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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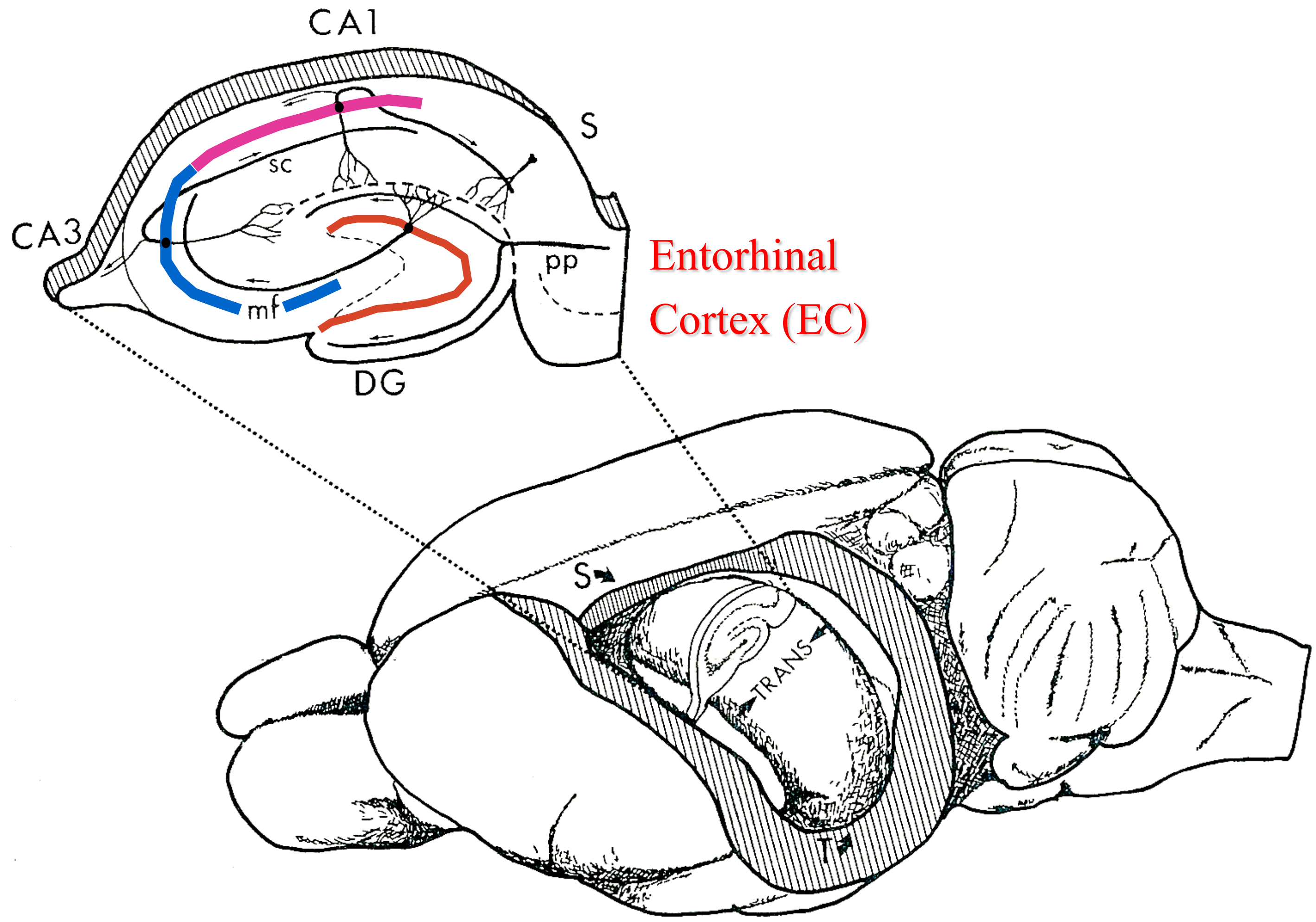
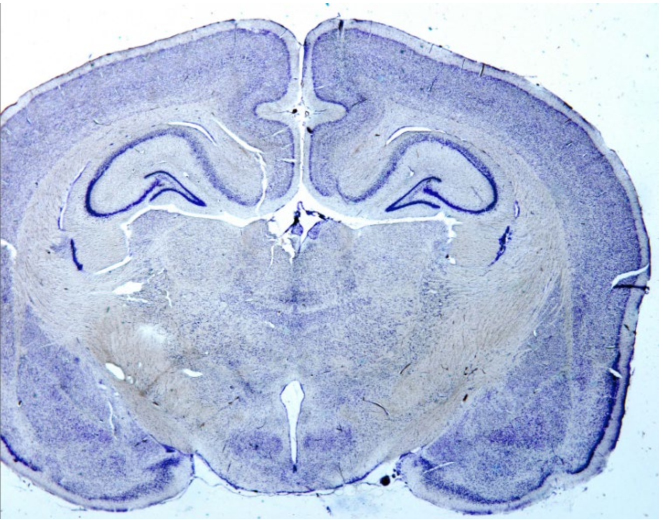
The hippocampus



(Amaral and Witter 1989)

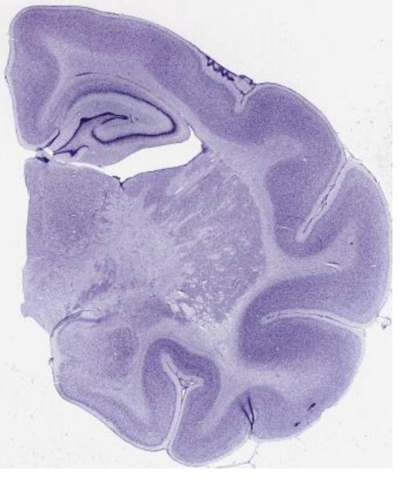
The hippocampus is highly conserved across mammals

Egyptian fruit bat



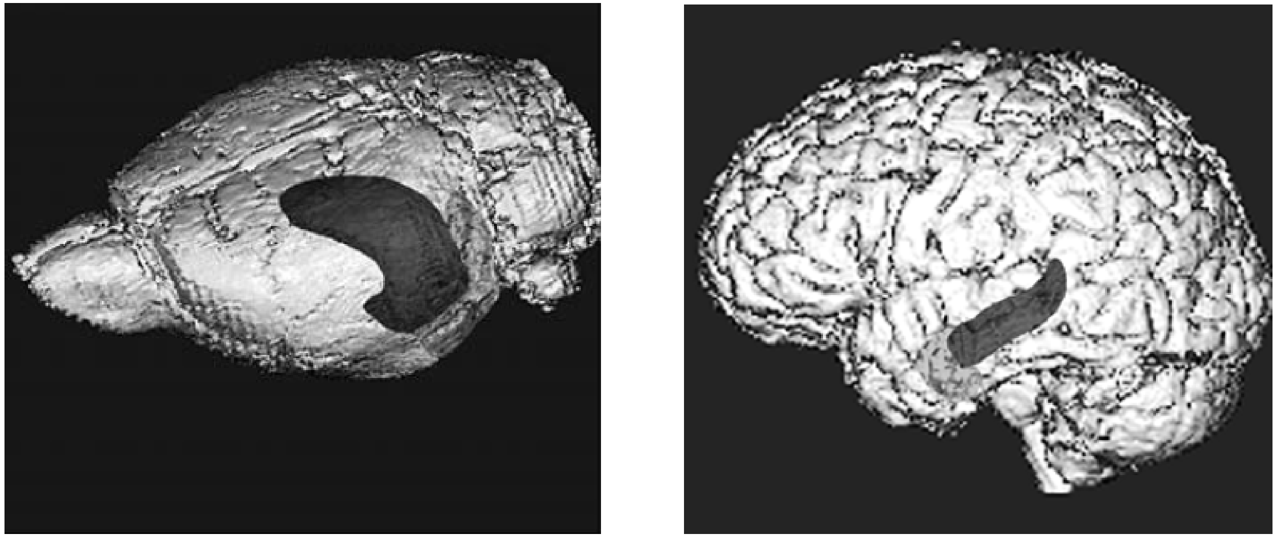
Rat

Echidna
(ancient egg-laying mammal)

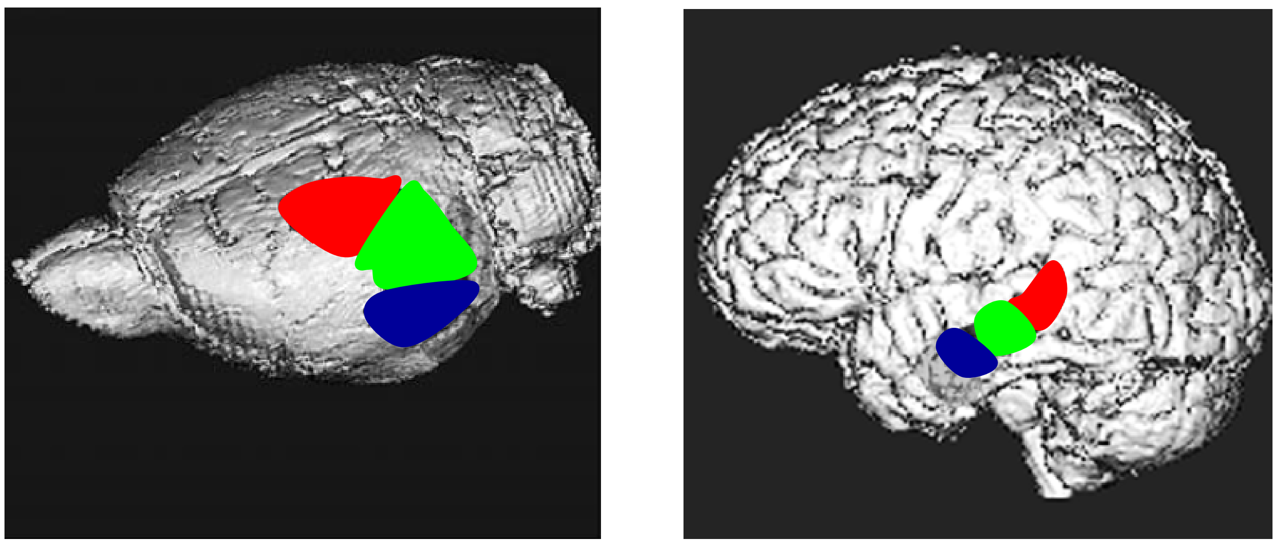


Highly conserved brain structure across all mammals, including humans (exists also in birds, but looks quite different)

The hippocampus is highly conserved across mammals



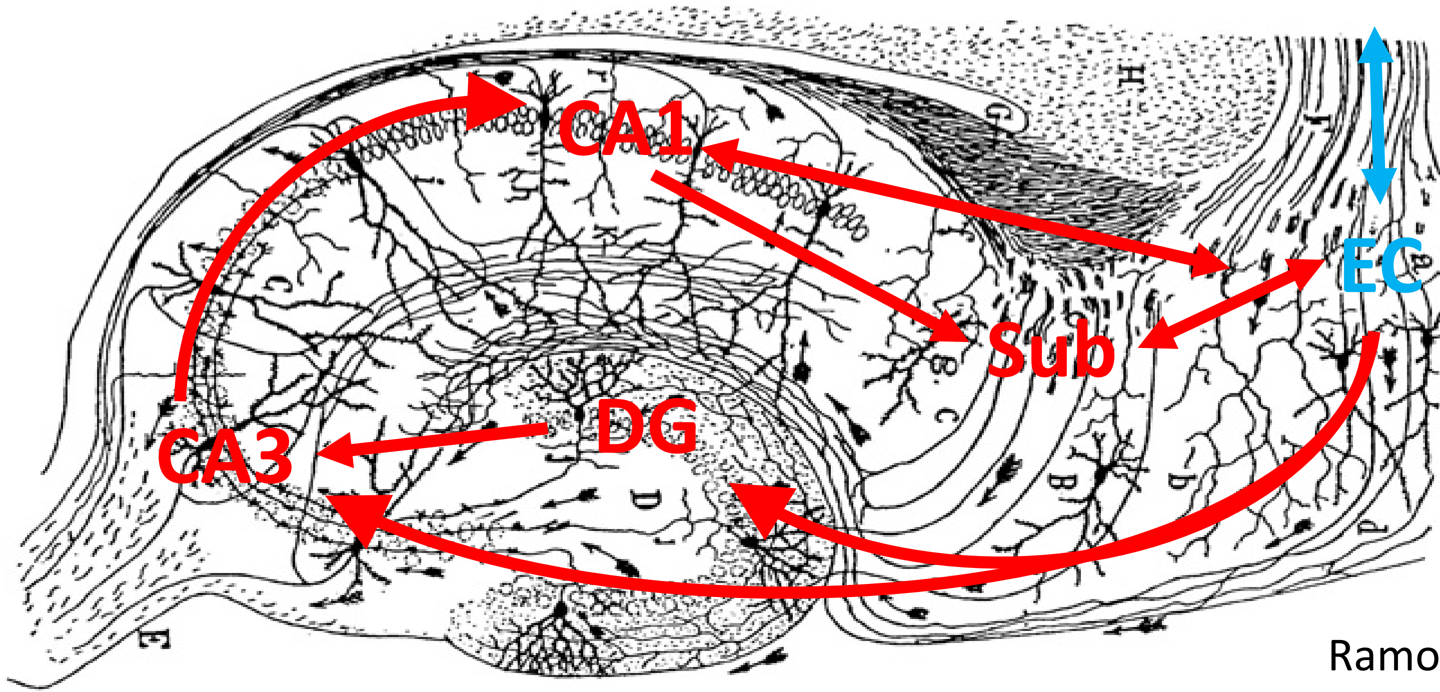
Rat Human



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

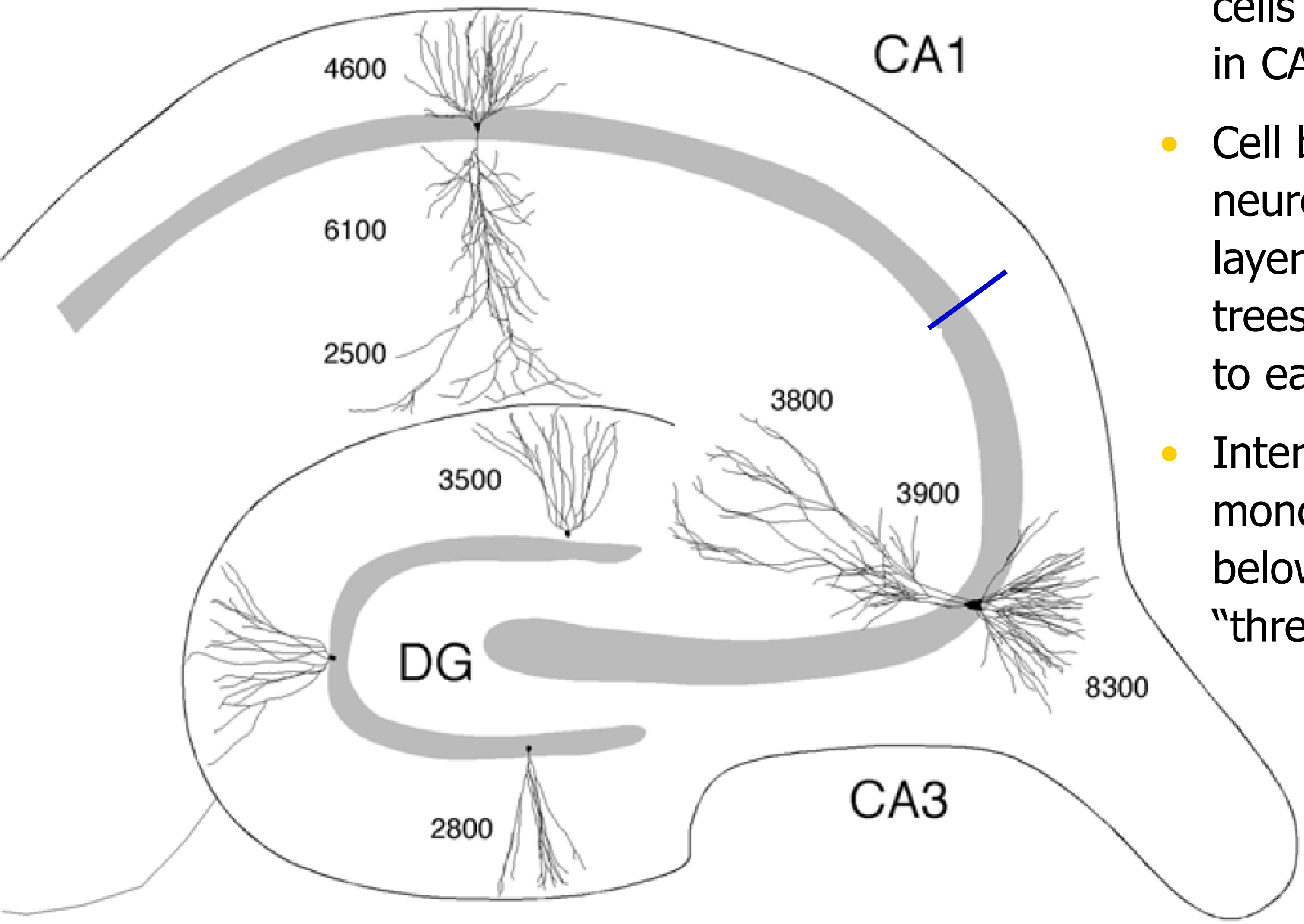


Ramon y Cajal

EC	Entorhinal Cortex
CA1	Cornu Ammonis 1
CA3	Cornu Ammonis 3
DG	Dentate Gyrus
Sub	Subiculum

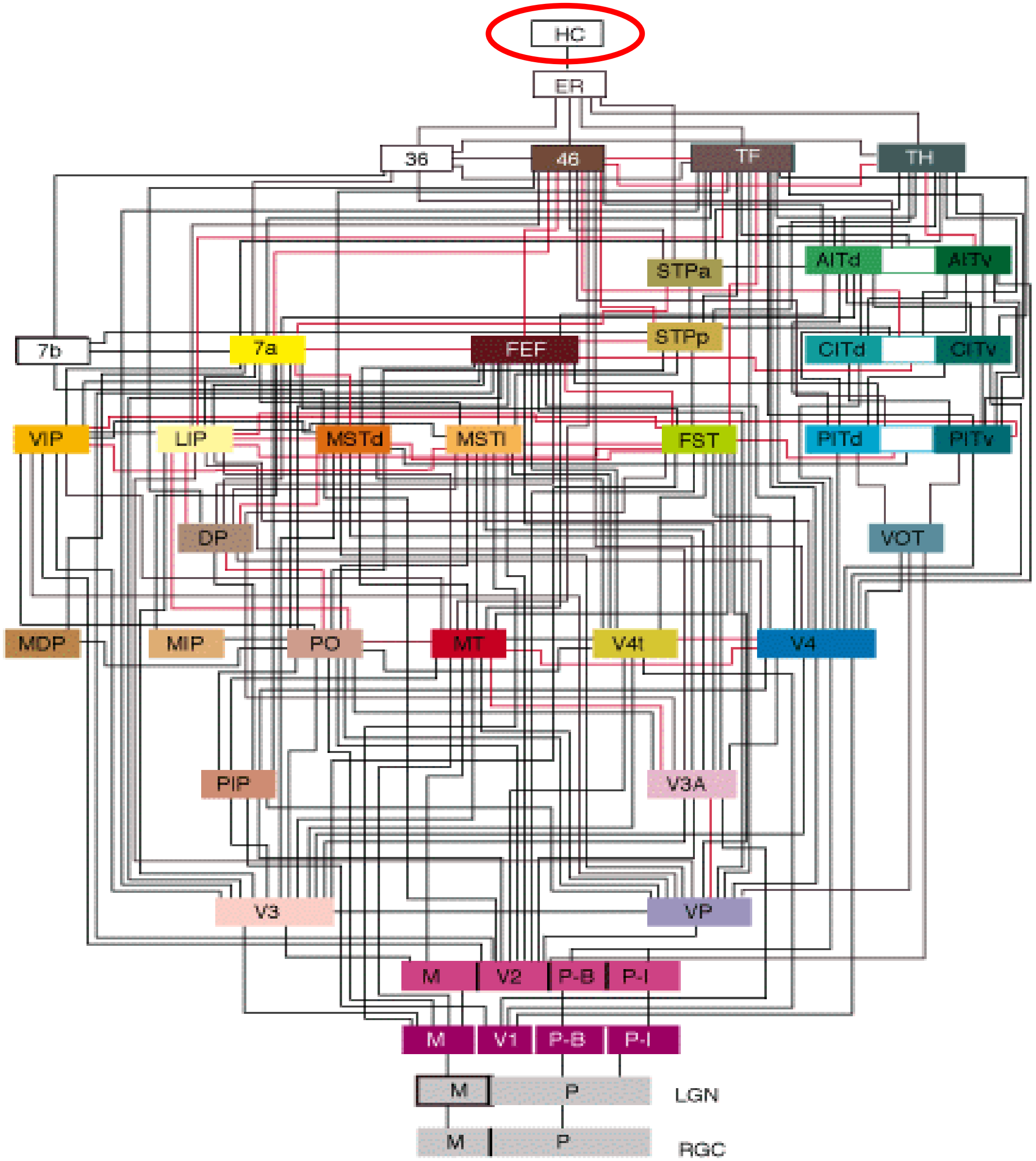
- This uni-directional connectivity is quite different than what is typically found in neocortex, where connectivity is usually bi-directional (i.e., if area A projects to B, then B also projects to A).

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



Felleman & Van Essen, *Cereb Cortex* 1, 1-47 (1991)

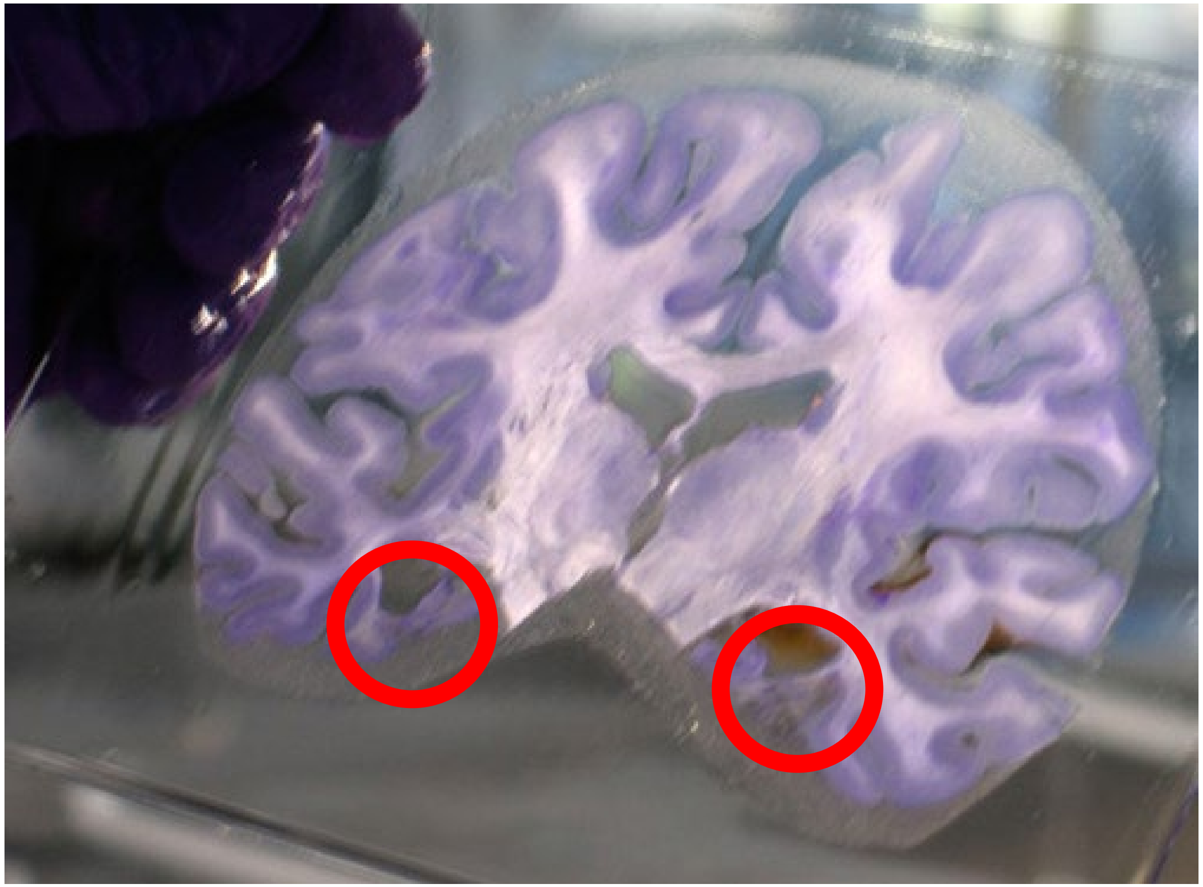
- Huge amount of visual processing until any external sensory information reaches the hippocampus
- In other senses (auditory, somatosensory) there is similarly complex processing upstream of the hippocampus – except olfactory inputs that reach the hippocampus much more directly (olfactory bulb → entorhinal 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)

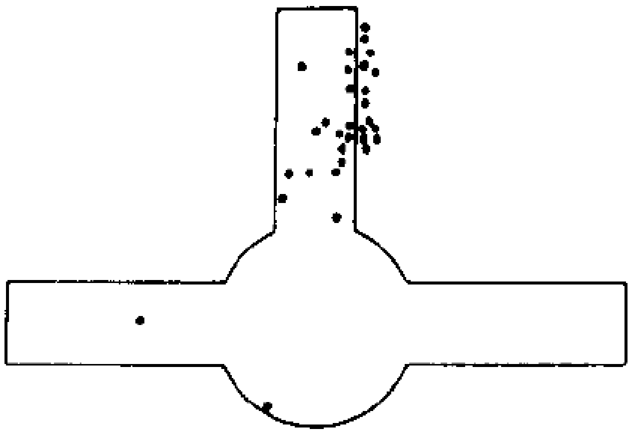
Henry Mollaison (H.M.), 1926-2008



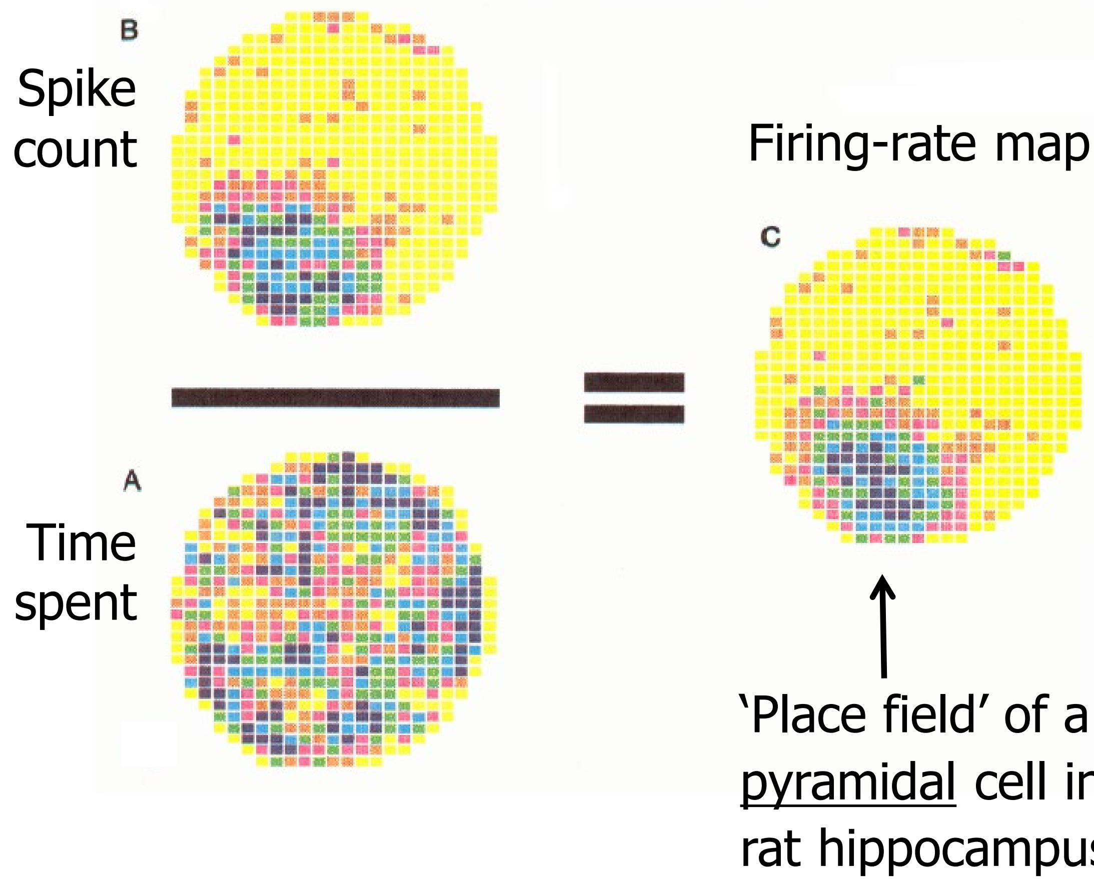
Scoville & Milner, *J Neurol Neurosurg Psychiatry* 20, 11 (1957)

- 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.

