A Study Of Spatial Cell Representations In Complex Environment Using Oscillatory Networks

A project report

Submitted in partial fulfillment of the requirement for the award of the degree of

Dual Degree in Electrical Engineering (B.Tech and M.Tech)

Submitted by

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THESIS CERTIFICATE

This is to certify that the thesis entitled **" A Study Of Spatial Cell Representations In Complex Environment Using Oscillatory Networks"** submitted by **G Rajat Kumar** to the Indian Institute of Technology, Madras for the award of the degree of **Dual Degree in Electrical Engineering (B.Tech and M.Tech)** is a bona fide record of research work carried out by him under my supervision. The contents of this thesis, in full or in parts, have not been submitted to any other Institute or University for the award of any degree or diploma.

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ABSTRACT

The field of computational neuroscience seeks to break down the functioning of the internal biological processes of organisms. Many of these processes are involuntary and taken as a given from nature. One such process is how organisms locate themselves in an environment. Using previous models, which were based on a simplistic framework, this thesis applies a combination of Velocity Driven Oscillatory Networks (VDON) and Lateral Anti-Hebbian Network (LAHN) to more complex environments (trajectories) such as grid and mazes to infer the patterns of the simulated cell firings in the neural networks.

Keywords: *Place Cells. Grid Cells. Oscillatory Networks. Velocity Driven Oscillatory Networks. Locomotion Driven Oscillatory Networks. Lateral Anti-Hebbian Network.*

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Chapter 1

INTRODUCTION

1.1. A Basic Insight Into The Thesis

Survival of an animal depends on its ability to navigate the complexities of the environment it lives in and accurately estimating its location in the environment is central to this process. The animals (including us human beings) use sensory cues such as vision and proprioception (feedback from movement of limbs) to familiarize itself with the environment and thus locate itself in it. The unscrambling of the scientific processes that enable the animal to be inherently aware of its location has been a subject of constant query and research. When experiments were carried out on animals to investigate the neural architecture responsible for this, it was concluded that a hierarchy of neurons in the Hippocampus region of the brain that seemed to respond to the animal's position, speed and direction.

Further experiments done on animals navigating simple mazes revealed the manner in which the neurons in this hierarchical order are connected. Inputs from visual and proprioceptive neurons feed into sets of neurons called Self Organizing Maps (SOMs) which act as encoders to map the input onto a finite set of values. These two types of programmed inputs are then combined in the Sensory Integration (SI) layer using a weighted average, which depends on the dependability of incoming information. If there is enough light for reliable visual information, the visual SOM's value will dominate, and vice-versa. At this point, the SI layer's neurons have information on the direction and velocity of the animal (Soman, K., Muralidharan, V. & Chakravarthy, V.S. 2016)

The SI layer feeds into the Path Integration (PI) layer via one-on-one connections. As the name suggests, these neurons integrate the incoming velocity information, encoded in the form of phase difference w.r.t theta oscillations (constant, low frequency oscillations independent of Hippocampus). Finally, the PI layer feeds into a Lateral Anti-Hebbian Network (LAHN) of neurons in a fully connected manner. These neurons encode the incoming information in a manner similar to Principal Component Analysis. Ultimately, the LAHN neurons help the animal locate itself as these neurons fire only when the animal is in certain locations in the environment i.e. the firing patterns have relevant spatial information

(Soman, K., Muralidharan, V. & Chakravarthy, V.S. 2016). These "spatial cells" are the main subject of this study.

Study of the firing patterns of these LAHN neurons in different environments can help us better understand the way in which animals navigate their environments. This could eventually help us improve artificial techniques of navigation in inaccessible environments where conventional systems like GPS are not viable.

1.1.1. Spatial Cells

Grid cells and **place cells** are part of a space mapping circuitry that seems to be a constant across the spectrum of mammalian evolution. In the rodent families, the grid cells function as a mapping system which identifies any location the animal visits. A location independent coordinate map of multiple length scales to uniquely identify any space is created. The location independency of the map is an absolute form, it is reused in every situation. However, the coordinate map is not just one grid with fixed spacing between grid points. Instead, the coordinate map is composed of multiple grid layers, each with a different length scale between grid points - that is the distance between points on the grid is fixed in each grid layer, but different across layers. For example, one layer may have grid points spaced 54 cms apart and another layer may have grid points spaced 34 cms apart. This arrangement enables the location independent coordinate map to produce a unique identification for a location by combining the grid layers - the coactivity of the grid points from the different layers creates a unique combination of coactivity for any location the animal visits - and that is encoded in place cells. Coactivity of grid cells does not imply "spatial intersection" (firing at the same place) of grid cells from different layers, but “temporal intersection" (firing at the same time) of grid cells from the different layers.

A research article published in Science (Miller, Jonathan F., Markus Neufang, Alec Solway, Armin Brandt, Michael Trippel, Irina Mader, Stefan Hefft et al. 2013) gave impetus to the concept of spatial coding of the "place cell system". This gives further weight to the conceptualisation of spatial coding of the "place cell system" as part of a more general mechanism of storage of events in temporal sequence, where items become associated with their spatiotemporal context, and retrieval of items reinstates the context. This study was carried out on human subjects.

While most findings of this space mapping circuitry were observed in the rodent families, they have been also recently experientially seen in bats (Space Bats: Multidimensional Spatial Representation in the Bat, Science November 2013). Grid cells have been recognized in monkeys (A map of visual space in the primate entorhinal cortex Nature 2012) as well as in humans in a virtual reality task (Direct recordings of grid-like neuronal activity in human spatial navigation Nature 2013). Place cells in humans were known back in 2003 (Cellular networks underlying human spatial navigation Nature). Grid-like cells have been detected near the Avian Hippocampus although their exact location remains a subject of intense debate. (Neuronal implementation of hippocampus: Behavioral Cognitive Neuroscience Rev. 2006).

Where do grid and place cells lie in the hierarchy of information processing of visual input?

In Figure 1 below, place cells are right on top at the root node and are categorized as HC (Hippocampus) and grid cells are in ER (Entorhinal cortex), the child node of the root node HC.

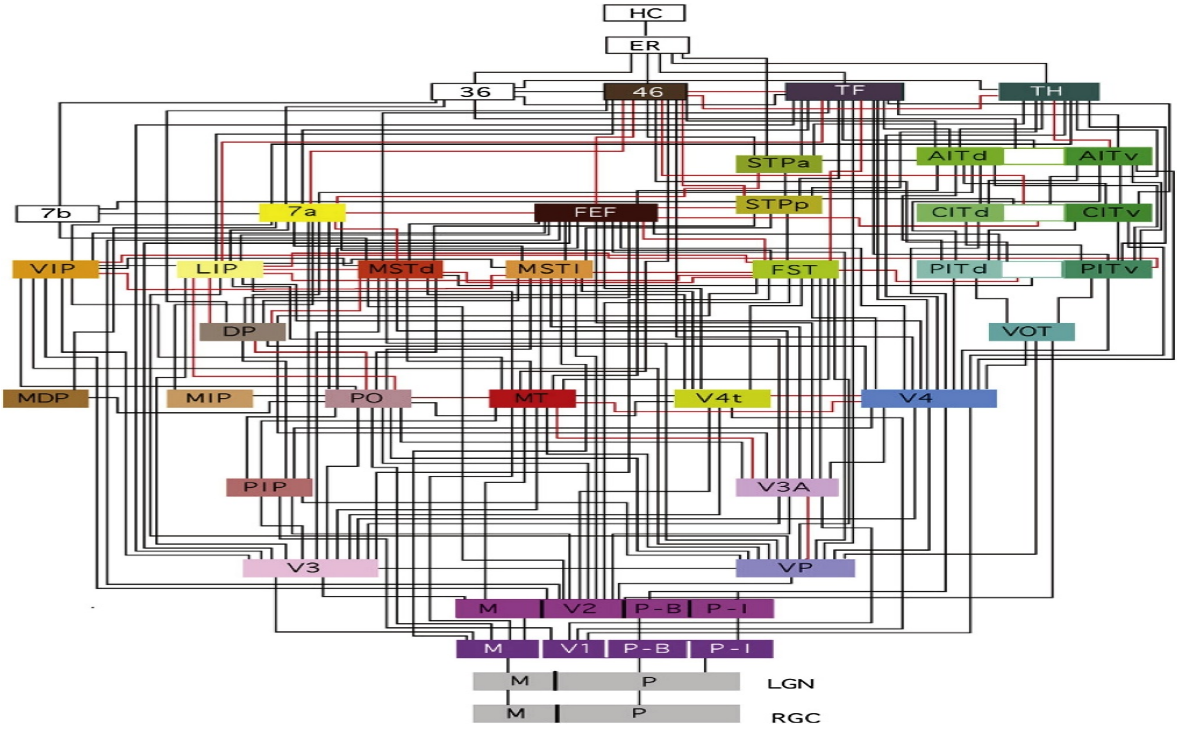


Figure 1. Connectivity of the visual cortex with visual input processing starting at the bottom and ending at the root node on top, HC (Hippocampus). (Cell. *www.cell.com- Grid Cells and Neural Coding in High-End Cortices*.)

The coordinate map:

Each grid cell will fire at fixed points creating a repeating triangular activity pattern (or coordinate map) creating a tiled representation of the complete locational space covered by the animal (Grid Cells and Neural Coding in High-End Cortices, Neuron October 30, 2013).

