Grid Cells through Attractor Dynamics

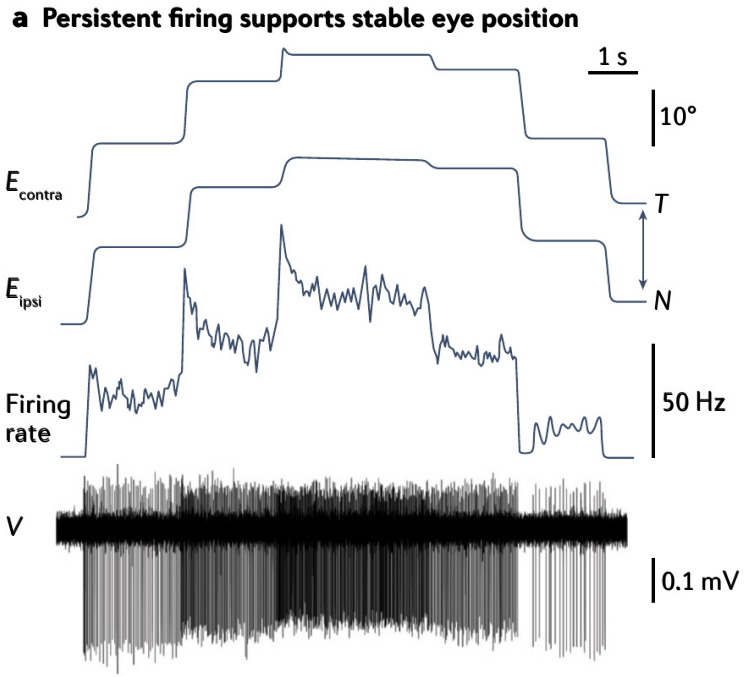
Recitation 1

Computational Neuroscience

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Why Does the Brain Need Persistent States?

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Goldfish gaze holding

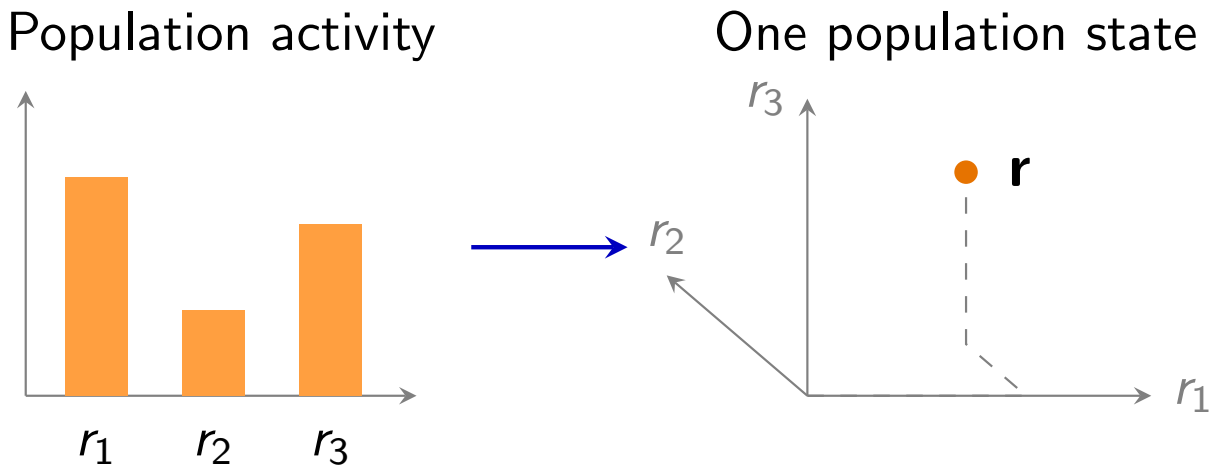
Brief movement commands lead to sustained eye positions.

Neural firing persists between eye movements.

How can a circuit maintain a state longer than its individual activity variables?

From Neurons to Population States

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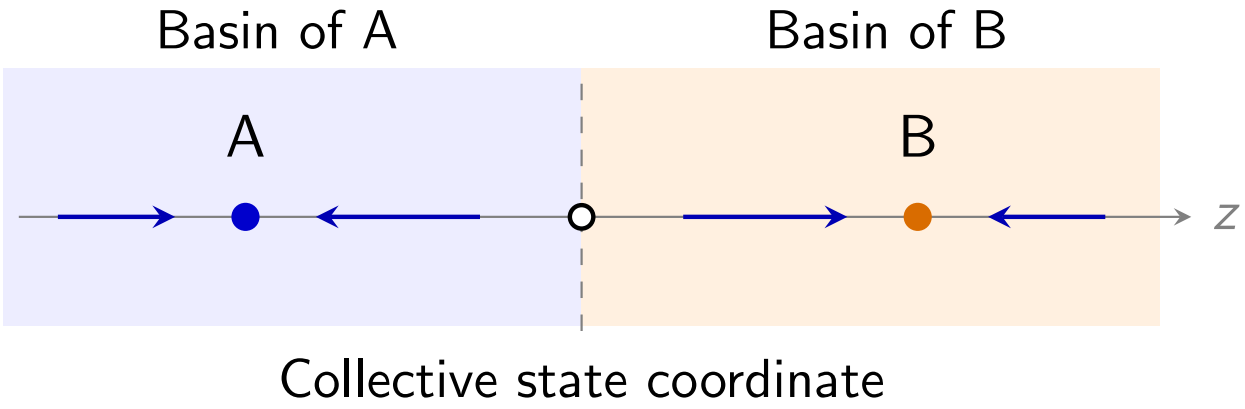


$$\mathbf{r} = (r_1, \ldots, r_N), \qquad \dot{\mathbf{r}} = F(\mathbf{r}; \mathbf{u}).$$

One point describes the whole population at one instant.

Hold the input $\mathbf{u}$ fixed to study the circuit's intrinsic dynamics.

Stable States Can Store Memories



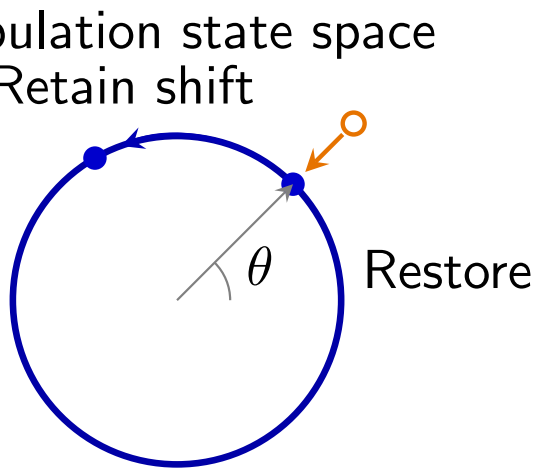
At a stable fixed point, $\dot{\mathbf{r}} = \mathbf{0}$.

- An input can place the circuit in the basin of A or B.
- After the input ends, the circuit retains the selected state.
- Small perturbations within a basin return to the same state.

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Continuous Variables Need a Family of States

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Angle labels the stored state

A continuous attractor stores an angle in a family of stationary states.

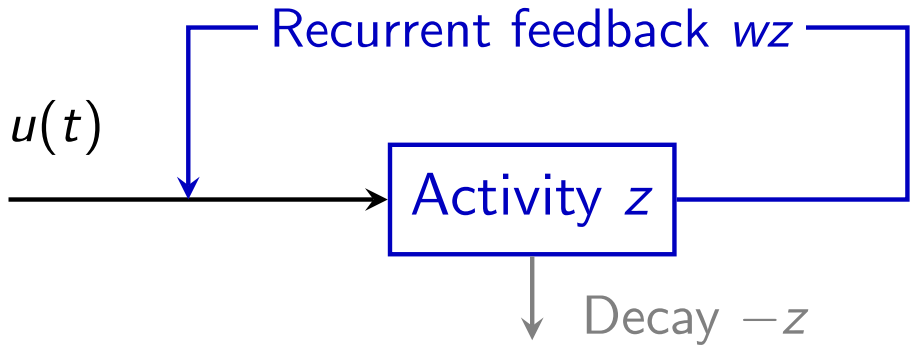
Across the family:
perturbations decay.

Along the family:
a shifted state can persist.

The ring lies in state space. Each point represents a different activity pattern.

How Can Recurrence Create Persistence?

