Weight dependent synaptic plasticity rules

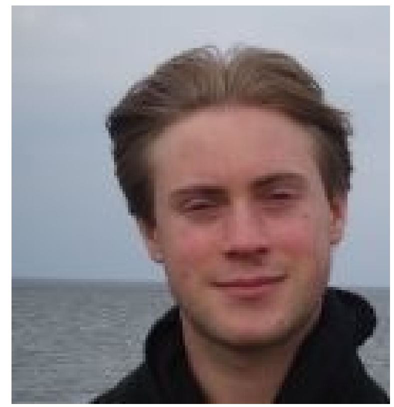
Mark van Rossum

Institute for Adaptive and Neural Computation
University of Edinburgh, UK

Acknowledgements

Guy Billings

Cian O'Donnell



Adam Barrett

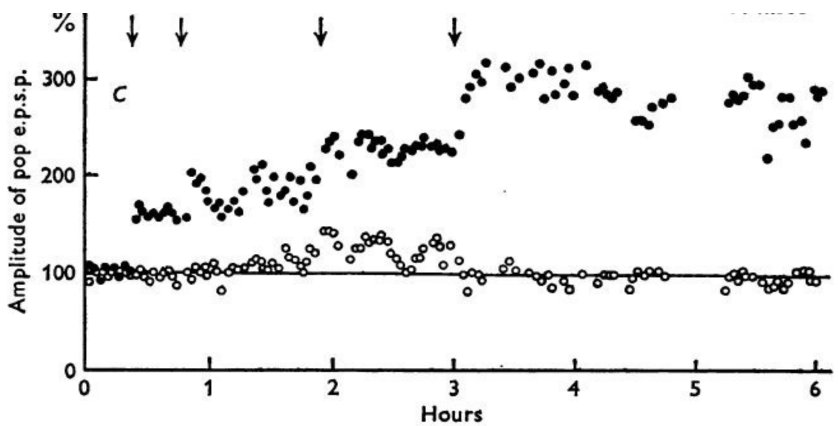
Maria Shippi

EPSRC Engineering and Physical Sciences Research Council

HFSP

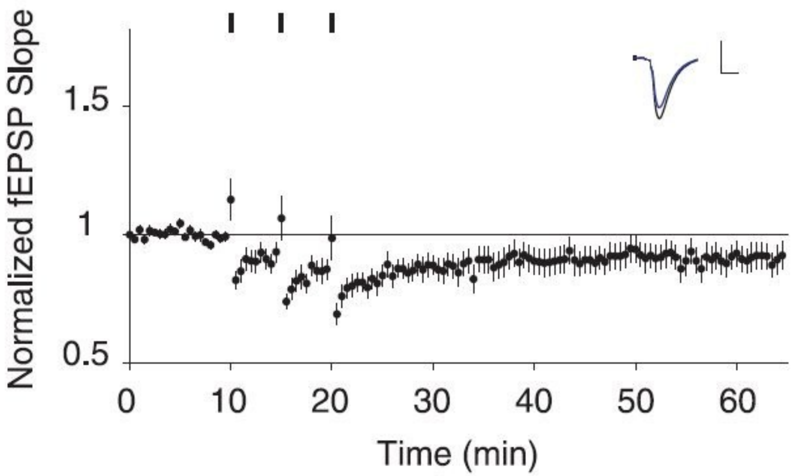
Hebbian long term plasticity

LTP



[Bliss & Lomo '73]

LTD



[O'Connor & Wang '05]

Pairing high pre- and post synaptic activity =>
Long term potentation

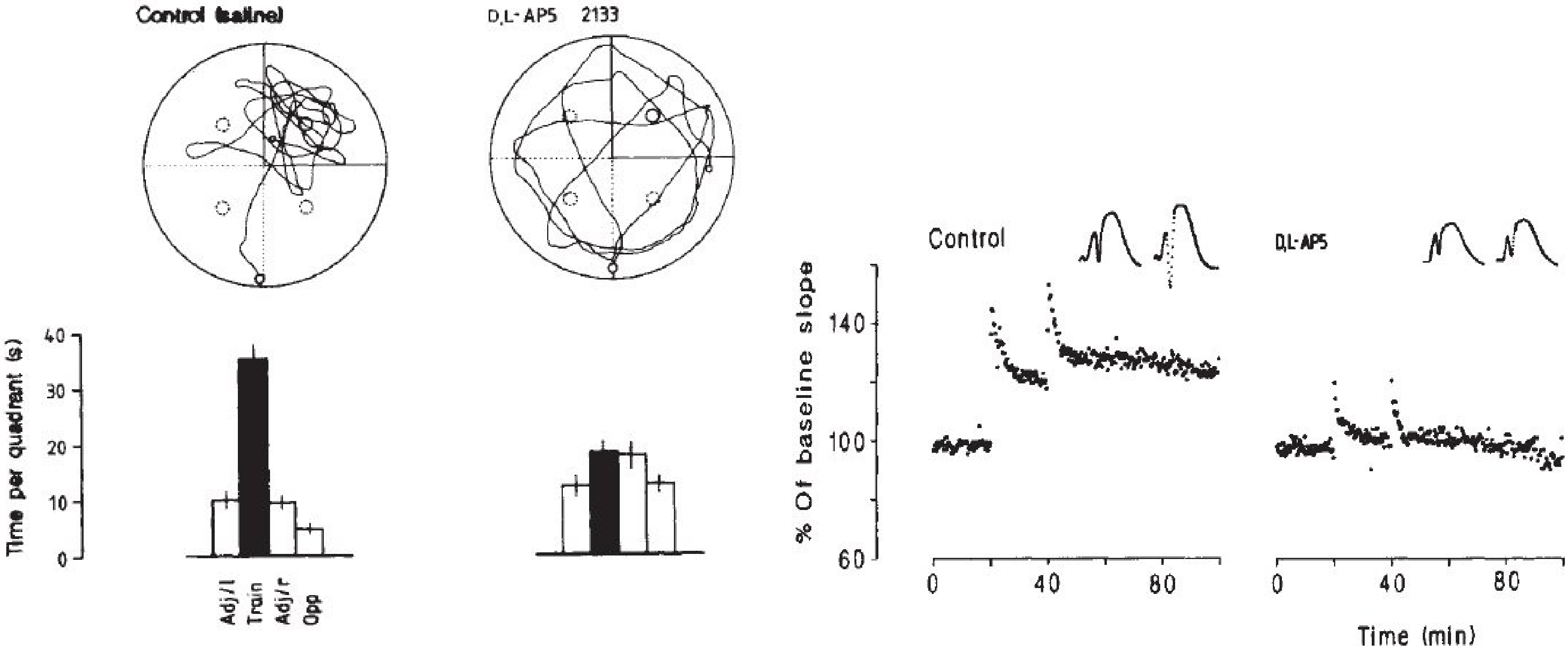
Pairing with low activity =>
Long term depression

Synaptic plasticity = memory?

[Martin, Greenwood, Morris, '00]

- Anterograde alteration
  prevent synaptic plasticity → anterograde amnesia
  Yes (NMDA-block)

AP5 blocks learning



[Morris et al '86]

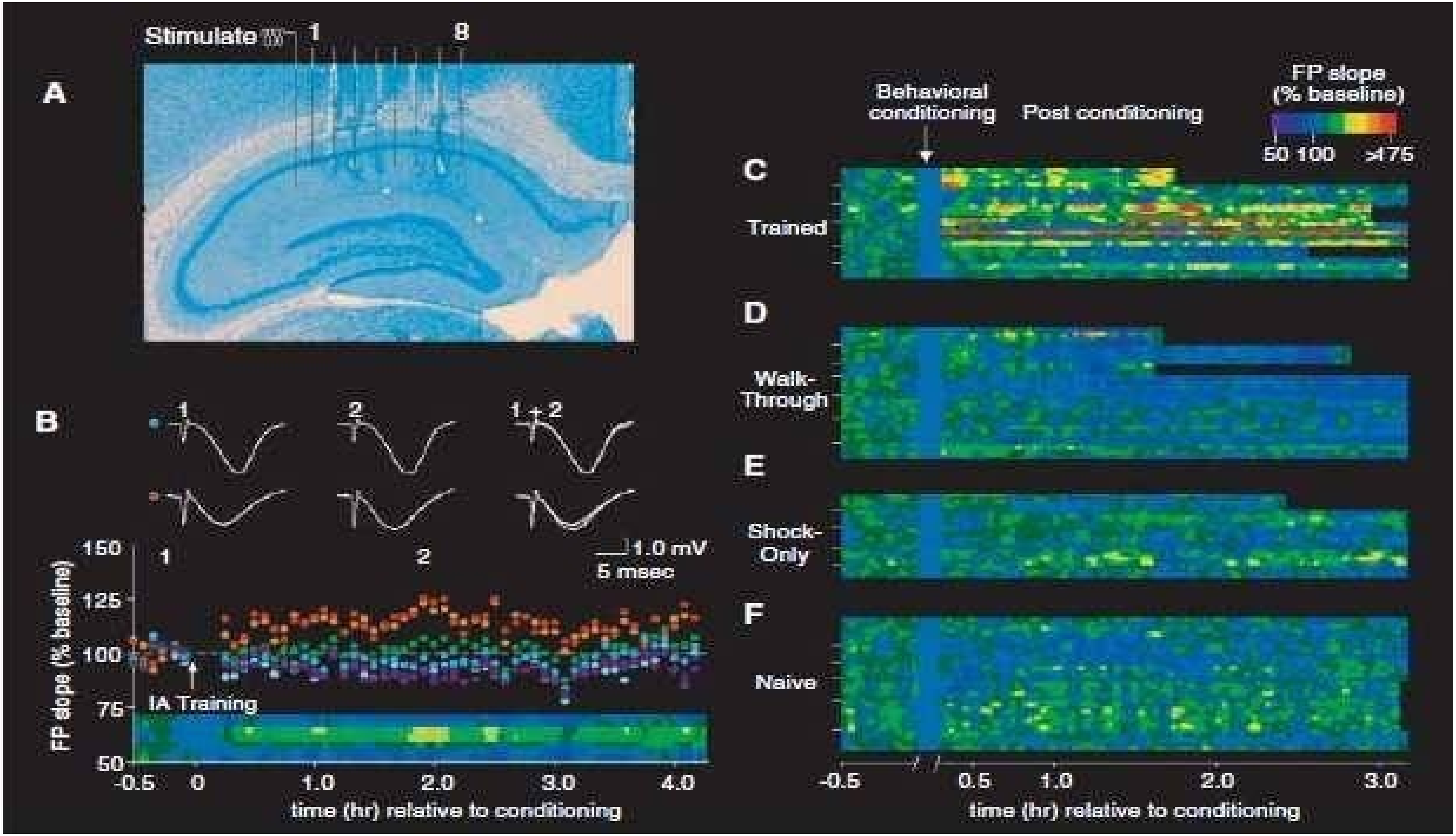
Synaptic plasticity = memory?

[Martin, Greenwood, Morris, '00]

- Anterograde alteration
  prevent synaptic plasticity → anterograde amnesia
  Yes (NMDA-block)

- Detectability
  changes in behaviour and synaptic efficacy should be correlated
  Yes (Whitlock et al.)

Synaptic plasticity=memory?



[Whitlock,.. and Bear '06]

Synaptic plasticity = memory?

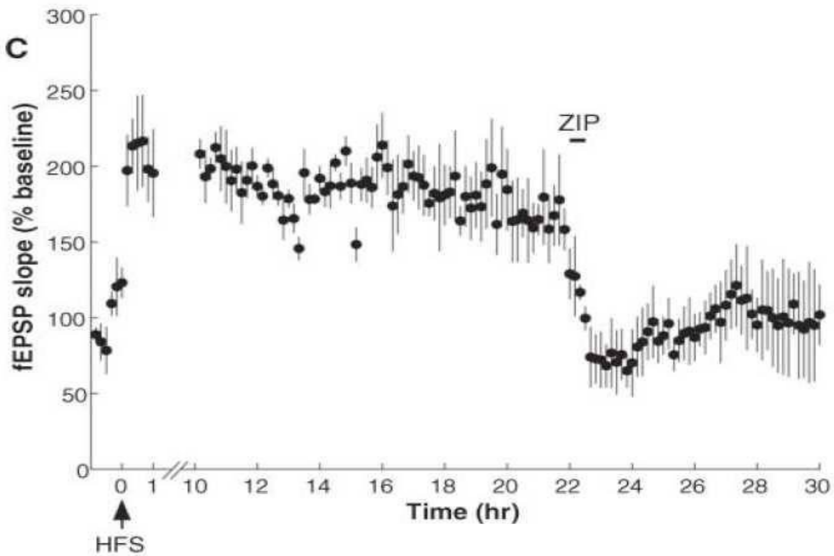
[Martin, Greenwood, Morris, '00]

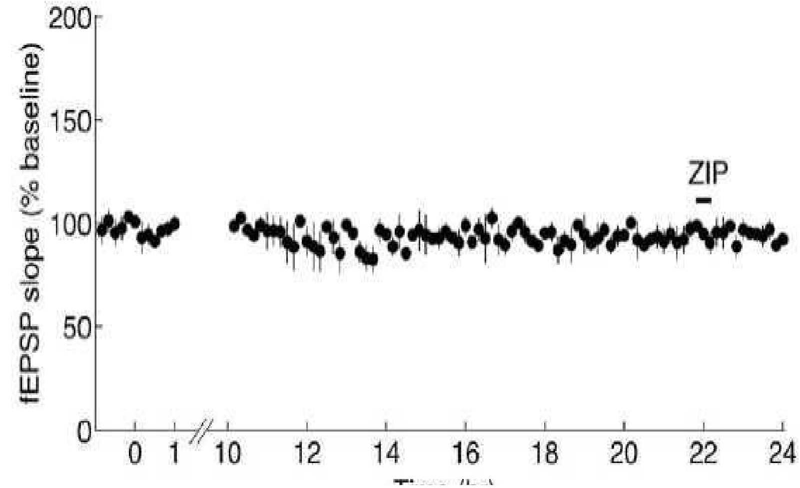
- Anterograde alteration
  prevent synaptic plasticity → anterograde amnesia
  Yes (NMDA-block)

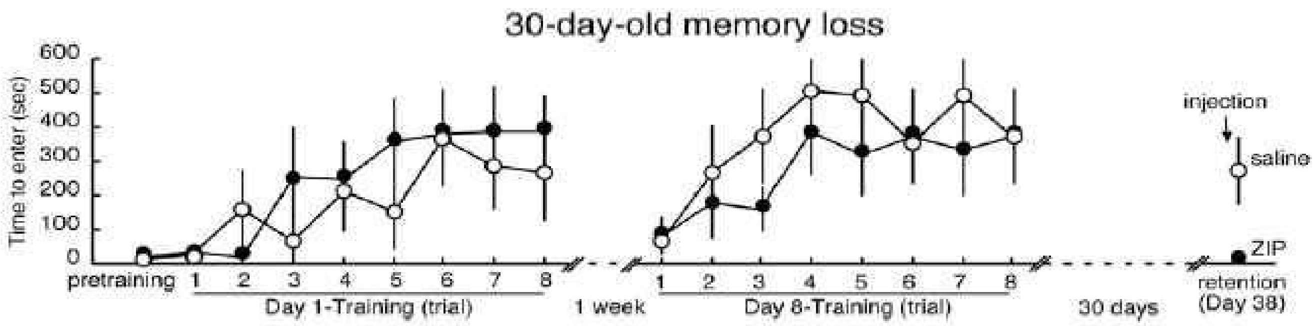
- Detectability
  changes in behaviour and synaptic efficacy should be correlated
  Yes (Whitlock et al.)

- Retrograde alteration
  alter synaptic efficacies → retrograde amnesia
  Yes (PKMζ), but...

Late LTP maintenance as an active process







ZIP disrupts one month old memory

[Pastalkova et al '06]

Synaptic plasticity = memory?

[Martin, Greenwood, Morris, '00]

- Anterograde alteration
  prevent synaptic plasticity → anterograde amnesia
  Yes (NMDA-block)

- Detectability
  changes in behaviour and synaptic efficacy should be correlated
  Yes (Whitlock et al.)

- Retrograde alteration
  alter synaptic efficacies → retrograde amnesia
  Yes (PKMζ), but...

- Mimicry
  change synaptic efficacies → new 'apparent' memory
  Not quite yet...

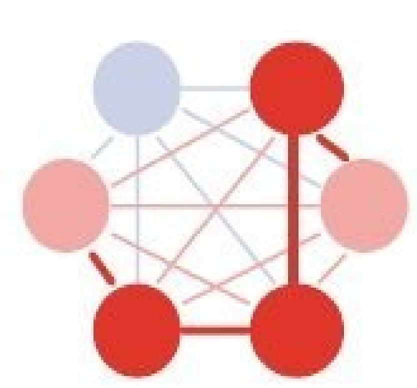
Computational modelling of synaptic plasticity

Ultimate goal: Quantitative, accurate models in health and disease

Complicated rules. Plasticity depends on:

- pre and post activity,
- reward, modulation, history, other synapses, homoeostasis..
- **synaptic weight itself**

Most models are oversimplified



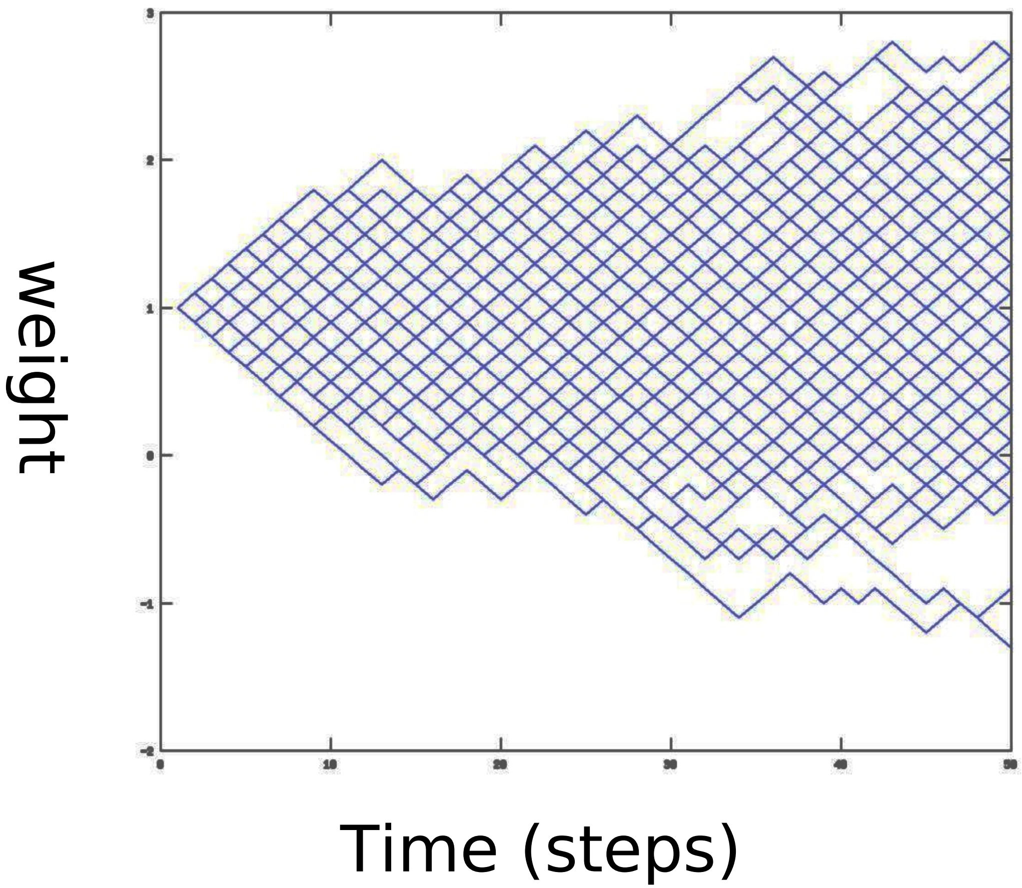
Plasticity due to random patterns: random walk

Random, independent sequence of LTP and LTD

weight

index

Synaptic weights divergence



- Diffusion of weights (Sejnowski '77)
- Run away, so need bounds on the weights

Dealing with synaptic weights divergence

Some possible solutions:

- Hard bounds
- BCM (*)
- Normalization/homeostasis (*)

$$\sum_i w_i = 1$$
$$\sum_i w_i^2 = 1$$

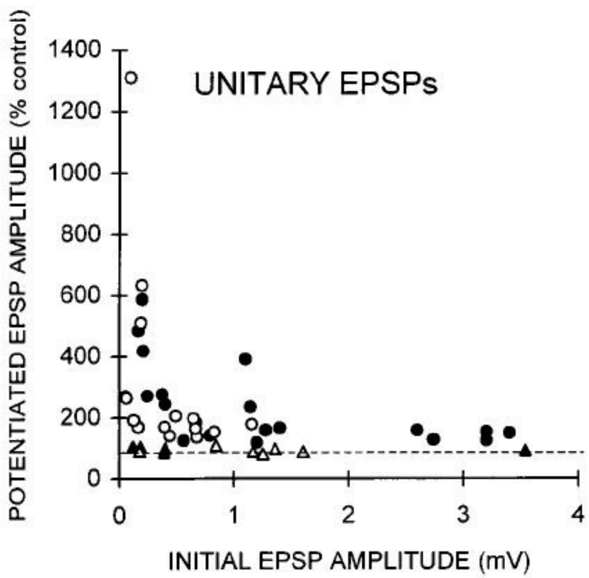
- Non-linear STDP (*)

- What is does biology say?
- The outcome of the rules depends strongly on the chosen solution...

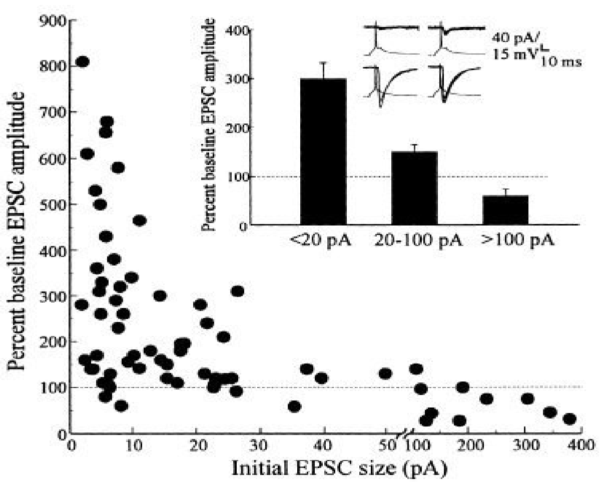
(*) Competitive

LTP/LTD is weight dependent

Long term potentiation

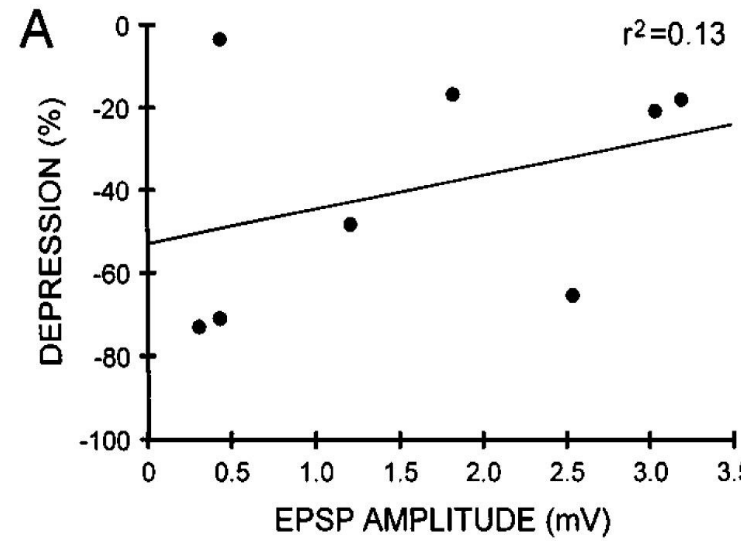


[Debanne '99]



[Montgomery '01]

Long term depression



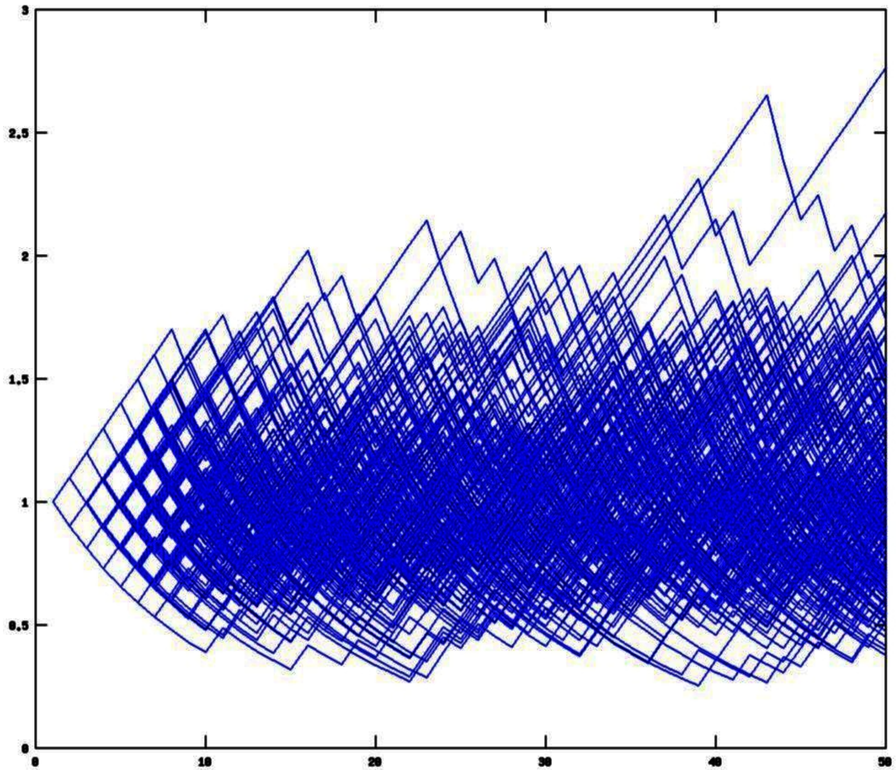
[Debanne '96]

Weight dependent random walk

weight

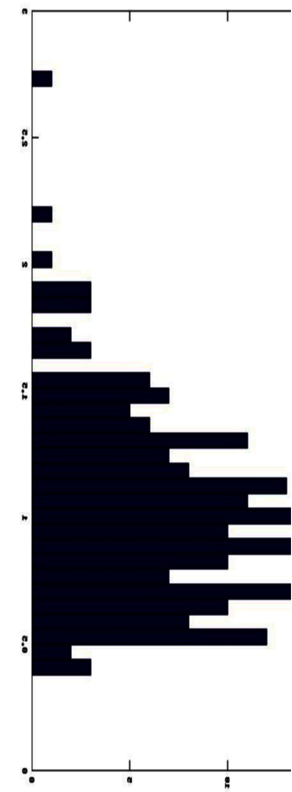
index

Weight dependent learning rules



weight

Time (steps)

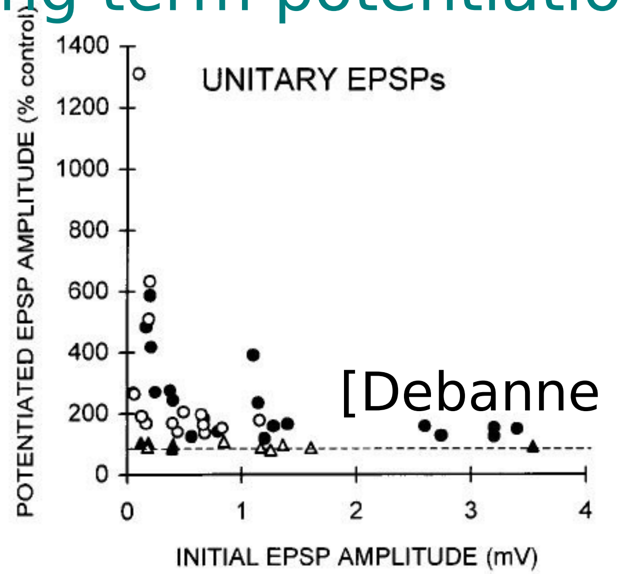


P(w)

- Weight dependent plasticity prevents run away
- Leads to realistic weights distributions [MvR et al.'00]

