A Grid & Place Cell Model of Path Integration Utilizing Phase Precession Versus Theta

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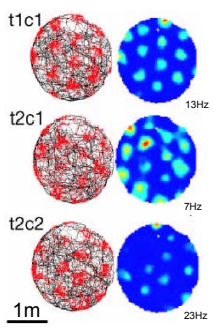
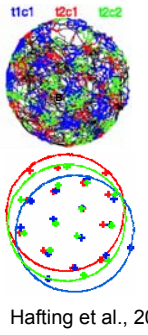
Grid cells in dorsomedial Entorhinal cortex

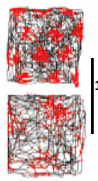
fire in a strikingly regular array of locations as a rat explores (Hafting et al., 2005). Nearby grid cells have similar orientation and scale, but shifted to tile the environment



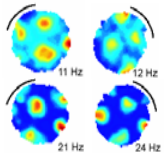


Hafting et al., 2005

Grid scale increases as recording site moves from dorsal to ventral

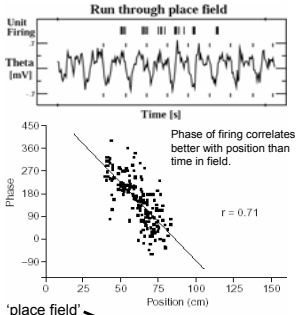


Grid orientation follows sensory cues



Does the cyclical firing pattern reflect interference?

Theta-phase of place cell firing precesses from late to early as the rat runs through the place field:

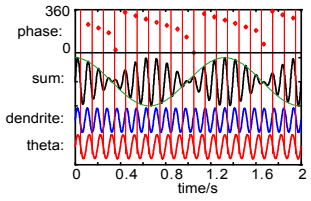


'place field'

Firing rate:

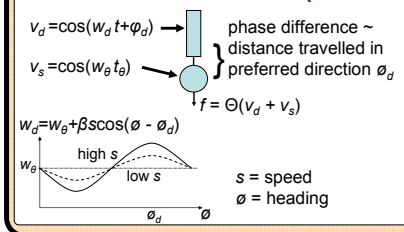
O'Keefe & Recce, 1993

This may reflect interference of theta with a dendritic membrane potential oscillation (MPO):

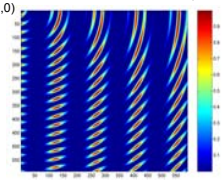


If MPO is voltage-controlled and input ~speed, interference peaks correlate with position (& more so than with time). See also Lengyel et al., 2003; O'Keefe & Burgess (2005).

1-D interference: 'band cells' (could be cells or dendritic sub-units)

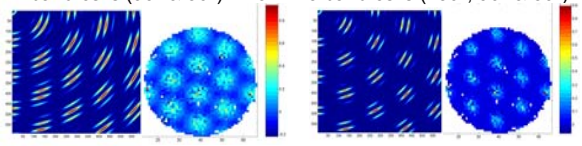


Straight runs from (0,0), $\varnothing_d$=0



Combining band cells to make grid cells (taking product of firing)

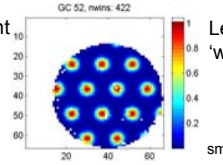
2 band cells (90° & 30°) or 3 band cells (150°, 90° & 30°) will do



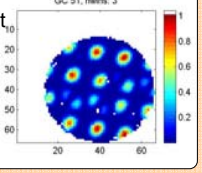
Straight runs from (0,0) 10mins real trajectory

But 3 band cells => 60°/120° separation for max firing of grid cell:

Most frequent 'winner'/100 random selections of 3 band cell orientations:



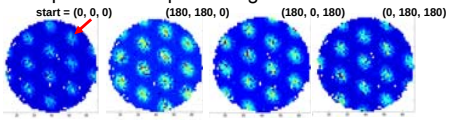
Least frequent 'winner'/100:



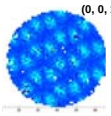
smoothed plots

3 band cells require phase reset at a location for correct alignment and correction of error in path integration (PI).

