

Cognitive Neuroscience Space

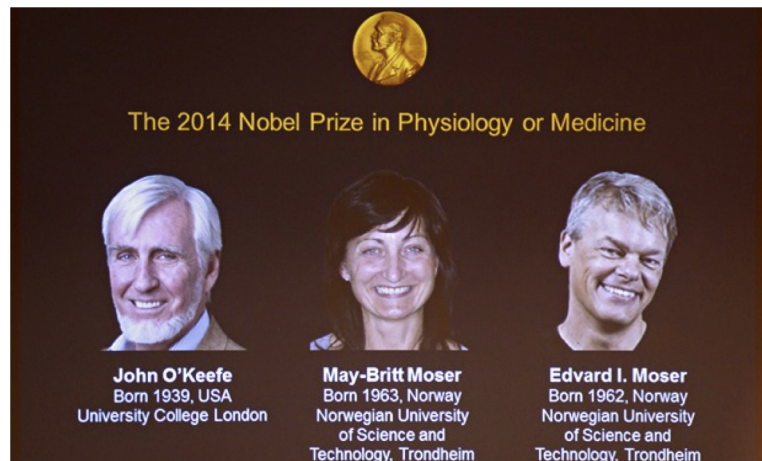
Cinzia Chiandetti, PhD
A.A. 2019-2020

1CFU

Hippocampus

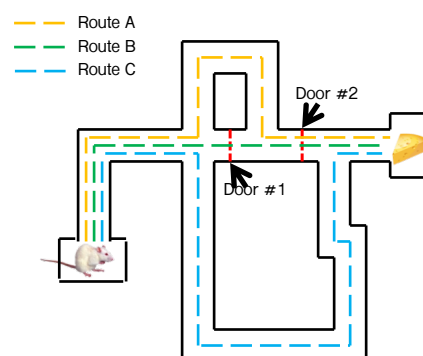
1. Electrophysiological data
2. Neuropsychological data
3. Specific animal model
4. Lesioning studies

GPS in the brain



Latent learning

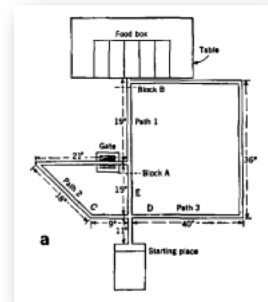
- Type of learning that is possible without a reward, rather thanks to a mental representation –or cognitive map– of the solution
 - it is formed after several trials and errors



Latent learning

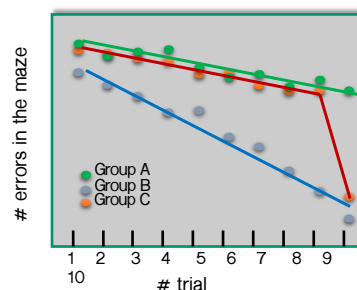
- Tolman & Honzik (1930)

- 3 groups of rats were placed 10 times (one per day) in a maze from which they had to escape
- Group A: no reward at the exit
- Group B: reward every time they found the exit
- Group C: no reward for the first 8 trials; reward at the 9th trial



Latent learning

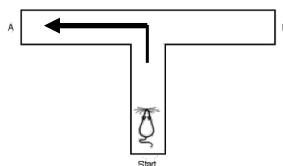
- At the 10th trial?
 - Group A: several errors at every trial but a general improvement of the performance over time
 - Group B: the n. of errors decreases faster than in group A
 - Group C:
 - Trials 1 to 9 - they behave in the same way of group A
 - At trial 10 - they behave as group B



Latent learning

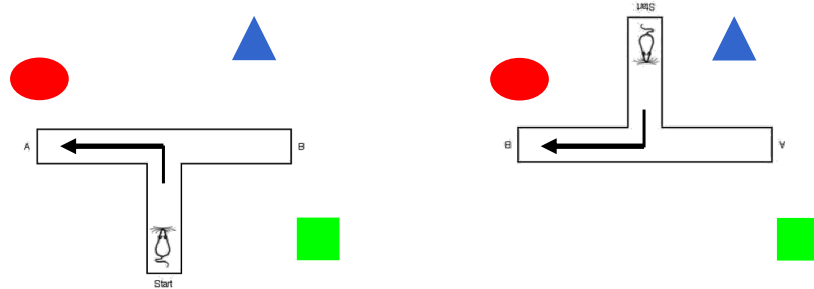
- rats of *group C showed latent learning*: in the days preceding the reward they created a mental map of the maze
- rats who did not get the reward, did not use the info acquired during navigation until there was a reason to do so (e.g., the presence of the reward): the reward is important **for the learning to show up**
- Goals are fundamental: the learning is evident only when the behaviour or the action has a goal; even if the performance does not change during the trials, or it seems by chance, this does not mean that the animal is not learning properties and features of the environment

Cognitive map



Tolman vs. Hull

Cognitive map



Tolman vs. Hull

Cognitive map

- Tolman
 - proposed that rats learn comprehensive maps of their environments, which can guide flexible goal-directed behaviors
 - coined the term “cognitive map” and speculated how these maps might underlie psychological functions

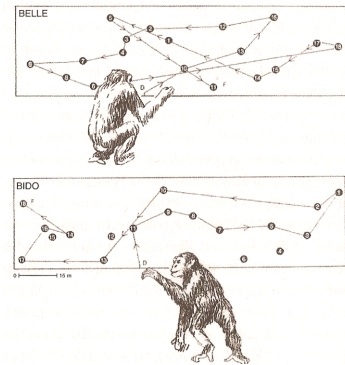
Cognitive map

- the cognitive map is a mental representation that lies in between the stimulus and the response
 - the behaviour is regulated by intentions
 - this means that the animal behaves in a certain way in order to get a specific goal or in virtue of a certain reason; it is not just or solely mechanically guided by external stimuli: there is something in between
- Such internal variable is used by the animal to anticipate the consequences of its behaviour *and to choose* how to behave in order to get to the target

Cognitive map

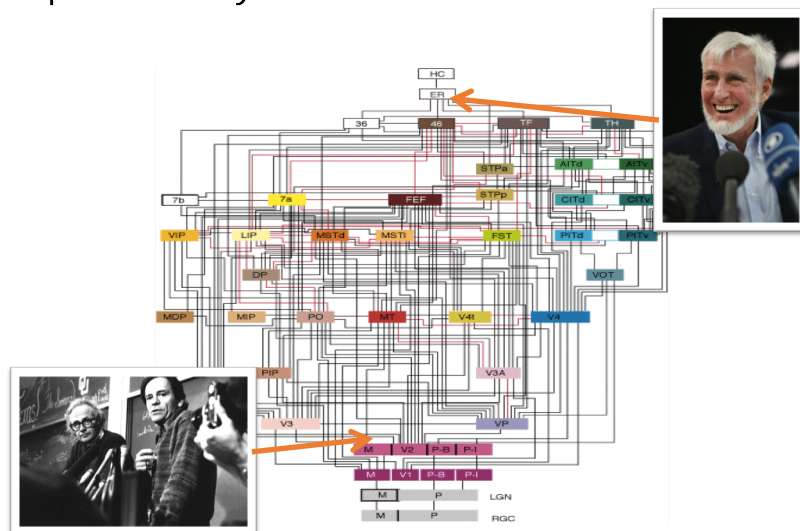
- **There are several advantages in possessing such allocentric representation of the environment:**
 - the organism can navigate using shortcuts – since there is an accurate memory of several reference points, they can be connected and the shorter route can be chosen (Dennet 1996)
 - the organism can reach the target position by initiating the navigation from virtually all possible starting places – since there is an accurate representation of the relations between the separate landmarks (Tolman 1948)
 - the organism can optimize the route (Menzel, 1973)

