



# 外界をモデル化する脳の回路メカニズム —海馬と大脳皮質—

Brain's network mechanisms to model the external world

深井 朋樹

理化学研究所 脳科学総合研究センター

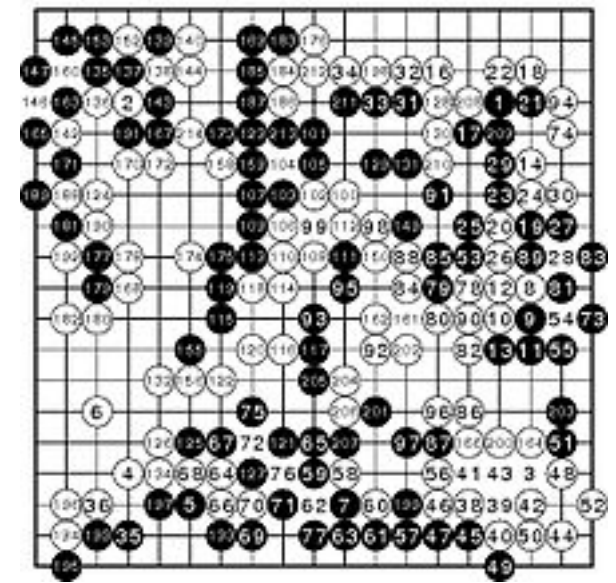
2017年8月4日 @ 電気通信大学

# 頂上決戦 !!

## Game of GO (碁)

2016 Mar: 李世乜(イ・セドル)九段 vs Alpha GO

2017 May: Alpha GO vs 柯潔(か・けつ)九段



李世乜  
(Wikipedia)



柯潔  
(Google)

# ディープ Qラーニング

$$Q^*(s,a) = \max_{\pi} \mathbb{E}_s [r_t + \gamma r_{t+1} + \gamma^2 r_{t+2} + \dots | s_t = s, a_t = a, \pi]$$

big data of past game record

value evaluation of current state

machine vs. machine

Silver et al., Nature 2016

「論理的思考」ではなく「経験と勘」を養うことによる勝利

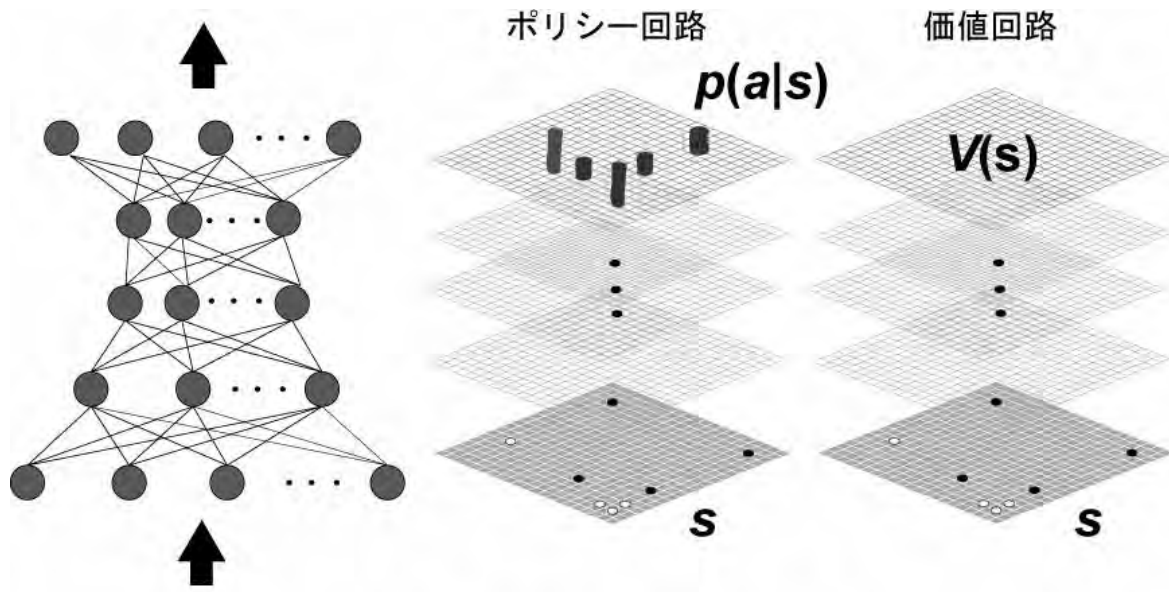


図3：深層学習による碁の習得

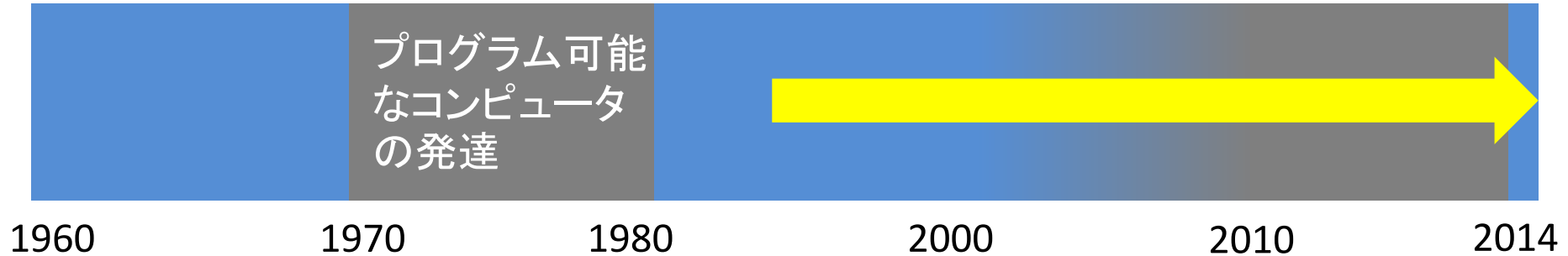


# 脳の計算理論の発展

第一次ブーム

第二次ブーム

第三次ブーム



神経回路網(McCulloch & Pitts、**甘利**)  
パーセプトロン  
視覚の計算理論 (Marr)

誤差逆伝搬学習  
教師なし学習(自己組織化)  
強化学習(意思決定)  
時間誤差学習  
予測符号化  
連想記憶モデル  
シンファイア・チェーン  
スパイク時間依存シナプス可塑性  
液体状態マシン ...

ディープ学習  
機械学習  
人工知能( $\alpha$ 碁)  
リザーバ・マシン  
ニューロモルフィック  
全脳の階層モデル  
社会性の脳科学  
...

データ・サイエンス



# 脳は学習する。何のために？

→ 外界の特徴を検出し、外界をモデル化するため



では何のためにモデル化する

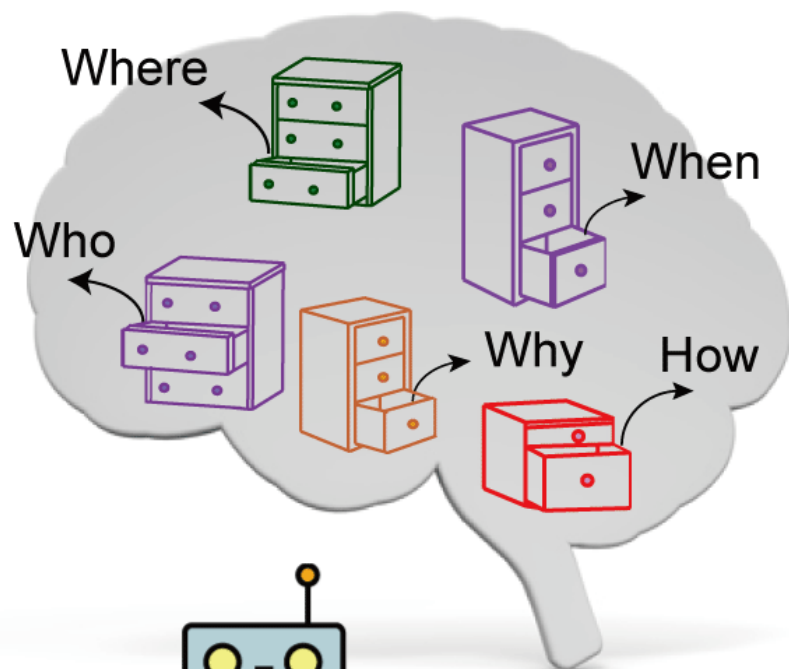
→ 世界の動きを予測し、行動を計画するため



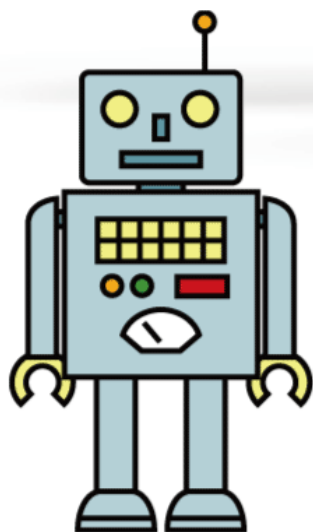
統計的モデル



# 脳は記憶というビッグデータをどう扱っているのか？



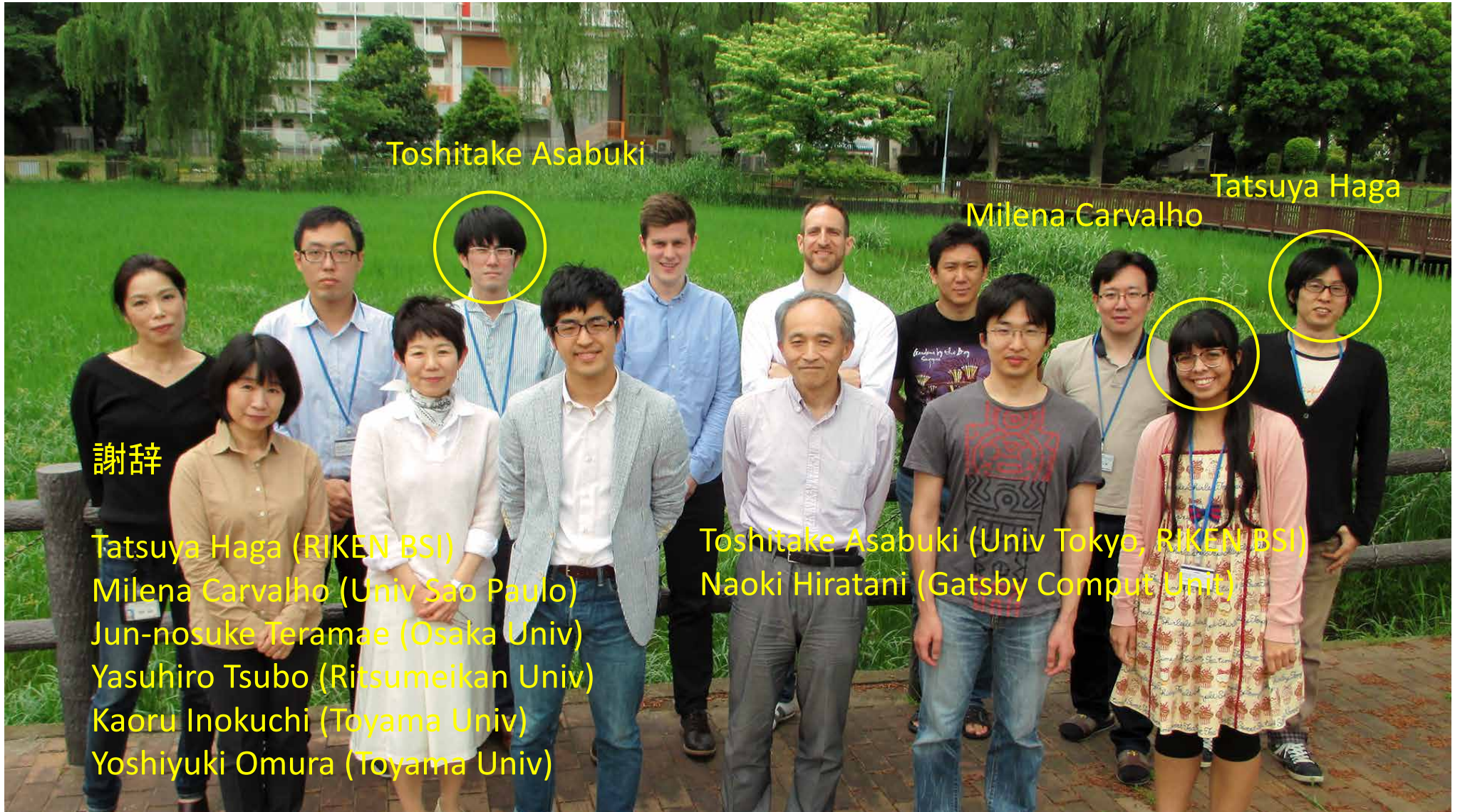
- 素早い記憶 (one-shot learning)
- 文脈依存の想起
- 報酬依存の記憶・学習



Human-like memory systems will  
make AI more human-like



# Laboratory for Neural Circuit Theory



Toshitake Asabuki

Tatsuya Haga

Milena Carvalho

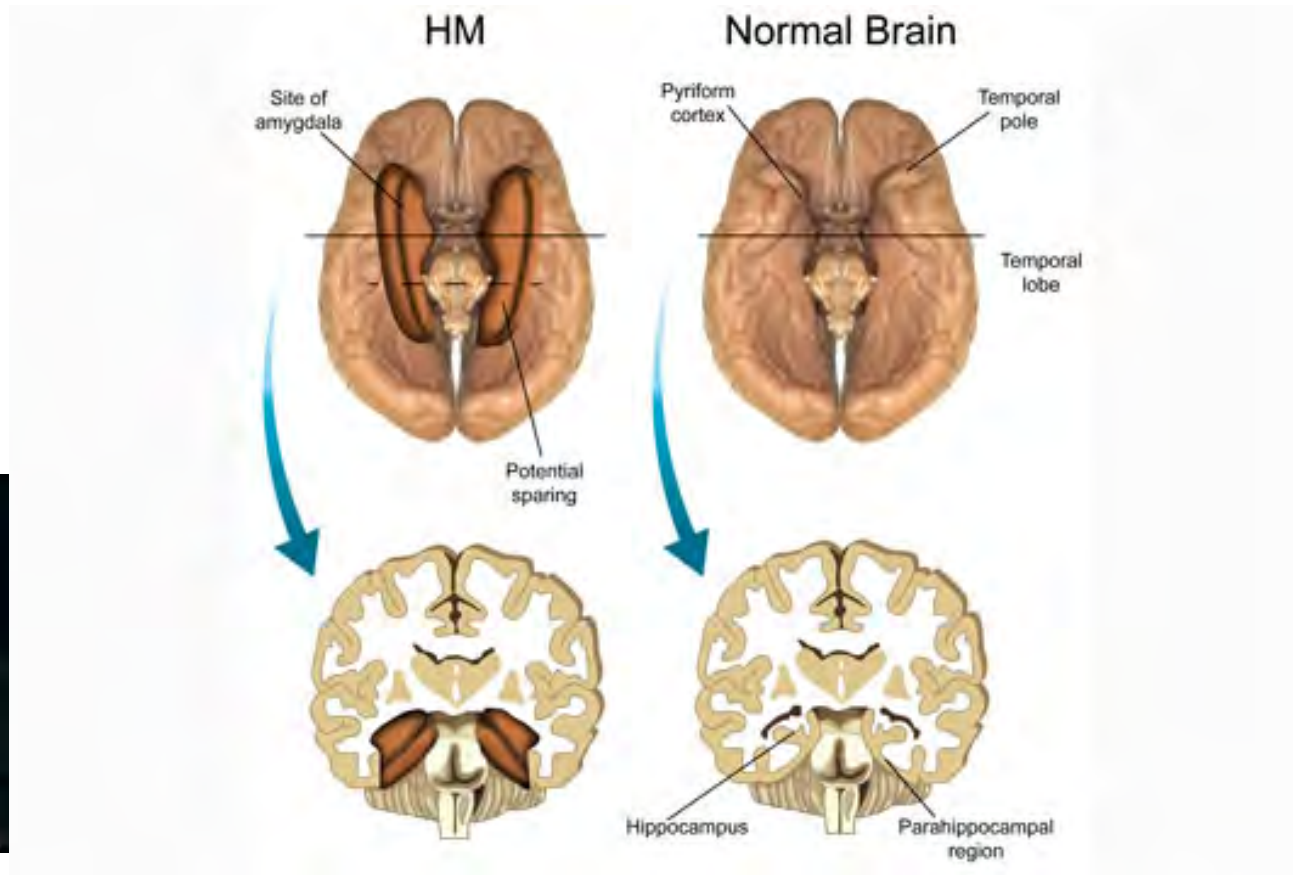
謝辞

Tatsuya Haga (RIKEN BSI)  
Milena Carvalho (Univ Sao Paulo)  
Jun-nosuke Teramae (Osaka Univ)  
Yasuhiro Tsubo (Ritsumeikan Univ)  
Kaoru Inokuchi (Toyama Univ)  
Yoshiyuki Omura (Toyama Univ)

