### **N. Yu, H. Yu, L. Wang, Y. Liao and C. Yin, "A Model of Information Circulation and Transmission Network of Grid Cells in Entorhinal Cortex and Place Cells in the Hippocampus of Rat," 2020 IEEE 9th Joint International Information Technology and Artificial Intelligence Conference (ITAIC) 2020, pp. 838-844, doi: 10.1109/ITAIC49862.2020.9338829.**

Cyclic relationship between grid cells and place cells

Combination of GC and PCs provides information on where a rat is and how to travel to a target location

Place cells dont require grid cells in development but do become stable when grid cells become mature (Laurenz et al)

When MEC is injured place fields becpme smaller - consistent with place cell firing derived from grid cells of several scales (Neher et al)

+Grid cells need excitatory input from place cells (Bonnevie et al)

entorhinal cortex and the hippocampus have mutual inputs during the process of information transmission

entorhinal cortex transmits information to the CA3 area of the hippocampus, and then the information reaches the CA1 area of the hippocampus through neuron exchange. Finally, the CA1 area transmits the information back to the entorhinal cortex

MODULE 1 Place to Grid

Place cell firing is determined by position

A grid cell receives input from n place cells in different locations in the second module

Competitive network model -> only one place cell can control grid cell firing at one time?

MODULE 2 Grid to place

a place cell in the second module receives input from n grid cells with different spatial characteristics in the first module

**Hebb learning was used to calculate the discharge rate of the position cells according to the area with the largest discharge rate of grid cells, as shown in equation**

**Grid cells with different phases and spacing were weighted differently**

Place cells and surrounding grid cells provide inhibitory input to grid cells

And grid cells and surrounding place cells inhibit place cells

Grid cells provide coordinate system of the environment

* 2D twisted torus continuous attractor

Also 2D continuous attractor for place cells

* Get inpot from grid cells and surrounding place cells

Plasticity in connections between place and grid cells

* Hebbian learning for excitatory synapses
* Steady state plasticity rule for inhibitory synapses

Synaptic plasticity will occur, changing the connection weight between the cells corresponding to the current position and the grid cells to generate a node of the grid field. Each new synaptic plasticity event will add a new grid field node until the hexagonal grid field spreads throughout the whole space environment of the mouse.

### 

### 

### **Chen, G., Lu, Y., King, J.A. et al. Differential influences of environment and self-motion on place and grid cell firing. Nat Commun 10, 630 (2019).** [**https://doi.org/10.1038/s41467-019-08550-1**](https://doi.org/10.1038/s41467-019-08550-1)

### **Milford MJ, Wiles J, Wyeth GF. Solving navigational uncertainty using grid cells on robots. PLoS Comput Biol. 2010 Nov 11;6(11):e1000995. doi: 10.1371/journal.pcbi.1000995. PMID: 21085643; PMCID: PMC2978698.**

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### **Chen G, Lu Y, King JA, Cacucci F, Burgess N. Differential influences of environment and self-motion on place and grid cell firing. Nat Commun. 2019 Feb 7;10(1):630. doi: 10.1038/s41467-019-08550-1. PMID: 30733457; PMCID: PMC6367320.**

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### **Diehl GW, Hon OJ, Leutgeb S, Leutgeb JK. Grid and Nongrid Cells in Medial Entorhinal Cortex Represent Spatial Location and Environmental Features with Complementary Coding Schemes. Neuron. 2017 Apr 5;94(1):83-92.e6. doi: 10.1016/j.neuron.2017.03.004. Epub 2017 Mar 23. PMID: 28343867; PMCID: PMC5444540.**

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### **Chen G, Manson D, Cacucci F, Wills TJ. Absence of Visual Input Results in the Disruption of Grid Cell Firing in the Mouse. Curr Biol. 2016 Sep 12;26(17):2335-42. doi: 10.1016/j.cub.2016.06.043. Epub 2016 Aug 4. PMID: 27498565; PMCID: PMC5026695.**

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### **Park SW, Jang HJ, Kim M, Kwag J. Spatiotemporally random and diverse grid cell spike patterns contribute to the transformation of grid cell to place cell in a neural network model. PLoS One. 2019 Nov 14;14(11):e0225100. doi: 10.1371/journal.pone.0225100. PMID: 31725775; PMCID: PMC6855461.**

