spike of the postsynaptic neuron coincides with the trace left by the presynaptic spike, a change happens (proportional to the monentary value of the trace.

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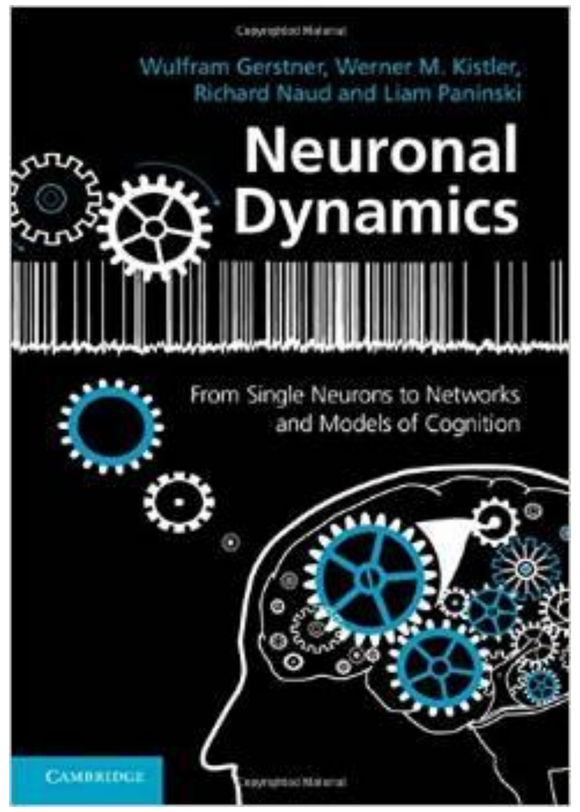
Cambridge Univ. Press



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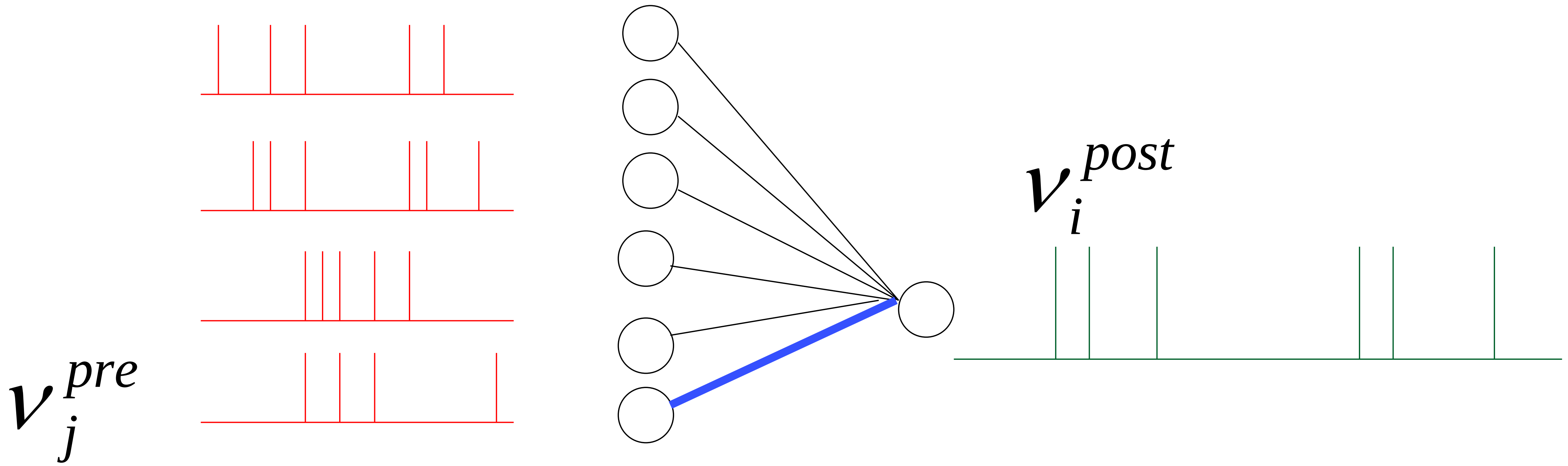
- STDP as Hebbian learning
- Model of STDP: synaptic traces

6. From STDP to rate models

7. Triplet STDP model

8. Online learning of memories

6. from STDP to rate models

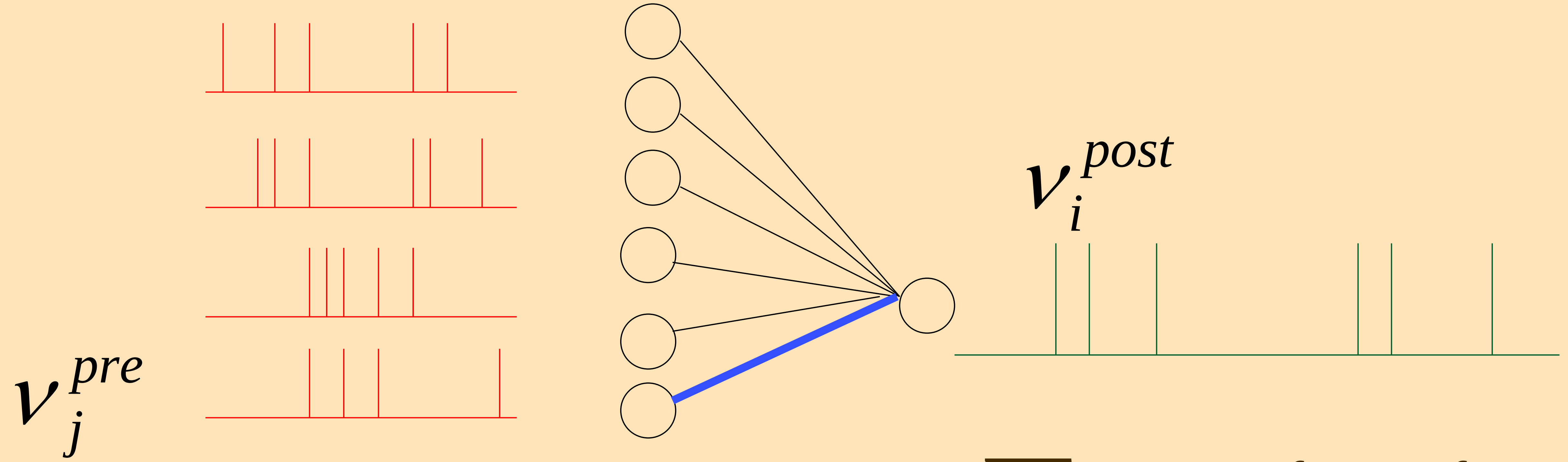


$$\Delta w_{ij} = \sum_{f,f'} W(t_i^f - t_j^{f'})$$

$$\frac{1}{T}\Delta w_{ij} = \frac{1}{T}\int_0^T \int_{-\infty}^{\infty} W(s) S_i(t) S_j(t+s)\, ds$$

Exercise 4a: STDP to rate now:

Take 8 minutes = Discussion of ex At 11:20



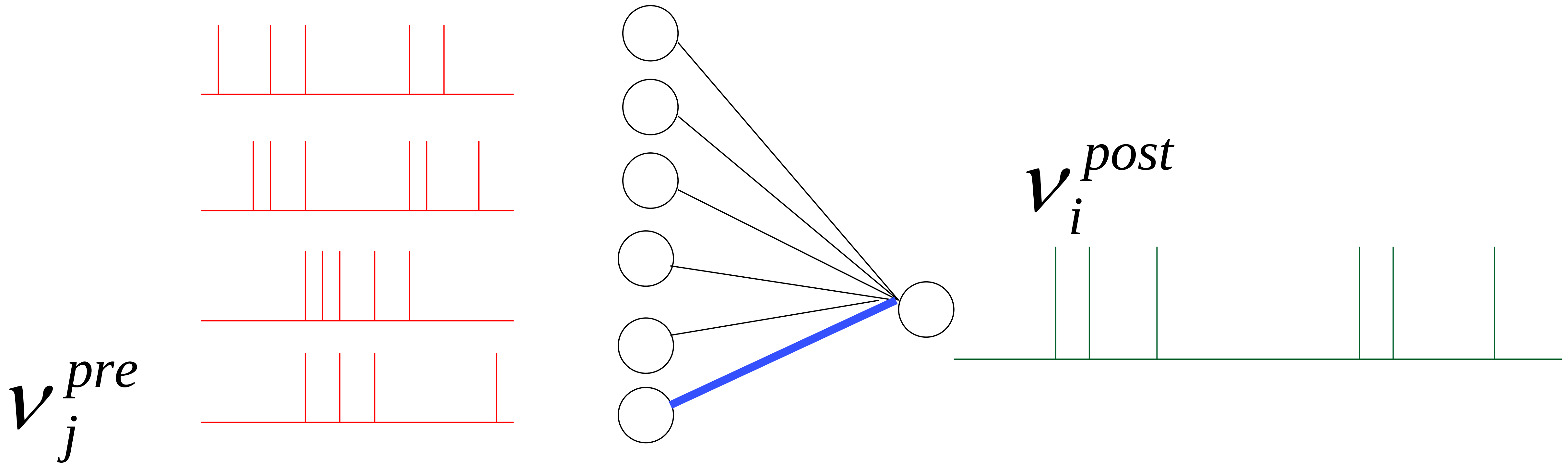
$$\Delta w_{ij} = \sum_{f,f'} W(t_i^f - t_j^{f'})$$

Assume presynaptic spikes are generated by Poisson process with rate ν_j^{pre}

Assume postsynaptic spikes are generated by Poisson process with rate ν_i^{post}

What is the expected change of weights in a time T? $(T >> \tau^{LTP}, \tau^{LTD})$

6. from STDP to rate models

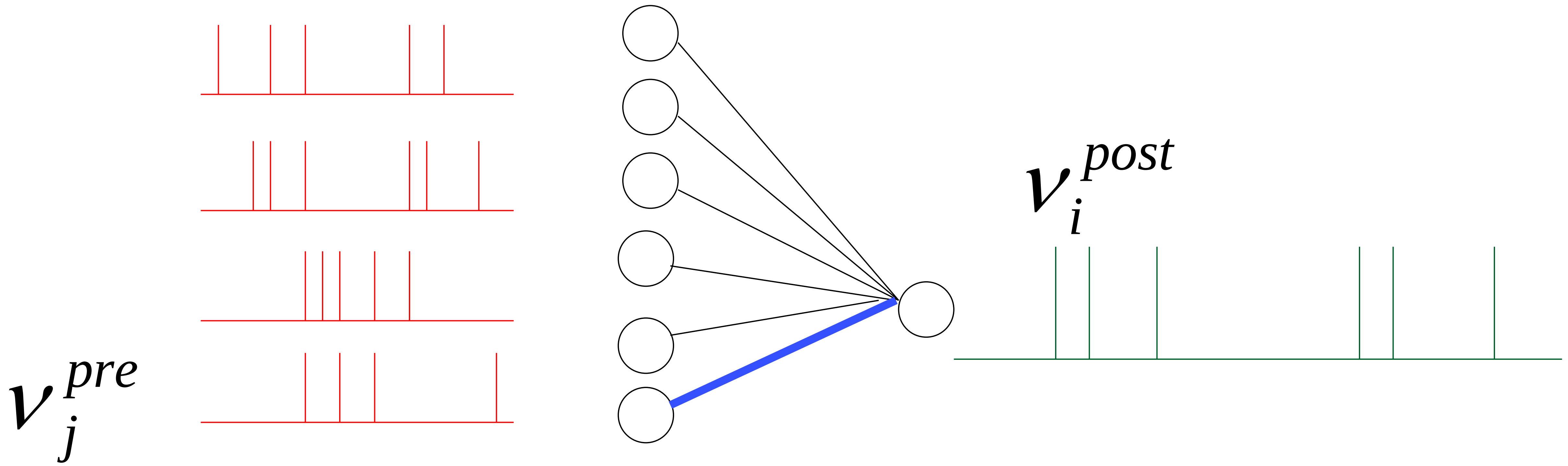


Blackboard2

$$\Delta w_{ij} = \sum_{f,f'} W(t_i^f - t_j^{f'})$$

$$\frac{1}{T}\Delta w_{ij} = \frac{1}{T}\int_0^T \int_{-\infty}^{\infty} W(s) S_i(t) S_j(t+s) ds$$

6. from STDP to rate models



$$\Delta w_{ij} = \sum_{f,f'} W(t_i^f - t_j^{f'})$$

$$\frac{1}{T}\Delta w_{ij} = \frac{1}{T}\int_0^T \int_{-\infty}^{\infty} W(s) S_i(t) S_j(t+s)\,ds$$

$$\frac{d}{dt} w_{ij} = S_i(t)\int_0^{\infty} W_+(-s) S_j(t-s)\,ds + S_j(t)\int_0^{\infty} W_-(s) S_i(t-s)\,ds$$

6. Summary: from STDP to rate models

In an STDP model, changes of synapses depend on the exact timing of pre- and postsynaptic spikes.
However, if we assume that both presynaptic and postsynaptic spike trains are generated by a homogeneous Poisson Process (with stationary firing rates ν_i and ν_i), we can translate the effect induced by STDP after many spikes into an equivalent rate model by evaluation the expected change.

