

# Interplay of synaptic plasticity and probabilistic brain theories

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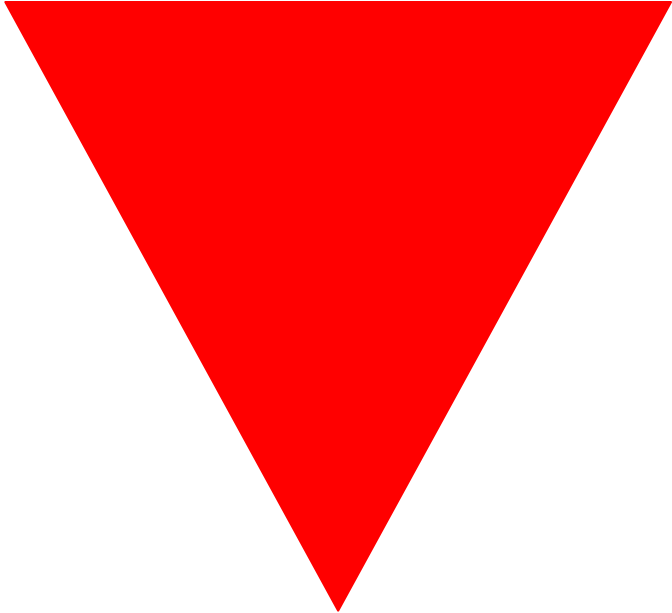
Joint work with:  
**Danilo J. Rezende**



Funding acknowledged:  
ERC, BrainScales, HBP,  
Swiss Natl. Sci. Foundation,

Probabilistic Brain  
Inference, Sampling

Machine Learning  
Optimal learning rules



Synaptic plasticity  
STDP

# Probabilistic Brain, Sampling, Bayesian Brain

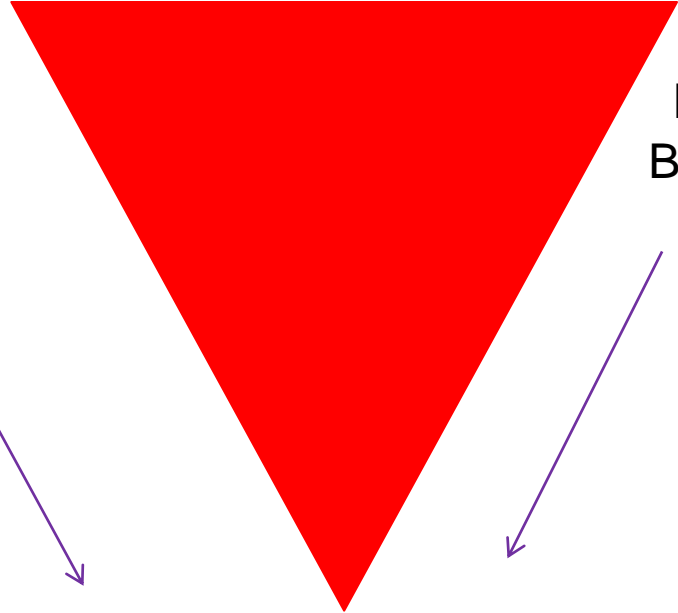
Kording and Wolpert 2004;  
Berkes et al. 2011;  
Knill and Pouget 2004

Nessler et al. 2013

# Machine Learning Optimal learning rules

Dayan 2000  
Friston and Stephan, 2007  
Beal and Gahrahmani, 2006

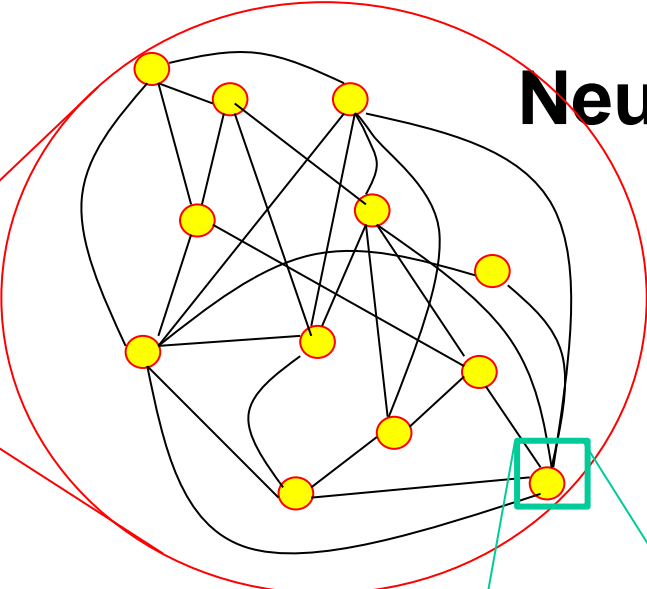
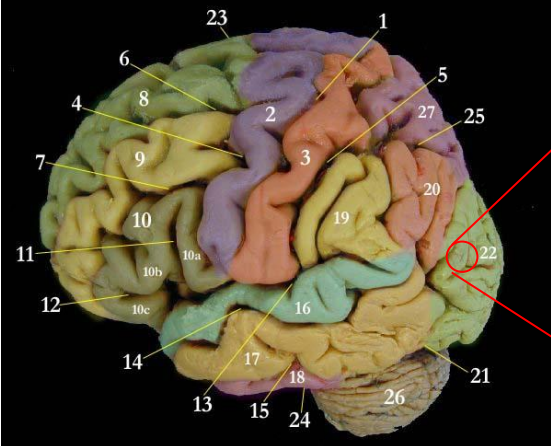
Pfister et al. 2006  
Brea et al. 2013



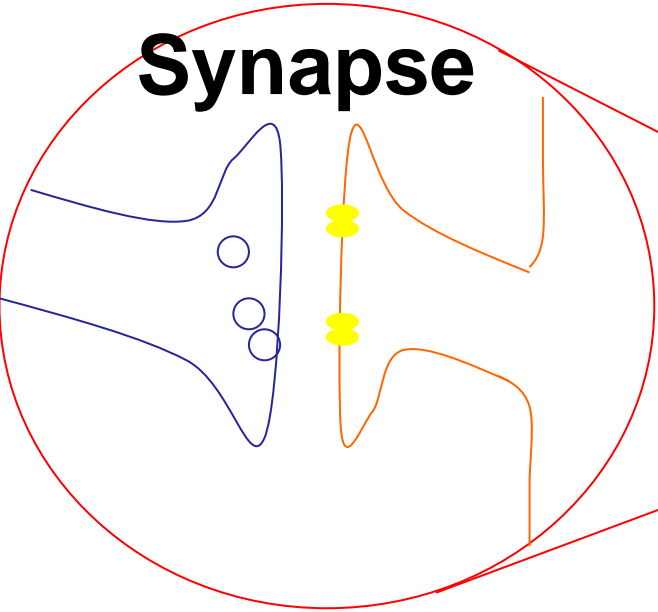
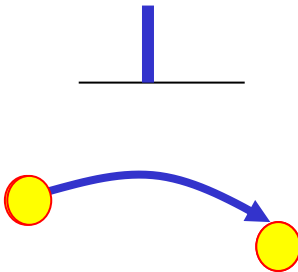
# Synaptic plasticity STDP

Markram et al. 1997; Bi and Poo 2001  
Artola and Singer 1993

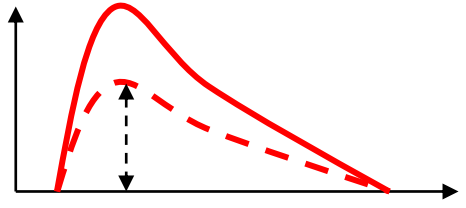
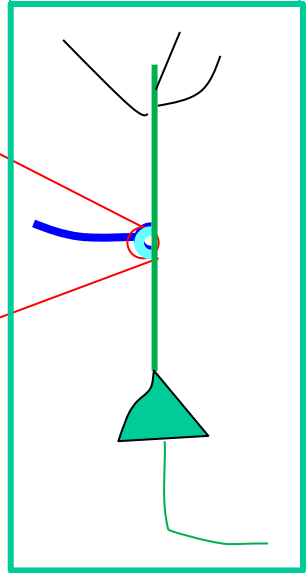
# Behavioral Learning – and synaptic plasticity



**Neurons**

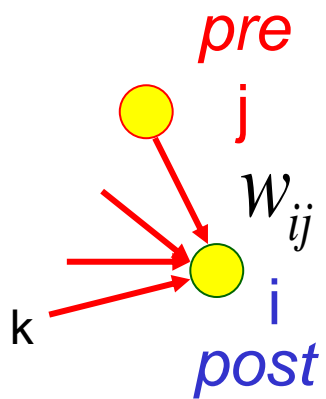


**Synapse**



**Synaptic Plasticity = Change in Connection Strength**

# Hebbian Learning



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

Spike arrival,  
EPSP

Postsyn. Spikes  
voltage

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*

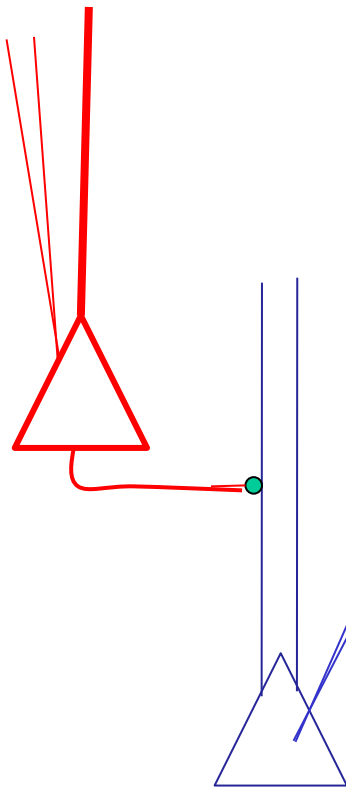
**Is Hebbian learning useful? –  
Developmental learning/rec. field development**

