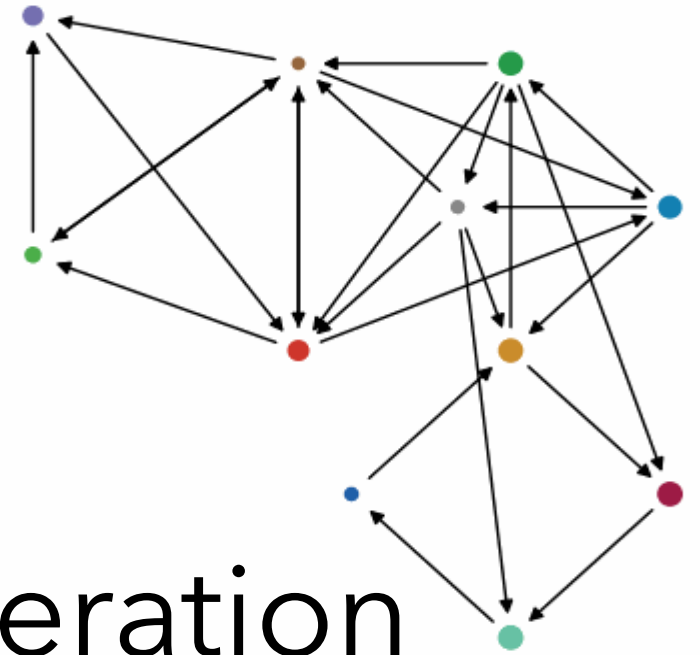
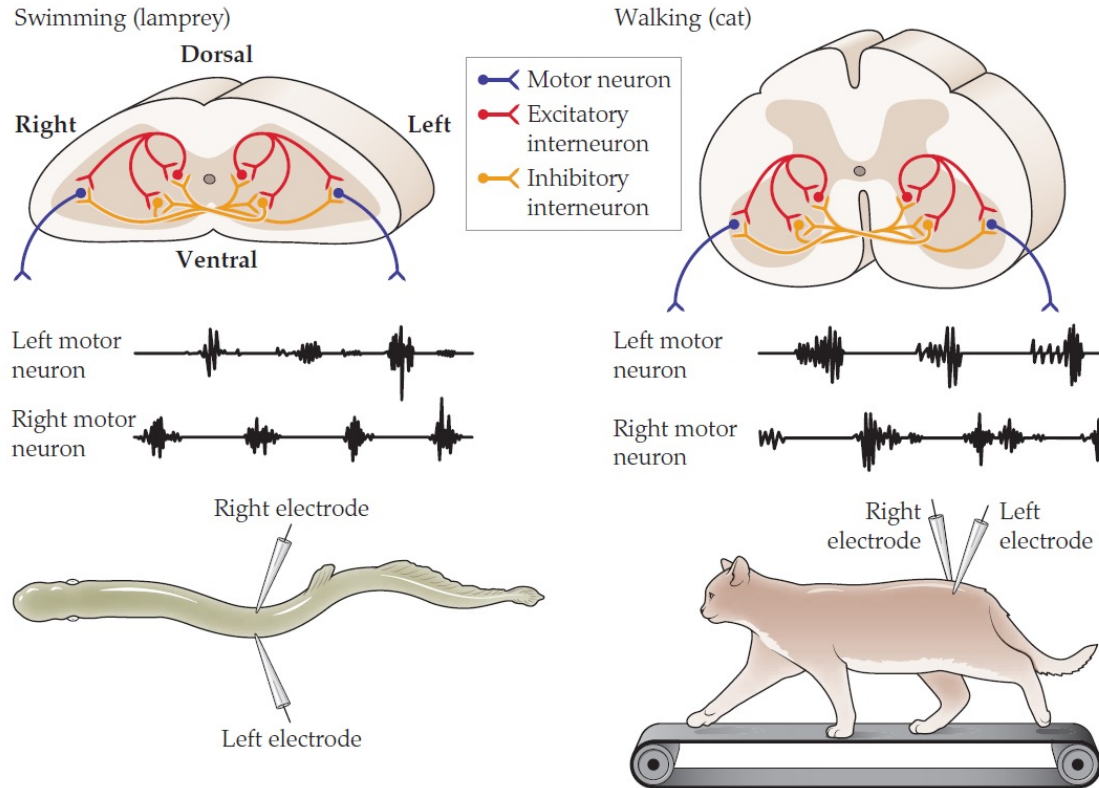


Attractor-based models for **sequences** and pattern generation in neural circuits



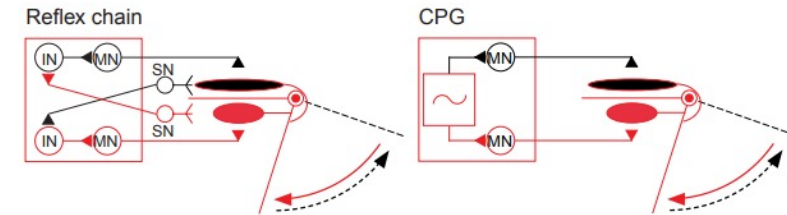
Juliana Londoño Álvarez
Applied Math, Brown University
with Carina Curto and Katie Morrison
August 2025

Oscillations arise in many brain processes

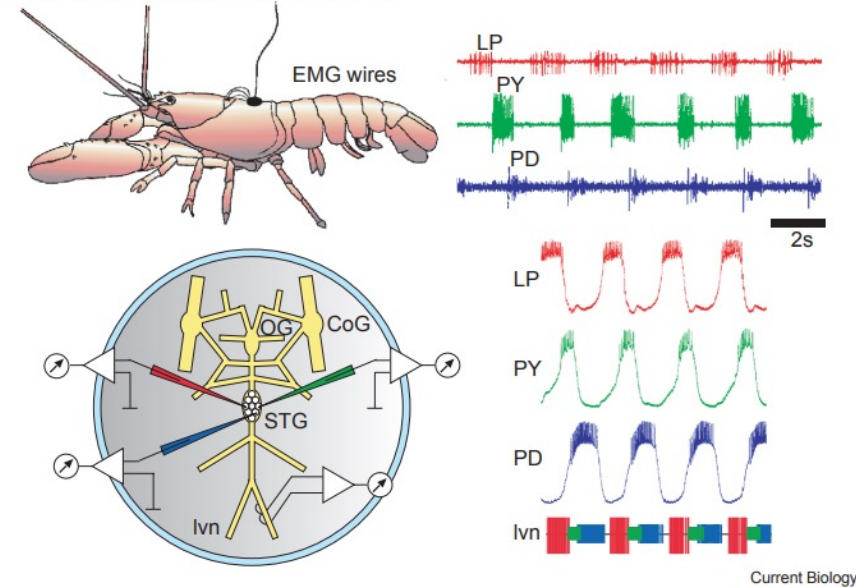


Eagleman & Downar, 2016, Brain and Behavior

(a) Reflexes vs central pattern generation

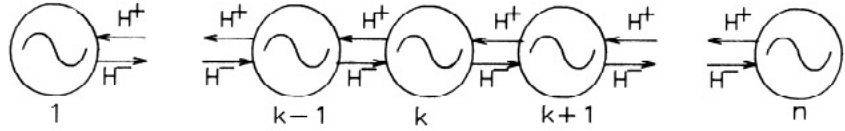


(b) *In vivo* and *in vitro* rhythmic activity



Marder & Bucher, 2001, Central Pattern Generators

Long history of coupled oscillator models in rhythm generation



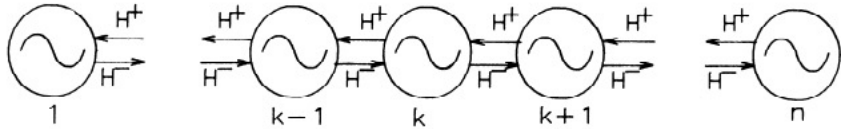
$$d\Theta_k/dt = \omega_k + H^+ (\Theta_{k+1} - \Theta_k) + H^- (\Theta_{k-1} - \Theta_k)$$

Williams et al., 1990, *Lamprey CPG*

Theoretical results &
locomotion models
(~80s to 00s):

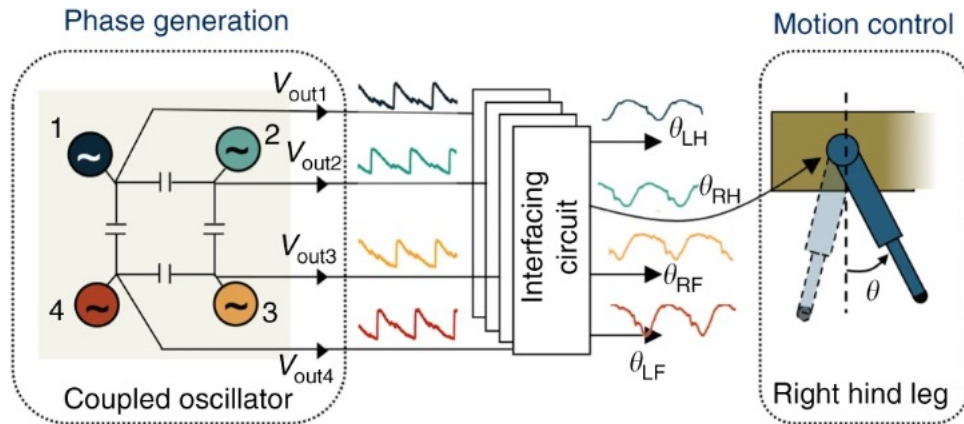
Nancy Kopell, Bard
Ermentrout, A.H. Cohen,
Martin Golubitsky, Ian
Stewart, Pietro-Luciano
Buono, J.J. Collins and
many more...

Long history of coupled oscillator models in rhythm generation



$$d\Theta_k/dt = \omega_k + H^+ (\Theta_{k+1} - \Theta_k) + H^- (\Theta_{k-1} - \Theta_k)$$

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Dutta et al., 2019, *Programmable coupled oscillators*

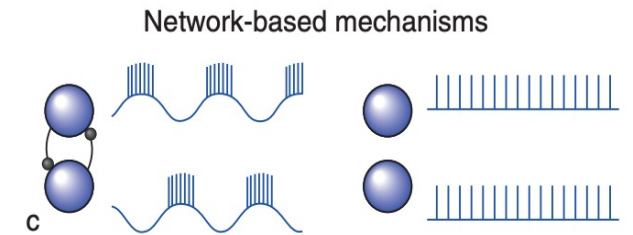
Theoretical results & locomotion models (~80s to 00s):

Nancy Kopell, Bard Ermentrout, A.H. Cohen, Martin Golubitsky, Ian Stewart, Pietro-Luciano Buono, J.J. Collins and many more...

Robotics:

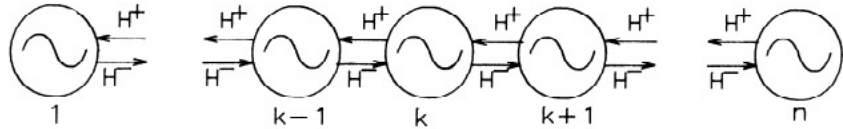
Auke Ijspeert, Suman Datta and many more...

- ☺ lots of theoretical results available
- ☹ periodic solutions might be fine-tuned (not attractors)
- ☹ not all neurons are pacemakers



Bucher, 2009, *Central pattern generators*

Long history of coupled oscillator models in rhythm generation



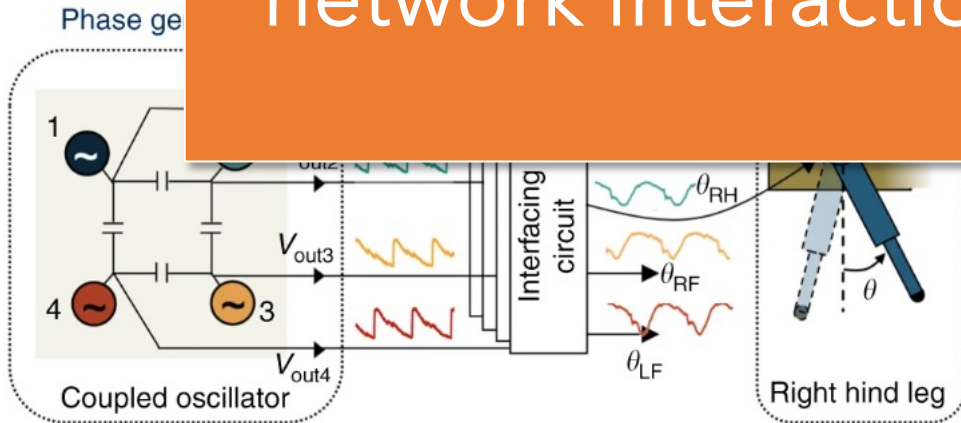
$$d\Theta_k/dt = \omega_k + H^+ (\Theta_{k+1} - \Theta_k) + H^- (\Theta_{k-1} - \Theta_k)$$

Williams et al.

Theoretical results & locomotion models (~80s to 00s):

- ☺ lots of theoretical results available
- ☹ periodic solutions might be fine-tuned (not

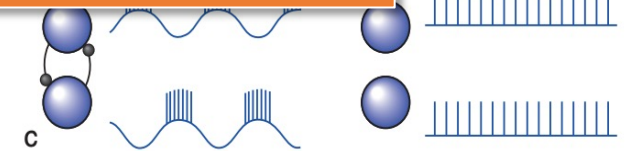
How do (robust) oscillations emerge from network interactions between non-oscillating units?



Dutta et al., 2019, *Programmable coupled oscillators*

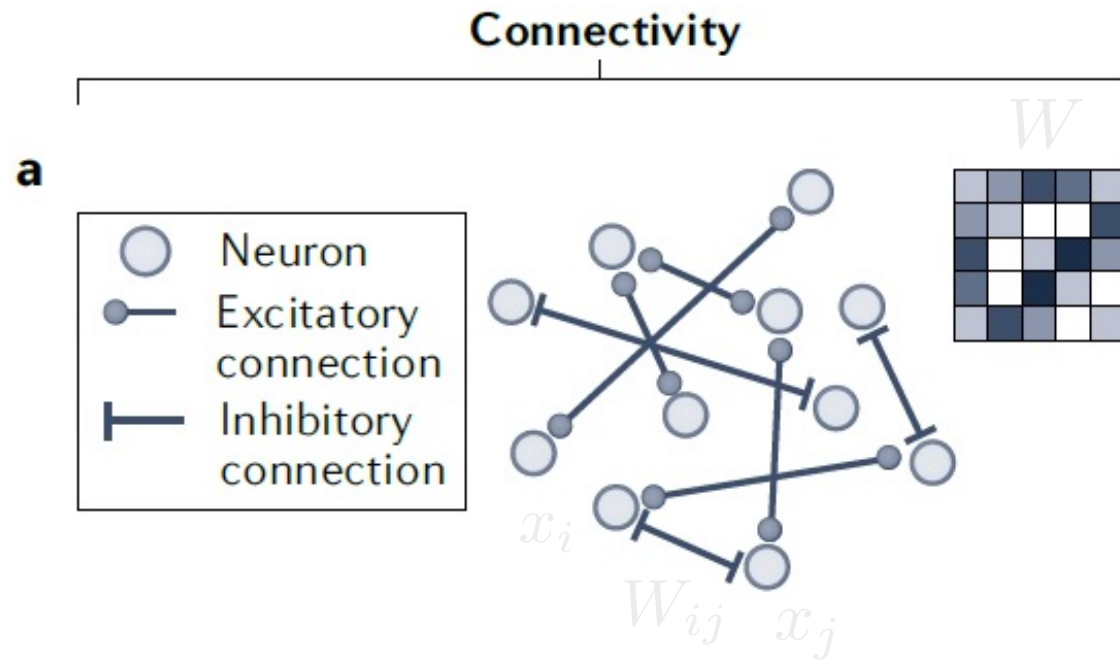
Robotics:

Auke Ijspeert, Suman Datta and many more...