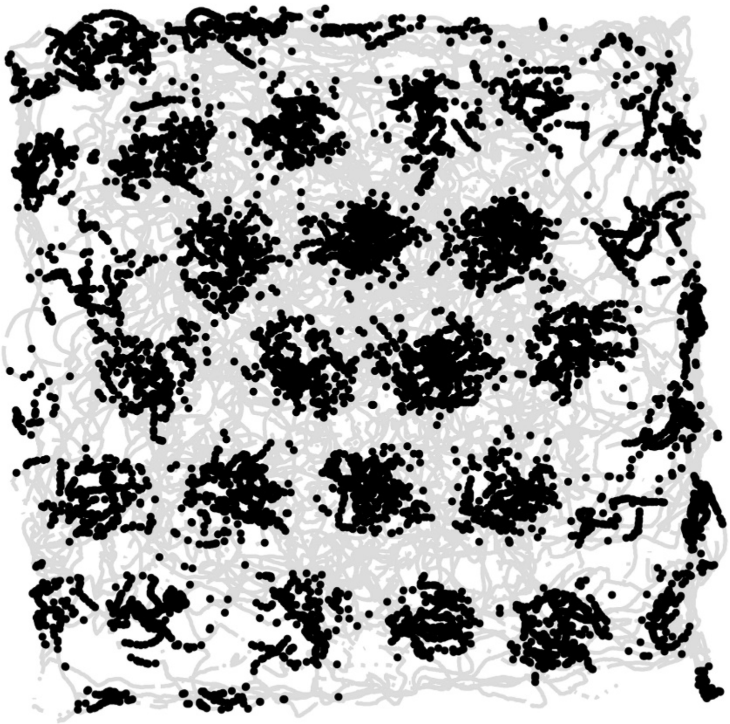


Figure 2. Recording from a single grid cell in Entorhinal Cortex (ER) of a rat brain. The gray trace is the trajectory of a rat that is foraging in a 2.2 m wide enclosure. Spike locations of the grid cell are superimposed on the track. Each black dot corresponds to one spike. Note the regular spacing between spike clusters. That is the length scale of this particular grid cell's coordinate map. The spiking pattern of this grid cell will be the same in a different environment - making the firing pattern of a grid cell location independent. A topographically adjacent grid cell may have a different length scale than this grid cell. (Cell.*www.cell.com- Grid Cells and Neural Coding in High-End Cortices*)

Each grid cell creates a coordinate map of a static length scale such that each spike is at the center of a hexagon separated from neighboring spike vertices by the same length. Thus, when an animal runs in an environment even in the dark, the spike pattern spacing remained the same regardless of the speed and direction of the animal, indicating that grid cells had access to path integration (computation of the negative value of a result vector that gives the sum of individual vectors, where each vector captures the speed and direction of the rodent. Also termed as '*dead reckoning'*). Alongside grid cells are **head direction cells** that fire specifically when the animal faces a certain direction regardless of location. Many head direction cells were also grid cells, firing only when the animal passed through the grid vertices with its head in a certain direction. There is a third type of cell, border cell, fired only when the animal was near one of the borders of the local environment, such as a wall or an edge. Grid cells, head direction cells, and **border cells**, together form an overlay coordinate map over the space covered by an animal as it moves around in its environment.

Moving on to the second type of cell being deal this in this thesis, **Place cells** are neurons in the hippocampus that fire when the animal occupies a specified location within its environment. As different place cells have different place fields (locations where they fire), they are thought to provide a cognitive map for the rat. A given place cell will have only one, or a few, place fields in a typical small laboratory environment, but more in a larger region (Fenton 2008). There is no apparent topography to the pattern of place fields, unlike other brain areas such as visual cortex—neighboring place cells are as likely to have nearby fields as distant ones (O'Keefe 1998). In a different environment, typically about half the place cells will still have place fields, but these will be in new places unrelated to their former locations.

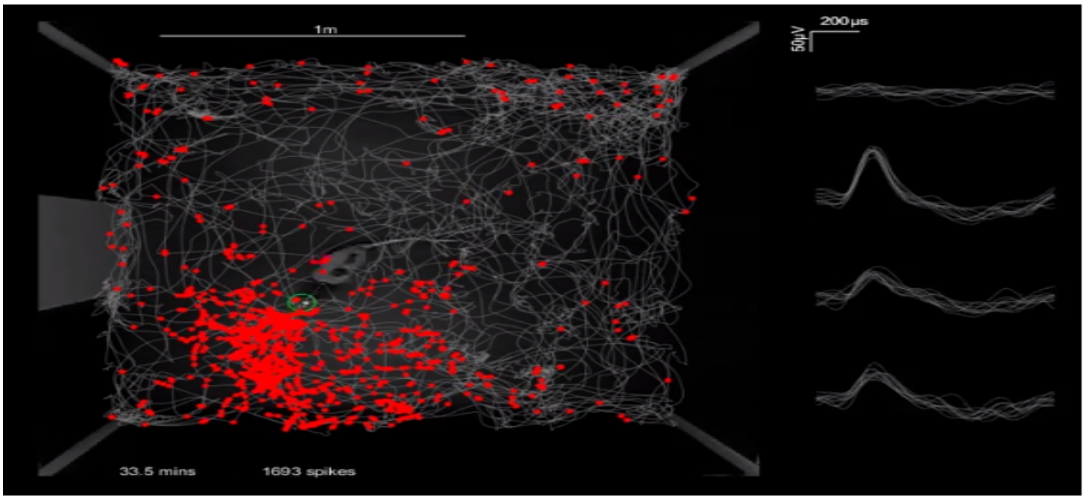


Figure 3: A place cell recorded (wirelessly) as a rat explores a square open field environment. This cell has a place field towards the bottom left of the enclosure. More often than not when the rat visits this location the cell fires, which is indicated by the red markers. The waveforms of the last 10 action potentials can also be seen to the right of the camera feed. *(Youtube: www.youtube.com- Place Cell Recorded at University College London, in the Institute for Behavioural Neuroscience by Professor Kate Jeffery,2017)*

Place cells are thought, collectively, to act as a cognitive representation of a specific location in space, known as a cognitive map. Place cells work with other types of neurons in the hippocampus and surrounding regions to perform this kind of spatial processing, but the ways in which they function within the hippocampus are still being researched. Studies with rats have shown that place cells tend to fire quickly when a rat enters a new, open environment, but outside of a firing field, place cells tend to be relatively inactive (Bures 1997). Together place cells are thought to form a "cognitive map" in which they have localized firing patterns called place fields (Jeffery 2007). External sensory information and the local environment often determine place cell firing patterns. Place cells have proven to have the ability to suddenly change their firing pattern from one pattern to another, a phenomenon known as "re-mapping" and though place cells do change according to the external environment, they are stabilized by attractor dynamics which "enable the system to resist small changes in sensory input but respond collectively and coherently to large ones" (Jeffery 2007).

Although place cells are part of a non-sensory cortical system, their firing behavior is strongly correlated to sensory input. Place cells fire when an animal is located in parts of the environment known as place fields (Smith 2006). These circuits may have important implications for memory, as they provide the spatial context for memories and past experiences (Smith 2006). Like many other parts of the brain, place cell circuits are dynamic. They are constantly adjusting and remapping to suit the current location and experience of the brain. Place cells do not work alone to create visuo-spatial representation; they are a part of a complex circuit that informs place awareness and place memory (Smith 2006).

1.1.2. Oscillatory Networks

An oscillatory neural network (ONN) is an artificial neural network that uses coupled oscillators as neurons. Oscillatory neural networks are closely linked to the **Kuramoto** model, and are inspired by the phenomenon of neural oscillations in the brain. These are assemblages of neurons responsible for a wide variety of periodic behavior patterns. Most of the current understandings about the neuronal basis of rhythmic behaviors has been derived from the analysis of oscillatory neural networks in invertebrates. With invertebrates it is possible to identify component cells and synapses and work with them repeatedly. These kind of networks are those capable of generating oscillatory activity without requiring some sensory input, although many do require some form of tonic excitation. Such networks are commonly referred to as Central Pattern Generators (CPGs), and the goal of most efforts towards their analysis has been to explain their operation in terms of the cellular and synaptic properties of the neurons involved. To fully consider oscillatory networks, it will not only be necessary to examine their mechanisms when completely isolated but also when under the influence of neuro-modulatory pathways.

1.2. Objective Of The Work

This thesis attempts an investigation of the current prevalent models to further the understanding of neural network and then to help bring into focus the locationalization capabilities of animals. These objectives are further elaborated as follows:

1. To analyze the oscillatory model and its advantages over the other models available.

2. To study the neuron firings in custom built trajectories (maze/grid) in L1, L2, L3 layers of LAHN.

3. To find any new kind of cell firings in various layers of and study their predominance and direction dependence.

4. To broaden the scope to include more possible complex environments and their respective cell firings

Chapter 2

LITERATURE REVIEW

2.1. Introduction

Spatial cells in the hippocampal complex play a pivotal role in the navigation of an animal but the precise neural principles guiding these spatial cell responses have not been completely understood. For the purposes of this thesis, we look at two models for spatial cells, namely the **Velocity Driven Oscillatory Network (VDON)** and **Locomotor Driven Oscillatory Network**. Both models have three stages in common such as direction encoding stage, path integration (PI) stage, and a stage of unsupervised learning of PI values. In the first model, the following three stages are implemented: head direction layer, frequency modulation by a layer of oscillatory neurons, and an unsupervised stage that extracts the principal components from the oscillator outputs. In the second model, a refined version of the first model, the stages are extraction of velocity representation from the locomotor input, frequency modulation by a layer of oscillators, and two cascaded unsupervised stages consisting of the **Lateral Anti-Hebbian Network**. The principal component stage of VDON exhibits grid cell-like spatially periodic responses including hexagonal firing fields. Locomotor Driven Oscillatory Network shows the emergence of spatially periodic grid cells and periodically active border-like cells in its lower layer; place cell responses are found in its higher layer. This model shows the inheritance of phase precession from grid cell to place cell in both one- and two-dimensional spaces. It also shows a novel result on the influence of locomotion rhythms on the grid cell activity. The study thus presents a comprehensive, unifying hierarchical model for hippocampal spatial cells.

