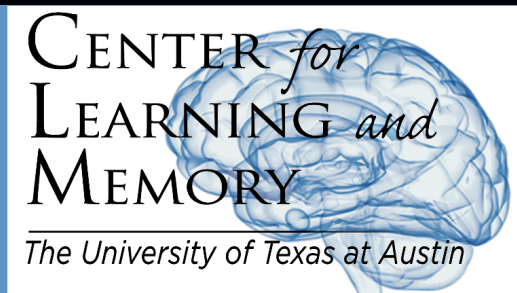
Mechanisms and the code for spatial representation in grid cells

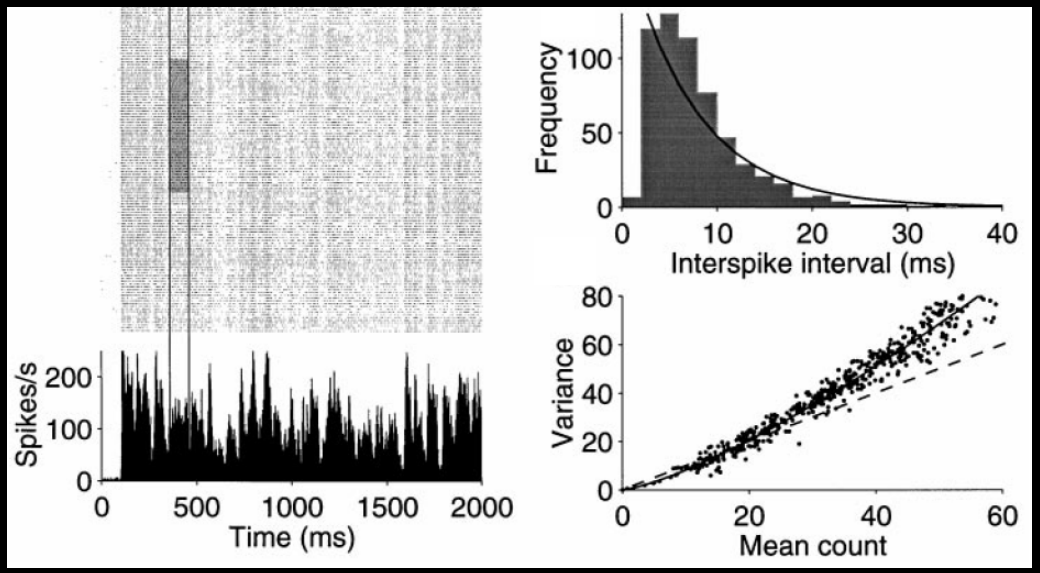
KITP Program: Neurophysics of space, time, and learning

Ila Fiete
The University of Texas at Austin



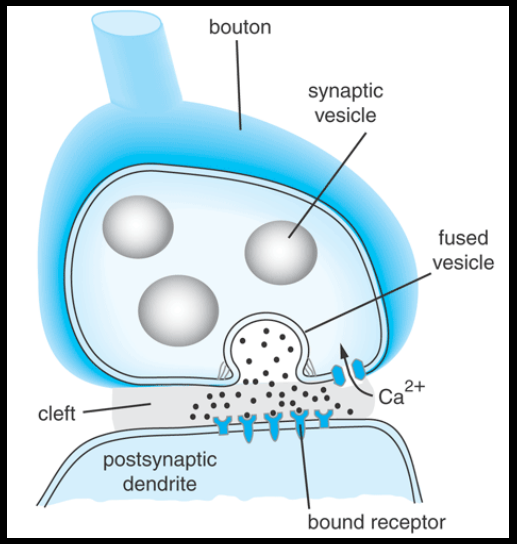
The computational elements of the brain are noisy

CV of cortical spiking ~ 1



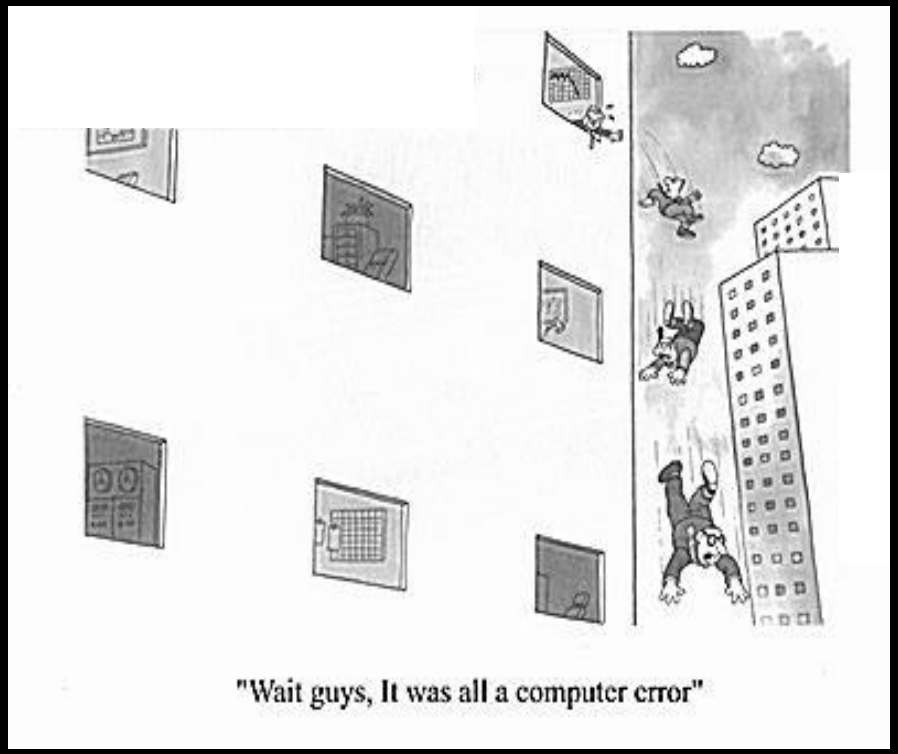
Softky and Koch, 1993
Shadlen and Newsome, 1998

probabilistic synaptic transmission

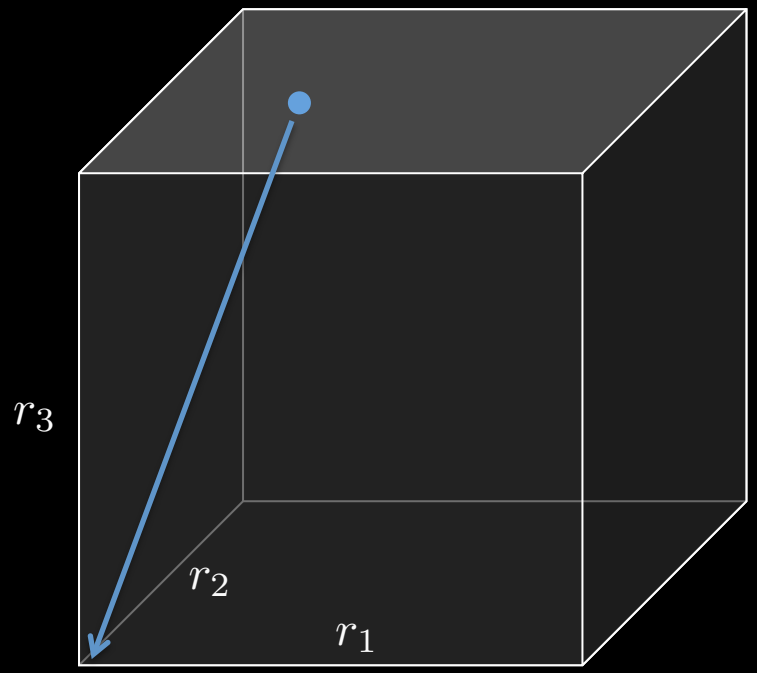


Katz, 1969
Raastad et al., 1992
Stevens 1994

Noise-induced errors can be problemmatic

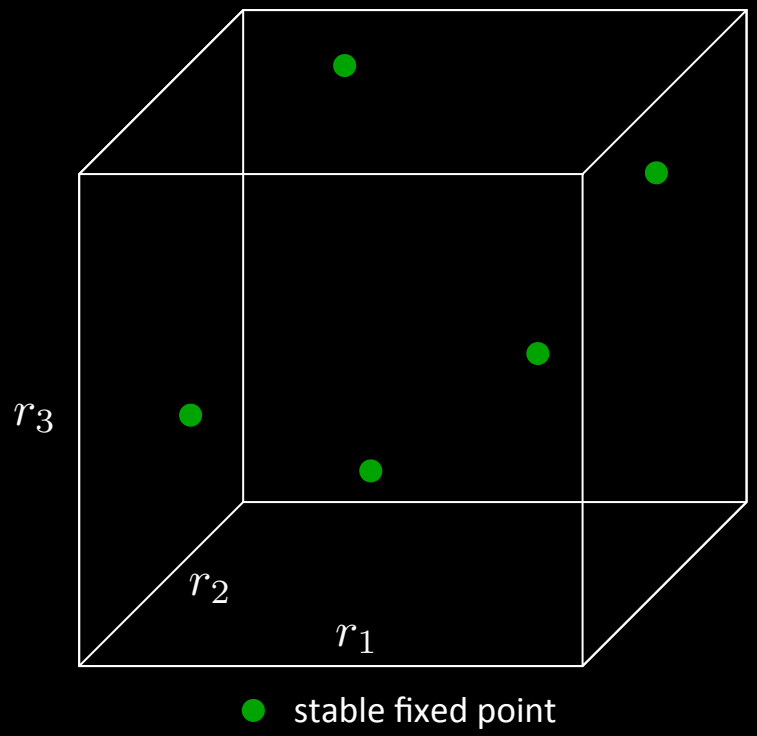


Huge state-space of N neurons



Large (N-dim) representational space. But no memory or noise tolerance.

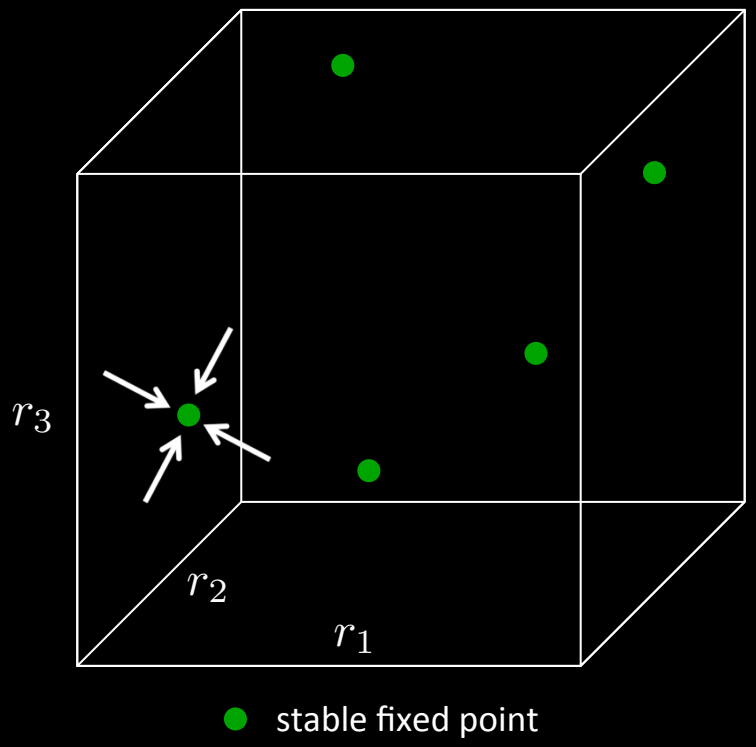
Specific recurrent connectivity: can stabilize some states at expense of others



Hopfield 1982;
various others on capacity of Hopfield nets.

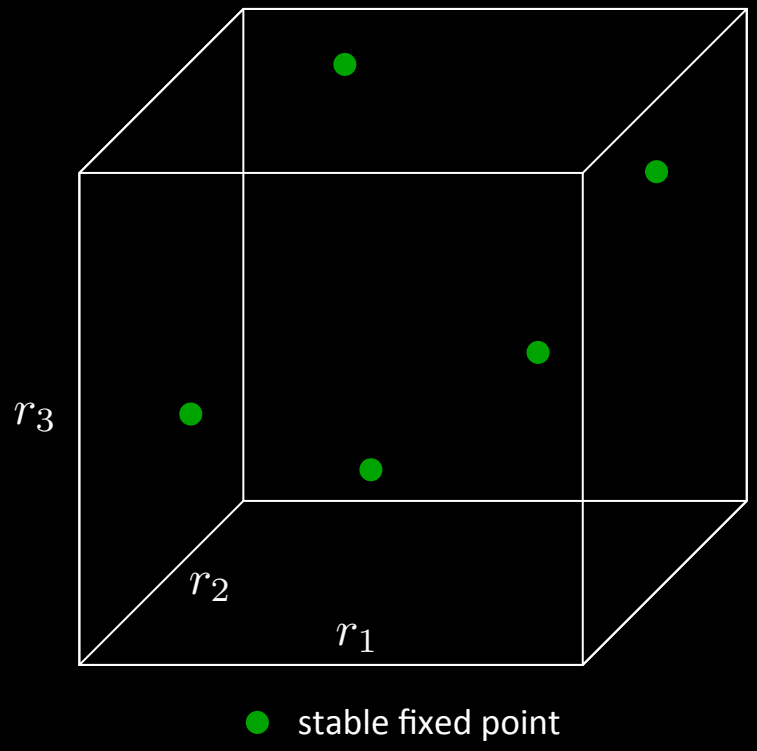
Decreased representational space (e.g. N-d → 0-d, or ~Q^N → ~N).

Advantage: noise tolerance (error correction)



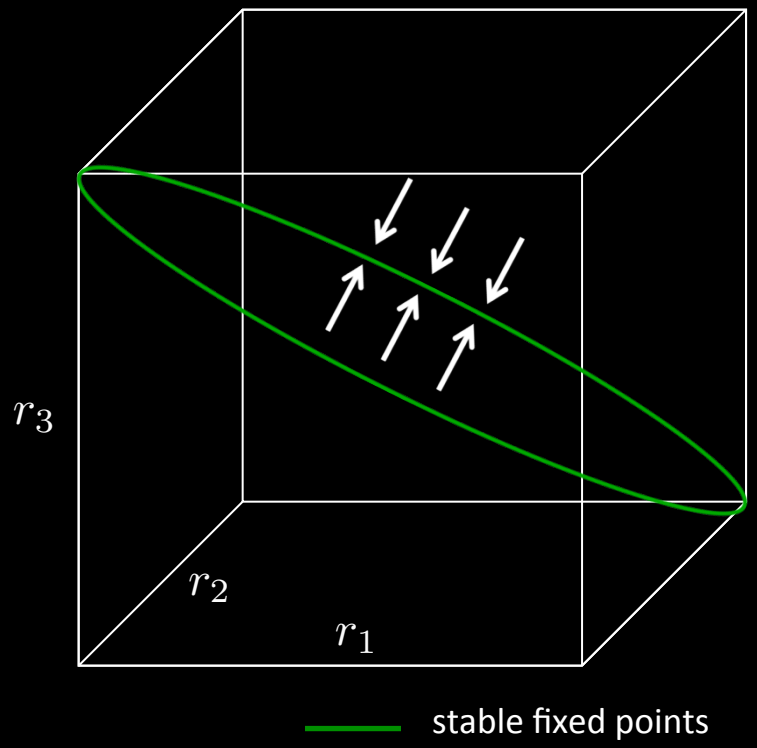
Perturbations away from the fixed points are corrected.

Advantage: persistent activity (memory states)



States stabilized by positive feedback do not decay rapidly and can hold a memory.

Continuous set of fixed points: can represent continuous variables



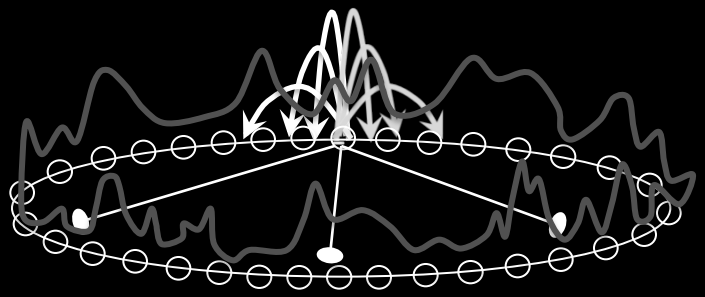
Ben-Yishai & Sompolinsky 1996
Zhang 1996
Seung 1996å

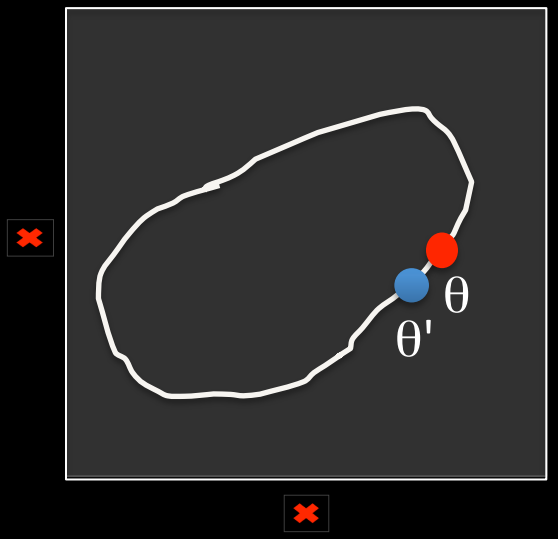
What is representational capacity?

