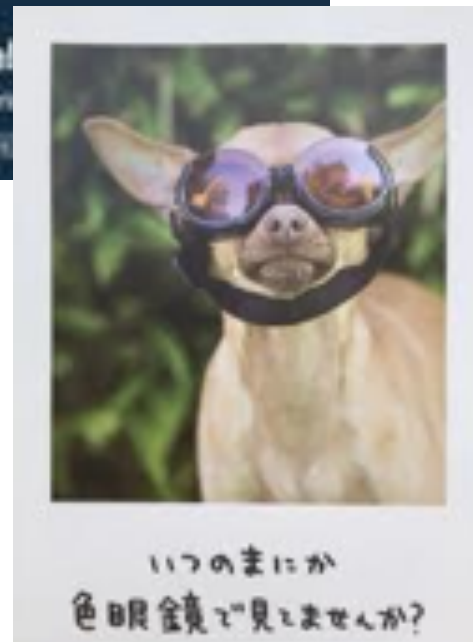
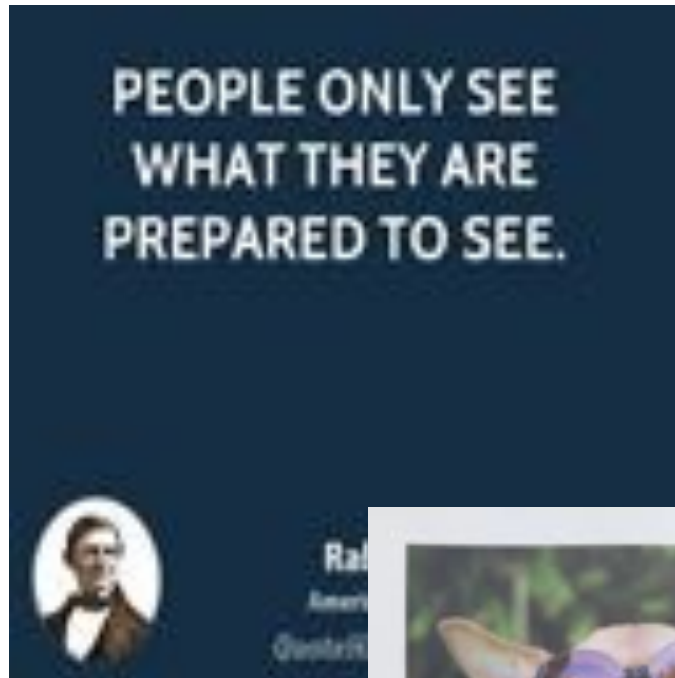




Synaptic plasticity in network models

Tomoki Fukai
RIKEN Brain Science Institute

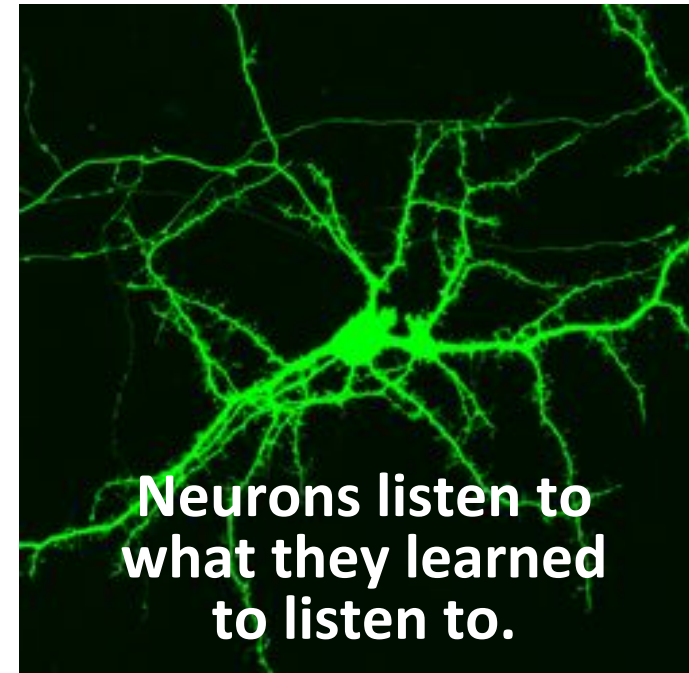
Matthieu Gilson (Univ Pompeu Fabra)
Naoki Hiratani (RIKEN)
Anthony Burkitt (Univ Melbourne)



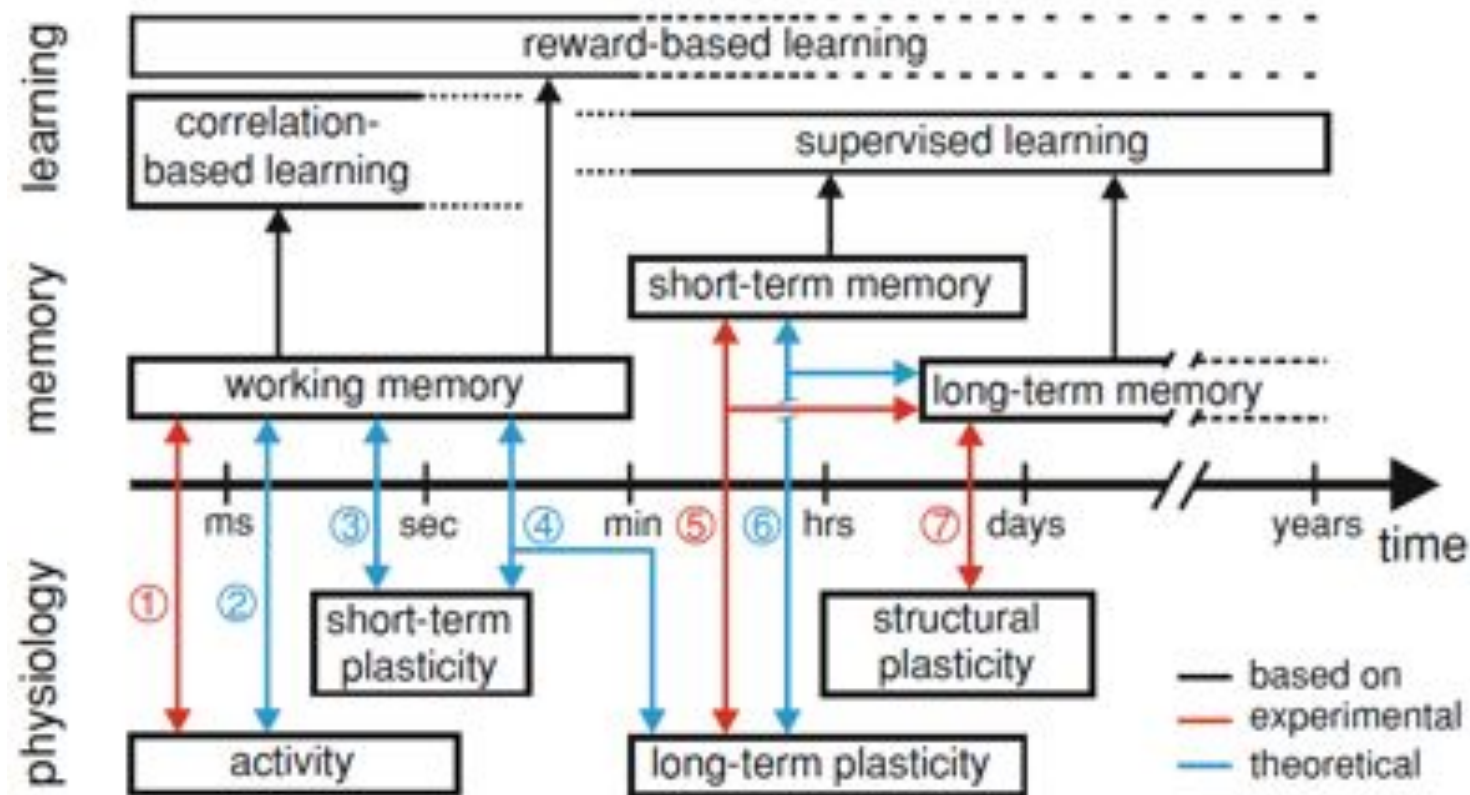
see things
through colored lens



Humans see what they want to see



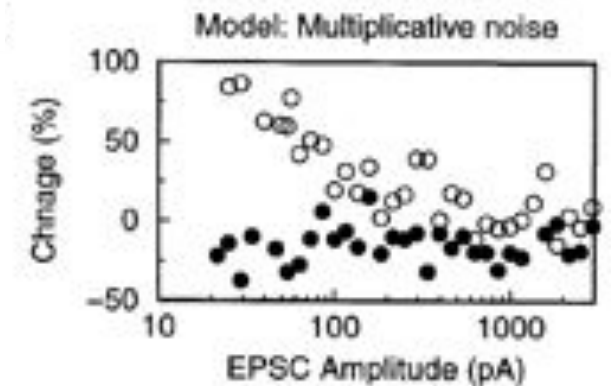
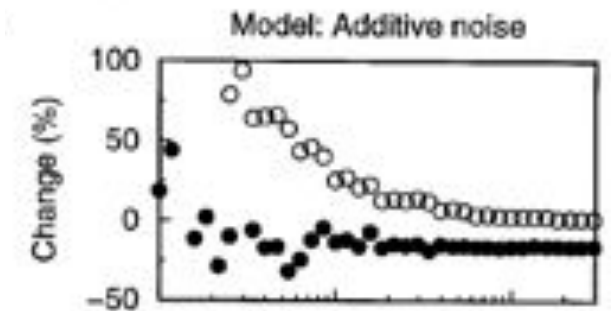
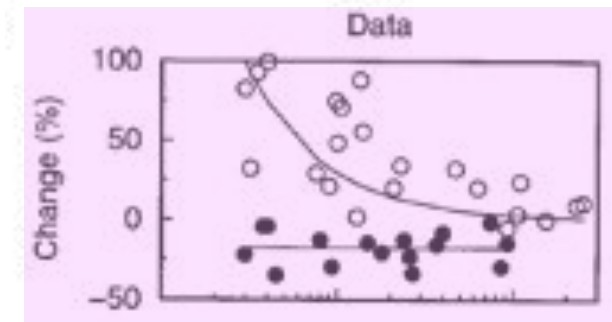
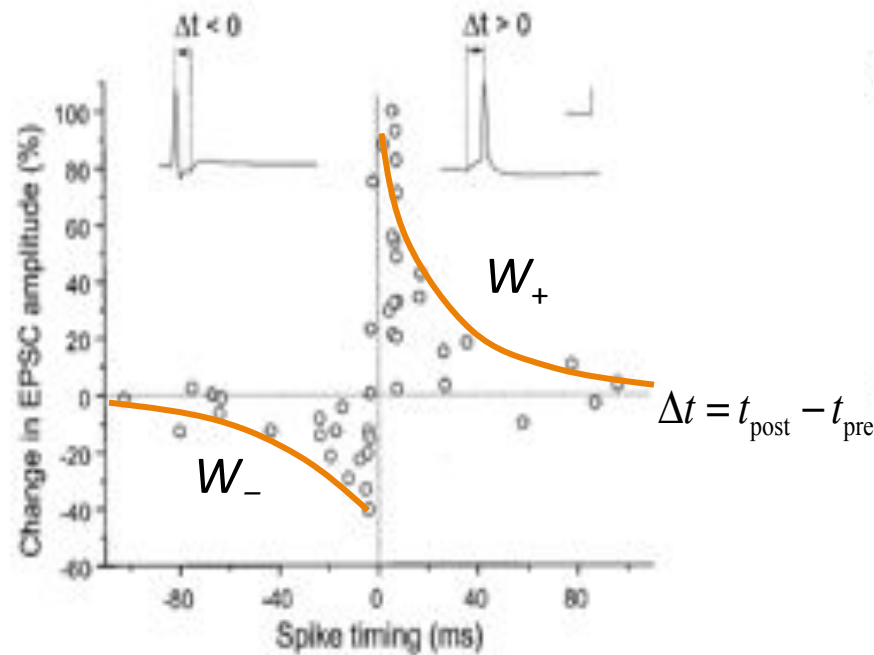
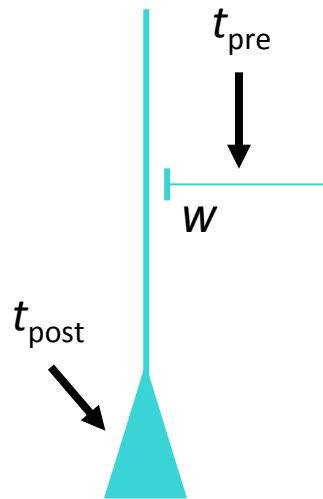
The brain has multiple plasticity rules having different time scales



(Tetzlaff et al., Biol Cybern 2012)

Spike-Timing-Dependent Plasticity

(Bi and Poo, 1998)

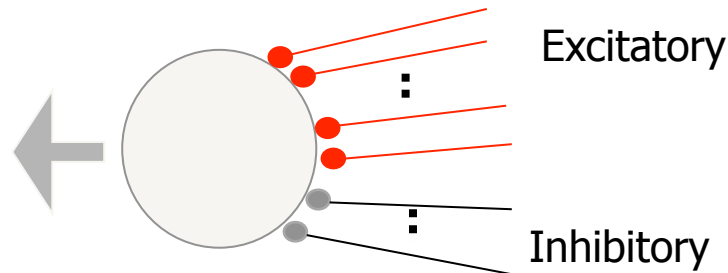


Multiplicative rule

$$\Delta w = \begin{cases} (c_+ + wn) \exp(-\Delta t / \tau_+) & \text{LTP} \\ (-c_- w + wn) \exp(\Delta t / \tau_-) & \text{LTD} \end{cases}$$

(van Rossum et al., 2000)

