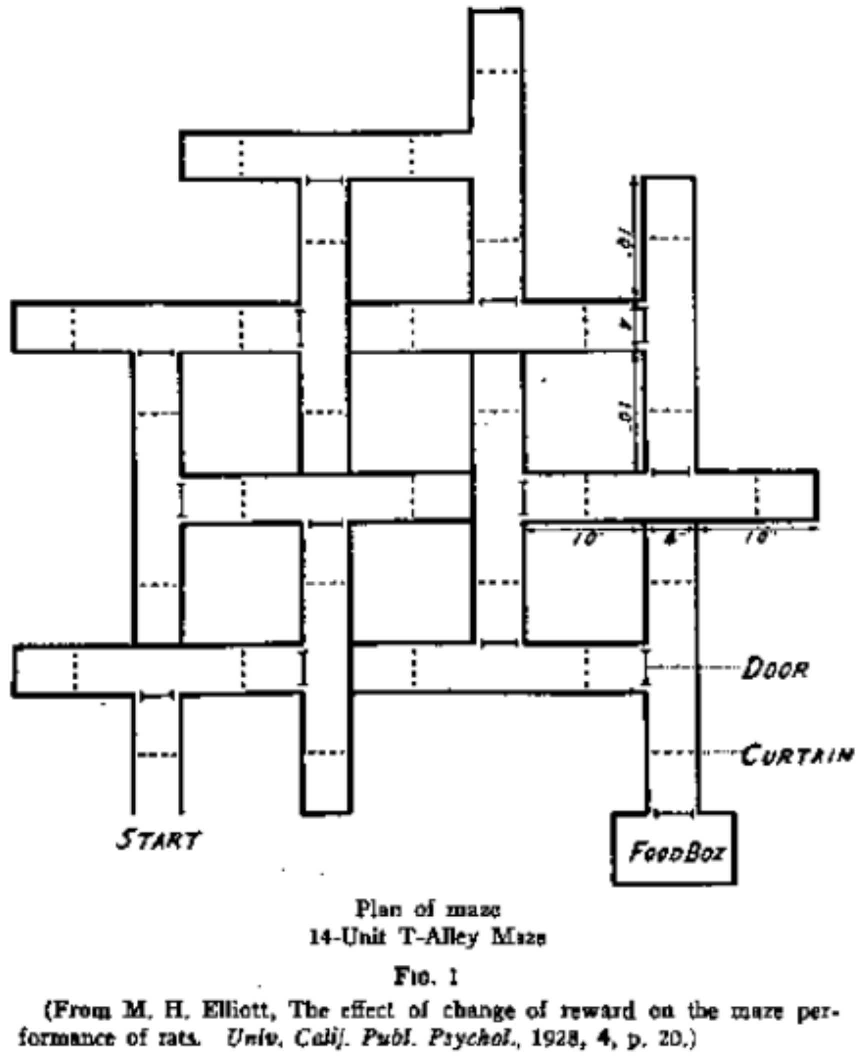
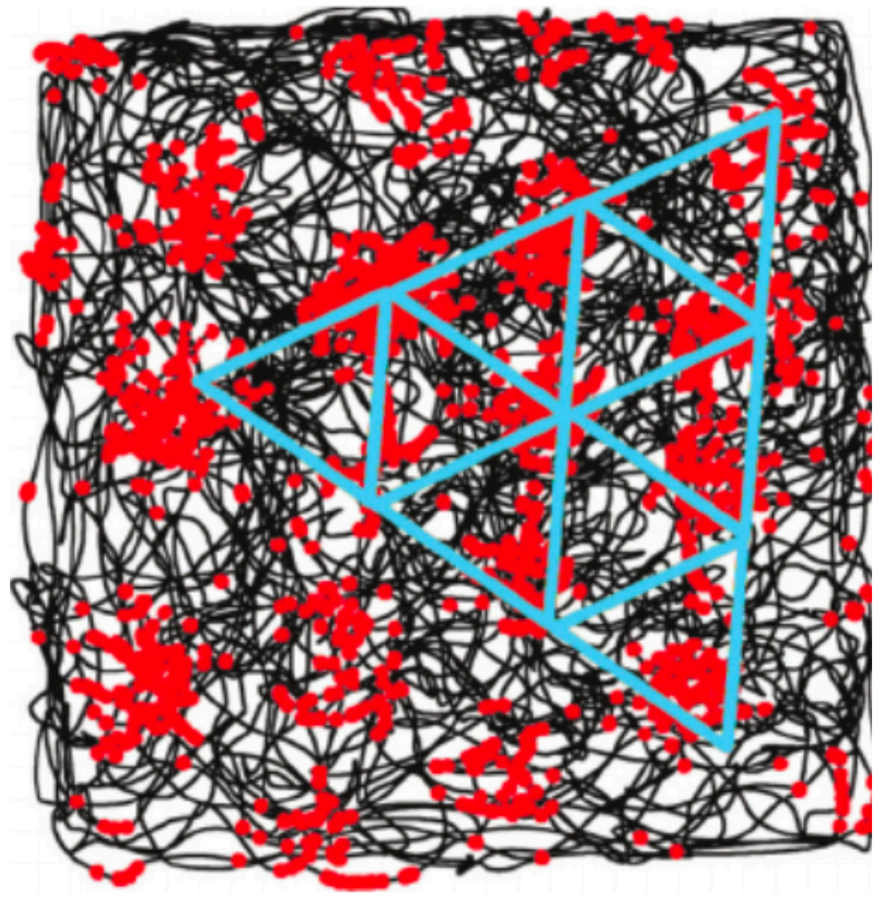




What is a cognitive map?
An overview of modern neuroscientific discoveries

Cognitive Maps Seminar
26th of October 2022

https://hmc-lab.com/Cogmaps.html

Overview

1. Admin recap, overview papers
    - Note: it is not mandatory to make an informed choice :)

2. *The cognitive map in humans: spatial navigation and beyond*
    - Focus on concepts, not details

3. [Additional important findings: cognitive maps beyond physical space]

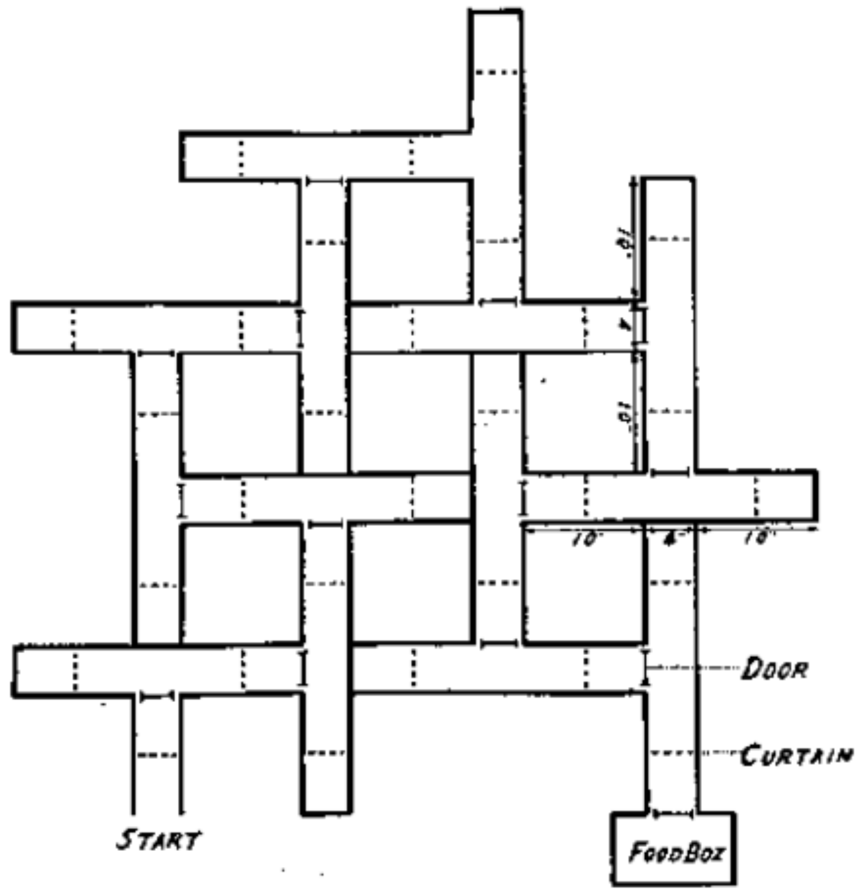
1. Admin and Key Papers

Admin Recap

- [Required] Attendance of at least 80% of sessions
- [30% of grade] Submit 1 engaging discussion question prior to every paper session
  - 16. November onwards
- [70% of grade] Give one presentation (90-minute session with discussion) on a relevant paper of your choice
  - In a group of 2-3 students
  - List: https://docs.google.com/spreadsheets

So, what do you think is a cognitive map?

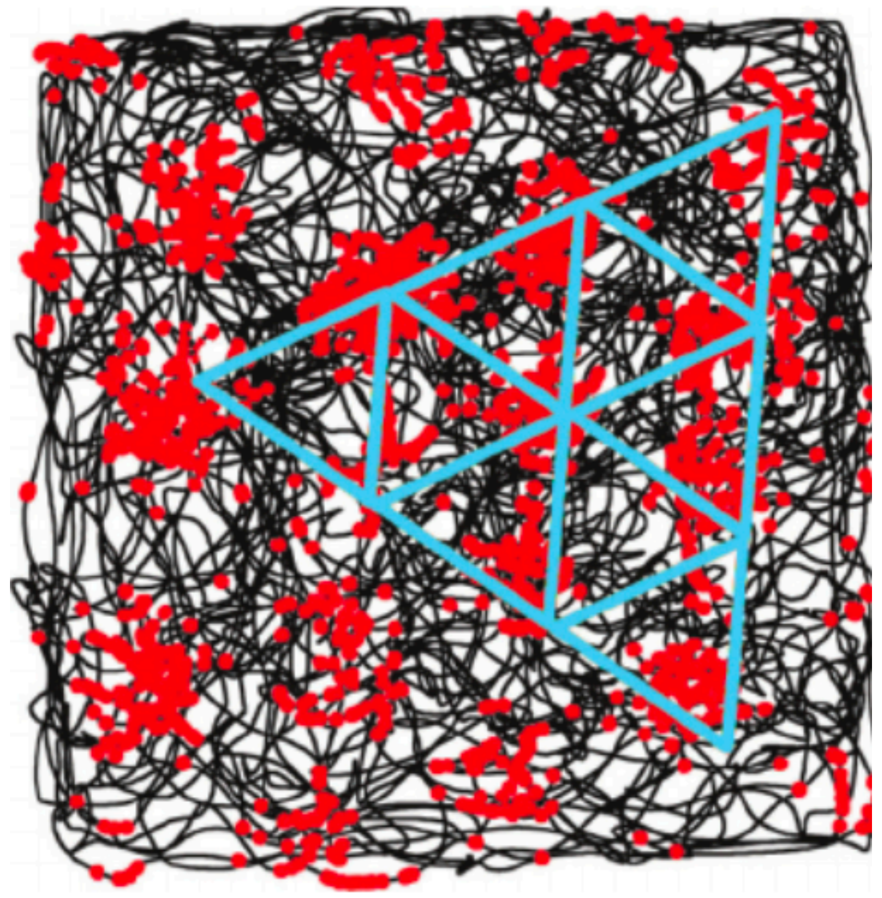
And how was the cognitive map apparent in the experiments from last week?



Plan of maze
14-Unit T-Alley Maze

FIG. 1

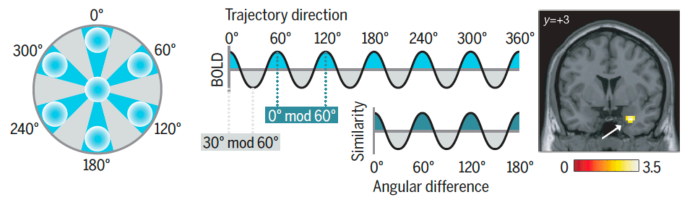
(From M. H. Elliott, The effect of change of reward on the maze performance of rats. *Univ. Calif. Publ. Psychol.*, 1928, 4, p. 20.)



Quick overview papers I

Cognitive maps for abstraction and values

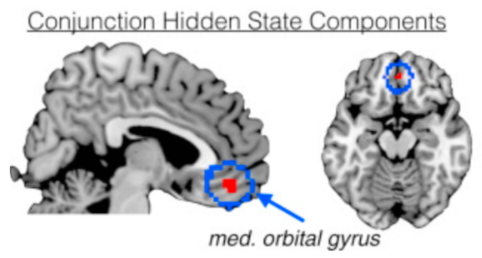
Navigating Cognition: Spatial Codes for Human Thinking

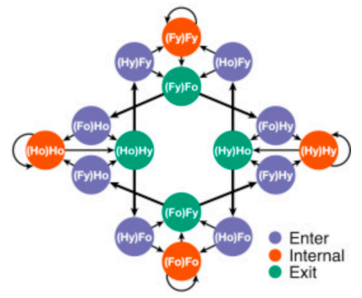


Jacob L.S. Bellmund[1,2,3*], Peter Gärdenfors[4,5], Edvard I. Moser[1], Christian F. Doeller[1,3*]

How can spatial maps afford general **cognition**?
Review - Theory - Experiment

Human Orbitofrontal Cortex Represents a Cognitive Map of State Space

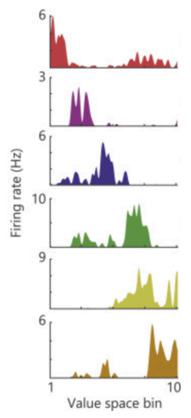




Nicolas W. Schuck[1, 3], Ming Bo Cai[1], Robert C. Wilson[2], Yael Niv[1]

Representing **task space** in reinforcement learning using cognitive maps
Review - Theory - **Experiment (fMRI)**

Hippocampal neurons construct a map of an abstract value space



Eric B. Knudsen[1, 3], Joni D. Wallis[1, 2]

Representing **values** in reinforcement learning using cognitive maps
Review - Theory - **Experiment (neuronal recordings)**

A map of abstract relational knowledge in the human hippocampal–entorhinal cortex

Mona M Garvert,[1,2,*] Raymond J Dolan,[1,3] and Timothy EJ Behrens[1,2]

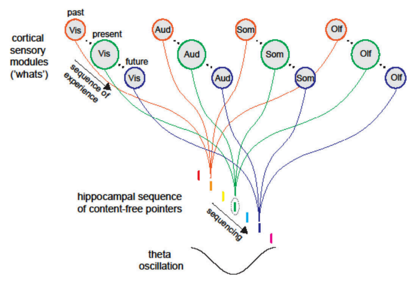
Conceptual (non-spatial) cognitive maps in humans
Review - Theory - **Experiment (fMRI)**

Quick overview papers II

The neural substrate of cognitive maps

Space and time: The hippocampus as a sequence generator

György Buzsáki[1,2,3,4] and David Tingley[1]

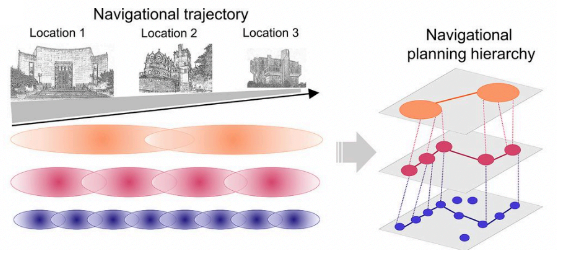


Space and time = sequence generation in hippocampus
Review (neuro) - Theory - Experiment

Predictive Representations in Hippocampal and Prefrontal Hierarchies

Iva K. Brunec and Ida Momennejad

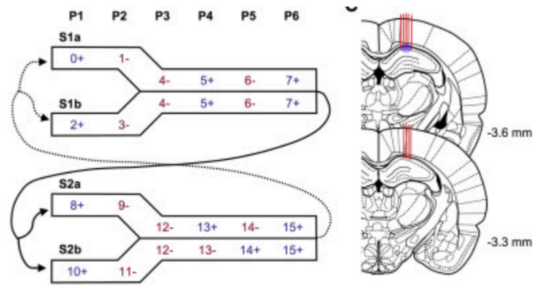
Journal of Neuroscience 12 January 2022, 42 (2) 299-312; DOI: https://doi.org/10.1523/JNEUROSCI.1327-21.2021



Hierarchical (multiscale) planning using cognitive maps
Review - **Theory** - **Experiment (fMRI)**

Complementary Task Structure Representations in Hippocampus and Orbitofrontal Cortex during an Odor Sequence Task

Jingfeng Zhou[1], Marlian Montesinos-Cartagena[1], Andrew M. Wikenheiser[1], Matthew P.H. Gardner[1], Yael Niv[2], Geoffrey Schoenbaum[1, 3, 4, 5]



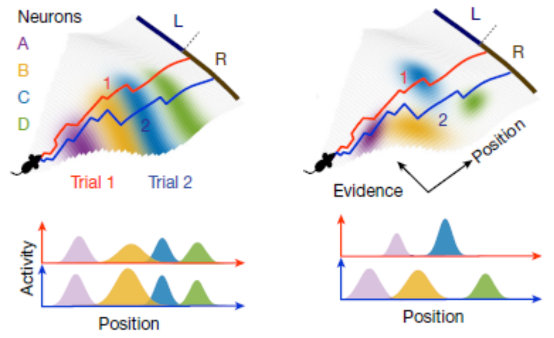
State-of-the-art experiments on **task representations**
Review - Theory - **Experiment (neural recording)**

Evolving schema representations in orbitofrontal ensembles during learning

Jingfeng Zhou, Chunying Jia, Marlian Montesinos-Cartagena, Matthew P. H. Gardner, Wenhui Zong & Geoffrey Schoenbaum

Geometry of abstract learned knowledge in the hippocampus

Edward H. Nieh, Manuel Schottdorf, Nicolas W. Freeman, Ryan J. Low, Sam Lewallen, Sue Ann Koay, Lucas Pinto, Jeffrey L. Gauthier, Carlos D. Brody & David W. Tank



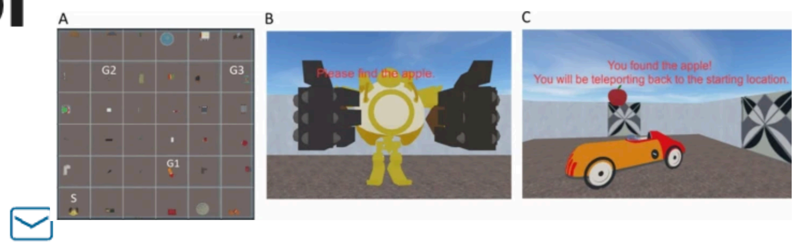
Compelling evidence for cognitive maps **beyond space** in rodents
Review - Theory - **Experiment (neural recording)**

Quick overview papers III

Computational models of the hippocampal formation - How are maps formed?