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$$\tau \dot{z} = -z + wz + u(t) = -(1 - w)z + u(t).$$

After the input ends, $u = 0$:

$w < 1$ Activity decays toward zero.

$w = 1$ Feedback balances decay and the state persists.

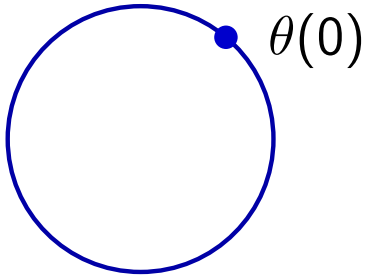
$w > 1$ Nonzero activity grows in this linear model.

Exact balance gives neutral memory. Transverse stability needs more structure.

An Attractor Is Not Yet an Integrator

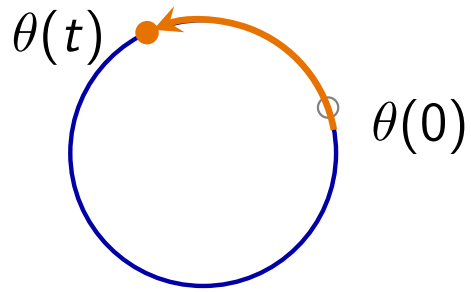
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Storage



$\dot{\theta} = 0$

Controlled updating



$\dot{\theta} = g\,u(t)$

$$\theta(t) = \theta(0) + g \int_0^t u(s)\,\mathrm{d}s.$$

Inputs must move the state along the family while preserving its shape.

Discuss: does the ability to remember an angle guarantee correct updating?

From a Computational Goal to a Network Model

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1. Choose the variable and its population representation.
2. Propose dynamics that maintain and update the state.
3. Construct connections that could realize those dynamics.
4. Test persistence and predicted responses to perturbation.

A low-dimensional activity pattern alone does not establish an attractor.

Next: Navigation

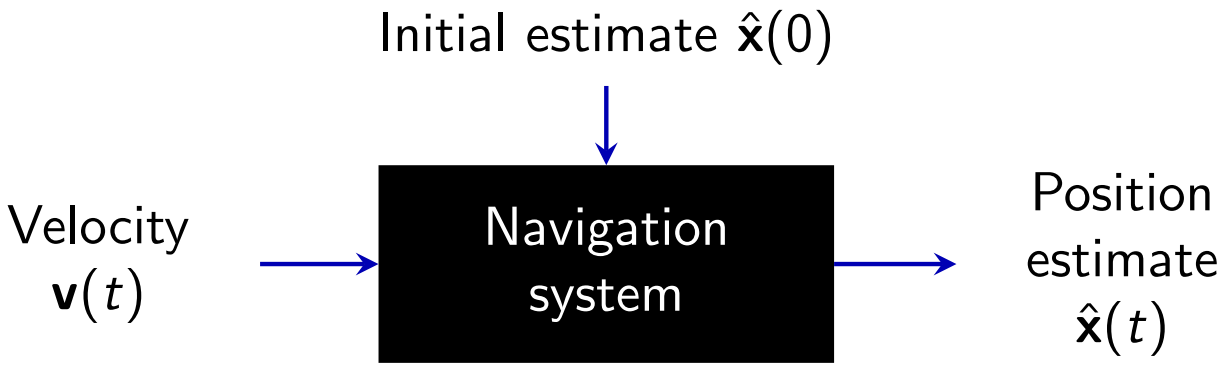
What internal state should the network maintain?

How should movement inputs update it?

A Navigation System

There are plenty of cases to show that rodents can estimate its position with limited cue, with an assumption that the environment is invariant during the time period.

How can movement update an internal estimate of location?



Modeling task: update location from movement cues between external corrections.

Question: what must the circuit store when the animal stops?

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The Computation: Path Integration

Starting from an initial estimate, add each displacement:

$$\hat{\mathbf{x}}(t + \Delta t) \approx \hat{\mathbf{x}}(t) + \mathbf{v}(t)\,\Delta t.$$

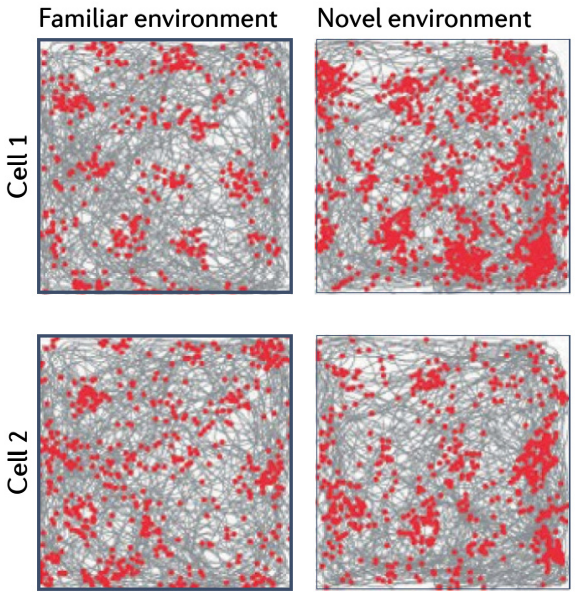
In continuous time, this becomes

$$\hat{\mathbf{x}}(t) = \hat{\mathbf{x}}(0) + \int_0^t \mathbf{v}(s)\,\mathrm{d}s.$$

At rest: preserve the accumulated estimate.
During movement: update it with speed and direction.

The integral specifies the computation. The circuit implementation is still open.

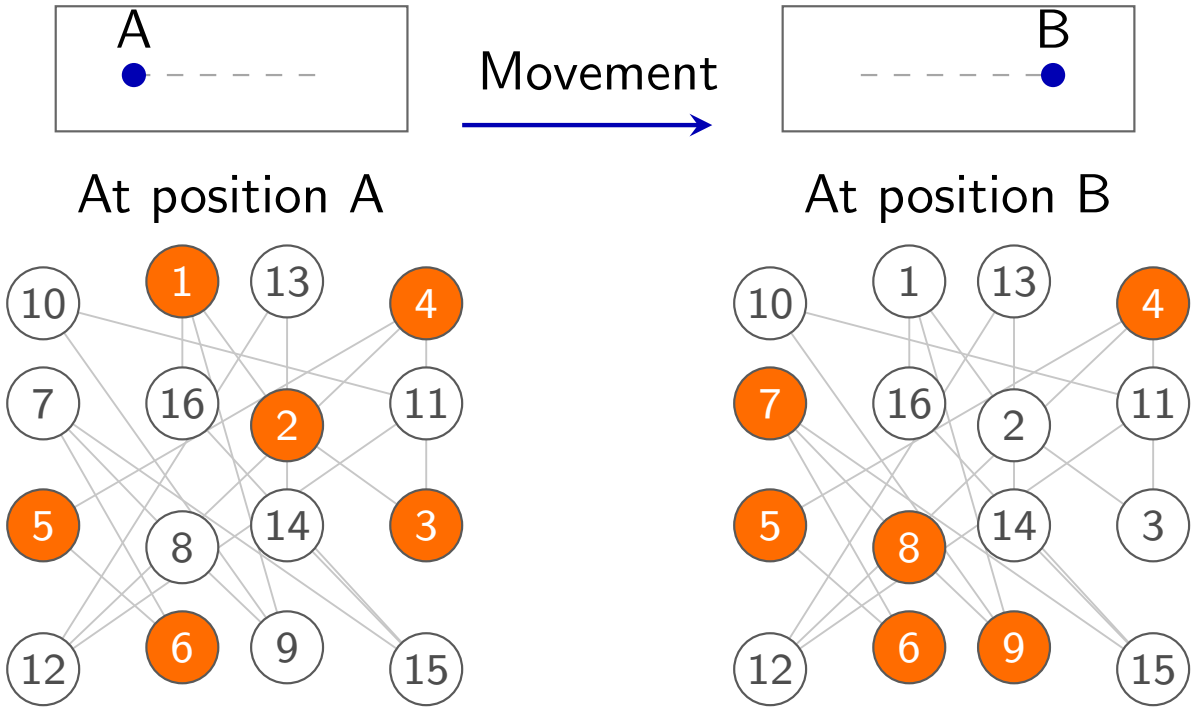
Grid Cells and Spatial Phase



- Firing fields repeat on a triangular lattice.
- Within a module, cells share scale and orientation but differ in phase.
- One module identifies position only modulo its lattice.