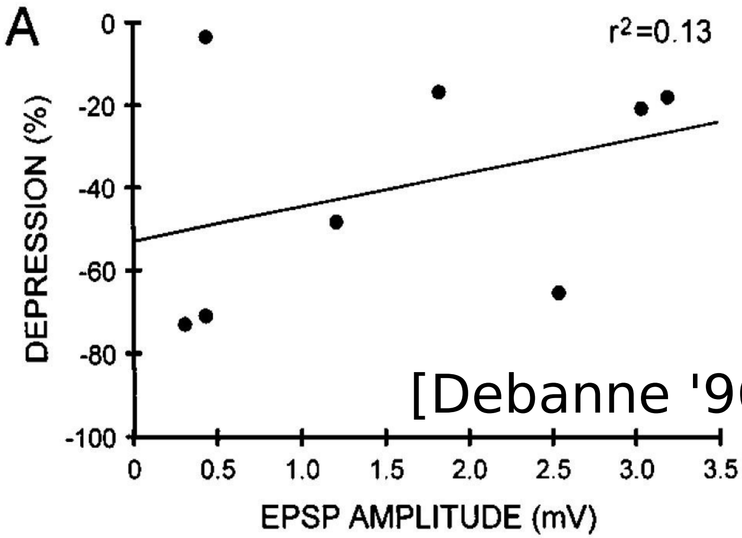
Simple model

Long term potentiation



[Debanne '99]

Long term depression



[Debanne '96]

<u>Simple description</u>

Relative change:

$$\frac{\Delta W^-}{W} = -c_1; \quad \frac{\Delta W^+}{W} = \frac{c_2}{W}$$

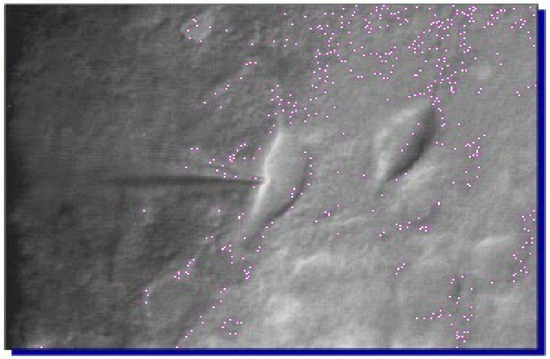
Absolute change:

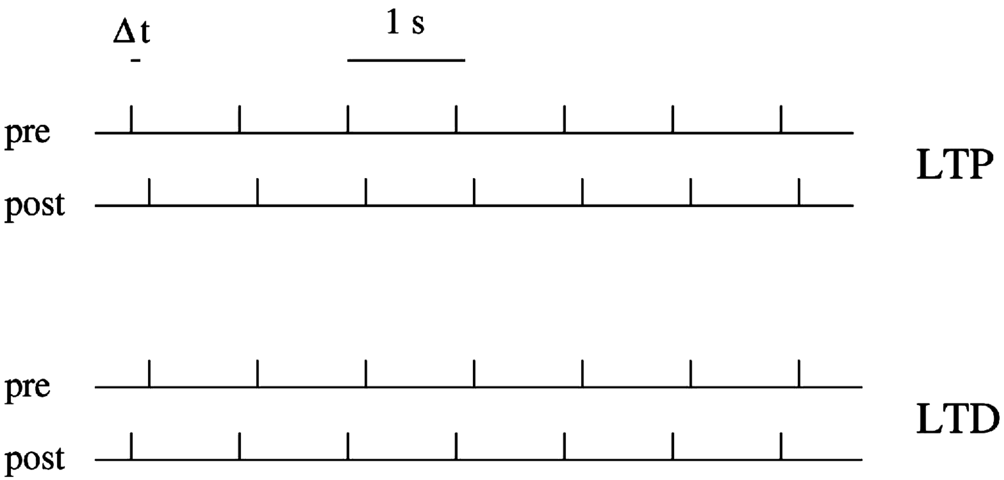
$$\Delta W^- = -c_1 W; \quad \Delta W^+ = c_2$$

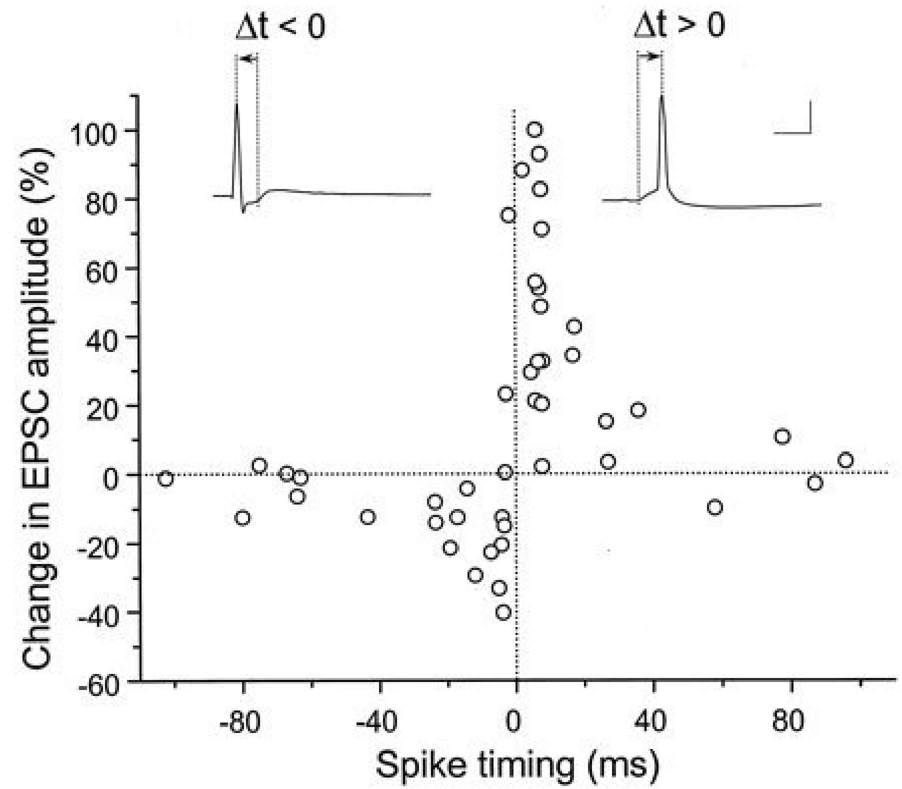
Table of contents

- **Weight dependent STDP in single neurons and networks**
- Spine volume dynamics can implement weight dependence
- Weight dependence increases information capacity

Spike Timing Dependent Plasticity
Experimental data

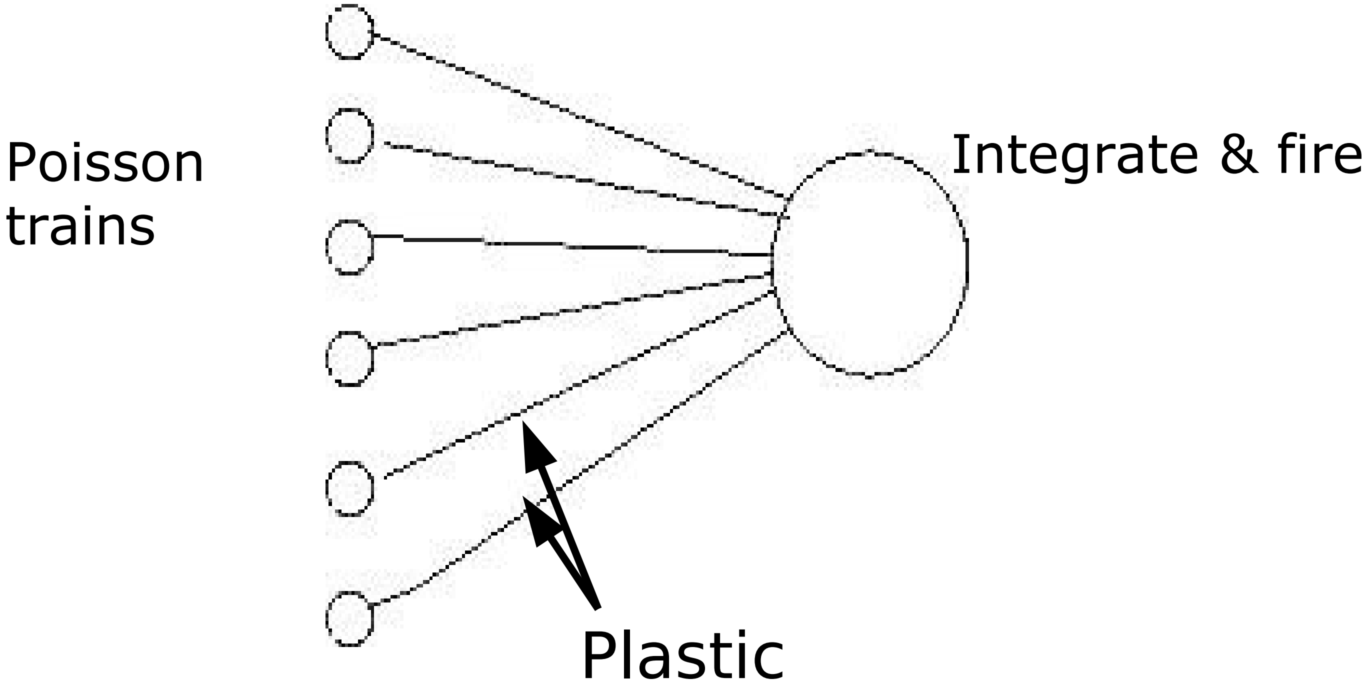




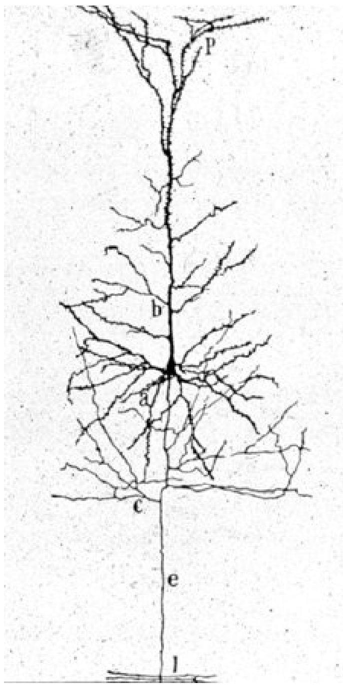


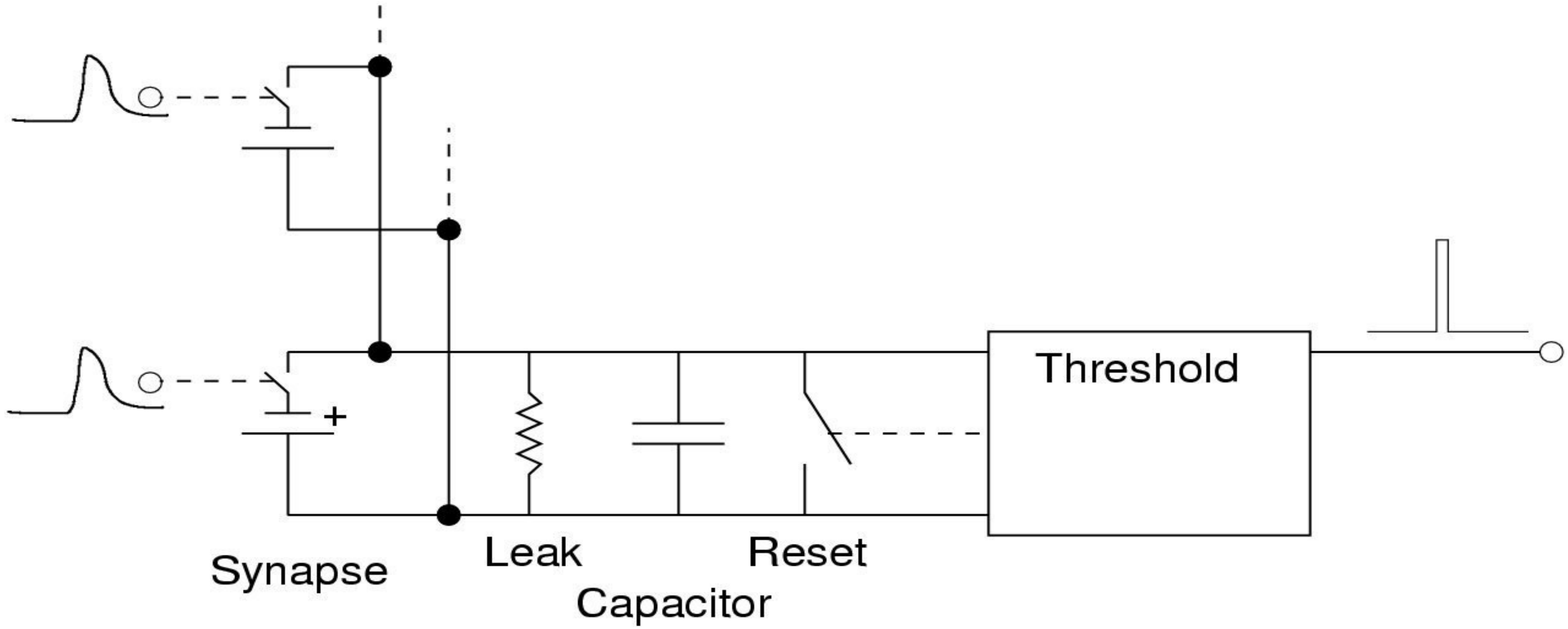
[Bi & Poo 1998]

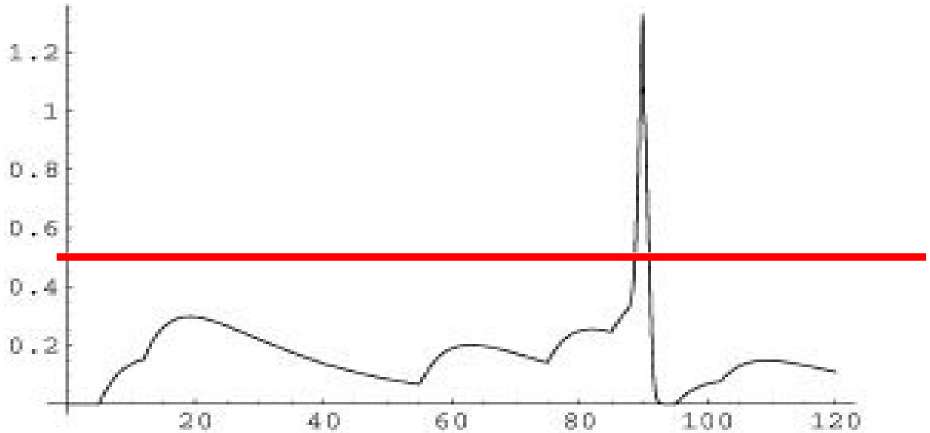
Modelling STDP



Integrate-and-fire neurons

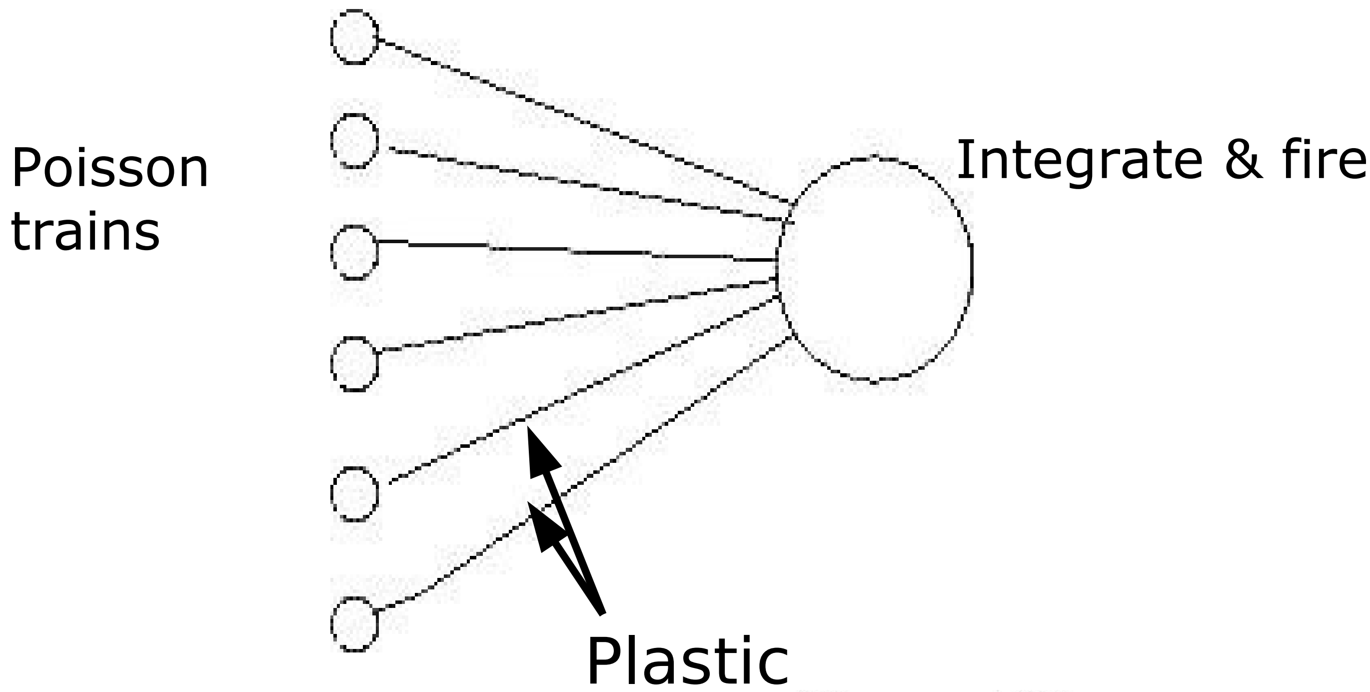


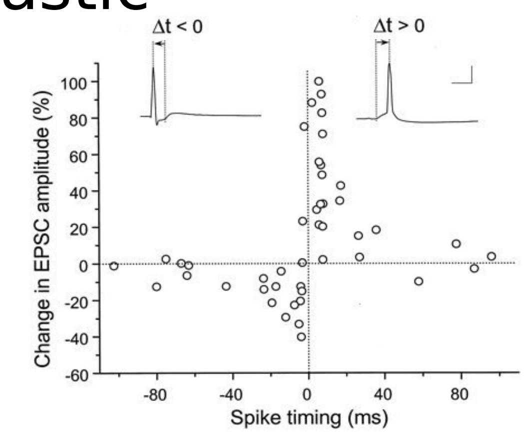




[Lapicque 1907,
Brunel & MvR 2007]

Modelling STDP



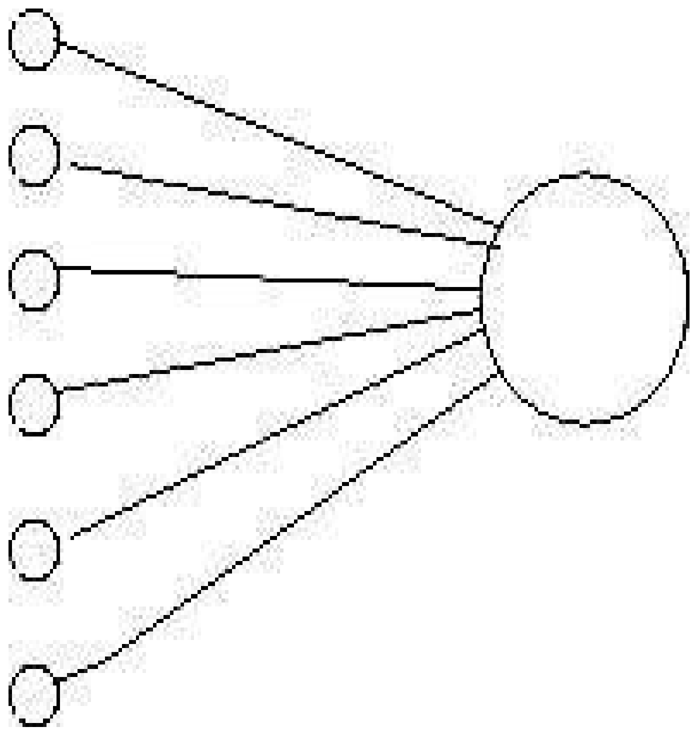


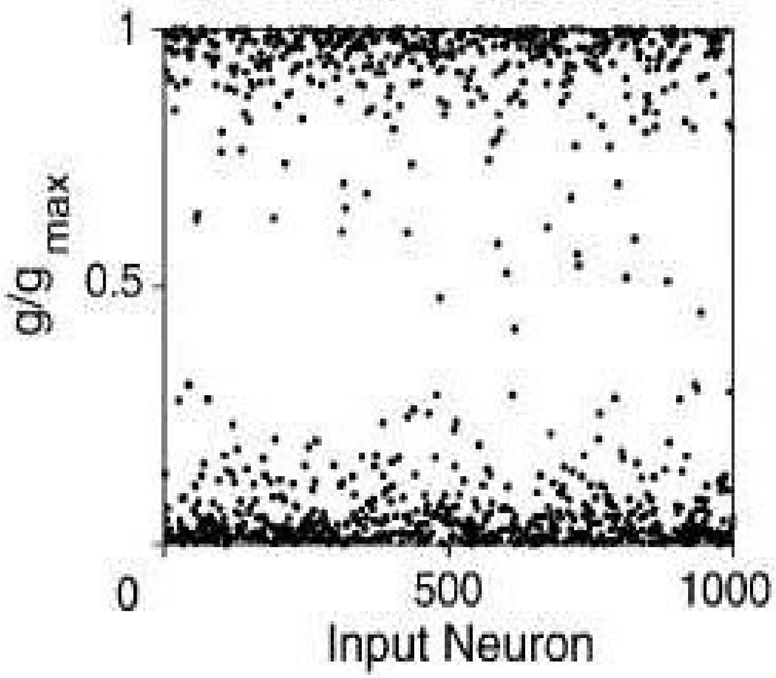
$$\Delta w = -A_{-} e^{-(t_{post} - t_{pre})/\tau_{-}}$$

$$\Delta w = A_{+} e^{-(t_{pre} - t_{post})/\tau_{+}}$$

Modelling STDP

Poisson trains

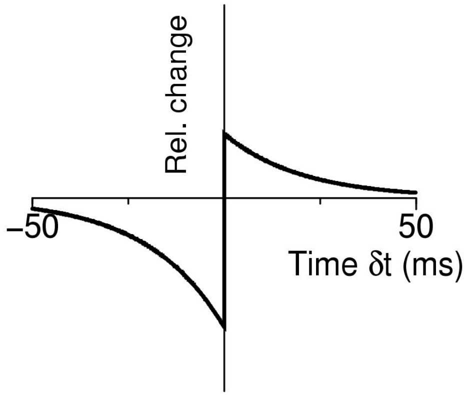




Fokker-Planck approach

$$\Delta w = -A_{-} e^{-(t_{post} - t_{pre})/\tau_{-}}$$

$$\Delta w = A_{+} e^{-(t_{pre} - t_{post})/\tau_{+}}$$

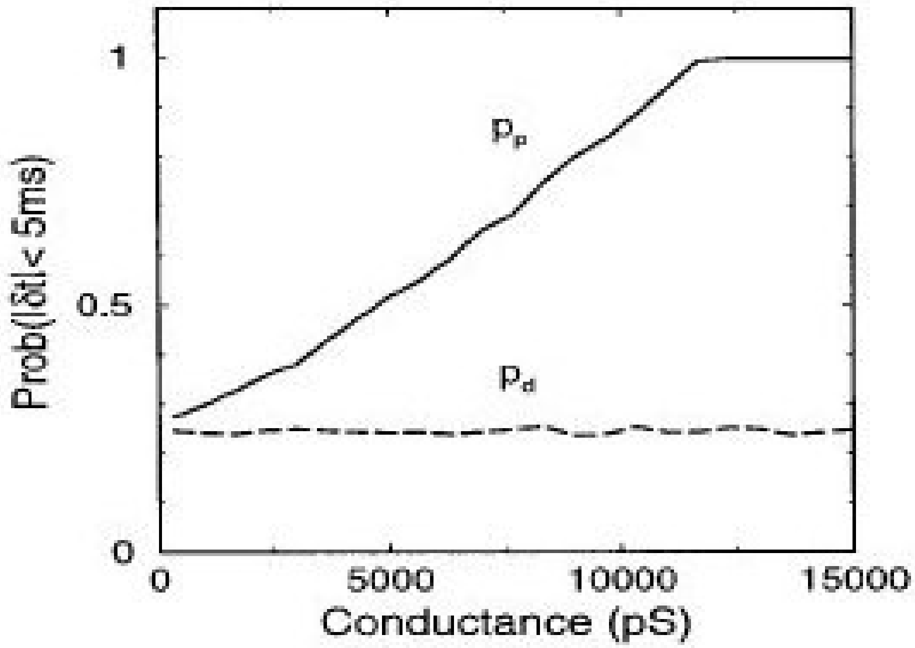


drift diffusion

$$\frac{\partial P(w,t)}{\partial t} = \frac{-\partial}{\partial w}[A(w)P(w,t)] + \frac{1}{2}\frac{\partial^2}{\partial w^2}[D P(w,t)]$$

$$A(w) = -p_d A_{-} + p_p A_{+}$$

Modelling STDP

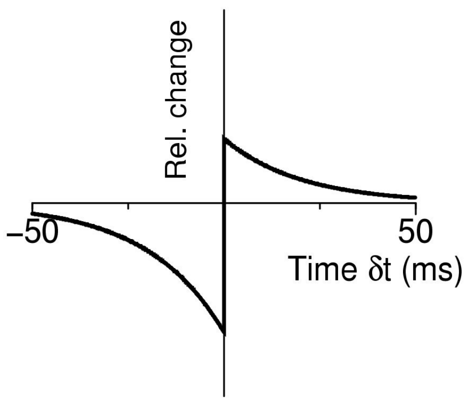


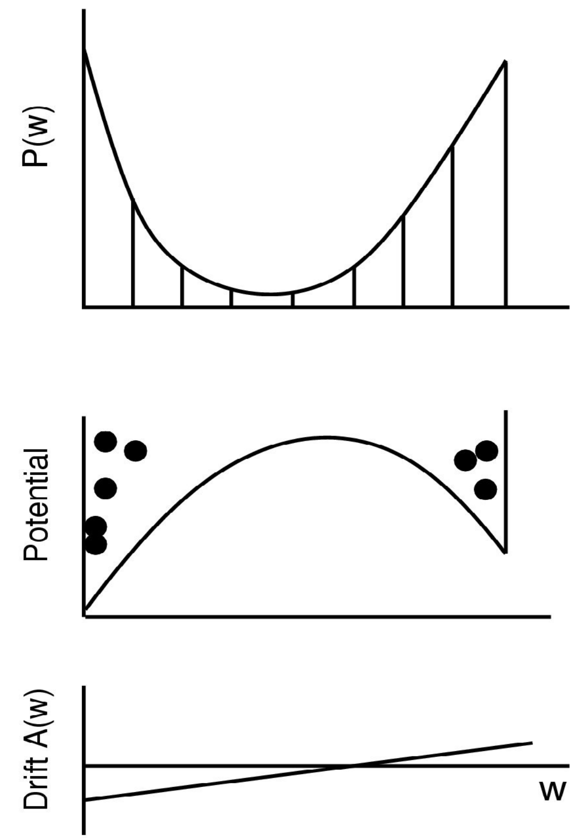
$$p_p = p_d\left(1 + w / \Sigma w\right)$$