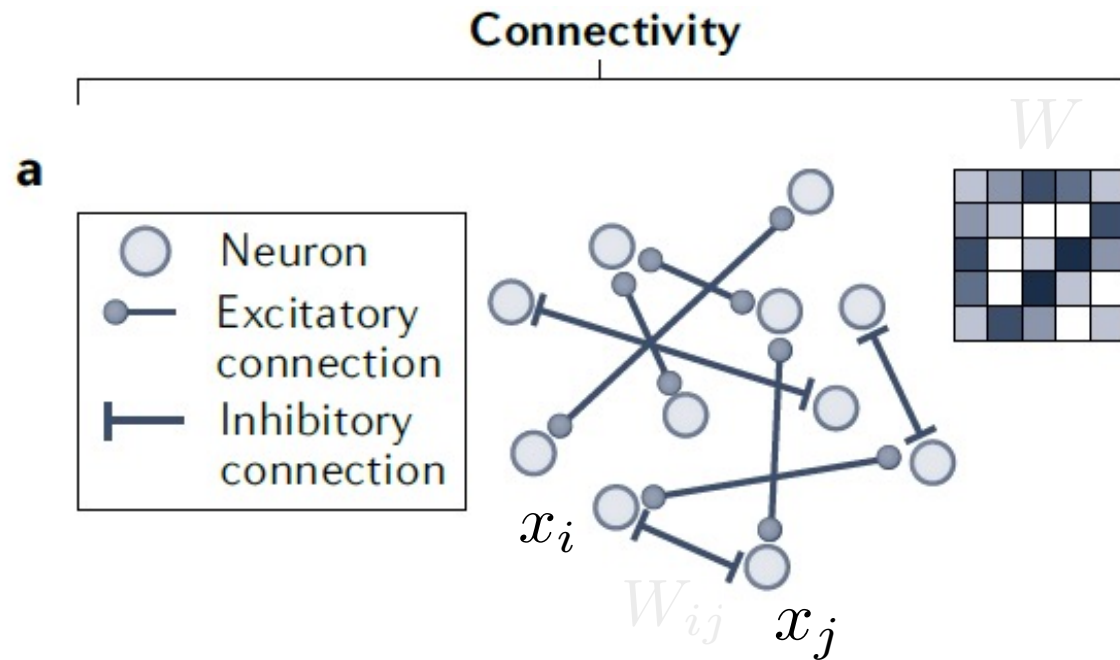
Bucher, 2009, *Central pattern generators*

Attractor networks are good at isolating the role of connectivity



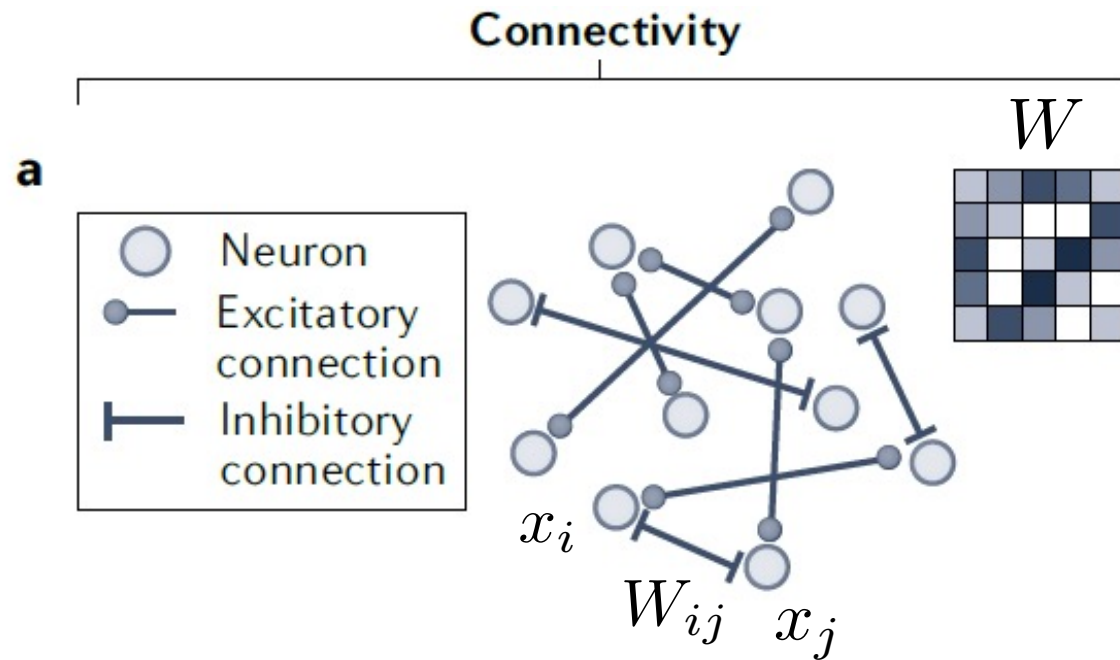
$$\frac{dx_i}{dt} = -x_i + \varphi \left(\sum_{j=1}^n W_{ij} x_j + b_i \right)$$

Attractor networks are good at isolating the role of connectivity



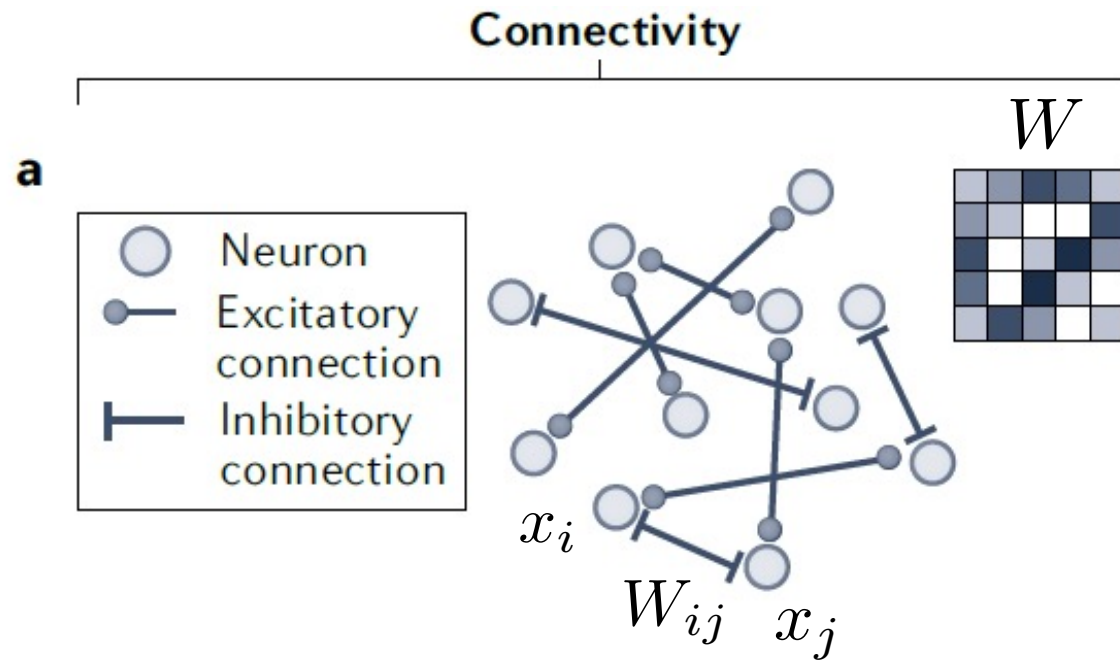
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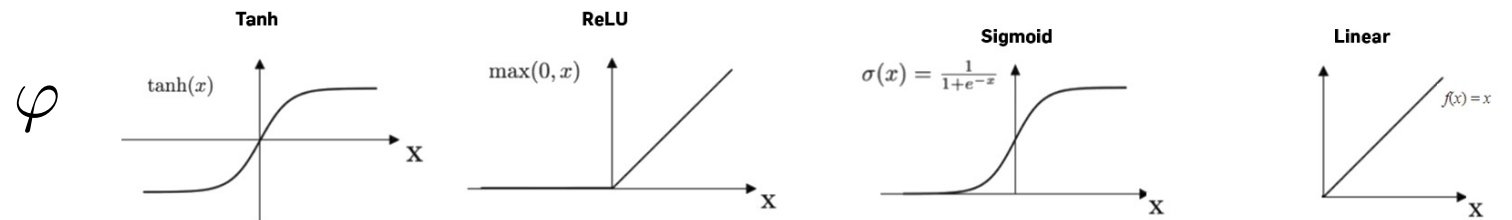


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Attractor networks are good at isolating the role of connectivity

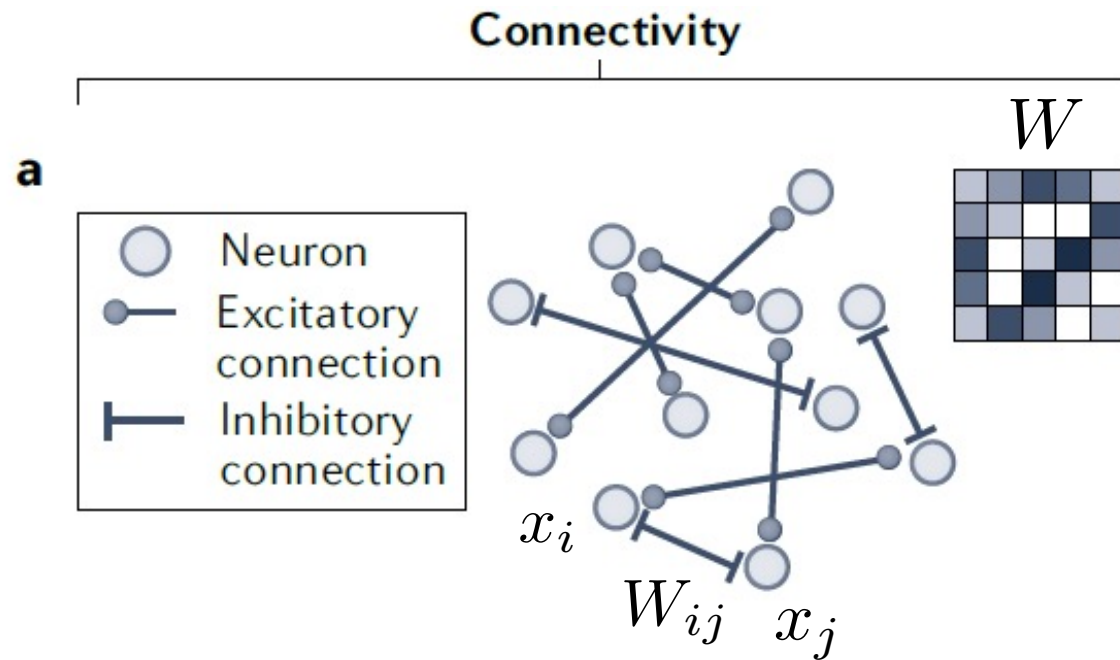


$$\frac{dx_i}{dt} = -x_i + \varphi \left(\sum_{j=1}^n W_{ij} x_j + b_i \right)$$

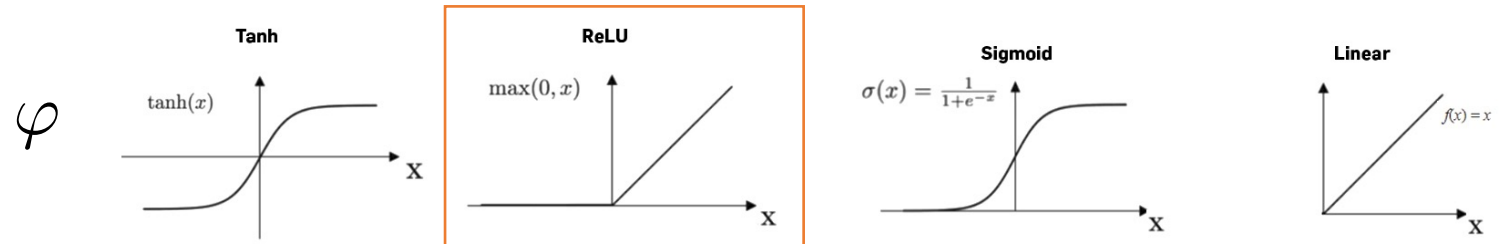


AI Wiki

Attractor networks are good at isolating the role of connectivity

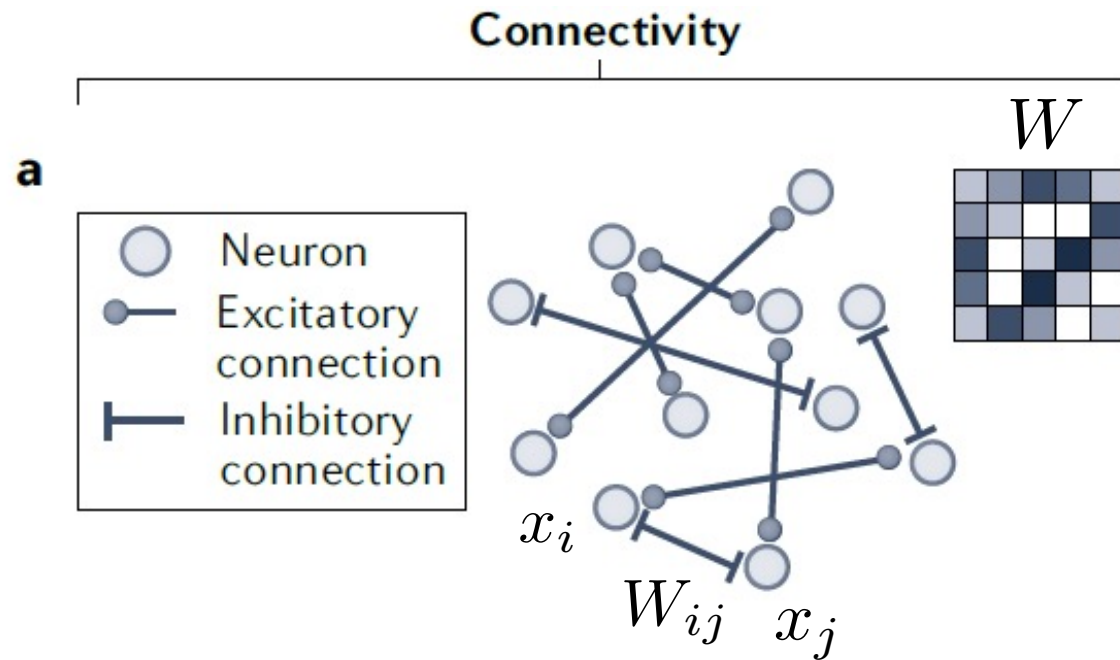


$$\frac{dx_i}{dt} = -x_i + \varphi \left(\sum_{j=1}^n W_{ij} x_j + b_i \right)$$



AI Wiki

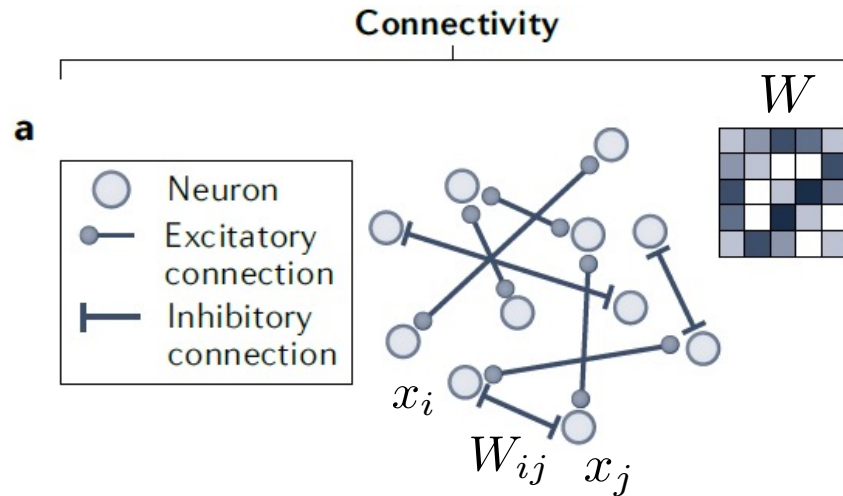
Attractor networks are good at isolating the role of connectivity



$$\frac{dx_i}{dt} = -x_i + \varphi \left(\sum_{j=1}^n W_{ij} x_j + b_i \right)$$

Recurrent **dynamical** network

Attractors are widely used in neuroscience as representations of cognitive processes



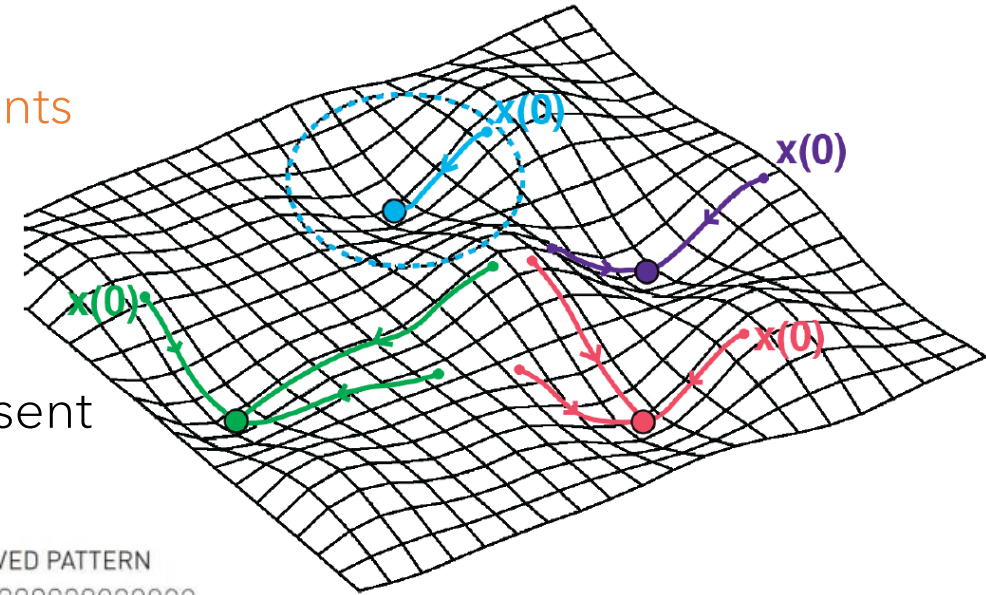
$$\frac{dx_i}{dt} = -x_i + \varphi \left(\sum_{j=1}^n W_{ij} x_j + b_i \right)$$

