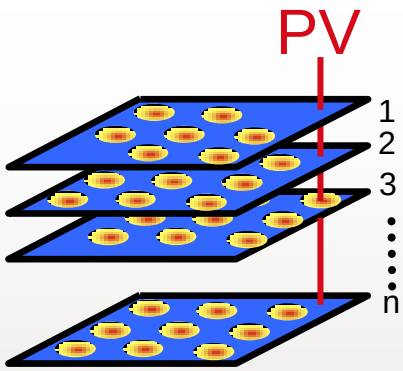
SISSA

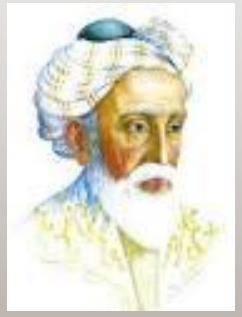
Self-organizing
Spatial representations

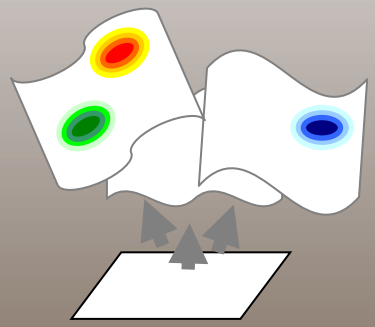
Alessandro Treves



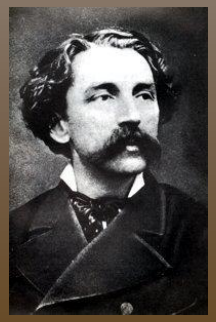
Plan

1. *The neuronal fatigue model*
2. *Differentiating the layers*
3. *Running behind Edvard and Nachum*
4. *Wondering about parallel lines*





5. *Why ruin mEC beauty with DG?*
6. *Are CA3 charts good for navigation?*
7. *Wandering across parallel spaces*



Many models have been proposed..

Grid cell model	Position representation	Updating mechanism
Conklin and Eliasmith (2005)	Torus attractor, single bump	Direction-conjunctive cells
O'Keefe and Burgess (2005)	[Torus attractor, single	[Direction modulated

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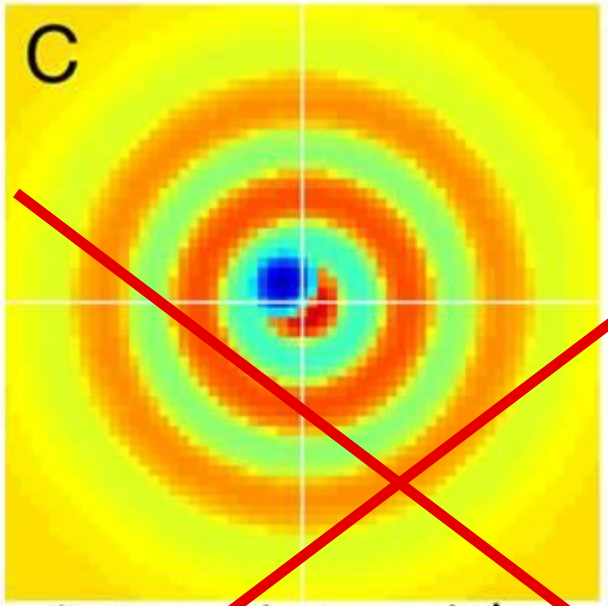
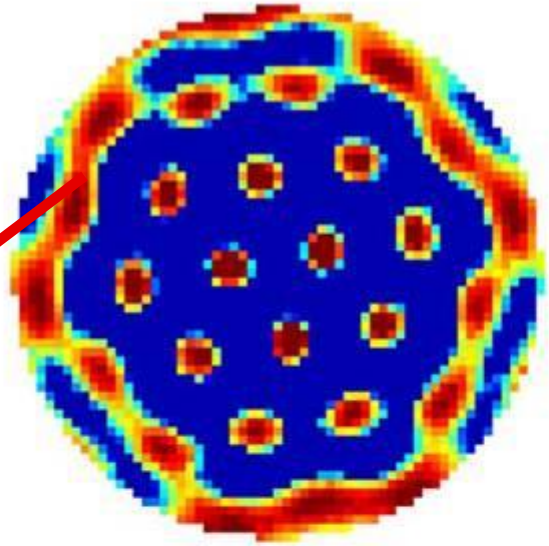


Connection weights



Firing rate map

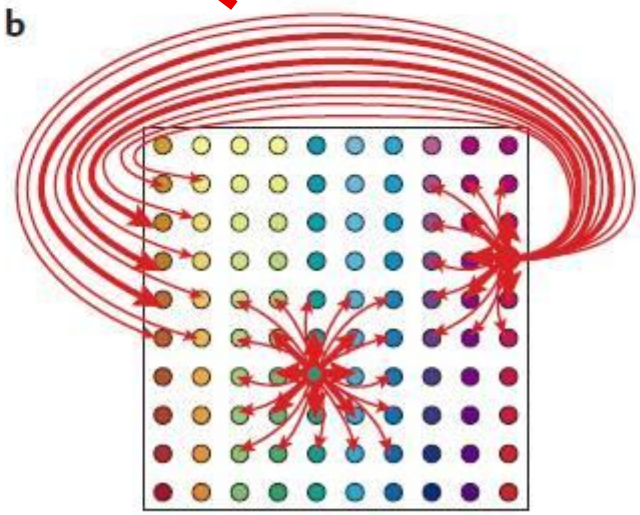
Recurrent Network

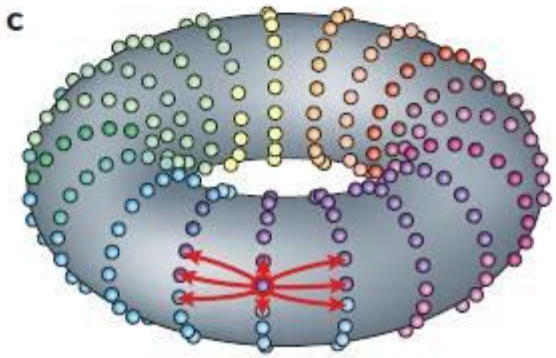
creating a single

Continuous Attractor

?

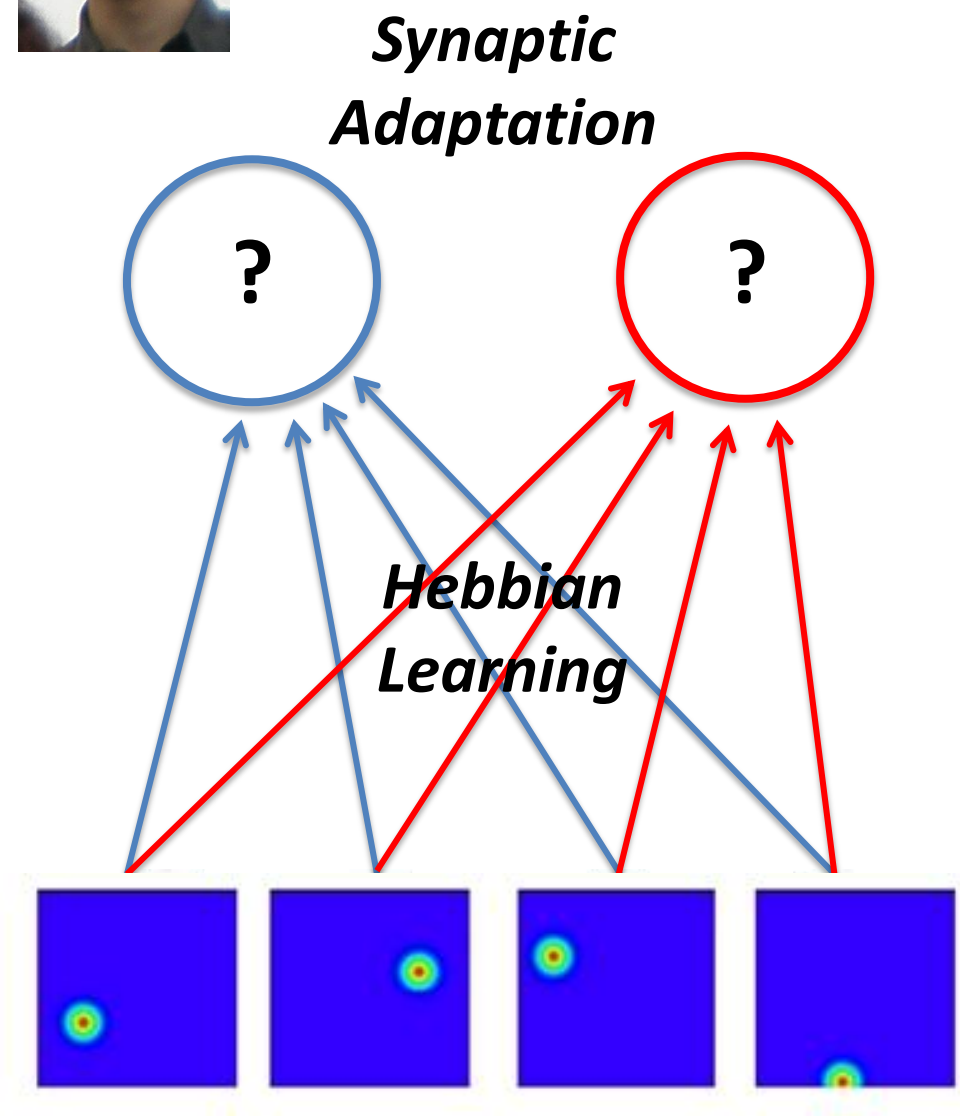
Solving both boundary & periodicity problems in one shot





slides by Federico Stella

A Model Based on Neural Fatigue



Treves et al, SfN 2005

- The model should generate grid patterns from already existing **spatially modulated activity**.
- It is based on the effects of **neural fatigue** on mEC units.
- The feedforward connections have no pre-wired structure and (should) develop through **self-organization**.

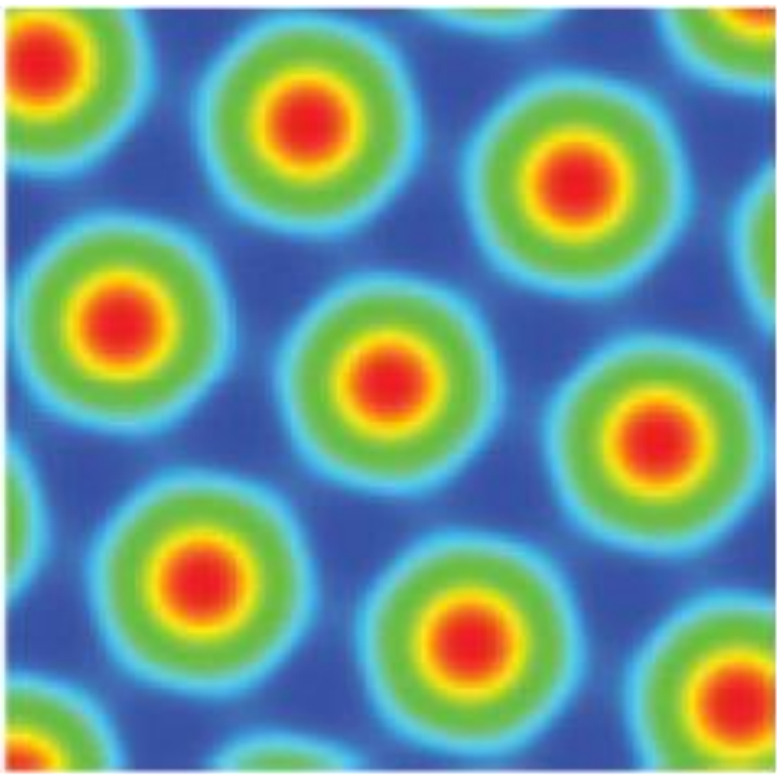
Erika Cerasti

Grid Cell Self-Organization

2D-case

Analytical Solution

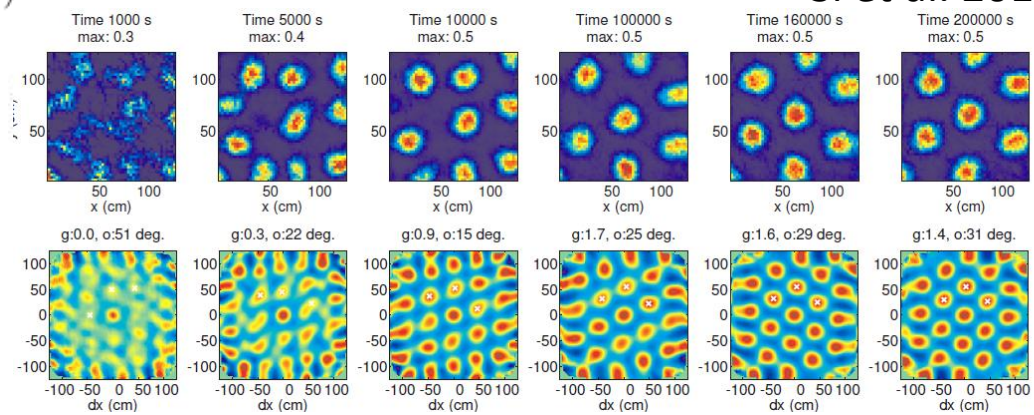
$$L = \int d\mathbf{x}[\nabla\psi(\mathbf{x})]^2 + \gamma \int d\mathbf{x} \int dt' \psi(\mathbf{x}(t))K(t-t')\psi(\mathbf{x}(t'))$$



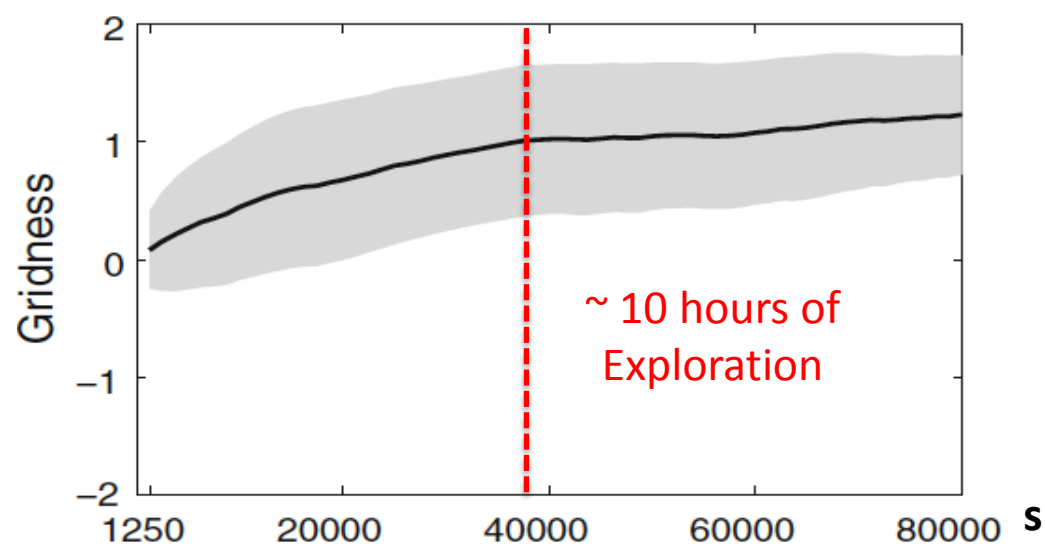
Kropff & Treves 2008

Simulation Results

Si et al. 2012

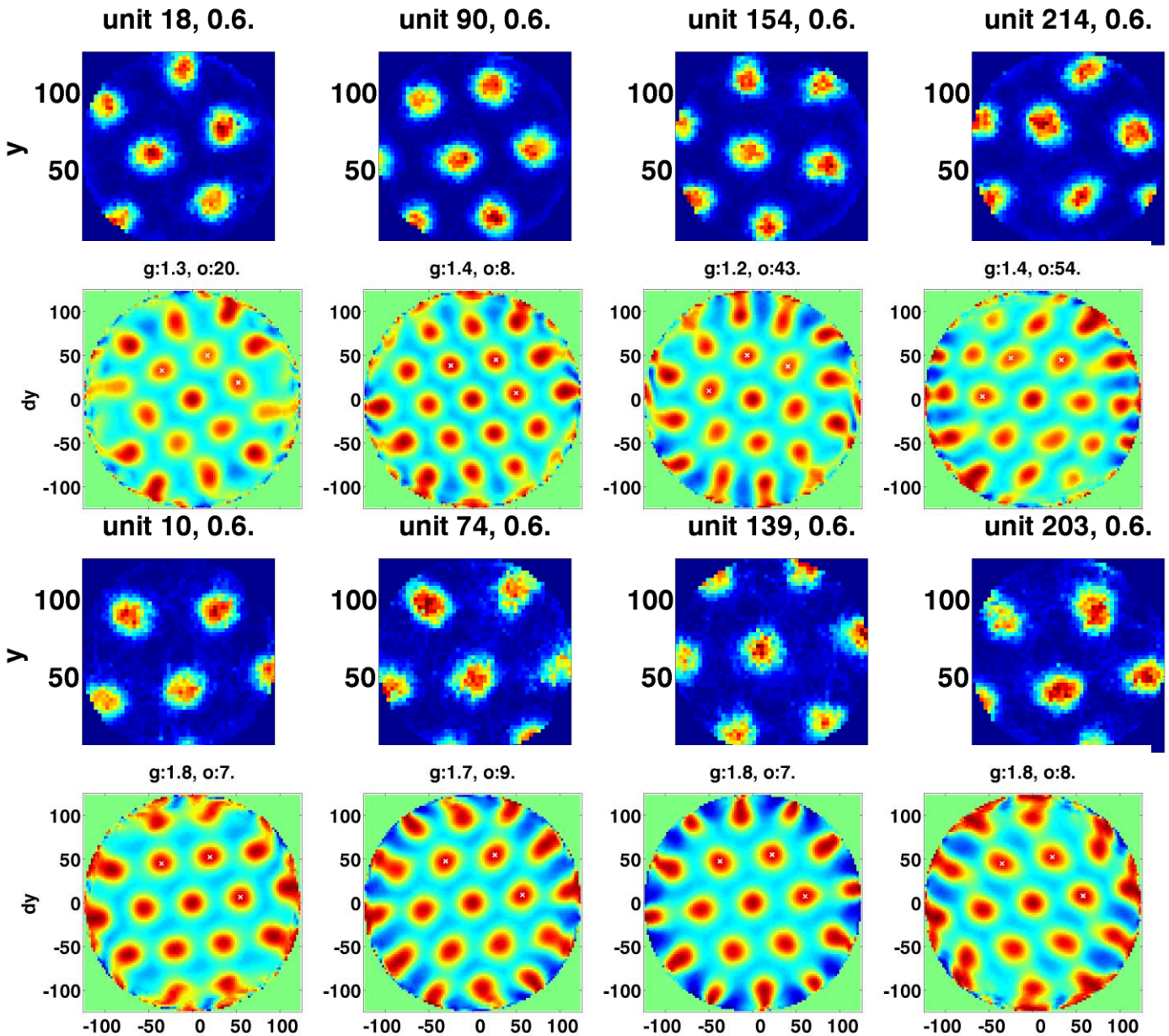


Time →



Our results suggest a single-cell mechanism, however, the grid axes may differ in different cells