The standard STDP window gives then a rate model

$c\ \nu_i\ \nu_j$

where c is the integral over the STDP window.

Expectations and Correlations of Poisson spike train:
see week 11.2 or
Watch vide video ‘Membrane Potential fluctuations’ on:
http://lcn.epfl.ch/~gerstner/NeuronalDynamics-MOOC1.html
direct link:
https://www.youtube.com/watch?v=YTQqOyrFQQ4

Computational Neuroscience: Neuronal Dynamics of Cognition

EPFL

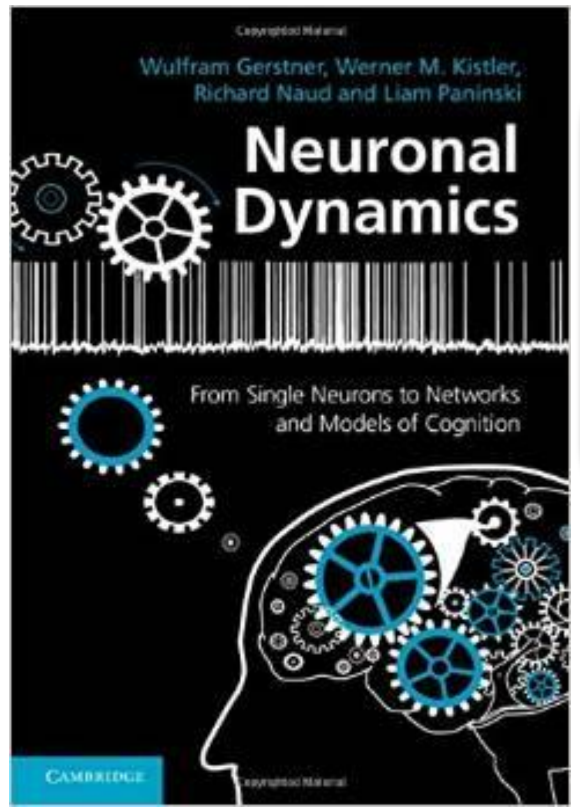
Synaptic Plasticity and Learning

Wulfram Gerstner

EPFL, Lausanne, Switzerland

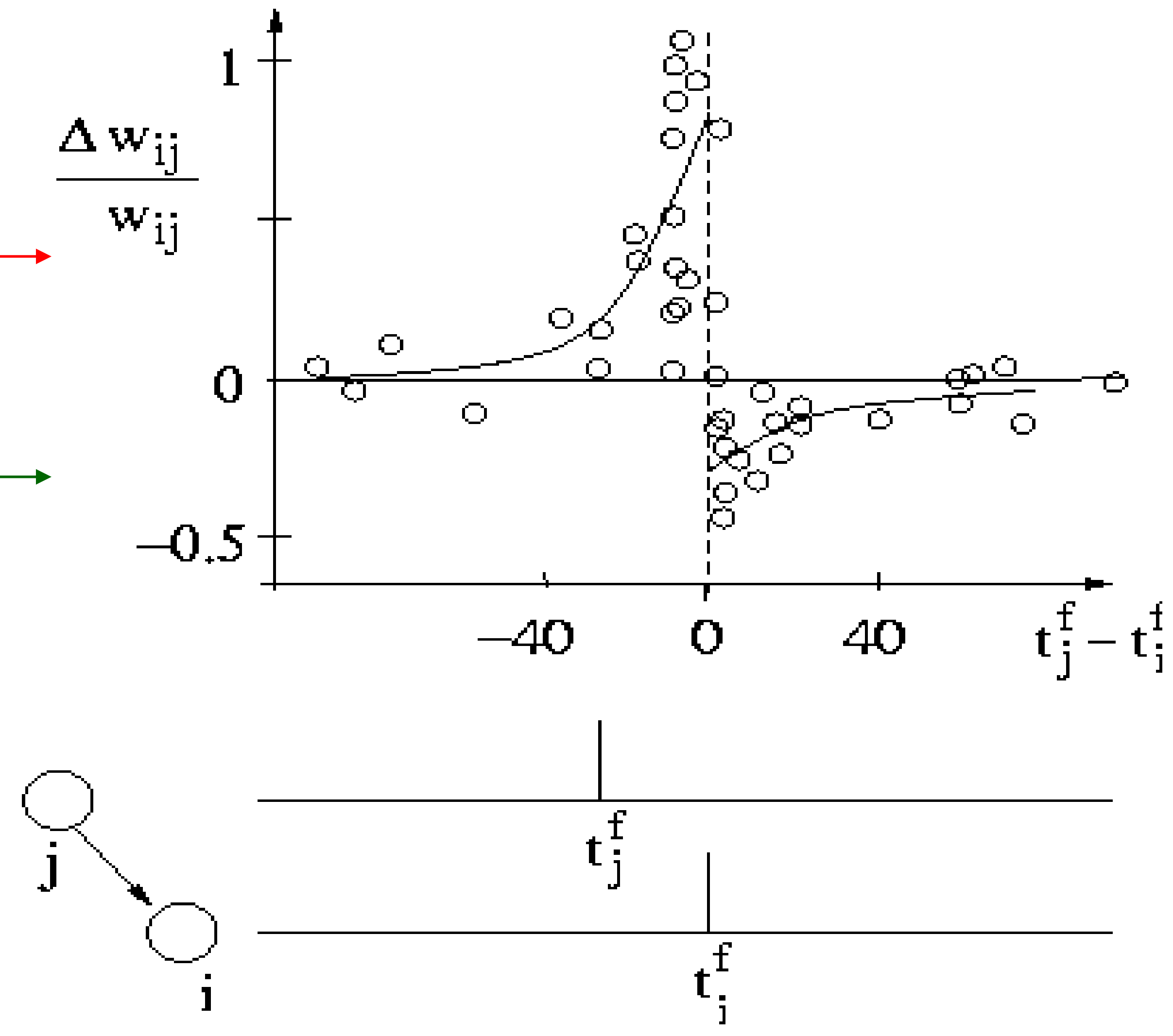
Reading for plasticity:
NEURONAL DYNAMICS
- Ch. 19.1-19.3

Cambridge Univ. Press



1. **Synaptic plasticity: aims**
2. **Classification of plasticity**
3. **Model of short-term plasticity**
4. **Models of long-term plasticity**
5. **Spike-Timing Models of plasticity**
   - STDP as Hebbian learning
   - Model of STDP: synaptic traces
6. **From spiking models to rate models**
7. **Triplet STDP model**
   - Relation to experiments
   - Relation to BCM rule
8. **Online learning of memories**

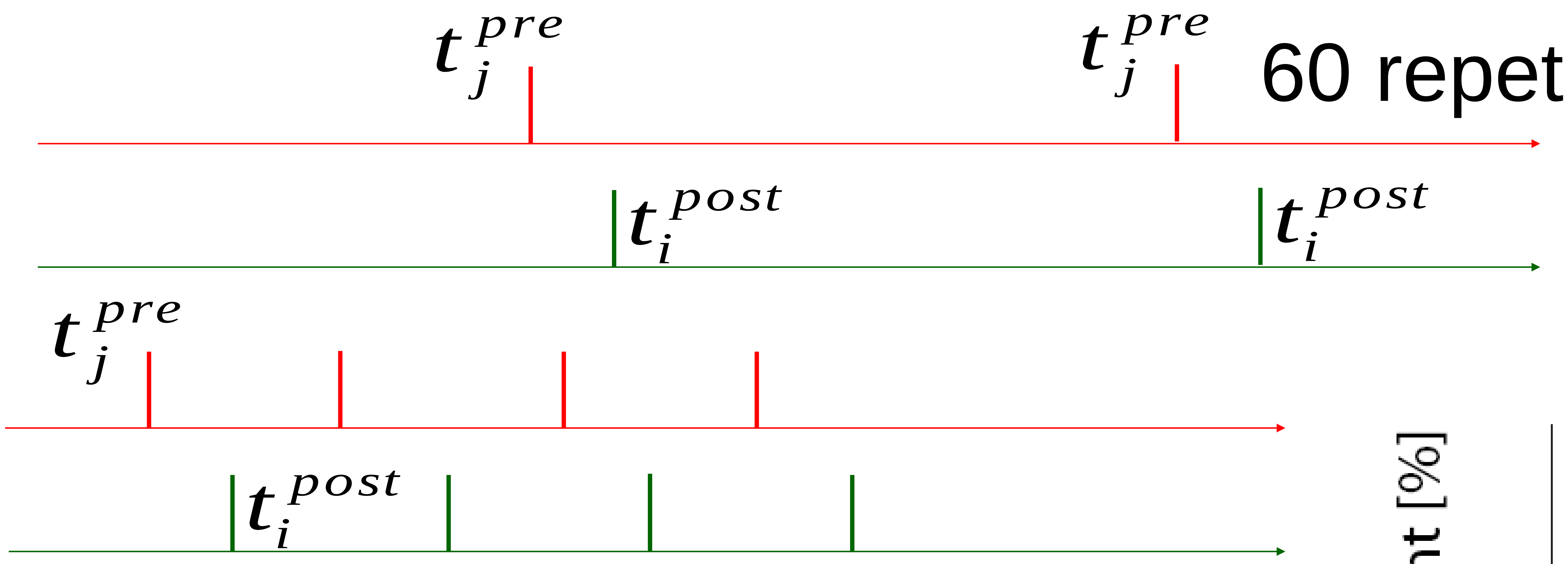
7. Why do we need a Triplet STDP model?



