The Hippocampus as a Cognitive Map

Computational Models of Neural Systems

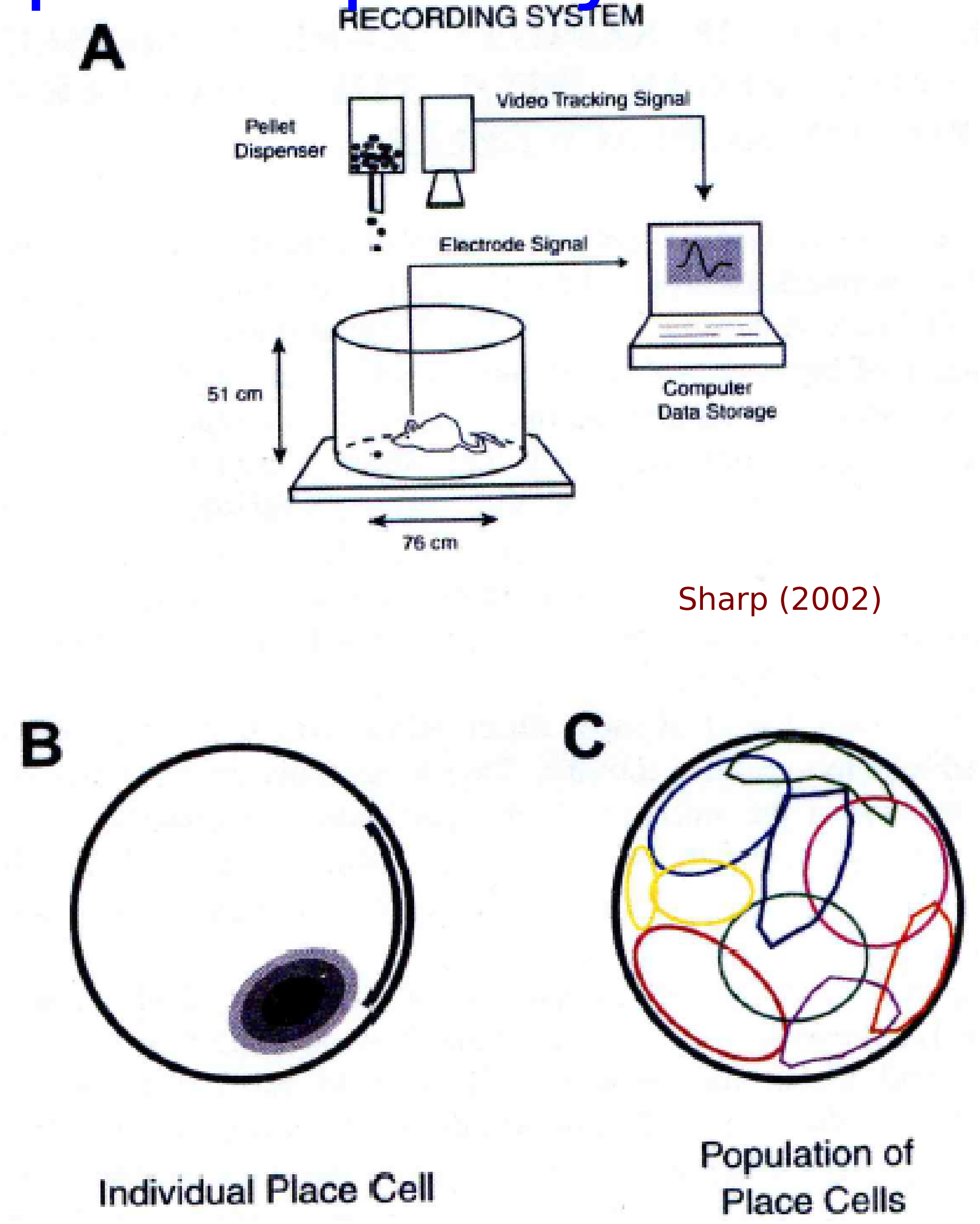
Lecture 3.5

David S. Touretzky

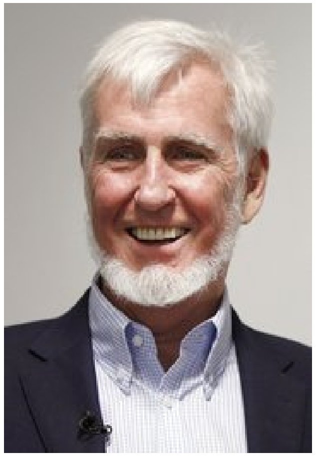
October, 2025

Place Cells Are Found Throughout the Hippocampal System

- Place cells discovered in CA1 in rats by O'Keefe and Dostrovsky (1971)
- Continuous firing fields with gaussian falloff.
- Place fields cover the physical space, forming a “cognitive map” of the environment.



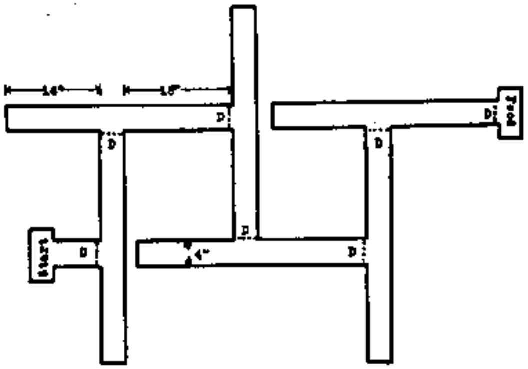
Sharp (2002)



John O'Keefe
2014 Nobel Laureate in Physiology or Medicine

The Hippocampus as a Cognitive Map

- Psychologist E. C. Tolman coined the term “cognitive map” to describe an animal's mental representation of space.
  - Tolman, EC (1948) Cognitive maps in rats and men.
    Psych. Review 55(4):189-208.



6-Unit Alley T-Maze

Fig. 4

(From H. C. Blodgett, The effect of the introduction of reward upon the maze performance of rats. *Univ. Calif. Publ. Psychol.*, 1929, 4, No. 8, p. 117.)

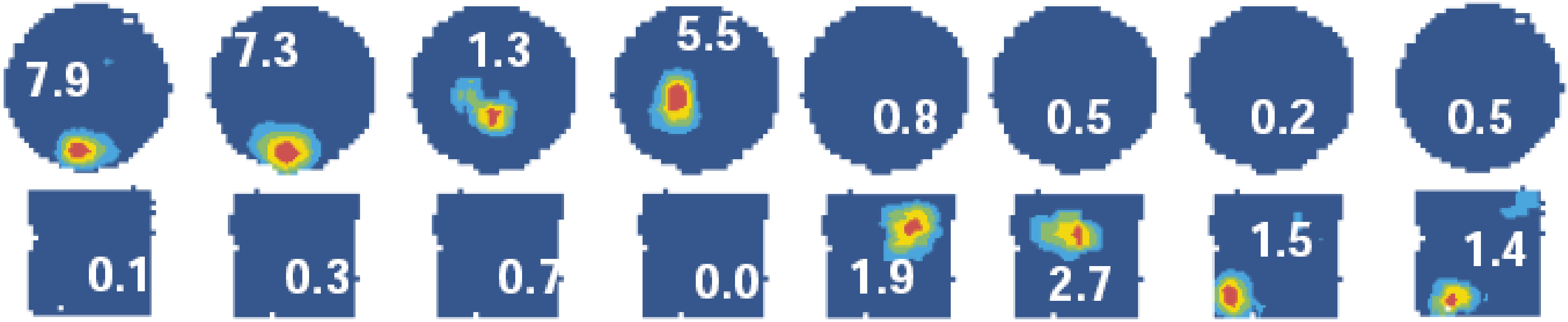
- O'Keefe and Nadel's book about place cells drew its title from Tolman's phrase.
  - O'Keefe, J and Nadel, L. (1978) The Hippocampus as a Cognitive Map. Oxford University Press.
  - Now online at https://discovery.ucl.ac.uk/id/eprint/10103569/

Properties of Place Fields

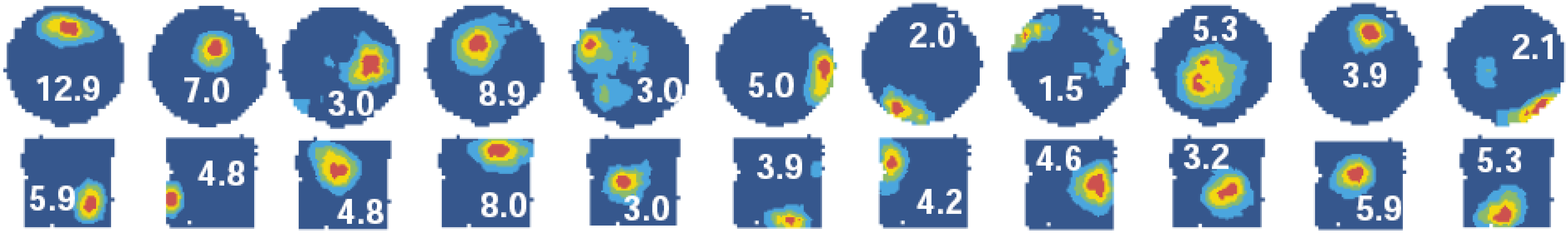
- Appear instantly in a new environment, but take 10-20 minutes to fully develop.
- Can be controlled by distal visual cues. (Rotate the cues and the fields will rotate.)
- Persist in the dark – so not *dependent* on visual input.
  - Driven by path integration?
- Only about 1/3 of place cells have fields in a typical small environment.
- Cells have <u>unrelated</u> fields in different environments.

Place Fields in a Cylindrical and Square Arena

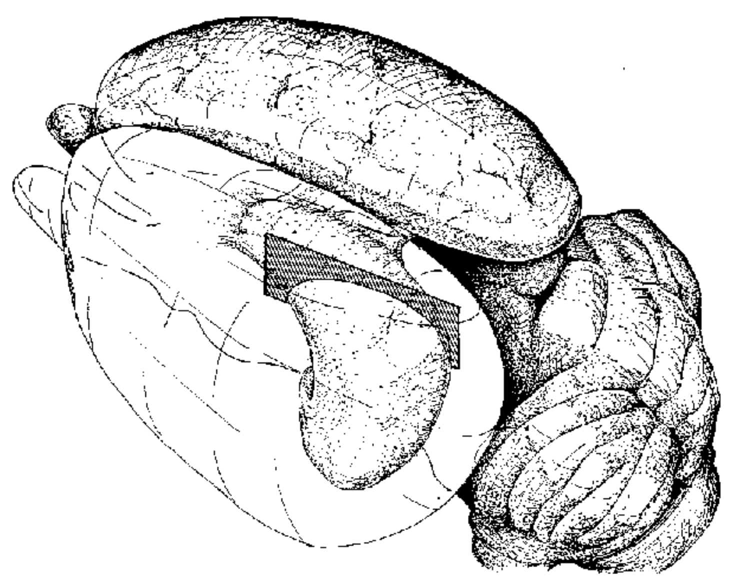
- Roughly gaussian
- Modest peak firing rates (5-10 Hz)
- Largely unrelated fields in the two environments



