(Relating attractors to the) topological organization of neural networks

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Applied Algebraic Topology 2017

Hokkaido University, Sapporo

Aug 11, 2017

Plan of the talk

- Attractors in neuroscience
- Network structures/motifs
- Threshold-linear networks, CTLNs
- Early explorations...
- Graphical analysis of fixed points of CTLNs

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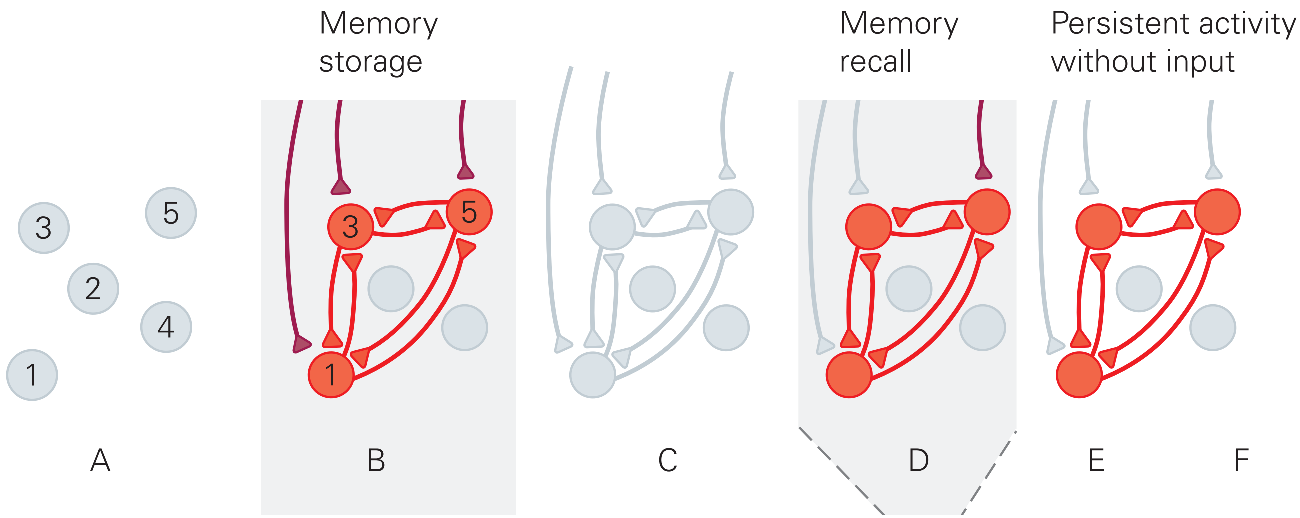
Memory states as attractors of a neural network



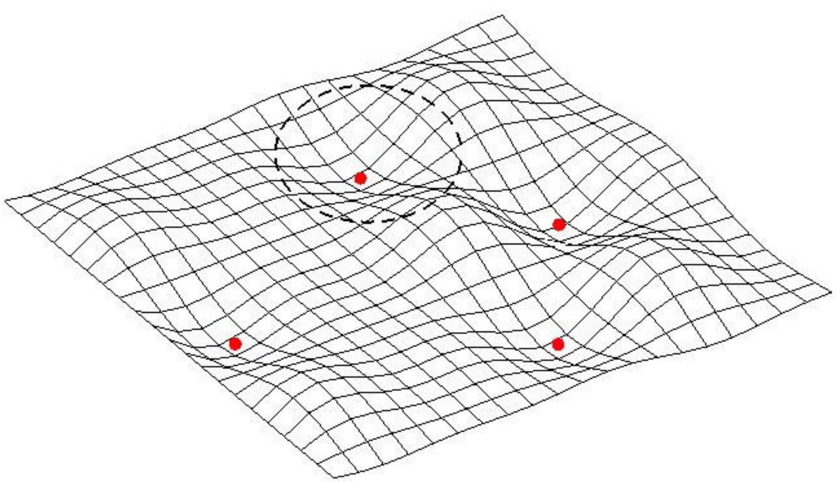
Appendix E of Kandel (Seung & Yuste)

memory patterns ⟷ fixed point attractors

Classical model - Hopfield networks

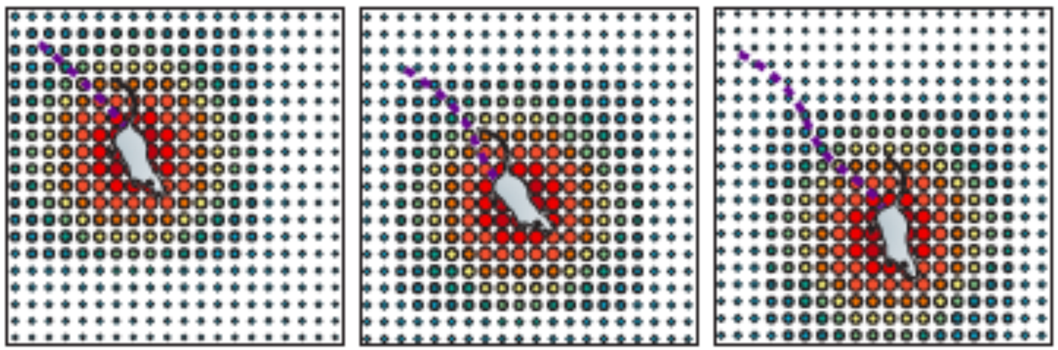
memory patterns ⟷ fixed point attractors

famous Hopfield result: guaranteed convergence
to a fixed point for symmetric interaction matrix



Example: place cell activity in hippocampus

memory patterns (animal position) ⟷ fixed point attractors ("bump" attractors)

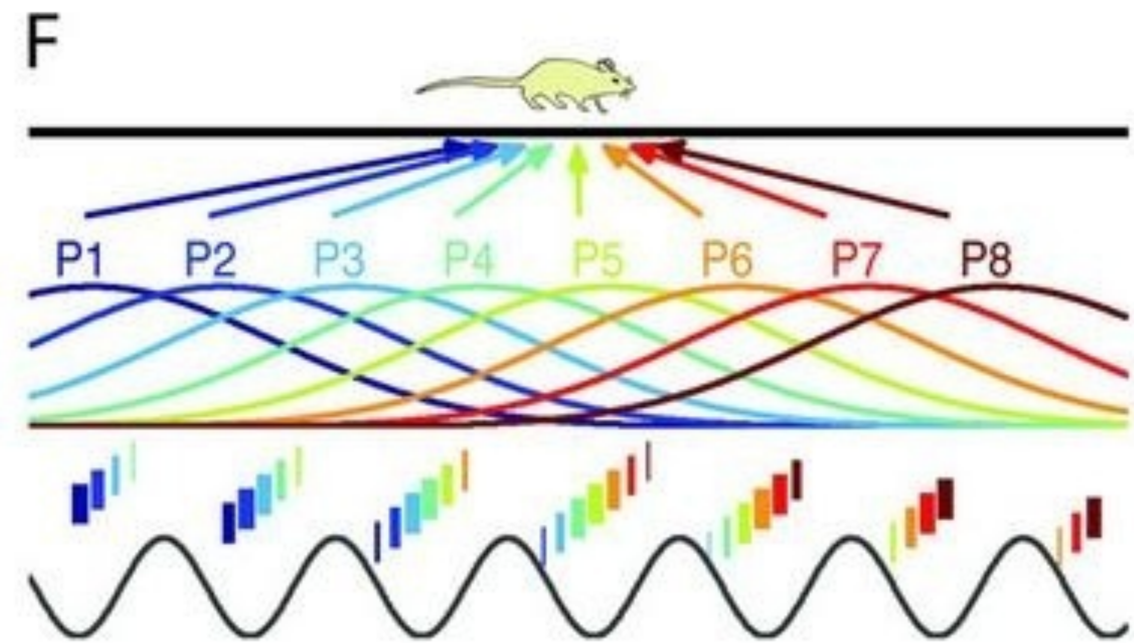


McNaughton et. al., Nature Rev. Neurosci. 2006

Tsodyks & Sejnowski 1995,
Samsonovich & McNaughton 1997

Example: place cell activity in hippocampus

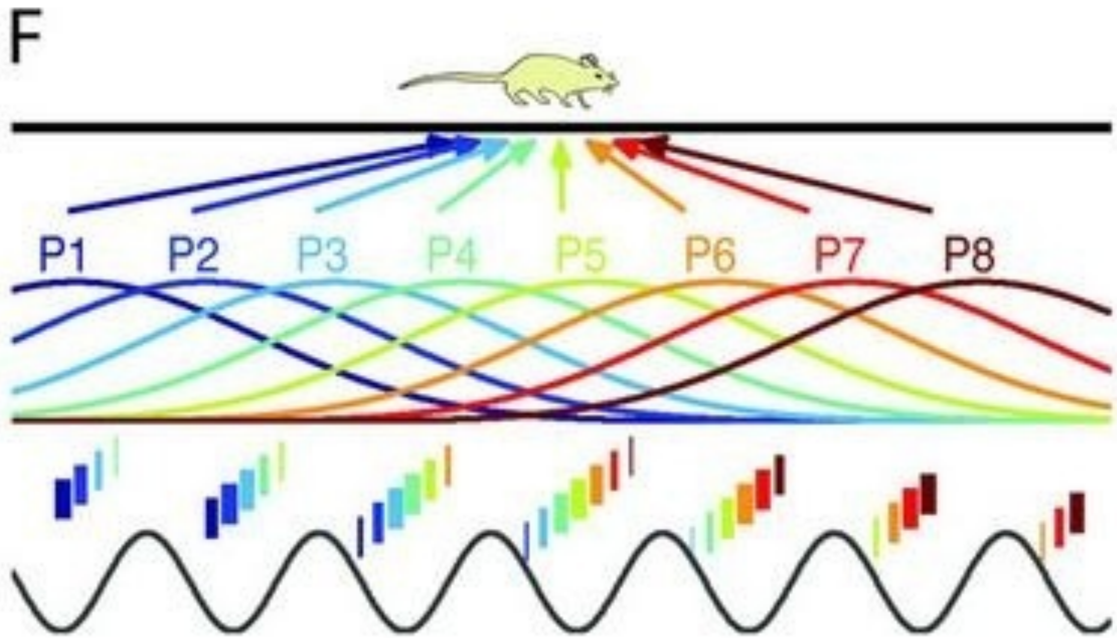
memory patterns (animal position) ⟷ fixed point attractors ("bump" attractors) ??



Individual positions do not correspond to fixed points, but sequences...

Example: place cell activity in hippocampus

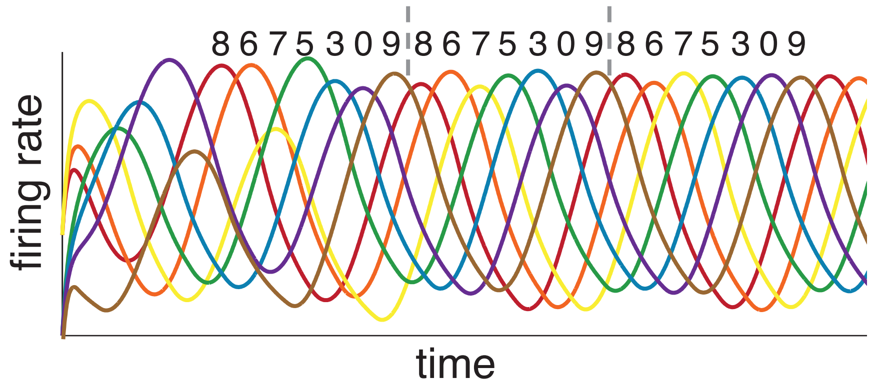
memory patterns (animal position) ⟷ periodic attractors ?

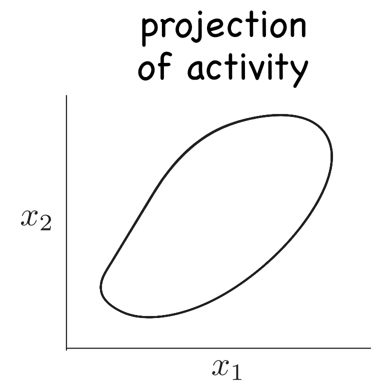


Individual positions do not correspond to fixed points, but sequences…

What other types of attractors are important for neural computation?

Example: You want to remember Jenny's phone # 867-5309





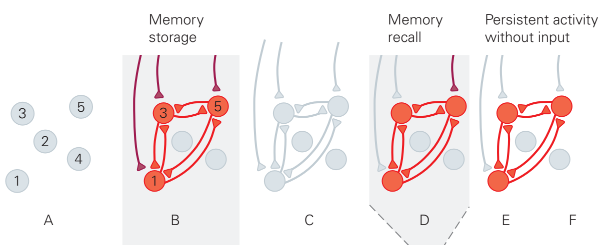
Limit cycles are also useful for modeling central pattern generators (CPGs) that govern respiration, locomotion, etc.

Evidence for memories as sequential attractors (and the dangers of an overly large basin of attraction)

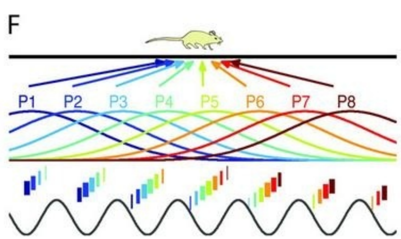
https://www.youtube.com/watch?v=HNRNHgi1RzU

Memory states as attractors of a neural network

static memory patterns ⟷ fixed point attractors (including continuous attractors/ "bump" attractors)



dynamic memory patterns ⟷ periodic attractors (sequences, rhythms)



[other periodic attractors:
central pattern generators (CPGs) -
biological rhythms, locomotive gaits, etc.]

memory patterns ⟷ chaotic attractors
?

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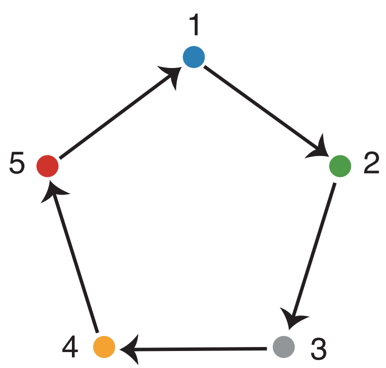
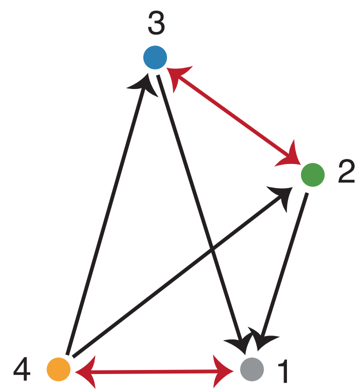
Recurrent vs. feedforward architecture

Recurrent motifs
(attractors)

cycle



directed clique

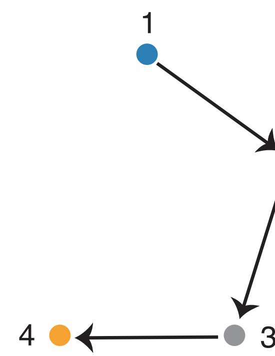


<u>directed clique</u>: there exists an ordering on the nodes such that

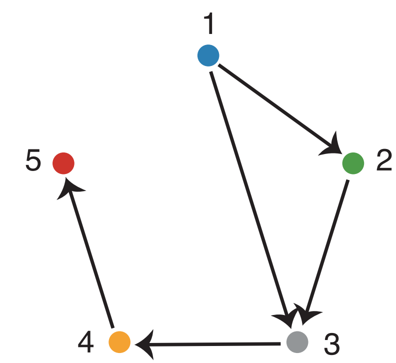
$$i \to j \text{ if } i > j$$

Feedforward motifs
(FF flow of information)

path



FF graph



<u>feedforward graph</u>: there exists an ordering on the nodes such that

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2005

Highly Nonrandom Features of Synaptic Connectivity in Local Cortical Circuits

Sen Song[1], Per Jesper Sjöström[2,3], Markus Reigl[1], Sacha Nelson[2], Dmitri B. Chklovskii[1*]

- local cortical circuits
- layer 5 pyramidal neurons
- rat visual cortex
- simultaneous quadruple whole-cell recordings