STDP window
is only part of story

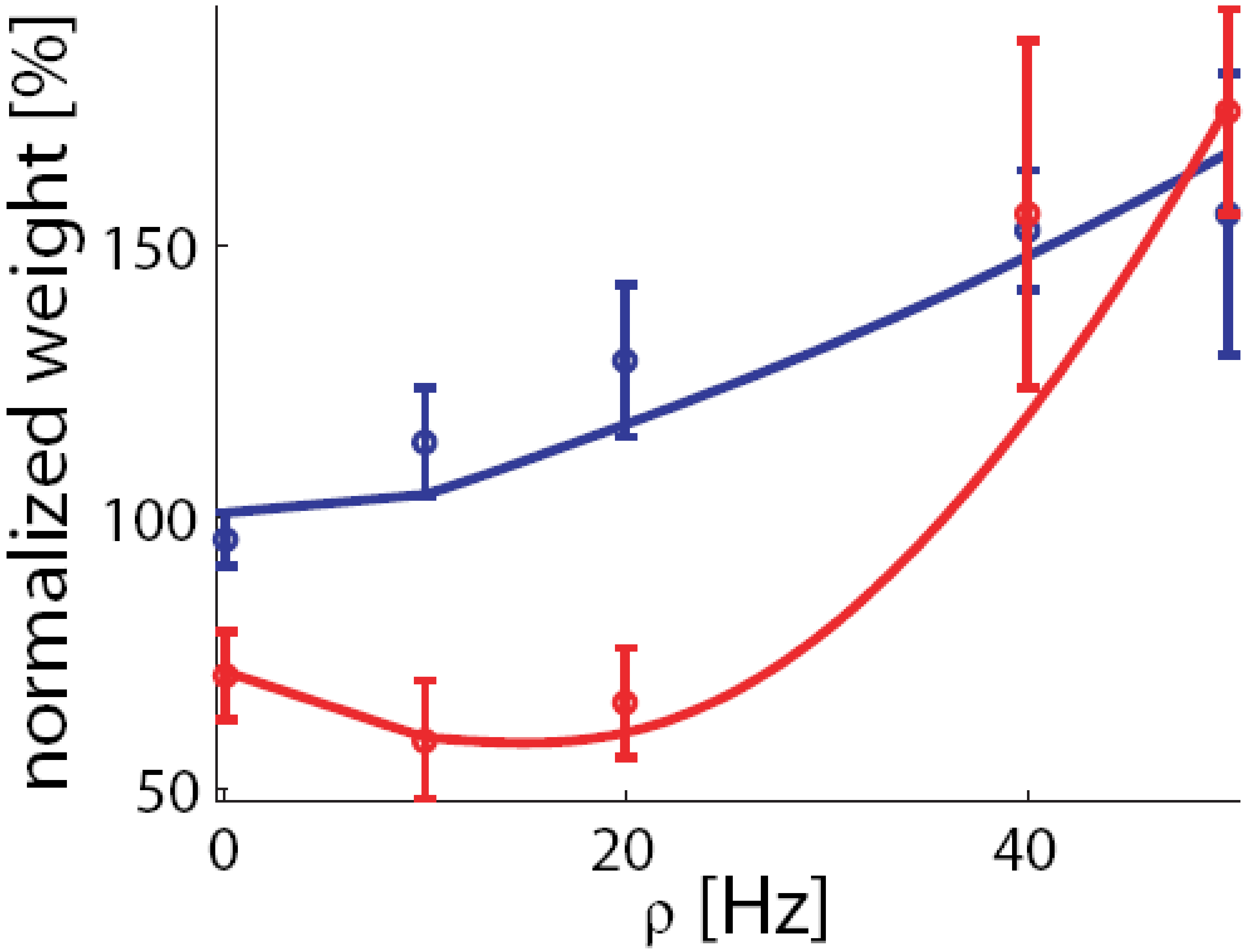
Pair-based STDP model
is not sufficient

7. frequency dependenc of STDP



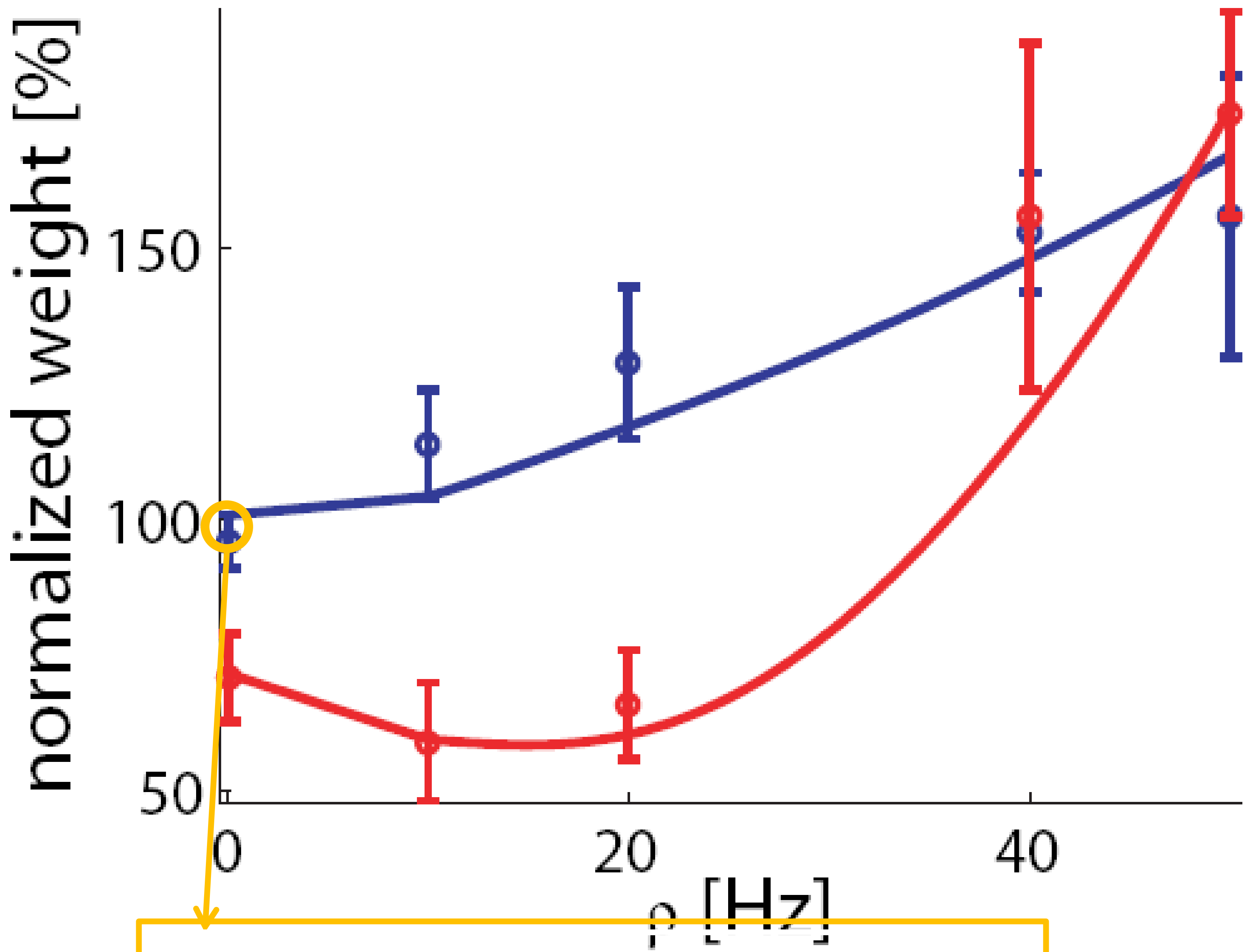
60 repetitions

Sjostrom et al. 2001
See also:
Markram et al. 1997,
Senn et al. 2001,



7. frequency dependence of STDP

- Repetition frequency important
- No LTP at 0.1Hz

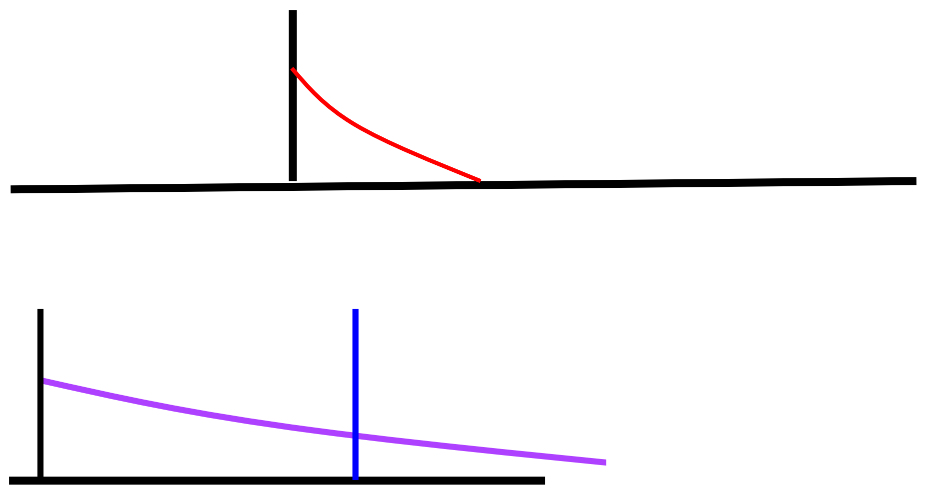


No plasticity
At low frequency

7. Triplet STDP model

Triplet
LTP

$$\frac{d}{dt} w_j^+ = +A^+ z_j^+ \; z_i^{slow} \, \delta(t - t_i^{post})$$



pre post post

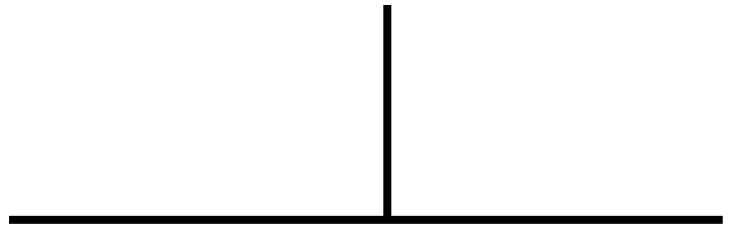
Triplet

7. Triplet STDP model

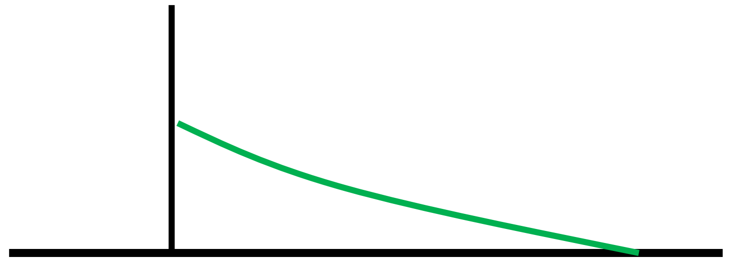
Pfister and Gerstner, 2006

$$\frac{d}{dt} w_j =$$

$$-B\, z_i^- \,\delta\left(t - t_j^{pre}\right)$$

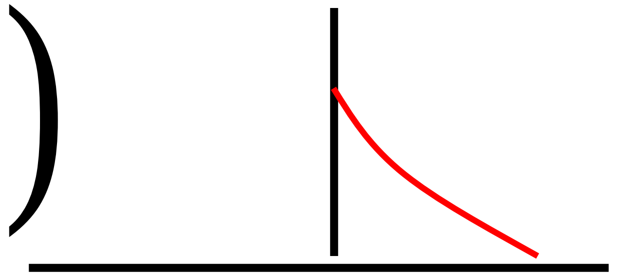


Pre: spike

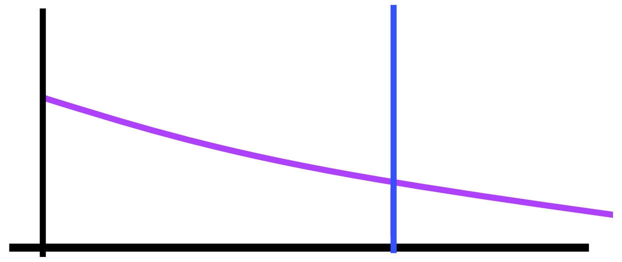


Post: spike-trace

$$+A^+ z_j^+ \; z_i^{slow}\, \delta\left(t - t_i^{post}\right)$$



Pre: spike-trace



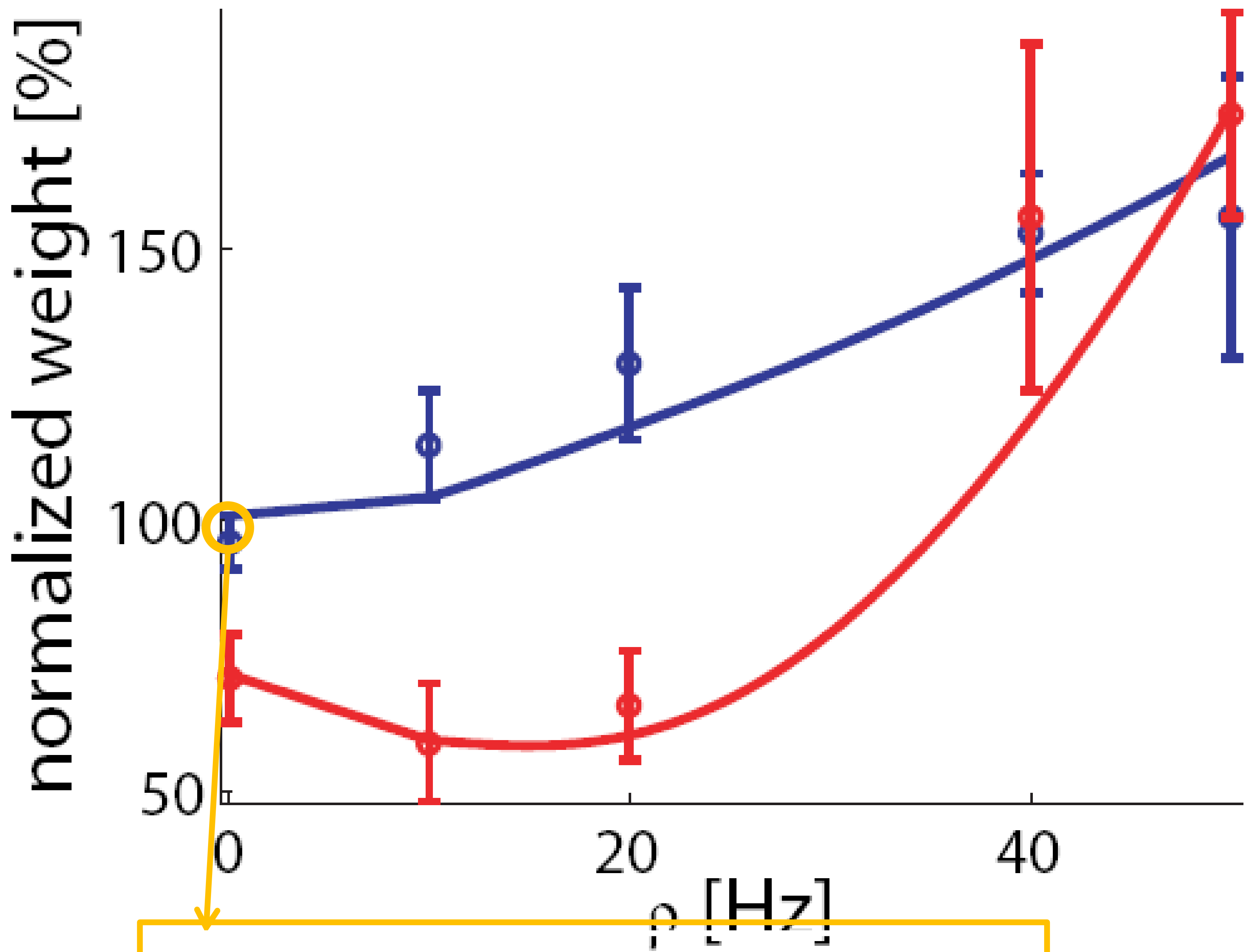
Post: spike-now

spike-trace

7. Triplet STDP model

Pfister and Gerstner, 2006

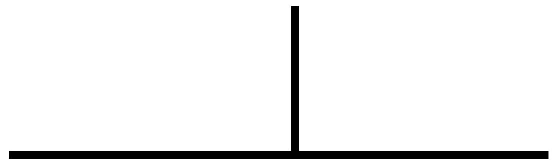