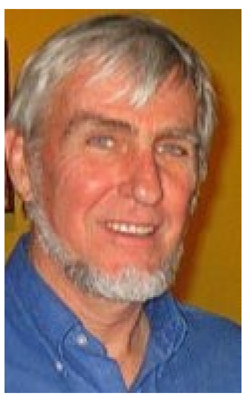
50 years ago – A surprisingly simple discovery for such a high-level brain area: Hippocampal place cells in rats



(O'Keefe & Nadel 1978)
(O'Keefe & Dostrovsky 1971)



(Muller et al. 1987)



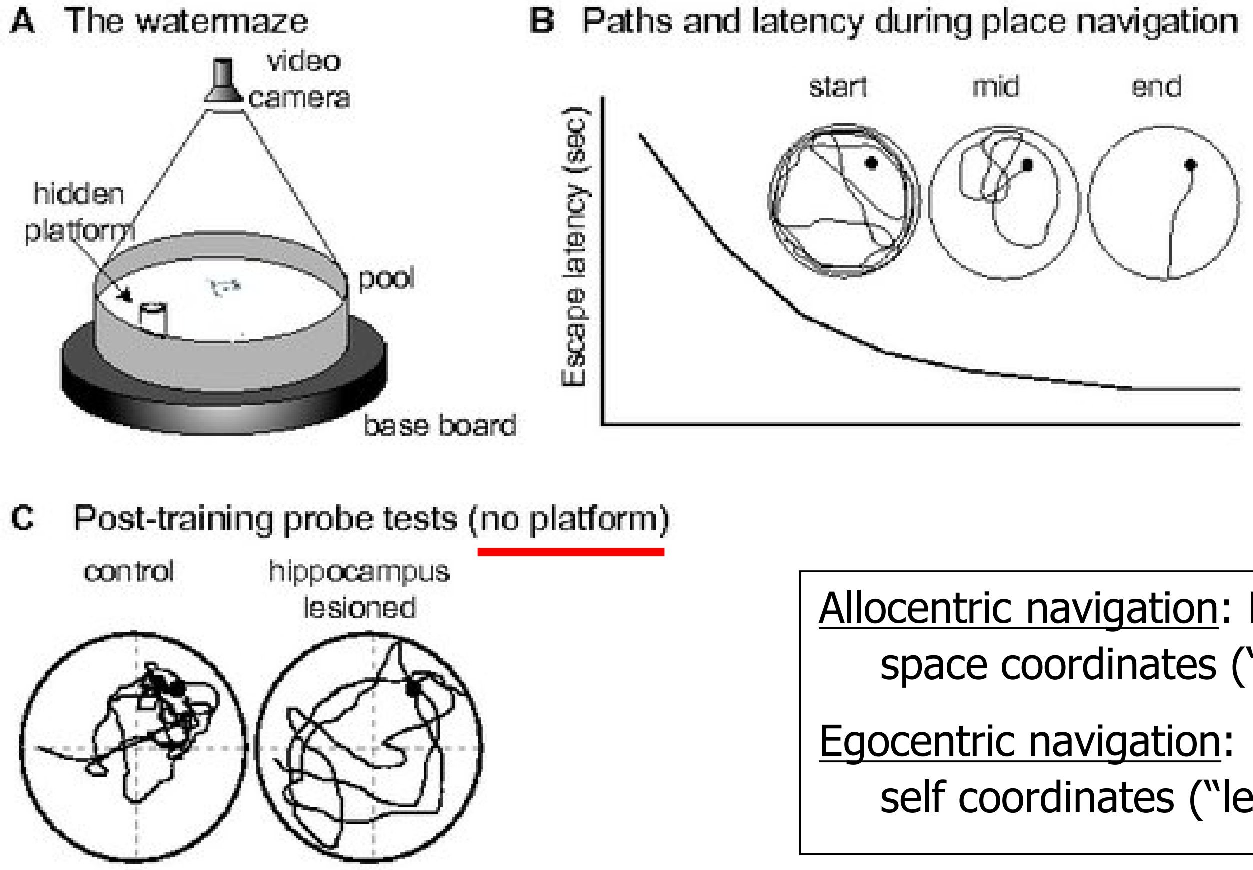
John O'Keefe

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)



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

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

- These deficits of spatial memory occur after lesions in <u>dorsal</u>, not ventral hippocampus
- In rats <u>over-trained</u> 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 ?

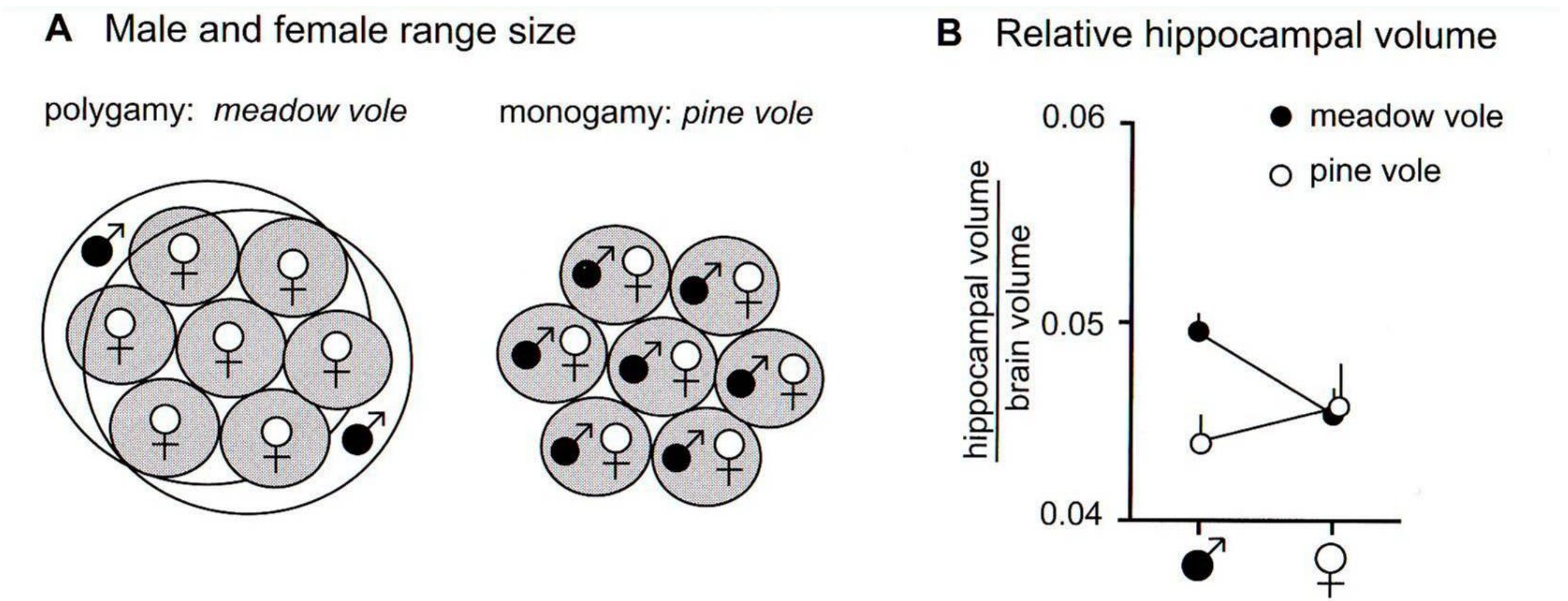
- Navigation and moving through space are key behaviors in all animals: important for survival.

- 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) higher brain functions, or (iii) learning & memory – study the case of navigation and spatial memory.

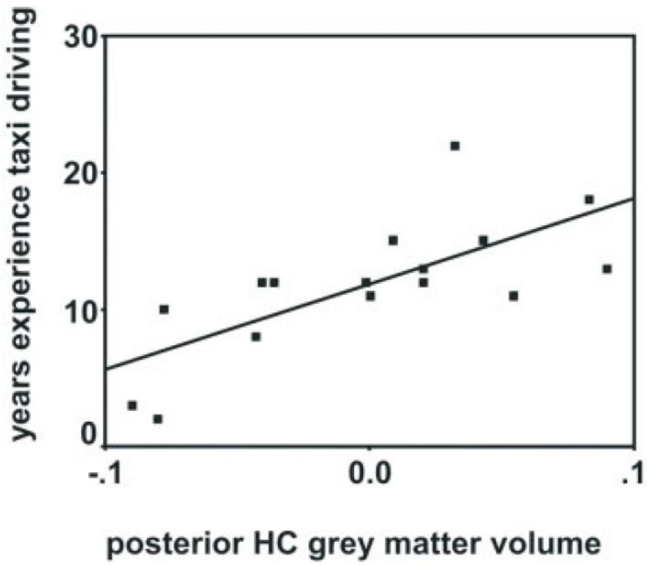
Hippocampal volume correlates with navigational load in rodents



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)

Interpretations:

- The hen and the egg problem: Does posterior hippocampus grow with experience (plasticity), or is a large hippocampus needed in order to do well and “survive” for many years in the demanding profession of a London taxi driver?
- Navigation based on a cognitive-map, allocentric strategy (taxi drivers) requires/causes a larger hippocampus than route-based, egocentric navigation (bus drivers) ?

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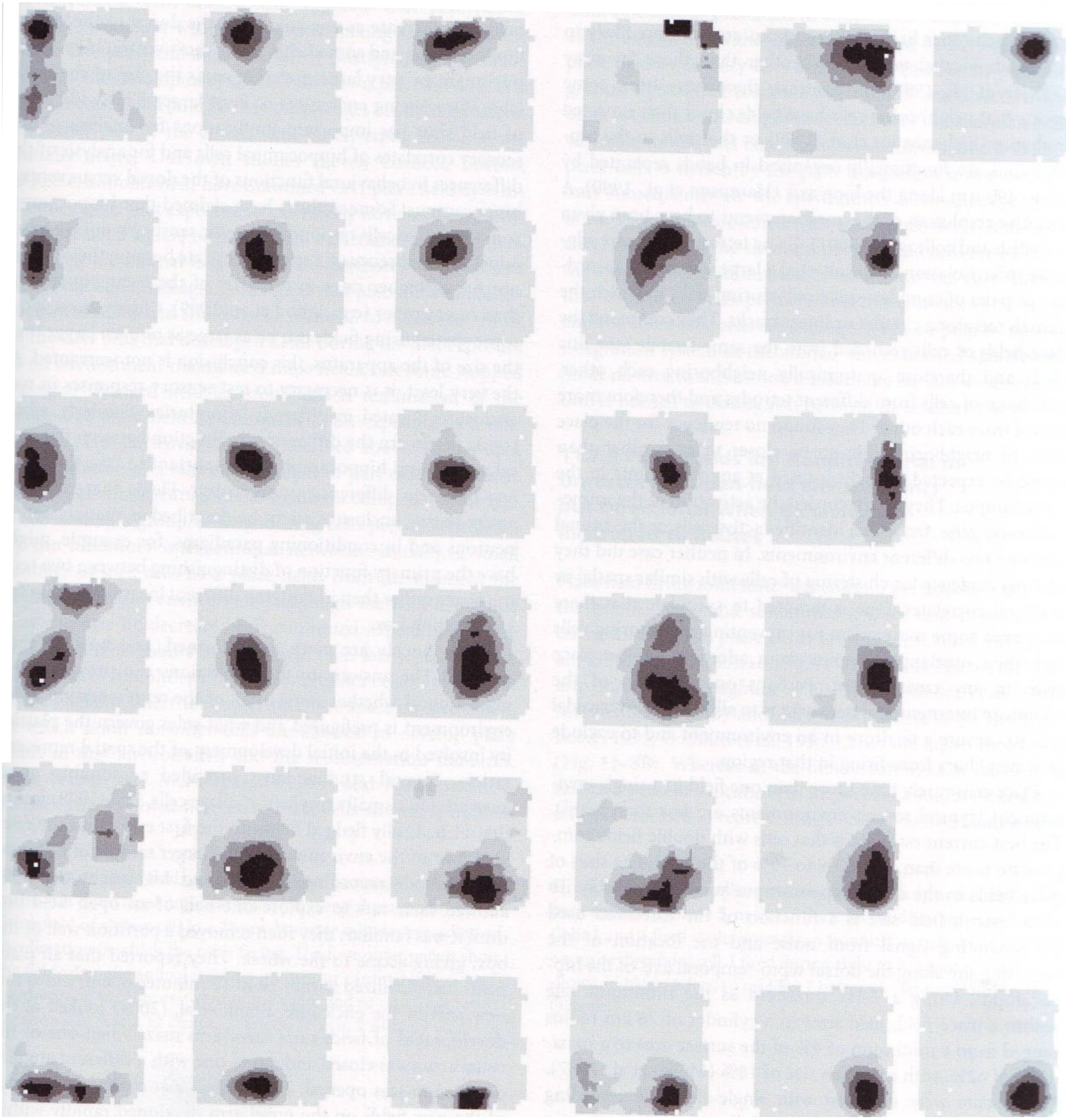
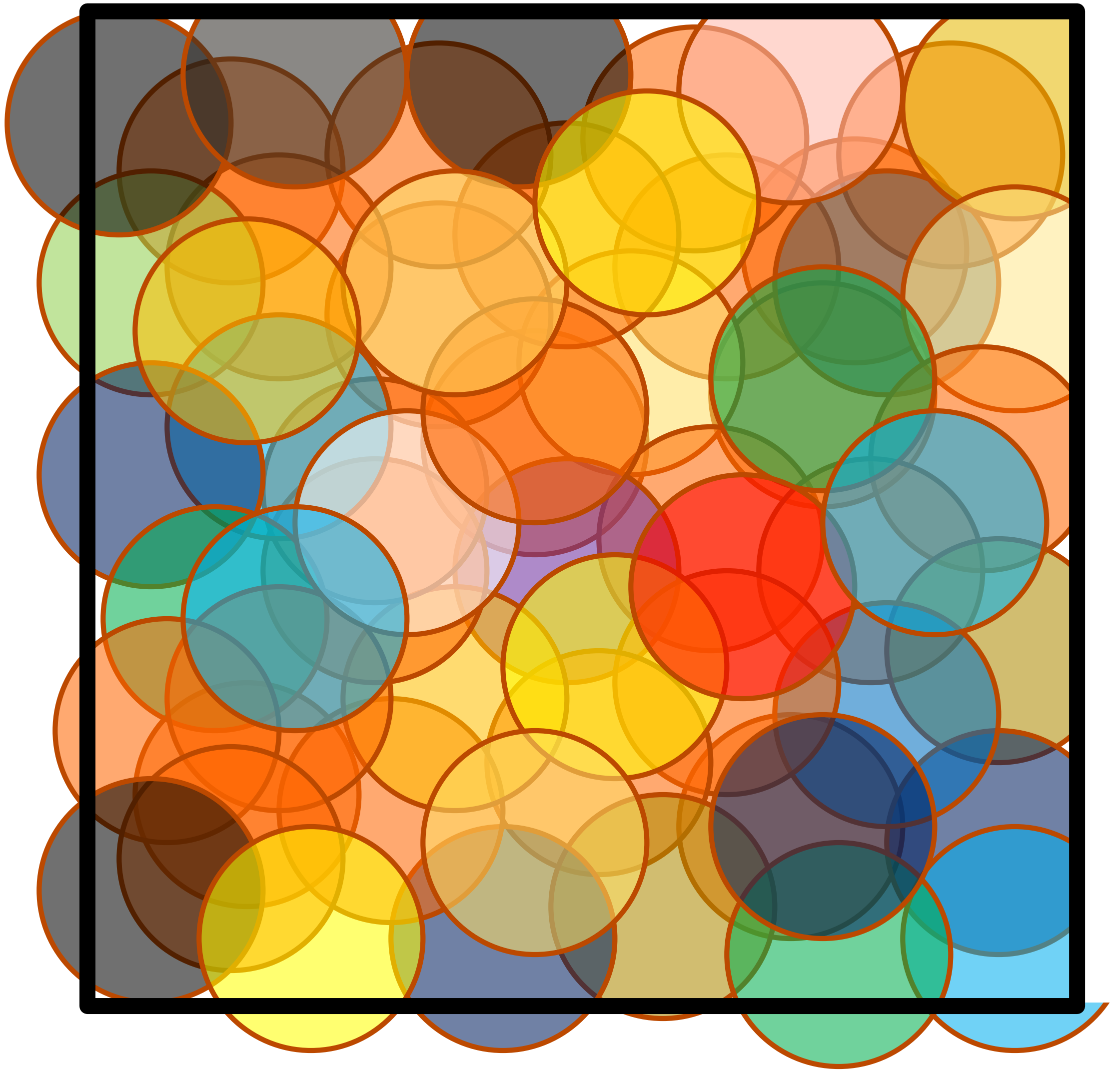
The place fields of hippocampal place cells tile the environment

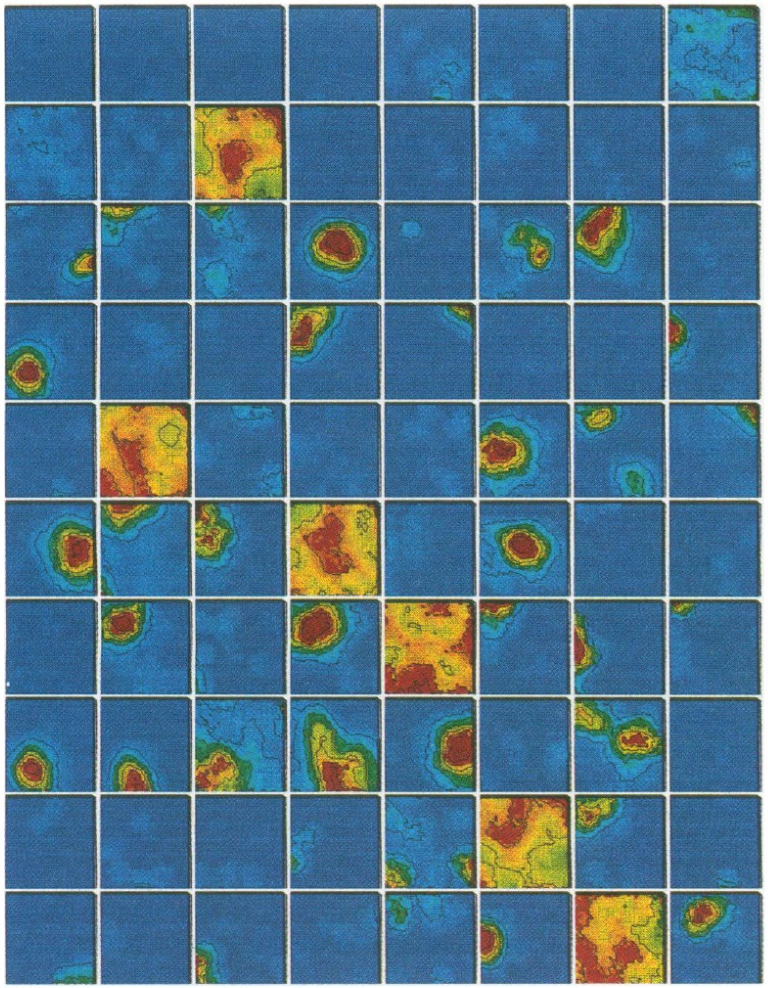


The place fields of hippocampal place cells tile the environment



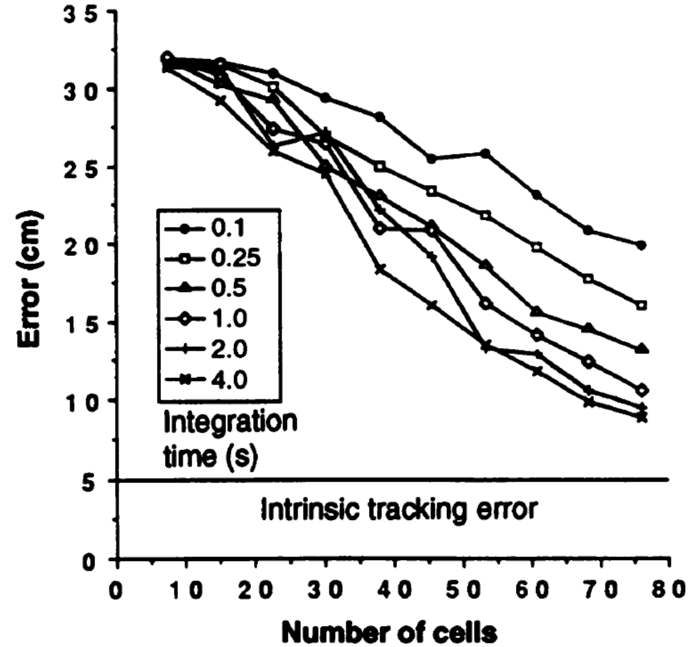
The rat's location can be reconstructed from the activity of an ensemble of simultaneously-recorded place cells

Tetrode recording of 80 neurons simultaneously



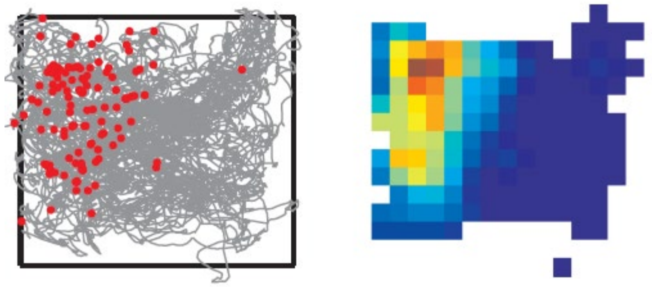
Putative pyramidal neuron (place cell)

Interneuron (very little spatial modulation)

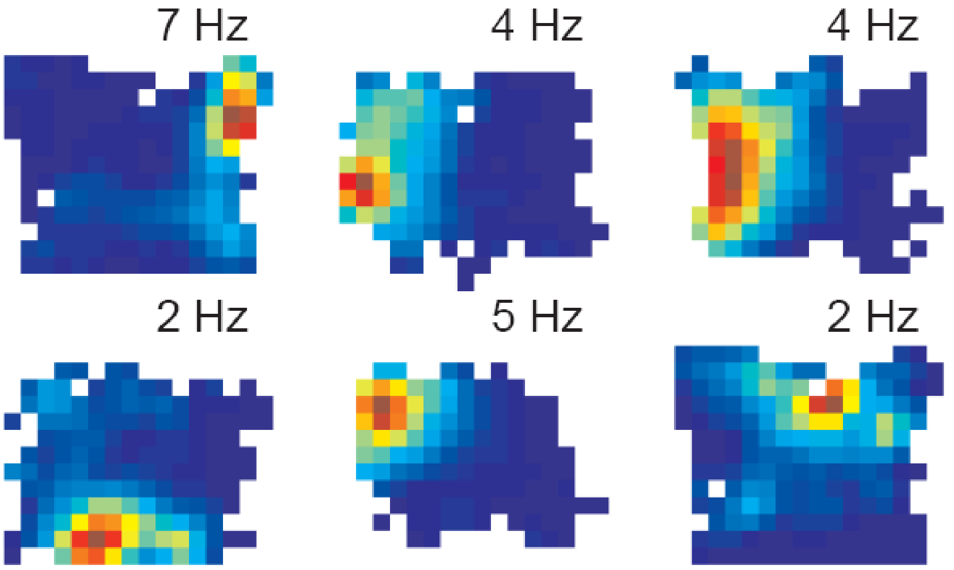


Wilson and McNaughton, *Science* (1993)

Place cells exits also in other species: Big brown bats



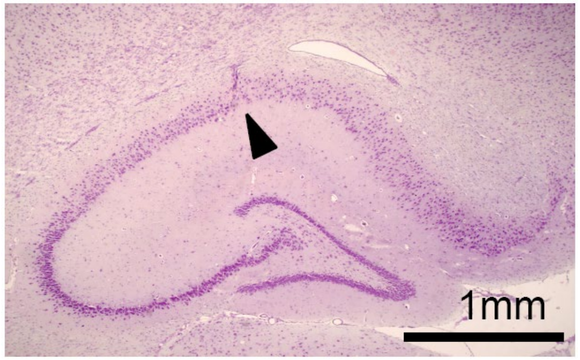
A single cell

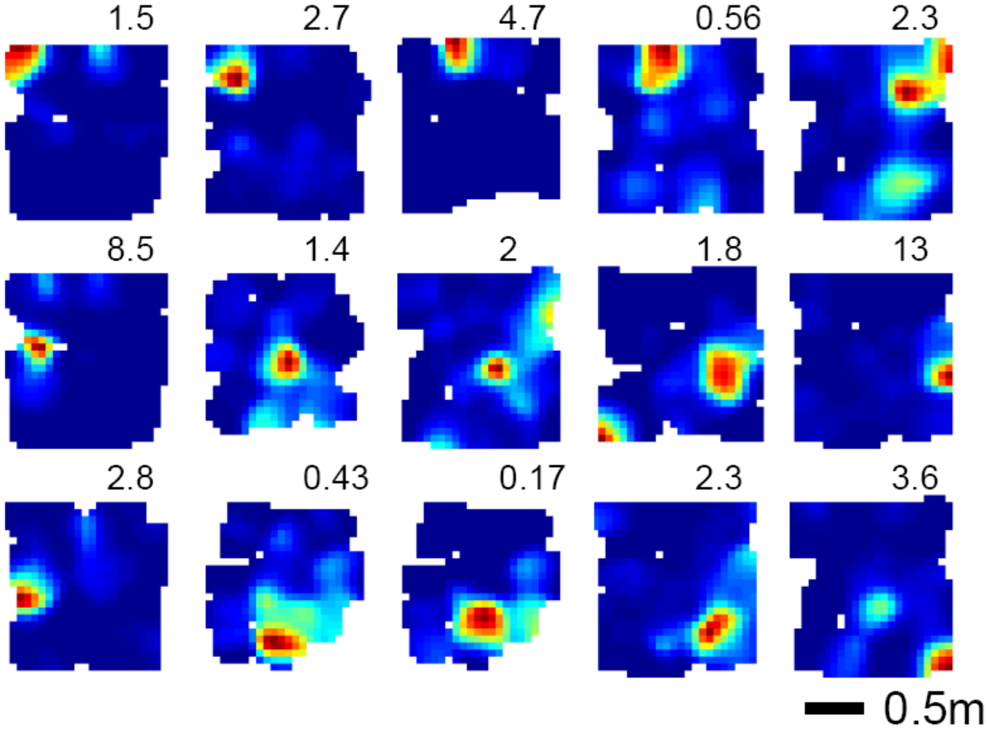


More examples of place fields from 6 neurons

Ulanovsky & Moss, *Nature Neurosci.* (2007)

And in another bat species: Egyptian fruit bat



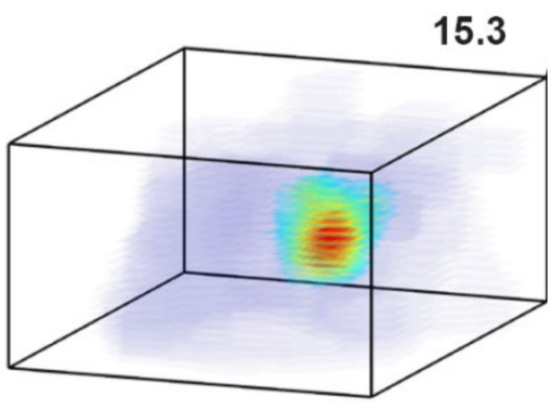


Examples of hippocampal place fields from our current study species, the Egyptian fruit bat.