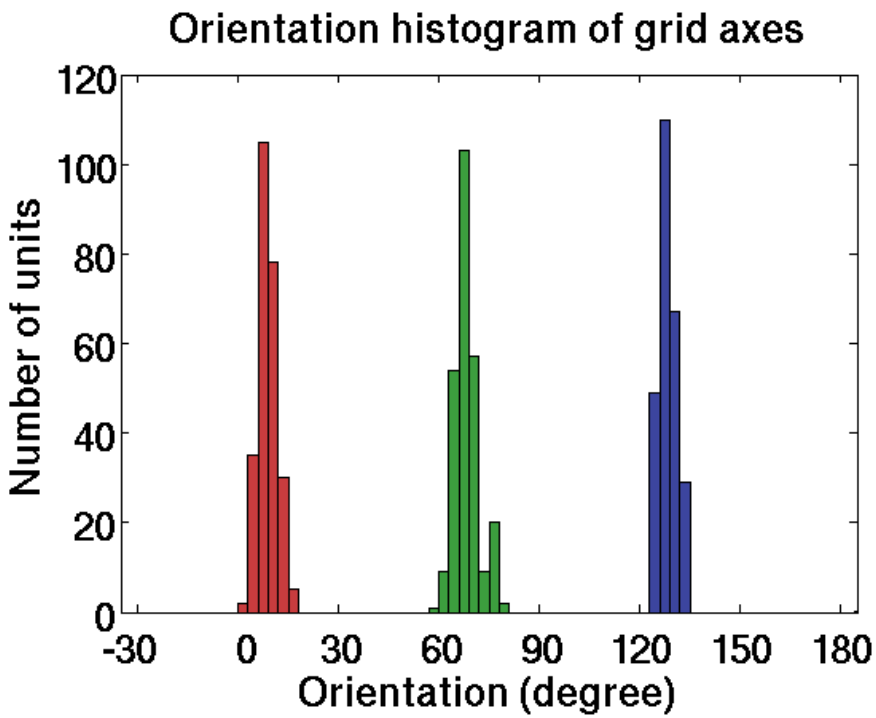
Recurrent connections are needed, however, to align the grid axes

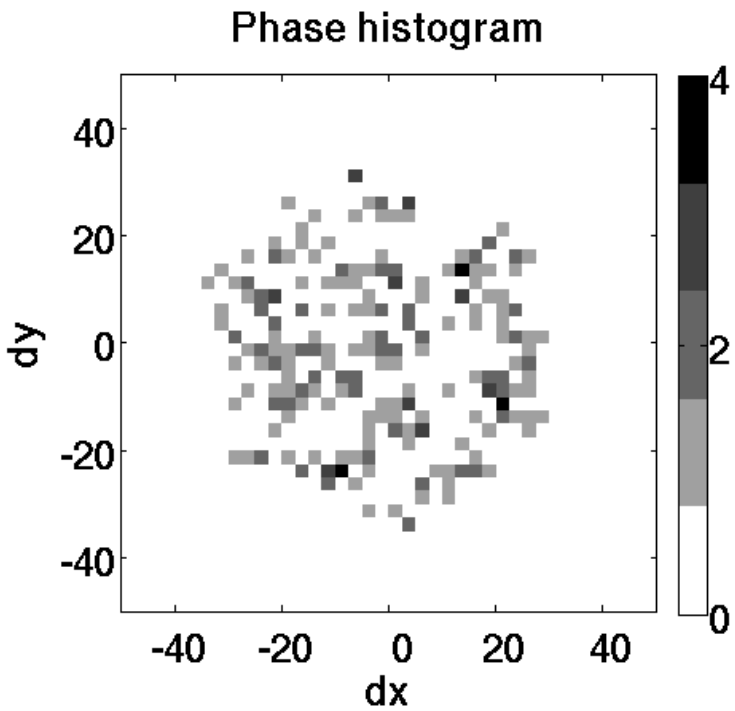


With collaterals

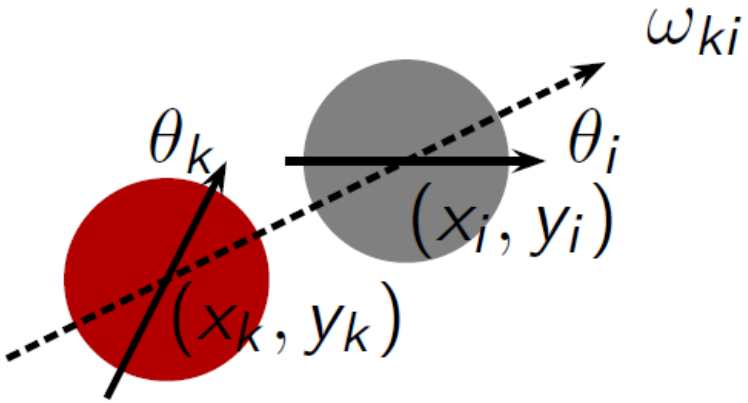
Grids Align with Distributed Phases

- grid axes align to common orientations
- spatial phases are randomly distributed





collateral weights may self-organize, however they appear to require head-direction modulation

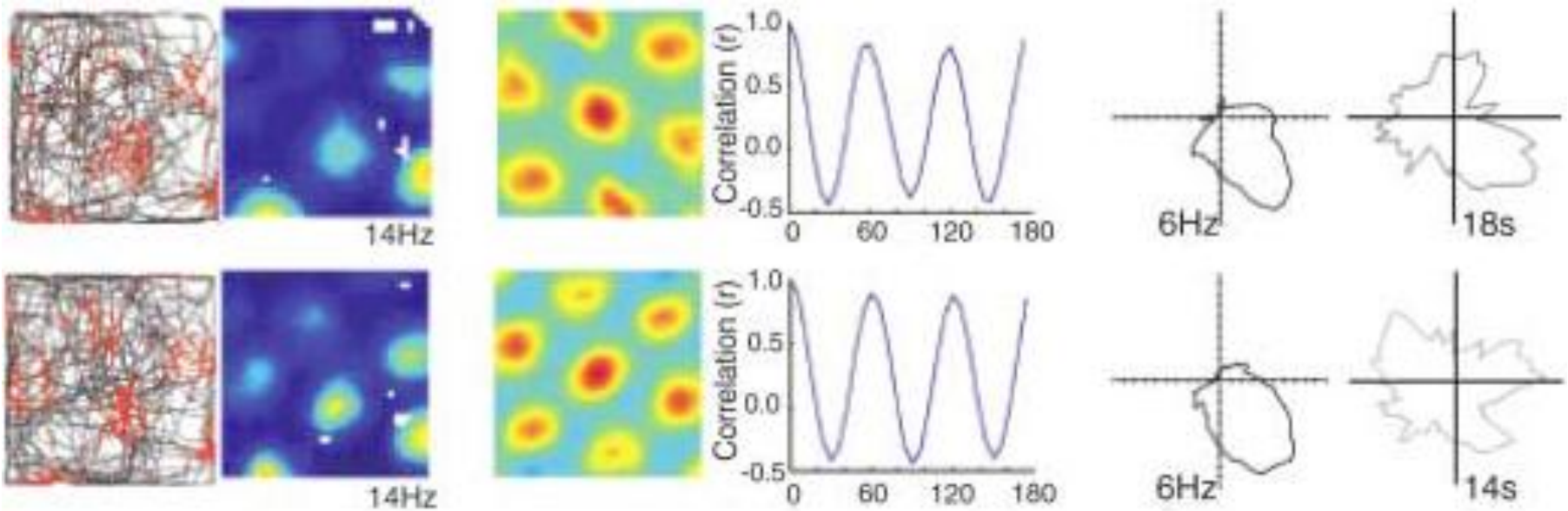


- temporarily assign an auxiliary field to each unit
- *assign* or *learn* a strong collateral connection between two units if they

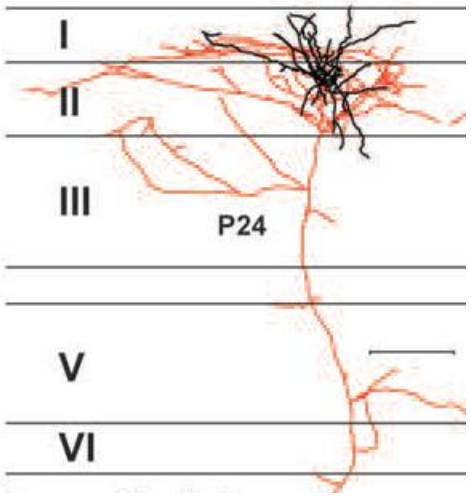
a) have similar preferred HDs: fields form along one direction

b) have auxiliary fields some distance away: avoid co-activation

Conjunctive grid x head-direction cells are observed in mEC, but in layers III and below

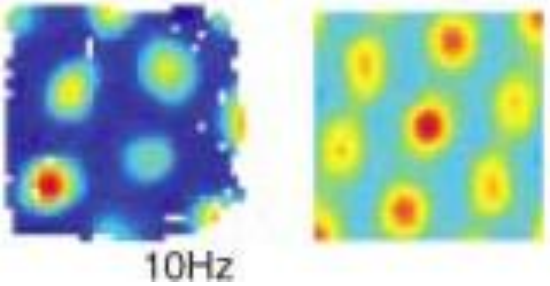


Sargolini et al, 2006

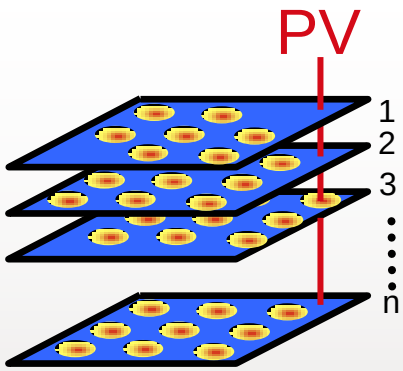


..whereas in layer II only "pure" grid cells are seen,

and they seem to have no excitatory recurrent collaterals at all!

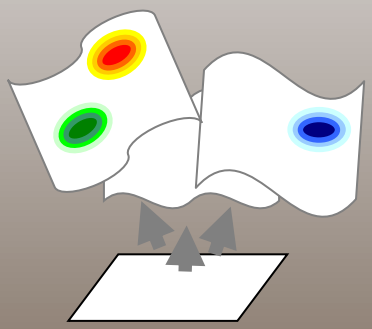


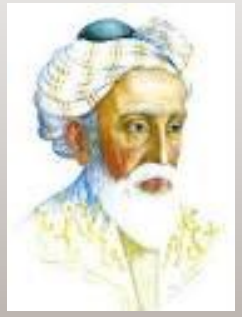
Couey et al, 2013

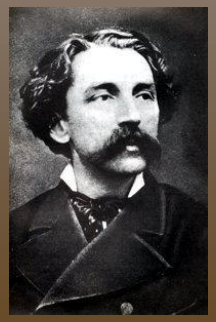


1. The neuronal fatigue model requires HD-dependent collateral interactions to align

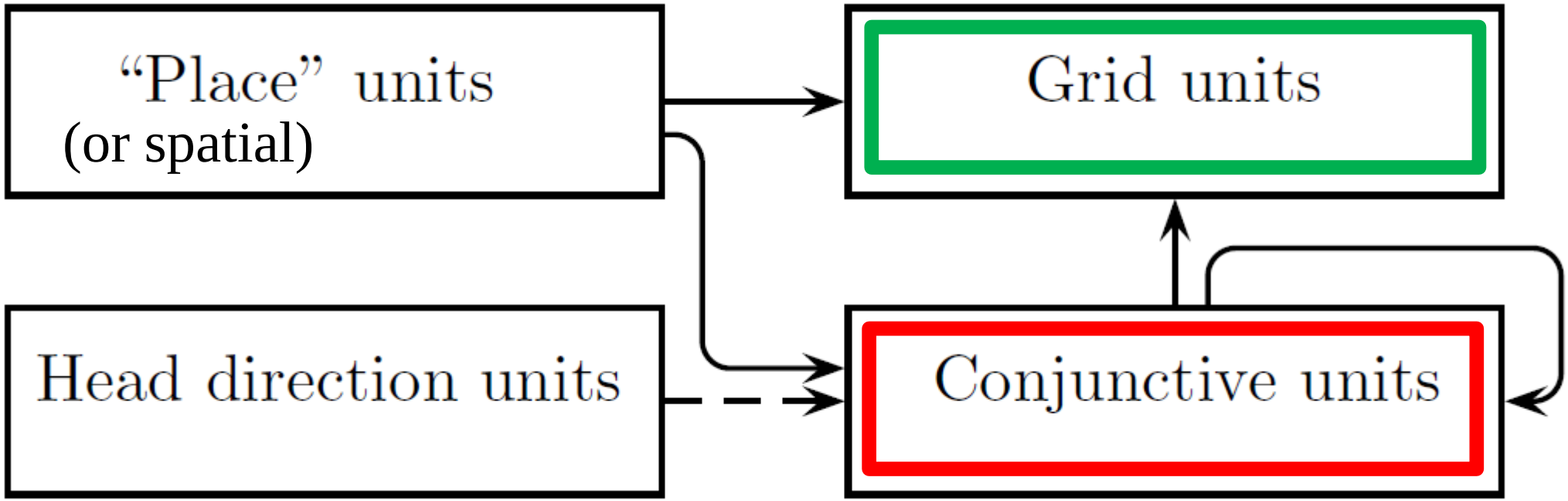
Differentiating the layers







Try then a «layer» model



All weights in the network self-organize when the virtual rat explores the environment. The weights from place units to grid units or conjunctive units are changed according to a Hebbian rule

$$\Delta W_{nj}^{t} = \epsilon(\psi_n^t r_j^t - \bar{\psi}_n^{t-1} \bar{r}_j^{t-1}). \tag{9}$$

The collateral weights between conjunctive units are adapted according to

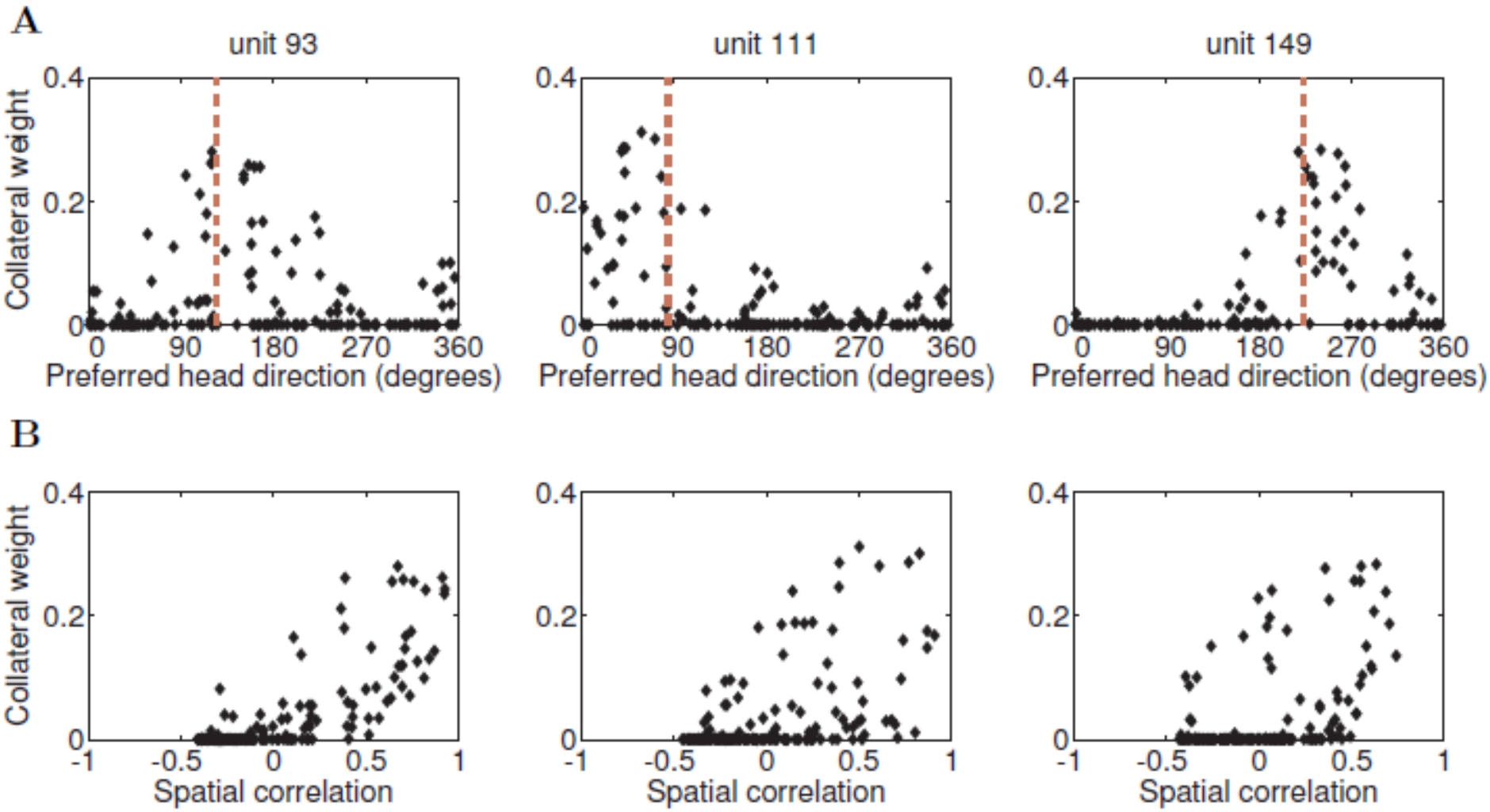
$$\Delta W_{ik}^{t} = \zeta \psi_i^t (\psi_k^{t-\tau} - \kappa), \tag{11}$$