Dilemma of STDP

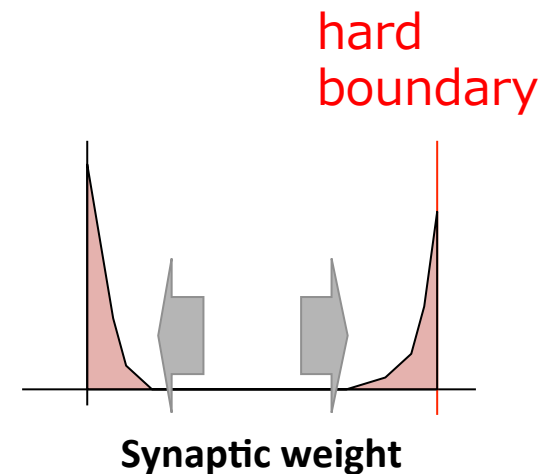


Additive STDP (no weight-dependence)

Song, Miller and Abbott (2000)

Synaptic competition, interesting functions

Unstable dynamics

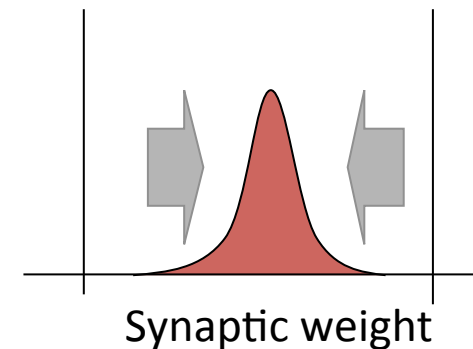


Multiplicative STDP (weight-dependent)

van Rossum, Bi and Turrigiano (2000)

No synaptic competition, almost no function,

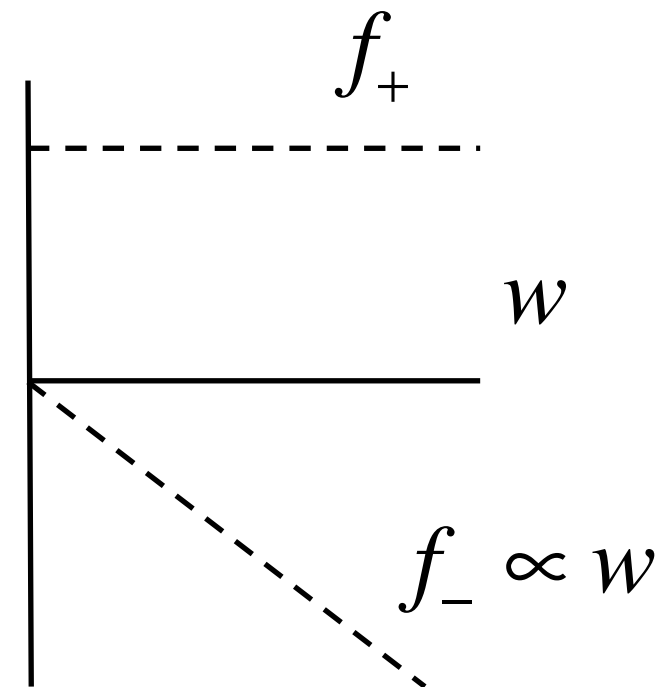
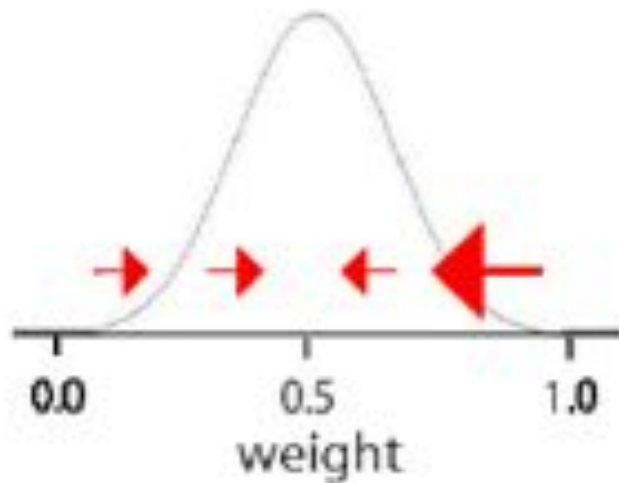
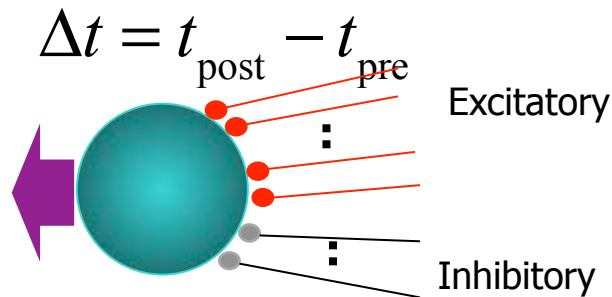
Stable dynamics



Multiplicative STDP

(van Rossum et al., 2000)

$$\Delta w = \begin{cases} (f_+(w) + \text{noise}) \exp(-\Delta t / \tau_P) & (\Delta t > 0) \\ -(f_-(w) + \text{noise}) \exp(\Delta t / \tau_D) & (\Delta t < 0) \end{cases}$$

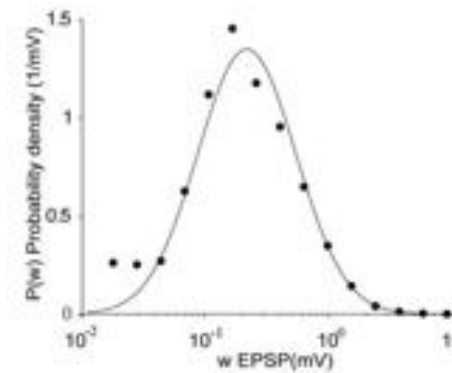
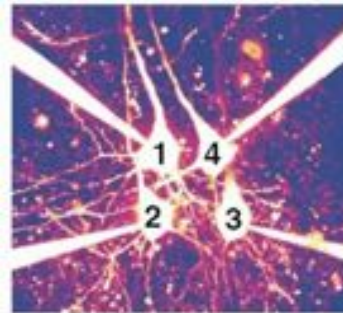


Heavy-tailed EPSP distributions of cortical synapses

Strong-sparse synapses vs. weak-dense synapses

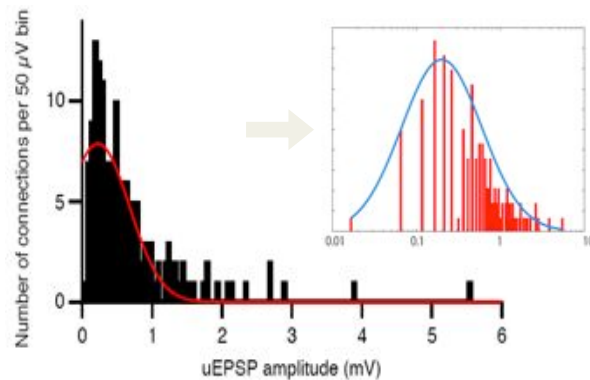
rat visual cortex

Song et al., PLoS Biol (2005)



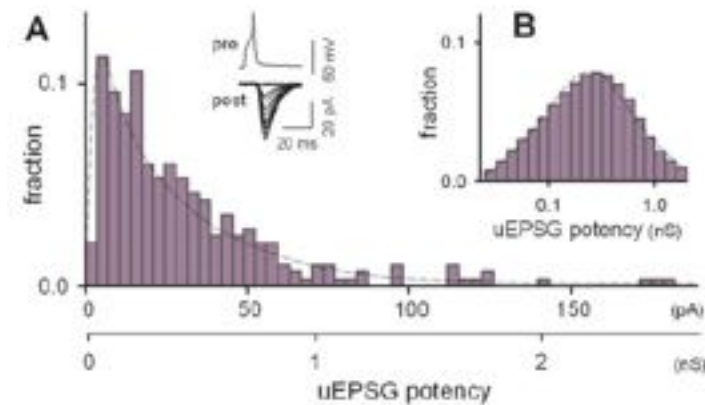
mouse somatosensory cortex

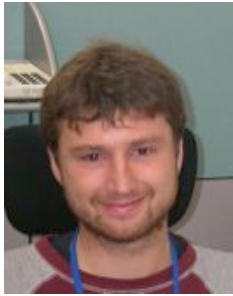
Lefort et al. Neuron (2009)



rat hippocampus

Ikegaya et al., Cereb Cortex (2013)

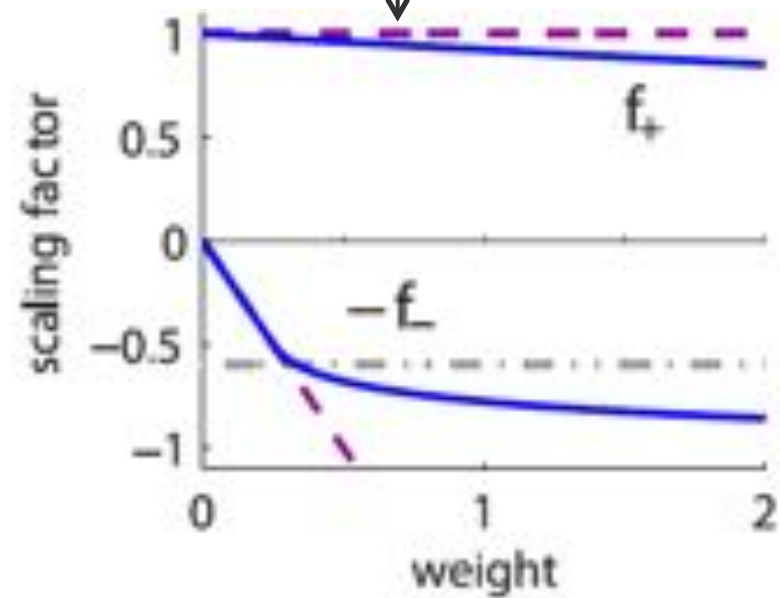
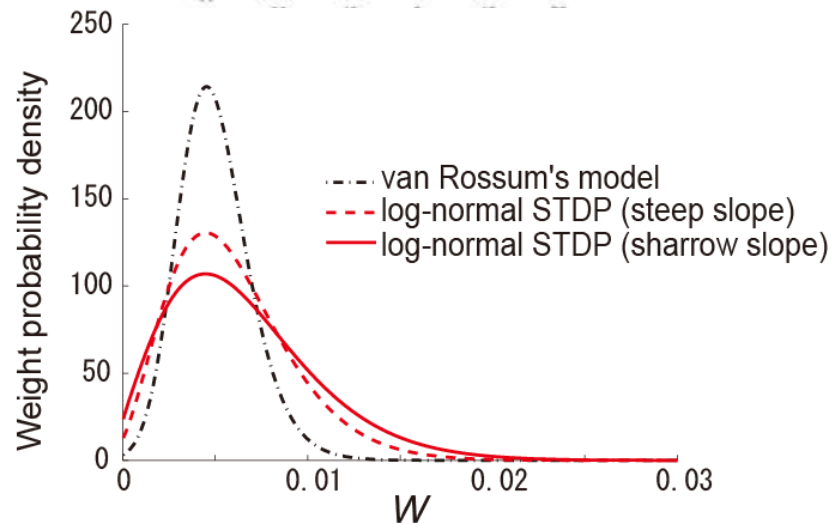
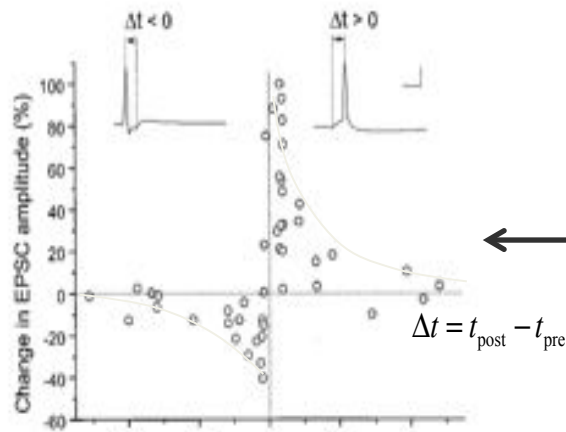




