Biological Modeling of Neural Networks

ÉCOLE POLYTECHNIQUE FÉDÉRALE DE LAUSANNE

Week 13

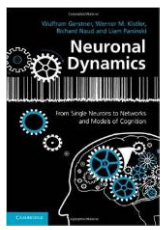
Synaptic plasticity and Learning

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

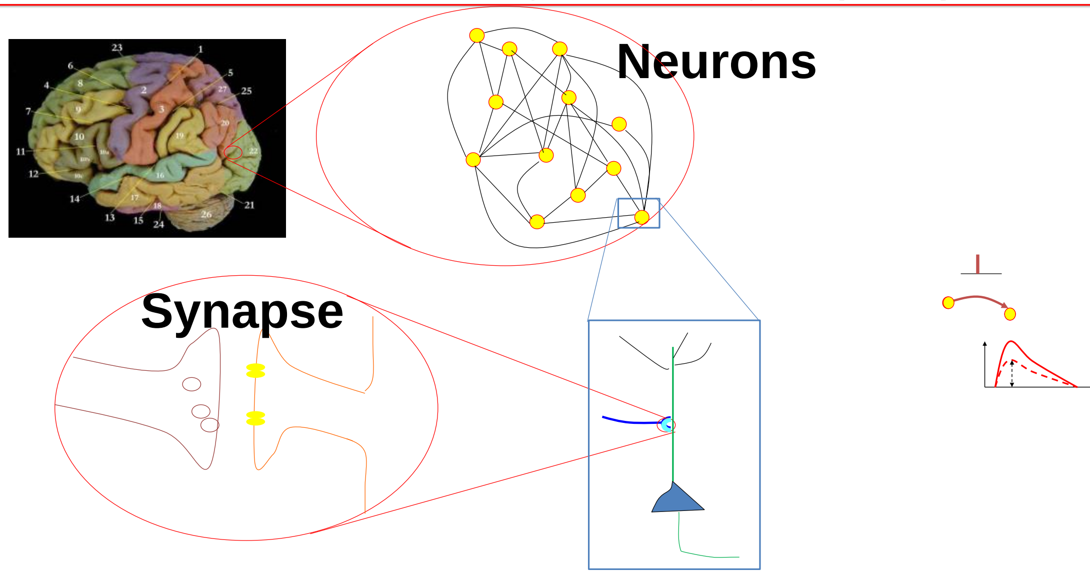
6. Online learning of memories

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

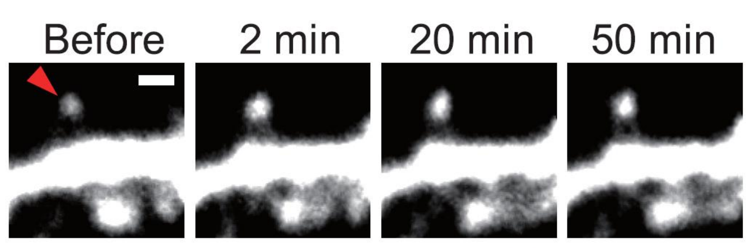
which parking spot?

1. Behavioral Learning – and synaptic plasticity



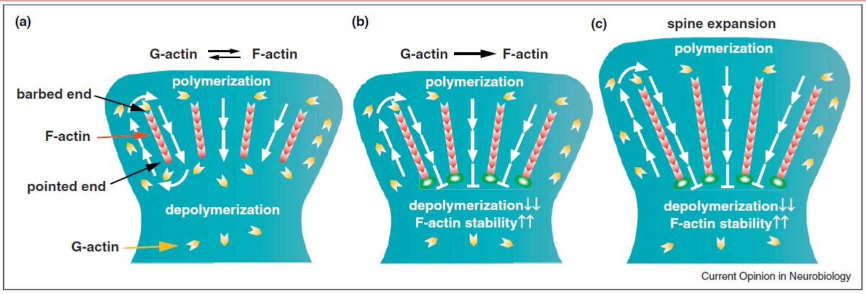
Synaptic Plasticity =Change in Connection Strength

1. Synaptic plasticity – structural changes

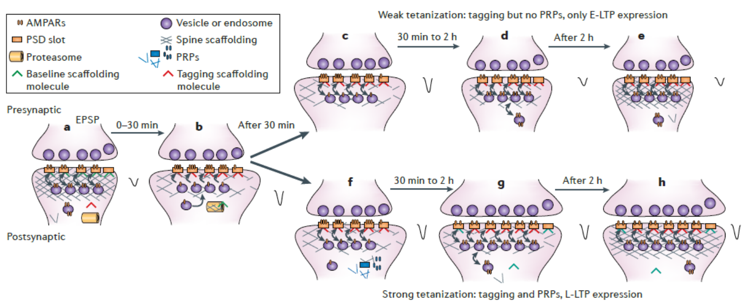


Yagishita et al.
Science, 2014

1. synaptic plasticity – molecular changes

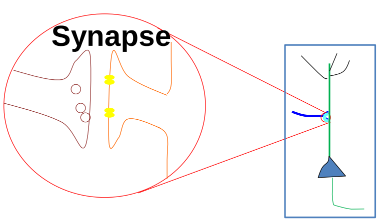


Bosch et al. 2012, Curr. Opinion Neurobiol.



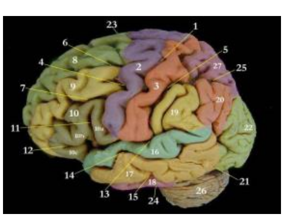
Redondo and Morris 2011, Nature Rev. Neurosci.

1. synaptic plasticity – connections change



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

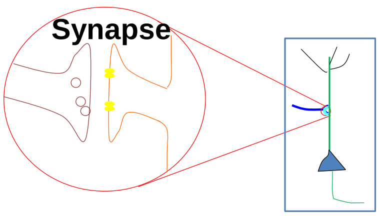
Amunts et al. Human Brain Map. 1997
Gaser and Schlaug, J. Neuosci. 2003

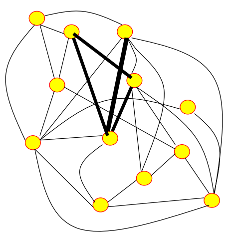


More space in hippocampus allocated
- London taxi driver vs bus driver

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

Biological Modeling of Neural Networks

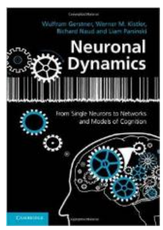
Week 13

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

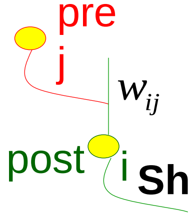
2. Classification of plasticity
short-term vs. long-term
unsupervised vs. reward modulated

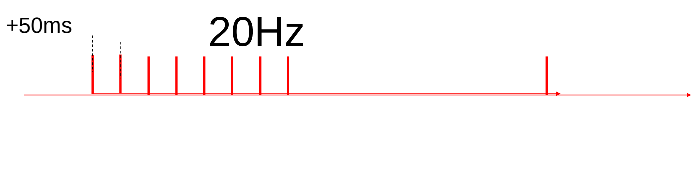
3. Model of short-term plasticity

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

5. Spiking Models of plasticity

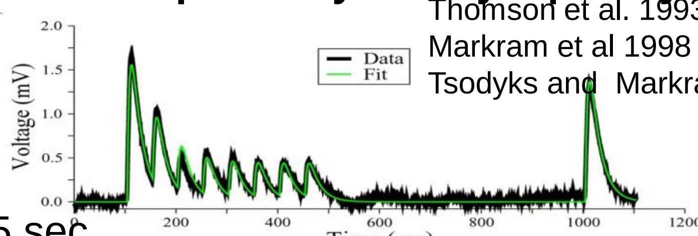
2. Classification of synaptic changes: Short-term plasticity