Similar triplet mechanism in
Senn et al. 2001,
Rubin et al. 2005,
Clopath et al. 2010



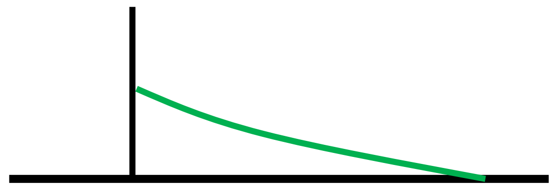
No plasticity
At low frequency

7. Triplet STDP model → BCM model

$$\frac{d}{dt} w_j = -B\, \underline{z_i^-}\, \delta(t - t_j^{pre})$$

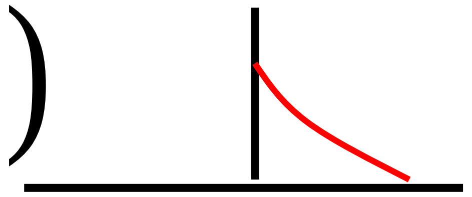


Pre: spike

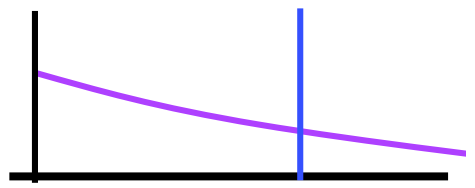


Post: spike-trace

$$+A^+ z_j^+\; z_i^{slow}\, \delta(t - t_i^{post})$$



Pre: spike-trace



Post: spike-now

slow spike-trace

Assume Poisson firing

$$\frac{d}{dt} w_j =$$

7. Summary: Triplet STDP → BCM model

Triplet STDP model

- parameters can be extracted from experimental data
- for Poisson spikes closely related to rate-based BCM
- but captures addition spike-timing effects
- simple pair-based STDP model is not sufficient, because STDP depends also on repetition frequency (and not only on relative timing of pairs of spikes).

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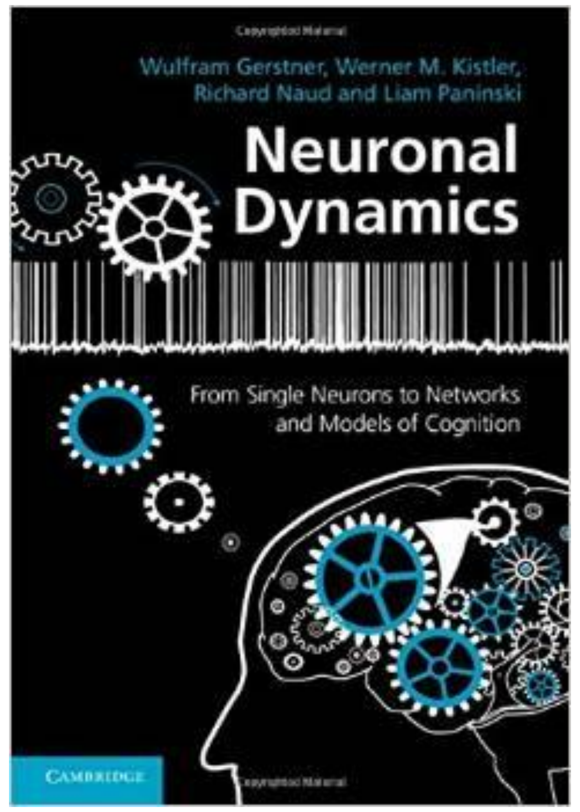

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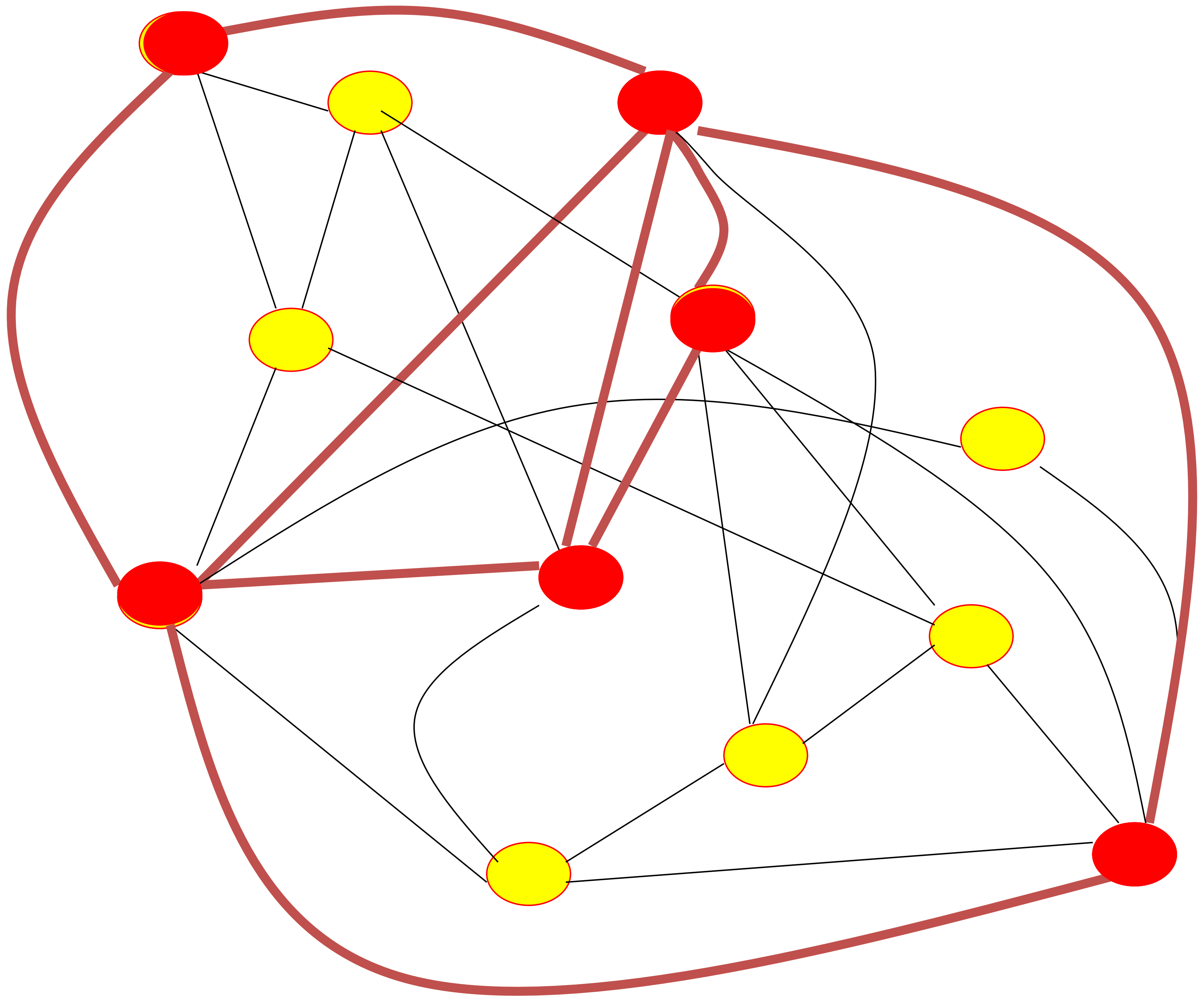
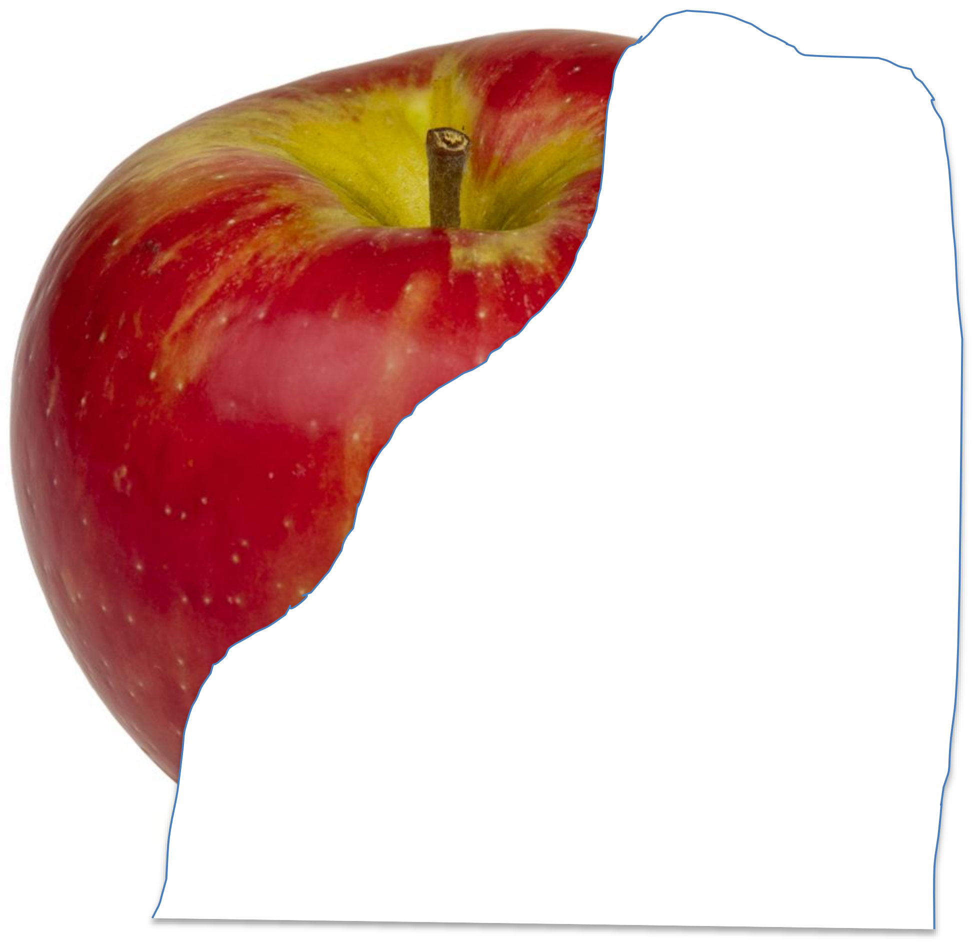
8. Online learning of memories