Recurrent dynamical network

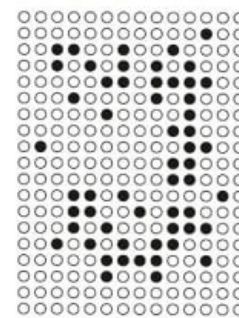
Hopfield networks

Attractors are
stable fixed points

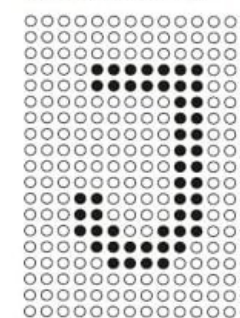
Attractors represent
memories



INPUT PATTERN



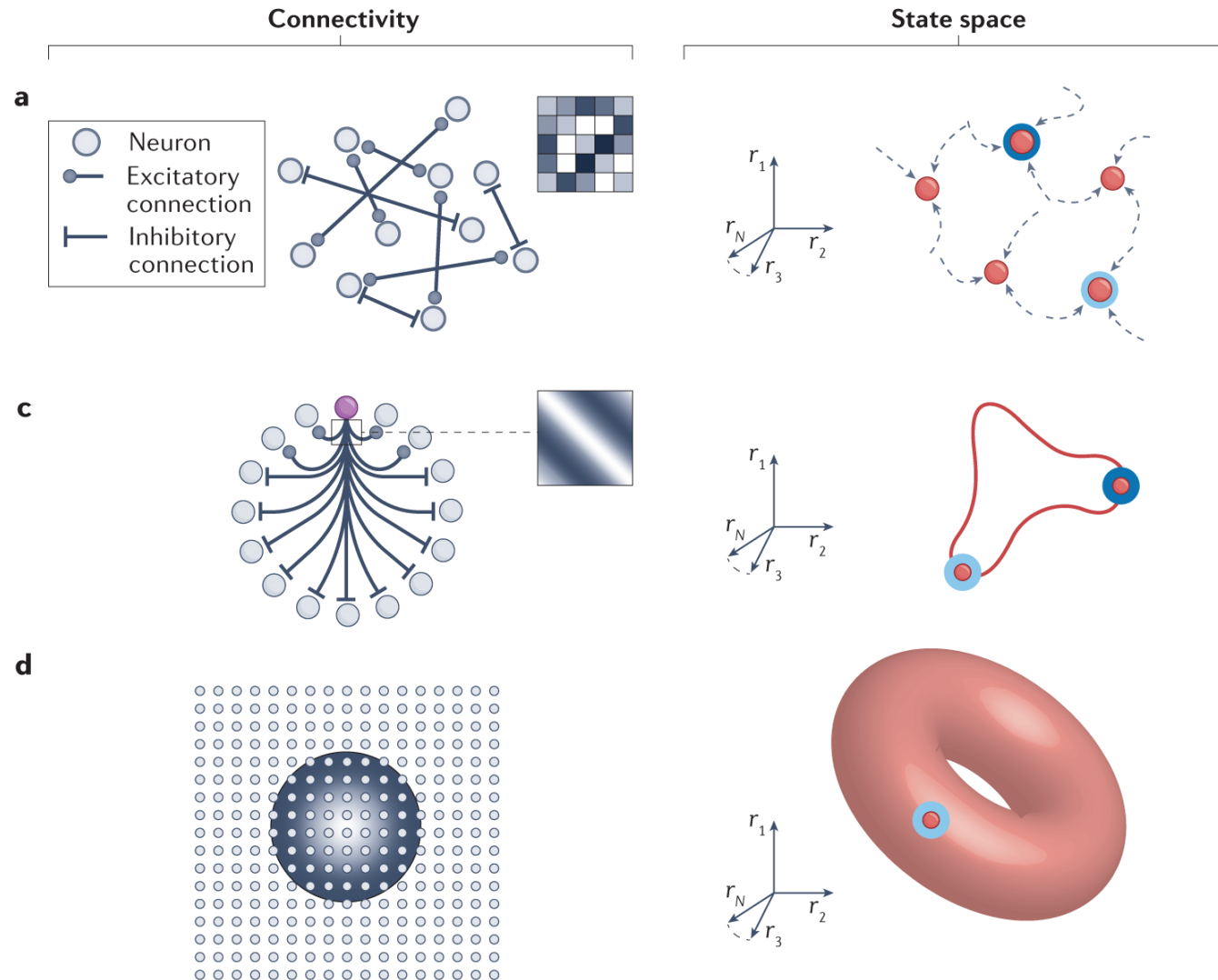
SAVED PATTERN



Curto & Morrison, 2023, graph rules for recurrent neural network dynamics

© Johan Jarnestad/The Royal Swedish Academy of Sciences

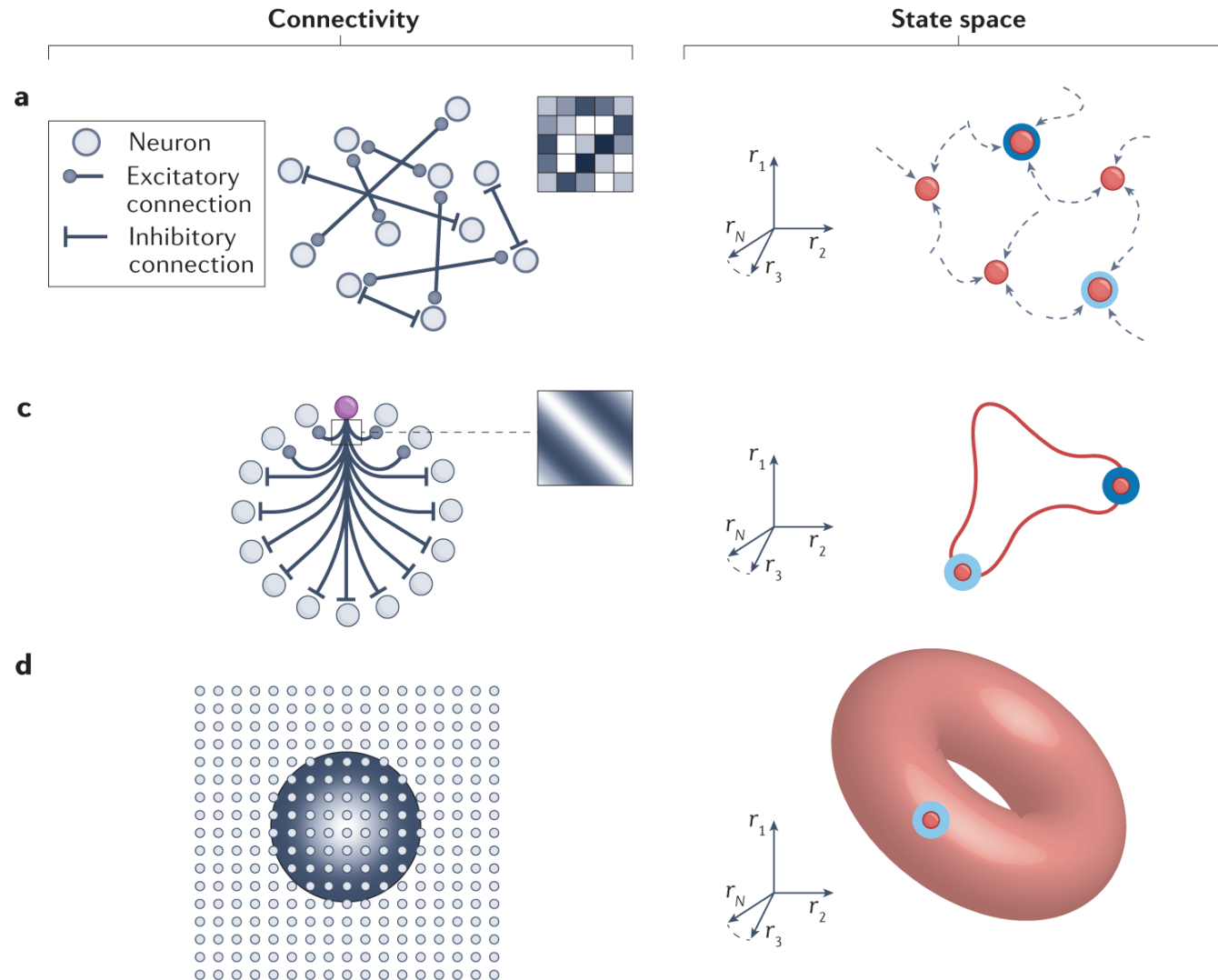
Attractors are widely used in neuroscience as representations of cognitive processes



☺ neurons are not pacemakers

$$\frac{dx}{dt} = -x + \varphi(Wx + b)$$

Attractors are widely used in neuroscience as representations of cognitive processes

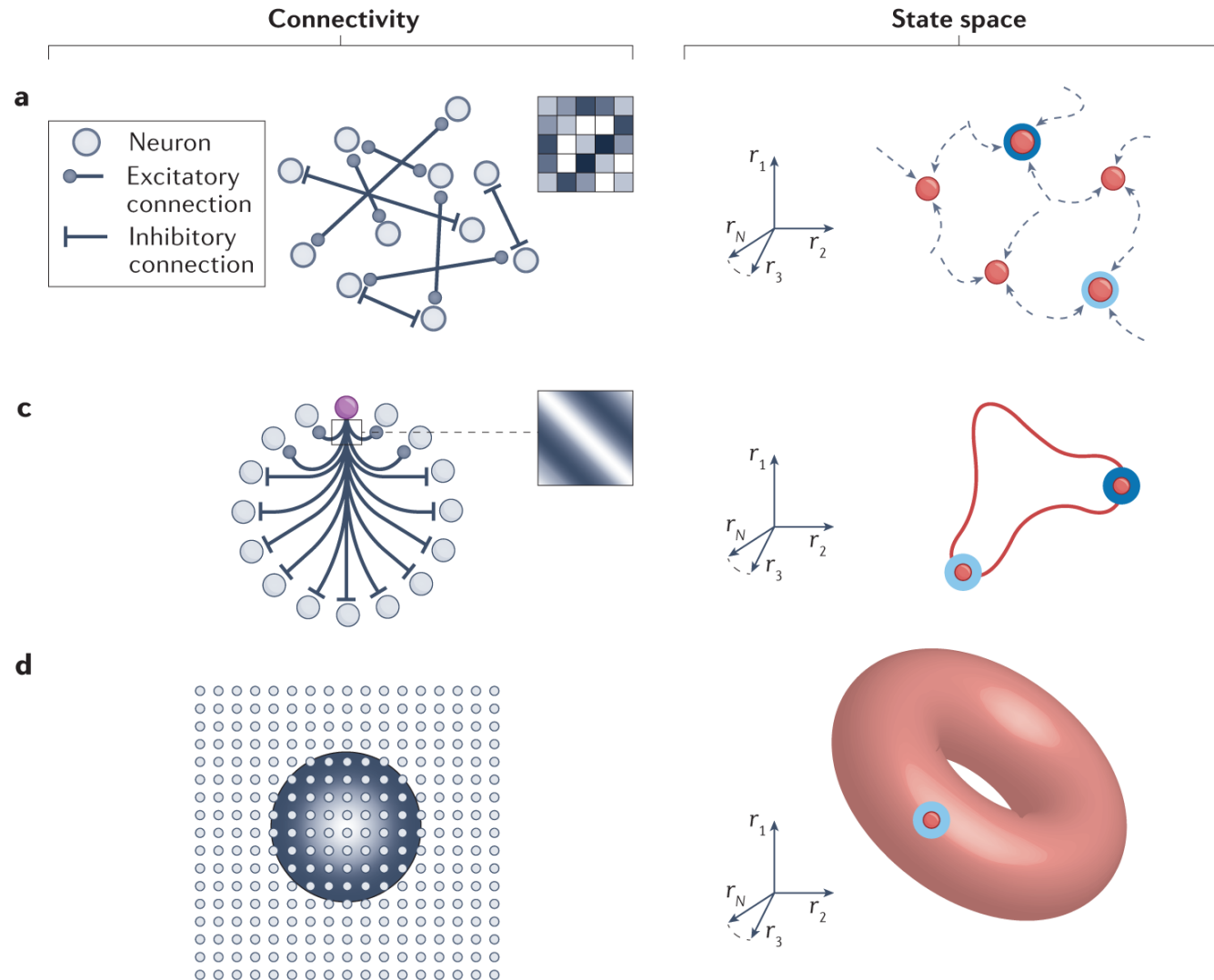


☺ neurons are not pacemakers

$$\frac{dx}{dt} = -x + \varphi(Wx + b)$$

☺ patterns are attractors of the network

Attractors are widely used in neuroscience as representations of cognitive processes



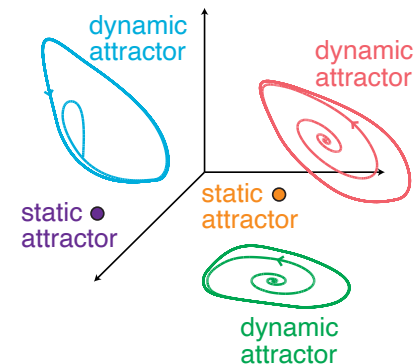
☺ neurons are not pacemakers

$$\frac{dx}{dt} = -x + \varphi(Wx + b)$$

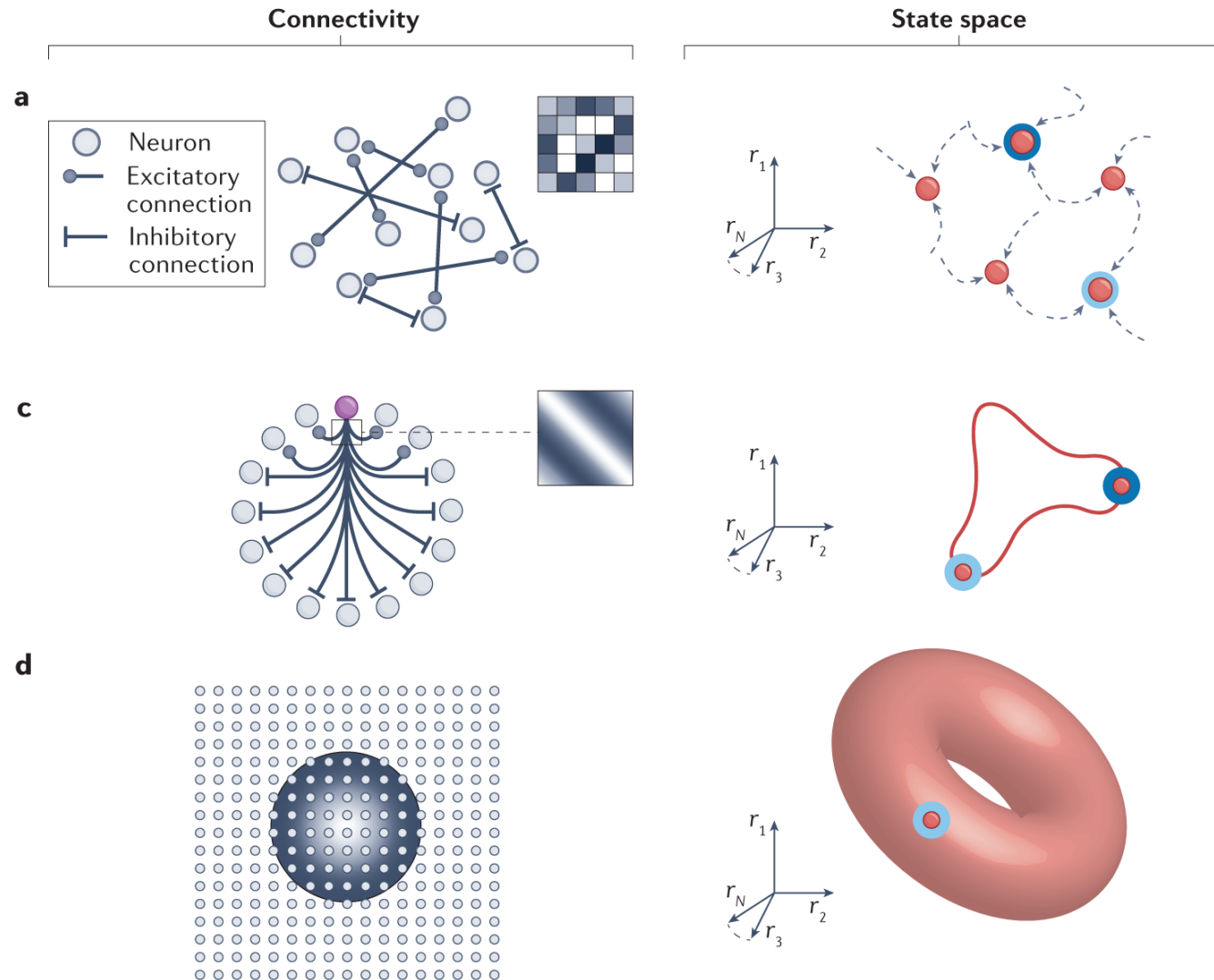
☺ patterns are attractors of the network

☺ lots of theoretical results available...