Fokker-Planck approach

$$\Delta w = -A_{-} e^{-(t_{post} - t_{pre})/\tau_{-}}$$

$$\Delta w = A_{+} e^{-(t_{pre} - t_{post})/\tau_{+}}$$





drift diffusion

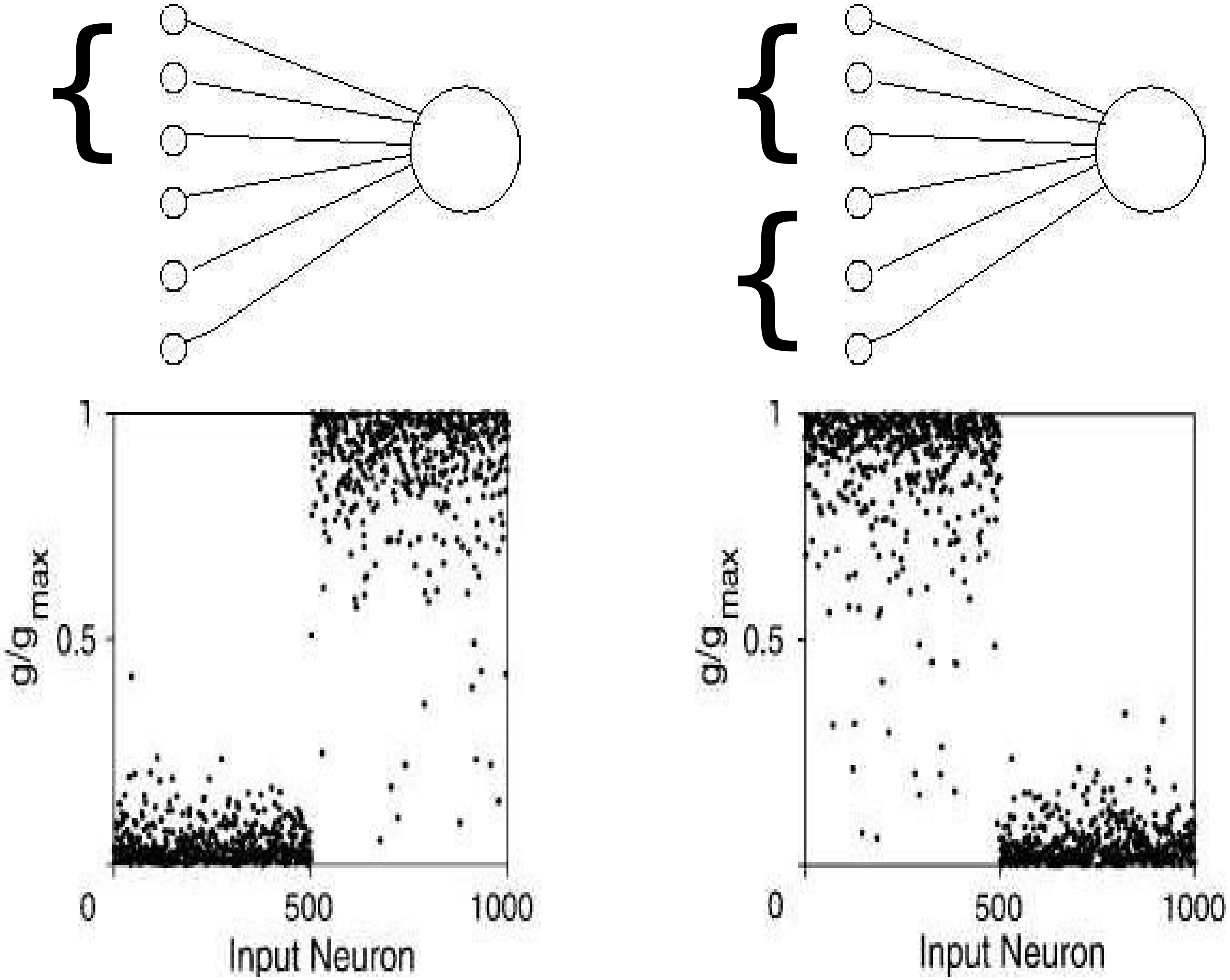
$$\frac{\partial P(w,t)}{\partial t} = \frac{-\partial}{\partial w}[A(w)P(w,t)] + \frac{1}{2}\frac{\partial^2}{\partial w^2}[D P(w,t)]$$

$$A(w) = -p_d A_{-} + p_p A_{+}$$

$$A_{-} = (1+\epsilon) A_{+}$$

Modelling STDP

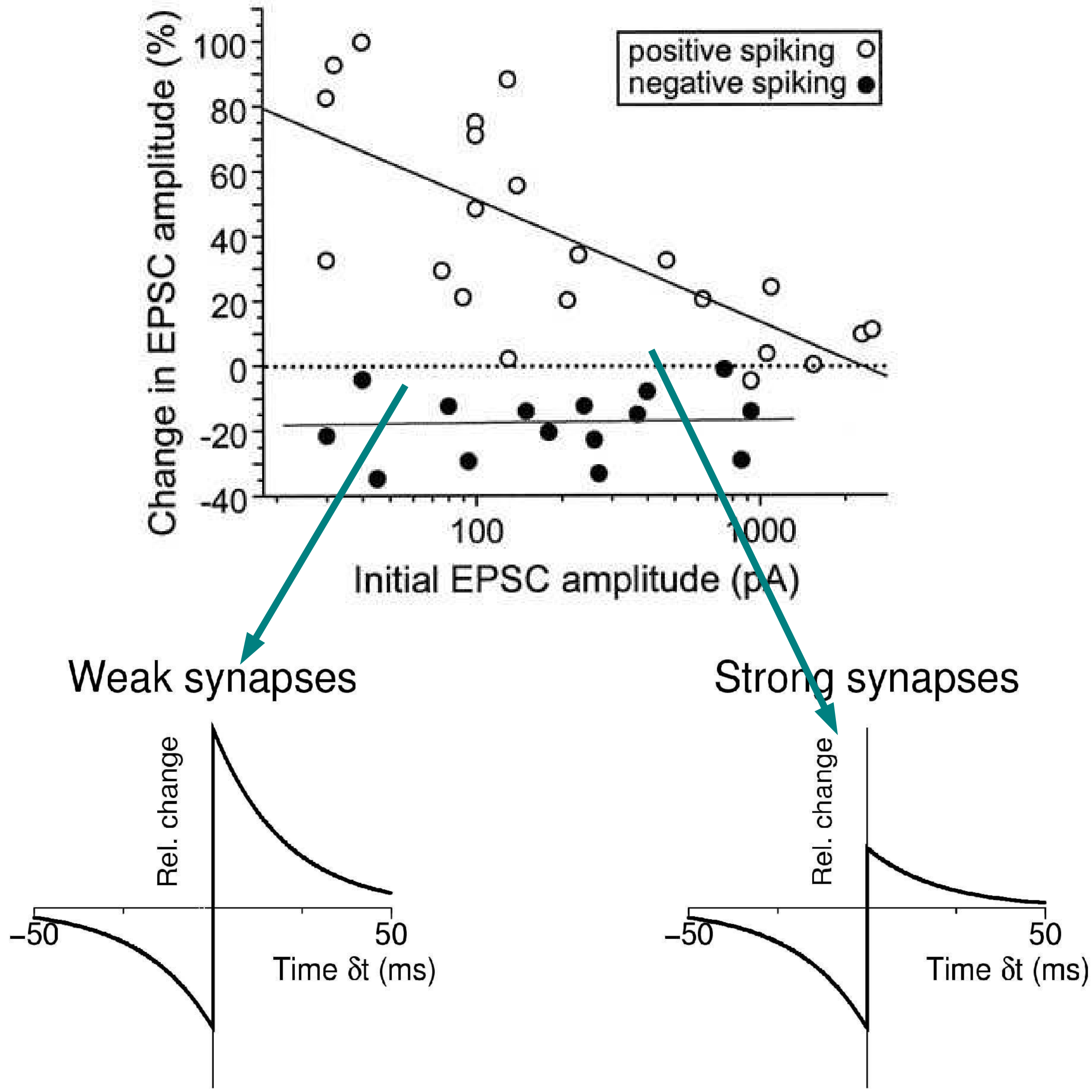
Correlated
Poisson trains



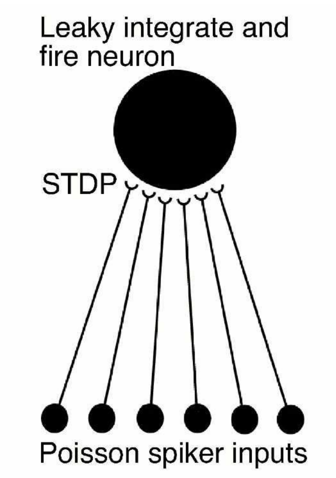
- Require hard bounds on weights
- Competitive

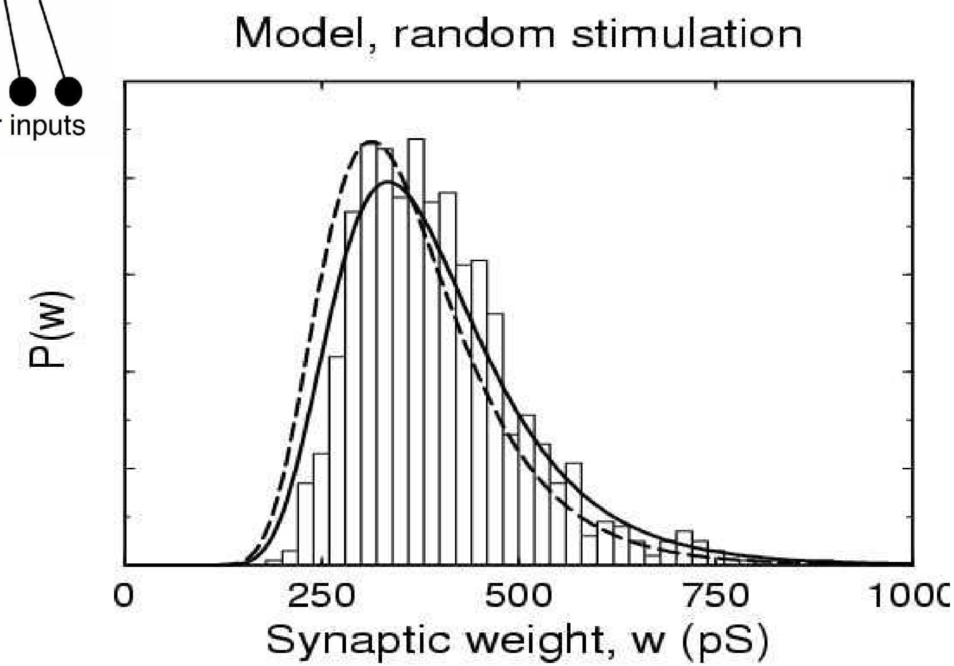
[Song & Abbott '01]

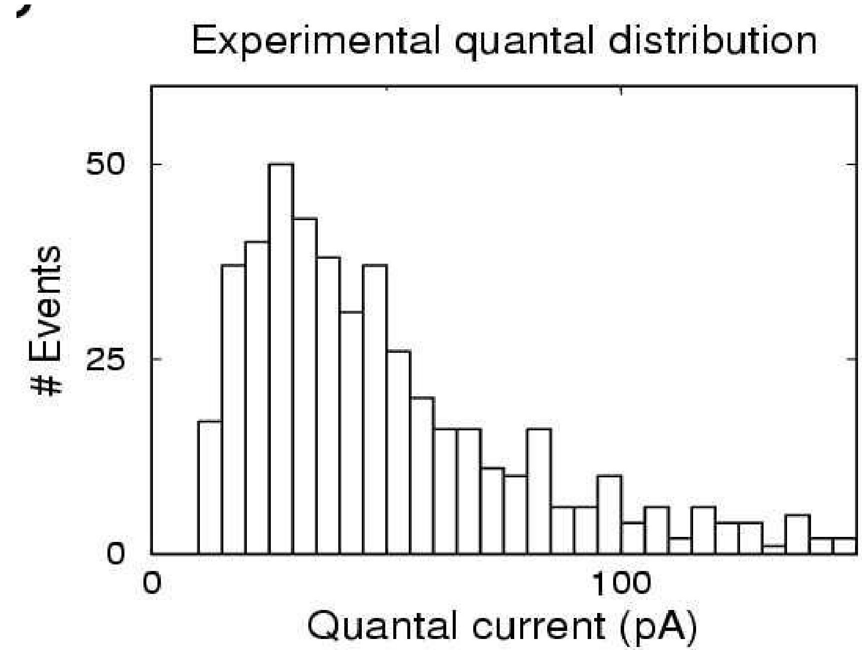
However, STDP is weight dependent ('soft bounds')

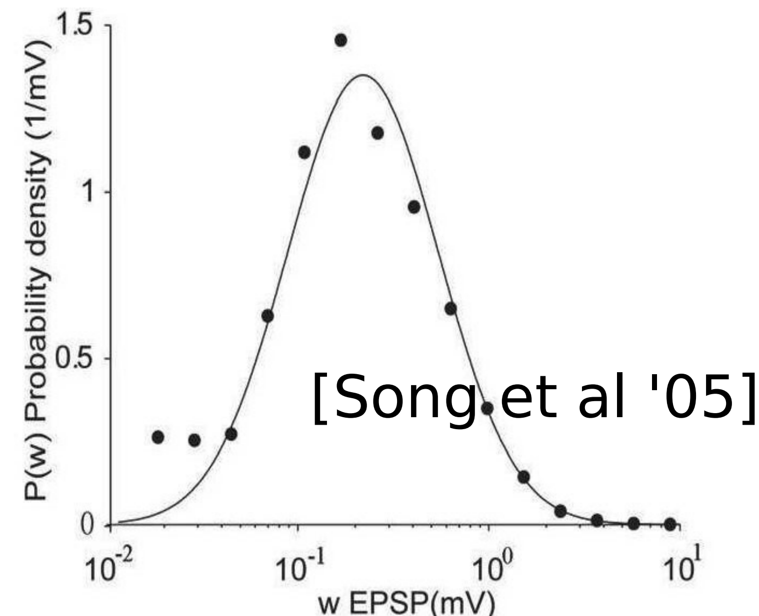


Weight dependence leads to observed weight distribution





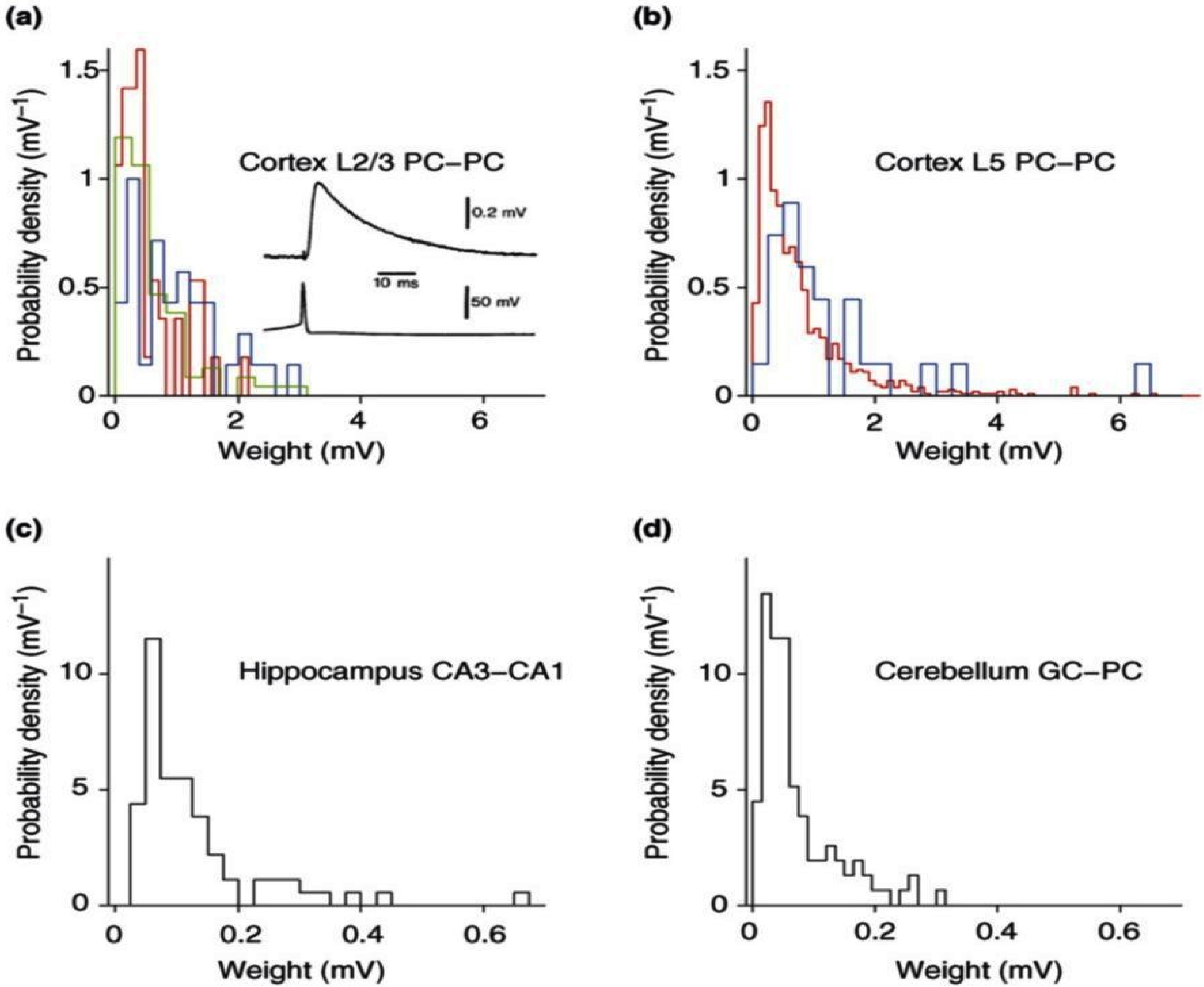




[Song et al '05]

[MvR, Bi, Turrigiano '00]

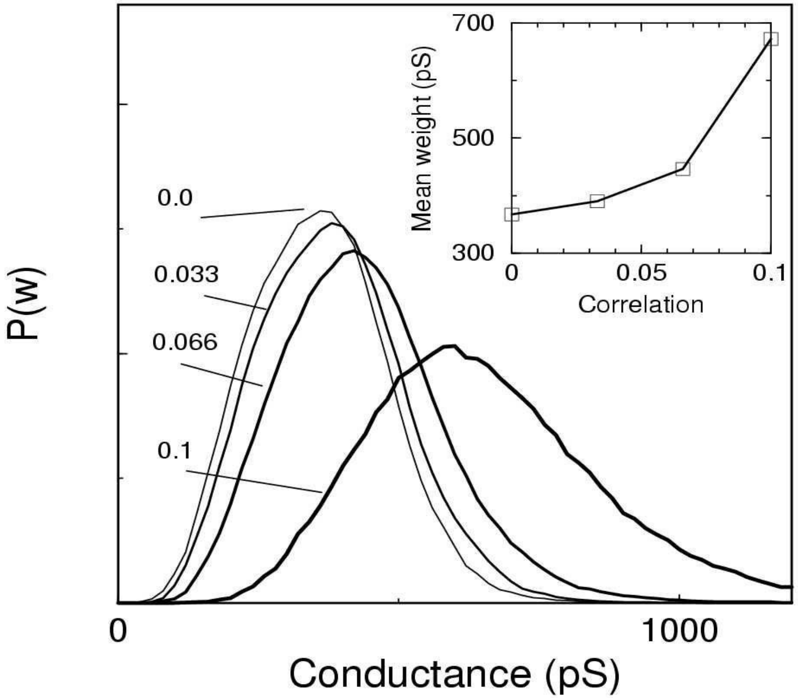
Data on weight distribution

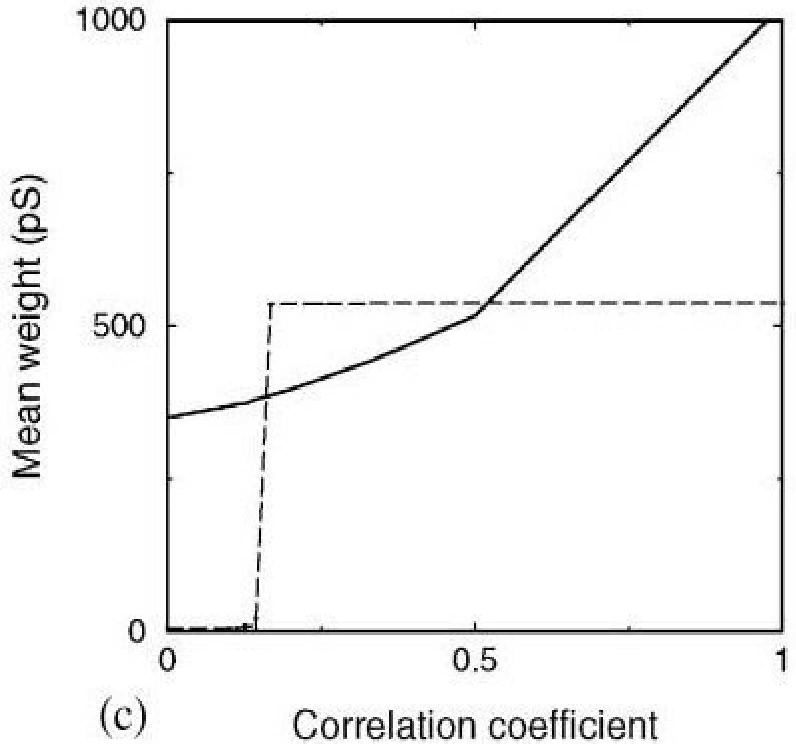


[Barbour et al. '07]

Note many confounding factors

Learning correlations

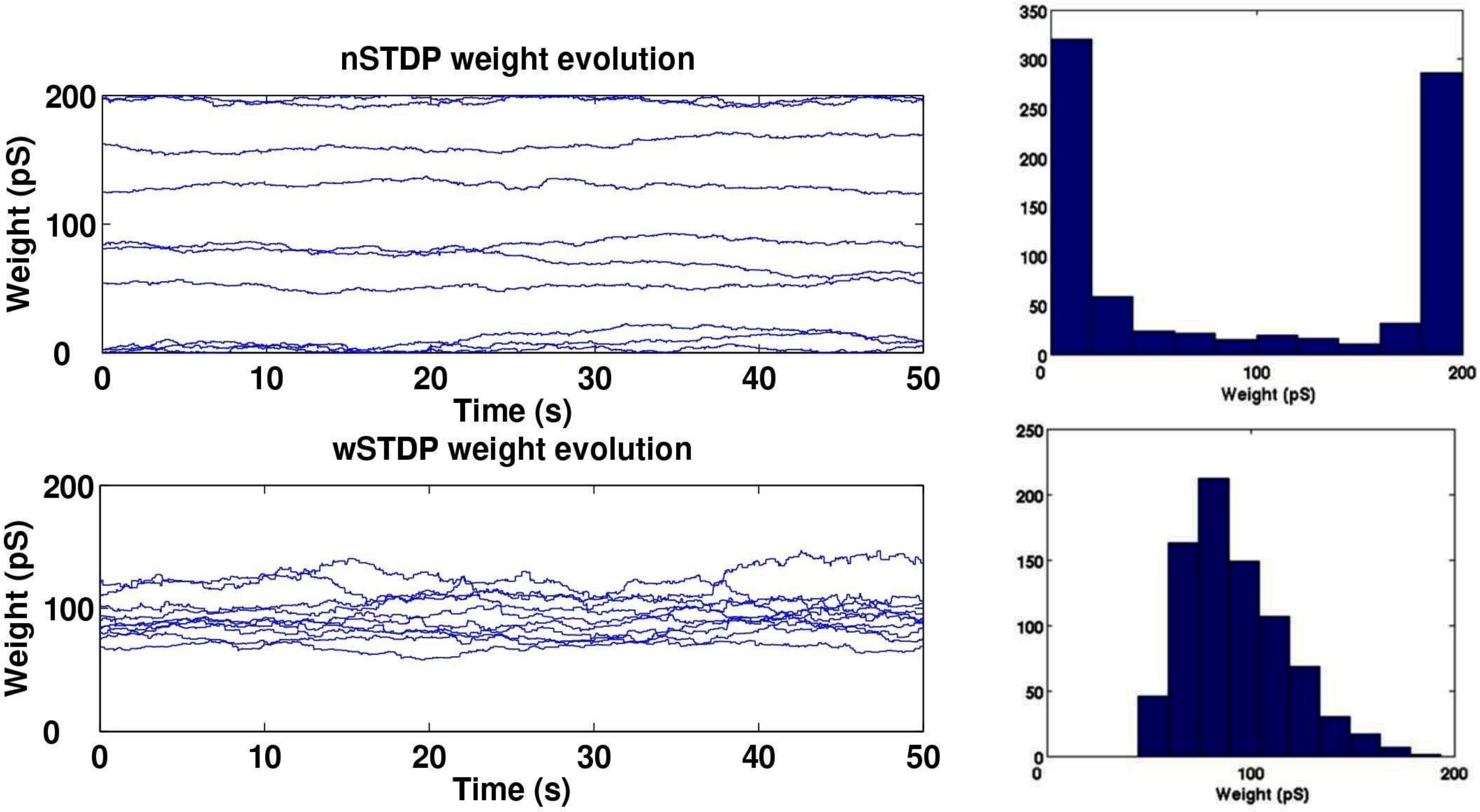




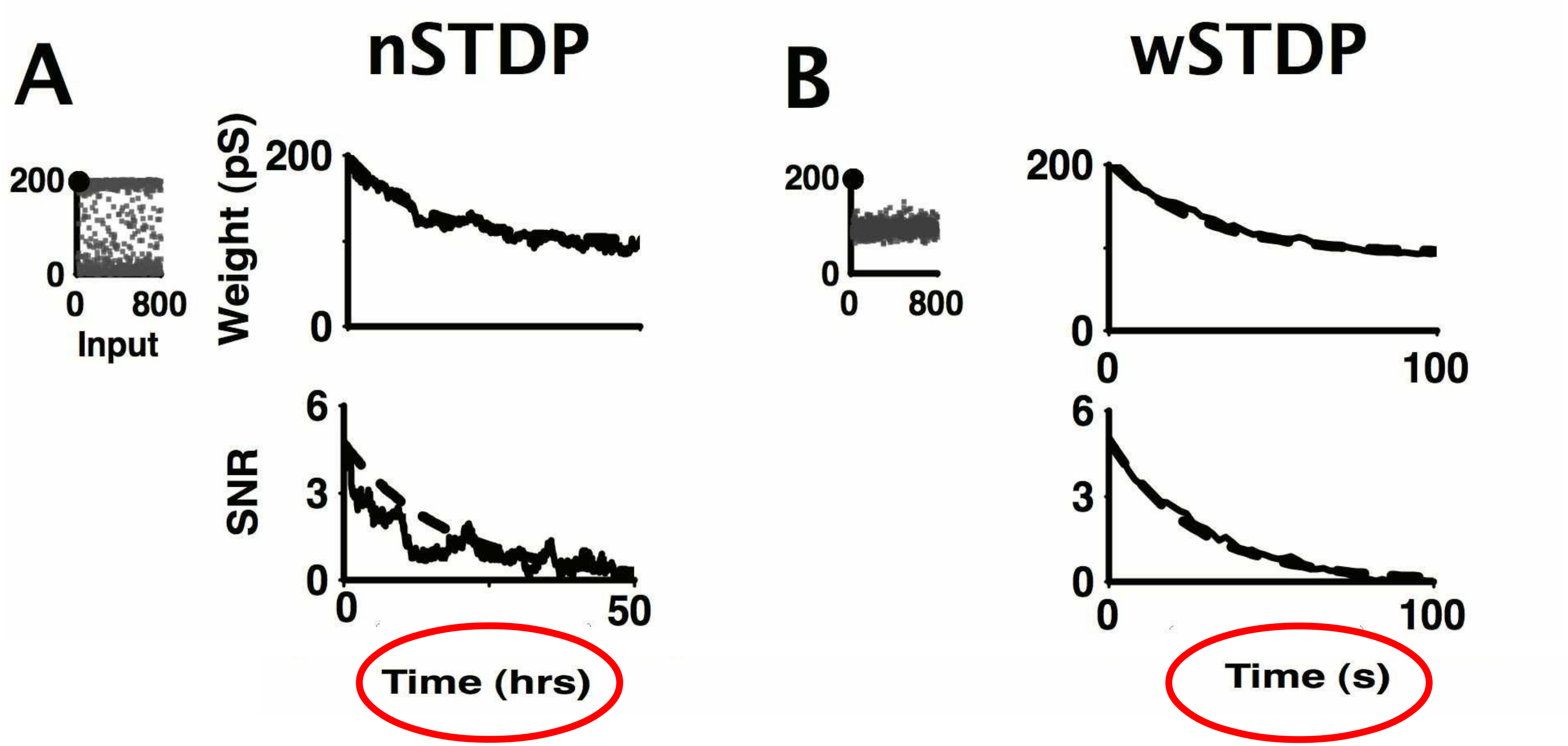
Similar to Oja's rule.
Weakly competitive.

