An Exploration of a Grid Cell Model

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Abstract—**Grid cells found in the brains of mammals exhibit periodic firing responses that encode animal locations. The error correction mechanism of Grid cell networks assists animals in making precise estimations of their current location. This report has replicated the work in [1] using Python. Additionally, we have conducted comprehensive explorations to determine how network size, spatial period, and noise influence the error correction ability of a given network, as well as to identify the optimal distance for maximum error correction ability.**

Index Terms—**Grid cell, Error Correction, Neural networks**

I. INTRODUCTION

Grid cells are nerve cells found in the medial entorhinal cortex (MEC) of the brain that aids in the navigation of mammals from one location to other. Unlike place cells in Hippocampus grid cells are not active for one specific location, rather they form a symmetric grid-like space as shown in Fig.1.a and are active at the center and edges of this space. These spaces are also formed under different combinations of grid scale, grid orientation, and grid phase as shown in Fig.1.b.

These grid mappings form a coordinate for the real-world environment and are also dynamically shifted in relation to the subject's movement. Experiments have confirmed that with the removal of visual or olfactory landmarks, the grid cell was able to retain its grid spaces, and grid cell pairs were able to maintain spatial firing relationships across different environments [2]. This implies that the grid cell representation primarily depends on the self-motion inputs and is secondary to stationary cues.

Being highly influenced by motion cues, grid cells along with place cells play a significant role in the path integration of mammals. Path integration is a process by which the spatial displacement between a reference point and the movement is calculated by integrating linear and angular running speeds over time (received from speed cells) [3]. With path integration associated with inputs from stationary cues mammals then determine their absolute position.

As mentioned earlier grid cells are located in the cortex which is a noisy system where the neurons exposed to repeated stimuli are often stochastic [4], and synaptic activation is probabilistic [5]. In the context of location encoding or path integration using the grid cells, the presence of noise can significantly affect the coordinate mappings of the grid cells. As the computation here is recursive, the noise can integrate and propagate through every time step, which eventually
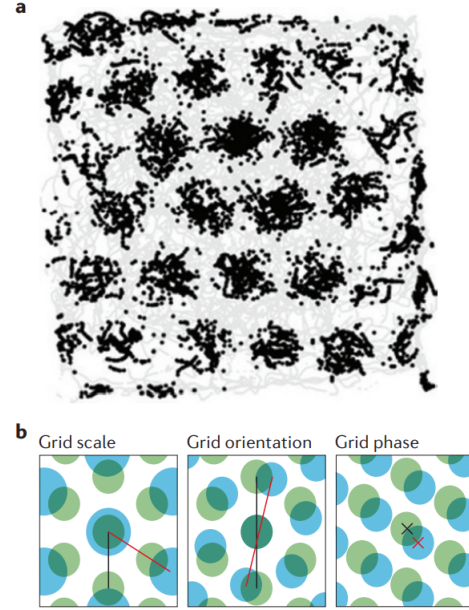

Fig. 1. a. This is the grid mapping/spatial firing pattern of a grid cell from layer II of the rat MEC in a 2.2 m wide square enclosure [6]. This firing rate mapping shows the periodic hexagonal pattern fields formed by the grid cells where a spike is represented by a single black dot. b. Demonstrating Grid field variations with two grid cell spiking. The first box shows the difference in grid-scale between two grid cells, the distance between the center of the grid space to the edges. The second one is the grid orientation which is the rotation of space, and then the grid phase where two grid cells have a phase shit in their grid spaces.

makes the representation incorrect. But how do Mammals able to perform these actions very precisely?

Sreenivasan and Fiete hypothesize that grid cells generate an analog error-correcting code-named Grid Population Code(GPC) to do accurate path integration over time [1].