A comparison of reinforcement learning models of human spatial navigation

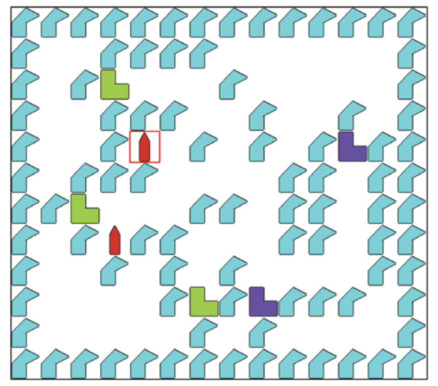
Qiliang He, Jancy Ling Liu, Lou Eschapasse, Elizabeth H. Beveridge & Thackery I. Brown



Compare **RL models** under different navigation requirements
Review - **Theory** - **Experiment (Behaviour)**

What Is the Model in Model-Based Planning?

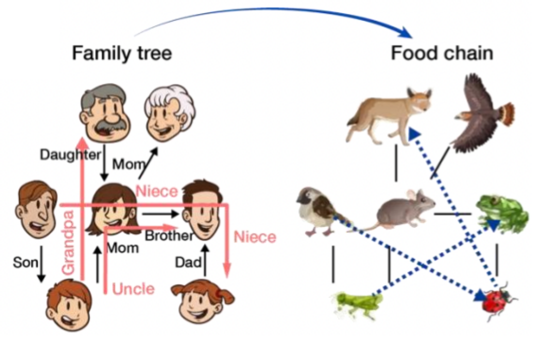
Thomas Pouncy,[a] Pedro Tsividis,[b] Samuel J. Gershman[a,c]



What are task representations that allow humans to **generalise**?
Review - **Theory** - **Experiment (Behaviour)**

Do grid codes afford generalization and flexible decision-making?

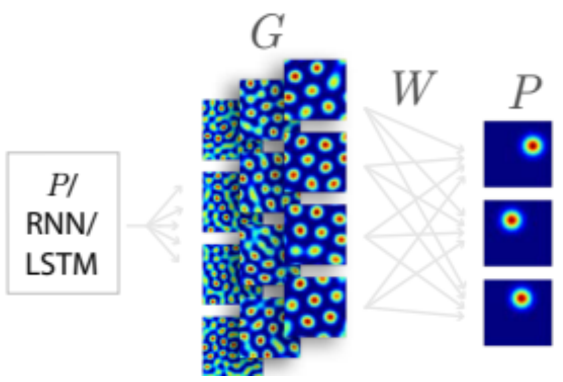
Linda Q. Yu [*,◊,a], Seongmin A. Park [*,◊,b], Sarah C. Sweigart [b,c], Erie D. Boorman [b,c,†], Matthew R. Nassar [a,†]



Discuss **competing views** on what cognitive maps are
Review - Theory - Experiment (Behaviour)

A unified theory for the origin of grid cells through the lens of pattern formation

Ben Sorscher*[1], Gabriel C. Mel*[2], Surya Ganguli[1], Samuel A. Ocko[1]
[1]Department of Applied Physics, Stanford University
[2]Neurosciences PhD Program, Stanford University



Theoretical model on **emergence of grid cells**
Review - **Theory (heavy)** - Experiment (Behaviour)

Quick overview papers IV

The role of hippocampal replay in navigation

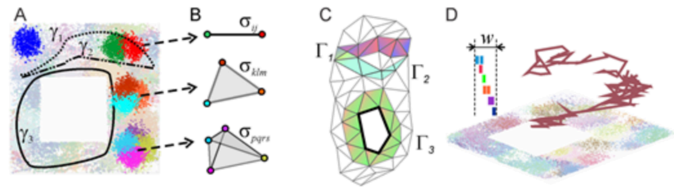
Prioritized memory access explains planning and hippocampal replay

Marcelo G. Mattar & Nathaniel D. Daw

Influential theory of the role of **replay in RL**
Review - **Theory** - Experiment

Replays of spatial memories suppress topological fluctuations in cognitive map

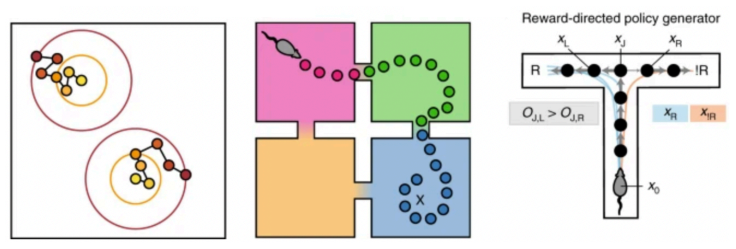
Andrey Babichev, Dmitriy Morozov, Yuri Dabaghian



Replay to **stabilise/learn** cognitive map of space
Review - **Theory (heavy)** - Experiment

Flexible modulation of sequence generation in the entorhinal–hippocampal system

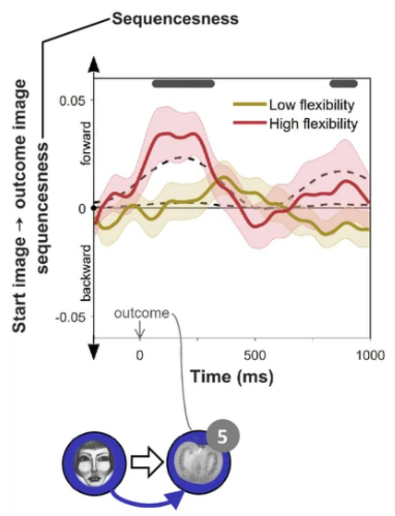
Daniel C. McNamee, Kimberly L. Stachenfeld, Matthew M. Botvinick & Samuel J. Gershman



Distinct modes of replay in exploration, consolidation and planning
Review - **Theory** - Experiment

The roles of online and offline replay in planning

Eran Eldar, Gaëlle Lièvre, Peter Dayan, Raymond J Dolan

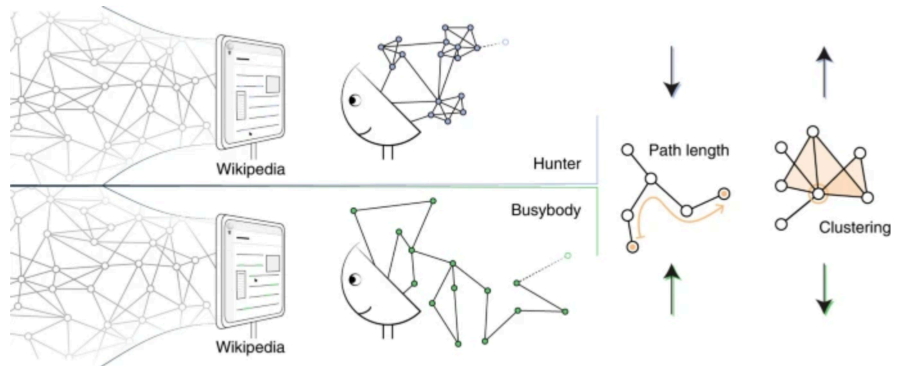


Roles of replay during **decision-making and learning**
Review - Theory - **Experiment (MEG)**

Quick overview papers V
Navigating graphs

Hunters, busybodies and the knowledge network building associated with deprivation curiosity

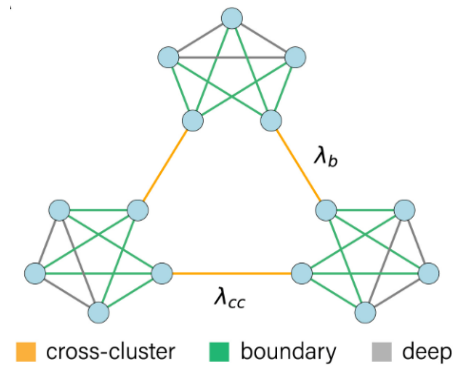
David M. Lydon-Staley, Dale Zhou, Ann Sizemore Blevins, Perry Zurn & Danielle S. Bassett



Naturalistic investigation of **structured concept learning**
Review - **(Graph) Theory** - **Experiment (Behaviour)**

Optimizing the human learnability of abstract network representations

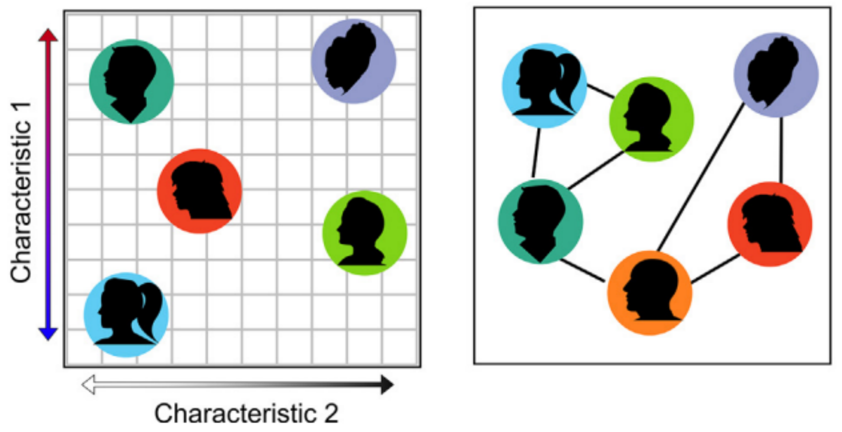
William Qian, Christopher W. Lynn, Andrei A. Klishin, +2, and Dani S. Bassett Authors Info & Affiliations



What optimises the **learnability** of concept networks?
Review - **Theory** - Experiment

Structuring Knowledge with Cognitive Maps and Cognitive Graphs

Michael Peer,[1,3] Iva K. Brunec,[2,3] Nora S. Newcombe,[2] and Russell A. Epstein[1,*]



Types of representation: **Graphs vs. Euclidean**
Review - Theory - Experiment

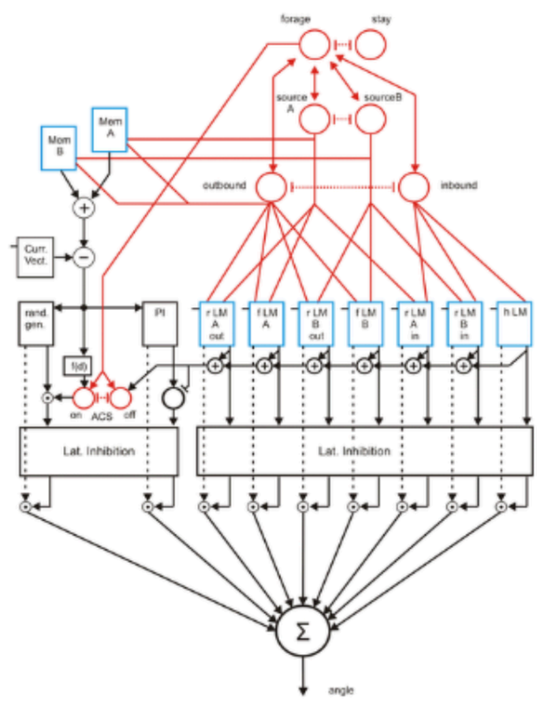
Quick overview papers VI

Do Insects use Cognitive Maps?

@Paige :)

No Need for a Cognitive Map: Decentralized Memory for Insect Navigation

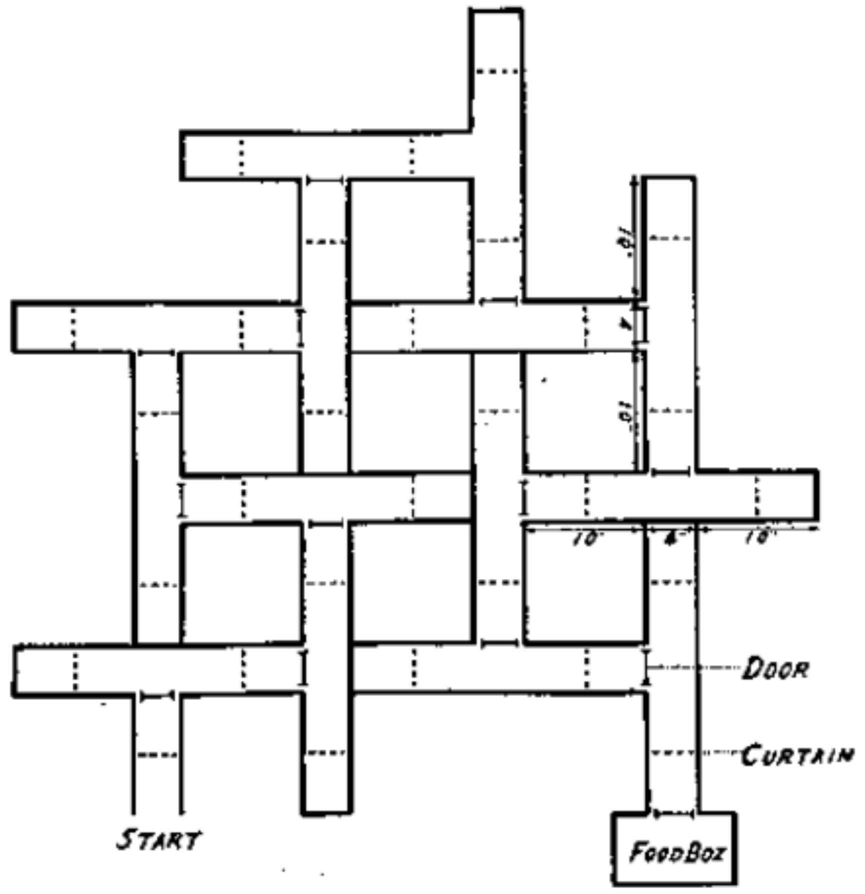
Holk Cruse, Rüdiger Wehner



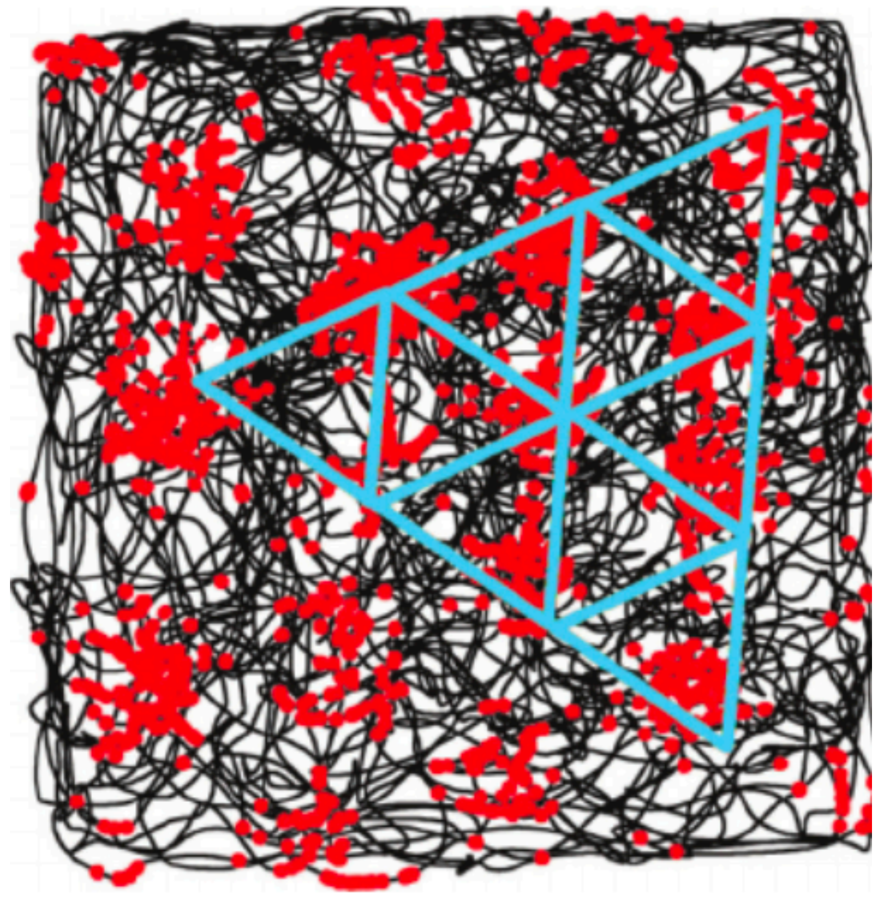
Principles of navigation **without a cognitive map**

Review - **Theory (Neural Network)** - Experiment

Any Questions?



Plan of maze
14-Unit T-Alley Maze
FIG. 1
(From M. H. Elliott, The effect of change of reward on the maze performance of rats. *Univ. Calif. Publ. Psychol.*, 1928, 4, p. 20.)

