Memories, time, space and [of course] cognitive maps

Georgy Antonov

Cognitive Maps Seminar

23/11/22

7. Dec 2022	4th floor	Philipp	Group presentation 1: Aleksejs Timcenko, David Müller, Paula de Oliveira, & Ayberk Asik	Peer, M., Brunec, I. K., Newcombe, N. S., & Epstein, R. A. (2021). Structuring knowledge with cognitive maps and cognitive graphs. Trends in cognitive sciences, 25(1), 37-54.
14. Dec 2022	Ground floor	Philipp	Group presentation 2: Katja Schach, Paula Verde Puerto, & Franziska Gekeler	Brunec, I. K., & Momennejad, I. (2022). Predictive representations in hippocampal and prefrontal hierarchies. Journal of Neuroscience, 42(2), 299-312.
11. Jan 2023	4th floor	Charley	Group presentation 3: Peter Wolters, & Simon Heuschkel	He, Q., Liu, J. L., Eschapasse, L., Beveridge, E. H., & Brown, T. I. (2022). A comparison of reinforcement learning models of human spatial navigation. Scientific Reports, 12(1), 1-11.
18. Jan 2023	4th floor	Charley	Group presentation 4: Yirong Xiong, Shweta Prasad, Ali Gholamzadeh, & Dennis Grötzinger	Pouncy, T., Tsividis, P., & Gershman, S.J. (2021). What is the model in model-based planning? Cognitive Science, 45, e12928.
25. Jan 2023	4th floor	Charley	Group presentation 5: Jiatong Liu, Ruben Tammaro, Yuguang Lin, & Laura García	Buzsáki G, Tingley D. Space and Time: The Hippocampus as a Sequence Generator. Trends Cogn Sci. 2018;22(10):853-869. doi:10.1016/j.tics.2018.07.006
1. Feb 2023	4th floor	Charley	Group presentation 6: Paige Leerssen, Mark Bailey, Dan John, Chuyu Yang	Cruse, H., & Wehner, R. (2011). No need for a cognitive map: decentralized memory for insect navigation. PLoS computational biology, 7(3), e1002009.
8. Feb 2023	4th floor	Charley	Group presentation 7: Lena Mehnert & Gabriela Iwama	Eldar, E., Lièvre, G., Dayan, P., & Dolan, R. J. (2020). The roles of online and offline replay in planning. eLife.

Plan for today

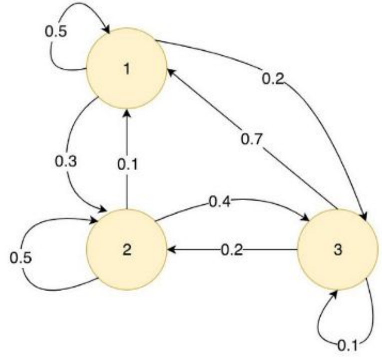
- Hippocampus and its role in memory
- Neural substrates of memory
- Causally manipulating spatial memories
- Temporal coding of events
- How are space & time integrated?

What is the model in model-based RL?

Ingredients:

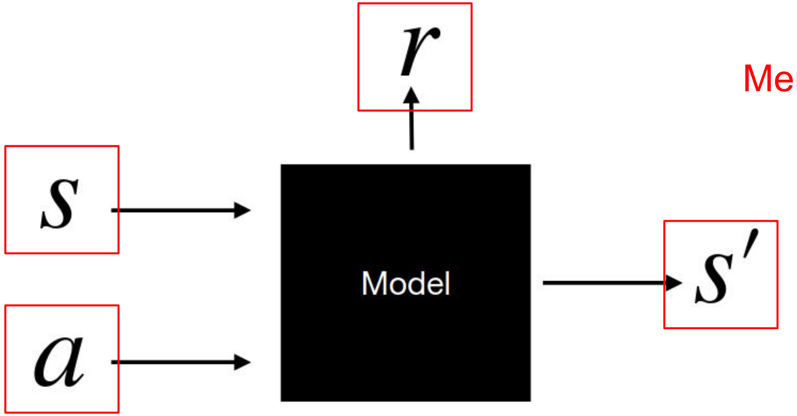
- Transition model T
- Reward function R
- State space $s \in \mathcal{S}$
- Action space $a \in \mathcal{A}$

MDP

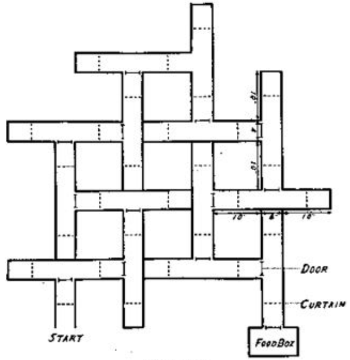


Transition Matrix

$$\begin{array}{c c} & \begin{array}{ccc} S_1 & S_2 & S_3 \end{array} \\ \begin{array}{c} S_1 \\ S_2 \\ S_3 \end{array} & \begin{bmatrix} 0.5 & 0.1 & 0.7 \\ 0.3 & 0.5 & 0.2 \\ 0.2 & 0.4 & 0.1 \end{bmatrix} \end{array}$$



Memories?



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.)

What is the model in model-based RL?

Temporal order of events is important for credit assignment – i.e., figuring out which actions and in which order lead to reward

Also known as model inversion – given you know where the goal is, how can it be reached?

