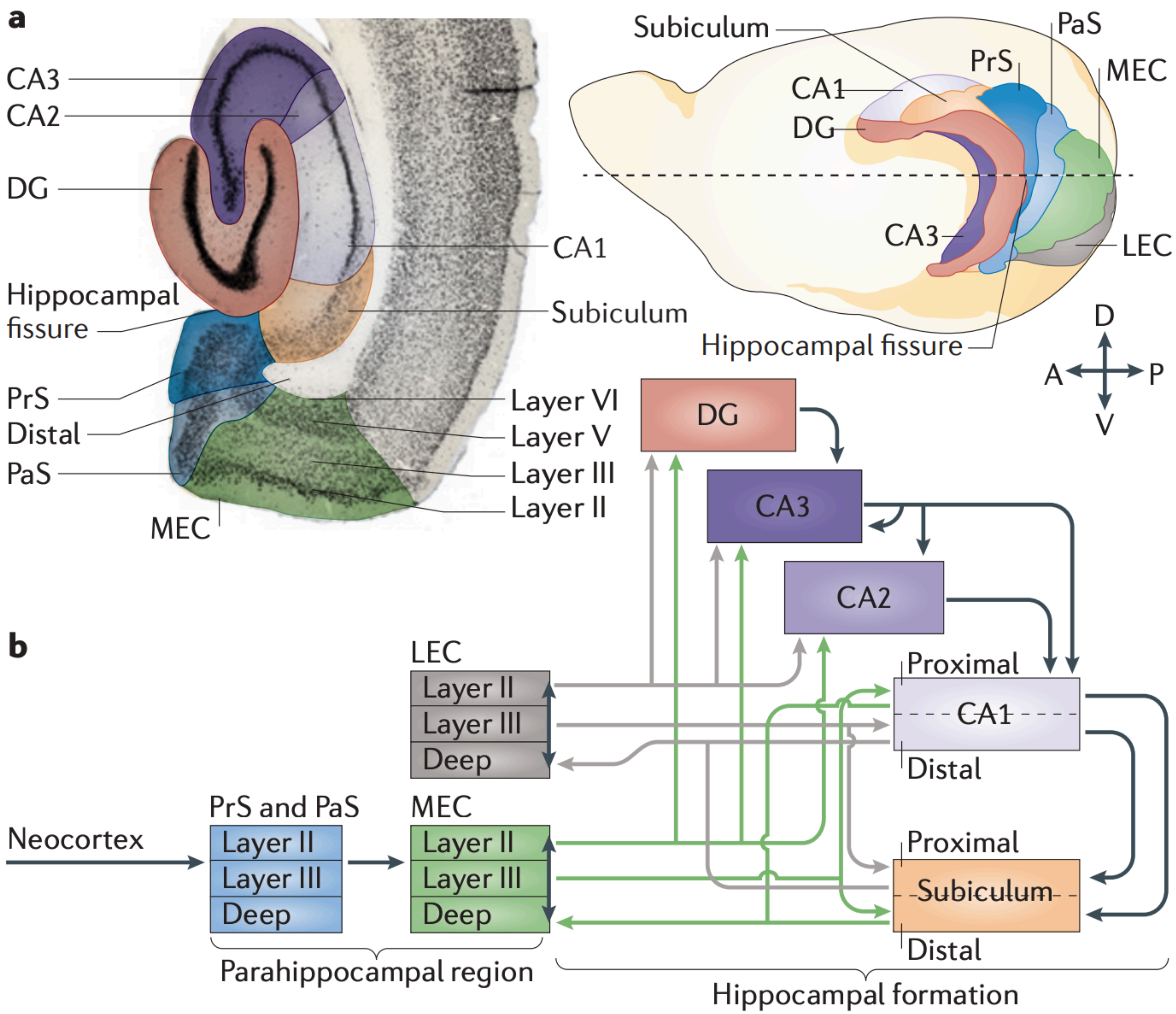
On the optimality of grid cells

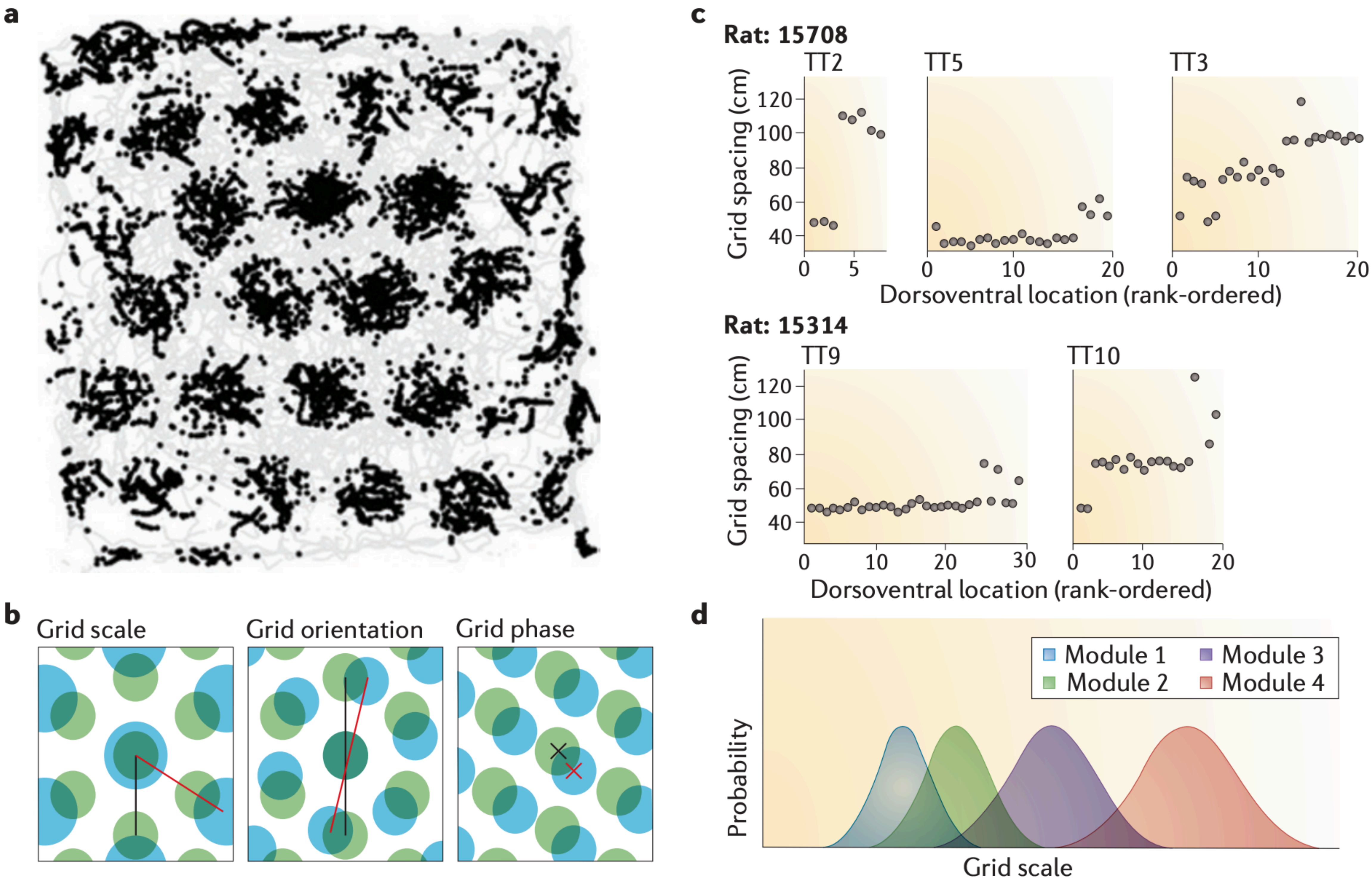
Anatomy



Moser et al. 2014

Background

- Grid cells are discovered in Moser et al. 2005 in mEC
- It fires in hexagonal grid like pattern spatially with different phases, spacing and orientation
- Distinct neurons then will fire at different locations and hence form a internal spatial map
- It is believed that the neurons do path integration to update the location



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Moser et al. 2005

Theoretical Question

- How does the grid-like formation occur? Fuhs & Touretzky 2006, Burak & Fiete 2009
- Why does the module size increase geometrically? Mathis et al. 2012, Wei et al. 2013
- What are the underlying computational principles of grid cells? Papadimitriou 2016

Setup

- N neurons on a circle
- Respond to input $\theta \in [0,2\pi]$
- And the tuning curve of the ith neuron is $f_i(\theta)$
- We assume that $f_{(i+1) \bmod N}(\theta) = f_i(\theta + \frac{2\pi}{N})$

Setup

- Given θ, the response $r_i(\theta) = f_i(\theta) + \eta_i$ where η_i is Gaussian noise
- Furthermore, the correlation matrix of the noise is C
- And C_{ij} is only a function of $|i - j|$ independent from θ
- Total signal power is bounded i.e. $\dot{f}(\theta)^T \dot{f}(\theta) \leq 1$
- Would like to decode $\Delta\theta$ from Δr