II. THE GPC MODEL

To estimate the animal's changing location, the entorhinal cortex contains multiple sets of cells that respond with various spatial periods to be integrated. Each set is a network. Within the same grid-cell set, each neuron shares the same period but fires at different phases. A Grid Population Code (GPC) is an integration of coded locations for all networks. A population code generated by grid networks collectively encodes the target variable. This type of network model is commonly found in sensory, motor, and some cognitive areas [1], [7]–[11].
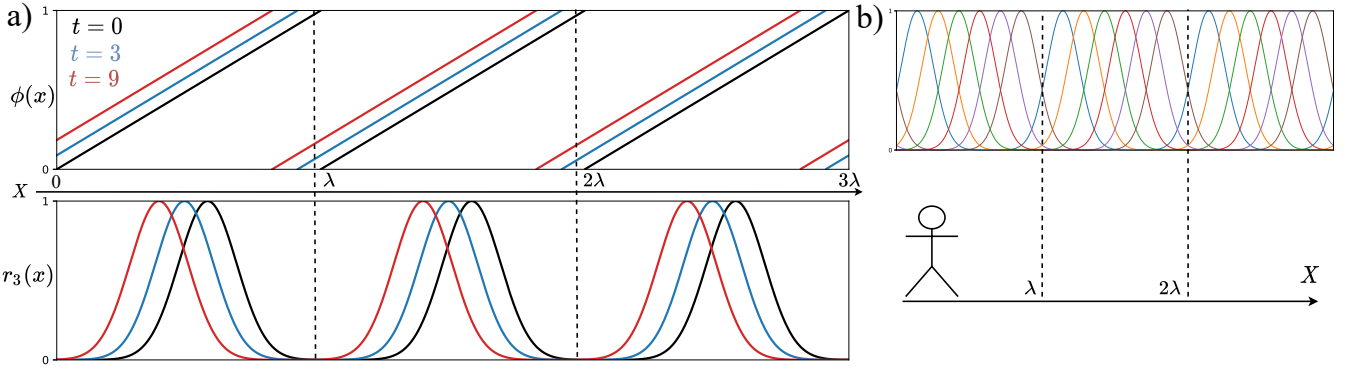
Fig. 2. a) Phase response (ϕ) and neural tuning curve for a single neuron shown over three spatial periods λ and over three different time steps, generated using our code. Noise results in a phase shift according to equation 2, and this in turn affects the neural tuning curve as shown in equation 3. Values of noise standard deviation were taken from [1]; the particular value used here is .04. b) Neural tuning responses for all neurons in the grid network over three spatial periods. Note how each neuron peaks at a different preferred periodic phase point as our person is at different distance x. Values of the neural tuning curve standard deviation were also taken from [1], the value used here is 0.11.
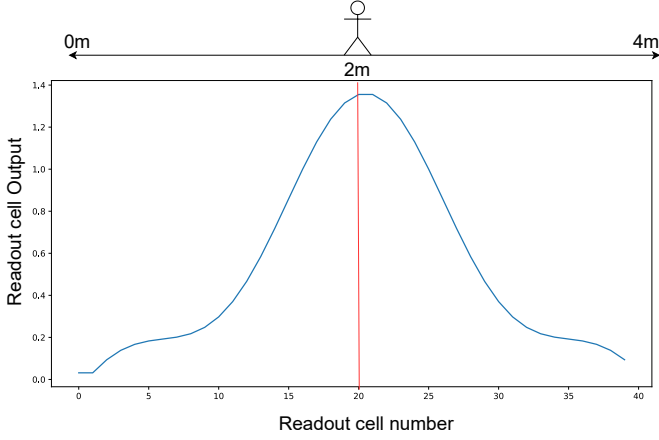

Fig. 3. A 2-layer neural network with 4 grid cell neurons each, is trained to find the input location in 4 meters of 1D space using 40 readout cells. Within the span of 4m, each readout cell represents a position with a 0.1m interval. An input location of 2m is given to the network and the response of the readout cells is shown, in which the 20th readout cell is highly active implying that the subject is at 2m.

Read-out cells will decode the GPC results and then generate the predicted locations.