Cognitive map



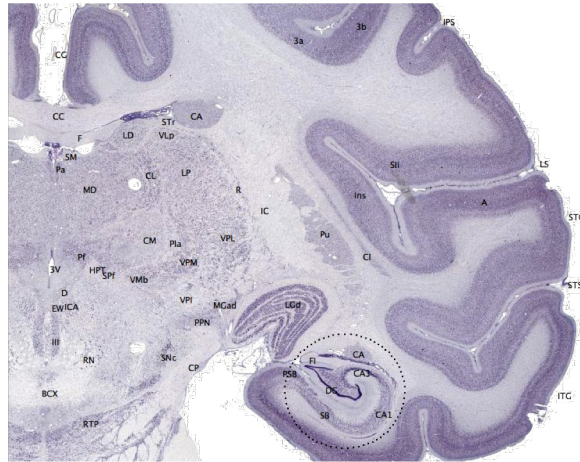
Menzel, 1973

Visual pathways

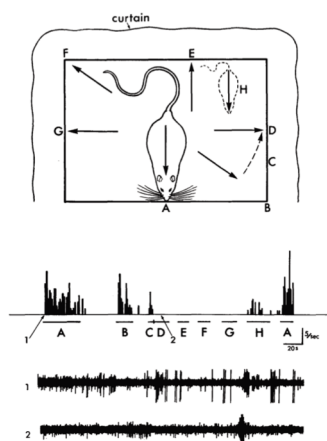


Fellman and Van Essen, 1991

Hippocampal circuit



The “revolutionary” study



- *“These findings suggest that the Hippocampus provides the rest of the brain with a spatial reference map...it could not learn to go from where it happened to be in the environment to a particular place independently of any particular route (as in Tolman’s experiments)”*

O’Keefe & Nadel

www.cognitivemap.net

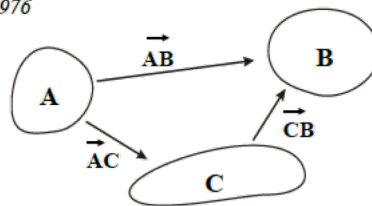


THE
HIPPOCAMPUS
AS A COGNITIVE MAP

JOHN O'KEEFE
AND
LYNN NADEL

Spatial map

O'Keefe 1976



topology



topology

- Topology, in its specific meaning within geometry, expresses the possibility of defining a place devoid of all metric attributes, but comprising the concepts of
 - order
 - enclosure
 - adjacency
- Piaget and Inhelder (1956) proposed that children initially represent space only in topological terms
 - the conception of metric, instead, would emerge only after the shift from a egocentric to an allocentric representation
- Nowadays we know that this idea is incorrect, since it has been demonstrated that even young infants, early in development, represent and respond to metric information (for a review, see Newcombe & Huttenlocher, 2000)

topography

- It is really doubtful that animals' navigation is topological because notions of
 - direction
 - distance
 - elevation
 - size
- are used to move from and towards important places (see for examples Gallistel, 1990)
- while moving and approaching a target, an animal has to perceive the distance and the direction of its own position with respect to the landmark, to remember the distance between the landmark and the goal and the intervening direction between those points, and then to implicitly calculate the distance and direction from its position to the goal

Munduruku



- Isolated villages
- Lack of rulers, compass, maps, ...
- Lack formal education
- A few words or phrases to refer to geometrical or spatial concepts

Munduruku

3.2. Geometrical terms

Figures

iroyruy'at	Curved figure, circle
iwaketkut'at	Curved figure

Points and lines

yabi	Dot, point, beginning, end (literally "the mouth of the round thing")
ibucūg	Curve, line (literally "his straight finger")
kadi	Side (literally "bank (of a river)")

Proportions

i'in	Part of
i'in pūg	One part of
ipidase	Center, middle, half (literally "on the mouth/skin of the earth/ground"; The earth/ground occupies the middle layer of the universe according to Mundurukū cosmology)
ipidasesu	Right in the middle
ipidasese	Quarter (reduplication of last syllable of ipidase)

Munduruku

Here/there

bodiku	Over there (literally "right over this side")
bodiweku	From over there (literally "from right over this side")
bodimaku	Exactly there (literally "exactly over this side")
bodimaweku	From exactly there (literally "from exactly over this side")
goku	Right there in front of me
iboce	There (literally "the place over there where he is")
ibocewi	There from (literally "from the place over there where he is")
ijoce	Here (literally "the place here where he is")
ijocewi	Here from (literally "from the place where he is")

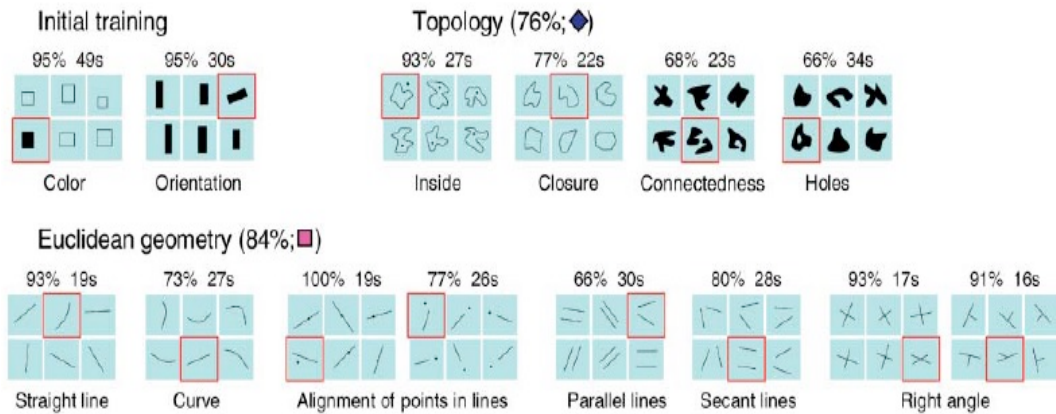
Near/far

ijastūn	Near
wuy jijā	Far

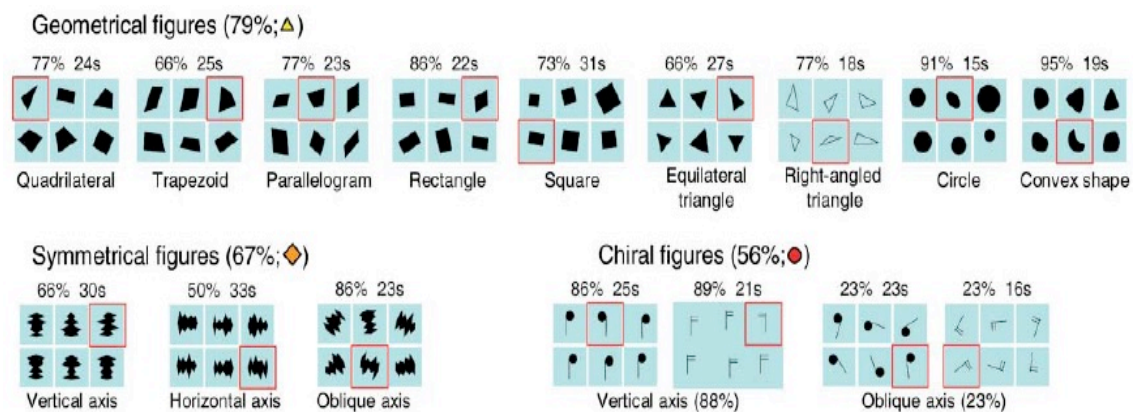
Directions

kaxi jem ap	Sunrise, east (literally "the place from which the sun rises")
kaxi a cap	Sunset, west (literally "the place at which the sun declines")
tiakay	Upstream (literally "to the water")
deim	Downstream (literally "the place of those who leave downstream")

