Representing complex spaces

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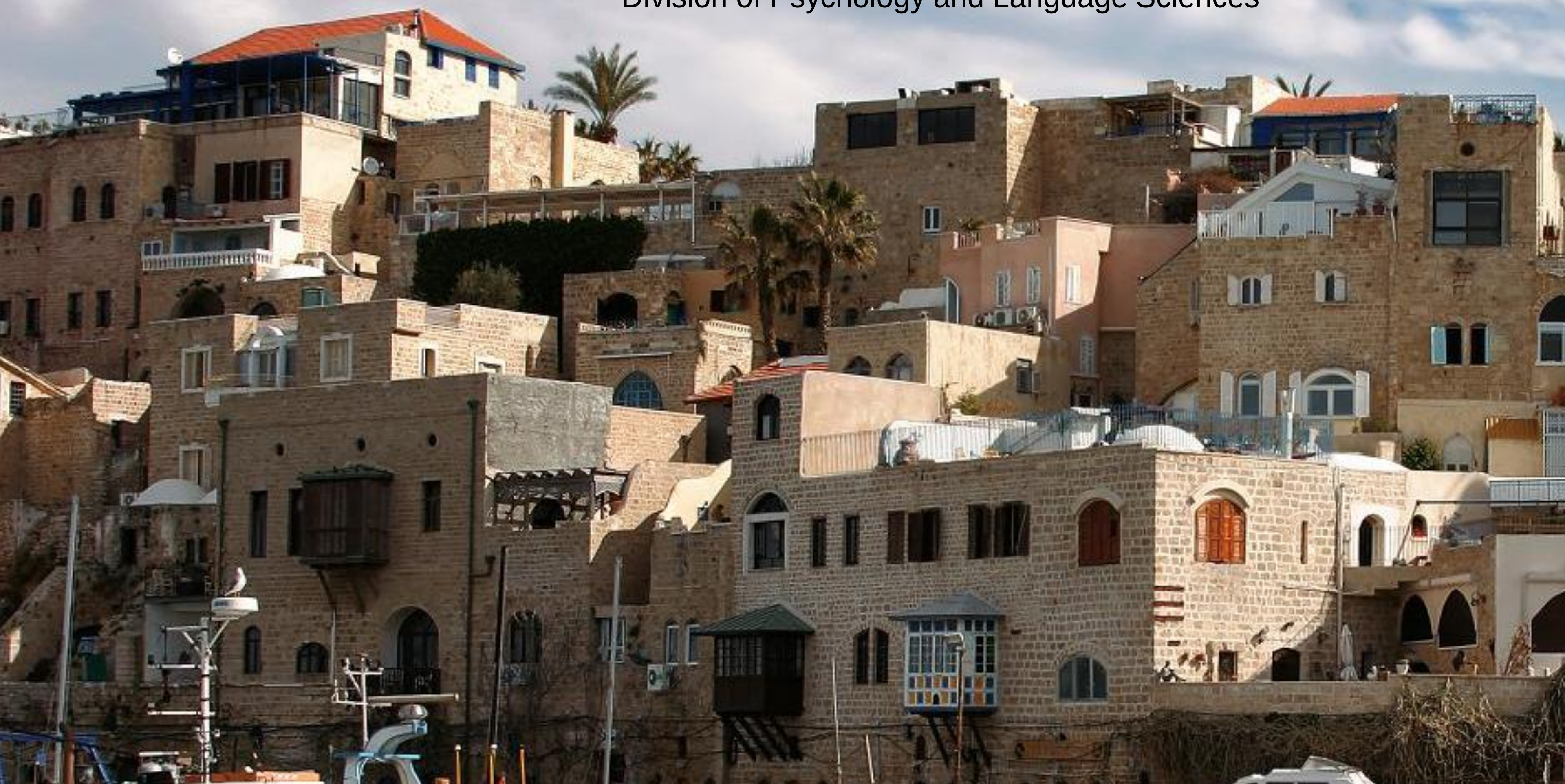
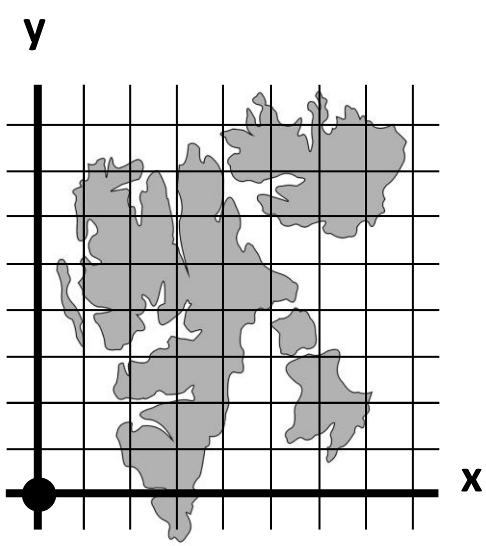


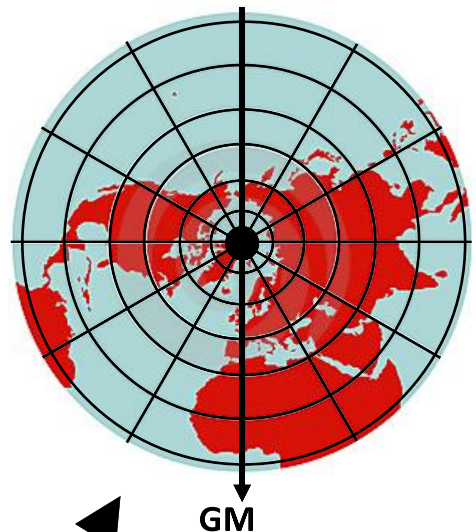
To represent space one needs a map

Types of maps that humans use:

Cartesian



Polar

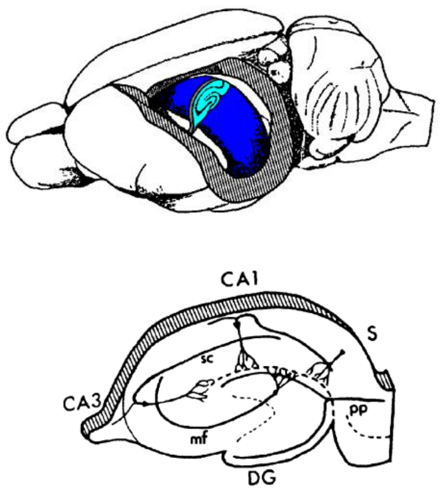


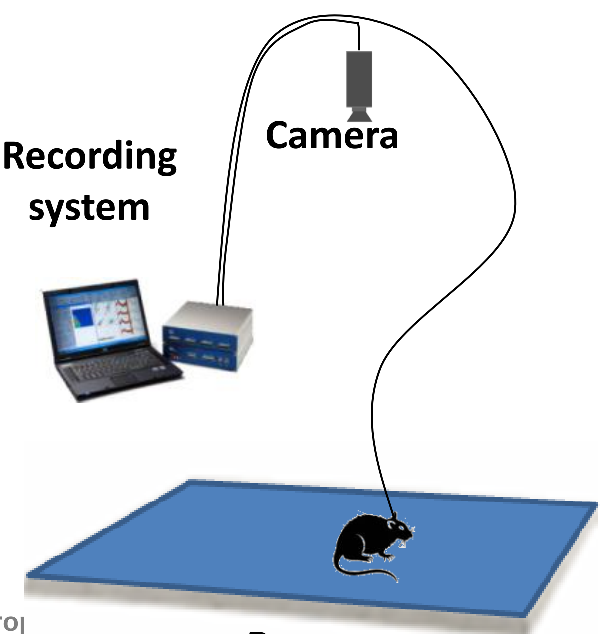
Topological

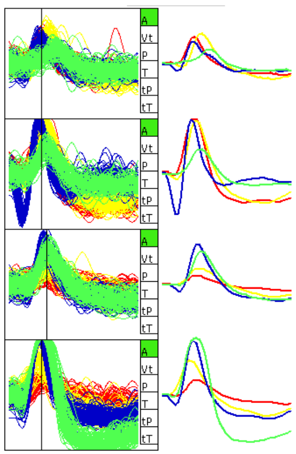
These ones are metric

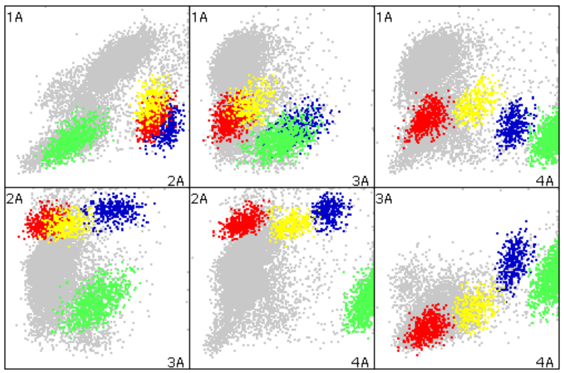
This one is non-metric

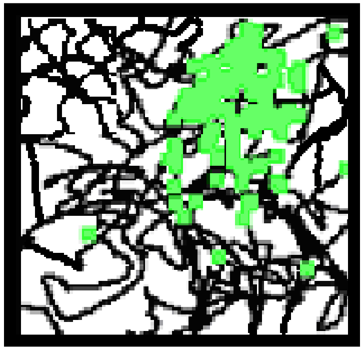
Methods for studying spatial encoding by neurons

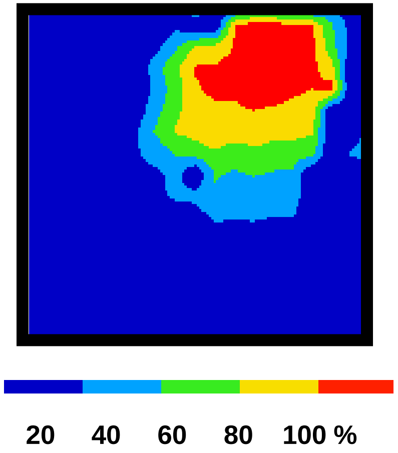






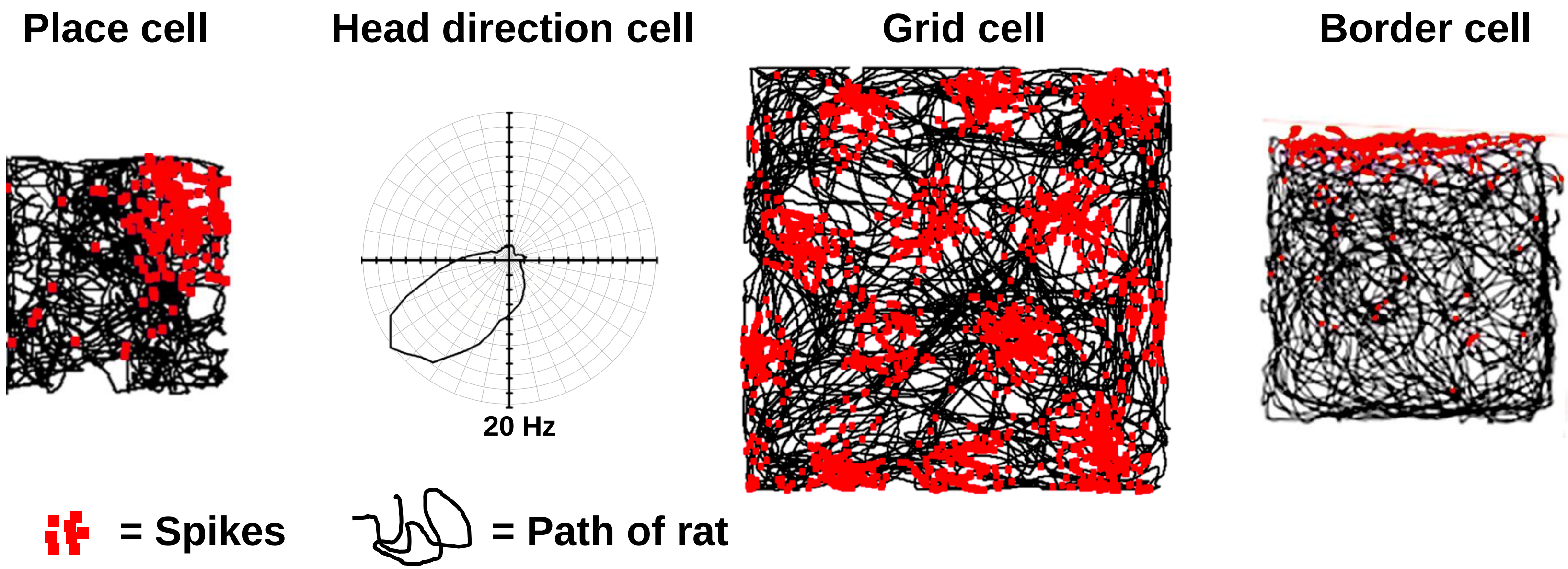






O'Keefe and Dostrovsky, *Brain Res* 1971

Spatial representation has focused on place cells, head direction cells, grid cells, border cells



How do these neurons encode complex spaces?