Toshitake Asabuki (Univ Tokyo, RIKEN BSI)  
Naoki Hiratani (Gatsby Comput Unit)



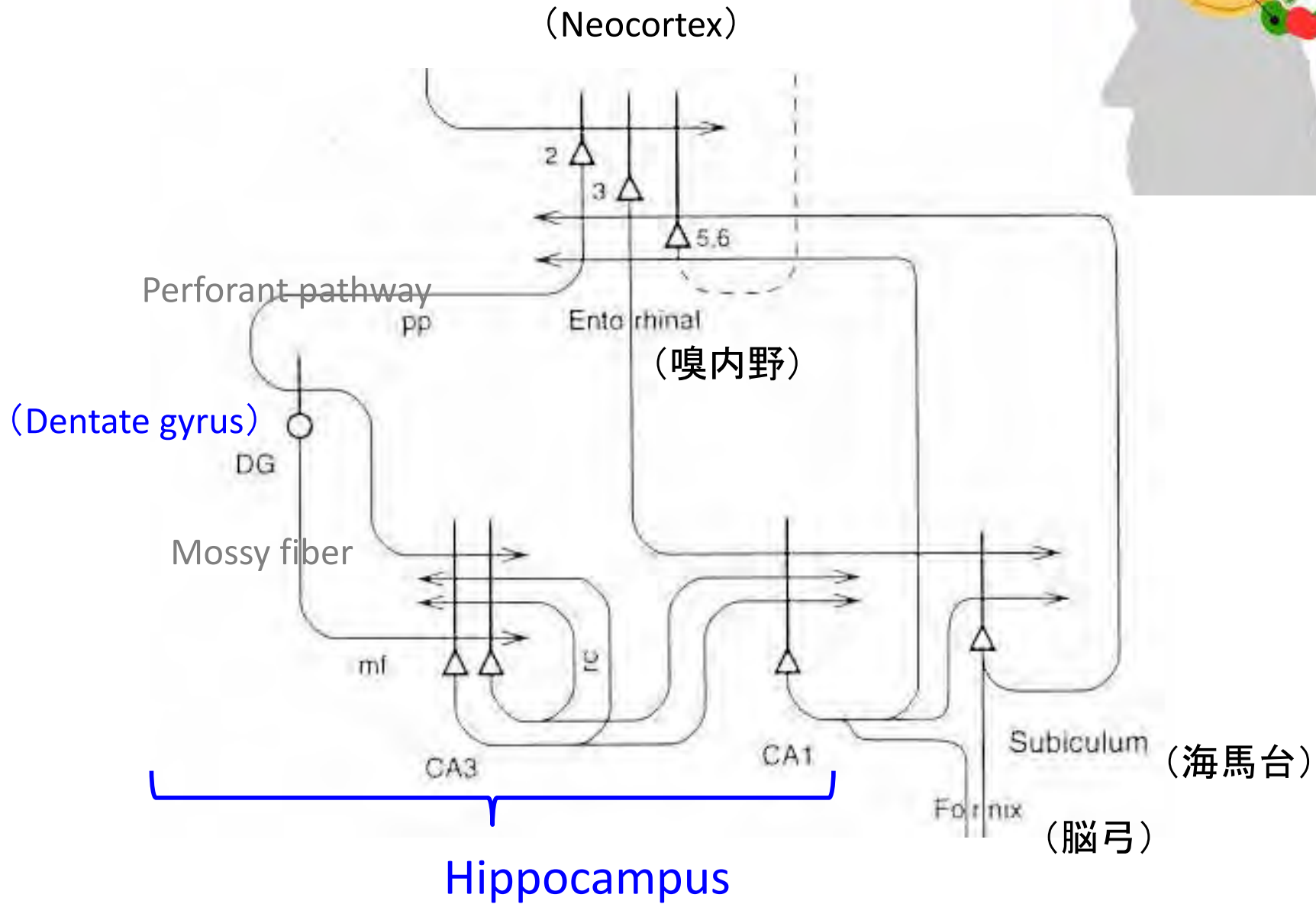
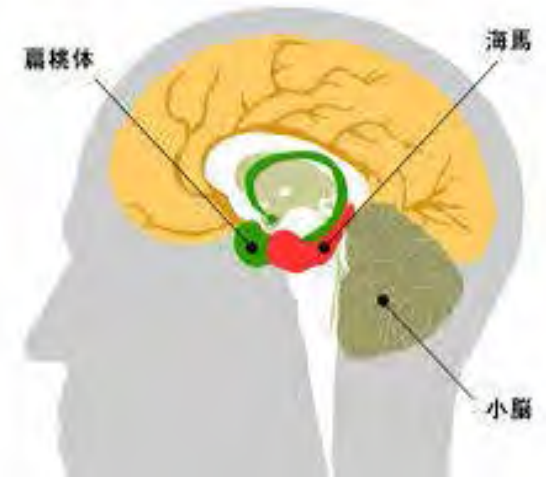
# H.M.



In the case of H.M., the memory deficiency remained permanent. Even a half-century later, H.M. still leads a life of quiet confusion. He lives in a hospital but must be re-introduced to his doctors every day. He does not recognize terms such as "VCR" or "Jacuzzi" and other things that have been invented since his surgery. And though he remembers the date of his birthday, he typically underestimates his age when asked. In many ways, H.M.'s memory remains "trapped" in a world of a half-century ago.



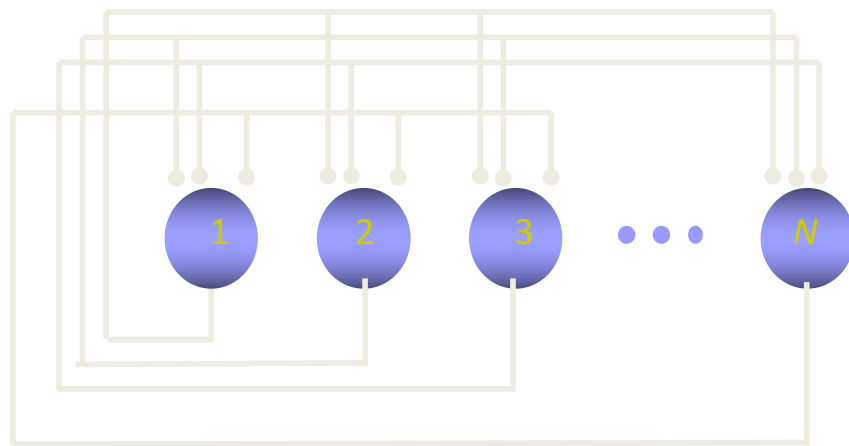
# Memory-related circuits



# Hopfieldの連想記憶モデル

(Hopfield, 1982)

## $P$ 個の活動パターンを記憶させる



ネットワークの時間発展

$$S_i(t+1) = \begin{cases} 1 & \text{if } \sum_{j=1}^N J_{ij} S_j(t) > h \\ 0 & \text{それ以外の場合} \end{cases}$$

状態 “ $S=1$ ” → “発火”

状態 “ $S=0$ ” → “非発火”

ニューロン間のシナプス結合

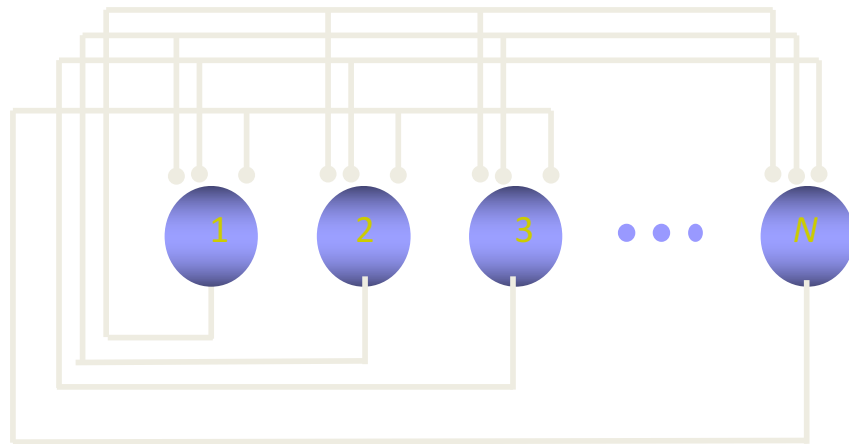
$$J_{ij} = \frac{1}{N} (A_i A_j + B_i B_j + C_i C_j + \dots)$$

$$i, j = 1, 2, \dots, N$$

# Hopfieldの連想記憶モデル

(Hopfield, 1982)

## P個の活動パターンを記憶させる

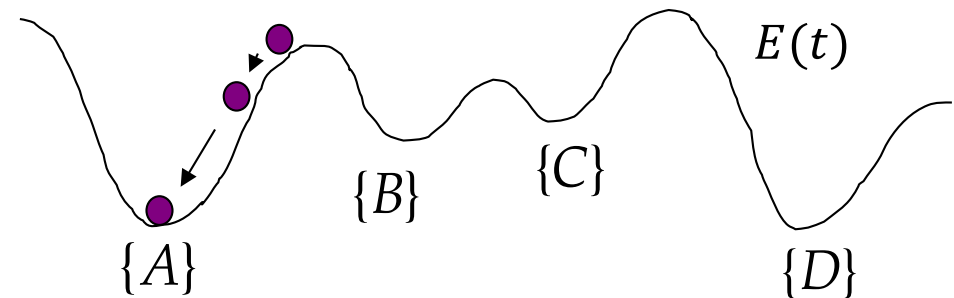


状態空間のランドスケープ

$$E(t) = -\frac{1}{2} \sum_{j \neq i}^N J_{ij} S_i(t) S_j(t) + \sum_{i=1}^N h_i S_i(t)$$

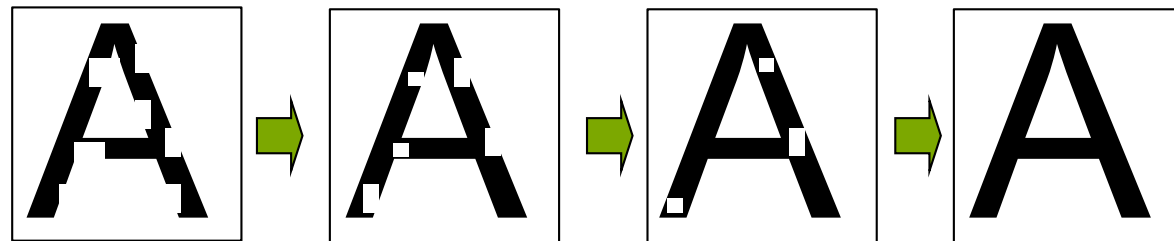
アトラクターカ学

状態空間



- S=0 をとる細胞
- S=1 をとる細胞

“パターン補完”



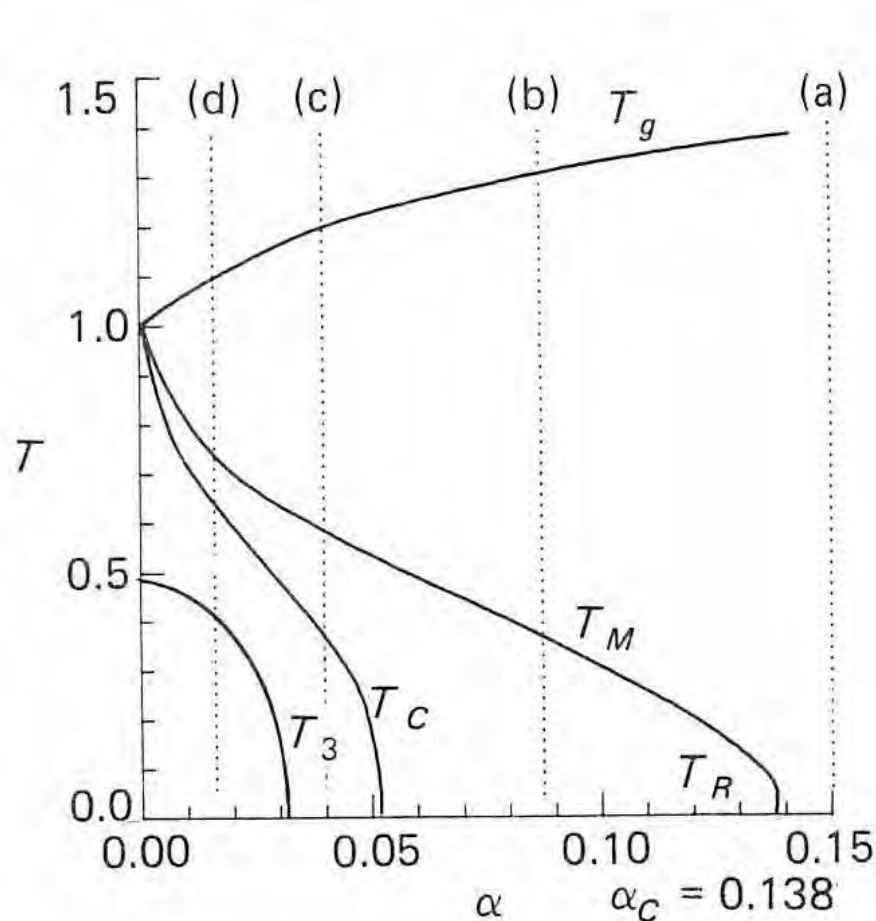
# 連想記憶のスピングラス理論： 臨界記憶容量

Amit, Gutfreund, Sompolinsky, Phys Rev Lett (1985)

Shiino and Fukai, Phys Rev E (1993) SCSNA

...

Probabilistic retrieval dynamics



$$S_i(t+1) = \begin{cases} 1 & \text{probability } p = \frac{1}{1 + \exp(-(h(t) - \theta)/T)} \\ 0 & \text{probability } 1 - p \end{cases}$$

Local fields  $h_i(t) = \sum_{j=1}^N J_{ij} S_j(t)$

$T$ : temperature parameter

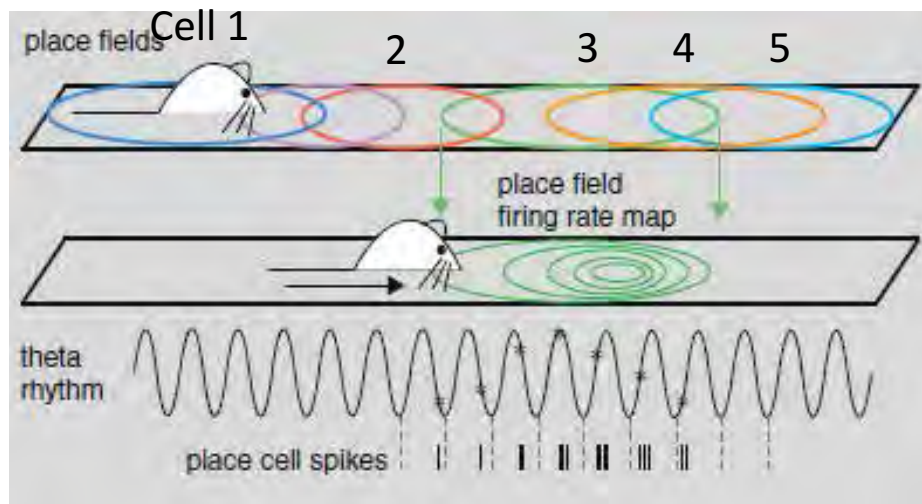
$\alpha = \frac{P}{N}$  : storage capacity



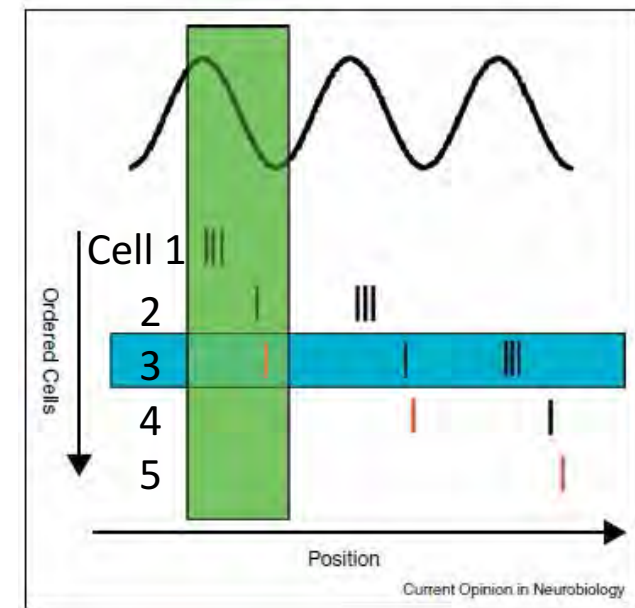
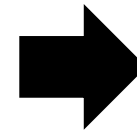
# Sequence memory in the hippocampus: place cells