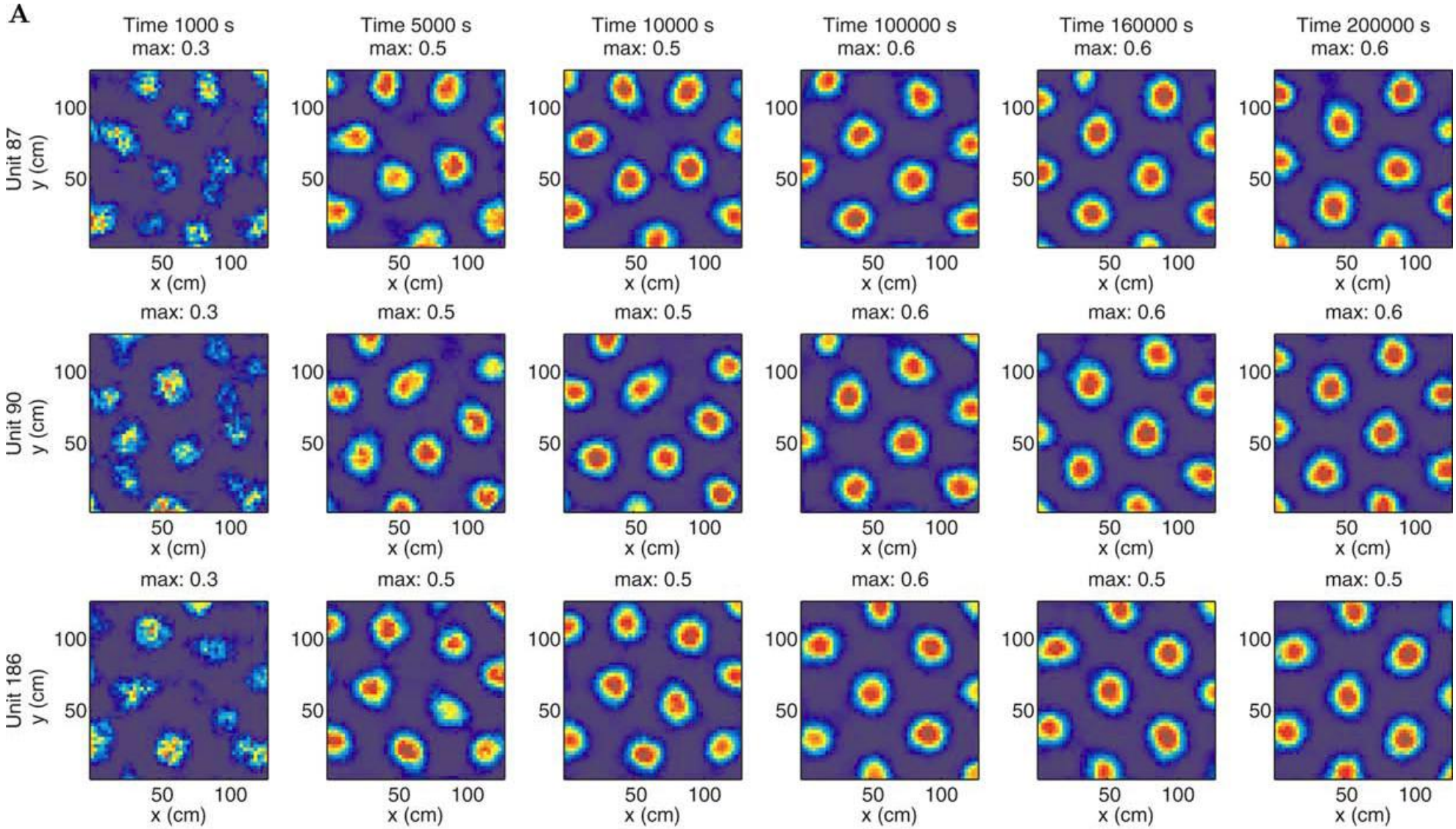
and the weights from conjunctive units to grid units are learned by a similar Hebbian rule

$$\Delta W_{mi}^{t} = \zeta \psi_m^t \psi_i^t. \tag{12}$$

The conjunctive units

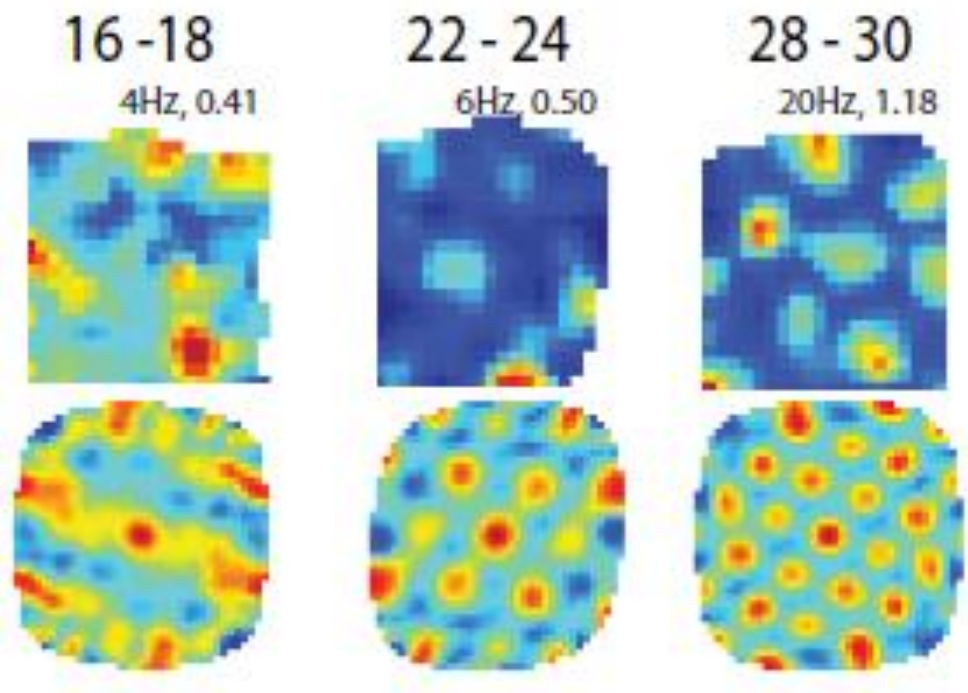
The recurrent weights reflect the similarity in preferred head direction, and the spatial correlation between pre- and postsynaptic units





The pure grid units

When do grids emerge ?

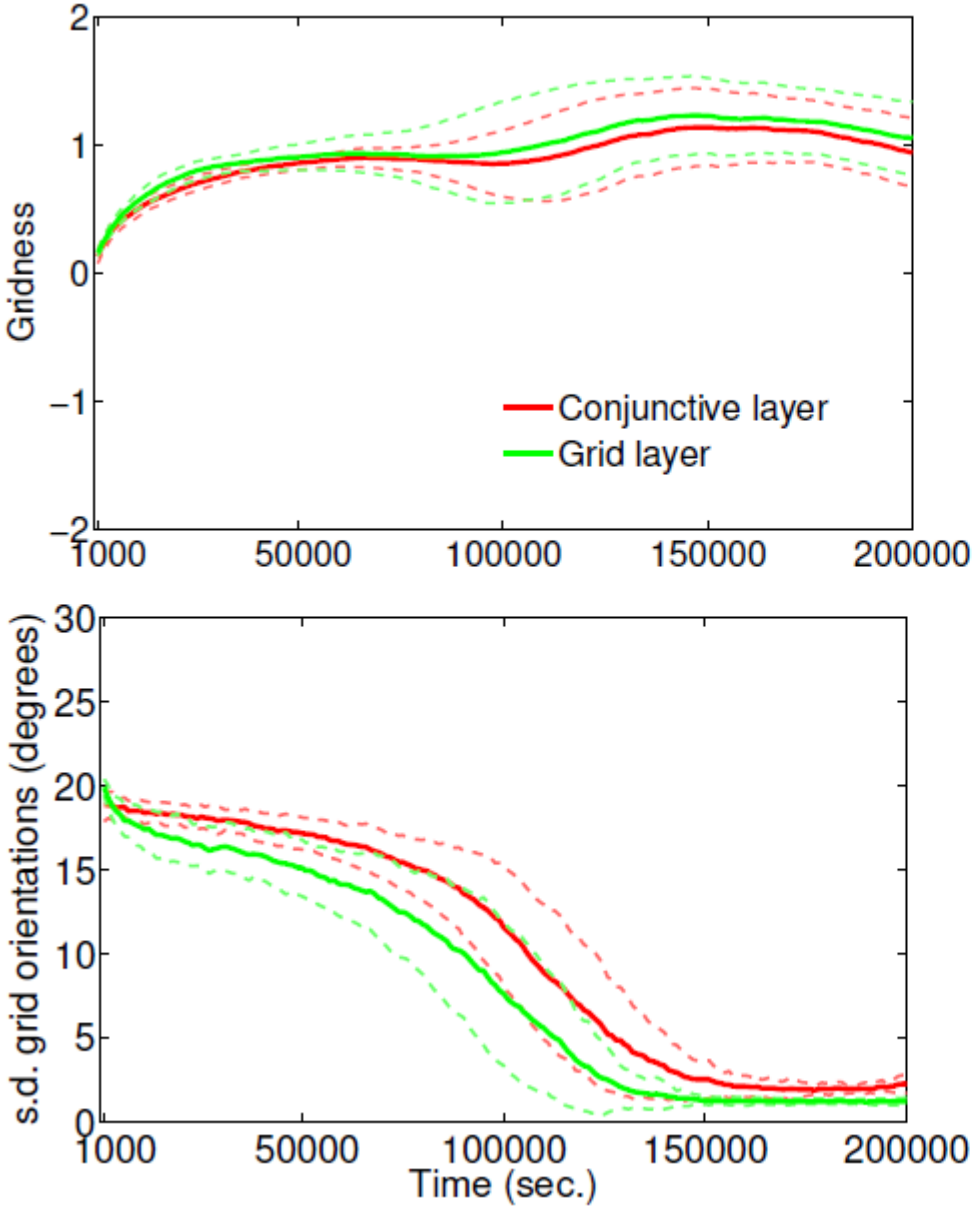


Langston et al, 2010
Ainge & Langston, 2012

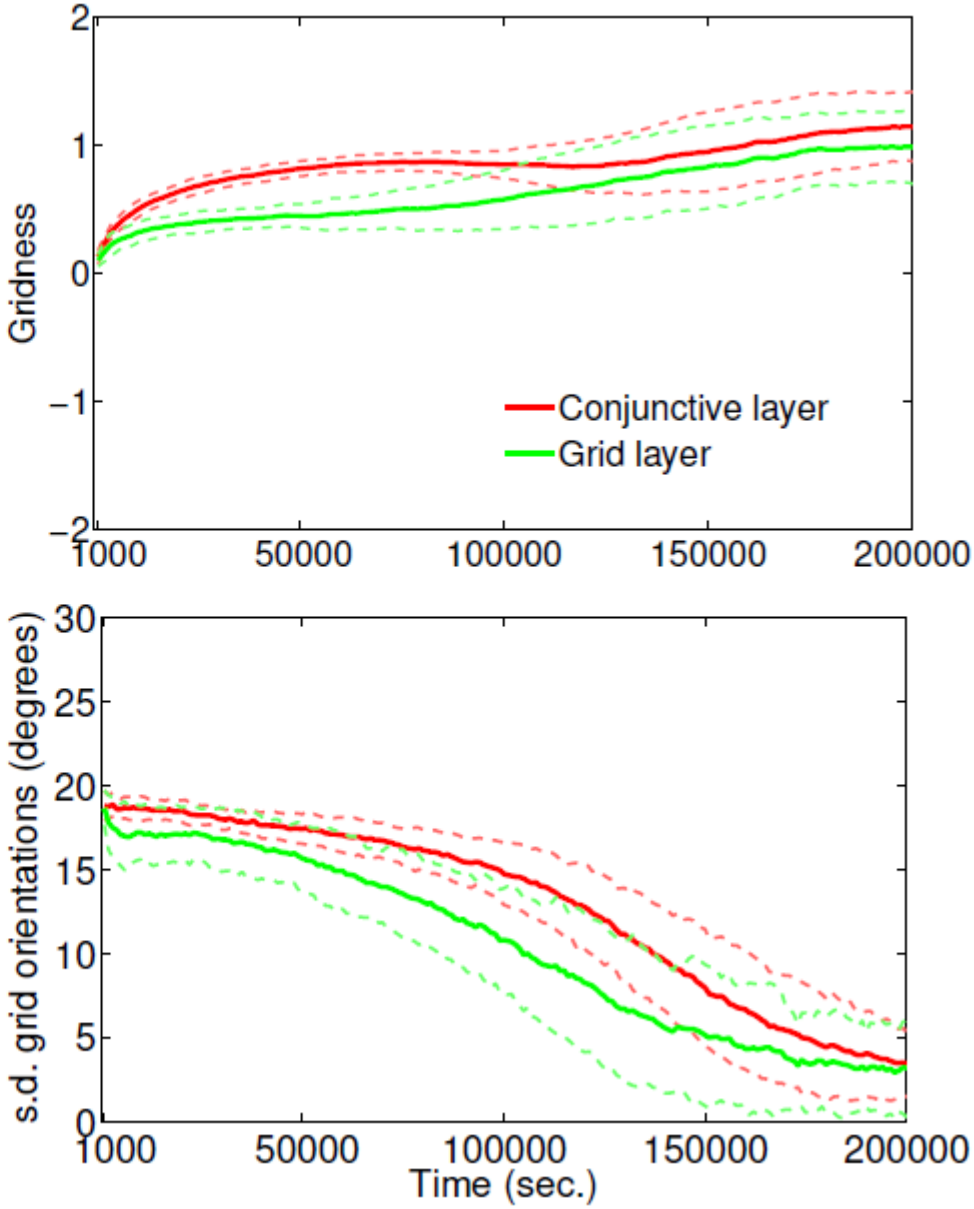
Compatible with
experimental observations

The details of the model do not matter too much

Large learning rate

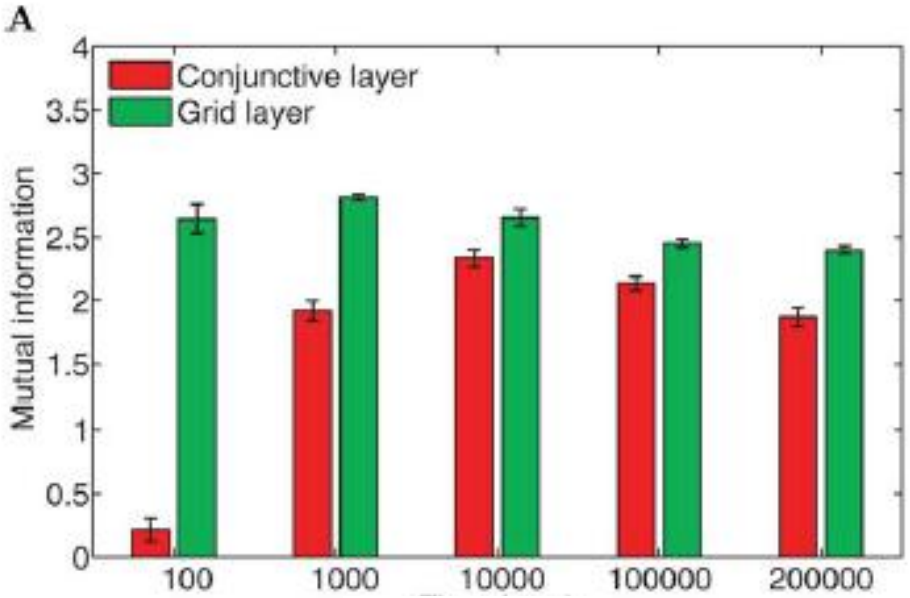


No place inputs to pure grids

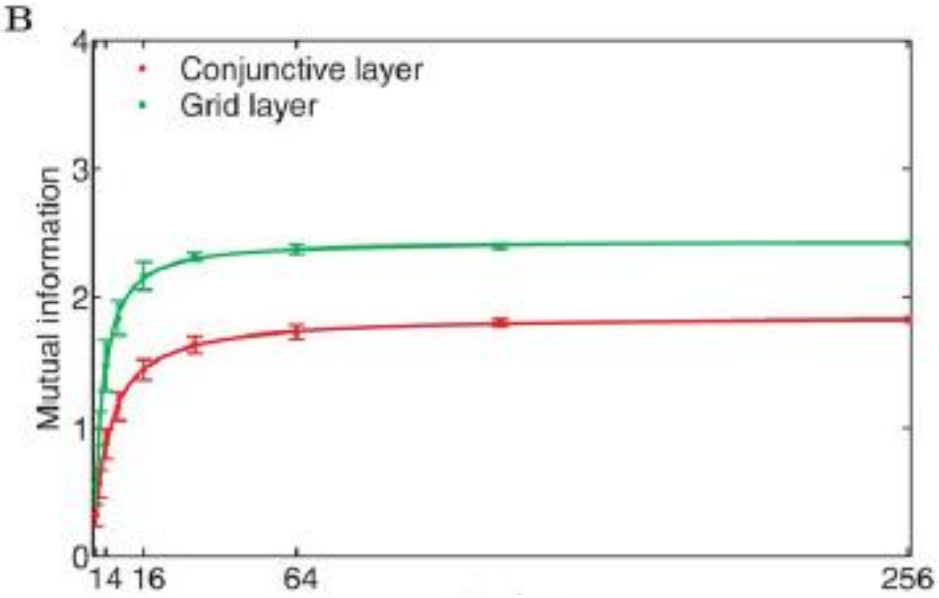


pure grid units are more informative about position

at all times and for all sample sizes



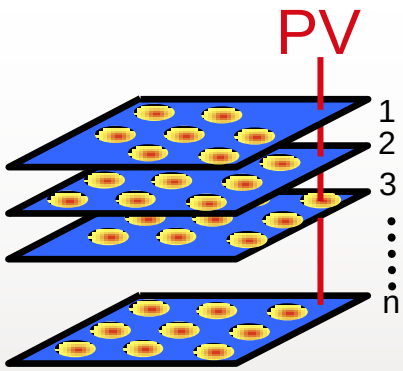
Time (sec)



Number of units

..is this what drives the differentiation in the real system?