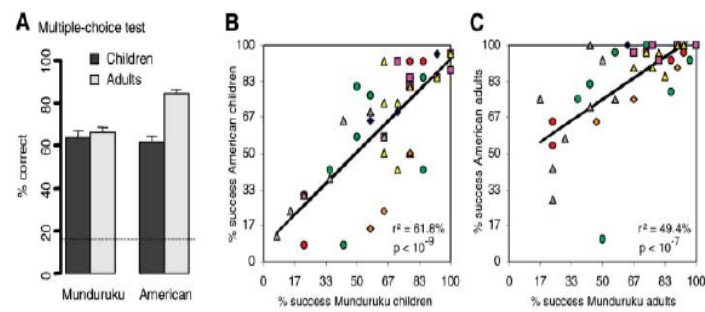
Munduruku



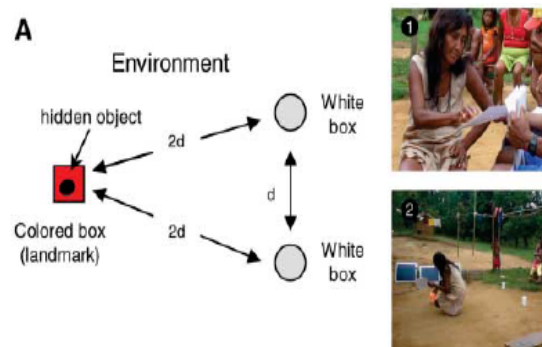
Munduruku



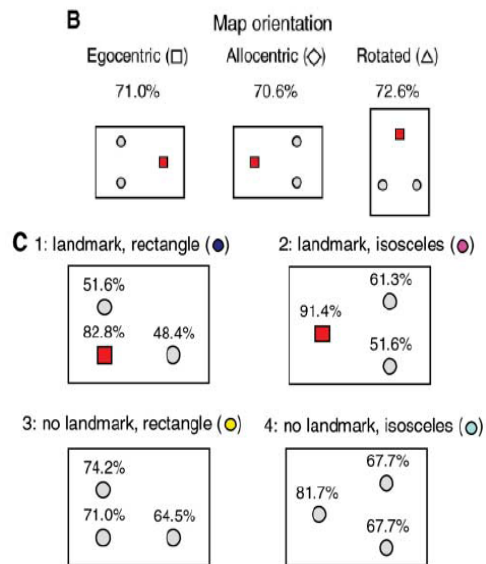
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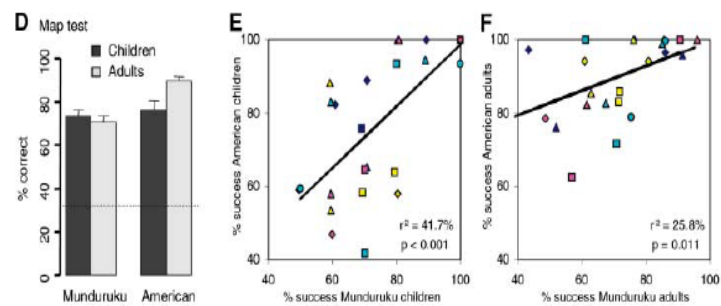
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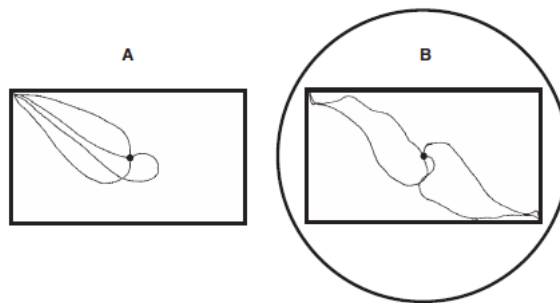
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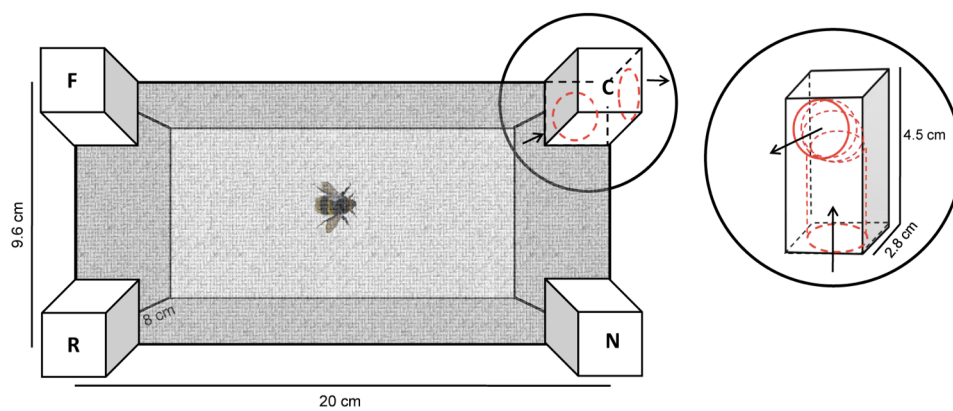
Munduruku



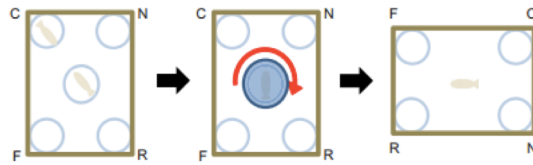
Geometric module



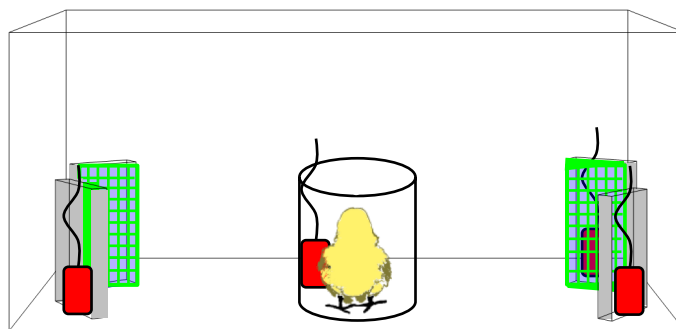
Geometric module



Geometric module

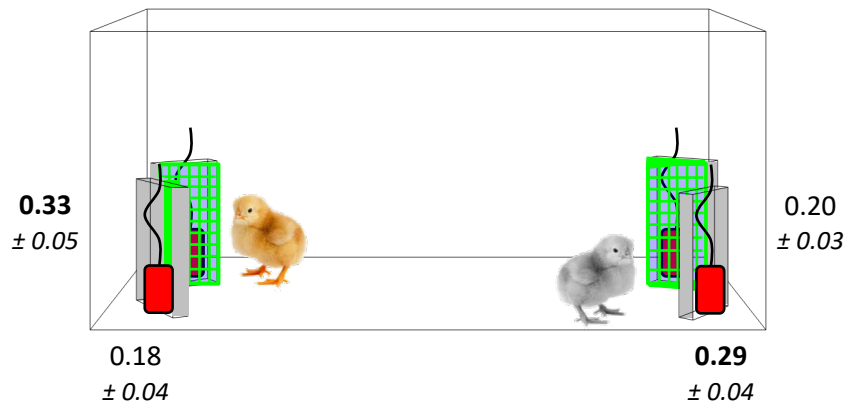


Geometric module task



Chiandetti Spelke Vallortigara, 2015

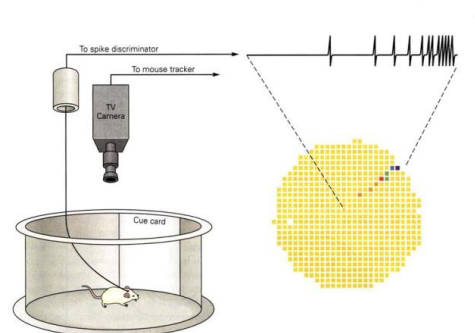
Geometric module task



Chiandetti Spelke Vallortigara, 2015

Place cells

- the rat moves around freely in an open arena
- some neurons become active as the rat reaches a specific place in the arena
- different place cells are activated in different places
- their combination creates a map of a specific environment



