Grid Cells and Path Integration

Computational Models of Neural Systems

Lecture 3.6

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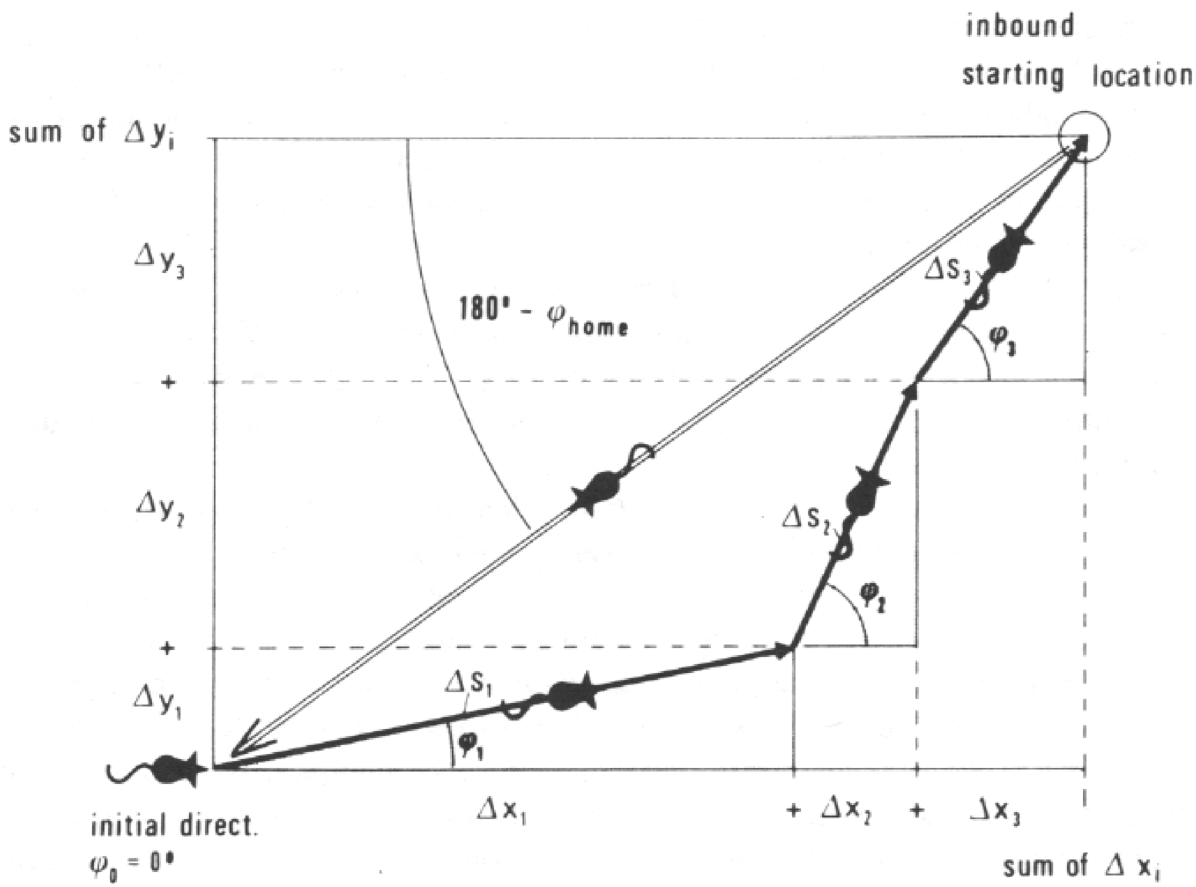
Outline

- Models of rodent navigation
  - Where is the path integrator?
- Grid cells in entorhinal cortex
- Grid cell models
  - Fuhs & Touretzky (many bumps, one sheet)
  - McNaughton et al. (one bump on a learned torus)
  - Burgess et al. (oscillatory interference)
- Outstanding questions about grid cells

Path Integration in Rodents

Mittelstaedt & Mittselstaedt (1980): gerbil pup retrieval



Where Is the Path Integrator?

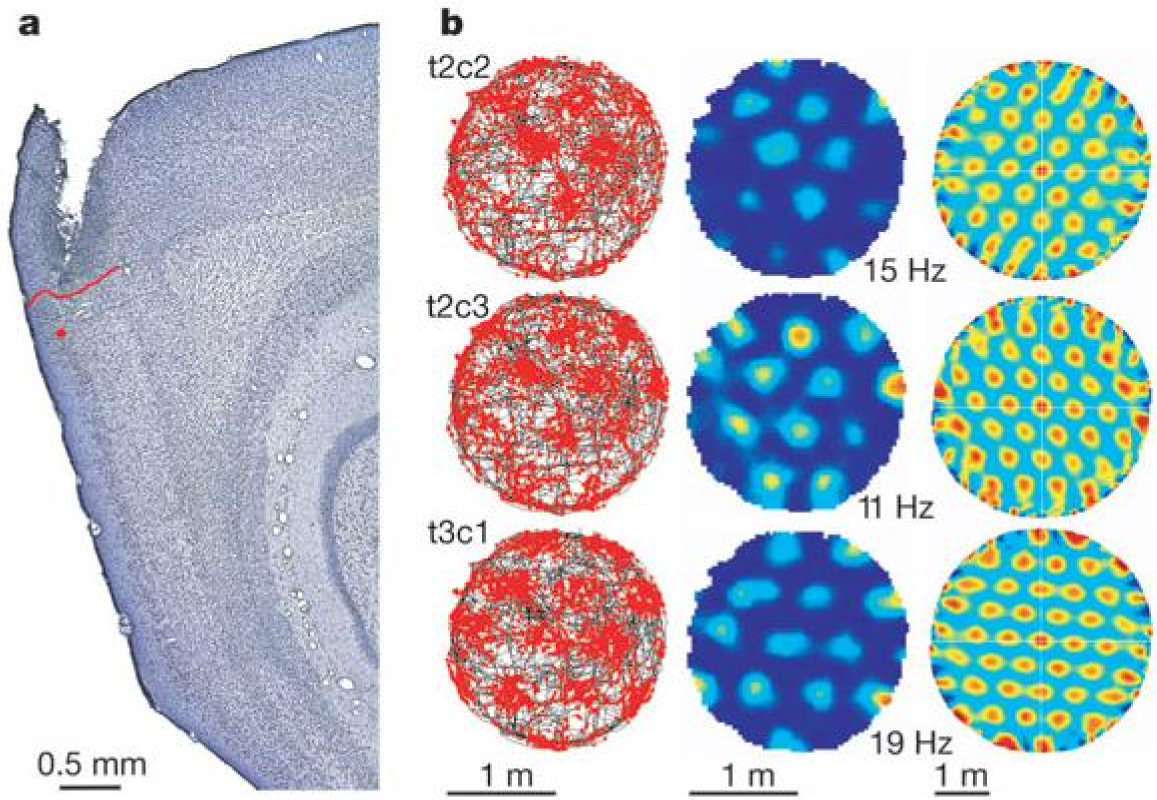
- Early proposals put the path integrator in hippocampus.
- Problem: accurate path integration on one map is hard.
- Doing it on multiple co-existing maps is much harder!
  - Not enough connections?
  - Won't work for spontaneously created maps.
- Redish & Touretzky (1997) argued that the path integrator must be independent of hippocampus.
- So where is it???

Criteria for a Path Integrator (Redish & Touretzky, 1997)

1) Receives input from the head direction system.
2) Shows activity patterns correlated with animal's position (and doesn't remap across environments).
3) Receives information about self-motion from motor and vestibular systems.
4) Updates the position information using self-motion cues.
5) Sends output to an area associated with the place code.

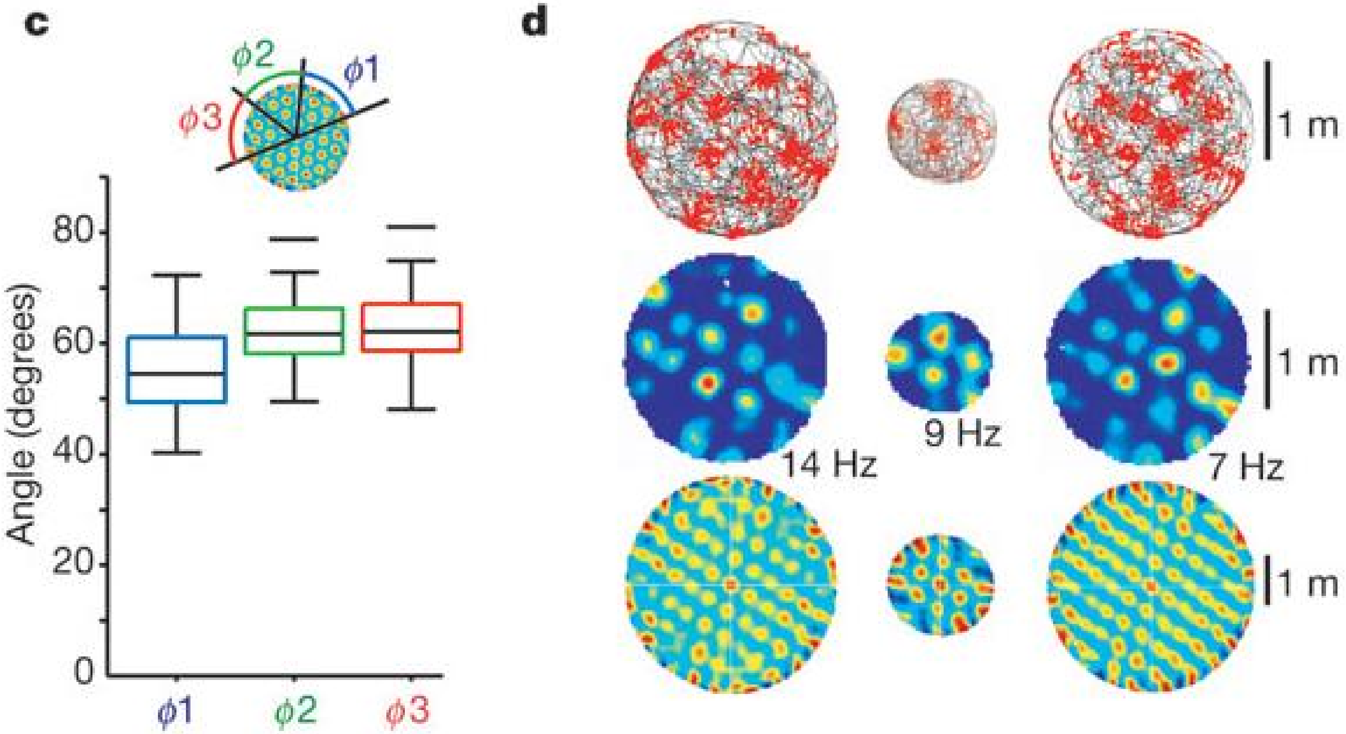
Grid Cells in Entorhinal Cortex (Fyhn et al., Science 2004)

