Path integration, continuous attractors and grid cells

Aims

- Understand the concept of path integration and how it might contribute to navigation and place cell firing
- Discuss the continuous attractor network model of place cell firing
- Describe the firing pattern of grid cells in entorhinal cortex and why they might be suited to provide the path integration input to place cells

References

Zhang (1996) Representation of spatial orientation by the intrinsic dynamics of the head-direction cell ensemble: a theory. Journal of Neuroscience 16: 2112-2126.

Samsonovich and McNaughton (1997) Path integration and cognitive mapping in a continuous attractor neural network model. Journal of Neuroscience 17: 5900-5920.

Etienne and Jeffery (2004) Path integration in mammals. Hippocampus 14:180-92.

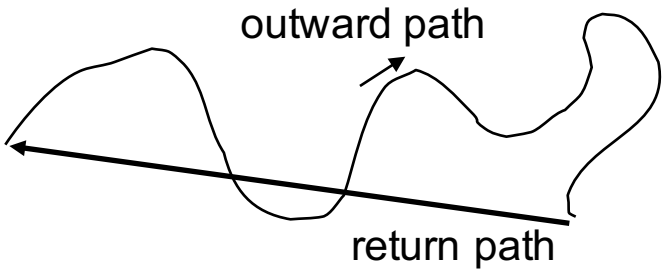
Hafting et al. (2005) Microstructure of a spatial map in the entorhinal cortex. Nature 436: 801-806.

O'Keefe and Burgess (2005) Dual phase and rate coding in hippocampal place cells: theoretical significance and relationship to entorhinal grid cells. Hippocampus 15: 853-866.

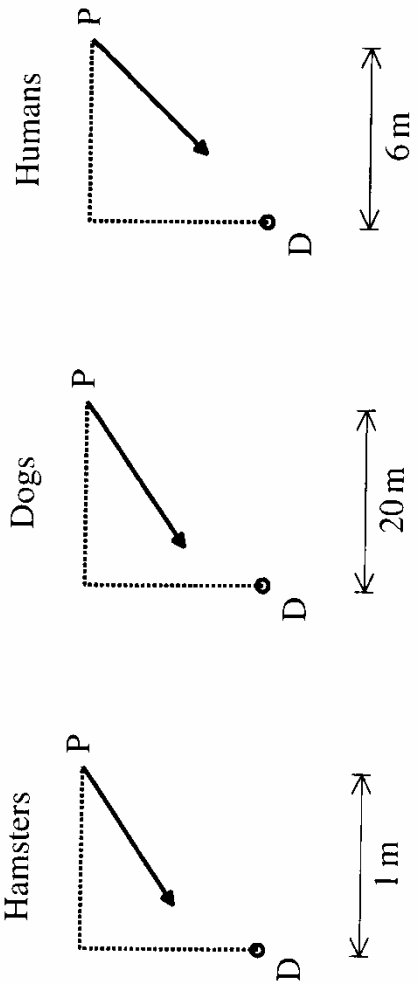
Jeffery and Burgess (2006) A metric for the cognitive map: found at last? Trends in Cognitive Science 10: 1-3.

‘Path integration’ in mammals

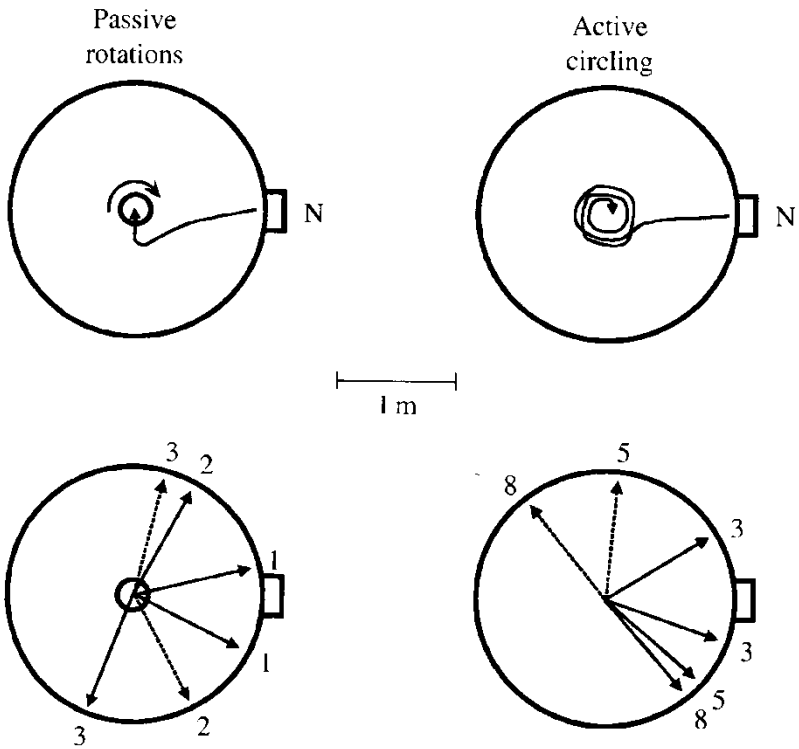
Many animals retain a sense of the total angle and distance travelled so that a return path can be made, even in total darkness



Although there are often biases…



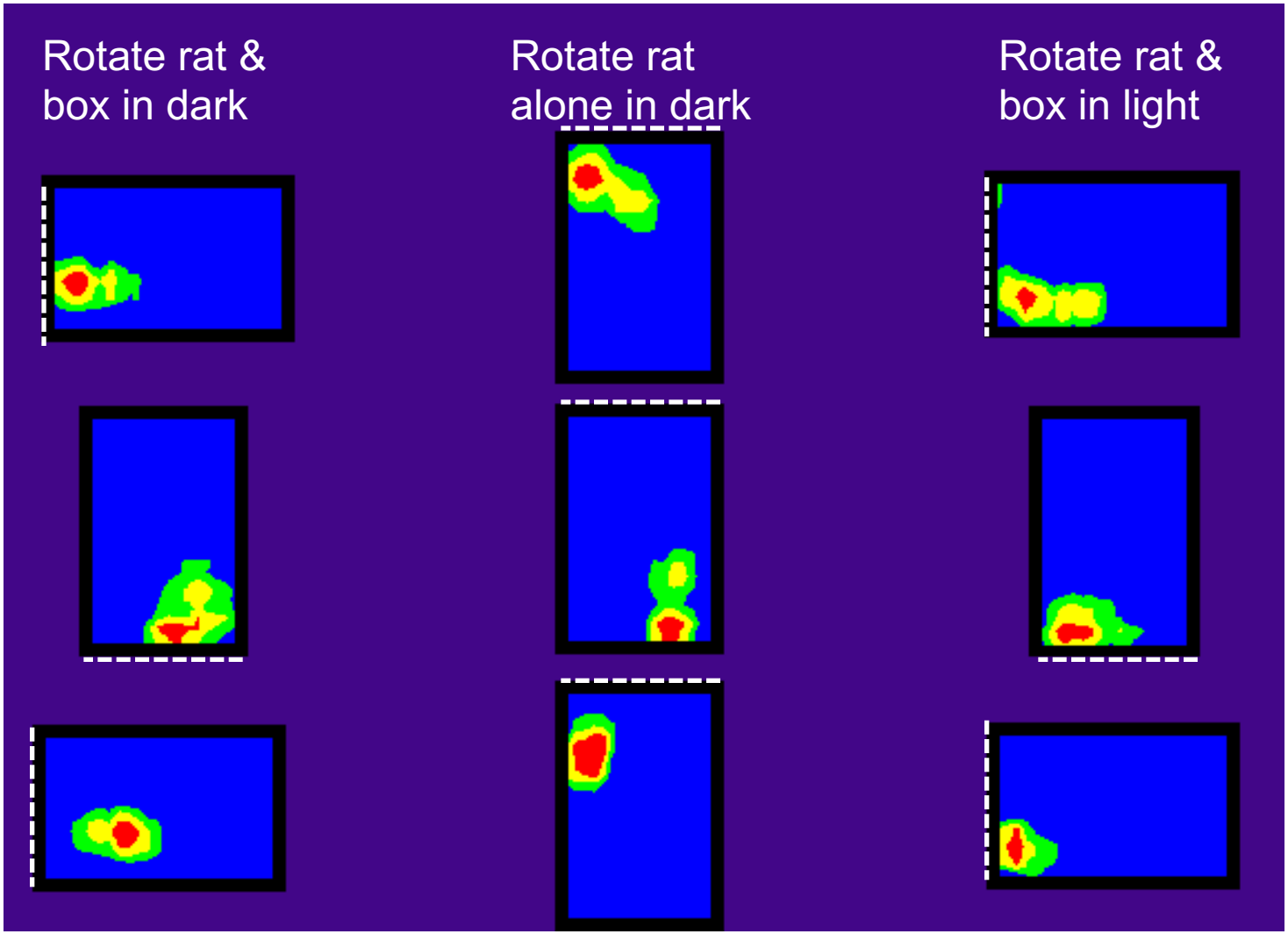
The capacity to retain this information is limited to around three passive or five active rotations in hamsters returning to the nest