**Is Hebbian learning linked to experiments?**

# Experimental Induction Protocols

*Markram et al. 1997, Bi an Poo 1998, Sjostrom et al. 2001*

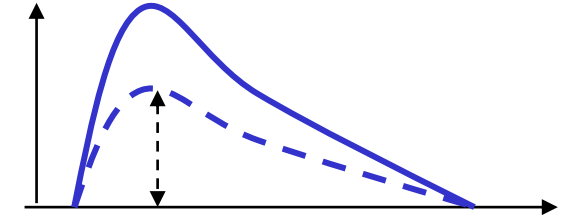
Intracellular  
electrode  
(pulses))



## STDP



+10ms



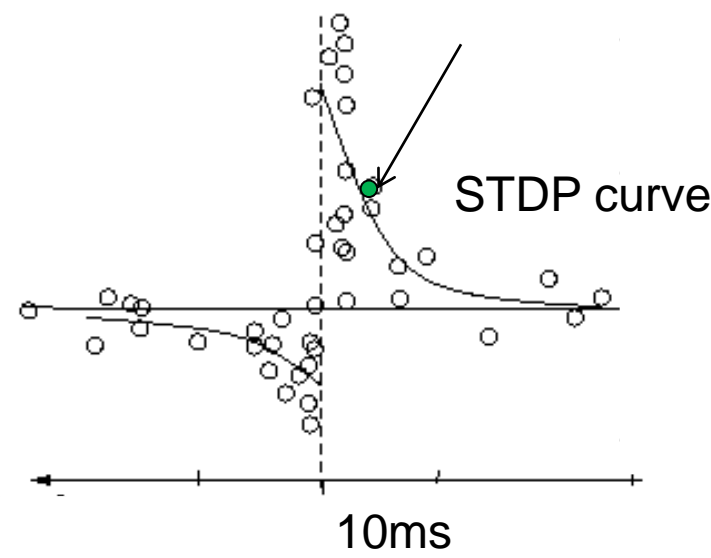
Pulse injection

Hebbian:

Pre-post = causal relation

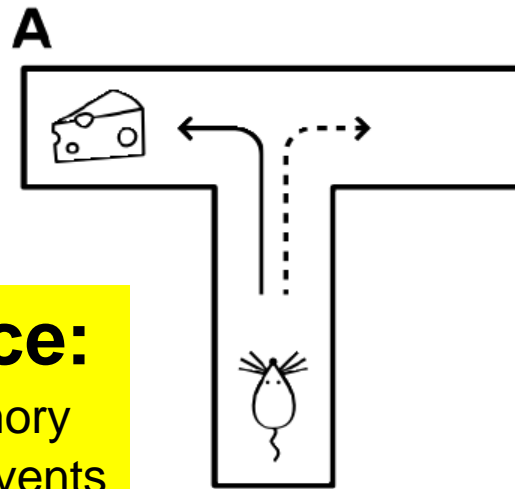
EPSP amplitude

Post:  
-spike timing  
-voltage

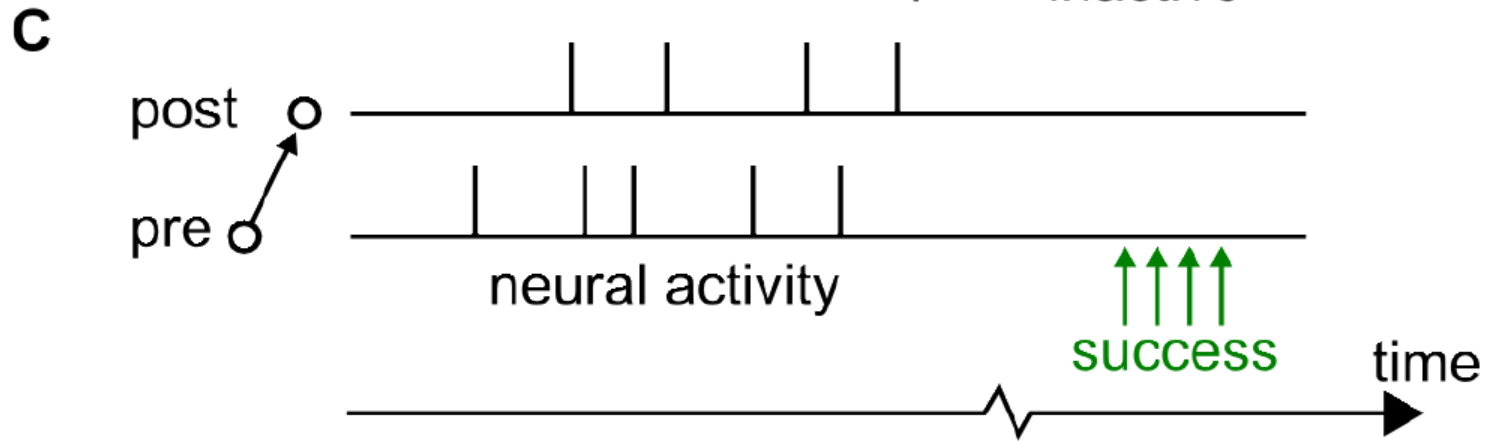
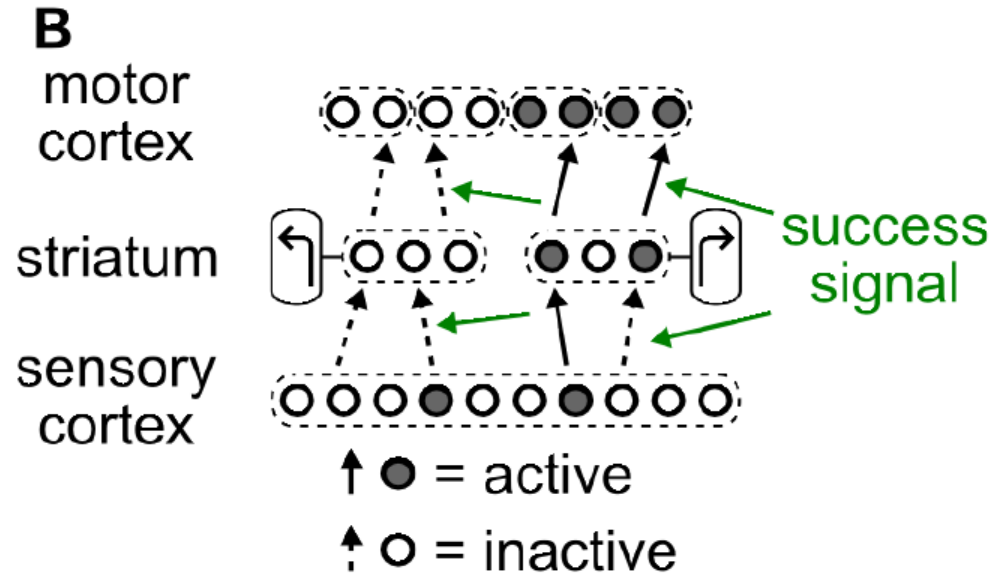


