Progress Report (Research Project)

A Model to Explain the Mechanisms of "Remapping" in Neuronal Coding for Navigation and Working Memory

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1 Literature Review

1.1 Place cells and grid cells

The discovery of hippocampal place cells, which fire when animals are in certain locations (Figure 1), the results are clearly visible.marked a new branch in neuroscience (O'Keefe & Dostrovsky, 1971) (O'Keefe & Nadel, 1978). These cells are thought to play a role in forming cognitive maps, which are used by animals for navigation (Tolman, 1948) (O'Keefe & Nadel, 1978). Place cells were discovered in both the CA1 and CA3 regions of the hippocampus. Place cells in area CA1 were found to maintain their place characteristics even after the CA3 input was eliminated (Brun, Leutgeb, & Leutgeb, 2002), suggesting that they receive input from the medial entorhinal cortex (MEC).

Neurons in MEC also show spatial selectivity, but with multiple firing fields rather than just one (Fyhn, Hafting, Treves, Moser, & Moser, 2004) (Hargreaves et al., 2005): In a series of experiments conducted in the early 2000s, the Mosers and their team recorded the activity of neurons in the entorhinal cortex of rats as they moved around a virtual maze. They found that some neurons exhibited a periodic firing pattern that formed a hexagonal grid, with the spacing between grid lines being consistent regardless of the animal's position or direction of movement (Moser & Moser, 2014) (Figure 1). Each grid cell has a slightly different set of x and y coordinates (Hafting, Fyhn, Molden, Moser, & Moser, 2005). The scale of the grid pattern increases from dorsal to ventral MEC (Fyhn, Hafting, et al., 2004) (Hafting et al., 2005) (Brun, Leutgeb, & Leutgeb, 2008).

The discovery of grid cells is generally attributed to the Norwegian scientists May-Britt Moser and Edvard Moser, who were awarded the Nobel Prize in Physiology or Medicine in 2014. Their discovery was groundbreaking because it provided the first evidence of a neural mechanism that could explain the animal's ability to form a map of its environment and navigate through it.

Several computational models (Fuhs & Touretzky, 2006) (McNaughton, Battaglia, Jensen, Moser, & Moser, 2006) (Burak & Fiete, 2009) (Burgess, Barry, Jeffery, & O'Keefe, 2007) and experimental evidence (Brun et al., 2002) (Van Cauter, Wyffels, & Verhagen, 2008) (Zhang & Ginzburg, 2013) suggest that grid cells are responsible for the spatial selectivity of place cells in the hippocampus. These models depend on the organization of the grid map at different functional levels, including grid spacing and orientation. While early studies suggested that grid cells always have a similar orientation (Hafting et al., 2005) (Fyhn, Hafting, Treves, Moser, & Moser, 2007), modern work has found that multiple orientation configurations may exist within the same animal (Krupic et al., 2012) (Stensola et al., 2012). This raises questions about the organization of the grid map, whether it is made up of smaller sub-maps or a single map with multiple configurations.