Etienne, Maurer & Seguinot (1996) Journal of Experimental Biology

Place cells and path-integration

Path integration appears to orient the place cell representation unless stable visual orientation cues are present

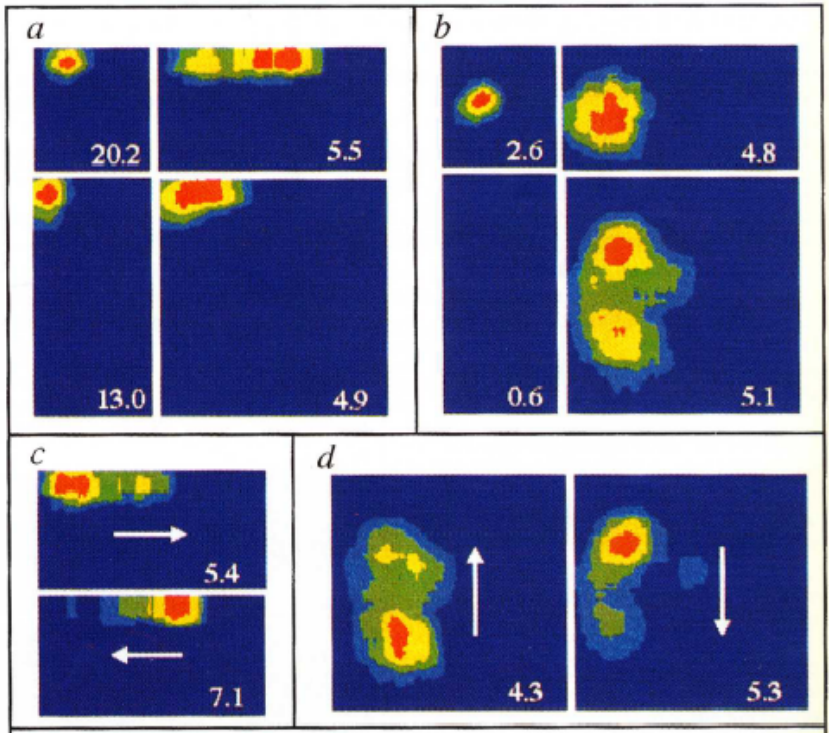


Jeffery et al. (1997) Experimental Brain Research

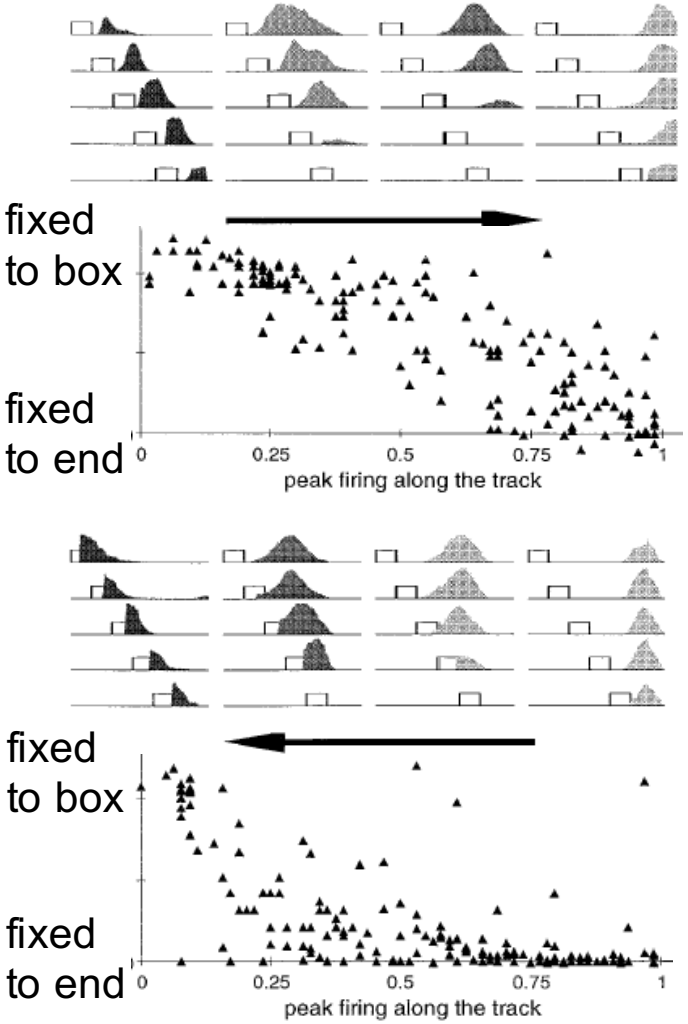
Place cells and path-integration

Path integration appears to provide additional information about a boundary that the rat has recently visited (i.e. behind it) compared to one ahead.