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### **Rowland DC, Roudi Y, Moser MB, Moser EI. Ten Years of Grid Cells. Annu Rev Neurosci. 2016 Jul 8;39:19-40. doi: 10.1146/annurev-neuro-070815-013824. Epub 2016 Mar 9. PMID: 27023731.**

## Review of findings upto 2016 from the Mosers

## Medial entorhinal cortex (MEC) + pre- and parasubiculum

## Seminal papers:

## grid cells (Hafting et al. 2005)

## border cells (Solstad et al. 2008)

## speed cells (Kropff et al. 2015)

## head direction cells (Boccara et al. 2010, Ranck 1985, Sargolini et al. 2006, Tang et al. 2016, Taube et al. 1990a)

## Grid cells - hexagonallu arranged tiling firing fields over 2D surface -> likely require input from other cell typed to produce their firing patterns and may drive place cell formation

## collection of place cells to create map of local environment, with individual cells in mutiple maps

## The cells probably require information on the environmemt and position based on path integration

## **Environmental cues control PC firing (remapping / rotation etc) - but can maintain firng pattern in darkness**

## dorsal MEC provides excitatory input to dorsal hippocampus (where best resolution place cells recorded)

## Fyhn et al (2004) -> recorded dorsal MEC and found PC with more than one field

## Hafting et al (2005) -> recorded in larger area and found hexagonal pattern

## mice (Fyhn et al. 2008), bats (Yartsev et al. 2011), monkeys (Killian et al. 2012), and humans (Doeller et al. 2010, Jacobs et al. 2013, Kunz et al. 2015)

## 

## only a few cells required to have full coverage of the environment

## neighbouring cells maintain relative firing patterns when moved between environments -? landmark independent (path integration based firing) -> firing pattern maintained regardless of changes in speed or direction

## 

## direction provided to grid cells from head direction cells, and speed cells for speed -> both also maintain firing properties independent of environment (unlike PC but like GC)

## 

## Grid cells htroughout all dorsal vetral axis of MEC

## Increase size and spacing of grid fields from dorsal to ventral (same as place fields)

## Distinct modules of grid cells which share common scale and orientation, asymetric distortion and spike phase relationships (stensola et al 2012)

## coherence between cells is only within a module

## Scale difference between modules is between 1.4 to 1.7 (geometric increase -> see Mathis et al 2013 for theory)

## Two classes for excitatory projection neurons - both can be grid cells:

## pyramidal cells

## stelate cells: only in layer II (where grid cells most abundant)

## superficially branching dendrites

## strong hyperpolarization-activated current

## only 50% of stellate cells are grid cells

## Development: HD (before eye open) -> border -> GC (likely have dedicated progenitor cell

## Two photo calcium imaging of MEC -> neighbouring cells show correlated activity

## Grid may emerge from long range inhibition and short range activation (attractor networks) porduce 'Turing patterns'

## Attractor networks

## for head direction

## cells arranged in ring according to directional turning

## each cell excites neighbours (distant dependant)

## get bump of activity

## bump moves around the ring with input of angular rotation of the head

## 2D ring attractor networks for grid cells (Fuhs et al 2005, McNaughton et al 2006, Guanella et al 2007)

## short range excitation and long range inhibition (mexican hat connectivity) produce grid

## also just long range inhibition (lincoln-hat connectivity) -> requires external source of excitation (maybe from PC or nonGCs)

## - stellate cells connected by all or noe inhibitory interneurons, but both excitatory and inhibitiory connection excist in the MEC between layers etc

## modules may be indipendant attractor networks

## attractor networks require precise wiring and are sensitive to noise

## Adaptation models

## Individual cells can produce grid firing -> hebbian learning using place cell inputs

## GCs adapt to spike frequency then is fatigued

## GC fires at the same time as a group of PCs and weights adapt. Grid cell is then not activated by the next PCs because fatigued, these connection weights become weeker. The GC is then recovered to be acactivated by the subsequent PCs -> repeat to get mature strong and week connections

## 'Periodic bouts of activation and fatigue cause some spatial cell–to–grid cell connections to strengthen and others to weaken, which in turn creates circular fields with minimal interfield spacing (i.e., a hexagon).'