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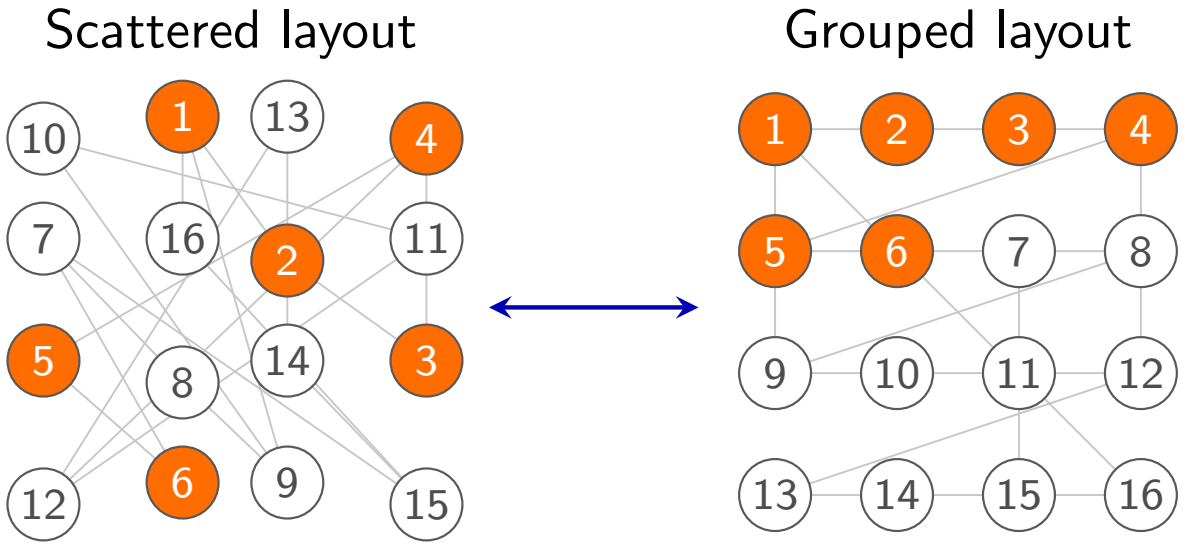
Position and Population Activity



Blue dots mark the rat's position. Orange cells are active.

Movement changes the active ensemble, with overlap. Gray lines illustrate assumed recurrent connections.

The Same Circuit in Different Layouts



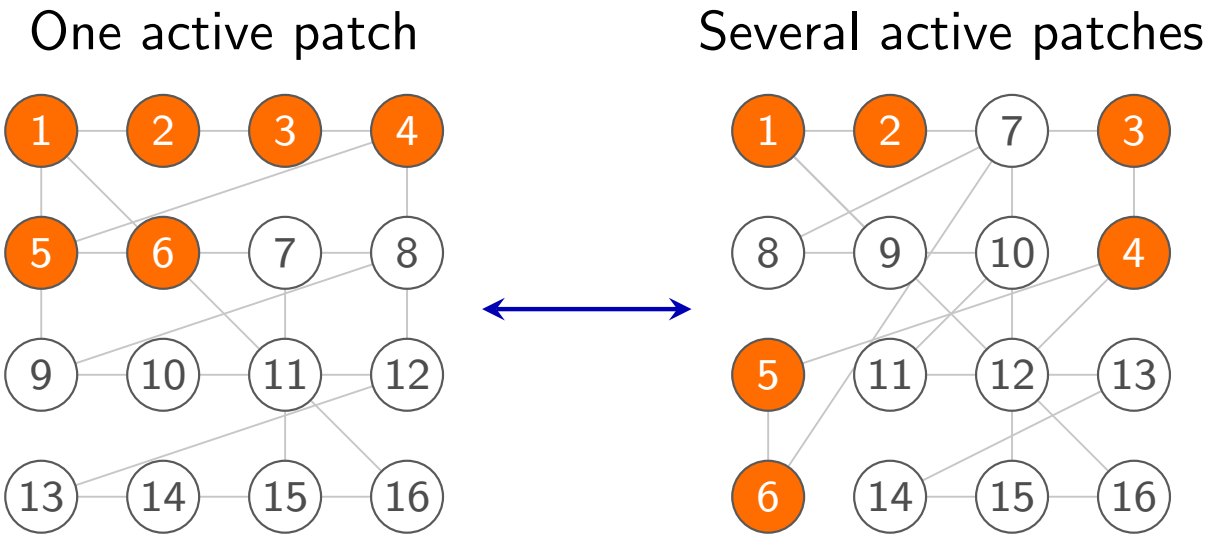
Follow the cell numbers: the active cells and connections are identical.

Reposition the drawing while preserving every weight and each cell's input. The model dynamics stay the same.

Anatomical proximity is optional for this model.

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Coactivity Can Occupy Several Patches



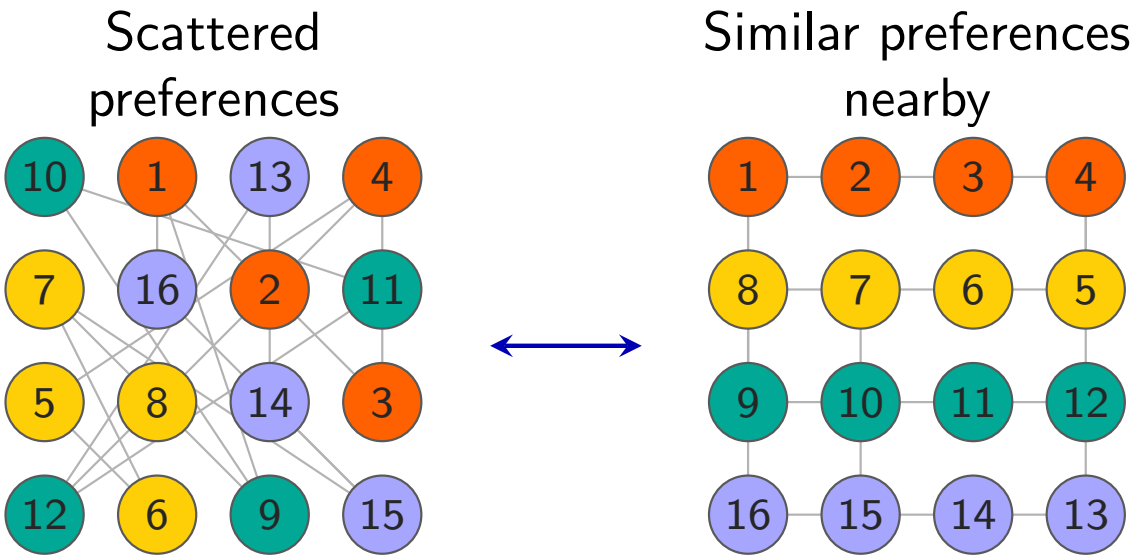
The same active cells can appear in one patch or several separated patches.

Next construction: Burak–Fiete use a regular, moving pattern with many activity peaks.

Its shape and motion require network dynamics.

Topography and Local Wiring

Place cells with similar spatial phase near one another.



Colours: similar spatial phases. Lines: assumed connections.

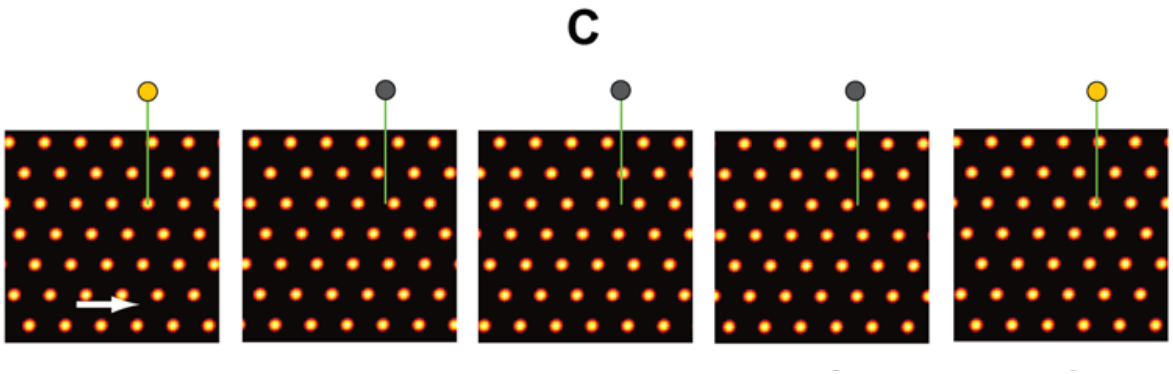
- Local axon and dendrite growth can simplify connection targeting.
- The same connections can require less total wiring.

