

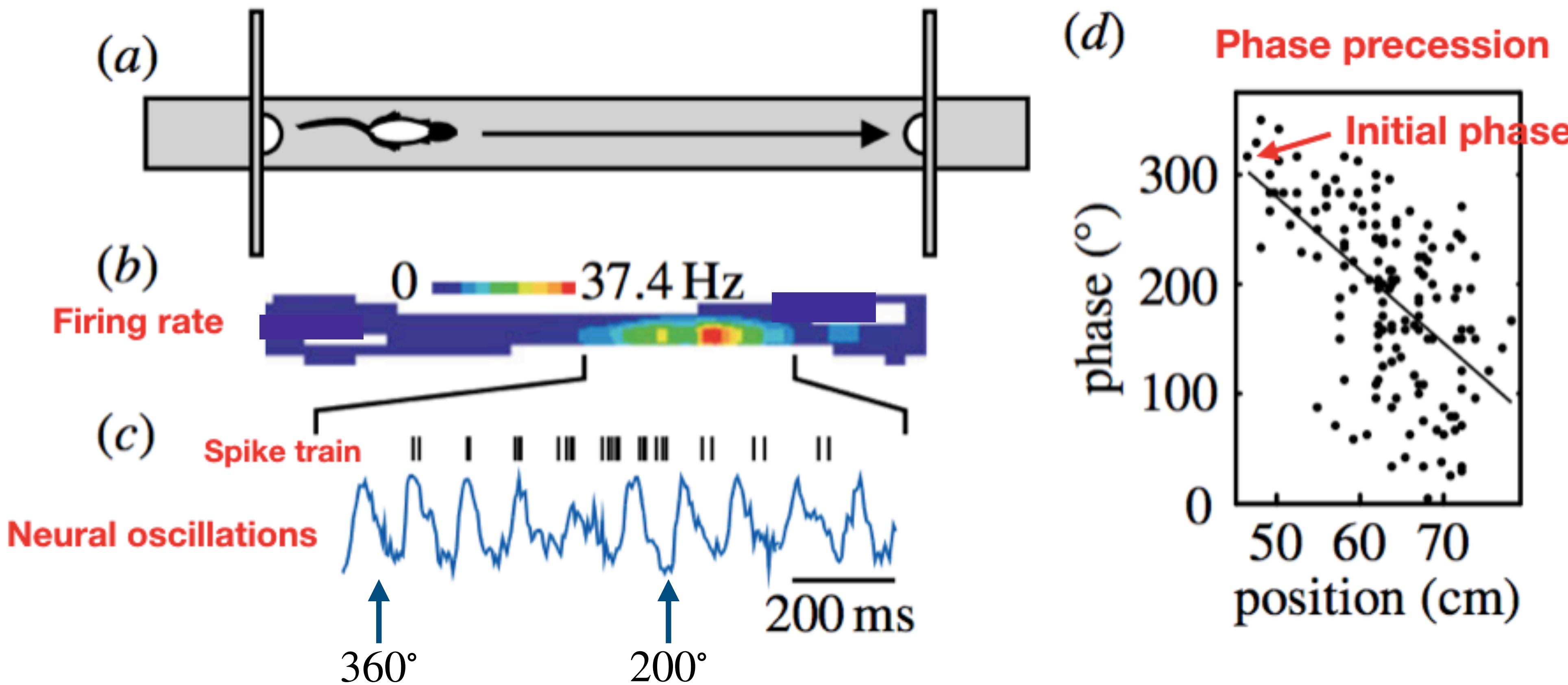
# Successor representation in hippocampus

Presented by Yusi Chen

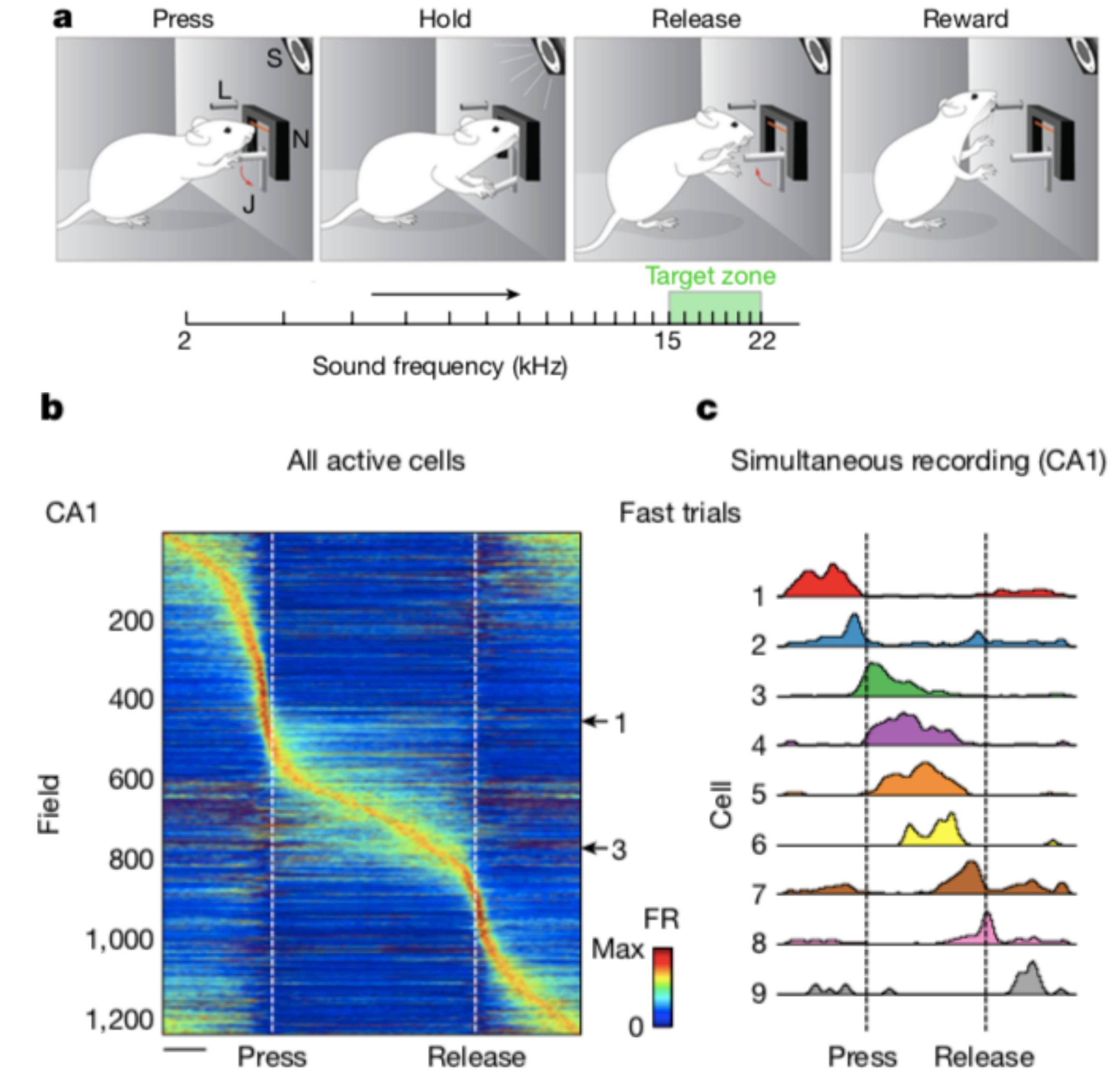
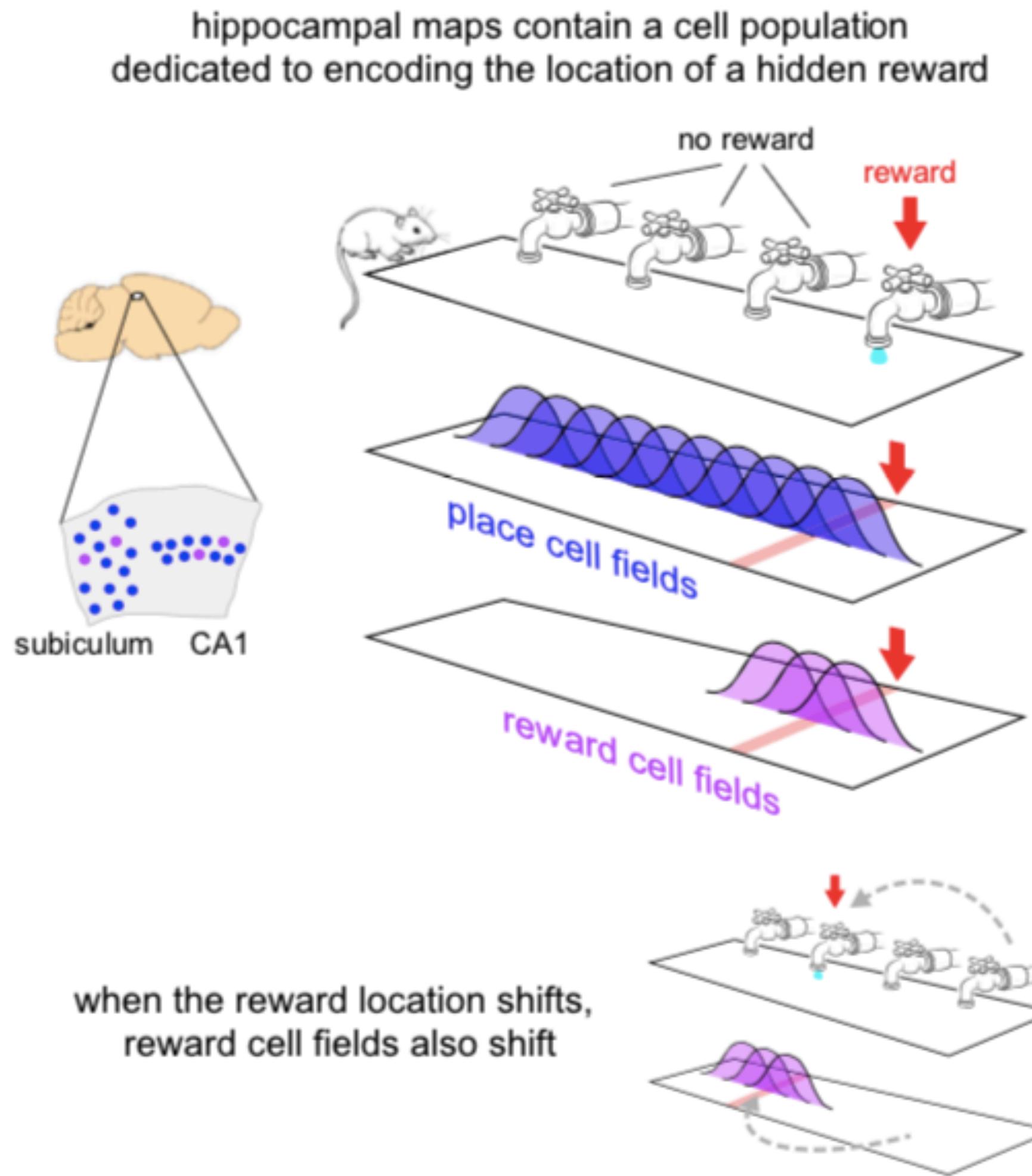
# Background

- Place cell: from spatial representation to successor representation (Tank lecture)
- Reinforcement learning: successor representation and temporal difference learning (Dayan\_Neural Computation\_1993)

# Spatial representation of place cells



# Non-spatial representation



- Results suggest grid cells and place cells build representations that represent adjacency in behavior; task performance, both in spatial navigation, and cognitive processes in general, activates a sequence of neural activity in the hippocampal formation in which firing fields are elicited parametrically with progress through behavior
- Representation learning is very general and cells are repurposed between spatial and non-spatial tasks

### Representation of continuous variables

- Time and Order, rodent and NHP

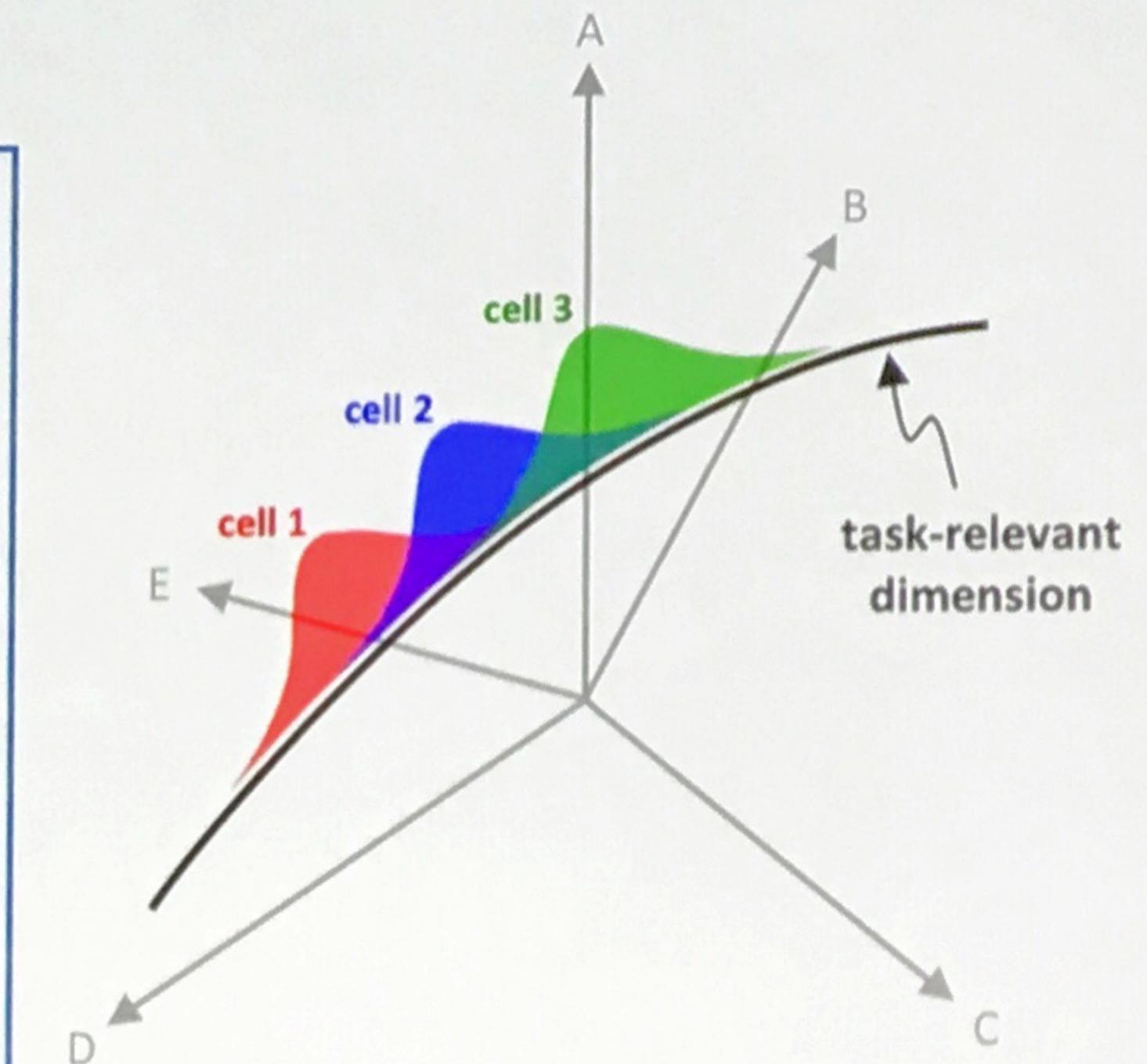
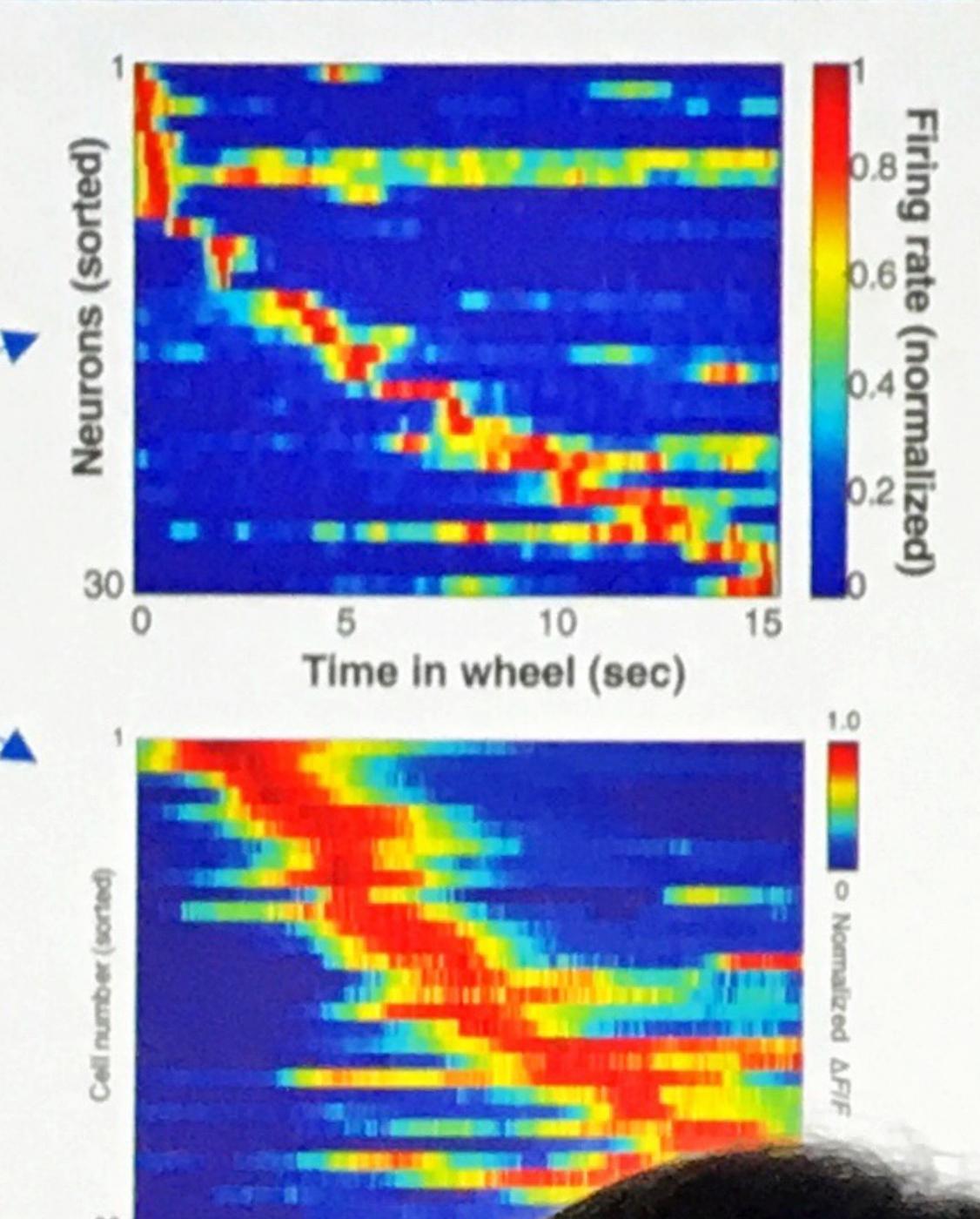
Manns, Howard, Eichenbaum (2007) odor sequences  
 Pastalkova,..., Buzsaki (2008) episode sequences  
 Naya, Suzuki (2011) time encoding between stimuli  
 Heys, Dombeck (2018) elapsed time, MEC