[MvR & Turrigiano '01]

Ongoing background activity leads to weight fluctuations

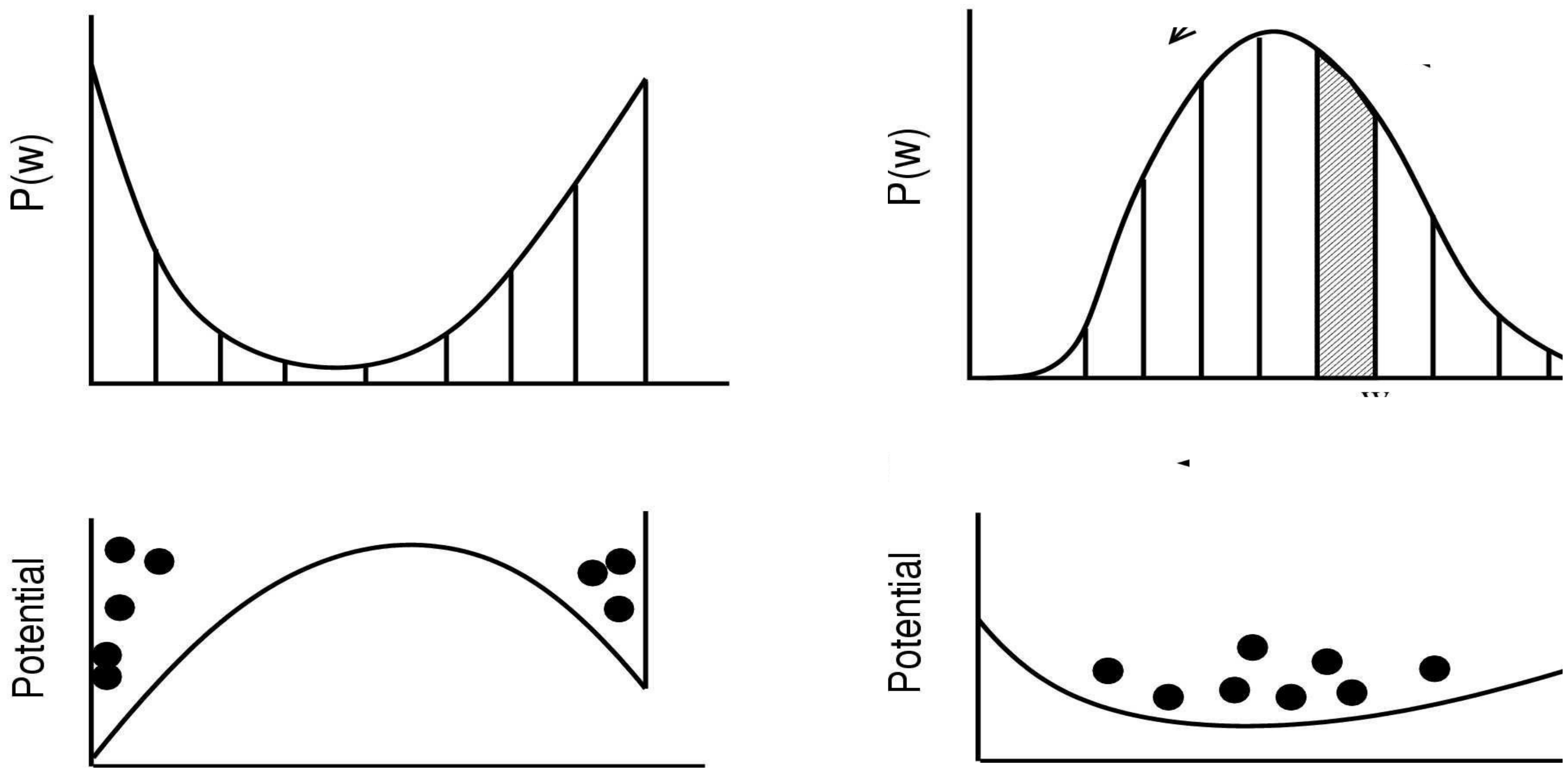


Weight dependence leads to volatile memories

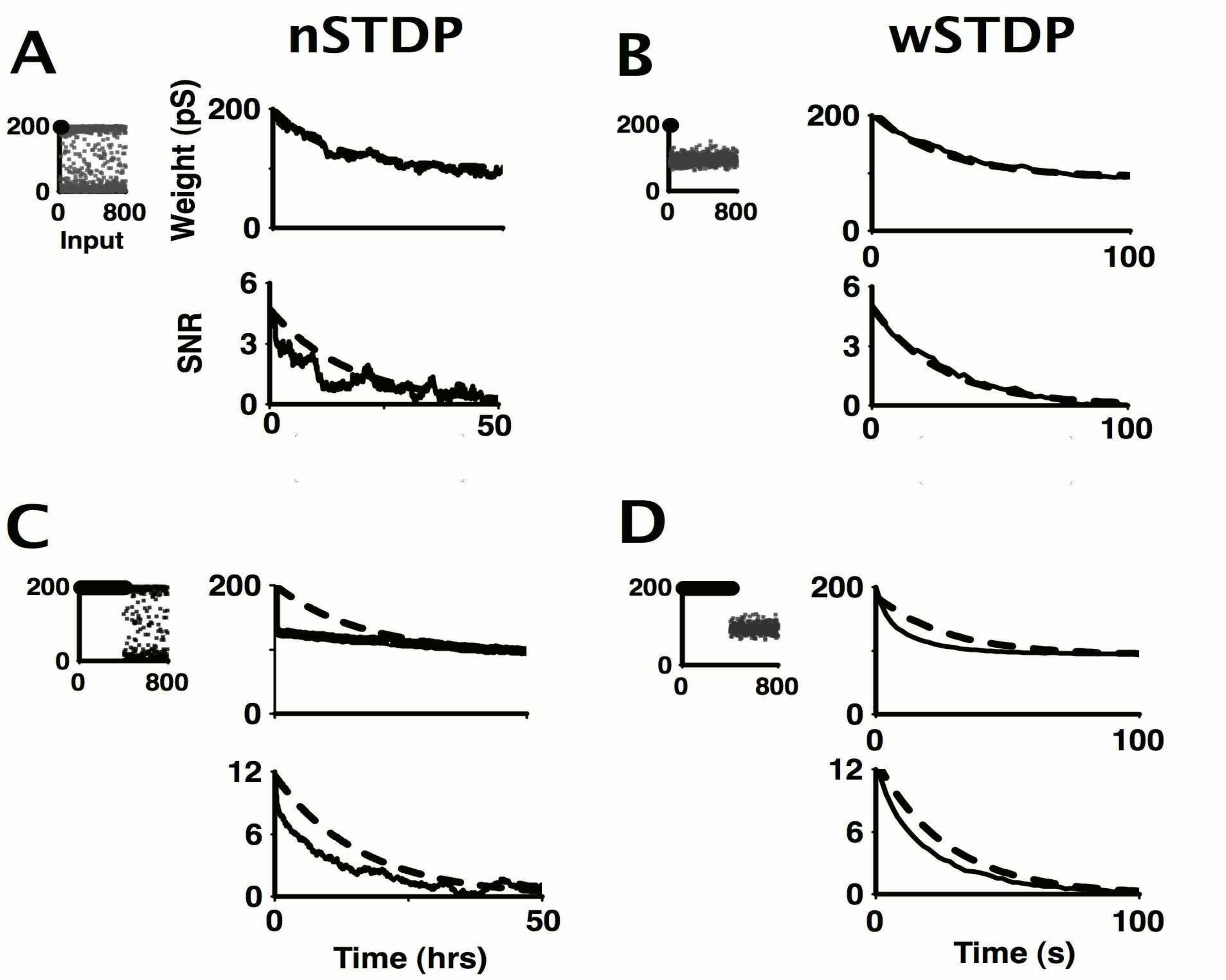


- Spontaneous activity leads to memory decay
- Decay is exponential
- Decay is much faster for weight dependent STDP

How weight dependence leads to quick forgetting

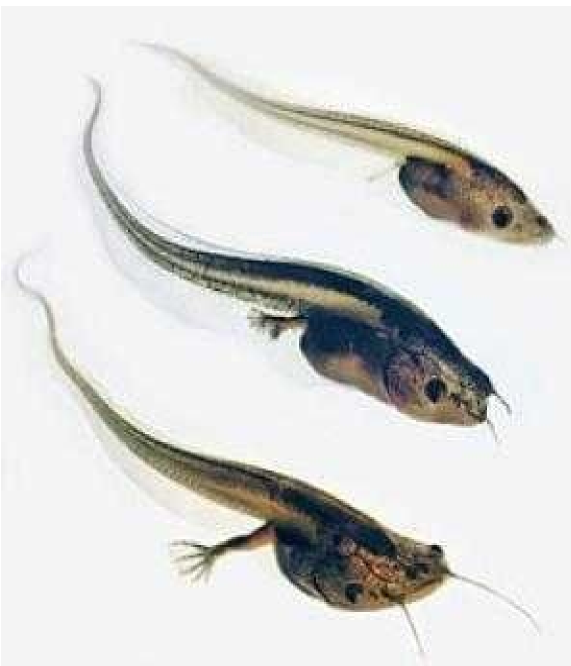


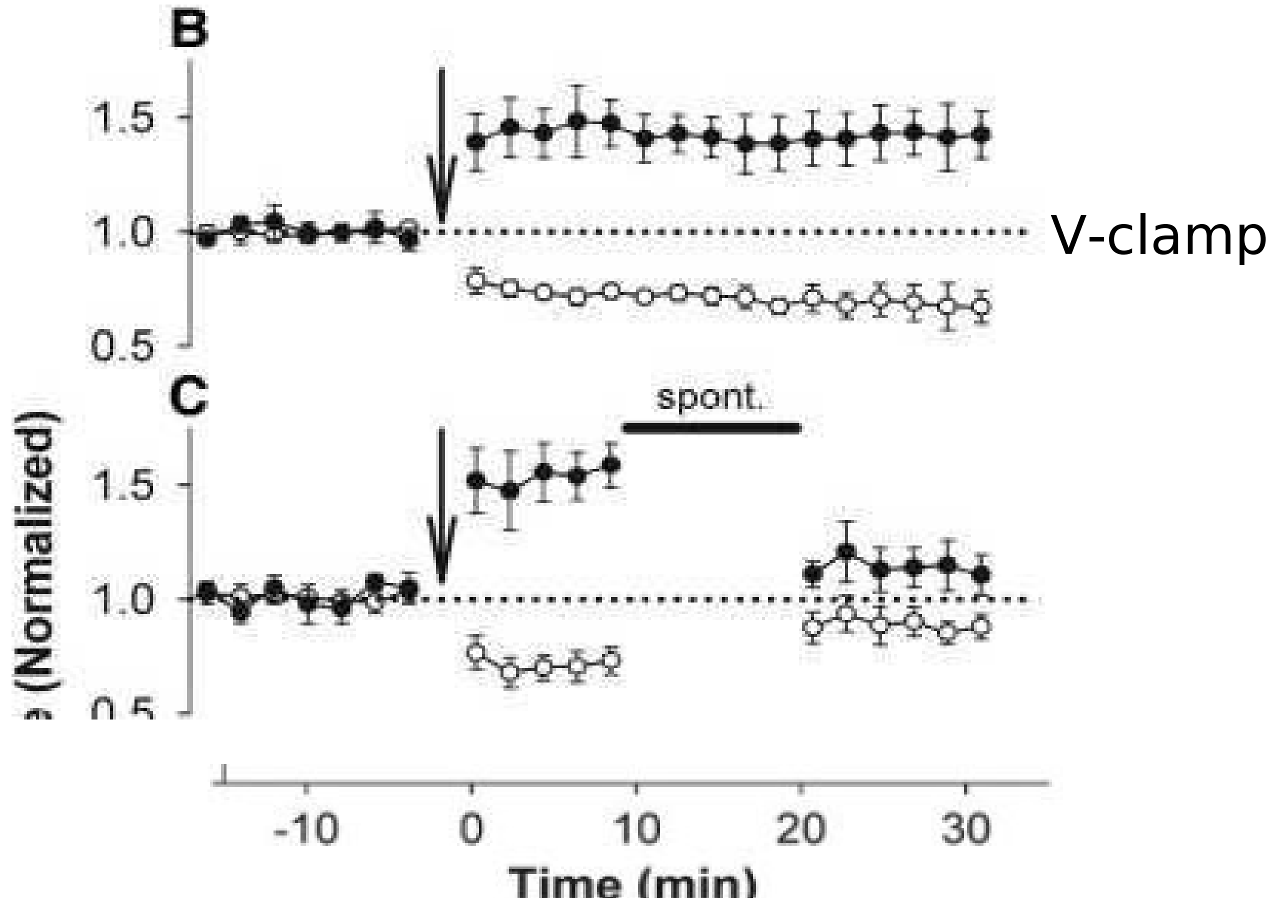
Weight dependence leads to volatile memories



[Billings & MvR '09]

Experimental data: erasure by spontaneous activity

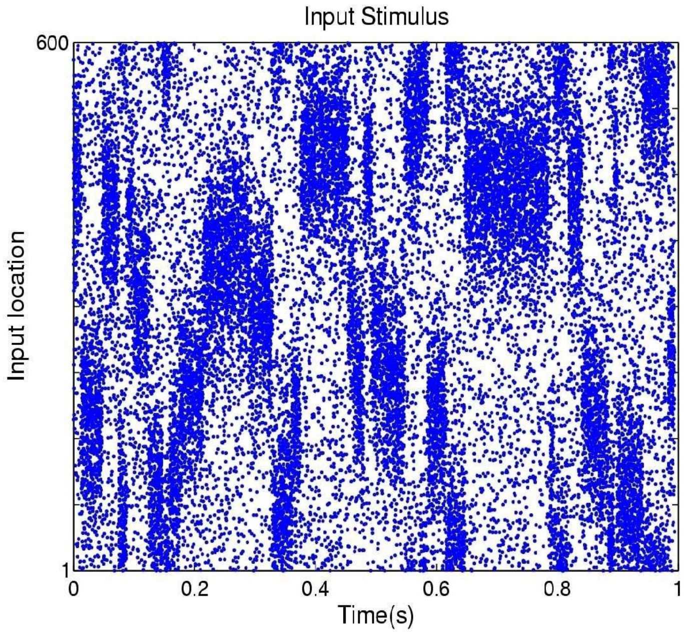


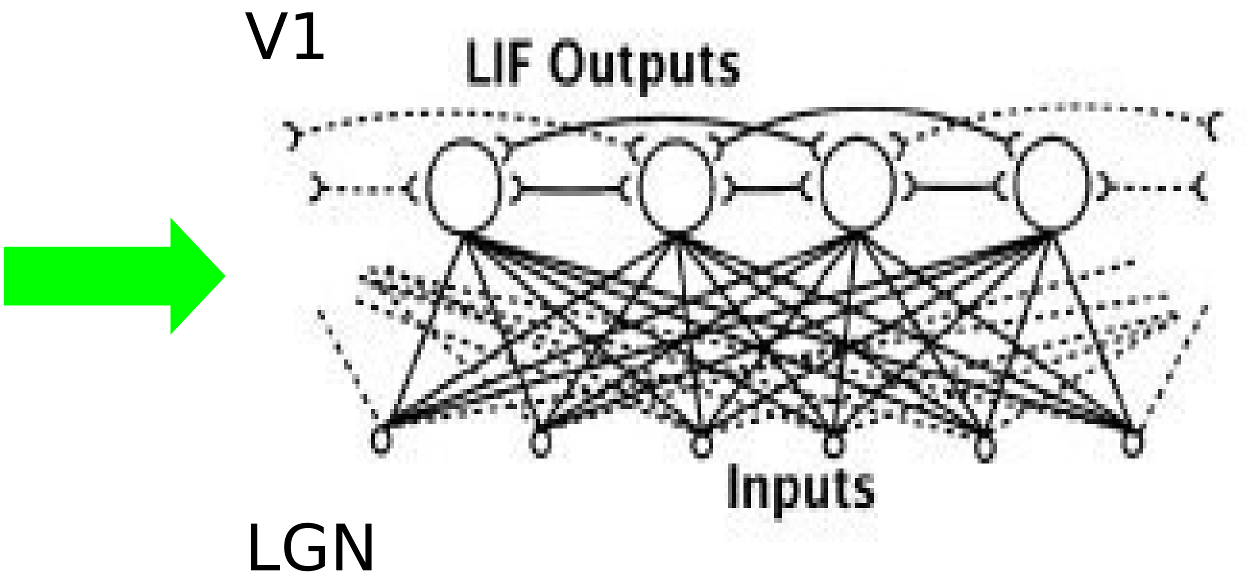


Xenopus tectum [Zhou & Poo, '03]

Are memories in *networks* are unstable?

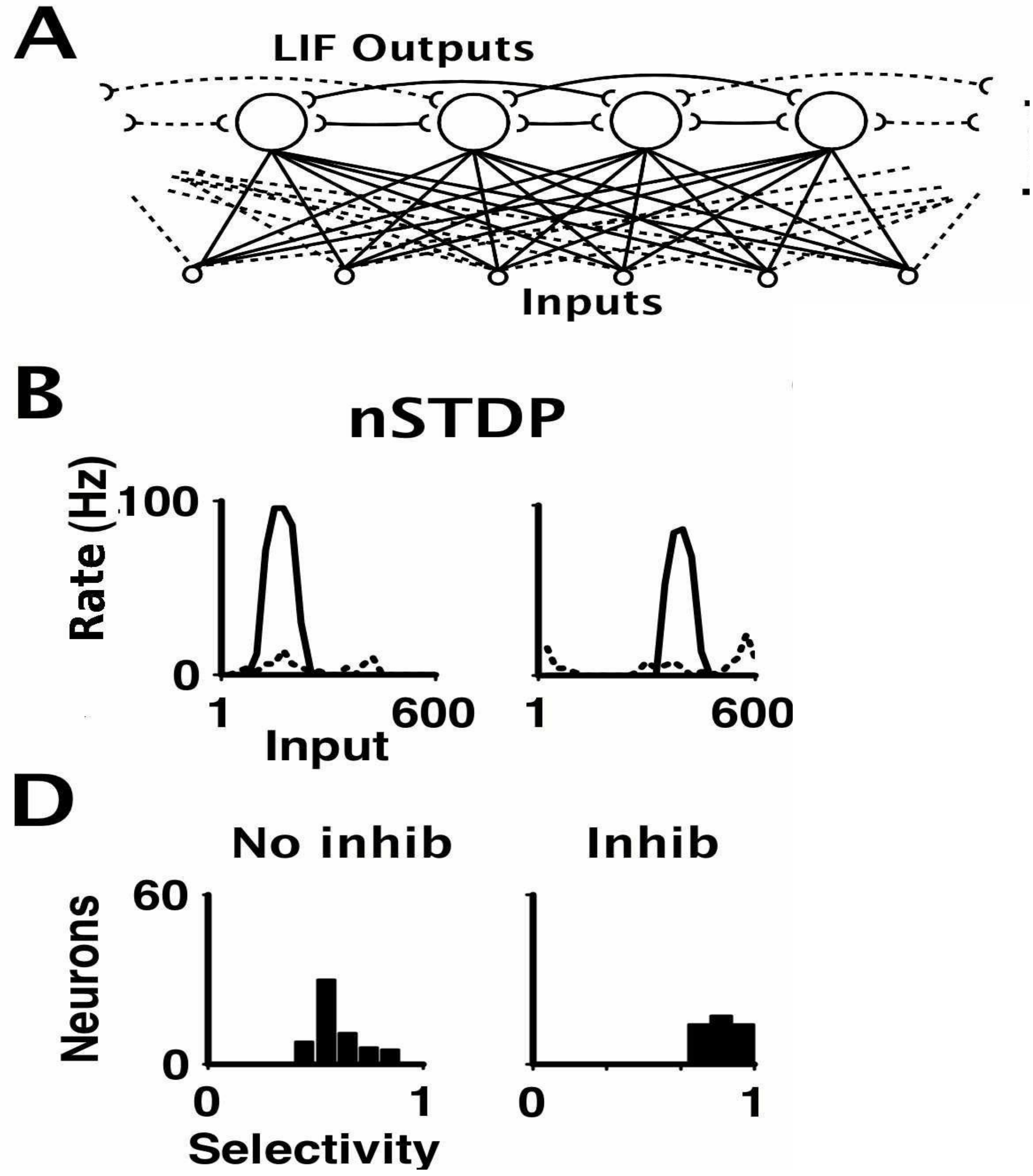
Stability of receptive fields in networks



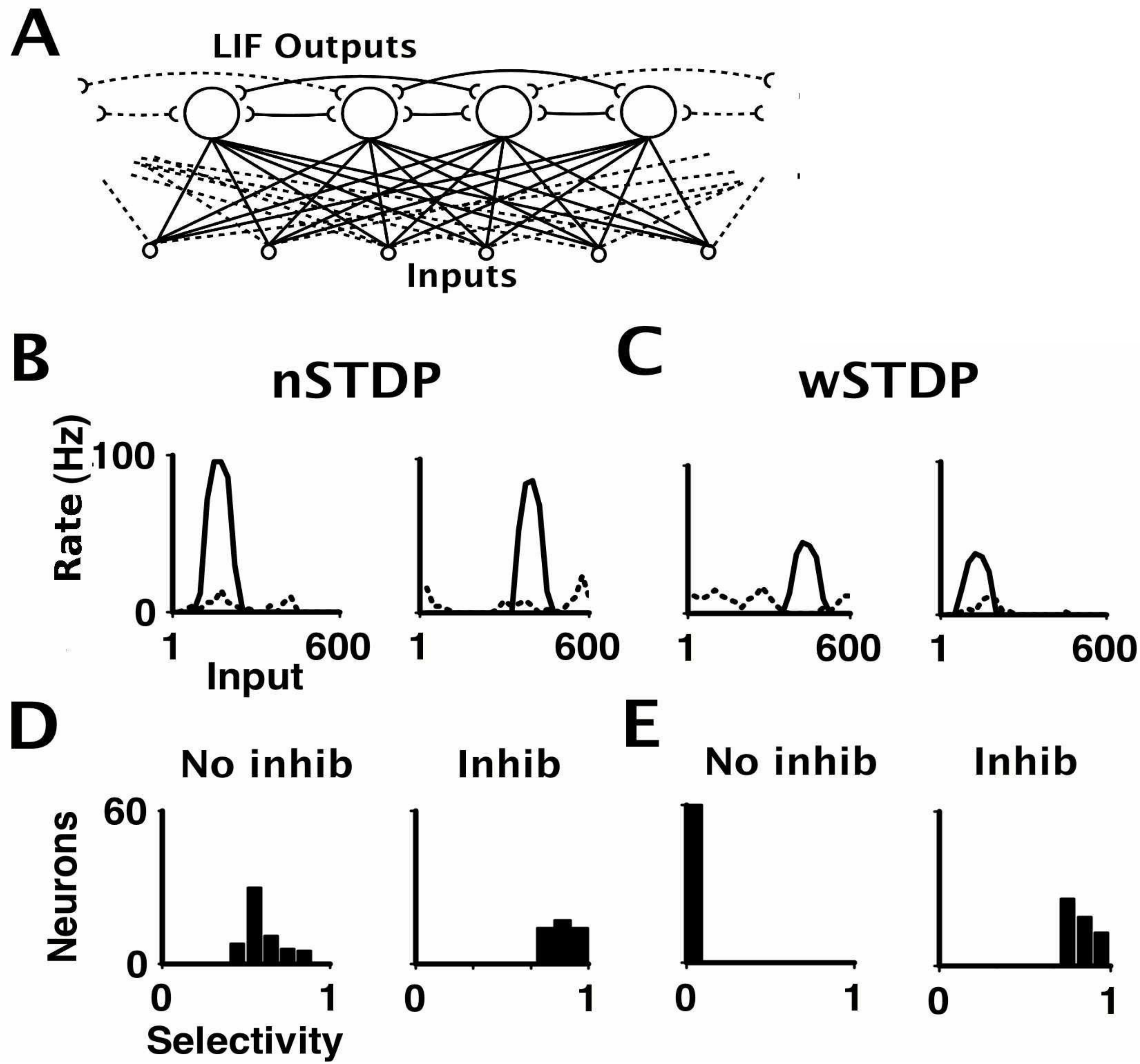


V1-like network

- Integrate and fire
- Variable lateral inhibition
- Sometimes plastic recurrent connections



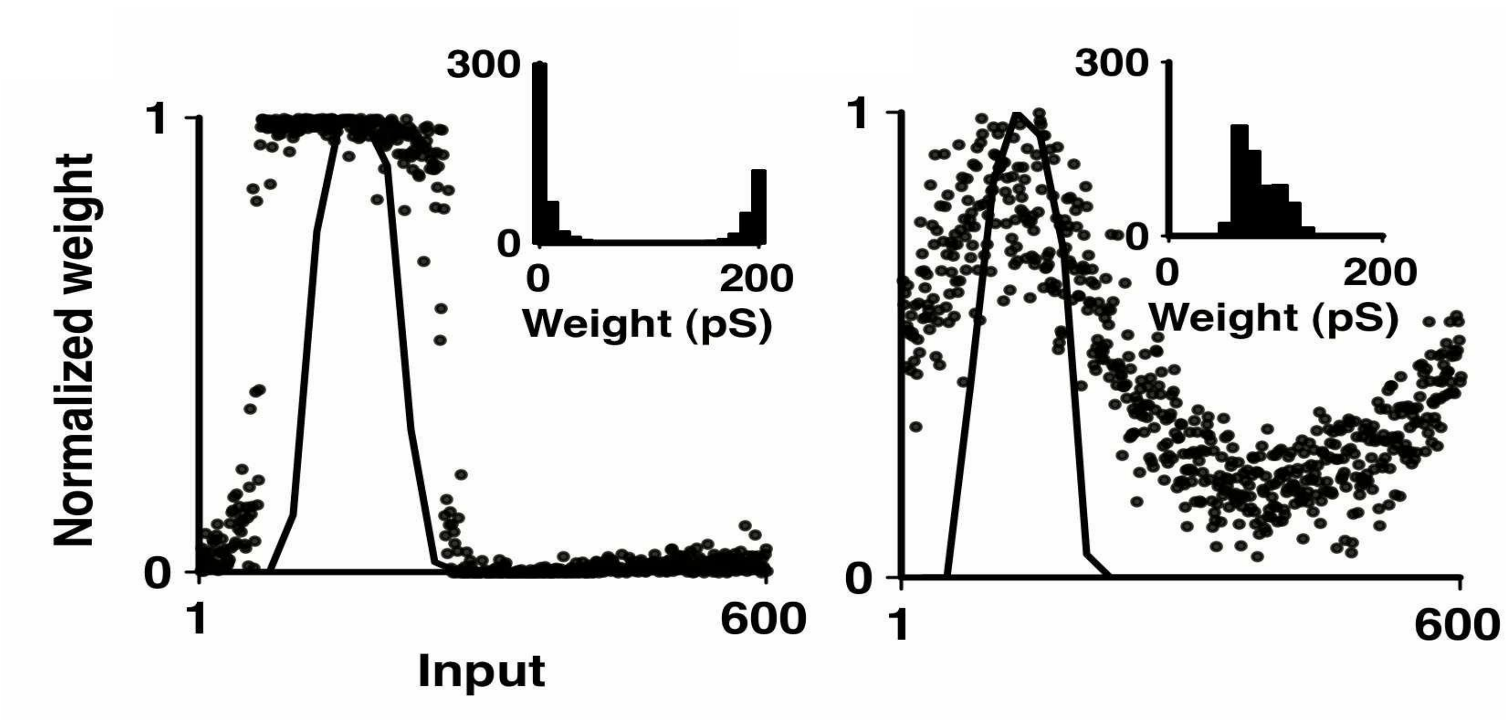
nSTDP: Spontaneous symmetry breaking [Song &Abbott '01]