Effect of running direction on firing rate of a stretched field:



Effect of running direction on firing location of a stretched field:



O'Keefe and Burgess (1996) Nature; Gothard et al. (1996) Journal of Neuroscience

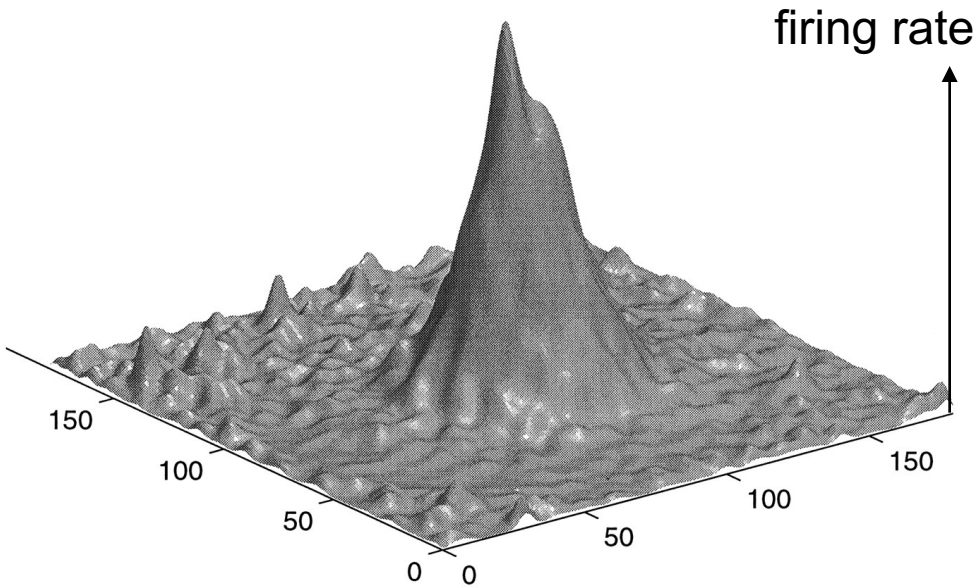
‘Continuous attractor’ network models of place cell firing

Attractor representations are patterns of neural activity to which similar patterns of activity evolve under the dynamics of the system, e.g. in the Hopfield model.

A ‘continuous attractor’ is a set of patterns to which other patterns are attracted but within which the pattern of activity can change smoothly from one to another.

Zhang (1996) and McNaughton et al. (1996) proposed that the patterns of activity shown by the place cells formed a continuous attractor: all of them can be thought of as having the same ‘bump’ shape:

Imagine the place cells arranged in a sheet so that each cell’s location reflects the location of its firing field in the environment. The bump indicates the rat’s location and moves as the rat moves.

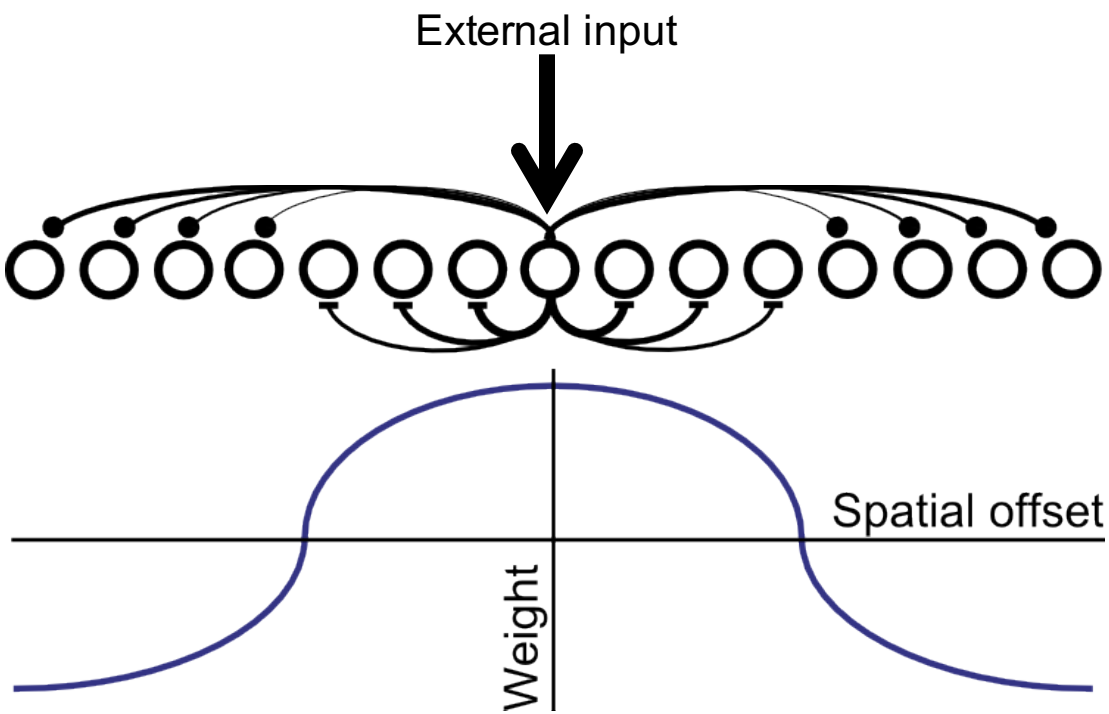


‘Continuous attractor’ network models of place cell firing

The simplest example of a continuous attractor network is on a linear track

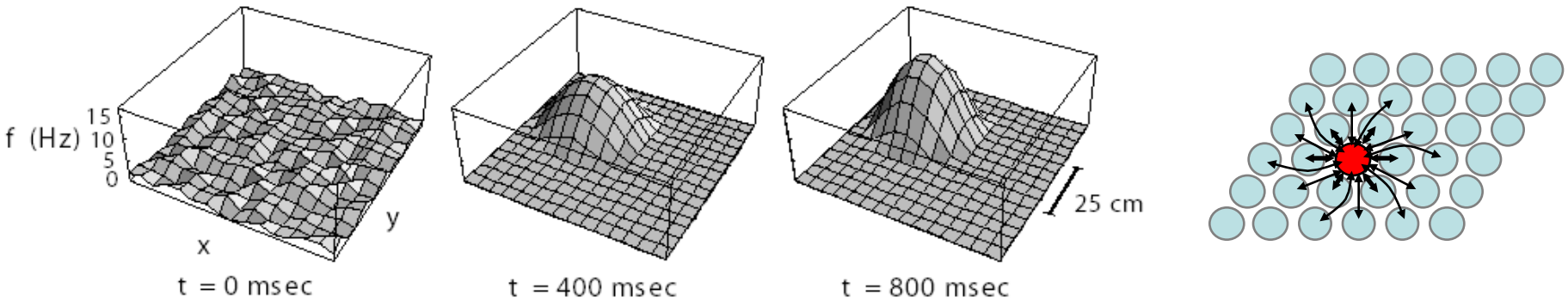
The requisite synaptic connectivity is often referred to as ‘Mexican hat’

It is important to remember that the physical arrangement of these cells in the brain does NOT reflect the arrangement of their firing fields in the environment

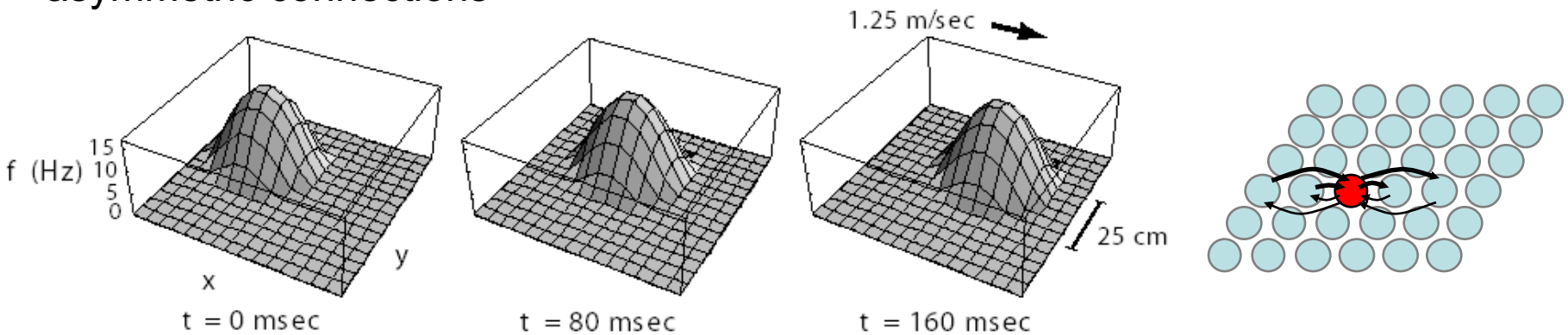


‘Continuous attractor’ network models of place cell firing

We can then generalise this model to two dimensions to form a continuous attractor, such that the ‘activity bump’ can move smoothly in any direction



