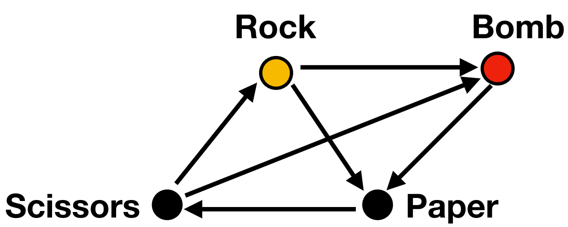
Graphical domination and inhibitory control for threshold-linear networks with recurrent excitation and global inhibition



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Workshop in Computational Neuroscience

July 2, 2025

Motivating ideas

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1. The brain is a dynamical system. ("The brain is a computer.")
2. By studying ANNs that are dynamical systems, we can generate hypotheses about the dynamic meaning/role of various network motifs.
3. Network motifs can be composed as dynamic building blocks with predictable properties.
4. One network (by architecture/connectivity) is really many networks in the presence of neuromodulation or external control.

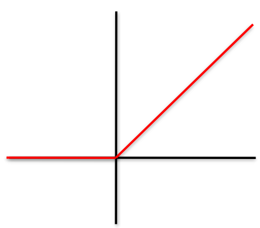
TLNs — nonlinear recurrent network models

Threshold-linear network dynamics:

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

W is an $n \times n$ matrix

$b \in \mathbb{R}^n$



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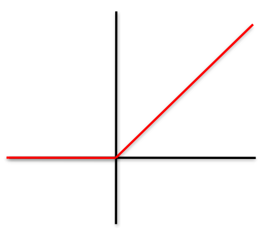

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Basic Question: Given (W,b), what are the network dynamics?

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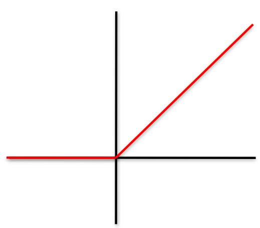


The TLN is defined by (W, b)

Linear network dynamics:

$$\frac{dx}{dt} = Ax + b$$

A is an $n \times n$ matrix

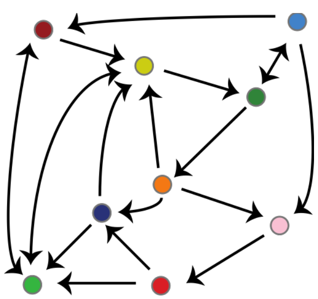
$b \in \mathbb{R}^n$

Long-term behavior is easy to infer from eigenvalues, eigenvectors — linear algebra tells us everything.

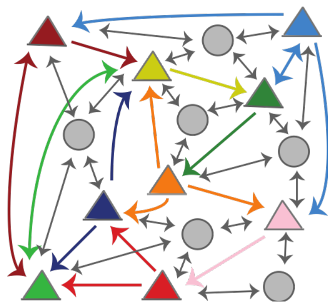
Basic Question: Given (W,b), what are the network dynamics?

The most special case: Combinatorial Threshold-Linear Networks (CTLNs)

graph G



Idea: network of excitatory and inhibitory cells



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:

$$\delta > 0 \quad \theta > 0 \quad 0 < \varepsilon < \frac{\delta}{\delta + 1}$$

TLN dynamics:

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

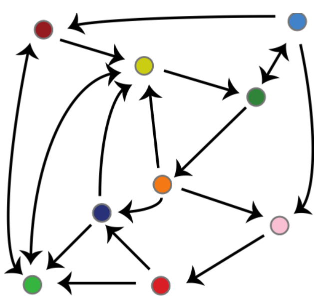
The graph encodes the pattern of weak and strong inhibition

Think: generalized WTA networks

For fixed parameters,
only the graph changes –
isolates the role of connectivity

Less special: generalized Combinatorial Threshold-Linear Networks (gCTLNs)

graph G



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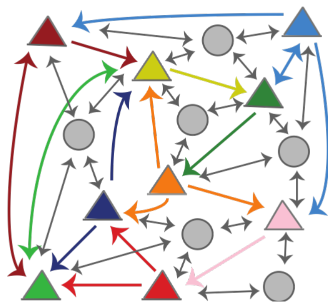

The gCTLN is defined by a graph G and two vectors of parameters: ε, δ

$$W_{ij} = \begin{cases} -1+\varepsilon_j & \text{if } j \to i, \\ -1-\delta_j & \text{if } j \not\to i, \\ 0 & \text{if } i = j. \end{cases}$$

weak inhibition

strong inhibition

TLN dynamics:

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The graph encodes the pattern of weak and strong inhibition

$b_i = \theta > 0$ for all neurons

(default is uniform across neurons, constant in time)

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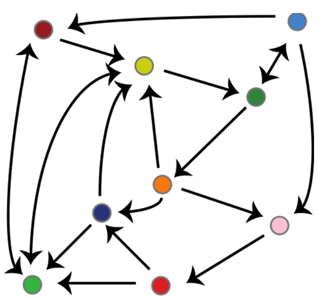

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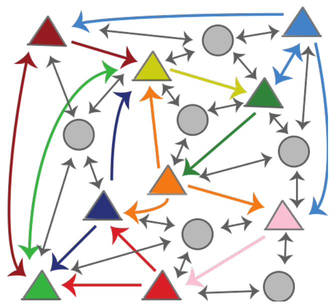

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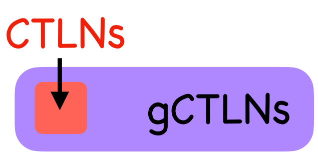
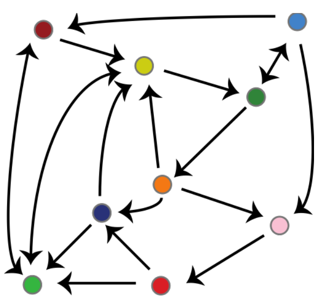


Special case: if the parameters ε_j, δ_j are the same for all neurons, we have a CTLN.

Less special: generalized Combinatorial Threshold-Linear Networks (gCTLNs)

graph G



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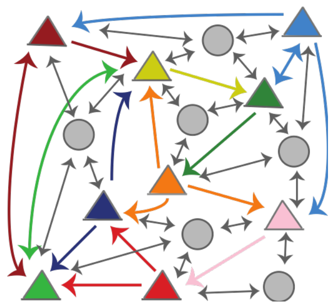
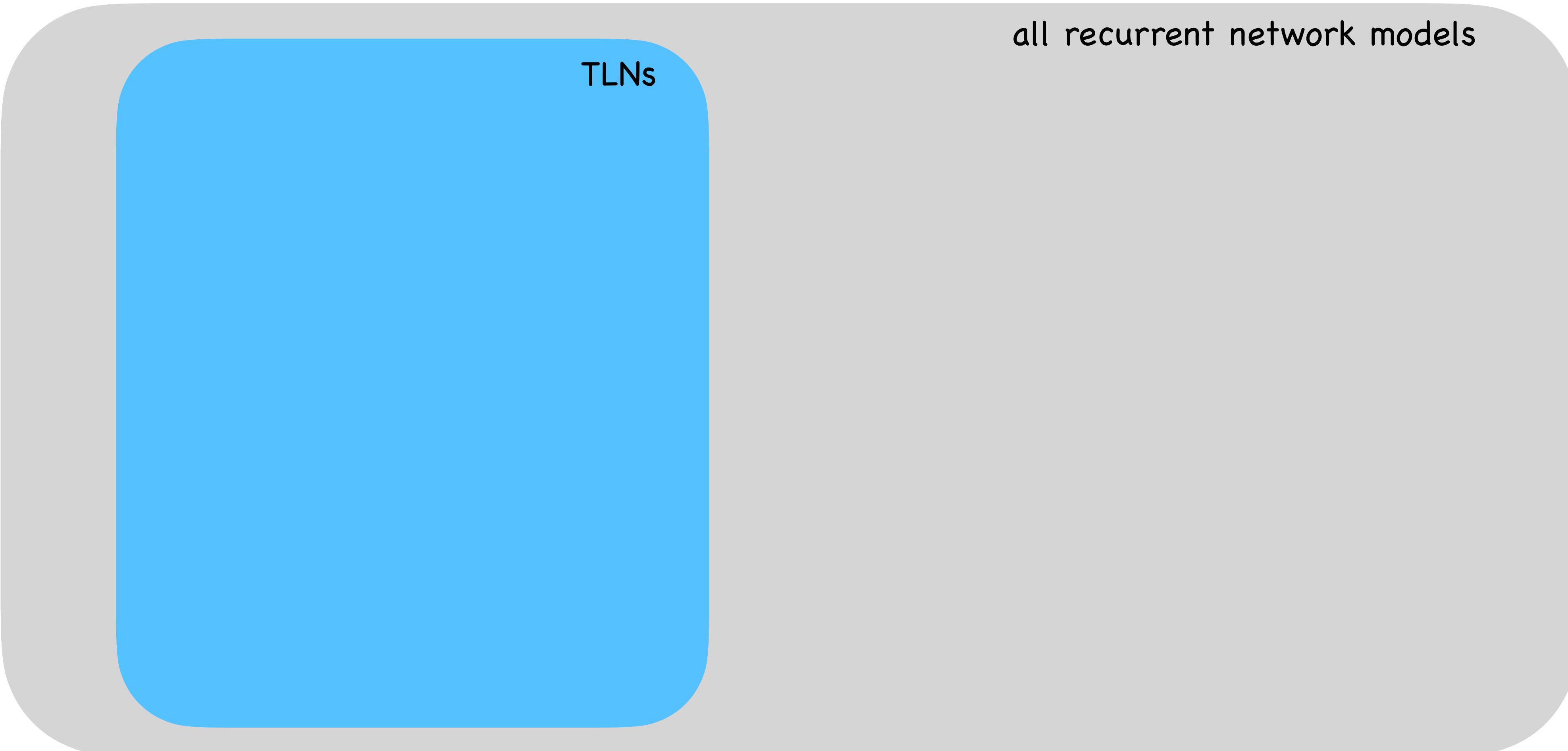


The central goal is to predict features of the dynamics (activity)

from the combinatorial structure of the graph G (connectivity).

TLNs, CTLNs, and gCTLNs



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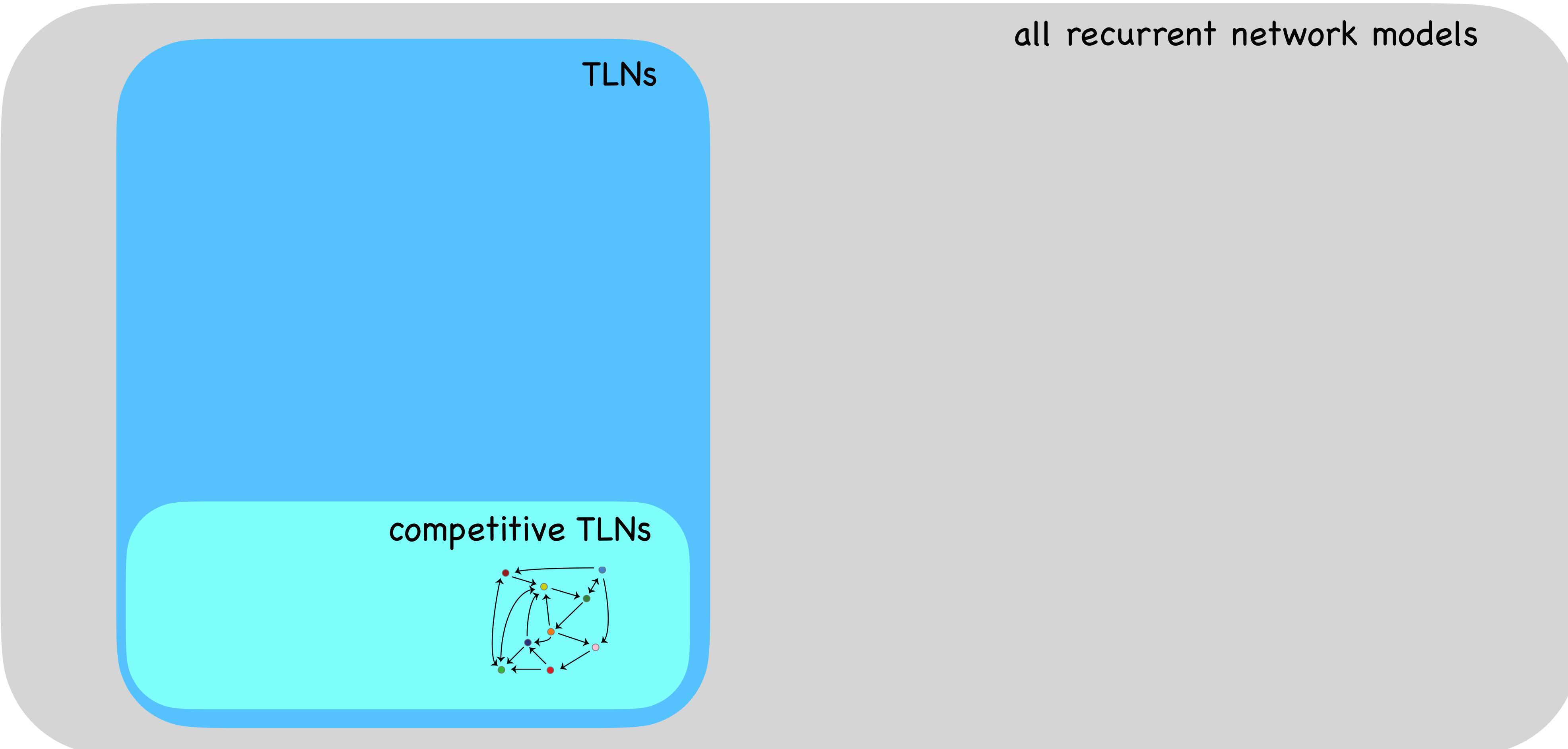

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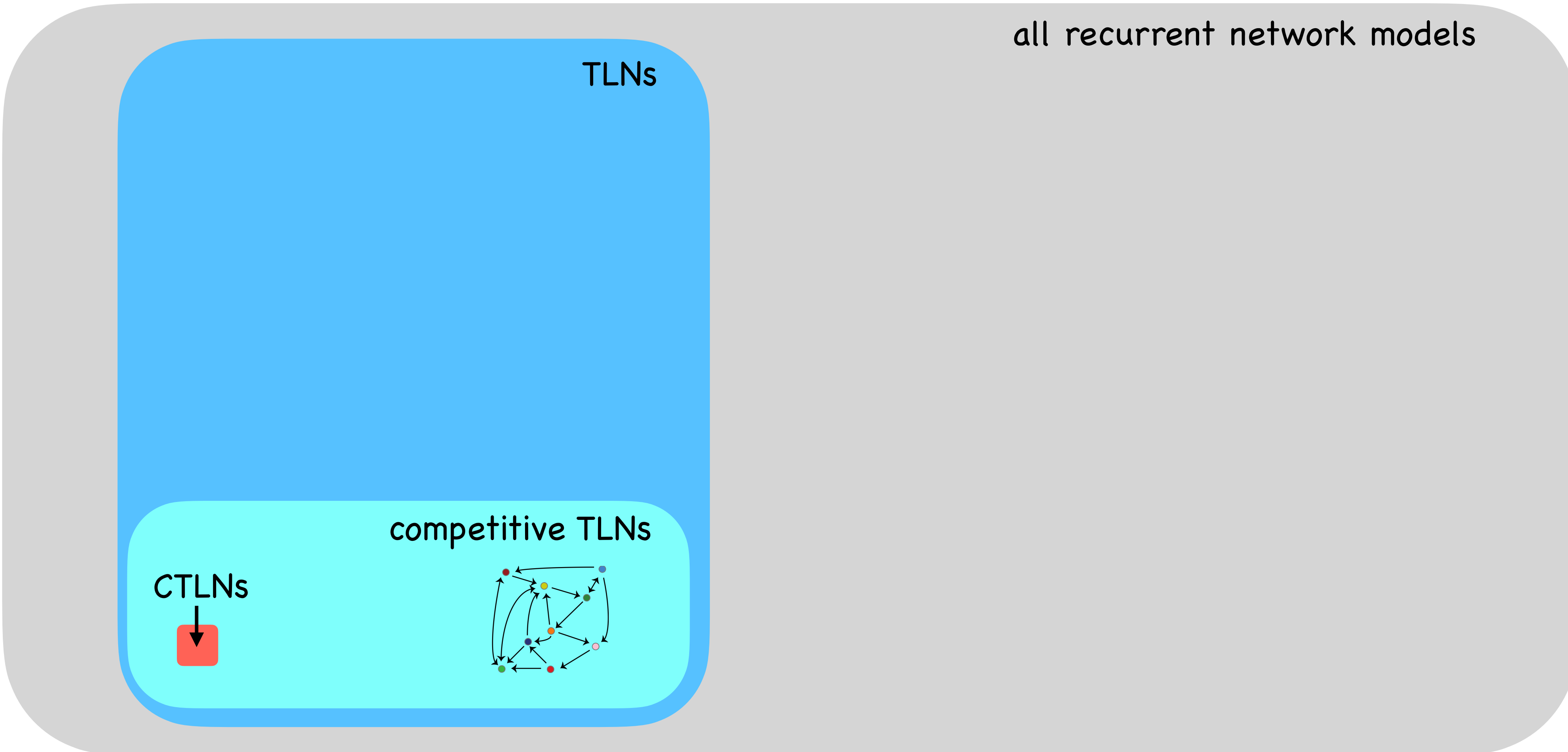