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

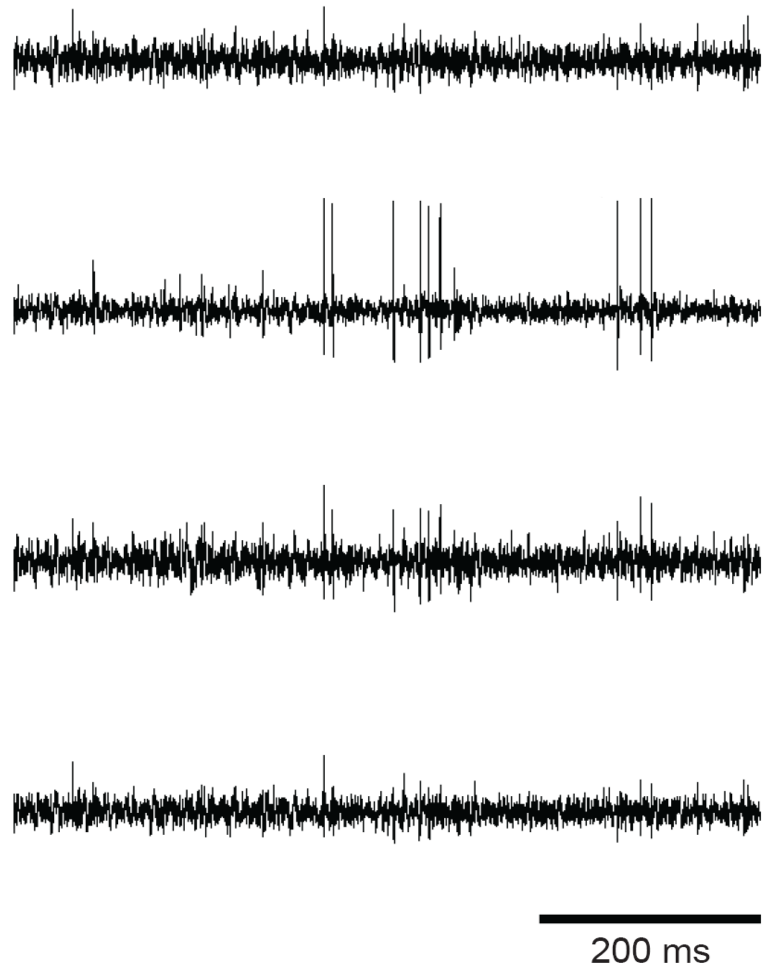
Yartsev, Witter, Ulanovsky
Nature (2011)

3-D place cells in bats



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

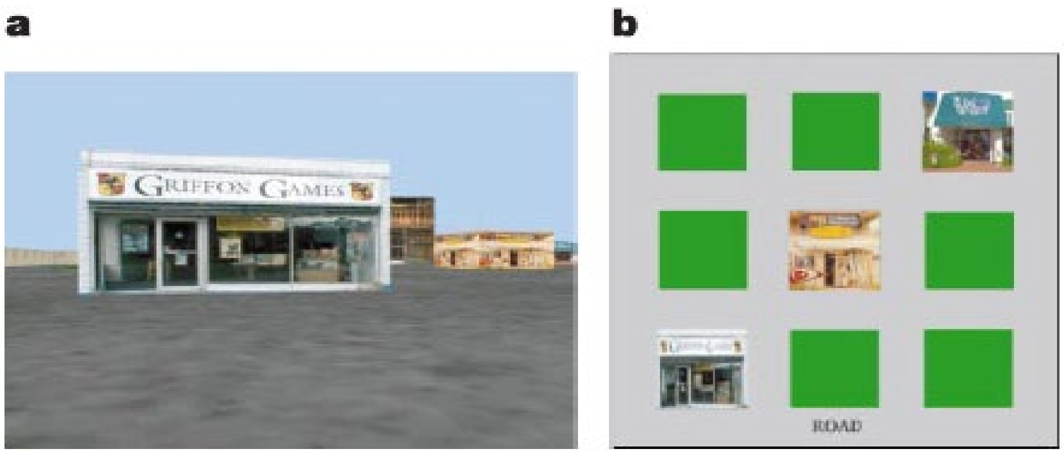
Wireless neural recordings in flying bats

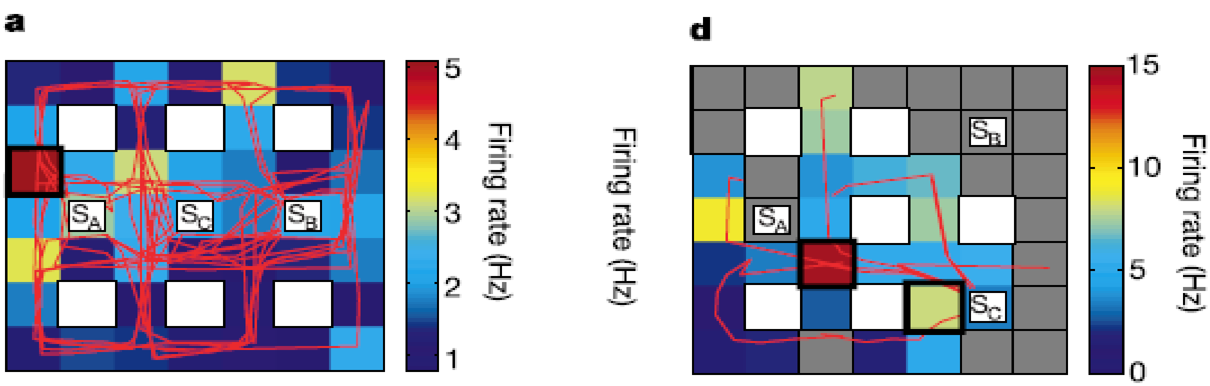


- **3-D place fields are spherical in shape (<u>isotropic</u>): Same resolution in all directions.**

Yartsev & Ulanovsky
Science (2013)

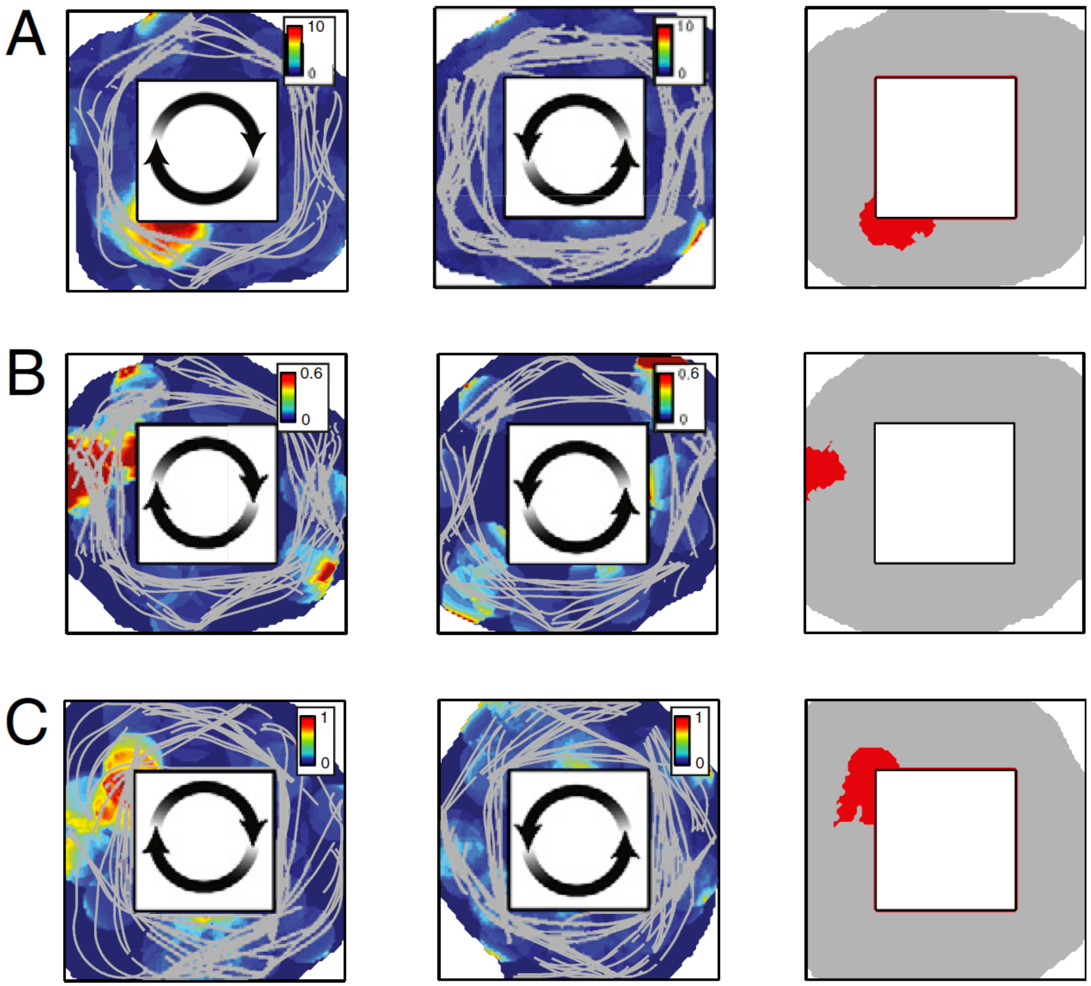
Place cells in humans





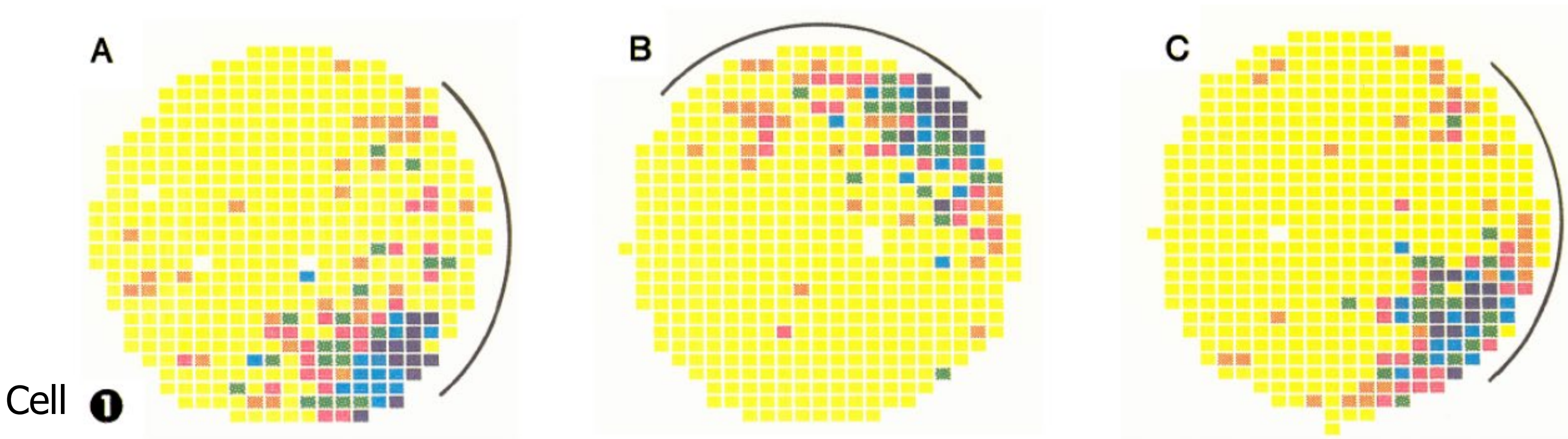
Ekstrom et al, *Nature* (2003)

Place cells in humans



Jacobs et al, *PNAS* (2010)

Place fields rotate with the rotation of prominent external landmarks

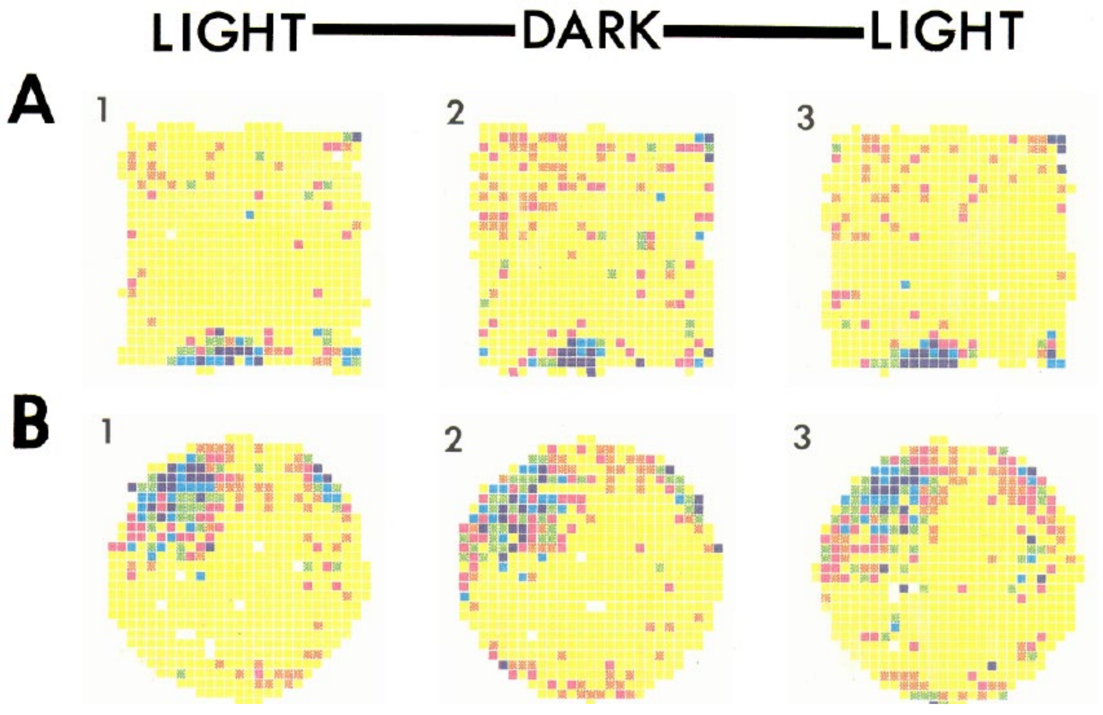


Rotation of cue card

(Muller and Kubie 1987)

Note that this place field is quite <u>stable</u>
(session A vs. session C)

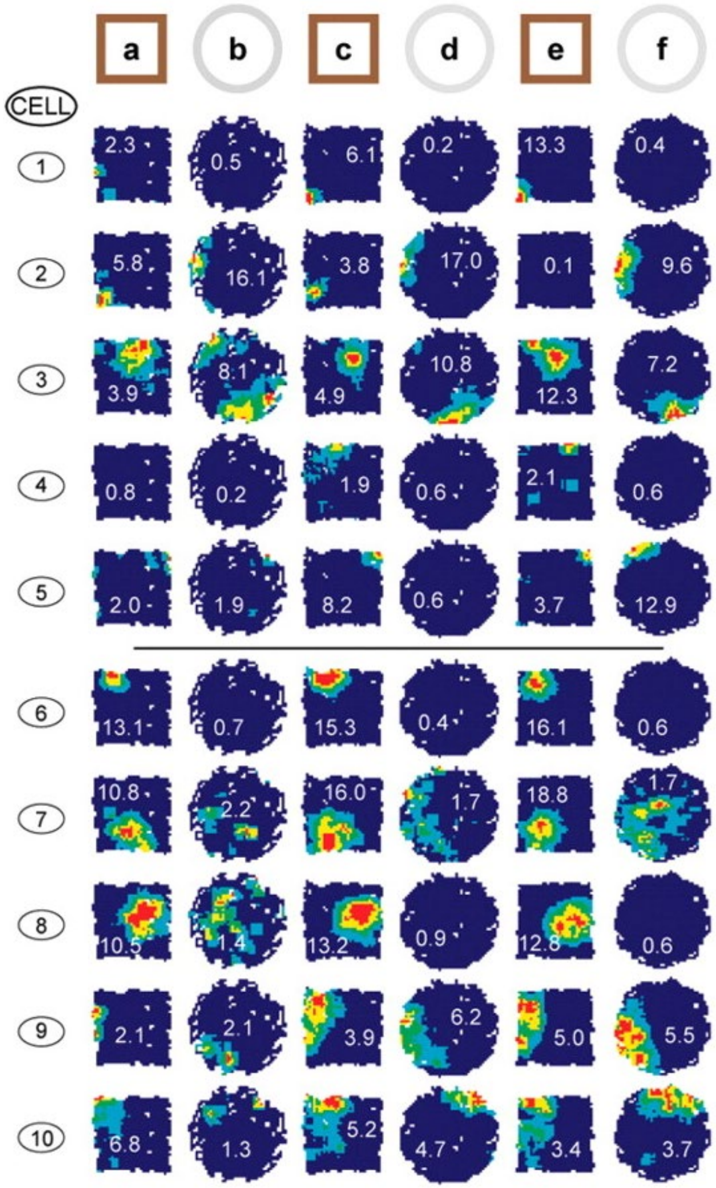
Place fields, however, are not purely visual, and are not even modality-specific – they are multi-modal



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

- In this experiment, the place-fields were likely determined mostly by <u>odors</u> 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

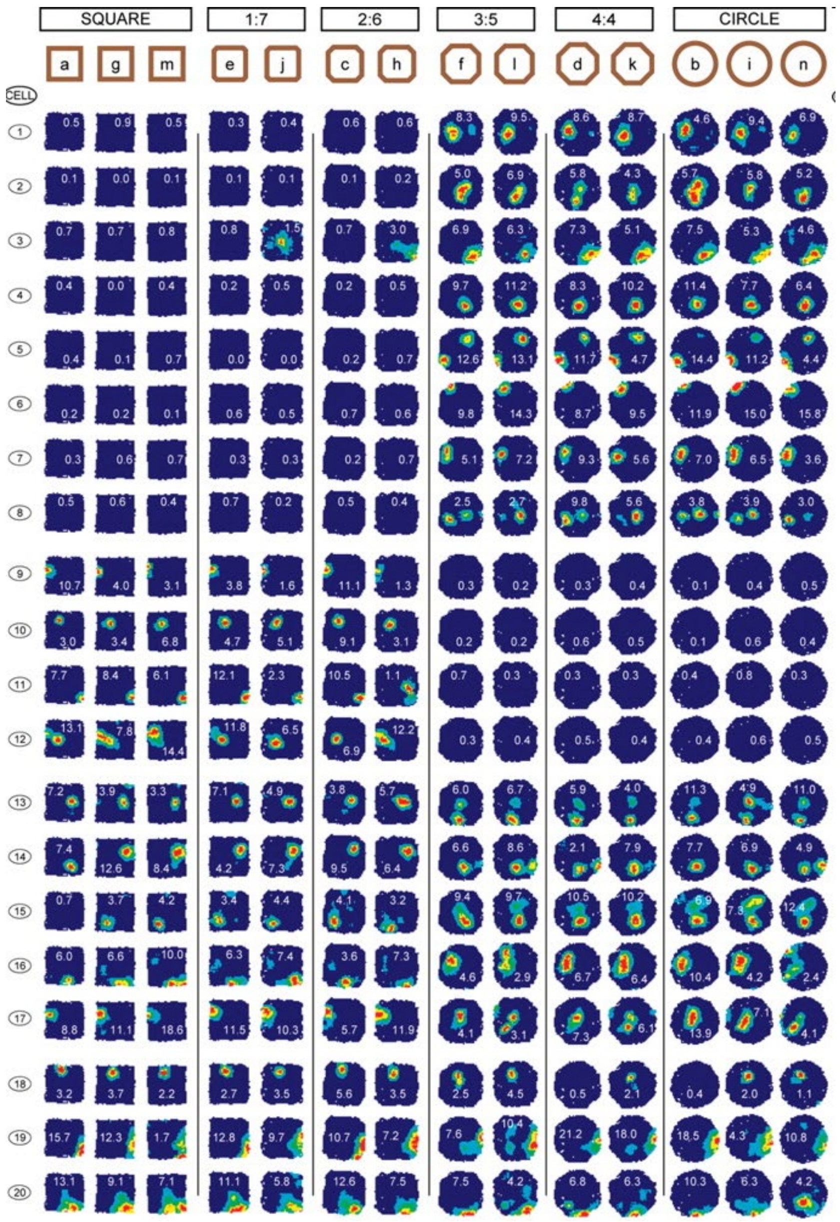
Multiple maps are stored simultaneously in rat hippocampus



<u>"Remapping"</u> between representations of square and circular environments.

Wills et al., *Nature* (2005)

Multiple maps are stored simultaneously in rat hippocampus

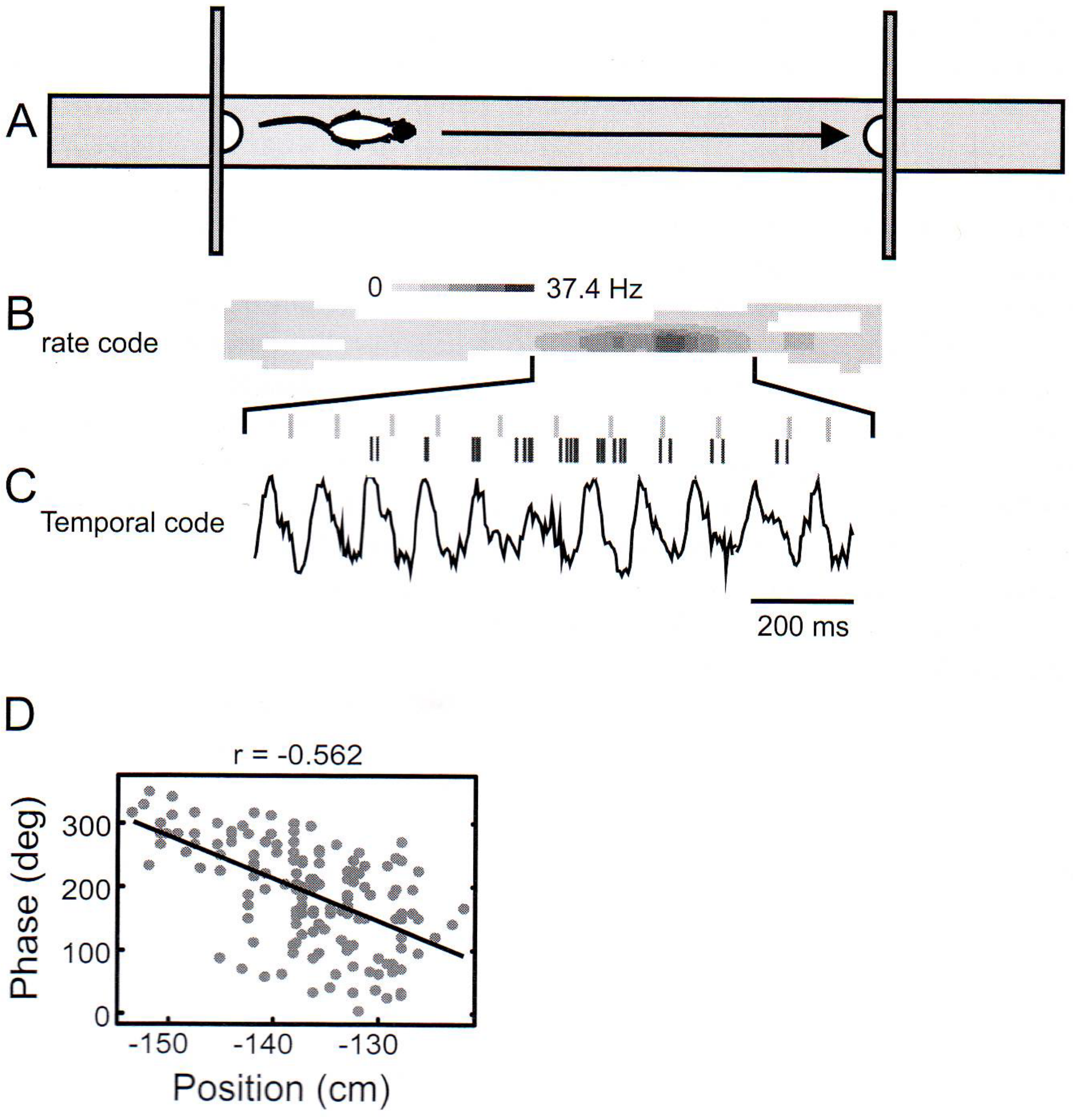


Abrupt **phase transition** between square-like and circle-like representations in intermediate octagonal environments: Evidence for **attractor dynamics** in the hippocampal network.

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

Wills et al., *Nature* (2005)

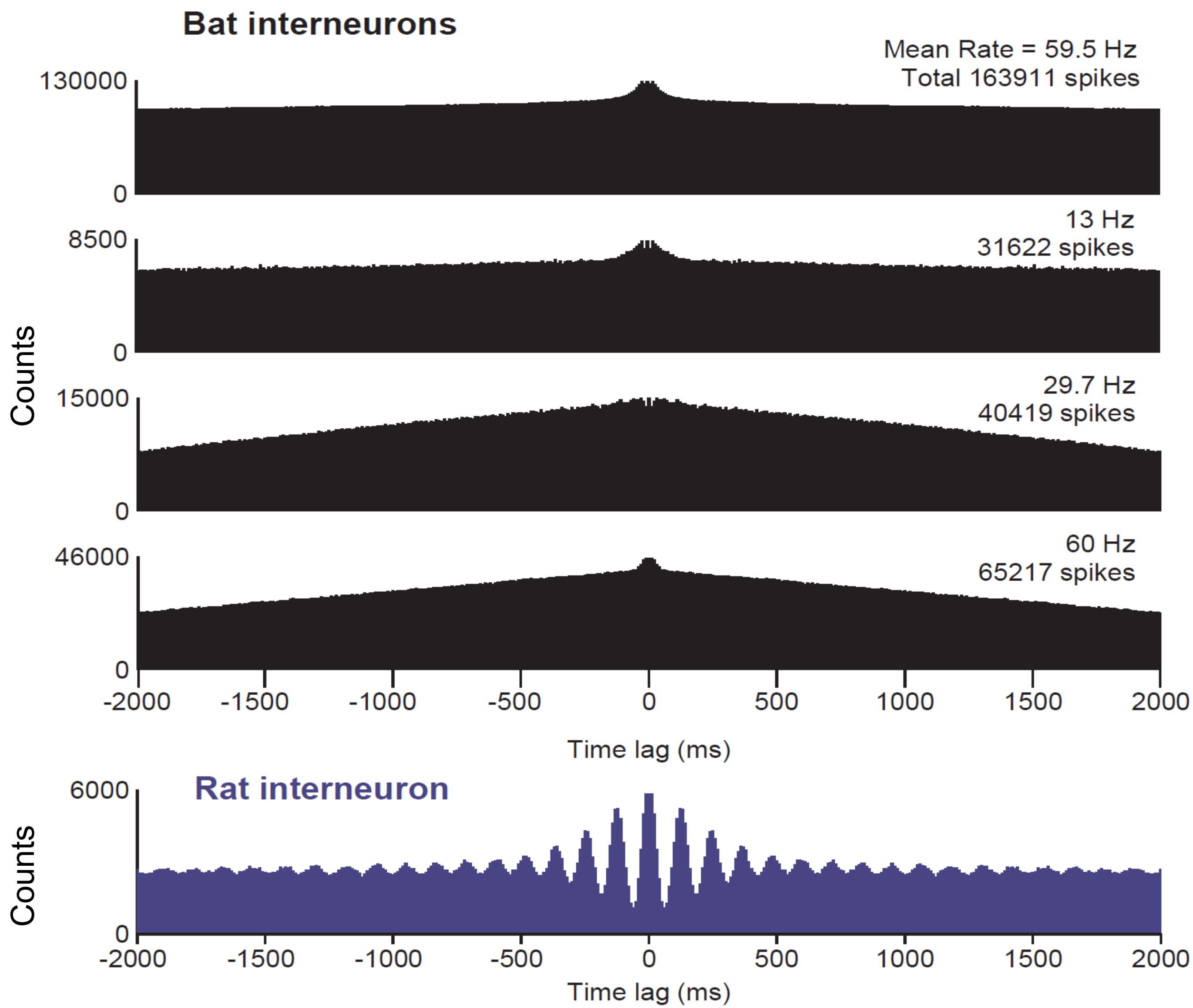
Temporal coding of position: Theta phase precession



<u>"Theta Phase precession"</u>: Place cells are firing at progressively earlier and earlier phases of the cycle of the **<u>theta oscillation</u>**, as the animal runs through the place field.