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



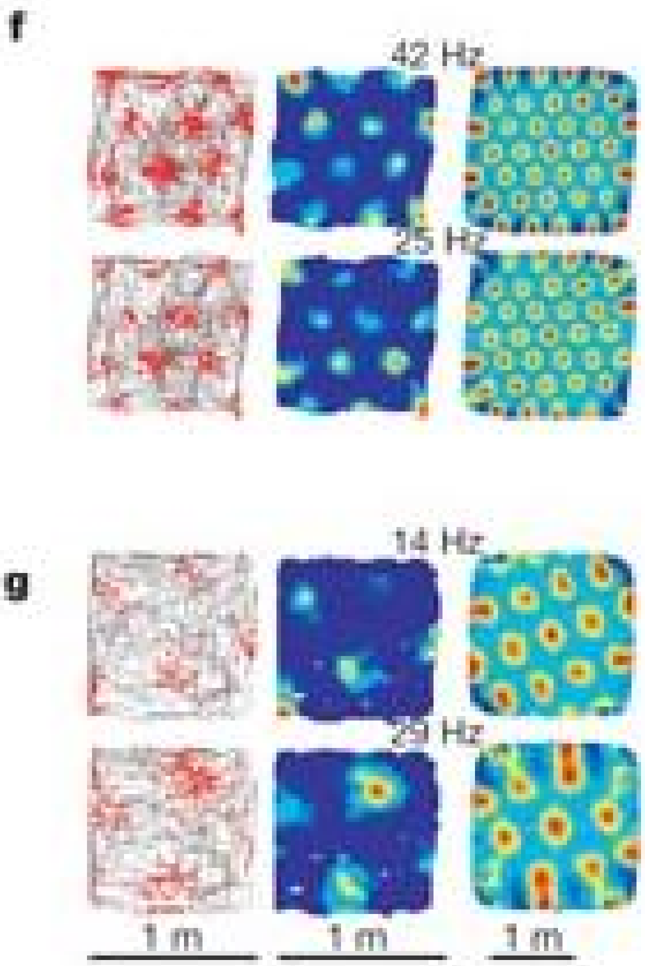
Hafting et al., 2005

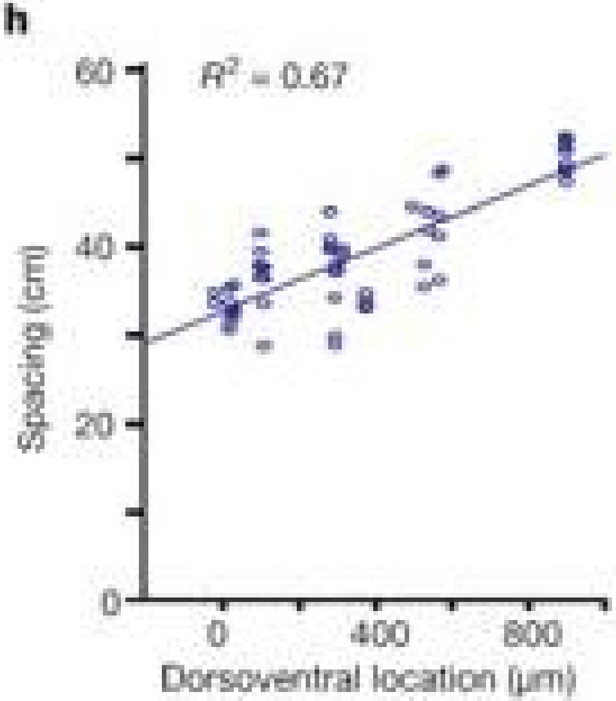
Grids are Hexagonal and Independent of Arena Size



Hafting et al., 2005

Multiple Grids: Spacing Increases From Dorsal to Ventral in Discrete Steps





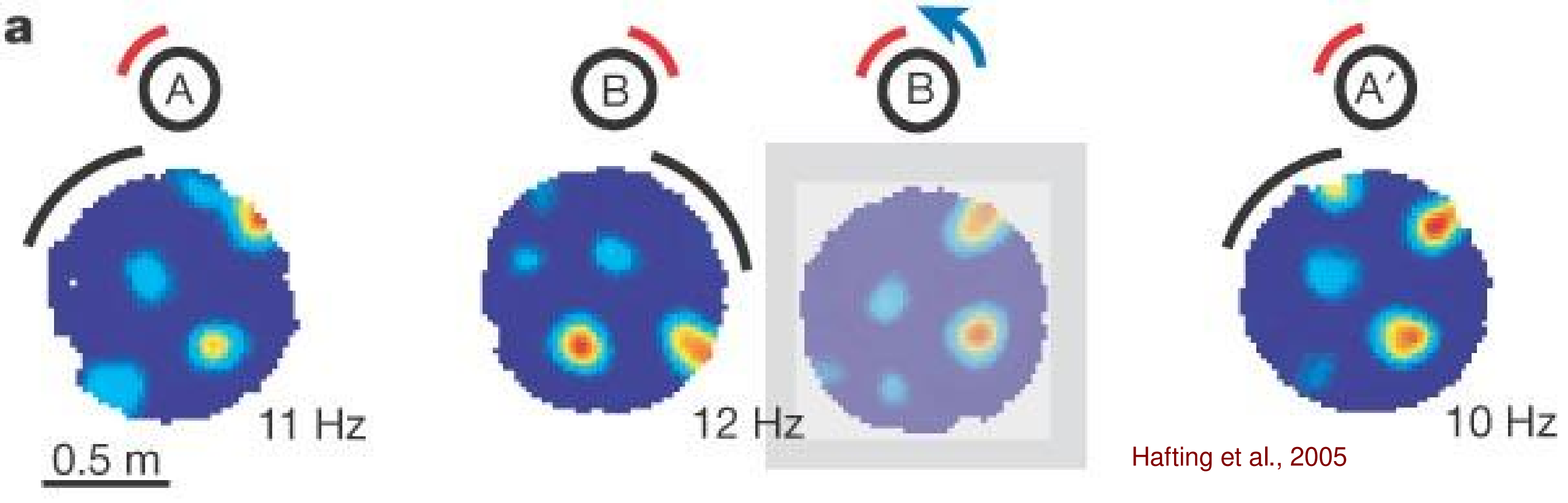
Hafting et al., 2005

More Grid Cell Properties

- Nearby grid cells have different spatial phases.
- Grids persist in the dark.
- Grid structure is expressed instantly in novel environments.
- Grids can have different orientations.
  - The original reports from the Moser lab suggested that grids could have different orientations
  - Some subsequent reports indicated a common orientation.
  - Later, more comprehensive studies show that the grid cell system is modular (each grid is a module), and orientations can differ (Stensola et al. 2012)

More Grid Cell Properties

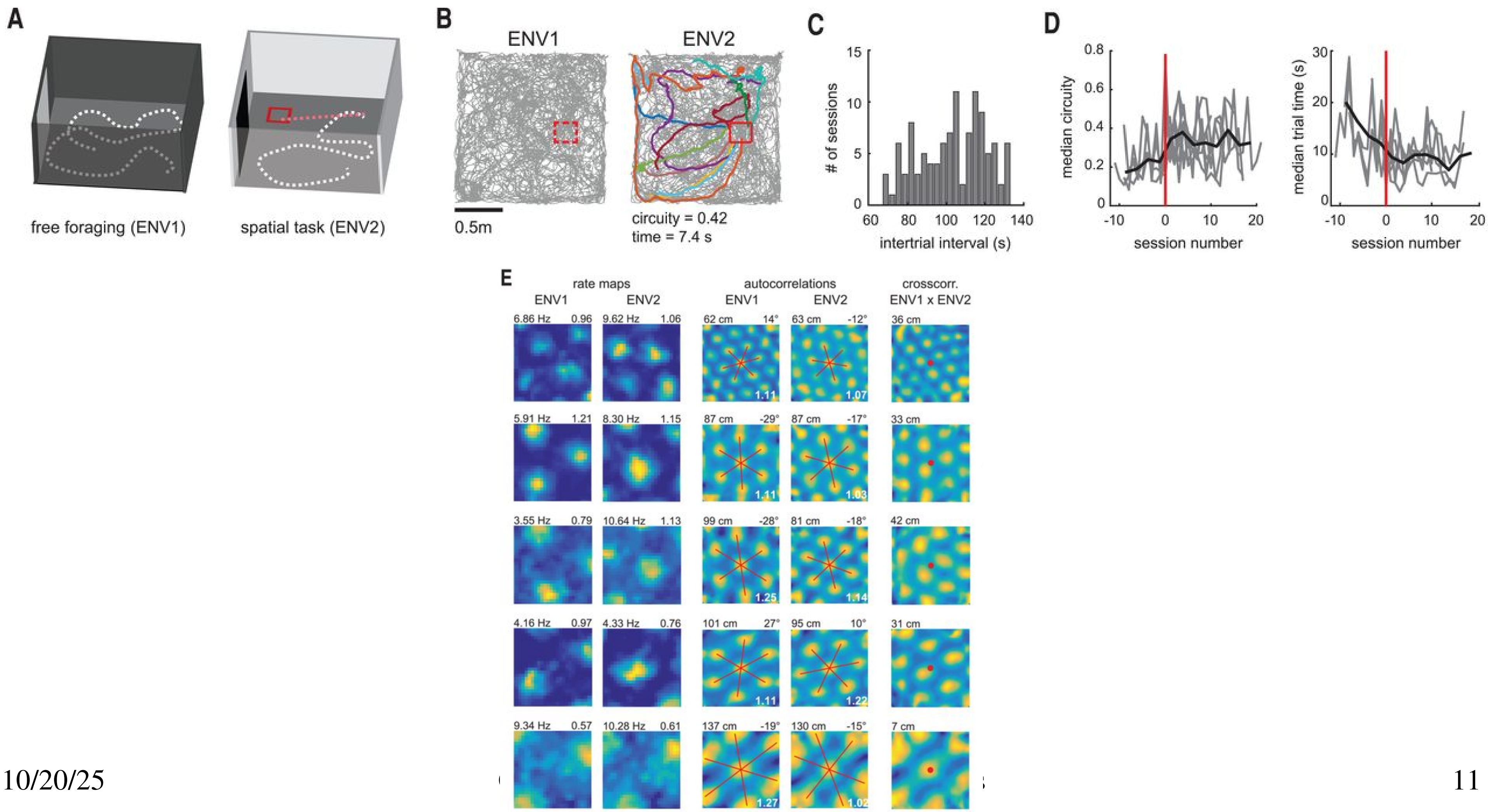
- Grids maintain alignment with visual landmarks.
- Different peaks in the grid have different amplitudes, reproducible across trials. (Suggests sensory modulation.)



Trials A and A': cue card in normal position: firing fields are the same.
Trial B: cue card rotated 90 degrees: firing fields have rotated.
Shaded plot: firing rate map for condition B, rotated by -90 degrees, closely matches the A and A' maps.