Mechanism: circuits for noise reduction and validation

Ring model: simple continuous attractor network

E.g.: ring network





Ben-Yishai, Bar-Or, Sompolinsky 1995;
Zhang 1996.

Reaching beyond analogy:

Does the brain contain and compute with continuous attractors?

Hypothesized continuous attractor systems

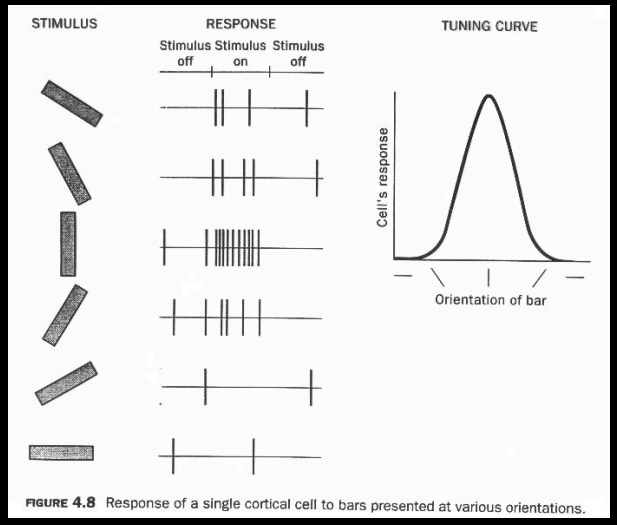
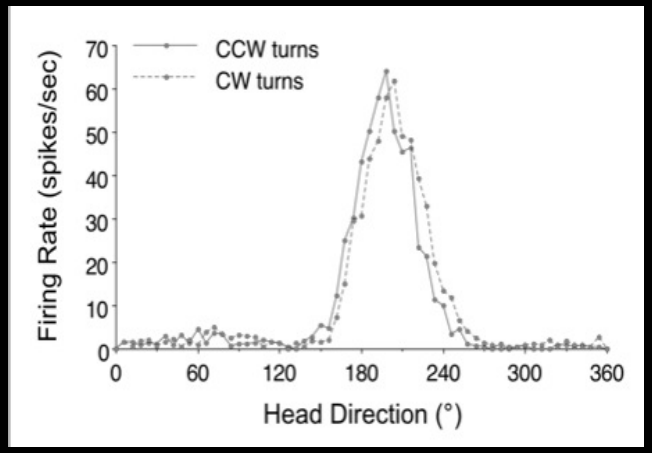
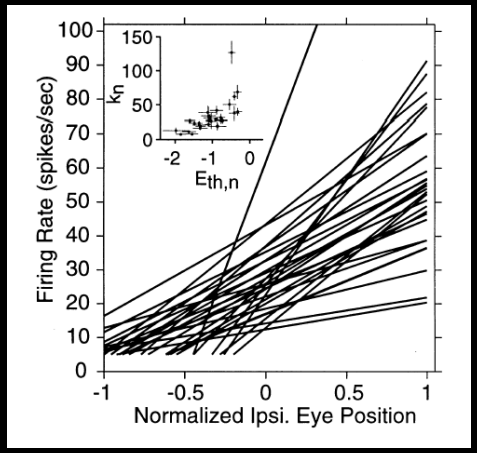


FIGURE 4.8 Response of a single cortical cell to bars presented at various orientations.

V1 orientation tuning
Hubel & Wiesel 1959
Ben Yishai, Bar-Or, Sompolinsky 1995



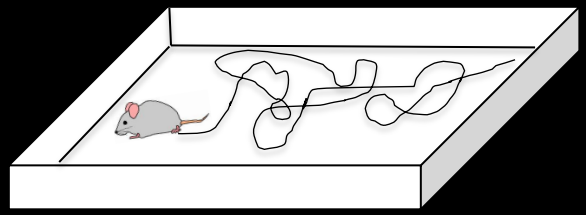
Head-direction cells
Taube et al.
Zhang 1996

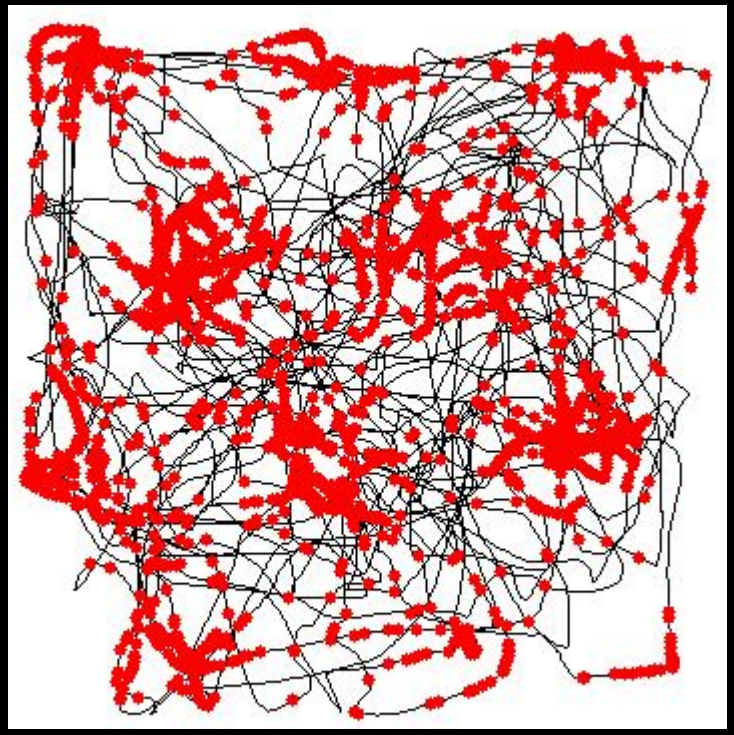


Oculomotor neurons
Cannon &Robinson
Aksay et al. 2001, 2003
Seung 1996

Stable tuning curves, short-term memory, integration, readouts for population codes

Grid cell response to 2-d location



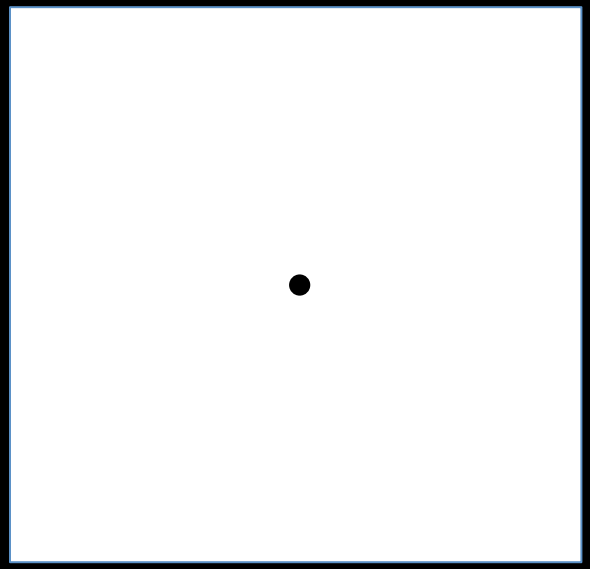


Layer II/III cell, entorhinal cortex.

Hafting et al., 2005

Static pattern formation

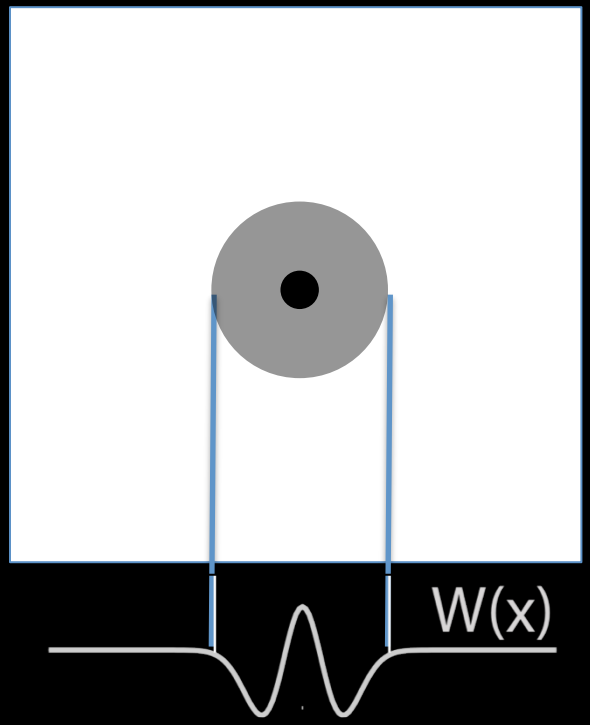
2-d neural sheet



$$\tau \frac{dr(\mathbf{x})}{dt} + r(\mathbf{x}) = f\left(\sum_{\mathbf{x}'} W(\mathbf{x}-\mathbf{x}')r(\mathbf{x}') + b(\mathbf{x})\right)$$

Fuhs & Touretzky 2006.
Burak & Fiete, 2006, 2009.

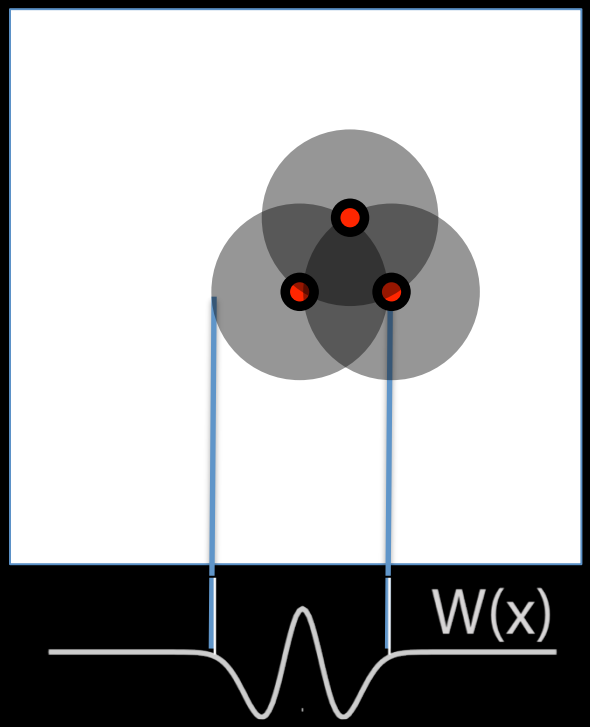
Static pattern formation

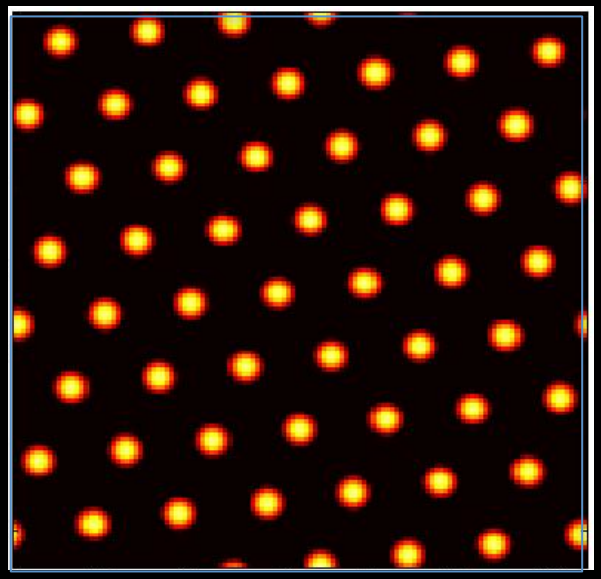


Center-surround connectivity

Burak & Fiete, 2006, 2009.

Static pattern formation

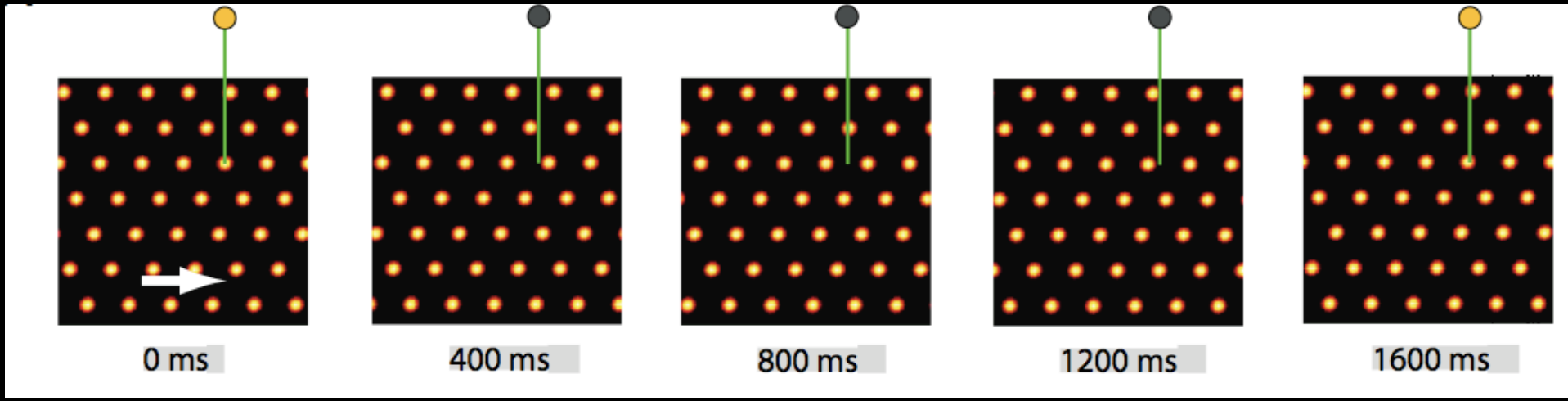




strong surround inhibition→ pattern formation in population

Fuhs & Touretzky 2006.
Burak & Fiete, 2006, 2009.

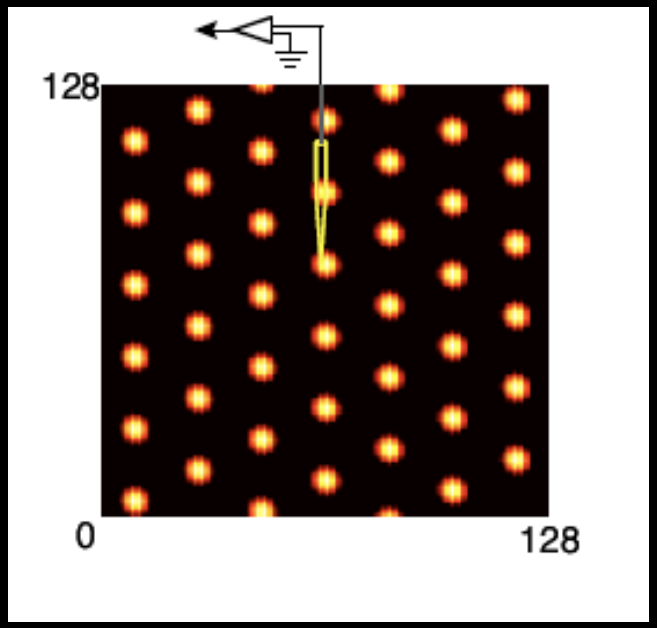
Pattern flow coupled to animal velocity generates periodic single-neuron responses



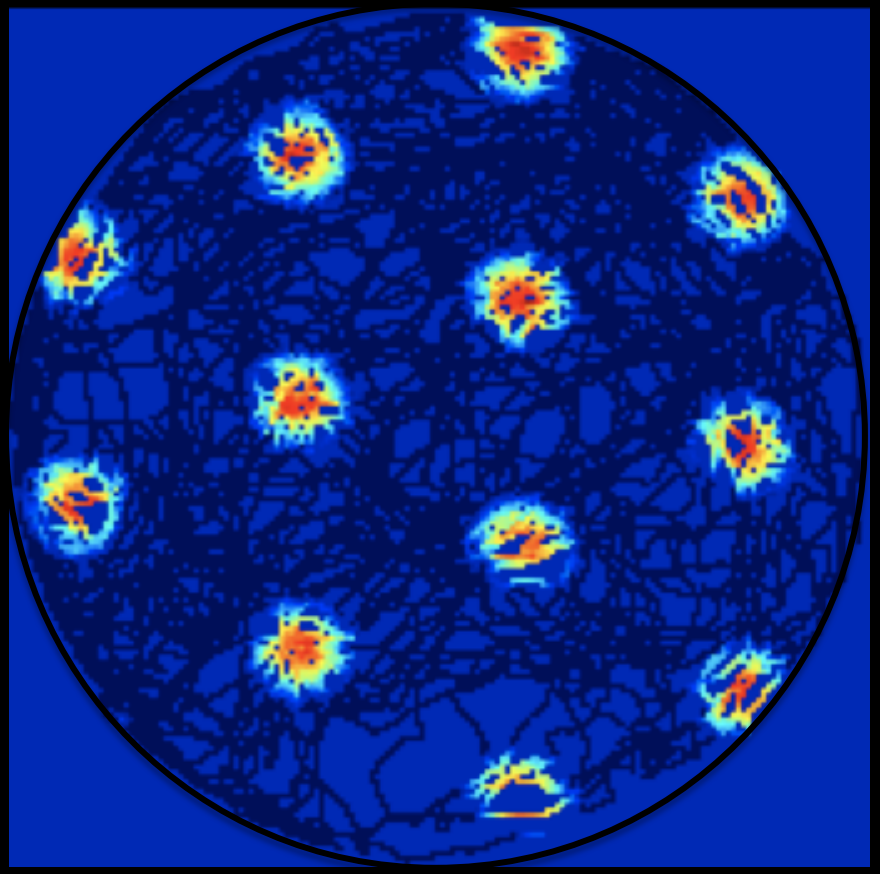
$$\tau \frac{dr(\mathbf{x},\theta)}{dt} + r(\mathbf{x},\theta) = f\left(\sum_{\mathbf{x}',\theta'} W(|\mathbf{x}-\mathbf{x}'|,\theta') r(\mathbf{x}',\theta') + b(\mathbf{x},\theta)\right)$$

Fuhs & Touretzky 2006.
Burak & Fiete, 2006, 2009.