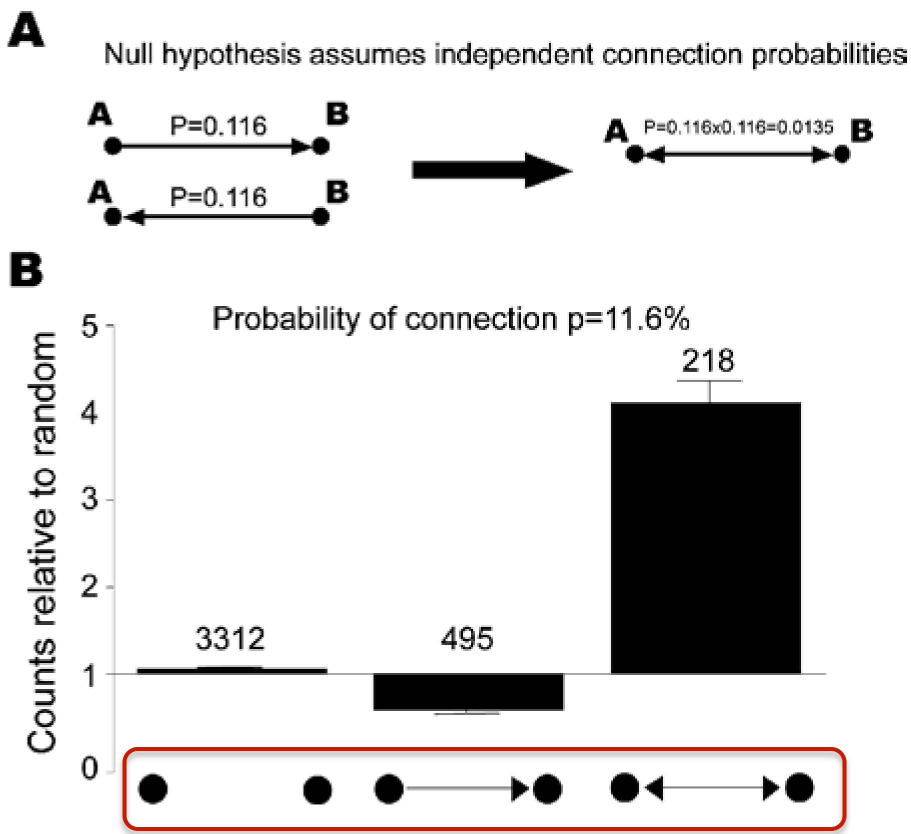

Figure 2. Two-Neuron Connectivity Patterns Are Nonrandom

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2005

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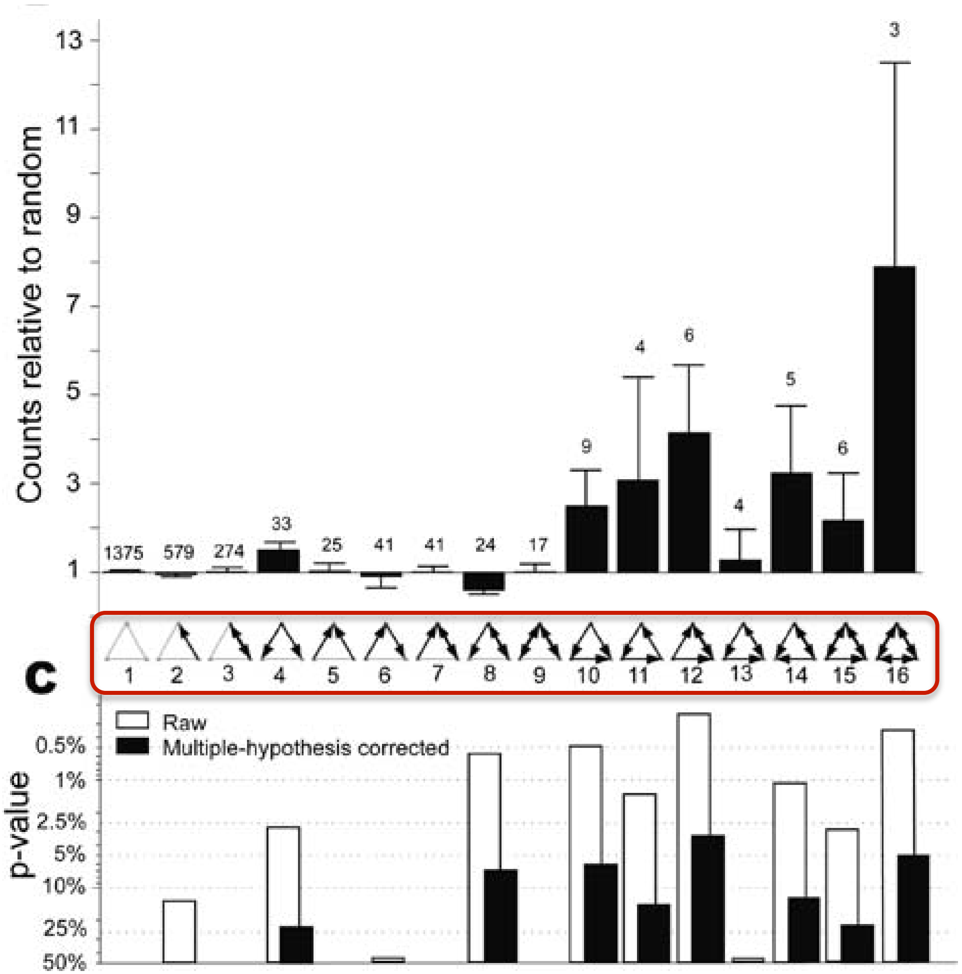
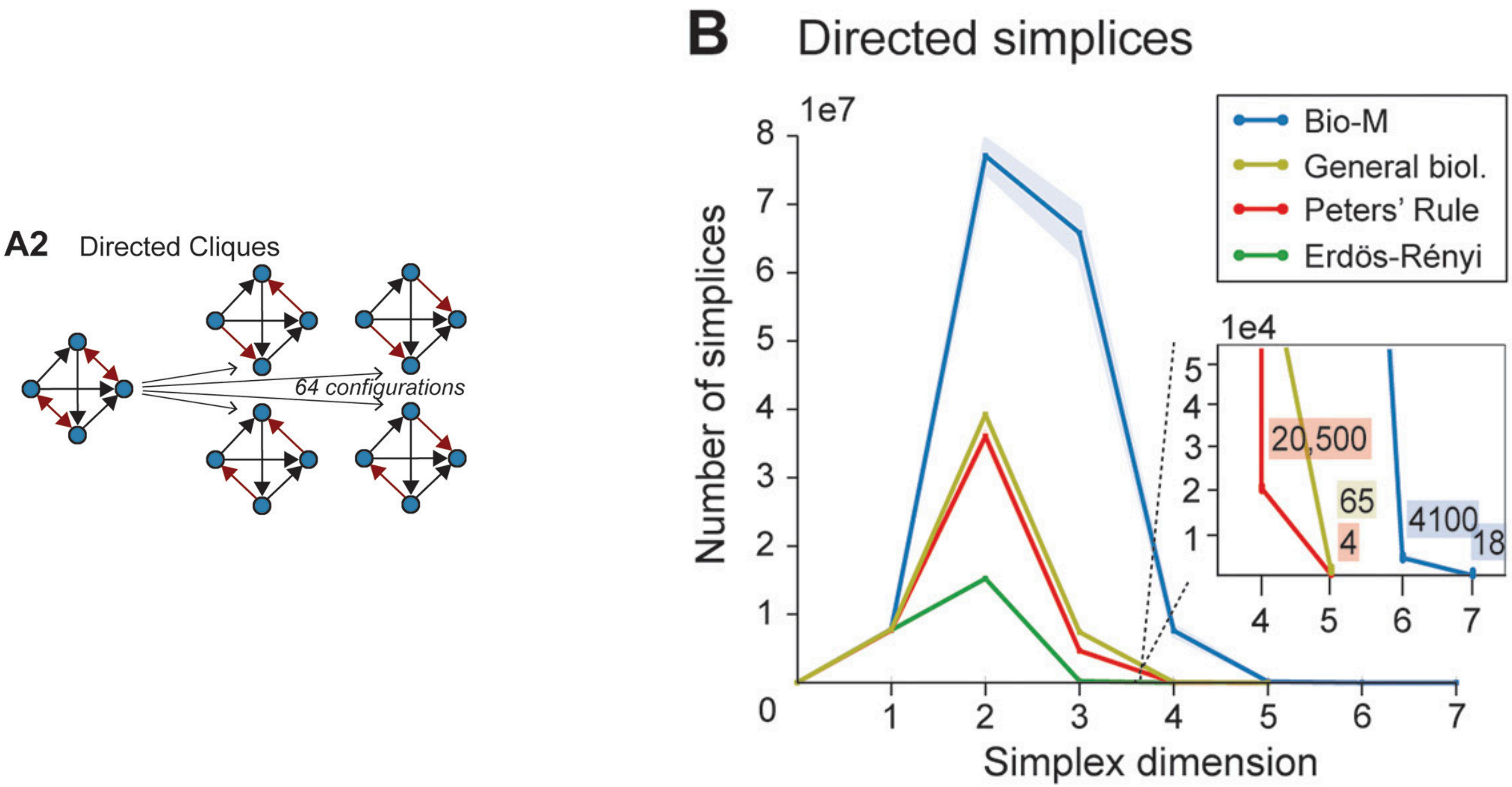


Figure 4. Several Three-Neuron Patterns Are Overrepresented as Compared to the Random Network

Cliques of Neurons Bound into Cavities Provide a Missing Link between Structure and Function

frontiers in Computational Neuroscience
June 2017 | Volume 11 | Article 48

Michael W. Reimann[1†], Max Nolte[1†], Martina Scolamiero[2], Katharine Turner[2], Rodrigo Perin[3], Giuseppe Chindemi[1], Paweł Dłotko[4‡], Ran Levi[5‡], Kathryn Hess[2‡] and Henry Markram[1,3*‡]*



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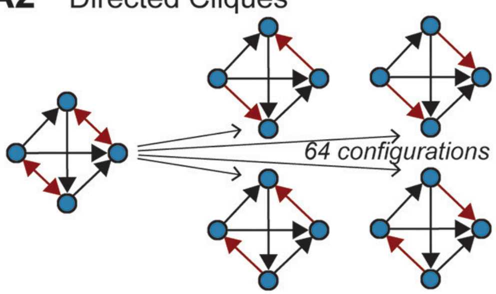
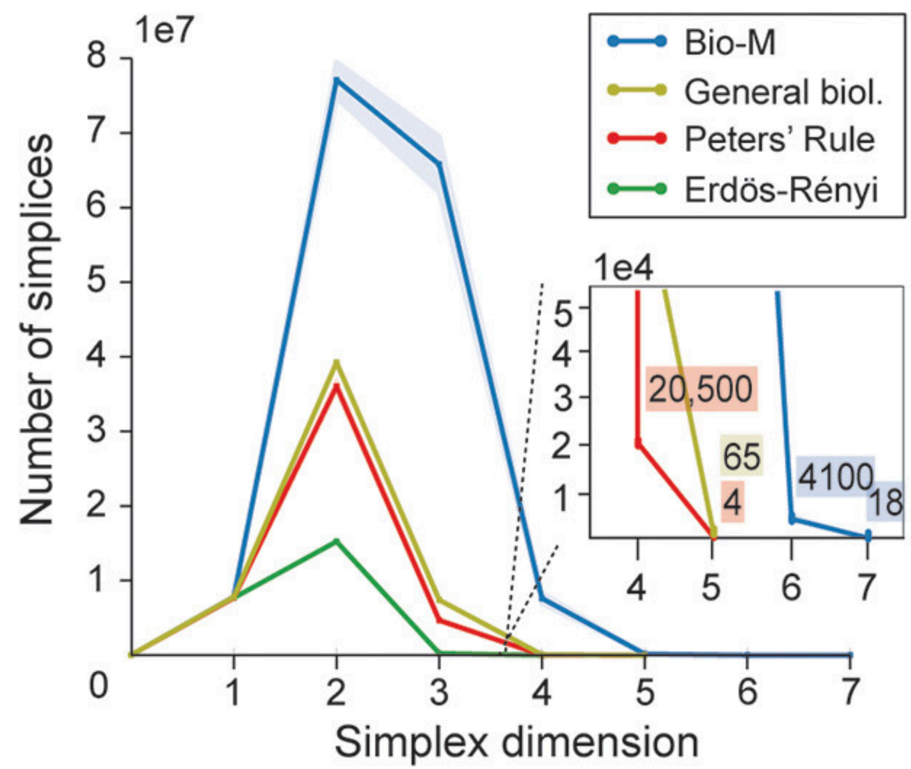
A2 Directed Cliques



B Directed simplices

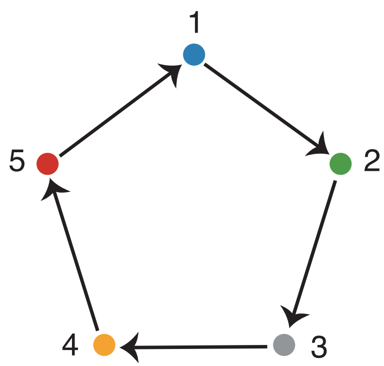


Directed cliques associated with "feedforward" flow of information!

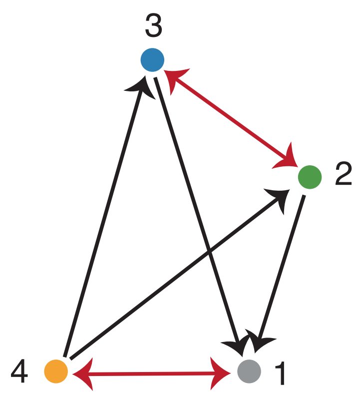
Recurrent vs. feedforward architecture

Recurrent motifs (attractors)

cycle



directed clique



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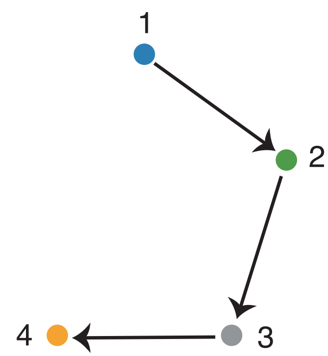
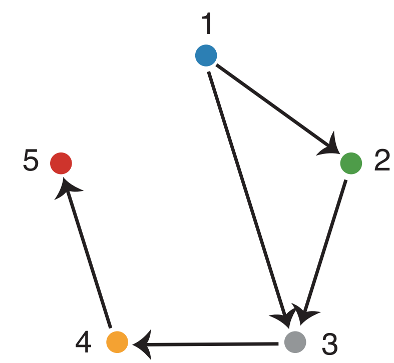
Feedforward motifs (FF flow of information)

path



FF graph



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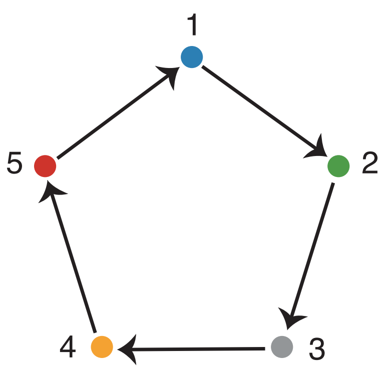

Feedforward motifs (FF flow of information)

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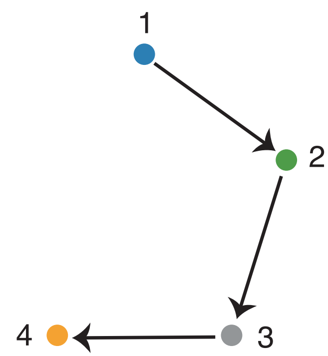

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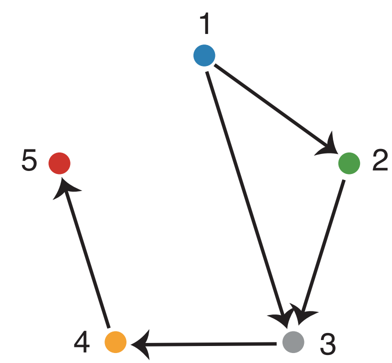
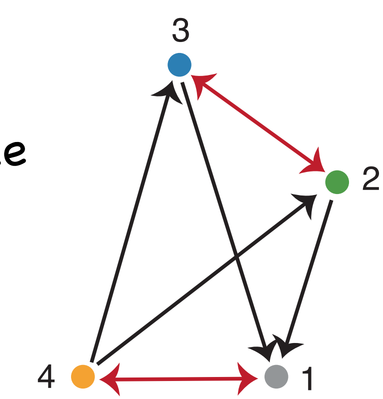


directed clique
goes here?



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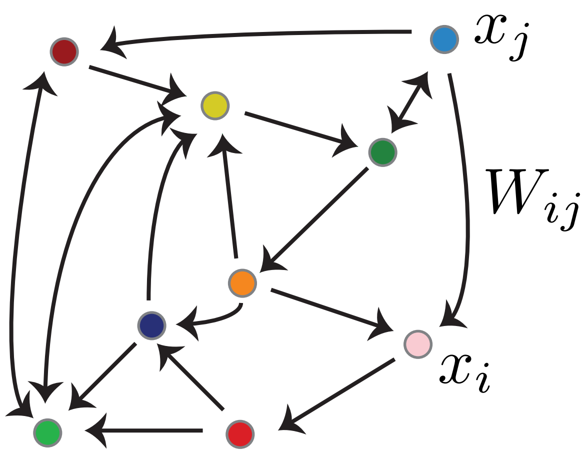
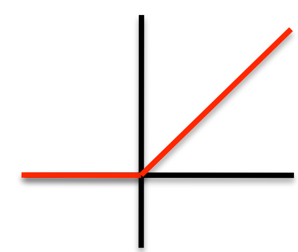
Threshold-linear networks



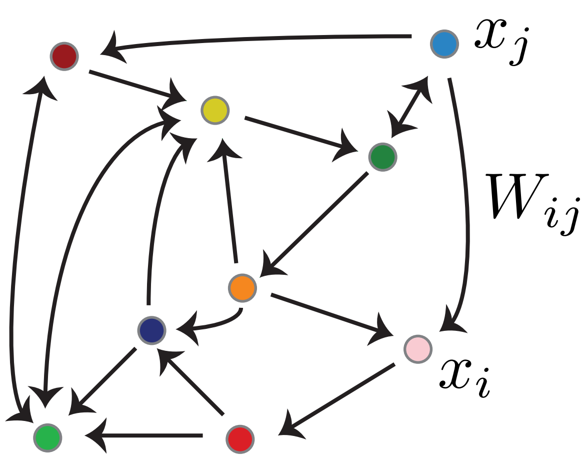
Threshold-linear dynamics

$$\frac{dx_i}{dt} = -x_i + \left[\sum_{j=1}^{n} W_{ij}x_j + \theta\right]_+$$



same as ReLU (rectified linear unit) in deep learning networks

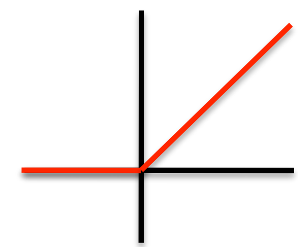
Threshold-linear networks



Threshold-linear dynamics

$$\frac{dx_i}{dt} = -x_i + \left[\sum_{j=1}^{n} W_{ij} x_j + \theta \right]_+$$

- multistability
- limit cycles
- chaos
- quasiperiodic attractors



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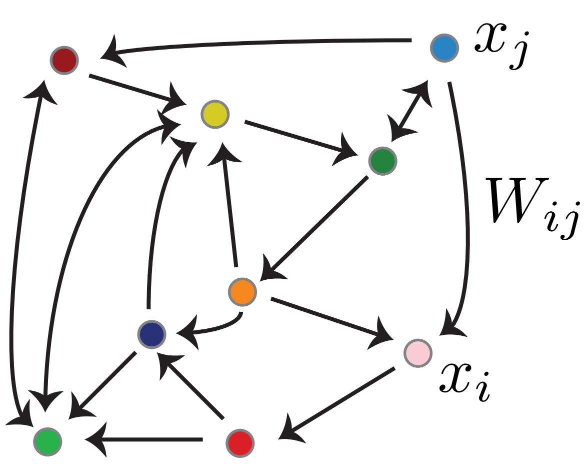
Fixed points/steady states/equilibria



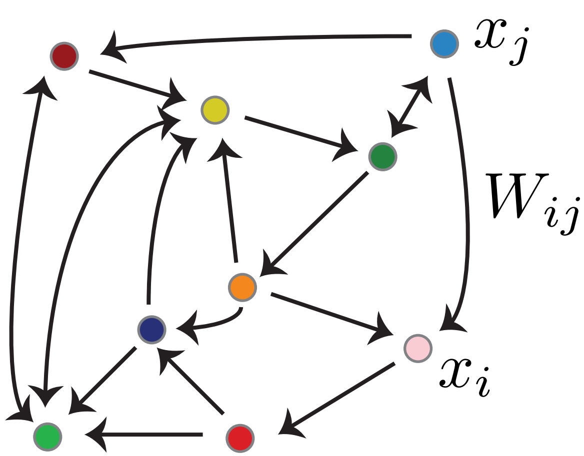
Fixed points:

set $dx_i/dt = 0$ for each $i \in [n]$

$$\frac{dx_i}{dt} = -x_i + \left[\sum_{j=1}^{n} W_{ij}x_j + \theta\right]_+$$

Fixed points arise when linear fixed points lie in the "correct" chamber of the hyperplane arrangement.

Fixed points/steady states/equilibria



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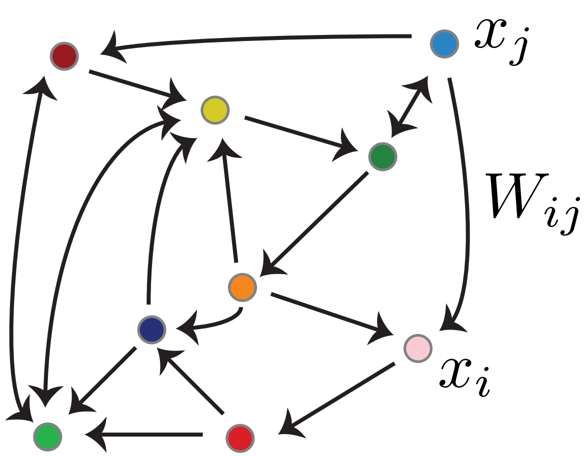
Fixed points arise when linear fixed points lie in the "correct" chamber of the hyperplane arrangement.