This motivates local, distance-dependent connections in the model.

A Moving Pattern in Model Coordinates

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Burak–Fiete simulation: each panel shows one population snapshot.



A fixed neuron becomes active as peaks pass its location.

Modeling question: what connections form the pattern, hold its phase at rest, and move it with velocity input?

What do we know at this point?

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The navigation task now becomes a circuit-design problem. Accroding to the discussion we made, there are some principles.

1. **Position selectivity:** Neurons prefer their own phase, i.e., a set of locations.
2. **Transition invariant:** All neurons have the same rule to connect with their fellows.
3. **Phase storage:** The recurrent network can hold the represented location when velocity is zero.
4. **Phase update:** The recurrent network can move the pattern in proportion to velocity.

Hint: We use "phase" here because the representation is periodic.

Model and Notation

We model each neuron using leaky dynamics and rectification:

$$\tau \dot{r}_i = -r_i + \left[\sum_j W_{ij} r_j + I_i(t) \right]_+ .$$

Design task: choose the recurrent weights W_{ij} and the external input $I_i(t)$.

$\mathbf{v}(t)$: velocity input

$\hat{\mathbf{x}}(t)$: position estimate

$\mathbf{q}_i$: neuron coordinate

$\theta(t)$: pattern phase

$r_i(t)$: activity of neuron i

$\mathbf{r}(t)$: population activity

Hint: Neuron coordinate means the **phase preference** *of the neuron.*

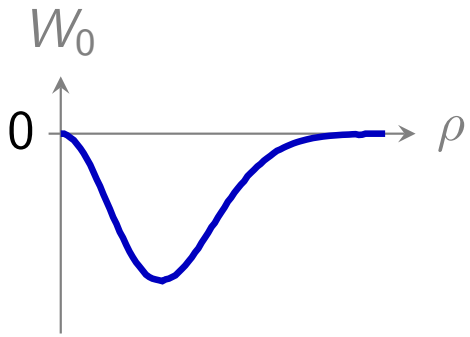
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Weight Design

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At zero velocity, use the same distance-based rule for every neuron:

$$W_{ij} = W_0(\mathbf{q}_i - \mathbf{q}_j).$$



Inhibitory surround

$$\rho = \sqrt{\beta}\,\|\mathbf{d}\|$$

- External excitation sustains activity.
- Weak inhibition near the center permits coactivity.
- A stronger inhibitory surround separates active regions.

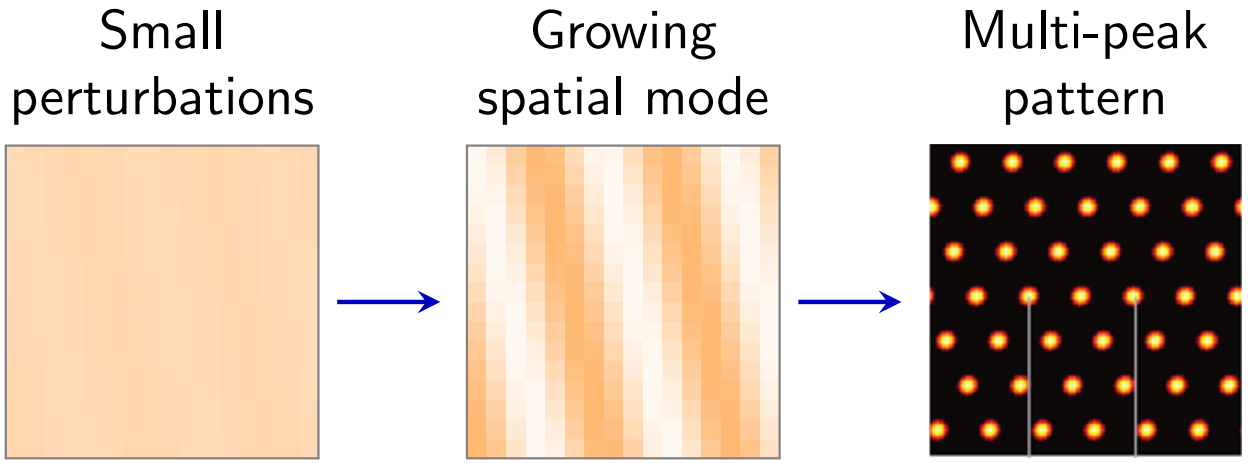
$$W_0(\mathbf{d}) = e^{-\gamma\|\mathbf{d}\|^2} - e^{-\beta\|\mathbf{d}\|^2}, \qquad \gamma = 1.05\beta.$$

All recurrent weights are nonpositive.

Hint: at this point, such gaussian-differential connection is just an **ansatz**. It helps us simplify the effort to find all possible solutions.

Pattern Formation

Begin near uniform activity, with small perturbations.



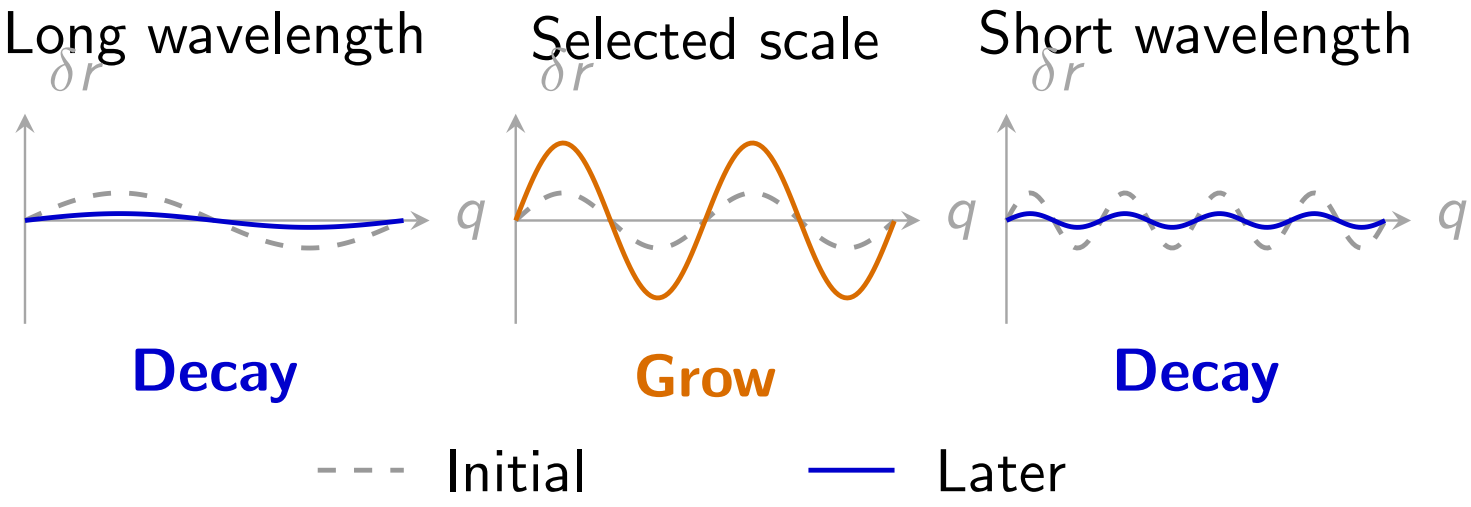
- External excitation and recurrent inhibition can amplify spatial differences.
- Nonlinear dynamics select the final pattern and its stability.

Why do some spatial variations grow?

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Turing Instability

Uniform changes can decay while spatial variations grow.