The relationship between grid cells and place cells is not fully understood, but it is thought that place cells may receive input from multiple grid cells with overlapping fields (Burgess et al., 2007). This overlap may be necessary for the precise location coding seen in place
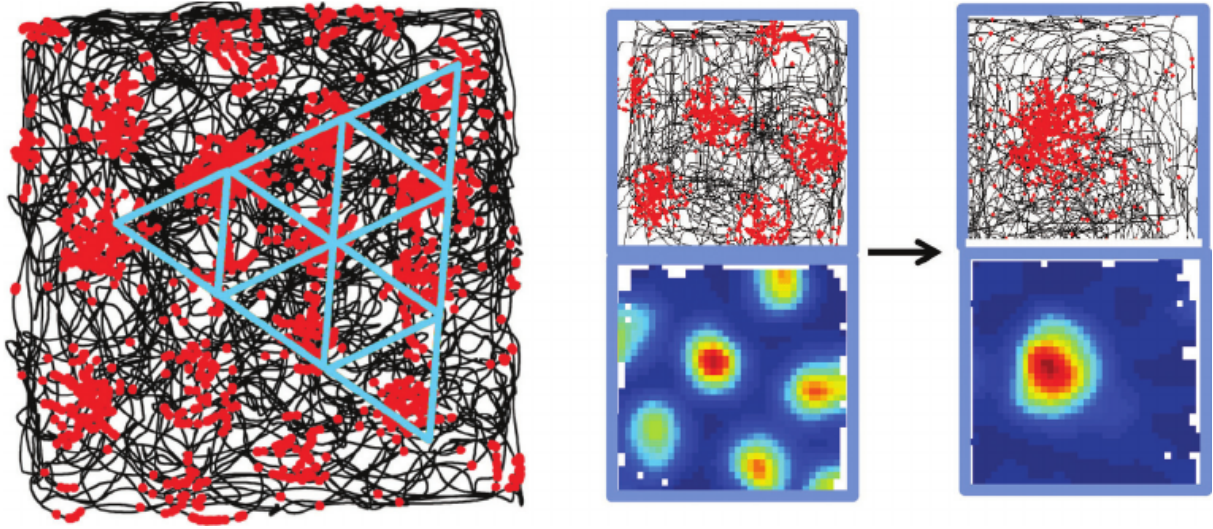
Figure 1: The figure shows the firing patterns of grid cells and place cells in the brain of a rat. The left panel shows a grid cell from the entorhinal cortex, which has a regular hexagonal firing pattern as the rat moves through a square enclosure. The right panel shows a grid cell and place cell, with the top panel showing the rat's trajectory and the bottom panel showing a color-coded map of the cells' firing activity (Moser et al., 2015)

cells (Fuhs & Touretzky, 2006). Additionally, theta rhythm oscillations (Berger, 1934), observed in both place cells and grid cells may play a role in integrating information from multiple grid cells (O'Keefe & Recce, 1993) (Sargolini et al., 2006)). Further research is needed to fully understand the precise function of theta oscillations in the relationship between place cells and grid cells.

In summary, the discovery of place cells and grid cells has provided important insights into the neural basis of spatial navigation and memory. While much has been learned about the relationship between these two cell types, there are still many questions that remain to be answered. Further research is needed to fully understand the mechanisms underlying the transformation of grid cell input into place cell activity, as well as the role of theta oscillations and other factors in this process.

