The influence of network structure on neuronal network dynamics

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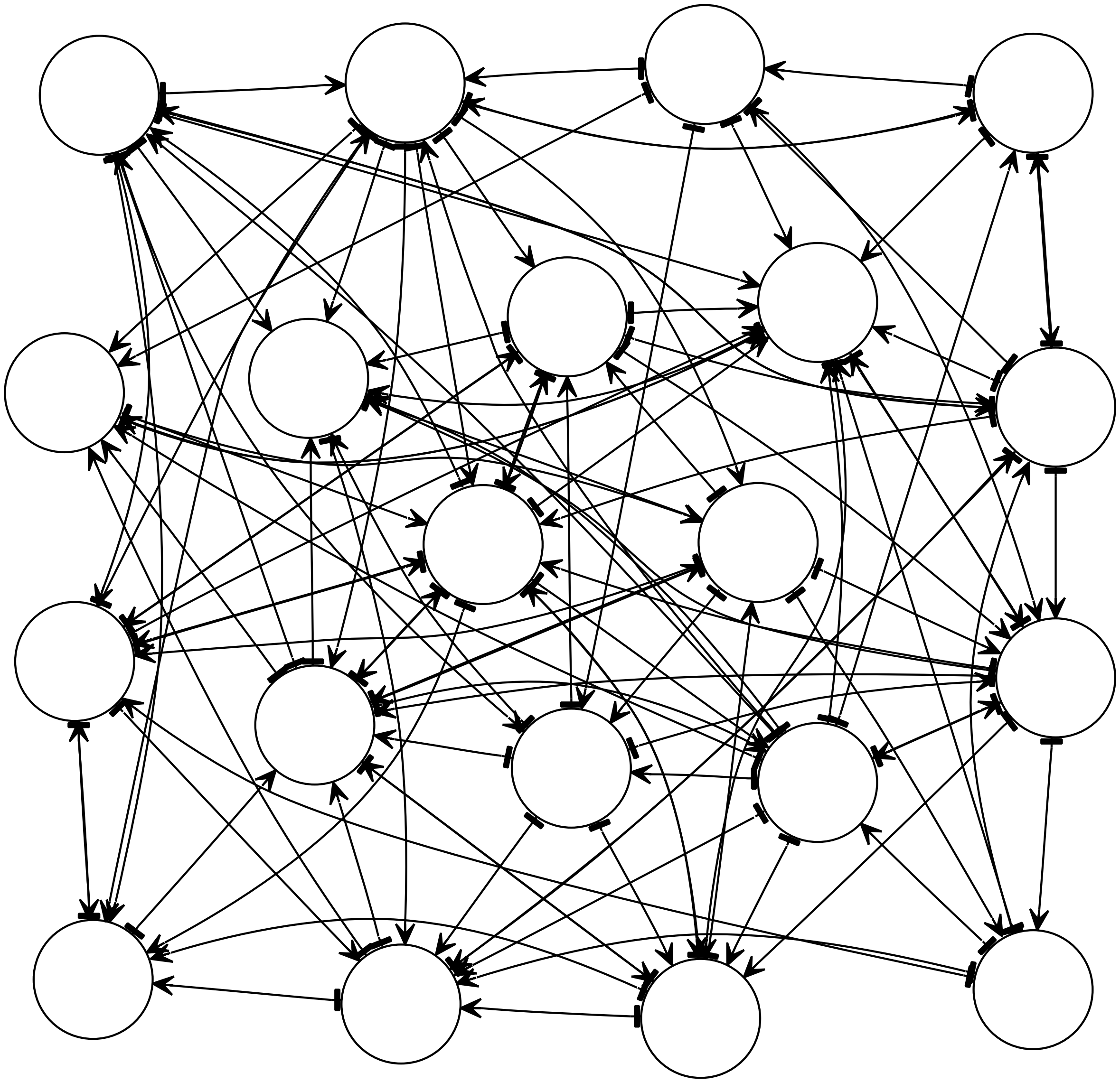
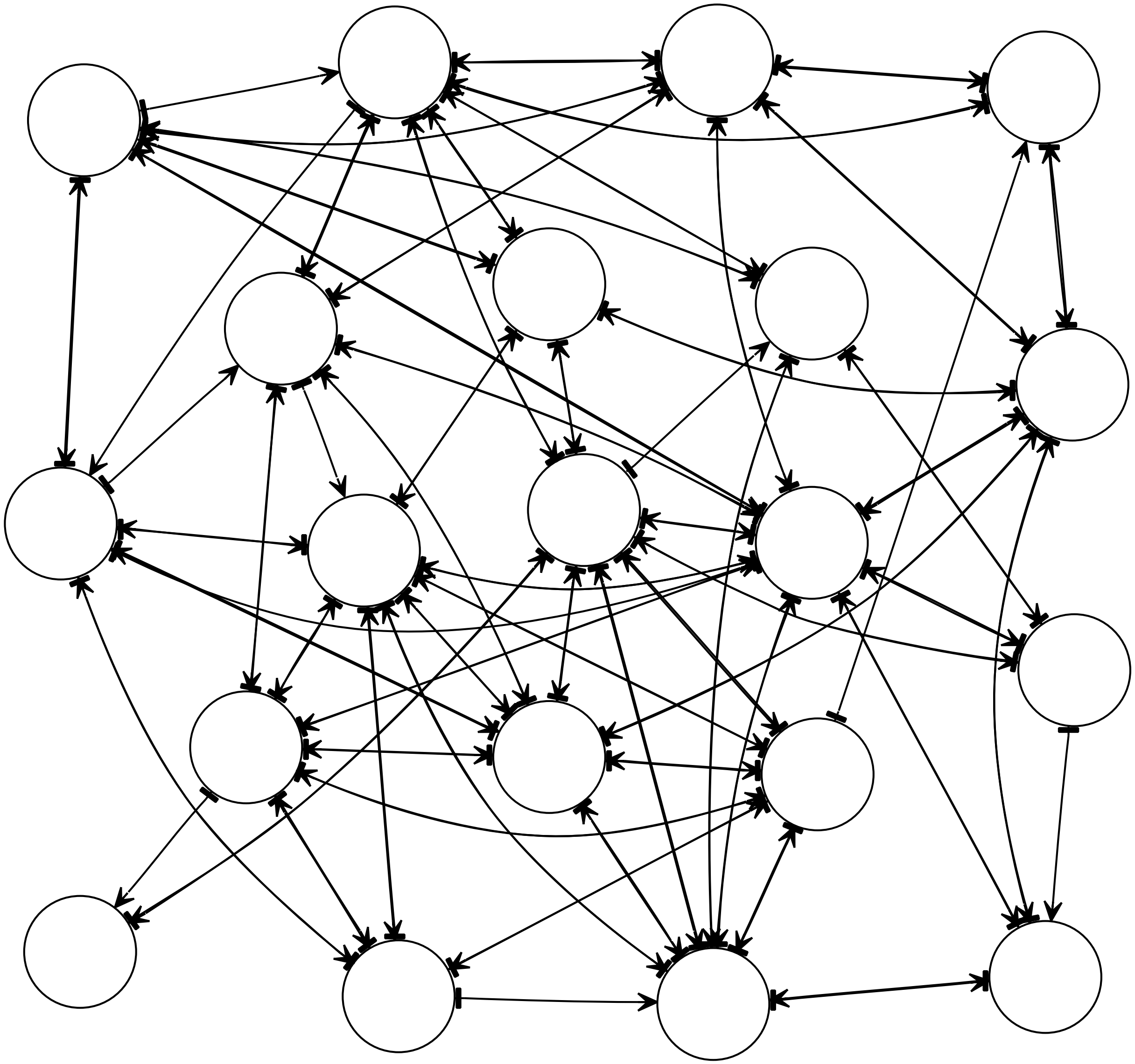
From network structure to dynamics



Computations in the brain are performed via complex networks of neurons.

The impact of this network structure on network dynamics remains virtually unexplored.

From network structure to dynamics



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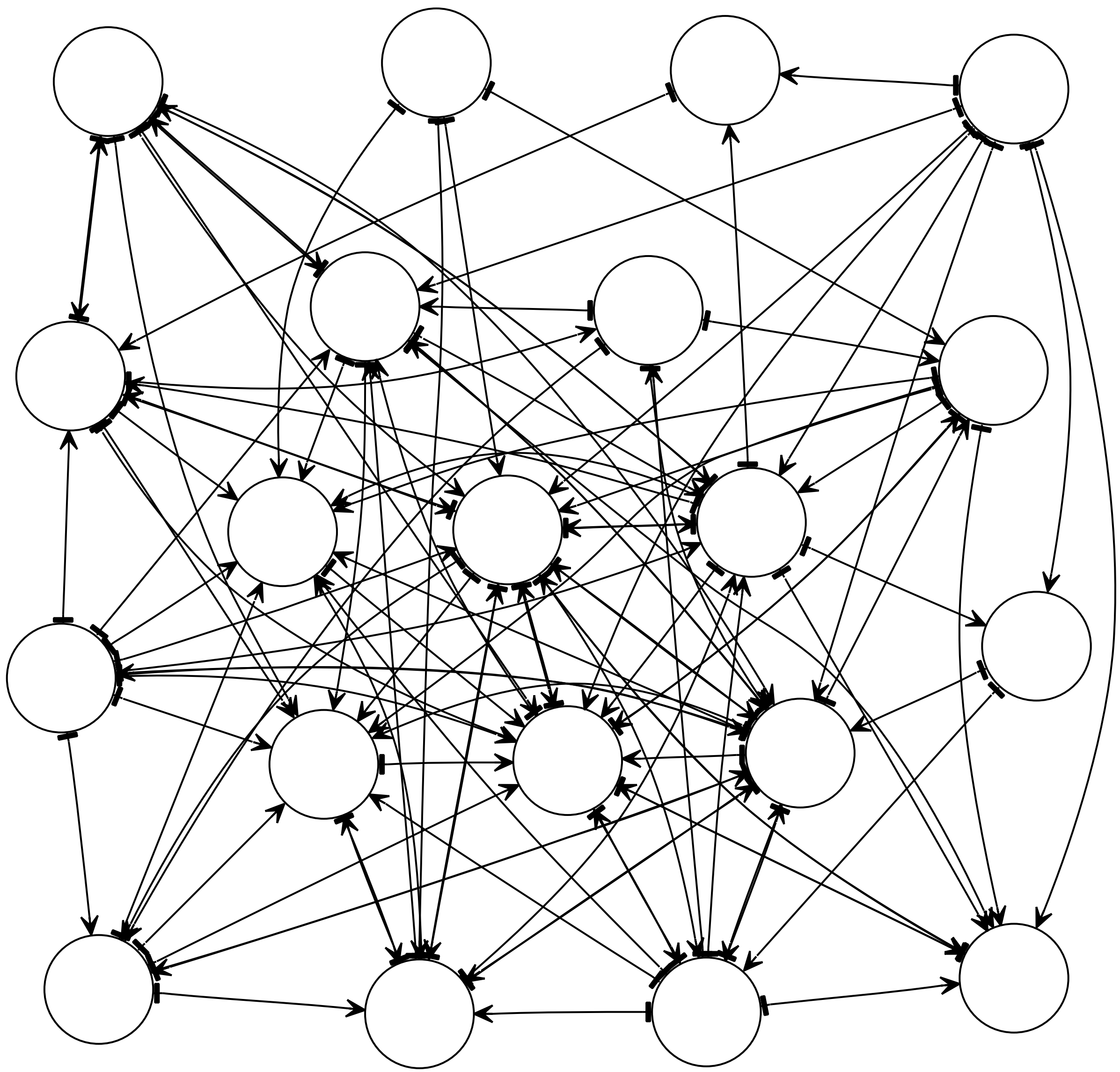

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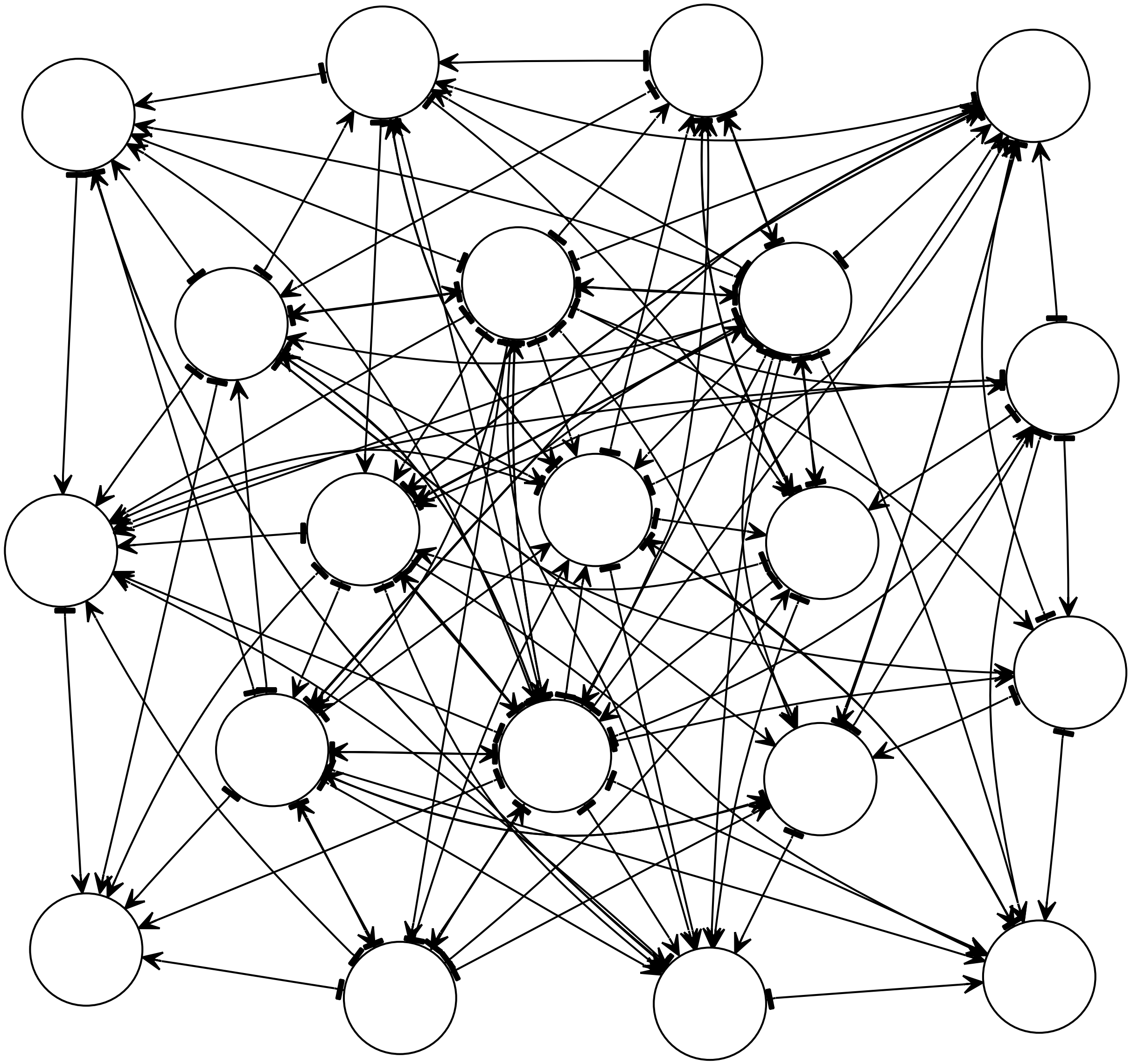

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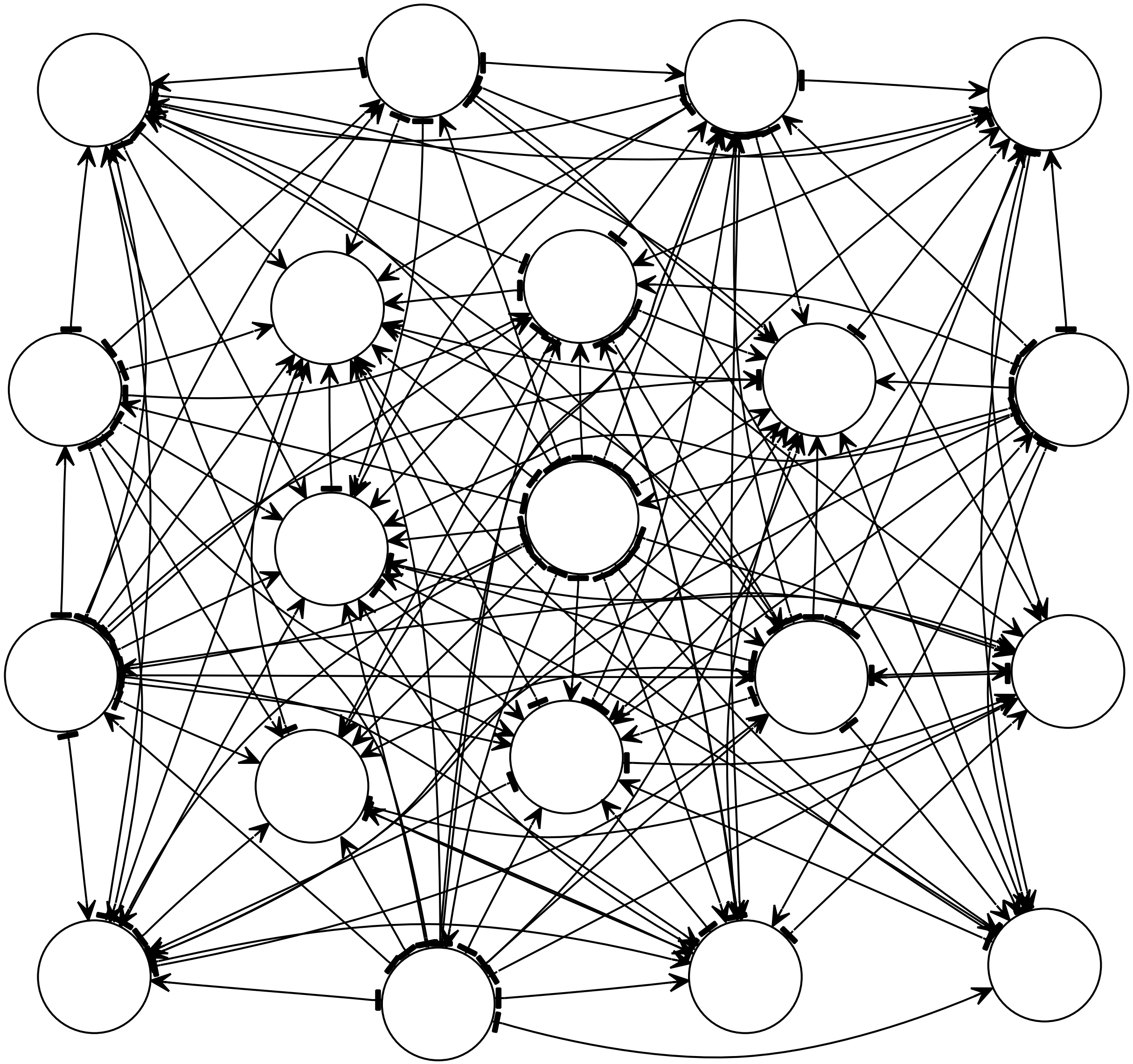

