計算神経科学ーモデルと解析

第二回：「学習」を表現する数式

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理化学研究所 脳科学総合研究センター

Activity-dependent plasticity

Hebbian plasticity

The interplay between activity and connectivity

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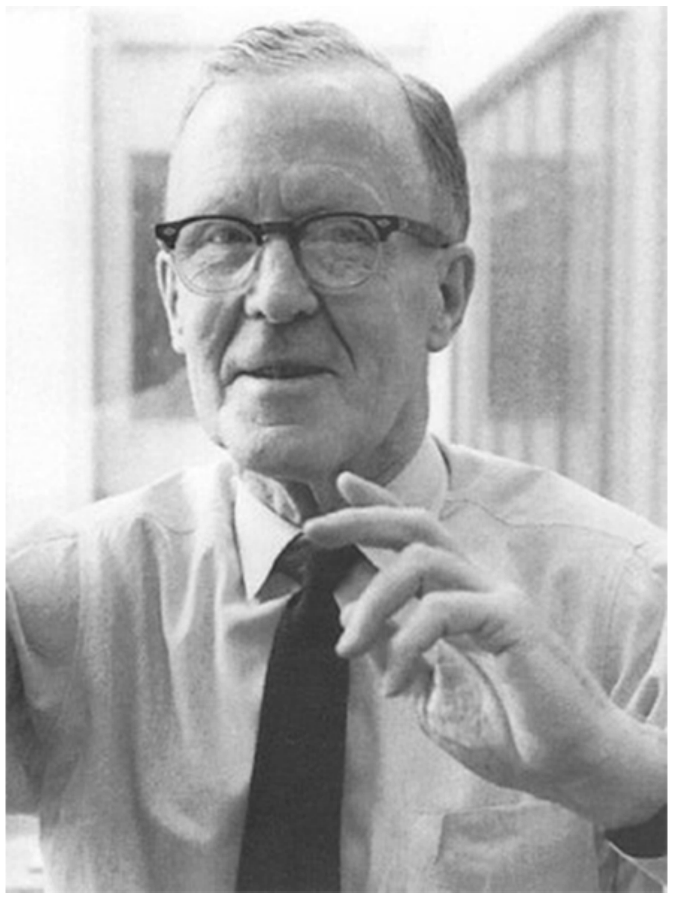
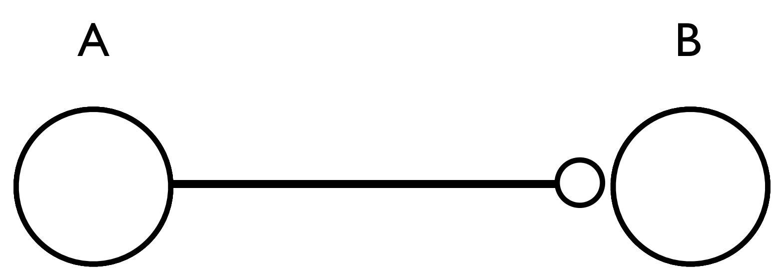


Donald Hebb

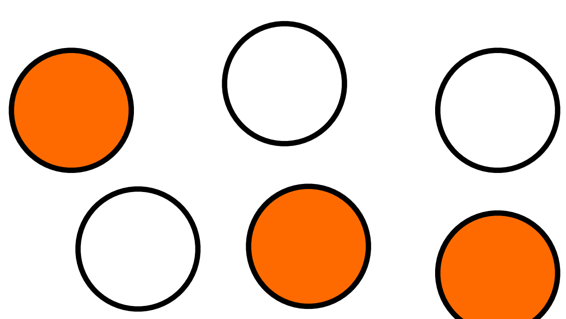
Markram et al. (2011) A history of spike-timing-dependent plasticity, Frontiers in Synaptic Neuroscience 3: 4, p. 6 Fig. 4: Donald Hebb. http://journal.frontiersin.org/article/10.3389/fnsyn.2011.00004/full

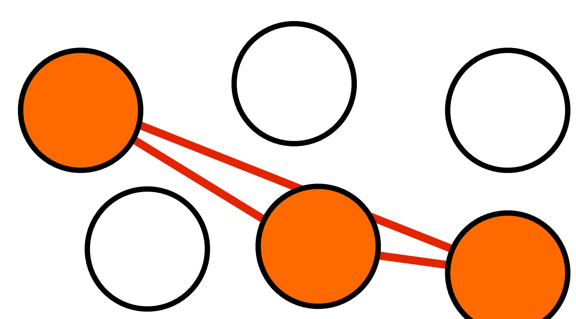
The Organization of Behavior (1949)

When an axon of cell A is near enough to excite cell B and repeatedly or persistently takes part in firing it, some growth process or metabolic change takes place in one or both cells such that A's efficiency, as one of the cells firing B, is increased

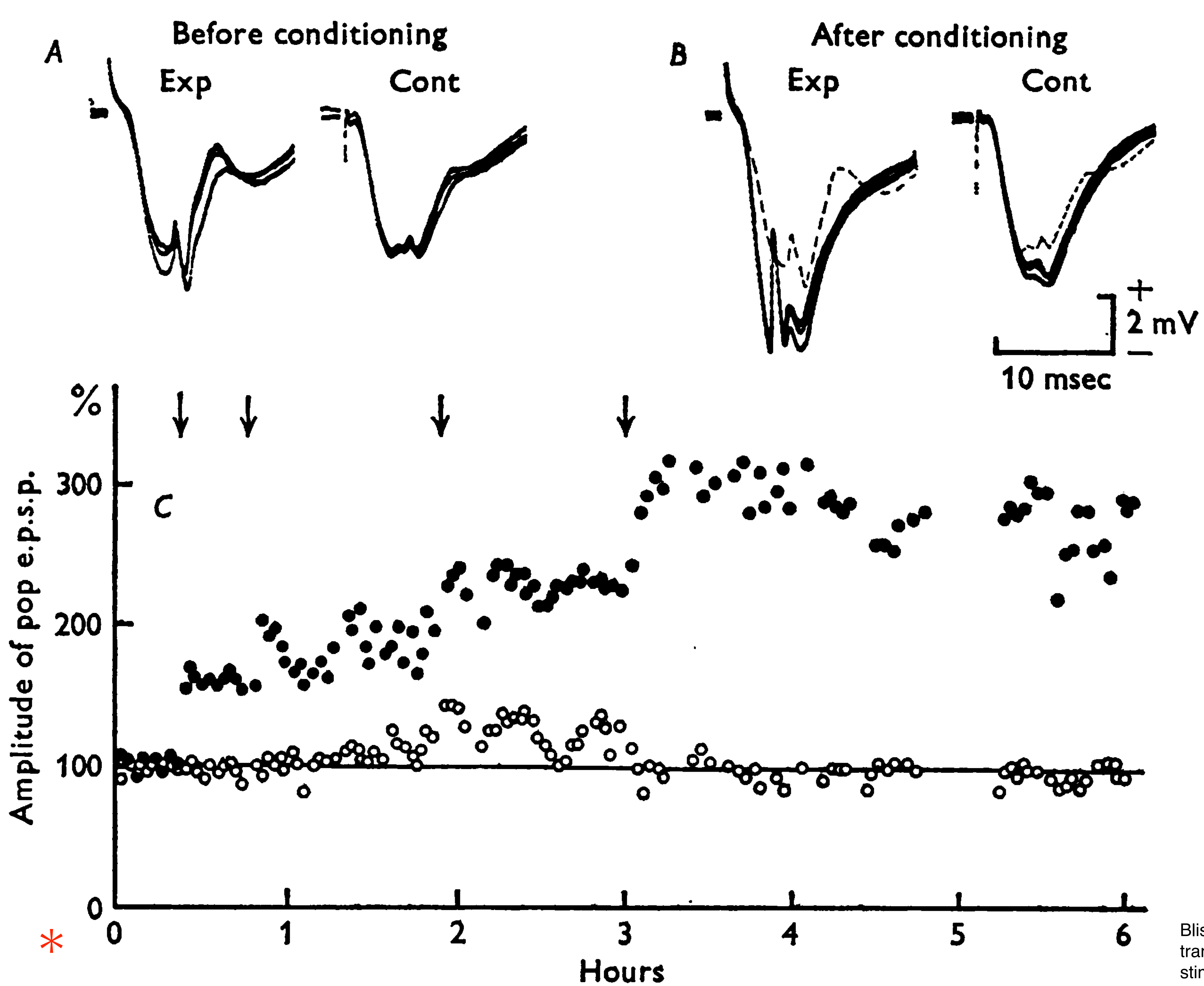


"Neurons that fire together wire together." → "cell-assemblies"



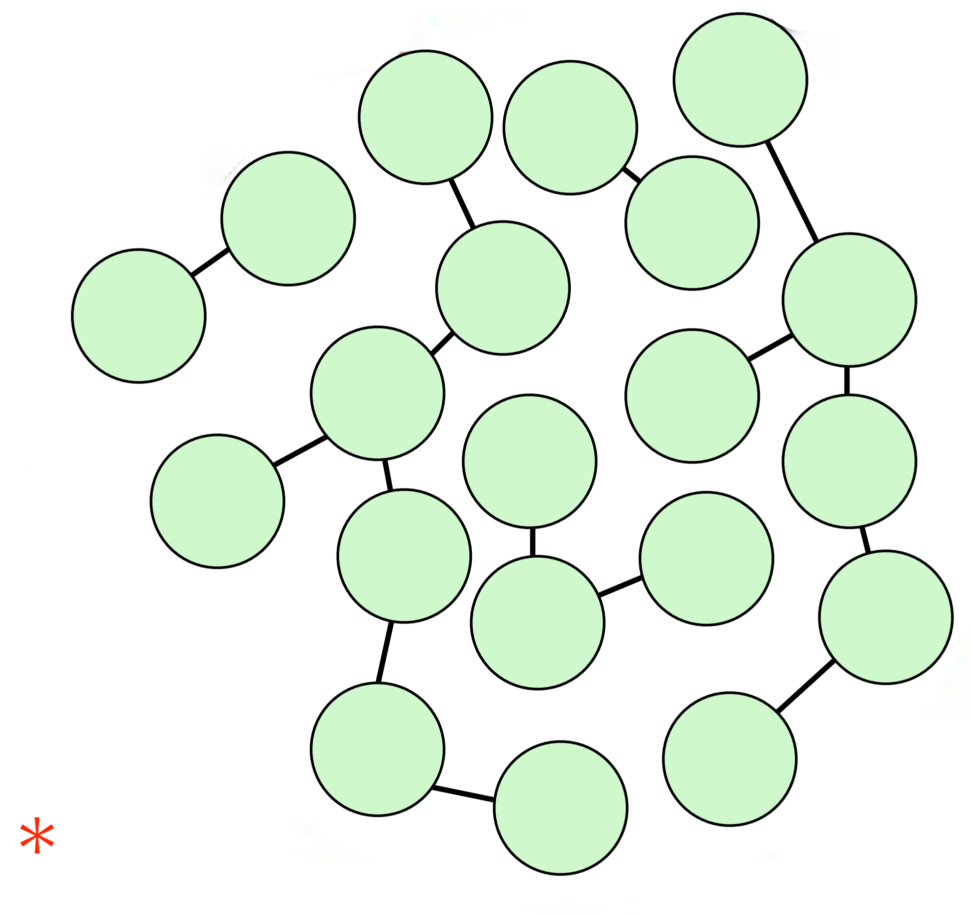


The discovery of long-term potentiation (LTP)



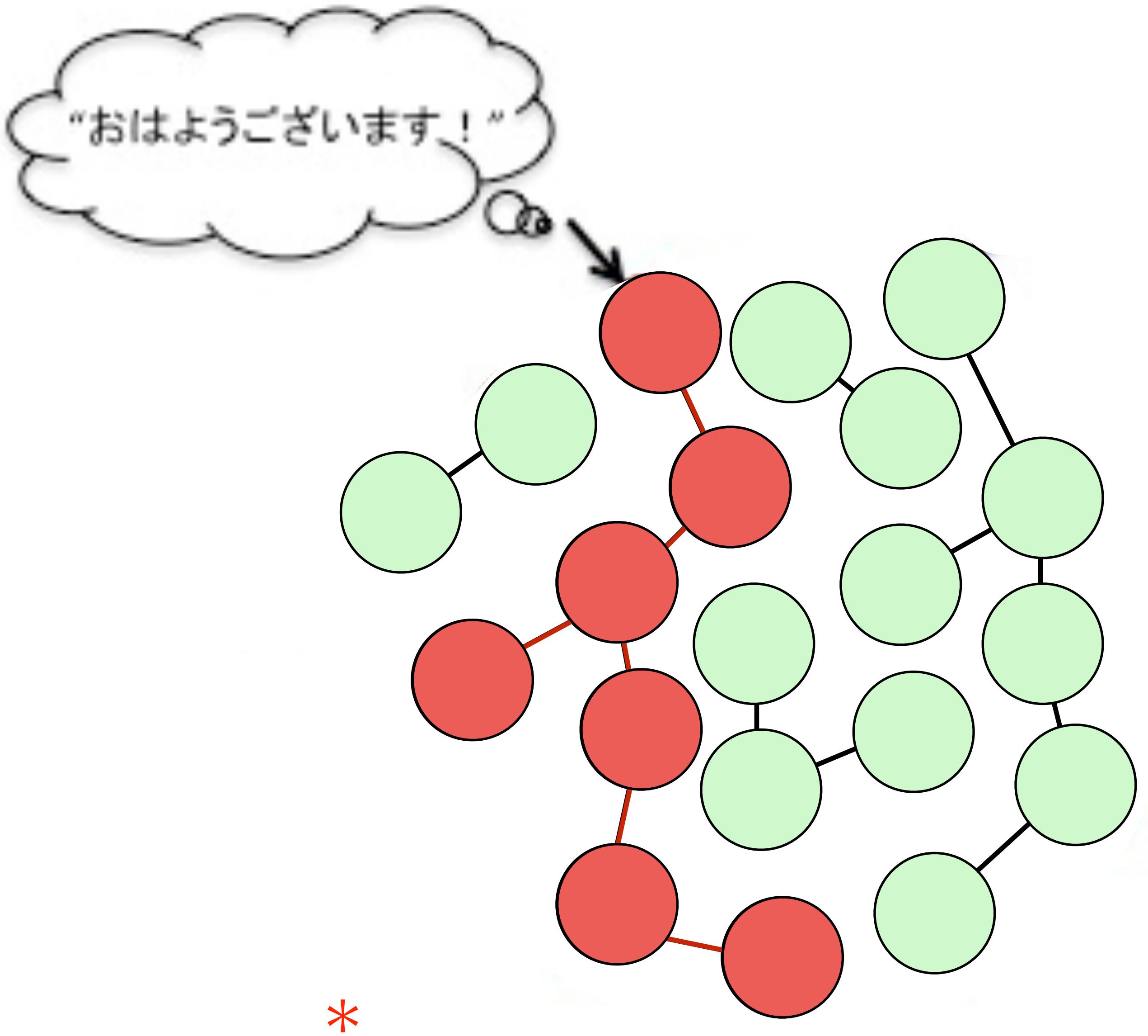
Bliss and Lømo (1973) Long-lasting potentiation of synaptic transmission in the dentate area of the anaesthetized rabbit following stimulation of the perforant path, The Journal of Physiology 232 (2): 331–356,p. 339 Fig. 4: An experiment in which all three standard parameters of the evoked response were potentiated. http://onlinelibrary.wiley.com/wol1/doi/10.1113/jphysiol.1973.sp010273/abstract

Associative memory and Hebbian plasticity



http://www.riken.jp/pr/press/2014/20141023_1/

Associative memory and Hebbian plasticity



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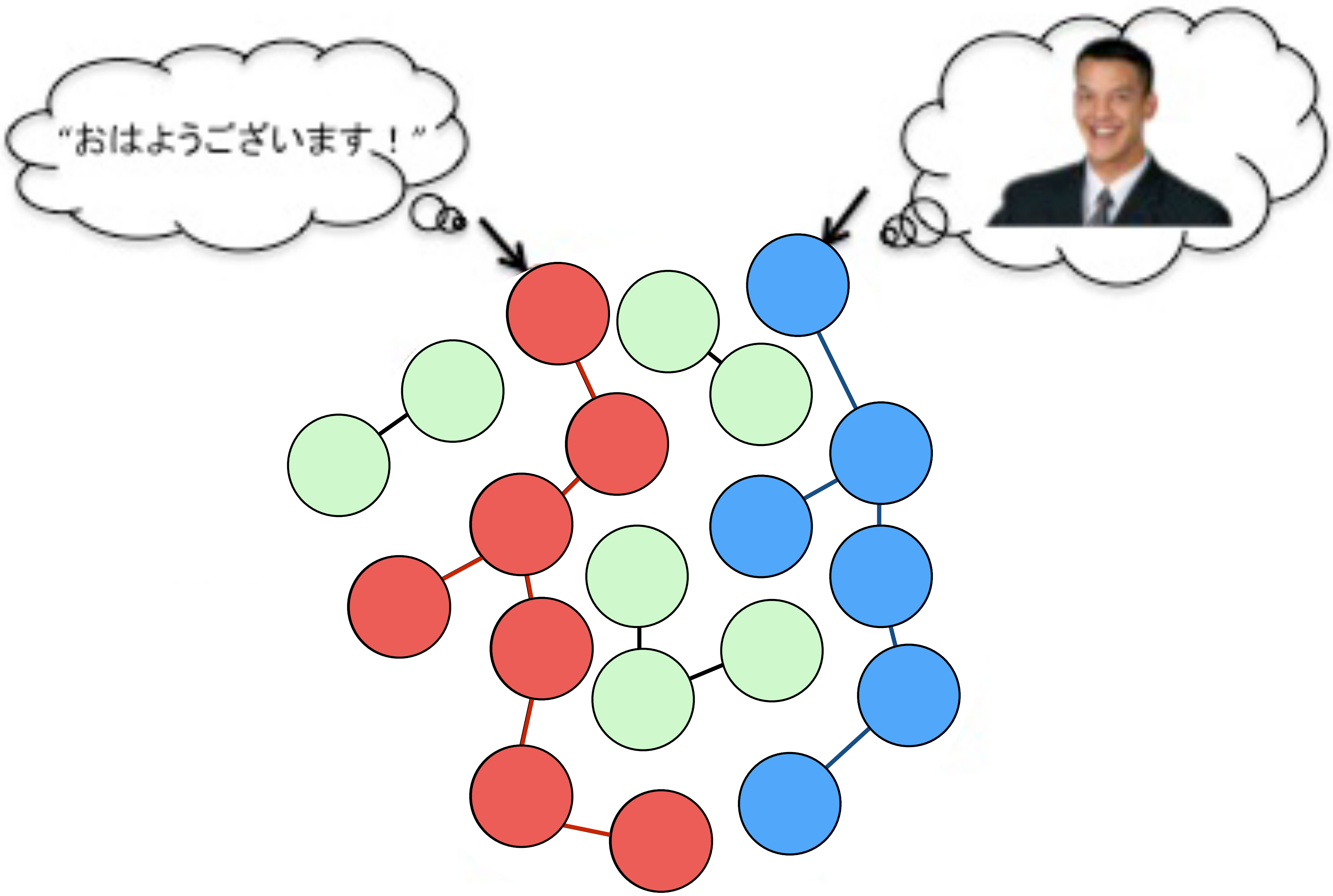
http://www.riken.jp/pr/press/2014/20141023_1/