Spatial tuning of individual neurons



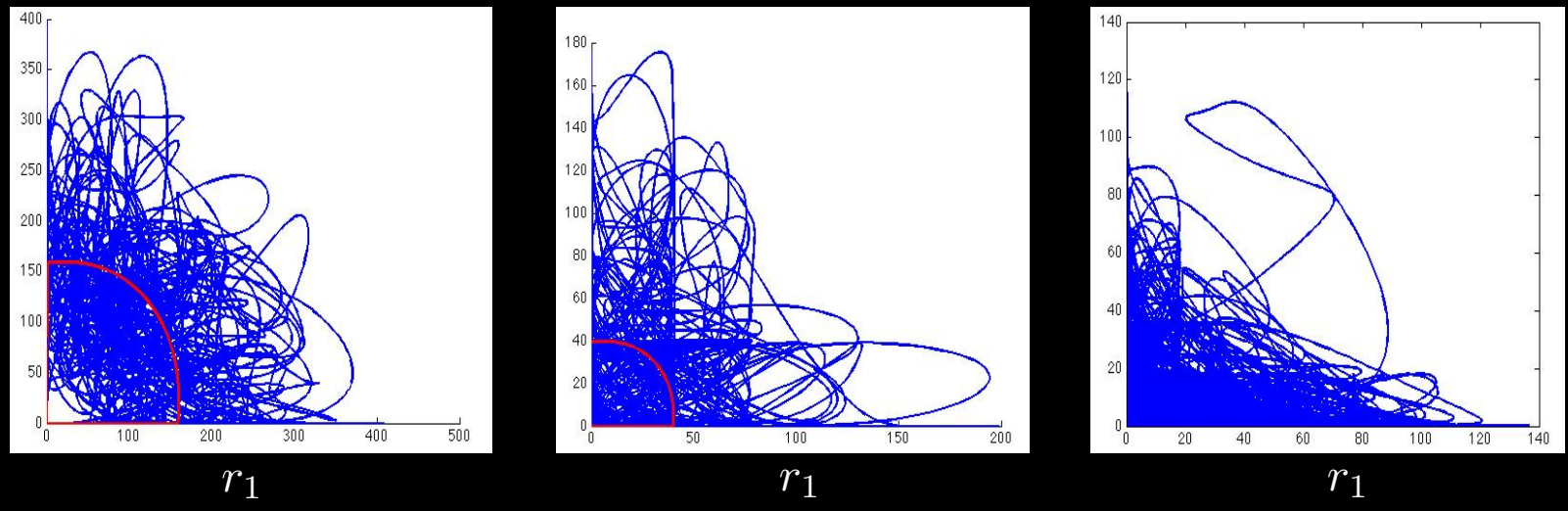
population response



single-neuron spatial tuning

Burak & Fiete, 2006, 2009.

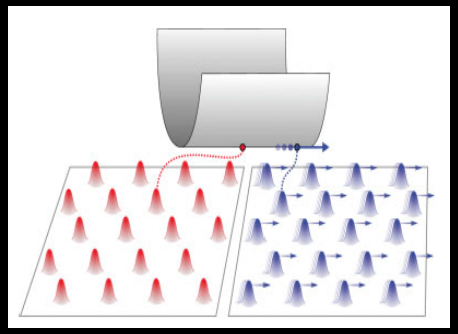
Direct visualization of low-dimensional structures in state-space?



Under realistic neural variability, difficult to learn whether there is low-dimensional structure from time-series responses (model-free).

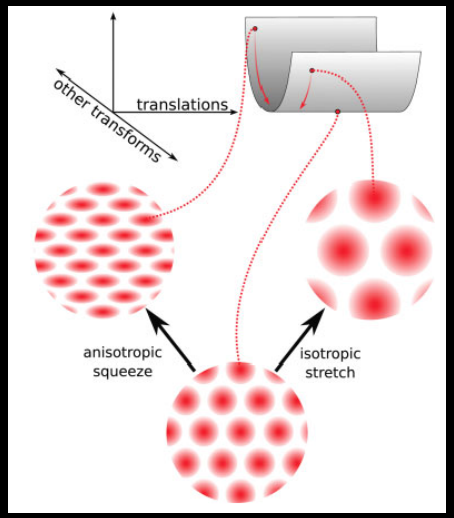
Key predictions

- Uniform distribution of relative phases.
- Identical tuning of neurons up to phase.



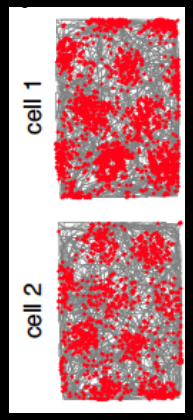
- Changes in population pattern not permitted
- (if network weights/biophysics unchanged):

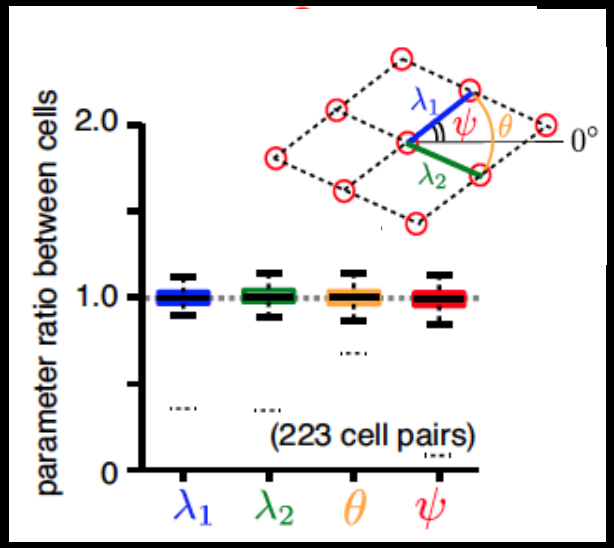
Absolute stability of relative phases,
regardless of changes in tuning

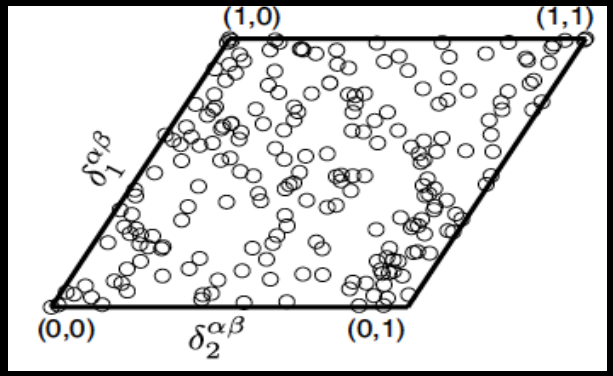


Burak & Fiete, 2006, 2009.
Yoon et al. 2013.

Tuning and relative phase distribution





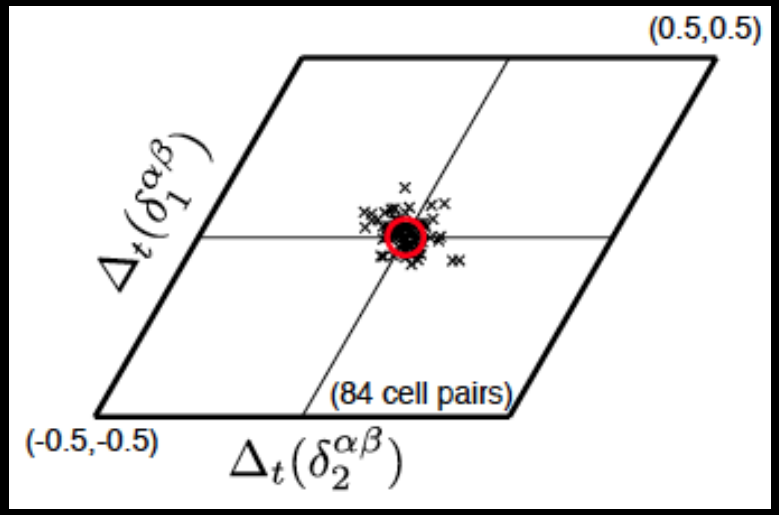


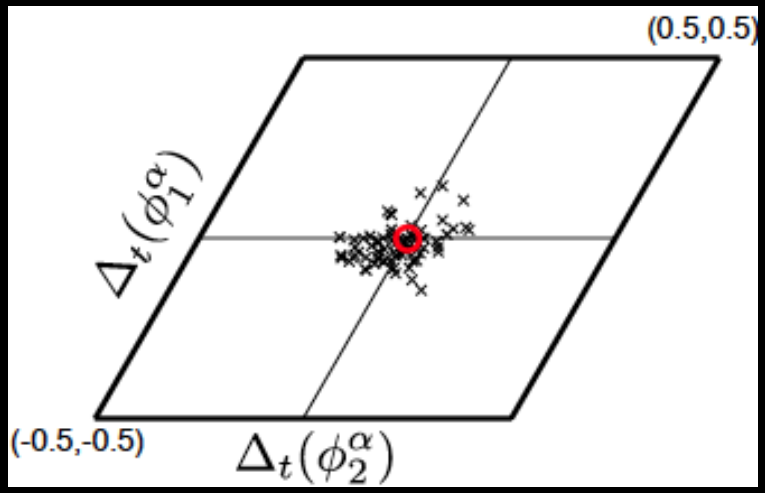
Data: Moser, Burgess, Jeffery labs

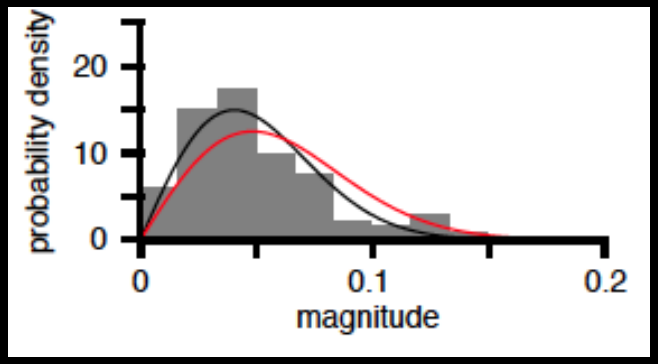
Yoon, Barry, Hayman, Burgess, Fiete, *Nature Neurosci* 2013

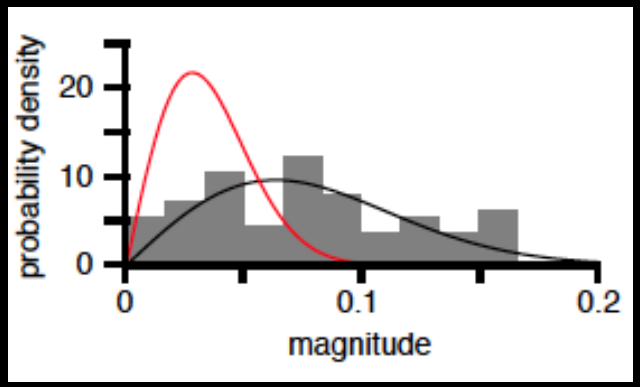
Simultaneously recorded cell pairs from a neighborhood with similar period: identical parameter ratios and uniform distribution of relative phases.

Relative phase conserved over 1-3 hours (even though phases themselves shift)





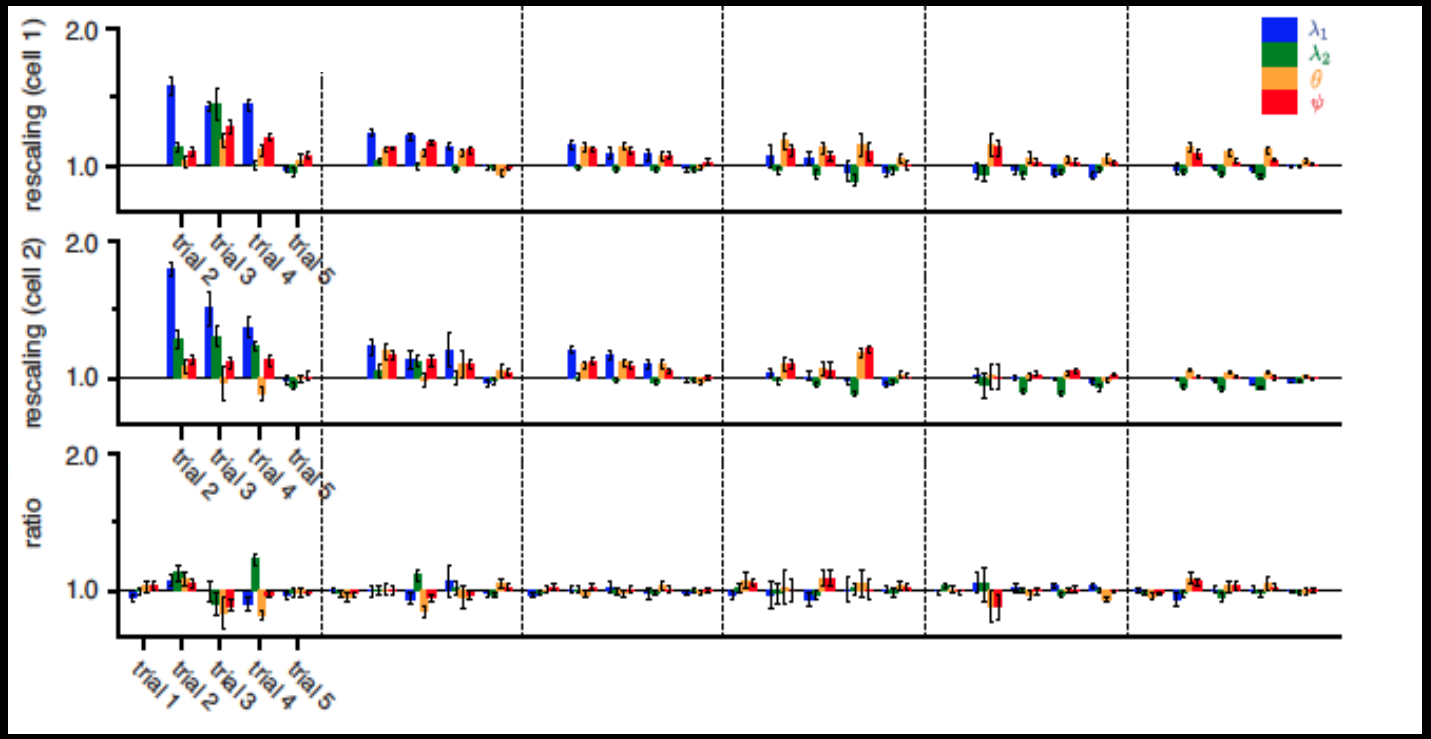




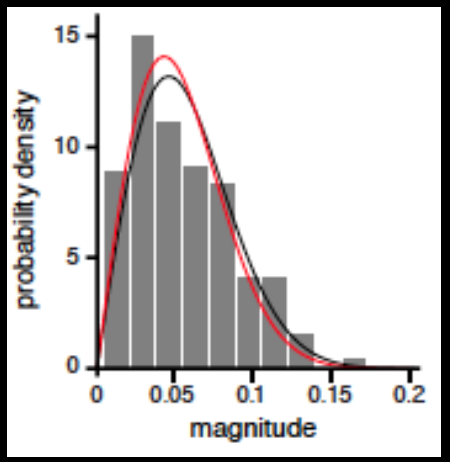
Yoon, Barry, Hayman, Burgess, Fiete, *Nature Neurosci* 2013

Relative phase more stable than absolute phases.
Relative phase stability *cannot* be ascribed to external cues.