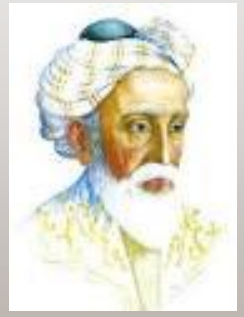
Si & AT, 2013

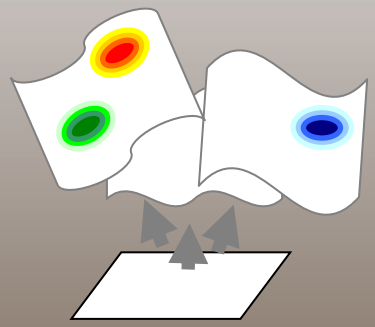


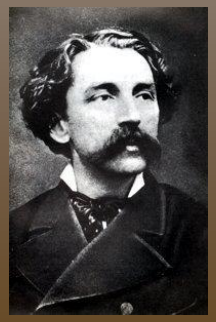
1. The neuronal fatigue model requires HD-dependent collateral interactions to align

2. Conjunctive units may help produce better «pure» grids

Running behind Edvard and Nachum





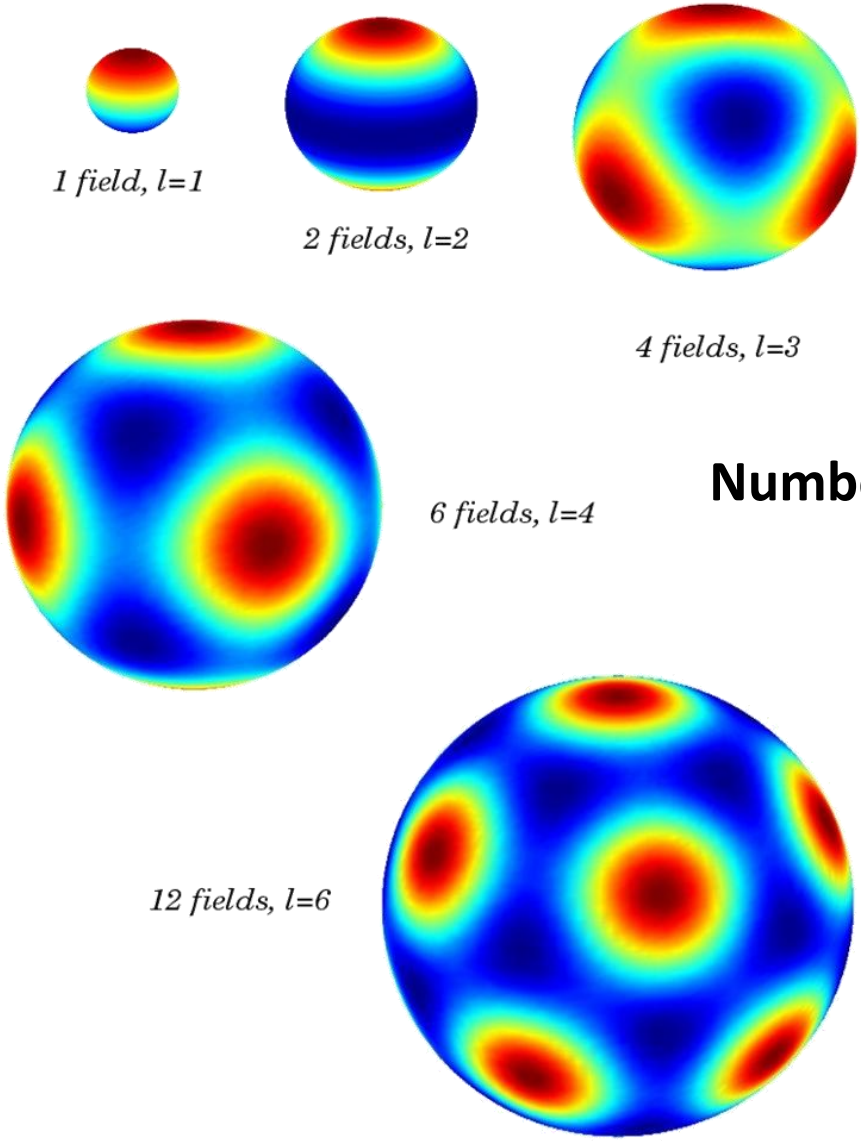


Spherical Environment

Rats in a Small World

Spherical Environment

Analytical Model

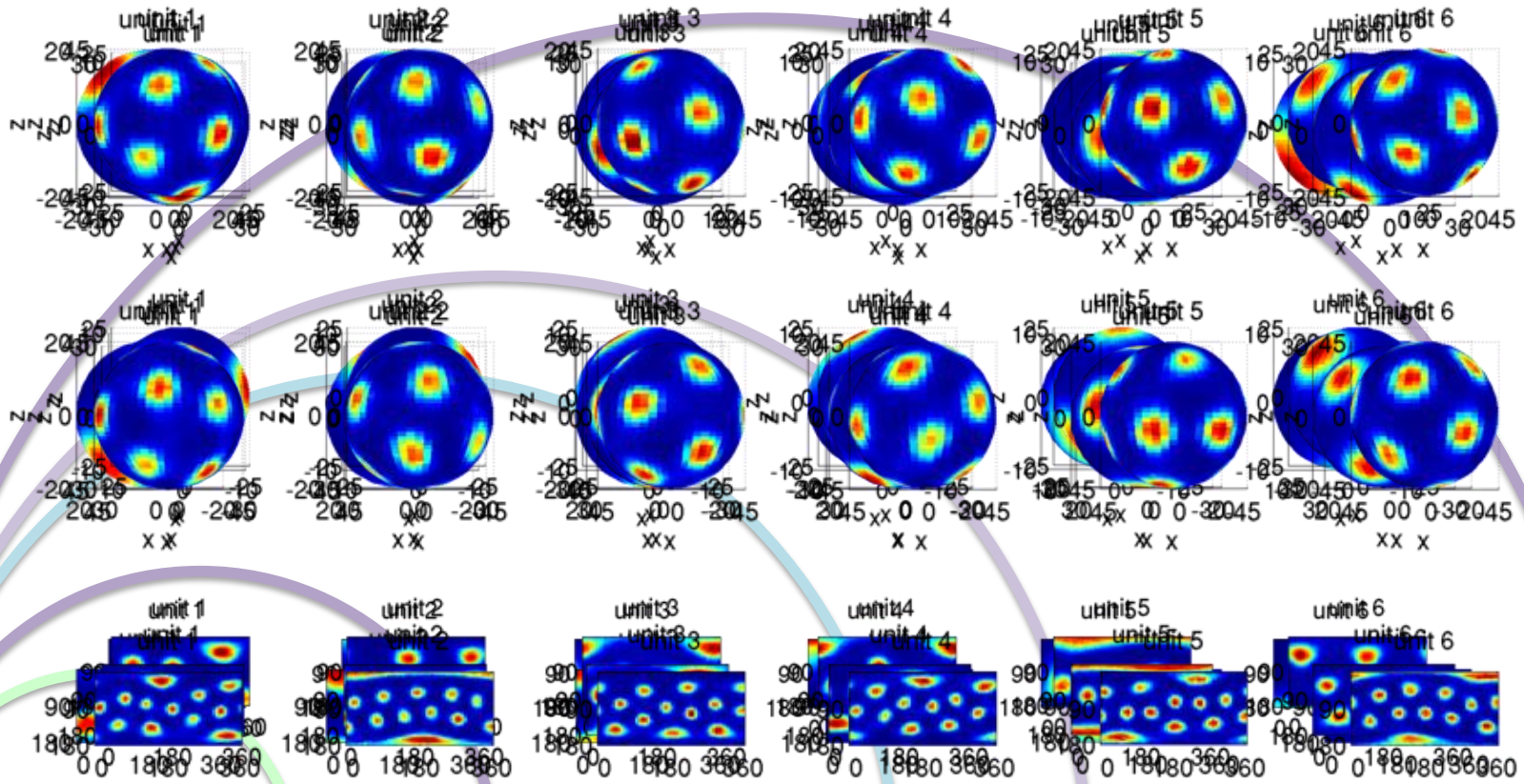


Number of Nearest Neighbors

< 6

Spherical Environment

Numerical Simulations

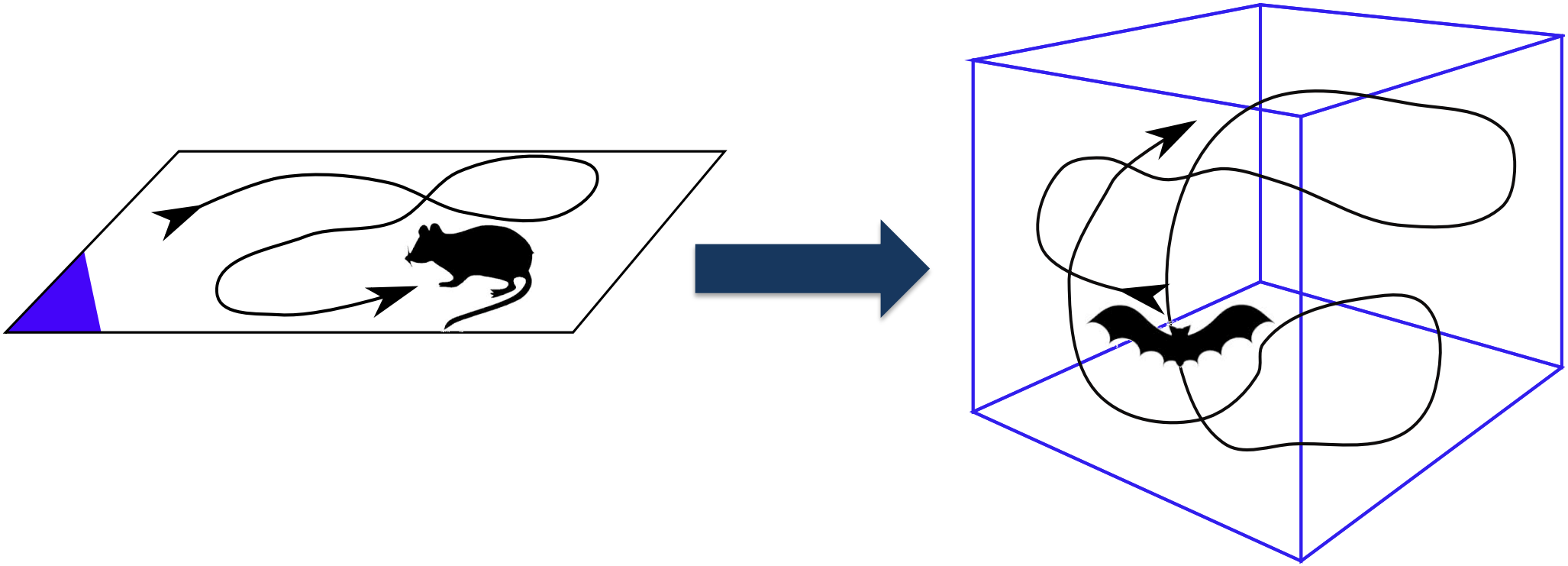


R = 10cmR = 15cm ***R = 25cmR = 30cm*** ***R = 45cm***

Grid Cells Self-Organization

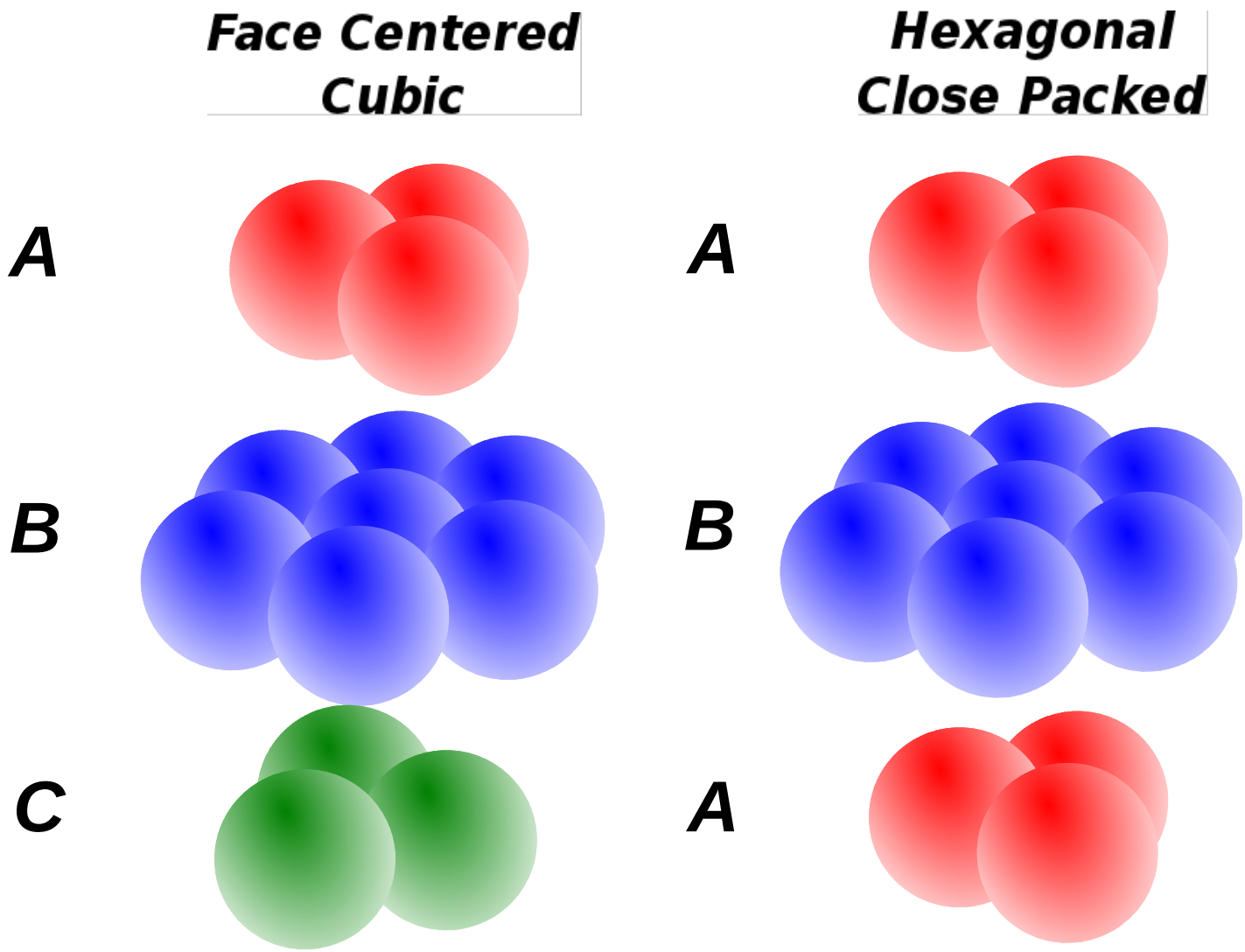
Adding dimensions

3D Case



Grids Development in 3-D

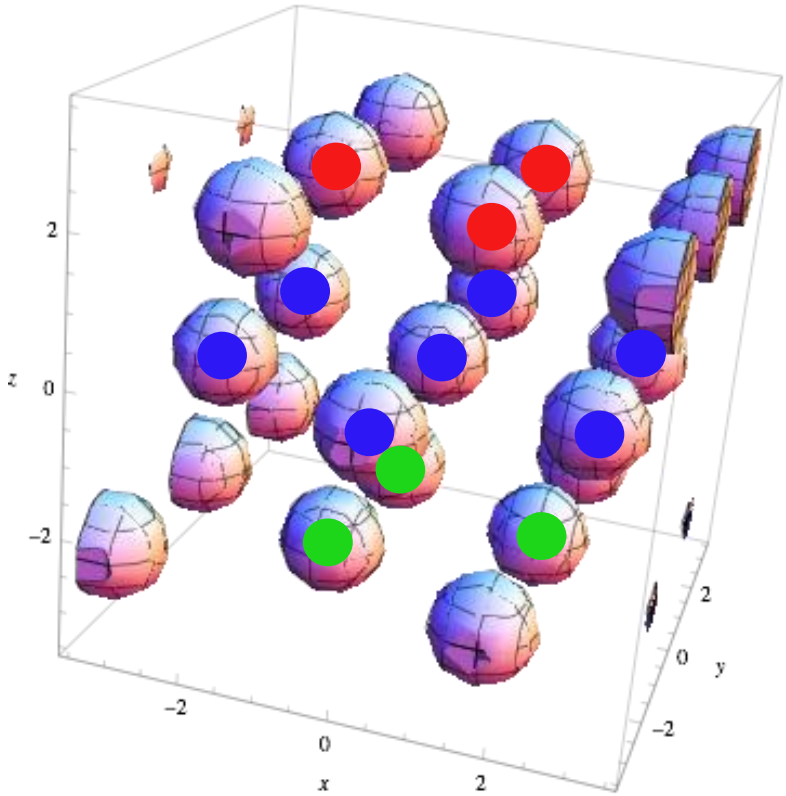
Optimal Sphere Packing



Grids Development in 3-D

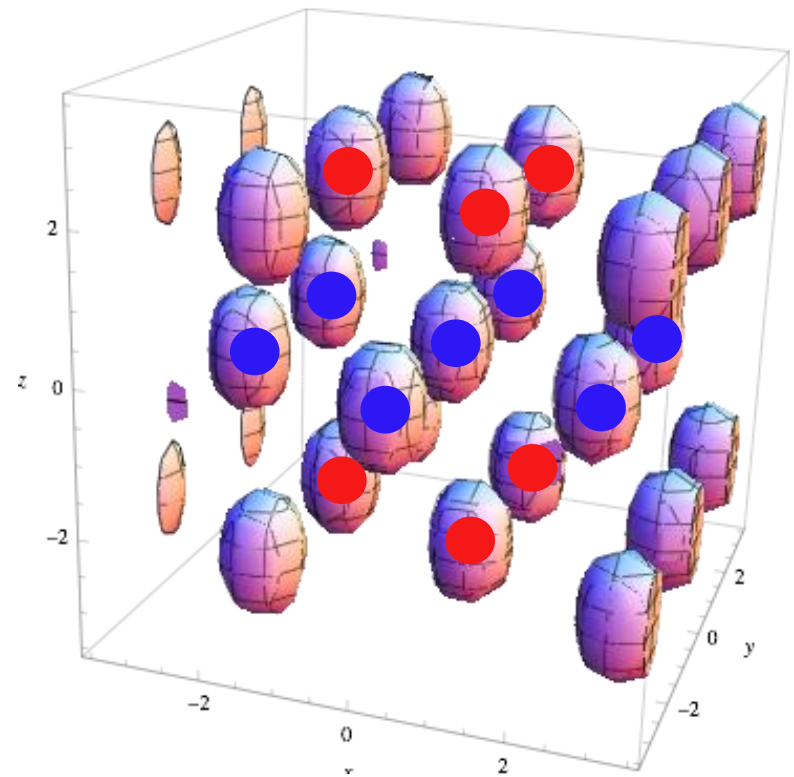
Analytical Solution