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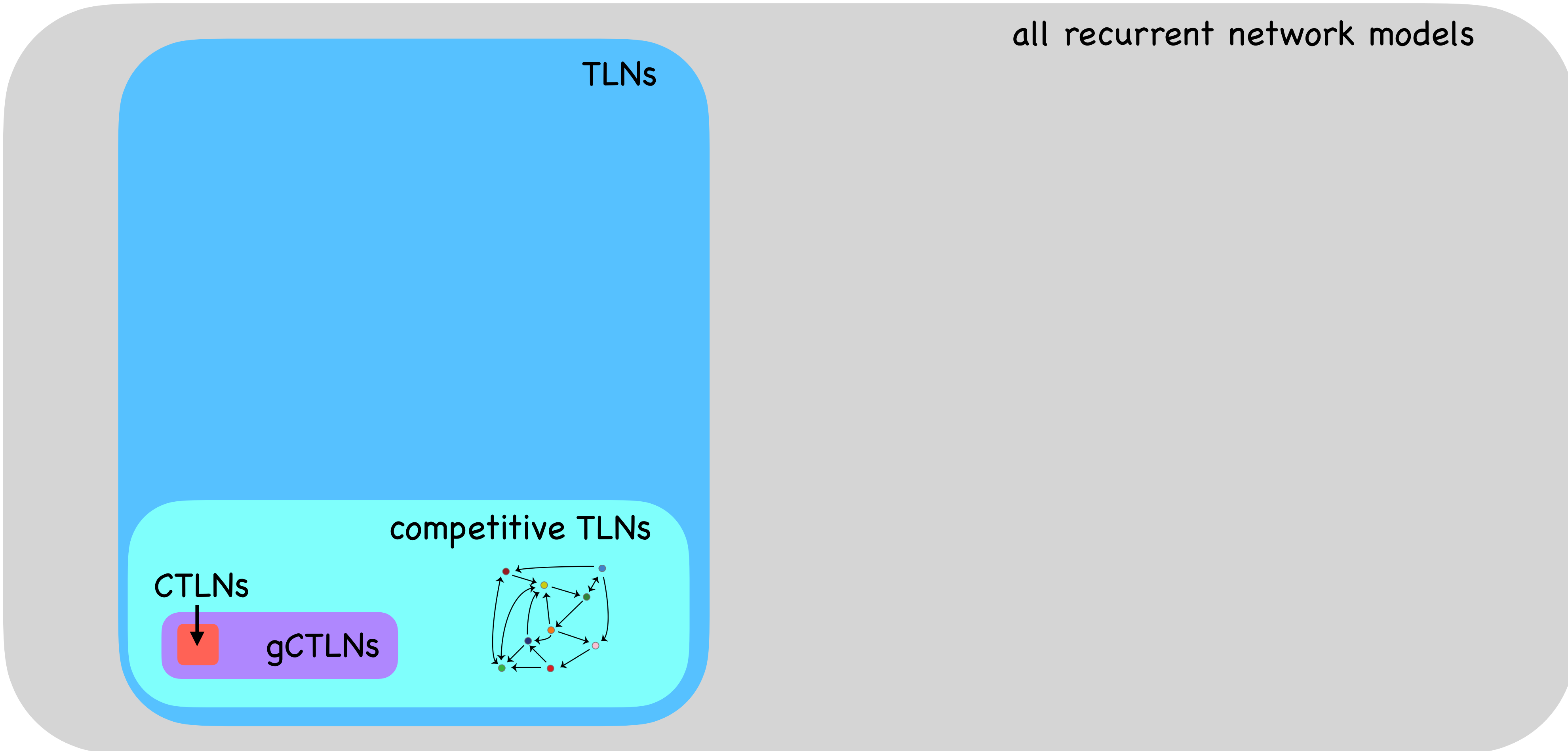

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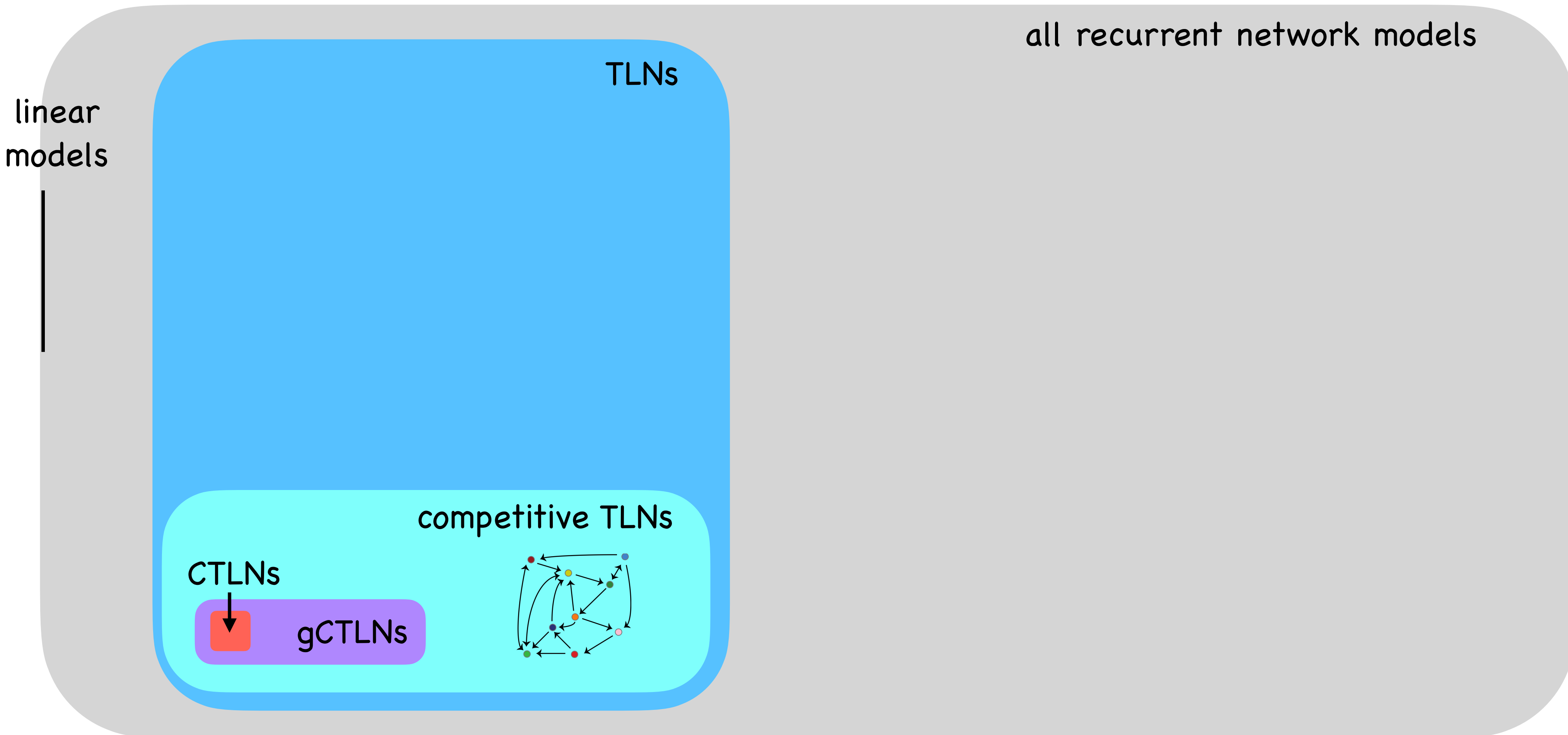
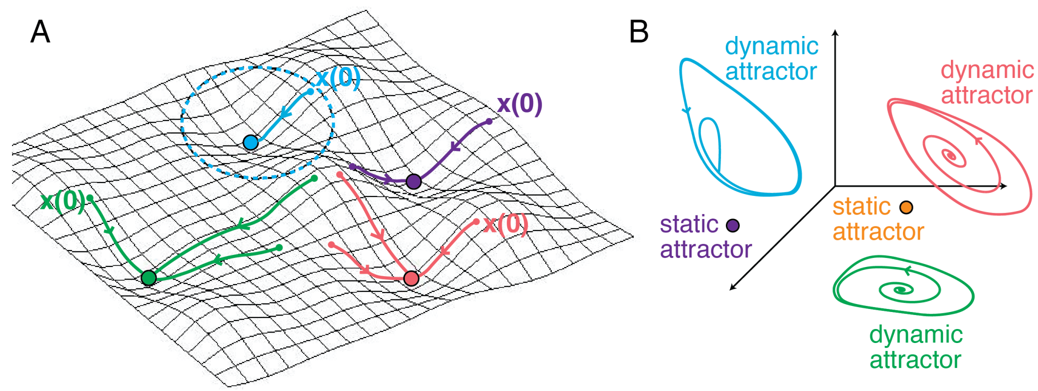


TLNs, CTLNs, and gCTLNs

1. Display rich nonlinear dynamics: multistability, limit cycles, chaos…

static attractors (fixed pts)

dynamic attractors
(correspond to certain unstable fixed pts)



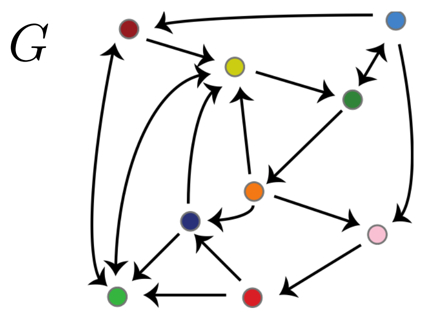
Curto & Morrison, 2023 (review paper)

TLNs, CTLNs, and gCTLNs

1. Display rich nonlinear dynamics: multistability, limit cycles, chaos...

2. Mathematically tractable: we can prove theorems directly connecting graph structure to dynamics.

graph structure



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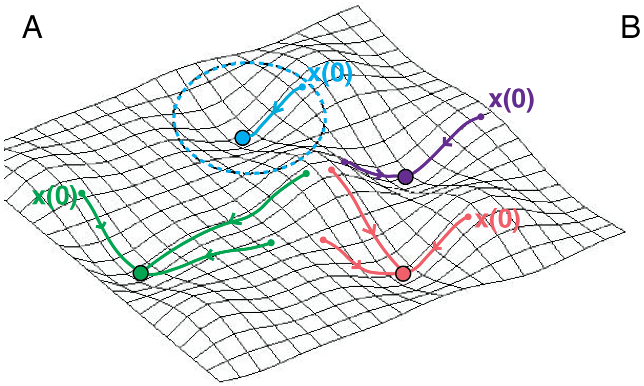

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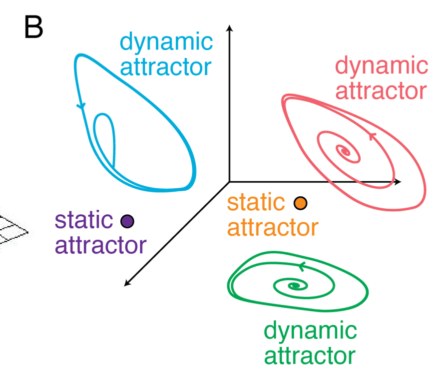

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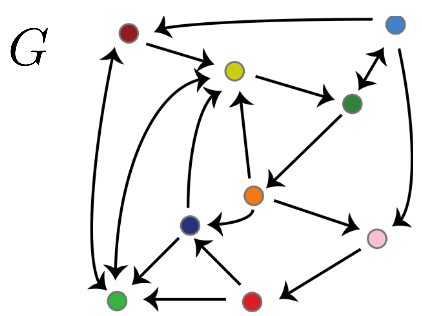
TLNs, CTLNs, and gCTLNs

1. Display rich nonlinear dynamics: multistability, limit cycles, chaos...
2. Mathematically tractable: we can prove theorems directly connecting graph structure to dynamics.
3. Both stable and unstable fixed points play a critical role in shaping the dynamics (the vector field).

graph structure



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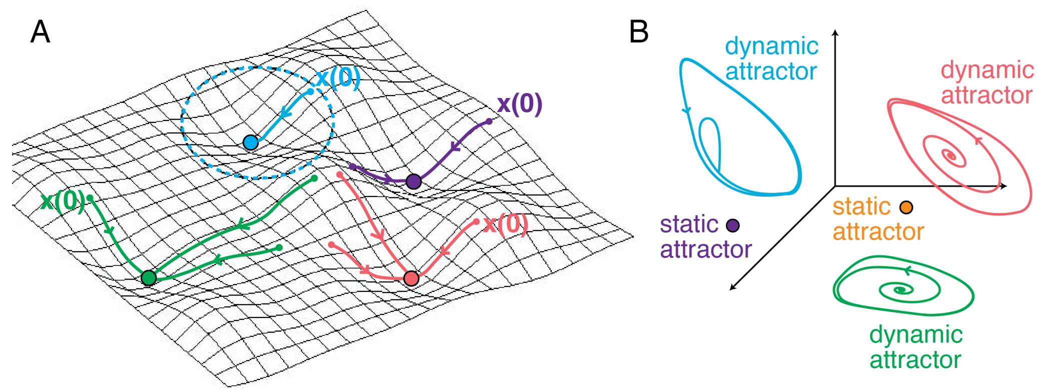
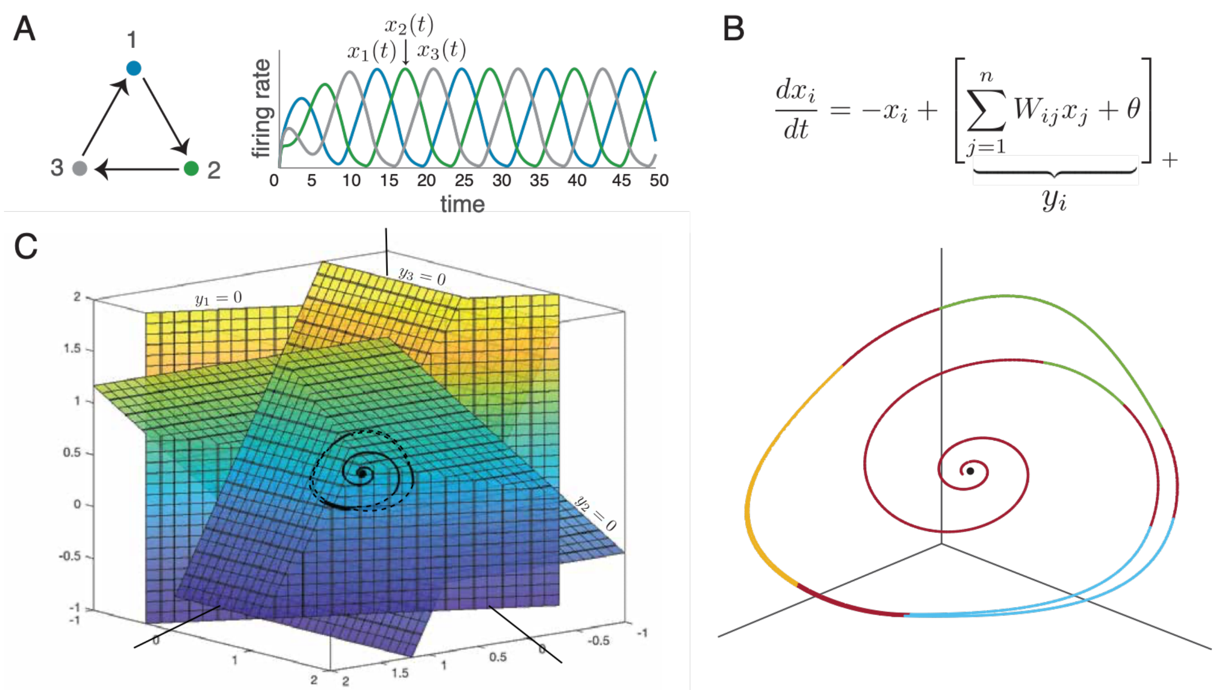


$$\mathrm{FP}(G) = \mathrm{FP}(G, \varepsilon, \delta) = \{ \text{ fixed points (stable and unstable) } \}$$

Curto & Morrison, 2023 (review paper)

Theorem: oriented graphs with no sinks

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



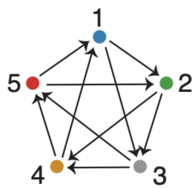
Existence of such limit cycles was established in Bel, Cobiaga, Reartes, and Rotstein, SIADS 2022.