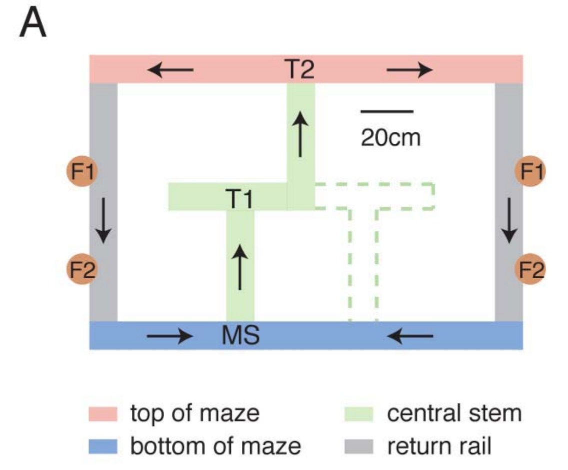
Lever et al., 2002

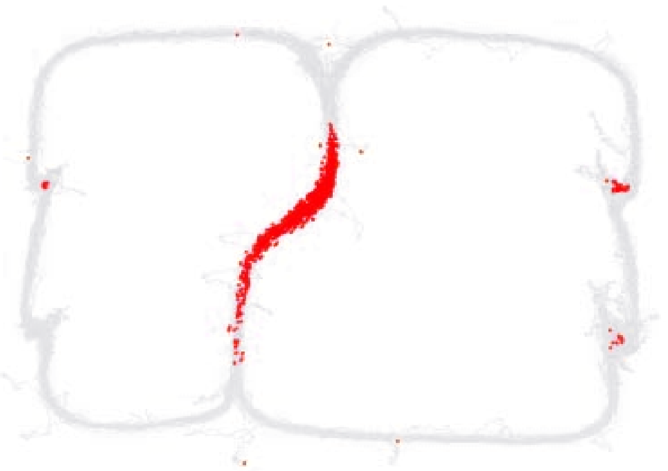


Place Fields On A Maze

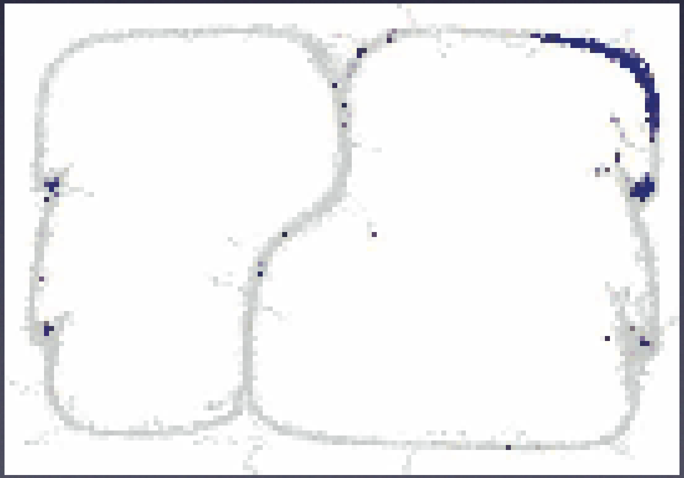


Slide courtesy of Anoopum Gupta





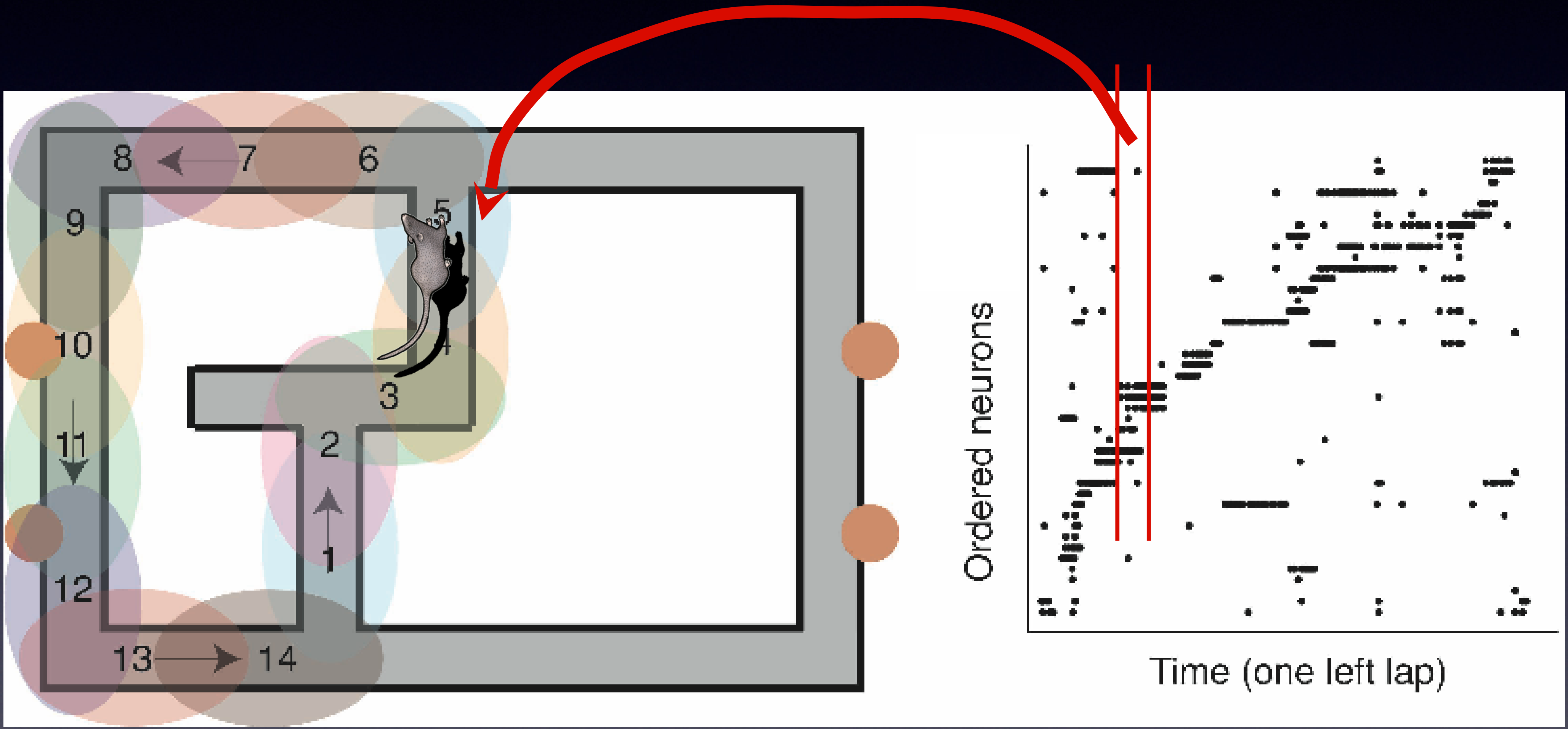
Cell 1



Cell 2

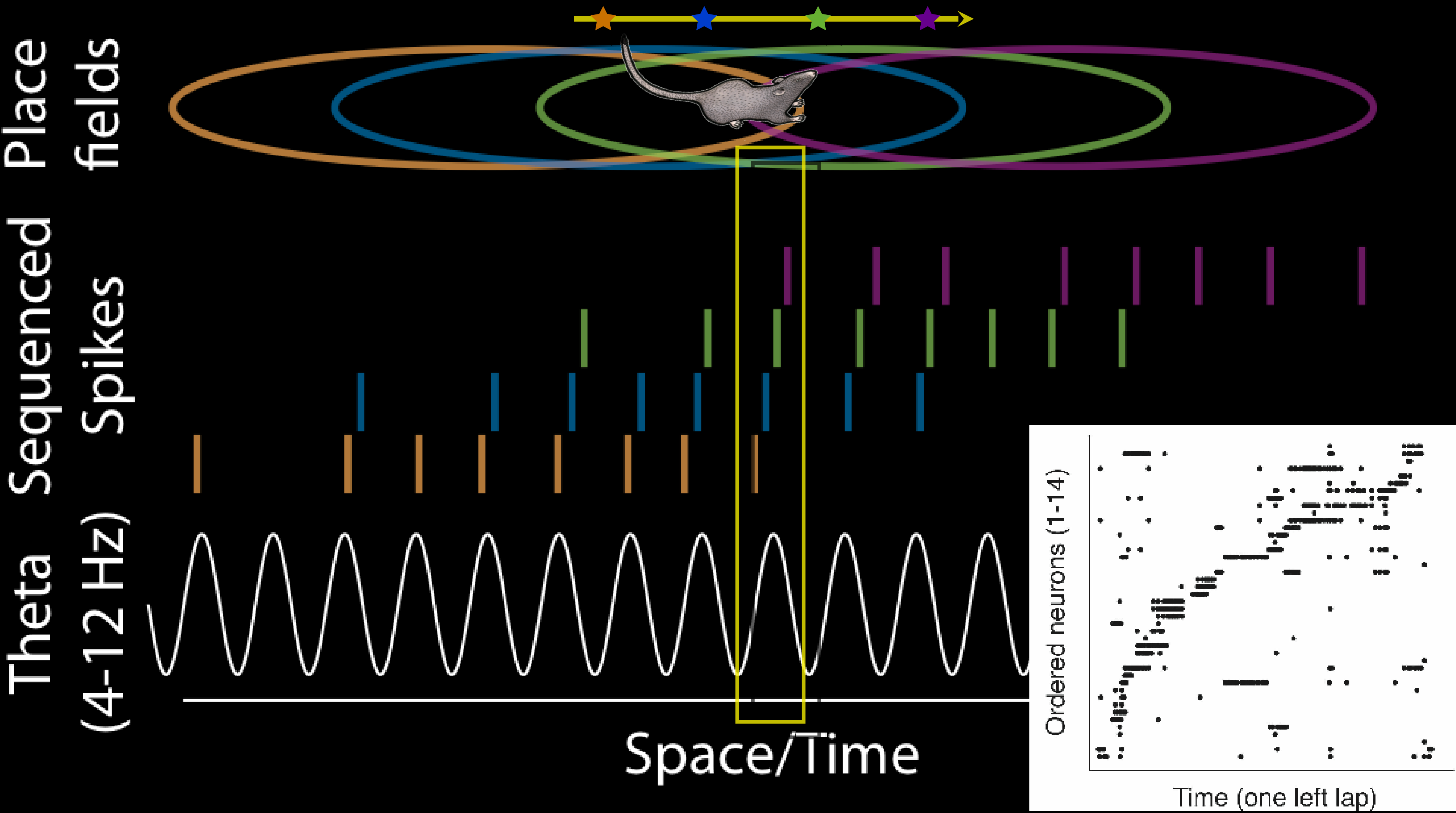
Slide courtesy of Anoopum Gupta

Neural activity during behavior



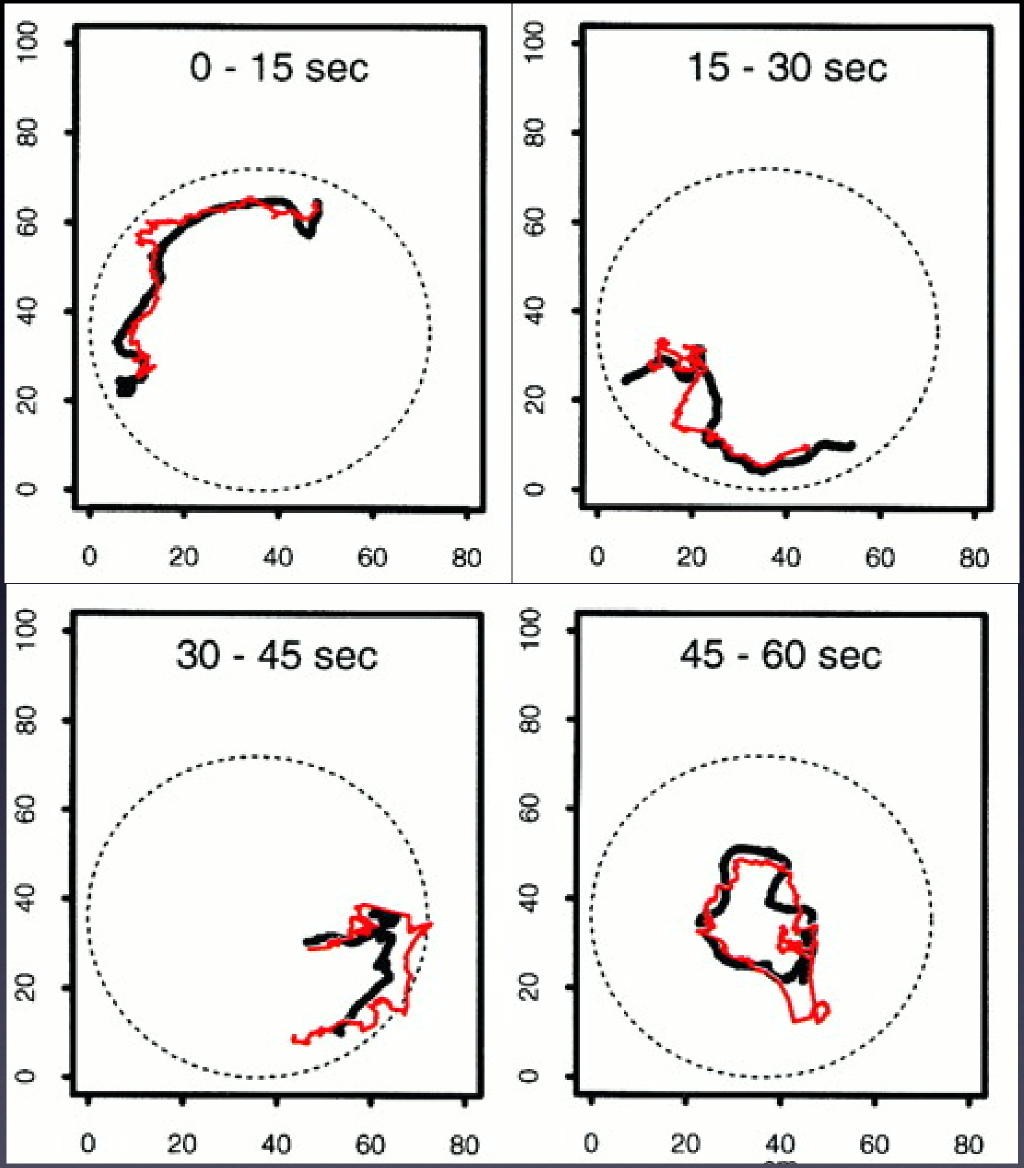
Slide courtesy of Anoopum Gupta

Theta Phase Precession



Slide courtesy of Anoopum Gupta

Decoded Paths

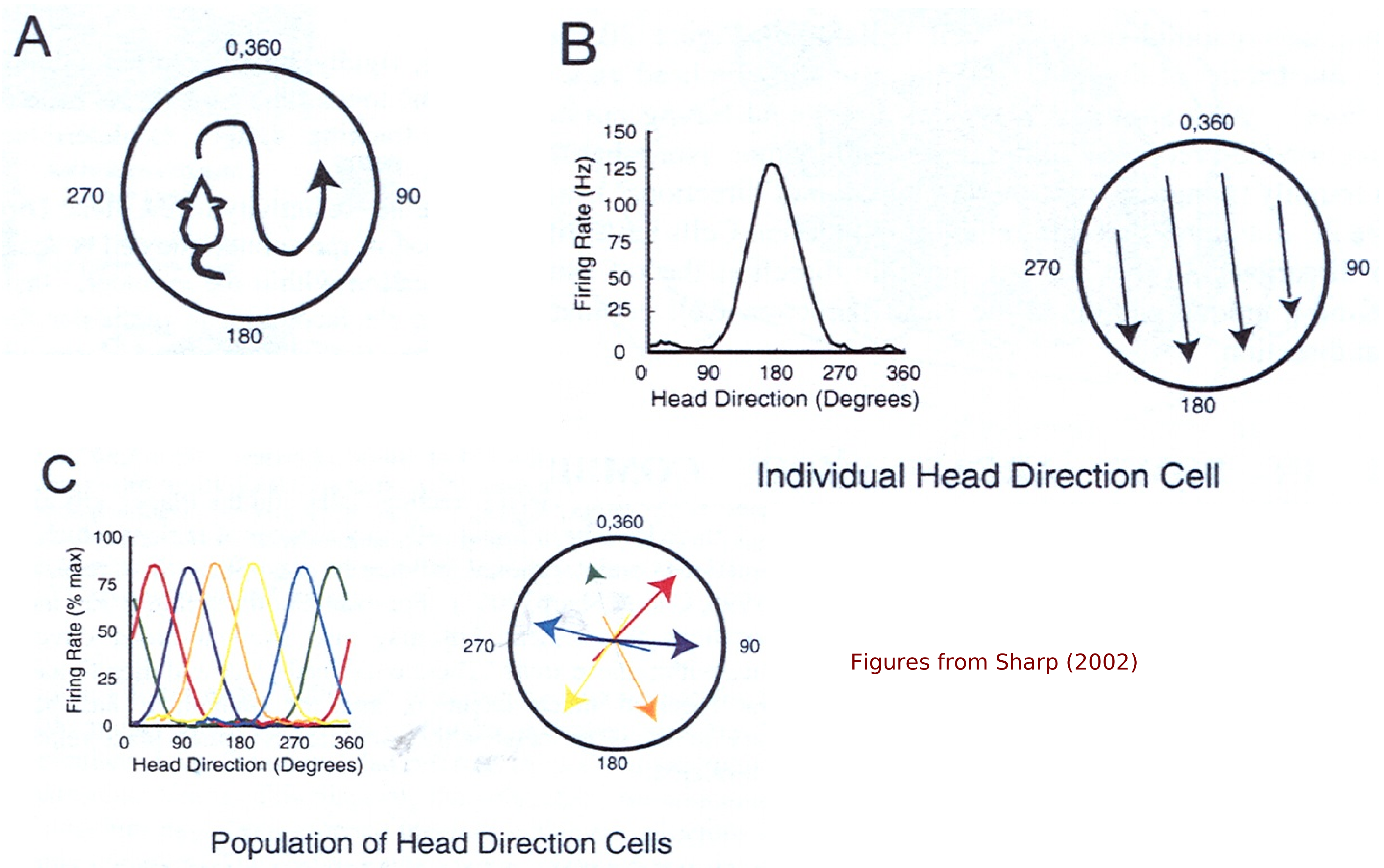


Brown et al., 1998

Eleanor Maguire:
Spatial Memory in Humans

- London cab drivers undergo 2-3 years of training to learn “The Knowledge” of London's complex streets.
- Cab drivers have larger posterior hippocampi than controls. Experienced drivers show greater enlargement than new drivers.
- When remembering complex routes, drivers show elevated activity in right posterior hippocampus; no increase when answering questions about historical landmarks.

Head Direction Cells (Ranck, 1989)