1.2   Grid cells organization and remapping of place cells

Muller and Kubie (1987) conducted a study on place cells that was a huge advance in our understanding of the relationship between the spatial map in the hippocampus and memory formation. They found that place cells were controlled by sensory cues in the environment, for example rotating a cue resulted in a consistent rotation of the place fields. Importantly, they also observed that when two recording environments differed beyond a certain magnitude, the activity of the recorded cells changed significantly between the environments (Muller & Kubie, 1987). This phenomenon, called "remapping," involved a reorganization of the firing locations of cells that were active in both environments, as well as a large portion of cells becoming inactive or active only in the second environment (Figure 2). It shows that the encoding of one environment is orthogonal to the encoding of the other one when they are different.
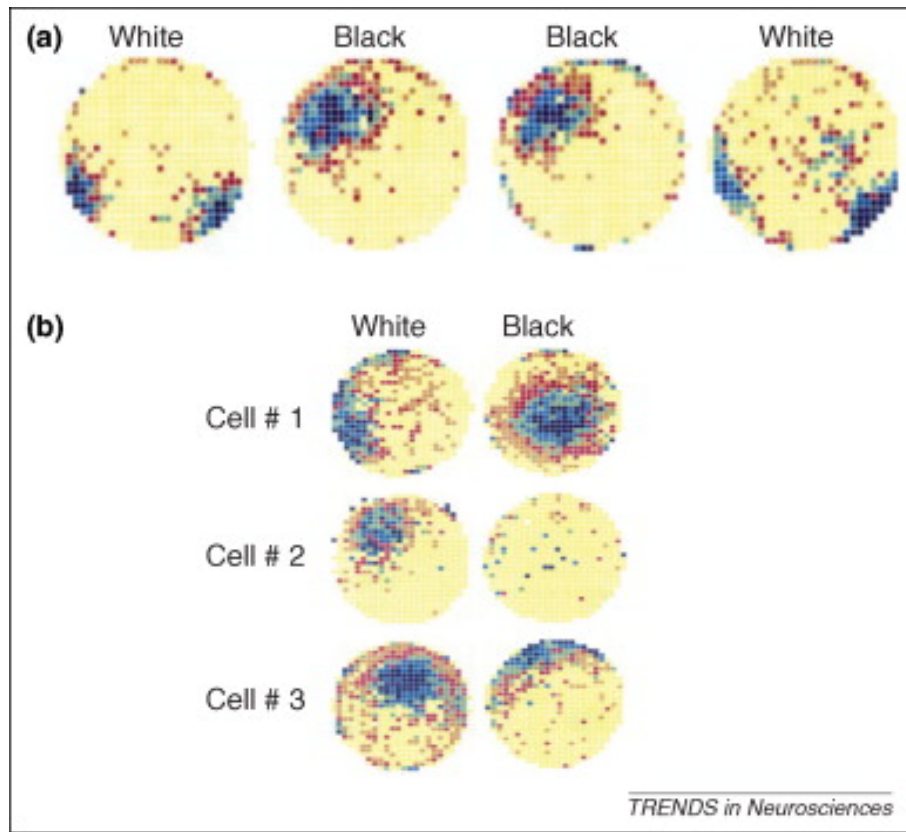
Figure 2: The figure shows firing rate maps for place cells in the hippocampus of a rat recorded during sessions in a cylinder with either a white or black cue card. The firing rate maps are color-coded, with yellow representing a firing rate of 0 Hz and purple representing the maximum firing rate. The place fields changed location or disappeared in response to the cue card substitution (Colgin et al., 2008)

The concept of grid modularity offers an explanation for remapping in the hippocampus. Maps from different grid modules could reorganize to produce completely new downstream population inputs and then new hippocampal place maps. Early research showed that grid cells realigned with the environment during remapping in simultaneously recorded place cells (Fyhn et al., 2007). This realignment involved a shift and a reorientation of the grid pattern relative to the environment's geometry. The realignment was coherent for all recorded grid cells, which means that the spatial relationships between the cells remained. But, it is still possible that distinct modules could present independent realignment, since the study was done on specific cells, having similar grid scales and located at the end of the dMEC.

The level of independence between grid modules affects the capacity of remapping. Grid modules have several characteristics that suggest they are autonomous (Stensola et al., 2012). For example, grid spacing relationships vary between animals, and grid orientation can be completely offset between modules. Grid modules also differ in terms of direction- ality, and deformation: Scale, and orientation can change independently across modules when the animal is exposed to a novel environment. These observations are consistent with an attractor mechanism for grid formation. However, it is surprising to find that

modules assumed one of only four distinct orientation configurations relative to the environment (Stensola et al., 2015). This constraint on orientation could be considered a disadvantage for generating distinct hippocampal inputs. However, it has been shown theoretically that remapping based on grid modules is more sensitive to the spatial phase offset between the modules than the relative orientation and spacing (Monaco & Abbott, 2011). Varying grid orientation caused less reorganization in the hippocampus compared to varying phases.