Matthieu Gilson

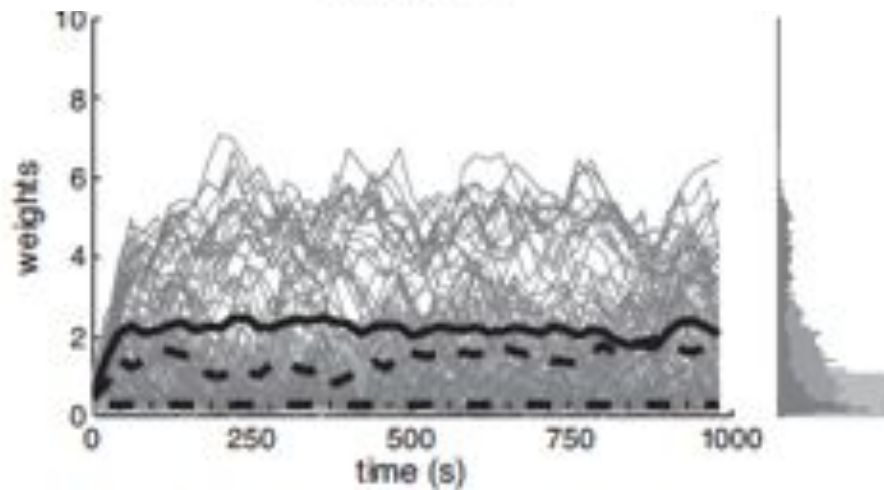
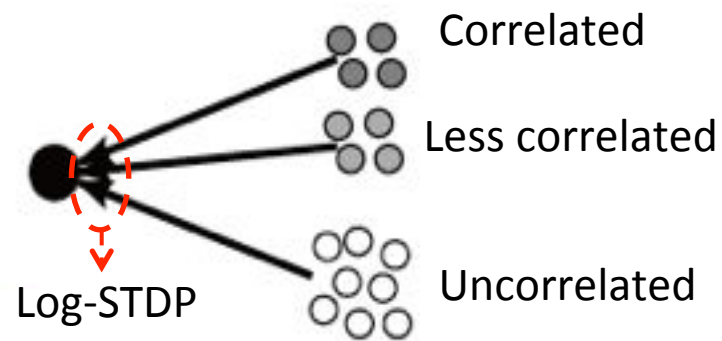
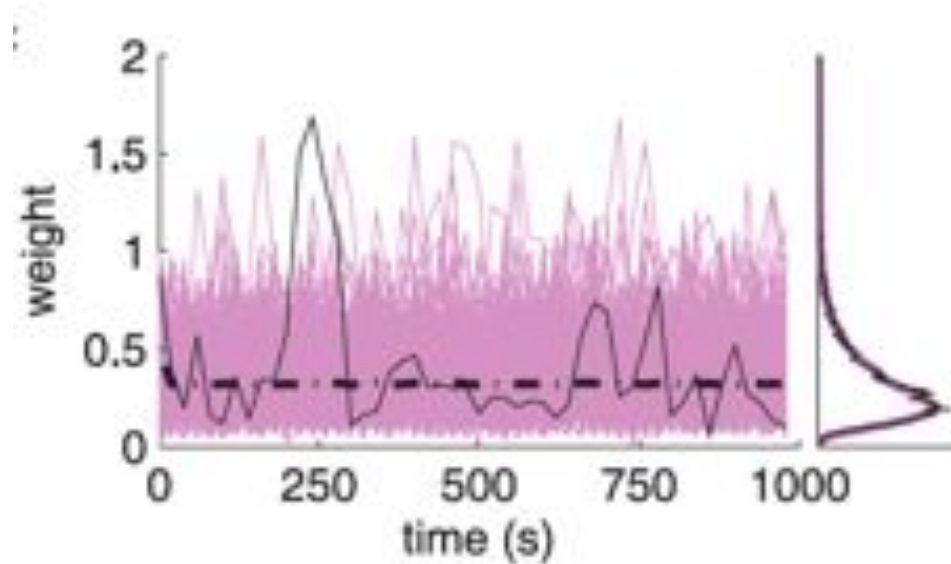
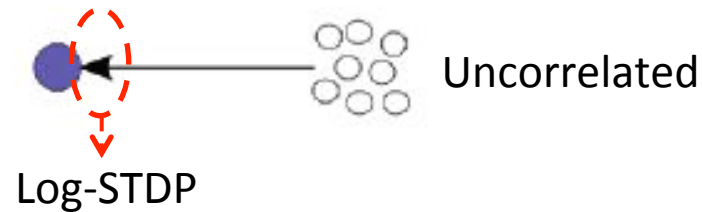
Log spike-timing-dependent plasticity

$$\Delta w_{ij}^{EE} = \begin{cases} +c_p e^{-\Delta t / \tau_p} \\ -c_d e^{-\Delta t / \tau_d} \log\left(1 + \alpha w_{ij}^{EE} / w_{EE}\right) / \log(1 + \alpha) \end{cases}$$



(Gilson and Fukai, PLoS One, 2011)

Correlated spike input drives synaptic weight towards long tail

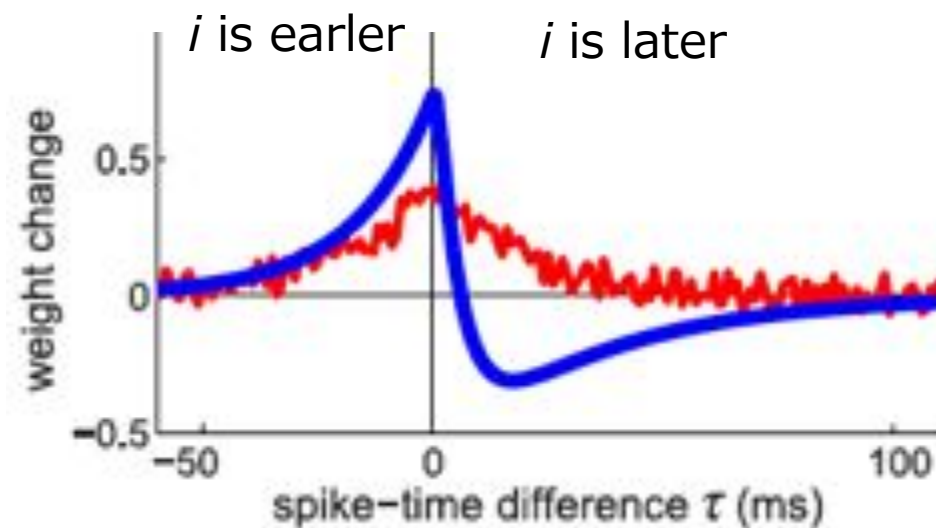
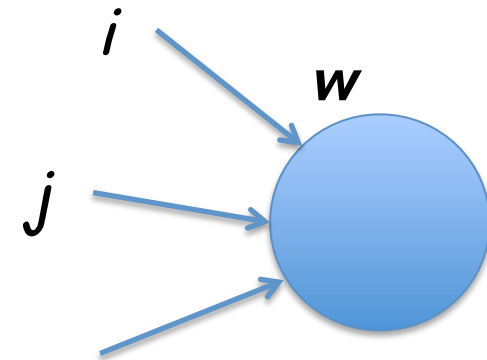


How weight i is modulated by input j

$$\dot{\mathbf{w}} \propto Y(\mathbf{w}; v_{\text{in}}; v_{\text{out}}) + \mathbf{w} C^{\chi}(\mathbf{w}),$$

$$C_{ij}^{\chi}(\mathbf{w}; t) = \int_{-\infty}^{+\infty} \chi_i(w_j; \tau) C_{ij}(t, \tau) d\tau,$$

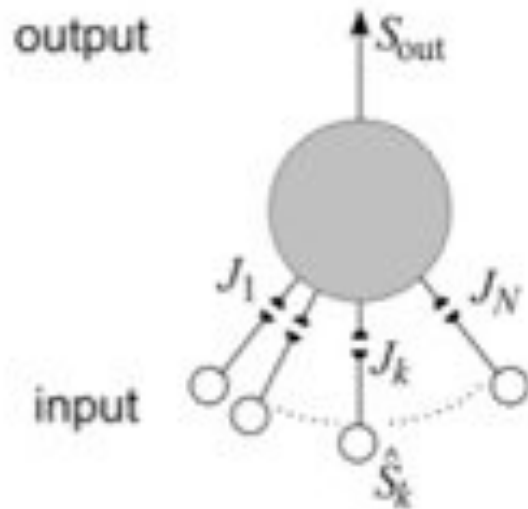
τ = timing of input i relative to j



(Gilson, Fukai and Burkitt, PLoS Comput Biol, 2012)

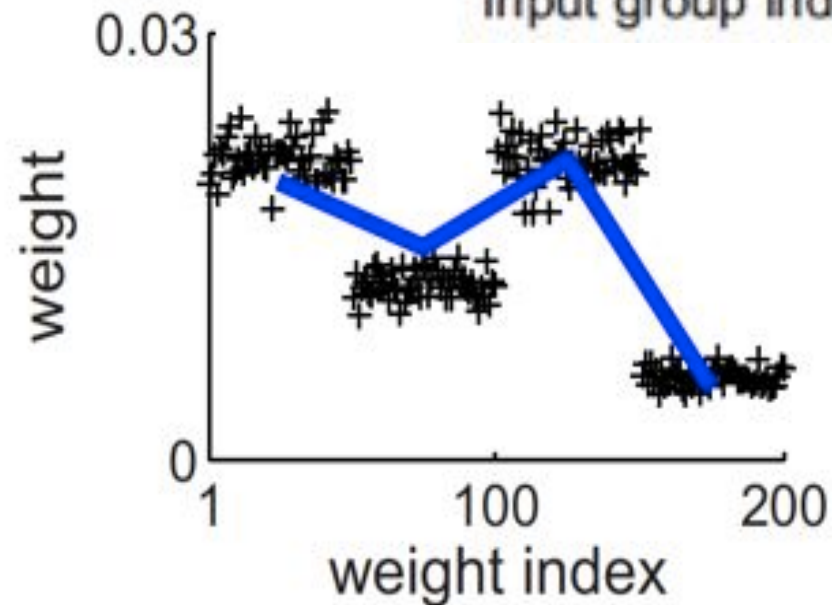
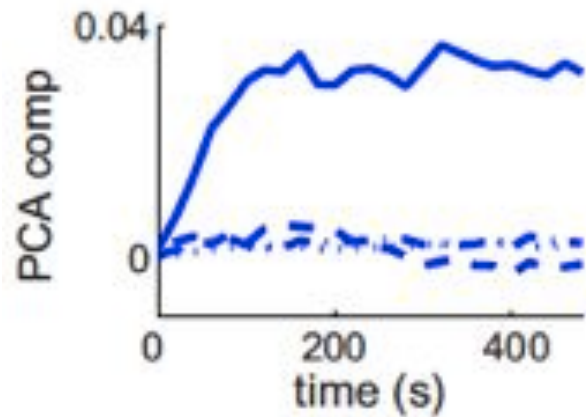
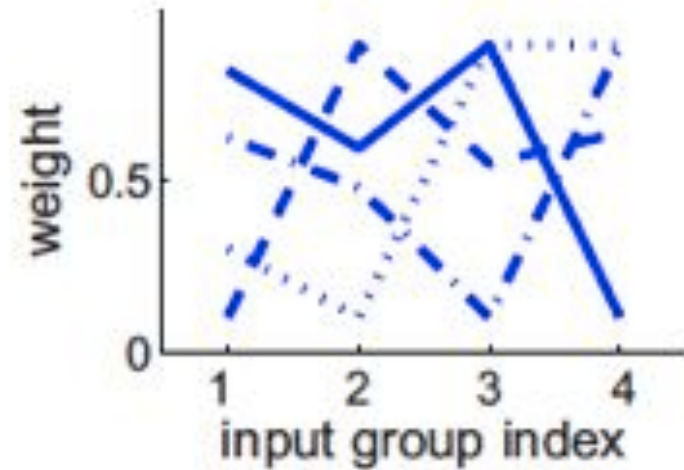
Log-STDP performs PCA in input correlation space

(Gilson, Fukai and Burkitt, PLoS Comput Biol, 2012)



Correlation matrix of input groups

$$\begin{pmatrix} 0.4 & 0 & 0.2 & 0 \\ 0 & 0.3 & 0.2 & 0.1 \\ 0.2 & 0.2 & 0.3 & 0 \\ 0 & 0.1 & 0 & 0.1 \end{pmatrix}$$



Log-STDP obeys stable plasticity dynamics and
uses a fat tail to detect correlated synaptic inputs

Cocktail Party Effect



Cocktail Party Effect (Blind Source Separation)

Independent component analysis ICA (Common, 1994)

Nonlinear PCA (Oja and Karhunen, 1995)

Entropy maximization (Bell and Sejnowski, 1995)

Natural gradient approach (Amari, Cichocki and Yang, 1995)

...

Yet, how the brain solves this problem is not known.

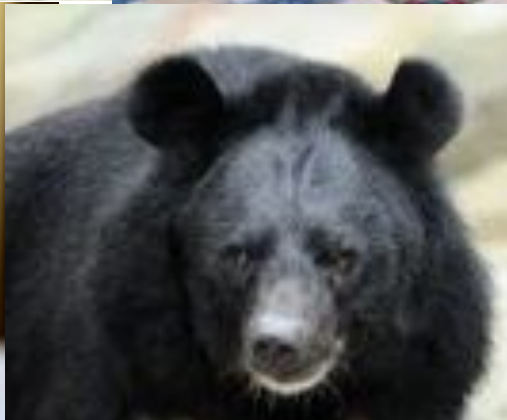
$$\mathbf{x}(t) = \mathbf{A}\mathbf{s}(t)$$