## Si et al. 2012 - adaptation model + recurrent connections

## adaptation model in development? to develop the phase dependant connectivity for attractor network?

## 

## Barry et al. 2012, Carpenter et al. 2015 takes time to develop a coherent grid -> adaptation mechanism to refine connections in new environments

## 

## When reexposed to an environment GCs firing in the same position as before -> achored by sensory cues

## If walls move the grids will expand or contract (Barry et al. 2007, Stensola et al. 2012)

## Walls cause rotation and deformation of the grid (shearing) (modle in Stensola et al. 2015)

## 'grid patterns are deformed by forces from the borders of the environment whose strength decreases with distance from the walls'

## 

## in environments with multiple conpartments get fractured grid -> new map for each compartment (Derdikman et al. 2009) -> caused by interacting sheer forces from walls -> with experience of the environement the maps merge (Carpenter et al. 2015)

## In very large space also get fracgmented maps which merge together -> quilt of different maps with different environmental references stitched toegther (may also merge with experience)

## 

## still dont know if 3D firing -> with rats encoding could just be in plane of motion -> peg board is just stacked horizonrtal planes (Jeffery et al. 2015)

## bats have volumetric place cells (Yartsev & Ulanovsky 2013) and three direction HD cells (Finkelstein et al. 2015), probs 3-D grid cells as well (Ginosar et al. 2015)

## 

## unique position - decoded from multiple grid cells of different scales and orientations from different modules (Mathis 2012, Wei et al. 2015, McNaughton et al. 2006) (distortion not a problem Stemmler et al. 2015) -can also decode distance to a landmark (distortion may be a problem)

## 

## 

## 

## Place cells are necessary for maintaining periodic firing in grid cells (Bonnevie et al. 2013)

## 

## 

### **Moser MB, Rowland DC, Moser EI. Place cells, grid cells, and memory. Cold Spring Harb Perspect Biol. 2015 Feb 2;7(2):a021808. doi: 10.1101/cshperspect.a021808. PMID: 25646382; PMCID: PMC4315928.**

## 

### **McNaughton BL, Battaglia FP, Jensen O, Moser EI, Moser MB. Path integration and the neural basis of the 'cognitive map'. Nat Rev Neurosci. 2006 Aug;7(8):663-78. doi: 10.1038/nrn1932. PMID: 16858394.**

## 

## Path integration = integration of linear and angular self motion

## 

## Convergence of periodic gric cell firing at mu;ltiple scales along the DV axis may produce none-periodic place cell firing in hippocampus

## PC gets environmental info + navigational info (nav info gates environmental input)

## 

## homing trajectories -? HD cells for angular path integration?

## 

## HD cells maintain directional turning rlative to each other

## -> but individuals may have different prefered firing directions in different contexts

## 

## 1D attractor map

## HD cells with sifferent direction preferences representing every angle

## arrange in circle according to relative PD

## those closs by get excitatory connections + global inhibition

## 

## rotation can be achieved with two types of conjunctive neuron which get info about angular velocity + info about current HD from the ring (cw and acw cells) 'hidden layer' cells drive activity bump arounfd the ring (\*\* do cells like this exist??)

## angualr velocity info from vestibular system (\*\* or robot odometry?? potentially even the motor command eg turn left etc. maybe a combo eg motor command + visual checks for correct rotation + odometry? - need to check vision because can be rotated passivly \*\* cant remember what the literature says about passive rotation)

## \*\* does this assume only one cell per head direction?

## 'conjunction of current HD + angular velocity'

## HD cells in modle encode relative orientation

## this type of network -> get drift but not jumps in activity from one bump to another

## 1D attractor network for HD -> can us 2D for location on a plane

## 

## 2D atteractor map

## arrange in 2D space acording to relative firing locations

## 2D hidden layer summation of position (from conninuous attracor network) + displacement vector (HD + speed)

## boundaries like a torus -> dont fall off the edge

## hidden layer conjunctive cells - conjunction of position on a plane and head orientation

## 

## neighboring grid cells have identical spacing and orientation but are offset from each other (different grid phase)

## the phase difference between two cells is constant

## 

## cells with both direction and place properties have been found 'Conjunctive cells'

## in layers III and V with extensive connecitons to II (where most grid cells are)

## 

## layer II may be output layer (integrating info from deperlatyers to produce non-directional representation

## 

## association with landmarks may occur in hippocampus or MEC (eg.influence of border cells on grids?)

## 

## HWAT DETERMINES SCALE

## During unrestricted natural locomotion, the amplitude of hippocampal theta waves increases essentially linearly with running speed