- Visual space, NHP

Killian, Jutras, Buffalo (2012)

- Human (Social, Conceptual)

Tavares,..., Schiller (2015)  
 Constantinescu, O'Reilly, Behrens (2016)



# Do Hippocampal Pyramidal Cells Signal Non-Spatial as Well as Spatial Information?

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University College London, London, United Kingdom*

**ABSTRACT:** It is generally agreed that the rat hippocampus is involved in spatial memory. Whether this is its sole or primary function, or merely one component of a broader function, is still debated. It has been suggested, for example, that the hippocampus stores information about flexible relations between stimuli, both spatial and non-spatial. In this paper, I reiterate the basic tenet of the cognitive map theory that the processing and storage of spatial information is the primary and perhaps the exclusive role of the hippocampus in the rat, and that data that appear to contradict this have been misinterpreted. These data are found in

map theory states that this is the sole function of the hippocampus in the rat, that the structure was designed to carry out this specific function, and that its components are wired up to achieve that purpose. It is, of course, possible to modify such a system to accomplish different or additional functions by adding components or by changing the data that is fed into it. For example,

# Successor representation (SR)

## Improving Generalisation for Temporal Difference Learning: The Successor Representation

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Computational Neurobiology Laboratory  
The Salk Institute  
PO Box 85800, San Diego CA 92186-5800

### Abstract

Estimation of returns over time, the focus of temporal difference (TD) algorithms, imposes particular constraints on good function approximators or representations. Appropriate generalisation between states is determined by how similar their successors are, and representations should follow suit. This paper shows how TD machinery can be used to learn such representations, and illustrates, using a navigation task, the appropriately distributed nature of the result.

- Successor representation: awarding similar representations to states that are nearby in some space
- Spatial space/frequency space/odor space
- Task/reward related states
- Theoretical basis of today's paper

# The hippocampus as a predictive map

Kimberly L Stachenfeld<sup>1,2</sup>, Matthew M Botvinick<sup>1,3</sup> & Samuel J Gershman<sup>4</sup>

A cognitive map has long been the dominant metaphor for hippocampal function, embracing the idea that place cells encode a geometric representation of space. However, evidence for predictive coding, reward sensitivity and policy dependence in place cells suggests that the representation is not purely spatial. We approach this puzzle from a reinforcement learning perspective: what kind of spatial representation is most useful for maximizing future reward? We show that the answer takes the form of a predictive representation. This representation captures many aspects of place cell responses that fall outside the traditional view of a cognitive map. Furthermore, we argue that entorhinal grid cells encode a low-dimensionality basis set for the predictive representation, useful for suppressing noise in predictions and extracting multiscale structure for hierarchical planning.

# Reinforcement learning framework

- **$V(s)$ :** the value of a current state  $s$ , equals to expected discounted sum of the reward at each future state  $S_t$

$$V(s) = \mathbb{E} \left[ \sum_{t=0}^{\infty} \gamma^t R(s_t) \mid s_0 = s \right]$$

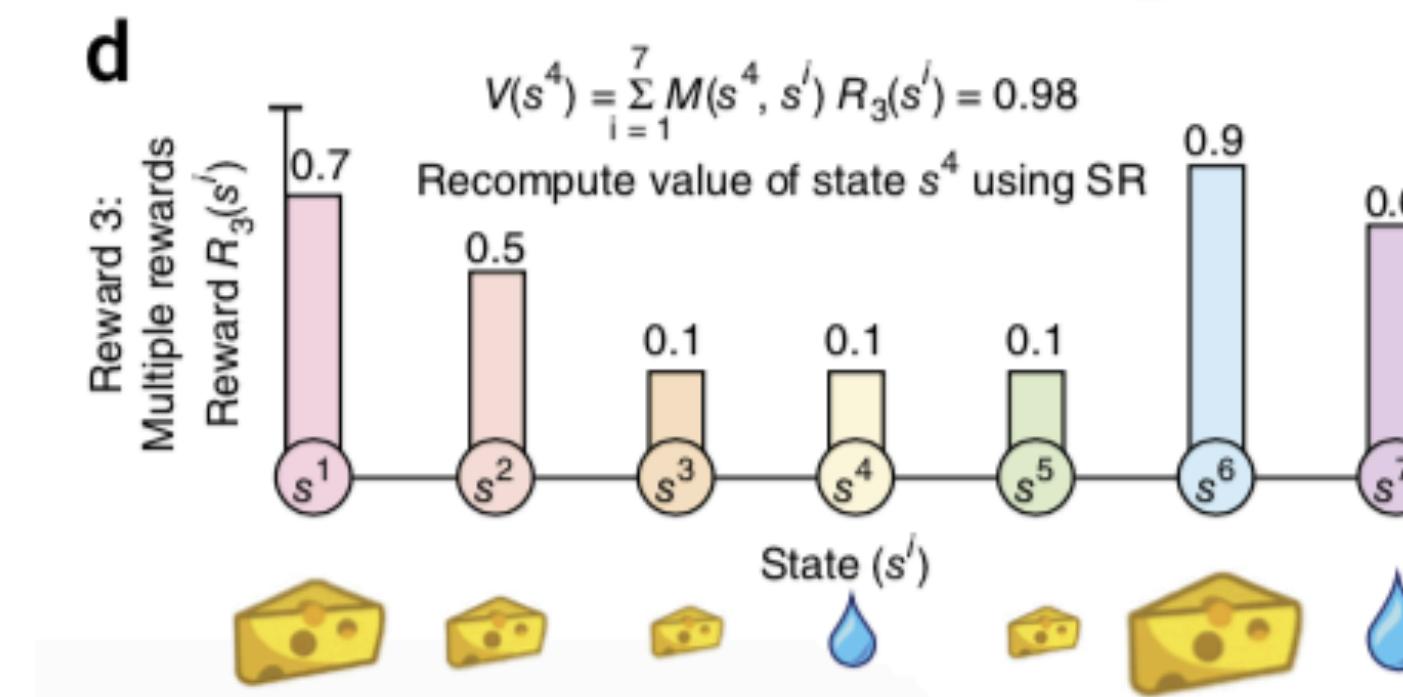
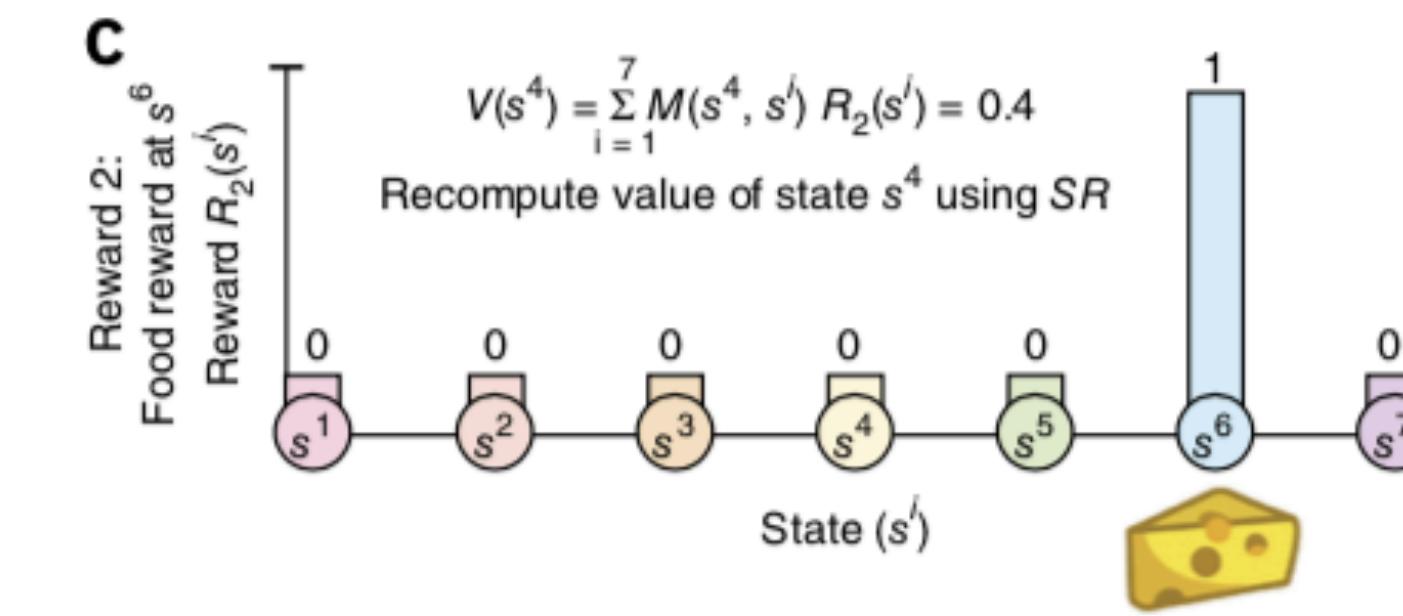
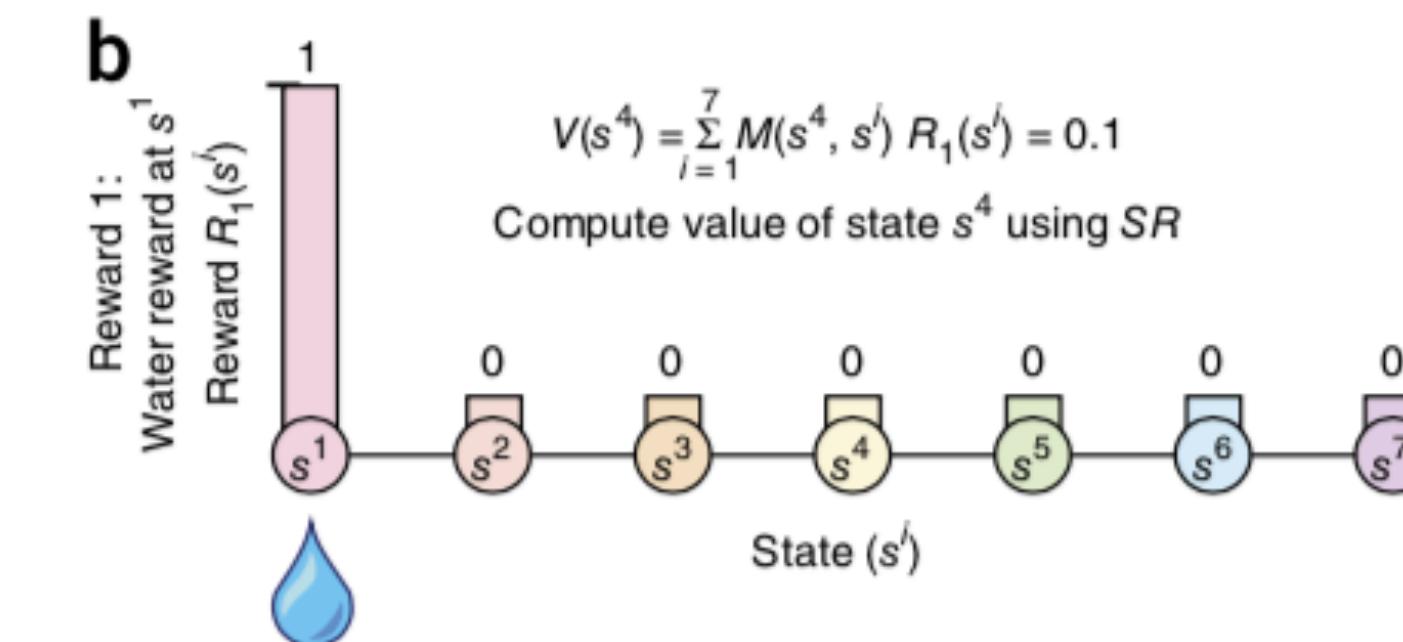
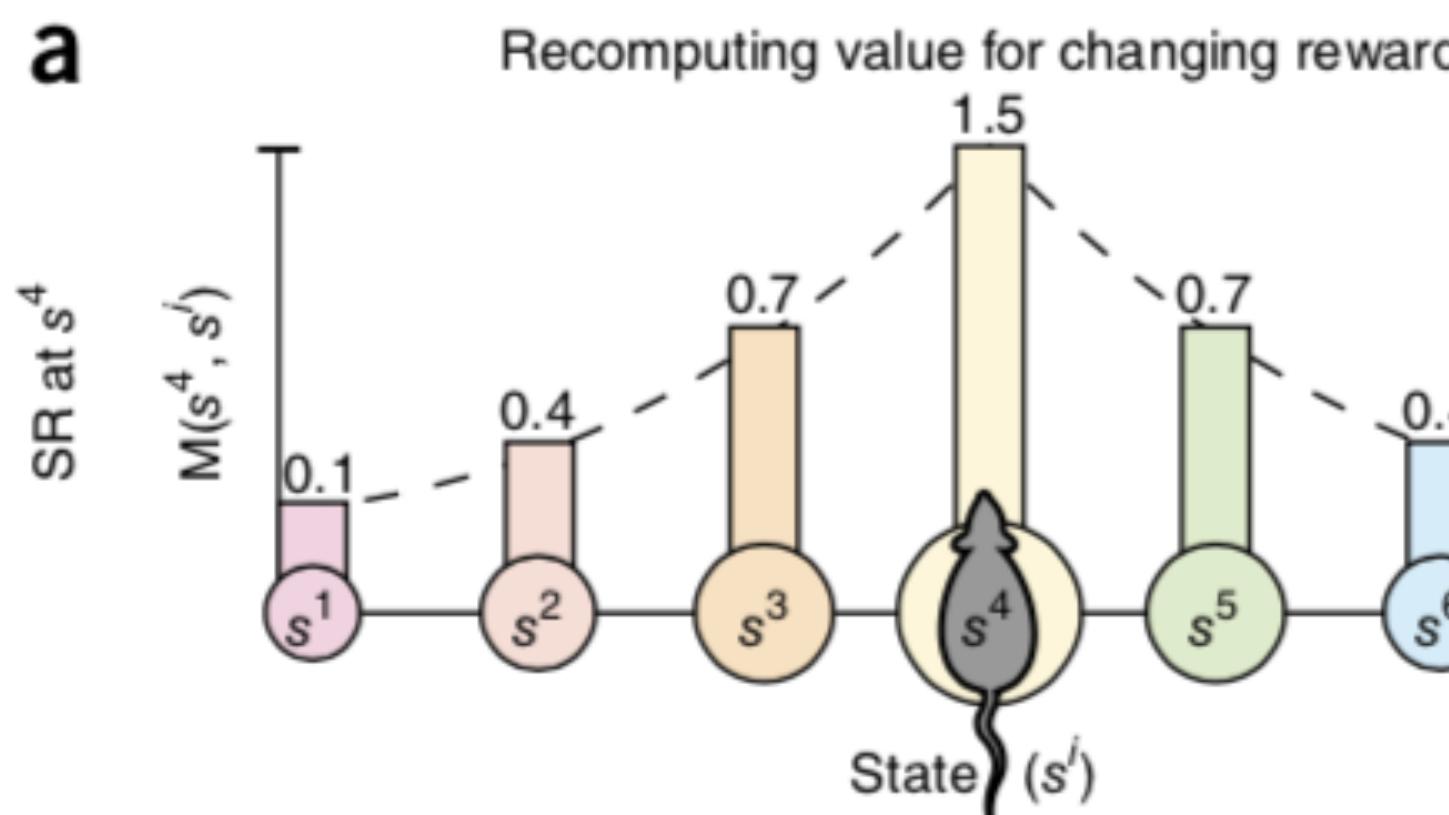
- **$V(s)$**  could be factorized into successor representation matrix (**M**) and direct reward function (**R**)

$$V(s) = \sum_{s'} M(s, s') R(s'),$$

- **$M(s, s')$ :** the expected number of times a single encoded location  $s'$  will be visited under current policy, starting from state  $s$