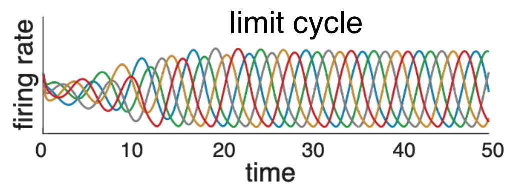
Fun examples!

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

Gaudí attractor

$\varepsilon = 0.1, \;\; \delta = 0.12, \;\; \theta = 1$





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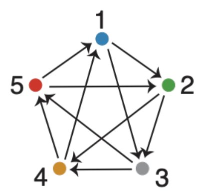
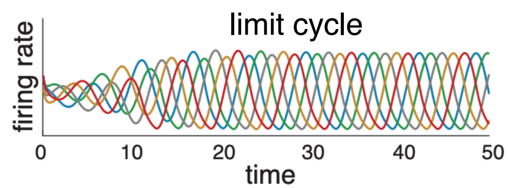
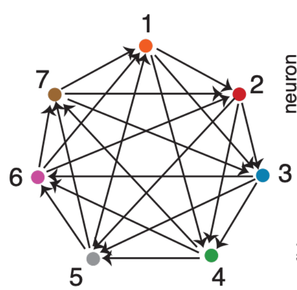
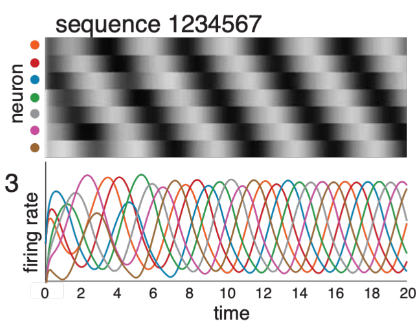
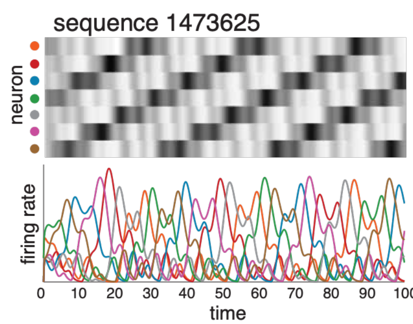


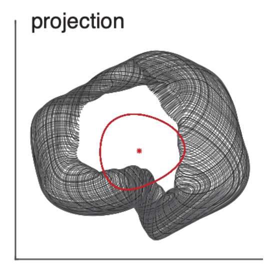


n = 7 star (another tournament)









Matlab code for all figures on Github:

Diversity of emergent dynamics in competitive TLNs, Morrison, et. al., SIADS 2024

TLNs as a patchwork of linear systems

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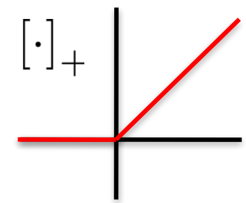
$[\cdot]_+$



Different linear system
of ODEs for each, indexed by:

$$\sigma \subseteq [n]$$

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

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

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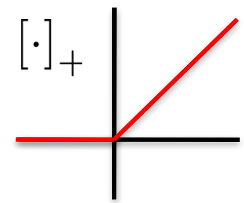

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$$\boxed{\mathrm{FP}(W,b) \overset{\text{def}}{=} \{\sigma \subseteq [n] \mid \sigma = \operatorname{supp} x^*, \text{ for some fixed pt } x^* \text{ of the associated TLN}\}}$$

1-1 correspondence between fixed points and allowed supports

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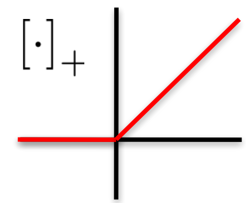
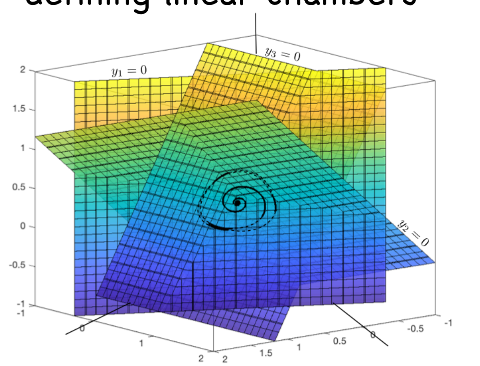


hyperplane arrangement
defining linear chambers



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TECHNICAL RESULTS
for fixed points of TLNs

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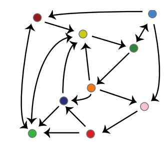


parity

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

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

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

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* $\sigma \subseteq [n]$,

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

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

Moreover, if $\sigma \in \mathrm{FP}(W, b)$ *then* $\mathrm{sgn}\, s_i^\sigma = \mathrm{sgn}\det(I - W_\sigma) = \mathrm{idx}(\sigma)$ *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* $j >_\sigma k$.

C. Curto, J. Geneson, K. Morrison. *Fixed points of threshold-linear networks.* (Neural Computation, 2019)

Graph rules for CTLN fixed point supports FP(G)

rule name	$G\|_\sigma$ structure	graph rule
Rule 1	independent set	$\sigma \in \mathrm{FP}(G\|_\sigma)$ and $\sigma \in \mathrm{FP}(G) \Leftrightarrow \sigma$ is a union of sinks
Rule 2	clique	$\sigma \in \mathrm{FP}(G\|_\sigma)$ and $\sigma \in \mathrm{FP}(G) \Leftrightarrow \sigma$ is target-free
Rule 3	cycle	$\sigma \in \mathrm{FP}(G\|_\sigma)$ and $\sigma \in \mathrm{FP}(G) \Leftrightarrow$ each $k \notin \sigma$ receives at most one edge $i \to k$ for $i \in \sigma$
Rule 4(i)	$\exists$ a source $j \in \sigma$	$\sigma \notin \mathrm{FP}(G)$ if $j \to k$ for some $k \in [n]$
Rule 4(ii)	$\exists$ a source $j \notin \sigma$	$\sigma \in \mathrm{FP}(G\|_\sigma) \Leftrightarrow \sigma \in \mathrm{FP}(G\|_{\sigma \cup j})$
Rule 5(i)	$\exists$ a target $k \in \sigma$	$\sigma \notin \mathrm{FP}(G\|_\sigma)$ and $\sigma \notin \mathrm{FP}(G)$ if $k \not\to j$ for some $j \in \sigma$
Rule 5(ii)	$\exists$ a target $k \notin \sigma$	$\sigma \notin \mathrm{FP}(G\|_{\sigma \cup k})$ and $\sigma \notin \mathrm{FP}(G)$
Rule 6	$\exists$ a sink $s \notin \sigma$	$\sigma \cup \{s\} \in \mathrm{FP}(G) \Leftrightarrow \sigma \in \mathrm{FP}(G)$
Rule 7	DAG	$\mathrm{FP}(G) = \{\cup s_i \mid s_i \text{ is a sink in } G\}$
Rule 8	arbitrary	$\|\mathrm{FP}(G)\|$ is odd

Table 1: Summary of derived graph rules.

C. Curto, J. Geneson, K. Morrison. *Fixed points of threshold-linear networks.* (Neural Computation, 2019)

Observations about competitive TLNs

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

1. Directed graphs (non-symmetric W) is necessary to get dynamic attractors that (as opposed to fixed points).

2. Unstable fixed points matter — b/c of the Perron-Frobenius theorem.

3. Degeneracy: attractors can be preserved with changing weights (selectively).

4. Architecture provides serious constraints, not everything is possible!

5. The same in/out-degree distribution can correspond to networks with wildly different dynamics.

6. Sequences emerge very naturally because of the inhibition. There is no need for a synaptic chain in the architecture.

recent survey if you want to know more:

Curto & Morrison, Notices of the AMS, 2023

Focus on one very important graph property:

domination

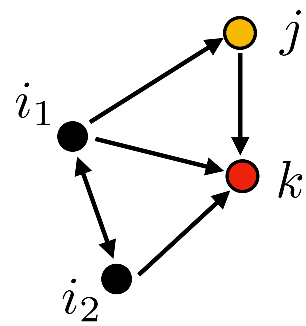
Domination

Definition 1.1. Let $j, k \in [n]$ be vertices of G. We say that k *graphically dominates* j in G if the following two conditions hold:

(i) For each vertex $i \in [n] \setminus \{j, k\}$, if $i \to j$ then $i \to k$.

(ii) $j \to k$ and $k \not\to j$.

If there exists a k that graphically dominates j, we say that j is a *dominated node* (or *dominated vertex*) of G. If G has no dominated nodes, we say that it is *domination free*.



$k > j$

"k dominates j"

"j is a dominated node"

Curto, Geneson, Morrison, 2019

domination is a property of G

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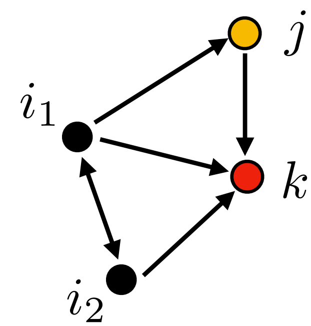

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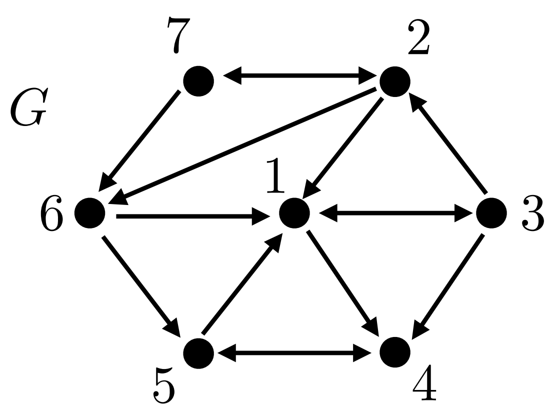

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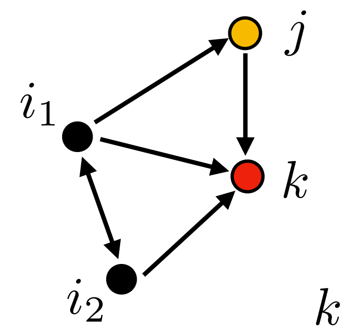

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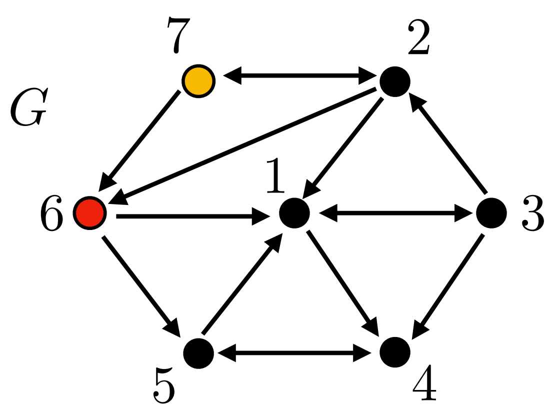

$6 > 7$

domination is a property of G

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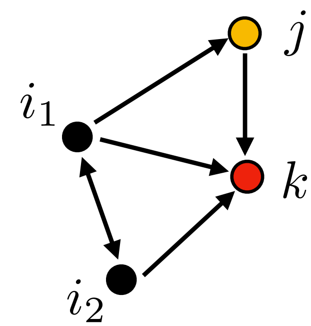

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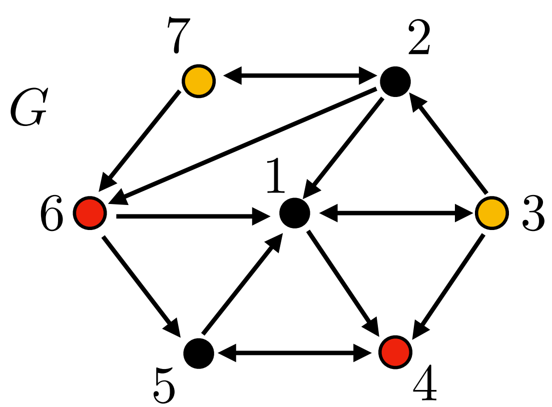


$6 > 7$

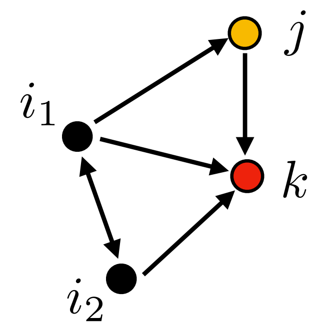
$4 > 3$

domination is a property of G

Domination

Old Theorem (2019)
If k dominates j in G, then j, k cannot both be active at any fixed point of a CTLN built from G.

$$\{j, k\} \not\subseteq \sigma \text{ for any } \sigma \in \mathrm{FP}(G)$$



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Curto, Geneson, Morrison, 2019

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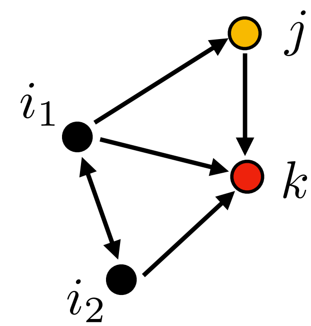

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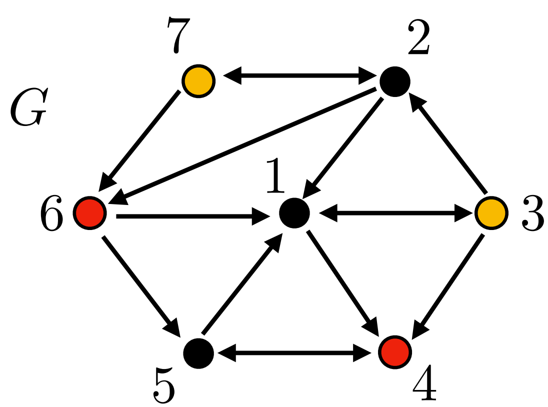


$6 > 7$

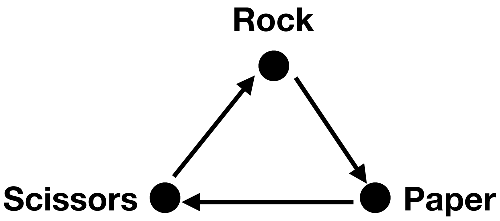
$4 > 3$

Old Theorem says: for any CTLN built from G, FP(G) cannot have any fixed points with both {6,7} or both {3,4}.

But it's not like we can remove 3 and 7; they may still affect or participate in other fixed points (for all we know).