Weight dependent plasticity requires inhibition for selectivity

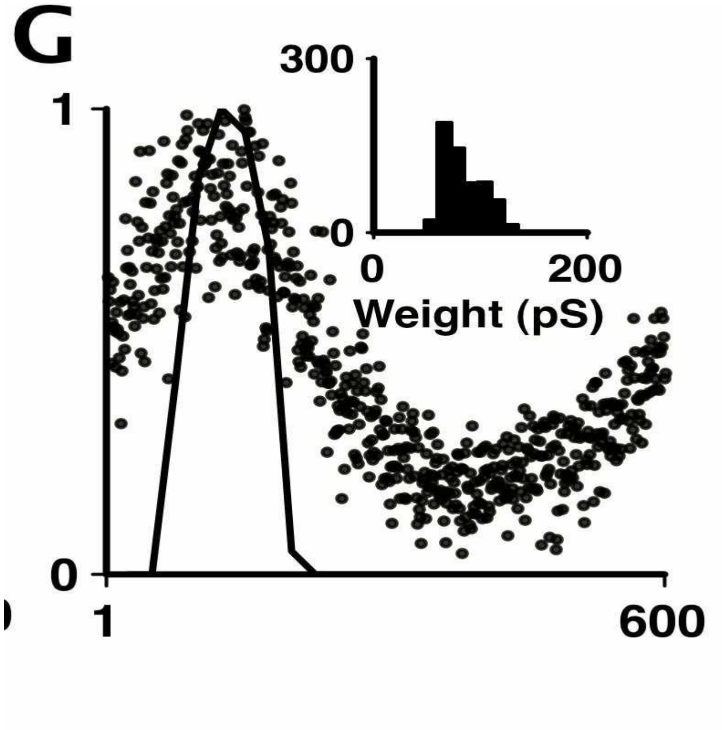
Broad tuning underlies receptive field

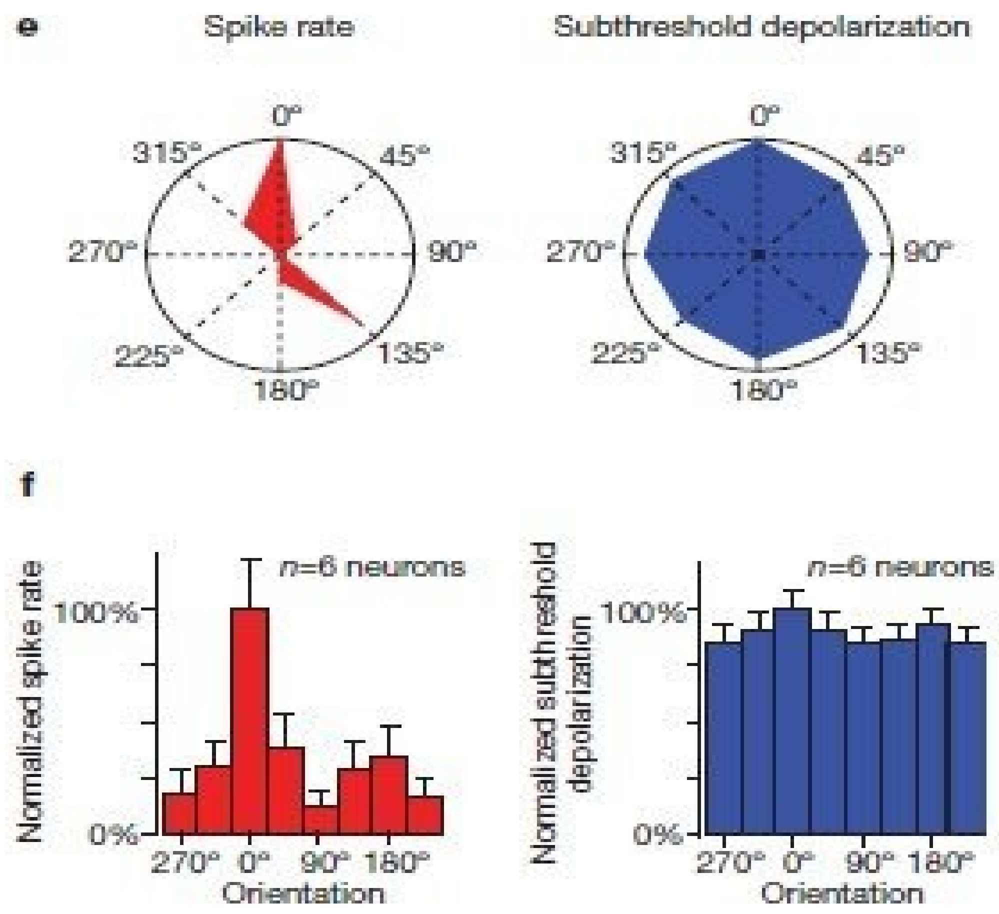
nSTDP wSTDP



Input tuning in experiments

wSTDP

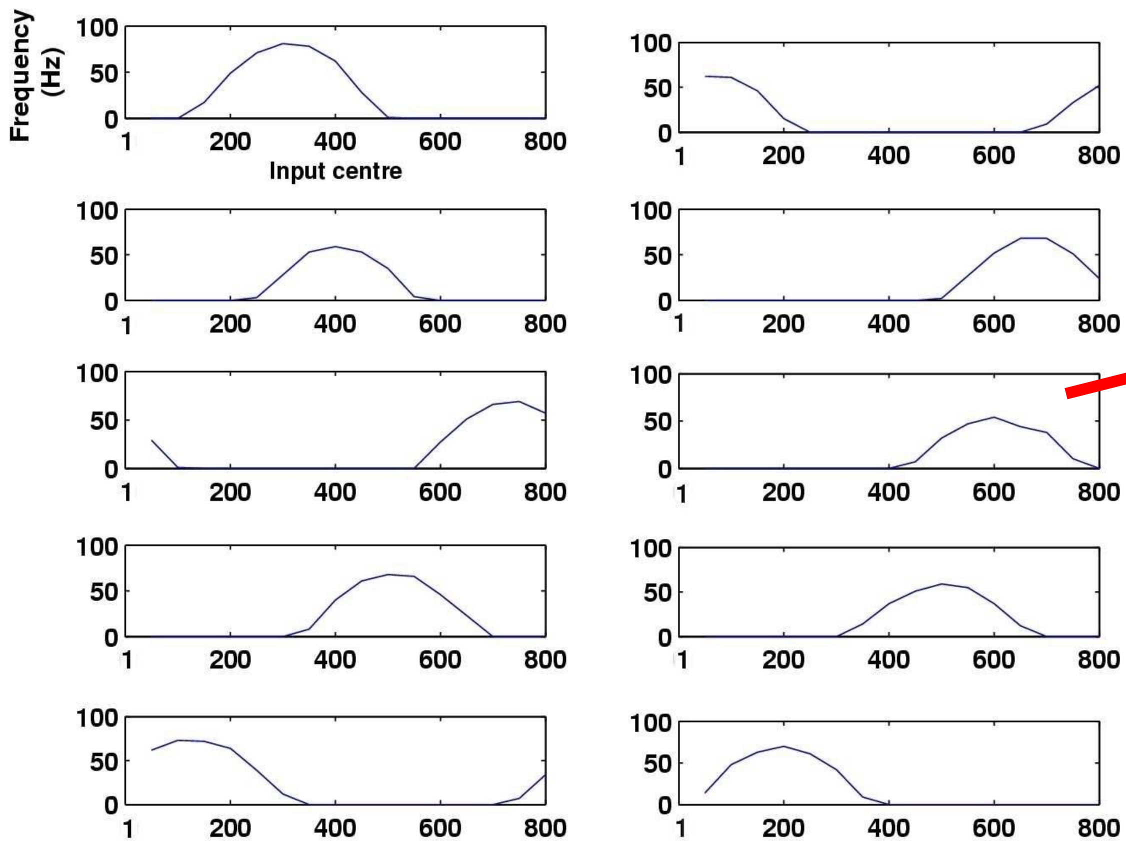




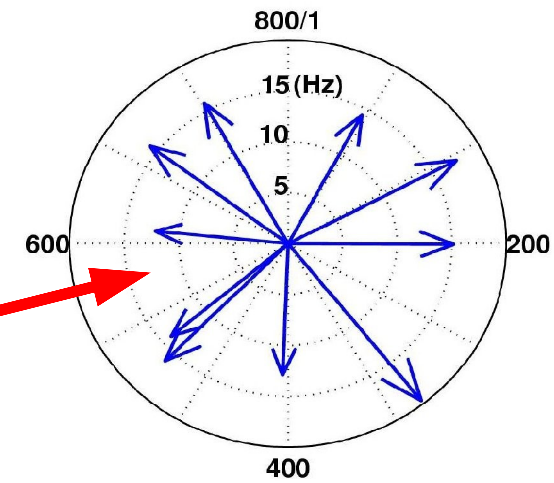
[Jia and Konnerth 2010]

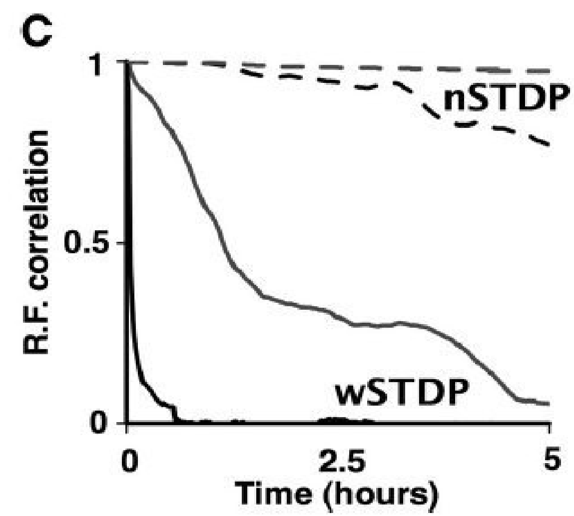
Stability of receptive fields

Receptive fields

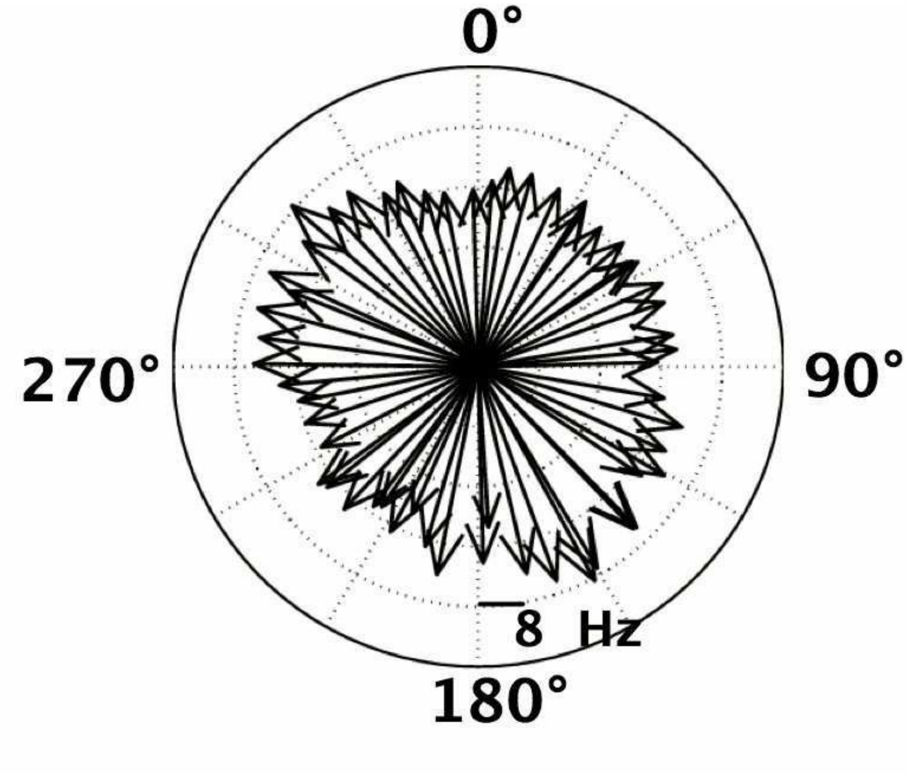


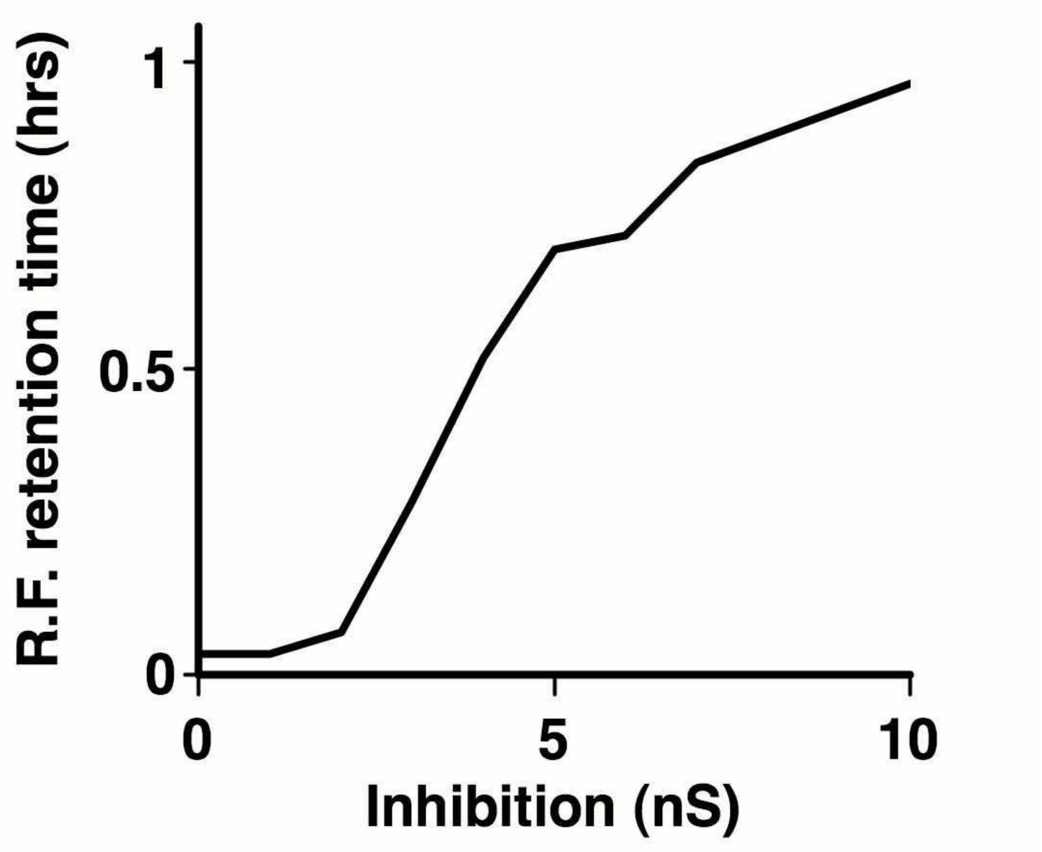
Population vectors





Inhibition rescues network stability

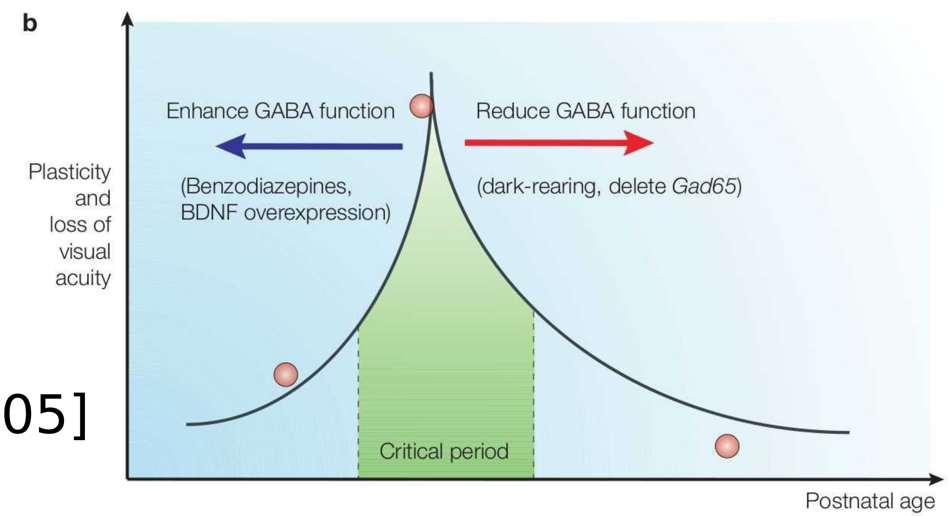




[Billings & MvR 2009]

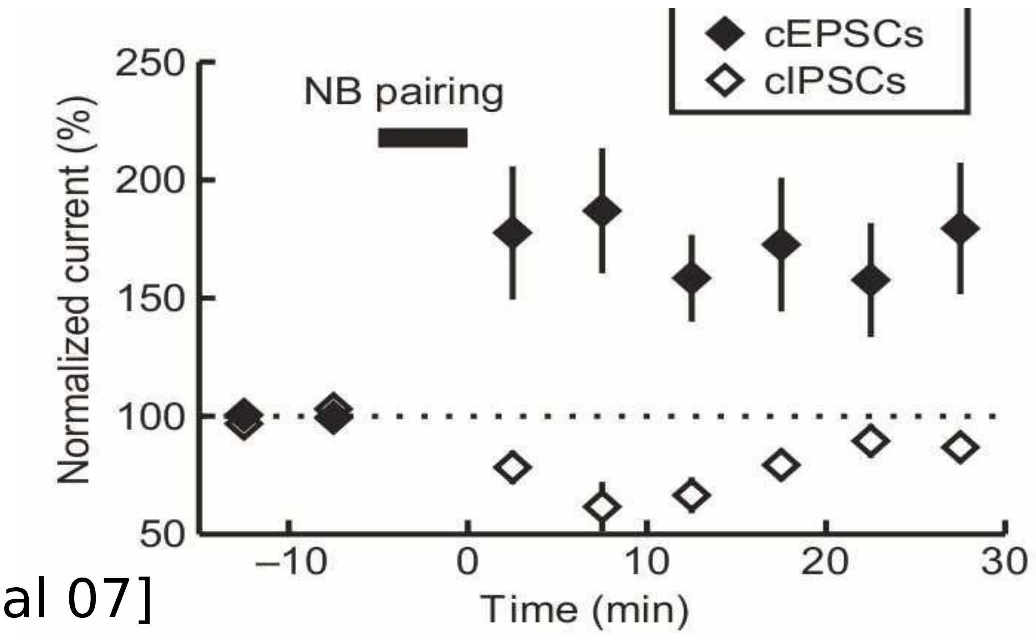
Experimental evidence for effect of inhibition on stability

- Ocular Dominance plasticity regulated by GABA?



[Hensch '05]

- Reduced inhibition in auditory plasticity



[Froemke et al 07]

Table of contents

- **Weight dependent STDP in single neurons and networks**
  - **- The observed weight dependence leads to realistic weight distributions**
  - **- The receptive fields are much less stable, but lateral inhibition can rescue and modulate retention**

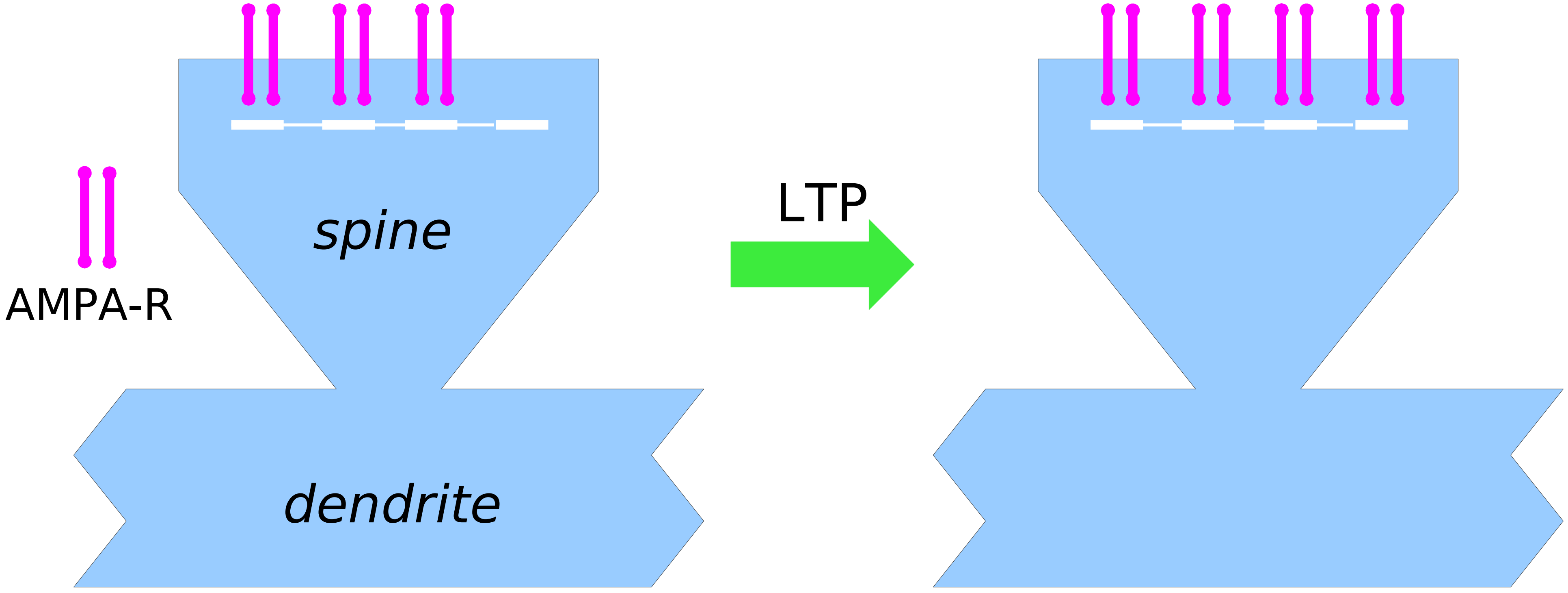
- Spine dynamics can implement weight dependence

- Weight dependence increases information capacity

Table of contents

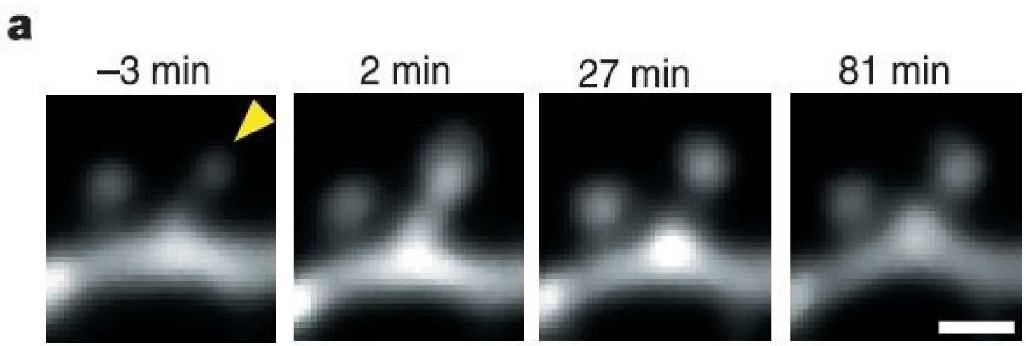
- Weight dependent STDP in single neurons and networks
- **Spine dynamics can implement weight dependence**
- Weight dependence increases information capacity

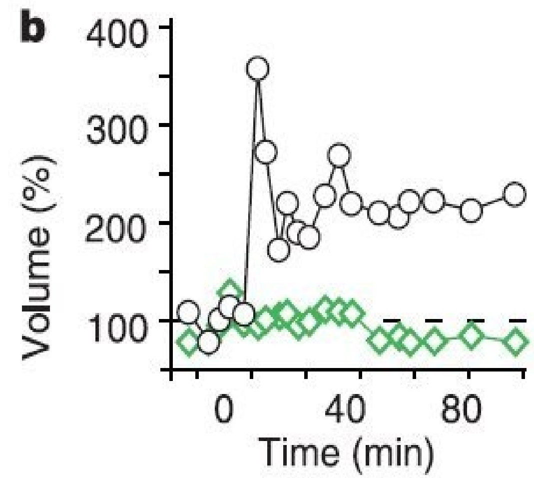
Biophysical implementation

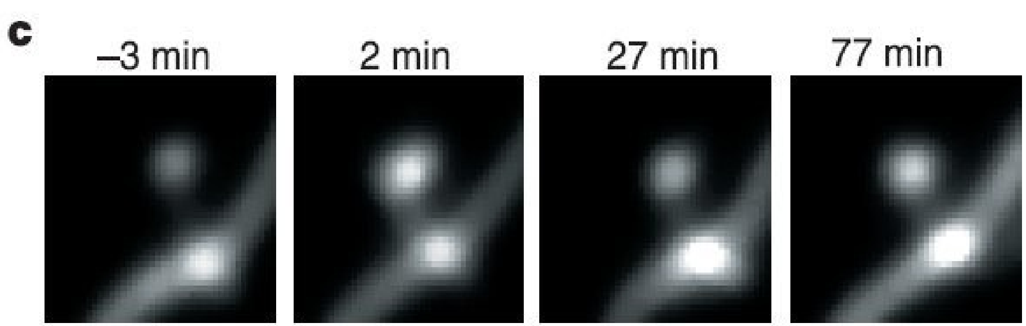


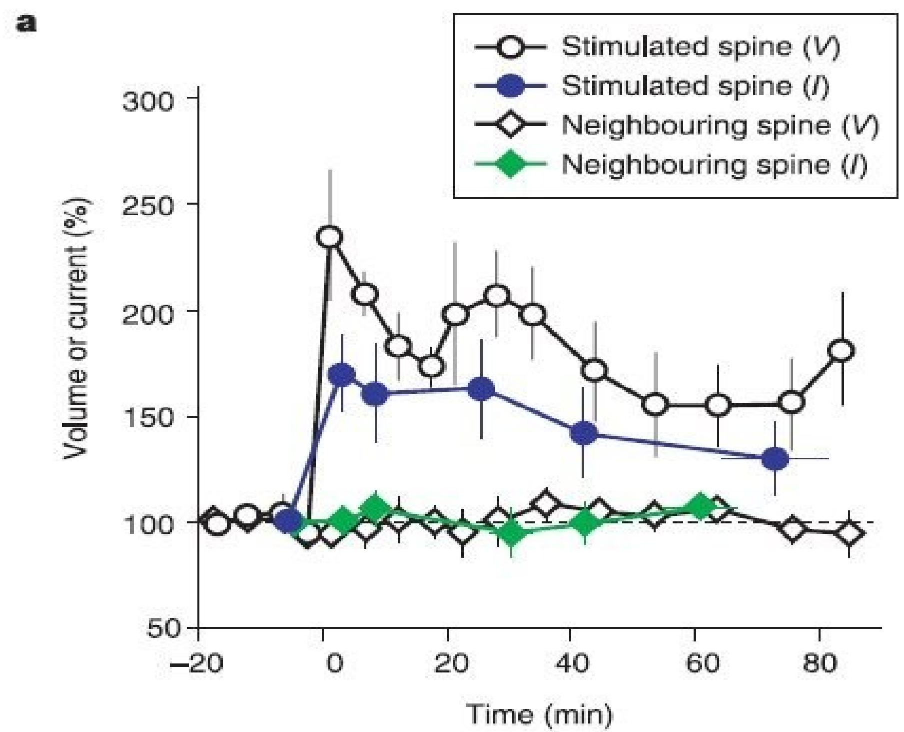
Simple model for weight dependence: biophysical saturation

Spine morphology is remarkably plastic





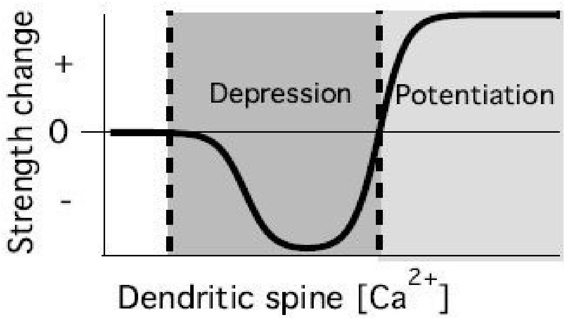


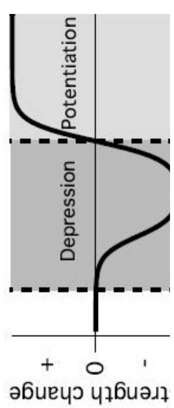


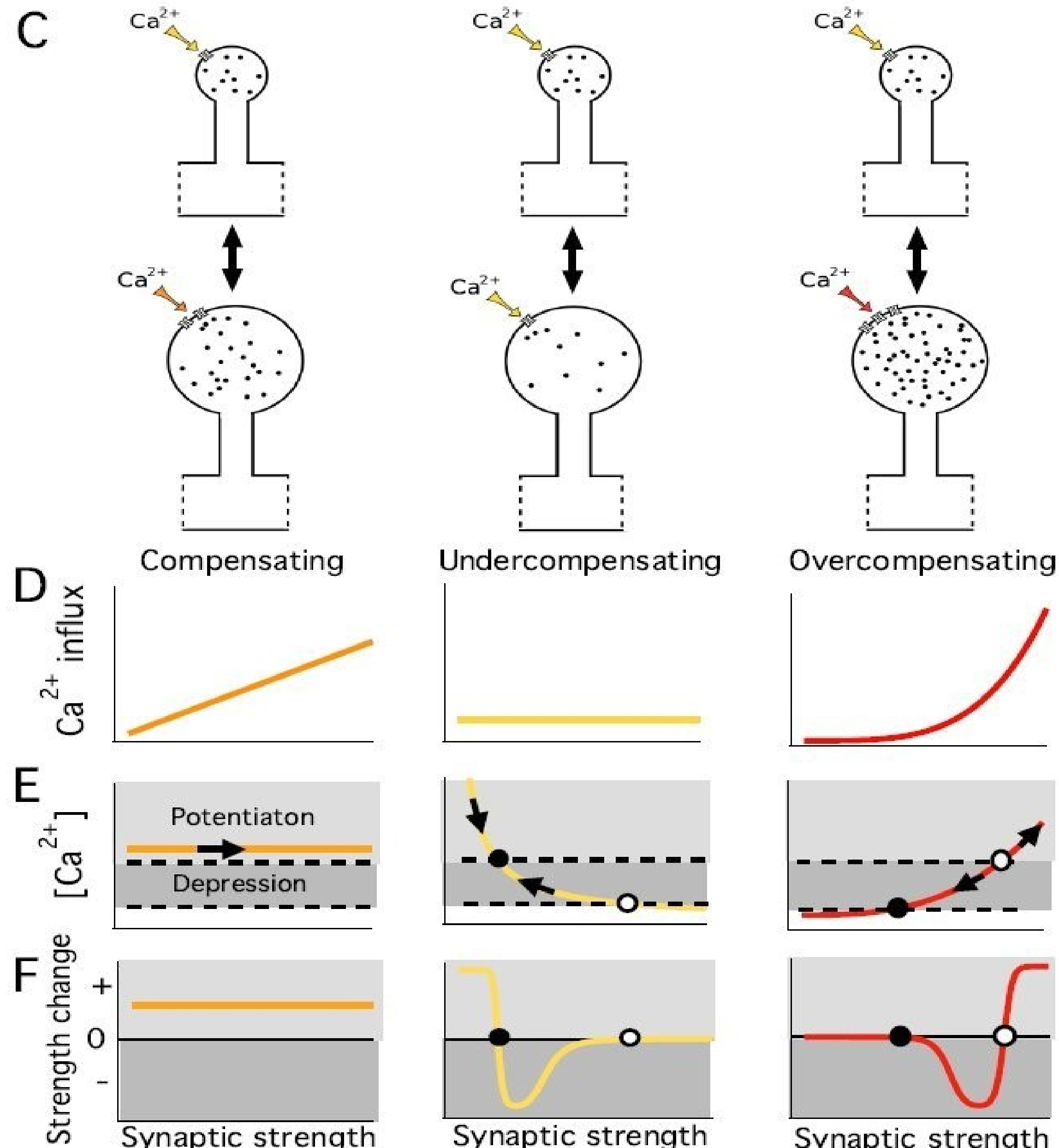
[Matsuzaki '04, Glu uncaging]