DYNA does this by sampling experiences (accessing memories) and propagating reward information towards preceding states

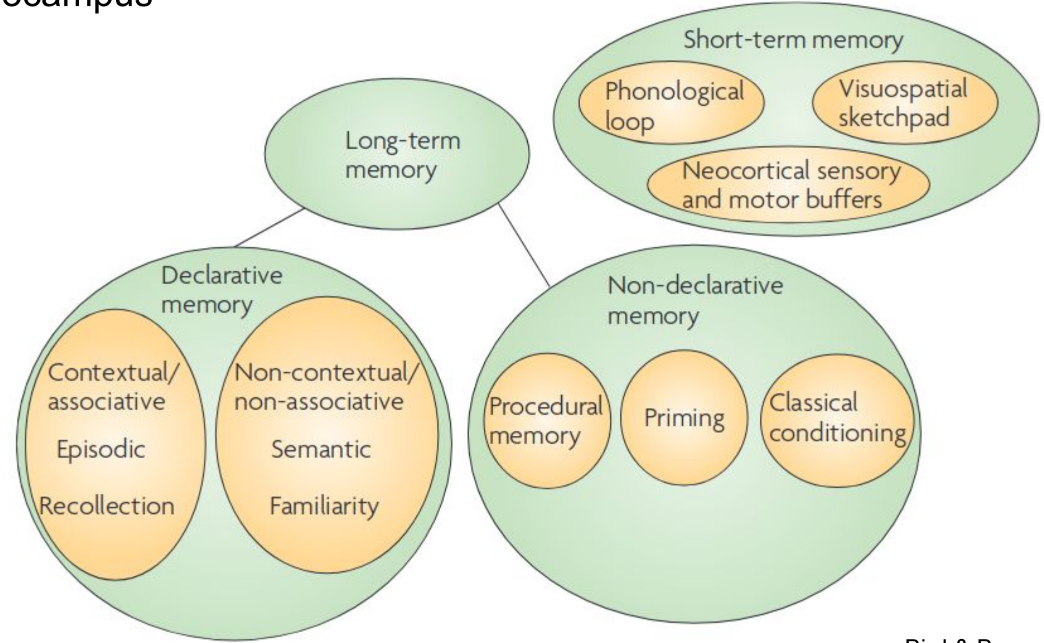
Knowing the model (structural and temporal dependencies between states and actions) is necessary for learning a good policy

Memory taxonomy

- **Short-term memory** is the ability to maintain information over a few seconds. Manipulating items in the short-term memory is usually referred to as working memory

Hippocampus

- **Declarative** (or explicit) **memory** is something that can be consciously recalled based on experience
    - **Semantic memory** refers to factual knowledge (e.g., one can eat food with their favourite utensils)
    - **Episodic memory** relates to specific events in our lives



Bird & Burgess (2008)

Hippocampus

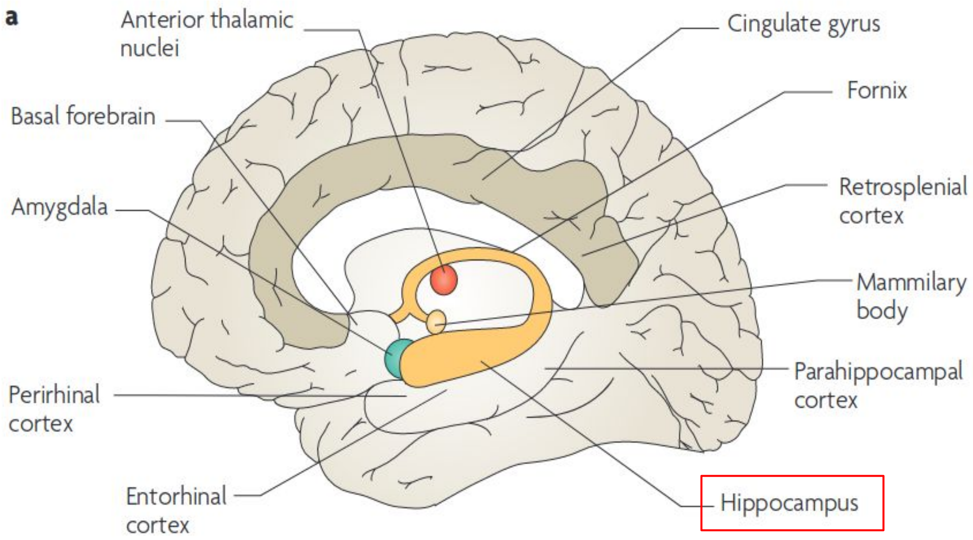
How do we know its role in memory?

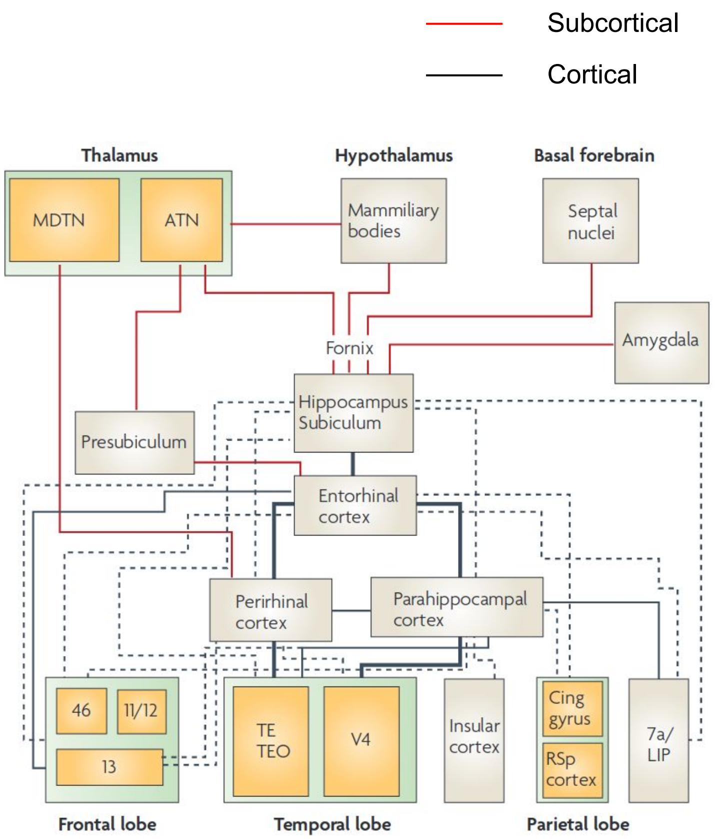
- Memory deficits following damage to HPC (e.g., patient HM)
    - Mostly episodic memories; those acquired prior to damage remain intact
- Recent studies causally manipulate HPC activity to affect memory