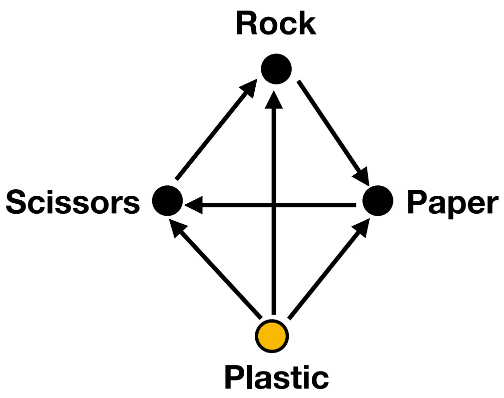
Curto, Geneson, Morrison, 2019

Rock-Paper-Scissors: a true story



March 2024

Rock-Paper-Scissors: a true story

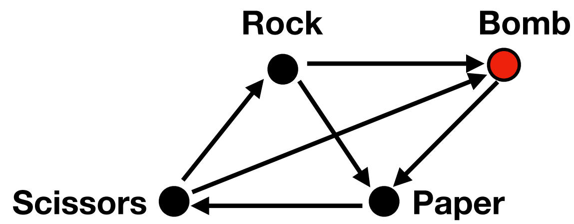


Plastic loses to everyone, so nobody would ever pick it as a strategy.

It drops out.

March 2024

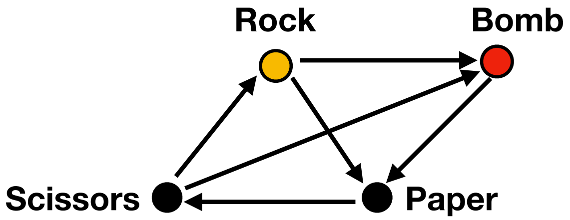
Rock-Paper-Scissors: a true story



Bomb beats Scissors and loses to Paper, just like Rock.
But Bomb also beats Rock.

March 2024

Rock-Paper-Scissors: a true story



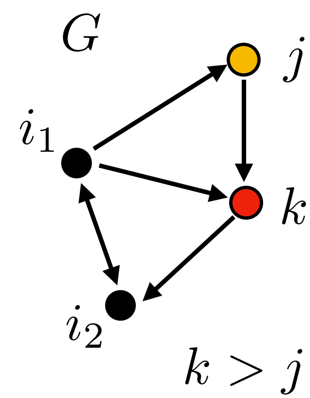
Bomb beats Scissors and loses to Paper, just like Rock.
But Bomb also beats Rock.

So now nobody would ever pick Rock as a strategy.
Rock drops out!

March 2024

Domination - New Theorems

Theorem 1 (2024)
If j is a dominated node in G, then it drops out!
I.e., in any gCTLN, we have: $\mathrm{FP}(G) = \mathrm{FP}(G|_{[n]\setminus j})$



Curto 2024 (unpublished)

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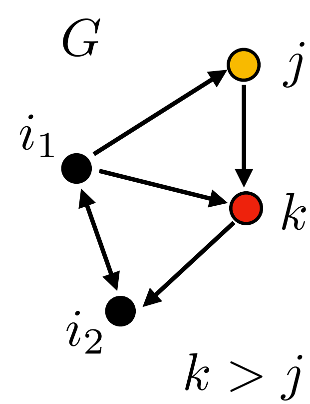

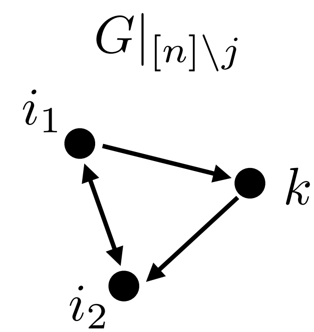

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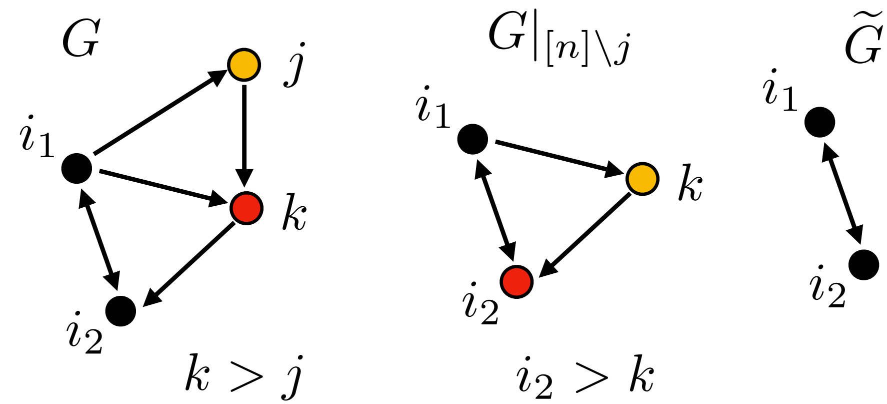

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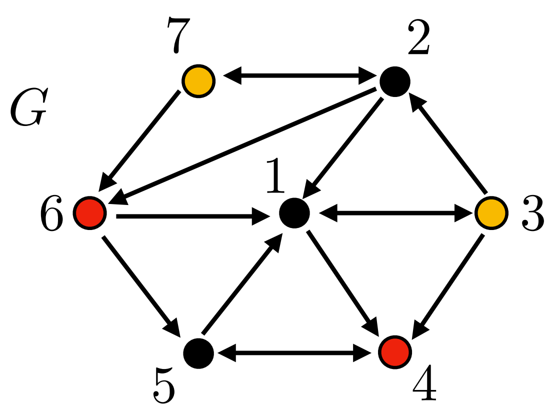

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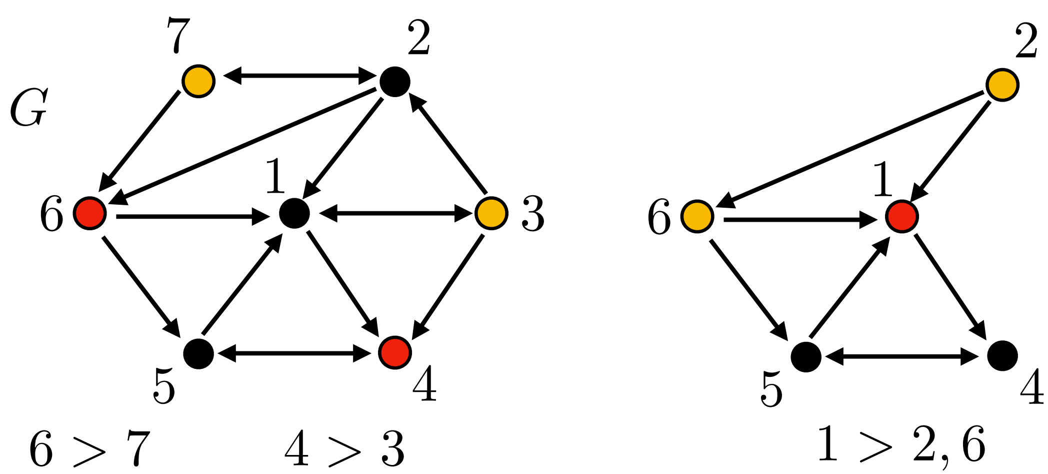

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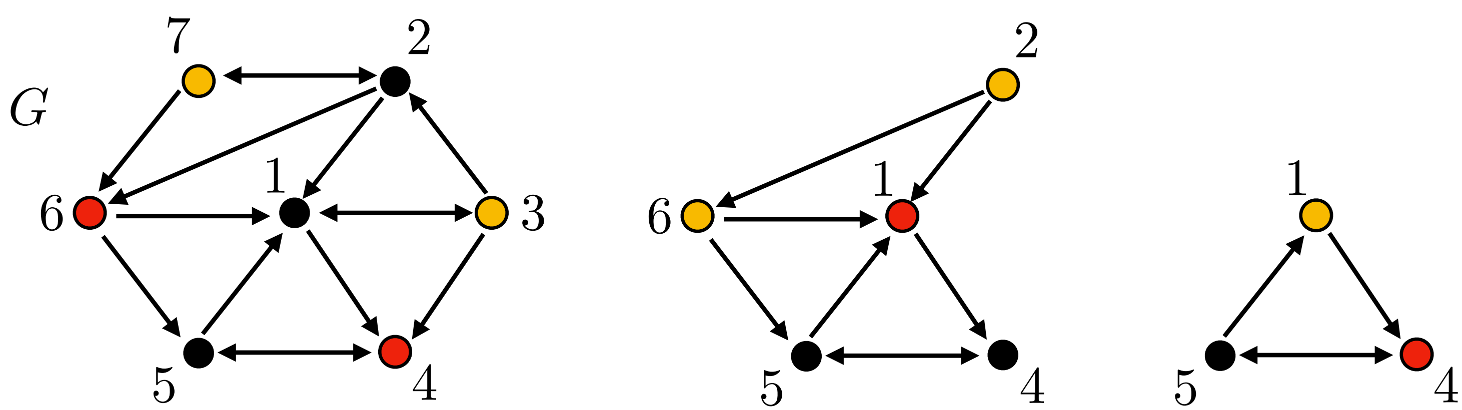

$6 > 7$ $\quad 4 > 3$ $\quad 1 > 2, 6$ $\quad 4 > 1$

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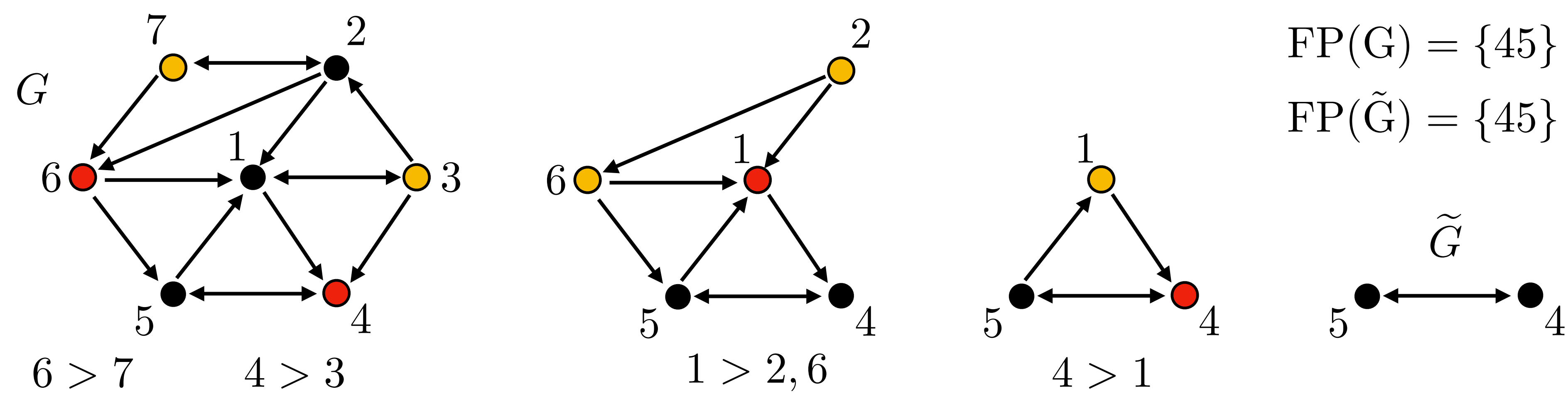
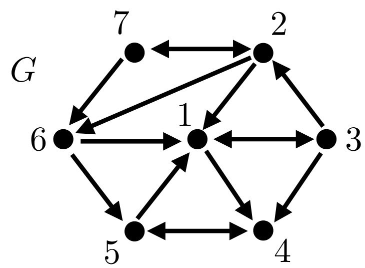


$\mathrm{FP(G)} = \{45\}$

$\mathrm{FP}(\tilde{\mathrm{G}}) = \{45\}$

Computational Experiments

Example



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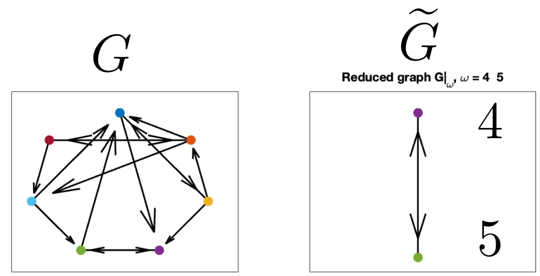

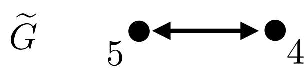

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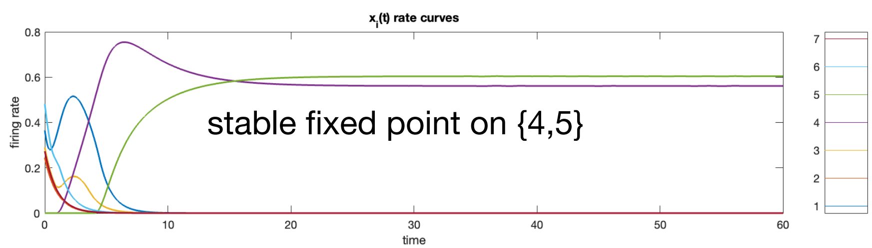

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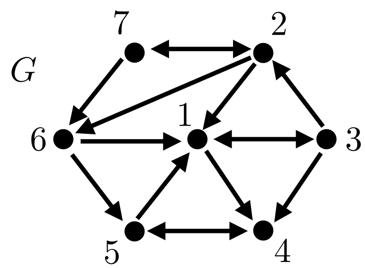

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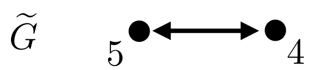