## 

## differnet grid scales must come about from multiple path integrator modules

## -> \*\* do see modules of grid cells?

## 

### **Banino et al (2018) Vector-based navigation using grid-like representations in artificial agents**

## 

## ‘Grid cells are thought to provide a multi-scale periodic representation that functions as a metric for coding space’

## vector based navigation - planning trajectories to goals

## 

## 1) trained recurrent network to do path integration -> get grid cell like representations out

## 2) deep reinforcement learning to use these representations to locate goals

## grid respesentations allowed for shortcut behaviour

## 

## velocity provided to place and head direction units

## 

## get grid like outcomes in network

## \*\* how i am not following..

## \*\* difficult paper maybe come back??

## 

### **Burak Y, Fiete IR (2009) Accurate Path Integration in Continuous Attractor Network Models of Grid Cells. PLoS Comput Biol 5(2): e1000291. doi:10.1371/journal.pcbi.1000291**

## 

## Figure 1

## In this model - local cells give inhibitory input + entire network feedforward excitation

## get blobs of activity on a triangular latice

## velocity coupling -?

## each cell recieves input from speed modulated HD cell and is connected to other cells in a dorresponding direction

## so if rat moves in a direction will shift activity along the 'sheet''asymetric connectivity'

## 

## 128^2(~10^4) neurons arranged in asquare sheet. Neurons close to each edge of the sheet formconnections with neurons on the opposite edg

## 

## Different grid cells receive different head direction input

## neutrons connectivity is centred on a cell in the corresponding direction not he neural sheet ->asymmetric connectivity drives network activity around the net in the direction of movement

## 

## HD input modulated by speed

## 

## Each patch on the neural sheet contains cells with all the preferred angles

## 

## Head direction input moves activity around the network of cells

## - the grid cells themselves don’t have a preferred direction in their firing

## 

## periodic (connections in a torus like shape) vs aperiodic

## 

## aperiodic - connections do not come round but new blobs of activity form based on the patterns of inhibition from the surrounding cells

## - need to solve the problem of distortion at the edges of the net due to lack of connectivity

## - they used tapered inputs (weaker input to cells at the edges) but then these cells are generally less active and have less influence on network dynamics

## 

## \*\* seems to me periodic network easier to start with

## 

## 

## spiking networks -> NOISE!!

## noise can cause the population pattern to move around the network

## reduce precision

## noisy because spikes are discrete events

## 

## ‘assuming that neural firing is an inhomogeneous Poisson process’

## performance is much worse in aperiodic network

## Altered spiking properties to be more regular and performace3 improved

## 

## 

## can explain grid field stretching in larger environments with this network -> by amplitude modulation of HD input

## 

## COME BACK TO THIS PAPER WHEN ACTIVLY SOLVING PROBLEMS

## 

## They used 10^4 neutrons which is similar to estimates of cells in MEC

## dMEC might consist of a very large number of very small networks with different grid periods

## continuous attractor models predict a large membership in each grid network, and correspondingly few different grids

## 

## separate attractor networks from different grid periods

## 

## ‘If neural locations in the cortical sheet are scrambled, while preserving the neural indices i and the pairwise weights Wij between neurons, the grid-like patterning in the cortical sheet will disappear, but there will be no change in the single neuron triangular lattice response or in any other dynamical property of the network. The underlying structure of the attractor manifold (e.g., whether or not it is continuous) is a function of network connectivity, but does not depend on the layout of neurons on the cortical sheet’

## 

## 

## 

### **Guanella A, Kiper D, Verschure P. A model of grid cells based on a twisted torus topology. Int J Neural Syst. 2007 Aug;17(4):231-40. doi: 10.1142/S0129065707001093. PMID: 17696288.**

