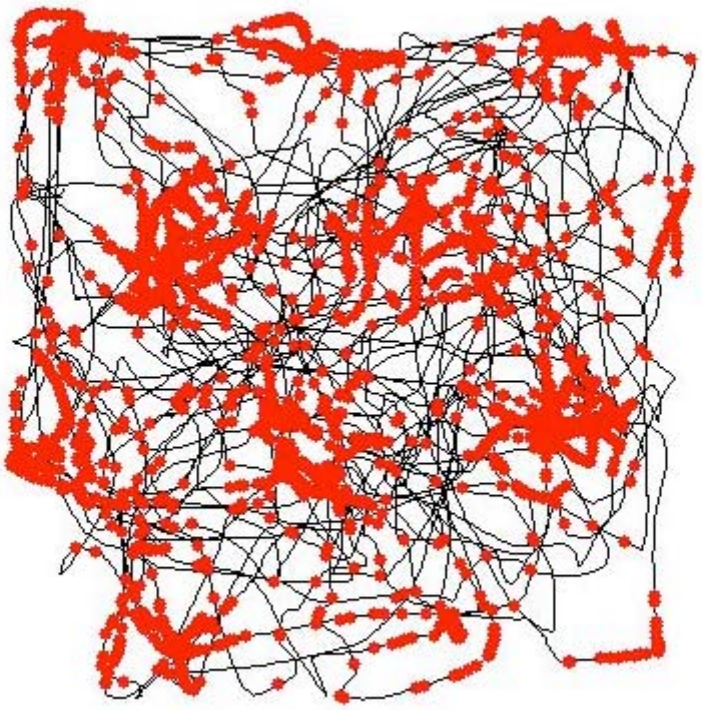
Dynamics in the grid cell network and the code for position in the rat brain.