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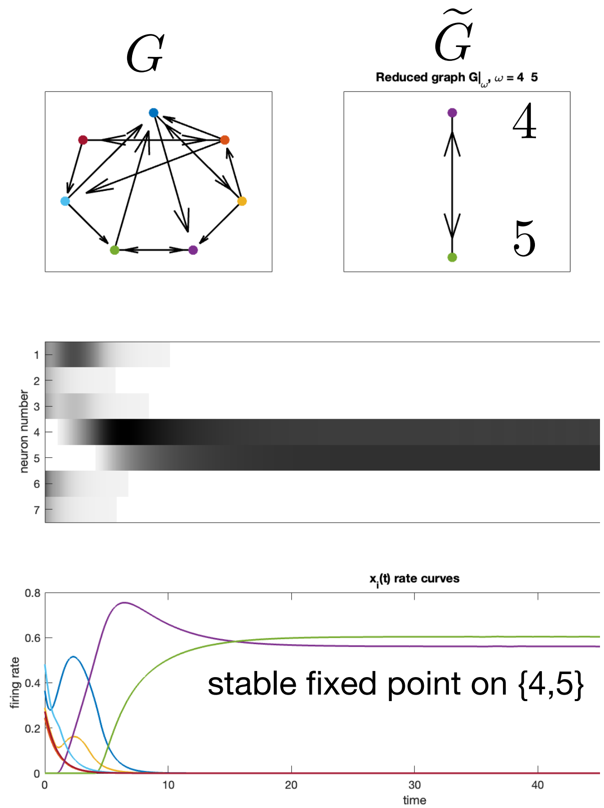
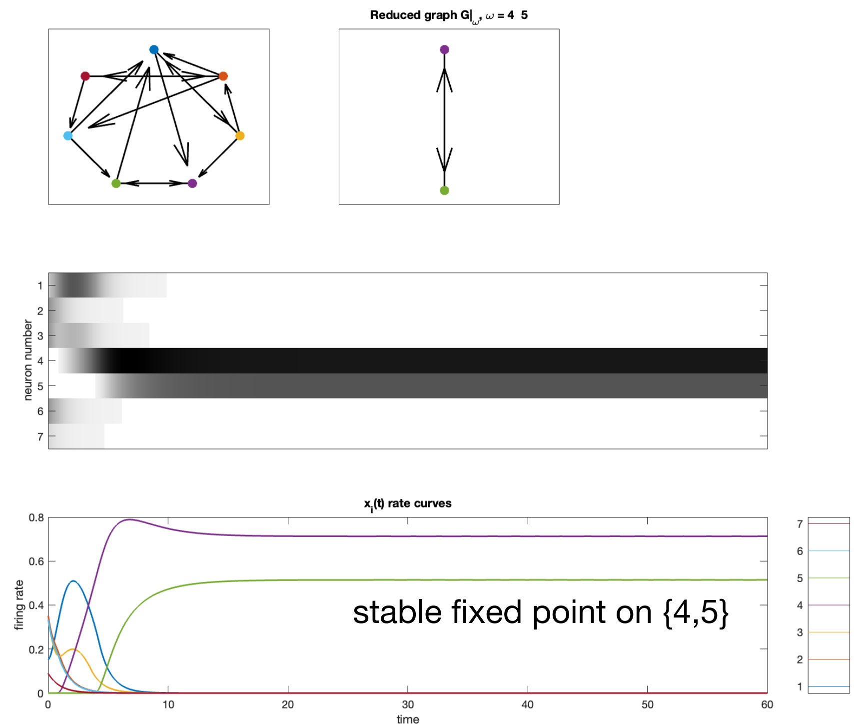
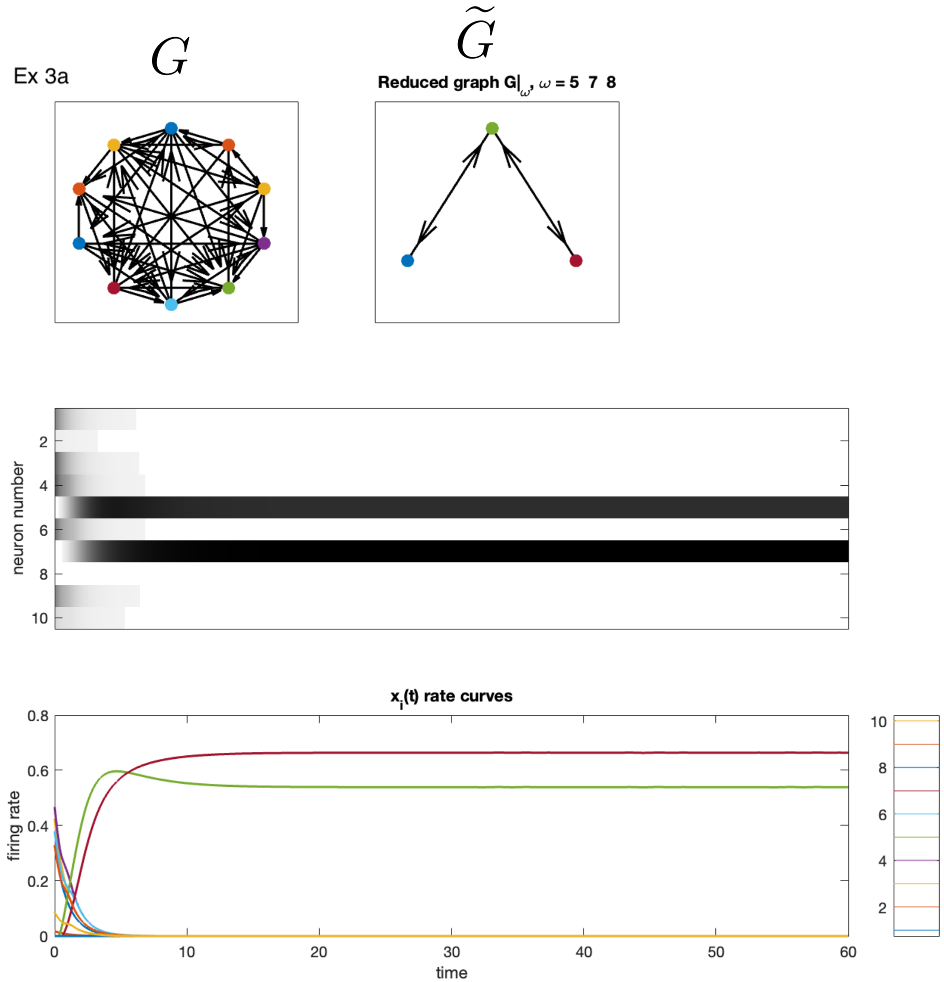


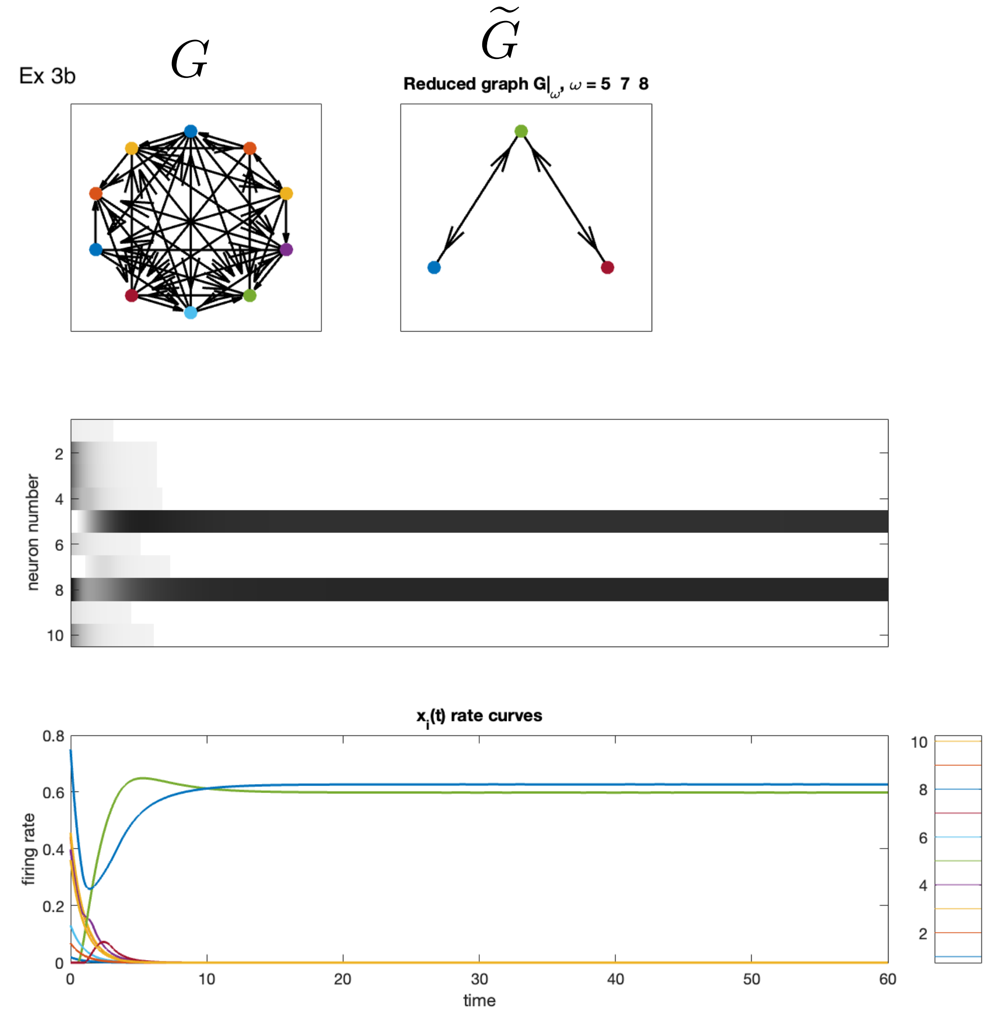
same graph, different gCTLN parameters



<u>Conjecture</u>: network activity flows from any initial condition on the graph to the reduced network $\widetilde{G}$

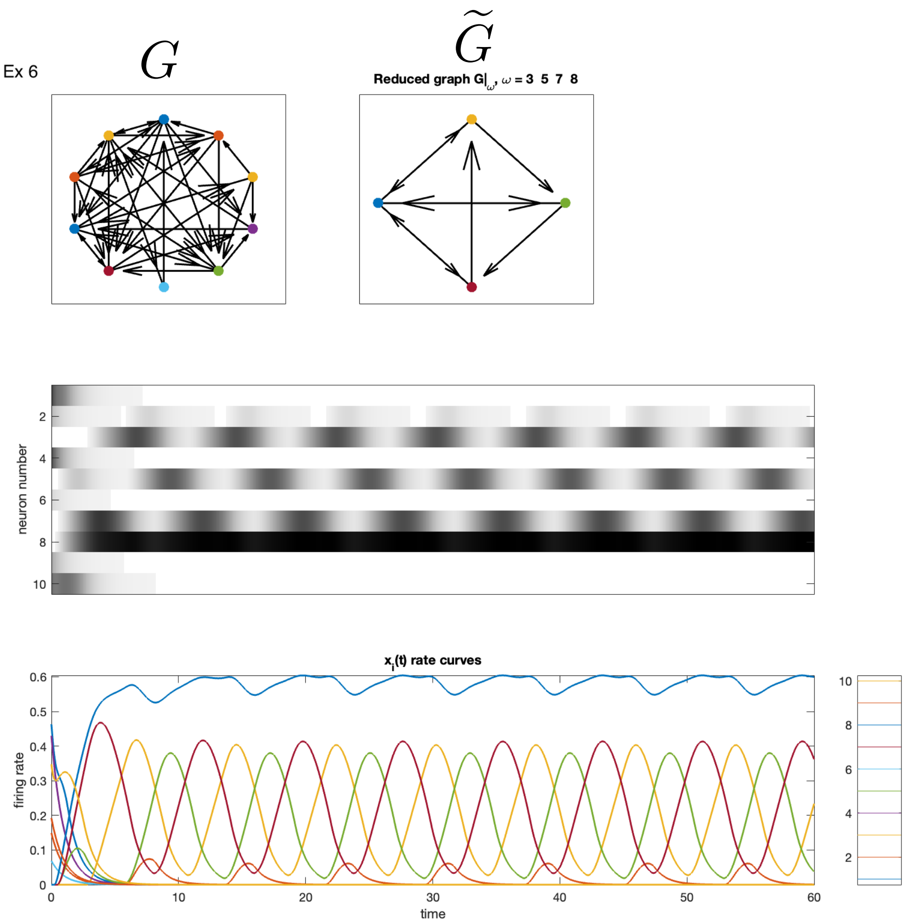
E-R random graphs with p=0.5



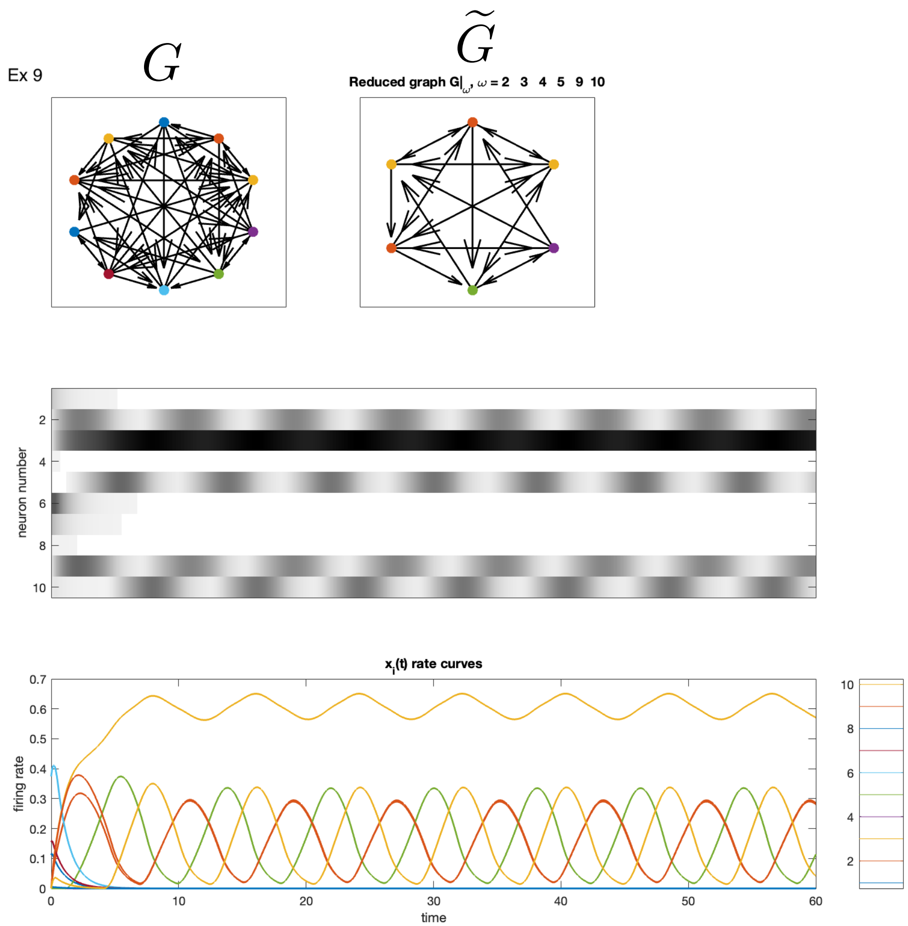


E-R random graphs with p=0.5

Ex 6



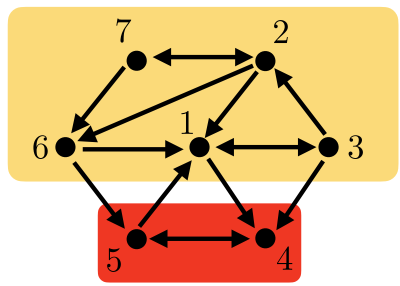
Ex 9



Dominoes!

<u>Conjecture</u>: network activity flows from any initial condition on the graph to the reduced network

G



$\mathrm{FP(G)} = \{45\}$

G_ω

$G_\tau = \widetilde{G}$

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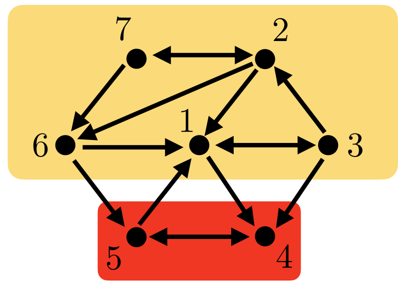

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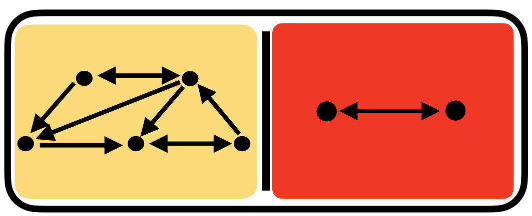
the "domino" of graph G



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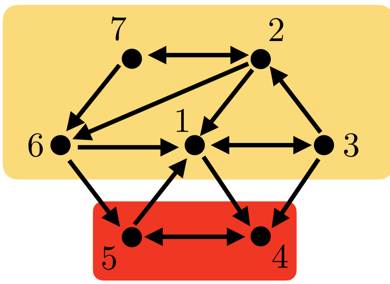

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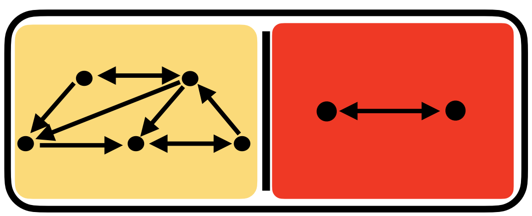


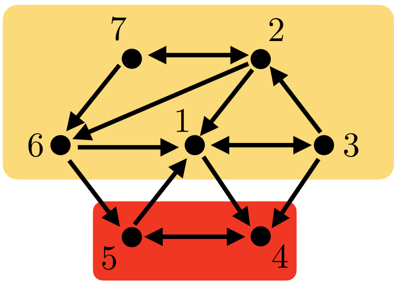
G_ω G_τ

<u>Fact (Thms 1 & 2)</u>: all the fixed points of G are supported in $G_\tau = \widetilde{G}$

<u>Conjecture</u>: network activity flows from $G_\omega \to G_\tau$

Dominoes!