## ===>>> main point is PC input to grid cells for correcting path integration error

## grid cells are topographi-cally organized in the MEC: first, neighboring cells share common grid orientation and spacing; second,the grid spacing isometrically increases along the dorsoventral axis (in Ref. 1, the grid spacing varies between 39 to 73 cm)

## 

## MEC lesions disrupt homing trajectories

## grid spacing remains constant in different sized environments but is deformed at boundaries and can be altered by changing boundaries

## ANN

## activity is shifted around the network due to asymmetric synaptic connections modulated by velocity

## network connectivity is appanages as a twisted torus -> can generate regular grids with same spacing an orientation but different phase

## They used 10 x 9 cell network

Number of cells in each row is 2/sqrt(3) times larger eg could have 40 x 35 cell network

Gaussian connectivity

Intensity I 0.3

Shift T 0.05

Width sig 0.24

Connections between cells are modulated by speed -> shift activity

Use floating normalisation function to ensure stability of network!!

Position of cells in sheet ci = (ci\_x,ci\_y)

Ci\_x = (ix - 0.5)/Nx

Ci\_y = sqrt(3)/2(iy - 0.5)Ny

Ix and iy are the column and row number of cell i

Dist\_tri (ci,cj) = ||ci - cj + sj|| (euclidean norm)

Distance between cell i and cell

See paper fro Sj values

The paper uses shifting weights to move the bump rather than conj cells

## use population of place cells to provide allothetic information (PCs encode unique regions in the environment)

## grid cells are recalibrated by place cells to correct large path integration errors

## 

## synaptic weights are shifted in direction of rat

## 

## regular torus would lead to rectangular grid - twisted torus gives triangular pattern

## 

## network gets velocity input

## v = (vx,vy) which does not depend on the animals location

## synaptic connections shirt int he direction of this speed vector

## 

## in this model place fields are view dependant representations of visual stimuli

## 

## hebbian synapses -> between PC and Grid cells -? ;earn associations between cells with correlated activity

## path integration error would then cause mismatch between place field and grid field (\*\* this assumes PC are a product of boundaries + visual landmarks?)

## attractor dynamics however would bring activity back to correct position

## 

## \*\* coupled with previous paper - maybe grid fields are disrupted when PC input removed because do not correct path integration error and get drift in firing??

## 

## model predicts that the different sixes of grids along the doors ventral axis is due to an exponential increase of the velocity gain along this axis

## twisted torus allows representation of large space with relatively few cells

## multiple sheets of cells connected like this with different properties???

## 

## problem with purely allotetic navigation in inability to disambiguate to similar scenes

## 

## 

## 

### **Castro L, Aguiar P. A feedforward model for the formation of a grid field where spatial information is provided solely from place cells. Biol Cybern. 2014 Apr;108(2):133-43. doi: 10.1007/s00422-013-0581-3. Epub 2014 Feb 28. PMID: 24577877.**

## 

## Most grid cell models assume place cells are produc of combination of grids

## 

## this is model fro emergence of grids from PC activity

## each PC provides either excitatory of inhibitory input to grid cells - connection type and strength is a function of distance to place filed centre

## PC compete for GC activation

## plasticity rules favour efficient packing of fields

## (feedforward connections have been found between CA1 and deep layers of MEC

## 

## In development get HD cells then place cells then grid cells (Langston et al 2010 and wills et al 2010)

## Grid fields are deformed when boundaries are moved -> therefore grid cells receive some sensory input (they suggest via place cells)

## inactivating hippocampus destroys grid firing (bonnevie 2013)

## disrupting grid cell firing does not impact place fields

## 

## In model each PC can both excite and inhibit a GC and each GC gets input from N PCs with place fields spread over the environment

## in model each GC was conencted to all PCs

## 

## grids form as animal explores the environment and passs through place fields which the contribute to the grid

## grid map is progressively extended as the animal explores

## 

## PCs compete for GC activation, the winning cell forces GC to fire in that PCs firing field, GCs can only recruit new place cells when the animal moves far enough out of the PCs firing field to be released from its inhibitory control

## 

## NO PATH INTEGRATION REQUIRED

## \*\* but we want to use grid cells for path integration

## 

## limitation of model is that with increasing size elf the grid the regularity of the lattice will decrease -> loose hexagonal structure

## also does not account for population properties of grid cells eg constant spatial properties of GC firing fields in different environments which have different place cell activity…

## they suggest HD may drive different orientations of grid cells -. local populations of grid cells with one HD preference (conjunctive cells are side effect)

## 

## 

## \*\*I don’t know how i feel about this…. \*\* throws a spanner in the works? \*\* probably the case that PCs do impact grids and grids to impact PCs and it is a nice and difficult to tease appart?