Associative memory and Hebbian plasticity



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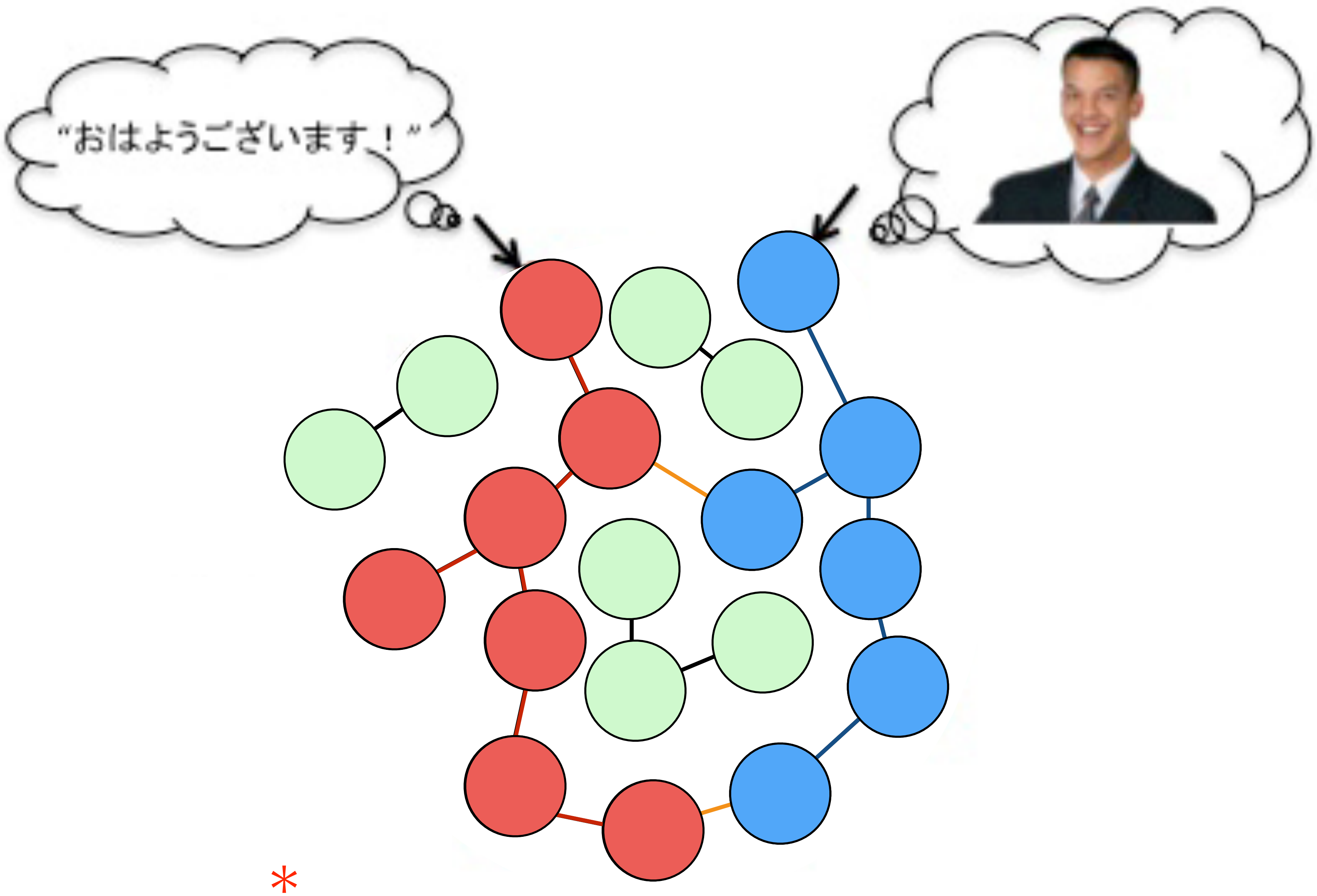
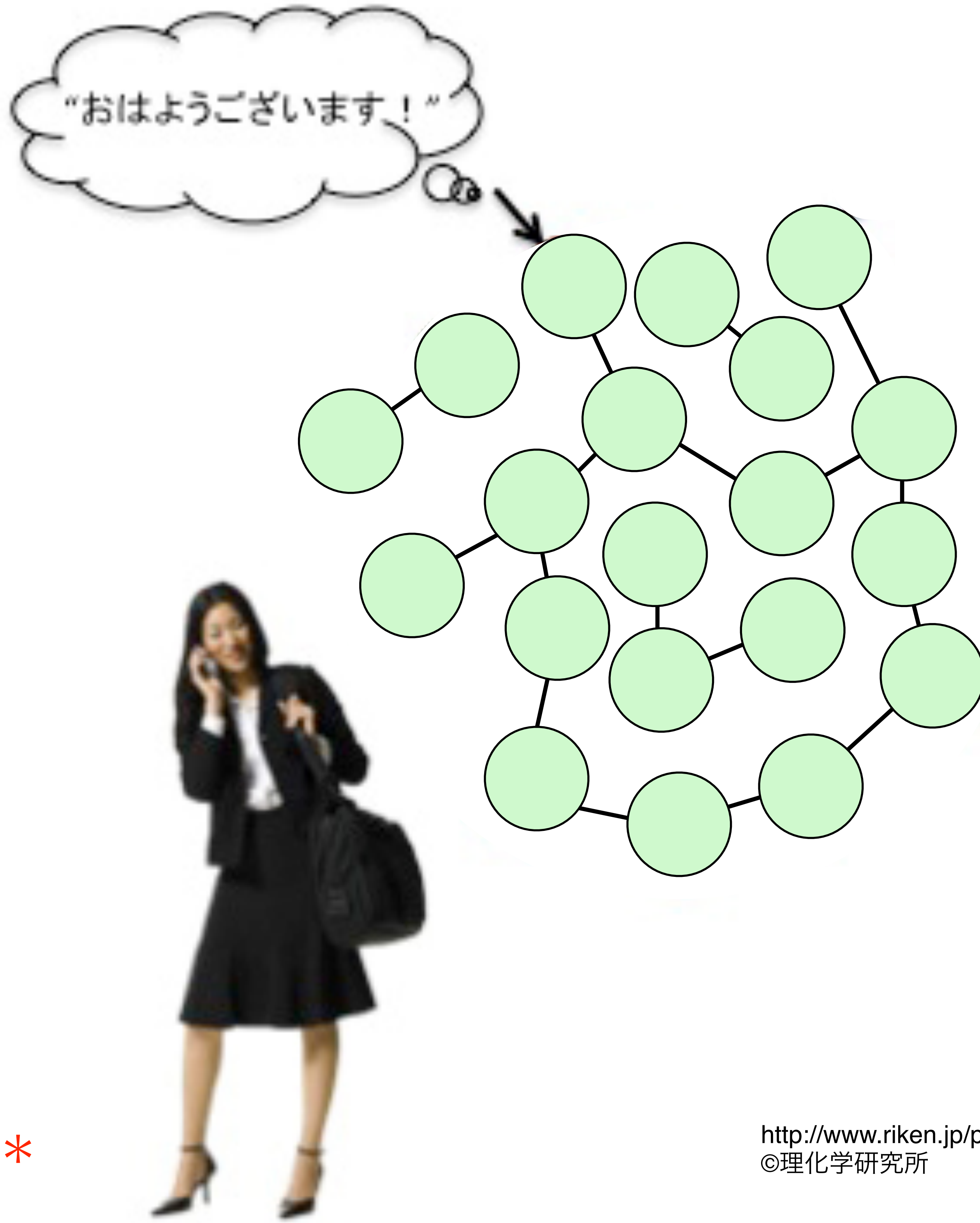
http://www.riken.jp/pr/press/2014/20141023_1/

Associative memory and Hebbian plasticity



Associative memory and Hebbian plasticity



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http://www.riken.jp/pr/press/2014/20141023_1/
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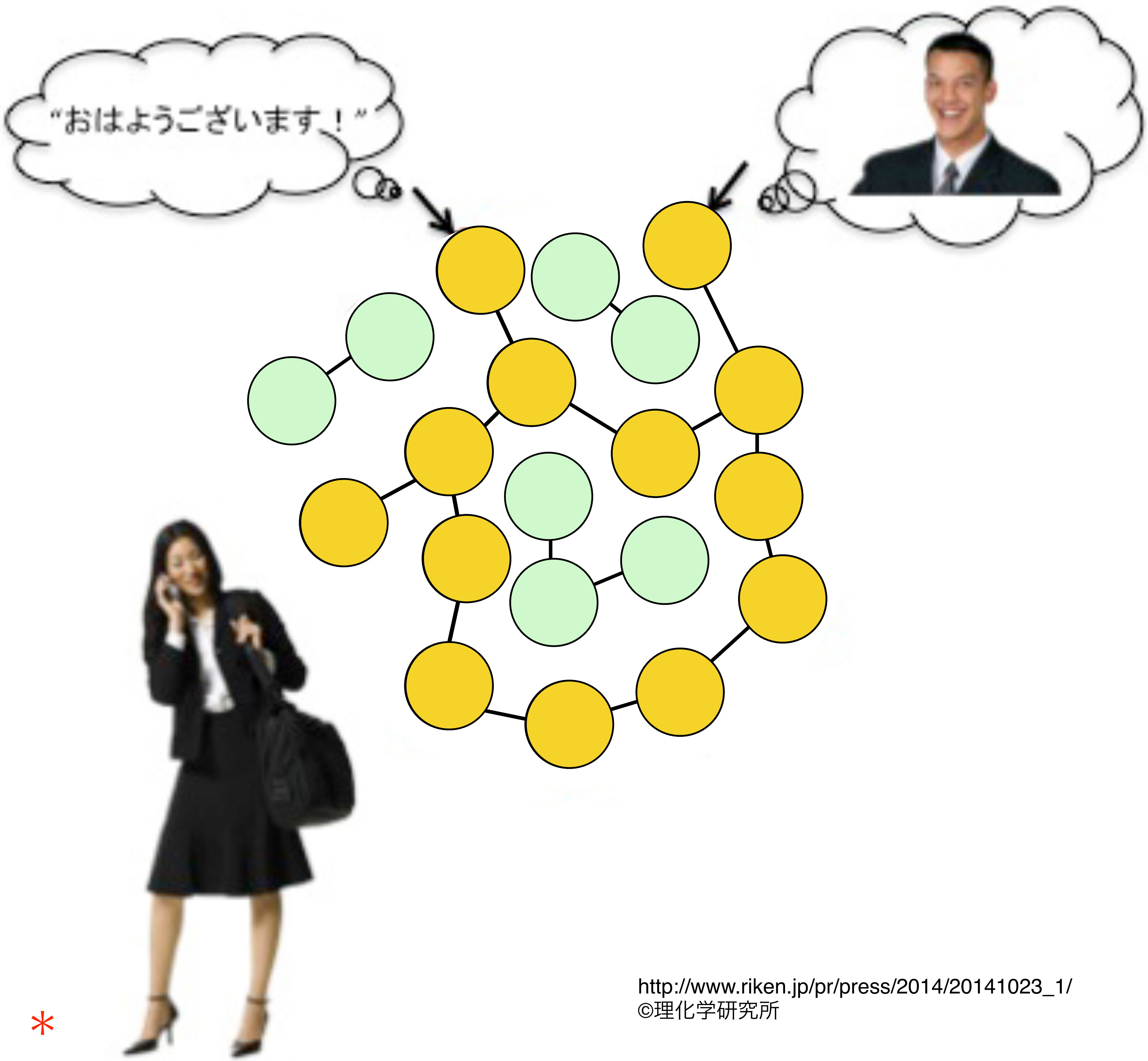
Associative memory and Hebbian plasticity



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http://www.riken.jp/pr/press/2014/20141023_1/

The Hopfield network

Little 1974
Hopfield 1982

著作権等の都合により、
ここに挿入されていた画像を削除しました

Hopfield network model
Simon S. Haykin (1999) Neural Networks: A Comprehensive Foundation, Prentice Hall.
p681,fig14.9

Memory pattern1

著作権等の都合により、
ここに挿入されていた画像を削除しました

バックスバニー、チップとデールの画像
Ruye Wang
http://fourier.eng.hmc.edu/e161/lectures/nn/node5.html

Memory pattern2

The Hopfield network

Little 1974
Hopfield 1982

著作権等の都合により、
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Hopfield network model
Simon S. Haykin (1999) Neural Networks: A Comprehensive Foundation, Prentice Hall.
p681,fig14.9

Memory pattern1

著作権等の都合により、
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バックスバニー、チップとデールの画像
Ruye Wang
http://fourier.eng.hmc.edu/e161/lectures/nn/node5.html

Memory pattern2

Learning rule:

$$w_{ij} \propto \xi_i^{(1)} \xi_j^{(1)}$$

$$\xi_i^{(p)} = \pm 1$$

The Hopfield network

Little 1974
Hopfield 1982

著作権等の都合により、
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Hopfield network model
Simon S. Haykin (1999) Neural Networks: A Comprehensive Foundation, Prentice Hall.
p681,fig14.9

Memory pattern1

著作権等の都合により、
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バックスバニー、チップとデールの画像

Ruye Wang
http://fourier.eng.hmc.edu/e161/lectures/nn/node5.html

Memory pattern2

Learning rule:

$$w_{ij} \propto \xi_i^{(1)} \xi_j^{(1)} + \xi_i^{(2)} \xi_j^{(2)}$$

$$\xi_i^{(p)} = \pm 1$$

The Hopfield network

Little 1974
Hopfield 1982

著作権等の都合により、
ここに挿入されていた画像を削除しました

Hopfield network model
Simon S. Haykin (1999) Neural Networks: A Comprehensive Foundation, Prentice Hall.
p681,fig14.9

Memory pattern1

Memory pattern2

著作権等の都合により、
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バックスバニー、チップとデールの画像

Ruye Wang
http://fourier.eng.hmc.edu/e161/lectures/nn/node5.html

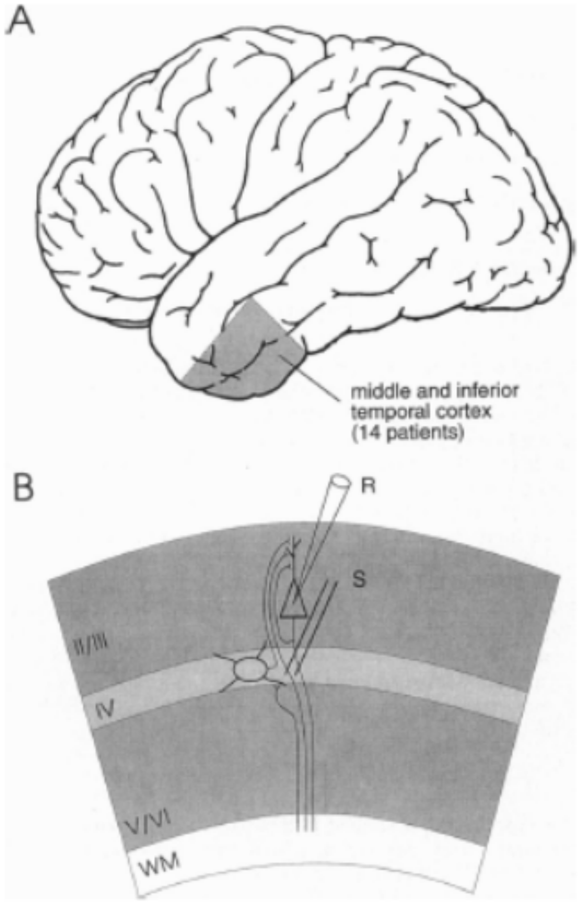
Learning rule:

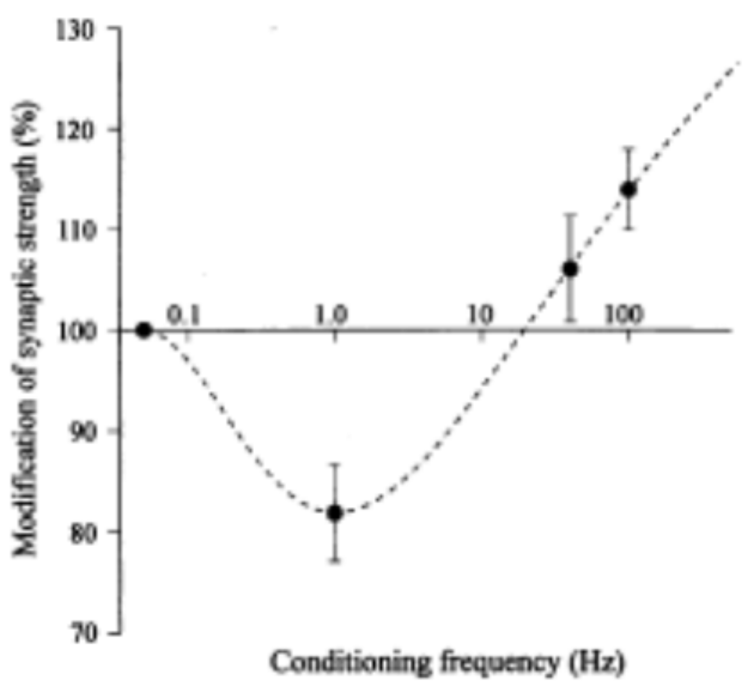
$$w_{ij} \propto \xi_i^{(1)} \xi_j^{(1)} + \xi_i^{(2)} \xi_j^{(2)}$$

$$\xi_i^{(p)} = \pm 1$$

Bidirectional synaptic modifications

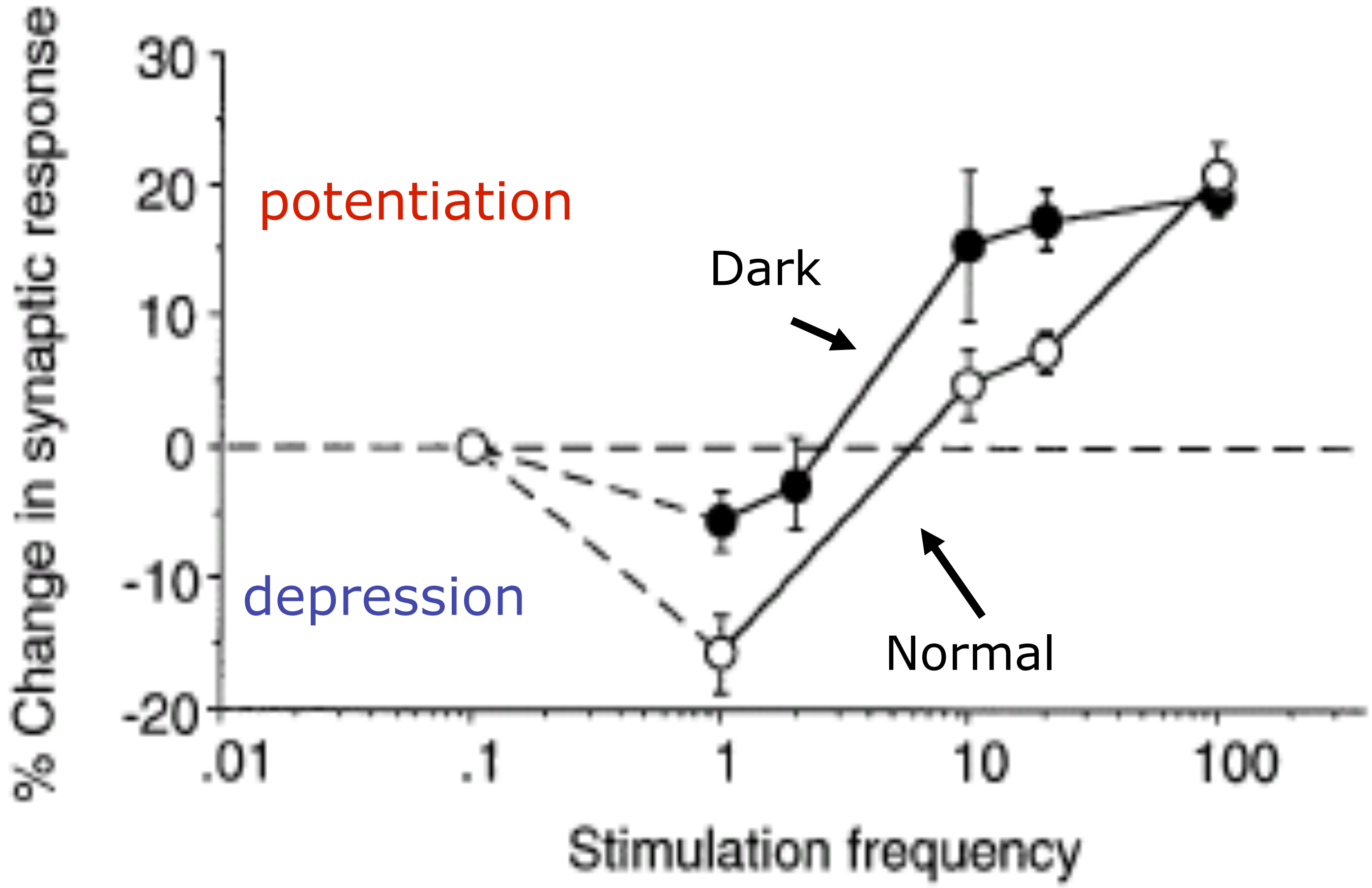
Recordings from human tissues





Chen, WR et al. (1996) Long-term modifications of synaptic efficacy in the human inferior and middle temporal cortex. Proceedings of the National Academy of Sciences USA 93(15): 8011-8015, p. 8012 Fig. 1.
http://www.pnas.org/content/93/15/8011.abstract

The balance of potentiation and depression

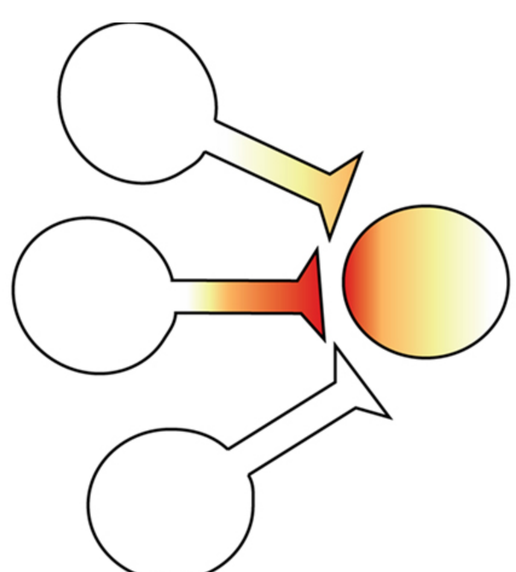


Kirkwood et al. (1996) Experience-dependent modification of synaptic plasticity in visual cortex, Nature 381: 526-528, p. 528 Fig. 4: Frequency-response functions derived from visual cortex of light-deprived (filled symbols) and normal (open symbols) rats. http://www.nature.com/nature/journal/v381/n6582/abs/381526a0.html

Kirkwood et al. 1996

Competitive Hebbian plasticity

$$\theta = \langle x^p \rangle$$



Watt and Desai (2010) Homeostatic Plasticity and STDP: Keeping a Neuron's Cool in a Fluctuating World, Frontiers in Synaptic Neuroscience 2: 5, p. 2 Fig. 1A. http://journal.frontiersin.org/article/10.3389/fnsyn.2010.00005/abstract