Several theories have been proposed:

- **Declarative theory** posits that HPC is critical for all forms of declarative memory but for a limited time; memories are ultimately consolidated (transferred) to cortex
- Relational (**cognitive map**) theory. HPC is important for learning predictive (model-based) associations.

Hippocampus





HPC receives inputs from major cortical areas

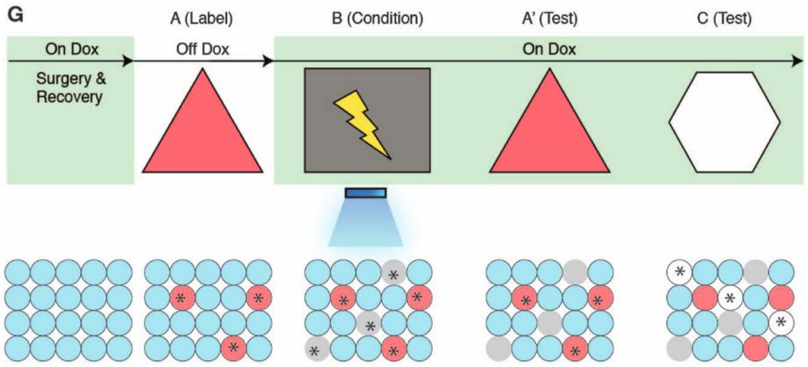
HPC is thus ideally positioned to integrate the sensory ‘what’ with the navigational ‘where’ information

Engrams – memory traces

Creating a False Memory in the Hippocampus

STEVE RAMIREZ, XU LIU, PEI-ANN LIN, JUNGHYUP SUH, MICHELE PIGNATELLI, ROGER L. REDONDO, TOMÁS J. RYAN, AND SUSUMU TONEGAWA Authors Info & Affiliations

SCIENCE • 26 Jul 2013 • Vol 341, Issue 6144 • pp. 387-391 • DOI: 10.1126/science.1239073



Activating the engram encoding ‘A’ in ‘B’ paired with foot shock led to animals subsequently freezing in ‘A’ but not a distinct ‘C’

Engrams and circuits crucial for systems consolidation of a memory

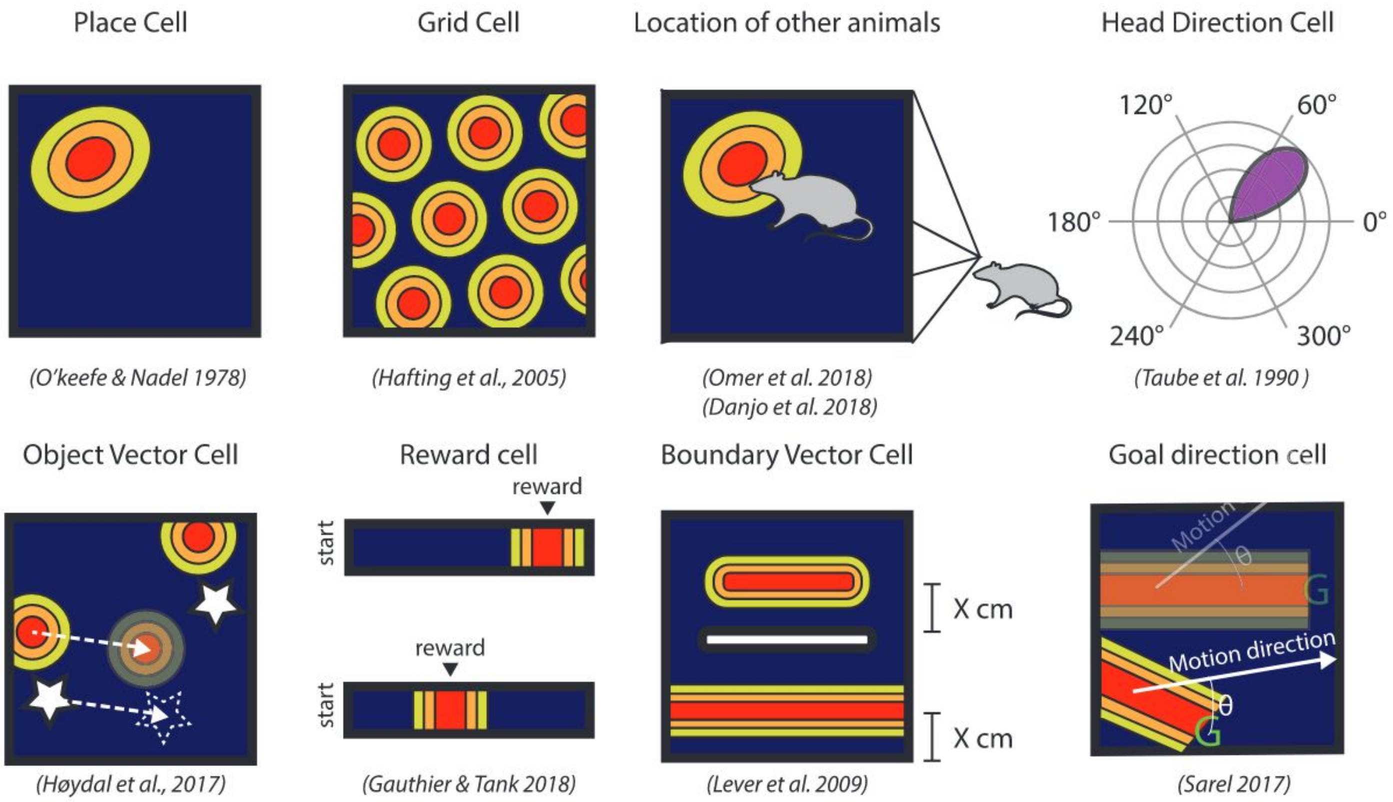
TAKASHI KITAMURA, SACHIE K. OGAWA, DHEERAJ S. ROY, TERUHIRO OKUYAMA, MARK D. MORRISSEY, LILLIAN M. SMITH, ROGER L. REDONDO, AND SUSUMU TONEGAWA Authors Info & Affiliations