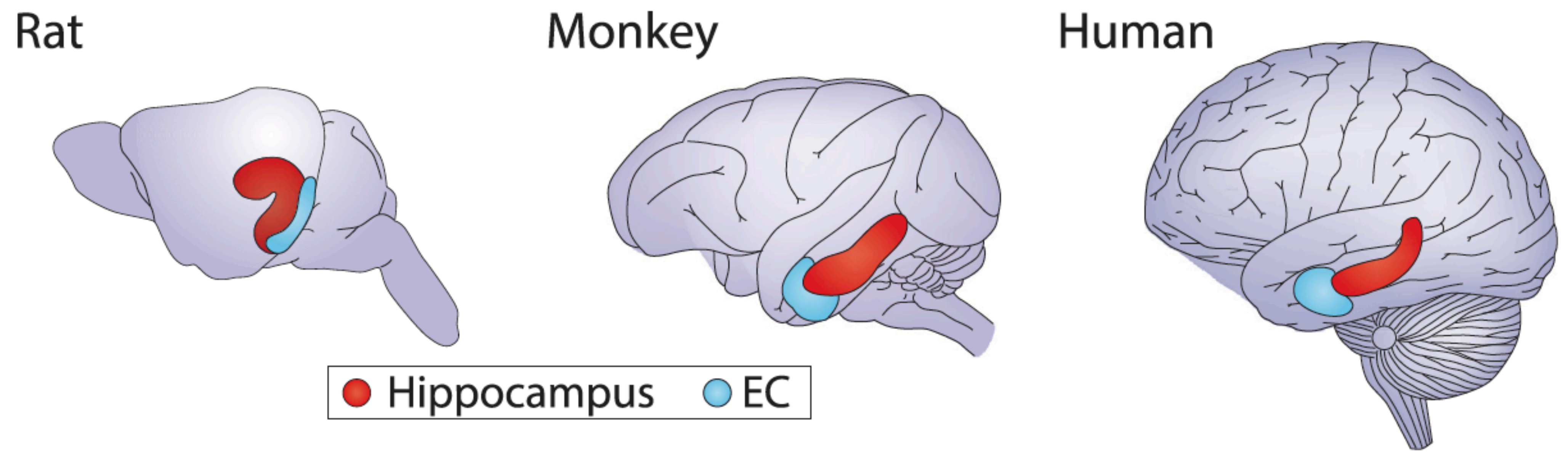


2. So, what's the neural basis of a cognitive map?

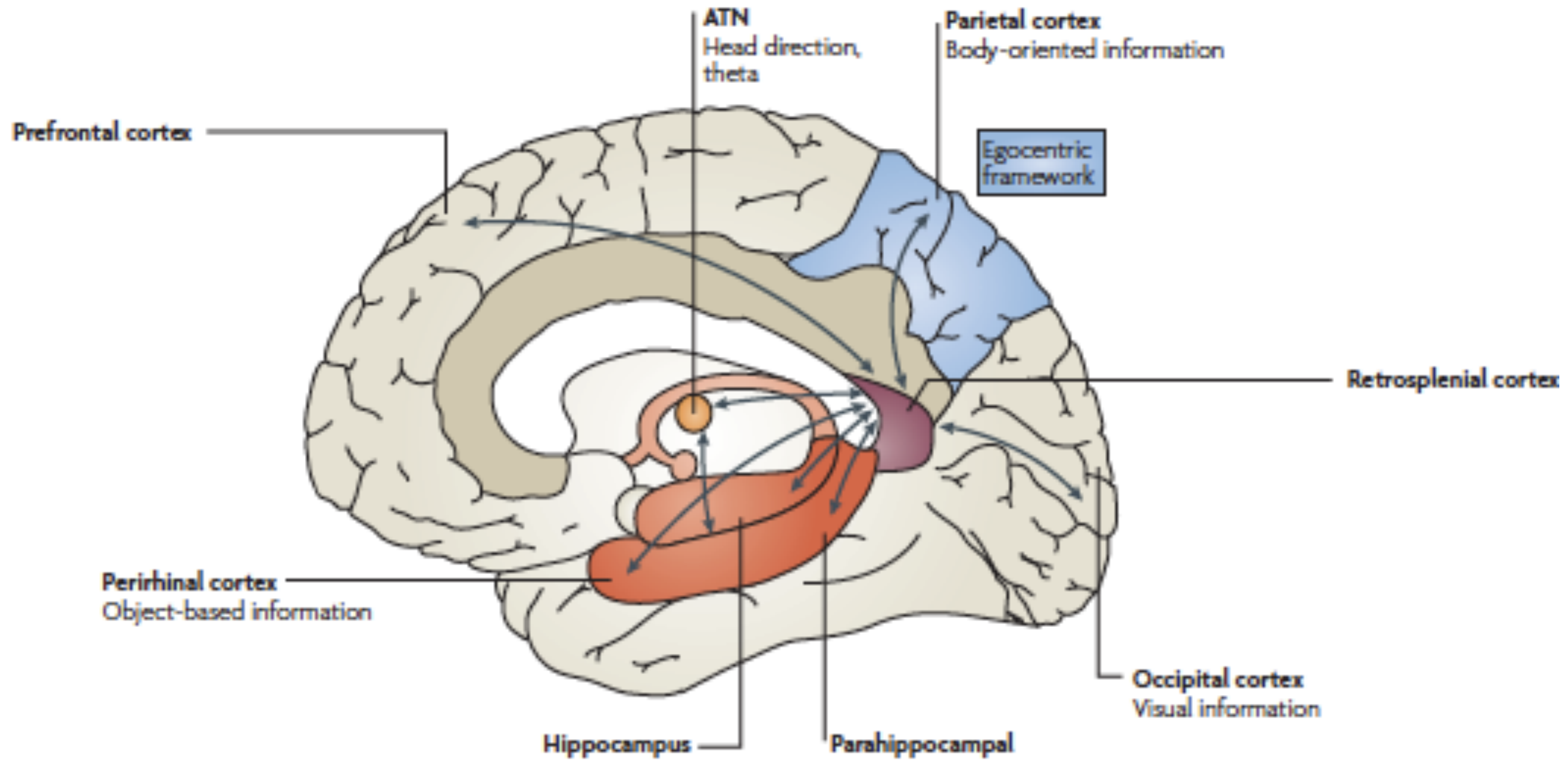
Cognitive maps in biological brains

Specific brain structures strongly associated with *learning* and *encoding* a cognitive map, especially
- **Hippocampus** (**HC**)
- **Entorhinal Cortex** (**EC**)

These structures are preserved across mammalian species:



Behrens et al. (2018). What is a cognitive map? Organizing knowledge for flexible behavior. Neuron

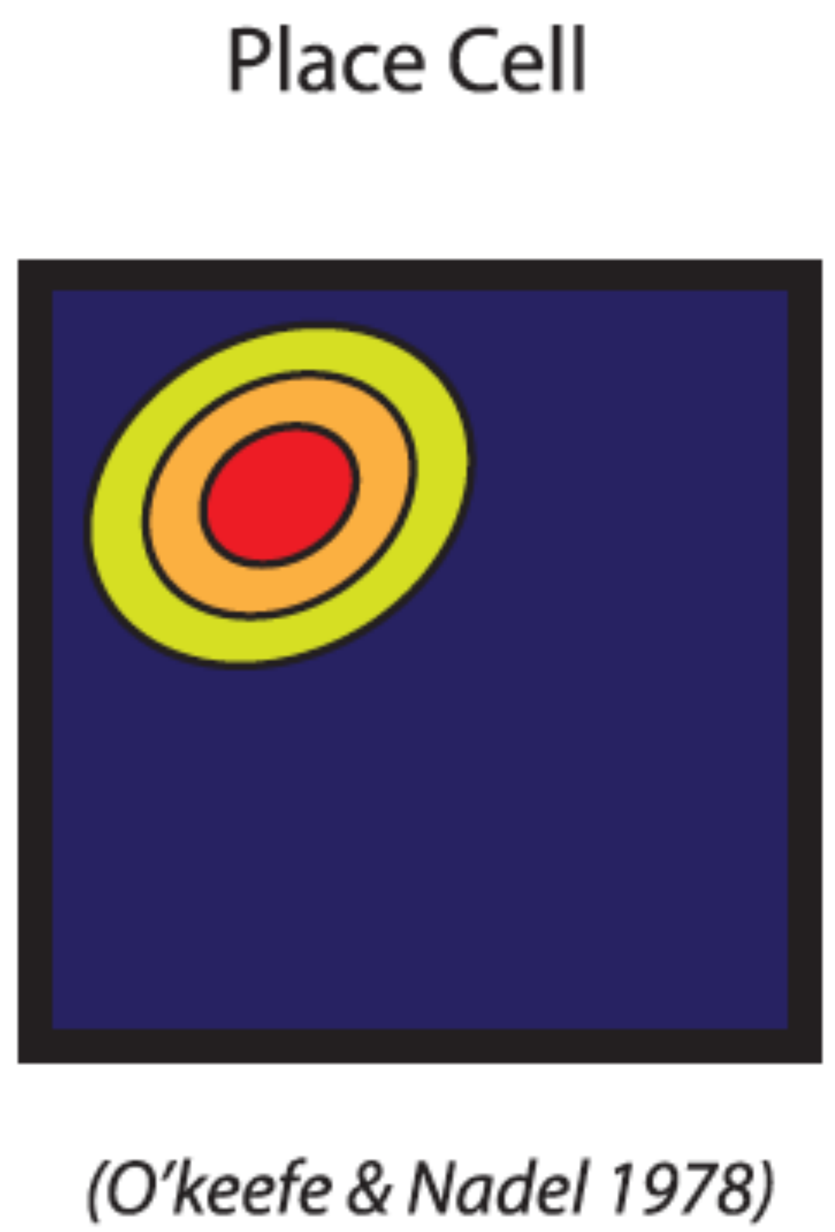


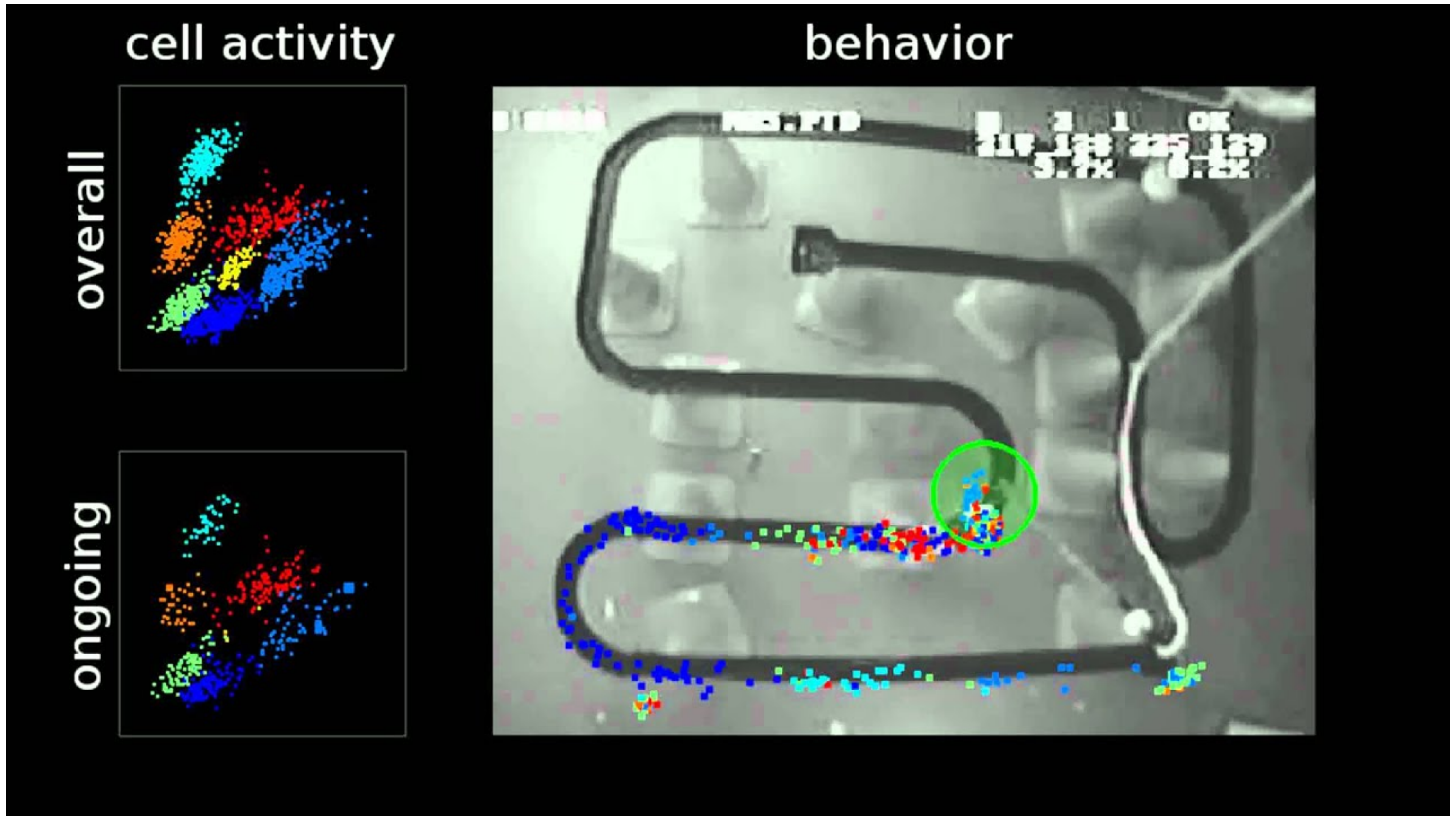
Vann et al. (2009). What does the retrosplenial cortex do? Nature reviews neuroscience

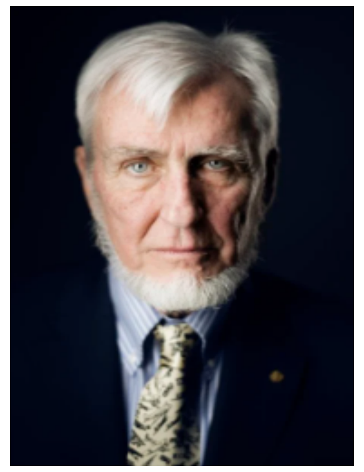
Together, they form the **Hippocampal Formation** (**HF**)

Cognitive maps in biological brains: Place Cells

Hippocampal **place cells** reflect an animals location in an environment





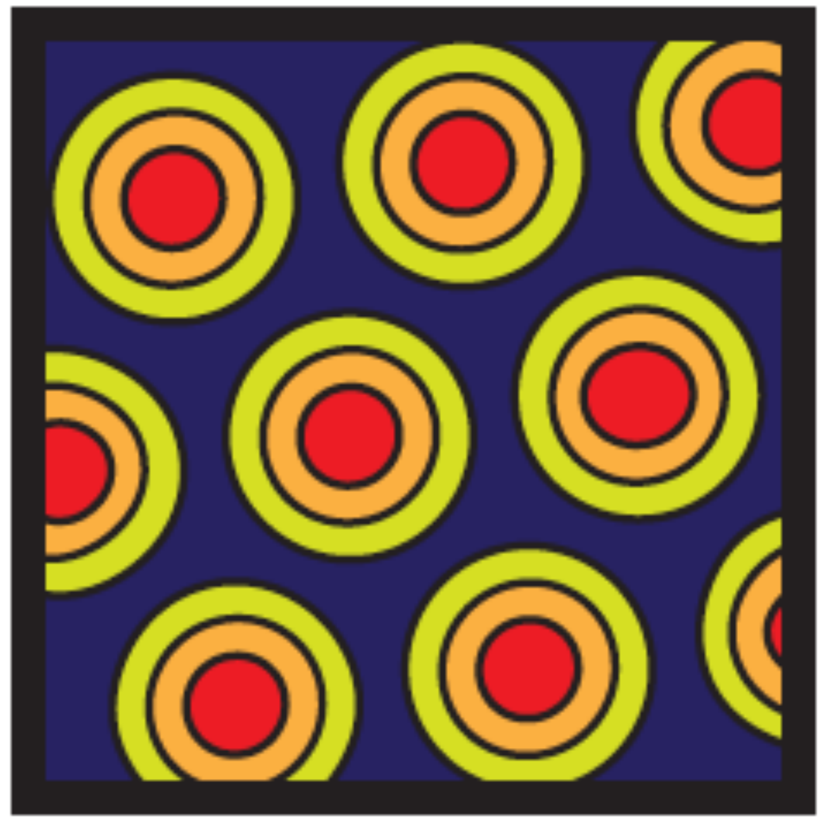


John O'Keefe
The Nobel Prize in Physiology or Medicine 2014

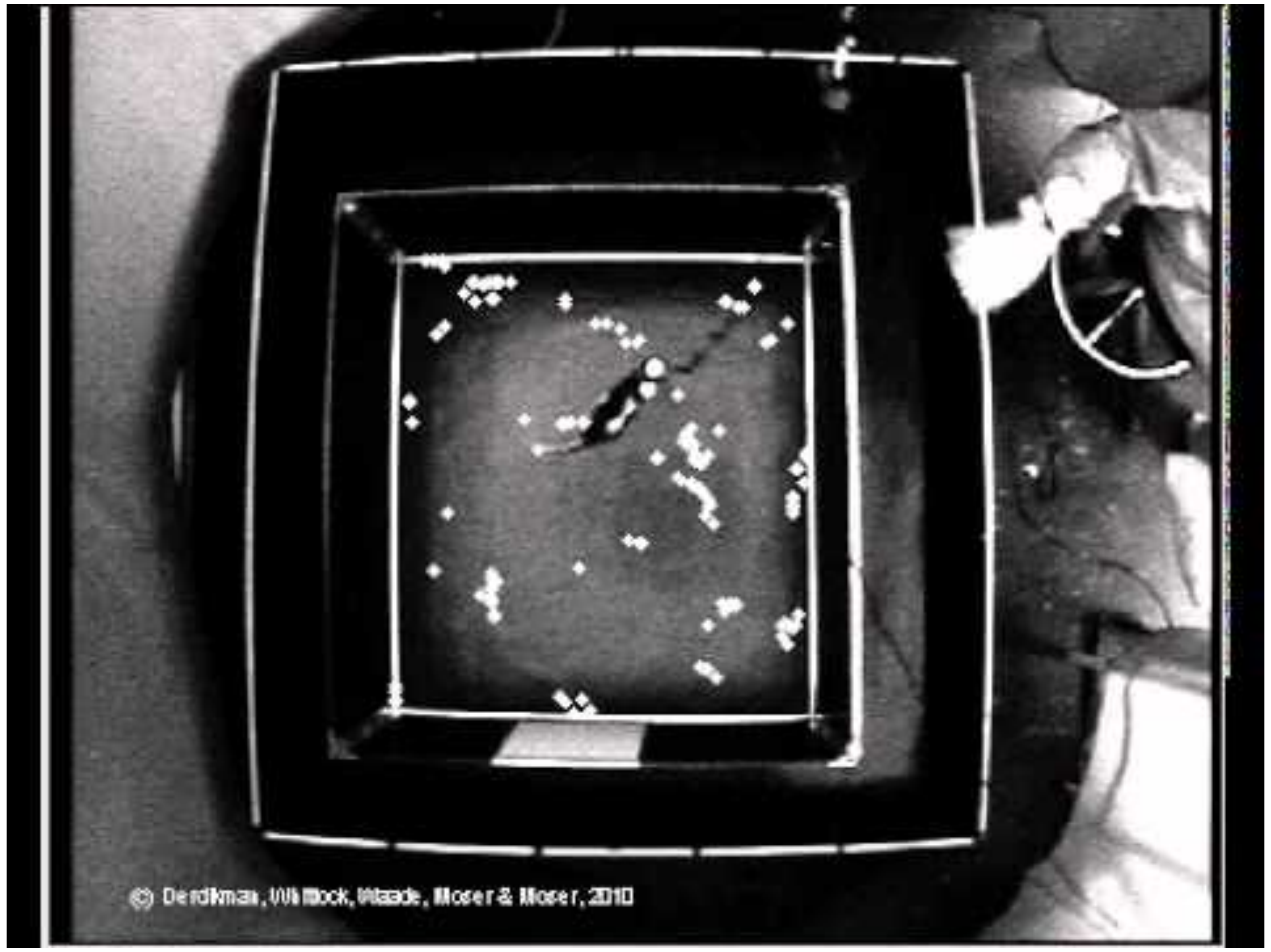
Cognitive maps in biological brains: Grid Cells