Watt and Desai 2010

The balance of potentiation and depression

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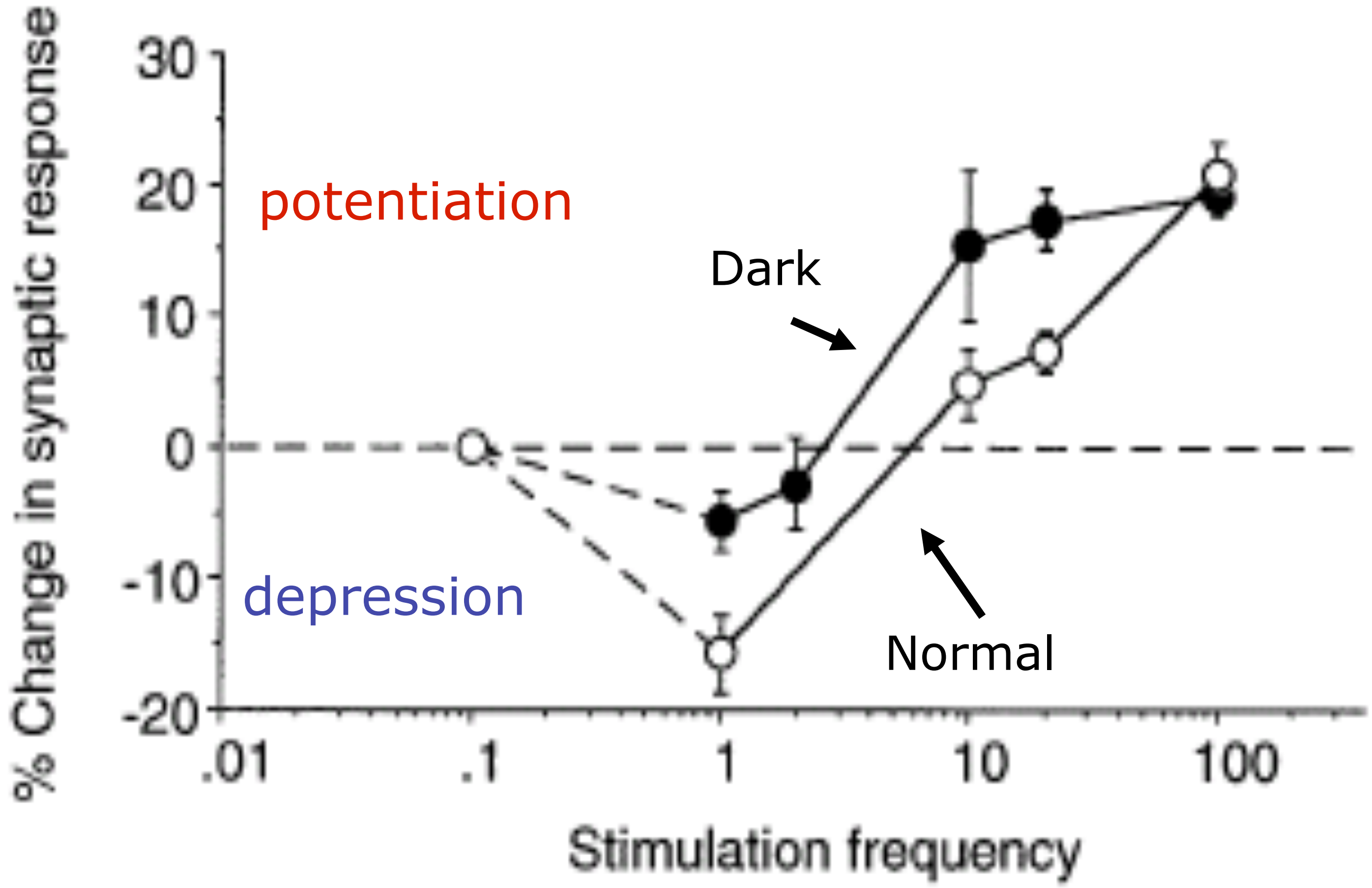

Kirkwood et al. (1996) Experience-dependent modification of synaptic plasticity in visual cortex, Nature 381: 526-528, p. 528 Fig. 4: Frequency-response functions derived from visual cortex of light-deprived (filled symbols) and normal (open symbols) rats.
http://www.nature.com/nature/journal/v381/n6582/abs/381526a0.html

Kirkwood et al. 1996

Gjorgjieva et al. (2011) A triplet spike-timing–dependent plasticity model generalizes the Bienenstock–Cooper–Munro rule to higher-order spatiotemporal correlations, Proceedings of the National Academy of Sciences of the United States of America 108 (48): 19383–19388, p. 19384 Fig. 2A.
http://www.pnas.org/content/108/48/19383.full

Competitive Hebbian plasticity

Watt and Desai (2010) Homeostatic Plasticity and STDP: Keeping a Neuron's Cool in a Fluctuating World, Frontiers in Synaptic Neuroscience 2: 5, p. 2 Fig. 1A.
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$$\theta = \langle x^p \rangle$$

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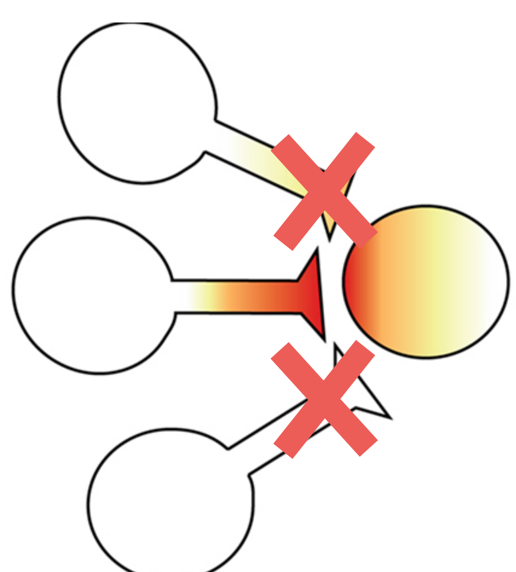

Watt and Desai 2010

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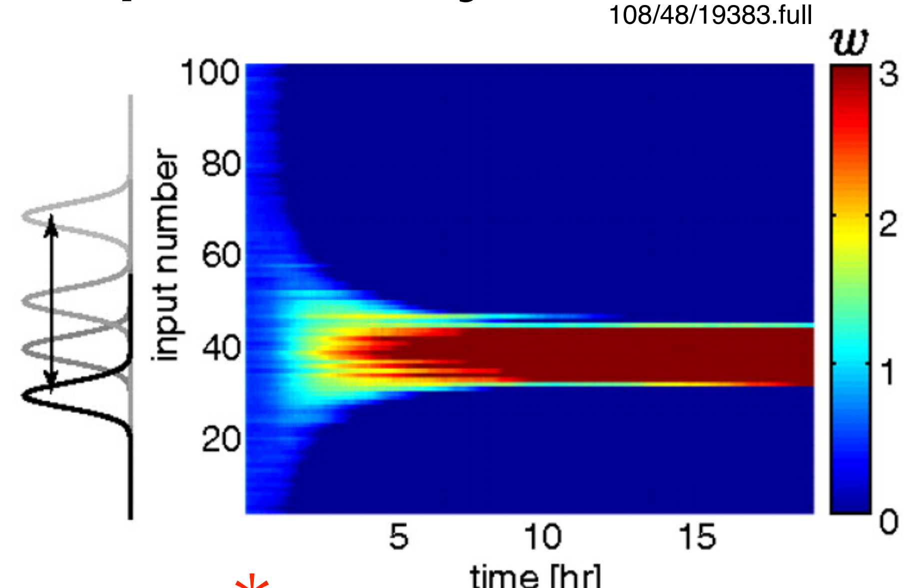
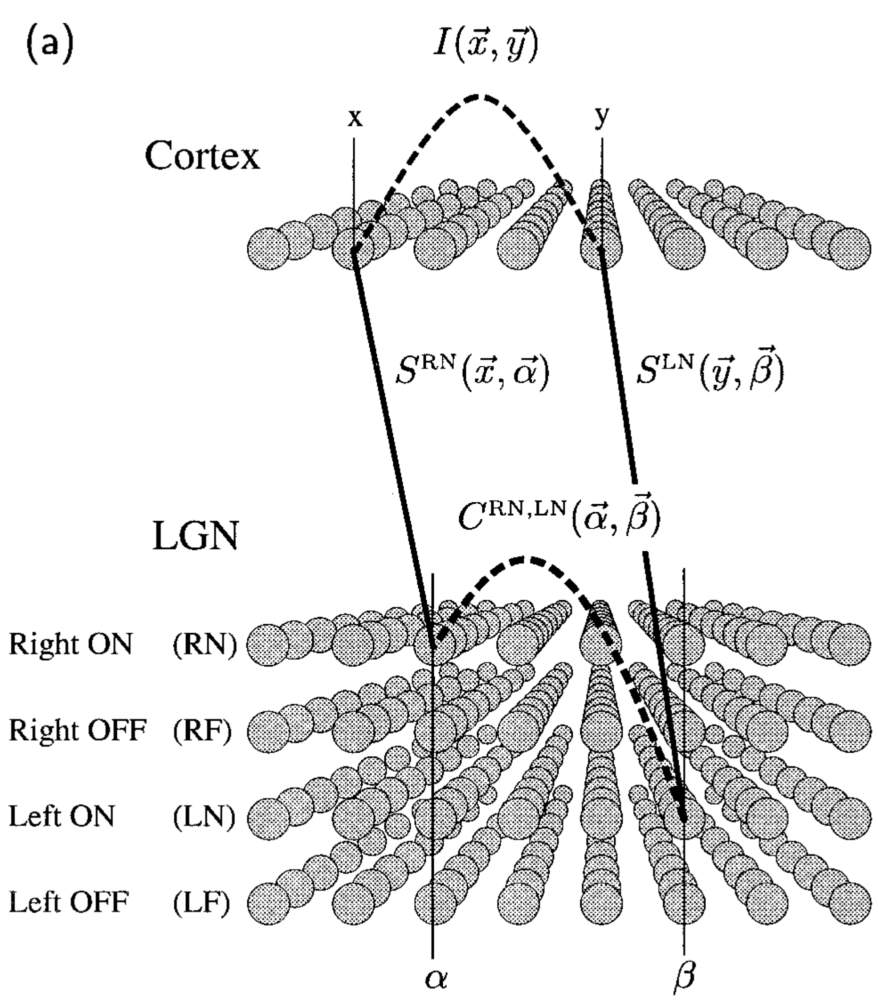


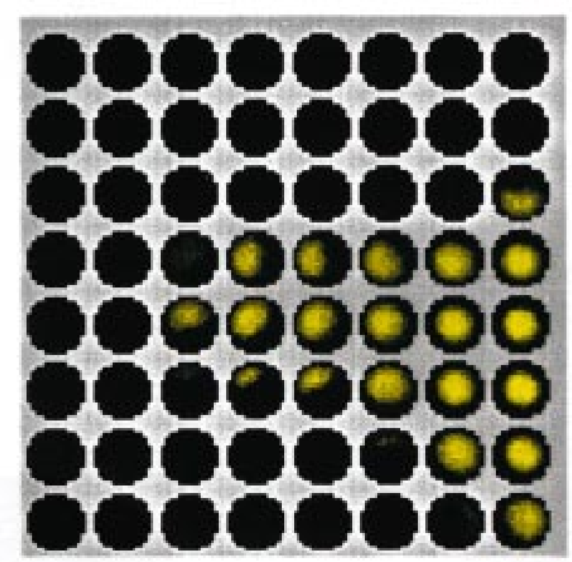
Bienenstock et al. 1982
Gjorgjieva et al. 2011

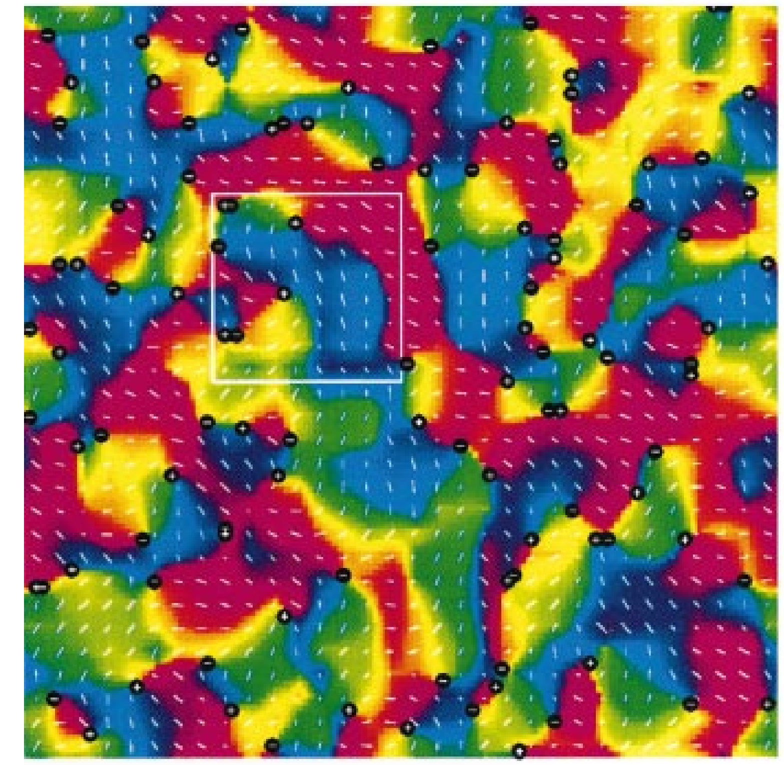
Development of cortical organization

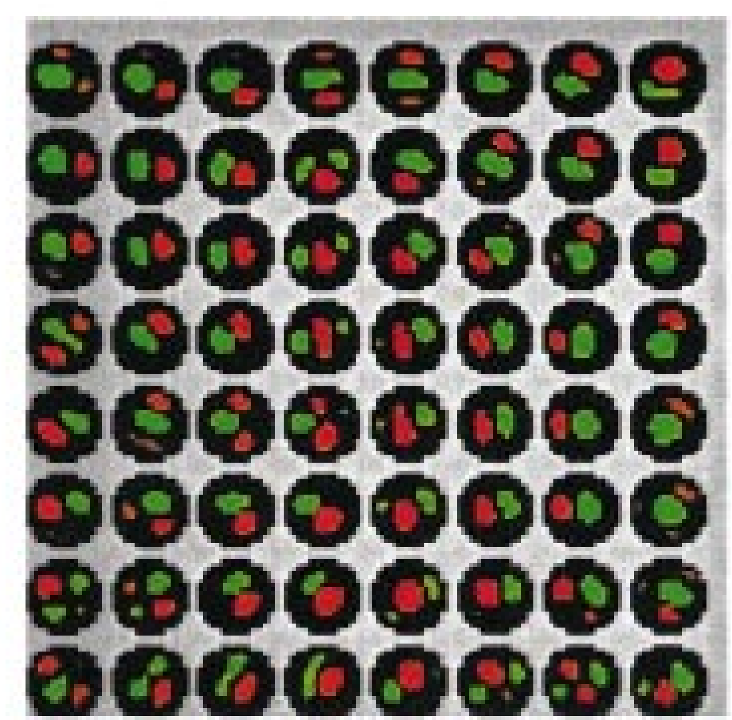


(a) OD Map

(c) Left Eye RFs

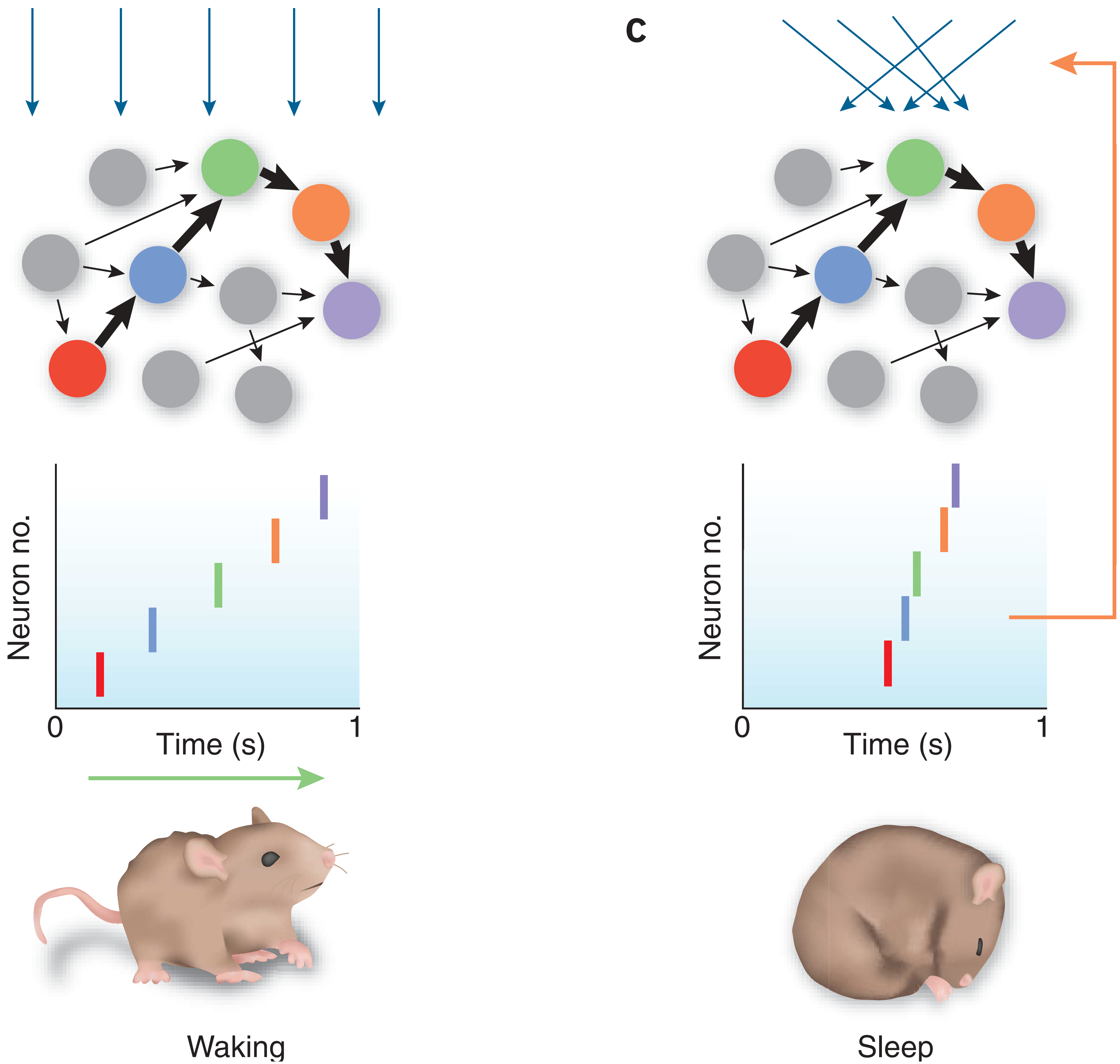






Erwin and Miller (1998) Correlation-Based Development of Ocularly Matched Orientation and Ocular Dominance Maps: Determination of Required Input Activities, The Journal of Neuroscience 18(23): 9870-9895, p. 9872 Fig. 1(a). http://www.jneurosci.org/content/18/23/9870.full

Sequences of episodes

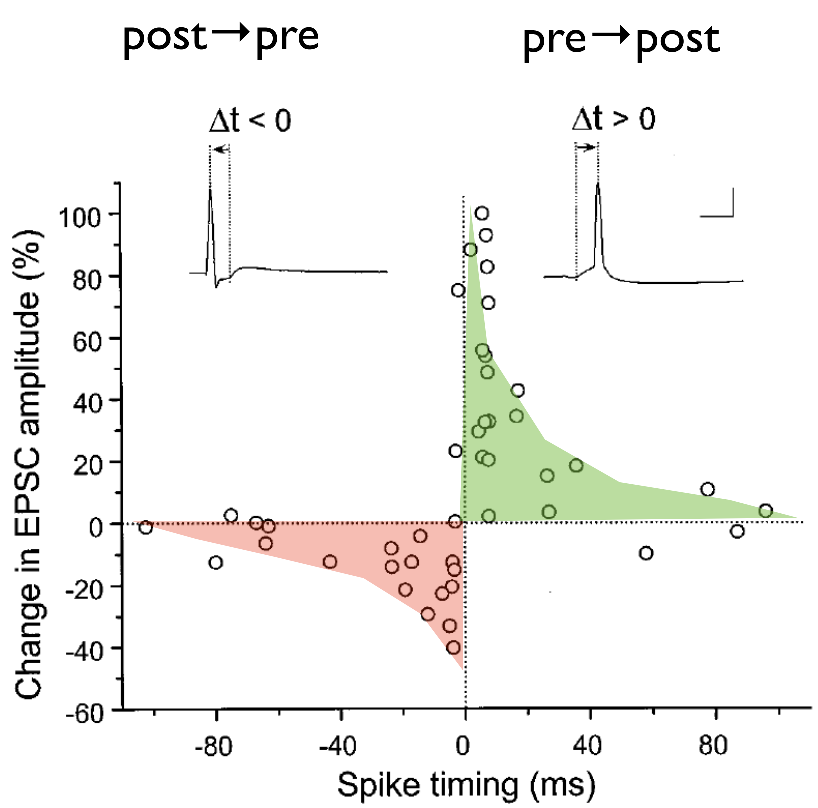


* M Mehta (2007) Cortico-hippocampal interaction during up-down states and memory consolidation, Nature Neuroscience 10 (1): 13-15, p. 14 Fig. 1 b, c. http://www.nature.com/neuro/journal/v10/n1/full/nn0107-13.html