Grid Encoding of Reward

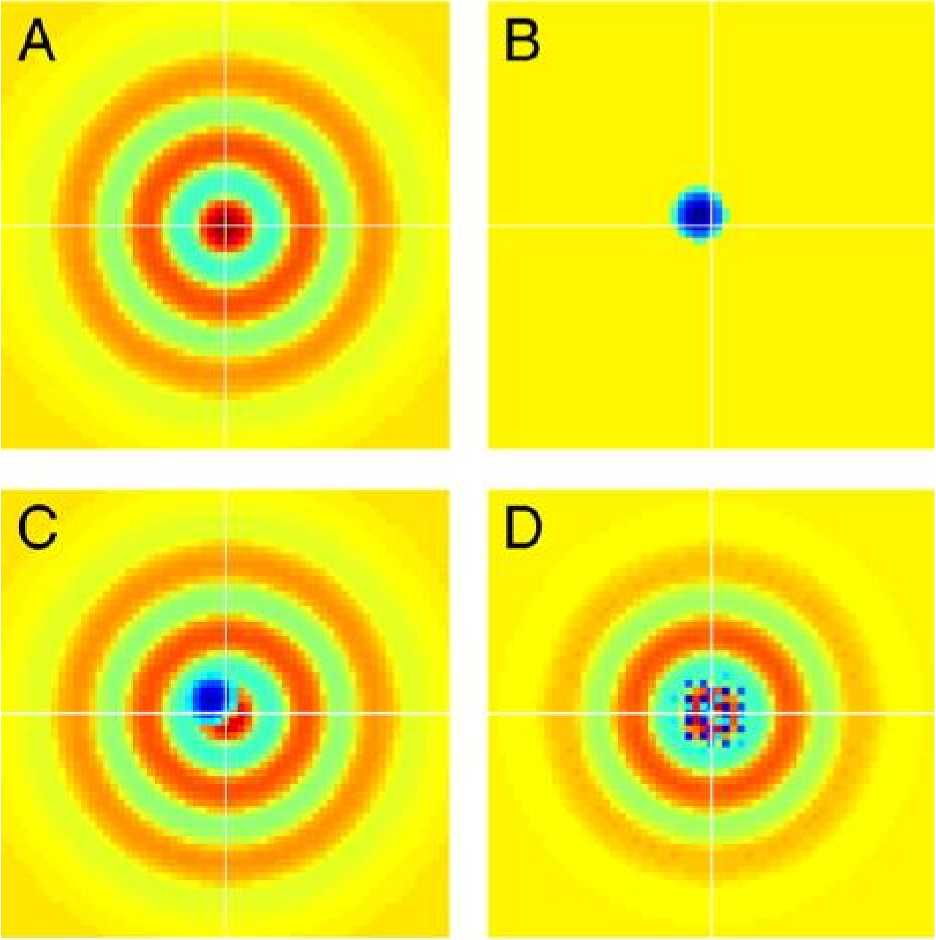
- In a foraging task with a defined reward location, grid cells showed higher firing rates near the reward location (Butler et al., 2019)



Fuhs & Touretzky Model: Many Bumps on a Sheet

J. Neurosci. 26(16):4266-4276, 2006

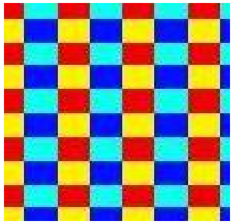
- Concentric rings of excitation/inhibition cause circular bumps to form.
- Most efficient packing of circles in the plane is a hexagonal array.
- Offset inhibition will cause the bumps to move.
- Panels A-C: output weights; panel D: input weights.



Fuhs & Touretzky, 2006

Velocity Input to Grid Cells Is Based on Preferred Direction

- Fuhs & Touretzky used four preferred directions.
- At every point where four pixels meet, all four preferred directions are represented.



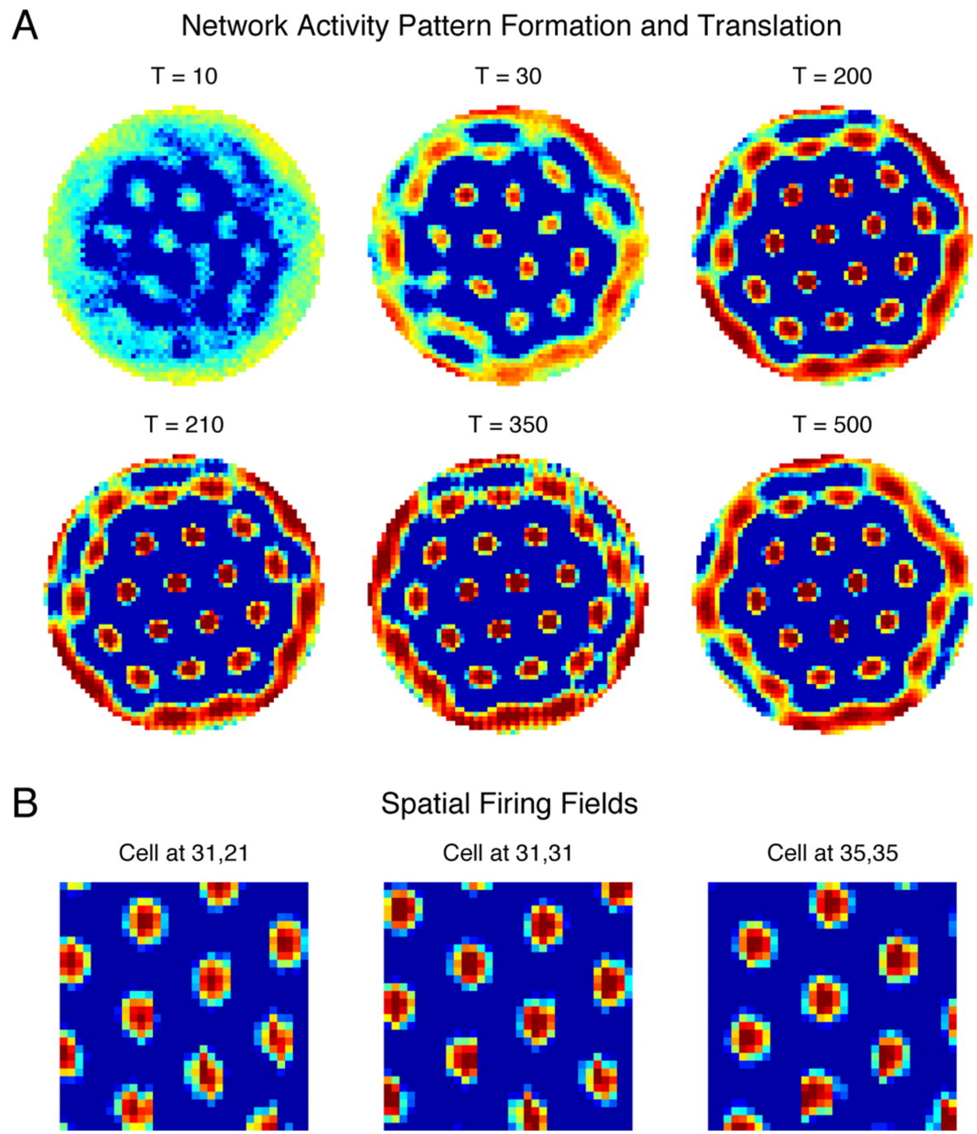
- Velocity tuning of cell must match direction of inhibitory component of weight matrix.

The Bump Array, and The Grid

- A) A hexagonal array of bumps forms over the sheet.

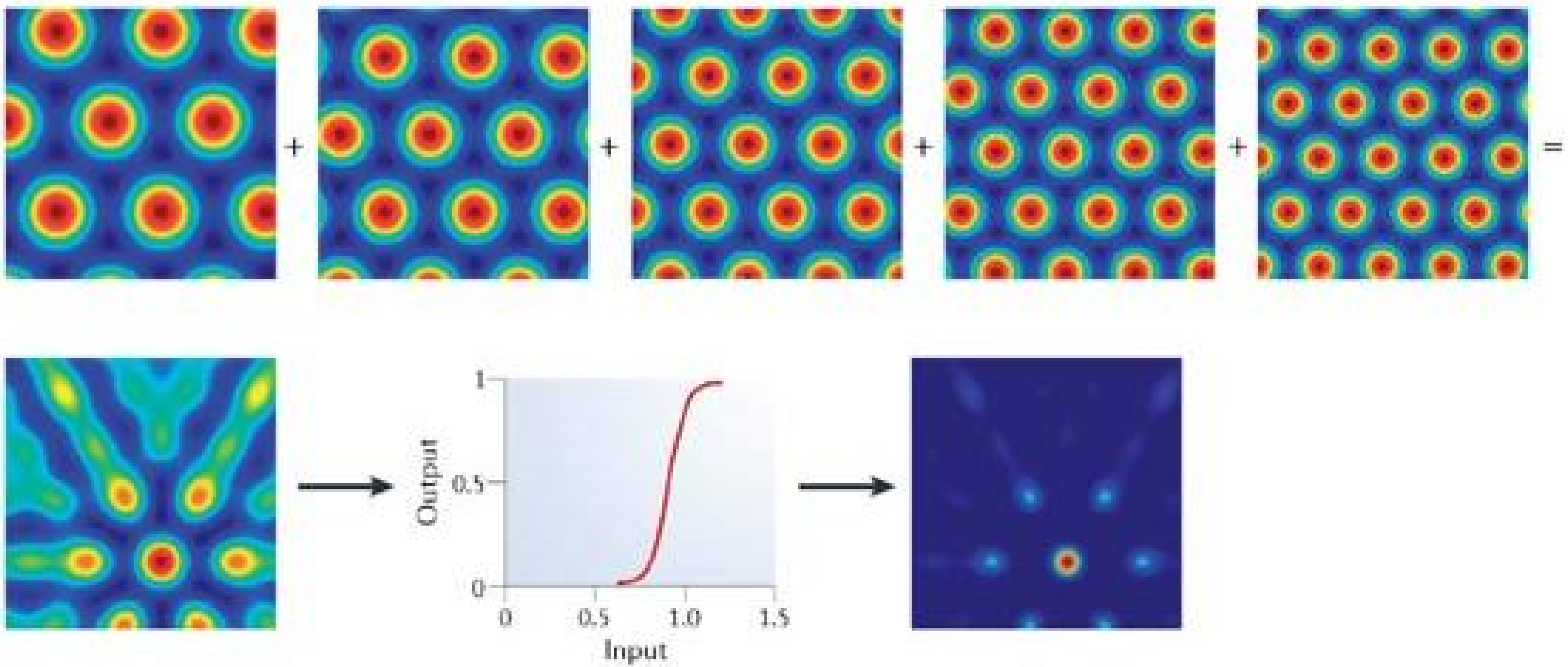
  Inhibition around the periphery allows bumps to smoothly "fall off the edge"

- B) The firing fields of individual cells show a similar hexagonal grid pattern as the bumps move over the sheet.