The differences in rescaling across grid modules may provide insight into the mechanisms underlying the rescaling of hippocampal place fields after changes in the environment's geometry (O'Keefe & Burgess, 1996). O'Keefe and Burgess recorded place cells in a rectangular environment that could be extended or compressed in any of the four cardinal directions. When the environment was extended or compressed, place fields followed the change in size, suggesting that they are rescaled according to the new geometry. It is thought that the grid cells provide the necessary signals for this rescaling, where the spacing between grid cells determines the degree of rescaling (Burgess et al., 2007). However, the mechanisms underlying this process are still fuzzy. One possibility is that the grid cells provide a metric for the size of the environment, which is then used to rescale the place fields (Burgess et al., 2007). Alternatively, it has been suggested that the place cells themselves may contain a metric for the environment's size, which is updated based on input from the grid cells (Moser & Moser, 2014).

2 Progress

2.1 Description of the computational model

There are several models explaining the grid cell activity recorded in dMEC and their utility in generating place cells (Fyhn, Molden, Witter, Moser, & Moser, 2004) (Fuhs & Touretzky, 2006). For this research project we will try to underline the mechanism of "remapping" in hippocampus place cells (Muller & Kubie, 1987) for a computational model developed by Gaussier and his team to study how grid cells and visual place cells (VPC) in the EC may be generated and integrated to generate strong place cells (Gaussier et al., 2007). The model suggests that grid cell activity in the dMEC arises from a long-distance path integration system located outside the hippocampus, while broad visual place cell activity in the MEC may result from the integration of visual information. The model also proposes that the merge of entorhinal visual place cell information and grid cell information in the EC or dentate gyrus (DG) allows the generation of precise place cells.

2.2 Visual place cells

The VPC in the entorhinal cortex are generated through the integration of "what" and "where" information from the visual flow: The "what" information, coded in the perirhinal cortexor local views, or other areas of ventral visual pathway of the temporal cortex (Rolls, Tovee, Purushothaman, & Cheng, 2003). The "where" information, or the absolute position of the local views is peripheral space, is provided by the parietal cortex through the parahippocampal region (Saunders & Rosene, 2013).

The "what" and "where" information is merged either in the EC, on the synapses of pyramidal neurons in the superficial layer of the EC (Gaussier et al., 2007). This merging allows for the activation of a neuron when a specific local view is recognized for a particular azimuth and elevation (Figure 3).
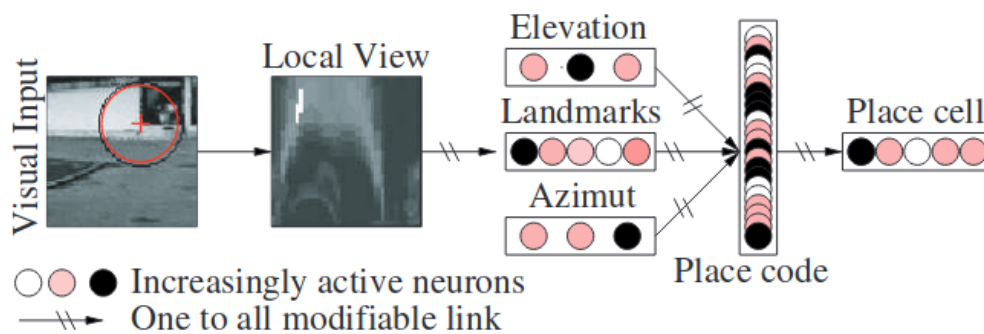

Figure 3: The figure shows a neural network architecture showing how visual place cells are built. (Gaussier et al., 2007)