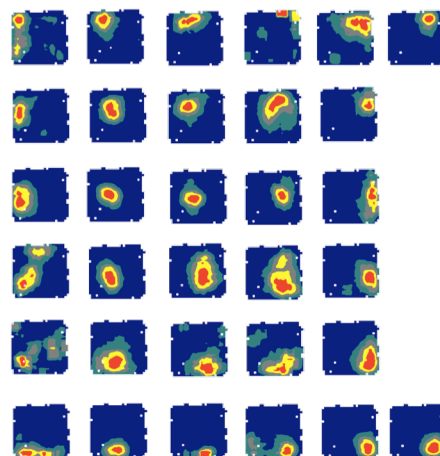
Place cells



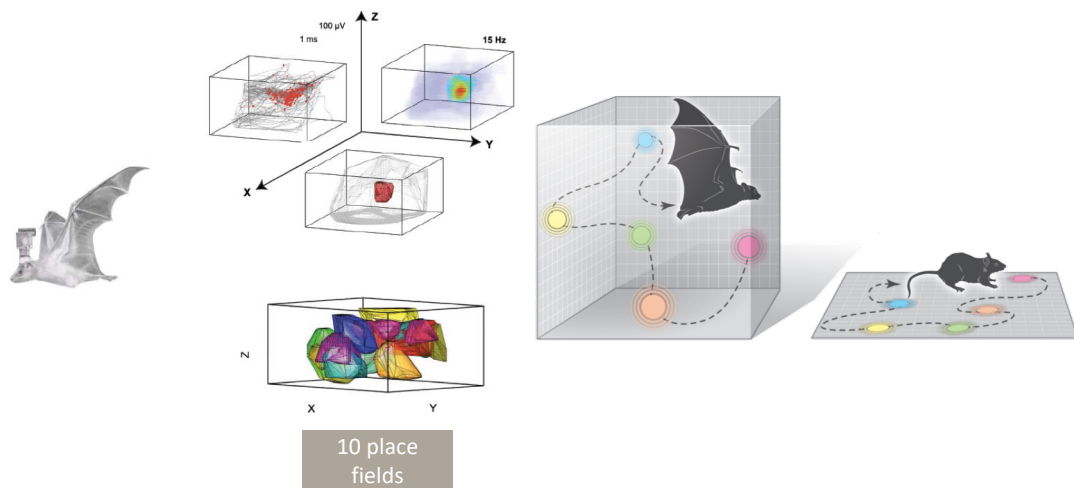
- Place cells are generally only active when an animal occupies the cell's preferred location.
- These cells were proposed by O'Keefe and Nadel as a potential neural substrate of Tolman's cognitive map

Place cells

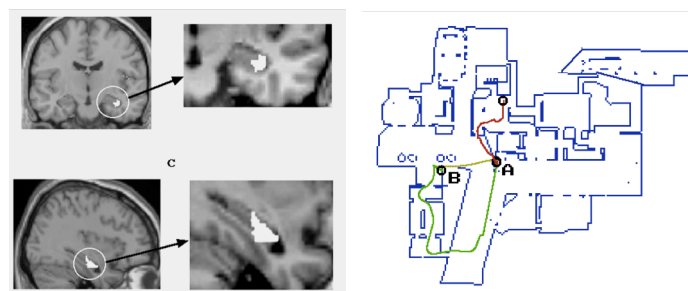
- Pyramidal cells in CA1
- place fields are established within minutes
- cells tend to be stable over repeated exposures to the same environment
- there is always an active cell in a certain position: the whole environment is "mapped"



3D representation

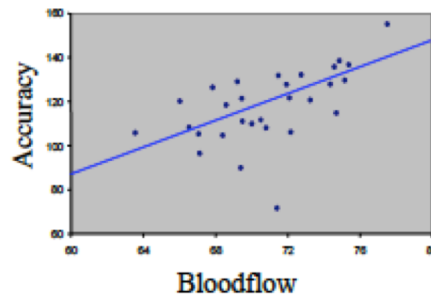


Place cells – the virtual town



Place cells

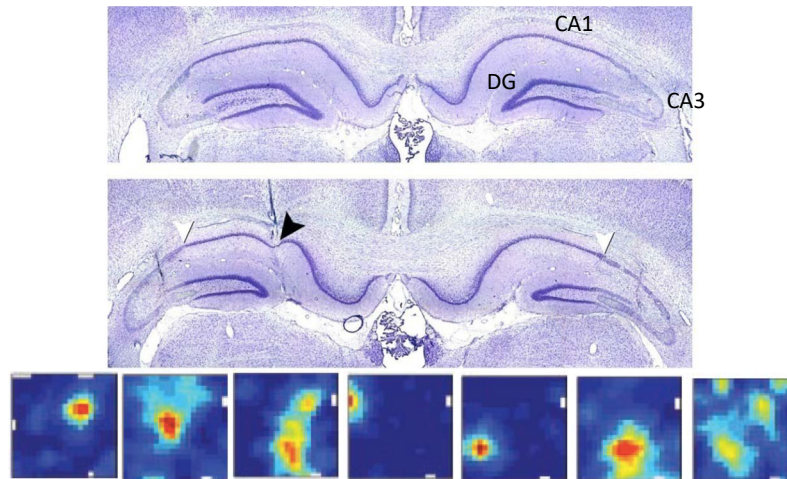
- the more the navigation is successful (mental planning and route following allow to reach the target area) the more blood arrives at the hippocampus



Place cells

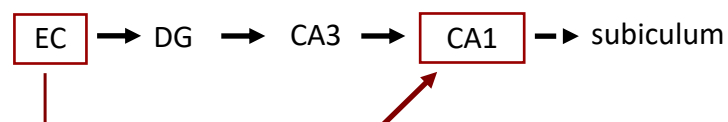
- In order to understand whether the activity is hippocampus-dependent, the Mosers started considering the connectivity of CA1: they recorded from CA1 after lesioning the areas sending input to the CA1.
 - PCs' activity could show relational properties that are encoded during the spatial learning and not necessarily spatial information *per se*
 - PCs's activity could depend on processing of other areas than the hippocampus (or could depend also by other external areas' activity)

Place cells



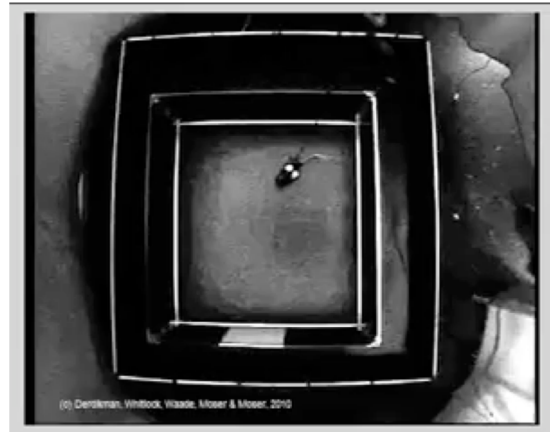
Place cells

- neurons in CA1 show their typical “place field” even after the lesion, suggesting that the source for the signal is external, is outside the CA1



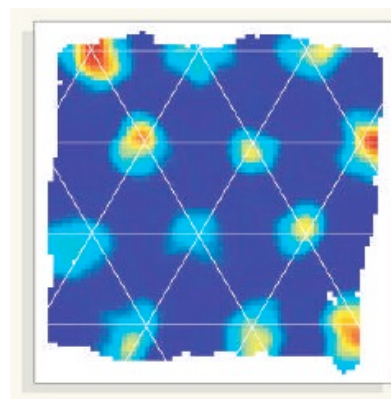
Entorhinal cortex

- the Mosers recorded from the dorsal medial entorhinal cortex, that sends the strongest input to the dorsal hippocampus where place cells were recorded



Grid cells

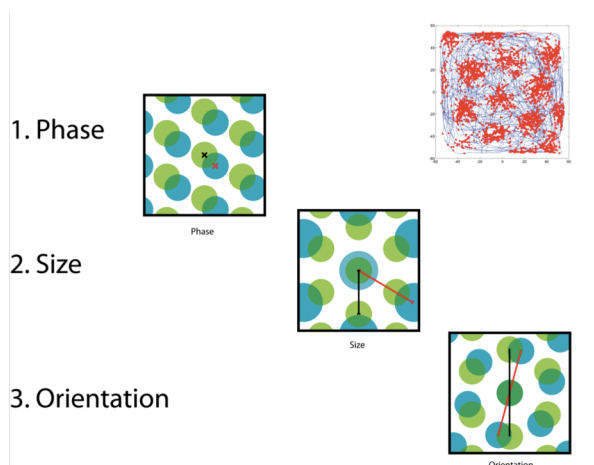
- Entorhinal cells show multiple spatial fields that exhibit a regular pattern
- The fields are organized at a regular hexagonal distance, like a grid, covering the entire space around
- The fields create a sort of grid, a metric map