Mehta 2007
Ji and Wilson 2007

Learning spatiotemporal patterns

Spike-timing dependent plasticity (experiment)



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Bi and Poo, 1998

Bi and Poo (1998) Synaptic Modifications in Cultured Hippocampal Neurons: Dependence on Spike Timing, Synaptic Strength, and Postsynaptic Cell Type, The Journal of Neuroscience 18(24): 10464-10472, p. 10470 Fig. 7. Critical window for the induction of synaptic potentiation and depression. http://www.jneurosci.org/content/18/24/10464.full

Sequence learning (model)

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ニューロンの働きを示すグラフ

Fiete et al. (2010) Spike-Time-Dependent Plasticity and Heterosynaptic Competition Organize Networks to Produce Long Scale-Free Sequences of Neural Activity, Neuron 65 (4): 563–576, p. 566 Fig. 2A.
http://www.sciencedirect.com/science/article/pii/S0896627310000917

Spike-timing dependent plasticity vs Hebbian plasticity

Spike frequency dependence

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グラフ:シナプス Spike frequency dependence

Sjöström, et al. (2001) Rate, Timing, and Cooperativity Jointly Determine Cortical Synaptic Plasticity, Neuron 32 (6): 1149–1164, p. 1151 Fig. 1D. p. 1157 Fig. 7B.
http://www.sciencedirect.com/science/article/pii/S0896627301005426

Calcium based model

Graupner and Brunela (2012) Calcium-based plasticity model explains sensitivity of synaptic changes to spike pattern, rate, and dendritic location, Proceedings of the National Academy of Sciences of the United States of America 109 (10): 3991–3996, p. 3994 Fig. 4A.
http://www.pnas.org/content/109/10/3991.full

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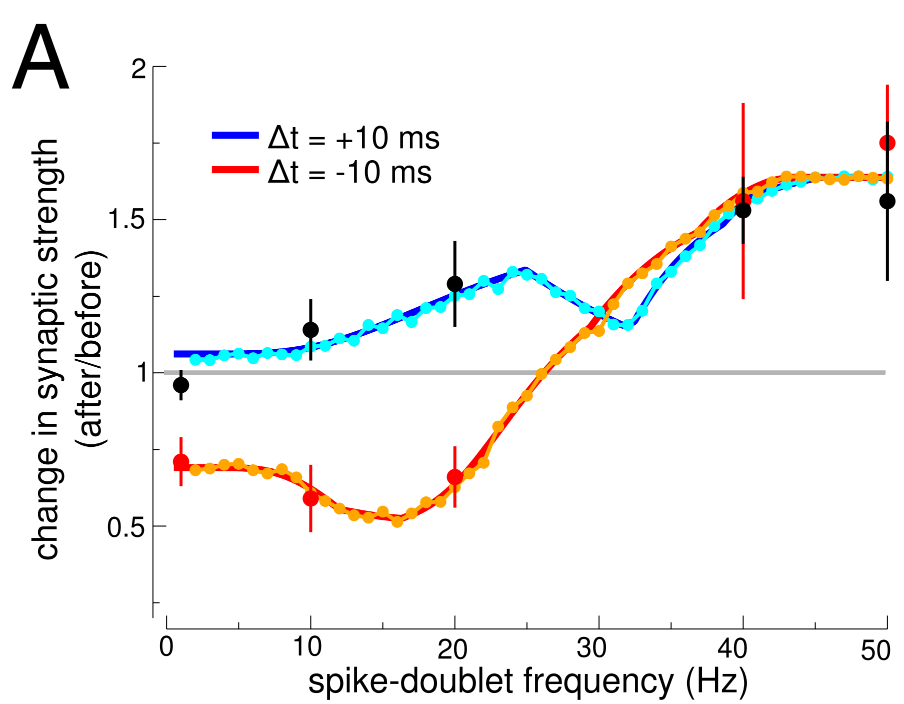

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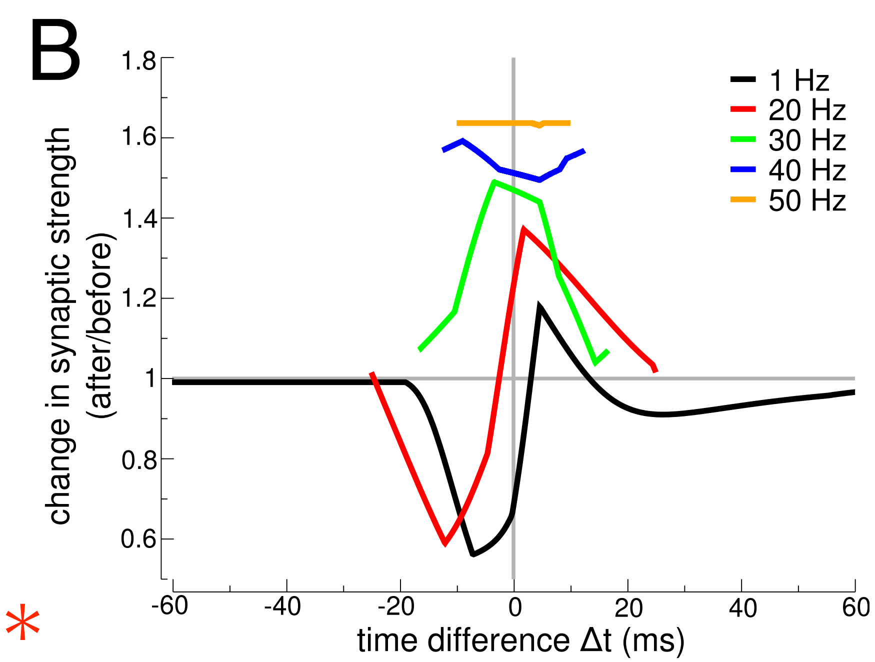
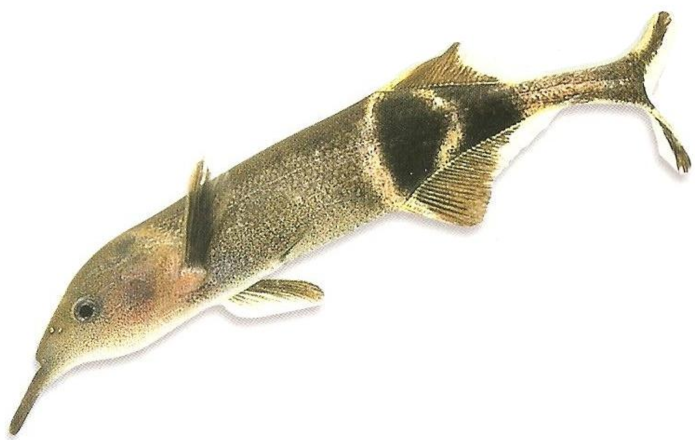


Anti-Hebbian plasticity

Bell et al. (1997) Synaptic plasticity in a cerebellum-like structure depends on temporal order, Nature 387 (6630): 278-281, p. 280 Fig. 4a. http://www.nature.com/nature/journal/v387/n6630/abs/387278a0.html

- Cerebellum-like structures in electric fish



post → pre　　　pre→ post

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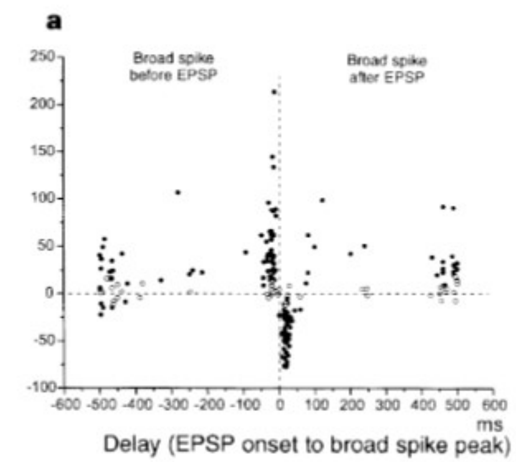

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電気魚の構造

Roberts and Bell (2000) Computational Consequences of Temporally Asymmetric Learning Rules: II. Sensory Image Cancellation, Journal of Computational Neuroscience 9 (1): 67-83, p. 69 Fig. 1: Connectivity of the ELL. http://link.springer.com/article/10.1023/A:1008938428112

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電気魚のシナプス機能のシミュレーション

Roberts and Bell (2000) Computational Consequences of Temporally Asymmetric Learning Rules: II. Sensory Image Cancellation, Journal of Computational Neuroscience 9 (1): 67-83, p. 76 Fig. 5: Comparison of experimental data with preliminary simulation. http://link.springer.com/article/10.1023/A:1008938428112

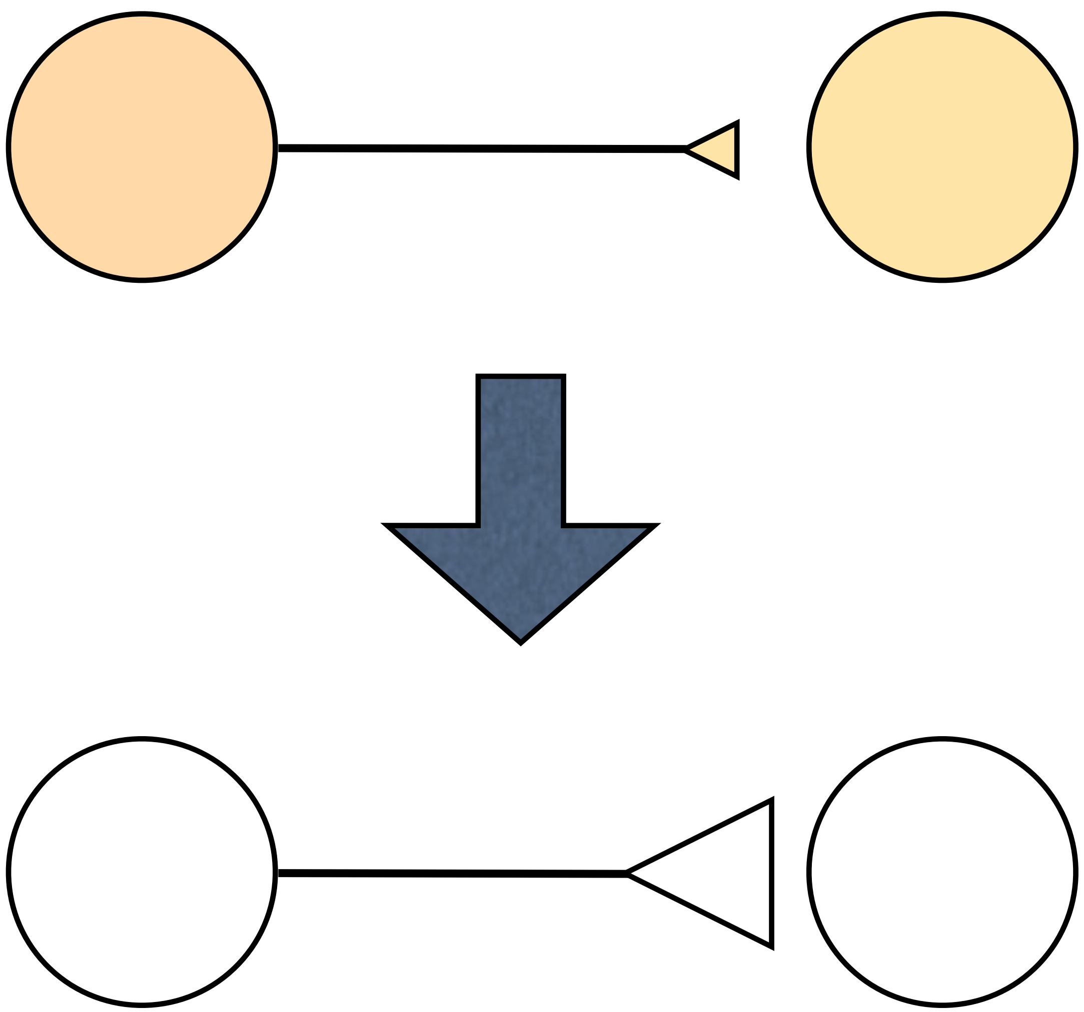
Hebbian and homeostatic plasticity

Hebbian plasticity

"neurons that fire together wire together"

homeostatic plasticity

scales synaptic strength to maintain activity



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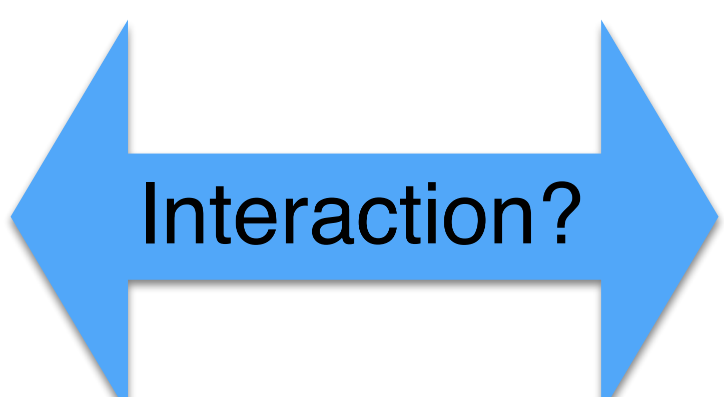
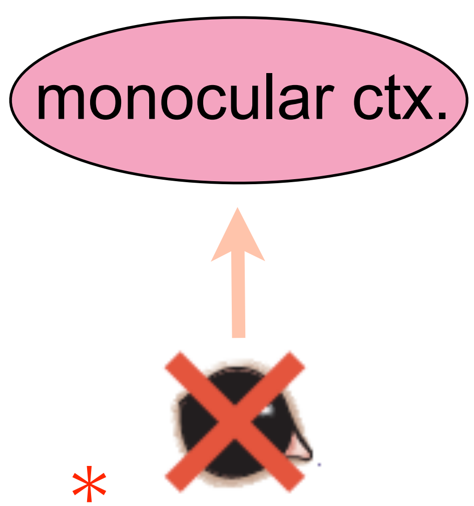
可塑性のグラフ

Kaneko et al. (2008) Tumor Necrosis Factor-α Mediates One Component of Competitive, Experience-Dependent Plasticity in Developing Visual Cortex, Neuron 58 (5): 673–680, p. 674 Fig. 1C.
http://www.sciencedirect.com/science/article/pii/S0896627308003772

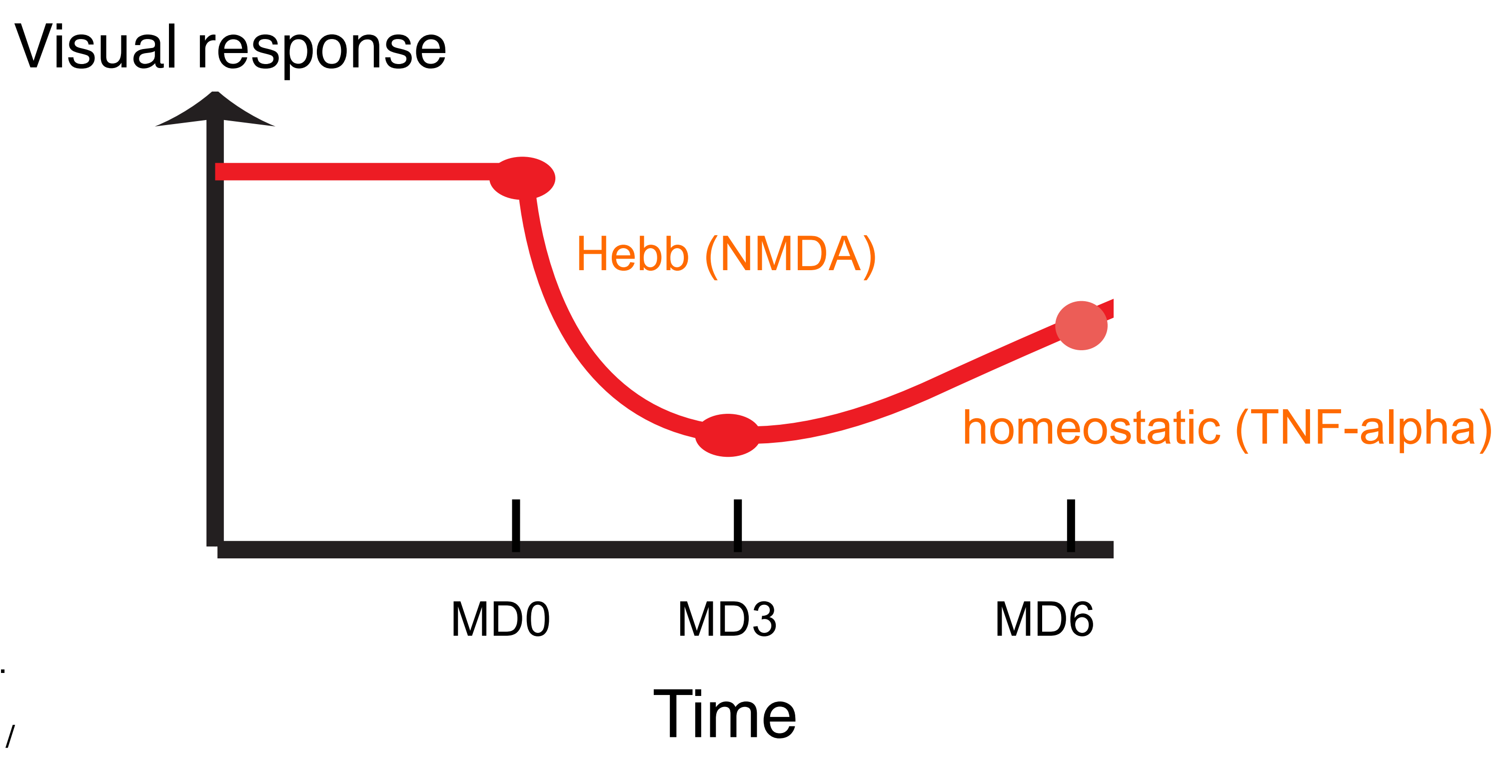


MD result in the monocular cortex

Fast Hebbian depression and slow homeostatic potentiation

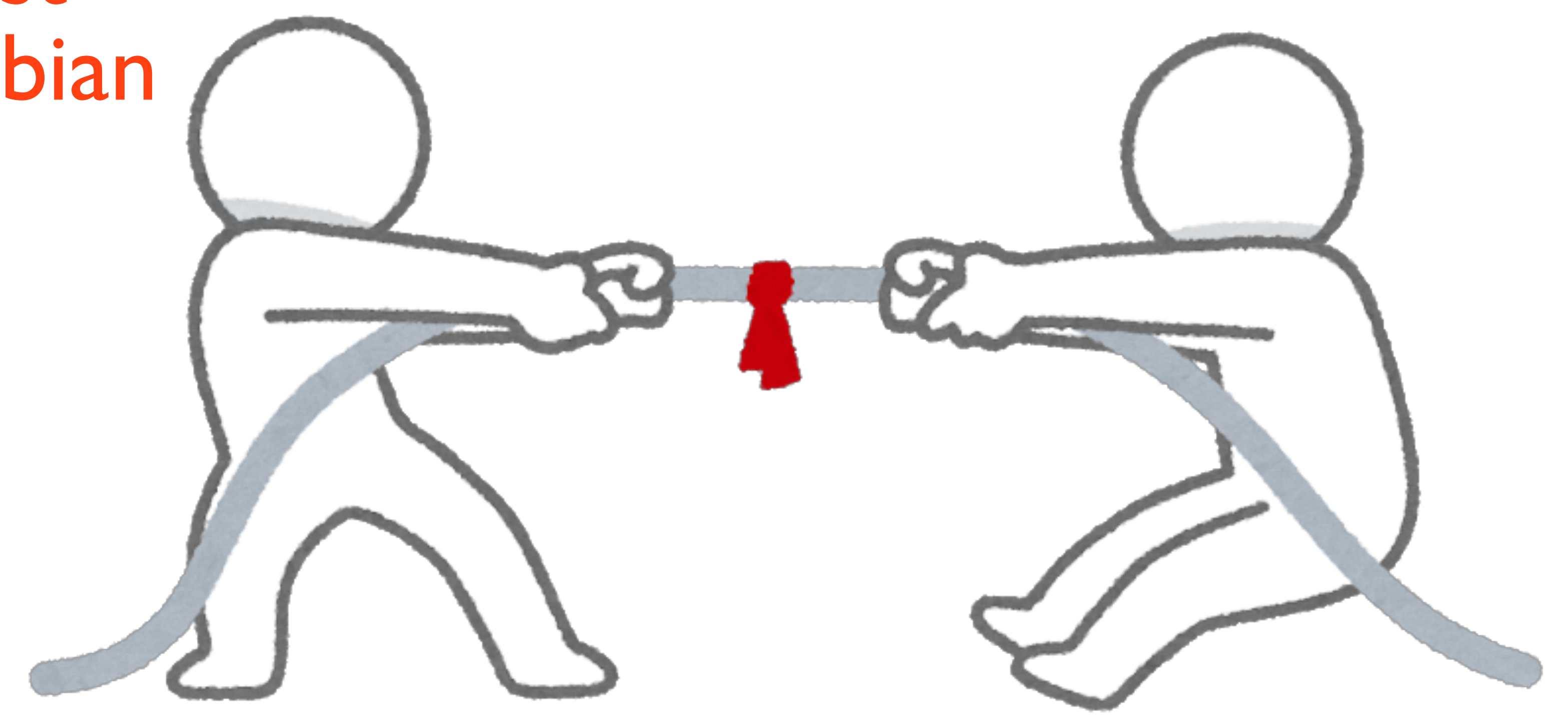


T Hensch (2005) Critical period plasticity in local cortical circuits, Nature Reviews Neuroscience 6(11): 877-888, p. 879 Fig. 2a.
http://www.nature.com/nrn/journal/v6/n11/full/nrn1787.html