Tight correlation weight and spine volume

Three Ca-volume scenarios

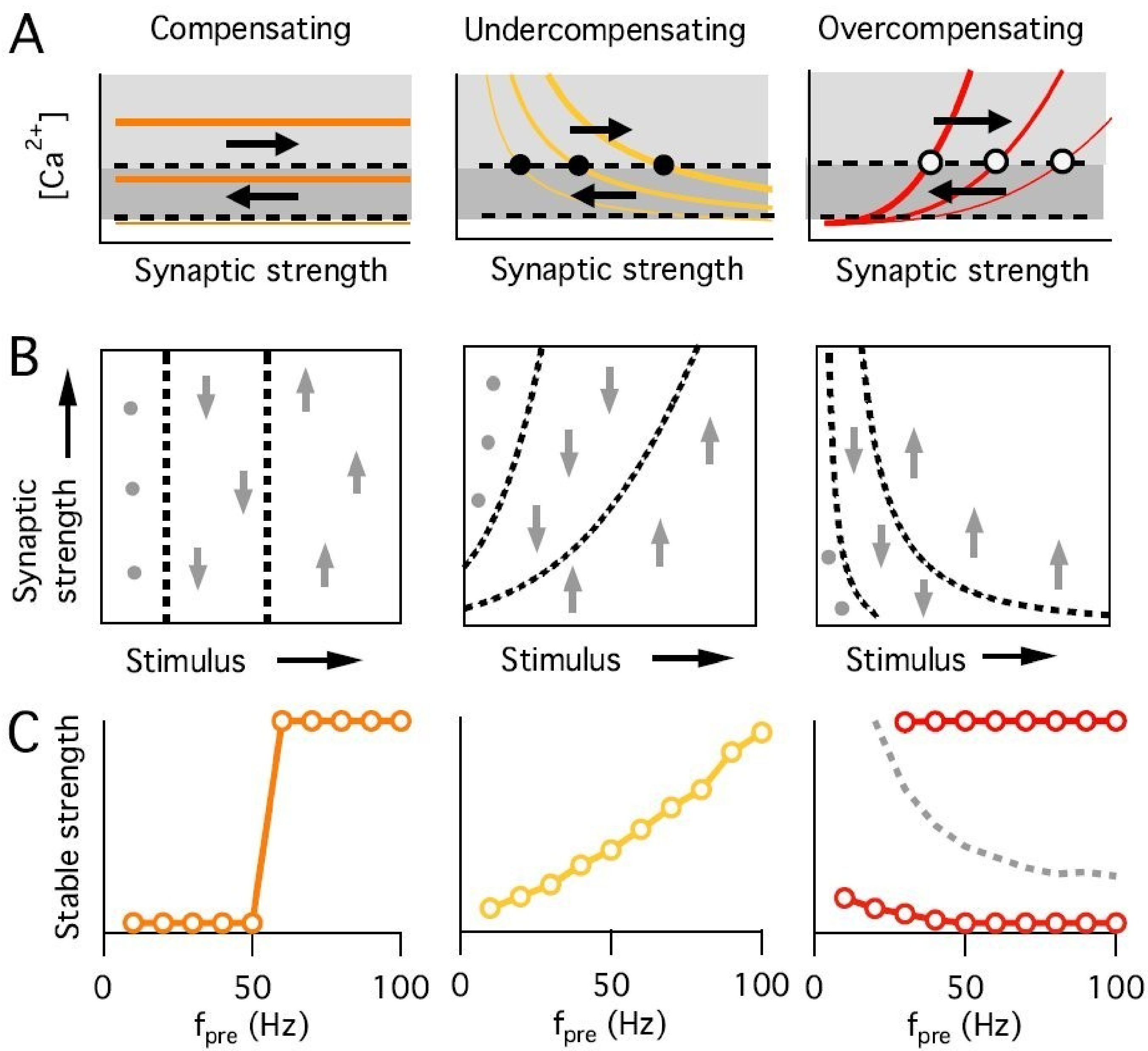




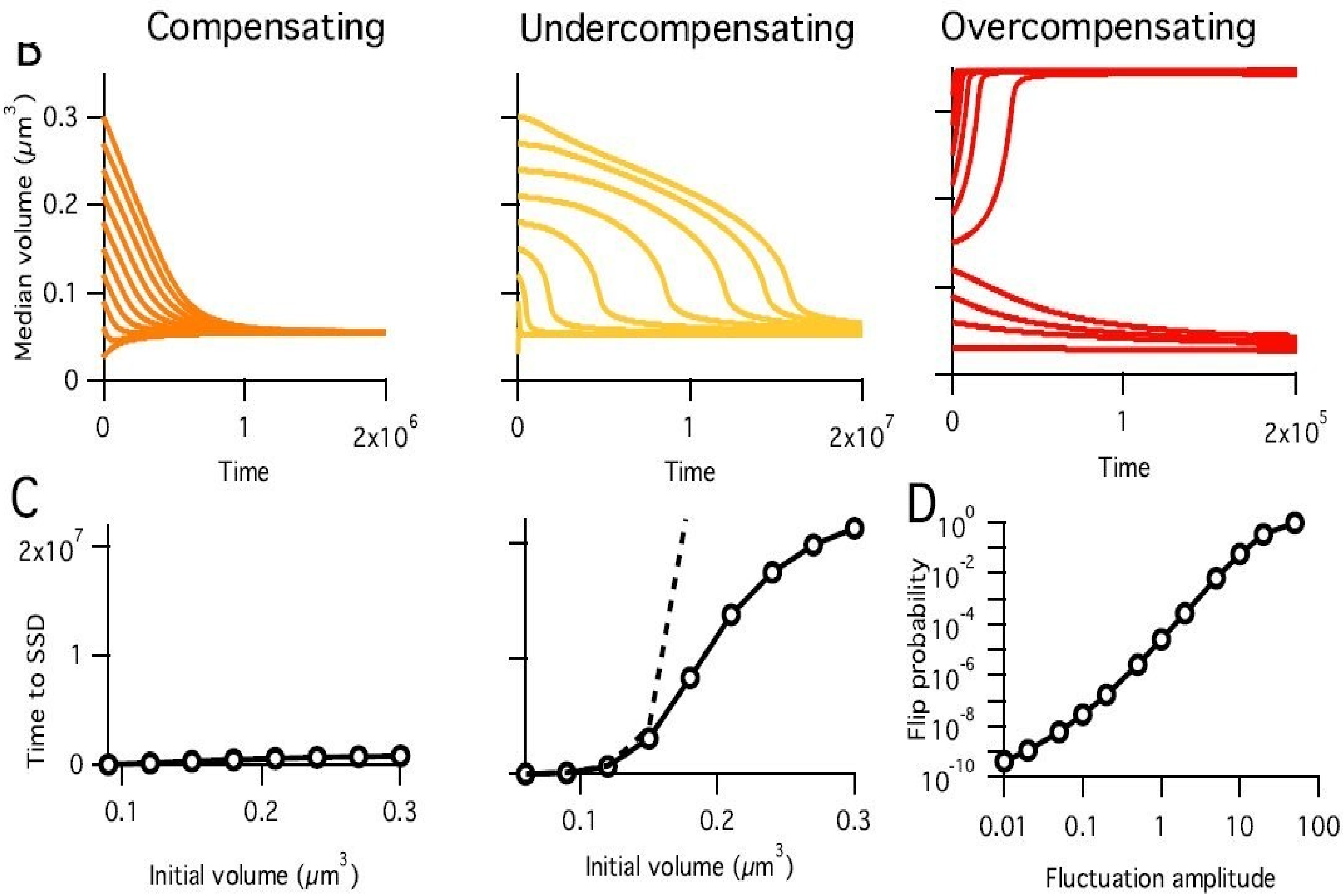


[O'Donnell & MvR, submitted]

Three scenarios

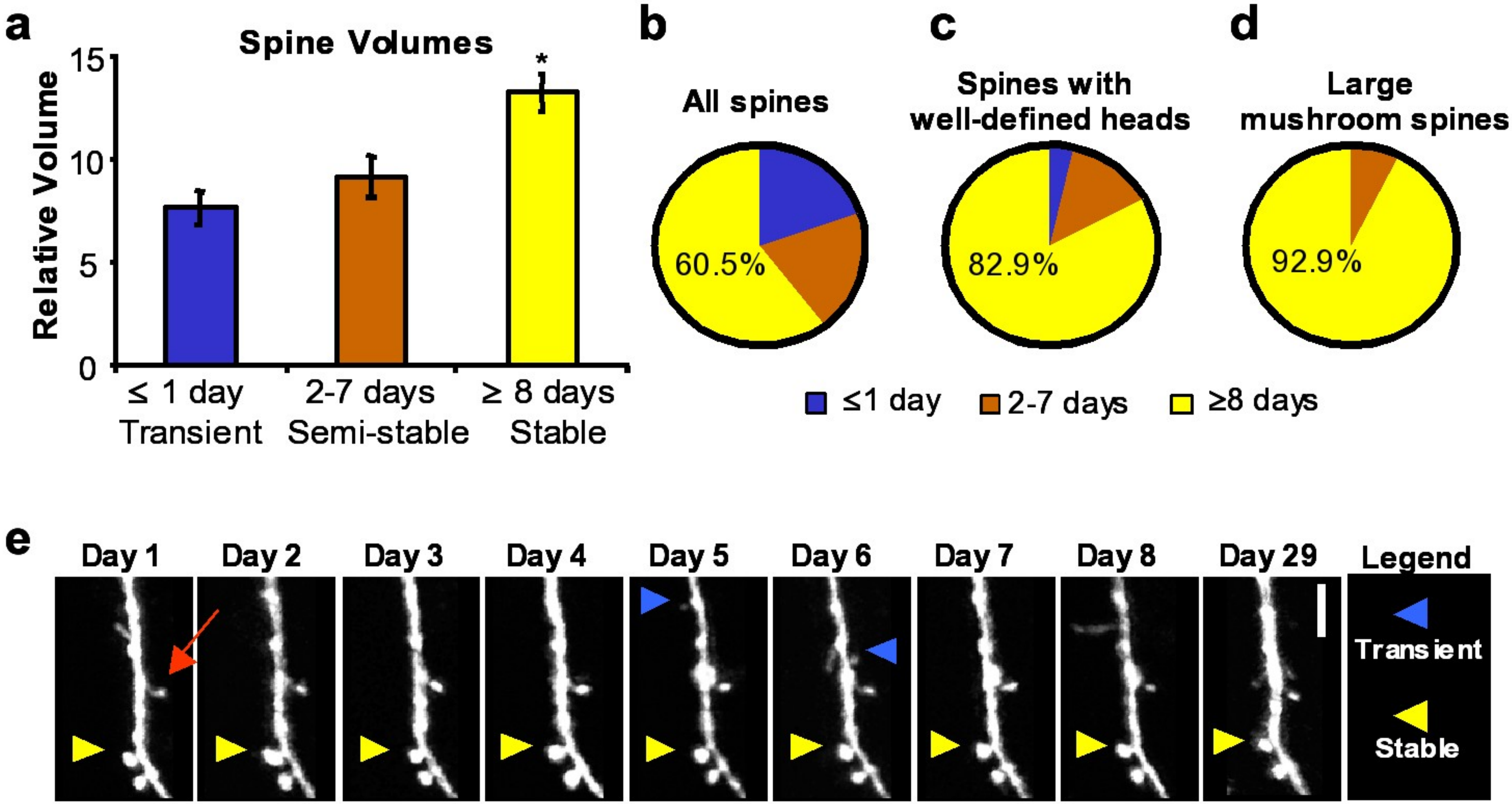


Undercompensating synapses freezes large weights



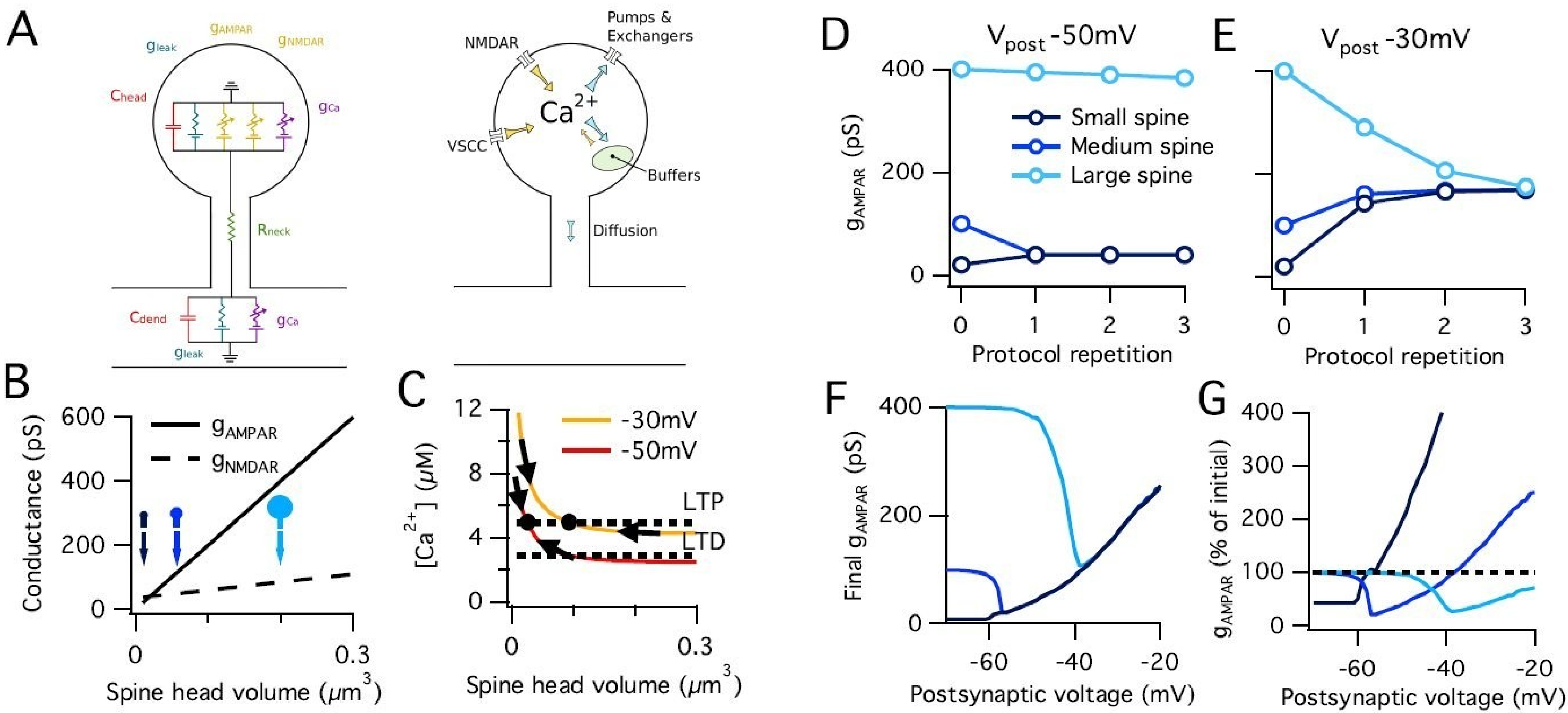
Note, contrasts with most softbound rules.

Large spines are more stable



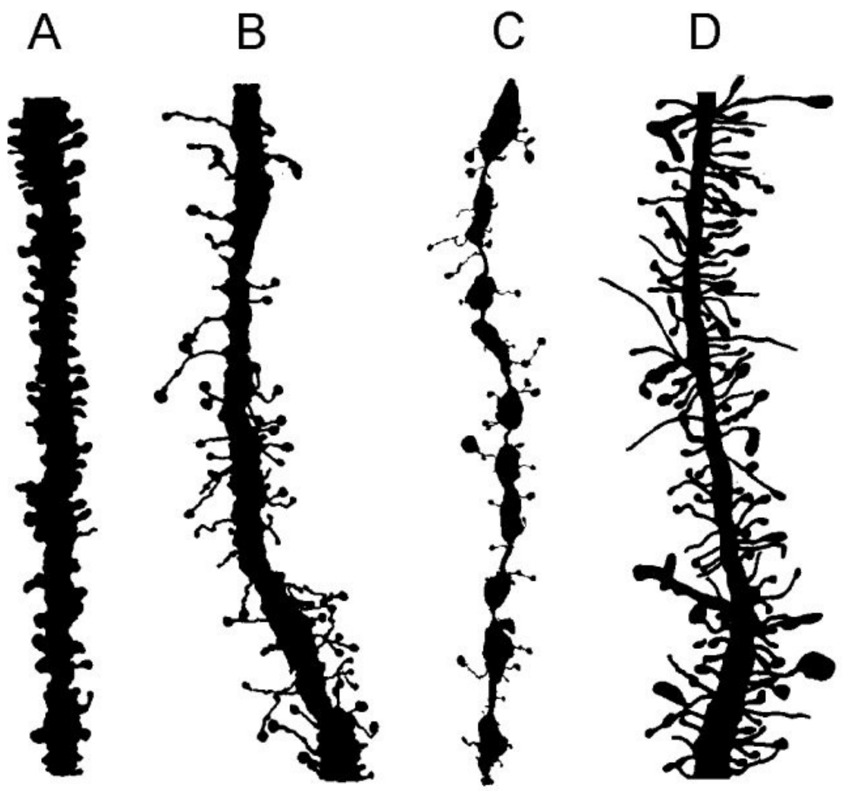
[from Trachtenberg '02 Supp Info]

Biophysical implementation

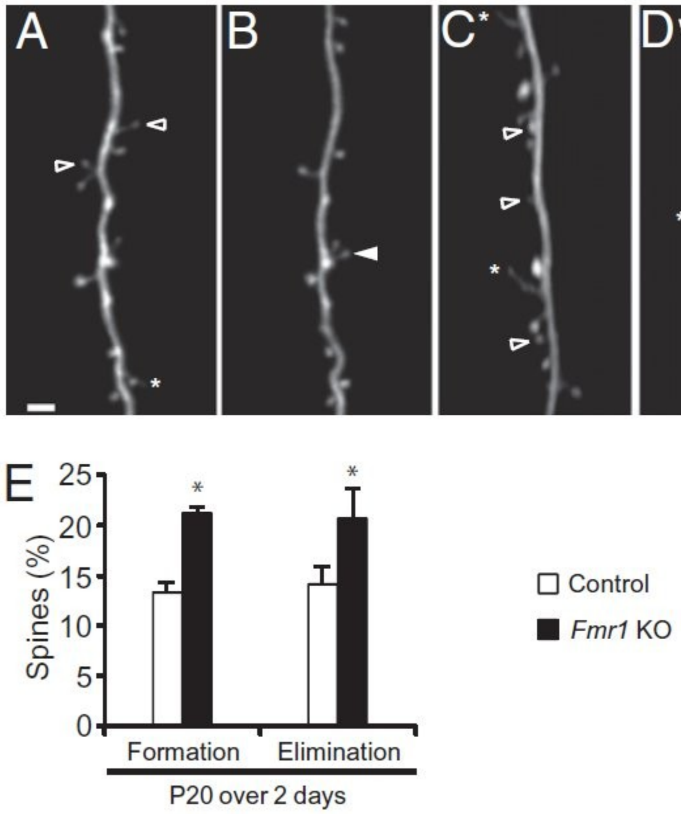


see also
[Kalantzis & Shouval '09]

Relation to disease?



[Fiala et al. '02]



[Pan et al. '10]

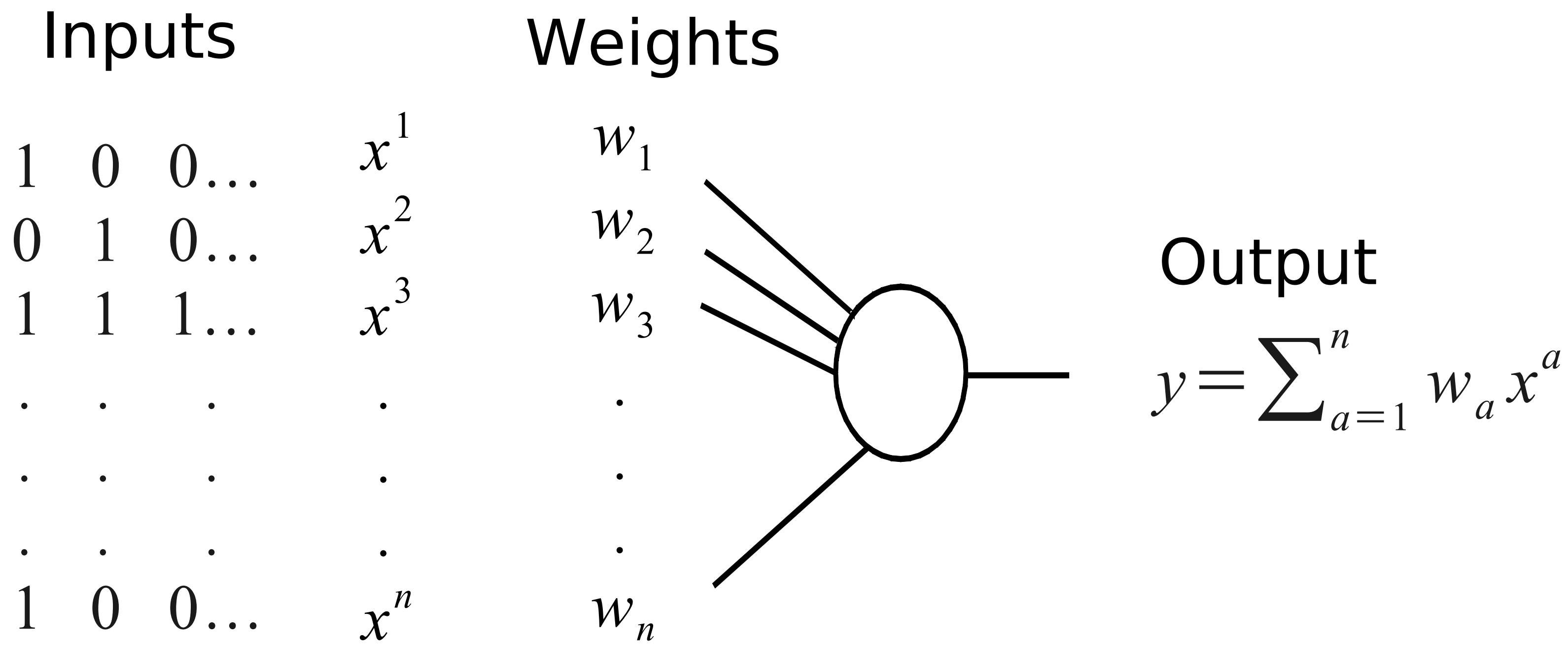
Table of contents

- Weight dependent STDP in single neurons and networks

- **Spine dynamics can affect plasticity rules**
  - **- Spine morphology likely under-compensates Ca influx**
  - **- Leads to weight dependent learning rules**
  - **- Leads to stabilization of large spines**

- Weight dependence increases information capacity

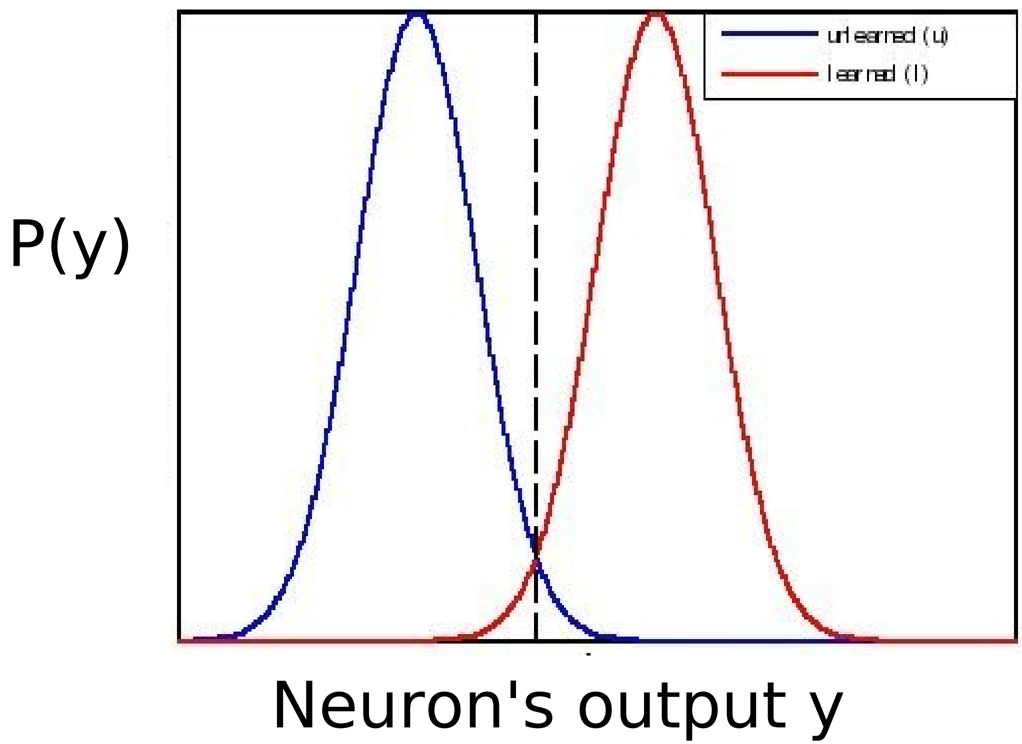
Weight dependent learning and information storage



- Binary patterns *x*
- Weights are bounded
- Ongoing learning, interrupted by recognition test

Measuring memory storage capacity

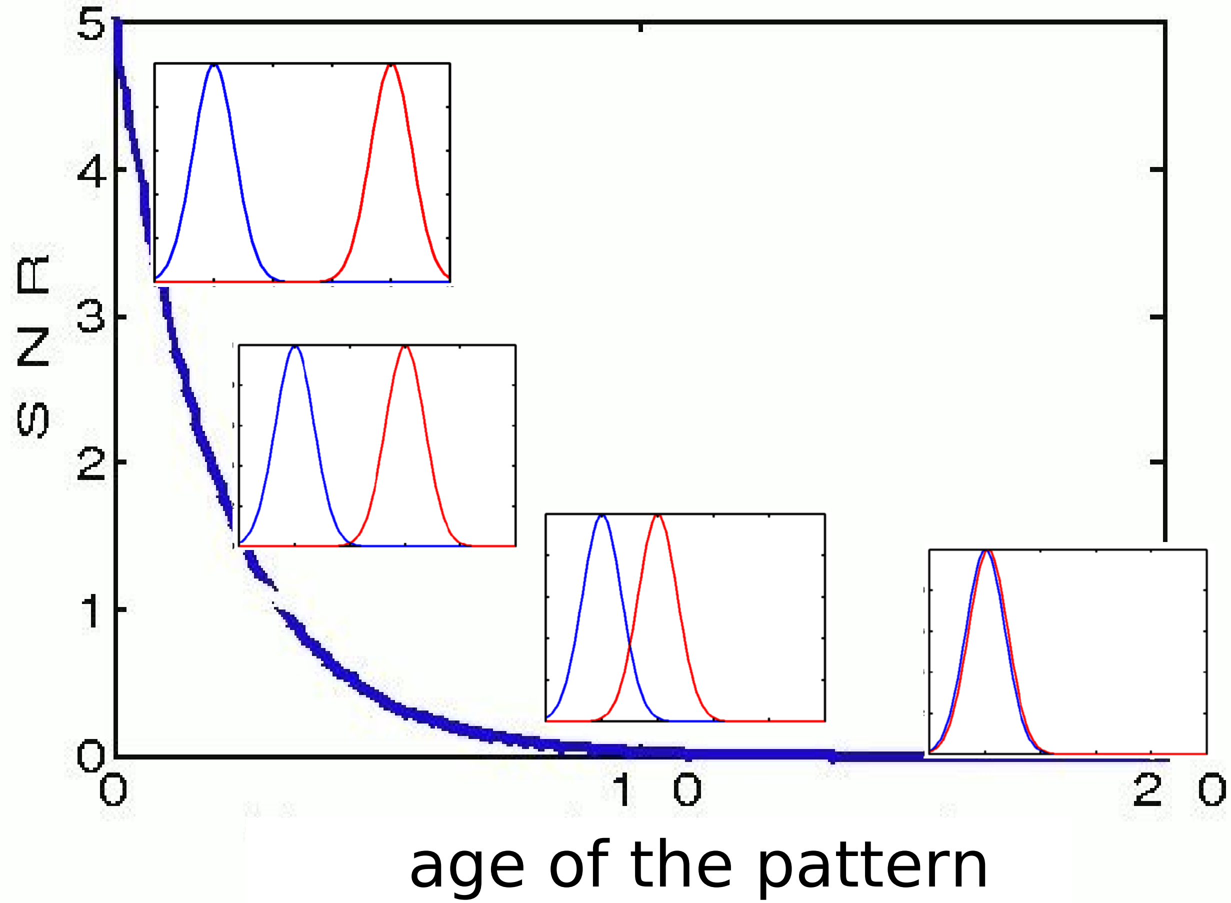
Separate learned from novel patterns ('lures')
Response in test phase:



Characterize with
Signal-to-Noise Ratio:

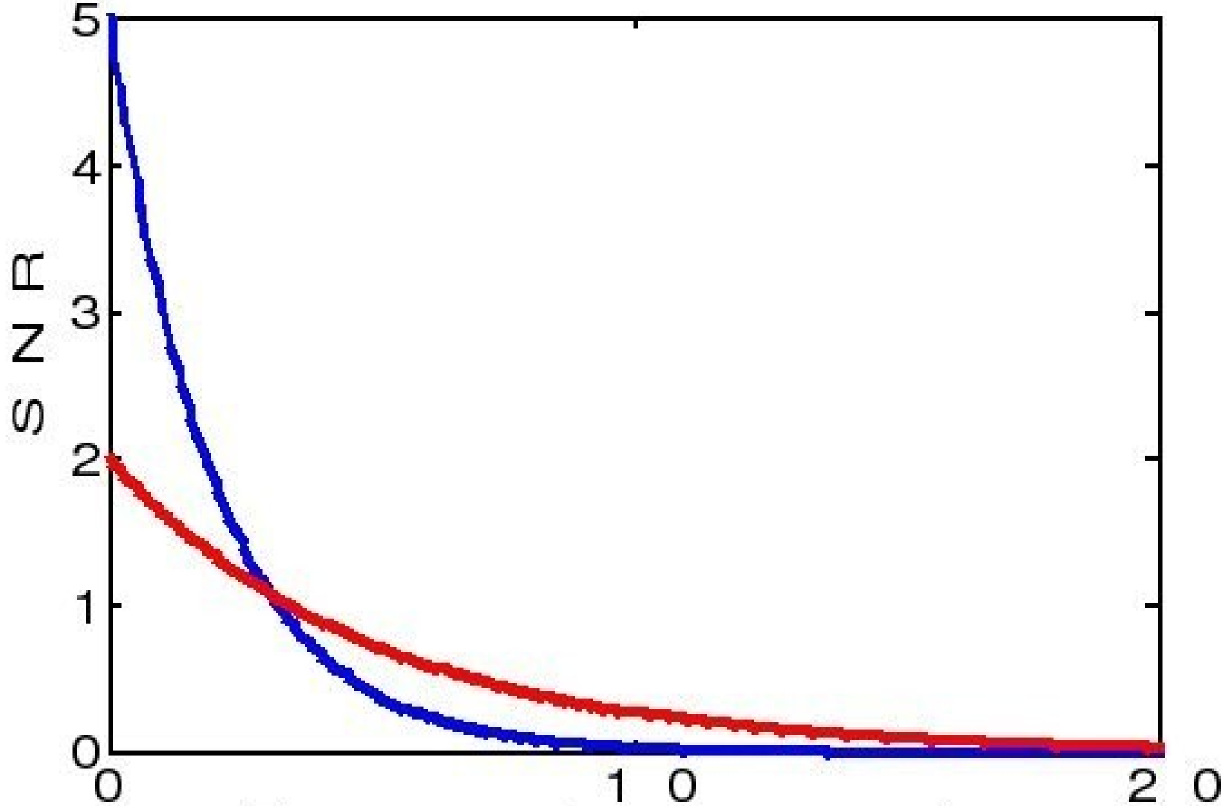
$$SNR = \frac{2\left[\langle y_u \rangle - \langle y_l \rangle\right]^2}{Var(y_u) + Var(y_l)}$$

Ongoing learning: new memories overwrite old ones



Exponential-like decay (but in principle many time-scales)

Trade-off: memory strength vs decay



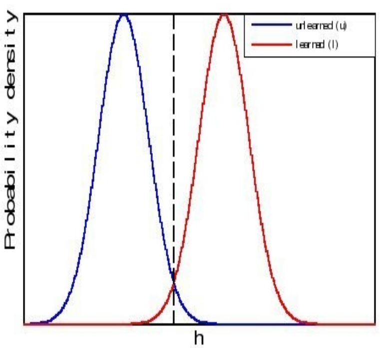
age of the pattern

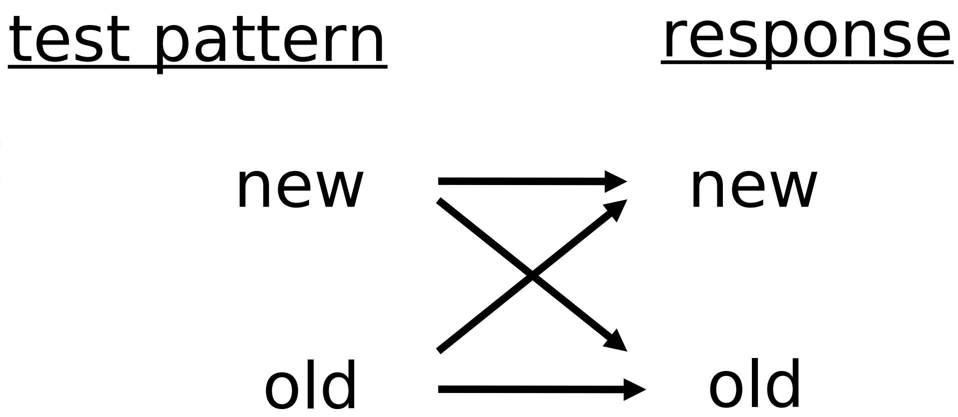
What is better:

- High initial SNR, or slow decay? [Fusi and Abbott '07]

Using Shannon information to resolve trade-off

How much **information** about the pattern is gained by inspecting the output?

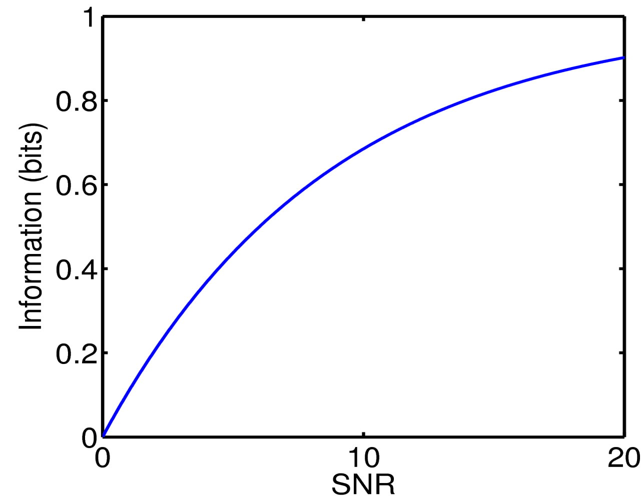




$$I = \sum_{s,r} P(r|s) P(s) \log_2 \frac{P(r|s)}{P(r)}$$

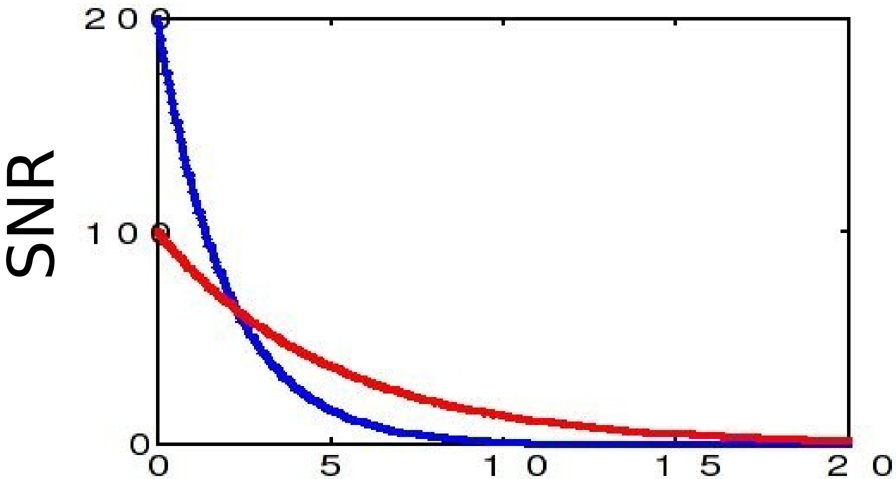
Always correct ~ 1 bit

Chance level ~ 0 bits



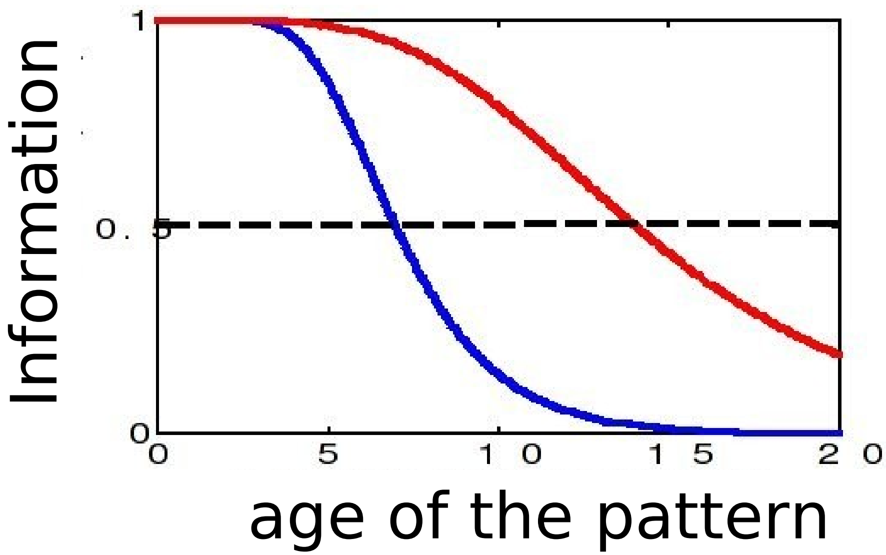
[Barrett and MvR' 08]

Relation between SNR and information



Independent patterns,
Total information **per** synapse:

$$I_{syn} = \frac{1}{N_{syn}} \sum_t I(t)$$



Best to store many patterns
with low SNR,
but what about weight dependence

Optimizing learning rules numerically

In general

$$\Delta w_i = f(x_i, y, w)$$

But patterns are binary:

$$\Delta w_i^{+} = f(x_i = 1, y = const, w)$$

$$\Delta w_i^{-} = f(x_i = 0, y = const, w)$$

Modelling learning

- Discretize array of possible weights (100 bins)
- Learning rule characterized by transition matrices M^{+} (high input), and M^{-} (low input) [Fusi and Amit '02].

$$M^{+} = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 1 & 1 \end{pmatrix} \qquad M^{-} = \begin{pmatrix} 1 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \end{pmatrix}$$

- Note, learning not stochastic.

Modelling learning

$$M^{-} = \begin{pmatrix} 1 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \end{pmatrix}$$

$$M^{-}\begin{pmatrix} 0 \\ 1 \\ 0 \\ 0 \\ 0 \\ 0 \end{pmatrix} = \begin{pmatrix} 1 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \end{pmatrix}$$

$$M^{-}\begin{pmatrix} 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 1 \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \\ 1 \\ 0 \\ 0 \end{pmatrix}$$

Modelling learning

- Learn from equilibrium weight distribution $\vec{\pi}_\infty$

Potentiation: $\vec{\pi} \rightarrow M^+ \vec{\pi}_\infty$

Depression: $\vec{\pi} \rightarrow M^- \vec{\pi}_\infty$

Expected update: $M = pM^+ + (1-p)M^-$

Signal decay: $\vec{\pi}_l(t) = M^t \vec{\pi}_l(0)$

$$M \vec{\pi}_\infty = \vec{\pi}_\infty$$

Weight independent learning

$$\Delta w_i^+ = f(x_i = 1, y = const, w)$$

$$\Delta w_i^- = f(x_i = 0, y = const, w)$$

0 th-order:

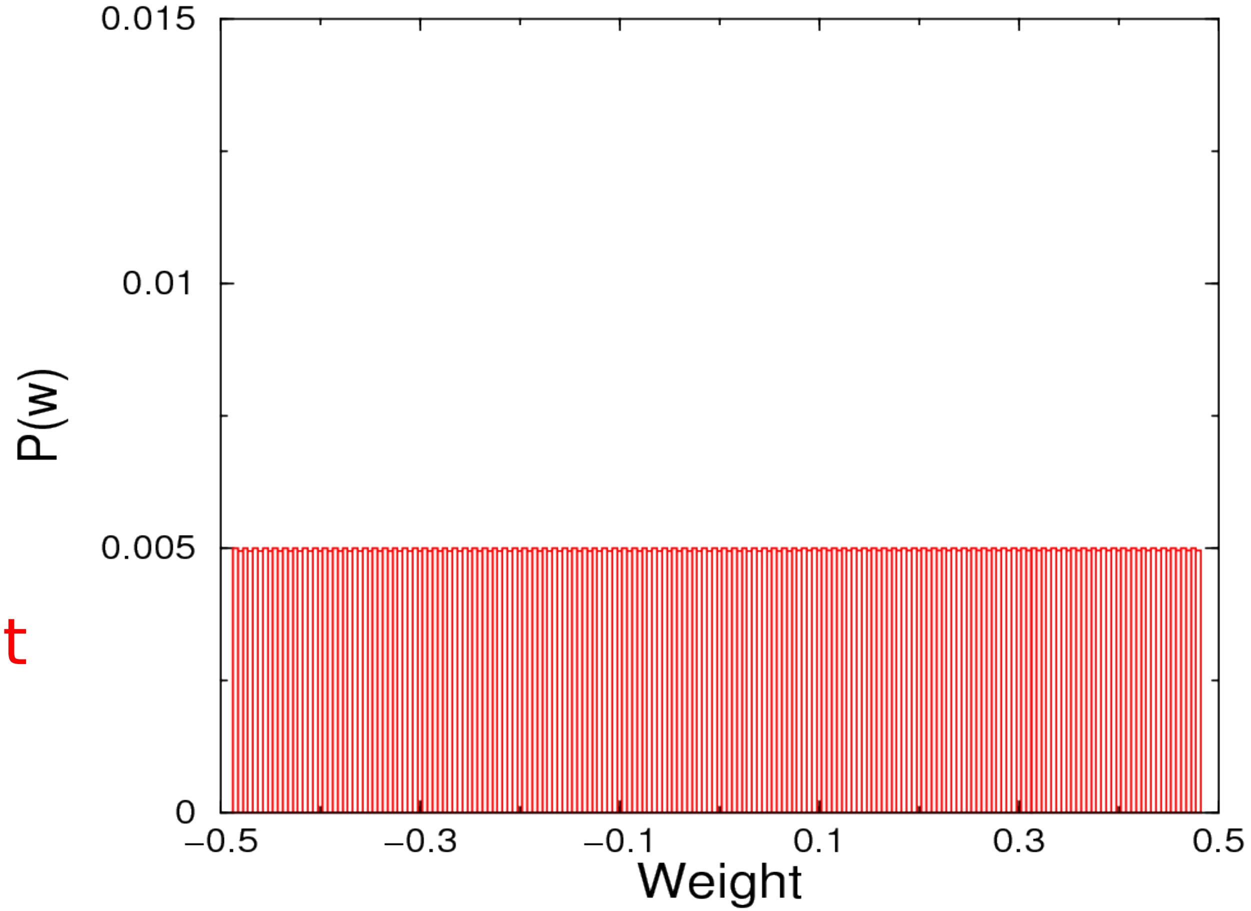
$$\Delta w_i^+ = a_1$$

$$\Delta w_i^- = -a_1$$

Weight independent learning

$$\Delta w_i^+ = f(x_i = 1, y = const, w)$$

$$\Delta w_i^- = f(x_i = 0, y = const, w)$$



0 th-order:

$$\Delta w_i^+ = a_1$$

$$\Delta w_i^- = -a_1$$

I_{syn}=0.047 bit

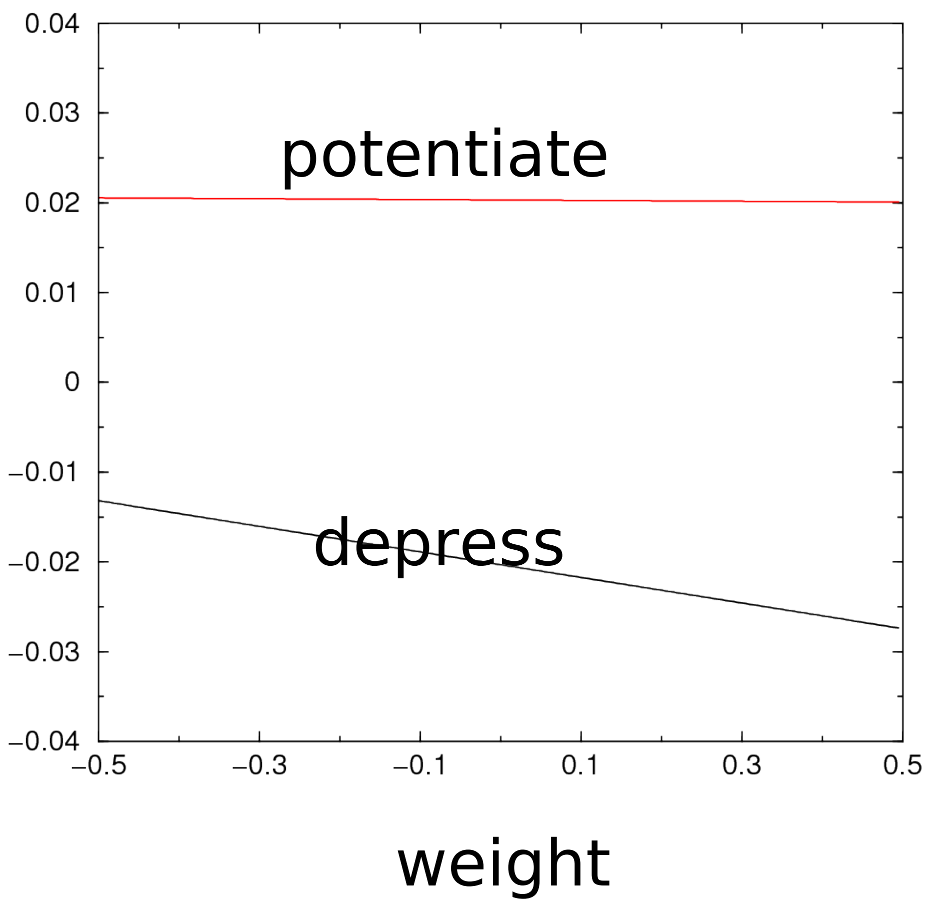
Optimal learning rule balances LTD against LTP

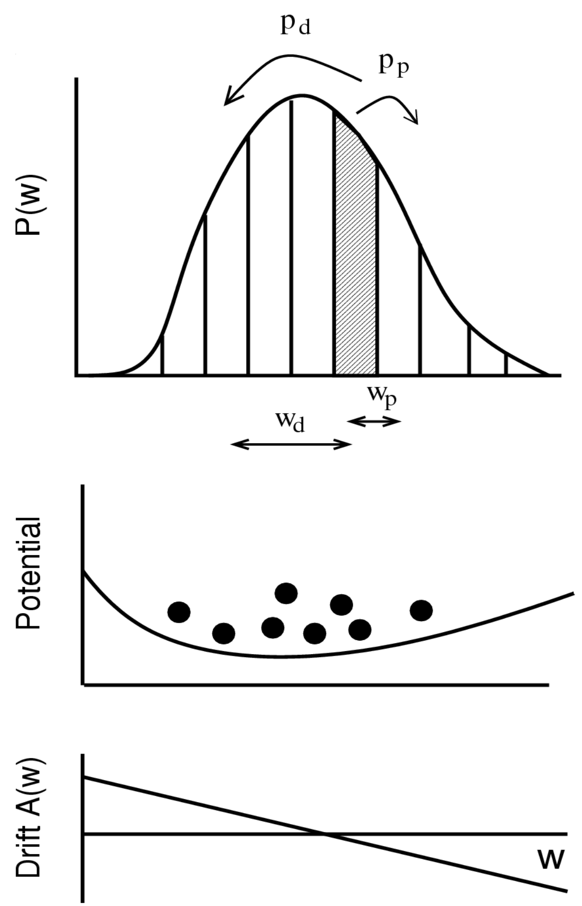
Weight dependent learning increases capacity

1 st -order:

$$\Delta w_i^+ = a_1 + b_1 w$$

$$\Delta w_i^- = a_2 + b_2 w$$





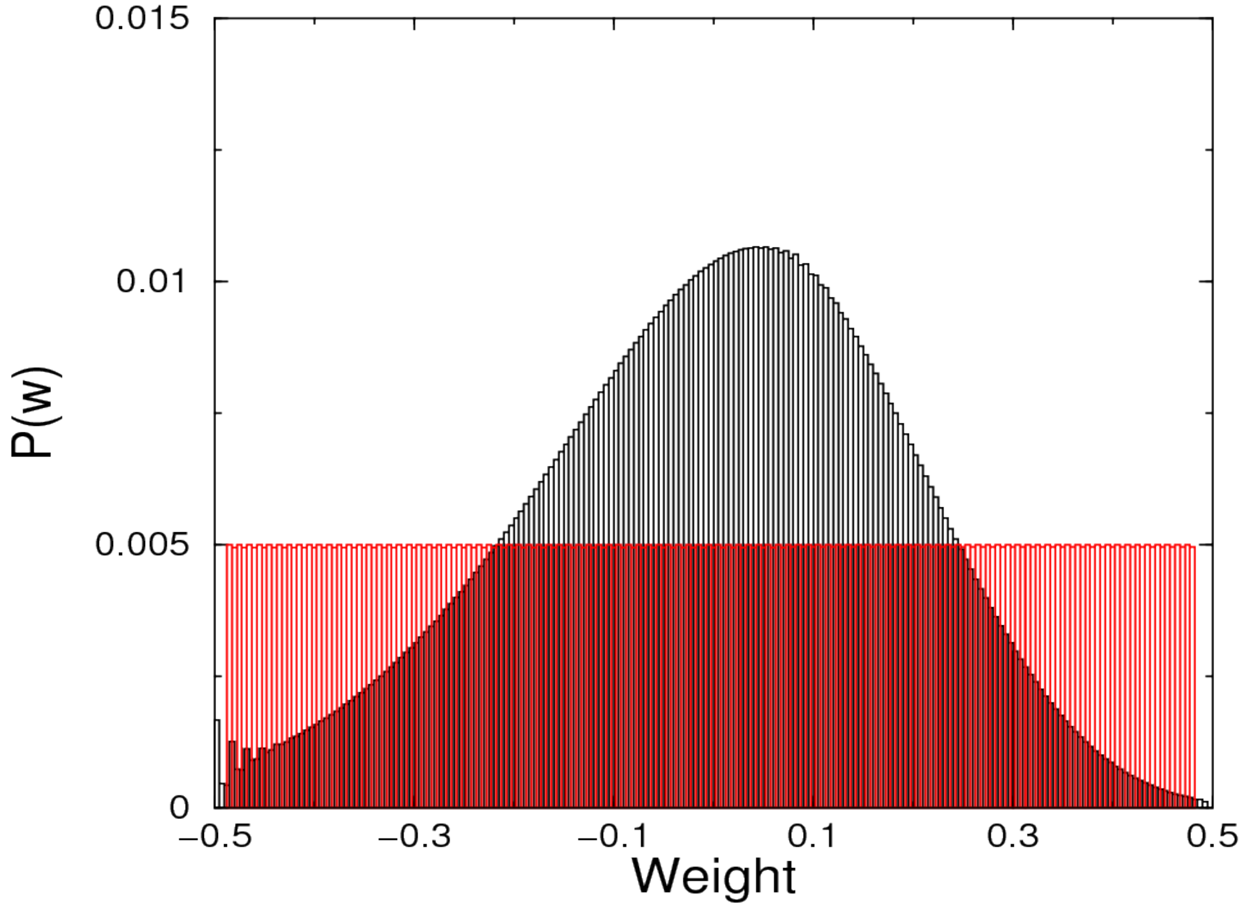
Weight dependent learning increases capacity

I_{syn}=0.047 bit

$$\Delta w_i^+ = a_1 + b_1 w$$

$$\Delta w_i^- = a_2 + b_2 w$$

I_{syn}=0.052 bit

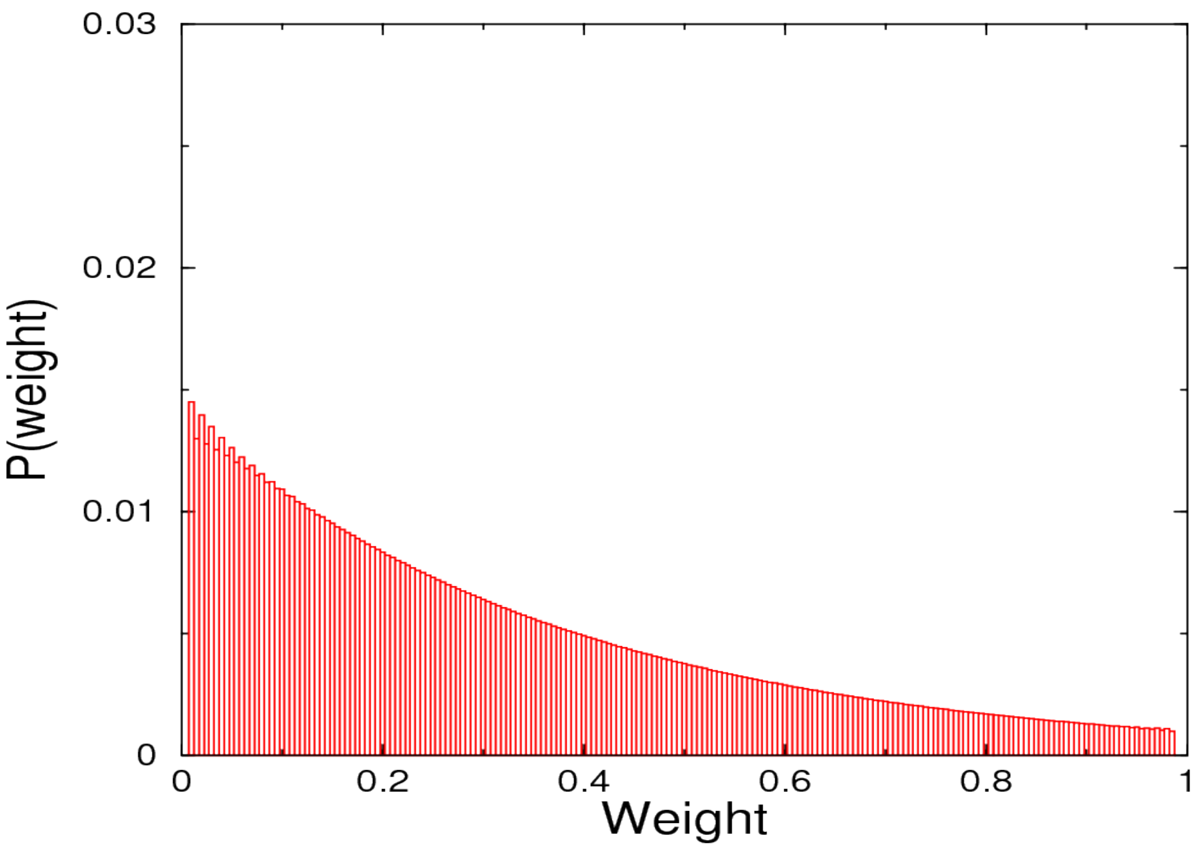


- Weight dependent learning increases capacity
- Higher order does not further increase capacity (significantly)

Restricting to excitatory synapses

0 th-order:

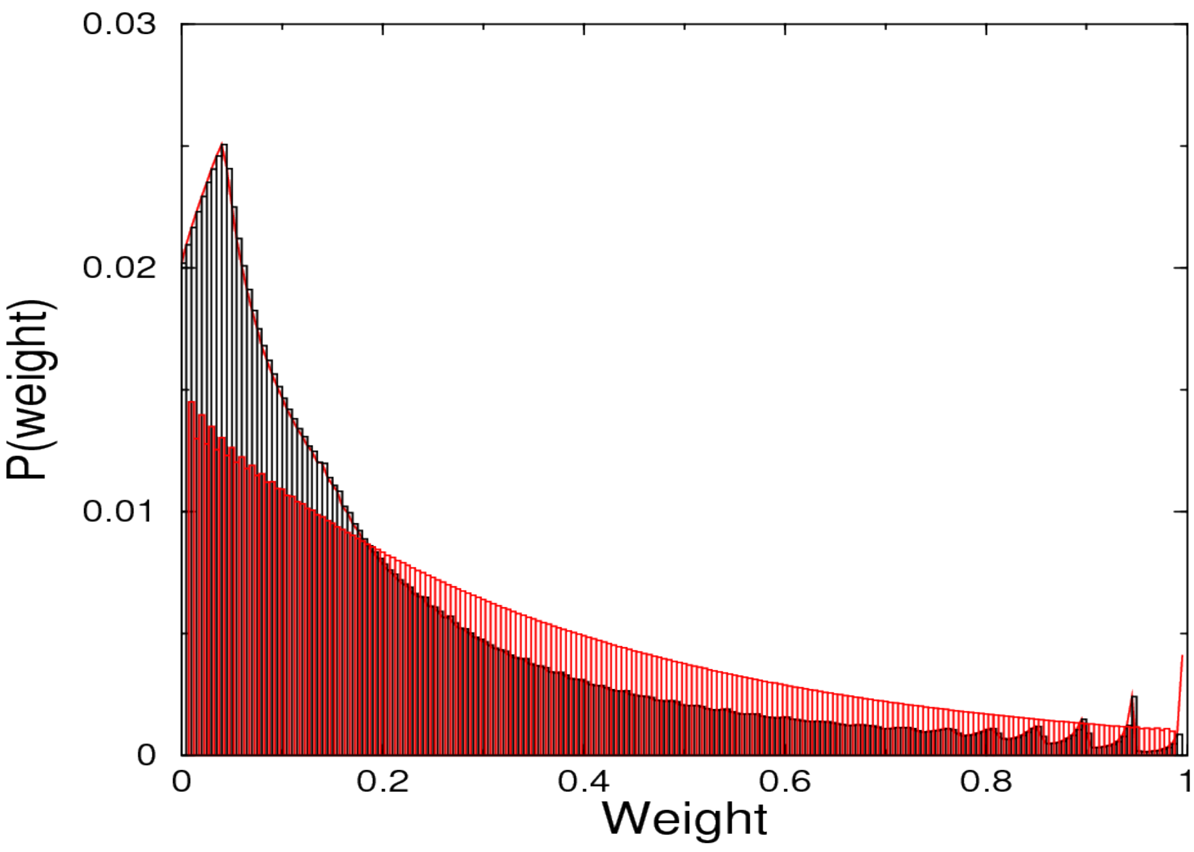
I_{syn}=0.022 bit



Restricting to excitatory synapses

I_{syn}=0.022 bit

I_{syn}=0.025 bit



- Using excitatory-only synapses reduces capacity
- Weight dependent rule is again better

Why does it matter that weights are excitatory?

$$SNR = \frac{2\left[\langle y_u \rangle - \langle y_l \rangle\right]^2}{Var(y_u) + Var(y_l)}$$

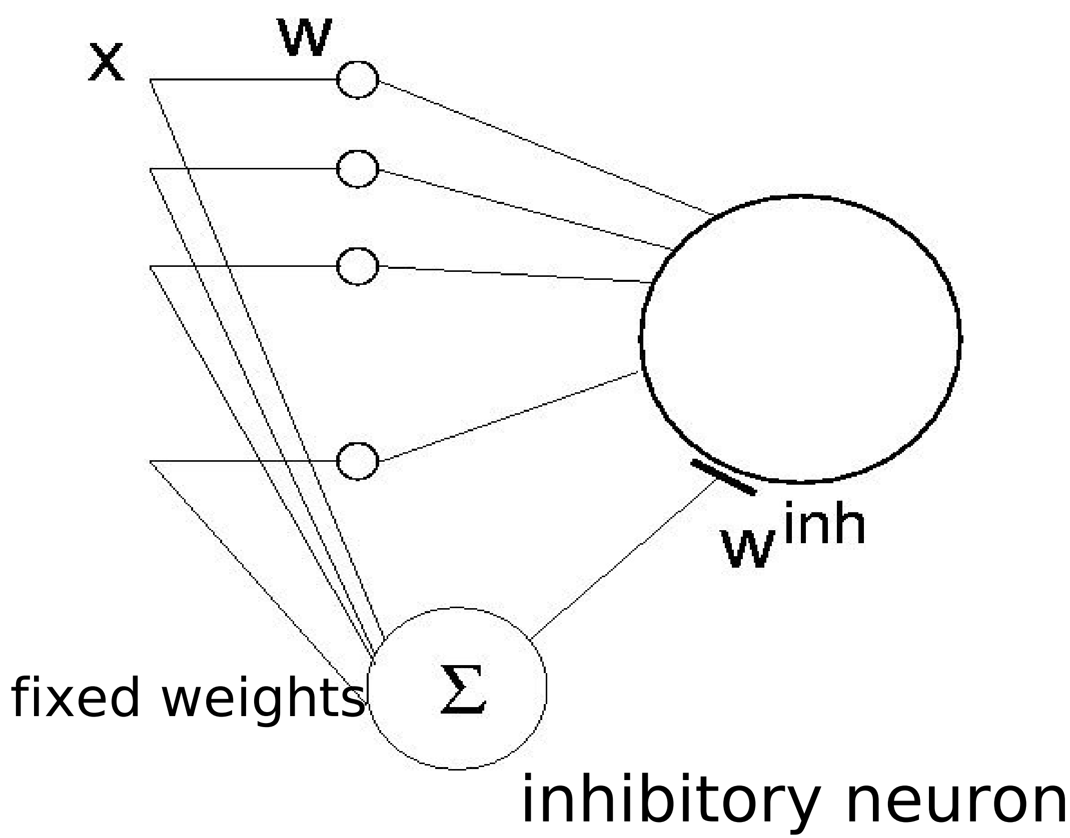
Note

$$\begin{aligned} var(y) &\propto var(wx) \\ &= var(x)\,var(w) + var(x)\langle w \rangle^2 + var(w)\langle x \rangle^2 \end{aligned}$$

So SNR is better if $\langle w \rangle = 0$

$$= var(x)\,var(w) + var(w)\langle x \rangle^2$$

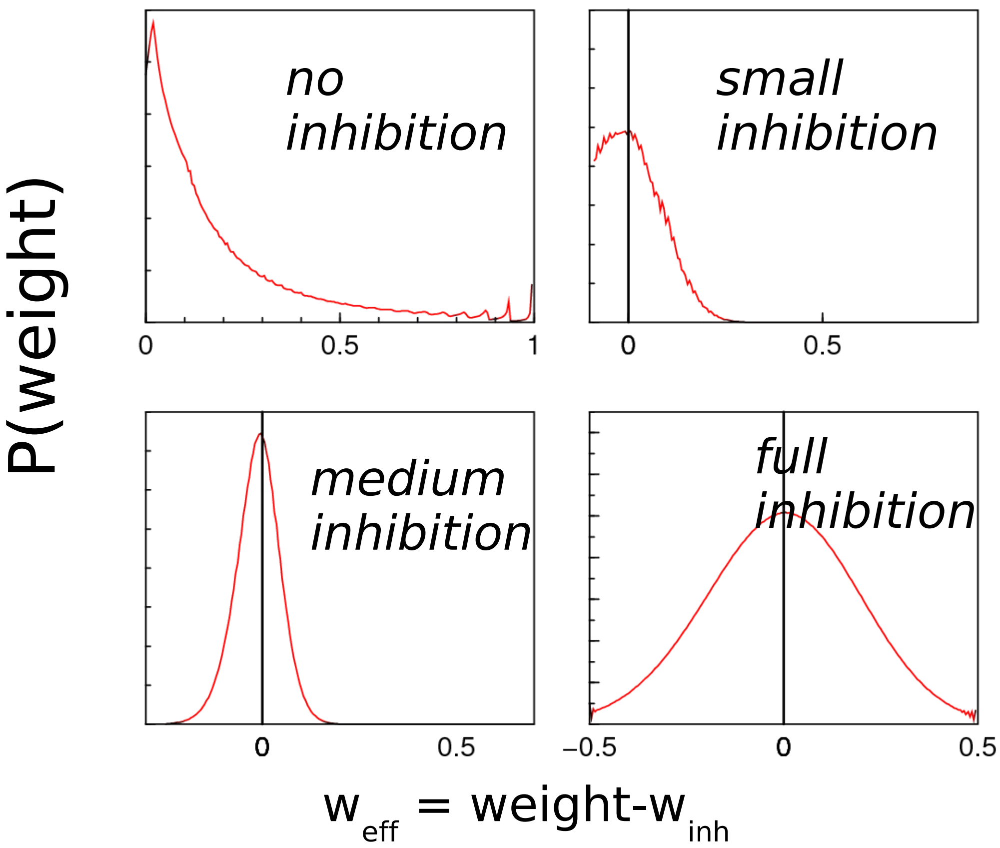
Increasing capacity by implementing feed-forward inhibition

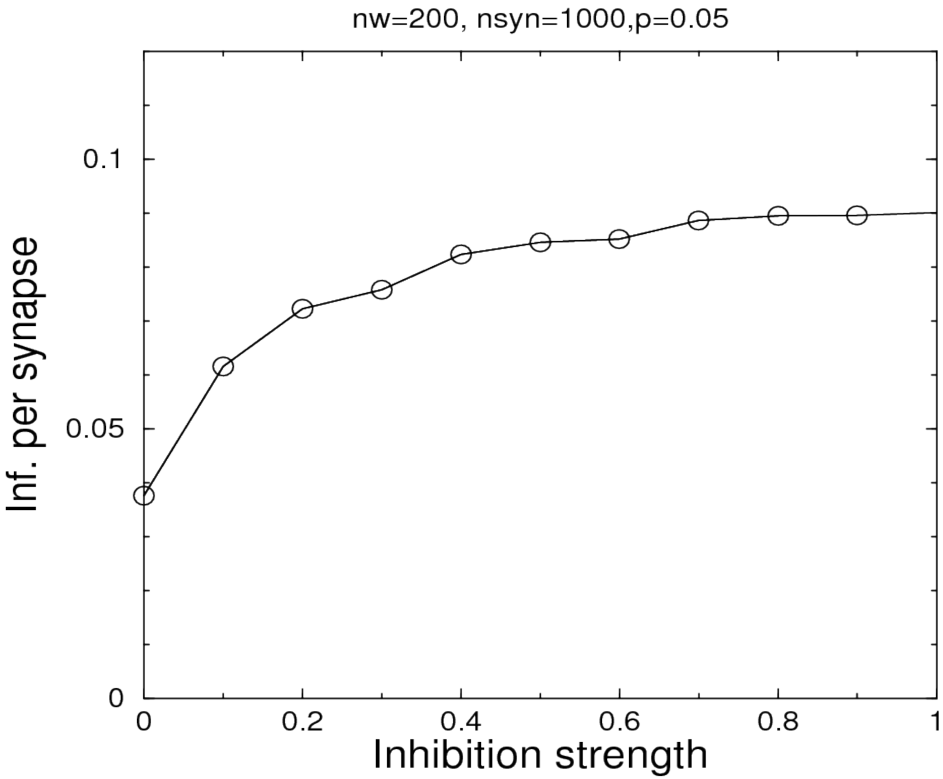


$$y = \sum_i w_i x_i - w^{inh} \sum_i x_i = \sum_i (w_i - w^{inh}) x_i$$

So $\langle w_{eff} \rangle = \langle w_i - w^{inh} \rangle$ can be made 0

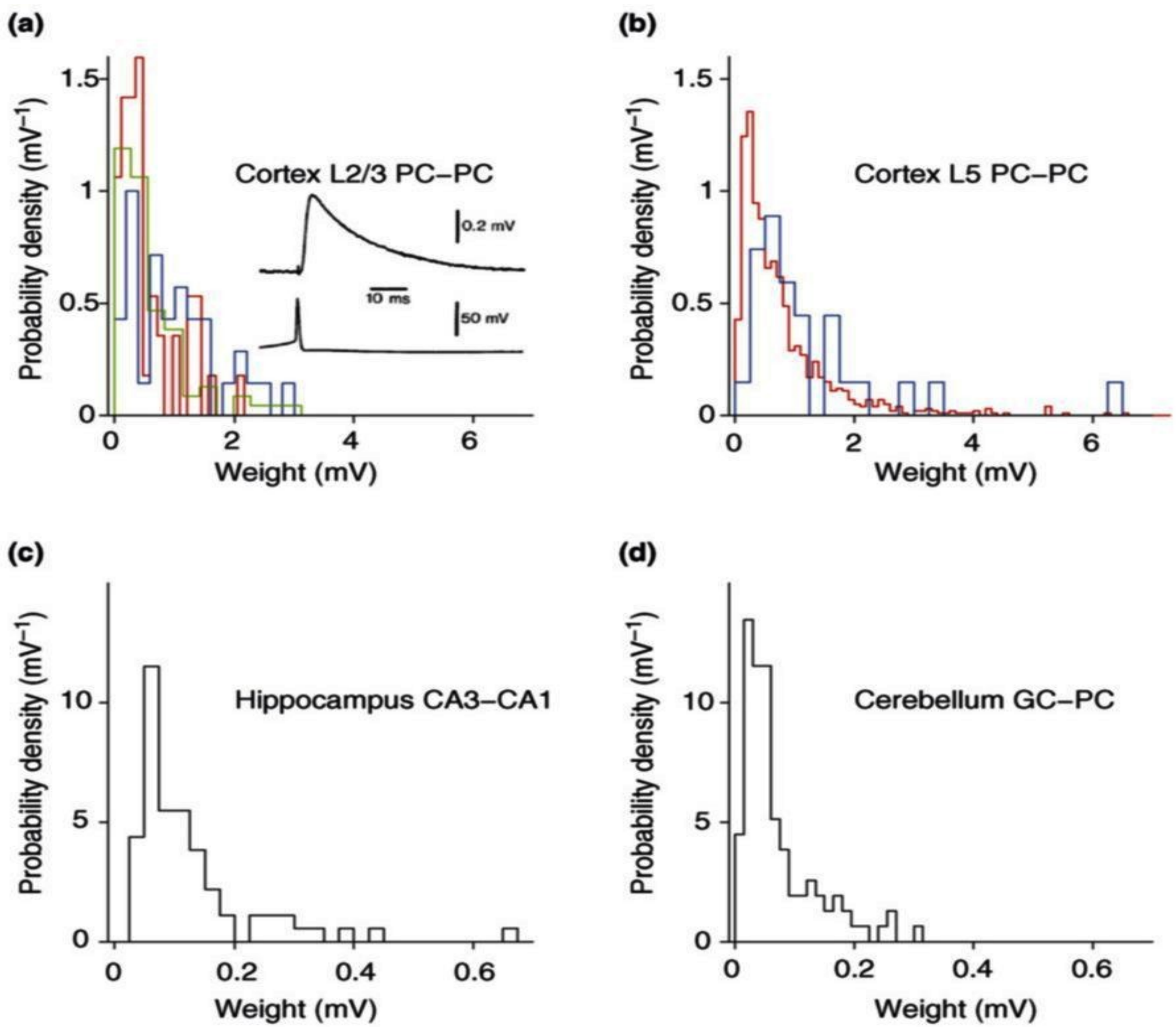
Weight distribution at various levels of inhibition





- Synapses cluster around effective weight 'zero' (balance)

Data on weight distribution



[Barbour et al. '07]

Further improvement: sparse patterns

$$SNR = \frac{\left(\langle y_u \rangle - \langle y_l \rangle\right)^2}{\frac{1}{2}\left(Var(y_u) + Var(y_l)\right)}$$

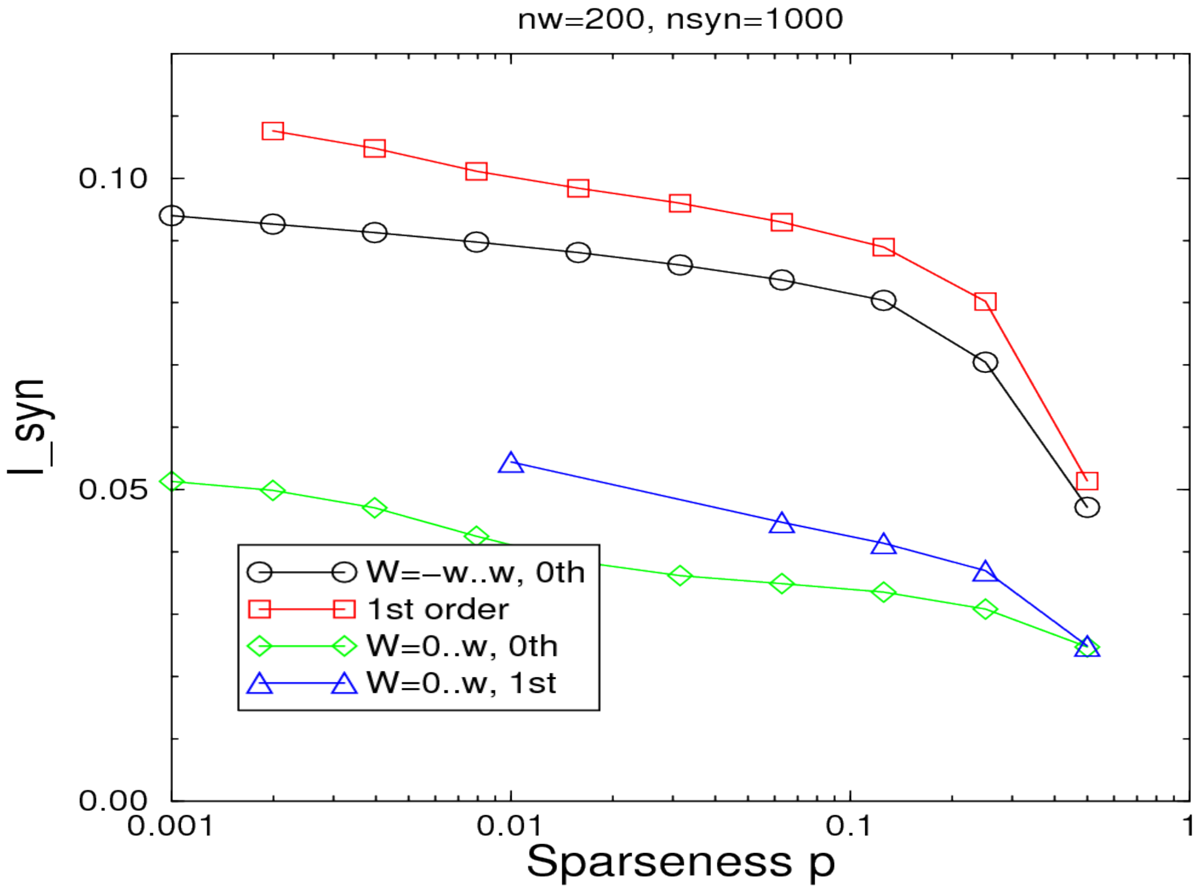
Note

$$\begin{aligned} var(y) &\propto var(wx) \\ &= var(x)var(w) + var(w)\langle x \rangle^2 \end{aligned}$$

So SNR is better if $\langle x \rangle = 0$

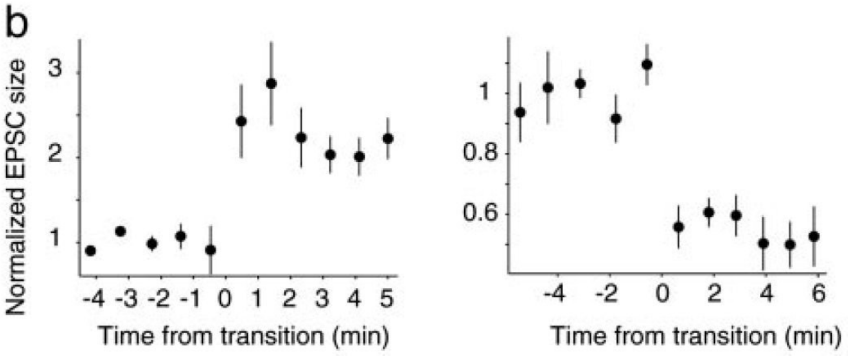
Use sparse patterns

Pattern sparseness increases capacity

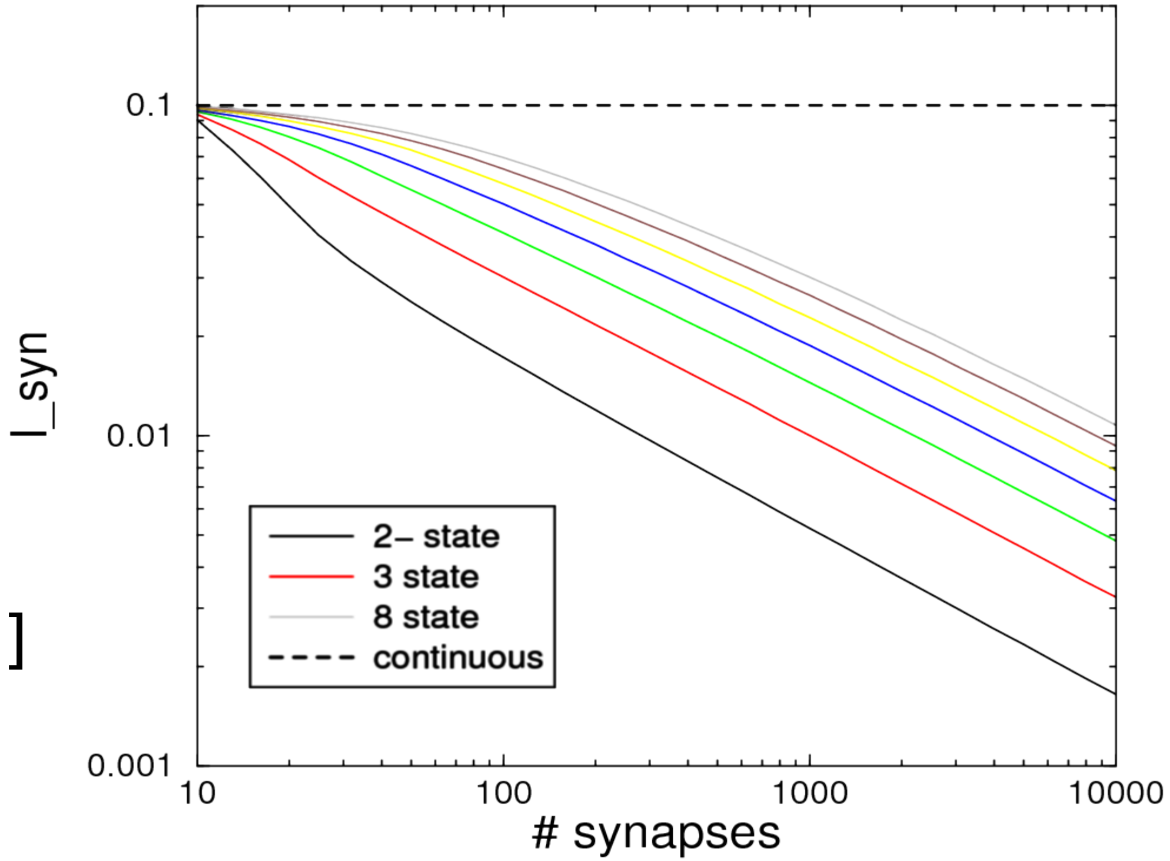


Sparse patterns further increase information capacity
(Little effect on distributions)

Comparison discrete synapses

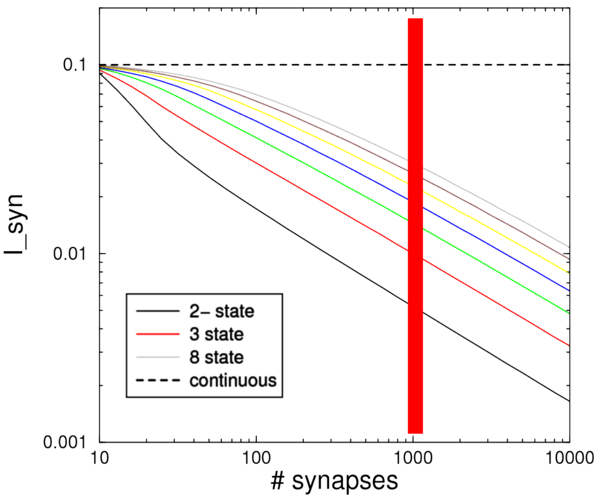


Discrete synapses?
[Petersen '98, O'Connor & Wang '05]



- Few synapses: discrete synapses perform well [Barrett, MvR '08]
- Decay $I_{syn} \propto 1/\sqrt{n_{syn}}$ as transitions are made stochastic
  [Fusi & Amit '02, Fusi & Abbott '07]

Equilibrium distribution for optimal learning depends on # states



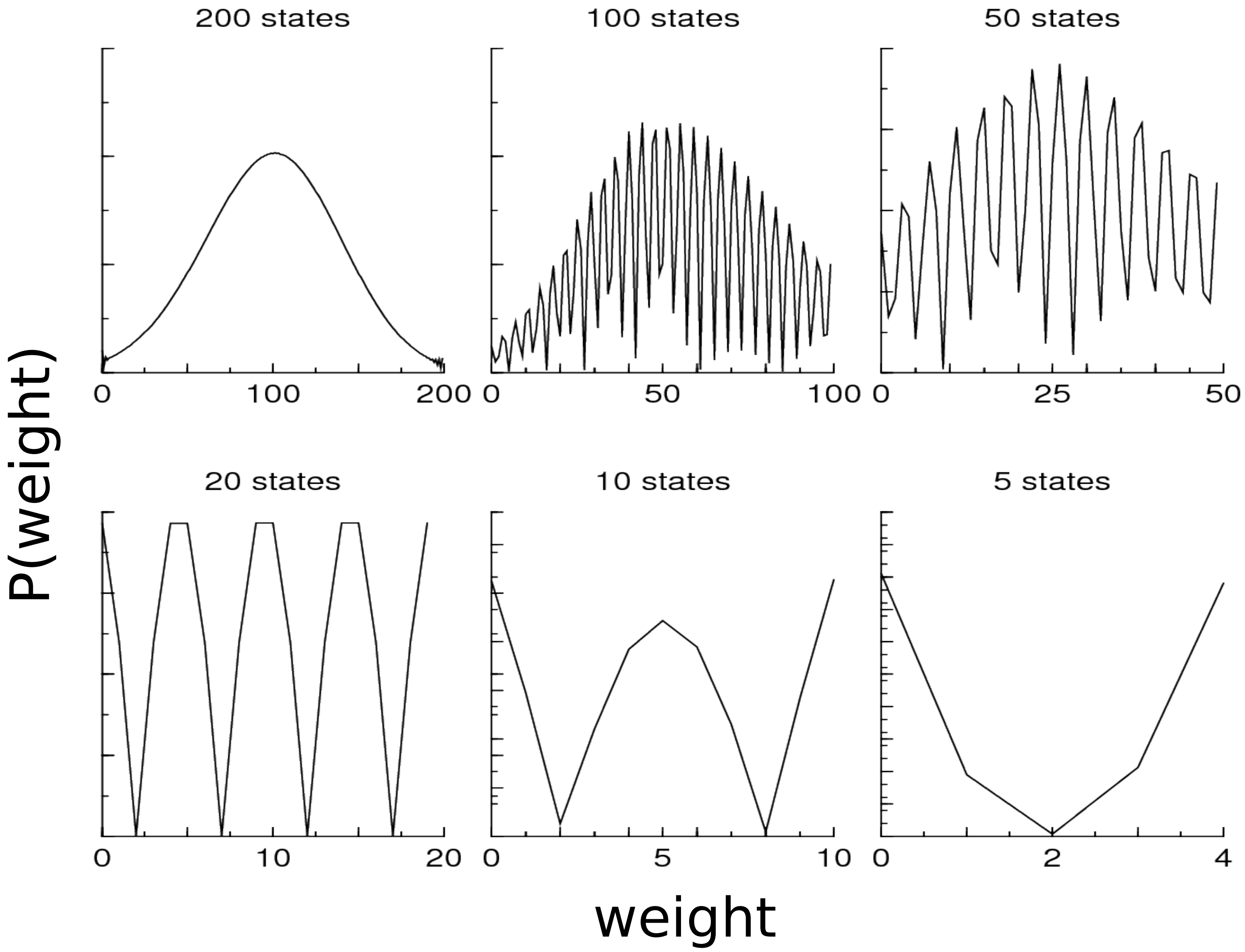


Table of contents

- Weight dependent STDP in single neurons and networks
- Spine dynamics can implement weight dependence
- **Weight dependence increases information capacity**
  - Small, significant increase
  - Feedforward inhibition and sparseness help
  - Might also hold in networks [Huang &Amit, in press]

Open questions

- Why are large spines more stable from a computational viewpoint?
- Relation to long term stability mechanisms, e.g. protein synthesis, synaptic tagging ?
- How general are these findings ?

Discussion

- Towards realistic models of synaptic plasticity

- Synaptic plasticity is weight dependent:
    - Realistic weight distribution
    - Shorter memory time, but is rescued by inhibition
    - Improves storage capacity

- Spine volume dynamics could underlie weight dependence