Spatial complexity includes:

- other compartments

- connected spaces that are not on the same plane

Three broad questions:

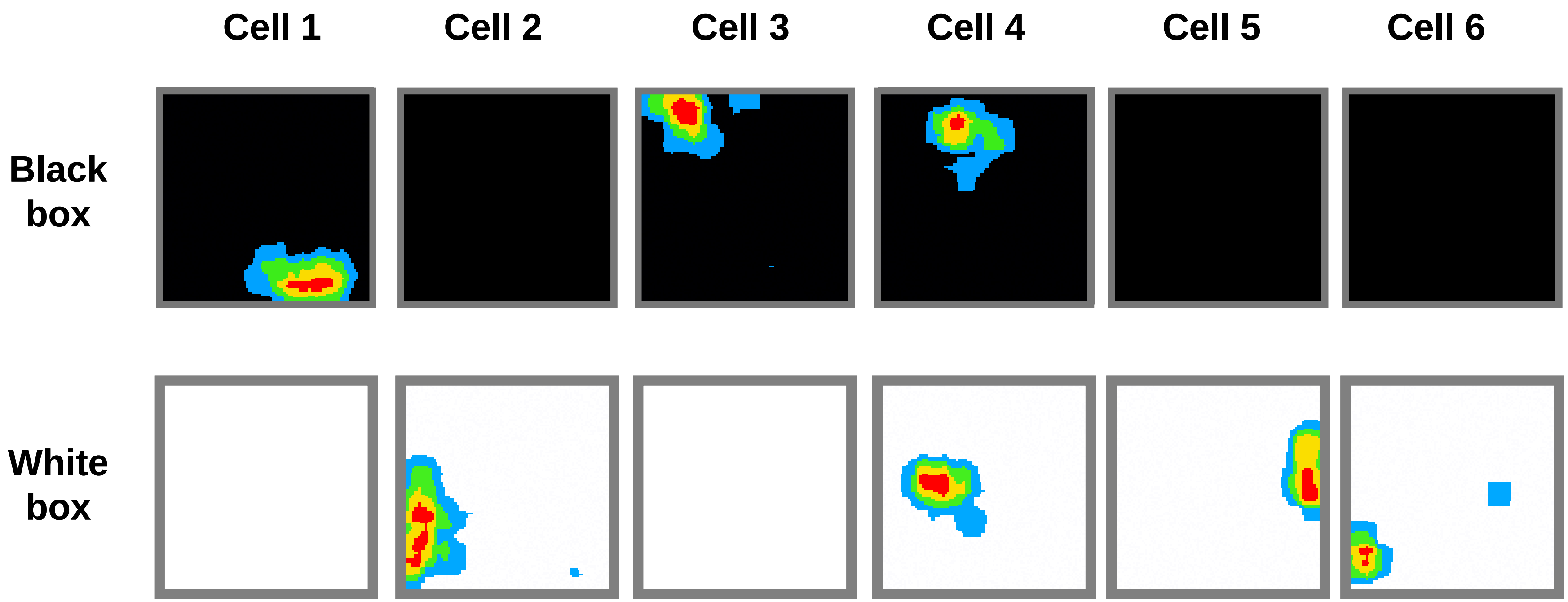
1. How to distinguish compartments from each other?

2. How to encode spaces that are three-dimensional?

3. How to relate compartments to each other in 3D space?

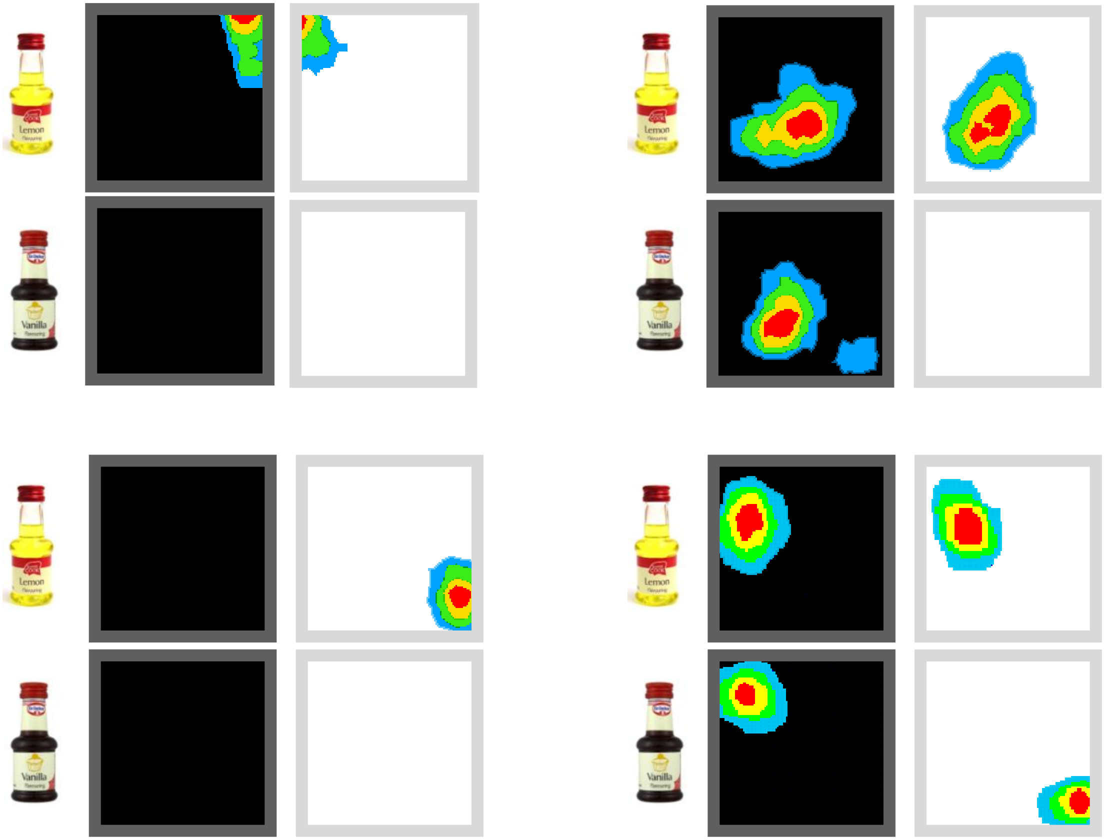
How to distinguish compartments from each other?

One possibility is associated non-metric context cues



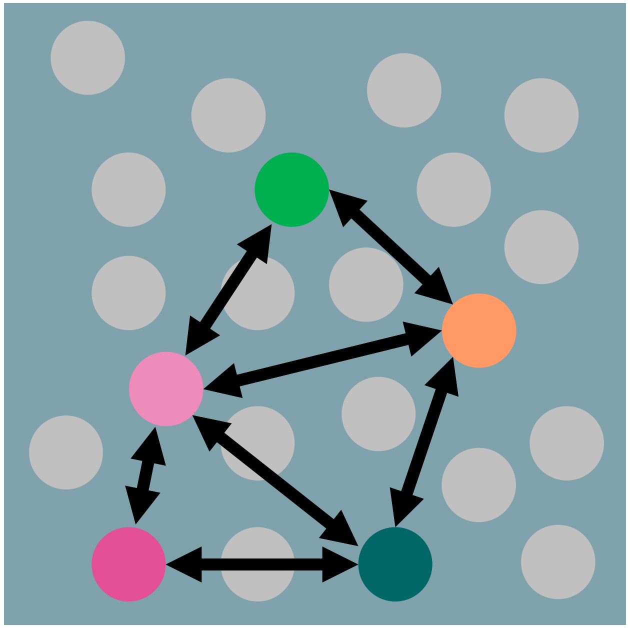
Muller and Kubie, *J Neurosci* 1987
Anderson and Jeffery, *J Neurosci* 2003

Place cells responding to context can be dissociated

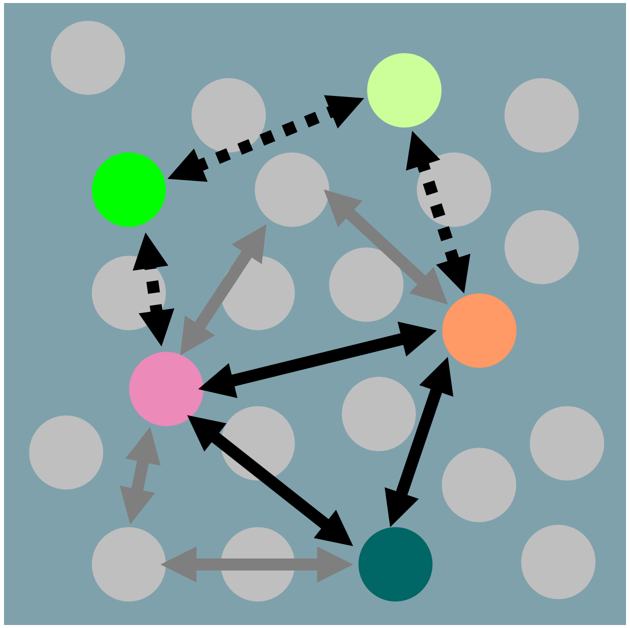


Anderson and Jeffery *J Neurosci* 2003

This partial remapping poses problems for local attractor-based accounts of remapping



Environment 1

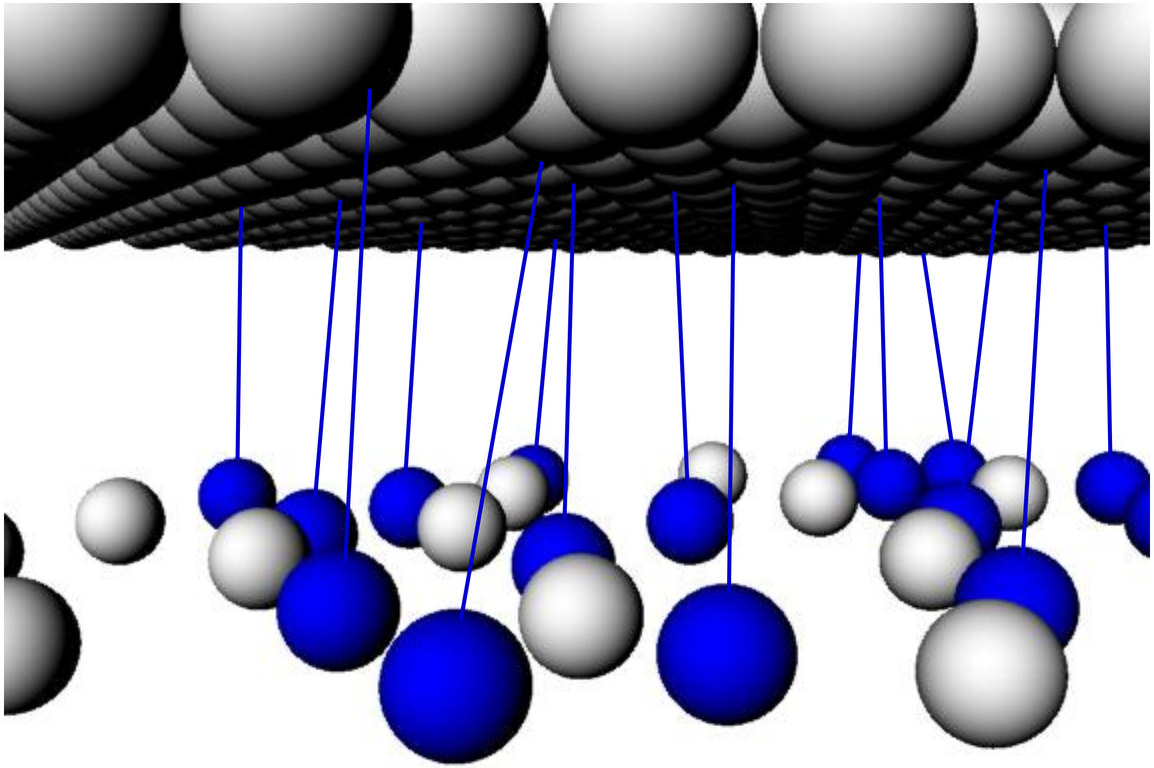


Environment 2

One solution is that maybe the continuous attractor dynamics reside in the grid cell sheet

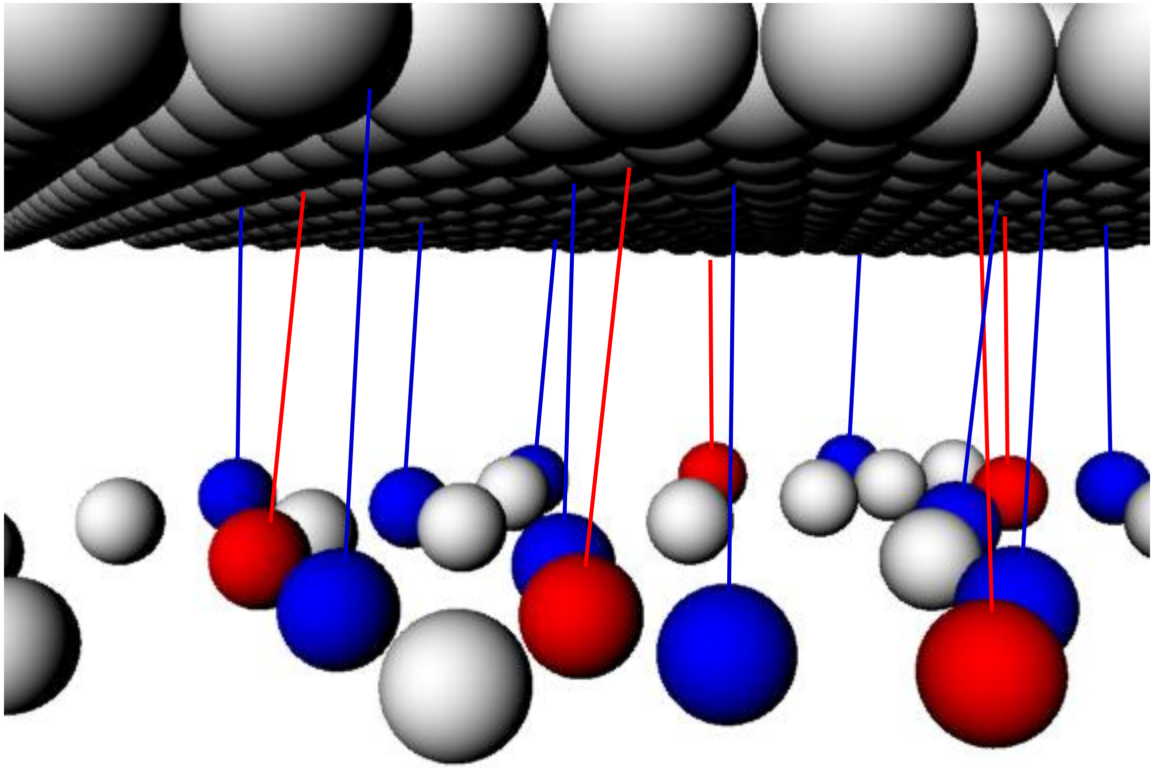
Grid cells

Place cells



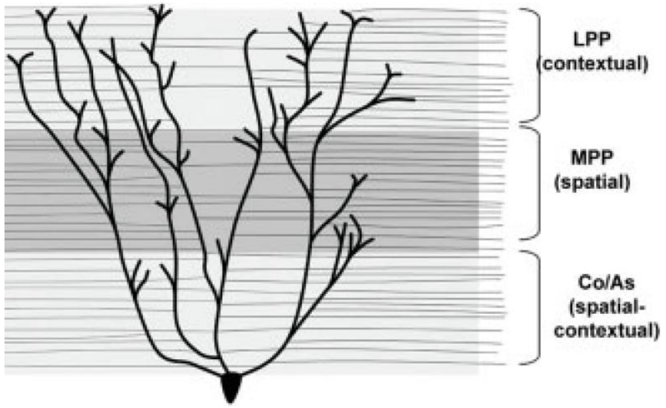
Partial remapping = mix of selected inputs