Fuhs & Touretzky, 2006

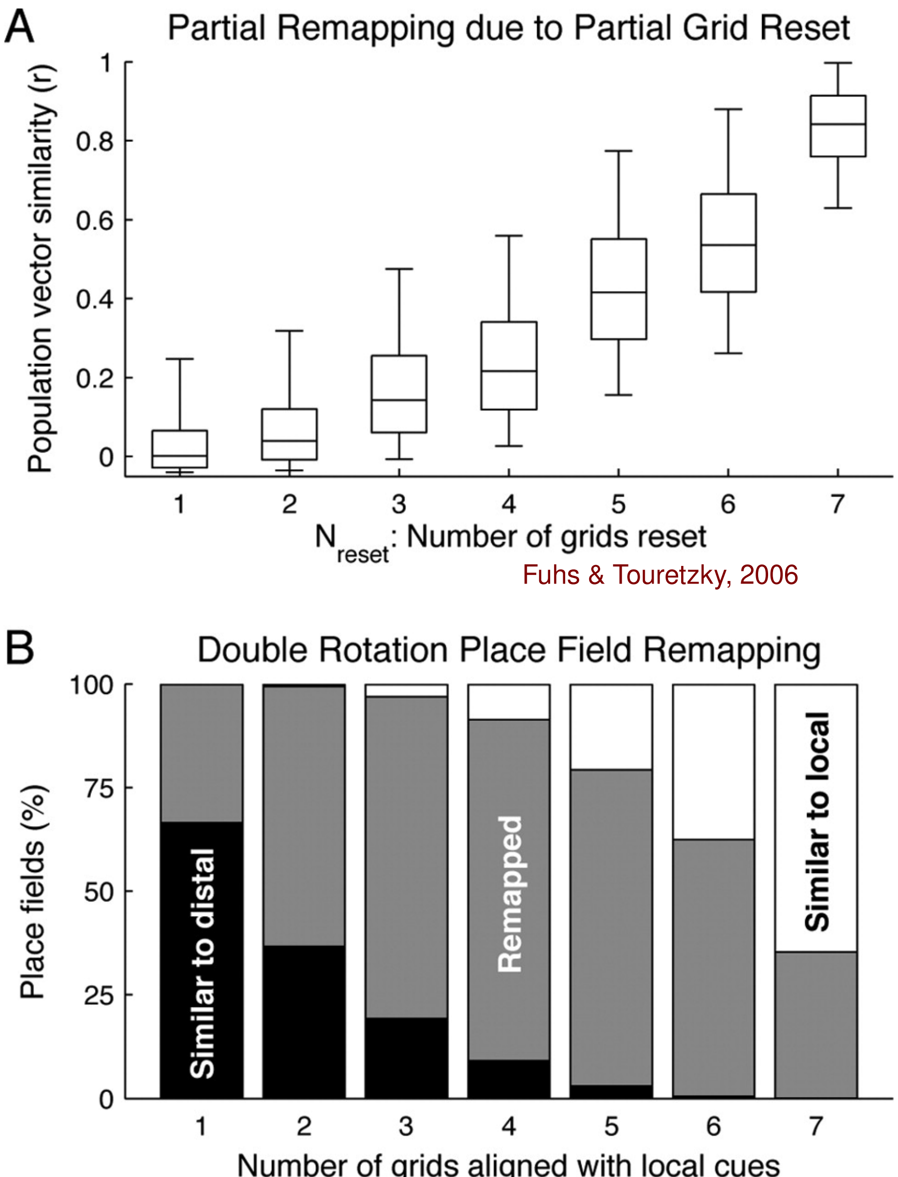
Conjunction of Multiple Grid Scales Yields Place Fields



McNaughton et al., 2006

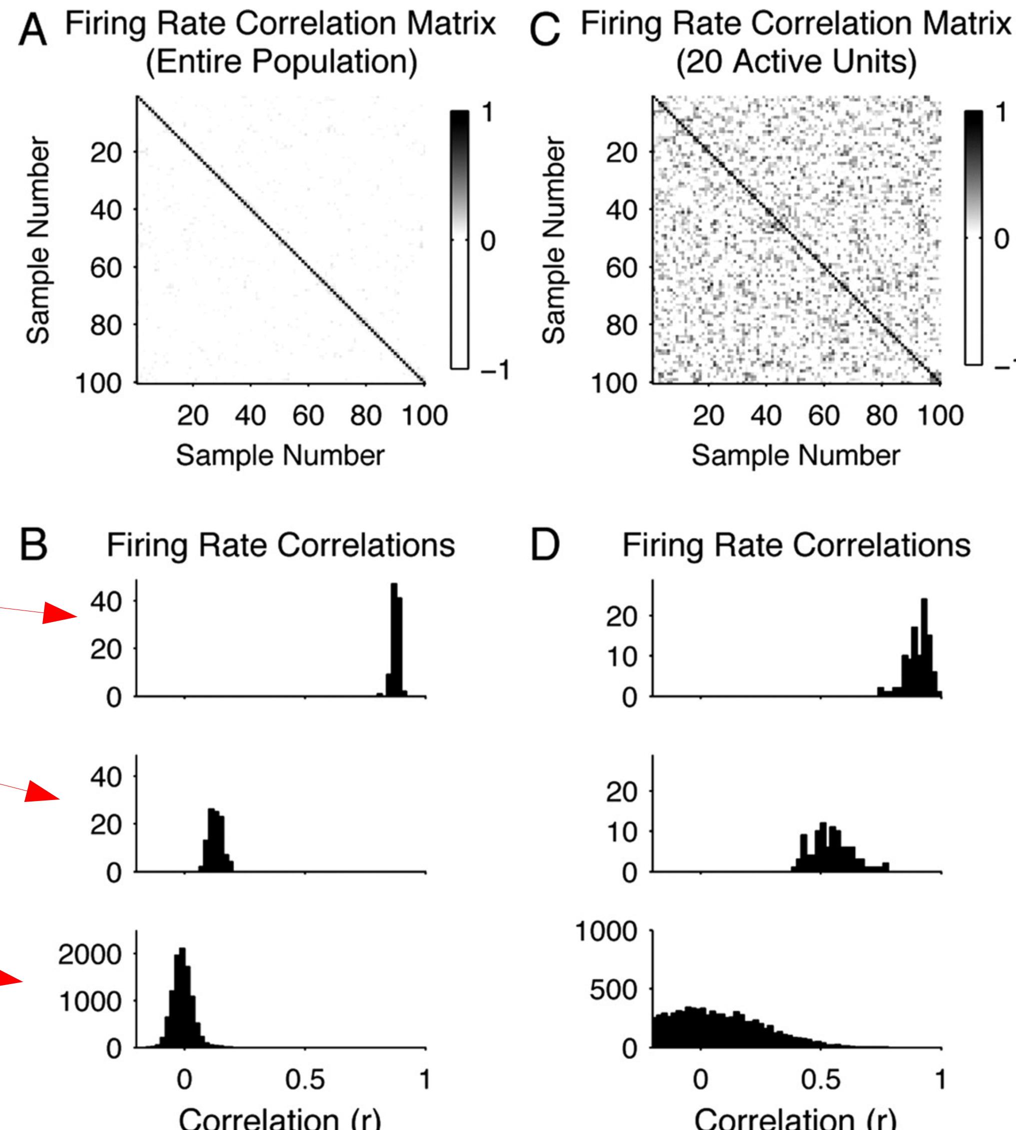
Resetting Only Some Grids Causes Partial Remapping

- A) Place code is more similar as more grids are reset.
- B) Partial remapping effects seen in double cue rotation experiments could be explained by different grids aligning with different cue sets (local vs. distal.)
- Alignment could be in terms of phase or orientation.



Sensory Modulation of Grid Cell Activity

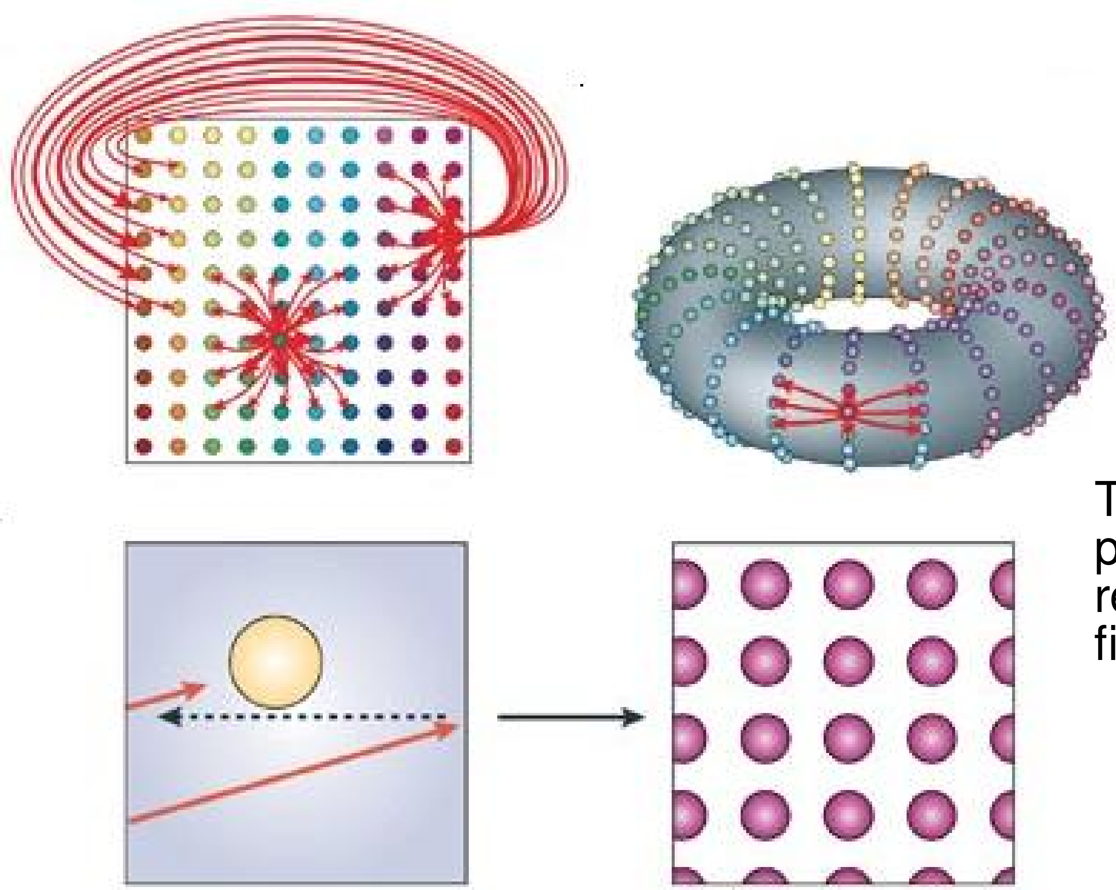
- 100 random input patterns over grid cell population.
- A,B: results using entire population
- C,D: results from sampling only 20 active cells.
- B1/D1: correlation between two presentations of the same random pattern.
- B2/D2: correlation with the next closest matching pattern.
- B3/D3: all off-diagonal correlations.