Short-term plasticity/fast synaptic dynamics

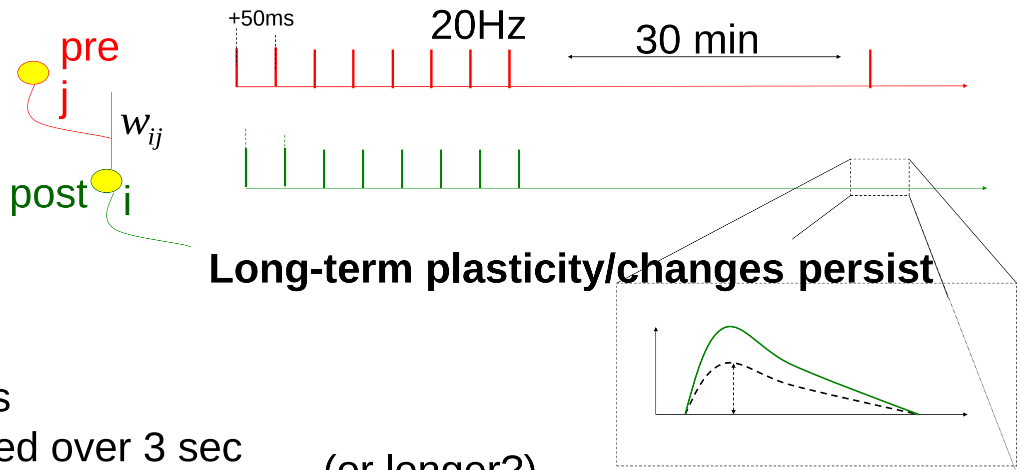
Thomson et al. 1993
Markram et al 1998
Tsodyks and Markram 1997



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

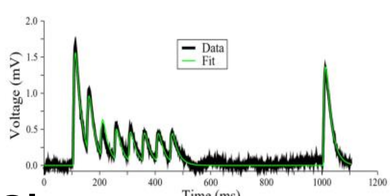


Long-term plasticity/changes persist

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

2. Classification of synaptic changes

Short-Term vs/ Long-Term



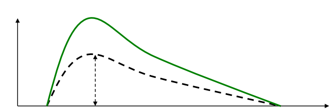
Changes
- induced over 0.1-0.5 sec
- recover over 1 sec

Protocol
- presynaptic spikes

Model
- well established

(Tosdyks, Pawelzik, Markram Abbott-Davan)

LTP/LTD/Hebb



Changes
- induced over 0.5-5sec
- remains over hours

Protocol
-presynaptic spikes + …

Model
- we will see

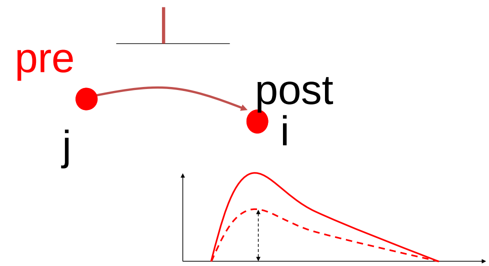
2. Classification of synaptic changes

Induction of changes

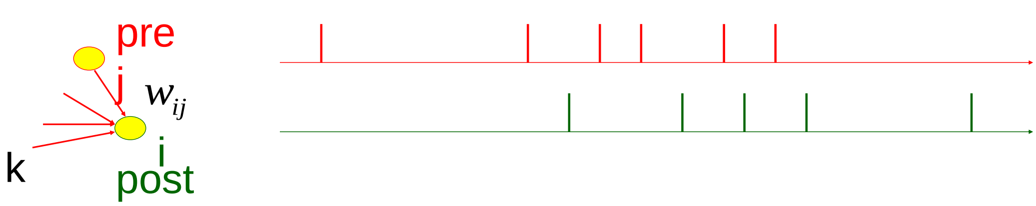
- fast (if stimulated appropriately)
- slow (homeostasis)

Persistence of changes

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



2. Review: Hebb rule



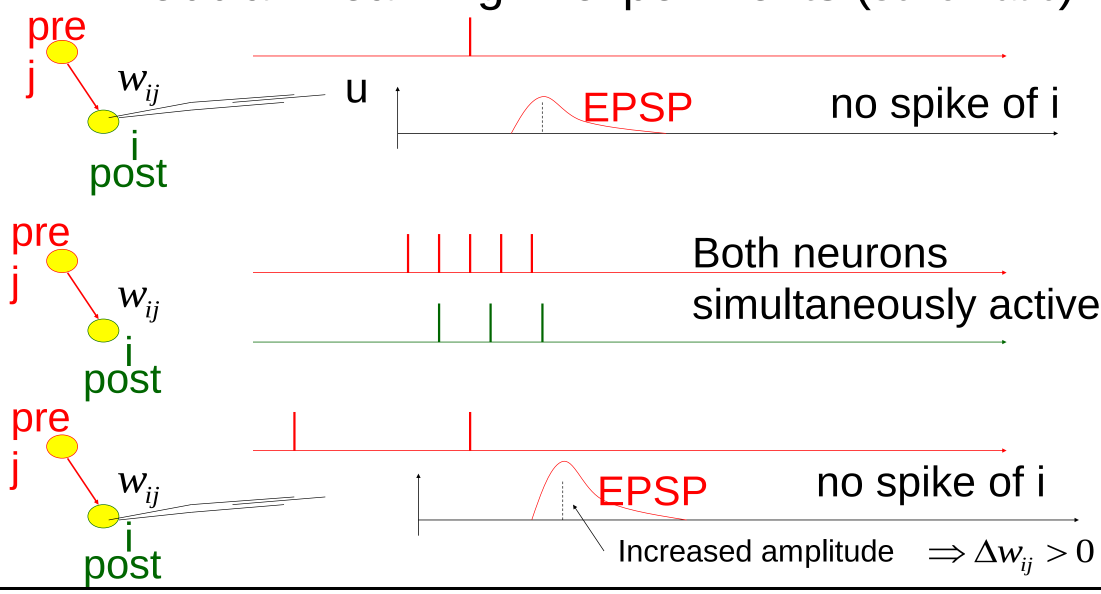
When an axon of cell **j** repeatedly or persistently takes part in firing cell **i**, then j's efficiency as one of the cells firing i is increased

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

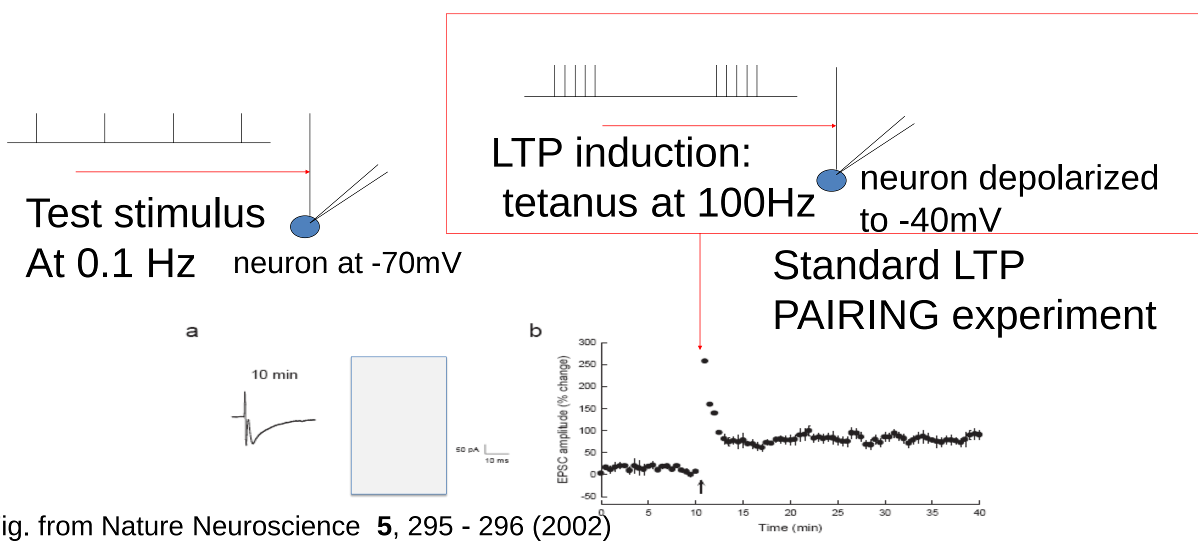
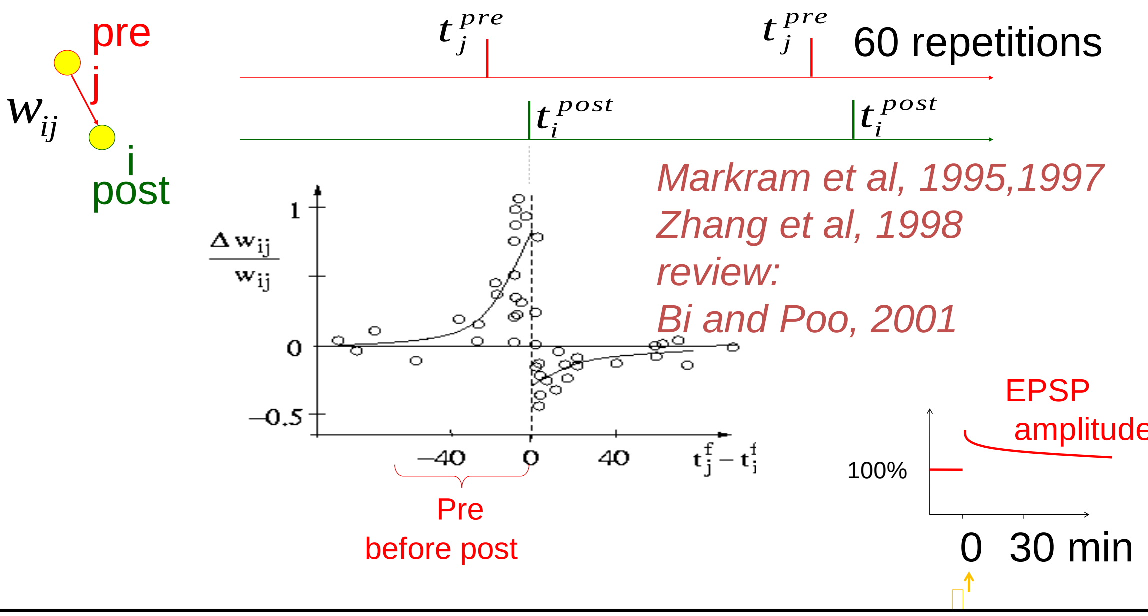