Face Centered Cubic



$$\psi^{FCC}(r) = \frac{8}{9}(1 + \frac{1}{4}\sum_{i=1}^{4} cos(k_i \cdot r))^2$$

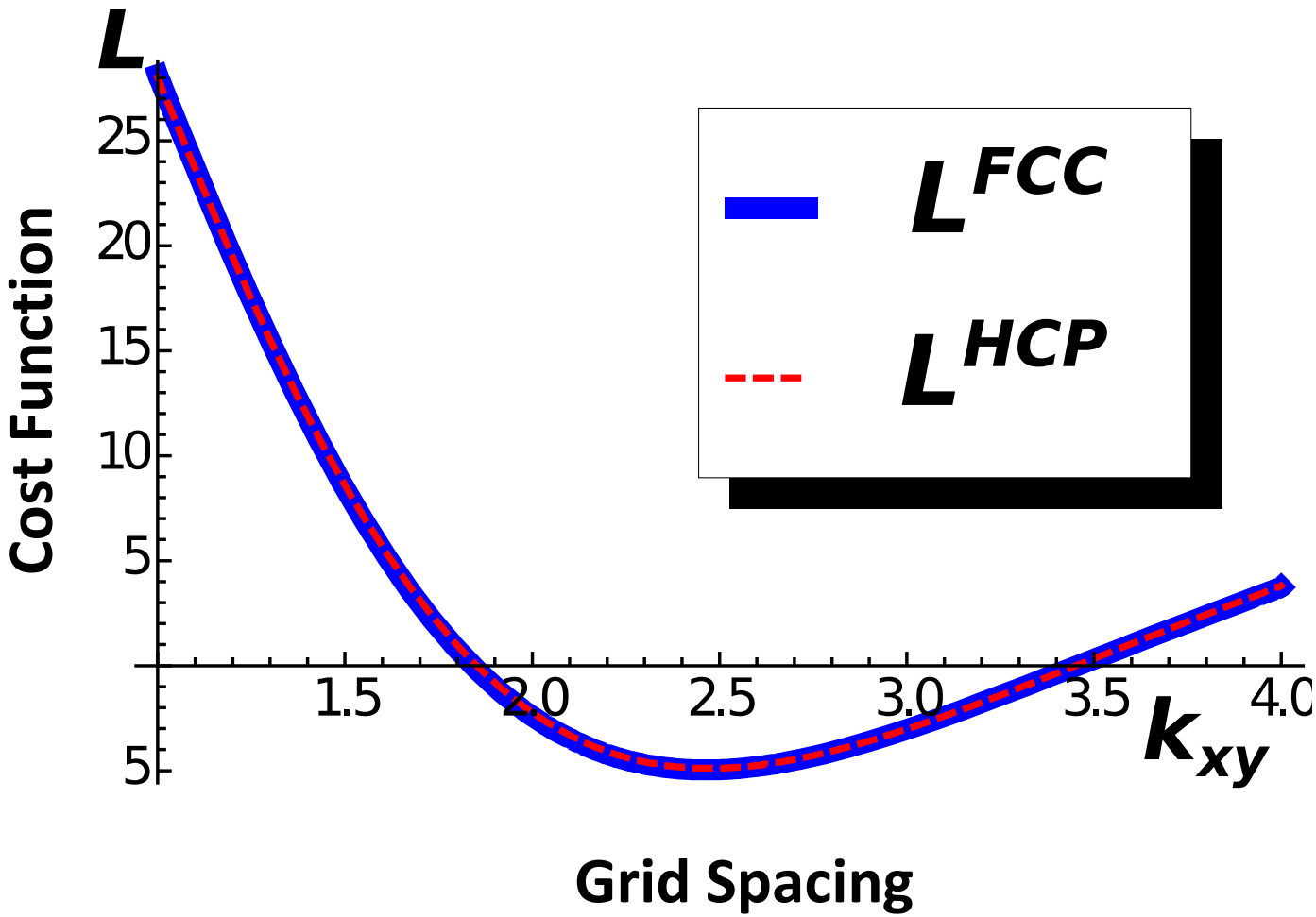
Hexagonal Close Packed



$$\psi^{HCP}(r) = (1/2 + 1/2cos(k_z \cdot r))\left[1 + \frac{2}{3}\sum_{i}^{3} cos(k_{xy}^{i}) \cdot r\right]$$
$$+ (1/2 + 1/2cos(k_z \cdot (r + \Delta z)))\left[1 + \frac{2}{3}\sum_{i}^{3} cos(k_{xy}^{i}) \cdot (r + \Delta x)\right]$$

Grids Development in 3-D

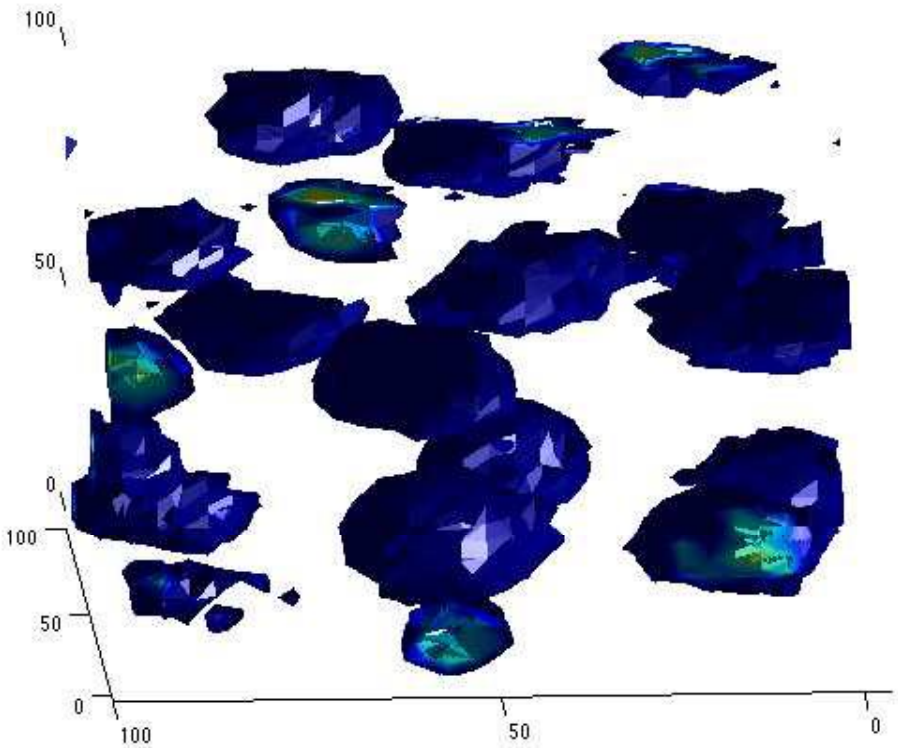
Analytical Solution



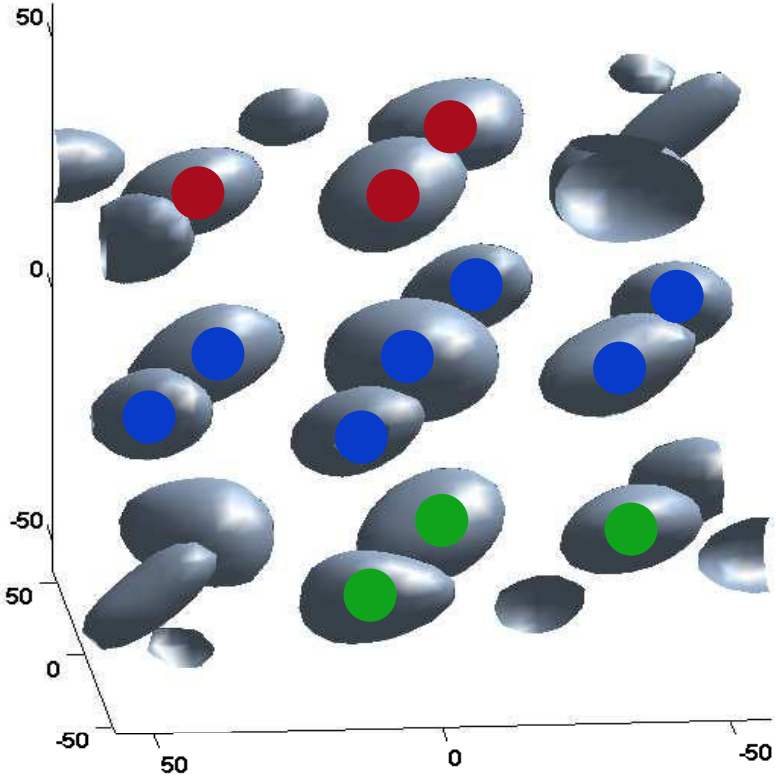
Grids Development in 3-D

Numerical Simulations

Rate Map



Autocorrelogram



Grids Development in 3-D

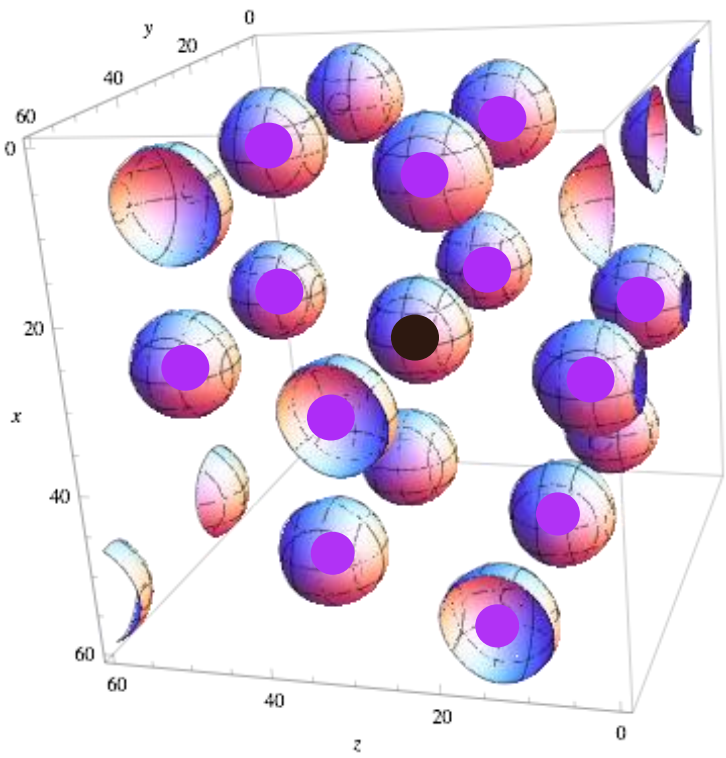
Numerical Simulations

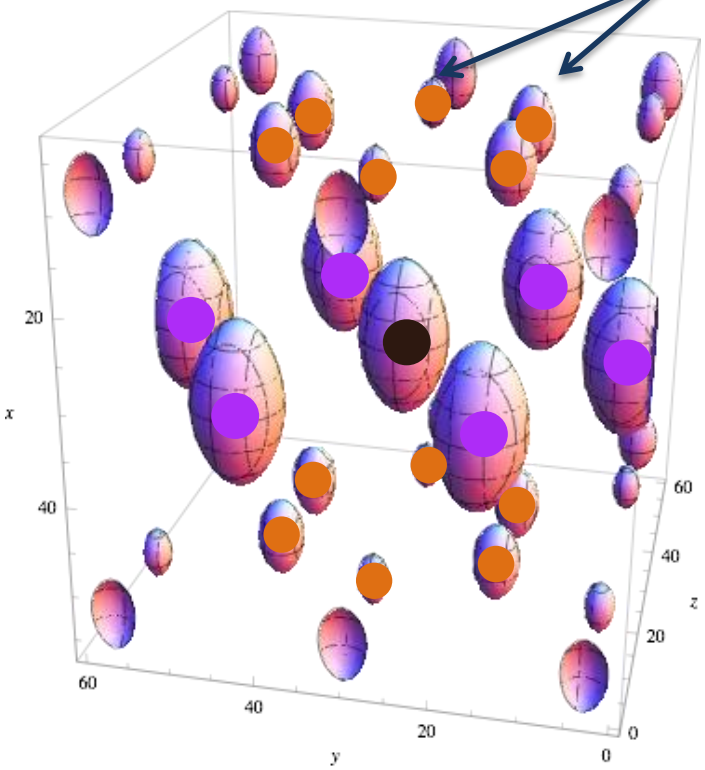
Face Centered Cubic

Hexagonal Close Packed

Autocorrelogram

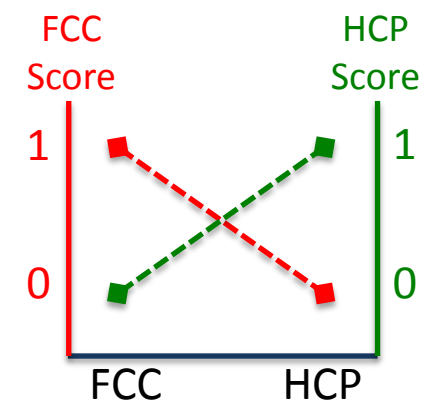
Half Peaks





Grids Development in 3-D

How to distinguish between the two configurations?