Grid cells



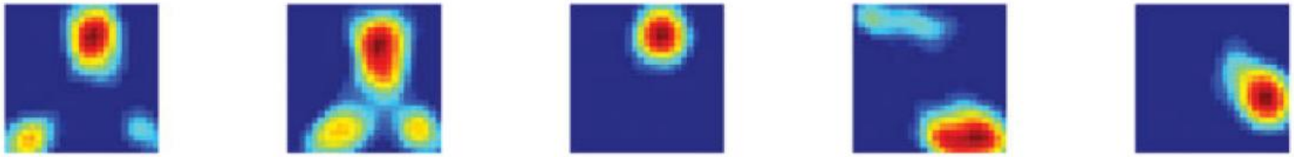
Place cells

Simulation of this context gating proposal produced graded remapping like that seen in DG



Hayman and Jeffery, *Hippocampus* 2008
Jeffery *Neural Plasticity* 2011

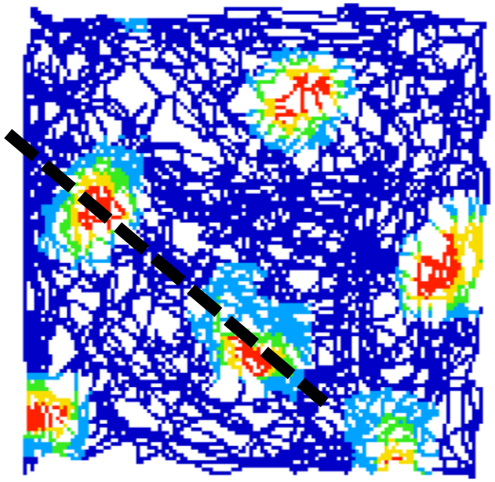
Simulation



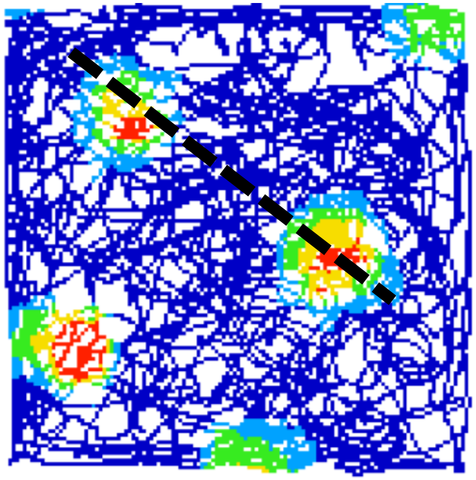
Leutgeb et al 2007

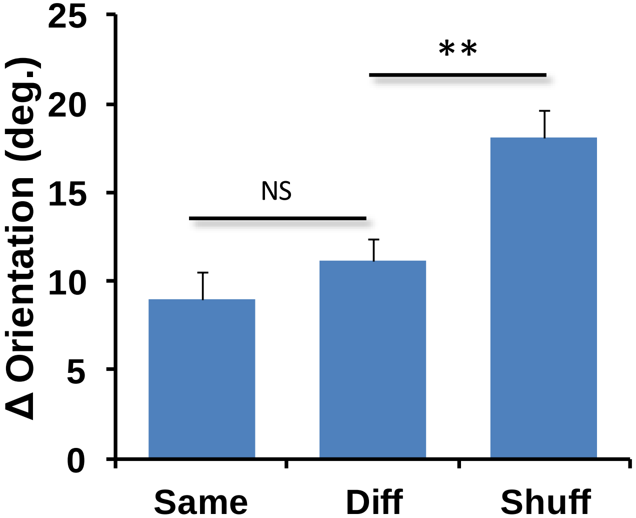
Grid cells are also responsive to context cues

Black-vanilla



White-vanilla





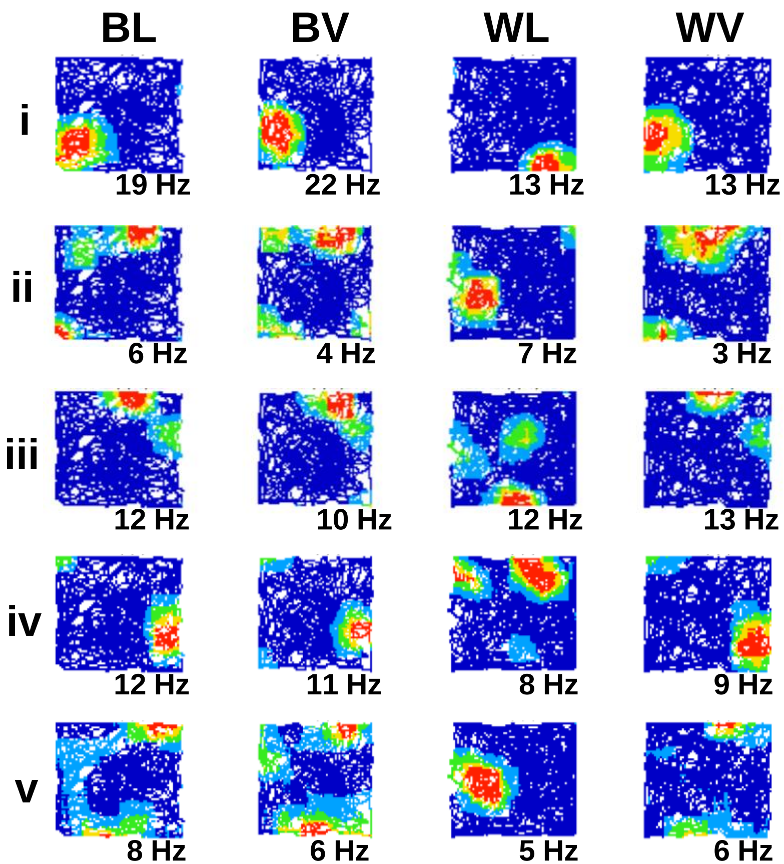
This affected position but not orientation of grid fields

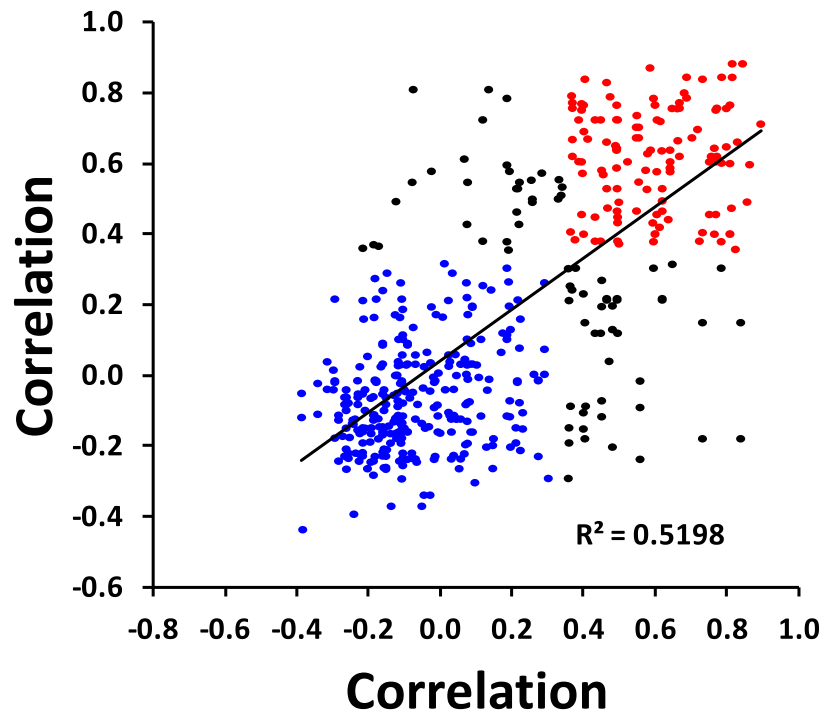
Liz Marozzi

Lin Lin Ginzberg

Andrea Alenda

Grid cells remapped homogeneously

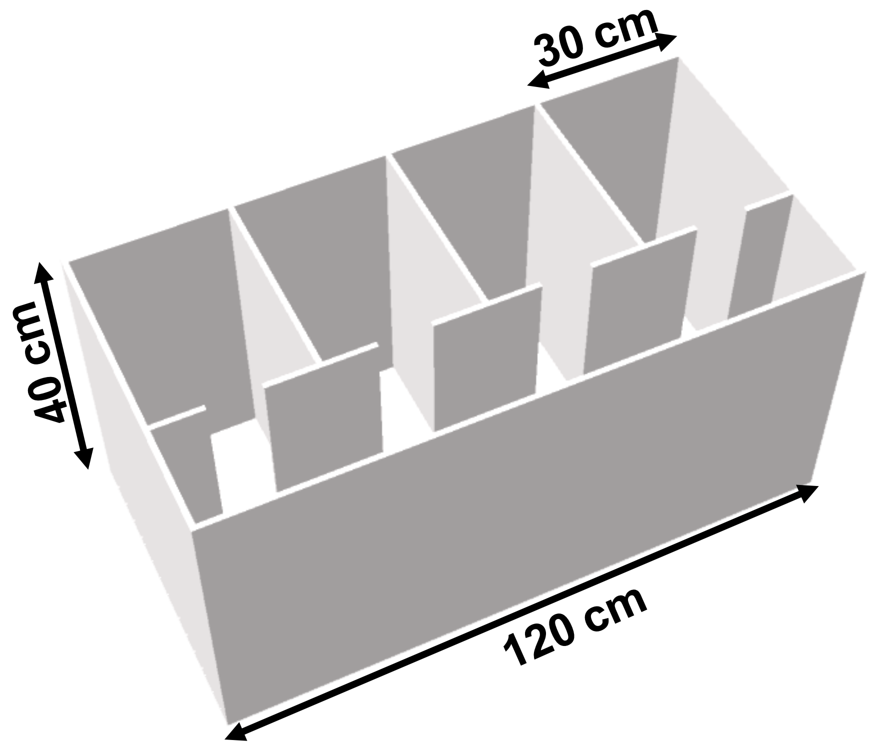




Ginzberg, Marozzi, Alenda and Jeffery in prep.

Thus, context cues position grid fields, and both select *and* position place fields

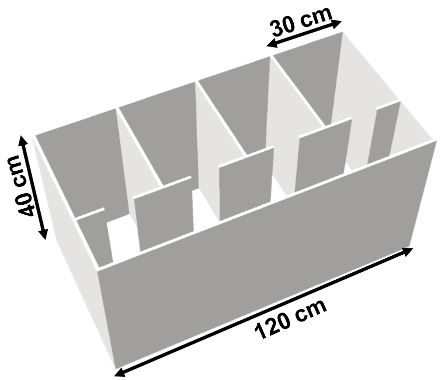
Can place and grid cells use path integration as a context cue to identify an environmental subcompartment?

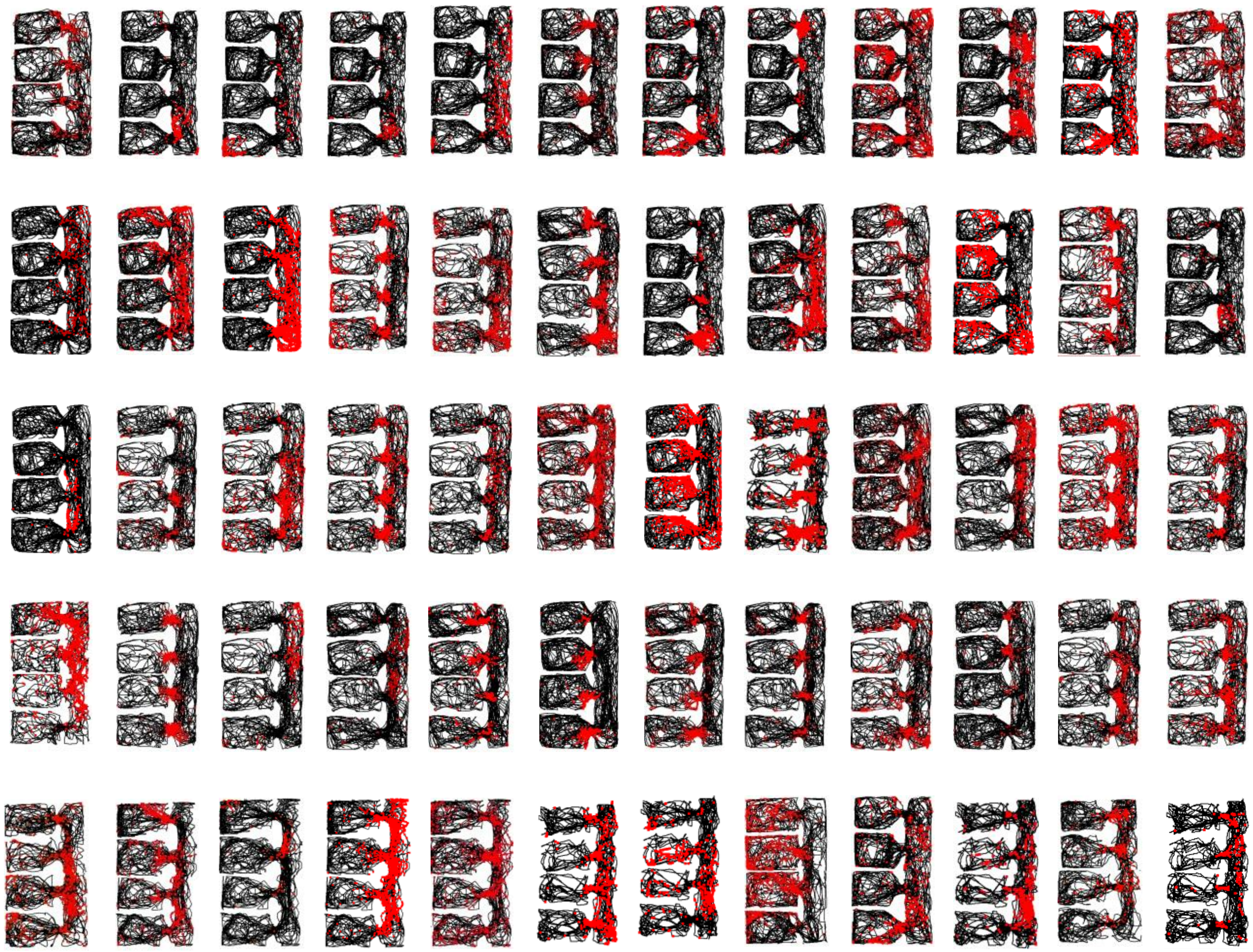


Hugo Spiers

Spiers, Hayman, Jovalekic, Marozzi, Jeffery *Cerebral Cortex* 2013

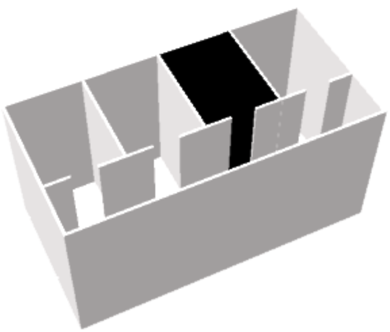
Path integration does not help identify compartments (much)