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

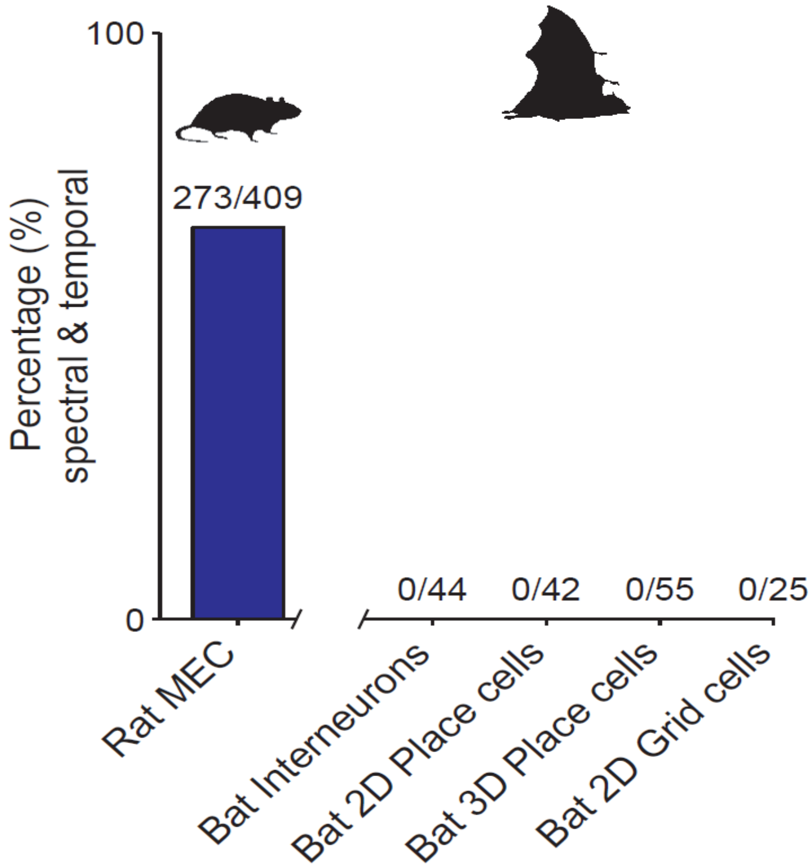
BUT: No theta oscillations in bat neurons (*nor in humans*)



Yartsev et al., *Nature* (2011)

Eliav et al., *Cell* (2018)

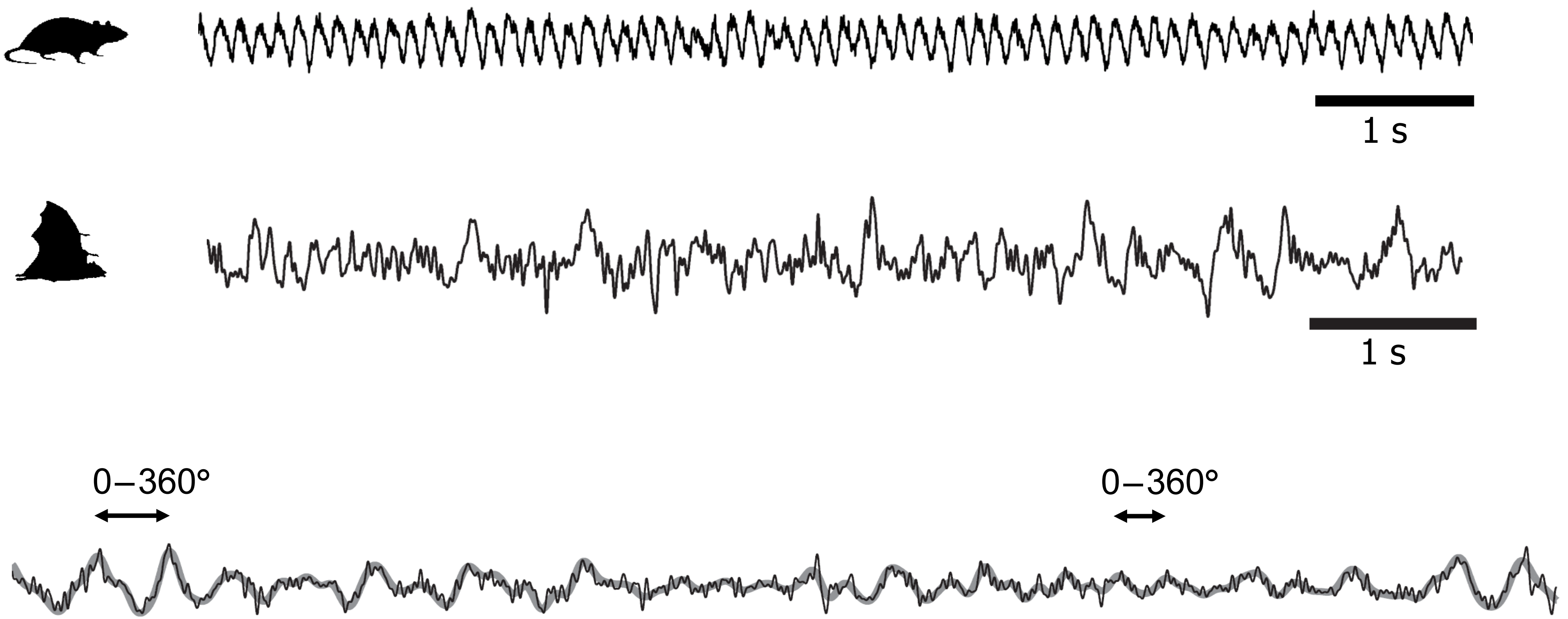
No movement-related oscillations at any frequency



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

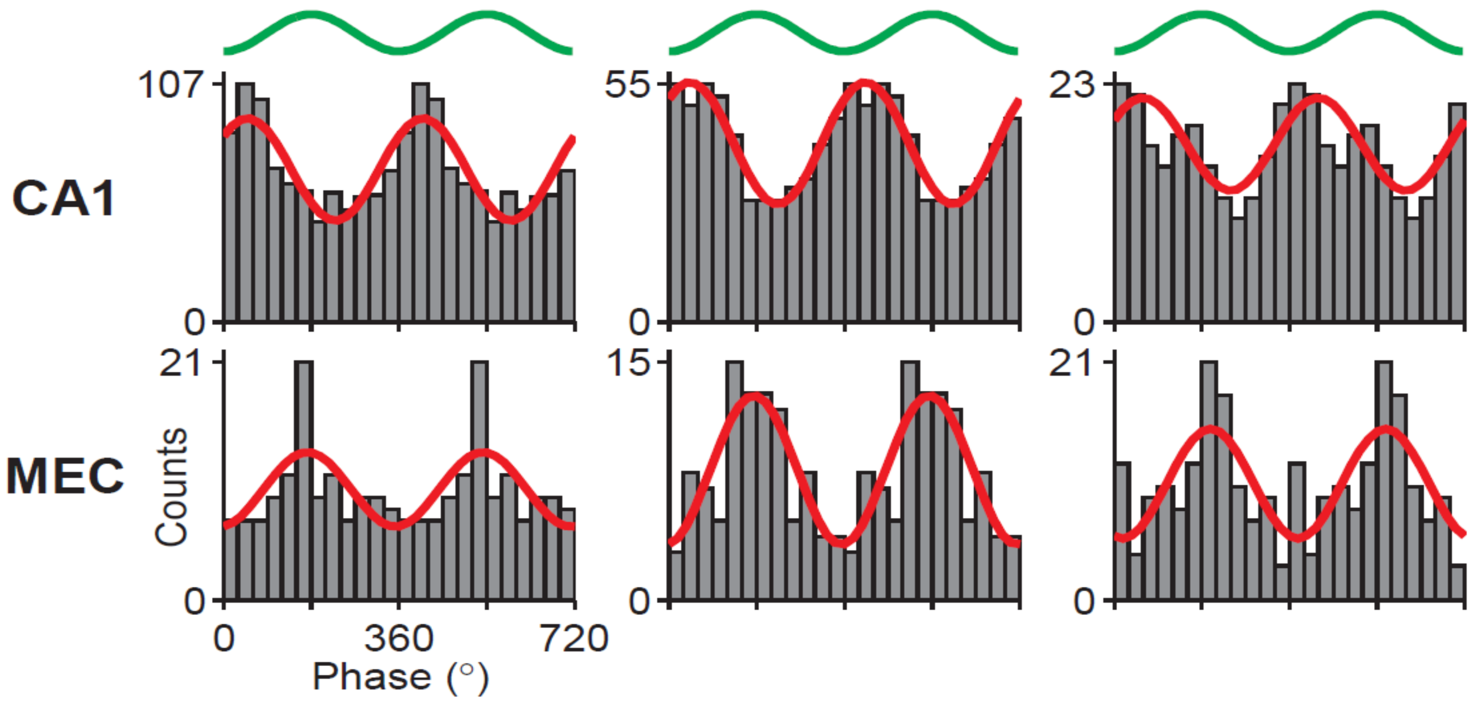
- 67% of rat neurons (273/409) are significantly oscillatory – almost all at ~8 Hz.
- 0% of bat neurons (0/166) are significantly oscillatory in the 1–20 Hz range.

A twist in the story



Eliav et al., *Cell* (2018)

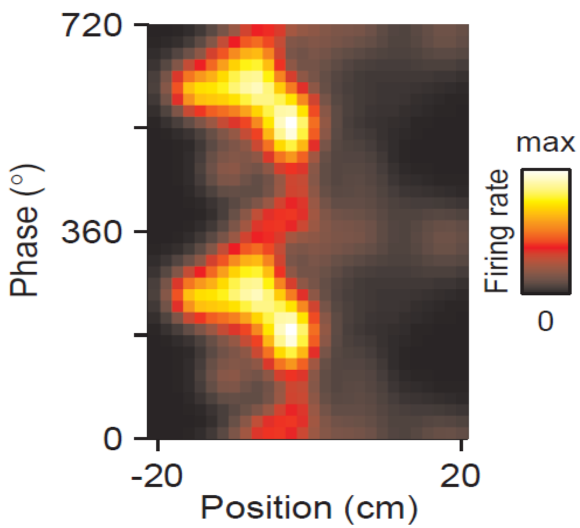
Nonoscillatory phase-locking in bats



- 44% of bat CA1 principal neurons (19/43) show significant nonoscillatory phase-locking.
- In the time-domain, these neurons are nonoscillatory.

Eliav et al., *Cell* (2018)

Nonoscillatory phase-coding of the animal’s position



- 38% of bat CA1 neurons (16/42) show significant nonoscillatory phase-coding of position.

Eliav et al., *Cell* (2018)

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:	Bats
✓ Oscillations (theta)	X Oscillations (theta)
✓ Synchronization	✓ Synchronization
✓ Coding (of position)	✓ Coding (of position)

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

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  - Grid cells
- Beyond the cognitive map: Hippocampus and memory
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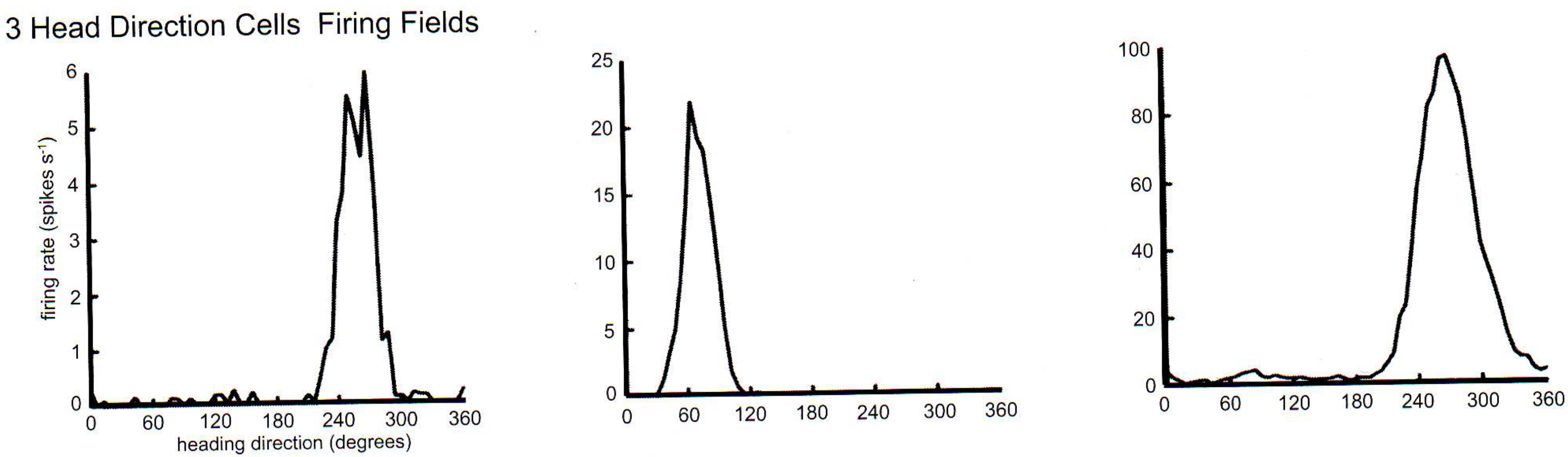
Head direction cells in dorsal presubiculum

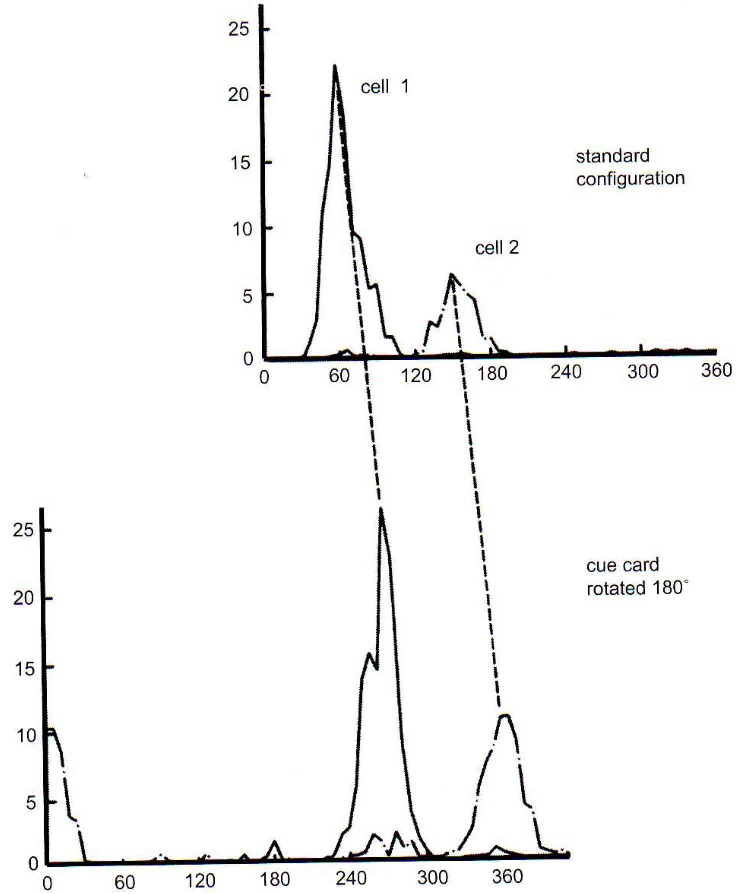


- Head direction cells are found in the dorsal presubiculum, anterior thalamus, medial entorhinal cortex, and in several other brain areas adjacent to the hippocampus.
- These cells are tuned to head direction, but *not* to place – i.e. they fire more or less uniformly with respect to the animal's location.

Head direction cells in dorsal presubiculum

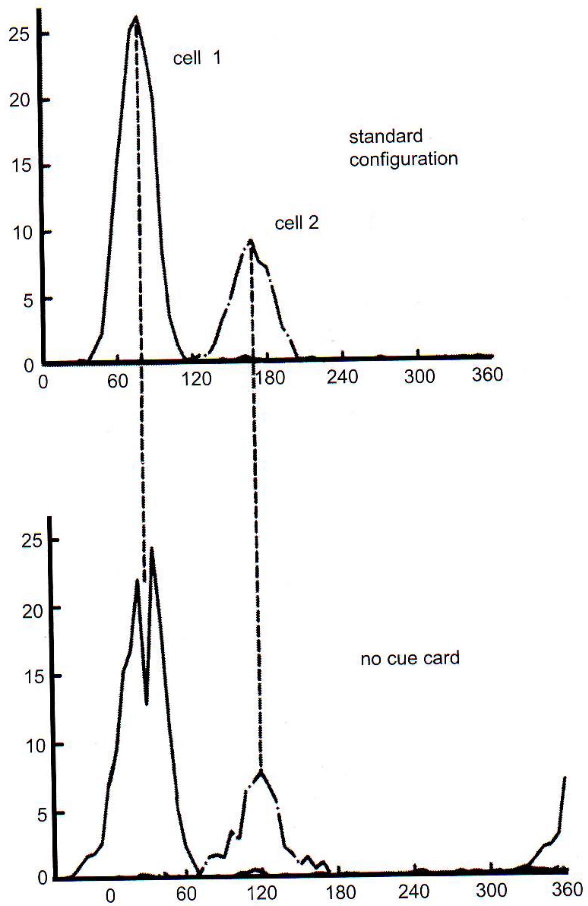
Head direction cells rotate together

Fields rotate with cue card



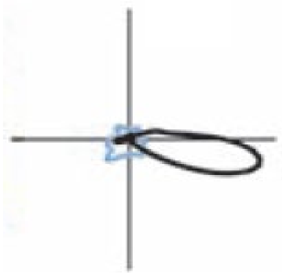
Head direction cells “remap” to a new random direction upon removal of cue card – but they remap together

Fields shift after cue card removal



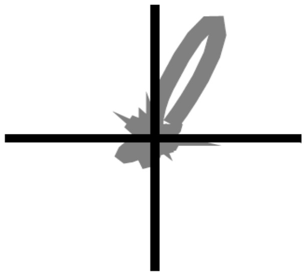
Is there a representation of 3-D head direction in the mammalian brain = “3-D neural compasses” ?

Head-direction cells
In rats



Solstad et al.
Science 2008

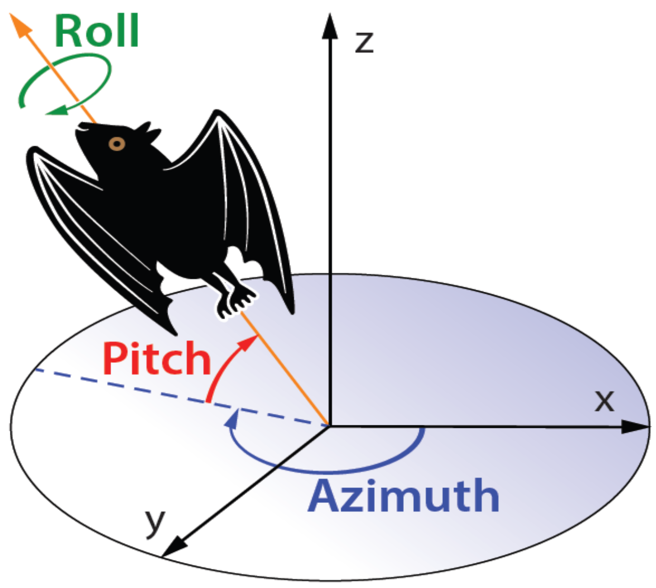
Head-direction cells
In bats



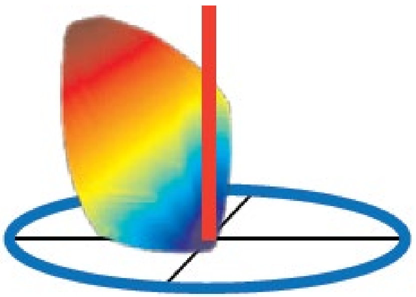
Yarsev, Witter, Ulanovsky
Nature 2011

3-D head direction cells in bats

Euler Angles



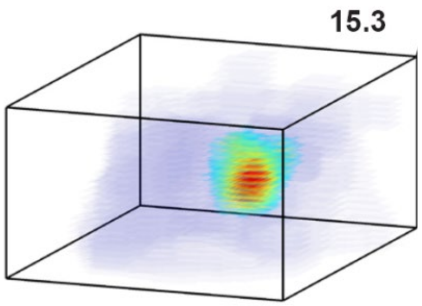
3D head-direction cell



Finkelstein et al, *Nature* (2015)

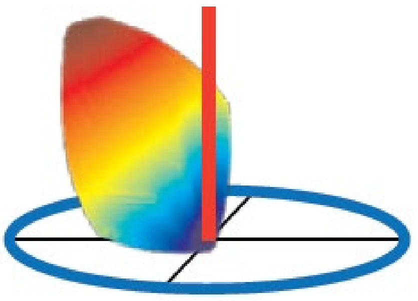
3D place cells and 3D head-direction cells were found also in rodents and primates

3D place cells



Yartsev & Ulanovsky
Science (2013)

3D head-direction cells



Finkelstein et al.
Nature (2015)

Recently, other groups found:

→ 3D head-direction cells:

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

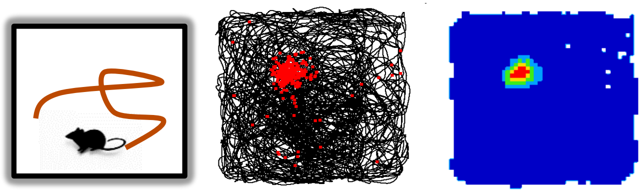
→ 3D place cells:

- Rats (Grieves…Jeffery 2020)

Neural basis of map-and-compass navigation ?

1. *Map* → *Place cells*

Hippocampus

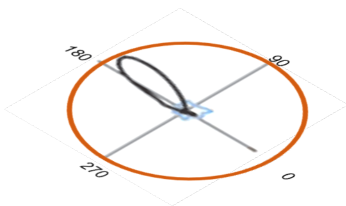


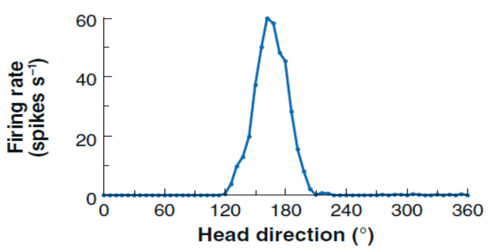
Movie courtesy of Dori Derdikman, 2010

2. *Compass* ↓

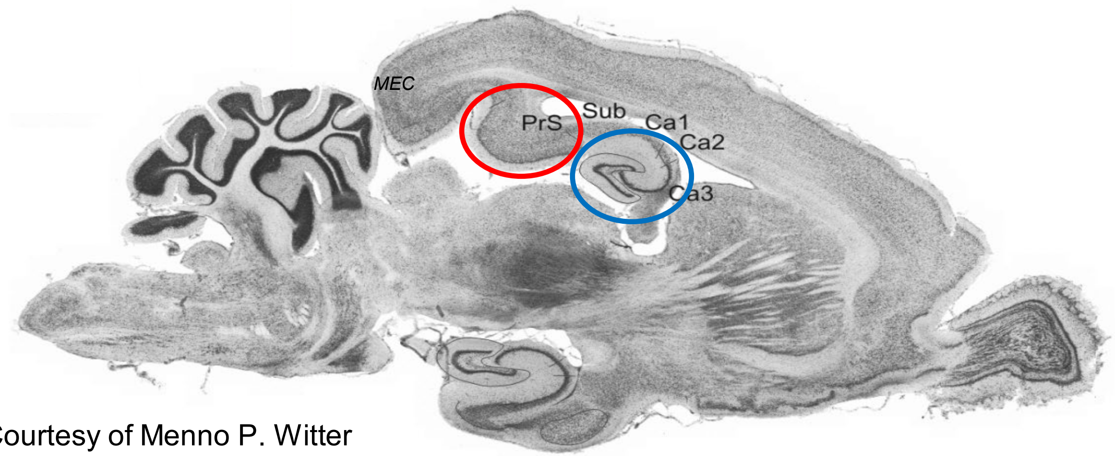
Head-direction cells

Presubiculum (PrS)





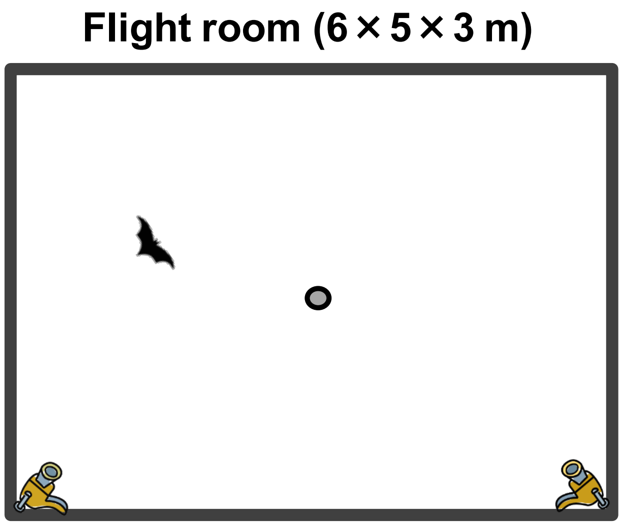
Ranck & Taube
JNS 1990



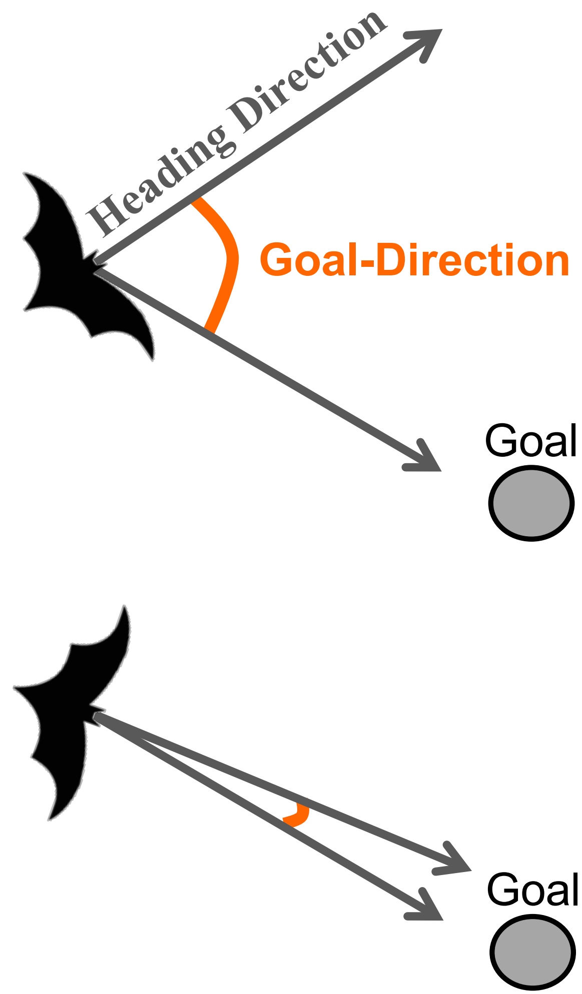
Courtesy of Menno P. Witter

Movie courtesy of Tor Kirkesola, 2010

The missing link: How do you navigate to goals ?