A. Grid Network Model

In the model proposed in [1], a GPC network is made of N different networks which each have M neurons. Spatial information is encoded in the networks spatial phase, ϕ_α, which is in context of its spatial period, λ_α, where α will be our index term for one of the N networks in the GPC. If there is no noise present, an ideal network would have a phase response to animal location as

$$\phi_\alpha = \frac{x \bmod \lambda_\alpha}{\lambda_\alpha} \equiv \frac{x}{\lambda_\alpha} \bmod 1 \qquad (1)$$

Noise is modeled from two different sources. The first, readout error, is a zero-mean Gaussian noise that approximates

the uncertainty in detecting the phase of network α from a finite amount of spikes. The second, integration error, models the error between actual location $x(t)$ and the phase location that the GPC encodes and is a cumulative zero-mean Gaussian noise over time. These errors combine to create phase noise in the mathematical model as follows

$$\phi_\alpha(x,t) = \left(\frac{x(t)}{\lambda_\alpha} + \xi_\alpha^I(t) + \sum_{t'=0}^{t} \zeta_\alpha^I(t') \right) \bmod 1 \qquad (2)$$

From the calculated phase, [1] goes on to relate this to a neural tuning curve for neuron i in network α. The curve is approximated as Gaussian, and given by

$$f_\alpha(\phi, \phi_i^*) = e^{-\frac{||\phi - \phi_i^*||^2}{2\sigma^2}} \qquad (3)$$

where ϕ_i^* is the preferred phase of neuron i; these preferred phases are evenly distributed between 0 and 1. Fig 2 shows how tuning curves and phase of a network are distributed, and how they can be affected by noise.

B. Readout Cells

Readout cells are the final computation stage of the grid cell neural network. As in the brain, most of the decision-making computation is executed by Winner Take All (WTA) dynamics, the readout cells here also depict the same kind. The readout cell that is highly active inhibits the other readout cells in the network, where the winner readout cell encodes the location of the subject at that instantaneous time t. These cells are spread out across a 1D distance of Rl, with a large number of them distributed over the distance, possibly indicating their precise tuning to specific positions. Readout cells receive inputs from all the grid cells from each of the networks and a collective weighted sum of all the tuning curve responses from the grid cells is computed like a multi-layer perception shown in equation (4). And finally a softmax function, WTA is applied at the end (equation (5)).
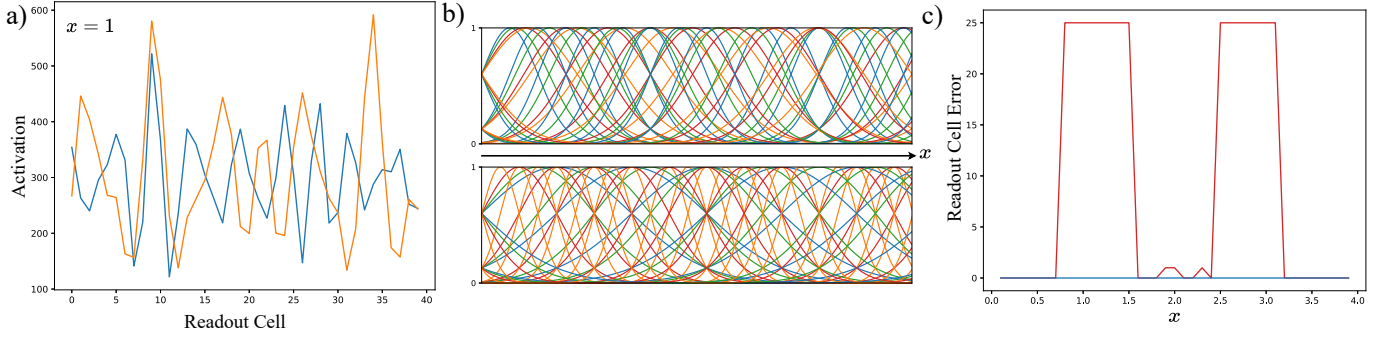
Fig. 4. a) Readout cell activations for two different sets of λ on an input of $x = 1$. The blue set correctly has a winner in readout cell 9 while the red curve has an error in a farther cell. Specifically the blue set has $\lambda = [.3, .36, .45, .51]$ while the red set has $\lambda = [.8, .6, .4, .2]$. b) The overlapping neural tuning responses of all neurons in each network for both trained GPCs. The top plot, corresponding to the blue curve in (a) and (c), has less overlap between networks than (c), and thus a more error-free response. c) Shows the error for different x with step sizes of 0.1m, from .1 to 4 meters for the two different networks.
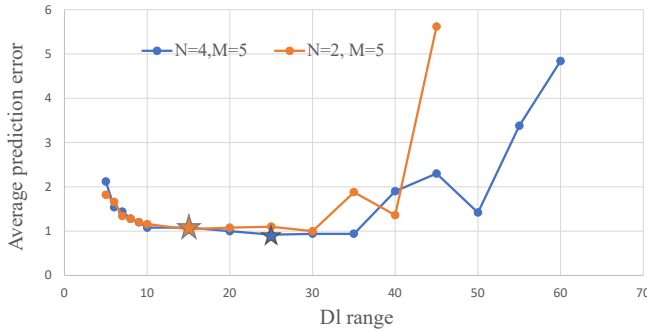