Grid cells

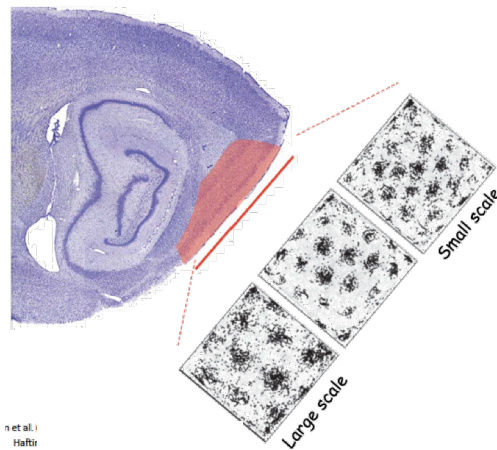
- Grid patterns
 - appear on the first entrance of an animal into a novel environment, and usually remain stable thereafter
 - do not require visual input
 - remain unchanged when all the lights in an environment are turned off
 - when visual cues are available, they exert strong control over the alignment of the grids
 - rotating a cue card on the wall of a cylinder causes grid patterns to rotate by the same amount (rotational remapping)
 - when an animal is moved into a completely different environment, grid cells maintain their "grid spacing"
 - the regularity in grid spacing does not derive from any regularity in the environment or in the sensory input available to an animal

Grid cells dimensions

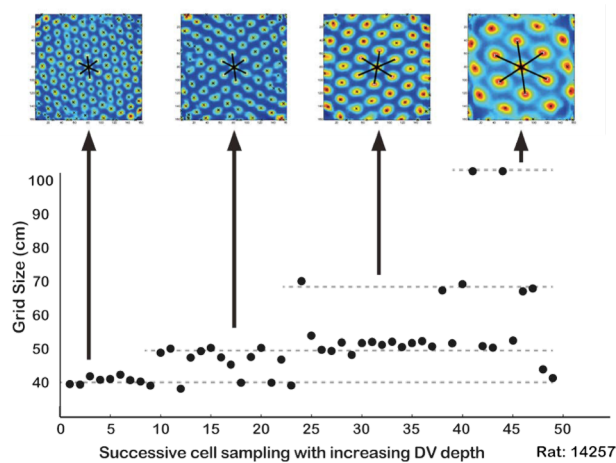


Grid cells: Scale

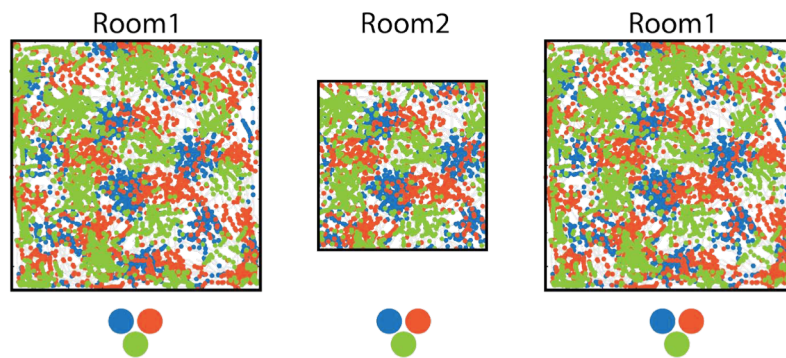
The scale of grid cells (spacing) follows a topographic dorso-ventral organization



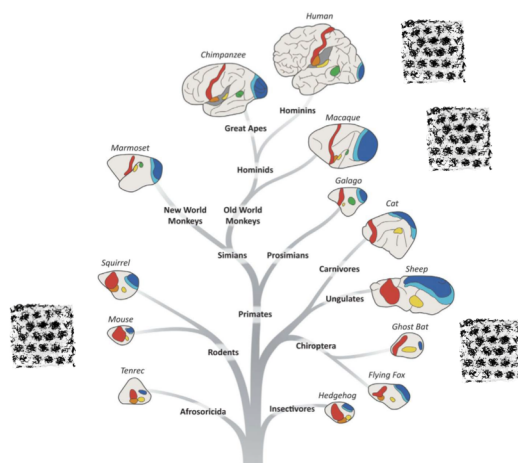
Grid cells: Scale



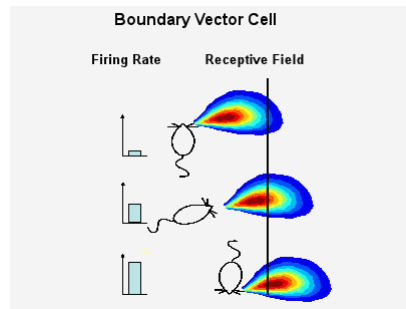
Grid cells: Orientation



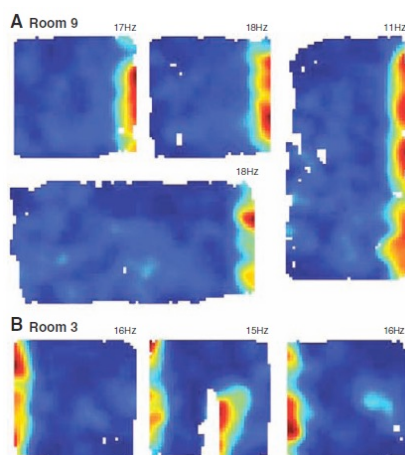
Grid cells: recent acquisition?



Other cells: mathematical model



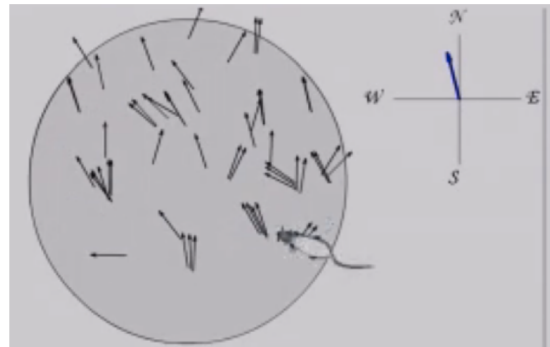
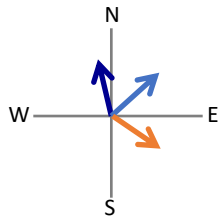
the model anticipated the real data



- Border cells
 - whenever the animal is at a certain distance from a landmark, a border, a wall
 - recorded in the subiculum and the EC

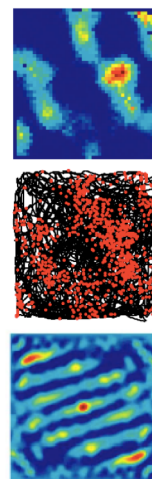
Other cells

- Head direction cells
 - between EC and Hp
 - independently from where the animal is
 - connected one with the other



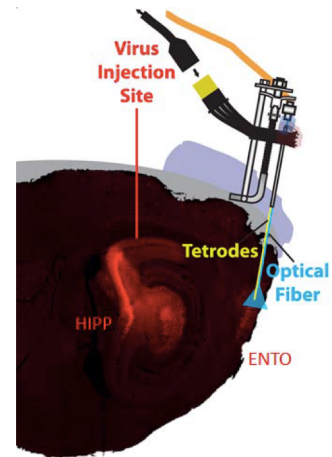
Other cells

- Band-like cells
 - parasubiculum
- probably they support the creation of place cells

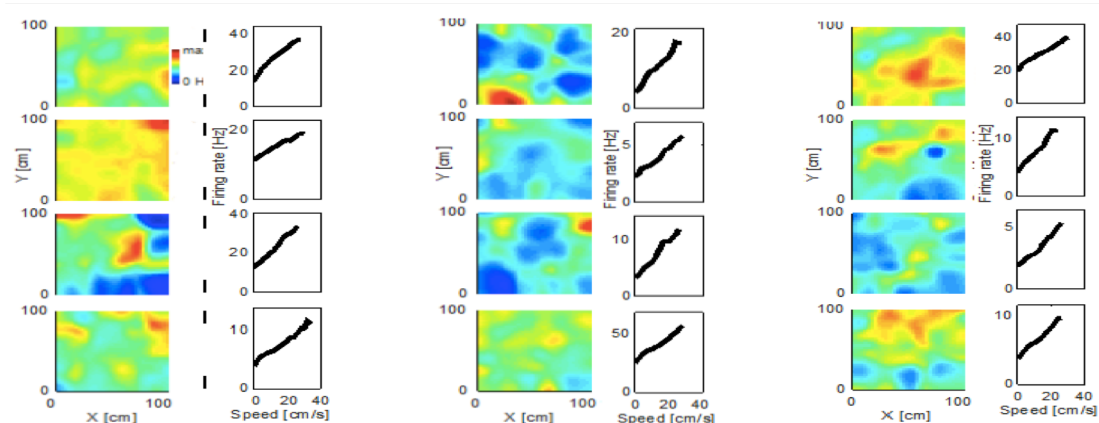


Other cells

- Which types of cells do project to the Hp?
- Grid cells, head direction cells, border cells and **non-spatial cells** responded with a certain latency to the photostimulation, suggesting that they all are hippocampus-projecting

