

Cognitive maps: A grid - like code?

Guglielmo Reggio - k1763271

1. Grid cells in the MEC

A **cognitive map** is described as a **mental representation** of one's **physical environment** [1] and was introduced by Edward **Tolman** in 1948. In general, the mapping system is one of many types of **memory systems** and is responsible for acquiring, coding, storing and decoding location information of metaphorical or real spatial environments.

The role of the hippocampus in generating cognitive maps was already appreciated in 1978, when **O'Keefe & Nadel** described it as the centre of a system that constructs and stores cognitive maps [2]. In particular, they described the **hippocampus** as one of the several spatial systems creating **allocentric representations**. In their study they described maps as created during exploration, rapidly acquired and used to guide animals through space in order to reach food or water supplies, a mate or a home base. In particular, they highlighted the flexible behaviour allowed by cognitive maps and the use of detours and shortcuts. Moreover, they predicted that a cognitive map not only requires location information (as provided by **place cells**, discovered in the hippocampus by **O'Keefe and Dostrovsky** in 1971 [3], but also direction and distance. The **integration of location with direction** will be proposed in the '90 in a series of papers on direction cells in the brain [4] and on a **continuous periodic attractor model** of **head direction cell** by angular velocity integration [5].

In 1997, a paper by **Samsonovich & McNaughton** introduced the concept of periodic boundaries in the model for a **continuous attractor network** underlying **path integration** and the **medial entorhinal grid cells** [6]. In the two years following this paper, two additional studies proposed the involvement of **loops including the entorhinal cortex (EC)** in the process of path integration [7] [8].

The **hippocampus**, which is part of the limbic system, contributes to the **consolidation of short-term to long-term memory of information** and plays an important role in particular in spatial and navigation memory. Moreover, **the entorhinal cortex acts as a hub connecting the hippocampus and the neocortex** and is part of the largely interconnected network responsible for navigation, memory and perception of time. **Together, the hippocampus and the EC contribute to the encoding of declarative and spatial memory.**

In the hippocampus, **place cells** (a type of **pyramidal neurons**), so called as they fire action potential when an animal is located in a distinct region of space (the place field of the cell), are **thought to generate cognitive maps** [2], as hypothesised by Edward Tolman. In 2005, **Moser** et al. discovered the existence of **grid cells** in the **medial entorhinal cortex (MEC)** [9]. Grid cells can be described as a type of place cells characterised by **regular patterns in their spatial activity**. They represent a **rhomboidal grid-like structure of place fields that repeat at regular intervals**. The rhombus composing the grid have internal angles of 60 and 120 degrees, as shown in Figure 1.

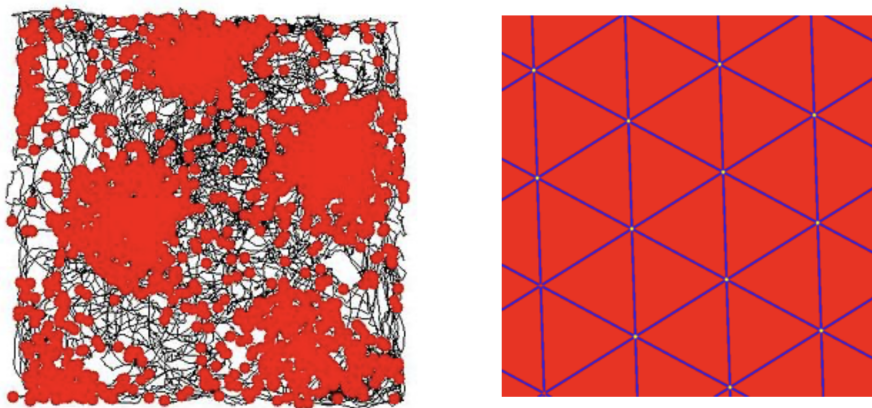


Figure 1: The grid cell hexagonally symmetric pattern.