There is at most one fixed point per support (subset of neurons):

$$\text{supp}(x) = \{i \in [n] \mid x_i > 0\}$$

Combinatorial Threshold-Linear Networks (CTLNs)



Threshold-linear dynamics

$$\frac{dx_i}{dt} = -x_i + \left[\sum_{j=1}^{n} W_{ij}x_j + \theta\right]_+$$

Graph to network connectivity

$$W_{ij} = \begin{cases} 0 & \text{if } i = j \\ -1+\varepsilon & \text{if } i \leftarrow j \text{ in } G \\ -1-\delta & \text{if } i \not\leftarrow j \text{ in } G \end{cases}$$

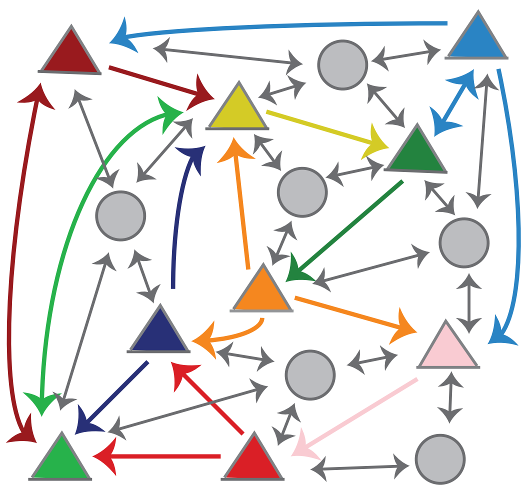
Parameter constraints

$\delta > 0$ $\theta > 0$

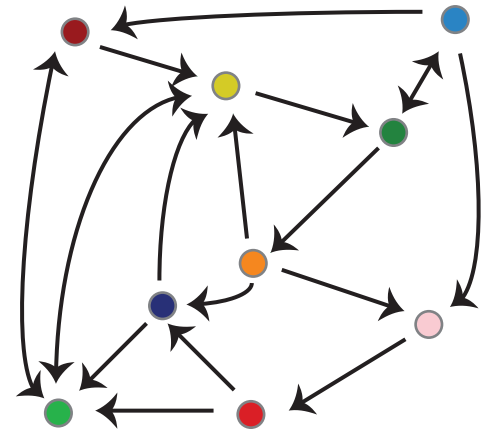
$$0 < \varepsilon < \frac{\delta}{\delta + 1}$$

Pyramidal neurons in a sea of inhibition

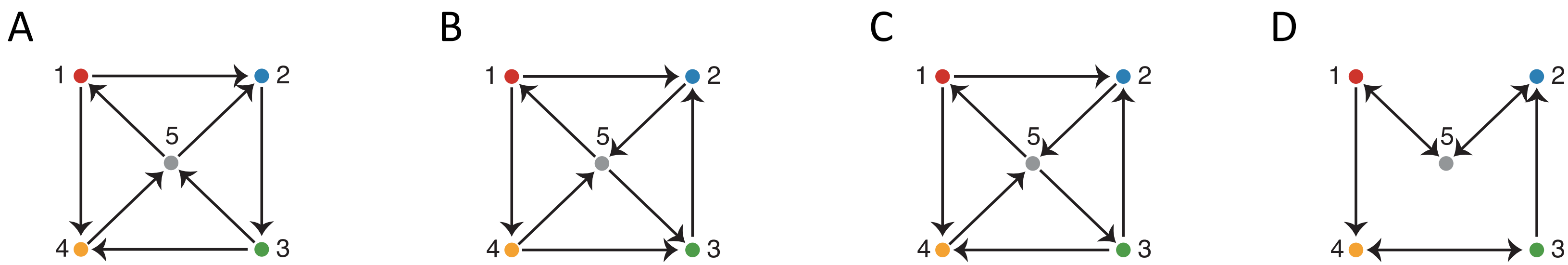
Network of excitatory and inhibitory cells



Graph of interactions among excitatory cells



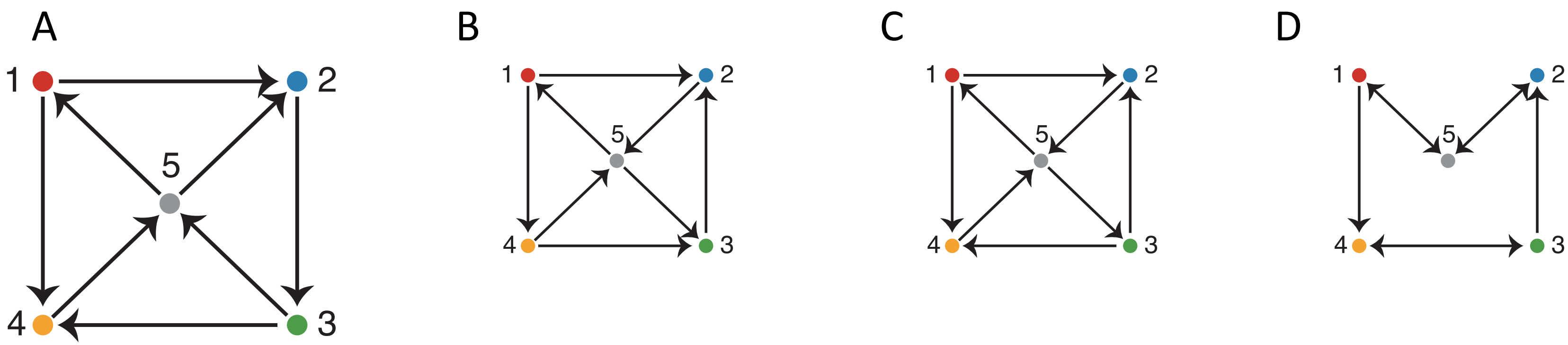
4 neural networks with matching degree sequence

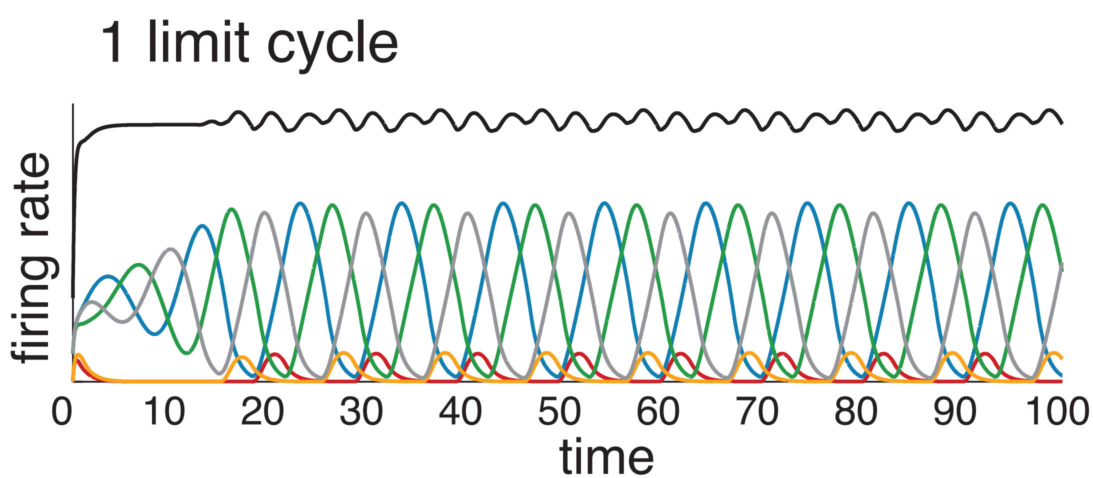


all graphs have the same
in/out-degree sequence:

(1,2), (1,2), (2,1), (2,1), (2,2)

examples of nonlinear network dynamics: limit cycles





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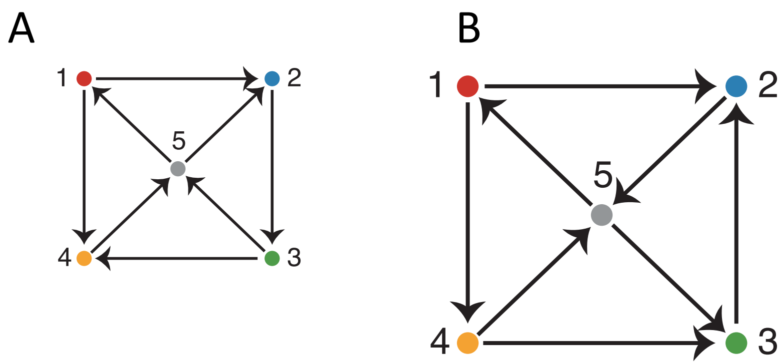
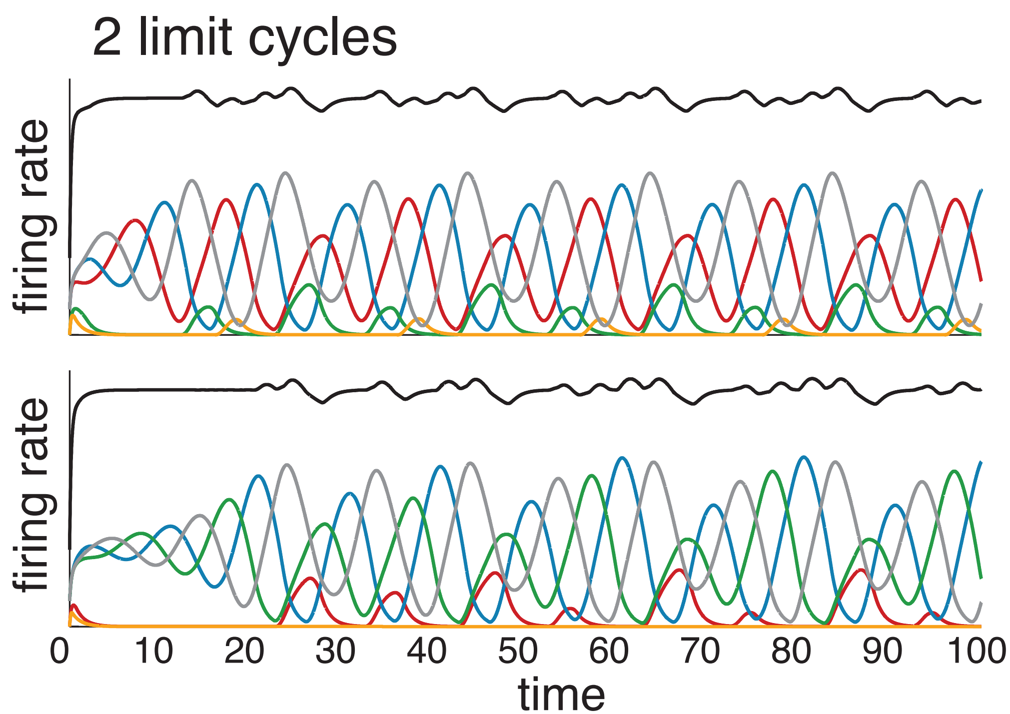
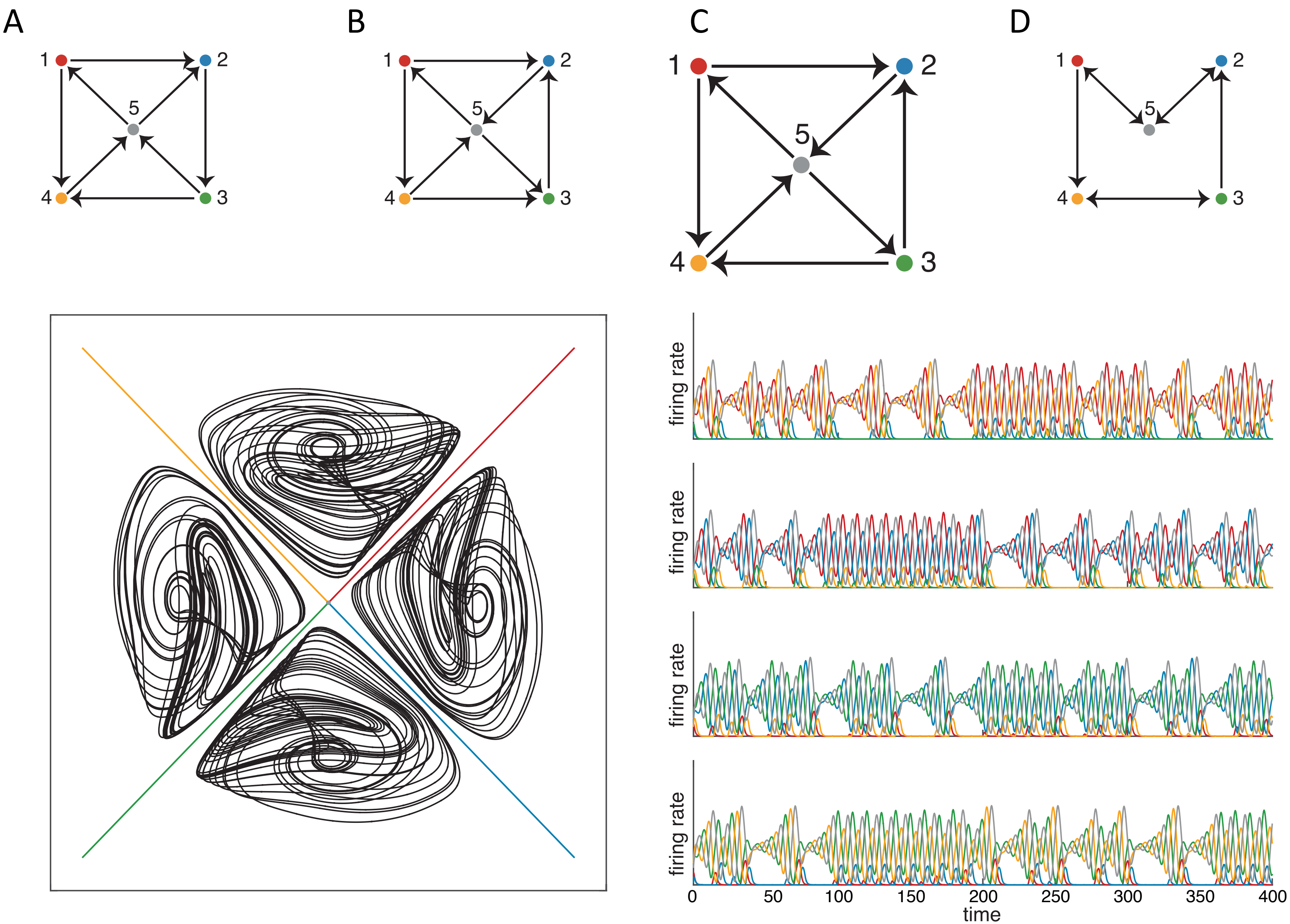
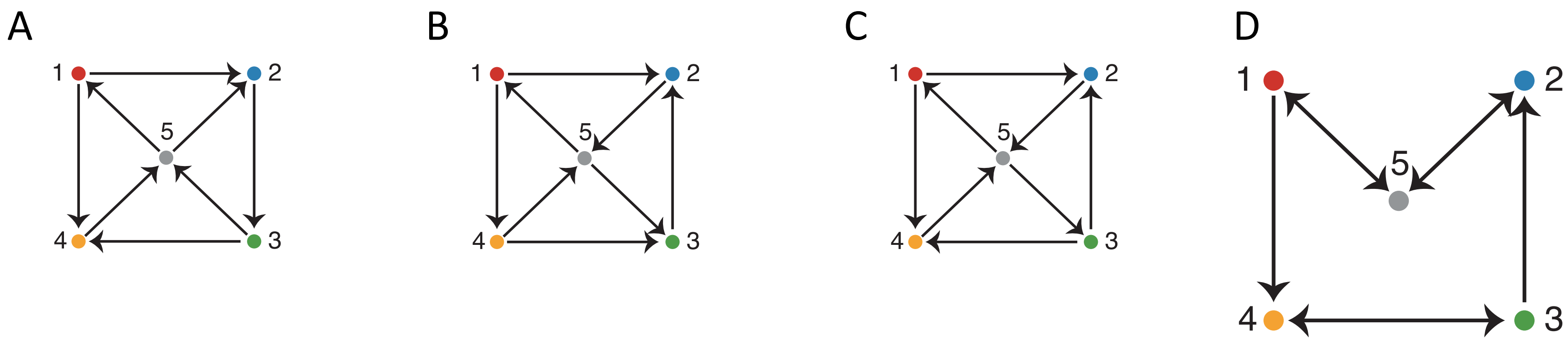




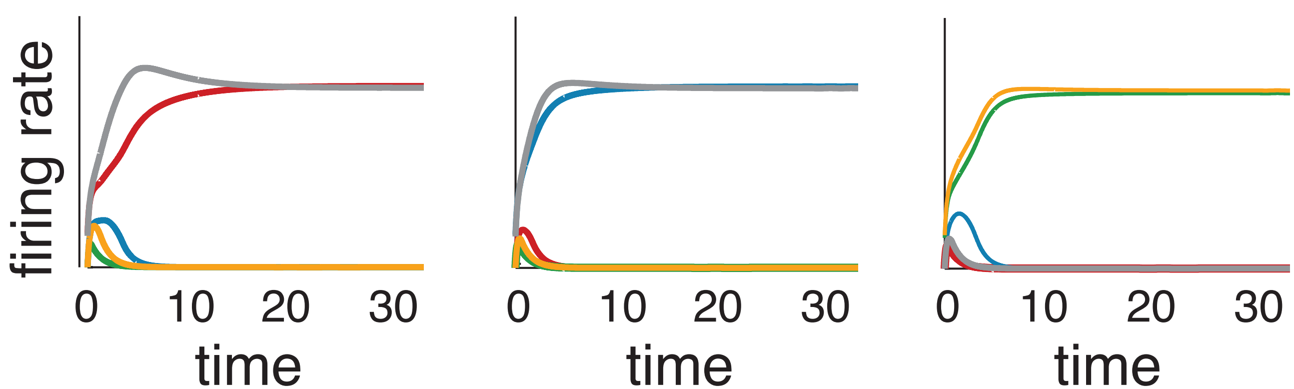
examples of nonlinear network dynamics: chaos



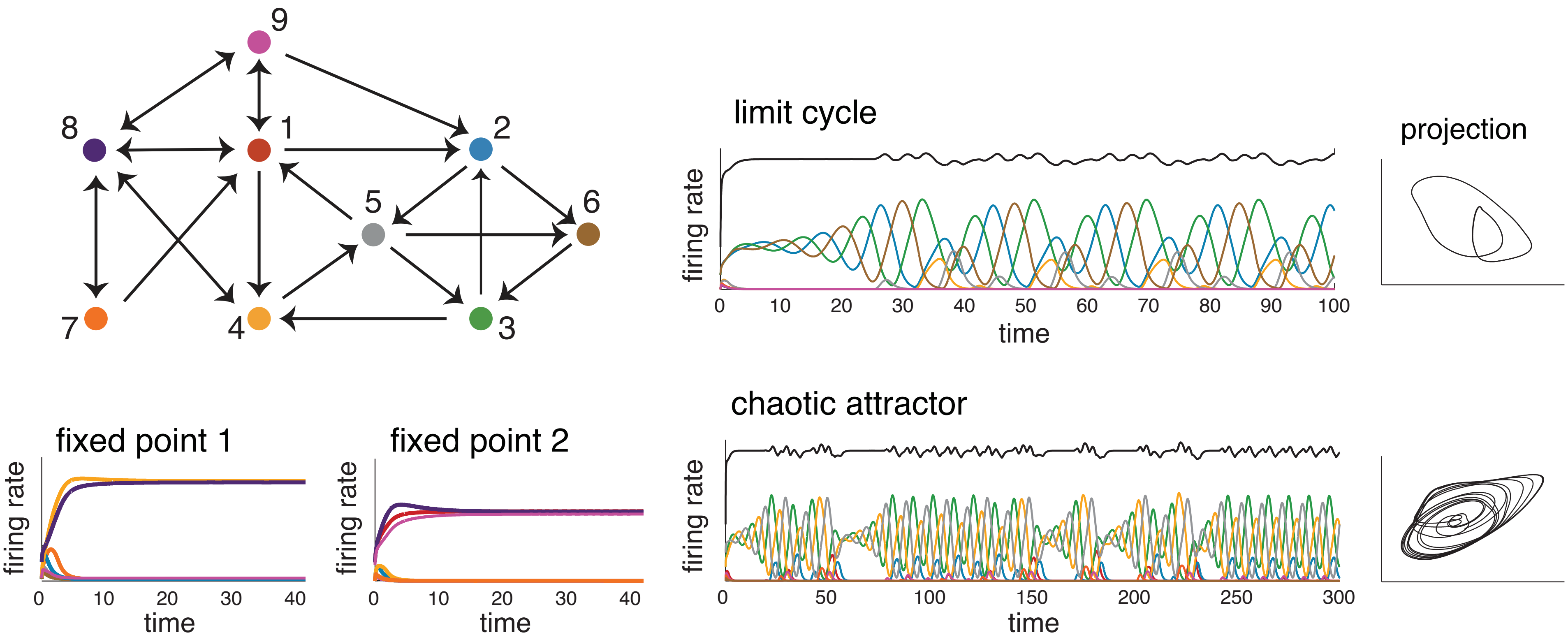
examples of nonlinear network dynamics: multistability