2.2. Background

Whenever the animal finds itself in a recognizable region, the place cells fire. This unearthing ensued the discovery of a larger class of hippocampal cells that represent space, collectively known as the ‘spatial cells’ (O'Keefe & Dostrovsky, 1971; Taube et al., 1990a,b; Hafting et al., 2005; Solstad et al., 2008). Taube et al. (1990a) discovered a group of neurons from the postsubiculum region that fired only when the animal's head was in a particular direction in the horizontal plane (yaw plane) (Taube et al., 1990a,b). These so-called head direction (HD) cells are thought to constitute an ‘internal compass’ that give a sense of direction to the animal (Valerio & Taube, 2012). Hafting et al. (2005) described a group of neurons in medial entorhinal cortex (MEC) that had a firing field with an astonishingly geometric regularity: multiple firing fields of a single neuron of this type roughly formed the *vertices of a hexagon*. As the firing field tessellated the ambient space into a hexagonal grid-like pattern, they were named the grid cells.

Efforts have been made to gain insight into spatial cell responses using computational models. With regard to grid cell modeling, existing models fall into two broad categories: oscillatory interference (OI) models and attractor network models. In the OI model, originally proposed for place cells by O'Keefe & Recce (1993), two subthreshold membrane potential oscillations (MPO), one with constant frequency and the other with variable frequency which in turn was a function of the velocity of the animal, were considered. The interference between them resulted in patterns that gave rise to spiking over spatially periodic locations. This was extended to explain the grid field formation on a two-dimensional space (Burgess et al., 2007). To account for the triangular/hexagonal grid formation, the directional modulation of the variable oscillations was assumed to differ by multiples of 60°.

Many variations of this model have been proposed which use coupled noisy spiking neurons instead of sinusoidal oscillators as VCOs, to generate the grid firing fields, and these models were also validated using experimental data (Blair et al., 2008; Hasselmo, 2008; Zilli & Hasselmo, 2010). The merit of interference models is that the resetting of path integration (PI) takes place naturally because of the inherent periodicity in the oscillations rather than using hard resets like modulo functions (Gaussier et al., 2007). These models also successfully explained many grid cell data and also came up with predictions on grid-scale variation. However, the drawback in these models was the assumption of 60° constraints on the direction modulation of the oscillators. There were modeling efforts to circumvent the aforementioned constraint problem such that 60° phase separation was formed through a self-organizing process (Mhatre et al., 2012). However, these models had a predisposition to explain specifically the grid field formation and could not explain the principle behind the formation of other spatial cells.

2.3. Methods

We study two models of spatial cells: Velocity Driven Oscillatory Network (VDON) and Locomotion Driven Oscillatory Network (LDON). VDON explains how the periodicity arises in the spatial cell responses although there is no periodicity in the input, nor is there any special symmetry in the network architecture. LDON is a refinement of VDON to produce spatial patterns more in agreement with the neurophysiology.

Both models have three common architectural elements viz. direction encoding layer/HD layer, PI layer, and layer of unsupervised neural network. Both models do not use any special symmetry in the HD layer. The HD layer responses are integrated in the next layer known as the PI layer. The PI layer in turn projects, via trainable connections, to another layer where a variety of spatial cells, particularly a variety of grid cells, naturally emerge.

A virtual animal is made to forage inside a square box of size two units. Trajectories of the animal, that involve an upper limit on curvature, are constructed. In VDON, the virtual animal is represented as a point, and its motion is represented explicitly in terms of speed, s, and direction, θ. In LDON, the virtual animal is represented as a four-legged creature and motion is represented in terms of four locomotor rhythms generated by the legs.

2.4. Velocity Driven Oscillatory Network

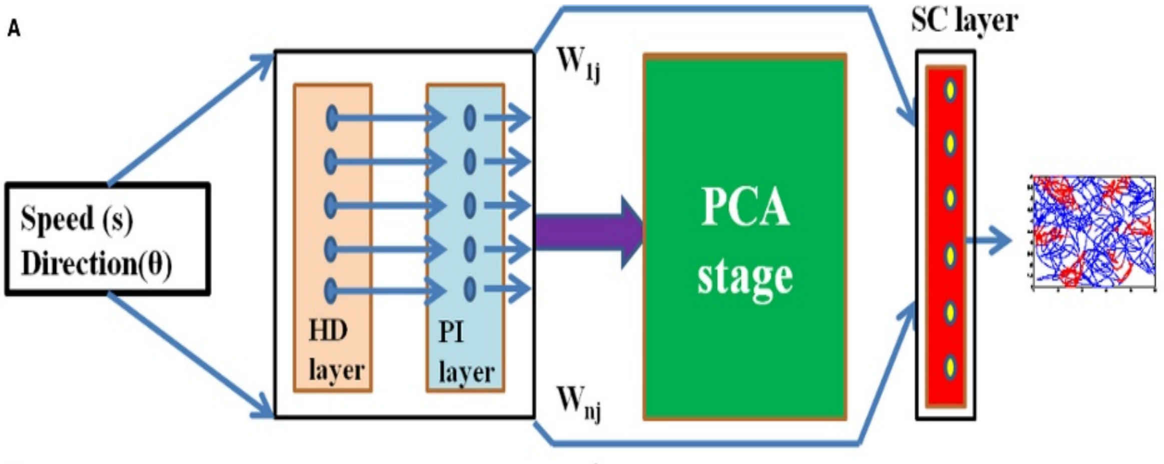


Figure 4. The network architecture of VDON including the head direction layer, followed by path integration and finally performing principal component analysis for the evolution of different spatial cells. (*Soman 2018*)

Head direction layer

Head direction layer is composed of array of neurons each having its own preferred direction. The response of ith HD cell is computed as the projection of the animal's current direction onto the ith preferred direction, given as,

$$HD_i = \cos(\theta - \theta_i)$$

where θ is the current heading direction of the animal, and θi is the preferred direction of ith HD cell.

Path integration layer

Path integration layer has an array of oscillators with one-to-one connection with the HD layer. To achieve PI, the frequency of the oscillator is modulated by the speed and the HD layer response. Hence, phase of the ith oscillator codes for the position of the animal in that preferred direction. This completes the PI process. Interference model also implemented position encoding using the phase of the velocity-controlled oscillators (VCO) (Burgess et al., 2007). Comparison to interference model is performed in the discussion section in detail. Frequency modulation of ith PI oscillator with a base frequency f_0 is given as

$$\mathrm{PI}_i = \sin\left[\int 2\pi(f_0 + \beta s \mathrm{HD}_i)\mathrm{d}t\right]$$

where β is the modulation factor, and s is speed of the animal.

State of ith PI neuron, PIi, is then thresholded by the following rule,

$$\mathrm{PI}_i^{\mathrm{Thr}} = \mathrm{H}(\mathrm{PI}_i - \varepsilon_{\mathrm{PI}}) \cdot \mathrm{PI}_i$$

where, H is the Heaviside function, and $\varepsilon_{\mathrm{pi}}$ is the threshold value.

Spatial cell layer

Spatial cell layer represents the region of Entorhinal Cortex (EC) to which the PI response vector converges as input (Fig. 1A). The thresholded PI values are projected via a linear weight stage (W^{PC}) to the SC layer. Weight (W^{PC}) from PI to SC neuron is computed by performing principal component analysis (PCA) over PI^{Thr}. PCA was performed analytically by extracting the top few Eigen vectors (selected based on the Eigen value spectrum) of the covariance matrix of the PIThr (Karhunen & Joutsensalo, 1995). The response of ith neuron in the SC layer is given as,

$$\mathrm{SC}_i = \sum_{j=1}^{N} \mathrm{H}\left[W_{ij}^{\mathrm{PC}} \cdot \mathrm{PI}_j^{\mathrm{Thr}} - \varepsilon_{\mathrm{SC}}\right]$$

where H is Heaviside function, N is the number of PI neurons, and ε_{SC} is the threshold value. W_{ij}^{PC} is the weight connection from jth PI neuron to ith SC neuron.

Neurons receiving the top few principal components (PC) will be shown to reveal a variety of spatial cell-like responses including grid cells (both hexagonal and square grid cells) and corner cells (whose firing fields are at the corners of the space) as shown in the results section. The emergence of spatially periodic firing field is due to the inherent periodicity in the PC weights The neurons that receive PCs whose peaks are separated by ≈60° show hexagonal grid cell-like activity. The current PCA approach has some resemblance to the model of Dordek et al. (2016) which used PCA to produce grid formation from place cell activity.