Fig. 5. This figure presents two configurations of the GPC networks' average error number under different Dl settings. The stars indicate the least error for each network. We can see the best Dl complies with equation (8). Another thing we can see is that a more complex network has more ability to encode a wider range of distances.

$$h_i = \sum_{ja} W_{ija} r_{aj}(x,t) + h_0 \qquad (4)$$

$$\hat{i} = argmax_i h_i \qquad (5)$$

In equation (4), a represents the network index, j is the index of neuron in ath network. h_0 is a constant containing non-grid cell information (inputs from external cues, learned priors, or inputs based on prediction).

Assuming the GPC network has p readout cells, $h_i(x,t)$ is the output that sums up corresponding inputs from all networks. x is the subject's location at instantaneous time t. $r_a i(x,t)$ is the tuning curve response of the i_{th} neuron in the a_{th} network. The h_i depends on the firing rate pattern r and learned grid cell–readout weights W. The weights are learned from the noiseless grid cell networks (which should be the ground truth). The weights are calculated once at the start using the Hebbian learning formulation, where the equation computes the weight values based on the grid cell's tuning curve peaks centered around the specific position $r_{aj}(\phi_a(x))$ with the readout neuron's local peak response in the location

$r_i(x)$ as indicated in equation (6). This shows that when the grid cell and readout cell for a specific position is highly active then the weight value is higher for this case compared to others, showcasing the Hebbian learning.

$$W(ija) = \sum_{x=0}^{Rl} r_i(x) r_{aj}(\phi_a(x)) \qquad (6)$$

The readout cells function as distance-encoded place cells, which become active specifically when the subject is located in the corresponding encoded position. Thus, we can infer the location by the index of the peak readout cell obtained from equation (7):

$$\hat{x}(t) = x_{\hat{i}} \qquad (7)$$

III. MODEL EXPLORATION

We had originally planned to explore readout with hierarchical neural networks, but implementation difficulties along with time constraints have not allowed us to do that. However, in the process of recreating this model ourselves we noticed several interesting features that were not discussed deeply in the original paper and have explored their effects on the grid code ourselves.

A. Redundancy in Spatial Periods

The basic idea behind the GPC is that location is encoded in different networks with various spatial periods λ, and then decoded with readout cells that span some total distance R_l. However we noticed that the choice of λ could affect even the idealized network response.

A GPC scheme was used with $N = 4$, $M = 8$ over a distance of $R_l = 4$m with 40 readout cells. While R_l should be much larger, we're approximating the learning of a large network on a smaller scale because of our limited computational power. As shown in Fig 4, the error massively changes for different spatial periods in the grid networks. Our explanation for the reason behind this is exemplified in Fig 4b: spatial periods can overlap in x, giving redundant information and leaving holes that cause errors.