Adding asymmetric connections in a particular direction makes the activity bump shift in that direction, with a speed proportional to the strength of the asymmetric connections

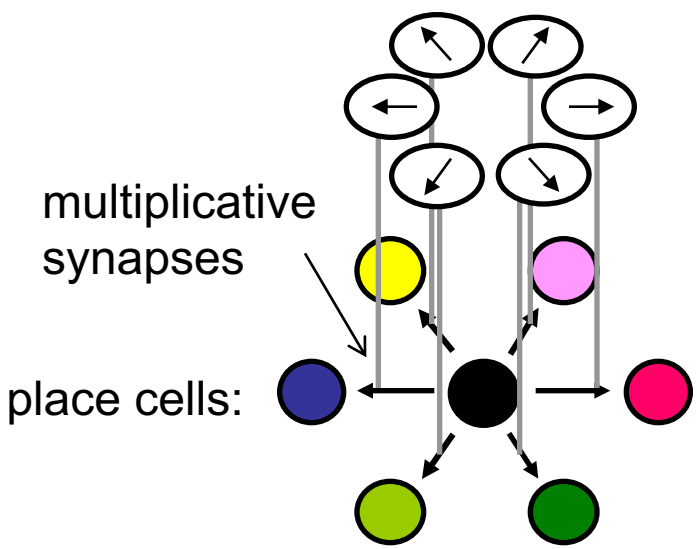


‘Continuous attractor’ network models of place cell firing

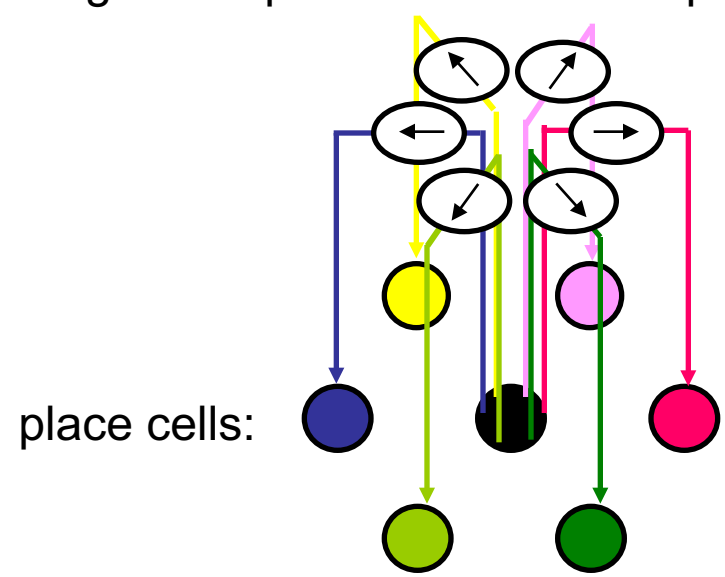
If the asymmetric connections between place cells along a given direction have weights proportional to the speed of movement in that direction, then the activity bump will automatically track the location of the rat using only these motion signals: i.e. the network performs ‘path integration’

This could be achieved in two ways:

1. ‘shifter cells’:
firing rate = direction x speed



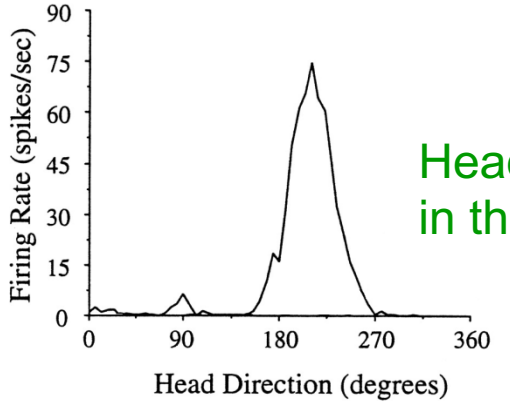
2. ‘shifter cells’:
firing rate = place x direction x speed



Summary: Continuous attractor network models of place cell firing and path integration

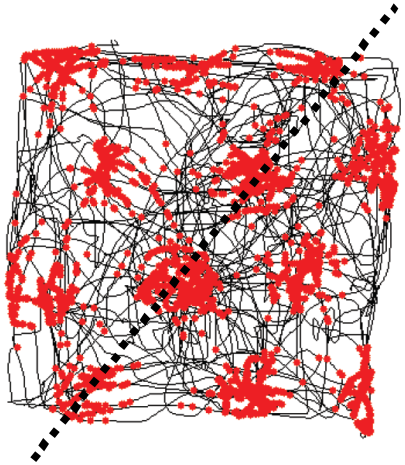
- Path integration is the process by which an animal updates its location - relative to some starting position – by keeping a cumulative record of internal movement information
- Connecting place cells with synaptic weights that increase with the proximity of the two cell's firing fields can produce a particular type of activity in a neural network - a 'bump' in which cells with nearby firing fields are active - and the set of all such patterns forms a continuous attractor
- The pattern of activation can change, within this set, so that the activity bump moves around the network. The speed of movement depends on the strength of asymmetric connections in the direction of motion
- 'Shifter cells' could be used to make the strength of asymmetric connections between place cells proportional to the rat's speed of movement in that direction. The activity bump would then automatically follow the rat's movement – thus performing path integration
- One issue with this model is that place cells are also driven by sensory input, not just path integration
- Another issue is that a large number of connection strengths have to be learned – one for movement in each direction from each place