Novel environments: parameters change but ratios and relative phase conserved from very first run



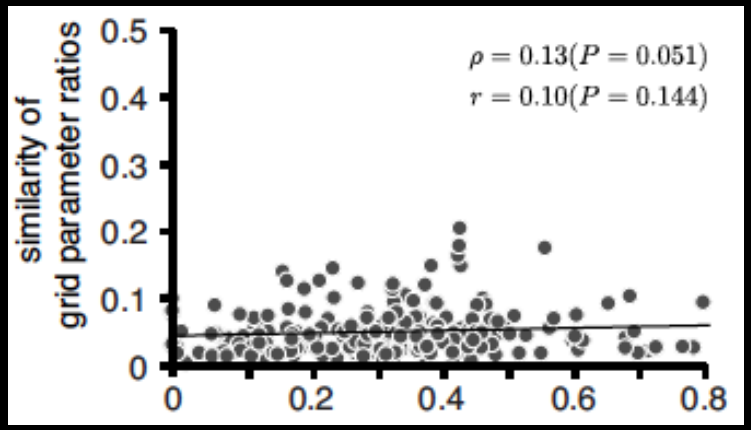
Magnitude of differences in relative phase

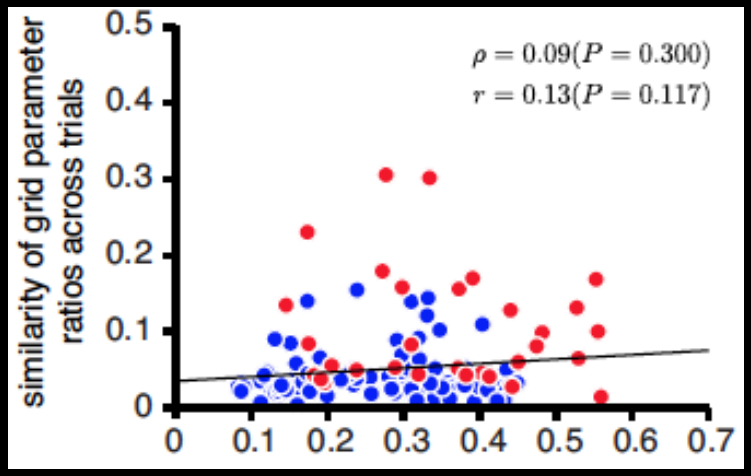


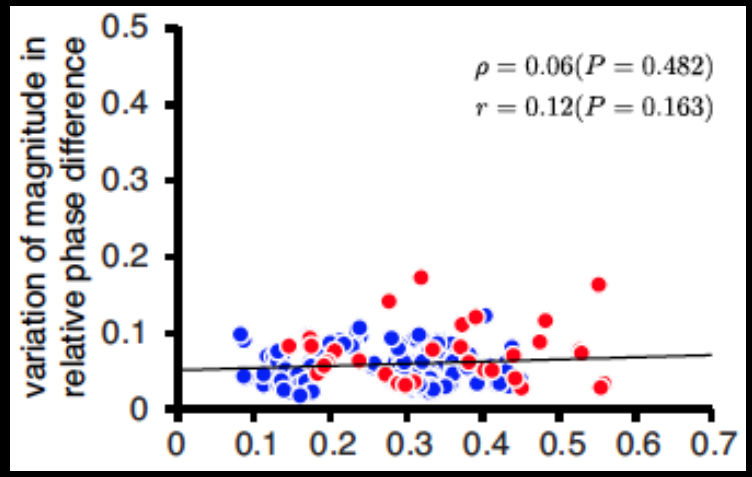
Yoon, Barry, Hayman, Burgess, Fiete, *Nature Neurosci* 2013

Parameter ratio stability cannot be attributed to place cells or environmental cues.

Stable states: discrete or continuous?

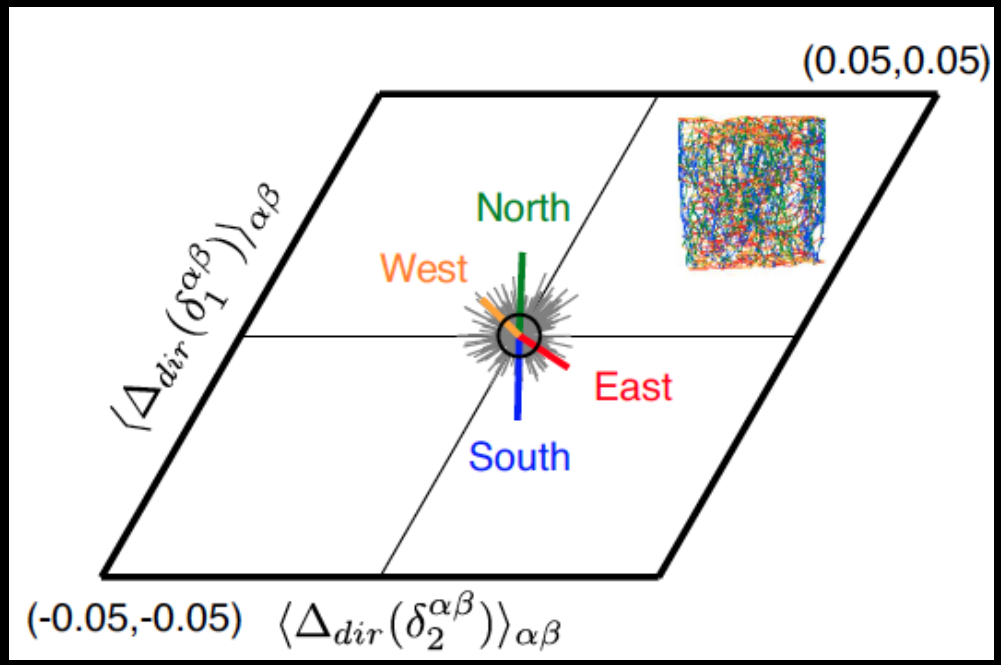






Parameter similarity, parameter ratio stability, and relative phase stability: not clustered by relative phase similarity. Continuous set of fixed points.

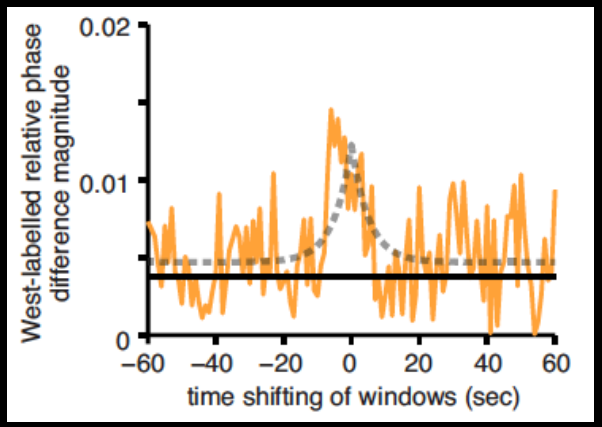
Perturbation: velocity inputs push the system *off* the manifold

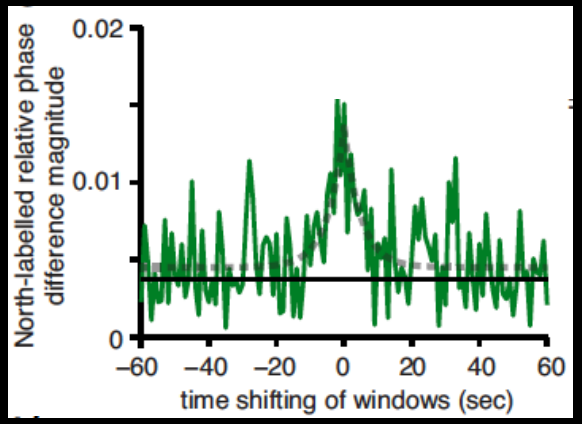


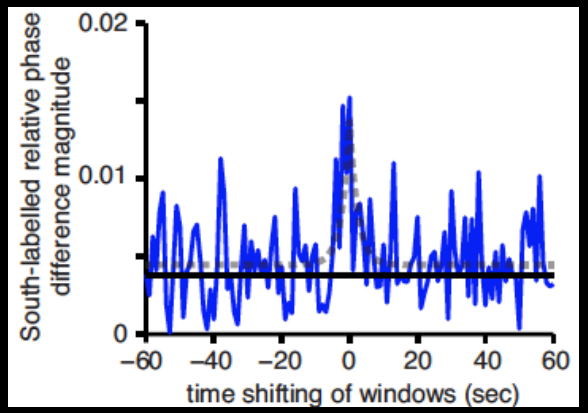
Yoon, Barry, Hayman, Burgess, Fiete, *Nature Neurosci* 2013

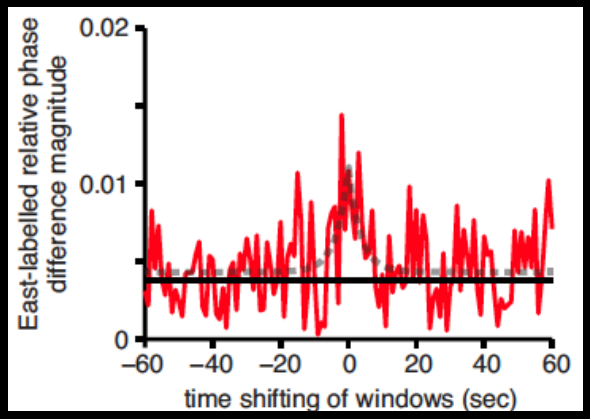
Velocity inputs perturb the relative phase relationships in consistent directions off the manifold.

Dynamics: *Restoration* of population to 2-d manifold





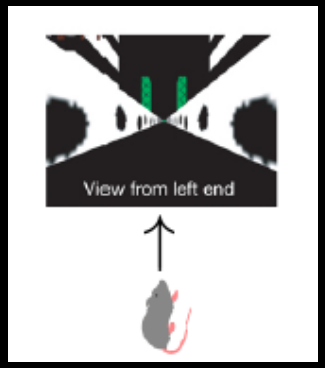


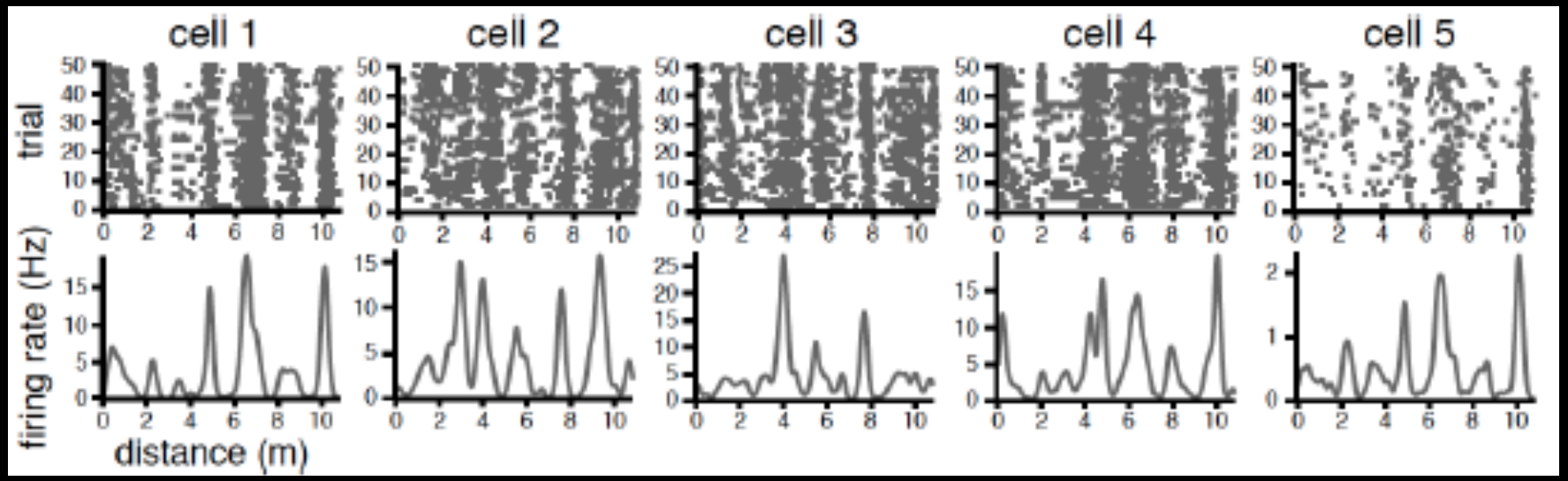


Yoon, Barry, Hayman, Burgess, Fiete, *Nature Neurosci* 2013

Perturbations decay to manifold at least as fast as the time-scale at which the perturbing (velocity) inputs change direction.

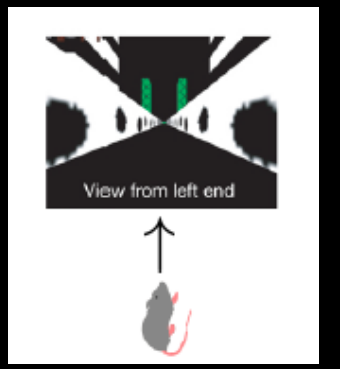
MEC cells in 1D environments

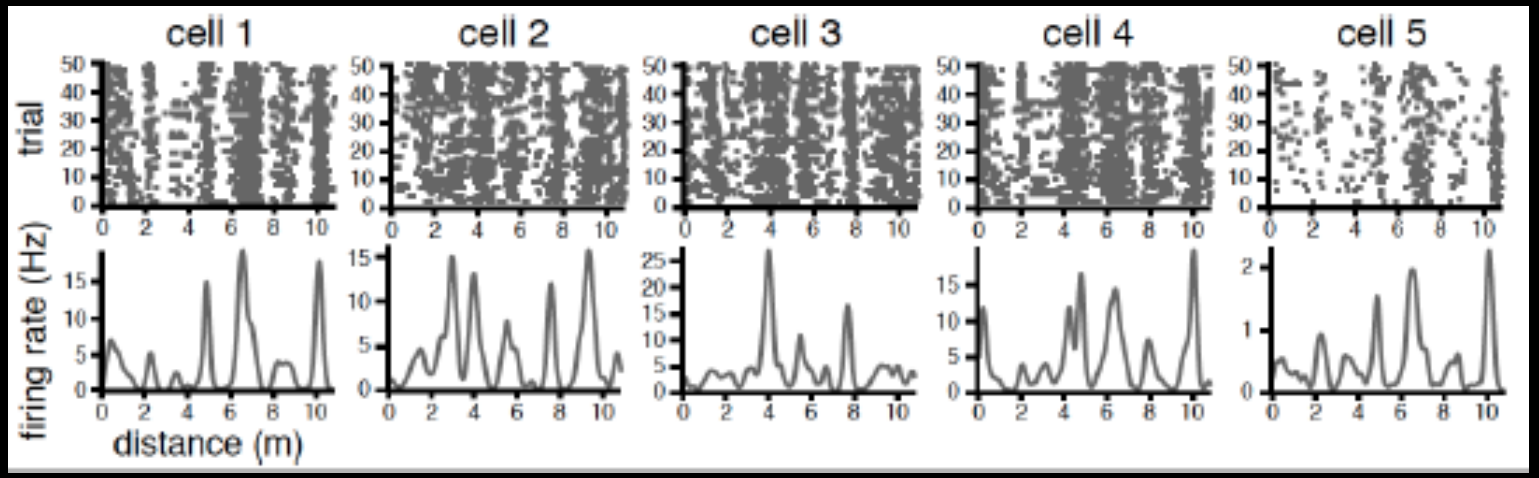


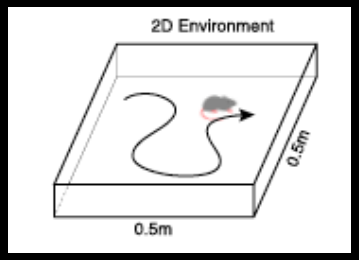


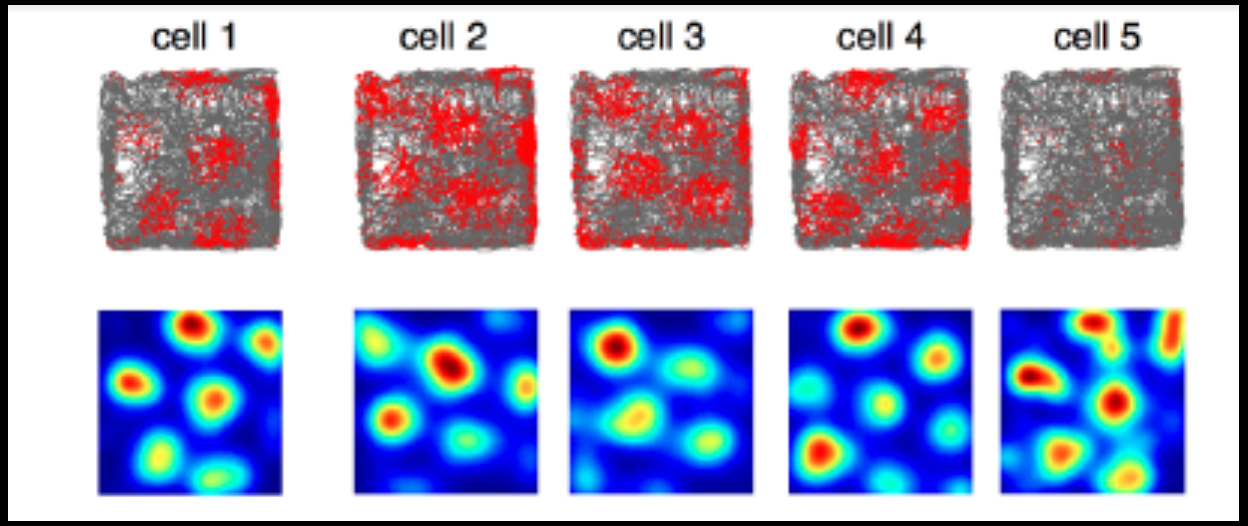
Non-periodic. Patterns differ in complex ways across cells. Much larger spacing between peaks: is the grid cell system higher-dimensional?