## $\theta$ -phase precession (Jon O'Keefe)



## $\theta$ - sequence

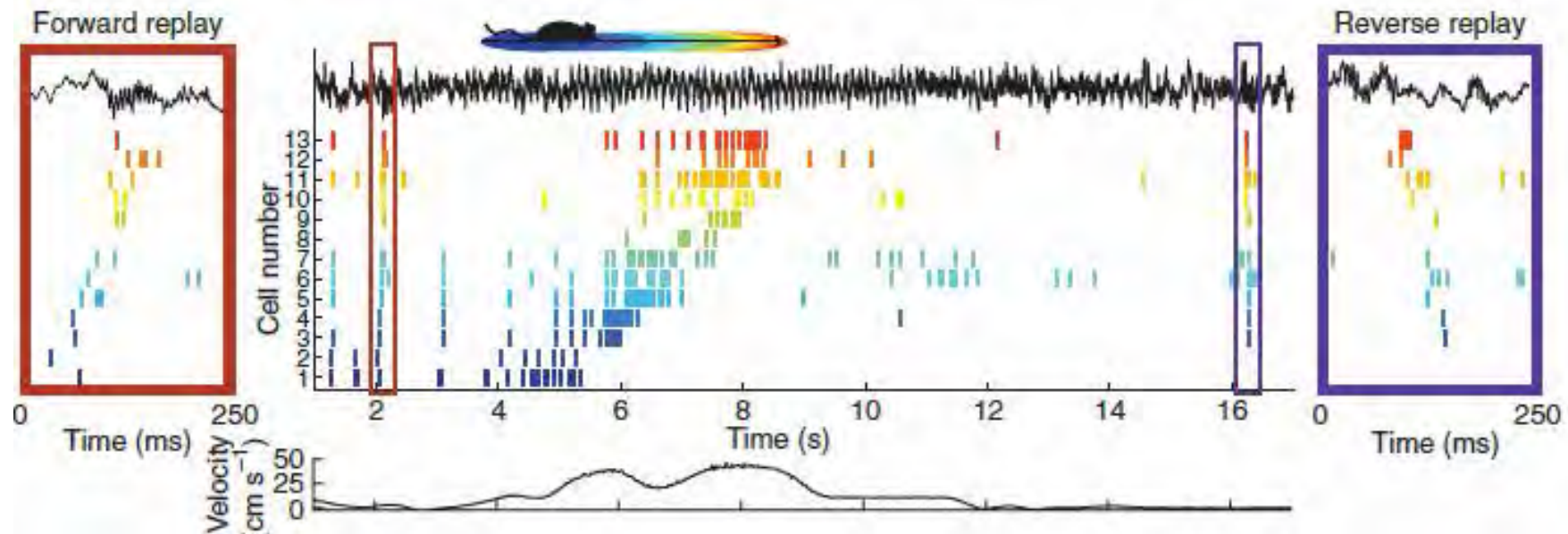


(Foster et al., 2012)

# 順行性及び逆行性Replay活動

Forward Replay

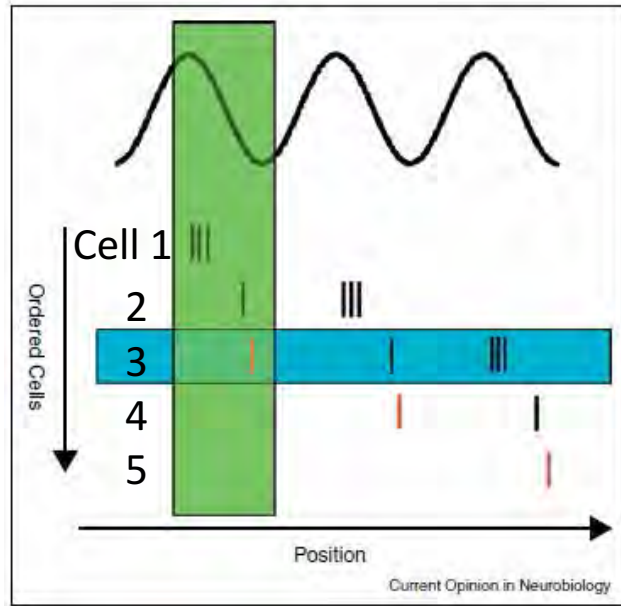
Reverse Replay



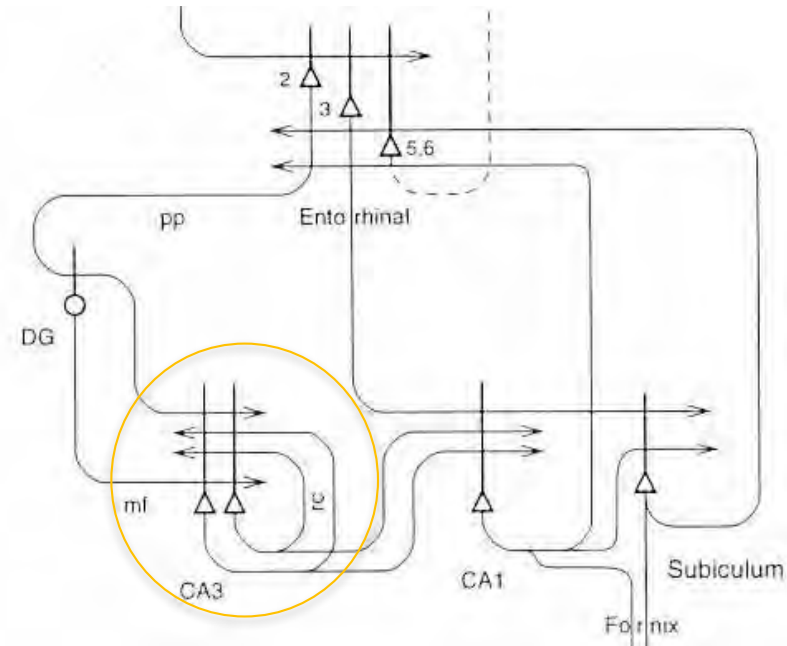
(Carr et al., 2011)

\*Replay活動は海馬CA3の反響神経回路で生成される  
(Nakashiba et al., 2009)

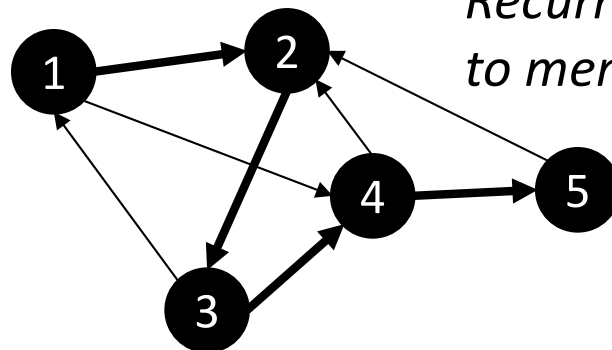
# Sequence memory in the hippocampus: place cells



(Foster et al., 2012)



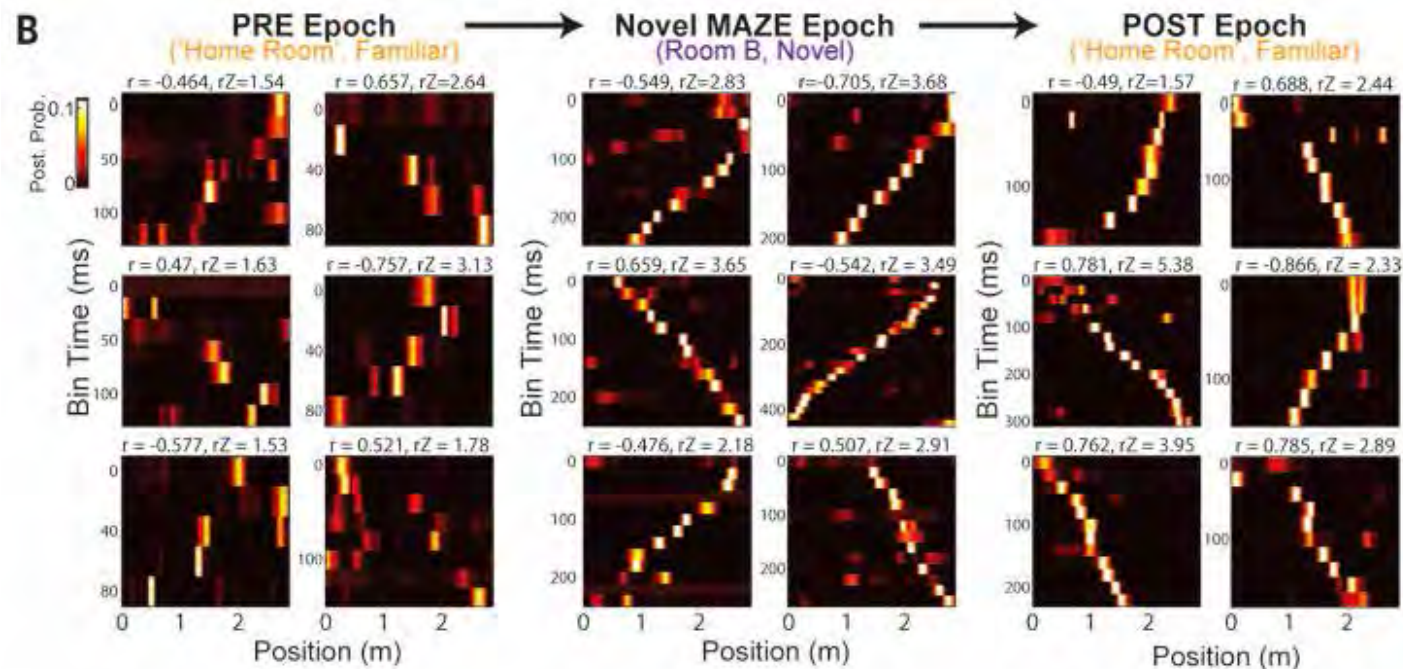
Standard view



*Recurrent circuit of CA3 is heavily remodeled to memorize firing sequences.*

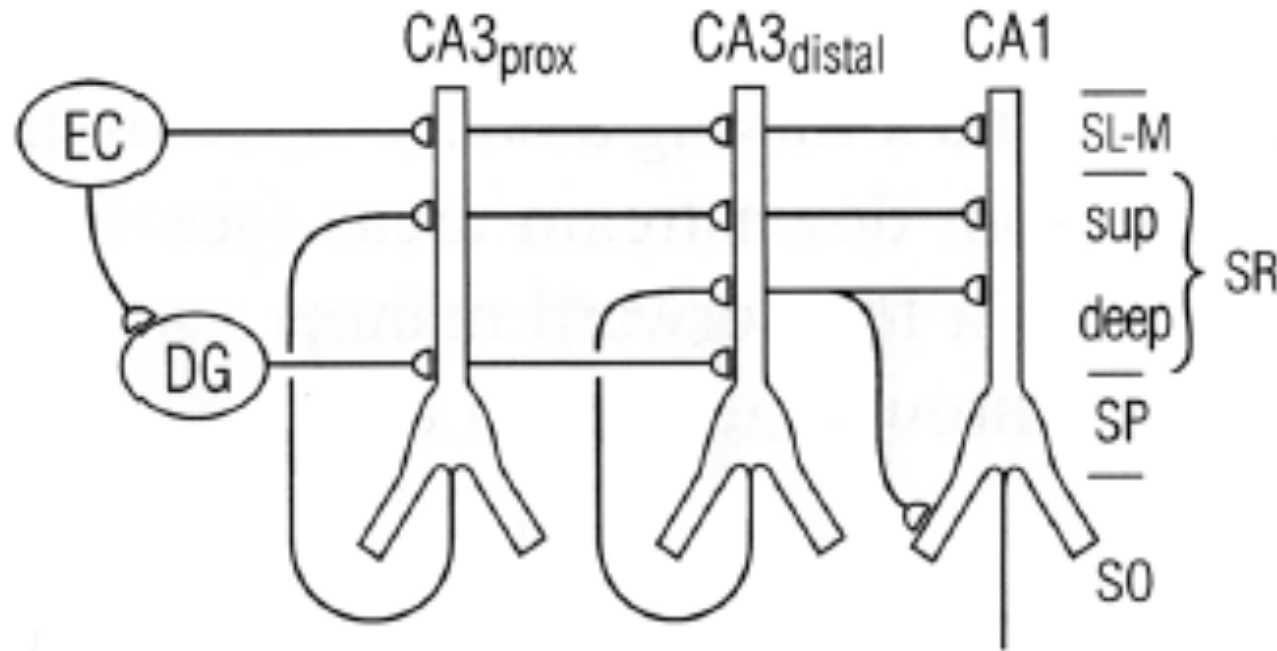
# Preplay suggests a novel framework of hippocampal memory processing

- 😊 Spontaneous activity *preceding* a novel spatial experience may contribute to the formation of new spatial memory. Dragoi and Tonegawa (2011) *Nature*
- 😞 Trajectory events across hippocampal place cells require previous experience. Silva, Feng & Foster (2015) *Nat Neurosci* 2015.
- 😊 Diversity in neural firing dynamics supports *both rigid and learned* sequences. Grosmark & Buzsáki (2016) *Science* (2016).

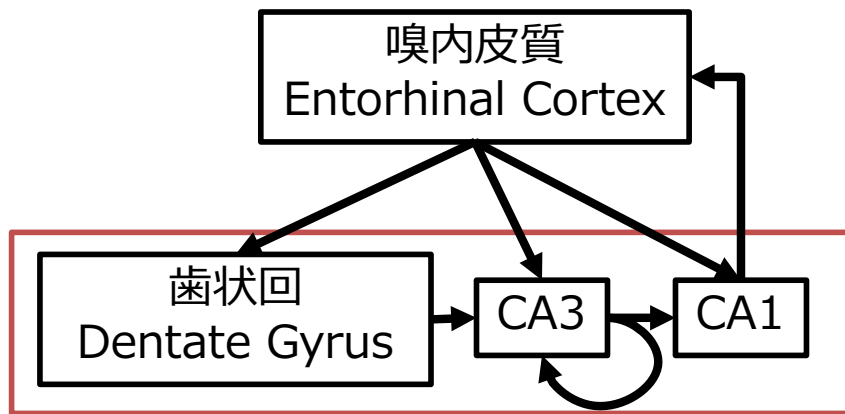




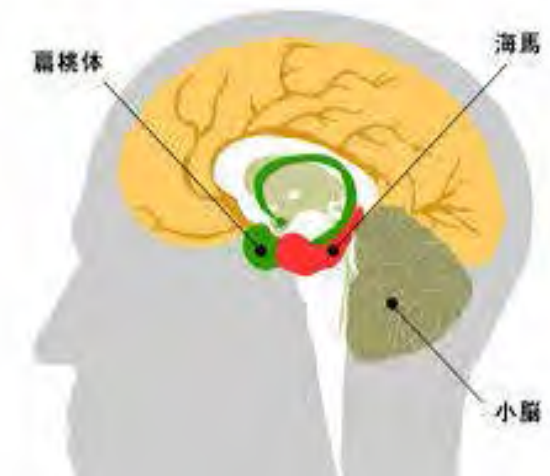
# Mesososcopic view of hippocampal structure



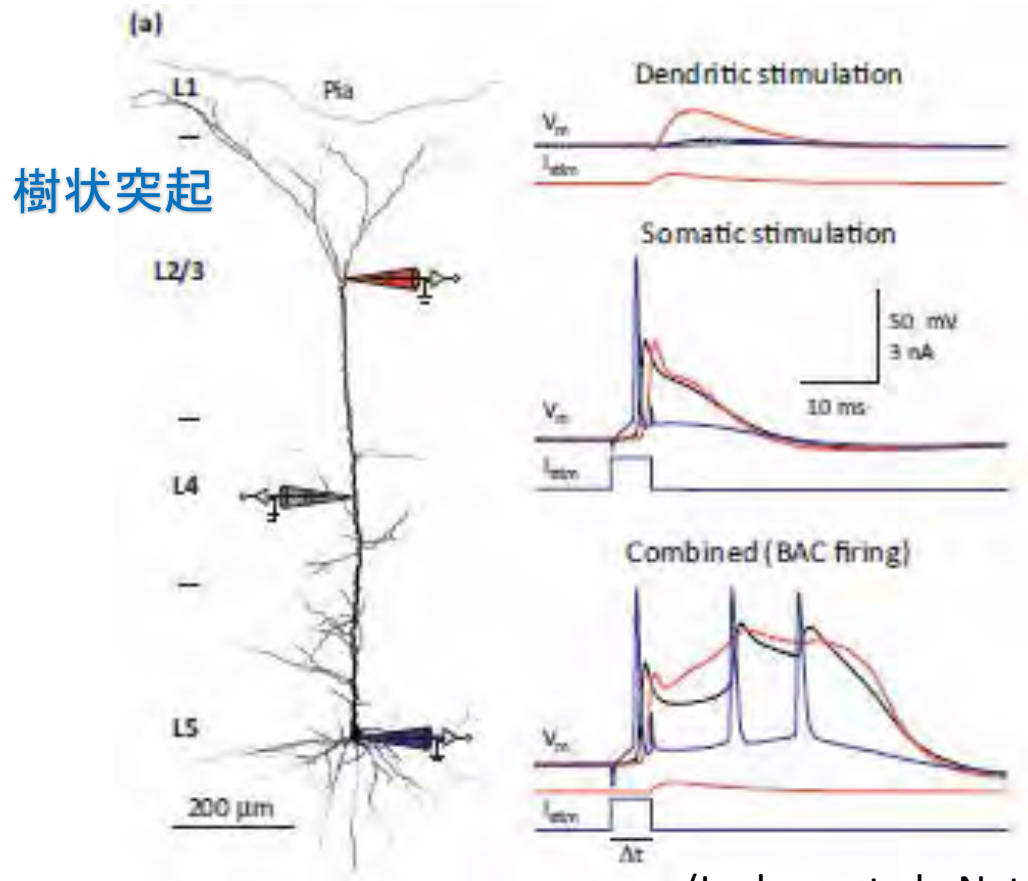
Shepherd, Front Neurosci 2011



海馬 Hippocampus



# Calcium spikes detect coincident inputs to proximal and distal dendrites



Uncorrelated inputs  
→ Rapid decay

Correlated inputs  
→ prolonged  $\text{Ca}^{2+}$  spikes

(Larkum et al., Nature 1999)