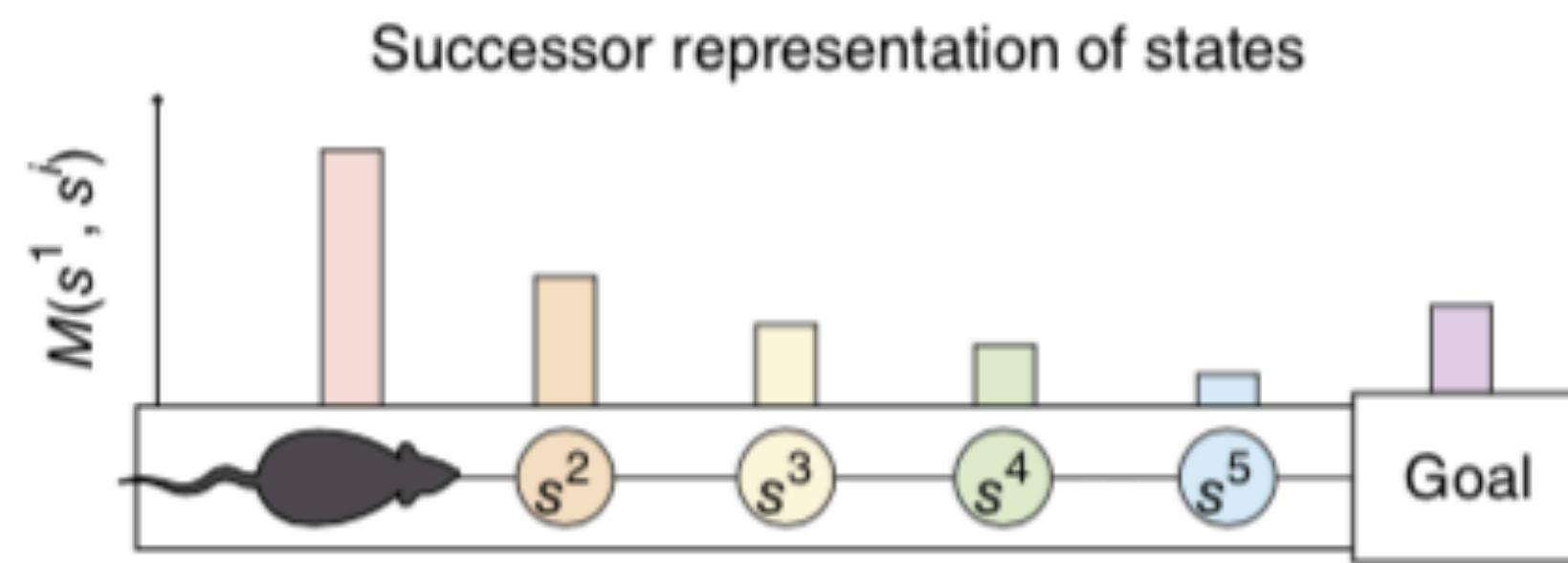
$$M(s, s') = \mathbb{E} \left[ \sum_{t=0}^{\infty} \gamma^t \mathbb{I}(s_t = s') \mid s_0 = s \right]$$

# Updating value using SR



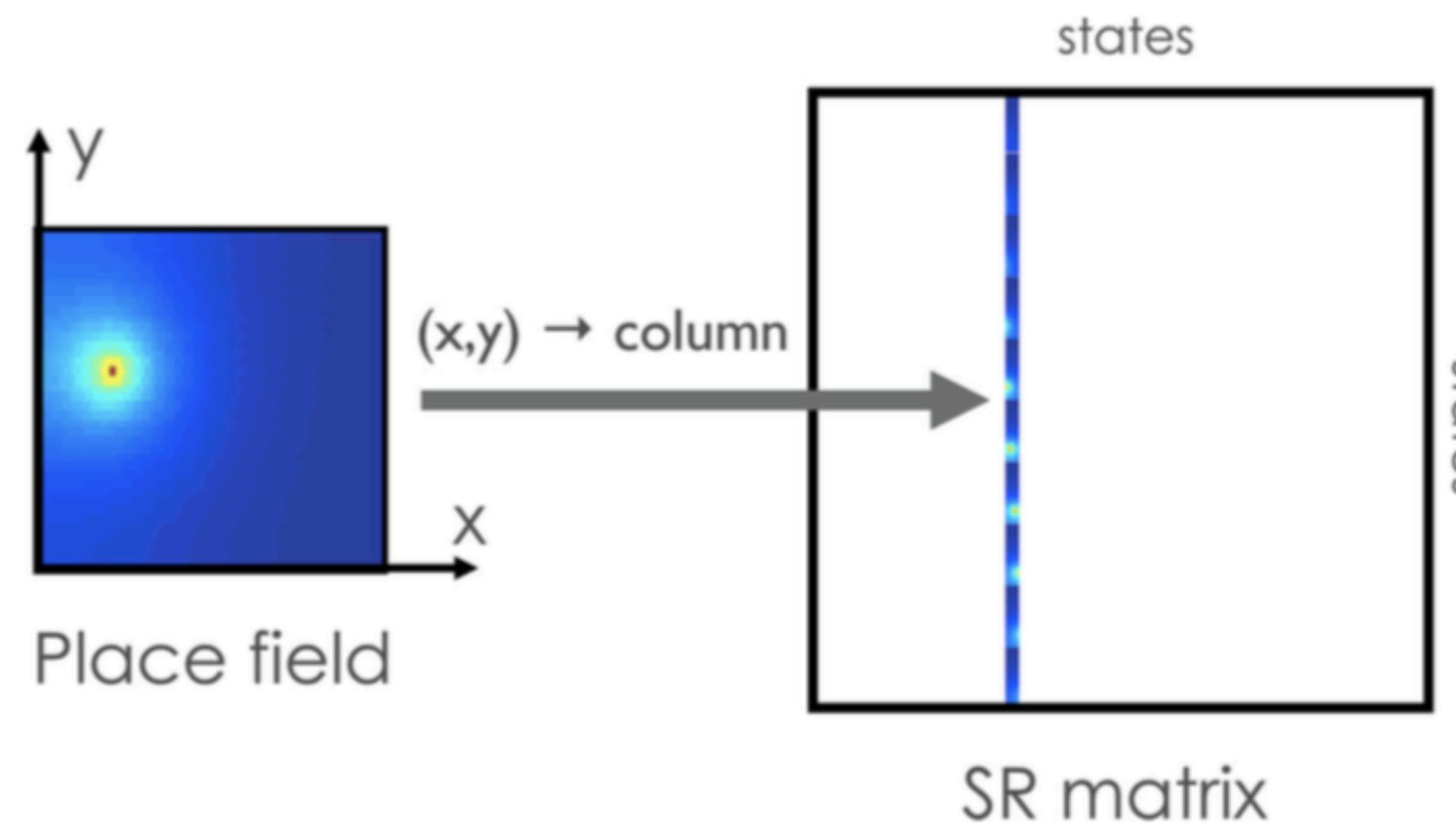
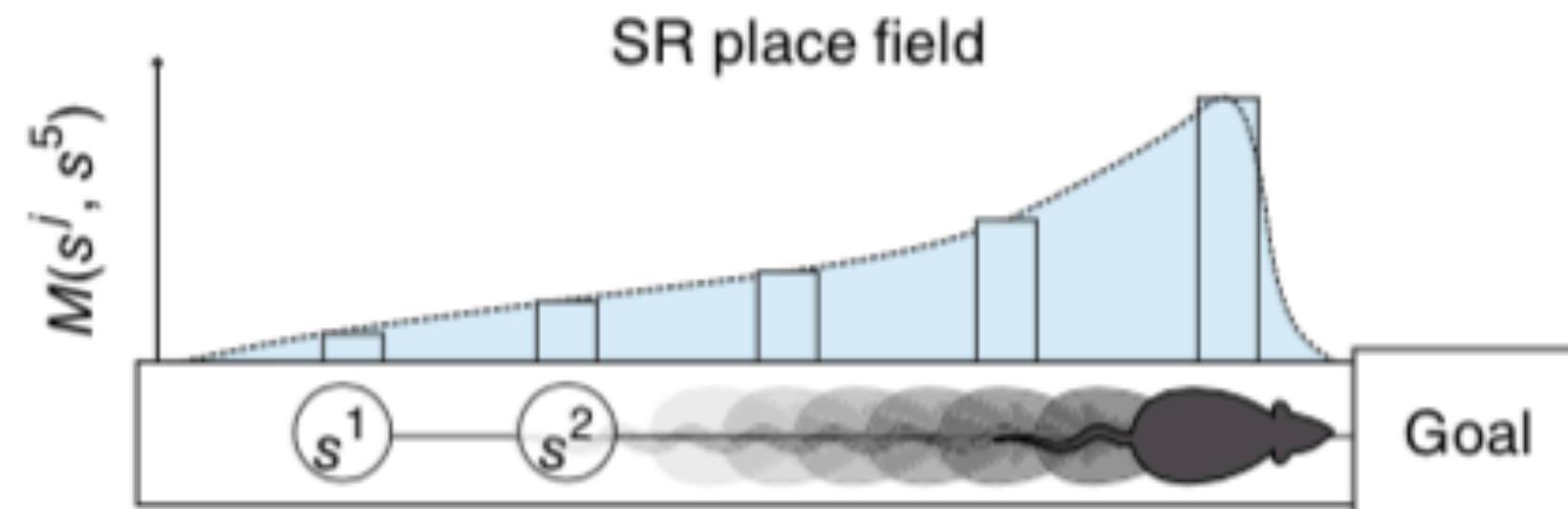
# Successor representation of a place cell

d



- $M(s, s')$ : the expected number of times a single encoded location  $s'$  will be visited under current policy, starting from state  $s$
- $M(:, s')$ : successor representation of one place cell indexed as  $s'$

e

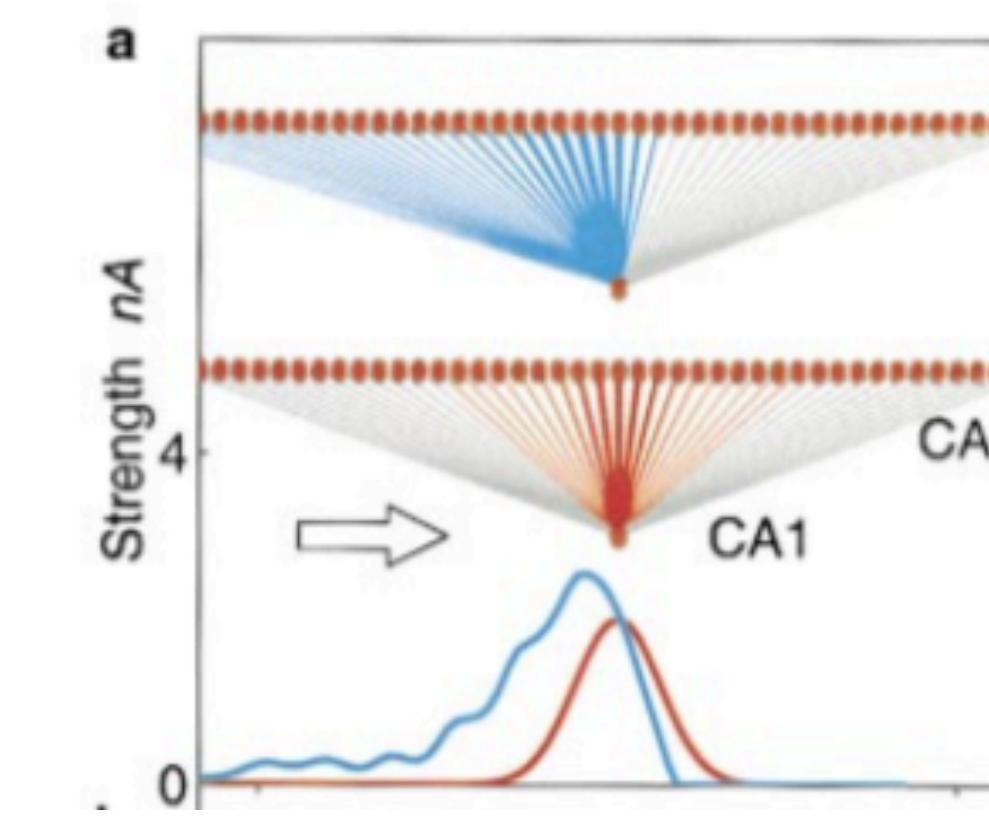
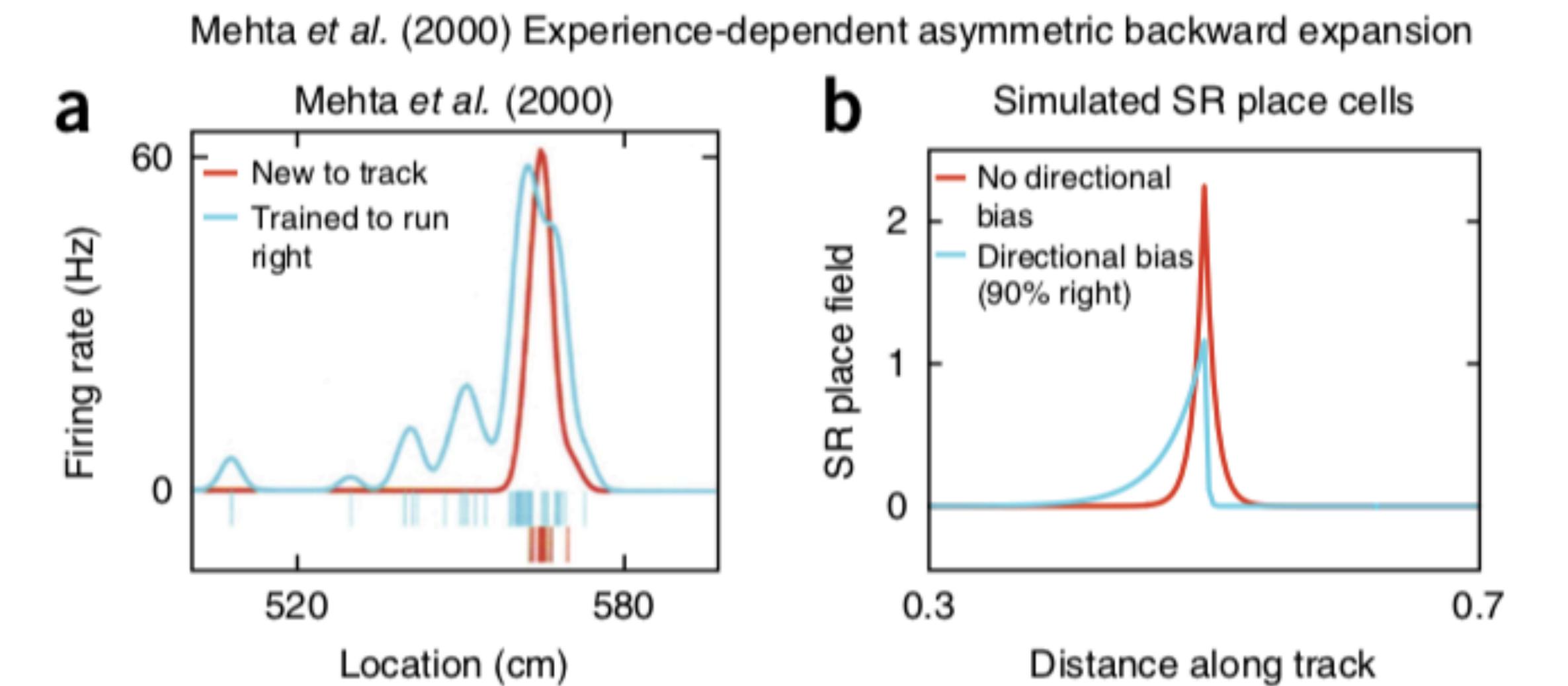
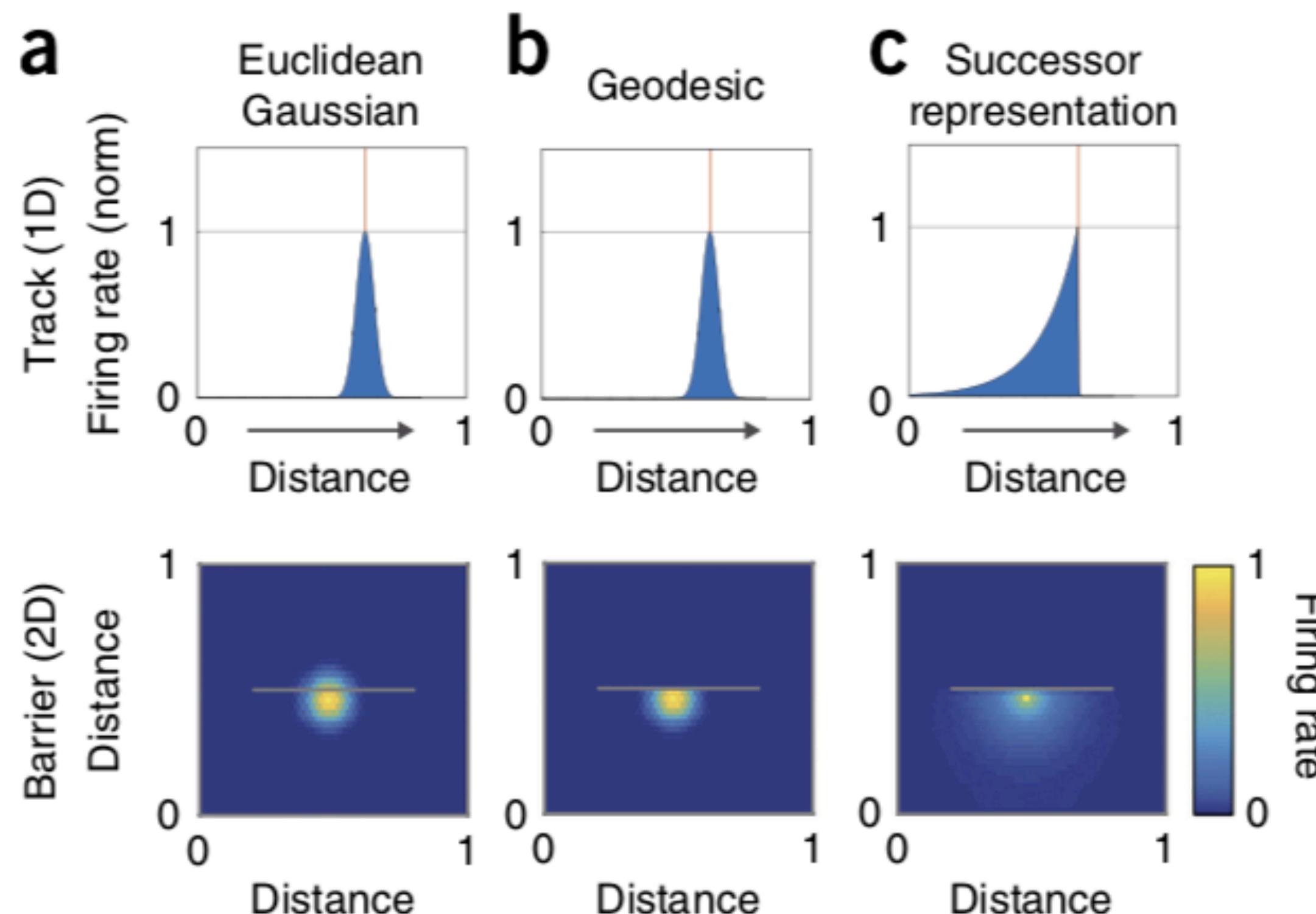