## \*\* i suppose we just have to pick a theory and run with it…

## 

## 

### **Solstad T, Moser EI, Einevoll GT. From grid cells to place cells: a mathematical model. Hippocampus. 2006;16(12):1026-31. doi: 10.1002/hipo.20244. PMID: 17094145.**

## place field diameters <20cm dorsal - several meters in very ventral

## Also dorsal ventral grid spacing increases

## 

## unlike place cells which are context dependant -> grids active in all environments

## place field could be generated from many grid fields with different spacings

## In model:

## - PC activity = weighted sum of excitatory inputs from N grid cells

## biggest wight from similarly sized firing field

## tried with 4,10,20 and 50 GC inputs to a single PC

## grid spacing was selected randomly with logarithmic sampling between two boundaries

## the number of GCs required to produce a single place field increases with the size of the arena

## ‘the average number of anatomical connections between a

## grid cell and a place cell may be somewhere between 100 and

## 1,000 depending on how many contacts each grid cell makes

## with each place cell’

## GC at same dorsal ventral level share the same orientation -> so place cells may receive GC input with different spacing but same orientation

## BUT to get one place field need varied orientations and spacings

## 

## integrate inputs from grid cells with different spacings, each place cell must be innervated by cells from different dorsoventral levels of the MEC

## PC remapping is accompanied by altered grid cell prepresentation (reorientation etc)

## Only need low number of GCs to get place field, os remapping could actually just be different combinations of cells driving the place field??????

## \*\* where does this context information come in??

## 

### **Kropff, E., Carmichael, J., Moser, M. et al. Speed cells in the medial entorhinal cortex. Nature 523, 419–424 (2015).** [**https://doi.org10.1038/nature14622**](https://doi.org/10.1038/nature14622)

## ‘activity is translated between grid cells in accordance with the animal’s displacement in theenvironment. For this translation to occur, grid cells must have continuous access to information about instantaneousrunning speed.’

## \*\* probably not required in robot?? get speed info from a) motor command/odometry/vision… suppose speed cell could have firing dependent on these things?

## FR of some grid cells modulated by speed

## ‘flintstones car apparatus’

## firing sharply follows changes in speed

## get speed conjunctive cells both with border, HD and GCs

## speed code is context-invariant

## firing rate of the MEC speed cells correlated better with future speed than simultaneous or past speed

## at faser speeds also prospective shift in layer II grid fields

## anticipatory shift of the grid fields increased during acceleration episodes - also theta dependent

## Speed calls make up 15% of all MEC cells across all layers

## indépendant of visual inputs

## may be derived from motor efferent information

## 

## 

### **Harland B, Grieves RM, Bett D, Stentiford R, Wood ER, Dudchenko PA. Lesions of the Head Direction Cell System Increase Hippocampal Place Field Repetition. Curr Biol. 2017;27(17):2706-2712.e2. doi:10.1016/j.cub.2017.07.071**

## place cells use a directional input to differentiate otherwise similar local environments

## without head direction input differentiation is abolished and get place field repetition in repetitive but differently oriented compartments

## Place Fields Are Driven by Borders and by Directional Inputs

## HD provides global reference regardless of local cues (mismatch between global direction and local boundaries

## unknown wether this is direct impact of HD on PC or via grids border cells

## but there is evidence for place fields mot dependant of grids (Bush, D., Barry, C., and Burgess, N. (2014). What do grid cells contribute to place cell firing? Trends Neurosci. 37, 136–145)

## 

## 

## 

## 

### **Carpenter, F., Manson, D., Jeffery, K., Burgess, N., and Barry, C. (2015). Grid cells form a global representation of connected environments. Curr. Biol.25, 1176–1182**

two compartments initially 2 grids then with experience one cohesive grid

### **Winter, S.S., Clark, B.J., and Taube, J.S. (2015). Spatial navigation. Disruption of the head direction cell network impairs the parahippocampal grid cell signal. Science 347, 870–874**