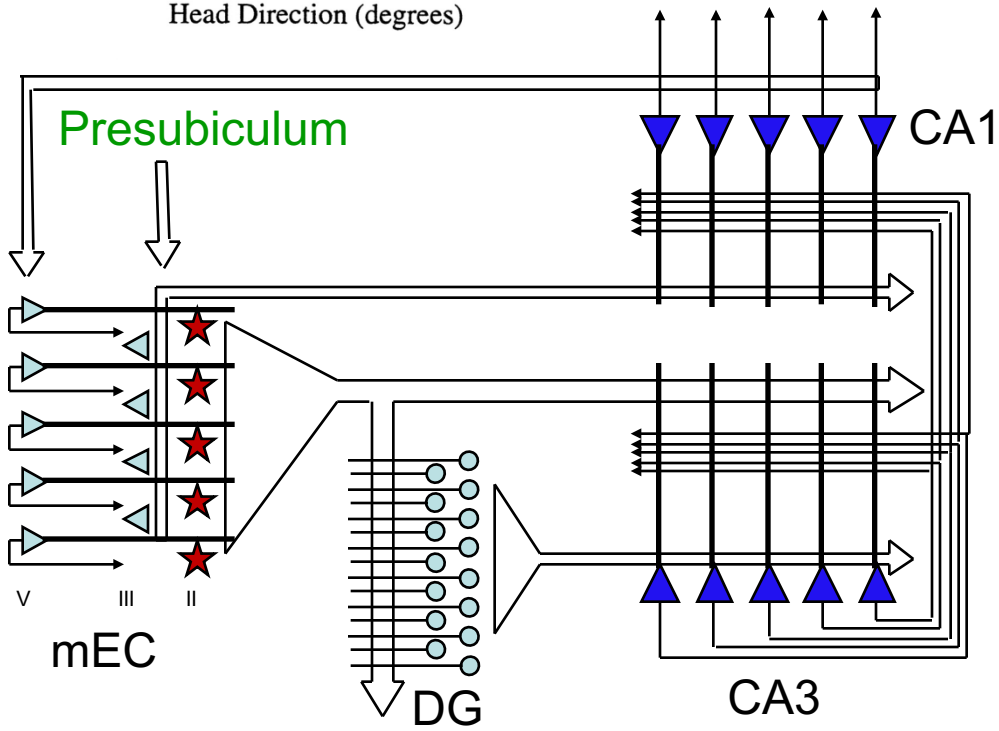
Spatially receptive cells in the hippocampal formation: Grid cells



Head-direction cells in the presubiculum

Grid cells in medial entorhinal cortex (mEC)





Place cells in CA1/CA3

Properties of grid cells

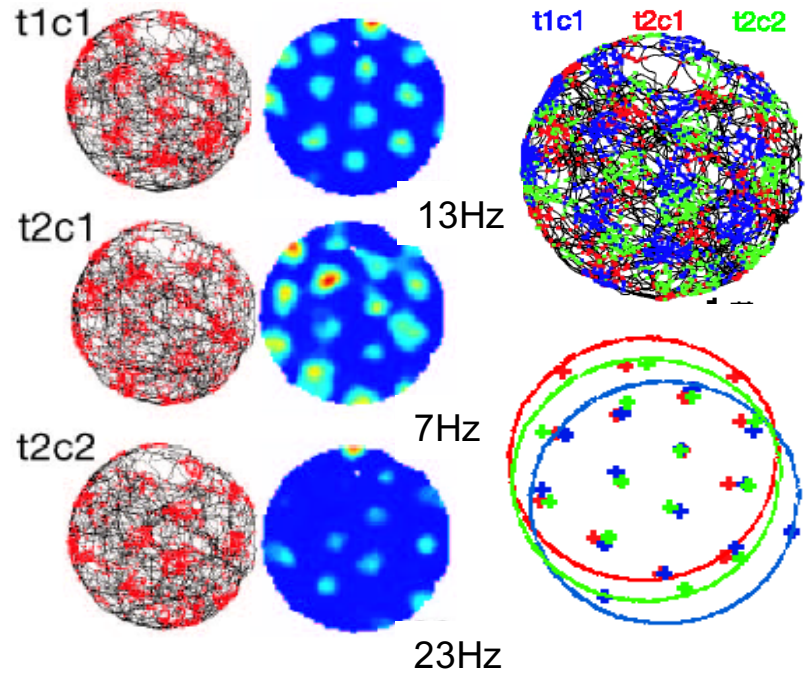
Spatially stable, regular hexagonal firing

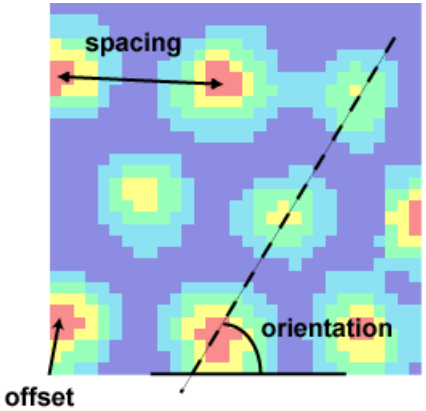
Orientation appears to be constant within each hemisphere

Local grids tile environment (random offset)

Spacing increases at more ventral locations

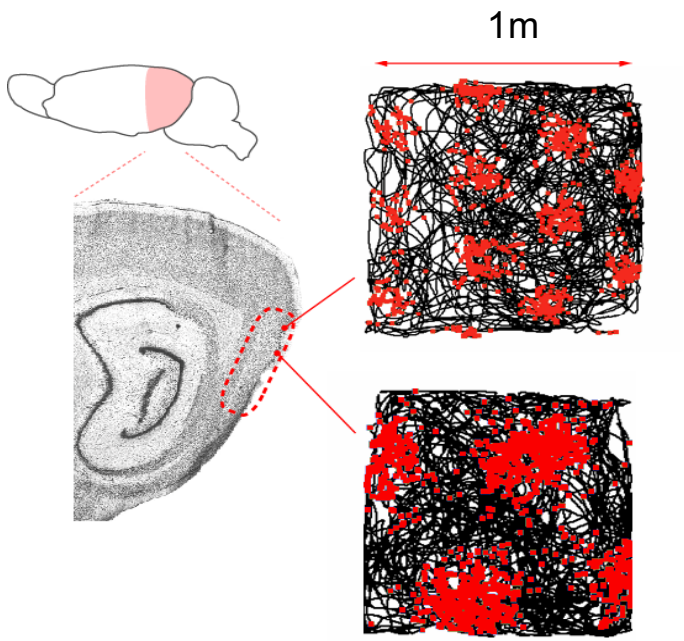
Code comprised of different scales is sufficient to localise the rat



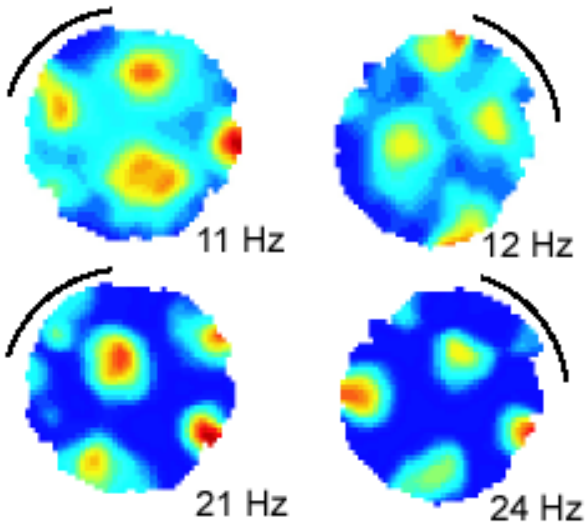


Hafting et al. (2005) Nature; Sargolini et al. (2006) Science

Properties of grid cells



Grid scale increases as recording site moves from dorsal to ventral



Grid orientation depends on environment

Hafting et al. (2005) Nature

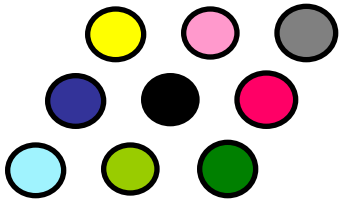
Properties of grid cells

The grid cell network is well suited for path integration via recurrent connections – i.e. as a continuous attractor