# SR computation

1. Policy optimization
2. Transition matrix computation 
$$T(s, s') = \sum_a \pi(a | s) P(s' | s, a)$$
3. SR could be computed analytically or through online learning using temporal difference update rule

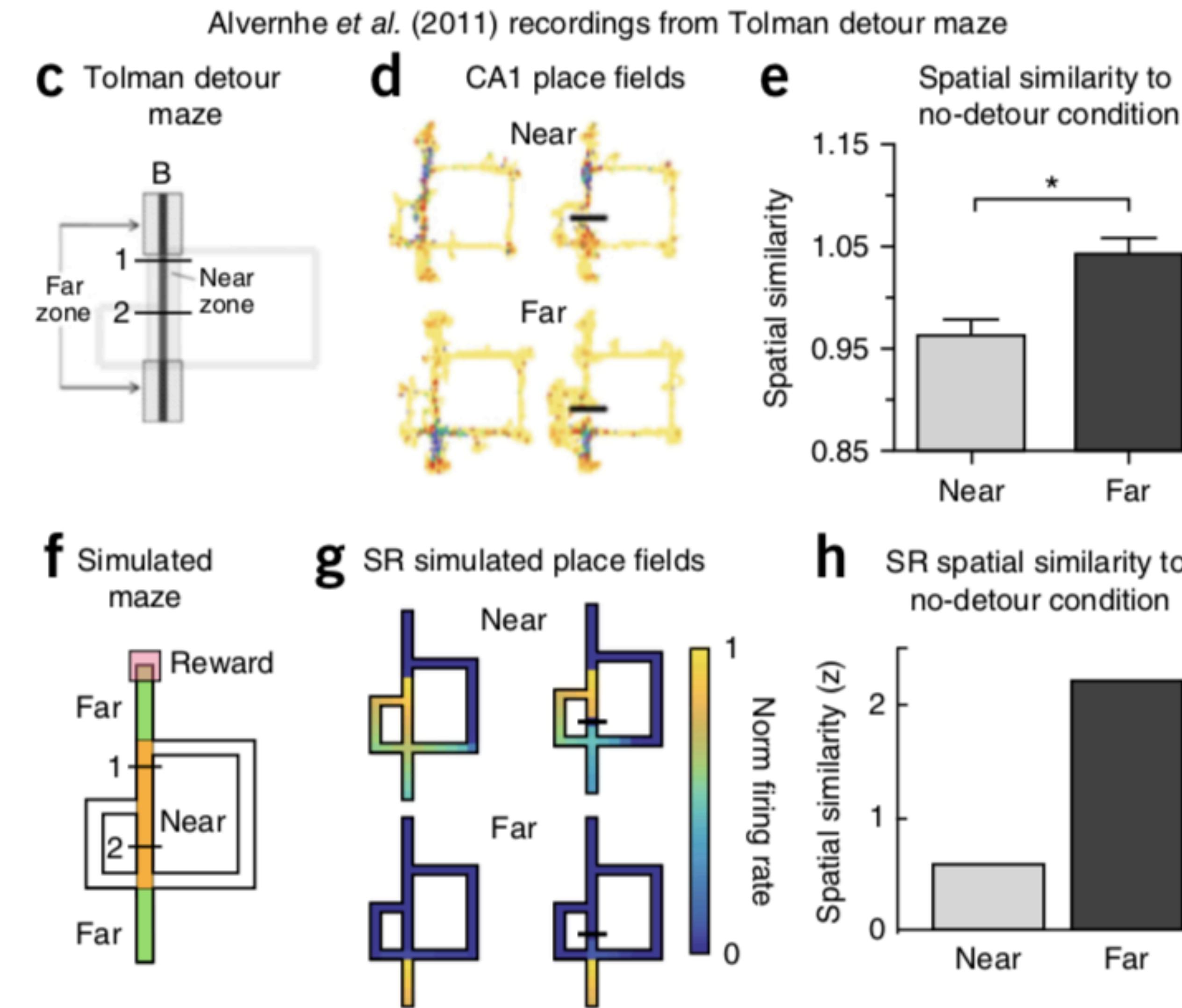
$$M = \sum_{t=0}^{\infty} \gamma^t T^t = (I - \gamma T)^{-1}$$
$$\hat{M}_{t+1}(s_t, s') = \hat{M}_t(s_t, s') + \eta \left[ \mathbb{I}(s_t = s') + \gamma \hat{M}_t(s_{t+1}, s') - \hat{M}_t(s_t, s') \right]$$

# Benchmark with other models



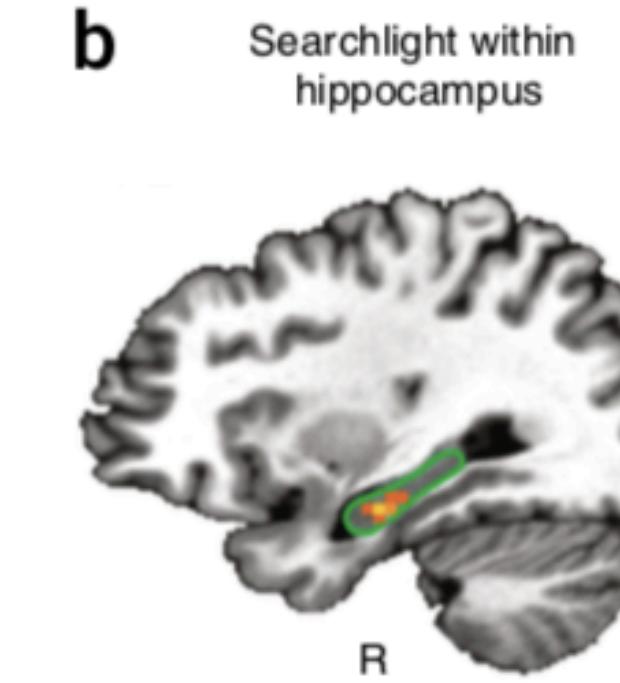
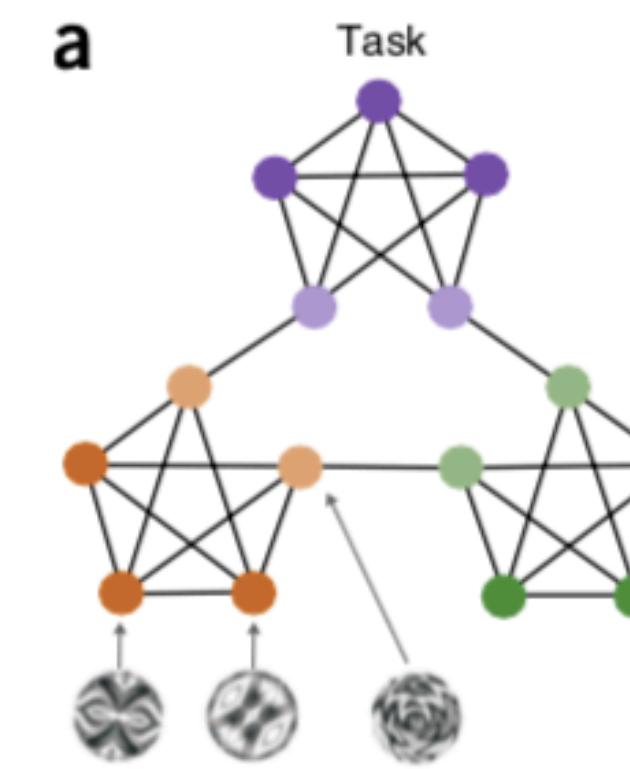
**STDP evolution of asymmetry  
in Euclidean model**

# Policy-dependent place field remapping

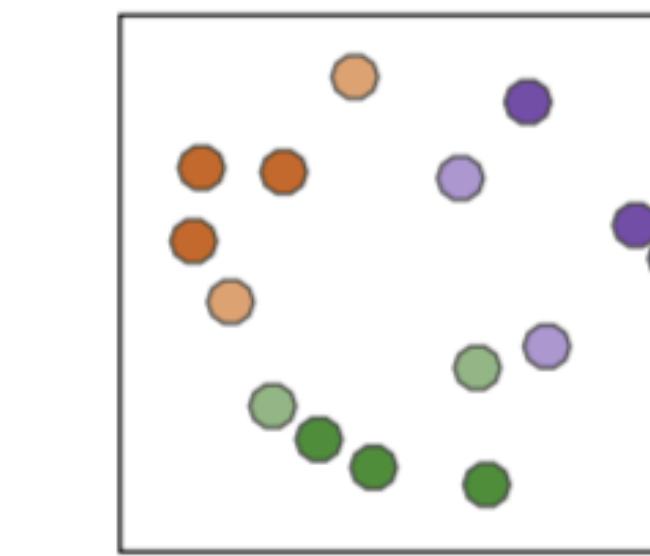


# Hippocampal representation in non-spatial task

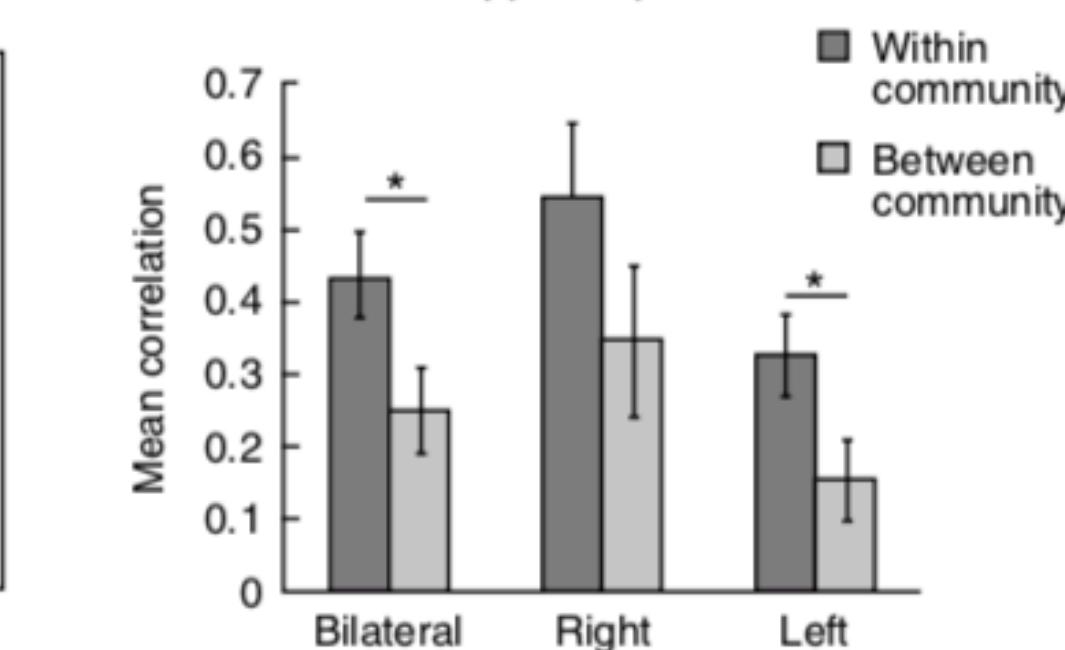
Schapiro et al. (2015)