Fisher Information

- For the decoding to be effective, we want small variance
- Variance is lower bounded by reciprocal of Fisher information by Cramer Rao's theorem $var(\hat{\theta}) \geq \dfrac{1}{I(\theta)}$
- So we seek to maximize F. I. $\dot{f}(\theta)^T C^{-1} \dot{f}(\theta)$
- Then, $\dot{f}(\theta)$ corresponds to the largest eigenvector of C^{-1}

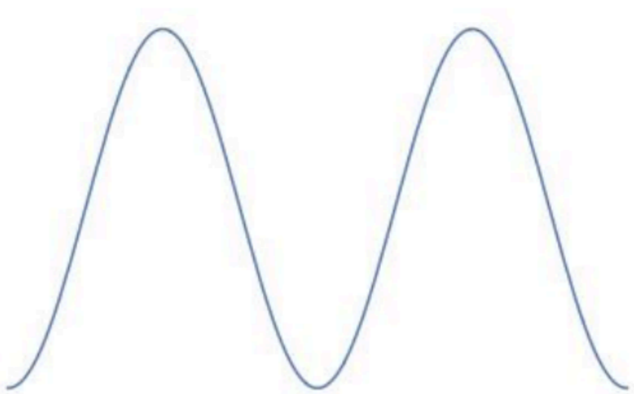
Solution

- Let λ_k be the smallest eigenvalue of C with eigenvectors
- $v_i = \cos((i-1)k\frac{2\pi}{N})$ and $w_i = sin((i-1)k\frac{2\pi}{N})$
- So $\dot{f}(\theta) = \alpha(\theta)v + \beta(\theta)v$ where $\alpha^2 + \beta^2 = 1$
- Now let $\alpha(\theta) = \sin(\phi(\theta))$ and $\beta(\theta) = \cos(\phi(\theta))$
- We get $\dot{f}(\theta) = \sin(\phi(\theta) + (i-1)k\frac{2\pi}{N})$

Solution

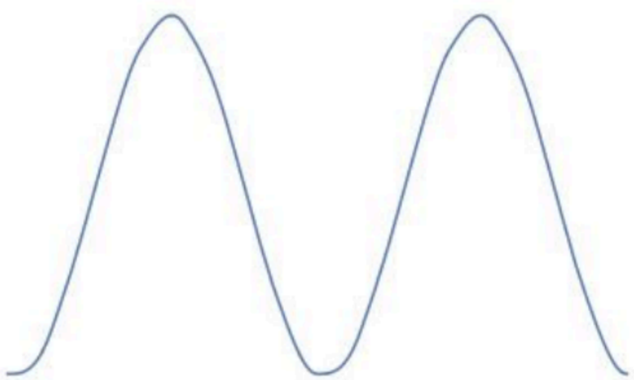
- By periodicity, we have $\sin(\phi(\theta + \frac{2\pi}{N}) + (i-1)k\frac{2\pi}{N}) = \sin(\phi(\theta) + ik\frac{2\pi}{N})$
- $\phi(\theta + \frac{2\pi}{N}) = \phi(\theta) + k\frac{2\pi}{N} + 2n\pi$ for some integer n
- Let $\psi(\theta) : [0,\frac{2\pi}{N}] \to \mathbb{R}$. For $\theta \in [0,2\pi]$, define $\theta' \in [0,\frac{2\pi}{N}]$ and $\theta'' \in \{0,\frac{2\pi}{N},\cdots,\frac{(N-1)2\pi}{N}\}$ from $\theta = \theta' + \theta''$
- Then $\dot{f}(\theta) = \sin(\psi(\theta') + \theta'')$ is a solution