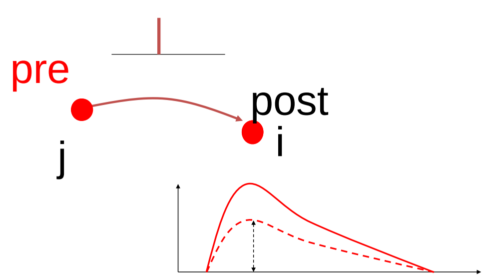
Fig. from Nature Neuroscience **5**, 295 - 296 (2002)
D. S.F. Ling, … & Todd C. Sacktor
See also: Bliss and Lomo (1973), Artola, Brocher, Singer (1990), Bliss and Collingridge (1993)

2. Spike-timing dependent plasticity (STDP)



2. Classification of synaptic changes

Induction of changes
- fast (if stimulated appropriately)
- slow (homeostasis)

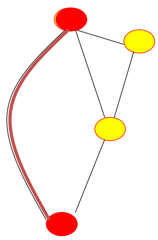


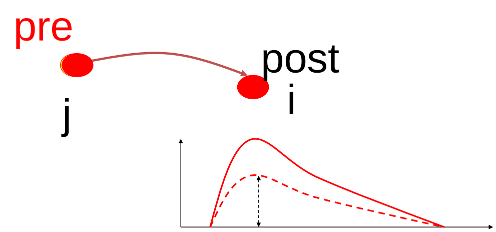
Persistence of changes
- long (LTP/LTD)
- short (short-term plasticity)

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

2. Classification of synaptic changes: unsupervised learning

Hebbian Learning
= unsupervised learning





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

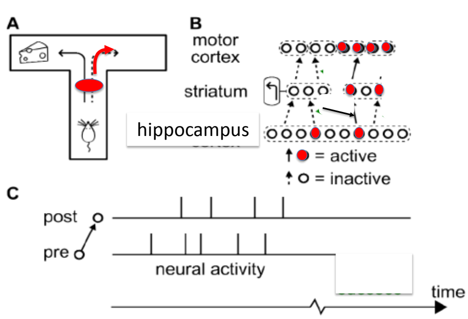
$$\Delta w_{ij} \propto F(pre, post)$$

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



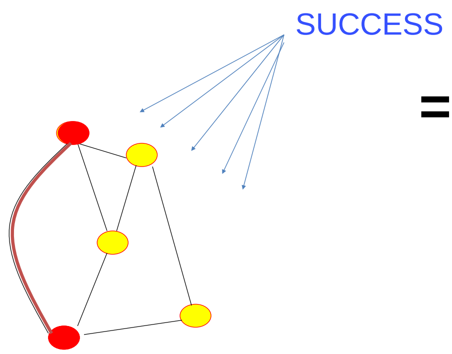
Dopamine:
Reward/success

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

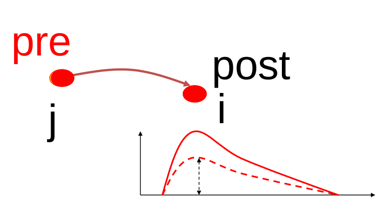
broadly diffused signal:
neuromodulator

2. Classification of synaptic changes

unsupervised vs reinforcement

LTP/LTD/Hebb
Theoretical concept

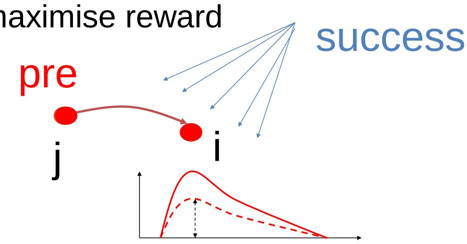
- passive changes
- exploit statistical correlations



Functionality
-useful for development
(wiring for receptive field)

Reinforcement Learning
Theoretical concept

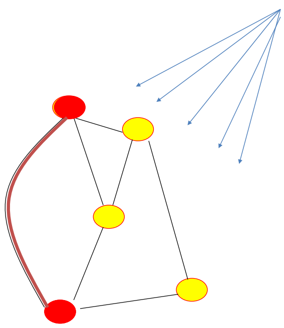
- conditioned changes
- maximise reward



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

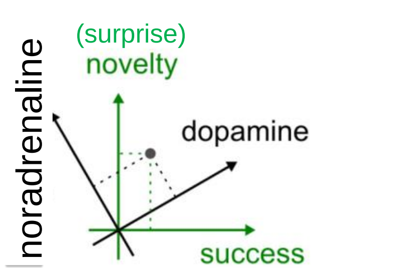
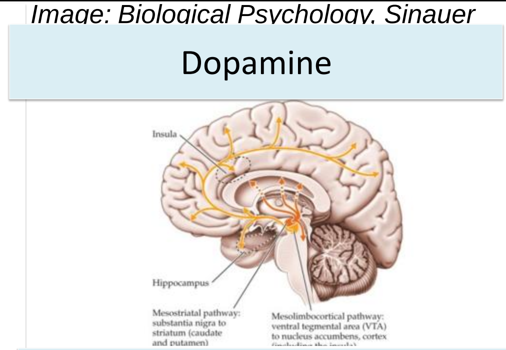
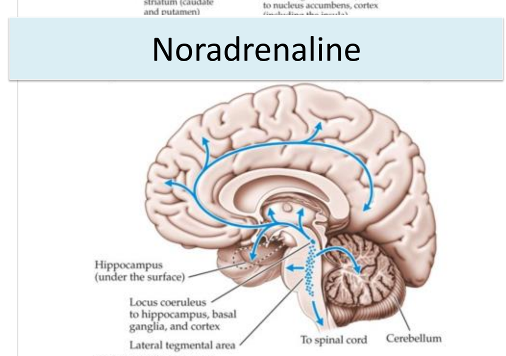


Image:
Fremaux and Gerstner, Frontiers (2016)

Image: Biological Psychology, Sinauer





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

Biological Modeling of Neural Networks

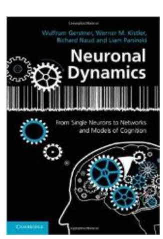
ÉCOLE POLYTECHNIQUE FÉDÉRALE DE LAUSANNE

Week 13
Synaptic plasticity and Learning

Wulfram Gerstner
EPFL, Lausanne, Switzerland

Reading for plasticity: NEURONAL DYNAMICS - Ch 3.1.3.

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

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

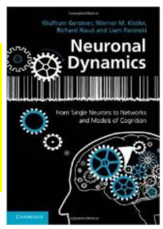
Part 1 - Synapses (15 min)

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



Biological Modeling of Neural Networks

ÉCOLE POLYTECHNIQUE
FÉDÉRALE DE LAUSANNE

Week 13

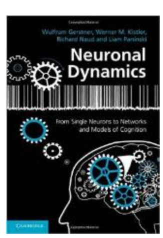
Synaptic plasticity and Learning

Wulfram Gerstner

EPFL, Lausanne, Switzerland

Reading for plasticity:
NEURONAL DYNAMICS
- Ch. 19.1-19.2.