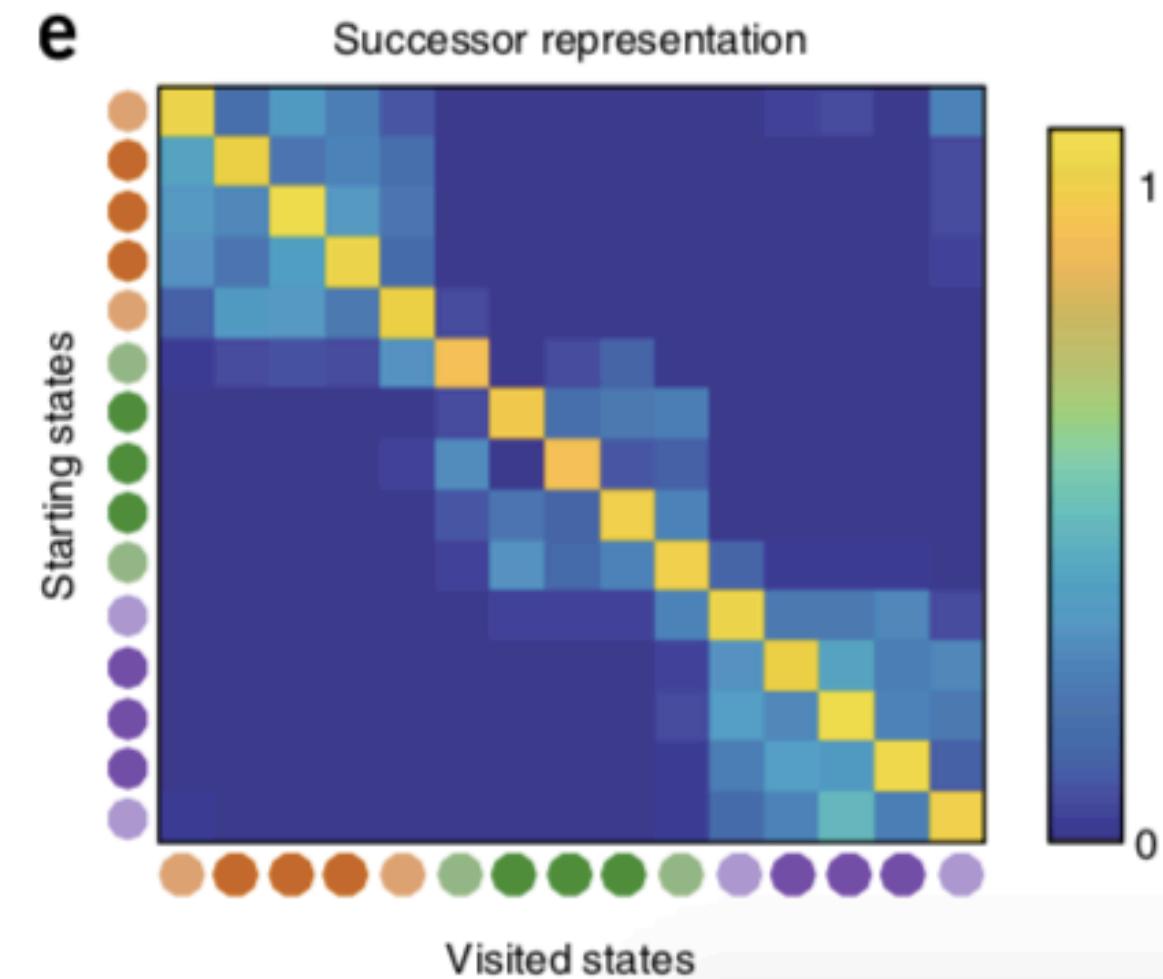
**c** Bilateral hippocampus MDS



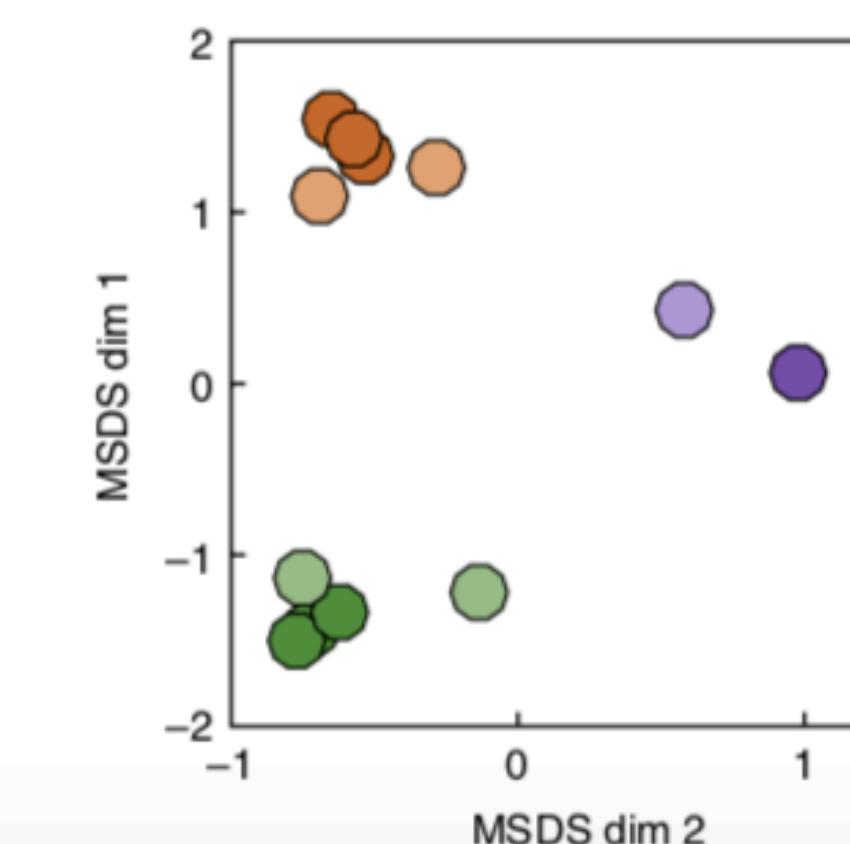
**d** Pattern analysis across hippocampus



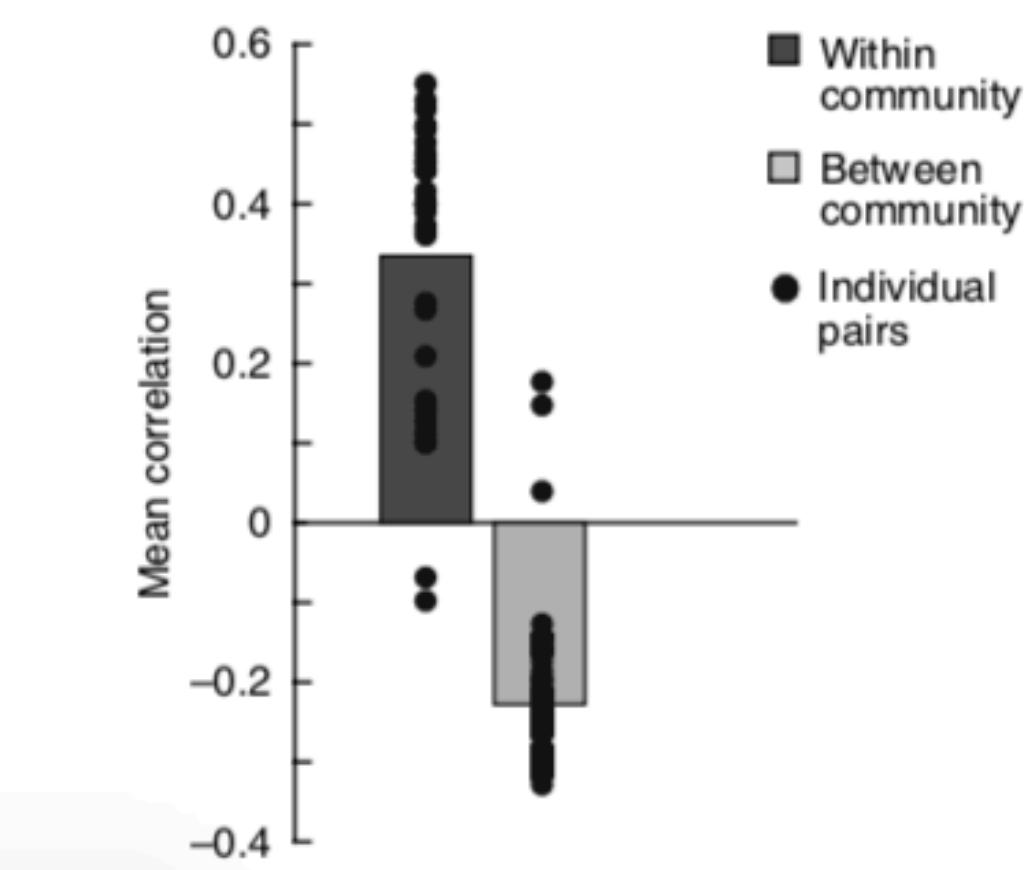
SR Simulations



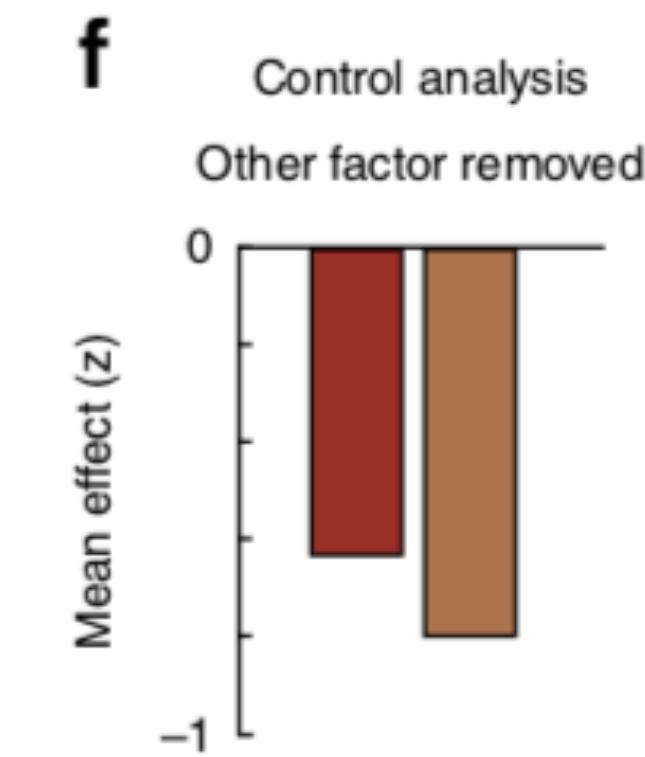
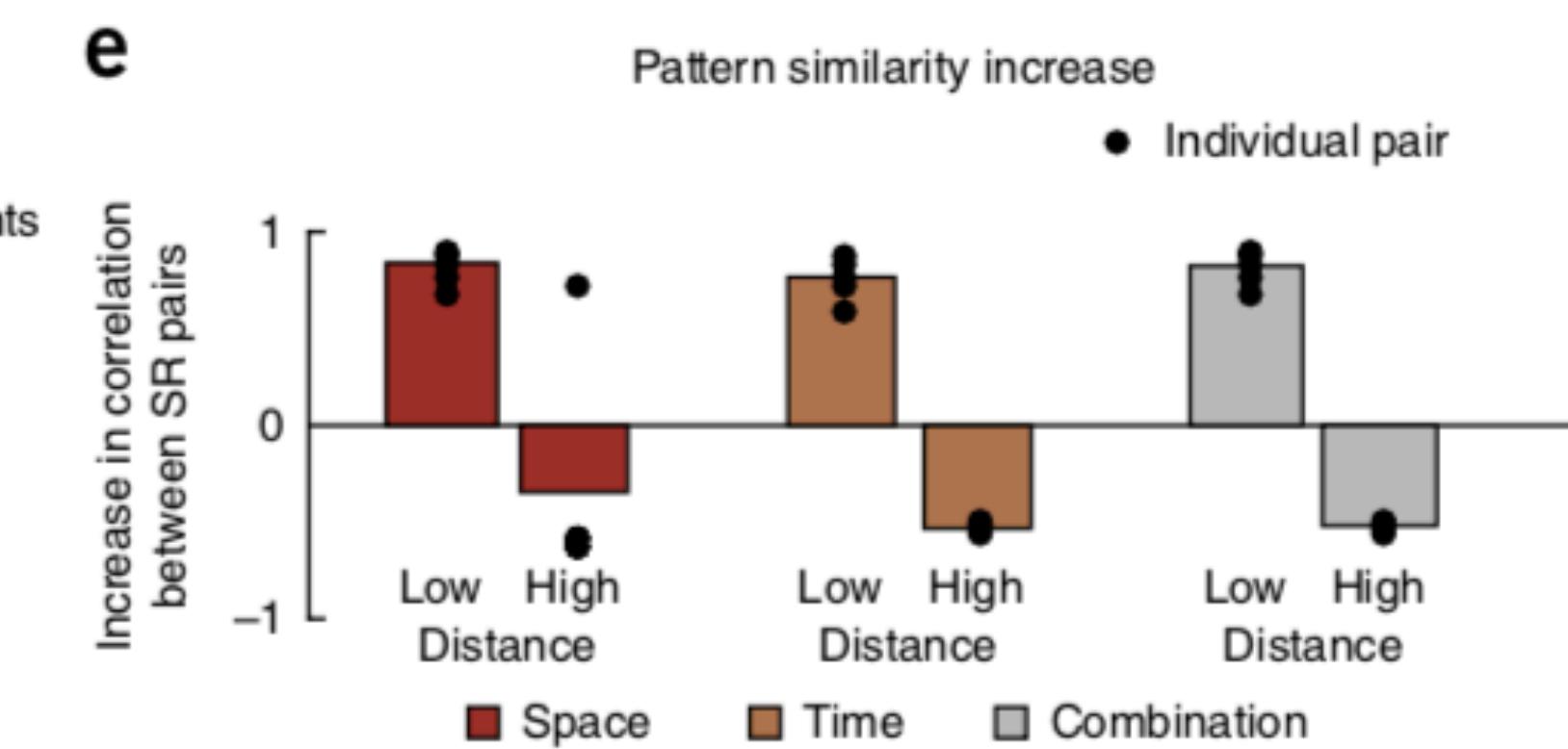
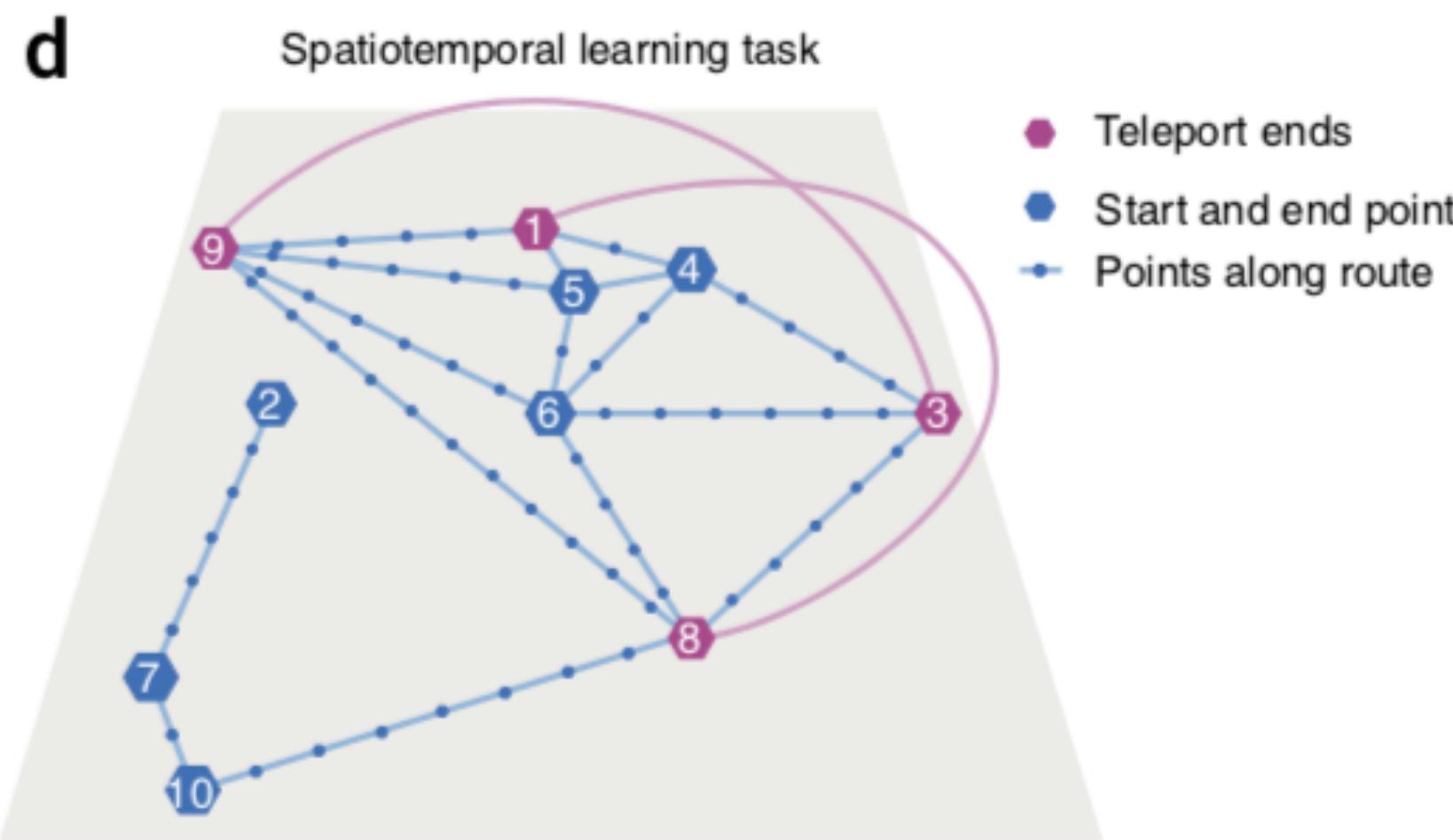
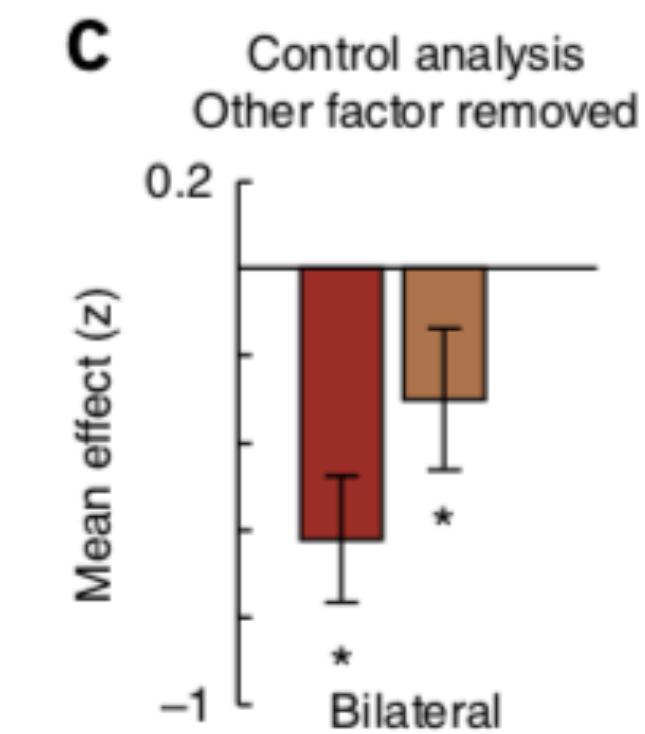
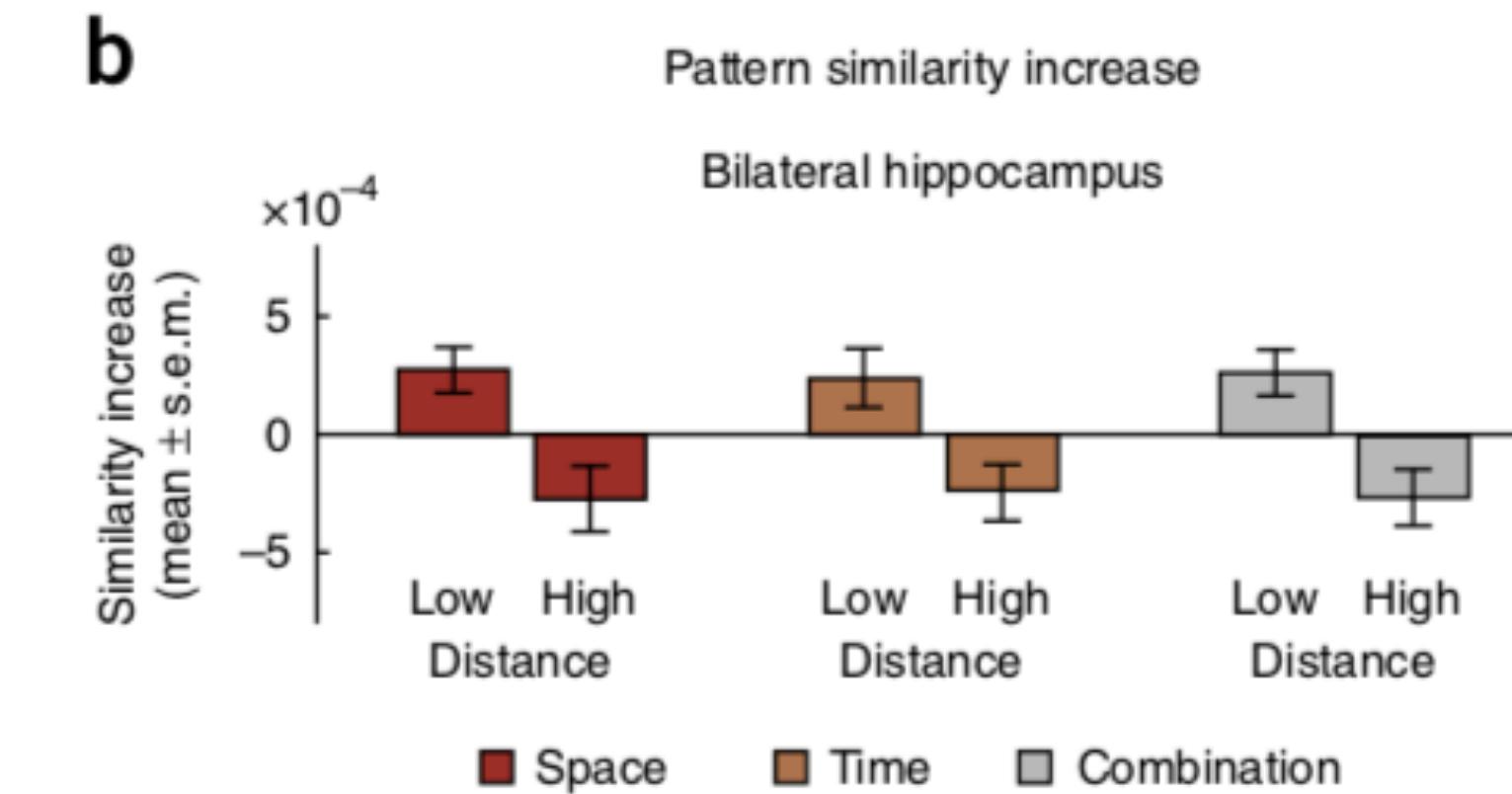
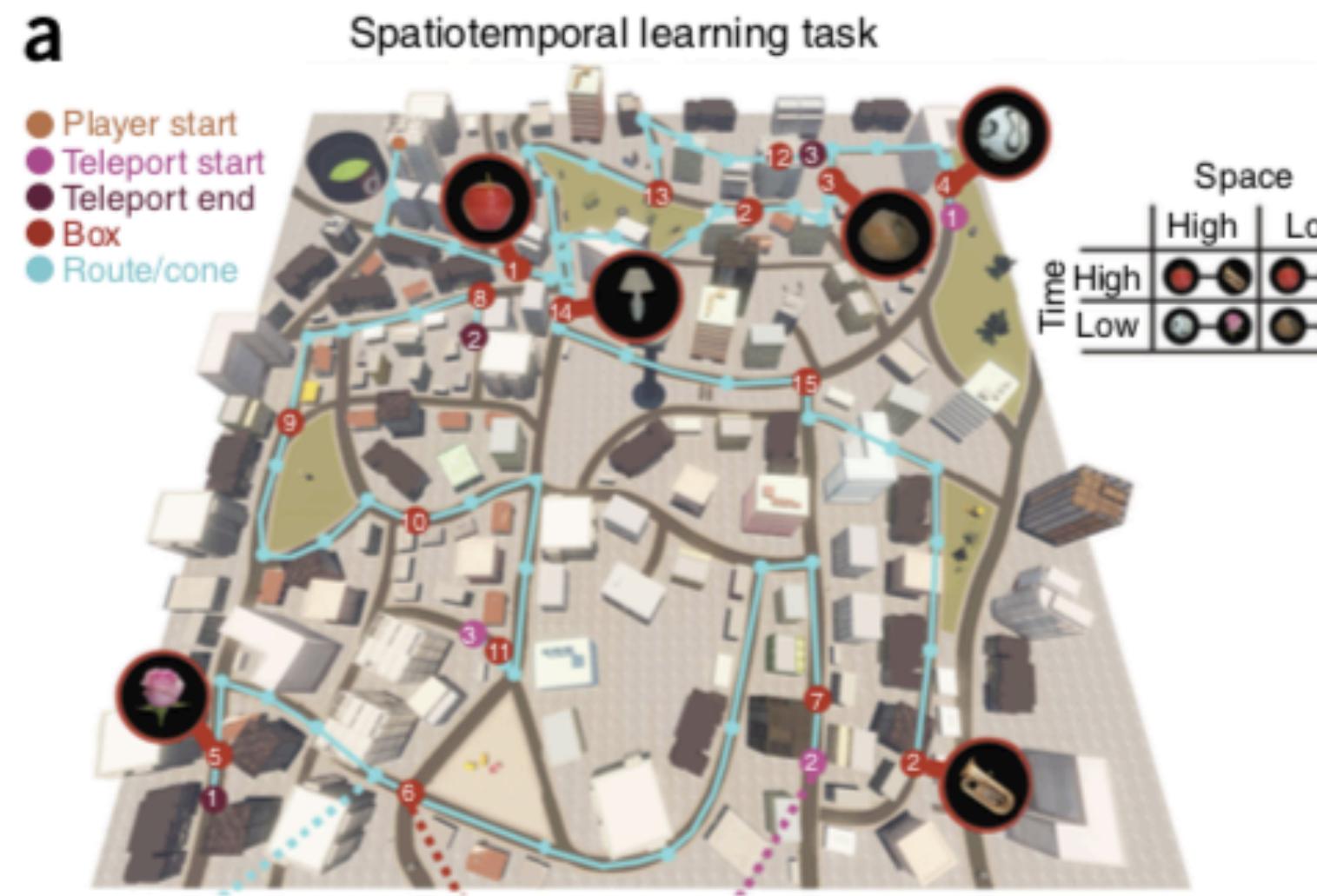
**f** Successor representation MDS