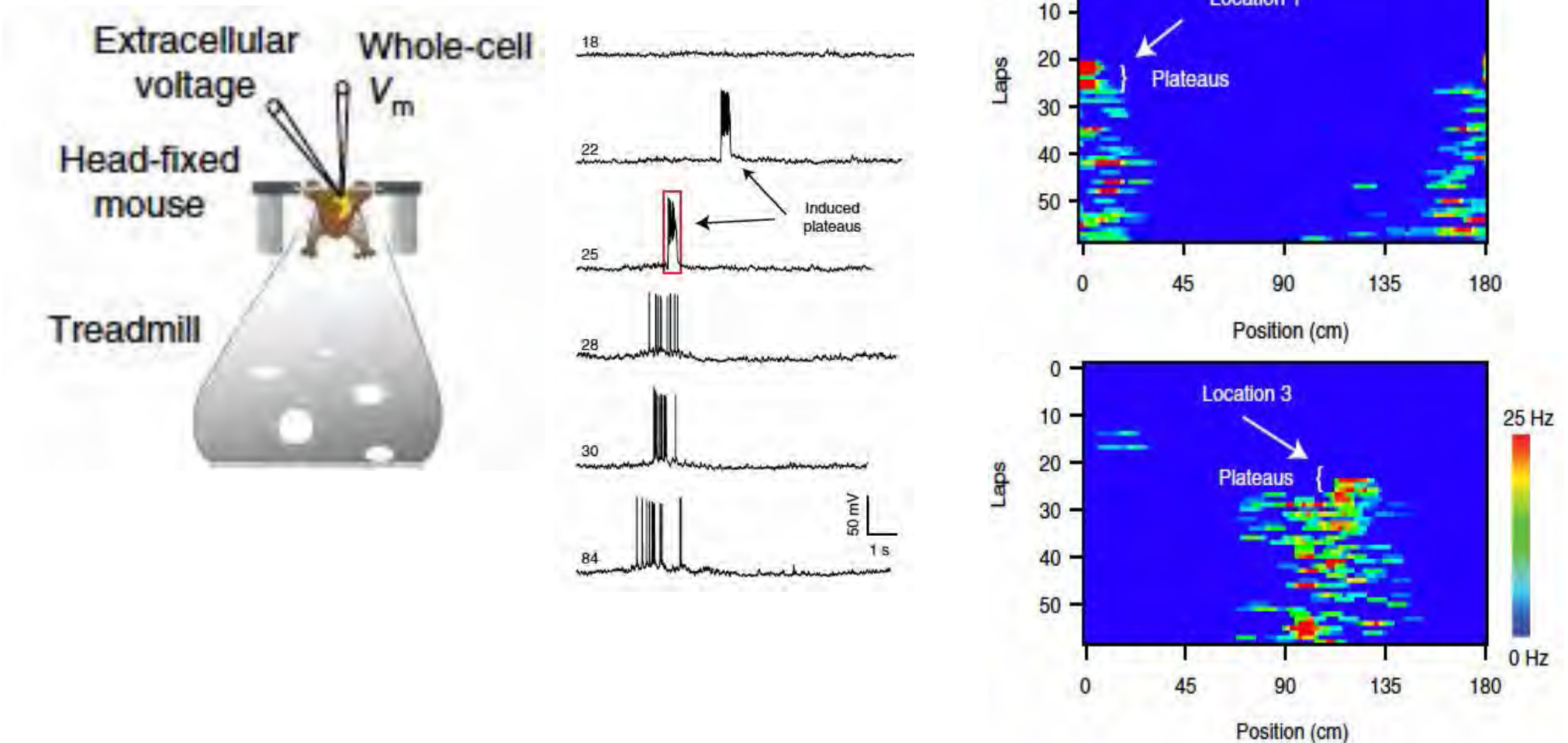
Back-propagation and  $\text{Ca}^{2+}$  spikes are necessary for LTP in vitro.

(Takahashi and Magee, 2009)

# Induced dendritic $\text{Ca}^{2+}$ plateaus is sufficient for new place-field formation

(Bittner et al., Nat Neurosci 2015)

Necessity of  $\text{Ca}^{2+}$  spikes for LTP has been known in vitro (e.g., Takahashi and Magee, 2009)



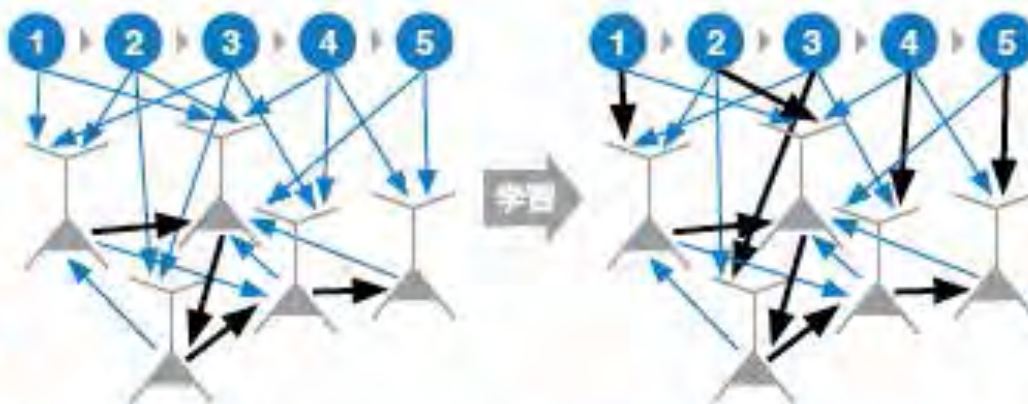
## 時系列を学習する神経回路

従来のモデル



相互結合の修正による学習

プリプレリのモデル



外界の時系列

樹状突起によるマッチング学習

自発発火の時系列

記憶の仕組みを示す。脳は学習するよりも前に、未来の経験を記憶するために必要な内部状態を有している。上の図（従来のモデル）では、●はニューロンを指し、番号はそのニューロンへの入力の種類、つまりそのニューロンの発火の順を指す。下の図では、上の●は入力とその順番、下の三角はニューロンを指す。番号は自発発火の順番。細い矢印は弱い結合、太い矢印は強い結合を示す。左の図は学習前、右の図は学習後で、学習によってシナプス結合が強まったことを示している。

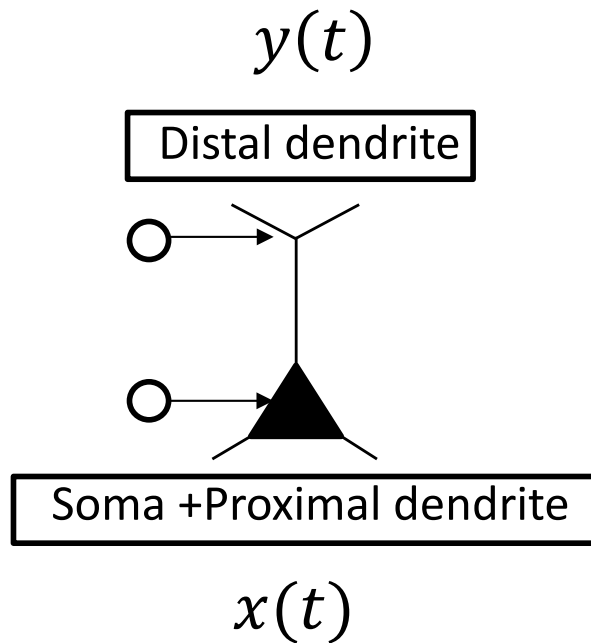
← 弱い結合  
← 強い結合



# Plasticity model

(Haga and Fukai, bioRxiv

doi: <https://doi.org/10.1101/165613>)



Learning rule for synapses in somatic compartments

$$\Delta w_j^{\text{som}}(t) = \eta \underbrace{(x(t)(x(t) - \theta^{\text{som}}))}_{\text{BCM theory for local activity}} + \underbrace{\alpha x(t)y(t)}_{\text{LTP by calcium spikes}} (1 - x(t)) \underbrace{I_j^{\text{som}}(t)}_{\text{Presynaptic input}}$$

BCM theory for  
local activity

LTP by  
calcium spikes

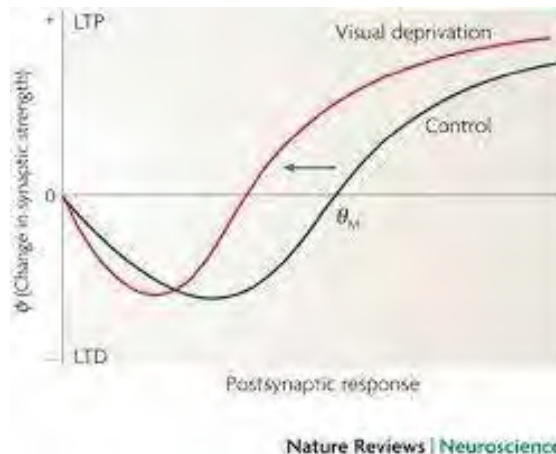
Presynaptic  
input

Learning rule for synapses in distal dendrites

$$\Delta w_j^{\text{dnd}}(t) = \eta \underbrace{(y(t)(y(t) - \theta^{\text{dnd}}))}_{\text{BCM theory for local activity}} + \underbrace{\alpha x(t)y(t)}_{\text{LTP by calcium spikes}} (1 - y(t)) \underbrace{I_j^{\text{dnd}}(t)}_{\text{Presynaptic input}}$$

Moving average

$$\theta^{\text{som}} = \frac{1}{r_0} E[x(t)]^2, \theta^{\text{dnd}} = \frac{1}{r_0} E[y(t)]^2$$

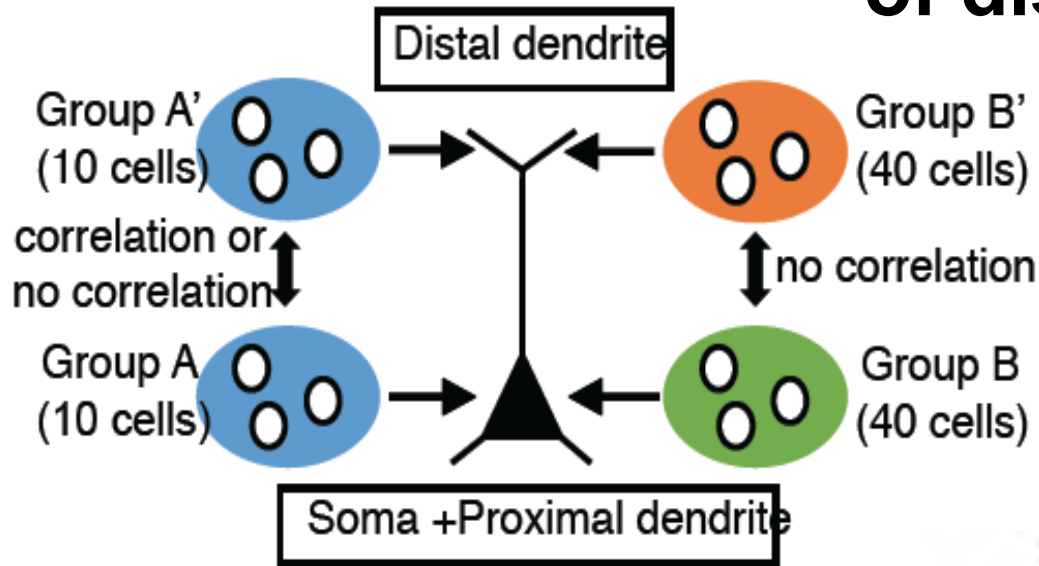


## Bienenstock-Cooper-Munro Theory of Hebbian plasticity (1982)

Sliding threshold for LTP/LTD

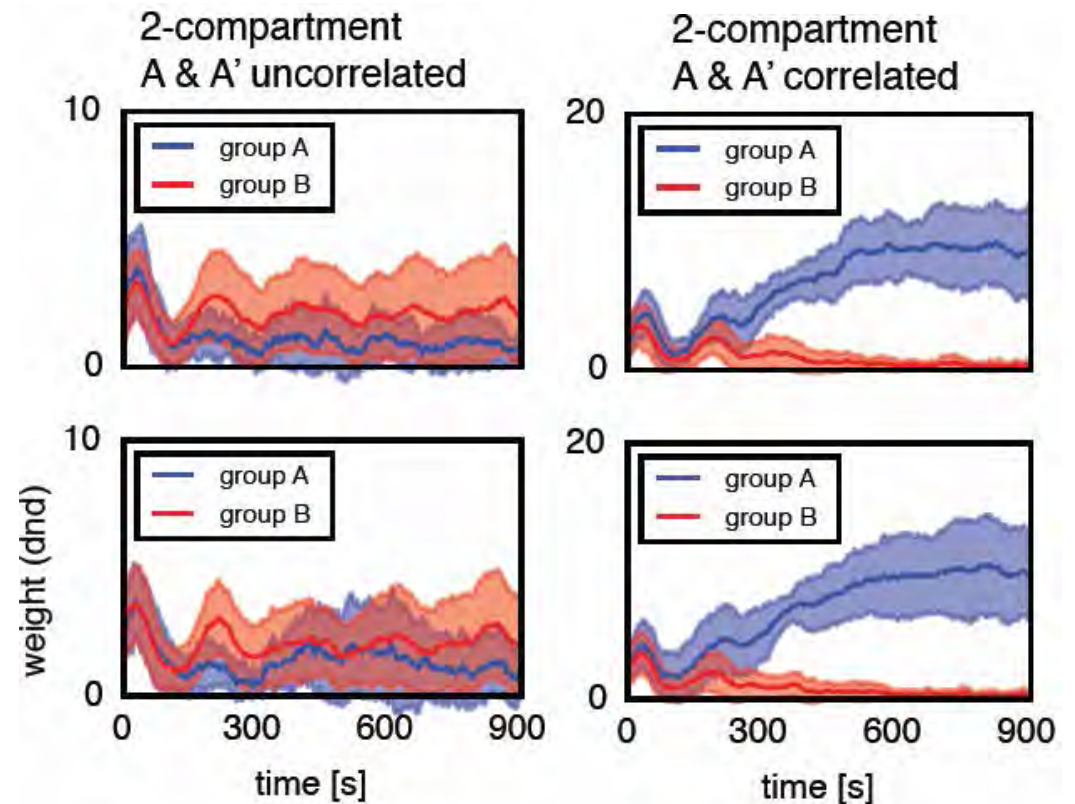
STDP is equivalent to BCM for random and uncorrelated neuronal firing