2.5. Lateral Anti-Hebbian Network (Lahn)

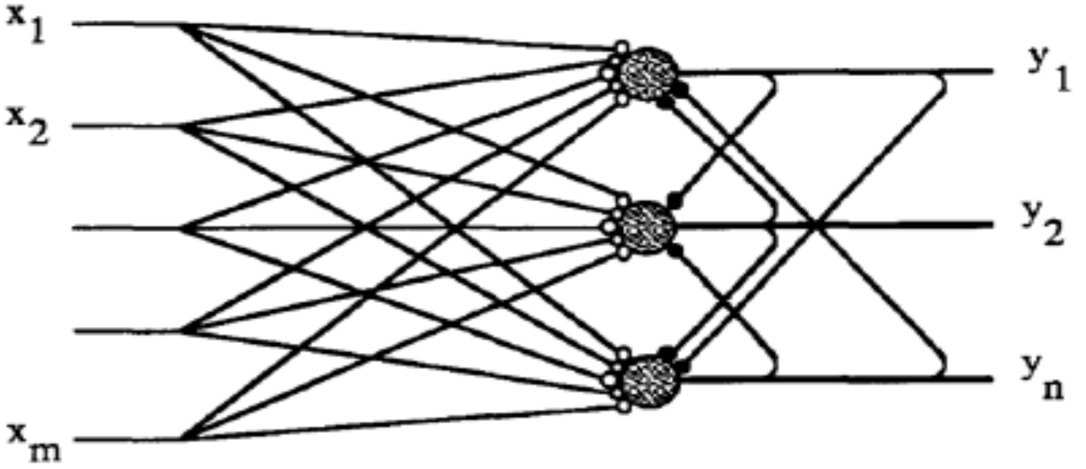


Figure 5. A sample LAHN. White circles - Hebbian connections. Black circles - anti Hebbian (*ResearchGate: Bahroun, Yannis.Hebbian/Anti-Hebbian Network with Lateral Connections. 2017*)

The LAHN is a set of neurons connected to each other such that incoming inputs are connected in a Hebbian manner (forward weights) and connections between neurons are connected in an anti-Hebbian manner (lateral weights). The anti-Hebbian connections act as a decorrelation network, removing correlations between incoming inputs as far as possible (P.Foldiak 1989). As a result, the LAHN acts as an effective dimensionality reduction network while maintaining maximum mutual information flow between input and output. Similar to PCA, this network projects the input onto a subspace of its largest principal components (dimensions with greatest variance) having least cross-correlation between them.

Training this network happens in an unsupervised manner, using simple localized rules for modification of connection weights. Not only is the training faster this way, it is also biologically more plausible than classical error propagation rules. The network training is said to have converged when the maximum change in weight of a connection (both forward and lateral) is less than a specified threshold.

The output of each neuron is as follows:

$$y_i = \sum_{j=1}^{m} q_{ij} x_j + \sum_{j=1}^{n} w_{ij} y_j$$

where wij and qij are forward and lateral weights respectively.

Written in matrix form:

$$\mathbf{y} = \mathbf{Qx} + \mathbf{Wy}$$

$$\mathbf{y} = (\mathbf{1} - \mathbf{W})^{-1} \mathbf{Qx}$$

During training, the rules for modification of these weights are as follows:

$$\Delta w_{ij} = -\alpha y_i y_j$$

$$\Delta q_{ij} = \beta (x_j y_i - q_{ij} y_i^2)$$

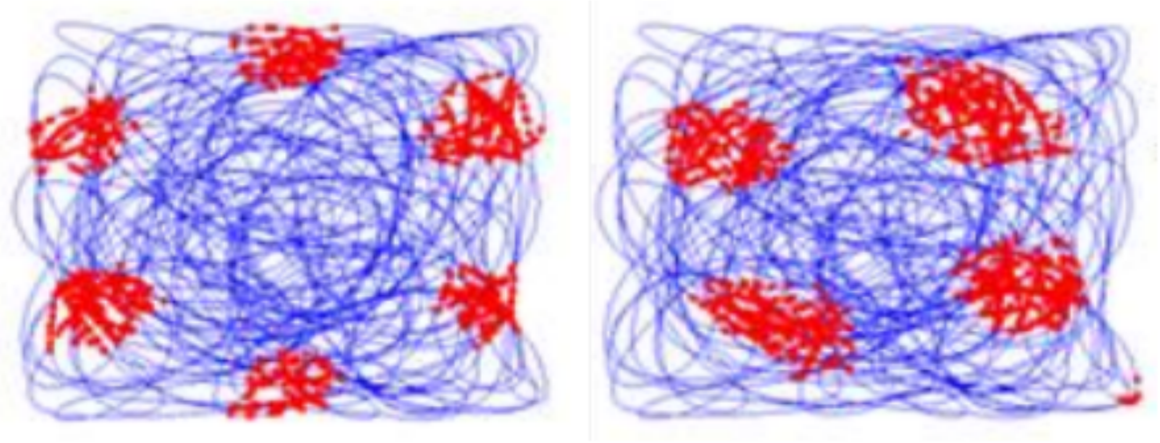
where α and β are the learning rates for each connection.

In the full model of the neural architecture, there are two sets of LAHNs - the spatial cell layer $\mathrm{LAHN_{SC}}$ and the place cell layer $\mathrm{LAHN_{PC}}$, each producing different types of firing fields. The simplified model, on the other hand, has just one layer of LAHN neurons.

2.6. Previous Work

Previous experiments and model simulations have been done in which the animal is constrained to a 2D plane (rats). The neuron firing fields obtained from the simulations contain a set of points where the neuron fires. This needs to be converted into a 2D map of strength of activation of the neurons at these points. The entire environment is divided into bins and if a point in the firing field exists in that bin, its value is increased. Cell firings are categorized as:

1. **Place cells** - These cells only fire when the animal is in the vicinity of a particular point in the environment.
2. **Grid cells** - These cells only fire when the animal is on the vertices of a repeating pattern on the environment. These repeating patterns may be overlapping hexagons or squares.
3. **Border cells** - These cells only fire when the animal is in the vicinity of a border of the environment.



(a) Hexagonal grid cell (b) Square grid cell

Figure 6: Sample firing fields of different LAHN neurons. Red dots indicate neuron firing at that location (*Soman 2018*)

Chapter 3

EXPERIMENTAL DETAILS

3.1. Methodology

This thesis employs a theoretical outlook to devise simulations for the above given problem statement on the basis of previous work carried out in this domain. We have drawn heavily from the work done by neuro-scientists to give a holistic bass to the coded work to root in the essential domain of biology. We look at the various steps involved in the methodology including a few code snippets showing the parameters involved. The whole methodology can be divided into four broad steps:

1. **Maze/Grid generation:** Building bounding boxes for custom trajectory generation

2. **Trajectory Generation:** Random trajectory generation in the generated bounding box with emphasis to continuity

3. **All cell firing fields:** Finding all neuron findings in L1, L2, L3 layers of LAHN

4. **Plots:** Devising a polar plot to check the direction dependency of the neuron firings

3.2. Maze/Grid Generation

We begin with the generation of the bounding box for our maze. The outer dimensions are 3x2.2 units rectangular with two boxes inside of size 1x1 spaced 0.2 units apart. The code snippet used for the maze generation is as follows:

```
sz=1;
delta=0.2;
[xbox,ybox]= sqrspc(sz);
[xbox1,ybox1]= sqrspc(sz);
xbox1=xbox1+1.2;

xbox_out=[1 1+2*sz+3*delta 1+2*sz+3*delta 1 1];
ybox_out=[1 1 1+sz+2*delta 1+sz+2*delta 1];
xbox_out= xbox_out-delta;
ybox_out= ybox_out-delta;

plot(xbox,ybox);hold on
plot(xbox1,ybox1);
   plot(xbox_out,ybox_out);
```

Snippet 1: Code showing the generation of bounding box. Here delta is the distance between the inner boxes and sz a unit length of 1.

3.3. Trajectory Generation

Our trajectory involves the subject making 4 iterative rounds around each inner box and 4 iterative rounds around the bigger box in a clockwise-anticlockwise manner. We use four functions namely leftgrid, rightgrid, cgrid_up and cgrid_down to direct the trajectories in each of their respective directions and leftgrid_ac and rightgrid_ac for anti-clockwise

```
for i=1:4
[xhist,yhist,prev_x,prev_y,x,y]=leftgrid_ac(prev_x,prev_y,x,y,sz);
x_left=[x_left xhist];
y_left=[y_left yhist];
[xhist,yhist,prev_x,prev_y,x,y]=cgrid_up(prev_x,prev_y,x,y,sz);
x_left=[x_left xhist];
y_left=[y_left yhist];
[xhist,yhist,prev_x,prev_y,x,y]=rightgrid(prev_x-1.2,prev_y,x-1.2,y,sz);
x_left=[x_left xhist+1.2];
y_left=[y_left yhist];
[xhist,yhist,prev_x,prev_y,x,y]=cgrid_up(prev_x+1.2,prev_y,x+1.2,y,sz);
x_left=[x_left xhist];
y_left=[y_left yhist];
end
```

direction.

Snippet 2: Code showing the iterative rounds around a single inner box for four times.