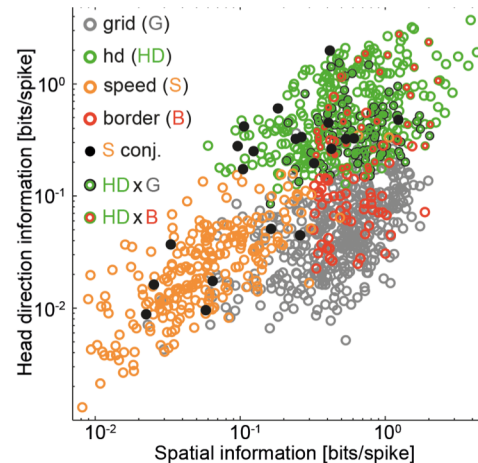


Other cells



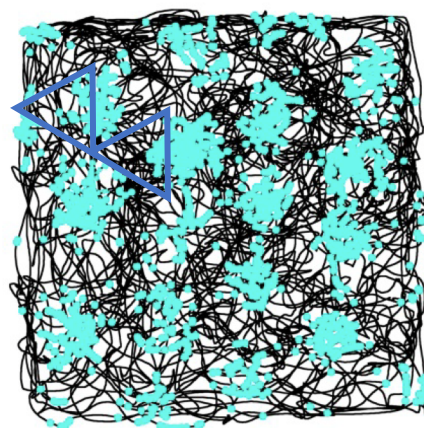
Speed cells

- Within the EC there are also the speed cells
- they update the grid pattern on the basis of the movement of the animal (distance=speed*time)
- discharging frequency follows the running velocity



Other cells

- By the integration of speed and head direction inputs, grid cells can be activated in specific positions



GPS in the brain

- **grid** and **band-like** cells support the creation of a cerebral map that gives the animal a “sense” of space and allows it to direct navigation within the environment following its metric
- **head-direction** cells act as a compass, by pointing toward a certain direction
- **border** cells are activated whenever the borders are encountered
- **TOGETHER** they create a complex network working as a positional system

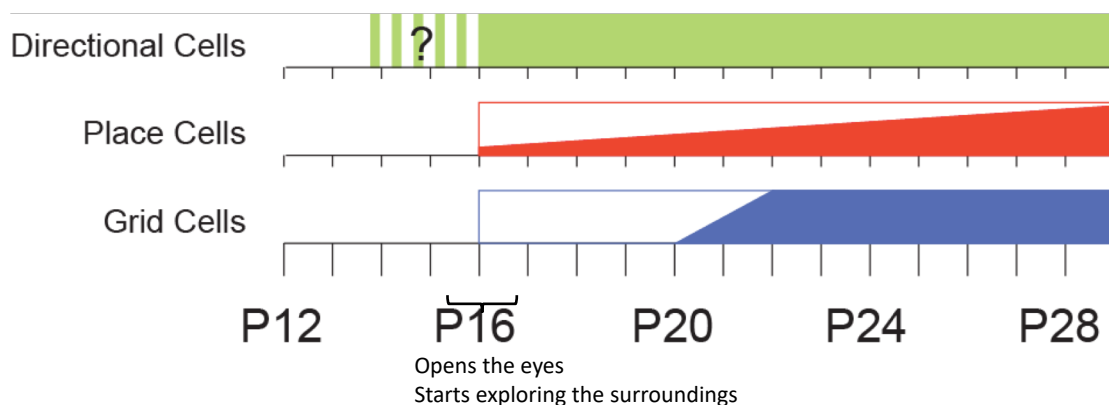
Imaginary navigation

- the same grid cell-like activity has been recently visualized (fMRI) during imaginary navigation, providing the first evidence that that this activity occurs in the absence of actual movements
 - 26 participants had to imagine while navigating a virtual mountainous environment and memorizing the location of a few objects within it
 - and also while just imagining that they were moving through it to retrieve those objects

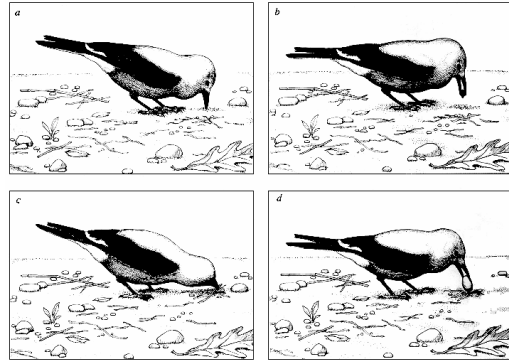
Imaginary navigation

- a signal that is consistent with grid cell-like activity in the entorhinal cortex was observed
 - during the navigational task
 - but also during periods when the participants merely imagined navigating through the environment to retrieve what they had seen earlier
- This suggests that grid cells not only track our movements during spatial navigation, but also contribute to path planning, perhaps by moving the viewpoint of the imagined environment

Ontogenesis



Hippocampus

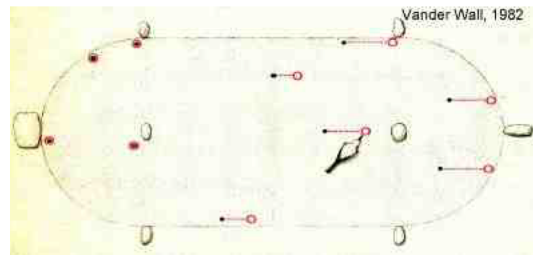


Hippocampus

- Are they using a simple rule?
 - ok, but then competitors could find them
- Are they remembering each single site?
 - safer strategy
 - but...thousands of coordinates in memory?

Hippocampus

- they memorize the hiding positions using *landmarks* (salient visual features)
- thousands of memory traces
- are they geniuses or do they possess a specific advantage? -> comparison between food storers and non-storers



Hippocampus

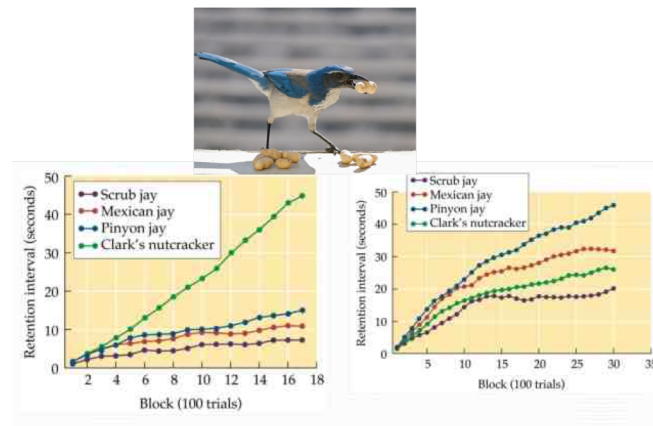
SPATIAL TASK

- find a reward on the basis of the position
 - two identical boxes, you have to learn if it is hidden in the one on the right or on the left

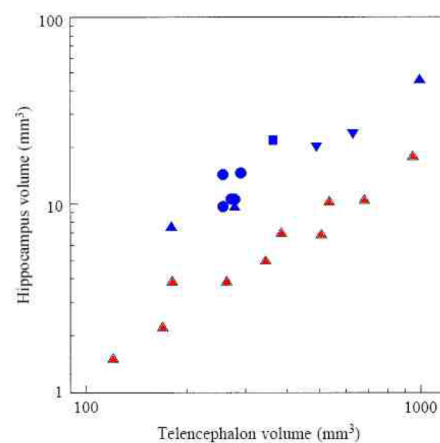
NON-SPATIAL TASK

- find a reward on the basis of a visual feature
 - two identical boxes that differ in colour, you have to learn if it is hidden in the green or the yellow box