30 min

# Three factor rules (schematic)



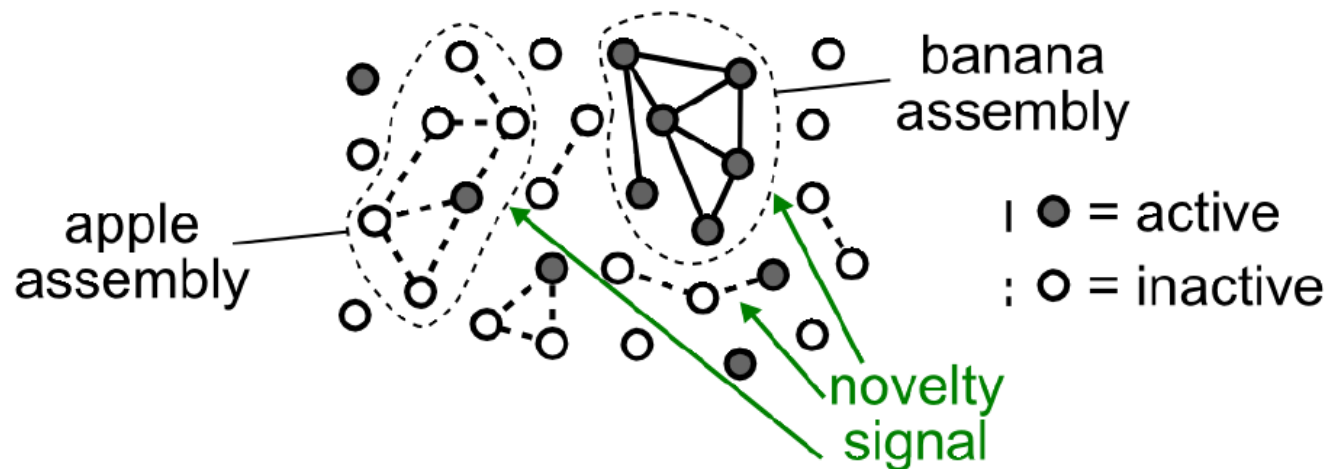
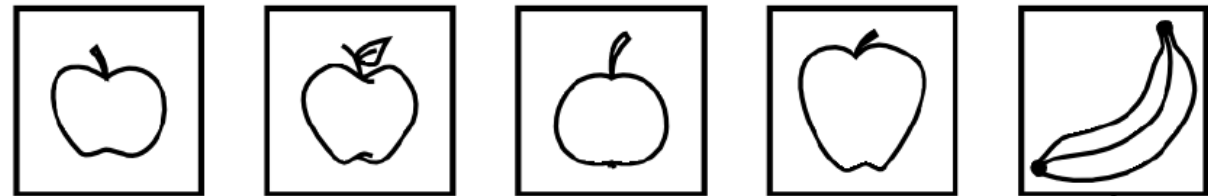
**Eligibility trace:**  
Synapse keeps memory  
Of pre-post Hebbian events



→ Reinforcement learning:  $\text{success} = \text{reward} - (\text{expected reward})$

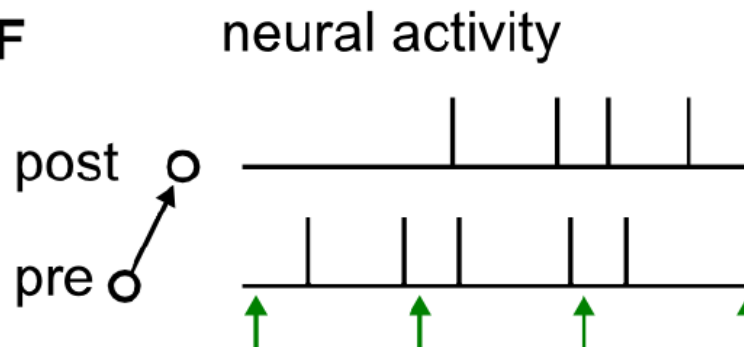
# Three factor rules (schematic)

D



**Neuromodulator:  
Novelty/surprise  
Reward/success**

F



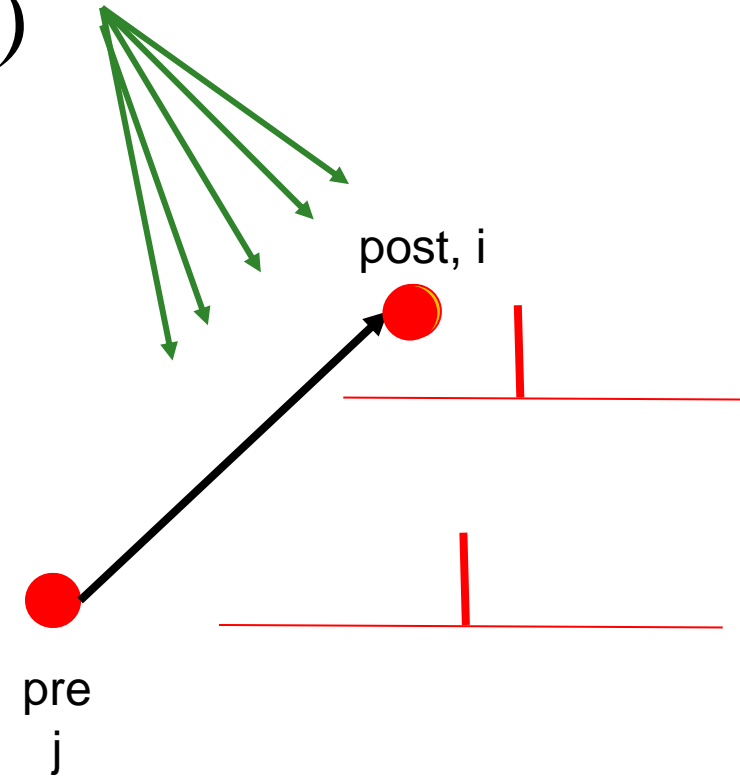
→ Novelty based learning: novelty = ?

time



# Three-factor rules in theory

$$\Delta w_{ij} \propto F(\textit{pre}, \textit{post}, \textit{3rd factor})$$



# R-STDP

(Izhikevich, 2007;  
Florian, 2007;  
Legenstein et al., 2008)