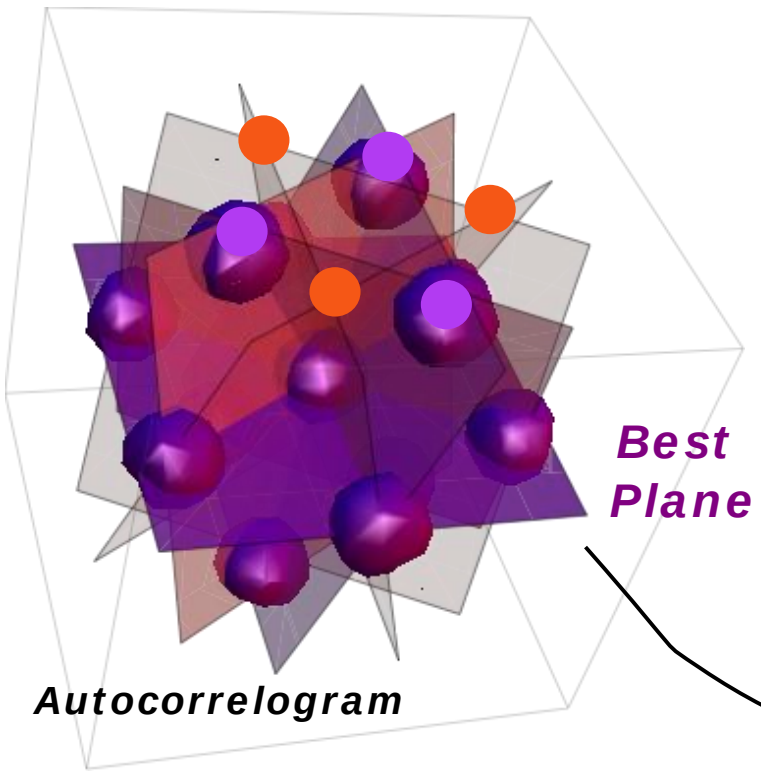


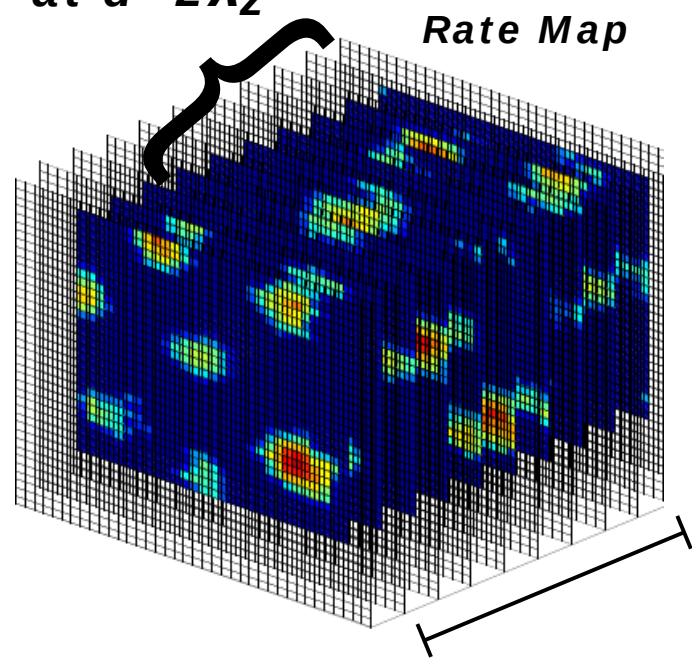
FCC Score

3 Other Planes for FCC and 6 (3+3) for HCP

HCP Score

Correlation at $d=2\lambda_z$

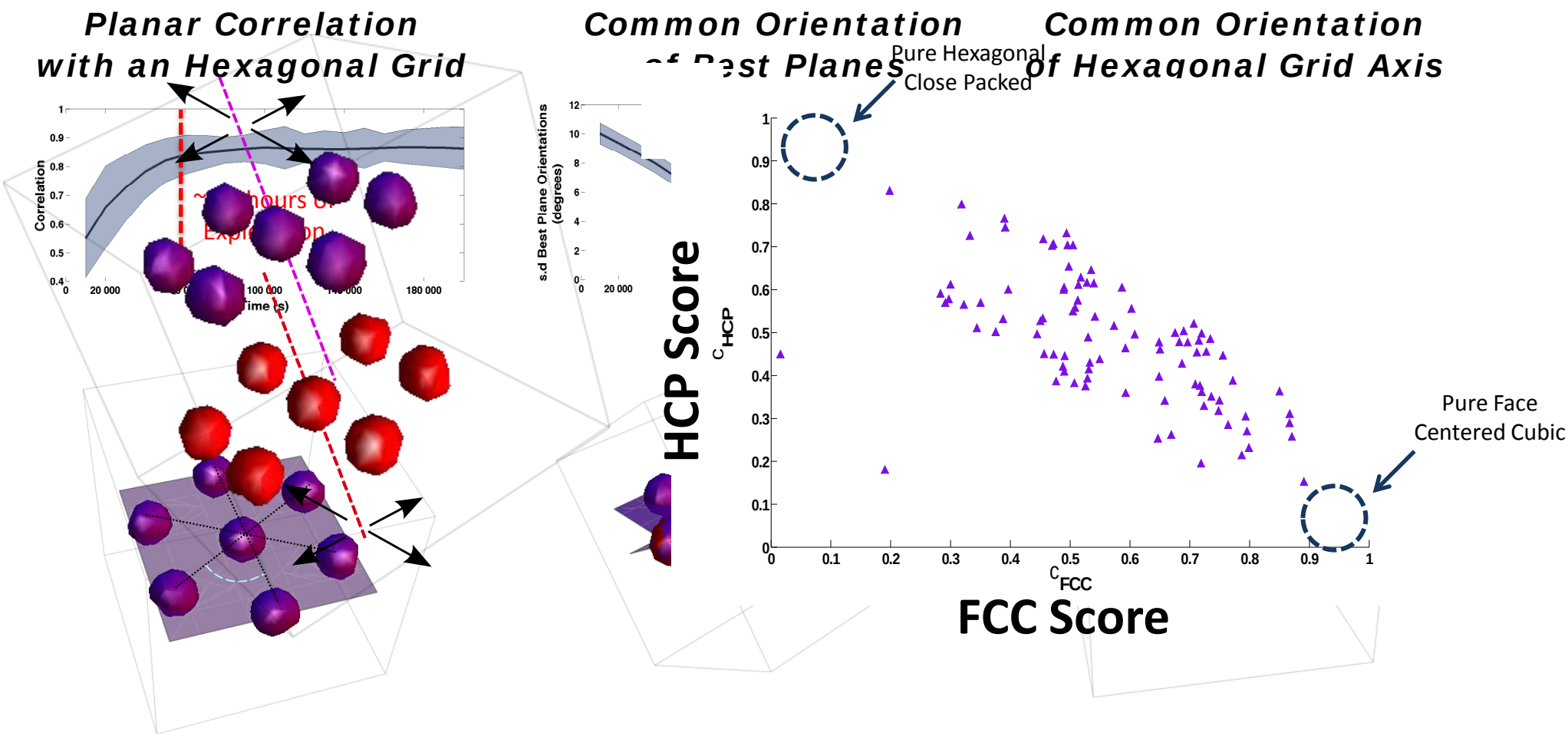


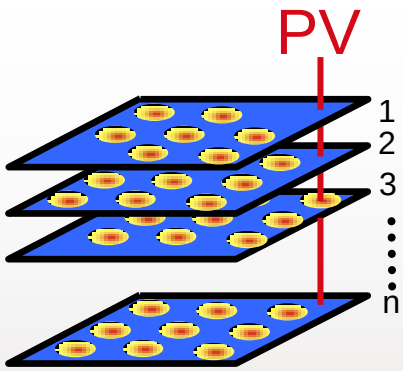


Slices parallel to the Best Plane

Grids Development in 3-D

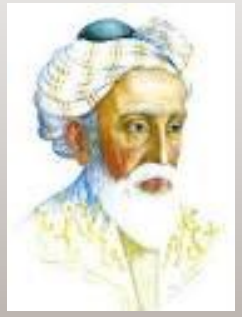
Grids Alignment

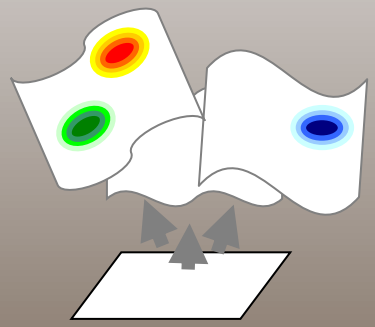


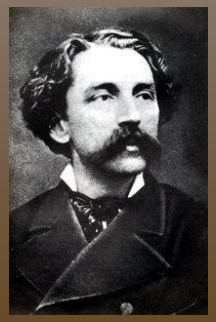


1. The neuronal fatigue model requires HD-dependent collateral interactions to align
2. Conjunctive units may help produce better «pure» grids
3. Rats may play soccer, while bats dwell in crystallography

Wondering about the parallels



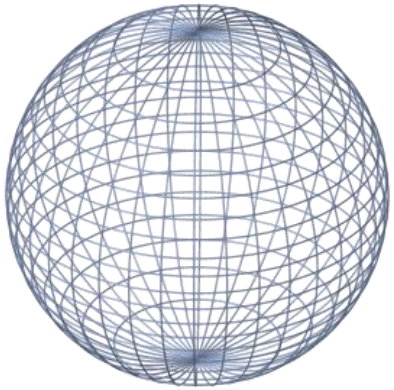




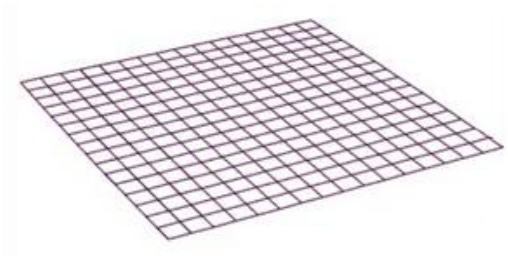
Development of grid cells in nonEuclidean geometry

slides by **Eugenio Urdapilleta**

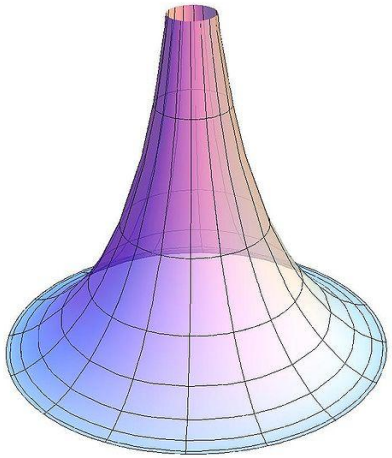
- Kropff & Treves 2008: Self-organizing model of grid cells
  - ➢ Adaptation-based generative model of grids:
    - ❑ Associative learning between position and grid cells
    - ❑ Competitive process among cells + collaterals
  - ➢ Exploration behavior determines grid structure (Si et al, 2012).
  - ➢ other non-Euclidean geometries? What about hyperbolic spaces?



Positive Curvature



Flat environment



Negative Curvature

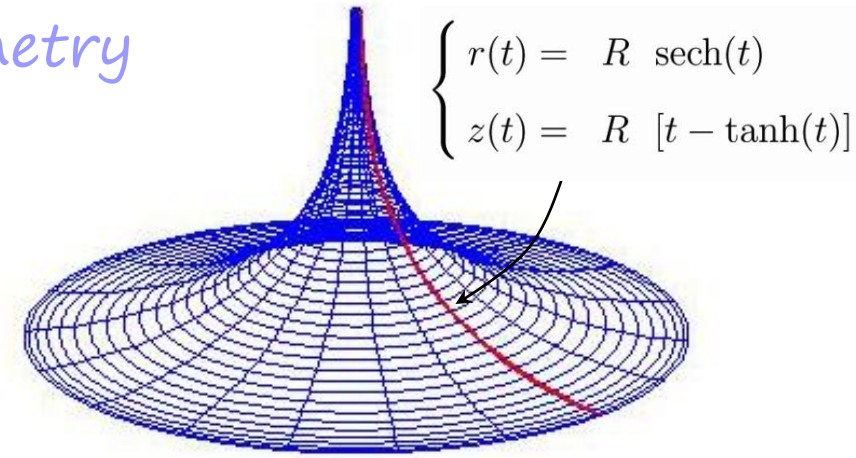
- ❑ Are grids on the **pseudosphere** different from a hexagonal pattern?
- ❑ Tessellations

Development of grid cells in hyperbolic geometries

- *Pseudo-sphere and hyperbolic geometry*

Pseudo-sphere of radius R (in R^3):

- Revolving a tractrix about its asymptote
- It is a surface of curvature $-1/R^2$.



Transformation to upper half-plane, H (u,v)

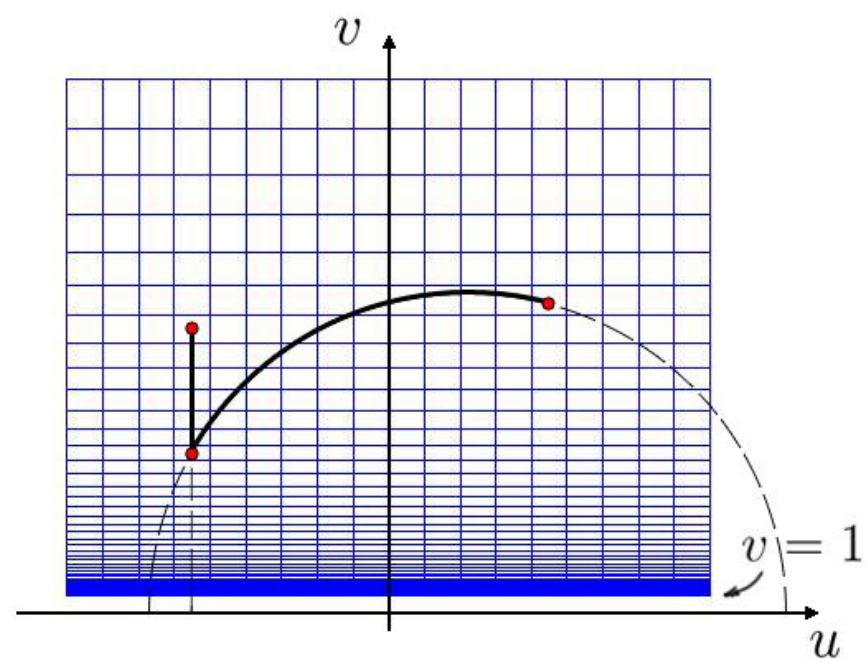
$$\begin{cases} u = \theta \\ v = \cosh(t) \end{cases}$$

- New metric

$$\frac{ds^2}{R^2} = \frac{dv^2 + du^2}{v^2}$$

- Distance (geodesics)

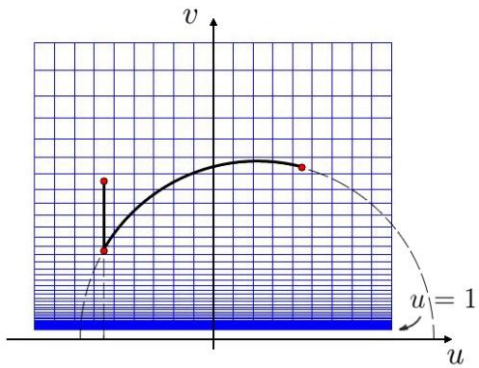
$$d = R \ \mathrm{acosh}\left[1 + \frac{(u_1 - u_2)^2 + (v_1 - v_2)^2}{2 \ v_1 \ v_2}\right]$$



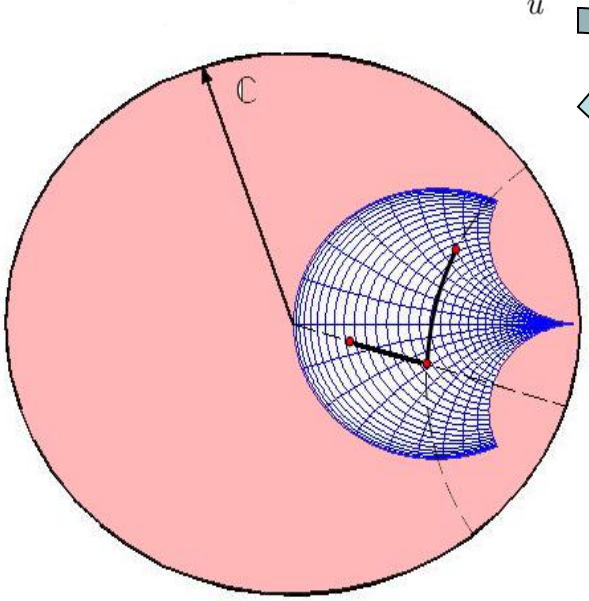
Development of grid cells in hyperbolic geometries

From upper half-plane, h (u,v), to Poincare Disk, C:

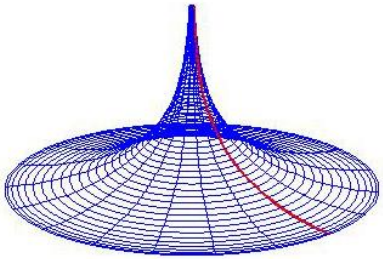
$$z = (u, v) \in \mathbb{H} \quad \rightarrow \quad \frac{z - \imath}{z + \imath} \in \mathbb{C}$$