HD required for normal grids

**Gerlei, K., Passlack, J., Hawes, I. et al. Grid cells are modulated by local head direction. Nat Commun 11, 4228 (2020).** [**https://doi.org/10.1038/s41467-020-17500-1**](https://doi.org/10.1038/s41467-020-17500-1)

Pure grid cells and conjunctive cells found in medialentorhinal cortex (MEC) both generate grid codes

May also have grid cells which are sensitive to multiple but not all directions

found pure grid cells do show selectivity for HD (multi directional) and this may come about from integrated input from multiple conjunctive cells

Cells may have a favoured and less favored trajectory

found individual firing fields had directional tuning (often multidirectional)

therefore directional modulation of grid cell firing depends on location

Continuous attractor: Pastoll et al. 2013 closest does not account

may come about from upstream directional grids

upstream cells would need differences in mean firing rate (spatially non-uniform - different mean firing rates in each field)

’spatially non-uniform conjunctive cell input model

local directional information may help with pattern separation downstream

stellate cells -? input to dentate gyrus and important for spatial memory but less than half of stellate cells are grid cells -> grid firing may then come about from that cells particular synaptic inputs

## PROBABLY SHOULD LOOK INTO METHODS

## 

### Shipston-Sharman O, Solanka L, Nolan MF. Continuous attractor network models of grid cell firing based on excitatory-inhibitory interactions. *J Physiol*. 2016;594(22):6547-6557. doi:10.1113/JP270630

### https://www.ncbi.nlm.nih.gov/pmc/articles/PMC5108899/

SUPER USEFUL FOR GRIS CELL MODEL!!!!

Alternatively, path integration could be achieved through interactions between a layer of heading‐independent grid cells and multiple layers of head direction‐modulated grid cells, which each integrate a single head direction input with speed signals and feedback from the heading‐independent grid layer (Samsonovich & McNaughton, [1997](https://www.ncbi.nlm.nih.gov/pmc/articles/PMC5108899/#tjp7075-bib-0039)). While the latter class of models require many more neurons to account for path integration, because separate layers are required for each heading direction, they have the advantage that they naturally account for direction modulated (or conjunctive) grid cells as well as pure grid cells.

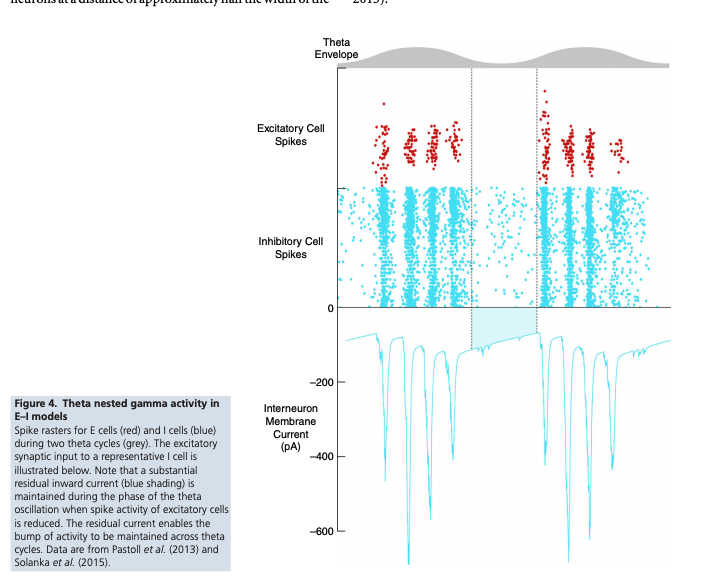
A network’s intrinsic connections can be configured so its preferred states will correspond to localised bumps of activity

Recommend twisted torus -> phase shift connectivity at one axis

When single bump attractors are implemented in E–I networks, each neuron’s connections extend over a relatively large fraction of the network (Fig. 2A). Thus, neurons making surround connections have their highest connection probability, or connection strength, with neurons at a distance of approximately half the width of the untwisted neural sheet.

\*\*\*Bursting behaviour is similar to theta:

Residual inward current is equivalent to the delay?