**g** SR similarity analysis

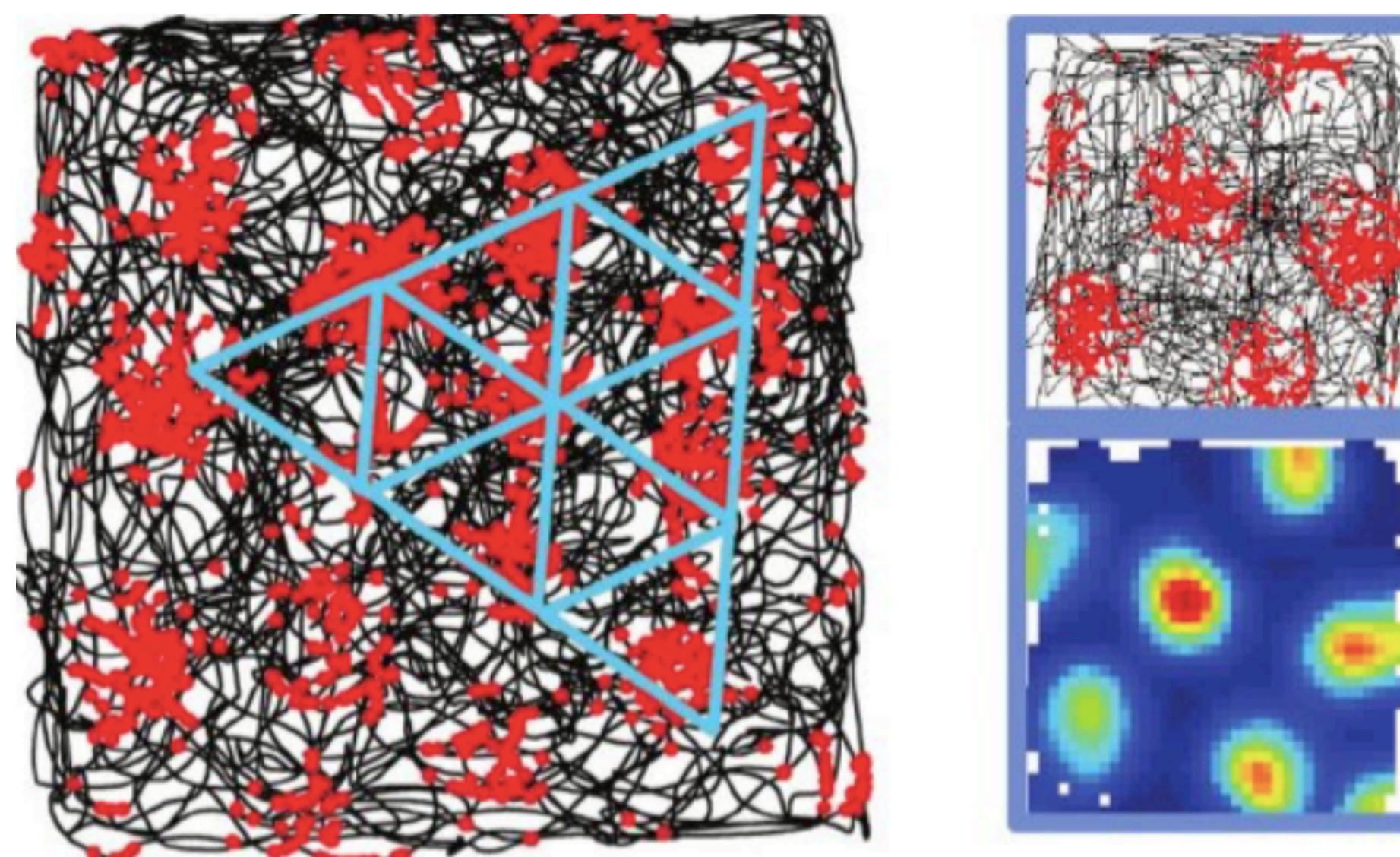


# In a spatiotemporal task



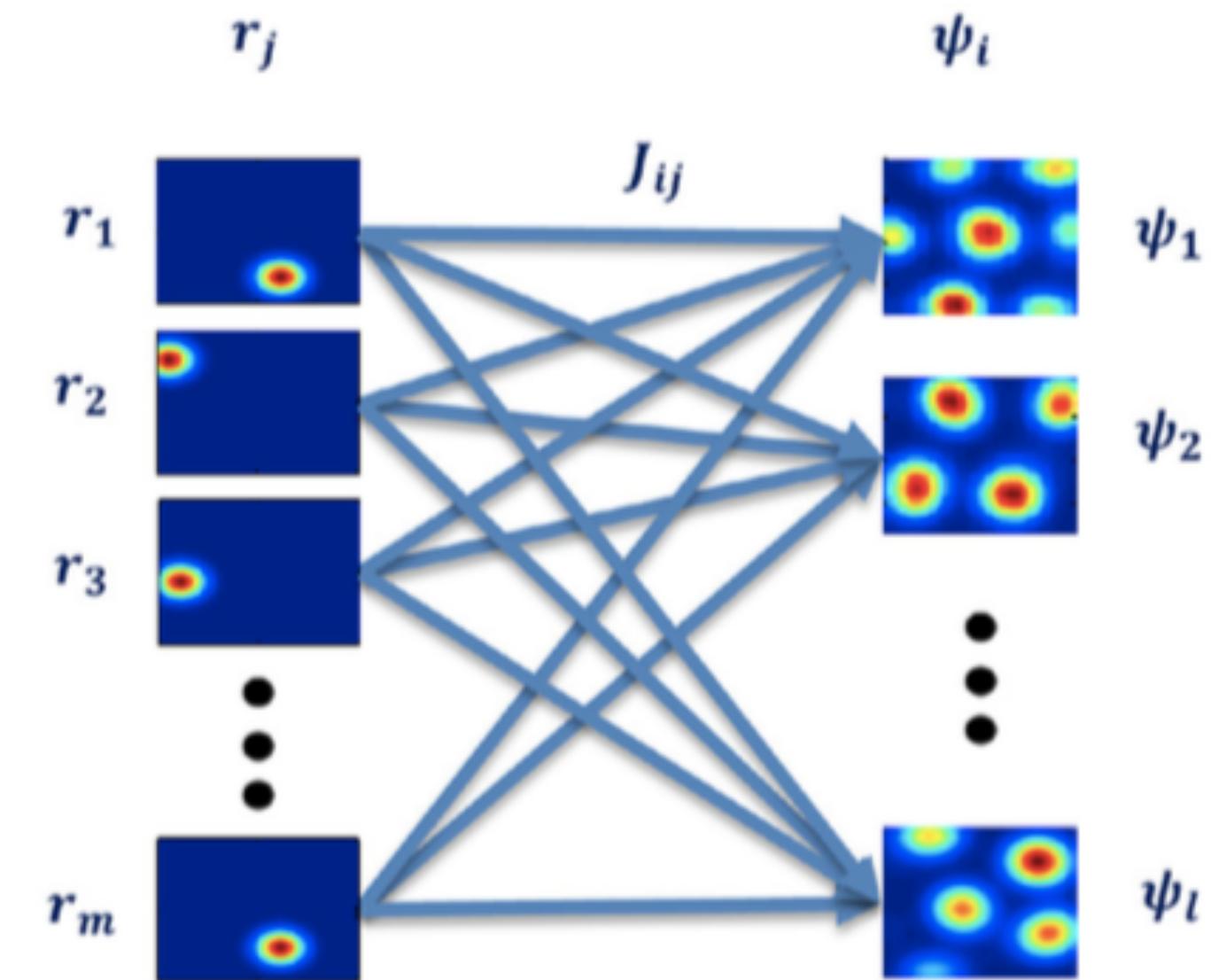
# Grid cell representation

## Entorhinal-hippocampal spatial circuit



- Allocentric grid cell: based on spatial relationships
- Idiothetic place cell: relative location from an arbitrary reference point
- Egocentric head direction cell: relative to body part axis

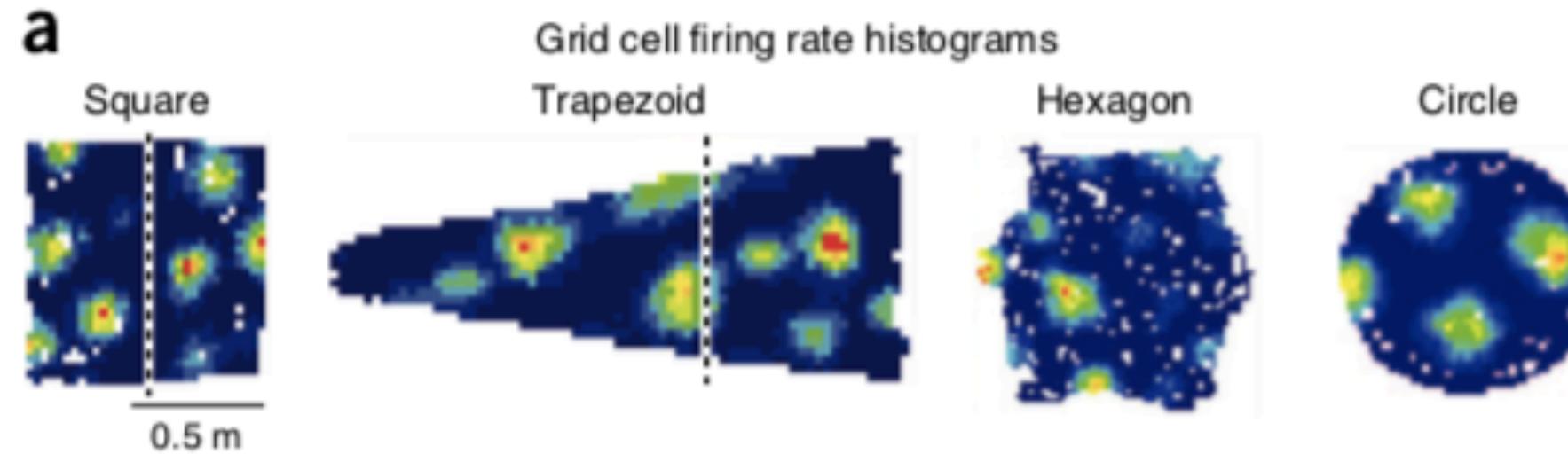
## Theoretical model: from place cell to grid cell