Cambridge Univ. Press



1. Synaptic plasticity
motivation and aims

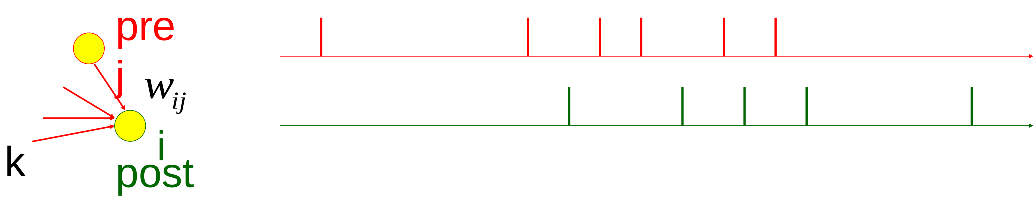
2. Classification of plasticity
short-term vs. long-term
unsupervised vs. reward modulated

3. Model of short-term plasticity

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

5. Spiking Models of plasticity

4. Hebbian Learning (rate models)



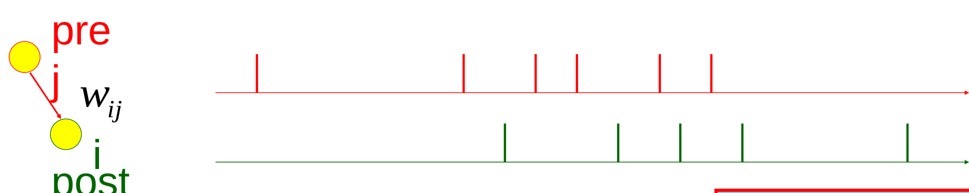
When an axon of cell **j** repeatedly or persistently takes part in firing cell **i**, then j's efficiency as one of the cells firing i is increased

Hebb, 1949

- local rule
- simultaneously active (correlations)

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

4. Rate-based Hebbian Learning



Blackboard1

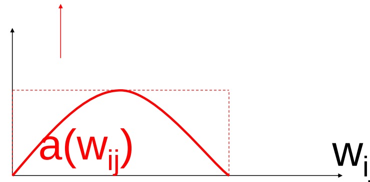
Local rule:

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

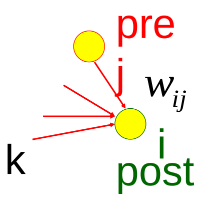
Taylor expansion:

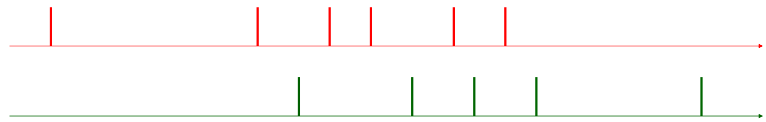
$$\frac{d}{dt} w_{ij} = a_0 + a_1^{pre}\nu_j^{pre} + a_1^{post}\nu_i^{post} + a_2^{corr}\nu_j^{pre}\nu_i^{post} + \dots$$

a = a(w_{ij})



4. Rate-based Hebbian Learning

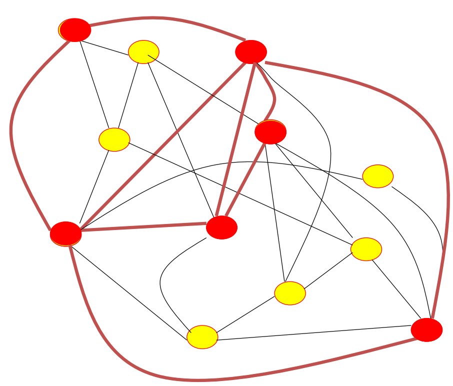




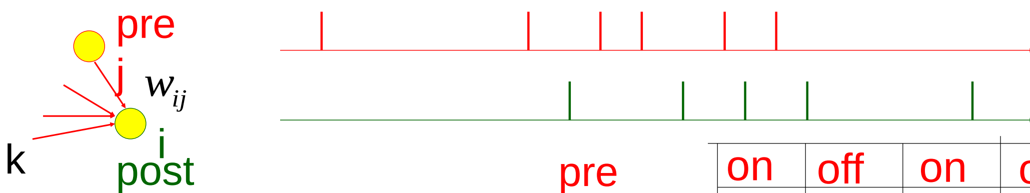
$$\frac{d}{dt} w_{ij} = a_2^{corr} \nu_j^{pre} \nu_i^{post}$$

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

Review from week 5: Hebbian Learning

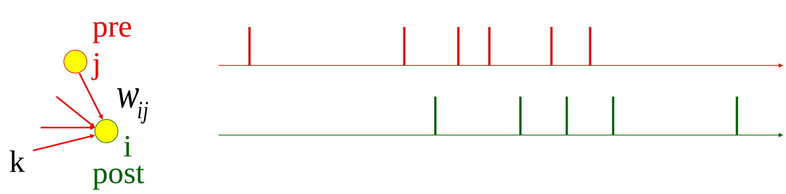


4. Rate-based Hebbian Learning



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

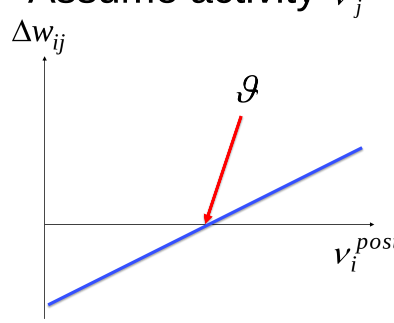
4. Presynaptically gated plasticity rule



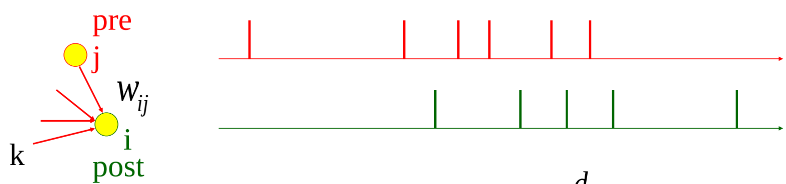
presynaptically gated

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

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



4. Bienenstock-Cooper-Munro rule



Bienenstock, Cooper Munro, 1982

presynaptically gated

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

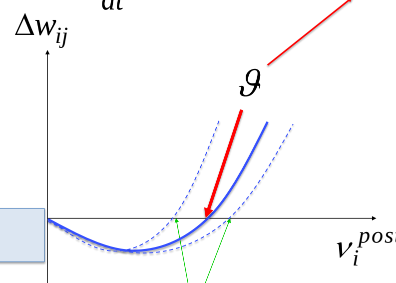
BCM: 3rd order ('triplet')

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

Map to
Taylor expansion?

triplet pair

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



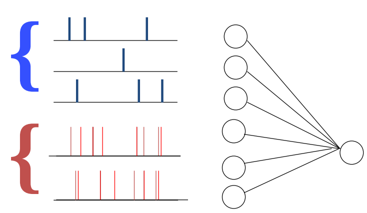
assume
$\nu_j^{pre} > 0$

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

4. Functional Consequence of Hebbian Learning

Fixed rate

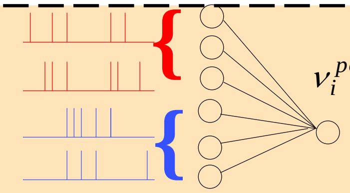
Jointly variing rate



Hebbian Learning detects correlations in the input

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

Exercise 1 now: Bienenstock-Cooper-Munro



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

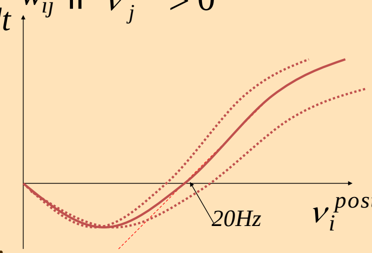
Take 8 minutes = Discussion of ex At 10:20

BCM rule

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

20Hz

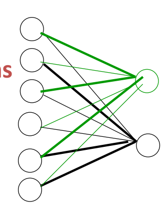
$\frac{d}{dt} w_{ij}$ if $\nu_j^{pre} > 0$



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?

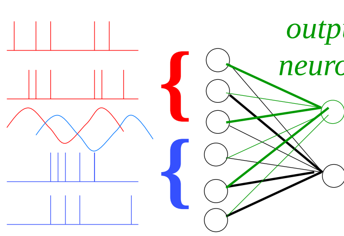
4. Synaptic Changes for Development of Cortex

Initial: random connections

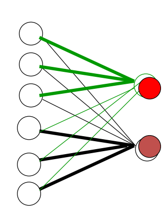


BCM leads to specialized Neurons (developmental learning);
Bienenstock et al. 1982

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



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

Biological Modeling of Neural Networks

ÉCOLE POLYTECHNIQUE FÉDÉRALE DE LAUSANNE

Week 13

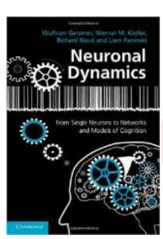
Synaptic plasticity and Learning

Wulfram Gerstner

EPFL, Lausanne, Switzerland

Reading for plasticity:
NEURONAL DYNAMICS
- Ch. 19.1-19.2; Ch 3.1.3.