$W = ??$



Attractors are widely used in neuroscience as representations of cognitive processes



☺ neurons are not pacemakers

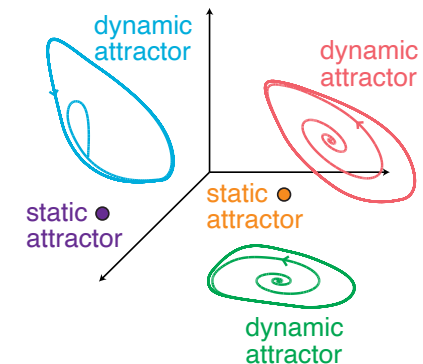
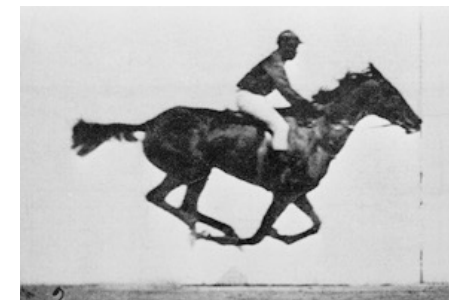
$$\frac{dx}{dt} = -x + \varphi(Wx + b)$$

☺ patterns are attractors of the network

☺ lots of theoretical results available...

☹ many of them for *fixed points*

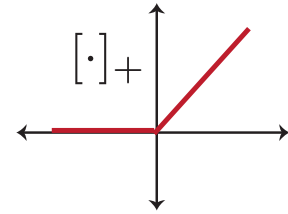
$W = ??$



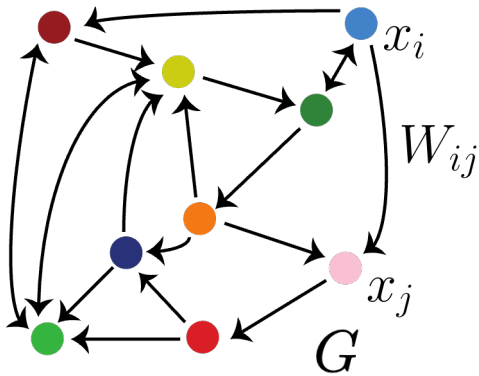
Combinatorial threshold-linear networks (CTLNs)

threshold-linear networks (TLNs):

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



whose connectivity matrix is defined by a directed graph:



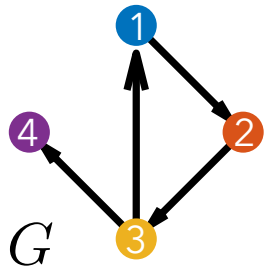
$$W_{ij} = \begin{cases} 0 & \text{if } i = j \\ -1 + \varepsilon & \text{if } j \rightarrow i \text{ in } G \text{ } j \text{ weakly inhibits } i \\ -1 - \delta & \text{if } j \not\rightarrow i \text{ in } G \text{ } j \text{ strongly inhibits } i \end{cases}$$

$$b_i = \theta \quad \text{Constant input}$$

$$\varepsilon, \delta > 0$$

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

Attractors of (C)TLNs



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

$$b = \begin{bmatrix} \theta \\ \theta \\ \theta \\ \theta \end{bmatrix}$$



$$\frac{dx}{dt} = -x + [Wx + b]_+$$



$$\frac{dx^*}{dt} = 0 \quad \downarrow \quad x_i^* = \left[\sum_{j=1}^n W_{ij} x_j^* + b_i \right]_+$$

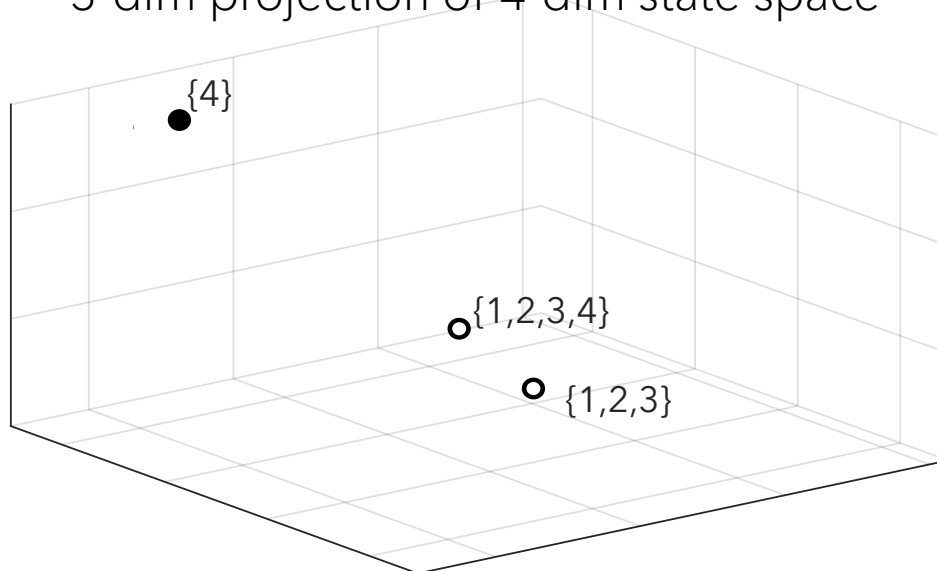
x^* fixed point

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

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

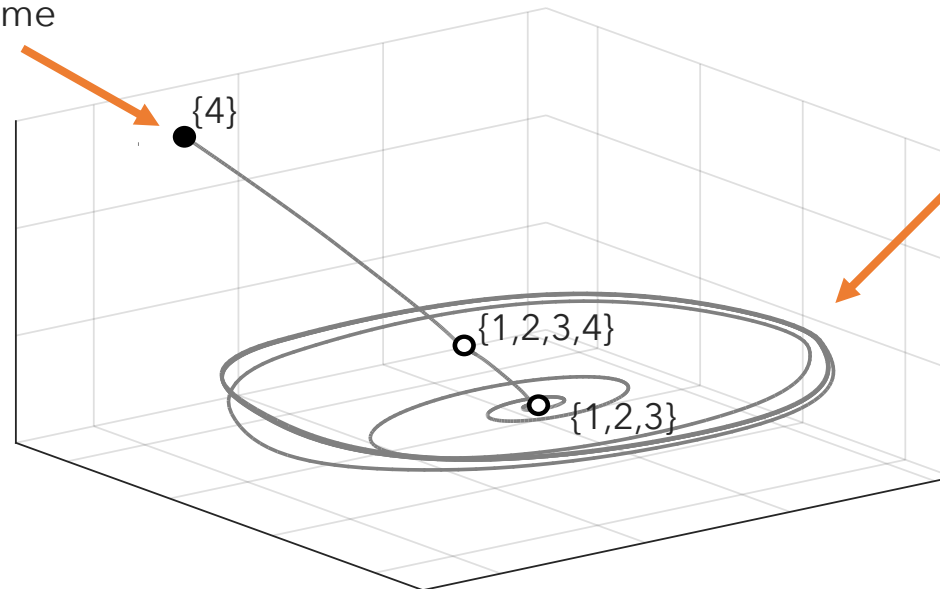
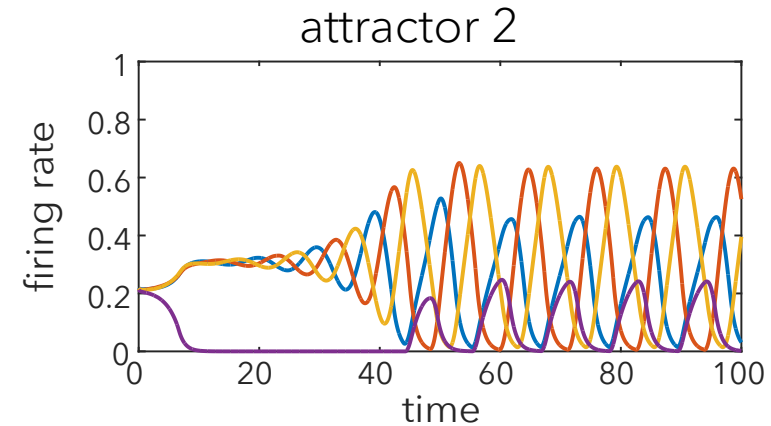
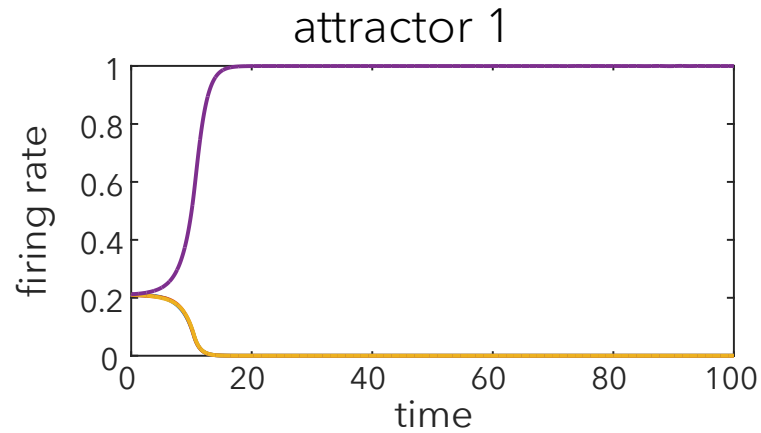
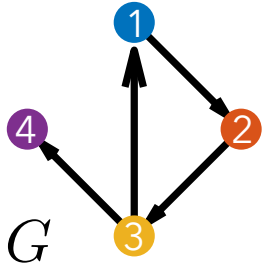
contains stable and unstable fixed points

3-dim projection of 4-dim state space



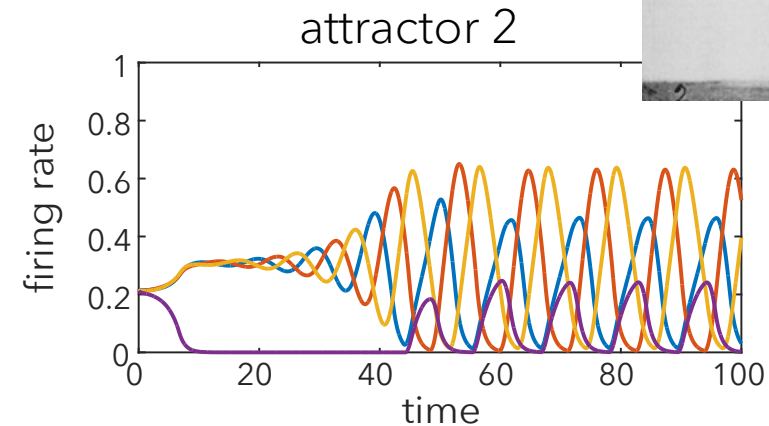
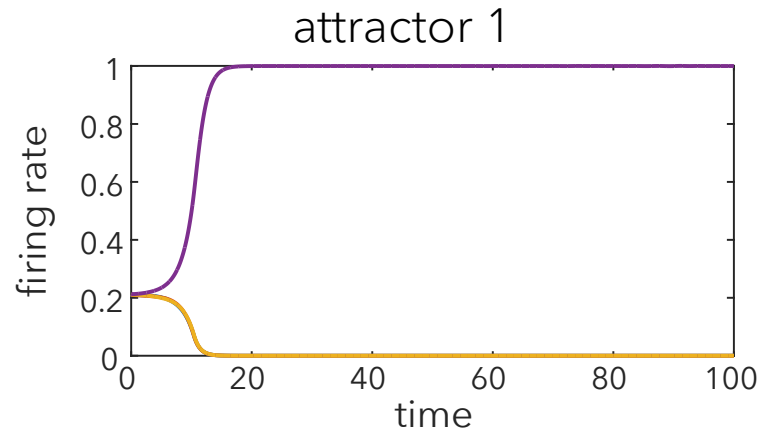
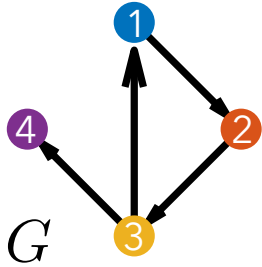
Heuristic: **minimal** fixed points *correspond* to attractors

$$FP(G) = \{\{4\}, \{1, 2, 3\}, \{1, 2, 3, 4\}\}$$



Heuristic: **minimal** fixed points *correspond* to attractors

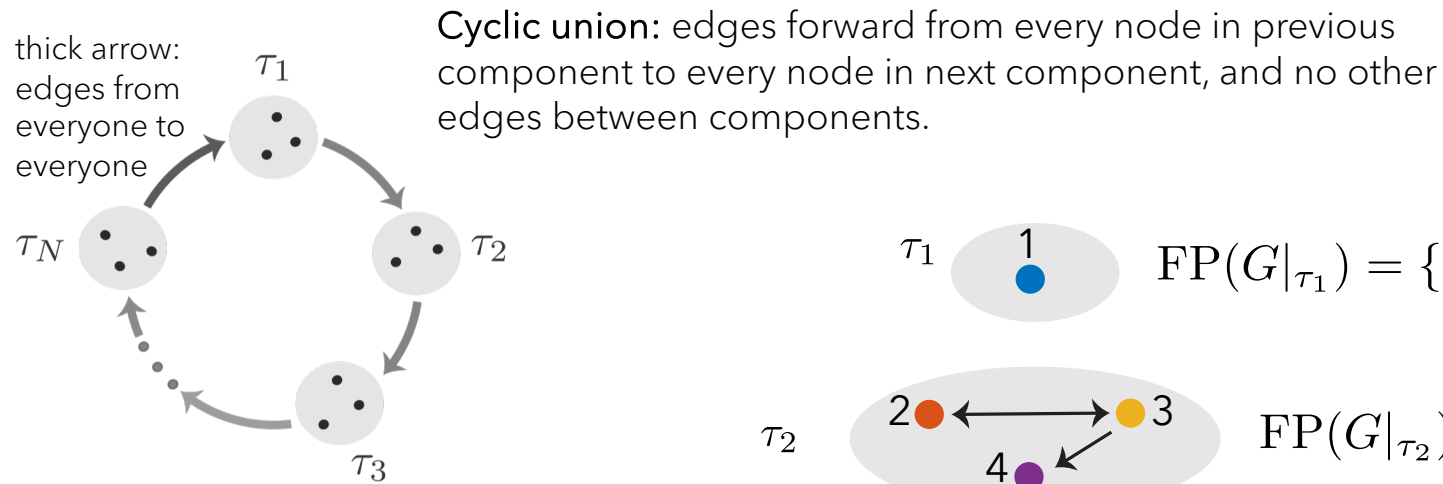
$$FP(G) = \{\{4\}, \{1, 2, 3\}, \{1, 2, 3, 4\}\}$$



Takeaways:

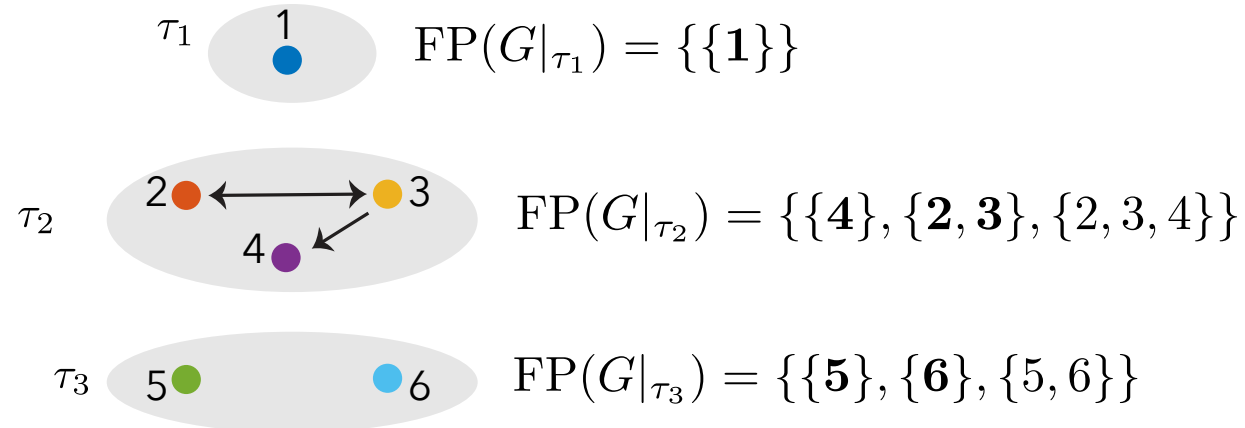
1. a single network can have many different attractors (which can be a mix of static and dynamic), accessible via different initial conditions
2. $FP(G)$ also gives information about the initial conditions needed to converge to its corresponding attractor
3. it seems easy to have dynamic attractors, **but what about more complex patterns of oscillations?**

For more complex patterns of oscillations: cyclic unions



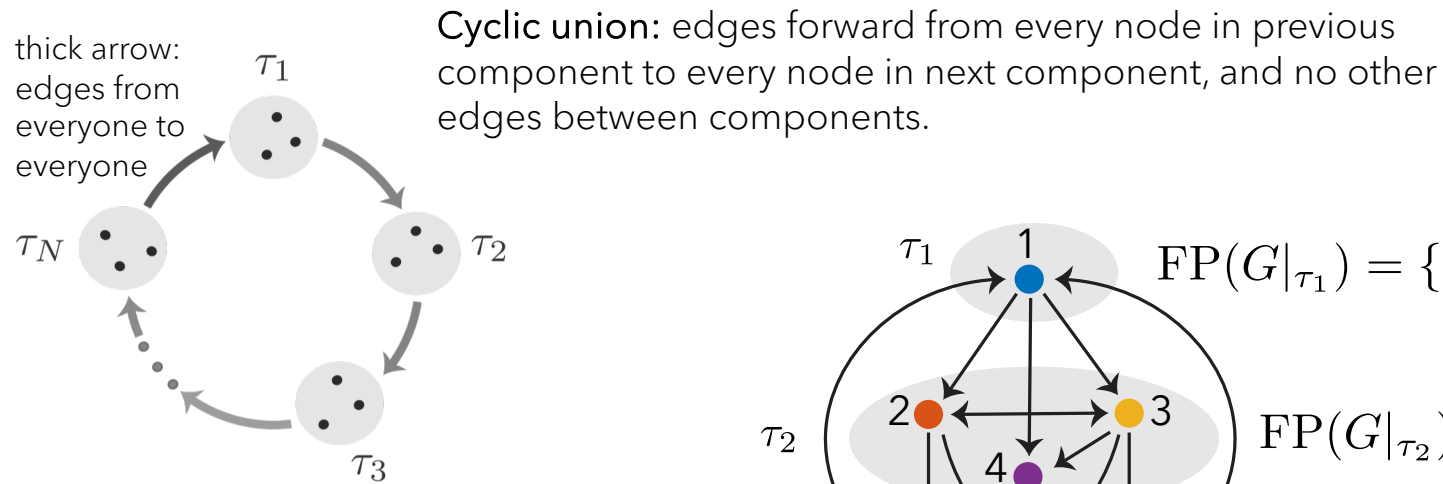
Theorem: for all $i \in [N]$
 $\sigma \in \text{FP}(G) \Leftrightarrow \sigma \cap \tau_i \in \text{FP}(G|_{\tau_i})$

$$|\text{FP}(G)| = \prod_{i=1}^N |\text{FP}(G|_{\tau_i})|$$



Parmelee, C., **Londono Alvarez, J.**, Curto, C., & Morrison, K. (2022). Sequential attractors in combinatorial threshold-linear networks. *SIAM Journal on Applied Dynamical Systems*, 21(2), 1597-1630.

For more complex patterns of oscillations: cyclic unions



Theorem: for all $i \in [N]$
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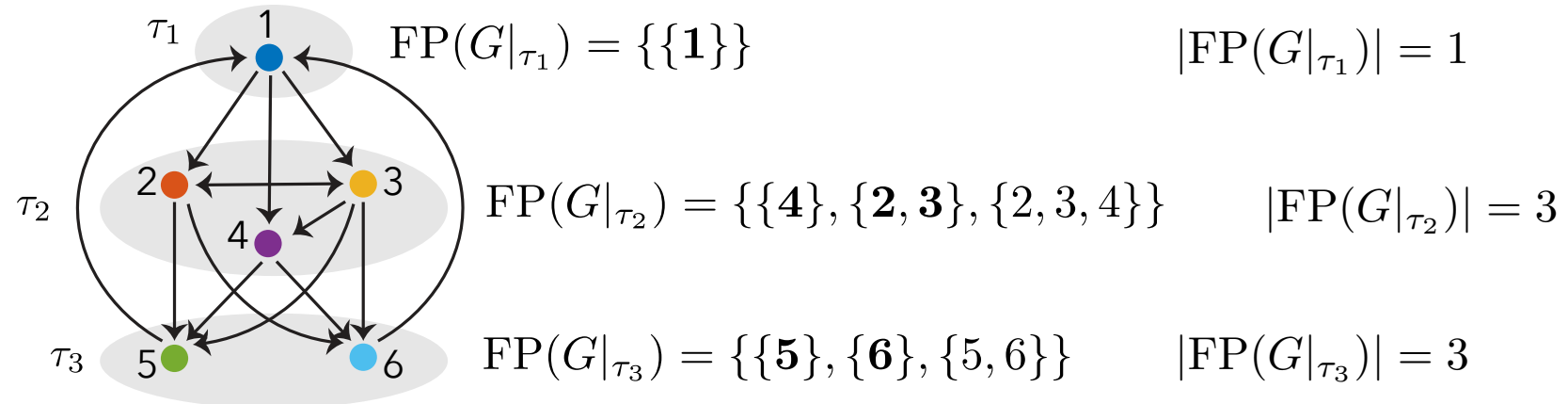
$$|\text{FP}(G)| = \prod_{i=1}^N |\text{FP}(G|_{\tau_i})|$$

theorem
says:

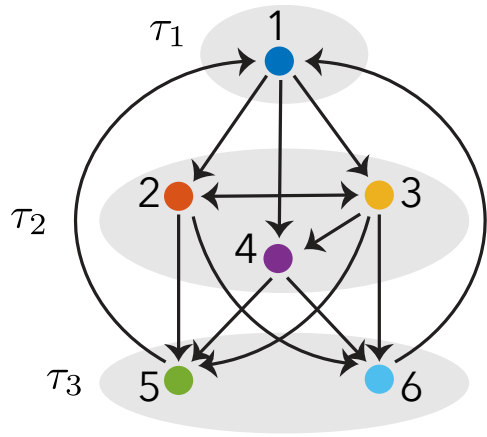
$$\begin{aligned} \text{FP}(G) = \{ & \{1, 4, 5\}, \{1, 4, 6\}, \{1, 2, 3, 5\}, \\ & \{1, 2, 3, 6\}, \{1, 4, 5, 6\}, \{1, 2, 3, 4, 5\}, \\ & \{1, 2, 3, 4, 6\}, \{1, 2, 3, 5, 6\}, \{1, 2, 3, 4, 5, 6\} \} \end{aligned}$$

$$|\text{FP}(G)| = 1 * 3 * 3 = 9$$

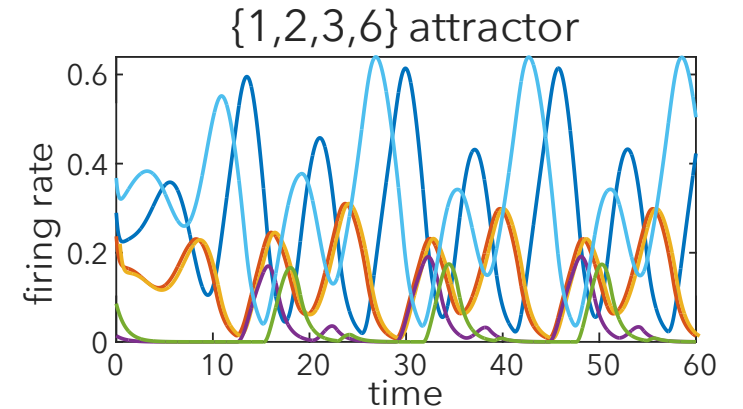
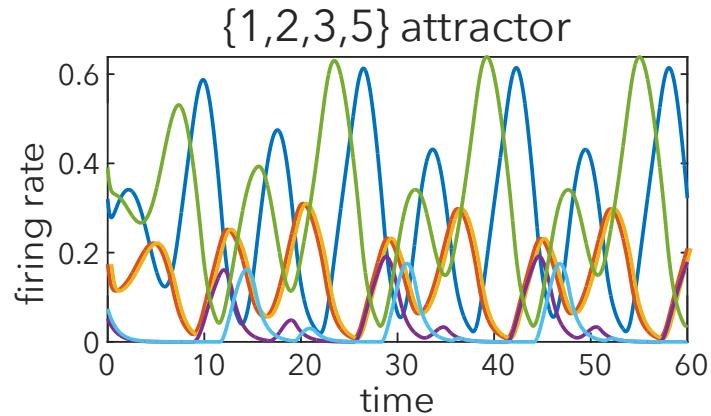
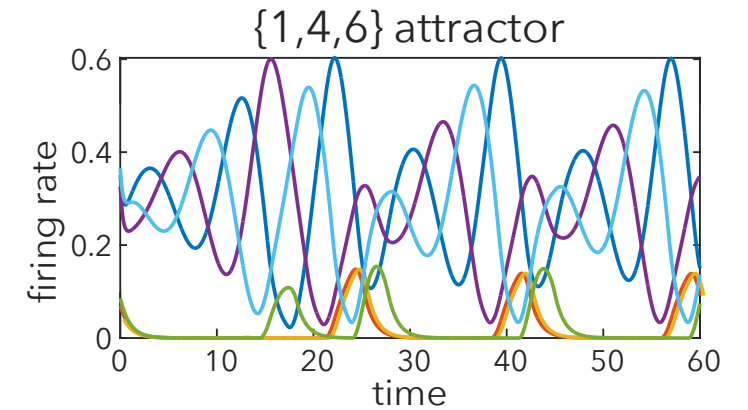
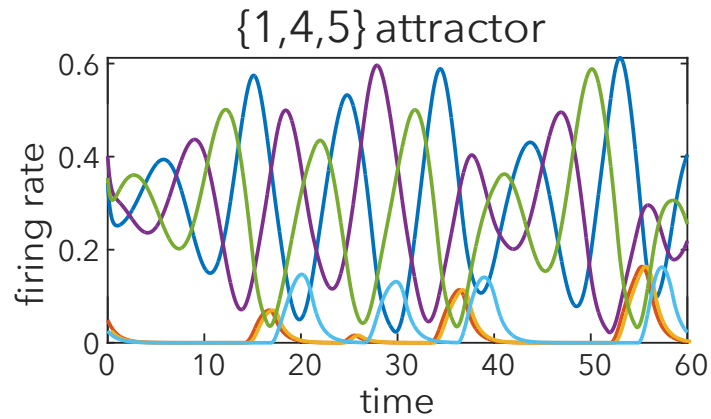
4 of them minimal



For more complex patterns of oscillations: cyclic unions

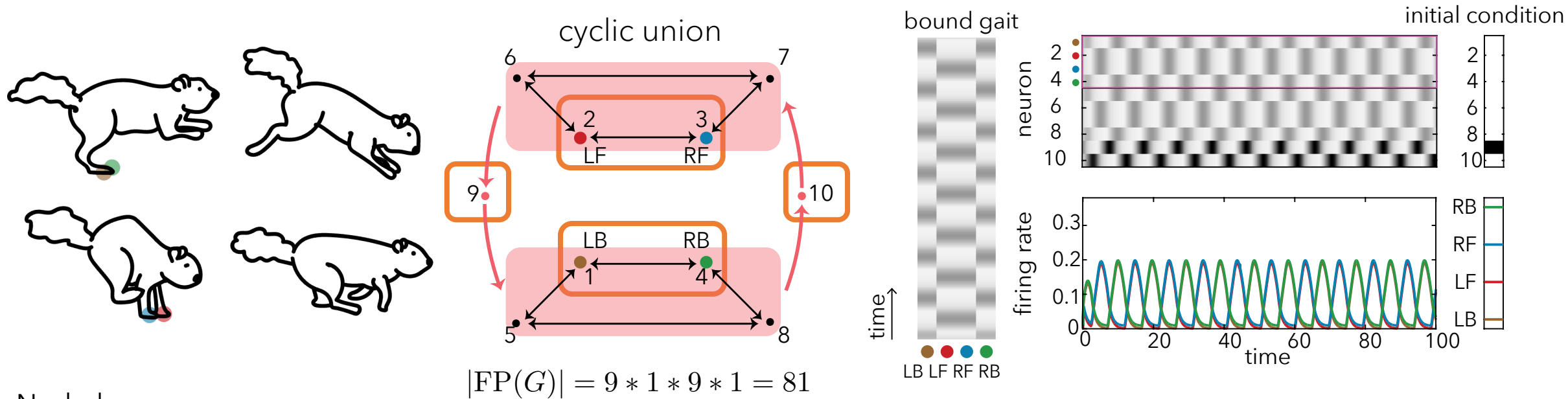


$$\text{FP}(G) = \{\{1, 4, 5\}, \{1, 4, 6\}, \{1, 2, 3, 5\}, \\ \{1, 2, 3, 6\}, \{1, 4, 5, 6\}, \{1, 2, 3, 4, 5\}, \\ \{1, 2, 3, 4, 6\}, \{1, 2, 3, 5, 6\}, \{1, 2, 3, 4, 5, 6\}\}$$



Cyclic union example: bound gait

Front legs are synchronized, back legs are synchronized, half a period apart.



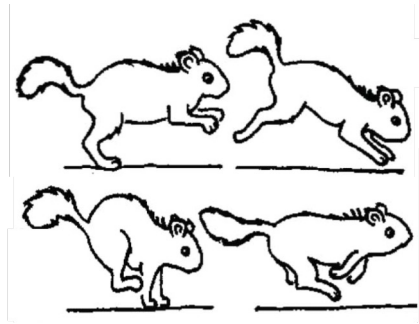
Node-leg
assignment



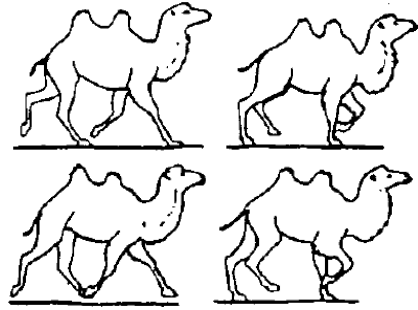
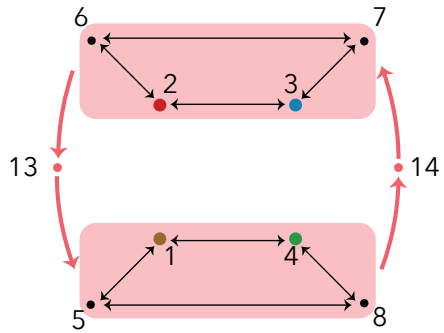
minimal supports = $\{\{1, 2, 3, 4, 9, 10\}, \{1, 2, 3, 5, 9, 10\}, \{1, 2, 4, 6, 9, 10\}, \{1, 2, 5, 6, 9, 10\}, \{1, 3, 4, 7, 9, 10\}, \{1, 3, 5, 7, 9, 10\}, \{1, 4, 6, 7, 9, 10\}, \{1, 5, 6, 7, 9, 10\}, \{2, 3, 4, 8, 9, 10\}, \{2, 3, 5, 8, 9, 10\}, \{2, 4, 6, 8, 9, 10\}, \{2, 5, 6, 8, 9, 10\}, \{3, 4, 7, 8, 9, 10\}, \{3, 5, 7, 8, 9, 10\}, \{4, 6, 7, 8, 9, 10\}, \{5, 6, 7, 8, 9, 10\}\}$

Londono Alvarez, J., Morrison, K., & Curto, C. (2025). *Attractor-based models for sequences and pattern generation in neural circuits*. bioRxiv.

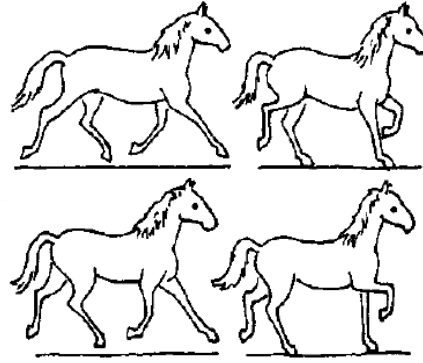
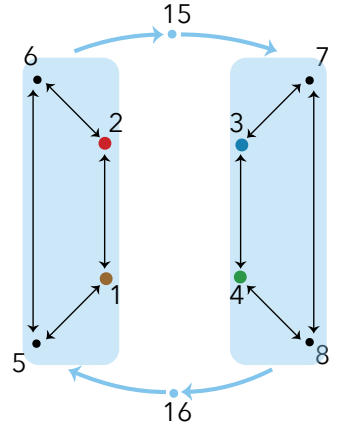
many patterns can be modeled this way



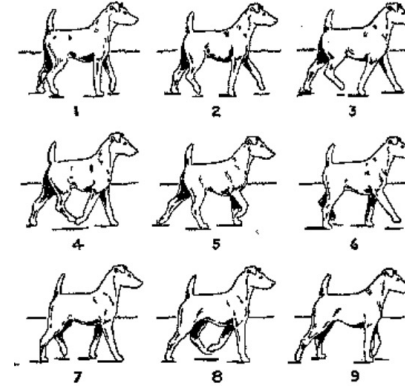
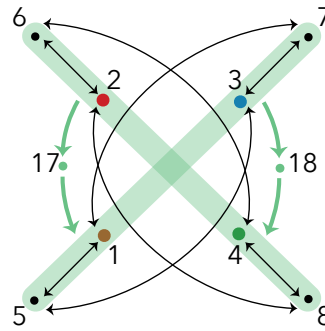
bound



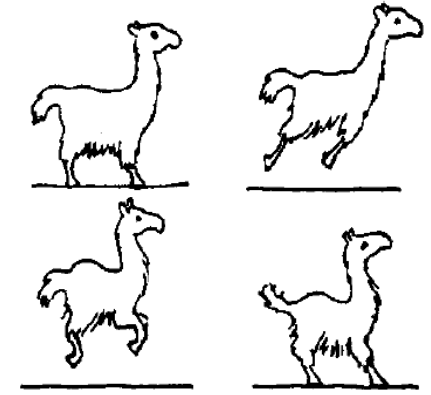
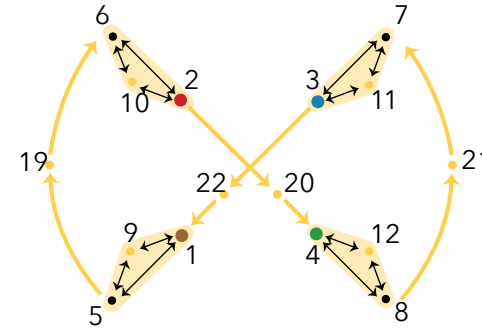
pace



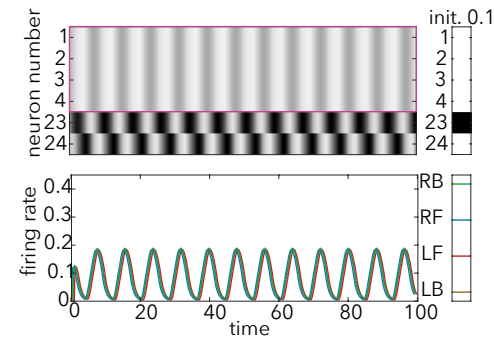
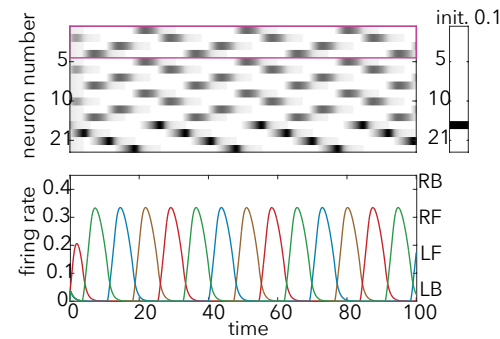
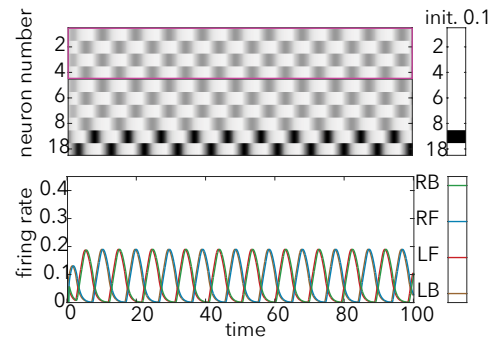
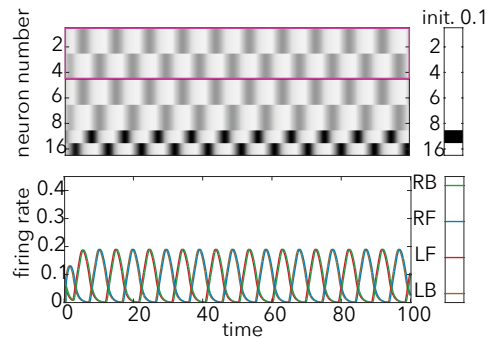
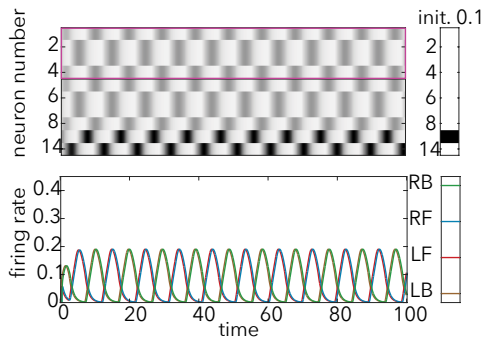
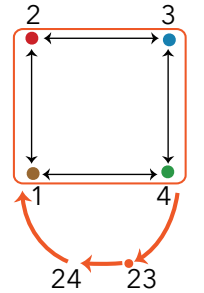
trot



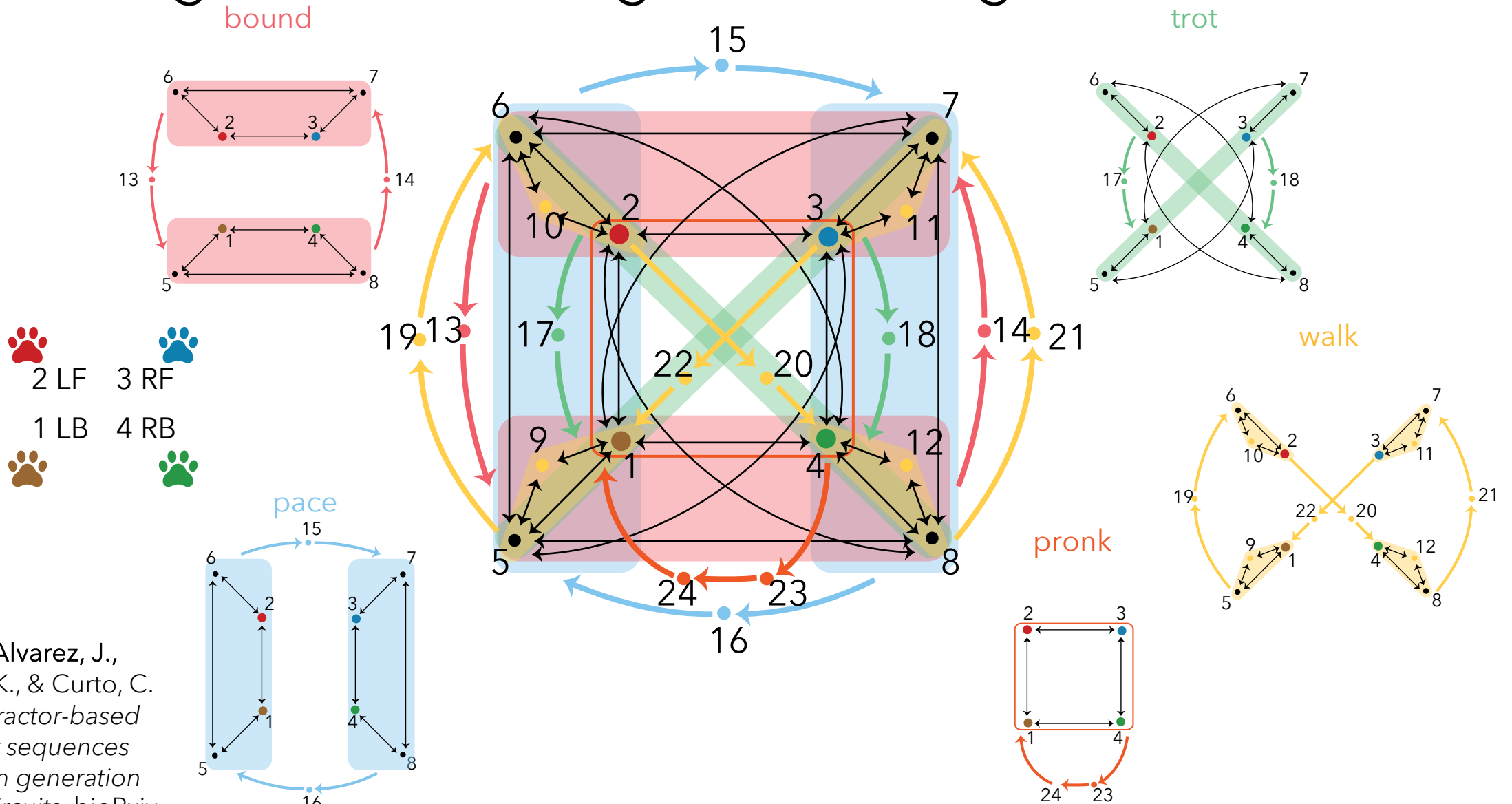
walk



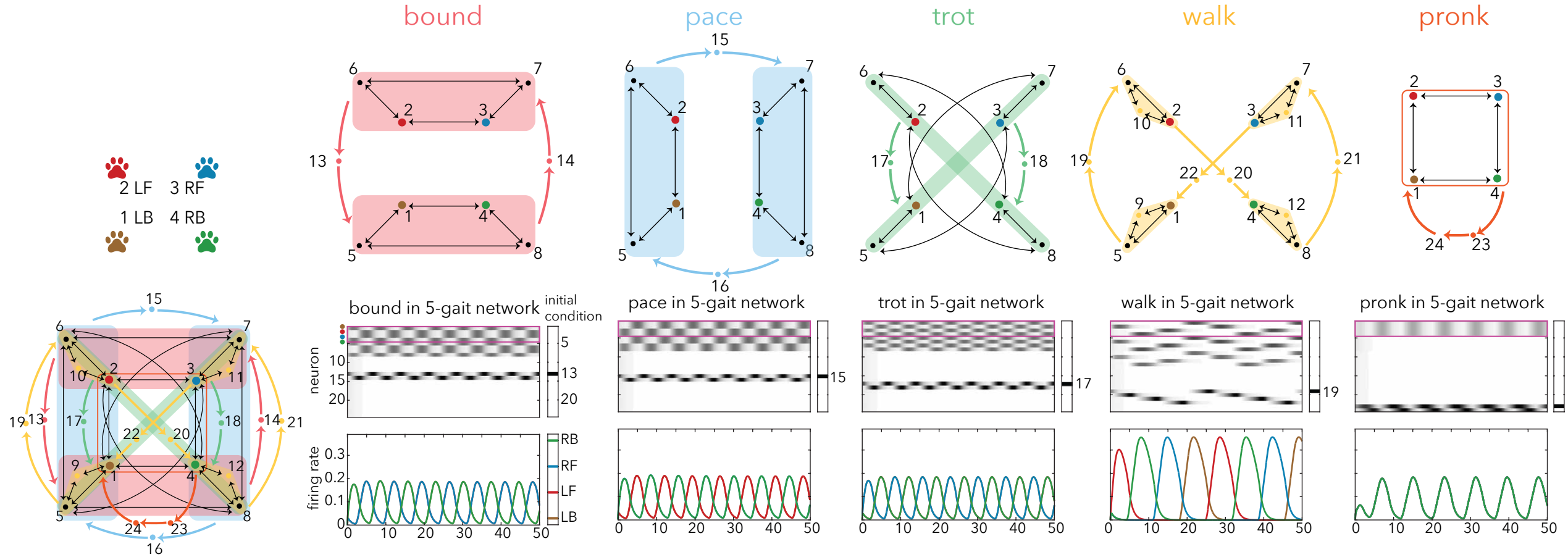
prong



remarkable (unexplained) robustness of construction: all gaits can be merged into a single network

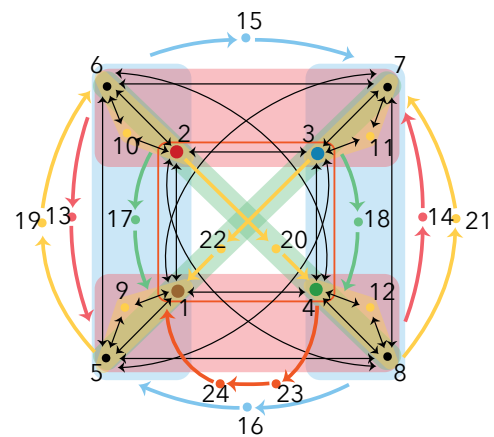


all attractors survive the merge

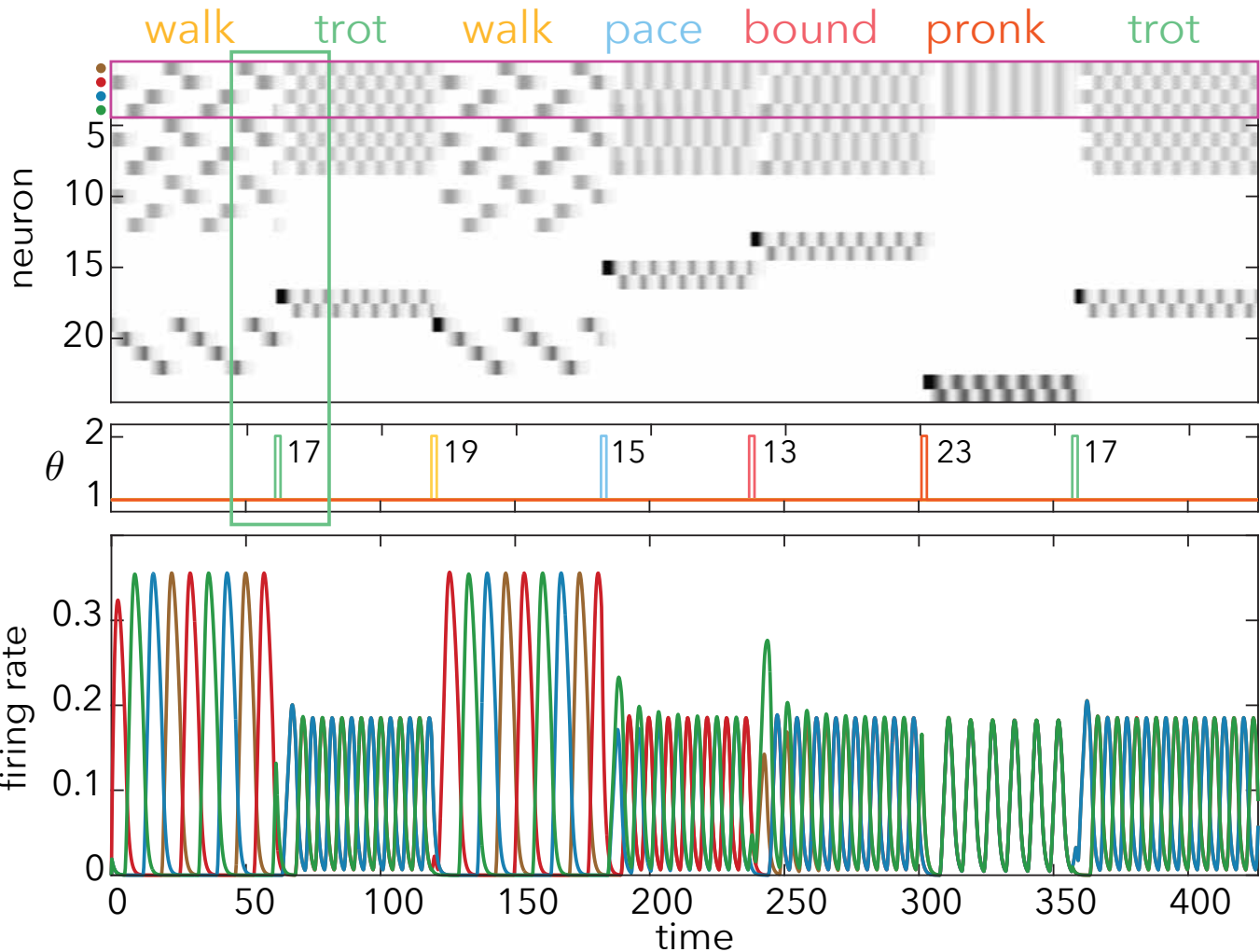


Londono Alvarez, J.,
Morrison, K., & Curto, C.
(2025). *Attractor-based
models for sequences
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network can easily transition attractors via pulses sent to auxiliary neurons



Londono Alvarez, J., Morrison, K., & Curto, C. (2025). *Attractor-based models for sequences and pattern generation in neural circuits*. bioRxiv.



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

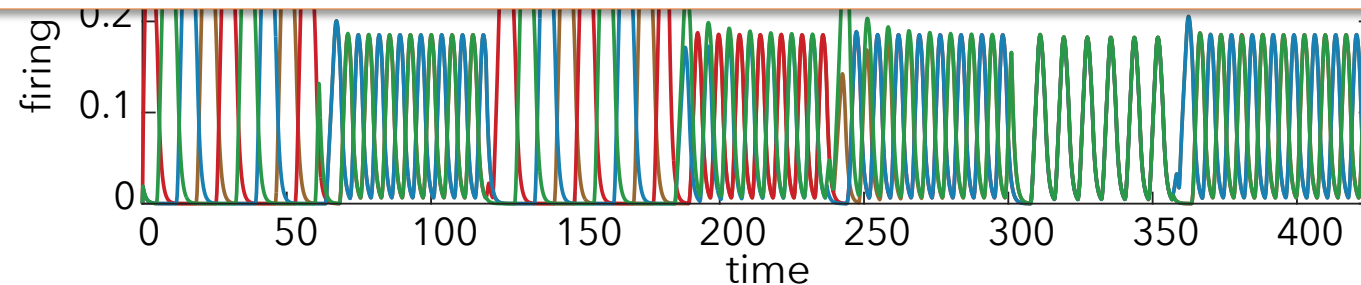
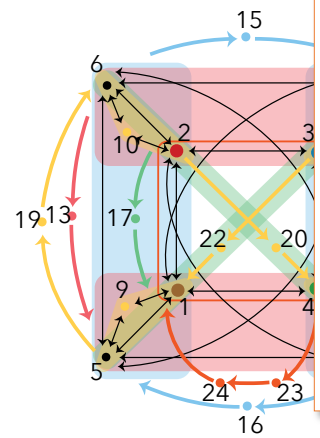
network can easily transition attractors via pulses sent to auxiliary neurons

walk trot walk pace bound pronk trot

This network:

1. has five different coexistent attractors, all engaging the same four limb neurons in different patterns
2. has all these attractors accessible without changing parameters (accessed via different initial conditions)
3. allows easy transitions between attractors by stimulating single neurons
4. has attractors that look nearly identical as the individually constructed gaits

What made these attractors so robust that they don't interfere with each other when "glued" together?

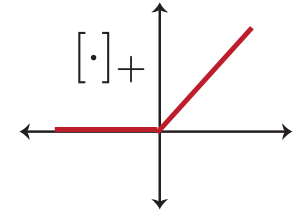


$$\left[\sum_{j=1}^n W_{ij} x_j + \theta \right]_+$$

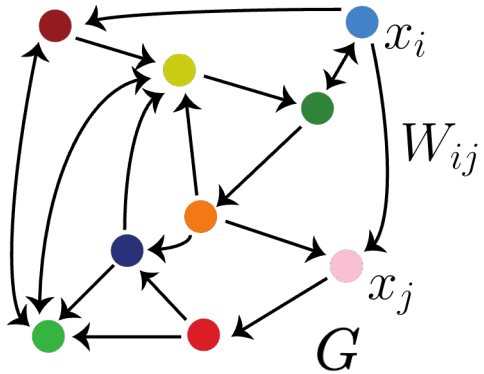
combinatorial threshold-linear networks (CTLNs)

threshold-linear networks:

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



whose connectivity matrix is defined by a directed graph:



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

$$b_i = \theta$$

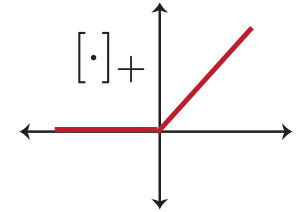
TLNs

CTLNs

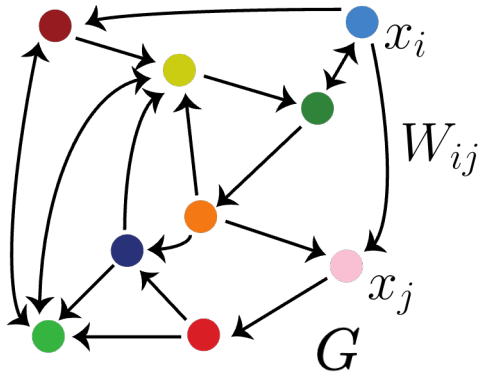
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cyclic union theorem holds

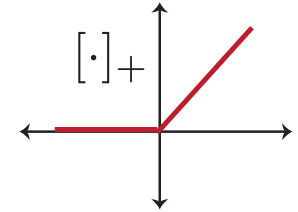
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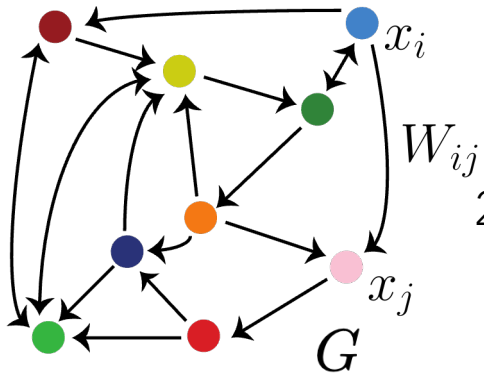
generalized combinatorial threshold-linear networks (gCTLNs)

threshold-linear networks:

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



whose connectivity matrix is defined by a directed graph:



CTLN prescription:

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

2 parameters

gCTLN prescription:

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

2n parameters

$$b_i = \theta$$

cyclic union theorem holds

TLNs

gCTLNs

CTLNs

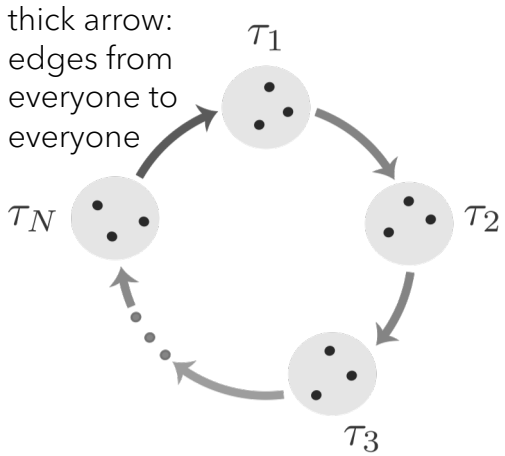
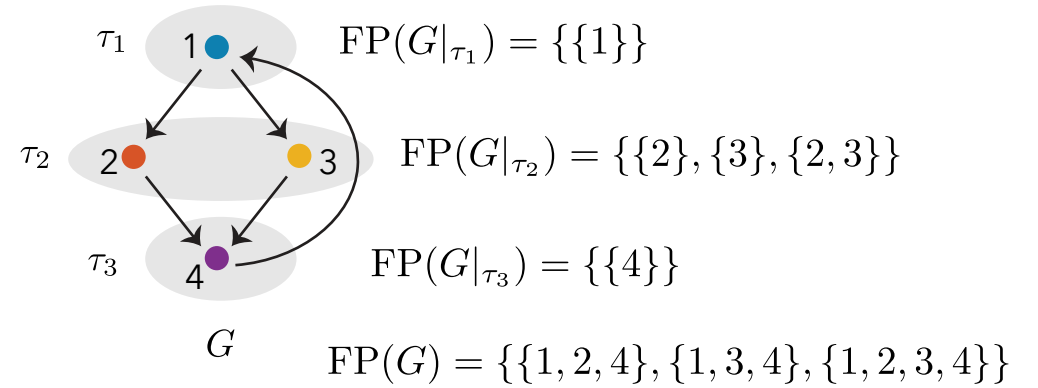
cyclic union theorem holds for gCTLNs!

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

CTLN version:

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

Theorem: for all $i \in [N]$
 $\sigma \in \text{FP}(G) \Leftrightarrow \sigma \cap \tau_i \in \text{FP}(G|_{\tau_i})$

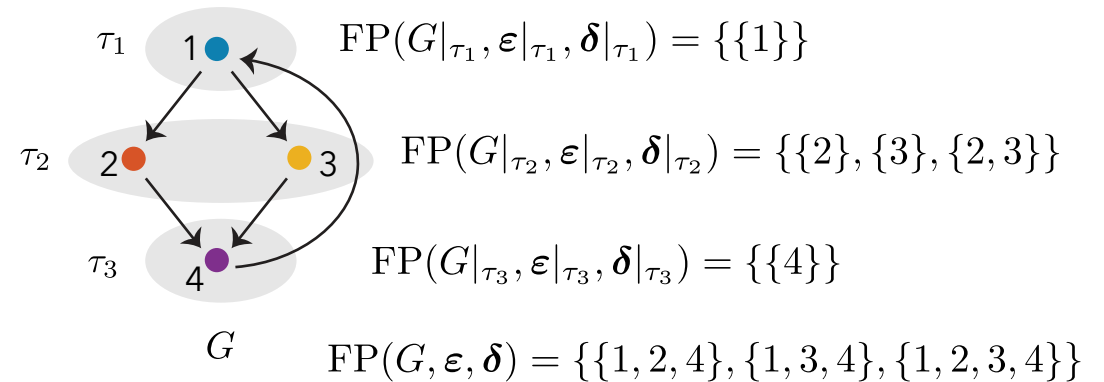


Cyclic union: edges forward from every node in previous component to every node in next component, and no other edges between components.

gCTLN version:

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

Theorem: for all $i \in [N]$
 $\sigma \in \text{FP}(G, \varepsilon, \delta) \Leftrightarrow \sigma_i \in \text{FP}(G|_{\tau_i}, \varepsilon|_{\tau_i}, \delta|_{\tau_i})$



The proof of the generalized cyclic union theorem for gCTLNs required several new ingredients (not so easy!)

1. menu theorem for TLNs (not graph-based!)

2. graphical domination results in gCTLNs

C simply-embedded partition

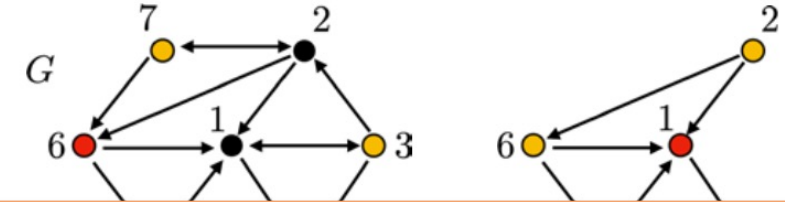
$$W = \left(\begin{array}{c|c|c|c|c|c} & W_1 & \begin{array}{c} \gamma_{t_1+1}^{(1)} \\ \vdots \\ \gamma_{t_2}^{(1)} \end{array} & \cdots & \begin{array}{c} \gamma_{t_{N-1}+1}^{(1)} \\ \vdots \\ \gamma_{t_N}^{(1)} \end{array} & \cdots \\ \hline \begin{array}{c} \gamma_1^{(2)} \\ \vdots \\ \gamma_{t_1}^{(2)} \end{array} & \cdots & W_2 & \cdots & \begin{array}{c} \gamma_{t_{N-1}+1}^{(2)} \\ \vdots \\ \gamma_{t_N}^{(2)} \end{array} & \cdots \\ \hline & & & \ddots & & \\ \hline \begin{array}{c} \gamma_1^{(N)} \\ \vdots \\ \gamma_{t_1}^{(N)} \end{array} & \cdots & \begin{array}{c} \gamma_{t_1+1}^{(N)} \\ \vdots \\ \gamma_{t_2}^{(N)} \end{array} & \cdots & & W_N \end{array} \right)$$

Theorem 3 (TLN menu). Let $\tau_1, \dots, \tau_N$ be a simply-embedded partition of the nodes of (W, θ) , with θ uniform input. For any $\sigma \subseteq [n]$, let $\sigma_\ell \stackrel{\text{def}}{=} \sigma \cap \tau_\ell$. Then

$$\sigma \in \text{FP}(W, \theta) \quad \Rightarrow \quad \sigma_\ell \in \text{FP}(W_{\tau_\ell}, \theta) \cup \{\emptyset\} \quad \text{for all } \ell \in [N].$$

In other words, every fixed point support of (W, θ) is a union of component fixed point supports σ_ℓ , at most one per component.

Londono Alvarez, 2025, *Fixed point decompositions for composite generalized combinatorial threshold-linear networks* (in preparation)



See Carina's talk on Wednesday 2:30pm: Graphical domination and inhibitory control in recurrent networks



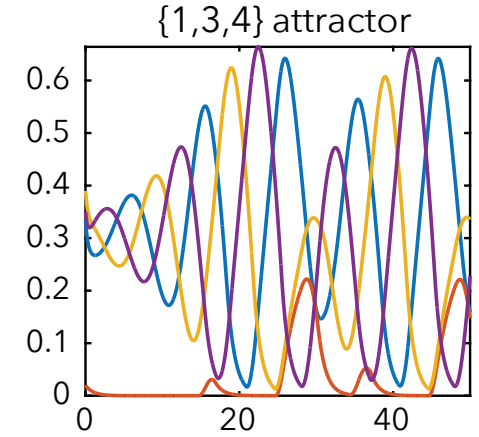
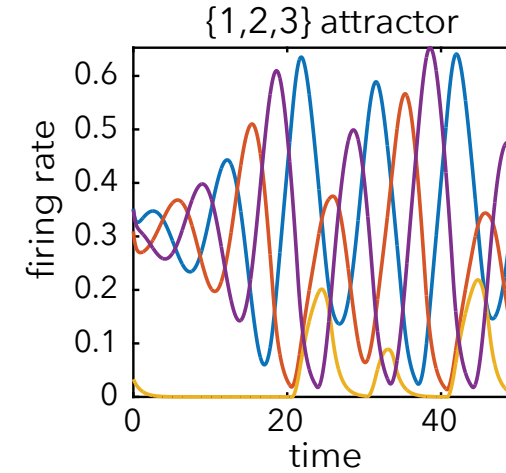
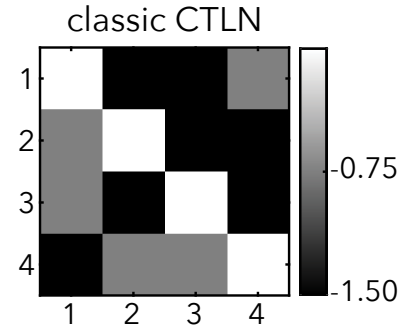
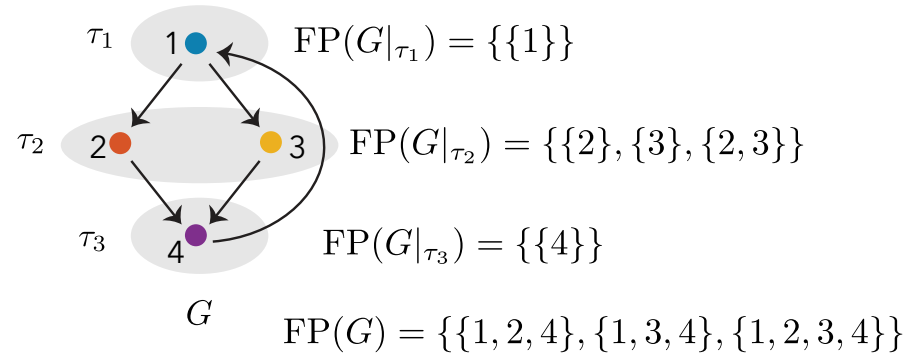
$$\text{FP}(G) = \text{FP}(\tilde{G}) = \{45\}$$

Curto, 2025, *Notes on graphical domination and inhibitory control for threshold-linear networks with recurrent excitation and global inhibition* (in preparation)

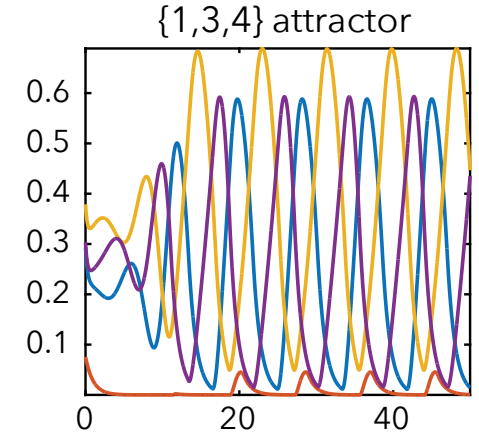
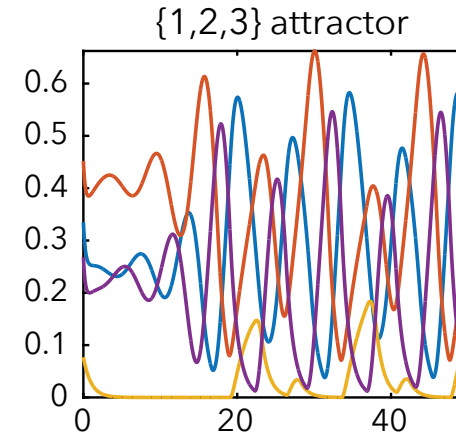
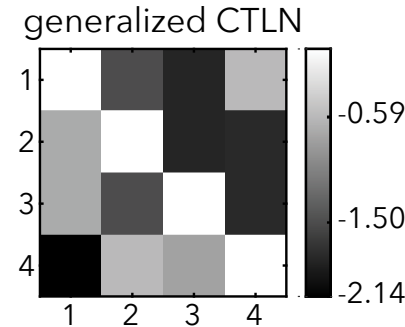
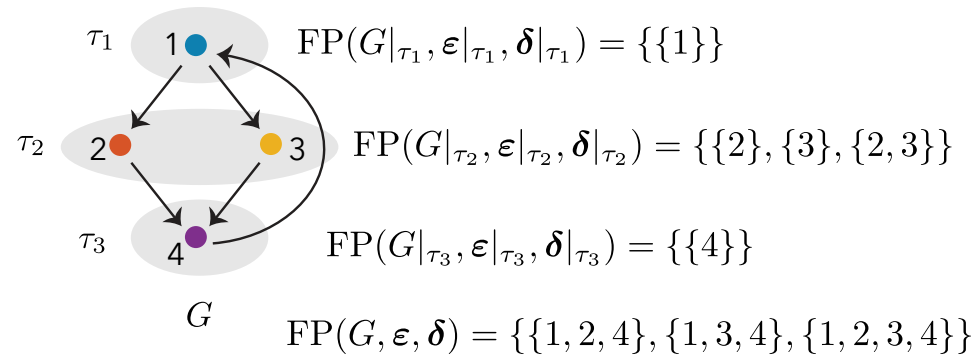
the attractor heuristic seems to still work