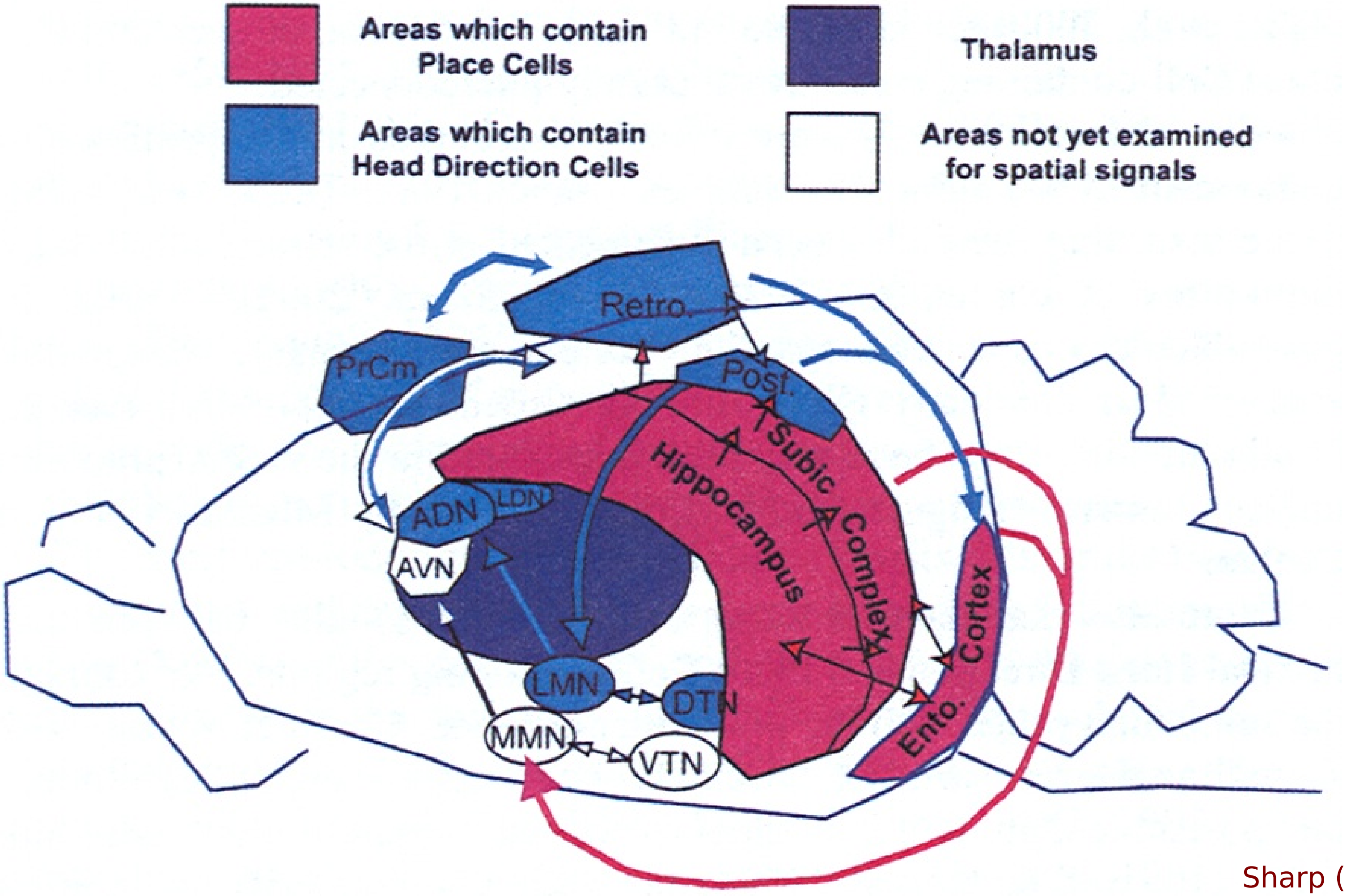


Individual Head Direction Cell

Population of Head Direction Cells

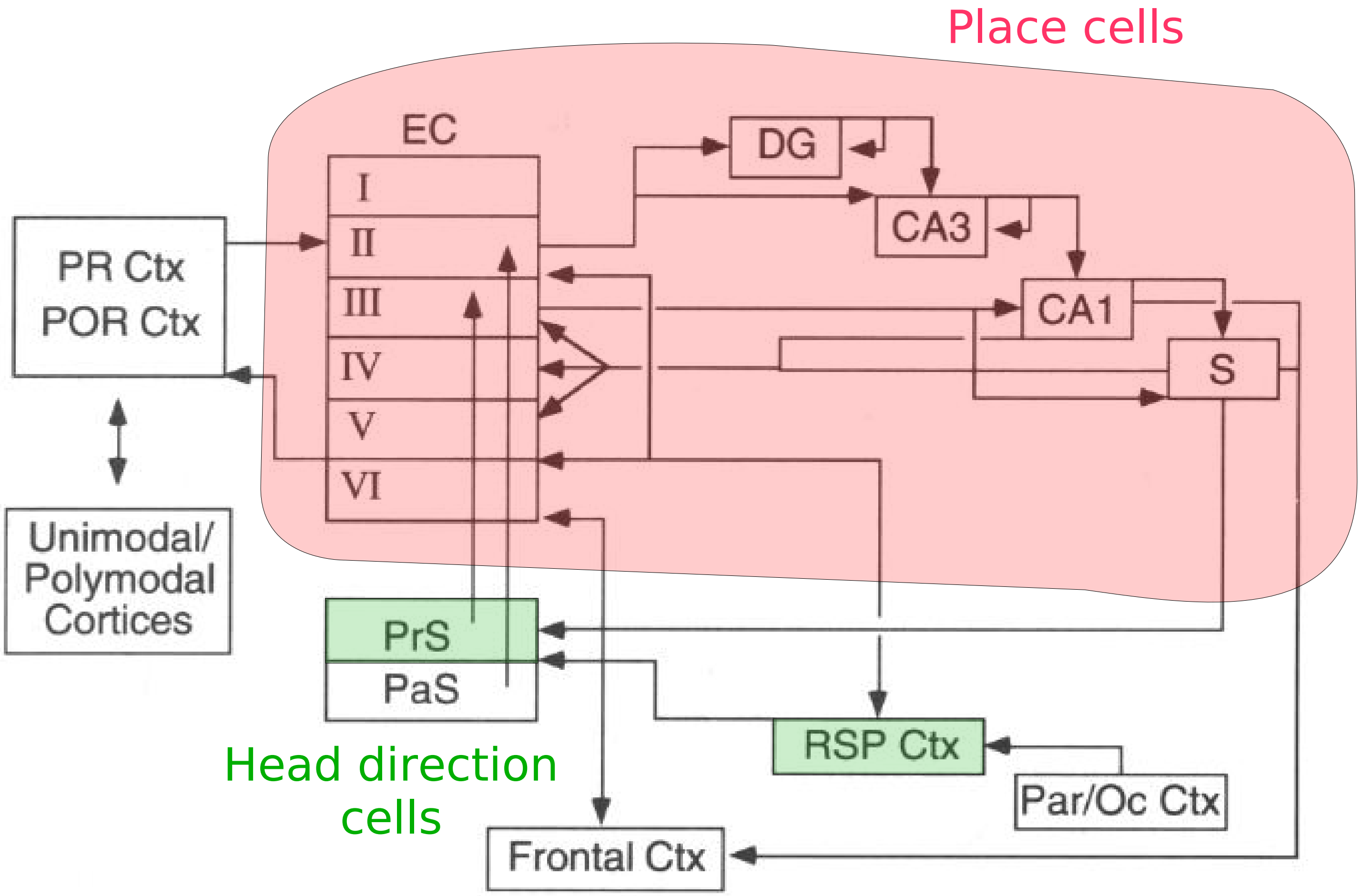
Figures from Sharp (2002)

Place and Head Direction Systems



Sharp (2002)

Rodent Navigation Circuit



Place cells

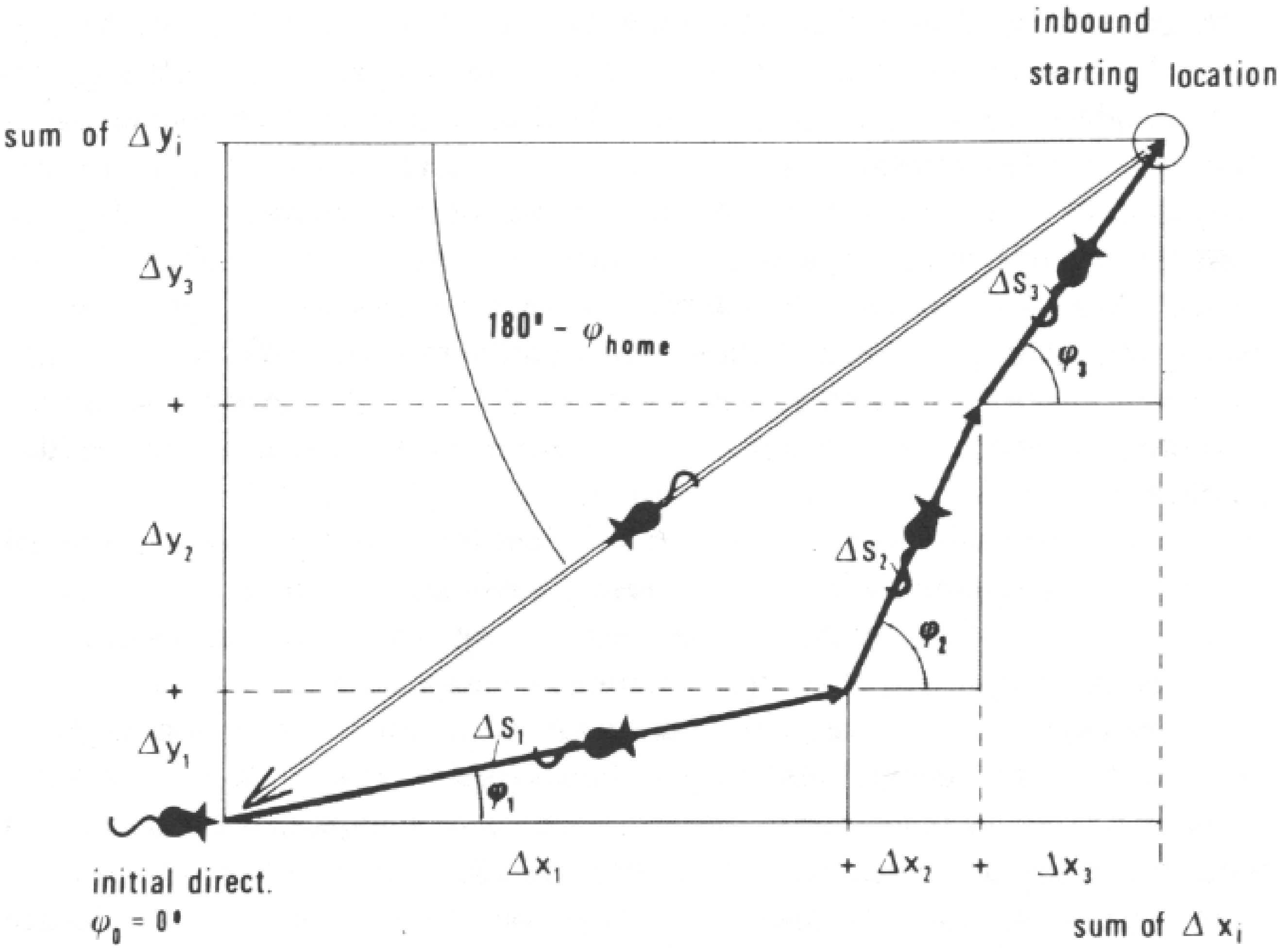
Head direction cells

From (Johnston & Amaral, 1998)

PR: perirhinal cortex; POR: postrhinal cortex; EC: entorhinal cortex; PrS: presubiculum; PaS: parasubiculum; DG: dentate gyrus; CA: Cornu amonis; S: subiculum; RSP: retrosplenial cortex; Par/Oc: parietal/occipital cortex

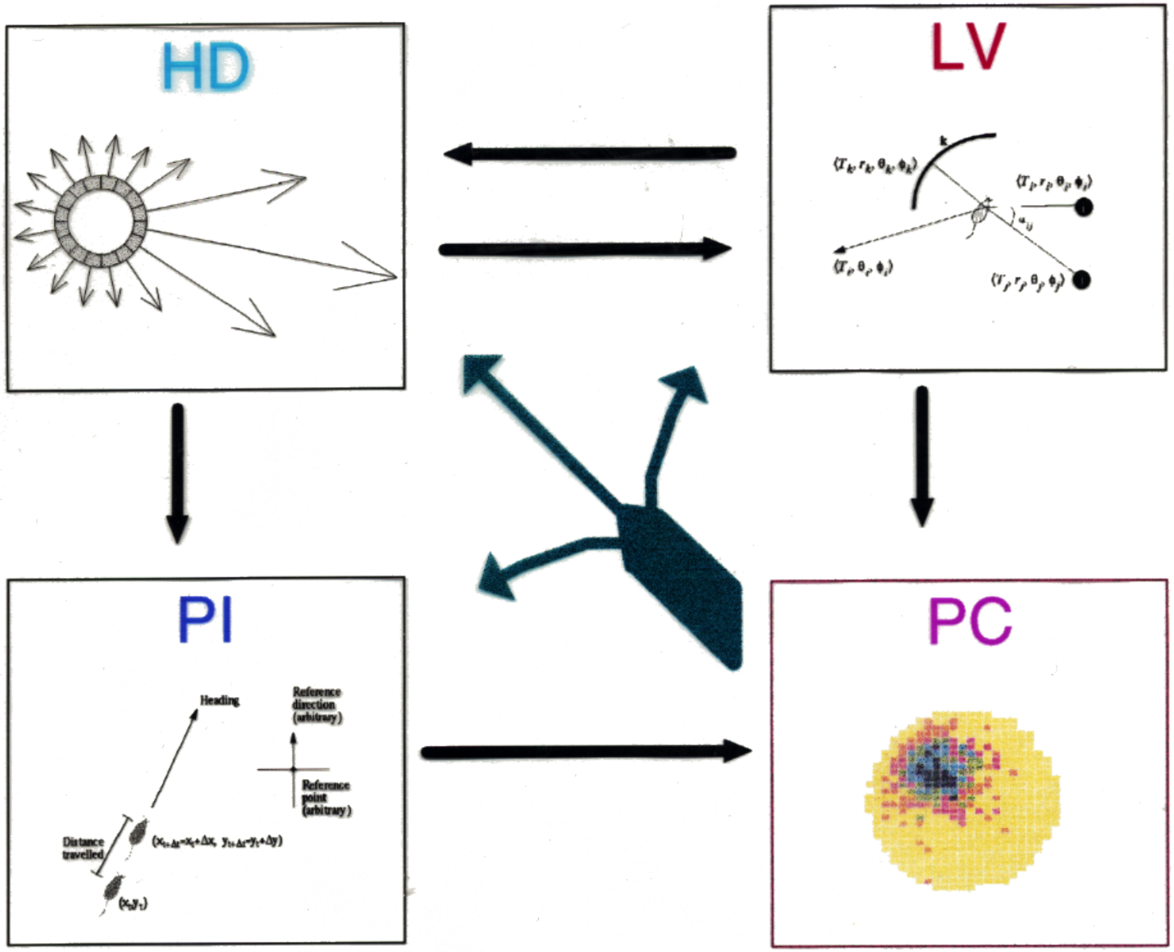
Path Integration in Rodents

Mittelstaedt & Mittselstaedt (1980): gerbil pup retrieval



Redish & Touretzky Model of Rodent Navigation

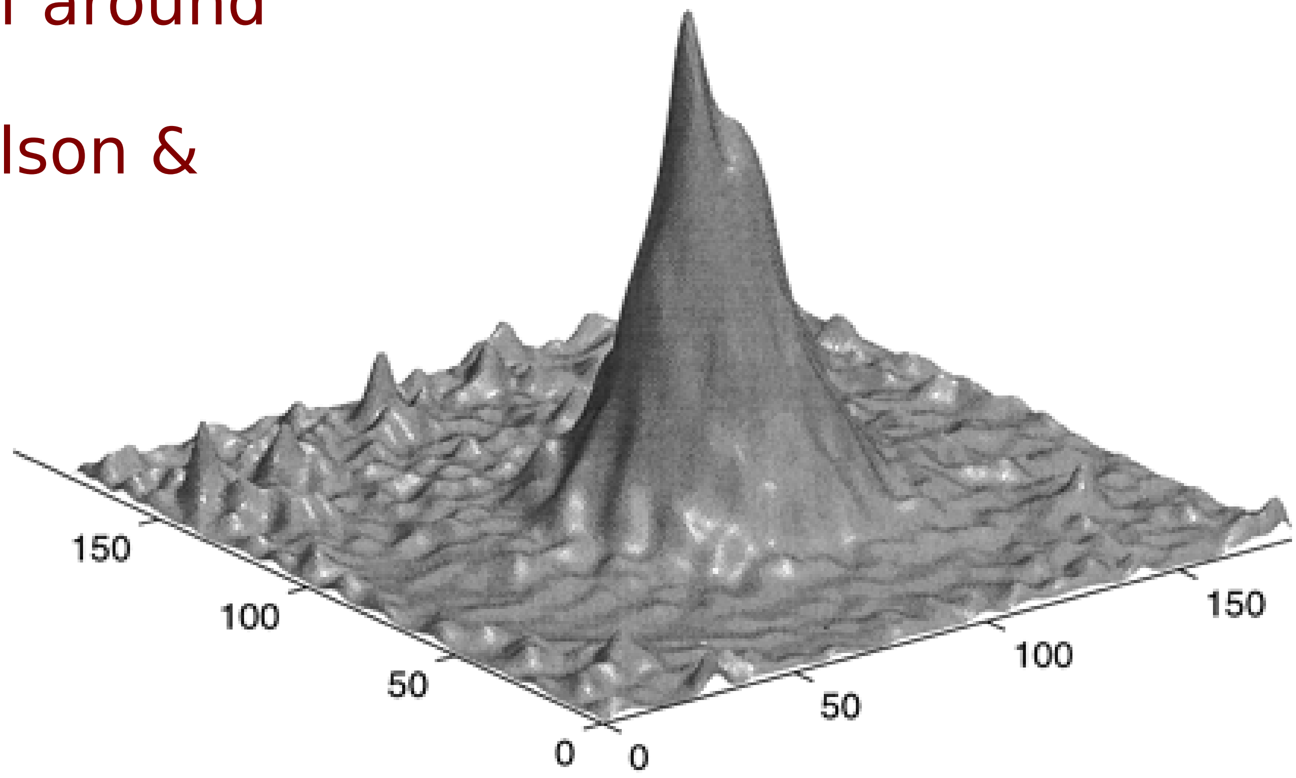
Place cells *learn* and *maintain* the correspondence between local view representations and path integrator coordinates.