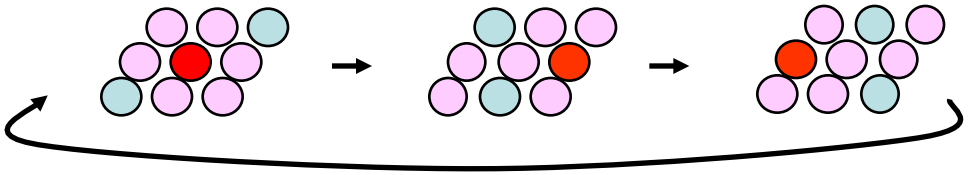
Far fewer neurons and connections are needed as the pattern is repeated – even across large environments

Connections can be fine-tuned regardless of the specific location and environment

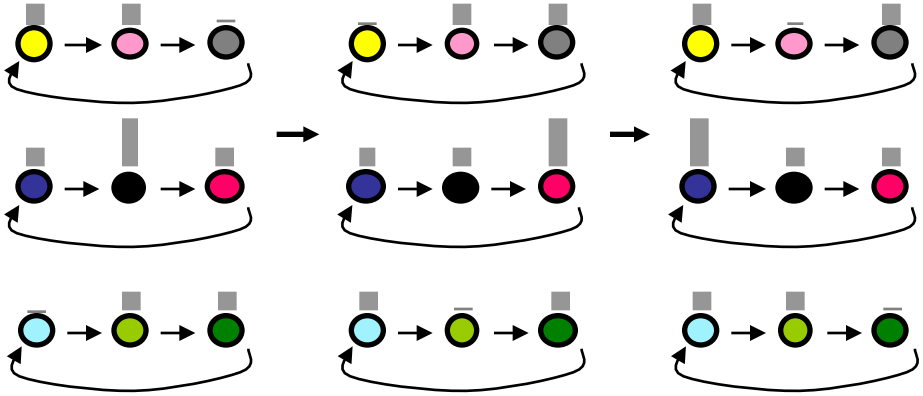
For example, nine grid cells are (just) enough to do path integration



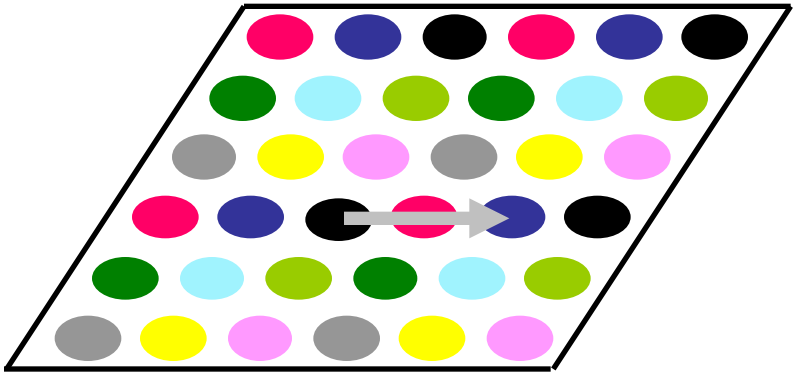
1. Sequence of activity



2. Connections and activity



Firing locations in the environment

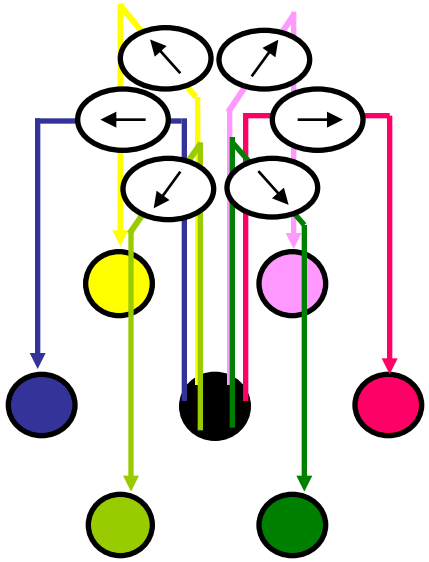


‘Conjunctive’ (grid x direction) cells

Conjunctive grid position x heading direction cells have also been identified in mEC

These provide an obvious correlate of the second group of postulated ‘shifter cells’ needed to perform path integration in a continuous attractor network

Conjunctive ‘shifter cells’:
firing rate = grid x direction x speed



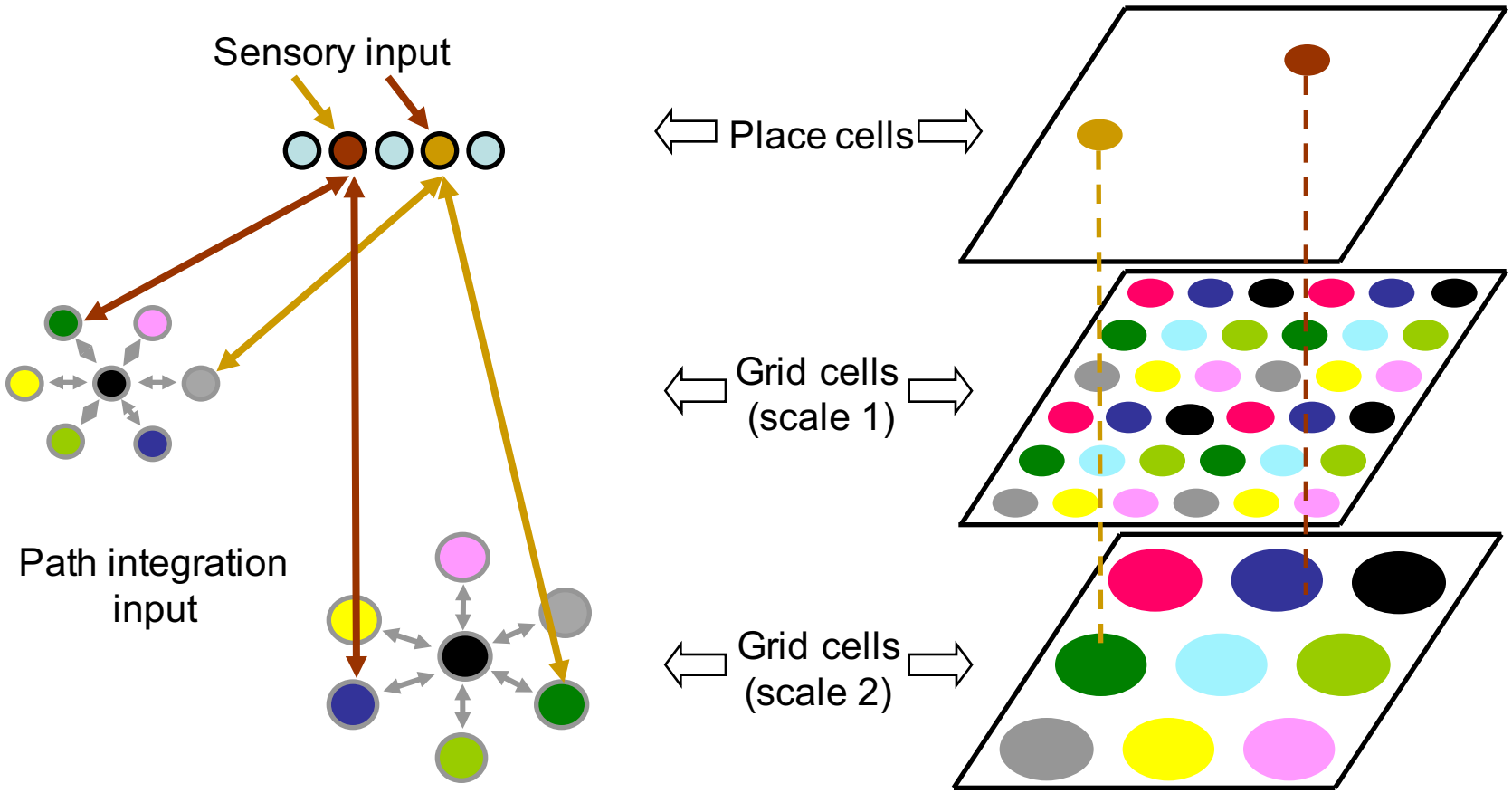
Grid cells

Sargolini et al. (2006) Science

Grid cell / place cell interactions

Associations between grid cells and the environment - and between grid cells with different orientations or spatial scale - must be made via place cells, as the relationship is only stable at one location