3.4. All Cell Firing Fields:

We generate three data files from the trajectory generation section viz. a coordinates file, head direction file and speed file. These files contain data in matrices enclosing the trajectory coordinates, the angle of the head direction (θ) and speed of the animal (s). We load this data in our model and feed the values to the HD layer to compute the HD responses.

```
%% HD response computing
speed = speed';
phase1d = zeros(100,1);
X=[];
 trj_hd_resp=[];
for ii = 1:size(speed,2)
    X1 = [cosd(theta_real_deg(1)) sind(theta_real_deg(1))]; X2 =
[cosd(theta_real_deg(ii)) sind(theta_real_deg(ii))];
    s1 = X2(1)*X1(2) - X1(1)*X2(2);  %sin(theta1-theta2)
    s2 = X2(1)*X1(1) + X1(2)*X2(2);  %cos(theta1-theta2)
    X=[s1 s2];
    y = respsom2dlinear(X,wt2);
    trj_hd_resp(:,:,ii) = y;
    ii
   end
```

Snippet 3: Computation of HD layer response

We feed the speed values and the HD layer responses to the PI layer.

```
%% PI osc
X = zeros(100,1); Y = ones(100,1); %Xarr=[]; Yarr=[];
dt = 0.01;
bf = 6*2*pi;
niter = size(trj_hd_resp,3);
betaa = 55; t = 0;
Xbg = 1; Ybg = 0;
tarr=[];
theta=zeros(100,1);
for ii = 2:niter
    ii
    y = trj_hd_resp(:,:,ii);
    inp1d = reshape(y,100,1);
    thetadot = bf + betaa*speed(ii)*inp1d*10;
    theta(:,ii)=theta(:,ii-1)+thetadot*dt;
   end
```

Snippet 4: Oscillatory output from the PI layer

We continue to perform PCA using the LAHN with an output neuron number of 25. The LAHN takes 2 iterations to converge. Loading the weights, we continue to find the neuron firings in L1 layer of the LAHN.

```
%% All cell firing field
load('L1-boxgrid2-weights.mat')
figure
% foldiak1respmat=[];
for ii=1:size(T,1)
    subplot(5,5,ii); w=T(ii,:);w = w';
    ot=w'*(PI1d); ot=ot';
    thresh=max(ot)*.65;
    firr=find(abs(ot)>thresh);
    foldiak1respmat(ii,:) = ((abs(ot)>thresh).*ot)';
    firposgrid=pos(firr,:);
    plot(pos(:,1),pos(:,2)); hold on;
plot(firposgrid(:,1),firposgrid(:,2),'.r', 'markersize', 10);
   end
```

Snippet 5: Plotting the neuron firings in the L1 layer of LAHN with a set threshold of 65%

We continue to perform PCA using LAHN for the second layer with an output neuron number of 16. The LAHN takes two iterations to converge. Loading the weights for L2, we continue to find the neuron firings in L2 layer of the LAHN.

```
%% All cell firing field
load('L2-boxgrid2-weights.mat')
figure
% foldiak1respmat=[];
for ii=1:size(T,1)
    subplot(4,4,ii); w=T(ii,:);w = w';
    ot=w'*(PI1d); ot=ot';
    thresh=max(ot)*.75;
    firr=find(abs(ot)>thresh);
    foldiak1respmat(ii,:) = ((abs(ot)>thresh).*ot)';
    firposgrid=pos(firr,:);
    plot(pos(:,1),pos(:,2)); hold on;
plot(firposgrid(:,1),firposgrid(:,2),'.r', 'markersize', 10);
   end
```

Snippet 6: Plotting the neuron firings in the L2 layer of LAHN with a set threshold of 75%

We continue to perform PCA using LAHN for the second layer with an output neuron number of 9. The LAHN takes two iterations to converge. Loading the weights for L2, we continue to find the neuron firings in L2 layer of the LAHN.

```
%% All cell firing field
figure
% foldiak1respmat=[];
for ii=1:size(T3,1)
    subplot(3,3,ii); w=T3(ii,:);w = w';
    ot=w'*(foldiak1respmat1); ot=ot';
    thresh=max(ot)*.85;
    firr=find(abs(ot)>thresh);
    foldiak1respmat2(ii,:) = ((abs(ot)>thresh).*ot)';
    firposgrid=pos(firr,:);
    plot(pos(:,1),pos(:,2)); hold on;
plot(firposgrid(:,1),firposgrid(:,2),'.r', 'markersize', 10);
   end
```

Snippet 7: Plotting the neuron firings in the L2 layer of LAHN with a set threshold of 85%

3.5. Plots:

In order to check for direction dependency of the neurons firing at the junctions we construct a polar plot and analyze the plot to check for firings in a particular direction among all the cells.

```
%% polar plot

for ii = 1: length(c)
    w=TT(Neuron_numbers(ii),:);w = w';
    ot=w'*PIpd; ot=ot';
    thresh=max(ot)*.75;
    firr=find(abs(ot)>thresh);
    foldiak1respmat(Neuron_numbers(ii),:) = ((abs(ot)>thresh).*ot)';
    firposgrid=pos(firr,:);
    dis = [];
    ang = [];
    c_x = 0;                      %@@@@@@@
    c_y = 0;                      %@@@@@@@
    cx = [c_x,c_y];
    Obj = repmat(cx , [length(pos) 1]);
    dis = pdist2(pos , cx);

    for i = 1:length(pos)
        a = atan2(pos(i,2)-c_y , pos(i,1)-c_x);

        ang = [ang; a ];
            [theta,rho] = cart2pol(pos(i,1),pos(i,2));

    end

        % load(['firr' num2str(i) '.mat']);
        dis_f = dis(firr);
        ang_f = ang(firr);
        figure ;
        polar(ang_f,dis_f,'.r');


        thetaticks(0:5:360);
        rticks(0:0.005:0.12);
        Ax = gca; % current axes
%         Ax.ThetaGrid = 'off';
%         Ax.RGrid = 'off';
        Ax.RTickLabel = [];
        Ax.ThetaTickLabel = [];
        title (['Neuron :  ' , num2str(Neuron_numbers(ii)), 'Object at
', num2str(cx)])
end
```

Snippet 8: The code for plotting a polar plot for all the cell firings at the junction with an offset of 0.1 units for the L2 layer

Chapter 4

RESULTS AND DISCUSSION

4.1. Results For Maze:

We will be looking at stepwise results in this section for maze bounding box and trajectory generated as followed in the methodology.

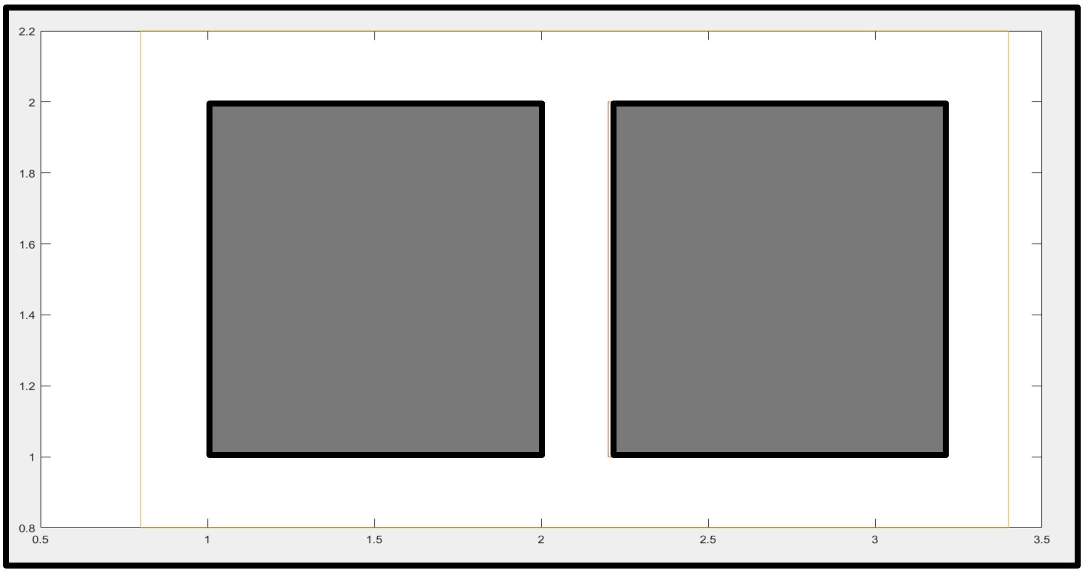


Figure 7: The maze outline generated from Section 3.2

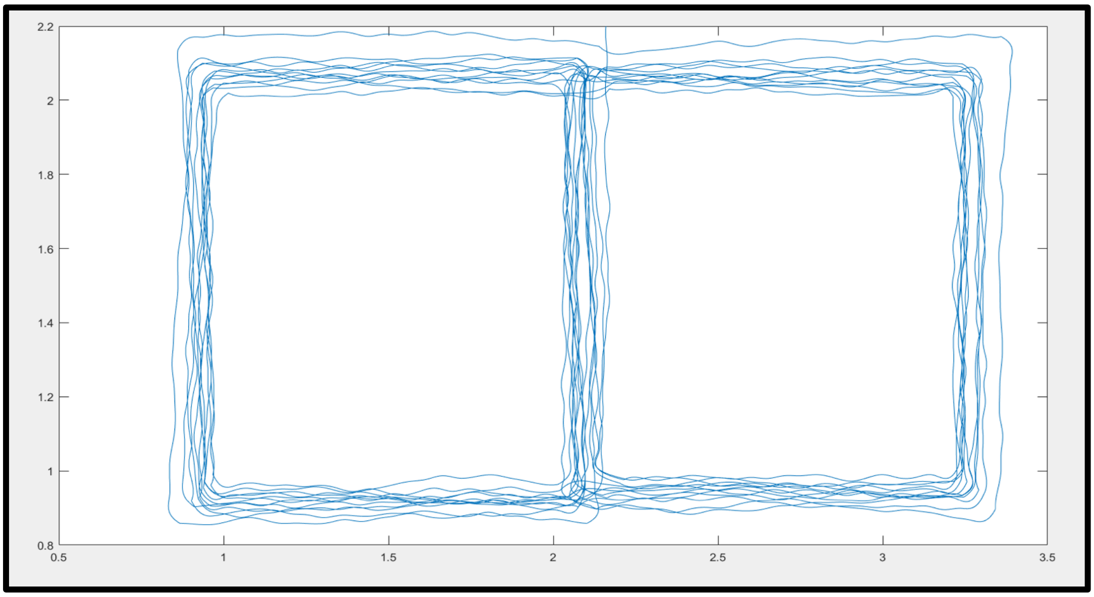


Figure 8: The trajectory generated for the maze outline generated as of Section 3.3