# Canonical Correlation Analysis of distal and proximal inputs

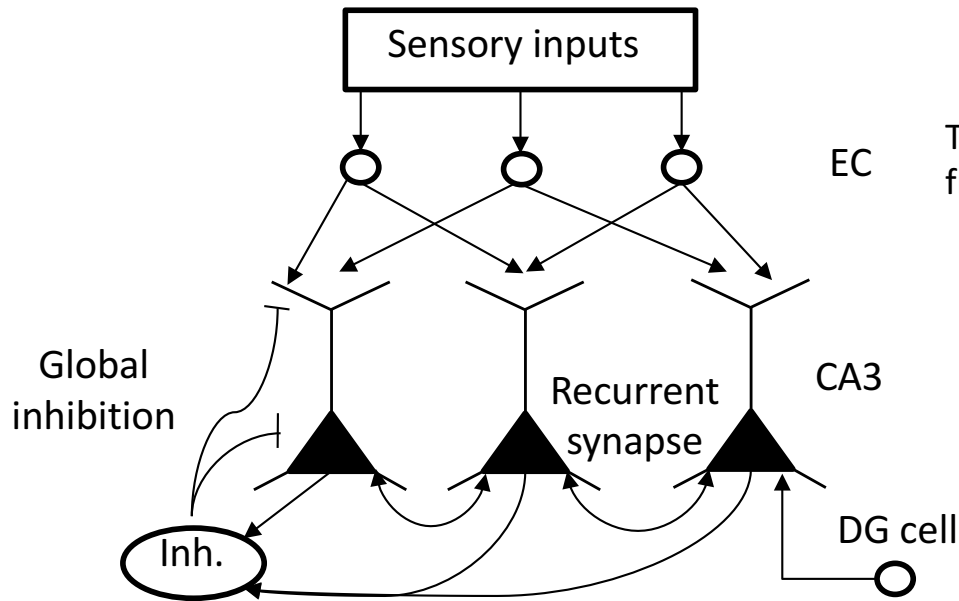


PCA-like

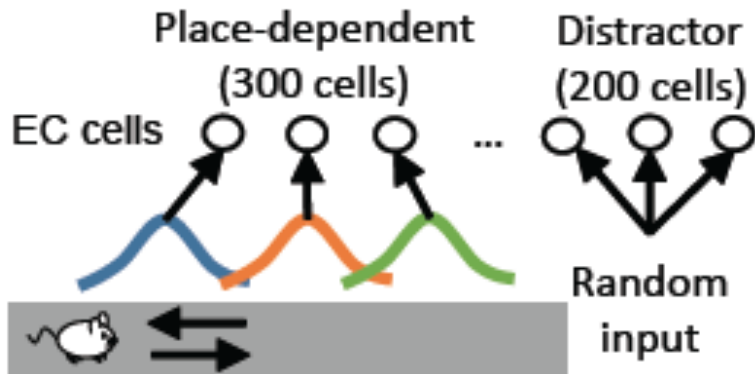
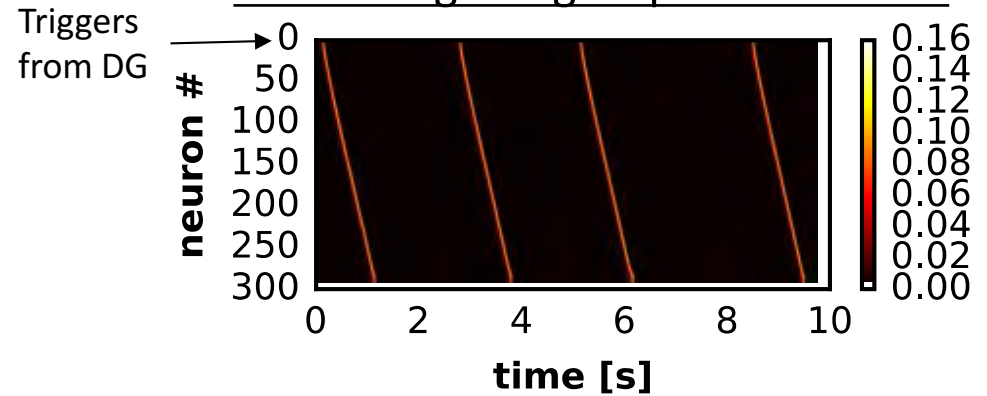
CCA-like



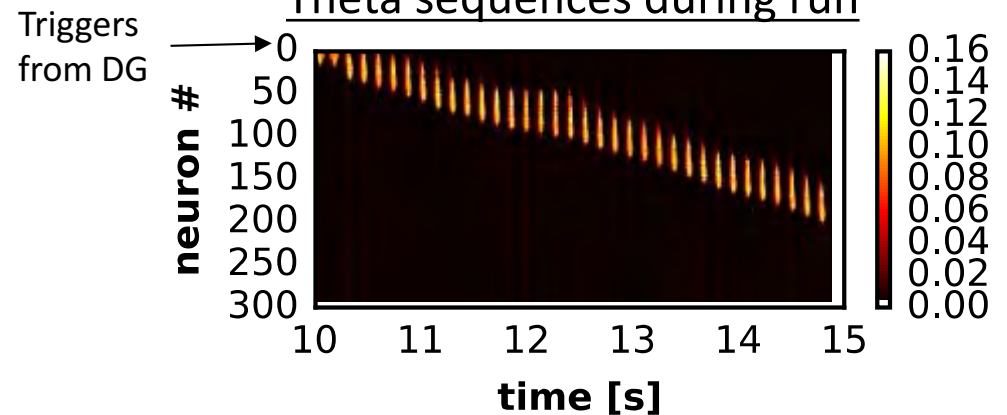
# Place coding by recurrent network model



Preexisting firing sequences in CA3

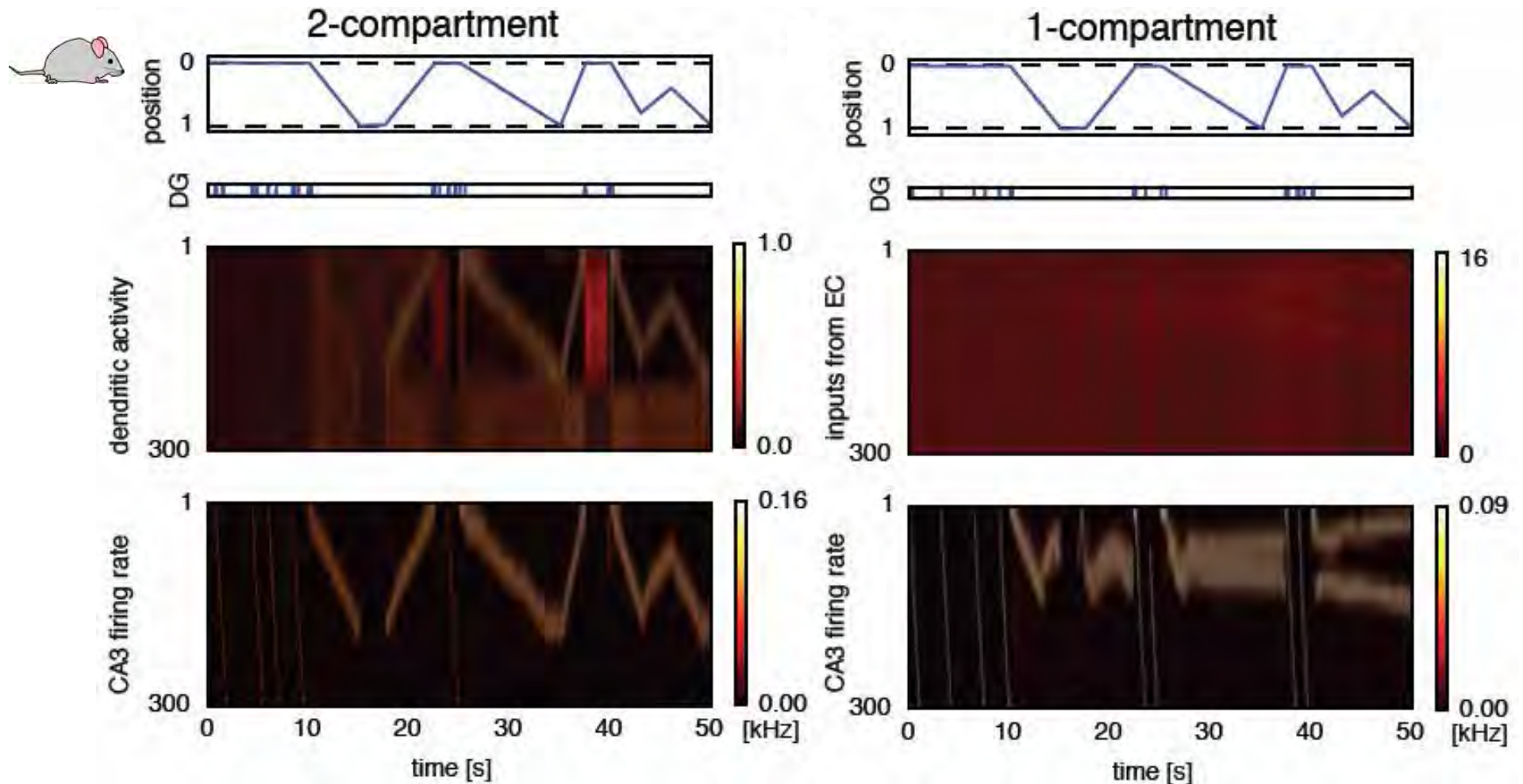


Theta sequences during run



# One-short learning of space info by preplay

Recurrent activity supervises learning of afferent synapses in the two-compartment model



# Recurrent connections (preplay) are crucial for memory formation

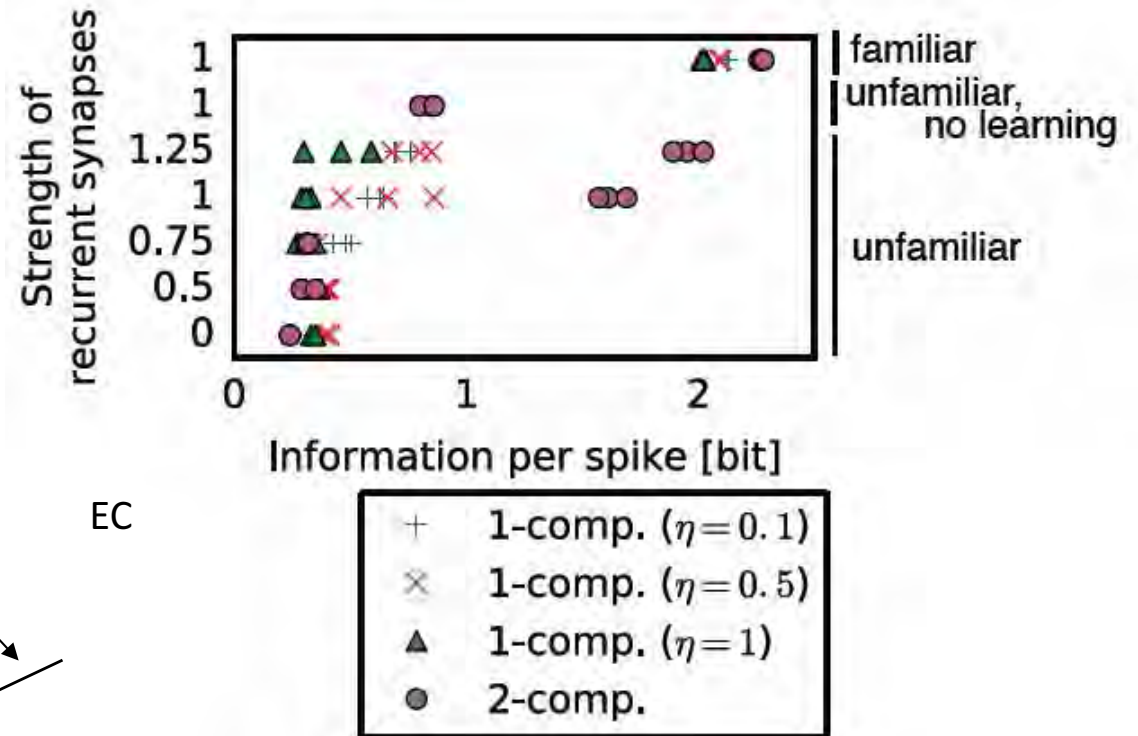
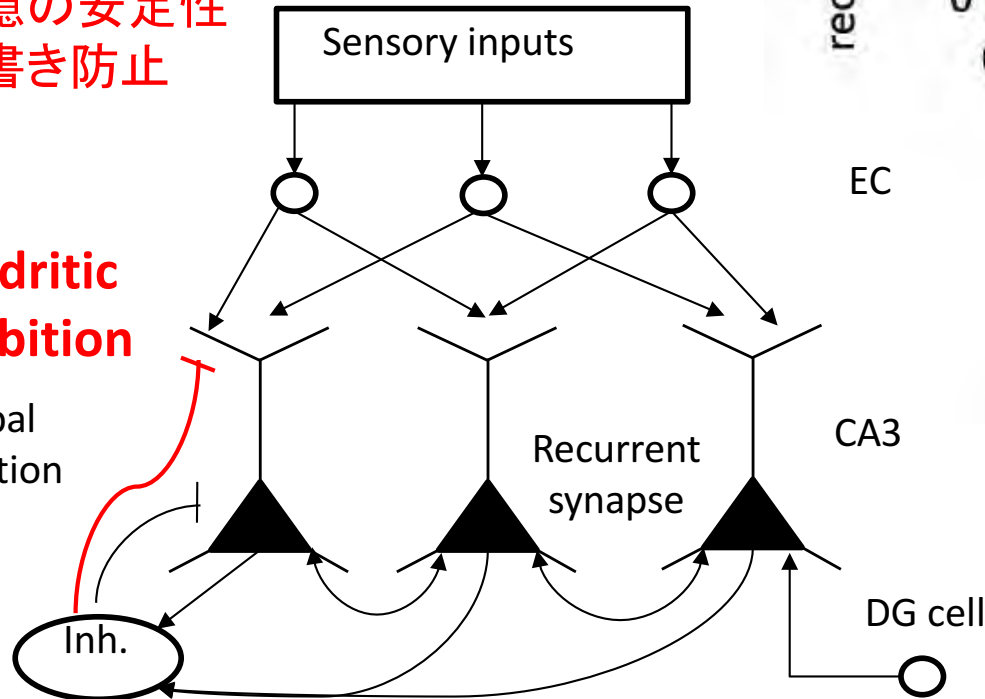
Mutual information between space and neural activity

樹状突起抑制の必要性

記憶の安定性  
上書き防止

dendritic inhibition

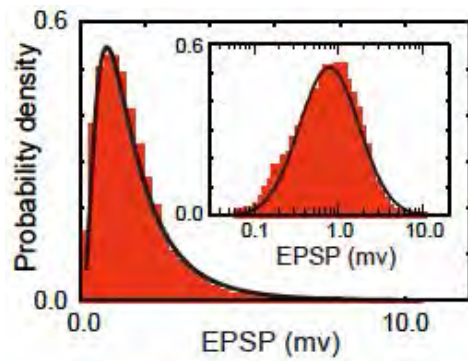
Global inhibition



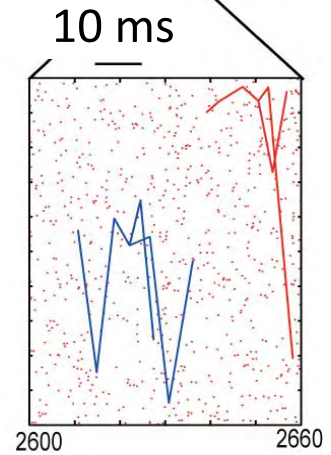
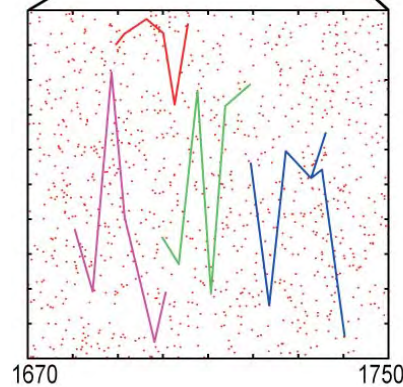
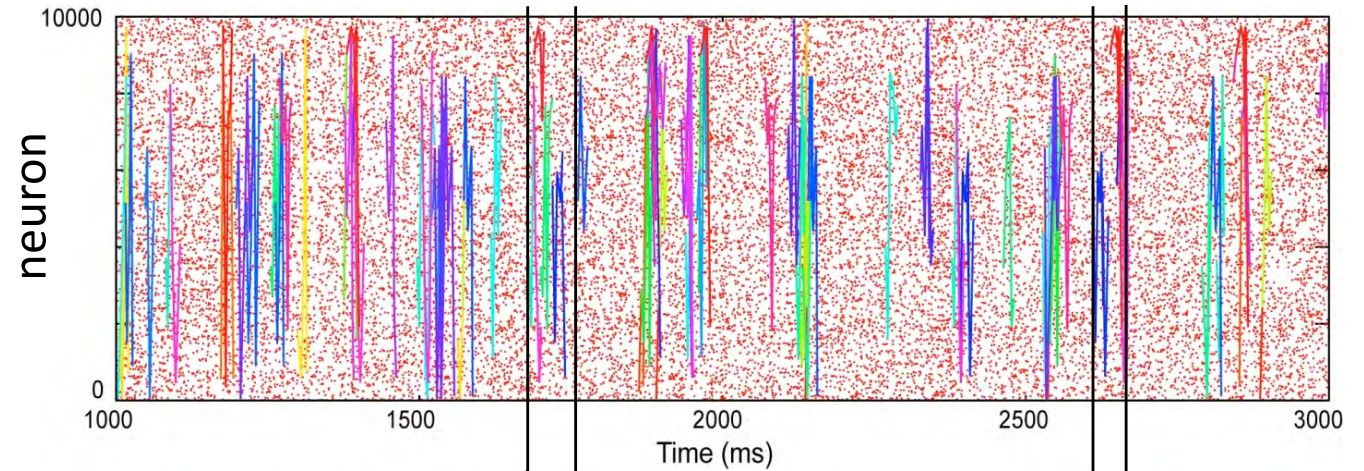
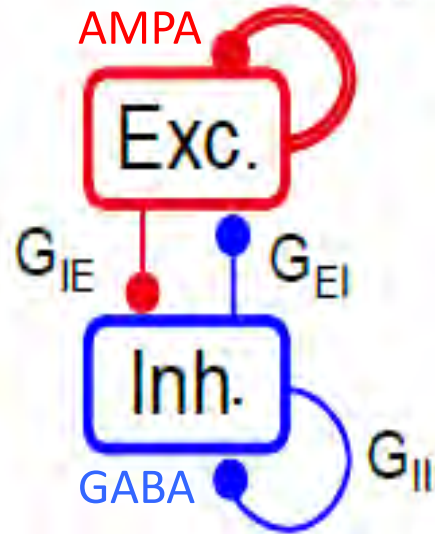