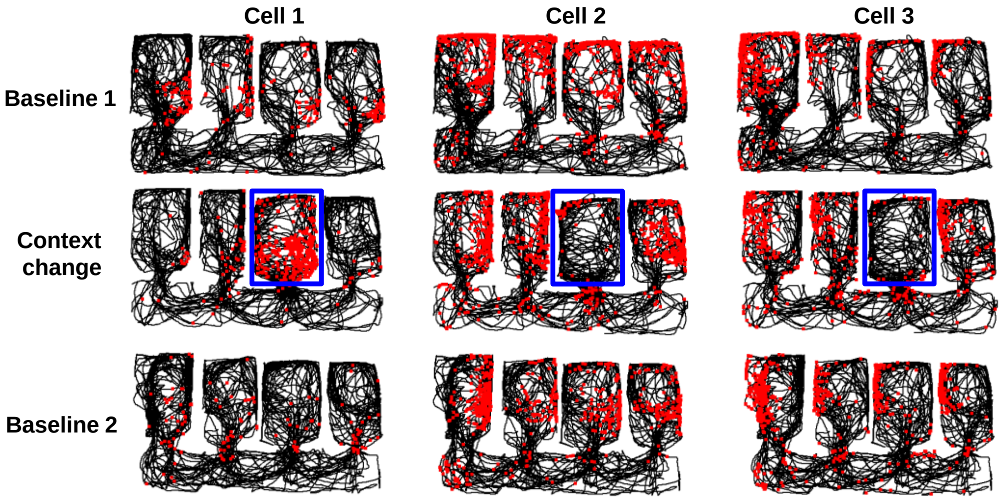


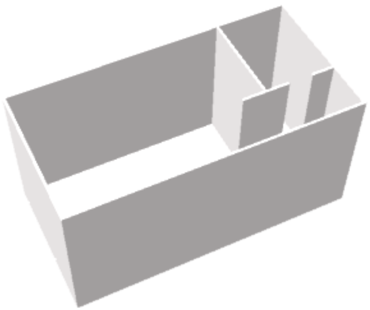


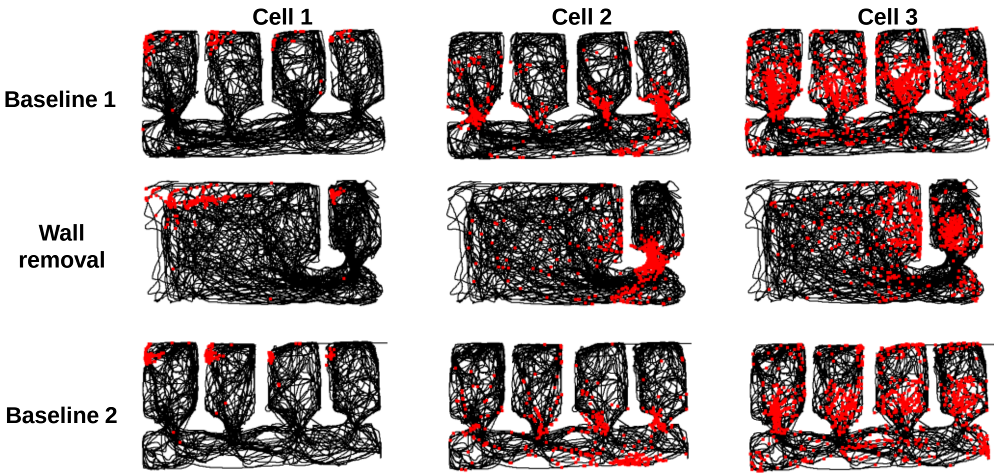
Spiers, Hayman, Jovalekic, Marozzi, Jeffery *Cerebral Cortex* 2013

The place cell representation seems to be local

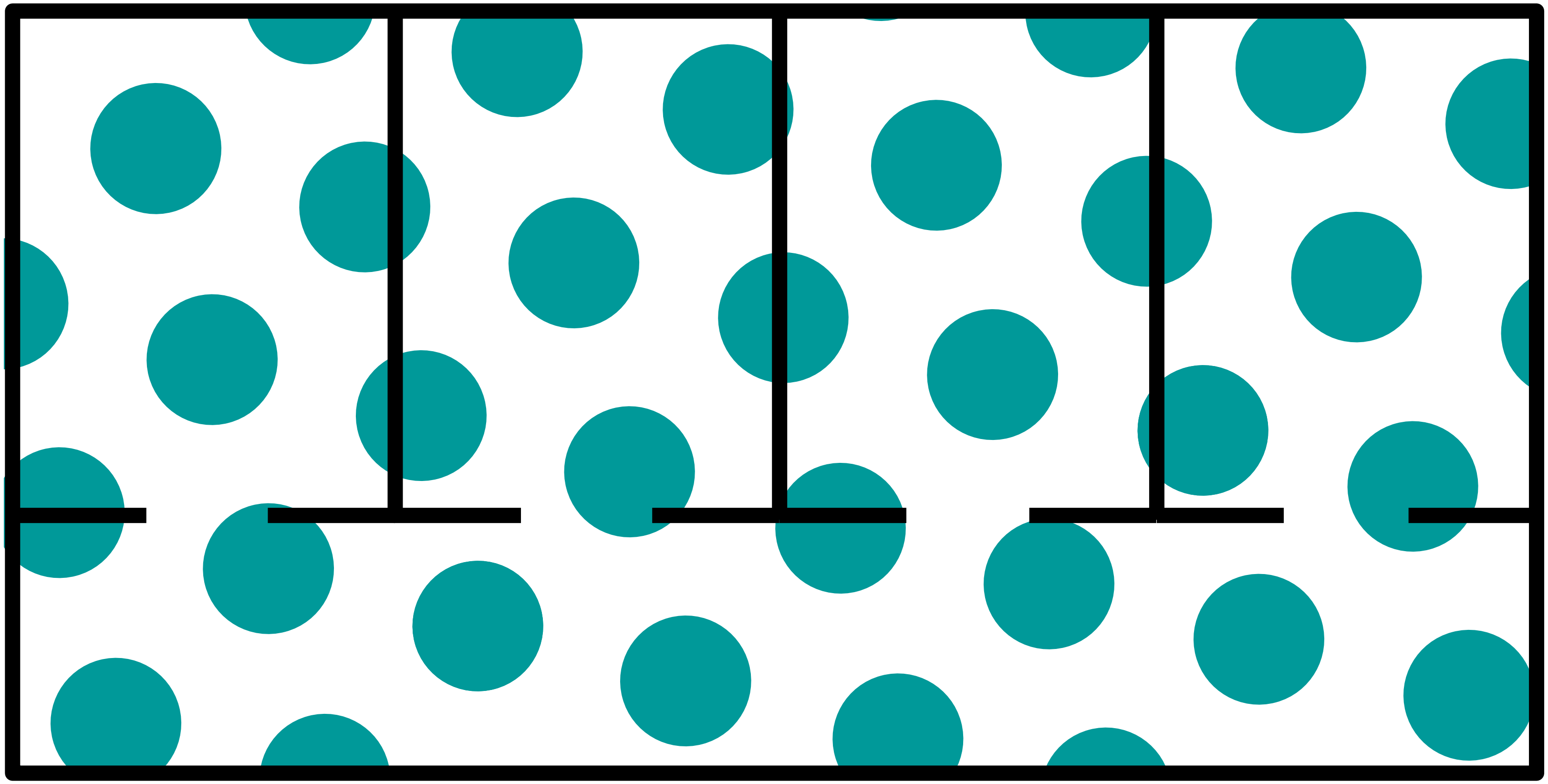








What would grid cells do? We don’t know yet

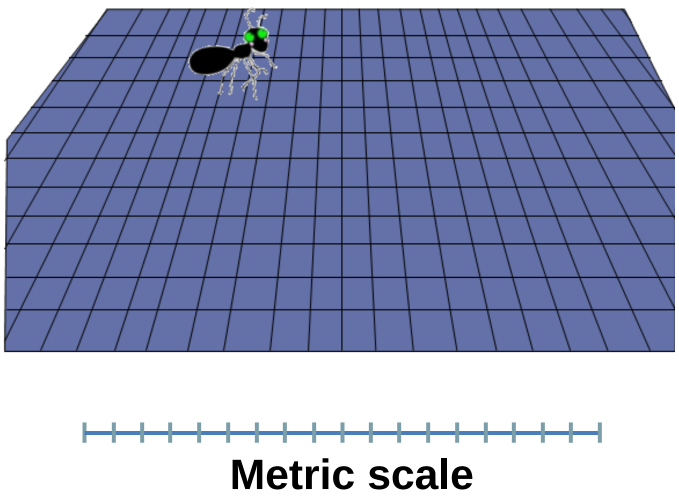


What is the dimensionality of the encoding in these environmental subspaces?

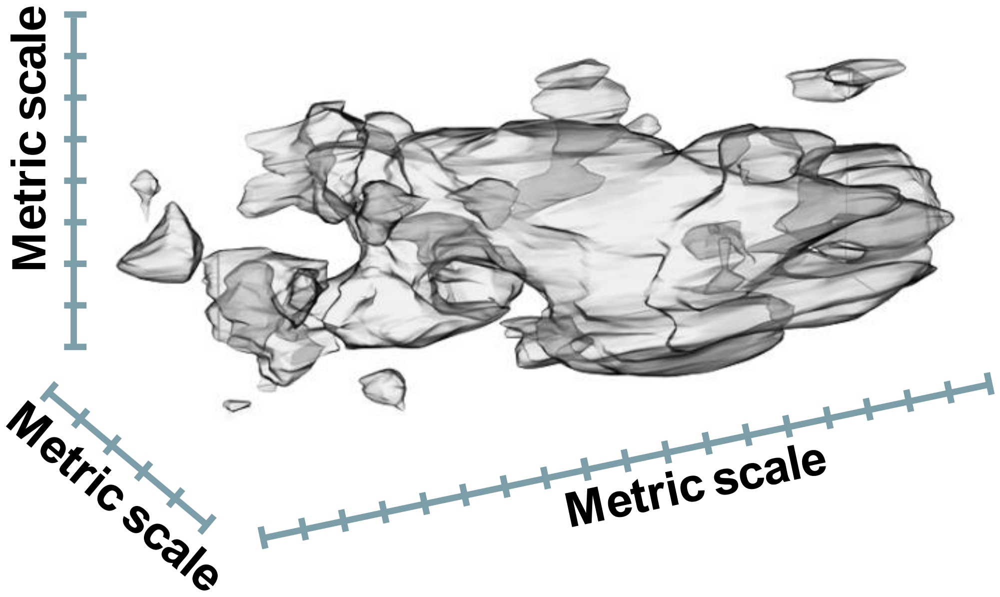
DIMENSIONALITY

Possible alternatives for dimensionality of the local spatial fragments:

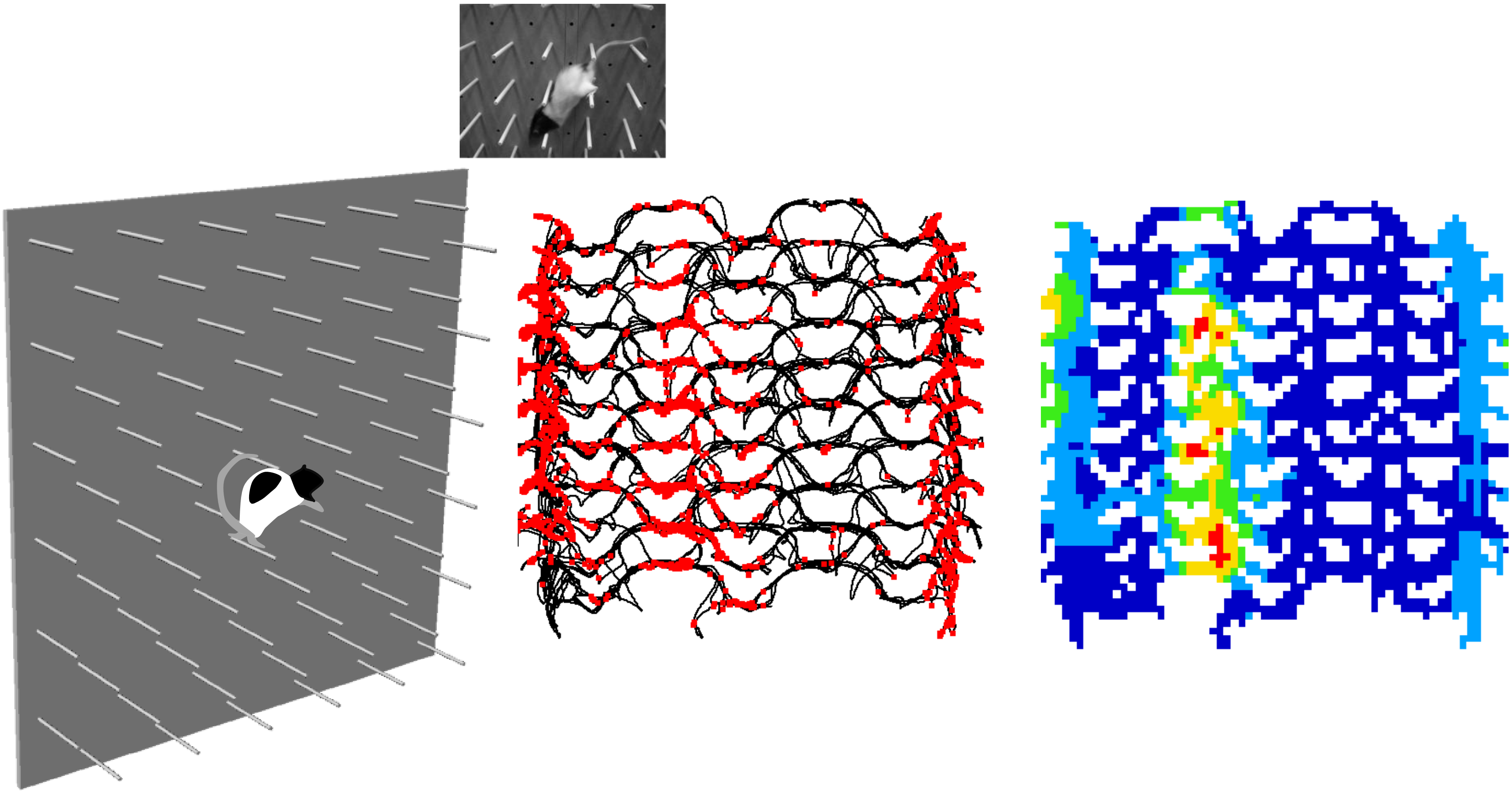
(i) Flat



(ii) Volumetric

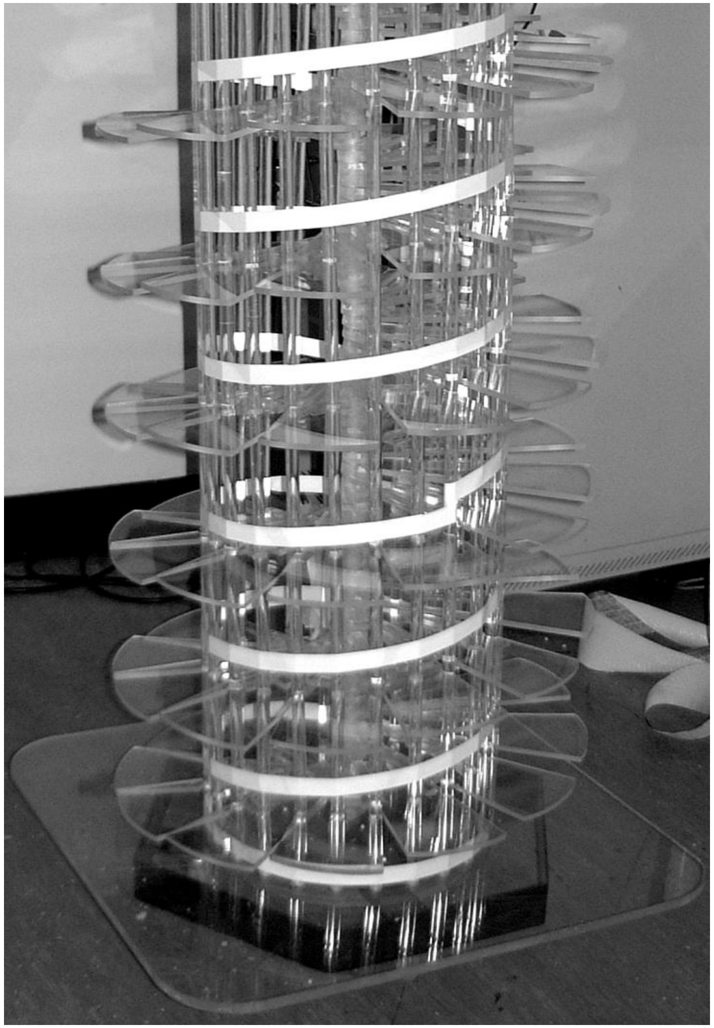


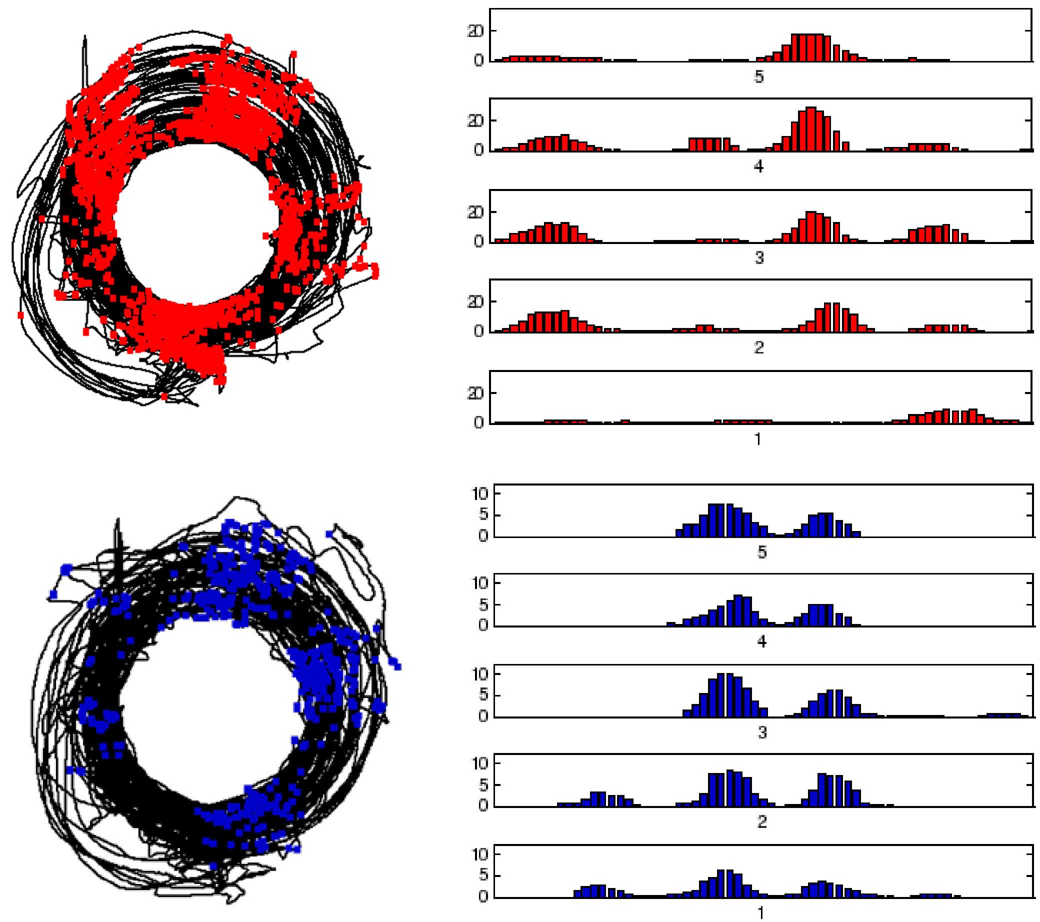
A suggestion that dimensionality is not volumetric...



Hayman, Verriotis, Jovalekic, Fenton, Jeffery, *Nat Neurosci* 2011

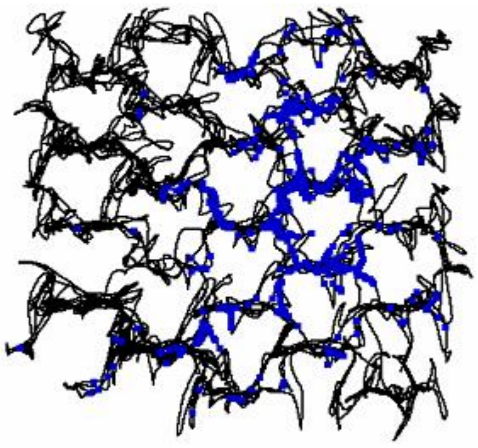
We saw a similar thing with a different apparatus

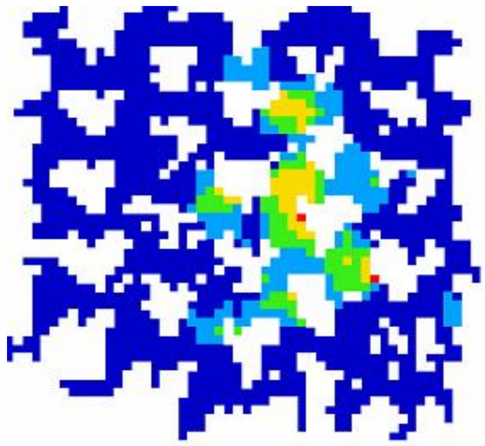


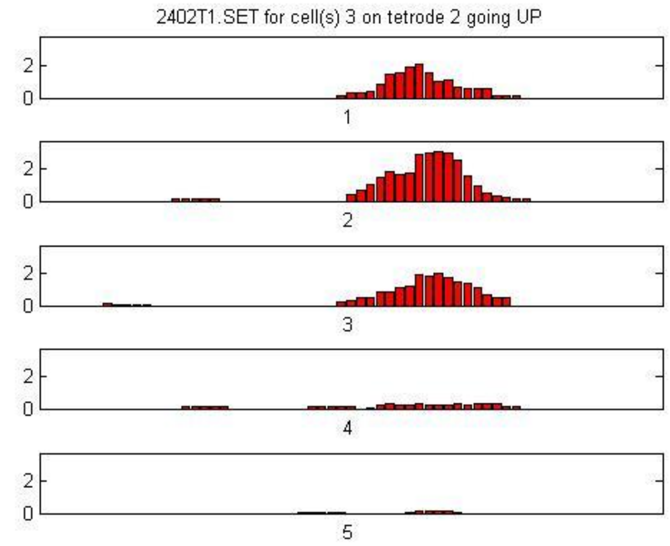


Hayman, Verriotis, Jovalekic, Fenton, Jeffery, *Nat Neurosci* 2011

However, place cells produced fields that were delimited in both vertical and horizontal dimensions – so *something* knows about height (map is not flat)

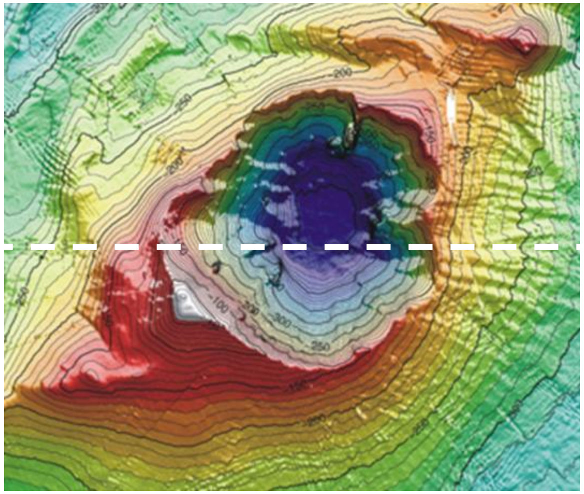


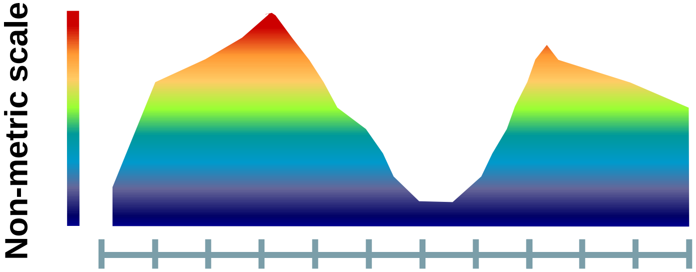




Hayman, Verriotis, Jovalekic, Fenton, Jeffery, *Nat Neurosci* 2011

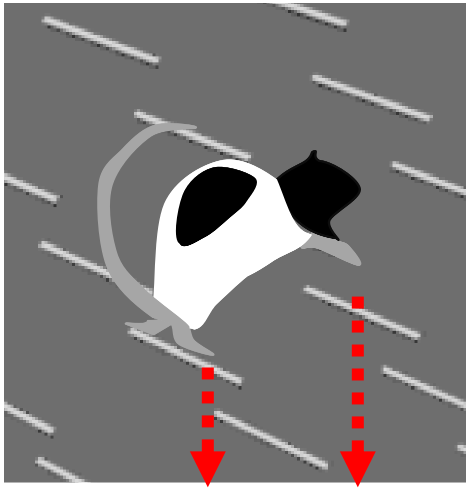
These findings led us to the *bicoded* hypothesis





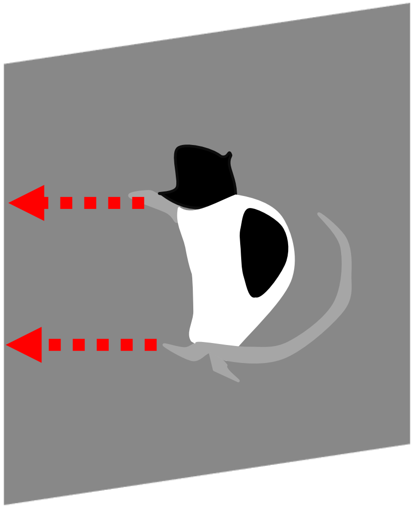
If spatial encoding only uses one metric plane, what defines that plane?

We suggested, following Taube, that the reference plane is defined by the *locomotor surface*



Reference plane = horizontal

Grid cells periodic in horiz. plane

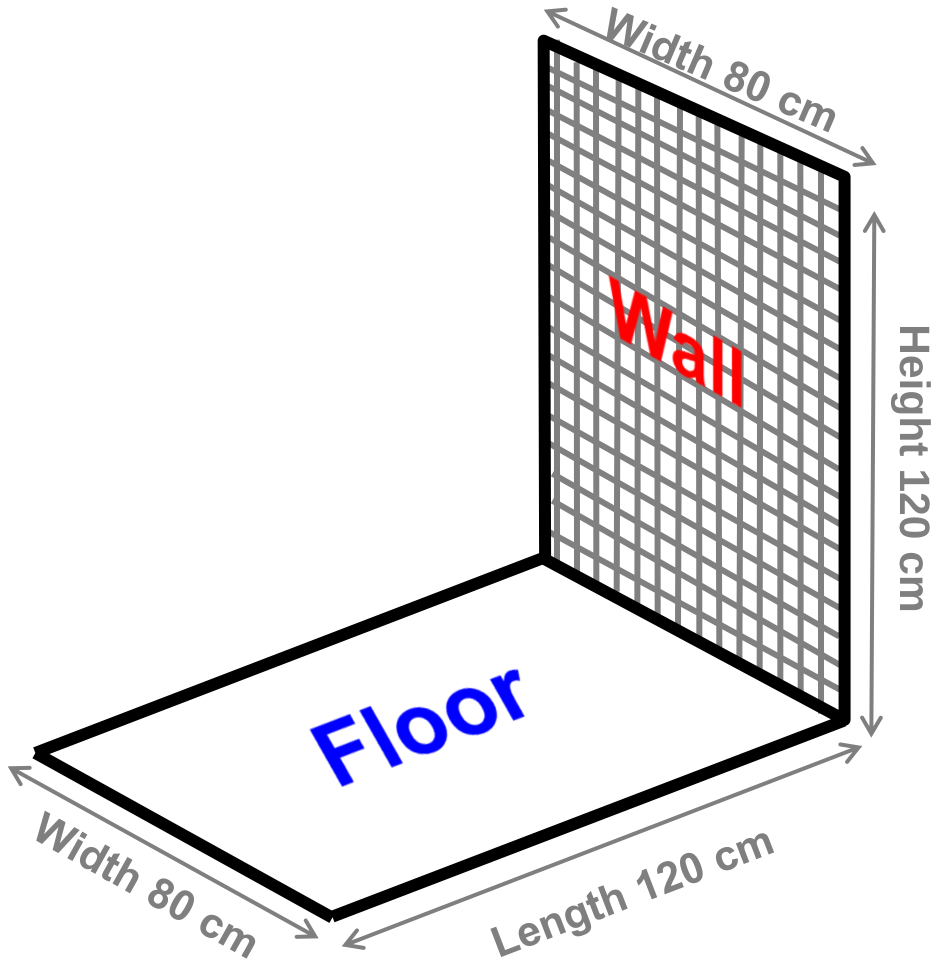


Reference plane = vertical

Grid cells periodic in vert. plane?