2. Continuous periodic attractor model of head direction cell

Path integration is thought to be performed in the hippocampal formation, which encodes relative spatial location, without relation to external indications. This is done by integration of linear and angular self-motion. In the MEC, the computation of path integration is performed by a periodic synaptic matrix through a symmetry breaking operation. The basis for a continuous attractor model for path integration was first proposed by McNaughton in 1991 [10] through an early version of the head direction path integrator. Four years later, in 1995, Tsodyks and Sejnowski published one of the first papers to advance the concept of a system of continuous attractors [11] and in 1996 Zhang proposed a periodic continuous attractor model of head direction cell by angular velocity integration [5].

An **attractor network** represents **a type of recurrent dynamical network which evolves over time toward a stable pattern**. Moreover, a **continuous attractor** represents **a continuous object embedded in the phase space, as opposed to a discrete set of points** [12]. Hebb's cell assembly theory is an example of attractor dynamics representing self-organising, self-sustaining neural activity.

The head direction (HD) cell cognitive map in rats can be modelled with a 1-dimensional continuous attractor network model, as in Figure 2 (left), considered active when a single locus of activity is generated by the orientation of the head in a specific absolute direction in the environment, regardless of other behavioural variables or even location in space. In a symbolical circular distribution of the head cells, representing the angular orientation of the rats head, the activity distribution shows an activity packet (a bump) which represents the single locus of activity, or the population vector code, generated by the head orientation [5]. This 1D model is characterised by three layers: an input layer corresponding to vestibular, rotational visual flow; an outer head direction cell layer where the activity packet is generated; a medial conjunctive cells layer which computes information from about the current state of the system (from the outer layer) and the direction of rotation (from the input layer) and generates the next state of the system by projecting to the appropriate neighbouring cell of the HD cell from which is receiving the outer layer input.

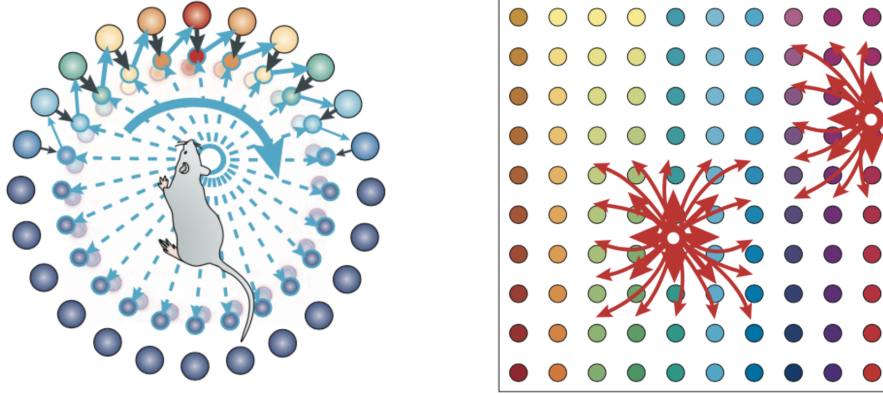


Figure 2: 1D and 2D continuous attractor network model.

The 2-dimensional version of this model, Figure 2 (right), is based on a grid of cells arranged on a 2D surface based on their relative firing locations in space. This grid is then represented with a recurrent synaptic matrix representing a graph with edges having strength, or weight, proportional to the physical distance between the cells place fields. The activity packet and the hidden layer would simply correspond to a 2D version of the one-dimensional ring described above. Path integration would then be achieved by the contributions of both the preceding activity state of the network and the distance and direction moved which would trigger the firing of one set of cells generating the new state, not directly influenced by the pattern of environmental stimuli at a given location (this might take place in the hippocampus which creates specific representations for different environments). In order to solve the periodic boundary problem [6], [13] proposed a toroidal topology which is topographically isomorphic to a two dimensional square with periodic boundaries, as shown in Figure 3.