Grid cells in medial entorhinal cortex fire in a structured way at several locations in an environment

Grid Cell

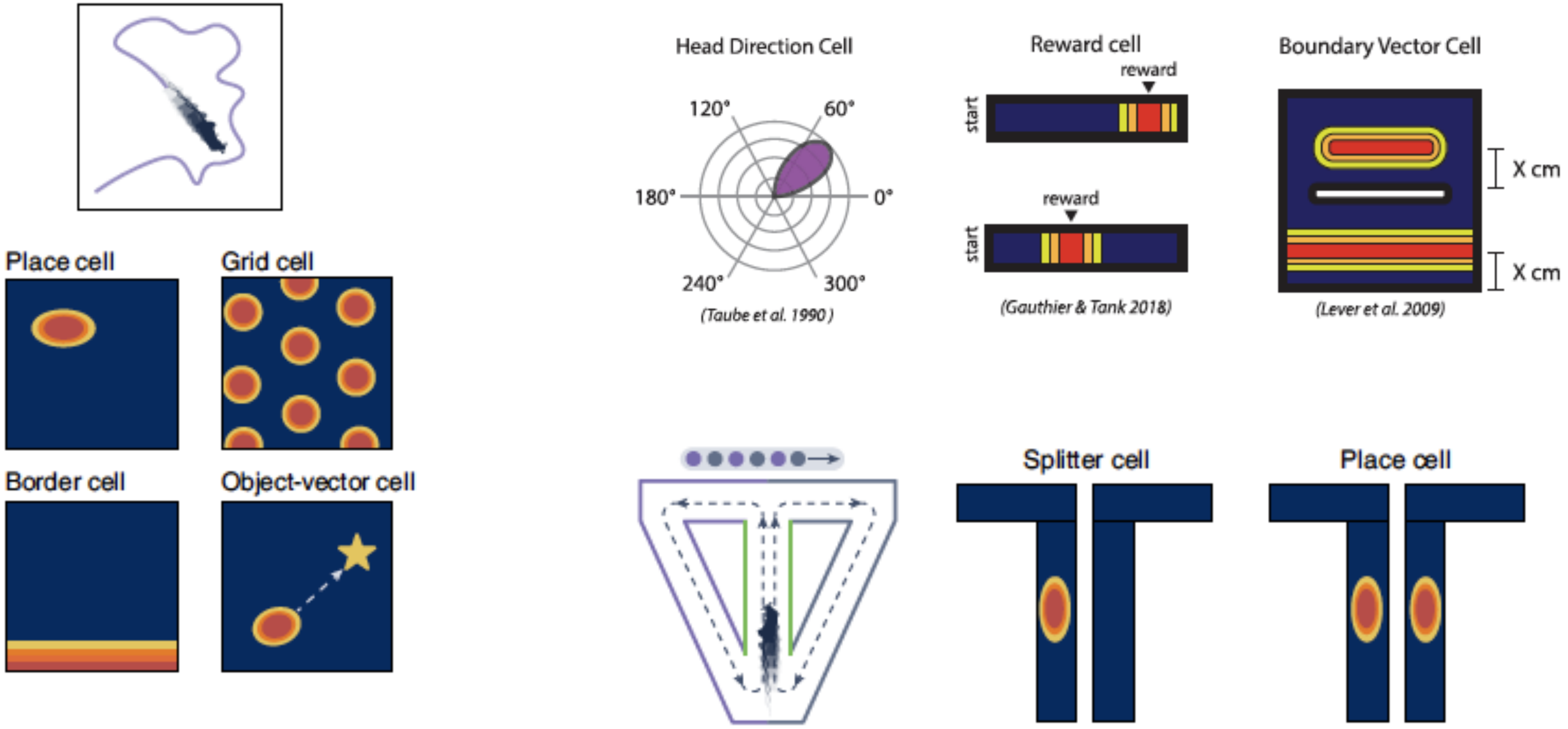


(Hafting et al., 2005)



May-Britt Moser and Edvard I. Moser
The Nobel Prize in Physiology or Medicine 2014

Actually, it’s more like a “Hippocampal Zoo”



Is this a **basis set** over world structures?

Whittington et al. (2022). How to build a cognitive map. Nature Neuroscience

Behrens et al. (2018). What is a cognitive map? Organizing knowledge for flexible behavior. Neuron

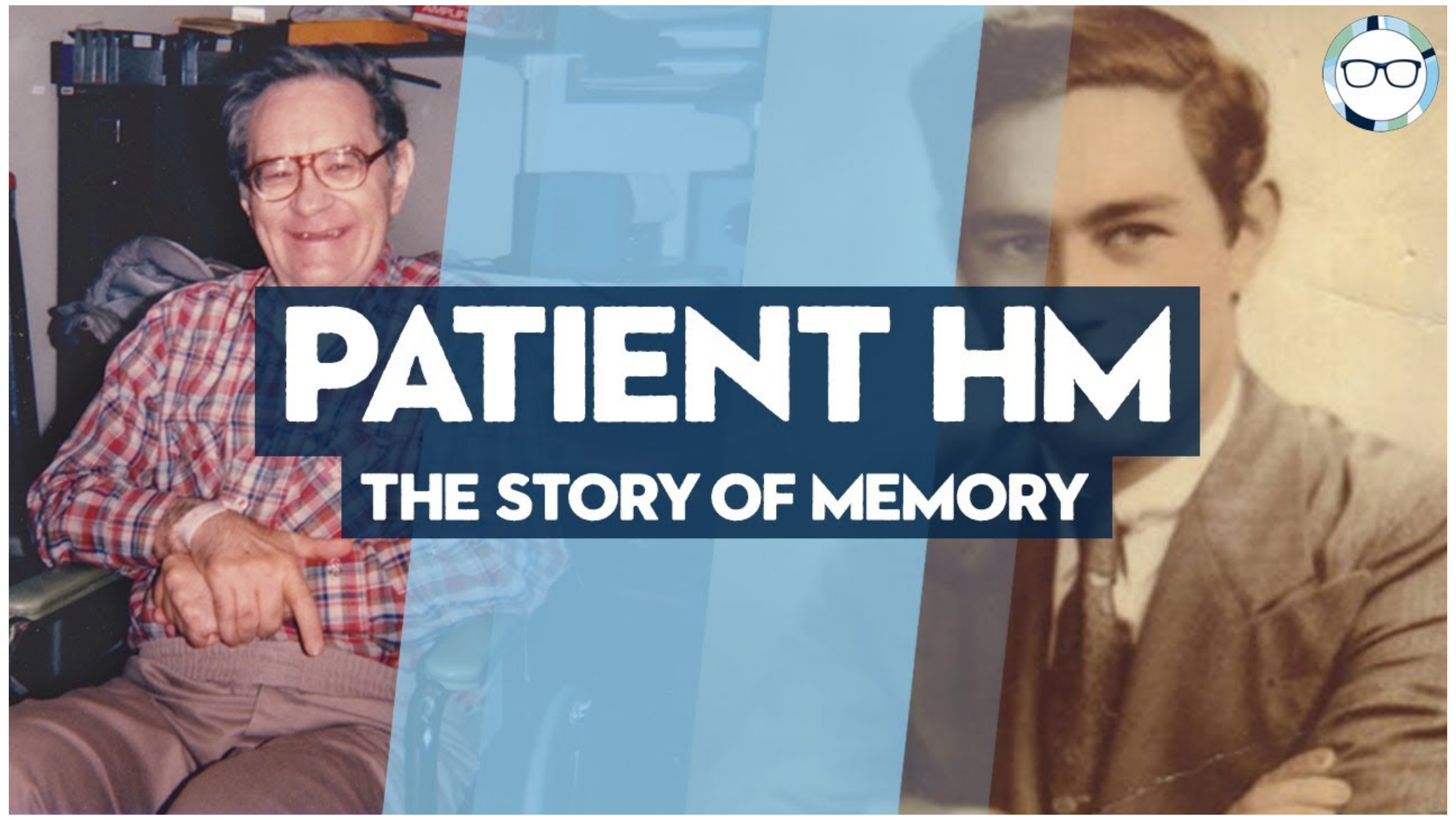
Wait, but isn't the hippocampus doing other stuff?

What else do you know about the hippocampus?

Henry Molaison - better known as H.M.

Widespread damage to his hippocampal formation after epilepsy surgery

Inability to form new long-term memories



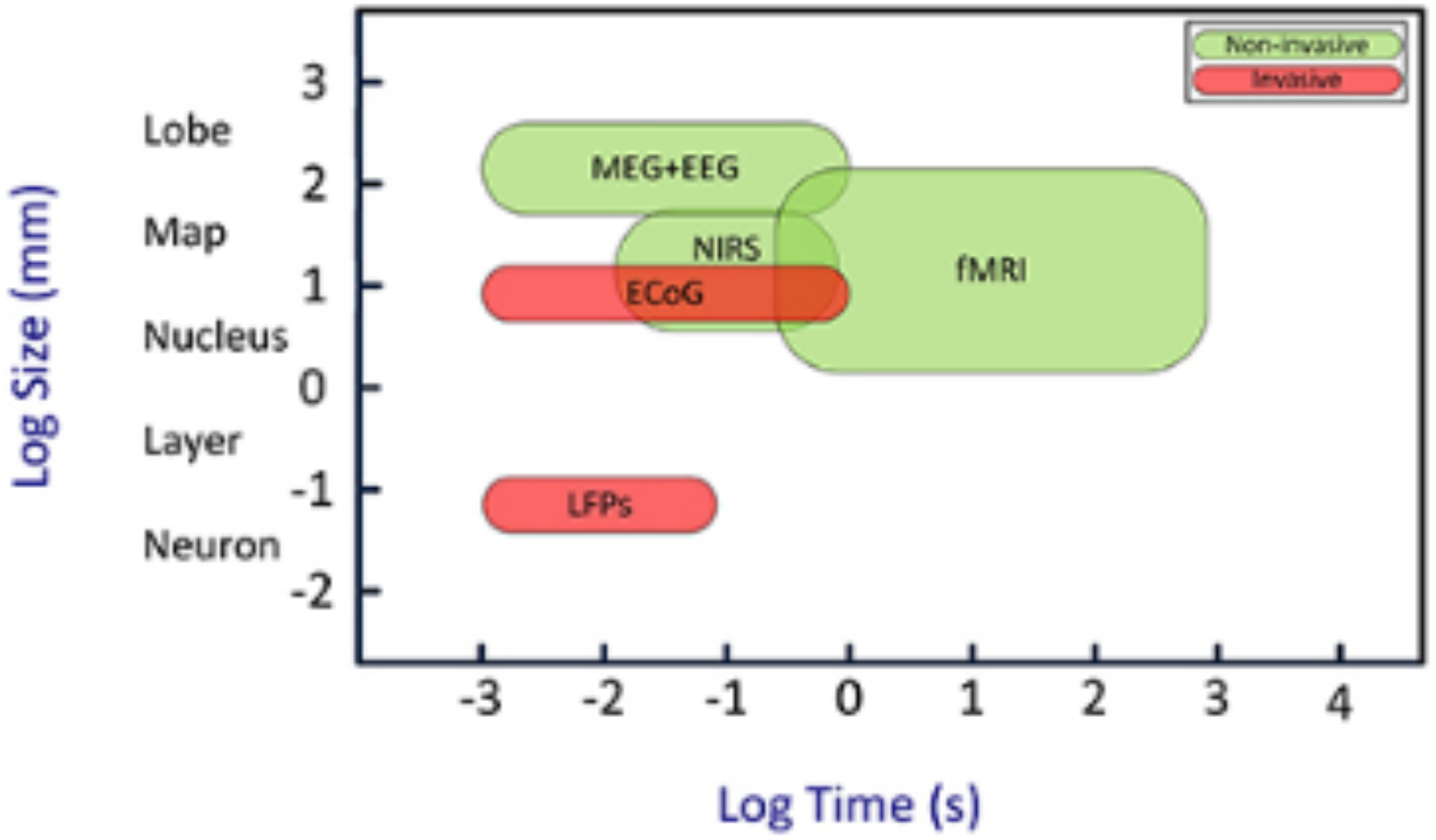
So… The hippocampus does memory? Or navigation? Or both?

It's a challenge to reconcile all these functions, we will come back to that many times..

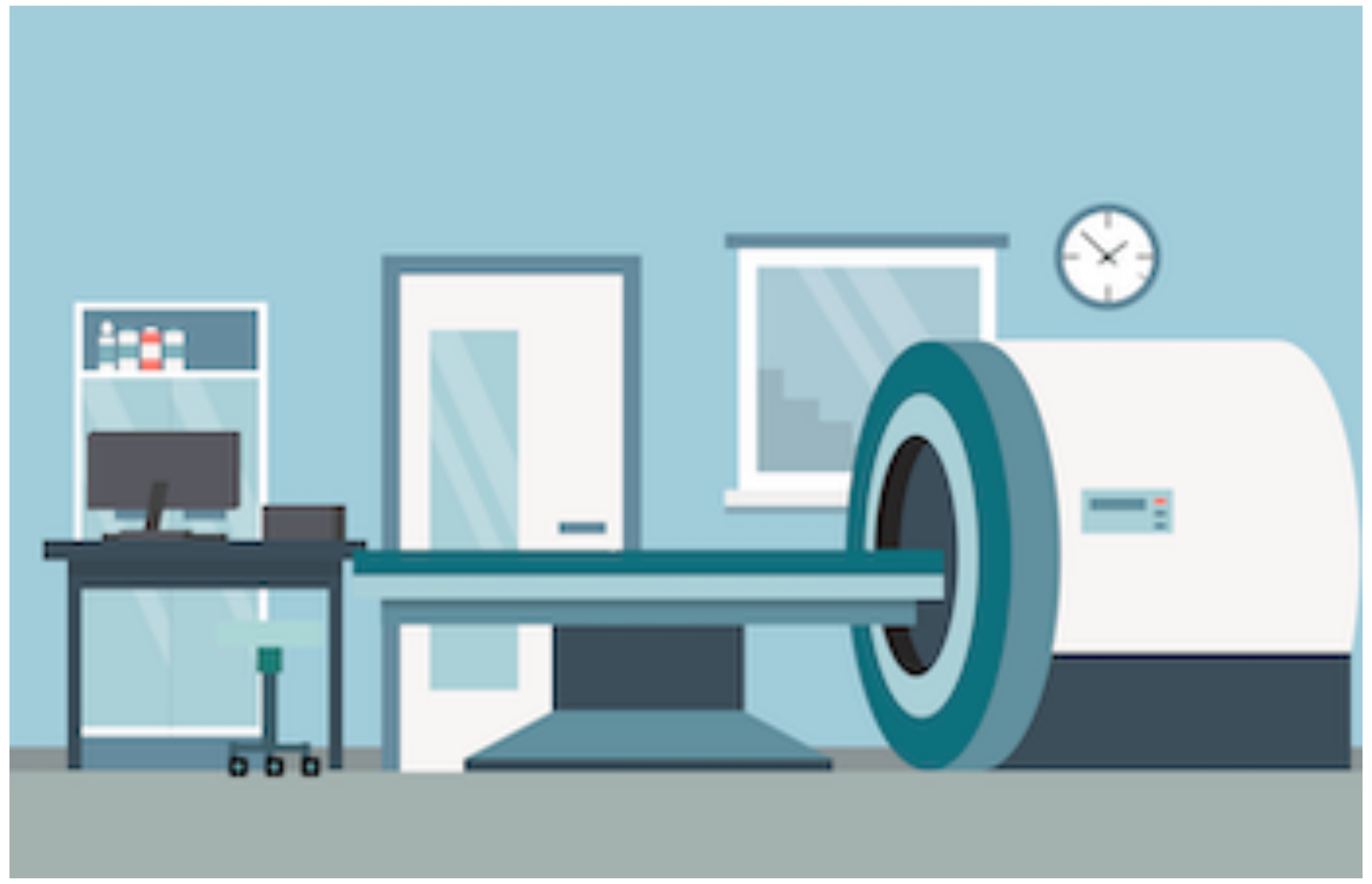
Cognitive maps across species

- Any relevance for humans? Or is this just navigation in rats?
    - We usually can’t obtain direct recordings in humans

- One solution: fMRI



Ordikhani-Seyedlar (2016). Neurofeedback therapy for enhancing visual attention: state-of-the-art and challenges. Frontiers in neuroscience



Published: 01 November 2017

The cognitive map in humans: spatial navigation and beyond

Russell A Epstein, Eva Zita Patai, Joshua B Julian & Hugo J Spiers

Nature Neuroscience **20**, 1504–1513 (2017) | Cite this article

The cognitive map in humans: spatial navigation and beyond

- To what extent are cognitive maps a principle of navigation in humans?