Near a uniform state, the growth rate of a spatial mode is

$$\sigma(\mathbf{k}) = \frac{-1 + g\widehat{W}_0(\mathbf{k})}{\tau},$$

$$\sigma(\mathbf{0}) < 0, \quad \sigma(\mathbf{k}) > 0 \text{ for some } \mathbf{k} \neq \mathbf{0}.$$

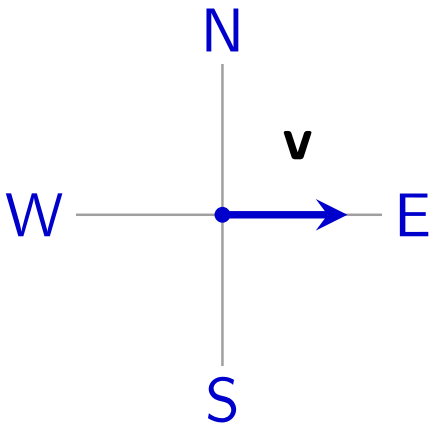
g: response gain; $\widehat{W}_0$: Fourier transform of the kernel.

Next: the pattern forms. How can velocity move it?

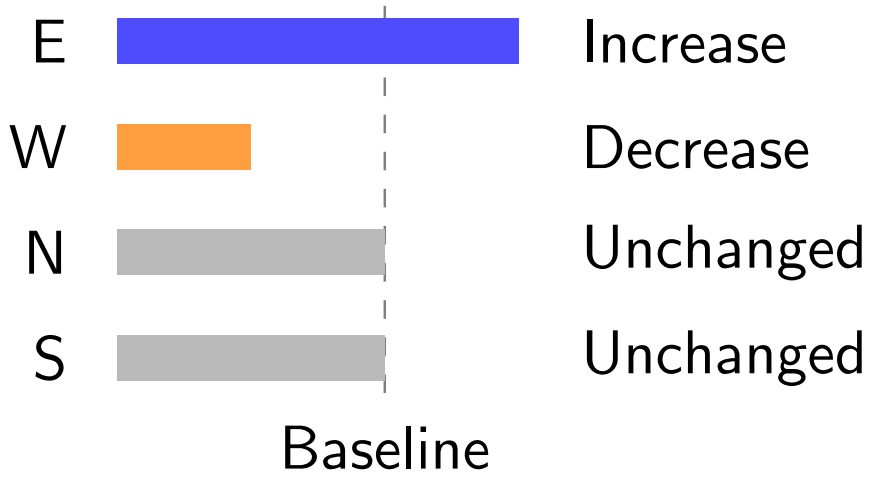
How Can Neurons Represent Velocity?

A simple choice: four preferred directions, E, W, N and S.

Preferred directions



Input during eastward motion



$$B_i(t) \sim I_i = A(\mathbf{q}_i)\big[1 + \alpha\, \mathbf{e}_i \cdot \mathbf{v}(t)\big].$$

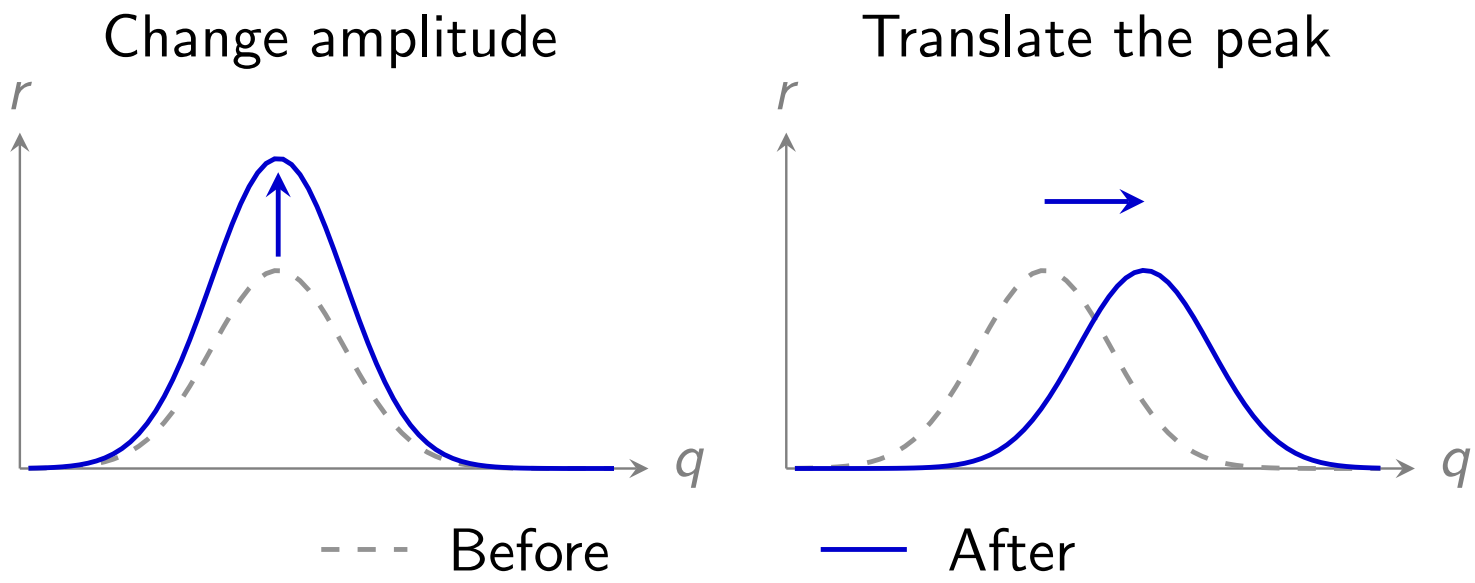
$\mathbf{e}_i$: preferred-direction unit vector.

A: baseline input; α: velocity sensitivity.

Hint: the **non-negativity** *of activity proposes us to use more that two groups.*

Is Direction Selectivity Enough?

Changing activity does not yet explain how a peak moves.



- A taller peak still represents the same phase.
- Translation needs increased activity ahead and decreased activity behind.

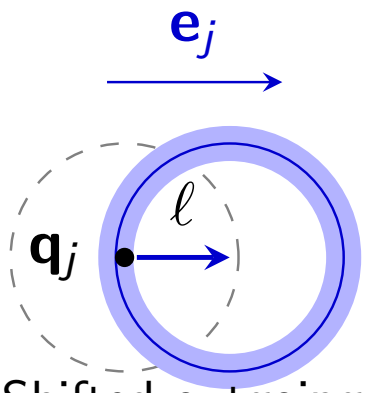
Hint: after input is removed, stable shape distortions decay. To accumulate displacement, velocity must drive the **phase**.

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Coupling Velocity to Pattern Motion

Use the same direction label for input tuning and connection shift:

$$W_{ij} = W_0(\mathbf{q}_i - \mathbf{q}_j - \ell \mathbf{e}_j).$$



Shifted outgoing inhibition

- $\ell \mathbf{e}_j$ shifts neuron j's outgoing weights.
- At rest, opposite directional drives balance.
- Velocity input breaks the balance and drives pattern motion.

With calibrated, weak drive: $\dot{\boldsymbol{\theta}} \simeq G\mathbf{v}$.

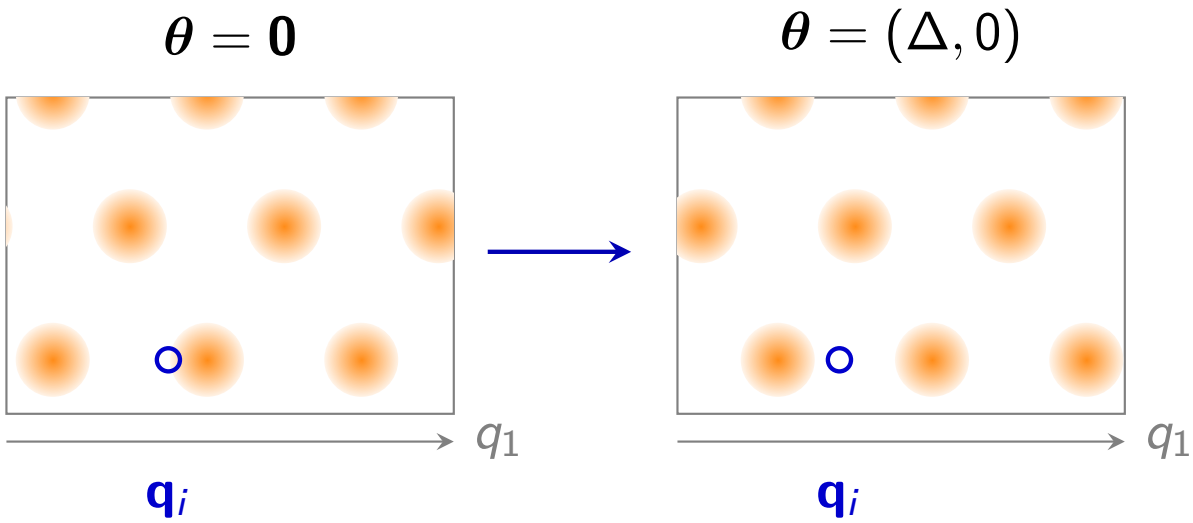
G converts movement velocity to phase velocity.