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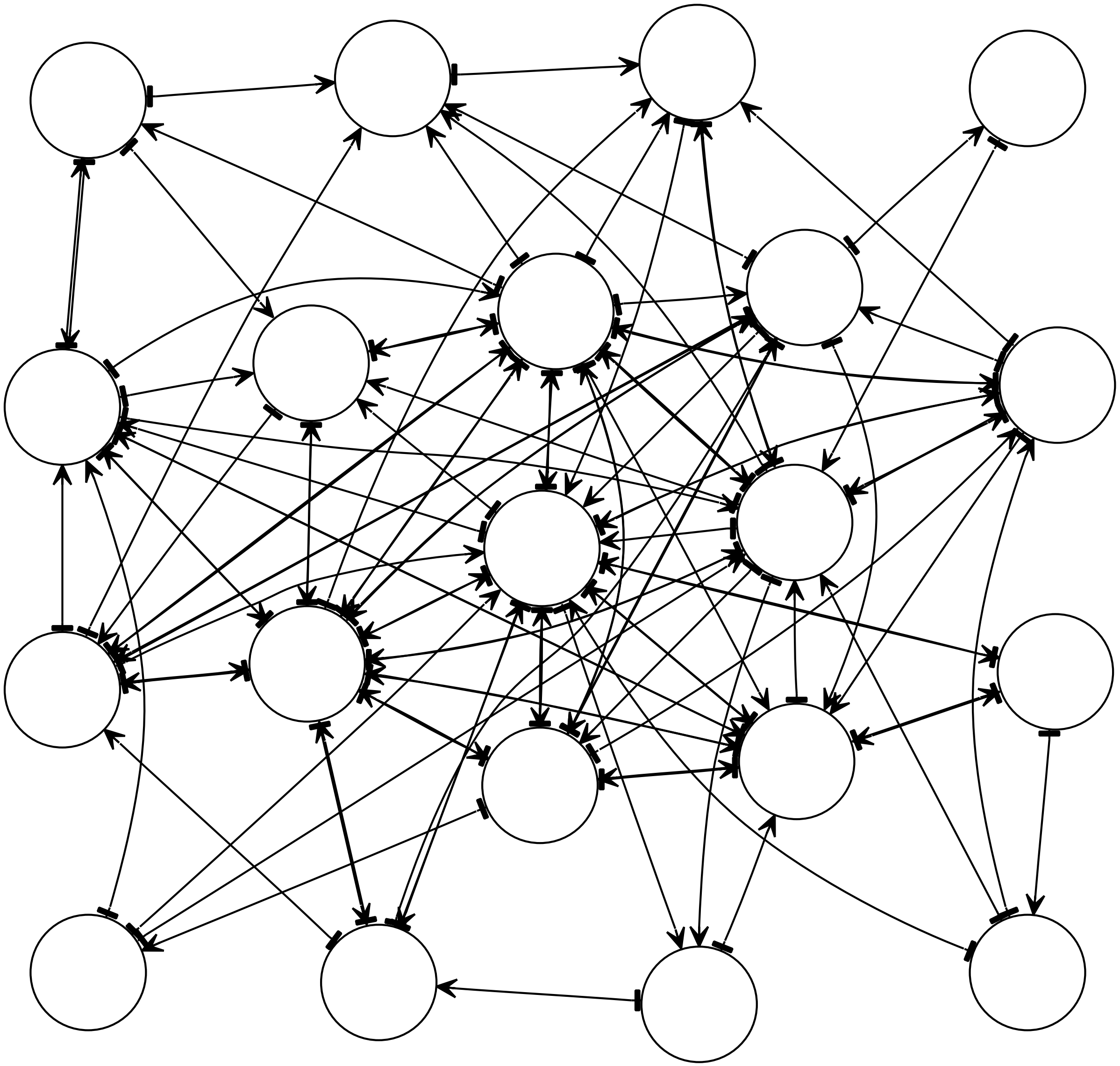

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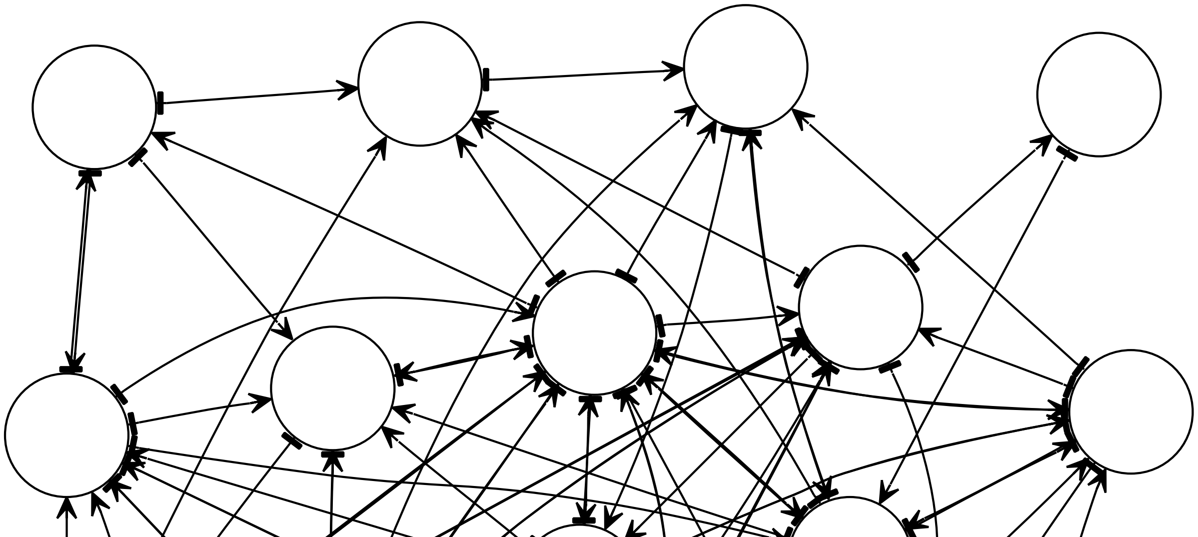

Computations in the brain are performed via complex networks of neurons.

- Can we extract key features of the network connectivity to obtain a useful low-dimensional description?
- Can we determine how these network features influence the dynamical state of neuronal networks?

Outline

1. Introduce SONETs (second order networks)
2. Influence on synchrony
3. Mean-field analysis
4. Multiple populations

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1. **Introduce SONETs (second order networks)**
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Add structure with few dimensions

Focus on connectivity among N nodes.

$W_{ij} = 1$ denotes a connection from node j to i. Else $W_{ij} = 0$.

Starting point: let each $W_{ij} = 1$ independent with probability p.

Get an Erdős-Rényi random graph.

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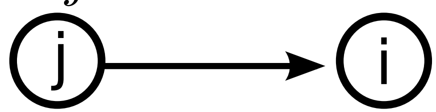
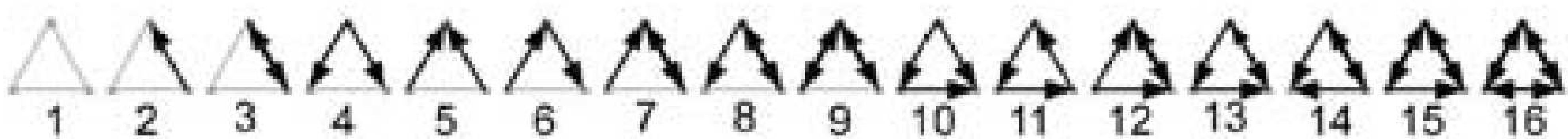


Get an Erdős-Rényi random graph.

But, neuronal networks appear to have additional structure.



Some motifs much more likely than predicted by Erdős-Rényi

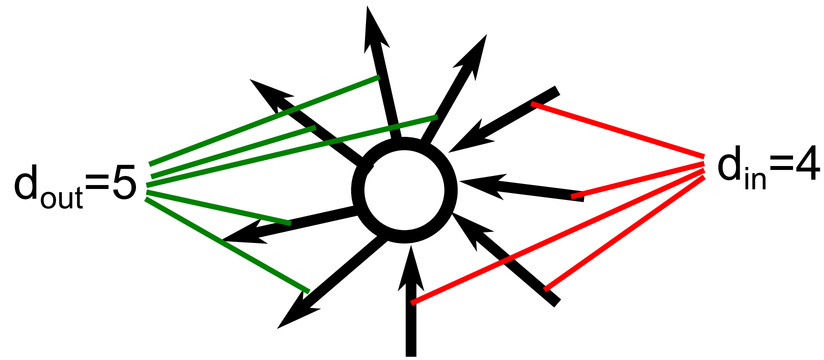
Song et al., PLoS Biology, 2005

Add structure with few dimensions

How to go beyond Erdős-Rényi?

- Standard approach: Add degree distribution $\rho(d_{in}, d_{out})$.

  Problem: many dimensions
  (one parameter for each degree)



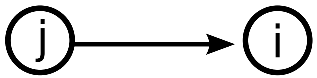
- Using 16 motifs from Song data is high dimensional and complicated.

Question: What is a low-dimensional way to add key structure to networks?

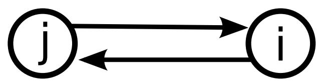
SONETs: second order networks

Idea behind SONETs: parametrize networks by first and second order connectivity statistics.

$$\Pr(W_{ij} = 1) = E(W_{ij}) = p$$

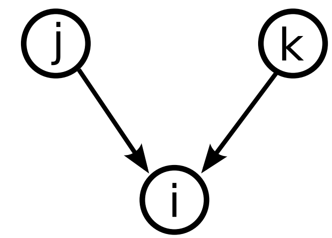


$$\alpha_{\text{recip}} = \frac{\text{cov}(W_{ij}, W_{ji})}{p^2}$$



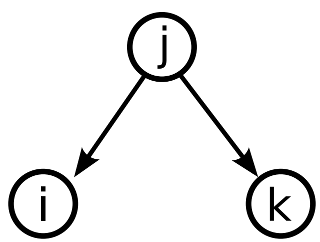
reciprocal connection

$$\alpha_{\text{conv}} = \frac{\text{cov}(W_{ij}, W_{ik})}{p^2}$$



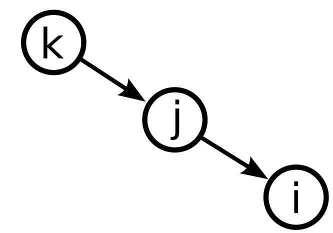
convergent connection

$$\alpha_{\text{div}} = \frac{\text{cov}(W_{ij}, W_{kj})}{p^2}$$



divergent connection

$$\alpha_{\text{chain}} = \frac{\text{cov}(W_{ij}, W_{jk})}{p^2}$$



chain connection

Define second order networks

Problem: There are many such probability distributions with given second order statistics.

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Solutions:

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   Choose the probability distribution with least structure, i.e., the maximum entropy solution. (Ising model.)

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   Use a joint Gaussian distribution to define $\tilde{W}_{ij}$ and let $W_{ij} = 1$ if $\tilde{W}_{ij} > \theta$ for some threshold θ.

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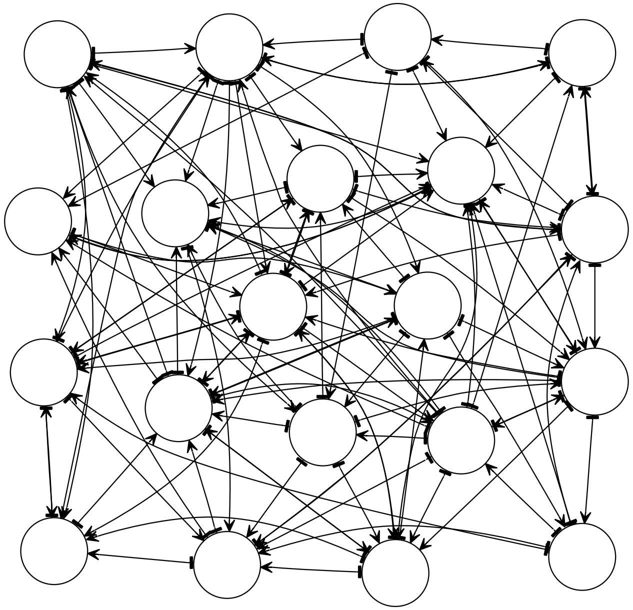
2. The wrong way

   Use a joint Gaussian distribution to define $\tilde{W}_{ij}$ and let $W_{ij} = 1$ if $\tilde{W}_{ij} > \theta$ for some threshold θ.

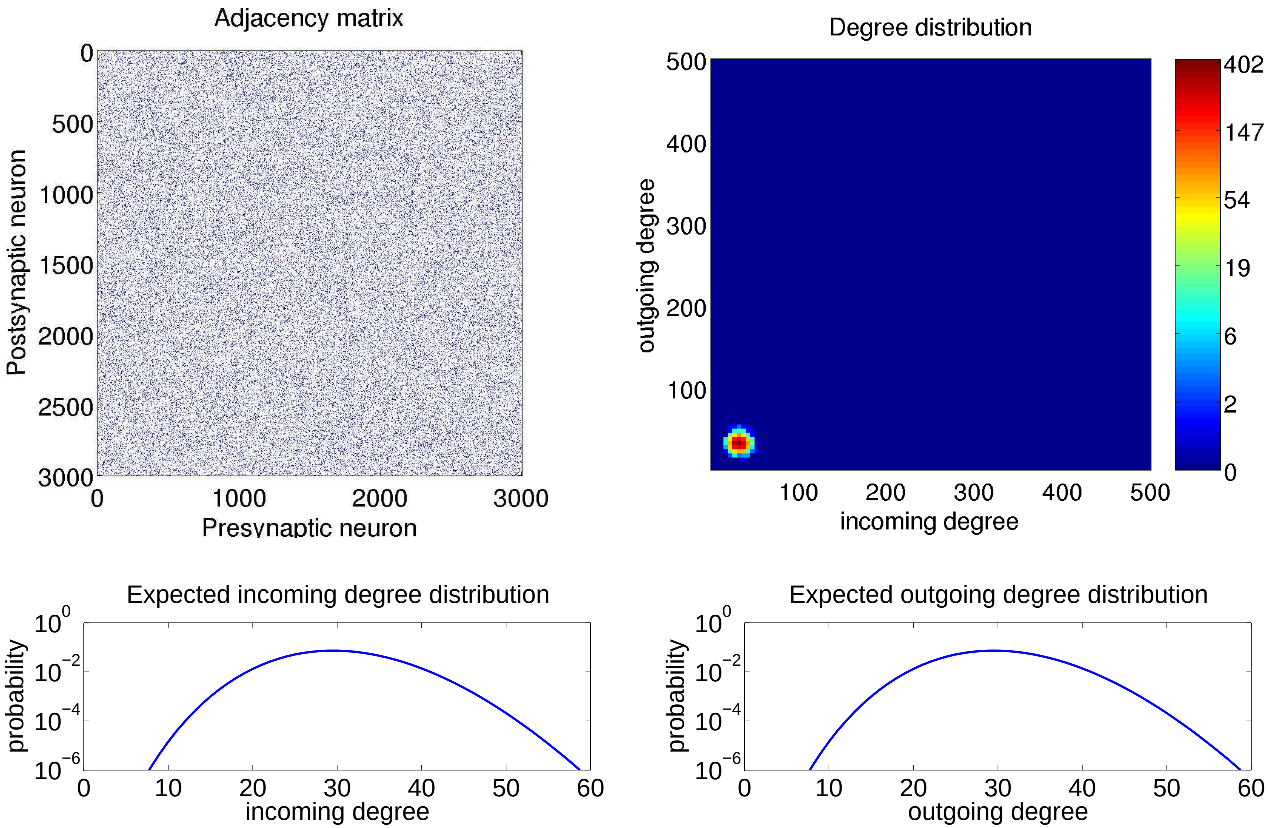
As matter of principle, choose the wrong way.

Properties of second order networks: Erdős-Rényi

The Erdős-Rényi random network

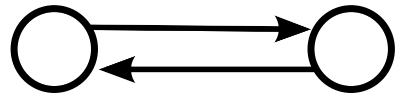


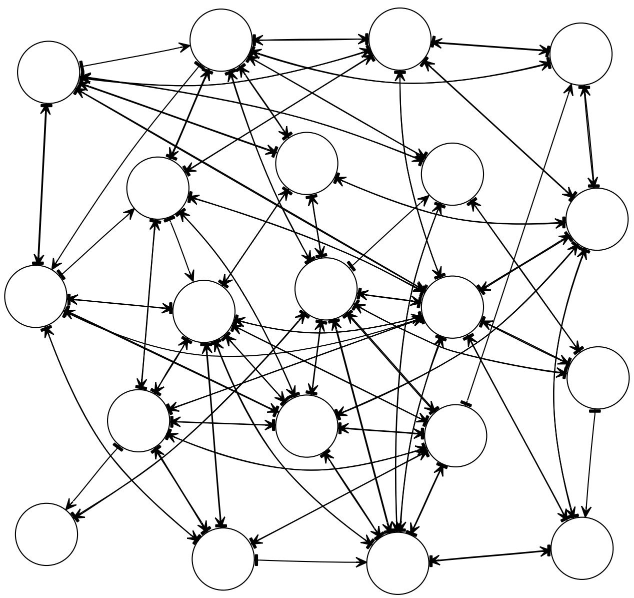
$N = 20,\ p = 0.3,\ \alpha_{\text{recip}} = -0.1,$
$\alpha_{\text{conv}} = 0,\ \alpha_{\text{div}} = 0,\ \alpha_{\text{chain}} = 0$



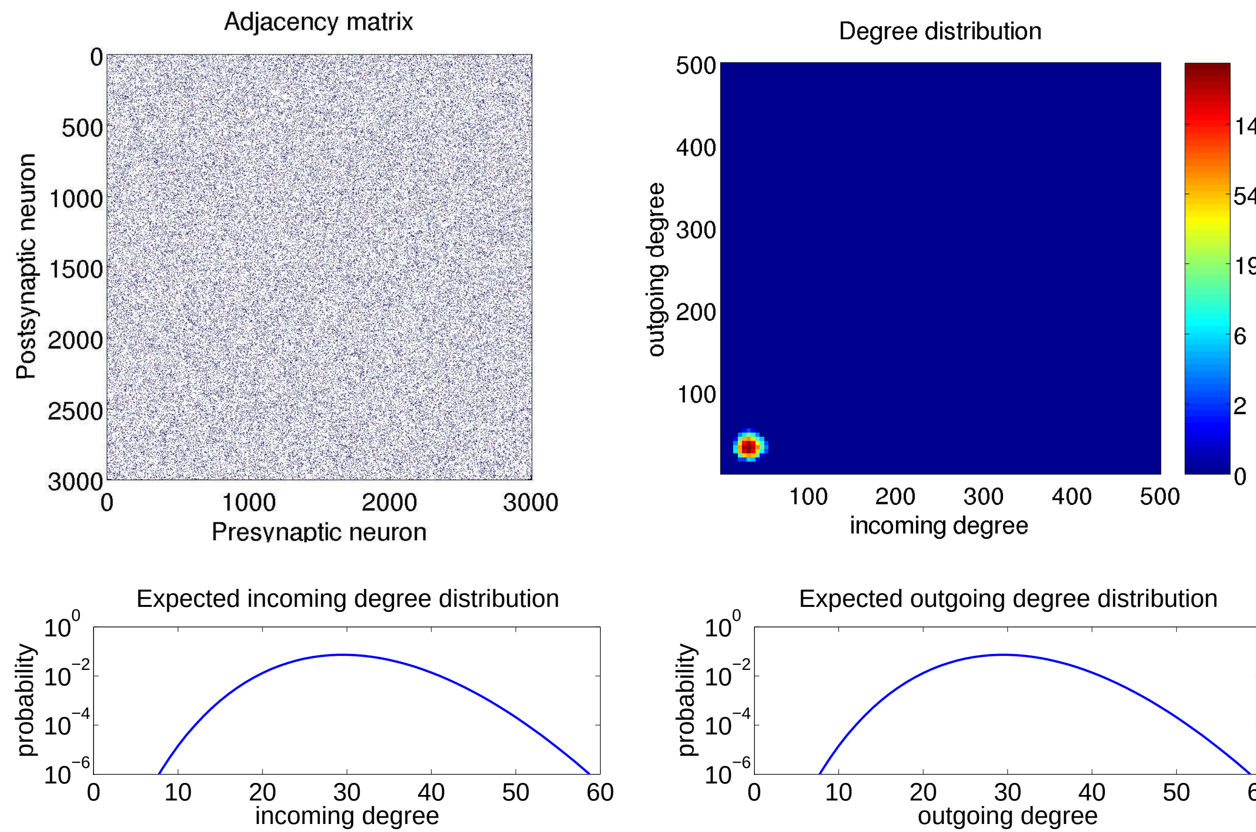
$N = 3000,\ p = 0.01,\ \alpha_{\text{recip}} = 0,\ \alpha_{\text{conv}} = 0,\ \alpha_{\text{div}} = 0,\ \alpha_{\text{chain}} = 0$