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

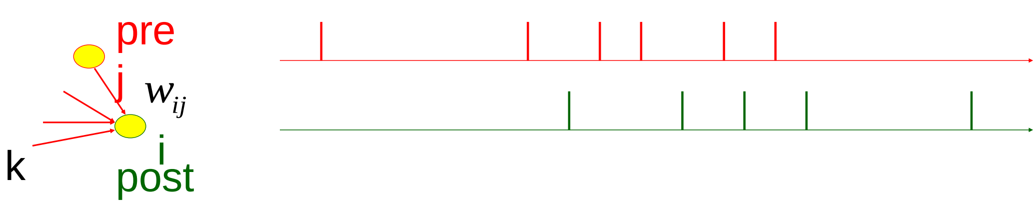
4. Models of long-term plasticity

- Hebbian learning rules
- Bienenstock-Cooper-Munro rule

5. Spiking Models of plasticity

6. Online learning of memories

Hebbian Learning

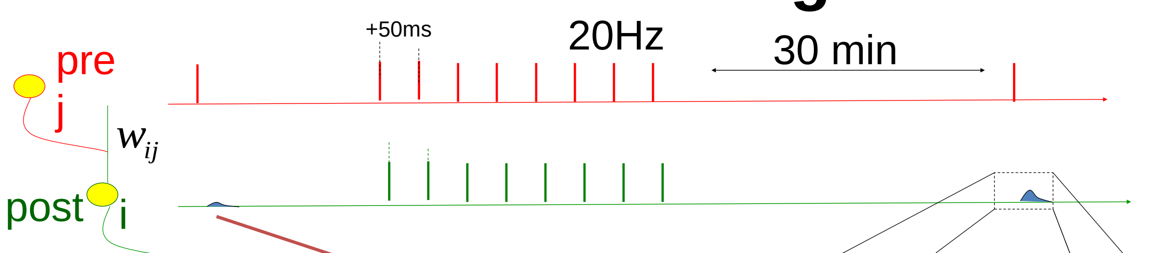


When an axon of cell **j** repeatedly or persistently takes part in firing cell **i**, then j's efficiency as one of the cells firing **i** is increased **Hebb, 1949**

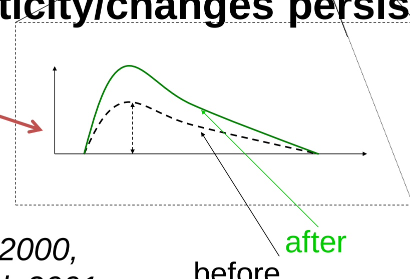
Experiments: Bliss and Lomo 1973, Levy and Stewart, 1983, …
Markram et al. 1997, Bi and Poo, 1998, …

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

STDP as Hebbian Learning



Long-term plasticity/changes persist

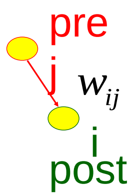


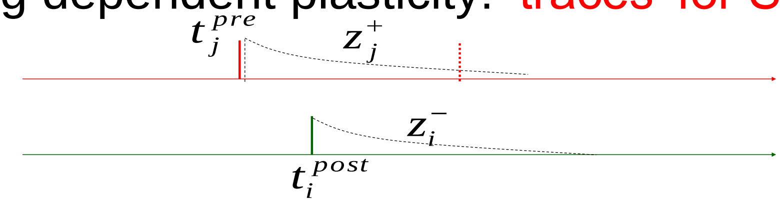
Changes
- induced over 3 sec
- persist over hours and days

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)

Spike-timing dependent plasticity: ‘traces’ for STDP



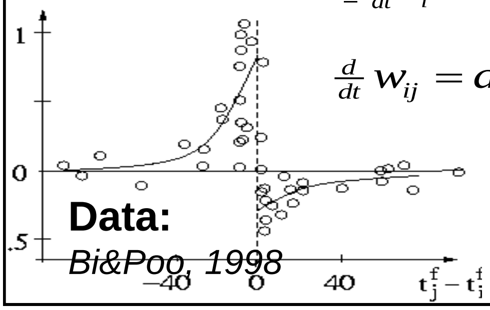


$$\tau_+ \frac{d}{dt} z_j^+ = -z_j^+ + \delta(t - t_j^{pre})$$ jump at presyn. spike

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

pair

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

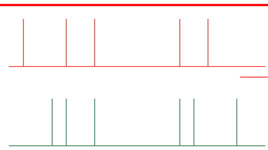


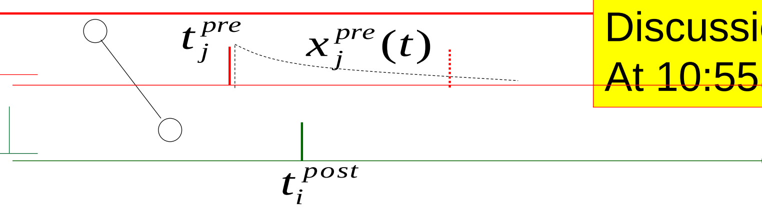
Data:
Bi&Poo, 1998

→ **Simple STDP model**
(Gerstner et al. 1996,
Song-Miller-Abbott 2000, etc)

Exercise STDP now:

Take 8 minutes =
Discussion of ex
At 10:55





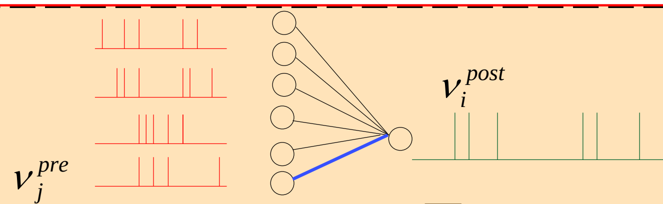
-What is the shape of the STDP window?

-calculate the effect of one pair of spikes

-calculate the effect of many pairs of spikes

Exercise STDP to rate now:

Take 8 minutes =
Discussion of ex
At 11:20



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

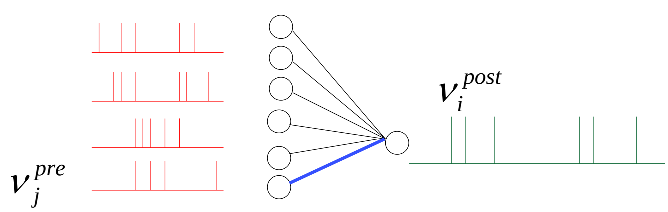
Assume presynaptic spikes are generated by Poisson process with rate ν_j^{pre}

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

What is the expected change of weights in a time T?

$(T >> \tau^{LTP}, \tau^{LTD})$

5. from STDP to rate models

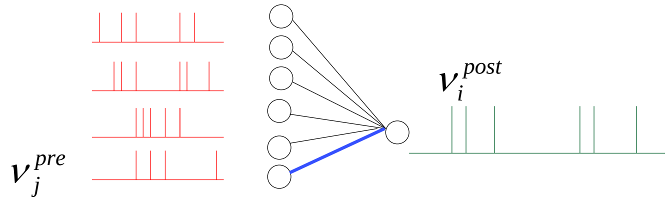


Blackboard2

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

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

5. from STDP to rate models



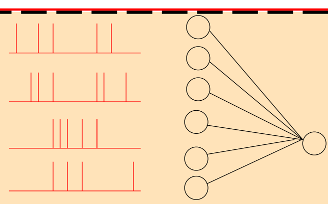
$$\Delta w_{ij} = \sum_{f,f'} W(t_i^f - t_j^{f'})$$

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

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

Exercise STDP to rate now:

Take 12 minutes =
Discussion of ex
At 11:40



$$\nu_i^{post}(t) = \sum_j w_{ij} \sum_f \varepsilon(t - t_j^f) \qquad (*)$$

assume that presynaptic spike are generated by Poisson pr.