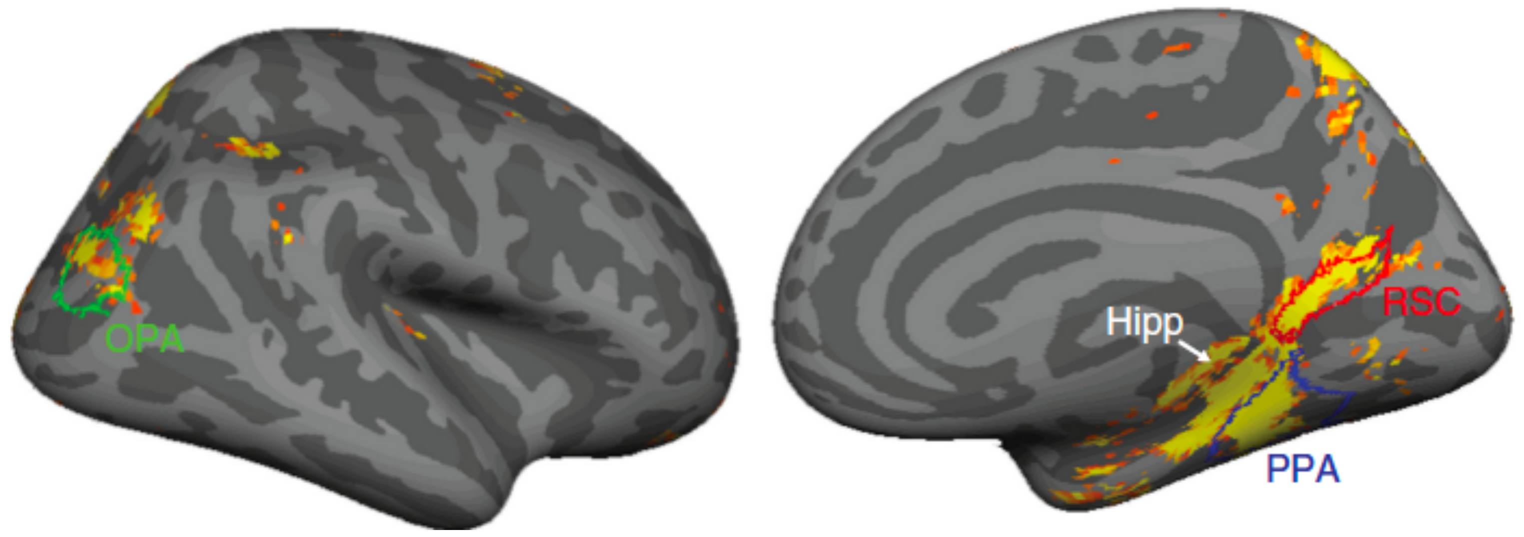
- Key points
  - Neural mechanisms of **spatial maps** are shared in the hippocampal formation
    - Place and grid fields, head direction cells, …
  - **Landmarks** help grounding cognitive maps into the real world
  - **Planning** in navigation relies on the interplay of different neural systems
    - Entorhinal cortex, hippocampus, prefrontal cortex

- This is not an anatomy or fMRI course - let's just focus on the key concepts

The cognitive map in humans: spatial navigation and beyond

I Spatial maps in human navigation

Most of what we know about human cognitive maps is based on fMRI research



Neuroimaging studies reveal a network of brain regions involved in spatial navigation (‘navigation network’)

Some neuroscience jargon - this is not critical! -

- **Repetition suppression**/ (fMRI) adaption
  - Repeated presentation of the same stimulus leads to a reduction in the fMRI signal
  - Adaptation across two different stimuli provides evidence for a common neural representation

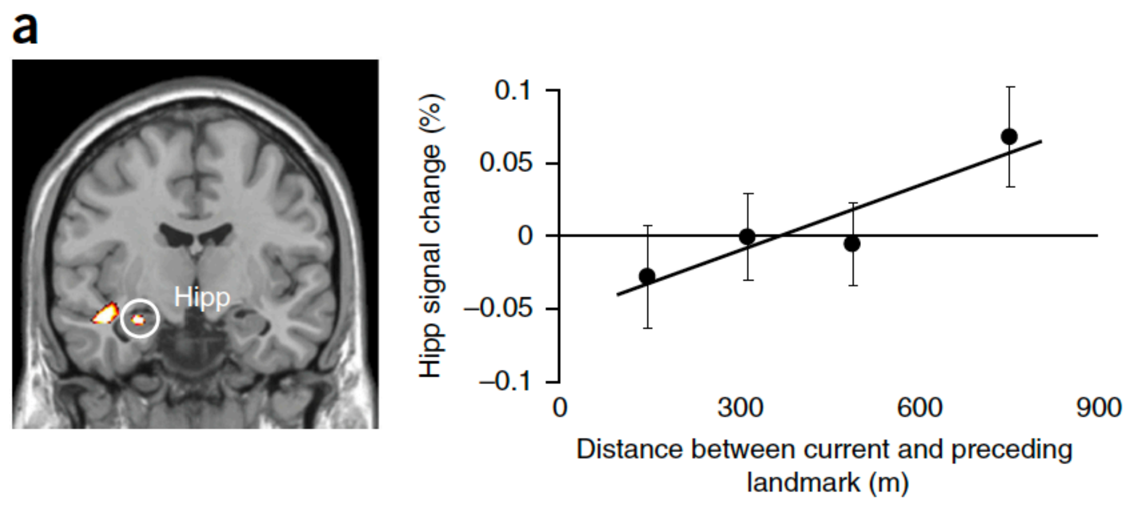
- **MVPA**
  - Analysing patterns of fMRI activity
  - Testing the information that can be decoded from these patterns

- **Decoding** vs. **Encoding model**
  - Decoding: predict stimuli based on neural responses
  - Encoding: predict neural response based on stimuli

The cognitive map in humans: spatial navigation and beyond

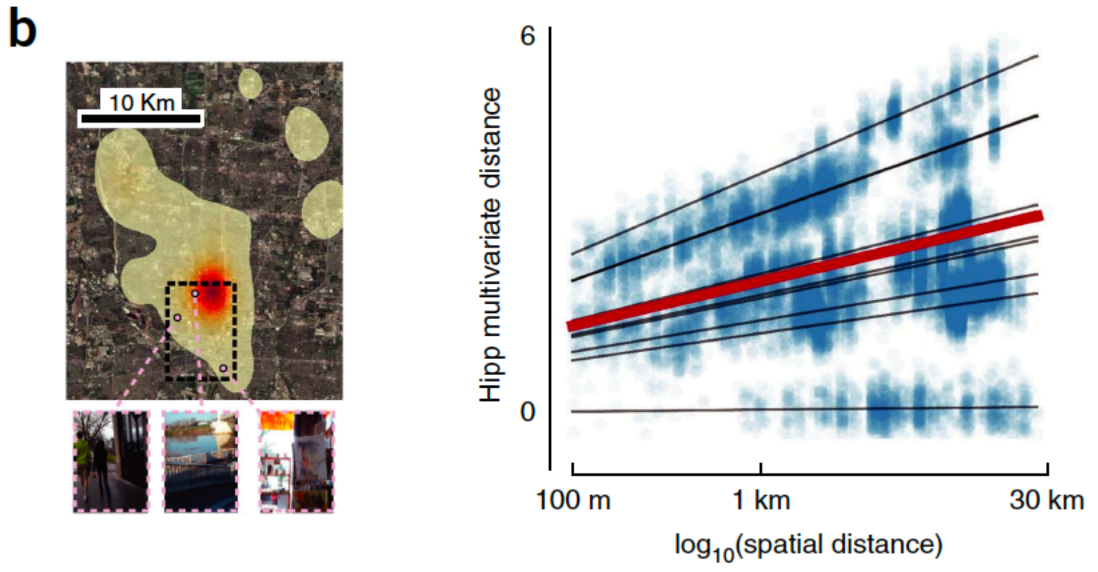
I Spatial maps in human navigation

Key feature of a map is that it preserves distance relationships:
- Entities closer in real world are closer on map

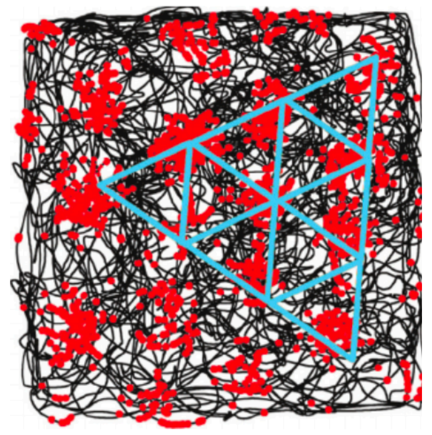


We find that in the hippocampus

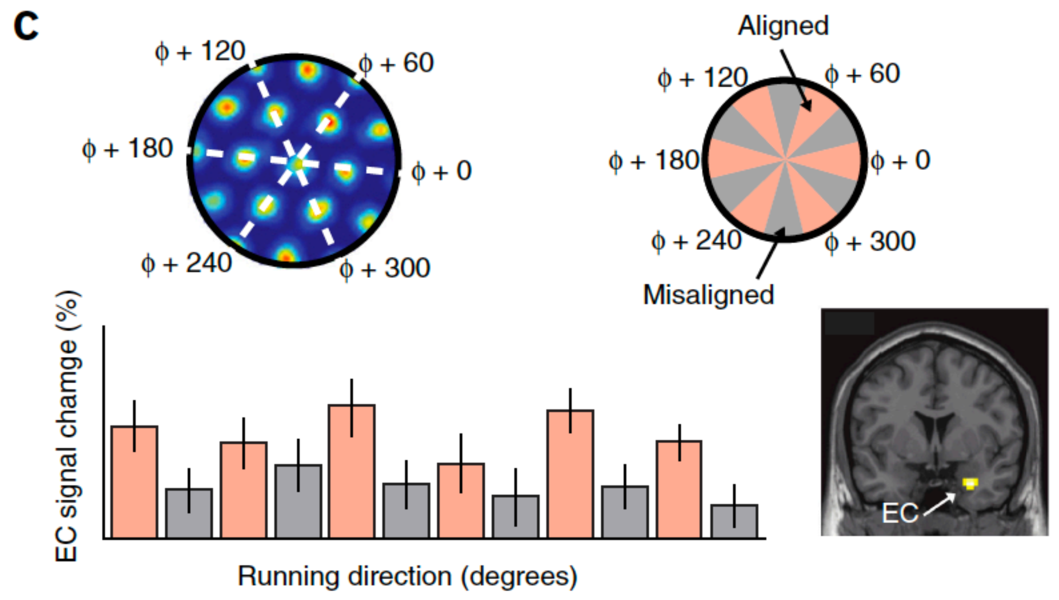
This is also true in real life navigation:



Anterior hippocampus reflects real life spatial and temporal proximities



Do we also find grid codes?



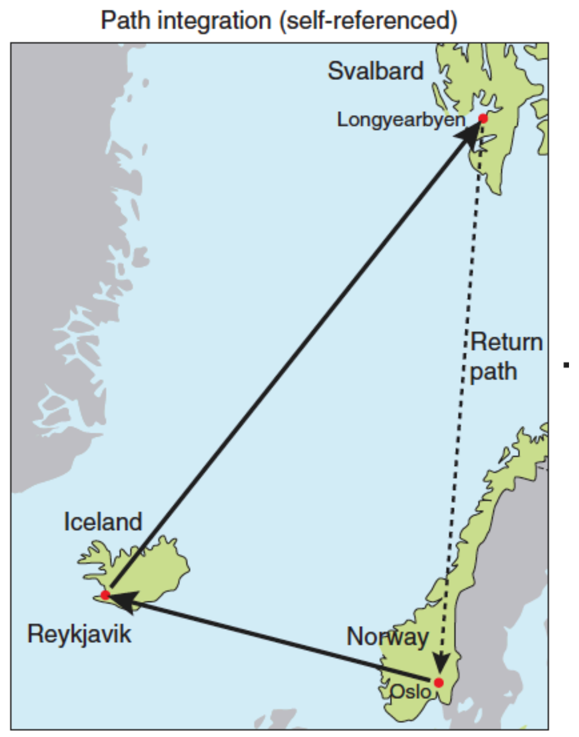
Yes! We can see those in human entorhinal cortex

The cognitive map in humans: spatial navigation and beyond

II Landmarks

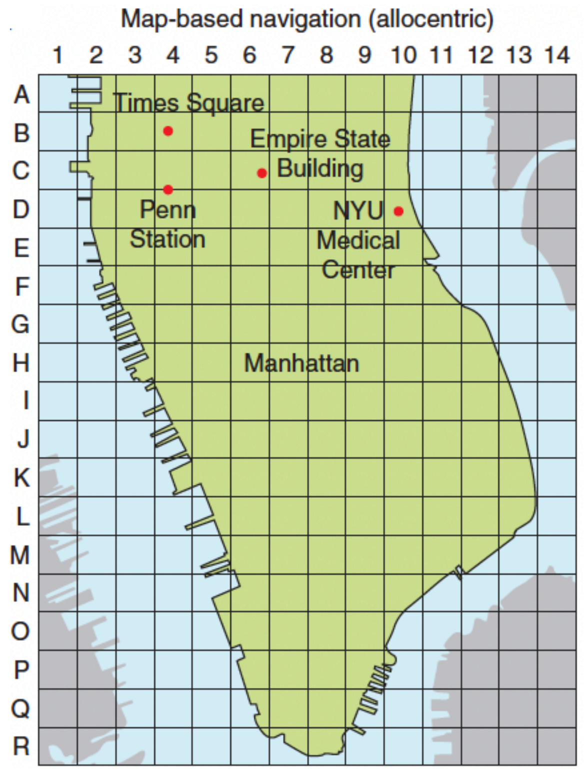
self-referenced navigation system

Entorhinal Cortex (EC)



Uncertainty-based arbitration

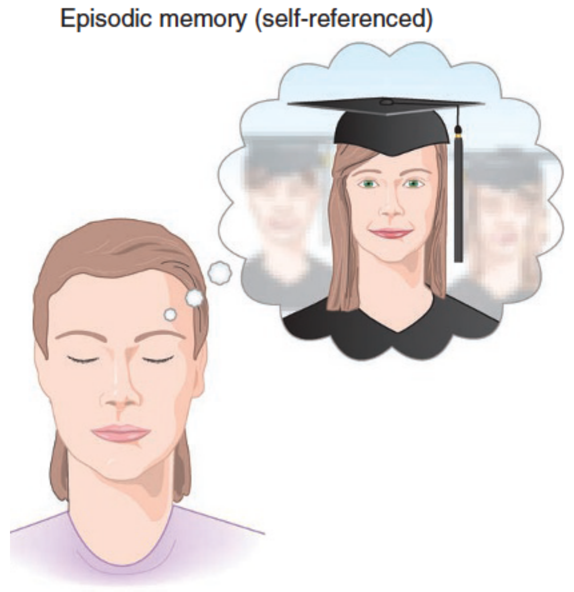
Landmarks



Hippocampus (HC)

One could speculate if this has an equivalent in memory

First person experience



Knowing stuff about things independent of yourself

Buzsáki & Moser (2013). Memory, navigation and theta rhythm in the hippocampal-entorhinal system. Nature neuroscience

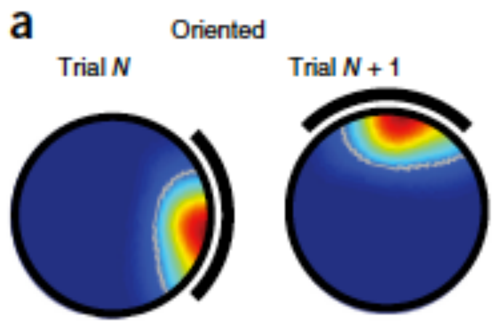
The cognitive map in humans: spatial navigation and beyond

II Landmarks

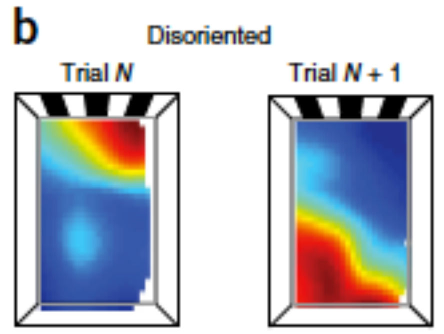
Landmarks are features (objects/boundaries) of the environment that help with orientation

Animals can rely on **path integration** based on head direction and grid cells if there are no landmarks

Oriented animal: place/grid fields rotate with rotated environment features



Disoriented animal: ‘geometric errors’
Search for goals and locations determined by geometric shape of environment



