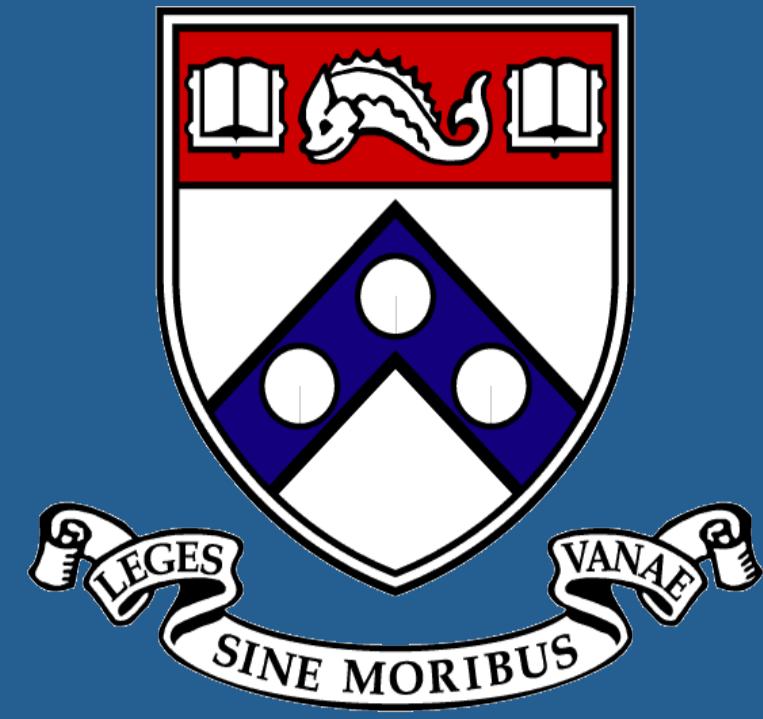


# A Potential Mechanism for Grid Cell Phase Shift: Leveraging Place Cell Remapping



Zachary P Sheldon, Ronald W DiTullio, & Vijay Balasubramanian  
University of Pennsylvania, Philadelphia, PA

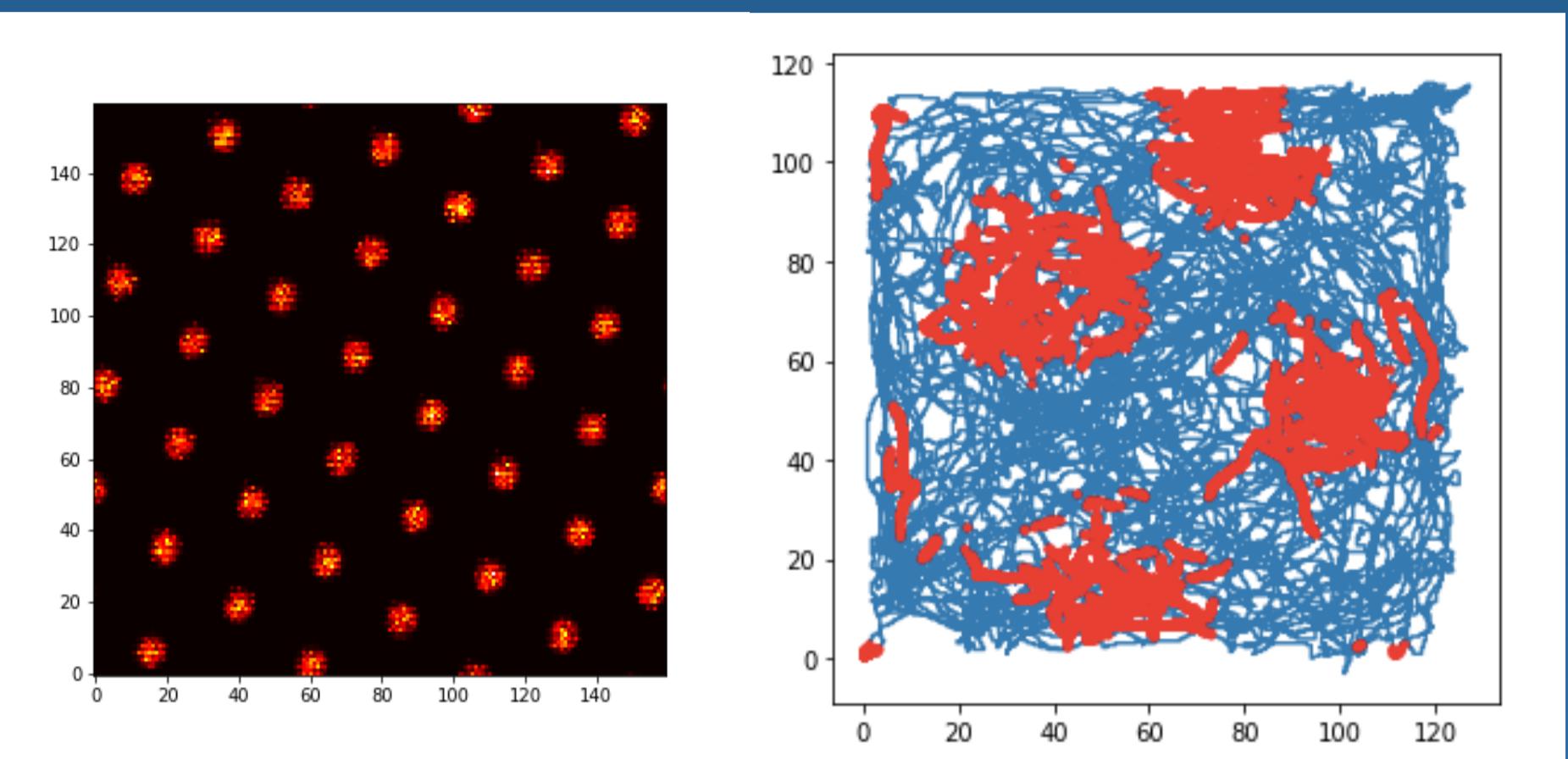
## Background

- Successful spatial navigation depends on an agent's ability to learn an internal representation of space, often referred to as a "cognitive map"<sup>1</sup>.
- The neuronal substrate of this cognitive map is believed to be made up of multiple types of specialized neurons in the hippocampus and entorhinal cortex, particularly place cells and grid cells<sup>14,15</sup>.
- Place cells have firing fields unique to a particular location within an environment, and are thought to encode specific contextual attributes of the environment<sup>14</sup>.
- Grid cells have firing fields that regularly tessellate across an environment, and are thought to be crucial to path integration, which is an agent's ability to determine its current location based on its velocity and previous position<sup>15</sup>.
- Place cells and grid cells undergo changes in certain qualities of their firing fields when the environment is manipulated<sup>3,7,9,12,13</sup>
- Allowing an animal to explore a multi-compartment enclosure leads to a shift in the starting location of the grid cell firing field<sup>9</sup>, otherwise known as a phase shift. However, there are currently no agreed upon mechanisms for how this environmentally-driven phase shift occurs.
- Based on the existence of recurrent connections between the CA1 region of the hippocampus and medial entorhinal cortex<sup>18</sup>, we posit a novel potential mechanism for spatial phase shift in which place cells drive changes in the grid cell firing fields.
- We test this hypothesis by constructing a novel Continuous Attractor Network (CAN) model of grid cells that incorporates place cell inputs.

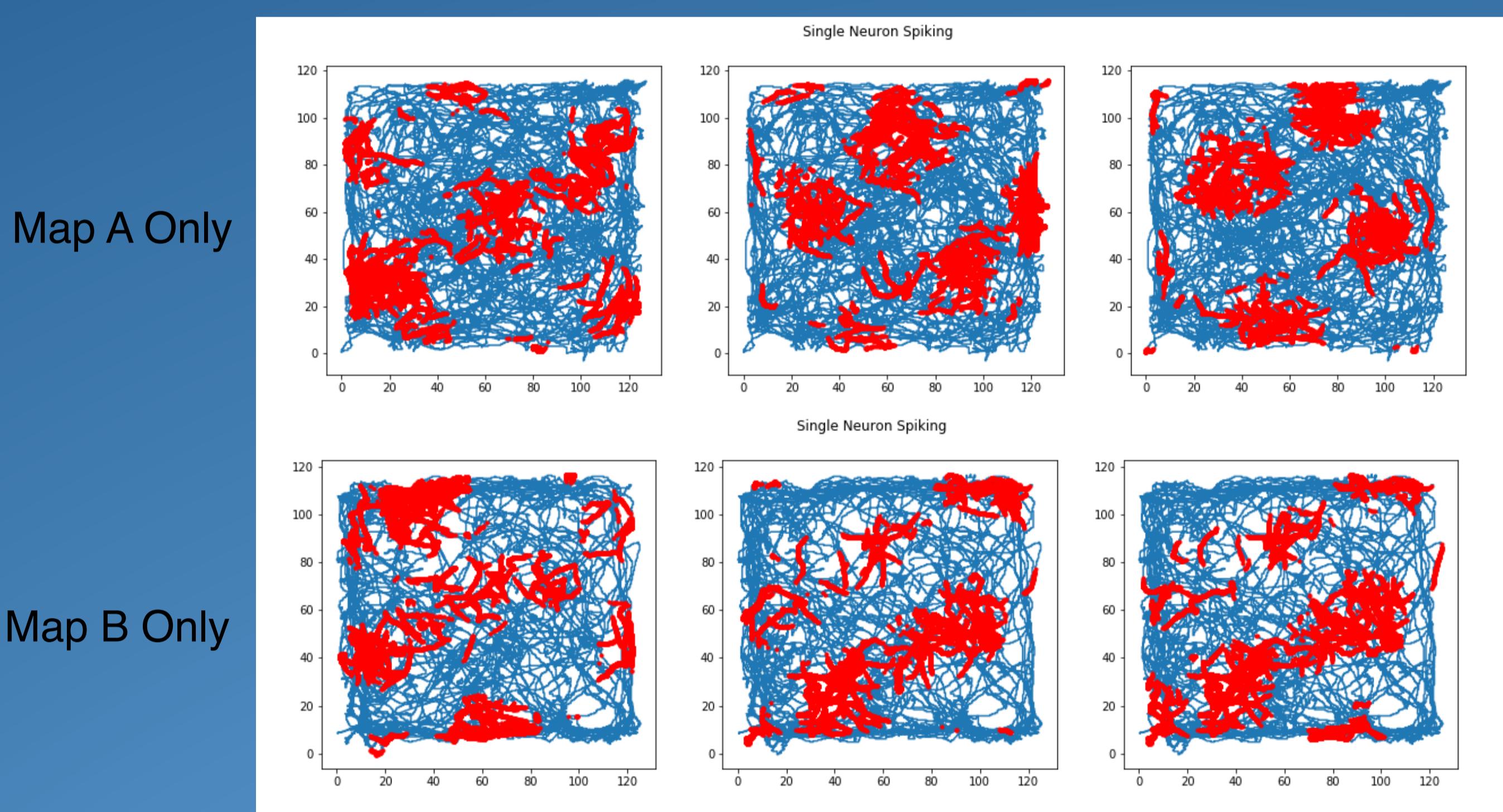
## Materials & Methods

- We implemented a spiking CAN model based off of Burak & Fiete<sup>8</sup>:
  - Periodic 160 x 160 neural sheet
  - Uniform global excitatory input and a local recurrent inhibition profile
  - Direction-sensitive neurons that alternatively tile the neural sheet
  - Global hippocampal excitation is modulated in proportion to the current velocity at each time-step
- We simulated a population of 16 place cells for each training environment to add as inputs into the CAN model:
  - Place cell firing fields are given by randomly centered 2-D Gaussians
  - Place-grid connections underwent competitive Hebbian learning during training
- We generated two orthogonal sub-populations of place cells and trained place-grid weights by using a unique rodent trajectory data-set.
- We tested the model on new trajectory data and switched between the two place cell sub-populations and their respective weights halfway through testing so as to simulate a switch between cognitive maps.

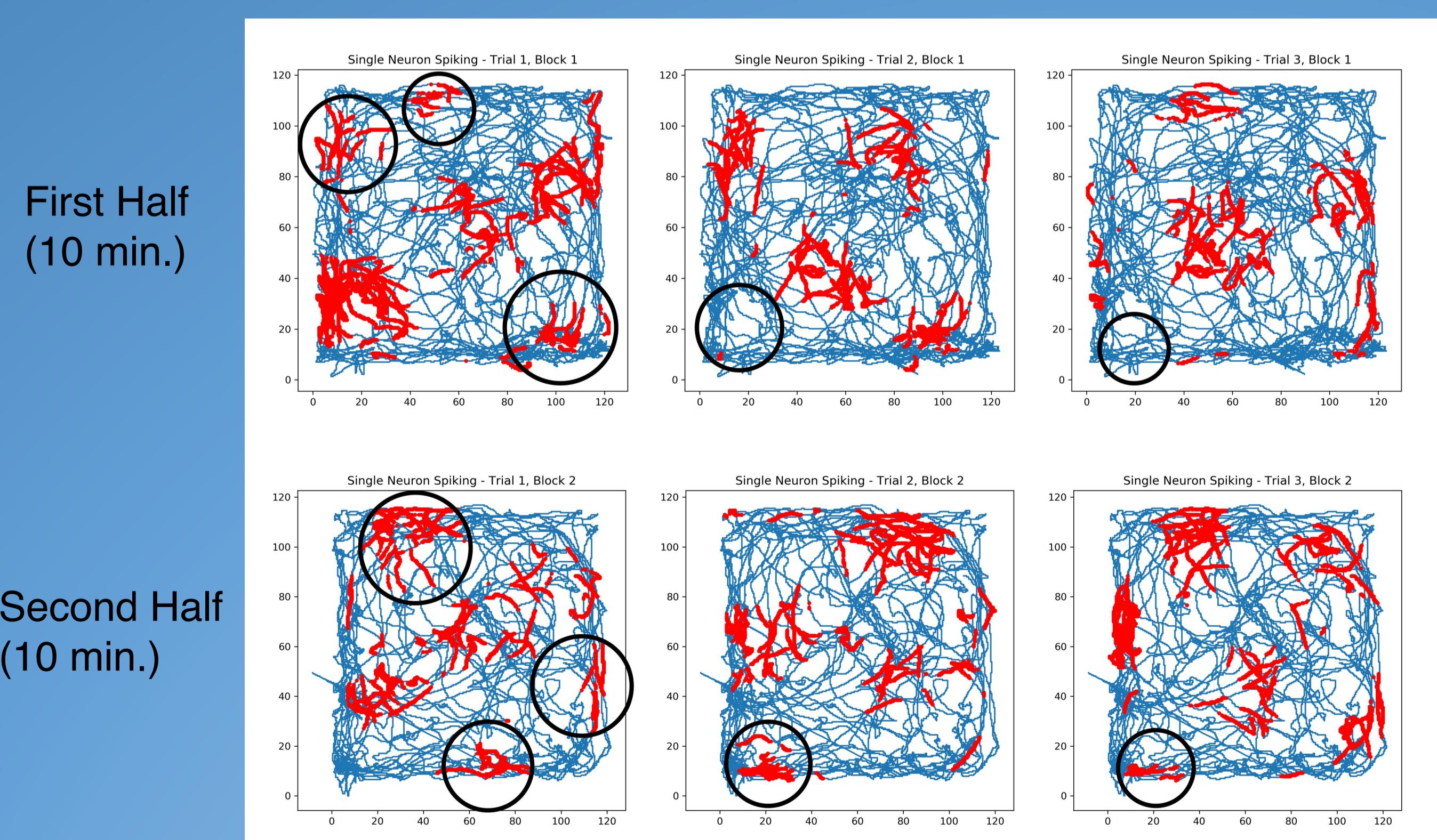
## Results



**1) Spiking, periodic CAN model without place cells.** Left: Overall grid cell population activity at one moment in time. Right: The activity of one grid cell (red) across an entire trial (approximately 20 minutes of trajectory data) plotted over the full trajectory of the rodent (blue).



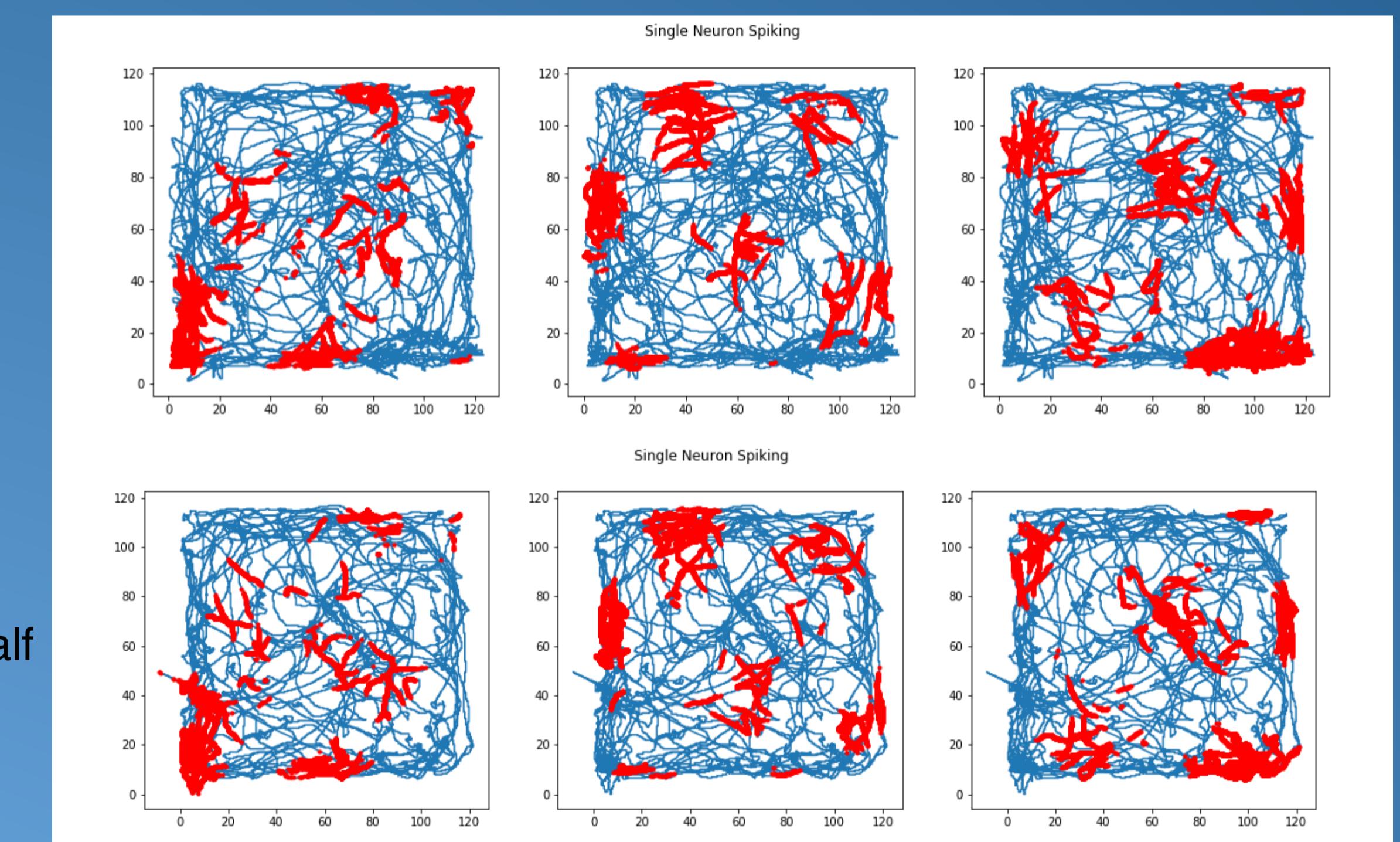
**2) Single-map training stage.** Top: Single neuron spiking results from three different neurons (left to right) from the map A grid cell network during 20 minutes of training. Bottom: Single neuron spiking results from three different neurons (left to right) from the map B grid cell network during 20 minutes of training.



**3) Map-switching experiment.** Top: Spiking results from three different neurons (left to right) from three different trials. Each of these neurons was recorded from a random position in the grid cell network during the first half of testing, using Map A. Bottom: Spiking results from the same three neurons (left to right) as above. These neurons were recorded during the second half of testing, using Map B.

## Discussion

- As a control trial, we also tested our model using only one cognitive map for 20 minutes (Fig. 4). Based on qualitative observation, it seems that the phase change in the experiment was not due to drift.
- Quantitative analysis of the extent of the phase shift during the map-switching experiment is currently underway.
- While we represented place cell remapping in the form of "global remapping"<sup>16</sup>, in which one distinct sub-population of place cells is active in each environment, it is important to note that place cells can exhibit more complex remapping behavior<sup>16</sup>.
- Because this is a novel model, we chose to model the more robust global remapping behavior of place cells in the CA3 region of hippocampus, which has indirect connections to medial entorhinal cortex via the CA1 region<sup>18</sup>.
- Future work in the field may focus on the role of place cells in the CA1 region that more frequently exhibit other forms of remapping.



**4) Single-map control trial.** Top: Spiking results from three different neurons (left to right) from the map A grid cell network during the first half of the control trial (10 minutes). Bottom: Spiking results from three different neurons (left to right) from the map A grid cell network during the second half of the control trial (10 minutes).

## Acknowledgements

- I would like to thank Dr. Vijay Balasubramanian and Ron DiTullio for advising me throughout this project, and Penn's Cognitive Science Program for giving me the Pinkel Award that allowed me to present my work internationally.

## References

- Tolman EC. (1960). Cognitive maps in rats and men. *The Psychological Review*, 55(4): 189–208.
- Giacomo LM, Moser MB, & Moser EI. (2011). Computational models of grid cells. *Neuron*, 71: 589–603.
- Jezek K, Henriksen EJ, Treves A, Moser E, & Moser MB. (2011). Theta-paced flickering between place-cell maps in the hippocampus. *Nature*, 476: 246–249.
- Burak F, & Fiete DR. (2012). Grid cell firing patterns signal environmental novelty by expansion. *PNAS*, 109(43): 17697–17705.
- Bush A, & Fiete DR. (2015). Using grids for navigation. *Neuron*, 87: 307–320.
- Kang J, & Balasubramanian V. (2018). A geometric attractor mechanism for self-organization of hippocampal place cell representations. *bioRxiv*, 71. <https://doi.org/10.1101/2018.01.11.189029>.
- Leutgeb S, Leutgeb J, Barnes CA, & Barnes CA. (2000). Hippocampal place cell responses in a multi-compartment environment. *Journal of Neuroscience*, 20(18): 7349–7359.
- Carrasco D, & Fiete DR. (2013). A geometric attractor mechanism for hippocampal place cell dynamics. *bioRxiv*, 103. <https://doi.org/10.1101/2013.06.10.250032>.
- Derdikman D, Whitlock JR, Tsao A, Fyhn M, Häfner T, Moser MB, & Moser EI. (2009). Fragmentation of grid cells in a multi-compartment environment. *Nature Neuroscience*, 12(10): 1323–1334.
- Hartley G, & Burgess N. (2012). Microstructure of the spatial map in the entorhinal cortex. *Nature*, 486(7405): 801–806.
- Keefe J. (1979). Place units in the hippocampus of the freely moving rat. *Experimental Neurology*, 51(1): 78–109.
- Lutjens P, Konkle O, Kohler L, & Allen K. (2018). Hippocampal remapping and its entorhinal origin. *Frontiers in Neuroscience*, 11(23): 177.
- Moser E, Knobf P, & Moser MB. (2008). Place cells, grid cells, and the brain's spatial representation system. *Annual Review of Neuroscience*, 31: 69–89.
- Kherim J. (2018). The hippocampus. *Current Biology*, 29(2): 1116–1121.