SCIENCE • 7 Apr 2017 • Vol 356, Issue 6333 • pp. 73-78 • DOI: 10.1126/science.aam6808

Communication between HPC-EC and cortical areas during memory acquisition is necessary for its maturation and successful retrieval

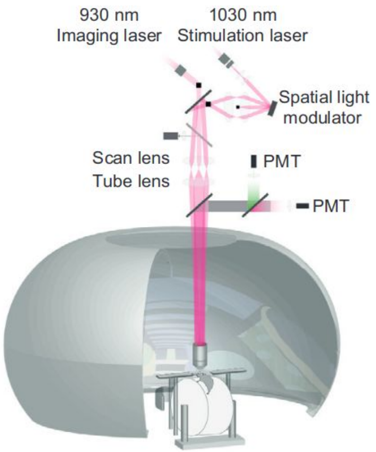
So it’s not quite true that HPC is solely responsible for the acquisition of new memories

Hippocampal zoo



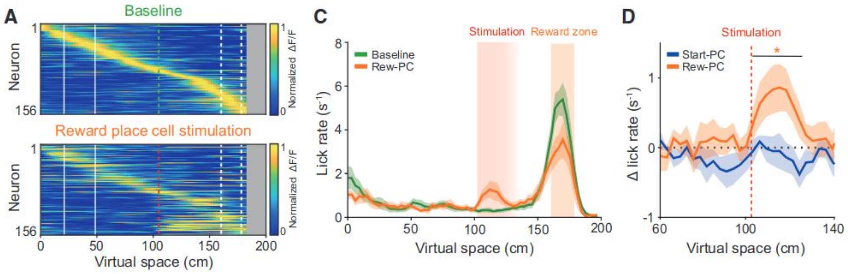
Behrens et al. (2018)

Manipulating spatial memories during behaviour

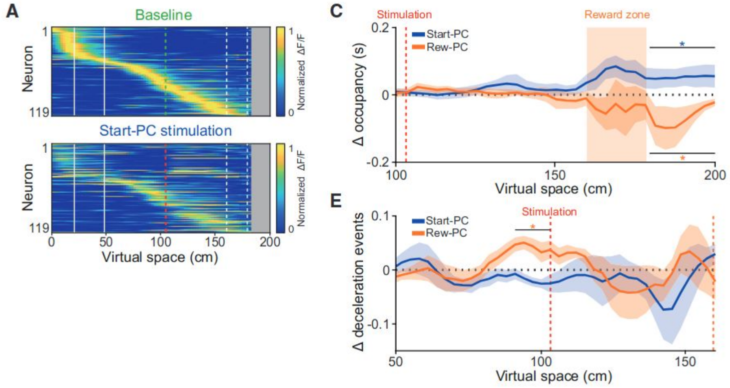


‘All-optical interrogation’ – optogenetic stimulation of dozens of functionally defined neurons + imaging at the same time

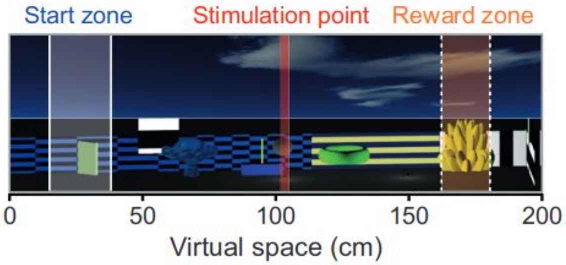
Stimulation of Reward Zone Place Cells



Stimulation of Start Zone Place Cells

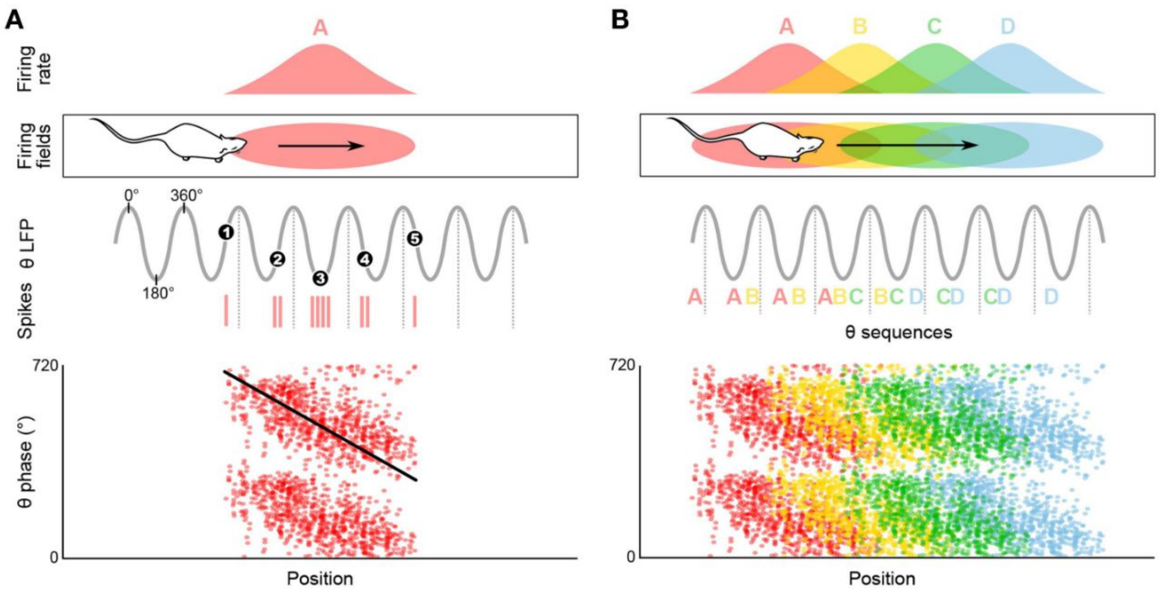


Virtual environment



Manipulating place cell activity affects behaviour

Theta precession



Place cells exhibit phase precession – their firing rate is modulated by the phase of the ongoing theta oscillation

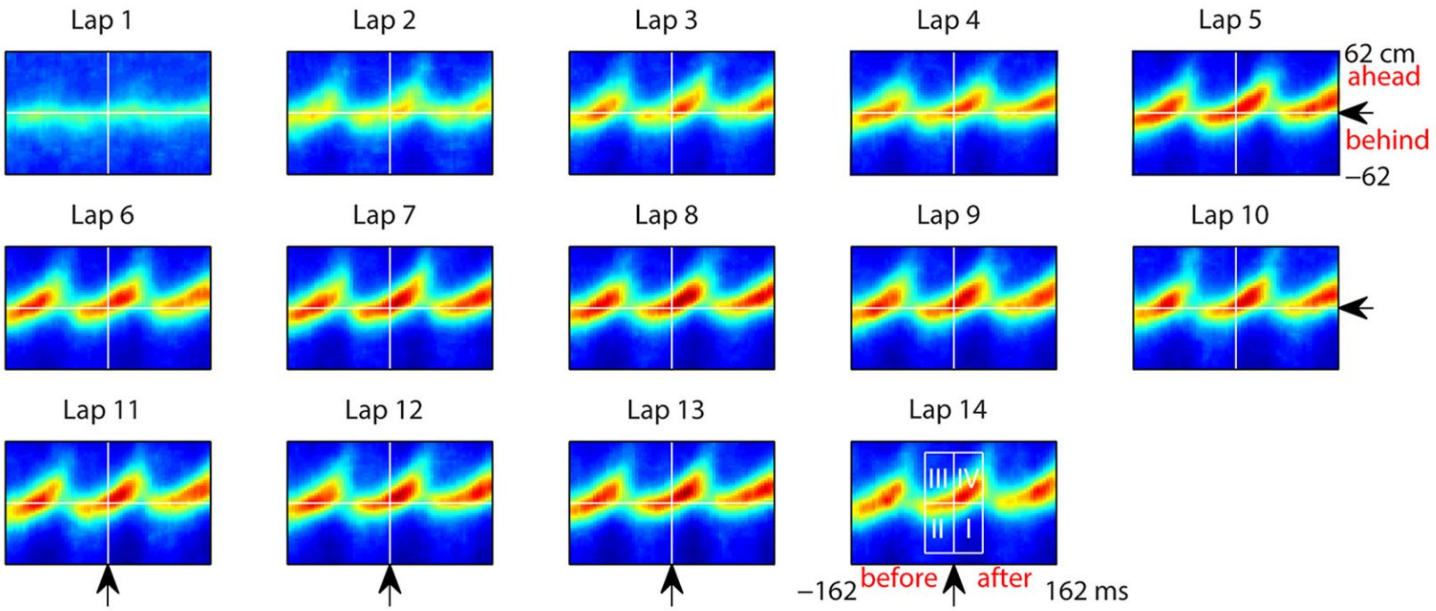
Theta sequences: the timing between each cell's firing is suitable for STDP – memory encoding?

Phase information is useful for estimating distance traversed through each receptive field

Hippocampus binds events across time and space into conjunctive memory representations

Drieu & Zugaro (2019)

How long does it take to acquire a ‘memory’?

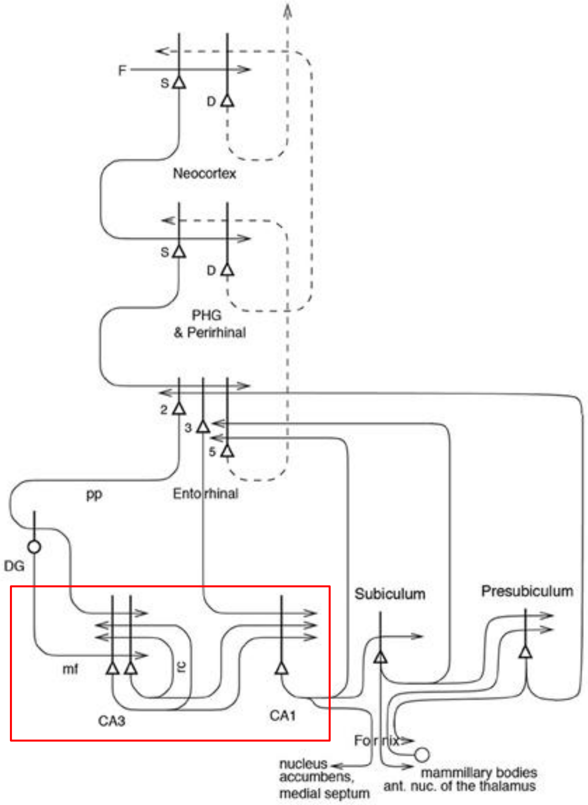


Theta sequences appear immediately after the very first experience of a novel environment

Feng, Silver, Foster (2015)

5-min break?

Are time and space coded independently?



CA3 and CA1 have independent inputs and outputs; it is therefore possible that there are differences in how the HPC subfields process / encode spatial and temporal information

CA3 (but not CA1) lesions impair object-place and odour-place associations; CA1 (but not CA3) lesions impair the learning of associations which involve temporal gaps. CA3, however, might be important for short interval associations

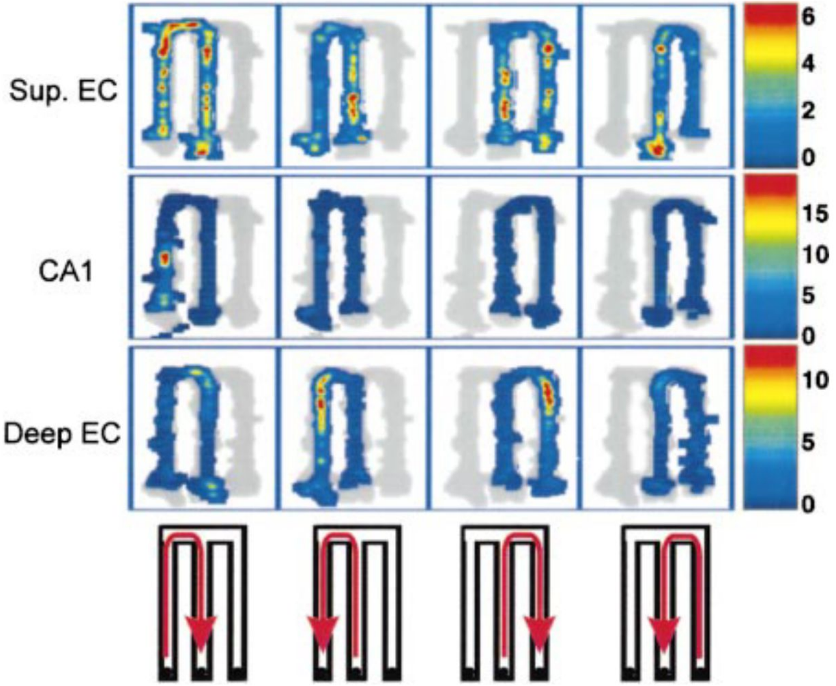
CA3 is critical for object-spatial associations and CA1 – for associations between objects across time? OR do they both encode (different) temporal information?

Rolls (2013)

Splitter cells

Spatial firing patterns in CA1 (but not CA3 and mEC) seem to depend on the animal's path history – i.e., they discriminate paths depending on a trajectory defined by the temporal context.

In RL terms, this can also be thought of as the animal's subjective belief state (see belief MDPs)

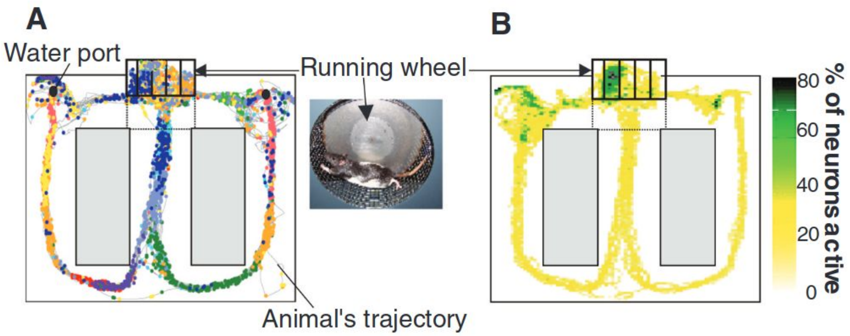


Frank, Brown, Wilson (2000)

Pastalkova et al. (2008)

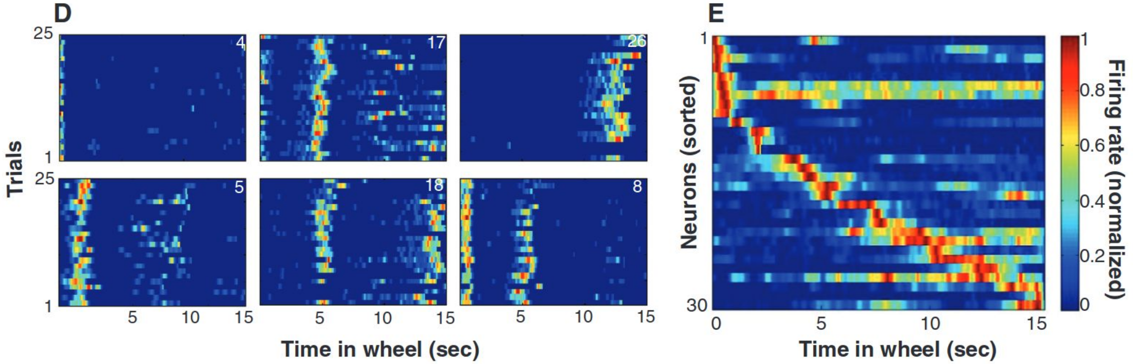
Time cells

Is time representation a consequence of the sequential / ordered nature of spatial experience?

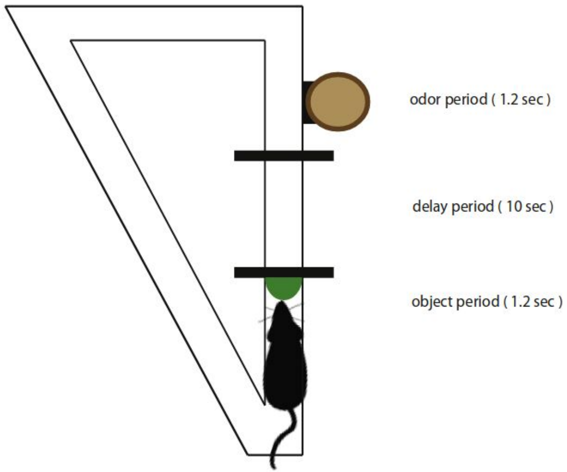


Alternating T-maze where in between each trial animals had to run steadily in the same direction on a wheel

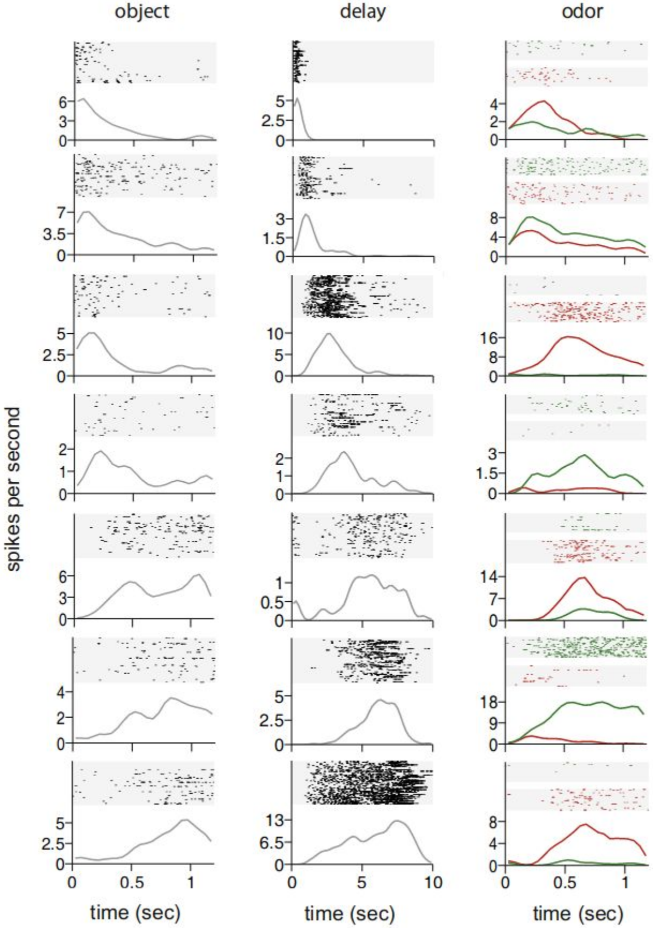
Some CA1 neurons selectively discharged at specific elapsed time intervals (also selective for left/right turn trials)

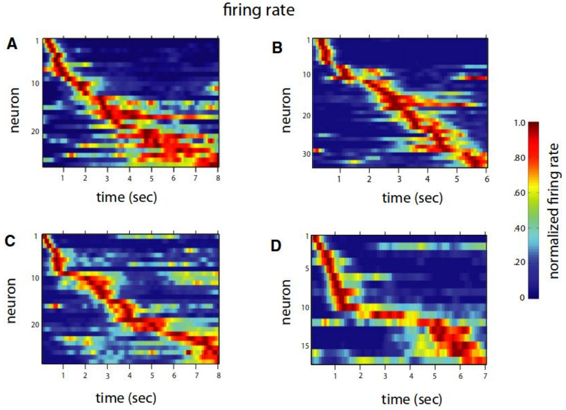


Time cells



- 2 objects, each paired with a distinct odour
- Temporal delay renders the task memory-dependent



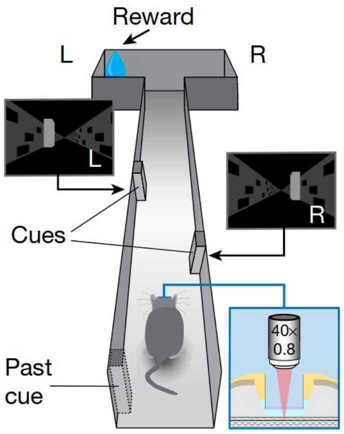


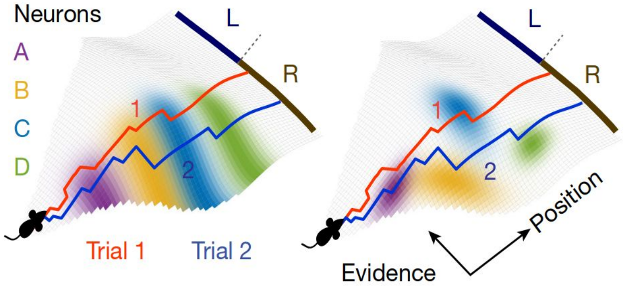
Hippocampal ‘time cells’ encode temporal information during the delay period

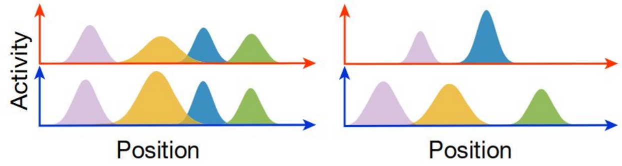
MacDonald et al. (2011)

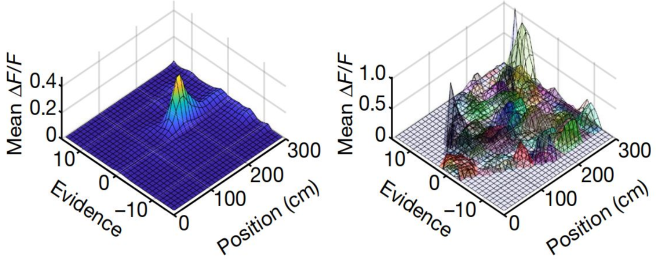
Conjunctive representations in CA1

Evidence accumulation task in virtual reality









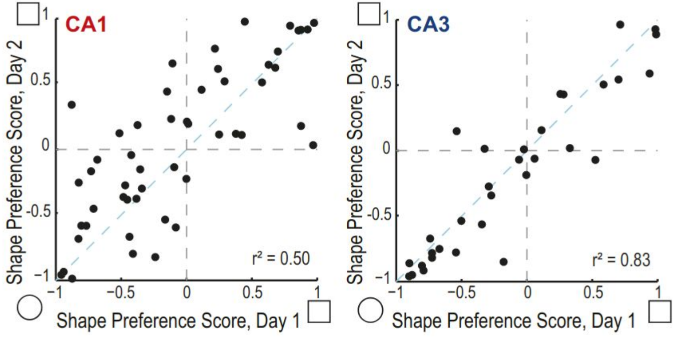
Conditional spatial representation by individual CA1 neurons looks noisy (trial-to-trial variability)

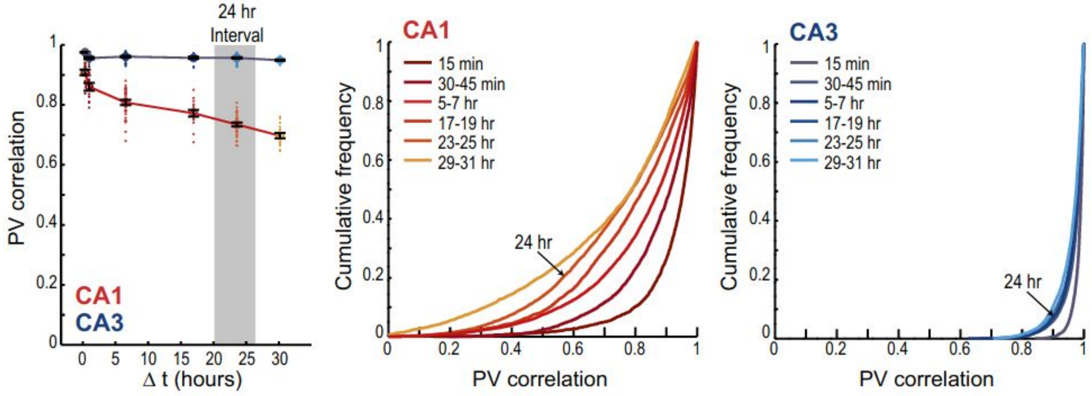
Joint representation (space + task evidence) – conjunctive encoding of multiple experience dimensions

Nieh et al. (2021)

Representational drift – temporal code?

Long-term memory requires stable activity patterns for accurate memory retrieval; however, variability in the activity can represent temporal distances between experiences





Both CA1 and CA3, however, still reliably dissociate 2 environments

Temporal fluctuations in firing activity are greater in CA1 than in CA3

Mankin et al. (2012)

Internally Generated Sequences

One prominent idea is that the HPC acts as a sequence generator – that is, it plays out sequences onto which incoming sensory data are mapped to create episodes of experience ordered in time

RESEARCH ARTICLE | BIOLOGICAL SCIENCES

Distinct preplay of multiple novel spatial experiences in the rat

George Dragoi and Susumu Tonegawa Authors Info & Affiliations

Trajectory events across hippocampal place cells require previous experience

Delia Silva, Ting Feng & David J Foster

One study reported sequential activations prior to experience which was then mapped onto those 'preplayed' sequences

Another study reported that their shuffling procedure produced spurious correlations, and those 'preplays' were chance events

So it's unclear…

Temporal Context Model

- Initially proposed to account for recency and contiguity effects in free recall in humans [Howard & Kahana (2006)]
- Recent events are more likely to be recalled first (recency); events that are near (in time) to those previously recalled follow suit
- Assumes a leaky (or exponentially decaying) trace of an event
- Temporal order can then be reconstructed by e.g. Laplace transform [Howard et al. 2014]
- Similar models have been developed for spatial coding [Momennejad & Howard 2018], as well as value representation [Tano & Dayan 2021]

Conclusions

- Hippocampus is important for episodic memory formation, although not solely
- Those memories are acquired rapidly, after single experience
- Recent studies casually probe the role of HPC in memory processing
- Spatial and temporal information is processed by overlapping (albeit not identical) networks, which all converge onto the HPC
- HPC encodes both time and space (and other task variables) conjunctively, yet there is likely to be a division of labour across the different HPC subfields
- More generally, HPC is thought to learn the predictive associational structure thus linking space and time in a predictive manner (next session)

Your questions