Fuhs & Touretzky, 2006

McNaughton et al. Model: Bump on a Learned Torus

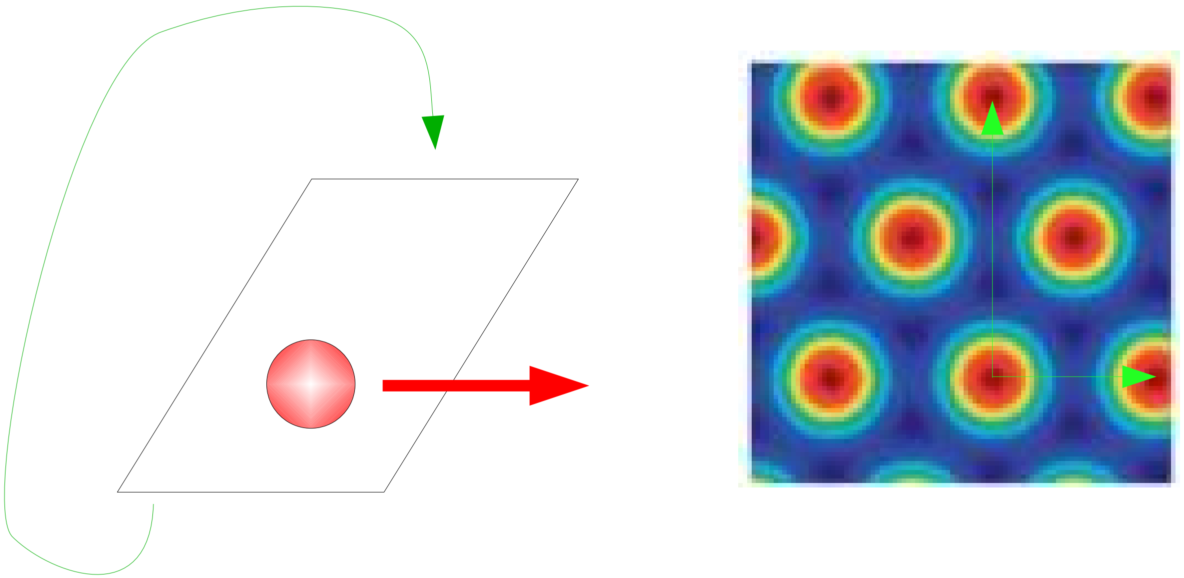
Nature Reviews Neurosci. 7:663-678, 2006



Toroidal connectivity produces a rectangular grid of firing fields.

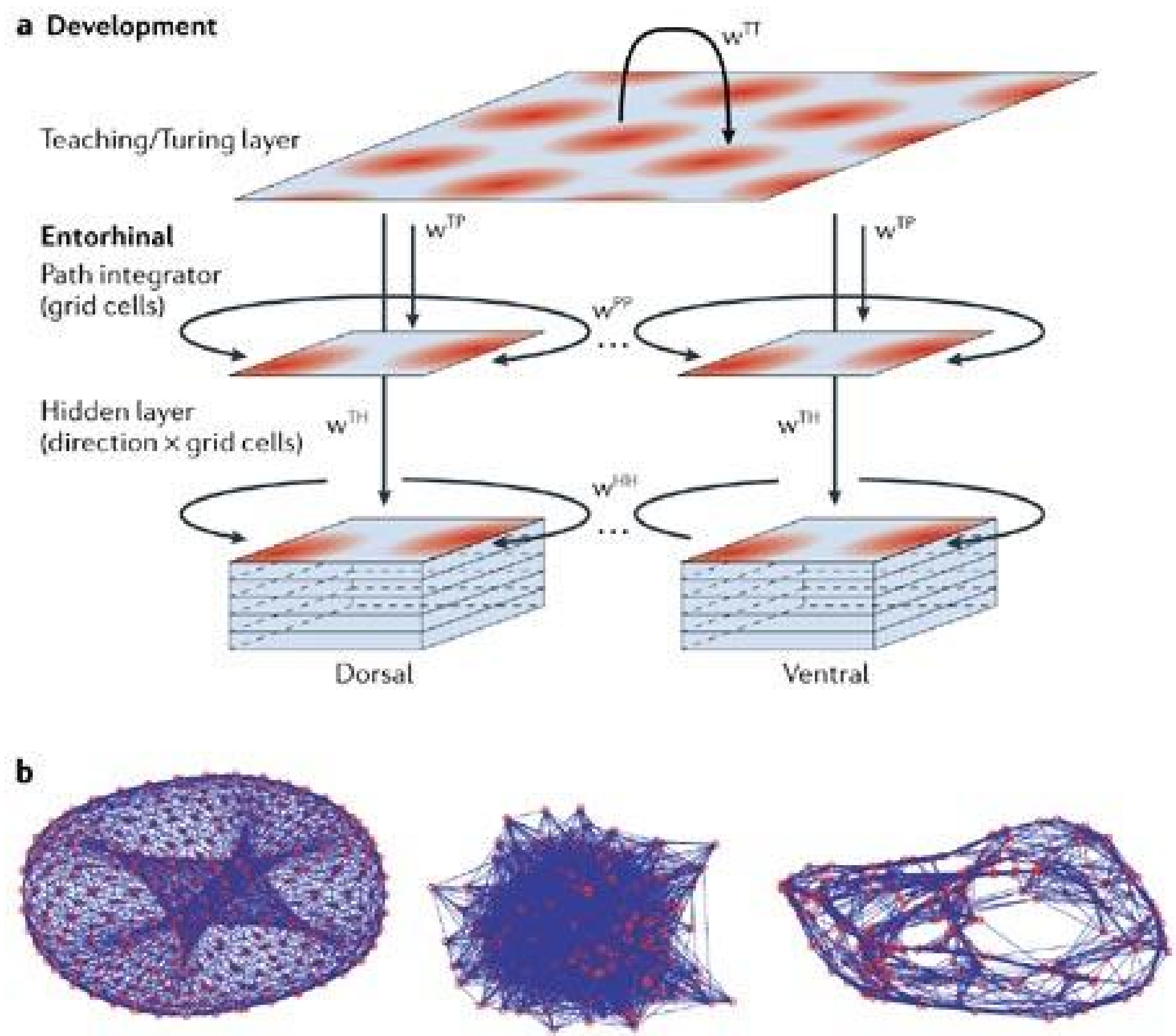
McNaughton et al., 2006

How To Get A Hexagonal Grid From A Torus



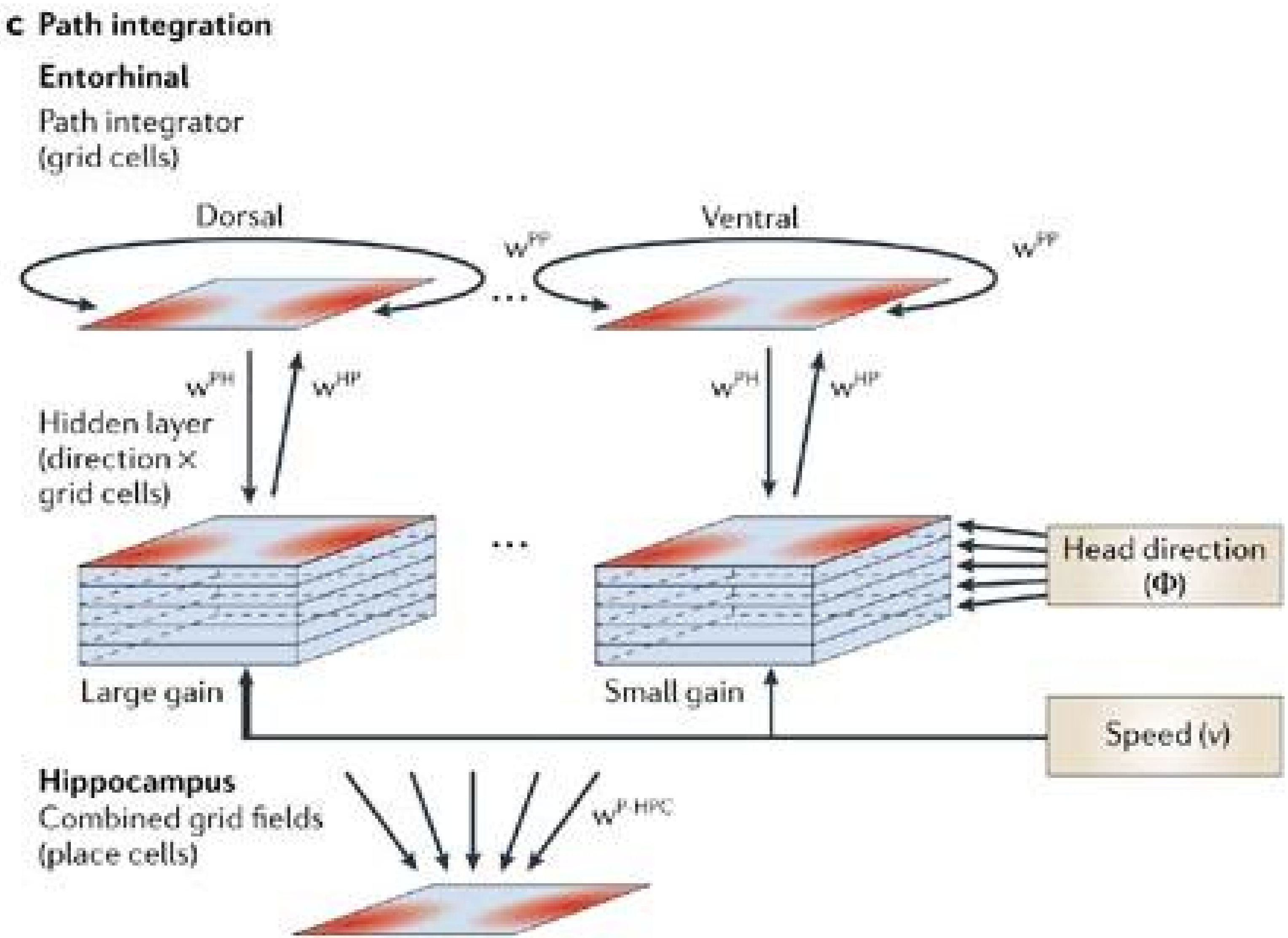
Development Stage

- Hexagonal array of bumps forms spontaneously in the “Turing cell layer”.
- Array drifts randomly but only by translation, not rotation.
- Hebbian learning trains the grid cells on the toroidal topology induced by the repeating activity patterns.