Properties of second order networks: reciprocal

Add reciprocal connections: 

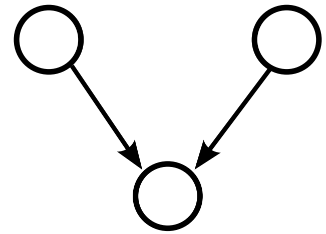


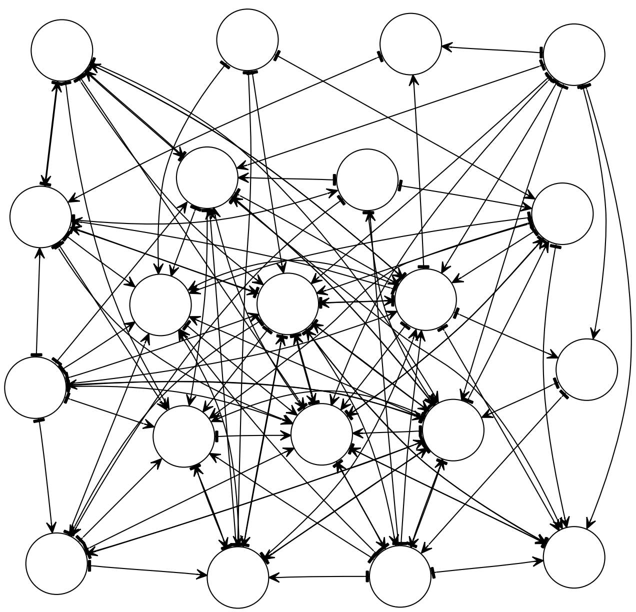
$N = 20$, $p = 0.3$, $\alpha_{\text{recip}} = 2.0$, $\alpha_{\text{conv}} = 0$, $\alpha_{\text{div}} = 0$, $\alpha_{\text{chain}} = 0$



$N = 3000$, $p = 0.01$, $\alpha_{\text{recip}} = 3$, $\alpha_{\text{conv}} = 0$, $\alpha_{\text{div}} = 0$, $\alpha_{\text{chain}} = 0$

Properties of second order networks: convergent

Add convergent connections: 



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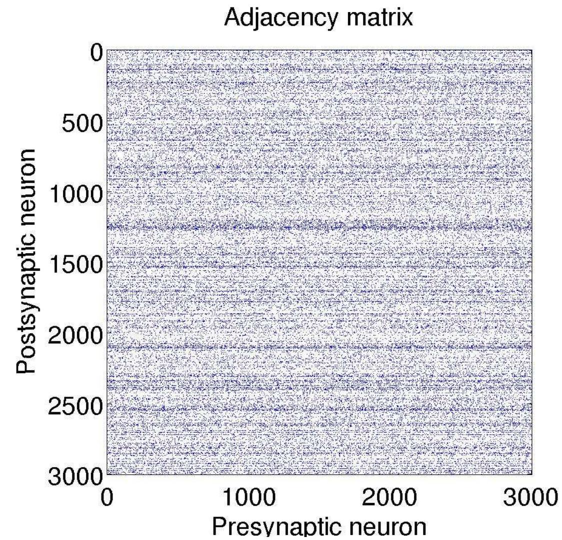
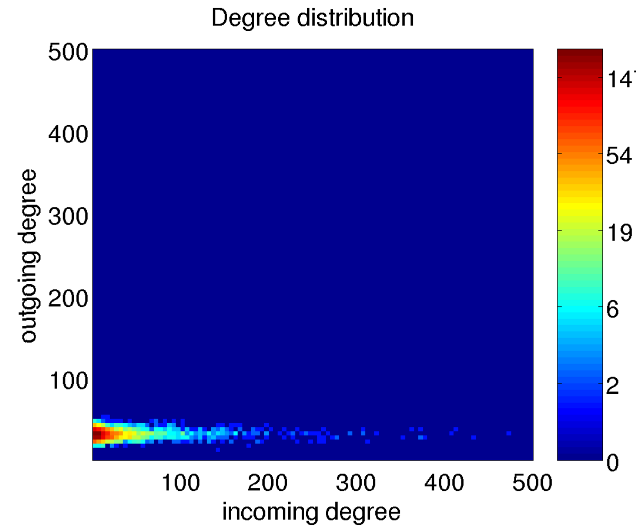
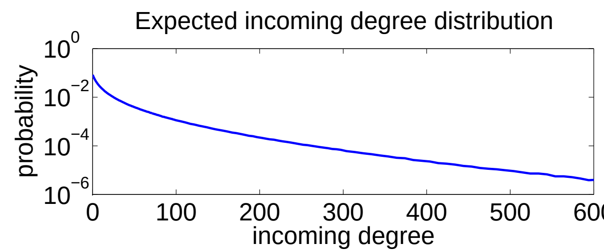
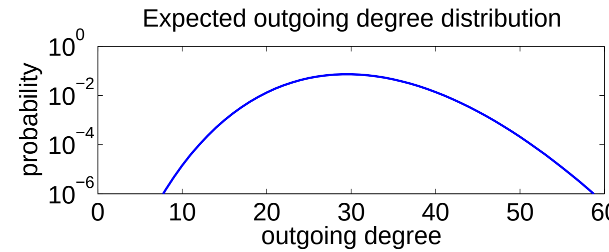




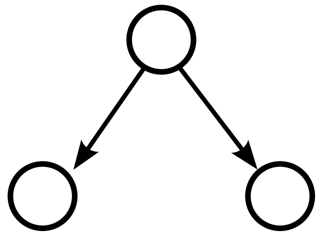


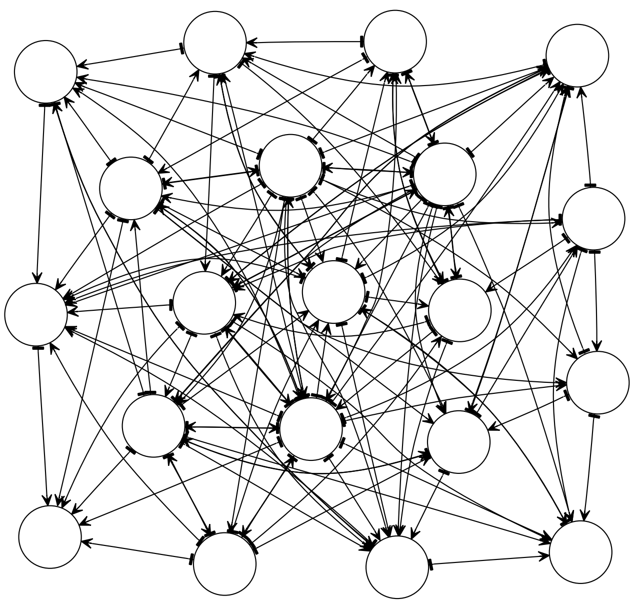


$N = 3000$, $p = 0.01$, $\alpha_{\text{recip}} = 0$, $\alpha_{\text{conv}} = 3$, $\alpha_{\text{div}} = 0$, $\alpha_{\text{chain}} = 0$

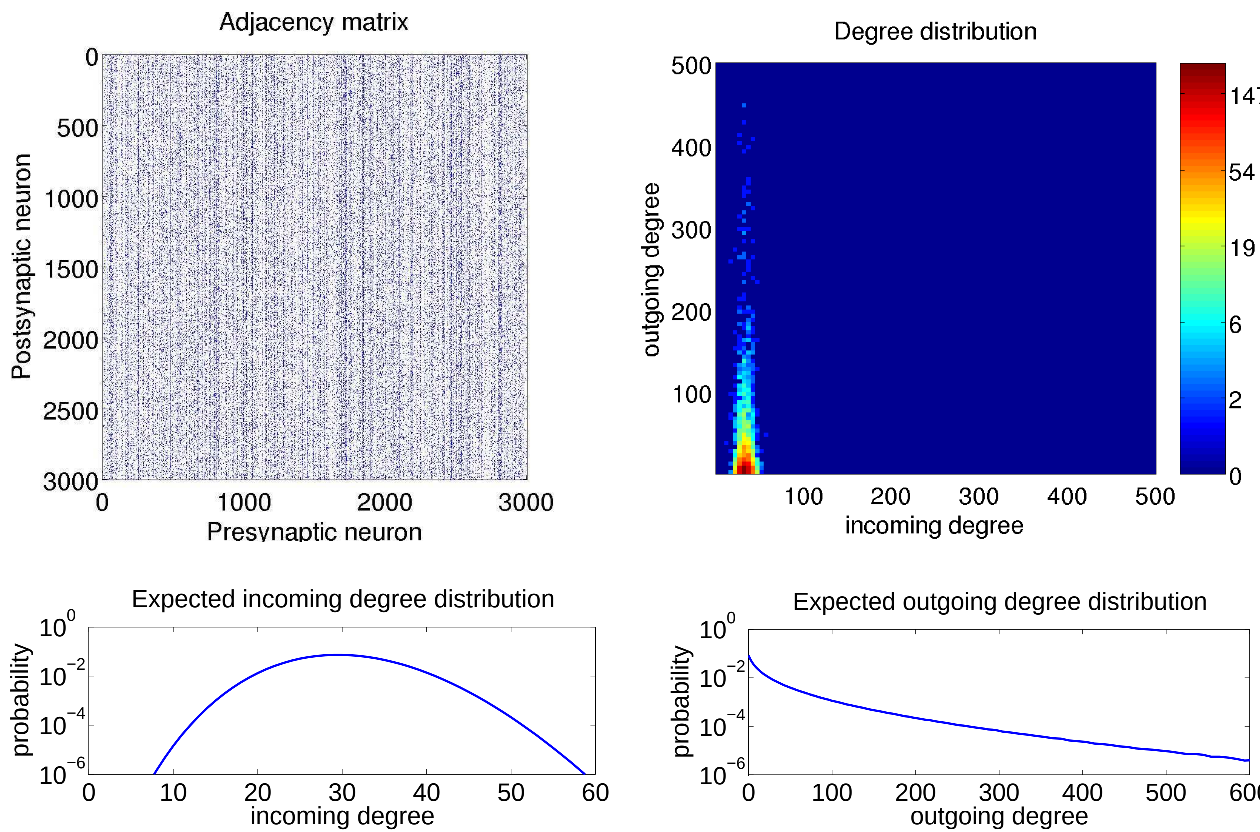
Properties of second order networks: divergent

Add divergent connections:





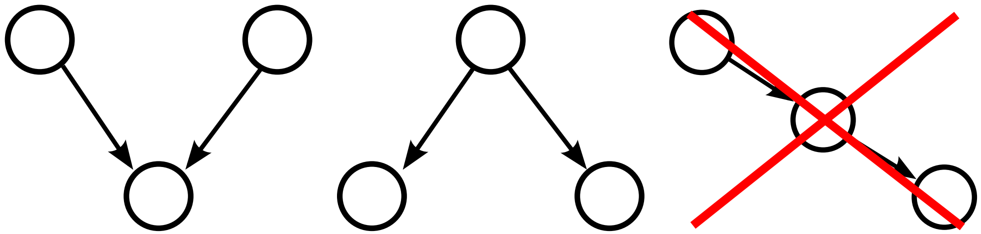
$N = 20$, $p = 0.3$, $\alpha_{\text{recip}} = -0.1$,
$\alpha_{\text{conv}} = 0$, $\alpha_{\text{div}} = 0.5$, $\alpha_{\text{chain}} = 0$

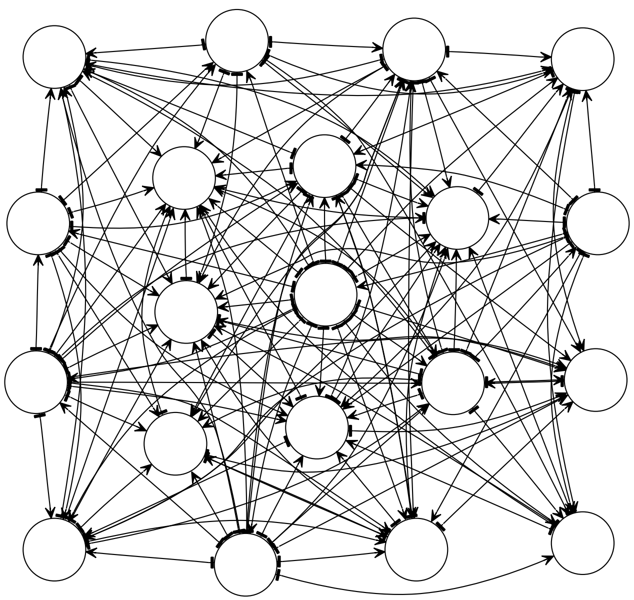


$N = 3000$, $p = 0.01$, $\alpha_{\text{recip}} = 0$, $\alpha_{\text{conv}} = 0$, $\alpha_{\text{div}} = 3$, $\alpha_{\text{chain}} = 0$

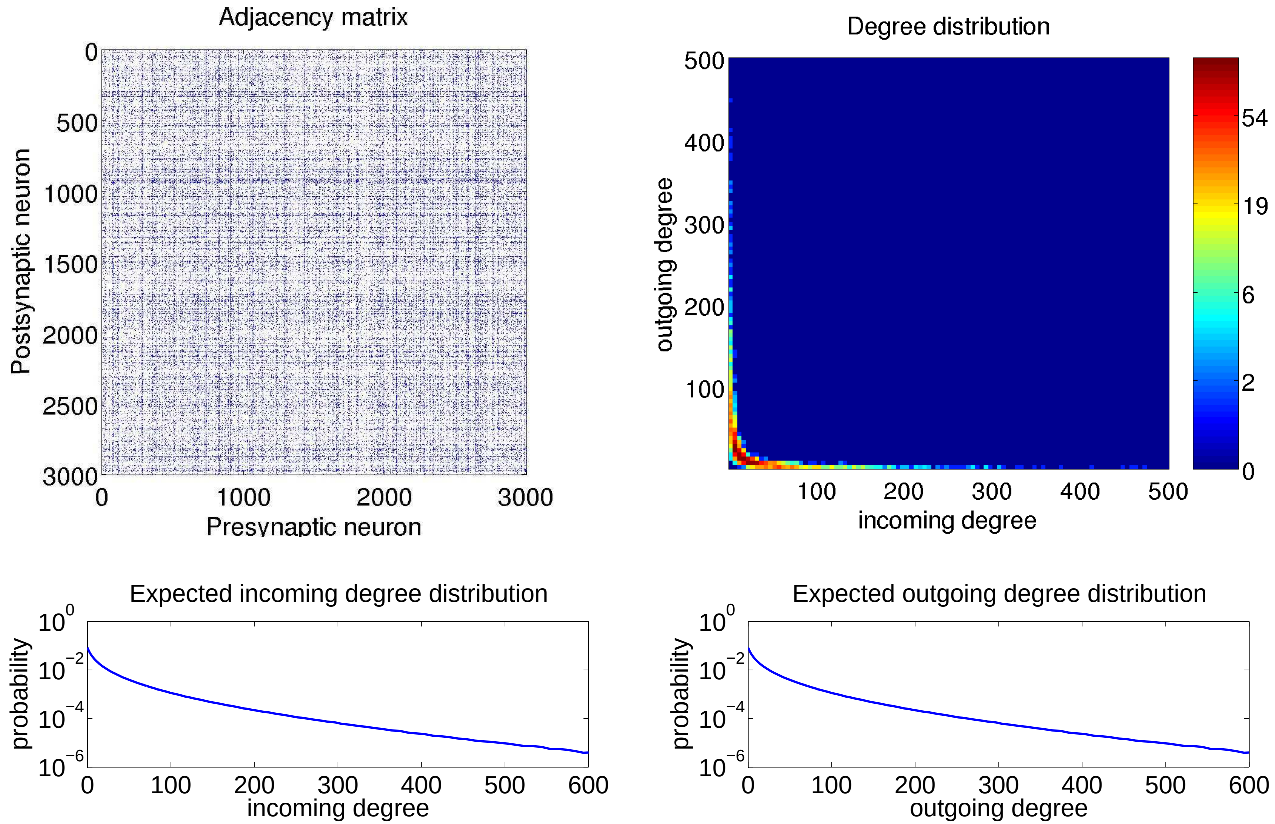
Properties of second order networks: no chains

Add convergent and divergent connections, reduce chains:





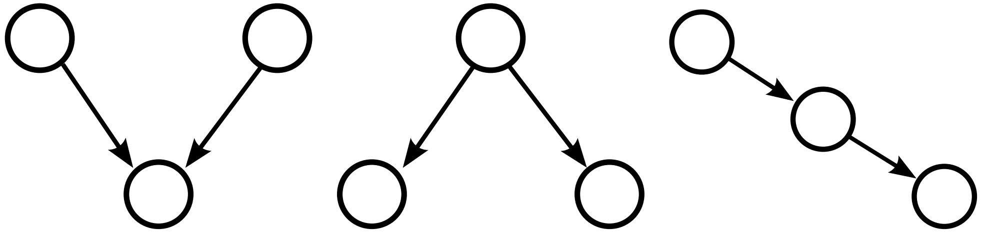
$N = 20$, $p = 0.4$, $\alpha_{\text{recip}} = -0.9$, $\alpha_{\text{conv}} = 0.3$, $\alpha_{\text{div}} = 0.4$, $\alpha_{\text{chain}} = -0.3$