8. Review: Hebbian assemblies

Recall:
Partial info

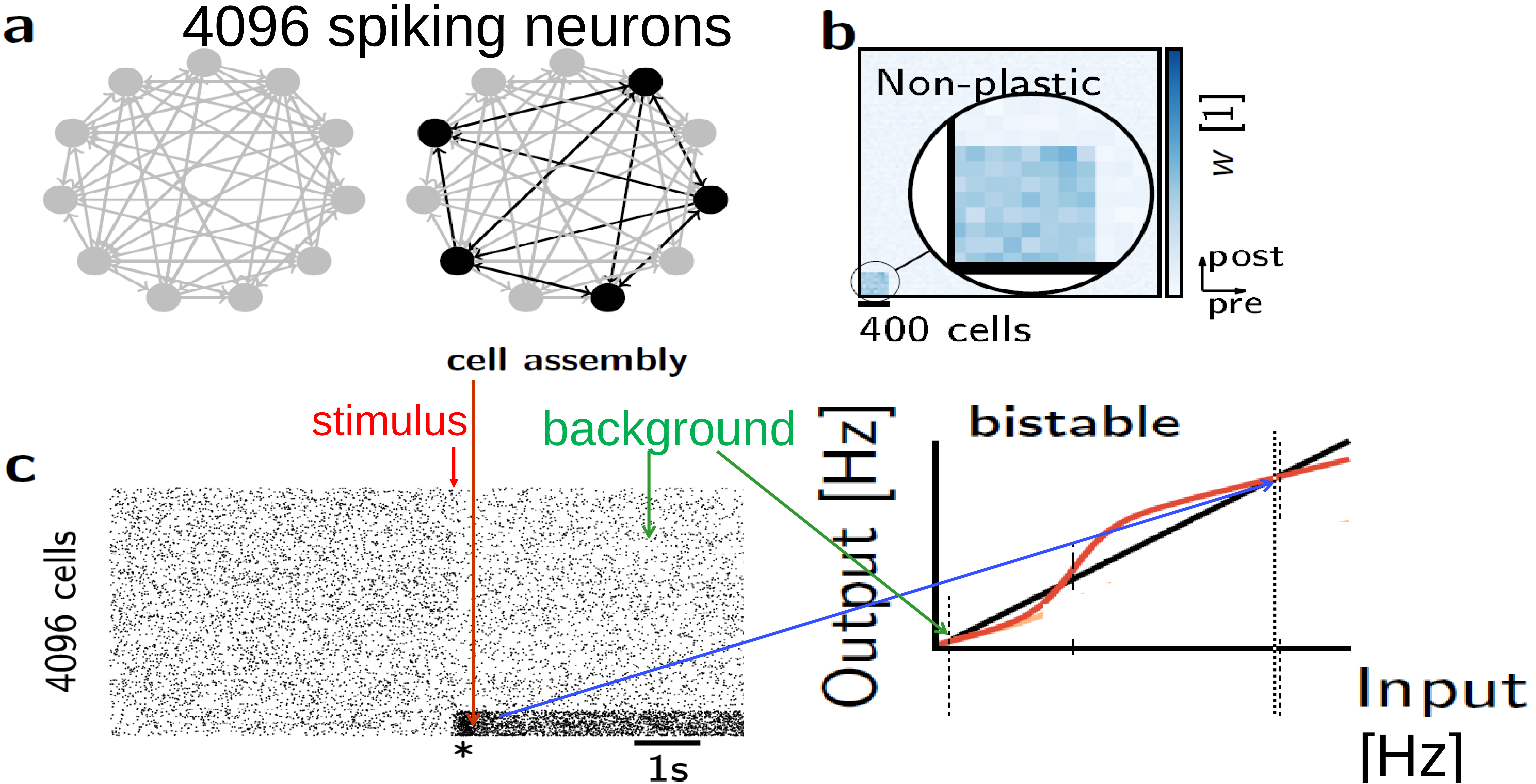




item recalled

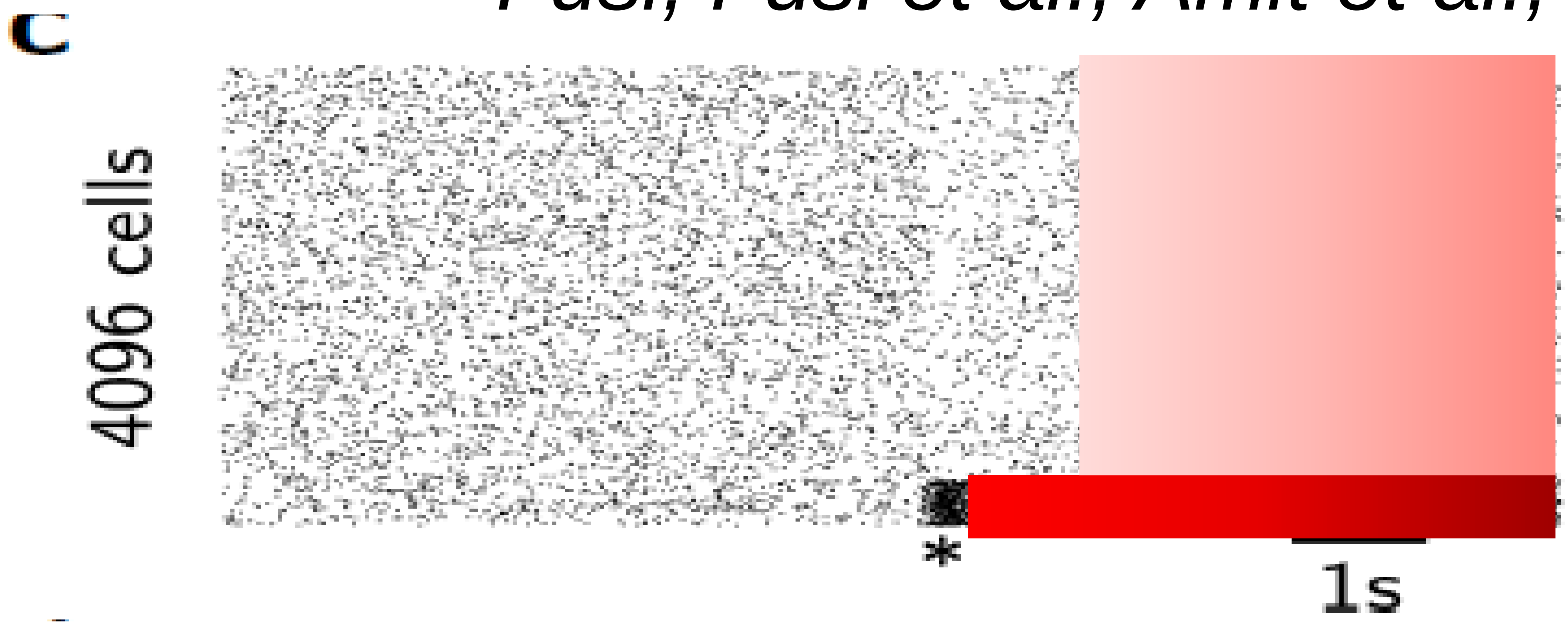
8. Preconfigured memory: bistable network

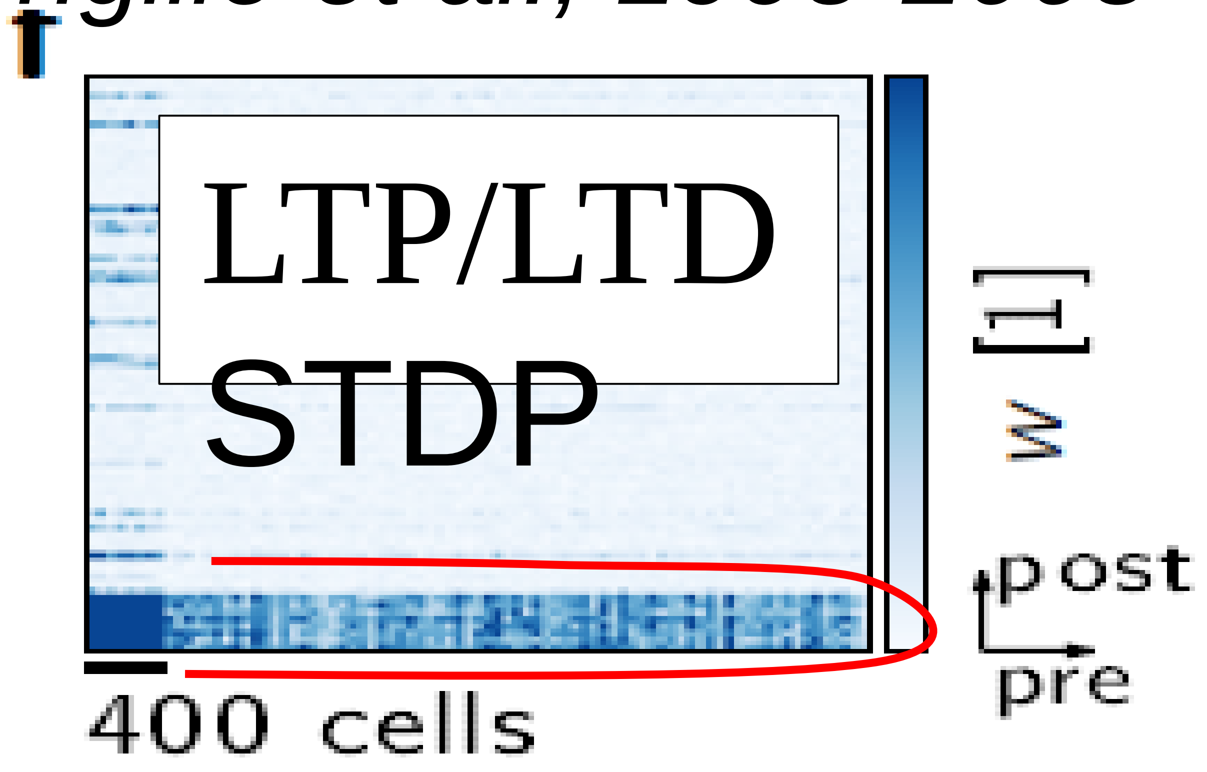
e.g., groups of Hopfield, Amit, Brunel, Fusi, Sompolinsky, Tsodyks,



8. Learning the memory: very hard

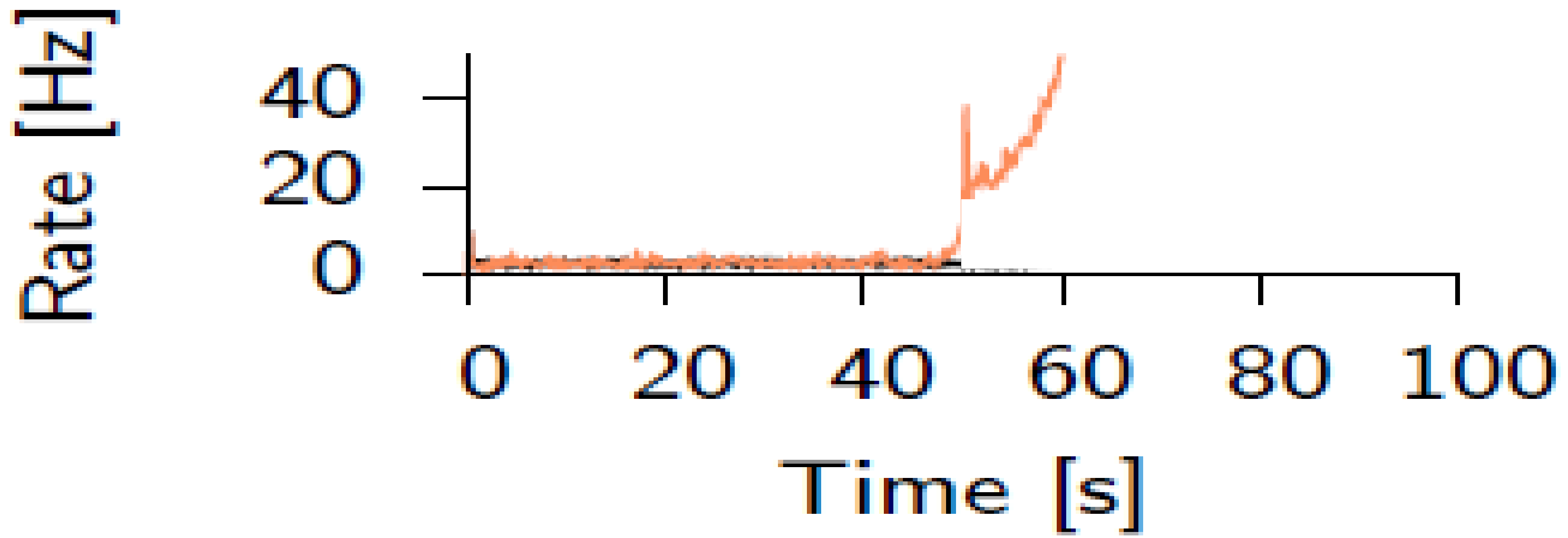
Fusi, Fusi et al., Amit et al., Mongillo et al., 1995-2005