McNaughton et al., 2006

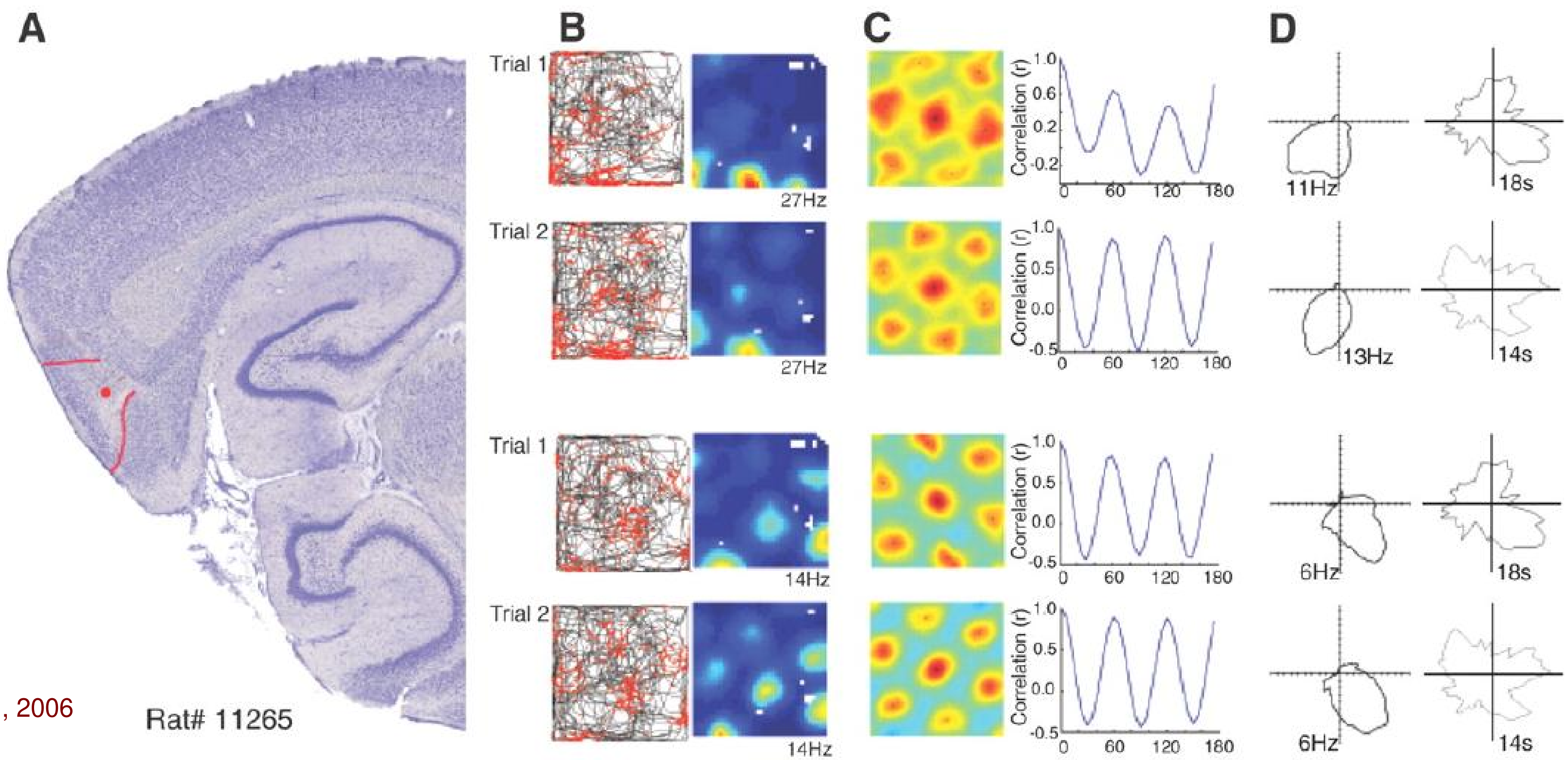
Mature Stage: "Turing Layer" Gone; Velocity Modulates Activity



McNaughton et al., 2006

Velocity Modulated Grid Cells

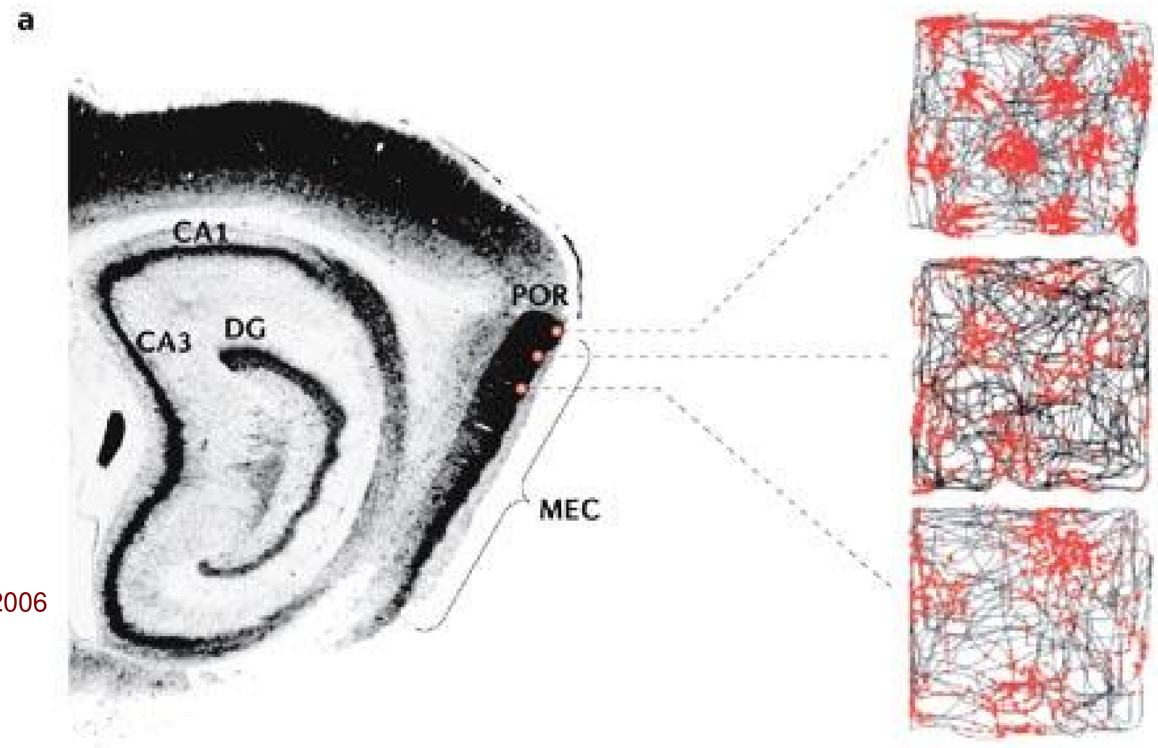
- Both models require that at least some grid cells must show velocity modulation.
- Confirmed by Sargolini et al. (2006): some EC layer III cells are grid $\times$ head direction cells, and sensitive to running speed.



Sargolini et al., 2006

McNaughton: Velocity Gain Can Determine Grid Spacing

- Cells with tighter packed grids should show greater firing rate variation with velocity.
- Some evidence for this in hippocampus: dorsal vs. ventral place cells (Maurer et al., 2005)



McNaughton et al., 2006

Differences Between The Two Models

Fuhs & Touretzky (2006):

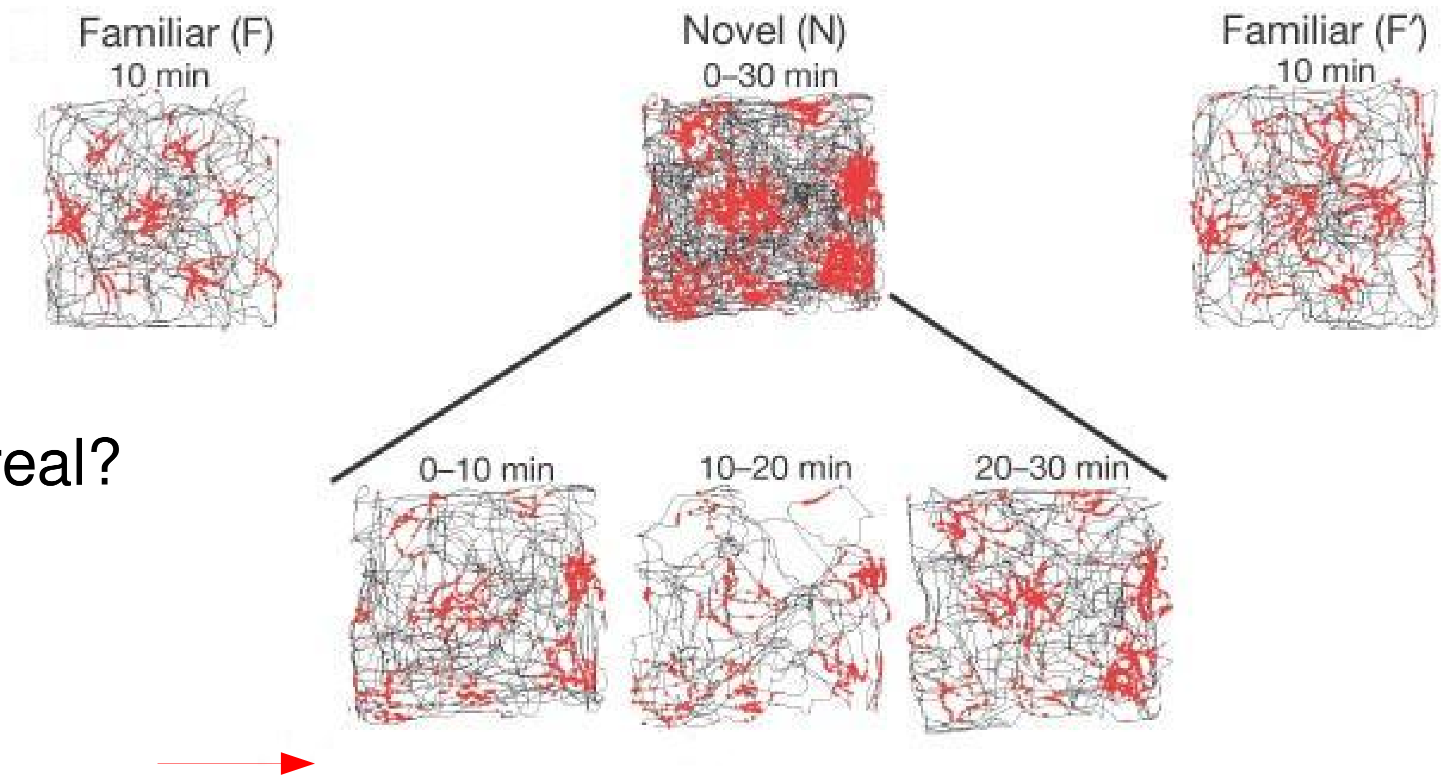
- No common grid orientation (confirmed by Stensola et al. 2012)
- Grids can rotate
- Irregular patterns (heptagons) are possible

McNaughton et al. (2006):

- Grids share same orientation due to common training signal
- Grids are fixed by the wiring
- Hexagonal pattern enforced by torus

Some Outstanding Questions

1) Can grids shift relative to each other across environments?
   - If not, how do we keep them from shifting? (Boundary effects?)
2) If grids don't shift, how is the phase relationship enforced?
3) Does velocity gain govern grid spacing? (Bump spacing constant.)
4) Are heptagons real?