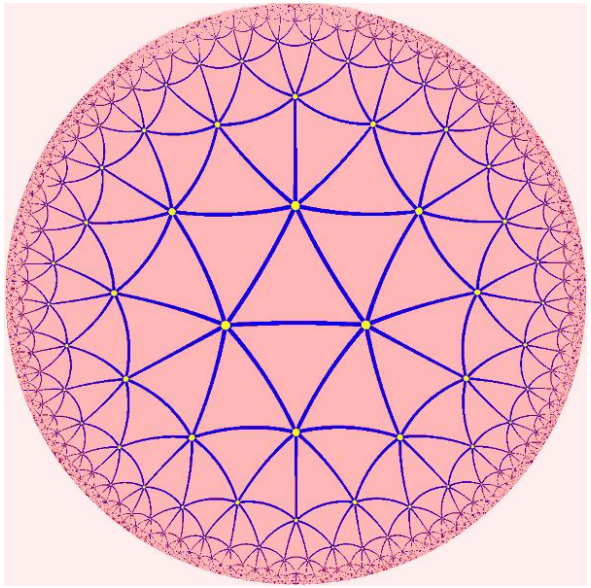


➢ New metric and geodesics

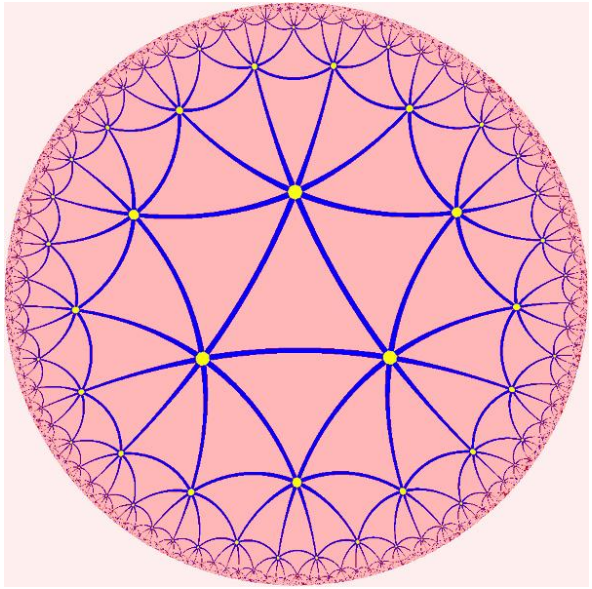


Tiling the space: Exact tessellations





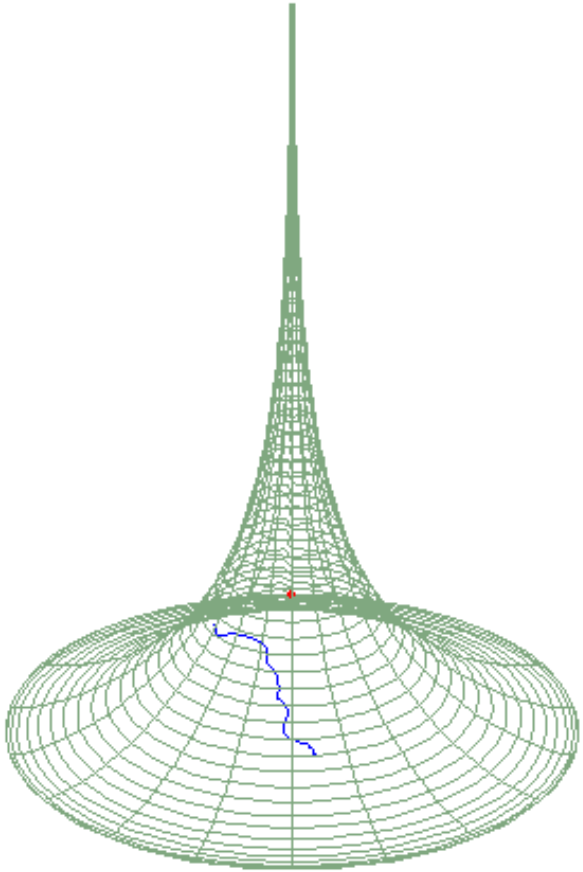
Heptagonal

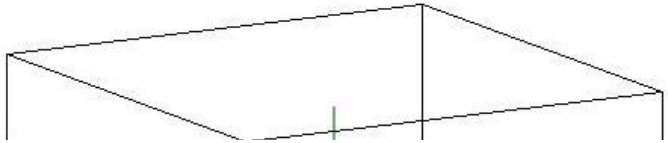


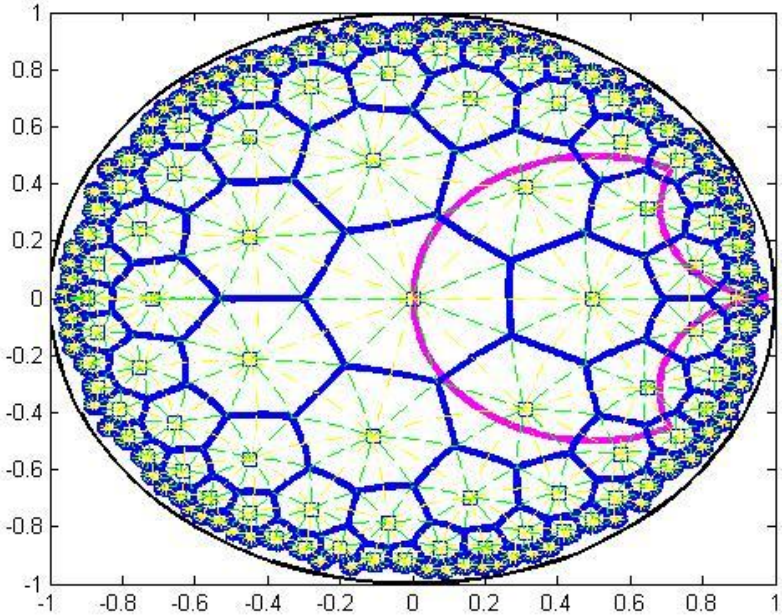
Octagonal

Development of grid cells in hyperbolic geometries

- A walk on the pseudo-sphere
  - Periodic continuation



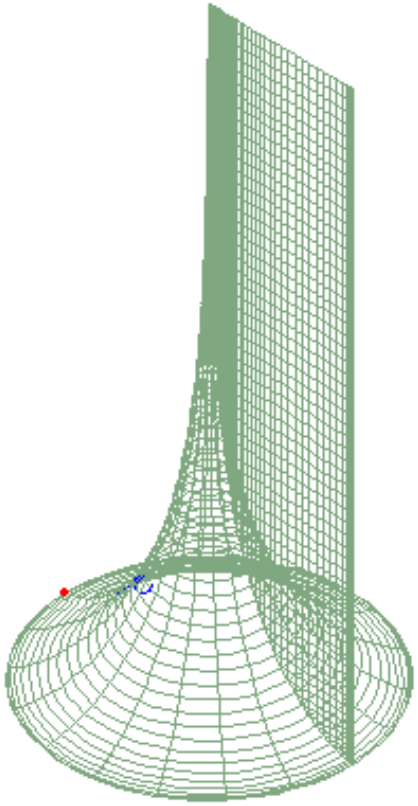


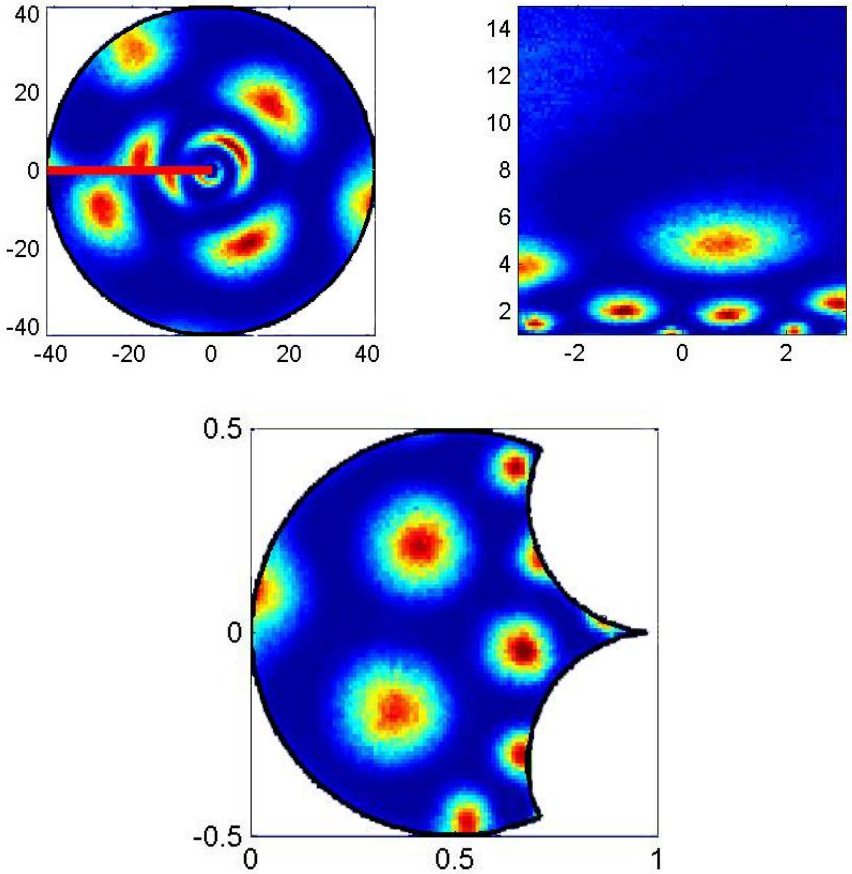


Regular grids do not satisfy this constraint

Development of grid cells in hyperbolic geometries

- A **smooth-walled** pseudo-sphere
  - Impossibility of closing the circumference (mirror condition on the wall)



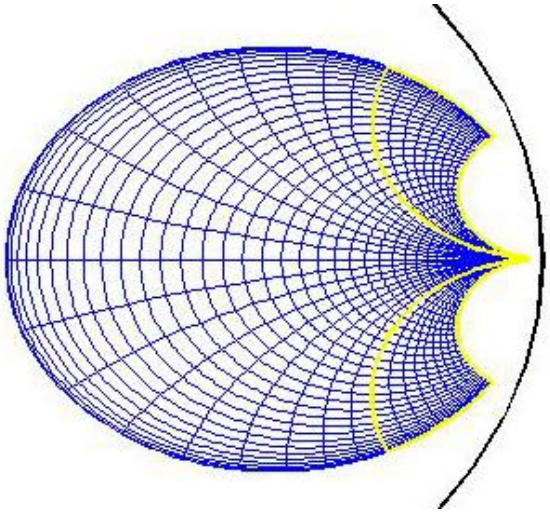


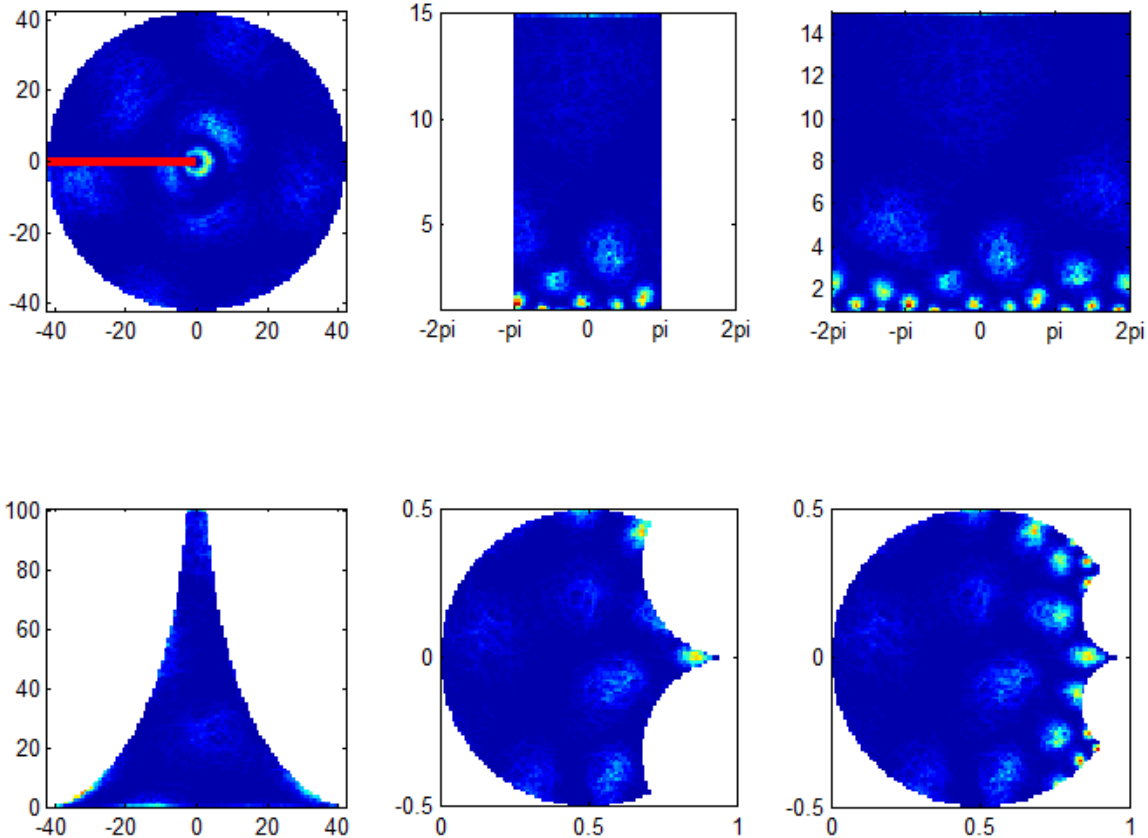
Tessellations: A major constraint given the ratio **grid spacing/pseudo-sphere radius**.

The pseudo-sphere cannot accommodate all the 8, 9, .. fields needed to assess it.

Development of grid cells in hyperbolic geometries

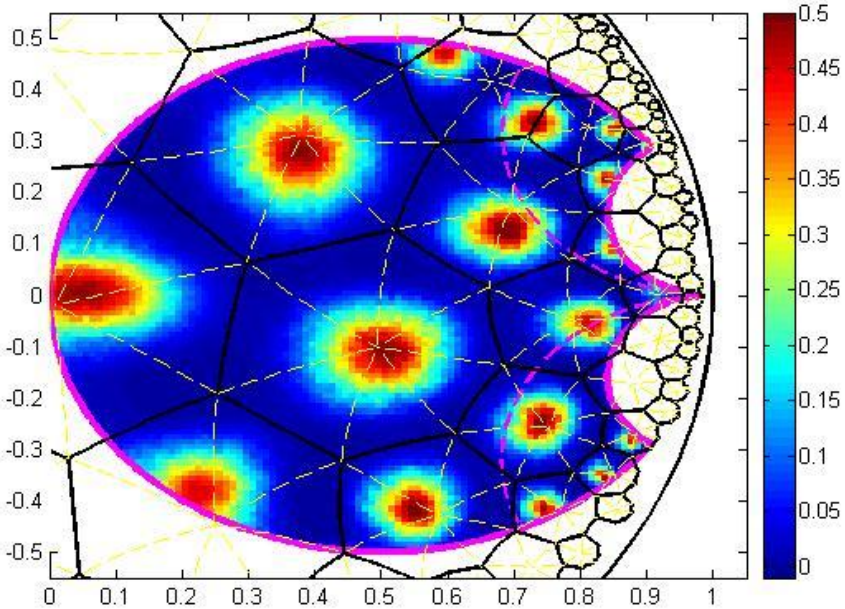
- The **folded** smooth-walled pseudo-sphere
  - Doubling the area available to develop grids
  - Visualizing in the upper half-plane / Poincare disk

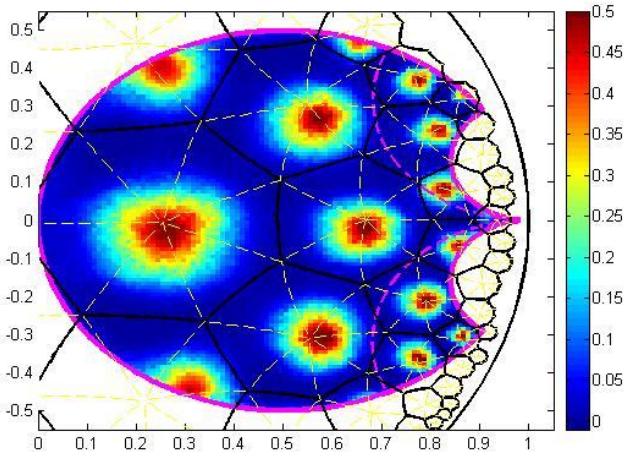


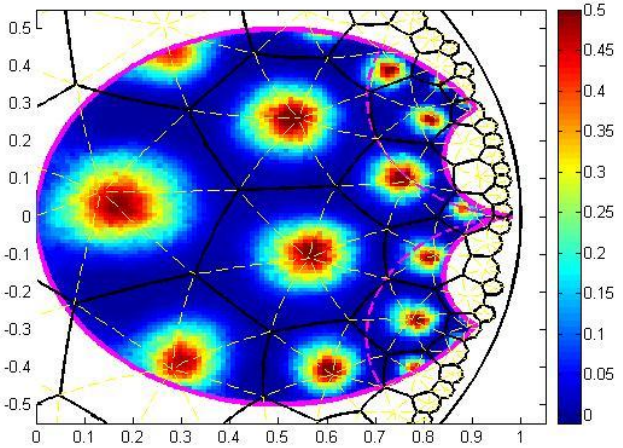


Development of grid cells in hyperbolic geometries

- Characterizing the grids
  - By theoretical tessellations



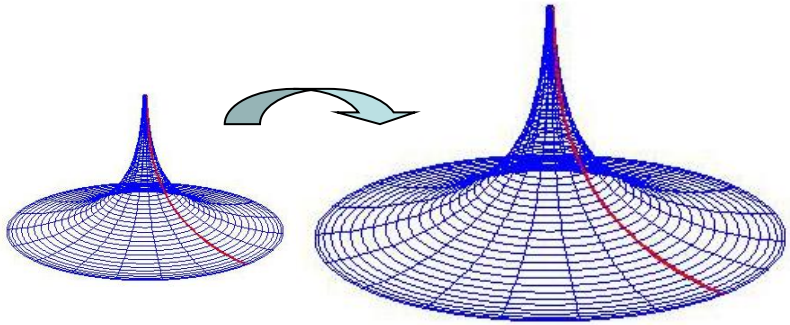


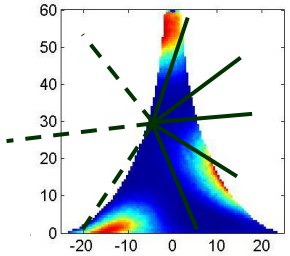


It is valid only for exact tessellations

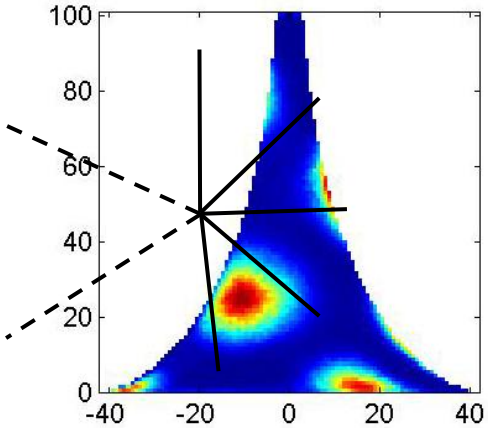
Development of grid cells in hyperbolic geometries