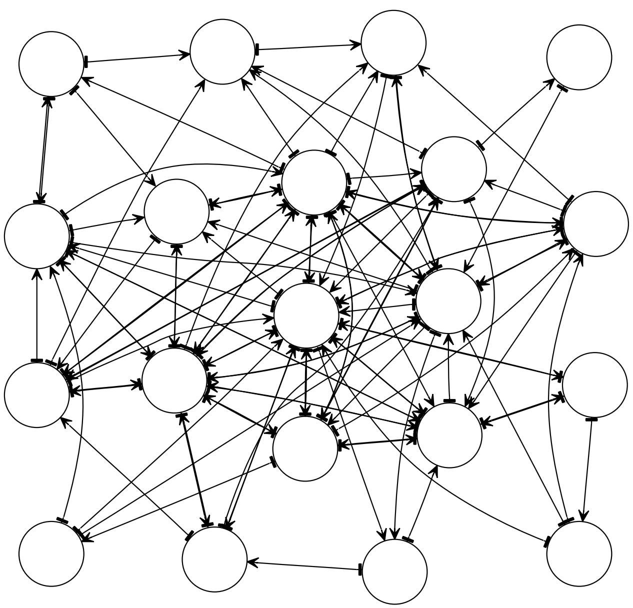


$N = 3000$, $p = 0.01$, $\alpha_{\text{recip}} = 0$, $\alpha_{\text{conv}} = 3$, $\alpha_{\text{div}} = 3$, $\alpha_{\text{chain}} = -0.9$

Properties of second order networks: chains

Add convergent and divergent connections with chains:





$N = 20$, $p = 0.3$, $\alpha_{\text{recip}} = 1.0$,
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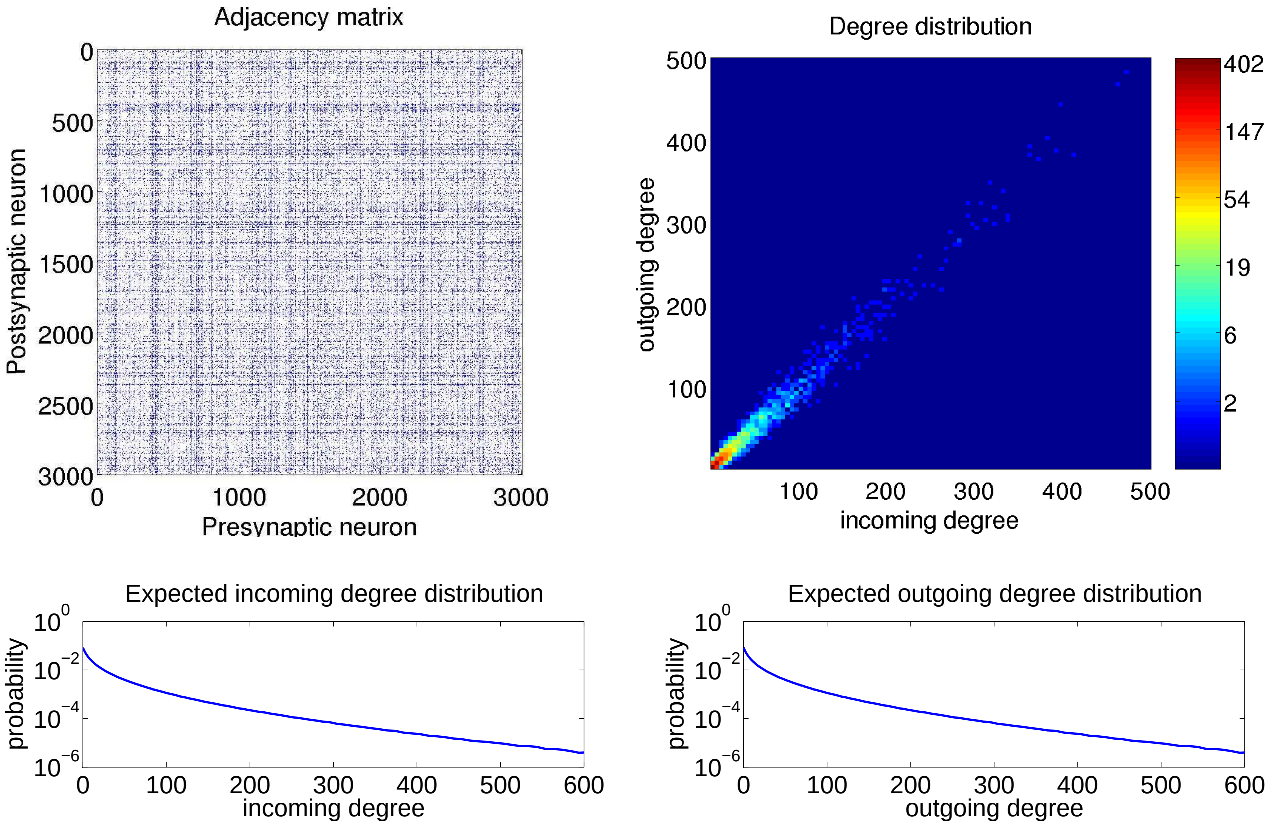

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Outline

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2. Influence on synchrony
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Influence of network structure on synchrony

Simulate network of excitatory phase response curve neurons.

$$\frac{\mathrm{d}\theta_i}{\mathrm{d}t} = \omega_i + \frac{J}{pN} f(\theta_i) \sum_{j \neq i} W_{ij} \sum_k \delta(t - T_j^k) + \sigma \xi(t)$$

Measure steady state synchrony with order parameter.

$$\text{synchrony} = \frac{1}{N} \left| \sum_{j=1}^{N} e^{i\theta_j} \right|$$

synchrony $= 0 \Rightarrow$ asynchrony
synchrony $= 1 \Rightarrow$ complete synchrony

f = phase response curve, T_j^k = time of kth spike of neuron j, S = coupling strength,
ω = intrinsic frequency, $\xi(t)$ = white noise

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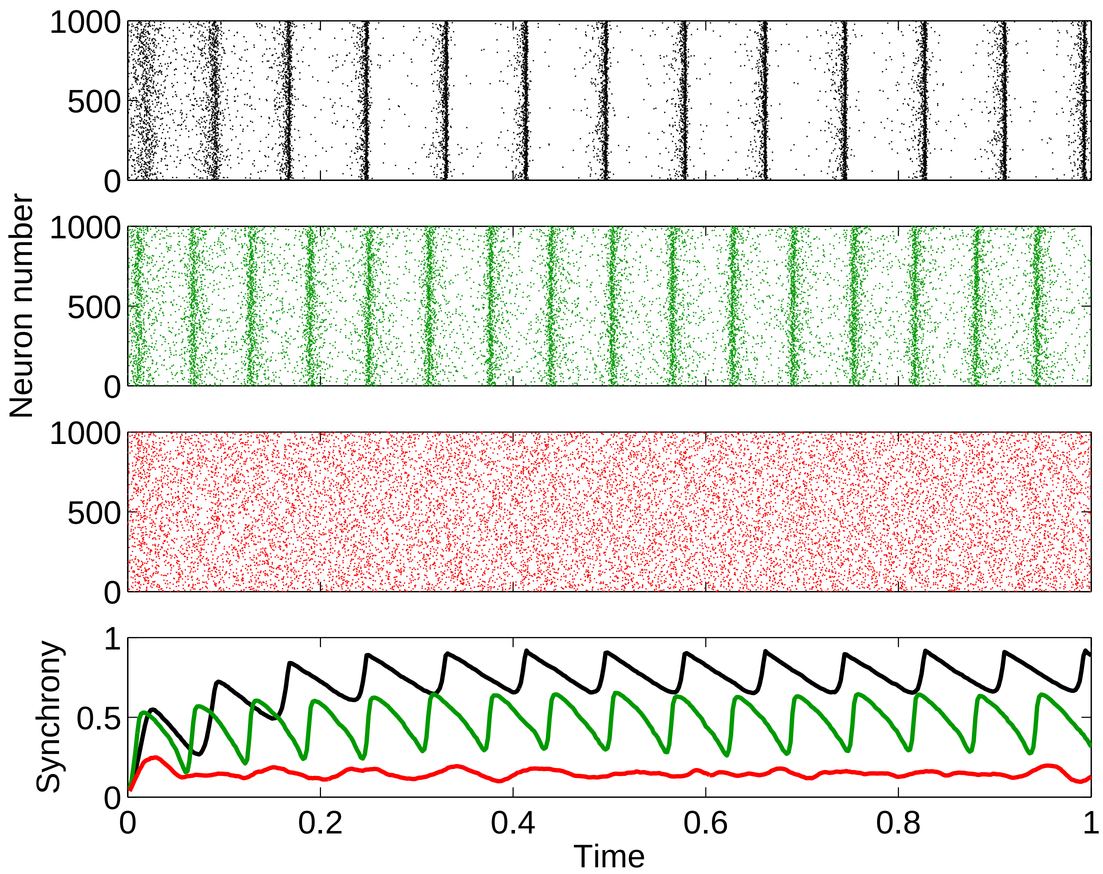
Adjust ω_i so that each neuron fires at 10 Hz.

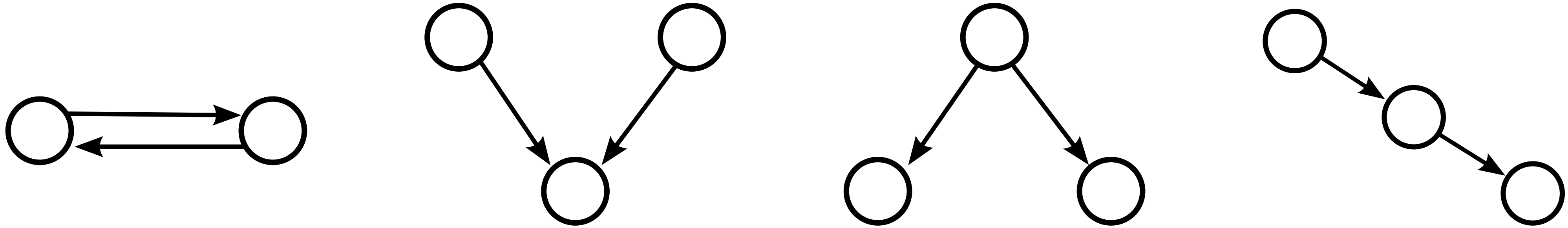
Illustrate synchrony

Simulate phase response curve models on SONETs.

Degree of synchronization varies across networks.

What network features most strongly modulate the synchrony?





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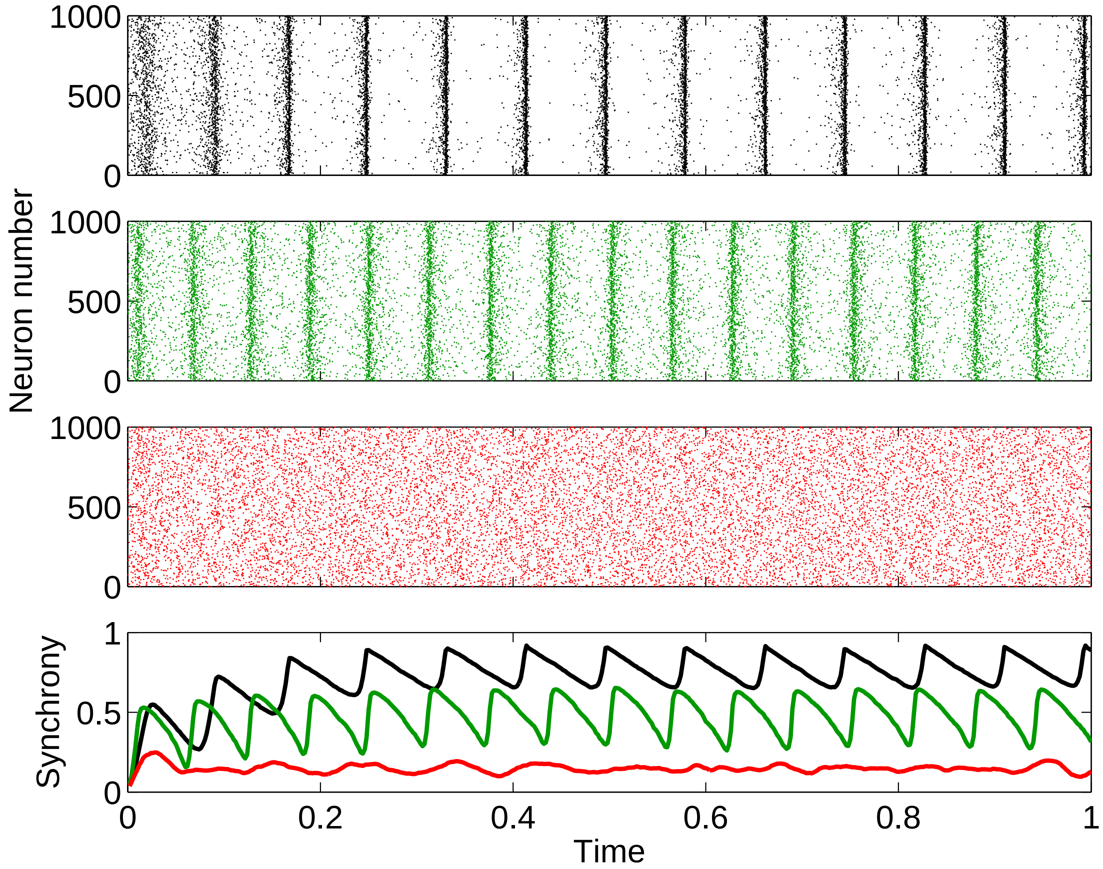
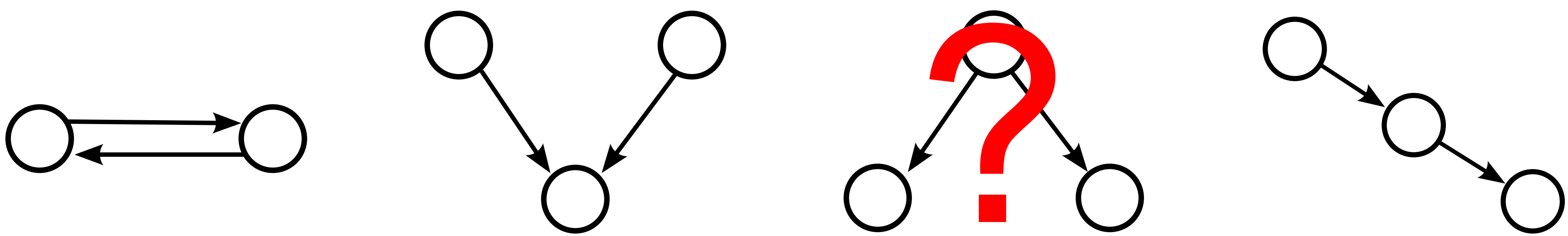
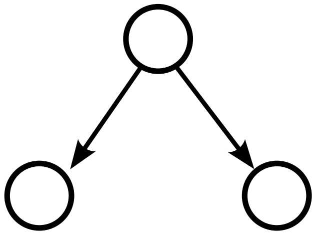




Does common input influence synchrony?

One idea: common input connections should encourage synchrony.



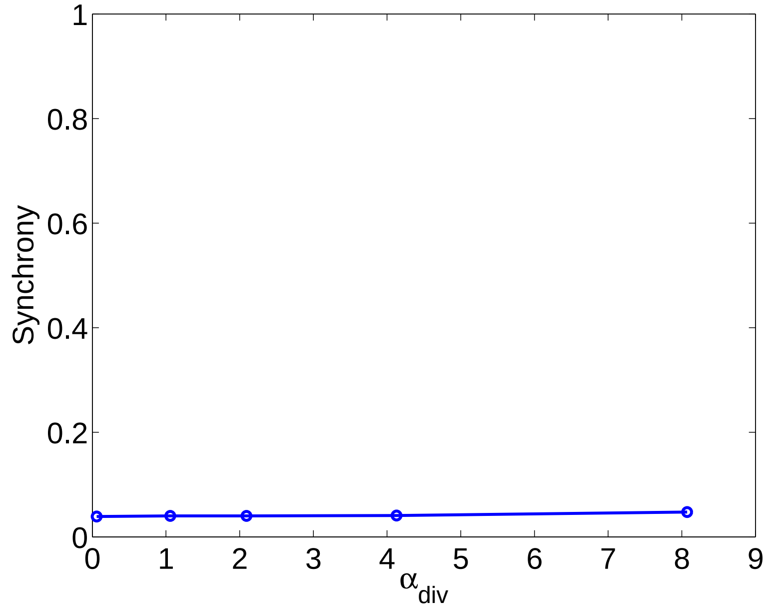
Intuition from feedforward networks:
common input
$\Rightarrow$ correlated input
$\Rightarrow$ correlated output
$\Rightarrow$ more correlated input downstream
$\Rightarrow$ development of synchrony

(But see Rosenbaum et al., 2010.)

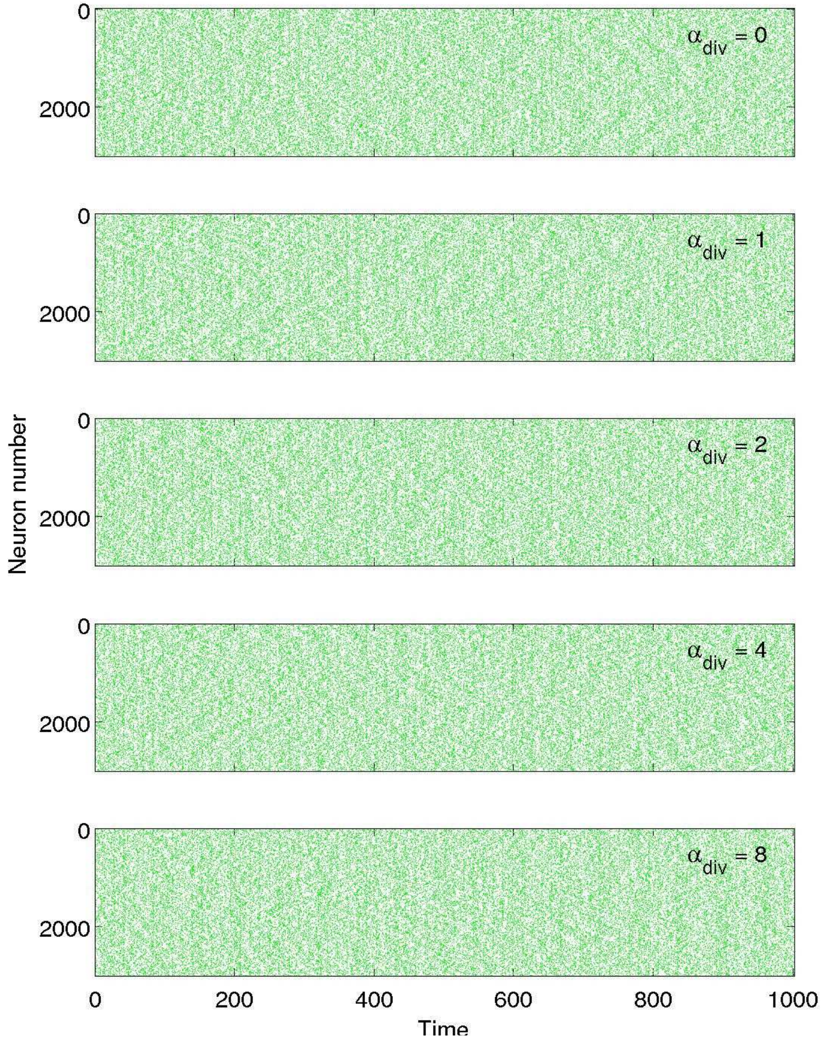
Test for recurrent networks through simulations of SONETs.

Simulations with divergence

Synchrony as function of divergence



Simulate five SONETs spanning range of divergence.