Tuning curve

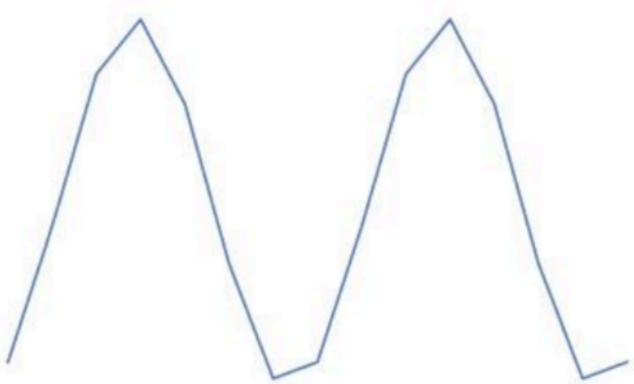


(a) $\psi(x) = x$

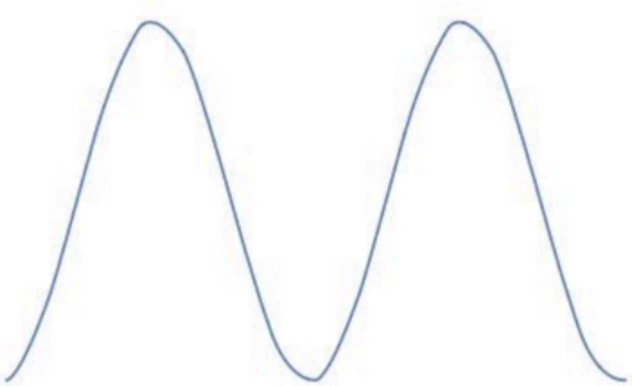
(b) $\psi(x) = 10x$



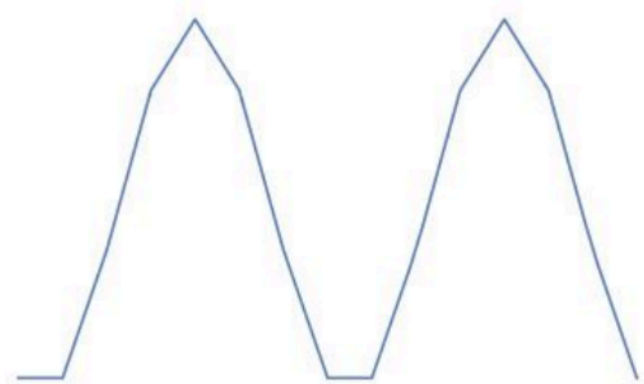
(c) $\psi(x) = \frac{x^2}{\delta}$



(d) $\psi(x) = 1$



(e) $\psi(x) = \sqrt{x\delta}$

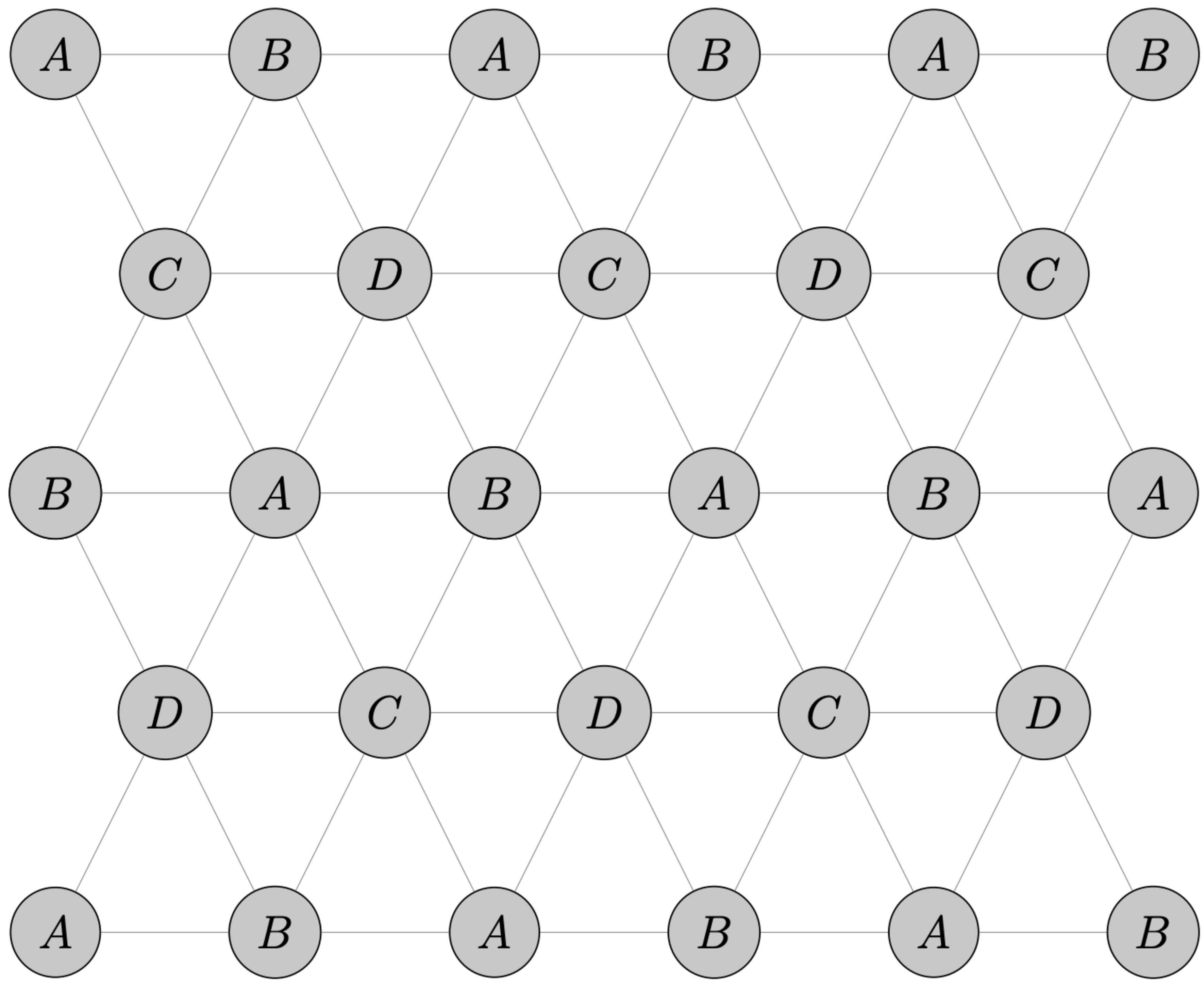


(f) $\psi(x) = 0$

Other points

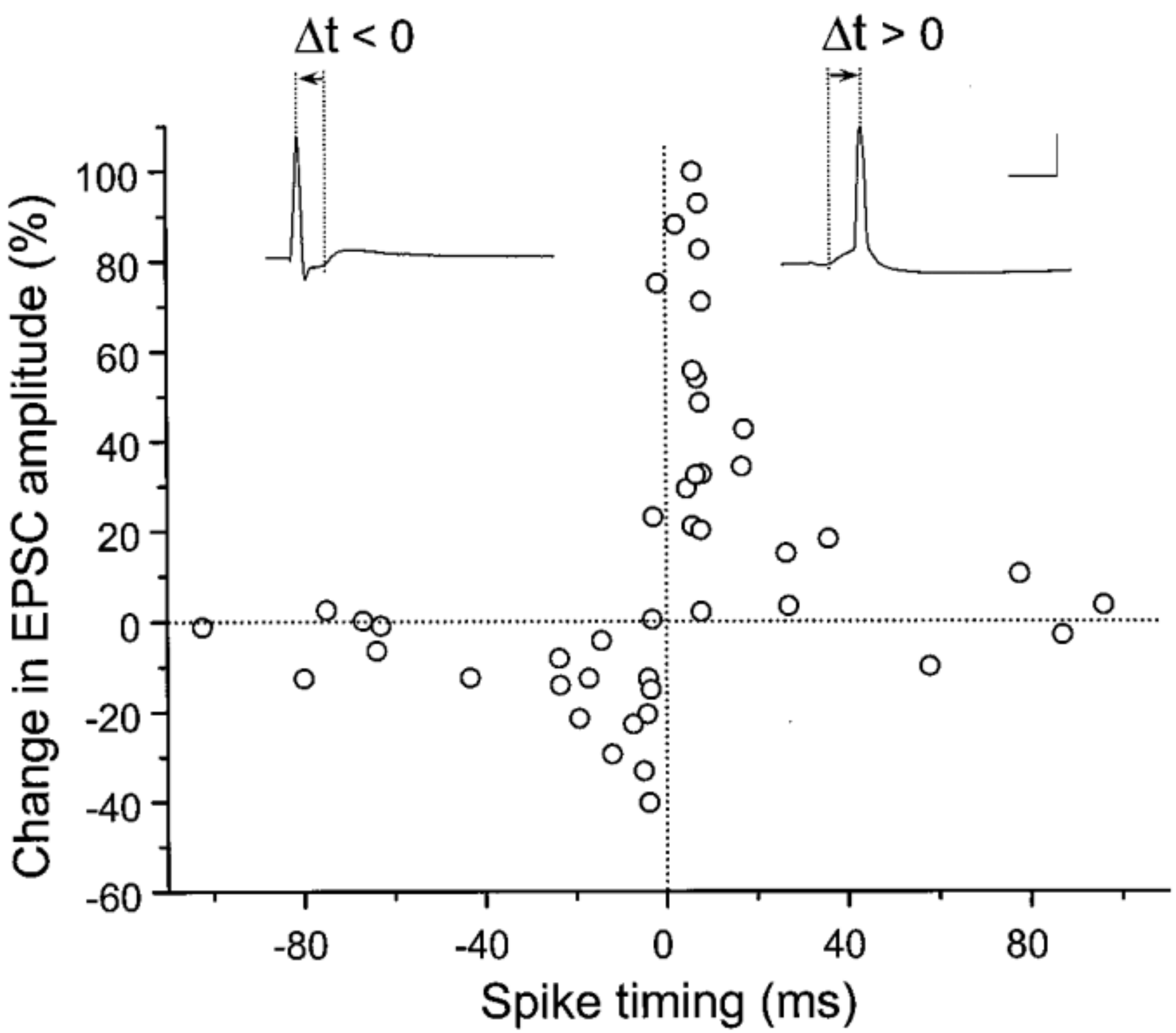
- One dimensional grid cells can efficiently compute the displacement with two copies of grid cells with phase orthogonal to each other.
- Two dimensional grid cells cannot generalize immediately unless we assume the fisher information can be maximized axis wise.
- In this case, the reason that two dimensional grid is hexagonal lattices might be of a computation one. You need four copies of grid cells to calculate displacement.