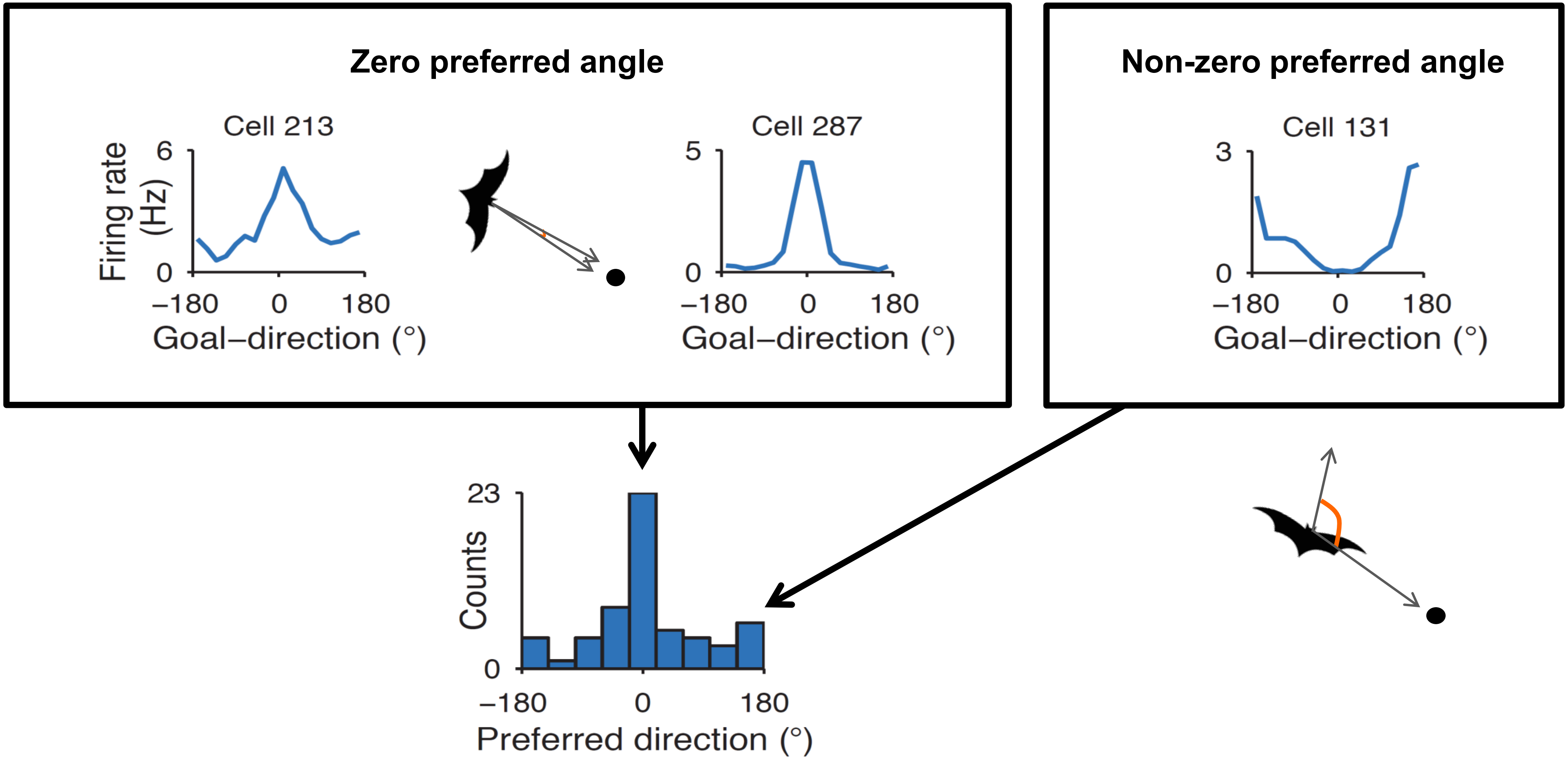


Recordings in hippocampal area CA1



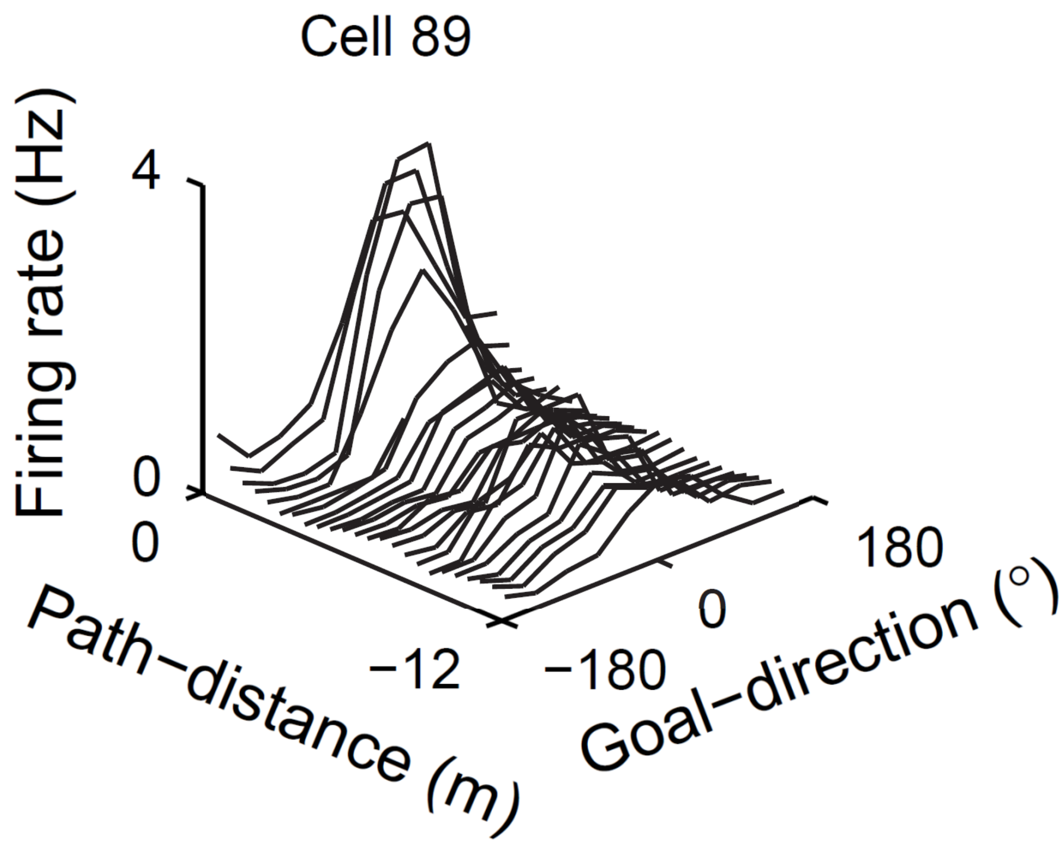
Sarel et al., *Science* (2017)

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



Sarel et al., *Science* (2017)

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



Sarel et al., *Science* (2017)

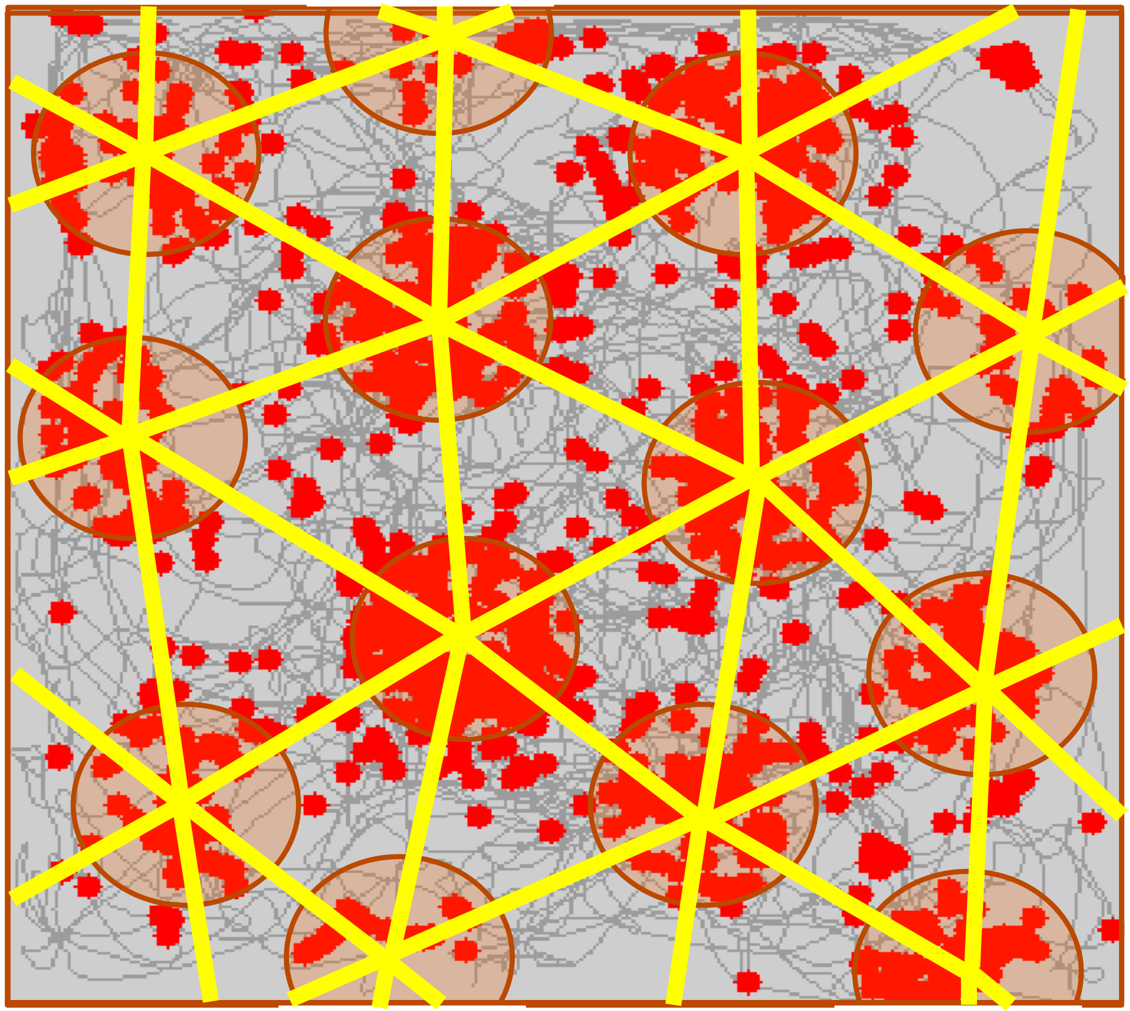
Outline of today's lecture

- **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



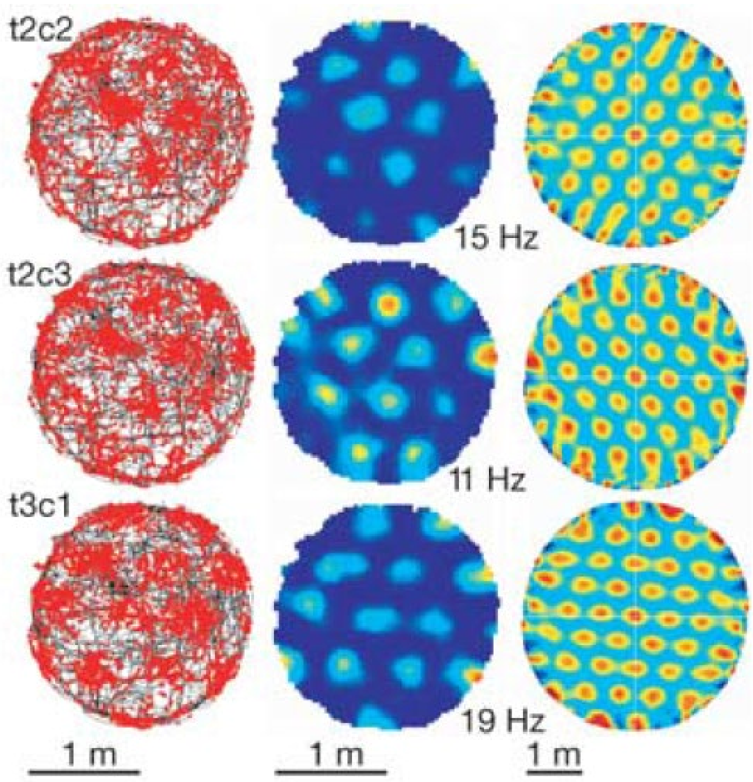
Marianne Fyhn

Torkel Hafting

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



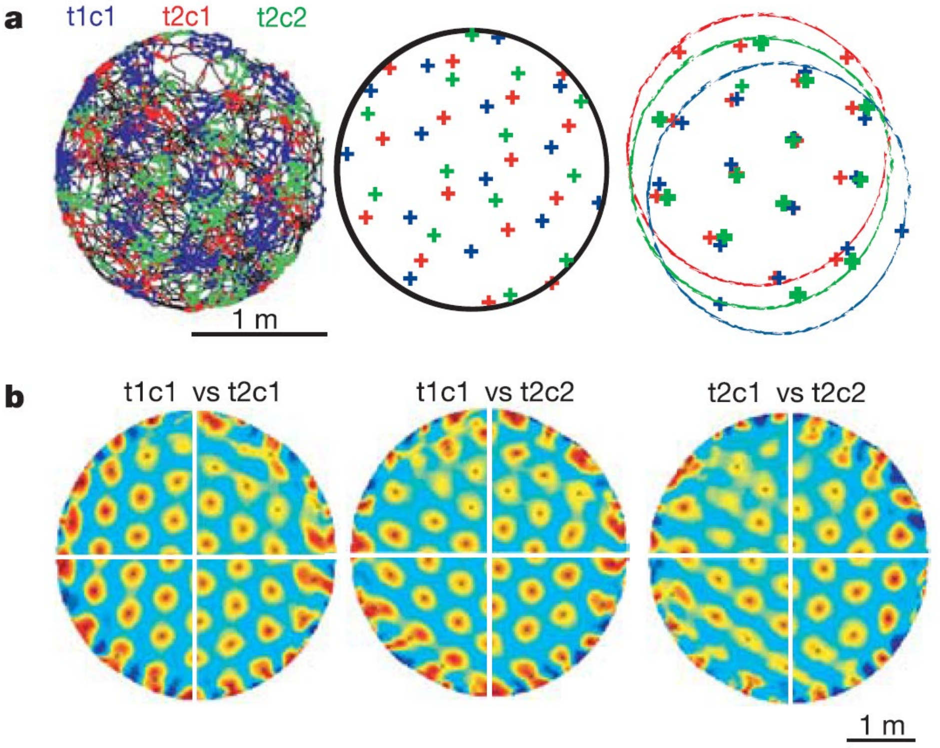
Cell 1

Cell 2

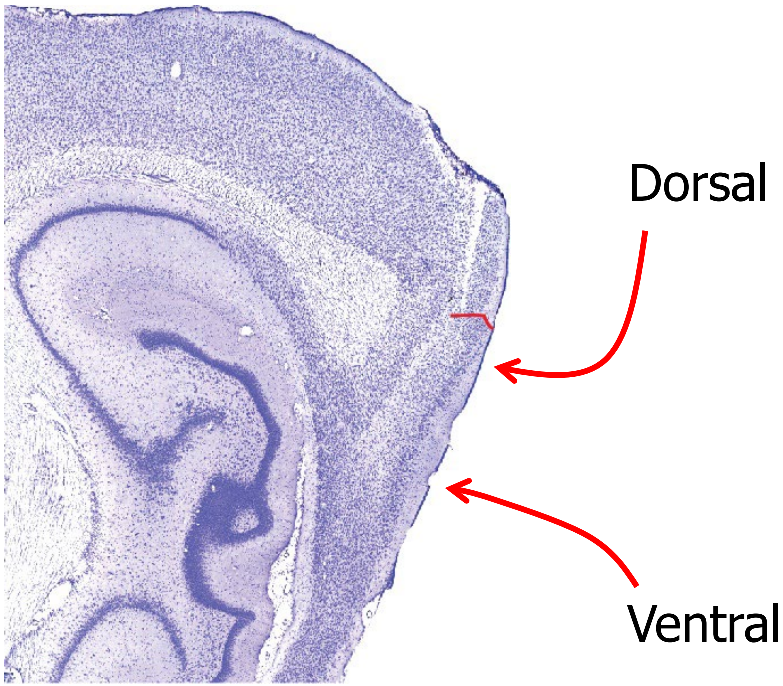
Cell 3

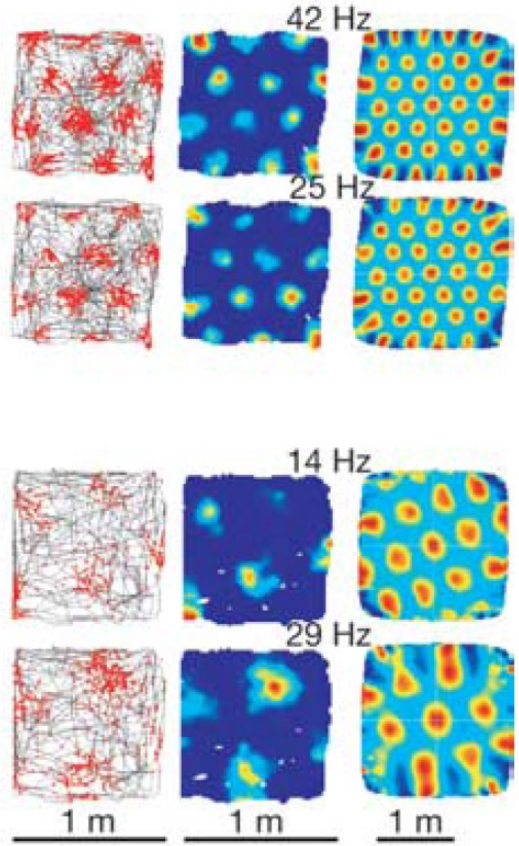
- Grids of simultaneously-recorded grid cells, from nearby locations in MEC, look quite similar

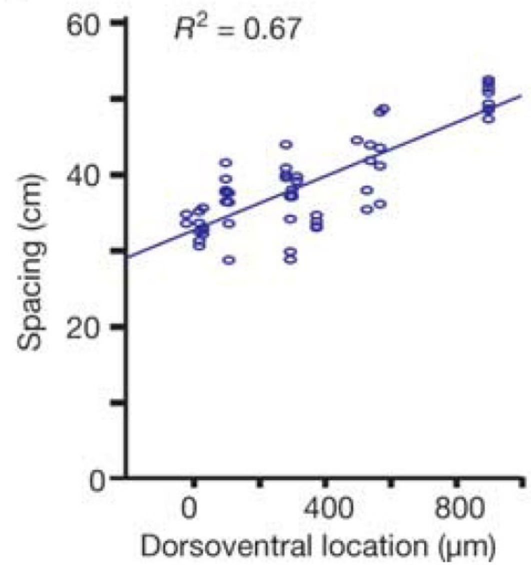
Nearby grid cells have the same grid spacing and orientation, but random grid phase



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

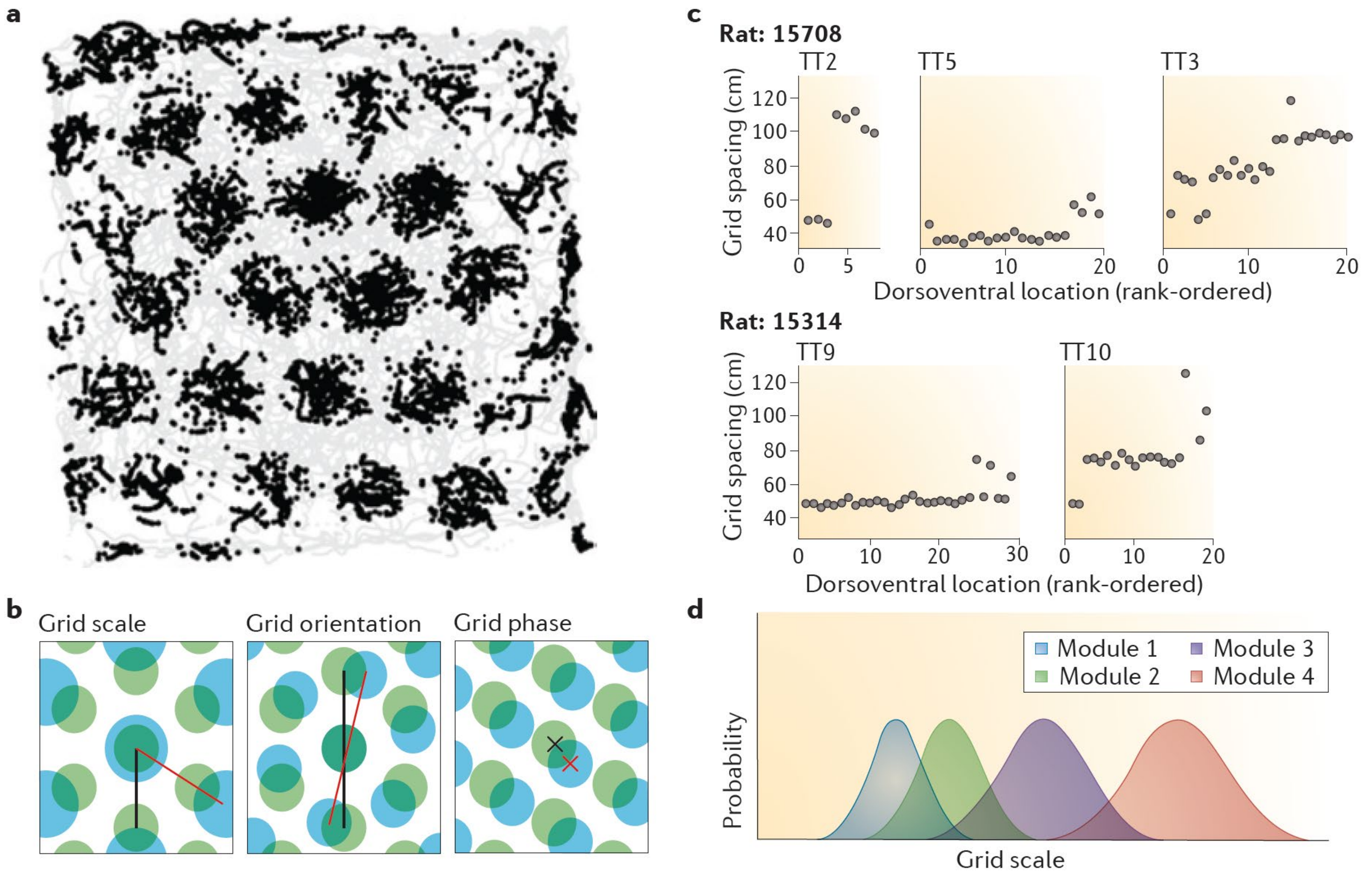






Data from multiple animals
pooled together

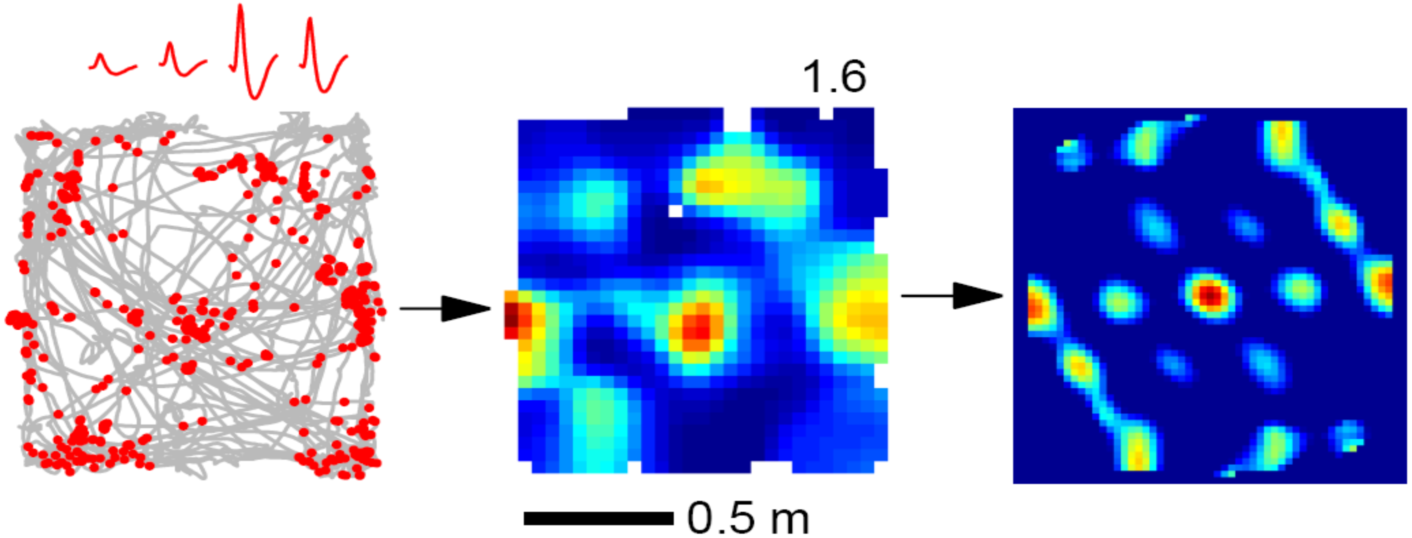
Support for the attractor network model of grid cells comes from the finding that grid cells are organized in *discrete* 'modules'



Stensola et al., *Nature* (2012)

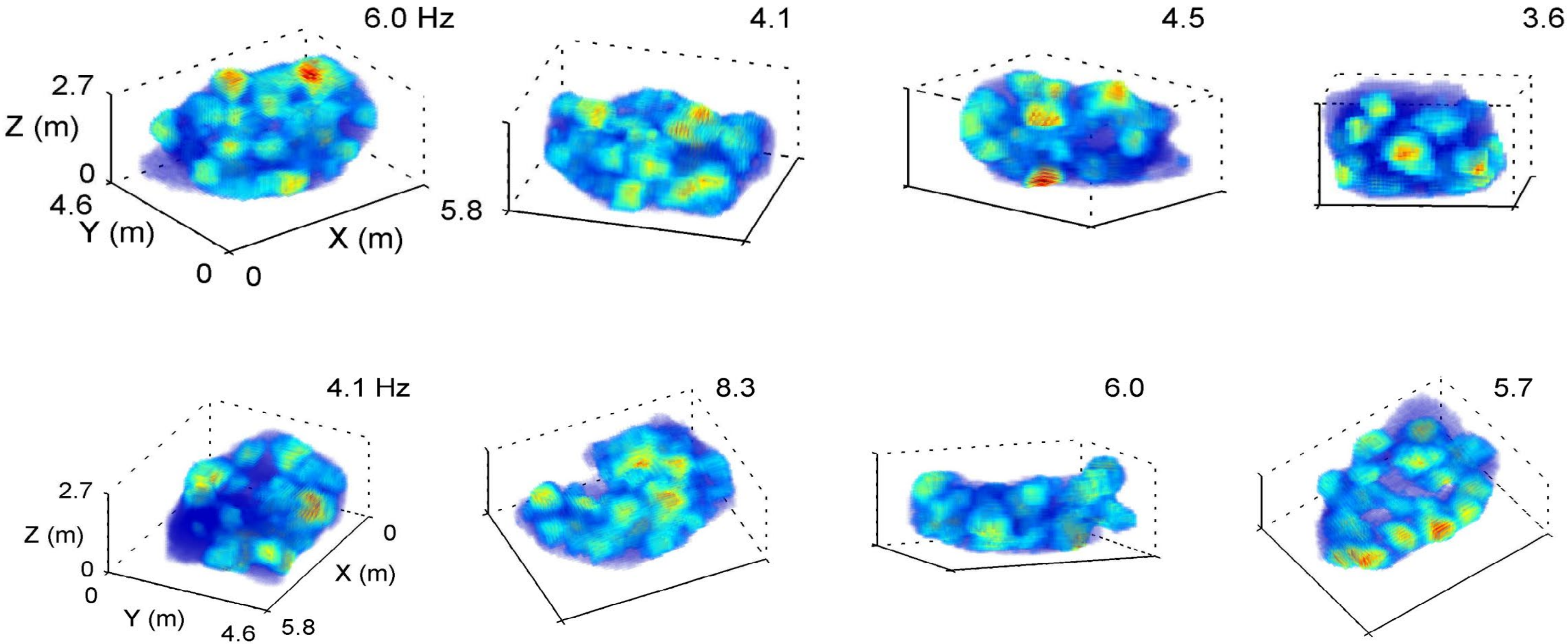
Moser et al., *Nat. Rev. Neurosci.* (2014)

2-D grid cells in bats



Yartsev et al., *Nature* (2011)

3-D grid cells in bats



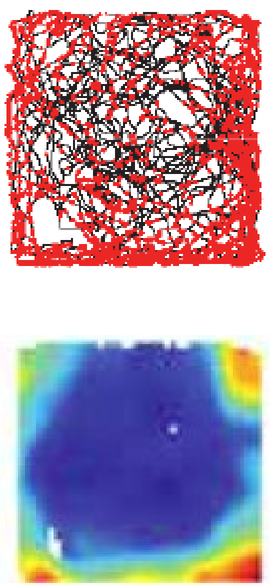
- Unlike 2D grids, 3D grids show a local distance metric but do not exhibit a global lattice → This argues against most current theories on the function of grid cells.