Example coherent phase alignments to θ at start



mis-aligned at start

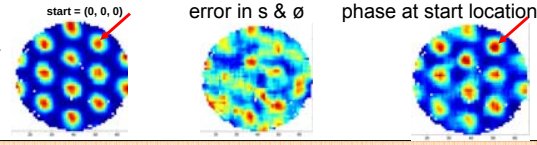


Perfect PI (i.e. s, ø)

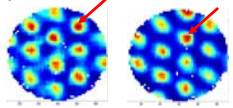
5% cumulative error in s & ø

5% err, band cells reset to θ phase at start location (41x)

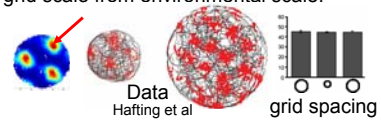
smoothed plots



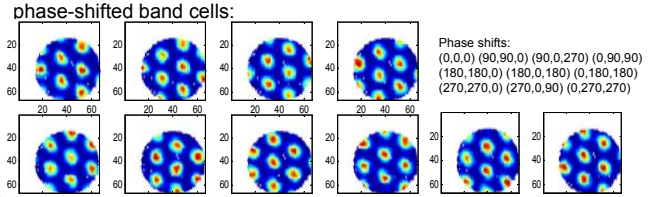
Grid position is determined by reset location:



Reset at a single location divorces grid scale from environmental scale:



Local sets of grid cells which tile environment may result from sets of phase-shifted band cells:



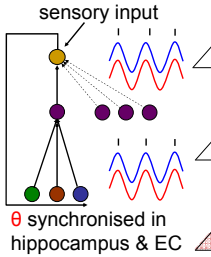
Phase shifts:
(0,0,0) (90,90,0) (90,0,270) (0,90,90)
(180,180,0) (180,0,180) (0,180,180)
(270,270,0) (270,0,90) (0,270,270)

Alignment of grid to environment: phase reset of band cells by place cells

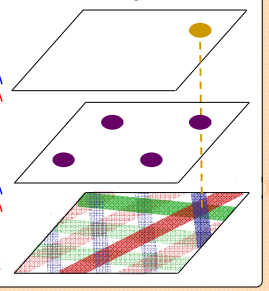
Place cell at peak rate (MPO in phase with θ)

Grid cell driving place cell (1 of many)

Band cells phase-reset by place cell (MPOs in phase with θ)

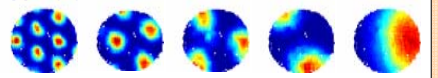


Firing fields

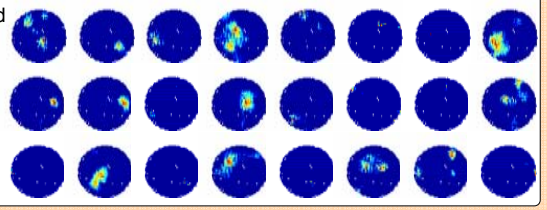


Place fields from overlapping grid cells

Simulate 600 grid cells:: 60 local sets (12 orientations, 5 scales, 60 reset points) of 10 grid cells with different offsets.

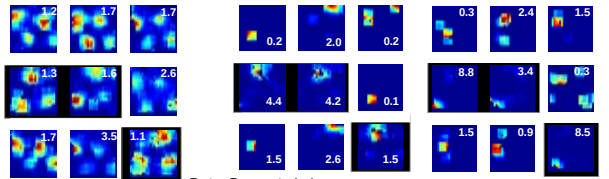


Thresholded sum of 60 randomly chosen grid cells gives realistic looking place fields:



Model is consistent with place fields 'remapping' while grids shift

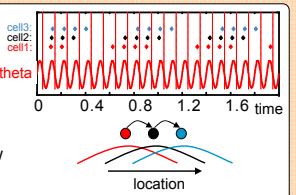
1 grid cell shifts in dark, while 2 simultaneously recorded place cells 'switch on'.



Data, Barry et al., in prep.

Recurrent connections from a band cell

will form predominantly to next cell with same preferred direction ($\varnothing_d$) and phase diff = lag of MPO response (90° = 25ms). Then phase will propagate correctly through the local set, only the band at start of run needing to be phase-reset, and band and grid cells will show predominantly late-early phase precession.



Once set up by interference, these connections would be support P.I. more efficiently than between place cells, as can be fine-tuned throughout environment.

The Boundary Vector Cell model (see Barry et al poster) is consistent with phase reset of grids by sensory input at edge of environment.

Conclusion: grid cell firing could result from interference of multiple MPOs with theta, phase reset by place cells.

References: Hafting T et al. (2005) Microstructure of a spatial map in the entorhinal cortex. *Nature* 436 801-806; Lengyel M et al. (2003) Dynamically detuned oscillations account for the coupled rate and temporal code of place cell firing. *Hippocampus* 13 700-714; O'Keefe J & Burgess N (2005) Dual phase & rate coding in hippocampal place cells: theoretical significance & relationship to entorhinal grid cells *Hippocampus* 15 853-866; O'Keefe J & Recce ML (1993) Phase relationship between hippocampal place units and the EEG theta rhythm. *Hippocampus* 3 317-330.