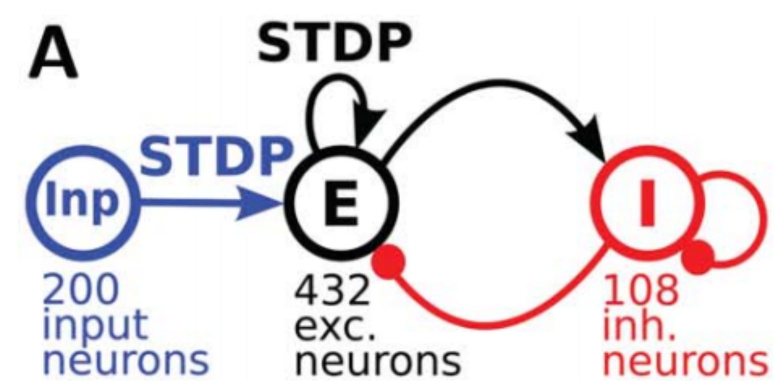
Hexagonal Grid



STDP forms associations between memory traces in networks of spiking neurons

STDP



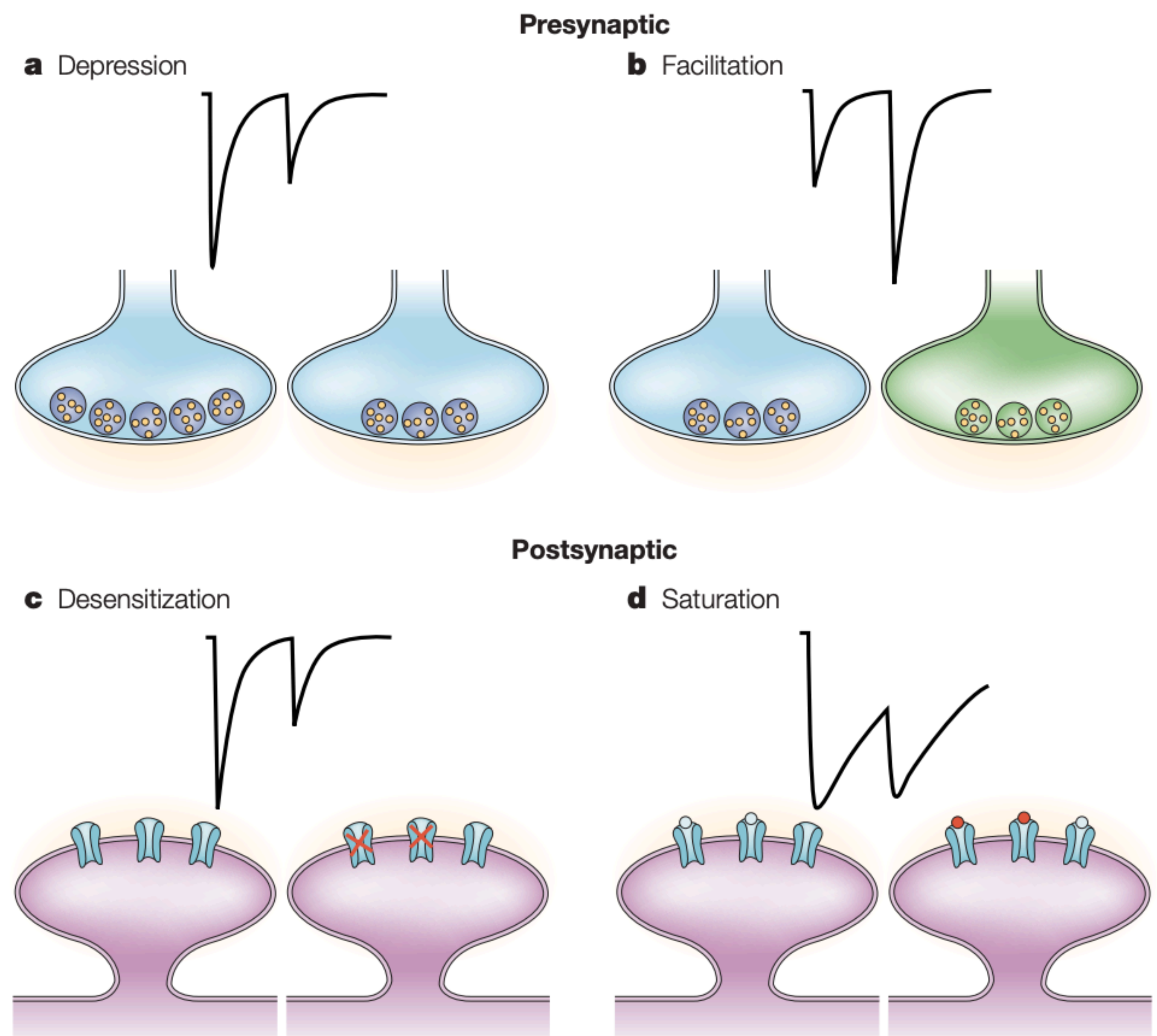


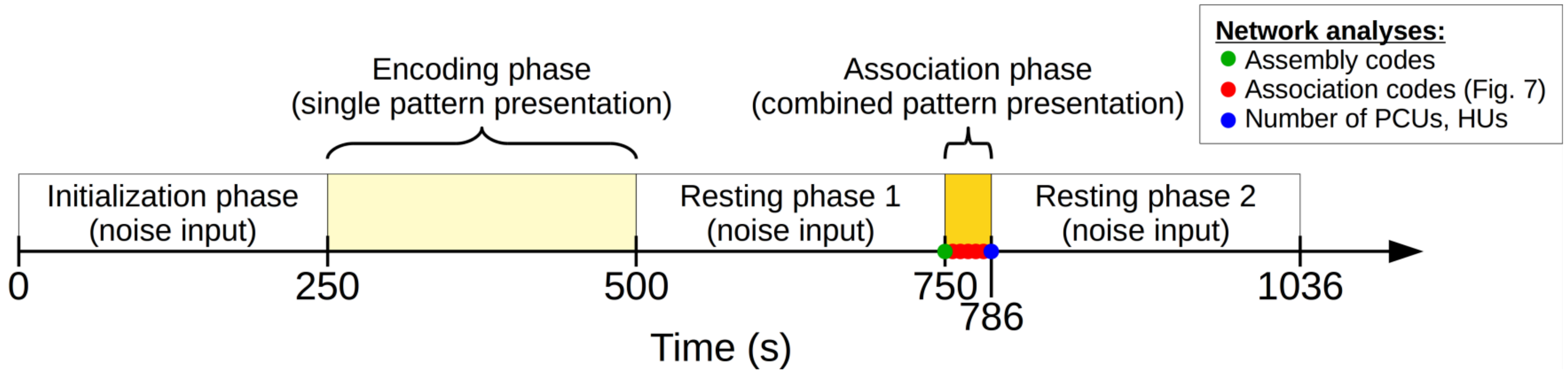
Bi & Poo 1998

Short Term Plasticity