Ginosar et al., *Nature* (2021)

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

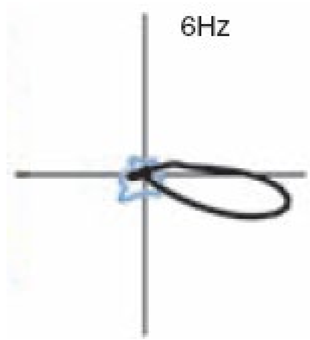
Medial entorhinal cortex

Border Cells



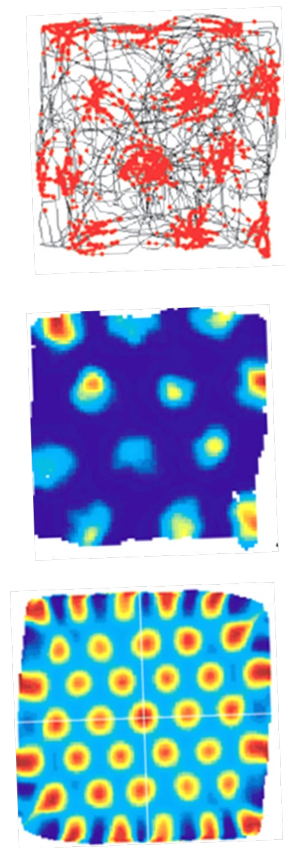
Mosers, O'Keefe, Knierim
2008

Head-direction cells



Ranck, Taube – 1980's

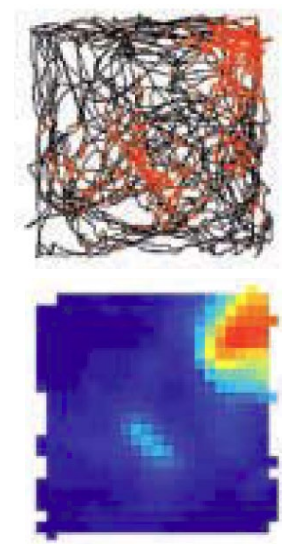
Grid cells



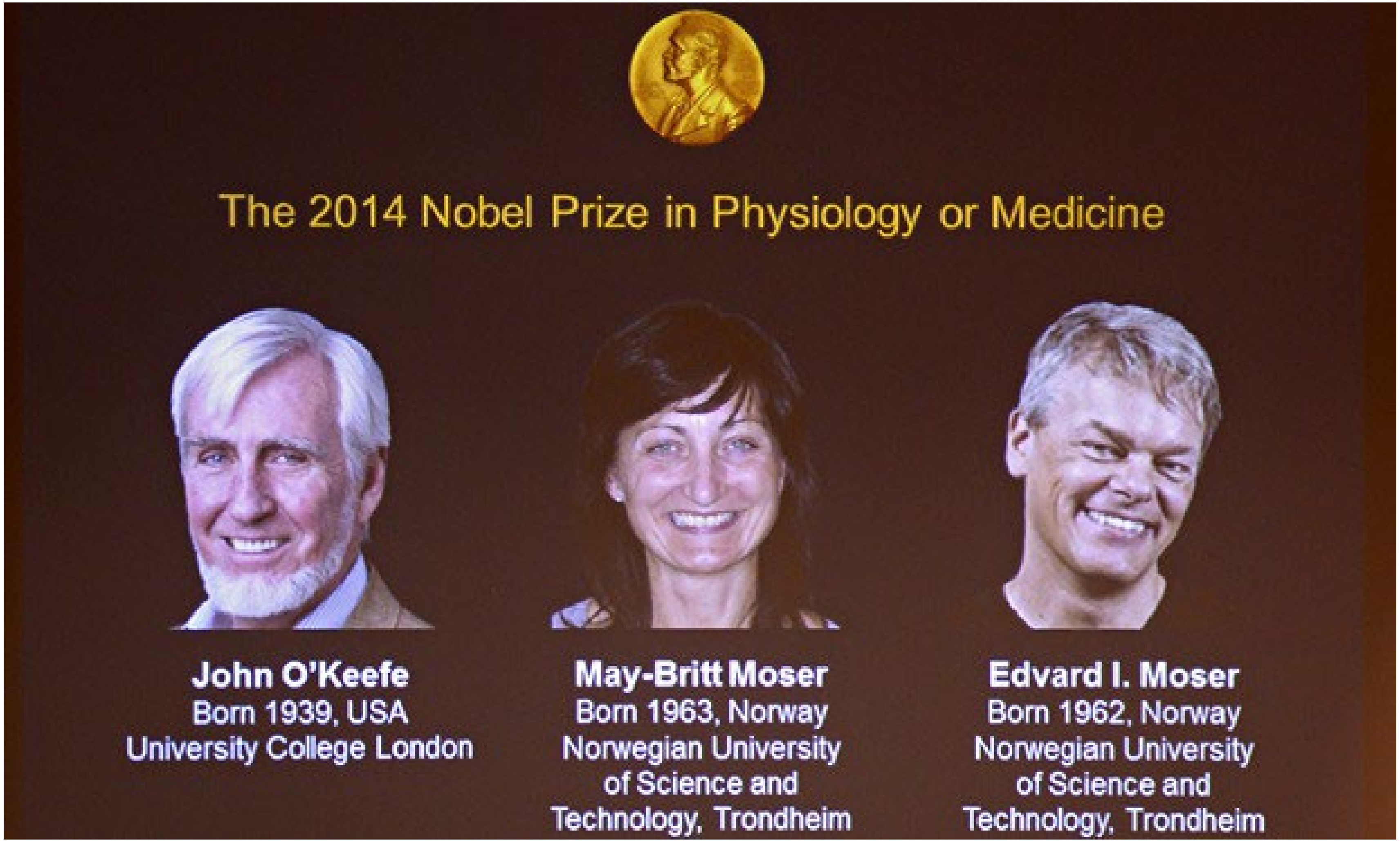
Mosers – 2005

Hippocampus

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

} Map

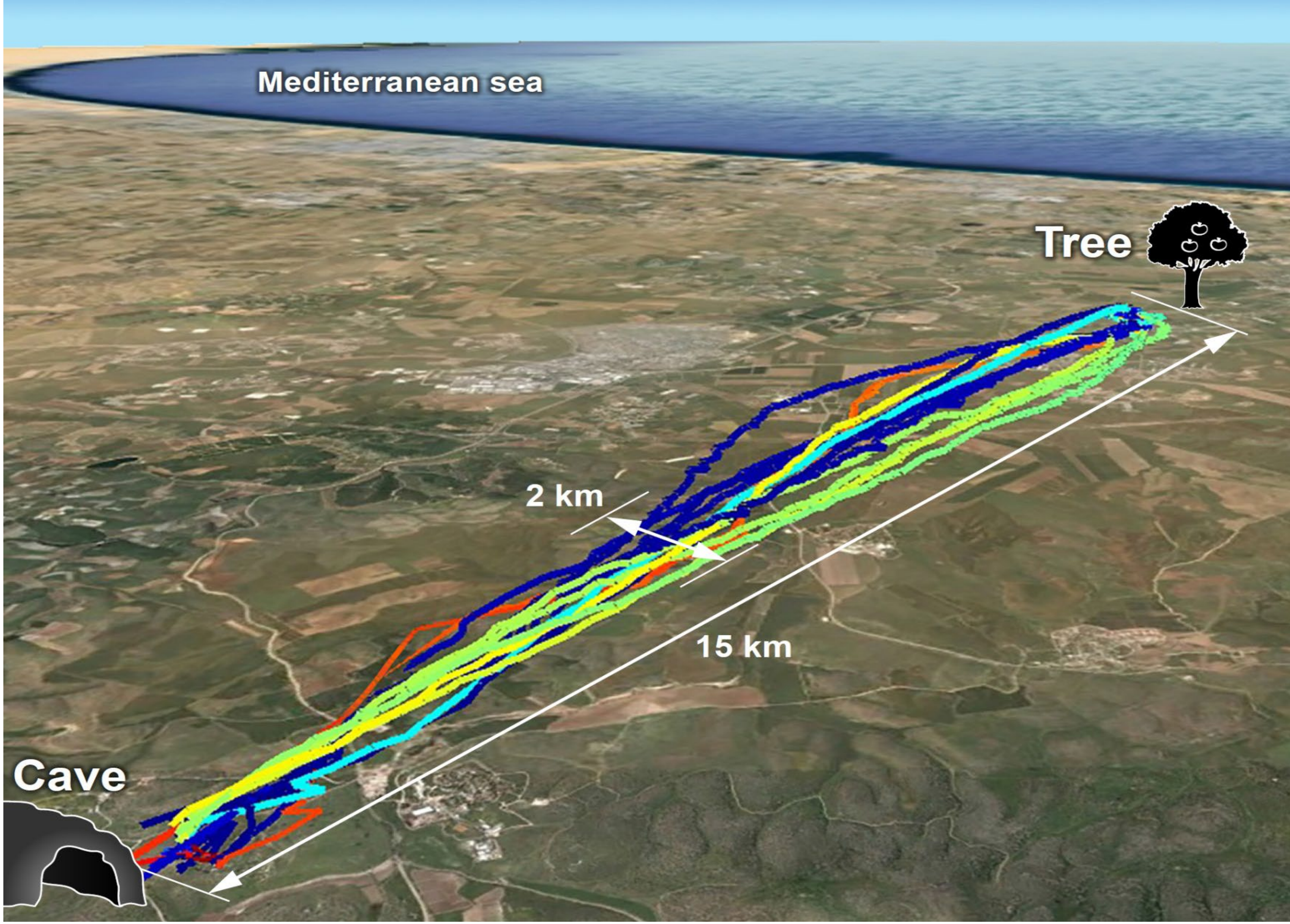
- **Head-direction cells** → Direction

} Compass

- **Goal-direction cells** → Goals

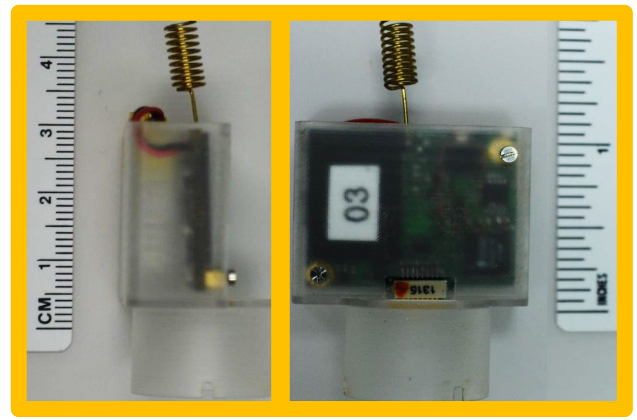
} "Waze"

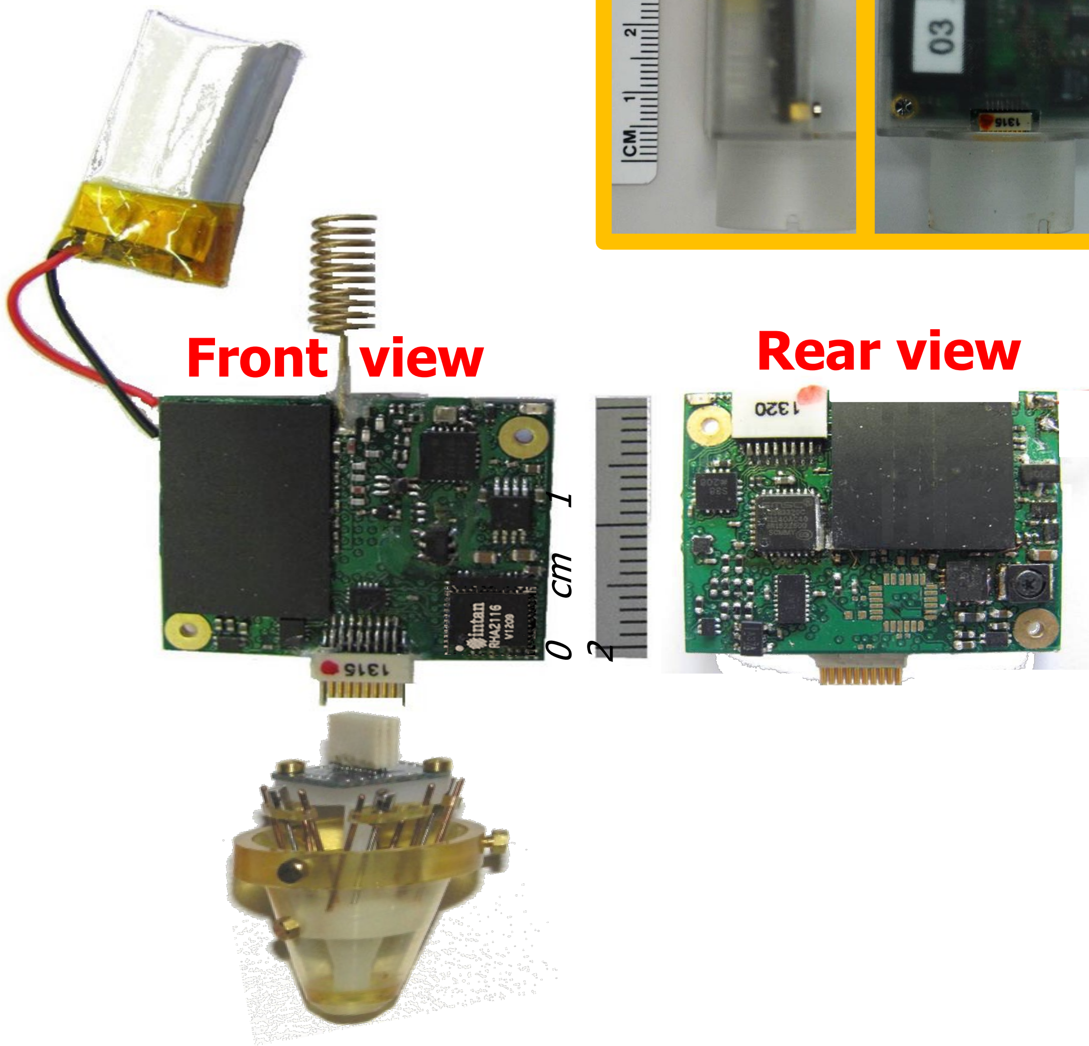
BUT:
How are large-scale spaces encoded in the brain?



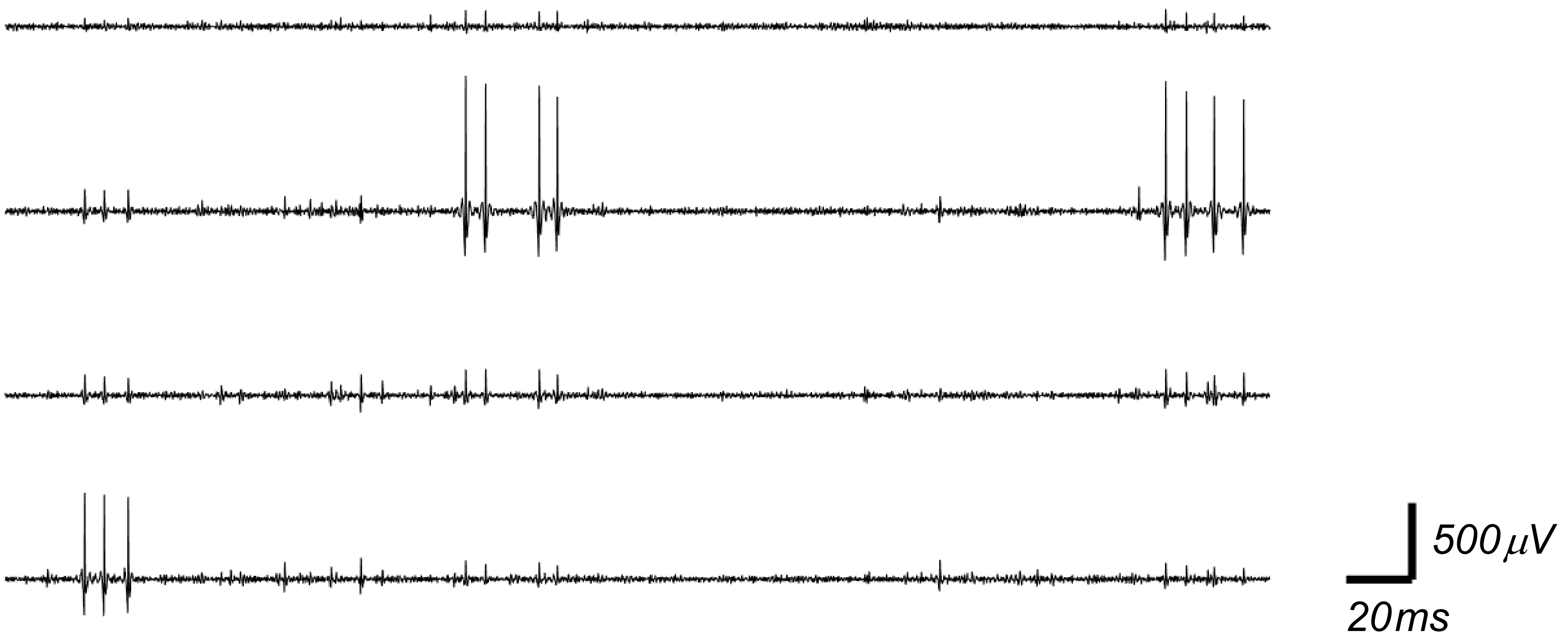
Geva-Sagiv, Las, Yovel, Ulanovsky
- Nature Rev. Neurosci., 2015
- PNAS, 2011

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



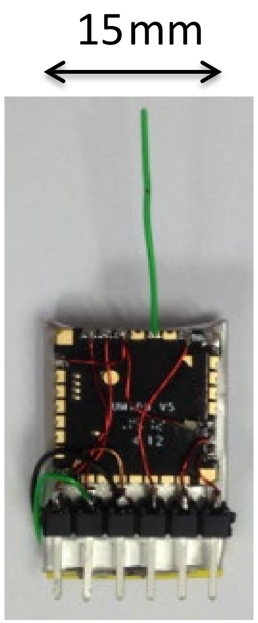


1. Developing on-board 64-channel neural logging system

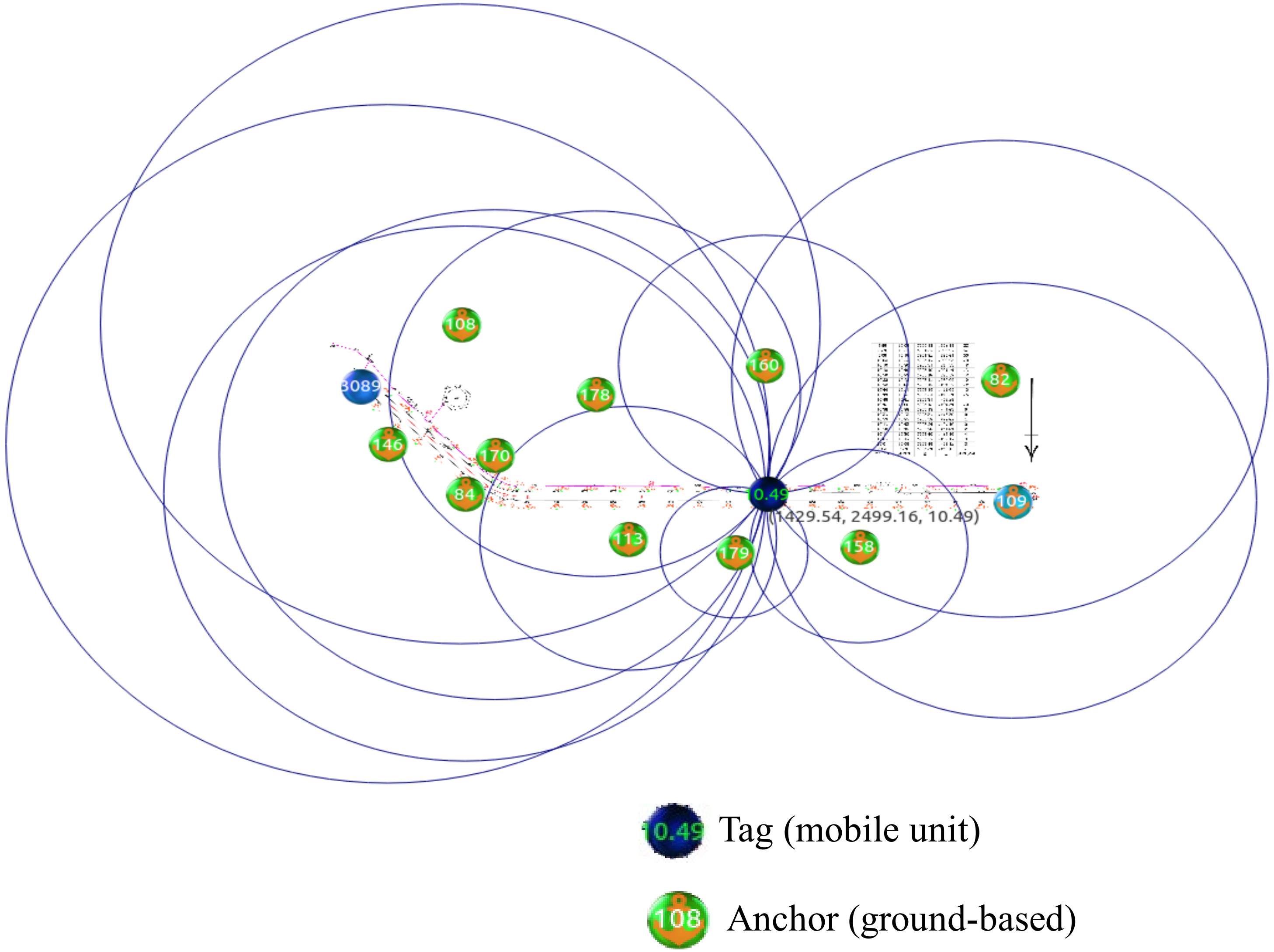


Eliav et al.
Science (2021)

2. Large-scale precise localization system



BeSpoon, Inc.

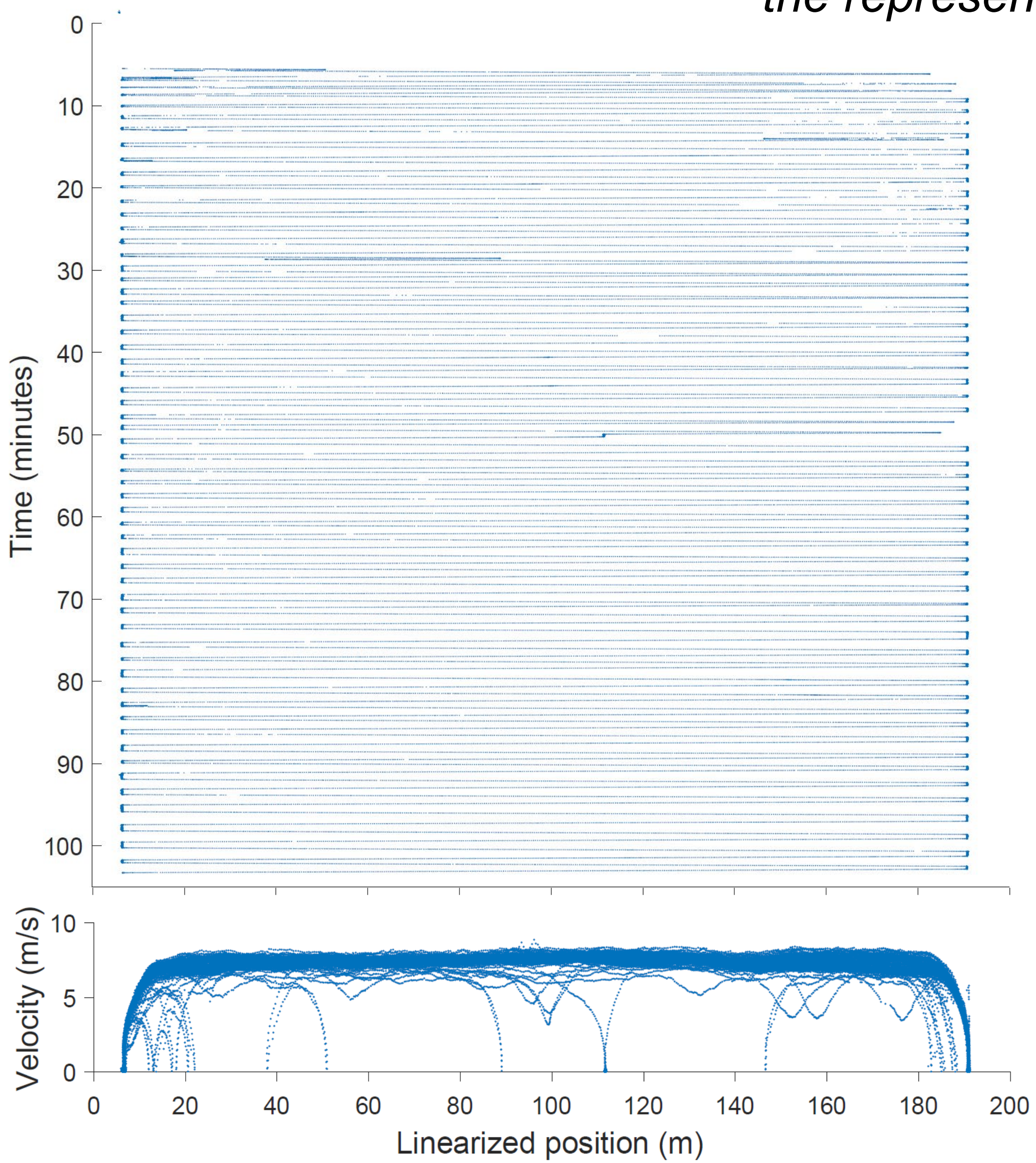


- 5-cm precision

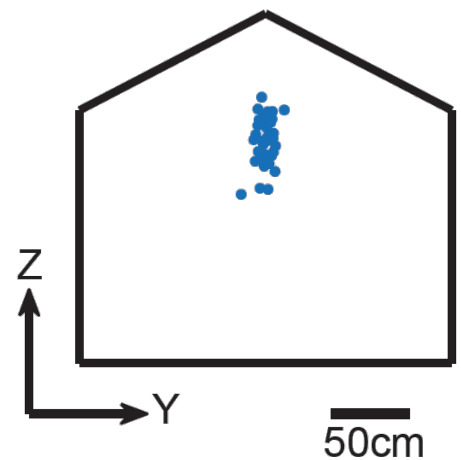
3. Large behavioral setup

Behavior

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

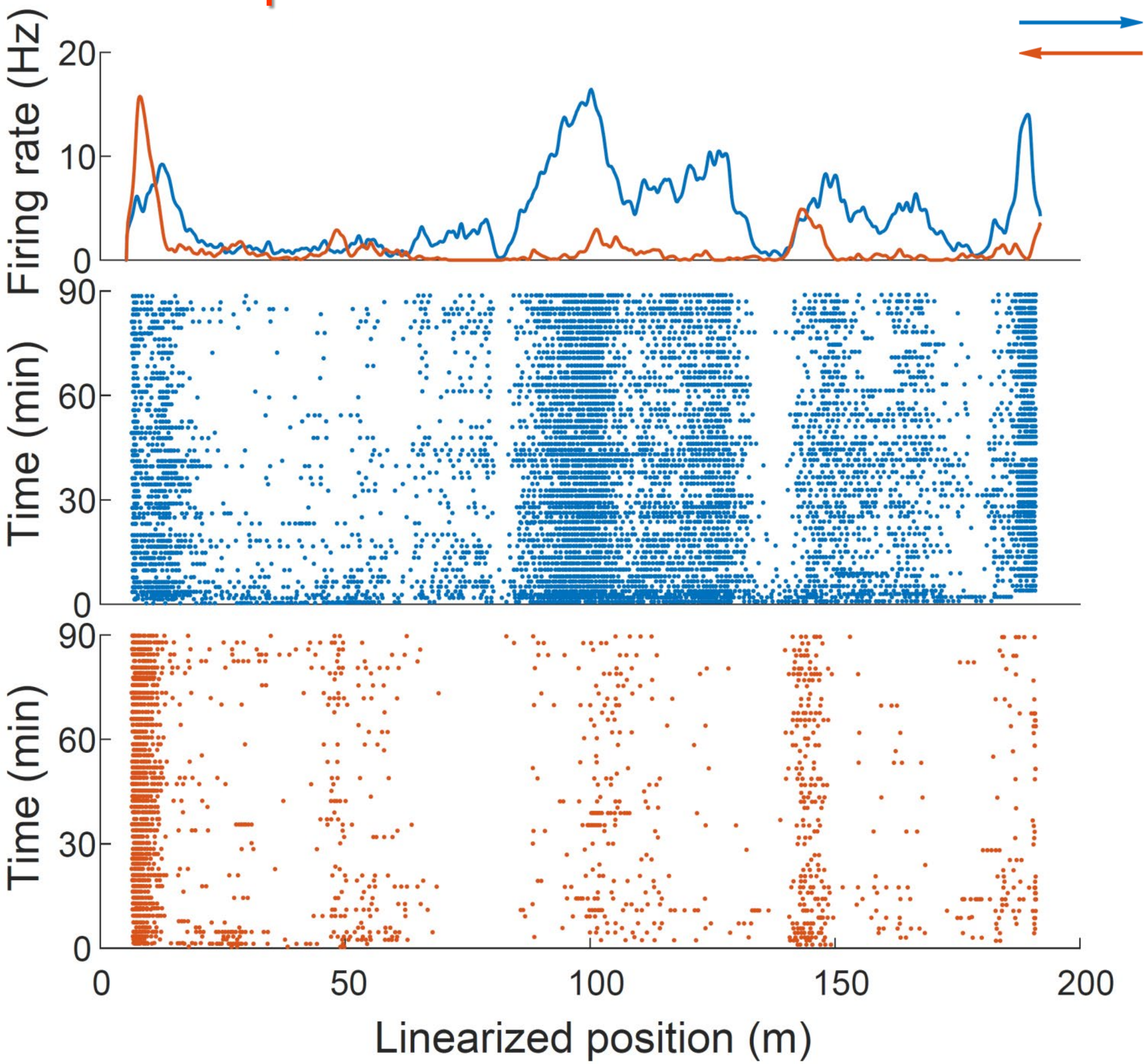


- Food rewards at both ends
- Direct flights from start to end
- 100 laps / session (20 km / 1.5 hrs)