The cognitive map in humans: spatial navigation and beyond

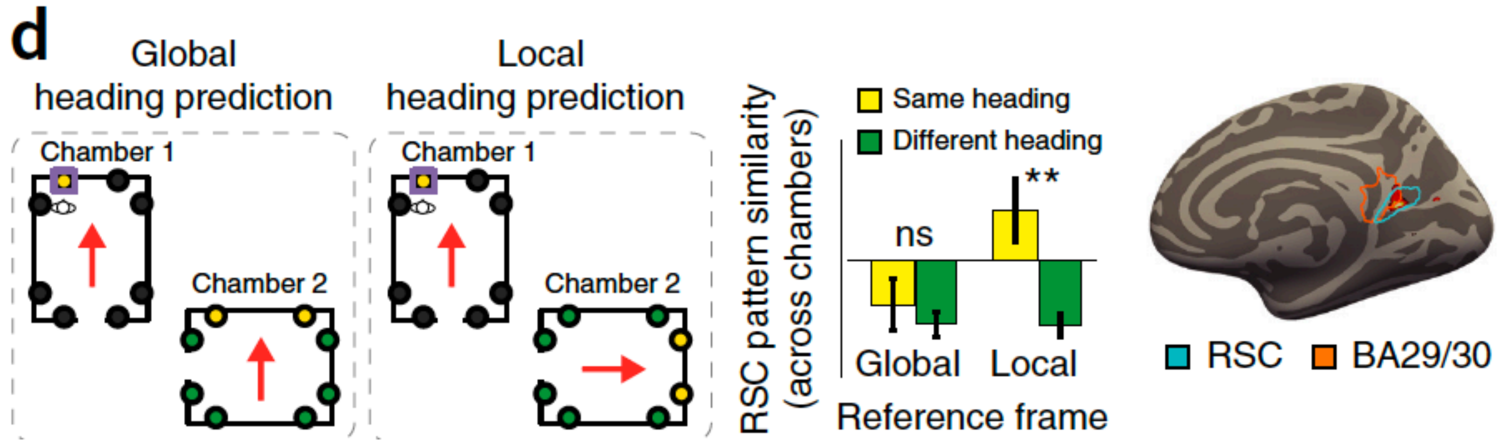
II Landmarks

Landmarks rely on the integration of **visual input** with cognitive map representations

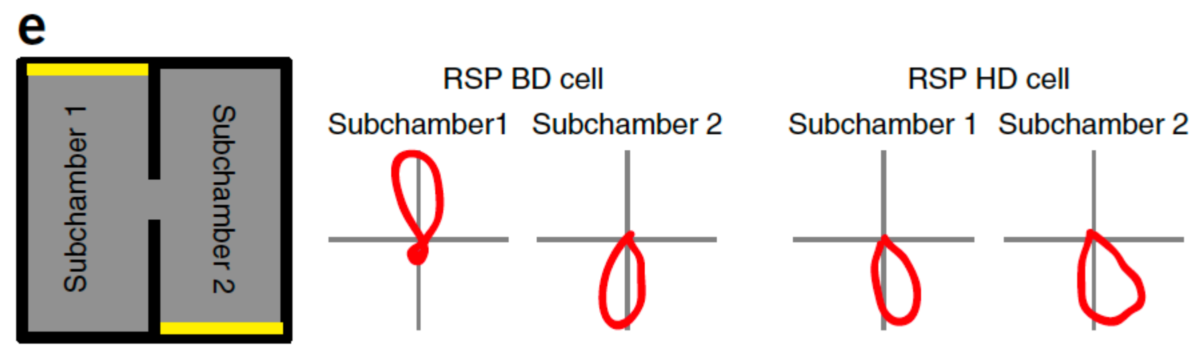
Key area in humans: **retrosplenial cortex**

Human brain represents heading direction

It does so in a local reference frame



In RSC, there are both head direction and environment-specific direction cells

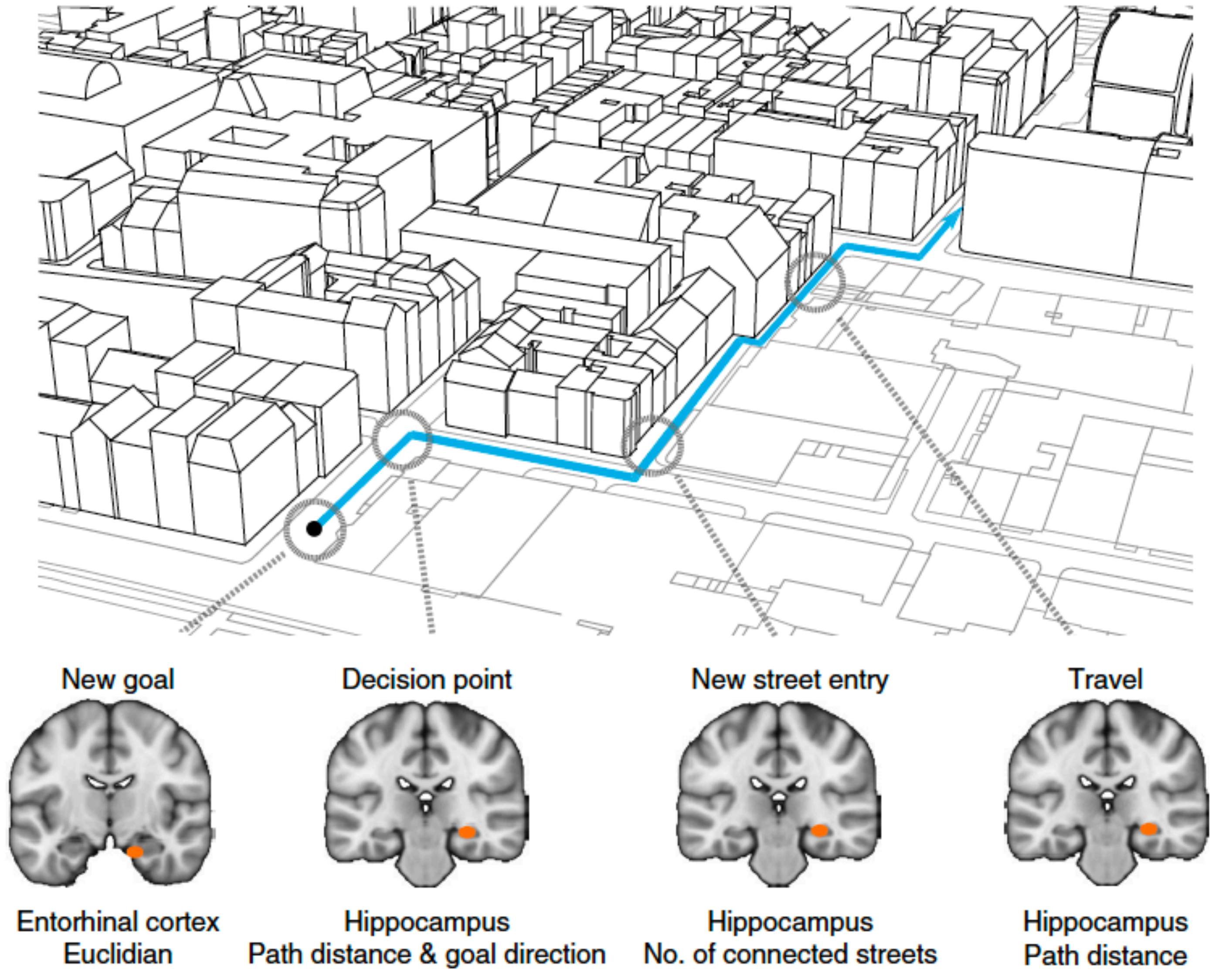


The cognitive map in humans: spatial navigation and beyond

III Cognitive maps for planning navigation

Cognitive maps also need to be useful for planning

a

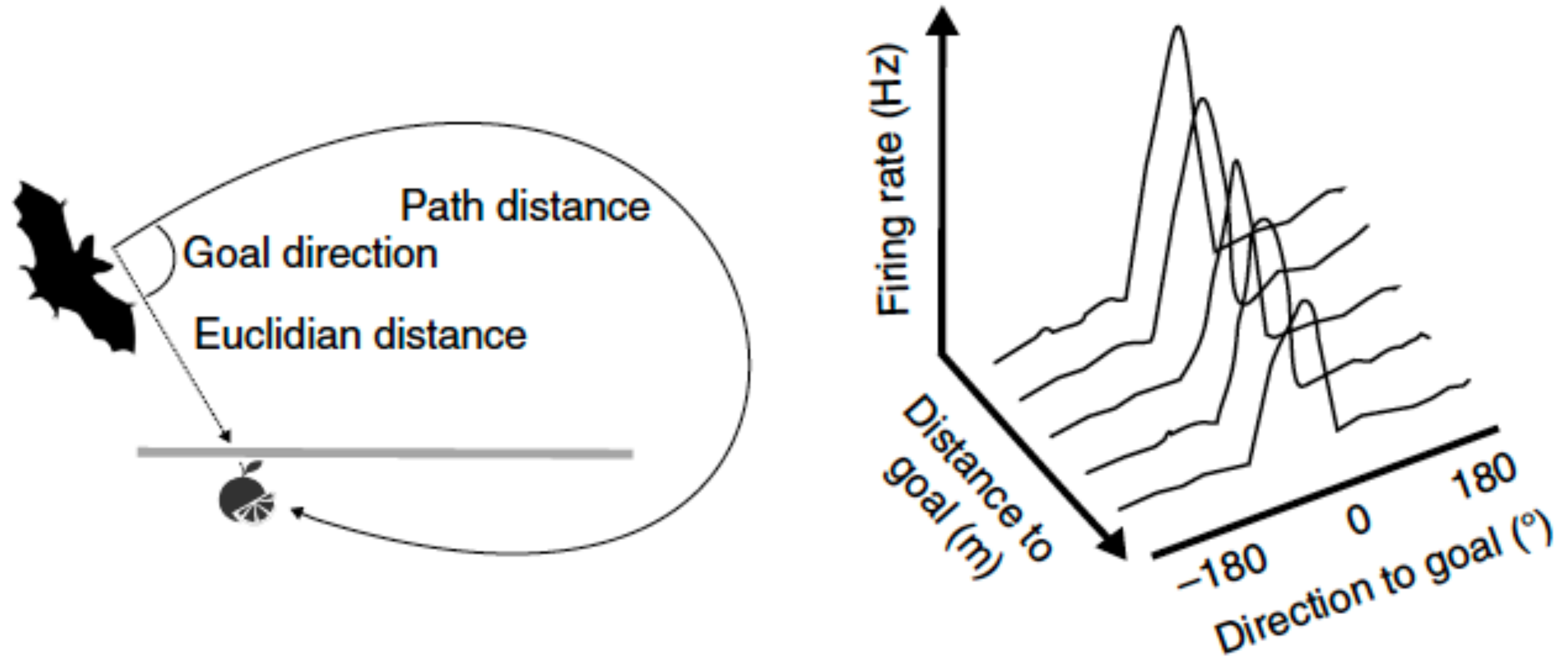


Entorhinal cortex reflects Euclidean distance to goal

Hippocampus: use distance info and compute path wrt obstacles

- Cf., neural *replay*

b

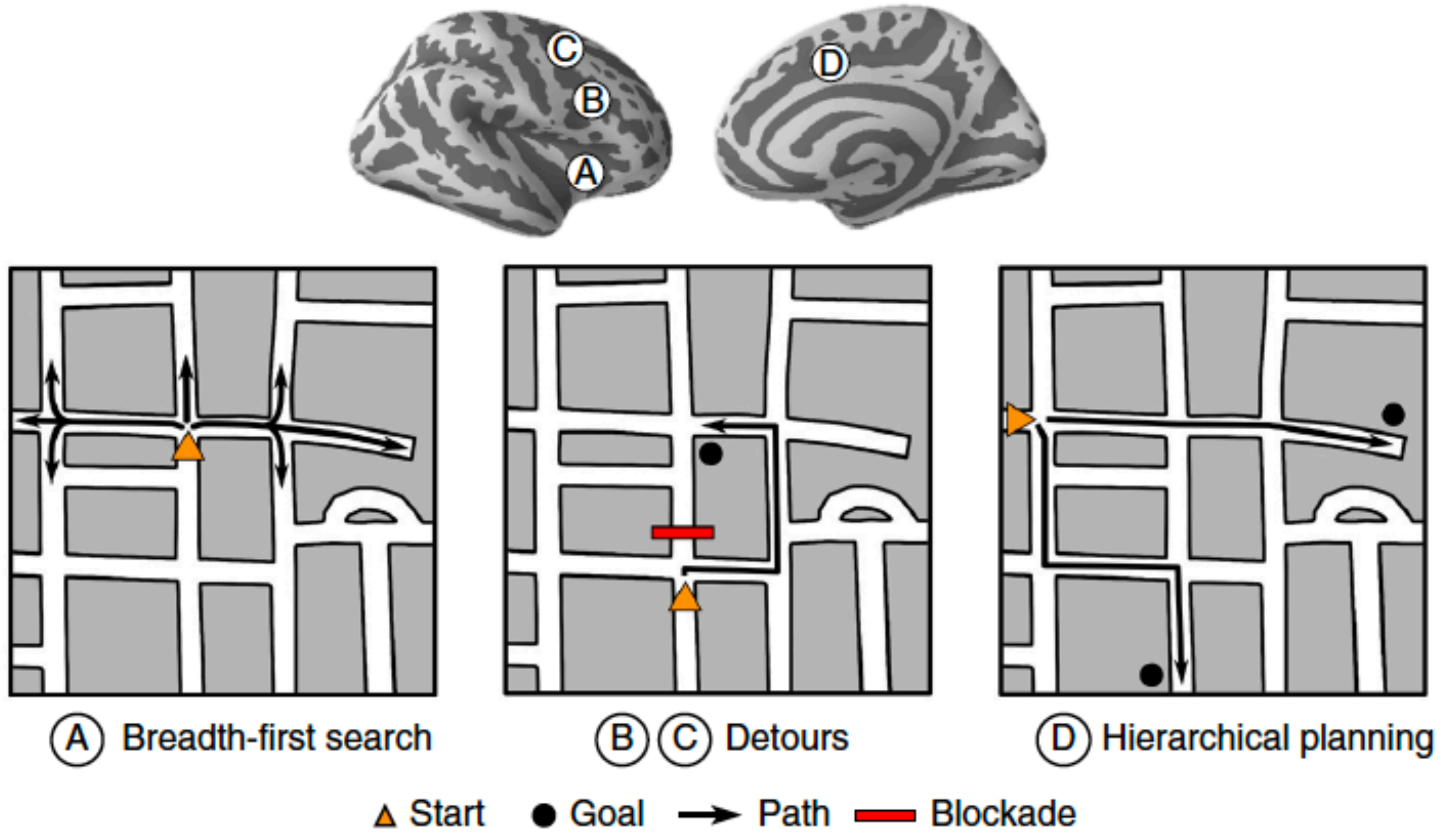


Goal direction (entorhinal) vs. path distance (hippocampus)

The cognitive map in humans: spatial navigation and beyond

III Cognitive maps for planning navigation

Cognitive maps also need to be useful for planning



Evaluation of paths in prefrontal cortex, such as

- Demands of breadth-first search
- Finding detours
- Hierarchical planning

The cognitive map in humans: spatial navigation and beyond

So, what have we learned?

- Neural mechanisms for spatial navigation in humans comparable to those of other mammals
- Map-like **spatial codes** in hippocampus formation
  - Hippocampus reflects distances, entorhinal cortex grid-like representations
- **Landmarks**
  - Used to anchor maps in real world
  - Cells reflecting head direction, direction within specific environment
  - Relies on visual input
- Cognitive maps for **planning**
  - Goal vs. path distance
  - Evaluation another important aspect - prefrontal cortex

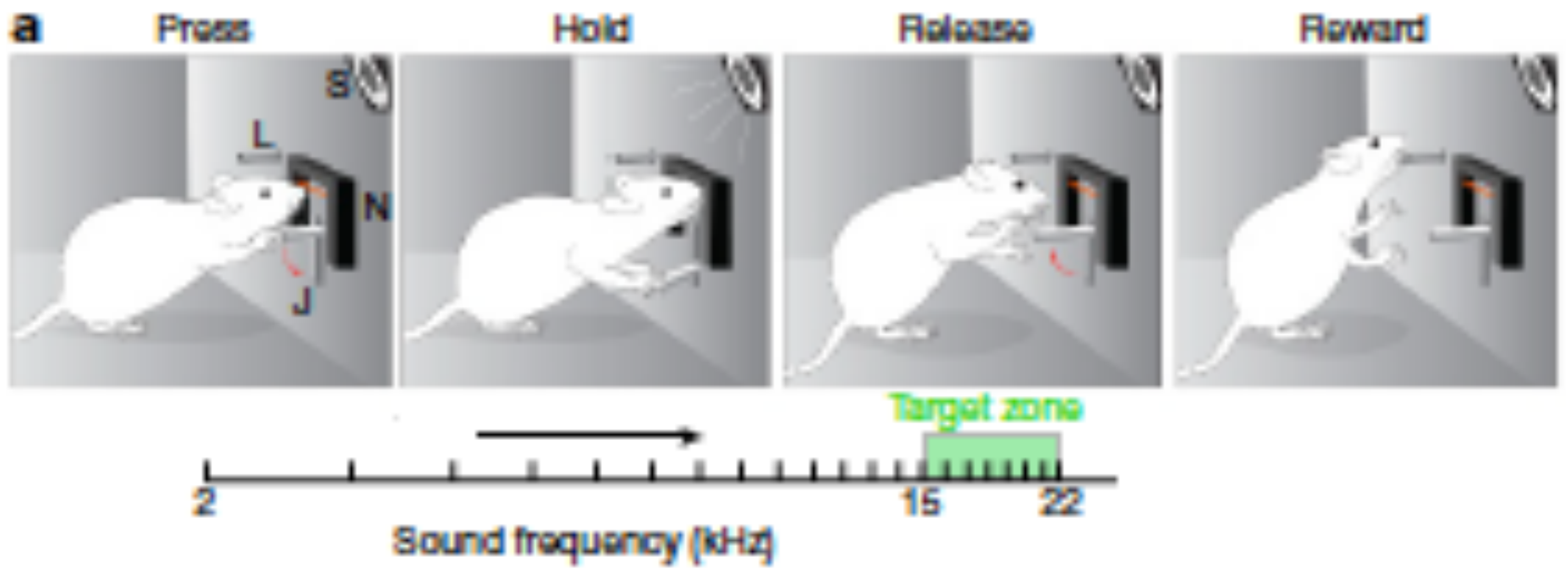
Cognitive Maps beyond space?