$$\Delta w_{ij} \propto F(\text{pre}, \text{post}, \text{3rd factor})$$

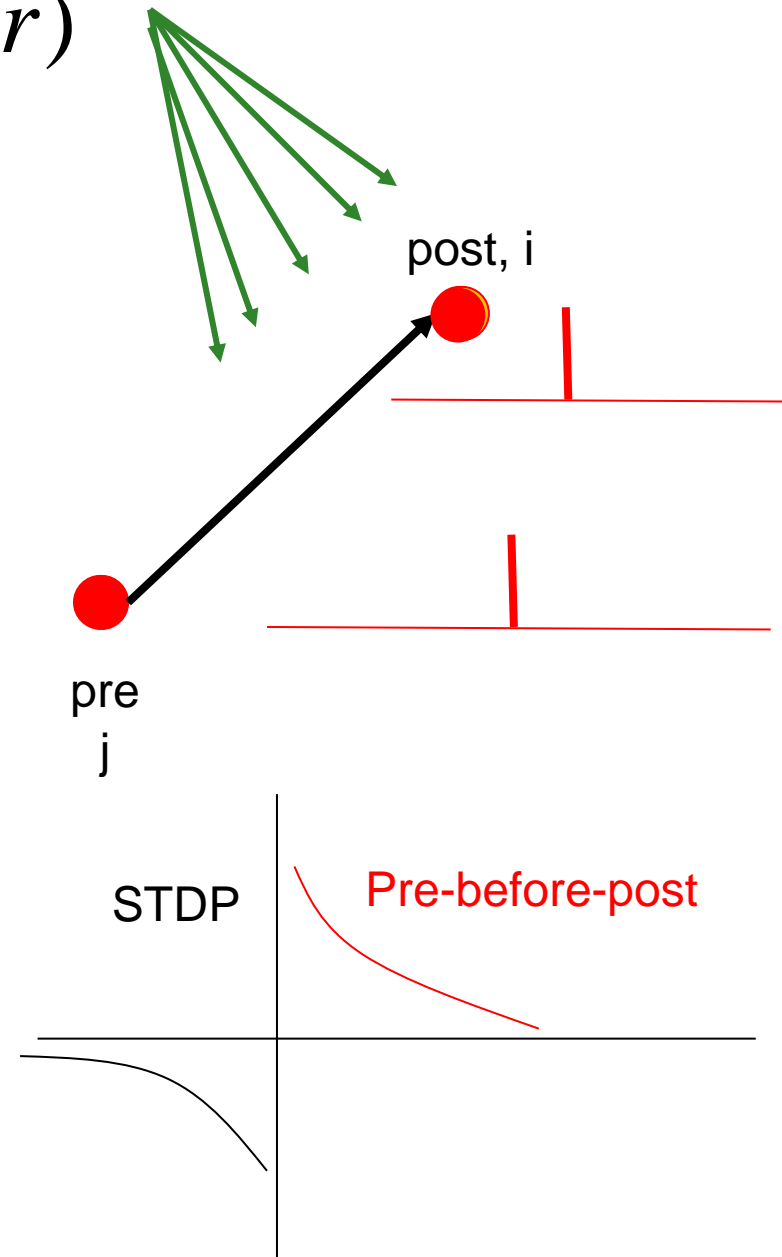
Success/gating/novelty

$$\Delta w_{ij} \propto \text{STDP} \times D$$

$$\Delta w_{ij} = H_{ij} \times D$$

Hebb rule

Success signal



# Neuromodulated STDP experiments

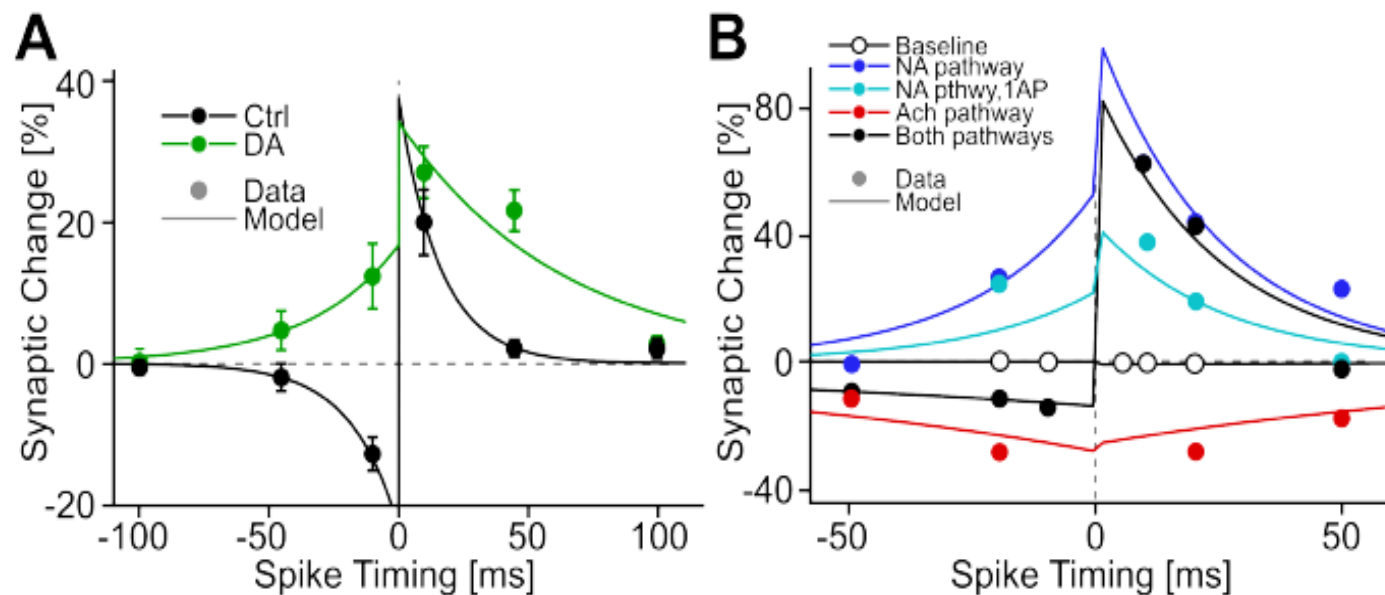
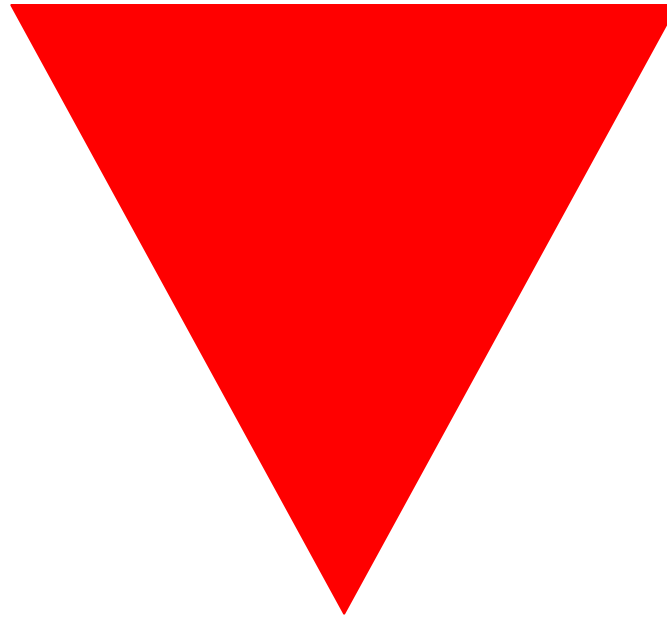


Figure 2: Fit of experimental neuromodulated STDP data with a simple phenomenological model. A: Fit of the data shown in Figure 3 in [Zhang et al., 2009]. Dots show the data (same as in Figure 1C), lines show the model fit, with parameters as in Table 2. B: Fit of the data in Figures 2B, 3C and 4B in [Seol et al., 2007]. Dots show the data, lines show the model fit, with parameters as in Table 2. Cyan points refer to a protocol using single postsynaptic action potentials for STDP induction, all the other points correspond to postsynaptic burst induction.

Probabilistic Brain  
Sampling

Machine Learning  
Optimal learning rules



Synaptic plasticity  
STDP

**Conclusion:**  
STDP experiments are unconvulsive  
Lot's of things possible

# Interplay of synaptic plasticity and probabilistic brain theories

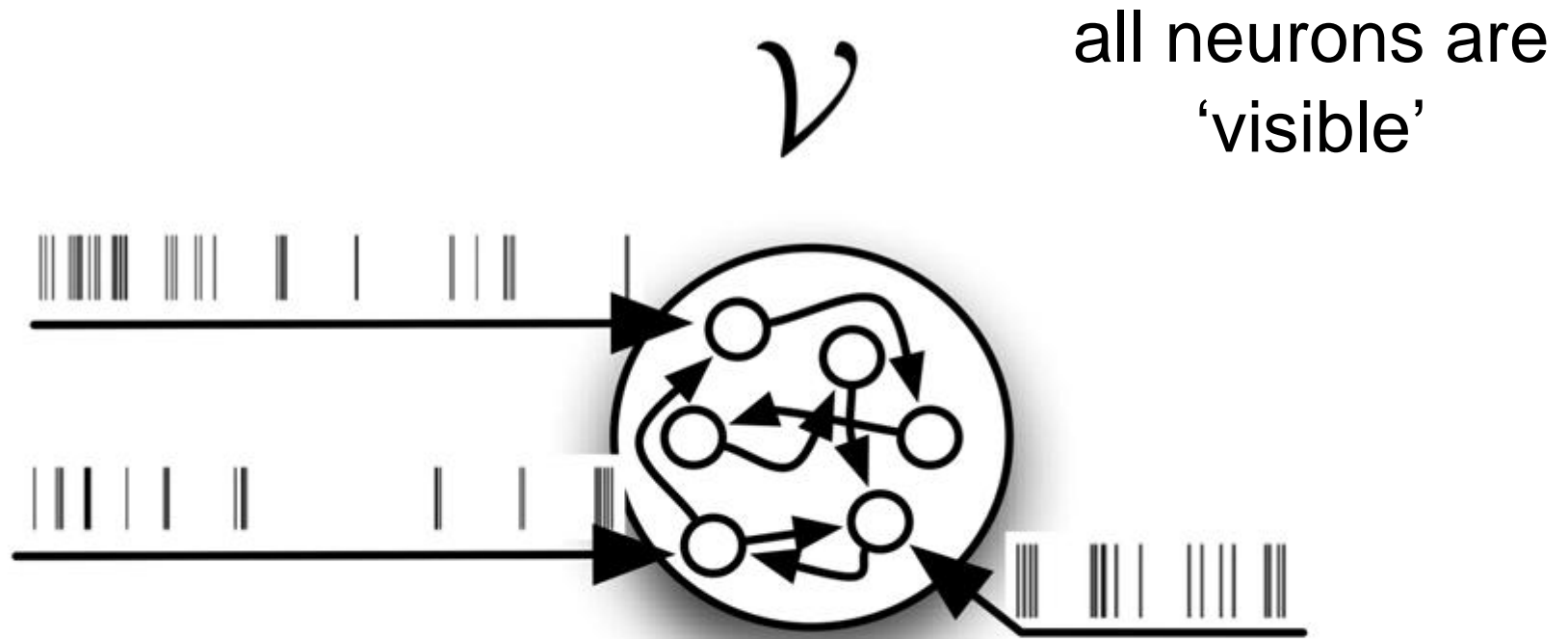
- Introduction

-  - Network and Task

- Math1: Likelihood in Spiking Neurons

- Math 2: Learning rule for network with hidden units

# Spiking Neural Network



**Observed  
neurons**

The task:

- 'slow' sequence

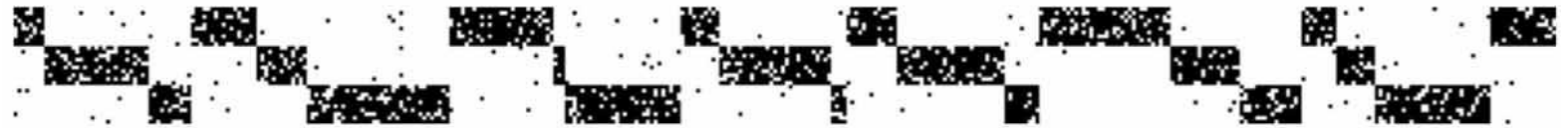
'lullaby, children song'

*frere Jacques, ....*

# Task: Sequence learning and Sequence Generation

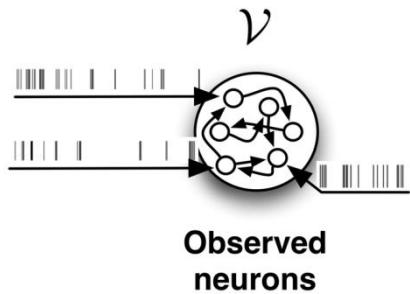
Target pattern (sample)

30 neurons



400ms

After learning, sequence generation, network of 30 neurons (all visible)