Redish (1997)

Hippocampal State:
A Moving Bump of Activity

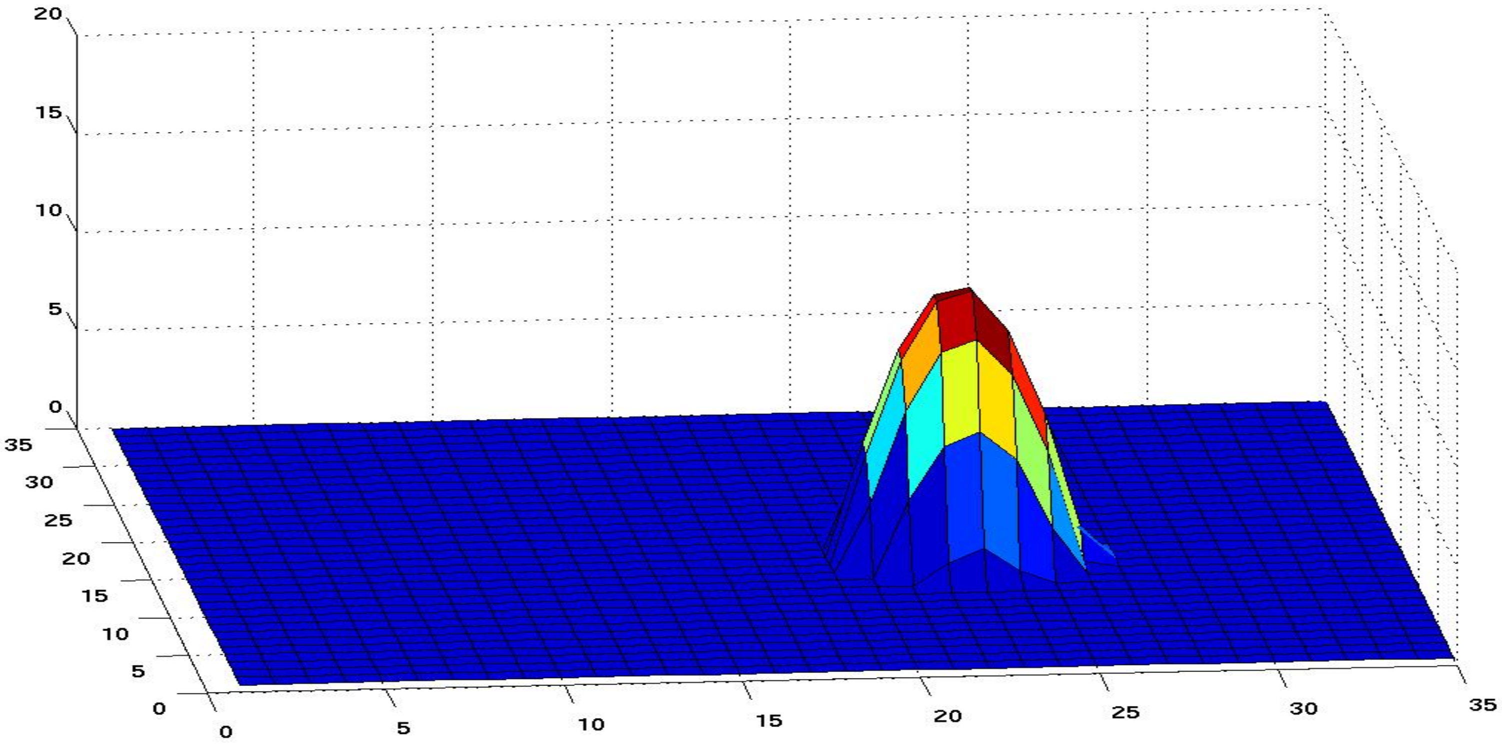
Activity packet reconstructed from firing patterns of around 100 cells recorded simultaneously by Wilson & McNaughton (1993)



Samsonovich & McNaughton (1997)

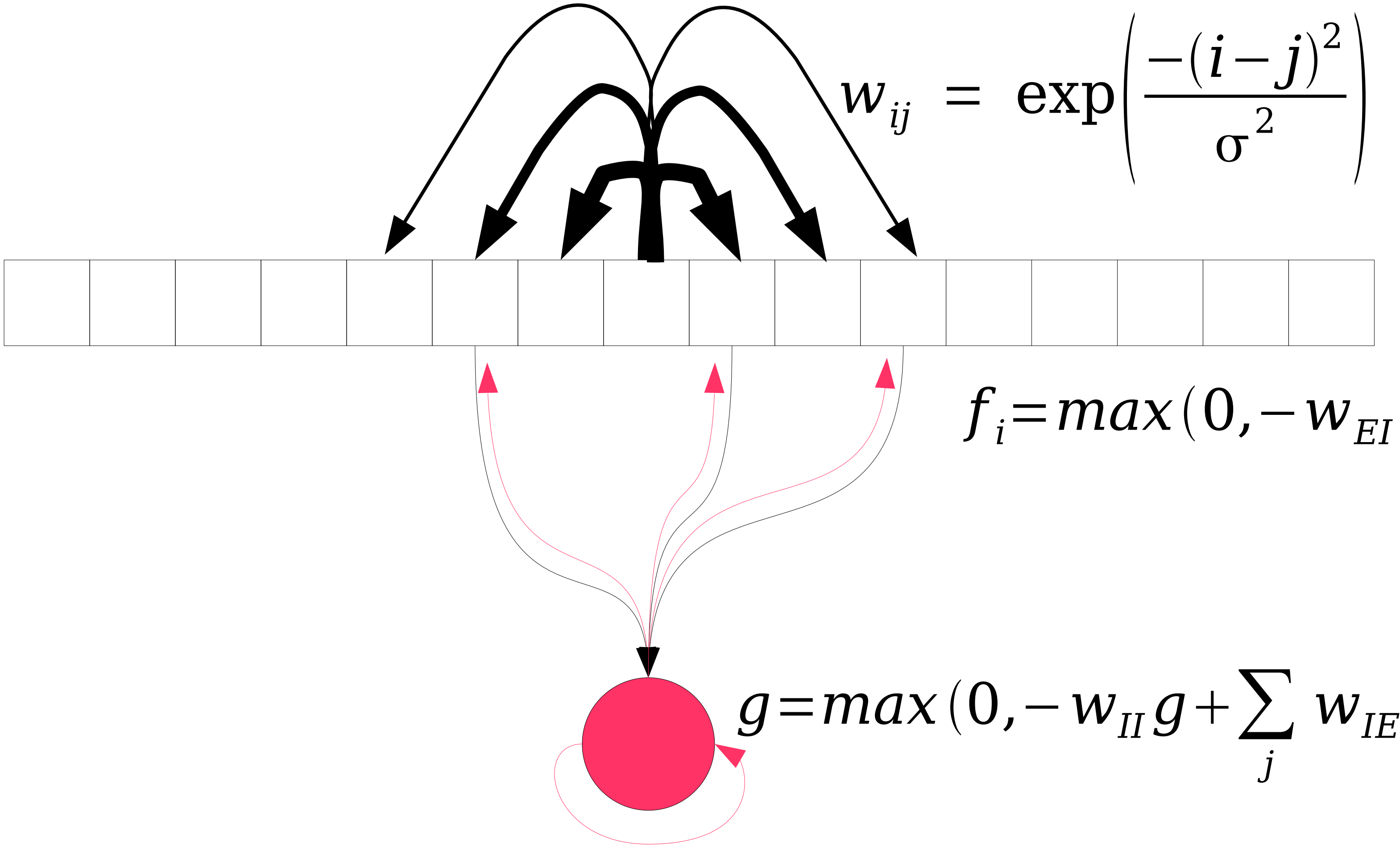
2D Attractor Bump Simulation

- In 1972, Amari, and Wilson & Cowan demonstrated continuous attractor bumps in a recurrent network.
- 25 years later: Samsonovich & McNaughton (1997): 2D attractor bump model of place cells.
- Bumps are easy to simulate and visualize in MATLAB.



How to make a bump (1D version)

Local excitation plus global inhibition:



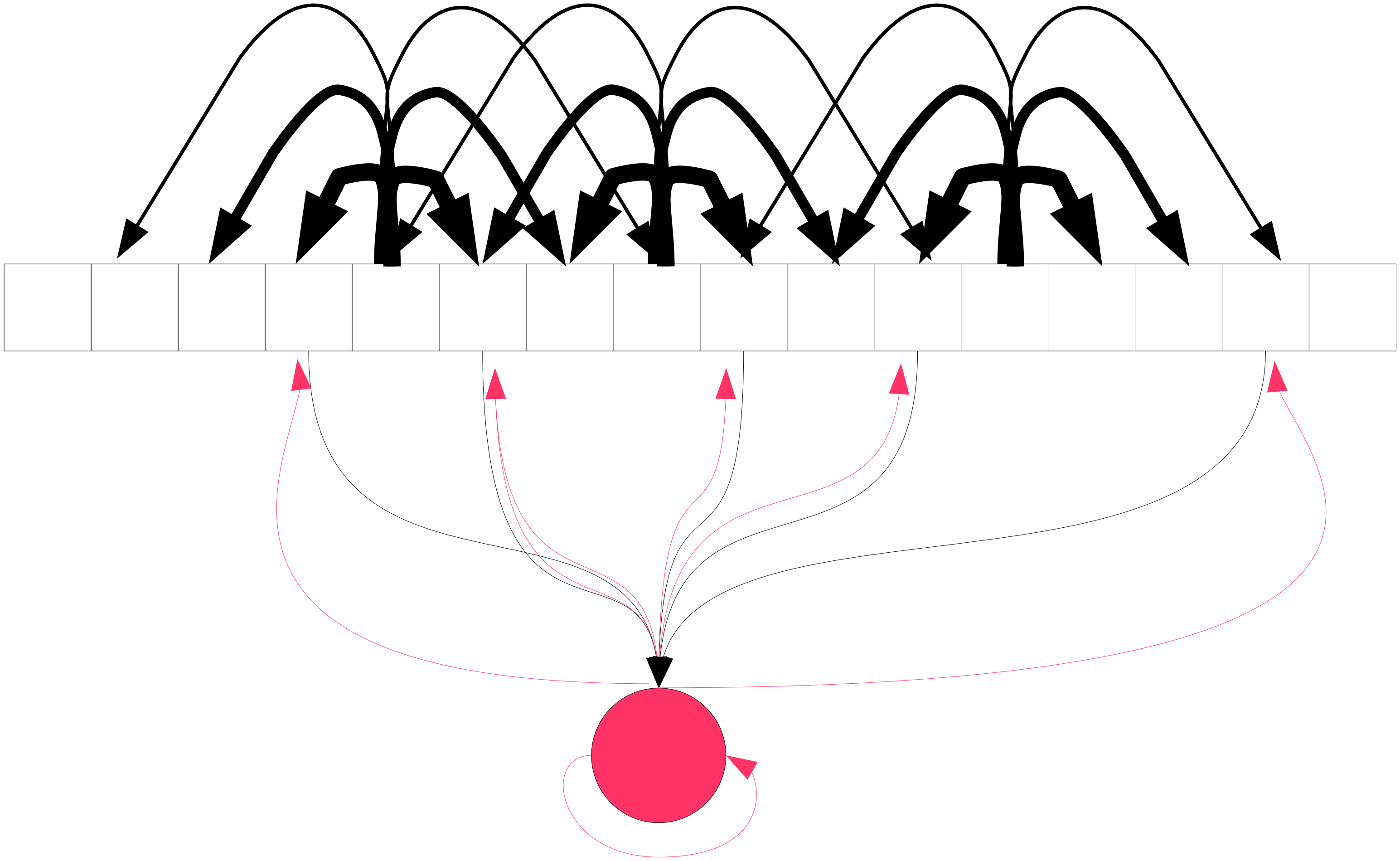
$$w_{ij} = \exp\left(\frac{-(i-j)^2}{\sigma^2}\right)$$

$$f_i = max(0, -w_{EI}\, g + \sum_j w_{ij} f_j)$$

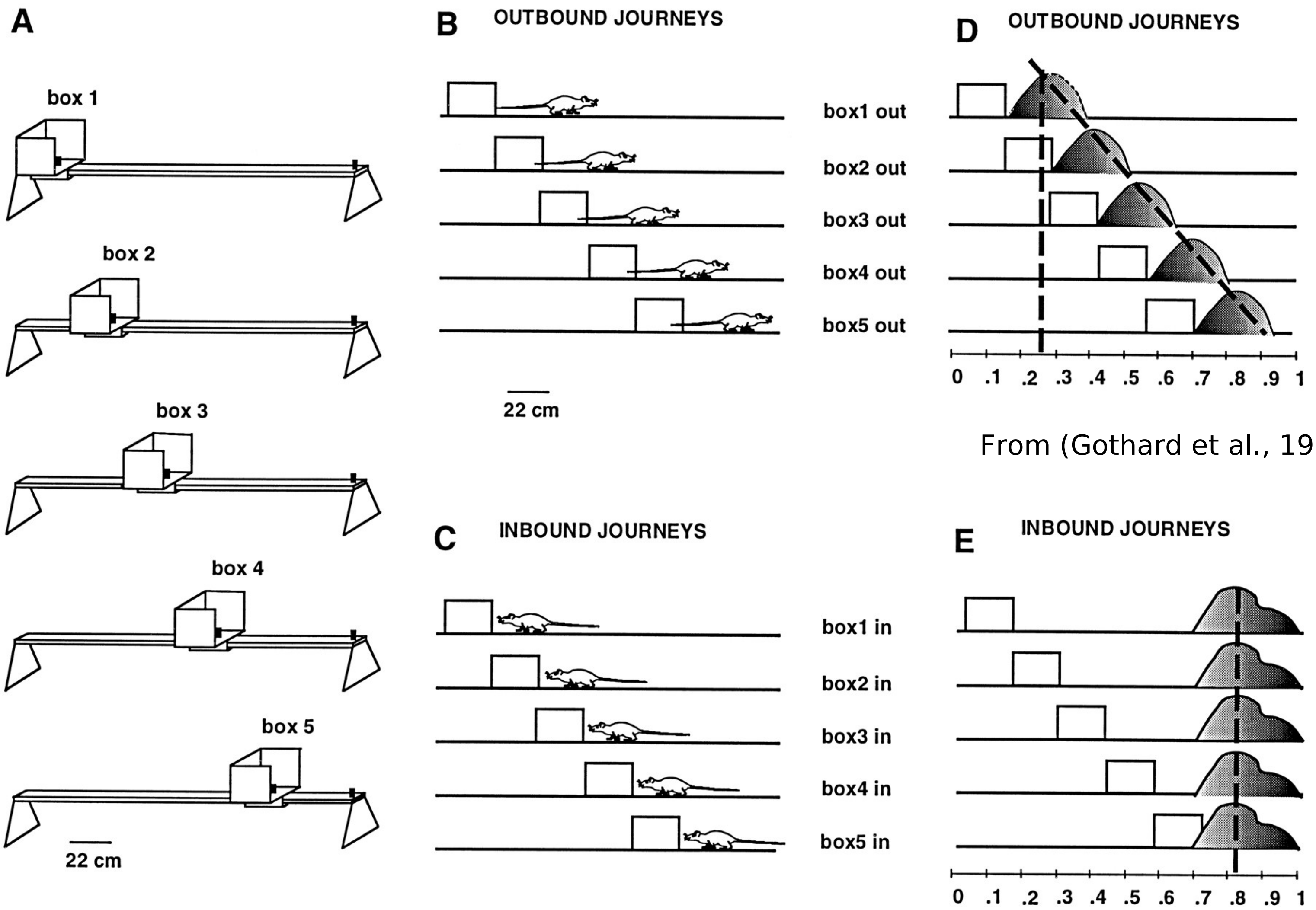
$$g = max(0, -w_{II}\, g + \sum_j w_{IE} f_j)$$

How to make a bump (1D version)

Same weights for every unit (shifted):

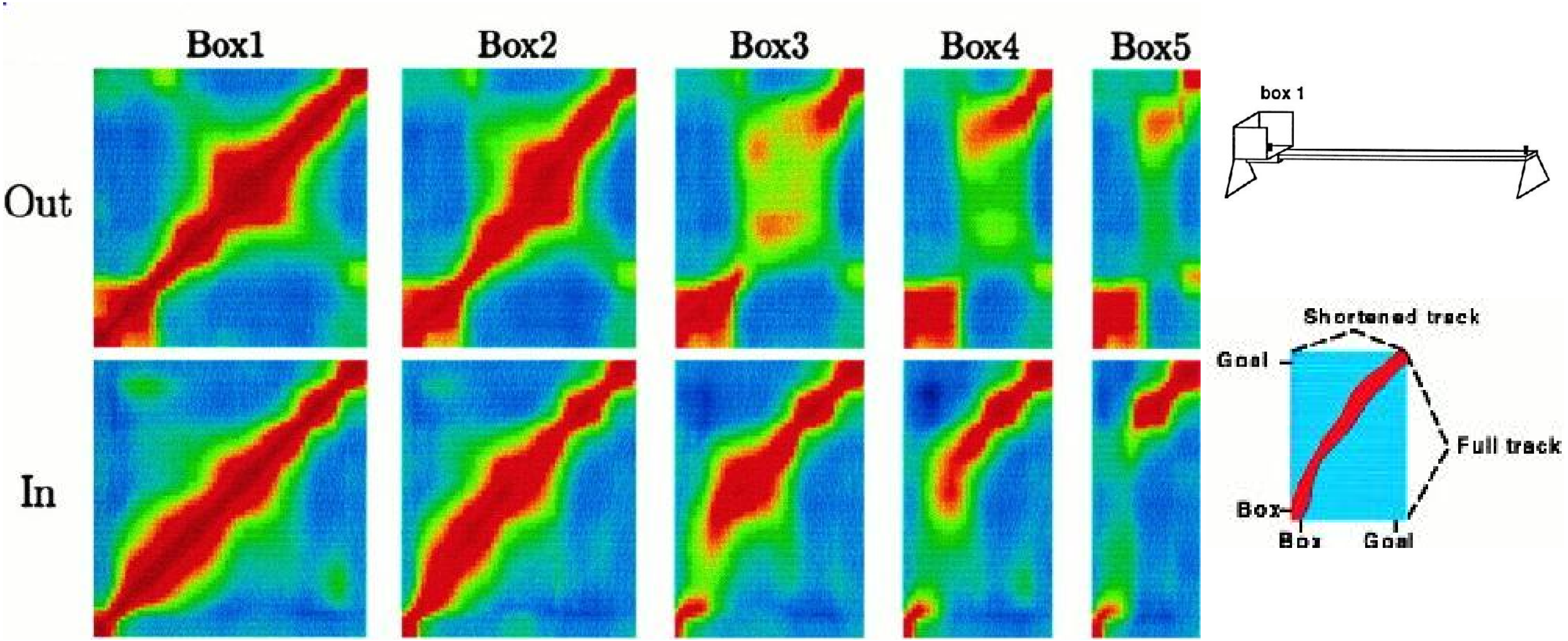


Gothard et al. (1996): bump jumps



From (Gothard et al., 1996)