As for the scale of the cognitive map generated in such a way, according to this model for path integration, the scale of the brain representation is generated by the contribution of both the speed of the rat in space and the speed of the activity packet in the network, particularly in the attractor layer. As for navigation in large environments, a combination of grids with different scales might provide the required spatial coordinate system and the repetition cycle could be increased by the beat interference pattern. Different scales could then be achieved by the weak interaction of multiple path integration models.

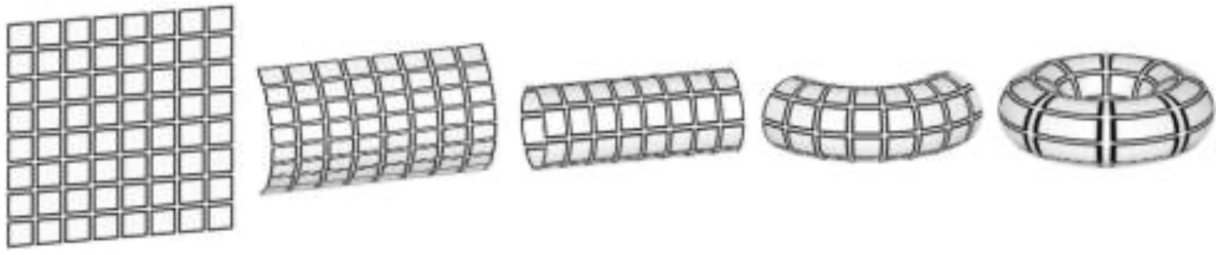


Figure 3: Isomorphic transformation from 2D square to torus.

3. Grid cells and memory in humans

After the discovery of grid cells in rats in 2005 [9], in 2010 a paper by Doeller et al. [14] provided evidence for grid cells in a human memory network. A speed-modulated six-fold rotational symmetry in running direction signal was found using fMRI. This signal appeared in a network of entorhinal/subicular, posterior and medial parietal, lateral temporal and medial prefrontal areas. Moreover, this directional signal was correlated with spatial memory performance. Not only they reported the first evidence that the human EC encodes virtual movement with six-fold symmetry, as previously found in rats [9] [15] [16], but the relationship to spatial memory of the directional coherence of potential grids across entorhinal cortex that they found represents a first signal that grid-like representations might usefully influence behaviour.

Six years later, in 2016, a study by Constantinescu et al. [17] confirmed this relationship between the hexagonally symmetric code used by grid cells and the organisation of spatial representations even for navigating conceptual relationships in a 2D knowledge space. In particular, they found that subjects with a wider hexagonal modulation performed better at the task of navigating a two-dimensional knowledge space in order to associate specific symbols or images with specific states of this concept space. Global relational codes, they suggested, may be used to organise non spatial conceptual representations, and when conceptual knowledge is represented in two continuous dimensions, these codes may produce a hexagonal grid-like pattern.