Hafting et al., 2005

Conclusions

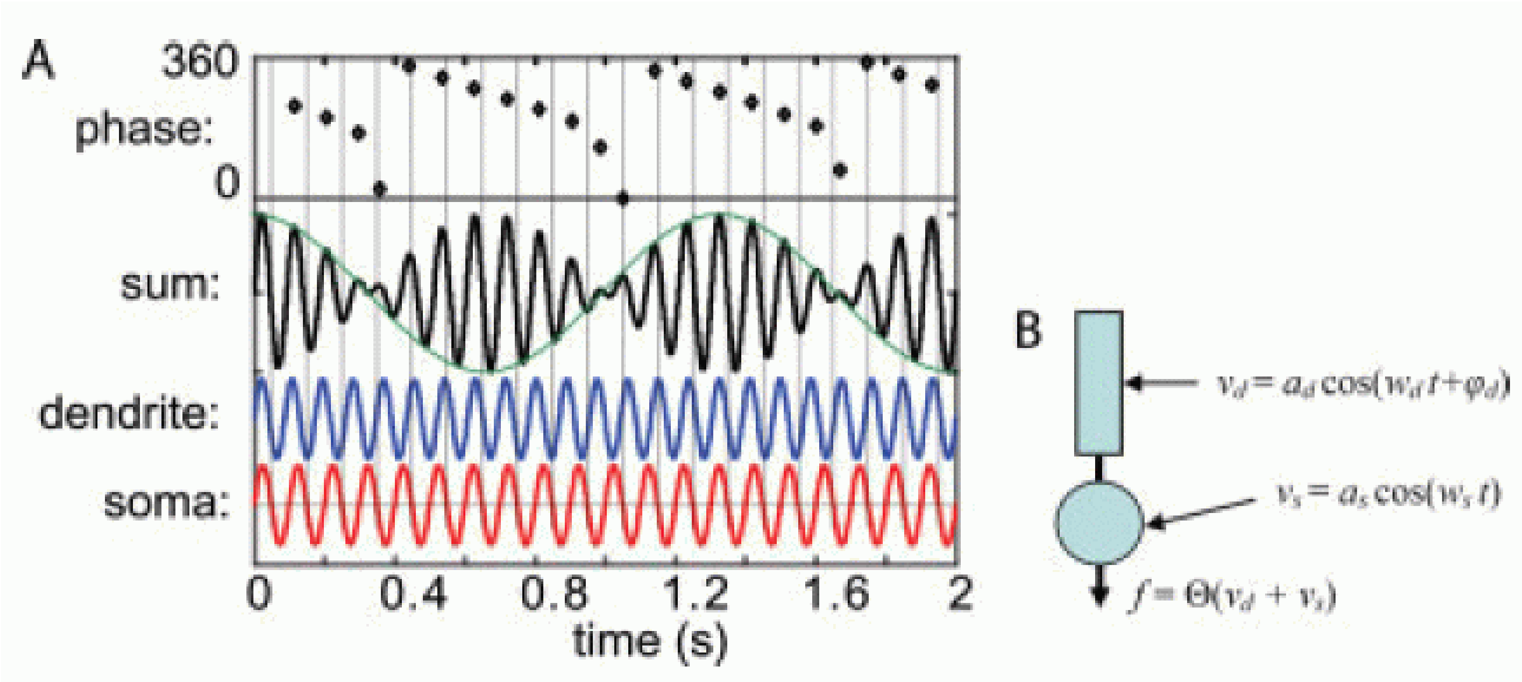
- The Moser lab has found the path integrator.
- Use of multiple grids allows fine-grained representation of position over a large area with a reasonable number of units.
  - How many grids? There is room for at least a dozen.
- How accurate is this integrator?
  - Error must eventually accumulate.
  - Even in the dark, rodents have sensory cues, so limited accuracy of a pure integrator may be okay.
- The brain really does compute with attractor bumps!
  - But Burgess et al. have a different view...

Burgess et al. Oscillatory Interference Model

- Burgess et al. (2007) proposed a radically different model of grid cells based on interference patterns between oscillators.
- The model is based on earlier work of theirs that attempts to explain phase precession via a similar interference mechanism.
- The somatic oscillator is located in the cell body (soma) entrained to the theta rhythm, possibly driven by pacemaker input from the medial septum.
- The dendritic oscillator is an intrinsic oscillator with a slightly higher frequency.

Somatic and Dendritic Oscillators

- The sum of somatic and dendritic oscillations determines the activation level of the cell, and the timing of spikes.
- The cell spike times precess relative to the peaks of the slightly slower theta rhythm, shown as vertical lines below.



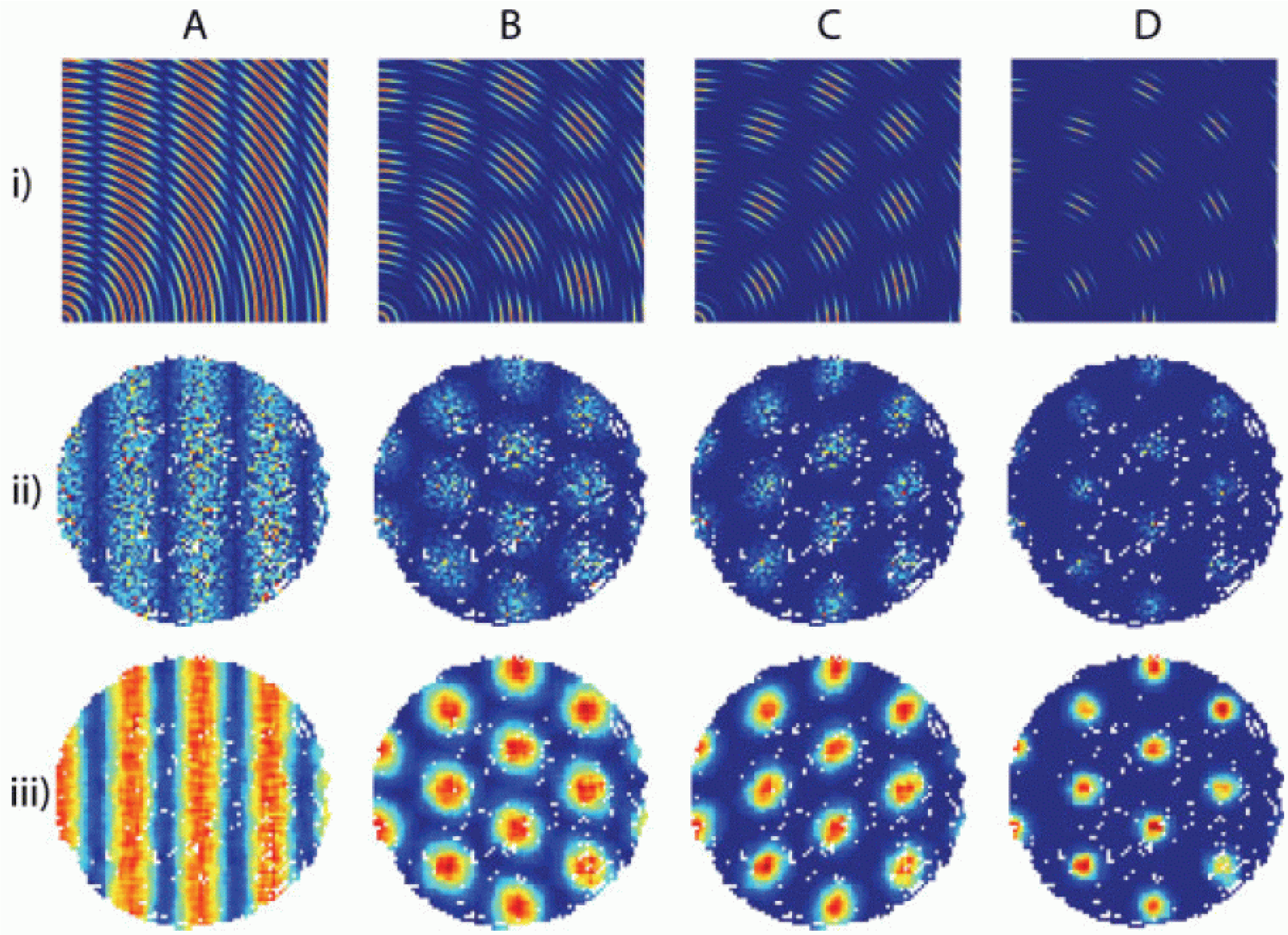
Extension to a 2D Model

- Assume the period of the dendritic oscillator is modulated by the animal's speed *s* and heading φ.
- Let φ_d be the dendrite's preferred direction, i.e., the direction where the oscillation is fastest.

$$w_d = w_s + \beta s \cdot \cos(\phi - \phi_d)$$

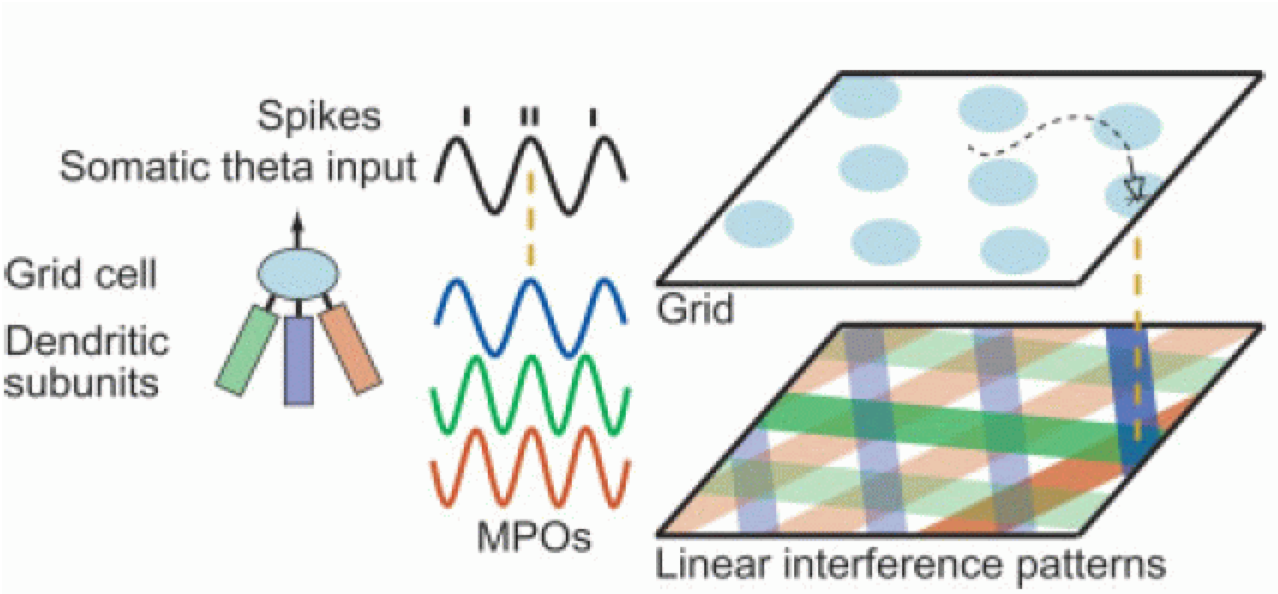
- For headings perpendicular to φ_d, $w_d = w_s$, and the two oscillators remain in phase.

