Dynamics in the grid cell network and the code for position in the rat brain.
Grid cell

Layer II/III cell, Hafting et al., 2005
Response (period, orientation) independent of enclosure size, shape.

Neighbors share period, orientation.
Range of periods: but narrow range

\[ \lambda_i: \ 30 \text{ cm} - 70 \text{ cm} \]

\[ \lambda_{\text{max}} \approx 2 \text{ m} \ll \text{rat range!} \]
- Why/why?

Why such a bizarre decomposition of 2-coordinate position?

Position determines firing, but does firing determine position? I.e., what is conveyed by the code?

*In collaboration with Y. Burak and T. Brookings*

- How?

How can network dynamics produce grid cells?

*In collaboration with Y. Burak*
Population readout in one lattice

modulo remainder: $\hat{x} = (x \mod \lambda)$

many-to-one mapping: position $\rightarrow$ phase
Population-of-populations code

\[(\lambda_1, ..., \lambda_N)\] \hspace{1cm} \text{set of grid periods}

\[\hat{x}_i = (x \mod \lambda_i)\] \hspace{1cm} \text{set of position phases}
Capacity
Idealized case

idealization: $x, \lambda_i$ whole numbers (dimensionless)

CRT: unique, invertible representation of $x$ in $[0, x_{\text{max}}-1]$

$$x_{\text{max}} = \text{LCM}(\lambda_i) = \prod_i \lambda_i \sim \lambda^n$$

modulii: (13, 15, 16, 17, 19)

20 = (7, 5, 4, 3, 1)

1000000 = (1, 10, 0, 9, 11)

$x_{\text{max}} = 1007760$
Actual (non-idealized) dMEC

- $x$, periods (modulii $\lambda$) non-integer, dimensional
- phases not modulo residues $\phi_i = 2\pi(x \mod \lambda_i)/\lambda_i$
- phase uncertainty: $\Delta\phi$ (across all lattices)

No mathematical results for range/capacity/invertibility.
What’s capacity?

Crude capacity estimate $\sim \lambda \Delta \phi \ (1/\Delta \phi)^N$

Actually, how far you can travel before landing within $\Delta \phi$ of a previously encountered set of phases.
Realistic case capacity

$x$ real-valued, dimensional; phase inexact

$N_{\text{eff}} \sim 10.5$

Scales like idealized case: capacity *combinatorial* in $N$
(even though wasteful within each lattice)
Why capacity is important: behavior

(1) Unique name-labels for large range~ 100 m x 100 m

(2) high-resolution position resolution for local path integration

Russell et al., Nature 2005

Whishaw & Maaswinkel, J Neurosci 1998

Maaswinkel et al., Hippocampus 1999
Comparison: EC, hippocampus

- $10^6$ HPC cells cover $<(20 \text{ m})^2$.
- Uniform coverage of large spaces impossible.
- Hippocampus not path integrator or locus of general purpose position representation.
Beyond capacity...
Narrow register range

<table>
<thead>
<tr>
<th>registers</th>
<th>capacity</th>
</tr>
</thead>
<tbody>
<tr>
<td>decimal</td>
<td>(10⁵, 10⁴, 10³, 10², 10¹, 10⁰)</td>
</tr>
<tr>
<td>modulo</td>
<td>(1003, 103, 13)</td>
</tr>
<tr>
<td>modulo</td>
<td>(18, 17, 16, 15, 14, 13)</td>
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</table>

<table>
<thead>
<tr>
<th>decimal</th>
<th>modulo</th>
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<tbody>
<tr>
<td>45</td>
<td>(9, 11, 13, 0, 3, 6)</td>
</tr>
<tr>
<td>800,000</td>
<td>(8, 14, 0, 5, 12, 6)</td>
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<tr>
<td>800,001</td>
<td>(9, 15, 1, 6, 13, 7)</td>
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</tbody>
</table>

Do not require network parameters to span several orders of magnitude. Lesions of any lattice equal.
Carry-free arithmetic

decimal \((10^2, 10^1, 10^0)\)

\[
\begin{array}{c}
1 \\
9 \\
+ \\
\hline \\
101
\end{array}
\]

modulo \((7,6,5)\)

\[
\begin{array}{c}
6 \\
1 \\
2 \\
+ \\
\hline \\
351
\end{array}
\]

No carry-over of information across lattices for position updating when rat moves
Metrics unrelated to real-space metrics

Not easy to make distance comparisons beyond
Downstream uses of dMEC responses?

- *Explicitly metric readout*: for spatial tasks like distance/direction vector computation in landmark-free homing.

- *Non-metric landmark labeling*: dMEC phases as name labels.
Explicit metric use of dMEC code

General phase $\rightarrow$ position/distance/vector reconstruction over large spaces for homing after random trajectories
Name-label use of dMEC code
large library of unique labels for different locations

Have arithmetic properties gone to waste?
No! Metric phase updating in dMEC allows recall of same label for landmark regardless of path
Novel abstract encoding scheme

<table>
<thead>
<tr>
<th>Representation</th>
<th>Capacity</th>
<th>Algorithmic rules for:</th>
<th>Carry-free</th>
<th>Narrow range</th>
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</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>rep(x)</td>
<td>x+y</td>
<td>x&gt;y?</td>
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<tr>
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<td>✓</td>
<td>✓</td>
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<td>x</td>
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<tr>
<td>modulo</td>
<td>~e_N</td>
<td>✓</td>
<td>✓</td>
<td>x</td>
</tr>
</tbody>
</table>

Continuous metric variable represented by arithmetic-friendly positional numeral system in population-of-populations code
What controls balance of $N, \Delta \phi$?

\begin{align*}
\text{total neurons} & \sim N^* (1/\Delta \phi) \\
\text{capacity} & \sim (1/\Delta \phi)^{N-1}
\end{align*}

Tradeoff between high capacity and accurate dynamics
How?

(1) Static pattern formation

Center-surround connectivity
(2) Pattern flow through velocity coupling

(a) Velocity input

(b) Shifted connections

Zhang 1996; Redish et al, 1996; Goodridge & Touretzky, 2000; Xie et al. 2002; Fuhs & Touretzky 2006.
Periodic boundaries

Works great, but unrealistic?
Boundary conditions not academic

- aperiodic
- periodic, multi-unit cell
- periodic, single unit cell

Experimental probes:

- distribution of maximum firing rates
- existence of defects
- tiling of defect if defect exists
Deduction of function from connectivity?

- $0^{th}$ order connections center-surround but possibly non-topographic.

- Very subtle connectivity shifts, depending on angular preference of neuron (1-neuron shift).

- Must functionally map phases of all neurons; then look for connectivity shifts as a function of phase.
Self-organization/learning

• Aperiodic+static pattern formation easy if topographic.
• Velocity shift mechanism?
• Isotropy?
• Non-topographic connectivity?
• Periodic boundary: many unit cells or one?
Collaborators

• Coding:
  – Yoram Burak (Harvard)
  – Ted Brookings (Brandeis)

• Dynamics
  – Yoram Burak (Harvard)
  – Peter Welinder (Caltech)