References

- [1] Lexico - cognitive map definition, https://www.lexico.com/en/definition/cognitive_map.
- [2] J. O'Keefe, L. Nadel, *The hippocampus as a cognitive map*, Clarendon Press, Oxford, United Kingdom, 1978.
- [3] J. O'Keefe, J. Dostrovsky, *The hippocampus as a spatial map. preliminary evidence from unit activity in the freely-moving rat*, *Brain Research* 34 (1) (1971) 171 – 175. doi: [https://doi.org/10.1016/0006-8993\(71\)90358-1](https://doi.org/10.1016/0006-8993(71)90358-1). URL <http://www.sciencedirect.com/science/article/pii/0006899371903581>
- [4] J. Taube, R. Muller, J. Ranck, *Head-direction cells recorded from the postsubiculum in freely moving rats. ii. effects of environmental manipulations*, *Journal of Neuroscience* 10 (2) (1990) 436–447. arXiv: <https://www.jneurosci.org/content/10/2/436.full.pdf>, doi: 10.1523/JNEUROSCI.10-02-00436.1990. URL <https://www.jneurosci.org/content/10/2/436>
- [5] K. Zhang, *Representation of spatial orientation by the intrinsic dynamics of the head-direction cell ensemble: a theory*, *Journal of Neuroscience* 16 (6) (1996) 2112–2126. arXiv: <https://www.jneurosci.org/content/16/6/2112.full.pdf>, doi: 10.1523/JNEUROSCI.16-06-02112.1996. URL <https://www.jneurosci.org/content/16/6/2112>
- [6] A. Samsonovich, B. L. McNaughton, *Path integration and cognitive mapping in a continuous attractor neural network model*, *Journal of Neuroscience* 17 (15) (1997) 5900–5920. arXiv: <https://www.jneurosci.org/content/17/15/5900.full.pdf>, doi: 10.1523/JNEUROSCI.17-15-05900.1997. URL <https://www.jneurosci.org/content/17/15/5900>
- [7] A. D. Redish, D. S. Touretzky, *The role of the hippocampus in the morris water maze (1998)*.
- [8] P. E. Sharp, *Complimentary roles for hippocampal versus subicular/entorhinal place cells in coding place, context, and events*, *Hippocampus* 9 (4) (1999) 432–443.
- [9] T. Hafting, M. Fyhn, S. Molden, M.-B. Moser, E. I. Moser, *Microstructure of a spatial map in the entorhinal cortex*, *Nature* 436 (7052) (2005) 801–806. doi: 10.1038/nature03721. URL <https://doi.org/10.1038/nature03721>
- [10] B. L. McNaughton, L. L. Chen, E. J. Markus, *dead reckoning, landmark learning, and the sense of direction: A neurophysiological and computational hypothesis*, *Journal of Cognitive Neuroscience* 3 (2) (1991) 190–202, PMID: 23972093. arXiv: <https://doi.org/10.1162/jocn.1991.3.2.190>, doi: 10.1162/jocn.1991.3.2.190. URL <https://doi.org/10.1162/jocn.1991.3.2.190>
- [11] M. Tsodyks, T. Sejnowski, *Associative memory and hippocampal place cells*, *International Journal of Neural Systems - IJNS* 6.
- [12] Scholarpedia - continuous attractor network definition, http://www.scholarpedia.org/article/Continuous_attractor_network.

- [13] J. Conklin, C. Eliasmith, *A controlled attractor network model of path integration in the rat*, *Journal of Computational Neuroscience* 18 (2) (2005) 183–203. doi: 10.1007/s10827-005-6558-z.
URL <https://doi.org/10.1007/s10827-005-6558-z>
- [14] C. F. Doeller, C. Barry, N. Burgess, *Evidence for grid cells in a human memory network*, *Nature* 463 (7281) (2010) 657–661. doi: 10.1038/nature08704.
URL <https://doi.org/10.1038/nature08704>
- [15] C. Barry, R. Hayman, N. Burgess, K. J. Jeffery, *Experience-dependent rescaling of entorhinal grids*, *Nature Neuroscience* 10 (6) (2007) 682–684. doi: 10.1038/nn1905.
URL <https://doi.org/10.1038/nn1905>
- [16] F. Sargolini, M. Fyhn, T. Hafting, B. L. McNaughton, M. P. Witter, M.-B. Moser, E. I. Moser, *Conjunctive representation of position, direction, and velocity in entorhinal cortex*, *Science* 312 (5774) (2006) 758–762. arXiv: <https://science.sciencemag.org/content/312/5774/758.full.pdf>, doi: 10.1126/science.1125572.
URL <https://science.sciencemag.org/content/312/5774/758>
- [17] A. O. Constantinescu, J. X. O'Reilly, T. E. J. Behrens, *Organizing conceptual knowledge in humans with a gridlike code*, *Science* 352 (6292) (2016) 1464–1468. arXiv: <https://science.sciencemag.org/content/352/6292/1464.full.pdf>, doi: 10.1126/science.aaf0941.
URL <https://science.sciencemag.org/content/352/6292/1464>