# 脳の自発発火は時系列で出来ている

(Lefort et al., Neuron 2009)



Lognormal



Teramae, Tsubo, Fukai (Sci Rep 2012)

Ohmura, Carvalho, Inokuchi, Fukai (J Neurosci 2015)

脳は学習する。何のために？

→ 外界をモデル化するため



統計的モデル

では何のためにモデル化する

→ 世界の動きを予測するため

# 予測符号化に基づく大脳皮質の階層的計算

脳は現実と予想の差を最小化している？

Srinivasan et al., 1982

Friston, 2005

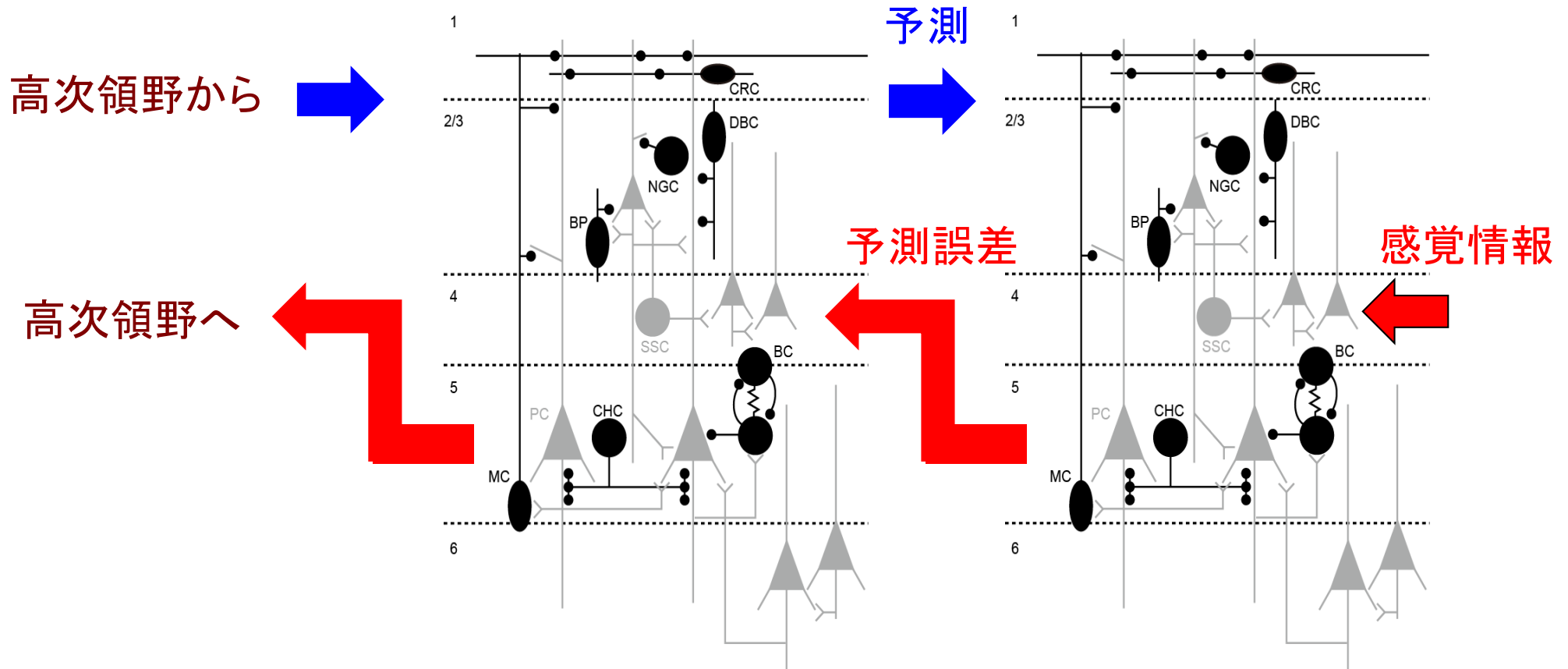
Smith and Lewicki, 2006

...

高次領野による情報の統合と外界の確率モデルの形成

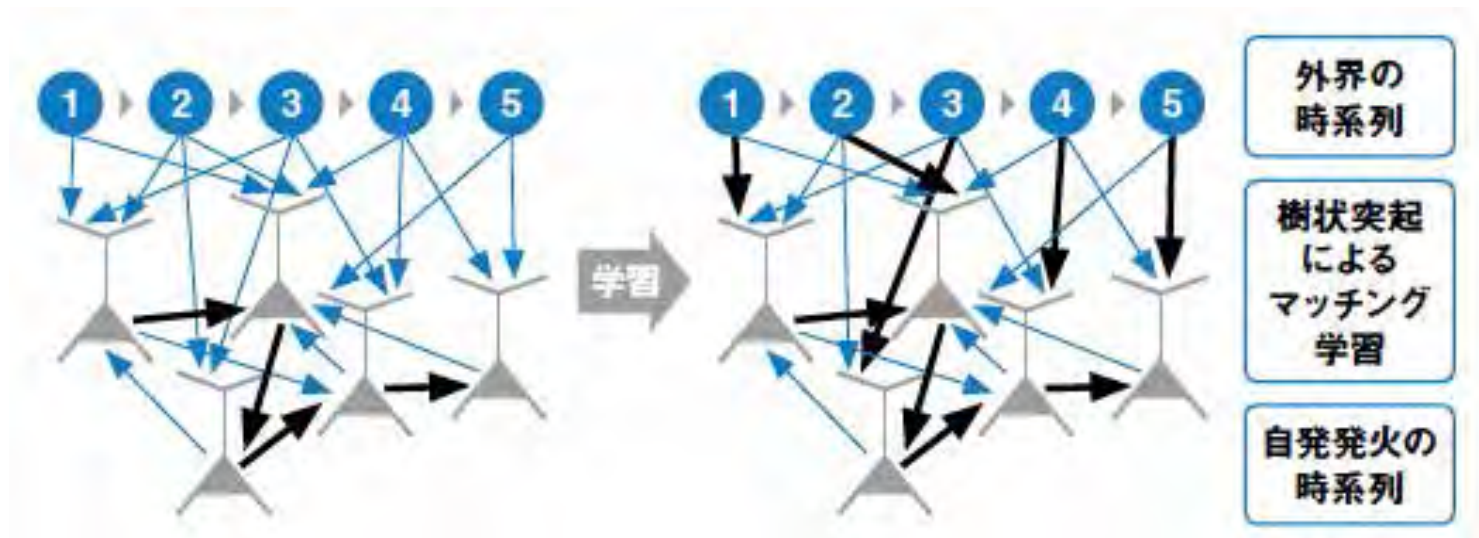
前領域の確率モデル

入力情報の特徴の解析



# まとめ1 プリプレイ的脳感

脳には記憶を表現する回路構造(自発活動)が予め備っており、  
学習により経験が「脳の内部状態」に関連付けられる



内部状態 = 意識のメカニズム？

# 外界に存在する規則性の検出

リザーバ計算による時系列のチャンク構造の学習

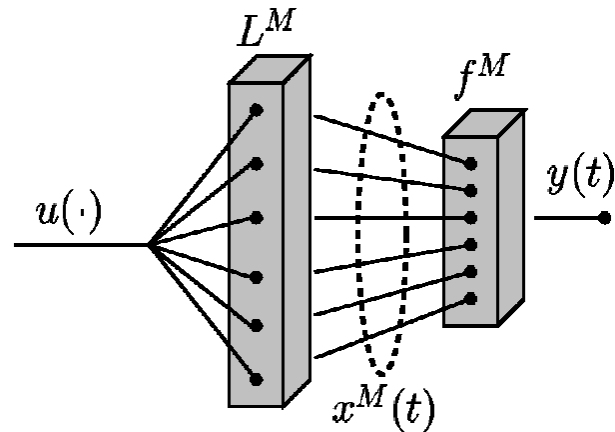
朝吹 & 深井 投稿準備中



# Conceptual models of cortical information processing

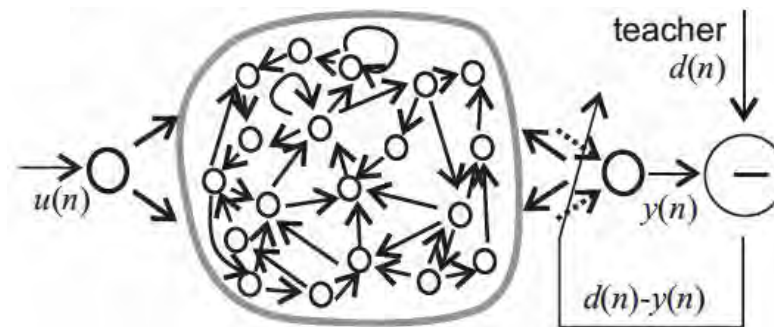
## Liquid state machine

Maass, Natschlaeger and Markram, Neural Comput (2002)



## Echo state machine

Jaeger and Haas, Science (2004)

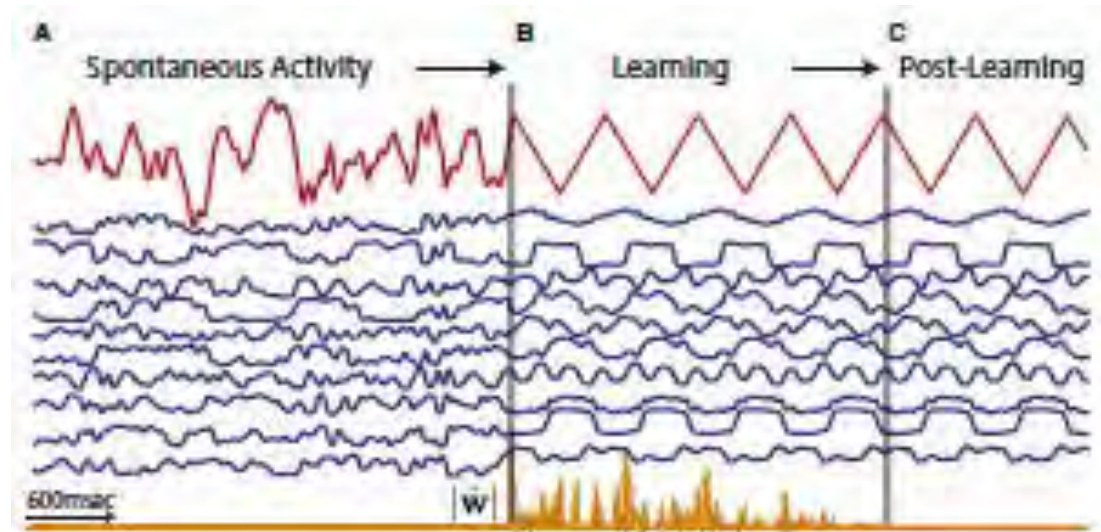
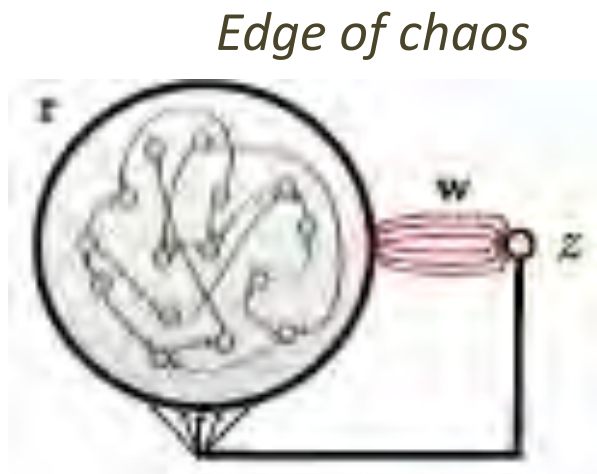


# Reservoir computing with strong E/I balance

Random networks

Synaptic strength scales as  $1/\sqrt{K}$

FORCE learning  $\Leftarrow$  Supervised learning



$$z(t) = \mathbf{w}^T \mathbf{r}(t).$$

$$\mathbf{w}(t) = \mathbf{w}(t - \Delta t) - e_-(t) \mathbf{P}(t) \mathbf{r}(t),$$

$$\mathbf{P}(t) = \mathbf{P}(t - \Delta t) - \frac{\mathbf{P}(t - \Delta t) \mathbf{r}(t) \mathbf{r}^T(t) \mathbf{P}(t - \Delta t)}{1 + \mathbf{r}^T(t) \mathbf{P}(t - \Delta t) \mathbf{r}(t)}.$$

(Sussillo and Abbott, Neuron 2009)

# Reservoir computing for motor control

→ Training in recurrent spiking networks

MacNeil and Eliasmith 2011

Boelin et al., 2013

Bourdoukean and Deneve 2015

Abbott et al., Nat Neurosci 2016 (Review)

Aditya and Gerstner, 2017

...

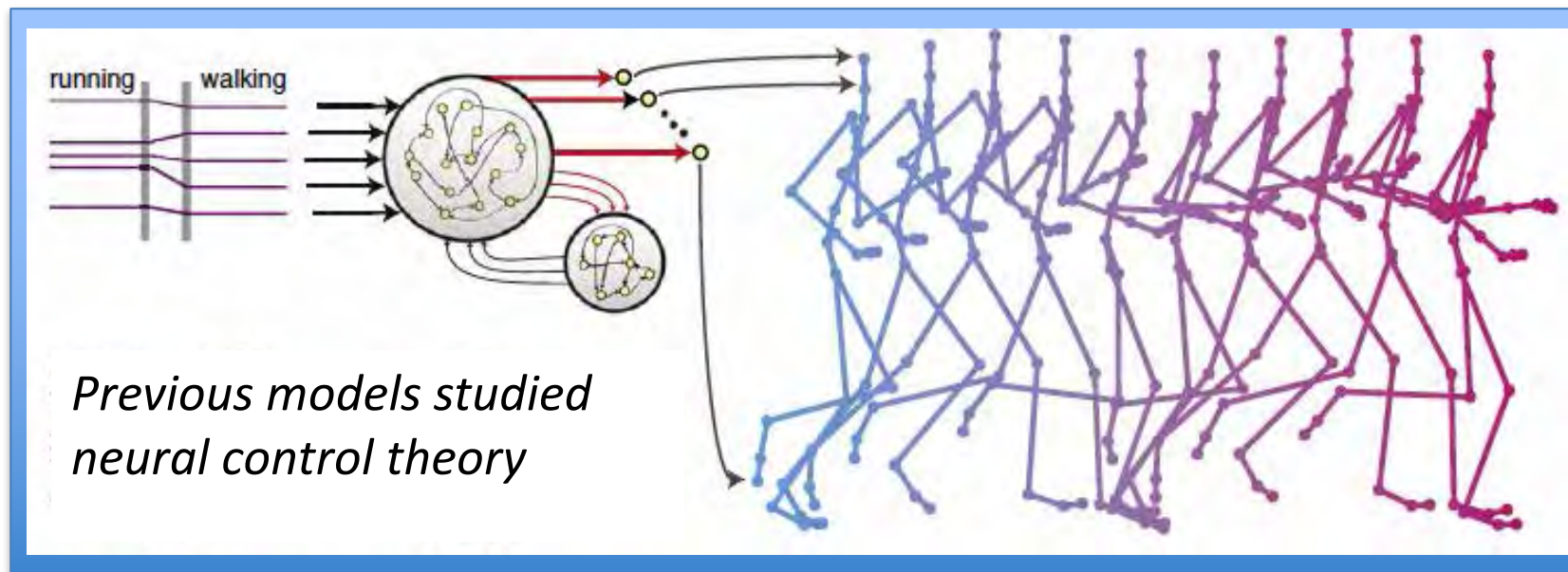
→ Theoretical studies

Toyoizumi and Abbott, Phy Rev E, 2011

Rivkind A, Barak O, Phys Rev Lett 2017

...

Q. より高次の機能を生成できるか？



(Sussillo and Abbott, Neuron 2009)

# Chunk learning

外界のコンパクトな表現を求めて



- Sensory scene analysis
- Motor routines
- Habituation
- Language acquisition
- Concept formation?

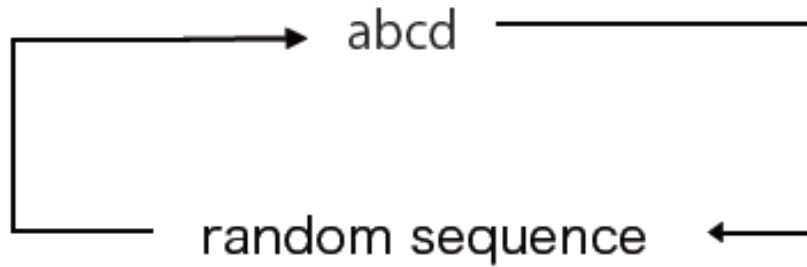
...