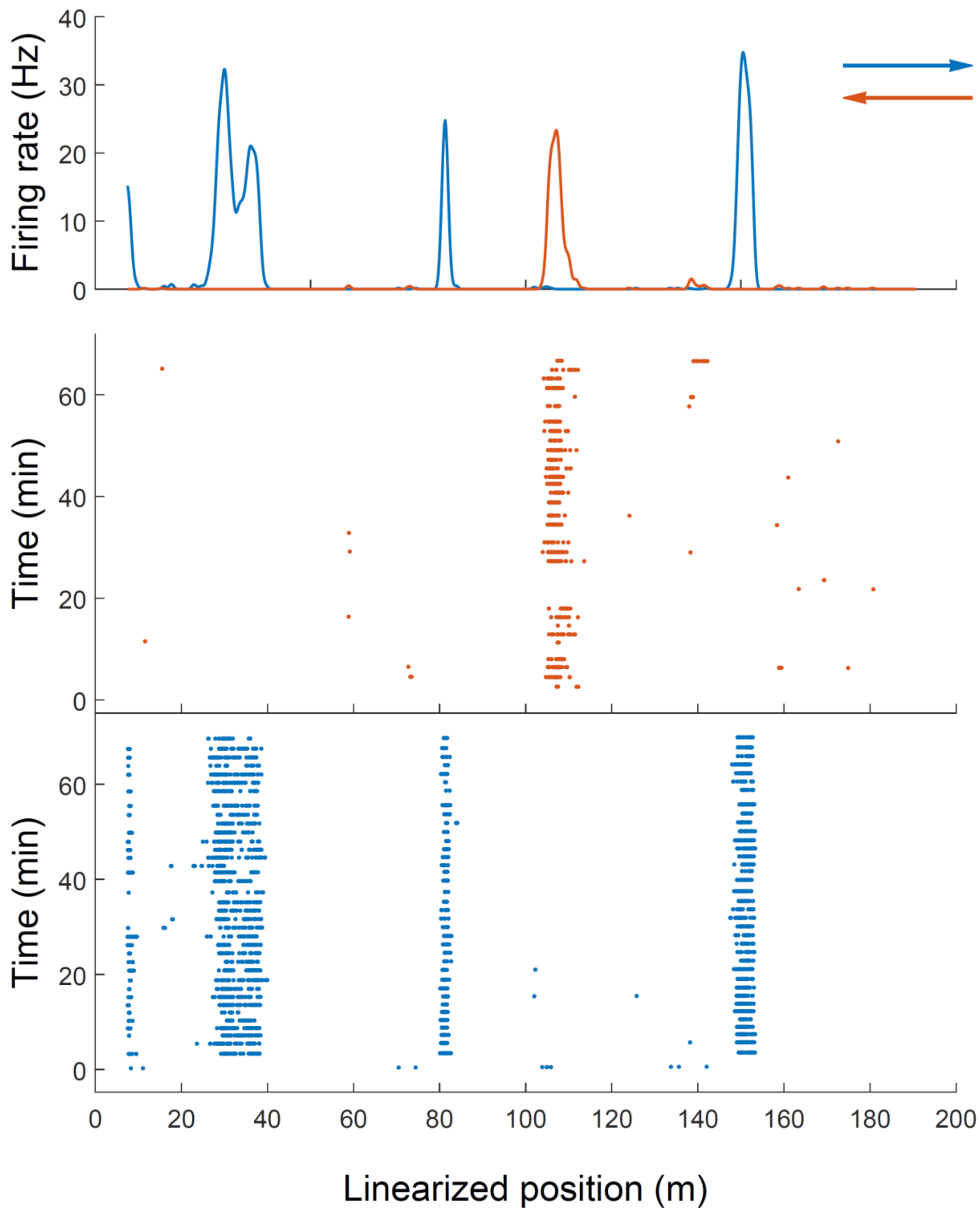
- Flight speeds: 7-8 m/s

Examples



Example cell from [dorsal CA1]

Eliav et al.
Science (2021)



[Example 2](#)

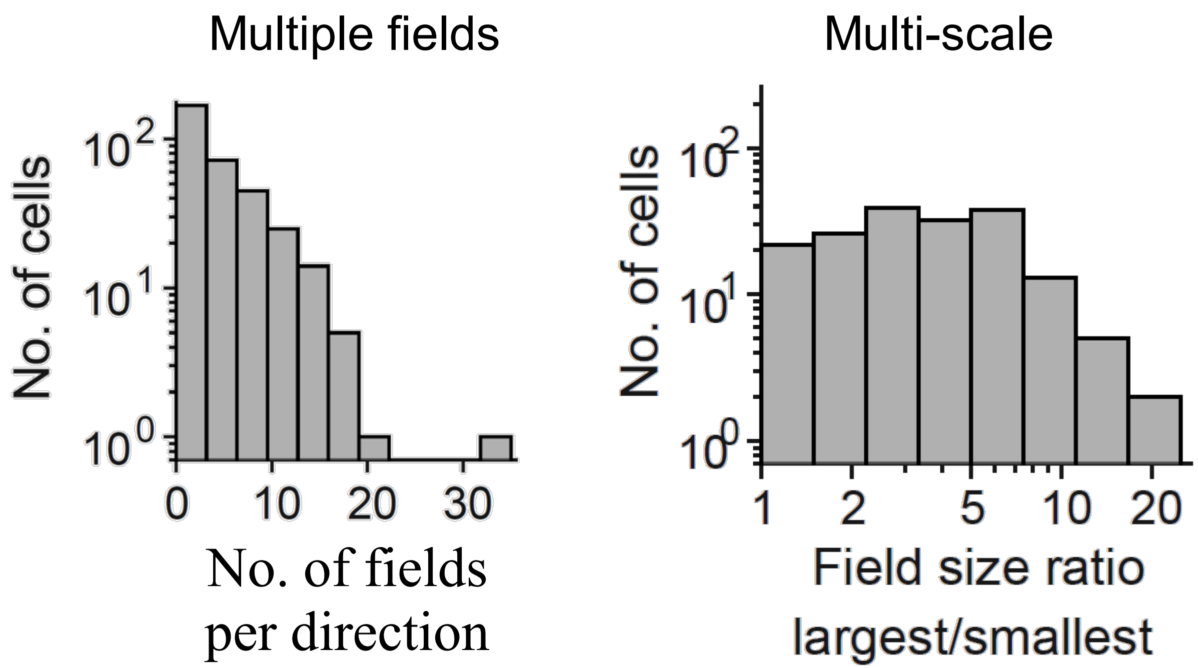
Properties of this spatial code:

- Large fields
- Multiple fields
- Multi-scale

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

Eliav et al.
Science (2021)

Population



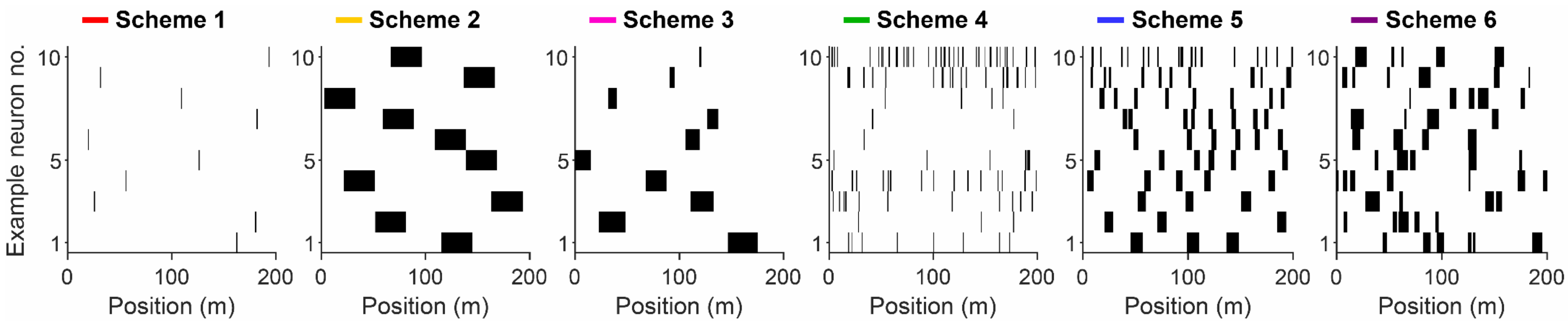
Properties of this spatial code:

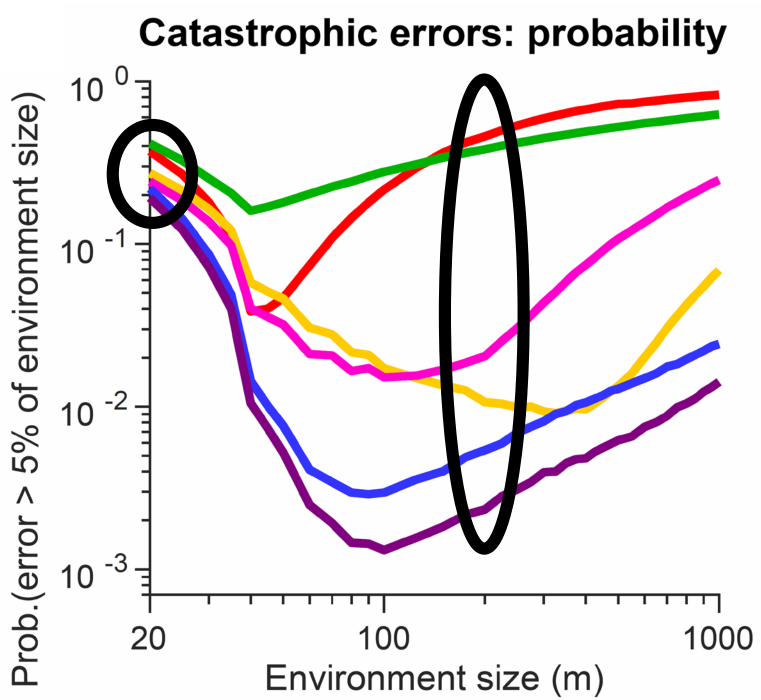
- Large fields
- Multiple fields
- Multi-scale

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

Eliav et al.
Science (2021)

Multi-Scale Coding reduces decoding errors in large environments



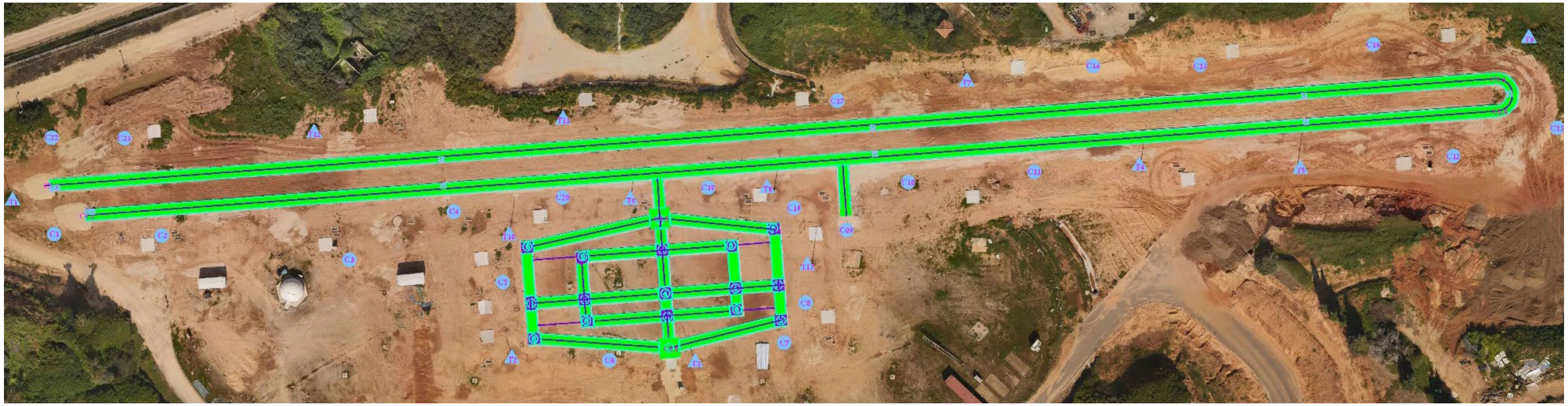


1: Single small field
2: Single large field
3: Single field, dorso-ventral gradient
4: Multiple small fields (Rich et al. 2014)
5: Multi-scale (population)
6: Multi-scale (single-cell), matching bat data

N = 50 neurons

Eliav et al.
Science (2021)

Building a 700-meter tunnel + large Maze (60 x 35 meters)



- **Tunnel:**
  - Coding of large spaces across hippocampal subregions.
  - Representation of multi-scale, multi-compartment environments.

→ Recording large ensembles of neurons in-flight.

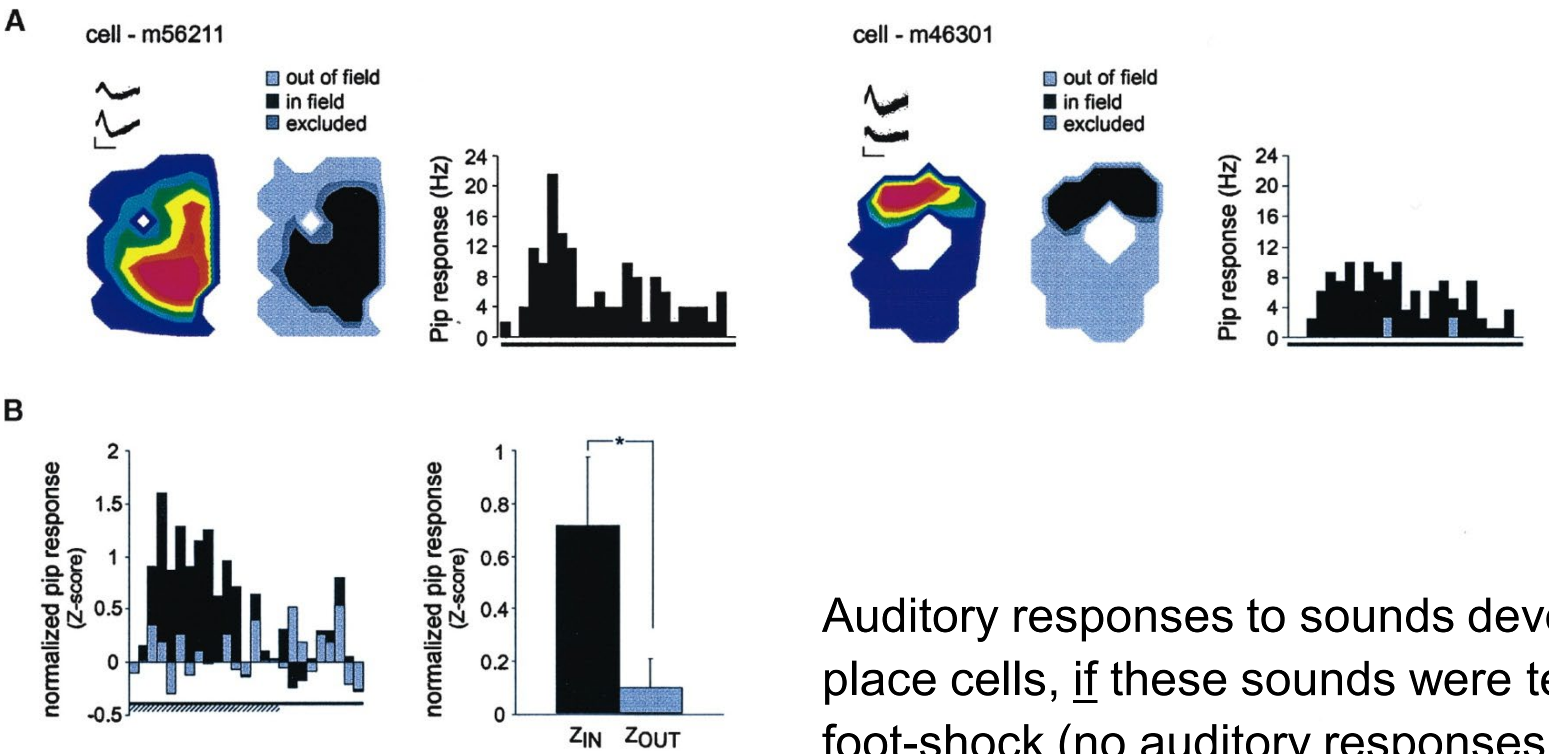
Building a 700-meter tunnel + large Maze (60 x 35 meters)

- **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.

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, <u>if</u> 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

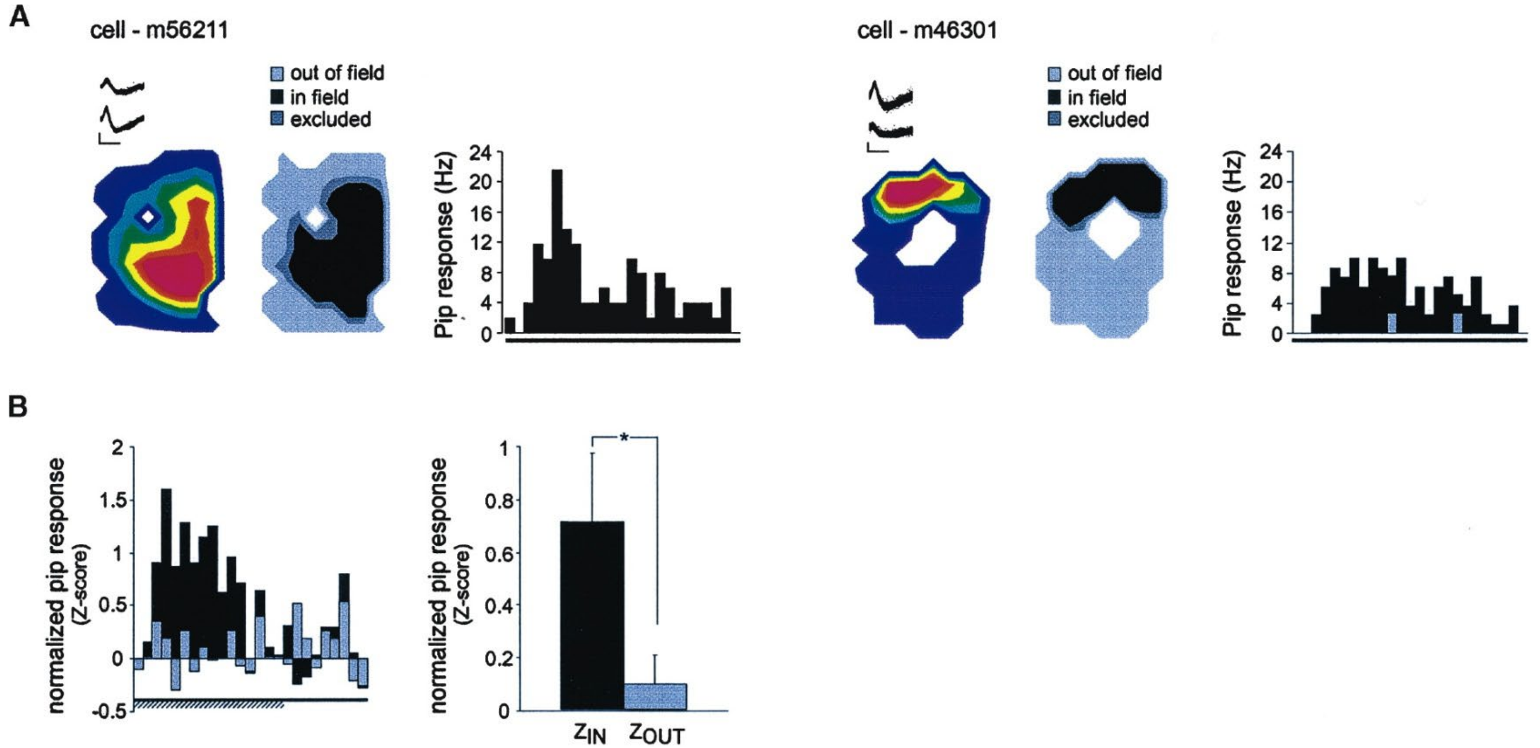
Do whatever (complex) computation the neuron is supposed to do

else

Do nothing

end

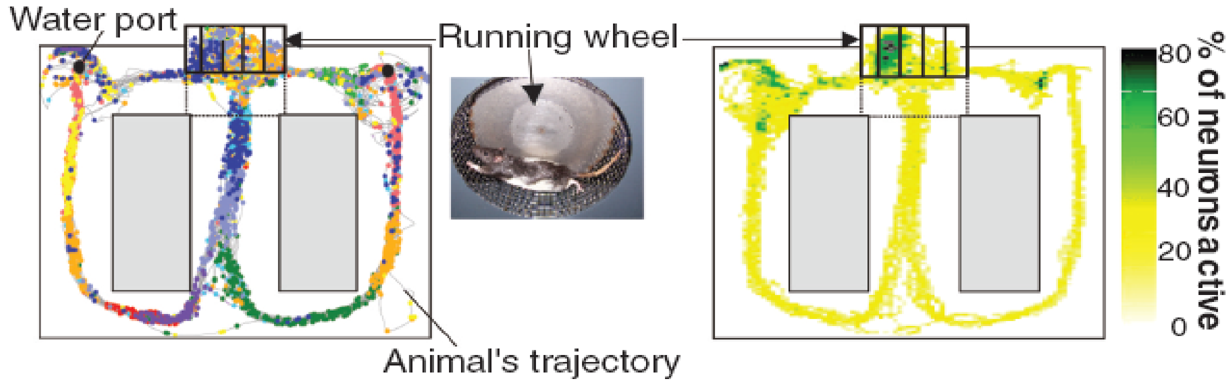
Coding of place is not everything: Gating of auditory responses by hippocampal place cells



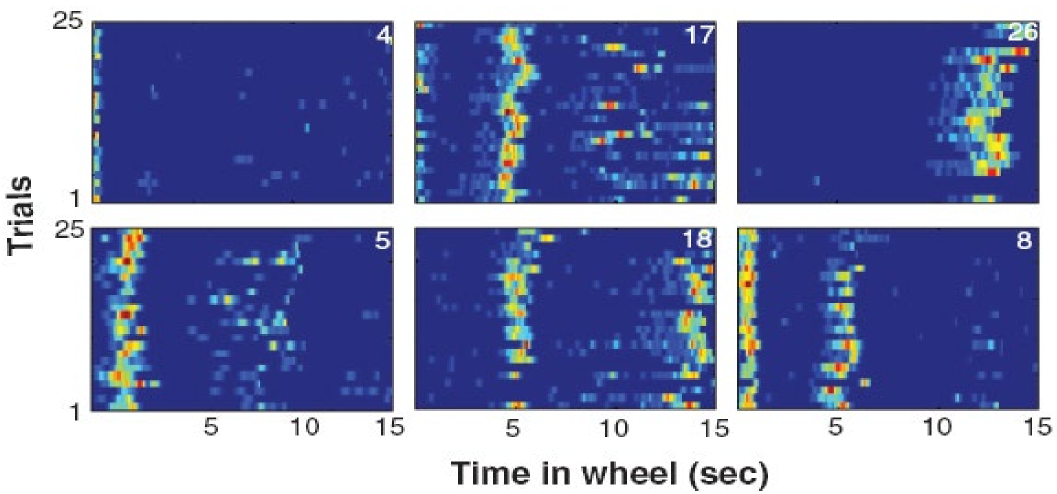
Moita et al., *Neuron* (2003)

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

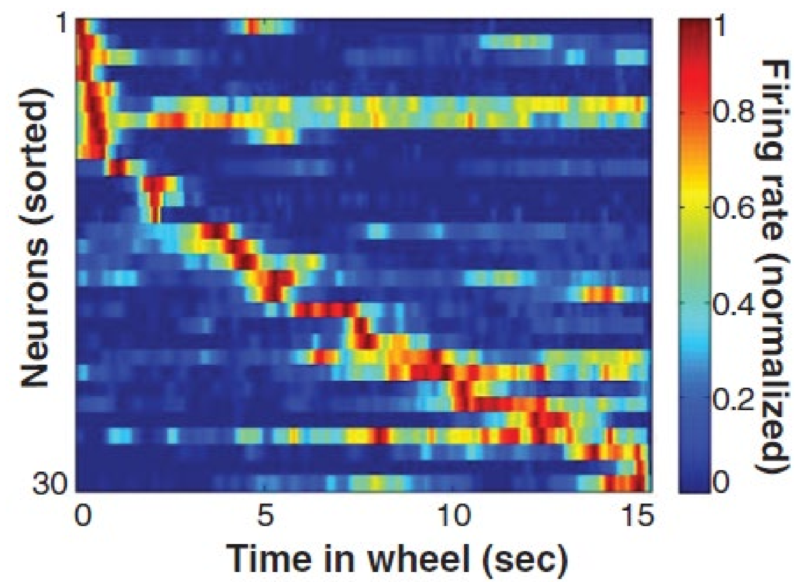
Time cells



Six neurons over multiple trials

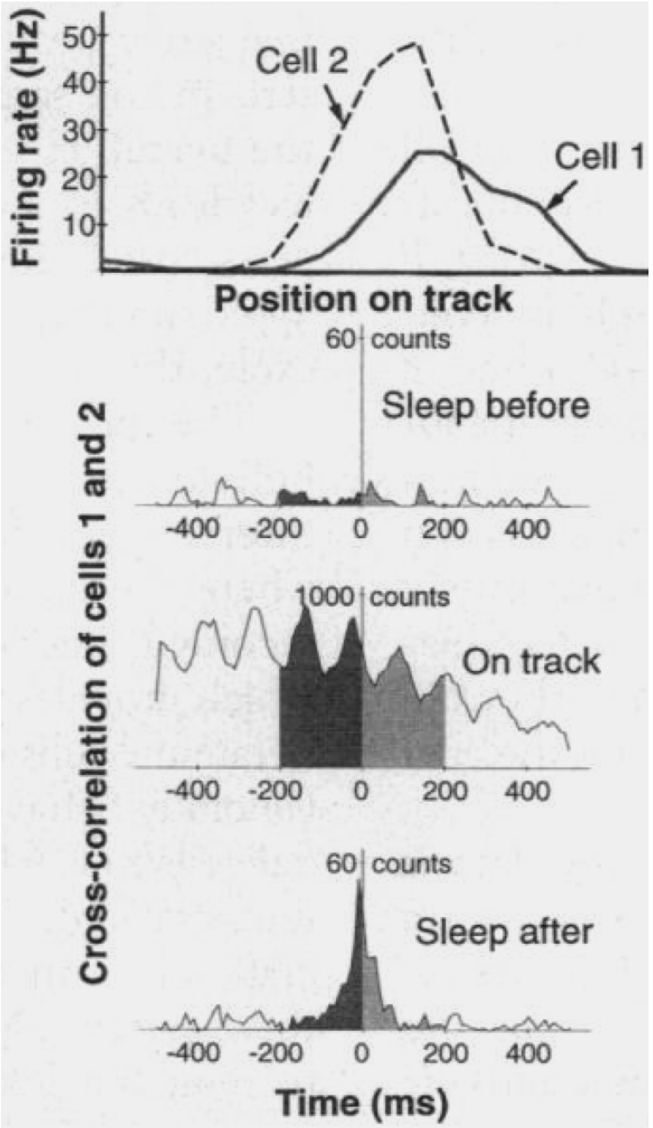


Simultaneously-recorded ensemble of 30 neurons



Pastalkova et al. , *Science* (2008)

Place cells and memory consolidation during sleep

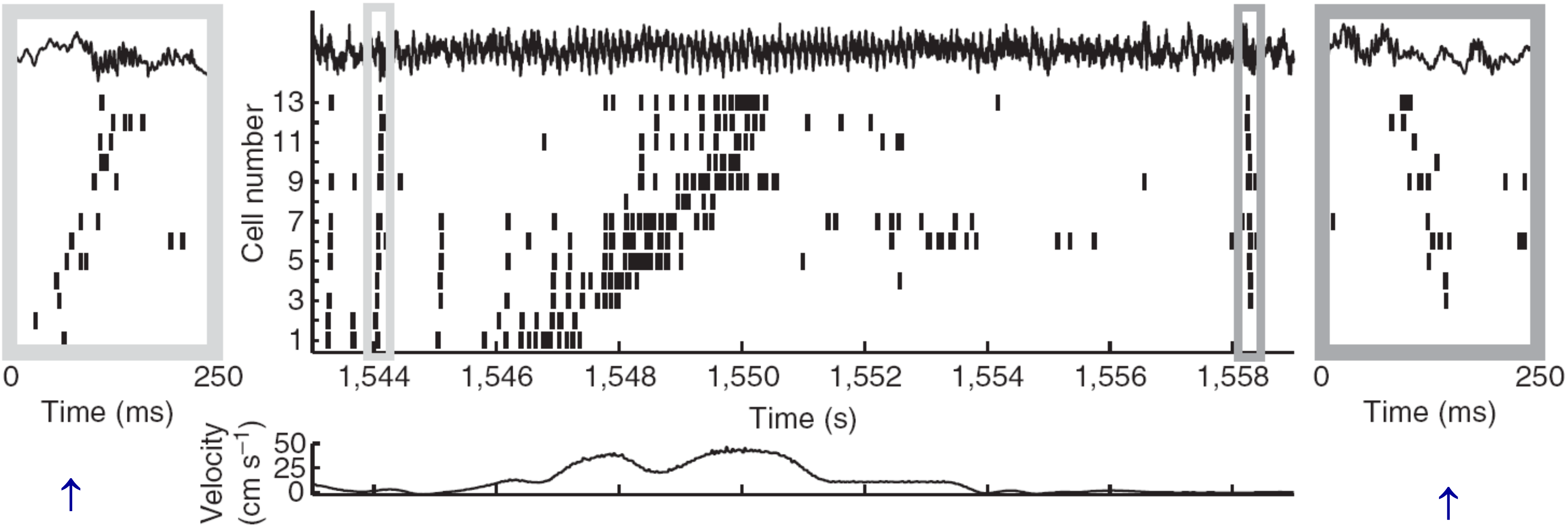


Increased correlations during post-behavior <u>sleep</u> periods, for <u>pairs</u> of cells that were activated together on the linear track.