Ila Fiete, Caltech

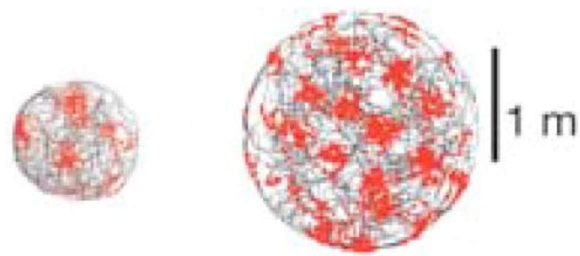
thebroadfoundations

Grid cell

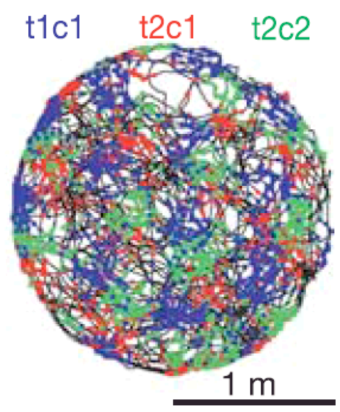


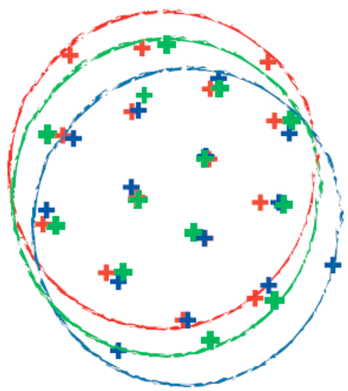
Layer II/III cell, Hafting et al., 2005

Response (period, orientation) independent of enclosure size, shap

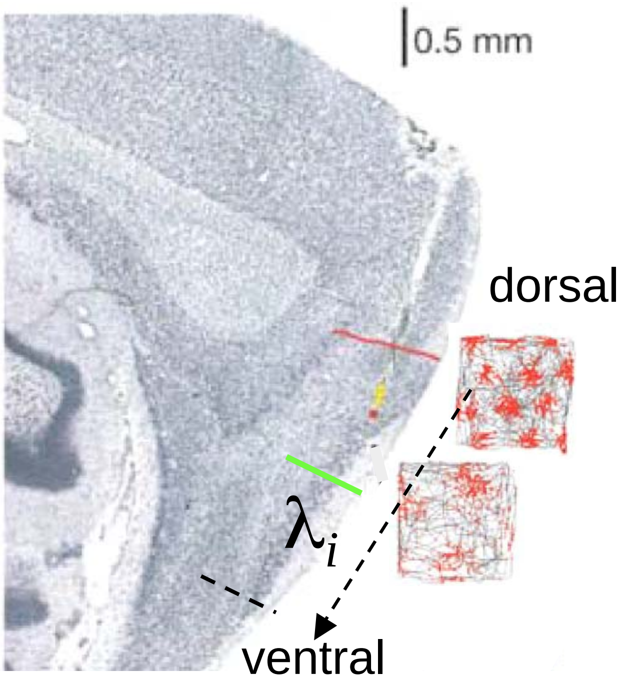


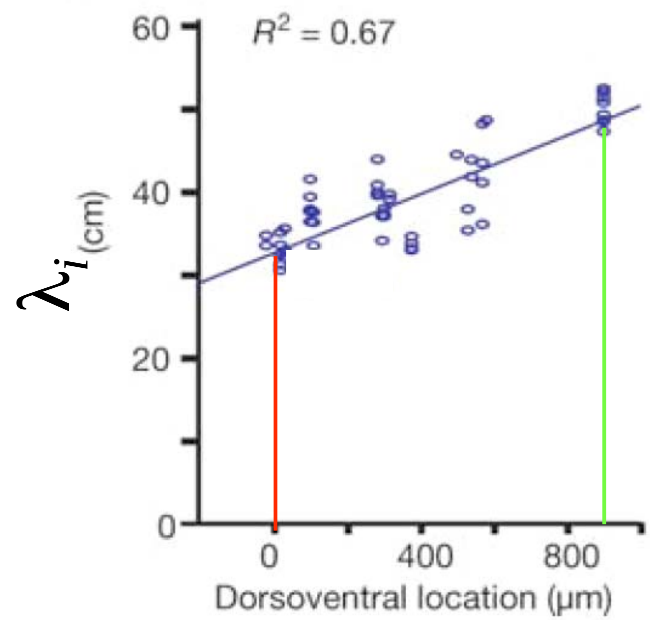
Neighbors share period, orientation





Range of periods: but narrow range





λ_i: 30 cm - 70 cm

λ_{max} <~ 2 m << rat range!?

- What/why?

Why such a bizzare decomposition of 2-coordinate position?

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

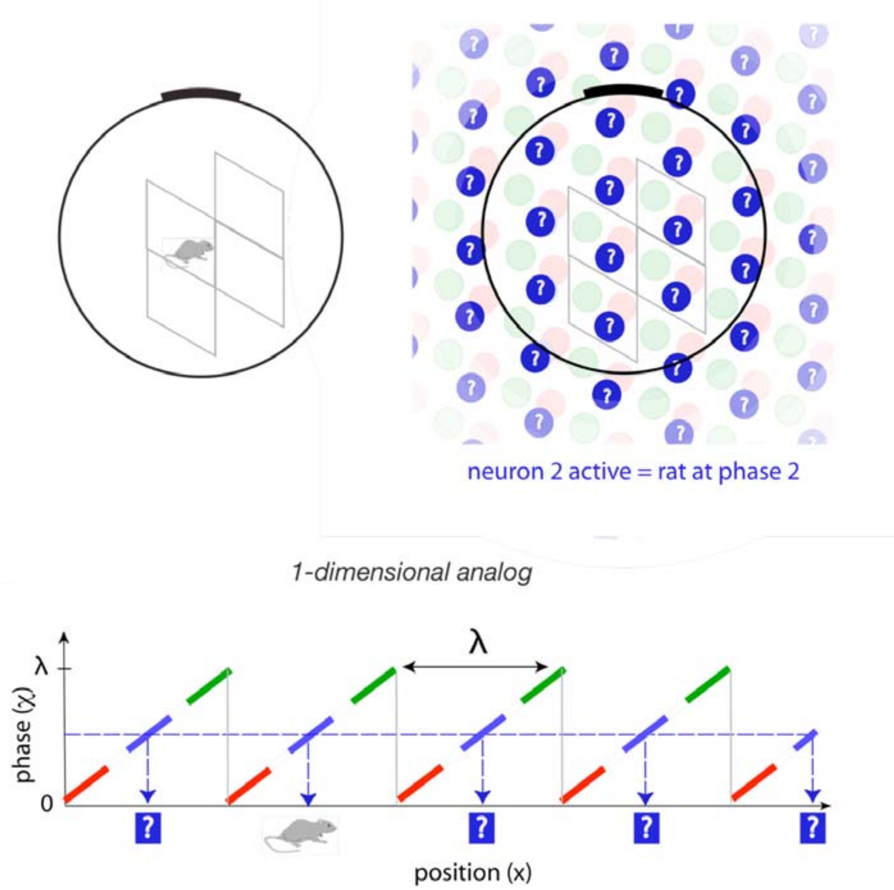
In collaboration with Y. Burak and T. Brookings