In 2D environments the cells have grid responses

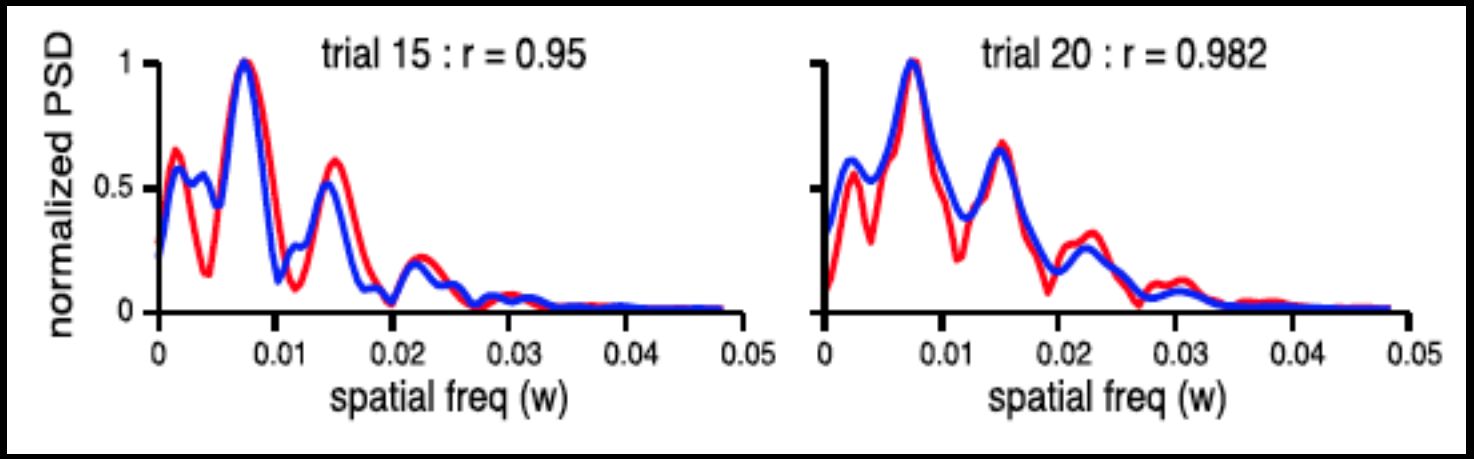




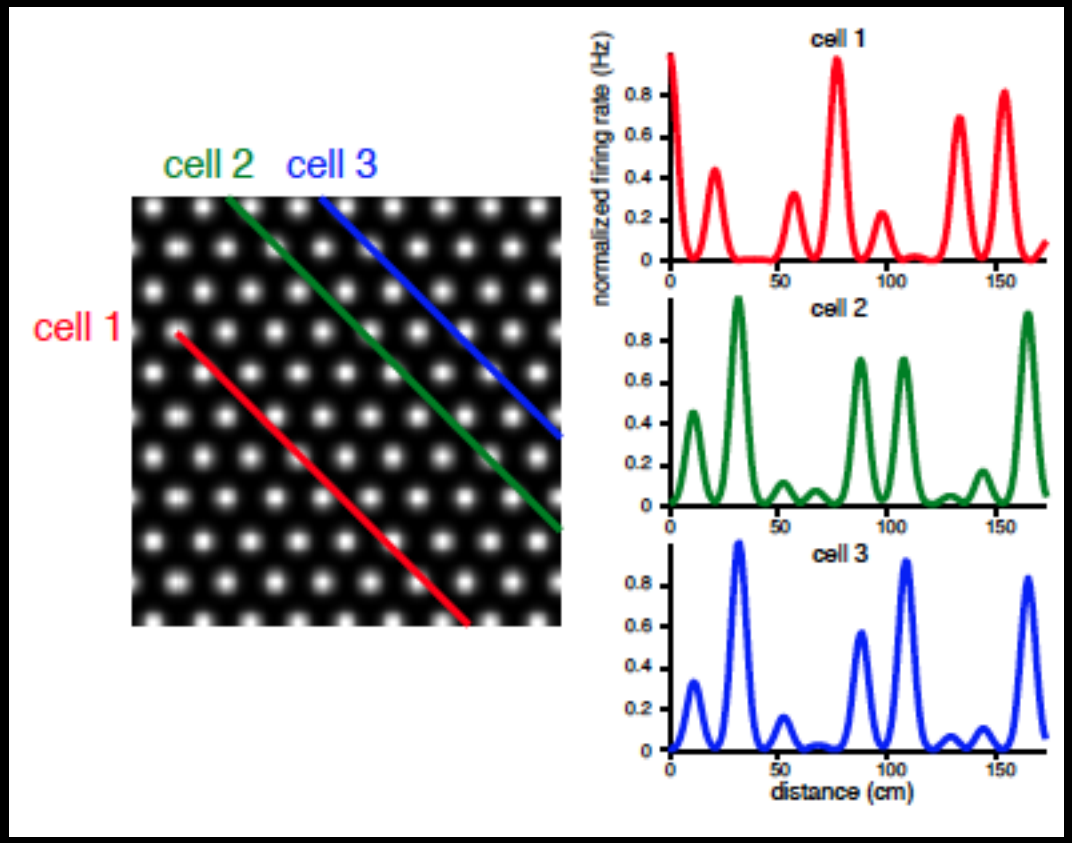


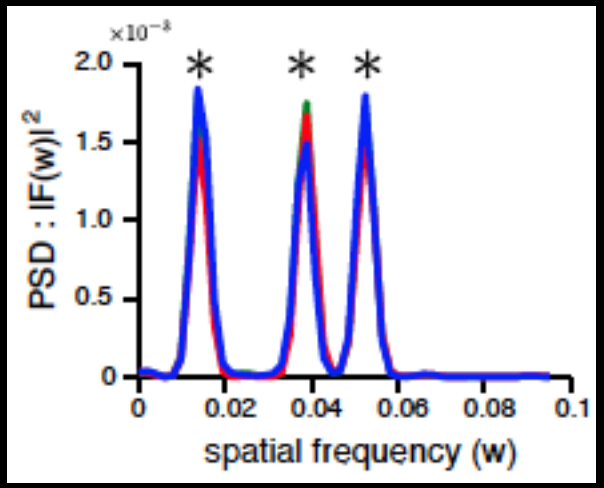


Identical Fourier power-spectra across cells (even if power spectrum changes a little from trial-to-trial)

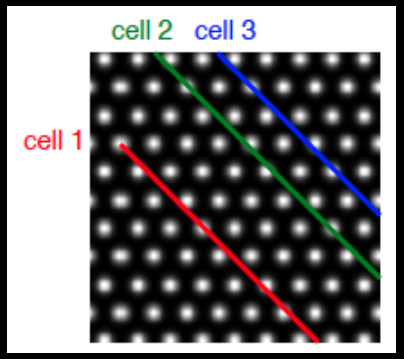


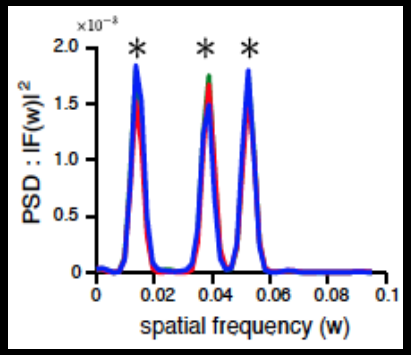
Schematic: properties of parallel slices through 2D lattices

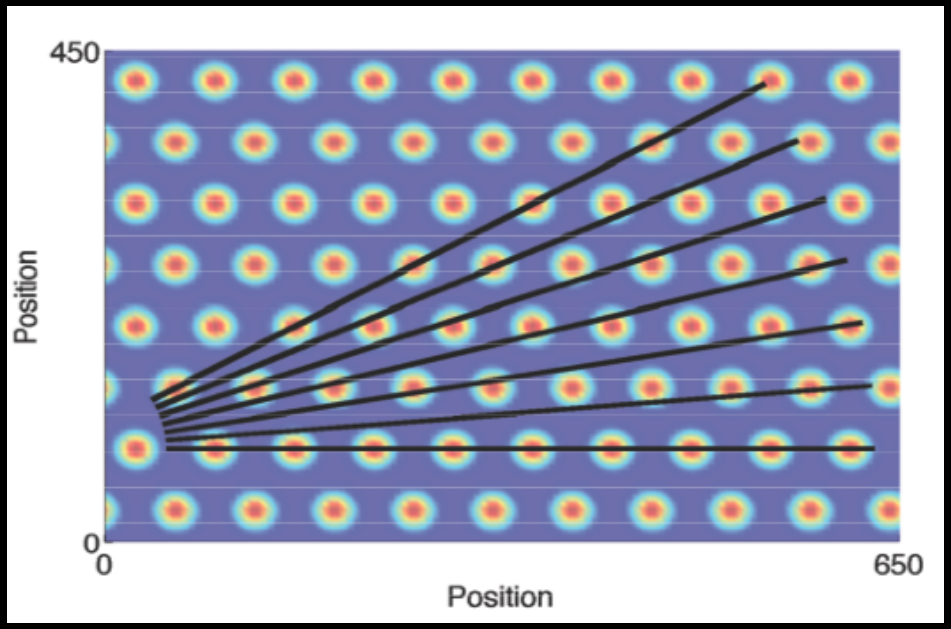




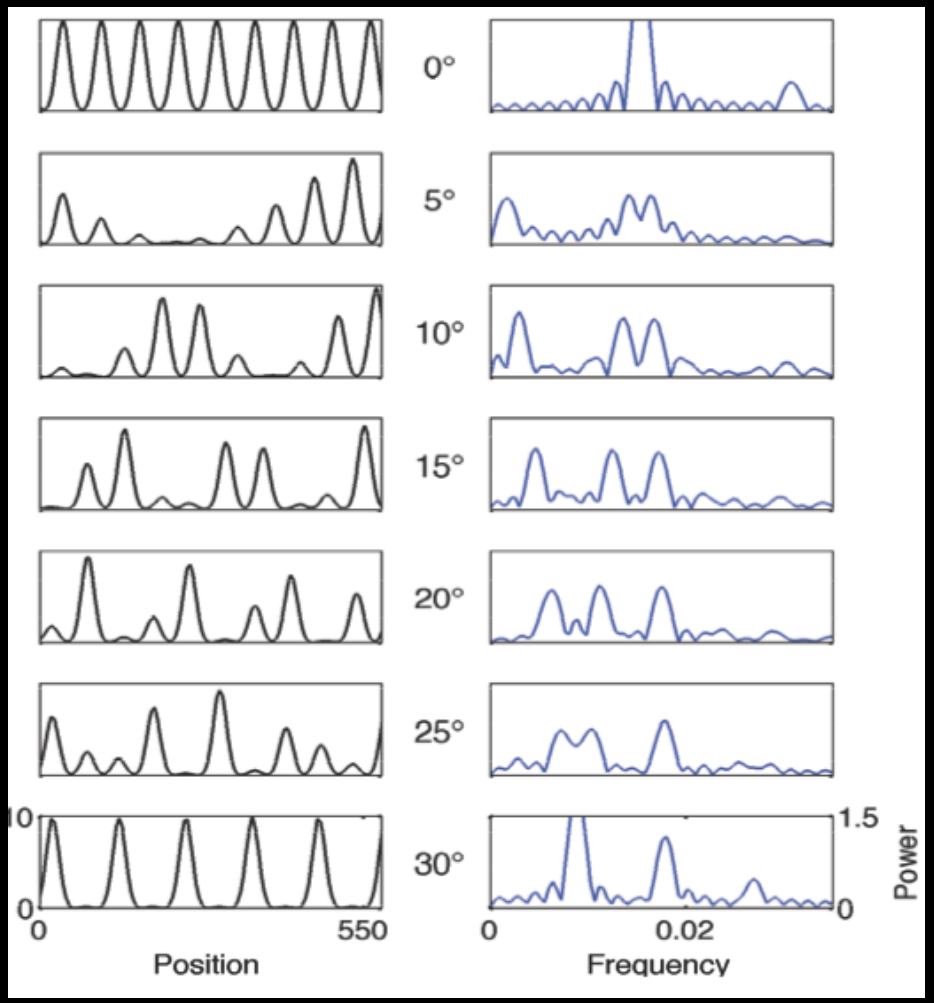
Power spectra of slices of a triangular lattice



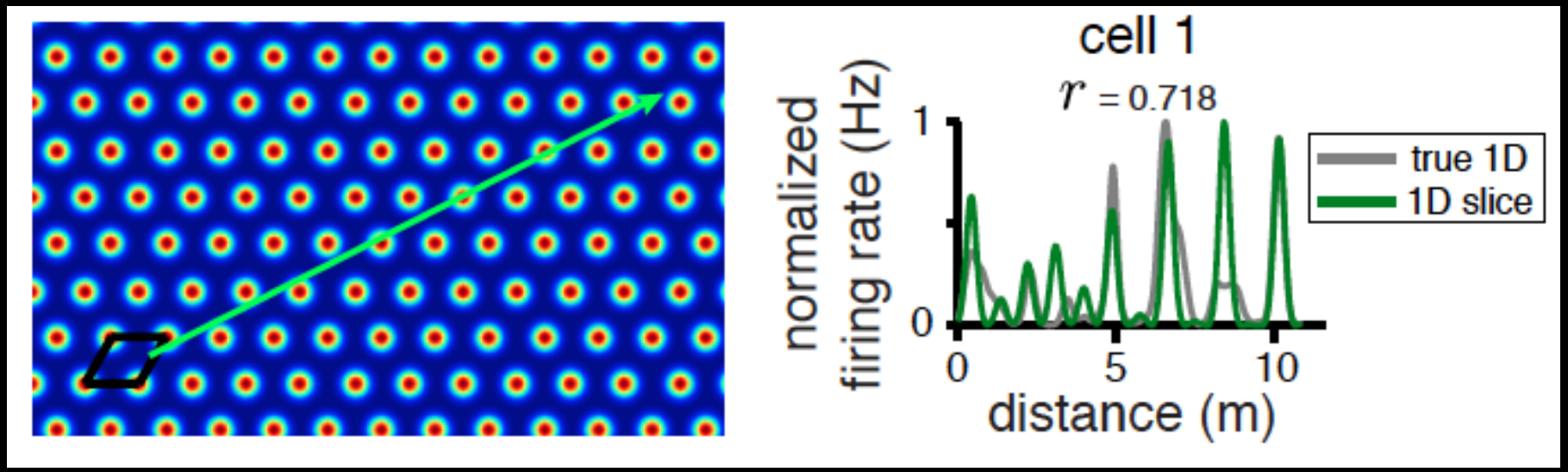




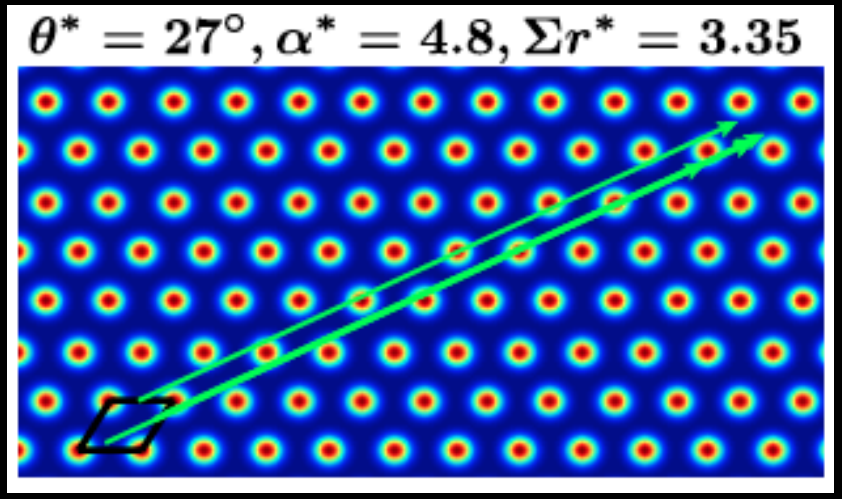
$k_1 + k_2 = k_3$

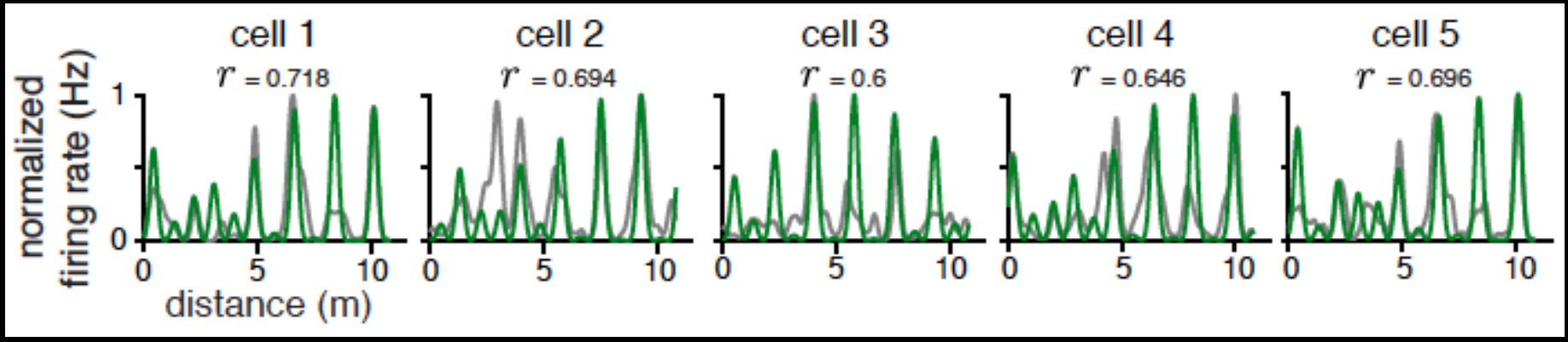


The 1D firing rate of cells is well-captured by a 1D linear slice through a triangular lattice