Extending the Model to 2D



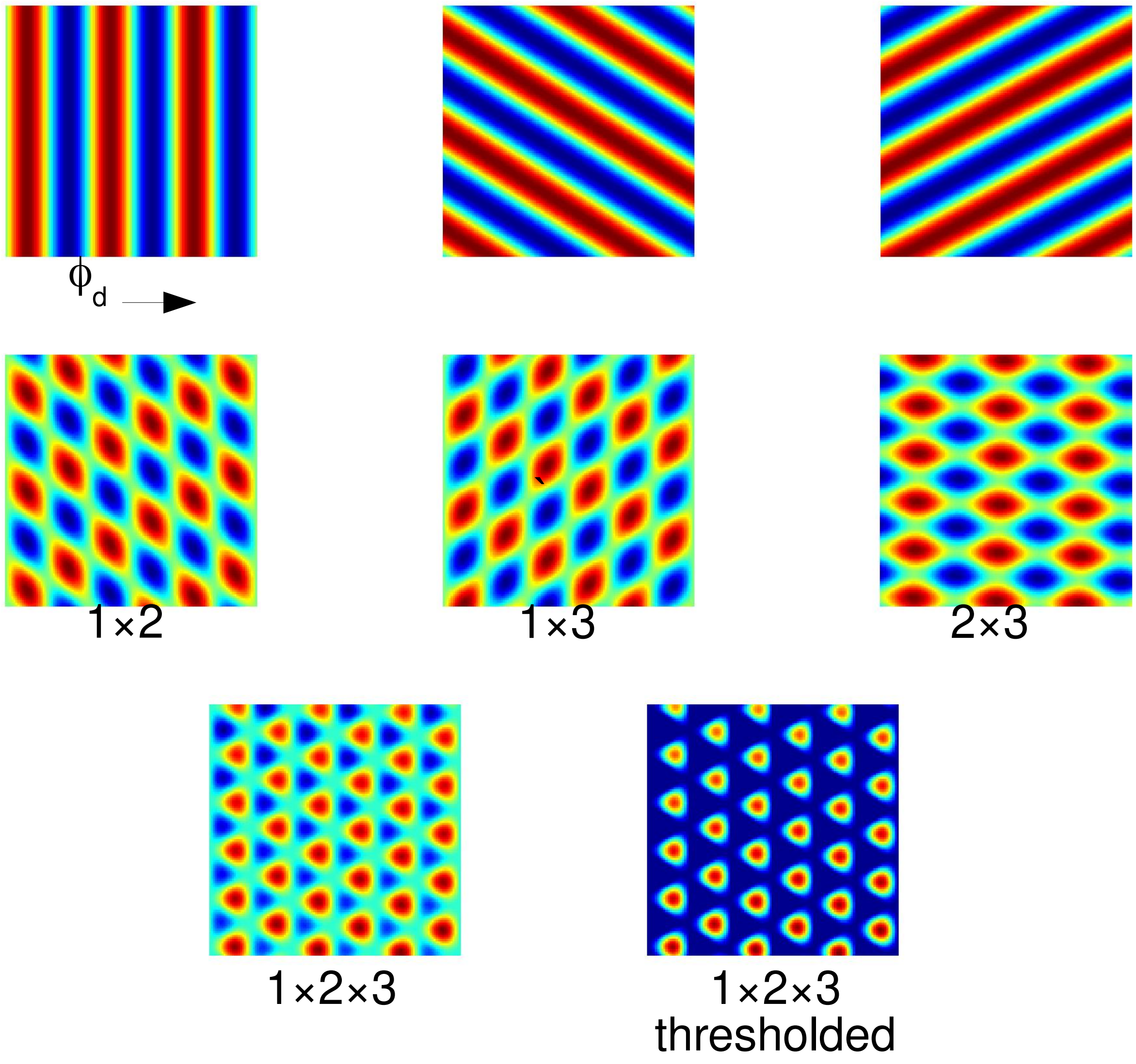
1 interference pattern 2 3 6

Each Dendritic Oscillator Interferes with the Somatic Oscillator

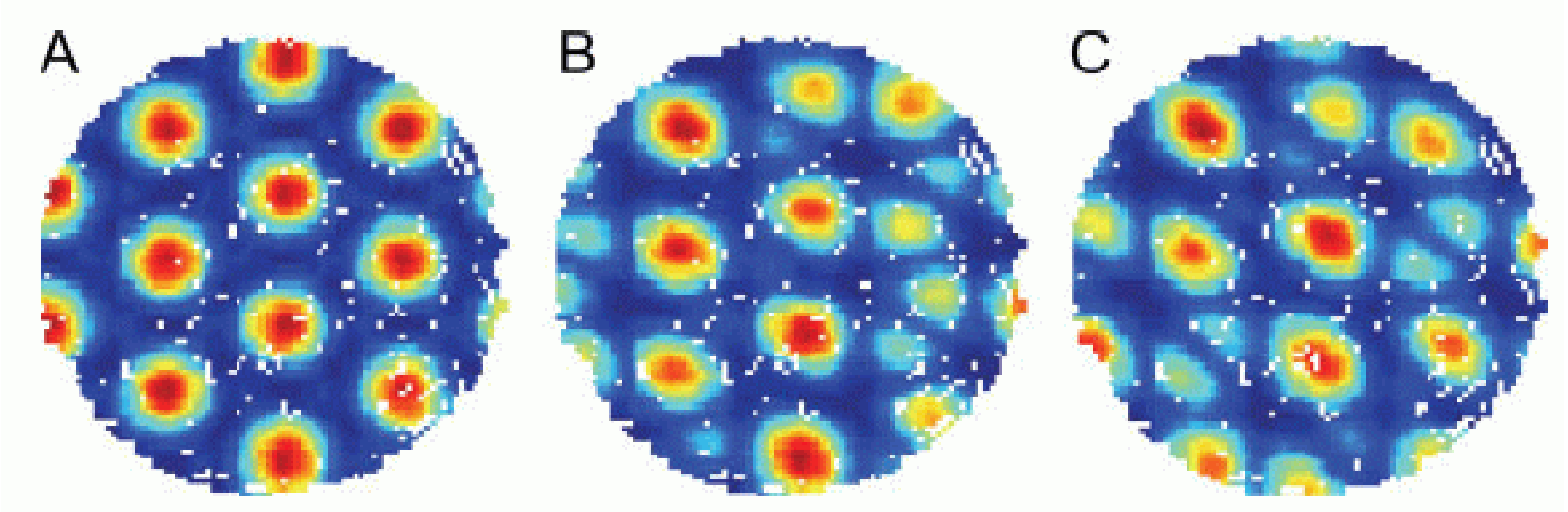


MPO = Membrane Potential Oscillator

The Product of Interference Patterns 60° Apart Gives Hexagonal Bumps



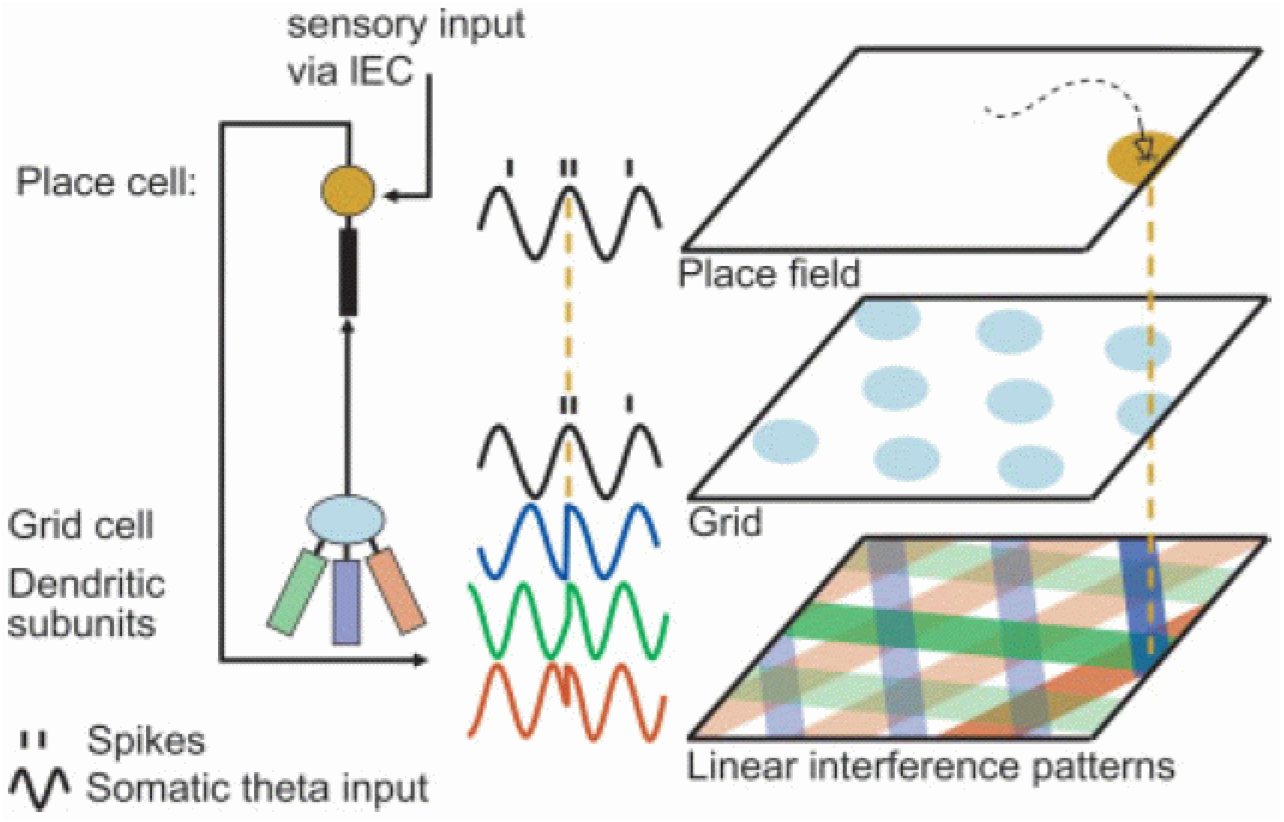
Separation by At Least 20° Suffices



A: cell with maximum firing rate; B: cell with median rate; C: cell with minimum rate. Simulation using three dendritic oscillators with different combinations of preferred directions.

How to Maintain Grid Alignment

- Path integration is subject to drift due to accumulated error.
- This can be corrected by resetting the phases of the dendritic oscillators when the rat is at a known location.



Is the Model Realistic?

- Stellate cells in layer II of dorsomedial entorhinal cortex show subthreshold oscillations.
- Giocomo et al. (2007) found that oscillation frequency correlates with grid size.
- The frequency of the intrinsic oscillation depends on the time constant of the h-current, which varies dorsoventrally.
- Grid cells in some layers of EC are modulated by head direction.
- The model also explains phase precession of grid cells.

Unresolved Issues

- No evidence yet for independent oscillators with different frequencies in different dendritic branches.
- The model treats each grid cell independently. Unlike the attractor model, there is no required interaction between grid cells.
  - How should cells interact to stabilize the grid?
- Is the grid reset mechanism realistic?