G



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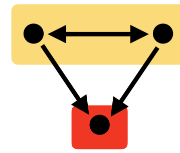
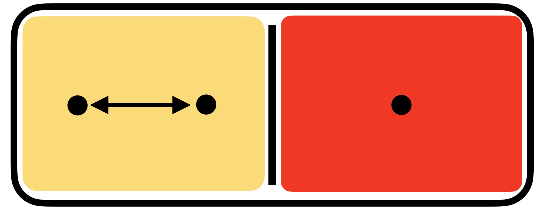
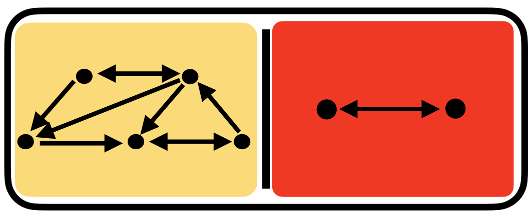




the "domino" of graph G



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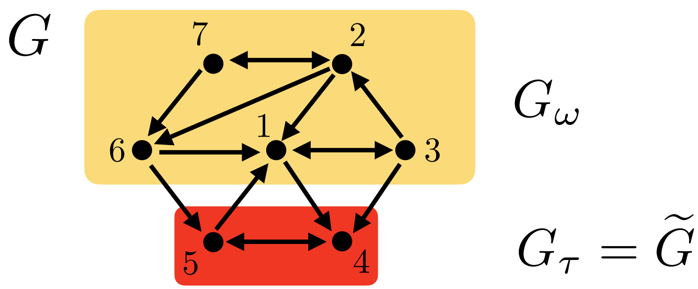

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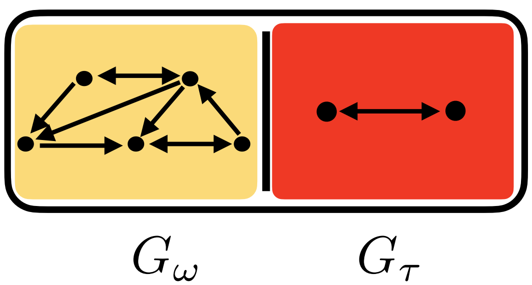

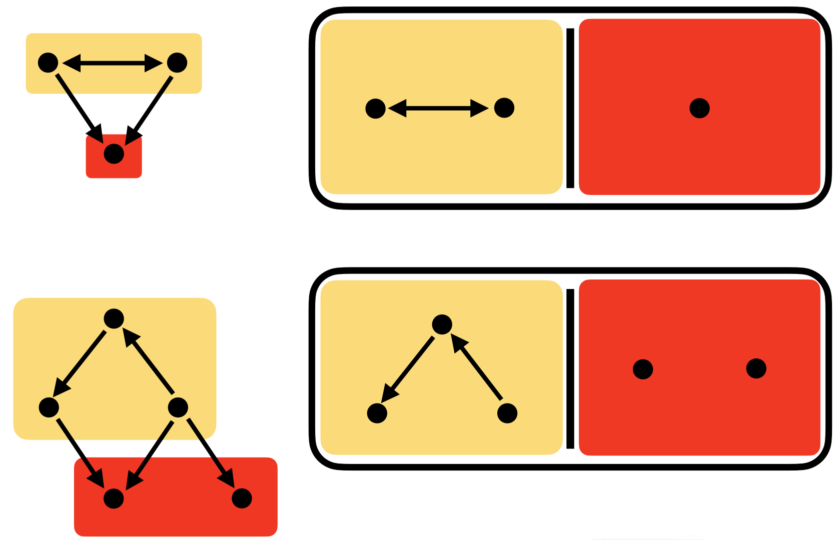

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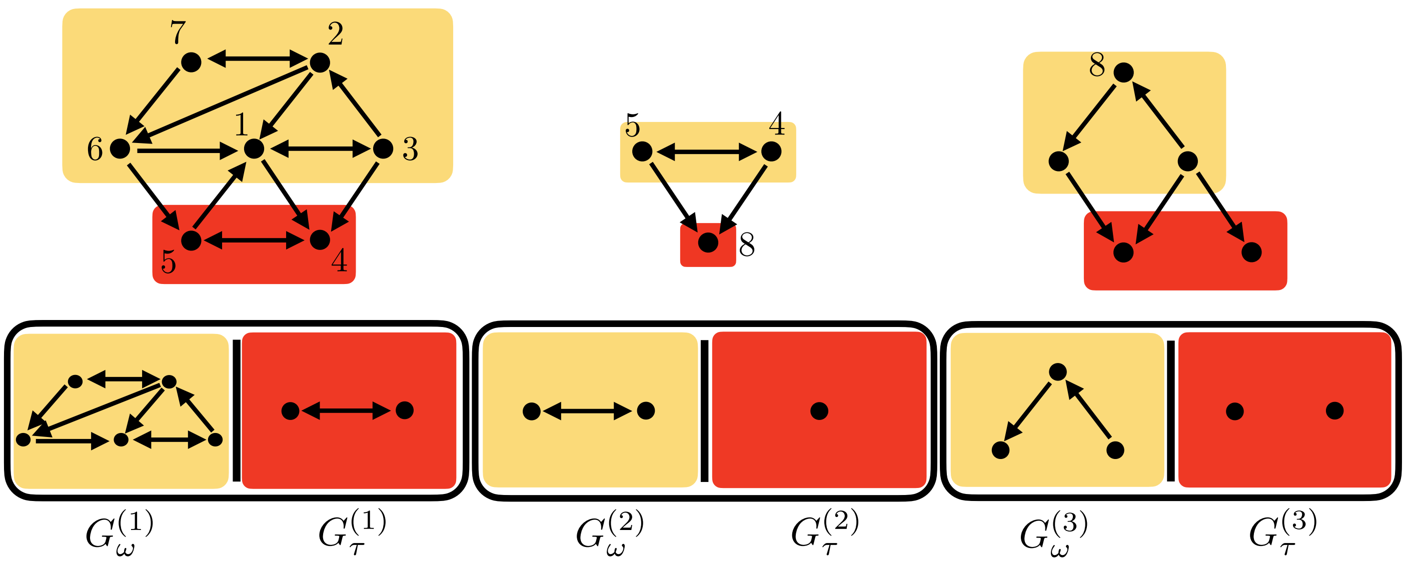
Conjecture: network activity flows from $\boxed{G_\omega} \to \boxed{G_\tau}$

Dominoes! We can chain them together...



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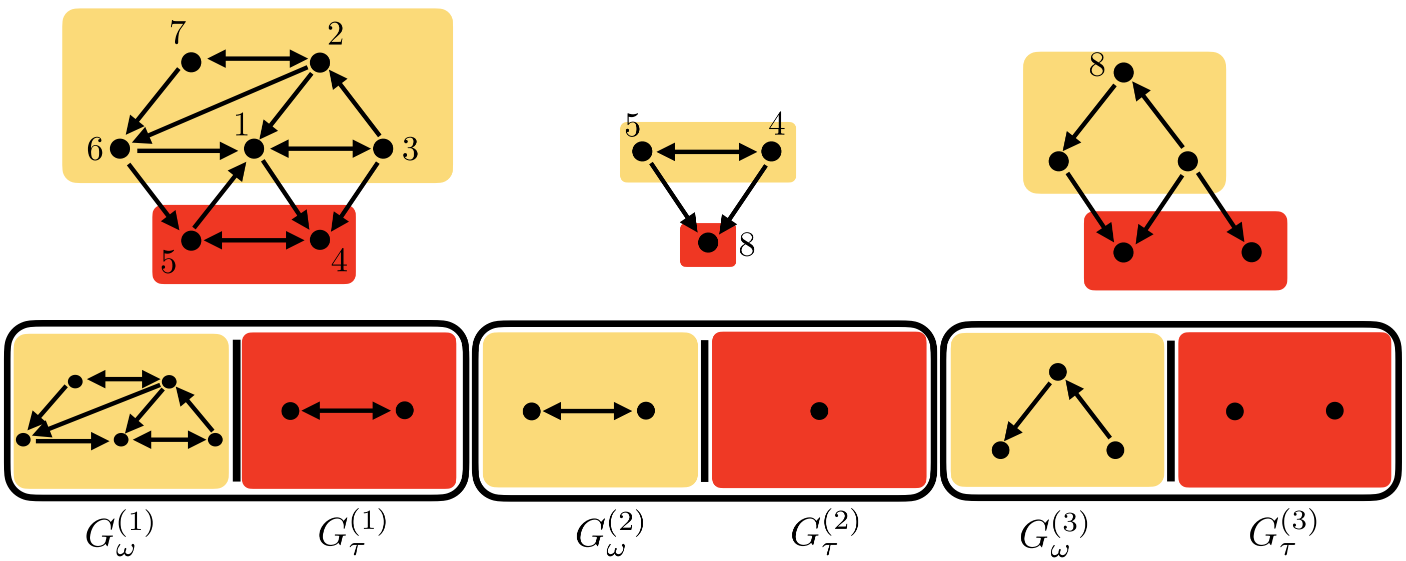

Theorem 3 (2024)
If we glue reducible graphs together along their dominoes, in a linear chain, so that G_τ of one is identified with a subgraph of G_ω of the next, then the glued graph reduces to the final $G_\tau^{(i)}$.

Curto 2024 (unpublished)

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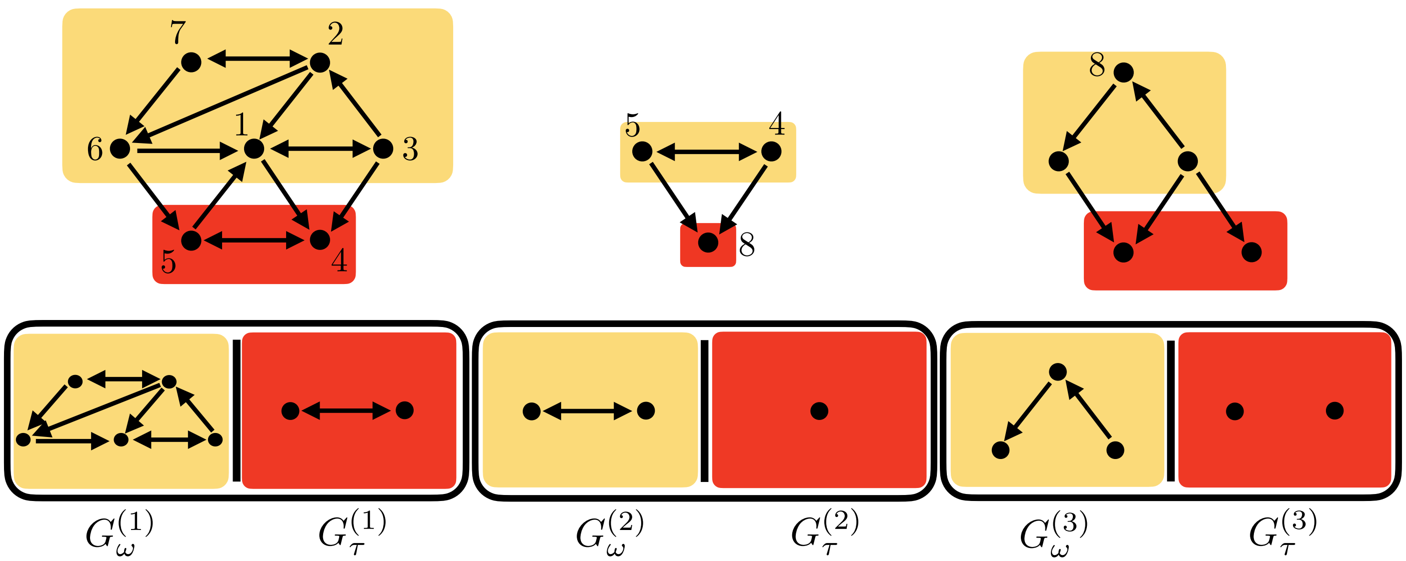
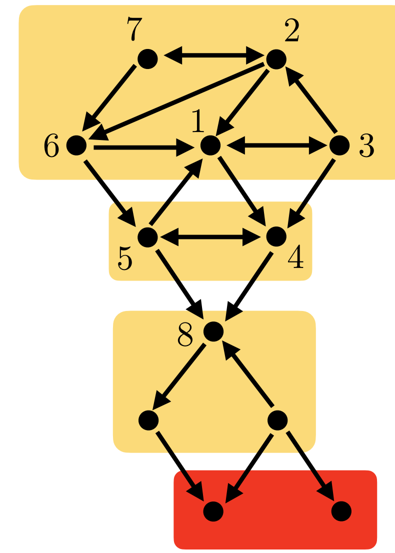


glued graph G



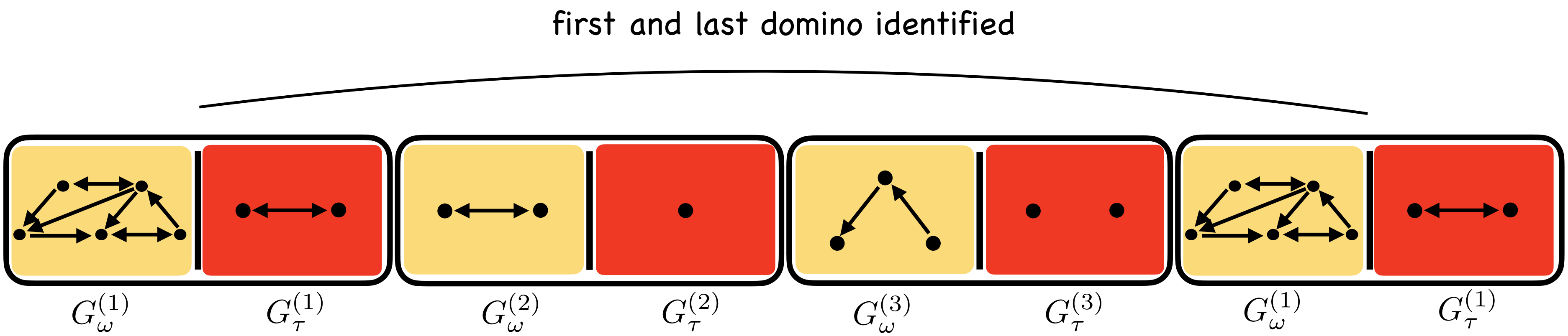
$$\widetilde{G} = G_\tau^{(3)}$$

$$\mathrm{FP}(G) = \mathrm{FP}(G_\tau^{(3)})$$

Theorem 3 (2024)
If we glue reducible graphs together along their dominoes, in a linear chain, so that G_τ of one is identified with a subgraph of G_ω of the next, then the glued graph reduces to the final $G_\tau^{(i)}$.

Curto 2024 (unpublished)

What about a cyclic chain?