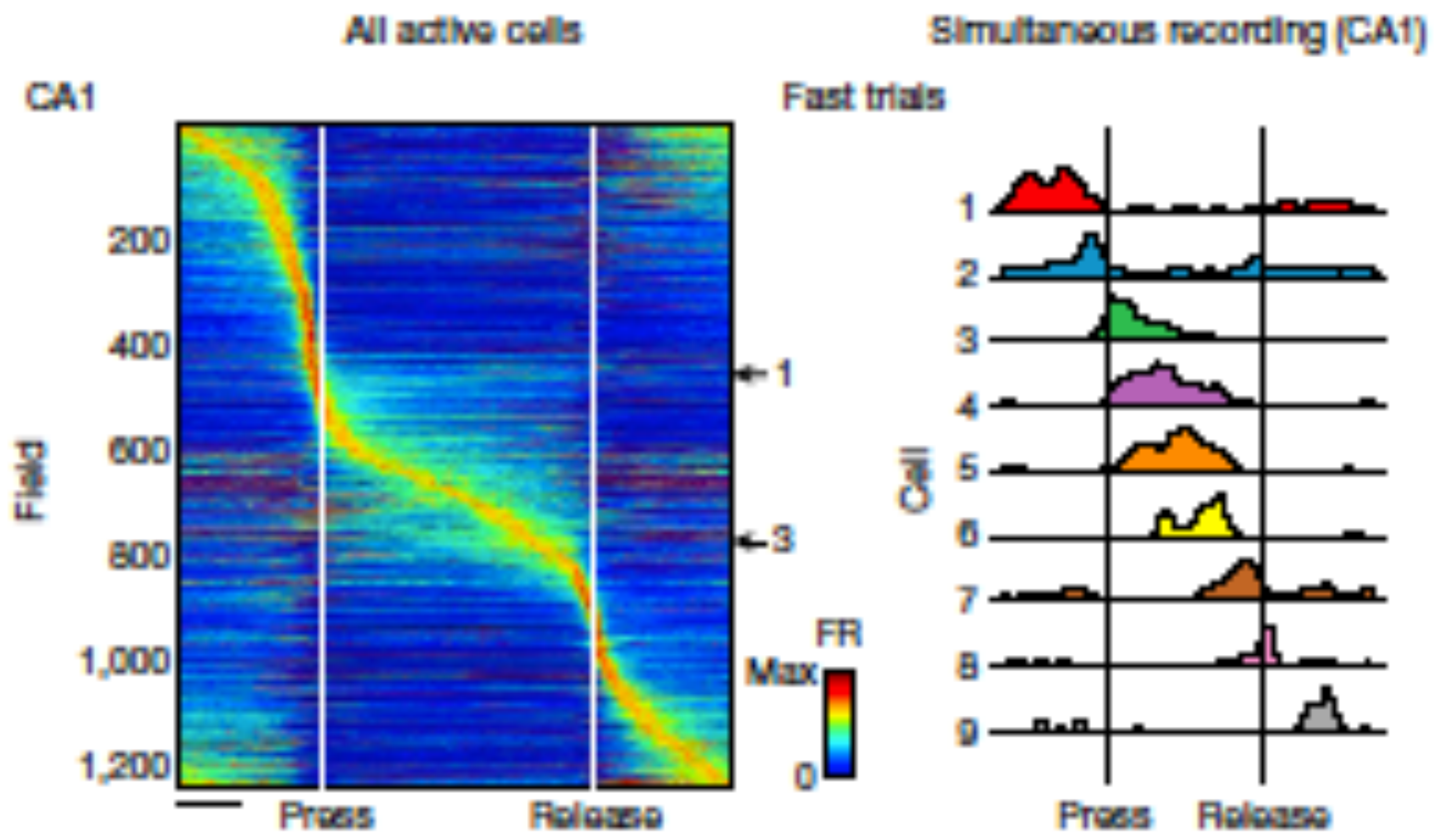
3. Additional important findings

Cognitive Maps across species?

Is the cognitive map just for space?

Place cells for sound:



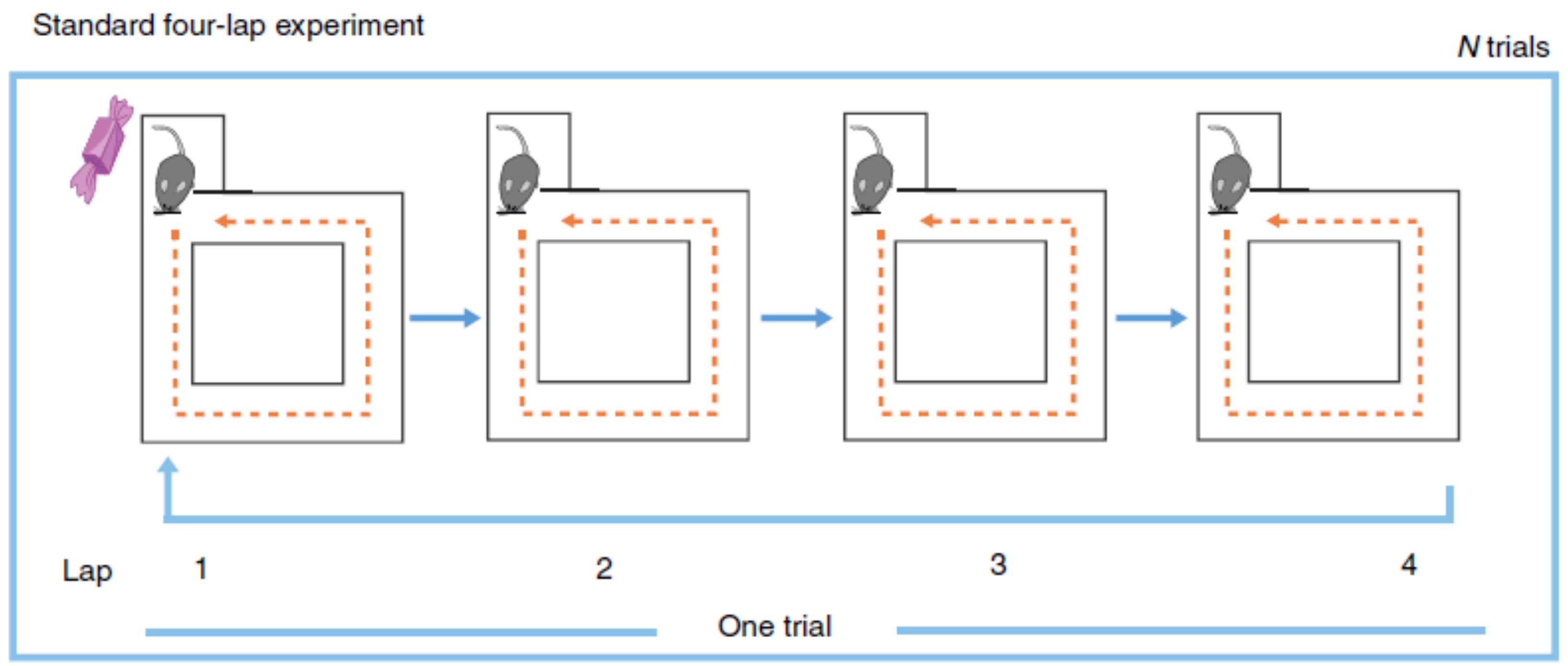


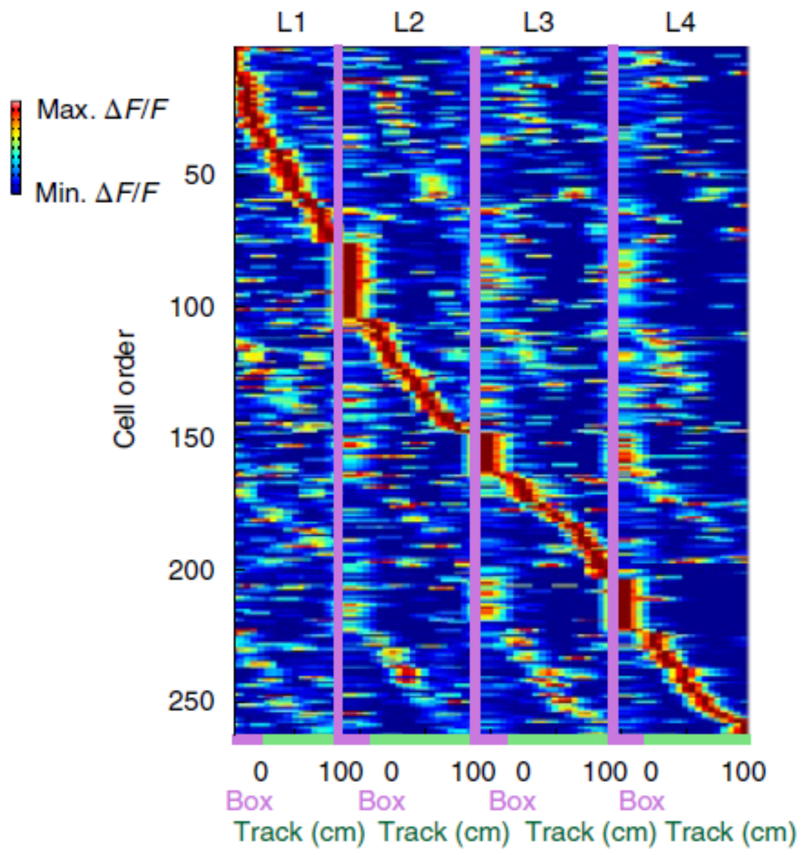
Important: cognitive maps might encode **task space**, rather than just physical space!

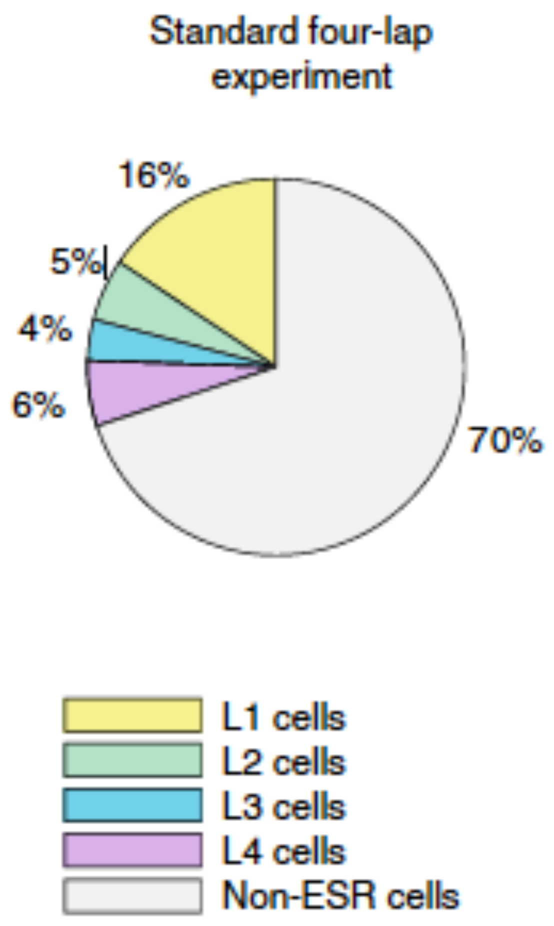
Aronov et al (2017). Mapping of a non-spatial dimension by the hippocampal–entorhinal circuit. Nature

Is the cognitive map just for space?

Place cells for lap counting:





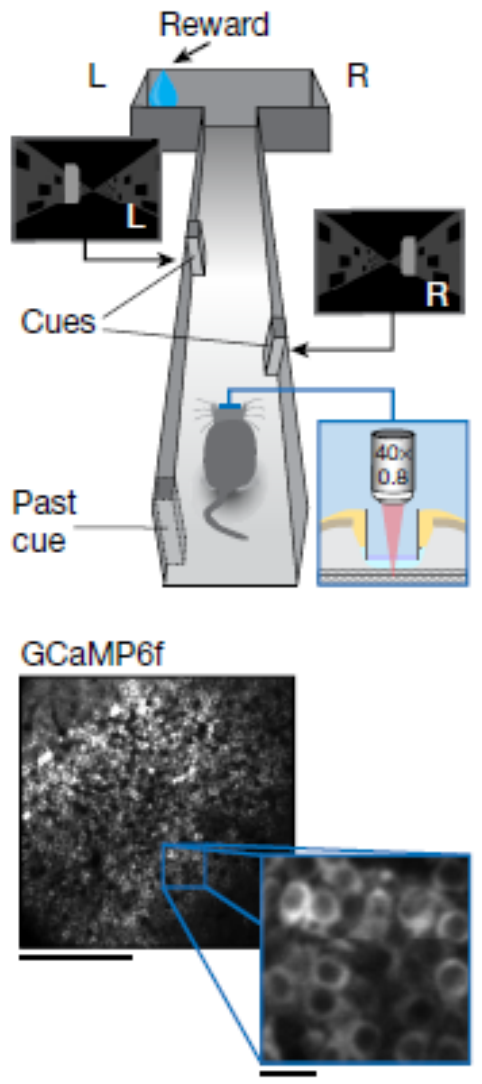


Important: cognitive maps might encode **task space**, rather than just physical space!

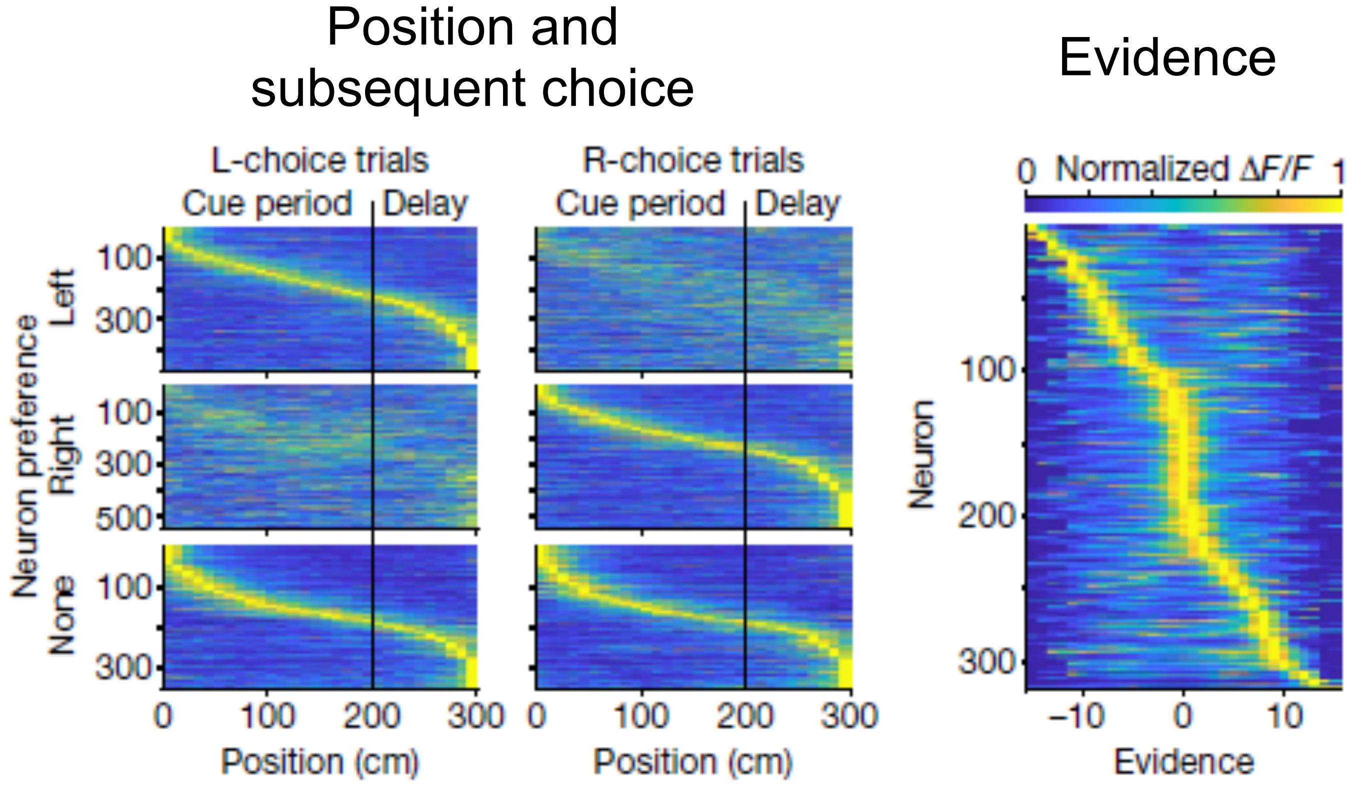
Sun et al. (2020). Hippocampal neurons represent events as transferable units of experience. Nature neuroscience

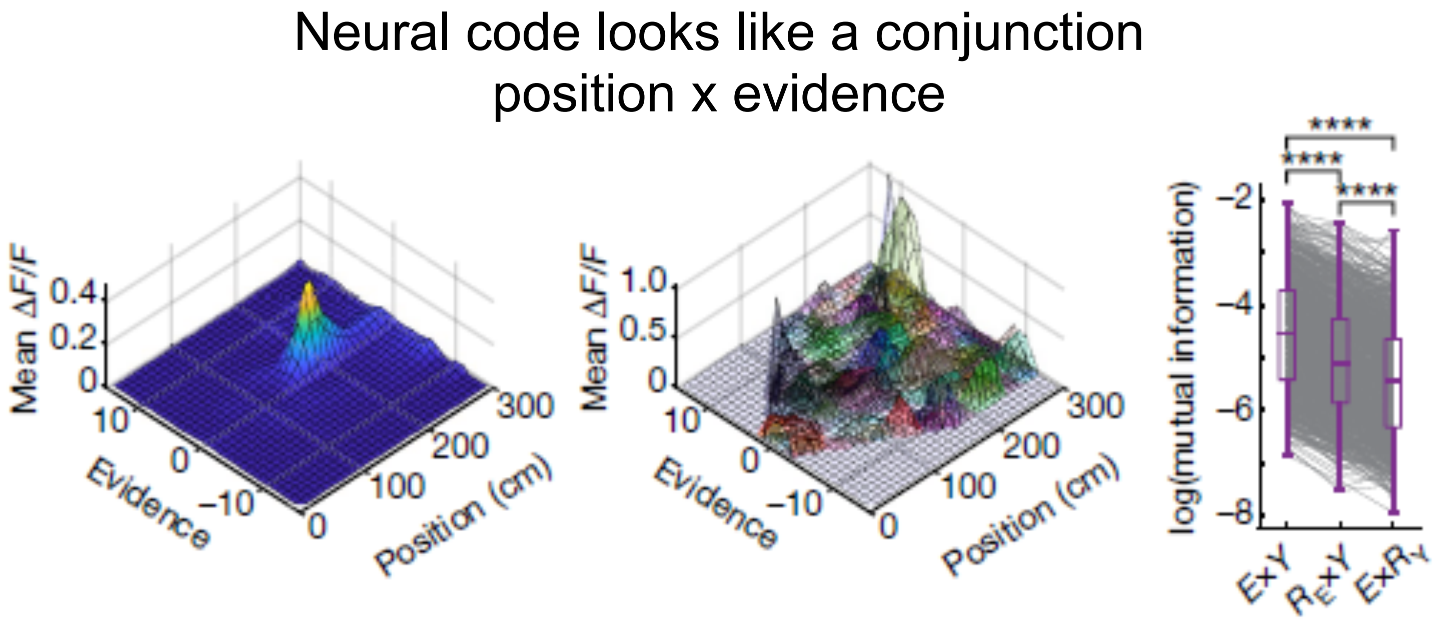
Is the cognitive map just for space?