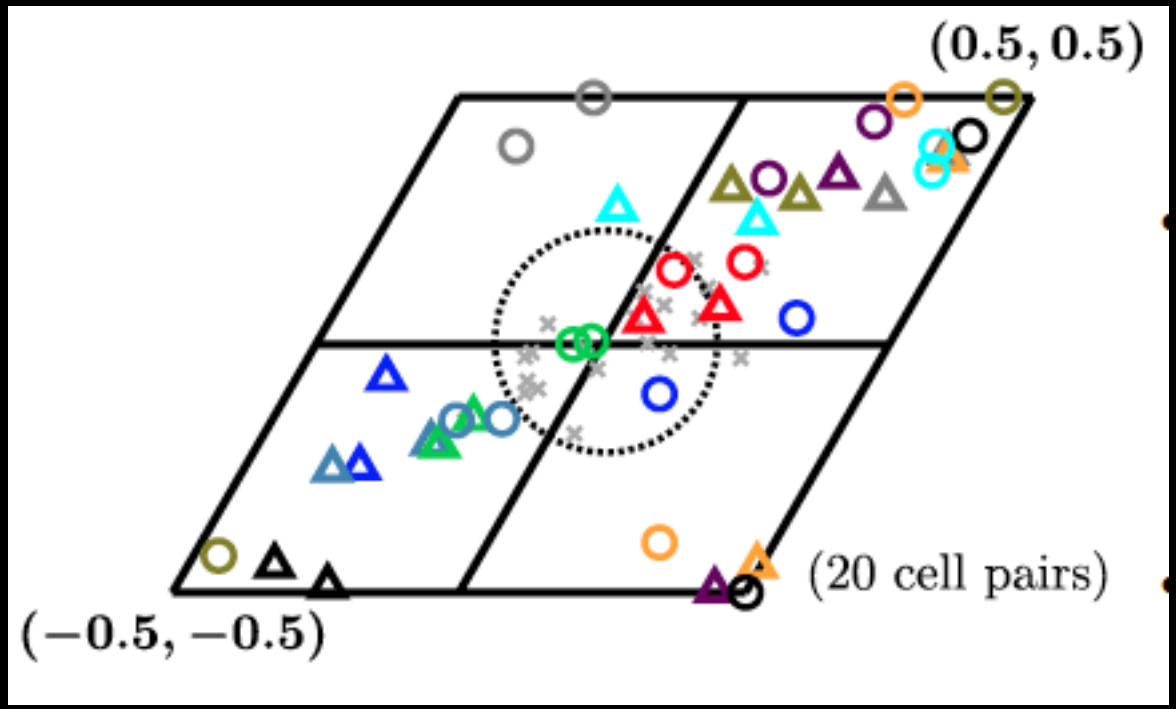


Multiple simultaneously recorded cells (same or neighboring tetrodes) are well-fit by parallel slices





2D attractor dynamics in 1D responses



Relative phases predicted by 1D analysis consistent with measured 2D relative phases. Different cells as parallel slices: consistent with dragging 2D pattern across network with animal motion

Implications

- Substantiation of the continuous attractor hypothesis: beyond analogy?

- Support for grid cell models based on recurrent pattern formation; suggest cells capable of memory/integration.

Fuhs & Touretzky 2006,
Burak & Fiete 2006,
McNaughton et al. 2006,
Burak & Fiete 2009.
consistent with Domnisoru, Kinkhabwalla, Tank 2013

- Severe constraint on alternate models (e.g. temporal interference): incorporate attractor dynamics into population responses.

- The system appears to remain in exactly the same, low-dimensional state space during navigation in 1D and 2D environments, suggesting a common computational role across diverse spatial environments.

Implications

- Substantiation of the continuous attractor hypothesis: beyond analogy?

- Support for grid cell models based on recurrent pattern formation; suggest cells capable of memory/integration.

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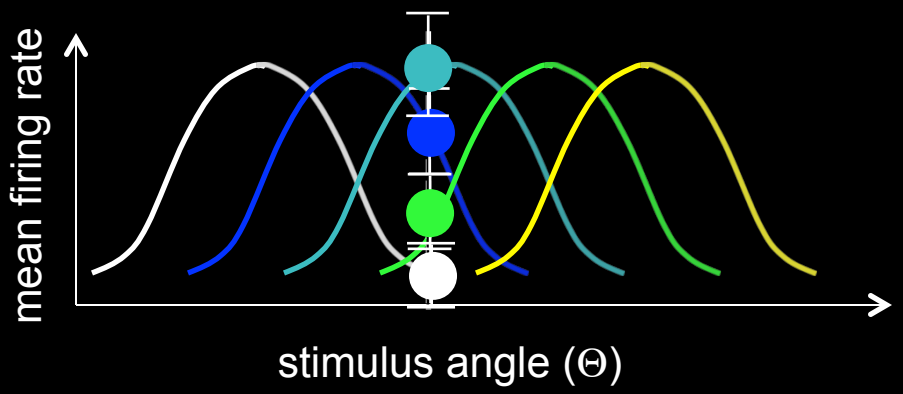
Codes for noise reduction

Population codes enable accurate representation of variables with noisy elements



$$r_i = \text{Poiss}(f_i(\theta)\Delta t)$$

$$\theta \rightarrow \mathbf{r} \rightarrow \hat{\theta}$$

Accuracy gain:

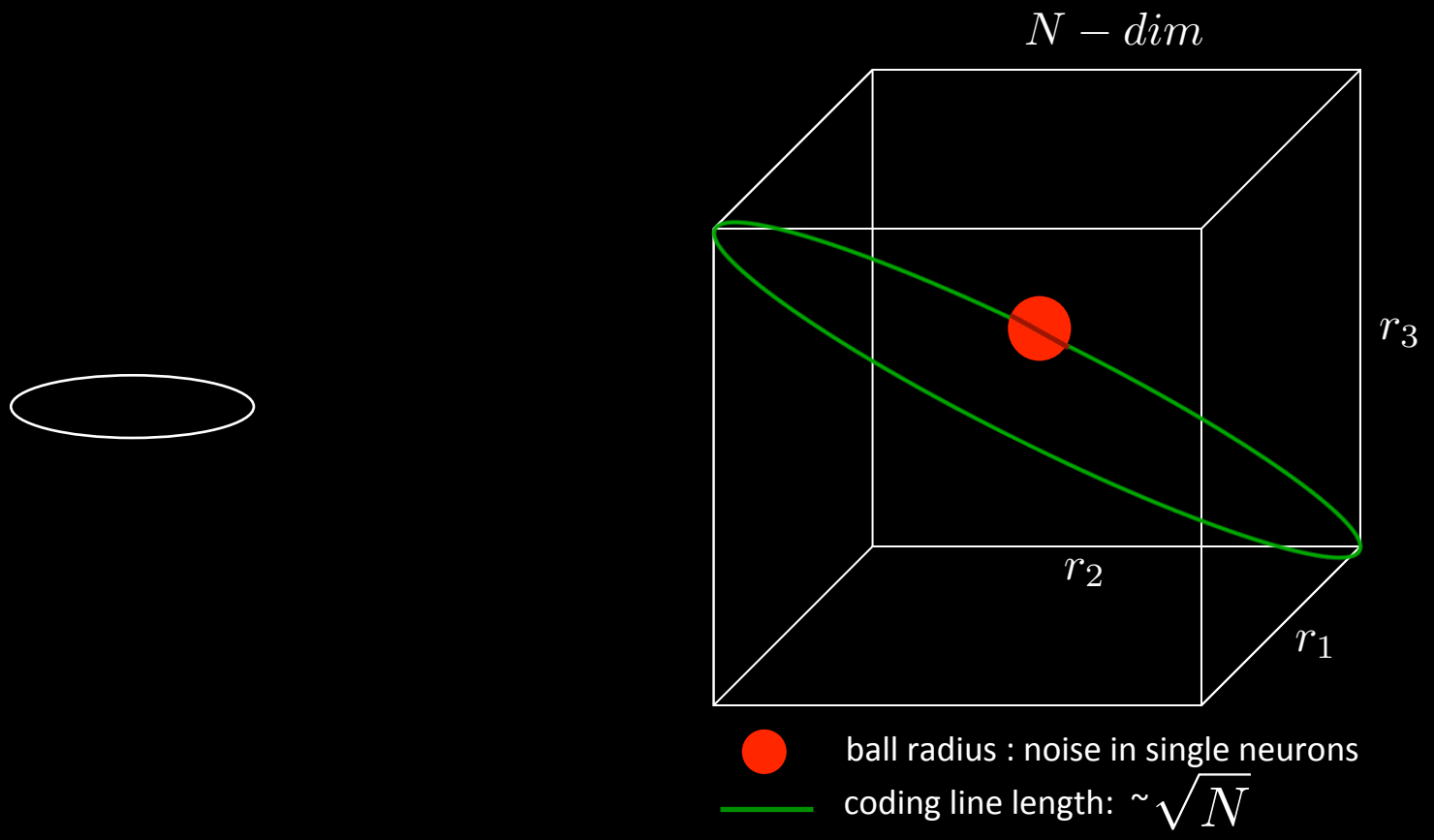
$$J(\theta) = -\langle \left(\frac{\partial \log P(\mathbf{r}|\theta)}{\partial \theta} \right)^2 \rangle \sim N$$

$$MSE \equiv \langle (\hat{\theta} - \theta)^2 \rangle \geq \frac{1}{J} \sim \frac{1}{N}$$

Seung & Sompolinsky, 1993
Brunel & Nadal, 1998
Abbott & Dayan, 1999
Latham et al. 2003

Polynomial (linear) gain in accuracy with *N*.
"Classical population code."

Back to a geometric view



$$fractional\ error \sim 1/\sqrt{N}$$

Fiete 2013.

Examples of classical population codes (CPCs)

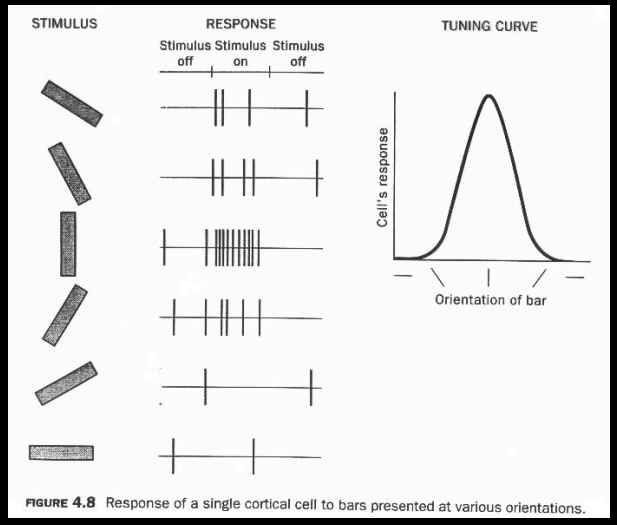
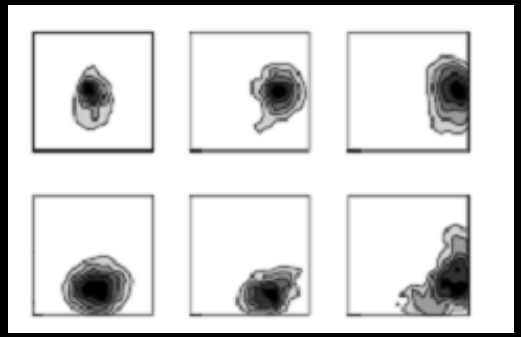


FIGURE 4.8 Response of a single cortical cell to bars presented at various orientations.

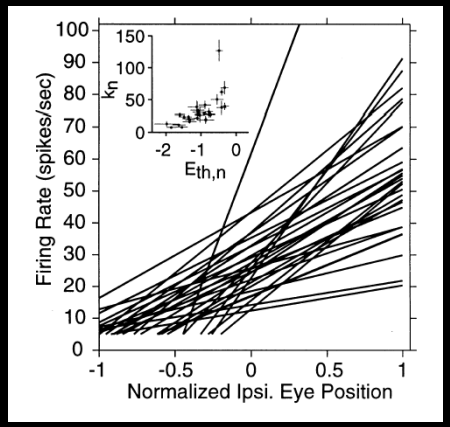
V1 orientation tuning

Hubel & Wiesel 1959



Place cell location tuning

O'Keefe, 1978



Oculomotor neurons

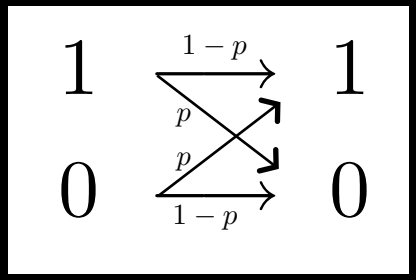
Cannon &Robinson

Aksay et al. 2001, 2003

Most codes in sensory, motor peripheries and some cognitive areas are CPCs.

Do CPCs make the best possible use of neural $$?

A simple code for discrete variables over noisy channels: repetition code



repetition code $\{0,1\}^N$: $0 \to 00\cdots0 \quad 1 \to 11\cdots1$

error probability: $p_{error} = \sum_{m=N/2}^{N} C(N,m)p^m(1-p)^{N-m} \quad \to 0 \text{ as } N \to \infty$

BUT! information rate: information bits/total bits: $\rho = \frac{1}{N} \to 0$

Exponentially vanishing error rate, at asymptotically zero info rate

Information rate in CPCs

$$\rho \sim \frac{I}{N} \sim \frac{\log(N)}{N} \to 0$$

Brunel & Nadal 1998

$$I \sim \log(J) \sim \log(N)$$

Repetition: Exponentially vanishing error rate, at asymptotically zero info rate
CPCs: Polynomially vanishing error size, at asymptotically zero info rate

Neurons aside: is it possible to do any better?

possible!

But does the brain contain such codes?

What classes are achievable by neurons?

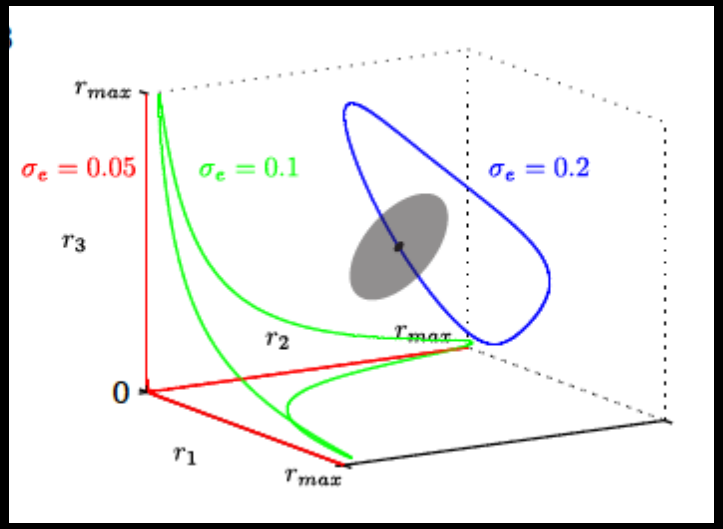
- linear scaling (~ aN, $a>0$)? yes
- super-linear polynomial scaling (~ N^a, $a>1$)? yes!
  (D. Schwab & I.R. Fiete)
- exponential scaling (~ e^{aN}, $a>0$)? grid cells!
  (S. Sreenivasan & I.R. Fiete)

First: is super-linear scaling possible?

$$FI \sim N/\sigma$$
$$FI \sim N^2 \quad (\text{if } \sigma \sim 1/N)$$
$$MSE \propto 1/N^2$$

FI-optimal scaling

Berens et al., PNAS 2011.