Hint: to be brief, the weight will activate those neurons whose **coordinates** *are on the direction of movement.*

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The Network Has No Preferred Phase

Ideal limit: zero velocity, uniform input, and continuous translation symmetry.



Relative coordinates are unchanged:

$$\mathbf{q}_i' = \mathbf{q}_i - \boldsymbol{\theta}, \qquad \mathbf{q}_i' - \mathbf{q}_j' = \mathbf{q}_i - \mathbf{q}_j.$$

Keep neuron identities fixed; translate their activity:

$$r_i(\boldsymbol{\theta}) = r_0(\mathbf{q}_i - \boldsymbol{\theta}).$$

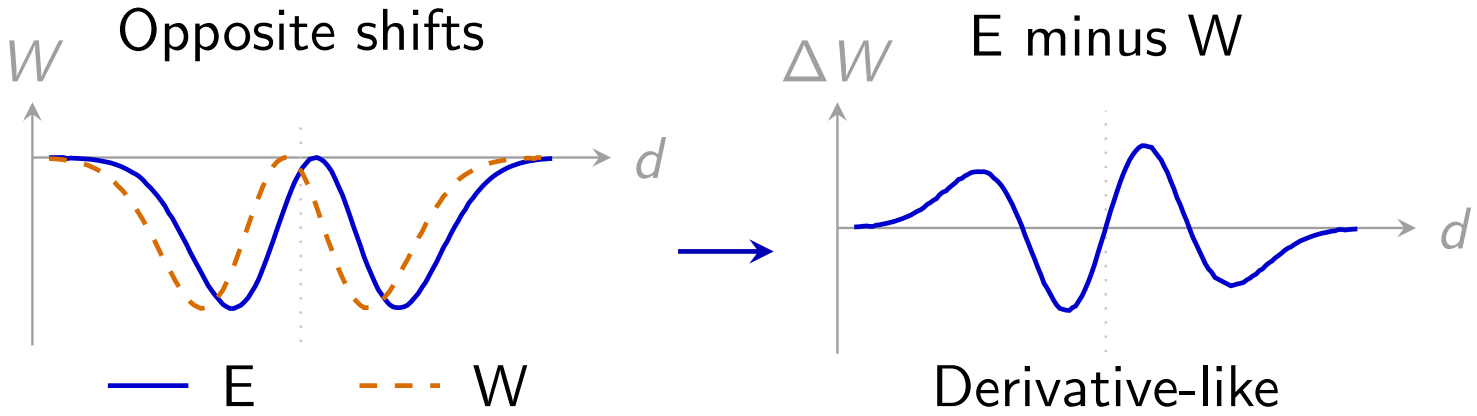
If one stable pattern exists, translation symmetry gives a continuous family of equivalent steady states.

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Why Do Shifted Connections Produce Motion?

Eastward motion increases E input and decreases W input. In a horizontal slice, $d = q_i - q_j$:

$$W_E(d) = W_0(d - \ell), \qquad W_W(d) = W_0(d + \ell).$$



$$\Delta W(d) = W_E(d) - W_W(d) \simeq -2\ell W_0'(d).$$

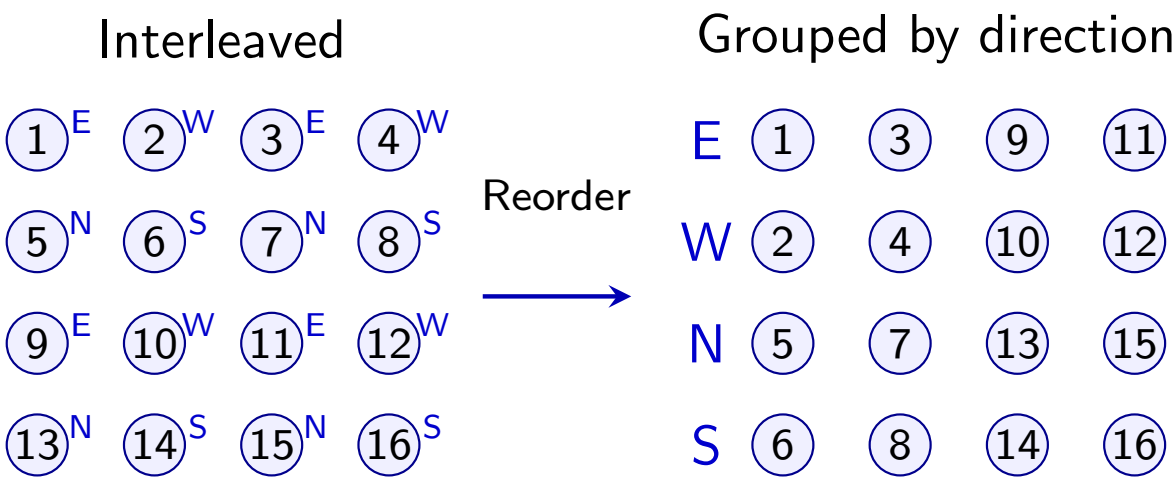
An E/W activity imbalance adds a spatial derivative of recurrent input, following the **current pattern**.

Compare with the change required for translation:

$$\partial_t r = -c\,\partial_q r, \qquad c = \dot{\theta}.$$

Weak shifts and drive: test $c \propto v_x$ and shape stability.

Four Directional Populations



All within- and between-group connections are retained.

Same cells, same model coordinates, same inputs and every connection.

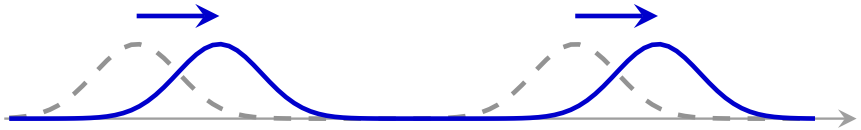
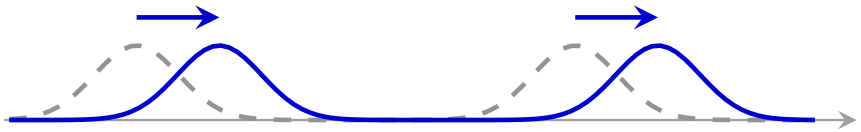
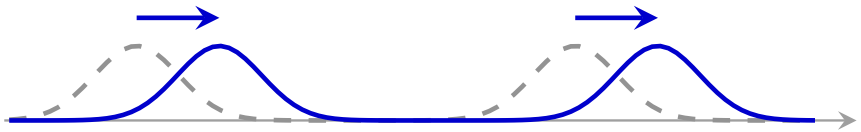
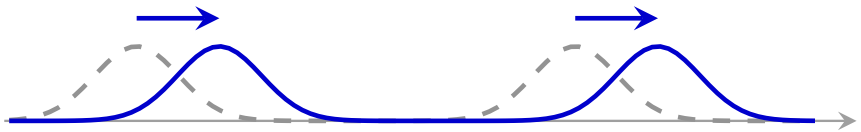
The four populations jointly maintain one pattern. Grouping them on the page preserves the dynamics.

Discuss: what changes if we remove connections between the groups?

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All Four Populations Move Together

Coherent motion: a common phase shift; amplitudes may differ.

Group	Input	Activity along q_x (schematic)
E	$B_E \uparrow$	
W	$B_W \downarrow$	
N	$B_N = A$	
S	$B_S = A$	

- - - Before — After $\Delta\theta_x > 0$ for all

$$H_i(t) = \sum_{d\in\{E,W,N,S\}} \sum_{j\in d} W_{ij} r_j(t).$$

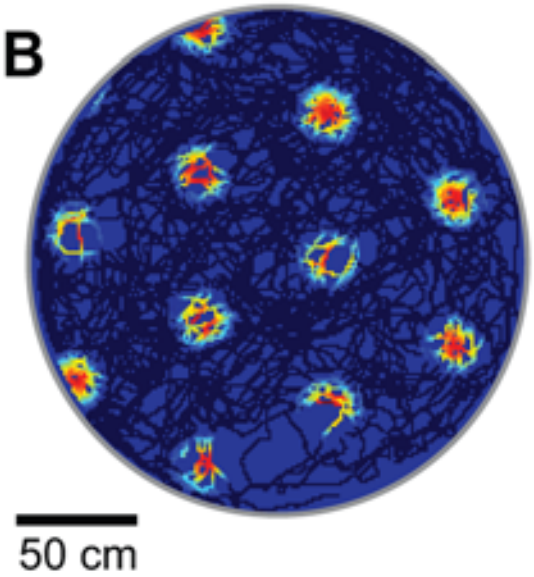
Each neuron receives recurrent input from all four groups.