Hippocampus

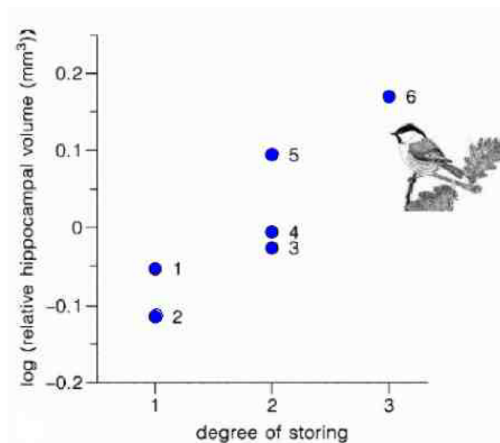


Hippocampus

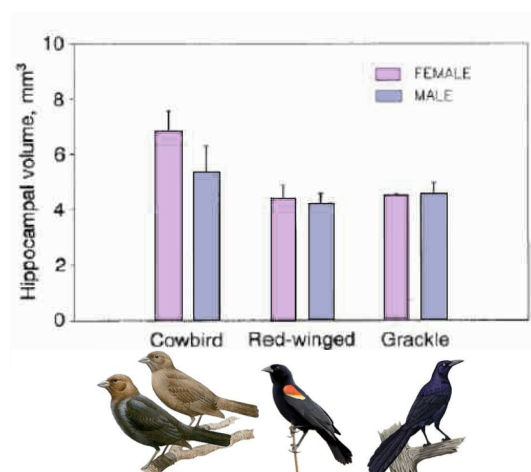


Storers
Non-storers

Hippocampus

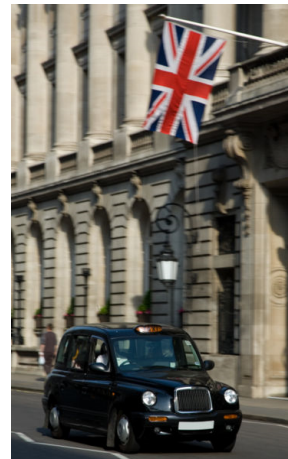


Hippocampus

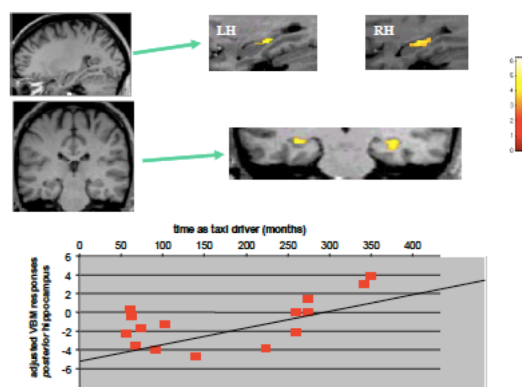


Hippocampus

- There is a human job requiring the very same ability that food storers have...
- guess...



Hippocampus



Maguire 2000

Hippocampus

- Taxists' brains were compared to those of participants of similar age, gender, socio-economical position...just doing other jobs
 - expansion of the posterior part of the Hp (involved in the formation of the cognitive map of the environment)
 - with a reduction of the anterior part (this has not been observed in the birds' brain)

Hippocampus



- Control group?
 - Comparable for
- ✓ experience of driving
- ✓ stress levels
- ☒ fixed routes

The Hp does not show the same increment

Hippocampus

- Let's go back to the storing behaviour of food storers
 - if the Hp is selectively lesioned, the storing itself is not compromised
 - what is compromised instead is the retrieving capability
- This means that motor skills and motivation, are independent from the Hp functionality which is crucial only for spatial memory

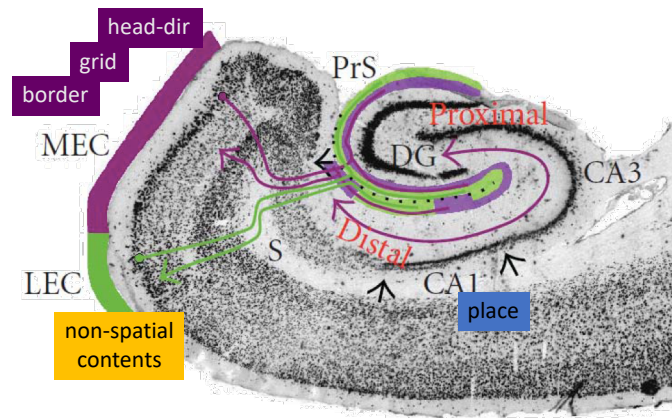
Hippocampus: space or memory?

"After operation this young man [H.M.] could

- no longer recognize the hospital staff
- nor find his way to the bathroom
- and he seemed to recall nothing of the day-to-day events of his hospital life"

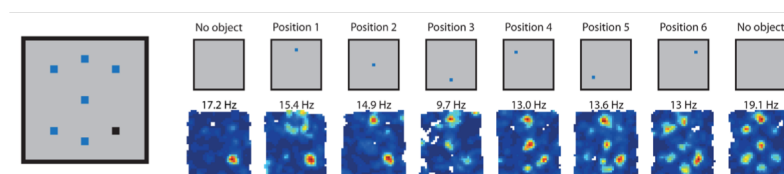


Entorhinal cortex (Medial and Lateral)

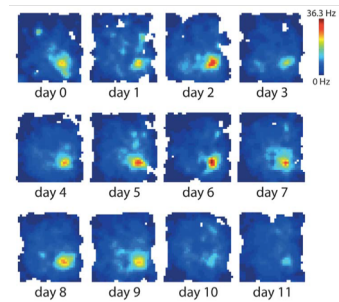


Entorhinal cortex (Medial and Lateral)

- By changing the position of an object, it leaves a memory-trace field in lateral entorhinal cells
- In every position, a trace field emerges one trial after the object presentation
- The trace fields accumulate in the following trials

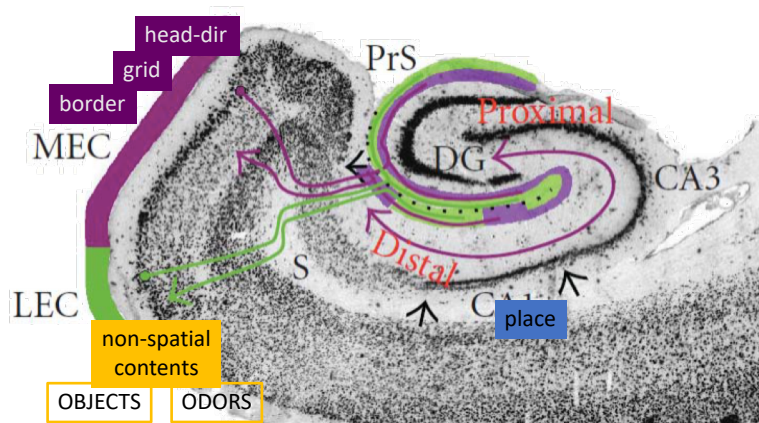


Entorhinal cortex (Medial and Lateral)



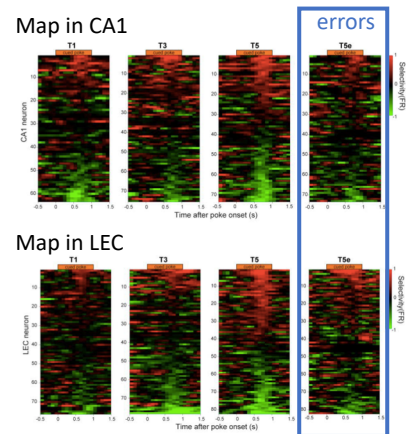
- When the training is prolonged, the trace field becomes persistent, it may last weeks after the first presentation
- the trace cell activity is not a mismatch response to the absence of the object

Entorhinal cortex (Medial and Lateral)