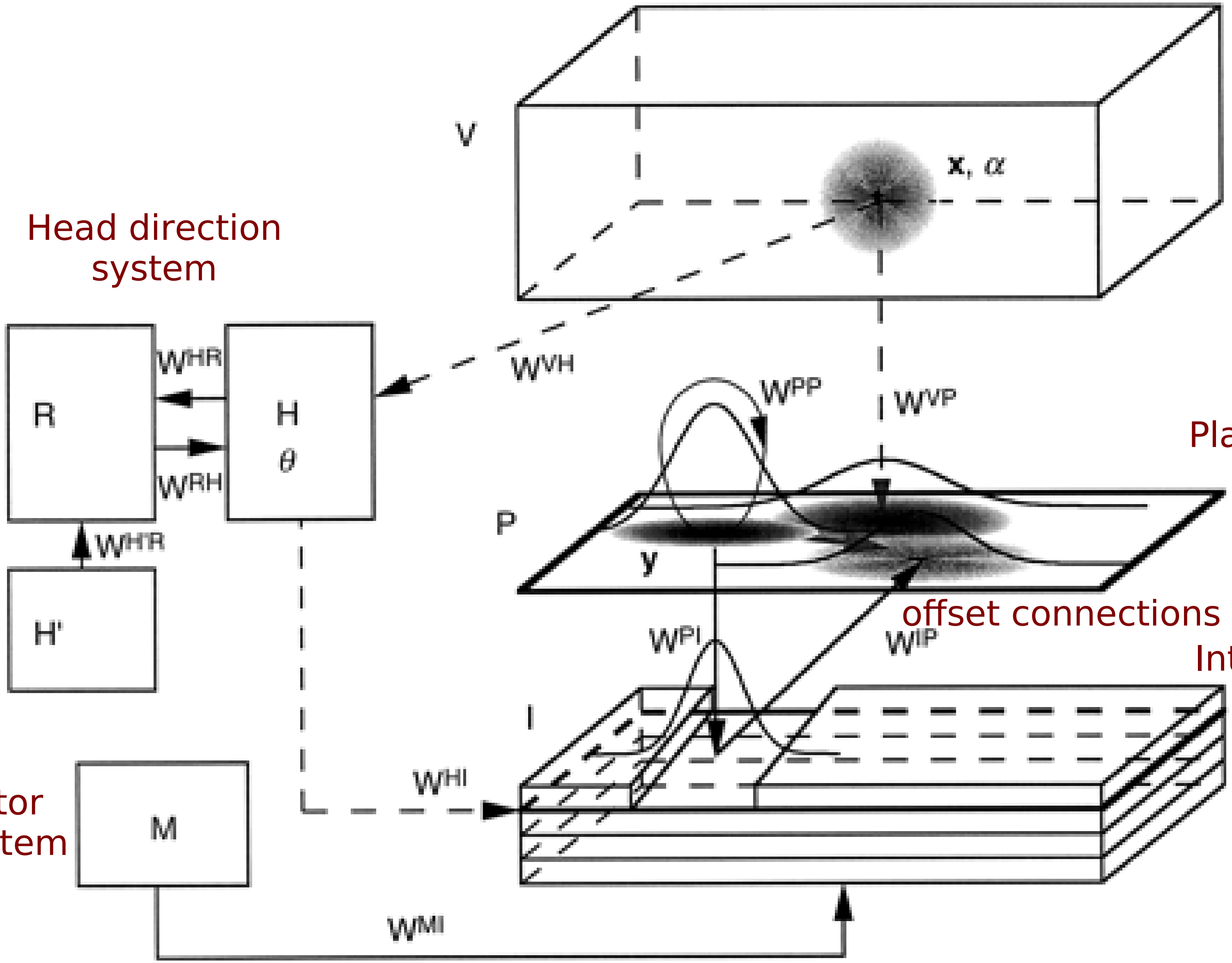
Watch the bump jump!



From (Gothard et al., 1996)

Cross-correlation plots of the ensemble activity patterns show a “jump” on the map as a discontinuity.

Samsonovich & McNaughton Model



Visual input

Head direction system

Place cells

offset connections

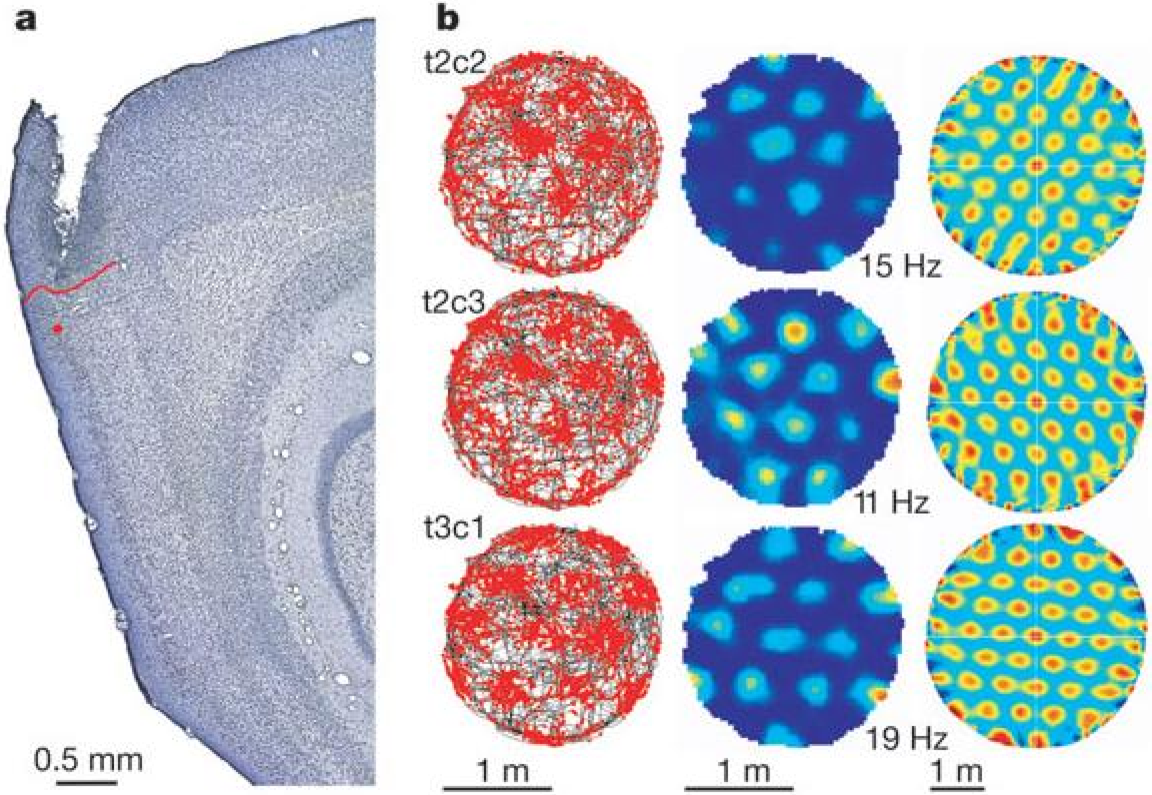
Integrator cells

Motor system

Where is the Path Integrator?

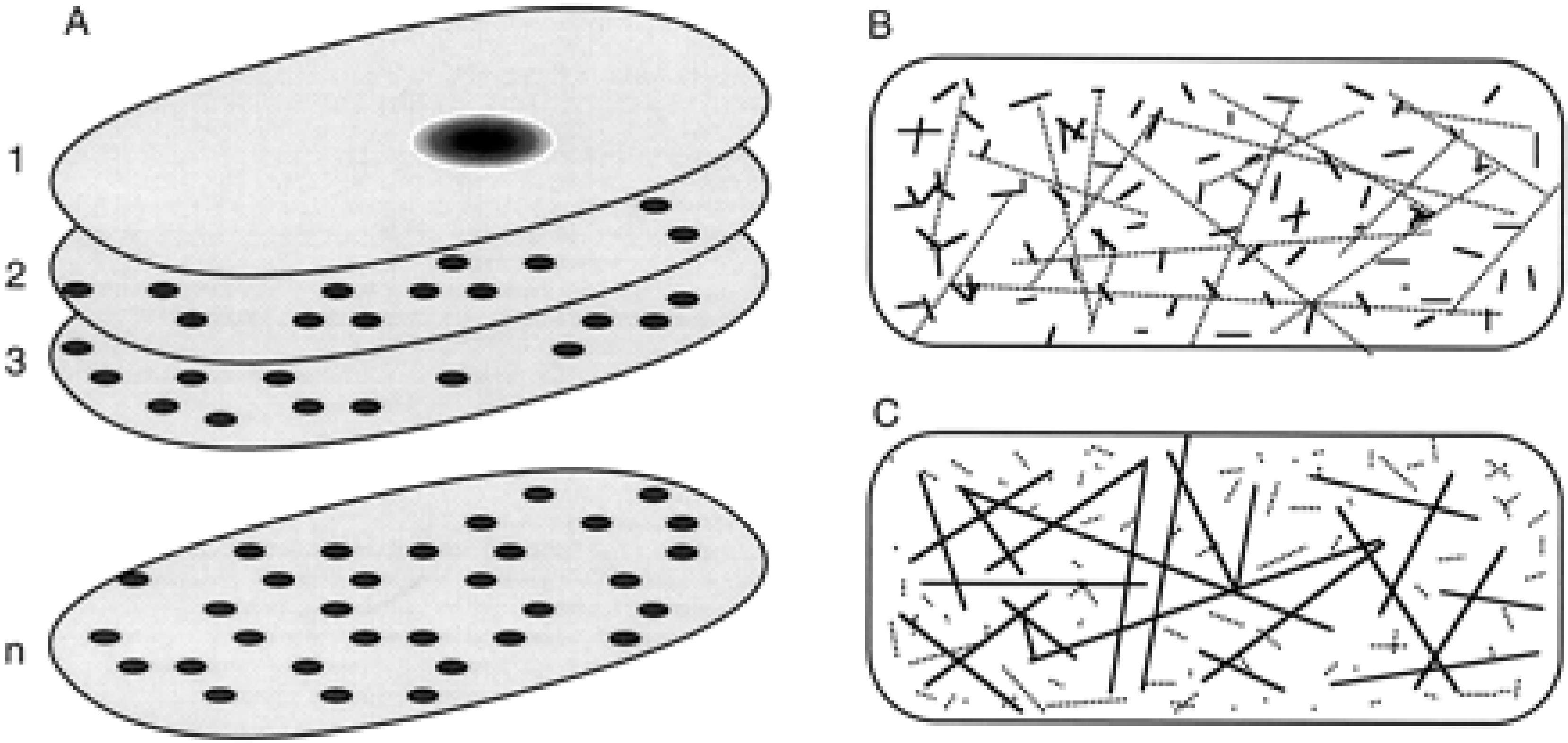
- Early theories (McNaughton) placed it in hippocampus.
- Redish & Touretzky: it can't go there, because multiple maps make it too hard to update position.
- Fyhn et al. (Science, 2004) found the PI in medial entorhinal cortex: “grid” cells.

May-Britt and Edvard Moser, 2014 Nobel Laureates in Physiology or Medicine

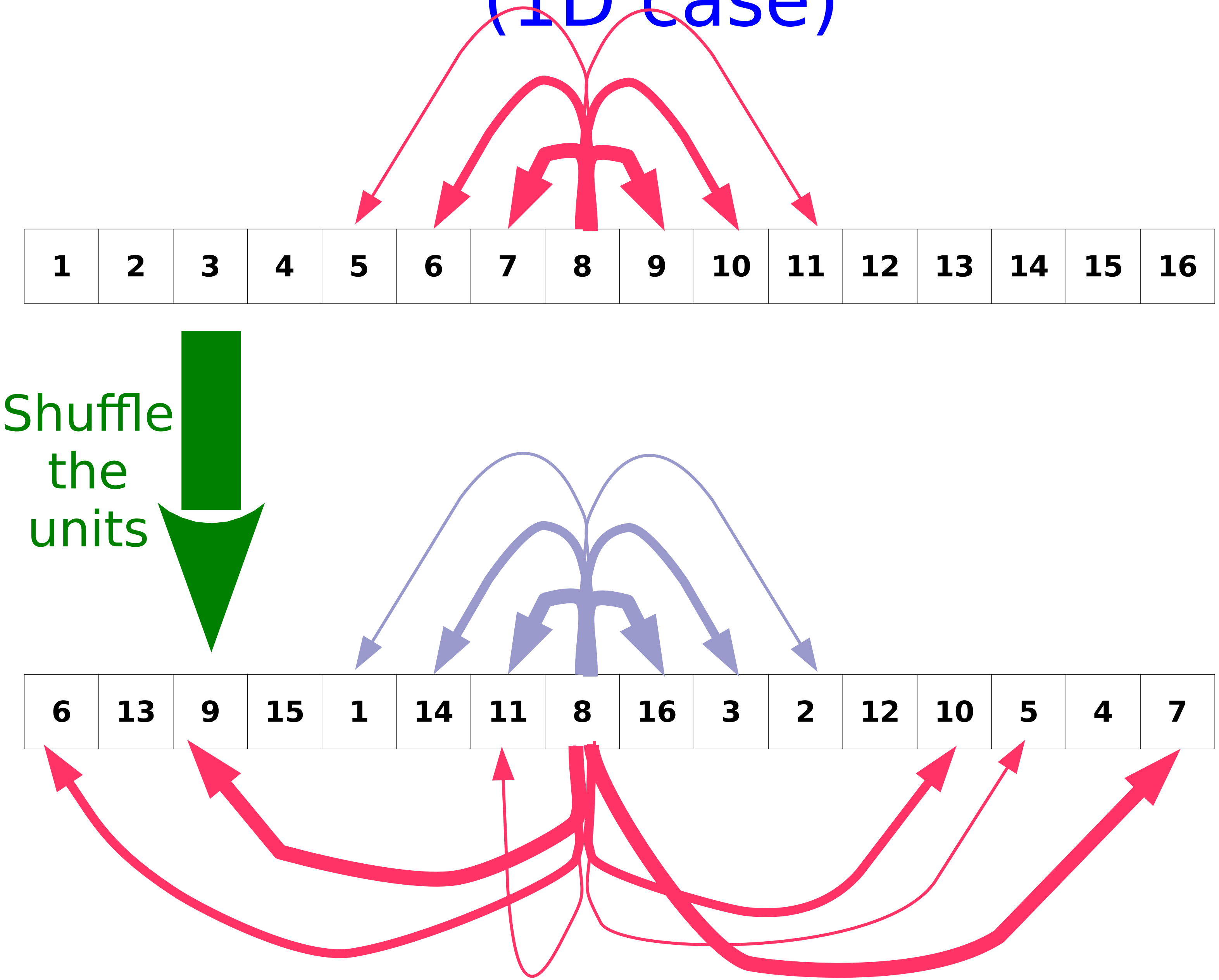


Multiple Maps in Hippocampus

Samsonovich & McNaughton's “charts” proposal:



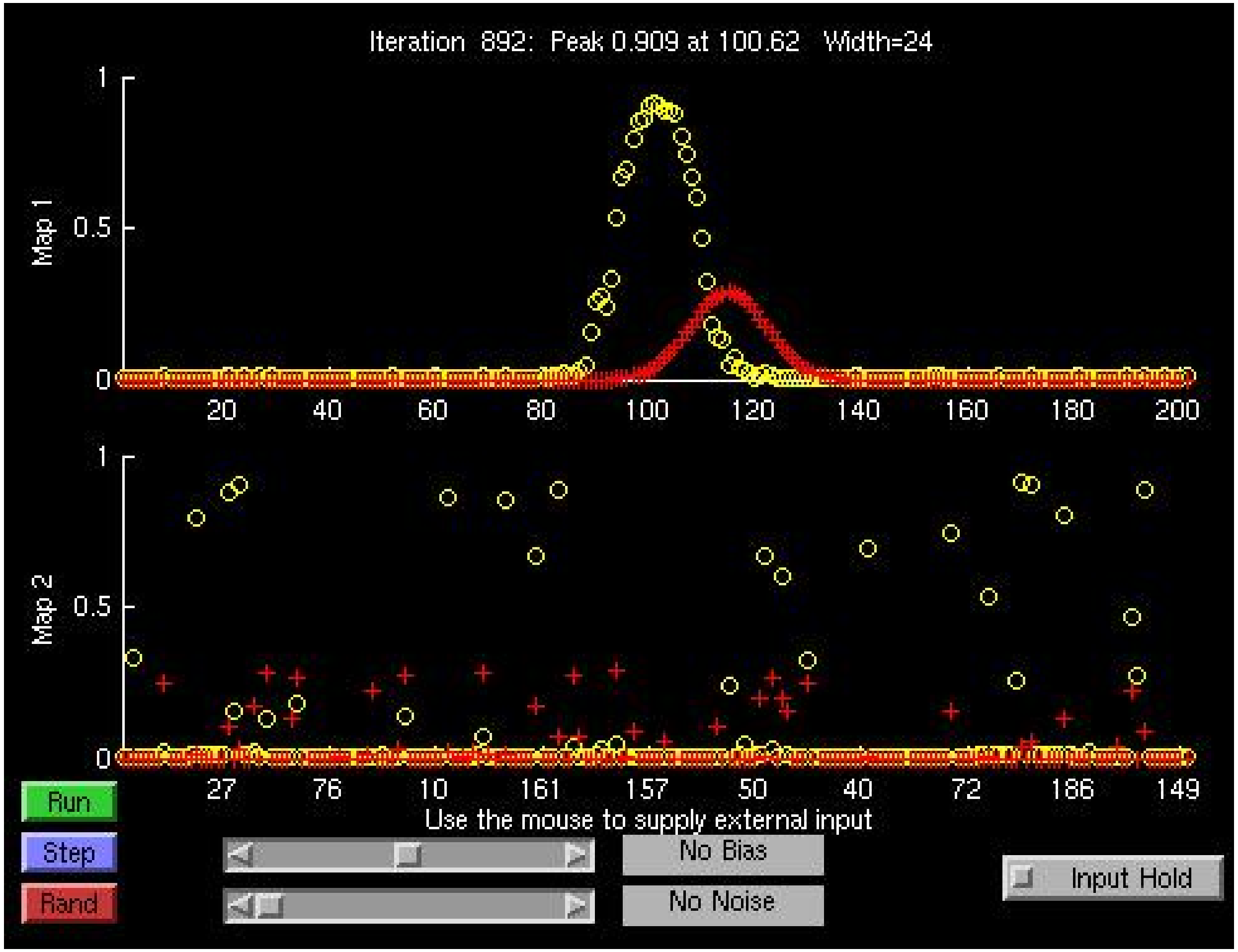
How to make multiple maps (1D case)