W input falls; its peak follows the network. Shared feedback recruits W cells at the new phase.

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From Pattern Motion to Grid Fields

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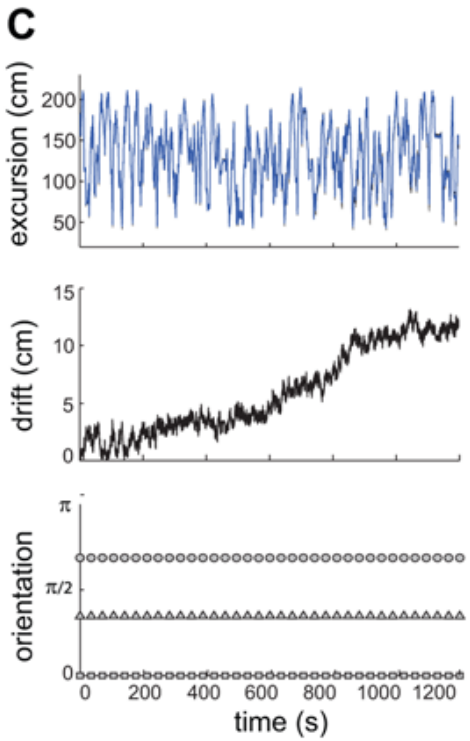


1. Fix one neuron at $\mathbf{q}_i$.
2. Move the population pattern as the animal moves.
3. Record this neuron's activity across physical positions.

$$r_i(t) = r_0(\mathbf{q}_i - \boldsymbol{\theta}(t)).$$

Repeated peaks give grid fields when phase tracks movement accurately.

Does It Really Integrate Velocity?



Drive the model with a recorded animal trajectory.

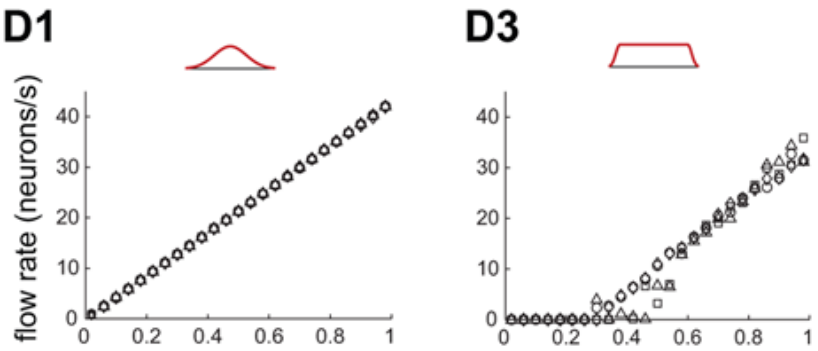
Compare true and inferred position; track error and pattern rotation.

Deterministic periodic example:
$\sim$20 min, $\sim$260 m;
error $\sim$15 cm,
grid period $\sim$48 cm.

A regular population pattern can still integrate velocity poorly.

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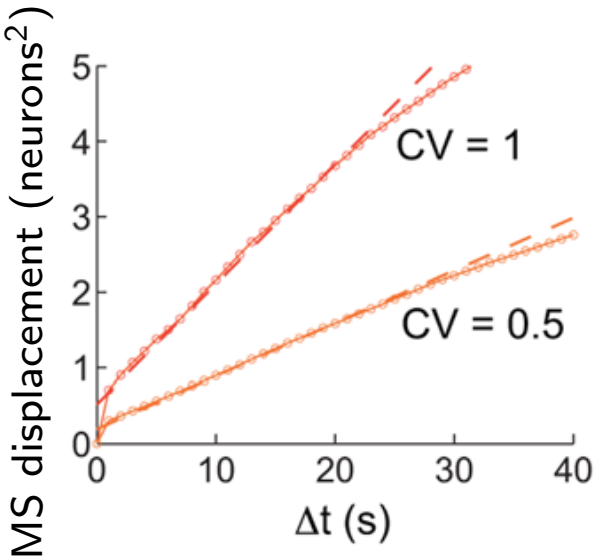
Boundary Conditions as a Model Test



Horizontal axis: input speed (m/s).

- **Periodic:** wrap connections across opposite edges.
- **Aperiodic:** edges can pin or rotate the pattern.
- Smoothly taper external input $A(\mathbf{q})$ to improve flow.

Stable Shape, Drifting Position



Shape errors can decay.

Noise along neutral directions changes phase, even at zero velocity.

Larger networks reduce drift in the tested model.

$$\mathbb{E}\|\boldsymbol{\theta}(t) - \boldsymbol{\theta}(0)\|^2 \simeq D_{\text{phase}}\, t.$$

MS means mean squared. Attractor stability does not fix absolute phase.

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A General Construction Problem

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1. **Choose the representation:** what should each network state encode?
2. **Construct the stable family:** which connections hold its shape?
3. **Construct motion:** which inputs move the state along that family?

B–F give a concrete construction for planar translation and test its accuracy.

Next: if we specify another target manifold, can we construct its connections and motion systematically?

What Can We Reuse from Existing Models?

System	Stored variable	Update input
Eye-position integrator	Gaze angle	Velocity command
Head-direction network	Heading	Angular velocity
Grid-cell module	Spatial phase	Translation velocity

The common computation

Hold a continuous state when input is zero.
Update that state according to a rate-of-change input.

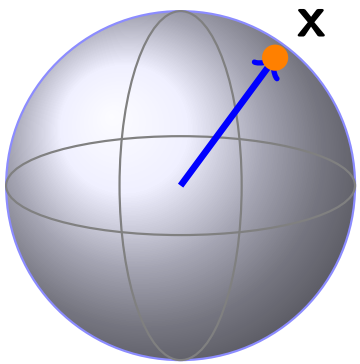
Can we **derive a construction recipe** instead of designing each circuit separately?

MADE: *Manifold Attractor Direct Engineering*.

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A New Task: Represent a Direction on a Sphere

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A direction has two degrees of freedom

External space $\mathcal{M}$: possible directions.

Neuron coordinates $\mathcal{P}$: labels used to define connectivity.

Activity manifold $\mathcal{N}$: the family of stored population states.

Goal: hold any direction; update it when a rotation signal arrives.

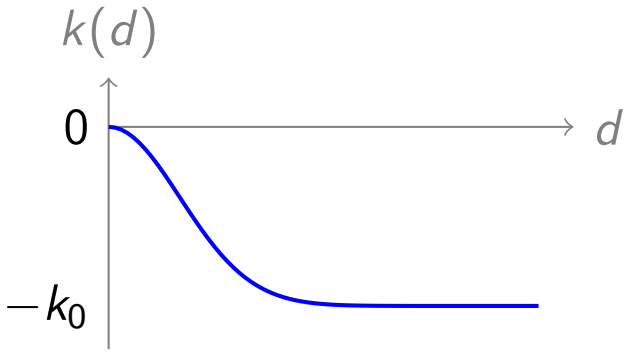
Neuron coordinates need not match positions in brain tissue.

Turn Geometry into Connectivity

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Choose neuron coordinates, then measure distances on the target surface:

$$W_{ij} = k(d_{\mathcal{P}}(\mathbf{q}_i, \mathbf{q}_j)) .$$



Weak inhibition nearby; strong inhibition far away.