- How?

How can network dynamics produce grid cells?

In collaboration with Y. Burak

Population readout in one lattice



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

many-to-one mapping: position → phase

Population-of-populations code

$(\lambda_1, ..., \lambda_N)$ set of grid periods

$\hat{x}_i = (x \bmod \lambda_i)$ set of position phases

Capacity

Idealized case

idealization: x, λ_i whole numbers (dimensionless)

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

$$x_{max} = \mathrm{LCM}(\lambda_i) = \prod_i \lambda_i \quad \sim \lambda^N$$

moduli: (13, 15, 16, 17, 19) $\quad x_{max} = 1007760$

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

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

Actual (non-idealized) dMEC

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

No mathematical results for range/capacity/invertibility.

What's capacity?

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

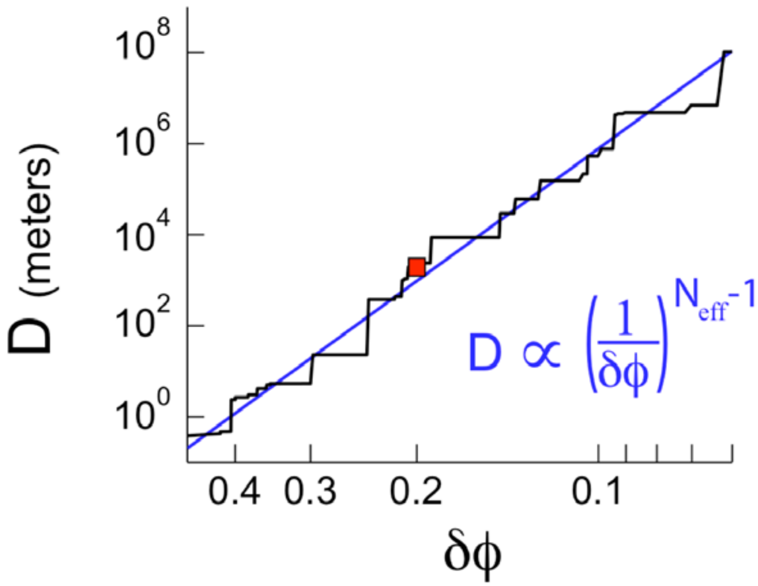
travel distance
to state transition

states

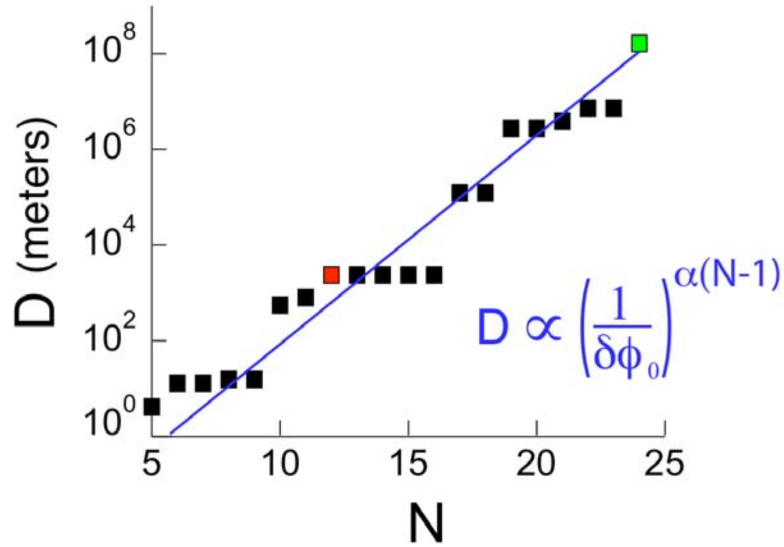
Actually, how far you can travel before landing within $\Delta\phi$ of a previously encountered set of phases.