Place cells for evidence accumulation:



Cells in hippocampus (CA1) code for



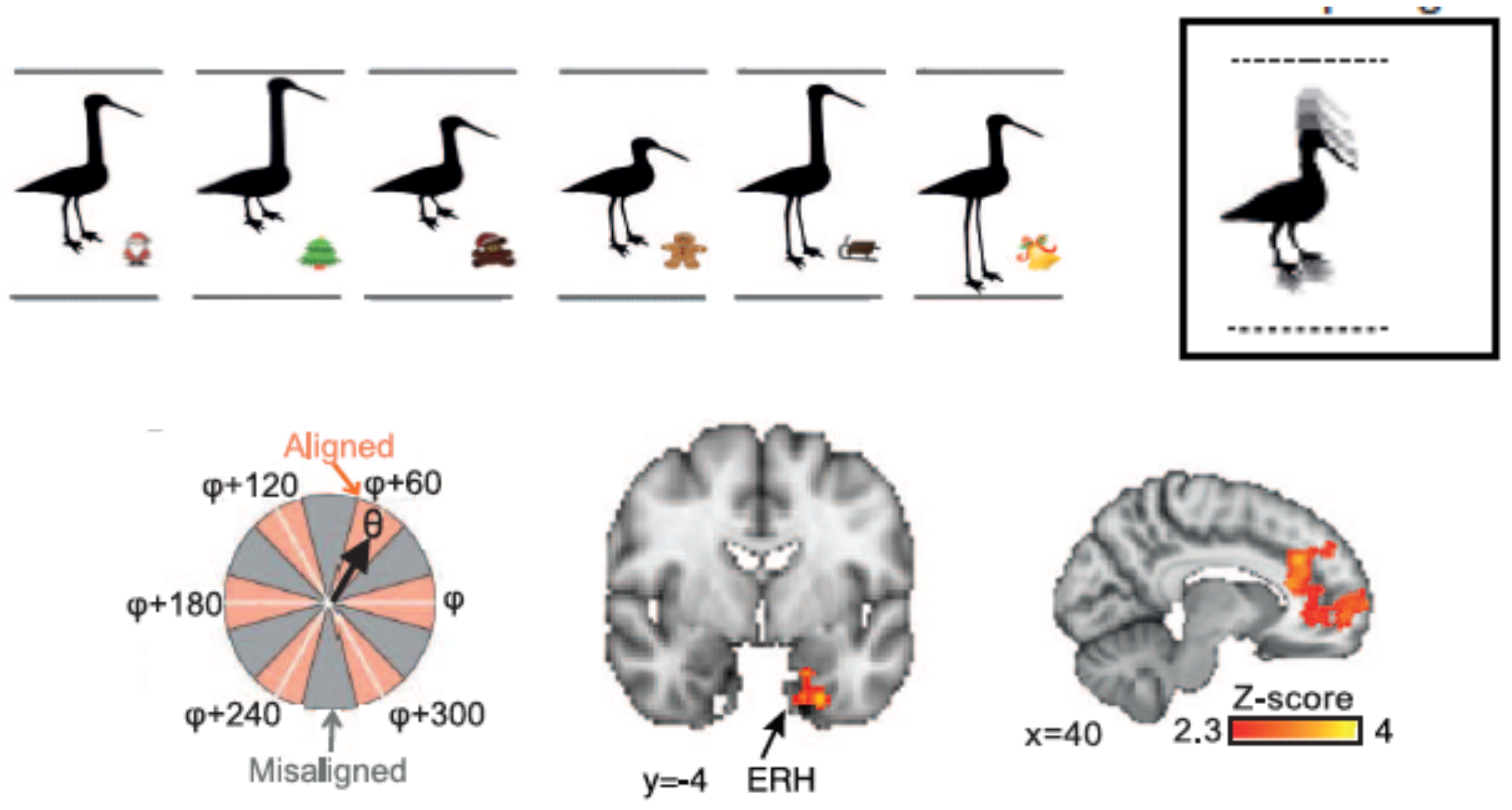


Important: cognitive maps might encode **task space**, rather than just physical space!

Nieh et al. (2021). Geometry of abstract learned knowledge in the hippocampus. Nature

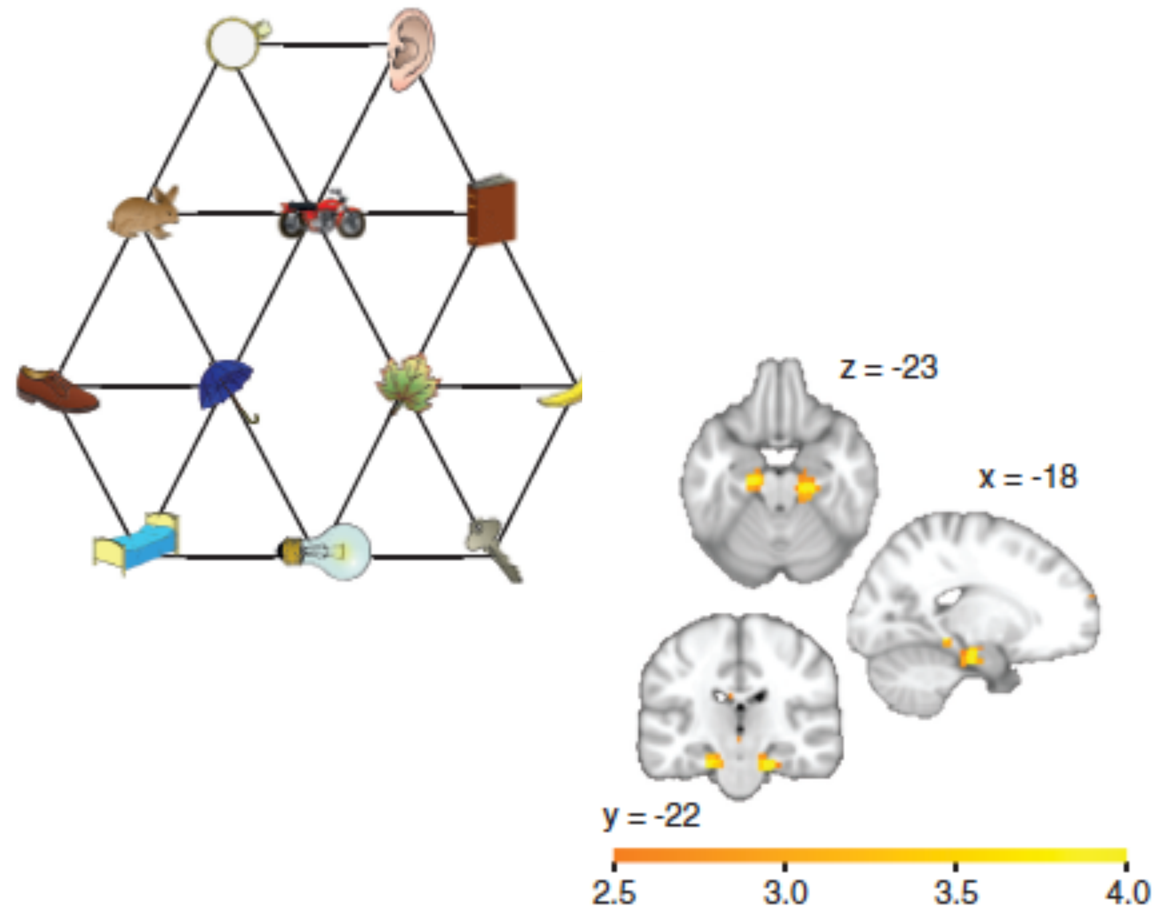
Is the cognitive map just for space?

Cognitive map of continuous conceptual space:



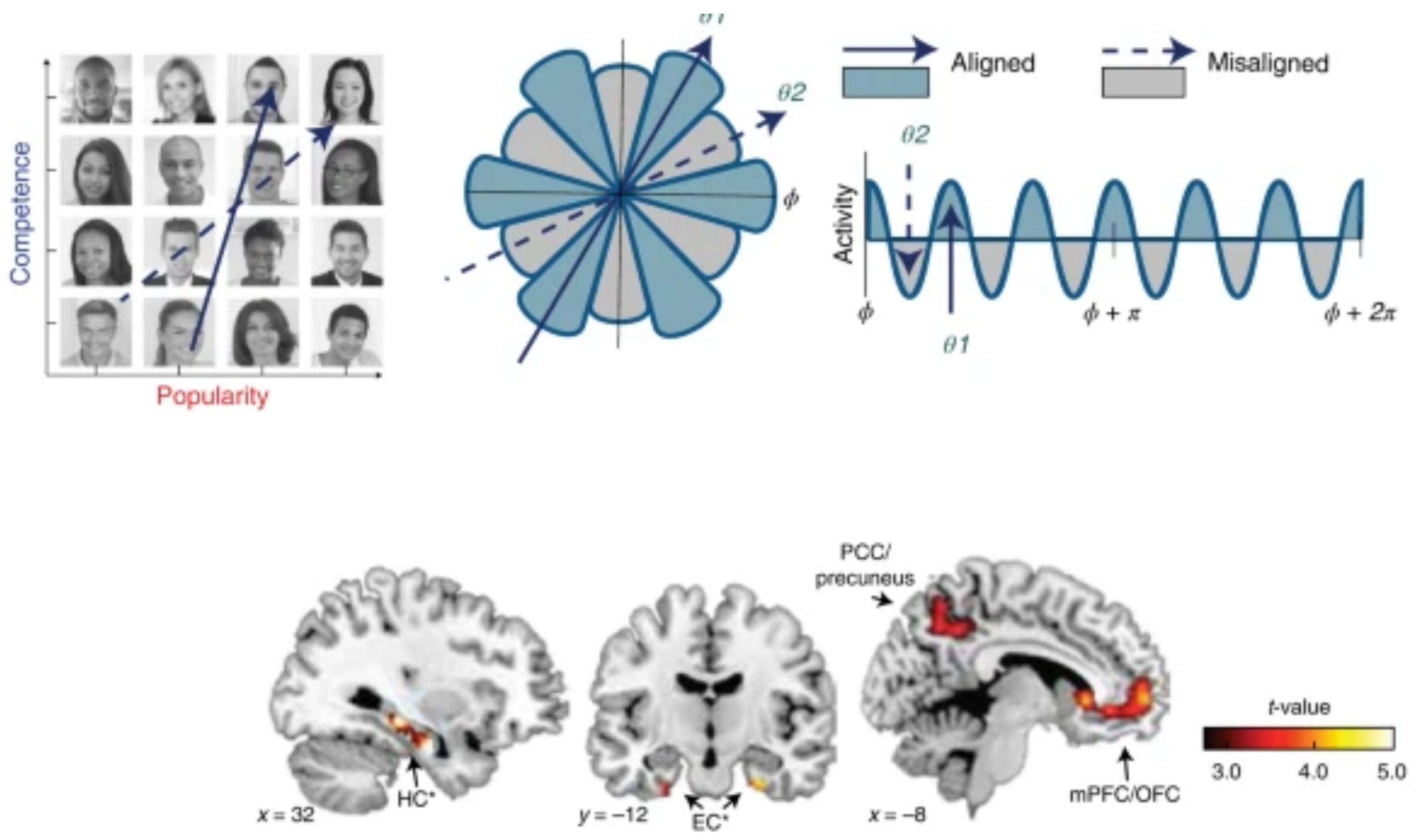
Constantinescu et al. (2016). Organizing conceptual knowledge in humans with a gridlike code. Science

Cognitive map of discrete conceptual space:



Garvert et al. (2017). A map of abstract relational knowledge in the human hippocampal–entorhinal cortex. elife

Cognitive map of social space:



Park et al. (2021). Inferences on a multidimensional social hierarchy use a grid-like code. Nature neuroscience

Important: cognitive maps might encode **task space**, rather than just physical space!

Discussion questions

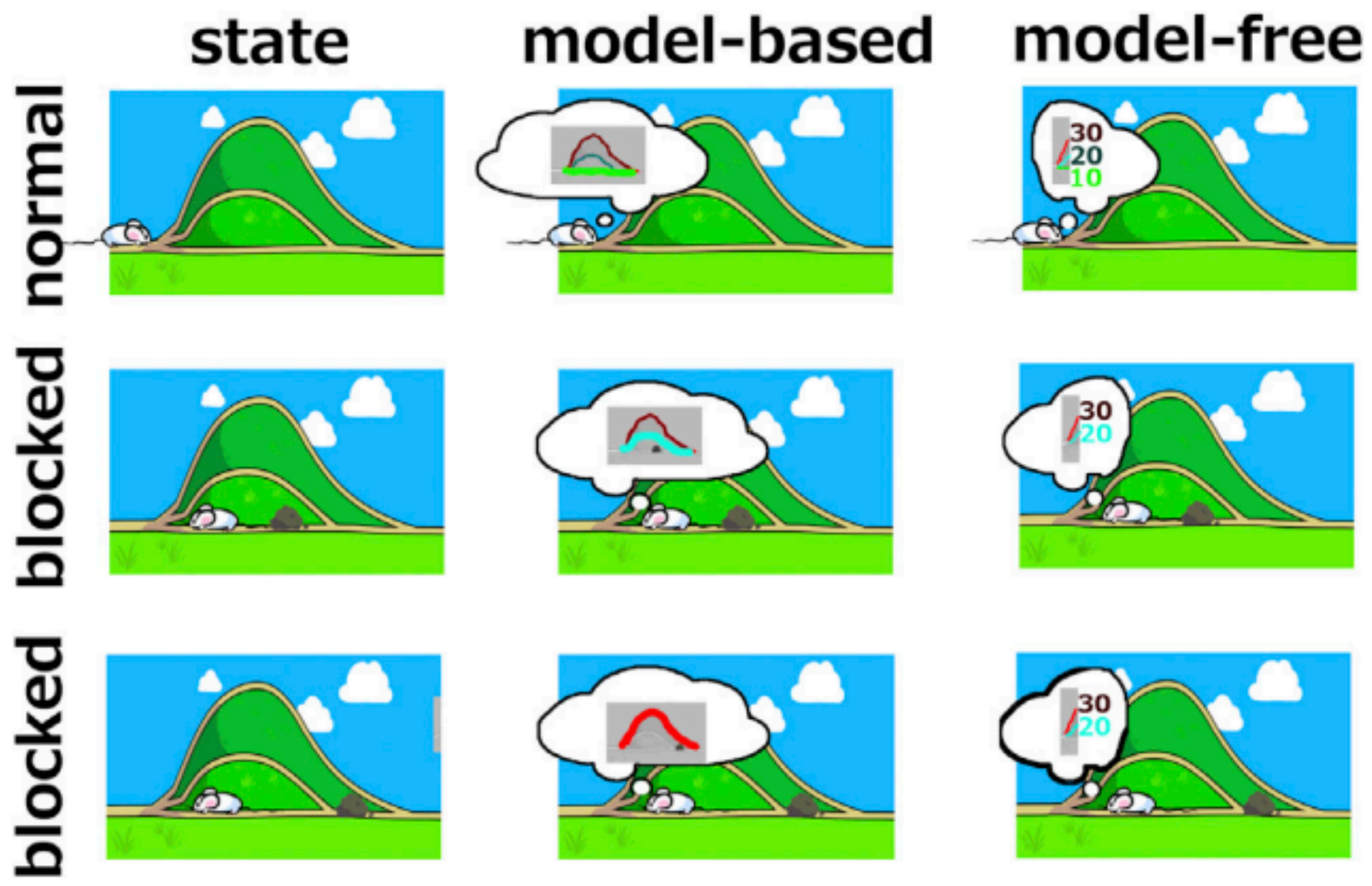
- Are cognitive maps a spatial, or is 2D physical space just a prime example?
- Do cognitive maps follow the same organisation across species, or to what degree are they adapted to a specific organism?
- You as a researcher: what do you think are important open questions and hypotheses to test?
- If have heard somewhere that the hippocampus is also relevant for memory (as well as ___, ___, …). Are these separate functions, or are they somehow related?
- What are possible head direction or boundary cells in conceptual space?

Next week

Introduction to reinforcement learning

$$V_{new}(CS_i) = V_{old}(CS_i) + \eta \left[\lambda_{US} - \sum_i V_{old}(CS_i) \right].$$

$$V_{new}(S_t) = V_{old}(S_t) + \eta(r_t + \gamma V_{old}(S_{t+1}) - V_{old}(S_t)).$$



Model-based and **model-free decision making** in a cartoon of a maze invented by Tolman and Honzik (1930)