First, we needed 3D-spatially competent animals

Are grid cells periodic on a vertical locomotor plane?

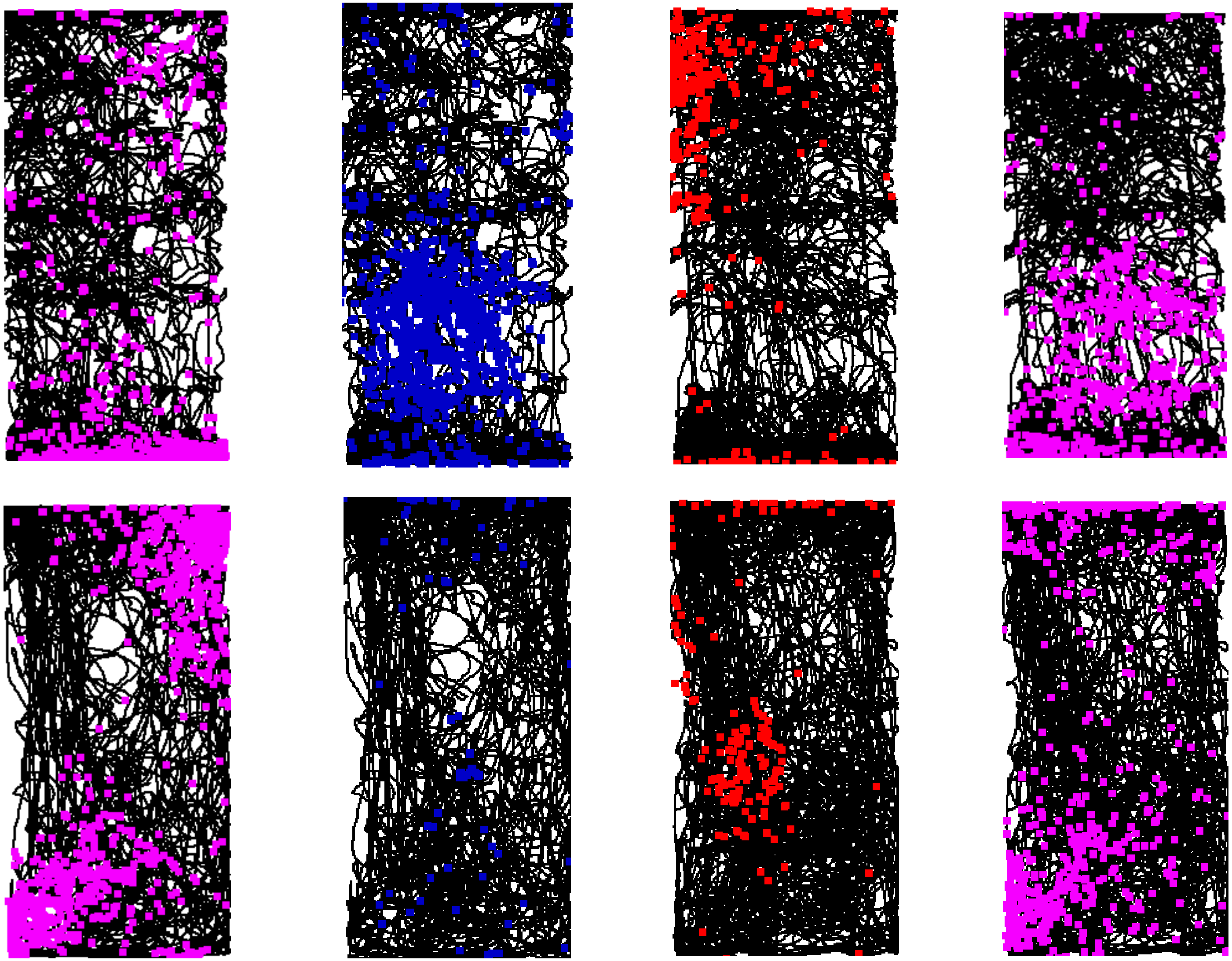


Giulio Casali

Place cells have fields on floor and wall

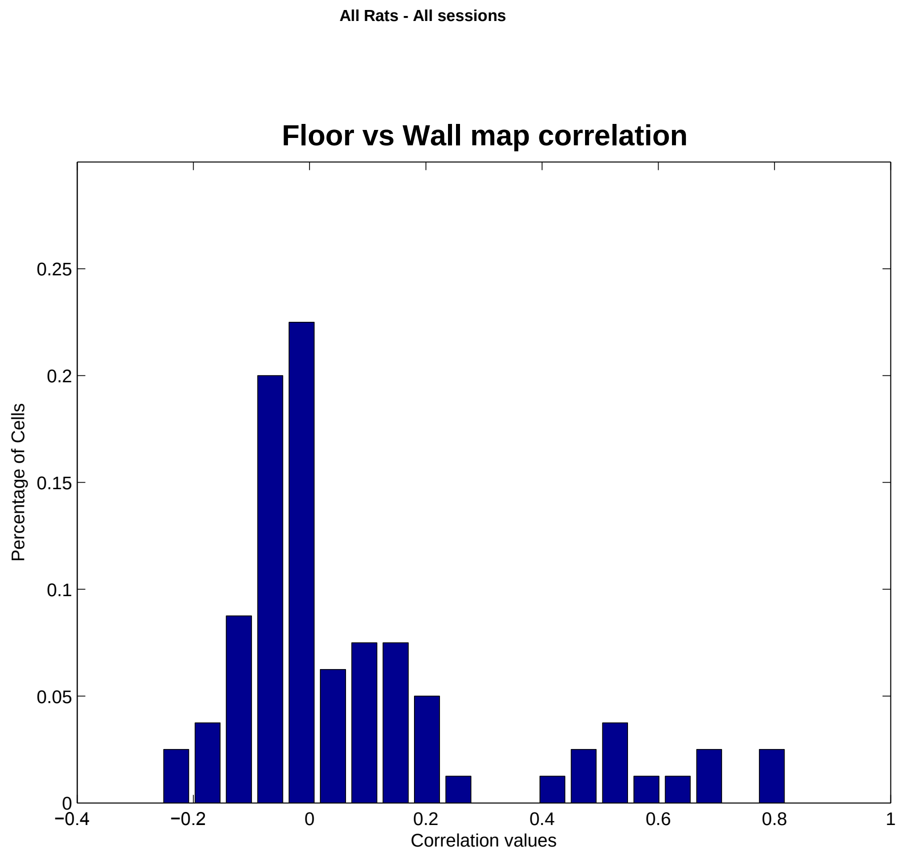
Wall

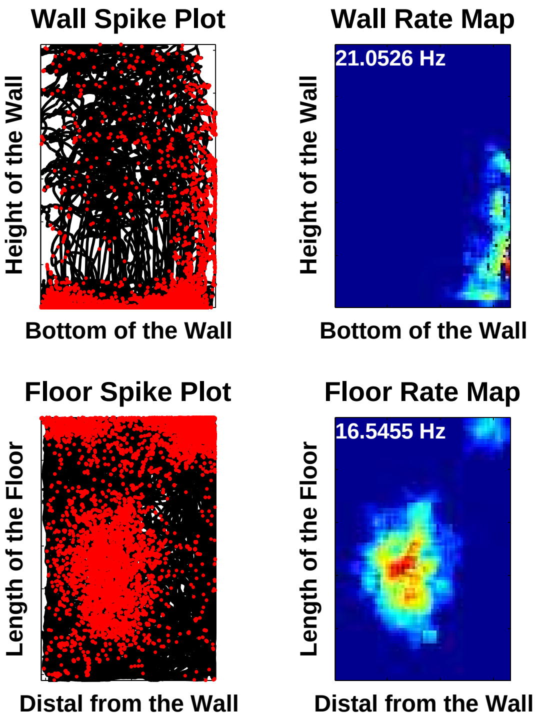
Floor



Giulio Casali

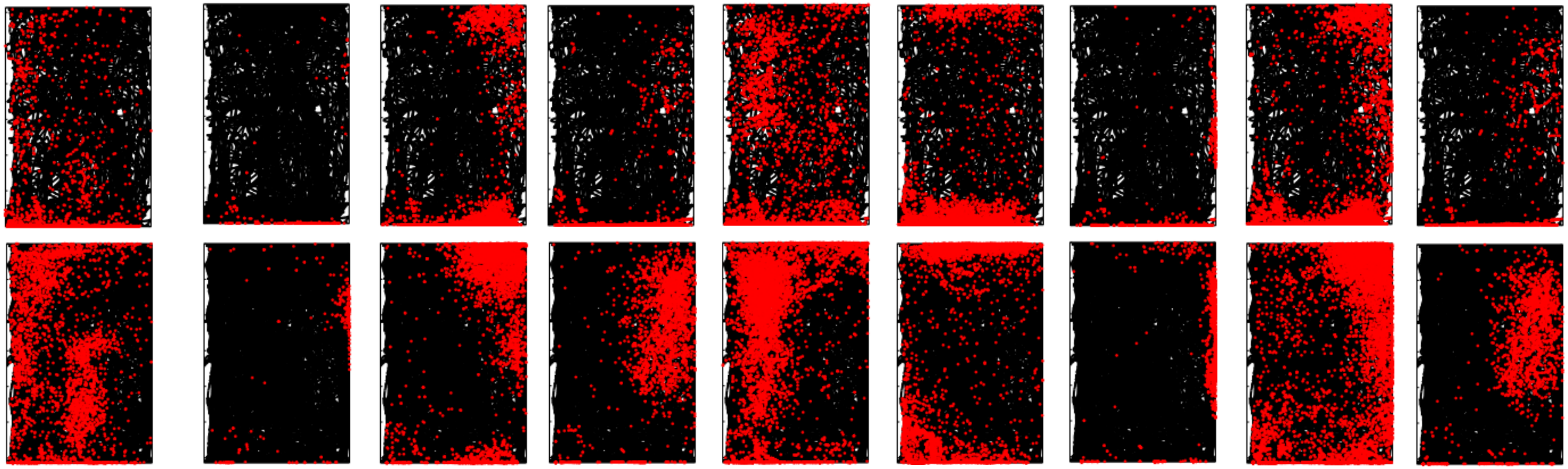
Generally there was no spatial correlation between floor and wall



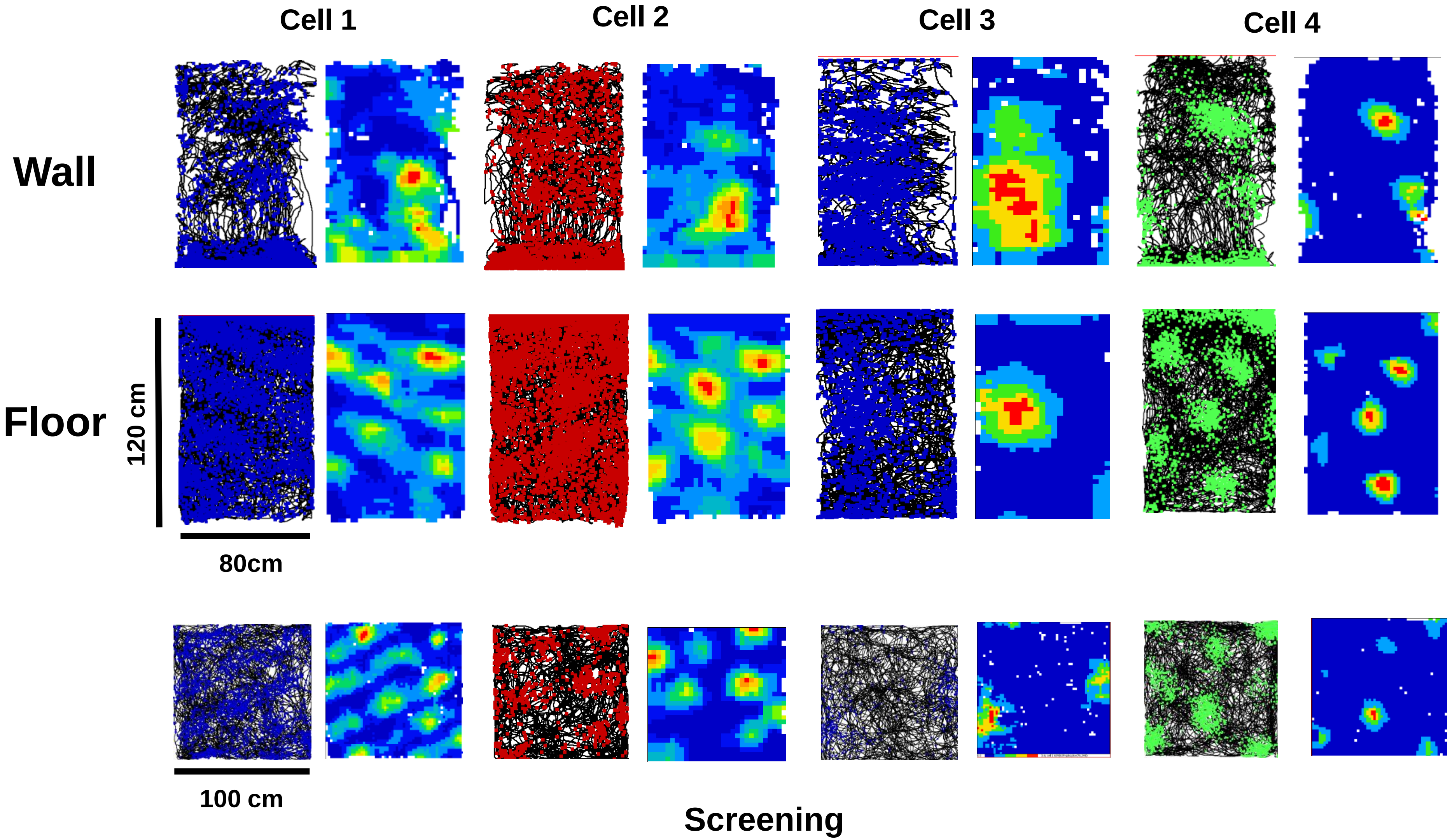


R = -0.03

However, one rat expressed same pattern on both surfaces, with decreased rate on the wall



Disrupted path integration on the wall?