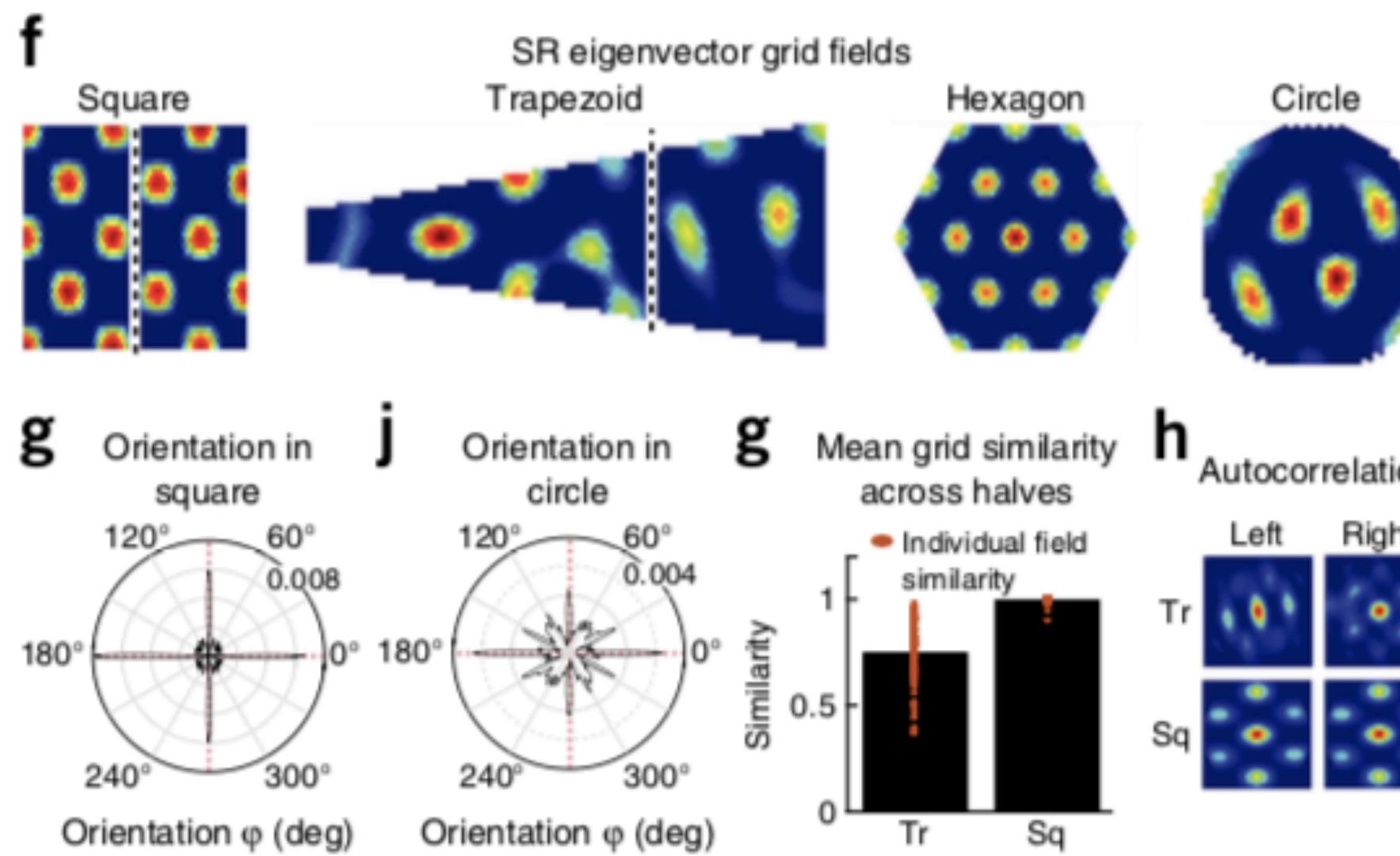
- Feedforward network with generalized Hebbian learning (PCA)
- Grid pattern is the eigenvector of place cell patterns

# Boundary sensitivity and effect of fragmentation

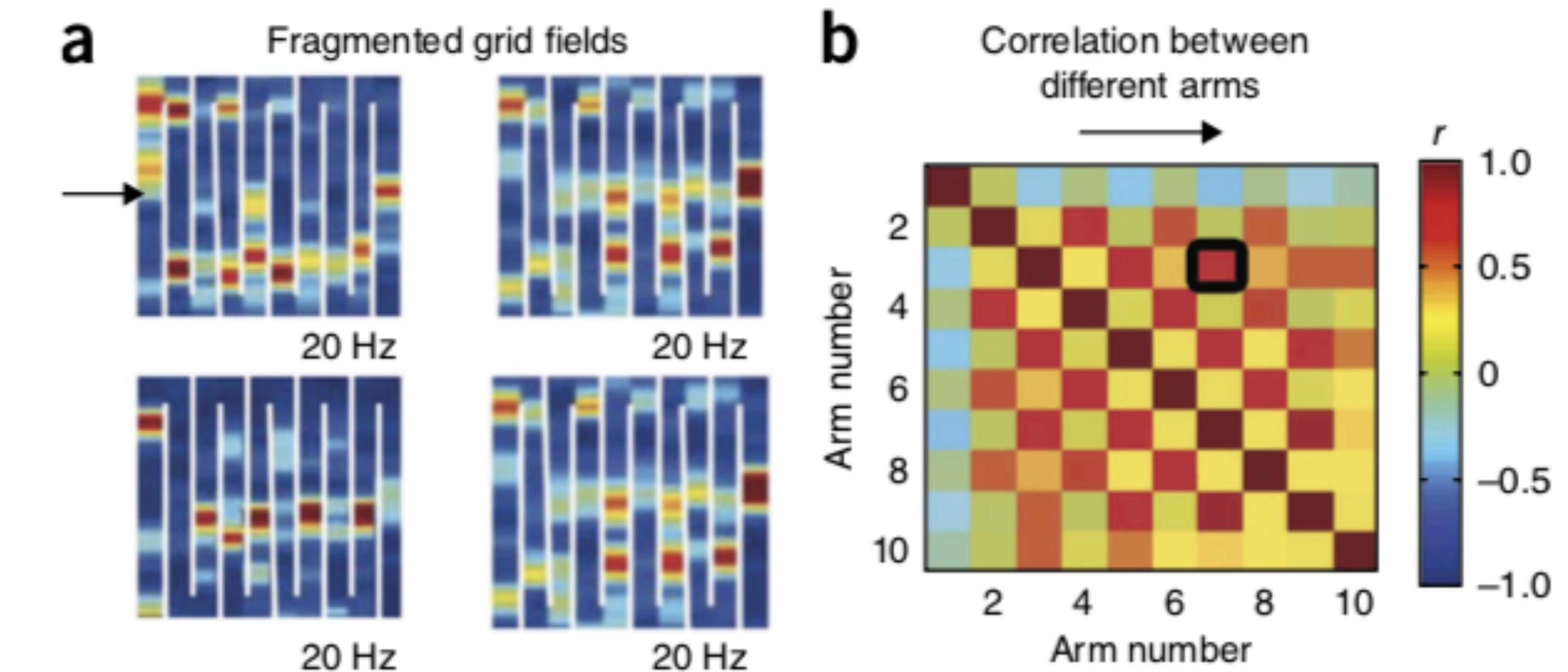
Krupic et al. (2015) Effects of environmental geometries



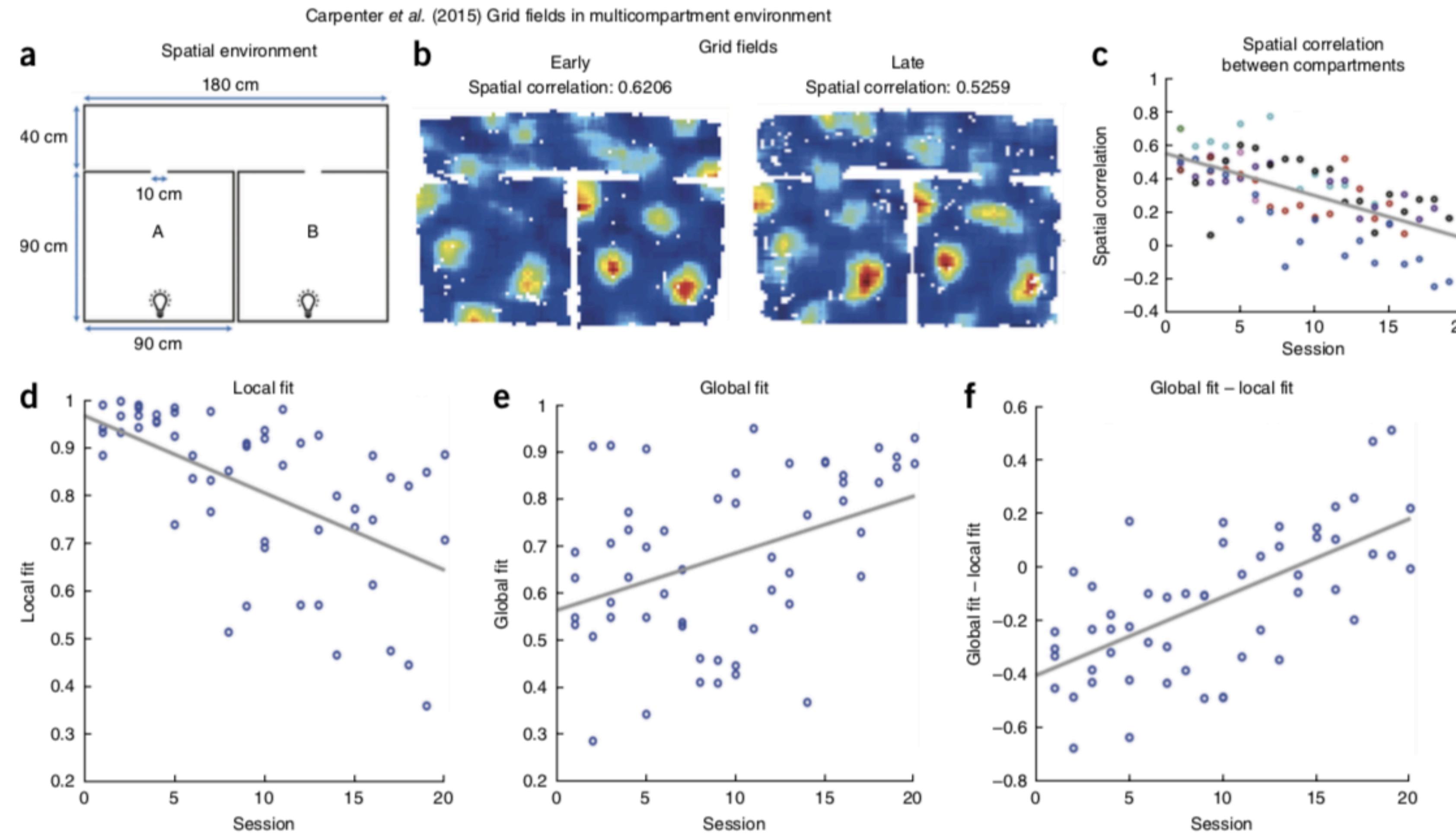
Effects of environmental geometries on SR eigenvectors