Realistic case capacity

x real-valued, dimensional; phase inexact



$N_{eff} \sim 10.5$



$\alpha \sim 0.9$

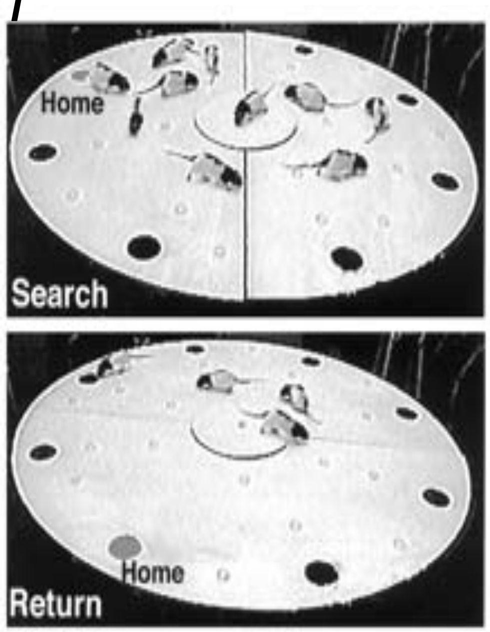
Scales like idealized case: capacity *combinatorial* in N (even though wasteful within each lattice)

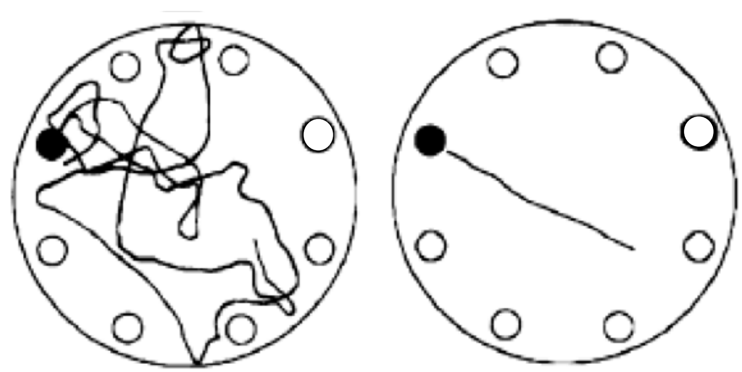
Why capacity is important: behavior

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

Russell et al., Nature 2005

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





Whishaw & Maaswinkel, J Neurosci 1998

Maaswinkel et al., Hippocampus 1999

Comparison: EC, hippocampus

N	$\delta\phi_0$	D (m)	# grid cells	# place cells
12	0.2	2×10^3	5×10^4	$\sim 10^{10}$
24	0.2	2×10^8	1×10^5	$\sim 10^{20}$

5000 neurons/grid
=5000 neurons/(30 cm)^2

10 neurons / (6 cm)^2

- 10^6 HPC cells cover <(20 m)^2.
- Uniform coverage of large spaces impossible.
- Hippocampus not path integrator or locus of general purpose position representation.

Beyond capacity...

Narrow register range

	registers	capacity
decimal	$(10^5, 10^4, 10^3, 10^2, 10^1, 10^0)$	1,000,000
modulo	(1003, 103, 13)	1,343,017
modulo	(18, 17, 16, 15, 14, 13)	1,113,840

decimal		modulo (18, 17, 16, 15, 14, 13)
45	=	(9, 11, 13, 0, 3, 6)
800,000	=	(8, 14, 0, 5, 12, 6)
800,001	=	(9, 15, 1, 6, 13, 7)