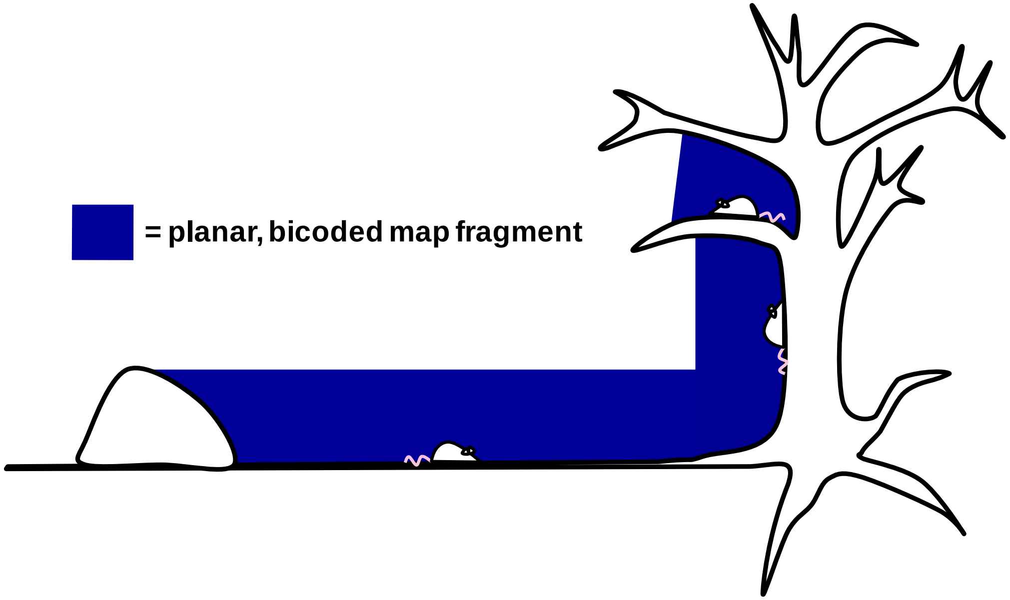


Does this mean the spatial frame of reference is the locomotor plane?

If this is true, then how could this be useful in practice?

If the map is mosaic, and the mosaic fragments can be oriented differently, how can the "master map" work properly?

It would need to know how these mosaic fragments are related to each other.

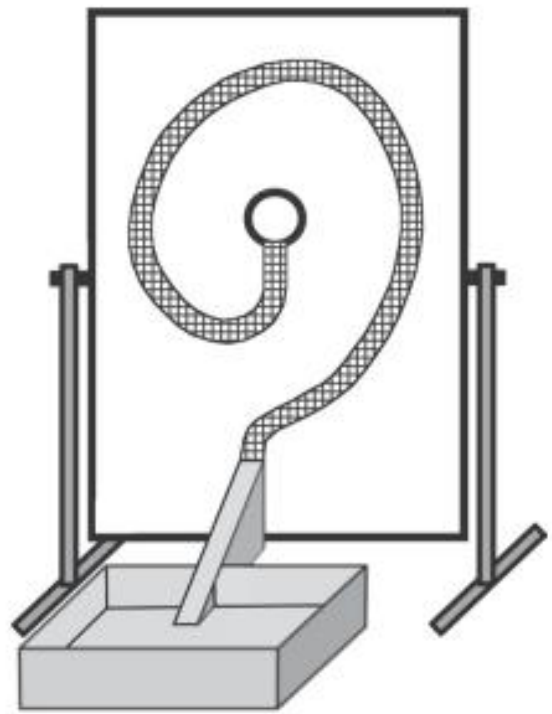


This means that some part of the brain would have to monitor movements through 3D space, to allow relating of the local fragments to each other.

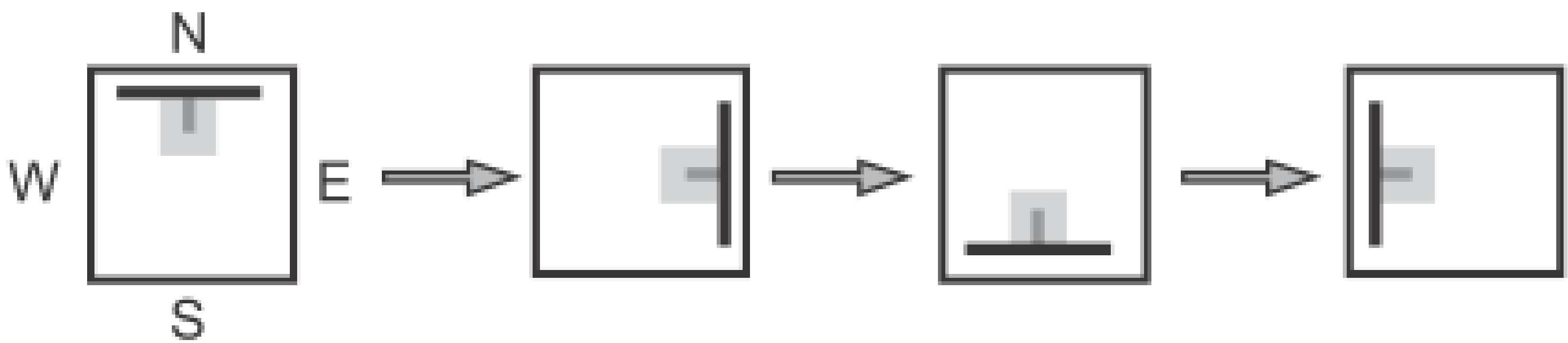
A possible linking substrate is the head direction cells, which monitor planar rotations in 2D space, and which serve to orient the fragments in the horizontal plane

So, do the reference frames of head direction cells in planes oriented differently in 3D space possess a "lawful“ relationship to each other?

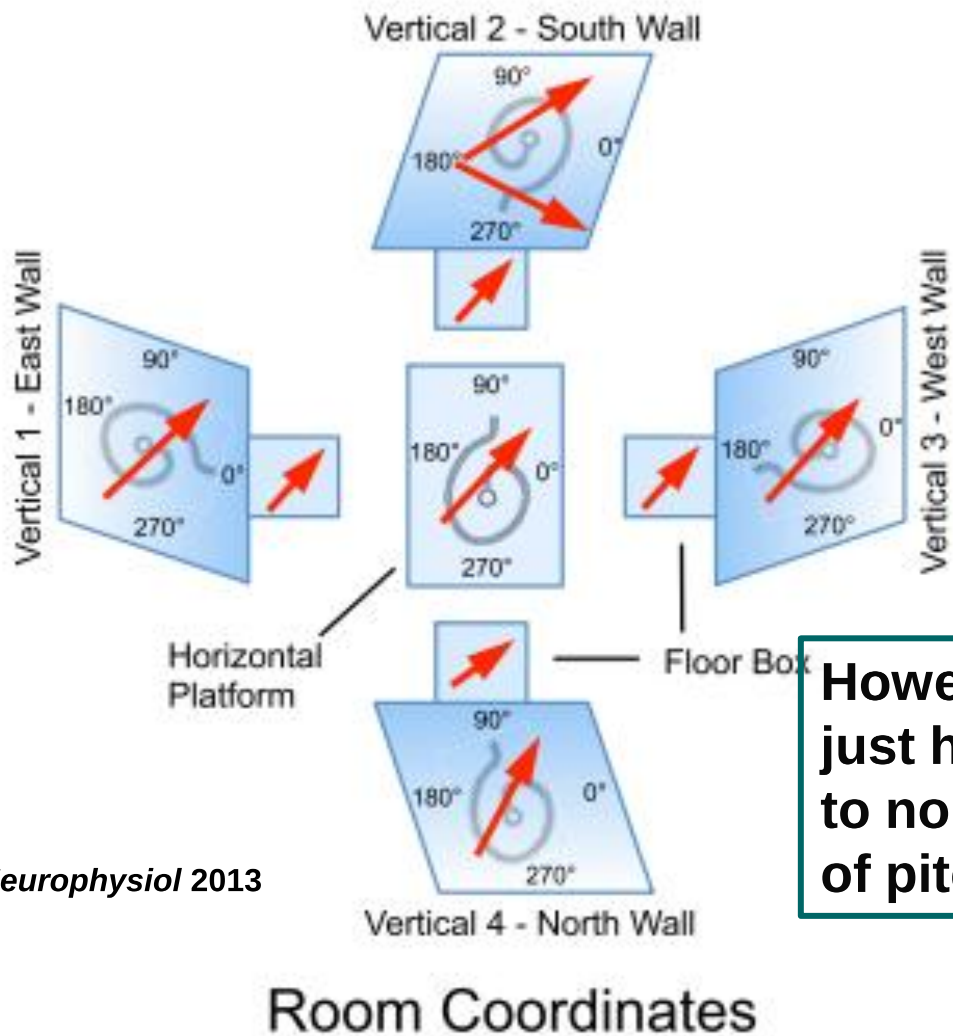
An experiment by Taube suggested maybe



Taube et al, *J Neurophysiol* 2013



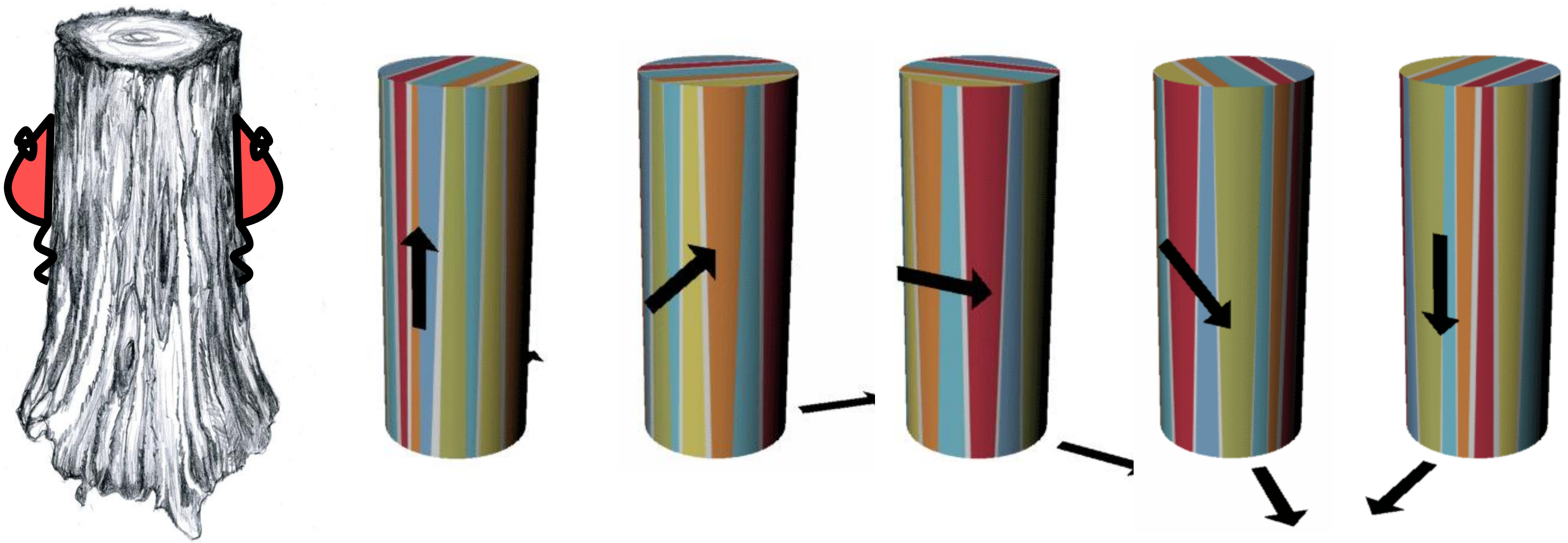
A study by Taube suggested a global reference frame for HD cells



Taube et al, *J Neurophysiol* 2013

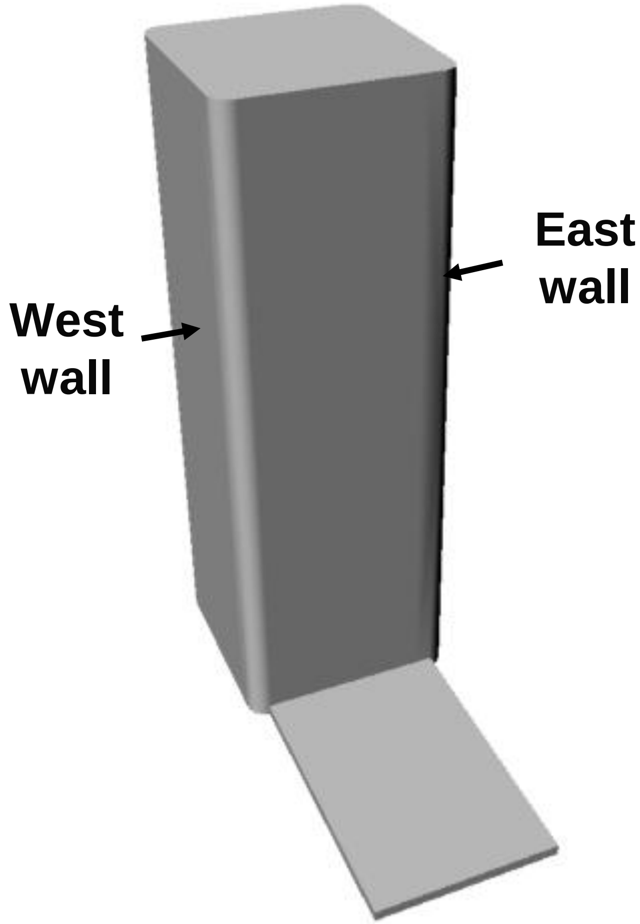
However, might this just have been due to non-processing of pitch?