$\mathbf{A} : n \times n$ nonsingular mixing matrix

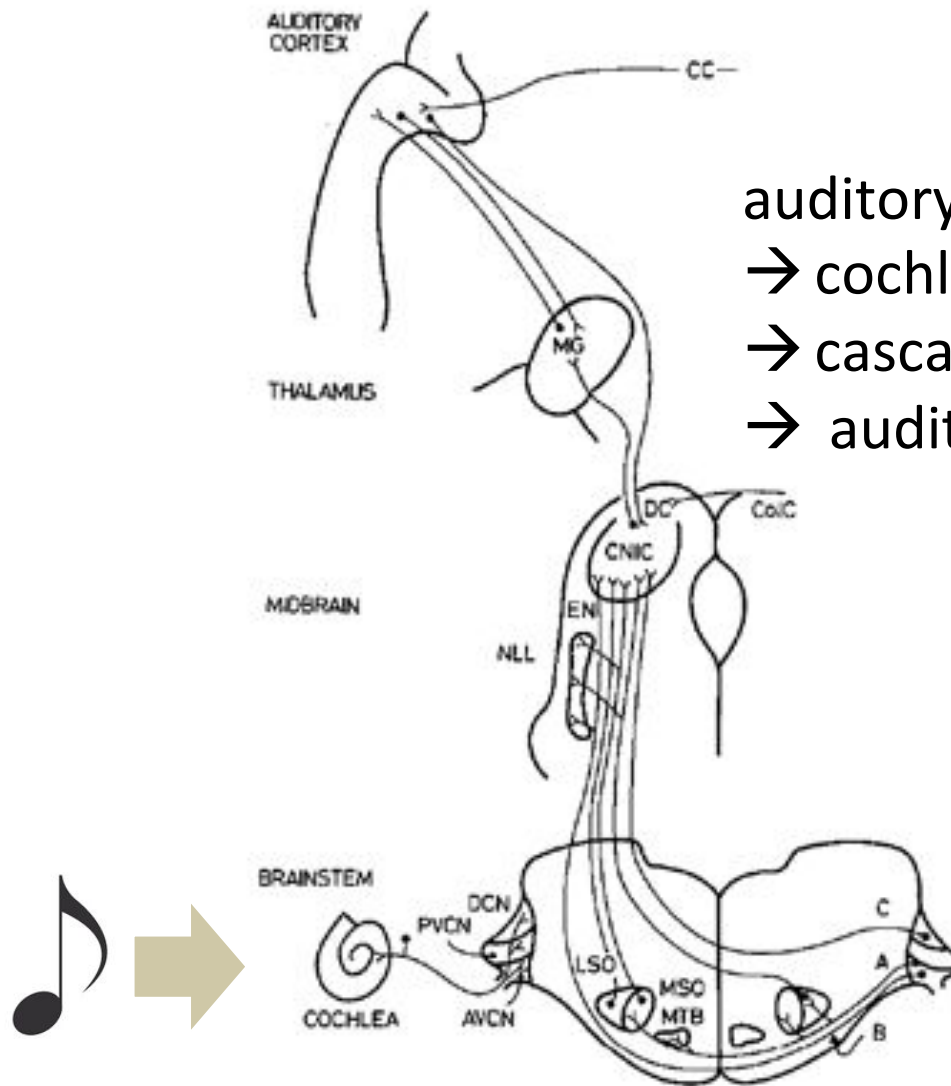
The problem is to find out a good estimate \mathbf{W} of \mathbf{A}^{-1}

$$\tilde{\mathbf{s}}(t) = \mathbf{W}\mathbf{x}(t)$$





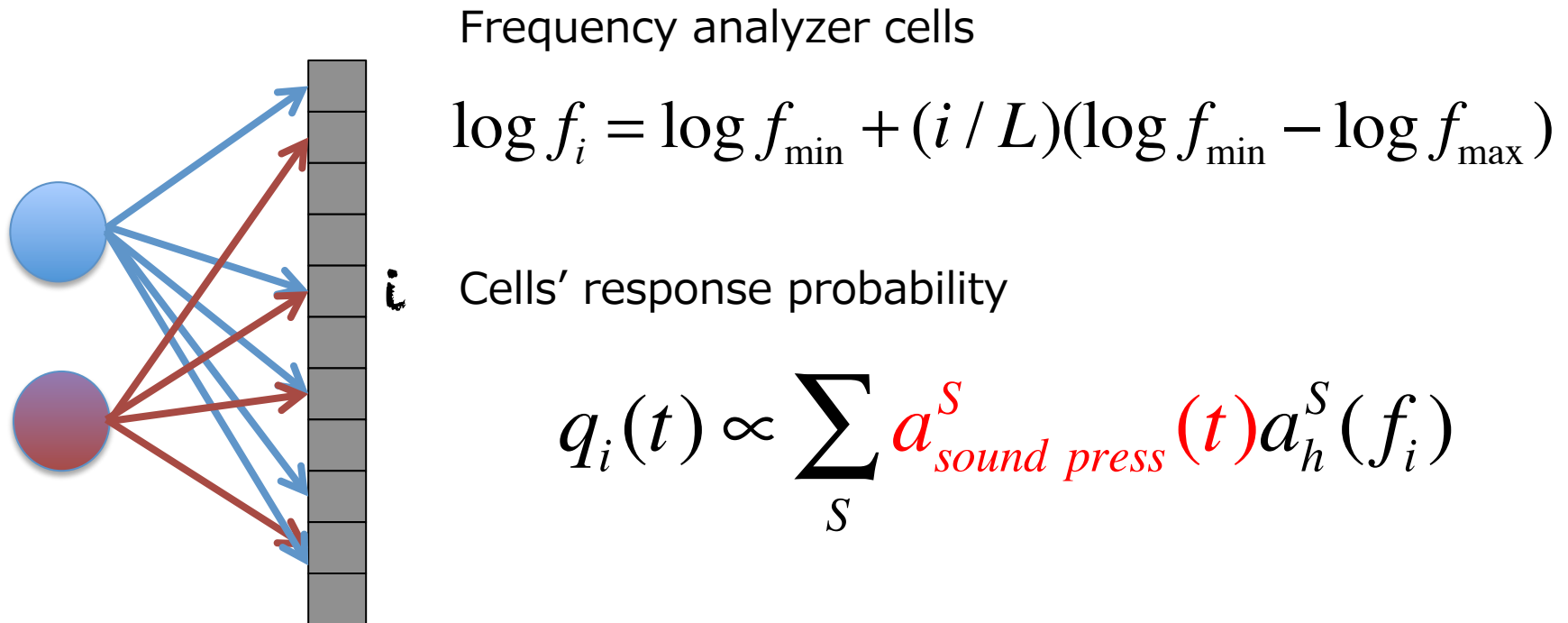
24 Organization of the subcortical auditory pathway



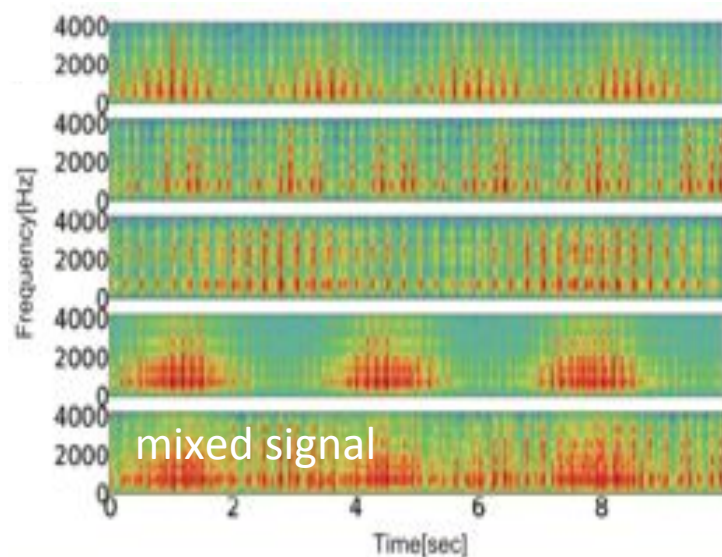
auditory signals
→ cochlear = frequency analyzer
→ cascade of thalamic nuclei
→ auditory cortex

Assumption in auditory information encoding

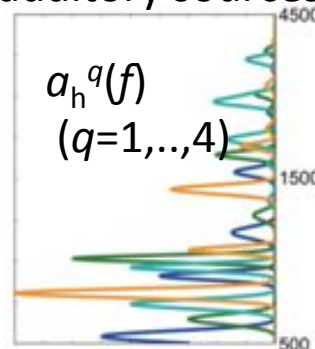
Frequency components belonging to the same auditory source exhibit larger spike correlations than components belonging to different sources.



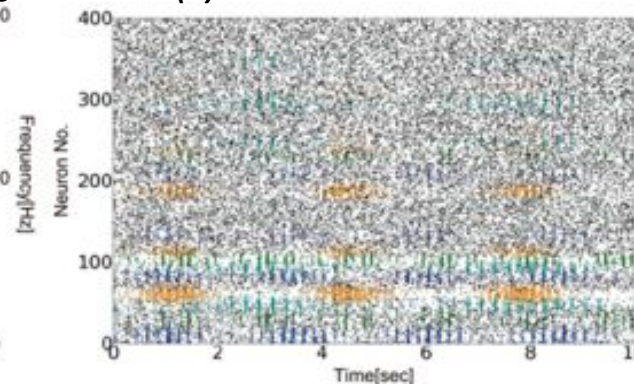
A solution to Cocktail Party Effect



Spectrums of auditory sources



$X(t)$

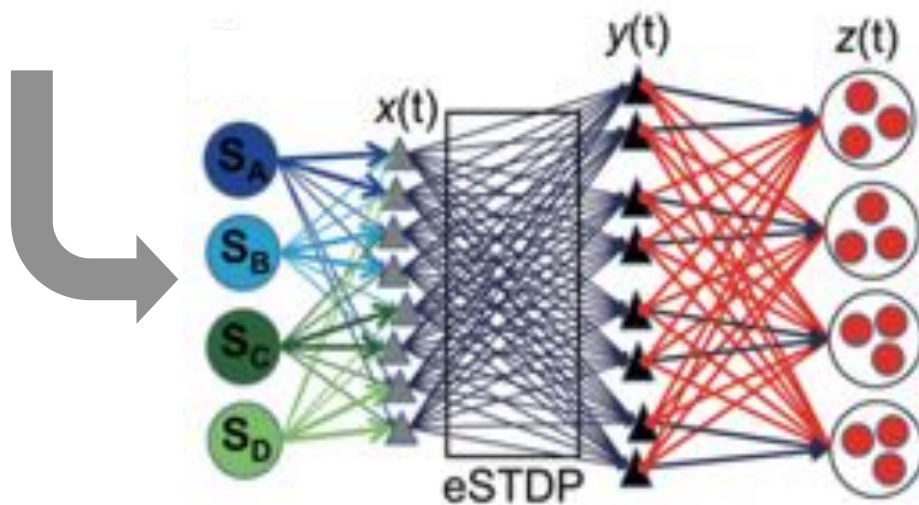


preferred frequency

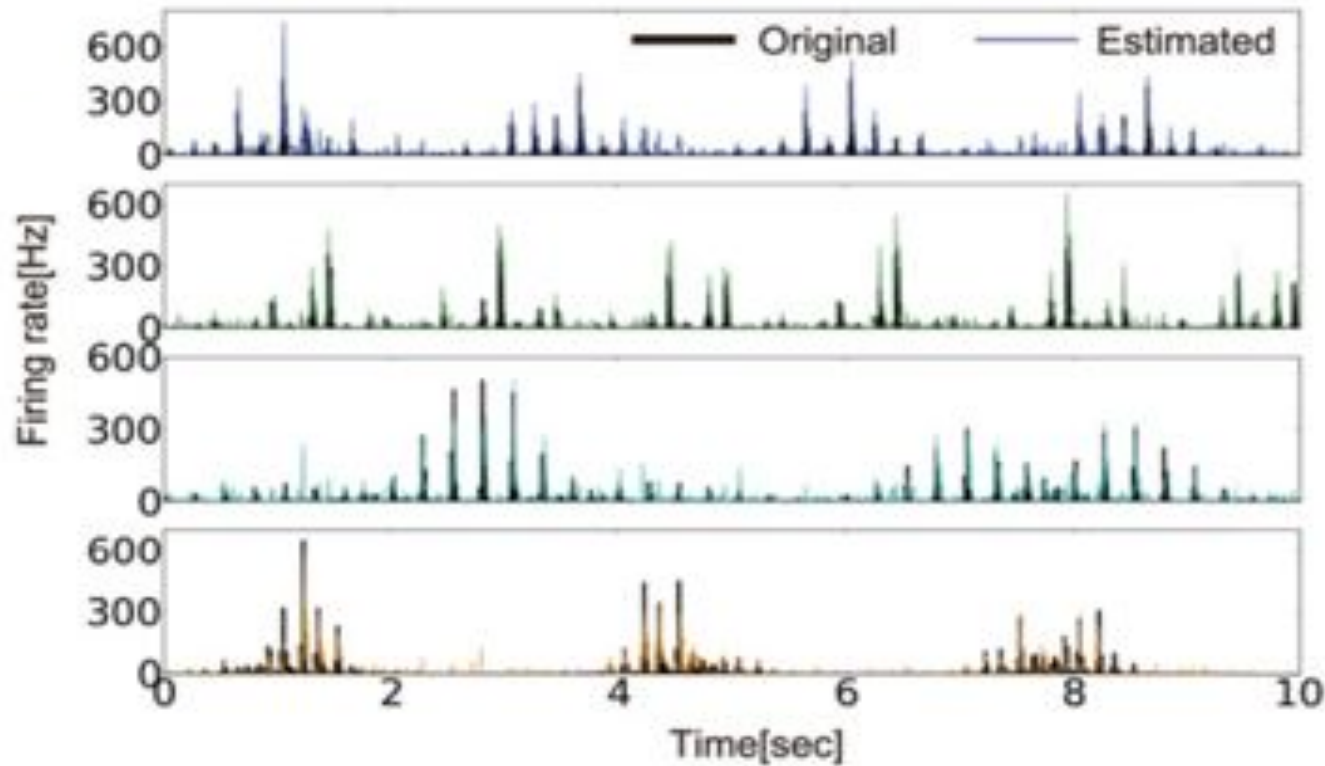
$$\log f_i = \log f_{\min} + (i / L)(\log f_{\min} - \log f_{\max})$$