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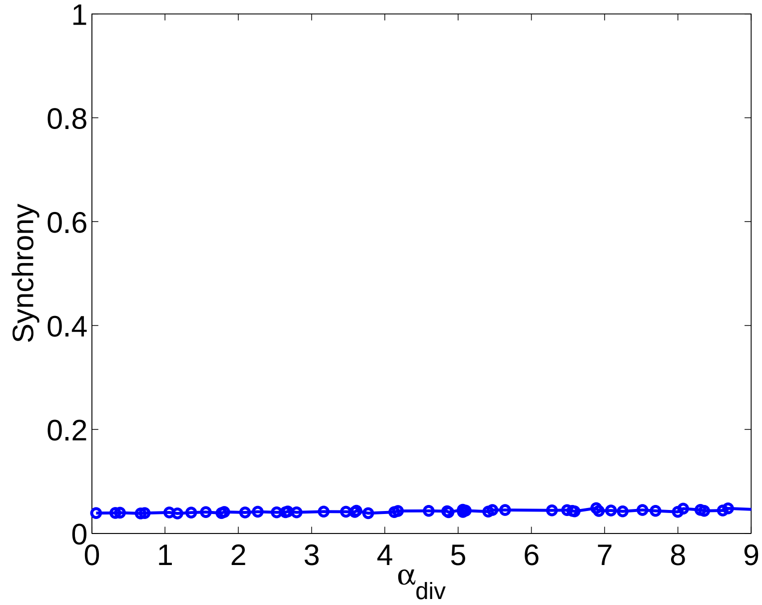
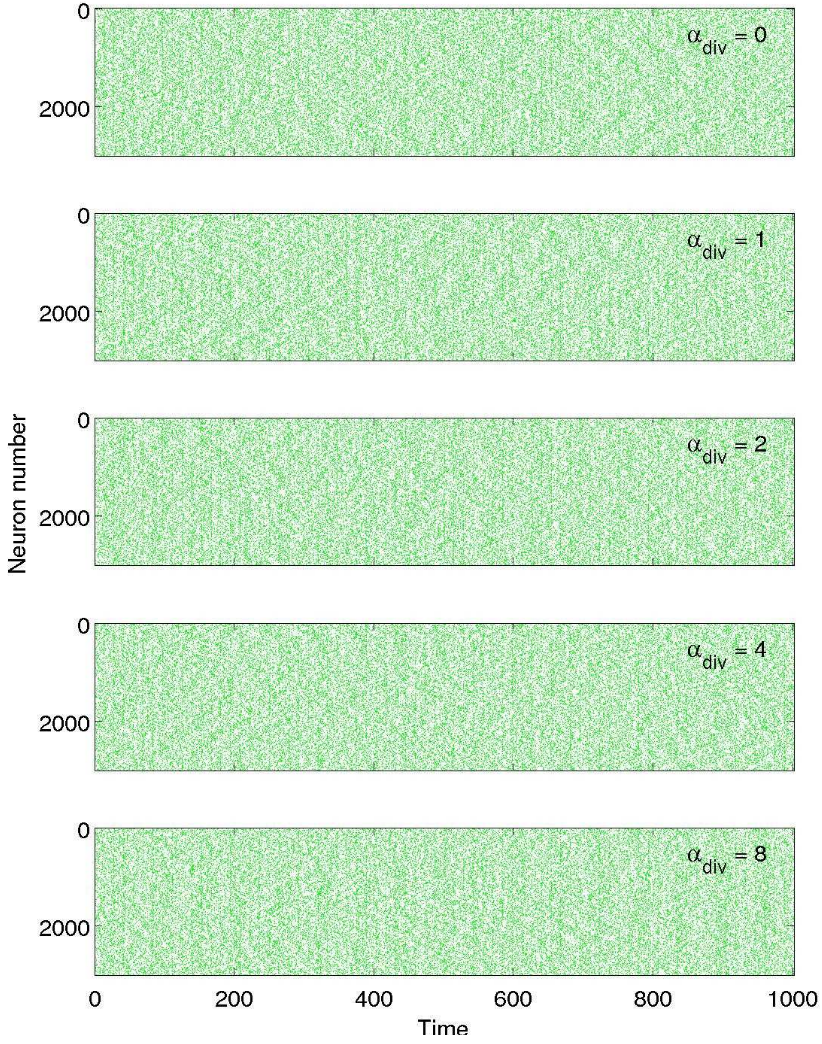


Simulate five SONETs spanning range of divergence.

Simulate a bunch more.

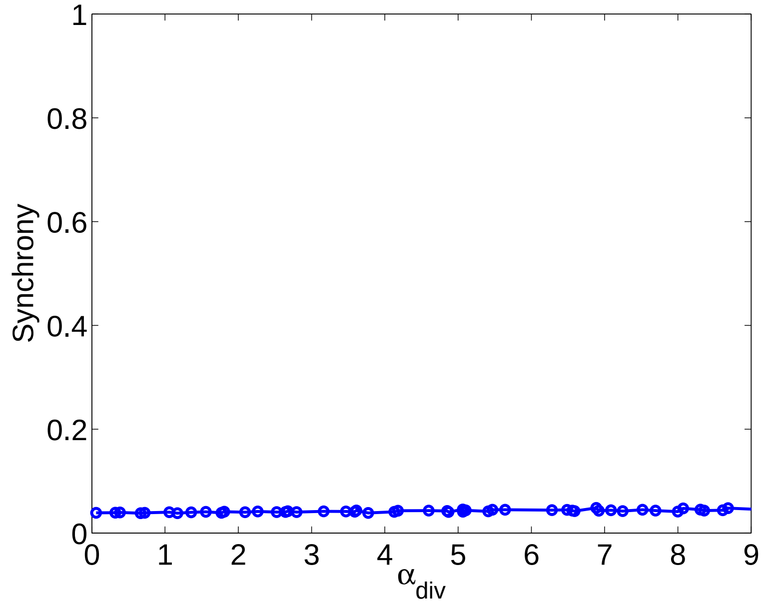


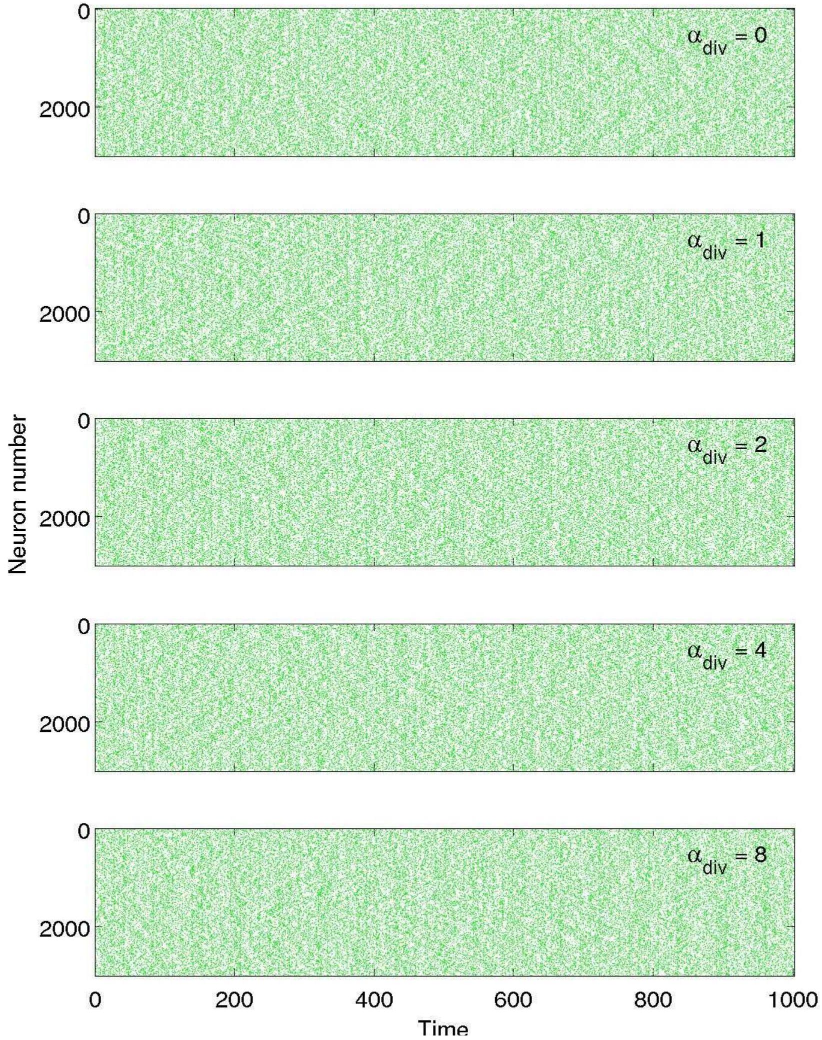
Conclude divergence doesn't influence synchrony, right?

Simulations with divergence

$J = 1$

Synchrony as function of divergence

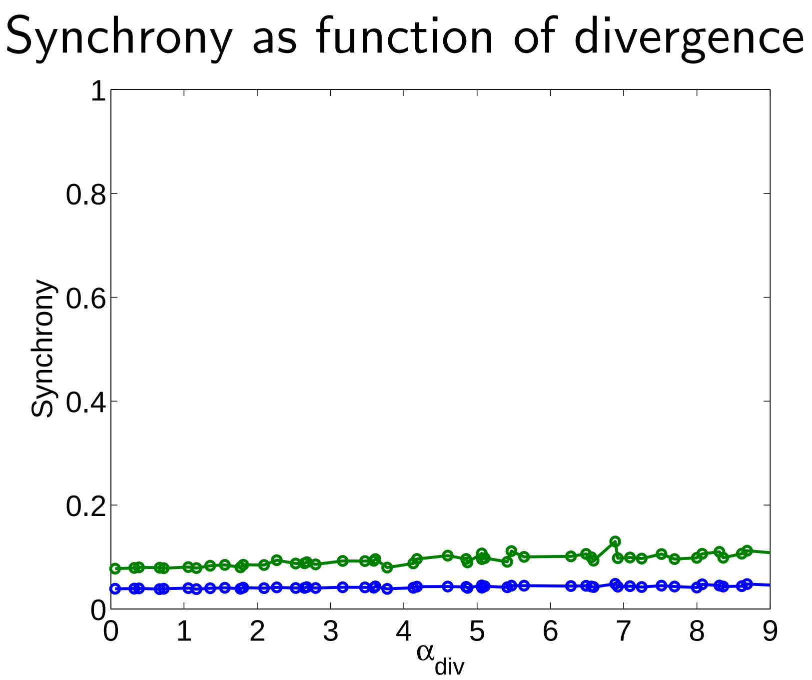




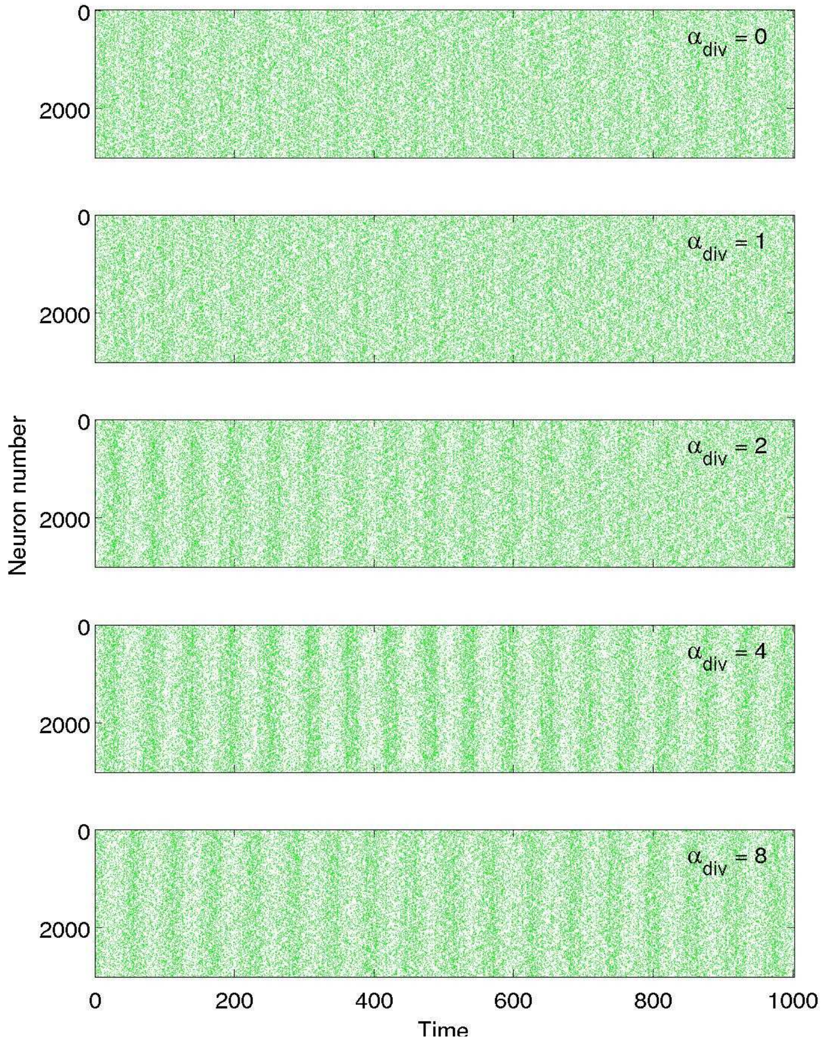
Simulate with increasing coupling strengths J

Simulations with divergence

$J = 2$



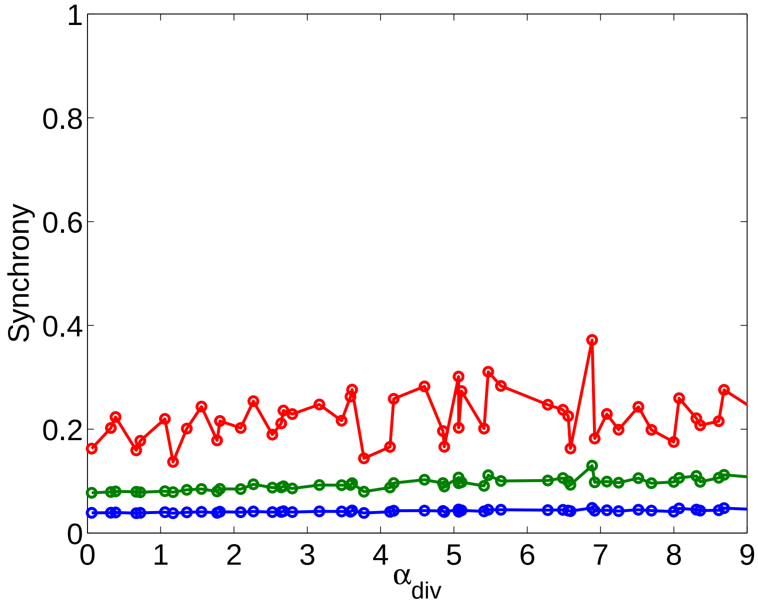
Simulate with increasing coupling strengths J

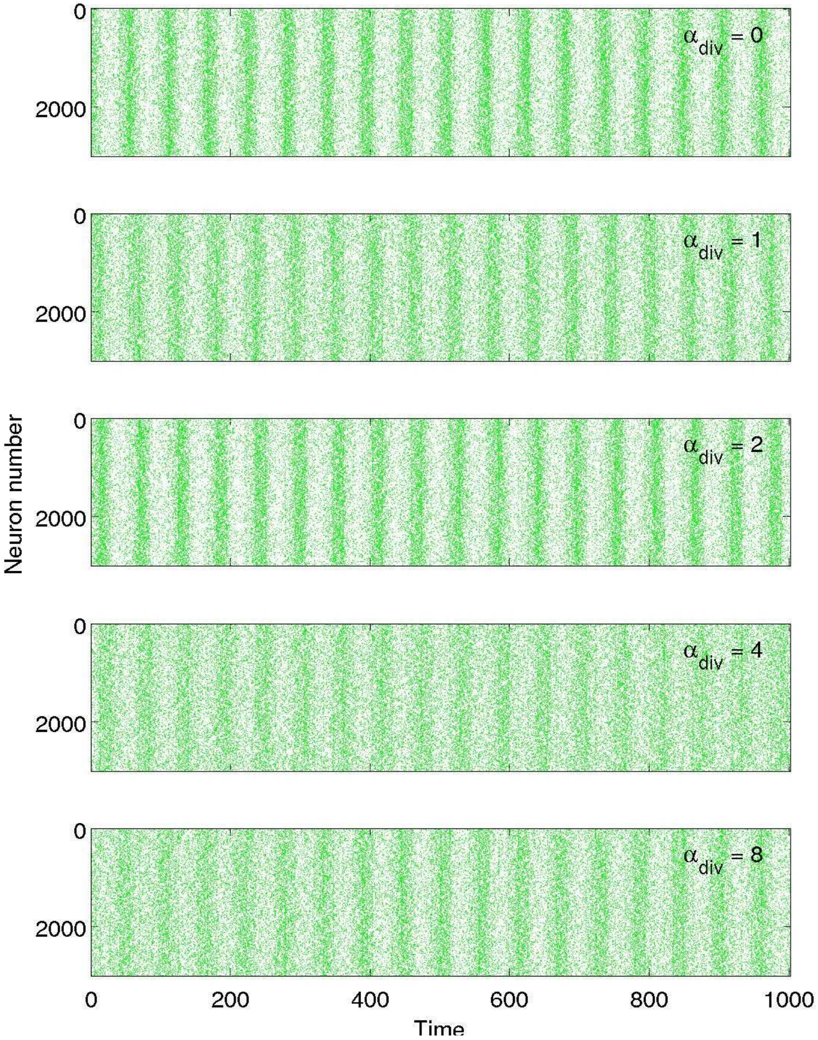


Simulations with divergence

$J = 2.6$

Synchrony as function of divergence



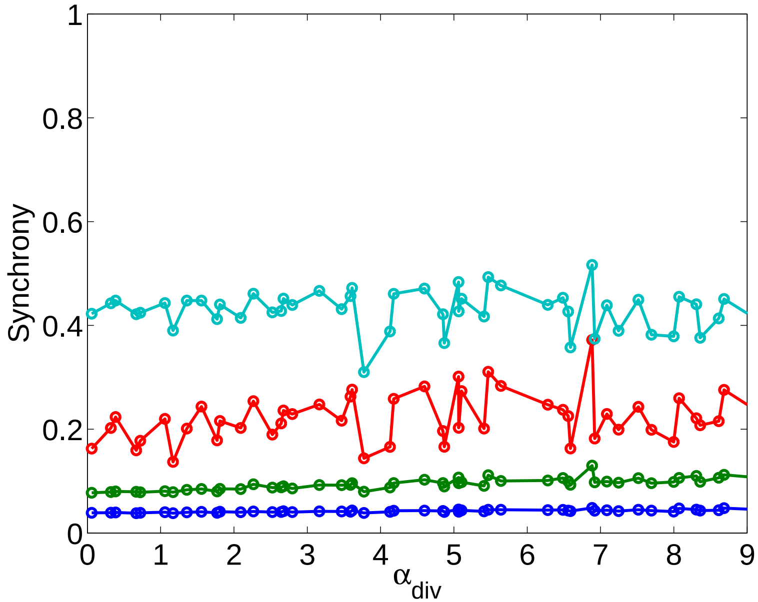


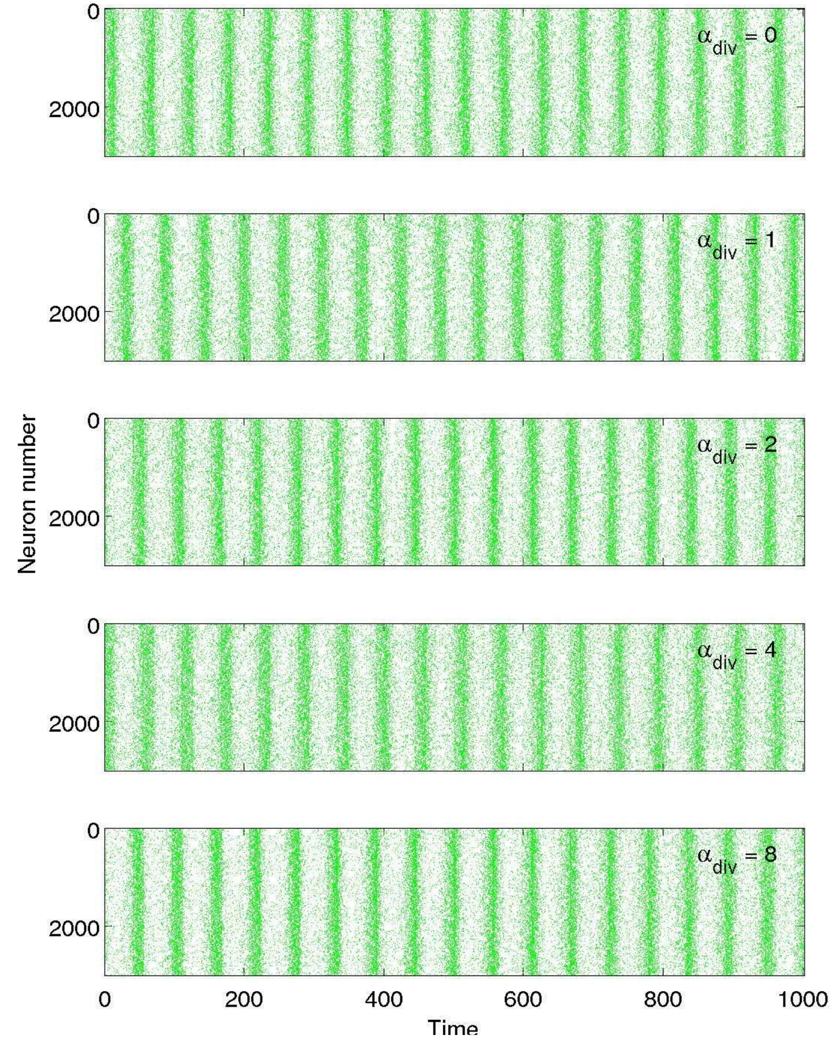
Simulate with increasing coupling strengths J