Place cells get sensory input from environment, and could get path integration input from all the grid cells that fire at the place field

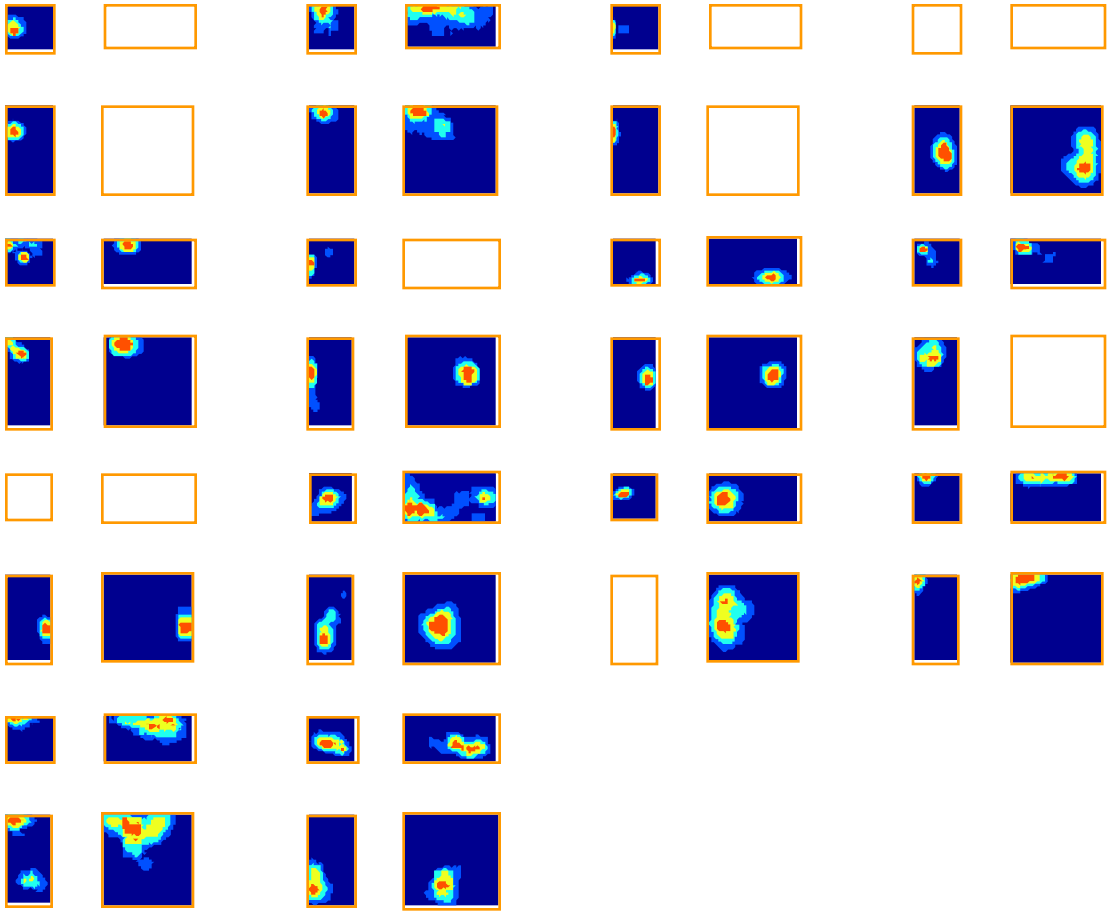


O'Keefe and Burgess (2005) Hippocampus

Grid cell / place cell interactions

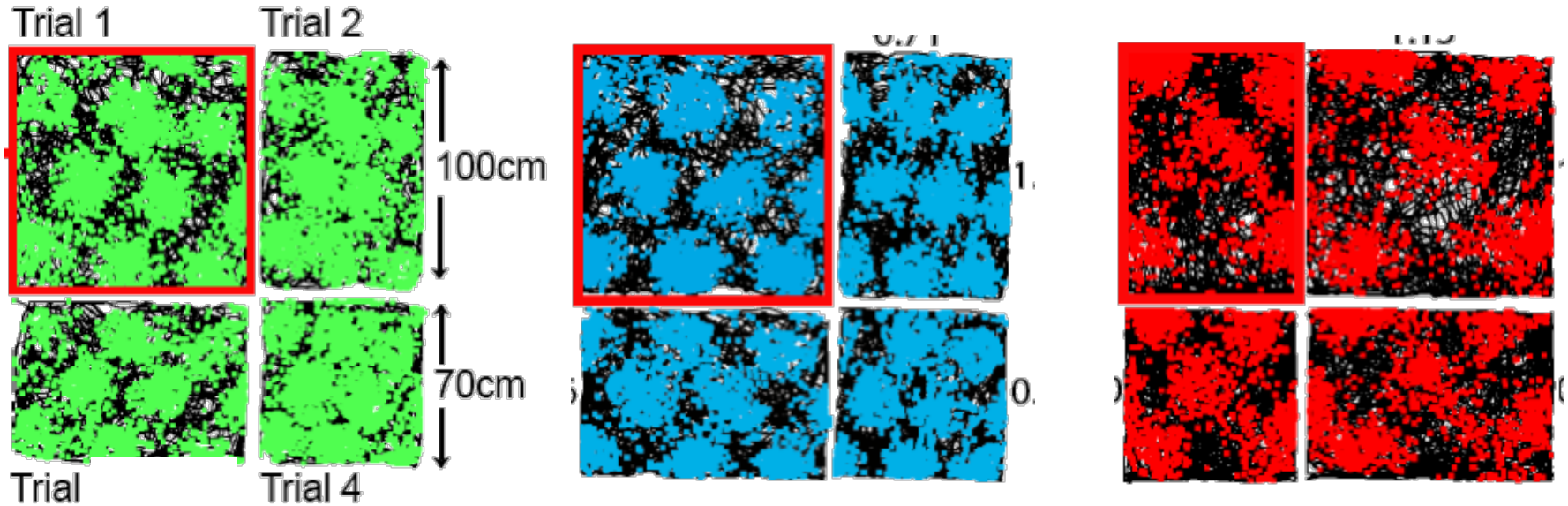
Peak place cell firing tends to maintain fixed distance to nearest boundary, but stretching / disappearance demonstrates some influence of more distant boundaries

So grid cells should also be reshaped by deformations of the environment?