Theorem 3 (2024)
If we glue reducible graphs together along their dominoes, in a linear chain,
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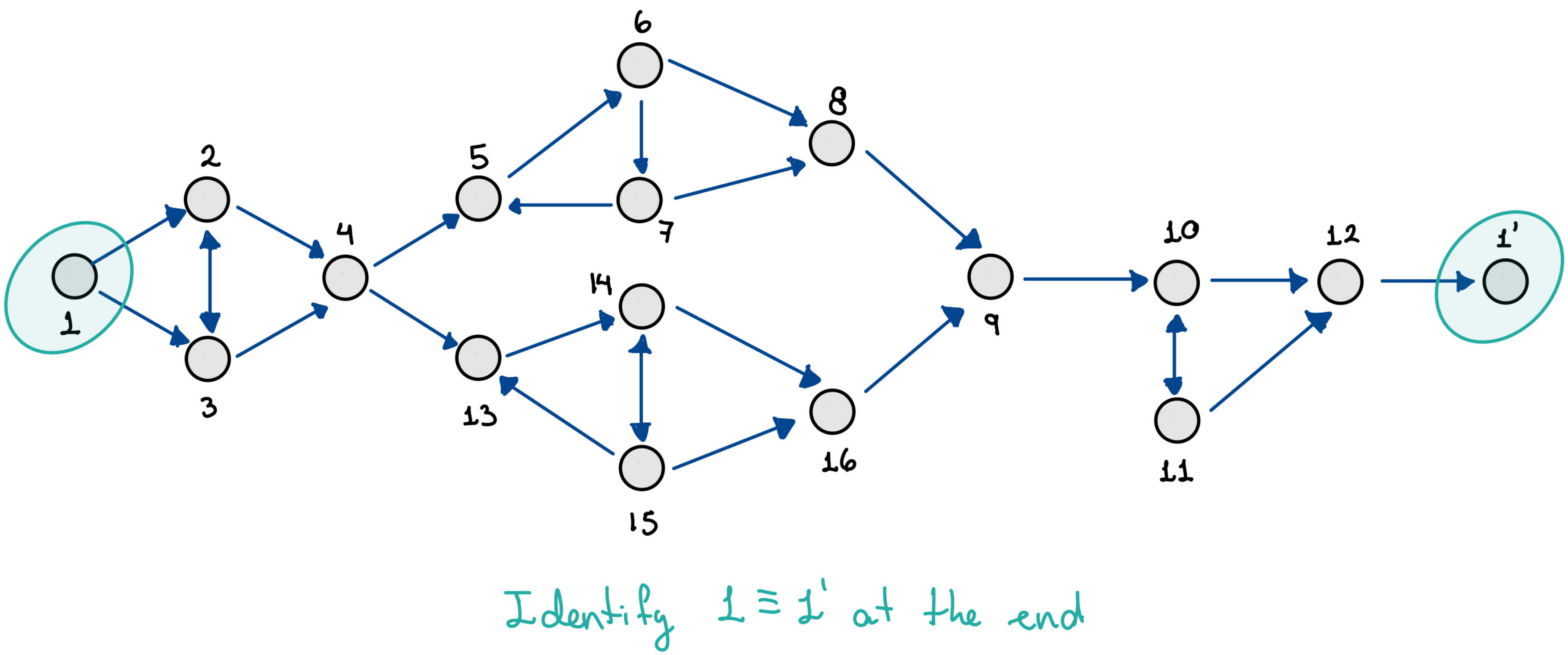
Cyclic chain example

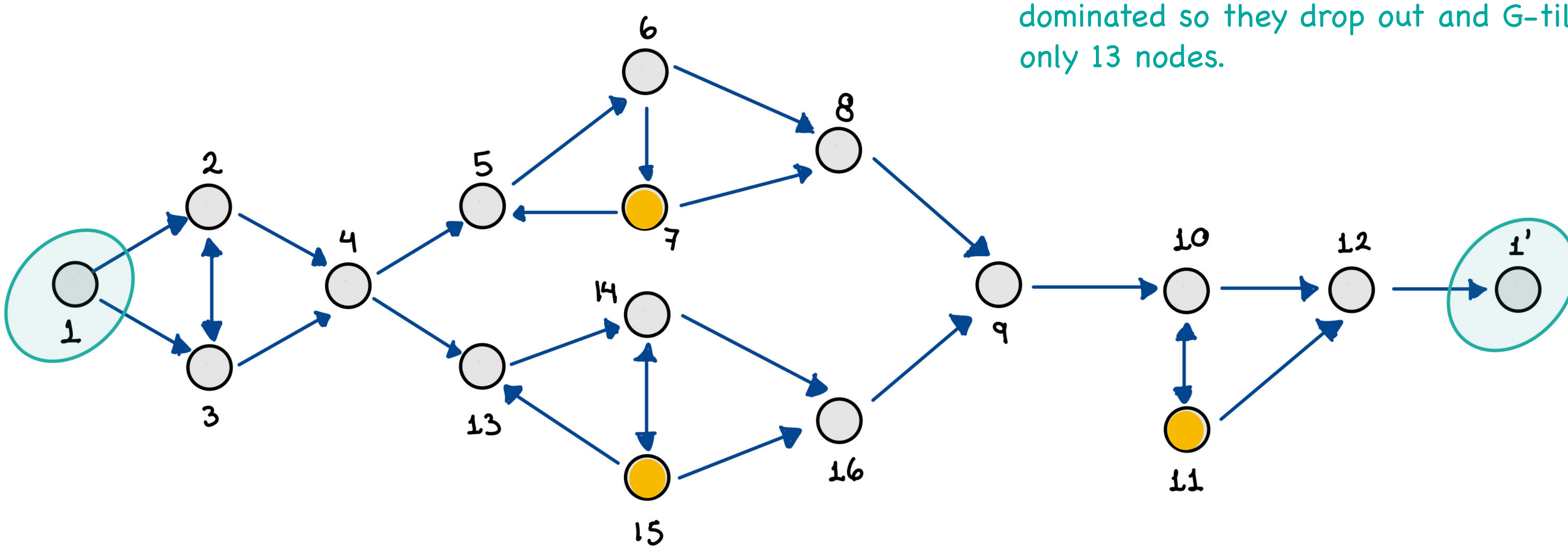


Domination reduction cannot be done, and the network activity will loop around.

Cyclic chain example

Domination reductions:

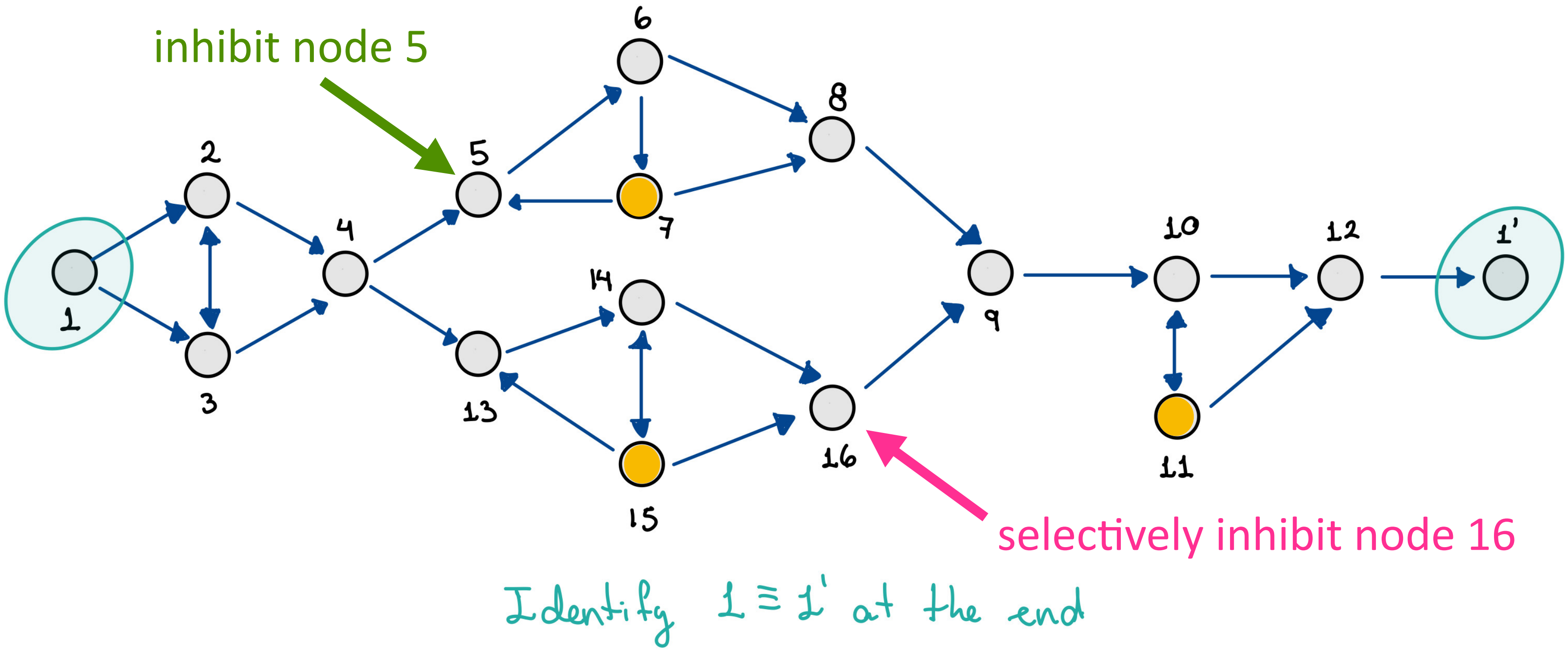
1) Without identifying 1′ and 1, G reduces to 1′
2) After identifying 1′ and 1, nodes 7, 11, 15 are dominated so they drop out and G-tilde has only 13 nodes.



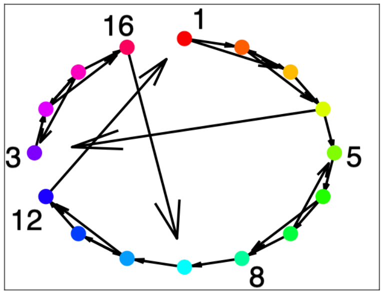
Identify 1 ≡ 1′ at the end

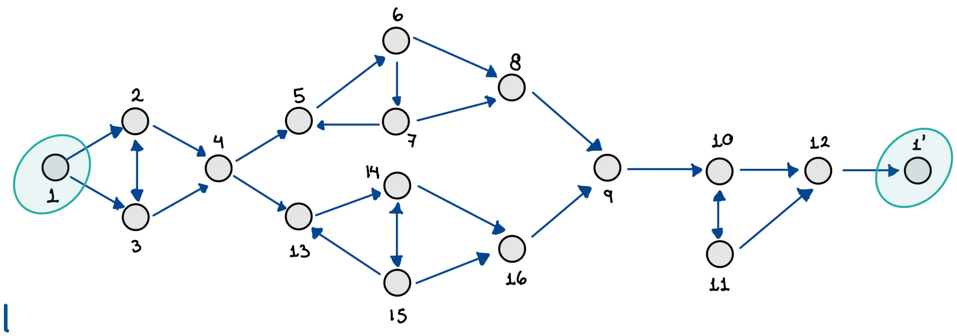
Domination reduction cannot be done, and the network activity will loop around.

Inhibitory control



What if you selectively inhibit one of the neurons?

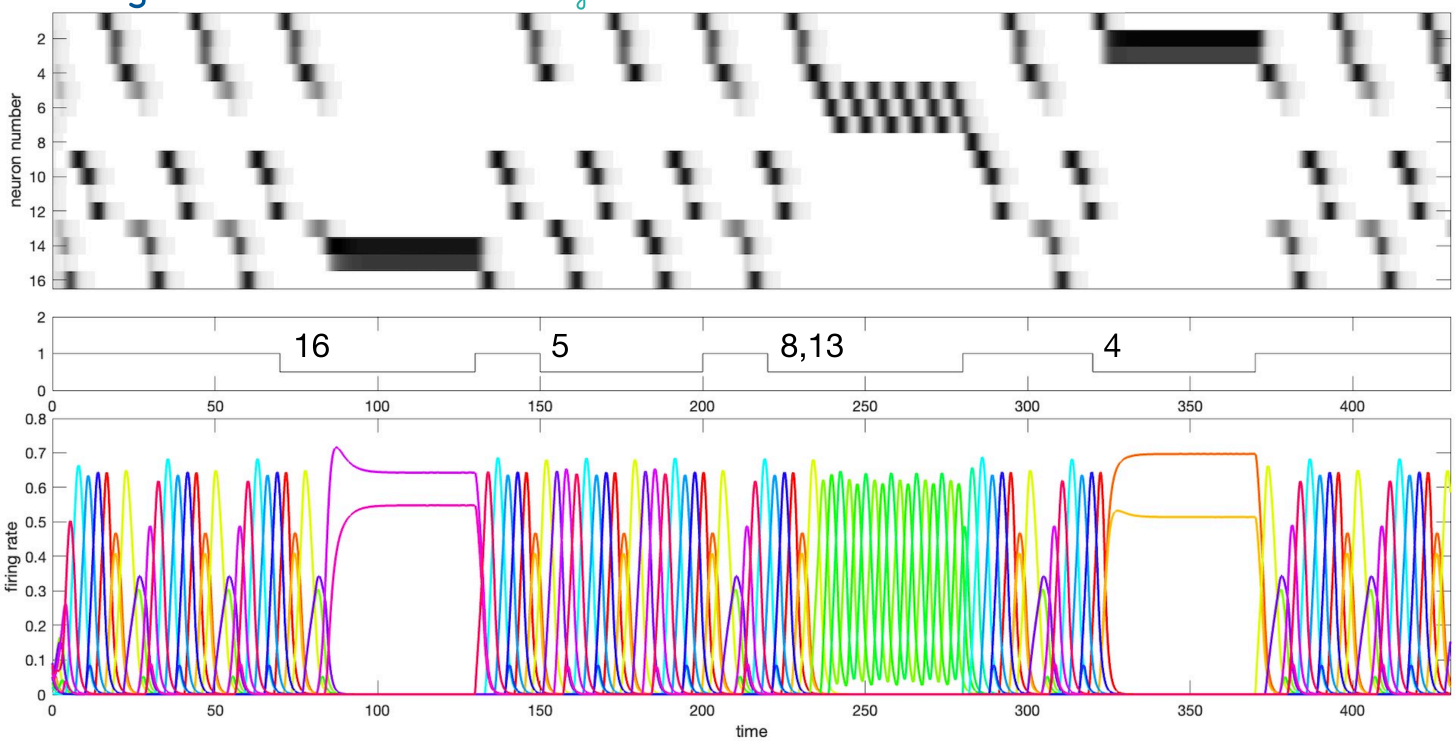




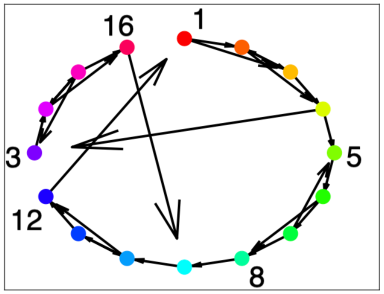
initial
“resting state”