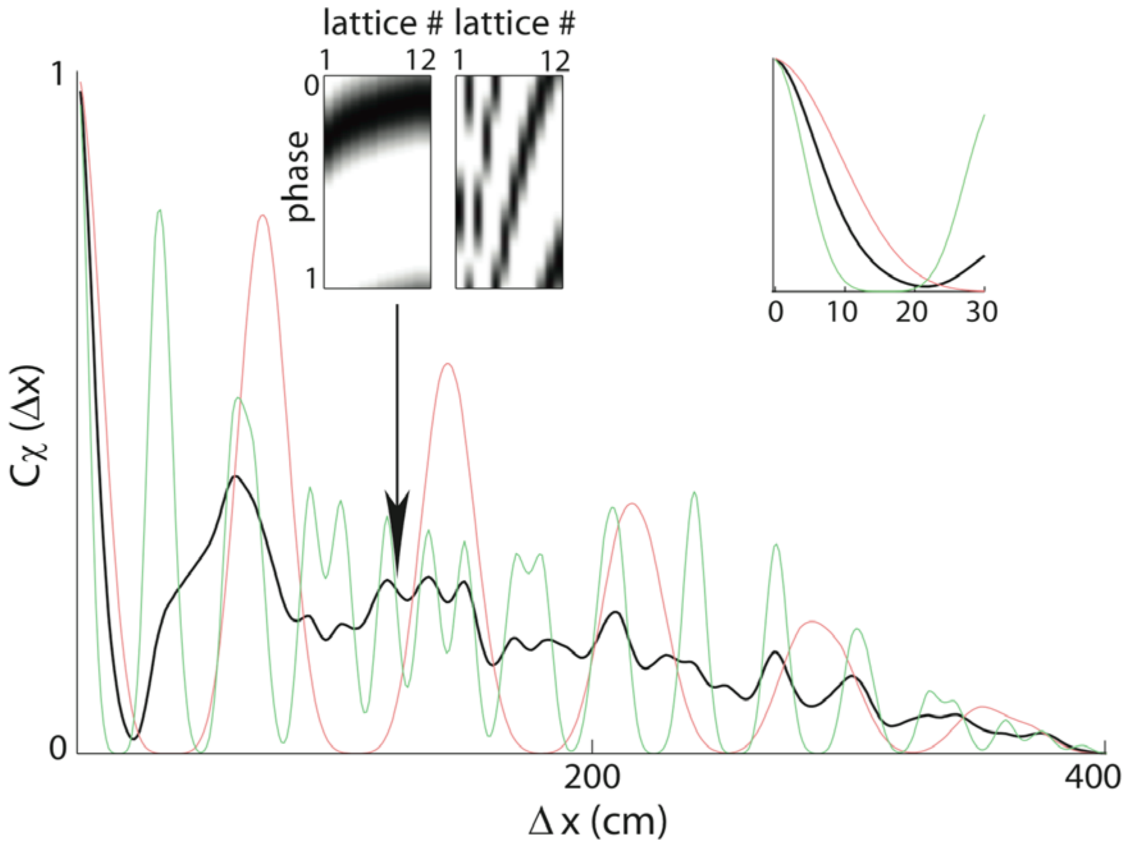
Do not require network parameters to span several orders of magnitude. Lesions of any lattice equal.

Carry-free arithmetic

decimal $(10^2, 10^1, 10^0)$	modulo (7,6,5)
1 1 (carries)	
9 7	6 1 2
+ 4	+ 4 4 4
1 0 1	3 5 1

No carry-over of information across lattices for position updating when rat moves