- *Characterizing the grids*
  - ➢ By angular relationships
  - ❑ How does the grids behave with environment size (which is given by the radius of curvature)?
  - ❑ For a generative model where grid spacing is ~ 45 cm, by varying the radius we find:

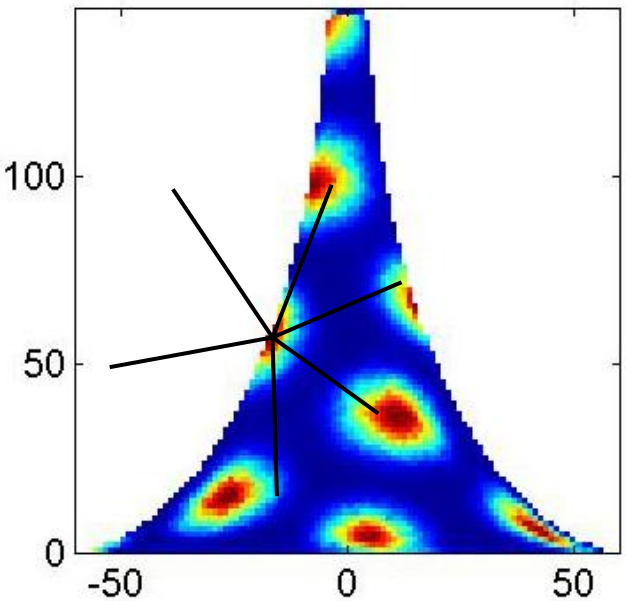




R = 25 cm



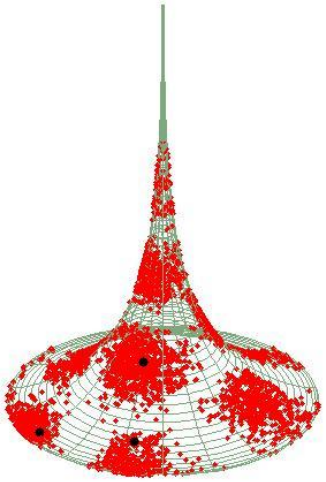
R = 42 cm

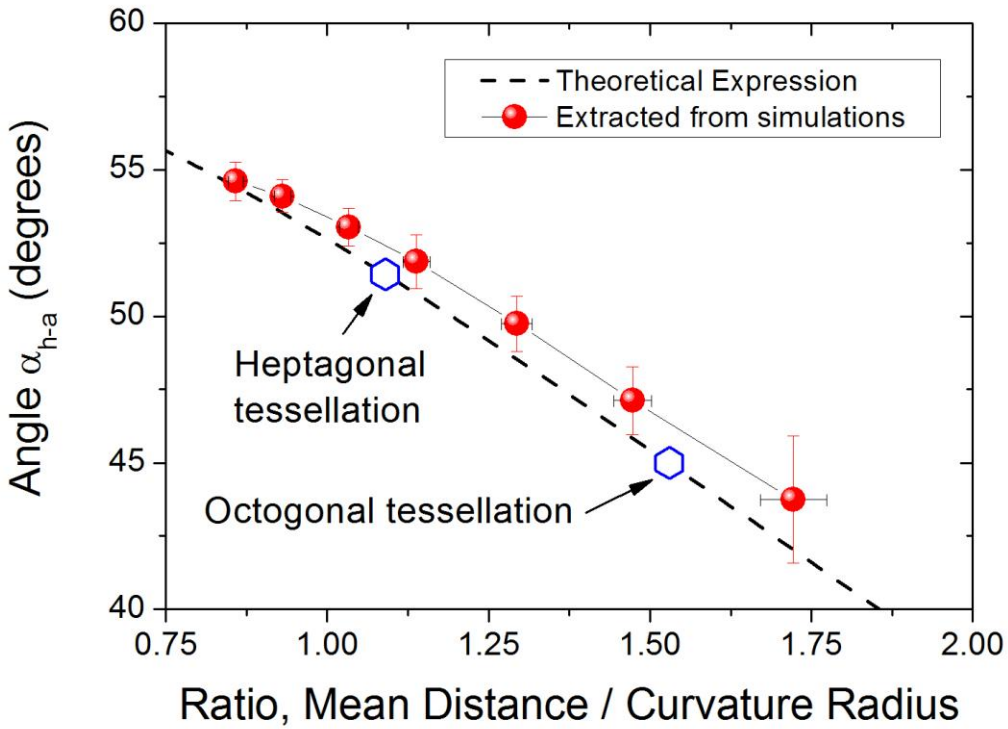


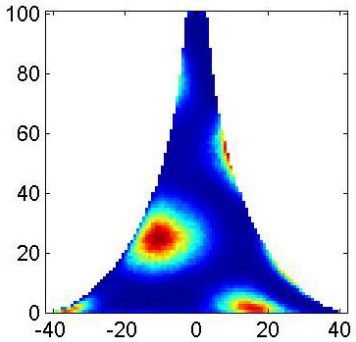
R = 60 cm

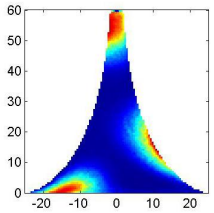
Development of grid cells in hyperbolic geometries

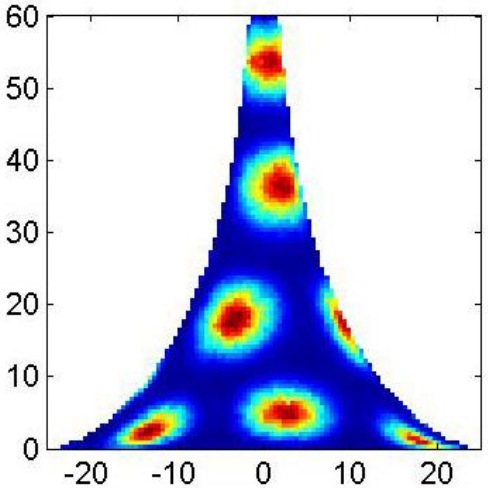
- *Characterizing the grids*
  - ➢ Angular relationships between triplets of spikes belonging to adjacent peaks.
  - ➢ Works well in planar environment (60 degrees).





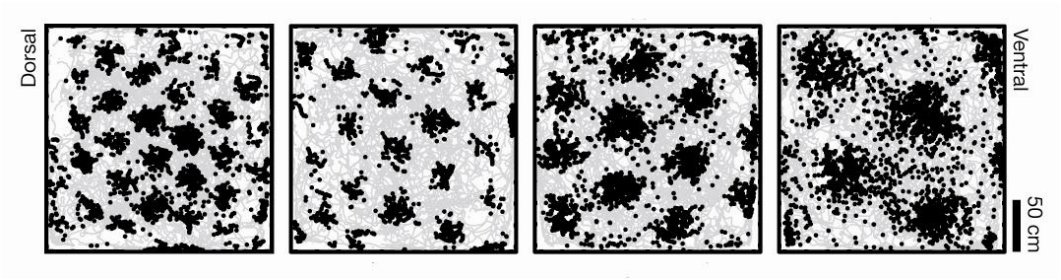






Formation of modules in heterogeneous populations of adapting mEC cells

- Grid cells have a modular organization



- How does this organization arise?

➢ Single cell model - Adaptation-based self-organization in grids

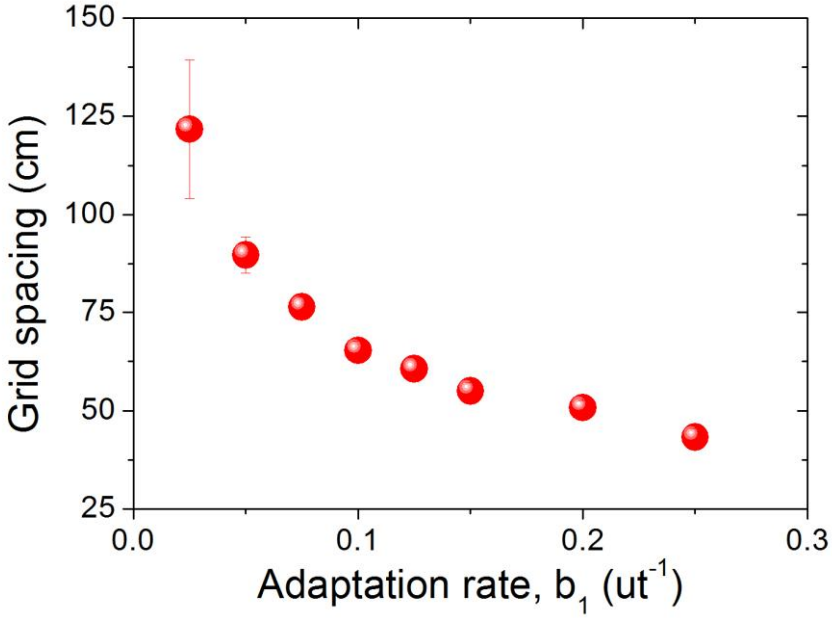
- ❑ Associative learning between position and grid cells
- ❑ Competitive process among cells

➢ Network model

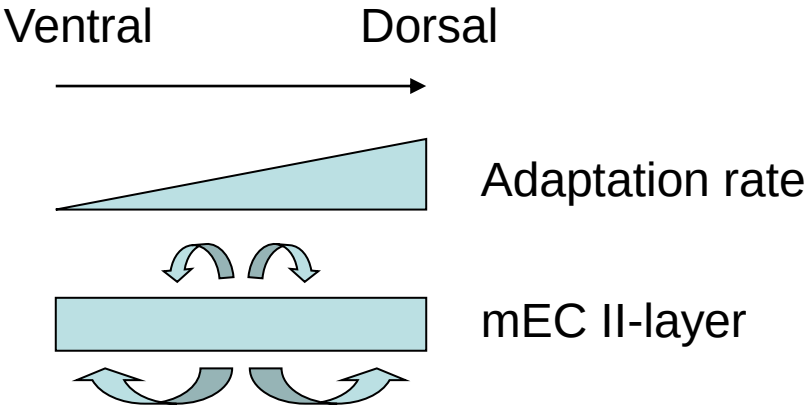
- ❑ Adaptation timescale depends continuously on depth (in the tissue)
- ❑ Smooth lateral connectivity
- ❑ **Does it produce modules?**

Formation of modules in heterogeneous populations of adapting mEC cells

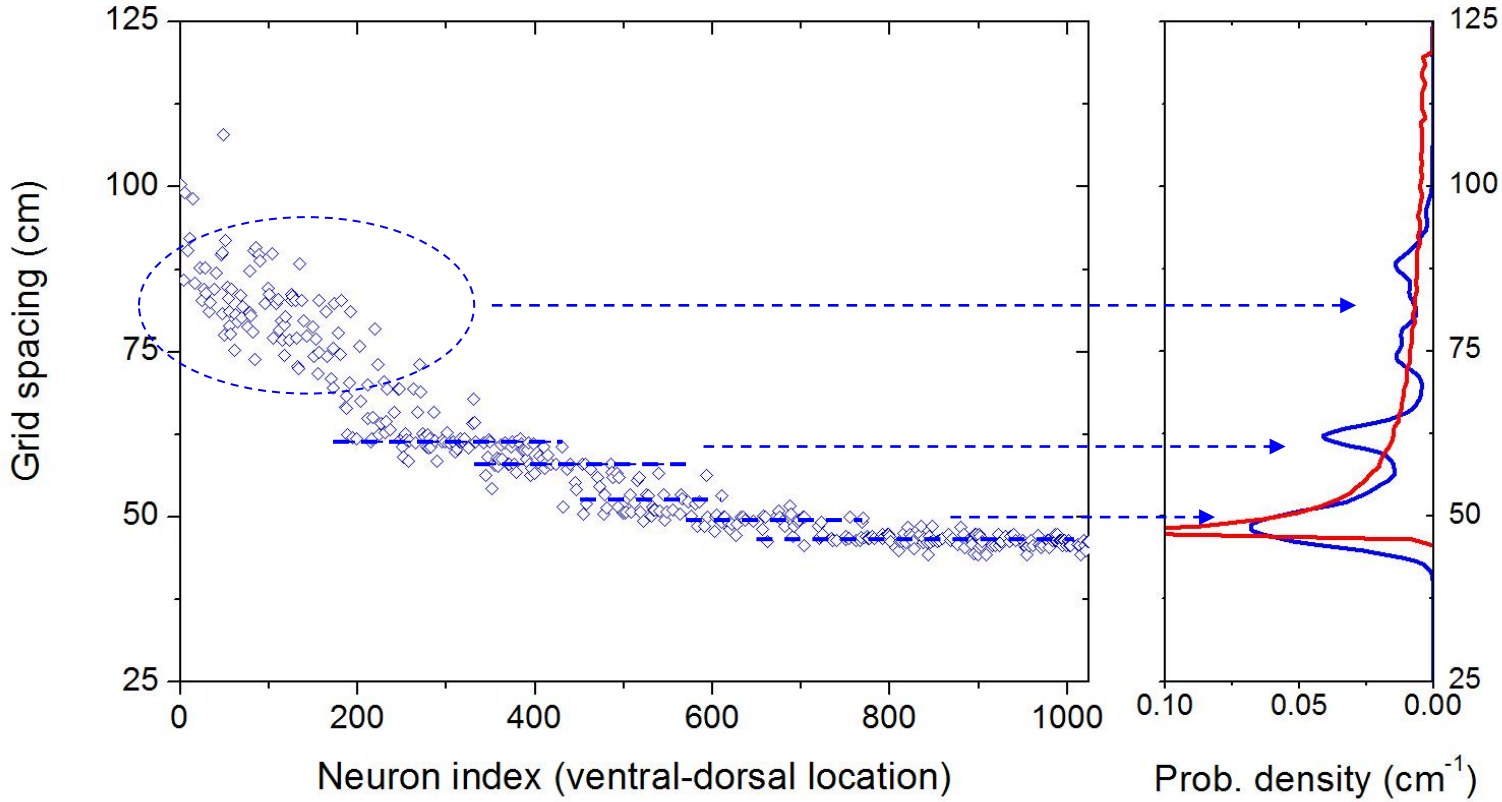
- Individual adapting cells, or a homogeneous network
  - ➢ Adaptation rate controls grid spacing



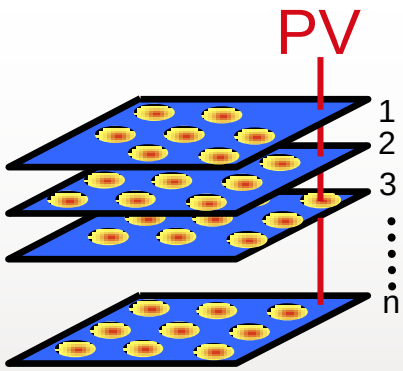
- Heterogeneous network of adapting neurons
  - ➢ **Individual unit adaptation rate** would lead to the expression of an "intrinsic" grid spacing.
  - ➢ **Collateral connectivity** makes units interact and leads to a clustering of their grid spacings.



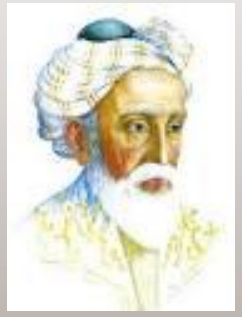
Formation of modules in heterogeneous populations of adapting mEC cells

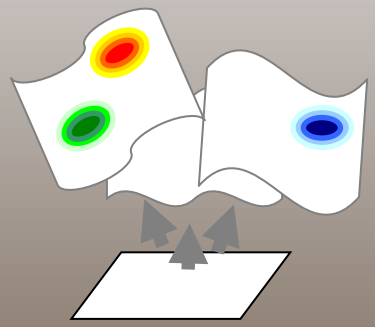


Modules can develop spontaneously within this model, if single cells with a gradient of adaptation timescales are linked with collaterals



1. The neuronal fatigue model requires HD-dependent collateral interactions to align
2. Conjunctive units may help produce better «pure» grids
3. Rats may play soccer, while bats dwell in crystallography
4. Non-Euclidean rodents may look just like ordinary ones





Why ruin mEC beauty with DG?

(……this will be postponed to another time)