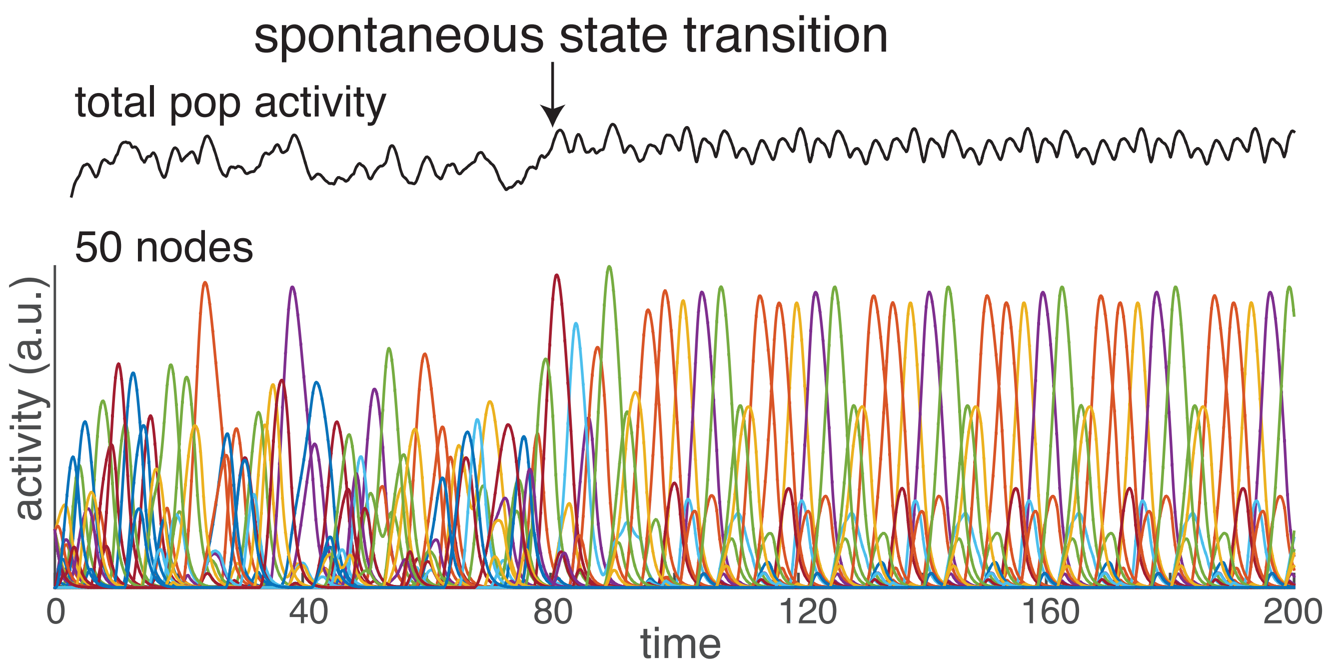
3 fixed points



A single network can display multiple attractors of different types

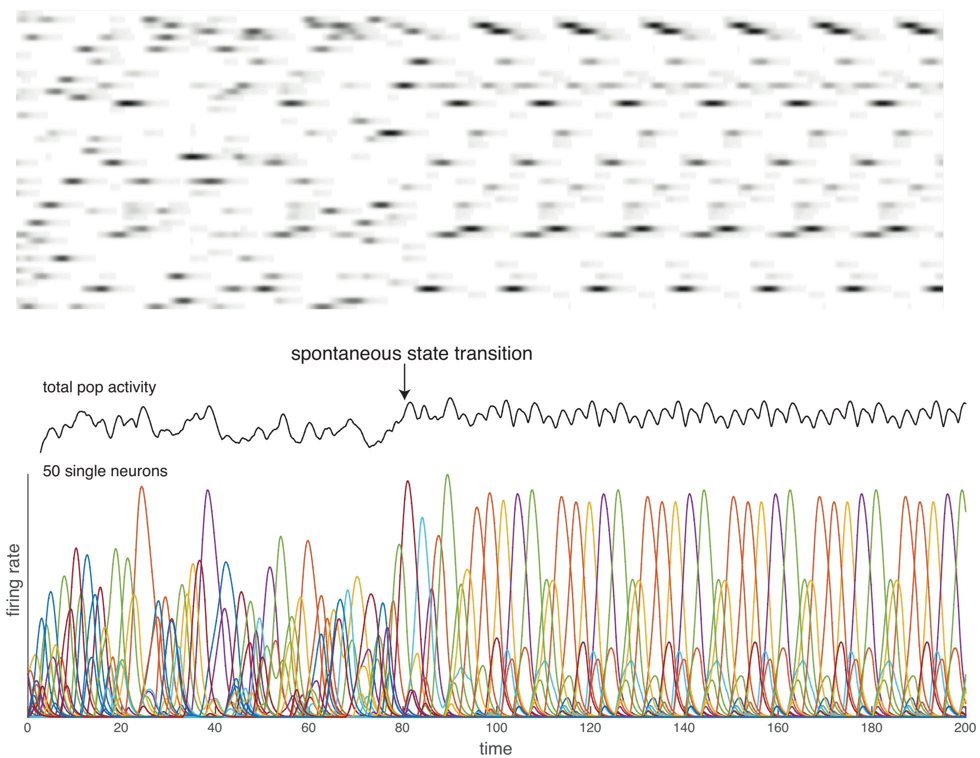


Spontaneous state transitions in large random networks

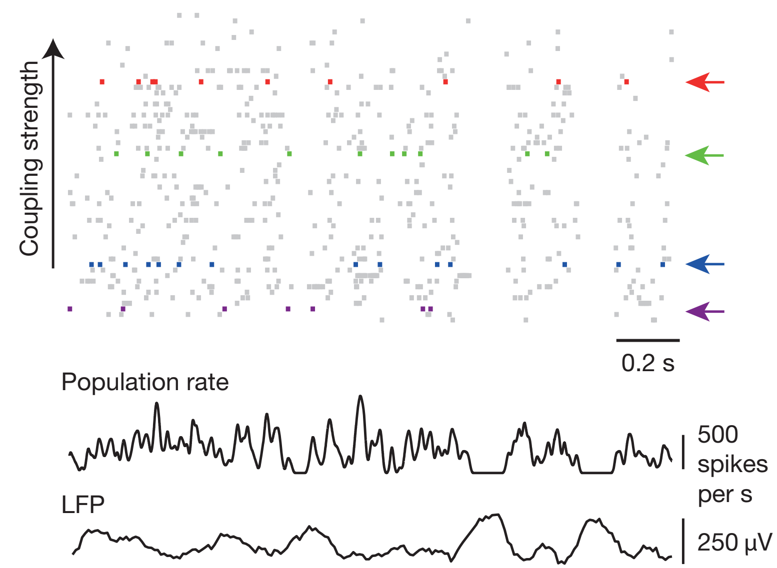


Spontaneous state transitions in large random networks

Model (50 neurons)



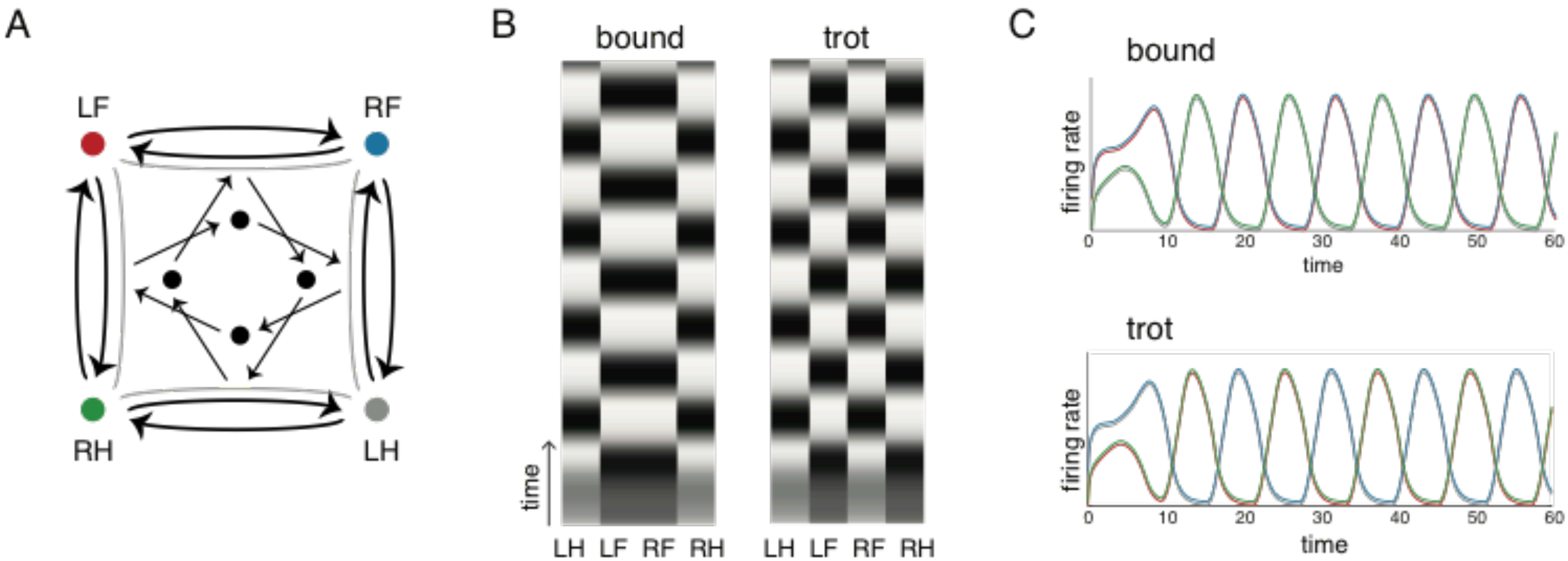
Data (66 neurons)



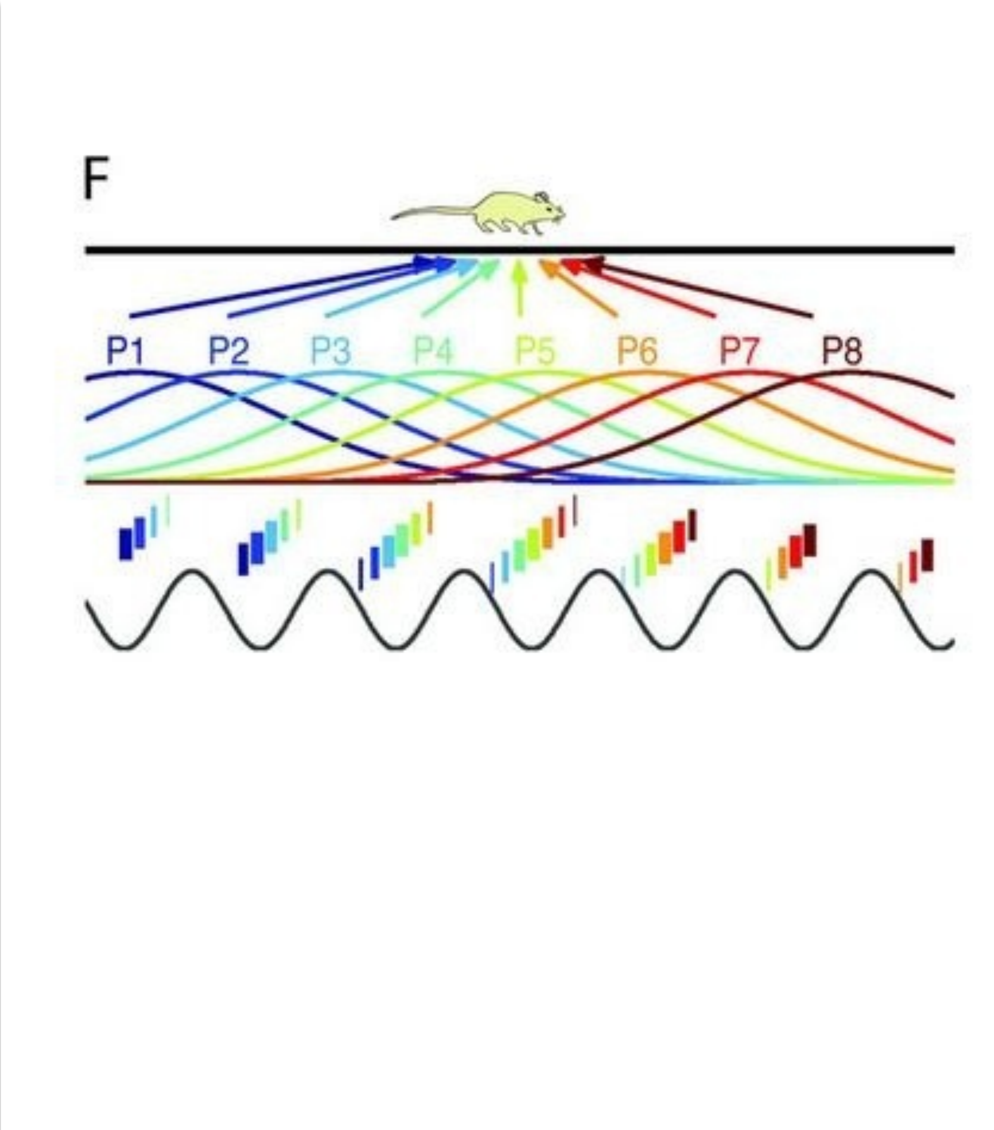
Okun et. al., Nature 2015

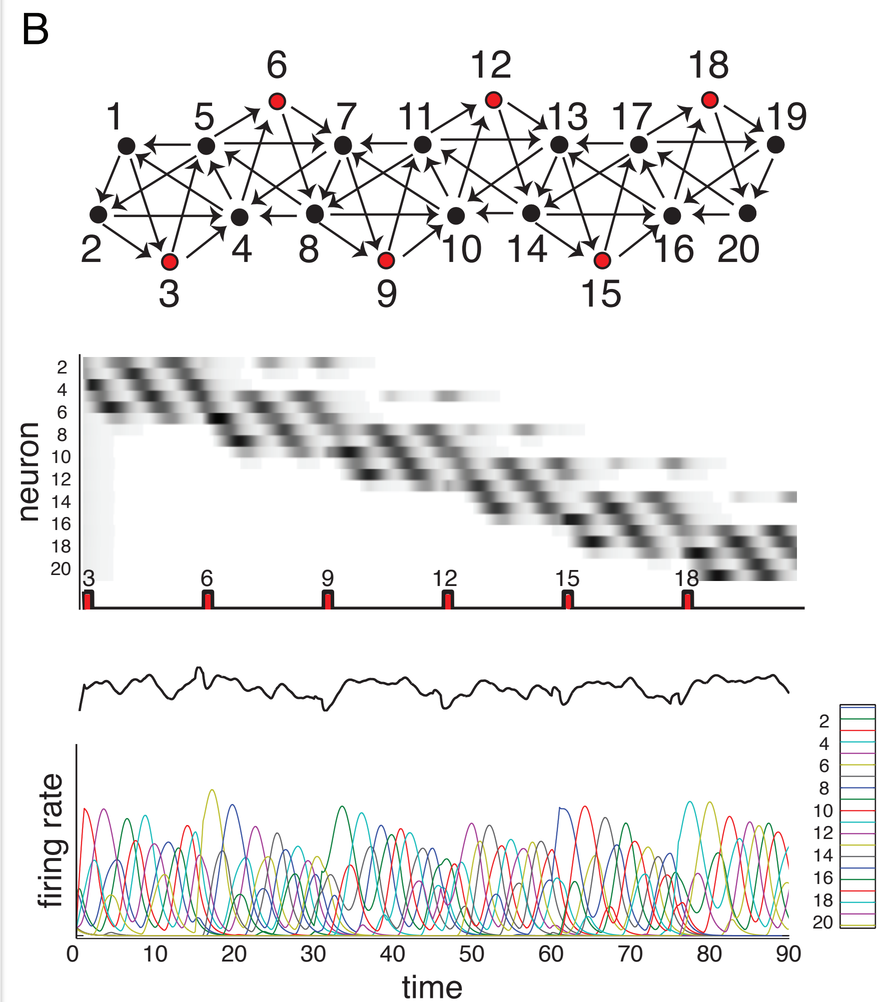
Central Pattern Generator (CPG)

quadruped motion

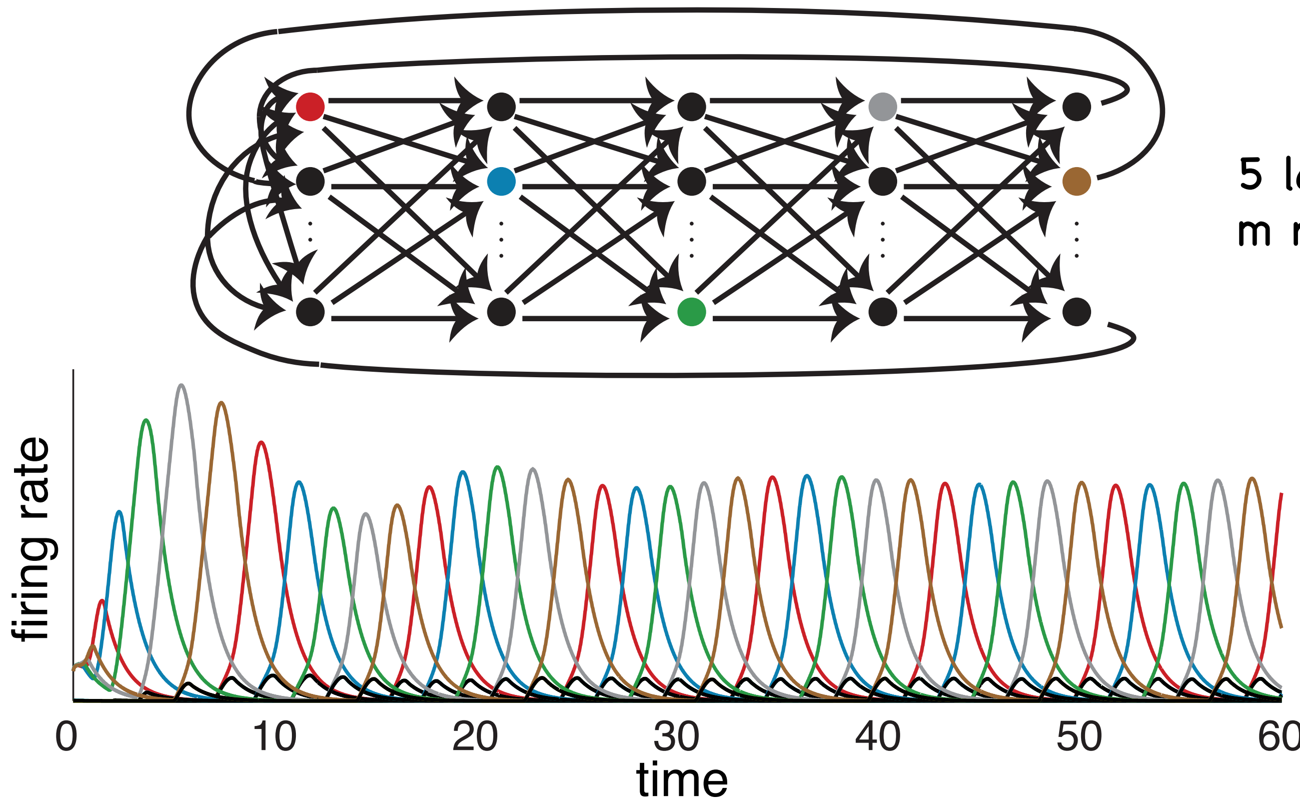


Patching together cyclic modules





phone number network



This network has m^5 limit cycles, like the one above.