Kaneko et al. 2008b

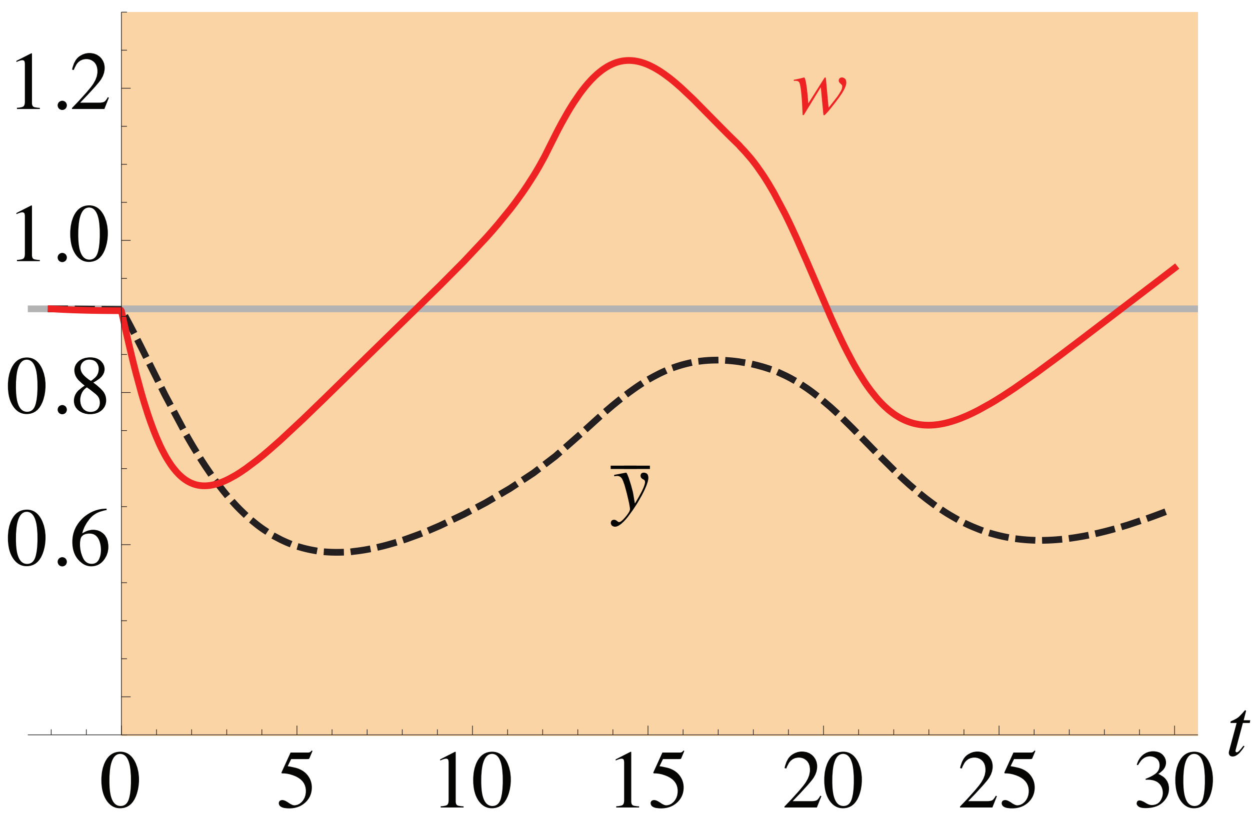
Conventional models assume that
the two kinds of plasticity cancel each other.



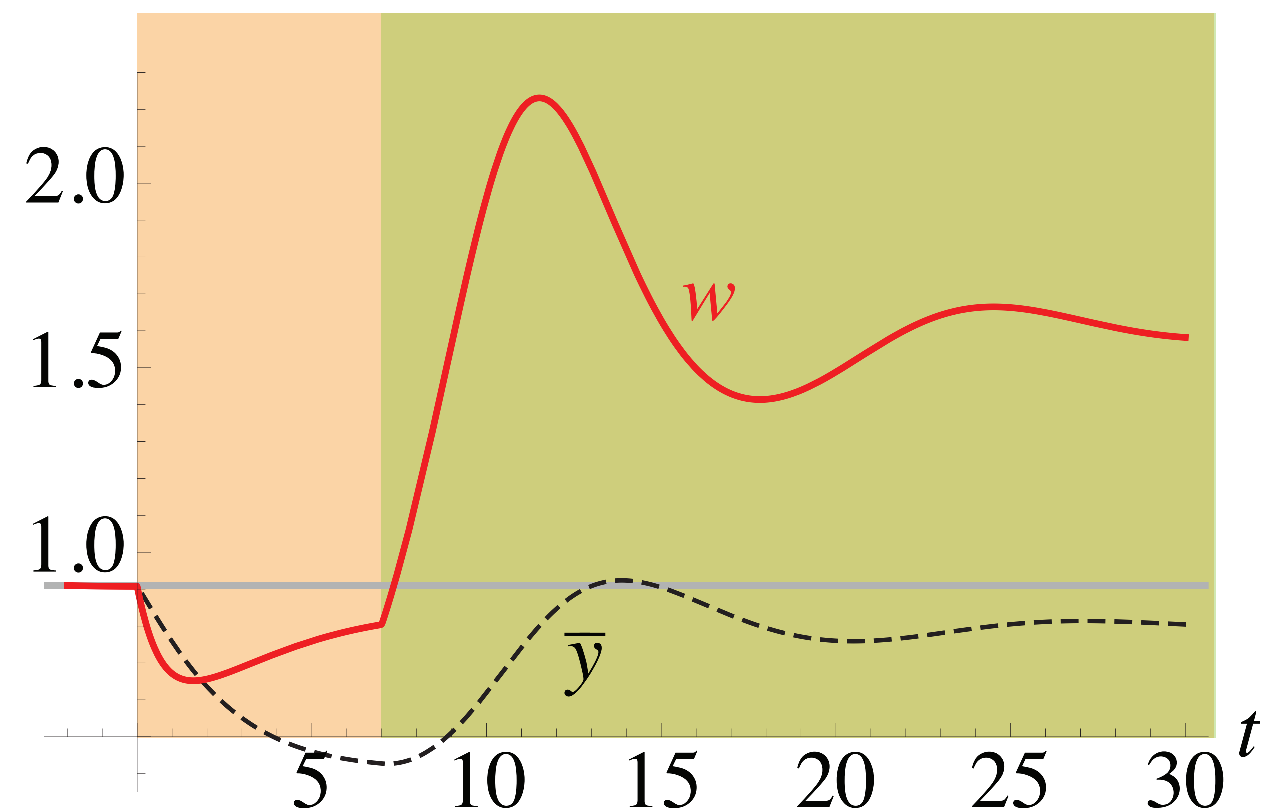
$$\Delta w = \Delta Hebb + \Delta homeo$$

Hebbian + homeostatic plasticity

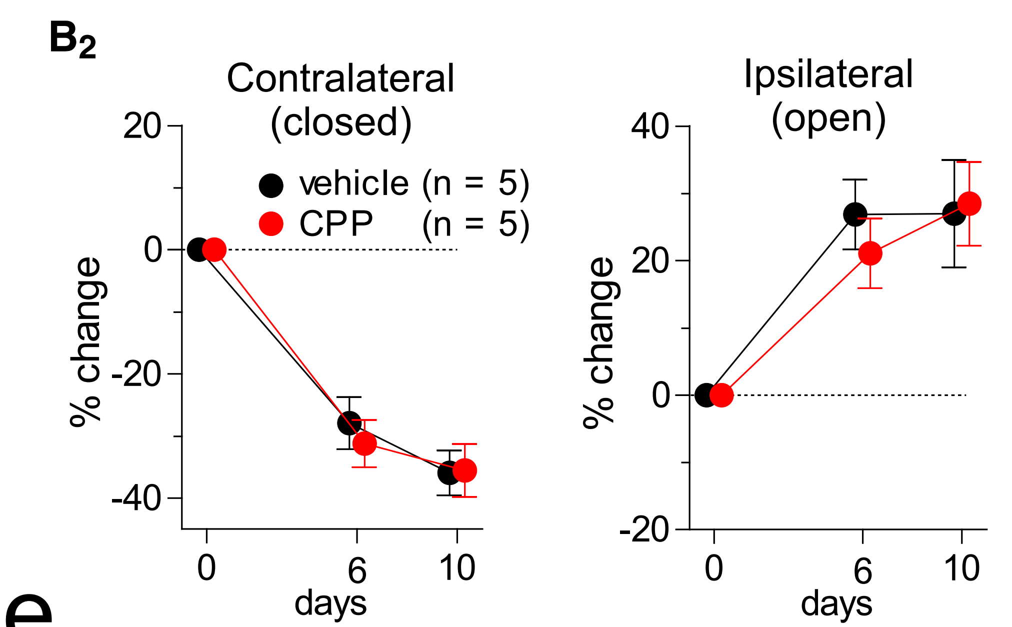
Monocular deprivation



Hebbian blockade (CPP)



This interaction predicts a change of visual response if Hebbian plasticity is blocked.



Toyoizumi et al. 2014

No change

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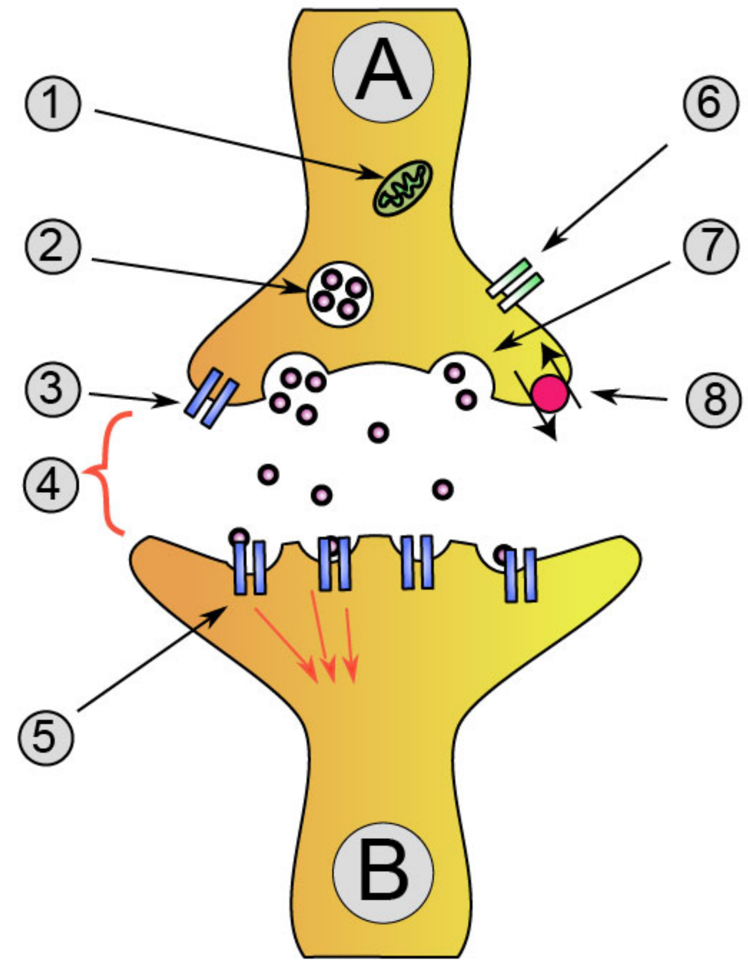
Toyoizumi et al. (2014) Modeling the Dynamic Interaction of Hebbian and Homeostatic Plasticity, Neuron 84 (2): 497–510, p. 500 Fig. 2B, C p. 501 Fig. 3B2. . http://www.sciencedirect.com/science/article/pii/S0896627314008940

The two-factor model:
synaptic strength as a product of Hebbian and homeostatic variables

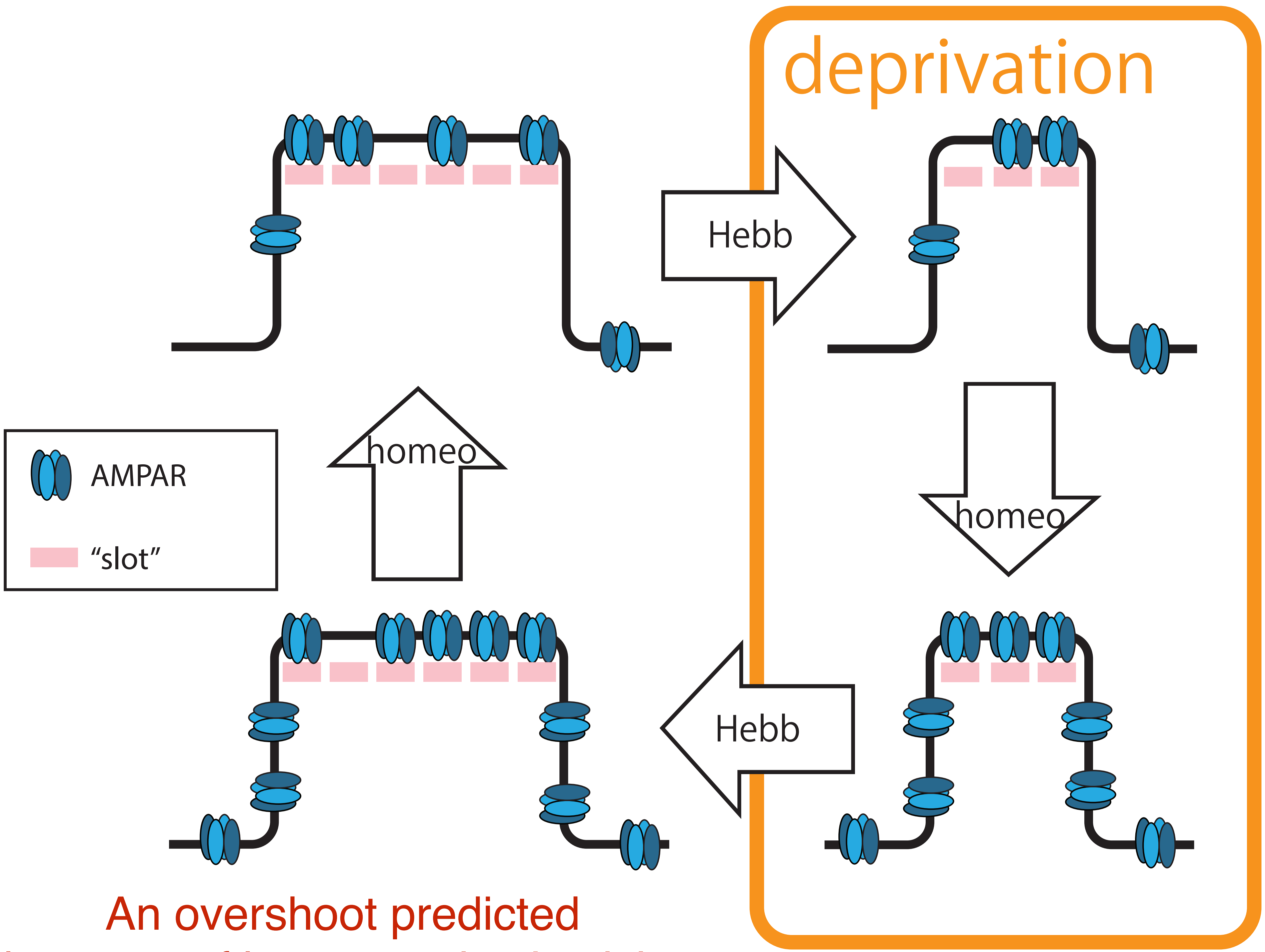
$$\Delta w = (\text{Hebb}) \times (\text{homeo})$$

Toyoizumi et al. 2014



https://commons.wikimedia.org/wiki/File:Synapse_diag1.png

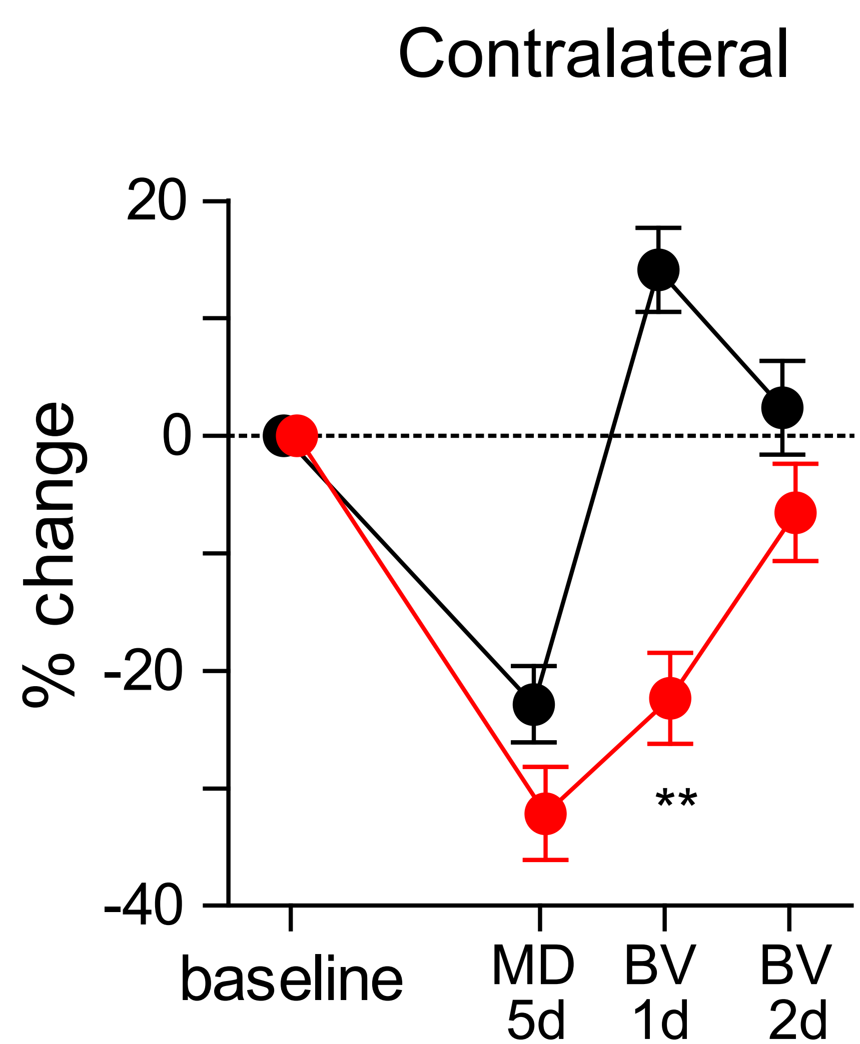
Schematic behavior:
a possible implementation



An overshoot predicted
because of homeostatic plasticity

Toyoizumi: http://www.jnss.org/150306-01/

Prediction confirmed:
The closed-eye overshoot is TNF-alpha dependent.