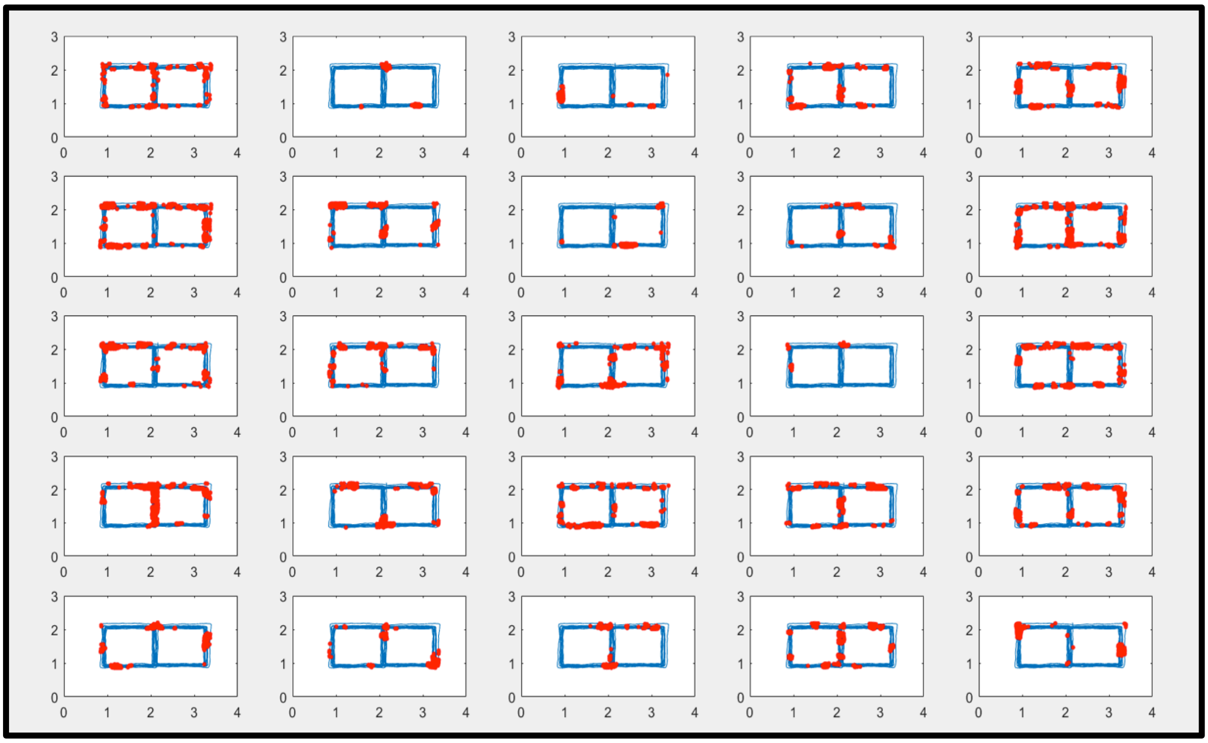


Figure 9: All cell firings in the L1 layer of LAHN (As per Section 3.4, set threshold of 65%)

Inferences:

1. We can predominantly observe three different cell firings.
2. Most of the neuron cells have firings at the junction of trajectory switch between the two inner boxes
3. Neuron firings at the entrance of the junction like in the 5th and 6th cell
4. Neuron firings at the boundary of the maze indicating the presence of boundary cells

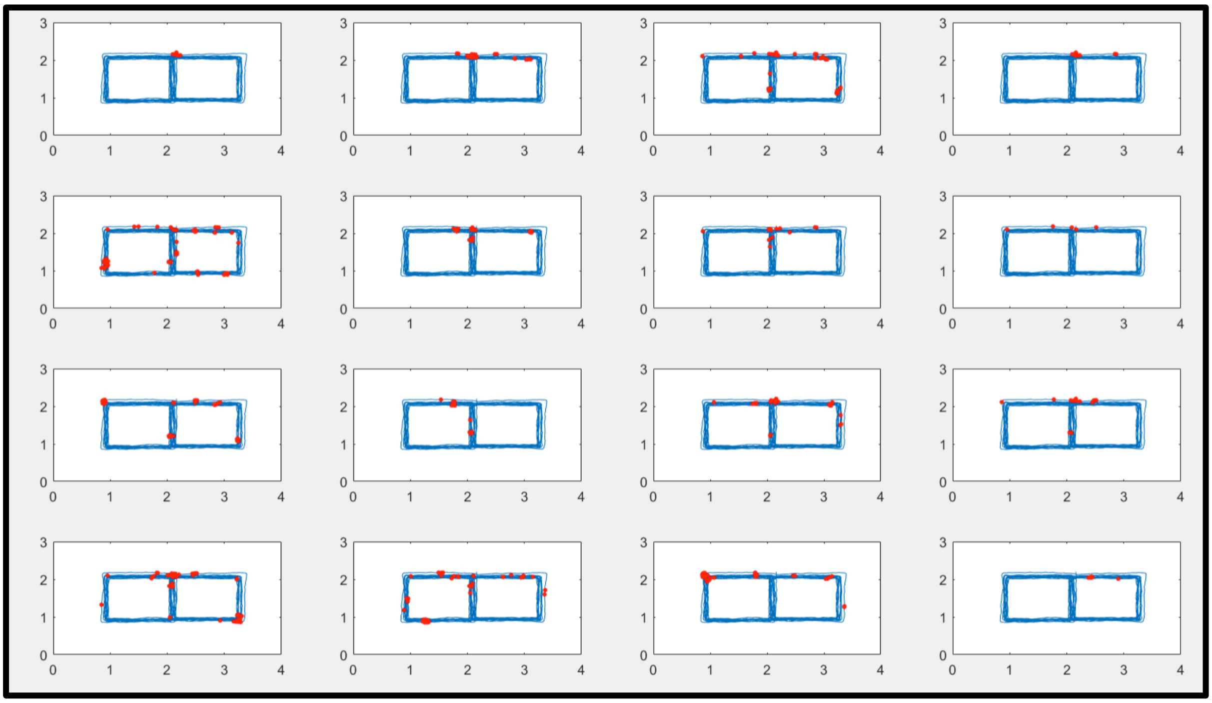


Figure 10: All cell firings in the L2 layer of the LAHN (As per Section 3.4, set threshold 75%)

Inference:

1. The junction firings have predominantly surfaced over the L1 layer
2. We can also find few boundary cells firing like in neuron 9 and 15

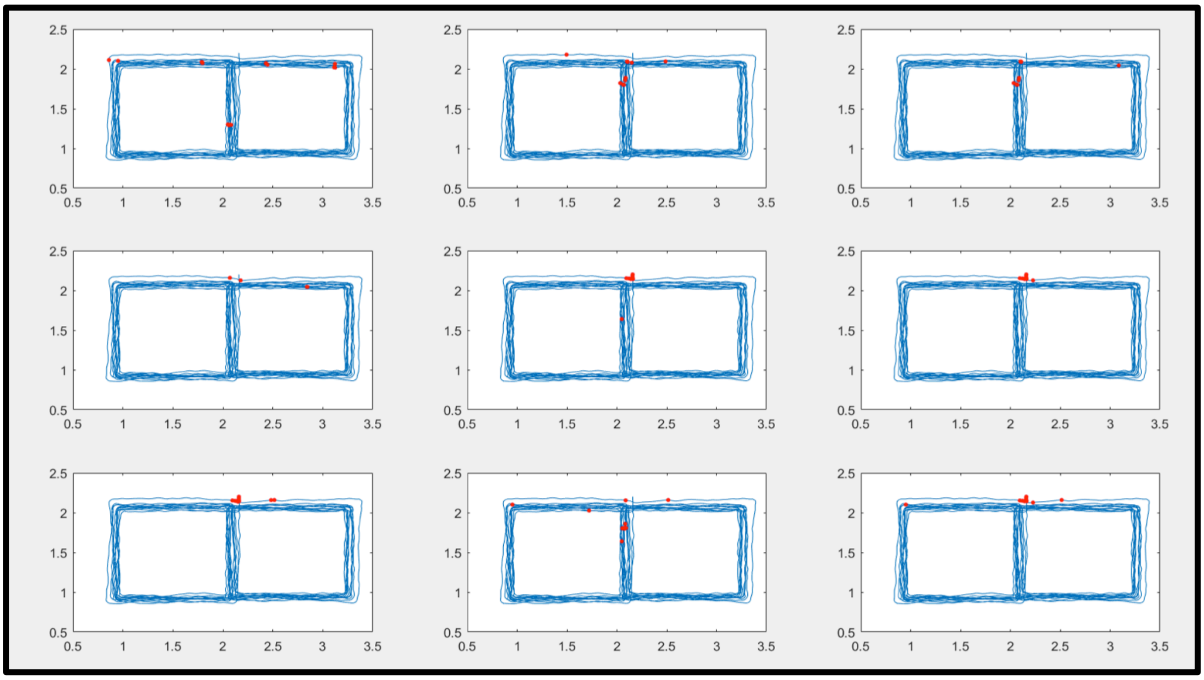


Figure 11: All cell firings in the L3 layer of the LAHN (As per Section 3.4, set threshold 85%)