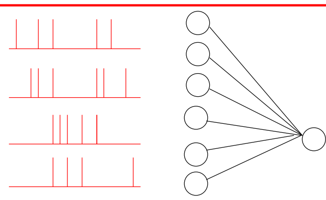
$$\nu_j^{pre}(t)$$

postsynaptic spikes are Poisson with stoch. intensity (*)

Calculate weight change $\Delta w_{ij} = \sum_{f,f'} W(t_i^f - t_j^{f'})$ in time T

STDP to rate now:

$\nu_j^{pre}(t)$



Poisson with stoch. intensity (*)

$$\nu_i^{post}(t) = \sum_j w_{ij} \sum_f \varepsilon(t - t_j^f) \qquad (*)$$

weight change

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

Blackboard3

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

Biological Modeling of Neural Networks

Week 13

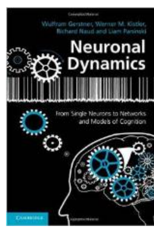
Synaptic plasticity and Learning

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

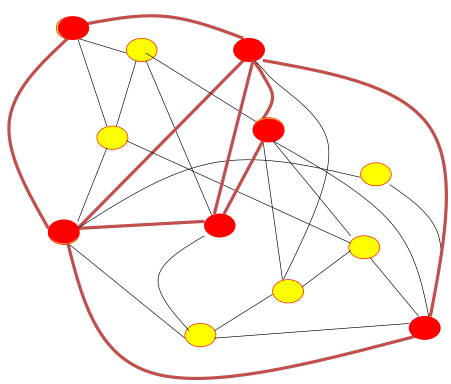
3. Model of short-term plasticity

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

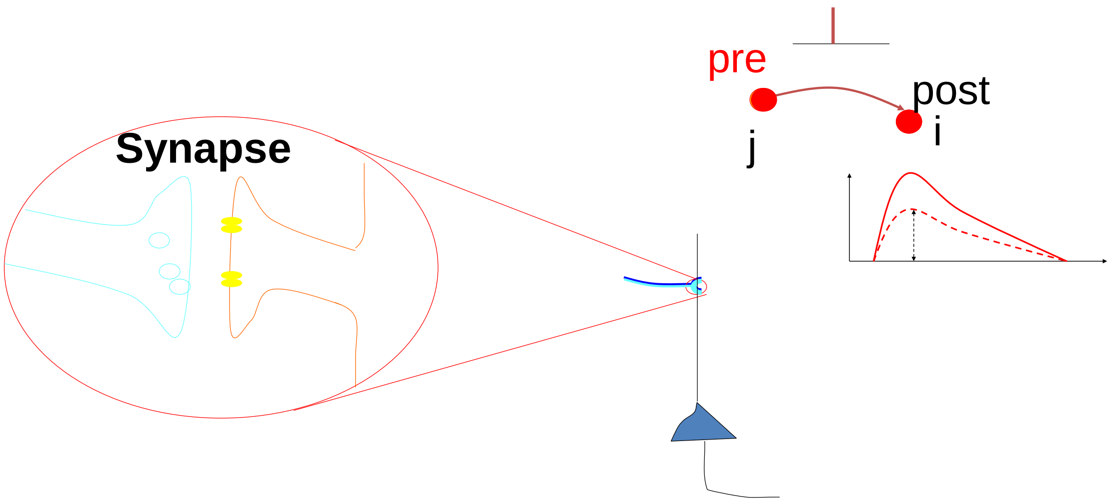
5. Spiking Models of plasticity

6. Online learning of memories

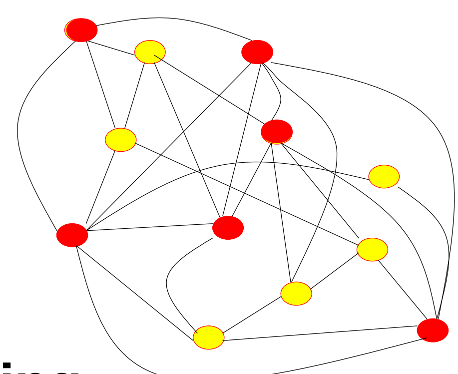
Review from week 5: Hebbian Learning



6. Synaptic plasticity

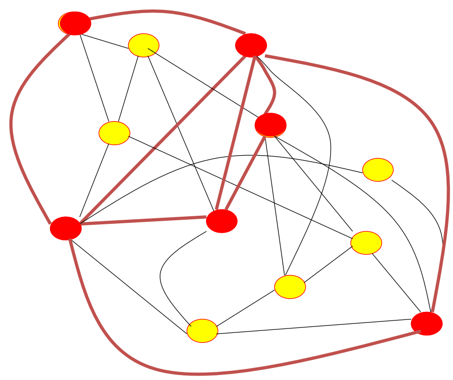


6. Synaptic plasticity: Hebbian Learning



Hebbian Learning

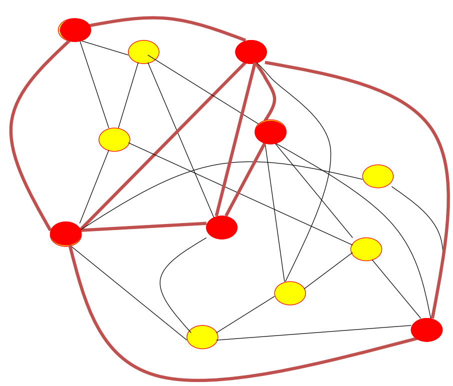
6. Synaptic plasticity: Hebbian Learning

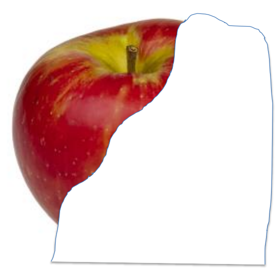


item memorized

6. Synaptic plasticity: Hebbian Learning

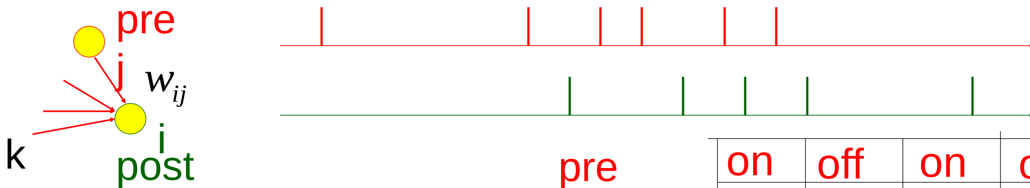
Recall:
Partial info





item recalled

6. Rate-based Hebbian Learning



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

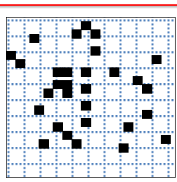
$$\frac{d}{dt}w_{ij} = a_2^{corr}\nu_j^{pre}\nu_i^{post} - c$$

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

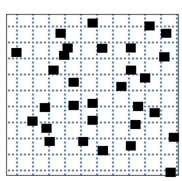
$$\frac{d}{dt}w_{ij} = a_2^{corr}(\nu_j^{pre} - \vartheta)(\nu_i^{post} - \vartheta)$$

pre / post	on / on	off / on	on / off	off / off
	+	0	0	0
	+	-	-	-
	+	0	-	0
	+	-	-	+

6. Review: Deterministic Hopfield model



Prototype $\vec{p}^1$



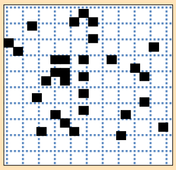
Prototype $\vec{p}^2$

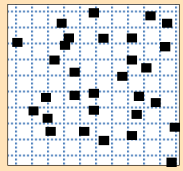
interactions $$w_{ij} = \frac{1}{N}\sum_{\mu} p_i^{\mu} p_j^{\mu}$$

Sum over all prototypes

Exercise 2 now: learning of prototypes

Prototype $\vec{p}^1$





Prototype $\vec{p}^2$

interactions

(1) $w_{ij} = \sum_{\mu} p_i^{\mu} p_j^{\mu}$

Sum over all prototypes

a) Show that (1) corresponds to a rate learning rule

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

Take 8 minutes,
start the exercise
Next lecture at 11:48

Assume that weights are zero at the beginning;

Each pattern is presented (enforced) during 0.5 sec (One after the other).

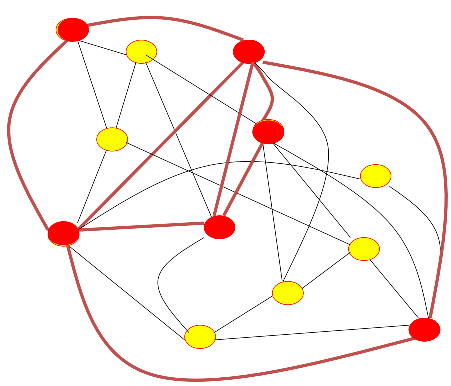
note that $p_j^{\mu} = \pm 1$ but $\nu_j \geq 0$

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

c) Is this unsupervised learning?