Shuffle the units

Multiple Maps Can Co-Exist In An Attractor Network

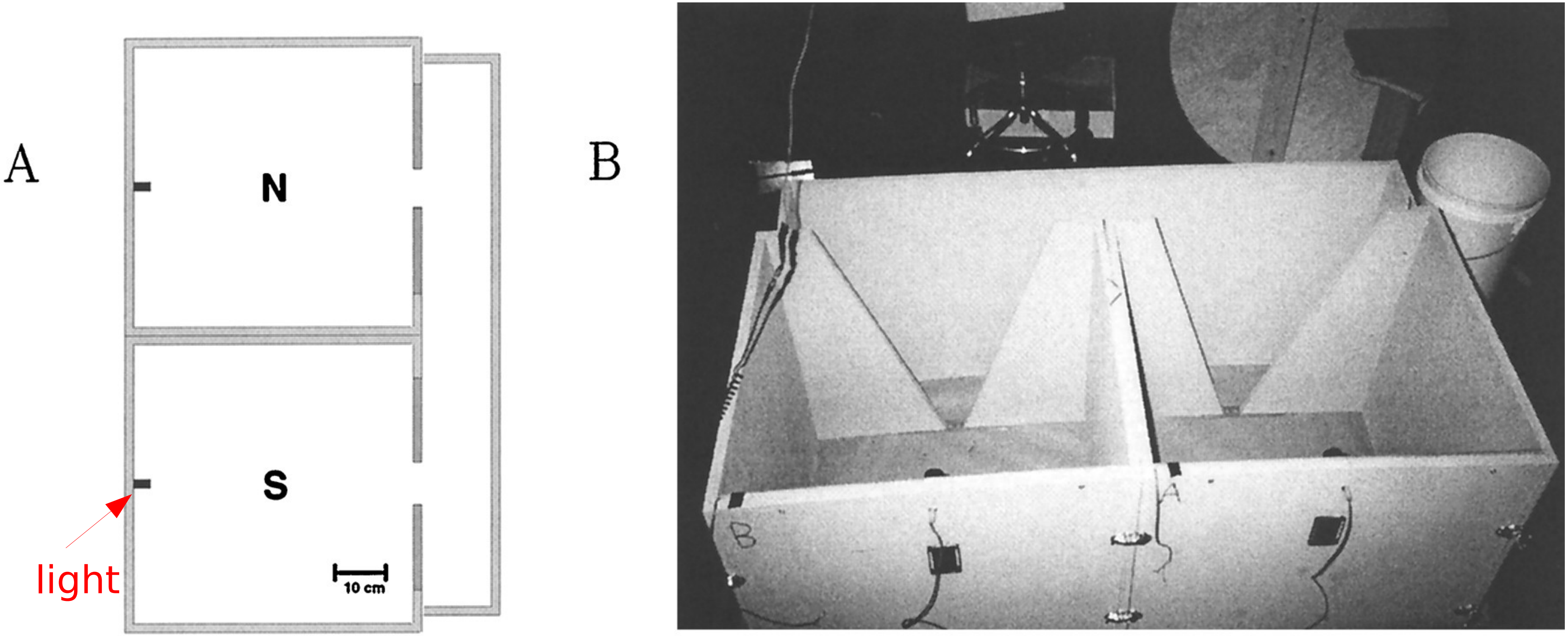
Because activity patterns are sparse, the weight matrix is also sparse. Interference isn't too bad.



Iteration 892: Peak 0.909 at 100.62 Width=24

Use the mouse to supply external input

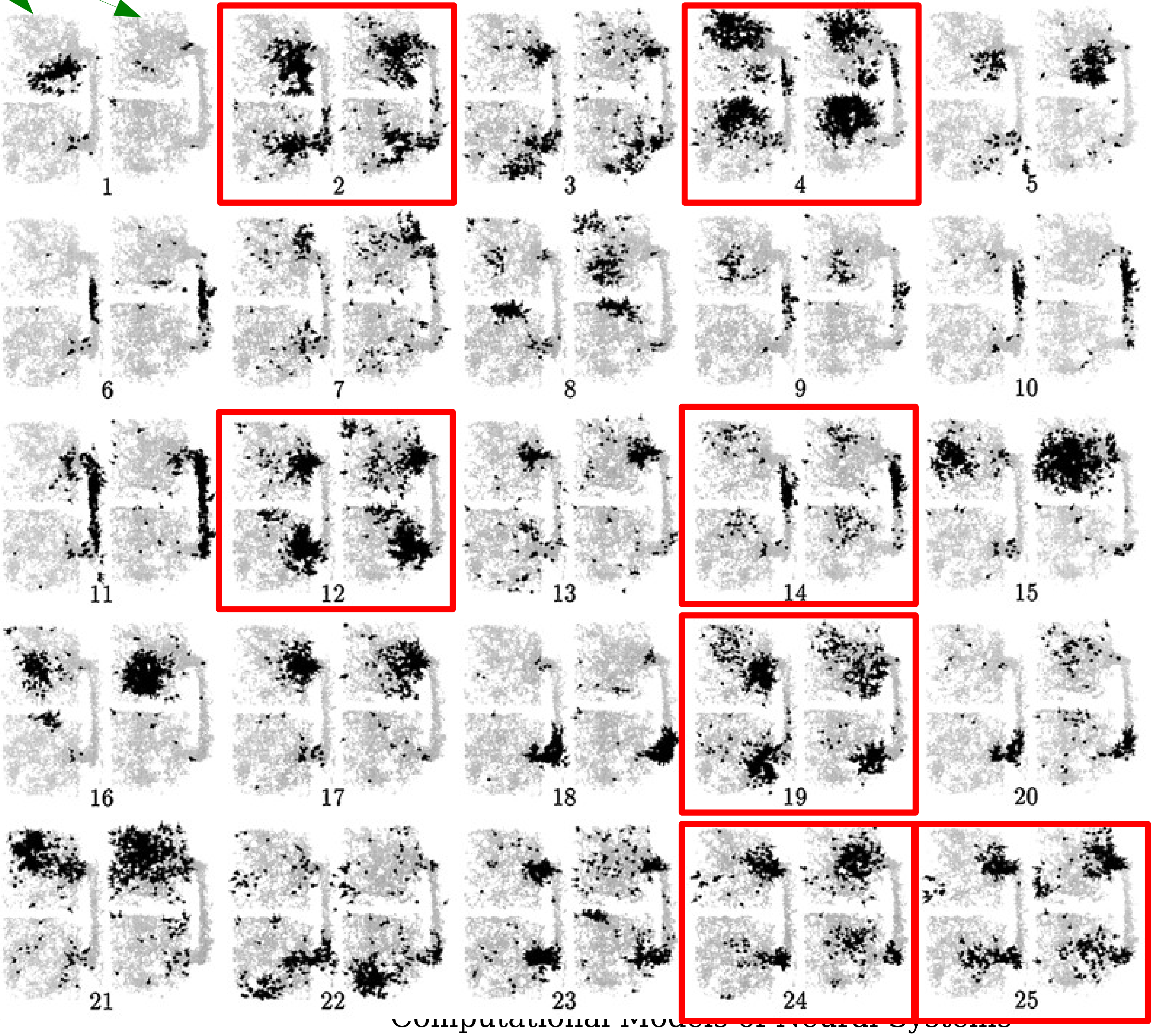
Skaggs & McNaughton (1998): Partial Remapping in Identical Environments



(Skaggs & McNaughton, 1998)

Identical Environments, Similar Fields in Both Boxes

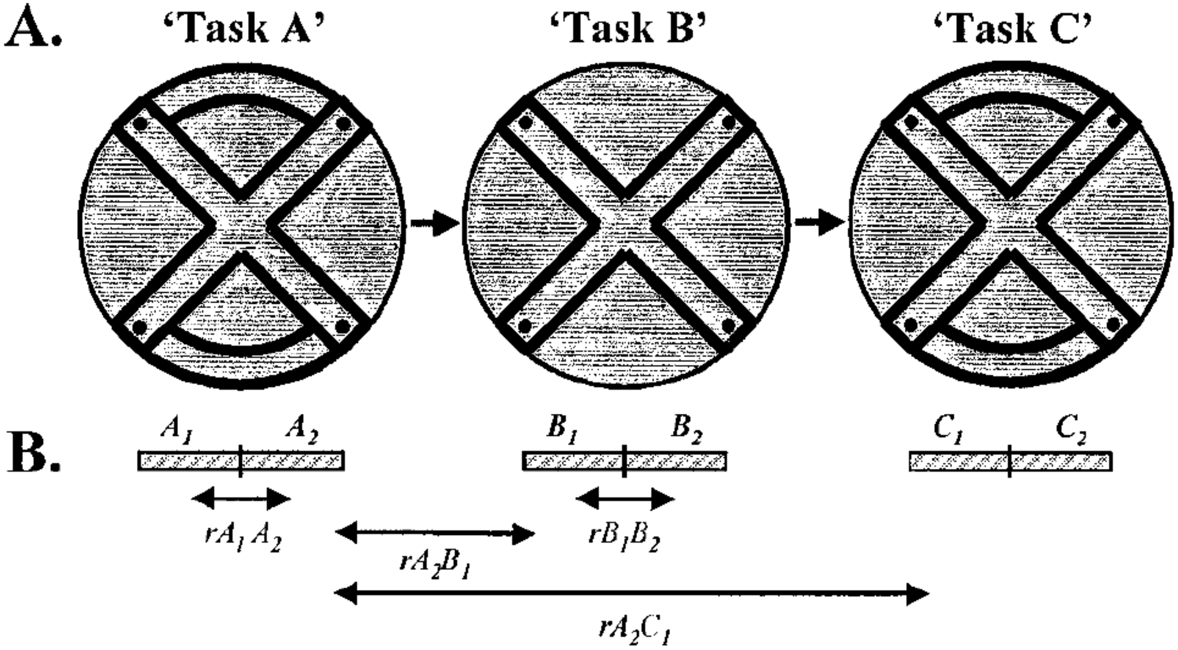
Same cell;
two sessions

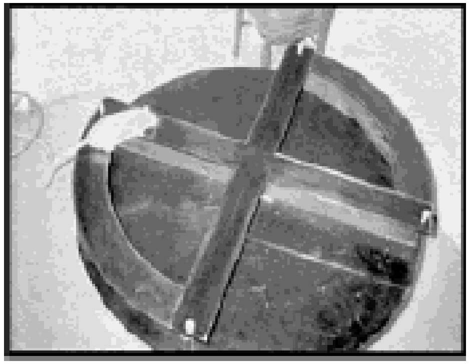


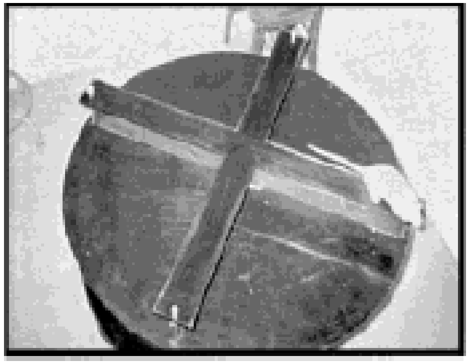
Skaggs & McNaughton (1998), Fig. 2.

Task-Dependent Hippocampal Remapping

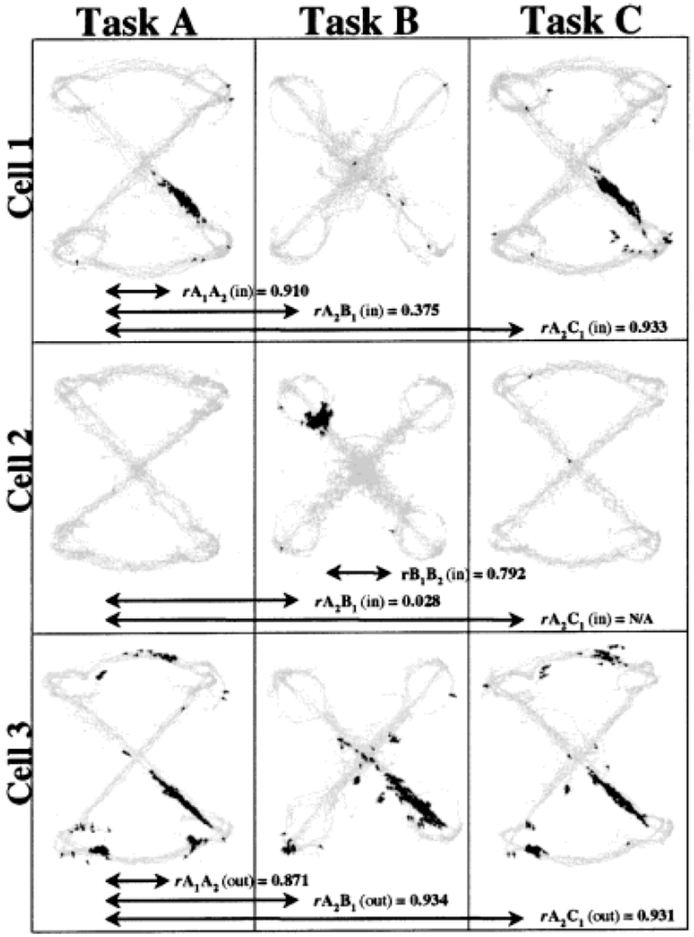
Oler and Markus (2000) recorded from DG, CA3, and CA1 while animals ran either on a Figure-8 or Plus maze.

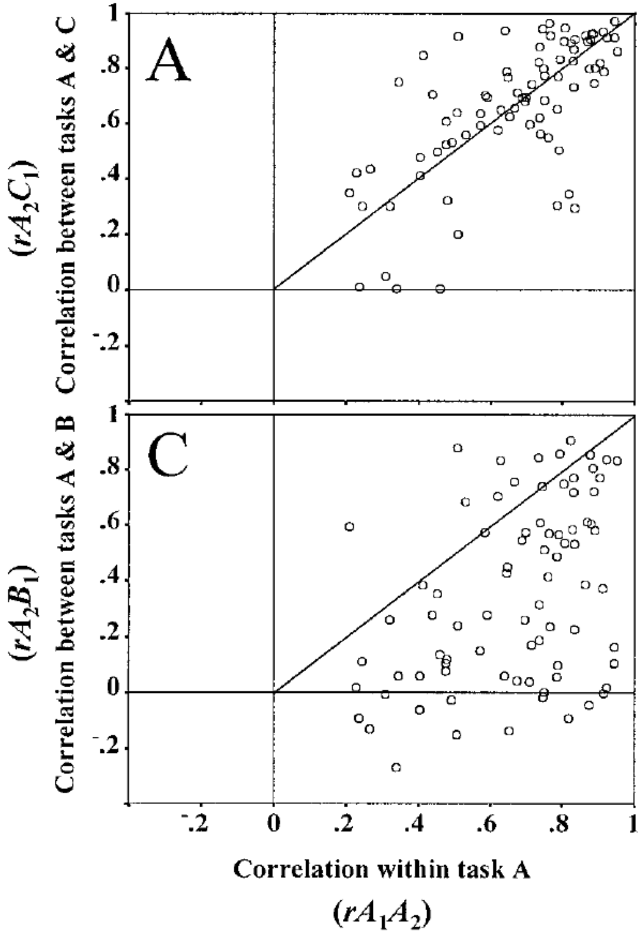






Task-Dependent Remapping





Some but not all fields remapped depending on which task was being performed .