Important Facts about CTLNs

- all nodes are identical
- for fixed parameters $\varepsilon, \delta, \theta$, only the graph matters
- many aspects of dynamics are invariant under parameter changes
- we can use this model to study emergent dynamics as shaped by connectivity alone (the graph)
- global properties of connectivity may matter more than local features
- mathematically tractable
- displays a rich variety of nonlinear dynamics

A competitive network theory of species diversity

Stefano Allesina[a,1] **and Jonathan M. Levine**[b]

[a]Department of Ecology and Evolution, Computation Institute, University of Chicago, Chicago, IL 60637; and [b]Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, CA 93106

5638–5642 | PNAS | **April 5, 2011** | vol. 108 | no. 14

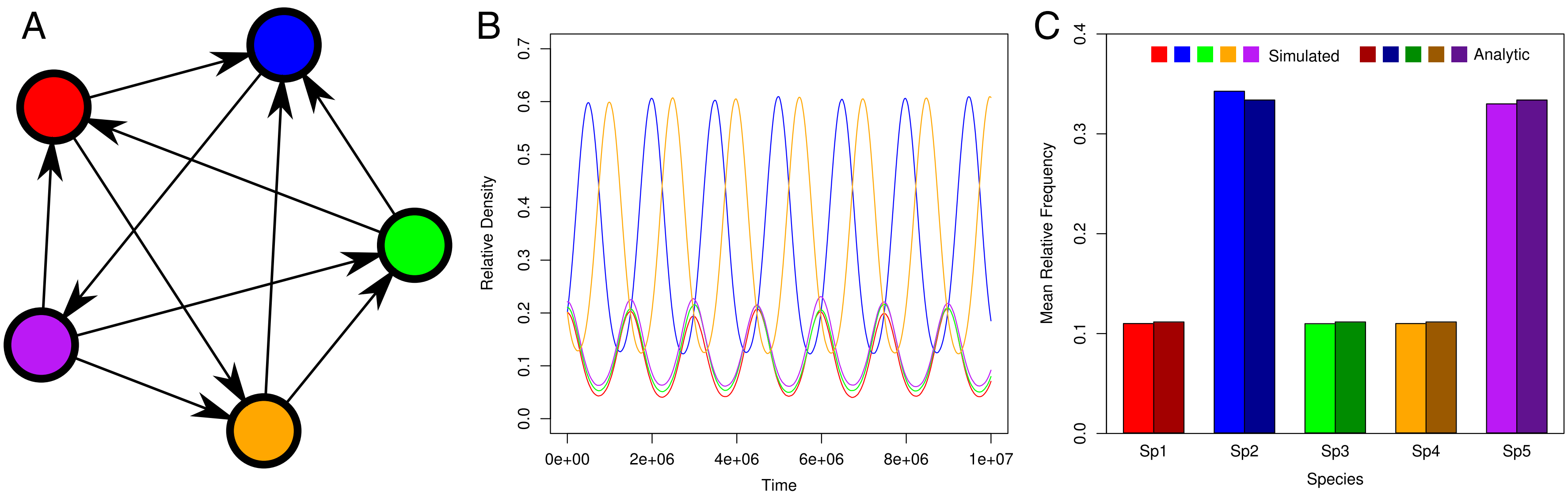


Fig. 1. (*A*) Species' competitive abilities can be represented in a tournament in which we draw an arrow from the inferior to the superior competitor for all species pairs. A tournament is a directed graph composed by n nodes (the species) connected by $n(n-1)/2$ edges (arrows). (*B*) Simulations of the dynamics for the tournament. The simulation begins with 25,000 individuals assigned to species at random (with equal probability per species). At each time step, we pick two individuals at random and allow the superior to replace the individual of the inferior. We repeat these competitions 10^7 times, which generates relative species abundances that oscillate around a characteristic value (*SI Text*). (*C*) The average simulated density of each species from *B* (shown in lighter bars) almost exactly matches the analytic result obtained using linear programming (shown in darker bars).

Discrete species competition model

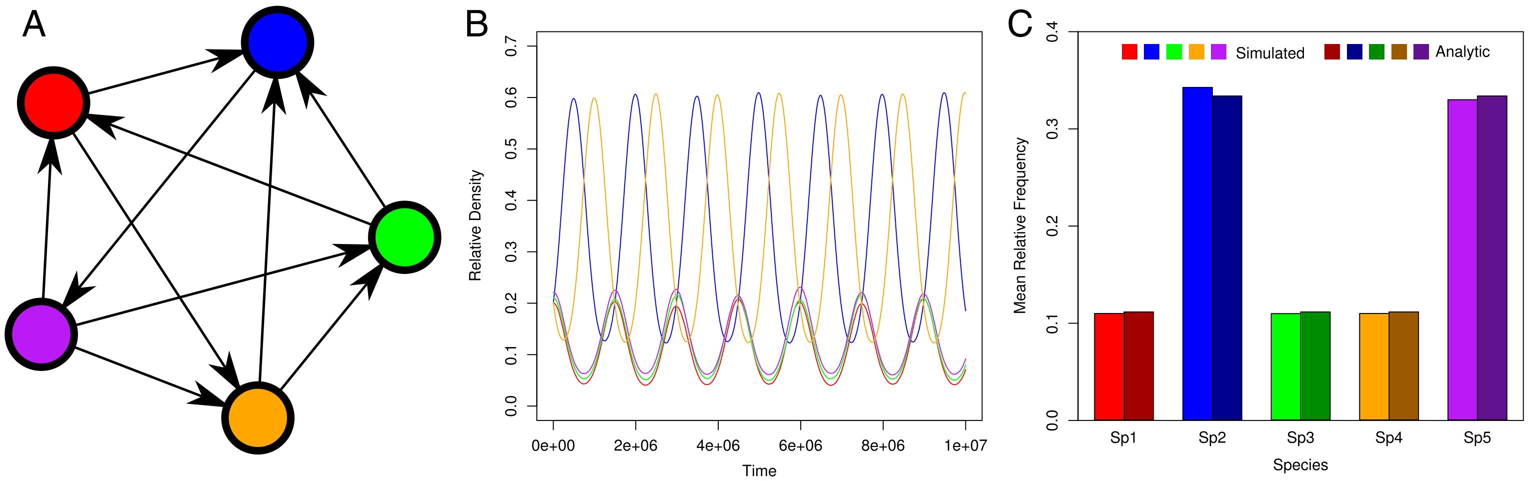
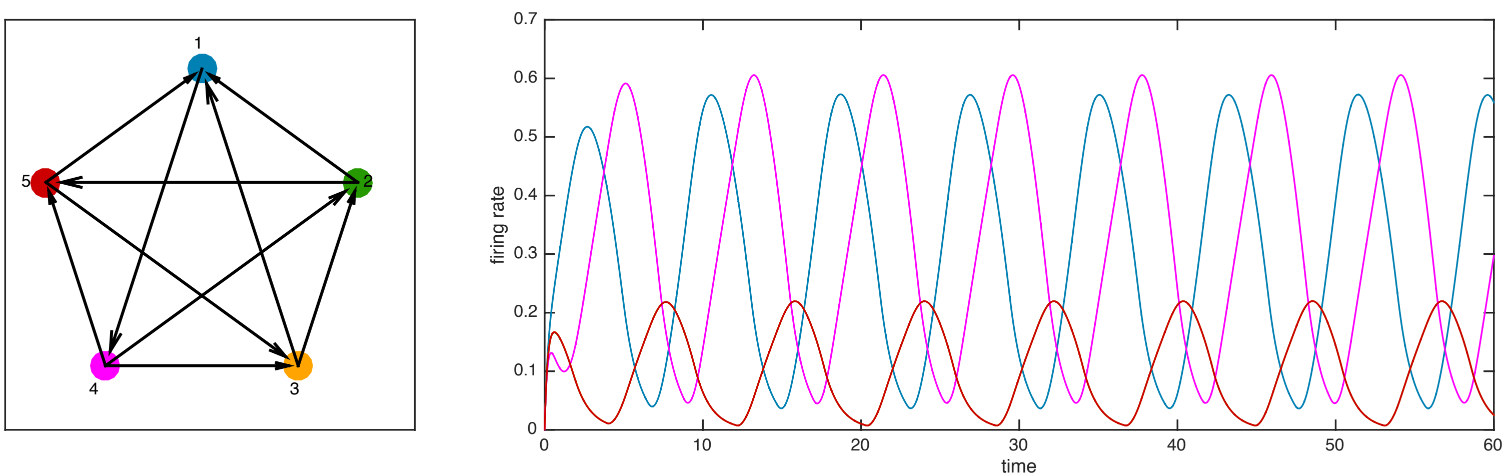


Fig. 1. (*A*) Species' competitive abilities can be represented in a tournament in which we draw an arrow from the inferior to the superior competitor for all species pairs. A tournament is a directed graph composed by n nodes (the species) connected by $n(n-1)/2$ edges (arrows). (*B*) Simulations of the dynamics for the tournament. The simulation begins with 25,000 individuals assigned to species at random (with equal probability per species). At each time step, we pick two individuals at random and allow the superior to replace the individual of the inferior. We repeat these competitions 10^7 times, which generates relative species abundances that oscillate around a characteristic value (*SI Text*). (*C*) The average simulated density of each species from *B* (shown in lighter bars) almost exactly matches the analytic result obtained using linear programming (shown in darker bars).

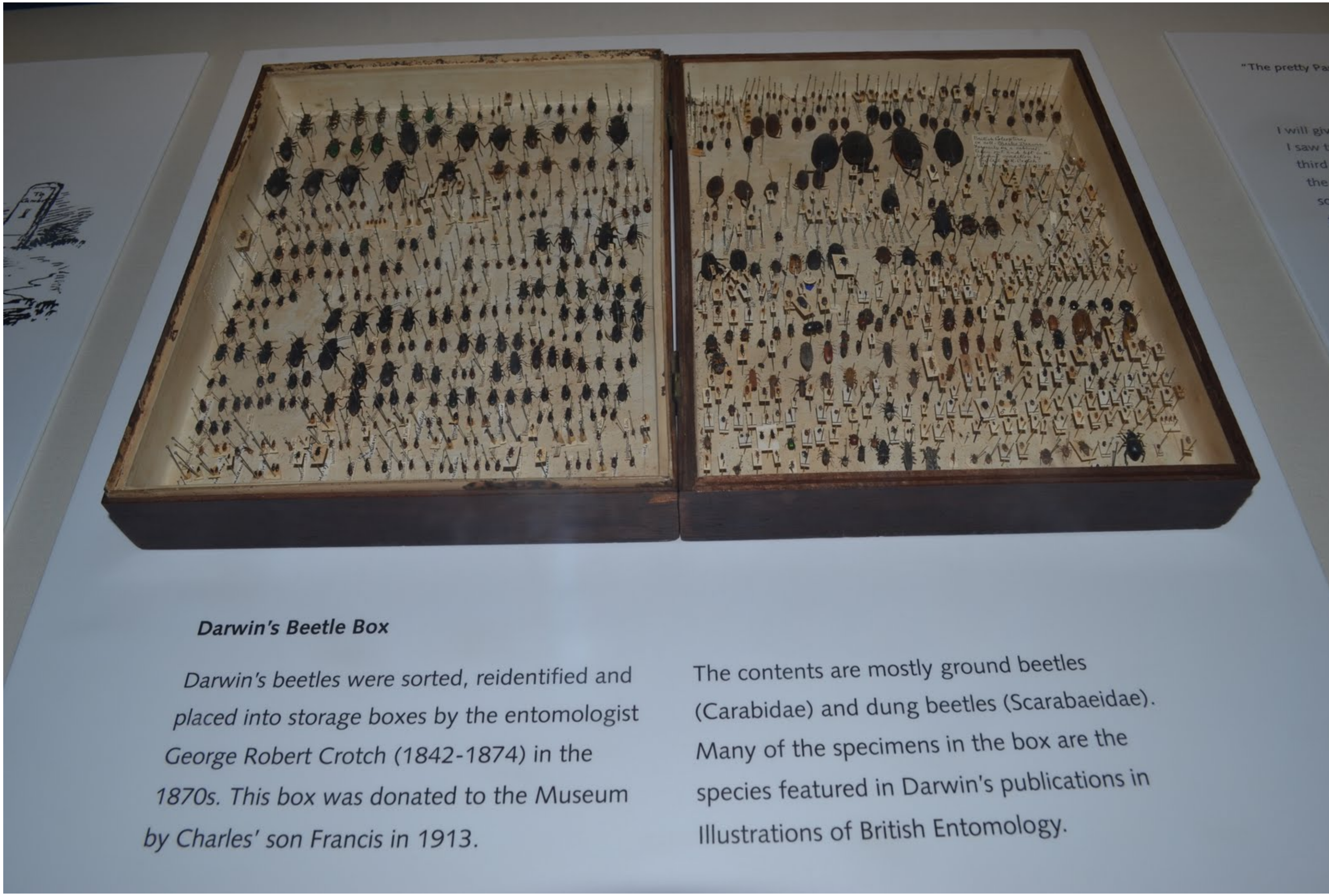
The CTLN model



Plan of the talk

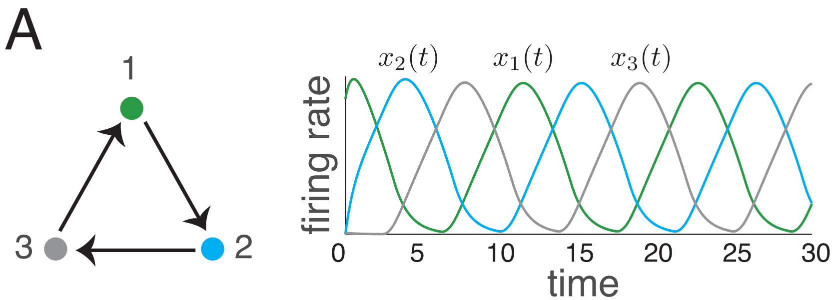
- Attractors in neuroscience
- Network structures/motifs
- Threshold-linear networks, CTLNs
- Early explorations...
- Graphical analysis of fixed points of CTLNs

What would Darwin do?



Early facts about stable fixed points

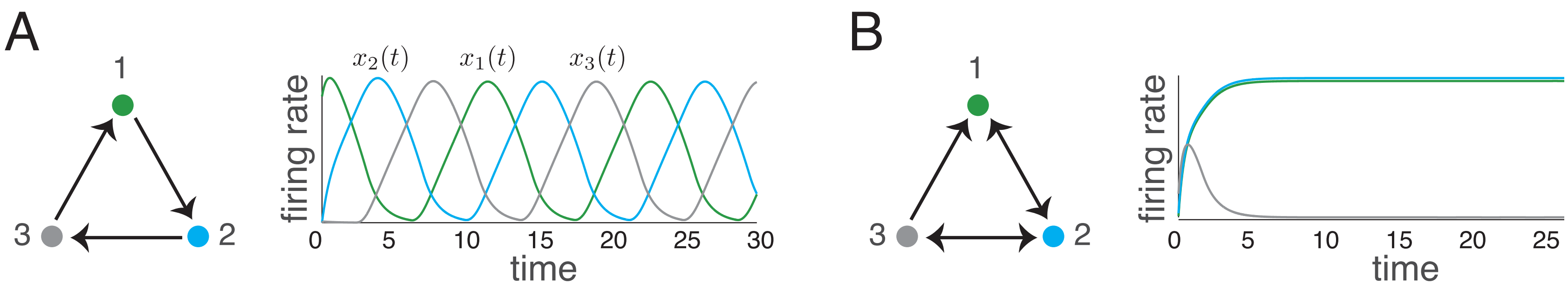
Thm 1. If G is an oriented graph with no sinks, then the network has no stable fixed points (but bounded activity).



Early facts about stable fixed points

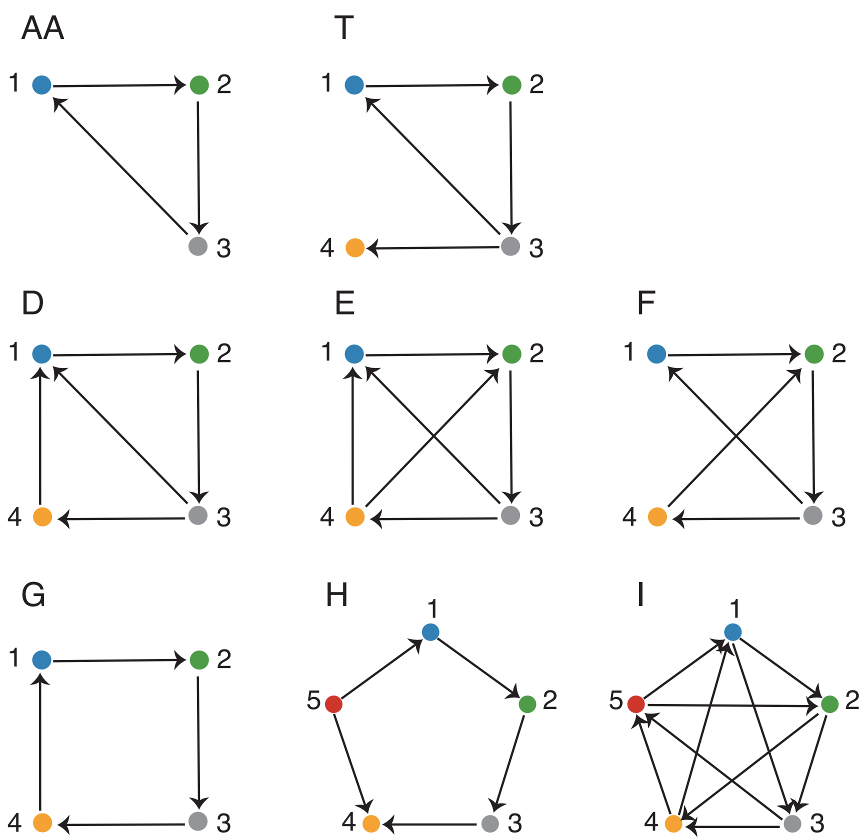
Thm 1. If G is an oriented graph with no sinks, then the network has no stable fixed points (but bounded activity).

Thm 2. For any G, a clique is the support of a stable fixed point if and only if it is a target-free clique.