Integrate-and-fire neurons

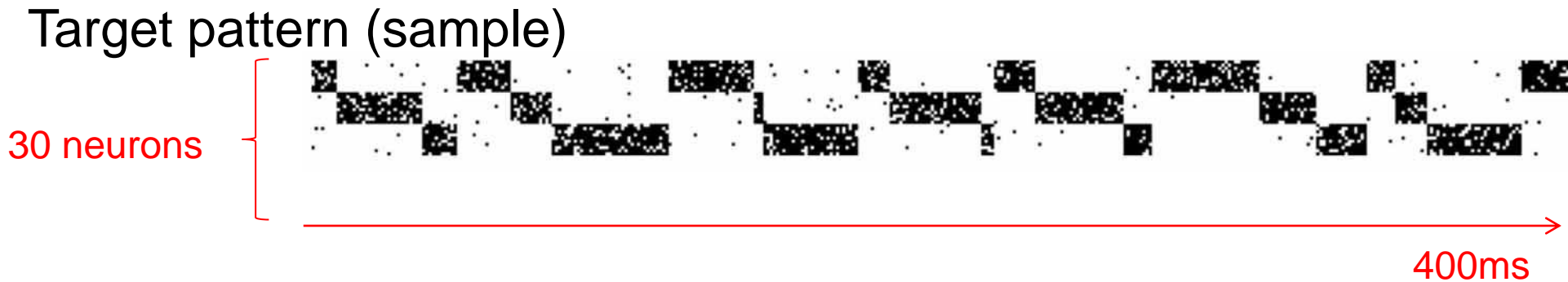
Neuronal time constant: 10ms

Duration of each step in sequence: 30ms +/- 20ms

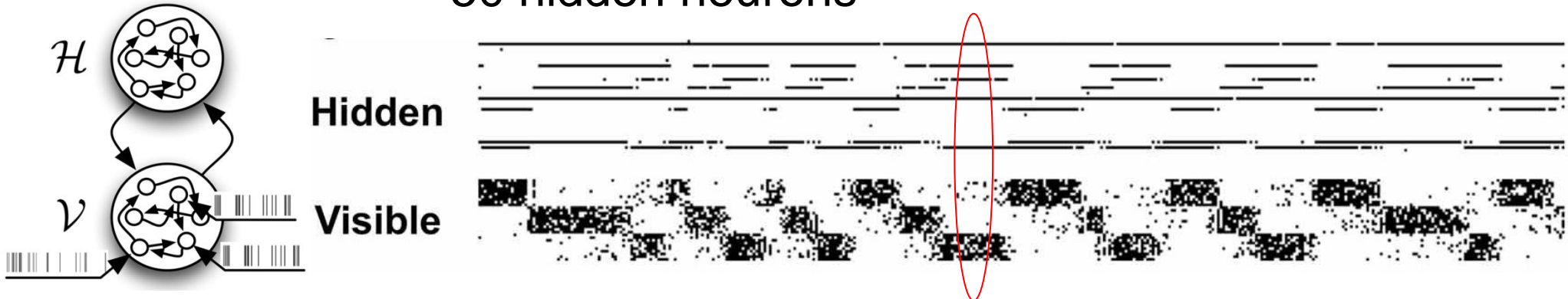
→ Network must keep 'memory'



# Task: Sequence learning and Sequence Generation



After learning, sequence generation, network with  
30 visible neurons  
50 hidden neurons



## **Hidden neurons**

- Memory
- Hidden causes
- Compressed explanation

... all well known in machine learning, Bayes theory, artificial neural networks, deep learning etc

### **Big question:**

- How can we learn the hidden representation?
- Biologically plausible?

# Interplay of synaptic plasticity and probabilistic brain theories

- Introduction

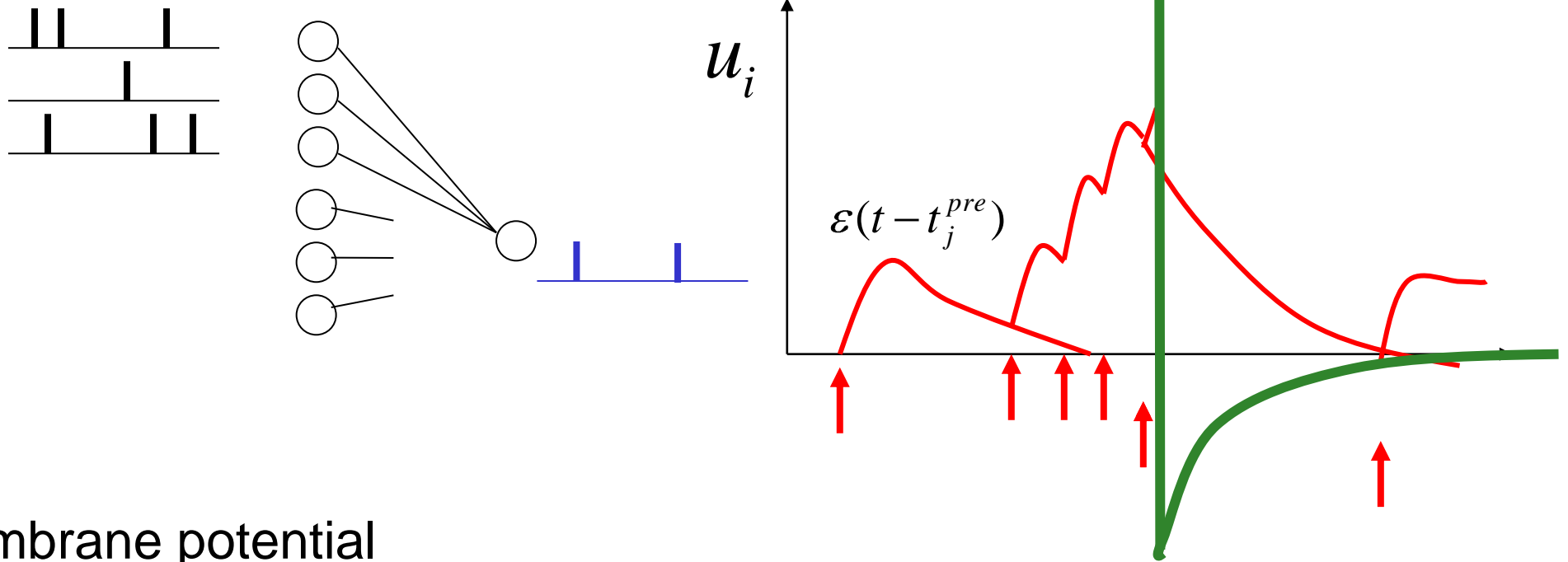
- Network and Task

-  - Math1: Likelihood in Spiking Neurons

- Math 2: Learning rule for network with hidden units

- Surprise

# Neuron model: Spike response model with stochastic firing.



Membrane potential

$$u_i(t | input) = u_{rest} + \sum_j w_{ij} \sum_{input\ spikes} \underline{\varepsilon(t - t_j^f)} + \sum_{output\ spikes} \underline{\eta(t - t_i^f)}$$

reset

Spike generation (probabilistic)

$$\rho(t | u_i) = \rho(u(t)) \propto \exp(\beta u(t))$$

The higher the potential,  
the more likely the  
neuron is to fire

# Likelihood of a spike train

## Spike Response Model with escape noise



$$L = P(\text{Spike train} | \text{input}) = \prod_n \rho(\hat{t}^n | u(\hat{t}^n)) \exp \left[ - \int_{\hat{t}^{n-1}}^{\hat{t}^n} \rho(t' | u(t')) dt' \right]$$

Past spike times, input spikes

known

$$u_i(t) = \sum_{\text{spikes of } i} \eta(t - t_i^f) + \sum_j \sum_{\text{input spikes}} w_{ij} \varepsilon(t - t_j^f)$$

Maximize likelihood to generate observed spike train:

→ Adjust weights

# Derivation of learning rule

- Maximize likelihood that (observed) spikes could have been generated by model

$$\frac{d}{dt} w_{ij} = \eta \frac{d}{dw_{ij}} \log \langle L \rangle$$

*Pfister, Barber, Gerster. 2006*

spiking neurons

$$\frac{d}{dt} w_{ij}(t) \propto \varepsilon(t - t_j^{pre}) [\delta(t - t_i^f) - \rho(u(t))]$$