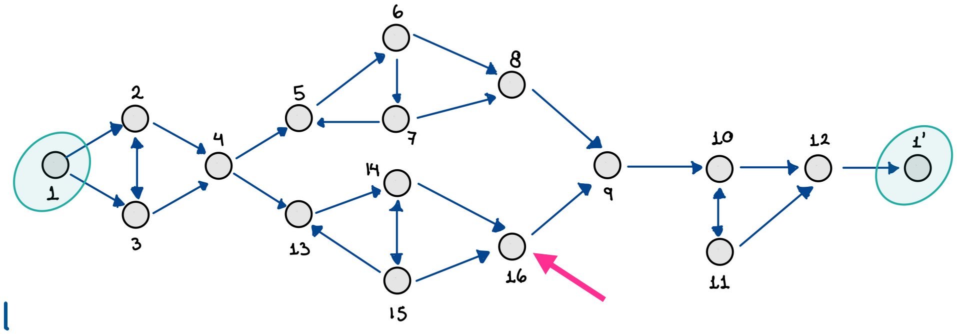
Identify $1 \equiv 1'$ at the end

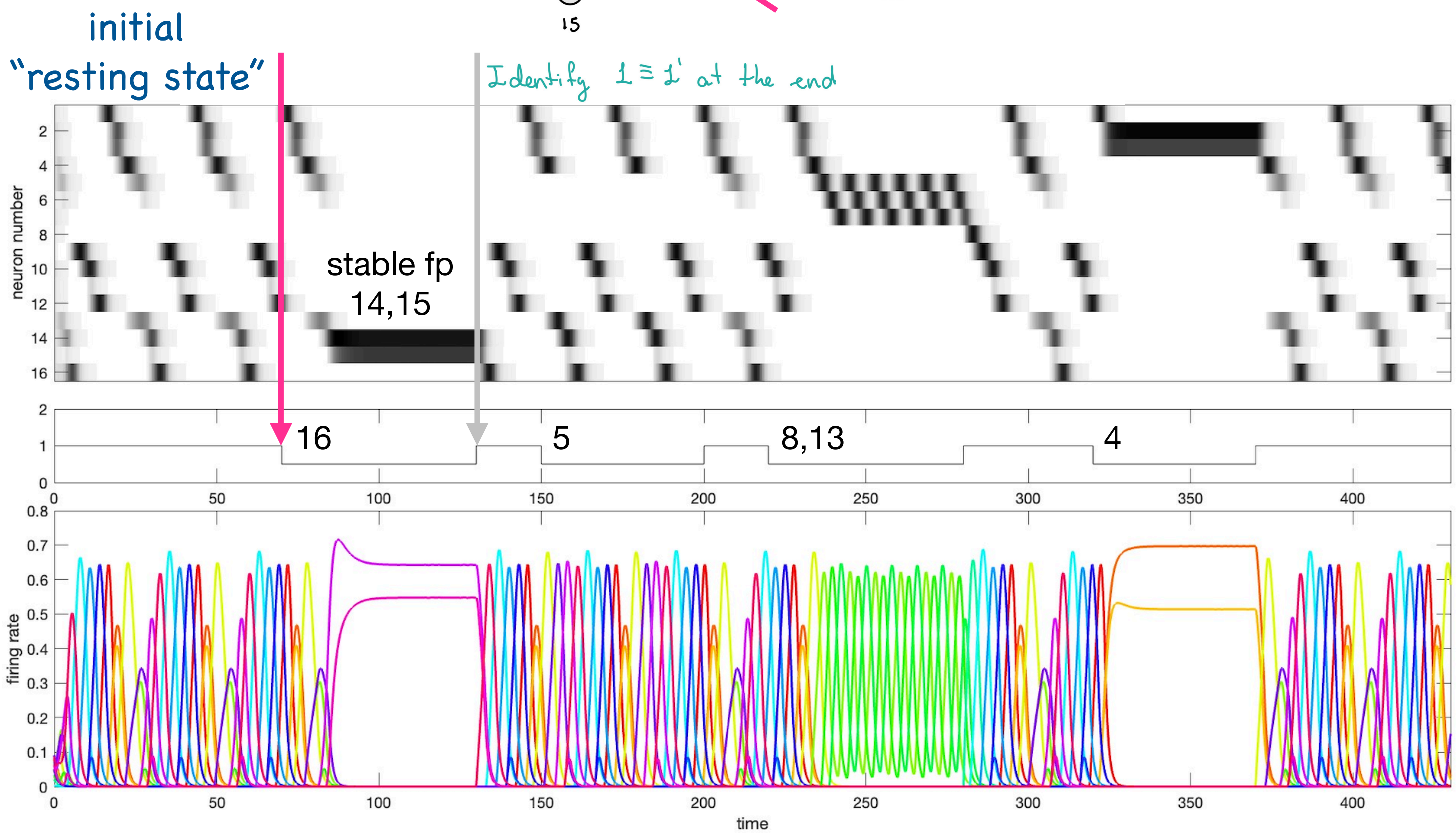
Control by inhibitory pulses:

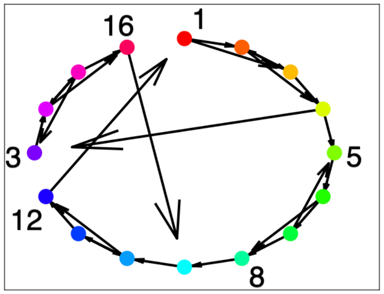


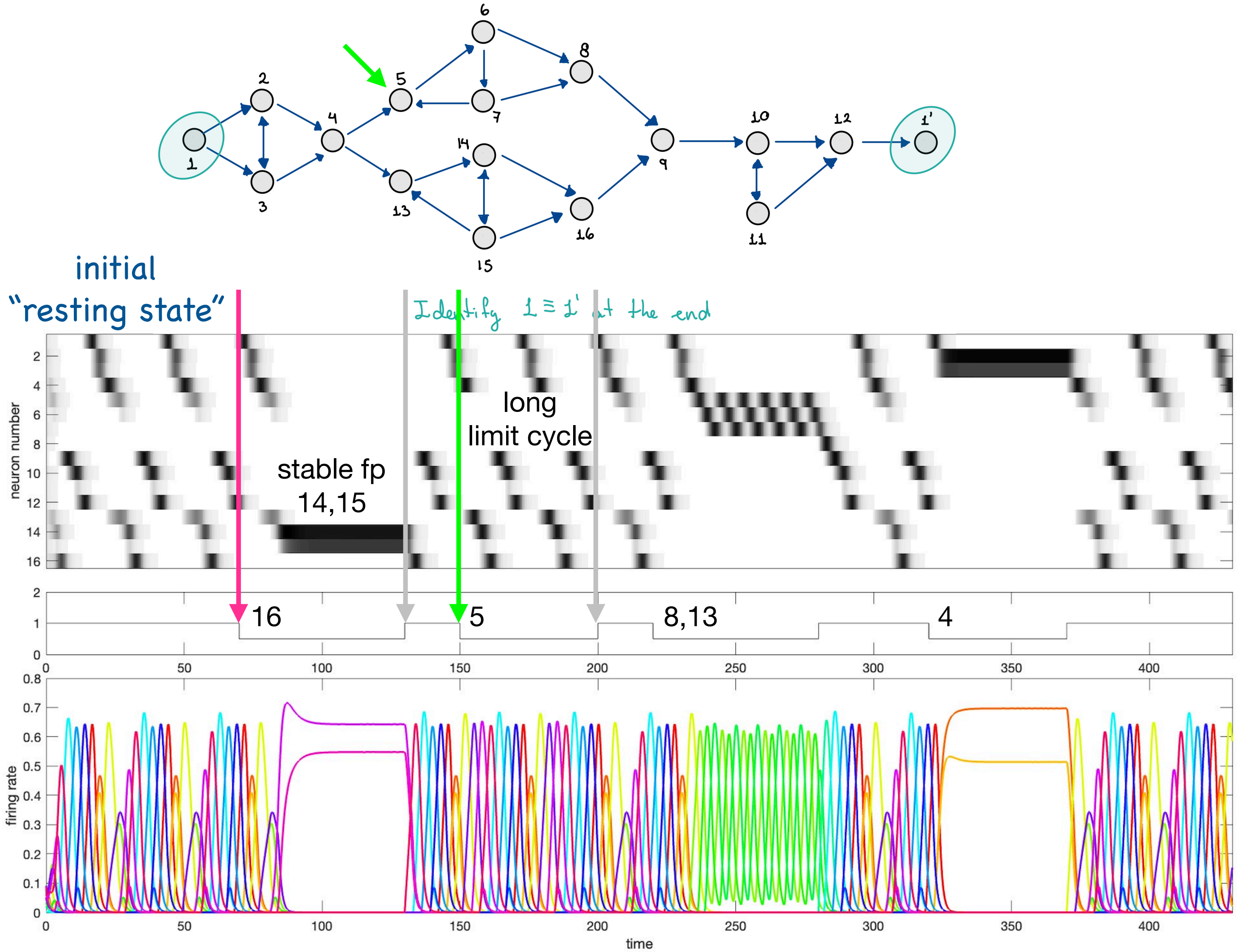
Control by inhibitory pulses:



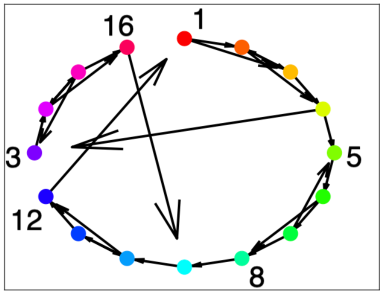


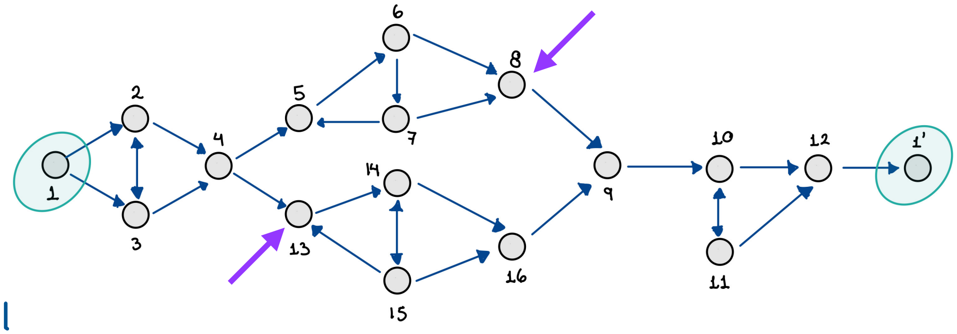




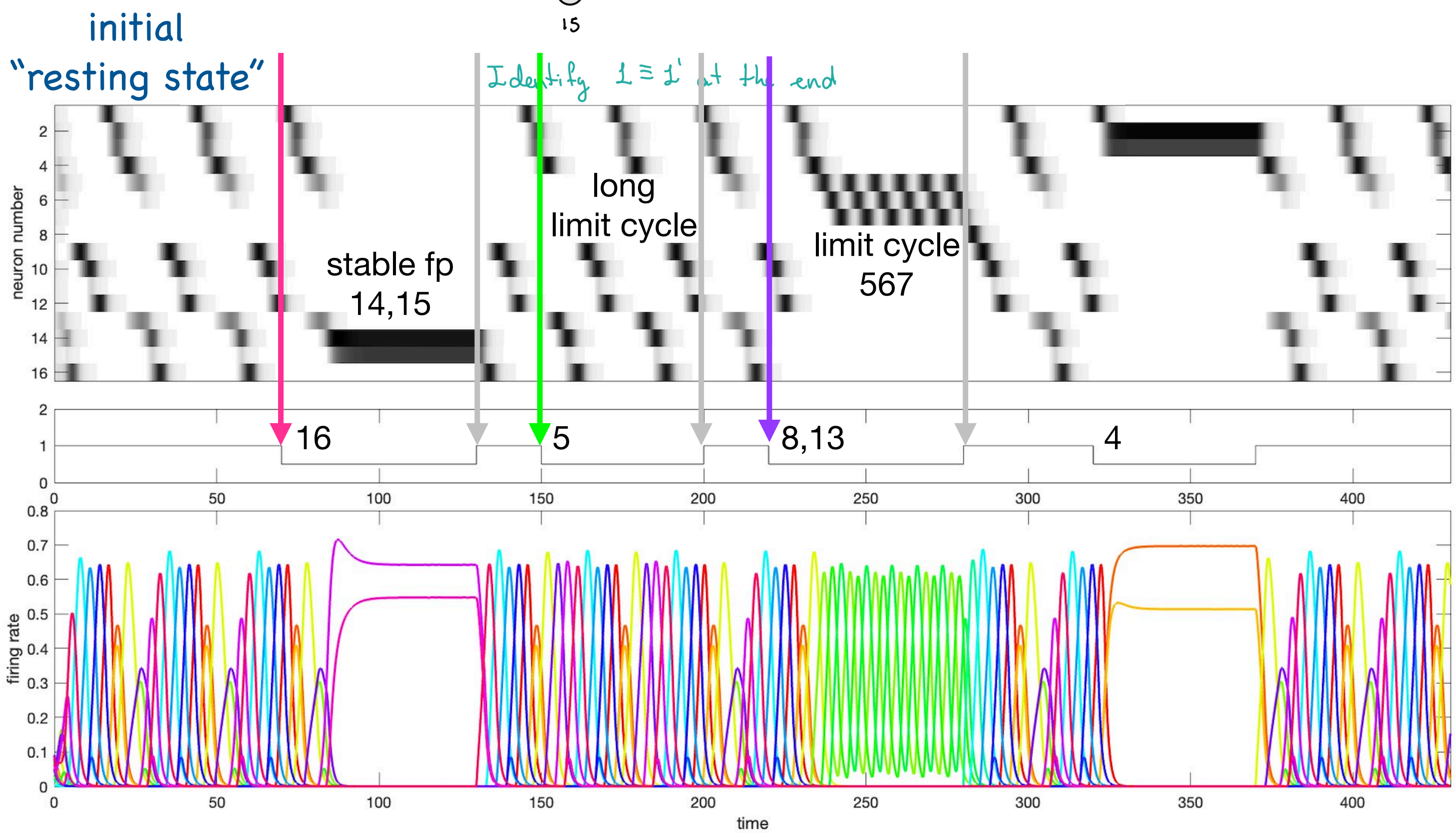


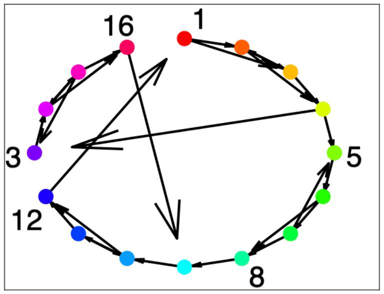
Control by
inhibitory pulses:

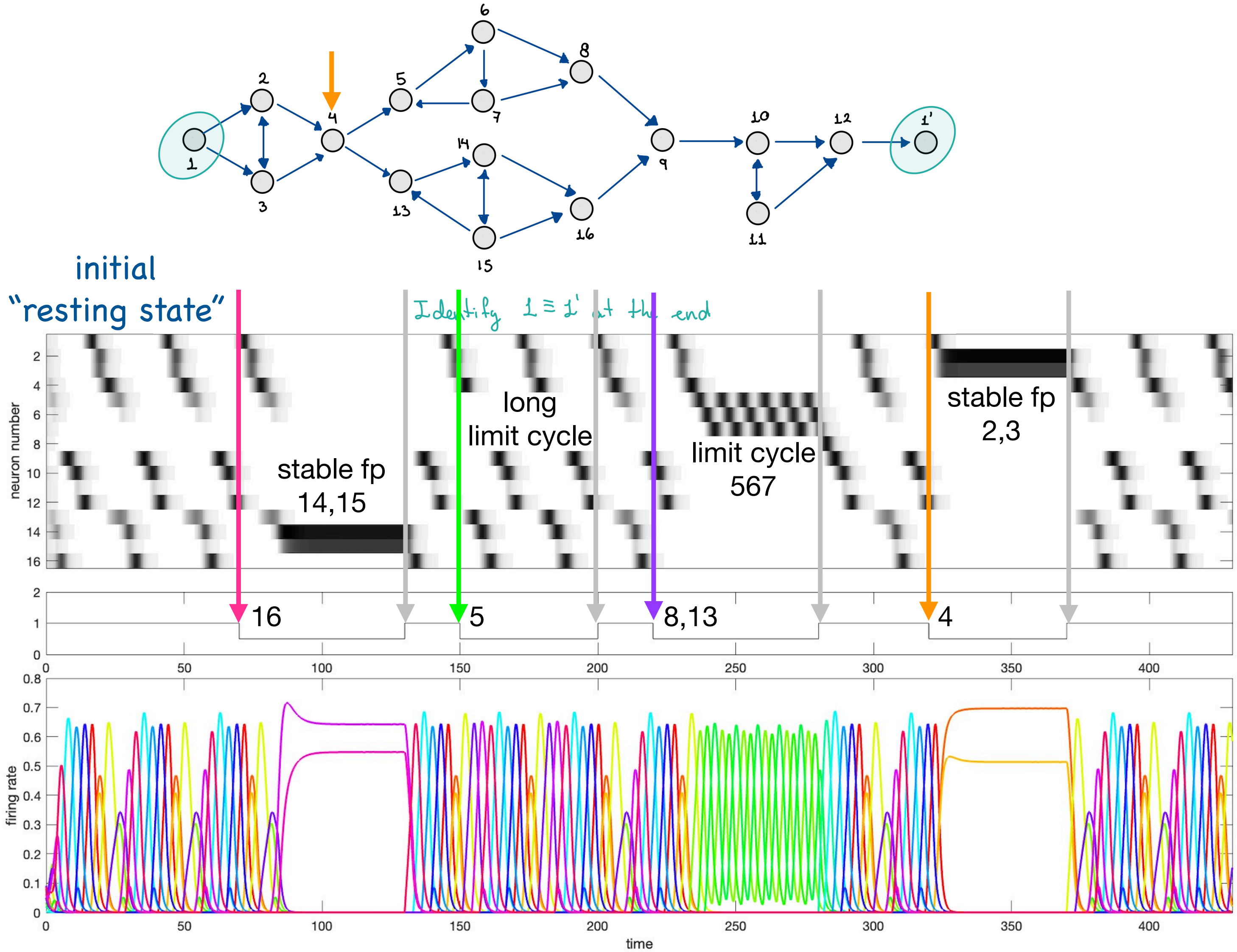




Control by inhibitory pulses:







Control by inhibitory pulses: