

Introduction to Neuroscience: Systems Neuroscience

The hippocampus in spatial navigation and memory consolidation

Nachum Ulanovsky

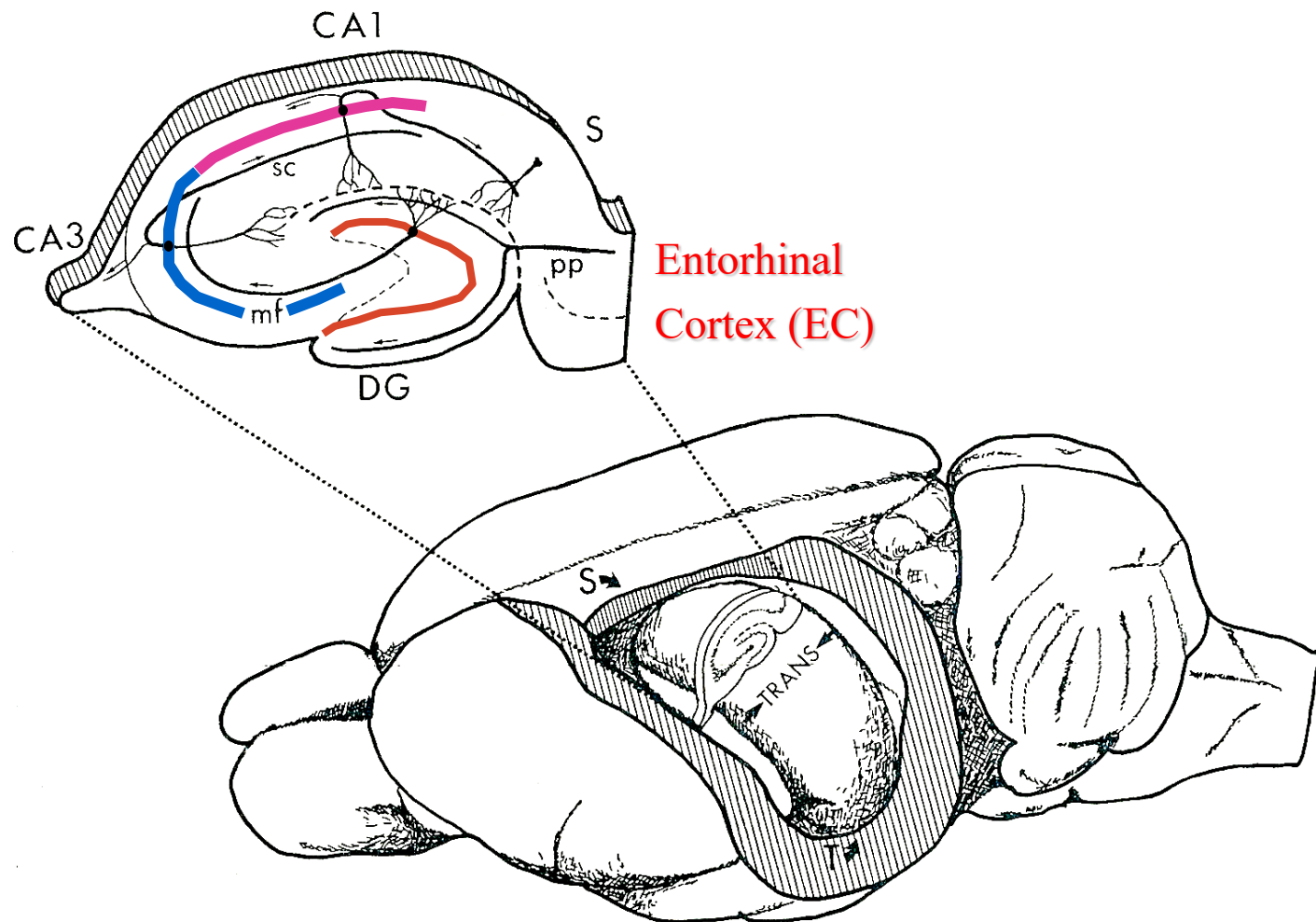
Outline of today's lecture

- **Hippocampus: Introduction and early discoveries**
- **Spatial maps in the hippocampus and related regions:**
 - **Place cells**
 - **Head direction cells**
 - **Grid cells**
- **Beyond the cognitive map: Hippocampus and memory**
- **Open questions**

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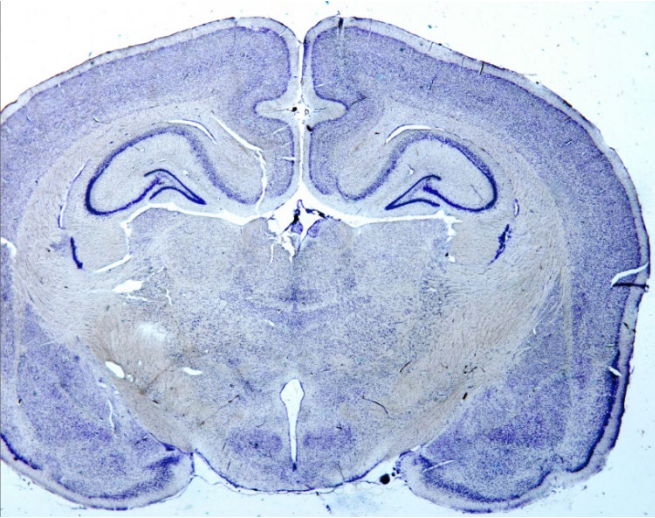
The hippocampus



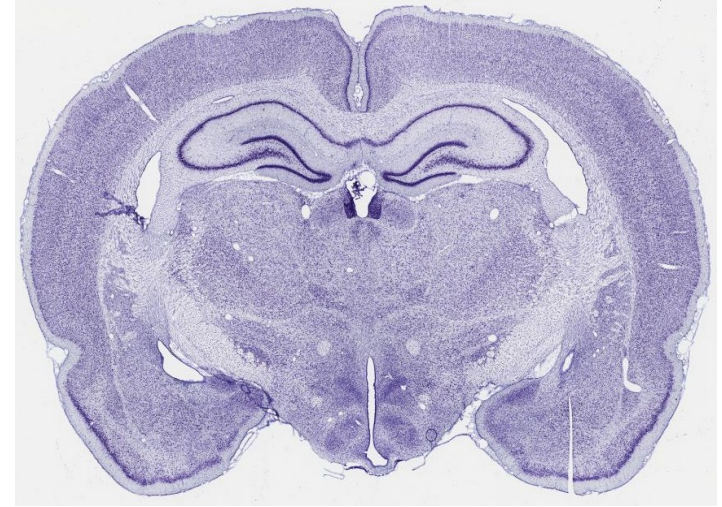
(Amaral and Witter 1989)

The hippocampus is highly conserved across mammals

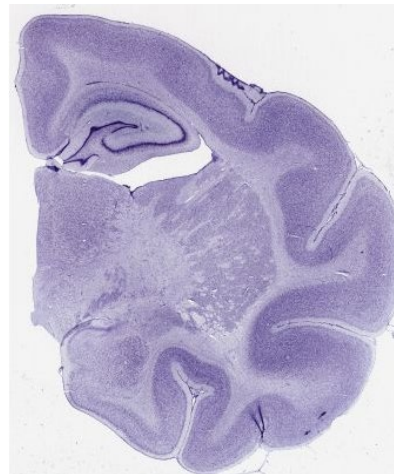
Egyptian fruit bat



Rat

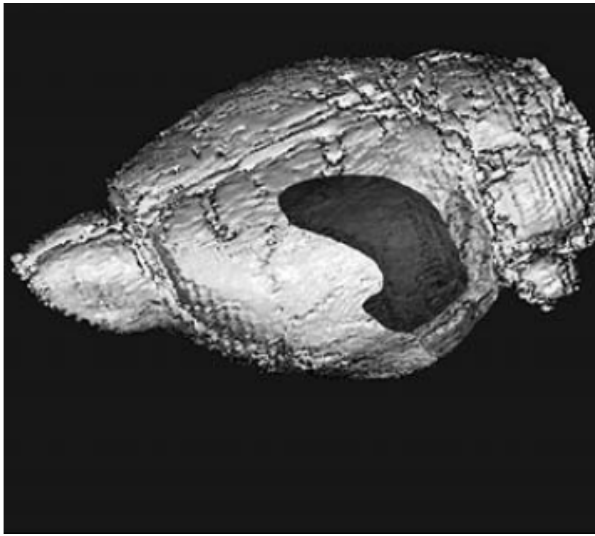


Echidna
(ancient egg-laying mammal)



Highly conserved brain structure across all mammals, including humans (exists also in birds, but looks quite different)

The hippocampus is highly conserved across mammals

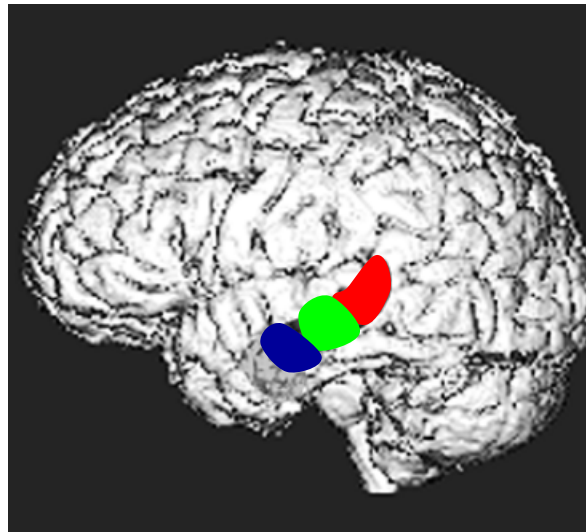
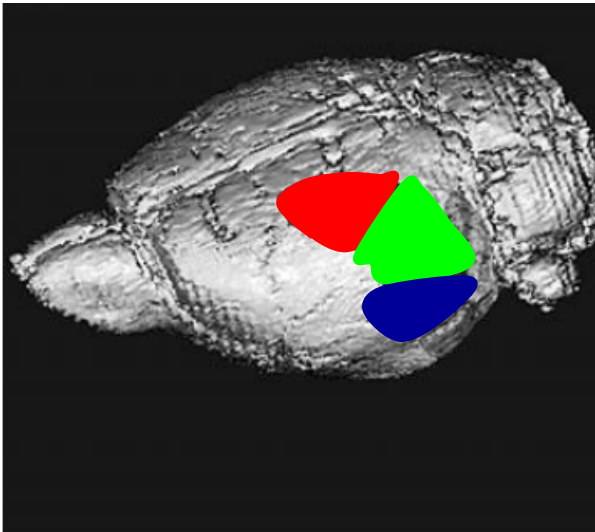


Rat



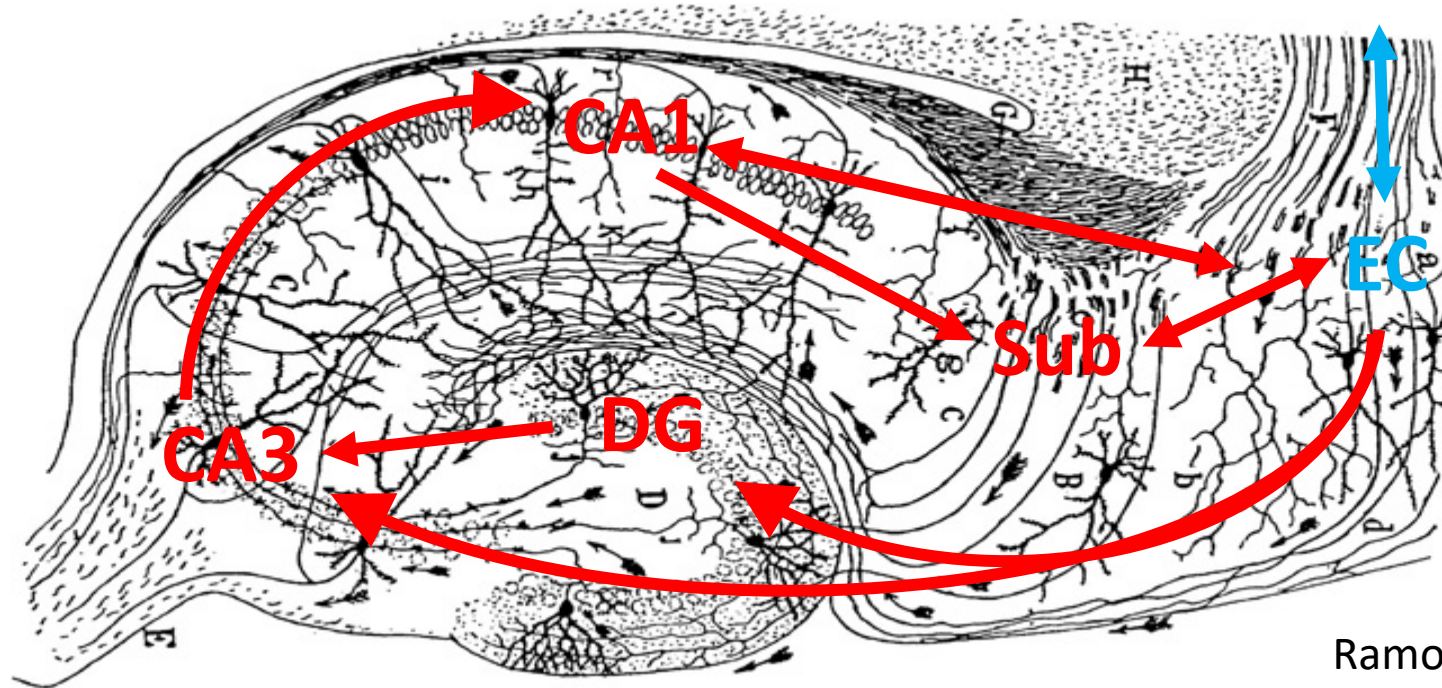
Human

In primates: The hippocampus is at the bottom of the brain and rotated 90° backwards compared to rats, but otherwise is very similar.



Posterior hippocampus in humans is equivalent to *dorsal (septal) hippocampus* in rats (**red**).

The hippocampus is part of a primarily uni-directional processing loop: entorhinal cortex → hippocampus → entorhinal cortex



Ramon y Cajal

EC Entorhinal Cortex

CA1 Cornu Ammonis 1

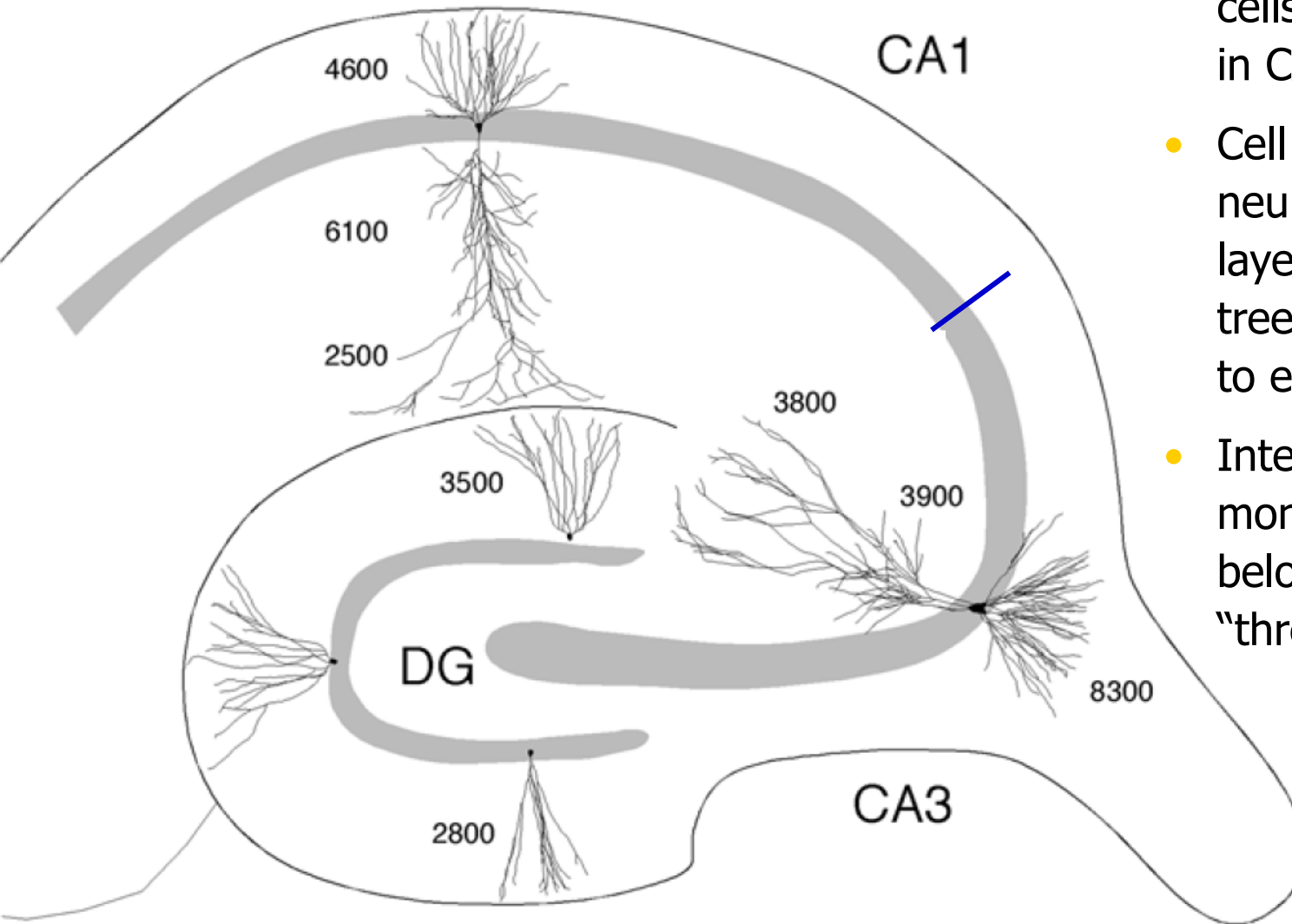
CA3 Cornu Ammonis 3

DG Dentate Gyrus

Sub Subiculum

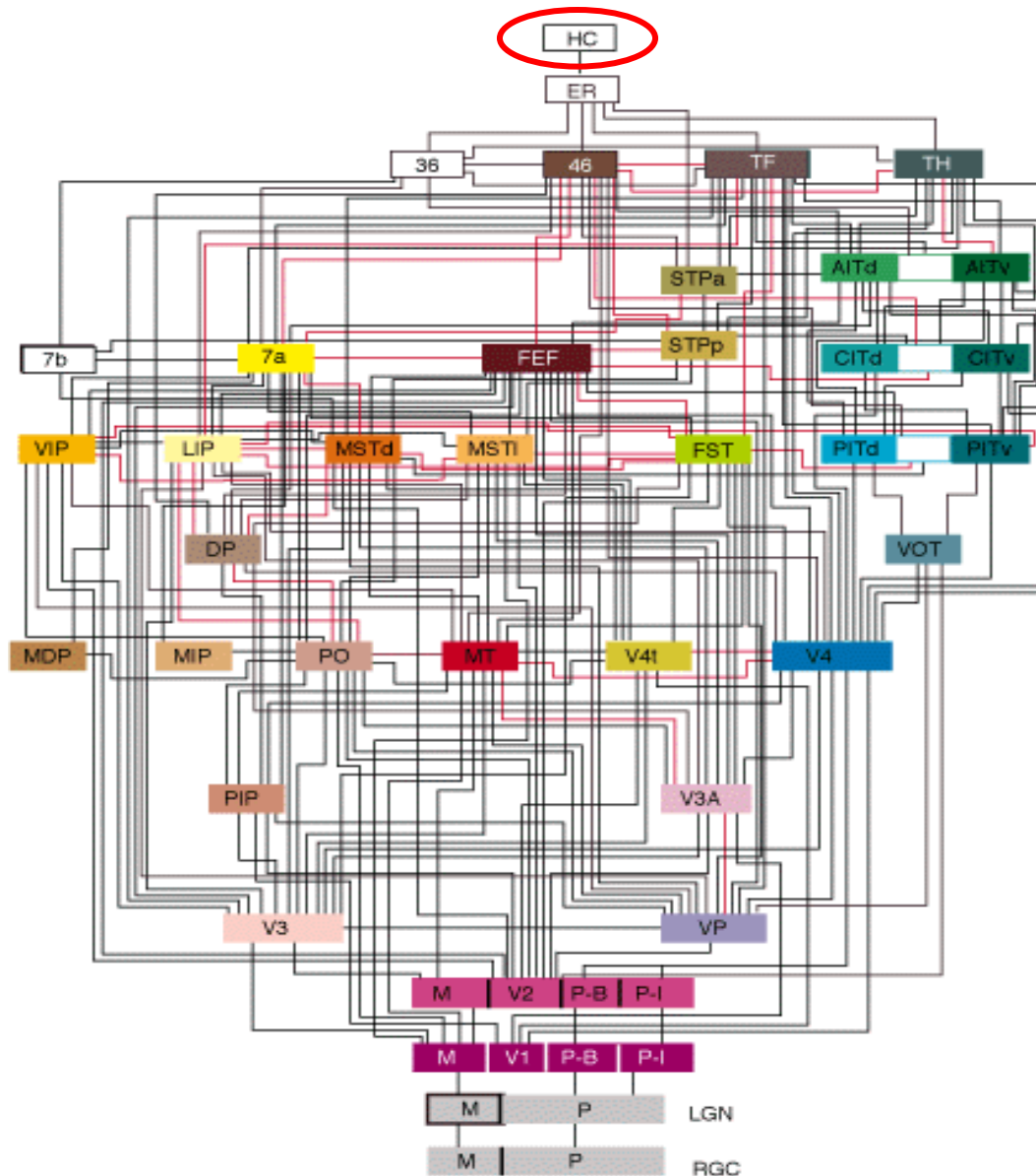
- This uni-directional connectivity is quite different than what is typically found in neocortex, where connectivity is usually bi-directional (i.e., if area A projects to B, then B also projects to A).

The hippocampus is a single-layer (or three-layer) cortex



- Projections neurons: Granule cells in DG and Pyramidal cells in CA1 and CA3
- Cell bodies of projection neurons form almost a mono-layer (in the rat), and dendritic trees are very orderly parallel to each other
- Interneurons are found in the mono-layer, but also above and below it (hence the term "three-layer cortex")

The hippocampus is a high-level brain region



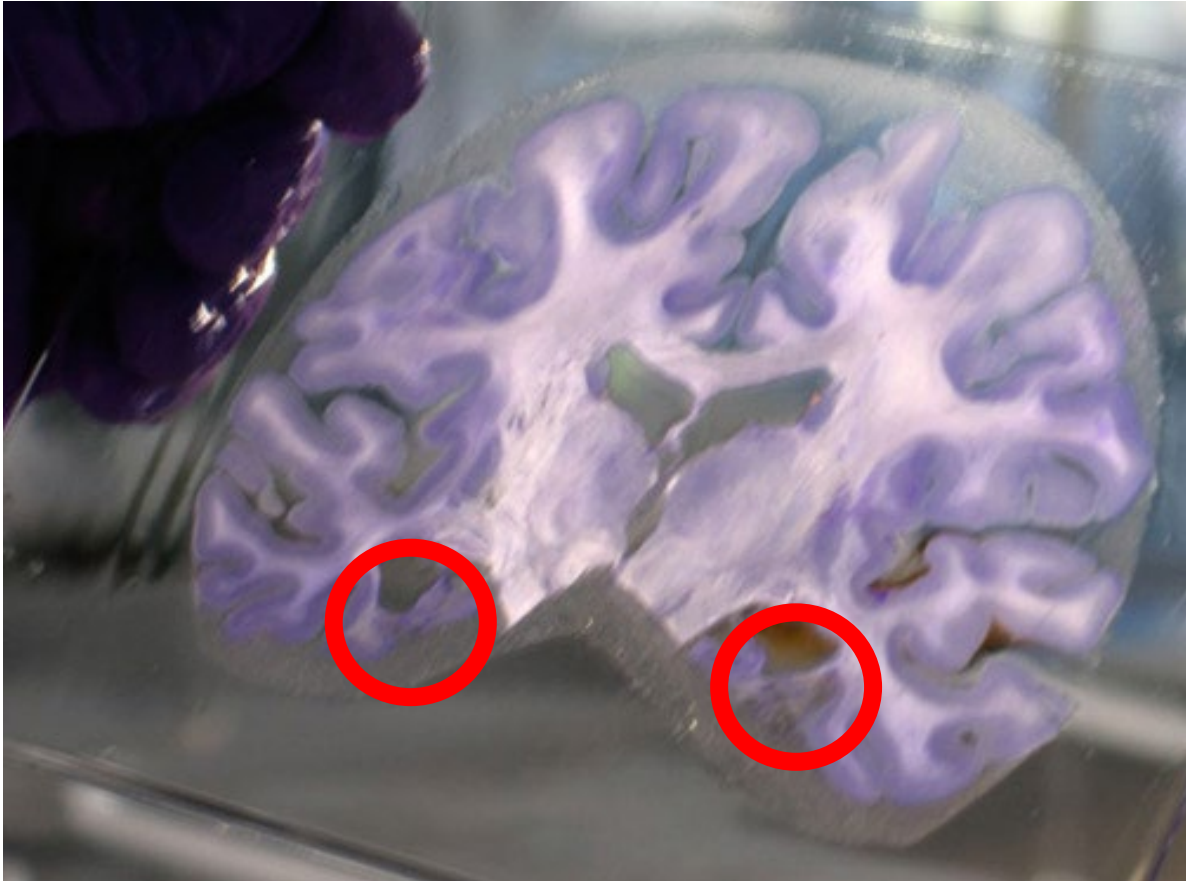
- Sits at the top of the processing hierarchy
- Huge amount of visual processing until any external sensory information reaches the hippocampus
- In other senses (auditory, somatosensory) there is similarly complex processing before the hippocampus – except olfactory inputs that reach the hippocampus much more directly (olfactory bulb → entorhinal cortex)
- Such high-level brain areas are expected to be notoriously difficult to understand: Presumably, responses must be extremely complex ?

Early ideas about hippocampal function (1920's, 30's, 40's)

- The hippocampus as part of the olfactory system (1920's) (rationale: there are strong *direct* inputs from the olfactory bulb to the entorhinal cortex, in both rat and monkey)
 - NOT TRUE: (i) Hippocampus receives multi-modal information; (ii) hippocampus exists also in anosmic animals totally lacking olfactory bulbs, such as dolphins
- The hippocampus and emotional processing
 - Papez circuit (1937)
 - Hippocampus as part of the Limbic System (one of the structures along the limbus, or edge of the 4th ventricle)
 - NOT TRUE: The Limbic System is not really a unitary functional “system”
 - The Amygdala is important for emotional learning, but the hippocampus much less so

The hippocampus and memory (1950's)

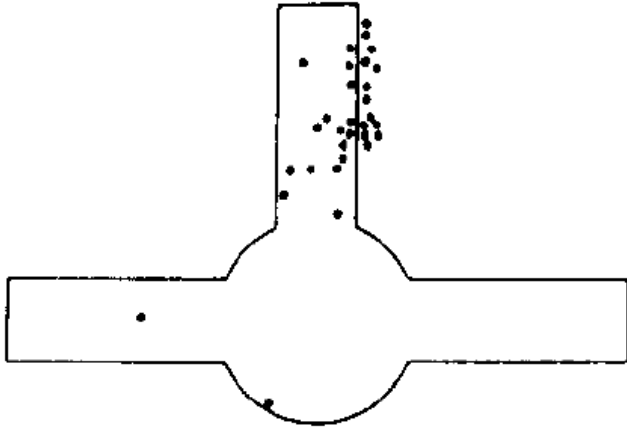
Henry Mollaison (H.M.), 1926-2008



Scoville & Milner, *J Neurol Neurosurg Psychiatry* 20, 11 (1957)

- Patient H.M. developed severe anterograde amnesia after a surgery to treat his intractable epilepsy, during which large portions of his hippocampus, entorhinal cortex, and amygdala were removed bilaterally.
- H.M. taught the Neuroscience community that:
 - The hippocampus is crucial for episodic memory – and later studies showed it is crucial for spatial memory.
 - There are different memory systems in the brain.
 - Long-term memories are not stored in the hippocampus.

50 years ago – A surprisingly simple discovery for such a high-level brain area: Hippocampal place cells in rats



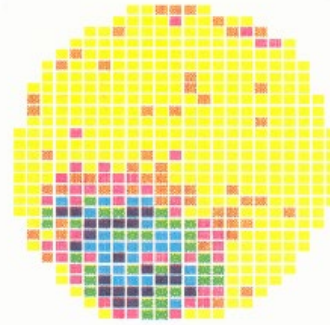
(O'Keefe & Nadel 1978)

(O'Keefe & Dostrovsky 1971)

John
O'Keefe



B
Spike
count



A
Time
spent



Firing-rate map



↑
'Place field' of a
pyramidal cell in
rat hippocampus

(Muller et al. 1987)

Movie of a rat hippocampal place cell in action



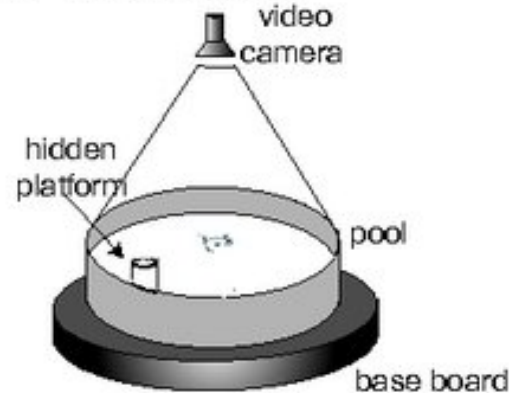
(Courtesy of Colgin, Moser & Moser)

Bilateral hippocampal lesions impair allocentric navigation

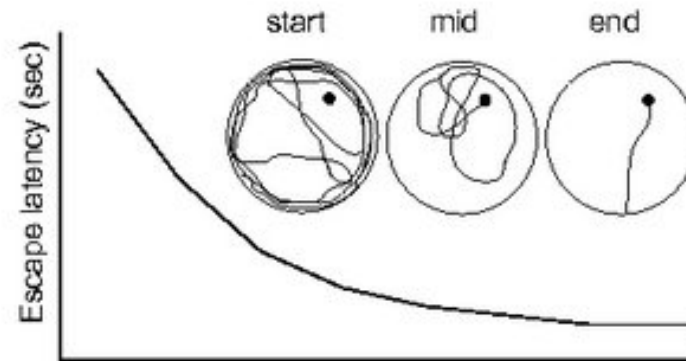


Richard Morris
(original finding:
1982)

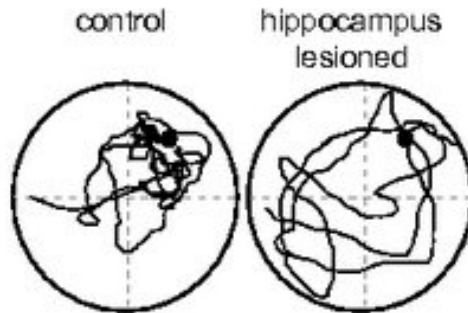
A The watermaze



B Paths and latency during place navigation



C Post-training probe tests (no platform)



Allocentric navigation: Based on absolute-space coordinates ("north/south")

Egocentric navigation: Based on body's self coordinates ("left/right")

- These deficits of spatial memory occur after lesions in dorsal, not ventral hippocampus
- In rats over-trained for months, animals do show improvements in probe tests after hippocampal lesions, suggesting the memory became (in part) independent of the hippocampus

These findings led the field into studying the neurobiology of navigation and spatial memory.

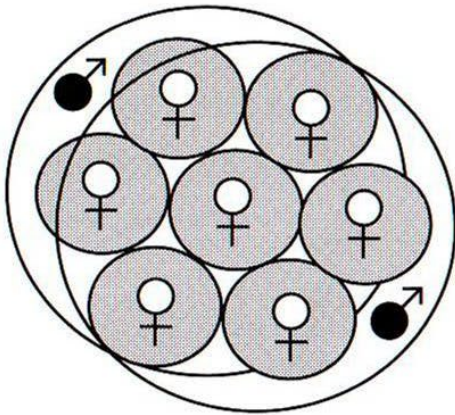
Intermezzo: Why are navigation and spatial memory interesting ?

- Navigation and moving through space are key behaviors in all animals: important for survival.
 - Spatial memory and navigation are good “models” for understanding higher cognitive functions more generally, because:
 - Space is Euclidian (notion of *distance*: allows mathematical modeling).
 - Navigation is quantifiable (accuracy, straightness, time).
 - Space is basic for human thought and cognition (Immanuel Kant).
- For these reasons, many neuroscientists who are interested more generally in (i) behavior, (ii) cognition, or (iii) learning & memory – study the case of navigation and spatial memory.

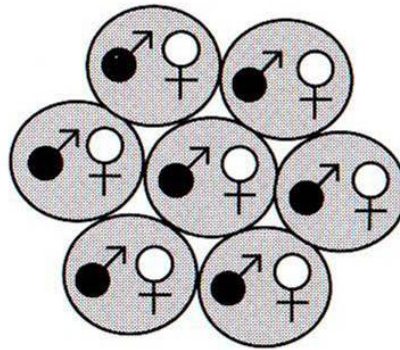
Hippocampal volume correlates with navigational load in rodents

A Male and female range size

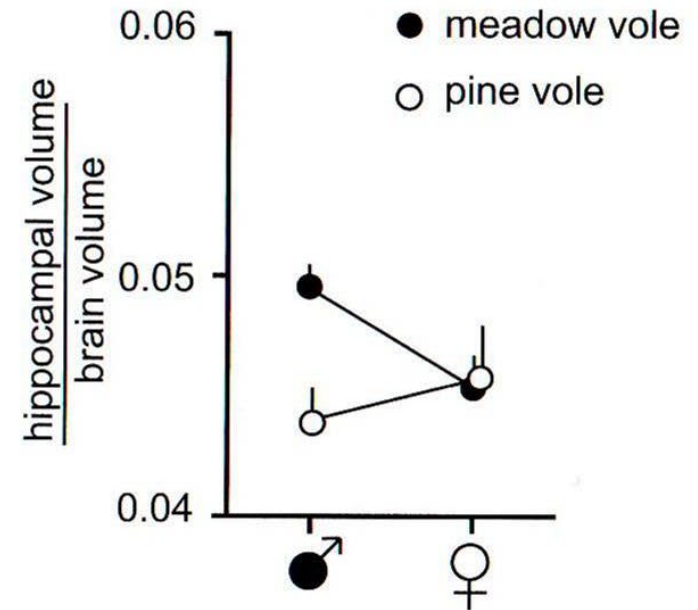
polygamy: *meadow vole*



monogamy: *pine vole*



B Relative hippocampal volume



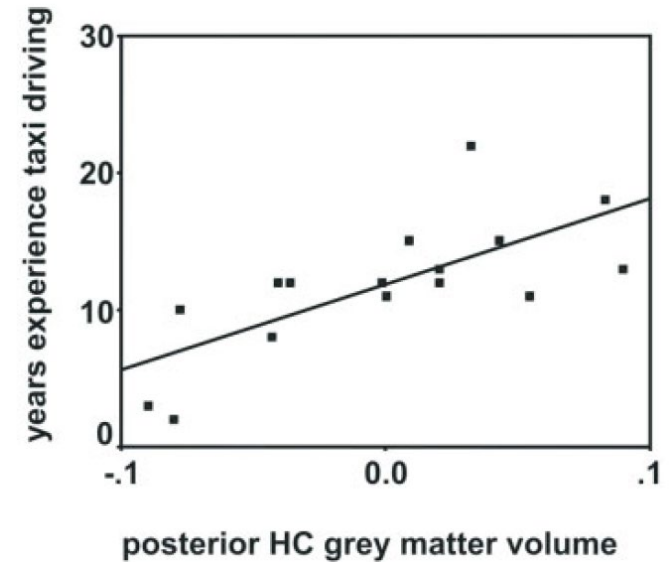
Hippocampal volume correlates with navigational load in humans

Volume of posterior hippocampus in humans (equivalent to dorsal hippocampus in rats):

- Larger in London taxi drivers than in age-matched controls.
- Correlated with time spent as a taxi driver.
- Larger in Taxi drivers than in experience-matched Bus drivers.
- In Bus drivers, no correlation with experience was found.

Maguire et al., *PNAS* (2000)

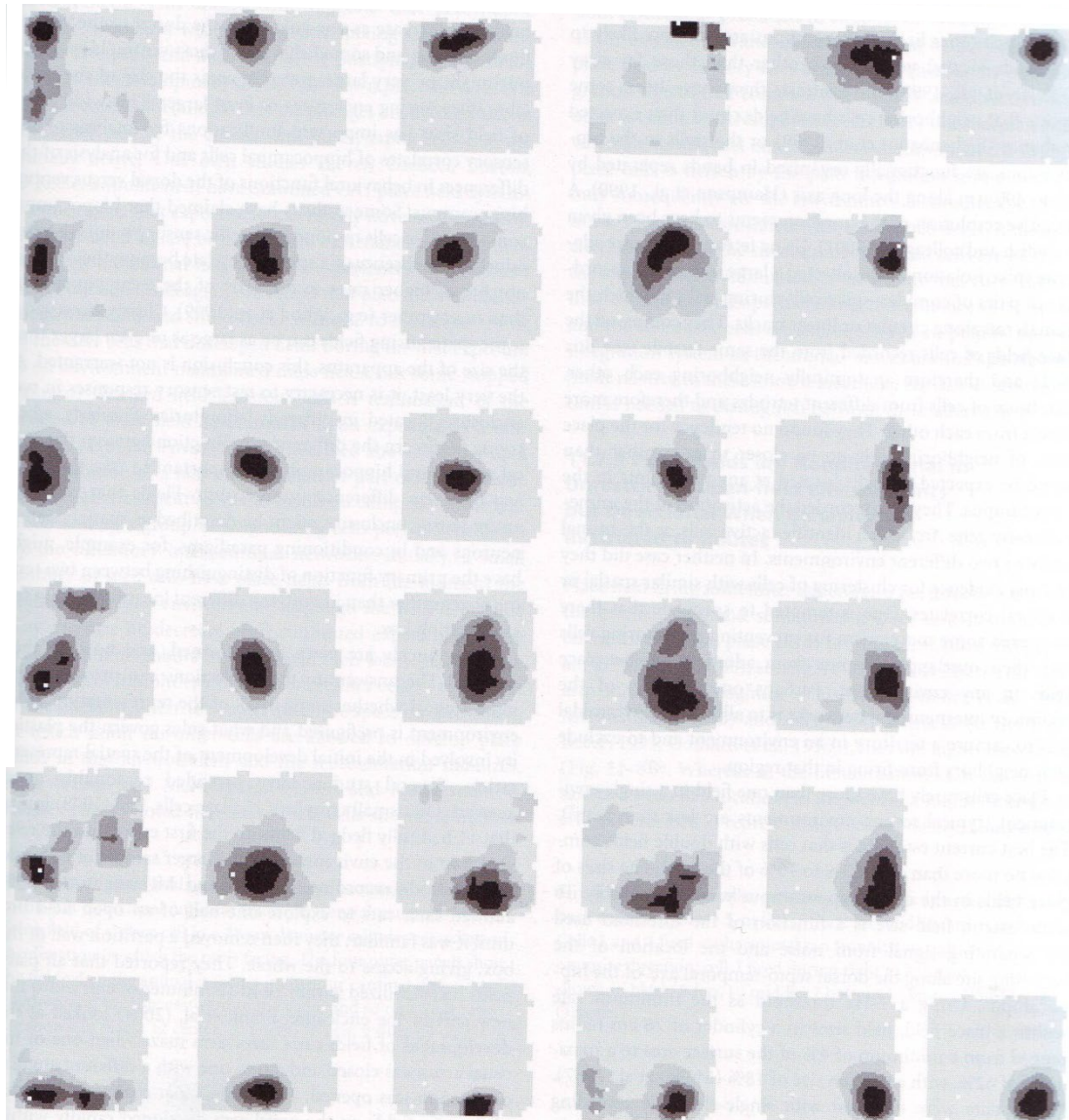
Maguire et al., *Hippocampus* (2006)



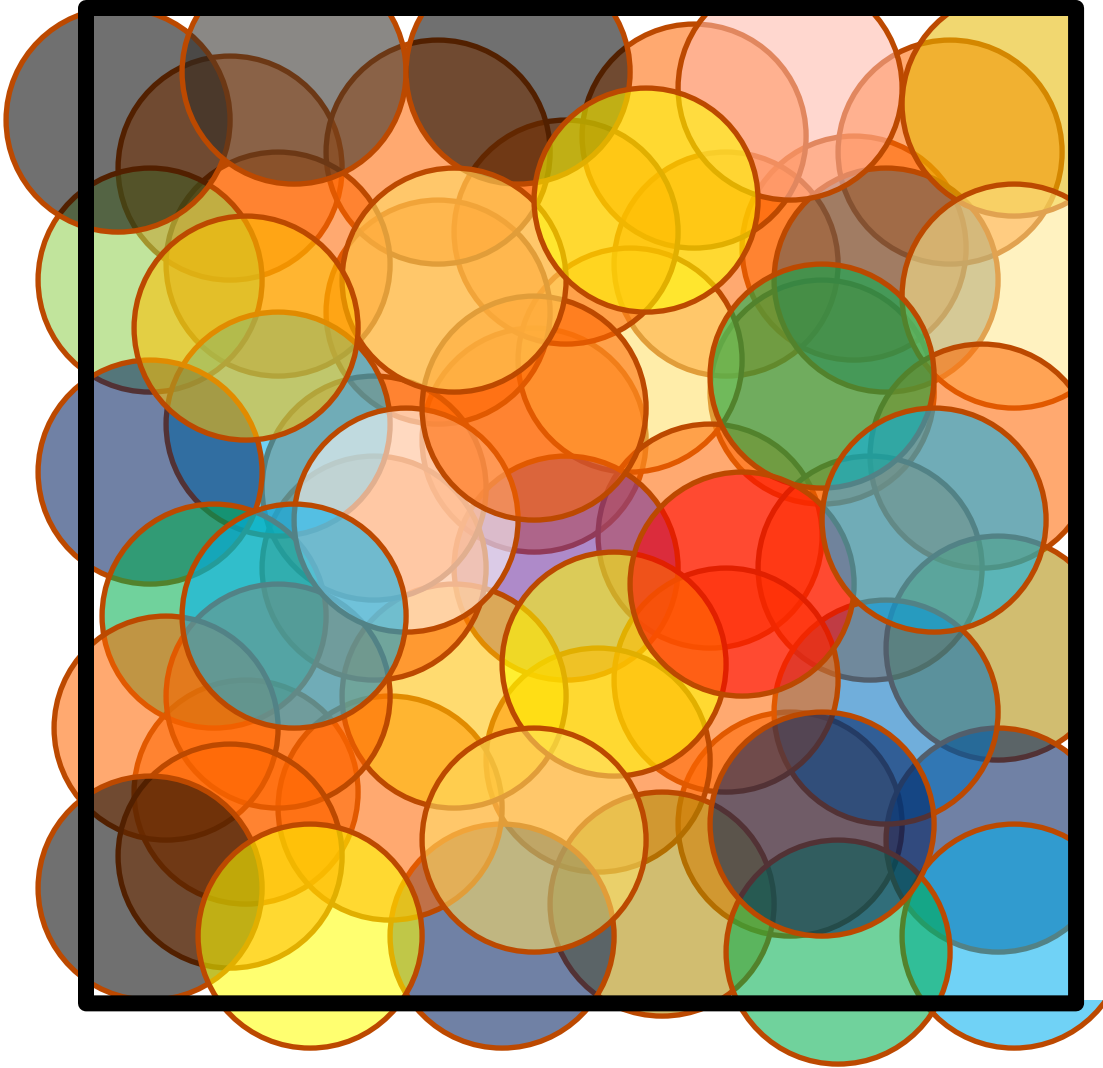
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The place fields of hippocampal place cells tile the environment

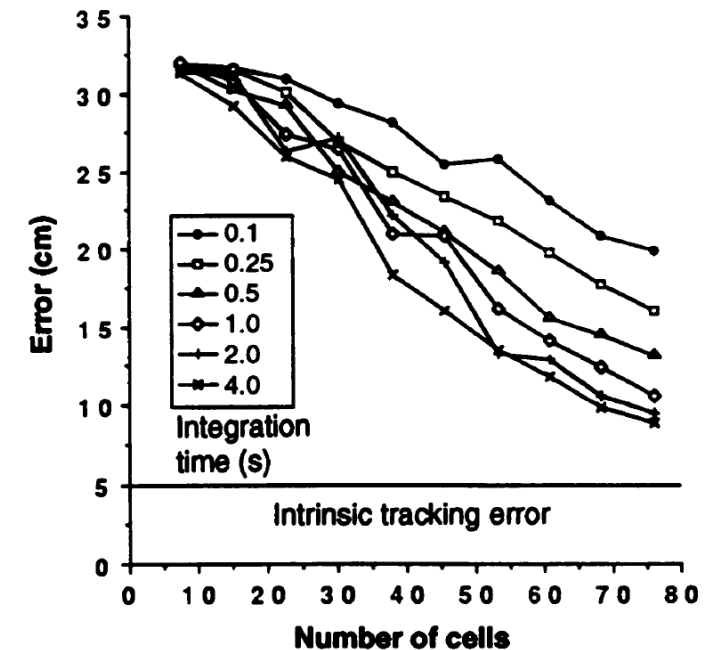
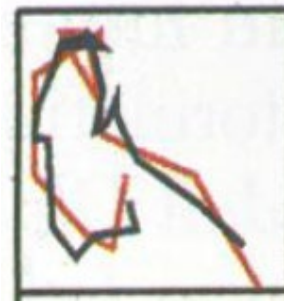
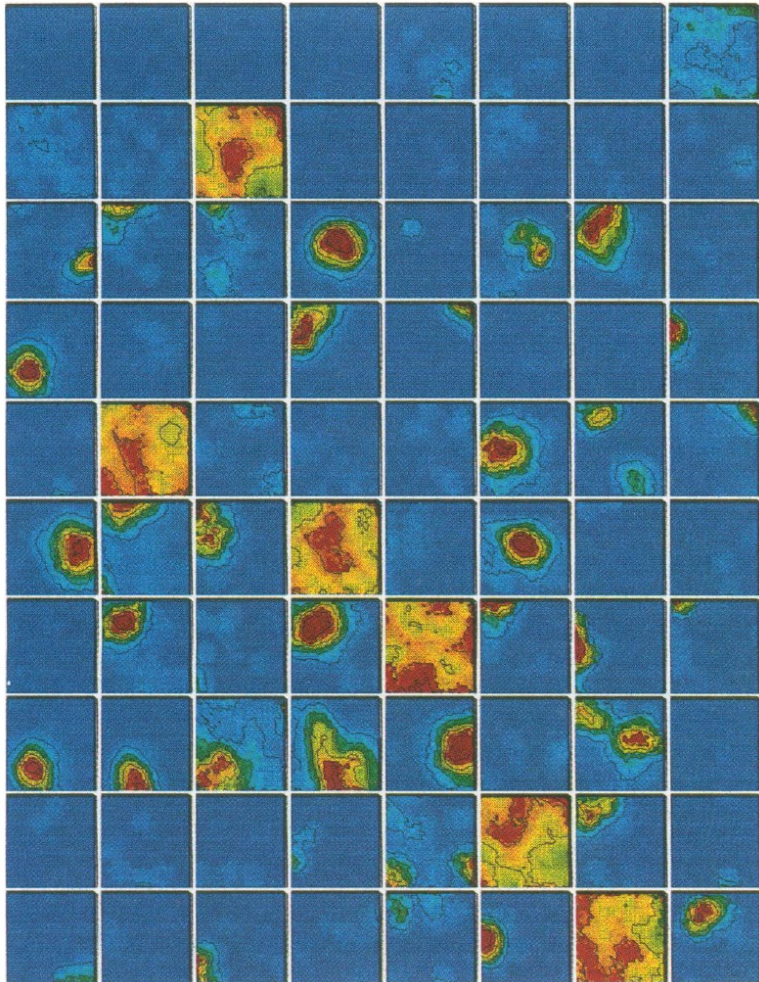


The place fields of hippocampal place cells tile the environment



The rat's location can be reconstructed from the activity of an ensemble of simultaneously-recorded place cells

Tetrode recording of 80 neurons simultaneously

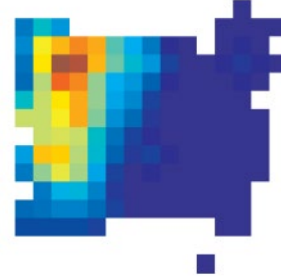
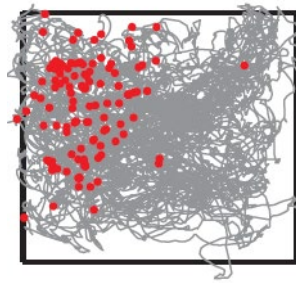


Putative pyramidal neuron (place cell)

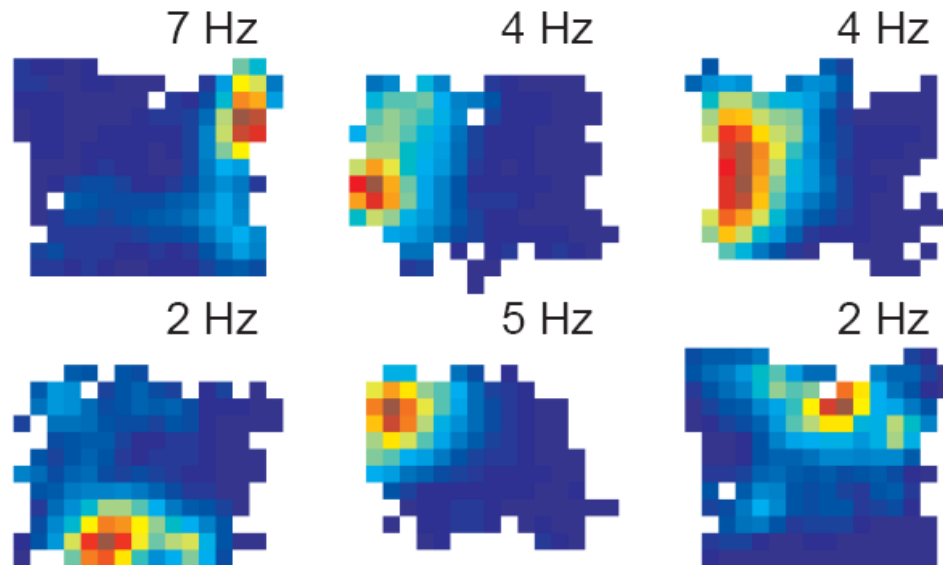
Interneuron (very little spatial modulation)

Wilson and McNaughton, *Science* (1993)

Place cells exist also in other species: Big brown bats

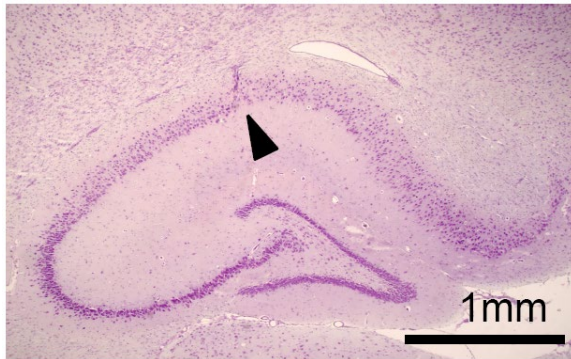


A single cell



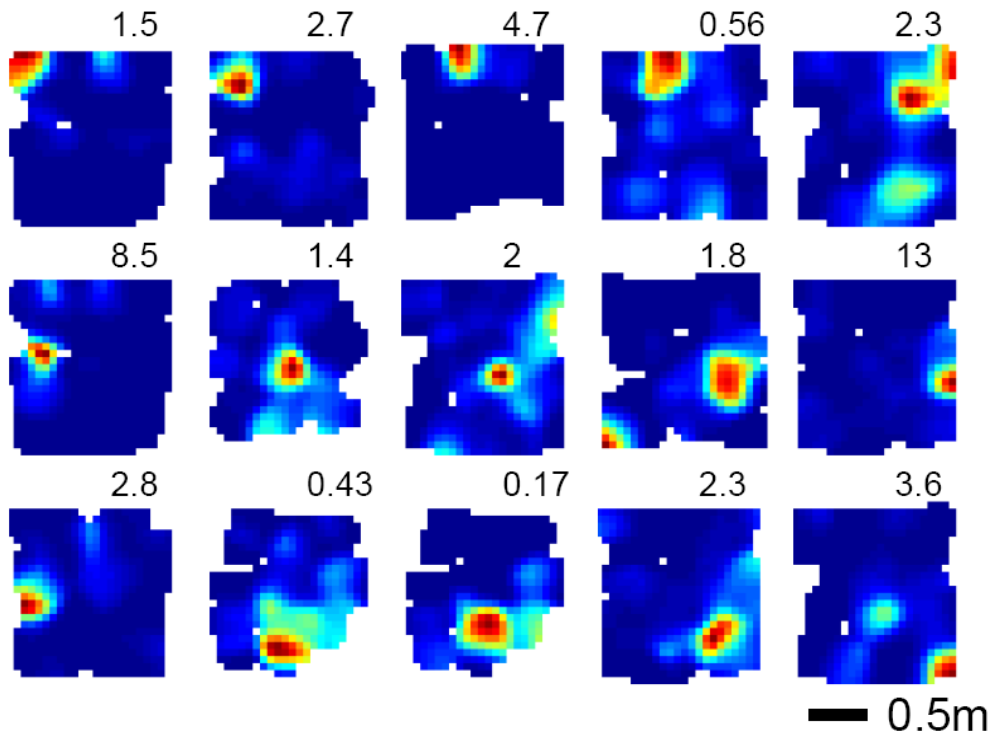
More examples
of place fields
from 6 neurons

And in another bat species: Egyptian fruit bat



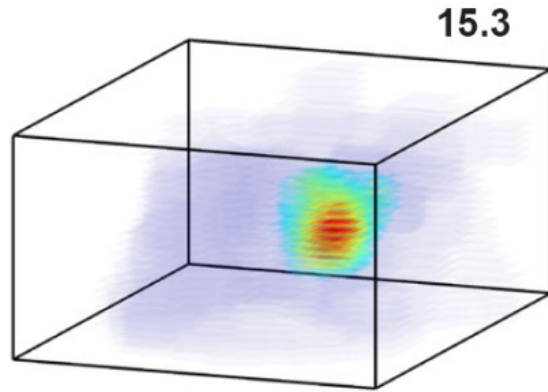
Examples of hippocampal place fields from our current study species, the Egyptian fruit bat.

As in rats, these place fields tile the environment, and represent the animal's spatial location.



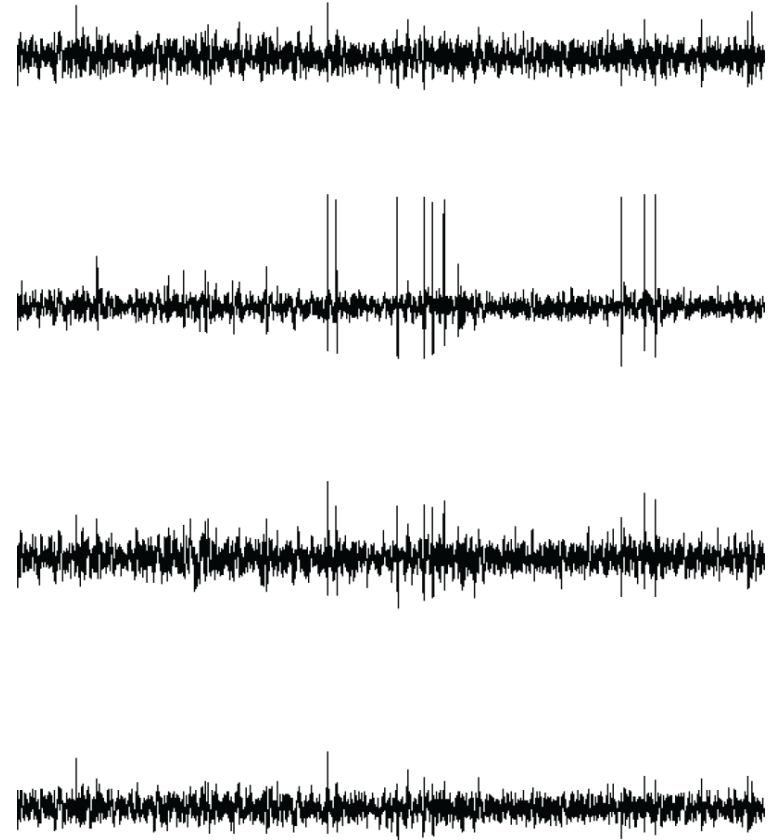
Yartsev, Witter, Ulanovsky
Nature (2011)

3-D place cells in bats



Place field of one hippocampal neuron recorded in a ~6 x 5 x 3 meter flight room

Wireless neural recordings in flying bats



200 ms

- **3-D place fields are spherical in shape (isotropic):**
Same resolution in all directions.

Yartsev & Ulanovsky
Science (2013)

Place cells in humans

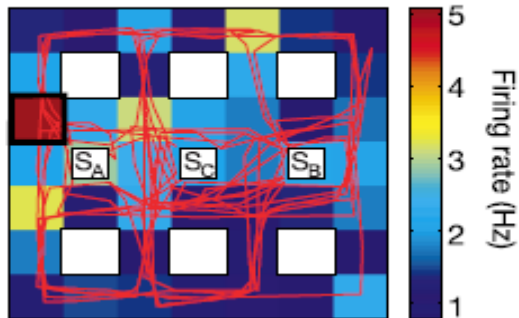
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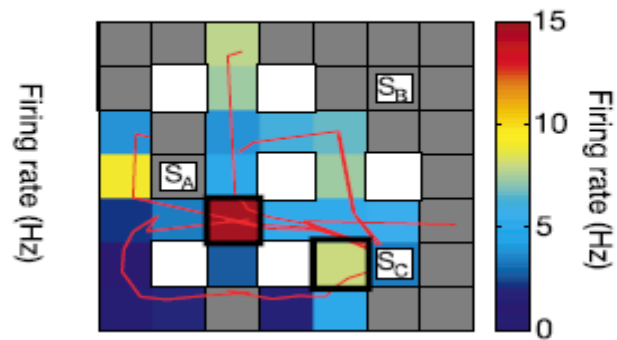
b



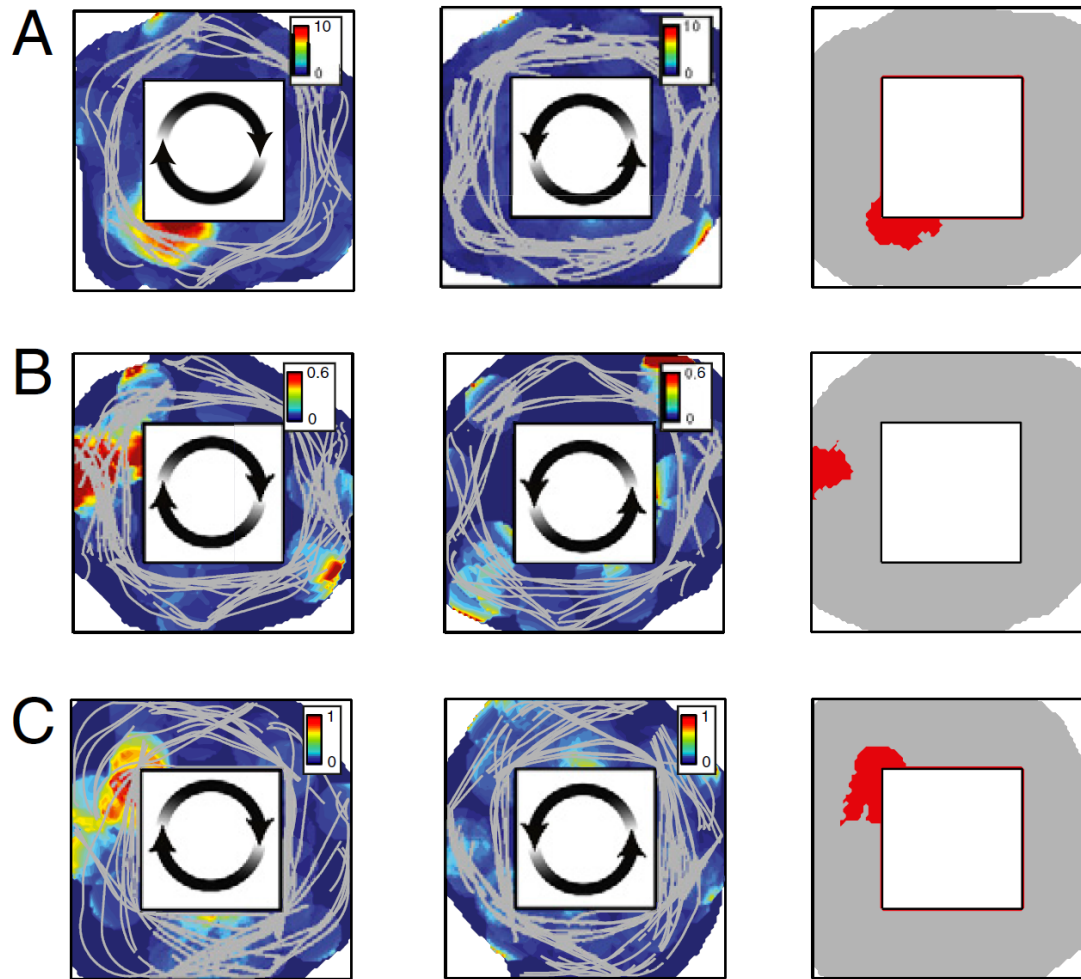
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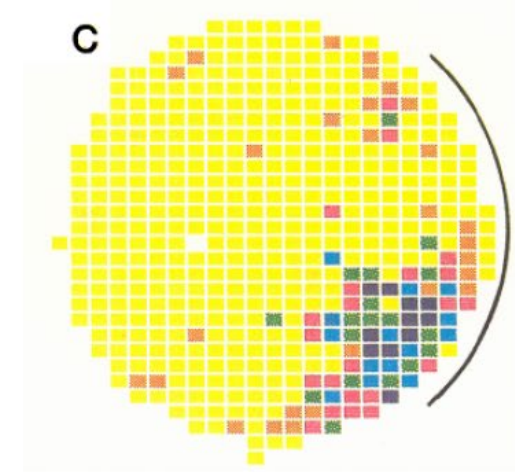
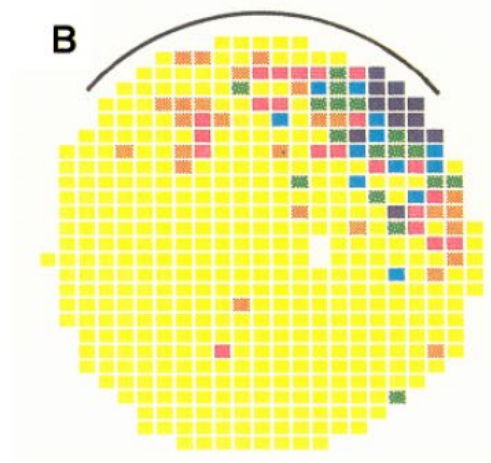
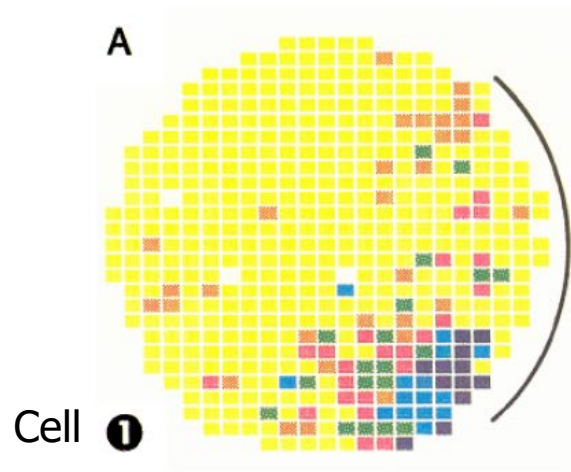
d



Place cells in humans



Place fields rotate with the rotation of prominent external landmarks

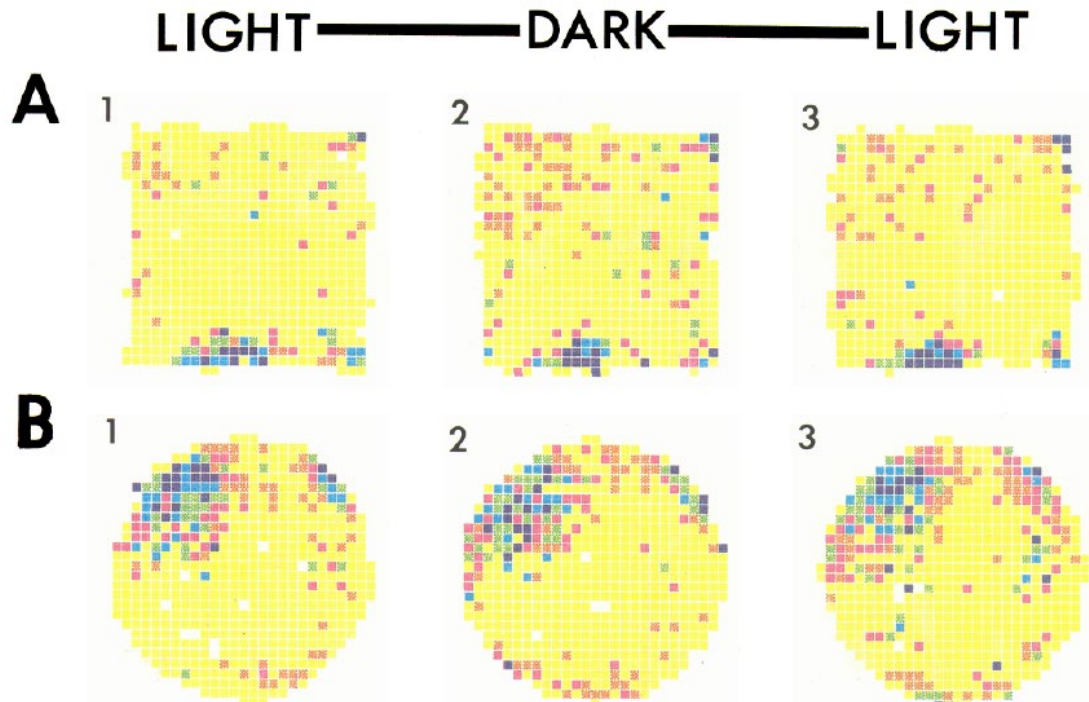


Rotation of cue card

(Muller and Kubie 1987)

*Note that this place field is quite stable
(session A vs. session C)*

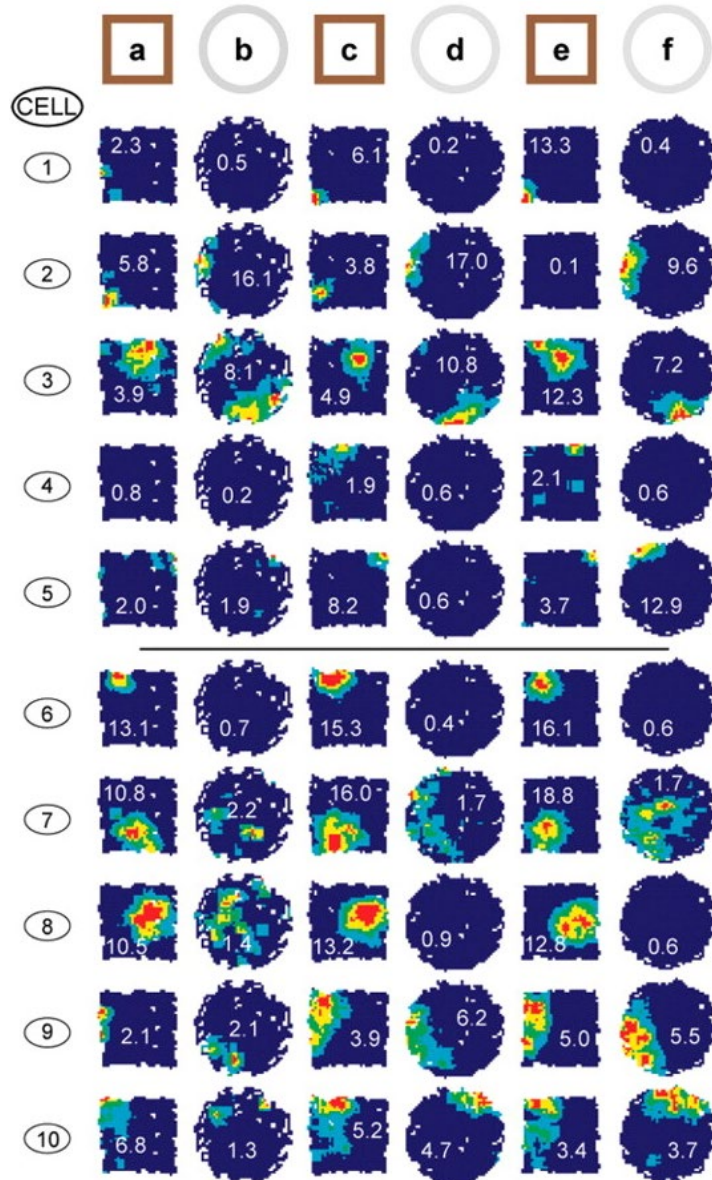
Place fields, however, are not purely visual, and are not even modality-specific – they are multi-modal



G. J. Quirk, R. U. Muller, J. L. Kubie (1990)

- In this experiment, the place-fields were likely determined mostly by odors on the floor
- In a later, very similar experiment (Save et al. 2000), when lights were turned off *and* odors were thoroughly cleaned, place-cell firing was severely disrupted

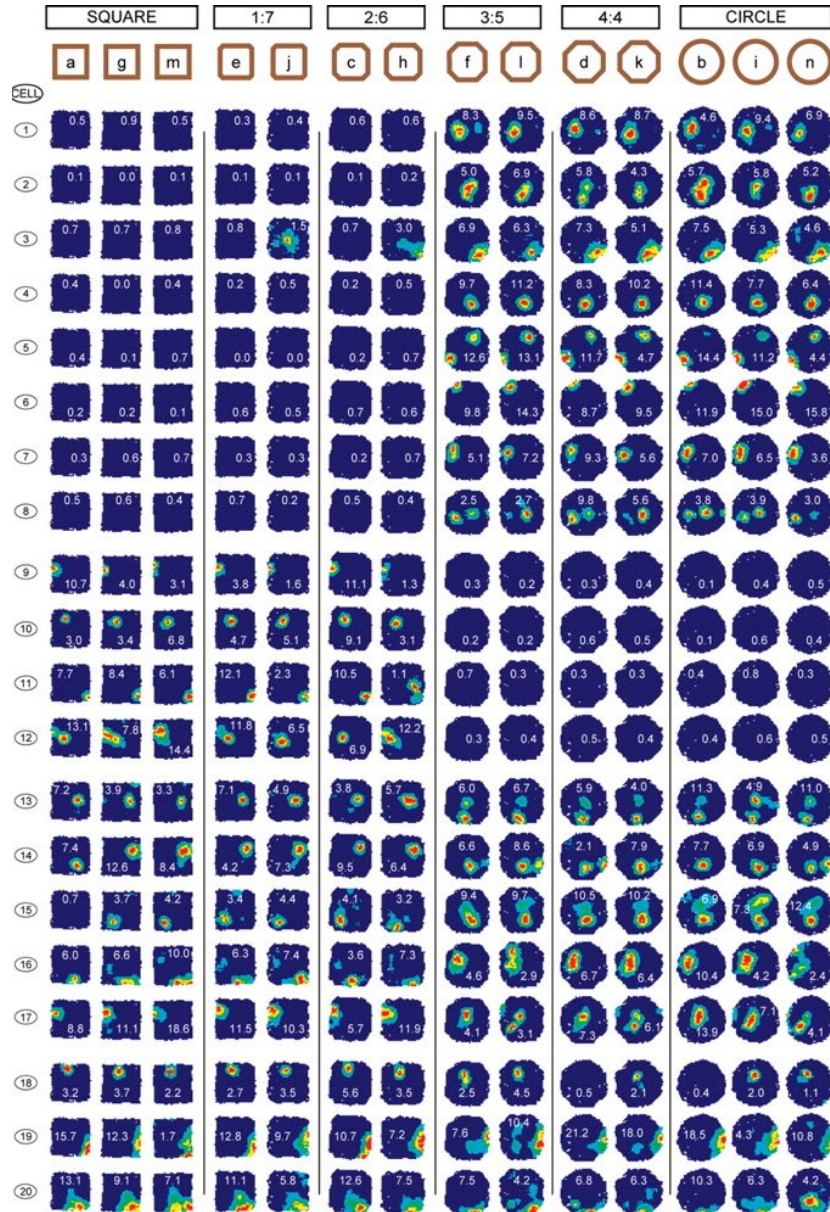
Multiple maps are stored simultaneously in rat hippocampus



“Remapping” between representations of square and circular environments.

Wills et al., *Nature* (2005)

Multiple maps are stored simultaneously in rat hippocampus

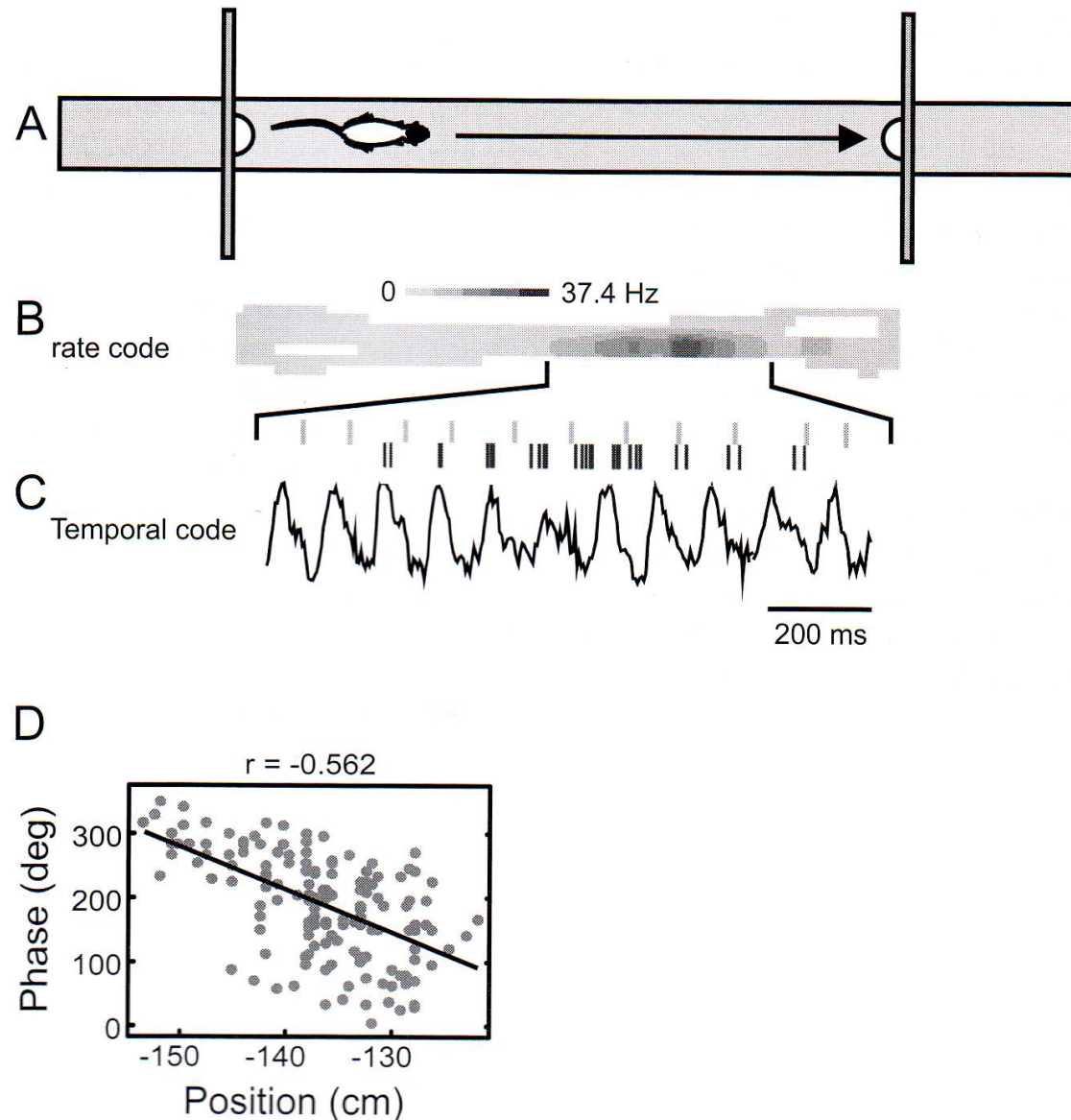


Abrupt phase transition between square-like and circle-like representations in intermediate octagonal environments: Evidence for attractor dynamics in the hippocampal network.

Attractor neural network models are useful as memory models – and we will come back to memory later on.

Wills et al., *Nature* (2005)

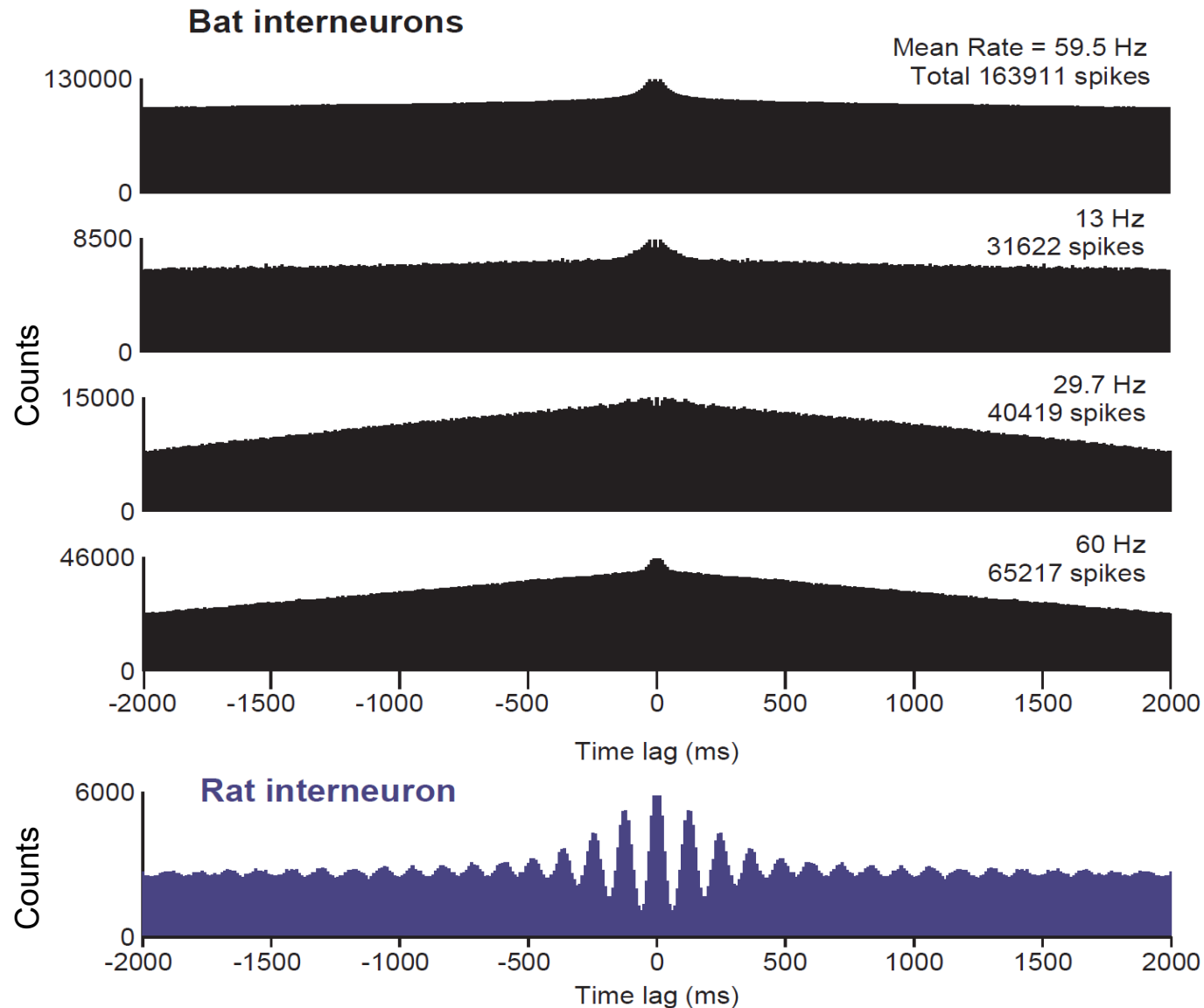
Temporal coding of position: Theta phase precession



“Theta Phase precession”:
Place cells are firing at progressively earlier and earlier phases of the cycle of the **theta oscillation**, as the animal runs through the place field.

Thus, spike phase relative to the theta oscillation provides information about the animal's position (**temporal code**), on top of the information from the place-field (**rate code**).

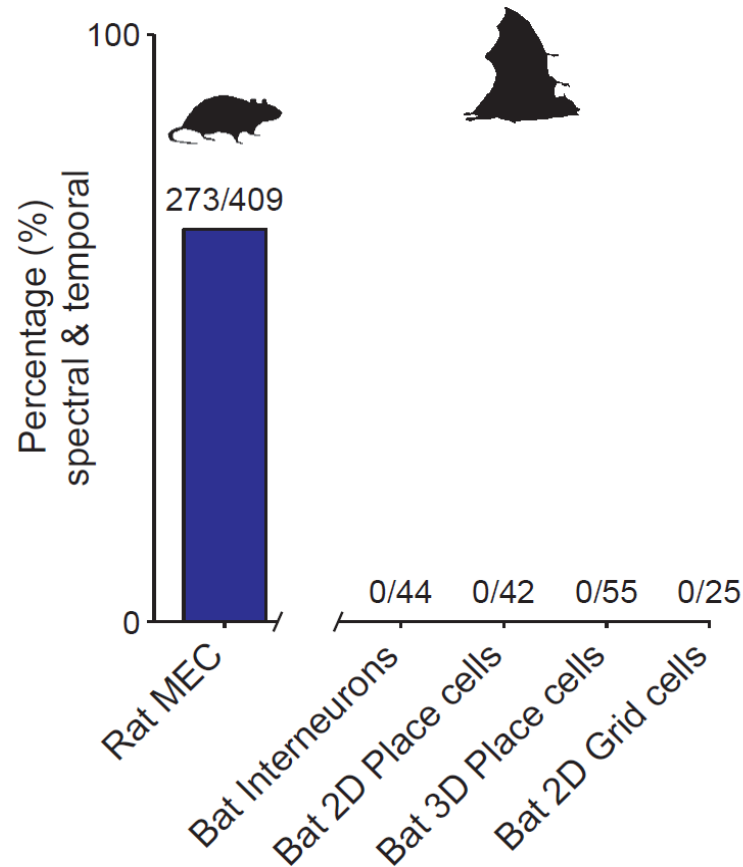
BUT: No theta oscillations in bat neurons (*nor in humans*)



Yartsev et al., *Nature* (2011)

Eliav et al., *Cell* (2018)

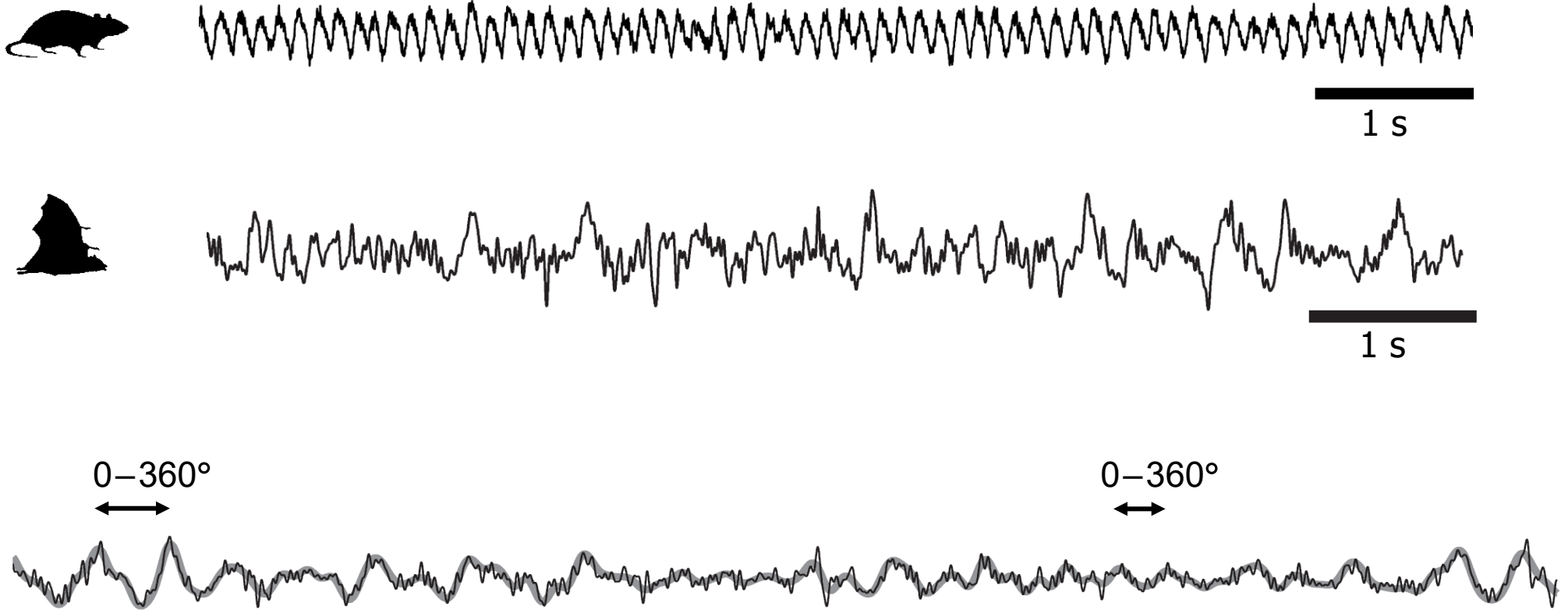
No movement-related oscillations at any frequency



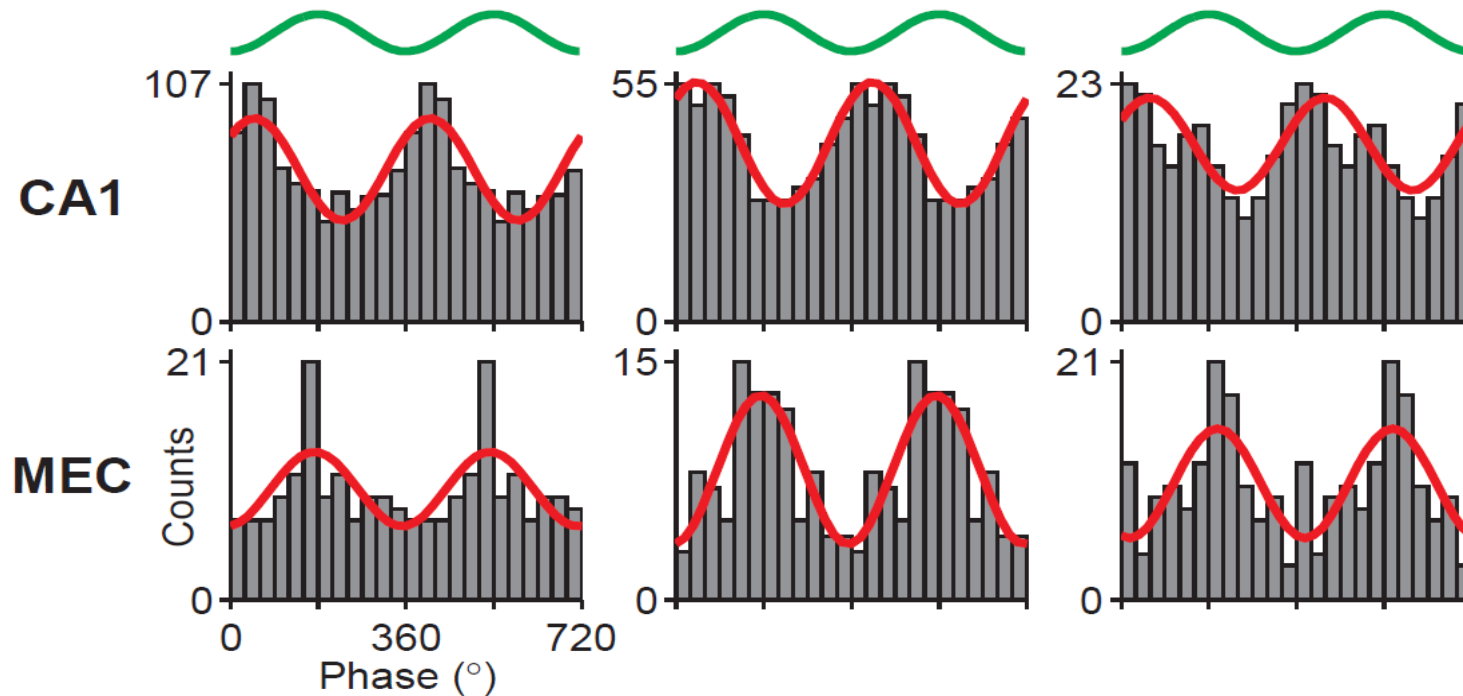
→ Does this mean there is no temporal coding (phase coding) in bats?

- 67% of rat neurons (273/409) are significantly oscillatory – almost all at ~8 Hz.
- 0% of bat neurons (0/166) are significantly oscillatory in the 1–20 Hz range.

A twist in the story

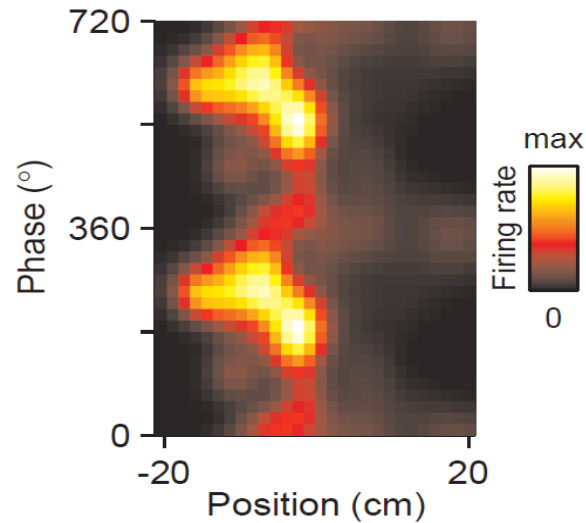


Nonoscillatory phase-locking in bats



- 44% of bat CA1 pyramidal neurons show significant nonoscillatory phase-locking.
- In the time-domain, these neurons are nonoscillatory.

Nonoscillatory phase-coding of the animal's position



- 38% of bat CA1 neurons show significant nonoscillatory phase-coding of position.

Conclusion: The importance of the Comparative Approach

- Analysis of in vivo data from bats did not reveal movement-related oscillations at any frequency – neither in grid cells, nor place cells, nor interneurons (“theta cells”) – neither in 2D nor in 3D flight.
- In rodents – 3 phenomena that are coupled together:

Rodents:

✓ Oscillations (theta)

✓ Synchronization

✓ Coding (of position)

Bats

✗ Oscillations (theta)

✓ Synchronization

✓ Coding (of position)

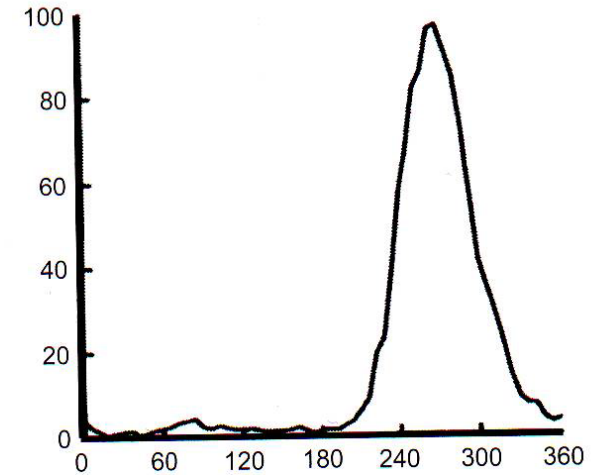
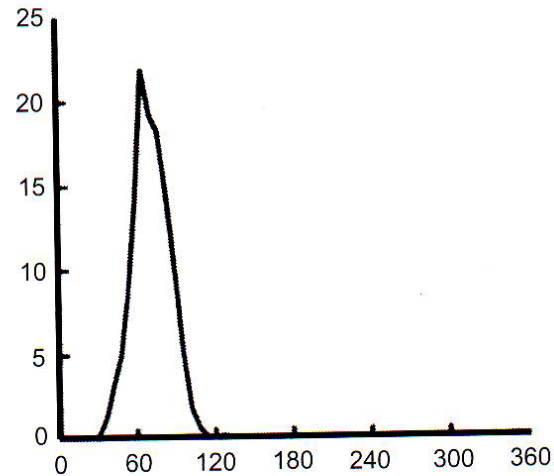
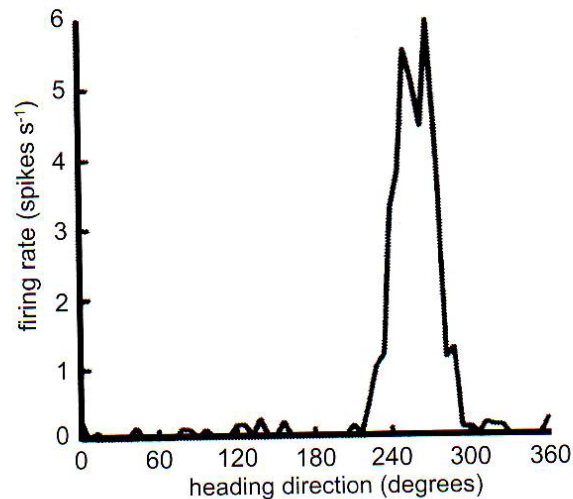
- The comparative approach allows to identify what is invariant across species – and what is not.
- Similar nonoscillatory coding was subsequently found also in humans, which lack continuous theta oscillations (Qasim et al., *Cell* 2021).

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Head direction cells in dorsal presubiculum

3 Head Direction Cells Firing Fields

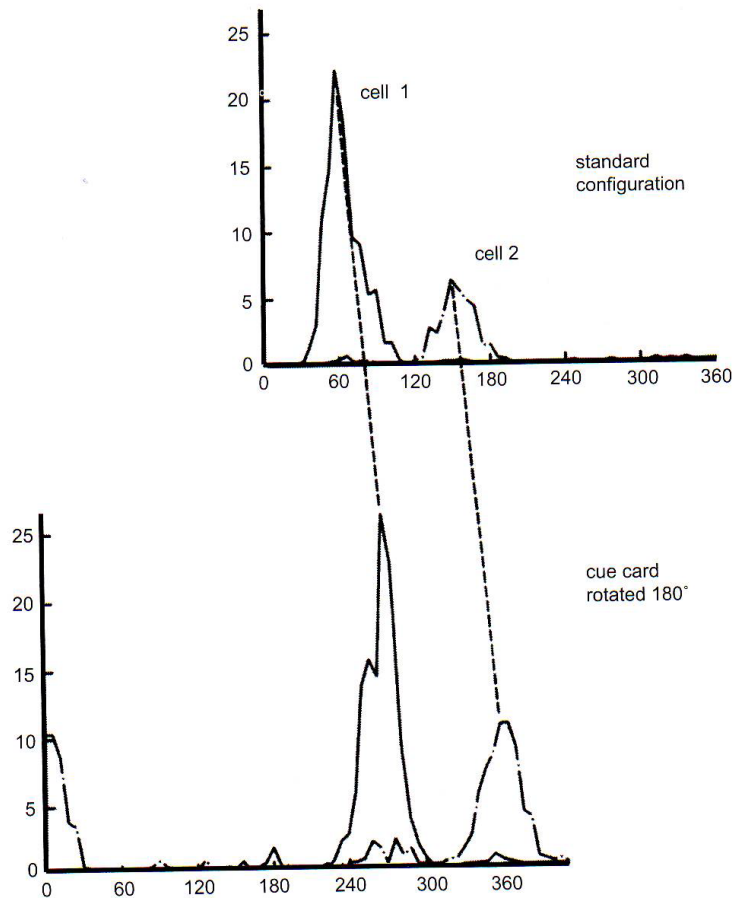


- Head direction cells are found in the dorsal presubiculum, anterior thalamus, medial entorhinal cortex, and in several other brain areas adjacent to the hippocampus.
- These cells are tuned to head direction, but *not* to place – i.e. they fire more or less uniformly with respect to the animal's location.

Head direction cells in dorsal presubiculum

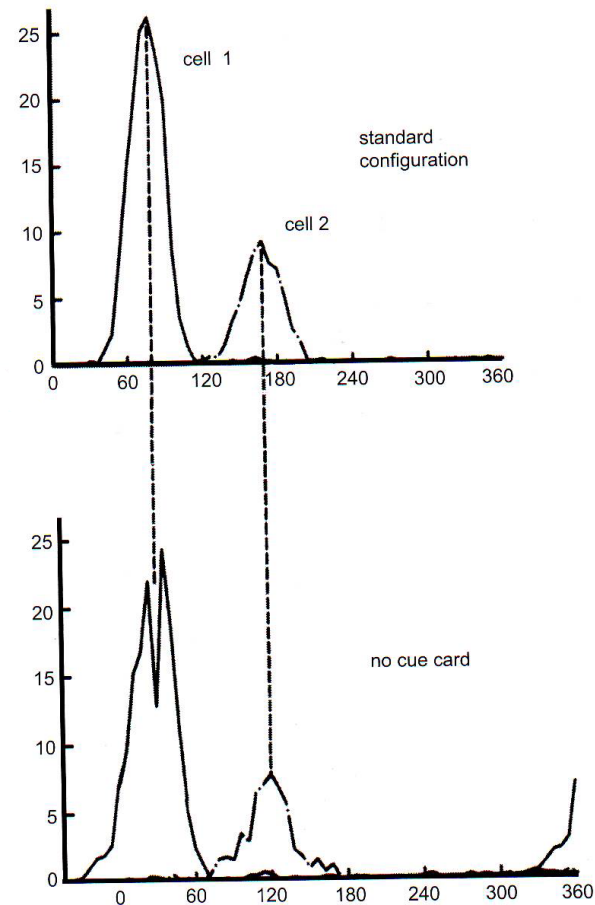
Head direction cells rotate together

Fields rotate with cue card



Head direction cells “remap” to a new random direction upon removal of cue card – but they remap together

Fields shift after cue card removal



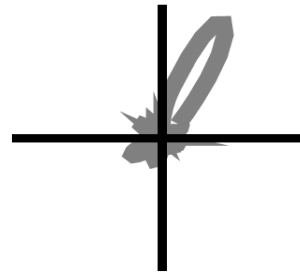
Is there a representation of 3D head direction in the mammalian brain = “3D neural compasses” ?

Head-direction cells
In rats



Solstad et al.
Science 2008

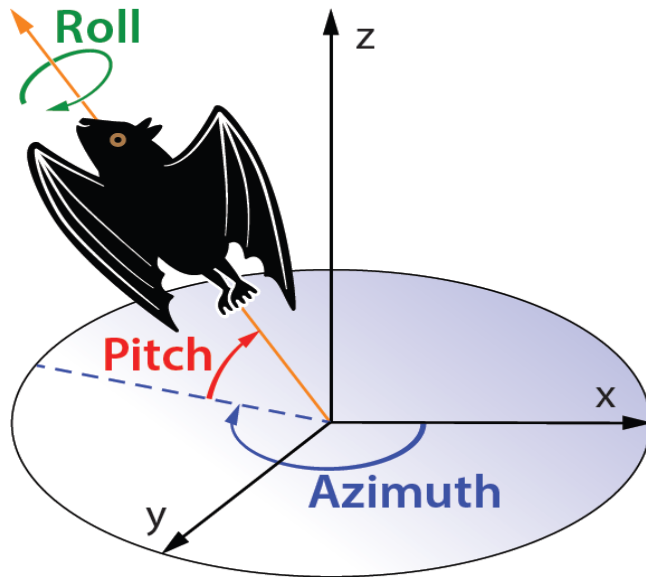
Head-direction cells
In bats



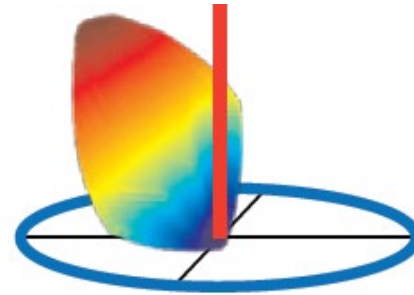
Yarsev, Witter, Ulanovsky
Nature 2011

3D head direction cells in bats

Euler Angles

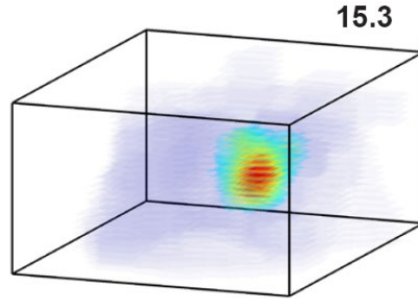


3D head-direction cell



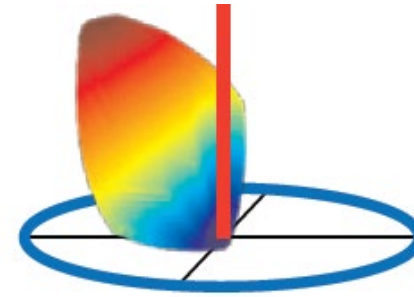
3D place cells and 3D head-direction cells were found also in rodents and primates

3D place cells



Yartsev & Ulanovsky
Science (2013)

3D head-direction cells



Finkelstein et al.
Nature (2015)

Subsequently, other groups found:

→ 3D head-direction cells:

- Monkeys (Laurens et al. 2016)
- Mice (Angelaki et al. 2019;
Mallory...Giocomo, 2021)

→ 3D place cells:

- Rats (Grieves...Jeffery 2020)



Neural basis of map-and-compass navigation ?

1. *Map*



Place cells

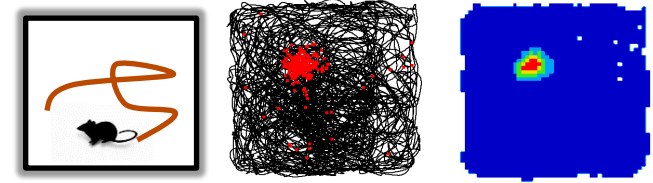
Hippocampus

2. *Compass*

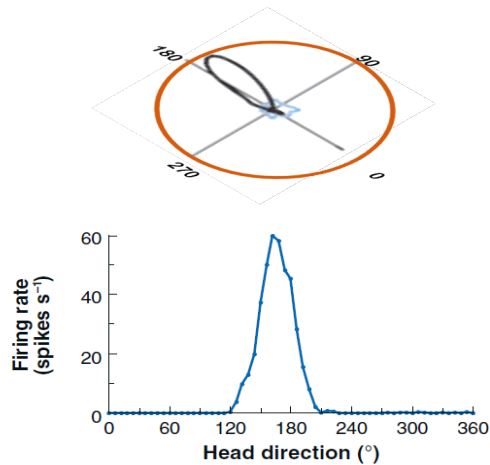


Head-direction cells

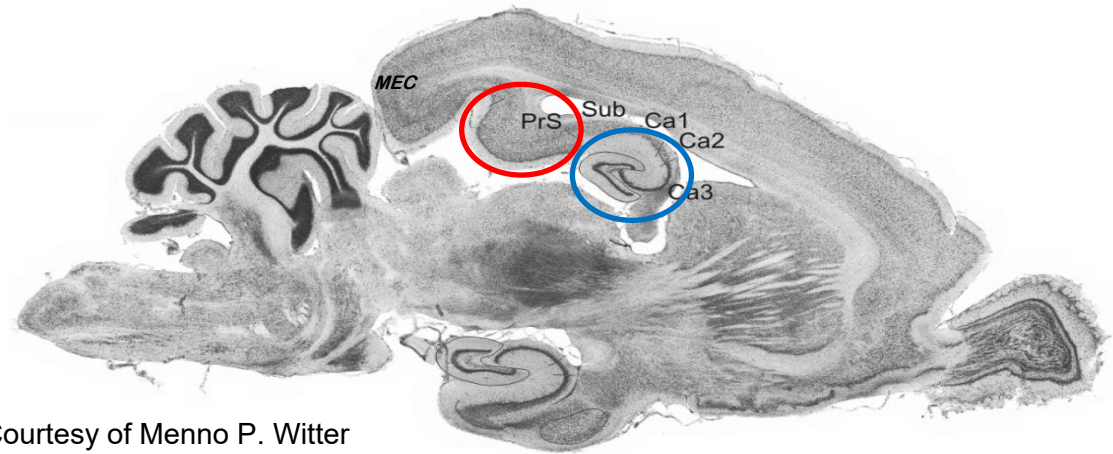
Presubiculum (PrS)



Movie courtesy of Dori Derdikman, 2010



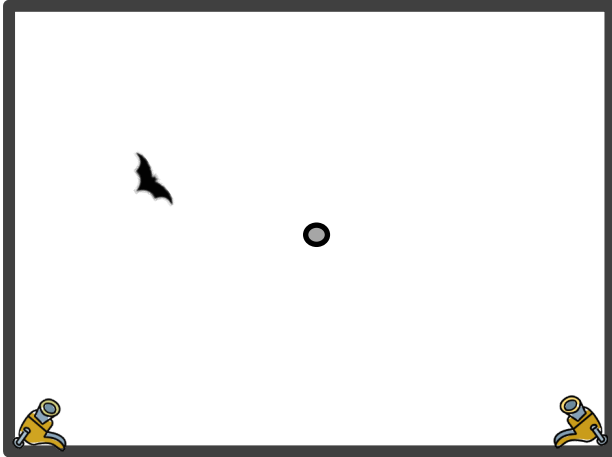
Ranck & Taube
JNS 1990



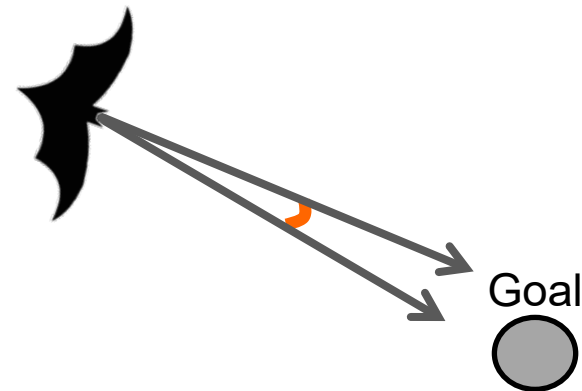
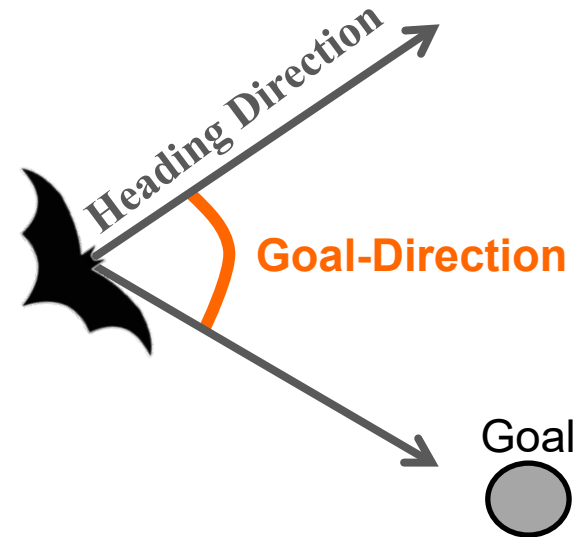
Courtesy of Menno P. Witter

The missing link: How do you navigate to goals ?

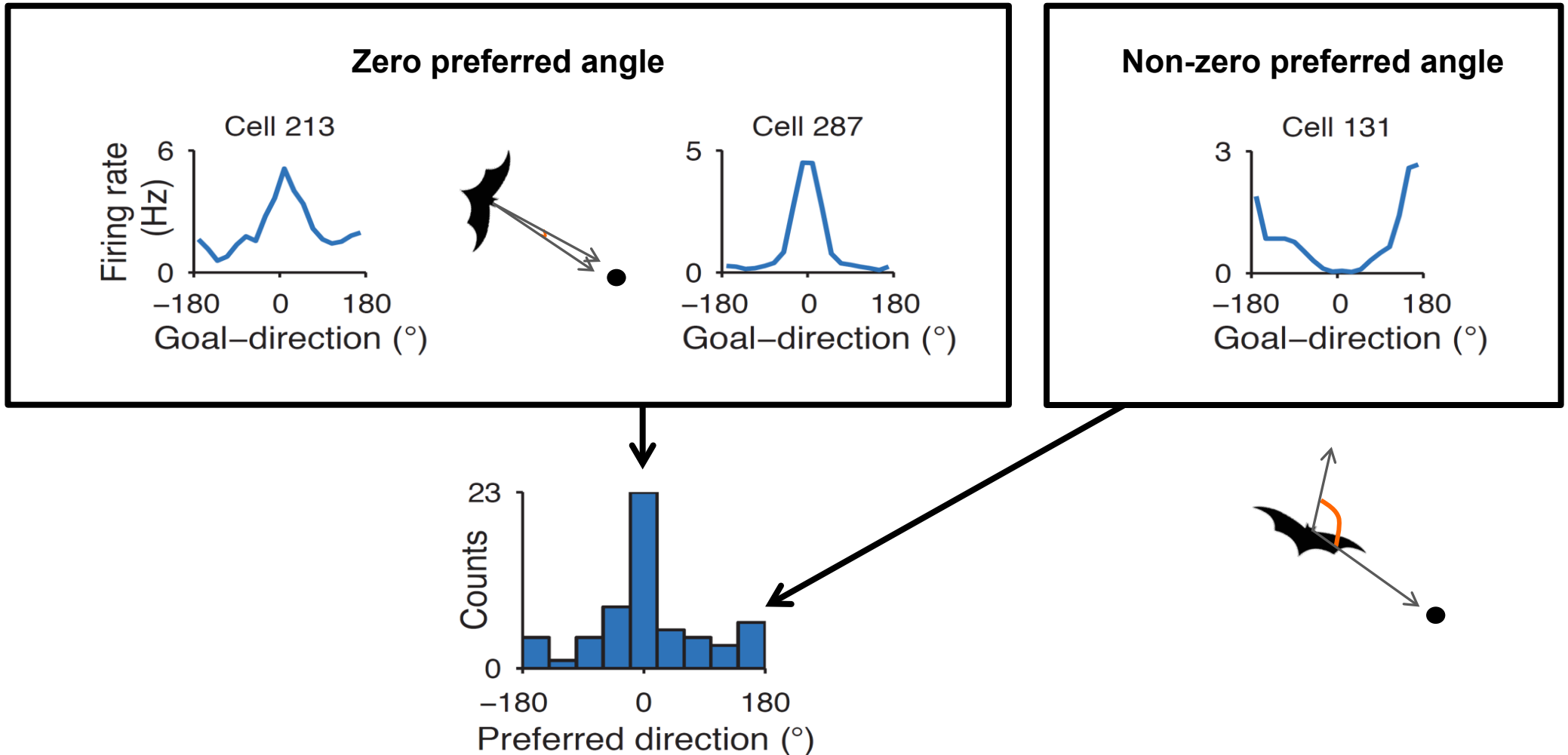
Flight room (6×5×3 m)



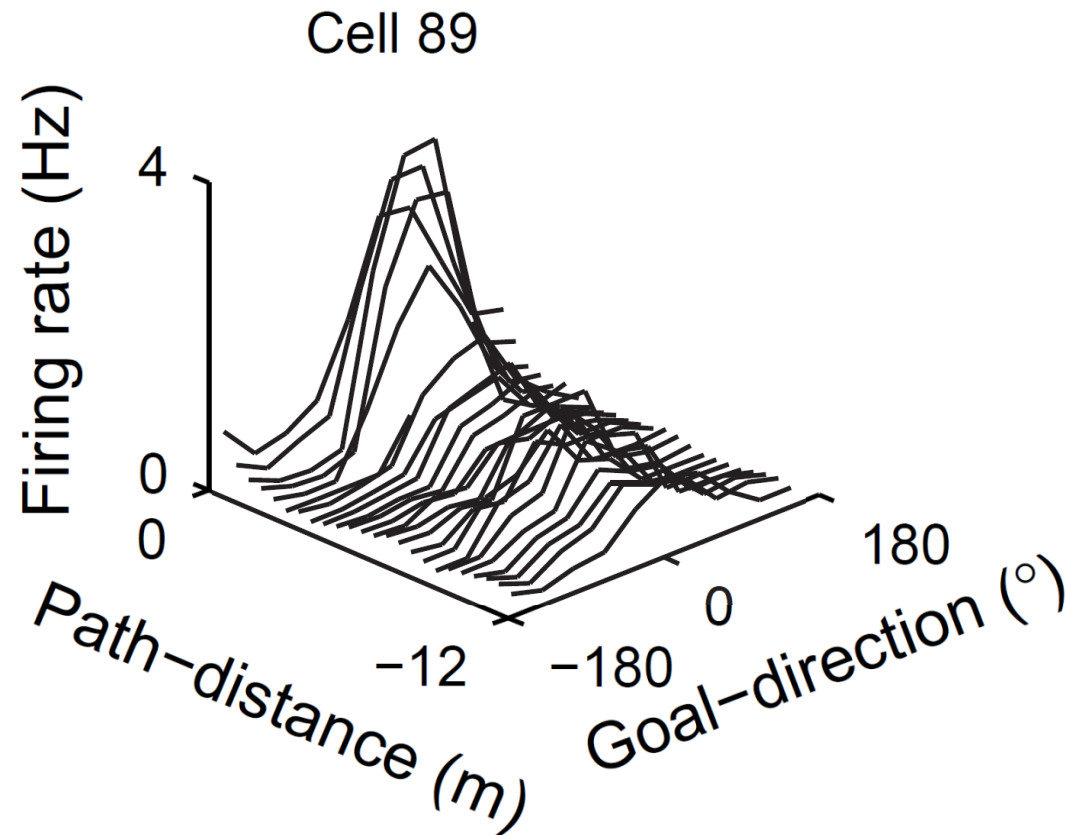
Recordings in hippocampal
area CA1



Goal-Direction cells: bat hippocampal CA1 cells with tuning to the goal's direction



Many neurons represent conjunctively the goal-direction and goal-distance: A vectorial representation of spatial goals



Outline of today's lecture

- Hippocampus: Introduction and early discoveries
- Spatial maps in the hippocampus and related regions:
 - Place cells
 - Head direction cells
 - **Grid cells**
- Beyond the cognitive map: Hippocampus and memory
- Open questions

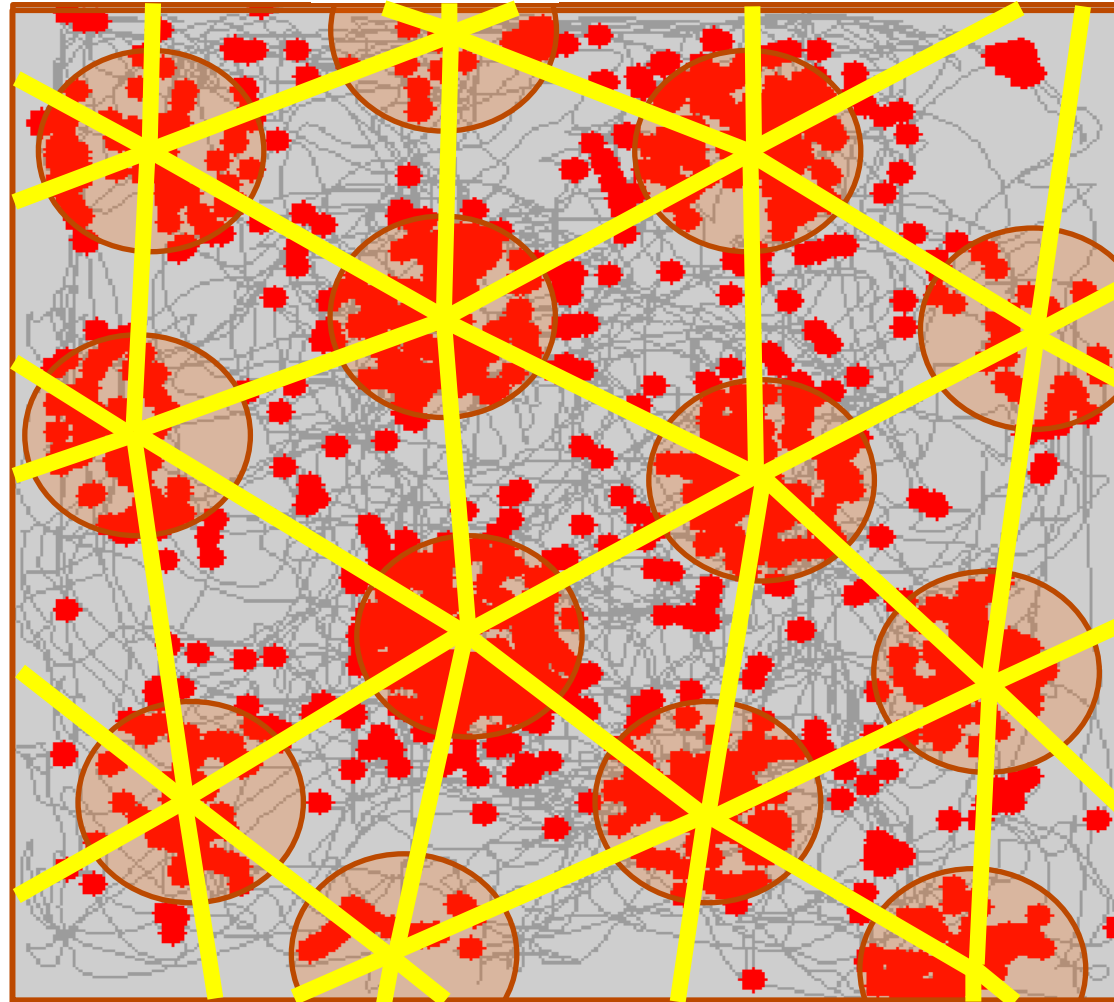
Grid cells



May-Britt Moser



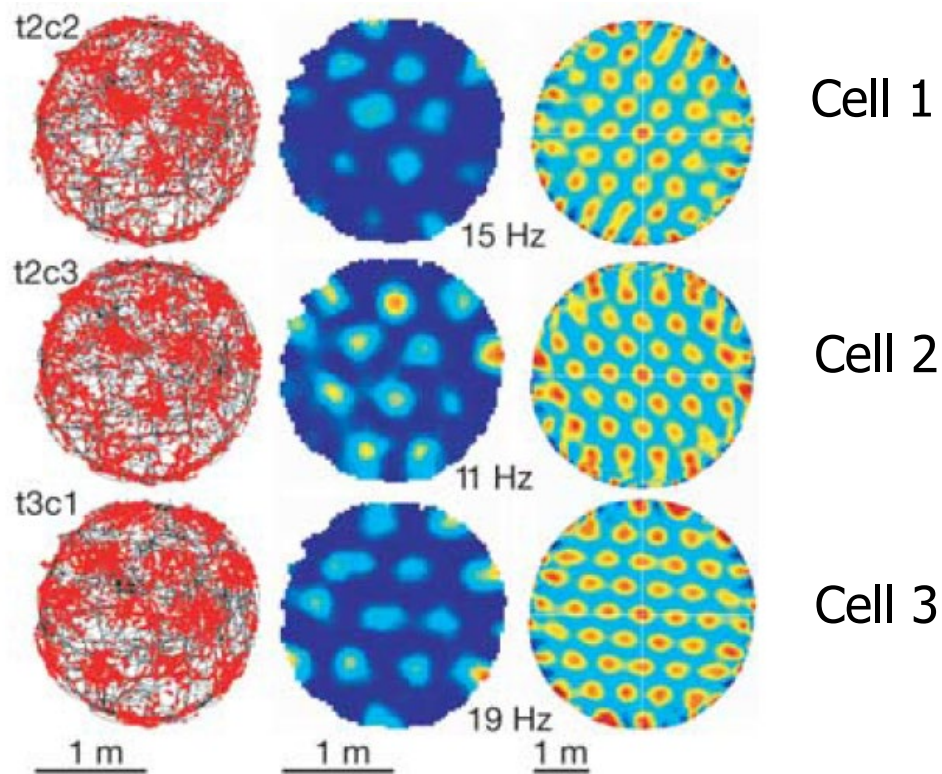
Edvard Moser



Hafting T, Fyhn M, Molden S, Moser MB, Moser EI (2005) Nature 436:801-806

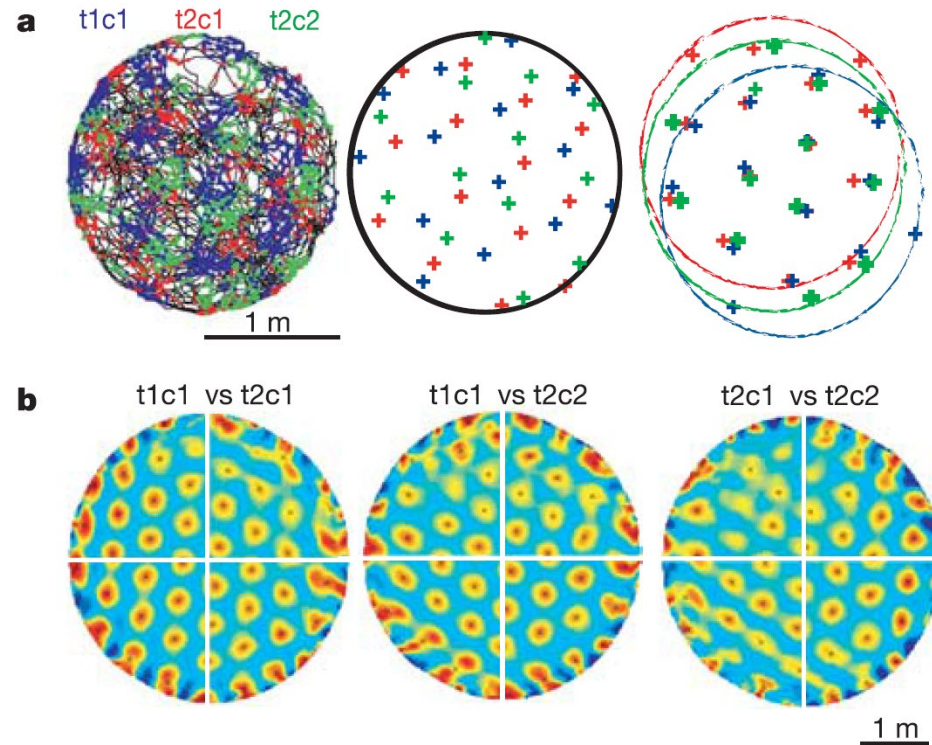
Grid cells in medial entorhinal cortex (MEC)

Three grid-cells recorded simultaneously on the same tetrode

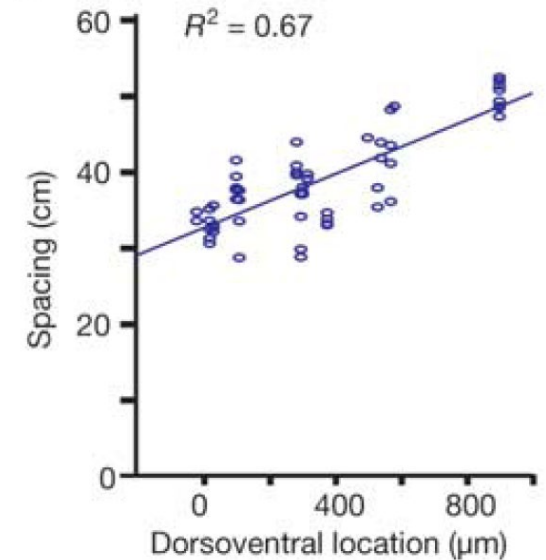
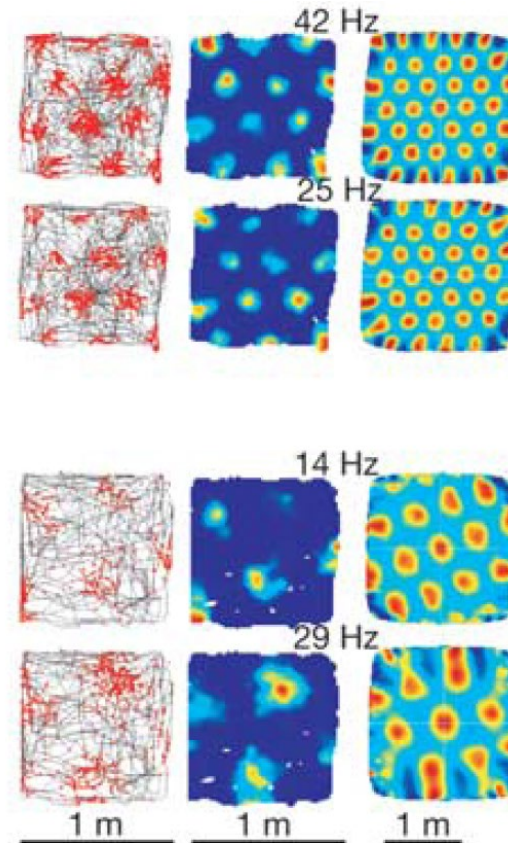
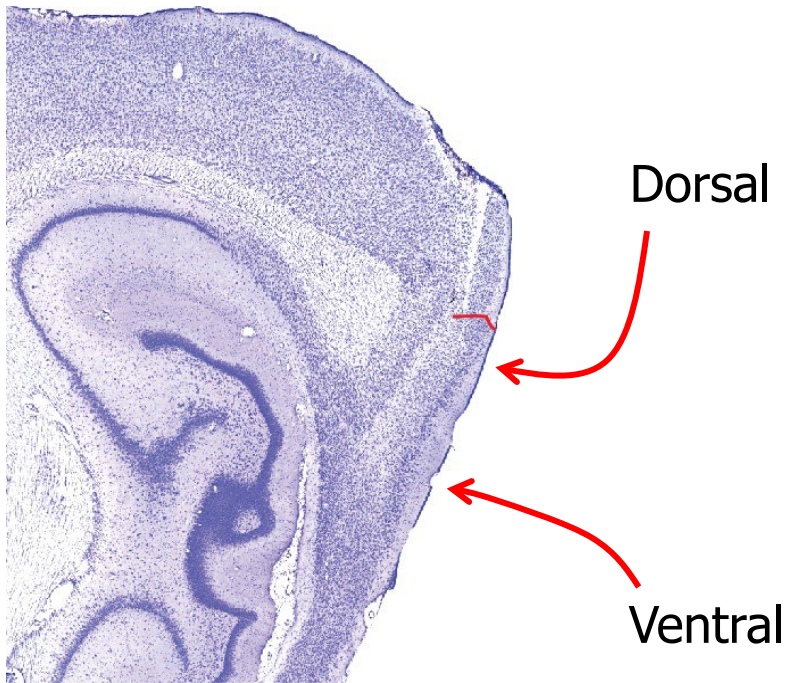


- Grids of simultaneously-recorded grid cells, from nearby locations in MEC, look quite similar

Nearby grid cells have the same grid spacing and orientation,
but random grid phase

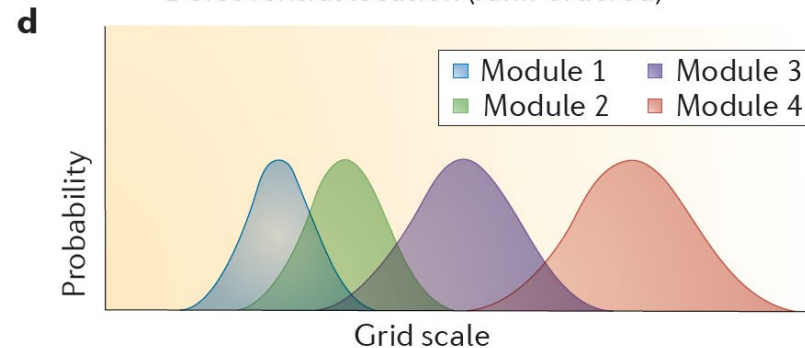
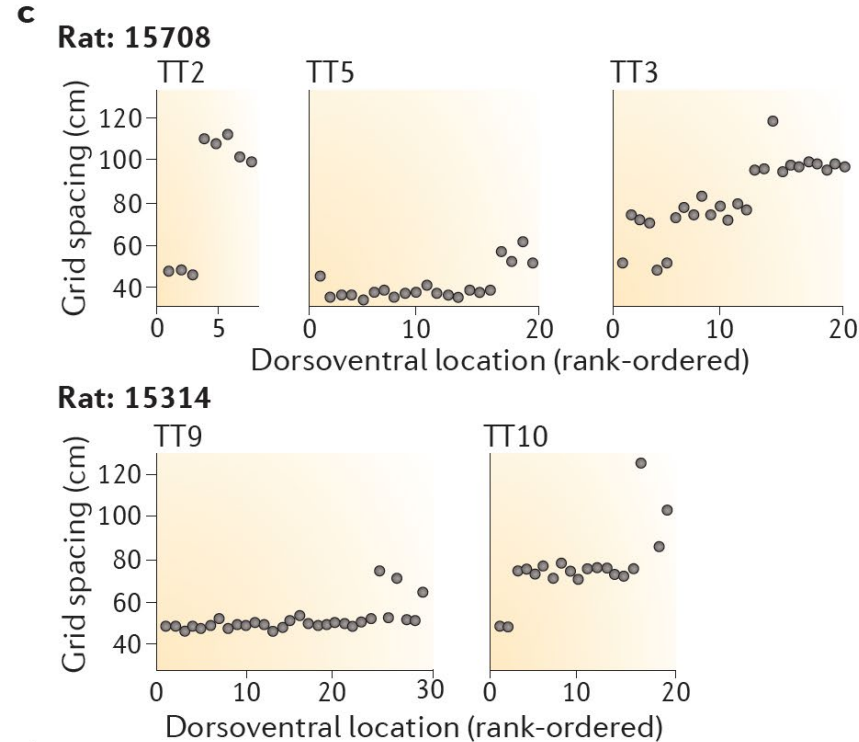
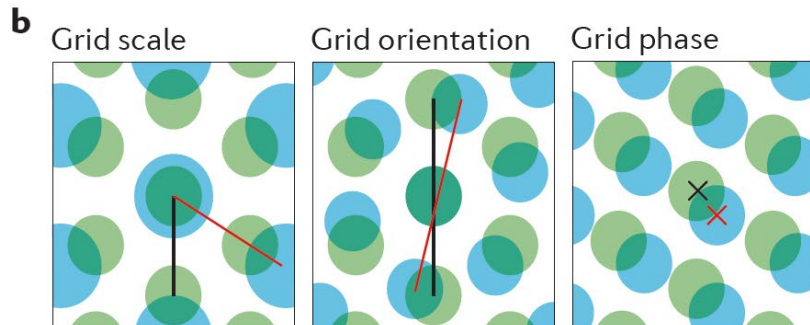
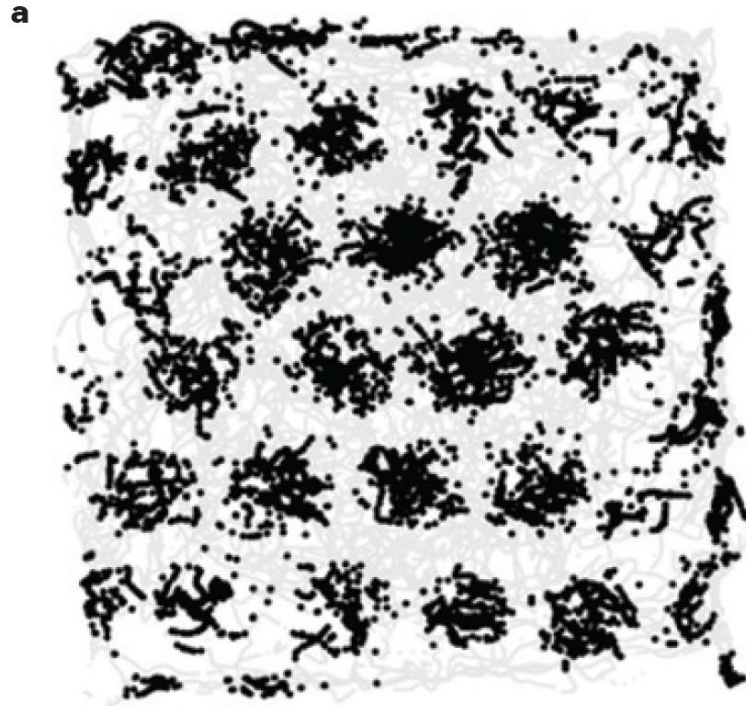


Grid spacing increases in size along the dorso-ventral axis of the entorhinal cortex



Data from multiple animals
pooled together

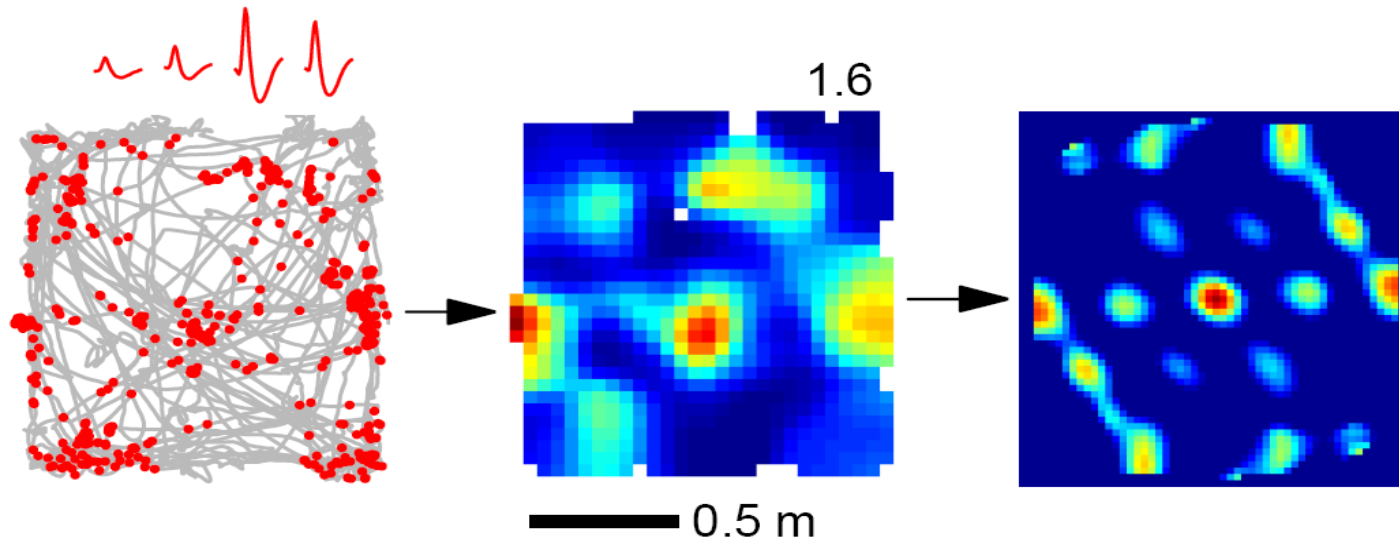
Support for the attractor network model of grid cells comes from the finding that grid cells are organized in *discrete* 'modules'



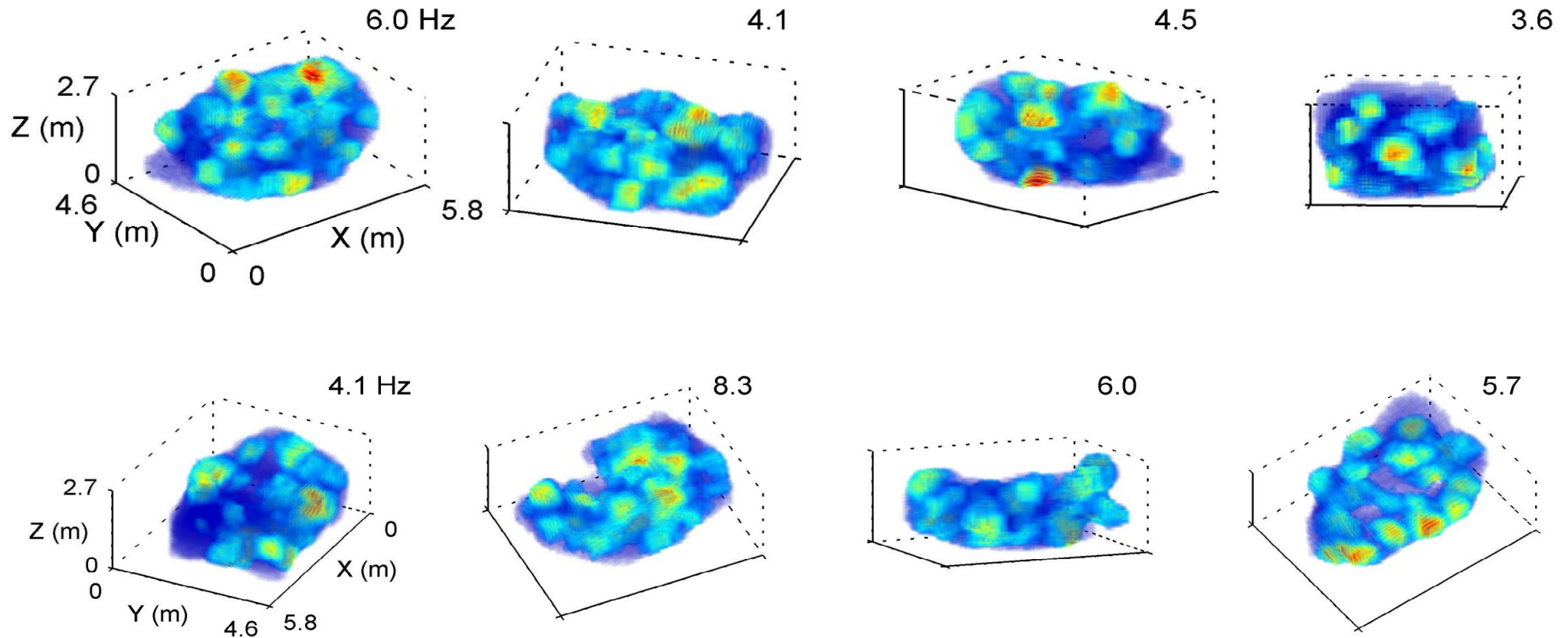
Stensola et al.,
Nature (2012)

Moser et al.,
Nat. Rev. Neurosci.
(2014)

2-D grid cells in bats



3-D grid cells in bats



- Unlike 2D grids, 3D grids show a local distance metric but do not exhibit a global lattice → This argues against most current theories on the function of grid cells.

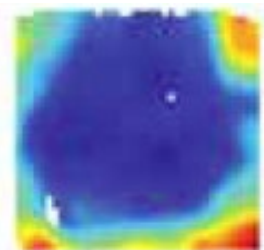
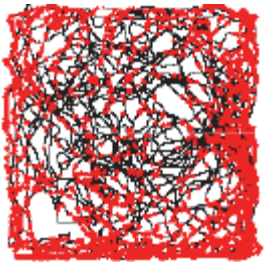
Ginosar et al.,
Nature (2021)

SUMMARY: Spatial cell types in the hippocampus and entorhinal cortex: The basic elements of the “brain navigation circuit”

Medial entorhinal cortex

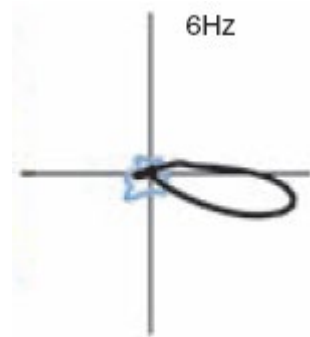
Hippocampus

Border Cells



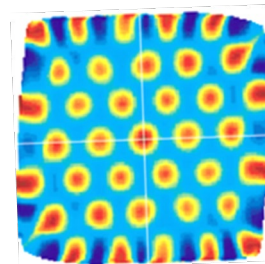
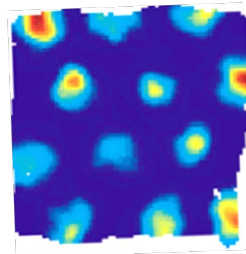
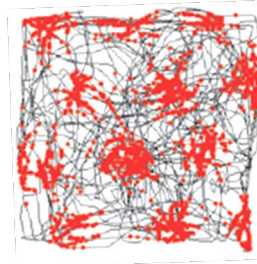
Mosers, O'Keefe, Knierim
2008

Head-direction cells



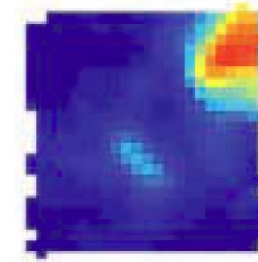
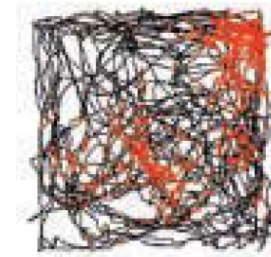
Ranck, Taube – 1980's

Grid cells



Mosers – 2005

Place cells



O'Keefe – 1971



The 2014 Nobel Prize in Physiology or Medicine



John O'Keefe
Born 1939, USA
University College London



May-Britt Moser
Born 1963, Norway
Norwegian University
of Science and
Technology, Trondheim



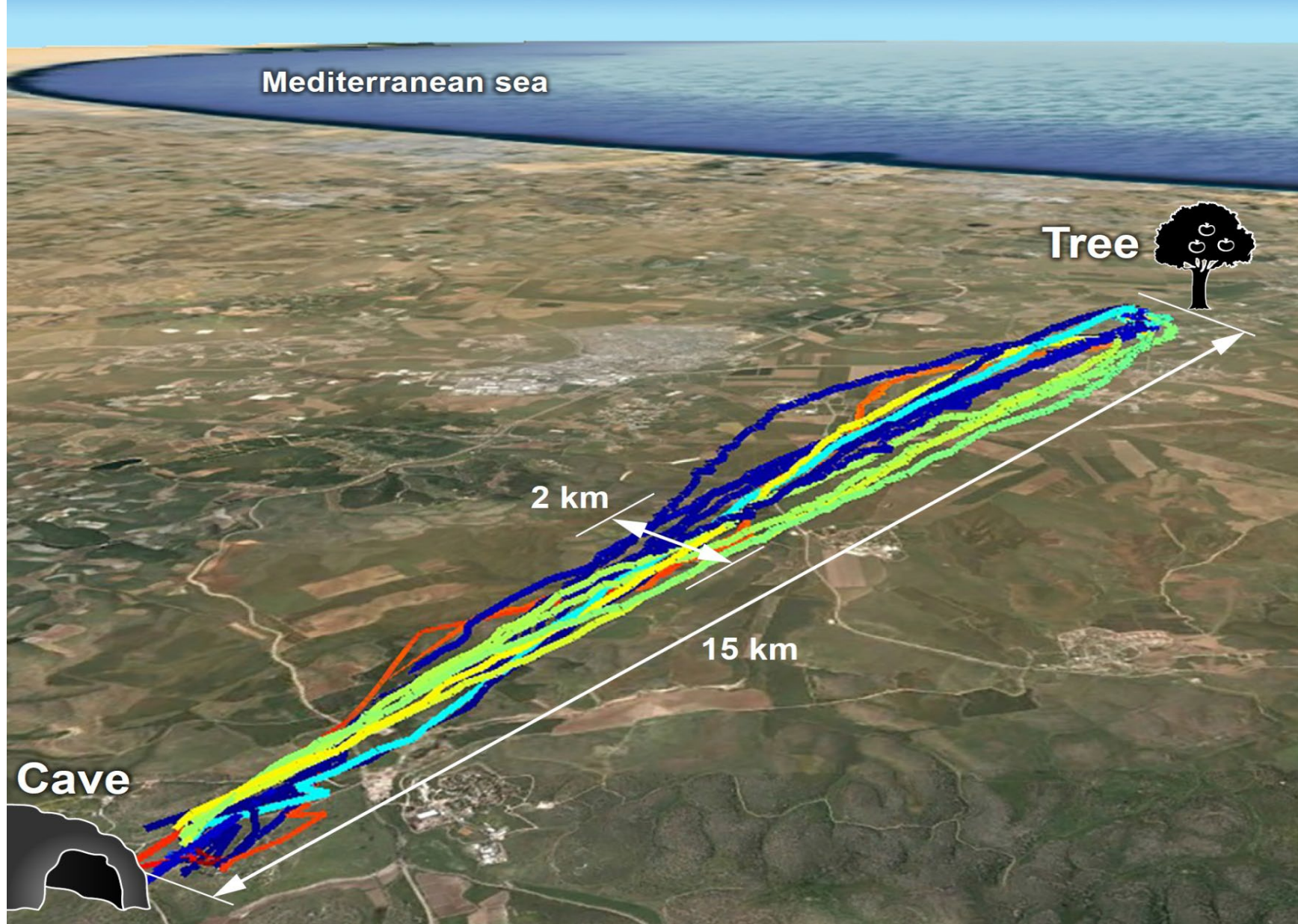
Edvard I. Moser
Born 1962, Norway
Norwegian University
of Science and
Technology, Trondheim

SUMMARY: Spatial cell types in the hippocampus and entorhinal cortex: The basic elements of the “brain navigation circuit”

SUMMARY:

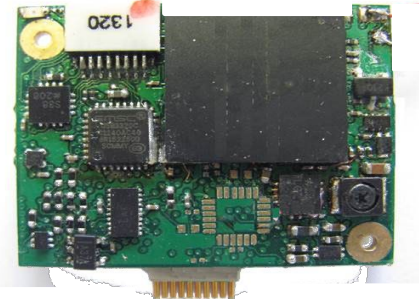
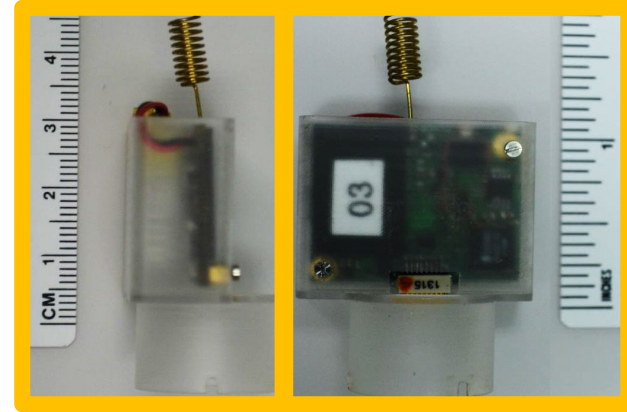
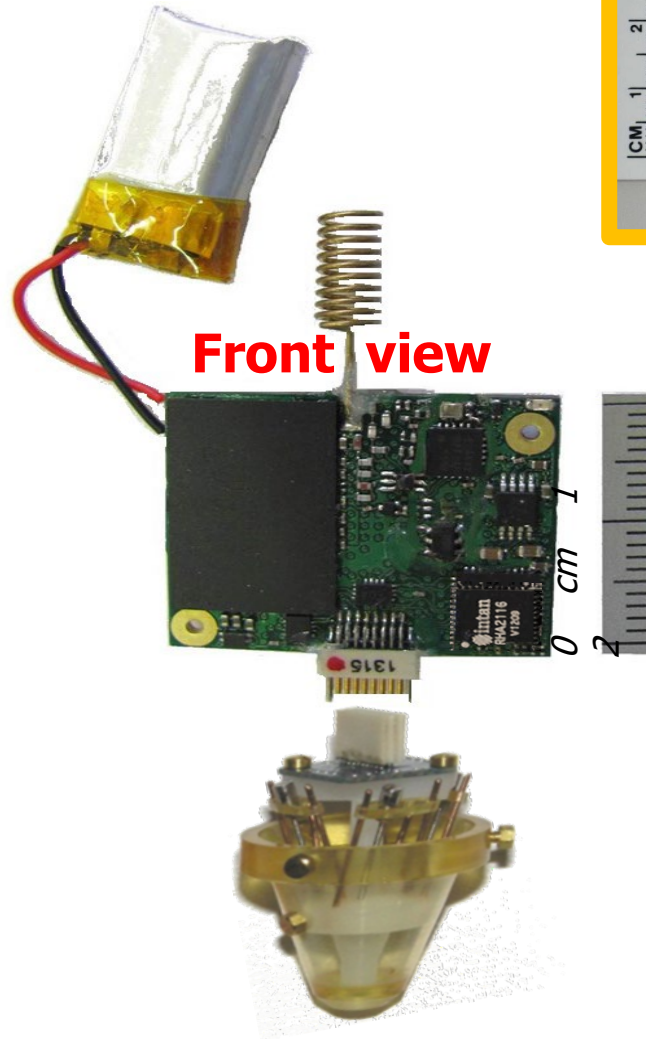
- **Place cell** → Position (where am I)
 - **Grid cells** → Position or Distance (“ruler”)
 - **Border cells** → Borders of the environment
 - **Head-direction cells** → Direction
 - **Goal-direction cells** → Goals
-
- The diagram uses blue curly braces to group the cell types into three functional categories:
- Map:** A large blue curly brace on the right side groups the first three cell types: Place cell, Grid cells, and Border cells.
 - Compass:** A blue curly brace on the right side groups Head-direction cells.
 - “Waze”:** A blue curly brace on the right side groups Goal-direction cells.

BUT:
How are
large-scale
spaces
encoded in
the brain?

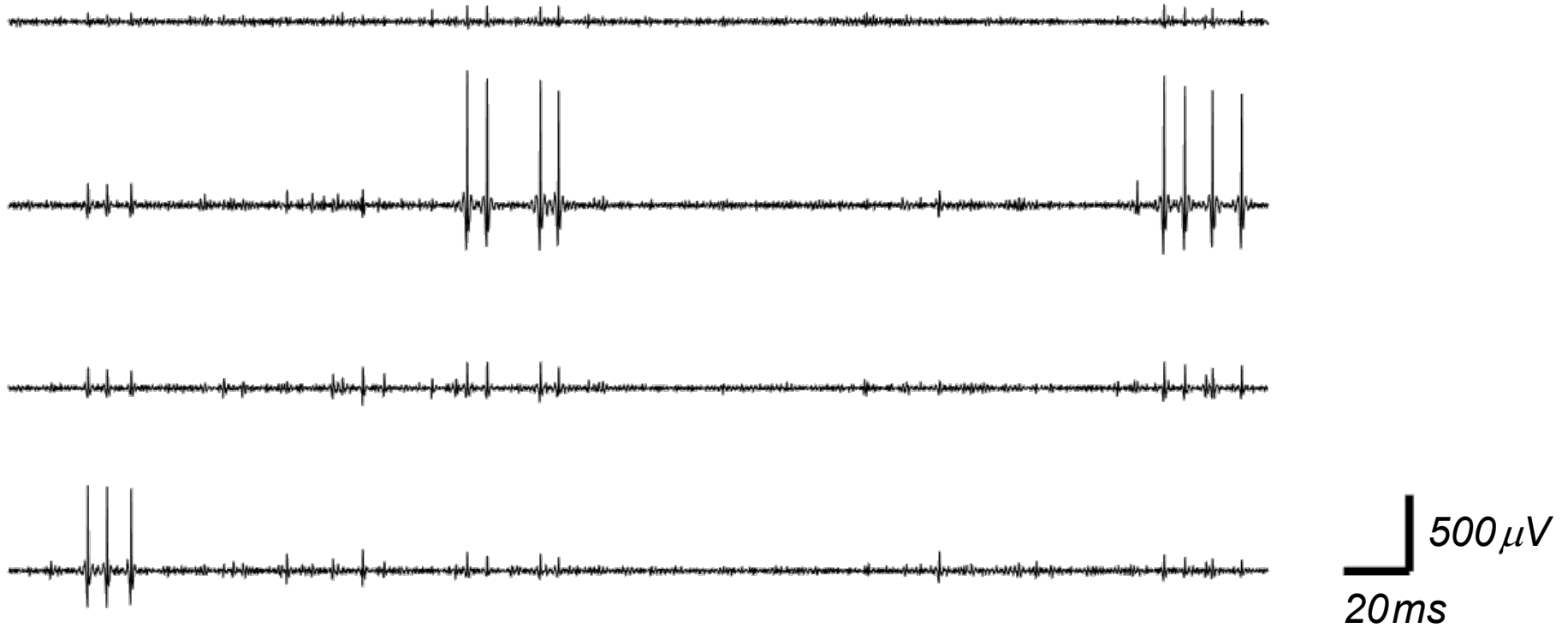


Geva-Sagiv, Las, Yovel, Ulanovsky
• Nature Rev. Neurosci., 2015
• PNAS, 2011

1. Developing on-board 64-channel neural logging system

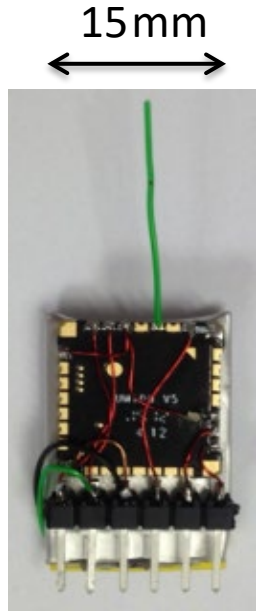


1. Developing on-board 64-channel neural logging system



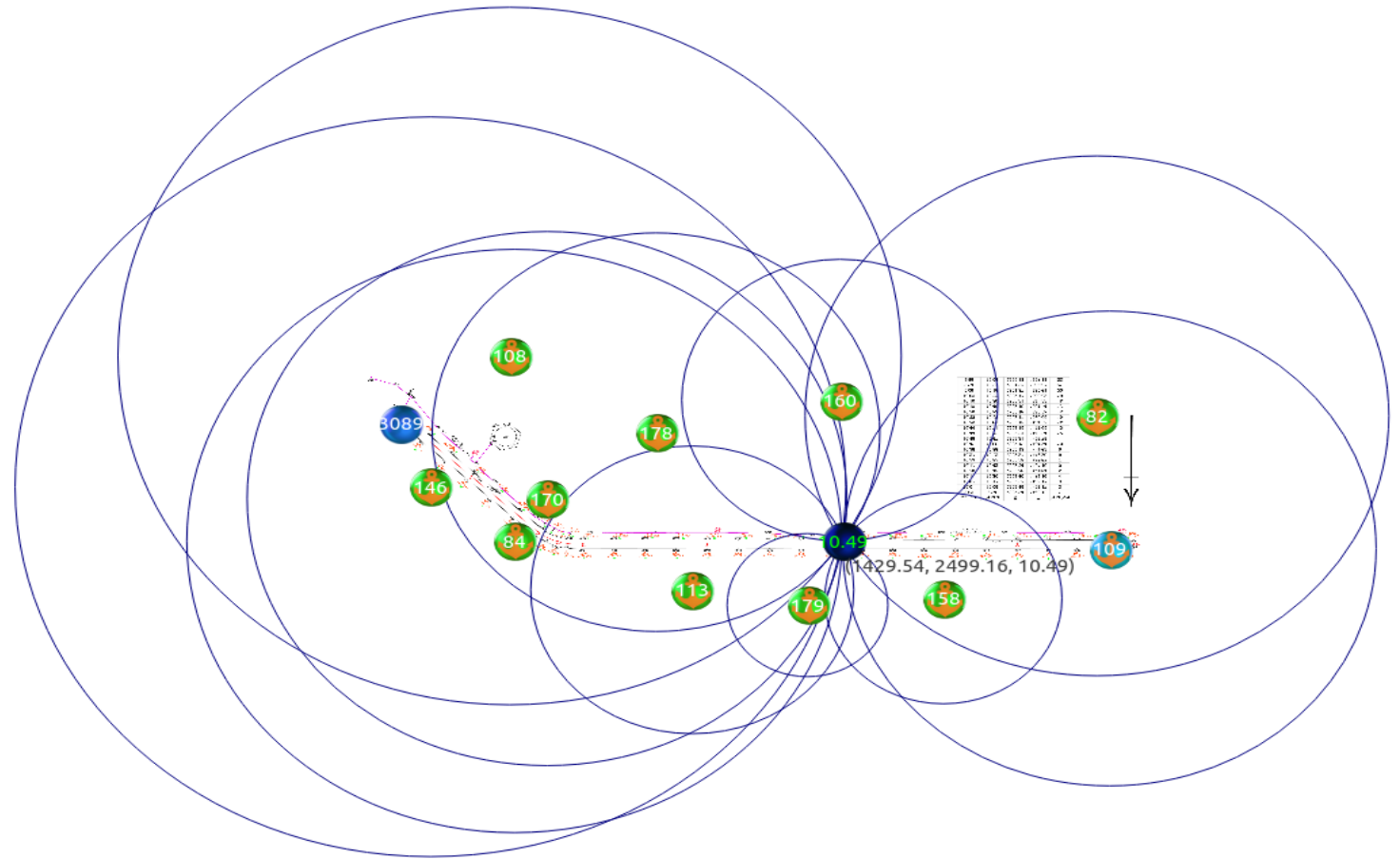
Eliav et al.
Science (2021)


2. Large-scale precise localization system




BeSpoon, Inc.

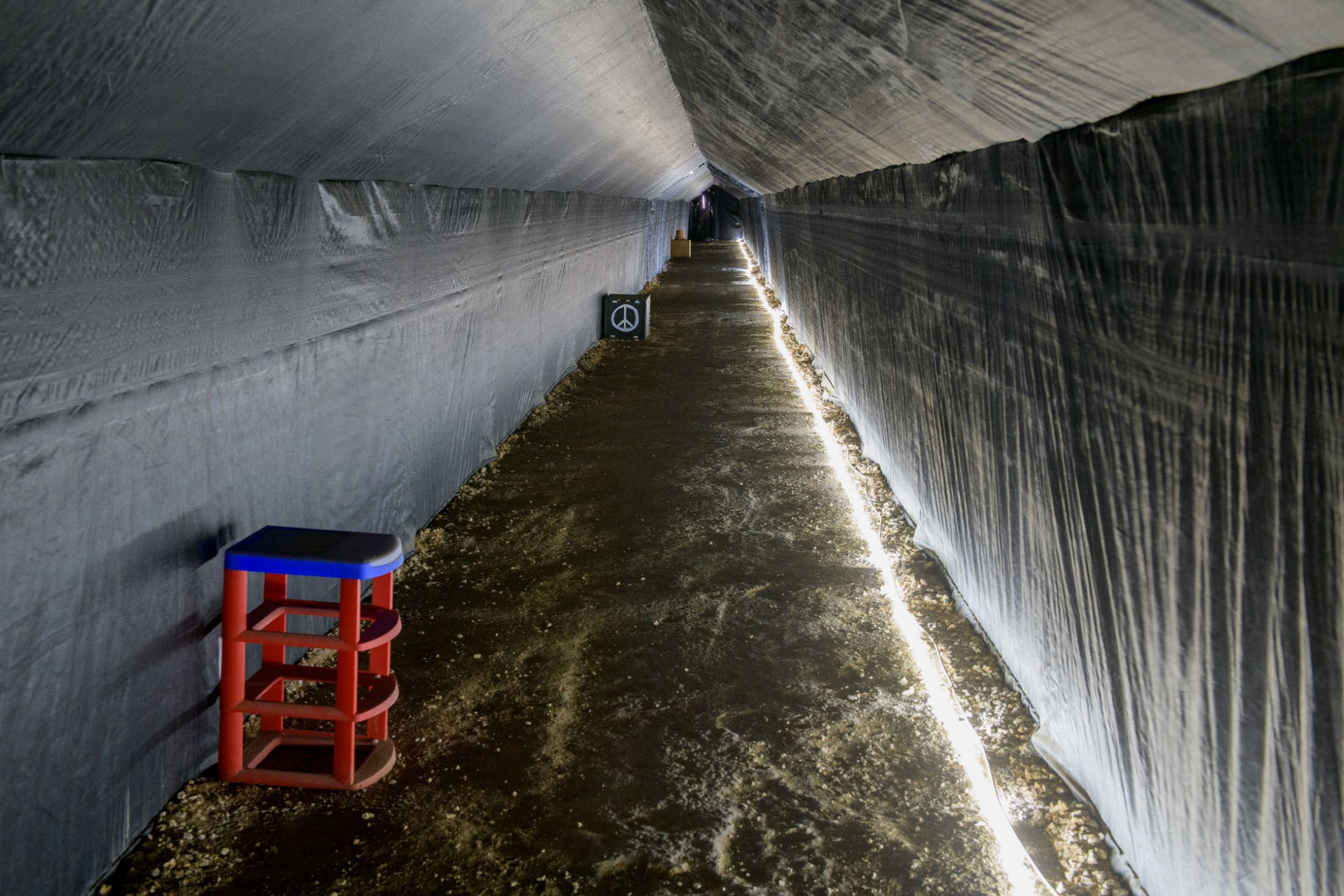
- 5-cm precision



 Tag (mobile unit)

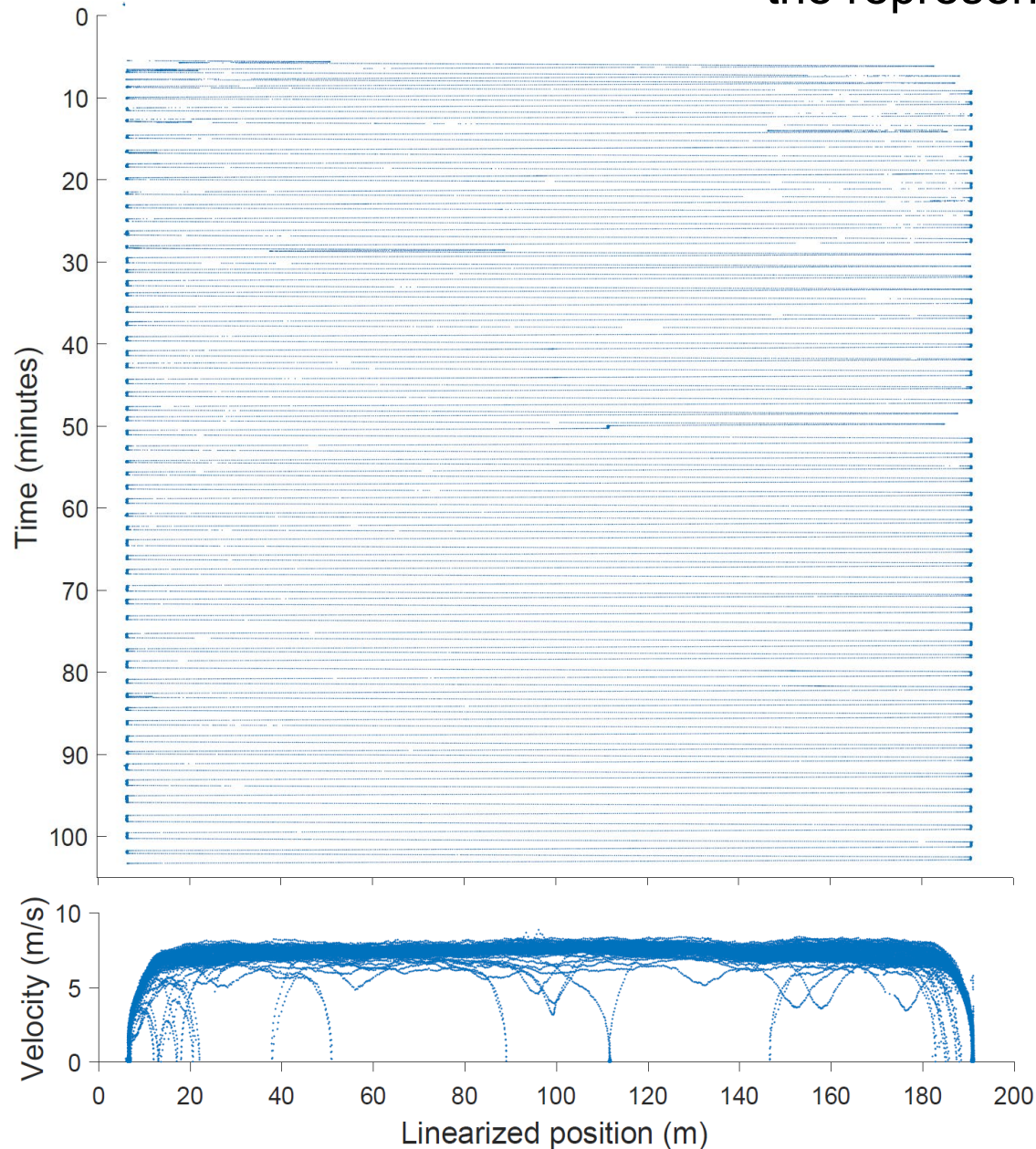
 Anchor (ground-based)

3. Large behavioral setup

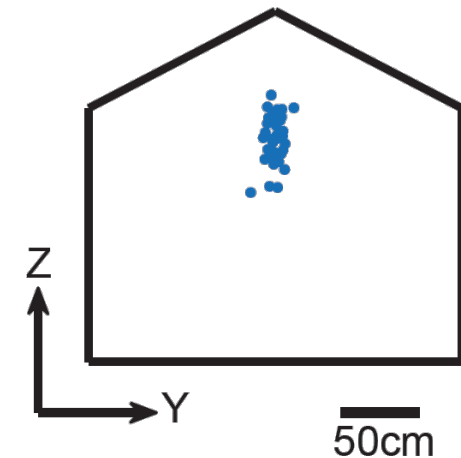


Behavior

→ Utilizing the bat's flight-speed to measure the representation of large spaces.

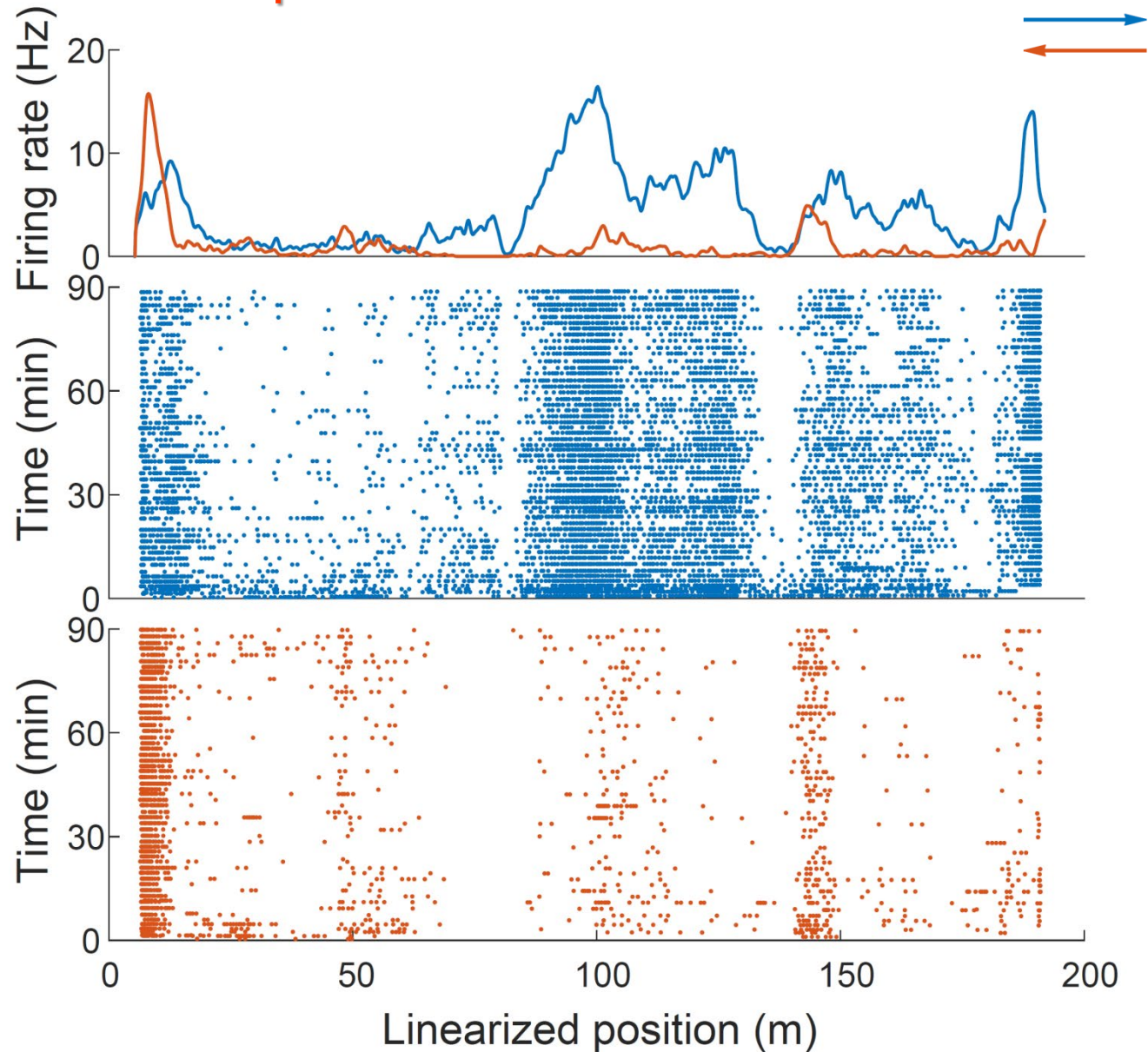


- Food rewards at both ends
- Direct flights from start to end
- 100 laps / session (20 km / 1.5 hrs)



- Flight speeds: 7-8 m/s

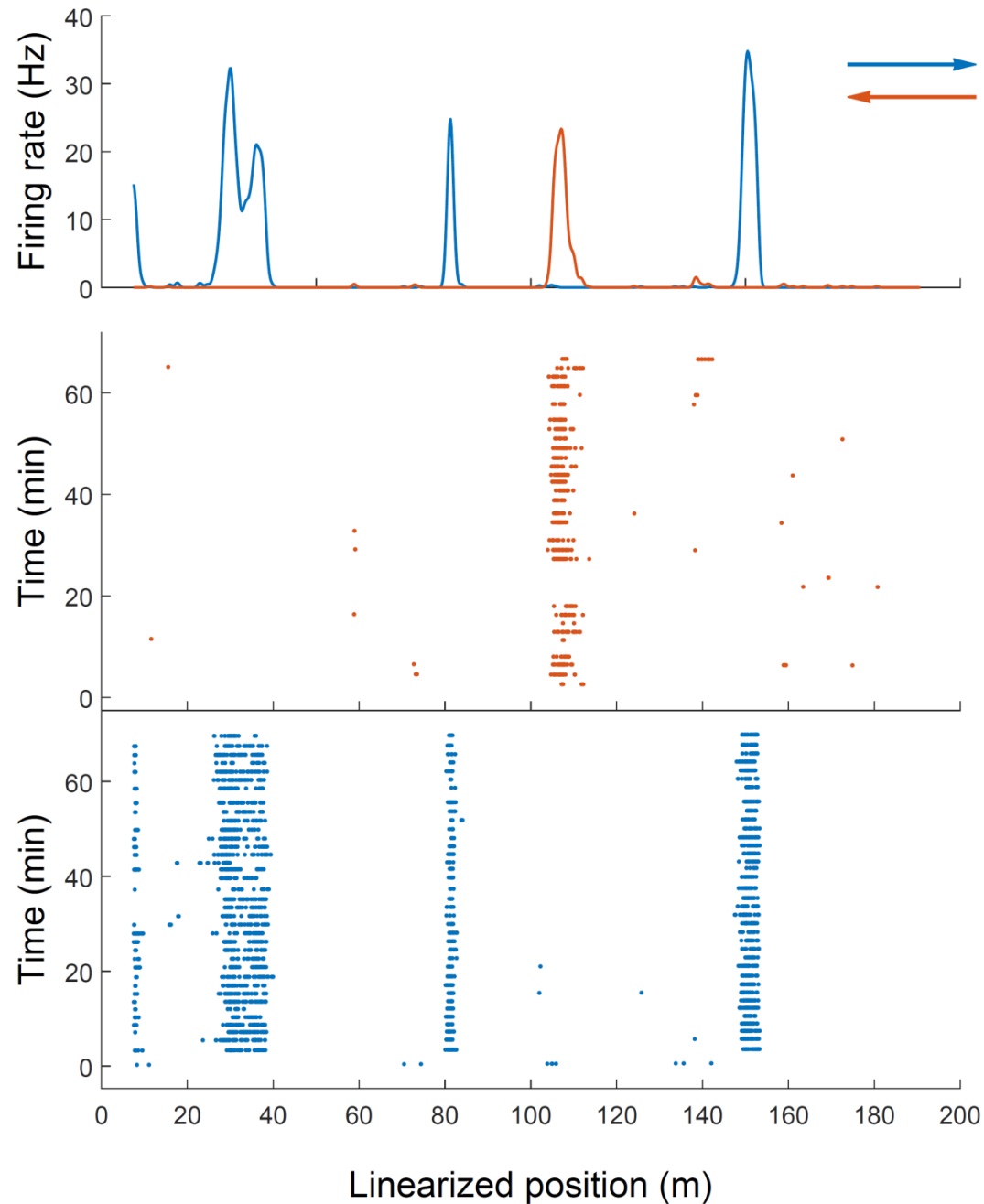
Examples



Example
cell from
dorsal CA1

Eliav et al.
Science (2021)

Example 2



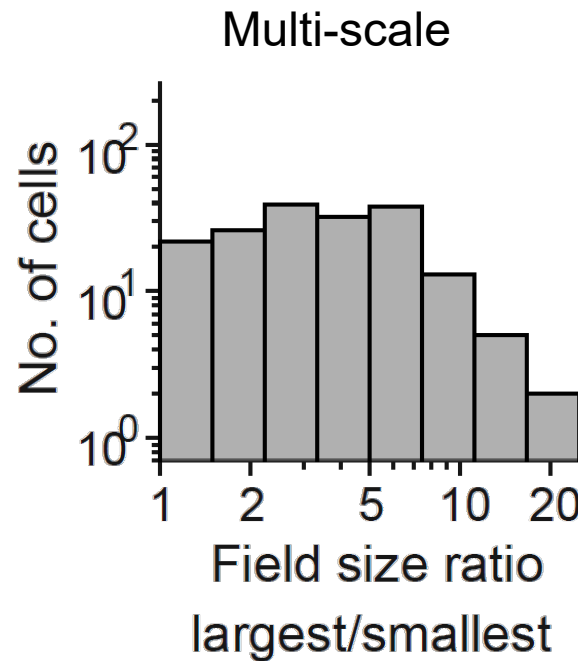
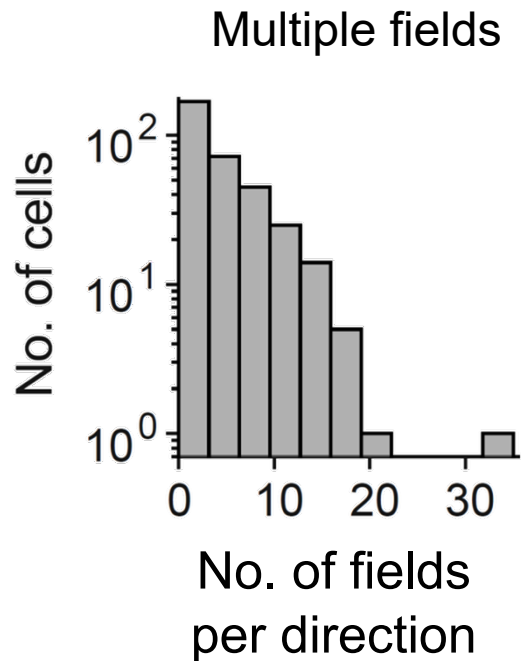
Properties of this spatial code:

- Large fields
- Multiple fields
- Multi-scale

→ Looks very different from place cells recorded in small lab setups !

Eliav et al.
Science (2021)

Population



Properties of this spatial code:

- Large fields
- Multiple fields
- Multi-scale

→ Looks very different from place cells recorded in small lab setups !

- Theoretical analysis of decoding errors explained why multi-scale coding is better for large environments.

Building a large Maze (60 x 35 meters)



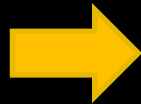
- **Maze:**

- How do we navigate in complex environments?
- Representation of multiple goals?
- What happens in the brain when we need to re-orient ourselves?
- Decision making.
- Planning.

→ Studying the higher-level cognitive aspects of navigation.

Question:

Neural coding in the “brain’s navigation circuit”
during NATURAL navigation – outdoors ?



Latham Island, Tanzania (70 km off the coast of Zanzibar)



Neuroscience Going Wild

Adding GPS + Altimeter to the Neural Logger

Neural Logger 2024:

- 64 neural channels (16 tetrodes)
- Ultrasonic Microphone
- Accelerometer, Gyro, Magnetometer
- GPS
- Altimeter

An entire on-board Flying ePhys Lab

NEW Neural Logger 2025 – logging *two* Neuropixels 2.0 probes:

- 768 neural channels
- Thousands of neurons simultaneously
- 7-8 brain areas simultaneously
- All of the above behavioral sensors (and more)

Neuroscience Going Wild



Neuroscience Going Wild

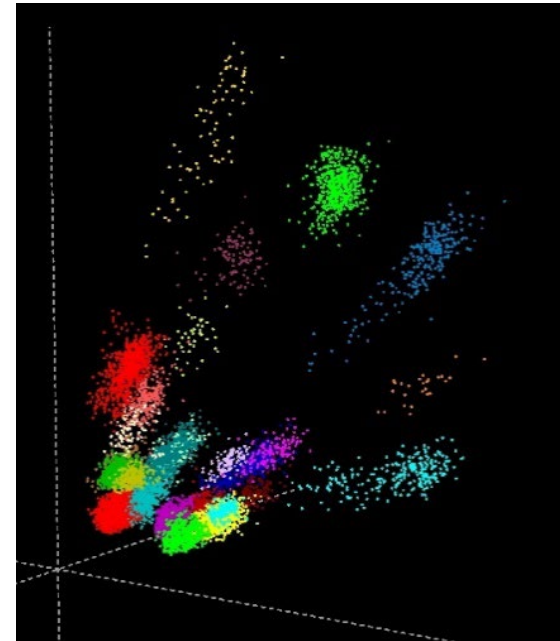








We recorded hippocampal place cells outdoors, on the island



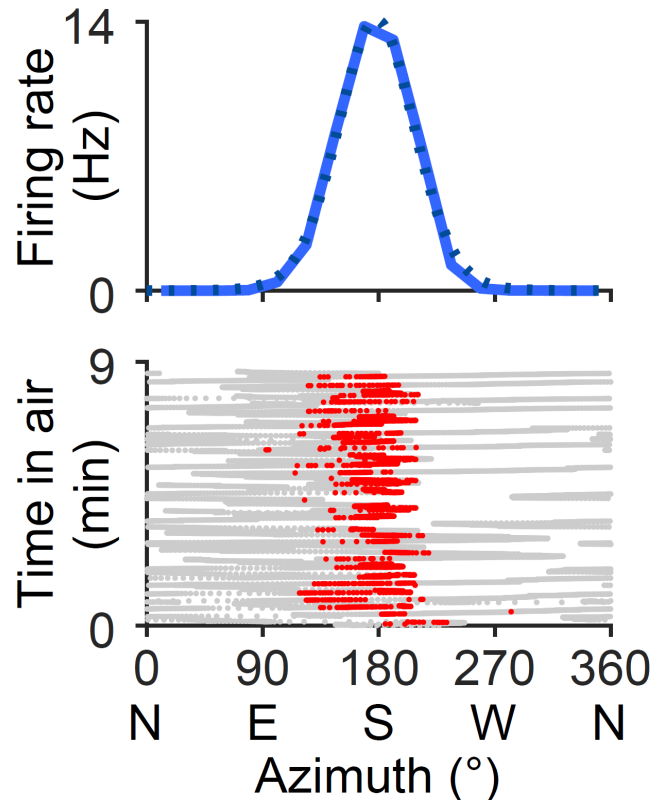
~100 neurons simultaneously

→ Analyze neural population manifolds during natural behavior, outdoors

We found head direction cells outdoors !

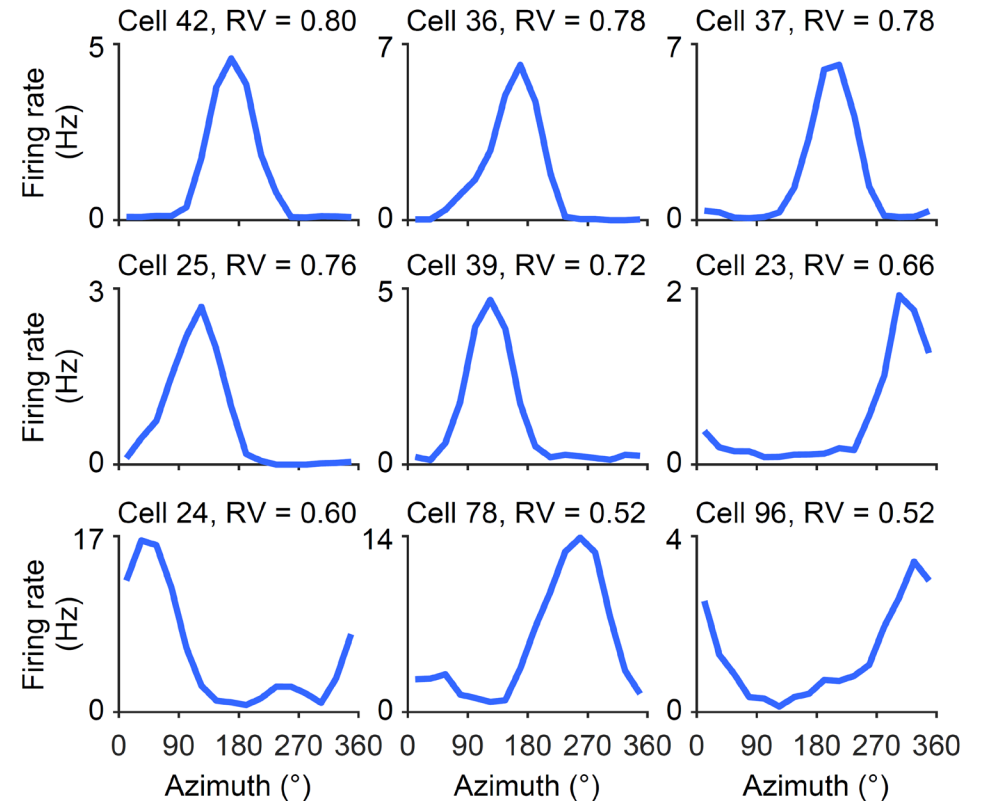
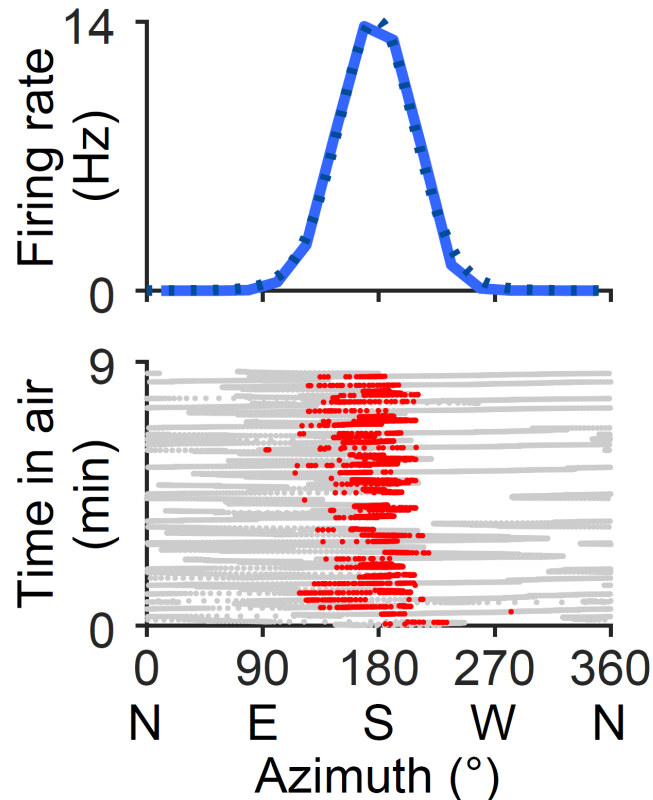
This head-direction cell points South.

Example of head-direction cell
recorded on the Island

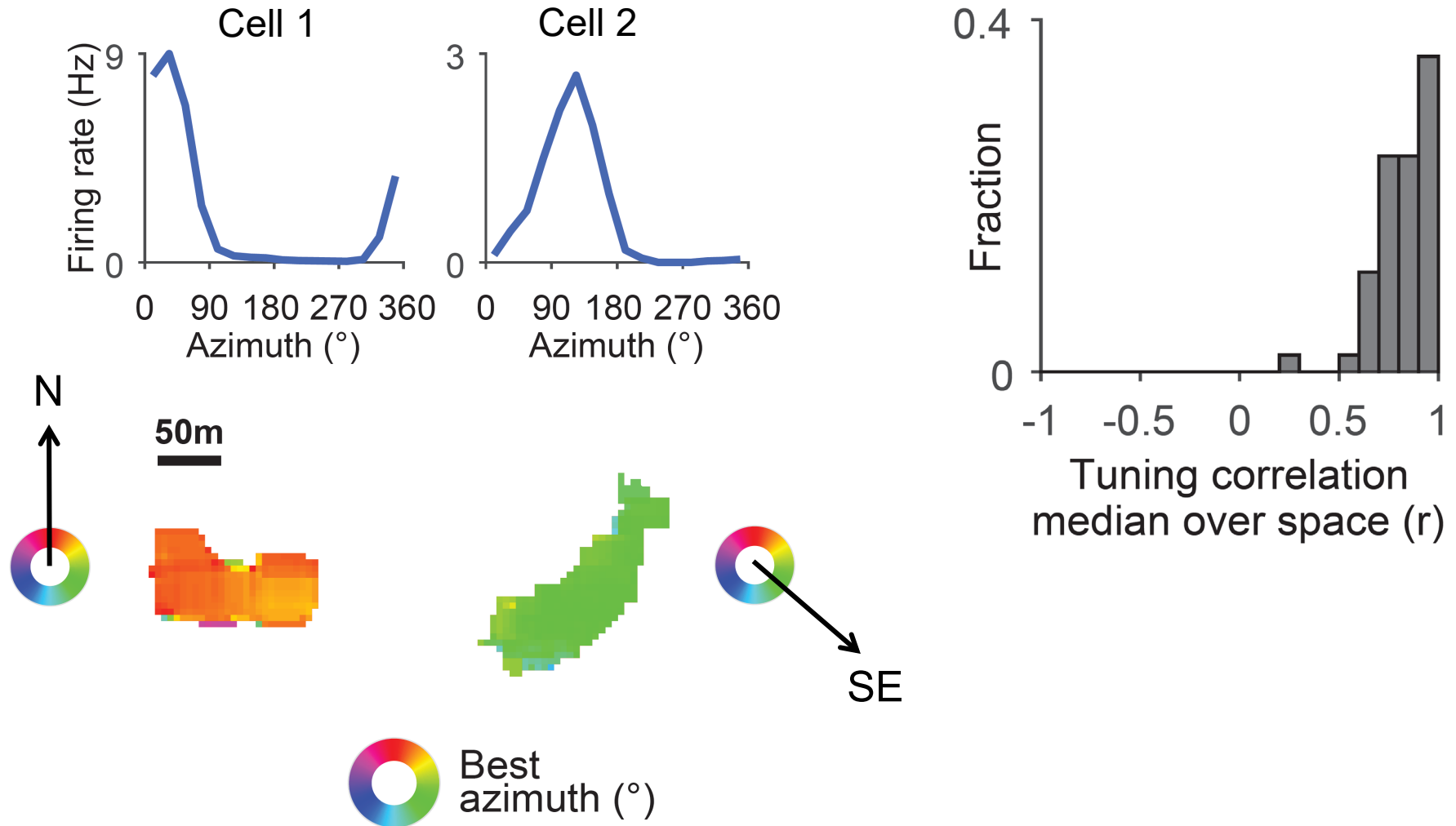


We found head direction cells outdoors !

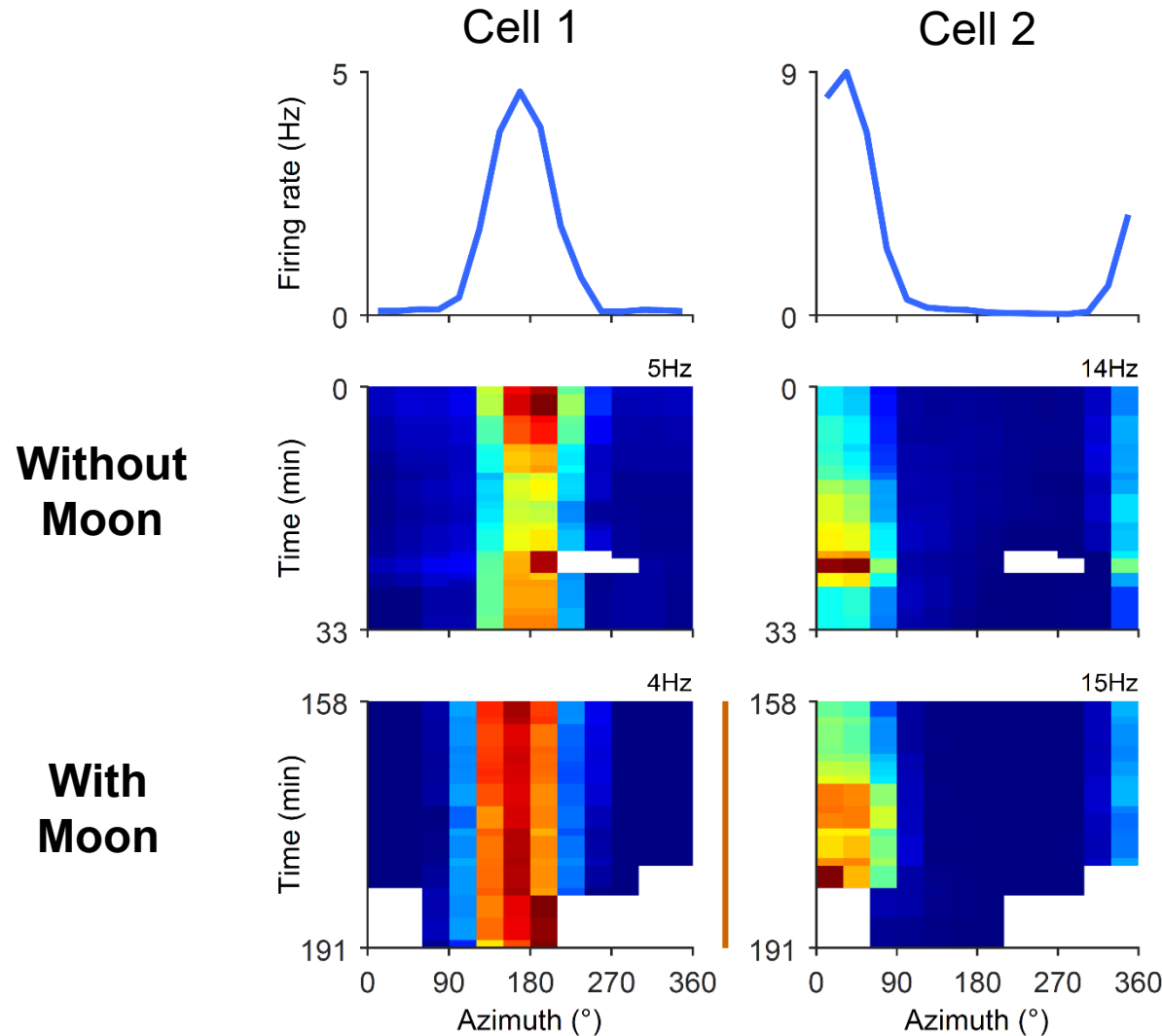
Example of head-direction cell recorded on the Island



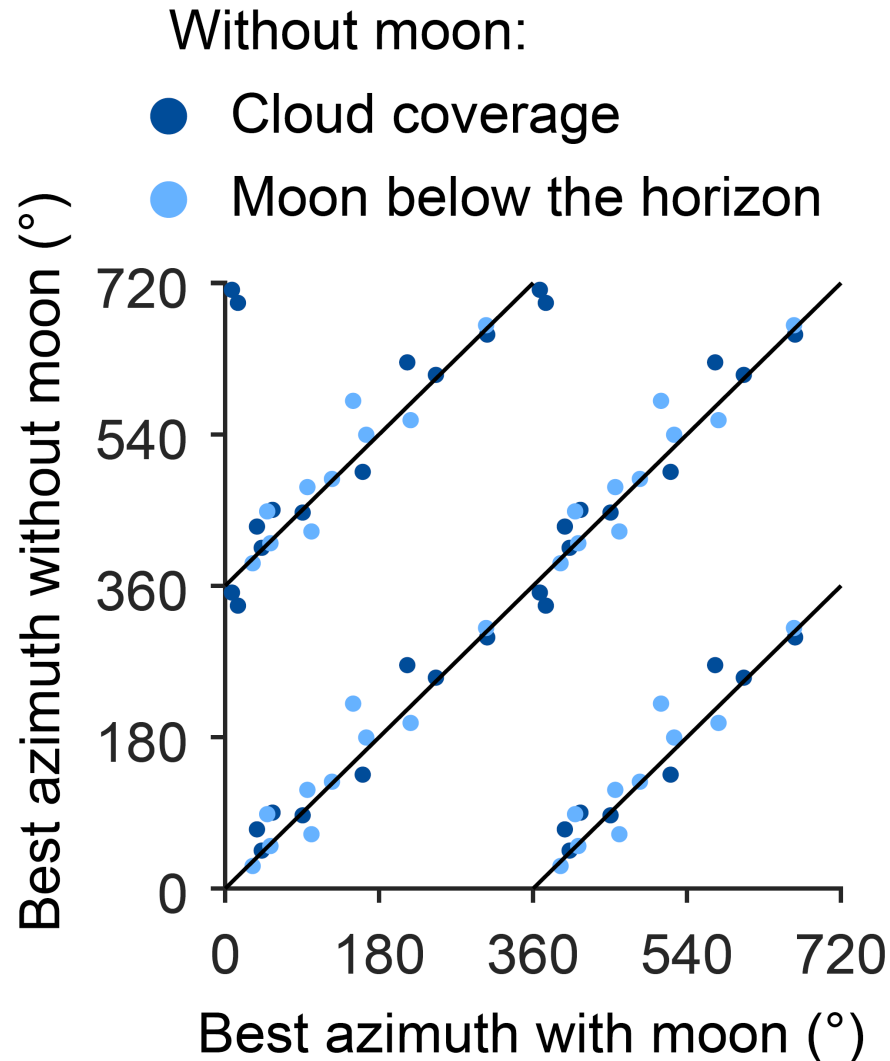
Direction of each cell was stable over geographical space



Direction of each cell was stable despite moon movements



Direction of each cell was stable despite moon movements,
and stable also on overcast cloudy nights (no moon / stars)



Preliminary results confirm the two major requirements for a “Neural Compass” – during real navigation, outdoors

- ✓ **Stability** of directional tuning **over geographical space**
- ✓ **Stability** of tuning despite **movement of moon & stars**

Additional findings

- Dynamics of the head-direction signal in the first days: *Learning*.
- Rotation in the head-direction signal indoors vs. outdoors.

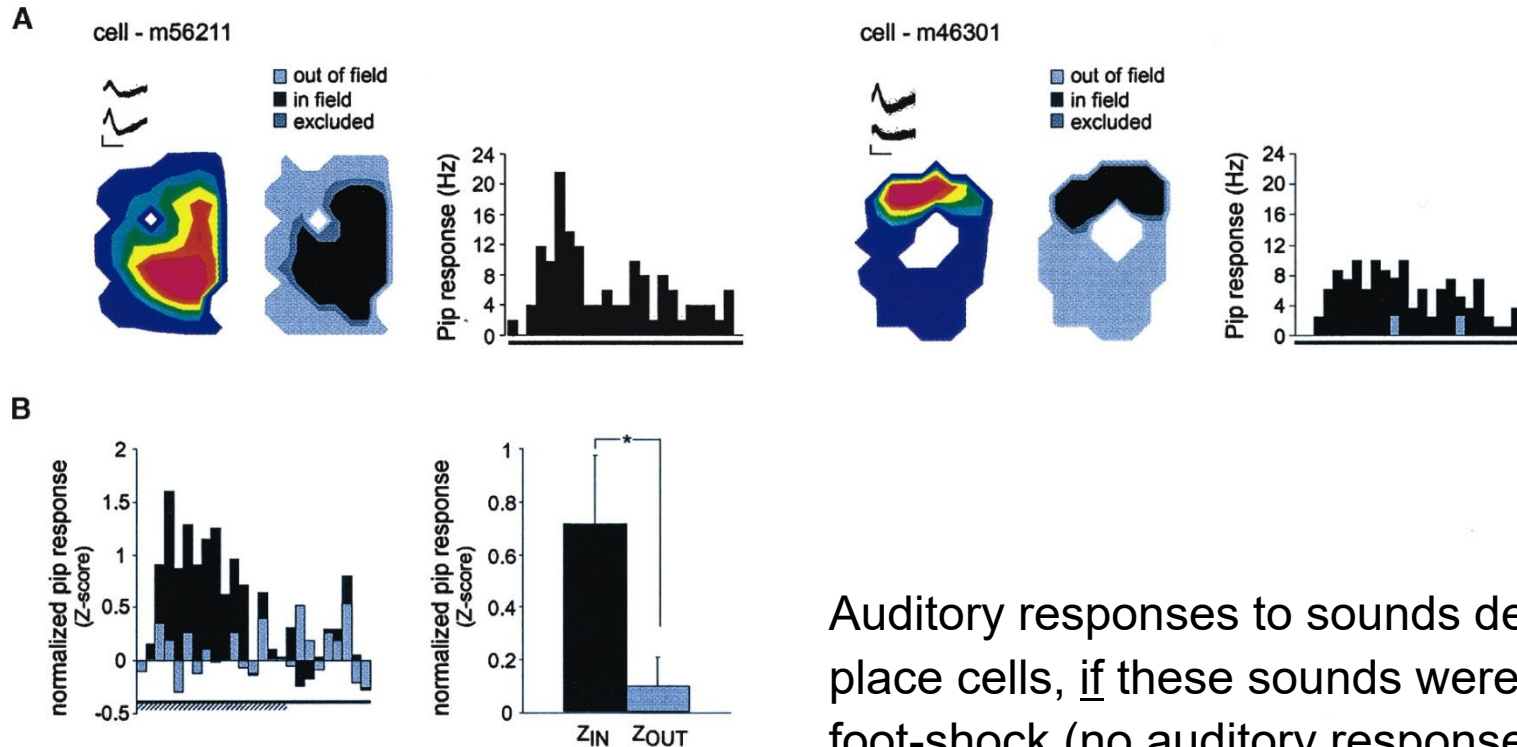
Take home messages

- Head direction cells **can** in fact serve as a neural compass for outdoors navigation.
- Head-direction representation is **global** not local.
- Head-direction tuning is likely **computed** from landmark configuration and/or island geometry.

Outline of today's lecture

- Hippocampus: Introduction and early discoveries
- Spatial maps in the hippocampus and related regions:
 - Place cells
 - Head direction cells
 - Grid cells
- **Beyond the cognitive map: Hippocampus and memory**
- Open questions

Coding of place is not everything: Gating of auditory responses by hippocampal place cells



Moita et al., *Neuron* (2003)

Auditory responses to sounds developed in hippocampal place cells, if these sounds were temporally-linked to a foot-shock (no auditory responses if the sounds and foot-shocks were presented randomly at the same rate but un-correlated to each other). Auditory responses occurred only when the animal was inside the place field of the neuron.

Receptive Fields – some properties

(reminder from lecture #1 about receptive fields of sensory neurons)

- The receptive field is NOT the key computational property of the neuron; instead, the receptive field can be thought as a “permissive property”:

if

Stimulus is within the receptive field of the neuron

then

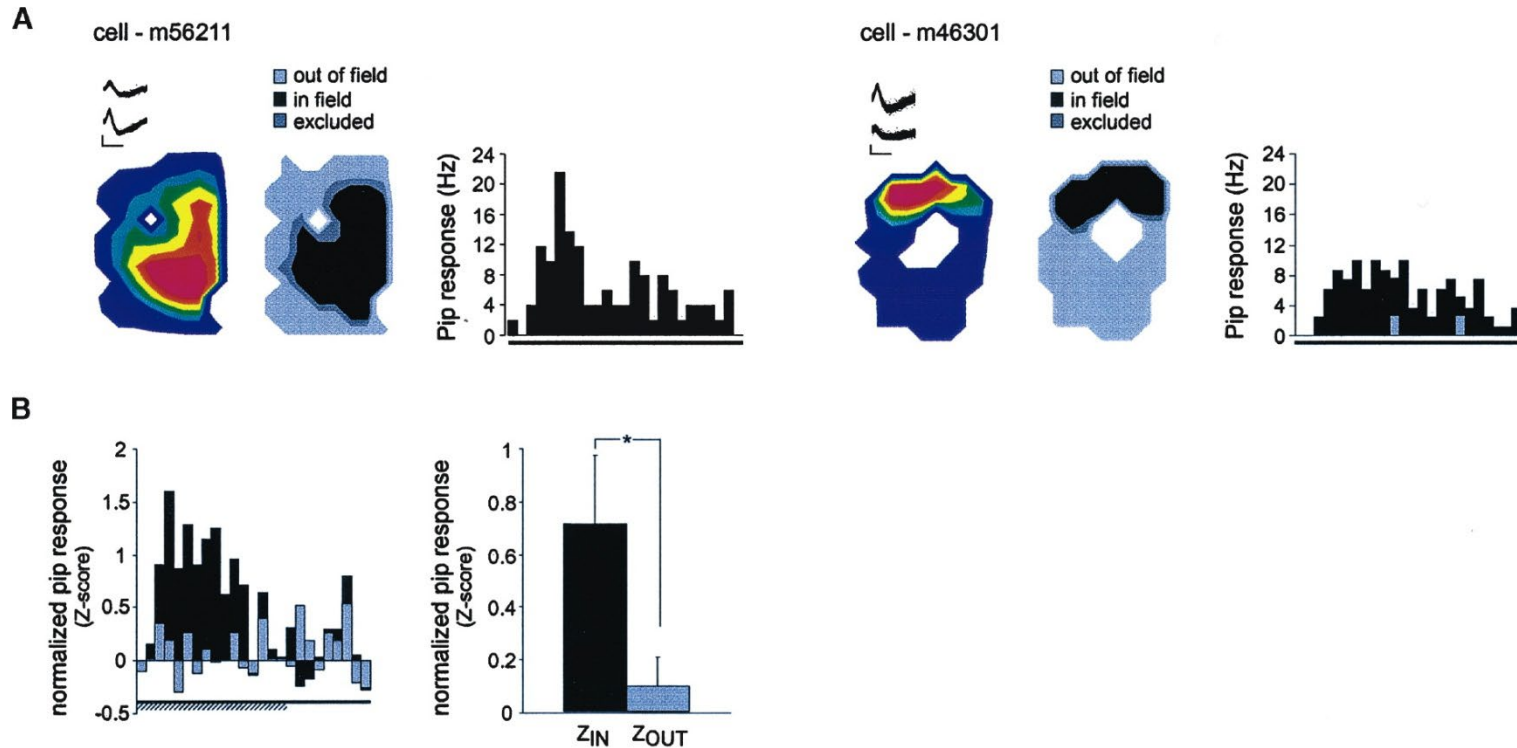
Do whatever (complex) computation the neuron is supposed to do

else

Do nothing

end

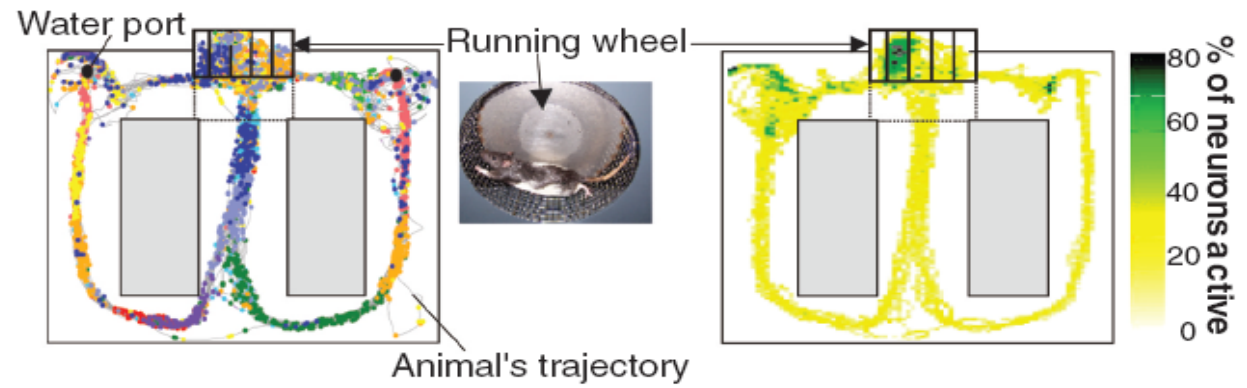
Coding of place is not everything: Gating of auditory responses by hippocampal place cells



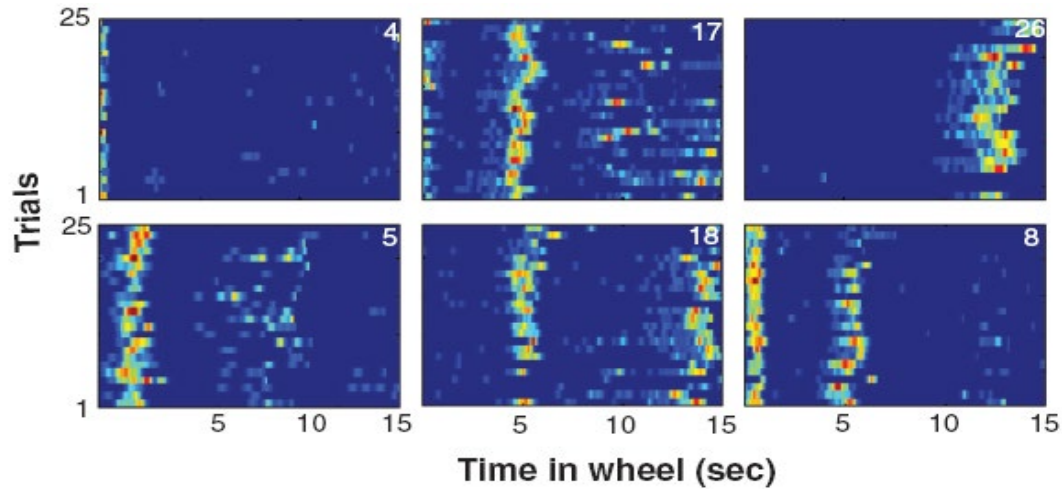
Moita et al., *Neuron* (2003)

Perhaps space is a “permissive property” in place cells, just as it is in the receptive fields of sensory neurons

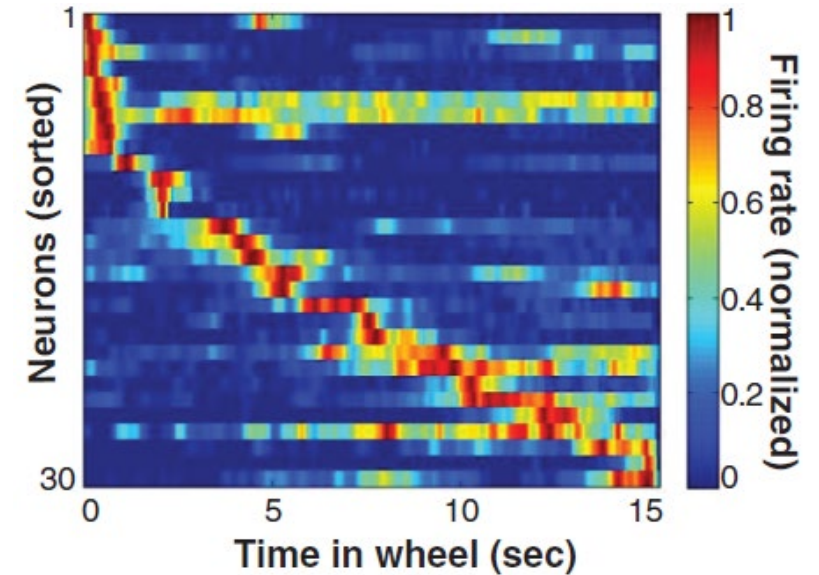
Time cells



Six neurons over multiple trials

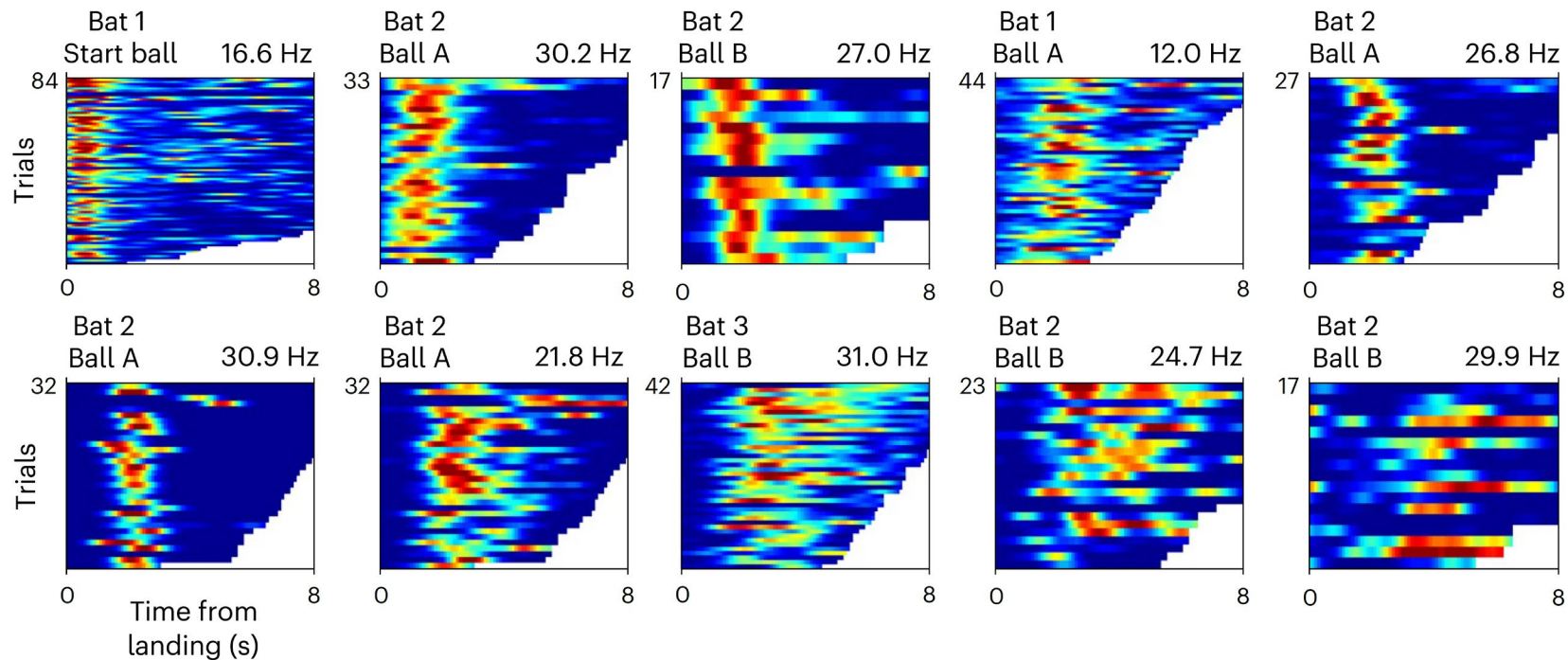


Simultaneously-recorded ensemble of 30 neurons

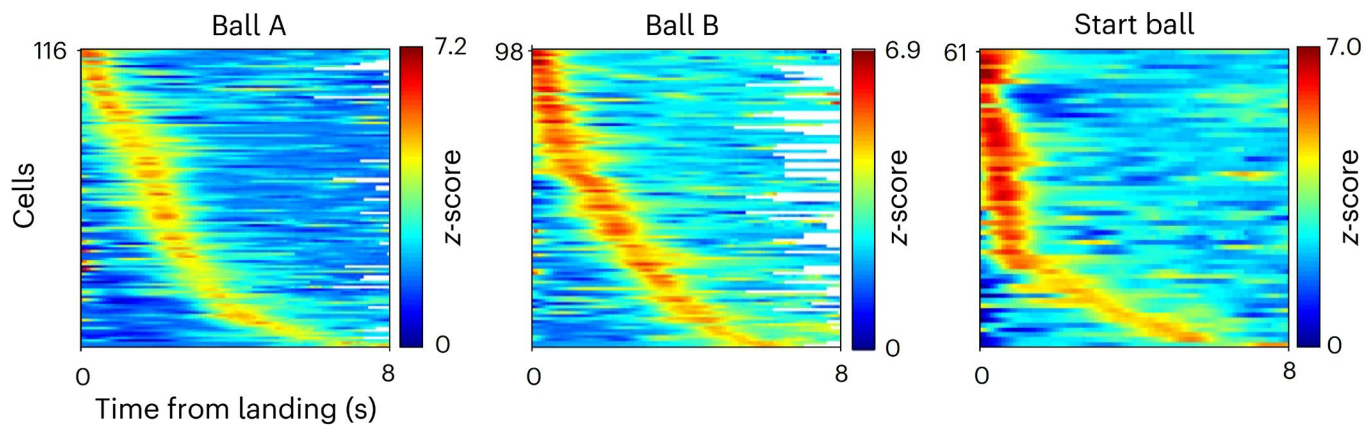


Time cells

Time cells in bats



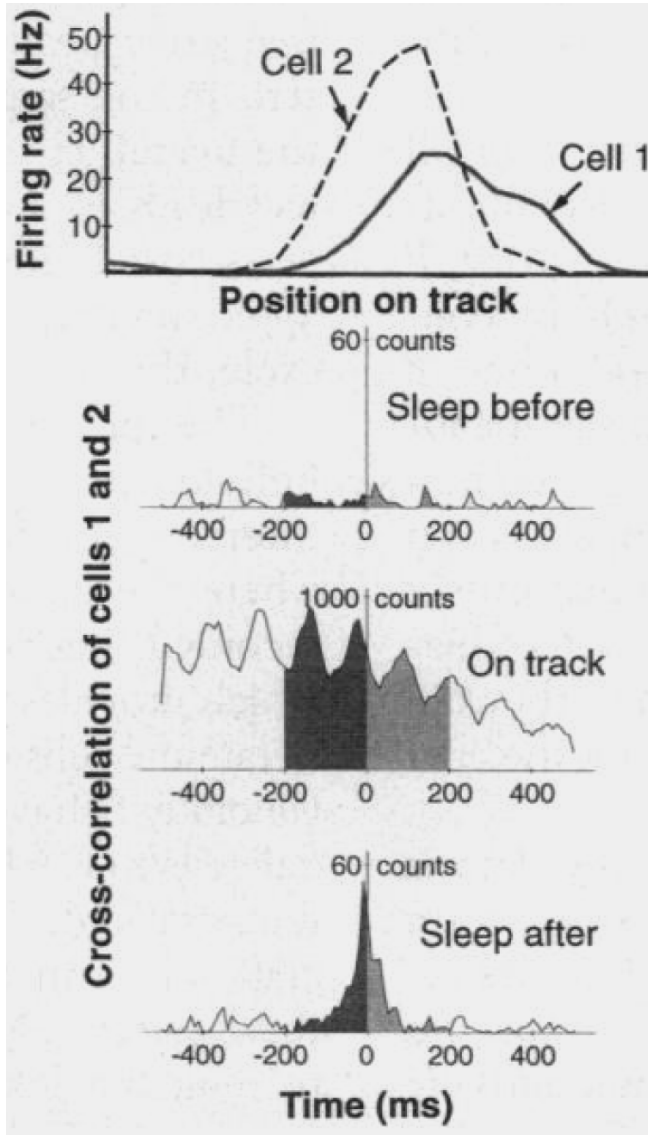
Examples



Population

Omer et al.
Nature Neurosci (2023)

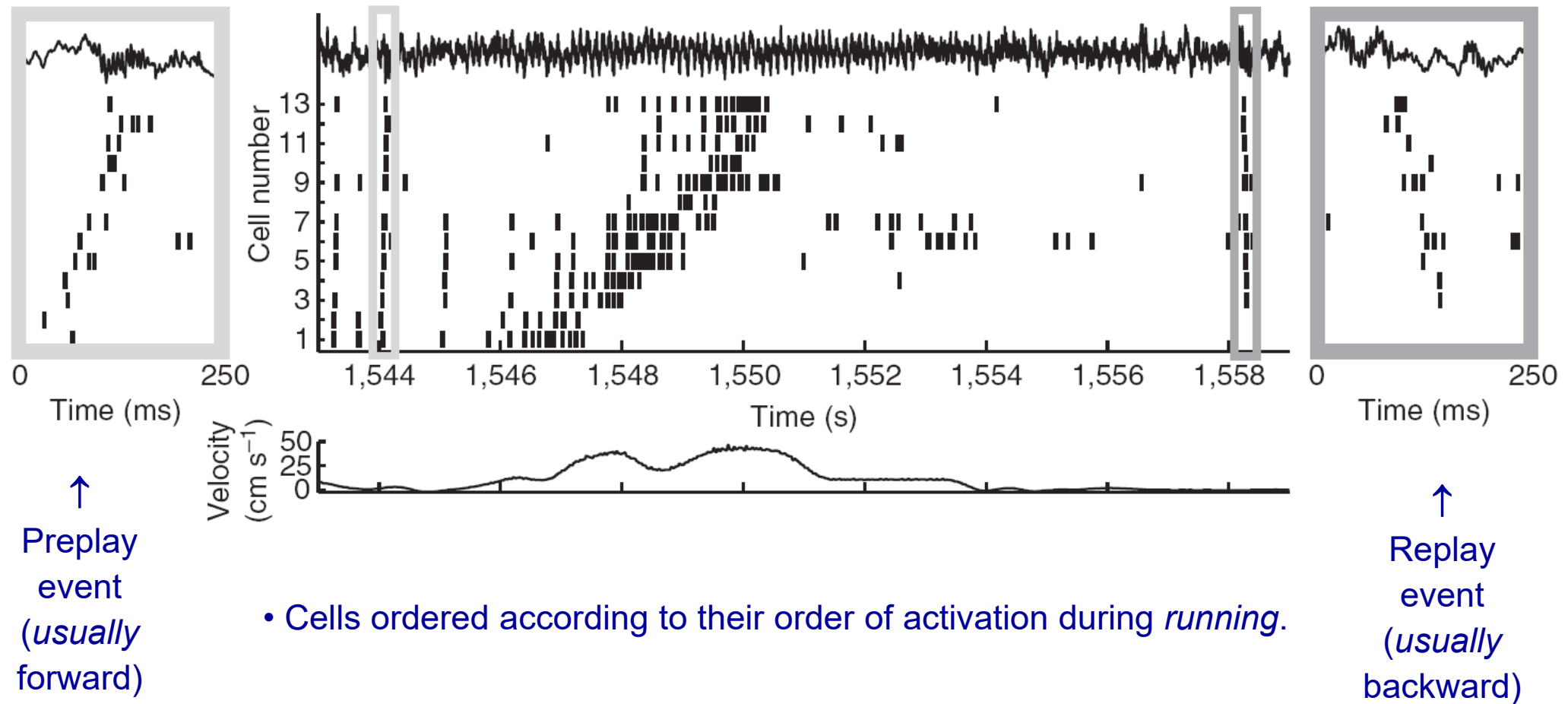
Place cells and memory consolidation during sleep



Increased correlations during post-behavior sleep periods, for pairs of cells that were activated together on the linear track.

→ Expected from basic synaptic-plasticity mechanisms (“fire together – wire together”)

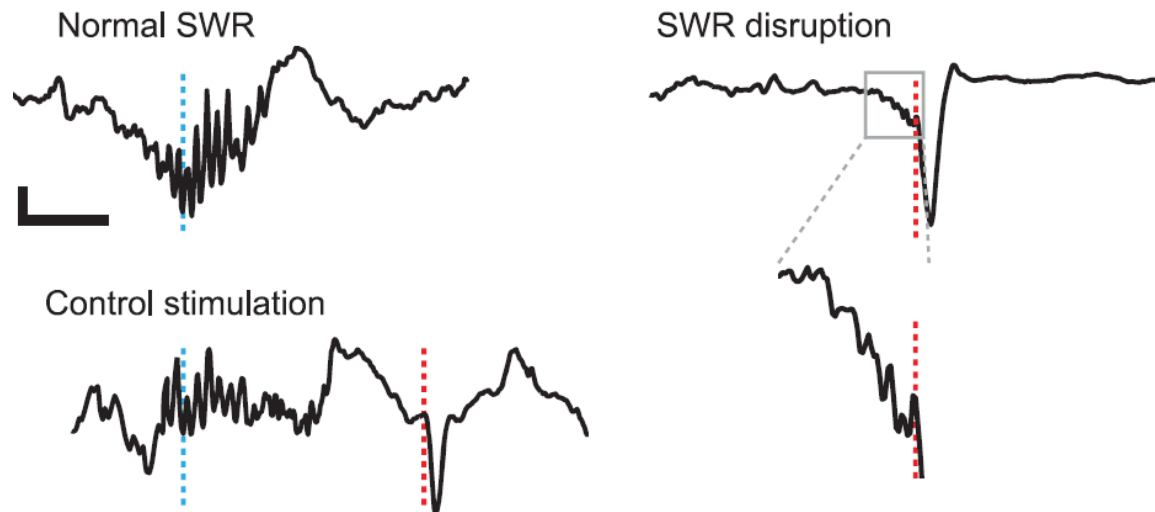
Replay and preplay of sequential activity of hippocampal cells, during pauses in behavior: A substrate for memory consolidation?



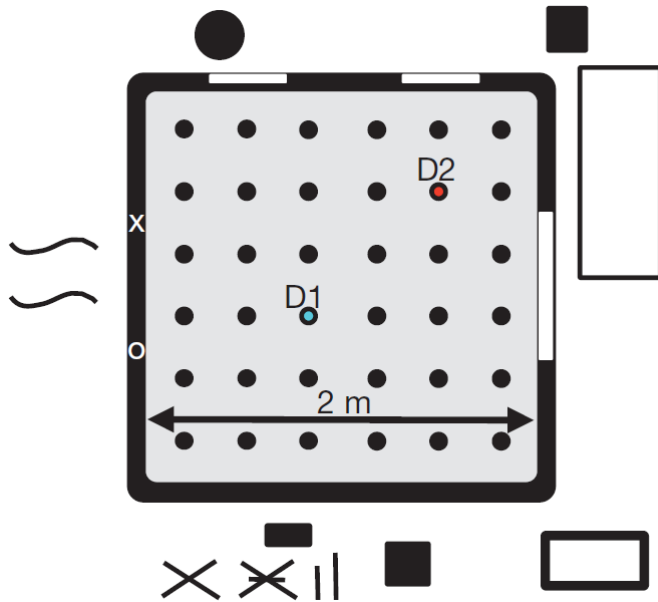
Diba and Buzsáki, *Nature Neurosci.* (2007)

Replay and preplay of sequential activity of hippocampal cells, during pauses in behavior: A substrate for memory consolidation?

- A notable theory proposes that memories become ultimately hippocampal-independent, in a “systems consolidation” process – and such replay sequences of events that were experienced during the day could be “packets of information” that transfer the information from hippocampus to neocortex, where these memories become hippocampus-independent.
- Preventing hippocampal ripples (and accompanying replay events) impaired performance of rats on a spatial working memory task (Jadhav et al., *Science* 2012).



Hippocampal preplay: Future planning

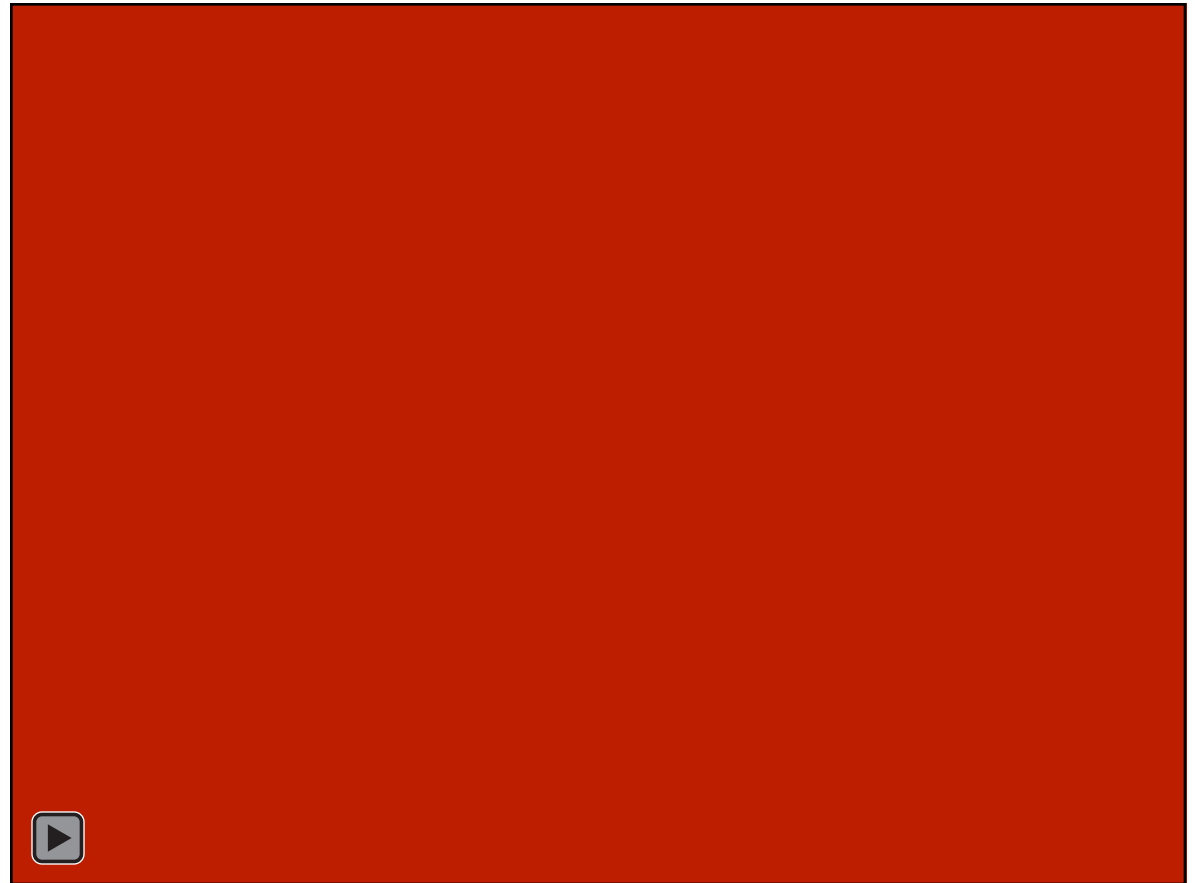


D1: *Home* on Day 1

D2: *Home* on Day 2

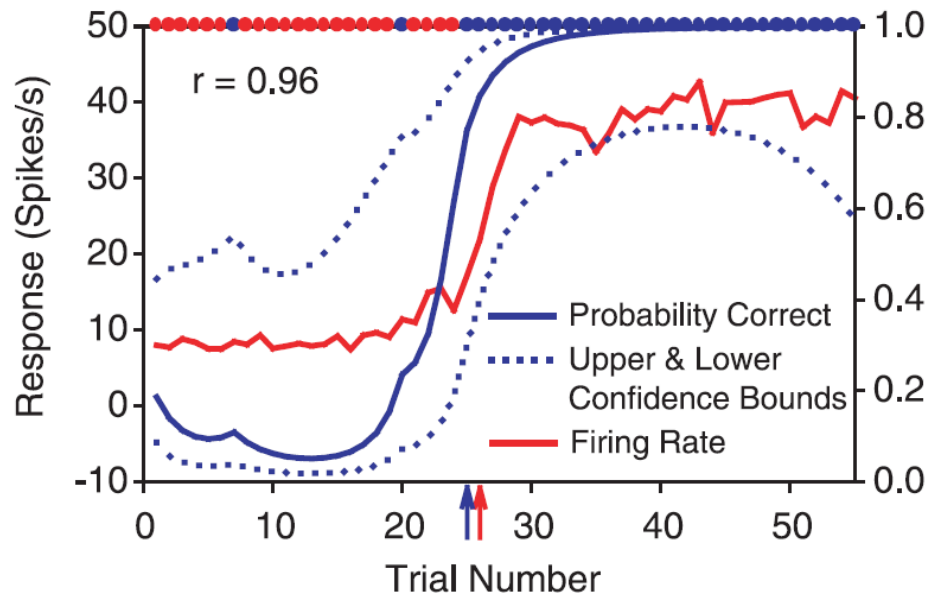
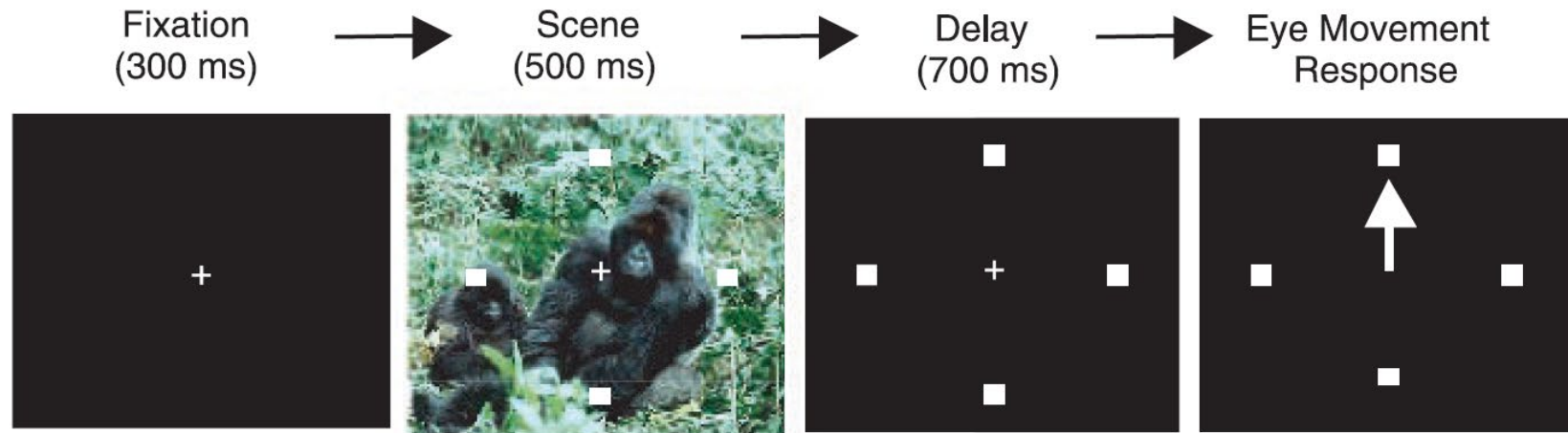
~200 neurons recorded
simultaneously with
electrophysiology

MOVIE: Trajectory decoding & Preplays towards *Home*
and from *Home* to the next goal



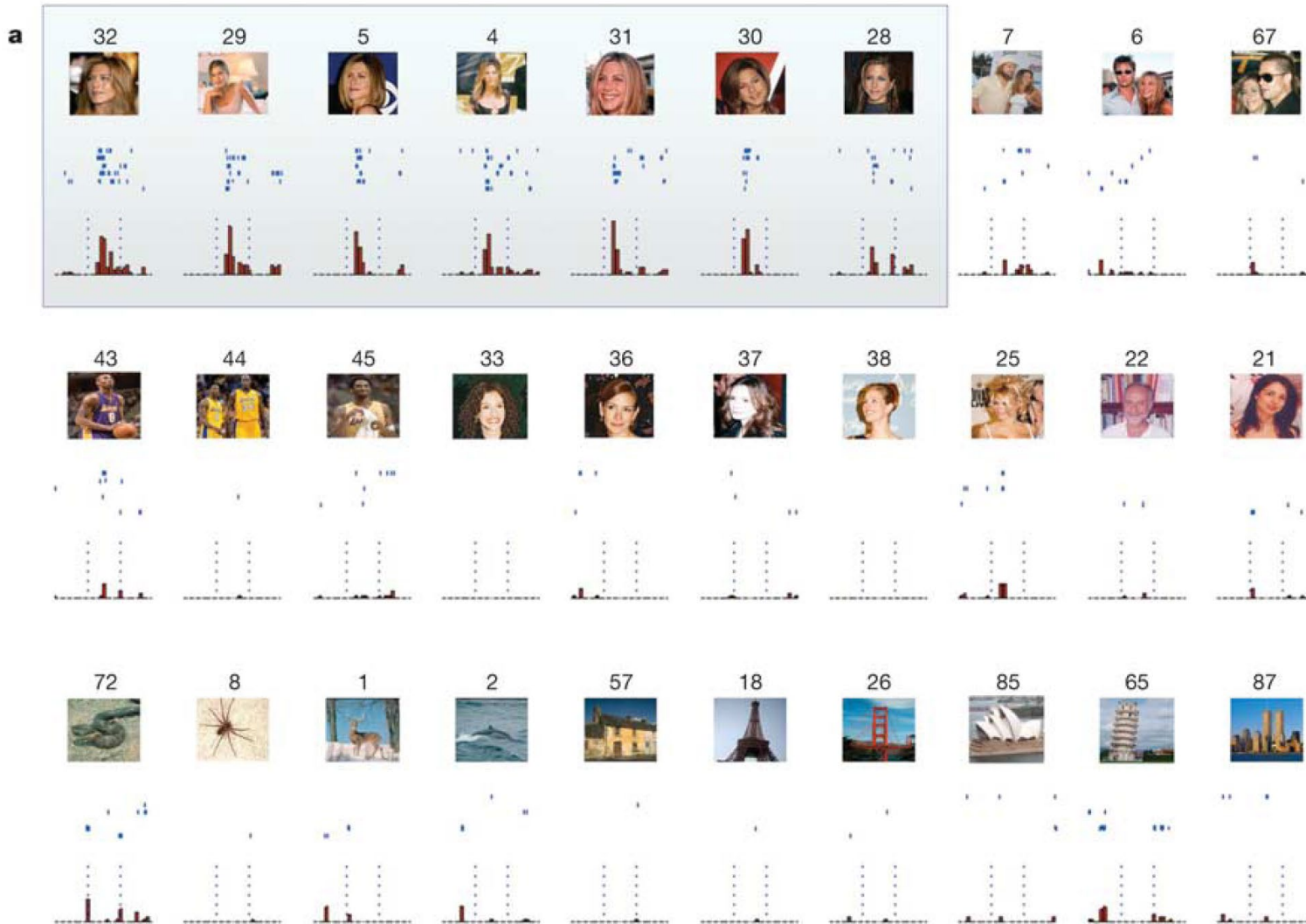
Pfeiffer and Foster, *Nature* (2013)

Hippocampal neural activity in monkeys: Beyond place cells



Example of a “changing cell” in monkey hippocampus, which increased its responses simultaneously with the behavioral “Aha moment” during learning of a new association.

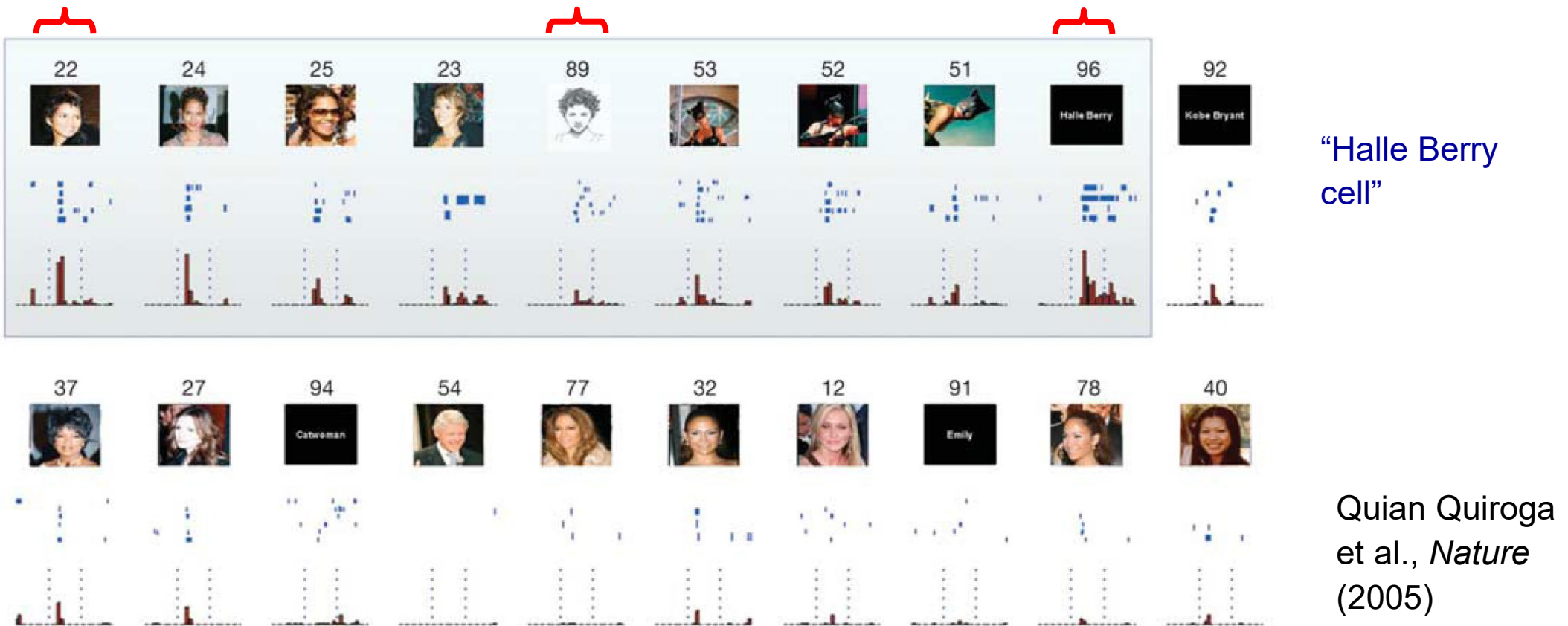
Hippocampal neural activity in humans: Beyond place cells



“Jennifer
Aniston cell”

Quian Quiroga et al.,
Nature (2005)

Hippocampal neural activity in humans: Beyond place cells



Although place-cells were found in human hippocampus, hippocampal neurons in humans can also show completely different activity patterns – highly specific responses to different instantiations of the same famous human / famous building. → **Social cells ? Concept Cells ? Invariance.**

Recent studies suggested the involvement of some hippocampal subregions in *social memory* in mice.

Social place-cells in the bat hippocampus



Bats are highly social mammals

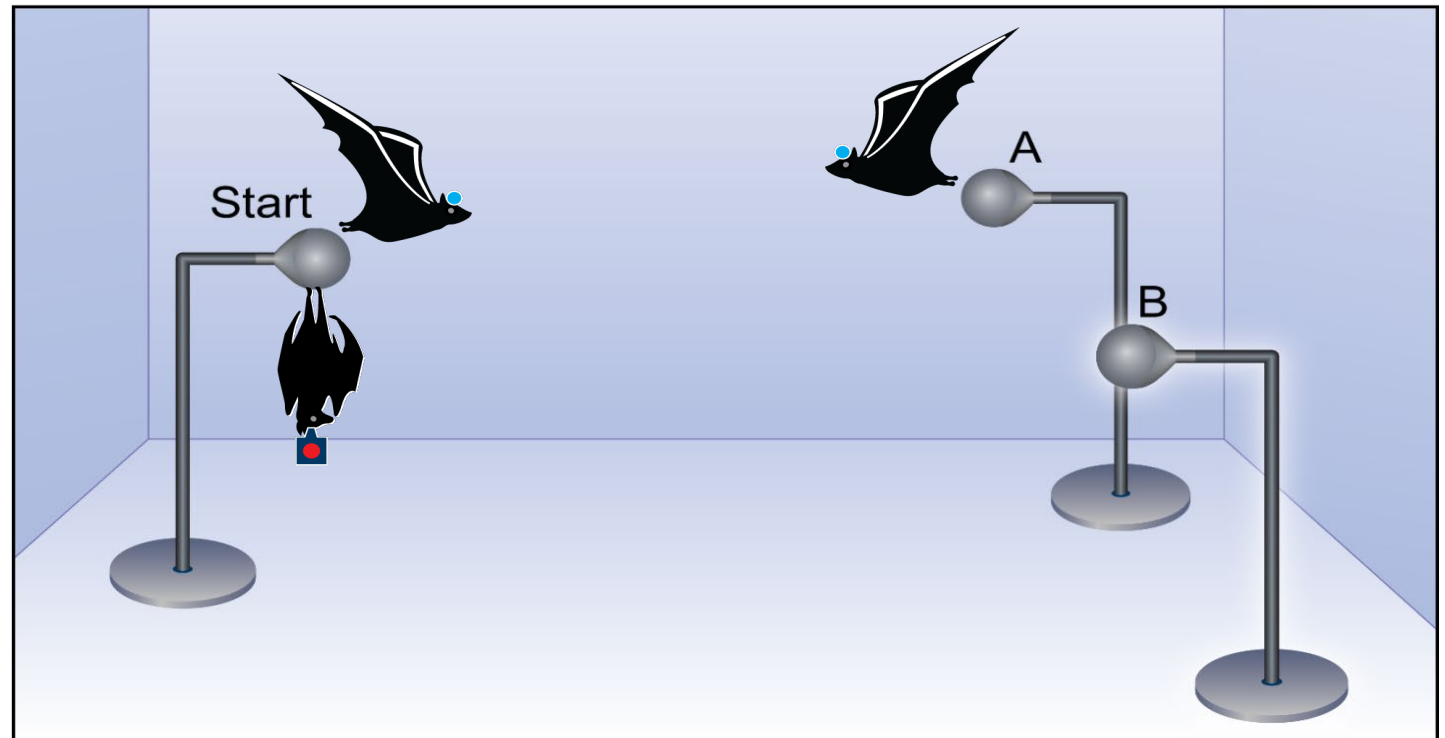


A delayed-match-to place task

Step 1: Other bat flying



Wireless
neural recordings
in the hippocampus



- Neural logger on implanted bat
- Tracking LED on other bat

A delayed-match-to place task

Step 2: Implanted bat flying



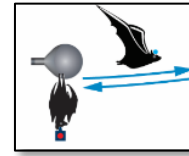
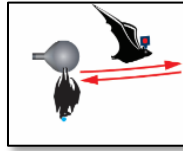
Wireless
neural recordings
in the hippocampus



- Neural logger on implanted bat
- Tracking LED on other bat

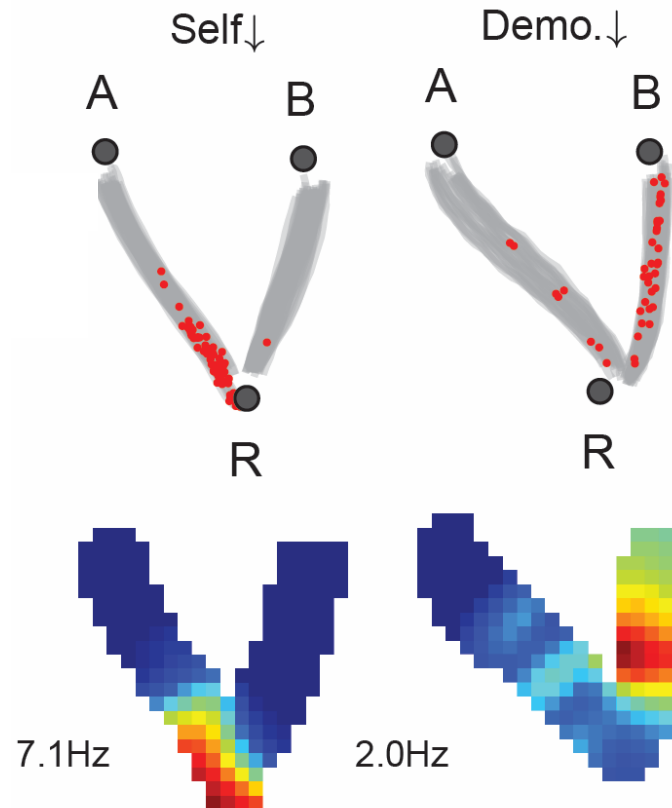
Example of a social place-cell in bat hippocampus

Observer
flying



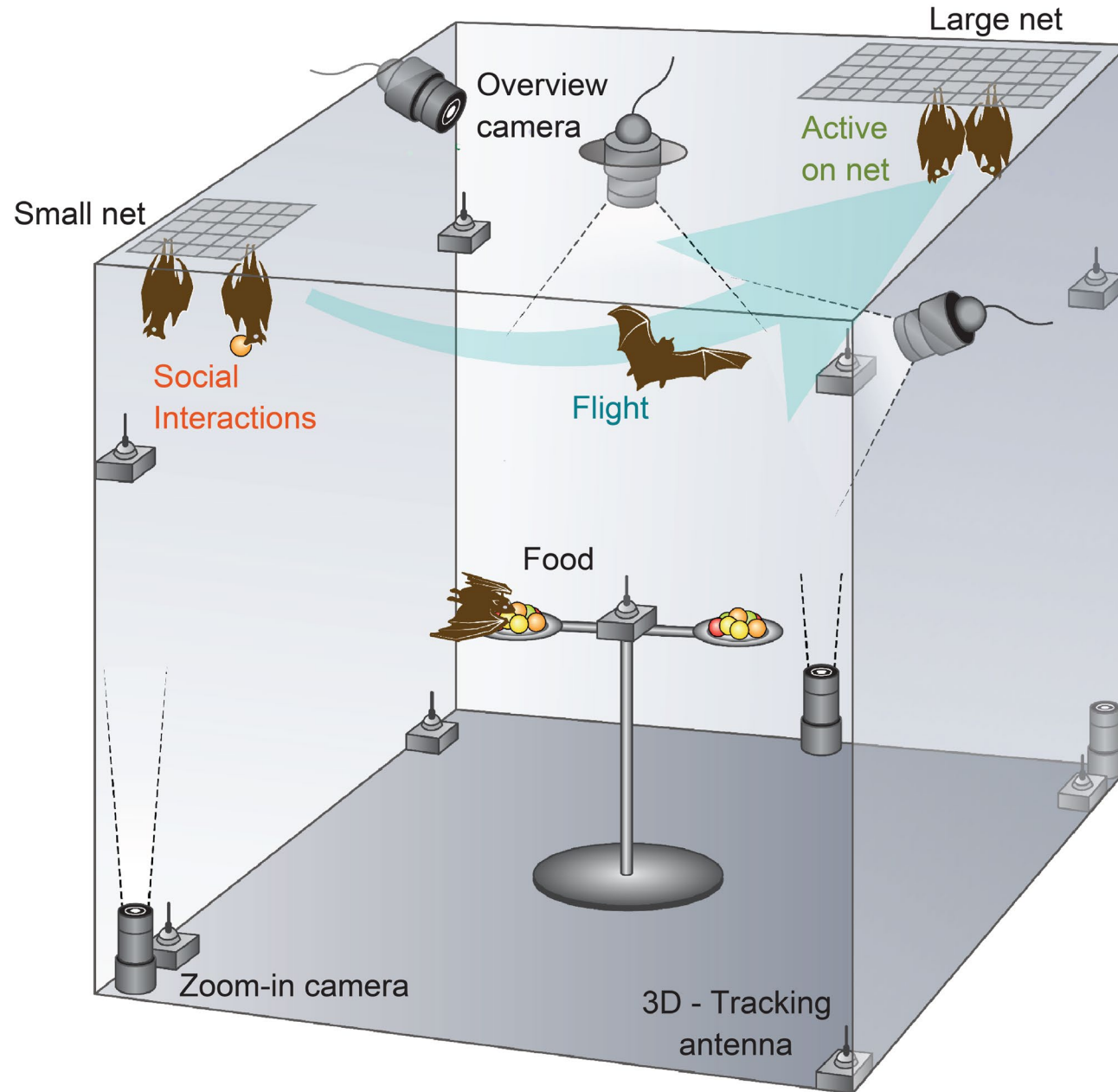
Demonstrator
flying

- Trajectory planning could not explain the results.
- Live conspecifics were represented differently than Objects.



- Social place cells may be important for social-spatial cognition: representing conspecifics, predators, prey...

Hippocampal CA1 recordings in a bat colony (5–10 wild bats)

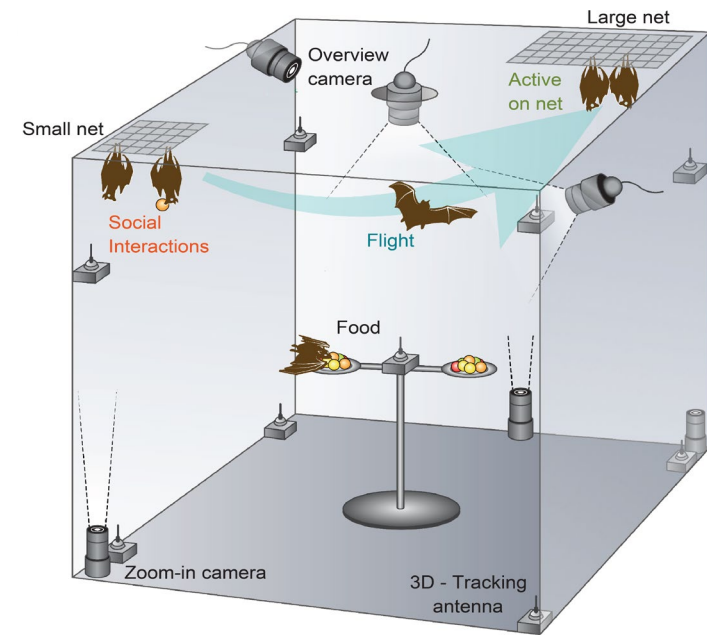


- Groups of 5 – 10 wild bats lived together 24/7 in the room. We recorded 3 hours/day.
- We tracked the identities, positions and head-directions of all bats using QR codes and RF tags.
- The bats formed a stable social network.

Key findings:

- Simultaneous representation of self and others
- Identity coding
- Same bats are identity-coded across contexts (in-flight, on-net): Social invariance → Akin to Jennifer Aniston cells
- Encoding of Sex, Social Hierarchy & Social Affiliation
- Responses to specific social interactions

→ In a highly-social situation, hippocampal CA1 neurons form a complex multi-dimensional representation of the world:
A social-spatial representation (socio-spatial cognitive map).



Outline of today's lecture

- Hippocampus: Introduction and early discoveries
- Spatial maps in the hippocampus and related regions:
 - Place cells
 - Head direction cells
 - Grid cells
- Beyond the cognitive map: Hippocampus and memory
- **Open questions**

Some open questions

- Hippocampus and Space:
 - **Gap in spatial scale:** Are place cells and grid cells relevant at all for large-scale navigation in the wild? How are large-scale spaces represented in the brain?
 - **Neural basis of goal-directed navigation:** Vectorial goal-direction and goal-distance cells... BUT: How do you plan your route optimally, or avoid obstacles, or re-orient when the way is lost ?
- **Hippocampus: Space versus memory?** Perhaps the hippocampus is a sequence encoder, which can bind sequences of events:
 - Spatial sequences → Spatial memory
 - Temporal sequences → Episodic memory
- **Hippocampus: Past vs. Future:** Remembering the past vs. Planning the future.
- **The Social Hippocampus.**



Thank you !

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