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Toyoizumi et al. (2014) Modeling the Dynamic Interaction of Hebbian and Homeostatic Plasticity, Neuron 84 (2): 497–510, p. 507 Fig. 7B.
http://www.sciencedirect.com/science/article/pii/S0896627314008940

Critical period plasticity

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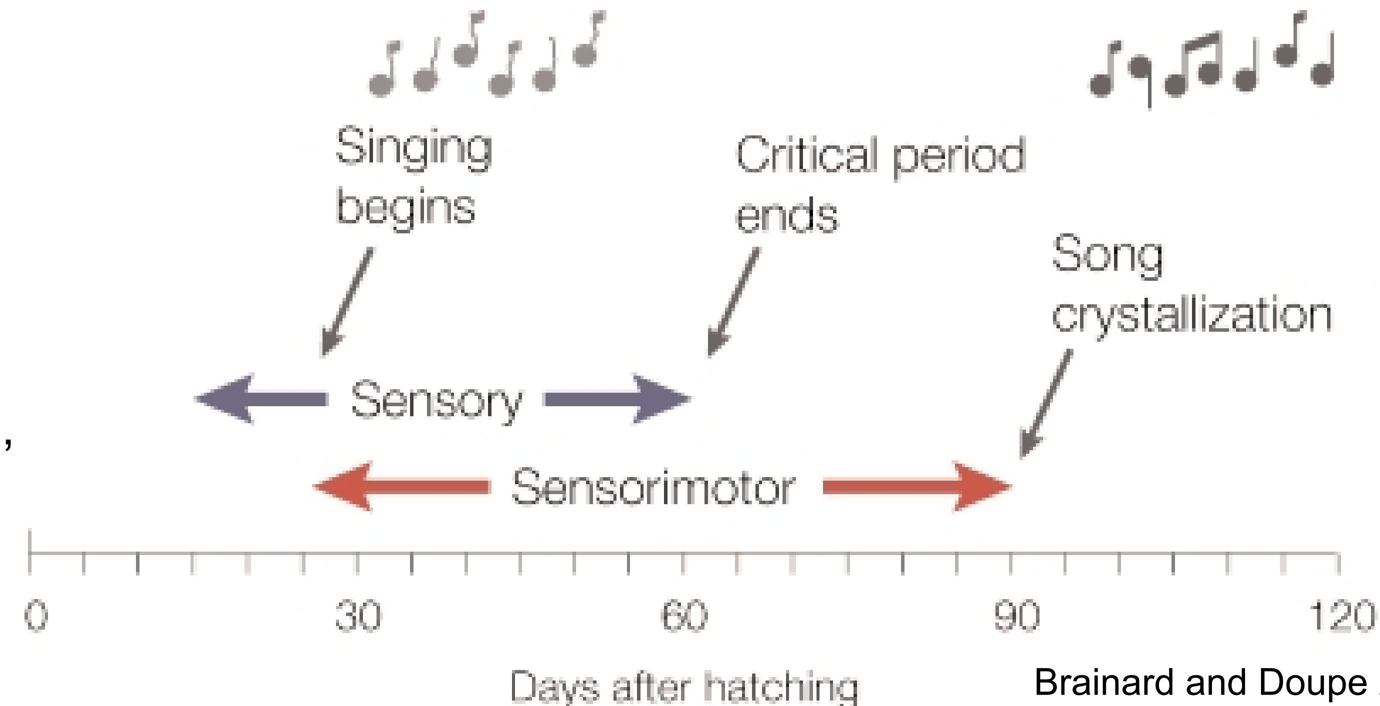
A sequence of critical periods

Critical periods can occur as a sequence of sensitivities to increasingly more complex aspects of experience.

(e.g. Werker et al. 2009, Hernandez and Li 2007, Scott et al. 2007)

Timeline for zebra finch song learning



Brainard and Doupe 2000

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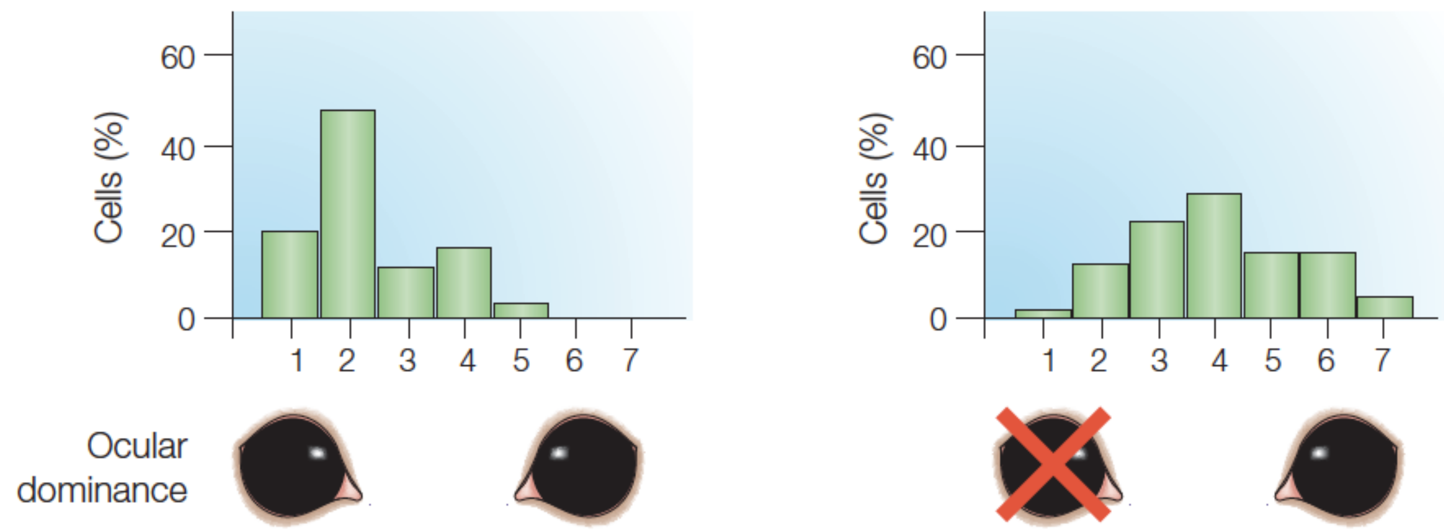
Brainard and Doupe (2000) Auditory feedback in learning and maintenance of vocal behaviour, Nature Reviews Neuroscience 1(1): 31-40, p. 32 Fig. 1: Timeline for zebra finch song learning. http://www.nature.com/nrn/journal/v1/n1/full/nrn1000_031a.html

How do critical periods start?

Maturation of inhibition initiates the CP for OD in mice

- Mice have a CP for OD.



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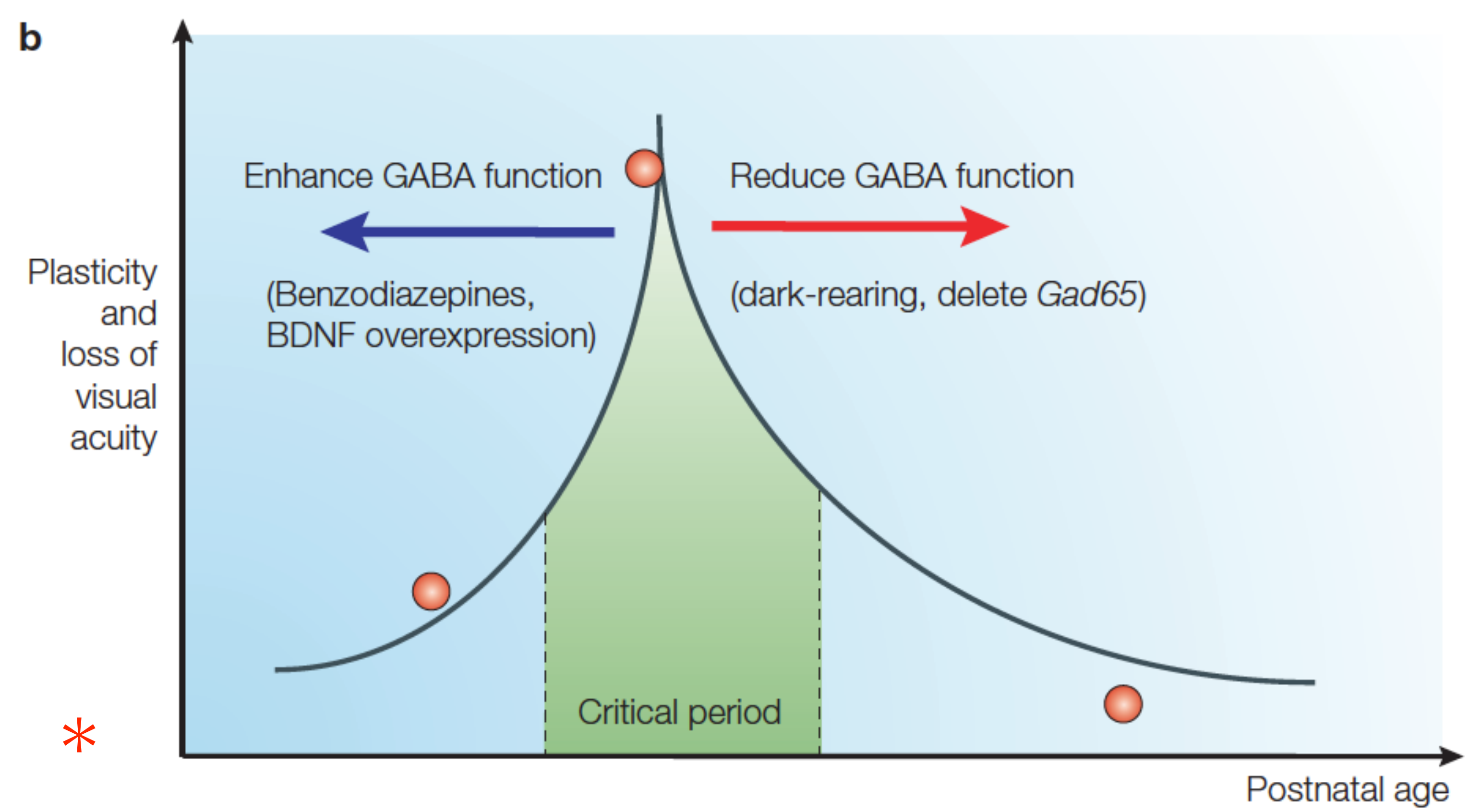
- Modulations of GABA function shift the critical period bidirectionally in time.

- Maturation of inhibition requires visual experience.



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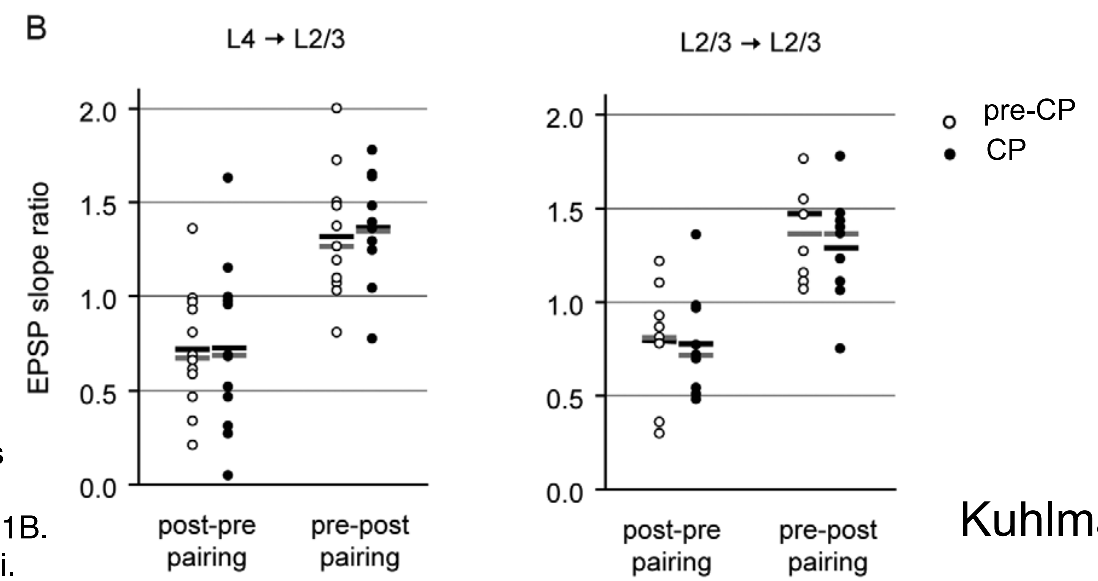
T Hensch (2005) Critical period plasticity in local cortical circuits, Nature Reviews Neuroscience 6(11): 877-888, p. 879 Fig. 2a. b
http://www.nature.com/nrn/journal/v6/n11/full/nrn1787.html

Hensch 2005

How maturation of inhibition initiates the CP?

1. Maturation of inhibition turns on plasticity specifically during the CP.

V1 shows activity-dependent plasticity during the pre-CP.



Kuhlman et al. (2010) Maturation of GABAergic Inhibition Promotes Strengthening of Temporally Coherent Inputs among Convergent Pathways, PLOS Computational Biology 6(6): e1000797, p. 3 Fig. 1B. http://journals.plos.org/ploscompbiol/article?id=10.1371/journal.pcbi.1000797

Kuhlman et al. 2010

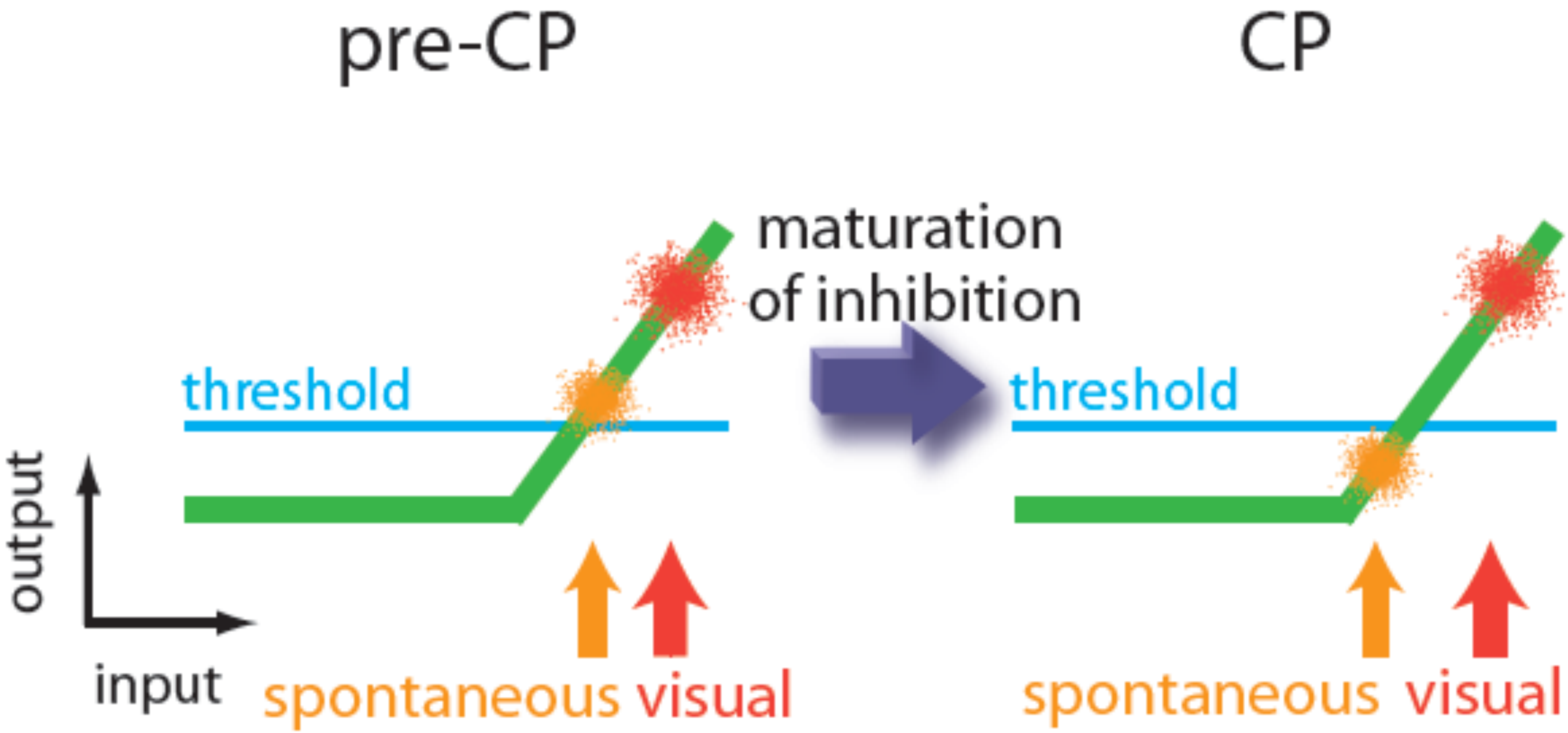
2. Before maturation of inhibition, all input patterns equally activate neurons. Hence, there is no competition between input patterns.

Experience-dependent refinement of retinotopy occurs in V1 during the pre-CP.

Questions

- Pre-CP: How can there be the experience-dependent refinement of retinotopy without a significant OD shift?
- CP: How does the maturation of inhibition make OD sensitive to MD?

Hypothesis



No change in plasticity rule

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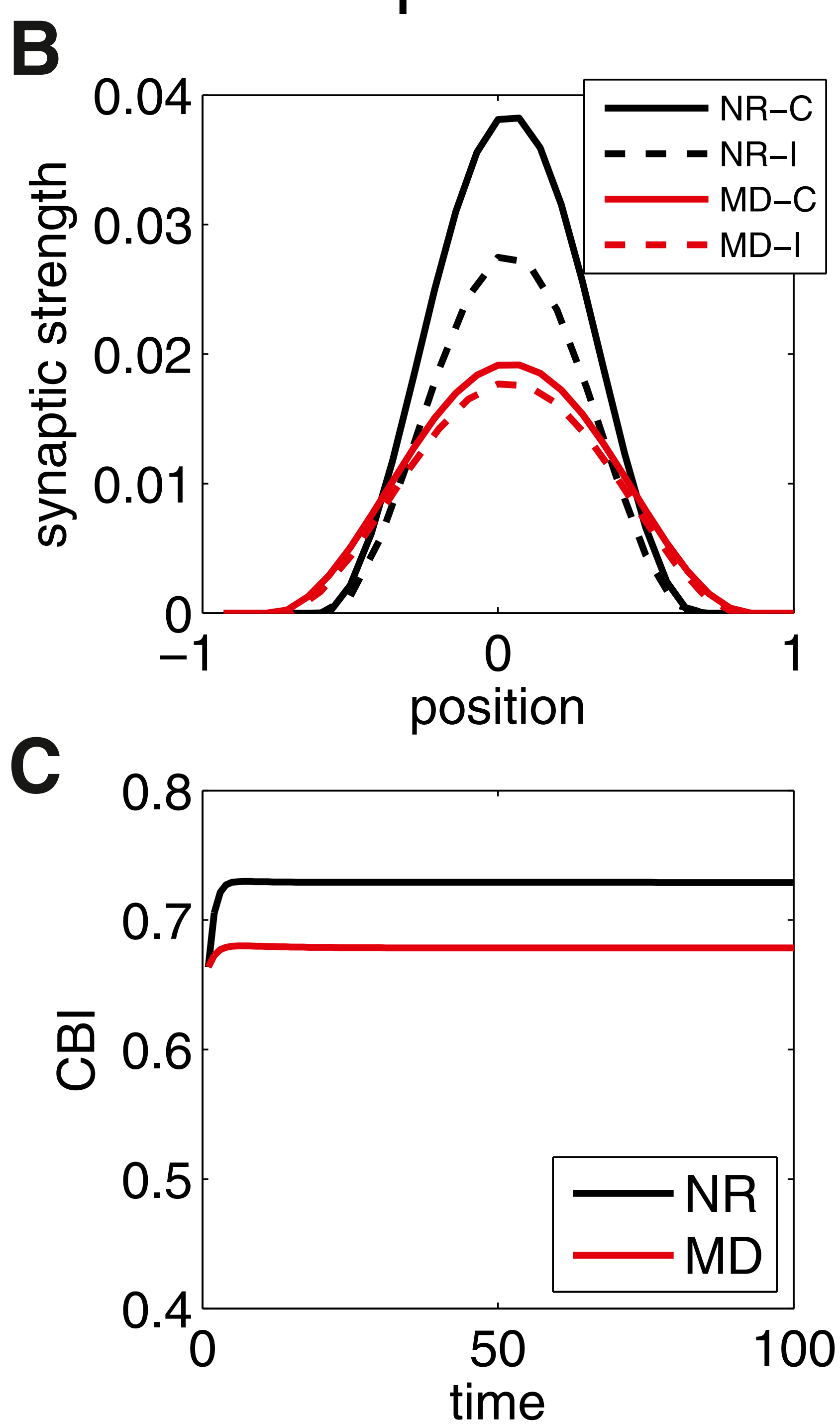
Toyoizumi et al. (2013) A Theory of the Transition to Critical Period Plasticity: Inhibition Selectively Suppresses Spontaneous Activity, Neuron 80(1): 51–63, p. 53 Fig. 1B. http://www.sciencedirect.com/science/article/pii/S0896627313006466