Simulations with divergence

$J = 3$

Synchrony as function of divergence



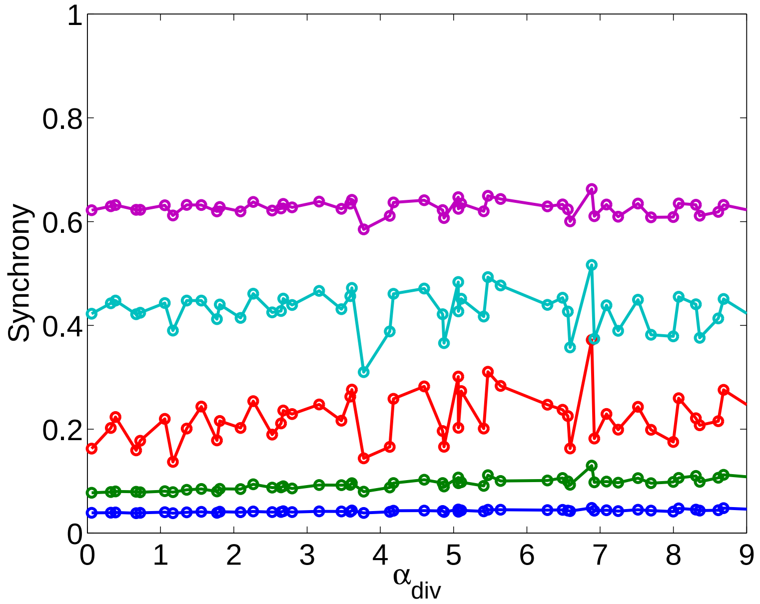


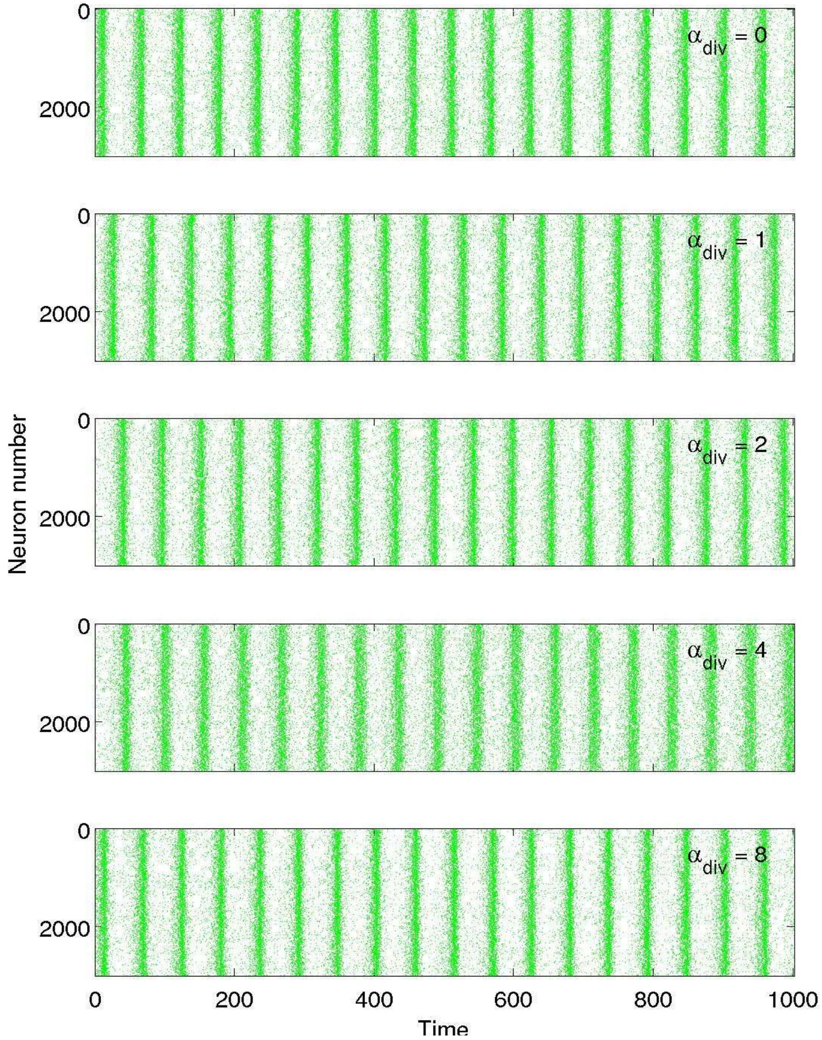
Simulate with increasing coupling strengths J

Simulations with divergence

$J = 4$

Synchrony as function of divergence



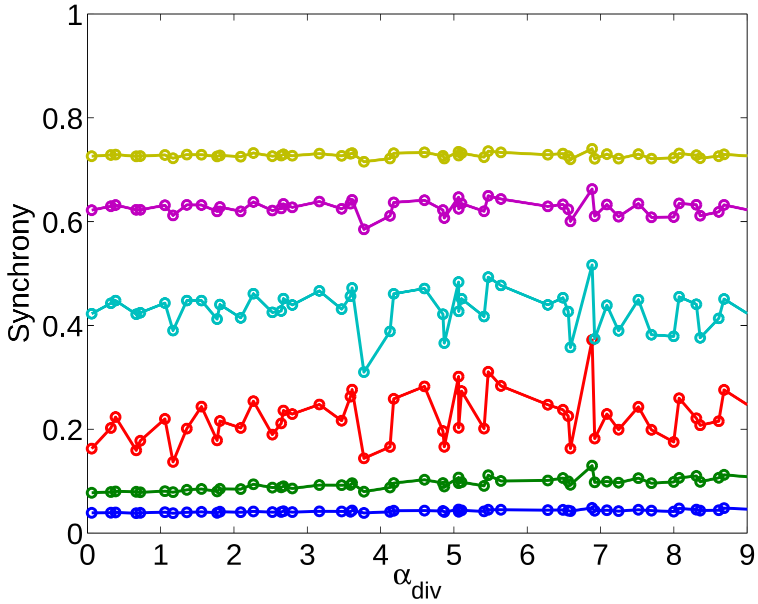


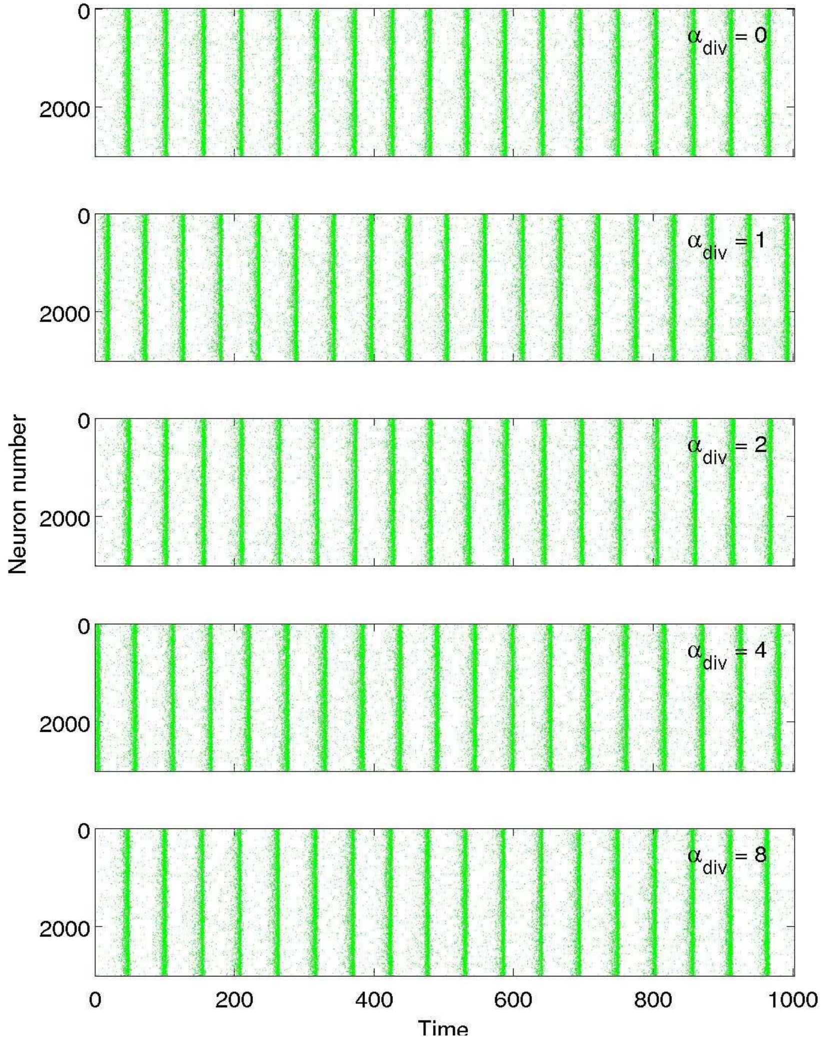
Simulate with increasing coupling strengths J

Simulations with divergence

$J = 6$

Synchrony as function of divergence



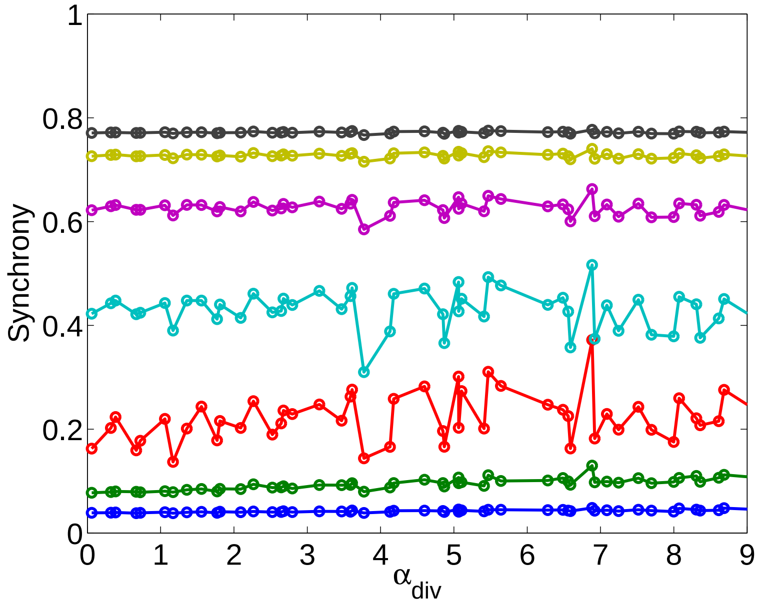


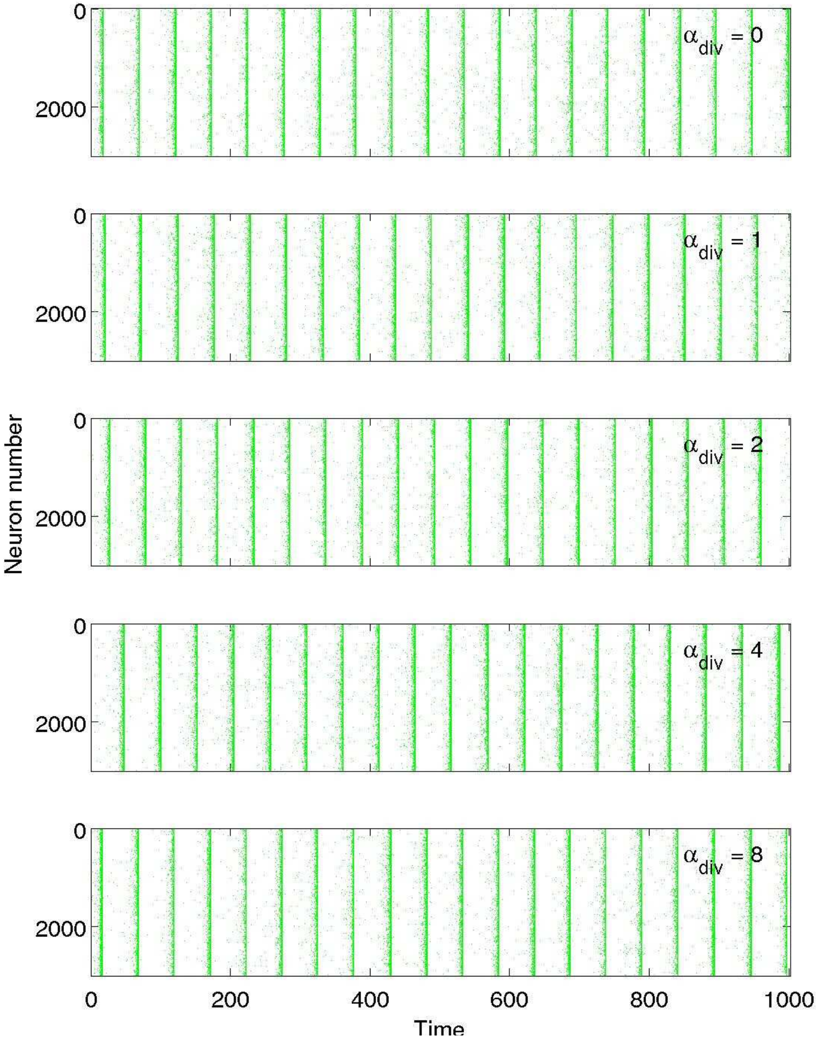
Simulate with increasing coupling strengths J

Simulations with divergence

$J = 10$

Synchrony as function of divergence



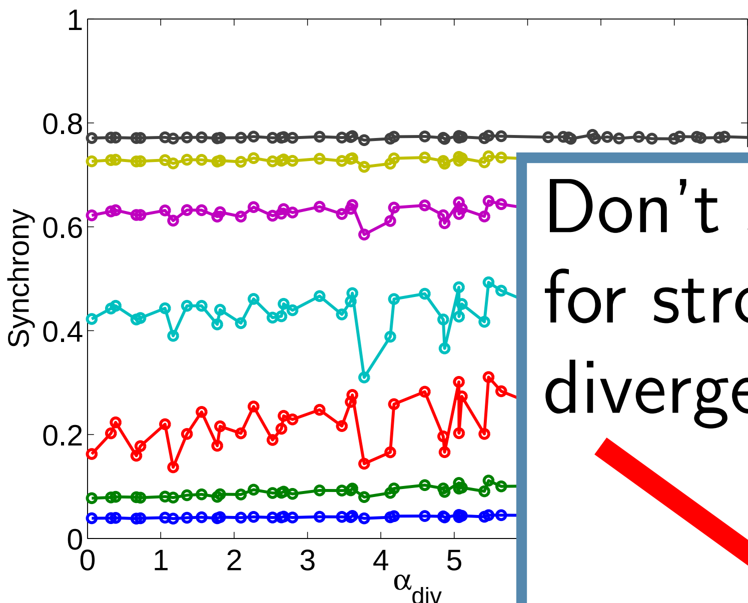


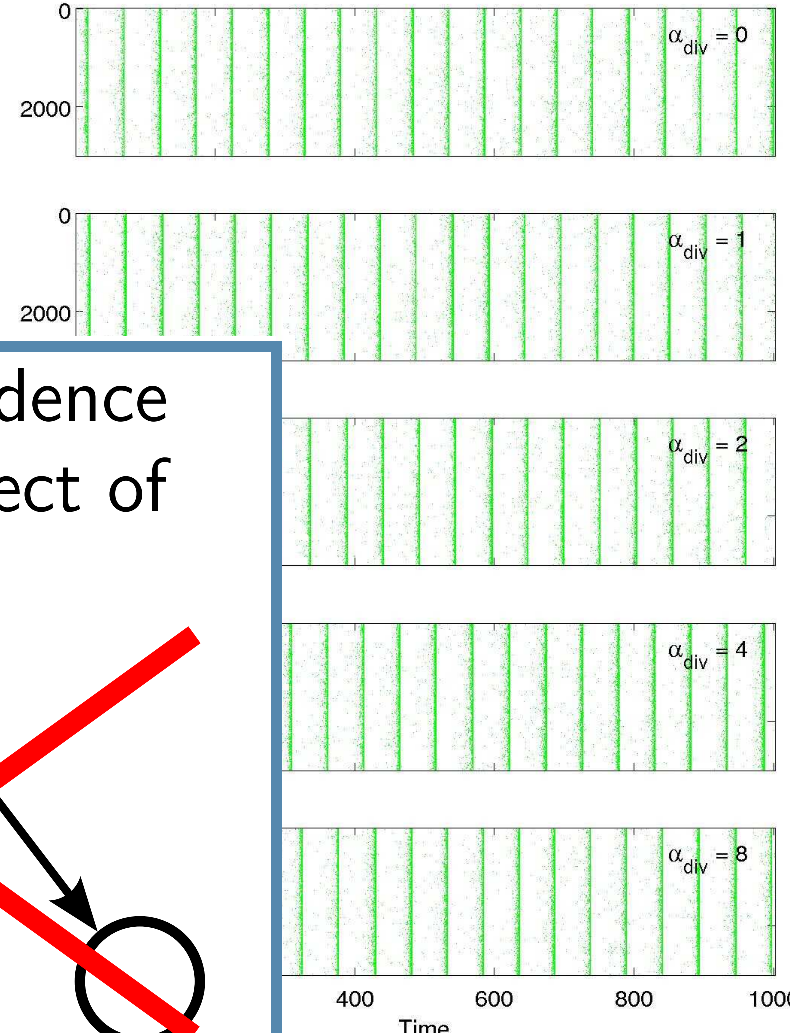
Simulate with increasing coupling strengths J

Simulations with divergence

$J = 10$

Synchrony as function of divergence

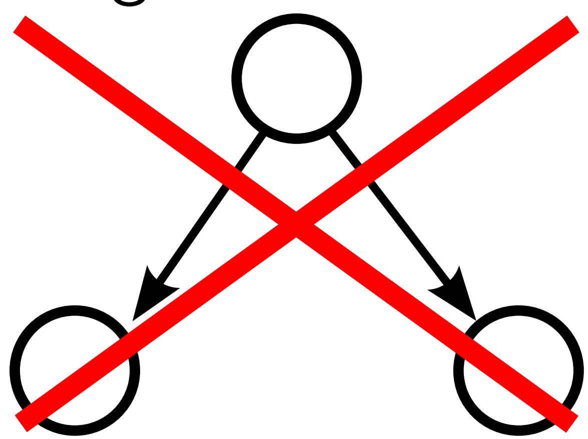




Simulate with increa

coupling strengths J

Don't see evidence for strong effect of divergence.