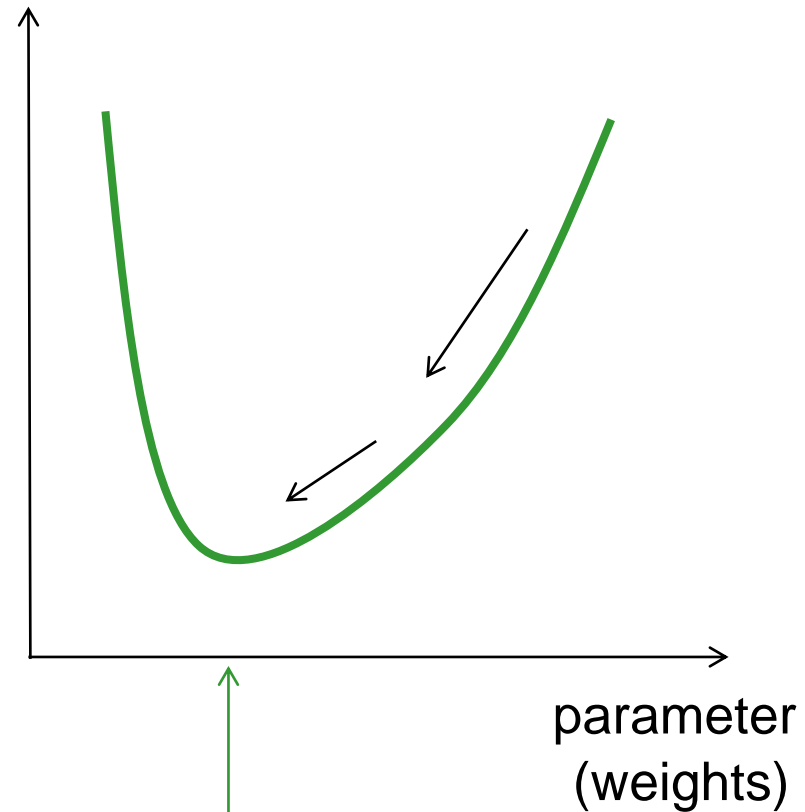
EPSP

Post

# Optimization is Convex

Work of Paninski

mismatch  
(spike times)

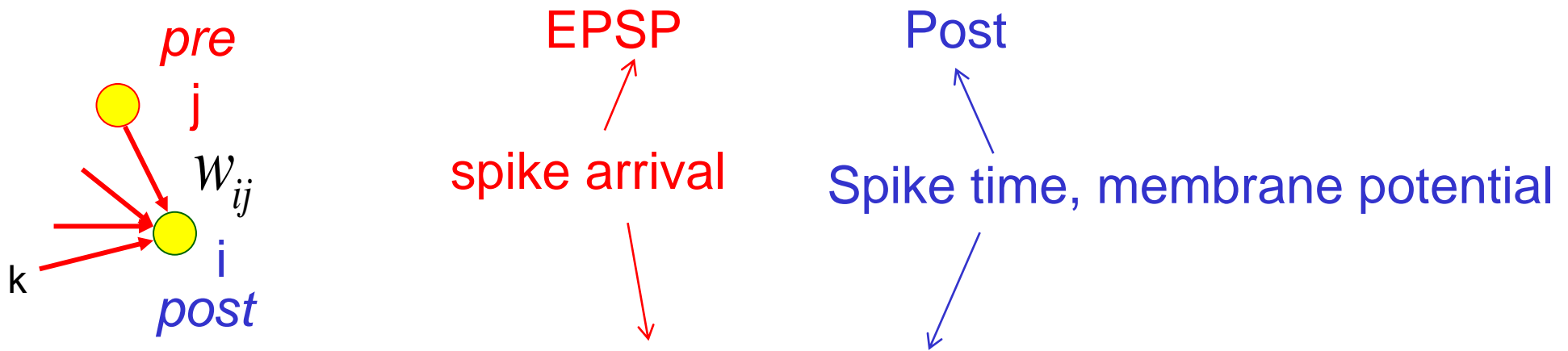


Optimal value

# Learning rule for fully observable network

$$\frac{d}{dt} w_{ij} = \eta \frac{d}{dw_{ij}} \log \langle L \rangle$$

$$\frac{d}{dt} w_{ij}(t) \propto \varepsilon(t - t_j^{pre}) [\delta(t - t_i^f) - \rho(u_i(t))]$$



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



# Interplay of synaptic plasticity and probabilistic brain theories

- Introduction

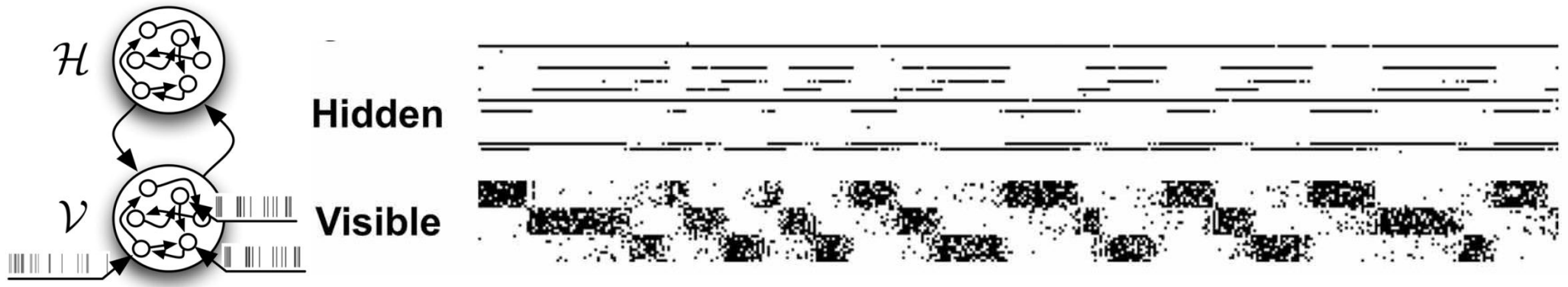
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- Surprise/novelty