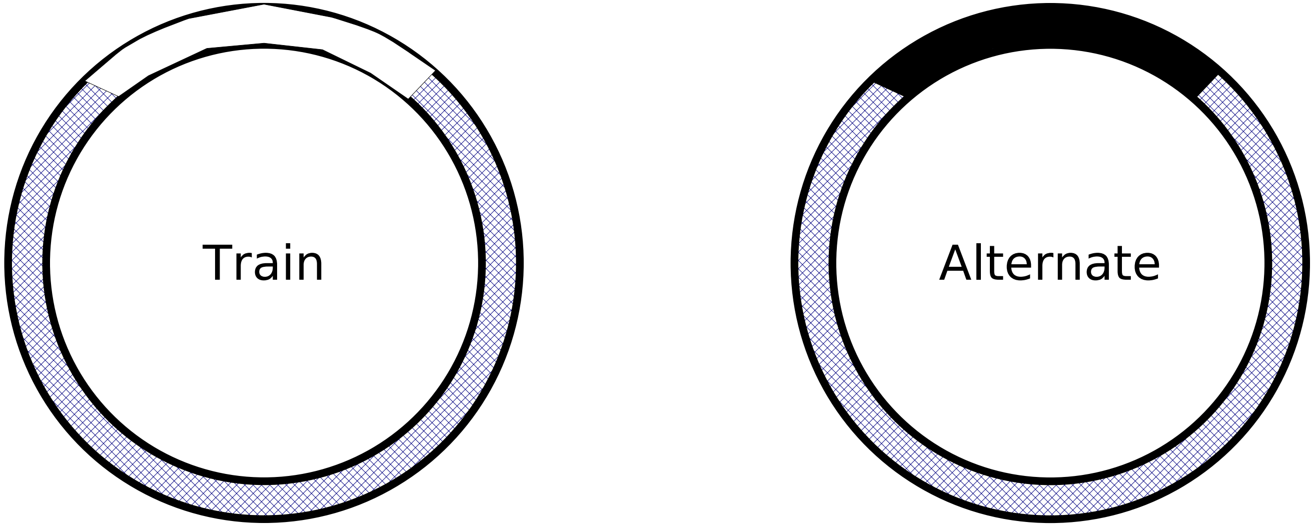
Experience-Dependent Remapping

In some circumstances, rats don't remap right away:

- **Onset** may be delayed.
  - So cannot be direct result of a <u>sensory</u> change.
  - Must reflect some <u>internal</u> change in the rat's representation of its environment: learning.
- **Rate** may be gradual.
  - The time course of remapping tells us something about the experience-dependent learning process.
- **Extent** may be partial or complete.
- What **learning algorithm** is reponsible for these experience-dependent changes**?**

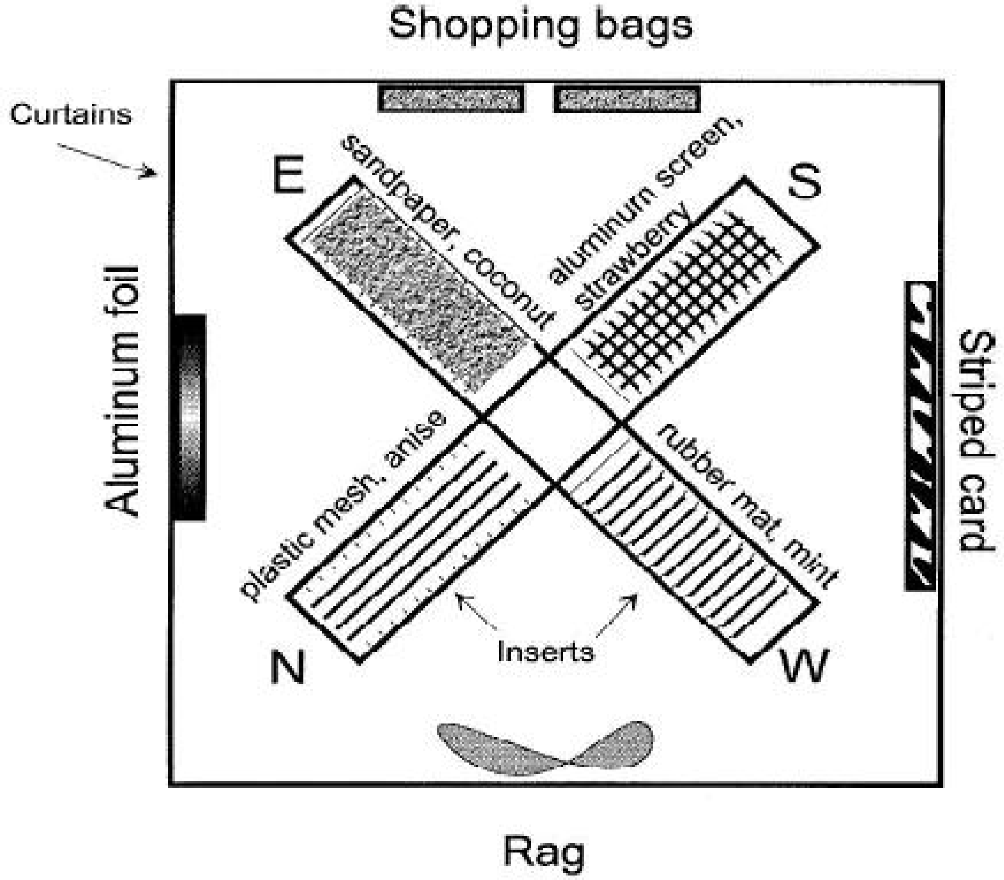
Bostock et al. (1991): Delayed Abrupt Complete Remapping

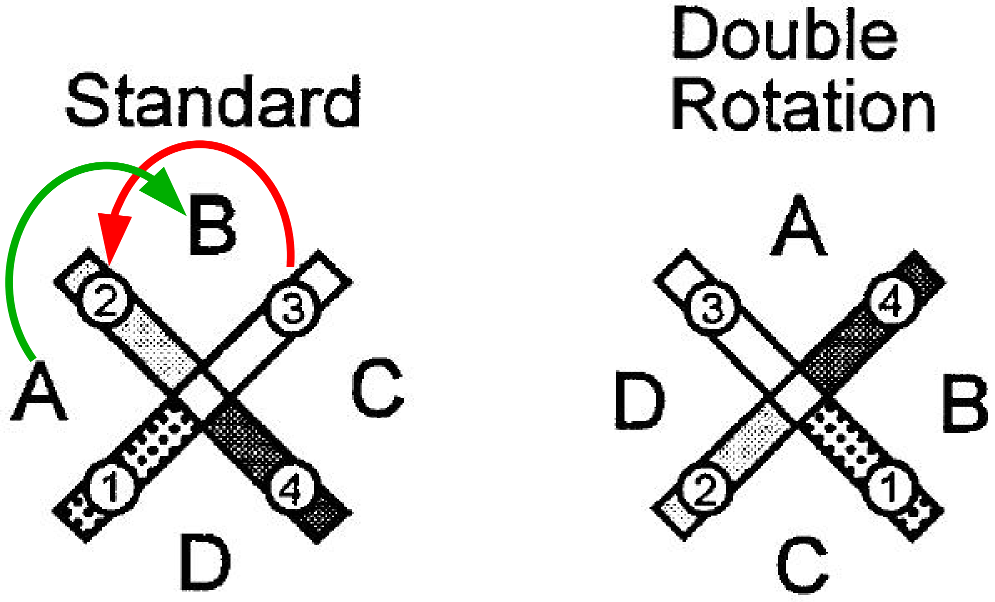
- Train in cylinder with white card, then alternate exposure to white and black cards.
- Most rats did not remap upon first exposure to black card.
- But once a rat remapped, it continued to do so.



Tanila et al. (1997): Gradual Remapping

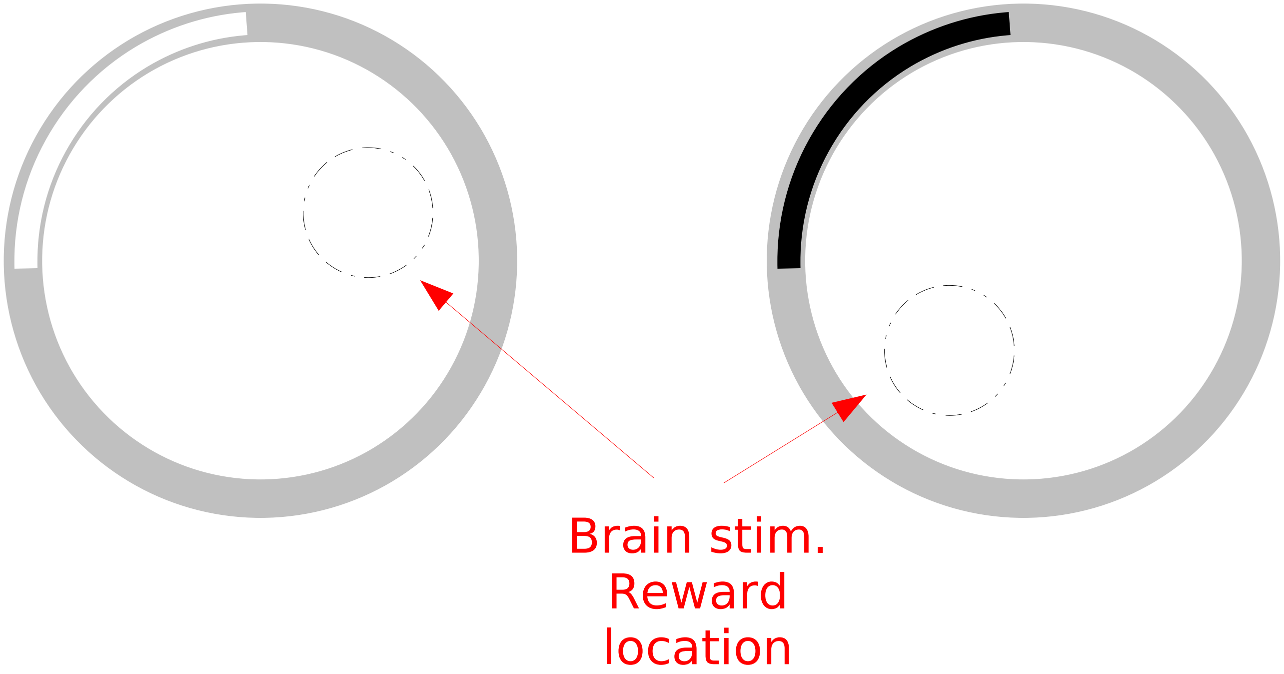
- Discordant responses: some cells followed local cues, some followed distal, some remapped. The extent of remapping appeared to increase over several days. (Based on data summed over rats.)
- Is the rat becoming more *certain* that the two environments are reliably different?





Does Remapping Matter?

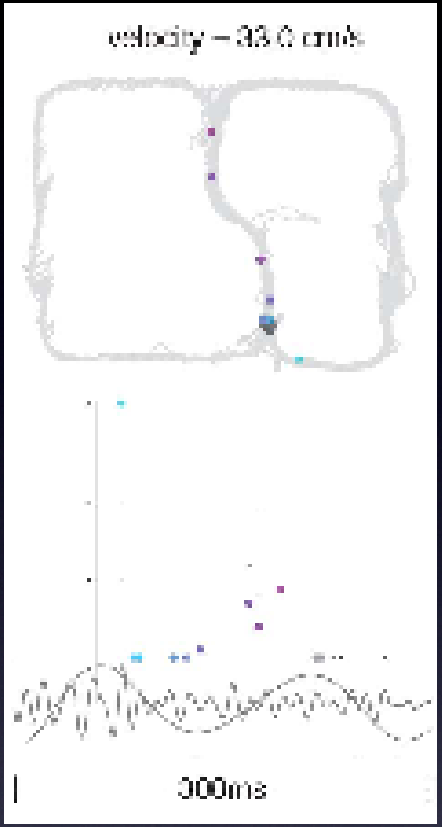
- Masters & Skaggs: remapping coincides with insight into a task:

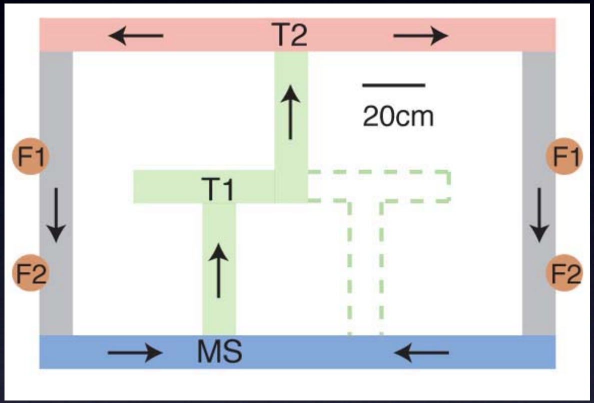


- One rat quickly remapped & learned the task; one never did. One rat didn't remap until day 11, when it suddenly “got” the task. Cause or effect?

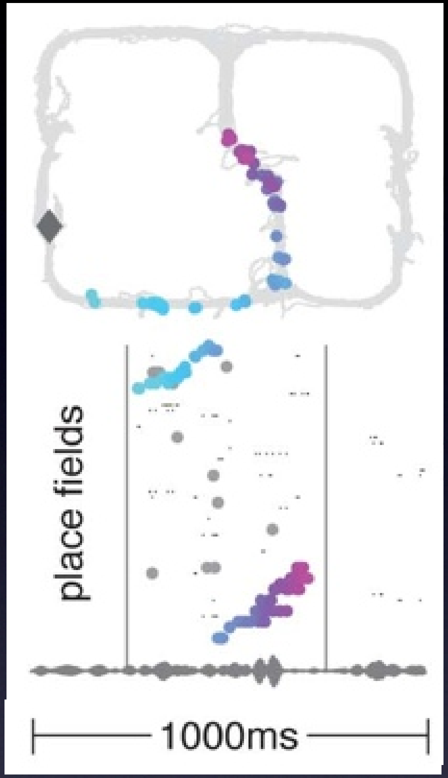
Theta vs Replay Sequences

Theta





Replay

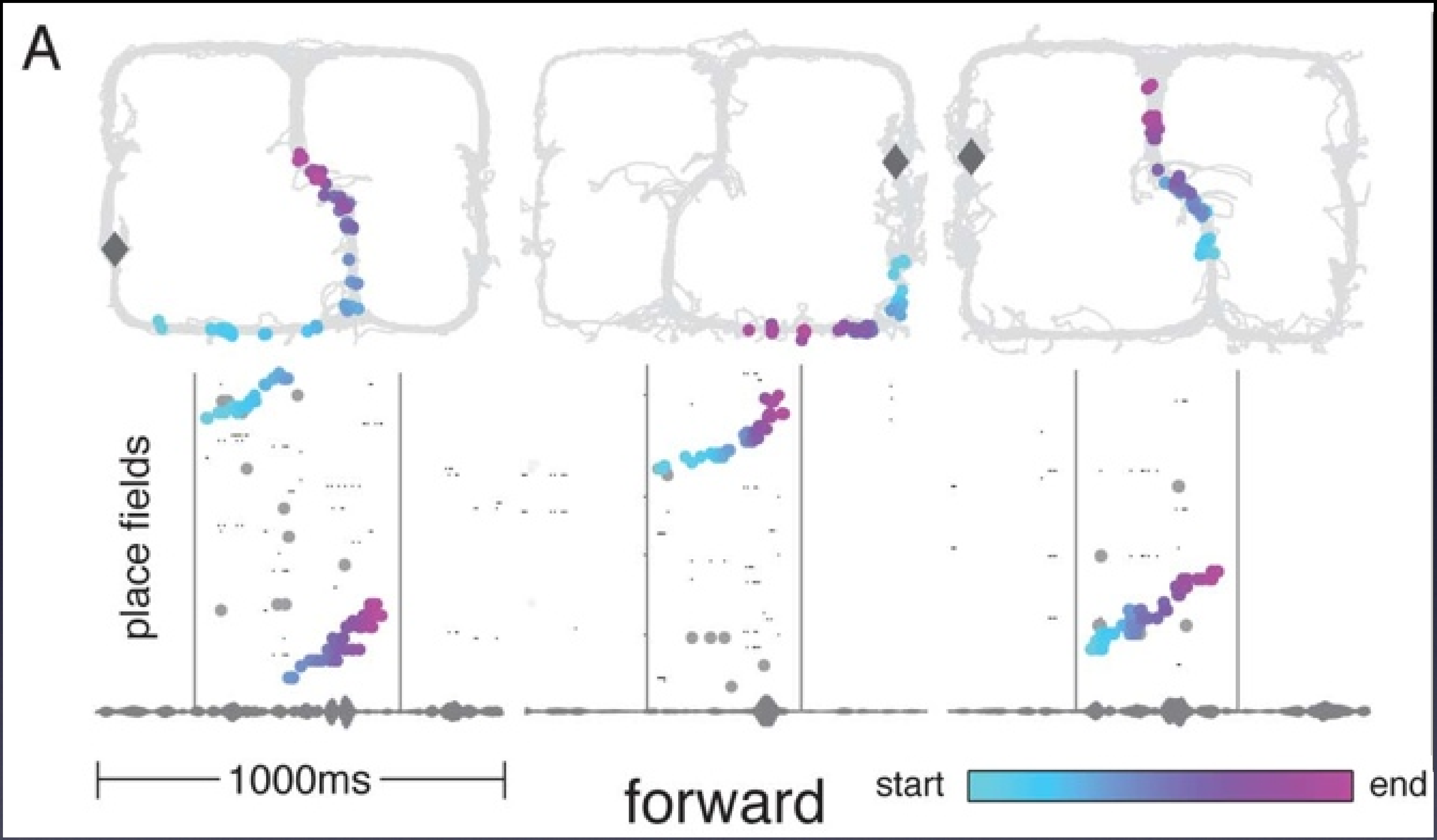


Occur during attentive behavior
Theta oscillation is present
Tied to the animal’s location
Forward sequence
Few neurons are active
Relatively short paths represented
Experience encoding and recall