Time-dependent response probability

$$q_i(t) = q_0 \sum_q a_{\text{sound press}}^q(t) a_h^q(f_i)$$



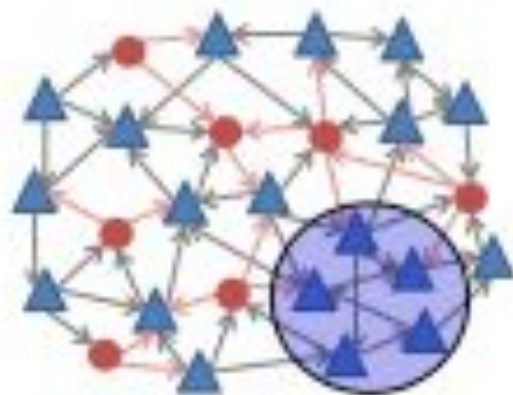
$$y(t)$$



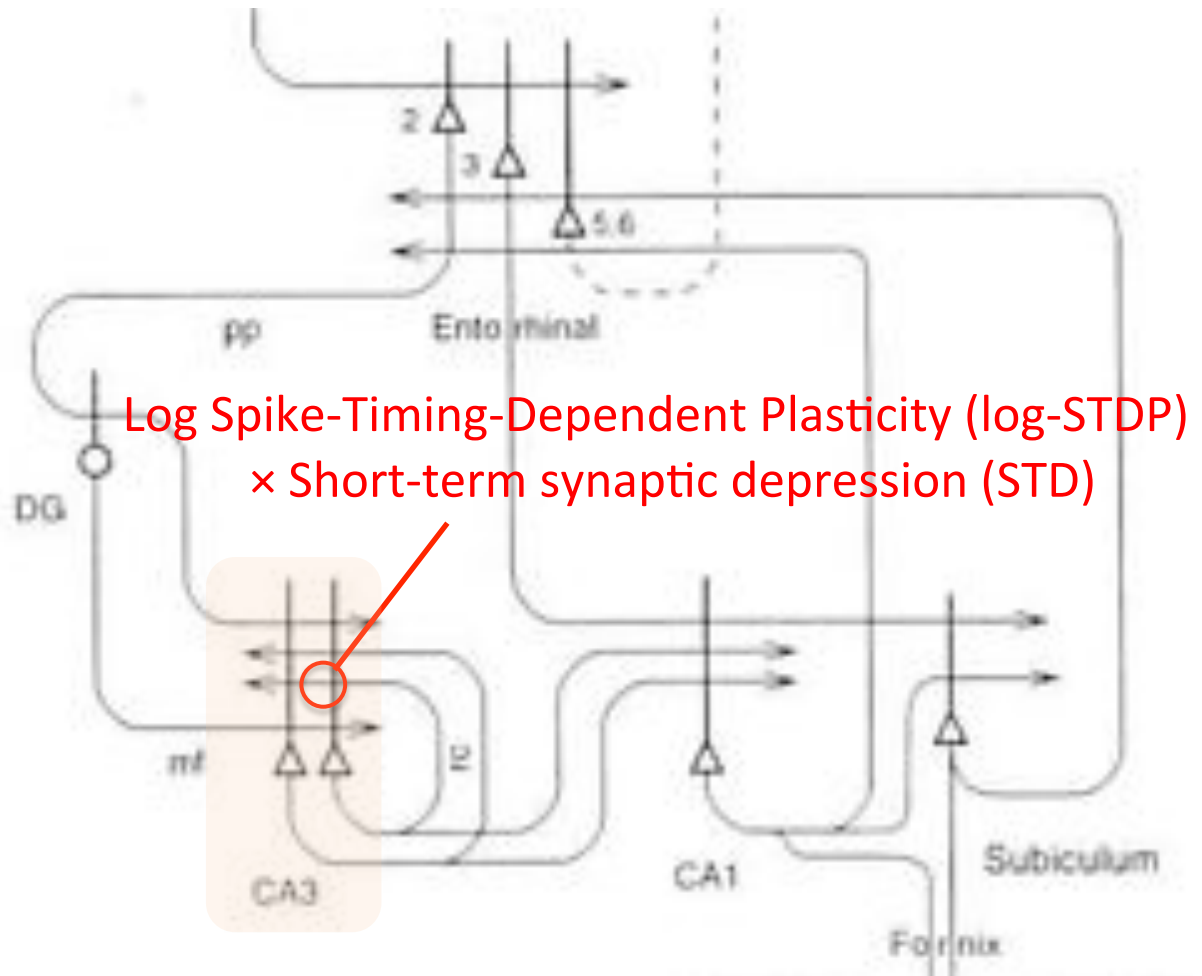
Spike correlations between different frequency channels may provide a cue to recombine independent signals.

Cell assembly formation/**maintenance**

Hippocampal memory traces are transformed into neocortical log-term memory about 4 weeks after learning experience.



External input
↗



Log-STDP (Gilson and Fukai, PLoS ONE, 2011)

Short-term depression (STD)

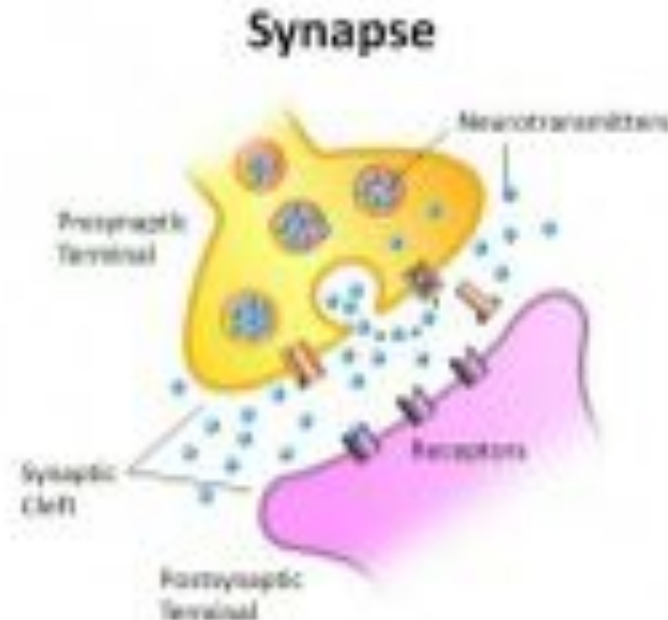
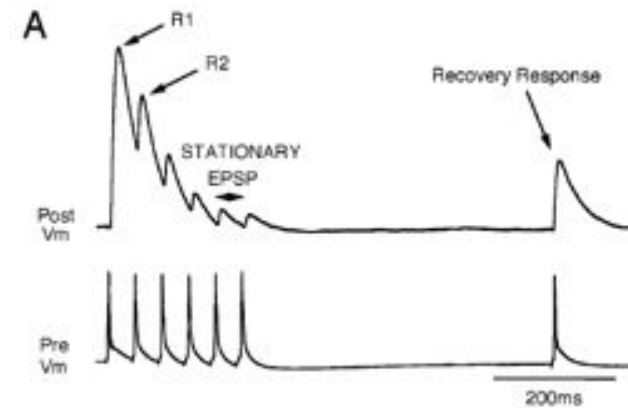
Neocortical pyr-pyr synapses:

Tsodyks and Markram, 1996

Abbott et al., 1997

CA3-CA3 synapses: Debanne et al., 1996

Saviane et al., 2002



Recycling dynamics of
presynaptic vesicles

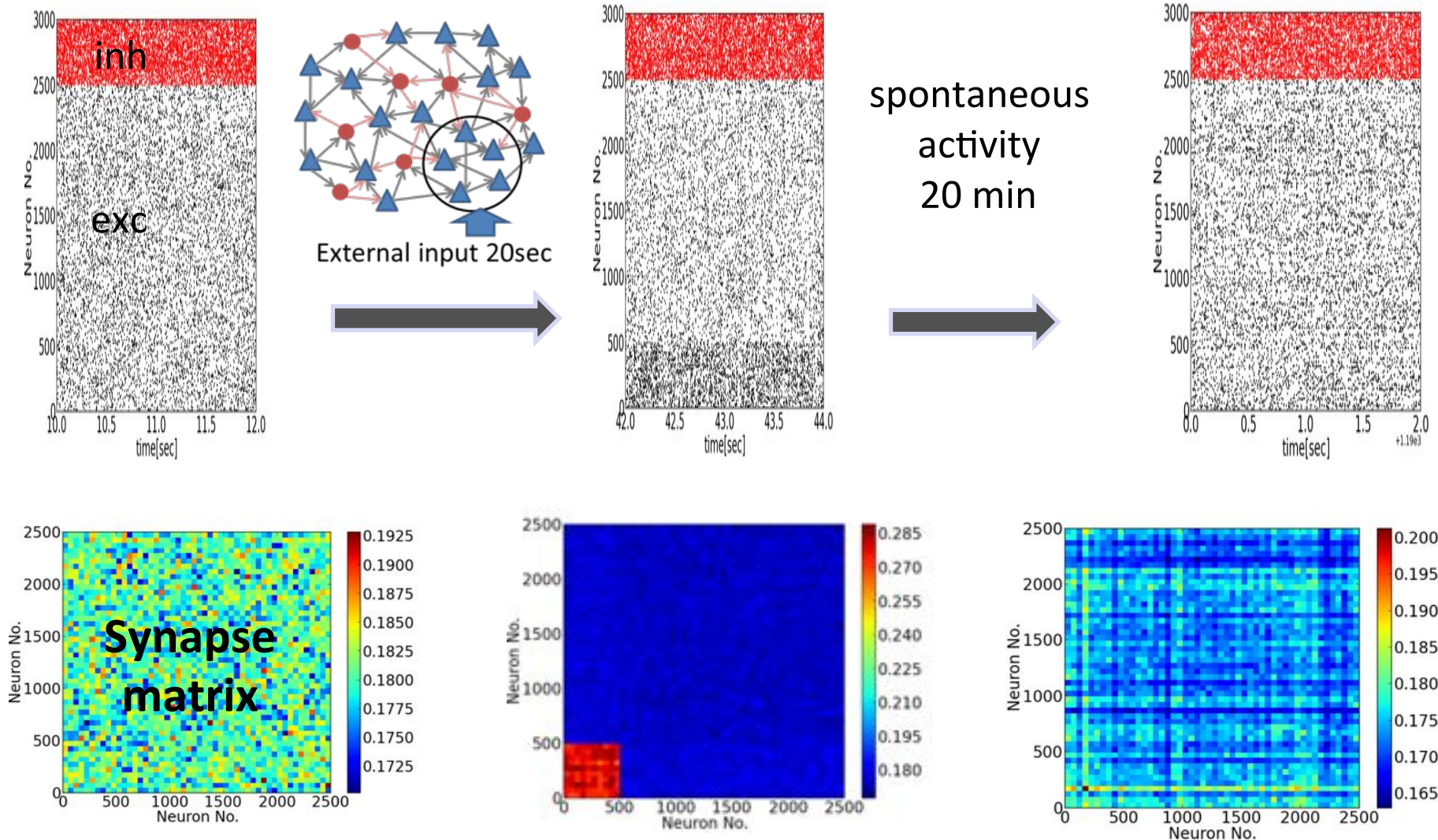
Release probability u

Time scale for recycling ≈ 1 sec

A cell assembly is unstable for strong STD

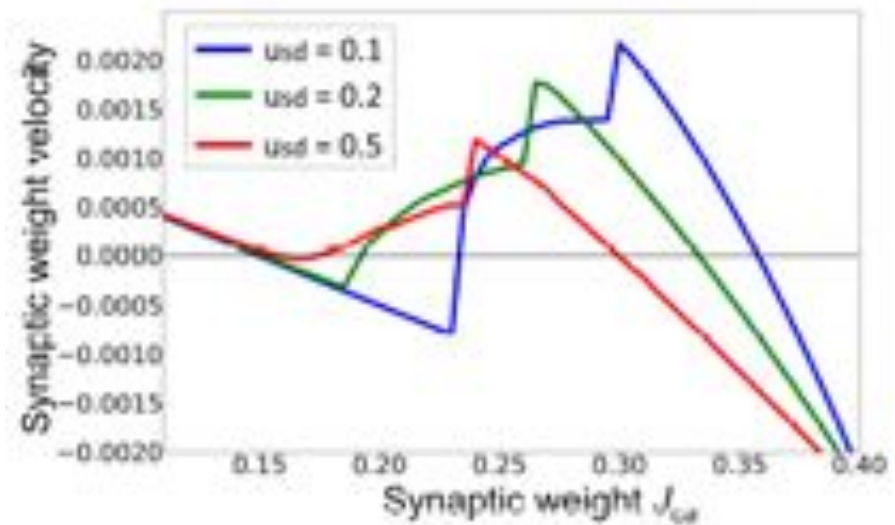
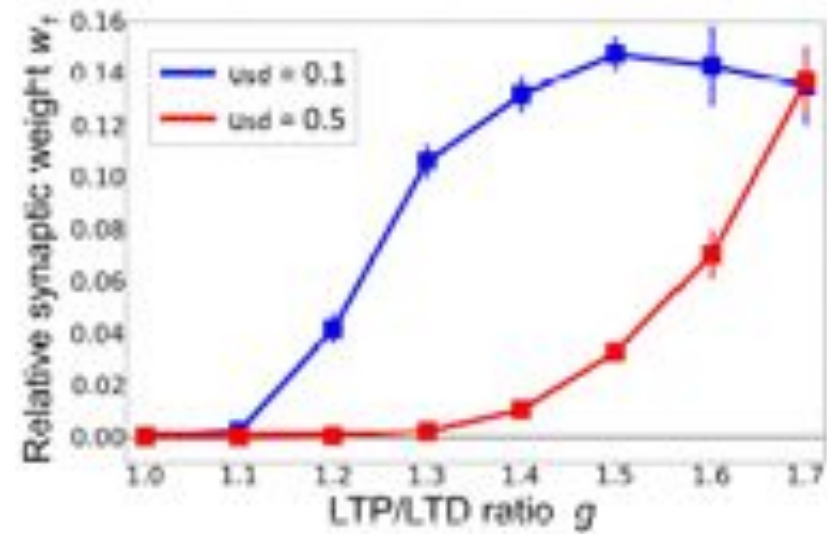
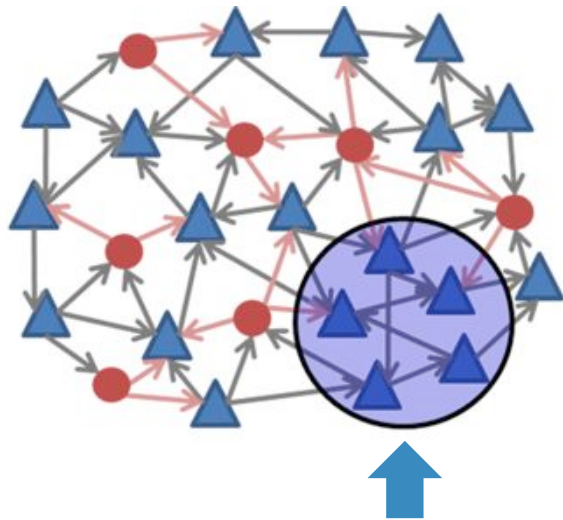
($u_{sd}=0.5$, $J_{EI}=0.155$)

(Hiratani and Fukai, PLoS One 2014)