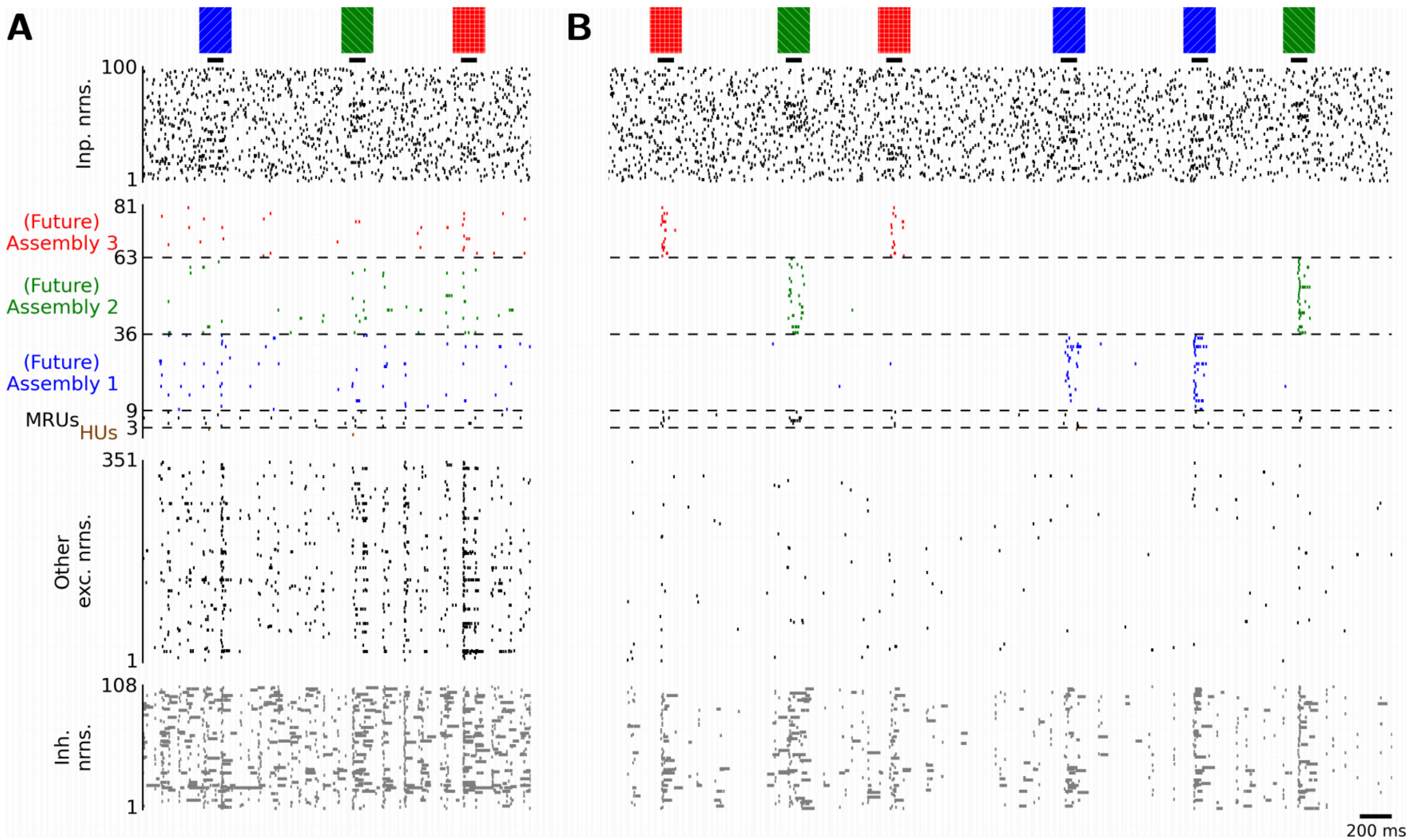
- Synaptic release probability (calcium)
- Synaptic availability (vesicle in the ready release zone)
- Short term plasticity is proportional to the product of these two
- This helps the network to stabilize