Inference: We can only the find the junction firings in the L3 layer

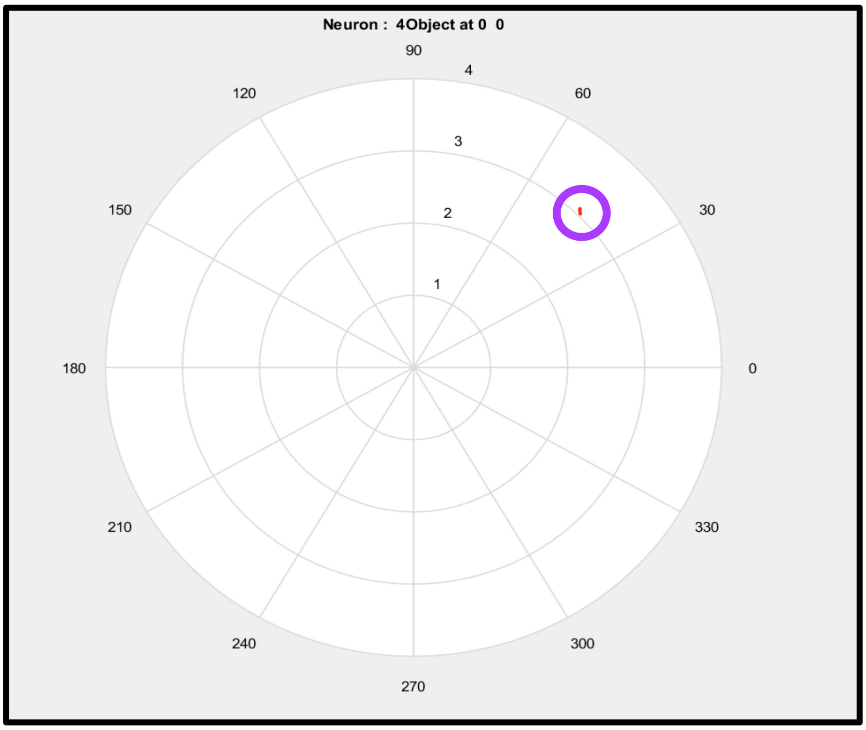
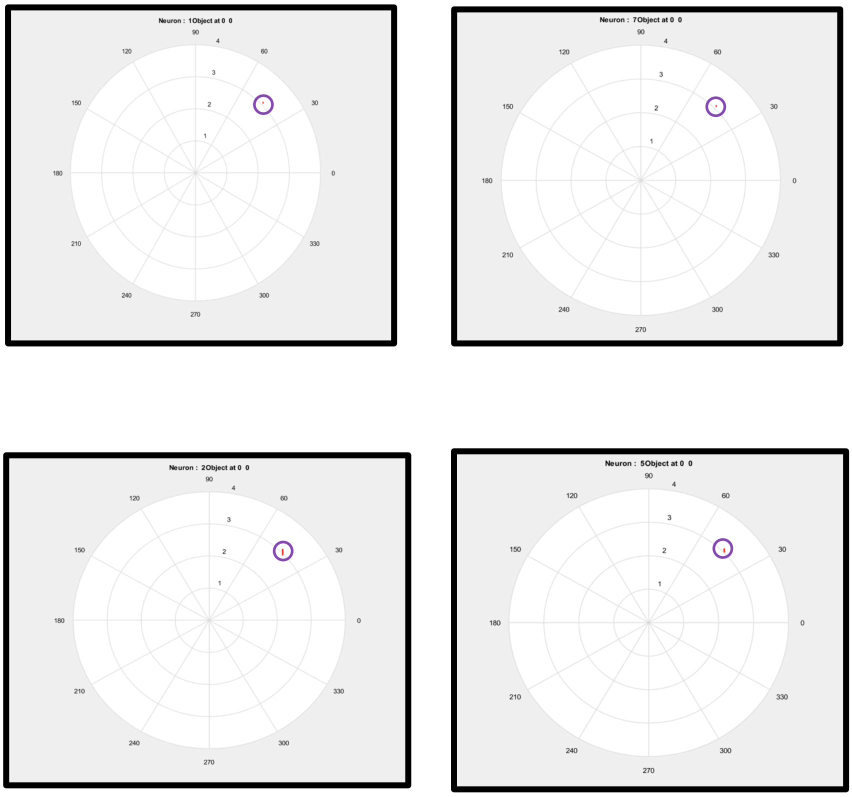


Figure 12: Polar plot for a single neuron in L2 layer firing at an angle of 45^{o}



Figures 13-16: Polar plots of few other neurons in the L2 layer.

Inference: We can find that the polar plot fires at a particular direction of 45^o at all the junctions indicating direction dependency for the cells firing.

4.2. Results For Grid (Further Work):

We find the results for a 3x3 grid type of a bounding box following the same methodology used in Section 3.

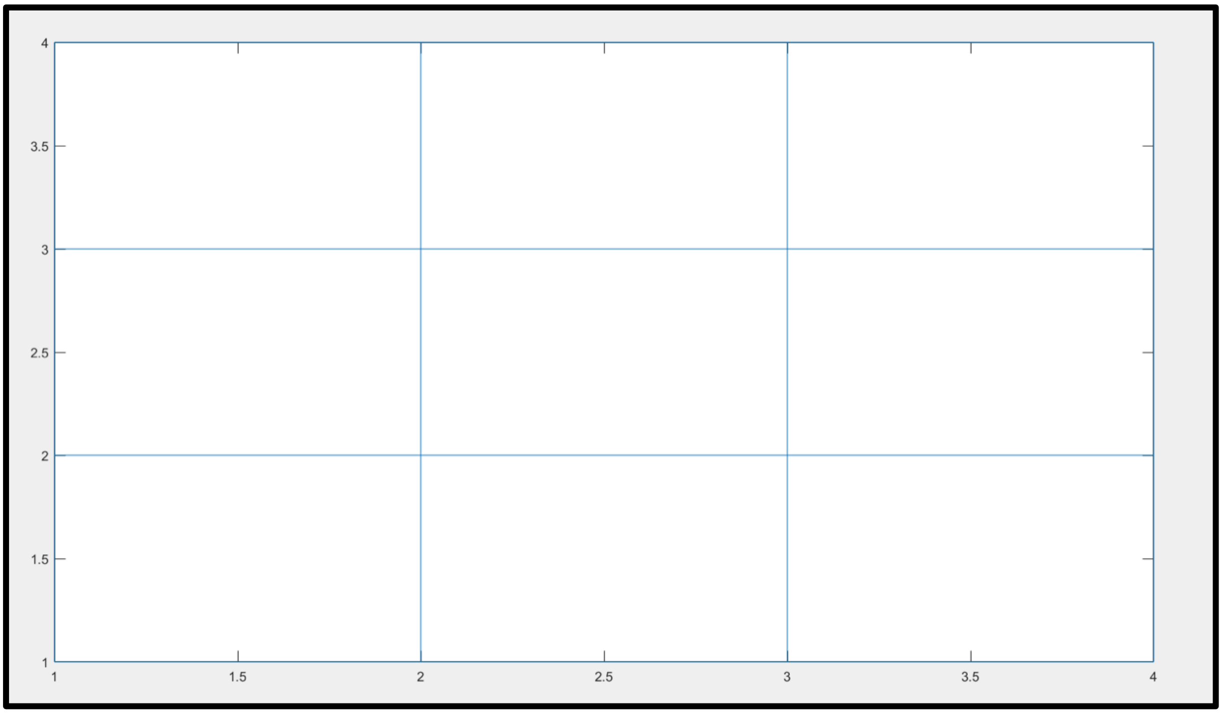


Figure 17: Trajectory generated for a 3x3 box grid

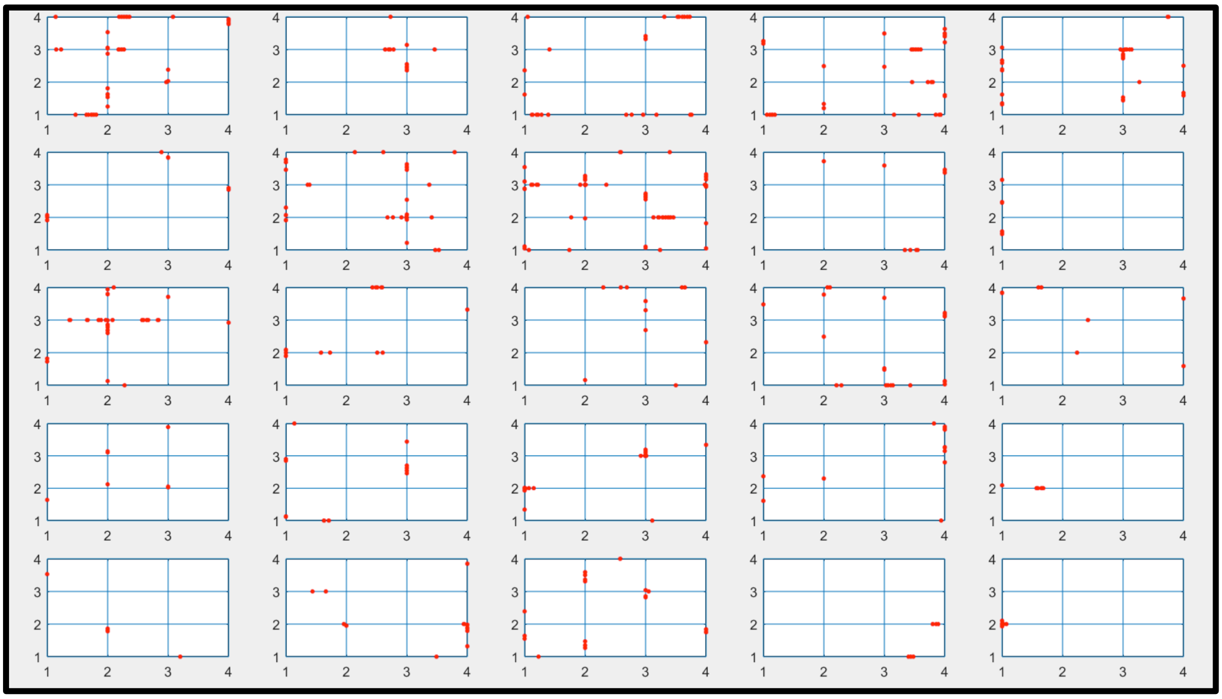


Figure 18: All cell firings for 3x3 grid in L1 layer of LAHN (As per Section 3.2, set threshold 65%)

Inferences:

1. Irregular patterns of cell firings in the L1 layer.
2. Predominant firings at certain junctions of the grid.
3. Certain boundary cell firings especially a the (1x2) junction.