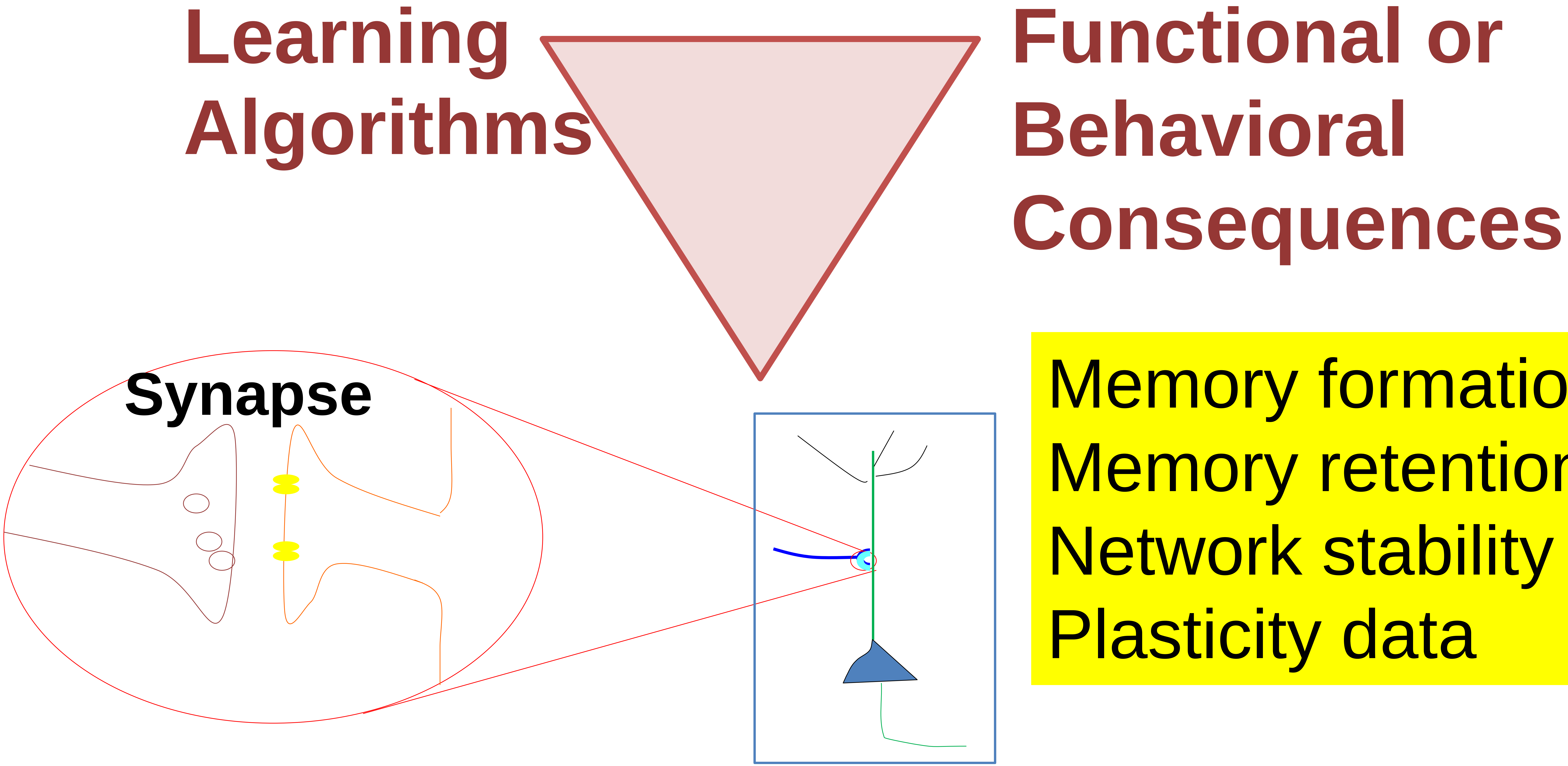


LTP/LTD
STDP

stimulus



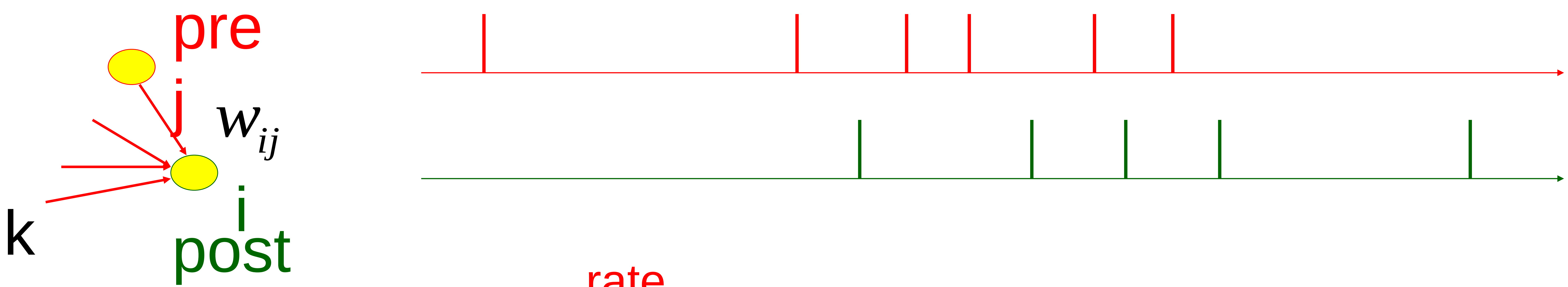
8. Learning: the task of modeling



Memory formation
Memory retention
Network stability
Plasticity data

Synaptic Plasticity

8. Review: Rate models of Hebbian learning



rate

rate

$$\frac{dw_{ij}}{dt} = F(w_{ij}; \nu_j^{pre}, \nu_i^{post})$$

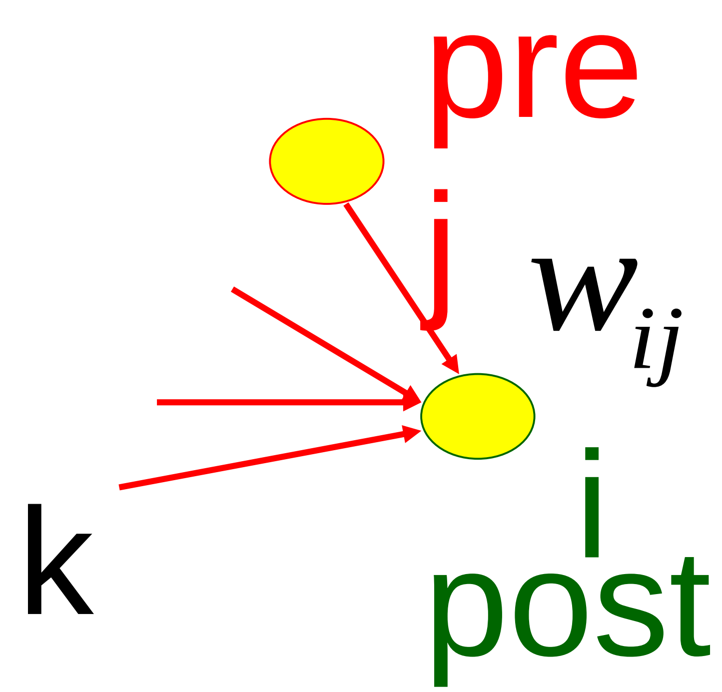
- local rule
- simultaneously active

pair

$$\frac{dw_{ij}}{dt} = a_0 + a_1^{pre}\nu_j^{pre} + a_1^{post}\nu_i^{post} + a_2^{corr}\nu_j^{pre}\nu_i^{post} +$$

depend on w_{ij}

8. Induction of Plasticity



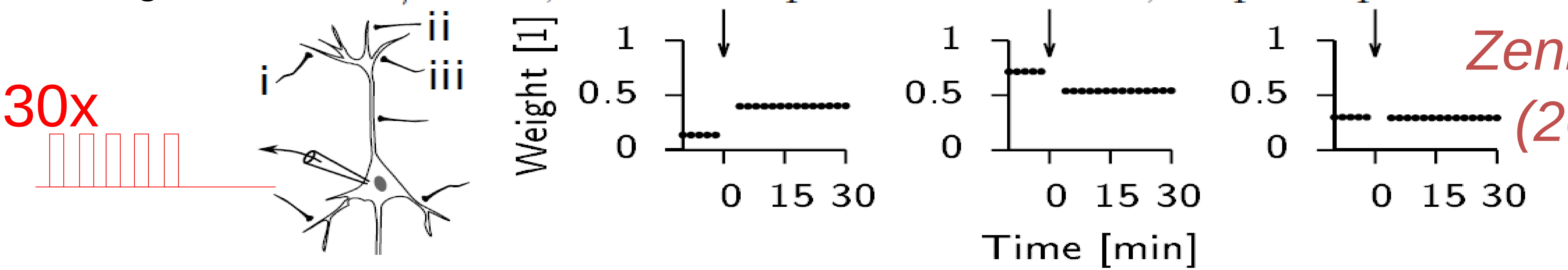
- **homosynaptic/Hebb** (‘pre’ and ‘post’)
- **heterosynaptic plasticity** (pure ‘post’-term)
- **transmitter-induced** (pure ‘pre’-term)

$$\frac{dw_{ij}}{dt} = a_0 + a_1^{pre}\nu_j^{pre} + a_1^{post}\nu_i^{post} + a_2^{corr}\nu_j^{pre}\nu_i^{post} +$$

$$+a_3^{BCM}\nu_j^{pre}(\nu_i^{post})^2 \quad +a_4^{post}(w_{ij})[\nu_i^{post}]^4$$

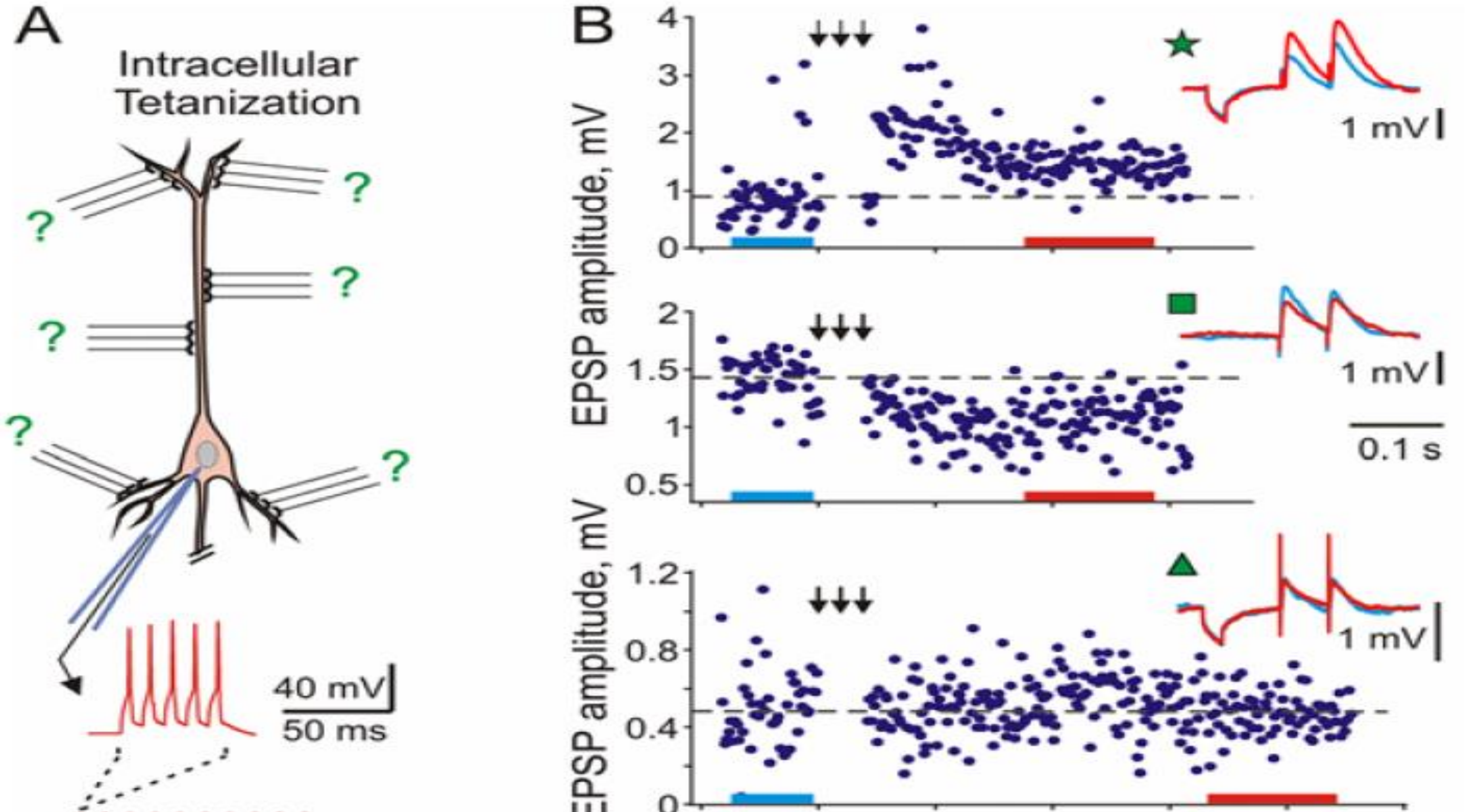
8. Heterosynaptic Plasticity (exper. and model)