Metrics unrelated to real-space metrics



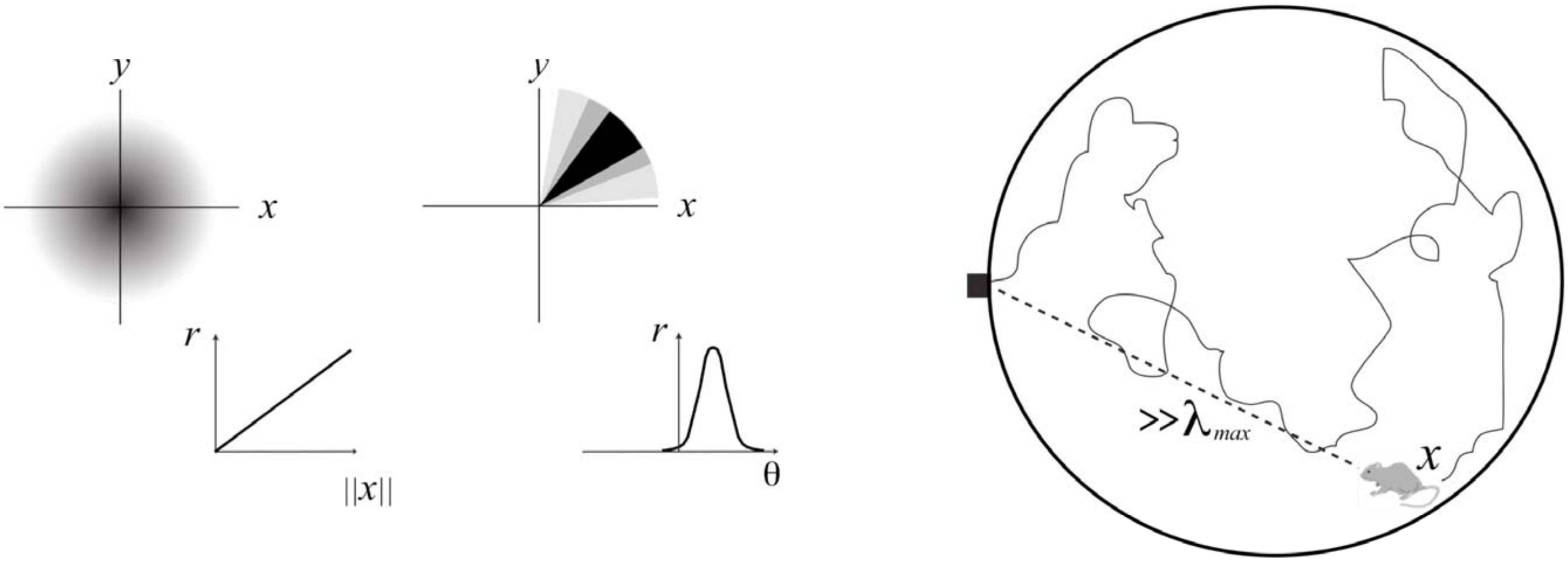
Not easy to make distance comparisons beyond

Downstream uses of dMEC responses?

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

- *Non-metric landmark labeling*: dMEC phases as name labels.

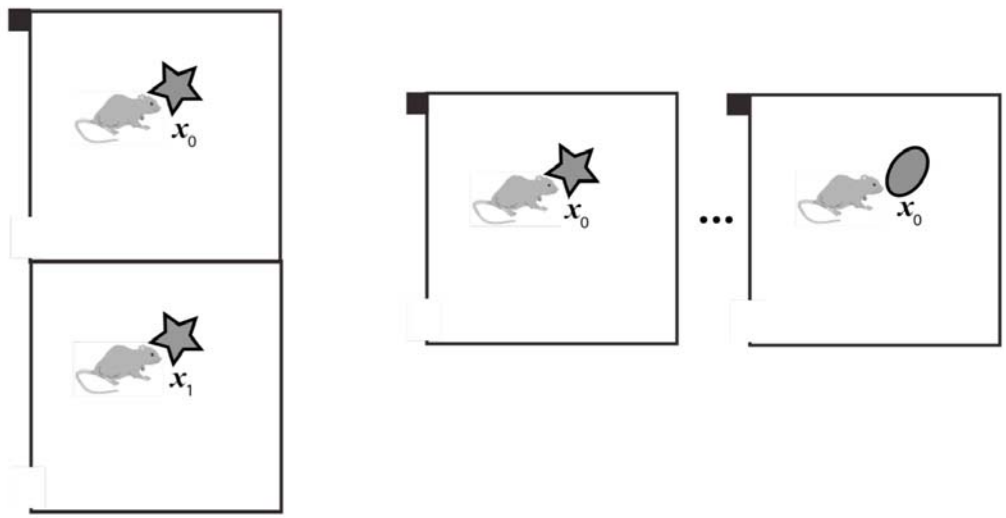
Explicit metric use of dMEC code



General phase→ 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



different locations, same appearance

same location, different appearance

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

Representation	Capacity	Algorithmic rules for: rep(x)	x+y	x>y?	Carry-free	Narrow range
unary	~N	✓	✓	✓	—	—
roman numeral	$\sim e^N$	✓	✗	✓	—	—
combinatorial name	$\sim e^N$	✓	✗	✗	—	—
fixed-base	$\sim e^N$	✓	✓	✓	✗	✗
modulo	$\sim e^N$	✓	✓	✗	✓	✓