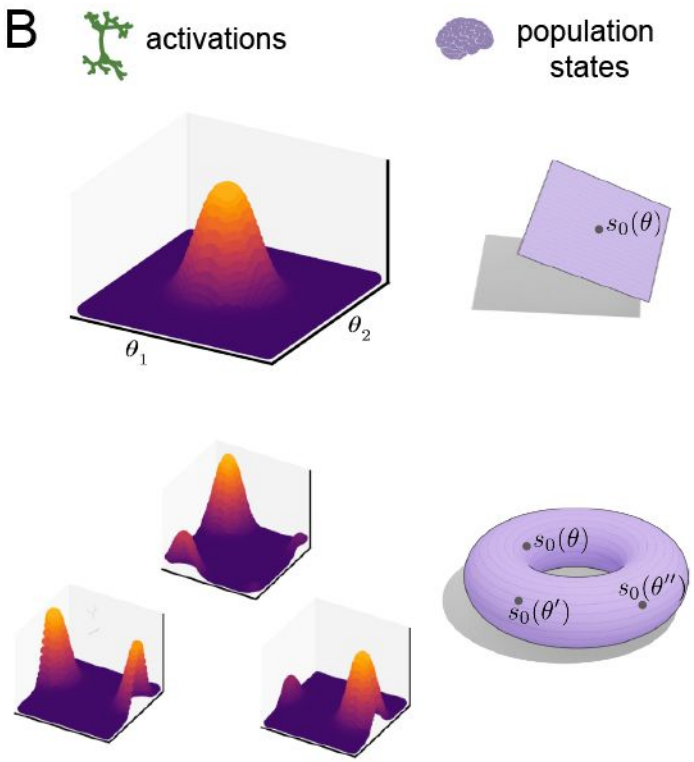
Local coactivity: nearby neurons inhibit each other less.

Global competition: distant activity is suppressed.

External excitation sustains a nonzero response.

Kernel strength, width and geometry must support a stable bump.

Let a Bump Represent the State



One bump center specifies one population state $\mathbf{r}^*(\boldsymbol{\theta})$.

Moving the center traces a family of states in activity space.

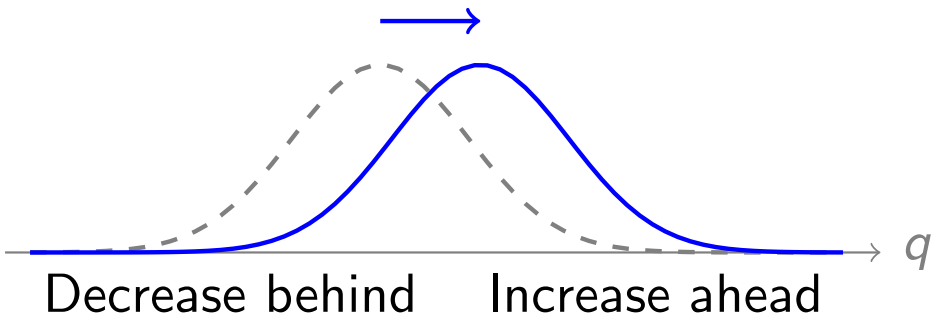
Required: shape errors decay; changes of represented state can persist.

B–F encode phase with a **multi-bump lattice**.
This MADE construction uses a **single bump**.

Periodic edge fragments belong to one wrapped bump.

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What Input Would Move the Bump?



$$r(q,t) = r_0(q - \theta(t)), \qquad \partial_t r = -\dot{\theta}\,\partial_q r.$$

The required activity change depends on the **current bump location**.

The design problem

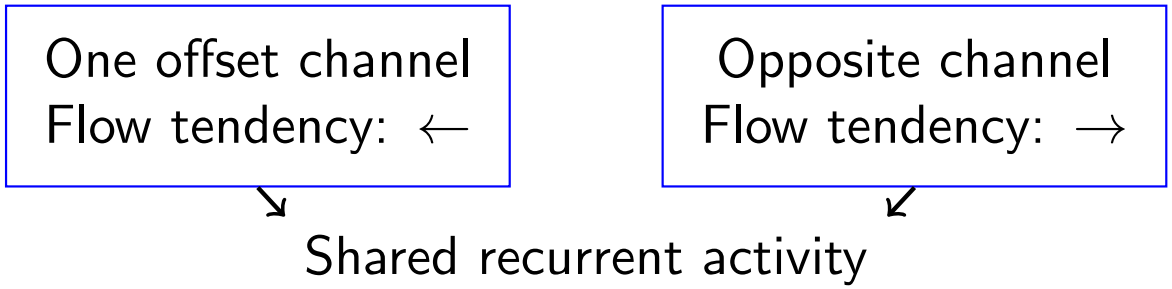
A velocity signal gives a speed and direction.
How can it select the right neurons to increase or decrease?

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Put the Motion Rule into the Connections

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A small **offset of the connection kernel** lets the current activity generate its own directional drive.

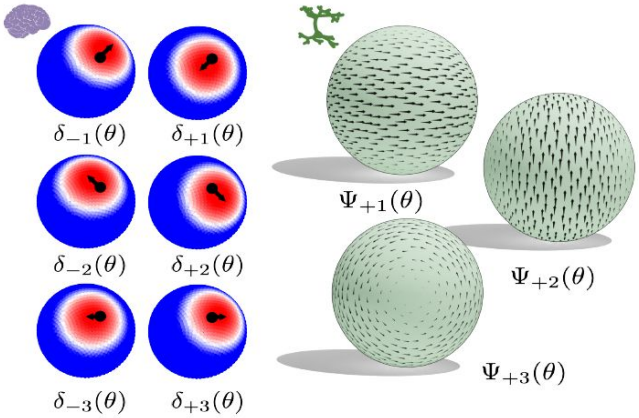


MADE calls the flowing building blocks **QANs**:
Quasiperiodic Attractor Networks.

B–F's E/W/N/S groups illustrate the same design principle:
fixed directional connections, input-controlled activity.

Why Curved Spaces Need Different Motion Rules

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On a sphere, replace a uniform planar shift with a **rotation**.

A **Killing field** specifies motion that preserves distances on the surface.

Each rotation axis has two fixed poles. Other axes supply motion there.

Three rotation generators, each with $+$ and $-$ channels, cover the sphere's possible tangent motions.

The geometry determines which motion channels are available.

Translate External Velocity into Neural Drive

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The represented state is a mapping of the external variable:

$$\boldsymbol{\theta} = \pi(\mathbf{x}), \qquad \dot{\boldsymbol{\theta}} = D\pi(\mathbf{x})\,\dot{\mathbf{x}}.$$

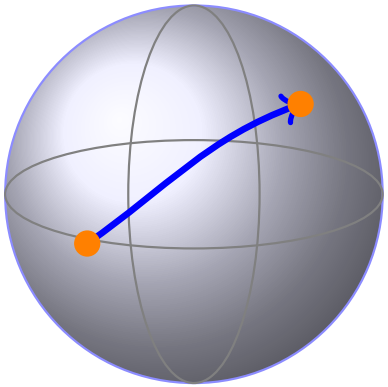
This is the chain rule: what internal motion corresponds to the external change?

1. Convert external velocity into a tangent velocity of the representation.
2. Express that motion using the available channels.
3. Modulate the channels' input strengths.

On curved spaces, the conversion may use the current state estimate.

$D\pi$: Jacobian of a **mapping**. J: Jacobian of the **neural dynamics**.

Assemble the Spherical Integrator



Bump center follows a path on the sphere

1. Place neuron coordinates on a sphere.
2. Use distance-based inhibition and background excitation.
3. Build paired rotation channels about three axes.
4. Let rotation inputs set their relative drive.

For a unit direction $\mathbf{p}$ and angular velocity $\mathbf{\Omega}$:

$$\dot{\mathbf{p}} = \mathbf{\Omega} \times \mathbf{p}.$$

Zero rotation input restores balanced drive and holds the represented direction.

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A Construction Recipe—and Its Tests

Recipe: choose a representation, construct stable states, then build and control its motion channels.

1. **Hold:** does zero input preserve different initial states?
2. **Recover:** do shape perturbations decay?
3. **Integrate:** is motion accurate across locations and directions?
4. **Stress-test:** what changes with noise and finite sampling?

Discussion

A bump moves correctly near one point. What remains to be established before calling the network a general integrator?

MADE is a constructive proposal with simulations (reviewed preprint v1); continuity and robustness need further tests.

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Claudi, F., Chandra, S. & Fiete, I. R. (2025). A theory and recipe to construct general and biologically plausible integrating continuous attractor neural networks. *eLife*, reviewed preprint v1, July 28, 2025. doi:10.7554/eLife.107224.1

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