# Math 2: Learning rule for network with hidden units



Hidden units

- + memory
- + hidden causes
- + compact representations

- hard to train

Aim: **visible** units

$$\mathcal{L} = P(\text{observed Spiketrain})$$

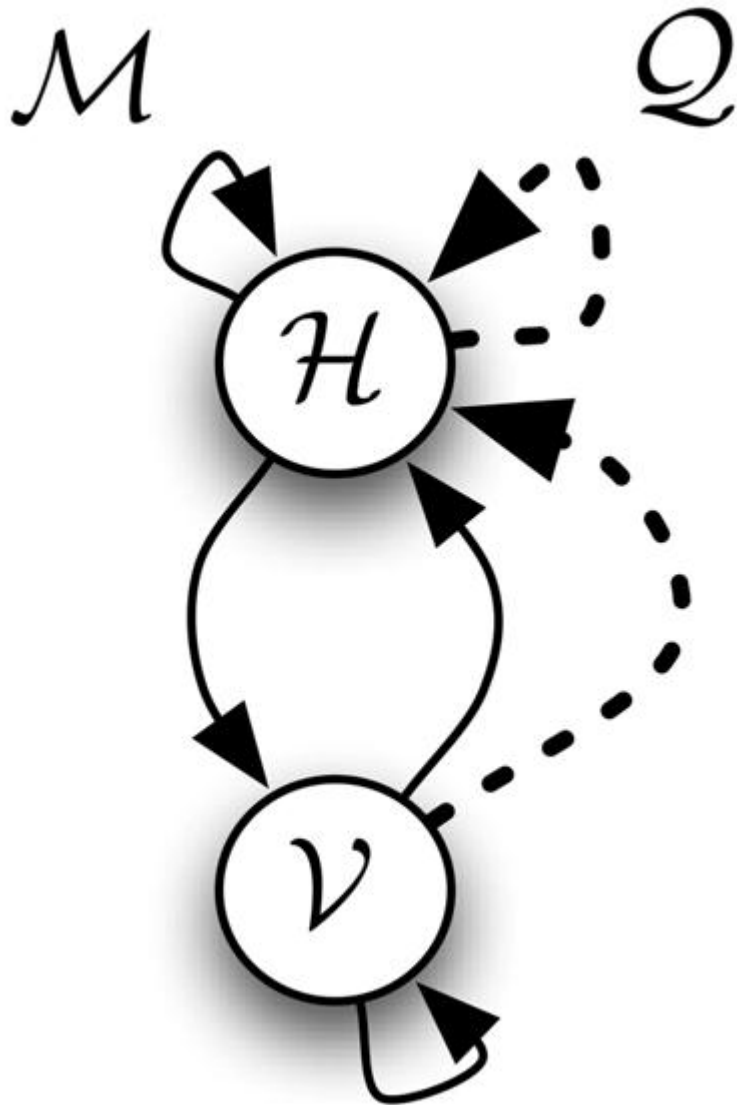
$$= P(X_v)$$

$$= \int P(X_v, X_H) dX_H$$

↑ ↑  
all hidden states

# Trick: Variational Learning (a.k.a: Free Energy)

*e.g. Friston 2005*



Approximate complicated network  $M$ ,  
by simpler network  $Q$

Minimize KL – divergence

$$KL(q; p) = \int q(X_H | X_v) \log \frac{q(X_H | X_v)}{p(X_H | X_v)} dX_H$$

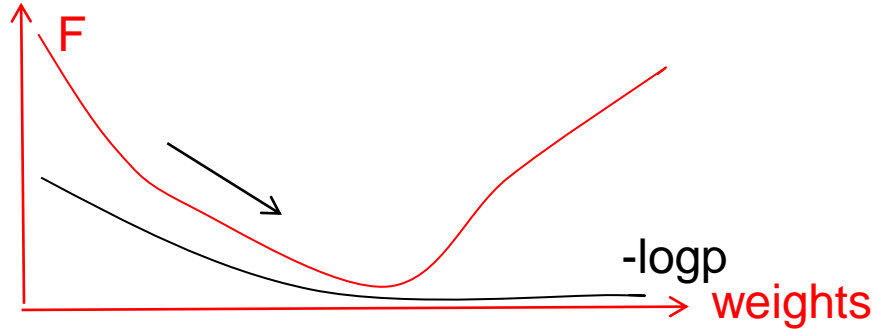
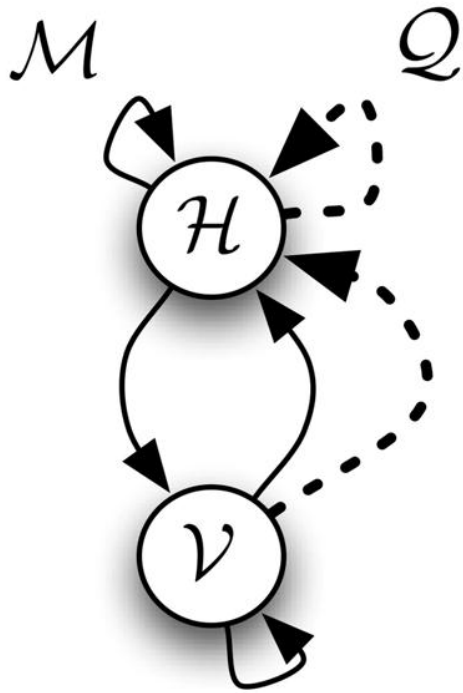
$$KL(q; p) = F + \log p(X_v)$$

$$F = \left\langle \log q(X_H | X_v) - \log p(X_H | X_v) \right\rangle_{q(X_H | X_v)}$$



average over samples from simple network

# Trick: Variational Learning (aka: Free Energy)



Minimize  $F \rightarrow$  maximize (upper bound of)  $\log p$

$$-\log p(X_v) \leq F$$

$$KL(q; p) = F + \log p(X_v) \geq 0$$

$$F = \left\langle \log q(X_H | X_v) - \log p(X_H | X_v) \right\rangle_{q(X_H | X_v)}$$



average over samples from simple network

e.g., Dayan 2000

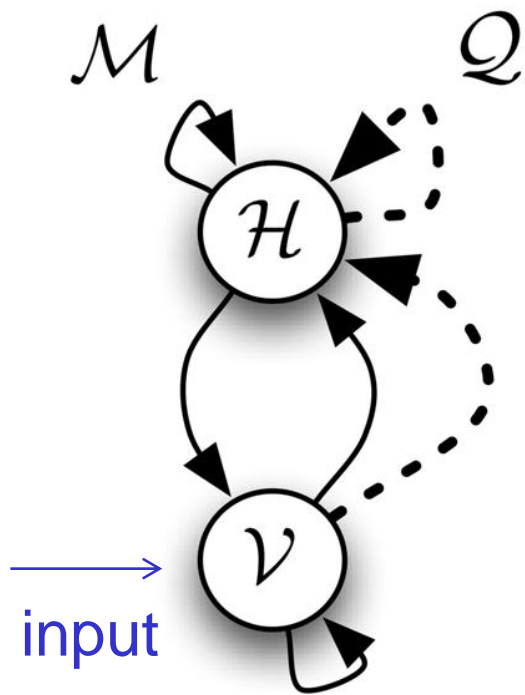
Friston, 2005

Friston and Stephan, 2007

Beal and Gahrahmani, 2006

# Math 2: Learning rule for network with hidden units

$$\frac{d}{dt} w_{ij} = -\eta \frac{d}{dw_{ij}} \log \langle F \rangle$$



For Q network

$$\frac{d}{dt} w_{ij}(t) \propto F \varepsilon(t - t_j^{pre}) [\delta(t - t_i^f) - \rho(u_i(t))]$$

generated by Q-network

For M network

$$\frac{d}{dt} w_{ij}(t) \propto \varepsilon(t - t_j^{pre}) [\delta(t - t_i^f) - \rho(u_i(t))]$$

→ M network takes Q network as teacher

# Biological implementation of learning rule

Hebbian learning leaves trace:

$$\frac{d}{dt} Hebb_{ij}(t) = \varepsilon(t - t_j^{pre}) [\delta(t - t_i^f) - \rho(u_i(t))] - Hebb_{ij}$$

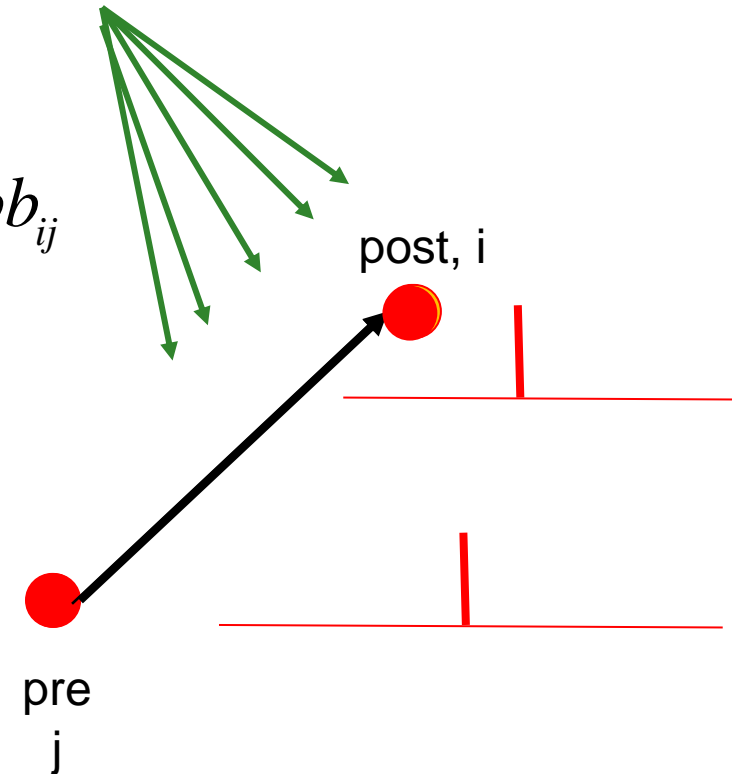
$$\frac{d}{dt} w_{ij}(t) = \eta \cdot Nov \cdot Hebb_{ij}$$

novelty/surprise

$$Nov = \hat{F} - \bar{F}$$


online estimate - running average  
of  
free energy

novelty/surprise



weights updated  
when we are more  
surprised than normally

# Interplay of synaptic plasticity and probabilistic brain theories

- Introduction
- Network and Task
- Math1: Likelihood in Spiking Neurons
- Math 2: Learning rule for network with hidden units
-  - Surprise/novelty

# Surprise/novelty

## Neuromodulator Ach

See: Gu 2002, Ranganath and Rainer 2003, Yu and Dayan, 2005

## Neuromodulators act on:

- Activity of neurons
- Synaptic plasticity

Our proposition: neuromodulator signal

$$\text{Novelty} = \text{surprise} - \text{expected surprise}$$

compare: reinforcement learning

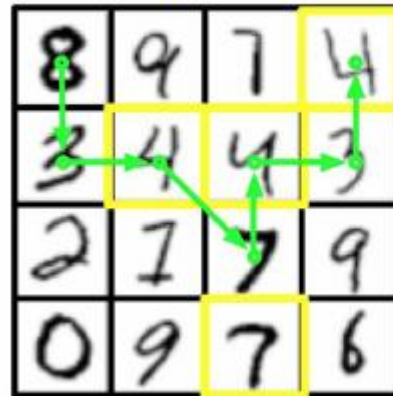
$$\text{Success} = \text{reward} - \text{expected reward}$$



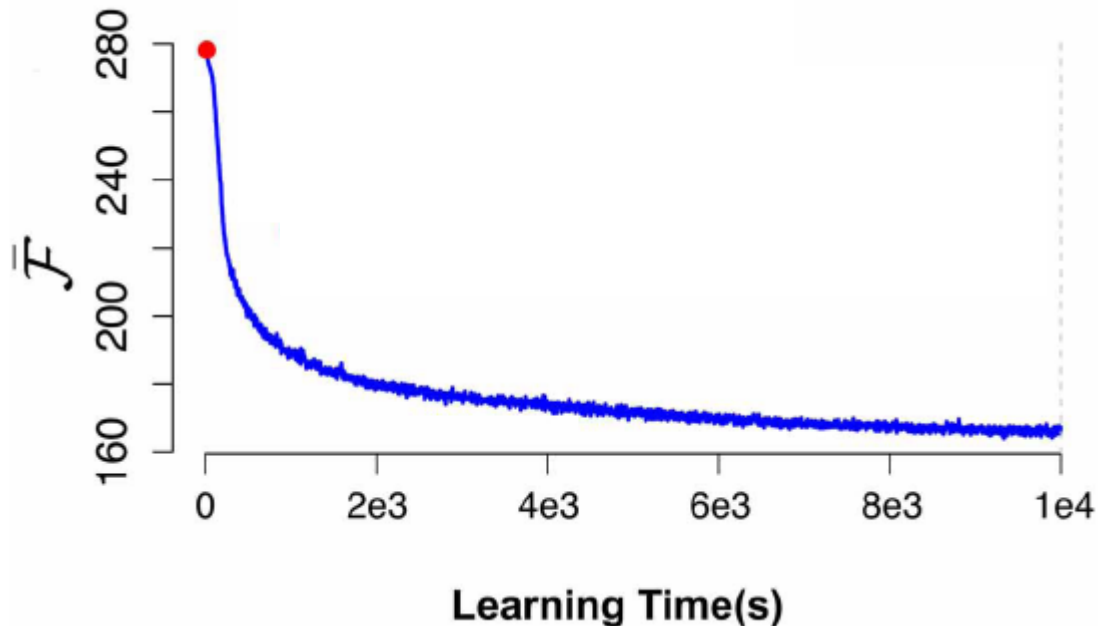
# Surprise/novelty

**Maze** of 16  
 MNIST pixel patterns  
 28x28 visible neurons  
 30 hidden neurons,  
 Actions are random,  
 every second