Short Term Plasticity

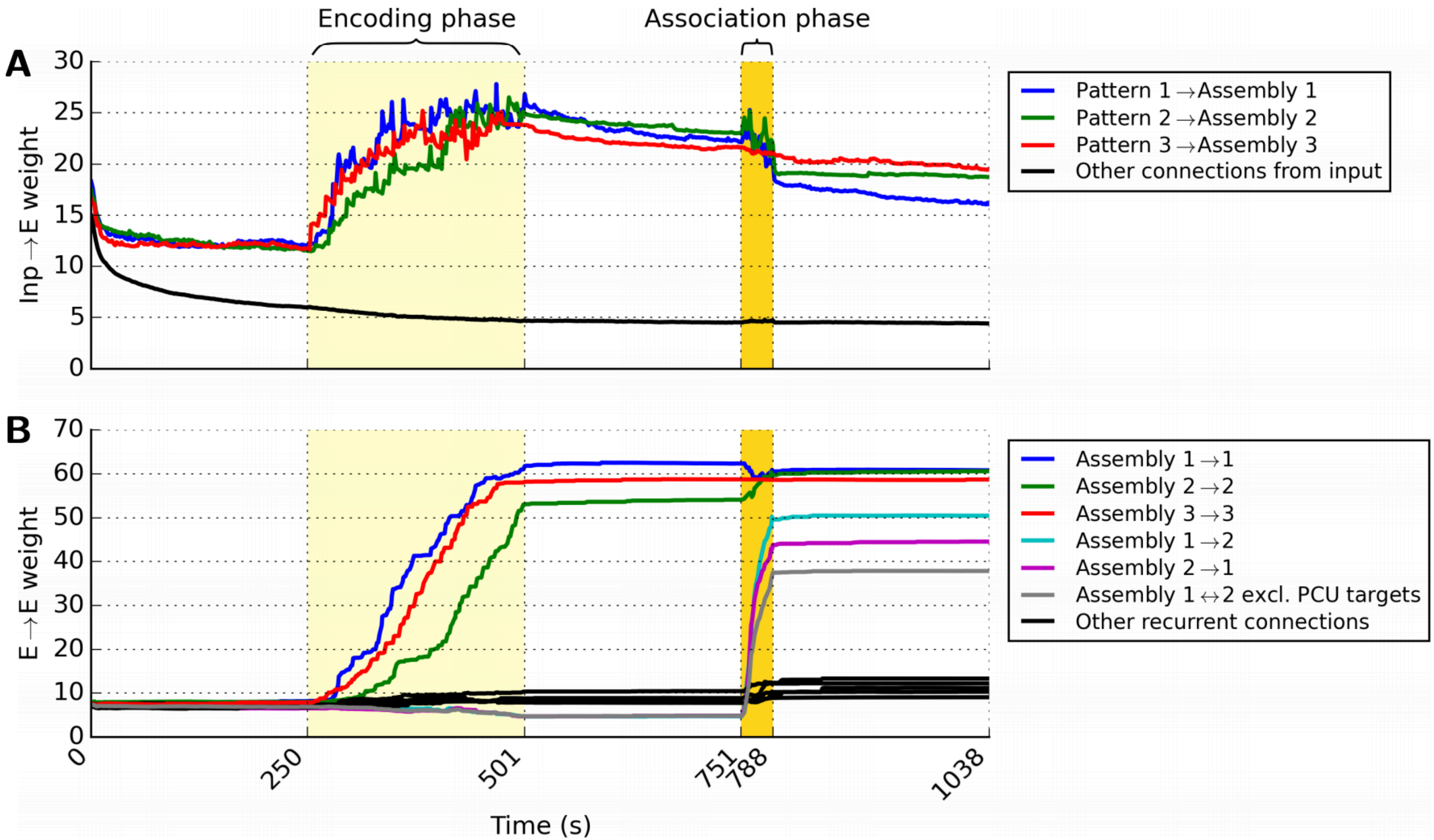




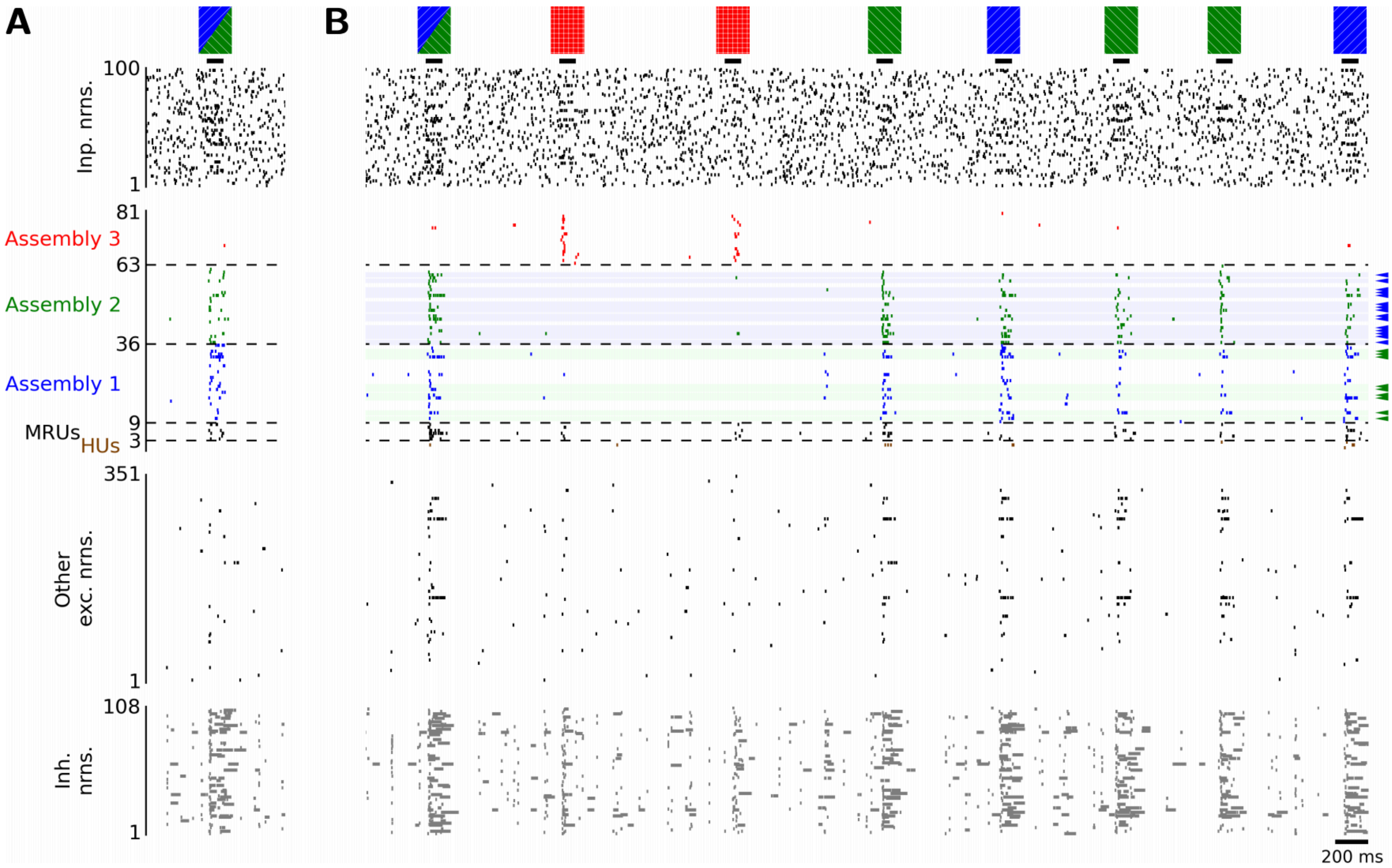
Network analyses:
Assembly codes
Association codes (Fig. 7)
Number of PCUs, HUs
Encoding phase
(single pattern presentation)
Association phase
(combined pattern presentation)
Initialization phase
(noise input)
Resting phase 1
(noise input)
Resting phase 2
(noise input)
0
250
500
750
786
1036
Time (s)