3 trains at 1/60 Hz, 10 bursts per train at 1 Hz, 5 spikes per burst at 100 Hz)



Zenke et al. (2015)

Experiments



Chen et al. 2013,
Chistiakova et al. 2014
See also:
Lynch et al. 1977

8. Induction of Plasticity (rate-based)

- nonlinear Hebb for potentiation

$$+a_3^{BCM} \nu_j^{pre} (\nu_i^{post})^2$$

- pre-post for depression

$$-a_2^{LTD} \nu_j^{pre} \nu_i^{post}$$

Bienenstock et al., 1982
Pfister and Gerstner, 2006

- heterosynaptic plasticity (pure 'post')

$$-a_4^{het} (w_{ij} - z_{ij}) [\nu_i^{post}]^4$$

- transmitter-induced (pure 'pre')

$$+a_1^{pre} \nu_j^{pre}$$

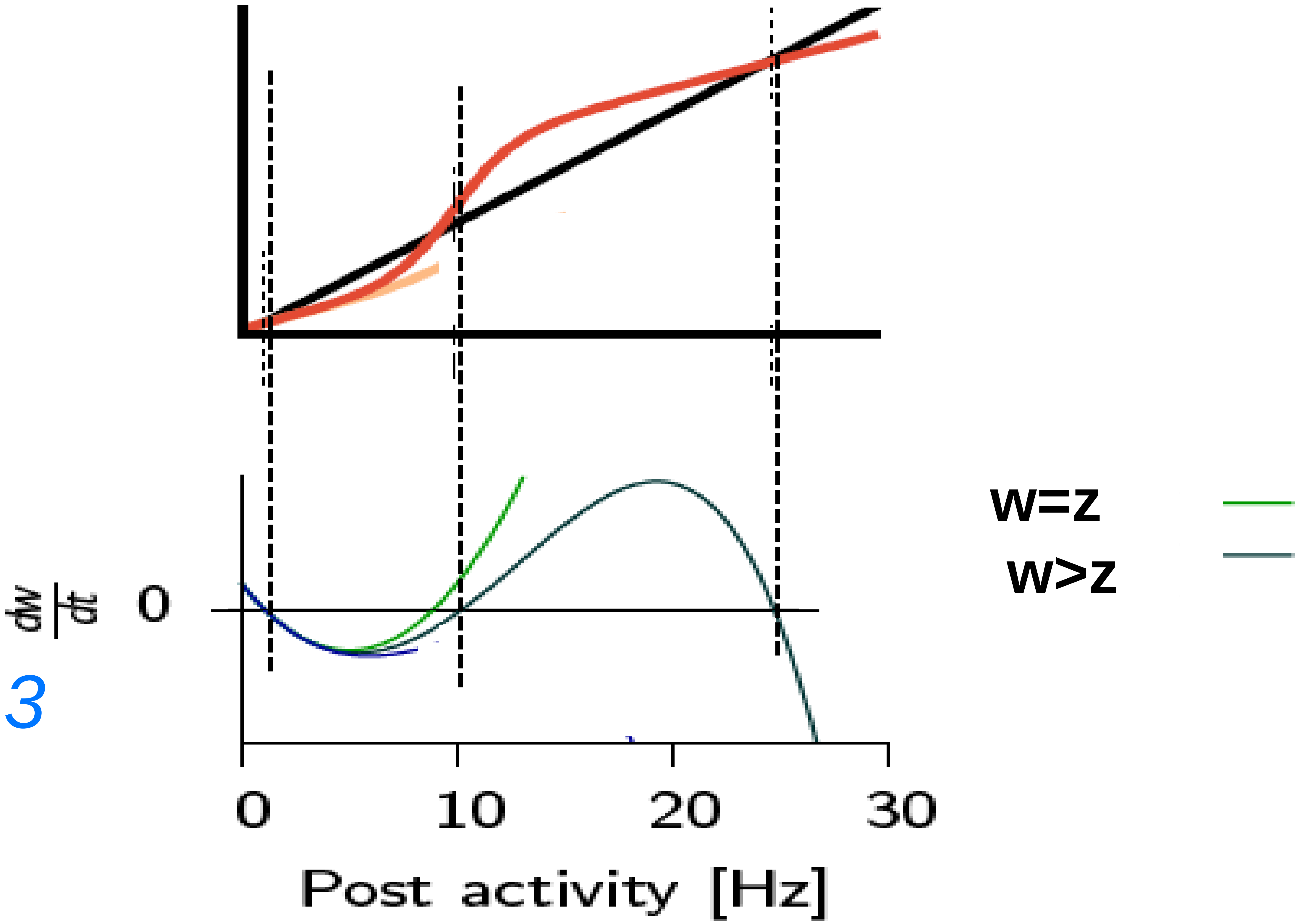
8. Plasticity model in network

$$\frac{dw_{ij}}{dt} = a_1^{pre}\nu_j^{pre} - a_2^{LTD}\nu_j^{pre}\nu_i^{post} + a_3^{BCM}\nu_j^{pre}(\nu_i^{post})^2 - a_4^{het}(w_{ij} - z_{ij})[\nu_i^{post}]^4$$

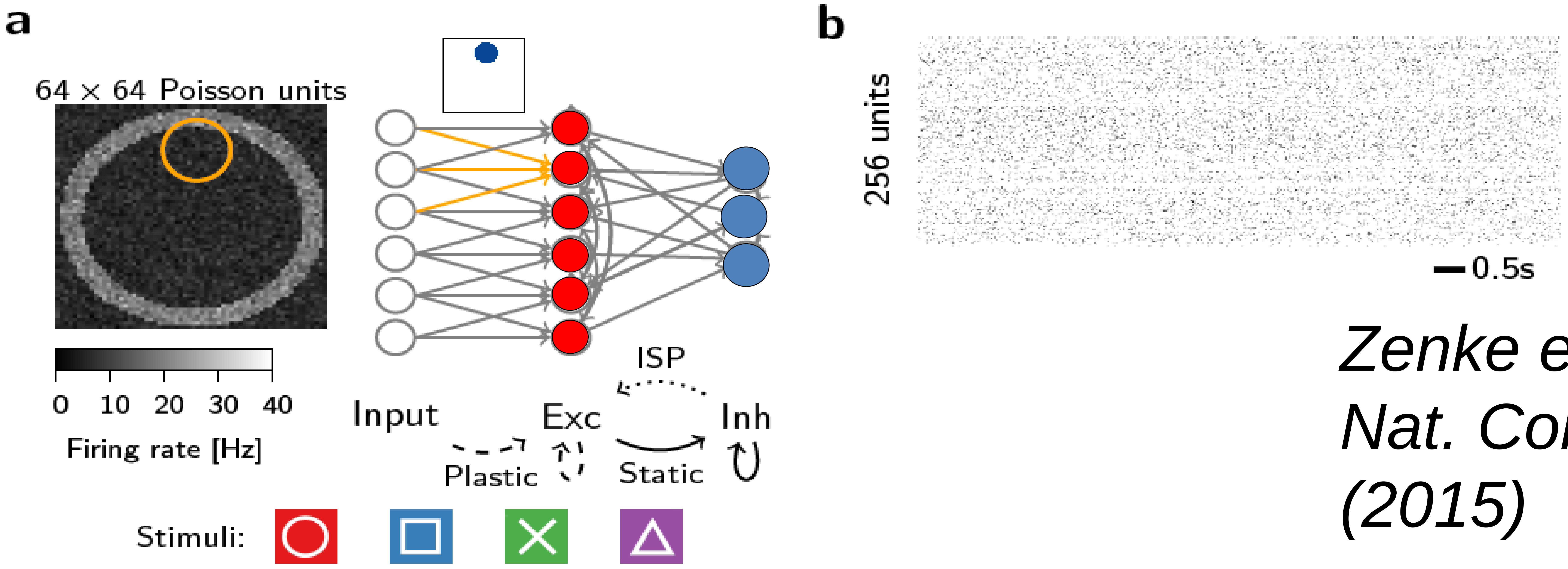
→Self-stabilizing!

Heterosynaptic plasticity
must act on the same time scale

Zenke+Gerstner, PLOS Comp. B. 2013
Zenke et al., Nat. Comm., 2015



8. Plasticity in feedforward /recurrent connections



Zenke et al., Nat. Comm. (2015)