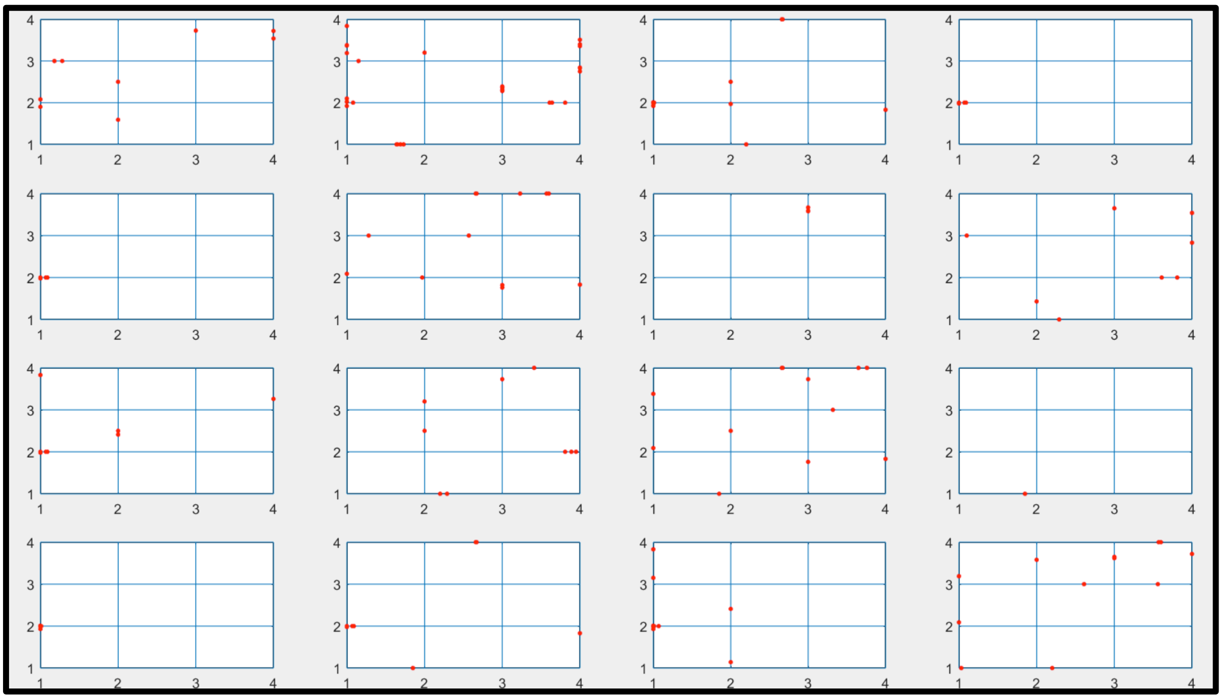


Figure 19: All cell firings for 3x3 grid in L2 layer of LAHN (As per Section 3.2, set threshold 75%)

Inference:

1. The irregular patterns fade in the L2 layer.
2. Predominant cell firings at the (1x2) junction.

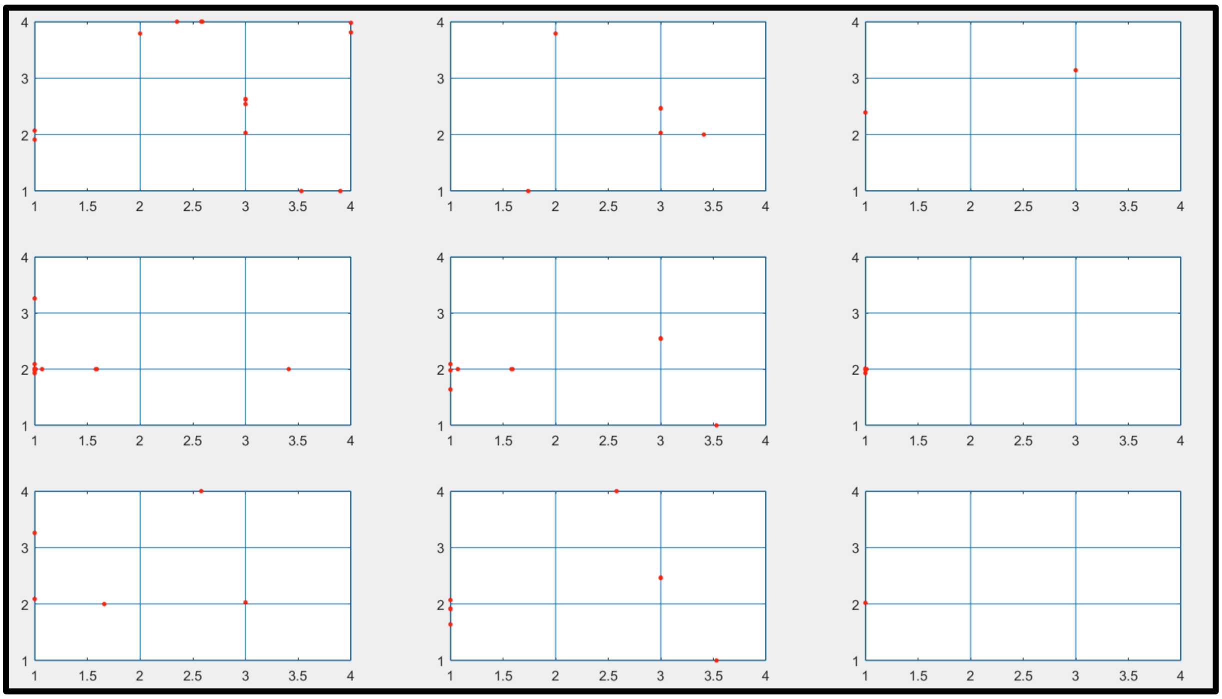


Figure 20: All cell firings for 3x3 grid in L3 layer of LAHN (As per Section 3.2, set threshold 85%)

Inference: Very few firings in the L3 layer to analyze any predominance. Although we can still find the (1x2) junction firings.

Chapter 5

SUMMARY AND CONCLUSIONS

This chapter is the compilation of the gist of the understandings developed based on the results and discussions carried out in the present work. The Oscillatory Model has assisted in extracting features from the neuron firing simulations from trajectories generated in complex environments. These features and results gives us a deeper understanding into the functioning of spatial cells in the brain. Locationalisation has been a subject which provokes a great deal of curiosity as well as a great deal of debate. It is important to unravel the scientific basis of the factual process of the same so as to negate the common sensical approach as well as the theoretical approach to working methods. This thesis makes an attempt to ossify the mathematical conceptualisation to move the research in this domain beyond theory.

Recommendations for the future work are as follows:

1. Improved feature extraction from the LAHN layer by adding a new dimensionality using visual input
2. The expansion of 3x3 grid to a bigger and more complex environment with obstacles and blocked paths in 2D as well as 3D

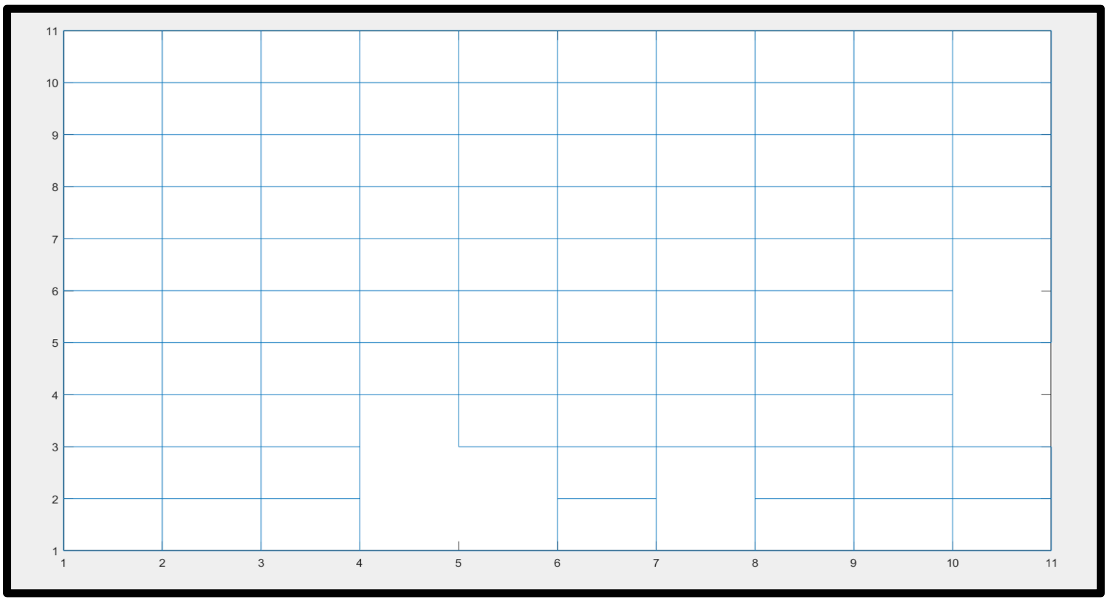


Figure 21: An example 10x10 grid for study in more complex environments

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