Yoo & Fiete, in preparation.

Why? "Threshold" errors: ~ *1* active neurons (not ~ *N*).

$$MSE \sim E_{th} p_{th} + E_{\not th}(1 - p_{th})$$

$E_{th} \sim 1$ $\quad p_{th} \sim p_0^{2\sigma N}$ $\quad E_{\not th} \sim \frac{\sigma}{N}$

$$\sigma \sim \log(N)/N$$
$$MSE \sim \log(N)/N^2$$

MSE-optimal scaling

D. Schwab & I. Fiete, in progress.

CPCs permit nearly ~N^2 performance. Truly sparse codes.

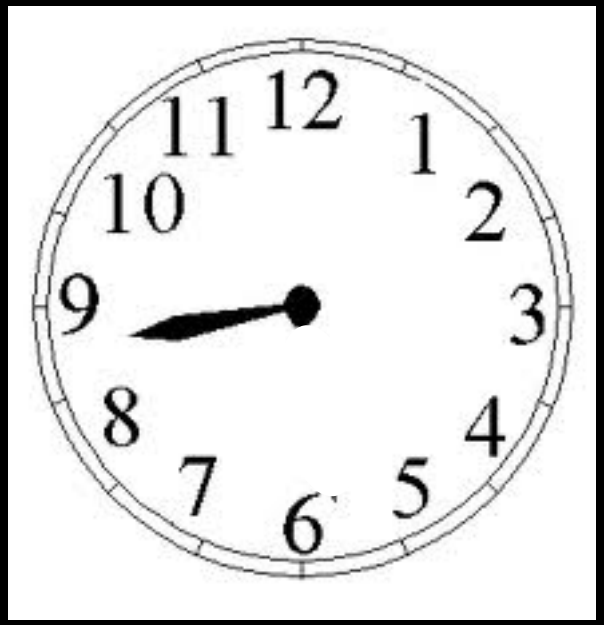
An entire grid cell population encodes location only as a spatial phase

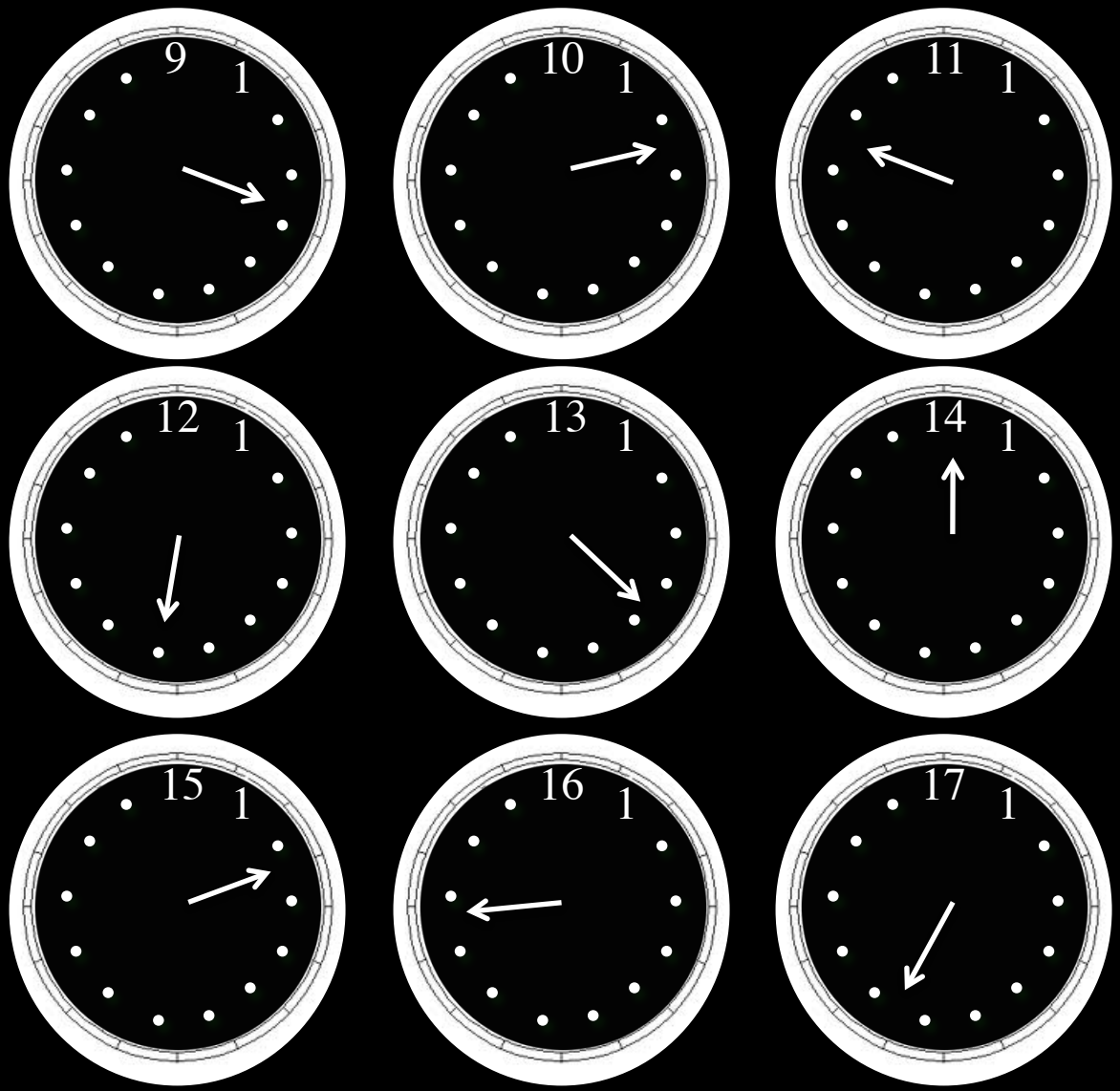
1-d analogue

$$\phi = \frac{x \bmod \lambda}{\lambda} = 1/4$$

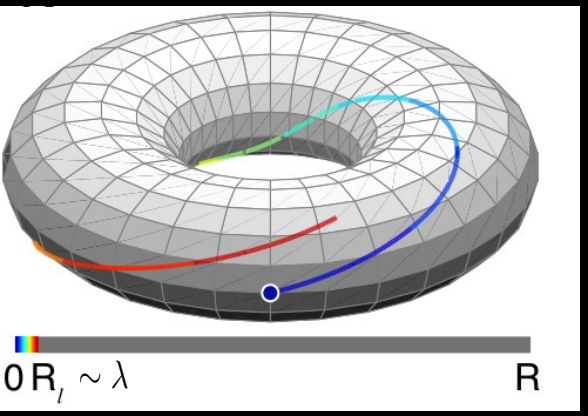
x

Population code of diverse populations





Unique representation for exponentially large range of locations

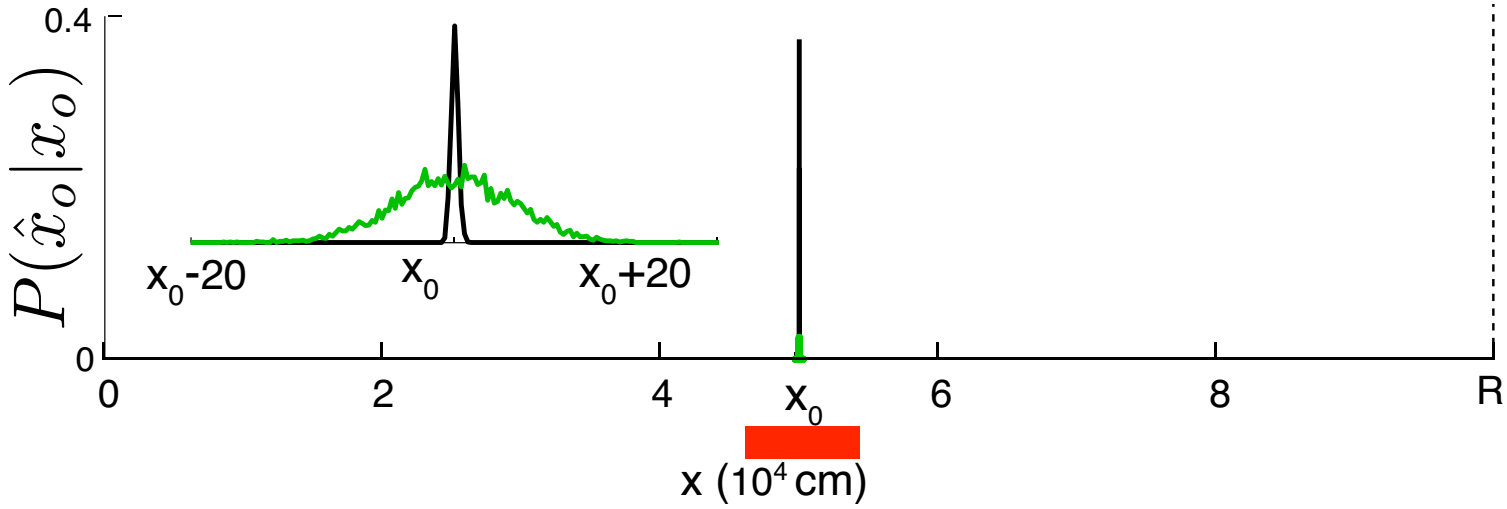


Fiete et al. 2008.
Sreenivasan & Fiete 2011.

Superior error control over range << R

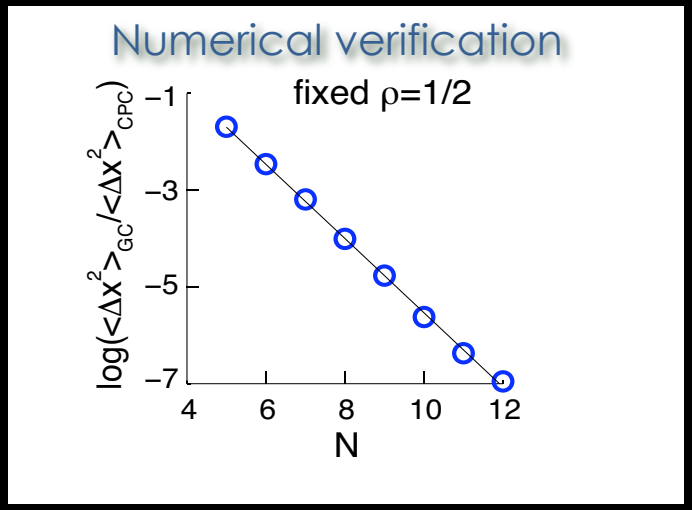
$$R_l \ll R$$

$$(\sim \lambda e^{\rho\beta N}) \quad (\sim \lambda e^{\beta N})$$



$$\text{information rate} :\sim \frac{\log R_l/\lambda}{\log R/\lambda} = \rho$$

How much better than CPCs?

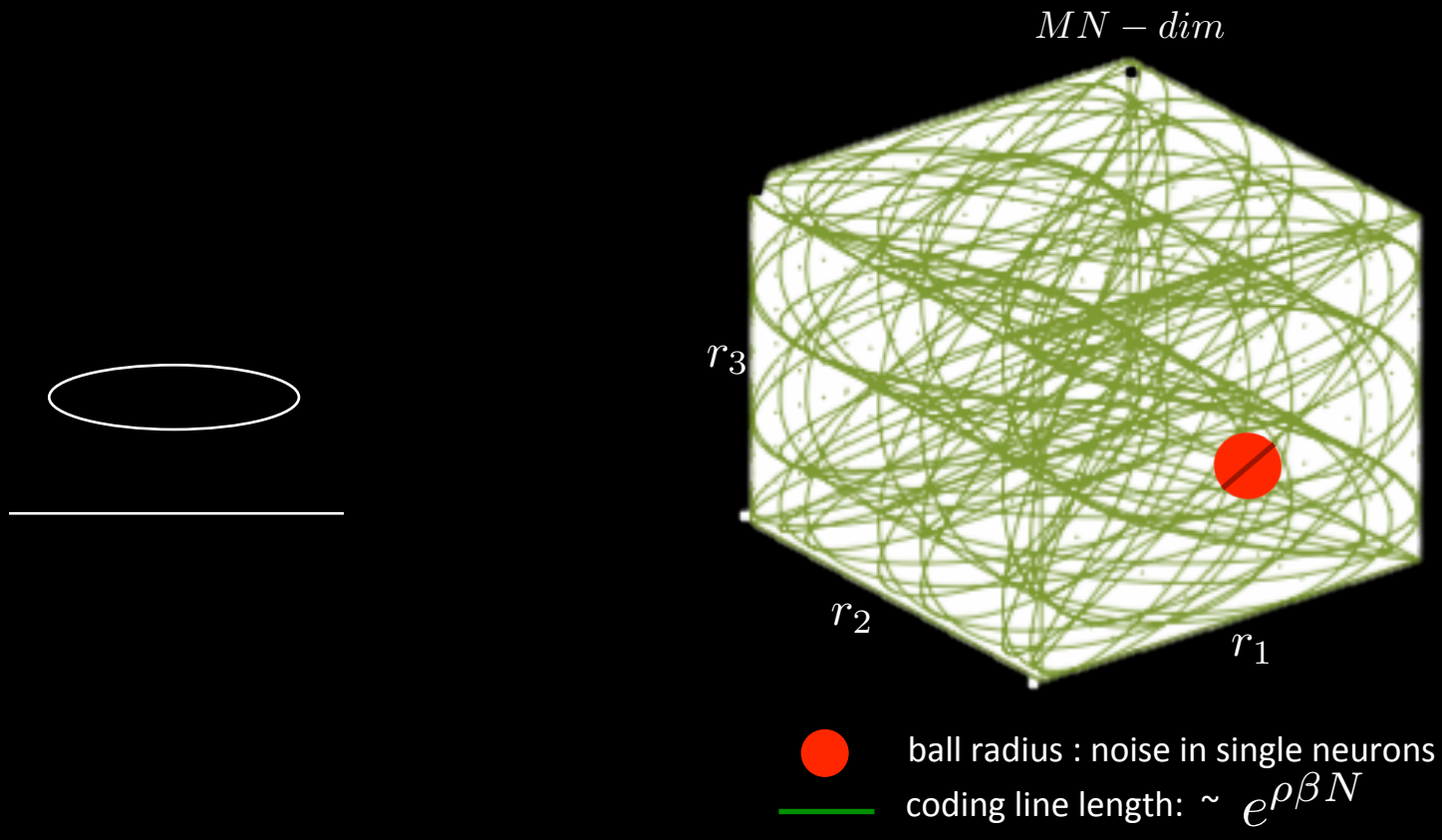


$$\frac{||\Delta x||_{GC}}{||\Delta x||_{CPC}} \sim e^{-\rho\beta N}\sqrt{N}$$

Sreenivasan & Fiete 2011
Mathis et al. 2012
Yoo et al. 2012.

Grid code enables *exponentially better* estimation accuracy than CPCs *at finite information rate,* ρ.

GC: low-dimensional coding line embedded in high-dimensional state space *at high density* permits large capacity AND error control



$$fractional\ \ error\ \sim e^{-\rho\beta N}$$

Sreenivasan & Fiete 2012.
Fiete 2014.

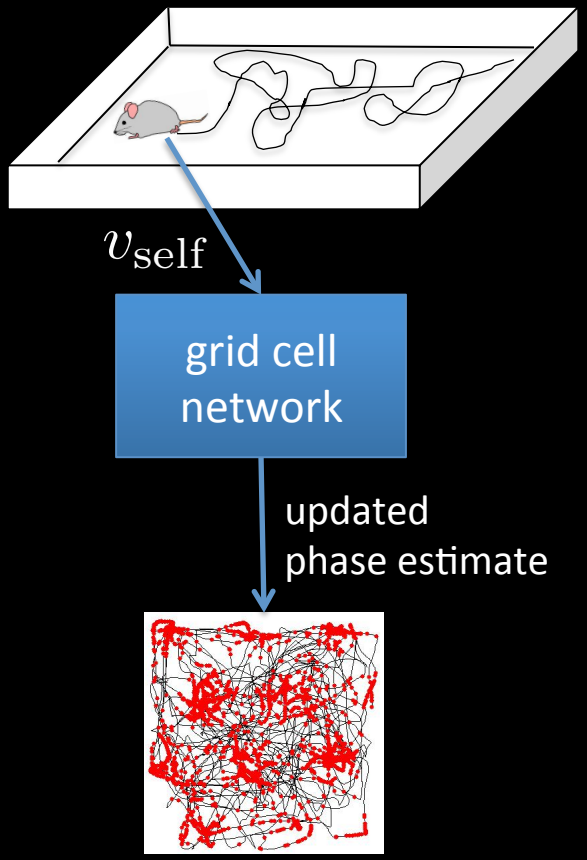
Exponentially strong codes in the brain?

- The grid cell code for location is the first potential example of an analog *exponentially strong population code* (EPC) in the brain.

- Exponential scaling is the signature of strong error-correcting analog codes: is this a new benchmark for efficiency in discussions on neural redundancy?