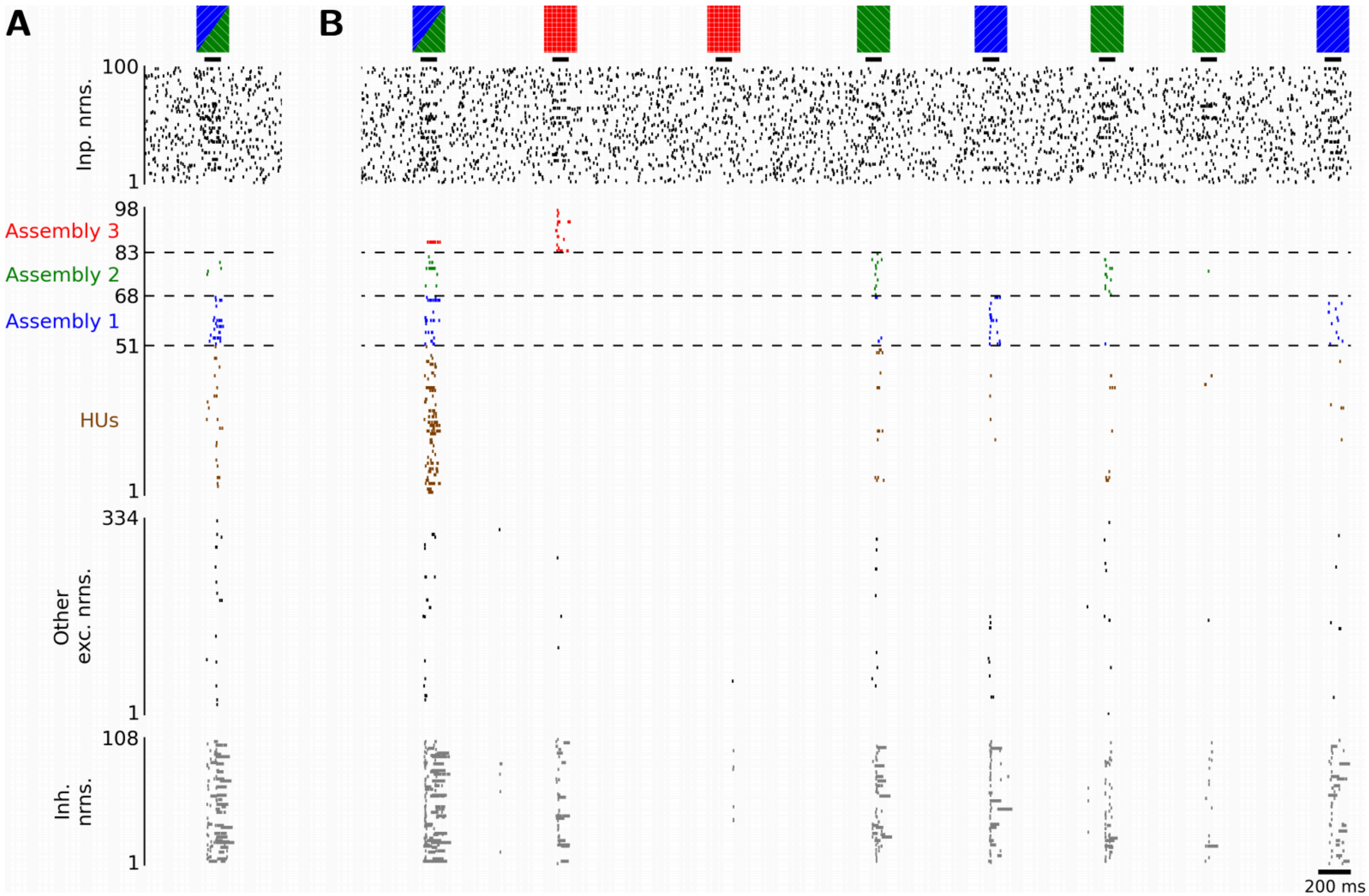


A
B
100
Inp. nrns.
1
81
(Future)
Assembly 3
63
(Future)
Assembly 2
36
(Future)
Assembly 1
9
MRUs
HUs
3
351
Other
exc. nrns.
1
108
Inh.
nrns.
1
200 ms



Encoding phase
Association phase
A
Inp → E weight
Pattern 1 → Assembly 1
Pattern 2 → Assembly 2
Pattern 3 → Assembly 3
Other connections from input
B
E → E weight
Assembly 1 → 1
Assembly 2 → 2
Assembly 3 → 3
Assembly 1 → 2
Assembly 2 → 1
Assembly 1 ↔ 2 excl. PCU targets
Other recurrent connections
0
250
501
751
788
1038
Time (s)


A
B
100
Inp. nrns.
1
81
Assembly 3
63
Assembly 2
36
Assembly 1
9
MRUs
3
HUs
351
Other exc. nrns.
1
108
Inh. nrns.
1
200 ms



A
B
Inp. nrns.
100
1
98
Assembly 3
83
Assembly 2
68
Assembly 1
51
HUs
1
334
Other exc. nrns.
1
108
Inh. nrns.
1
200 ms