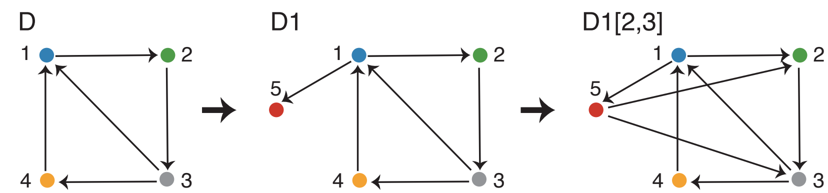


Taxonomy for oriented graphs on 5 neurons

Base graphs



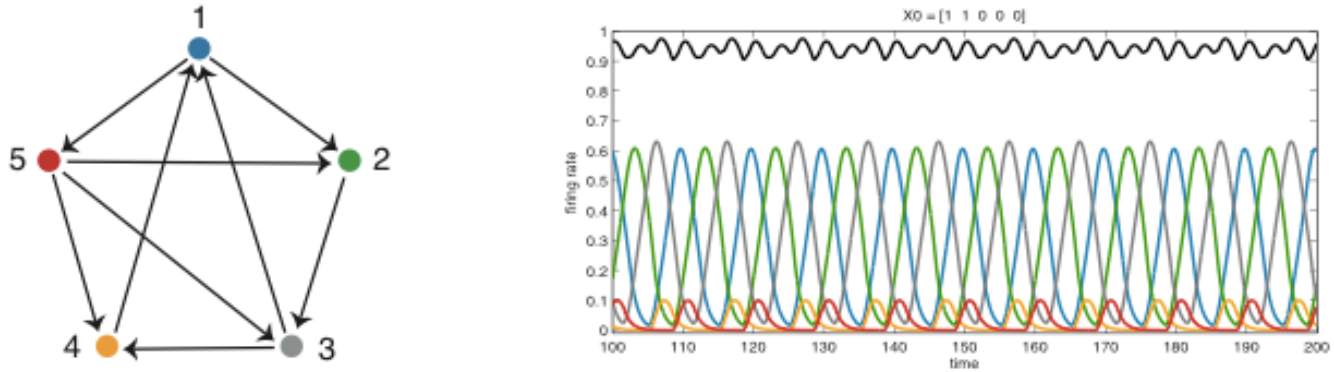
Every oriented graph with no sinks on n=5 can be built up and named using these base graphs:



Neuron numbering chosen to maximally align sequences in observed attractors

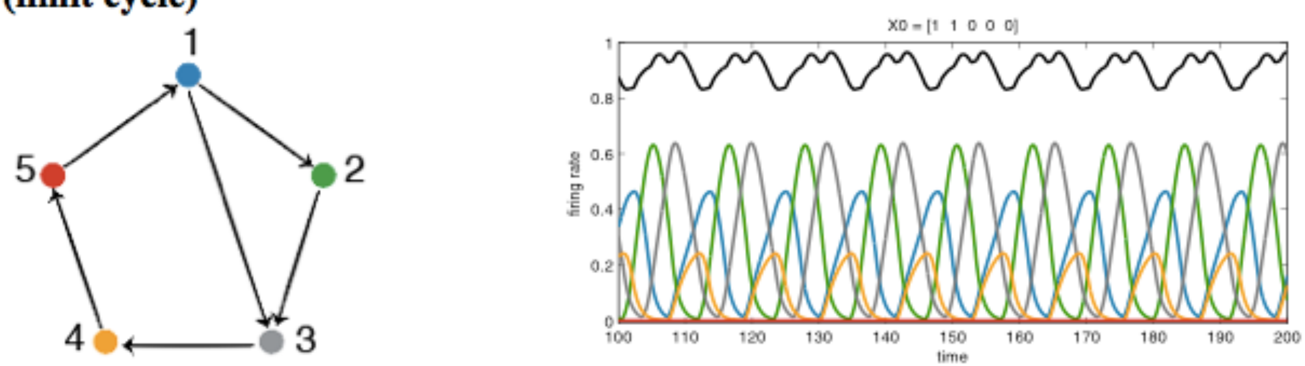
Dictionary of attractor types

AT-4 (limit cycle)



Rep. graph D1[2,3,4], seq 15234. All graphs: D1[2,3,4], D1[2,3] (aka E2[3]), D1[2,4], D1[2] (aka D2[3]), D2[1,3,4], D2[1,3] (aka E1[2]), D2[3,4], D3[4,*], E1[2,3,4], E1[2,4], E1[3,4], E1[3] (aka F2[1,3]), E1[4], E2[1,3,4], E2[3,4], E2[3] (aka D1[2,3]), E2[1,3] (aka E1[2,3]), E3[1,2,4], E3[1,4], E3[2,4], E3[4].

AT-11 (limit cycle)



Rep. graph T4[1], seq 1234. All graphs: T4[1,2,3], T4[1,2], T4[1,3], T4[2,3]_seq1 (aka D1[4]_seq2), T4[1], T4[2]_seq1 (aka G1[4]_seq2), T4[3]_seq1, T4[3]_seq2.

Dictionary of attractor types

Using the taxonomy, we could identify 19 attractor types and classify graphs based on which attractor types they exhibited –

this classification largely aligned with the taxonomy!

Attractor types include:

Limit cycles with simple cycles
Limit cycles with synchronous firing
Period-doubled limit cycles
Quasperiodic attractors
Chaotic attractors

Some things we learned…

1. 3-cycles supporting (unstable) fixed points yield attractors, while others do not.

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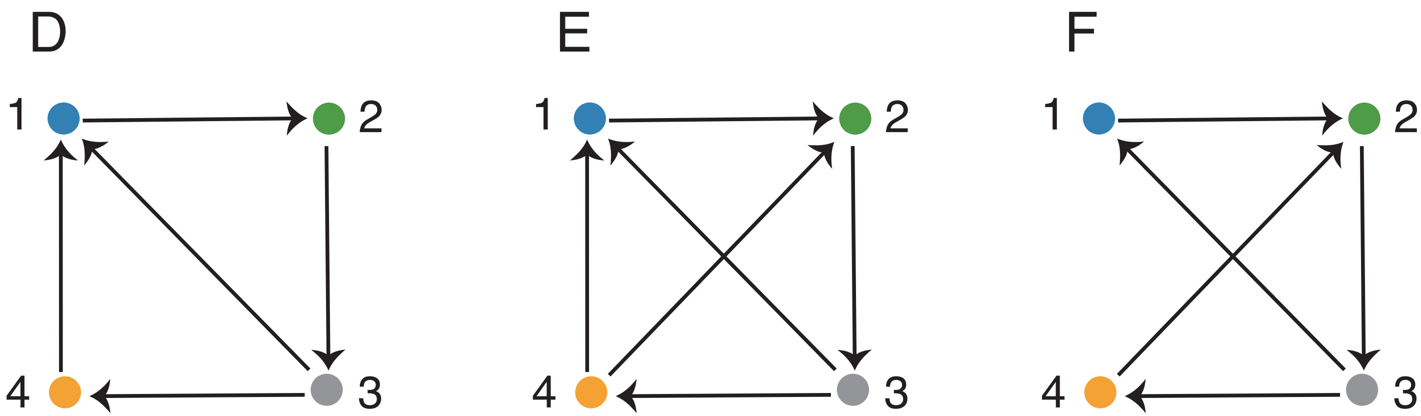
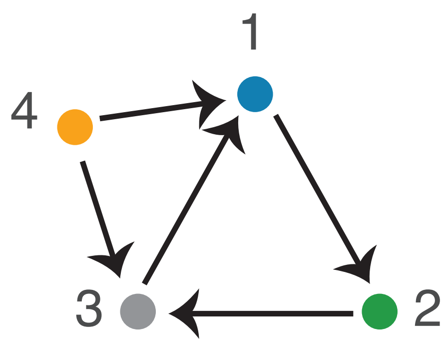


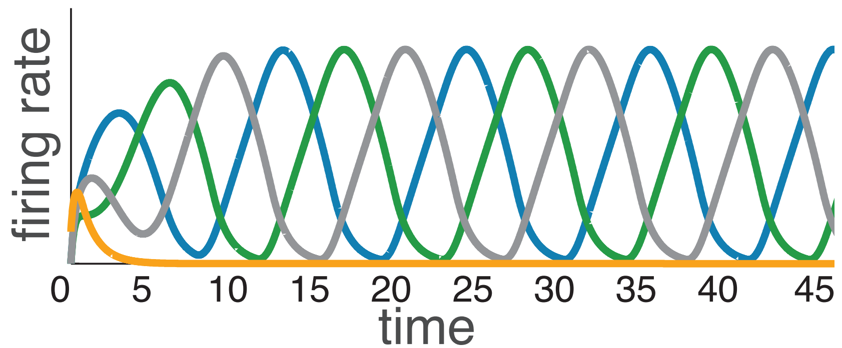
234 does not have a fixed point – nor a corresponding limit cycle!

Some things we learned…

1. 3-cycles supporting (unstable) fixed points yield attractors, while others do not.

2. Sources die – i.e., do not participate in any attractors.





Some things we learned…

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2. Sources die – i.e., do not participate in any attractors.

3. When two networks share certain common subgraphs, they tend to have at least one attractor in common.

   For $n \leq 5$ only 19 attractor types! (~200 observed attractors)

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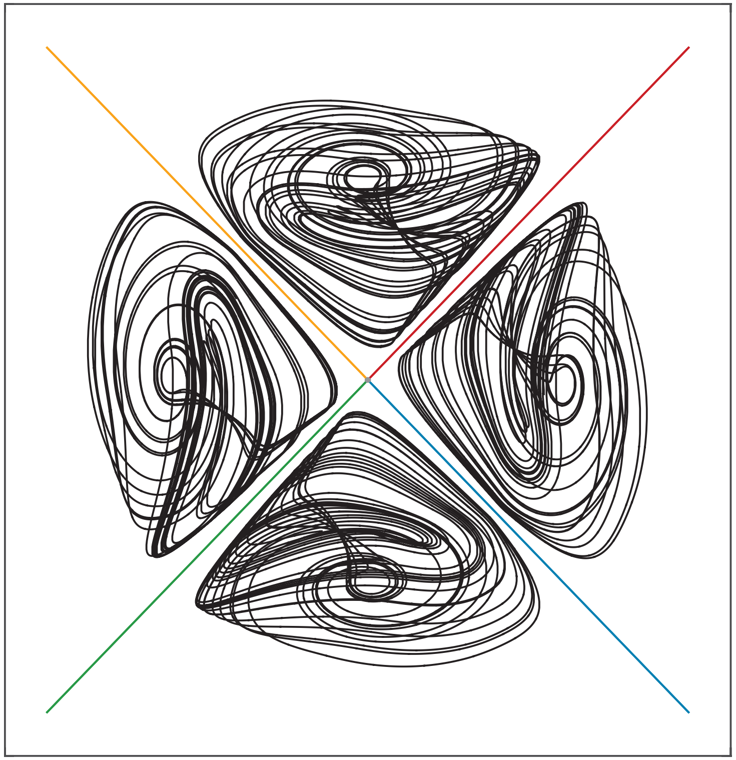
   For $n \leq 5$ only 19 attractor types! (~200 observed attractors)

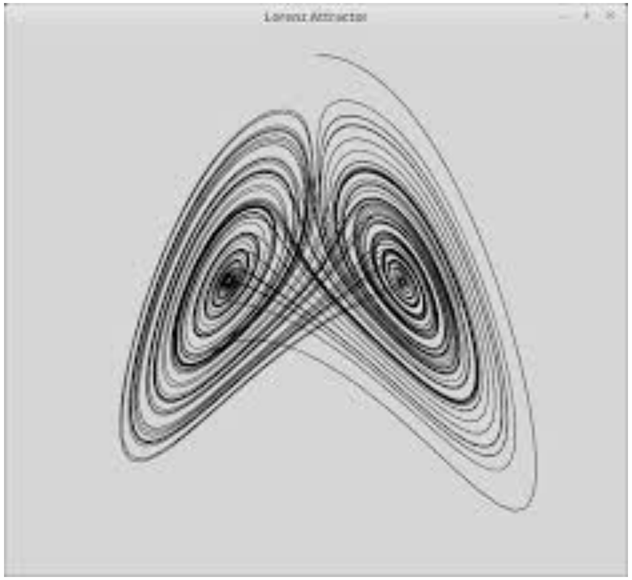
4. Unstable fixed points are closely related to – and predictive of – limit cycles and chaotic attractors

unstable fixed points in chaotic attractors

baby chaos: 4 attractors

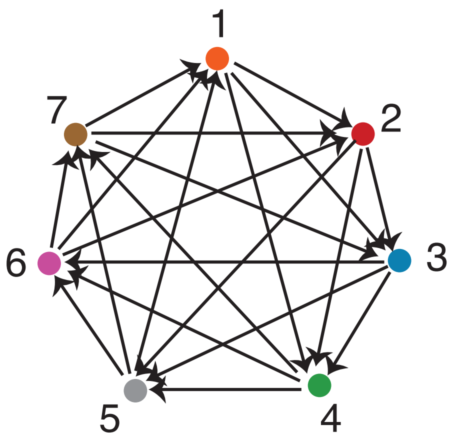


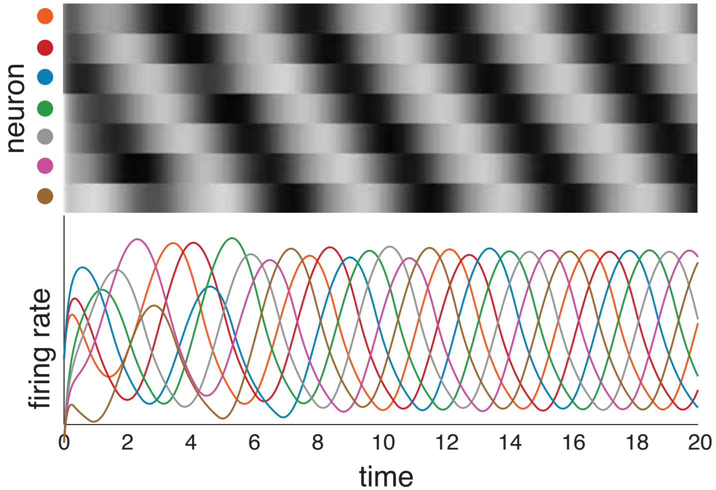
Lorenz attractor



A word of caution

1 (unstable) fixed point





Sequence 1234567

A word of caution

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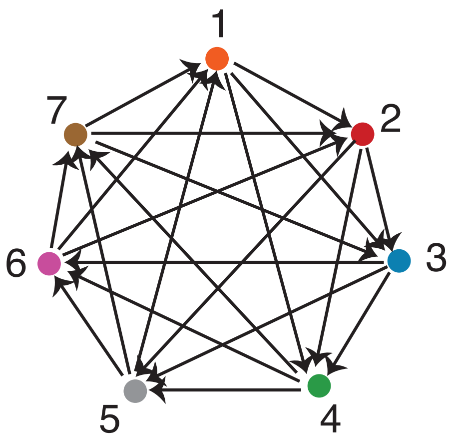
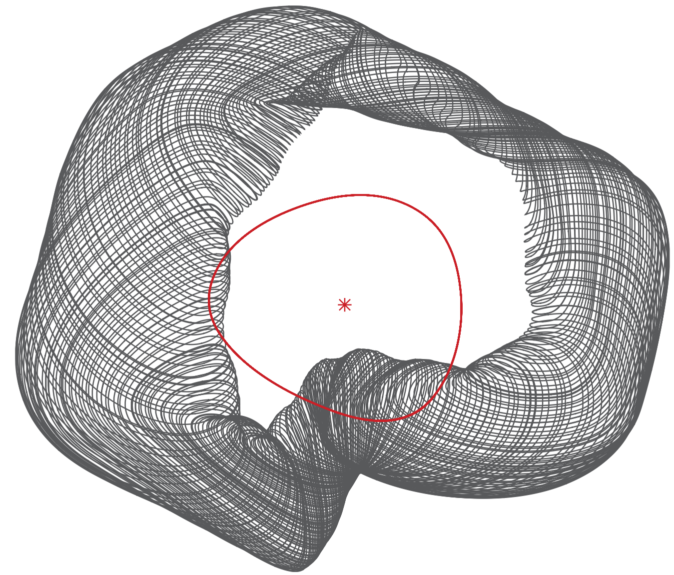
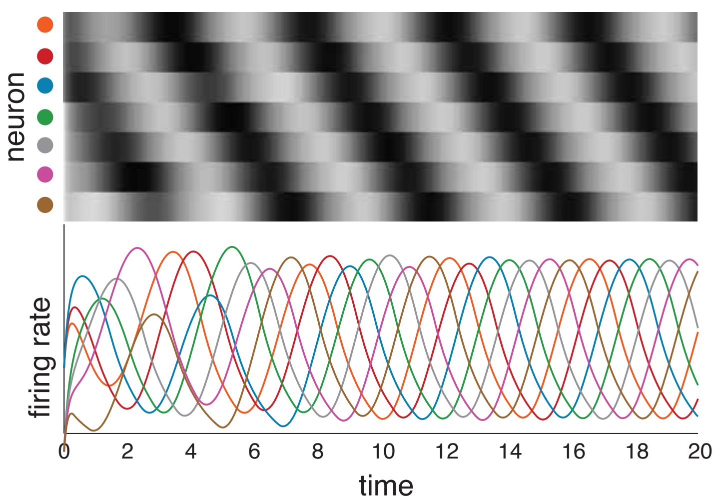
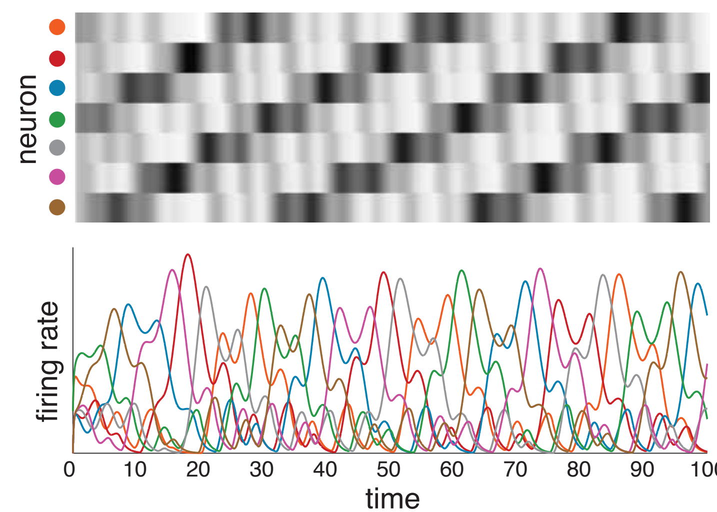


limit cycle + quasiperiodic attractor!