O'Keefe and Burgess (1996) Nature

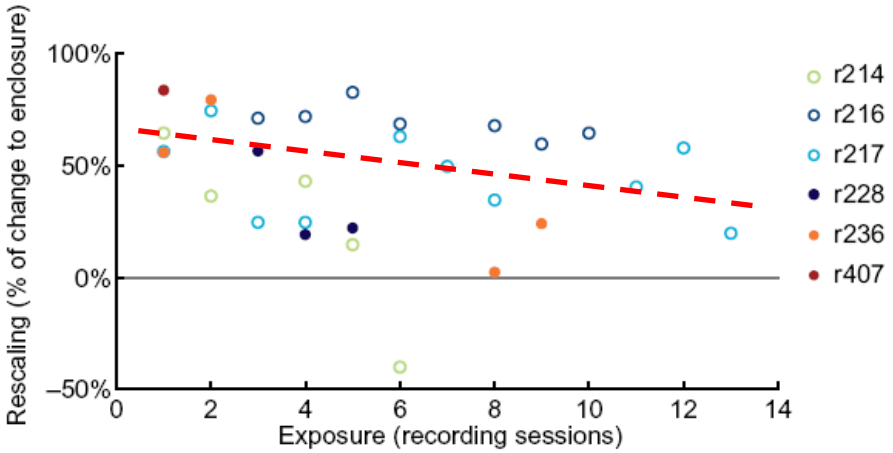
Grid cell / place cell interactions



Deformation of the environment causes a complementary change in grid scale

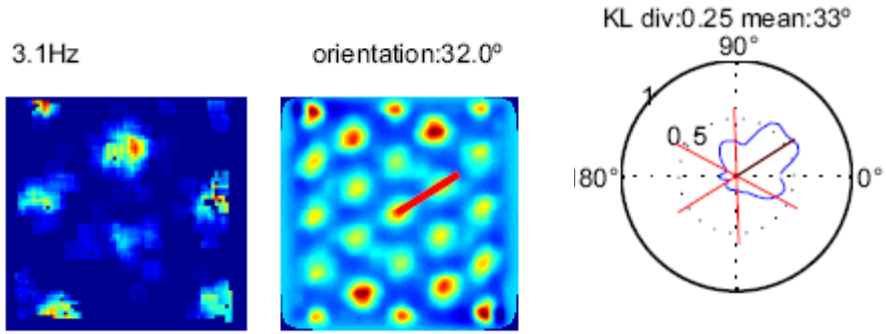
Similar effect to that seen in place cells

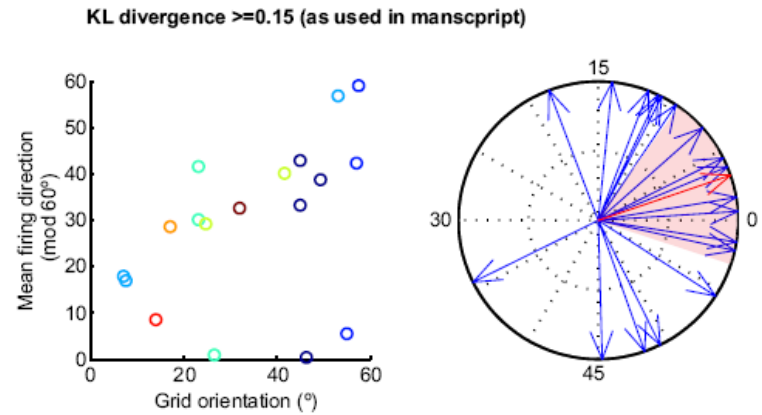
This supports the idea that place cells 'attach' grid cells to the sensory environment (or vice versa)

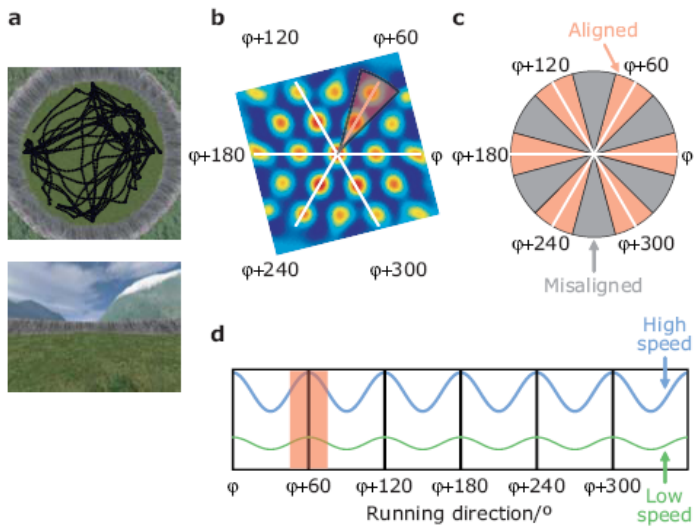


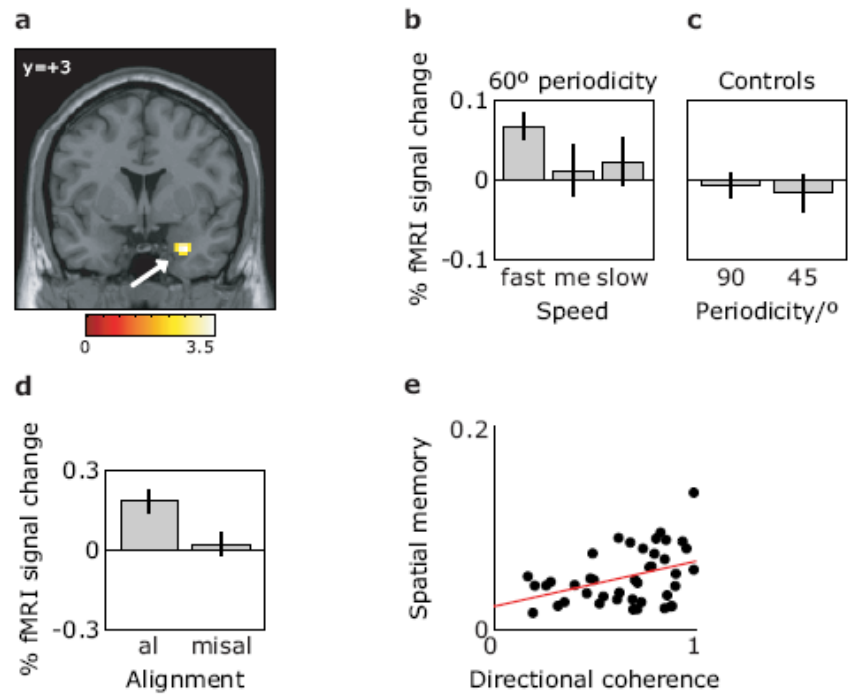
Barry et al. (2007) Nature Neuroscience

Grid cells in Humans?









Doeller et al. (2010) Nature; Jacobs et al. (2013) Nature Neuroscience

Grid cell summary

- Grid cells fire in multiple locations arranged on a hexagonal grid across the environment
- Nearby grid cells have a similar scale and orientation but tile the environment – the sub-peaks maintain a fixed spatial relationship to each other
- A small set of grid cells could perform path integration - updating their relative firing rates to track movement of the animal
- The requisite connections between grid cells could be learned at the multiple locations within an environment at which they fire
- The grid cells could thus provide the path integration input to place cells: place cells firing where all of the grid cell inputs overlap
- Equally place cells, with sensory input via lateral EC, could tie the grids to the environment