6. Review: Hebbian Assemblies

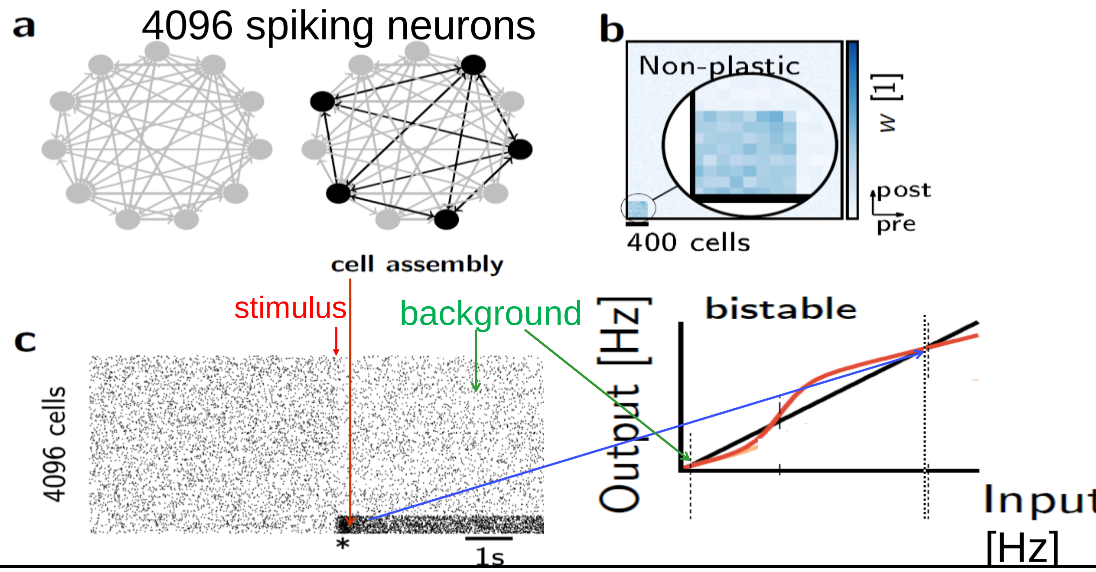
Recall:
Partial info



item recalled

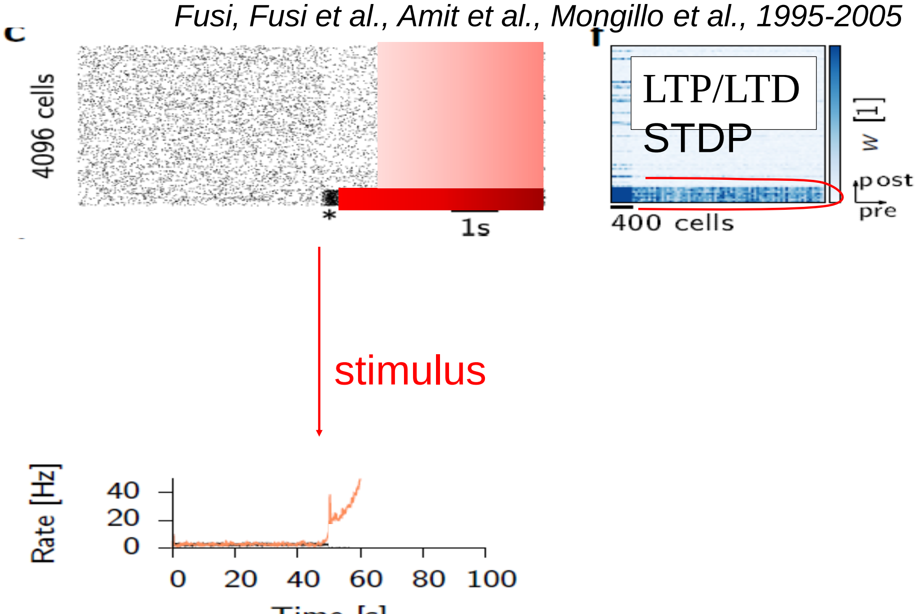
6. Preconfigured memory: bistable network

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



6. Learning the memory: very hard

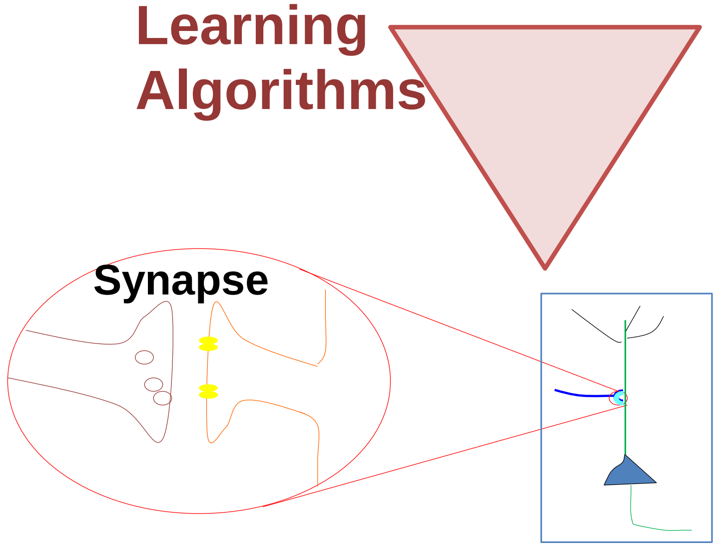
Fusi, Fusi et al., Amit et al., Mongillo et al., 1995-2005



6. Learning: the task of modeling

Learning Algorithms

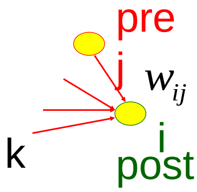
Functional or Behavioral Consequences

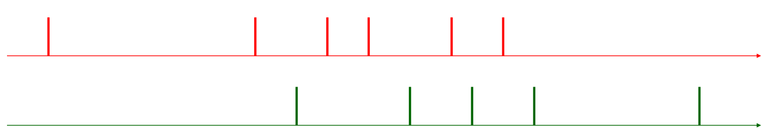


Memory formation
Memory retention
Network stability

Synaptic Plasticity

6. Review: Rate models of Hebbian learning





rate   rate

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

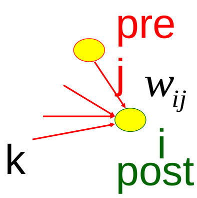
- local rule
- simultaneously active

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}

6. Induction of Plasticity



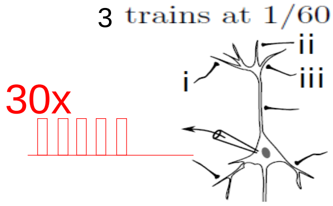
- **homosynaptic/Hebb** ('pre' and 'post')
- **heterosynaptic plasticity** (pure 'post'-term)
- **transmitter-induced** (pure 'pre'-term)

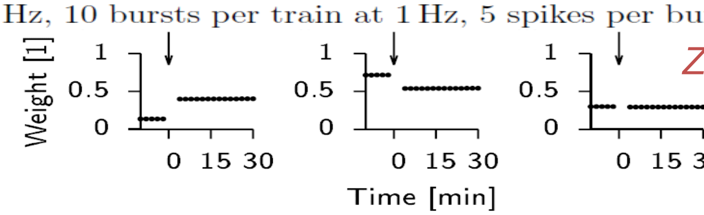
$$\frac{dw_{ij}}{dt} = a_0 + a_1^{pre} \nu_j^{pre} + a_1^{post} \nu_i^{post} + a_2^{corr} \nu_j^{pre} \nu_i^{post} +$$

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

6. Heterosynaptic Plasticity (exper. and model)

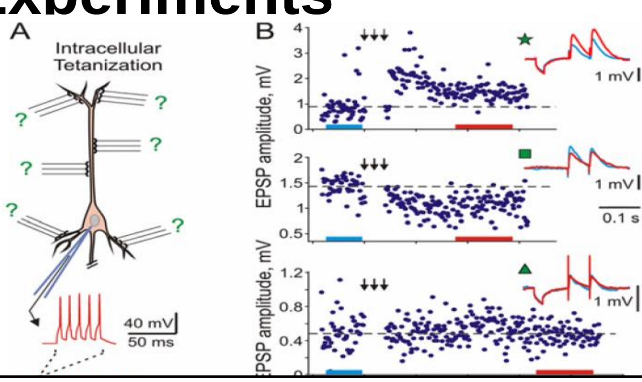
3 trains at 1/60 Hz, 10 bursts per train at 1 Hz, 5 spikes per burst at 100 Hz