This model is called Pr-Ph model, in more details (Figure 4), it consists of generating visual place cells and learning to recognize specific combinations of azimuths and landmarks by merging information from the perirhinal (Pr) and parahippocampal (Ph) structures (Jauffret, Cuperlier, & Gaussier, 2015). An action is then associated with this place cell through a winner-take-all competition, and the winning place cell is learned using a least mean square algorithm (Widrow & Hoff, 1960). Essentially, this model proposes that the perirhinal and parahippocampal structures play a role in representing spatial and object information, and that this information is used to guide actions through the activation of specific place cells.
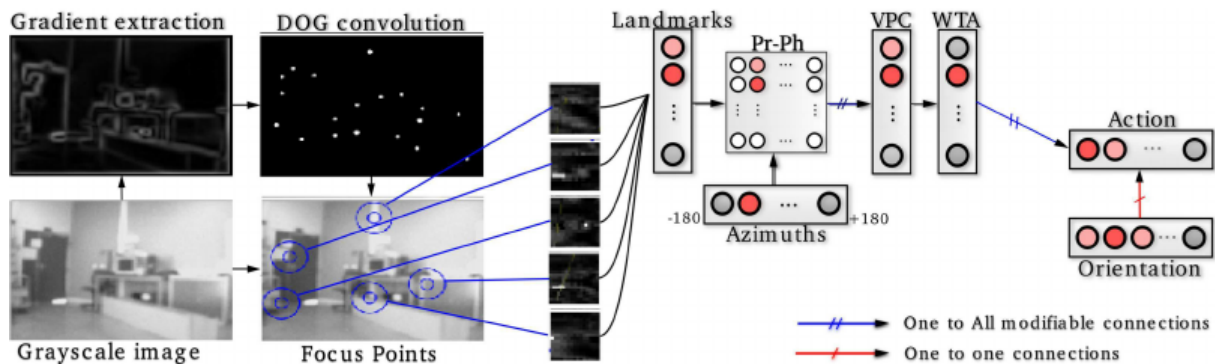

Figure 4: A neural network architecture showing the information flow used to build visual place cells from the surrounding environment (Jauffret et al., 2013)

2.3 Grid cells

Some models claim that emergence of grid cells is based particularly on self-motion information rather than visual information (Ekstrom, Yoganarasimha, Knierim, & Mc-Naughton, 2010) (Stensola et al., 2012) (Jacobs & Knierim, 2013). In the model that we study (Gaussier et al., 2007), the emergence of grid cells is based on long-path integration (Figure 5) considering just self-motion information.