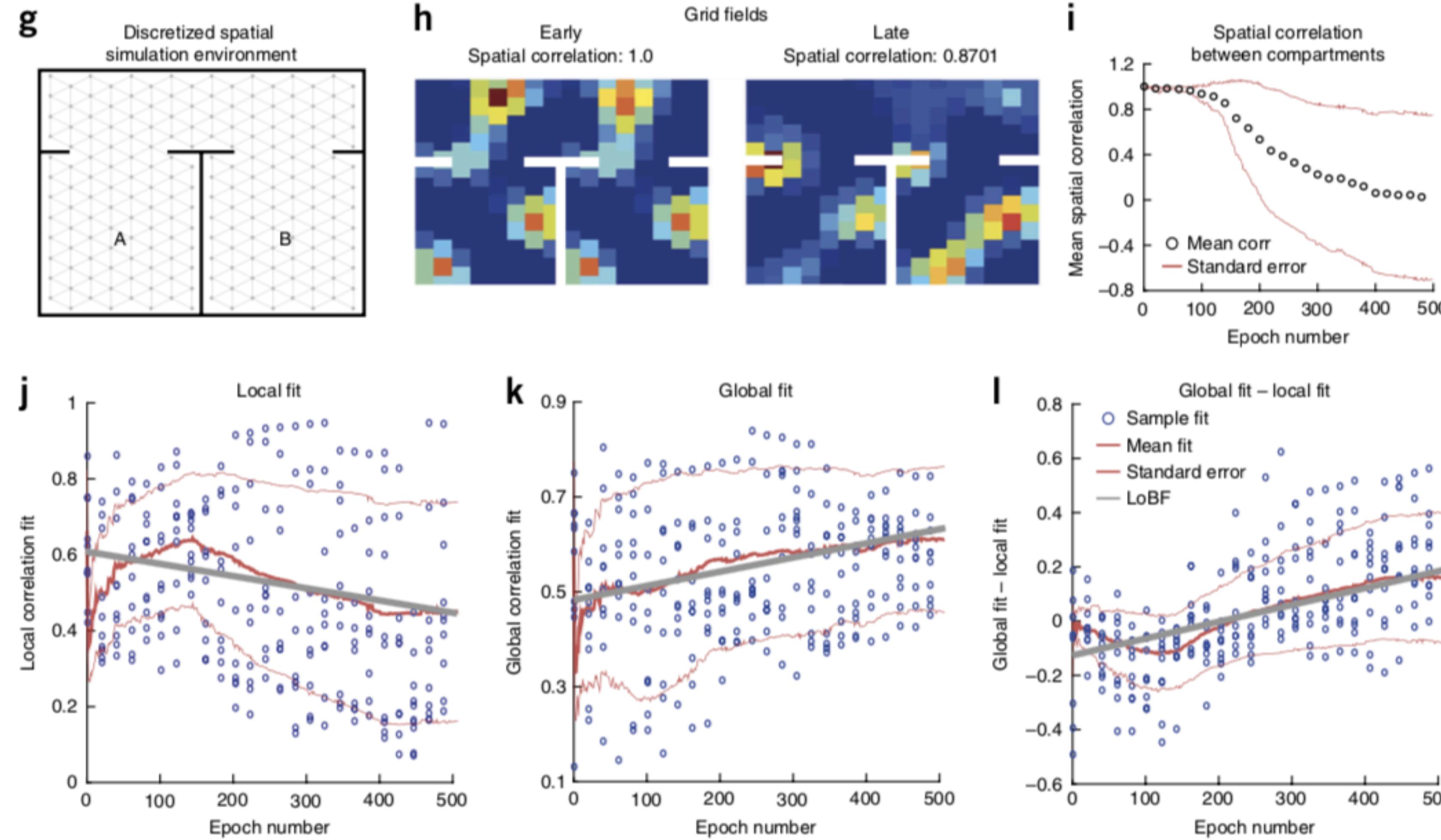
Derdikman et al. (2009) Hairpin maze



# Simulation of spatial learning

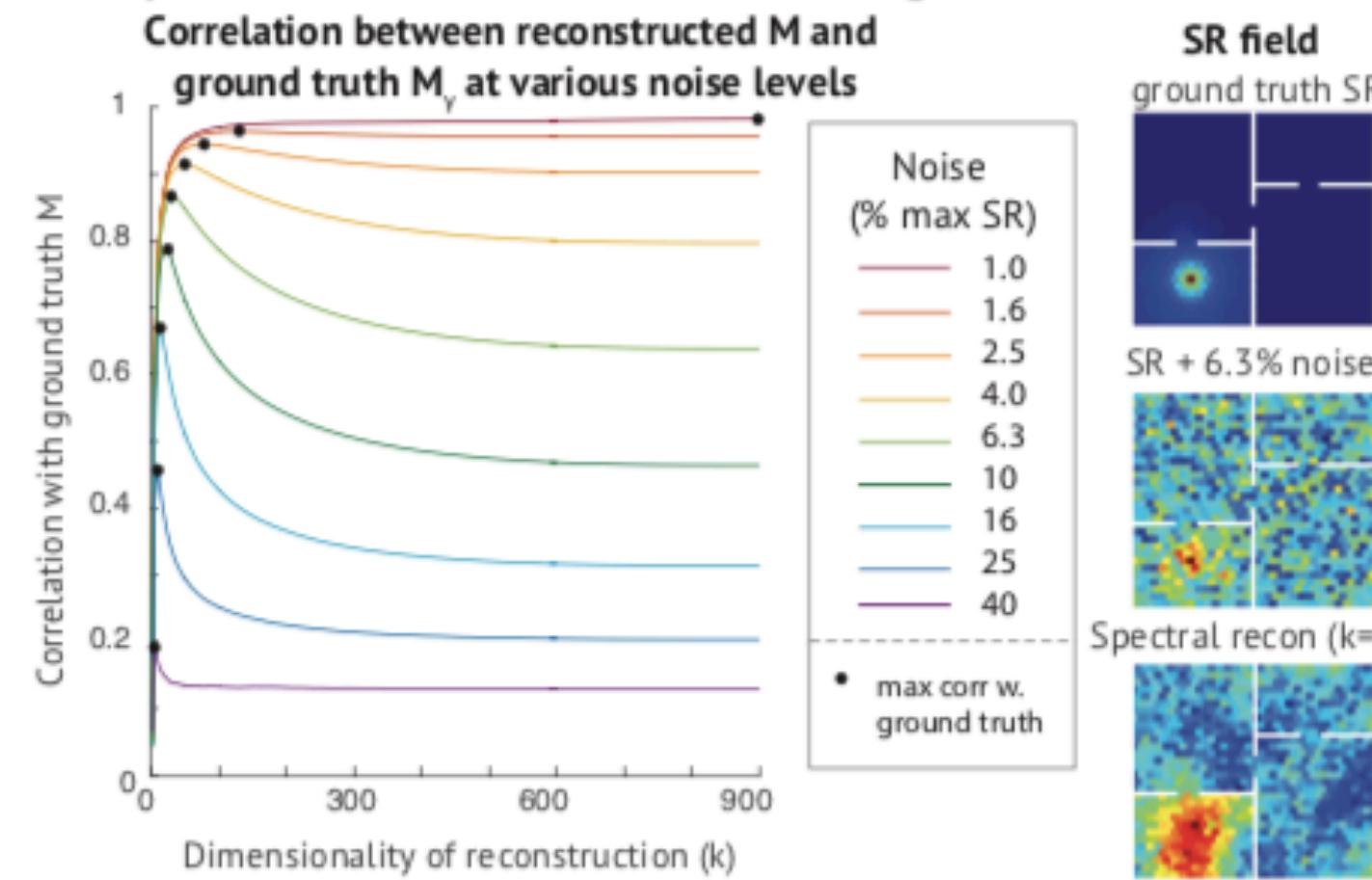


Eigenvector grid fields learned in multicompartiment environment

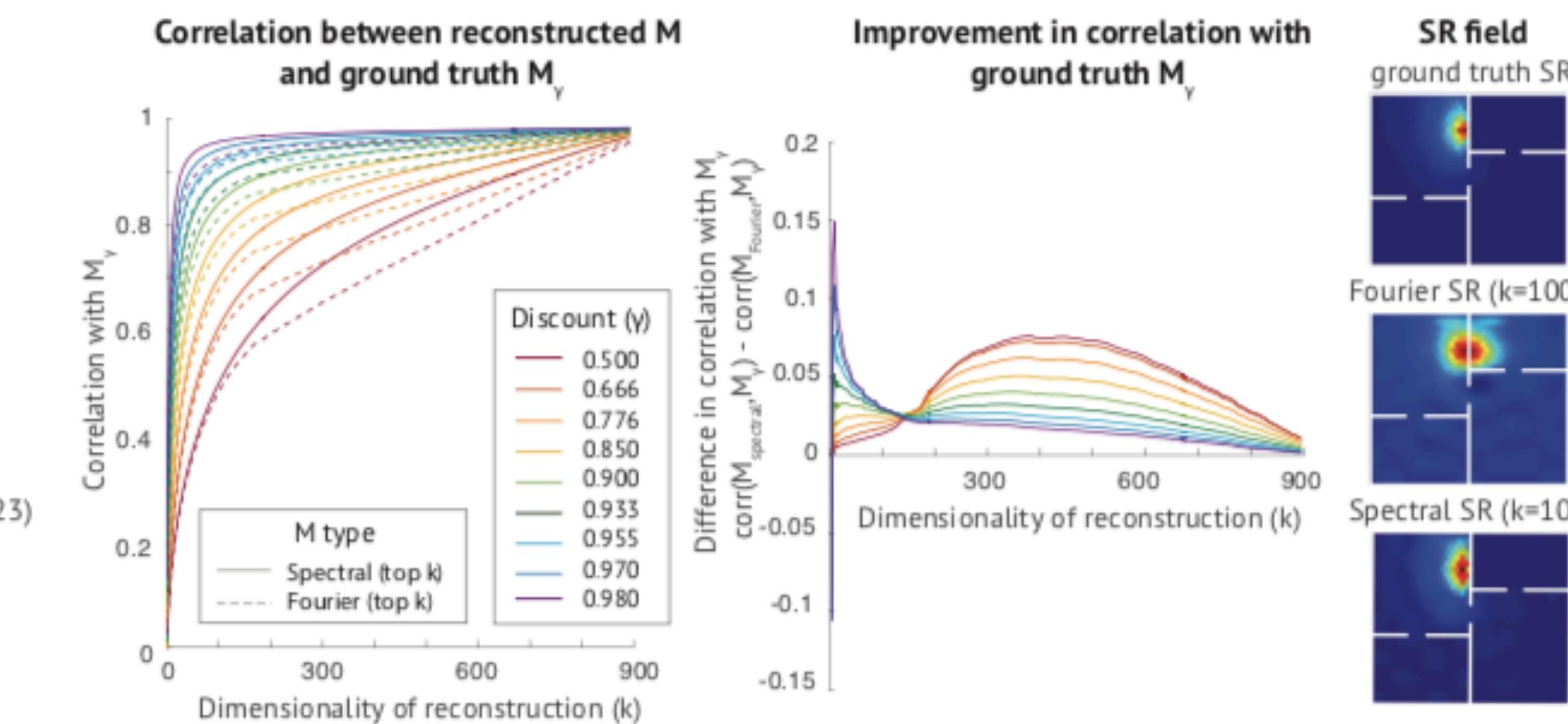


# De-noised reconstruction from grid cells

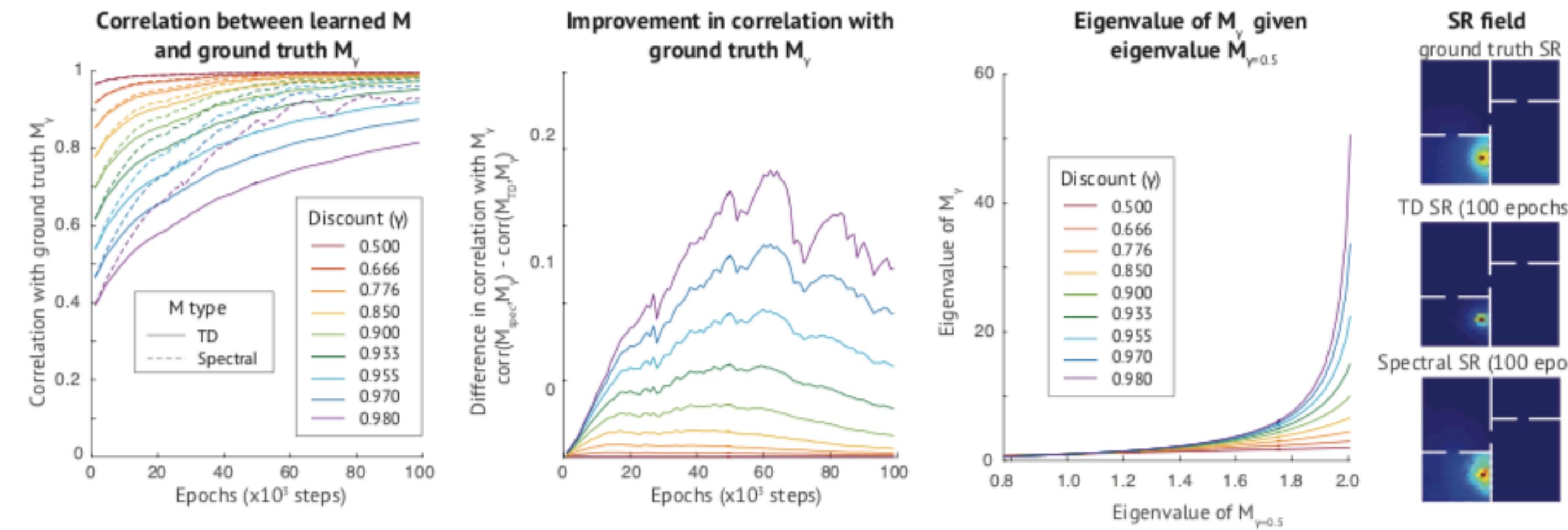
**A Spectral reconstruction for denoising**



**B Spectral improvement over Fourier for SR reconstruction**

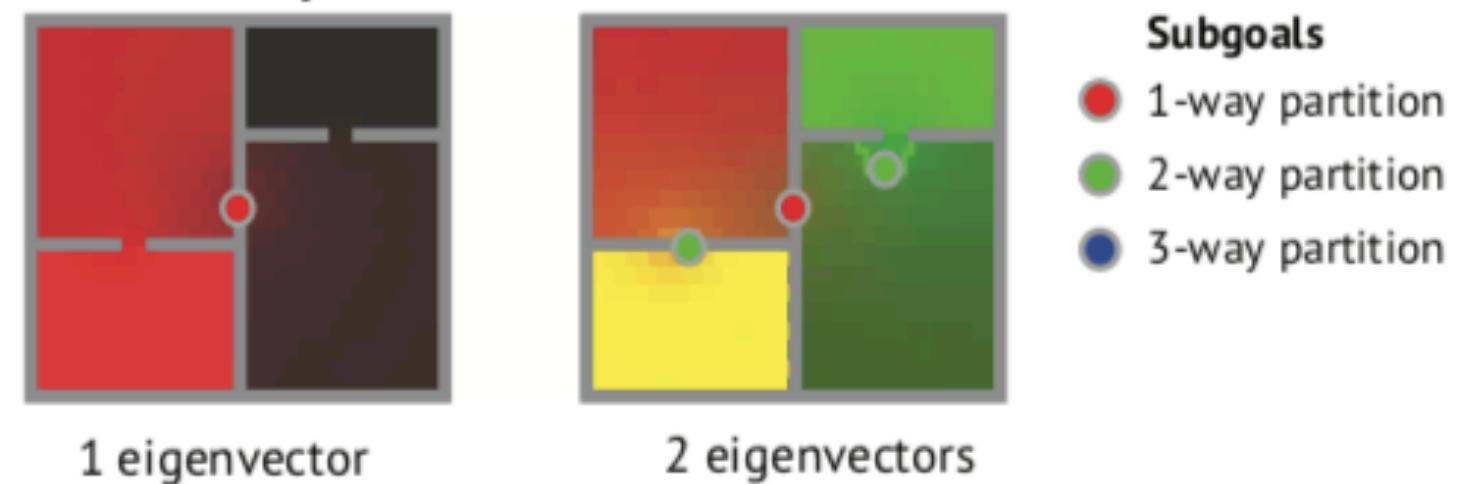


**C Spectral approximation converges faster than pure TD for SRs with large discounts**

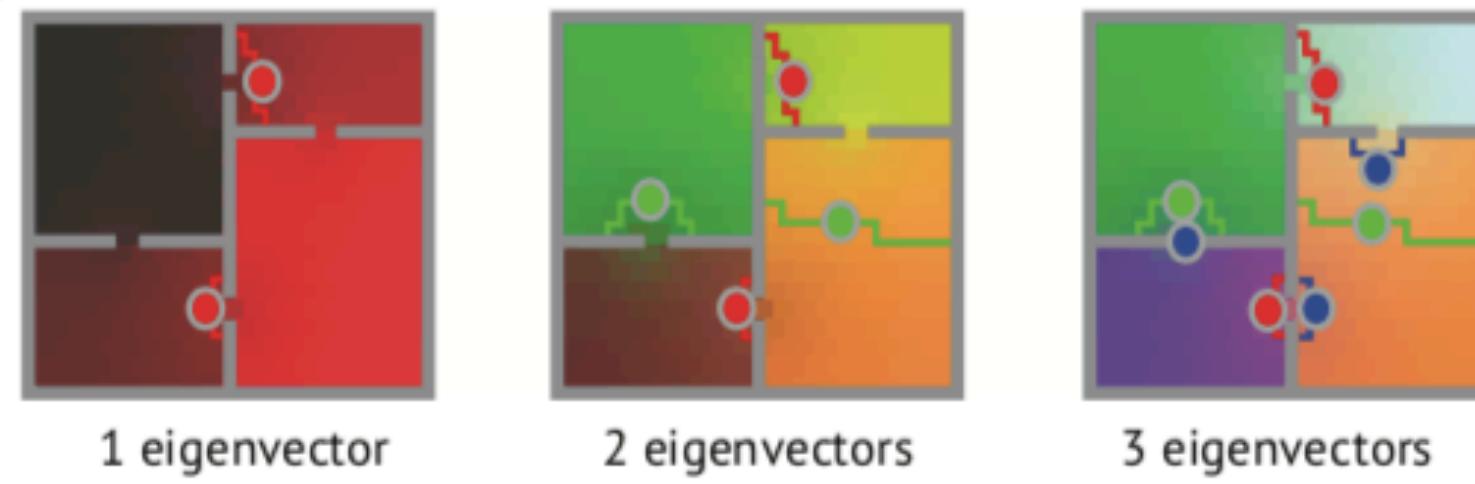


# Hierarchical planning

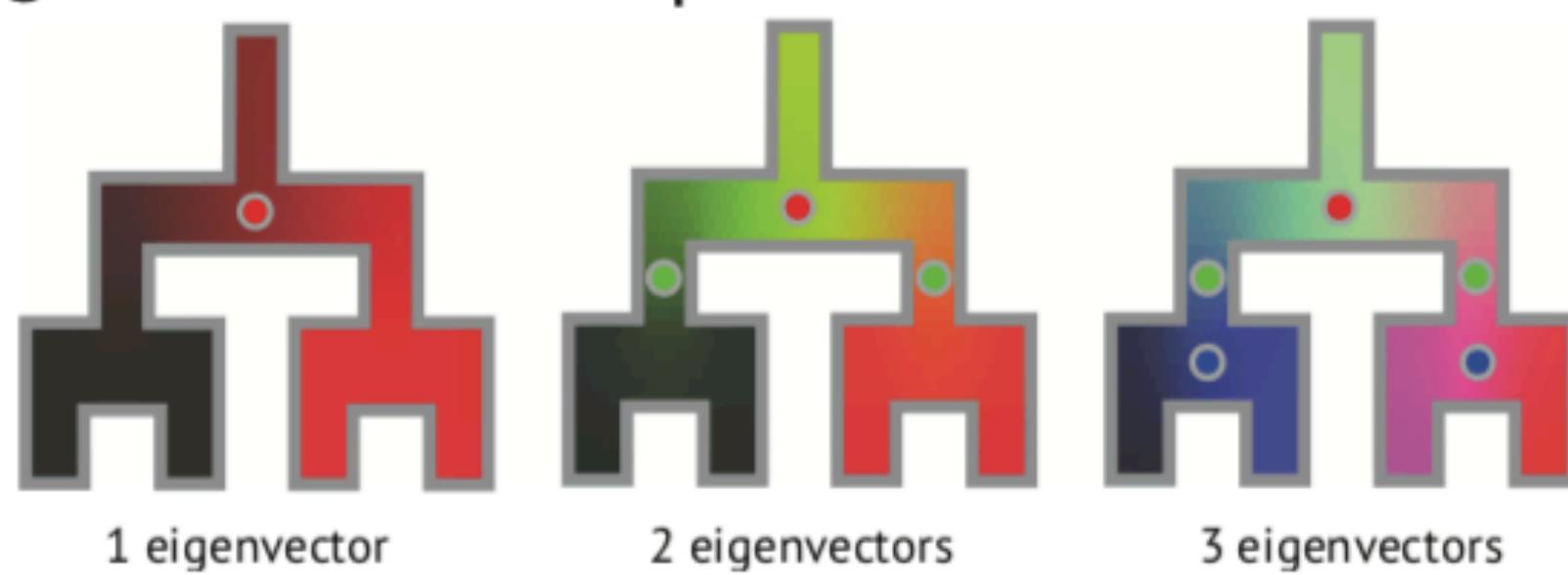
**A Multi-compartment environment I**



**B Multi-compartment environment II**

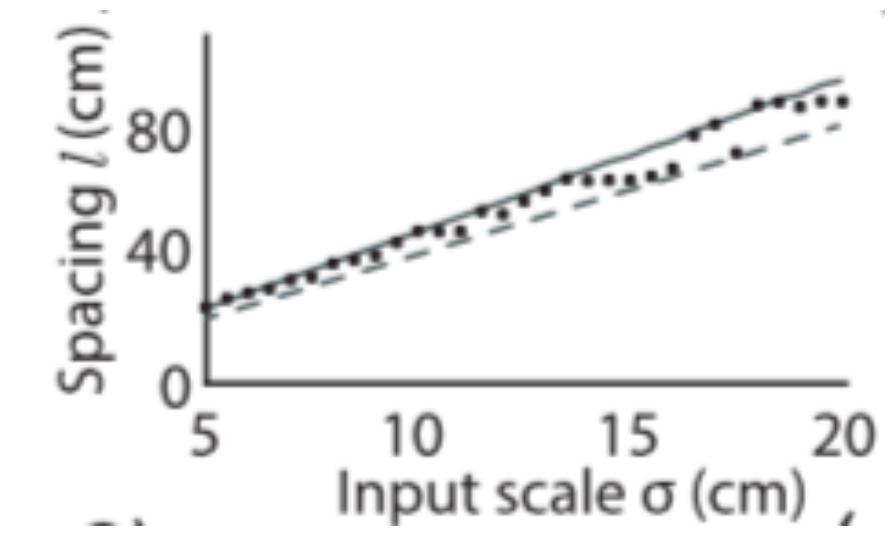


**C Normalized cuts on 2-step tree maze**



# Furthermore

- Phase precession (Drieu\_Science\_2018)
- Size of place field and grids (Mercado\_PRL\_2017)
- Navigation system (Banino\_Nature\_2018)



# Hippocampus-based navigation system

- RL framework
- Vector-based navigation