Models of interacting populations of excitatory and inhibitory exponential integrate and fire neurons can account for both grid firing and gamma oscillations (Pastoll et al. 2013; Solanka et al. 2015)

layer 2 stellate cells (L2SCs) and layer 2 pyramidal cells (L2PCs)

Both L2SCs and L2PCs may have grid firing fields, although the majority of neurons in each population do not appear to generate typical grid firing patterns (Tang et al. 2014; Sun et al. 2015)

grid-like firing patterns emerge as a result of path integration in continuous attractor networks composed of excitatory and inhibitory neurons, with membrane potential dynamics that approximate real neurons

A network’s intrinsic connections can be configured so its preferred states will correspond to localised bumps of activity

Given velocity inputs the activity bump(s) represent movement in space by propagating across the sheet

Alternatively, path integration could be achieved through interactions between a layer of heading-independent grid cells and multiple layers of head direction-modulated grid cell

A spatial input is required to oppose drift in the grid representation.

, In single bump models grid firing of excitatory cells can be generated by synaptic profiles that produce either surround excitation or surround inhibition. The surround connectivity is strongest for connections to neurons at a distance of about one-half the width of the sheet. Each neuron makes divergent connections to many target neurons, and receives convergent input from many presynaptic neurons

Removal of excitatory drive causes cells that previously had grid fields to encode head direction (Bonnevie et al. 2013)

-> this would not occur in my proposed network -> conjunctive grid cells would only fire with speed input???

use of local excitatory connections is inconsistent with evidence that L2SCs are not directly connected to one another (Dhillon & Jones, 2000; Couey et al. 2013; Pastoll et al. 2013), but instead interact indirectly via inhibitory interneurons (Couey et al. 2013; Pastoll et al. 2013).

## Models available on ModelsDB

Pastoll H, Solanka L, van Rossum MC, Nolan MF (2013) Feedback inhibition enables theta-nested gamma oscillations and grid firing fields. Neuron 77:141-54

<https://senselab.med.yale.edu/MicroCircuitDB/showModel.cshtml?model=150031>

Bush D, Burgess N (2020) Advantages and detection of phase coding in the absence of rhythmicity. [Hippocampus](http://dx.doi.org/10.1002/hipo.23199)

<https://senselab.med.yale.edu/MicroCircuitDB/showModel.cshtml?model=261878>

Bush D, Burgess N (2014) A hybrid oscillatory interference/continuous attractor network model of grid cell firing. [J Neurosci](http://dx.doi.org/10.1523/JNEUROSCI.4017-13.2014) 34:5065-79

<https://senselab.med.yale.edu/MicroCircuitDB/showModel.cshtml?model=218085>

Bush D, Barry C, Manson D, Burgess N (2015) Using Grid Cells for Navigation. [Neuron](http://dx.doi.org/10.1016/j.neuron.2015.07.006) 87:507-20

<https://senselab.med.yale.edu/MicroCircuitDB/showModel.cshtml?model=182685>

D'Albis T, Kempter R (2020) Recurrent amplification of grid-cell activity [Hippocampus](http://dx.doi.org/10.1002/hipo.23254)

<https://senselab.med.yale.edu/MicroCircuitDB/showModel.cshtml?model=262356#tabs-1>

Pilly PK, Grossberg S (2013) Spiking neurons in a hierarchical self-organizing map model can learn to develop spatial and temporal properties of entorhinal grid cells and hippocampal place cells [PLOS One](http://dx.doi.org/10.1371/journal.pone.0060599) 8(4):e60599

<https://senselab.med.yale.edu/MicroCircuitDB/showModel.cshtml?model=148035&file=/sGridPlaceMap/11207-21060501+02_t6c1.mat#tabs-1>

<https://senselab.med.yale.edu/MicroCircuitDB/ModelList.cshtml?id=83539>

Kim SS, Hermundstad AM, Romani S, Abbott LF, Jayaraman V (2019) Generation of stable heading representations in diverse visual scenes. [Nature](http://dx.doi.org/10.1038/s41586-019-1767-1) 576:126-131

<https://senselab.med.yale.edu/MicroCircuitDB/ShowModel.cshtml?model=261585>