Emergent dynamics from network connectivity: a minimal model

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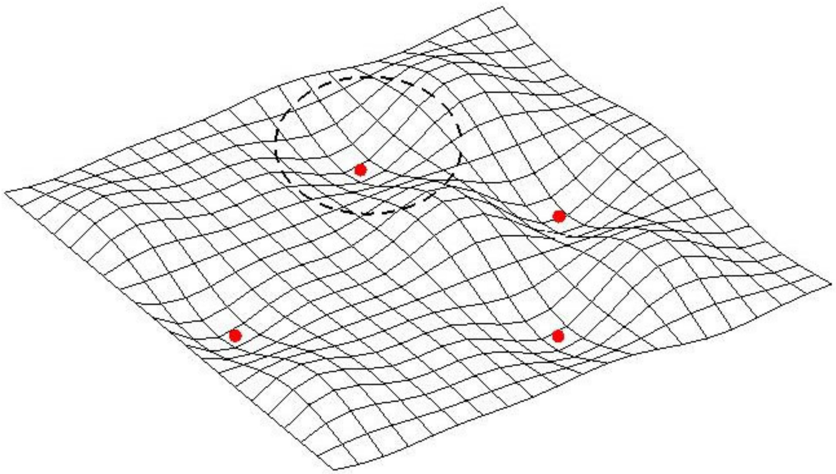
Mar 3 Denver, CO

Dynamic attractors in the brain

Classical model - Hopfield networks

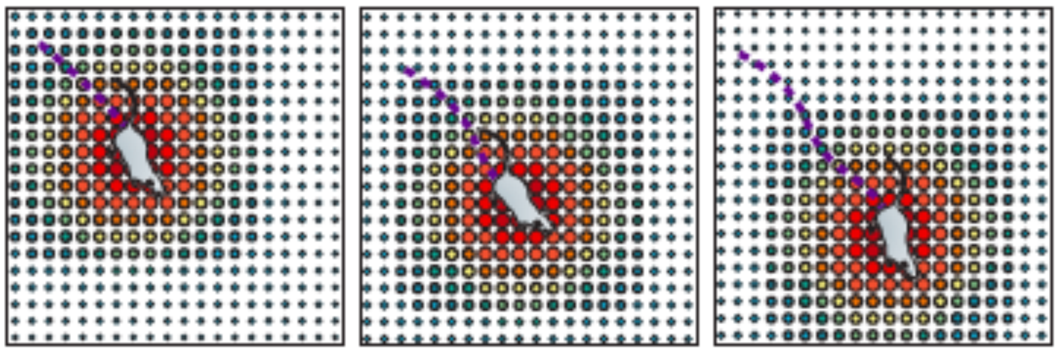
memory patterns $\longleftrightarrow$ fixed point attractors

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

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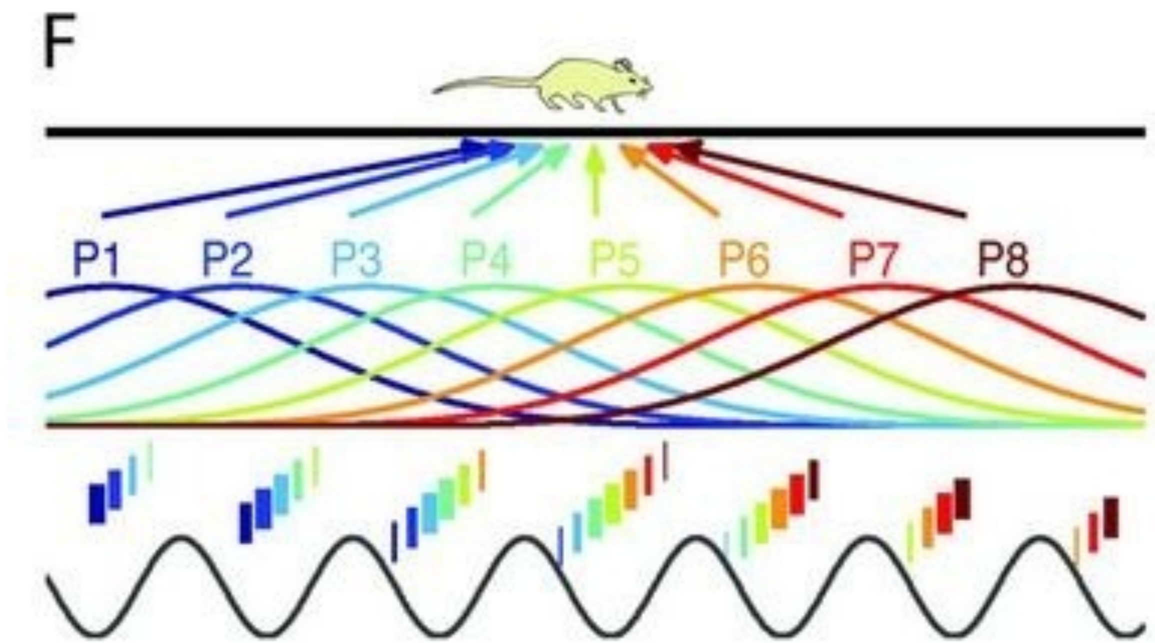
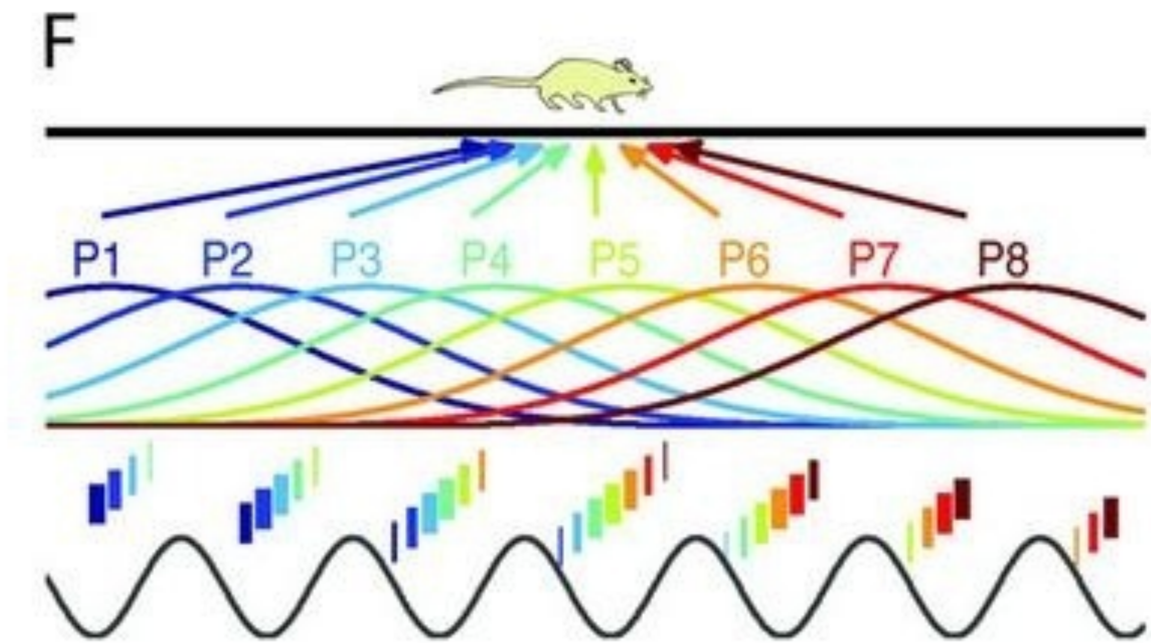


Individual positions do not correspond to fixed points, but sequences…

Example: place cell activity in hippocampus

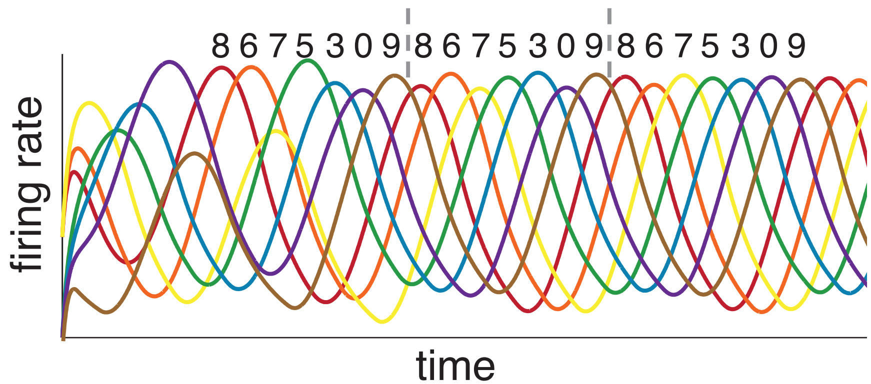
memory patterns (animal position) $\longleftrightarrow$ periodic/dynamic attractors ?

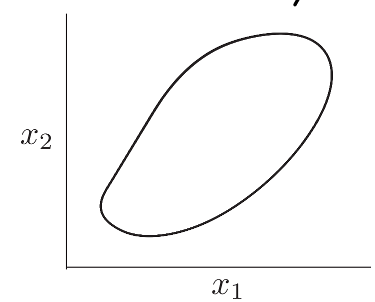


Individual positions do not correspond to fixed points, but sequences...

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

What features of a network shape emergent dynamics?

(e.g. dynamic attractors)

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intrinsic neuron dynamics (timescales, channel dynamics, etc.)
axonal delays
cell types
neuromodulators
dendrites
stochasticity of spikes
noise (other)
…
statistics of connectivity

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noise (other)
…
statistics of connectivity
precise pattern of connectivity – an important biological detail!

Our goal: to understand how precise connectivity shapes emergent dynamics

This is hard… mathematically, it's quite challenging to predict how network structure affects dynamics unless the structure is:

statistical/random or
very regular/geometric

Our approach: to develop a mathematical theory in a simple model

Success means: a kind of graphical calculus, where we can analyze the underlying directed graph and predict emergent attractors and sequences

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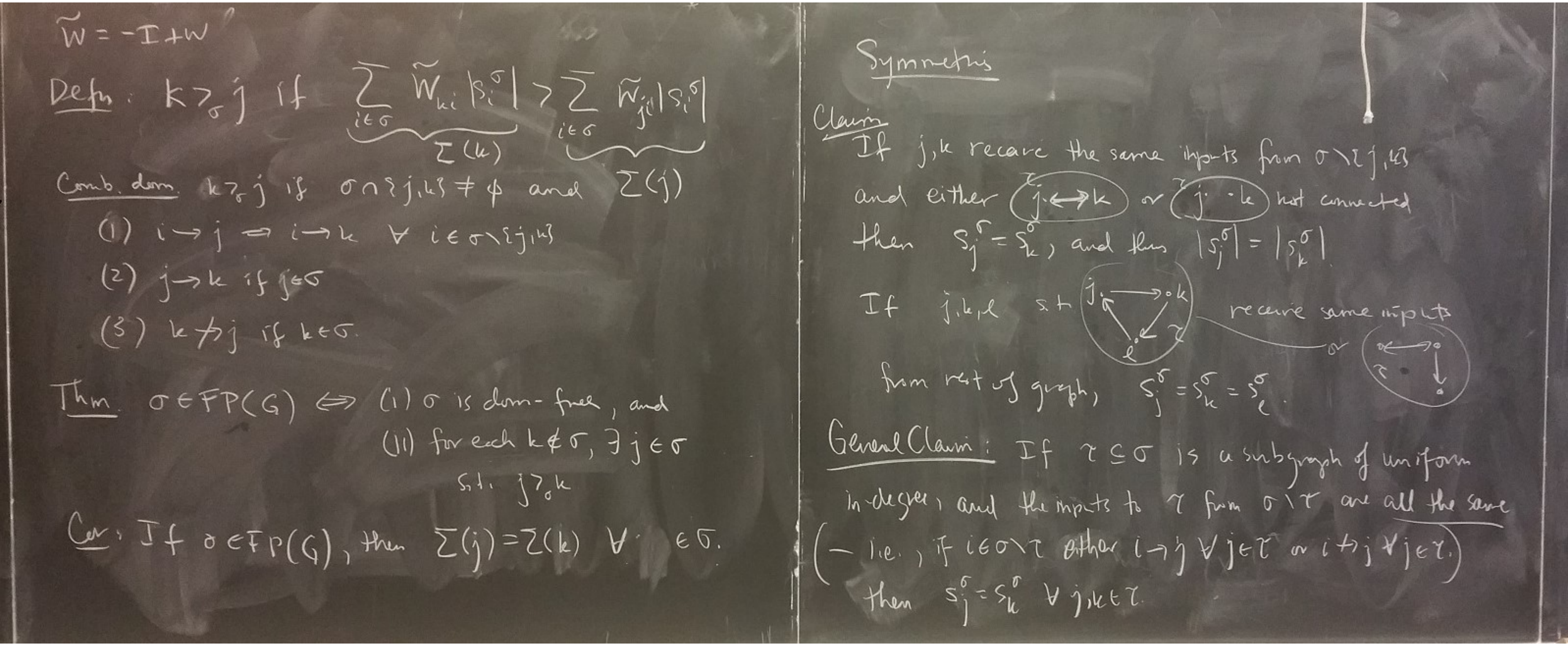
the lab



main contributors to this work:

Katie Morrison (U. of Northern Colorado)
Jesse Geneson (postdoc @ Penn State)
Chris Langdon (postdoc @ Penn State)
Caitlyn Parmelee (Keene State College)

some other collaborators:

Anda Degeratu (Stuttgart)
Vladimir Itskov (Penn State)
Eva Pastalkova
David Rolnick (MIT)

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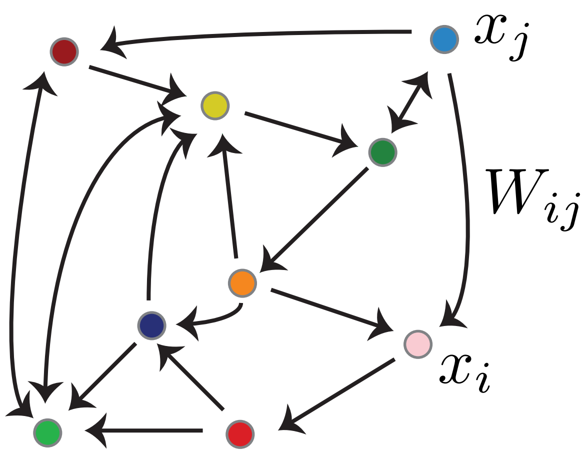
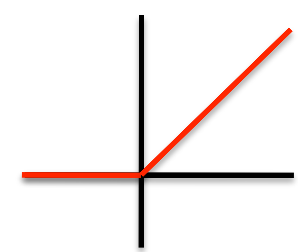
Threshold-linear networks

Threshold-linear networks (TLNs)



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

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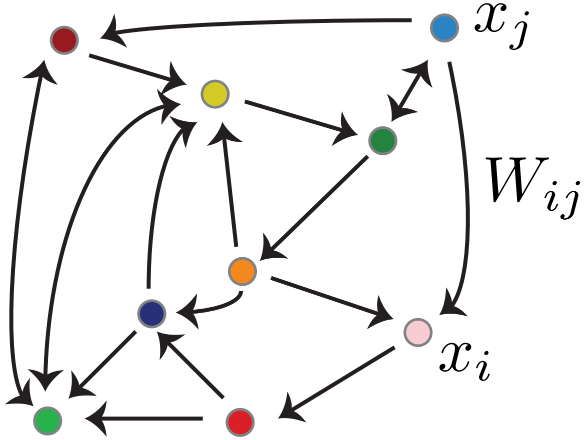
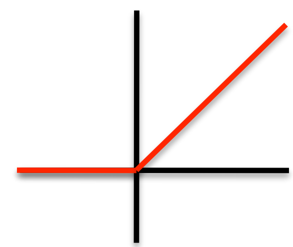


Threshold-linear dynamics

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

multistability
limit cycles
chaos
quasiperiodic attractors



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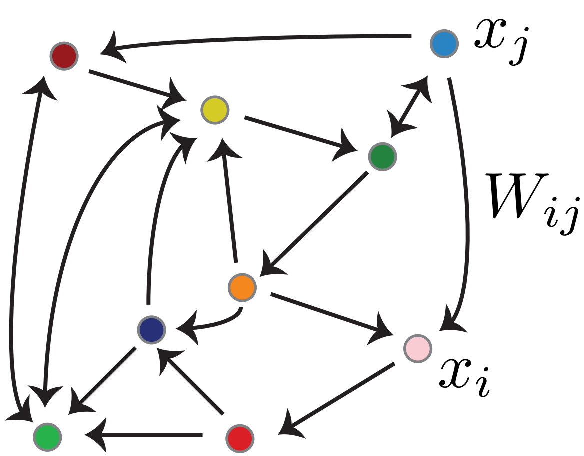

Threshold-linear dynamics

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

Q: Given (W,b), what can we say about the dynamics?

What are the static and dynamic attractors?

Some things we already knew about TLNs . . .

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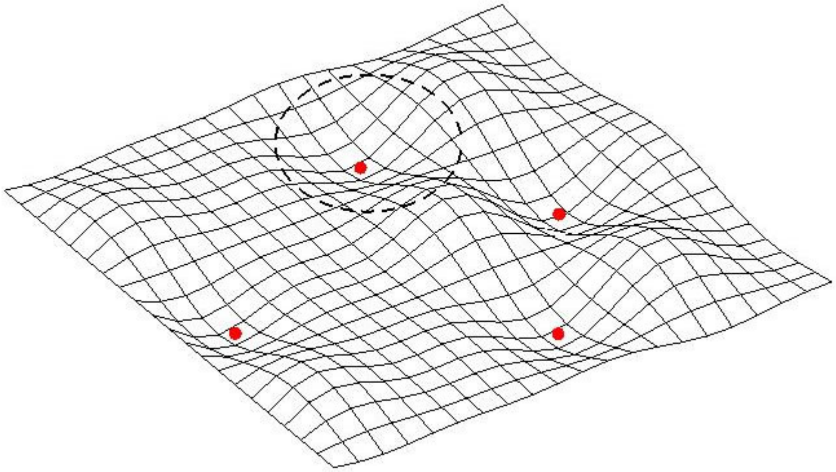
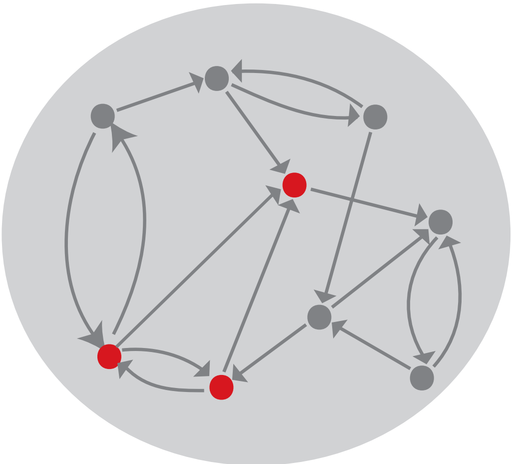


- For symmetric W, they generically exhibit multistability.

- For each support $\sigma \subseteq [n]$ there can be at most one fixed point.

- The fixed point is stable if and only if $(-I+W)_\sigma$ is stable.

- If W symmetric:
  - guaranteed convergence to a fixed pt
  - theory of permitted and forbidden sets



Results for TLNs with symmetric W
(all about stable fixed points)

X. Xie, R. H. Hahnloser, and H.S. Seung. Selectively grouping neurons in recurrent networks of lateral inhibition. Neural Computation, 2002.

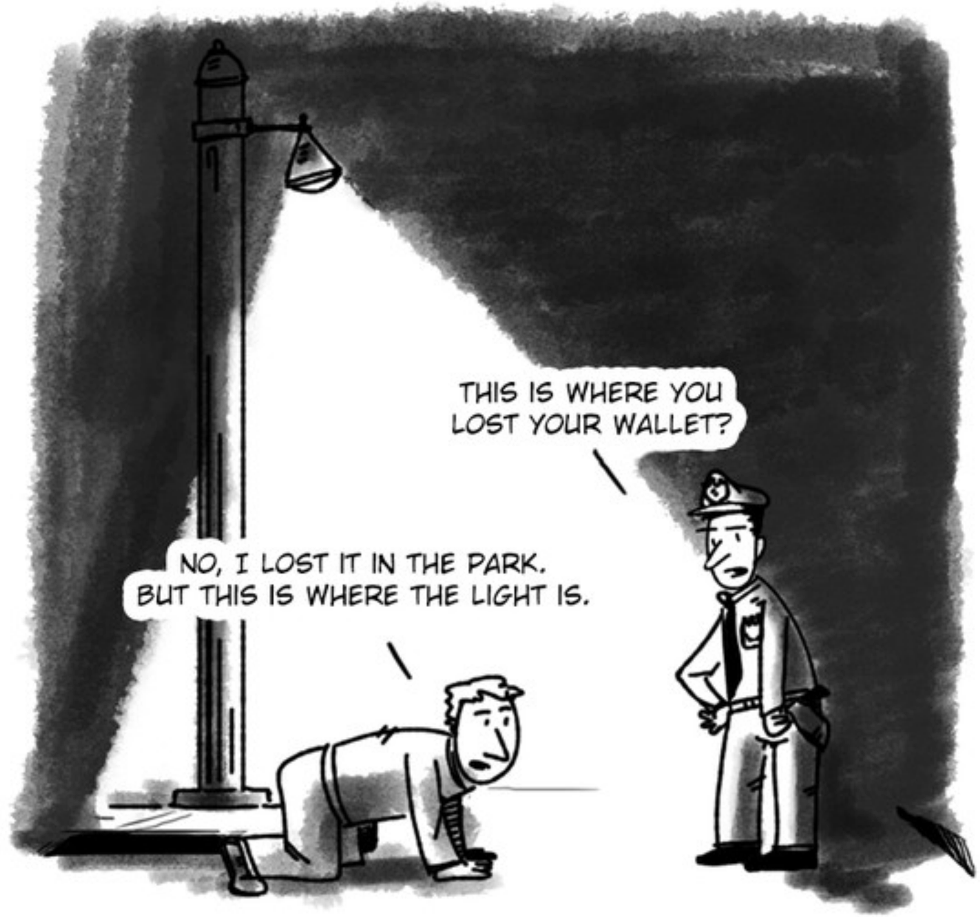
R. H. Hahnloser, H.S. Seung, and J.J. Slotine. Permitted and forbidden sets in symmetric threshold-linear networks. Neural Computation, 2003.

C. Curto, A. Degeratu, and V. Itskov. Flexible memory networks. Bull. Math. Biol., 2012.

C. Curto, A. Degeratu, and V. Itskov. Encoding binary neural codes in networks of threshold-linear neurons. Neural Computation, 2013.

C. Curto and K. Morrison. Pattern completion in threshold-linear networks. Neural Comp., 2016.

We are bored with stable fixed point –
where do we find other kinds of dynamics?



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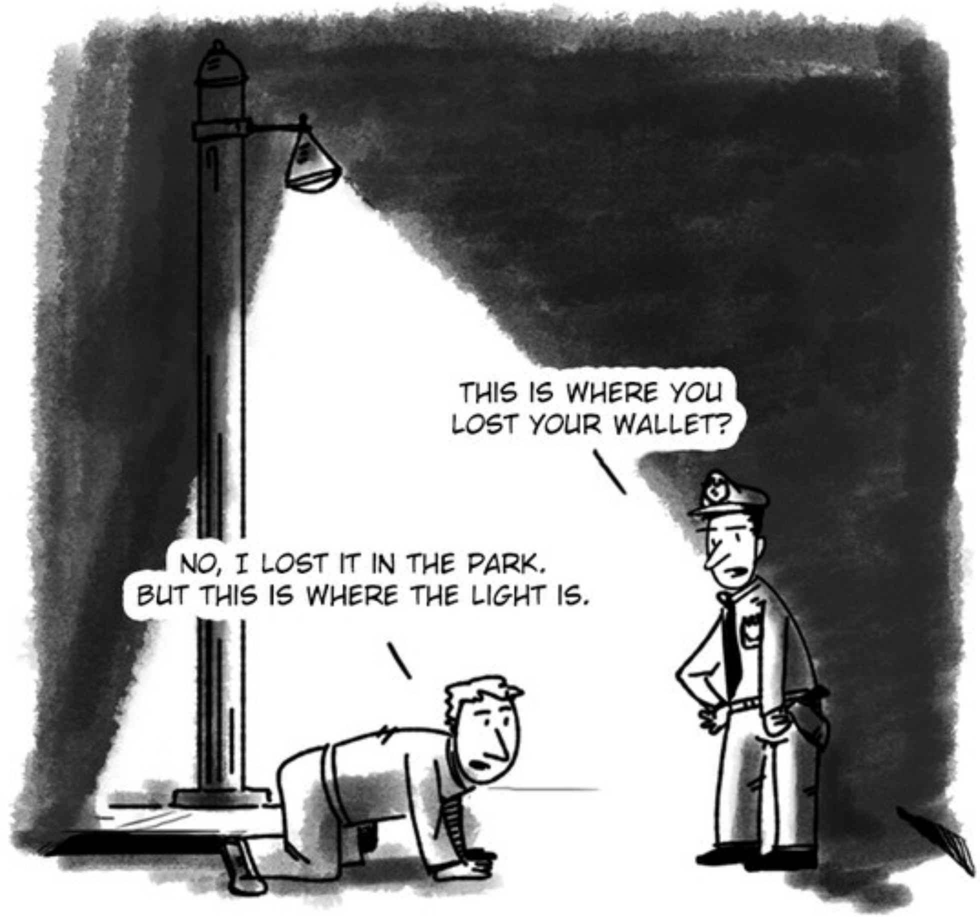
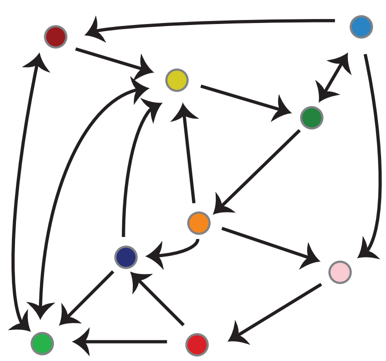


Idea: look for networks that have NO stable fixed points!

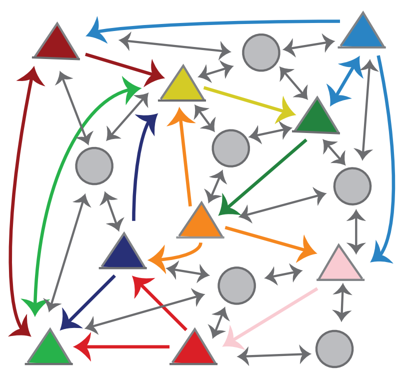
Combinatorial threshold-linear networks

Combinatorial Threshold-Linear Networks (CTLNs)

Directed graph G



Idea: network of excitatory and inhibitory cells



Same TLN dynamics:

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

Graph G determines the matrix W

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

parameter constraints:

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

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

CTLNs with no 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).

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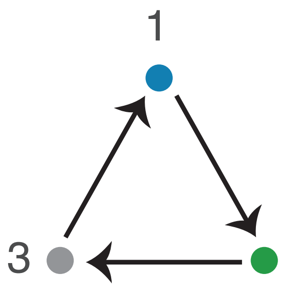
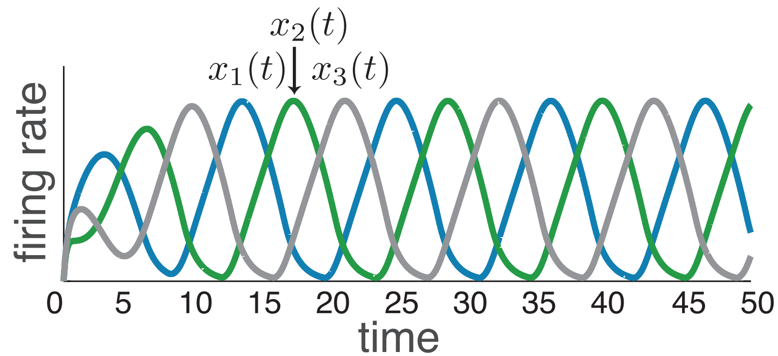
Example:
3-cycle





$$W = \begin{bmatrix} 0 & -1-\delta & -1+\varepsilon \\ -1+\varepsilon & 0 & -1-\delta \\ -1-\delta & -1+\varepsilon & 0 \end{bmatrix}$$

TLN dynamics:

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Parameter constraints:

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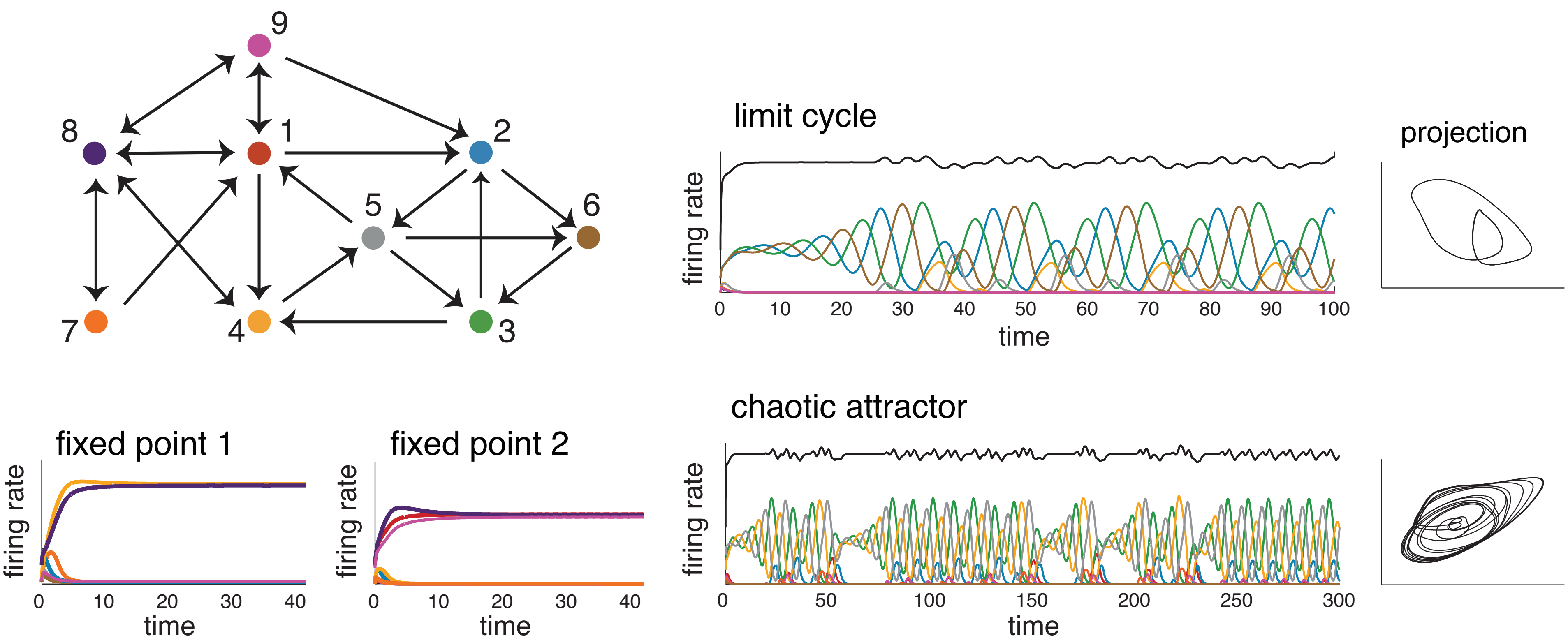
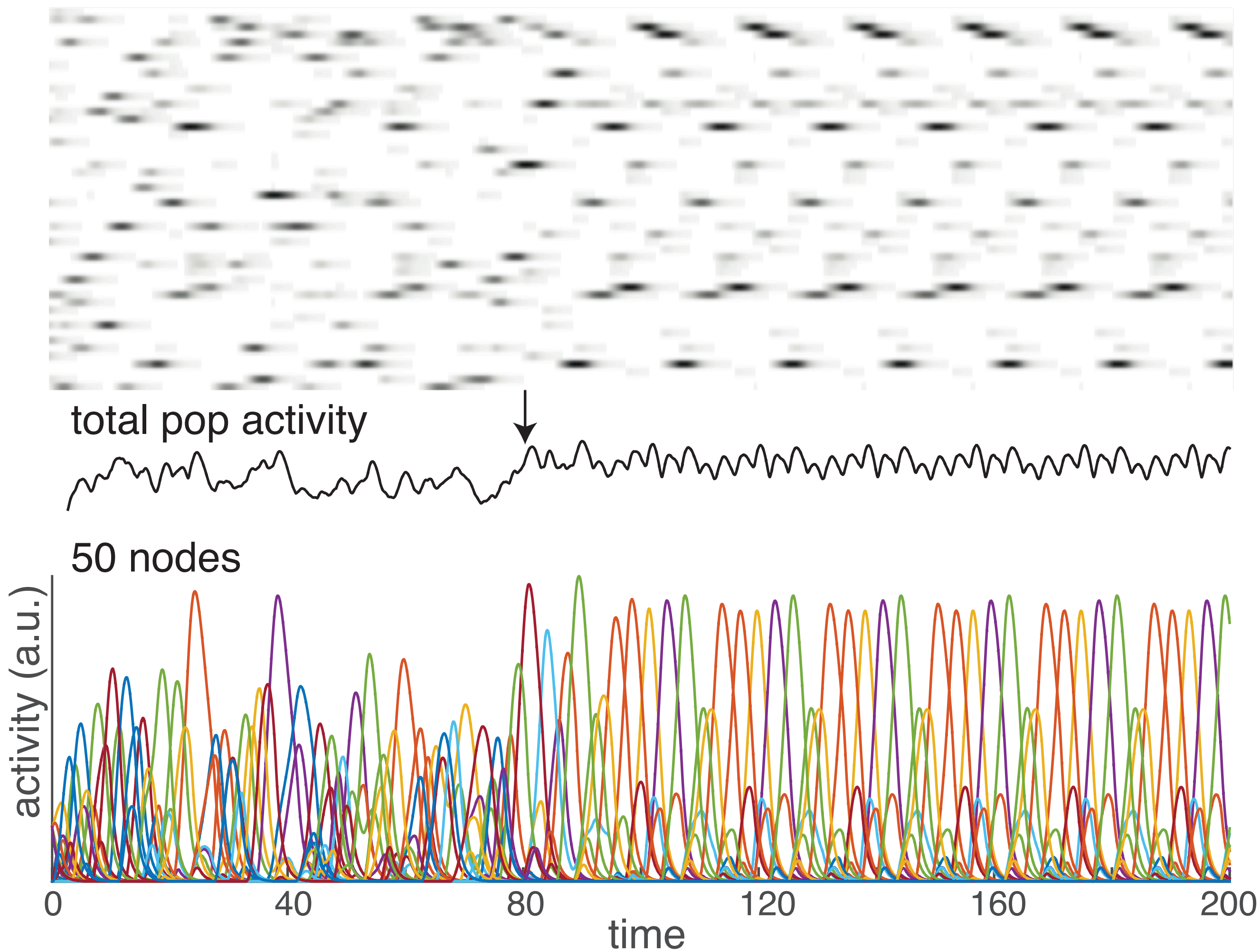
A single network can display multiple attractors of different types



Spontaneous state transitions in large random networks with no stable fixed points

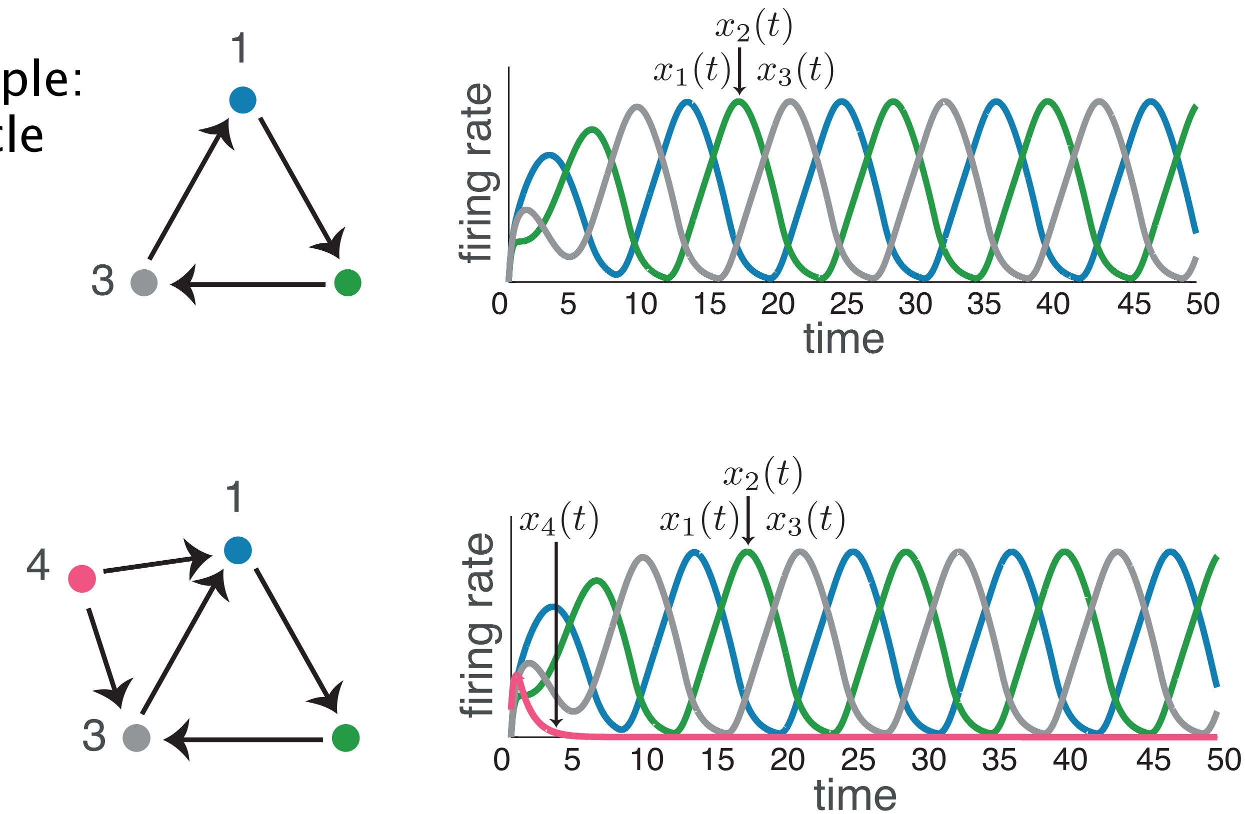


Important Facts about CTLNs

- display a rich variety of nonlinear dynamics
- mathematically tractable
- all nodes are identical
- for fixed parameters $\varepsilon, \delta, \theta$, only the graph changes between networks – isolates the role of connectivity
- many aspects of dynamics are invariant under parameter changes
- non-local properties of connectivity may matter more than local features

Embedding of motif matters

Example:
3-cycle



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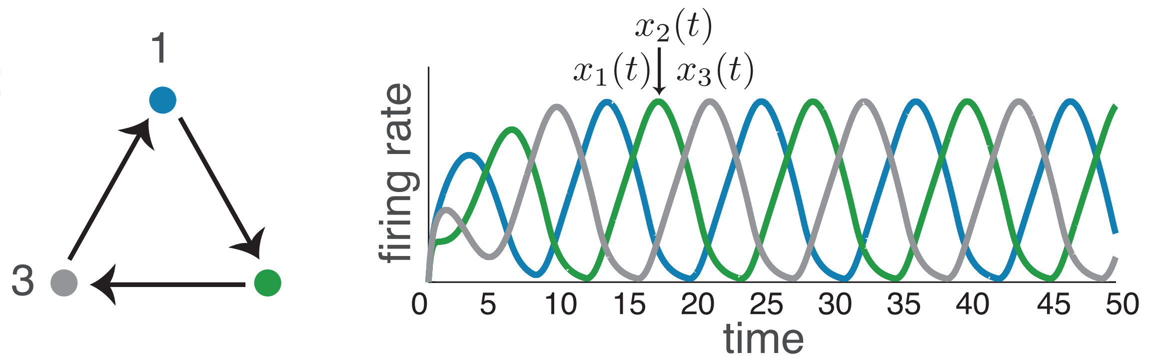
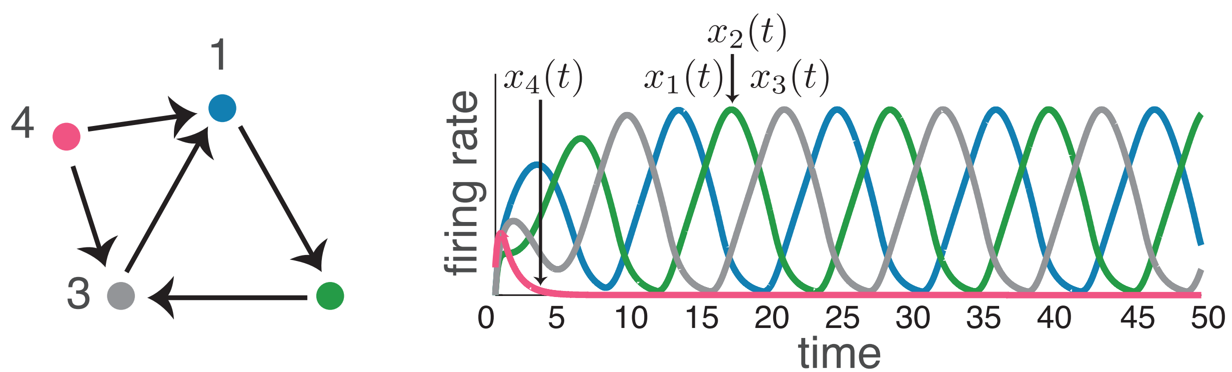
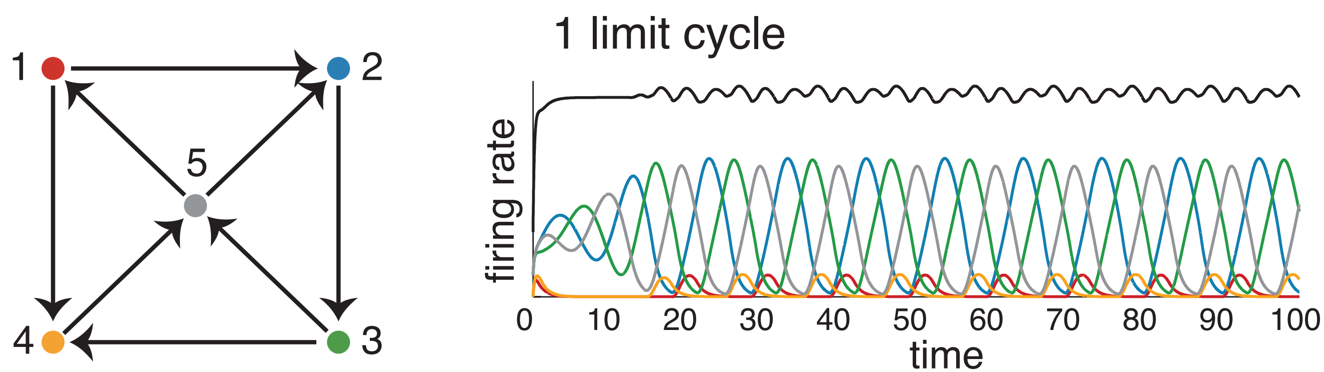




Is this a general principle, that added sources drop out of the dynamics?

Math Puzzle #1:

Which 3-cycles of the graph give rise to limit cycles in the dynamics?

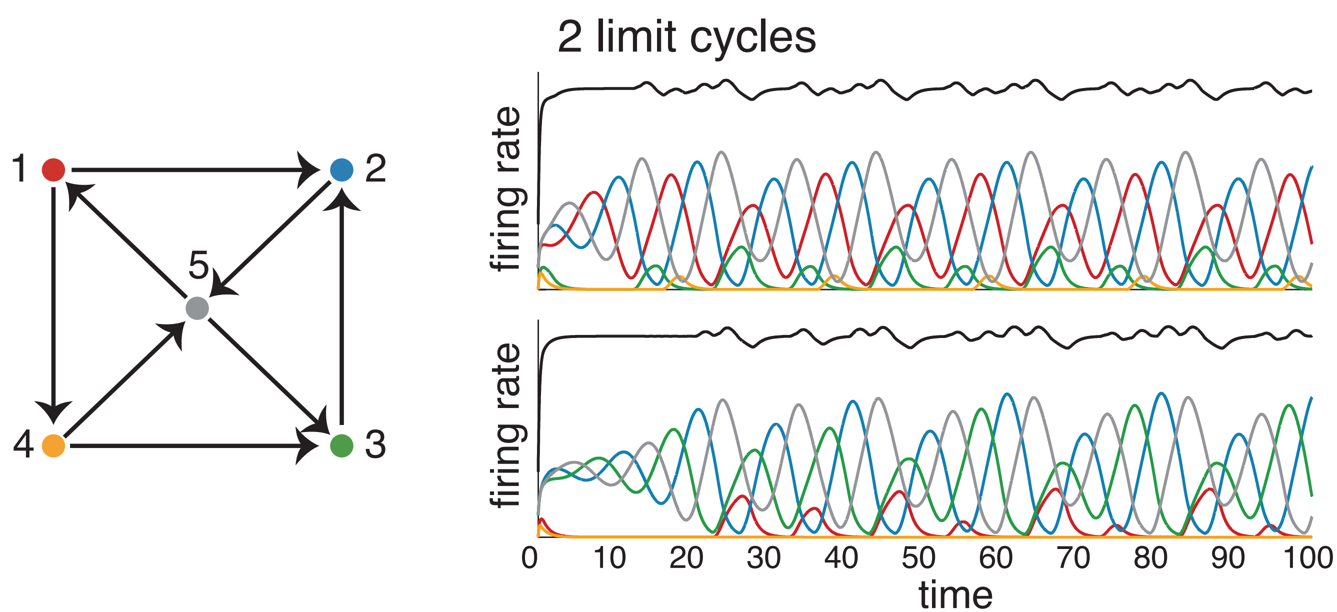


<u>3-cycles</u>

235, 145

<u>limit cycles</u>

235 only



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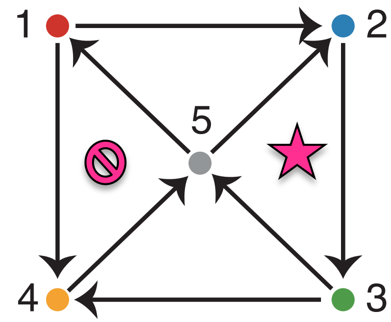

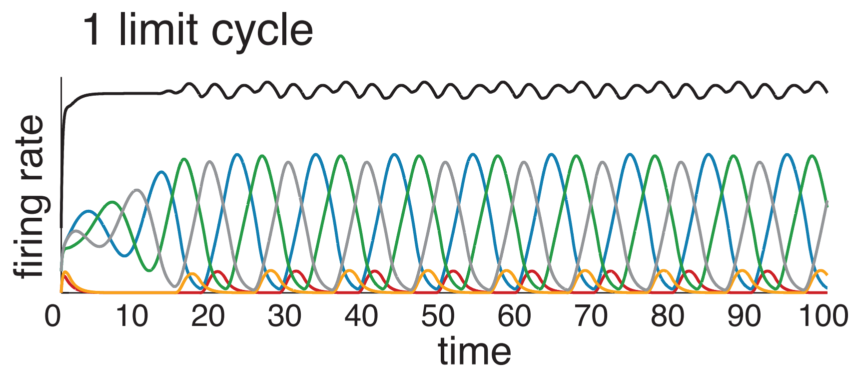

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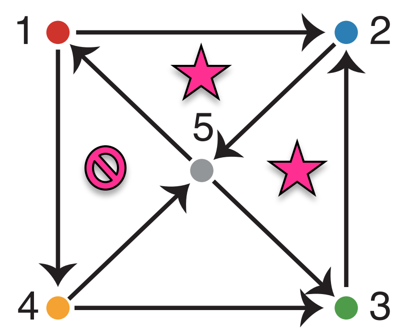

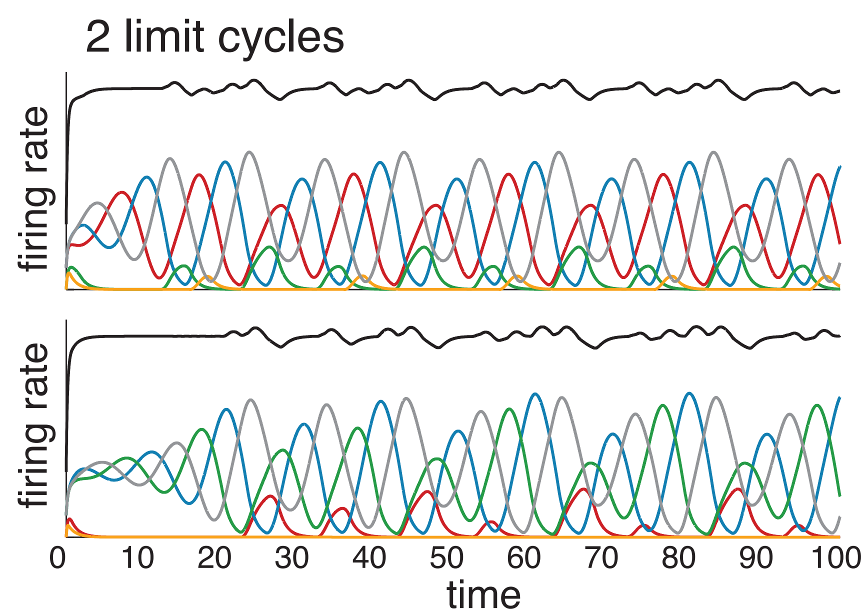

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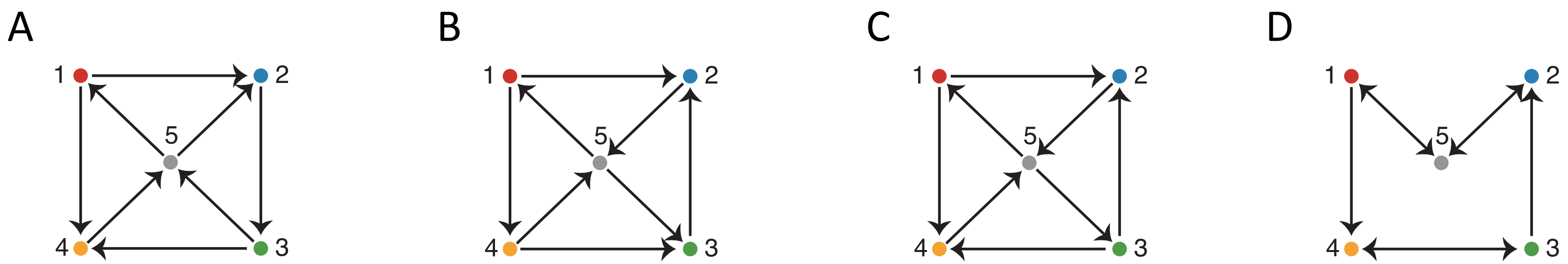
4 neural networks with matching degree sequence

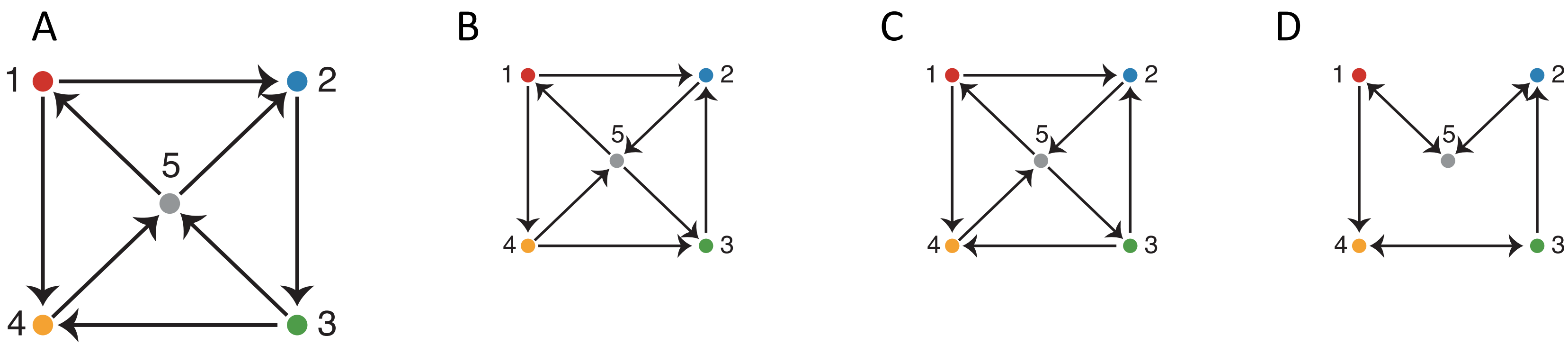


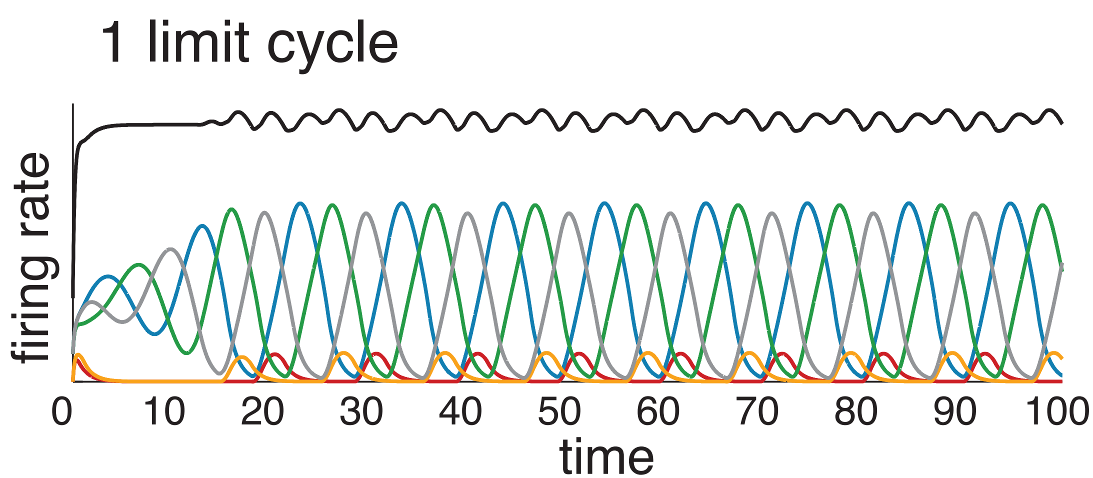
all graphs have the same in/out-degree sequence:

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

The four networks are locally identical.

examples of nonlinear network dynamics: limit cycles





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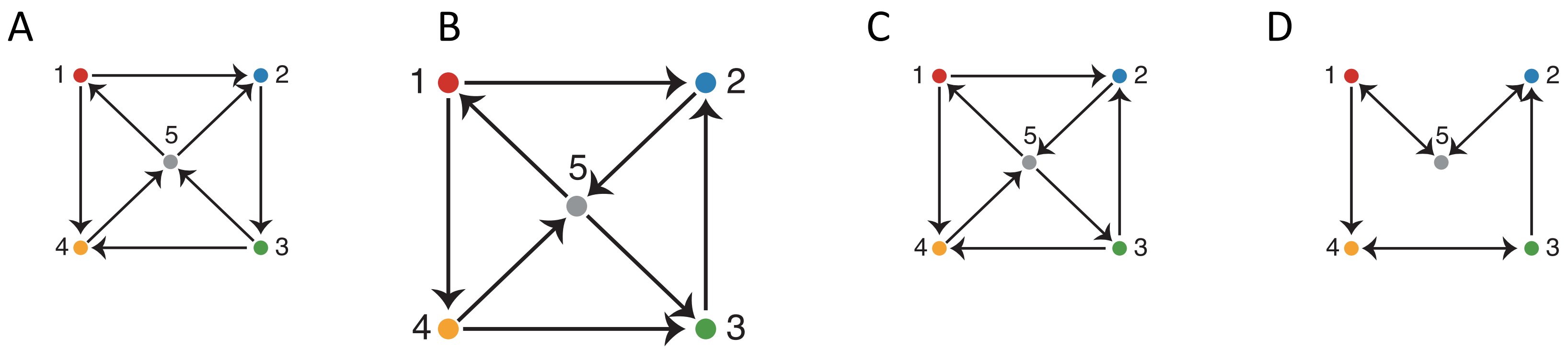
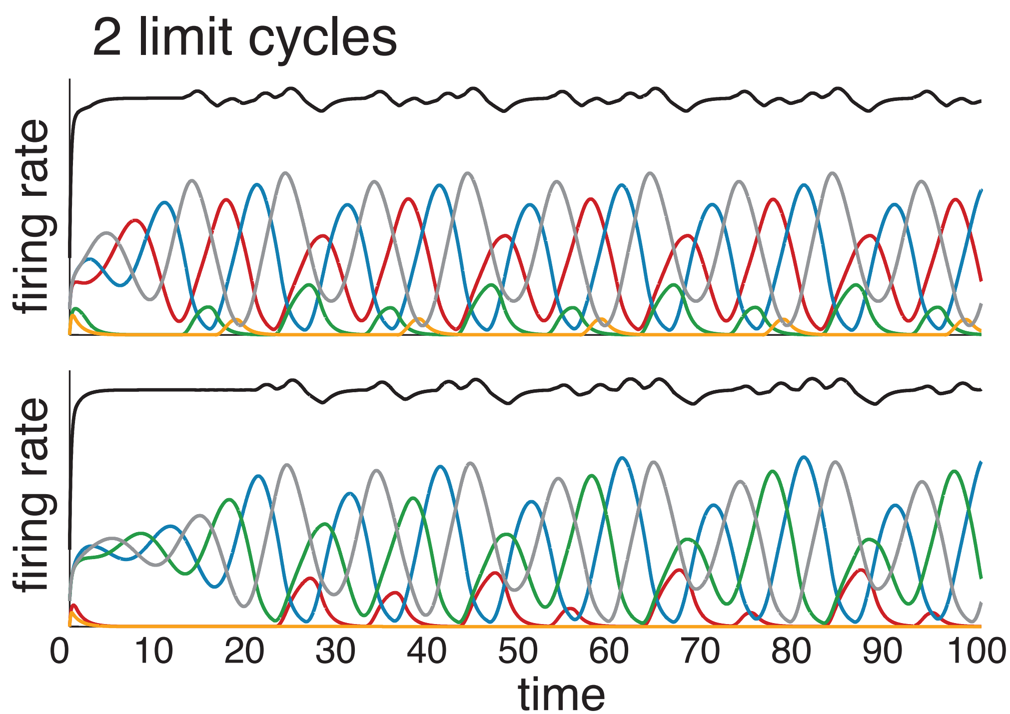
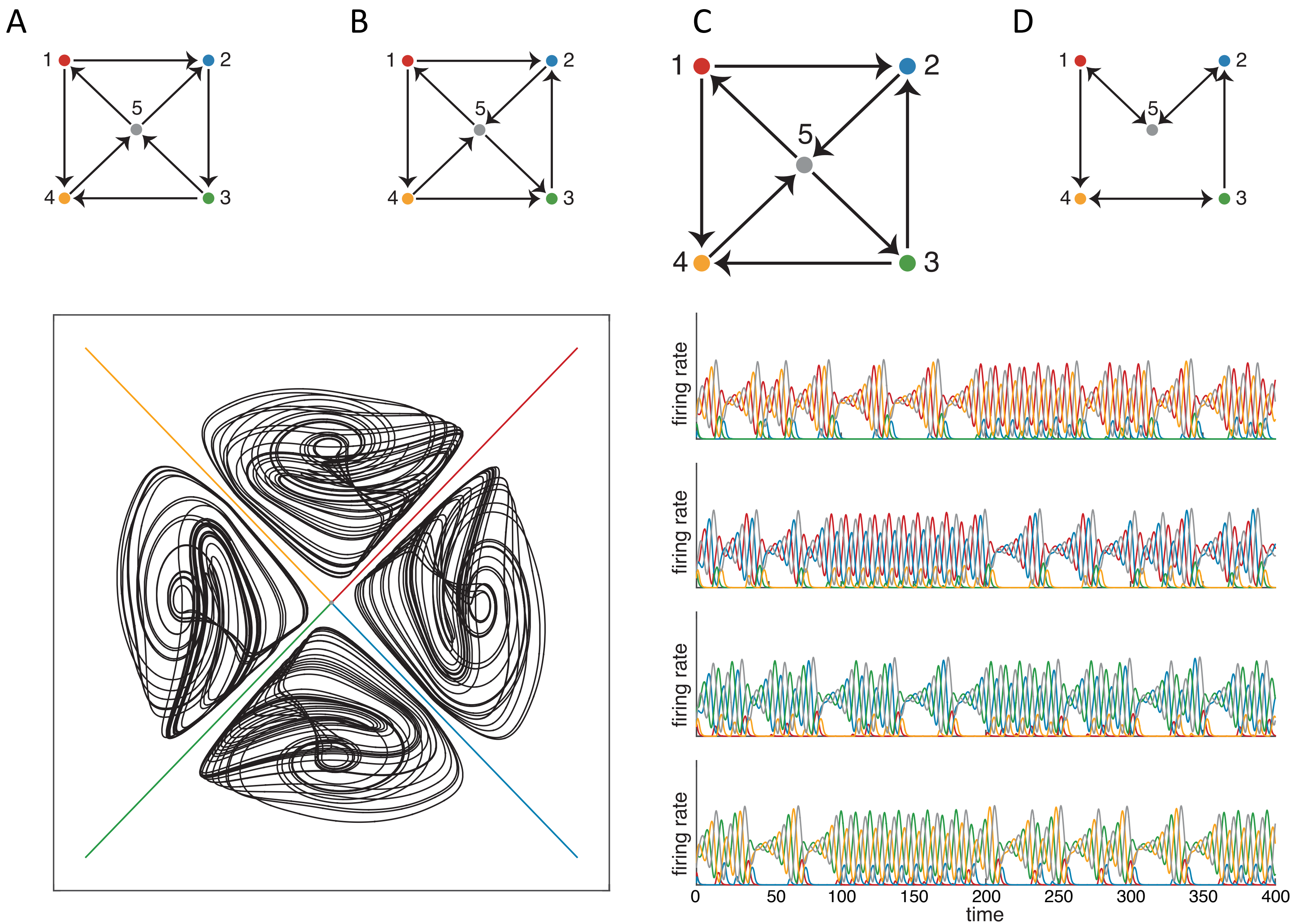
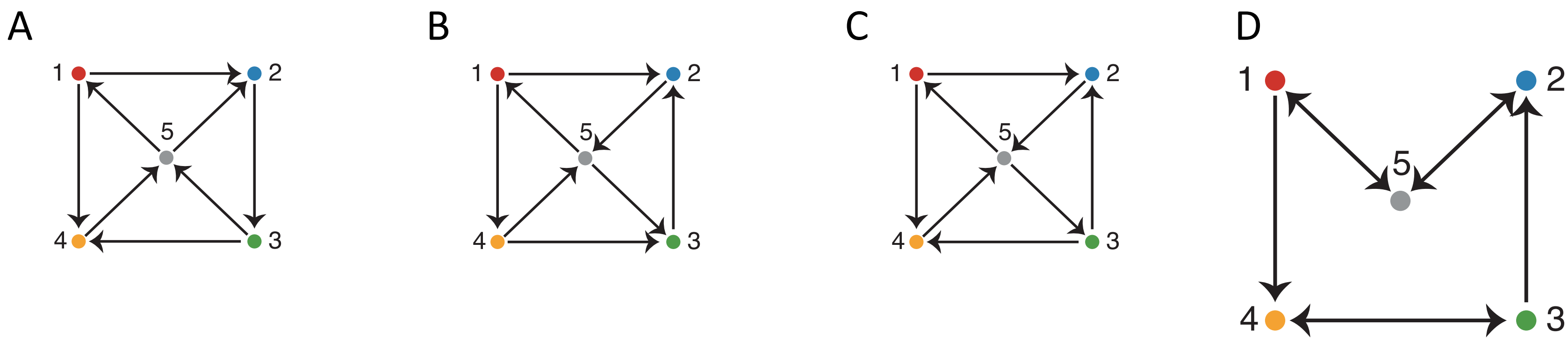


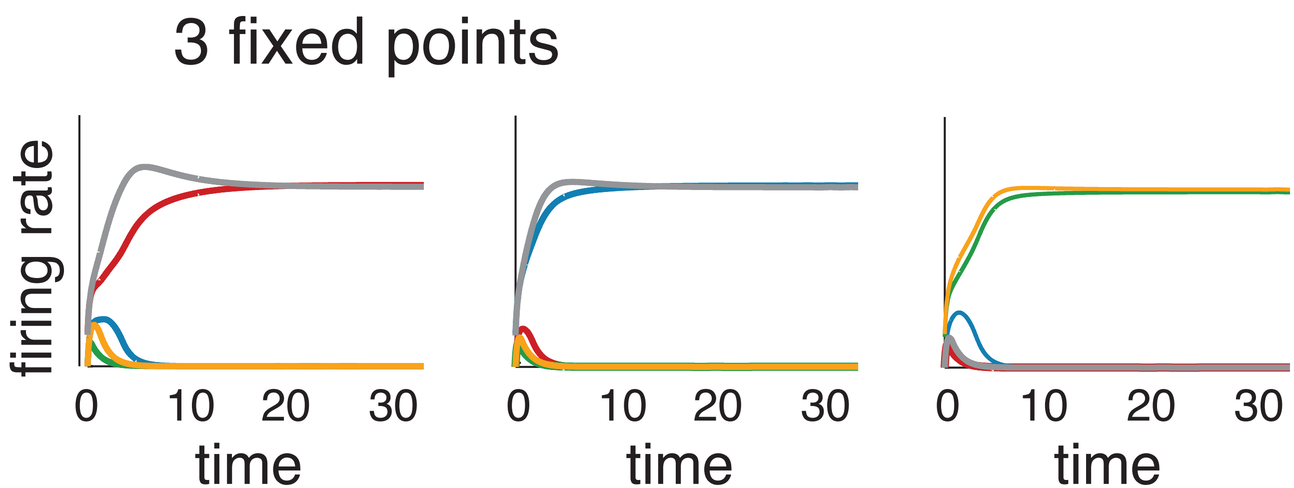


examples of nonlinear network dynamics: chaos



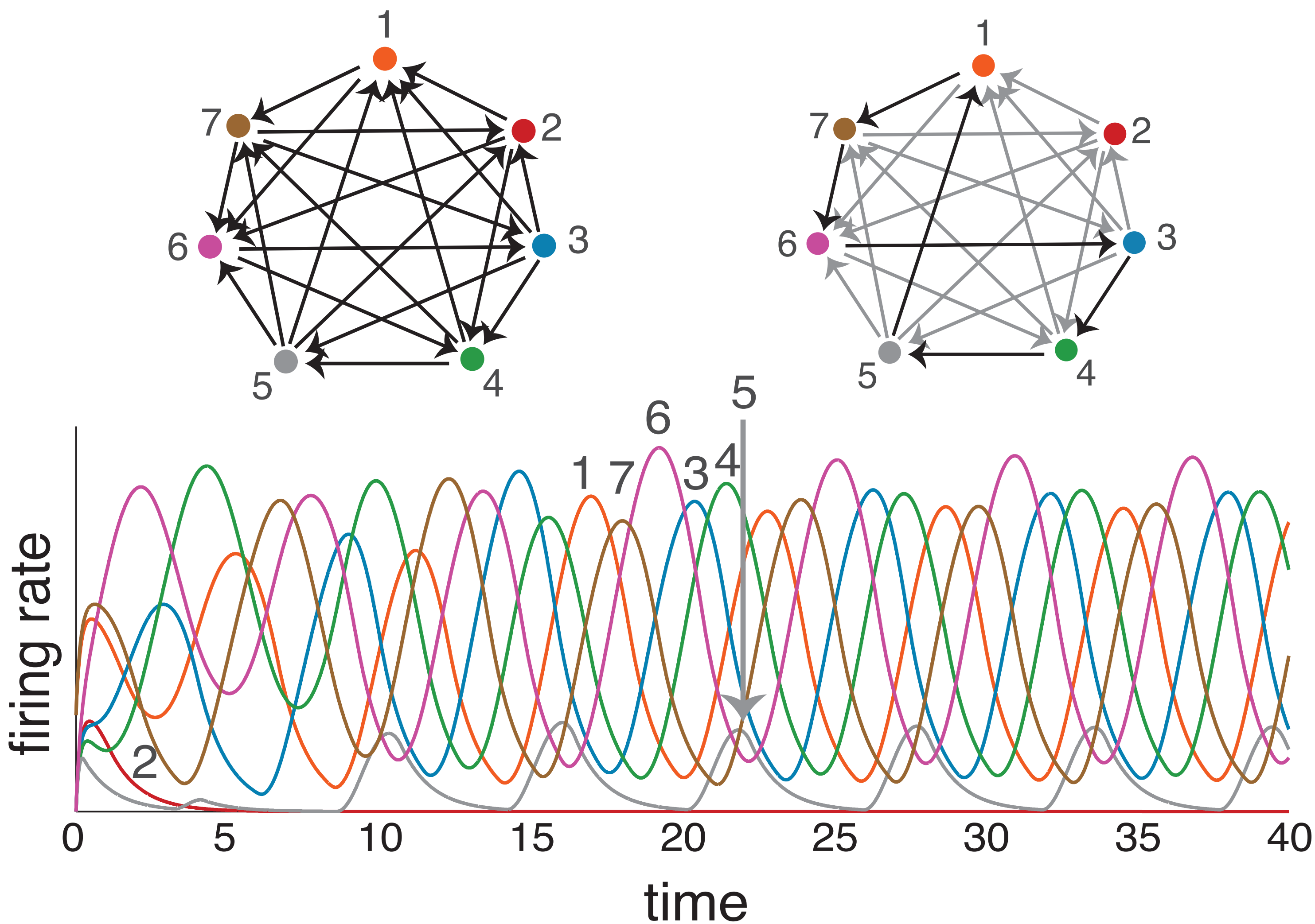
examples of nonlinear network dynamics: multistability





Math Puzzle #2:

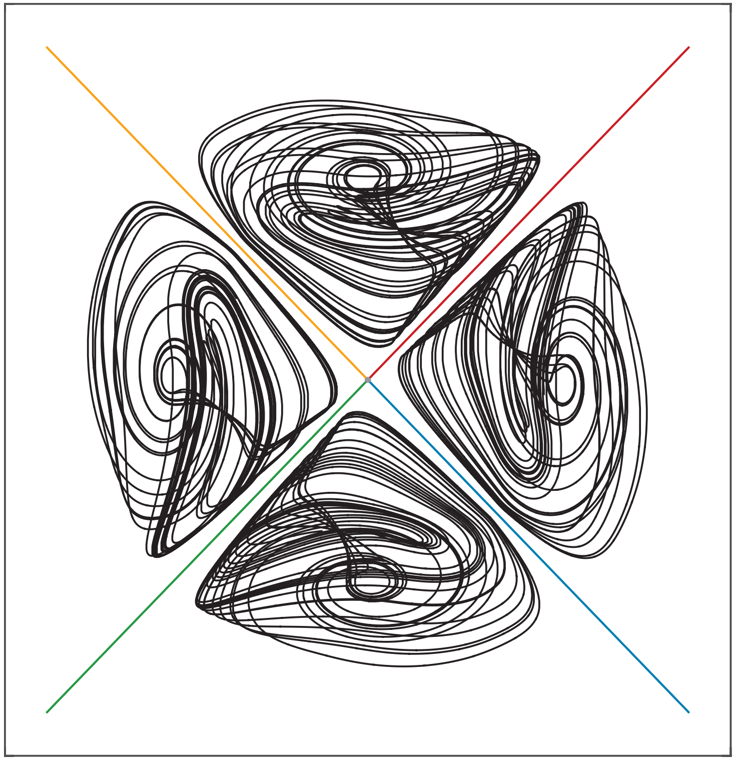
Why does the sequence 176345 emerge? Why does neuron 2 drop out?



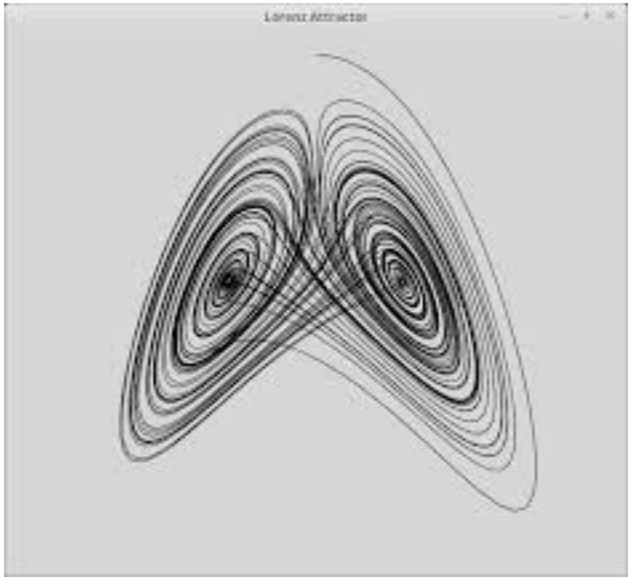
Fixed points (stable and unstable) of CTLNs

unstable fixed points in chaotic attractors

baby chaos: 4 attractors

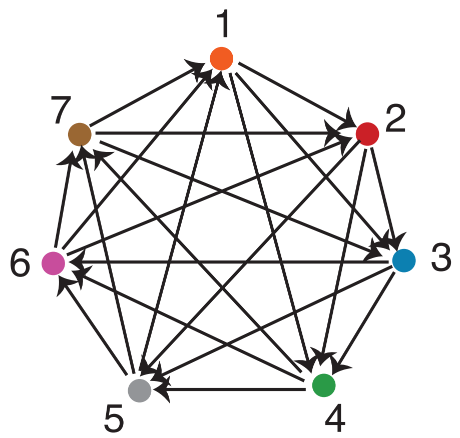


Lorenz attractor



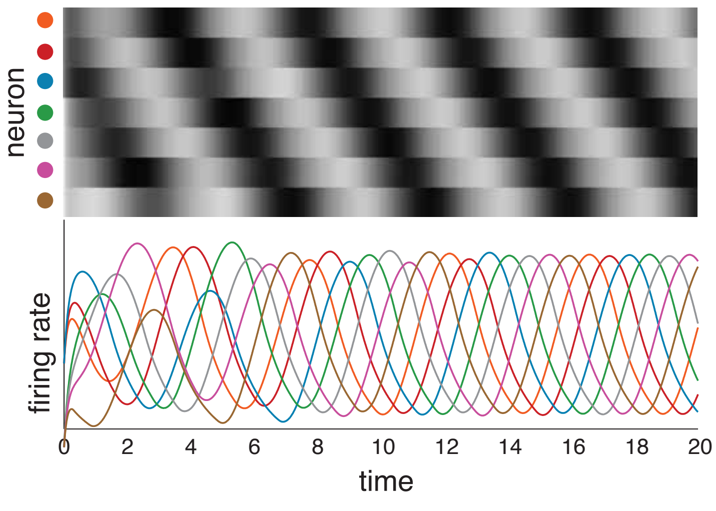
A word of caution

1 (unstable) fixed point



limit cycle

Sequence 1234567



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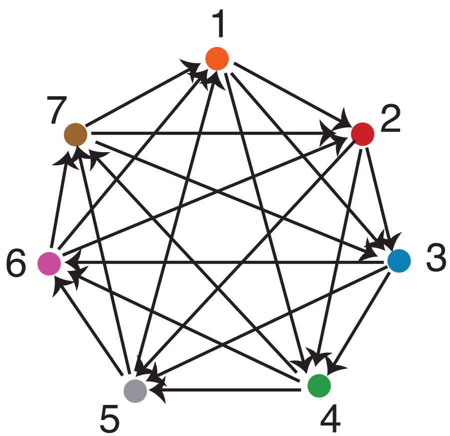
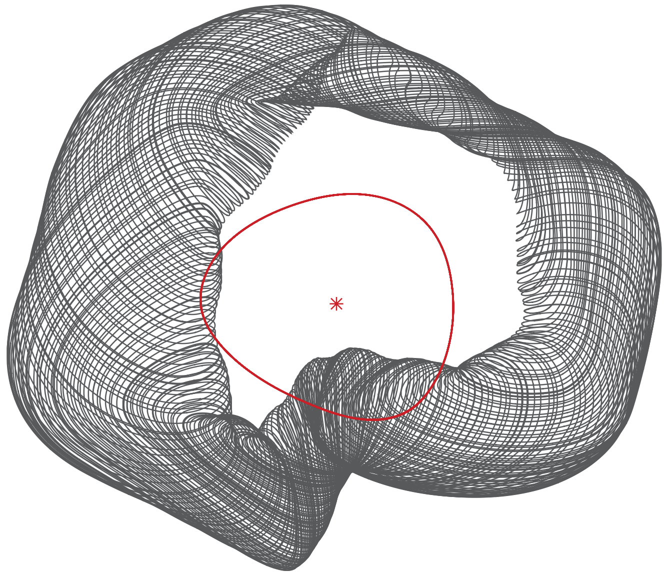


limit cycle + quasiperiodic attractor!



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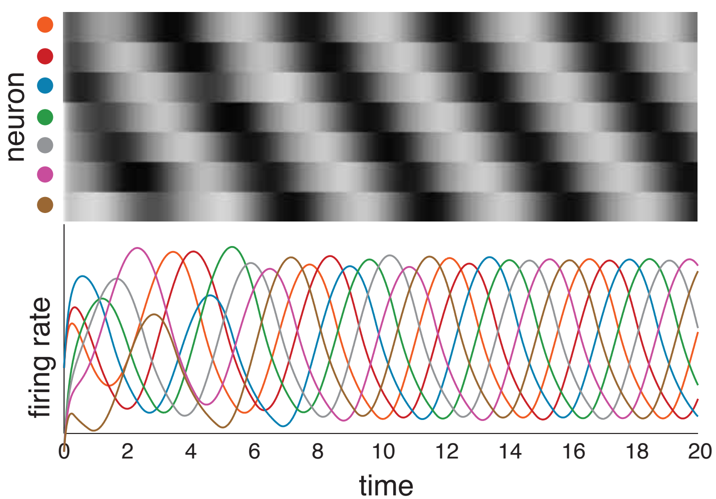
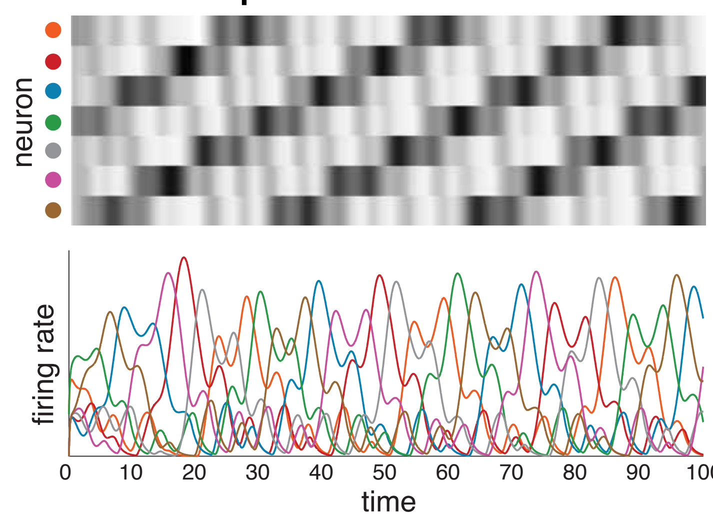


Sequence 1473625



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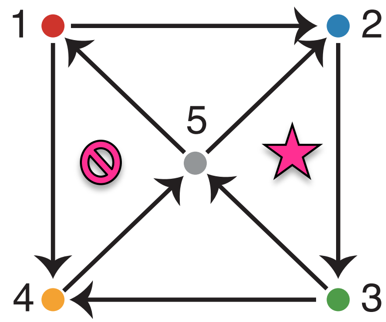
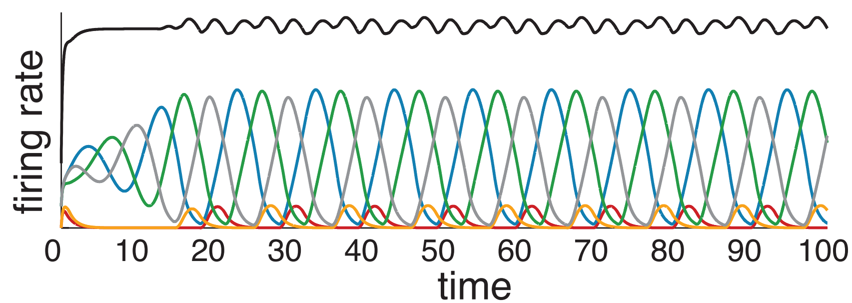


<u>3-cycle fixed pts</u>
235 only

1 limit cycle



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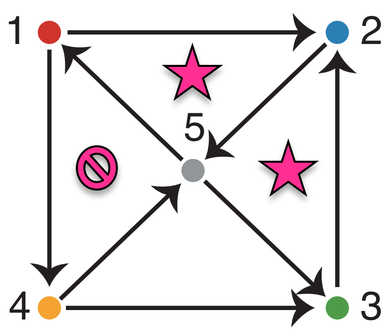
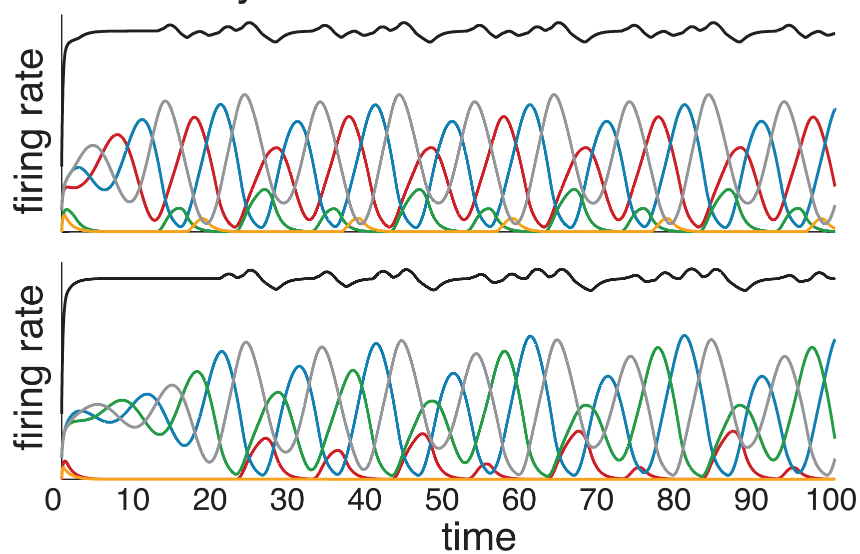


<u>3-cycle fixed pts</u>
125, 253 only

2 limit cycles



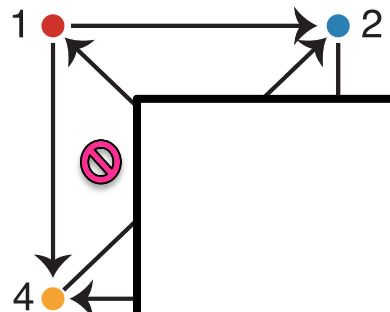
<u>3-cycles</u>
125, 253, 145

<u>limit cycles</u>
125, 253 only

Math Puzzle #1:

Which 3-cycles of the graph give rise to limit cycles in the dynamics?

1 limit cycle



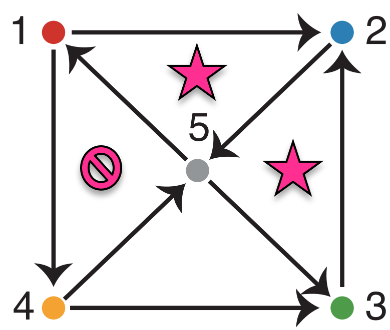
3-cycles

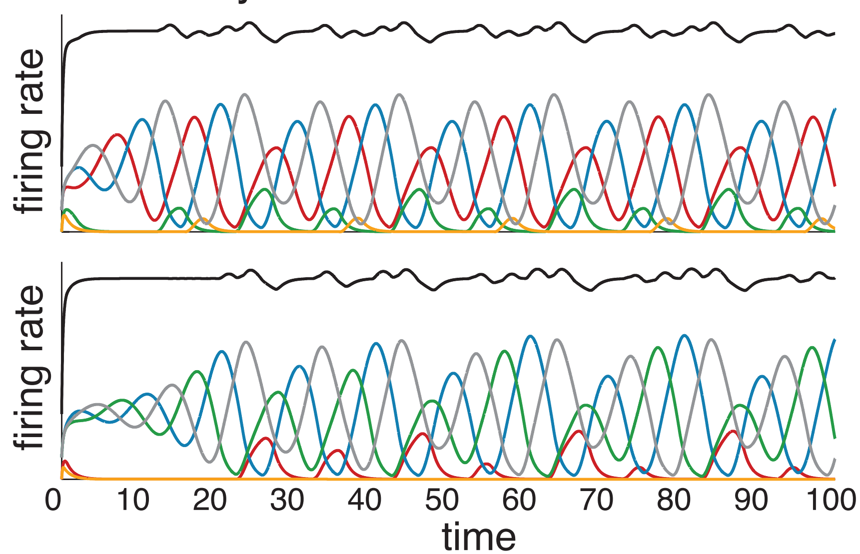
Which 3-cycles of the graph have surviving fixed points?

3-cyc

235 only

2 limit cycles





3-cycles

125, 253, 145

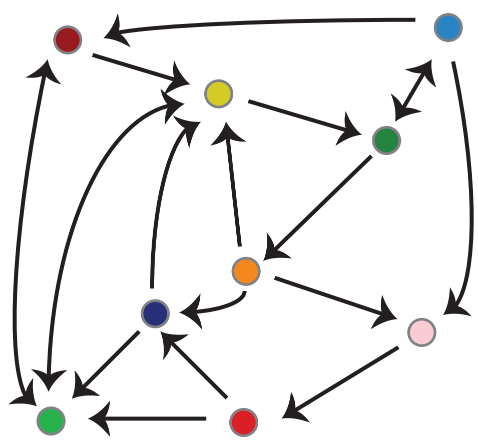
limit cycles

125, 253 only

3-cycle fixed pts

125, 253 only

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.)

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

$$\sigma = \mathrm{supp}(\mathbf{x}^*) = \{i \mid x_i^* > 0\}$$

Fixed points of CTLNs

$$\frac{dx_i}{dt} = 0 \text{ for all } i \in [n]$$

$$\begin{cases} \dfrac{dx_1}{dt} & = & -x_1 + \left[\sum_{j=1}^n W_{1j} x_j + \theta\right]_+ \\ \dfrac{dx_2}{dt} & = & -x_2 + \left[\sum_{j=1}^n W_{2j} x_j + \theta\right]_+ \\ & \vdots & \\ \dfrac{dx_n}{dt} & = & -x_n + \left[\sum_{j=1}^n W_{nj} x_j + \theta\right]_+ \end{cases}$$

Fixed points of CTLNs

$$\frac{dx_i}{dt} = 0 \text{ for all } i \in [n]$$

Different linear system of ODEs for each $\sigma \subseteq [n]$

$$\sigma = \{i \in [n] \mid y_i > 0\}$$

$$\begin{cases} \dfrac{dx_1}{dt} = -x_1 + \overbrace{\left[\sum_{j=1}^{n} W_{1j}x_j + \theta\right]}^{y_1}_+ \\ \dfrac{dx_2}{dt} = -x_2 + \underbrace{\left[\sum_{j=1}^{n} W_{2j}x_j + \theta\right]}_{y_2}{}_+ \\ \vdots \\ \dfrac{dx_n}{dt} = -x_n + \underbrace{\left[\sum_{j=1}^{n} W_{nj}x_j + \theta\right]}_{y_n}{}_+ \end{cases}$$

Fixed points of CTLNs

$$\frac{dx_i}{dt} = 0 \text{ for all } i \in [n]$$

Different linear system of ODEs for each $\sigma \subseteq [n]$

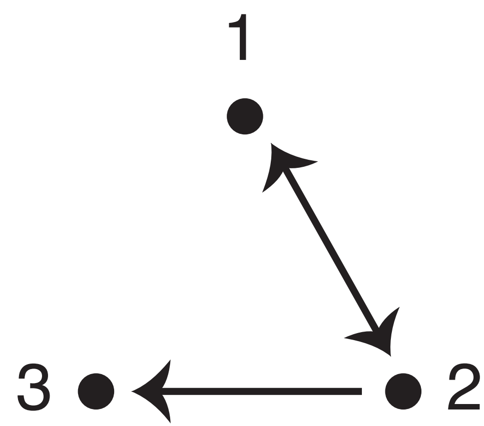
$$\sigma = \{i \in [n] \mid y_i > 0\}$$

$$\begin{cases} \dfrac{dx_1}{dt} &= -x_1 + \Big[\overbrace{\sum_{j=1}^n W_{1j}x_j + \theta}^{y_1}\Big]_+ \\ \dfrac{dx_2}{dt} &= -x_2 + \Big[\underbrace{\sum_{j=1}^n W_{2j}x_j + \theta}_{y_2}\Big]_+ \\ &\vdots \\ \dfrac{dx_n}{dt} &= -x_n + \Big[\underbrace{\sum_{j=1}^n W_{nj}x_j + \theta}_{y_n}\Big]_+ \end{cases}$$

Each linear system has a unique fixed point $\mathbf{x}^*$

This is a fixed point of the CTLN when $\begin{cases} x_i^* > 0 & \text{for all } i \in \sigma \\ y_k^* \leq 0 & \text{for all } k \notin \sigma \end{cases}$

Fixed points of example CTLN

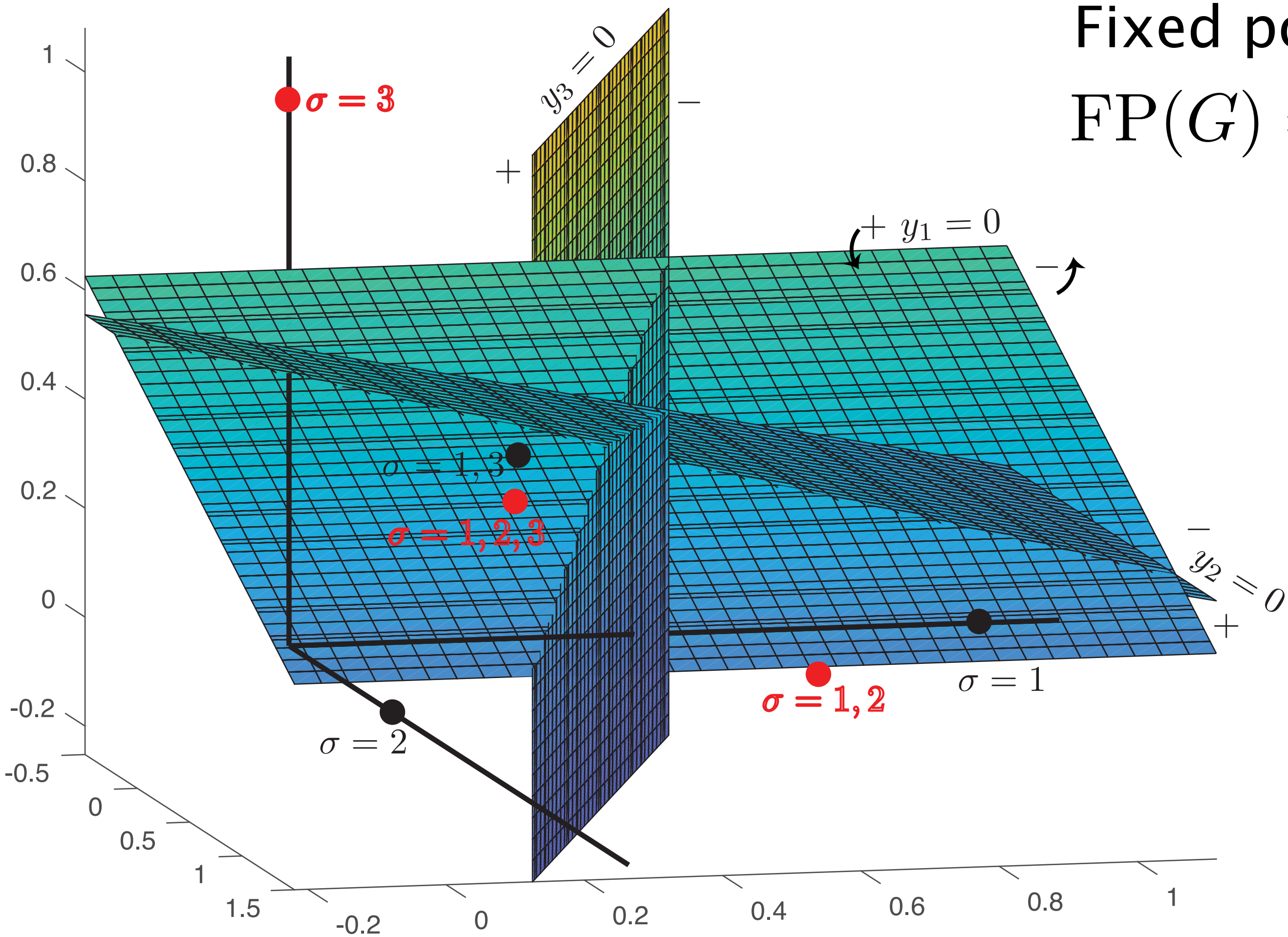


$$\frac{dx_1}{dt} = -x_1 + [\overbrace{(-1+\varepsilon)x_2 + (-1-\delta)x_3 + \theta}^{y_1}]_+$$

$$\frac{dx_2}{dt} = -x_2 + [\underbrace{(-1+\varepsilon)x_1 + (-1-\delta)x_3 + \theta}_{y_2}]_+$$

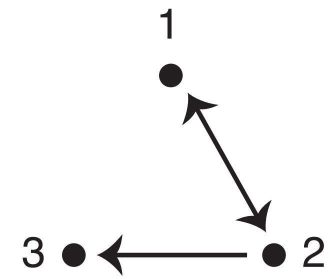
$$\frac{dx_3}{dt} = -x_3 + [\underbrace{(-1-\delta)x_1 + (-1+\varepsilon)x_2 + \theta}_{y_3}]_+$$

Fixed points of example CTLN



Fixed point supports:

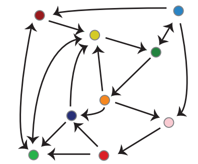
$$\mathrm{FP}(G) = \{3, 12, 123\}$$



Graph Rules

TECHNICAL RESULTS
for fixed points of TLNs

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



parity

Theorem 2.2 (parity [7])**.** *For any nondegenerate threshold-linear network* (W, b)*,*

$$\sum_{\sigma \in \mathrm{FP}(W,b)} \mathrm{idx}(\sigma) = +1.$$

$$\mathrm{idx}(\sigma) \stackrel{\text{def}}{=} \operatorname{sgn}\det(I - W_\sigma).$$

In particular, the total number of fixed points $|\,\mathrm{FP}(W,b)|$ *is always odd.*

Corollary 2.3. *The number of stable fixed points in a threshold-linear network of the form* (1.1) *is at most* 2^{n-1}*.*

sign conditions

Theorem 2.6. *Let* (W, b) *be a (non-degenerate) threshold-linear network with* $W_{ij} \leq 0$ *and* $b_i > 0$ *for all* $i, j \in [n]$*. For any nonempty* $\sigma \subseteq [n]$*,*

$$\sigma \in \mathrm{FP}(W,b) \quad \Leftrightarrow \quad \operatorname{sgn} s_i^\sigma = \operatorname{sgn} s_j^\sigma = -\operatorname{sgn} s_k^\sigma \text{ for all } i, j \in \sigma,\ k \notin \sigma.$$

$$s_i^\sigma \stackrel{\text{def}}{=} \det((I - W_{\sigma\cup\{i\}})_i; b_{\sigma\cup\{i\}})$$

Moreover, if $\sigma \in \mathrm{FP}(W,b)$ *then* $\operatorname{sgn} s_i^\sigma = \operatorname{sgn}\det(I - W_\sigma) = \mathrm{idx}(\sigma)$ *for all* $i \in \sigma$*.*

domination

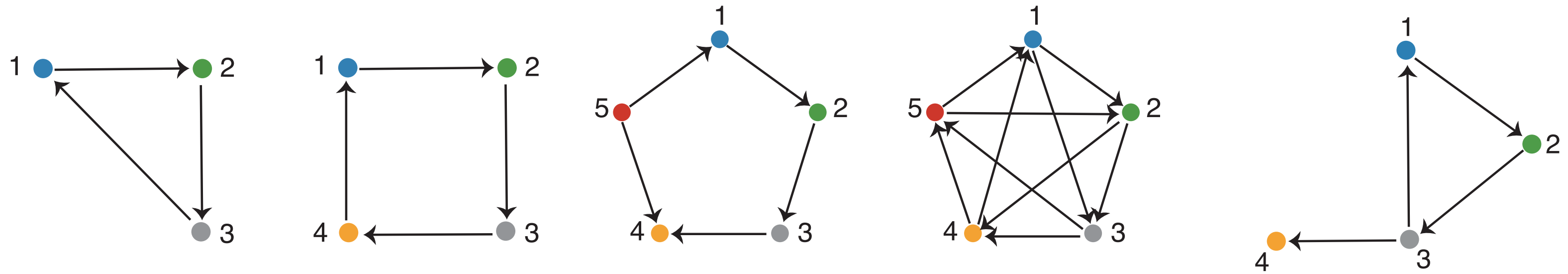
Theorem 2.11. *Let* (W, θ) *be a threshold-linear network. Then* $\sigma \in \mathrm{FP}(W, \theta)$ *if and only if the following two conditions hold:*

(i) σ *is domination-free, and*

(ii) for each $k \notin \sigma$ *there exists* $j \in \sigma$ *such that* $j >_\sigma k$*.*

Uniform in-degree fixed points

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



Uniform in-degree fixed points

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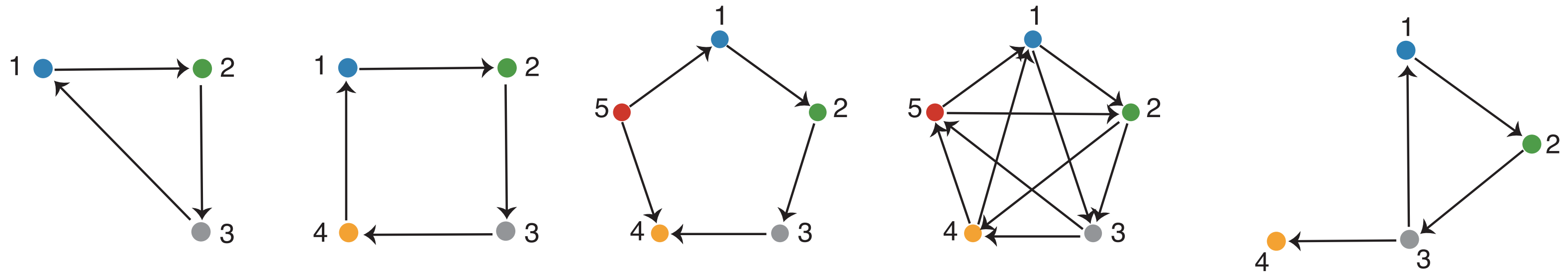

- If a subgraph is a fixed point support, this fixed point may or may not survive to the full graph!

Uniform in-degree fixed points

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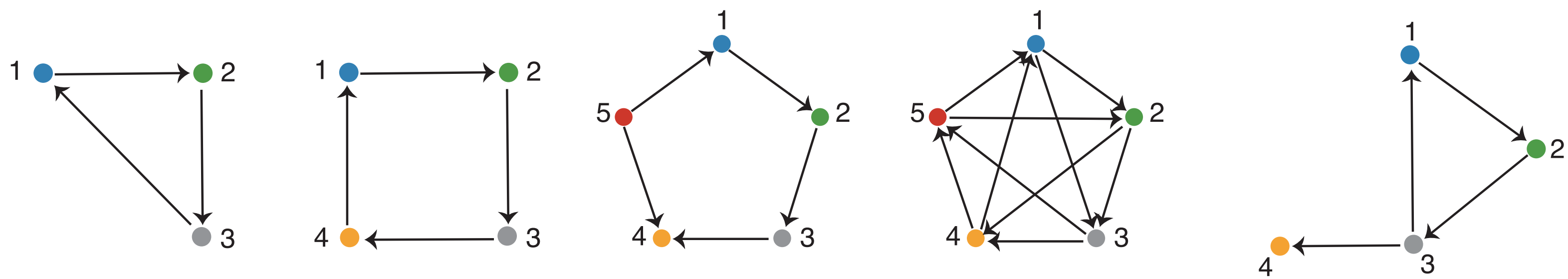


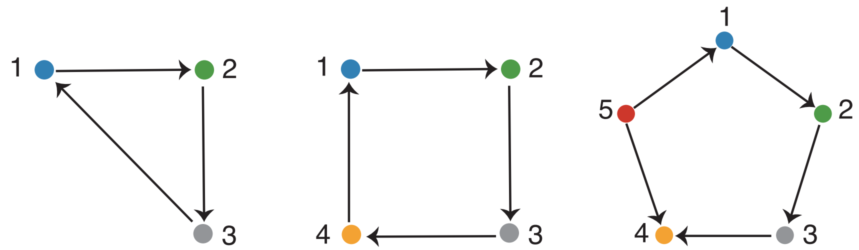
- If a subgraph is a fixed point support, this fixed point may or may not survive to the full graph!

Thm. G has uniform in-degree d.

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

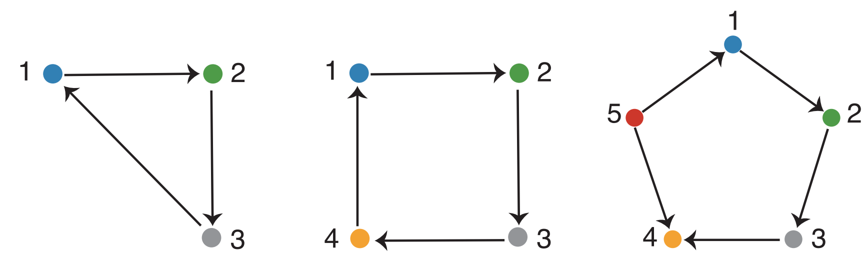
Uniform in-degree fixed points

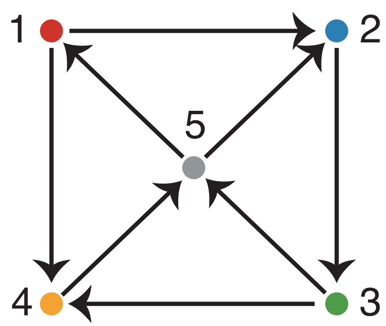
<u>Corollary:</u> Cycles (of any length) support fixed points if and only if there is no external node receiving 2 or more edges from the cycle.



Uniform in-degree fixed points

Corollary: Cycles (of any length) support fixed points if and only if there is no external node receiving 2 or more edges from the cycle.





3-cycles
235, 145

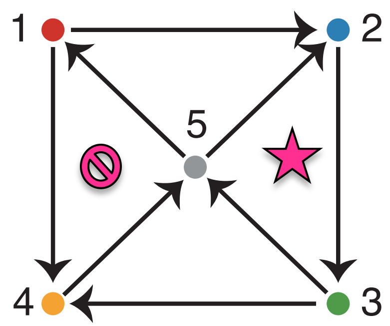
3-cycle fixed pts
235 only

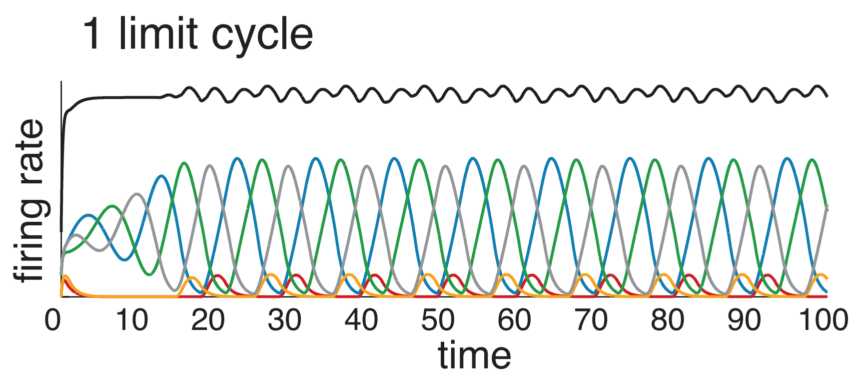
cycle 145 has an external node (2) receiving 2 edges

cycle 235 does not

Solution to Math Puzzle #1

Which 3-cycles of the graph give rise to limit cycles in the dynamics?

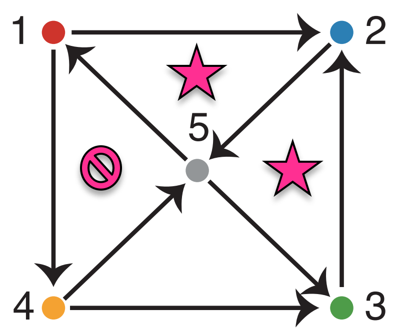


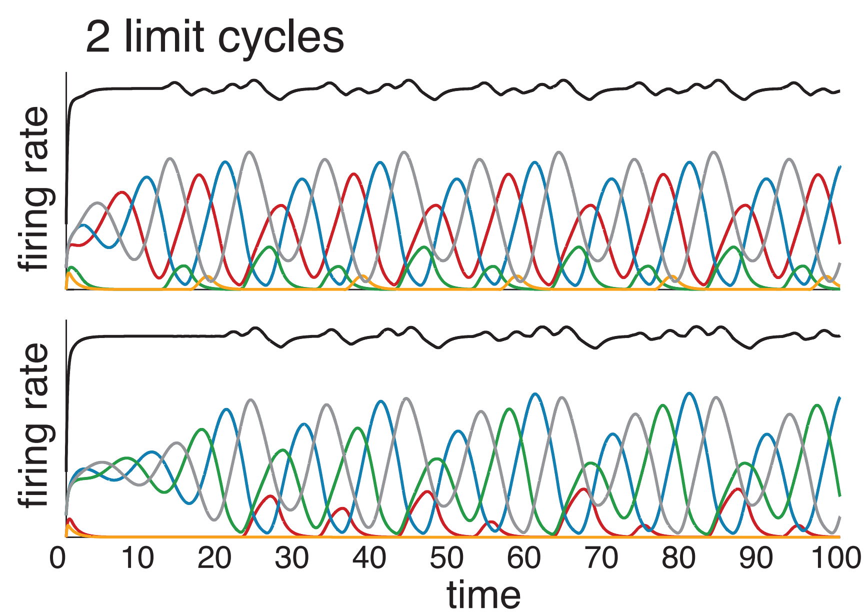


3-cycles
235, 145

limit cycles
235 only

3-cycle fixed pts
235 only





3-cycles
125, 253, 145

limit cycles
125, 253 only

3-cycle fixed pts
125, 253 only

A general principle: domination

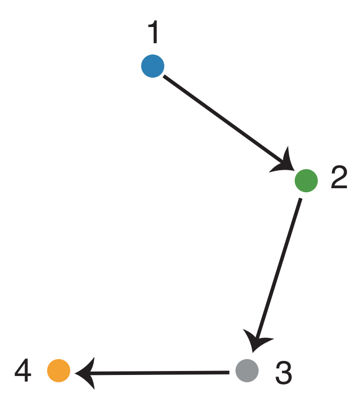
simplest version: $j, k \in \sigma$

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

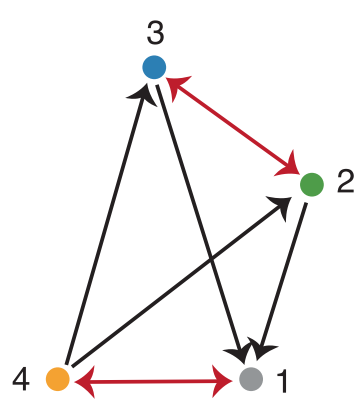
1. $j \to k, k \not\to j$

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

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



2 dominates 1



1 dominates 2 and 3

A general principle: domination

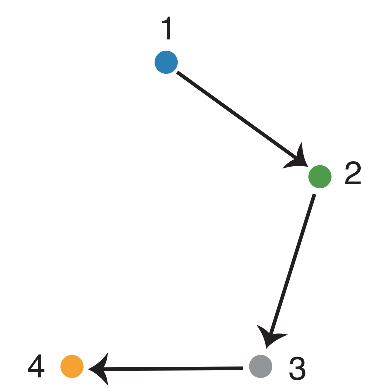
<u>Fact:</u> If there is domination inside σ then σ cannot be a fixed pt support.

A general principle: domination

Fact: If there is domination inside σ then σ cannot be a fixed pt support.

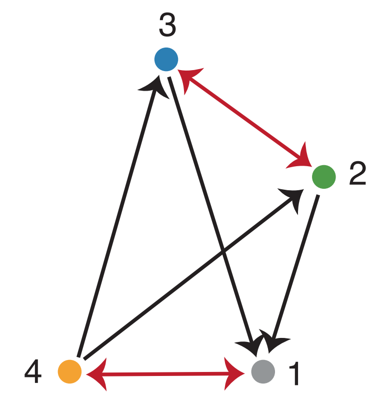
Some consequences:

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



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

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



Graph rules for CTLN fixed point supports

1. *Uniform in-degree.*

   For σ uniform in-degree, $\sigma \in \mathrm{FP}(G) \Leftrightarrow \sigma$ is target-free.
   If σ is a target-free clique, then σ supports a stable fixed point.

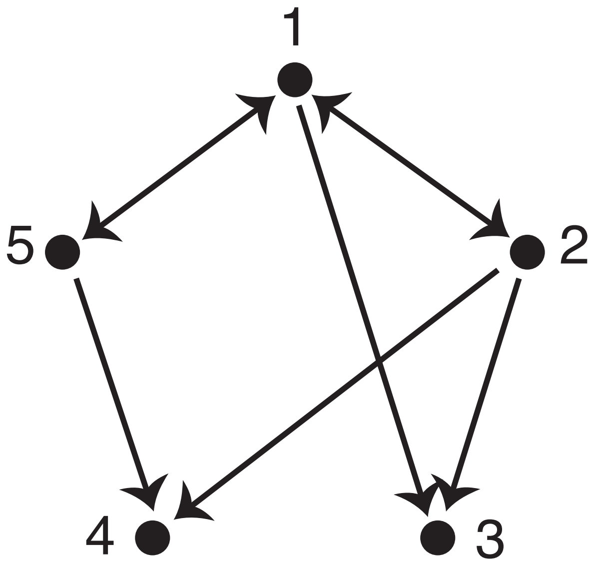
2. *Domination.* Suppose k dominates j w.r.t. σ
   (a) If $j, k \in \sigma$, then $\sigma \notin \mathrm{FP}(G)$.
   (b) If $j \in \sigma$ and $k \notin \sigma$, then $\sigma \notin \mathrm{FP}(G)$.
   (c) If $j \notin \sigma$ and $k \in \sigma$, then $\sigma \in \mathrm{FP}(G|_{\sigma \cup \{j\}}) \Leftrightarrow \sigma \in \mathrm{FP}(G|_\sigma)$.

3. *Sources.*
   (a) If $i \in \sigma$ is a proper source in $G|_\sigma$, then $\sigma \notin \mathrm{FP}(G)$.
   (b) If i is a proper source in G, then $\mathrm{FP}(G) = \mathrm{FP}(G \setminus \{i\})$.

4. *Sinks.*
   (a) A singleton $\{i\} \in \mathrm{FP}(G) \Leftrightarrow i$ is a sink in G.
   (b) An independent set $\sigma \in \mathrm{FP}(G) \Leftrightarrow \sigma$ is a union of sinks.

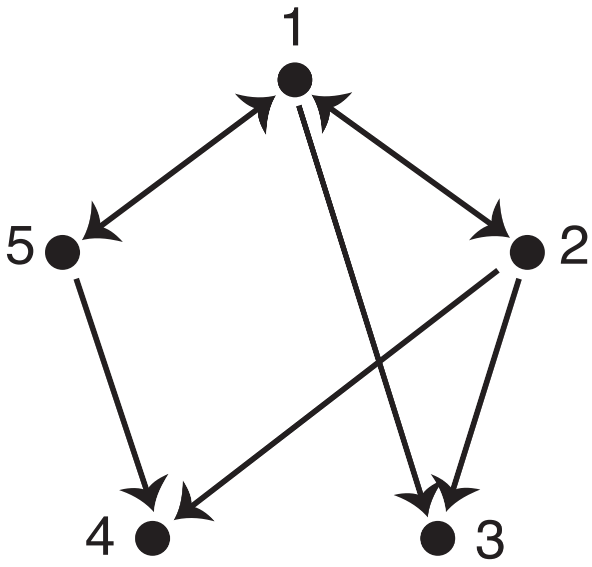
5. *Parity.* $|\mathrm{FP}(G)|$ is odd.

Finding FP(G) using graph rules



Elements of FP(G)

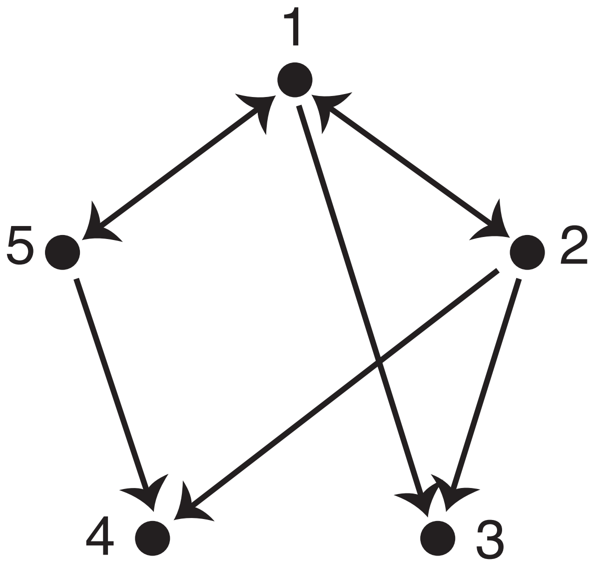
Finding FP(G) using graph rules



Elements of FP(G)

$\underline{|\sigma| = 1}: \quad 3,\ 4$

Finding FP(G) using graph rules

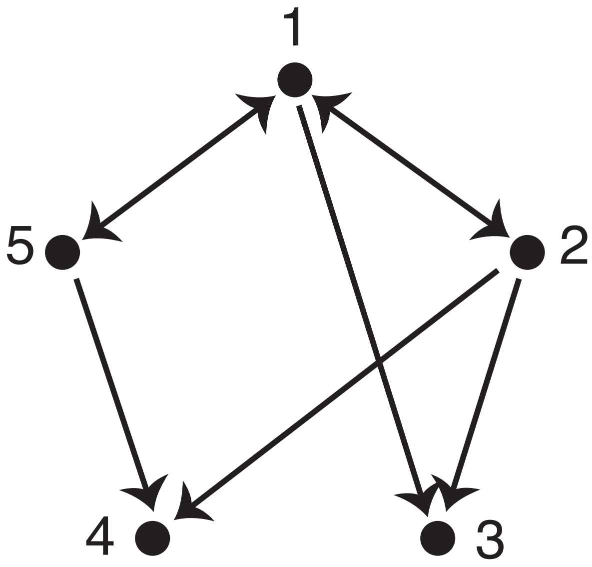


Elements of FP(G)

$\underline{|\sigma| = 1}$: $3,\ 4$

$\underline{|\sigma| = 2}$: $15,\ 34$

Finding FP(G) using graph rules



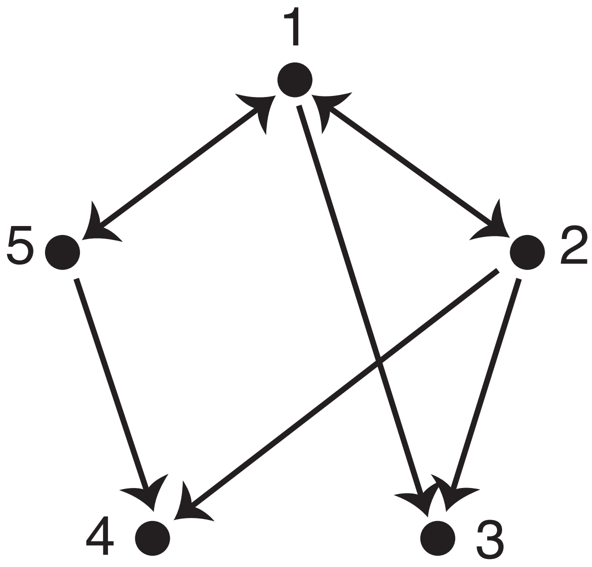
Elements of FP(G)

$\underline{|\sigma| = 1}:\quad 3,\ 4$

$\underline{|\sigma| = 2}:\quad 15,\ 34$

$\underline{|\sigma| = 3}:\quad 135,\ 145$

Finding FP(G) using graph rules



Elements of FP(G)

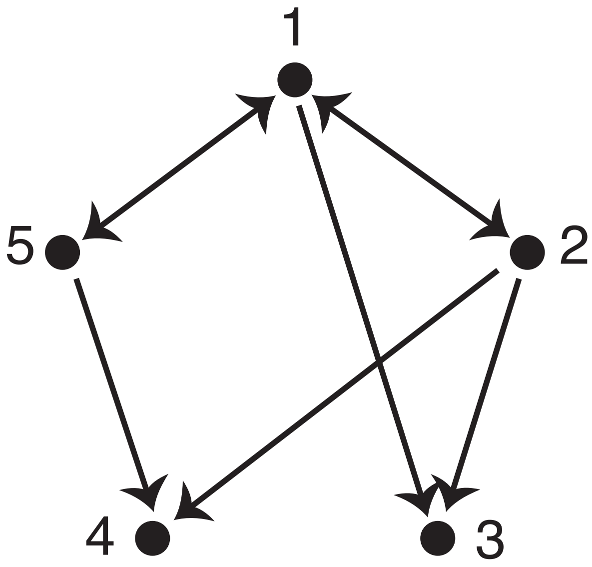
$\underline{|\sigma| = 1}:\quad 3,\ 4$

$\underline{|\sigma| = 2}:\quad 15,\ 34$

$\underline{|\sigma| = 3}:\quad 135,\ 145$

$\underline{|\sigma| = 4}:\quad 1345$

Finding FP(G) using graph rules



Elements of FP(G)

$\underline{|\sigma| = 1}:\quad 3,\ 4$

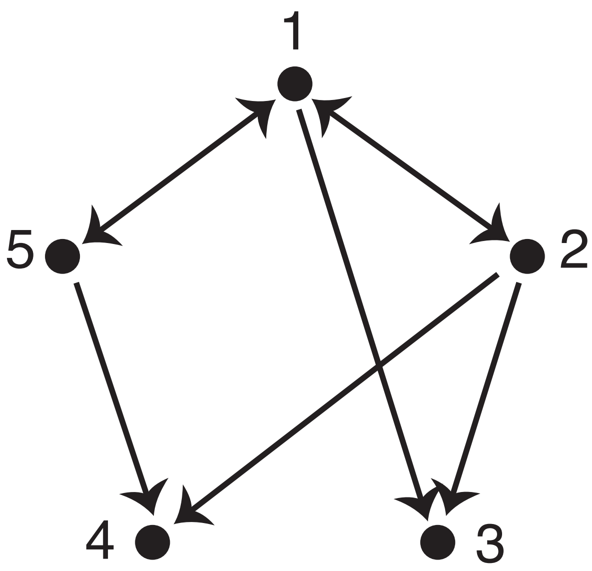
$\underline{|\sigma| = 2}:\quad 15,\ 34$

$\underline{|\sigma| = 3}:\quad 135,\ 145$

$\underline{|\sigma| = 4}:\quad 1345$

$\underline{|\sigma| = 5}:\quad \text{none}$

Finding FP(G) using graph rules



Elements of FP(G)

$\underline{|\sigma| = 1}:\quad 3,\ 4$

$\underline{|\sigma| = 2}:\quad 15,\ 34$

$\underline{|\sigma| = 3}:\quad 135,\ 145$

$\underline{|\sigma| = 4}:\quad 1345$

$\underline{|\sigma| = 5}:\quad \text{none}$

$$\mathrm{FP(G)} = \{3, 4, 15, 34, 135, 145, 1345\}$$

Because FP(G) was obtained from graph rules, this result is guaranteed to be parameter independent.

Lessons learned from graph rules

- We found specific motifs that support fixed points:

  cycles, uniform in-degree, cliques, independent sets, etc.

  and we also understand their survival rules, depending on how they are embedded in a larger network.

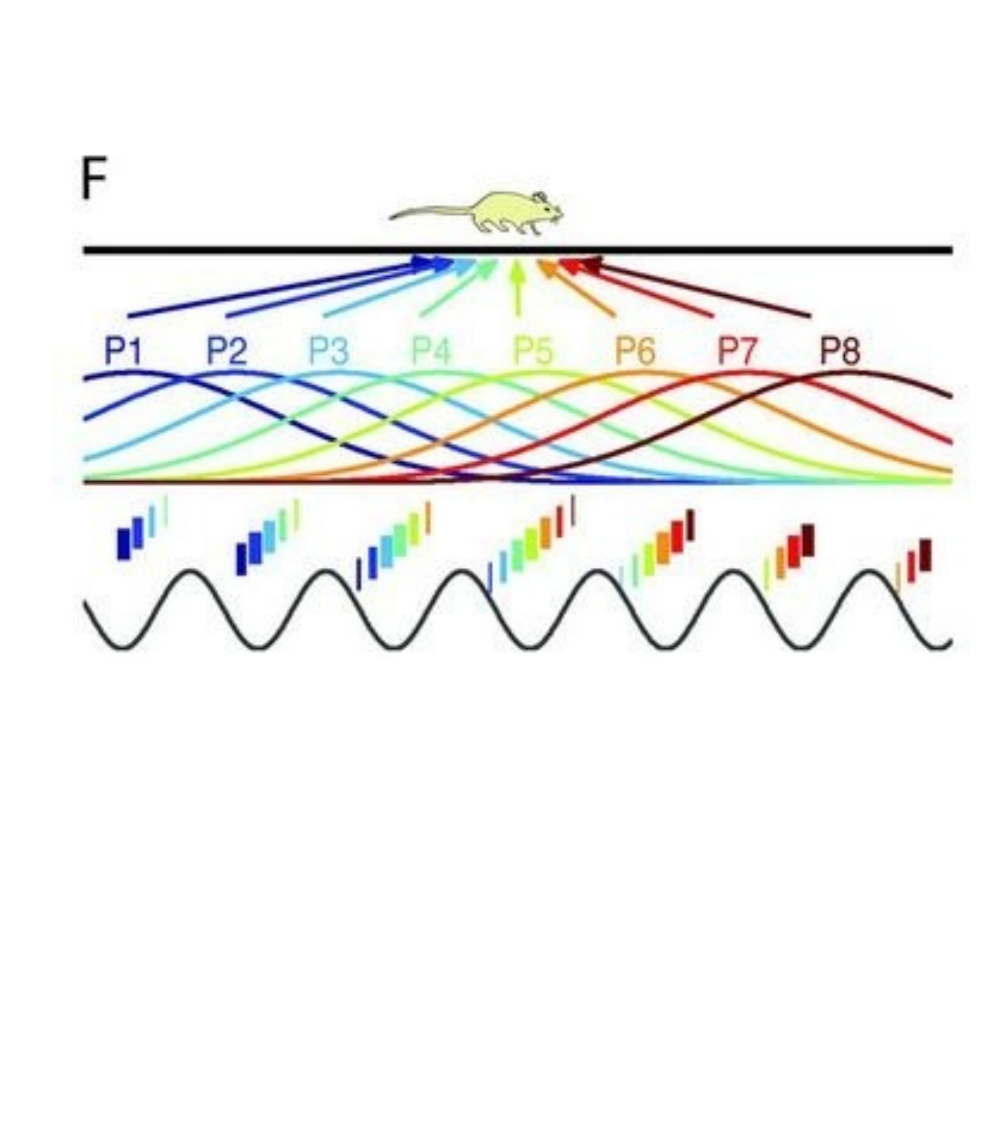
- Motifs supporting fixed points (and attractors) are domination-free.

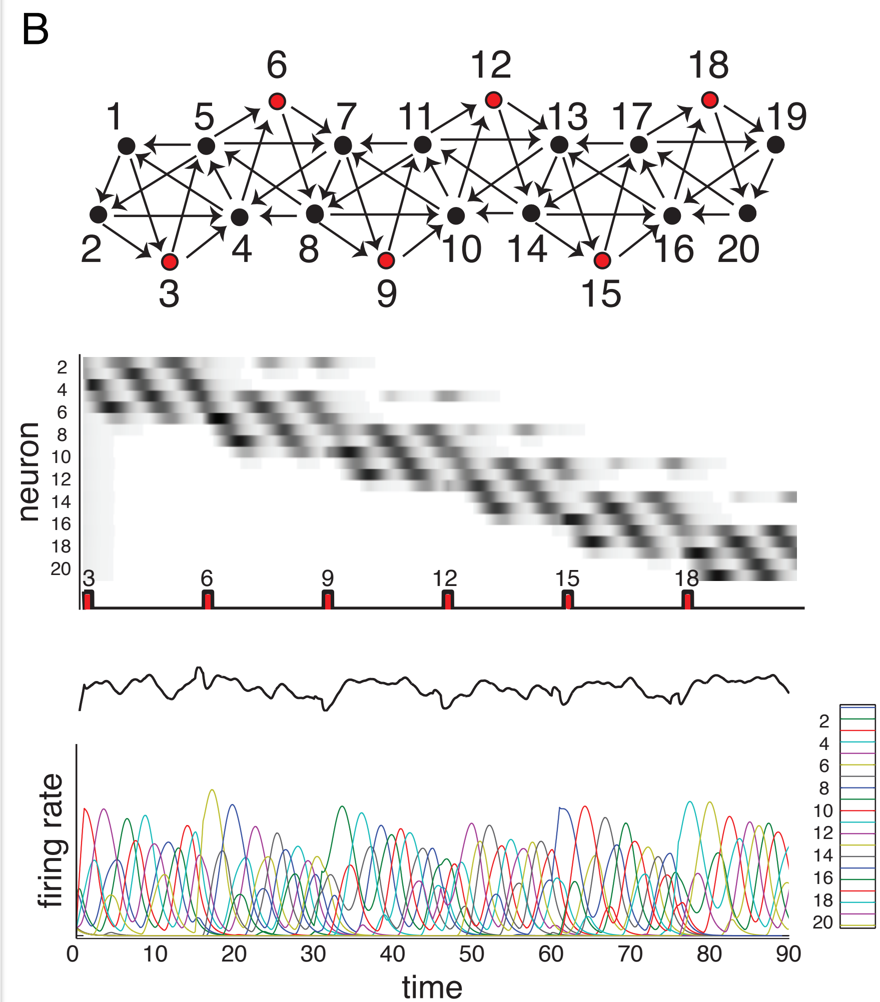
- Insights about how edges affect attractors for different motifs:
  -- edges out of a motif affect survival
  -- edges into a motif affect only the basins of attraction
  -- adding edges inside a motif may or may not preserve attractors

- Everything we've proven using graph rules is automatically parameter-independent. Connectivity is the only thing that matters.

Applications

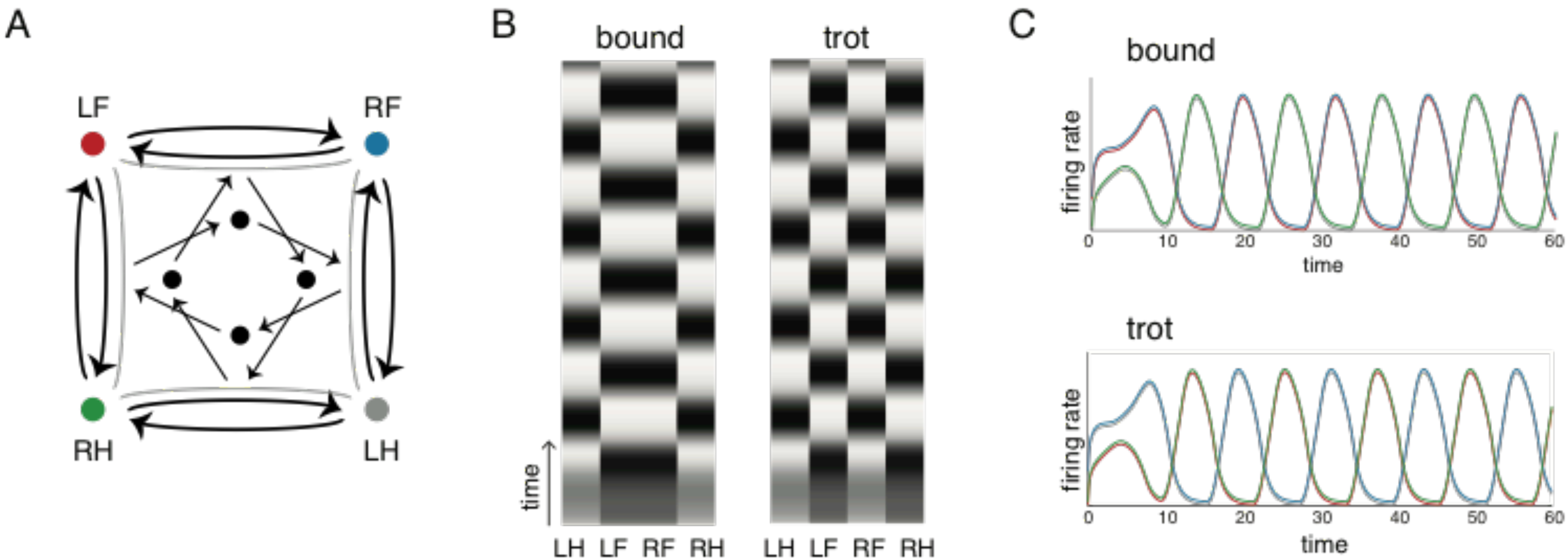
Patching together cyclic modules



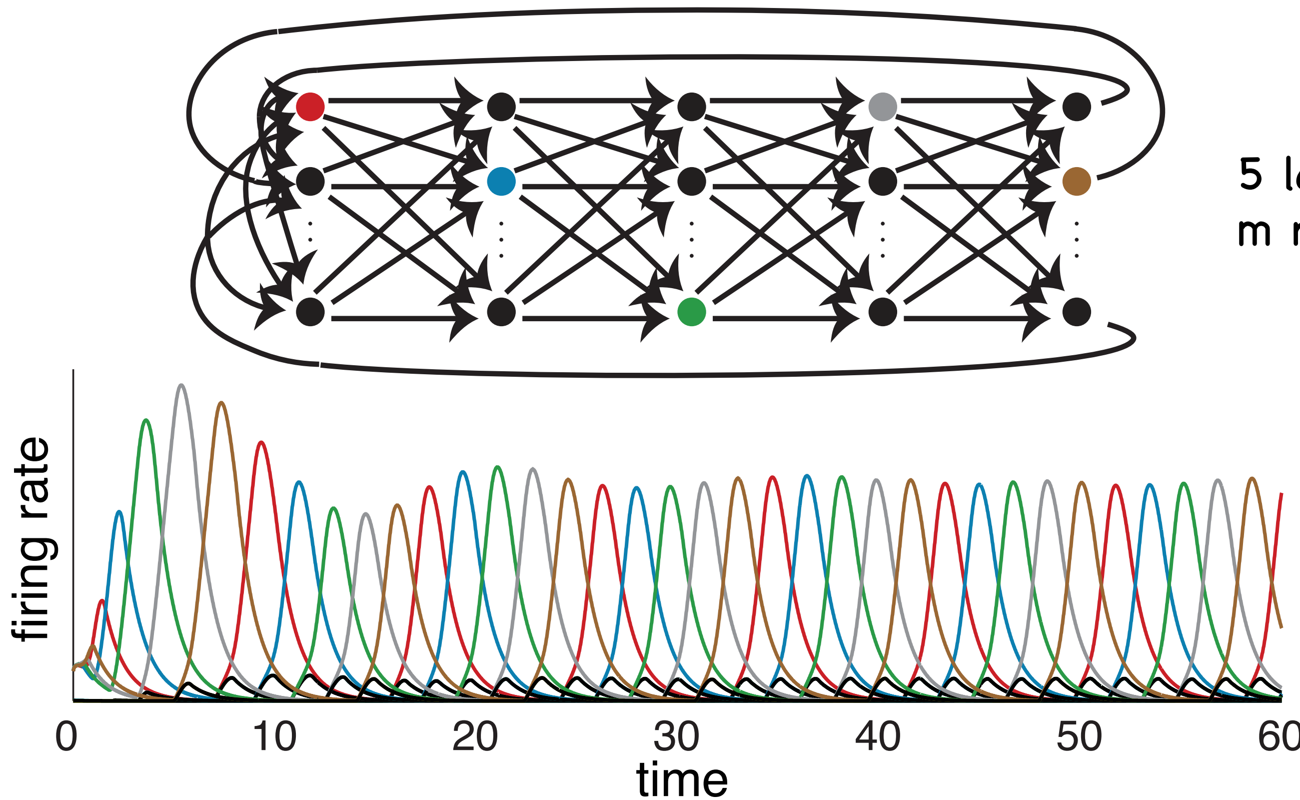


Central Pattern Generator (CPG)

quadruped motion



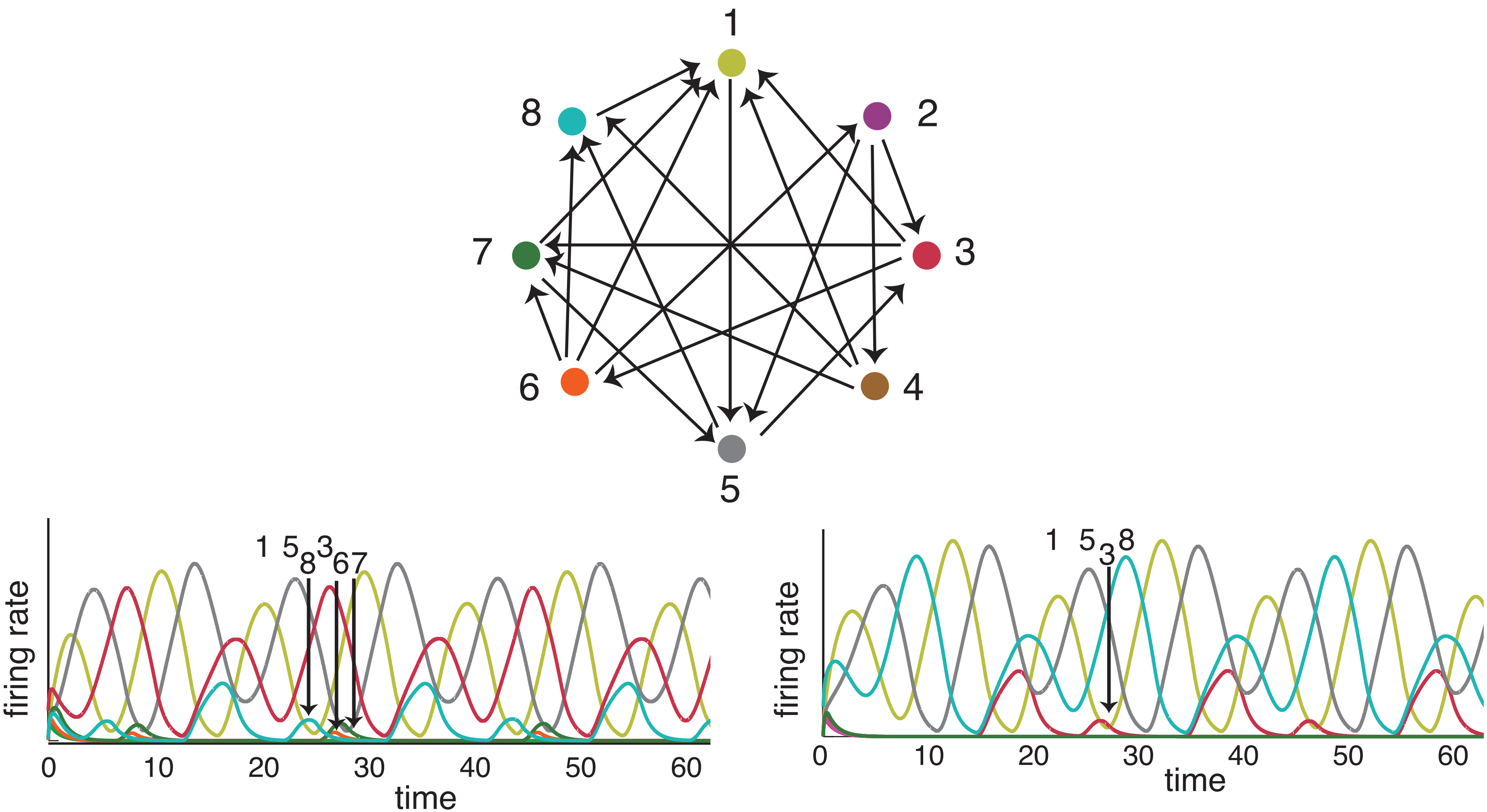
phone number network



5 layers
m neurons/layer

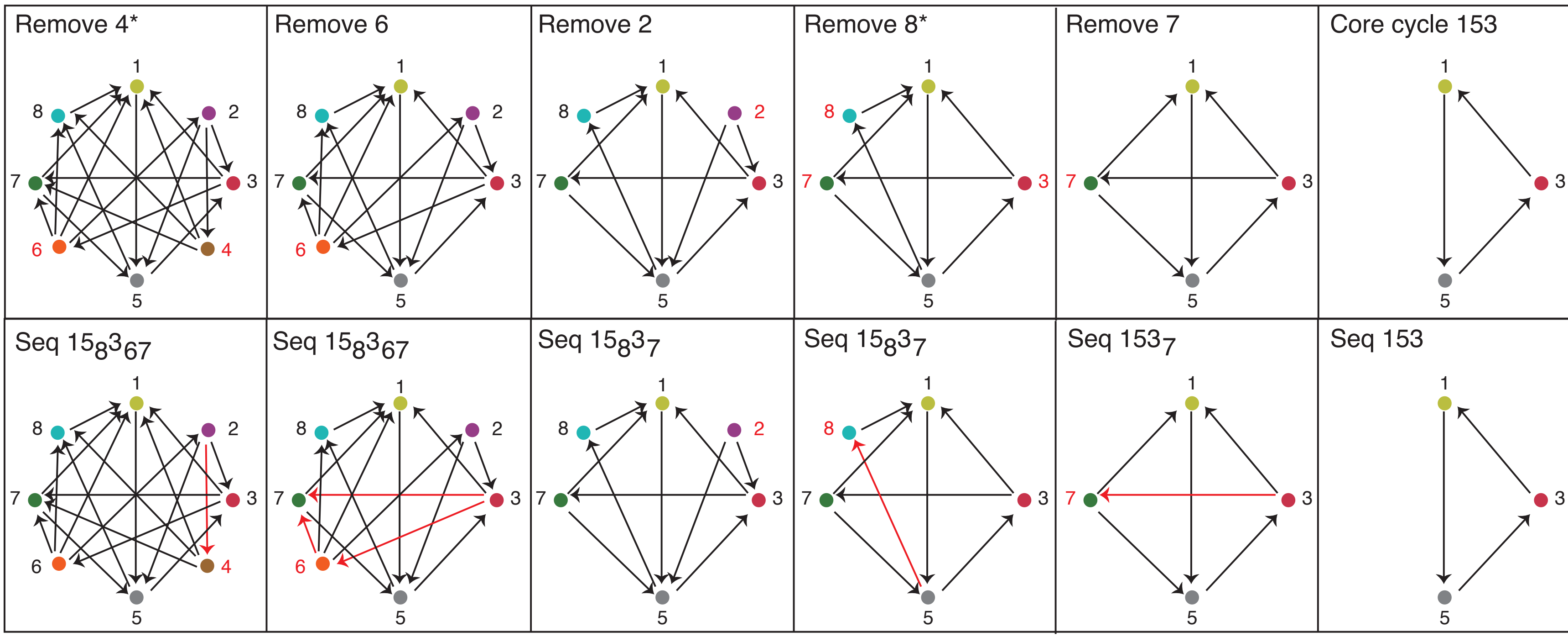
This network has m^5 limit cycles, like the one above.

Predicting sequences from graph structure



Predicting sequences from graph structure

Decompose graph →



Predicted Sequence: $15_{8}\,3_{67}$

← Reconstruct sequence

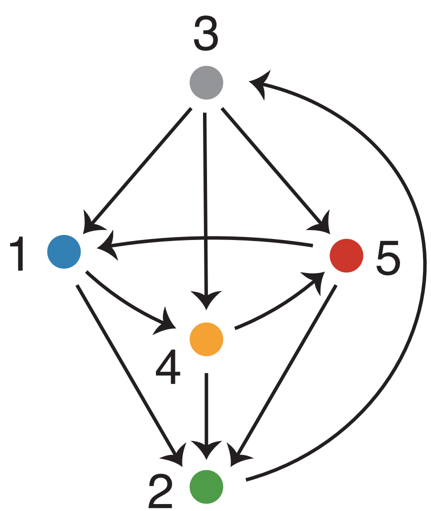
* indicates choice for nodes. The first choice between nodes 4 & 6 does <u>not</u> affect the sequence. The second choice between 3, 7 & 8 would have resulted in the other observed sequence $15_{3}8$.

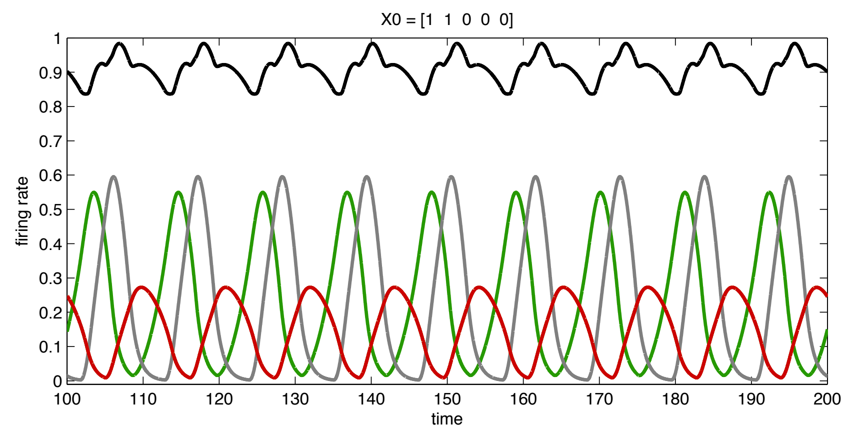
Algorithm prediction results

Complete analysis of attractors of the 160 non-isomorphic graphs on $n \leq 5$ neurons that are oriented with no sinks.

Algorithm correctly predicts the set of sequences of attractors for 156 of the 160 graphs.

Algorithm failure: unexpected synchrony - neurons 1,4,5 fire synchronously





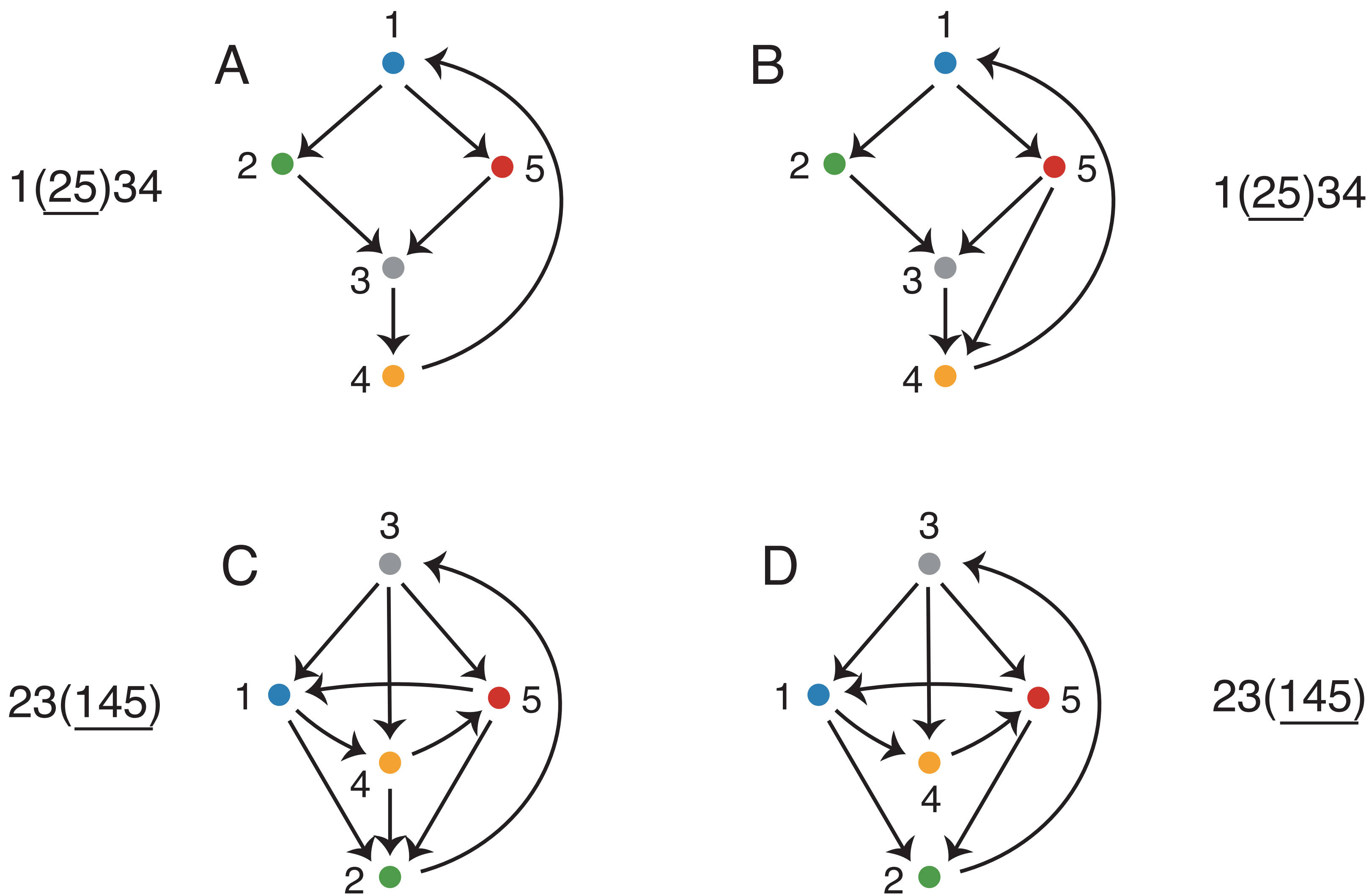
Algorithm output:

$123 \rightarrow 1_5 2 3_4$

$234 \rightarrow 2 3_5 4_1$

$154 \rightarrow 1_2 5 4$

Algorithm failures and graph automorphisms



References

CTLN project website

http://sites.psu.edu/mathneurolab/ctln/

Fixed points of threshold-linear networks
Carina Curto, Jesse Geneson, Katherine Morrison

contains proofs!

Predicting neural network dynamics via graphical analysis
Katherine Morrison and Carina Curto

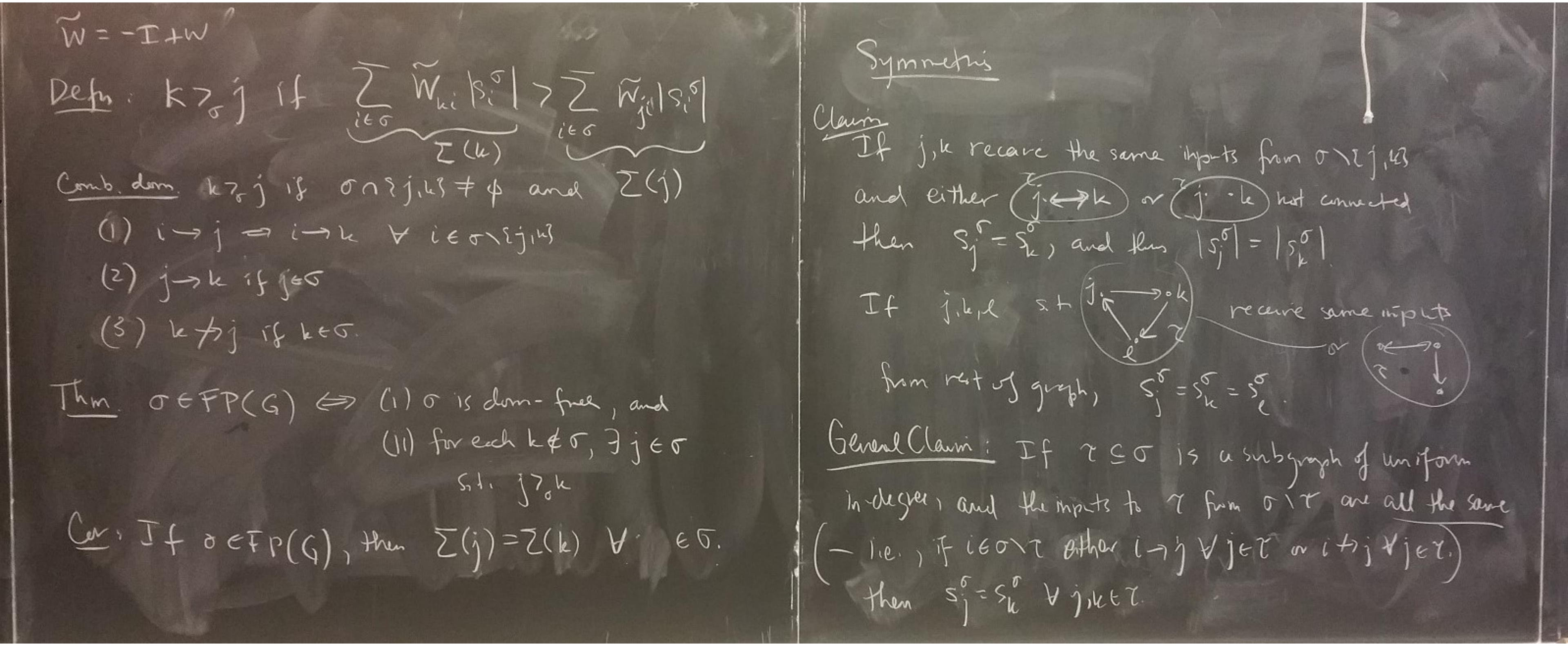
book chapter/ primer

Diversity of emergent dynamics in competitive threshold-linear networks: a preliminary report Katherine Morrison[1,2], Anda Degeratu[3], Vladimir Itskov[1] & Carina Curto[1]

In Prep

Predicting emergent sequences from network connectivity
Katherine Morrison, Caitlyn Parmelee, Samantha Moore, Carina Curto

Thanks!



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David Rolnick (MIT)

National Institutes of Health

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A competitive network theory of species diversity

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

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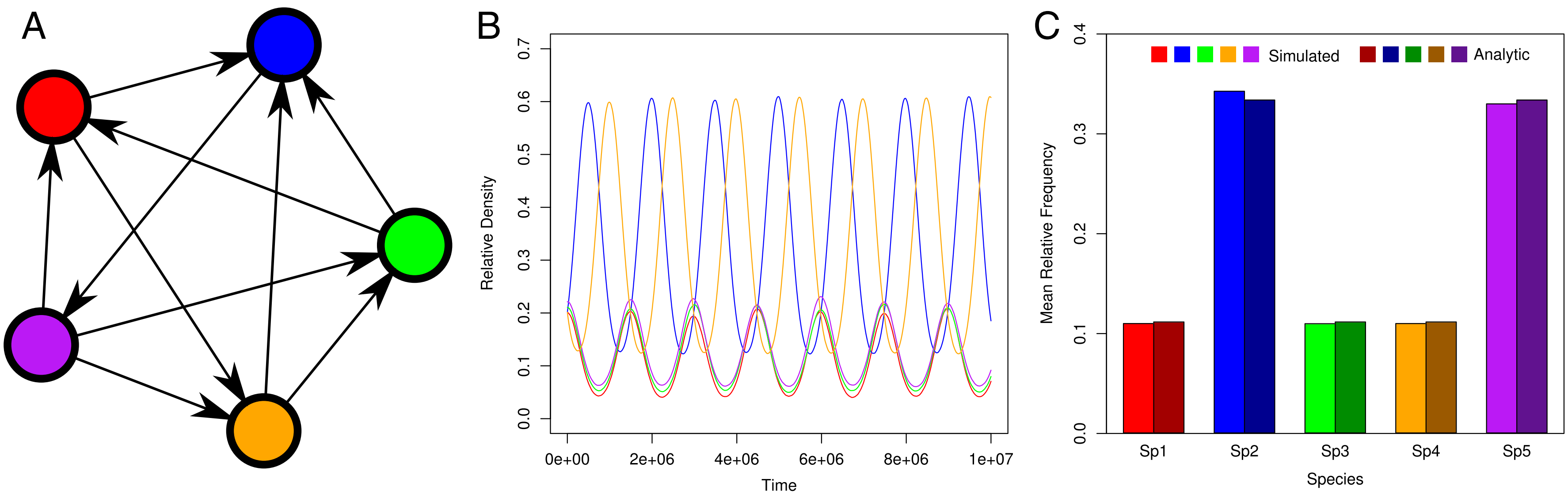


Fig. 1. (*A*) Species' competitive abilities can be represented in a tournament in which we draw an arrow from the inferior to the superior competitor for all species pairs. A tournament is a directed graph composed by n nodes (the species) connected by $n(n-1)/2$ edges (arrows). (*B*) Simulations of 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

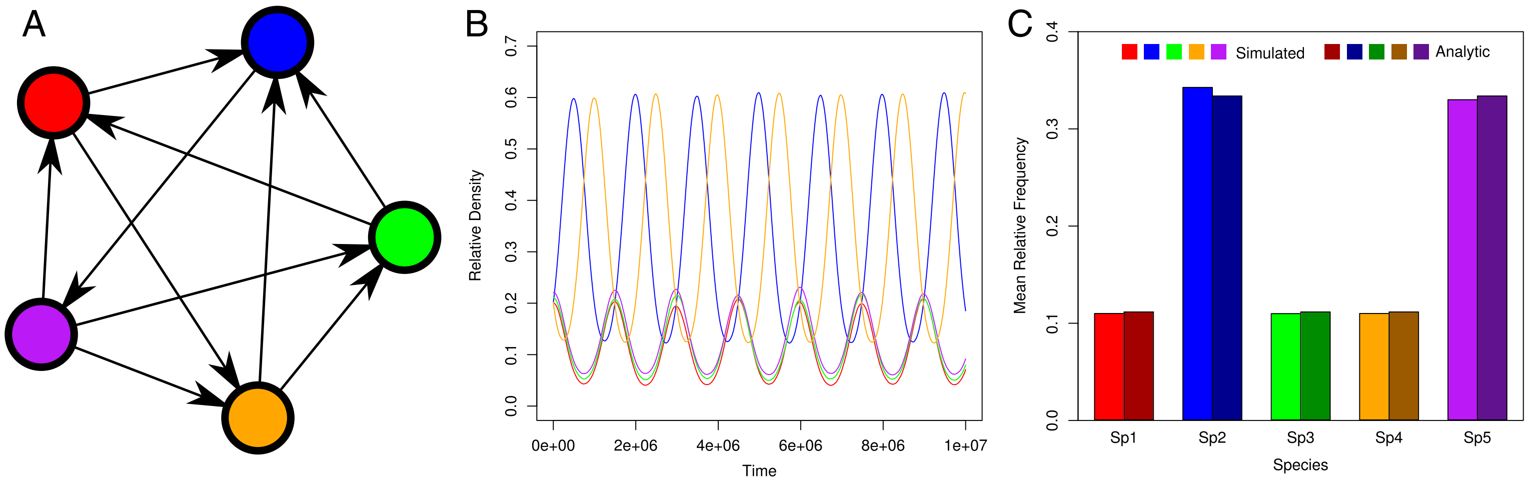
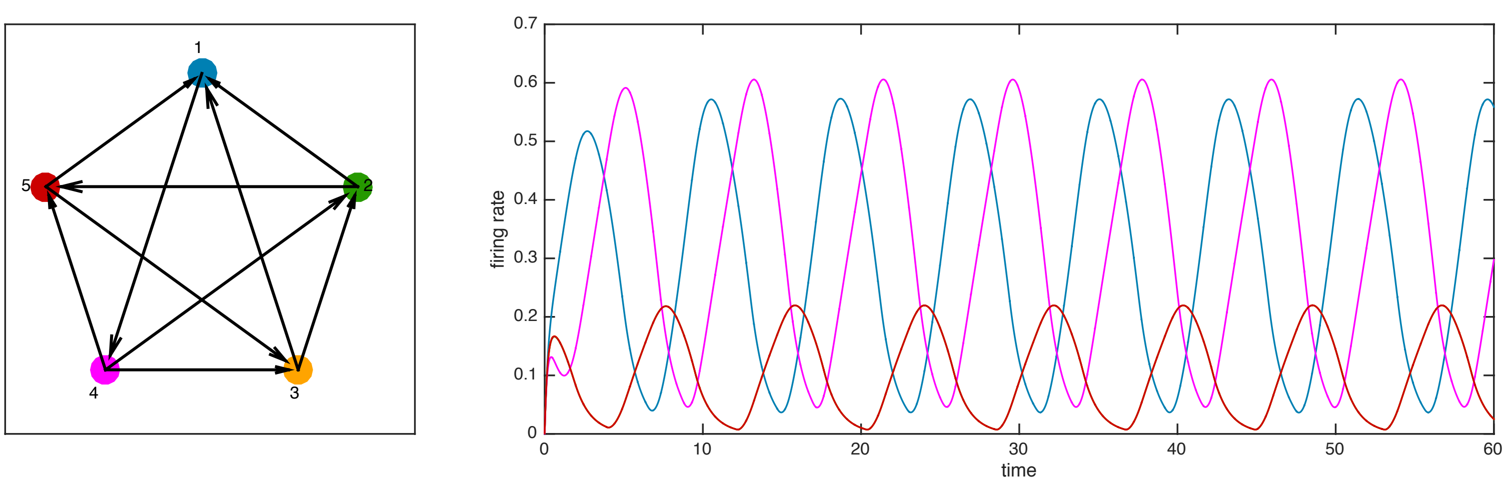


Fig. 1. (*A*) Species' competitive abilities can be represented in a tournament in which we draw an arrow from the inferior to the superior competitor for all species pairs. A tournament is a directed graph composed by n nodes (the species) connected by $n(n-1)/2$ edges (arrows). (*B*) Simulations of 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).

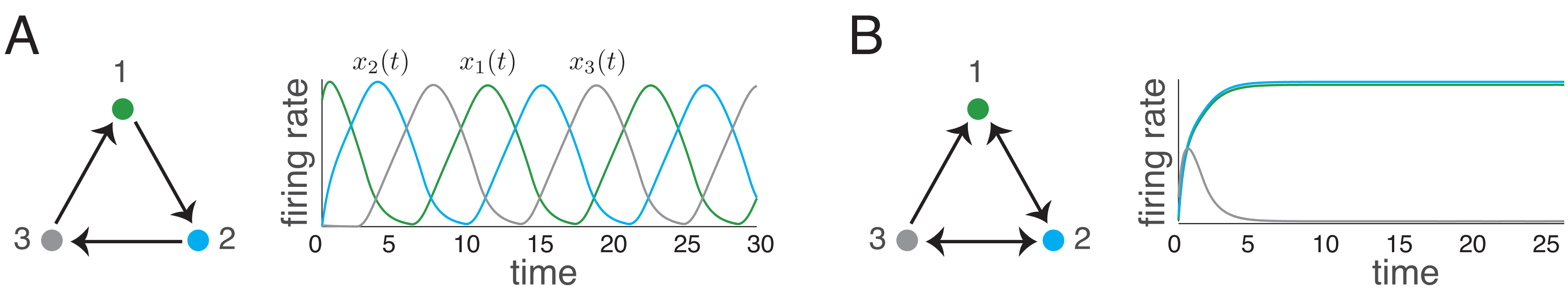
The CTLN model



Early facts about stable fixed points

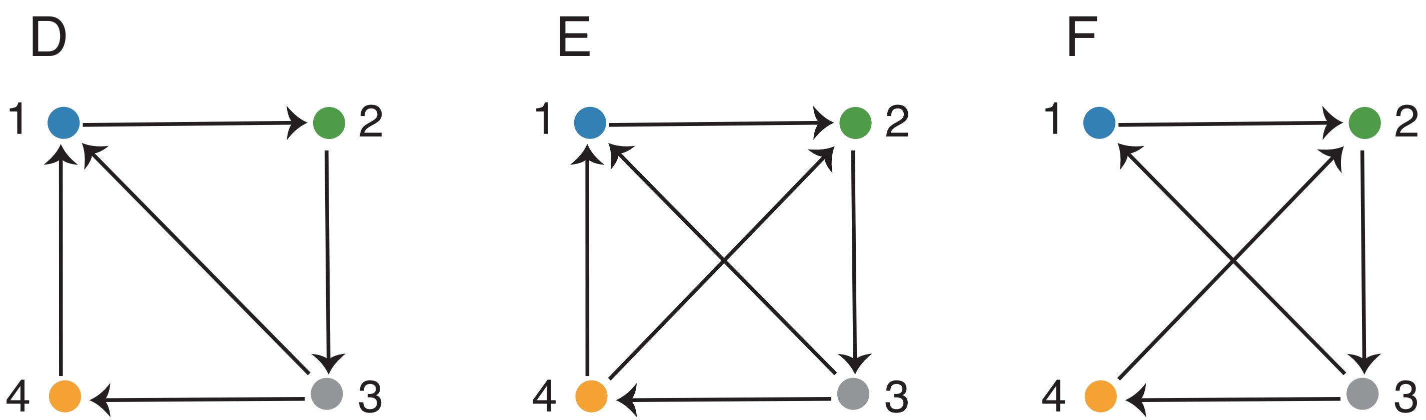
<u>Thm 1</u>. If G is an oriented graph with no sinks, then the network has no stable fixed points (but bounded activity).

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



Some things we learned…

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

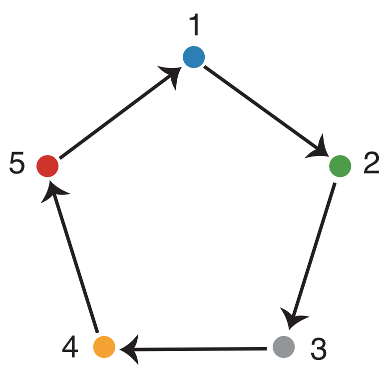


234 does not have a fixed point – nor a corresponding limit cycle!

Recurrent vs. feedforward architecture

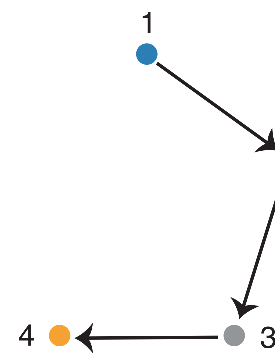
Recurrent motifs (attractors)

cycle

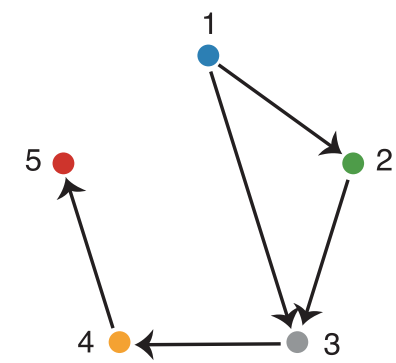


Feedforward motifs (FF flow of information)

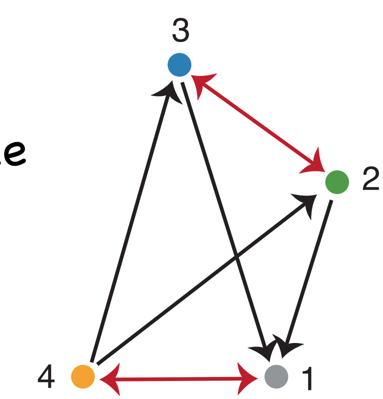
path



FF graph



directed clique goes here?



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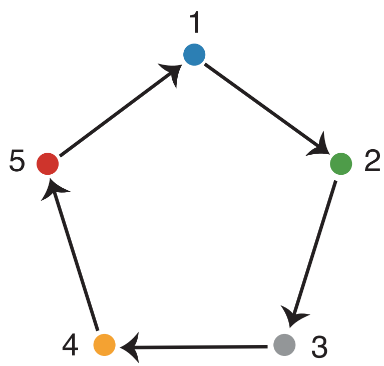
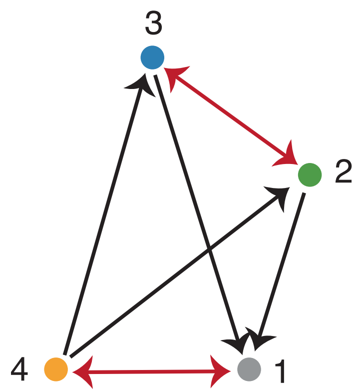


directed clique

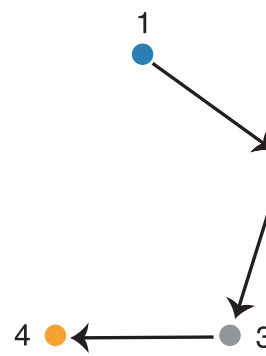


<u>directed clique</u>: there exists an ordering on the nodes such that

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

Feedforward motifs (FF flow of information)

path



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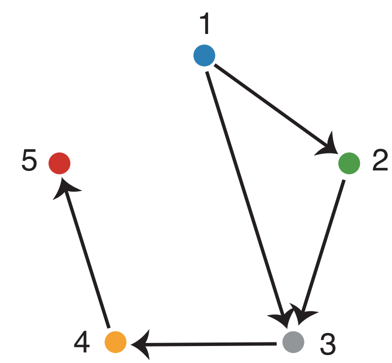

<u>feedforward graph</u>: there exists an ordering on the nodes such that

$$i \not\to j \text{ if } i > j$$

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

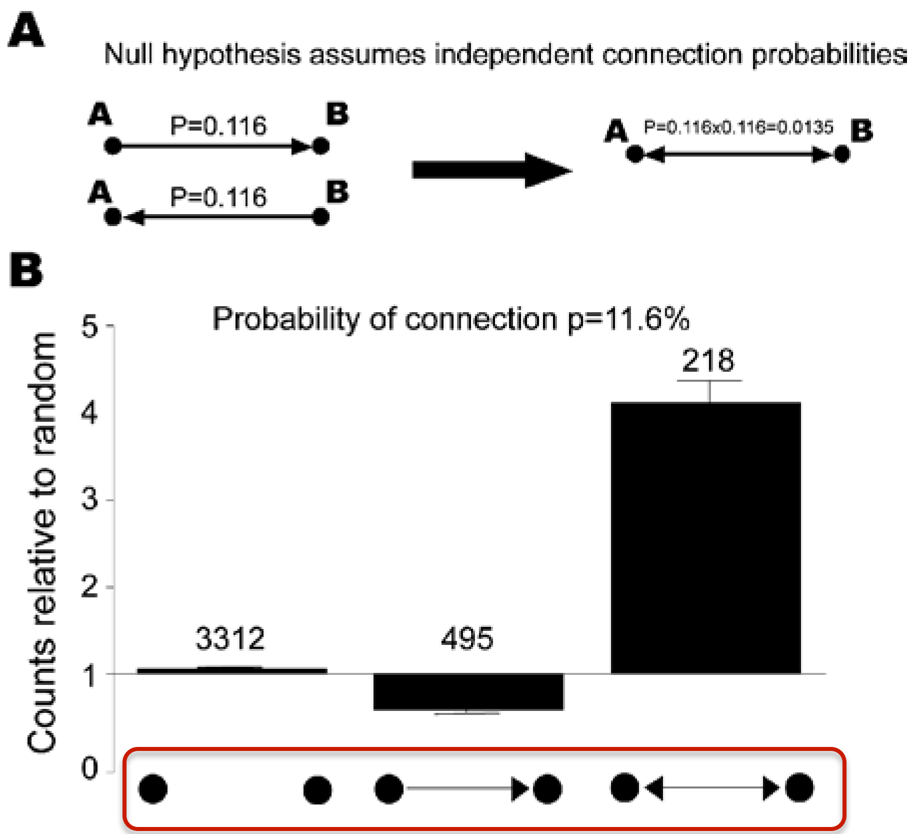

Figure 2. Two-Neuron Connectivity Patterns Are Nonrandom

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2005

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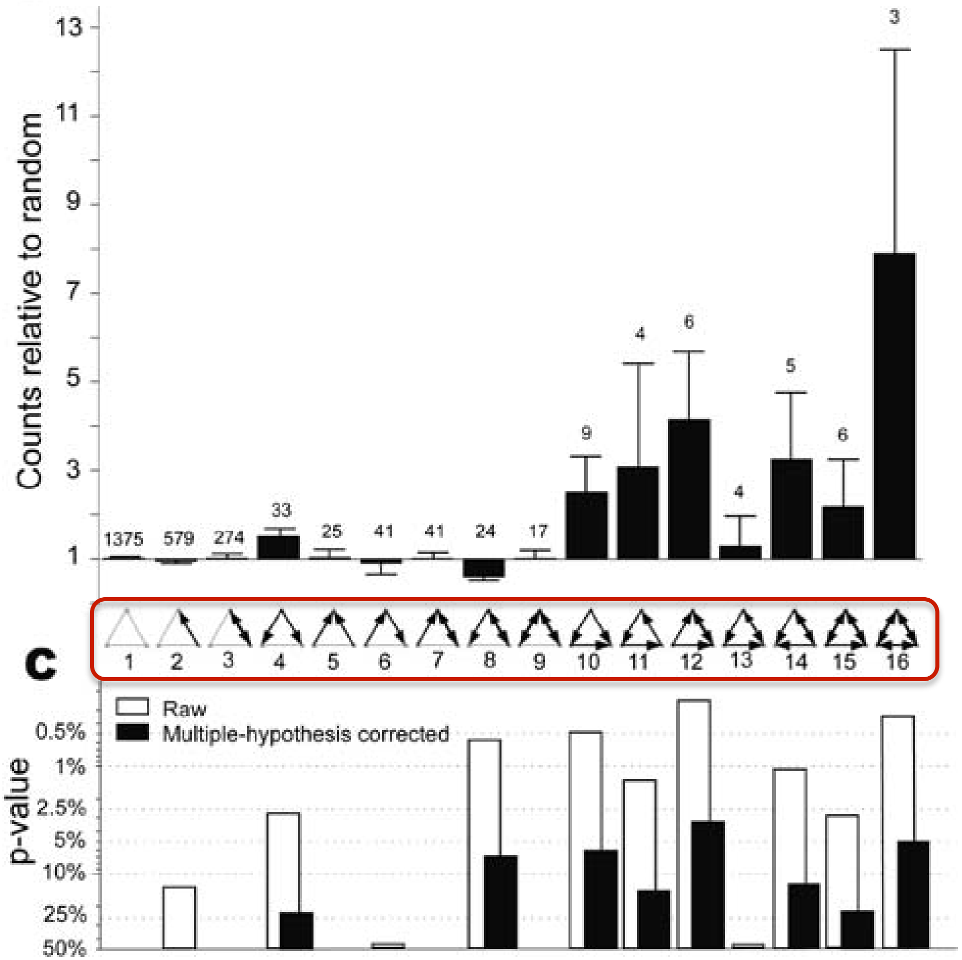

Figure 4. Several Three-Neuron Patterns Are Overrepresented as Compared to the Random Network

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

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

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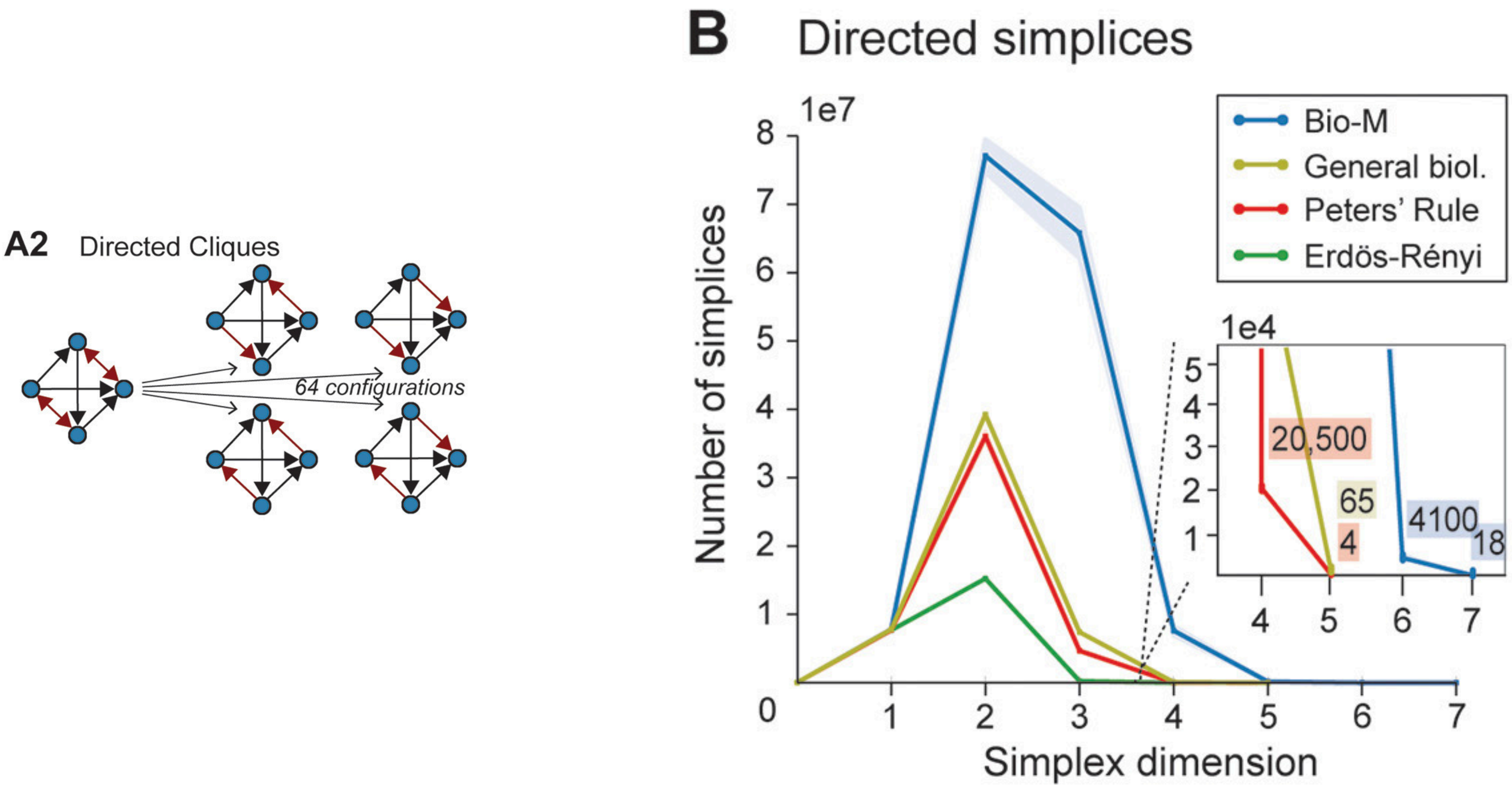

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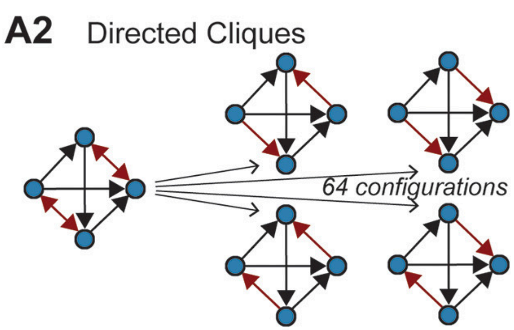
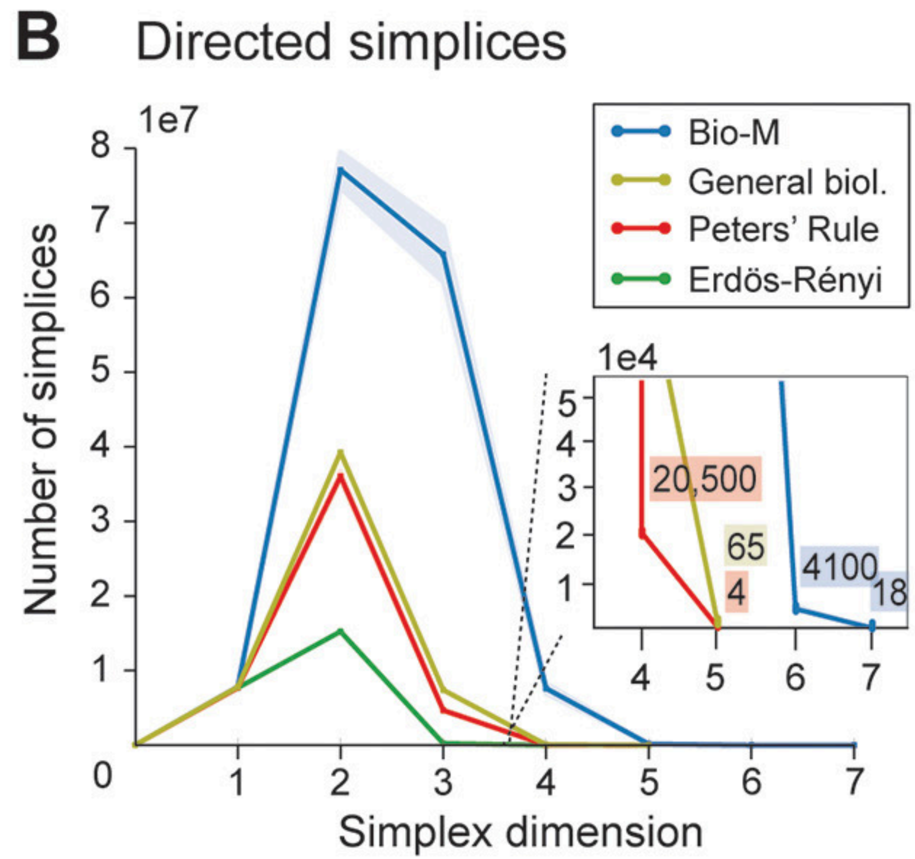


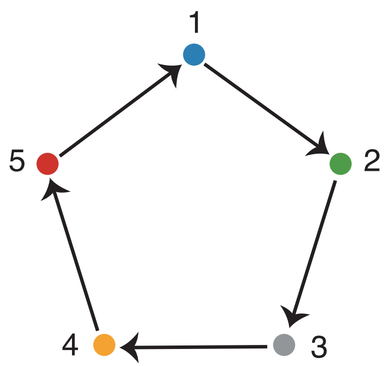


Directed cliques associated with "feedforward" flow of information!

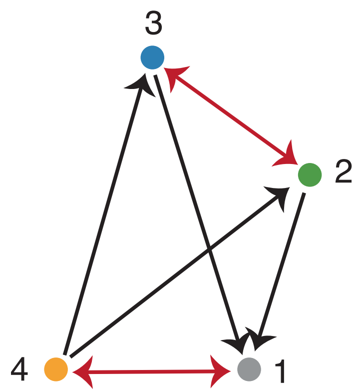
Recurrent vs. feedforward architecture

Recurrent motifs (attractors)

cycle



directed clique



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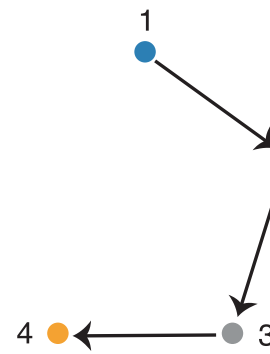
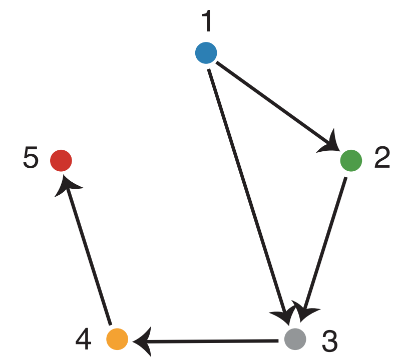
Feedforward motifs (FF flow of information)

path



FF graph



feedforward graph: there exists an ordering on the nodes such that

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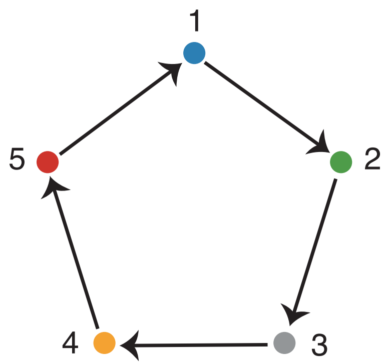

Feedforward motifs
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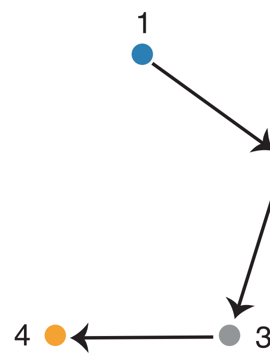

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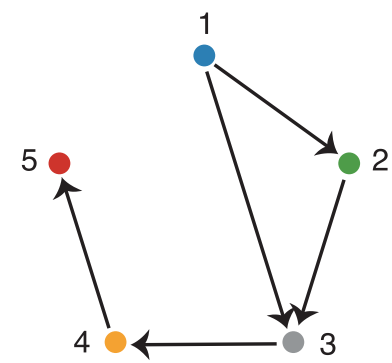
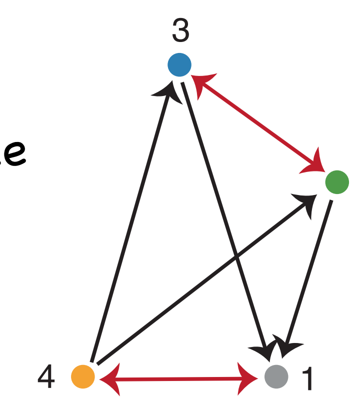
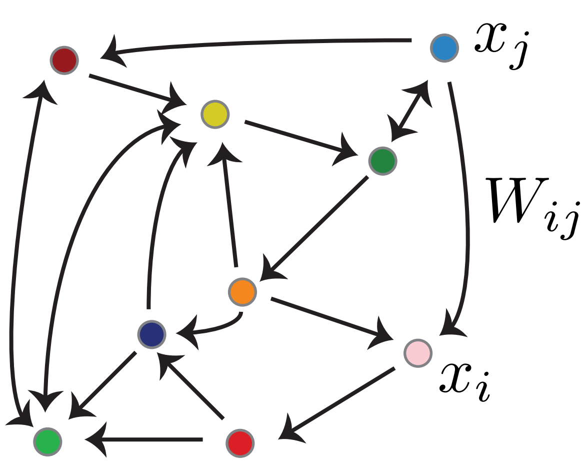


directed clique
goes here?



Fixed points/steady states/equilibria



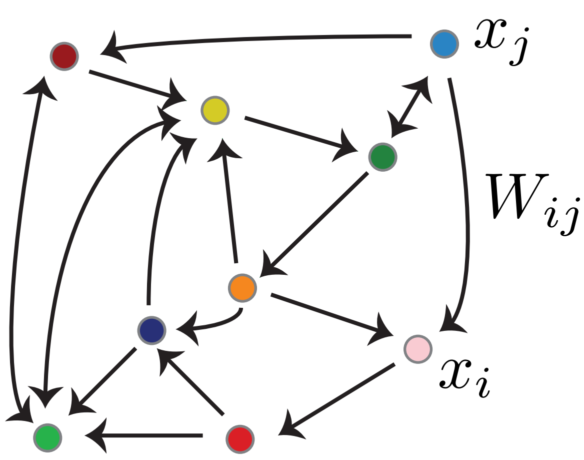
Fixed points:

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):

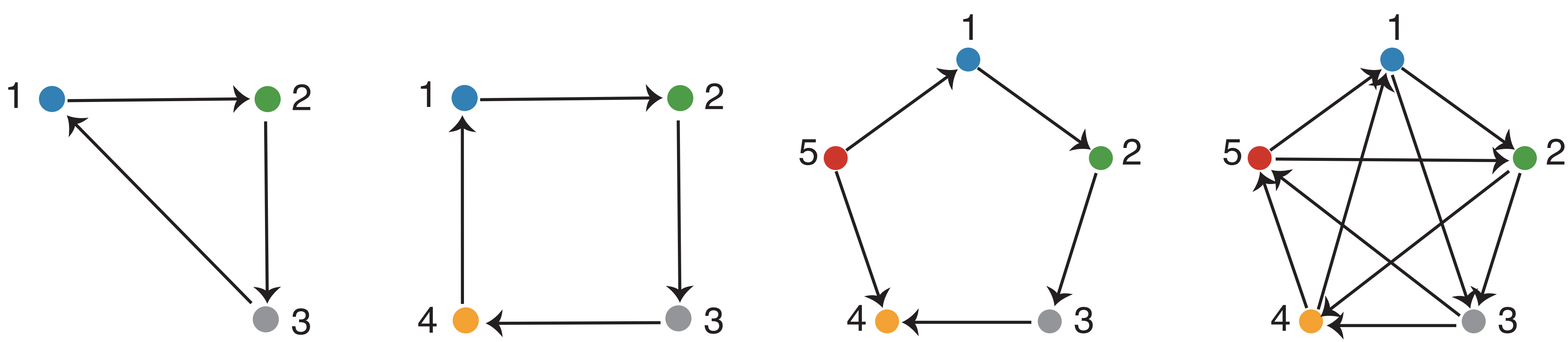
$$\mathrm{supp}(x) = \{i \in [n] \mid x_i > 0\}$$

V. Predicting emergent sequences

Sequence prediction algorithm

1. Remove the node with lowest in-degree that does **not** create a sink or remove the only target of a targeted 3-cycle. When there are multiple choices track all possible options.

Repeat Step 1 until no more nodes can be removed.
This typically yields a core cycle(s). The core cycle gives the high-firing neurons in the sequence.



example core cycles

Sequence prediction algorithm

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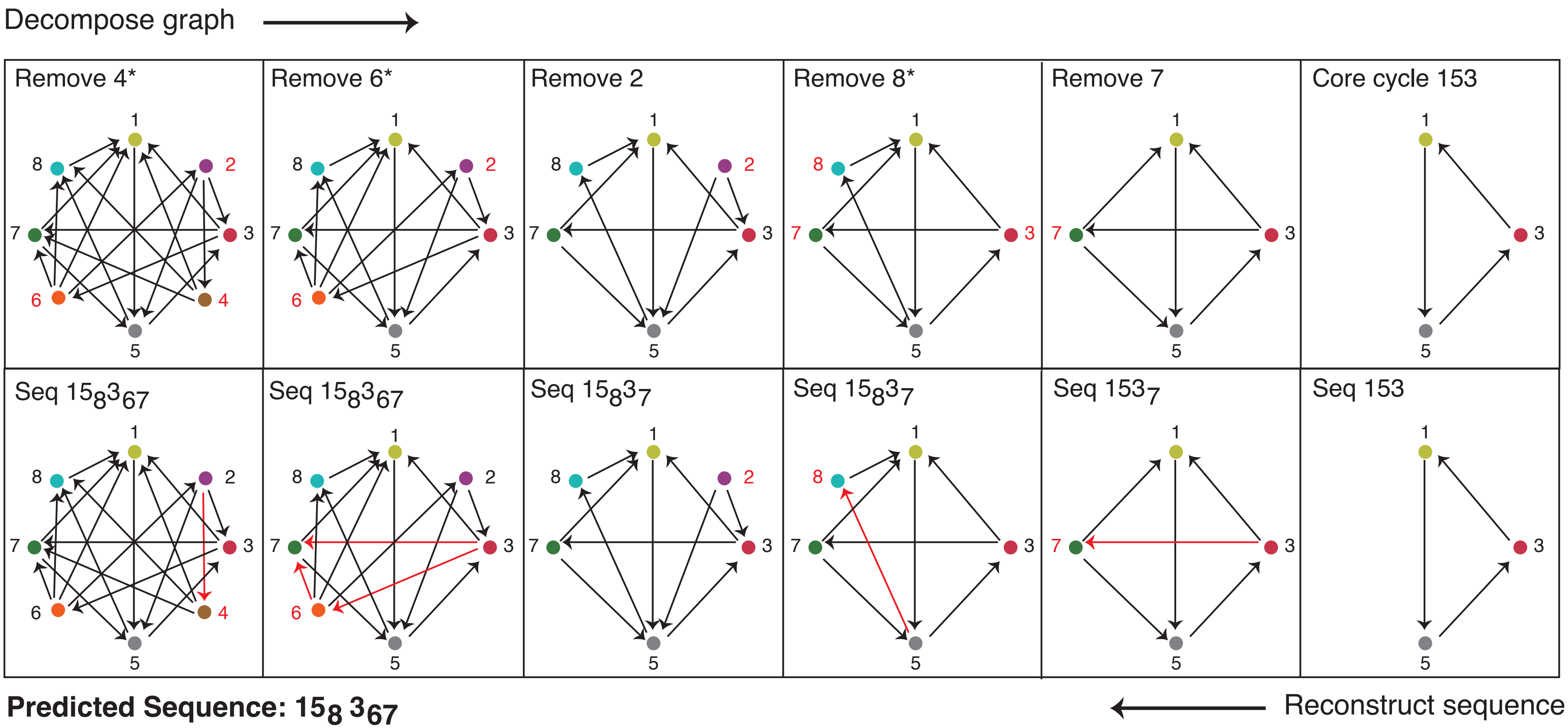
2. For each choice of removed nodes, re-insert nodes into the sequence if they receive input from the core cycle and insert them after the input node. These are low-firing neurons.

   If two nodes i and j are to be inserted in the same place, check how they interact. If $i \to j$, then insert i before j (or vice versa). If there is no edge, then i and j will fire synchronously as (ij).

Sequence prediction algorithm



* indicates choice for nodes. The first choice between nodes 4 & 6 does <u>not</u> affect the sequence. The second choice between 3, 7 & 8 would have resulted in another predicted sequence $15_3 8$.

Predicted sequences: $15_8 3_{67}$ and $15_3 8$

Sequence prediction algorithm

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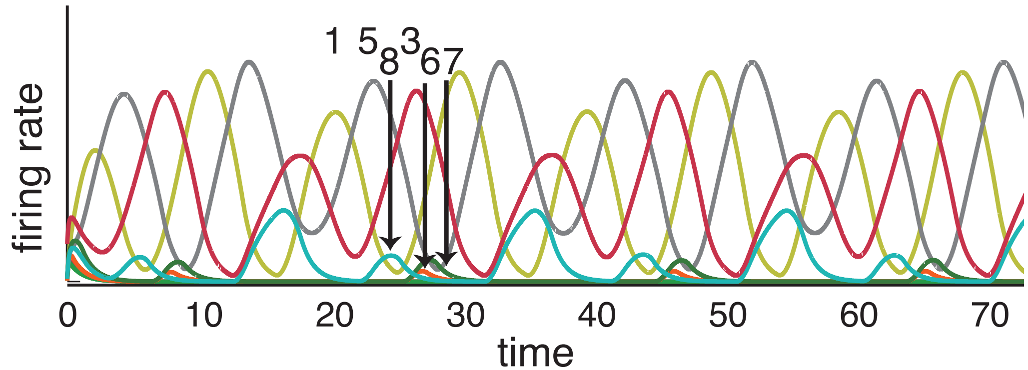
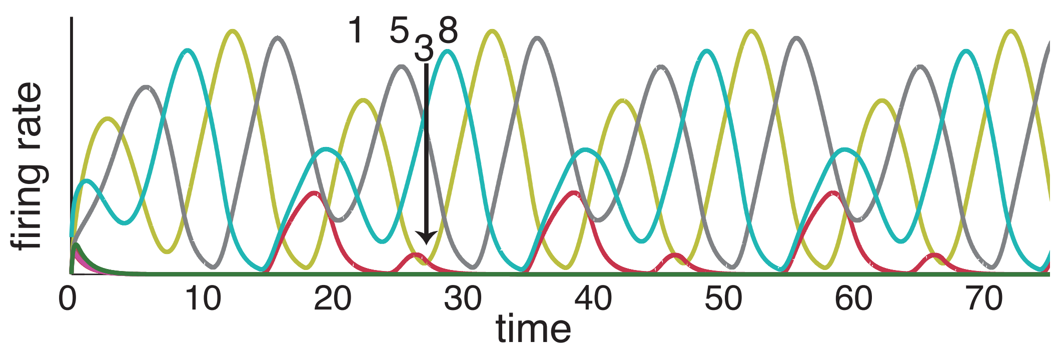
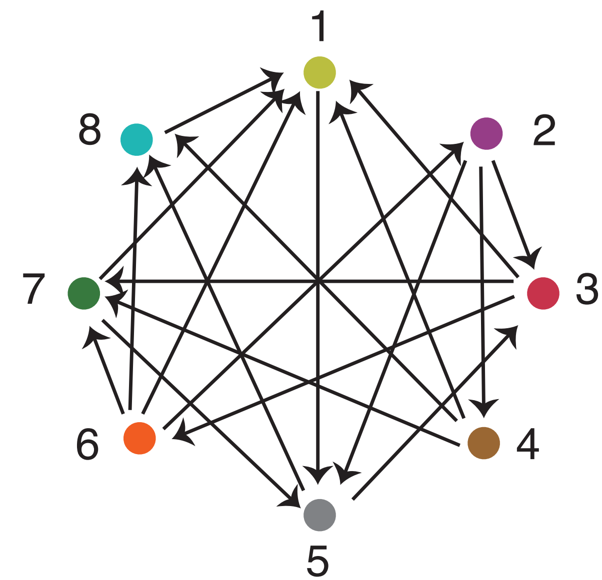






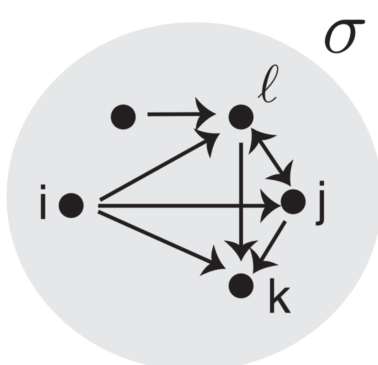
Only two attractors observed –
sequences precisely match those predicted by algorithm!

Domination

<u>Definition:</u> Given a subset $\sigma \subseteq [n]$ and $j \neq k$, with both $j \in \sigma$ and $k \in \sigma$, we say k dominates j with respect to σ if

1. For all $i \in \sigma$, if $i \to j$ then $i \to k$
2. $j \to k$ and $k \not\to j$

inside-in



k dominates j

k does not dominate l

j,k,l each dominate i (because i is a source)

<u>Thm:</u> If there is domination inside σ then σ cannot be a fixed pt support.

Subsets with uniform in-degree

<u>Definition:</u> A subset $\sigma \subseteq [n]$ has uniform in-degree d if all nodes have in-degree d in the induced subgraph $G|_\sigma$