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

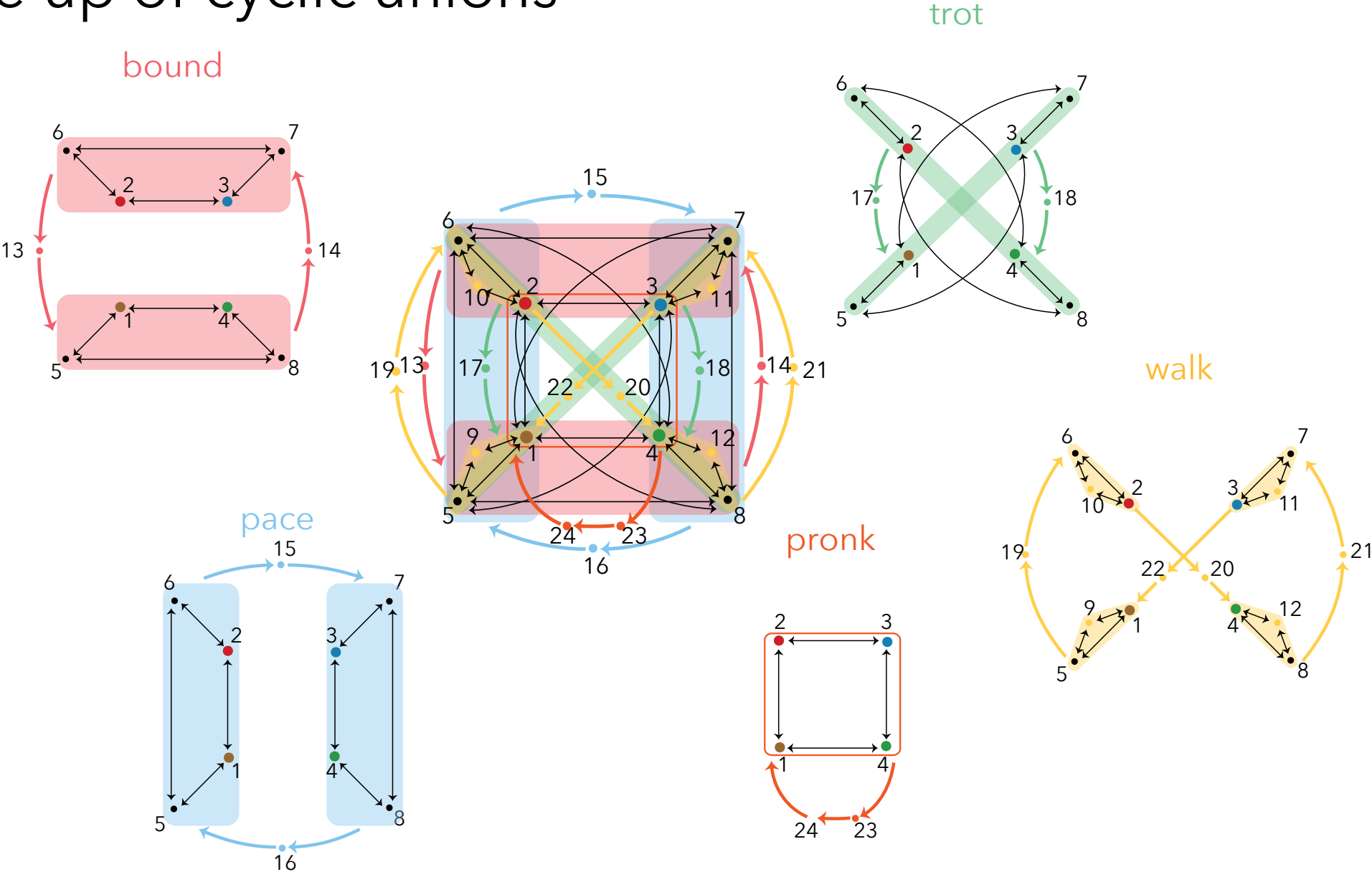
CTLN version:



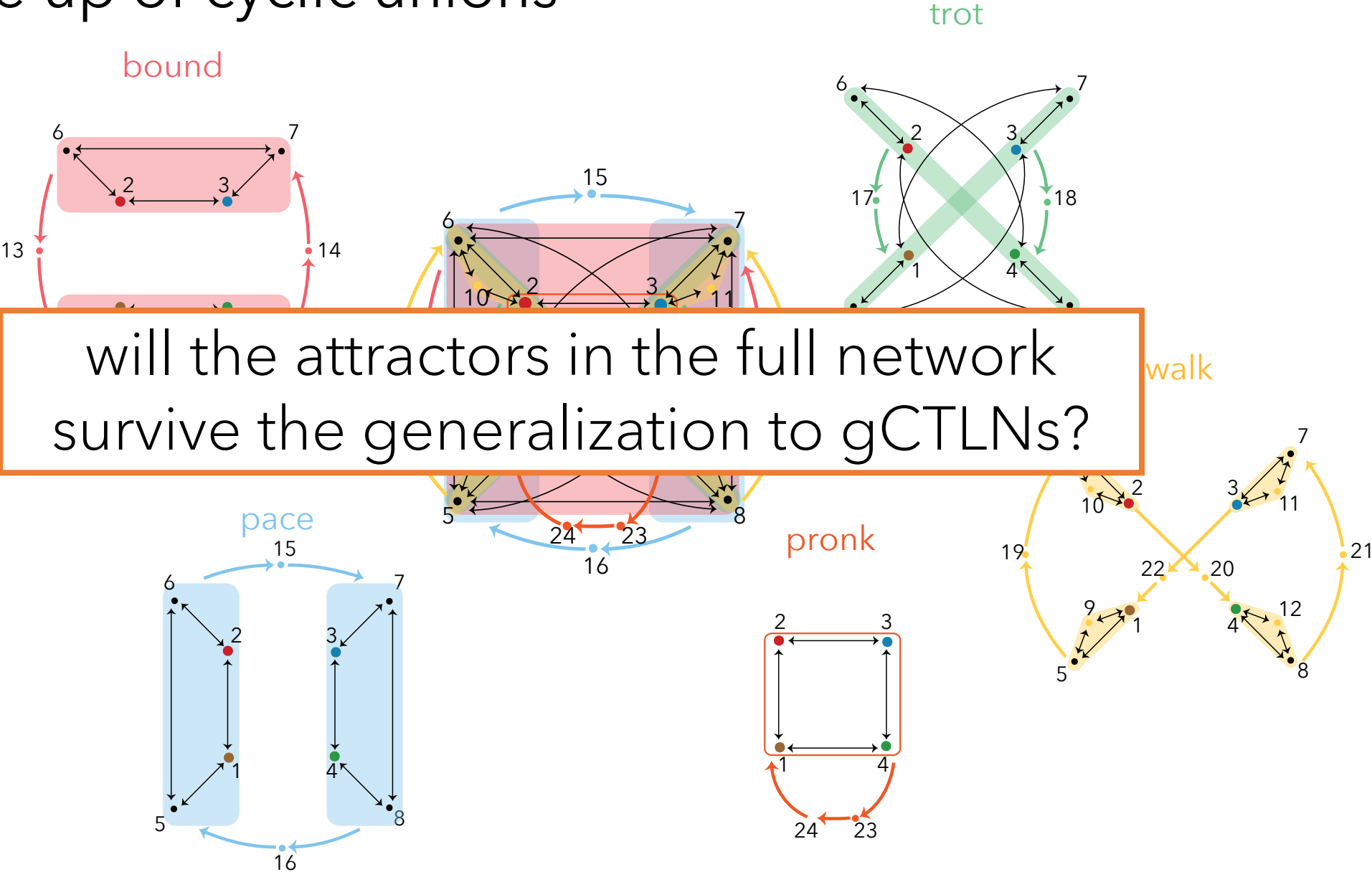
gCTLN version:



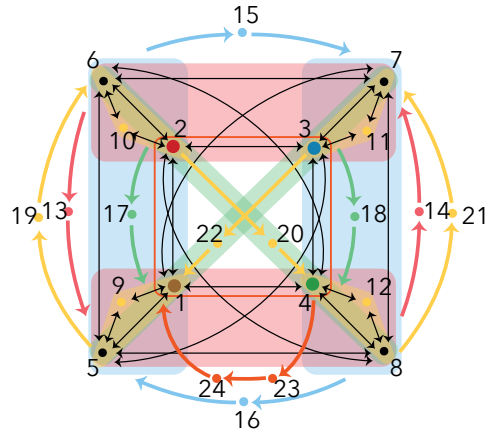
while full network was not technically not a cyclic union, it was made up of cyclic unions



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the answer is: sometimes

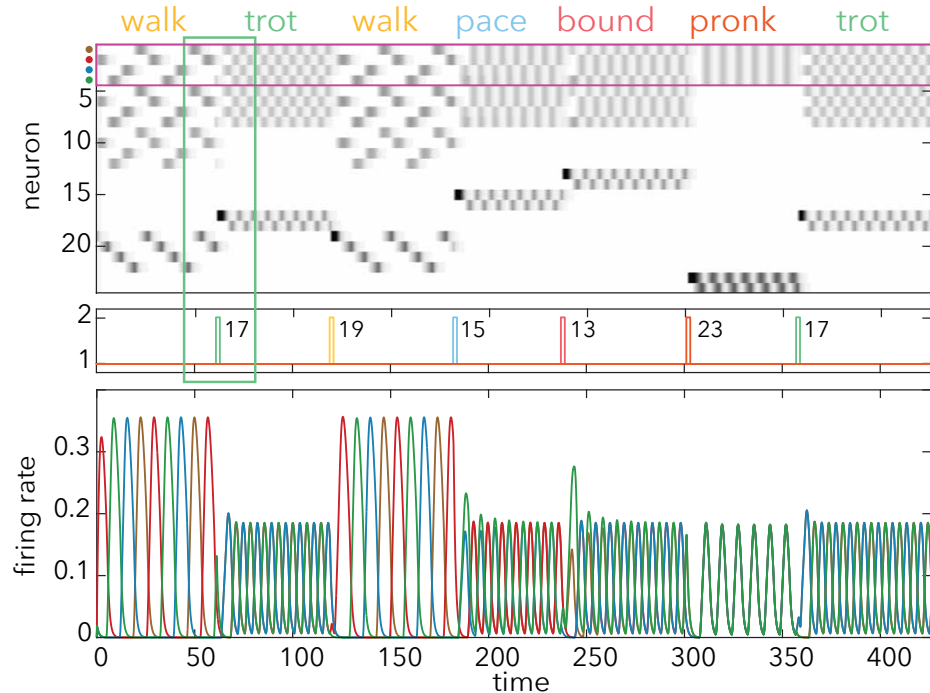


CTLN prescription:

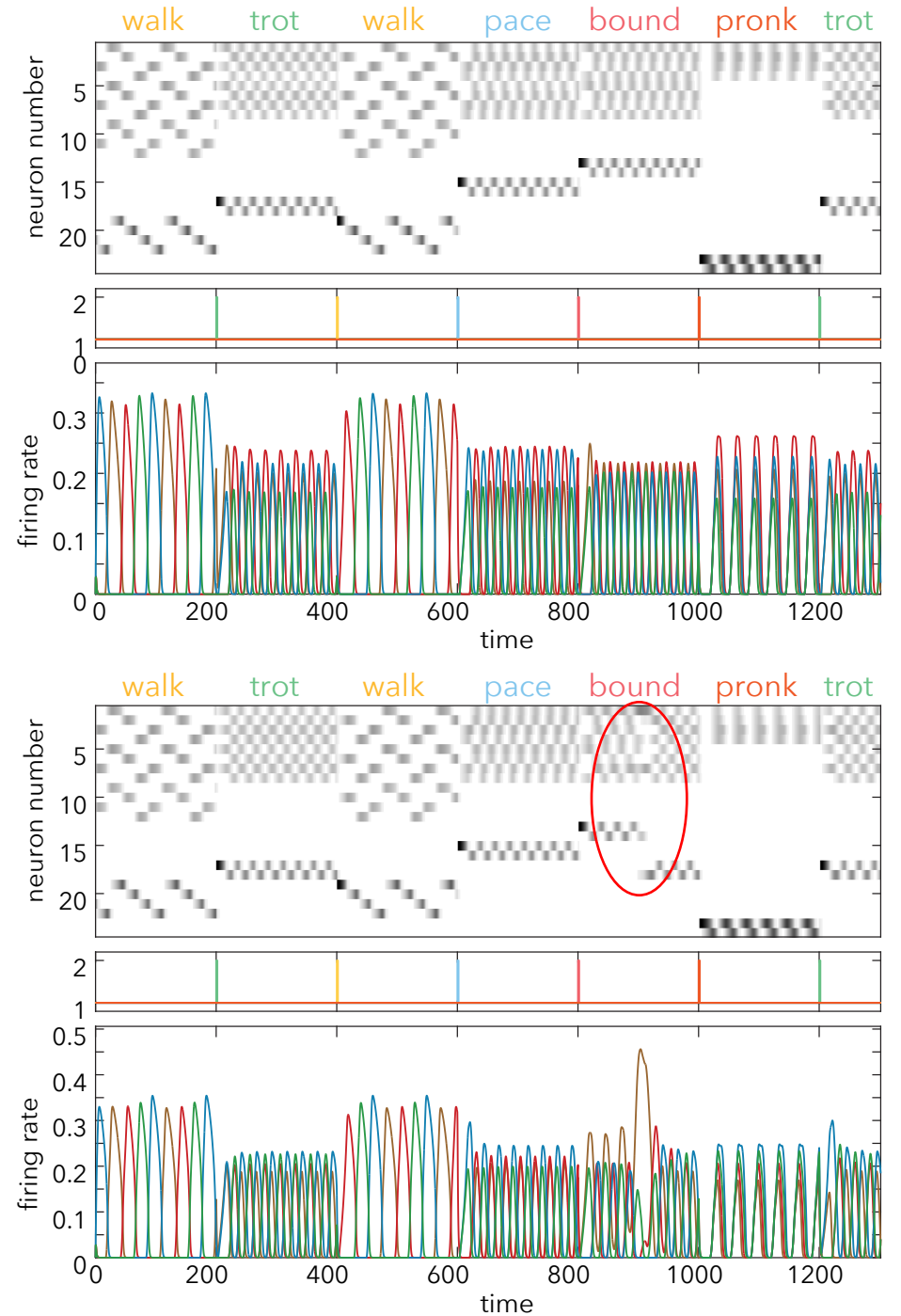
$$W_{ij} = \begin{cases} 0 & \text{if } i = j, \\ -1 + \varepsilon & \text{if } j \rightarrow i \text{ in } G, \\ -1 - \delta & \text{if } j \not\rightarrow i \text{ in } G, \end{cases}$$

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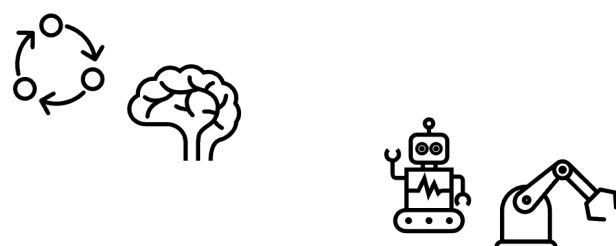
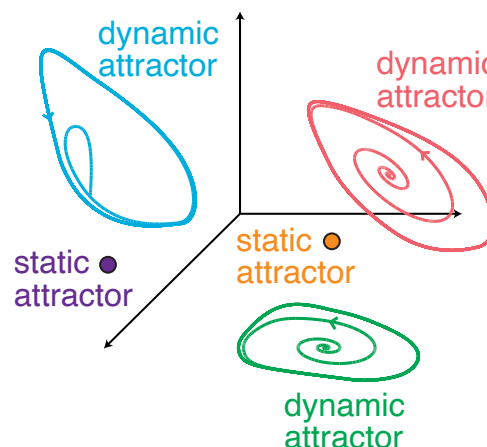


two gCTLNs
amounting to the
same level of
perturbation from
original
parameters:



Looking ahead:

- how much can we generalize these fixed point decomposition results?
- what controls the firing rates? bifurcations?
- how to “glue” attractors (as in quadruped gaits)?

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


cyclic union theorem holds

TLNs

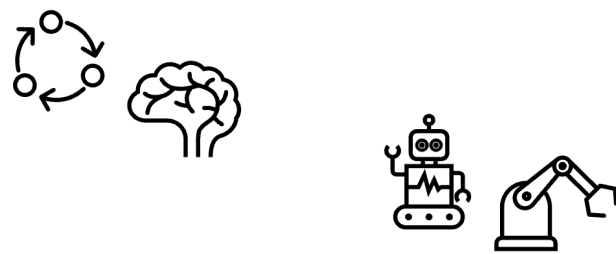
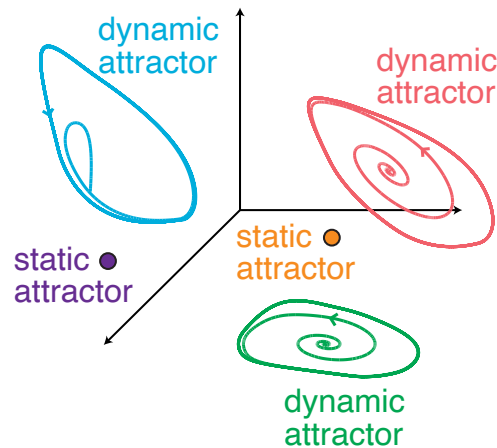
gCTLNs

CTLNs



In conclusion, TLNs are a nice framework for understanding structure-function relationships, and have potential as biological and artificial models

Thank you!

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In conclusion, TLNs are a nice framework for understanding structure-function relationships, and have potential as biological and artificial models



CTLN architectures giving rise to sequential attractors:

Parmelee, C., **Londono Alvarez, J.**, Curto, C., & Morrison, K. (2022). Sequential attractors in combinatorial threshold-linear networks. *SIAM Journal on Applied Dynamical Systems*, 21(2), 1597-1630.



Quadruped locomotion and more:

Londono Alvarez, J., Morrison, K., & Curto, C. (2025). *Attractor-based models for sequences and pattern generation in neural circuits*. bioRxiv.