Explore effect of SONET stats

Generate 186 SONETs with range of connectivity statistics: α_{recip}, α_{conv}, α_{div}, and α_{chain}. Simulate PRC model with connectivity strength $J = 6$ and measure synchrony.

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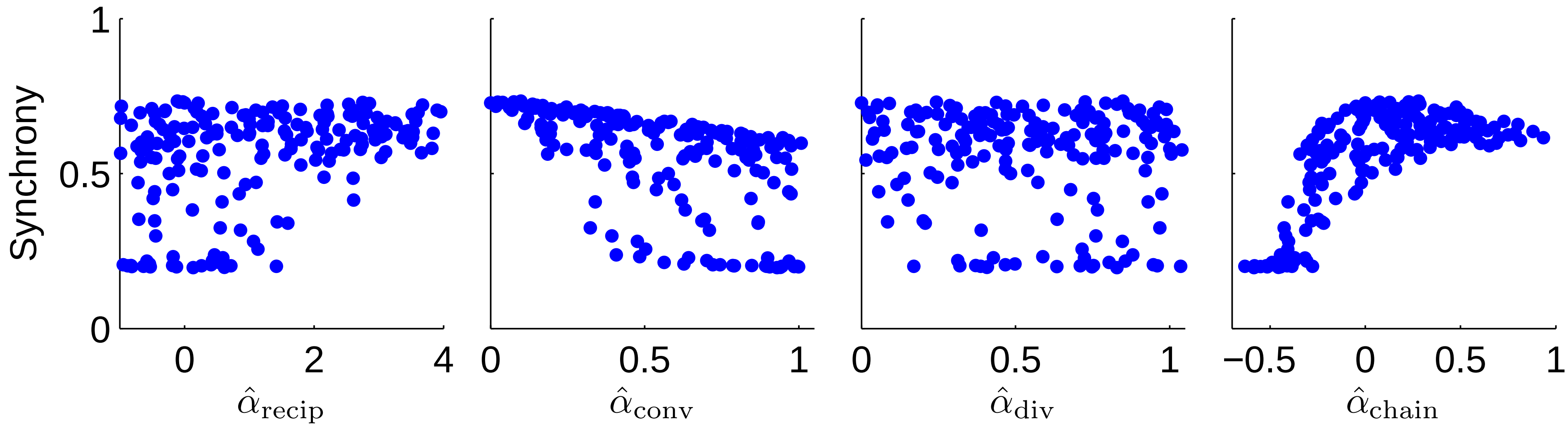


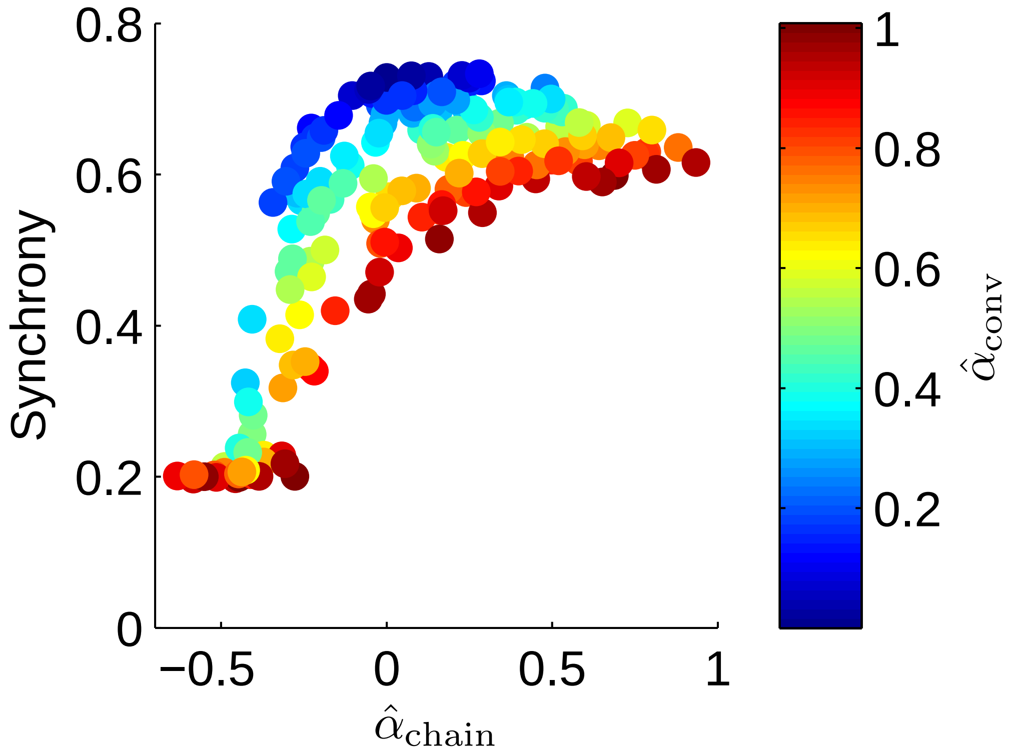
Explore effect of SONET stats

Generate 186 SONETs with range of connectivity statistics: α_{recip}, α_{conv}, α_{div}, and α_{chain}. Simulate PRC model with connectivity strength $J = 6$ and measure synchrony.

Discover that α_{chain} is critical for determining synchrony.

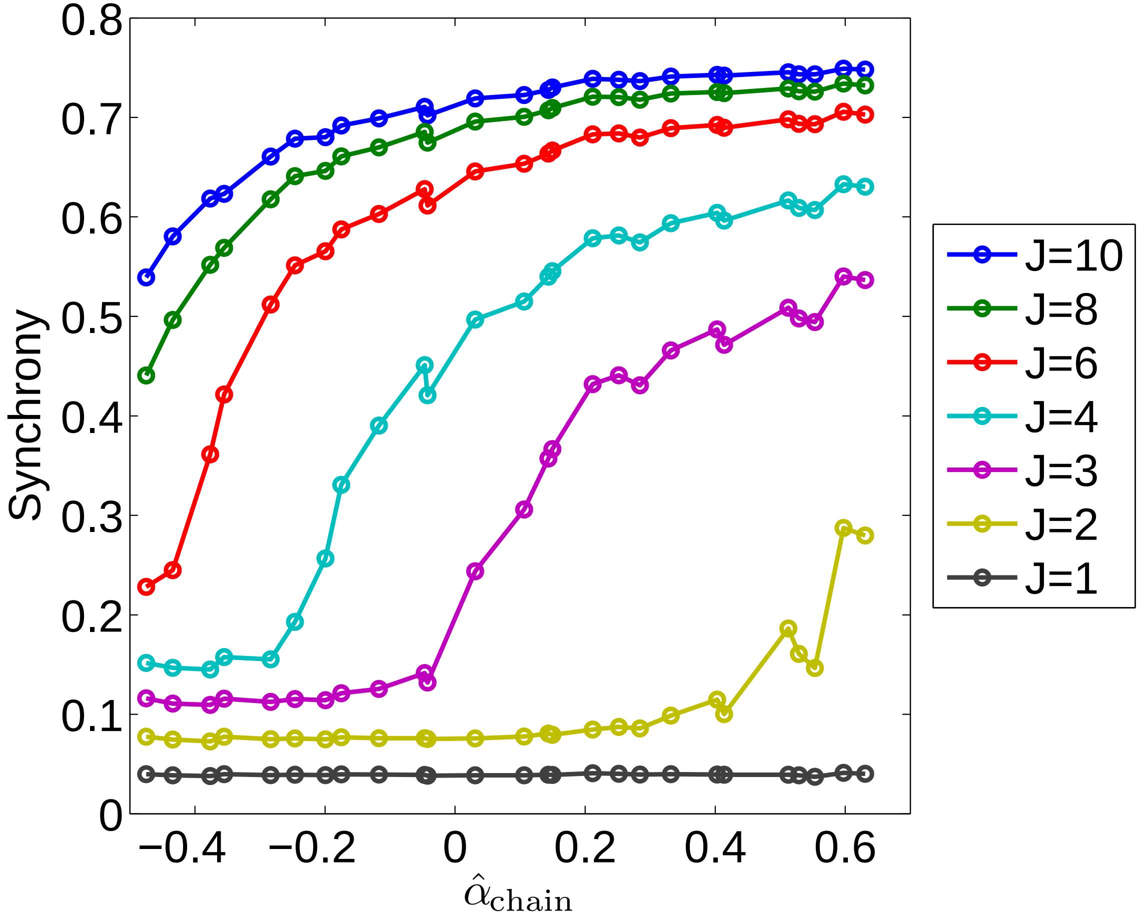
Synchrony increases dramatically with the frequency of chains.

Heterogeneity due to α_{conv} reduces synchrony.



Simulations with chains

If fix α_{conv}, synchrony appears to be a function of the coupling strength J and the frequency of chains.



Chains, not common input, highly influence synchrony.

Outline

1. Introduce SONETs (second order networks)
2. Influence on synchrony
3. Mean-field analysis
4. Multiple populations

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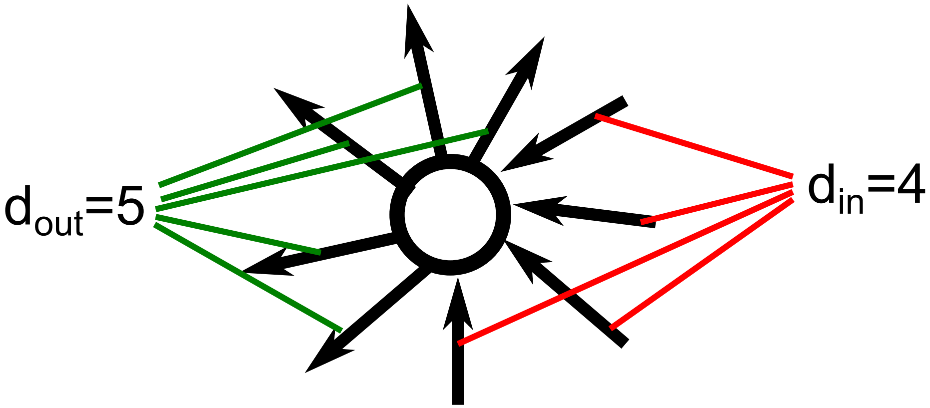
1. Introduce SONETs (second order networks)
2. Influence on synchrony
3. **Mean-field analysis**
4. Multiple populations

SONETs and degrees

in-degree d_{in}, out-degree d_{out}



normalized in- and out-degree:

$$x = \frac{d_{\text{in}}}{E(d_{\text{in}})}, \qquad y = \frac{d_{\text{out}}}{E(d_{\text{out}})}$$

SONETs and degrees

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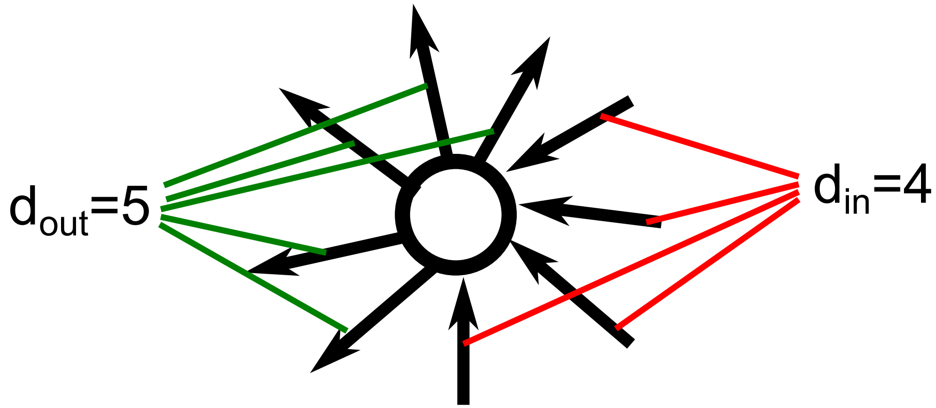

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SONET statistics are variances of the degree distribution:

$$\alpha_{\text{conv}} \approx \text{var}(x) \qquad \alpha_{\text{div}} \approx \text{var}(y) \qquad \alpha_{\text{chain}} \approx \text{cov}(x, y)$$

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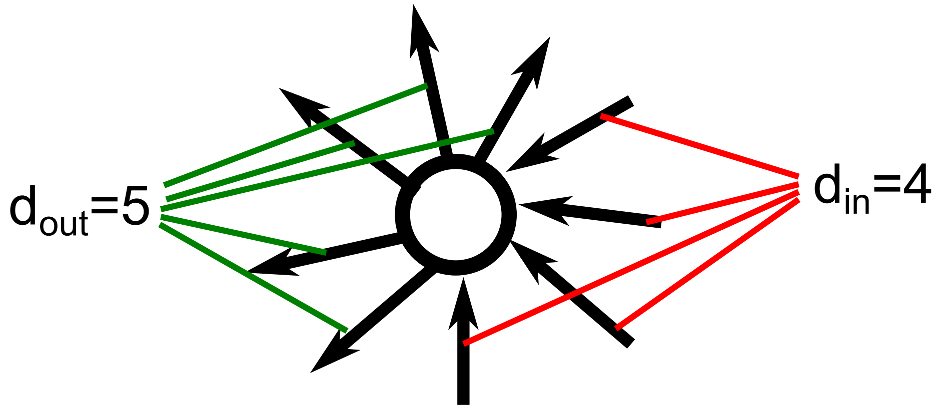

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$$\alpha_{\text{conv}} \approx \text{var}(x) \qquad \alpha_{\text{div}} \approx \text{var}(y) \qquad \alpha_{\text{chain}} \approx \text{cov}(x, y)$$

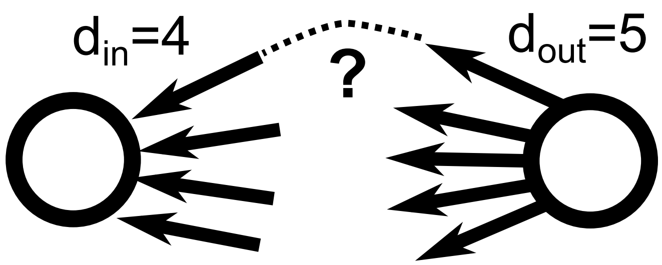
α_{chain} is covariance between (normalized) in- and out-degree.

Basis of rate equation

Given

- a postsynaptic neuron with in-degree x, and
- a presynaptic neuron with out-degree $\tilde{y}$,

connection probability from post to pre is proportional to $x\tilde{y}$.



Obtain rate equation

Let $r(x, y, t)$ be firing rate of neuron with degree (x, y).

Get rate equation

$$\frac{\mathrm{d}r}{\mathrm{d}t}(x,y,t) + r(x,y,t) = \Phi\left(\int \underbrace{Jx\tilde{y}}\underbrace{\rho(\tilde{x},\tilde{y})} r(\tilde{x},\tilde{y},t-D)\,d\tilde{x}\,d\tilde{y} + I\right)$$

- Φ: nonlinearity
- $Jx\tilde{y}$: coupling strength
- $\rho(\tilde{x},\tilde{y})$: degree distribution
- $r(\tilde{x},\tilde{y},t-D)$: presynaptic firing rate
- D: delay
- I: input

Coupling strength from presynaptic degree $(\tilde{x}, \tilde{y})$ onto postsynaptic degree (x, y) is $Jx\tilde{y}$.

Obtain rate equation

$$\frac{\mathrm{d}r}{\mathrm{d}t}(x,y,t) + r(x,y,t) = \Phi\Big(\int J x\tilde{y}\rho(\tilde{x},\tilde{y})r(\tilde{x},\tilde{y},t-D)d\tilde{x}d\tilde{y} + I\Big)$$

RHS does not depend on y; write rate as $r(x,t)$. Get

$$\frac{\mathrm{d}r}{\mathrm{d}t}(x,t) + r(x,t) = \Phi\Big(xJ\int \mu(\tilde{x})\rho(\tilde{x})r(\tilde{x},t-D)d\tilde{x} + I\Big)$$

Expected out-degree conditioned on in-degree:
$\mu(x) = \int y\rho(y|x)dy$

In-degree distribution: $\rho(x) = \int \rho(x,y)dy$

Independence of common input

$$\frac{\mathrm{d}r}{\mathrm{d}t}(x,t) + r(x,t) = \Phi\Big(xJ\int \mu(\tilde{x})\rho(\tilde{x})r(\tilde{x},t-D)d\tilde{x} + I\Big)$$

What if no chains: $\alpha_{\text{chain}} = \text{cov}(x,y) = 0$?

- expected out-degree conditioned on in-degree $\mu(x) = 1$
- $r(x,t)$ does not depend on out-degree distribution
- no influence of common input α_{div} at level of firing rate.

Mean-field equation

$$\frac{\mathrm{d}r}{\mathrm{d}t}(x,t) + r(x,t) = \Phi\left(xJ\int \mu(\tilde{x})\rho(\tilde{x})r(\tilde{x},t-D)d\tilde{x} + I\right)$$

Let $S(t)$ be average synaptic drive:
$S(t) = \int \mu(x)\rho(x)r(x,t)dx$.

Mean-field equation

$$\frac{\mathrm{d}r}{\mathrm{d}t}(x,t) + r(x,t) = \Phi\Big(xJ\int \mu(\tilde{x})\rho(\tilde{x})r(\tilde{x},t-D)d\tilde{x} + I\Big)$$

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Multiply by $\mu(x)\rho(x)$ and integrate to get mean-field equations

$$\begin{aligned}\frac{\mathrm{d}S}{\mathrm{d}t}(t) + S(t) &= \int \mu(x)\rho(x)\Phi\big(xJS(t-D) + I\big)dx \\ &= \tilde{\Phi}(JS(t-D), I)\end{aligned}$$

with effective nonlinearity $\tilde{\Phi}(s,I) = \int \mu(x)\rho(x)\Phi(xs+I)dx$.