Simulation: Refinement during pre-CP and OD-shift during CP

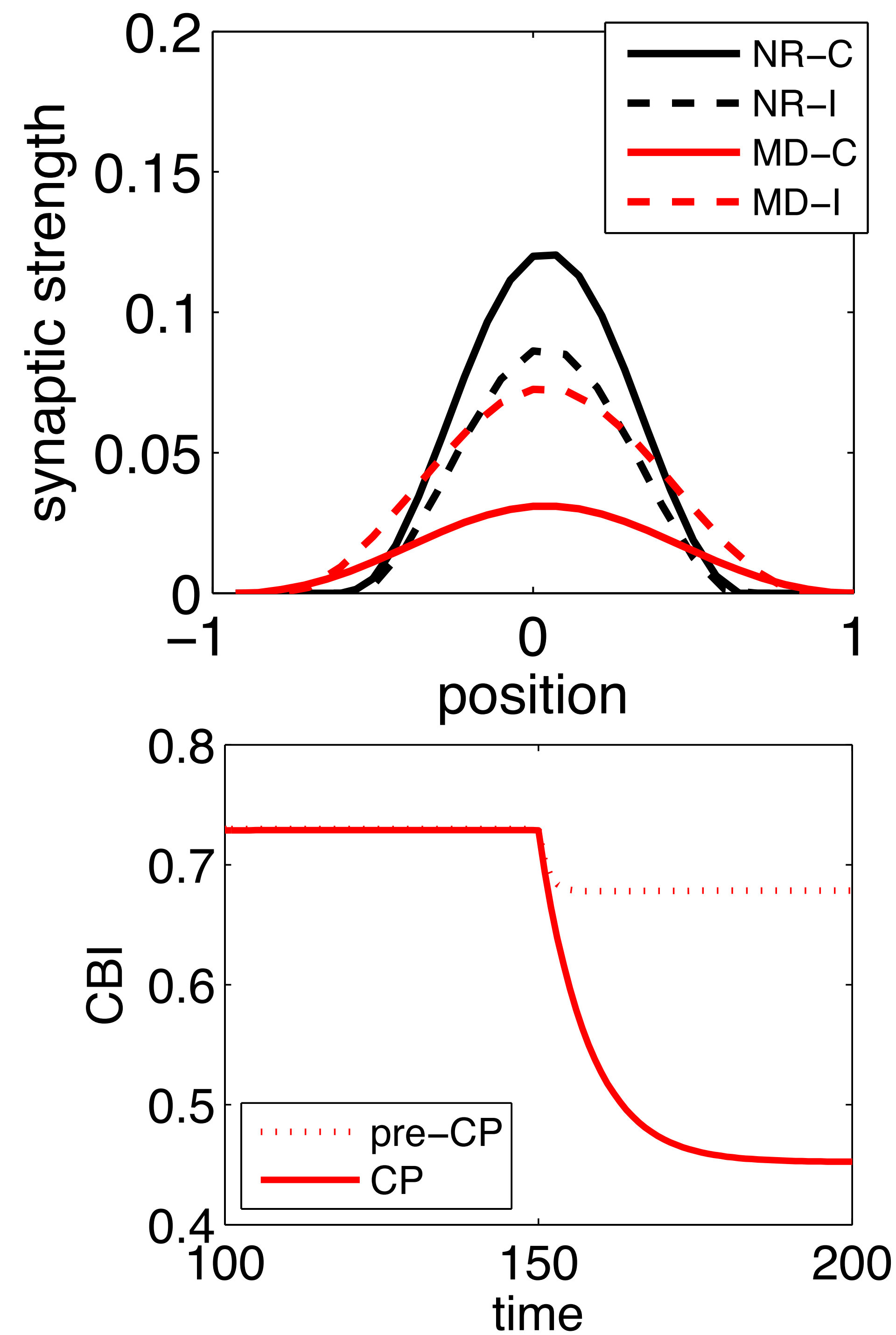
pre-CP



Inhibitory maturation

Suppressed spontaneous activity

CP



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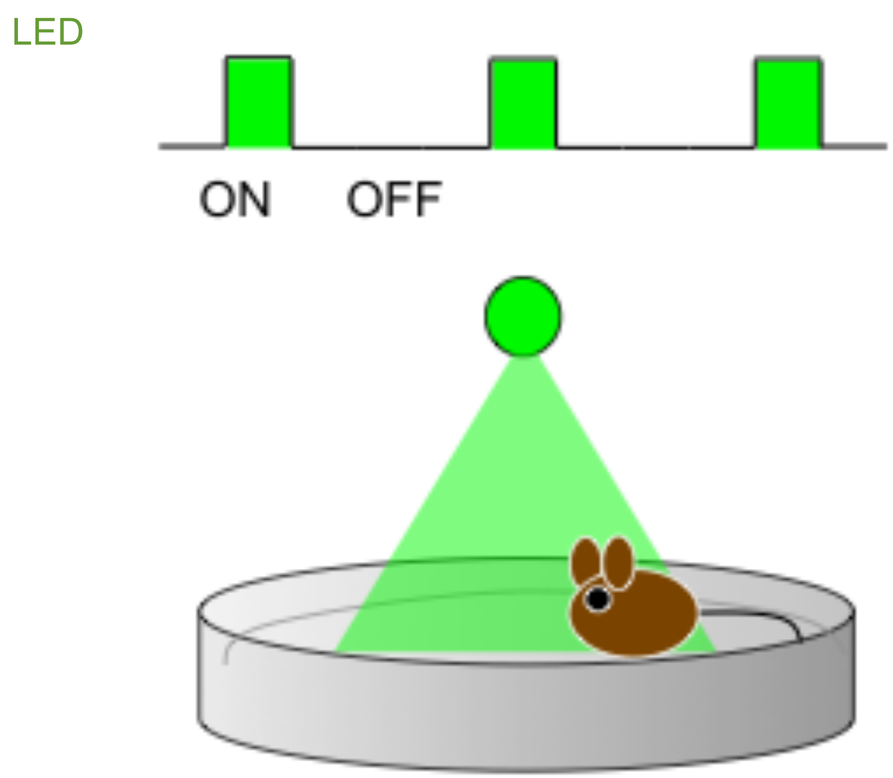
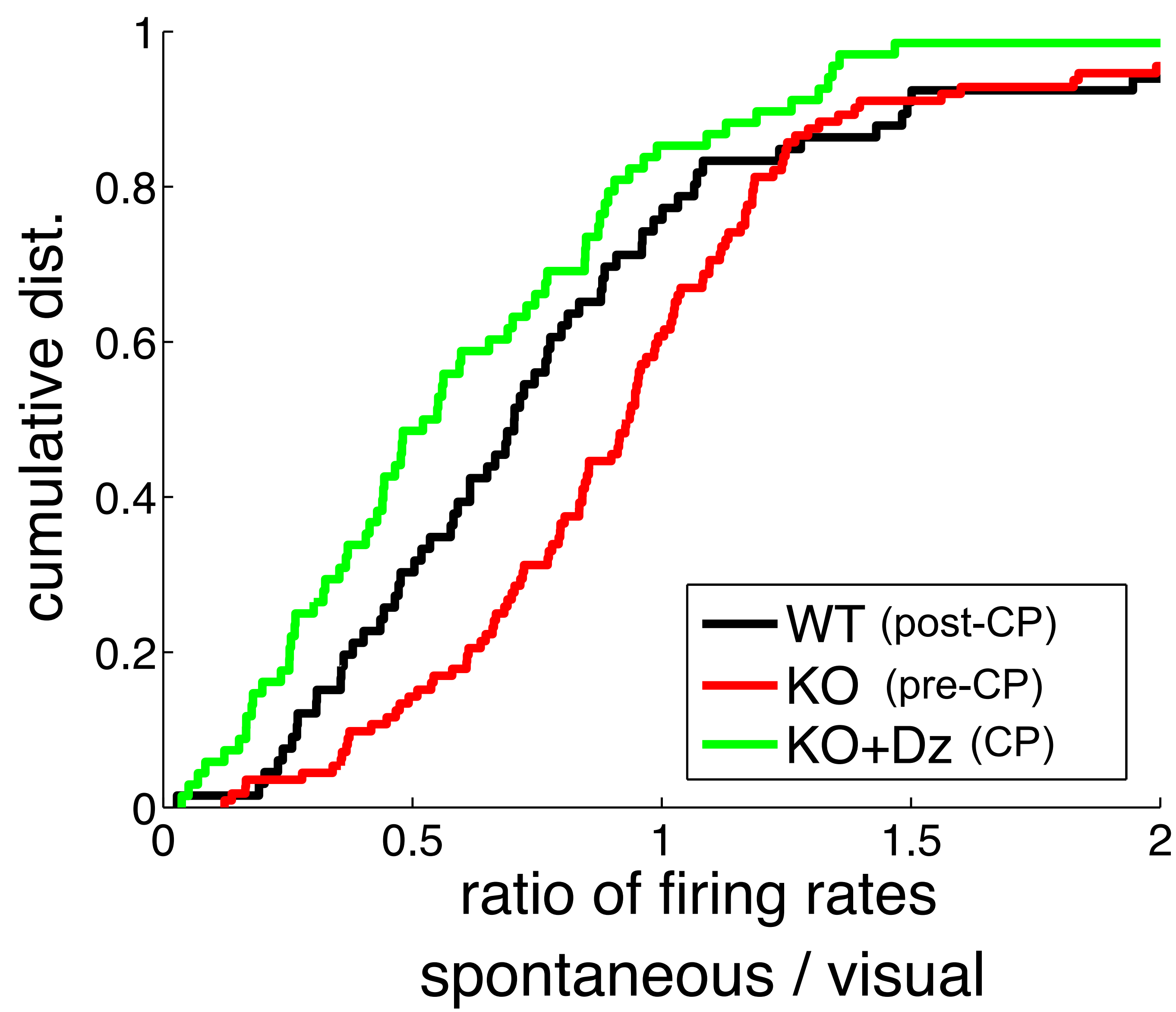
Toyoizumi et al. (2013) A Theory of the Transition to Critical Period Plasticity: Inhibition Selectively Suppresses Spontaneous Activity, Neuron 80(1): 51–63, p. 54 Fig. 2B, C.p. 56 Fig. 3B. p. 56 Fig. 3C.
http://www.sciencedirect.com/science/article/pii/S0896627313006466

Inhibition selectively suppresses spontaneous activity at the onset of the CP.

Tetrode recording from freely behaving adult mice



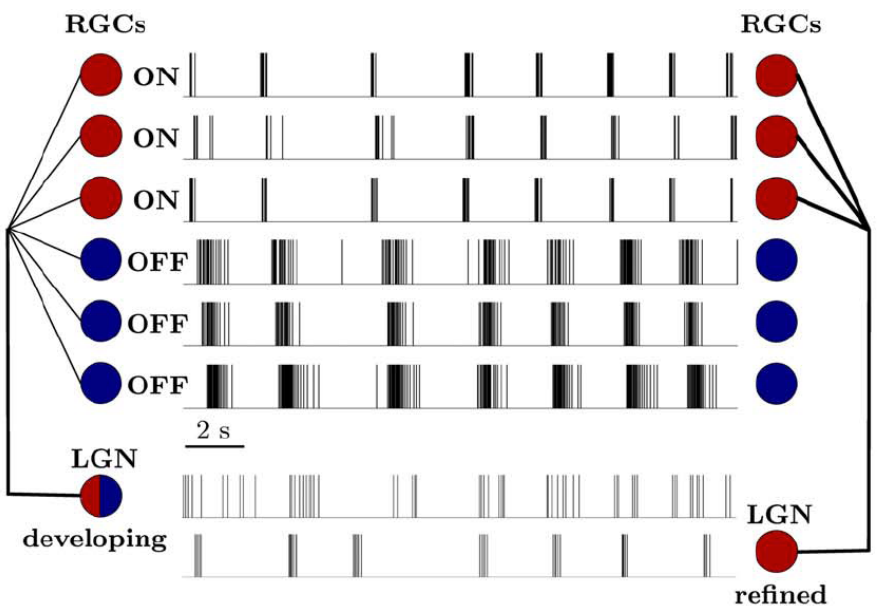


*

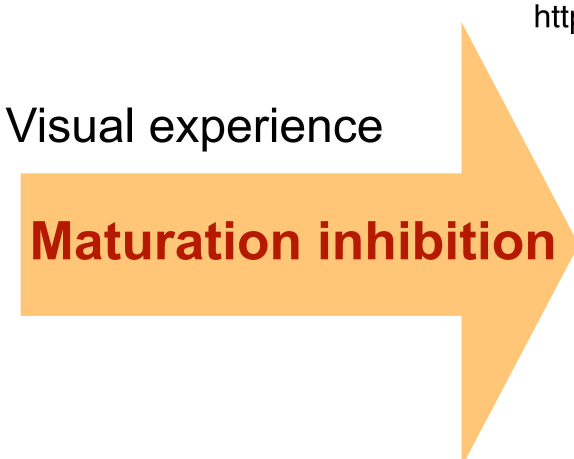
Toyoizumi et al. (2013) A Theory of the Transition to Critical Period Plasticity: Inhibition Selectively Suppresses Spontaneous Activity, Neuron 80(1): 51–63, p. 57 Fig. 4A. p. 57 Fig. 4D.
http://www.sciencedirect.com/science/article/pii/S0896627313006466

Switching of learning cues from internal to external sources

spontaneously driven



Gjorgjieva et al. 2009



Visually driven

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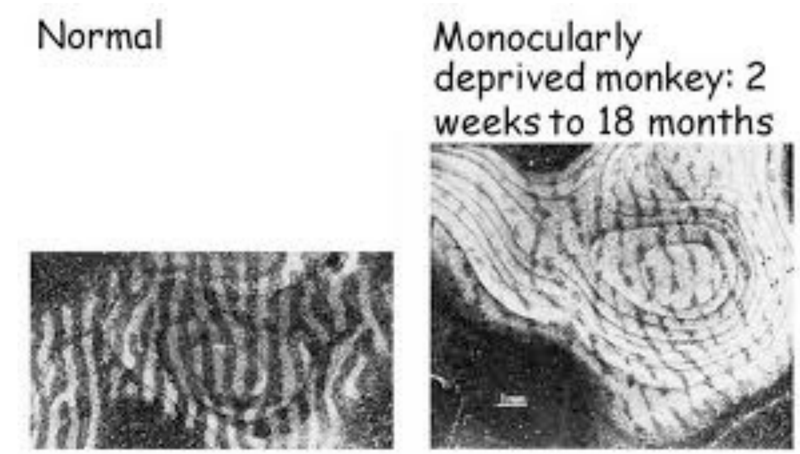

Wiesel, *Nature* 1982.

Chapman and Stryker 1993
Katz and Shatz 1996
Crair et al. 1998
White et al. 2001
Moody and Bosma 2005
Cang et al. 2005, 2008
Hooks and Chen 2006
Moody and Bosma 2006
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Timeline for zebra finch song learning

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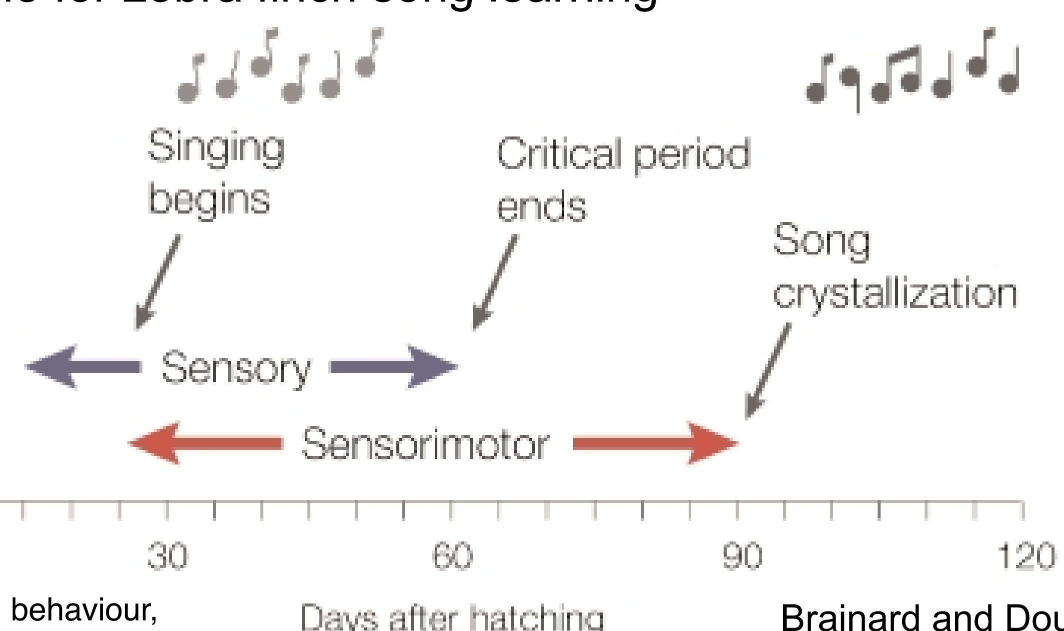


Brainard and Doupe 2000

Optimality-based approaches to adaptation and plasticity

The histogram equalization

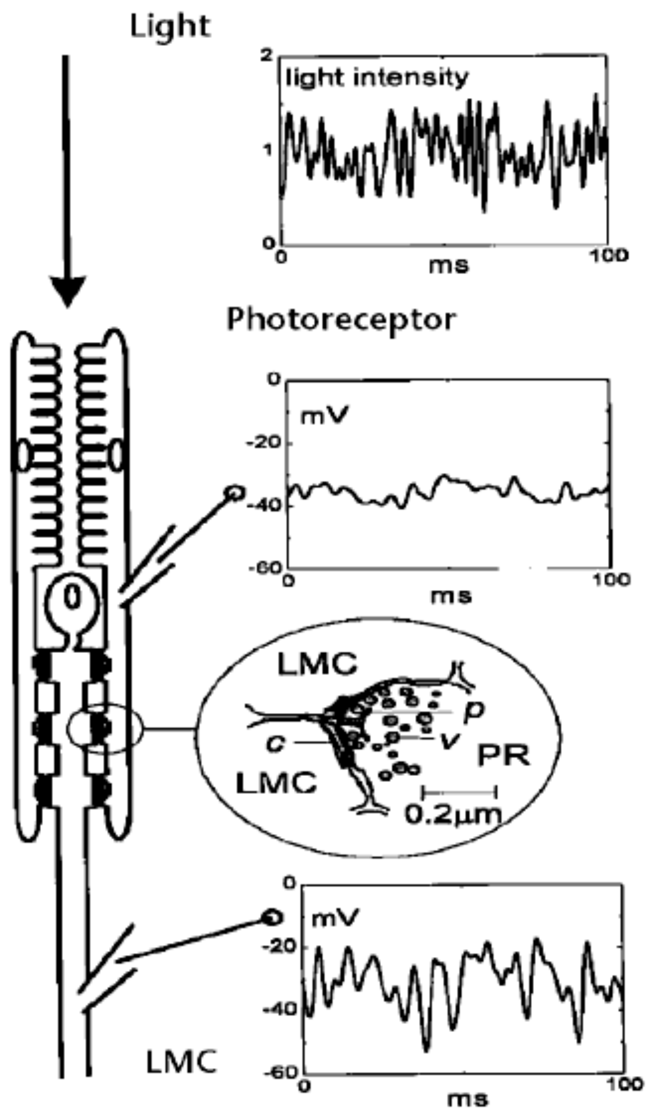
著作権等の都合により、
ここに挿入されていた画像を削除しました

グラフ:ニューロンの働き

Brenner et al. (2000) Adaptive Rescaling Maximizes Information Transmission, Neuron 26(3): 695–702, p. 699 Fig. 8: Optimizing Information Transmission.
http://www.sciencedirect.com/science/article/pii/S0896627300812052

Flies efficiently use neuronal dynamic range

Laughlin et al. (1998) The metabolic cost of neural information, Nature Neuroscience 1(1): 36 - 41, p. 37 Fig. 1: Cells, synapses and signals in blowfly compound eye. http://www.nature.com/neuro/journal/v1/n1/full/nn0598_36.html



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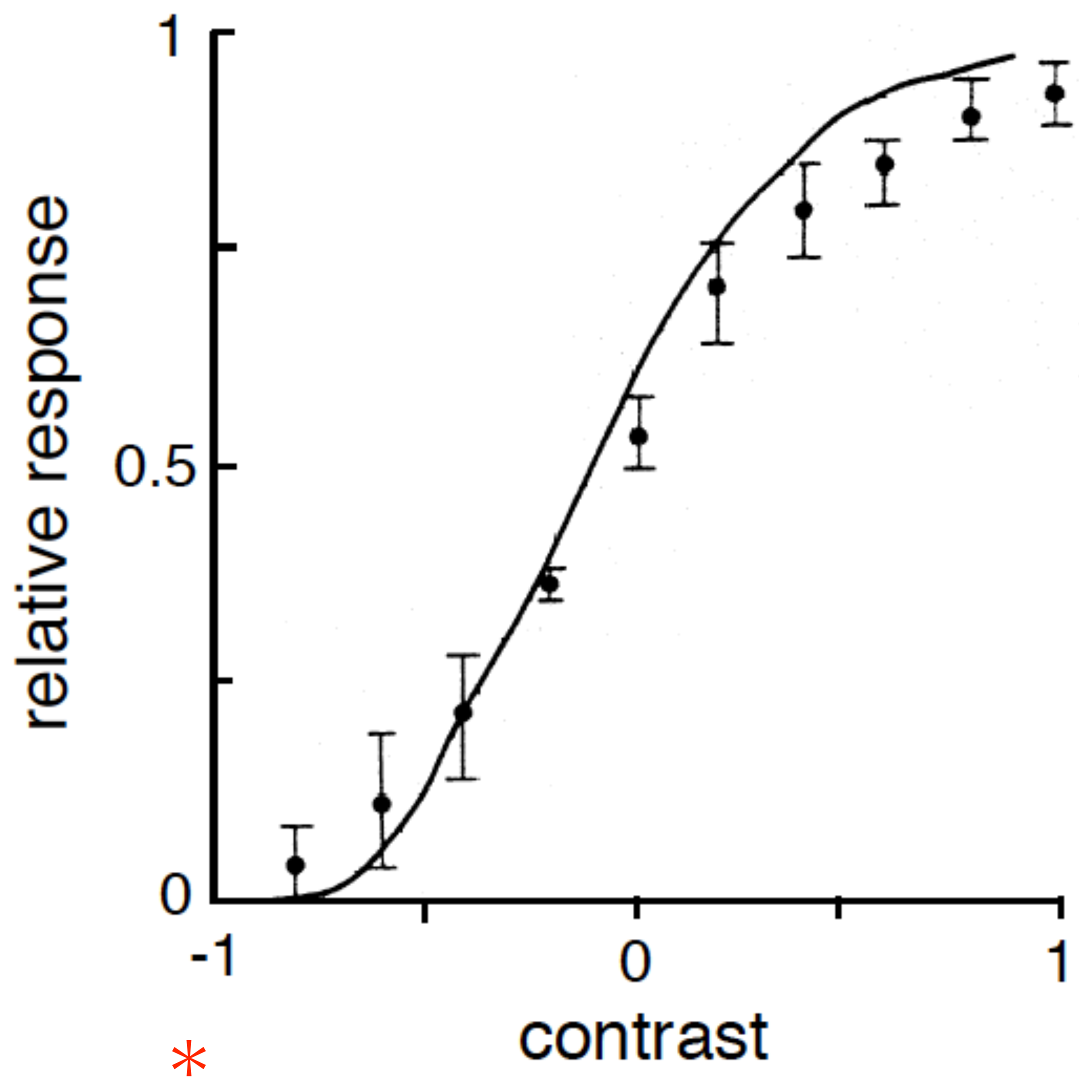
Laughlin, de Ruyter van Steveninck, and Anderson, 1998



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Laughlin, 1981

Dayan and Abbott, Theoretical Neuroscience: Computational and Mathematical Modeling of Neural Systems, MIT Press, 2001, p. 133, Fig. 4.2 Contrast response of the fly LMC (data points) compared to the integral of the natural contrast probability distribution (solid curve).