Episodic memory

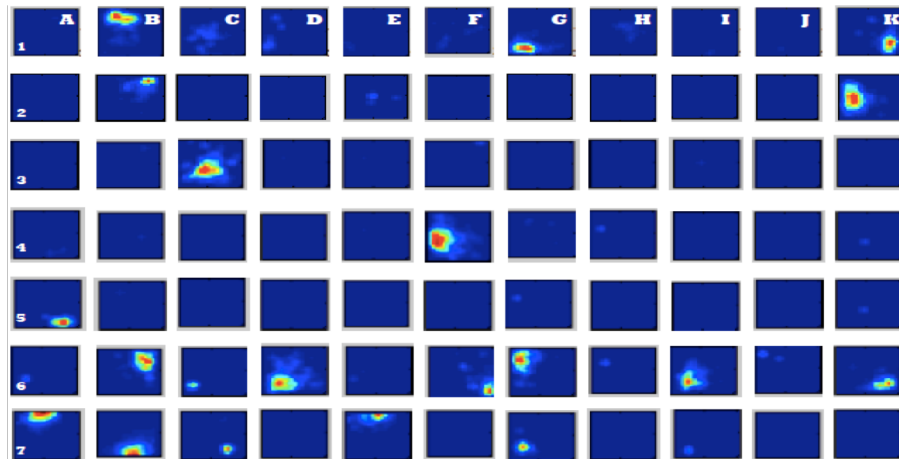
- The rat is trained to feed from container A when it recognizes “banana” and from B when it recognizes “chocolate”
- The number of odor-selective LEC neurons during the sampling of the cue increases during learning
- Selectivity for odors is lost in error trials
- This suggests that the expression of an olfactory map during cue sampling is predictive (maybe necessary) to recall the info



Episodic memory

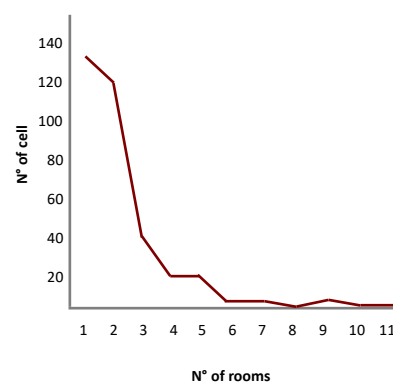
- The association between places and odors could get established thanks to coherent oscillations of Hp and LEC neurons
- The development of coherent activity in dCA1 or LEC could create unions of functional cells during learning, e.g. by making it possible synaptic plasticity. Such “unions” could be at the basis of odor memories.

Episodic memory



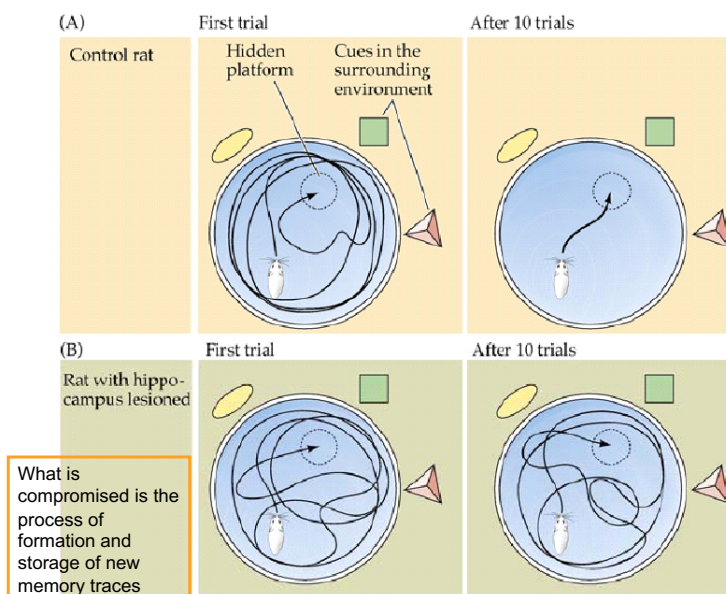
Episodic memory

- Each place cell is active in one or two rooms
- If active in more than one rooms, it has different coordinates in different rooms
- One trial is sufficient to encode the map
- The space is a cue to recall the memory and the memories associated to each space are kept separate

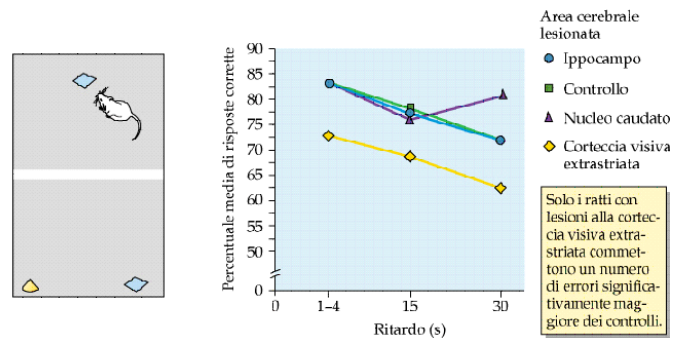


Hippocampus: explicit knowledge?

- he could learn new tasks
 - without being conscious of this learning
- he shows all forms of learning (associative and non-associative)
- he forms new implicit memories

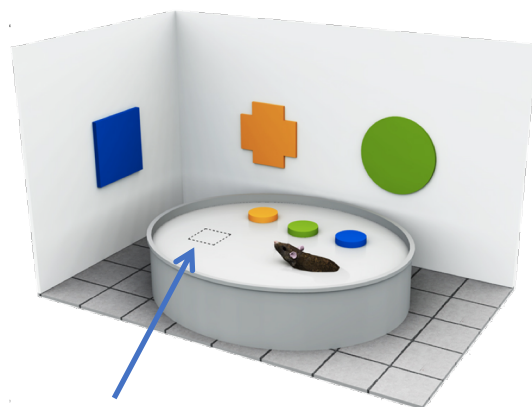


Different areas, different memories



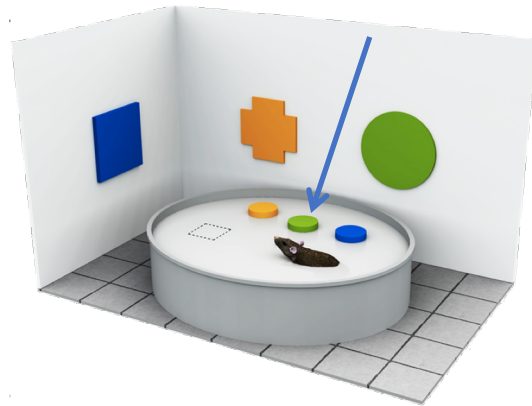
Different memories

- if the platform is not visible (dotted square), the rat uses the configuration of external objects to orient and find the safer position
 - spatial memory



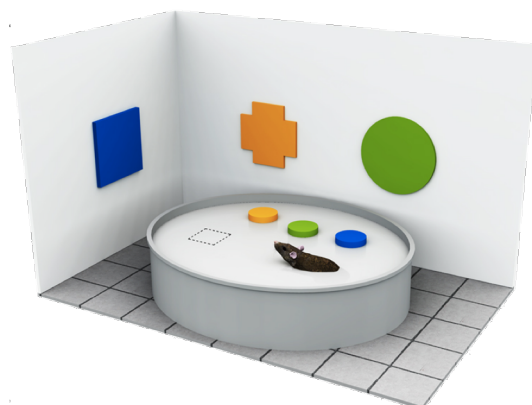
Different memories

- if the platforms are visible (coloured cylinders), and only one floats (the others sink) the rat has to learn to associate a response to a feature
 - procedural memory



Different memories

- the Hp is involved in the first task but not the second
- it learns the relational arrangement between external object not how to discriminate between two alternatives



Place cells and episodic memory

- The place cells
 - seem to encode declarative aspects
 - allowing to discriminate between different contexts in which specific facts may take place
- The Hp, it is not a mere spatial processor, rather it seems a relational processor of declarative memories (referred to facts and events)
- “Episodic memories can be formed by linking successive event representations and episodic trajectories into ensemble patterns stored in hippocampal networks for subsequent retrieval” Bellmund et al., 2018

Delay non-match to sample