Zenke et al. (2015)

Experiments



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

6. 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')**

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

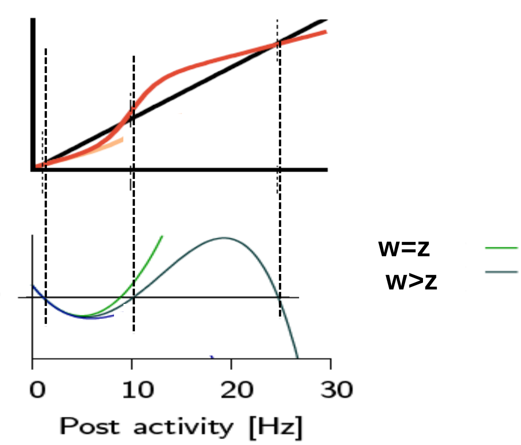
6. Plasticity model in network

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

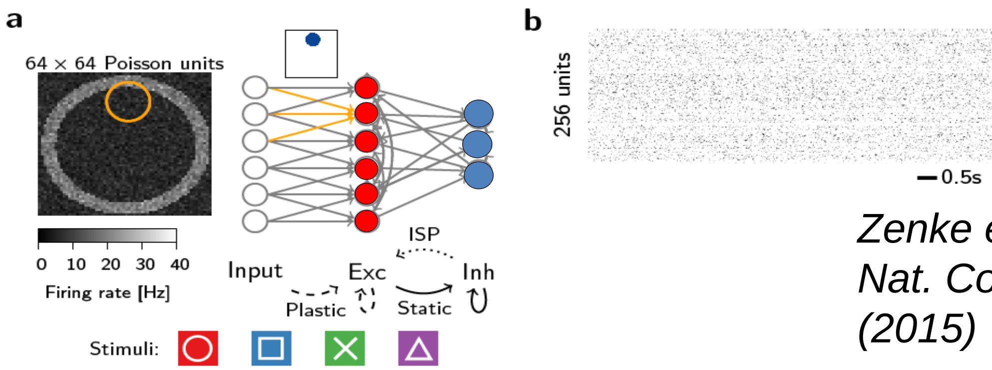
→Self-stabilizing!

Heterosynaptic plasticity
must act on the same time scale

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



6. Plasticity in feedforward /recurrent connections



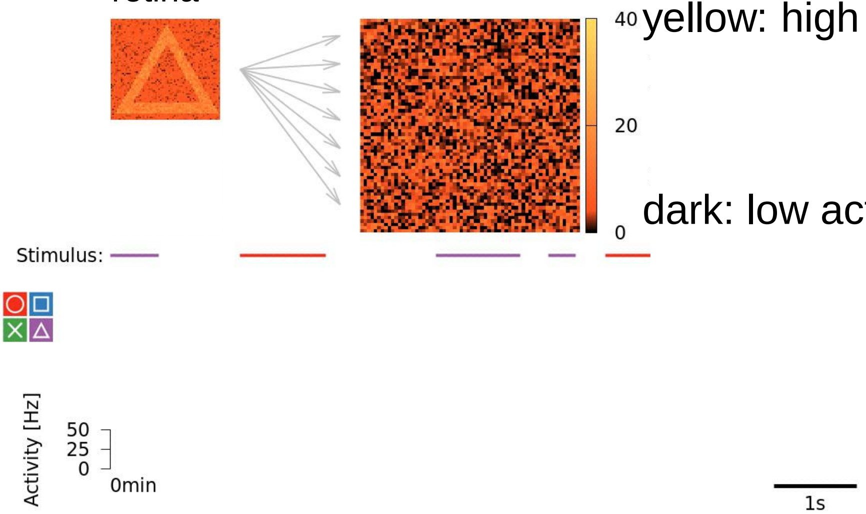
Zenke et al., Nat. Comm. (2015)

6. Theory and Simulation: first minute

stimulus

retina

Neuronal network



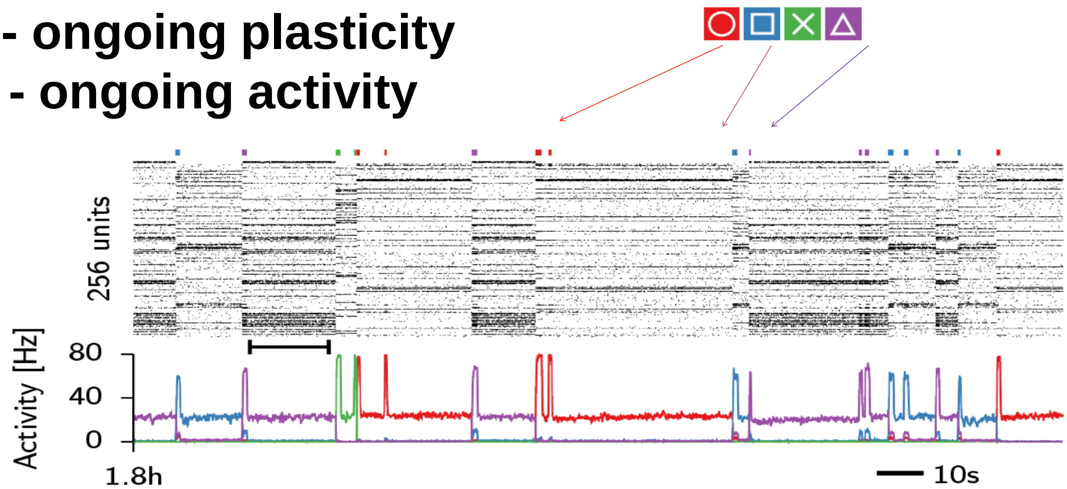
yellow: high activity

dark: low activity

6. Plasticity model in network: two hours later

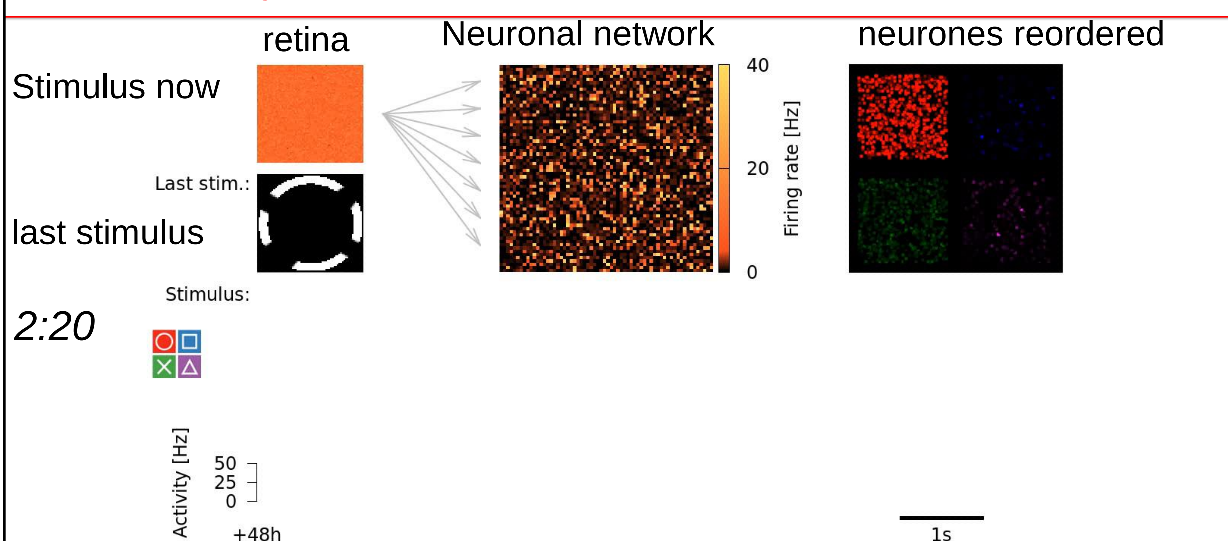
Stable memory recall despite

- ongoing plasticity
- ongoing activity



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

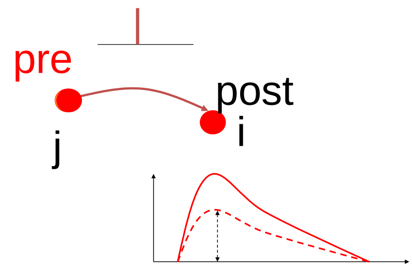
6. Theory and Simulation: after 2 hours



6. Synaptic changes – review and summary

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/new memories**
- useful for development (wiring for receptive field development)
- **useful for activity control in network (homeostasis)**
- useful for coding

The end