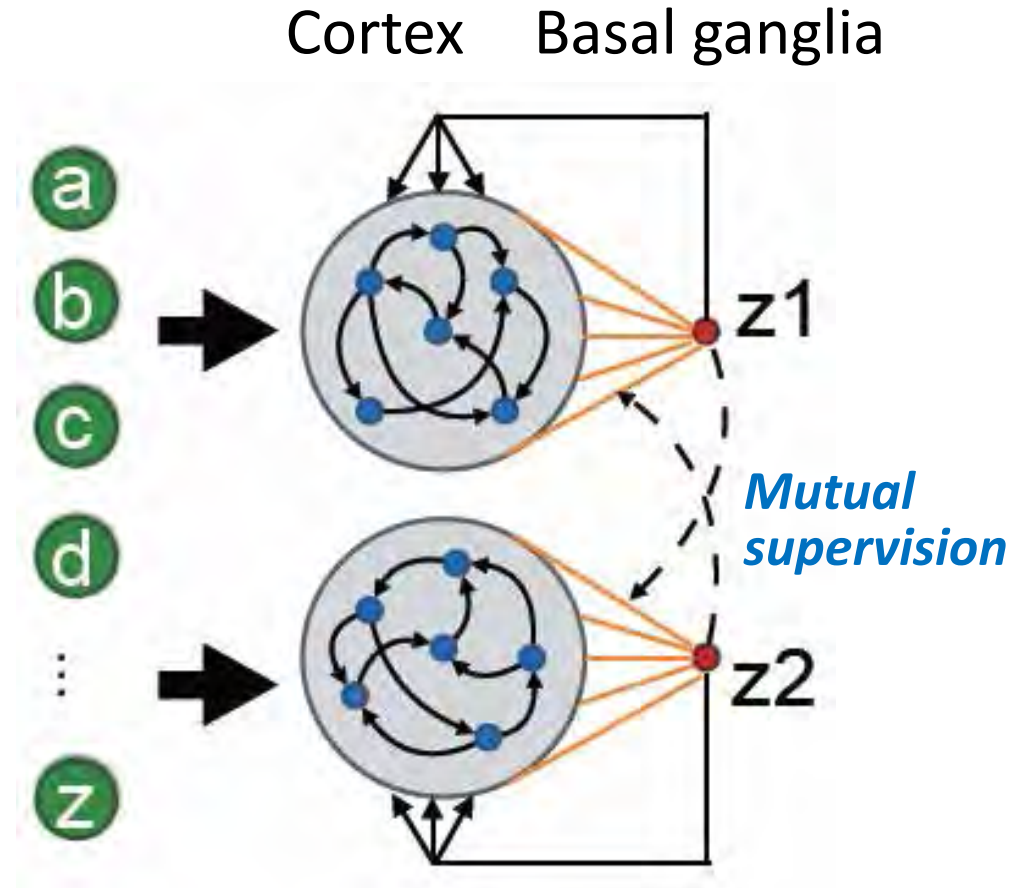
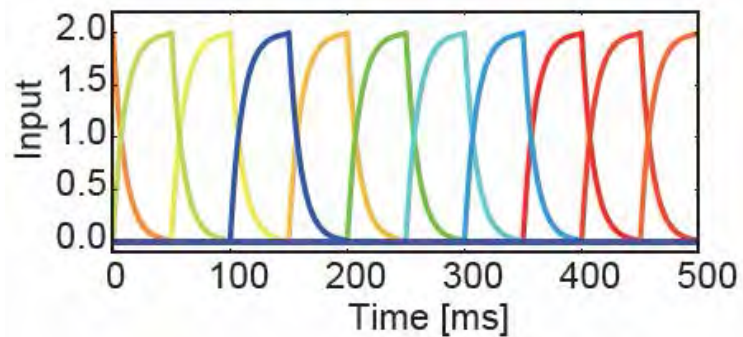


# Chunking by reservoir computing

*Detection of regularity in irregular sequences*



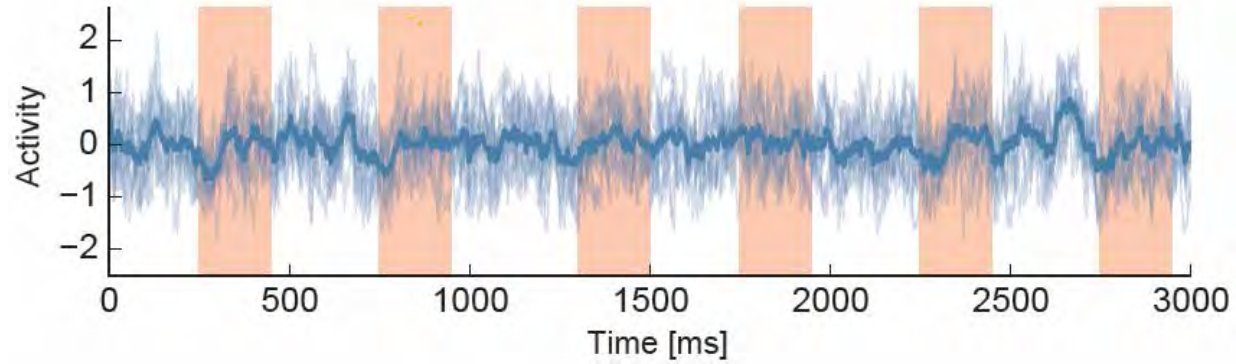
hdeo**abcd**lwfeir**abcd**nkcvuyehjda  
**bcd**hdeiowiifdkwrei**abcd**kdverioa  
**bcd**jqwhduezkg...



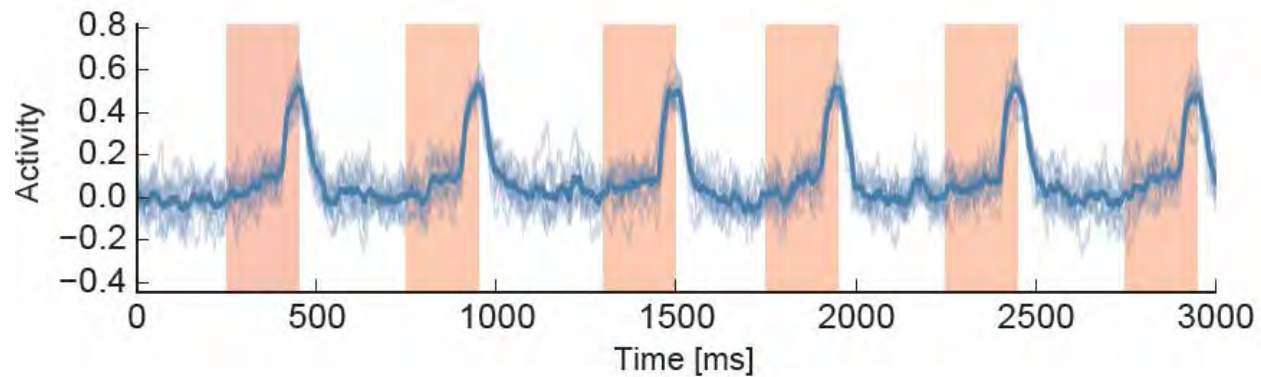
(Asabuki et al., in preparation)



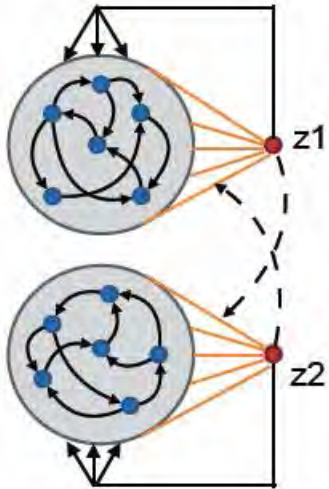
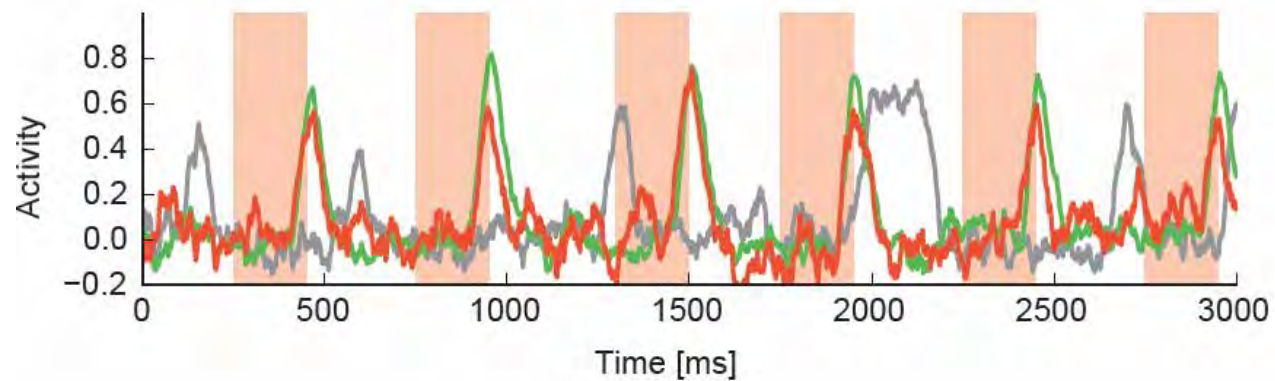
## Pre-learning readout activity



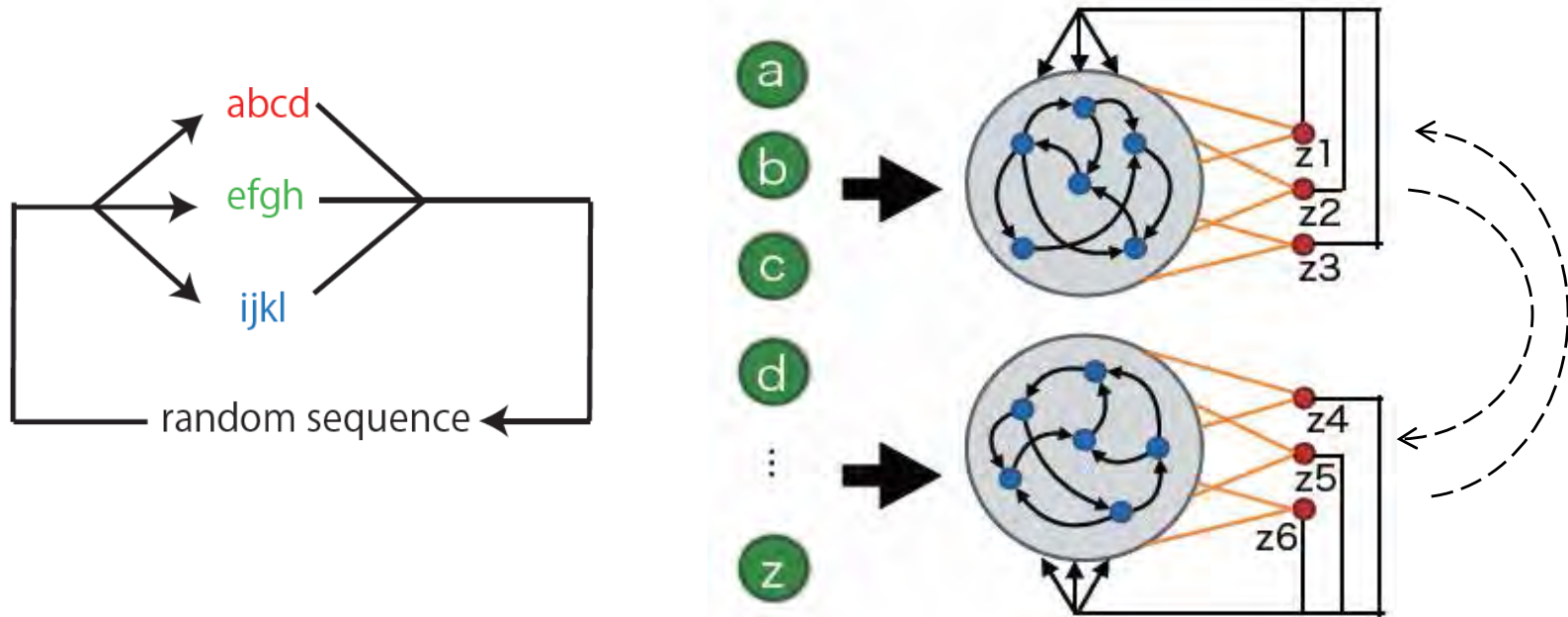
## Post-learning climbing activity of readout neurons



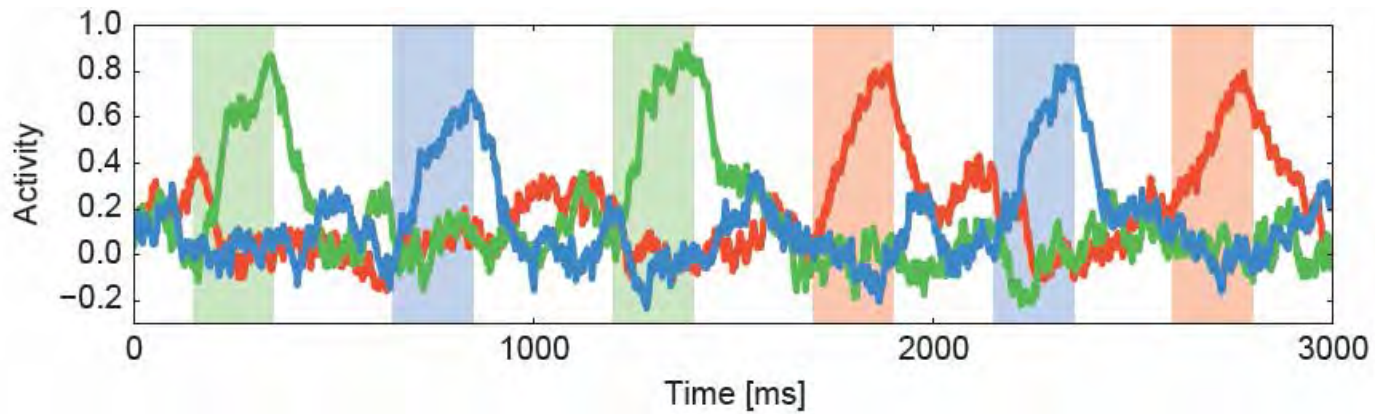
## Post-learning reservoir neuron activity