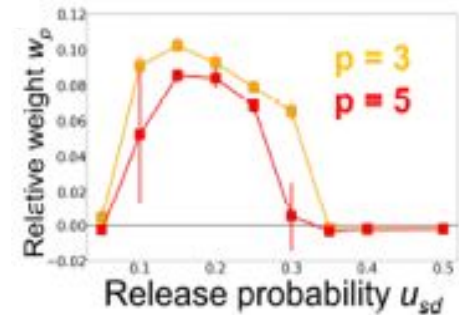
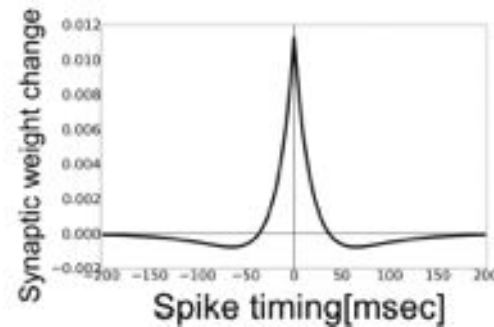
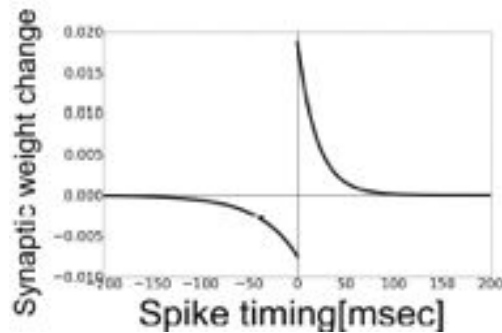


Stability of cell assembly crucially depends on STD

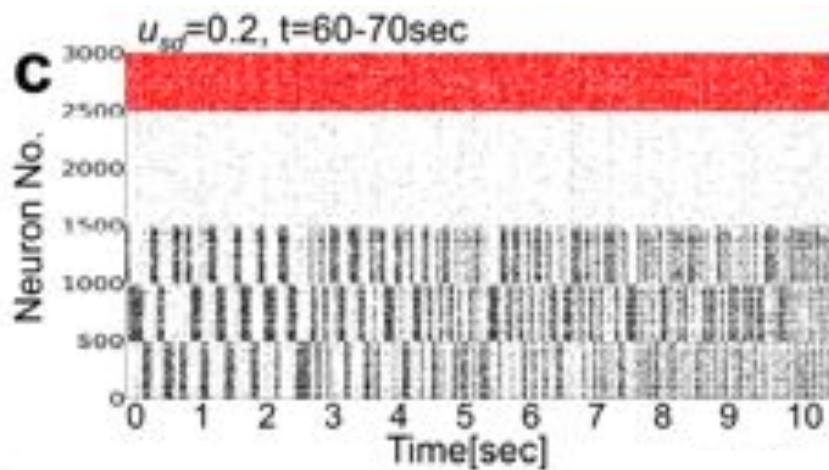
Mean-field analysis for $p=1$



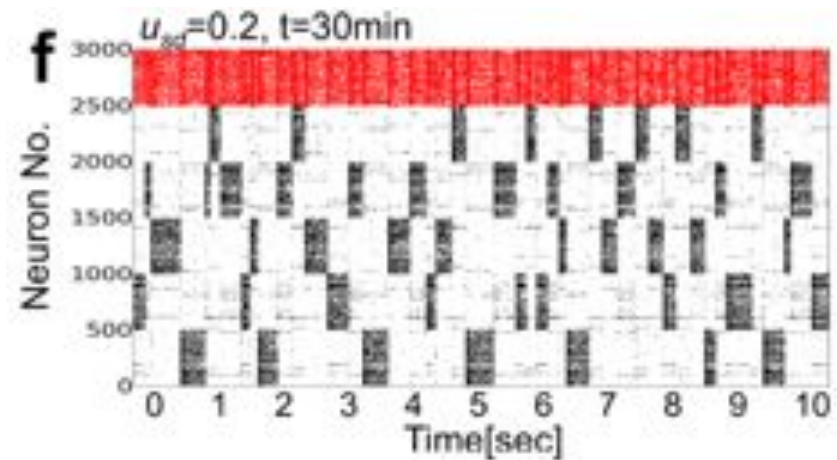
Symmetric STDP and modest STD stabilize multiple cell assemblies



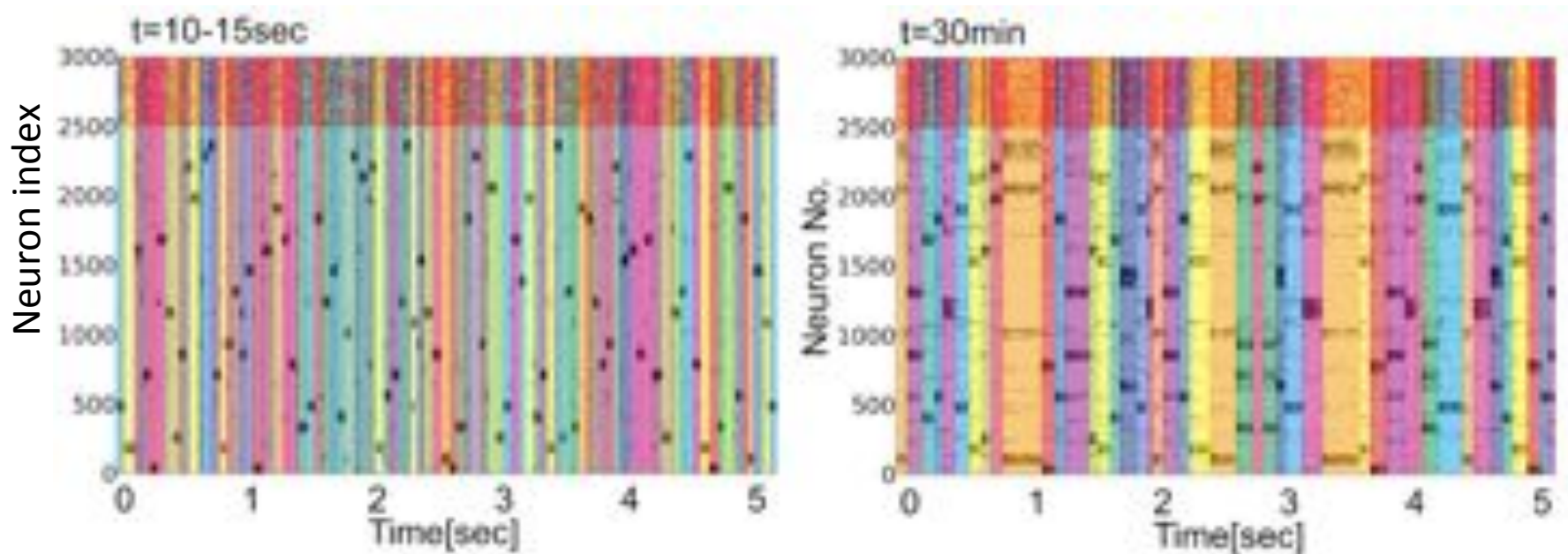
Transient synfire-like activity



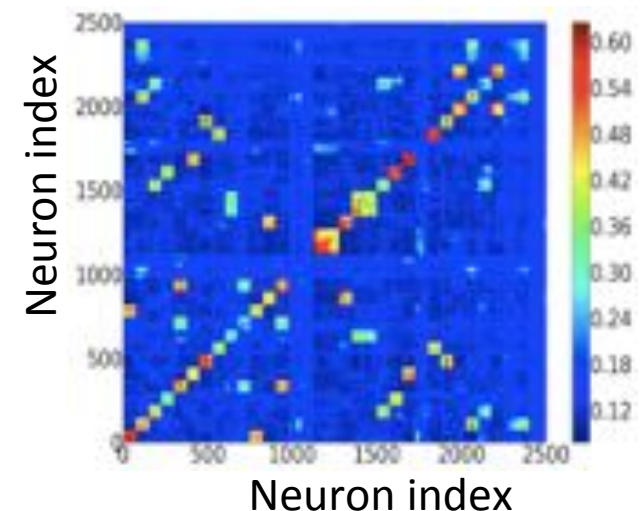
Stable irregular activity



Cell assemblies are dynamically reorganized during spontaneous firing



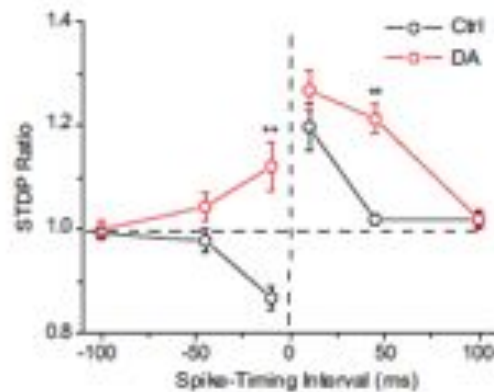
- Cell assemblies are most stable for moderate STD.
- A cell assembly with weak intra-connections tends to be eliminated.
- Multiple cell assemblies with strong initial interconnections tend to be merged.



symmetric STDP

1) dopaminergic modulations

Zhang et al., PNAS (2009)



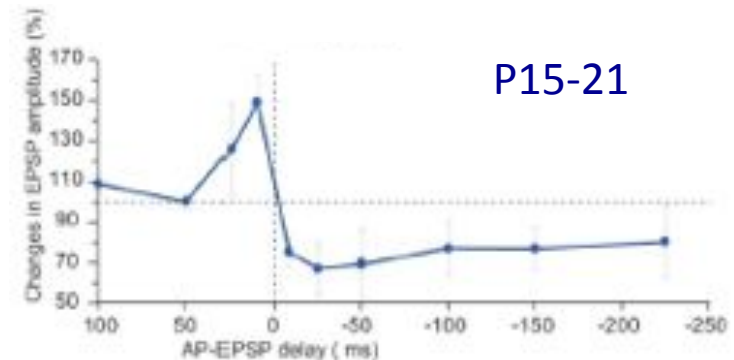
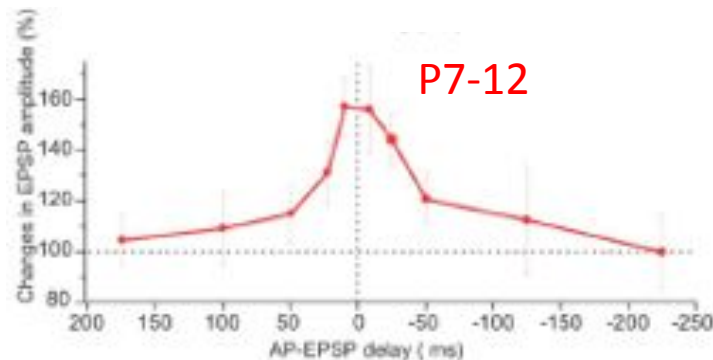
Schaffer collateral to CA1

D1-like DA receptor

NMDA dependent

2) during the development

Itami and Kimura, JNS (2012)

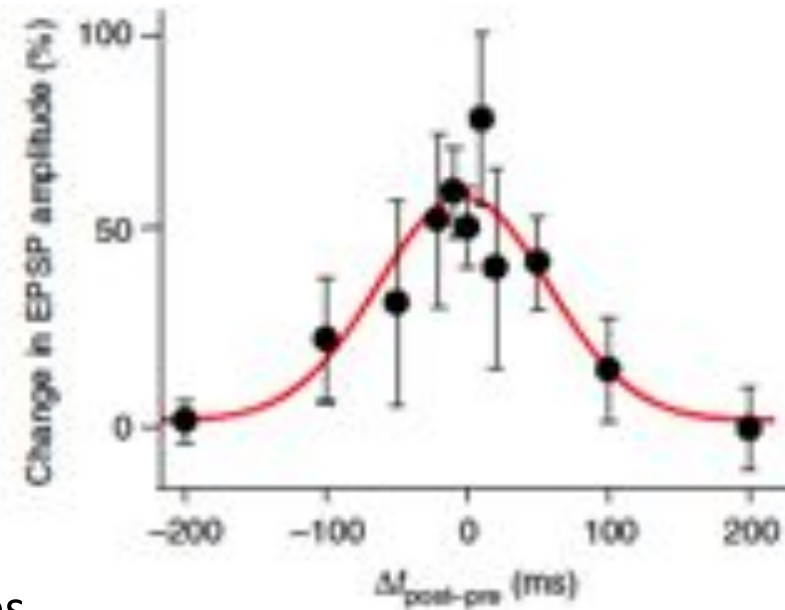
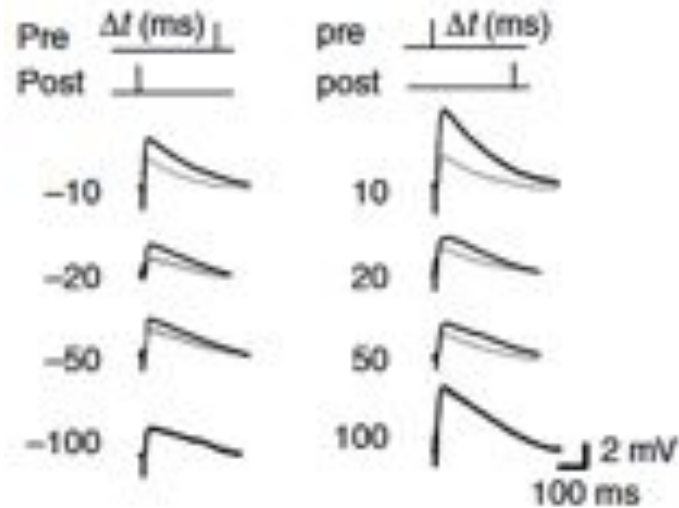


Rodent barrel cortex

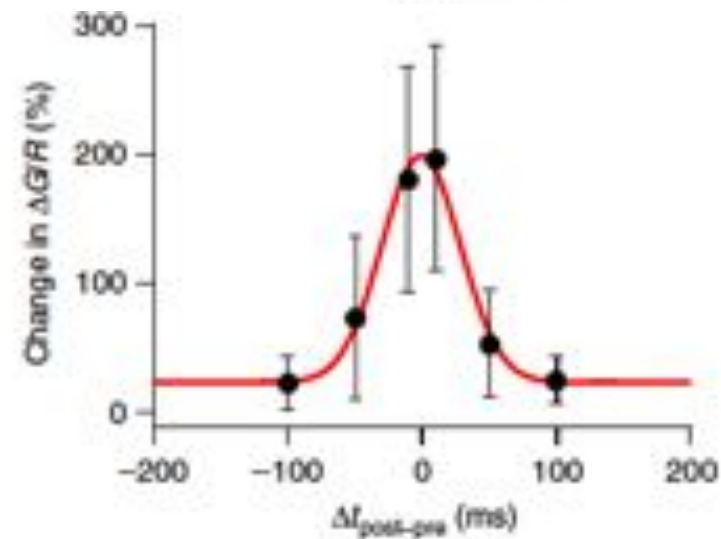
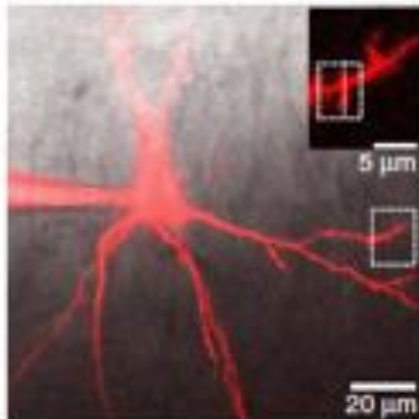
L4-L2/3 glutamate synapses

STDP at CA3-CA3 synapses is actually symmetric!