However, this could just reflect failure to process the pitch rotation from floor to wall. True updating should involve a *change* in orientation

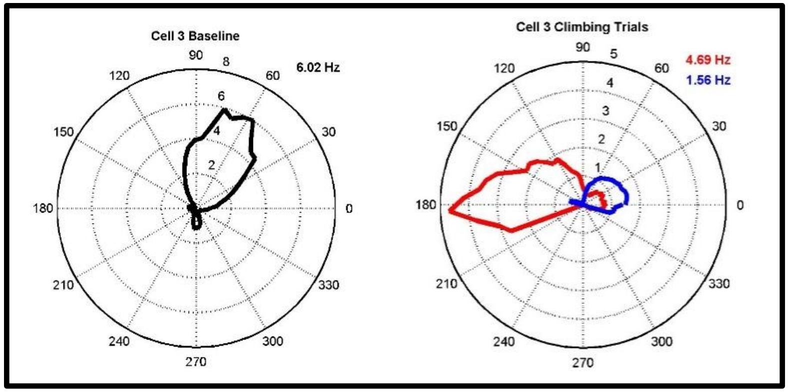


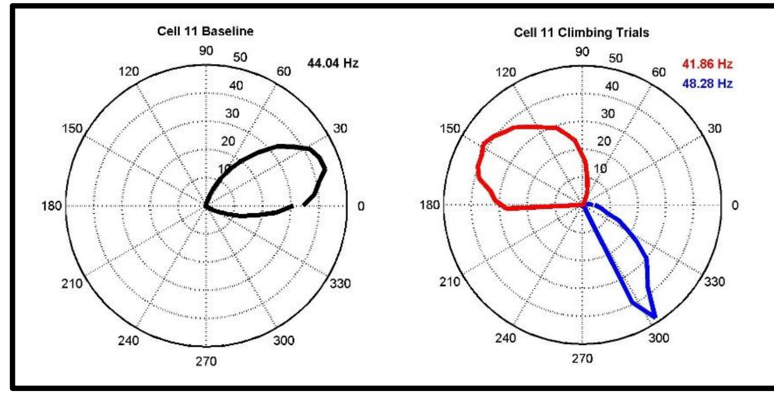
To rule this out we need to show active reference-frame updating by HD cells

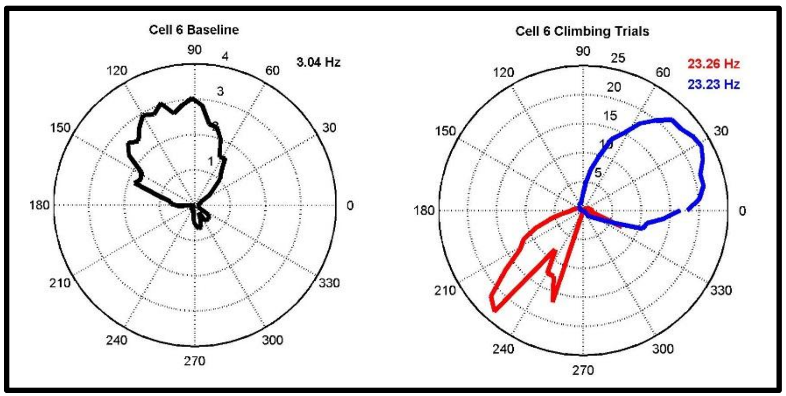
The tree-trunk maze

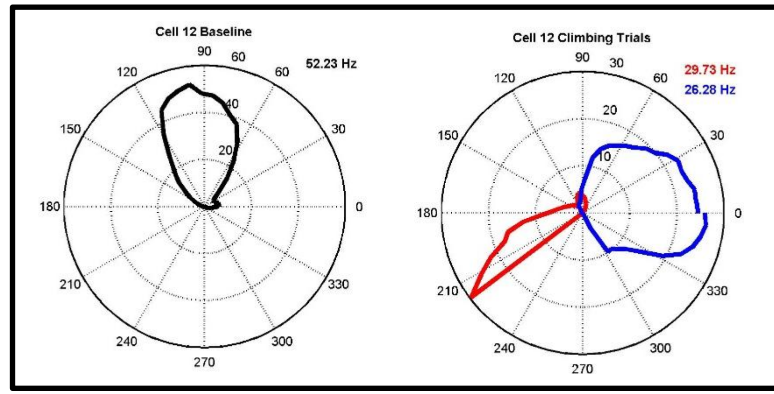


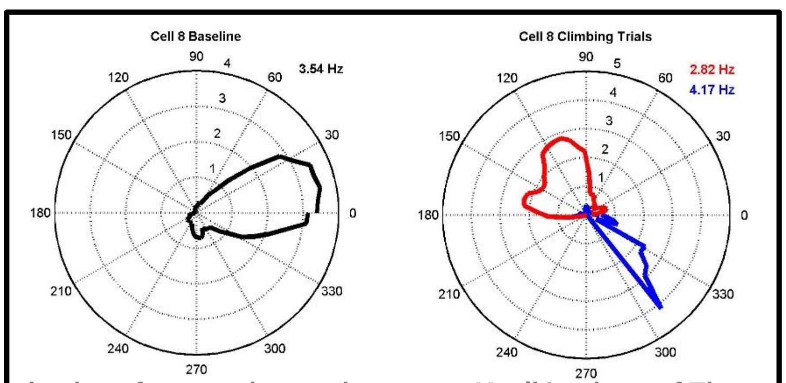
Jonathan Wilson

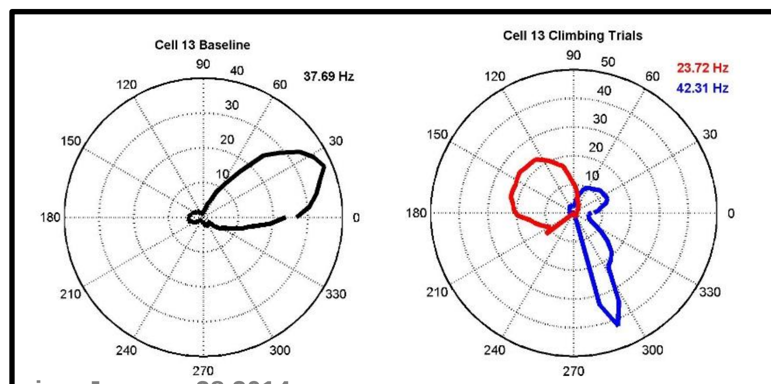

Cell 3 Baseline
6.02 Hz
Cell 3 Climbing Trials
4.69 Hz
1.56 Hz


Cell 11 Baseline
44.04 Hz
Cell 11 Climbing Trials
41.86 Hz
48.28 Hz

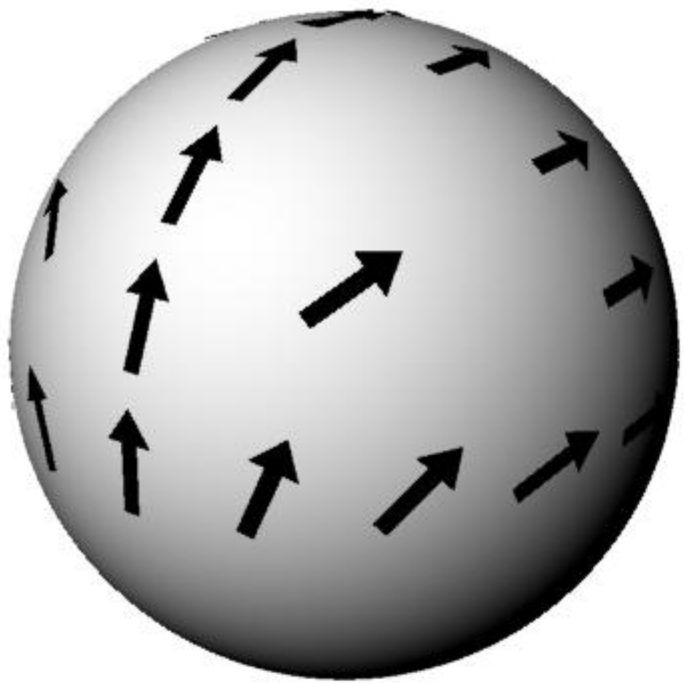

Cell 6 Baseline
3.04 Hz
Cell 6 Climbing Trials
23.26 Hz
23.23 Hz


Cell 12 Baseline
52.23 Hz
Cell 12 Climbing Trials
29.73 Hz
26.28 Hz


Cell 8 Baseline
3.54 Hz
Cell 8 Climbing Trials
2.82 Hz
4.17 Hz


Cell 13 Baseline
37.69 Hz
Cell 13 Climbing Trials
23.72 Hz
42.31 Hz

Does this transformation apply smoothly across all planes?



If so, where in the brain is the transformation signal coming from?

Recap:

1. Complex space representation may be multiple local fragments rather than One Big Map

2. Local fragments appear to be quasi-planar ("bicoded")

3. The metric reference frame for the bicoded map is the locomotor surface

4. The orientational reference frame for the planar map - the HD cell system - is lawfully related to other connected, but differently oriented planes

Hypothesis: The map of complex space (at least in rodents) is a three-dimensional, multiplanar mosaic

Acknowledgements

Lab members (past & present)

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Robin Hayman
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Bex Knight
Yave Lozano
Liz Marozzi
Dorothy Overington
Caitlin Piette
Madeleine Verriotis
Jonathan Wilson

Collaborators

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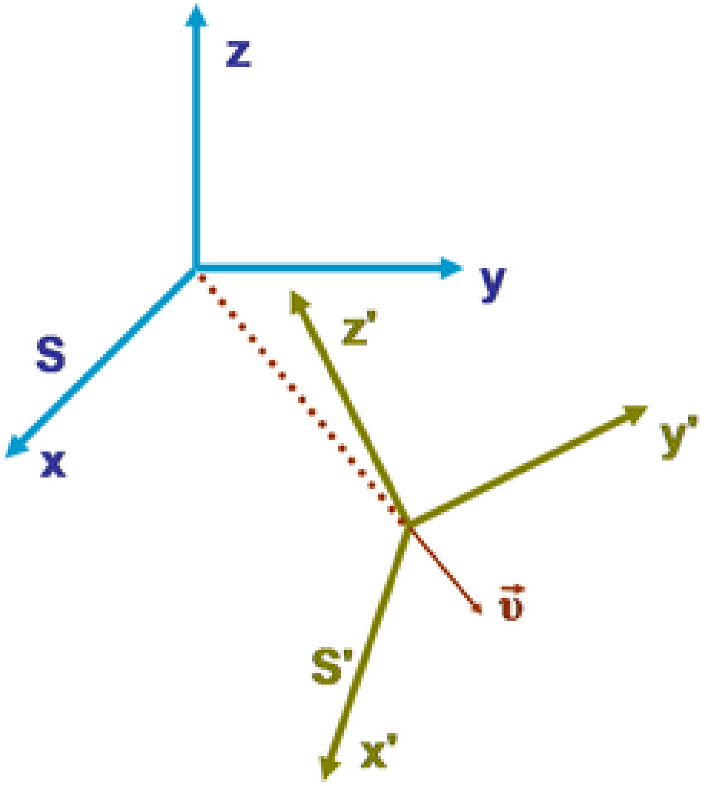
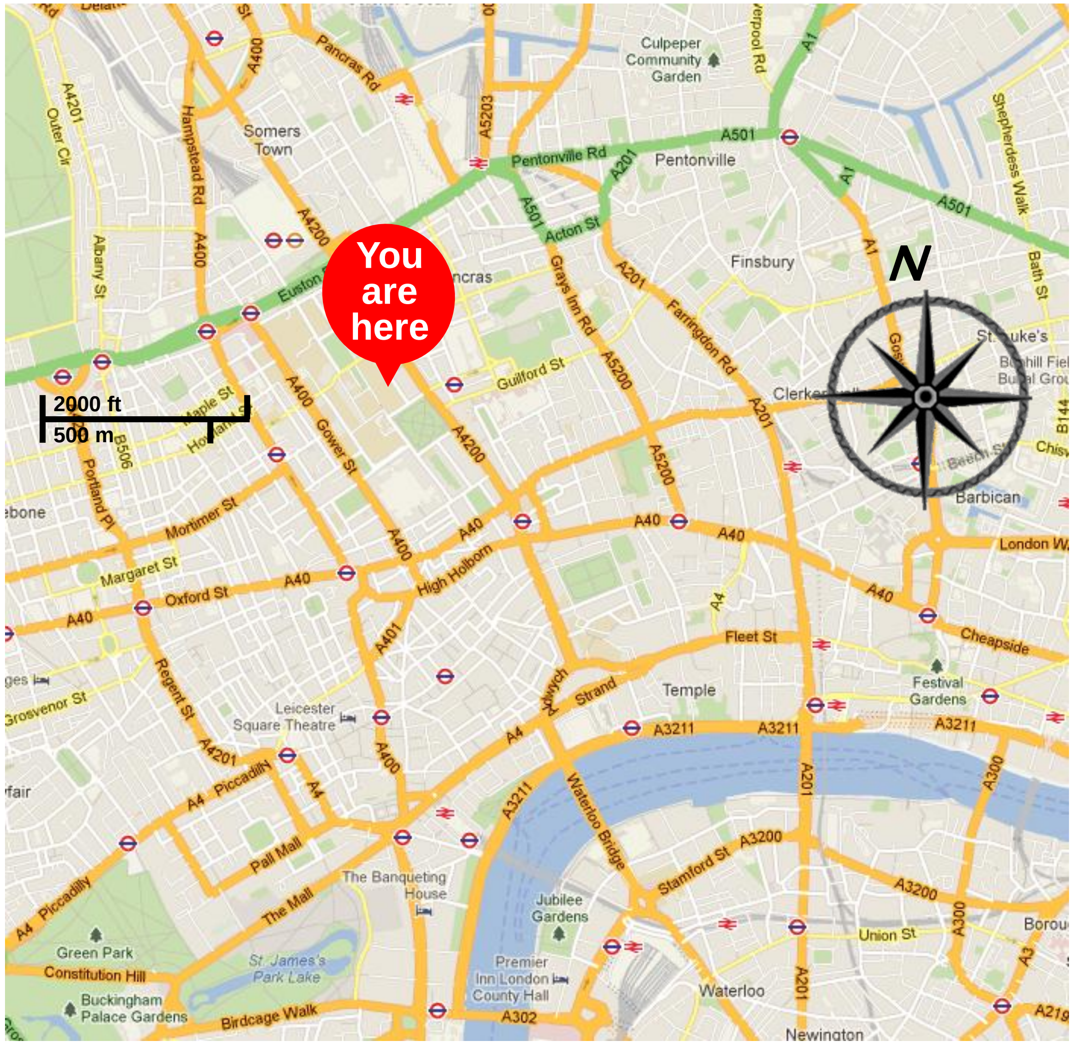
The core concept in spatial representation is that of the FRAME OF REFERENCE



…which has a distance metric …



…and a direction metric

Plus the navigator needs to know where it currently is on the map