8. Theory and Simulation: first minute

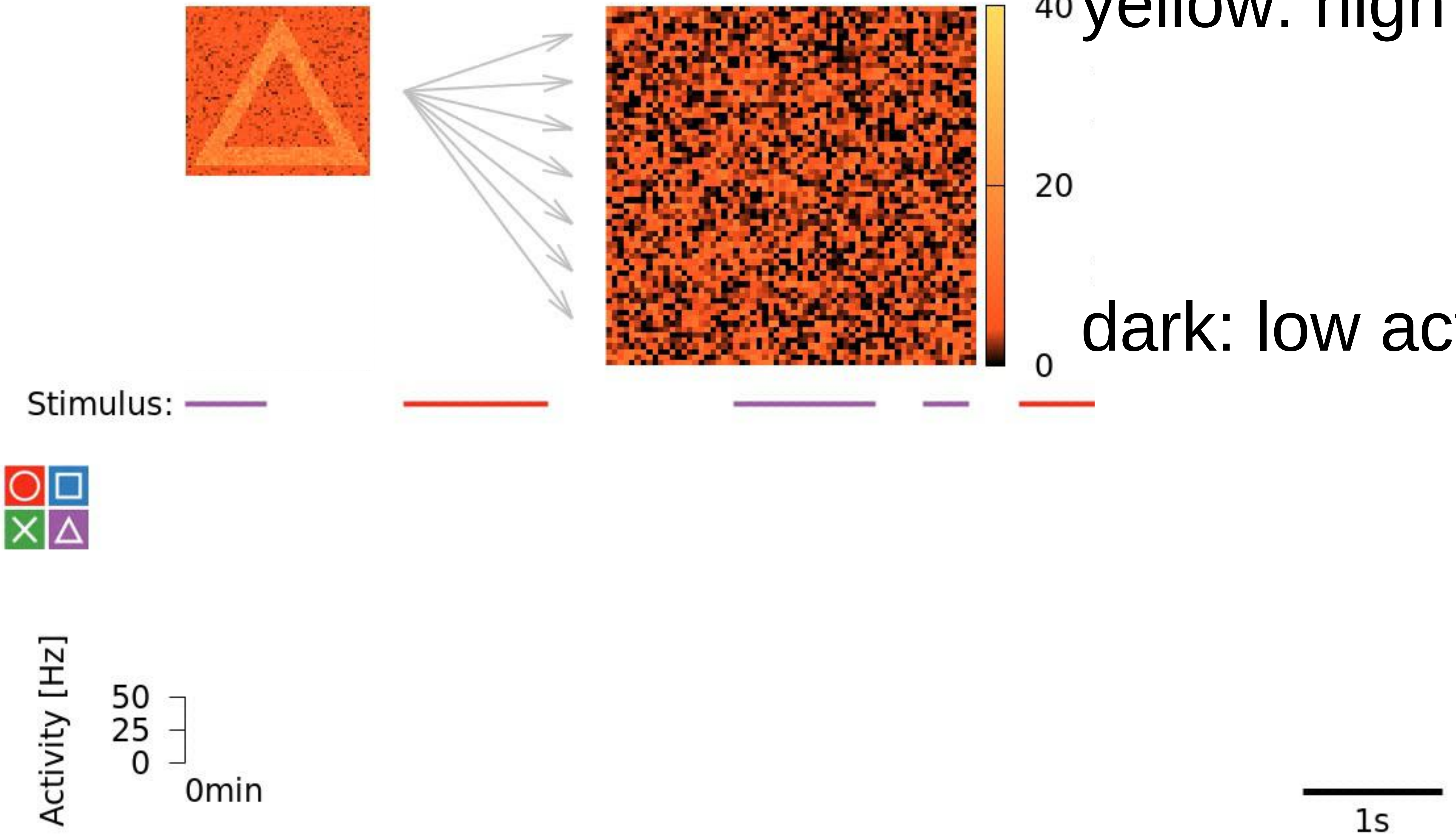
stimulus

retina

Neuronal network

yellow: high activity

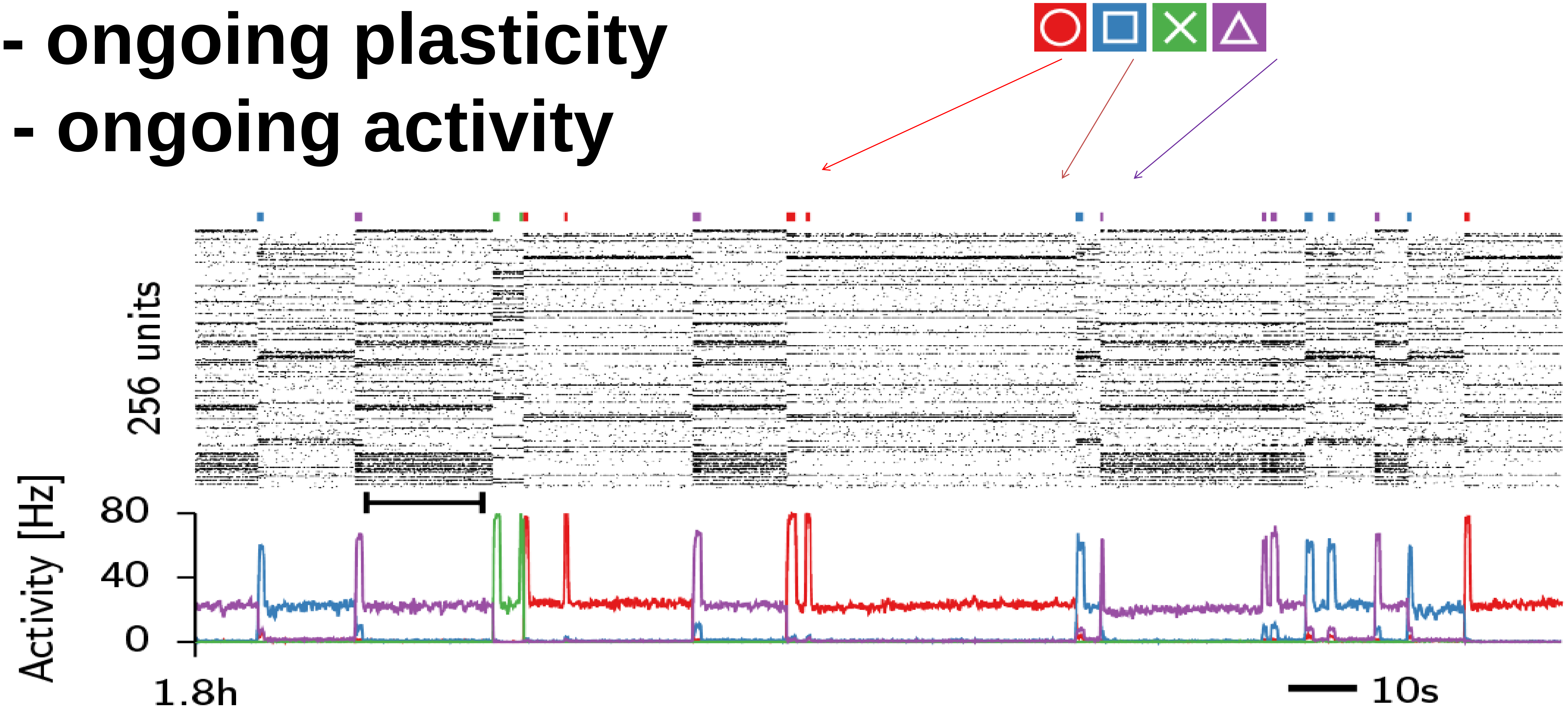
dark: low activity



8. Plasticity model in network: two hours later

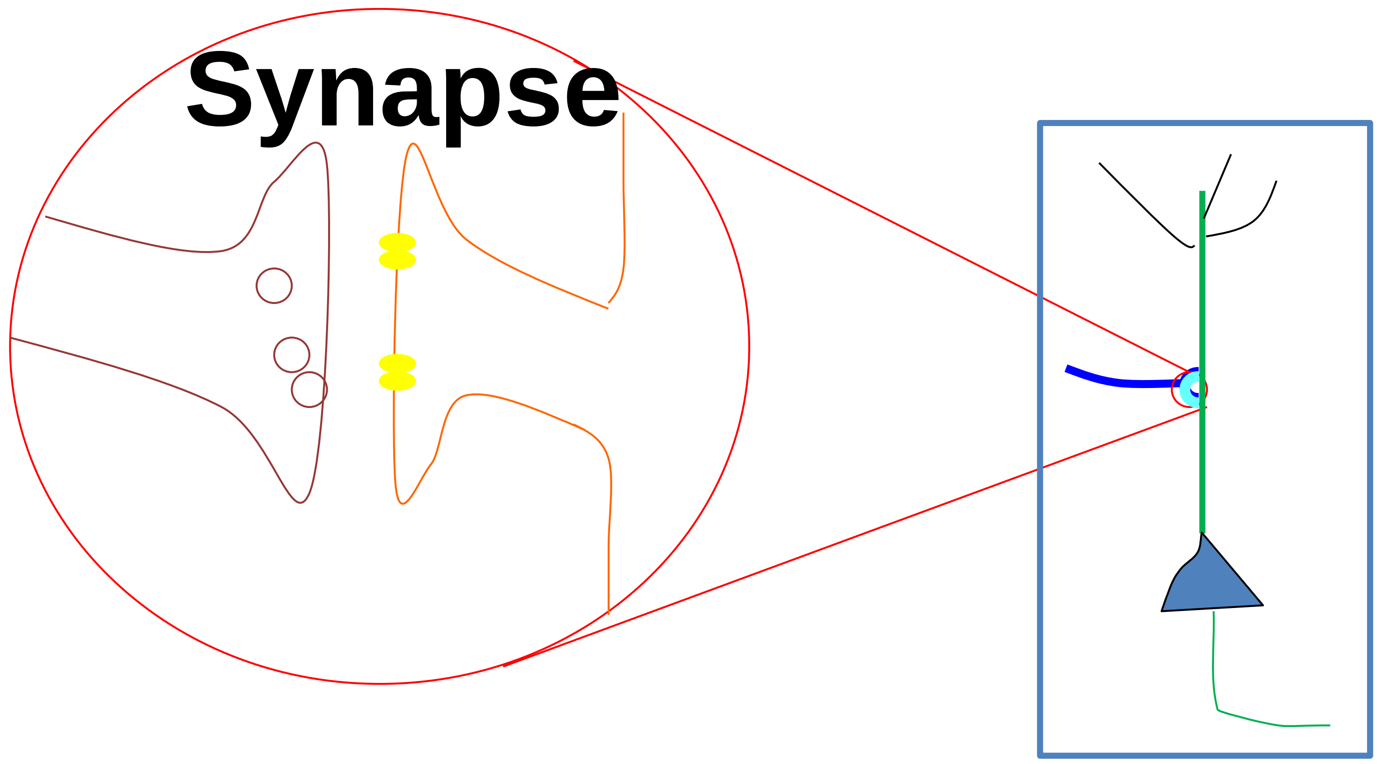
Stable memory recall despite

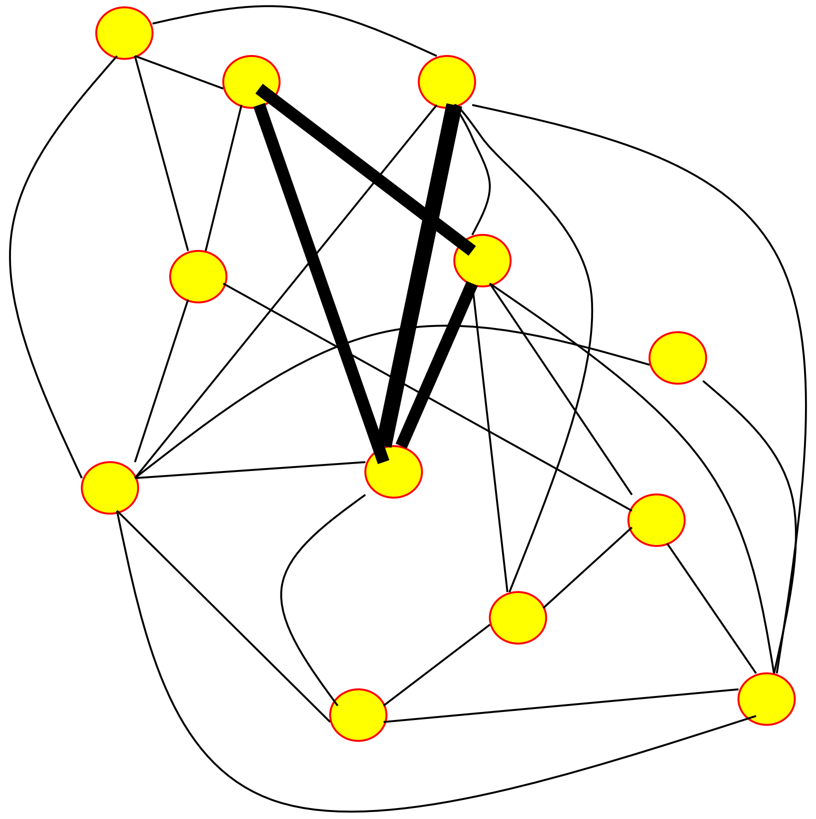
- ongoing plasticity
- ongoing activity



Zenke et al., Nat. Comm. (2015)

8. Synaptic plasticity, Learning and Memory





Should enable **Learning**

- adapt to the statistics of task and environments (receptive fields, allocate space etc)
- memorize facts and episodes
- learn motor tasks

Should avoid:

- blow-up of activity
- unnecessary use of energy

homeostasis

abstract models capture the essence
(but leave out many, many details)

8. Summary: Synaptic plasticity and Memory

Hebbian rules are a family of unsupervised learning rules which describe changes that only depend on presynaptic spike arrivals and the state (depolarization, firing rate, or bursts of spikes) of the postsynaptic neuron. If we make a Taylor expansion of local unsupervised rules, we find terms that depend on the correlations (Hebbian terms/homosynaptic terms) and terms that depend only on the state of the postsynaptic neuron (heterosynaptic terms). The heterosynaptic terms are useful to control the total firing activity of a neuron.
A clever combination of BCM-type homosynaptic terms (triplet STDP model) and of heterosynaptic terms (fourth-order in the postsynaptic firing rate) enables to build network models that learn to form stable attractors. These correspond to the attractors we have seen in the weeks on Hopfield model and memory; but now with true online learning: synaptic plasticity is always ongoing (and not switched off during retrieval).