Mishra et al., Nat Comm (2016)



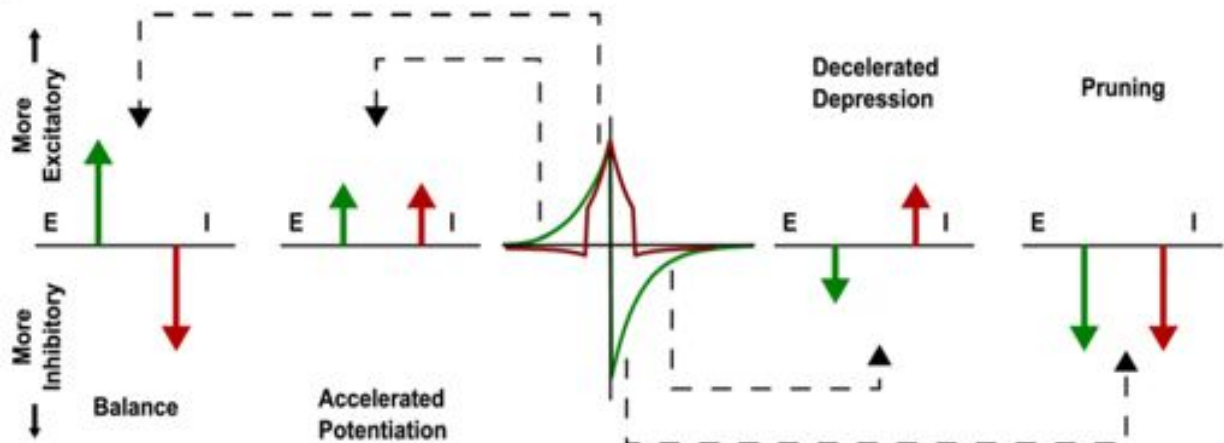
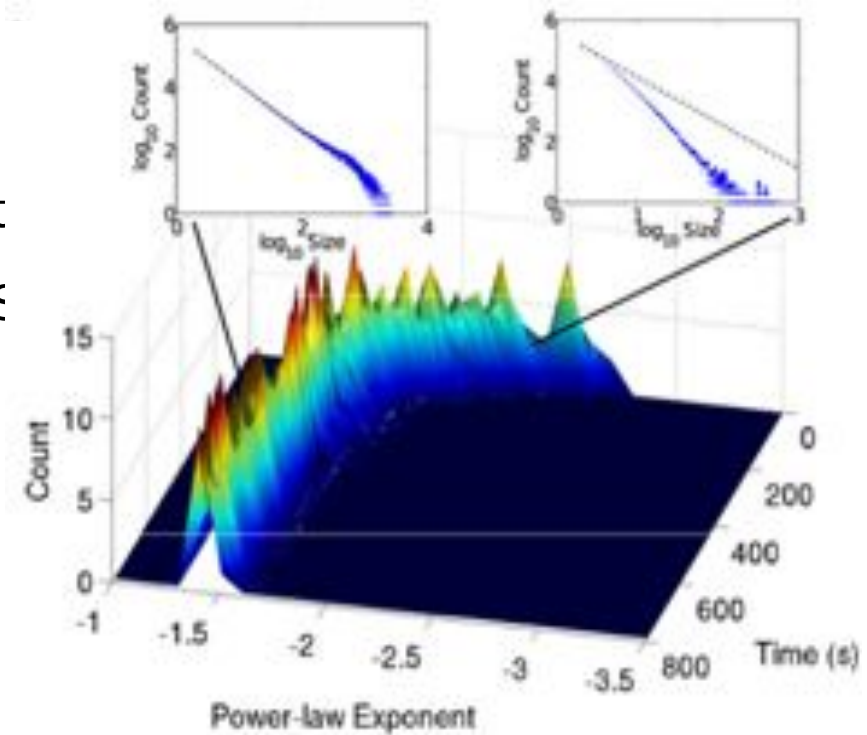
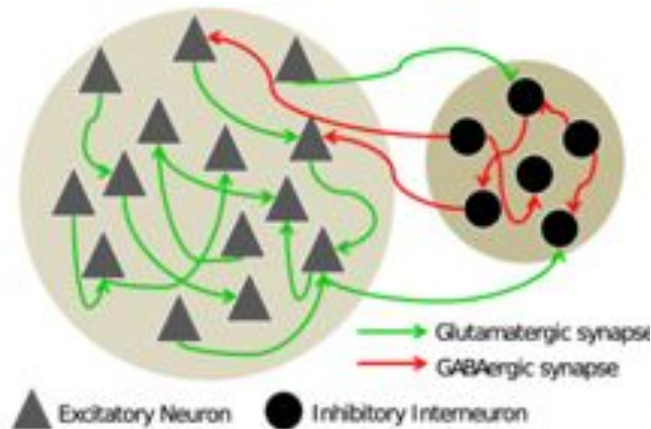
AP-induced Ca^{2+} transients in spines



Various plasticity rules have to orchestrate to maintain stable cell assemblies

Zenke, Agnes, Gerstner, Nat
Stepp, Plenz, Slinivasa, PLoS

...



Multiple cell assemblies can survive for moderate STD and symmetric STDP (recently shown in CA3).

Cell assemblies may interact with each other during spontaneous activity.

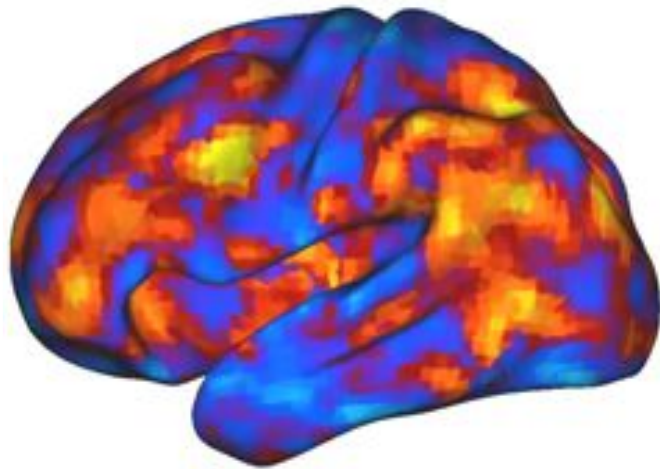
Bayesian computation

$$P(s | X) = \frac{P(X | s)P(s)}{\sum_s P(X | s)P(s)}$$

s 

prior $P(s)$ ~ the internal model of external world
~ spontaneous brain activity

(Berkes et al., Science 2011)



The brain is spontaneously cycling through distributed patterns of activity, which mimic activity patterns associated with sensory, motor, or cognitive events.

Vincent et al., J Neurophysiol (2006)



Questions

Q1. How is Bayesian computation implemented by neural circuits?

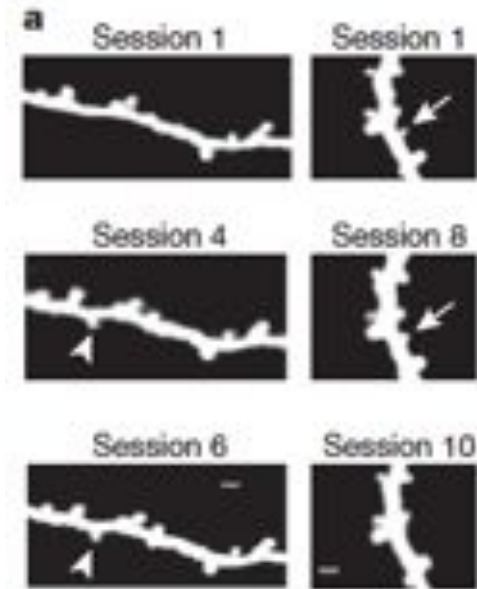
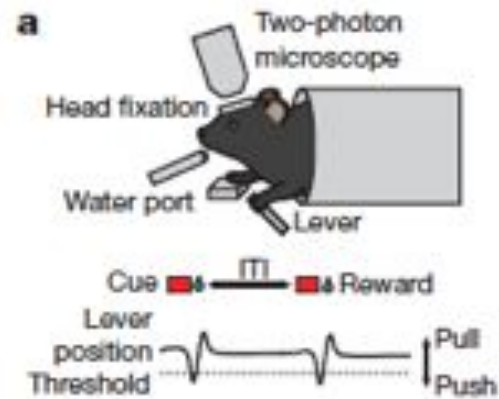
Q2. Can structural plasticity help this computation?

(Riken CDB)

Experience creates/eliminates spines in behaving animals

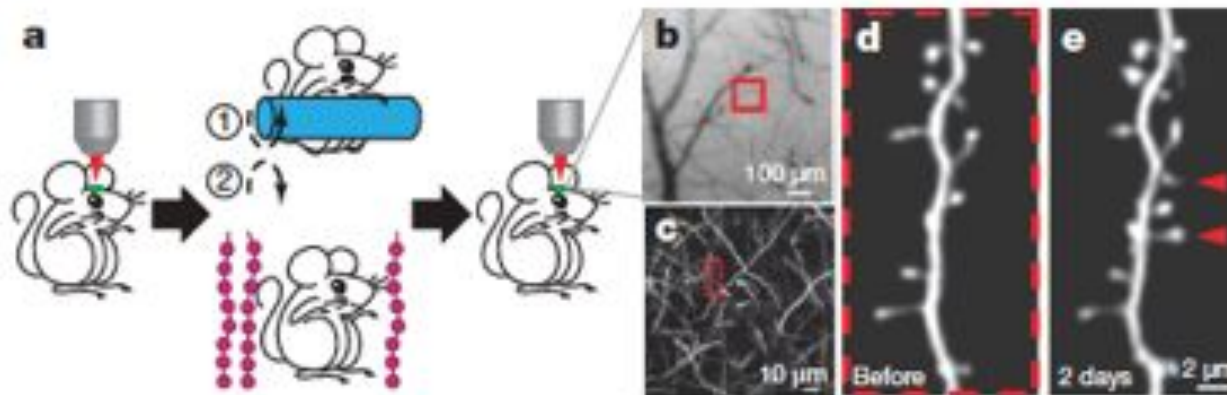
Peters et al., Nature 2014

Motor cortex, layer 2/3



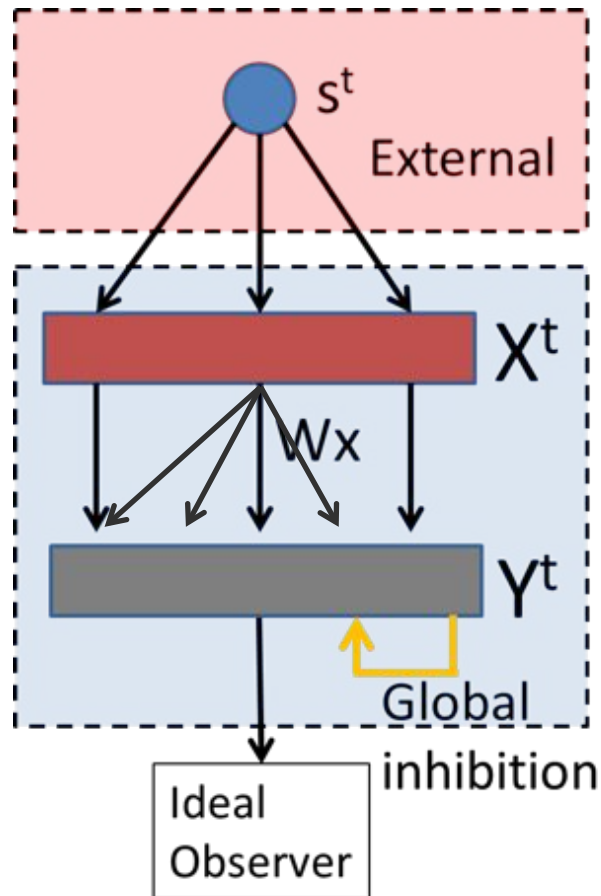
Motor cortex, layer 5

Yang et al., Nature 2014



Neural network for estimating hidden variables

Hiratani and Fukai, Front Neural Circuits, 2016



An external stimulus s^t obeys:

$$s^t \leftarrow p_s(s) \quad \text{S takes 10 discrete states}$$

s_1, s_2, \dots, s_{10}

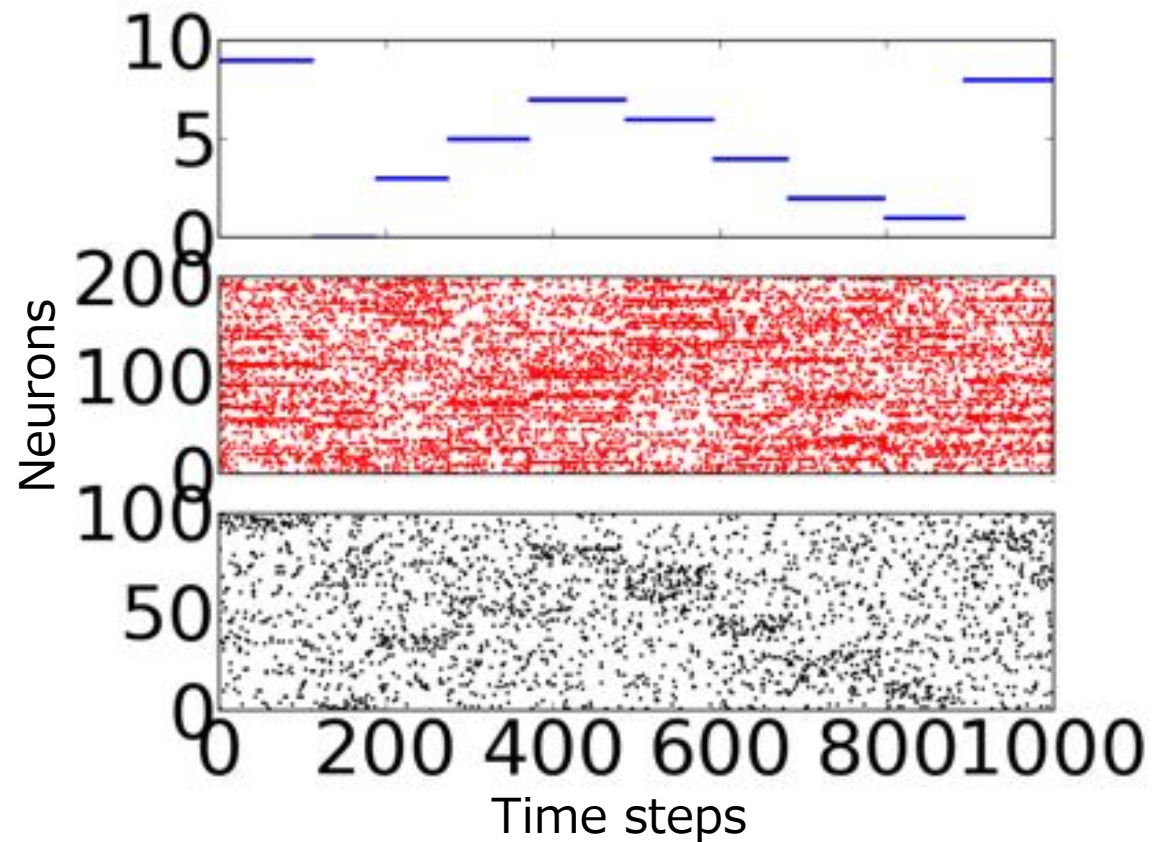
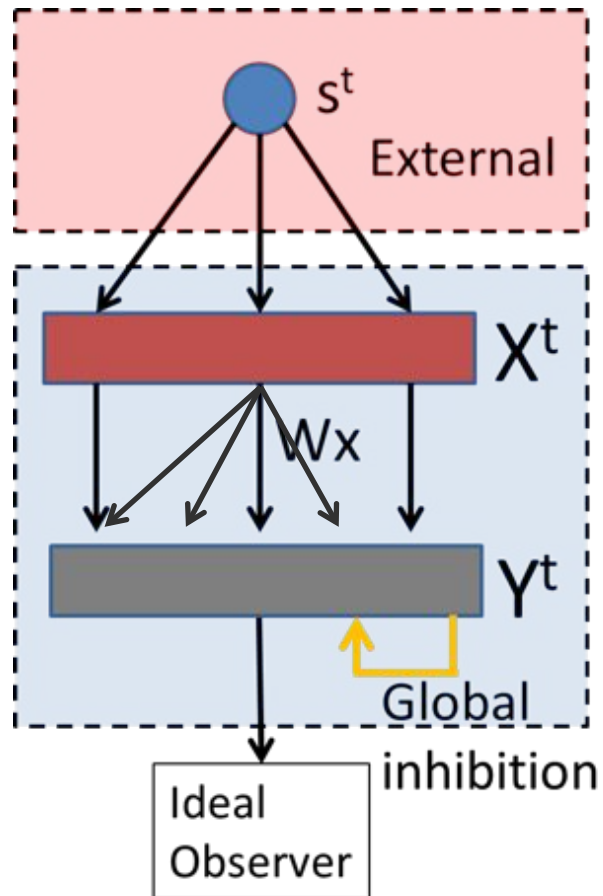
Input-layer neurons receiving the stimulus generate Poisson spike trains with firing probability:

$$\text{Prob}[X_j^t = 1 | s^t = s_\mu] = q_{j\mu}^*$$

An ensemble of Y cells self-organizes to decode some stimulus.

$$Y_i^t \propto p(s^t = s_{\sigma_i} | \mathbf{X}^t)$$

Pre-learning network responses

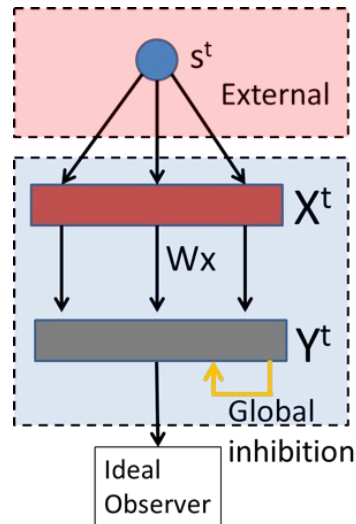


Y cells are sorted according to their response patterns.

Y cells should maximize

$$\log p(s^t = s_\mu | \mathbf{X}^t) = \log p(\mathbf{X}^t | s^t = s_\mu) + \log p(s^t = s_\mu) - \log p(\mathbf{X}^t)$$

Bayes formula



Firing probability

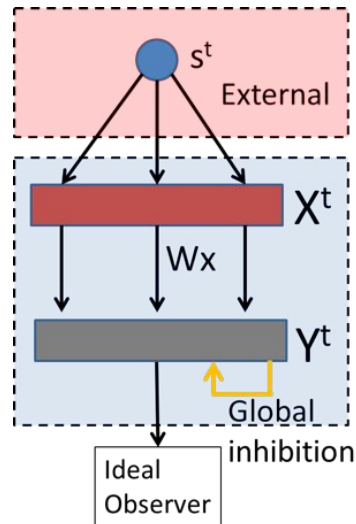
$$\log p(\mathbf{X}^t | s^t = s_\mu) \cong \sum_{j=1}^M \log(q_{j\mu}^*) X_j^t$$

$$= \sum_{j=1}^M \rho_{j\mu} w_{j\mu} X_j^t$$

$\rho_{\mu j}$:connection probability from X to Y for pattern μ

w_{ij} :synaptic weight from X_j to Y_i

membrane potentials of Y cells



$$v_i^t = \log p(s^t = s_\mu | \mathbf{X}^t) = \sum_j \rho_{\mu j} w_{ij} X_j^t + \alpha_\mu - I^t$$

$$\alpha_\mu = \log p(s^t = s_\mu) \quad \text{:prior distribution}$$

$$I^t = \log \left(\sum_\mu \exp \left[\sum_j \rho_{\mu j} w_{\mu j} X_j^t + \alpha_\mu \right] \right)$$

:global inhibition (normalization)

Learning rules for structural and non-structural plasticity

$$\log p(\mathbf{W}, \rho \mid \mathbf{X}^{1:T}) = \log p(\mathbf{X}^{1:T} \mid \mathbf{W}, \rho) + \log p(\mathbf{W} \mid \rho) + \log p(\rho) + c$$

Maximization with respect to synaptic weights and connection probabilities give dual Hebbian rules:

$$\Delta w_{ij} = \eta_w \left[Y_i^t \left(\rho_{ij} X_j^t - \rho_0 q_{\min} e^{\rho_0 w_{ij}} \right) - b_p (w_{ij} - 1) \right]$$

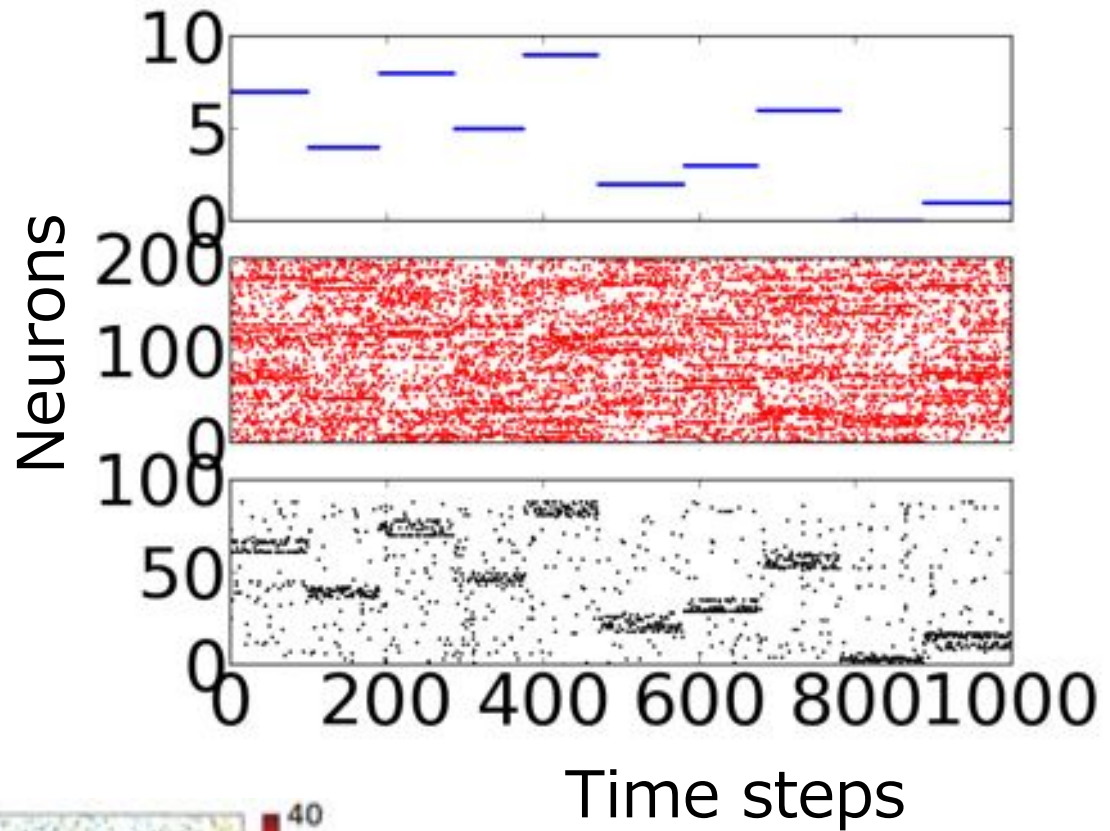
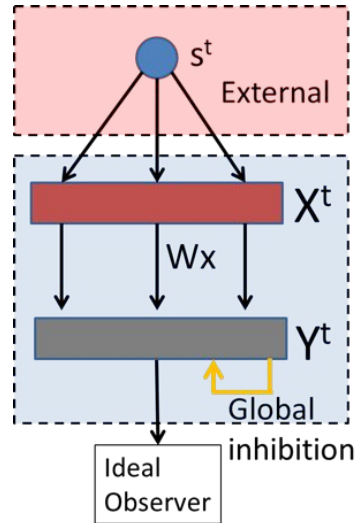
$$\Delta \rho_{ij} = \eta_c \left[Y_i^t \left(w_{ij} X_j^t - w_0 q_{\min} e^{\rho_{ij} w_0} \right) \right]$$

c.f. Kappel et al., Maass, PLoS Comput Biol (2015).

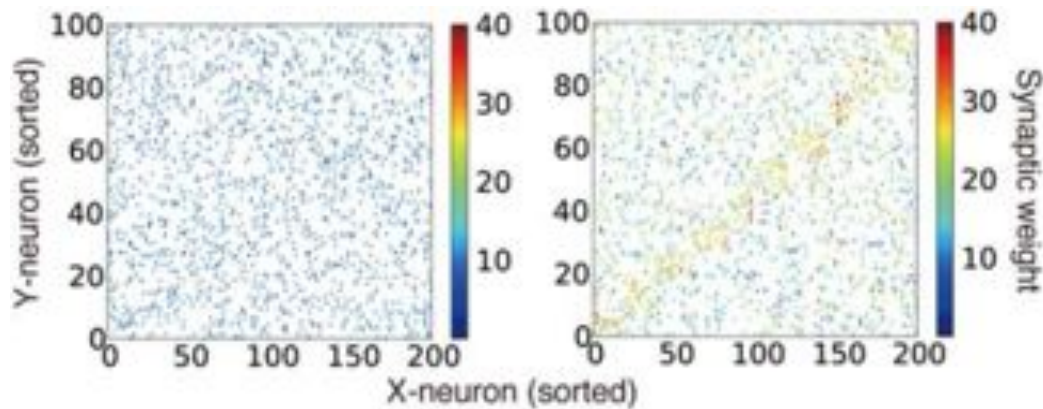
Synapses are randomly rewired at the rates of creation and elimination satisfying a detailed balance:

$$(1 - \rho_{ij})c(\rho_{ij}) = \rho_{ij}e(\rho_{ij})$$

Post-learning network responses



matrix W



Structural plasticity improves Bayesian computation if it is appropriately slow.