In this model (Gaussier et al., 2007) path integration information can be used to build grid cell activity without the need for a Cartesian coding. Just a one-dimensional neural field is used to code the global path integration of an animal. At the level of a blob in the MEC, the learning of the conjunction of two codes corresponding to the modulo compression of two projections of the path integration field is sufficient to obtain grid cells. The orientation of the grid is determined by the selection of modulo projections in two directions, and the spacing is determined by the modulo value and the radius of the firing field by the discretization factor of the path integration field. All combinations of neurons associated with the same angular difference produce the same grid cell activity (Figure 6).
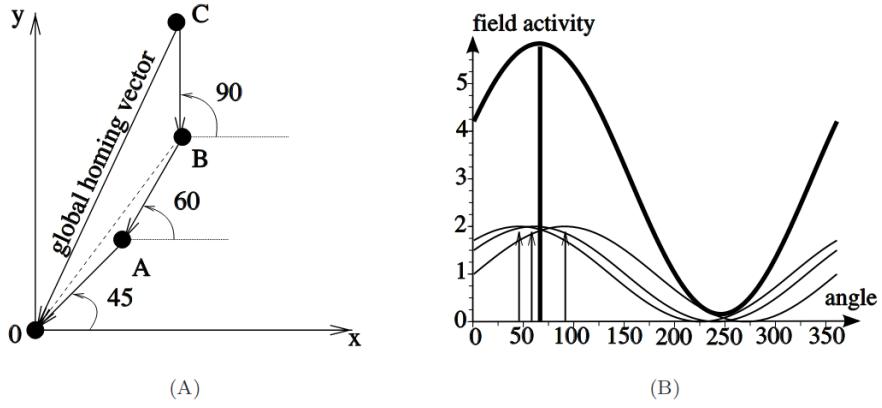
Figure 5: (A) A trajectory of three movements of the same length in different directions. The corresponding inputs are neural fields with a cosine shape centered on each movement direction. (B) The sum of these inputs has a maximum activity for the direction of the global movement. (Gaussier et al., 2007)
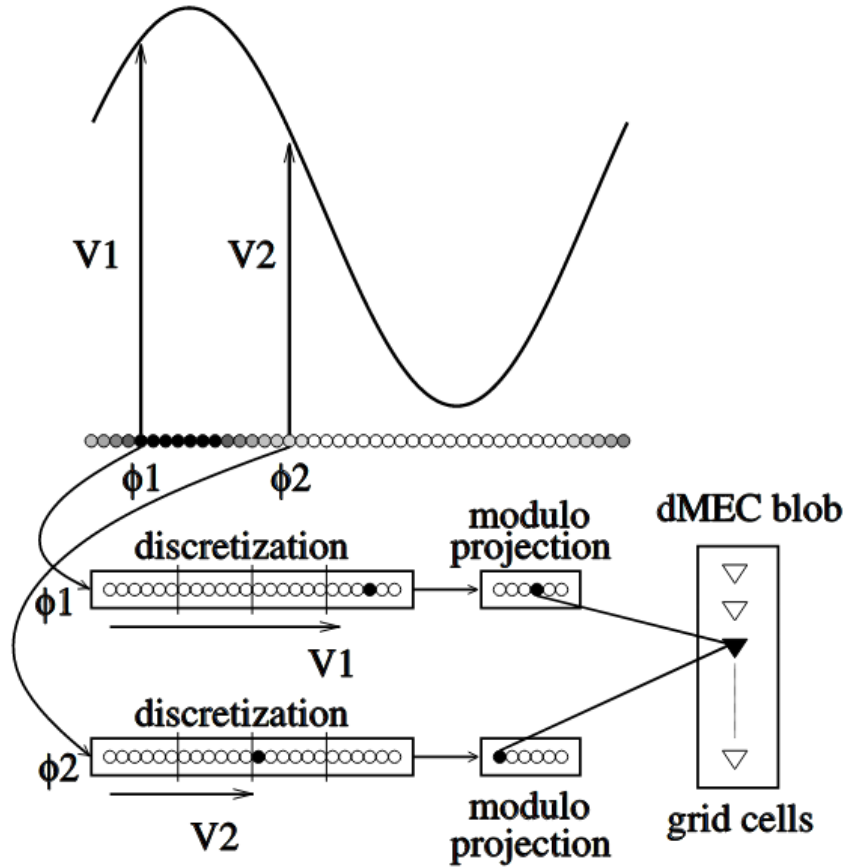

Figure 6: A neural network architecture used to build grid cells from path integration information (Gaussier et al., 2007)

2.4 Further work

One way that place cells can be remapped is by introducing a simulated agent to a new environment that has the same sensory cues as the original environment. For example, if an animal is trained to navigate a specific environment and the place cells in its hippocampus have become tuned to the features of that environment, introducing the animal to a new environment with the same sensory cues can cause the place cells to become active in the new environment as well. This process, known as "sensory remapping" (Gordon & Redish, 2010) allows the agent to use its existing spatial memory and navigation skills to explore and learn about the new environment.

It's also possible to observe the evolution of place cells organization and the evolution of the agent's origin while breaking the boundaries between two similar environments with the same sensory cues. For example, if the simulated agent is trained to navigate one environment and then given the opportunity to explore both that environment and a second environment with the same sensory cues, the place cells may begin to respond to locations in both environments. This process, known as "environmental remapping" (Wills & Redish, 2010) can allow the simulated agent to use its spatial memory and navigation skills to navigate both environments effectively.

By demonstrating the existence of hippocampal remapping for a simulated agent using the model described in the above subsections (Gaussier et al., 2007), we will be able to highlight the model's efficiency in terms of be able to evaluate the effectiveness of the model in terms of its ability to represent real-world navigation as well as its overall accuracy.

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