Sequence 1234567



Sequence 1473625

Plan of the talk

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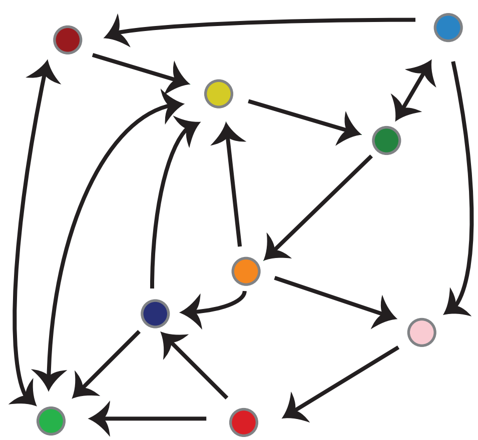
Graphical analysis of fixed points of CTLNs

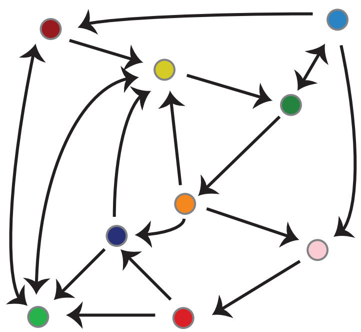


GOAL: Analyze the graph to predict the stable and unstable fixed points

(This gives insight into the dynamics.)

$$\mathrm{FP}(G) = \{\sigma \subseteq [n] \mid \sigma \text{ is a fixed point support } \}$$

How do we find the fixed point supports?



$$\frac{dx_i}{dt} = -x_i + \left[\sum_{j=1}^{n} W_{ij}x_j + \theta\right]_+$$

for $i \in \sigma, \sigma \subseteq [n]$

$$s_i^\sigma = \det((I - W_{\sigma\cup\{i\}})_i; 1)$$

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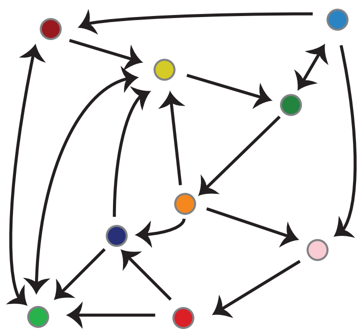

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for $i \in \sigma, \sigma \subseteq [n]$

$$s_i^\sigma = \det((I - W_{\sigma \cup \{i\}})_i; 1)$$

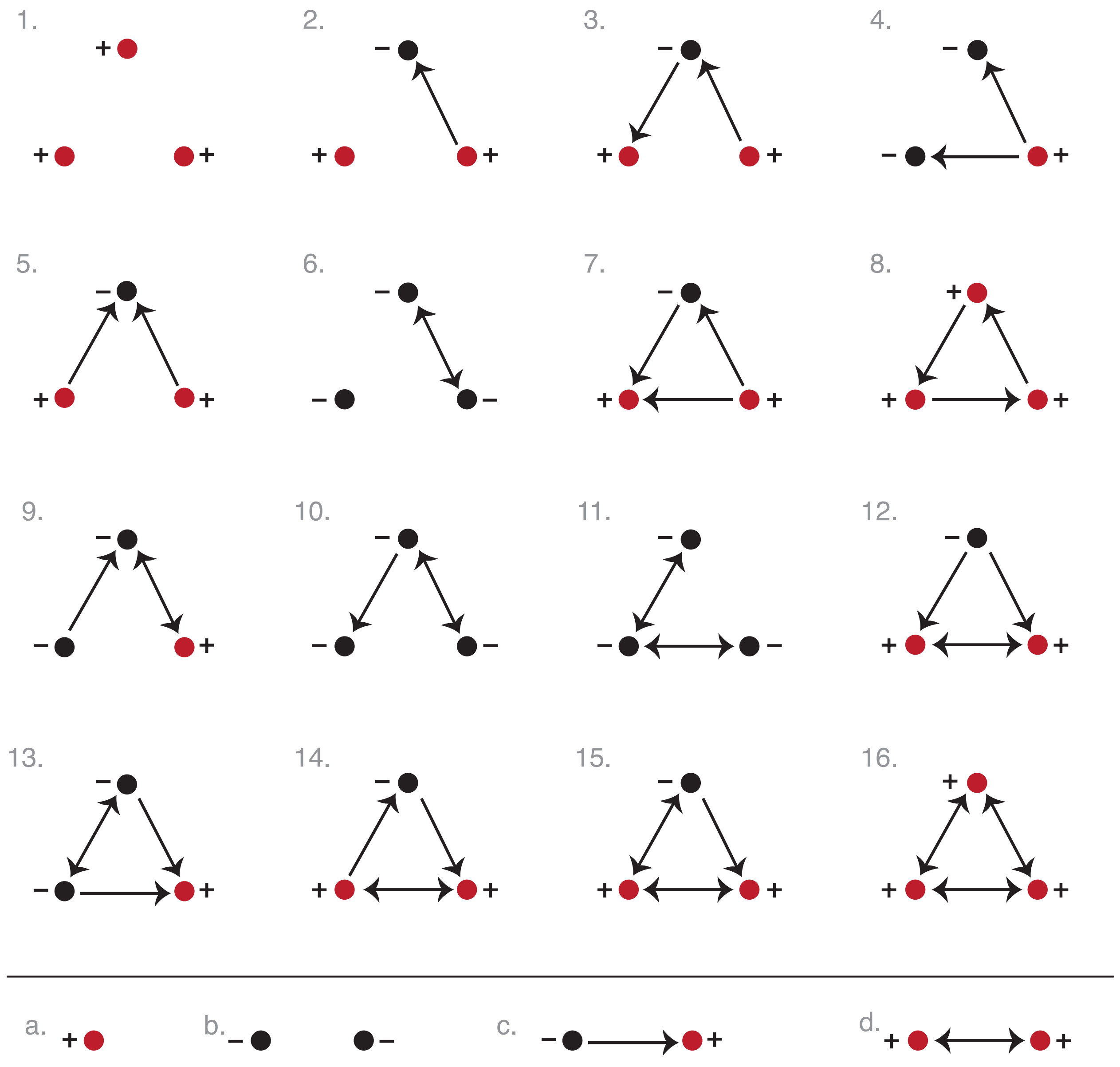
Lemma (fixed point supports)

$$\sigma \in \mathrm{FP}(G) \Leftrightarrow \operatorname{sgn} s_i^\sigma = \operatorname{sgn} s_j^\sigma = -\operatorname{sgn} s_k^\sigma$$

for any $i, j \in \sigma, k \notin \sigma$

Fixed point is stable iff $-I + W_\sigma$ is a stable matrix.

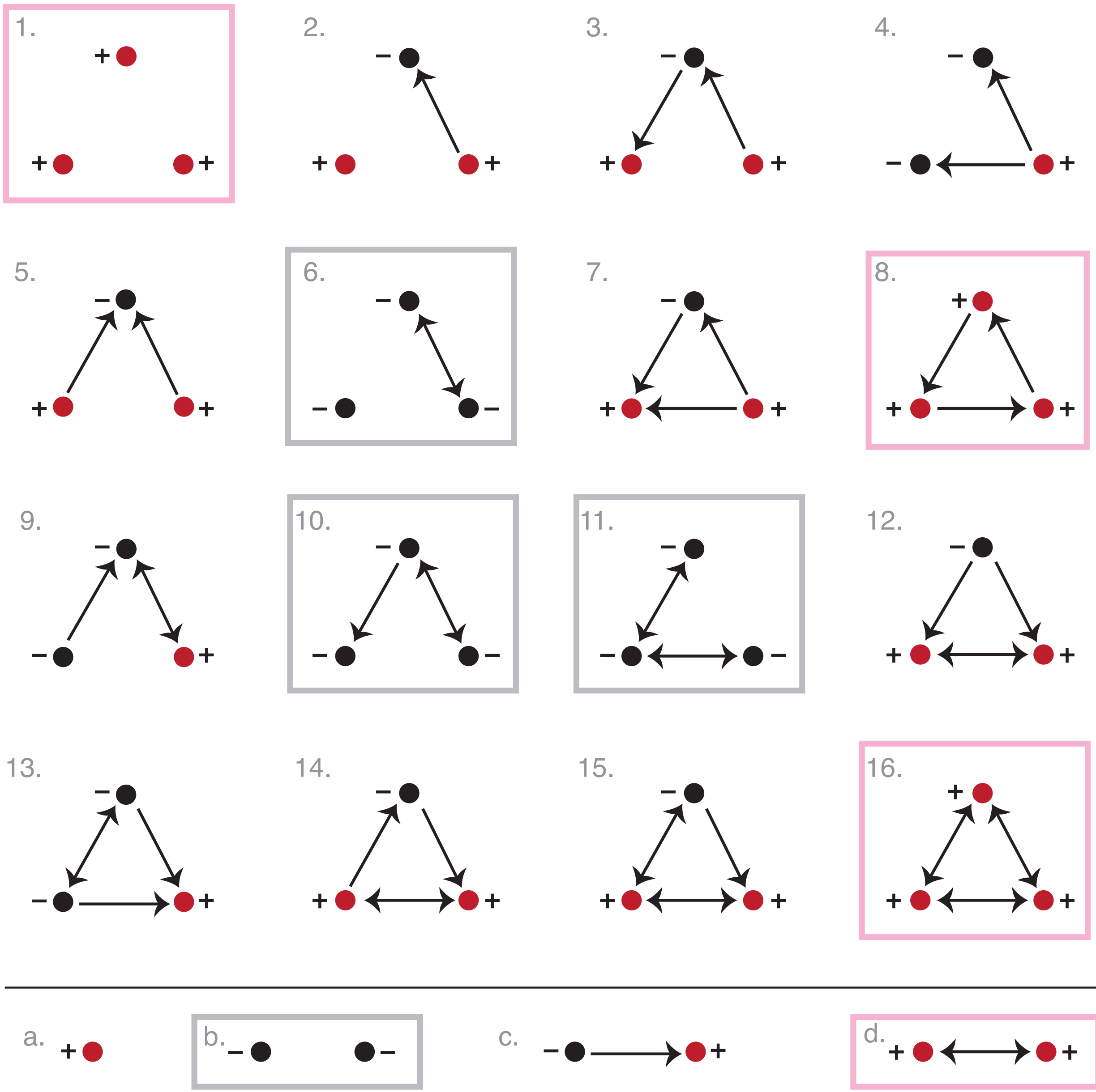
$$\operatorname{sgn} s_i^\sigma = +/-$$



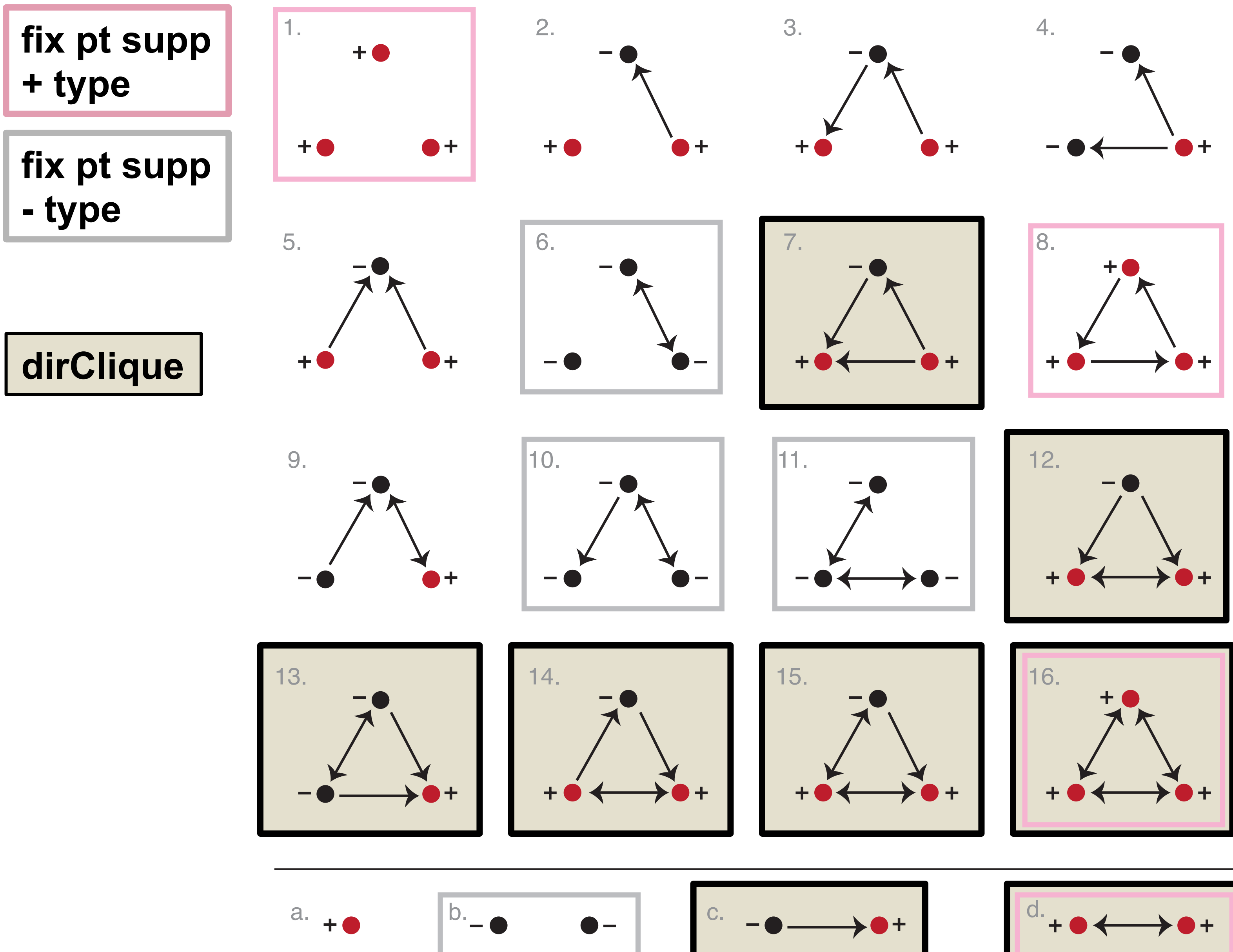
$$\operatorname{sgn} s_i^{\sigma} = +/-$$

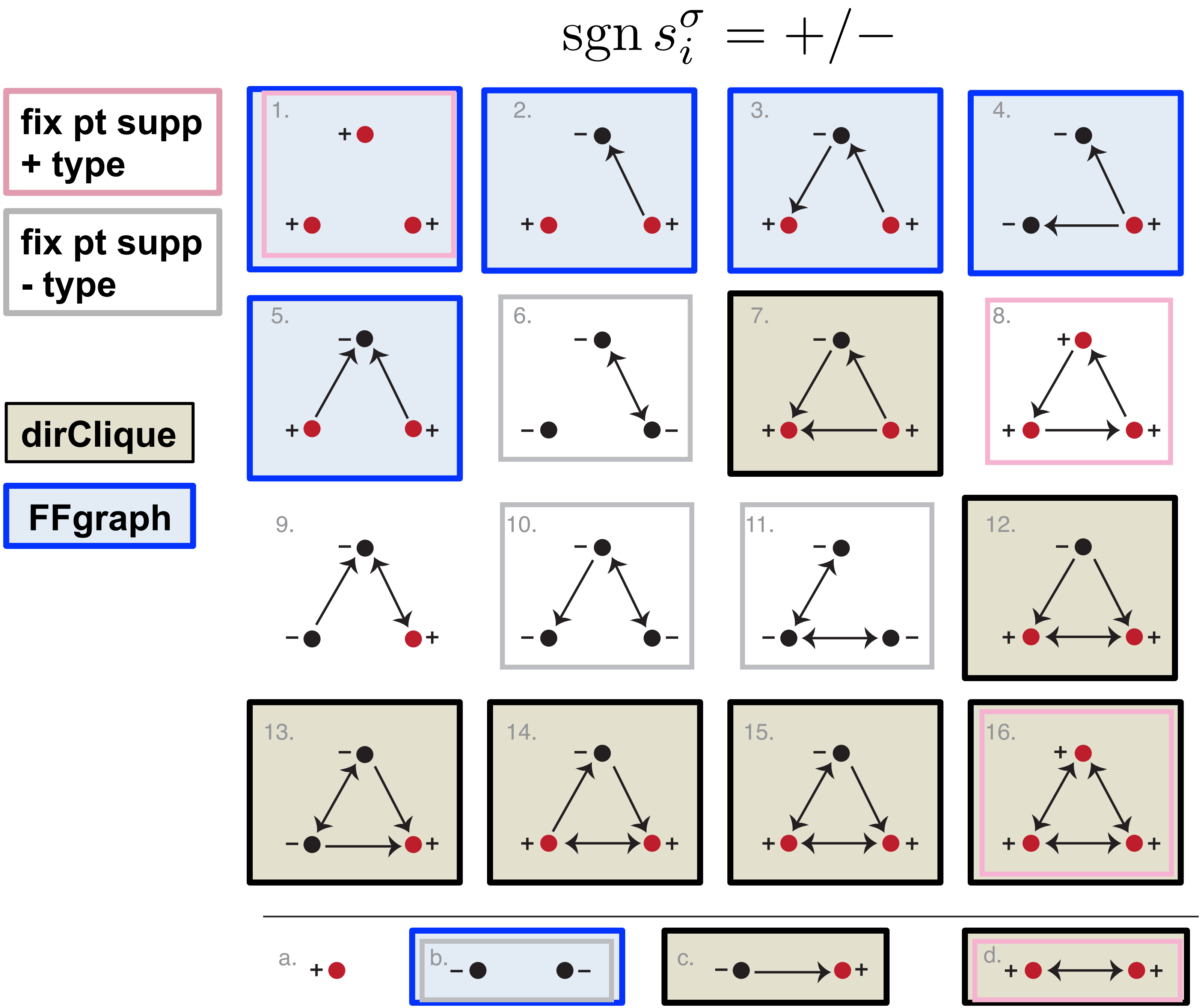
fix pt supp + type

fix pt supp - type

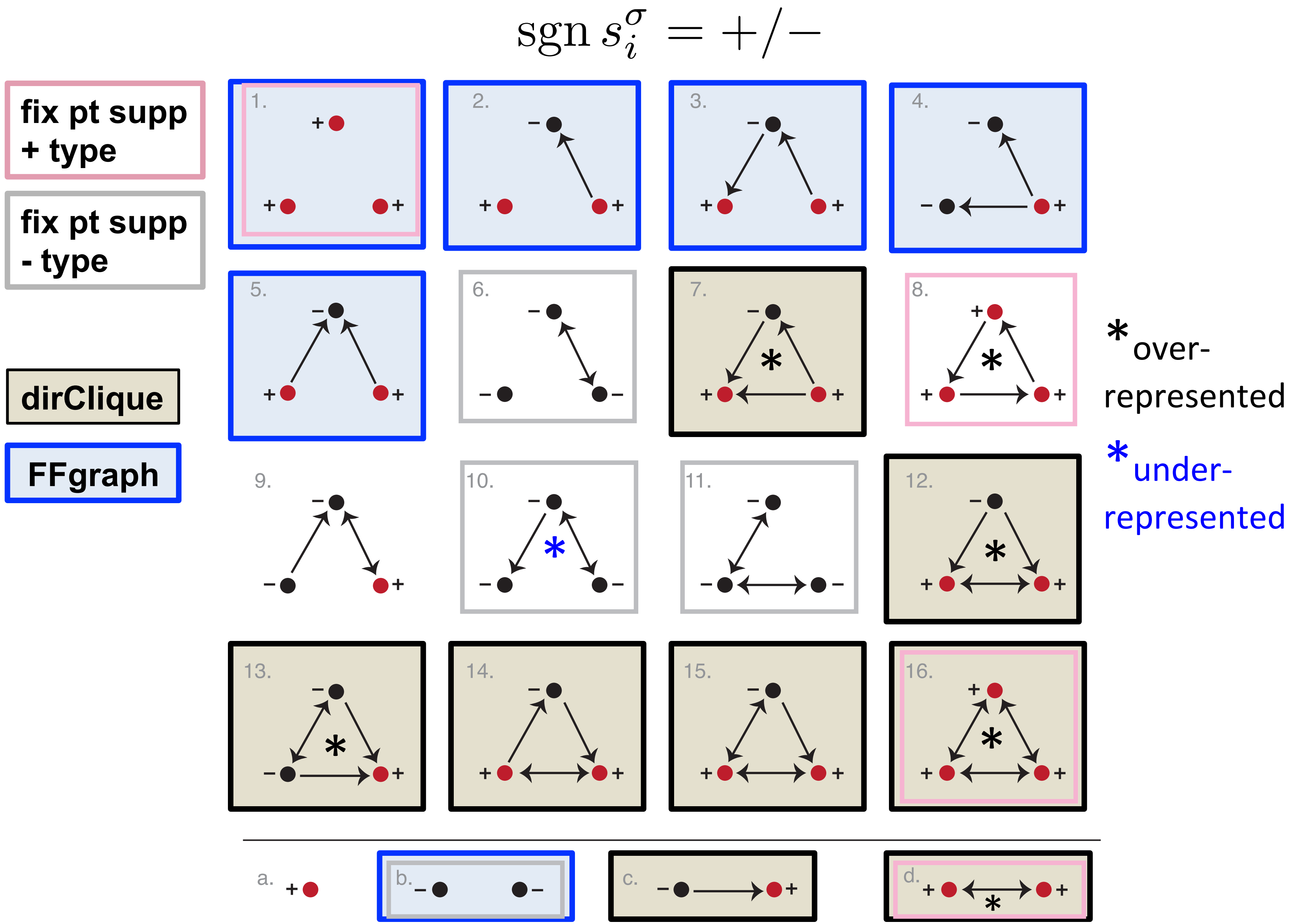


$$\text{sgn}\, s_i^{\sigma} = +/-$$





$\mathrm{sgn}\, s_i^\sigma = +/-$
fix pt supp + type
fix pt supp - type
dirClique
FFgraph
1.
2.
3.
4.
5.
6.
7.
8.
9.
10.
11.
12.
13.
14.
15.
16.
a.
b.
c.
d.



$\mathrm{sgn}\, s_i^\sigma = +/-$
fix pt supp + type
fix pt supp - type
dirClique
FFgraph
* over-represented
* under-represented
1.
2.
3.
4.
5.
6.
7.
8.
9.
10.
11.
12.
13.
14.
15.
16.
a.
b.
c.
d.

A general principle: domination

simplest version: $j, k \in \sigma$

k <u>dominates</u> j with respect to σ if

1. $j \to k, k \not\to j$

2. $i \to j \Rightarrow i \to k$ for each $i \in \sigma \setminus \{j, k\}$

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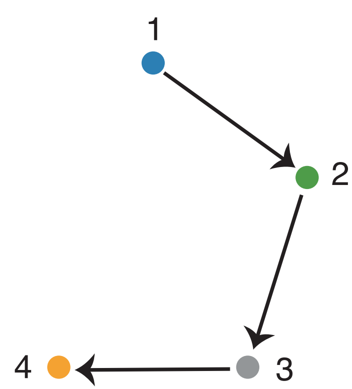
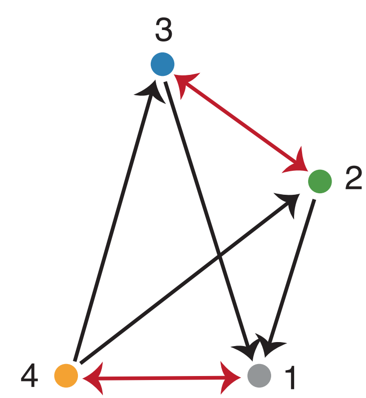
$$\sigma = \{1, 2, 3, 4\}$$



2 dominates 1



1 dominates 2 and 3

A general principle: domination

<u>Lemma</u>: $j, k \in \sigma$

If k dominates j with respect to σ then $\sigma \notin \mathrm{FP}(G|_\sigma)$

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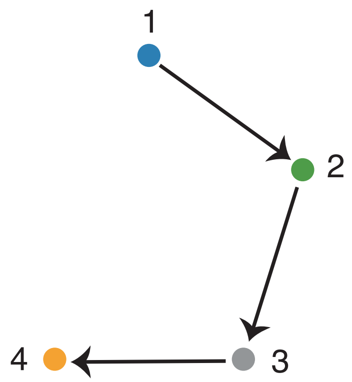
Some consequences:

1. Fixed point supports cannot have sources
   – rules out paths



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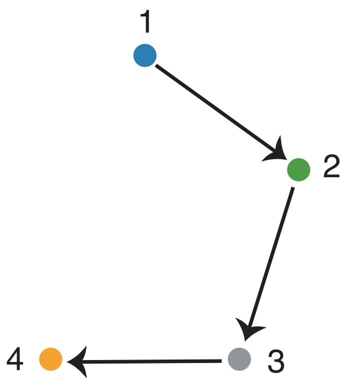

Some consequences:

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2. FF graphs cannot be fixed point supports
   (unless a union of isolated nodes)

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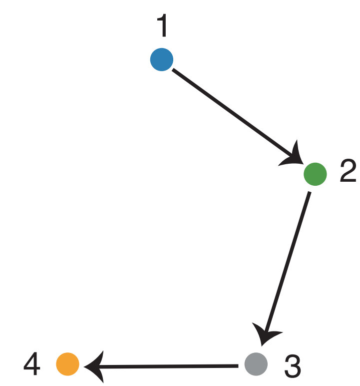

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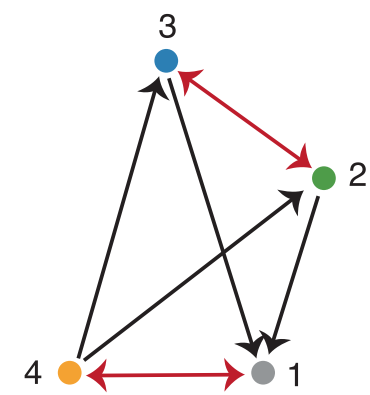
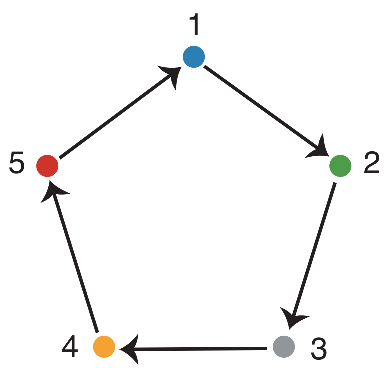


3. Directed cliques cannot be fixed points supports
   (unless it's a full bidirectional clique)

Recurrent vs. feedforward architecture

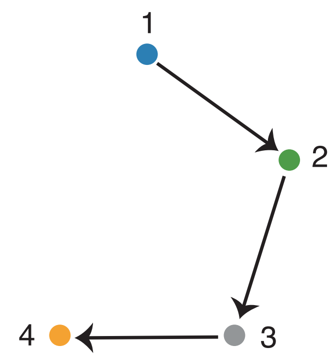
Recurrent motifs (attractors)

cycle

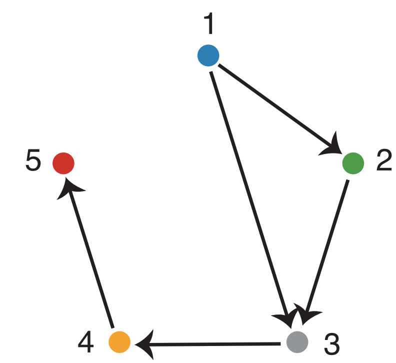


Feedforward motifs (FF flow of information)

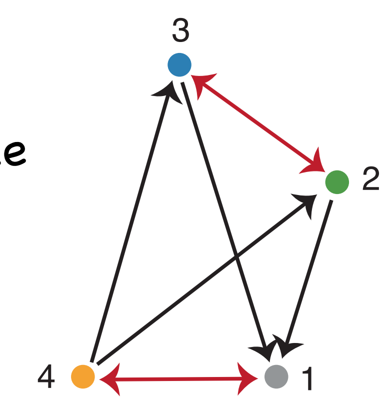
path



FF graph

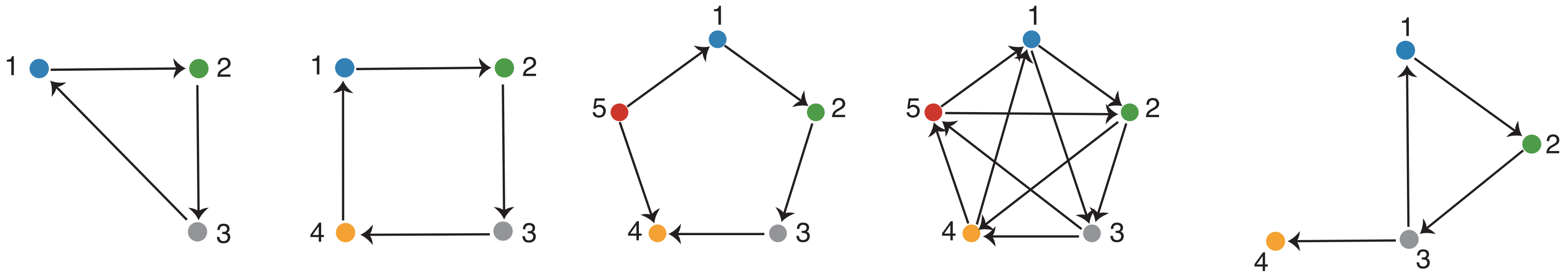


directed clique goes here?



More facts about (unstable) fixed points

- If G is has uniform in-degree, it supports a fixed point



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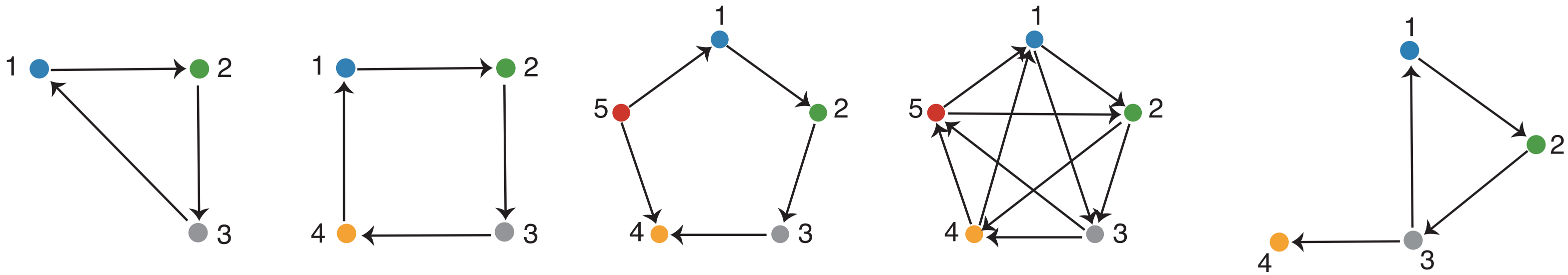

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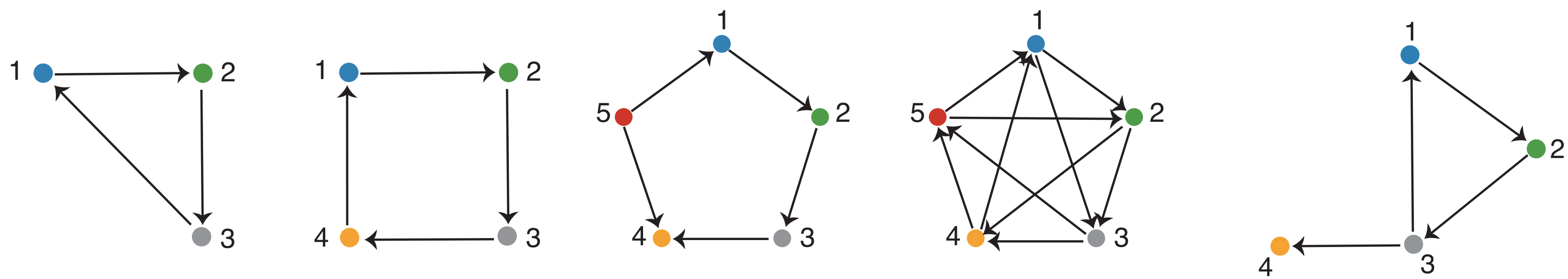


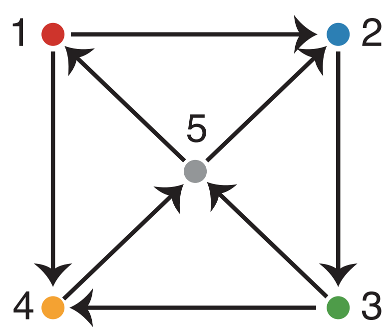
- If a subgraph is a fixed point support, this fixed point may or may not survive to the full graph!

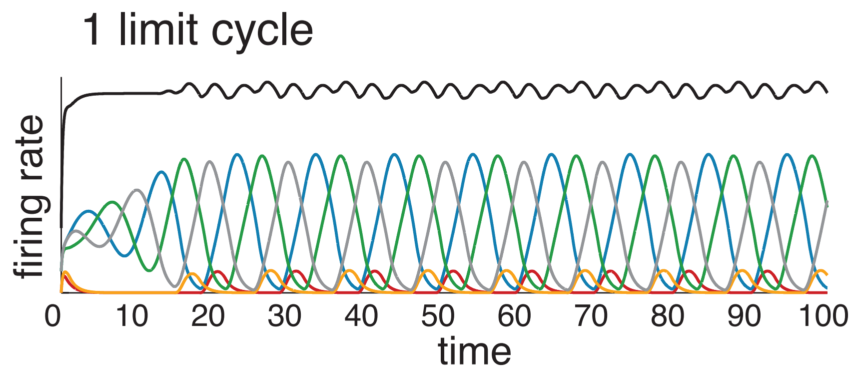
<u>Thm 3</u>. G has uniform in-degree d.

Fixed points survives $\Longleftrightarrow$ no node outside G receives d+1 (or more) edges from G

Which 3-cycles of the graph give limit cycles?

Those that correspond to surviving fixed points



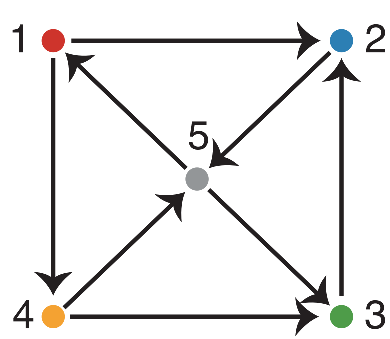


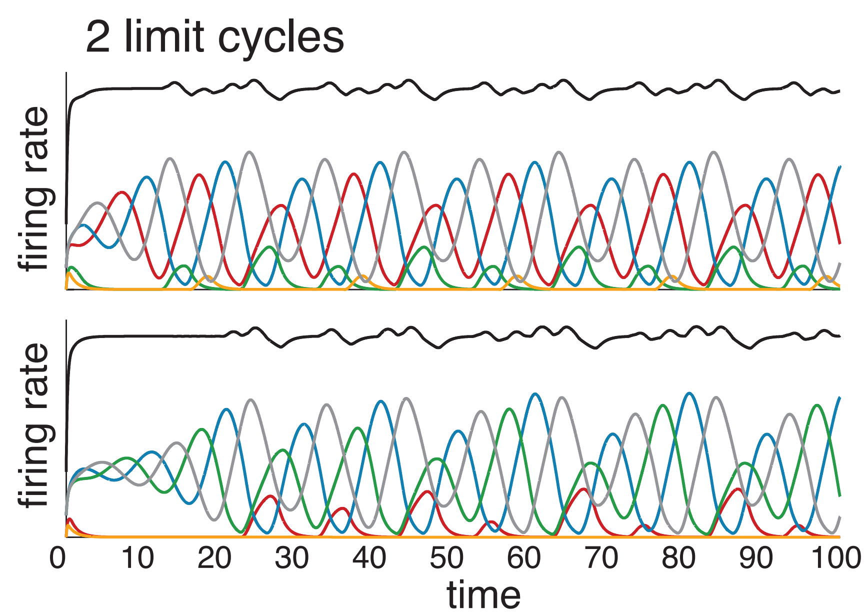
<u>3-cycles</u>

235, 145

<u>limit cycles</u>

235 only





<u>3-cycles</u>

125, 253, 145

<u>limit cycles</u>

125, 253 only

What can we learn using topology?

Naive Idea:

Make a simplicial complex from the network graph by filling in directed cliques...

Supergraphs theorem

Supergraphs theorem: if we replace each node i in a graph G by a subset ω_i with the same edges to obtain $\widetilde{G}$, then $\tilde{\sigma} \in \mathrm{FP}(\widetilde{G})$ if and only if $\tilde{\sigma} = \cup_{i\in\sigma}\tau_i$ where $\tau_i \in \mathrm{FP}(\widetilde{G}|_{\omega_i})$ for each $i \in \sigma$ and the index set $\sigma \in \mathrm{FP}(G)$. Moreover, $\mathrm{type}(\tilde{\sigma}) = \mathrm{type}(\sigma)\prod_{i\in\sigma}\mathrm{type}(\tau_i)$.

Summary

- CTLNs have rich nonlinear dynamics that are shaped by the graph of network connectivity
- Fixed point supports appear to depend only on properties of the graph, independent of parameters $\varepsilon, \delta, \theta$
- We can prove many facts about which (sub)graphs support fixed points, and when those fixed points survive to larger graphs
- Unstable fixed points are closely related – and predictive of – limit cycles and chaotic attractors
- A simplicial complex obtained by filling in directed cliques has the potential to tell us something about the attractors... if we figure out how to do it in the right way!

Thanks!

Collaborators:

Katie Morrison (University of Northern Colorado)
Caitlyn Parmelee (Keene State College)
Jesse Geneson & Chris Langdon (postdocs @ Penn State)

Anda Degeratu (Stuttgart)
Vladimir Itskov (Penn State)

National Institutes of Health

Funding: NIH R01 EB022862, NSF DMS 1516881

Plan of the talk

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- Network structures/motifs
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- Early explorations...
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A general principle: domination

Lemma 4.1. *k dominates j with respect to σ if the following three conditions hold:*

1. *if $i \to j$ then $i \to k$ for each $i \in \sigma \setminus \{j, k\}$,*
2. *if $j \in \sigma$, then $j \to k$, and*
3. *if $k \in \sigma$, then $k \not\to j$.*

Lemma 2.29 (domination)**.** *Suppose k dominates j with respect to σ. The following statements all hold:*

(a) If $j, k \in \sigma$, then $\sigma \notin \mathrm{FP}(G|_\sigma)$.

(b) If $j \in \sigma$, $k \notin \sigma$, then $\sigma \notin \mathrm{FP}(G|_{\sigma \cup \{k\}})$.

(c) If $j \notin \sigma$, $k \in \sigma$, and $\sigma \in \mathrm{FP}(G|_\sigma)$, then we also have $\sigma \in \mathrm{FP}(G|_{\sigma \cup \{j\}})$.

A general principle: domination

Definition 2.28. We say that k dominates j with respect to σ if the following three conditions hold:

1. $\sum_{i \in \sigma \setminus \{j,k\}} W_{ki} |s_i^\sigma| \geq \sum_{i \in \sigma \setminus \{j,k\}} W_{ji} |s_i^\sigma|$,
2. if $j \in \sigma$, then $W_{kj} > -1$ (i.e., $j \to k$), and
3. if $k \in \sigma$, then $W_{jk} < -1$ (i.e. $k \not\to j$).

Note that condition 1 is always satisfied if $W_{ki} \geq W_{ji}$ for all $i \in \sigma \setminus \{j, k\}$ – that is, if $i \to k$ whenever $i \to j$.

Lemma 4.1. *k dominates j with respect to σ if the following three conditions hold:*

1. *if $i \to j$ then $i \to k$ for each $i \in \sigma \setminus \{j, k\}$,*
2. *if $j \in \sigma$, then $j \to k$, and*
3. *if $k \in \sigma$, then $k \not\to j$.*