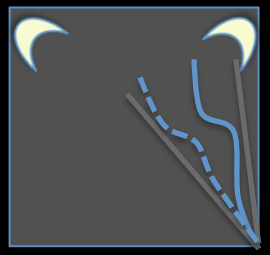
Spatial memory and the grid code

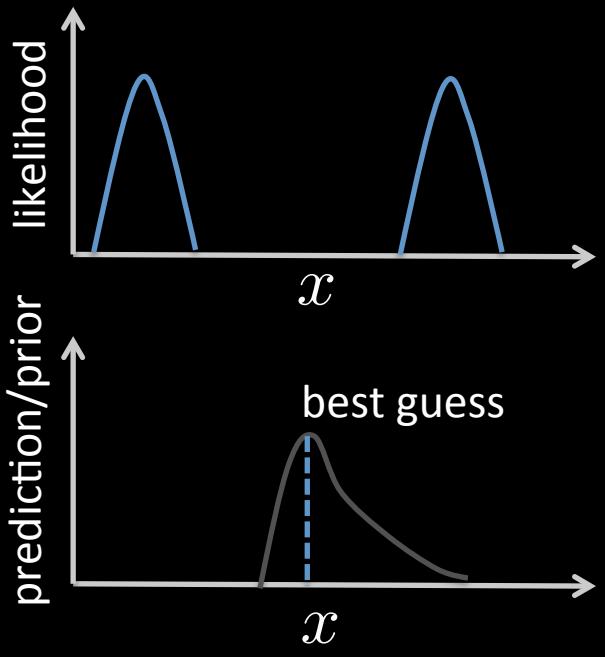
Theoretical models of grid cells predict they may be capable of path integration

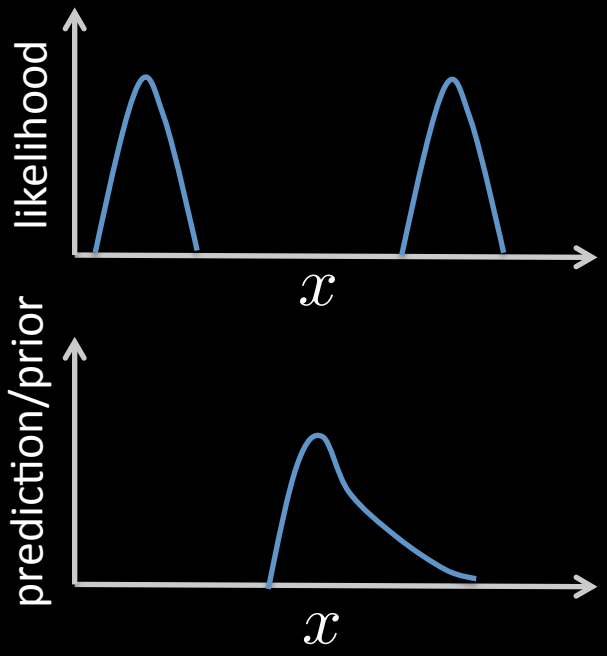


Through their hypothesized path integration role, grid cells are implicated in spatial short-term memory.

Navigation is a hard problem and probabilistic inference may be critical

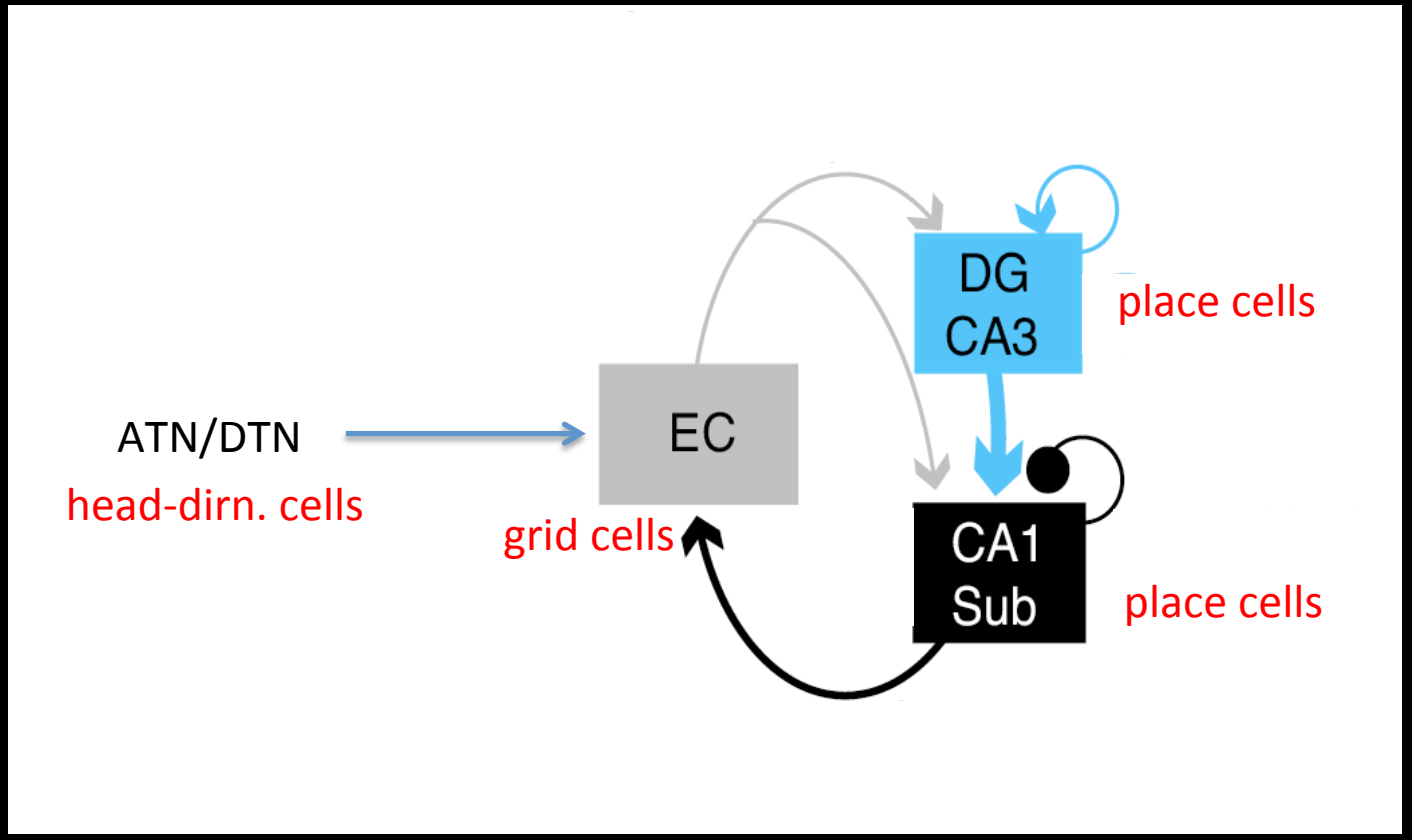






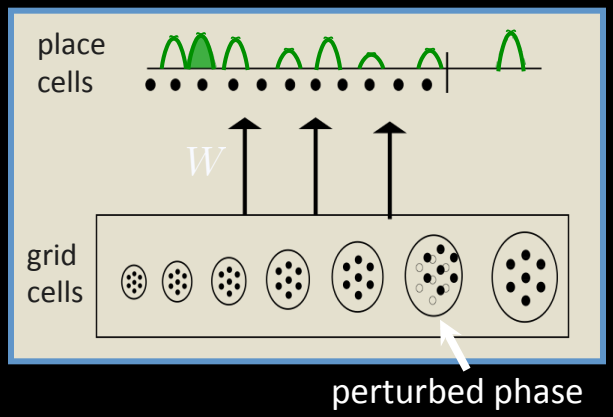
Single-hypothesis tracking is not sufficient to resolve ambiguity.

The entorhinal-hippocampal circuit



Natural interpretation of place cells as performing inference (decoding) with grid cell input

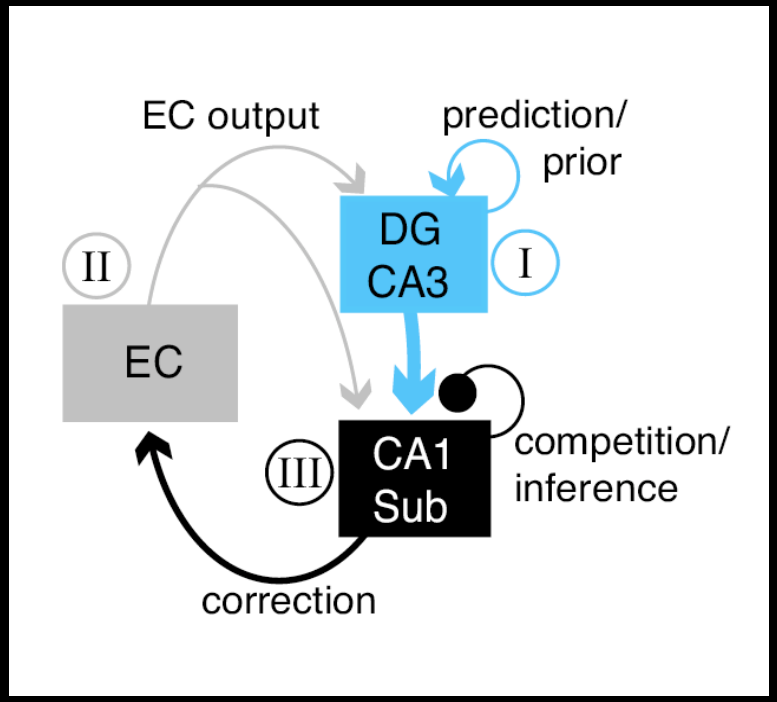
1. Forward drive



EC drives place cells.
If phase errors, many cells get comparable drive.

$$\hat{x} = \arg\min_{x \in R_l} ||\vec{\phi} - \underline{\vec{\phi}}(x)||$$

A hypothesis for spatial inference by the hippocampal-entorhinal circuit



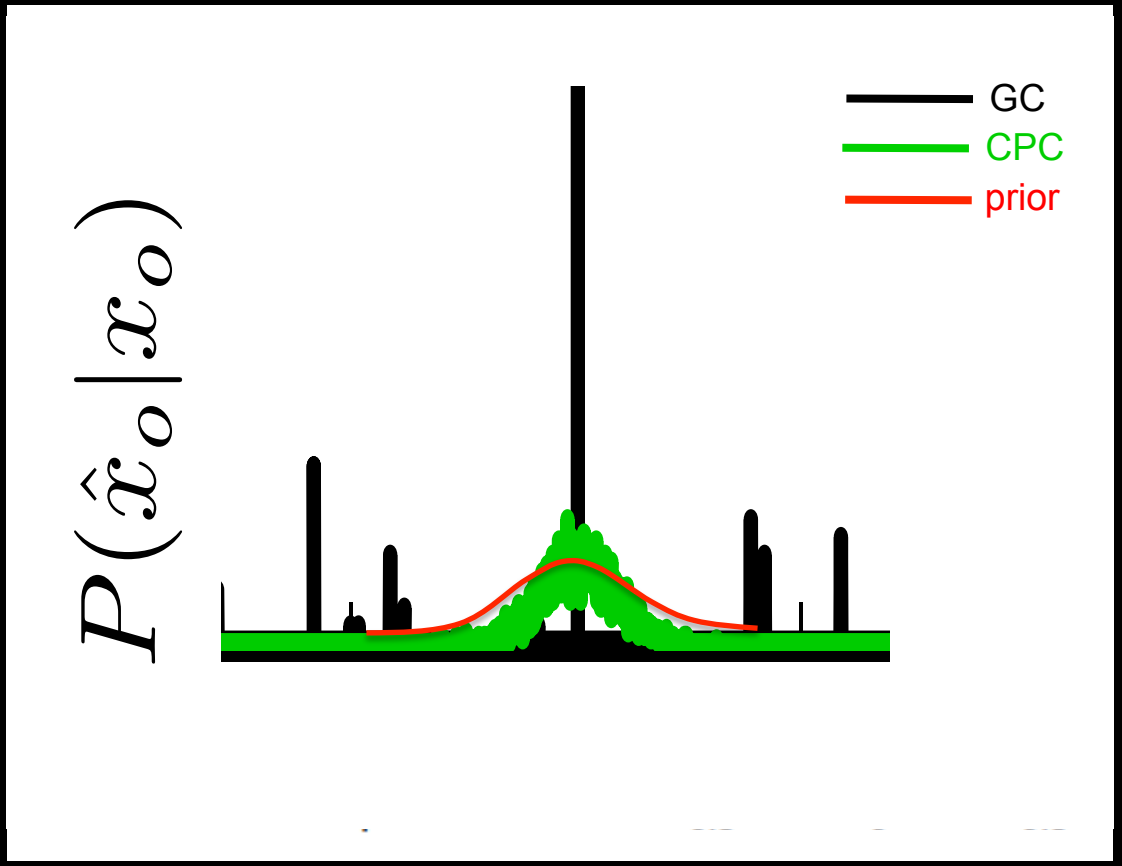
Sreenivasan & Fiete 2011

Ongoing with Wolbers, McNamara.

The grid code and the continuity prior are incoherent and synergistic

$x \in [0, R_l]$

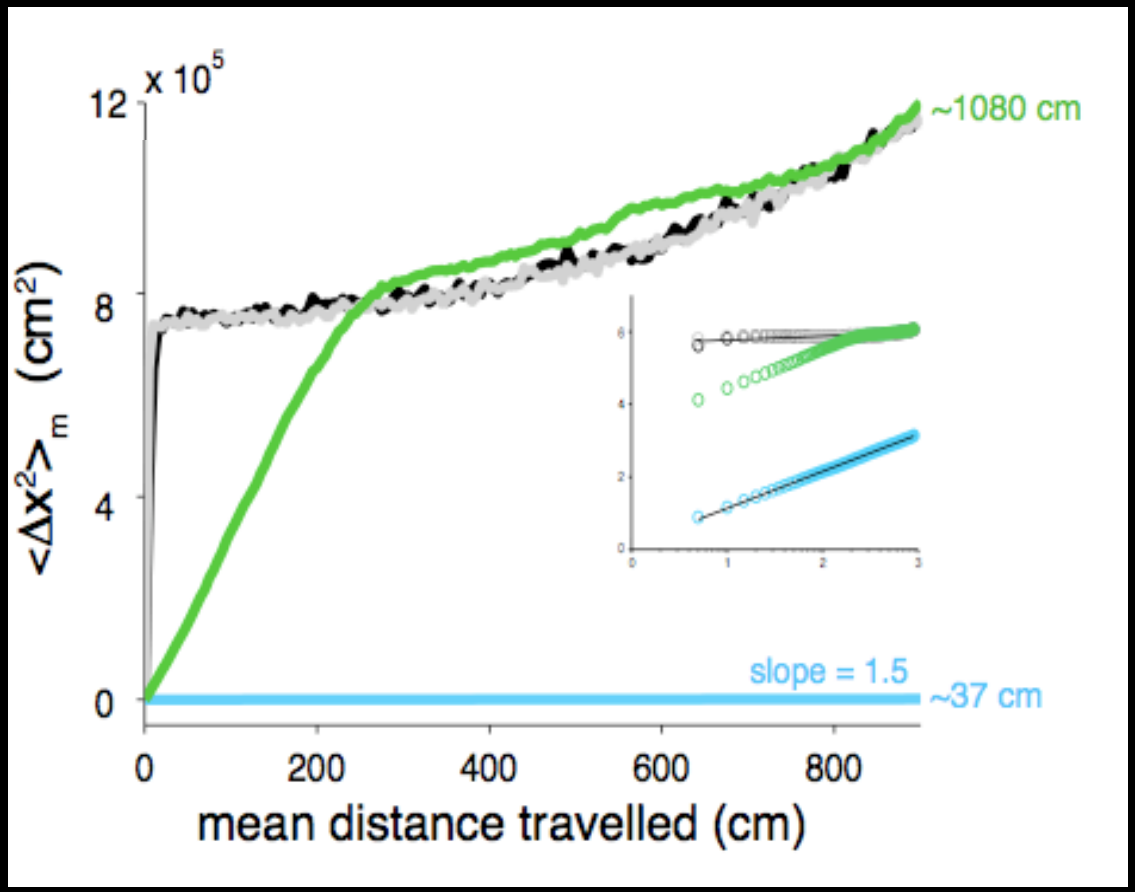
$x \in B(x^*)$



Sreenivasan & Fiete 2011,
Yoo et al., 2012.

A rough prior from continuity has far more value when combined with a grid cell code than a CPC.

Iterative error correction during path integration **without external cues**



Very little error accumulation. >10^4-fold improvement over CPC.

Acknowledgments

Kijung Yoon

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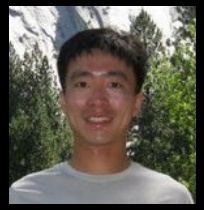
Sameet Sreenivasan



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Howard Eichenbaum
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Yoni Pertzov
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Thank you!