Adaptive rescaling maximizes information transmission

- Recordings from fly H1 neuron

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グラフ:ニューロンの働き

Brenner et al. (2000) Adaptive Rescaling Maximizes Information Transmission, Neuron 26(3): 695–702, p. 698 Fig. 6a, b.
http://www.sciencedirect.com/science/article/pii/S0896627300812052

Brenner, Bialek, and de Ruyter van Steveninck, 2000

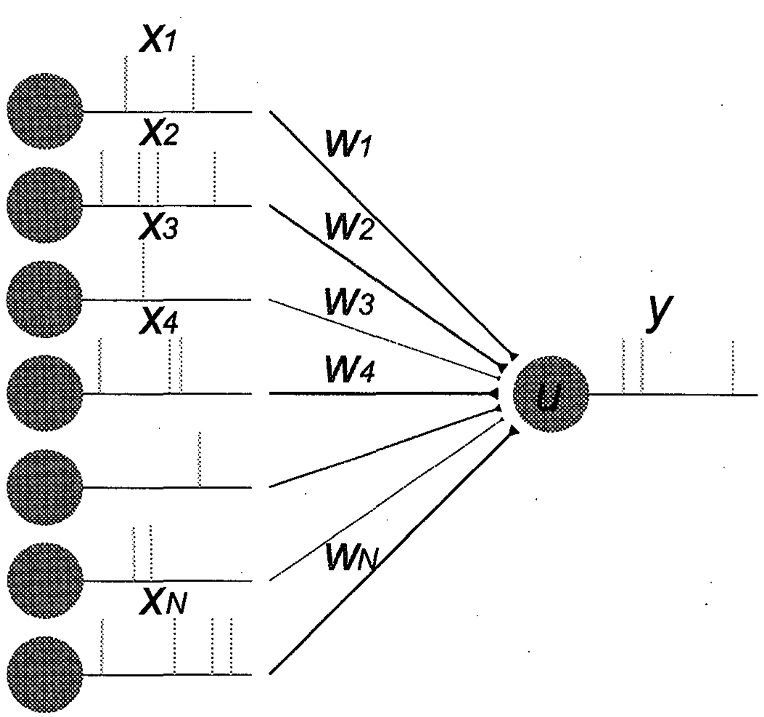
Plasticity for maximizing information transmission

$$L = I(\vec{x}(t); y(t)) - \gamma D[P(y(t))||\bar{P}(y(t))]$$

Information

Energy constraint

$$\frac{dw_i}{dt} = \frac{\partial L}{\partial w_i}$$



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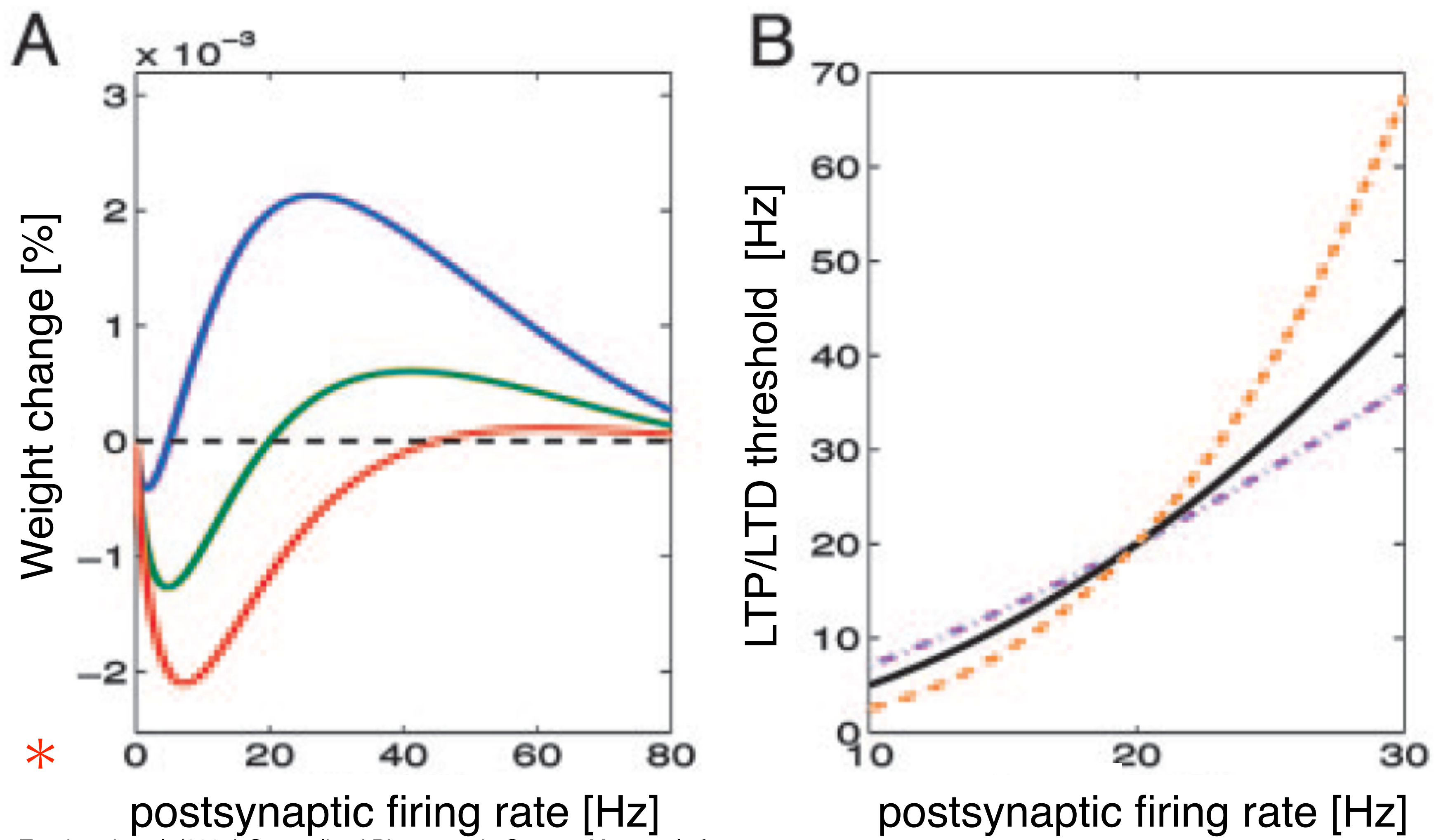
Toyoizumi and Aihara 計測と制御　４５（８）

http://toyoizumilab.brain.riken.jp/taro/papers/toyoizumi06mc.pdf 図１



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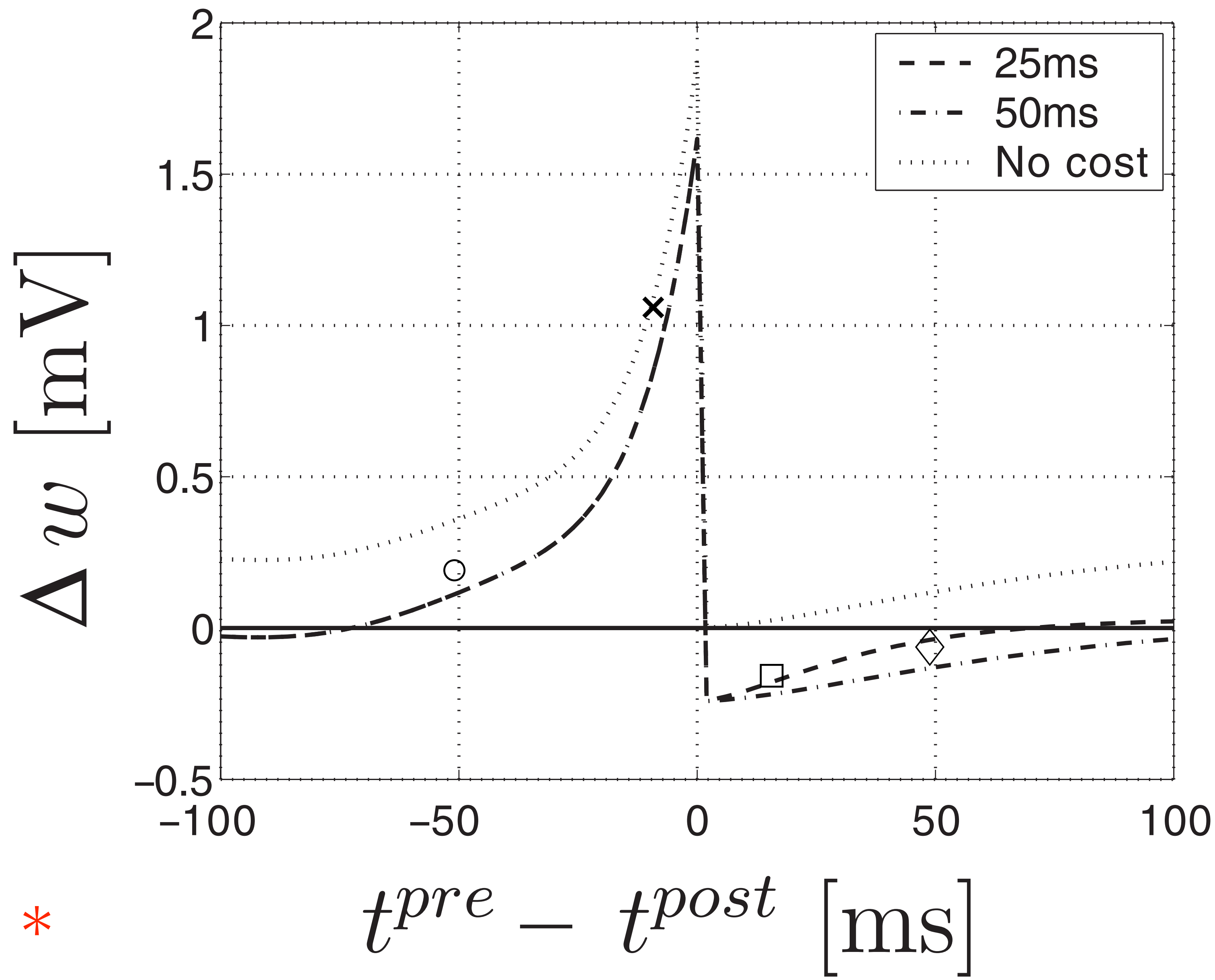
Toyoizumi et al. (2005) Generalized Bienenstock–Cooper–Munro rule for spiking neurons that maximizes information transmission, Proceedings of the National Academy of Sciences of the United States of America 102 (14): 5239–5244, p. 5241 Fig. 2: Relation to BCM rule. http://www.pnas.org/content/102/14/5239.full

Toyoizumi et al. 2005

Information maximization and STDP

With a cost of maintaining synapses….



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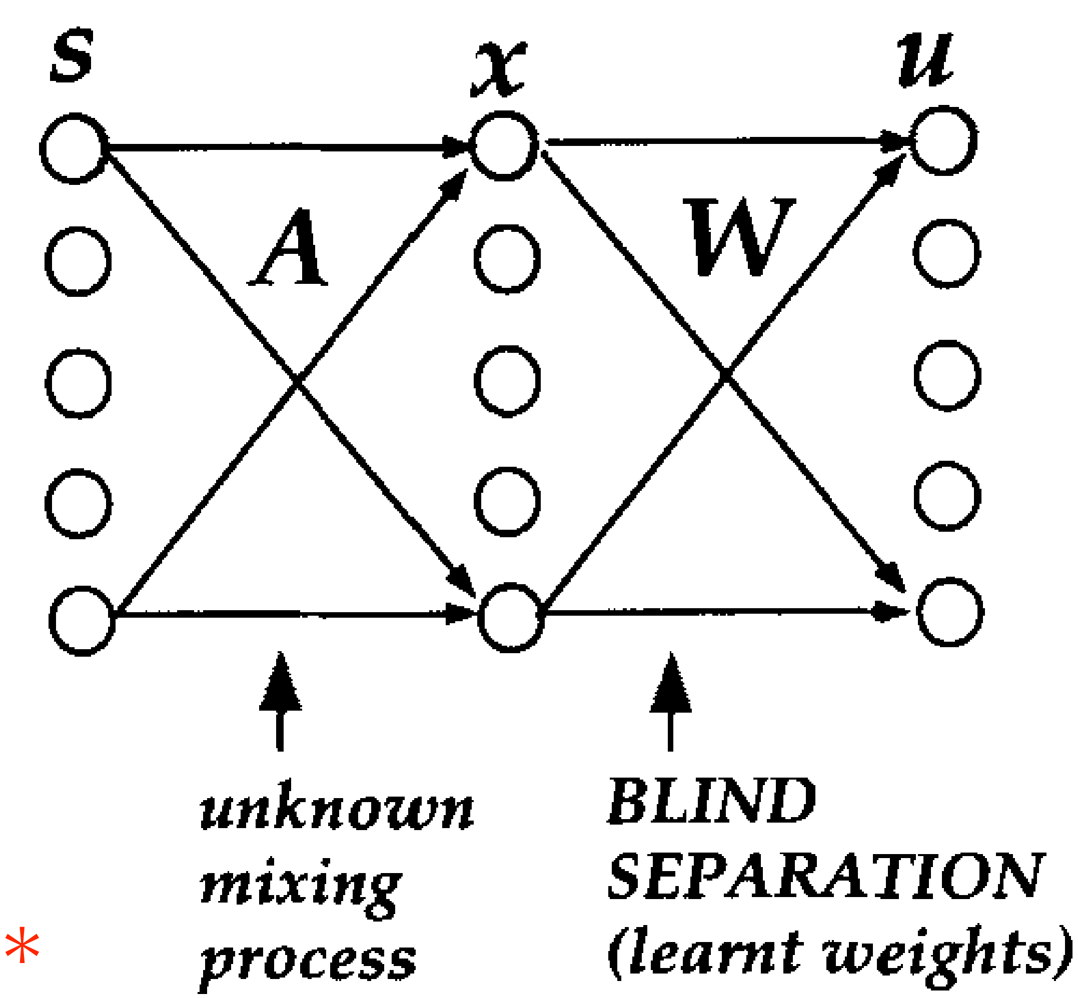
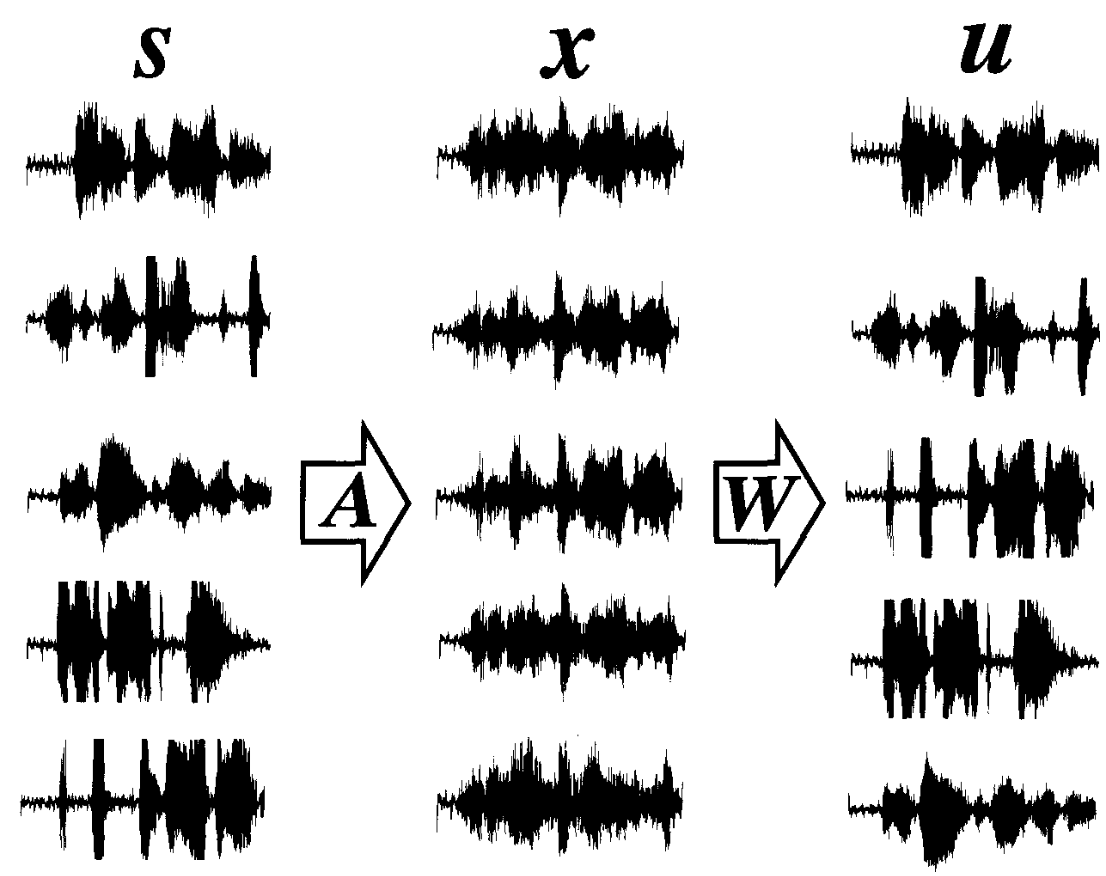
Toyoizumi et al. (2007) Optimality Model of Unsupervised Spike-Timing-Dependent Plasticity: Synaptic Memory and Weight Distribution, Neural Computation 19 (3): 639-671, p. 651 Fig. 3d.
http://www.mitpressjournals.org/doi/abs/10.1162/neco.2007.19.3.639#.VsFsI_msV8E

Information maximization using multiple output neurons

Independent component analysis





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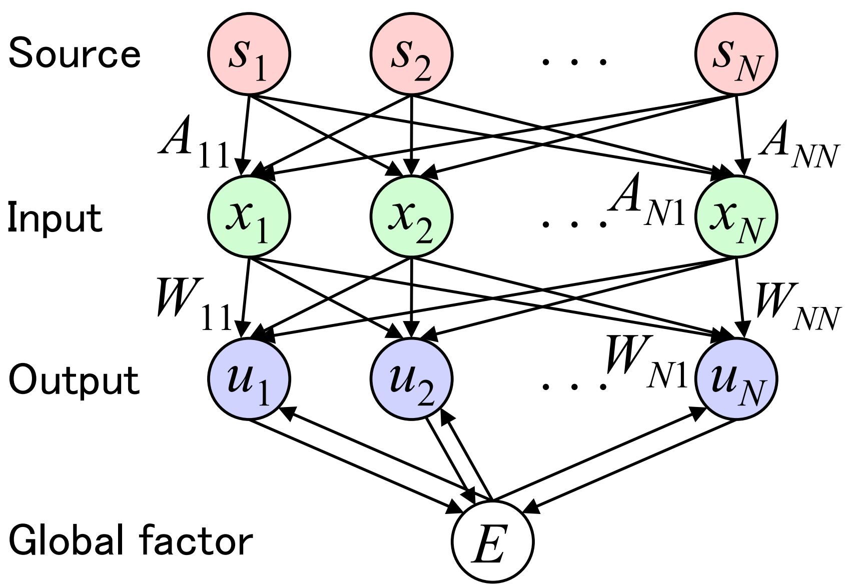
Bell and Sejnowski (1995) An Information-Maximization Approach to Blind Separation and Blind Deconvolution, 7 (6): 1129-1159, p. 1139 Fig. 3(a). p. 1145 Fig. 6. http://www.mitpressjournals.org/doi/abs/10.1162/neco.1995.7.6.1129#.VqcAzVlCOVM

Bell and Sejnowski 1995

A local ICA rule that approximates information maximization



T. Isomura and T. Toyoizumi,
Scientific Reports 6, 28073 (2016).
DOI:10.1038/srep28073
https://www.nature.com/articles/srep28073

Isomura and Toyoizumi, submitted

“Brain-like” computing

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脳とコンピュータの相同を示したパネル図

Merolla et al. (2014) A million spiking-neuron integrated circuit with a scalable communication network and interface, Science 345 (6197): 668-673, p. 670 Fig. 2: TrueNorth architecture.
http://science.sciencemag.org/content/345/6197/668.full