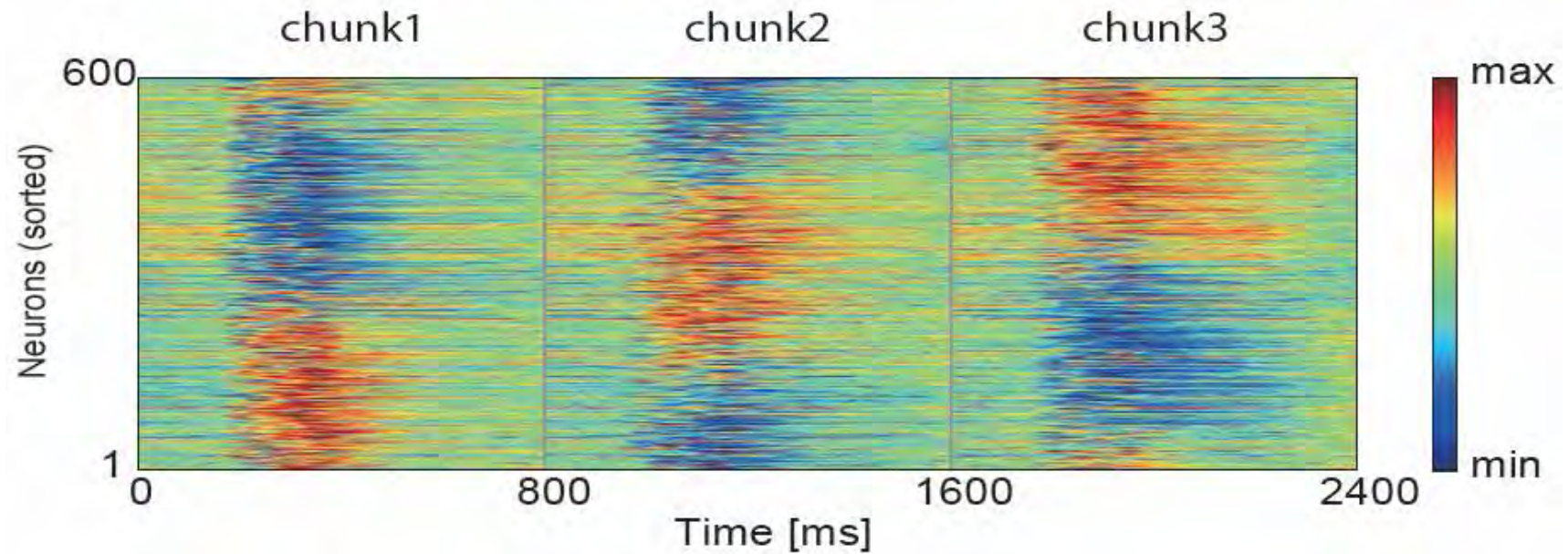
# Multiple chunks



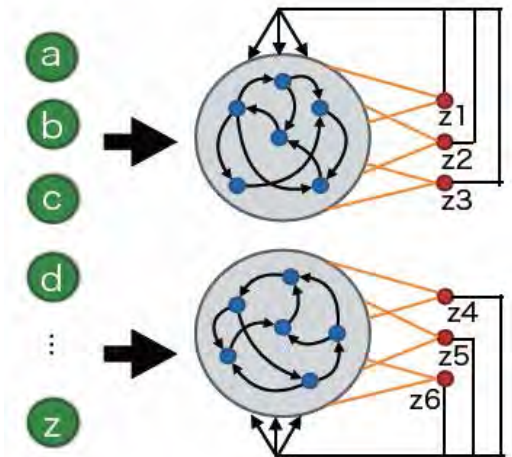
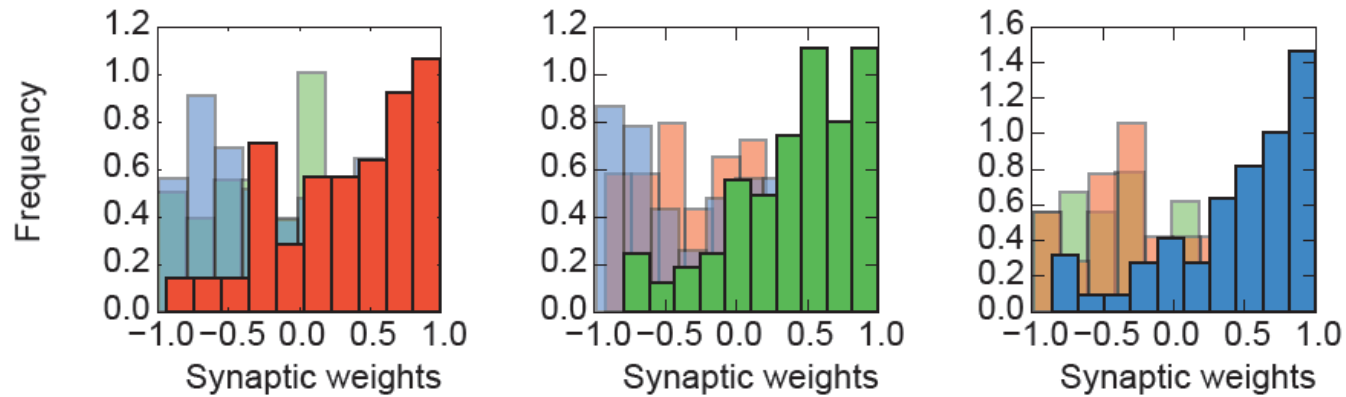
## Post-learning readout activity



# Synaptic wiring

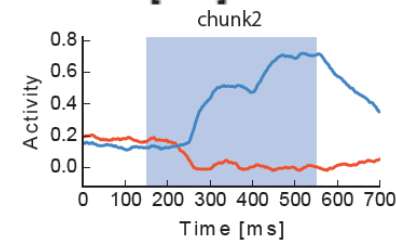
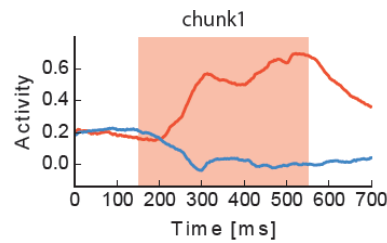
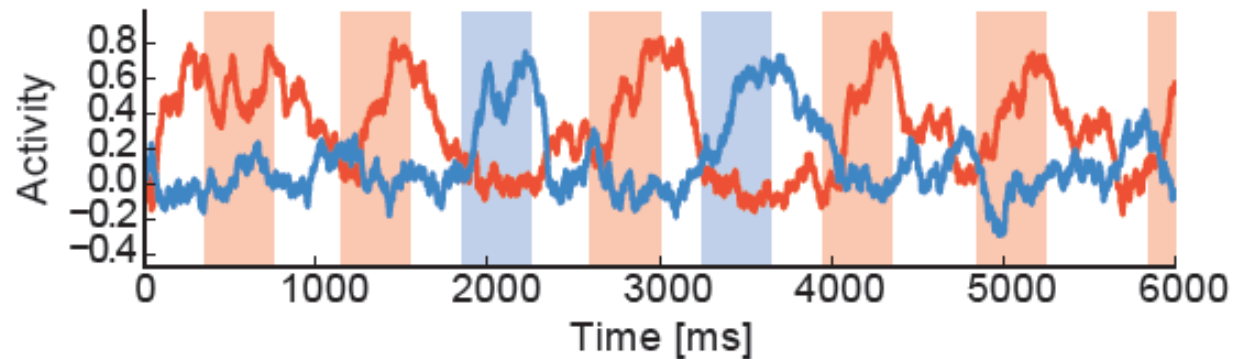
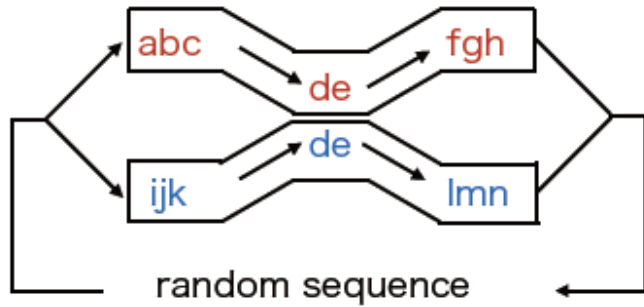
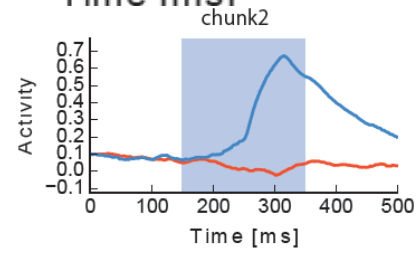
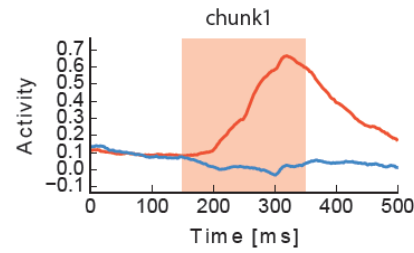
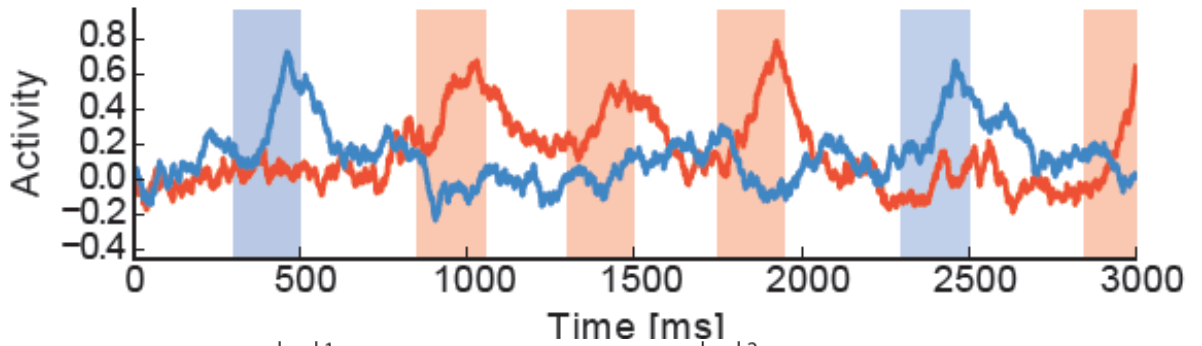
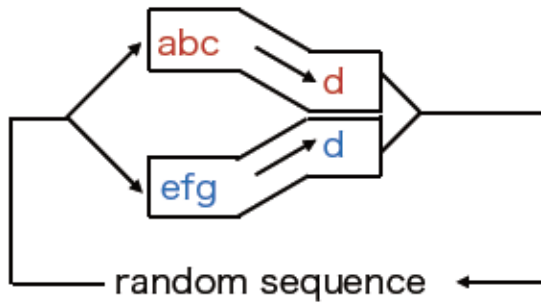


## feedback connections

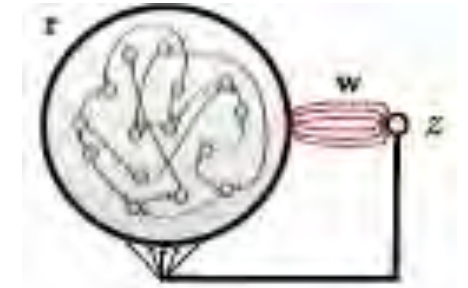




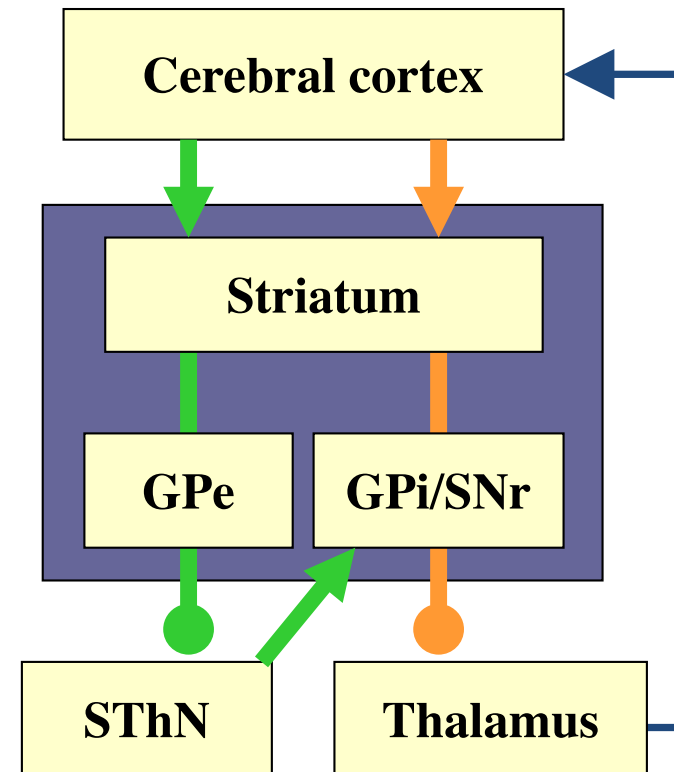
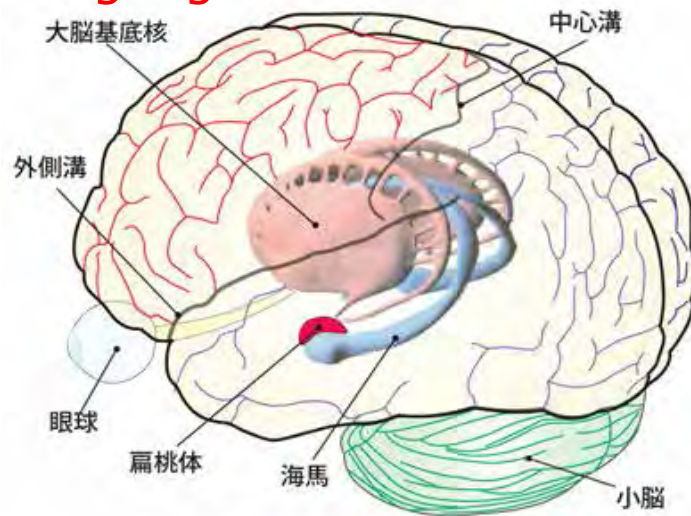
# Overlaps



# Cortico-basal ganglia loops for cognitive motor behavior



## Basal ganglia

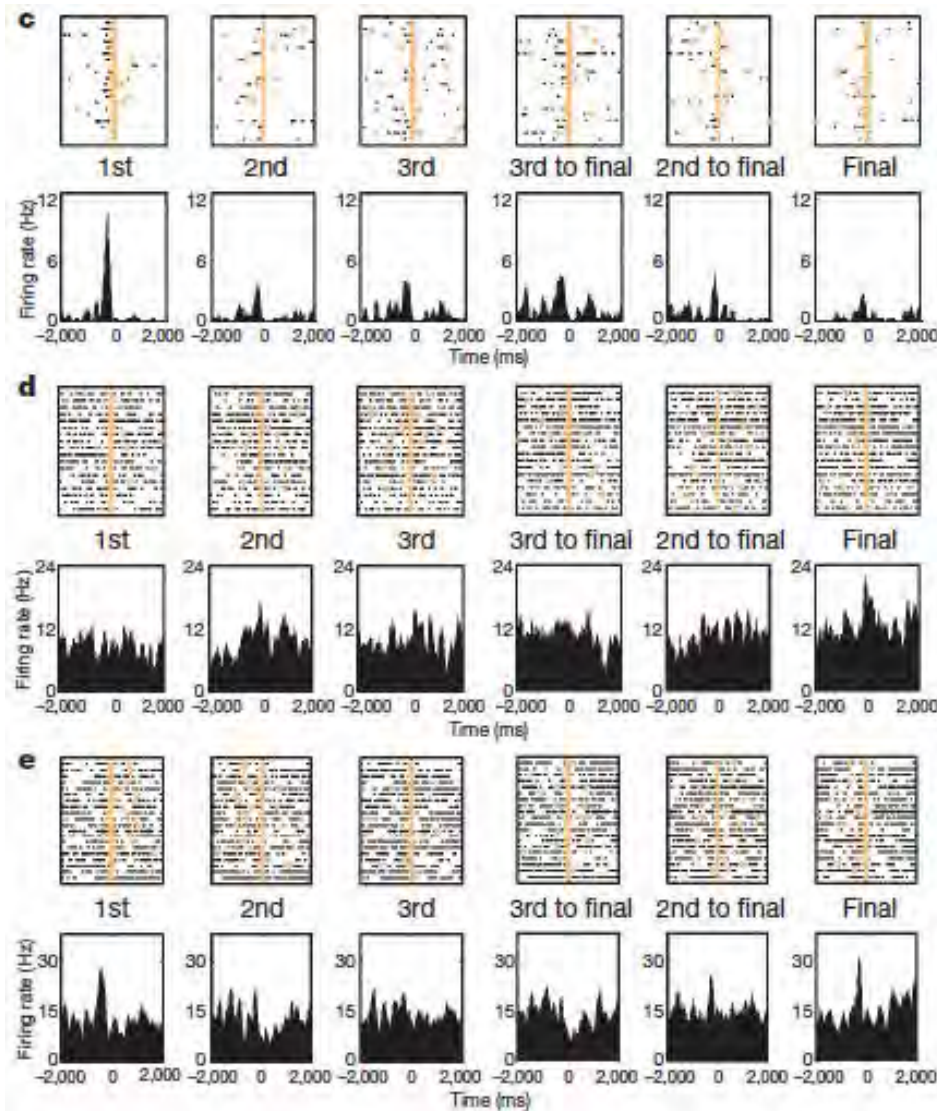




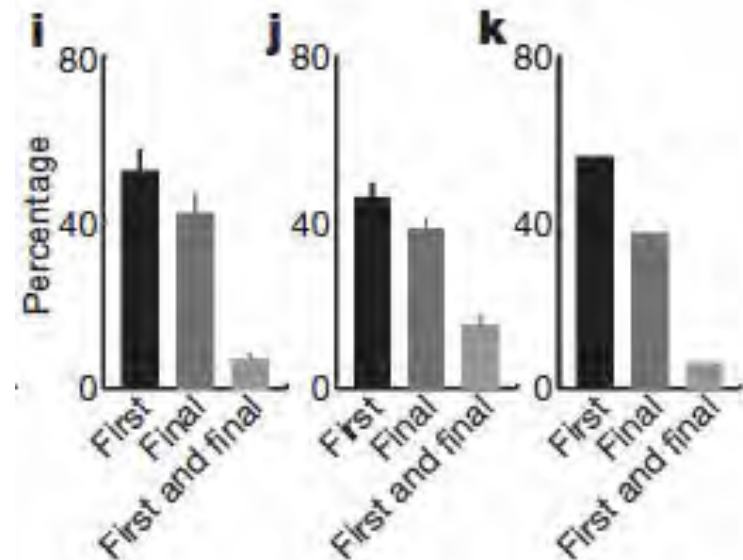
# Start/stop signals emerge in nigrostriatal circuits during sequence learning

Xin Jin<sup>1</sup> & Rui M. Costa<sup>1,2</sup>

Mice learned to generate a fixed number of lever press.



STR MSNs SN GABA SN DA



## まとめ2 リザーバ計算に基づく規則性の発見

- 相互に教え合うリザーバ計算機
- 大脳基底核のSTOP細胞に似た活動の生成

### まとめ

脳の学習メカニズムと、それにより外界をモデル化するメカニズムを実現できれば、ヒトらしいAIが創れるかもしれない。

# Summary

Reservoir computing systems can supervise each other to enable unsupervised learning of multiple chunks from random sequences.

The resultant systems can account for stop cells in the striatum.