Occur during awake rest
Sharp wave ripples present
Not always tied to the animal’s location
Forward or backward sequence
Many neurons are often active
Highly variable path lengths represented
Memory consolidation, learning of cognitive maps

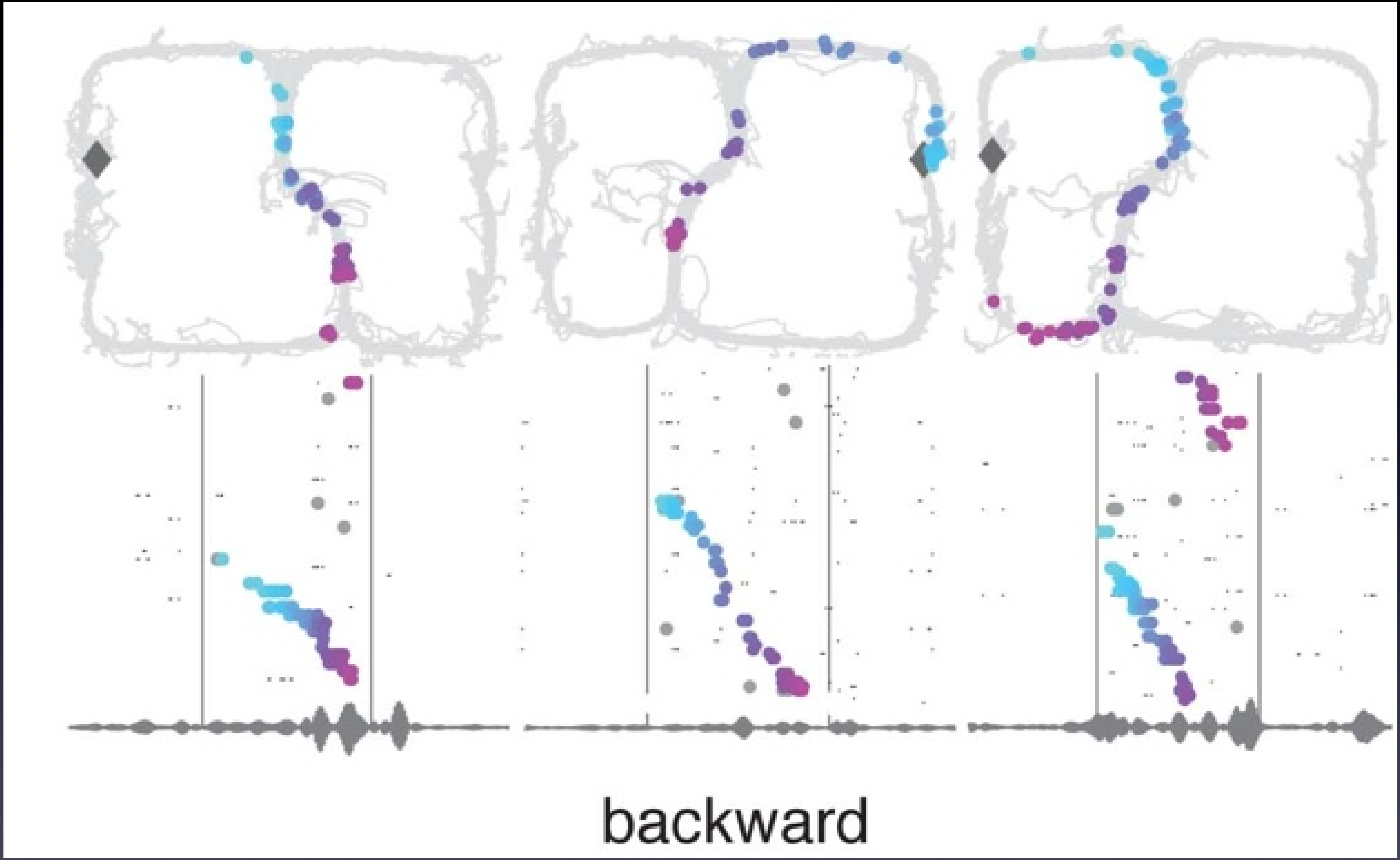
Slide courtesy of Anoopum Gupta

Forward Replay



Gupta, van der Meer, Touretzky, Redish, 2010

Backward Replay

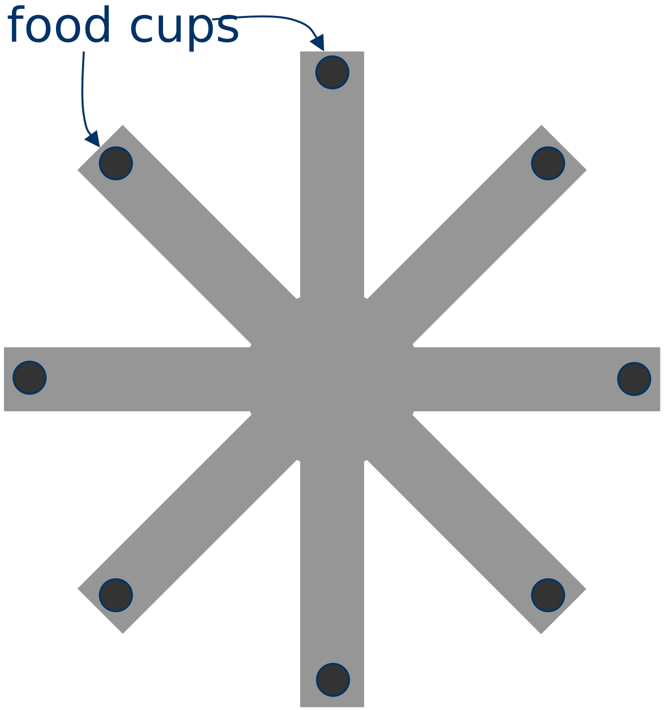


Gupta, van der Meer, Touretzky, Redish, 2010

Configural Learning

- Sutherland and Rudy suggested that hippocampus learns complex configurations of cues.
- After lesion, animals can still do tasks that depend on only one cue at a time.
- But tasks that depend on *relationships* among cues are impaired. Examples:
  - eight-arm radial maze
  - Morris water maze

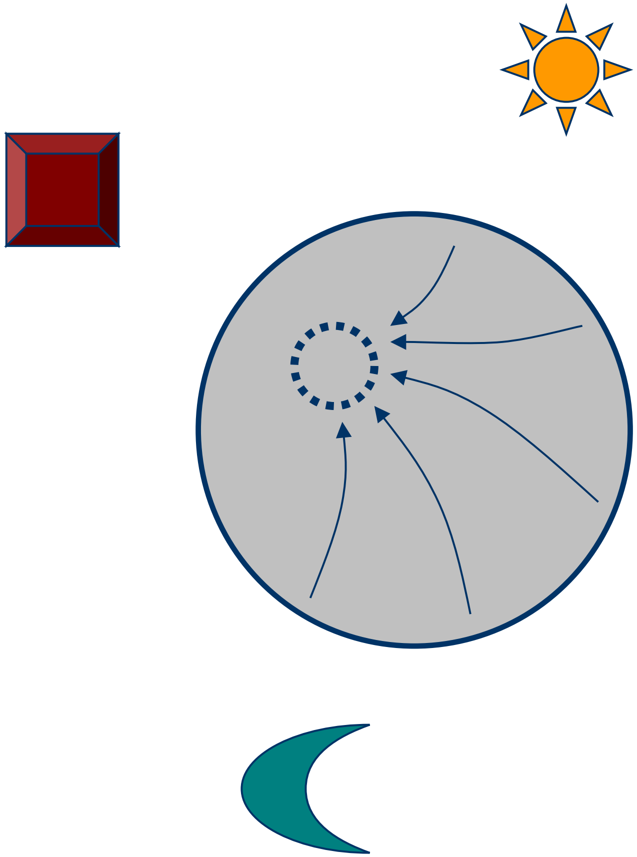
Spatial Working Memory



- Apparatus: 8-arm radial maze with food cups at each arm end
- All food cups are baited at the beginning of each trial
- During each trial, rats must remember which arms have already been visited. *A second arm visit provides no reward.*
- Rats with hippocampal lesions are severely impaired at this task (Neave et al., 1997)

Morris Water Maze

- Large pool filled with milky (opaque), cold water.
- A submerged platform is located at a fixed position in the pool.
- Distal landmarks outside the pool are located around the room; they never move.
- The rat is released from a random starting position and must swim to the platform to get out of the water.



Morris Water Maze

Sutherland and Rudy (1988):

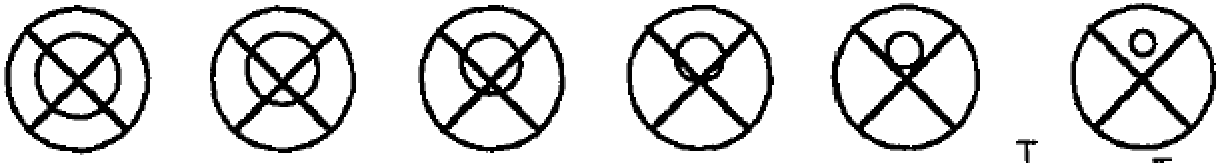
- Rats with fornix lesions can still navigate to a visible platform.
- But they are impaired at learning to find the hidden platform.
- Finding the hidden platform presumably requires recognizing a *configuration* of cues.

Morris Water Maze Revisited

- Rats with 48 training trials prior to lesioning the hippocampus showed no deficit (Morris *et al.*, 1990).

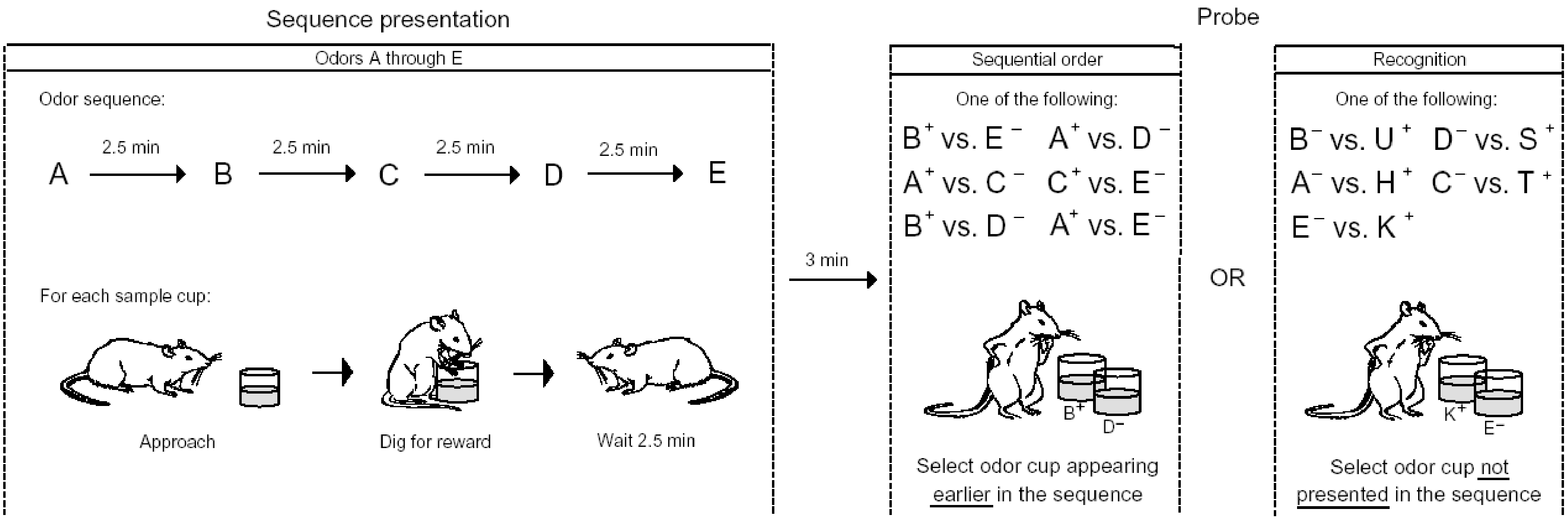
Hippocampal lesion causes a *learning* deficit!

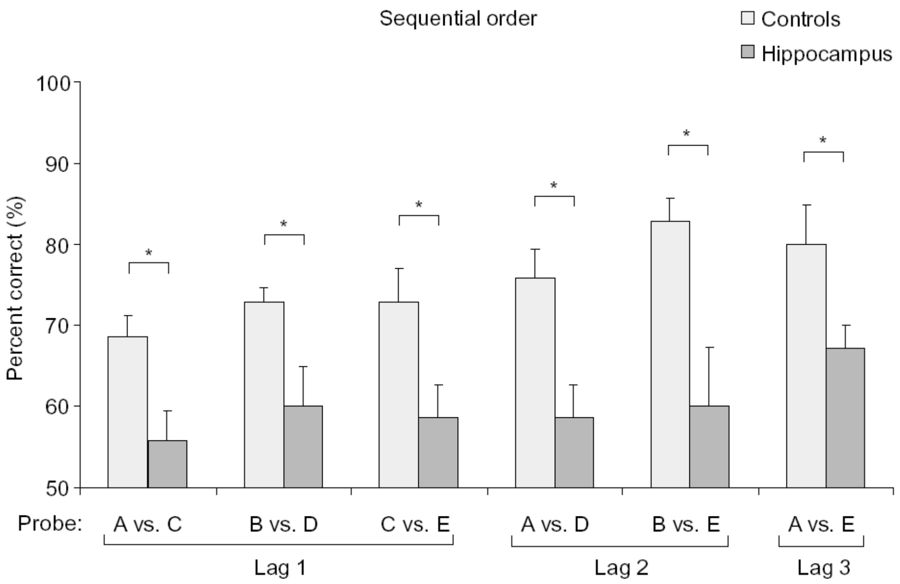
- Lesioned rats can gradually learn to find a hidden platform using successively smaller platforms (Schallert et al., 1996):

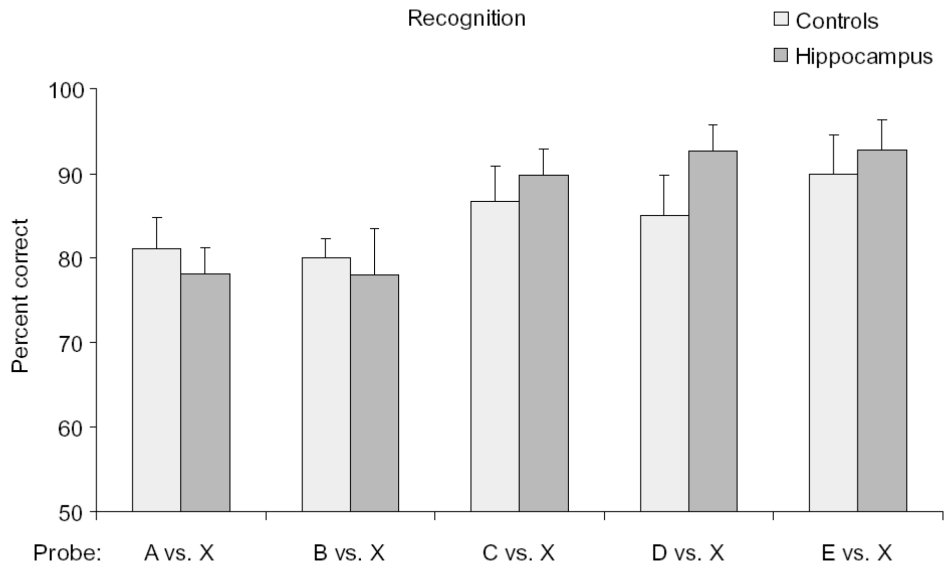


Hippocampal lesions cause impairment only when learning the whole path at once!

Sequence Learning







What Does the Hippocampus Do?

- Builds sparse random representations of complex configurations of sensory and behavioral information.
- Learns spatiotemporal associations between these, within appropriate context, e.g., for:
  - Learning paths to a goal
  - Learning odor sequences
- Retains representations for later use / consolidation.
  - Replay of paths during sleep
  - Recall of task state after delay:
    - DMS and DNMS tasks
    - Trace conditioning