Continuous metric variable represented by arithmetic-friendly positional numeral system in population-of-populations code

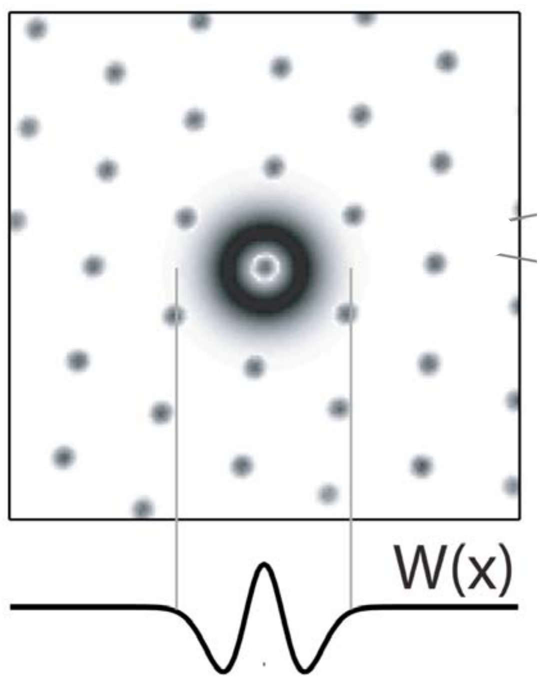
What controls balance of N, $\Delta\phi$?

total neurons	$\sim N*(1/\Delta\phi)$
capacity	$\sim (1/\Delta\phi)^{N-1}$

Tradeoff between high capacity and accurate dynamics

How?