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

Skaggs and McNaughton, *Science* (1996)

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



↑ Preplay event (*usually* forward)

↑ Replay event (*usually* backward)

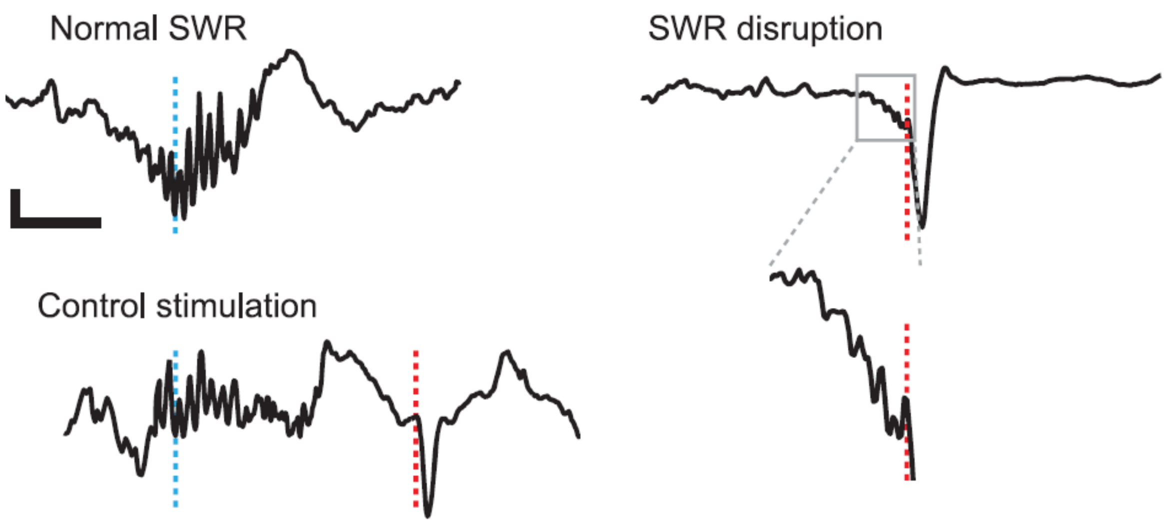
- Cells ordered according to their order of activation during *running*.

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

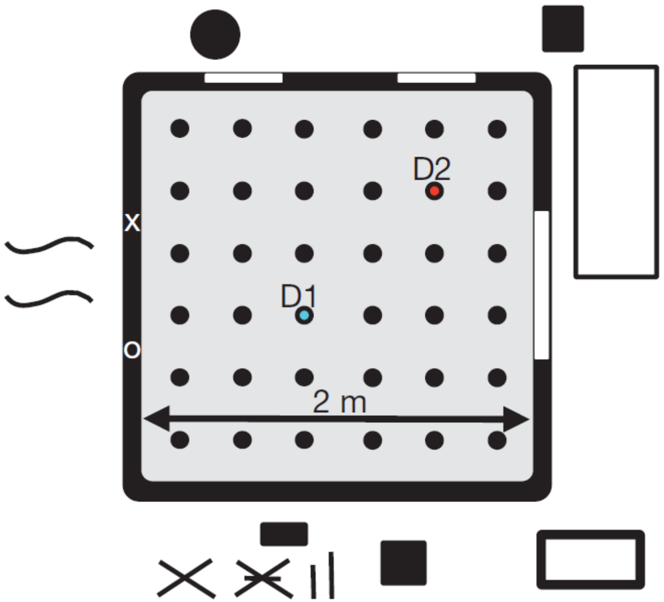
Replay and preplay of sequential activity of hippocampal cells, during pauses in behavior: A substrate for memory consolidation?

- 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

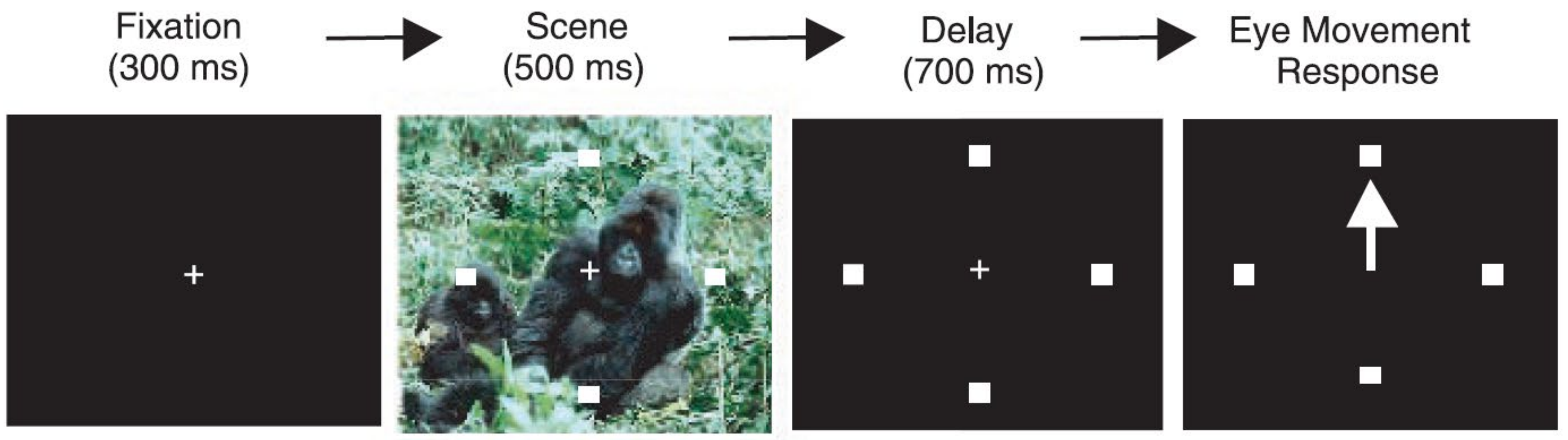
D2: *Home* on Day 2

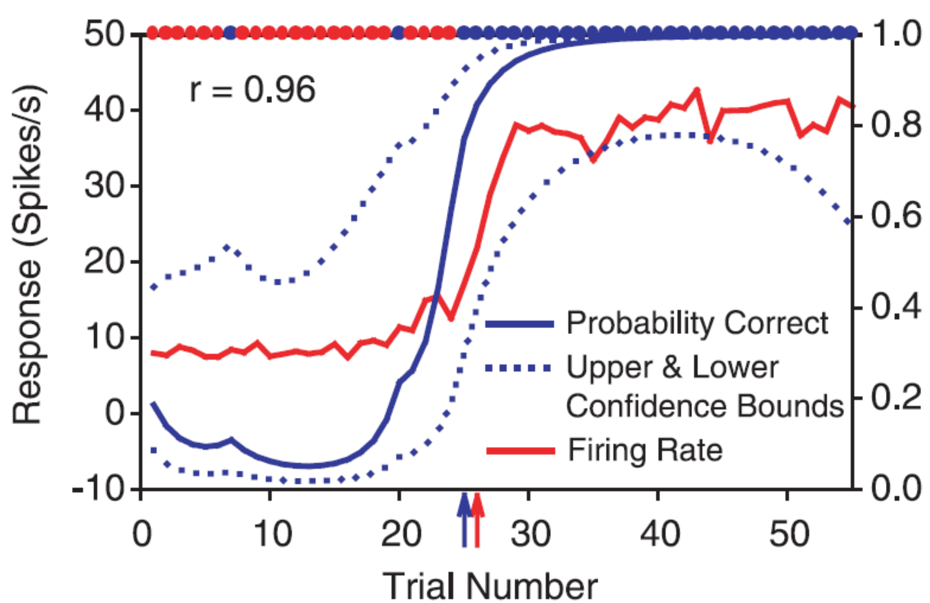
~200 neurons recorded simultaneously with electrophysiology

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

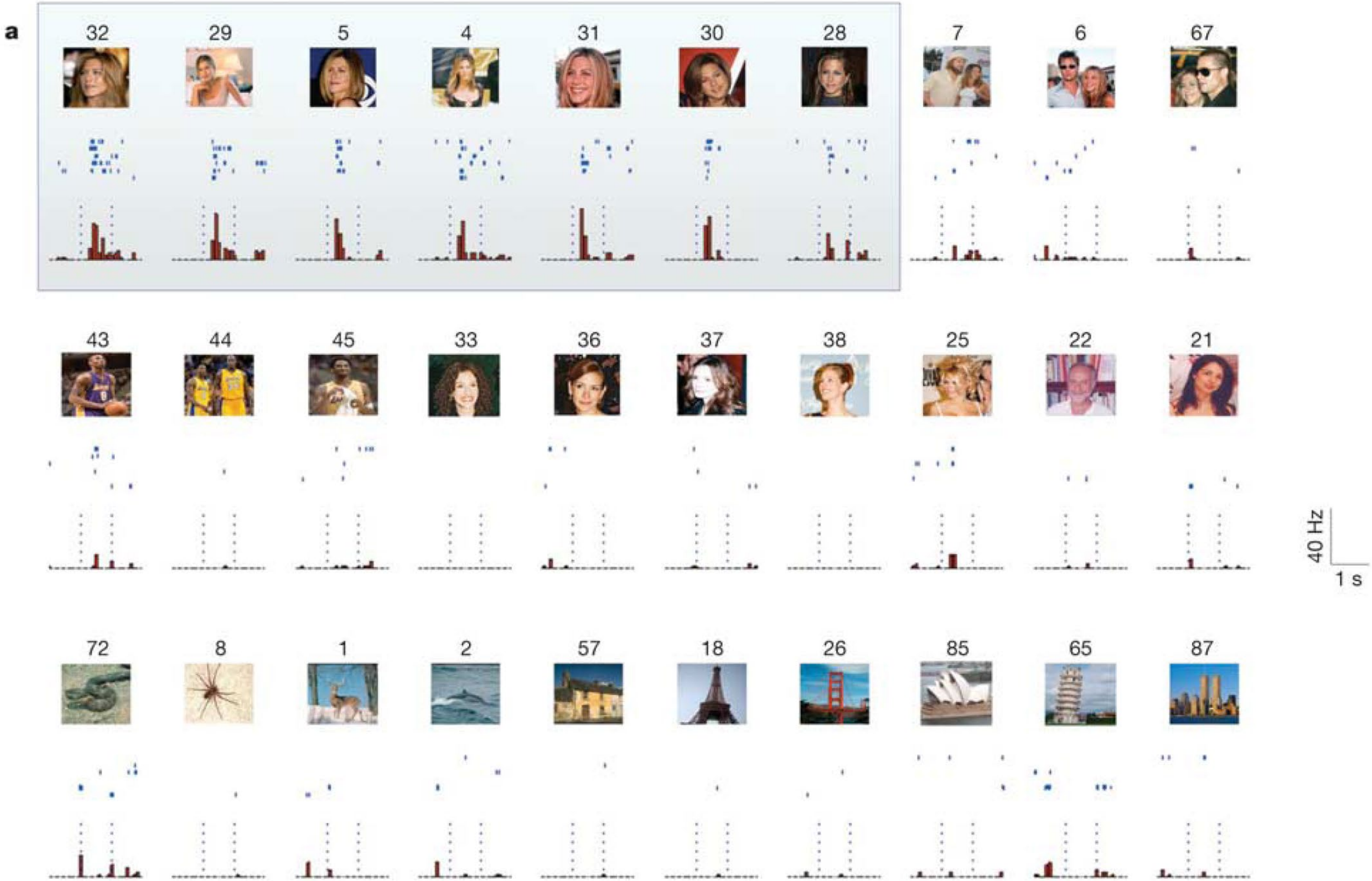




Example of a "changing cell" in monkey hippocampus, which increased its responses simultaneously with the behavioral "Aha moment" during learning of a new association.

Wirth et al., *Science* (2003)

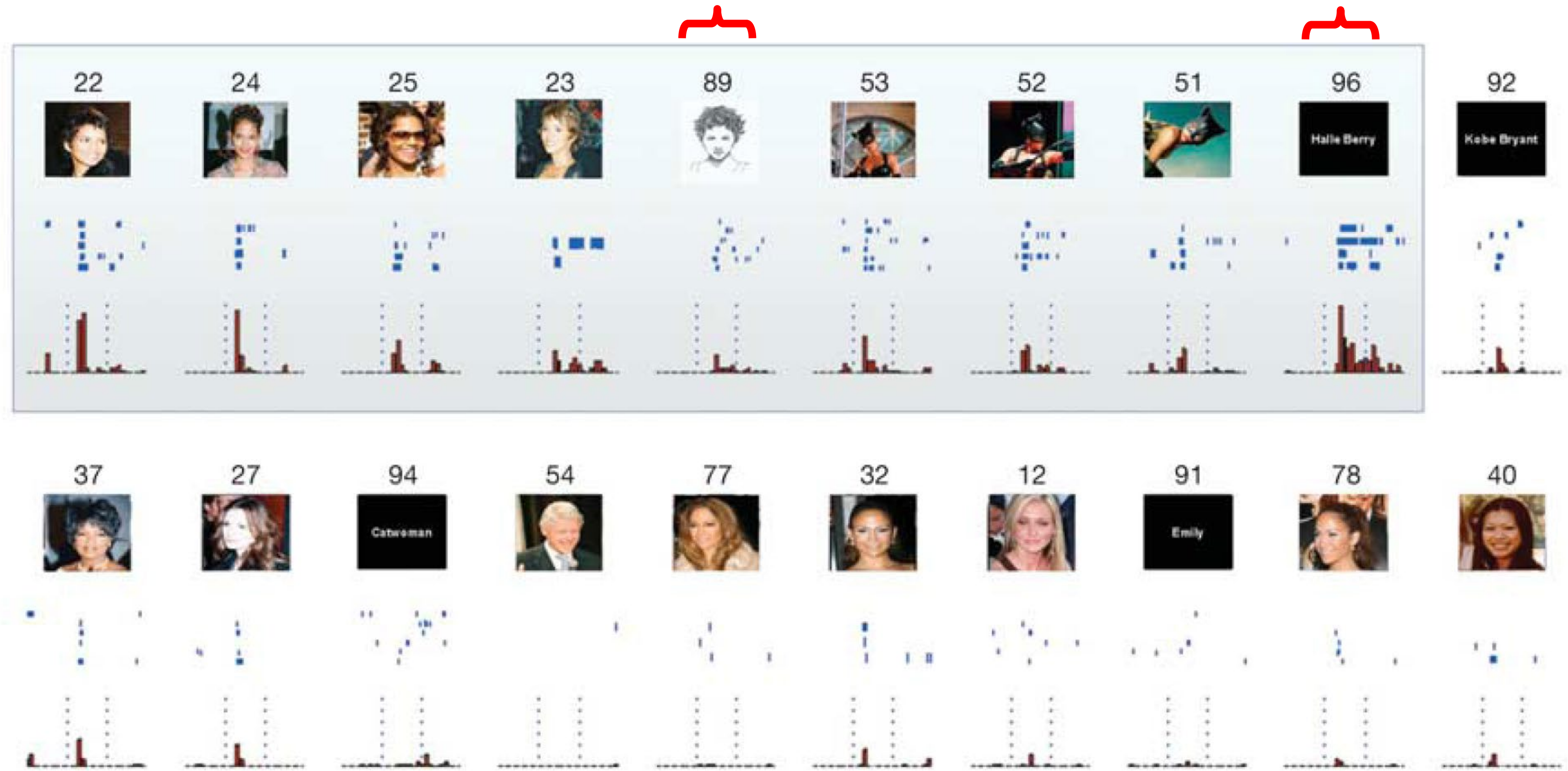
Hippocampal neural activity in humans: Beyond place cells



"Jennifer Aniston cell"

Quian Quiroga et al., *Nature* (2005)

Hippocampal neural activity in humans: Beyond place cells



"Halle Berry cell"

Quian Quiroga et al., *Nature* (2005)

Although place-cells were found in human hippocampus (epileptic patients undergoing electrophysiological recordings as preparation for surgery), hippocampal neurons in humans can also show completely different activity patterns – highly specific responses to very different instantiations of the same famous human (or the same famous building). → **Social cells ? Concept Cells ?**

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

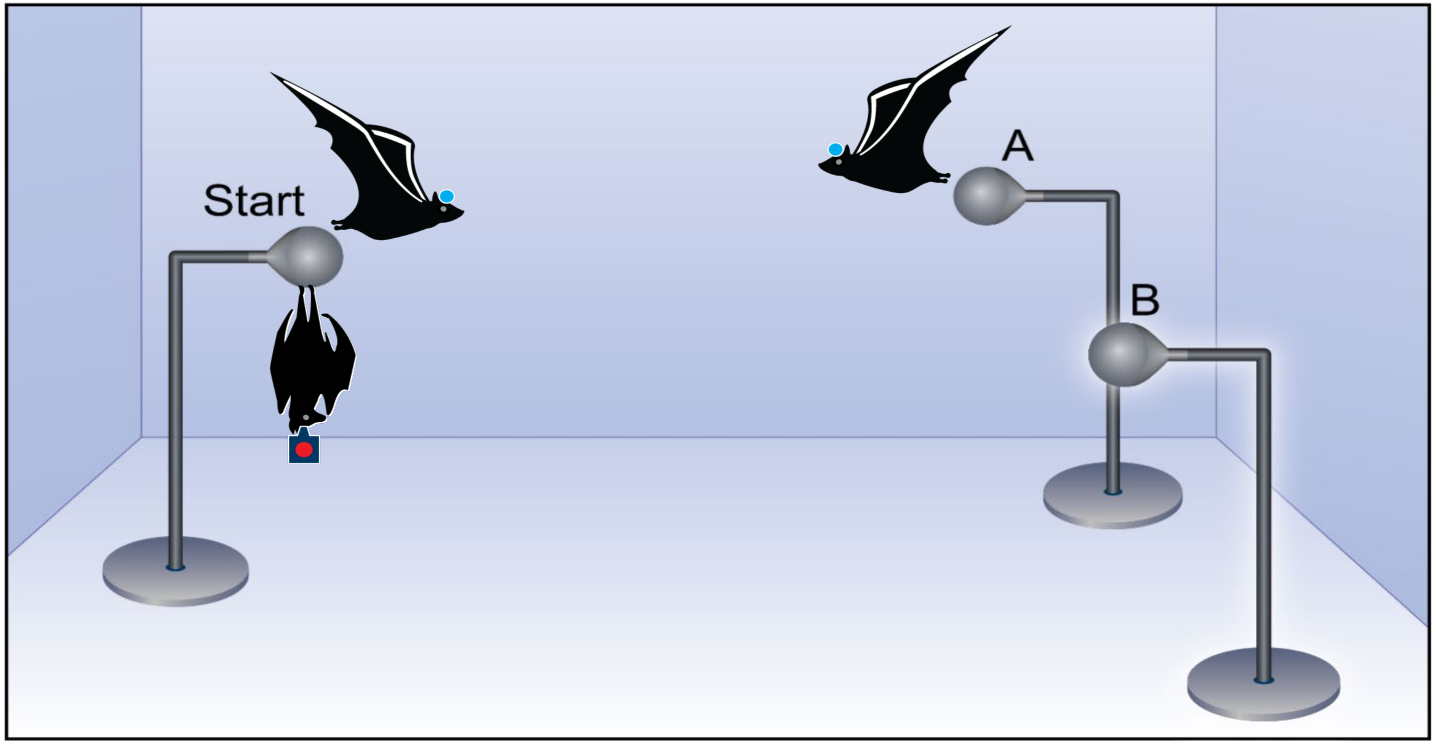
Social place-cells in the bat hippocampus

Bats are highly social mammals

A delayed-match-to **place** task

Wireless
neural recordings
in the hippocampus

Step 1: Other bat flying

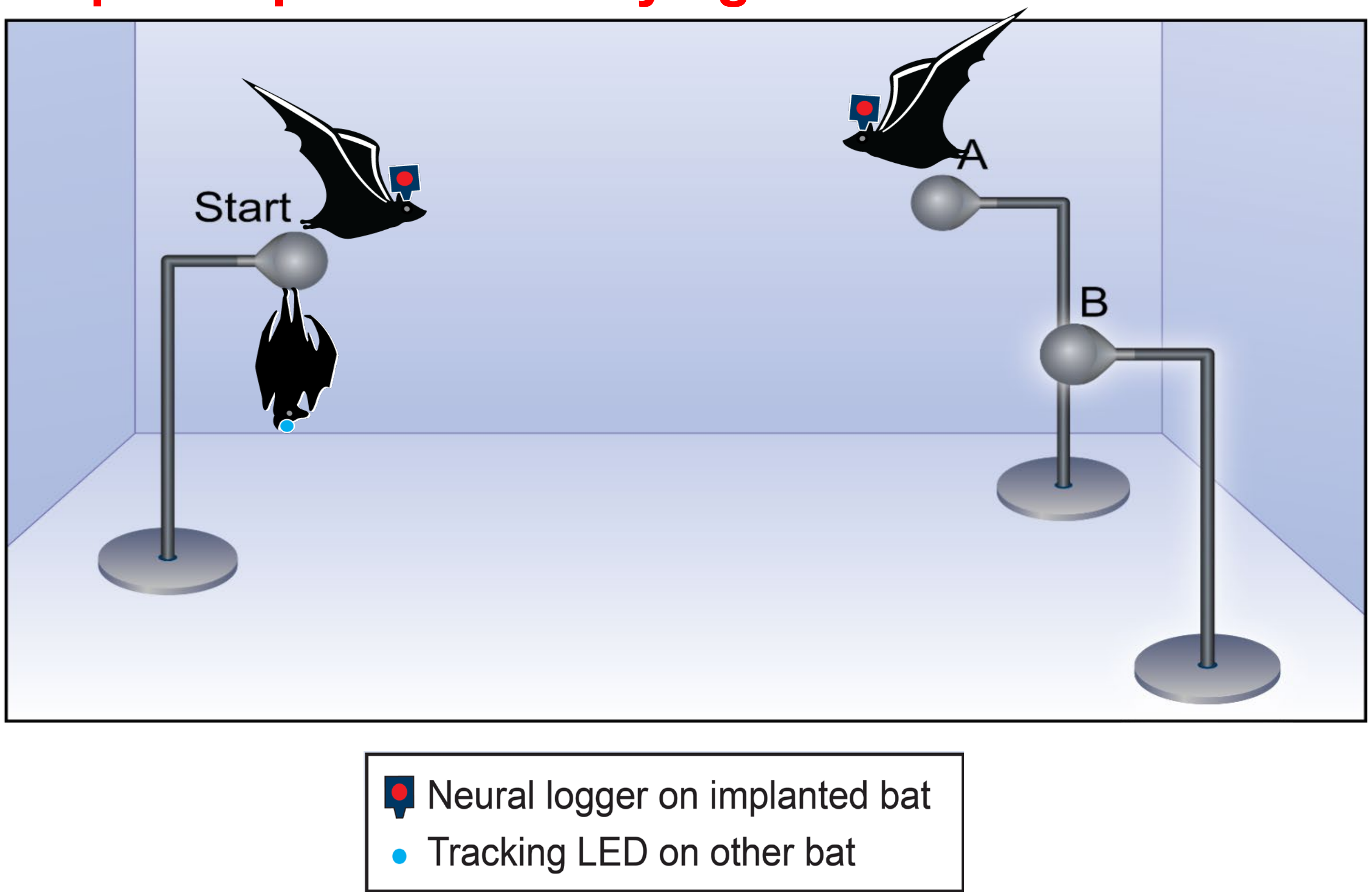


Neural logger on implanted bat
Tracking LED on other bat

A delayed-match-to **place** task

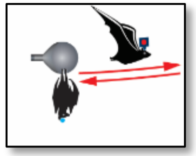
Wireless
neural recordings
in the hippocampus

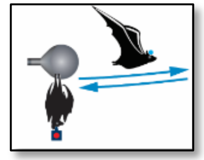
Step 2: Implanted bat flying



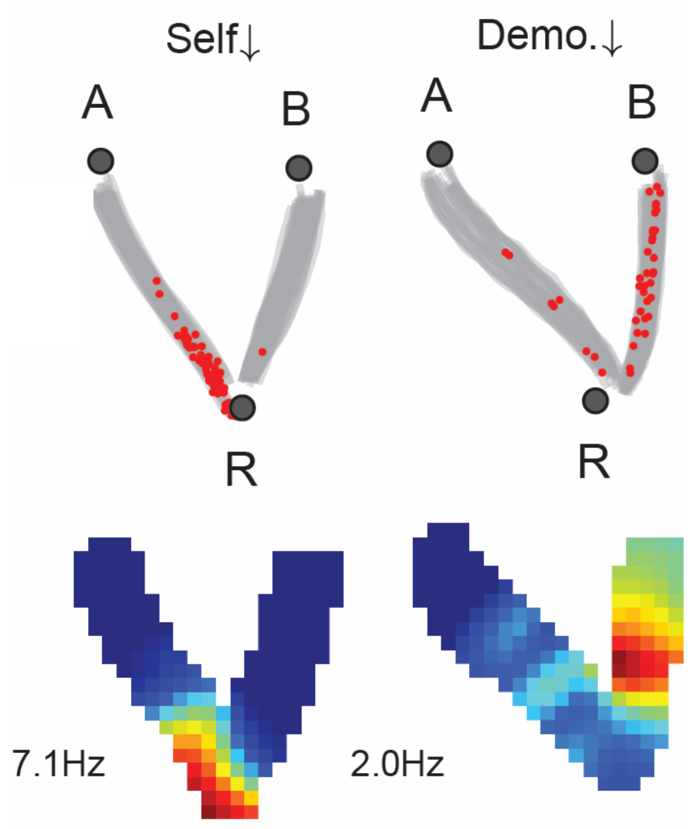
Example of a social place-cell in bat hippocampus

Observer flying





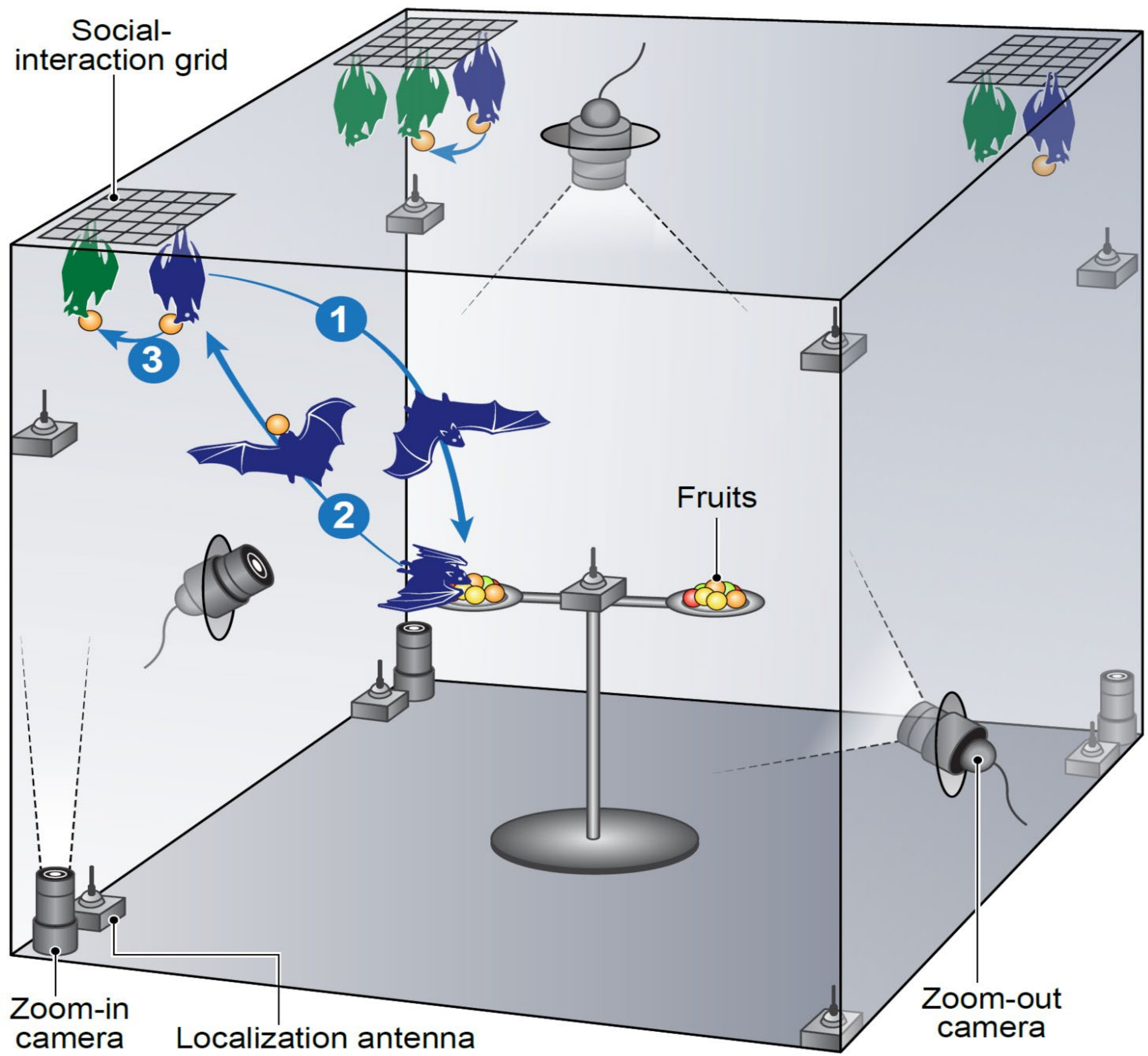
Demonstrator flying



- 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…

Omer et al., *Science* (2018)


Social-
interaction grid
1
2
3
Fruits
Zoom-in
camera
Localization antenna
Zoom-out
camera

Saikat Ray

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 !

Nachum Ulanovsky

nachum.ulanovsky@weizmann.ac.il