B. Noise Error Correction

The original model [1] put assumed two kinds of noise in the system: integration error noise and readout error noise. Both noises follow zero-mean Gaussian distribution. The integration error accumulates as time goes by while the readout error does not. The paper mentions that under a limited $Rl << R$ but $Rl >> \lambda$, the network shows extraordinary robustness to noises. However, the paper doesn't provide a quantitative range of the correlation among Rl, R, networks number N, and neuron number M. After exploration, we found that when:

$$\hat{Rl} \approx (N+1)M \tag{8}$$

The error correction robustness is the best. Two example configurations of the networks are presented in figure 5.

We also explore the sensitivity of the network to distance sampling density. If the sampling step is too small that Δx is around 10^{-1} cm, the error correction is more likely to make wrong inferences on the ends of the 1D space. Intuitively, this reveals that when the observation is too fine-grain, simple grid cell networks can not distinguish the nuances between two locations that are close enough. And under this condition, the ends are more error-prone is an interesting discovery that might indicate that animal grid cells might be more sensitive to the center of the foraging range. However, we suggest more neuron-level experiments be conducted to validate this because we didn't find any literature to support this discovery.

IV. Conclusion

This report delves into the GCP networks and their error correction operation, as demonstrated in [1]. In addition to replicating the model, we have extended our investigation to explore other aspects of grid network design and limitations, such as network size, spatial period, noise robustness, and distance sensitivity. Based on our findings, we provide a quantitative equation to estimate the optimal distance range for particular network configurations. Moreover, we have discovered that the error correction of grid cells becomes insensitive to distances on the order of $10^{-1} cm$.

References

[1] S. Sreenivasan and I. Fiete, "Grid cells generate an analog error-correcting code for singularly precise neural computation," *Nature neuroscience*, vol. 14, no. 10, pp. 1330–1337, 2011.

[2] M. Fyhn, T. Hafting, A. Treves, M.-B. Moser, and E. I. Moser, "Hippocampal remapping and grid realignment in entorhinal cortex," *Nature*, vol. 446, no. 7132, pp. 190–194, Feb. 2007. [Online]. Available: https://doi.org/10.1038/nature05601

[3] A. S. Etienne and K. J. Jeffery, "Path integration in mammals," *Hippocampus*, vol. 14, no. 2, pp. 180–192, 2004. [Online]. Available: https://doi.org/10.1002/hipo.10173

[4] W. Softky and C. Koch, "The highly irregular firing of cortical cells is inconsistent with temporal integration of random EPSPs," *The Journal of Neuroscience*, vol. 13, no. 1, pp. 334–350, Jan. 1993. [Online]. Available: https://doi.org/10.1523/jneurosci.13-01-00334.1993

[5] C. F. Stevens and Y. Wang, "Changes in reliability of synaptic function as a mechanism for plasticity," *Nature*, vol. 371, no. 6499, pp. 704–707, Oct. 1994. [Online]. Available: https://doi.org/10.1038/371704a0

[6] E. I. Moser, Y. Roudi, M. P. Witter, C. Kentros, T. Bonhoeffer, and M.-B. Moser, "Grid cells and cortical representation," *Nature Reviews Neuroscience*, vol. 15, no. 7, pp. 466–481, Jun. 2014. [Online]. Available: https://doi.org/10.1038/nrn3766

[7] D. H. Hubel, *Eye, brain, and vision.* Scientific American Library/Scientific American Books, 1995.

[8] J. O'Keefe and J. Dostrovsky, "The hippocampus as a spatial map: preliminary evidence from unit activity in the freely-moving rat." *Brain research*, 1971.

[9] C. E. Schreiner, H. L. Read, and M. L. Sutter, "Modular organization of frequency integration in primary auditory cortex," *Annual review of neuroscience*, vol. 23, no. 1, pp. 501–529, 2000.

[10] J. S. Taube, R. U. Muller, and J. B. Ranck, "Head-direction cells recorded from the postsubiculum in freely moving rats. i. description and quantitative analysis," *Journal of Neuroscience*, vol. 10, no. 2, pp. 420–435, 1990.

[11] M. A. Wilson and B. L. McNaughton, "Dynamics of the hippocampal ensemble code for space," *Science*, vol. 261, no. 5124, pp. 1055–1058, 1993.