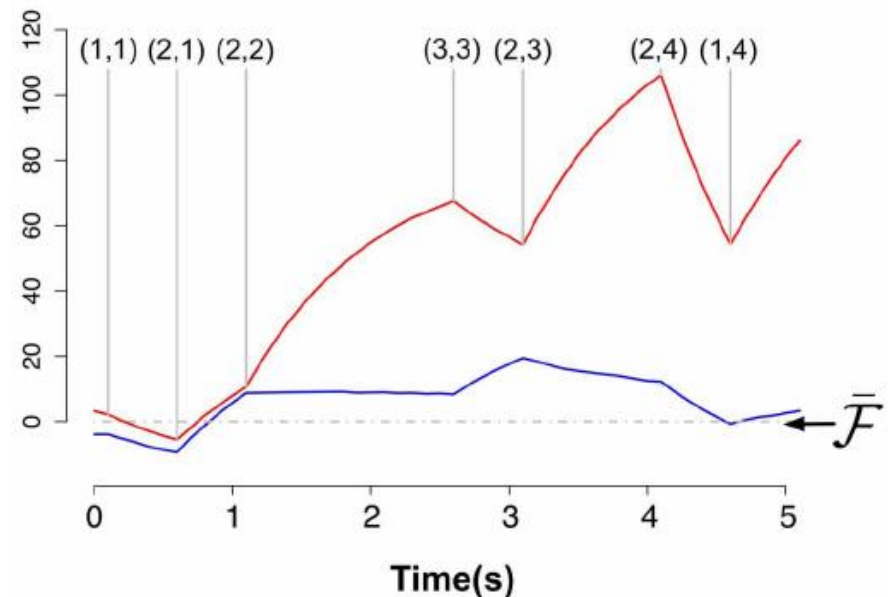
Target maze



Expected surprise (free energy)



novelty  $Nov = \hat{F} - \bar{F}$



Free Energy 'measures' mismatch of model to data

$$F \geq -\log p(X_v)$$

$\hat{F}$  = Online-single-sample estimate of  $F$

$\hat{F}$  'measures' surprise of present input

Our proposition: neuromodulator signal

**Novelty = surprise – expected surprise**

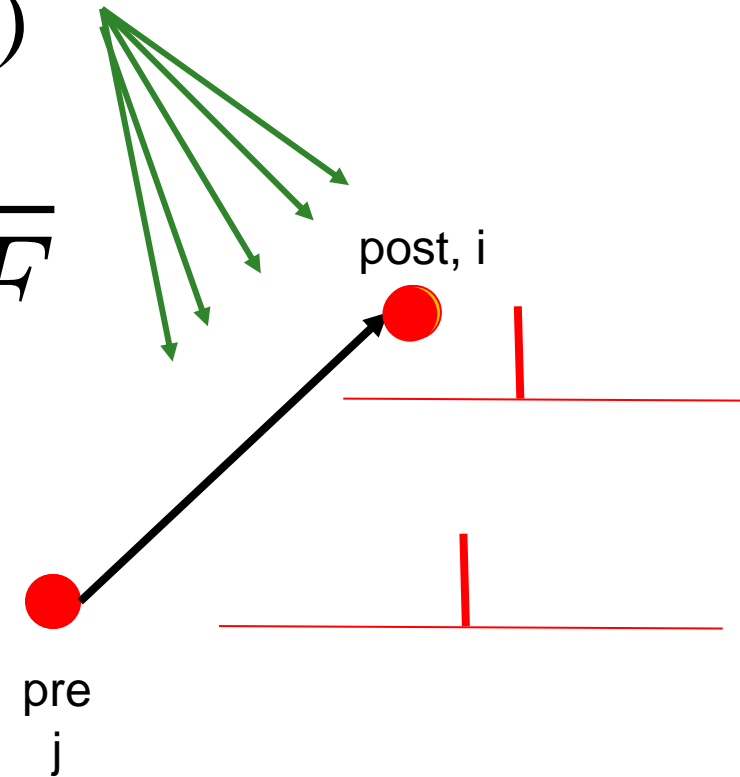
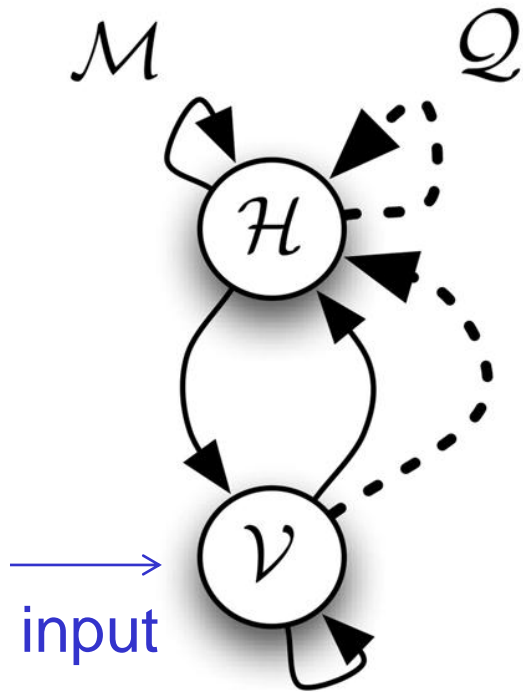
$$Nov = \hat{F} - \bar{F}$$

weights updated  
when we are more  
surprised than normally

# Conclusions

$$\Delta w_{ij} \propto F(\text{pre}, \text{post}, \text{3rd factor})$$

$$Nov = \hat{F} - \bar{F}$$



- Hidden neurons/network structure to form memories
- Hebb-rule/STPD for feedback connections
- 3-factor rule with 'novelty' for feedforward connections

*The end*

Thanks to

Danilo REZENDE

Daan WIERSTRA

Johanni BREA

Jimenez-Rezende, Wierstra, Gerstner, NIPS 2011

Brea, Senn, Pfister, J. Neuroscience 2013

Rezende and Gerstner, Frontiers Comp. Neurosci. 2014



# Classification

R-max Xie&Seung 2004, Pfister et al. 2006, Florian 2007, ...

$$\dot{w} = R \times (H(\text{pre}, \text{post}) - \langle H(\text{pre}, \text{post}) | \text{pre} \rangle) ,$$

$$\longrightarrow \langle \dot{w} \rangle = \text{Cov}(R, H(\text{pre}, \text{post})) .$$

R-STDP

Florian 2007, Farries&Fairhall 2008, Legenstein 2008, ...

$$\dot{w} = (R - \langle R | \text{pre} \rangle) \times H(\text{pre}, \text{post}) .$$

$$\longrightarrow \langle \dot{w} \rangle = \text{Cov}(R, H(\text{pre}, \text{post})) .$$

R-STDP with gating effect Izhikevich 2007

$$\langle \dot{w} \rangle = \text{Cov}(R, H(\text{pre}, \text{post})) + \langle R \rangle \langle H(\text{pre}, \text{post}) \rangle .$$

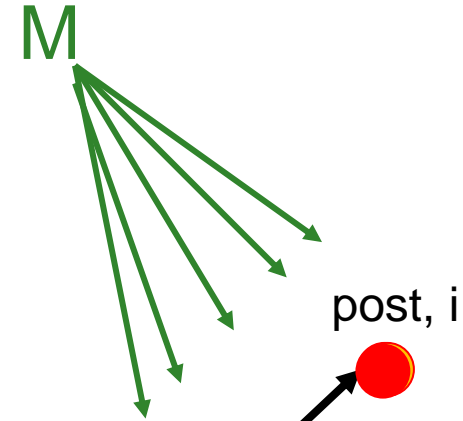
TD-STDP

Fremaux et al. 2013, to appear, PLOS Comput. Biol.

$$\dot{w} = \delta \times H(\text{pre}, \text{post}) .$$

# Classification

$$\dot{w} = M \times H(\text{pre}, \text{post})$$



{	$R - \langle R \rangle$	→	covariance-rule
	$\delta^{\text{TD}}$	→	TD learning
	$R$	→	gated Hebbian learning
	$S$	→	surprise/novelty-modulated STDP
	$const$	→	non-modulated STDP ,

pre  
j