(1) Static pattern formation

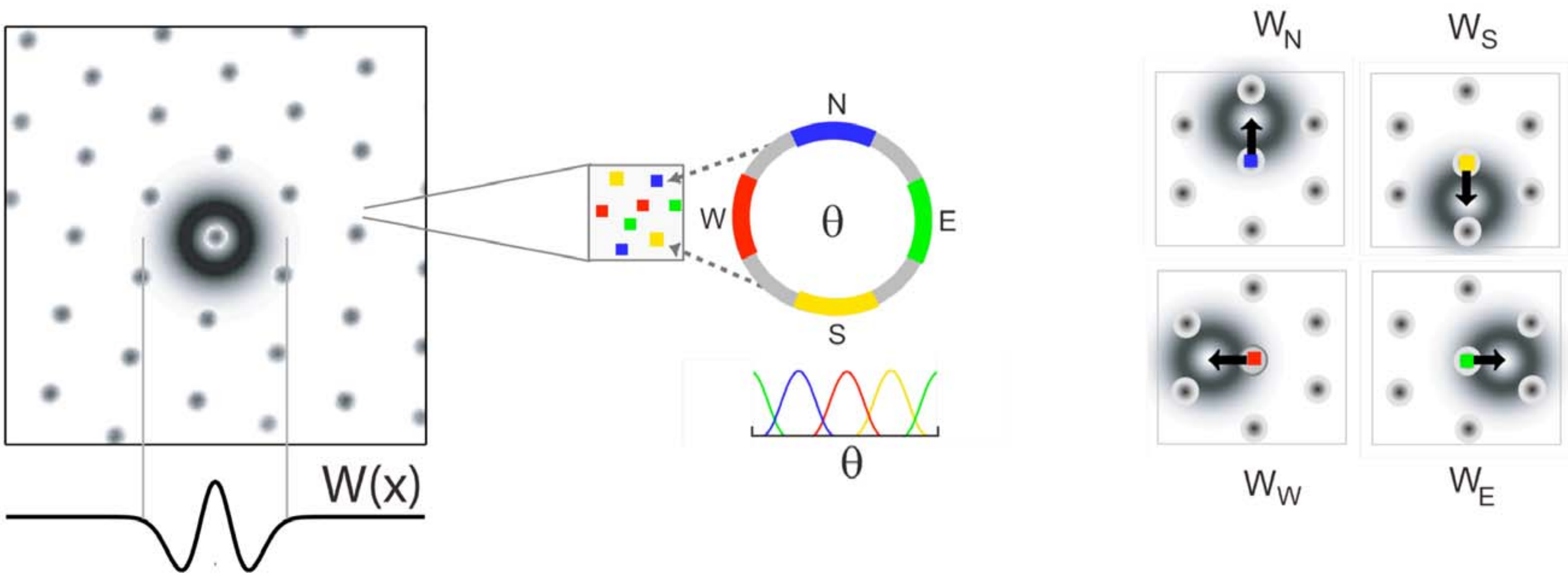


population response

Center-surround connectivity

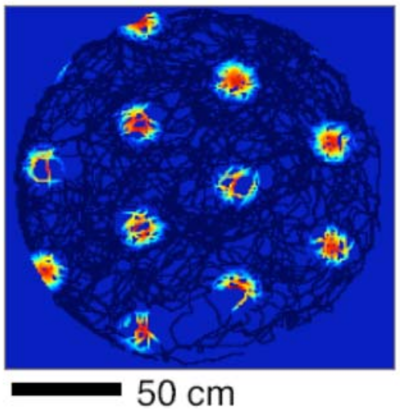
(2) Pattern flow through velocity coupling

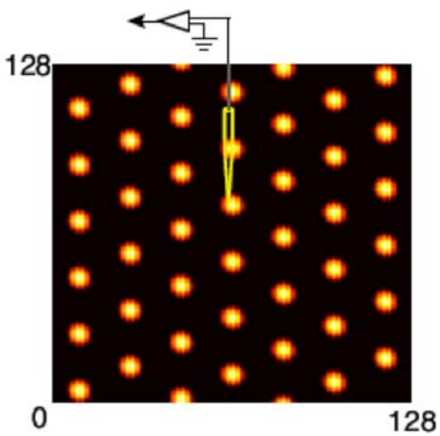
(a) Velocity input *(b) Shifted connections*

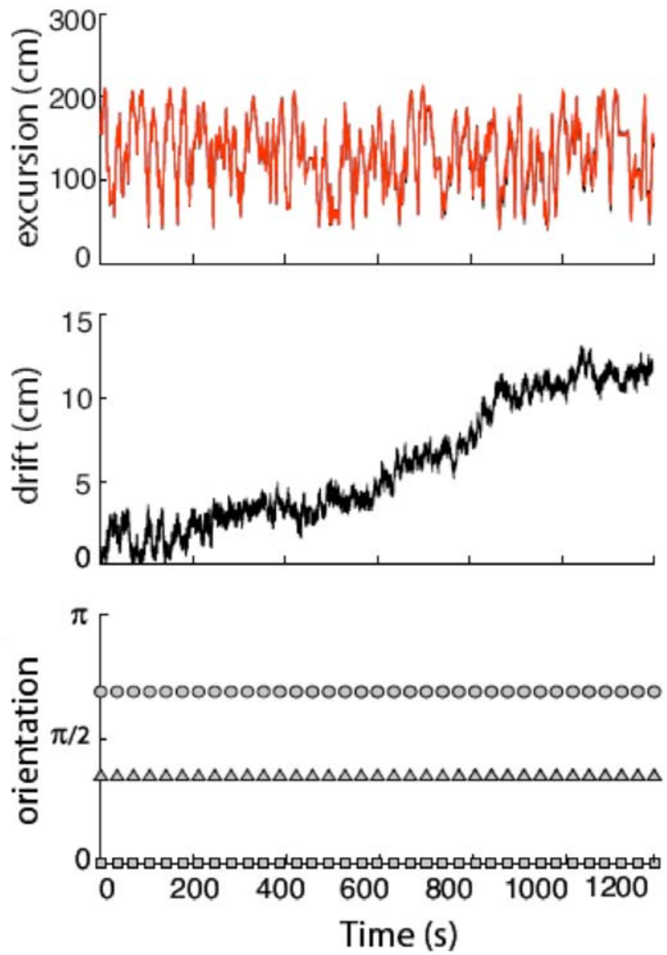


Zhang 1996; Redish et al, 1996;
Goodridge & Touretzky, 2000;
Xie et al. 2002; Fuhs & Touretzky 2006.

Periodic boundaries







~ perfect idiothetic path integration ove
~ 200 m and 20 min

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)