Get effect of chains from mean-field

In mean-field, synchrony comes from Hopf bifurcation leading to oscillations in firing rate.

Hopf bifurcation depends on derivative

$$\frac{\mathrm{d}}{\mathrm{d}S}\tilde{\Phi}(JS, I) = \frac{\mathrm{d}}{\mathrm{d}S}\int \mu(x)\rho(x)\Phi\big(xJS + I\big)dx$$
$$= J\int x\mu(x)\rho(x)\Phi'\big(xJS + I\big)dx$$

Note that $\int x\mu(x)\rho(x)dx = 1 + \mathsf{cov}(x, y) = 1 + \alpha_{\mathsf{chain}}$.

Get effect of chains from mean-field

Hopf bifurcation depends on derivative

$$\frac{\mathrm{d}}{\mathrm{d}S}\tilde{\Phi}(JS, I) = J \int x\mu(x)\rho(x)\Phi'\big(xJS + I\big)dx$$

$$= (1 + \alpha_{\text{chain}})J \times \text{weighted average of } \Phi'(\cdot)$$

Get effect of chains from mean-field

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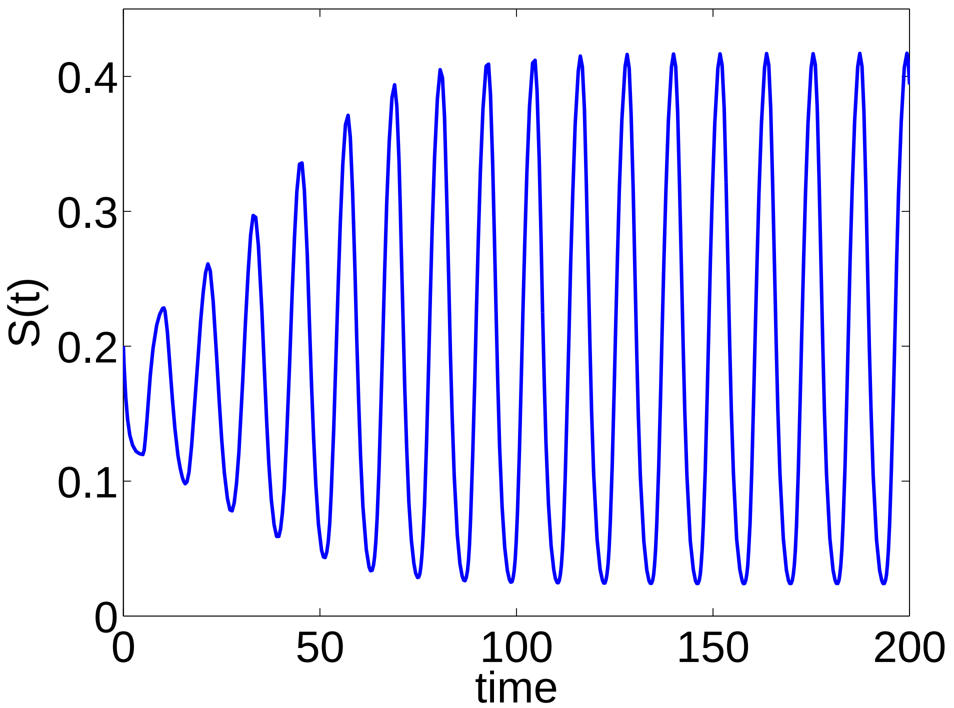
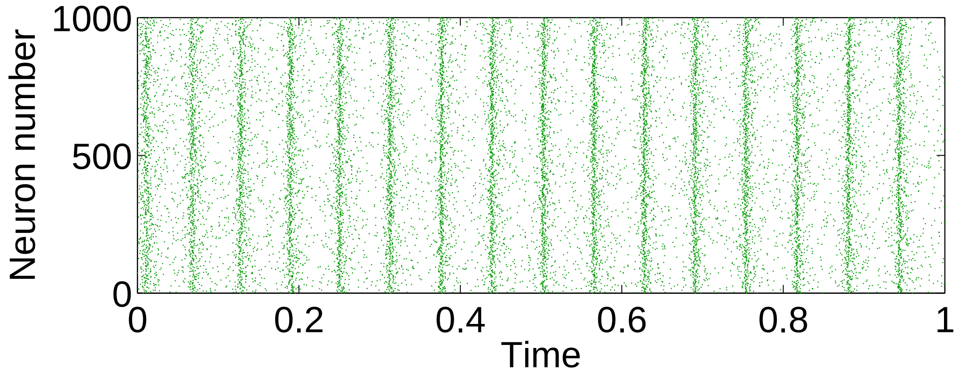
Hopf bifurcation leads to oscillations in synaptic drive $S(t)$.



Get effect of chains from mean-field

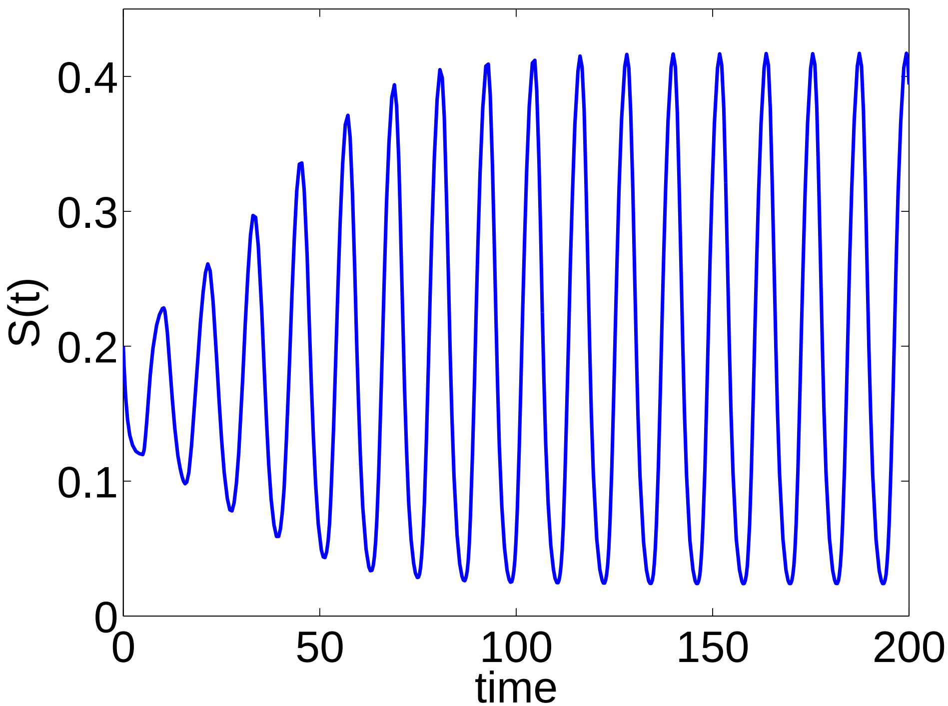
Hopf bifurcation derivative

$$\frac{\mathrm{d}}{\mathrm{d}S}\tilde{\Phi}(JS, I)$$
$$= (1 + \alpha_{\text{chain}})J \times \text{weighted}$$



Hopf bifurcation leads to oscillations in synaptic drive $S(t)$.

These oscillations correspond to synchronous oscillations in neuron spiking.



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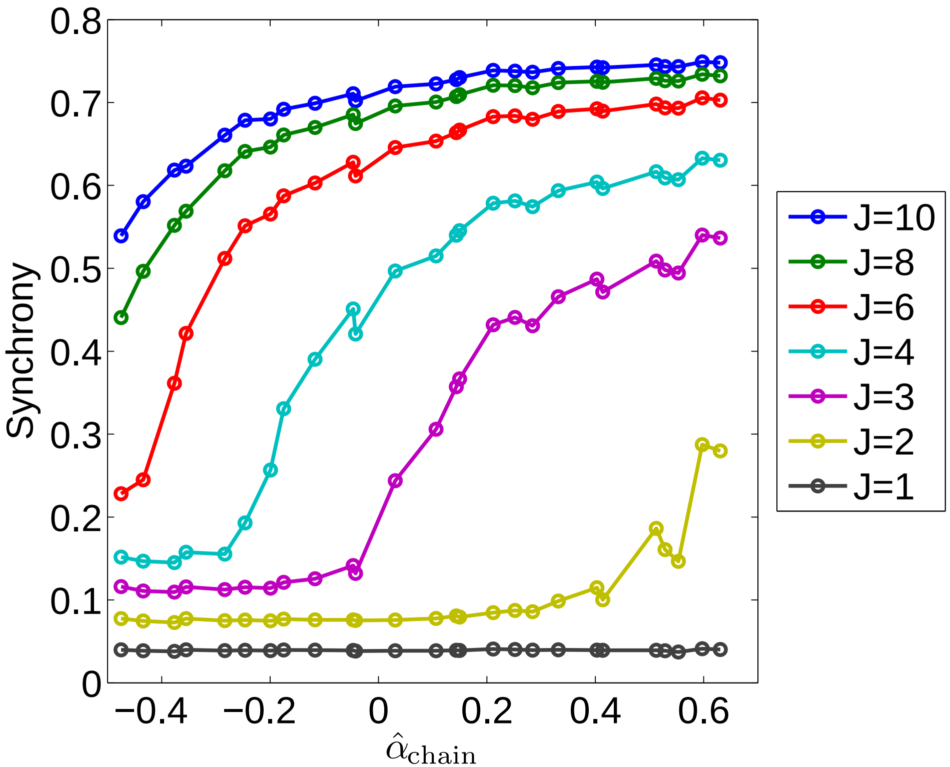
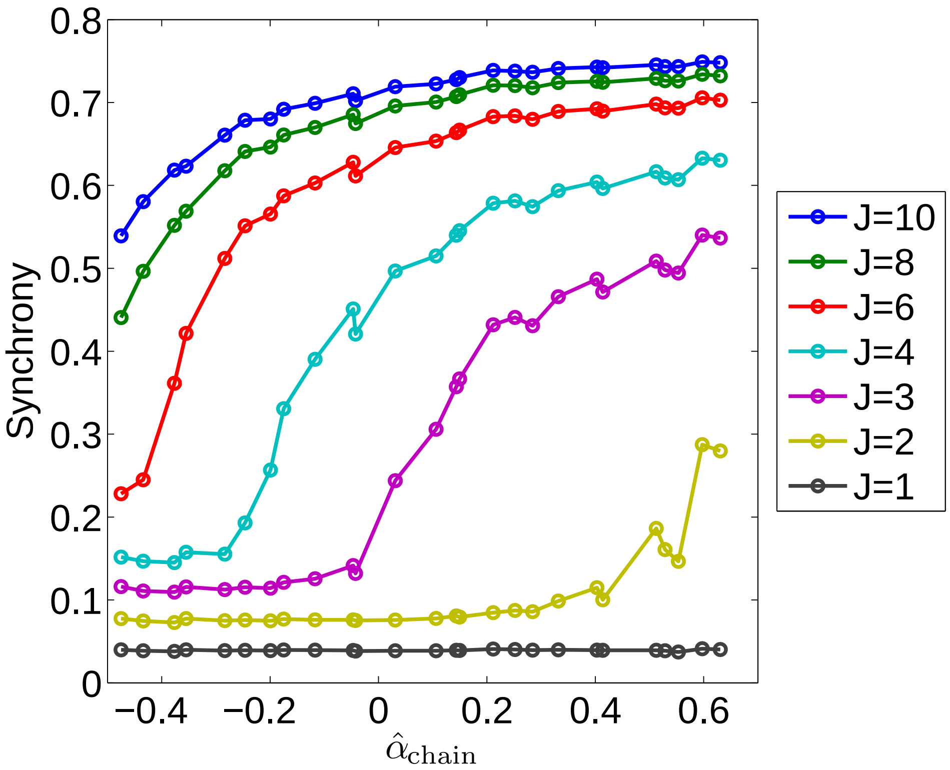


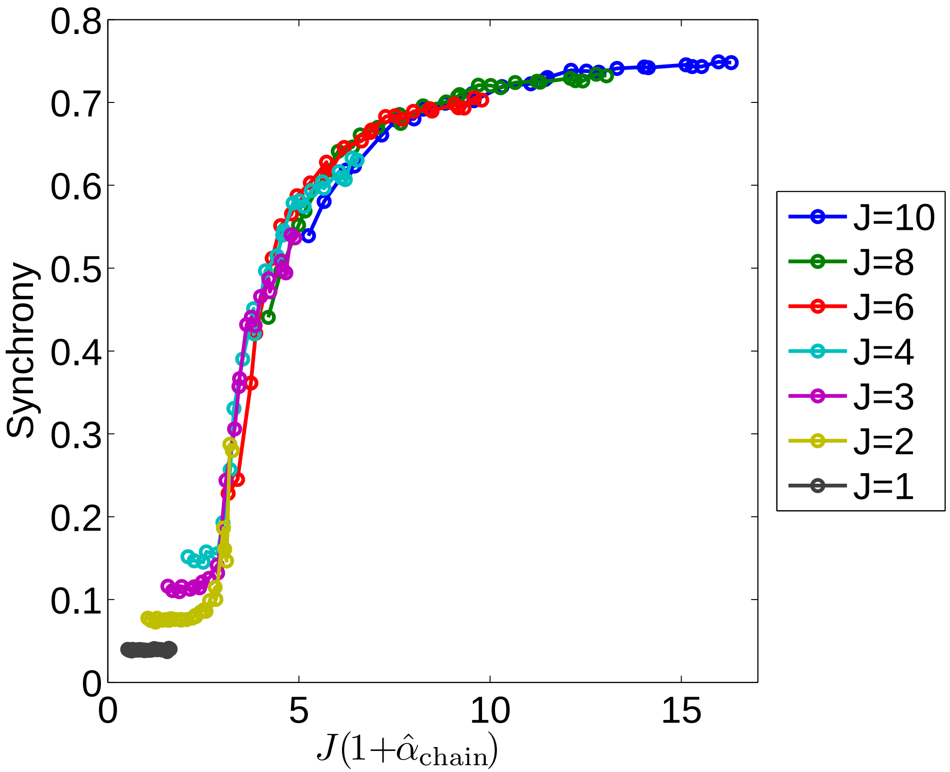
Primary effect of α_{chain}:

- decrease coupling strength at Hopf bifurcation
- increase synchrony for fixed coupling strength

Get effect of chains from mean-field

$$\frac{\mathrm{d}}{\mathrm{d}S}\tilde{\Phi}(JS, I) = (1 + \alpha_{\text{chain}})J \times \text{weighted average of } \Phi'(\cdot)$$





Mean-field explains main effect of chains on synchrony!

Outline

1. Introduce SONETs (second order networks)
2. Influence on synchrony
3. Mean-field analysis
4. Multiple populations

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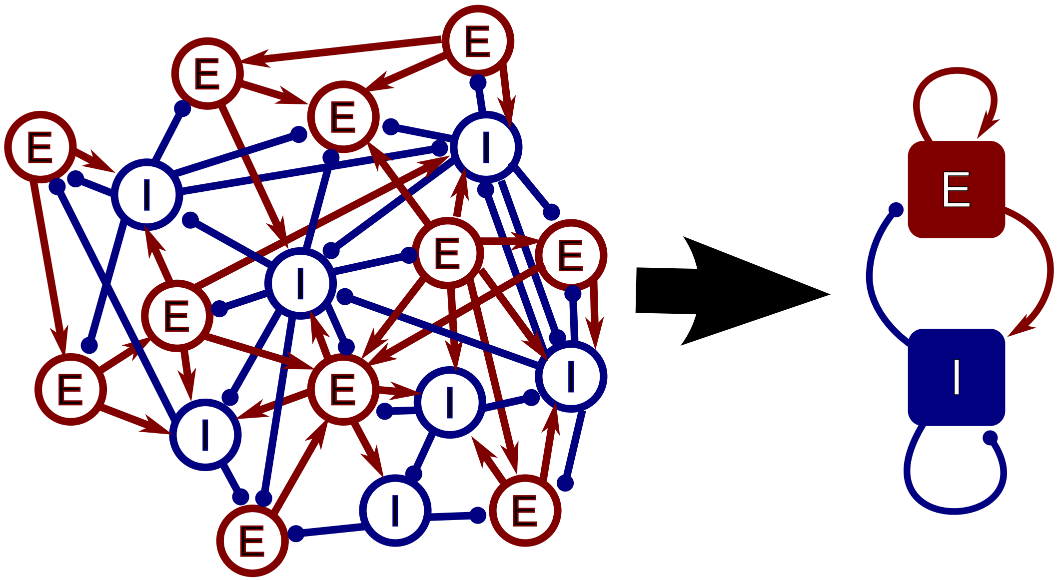
Excitatory and inhibitory network

Can a mean-field model capture influence of network structures of excitatory-inhibitory network?



Conclusion: Yes, but chains dramatically change the mean-field equations.

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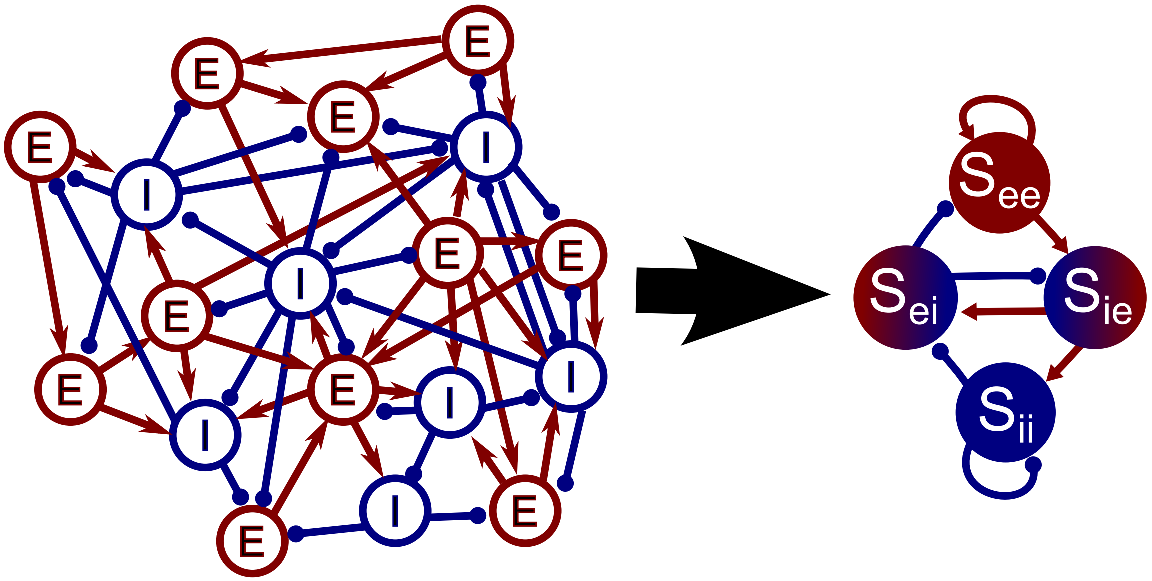
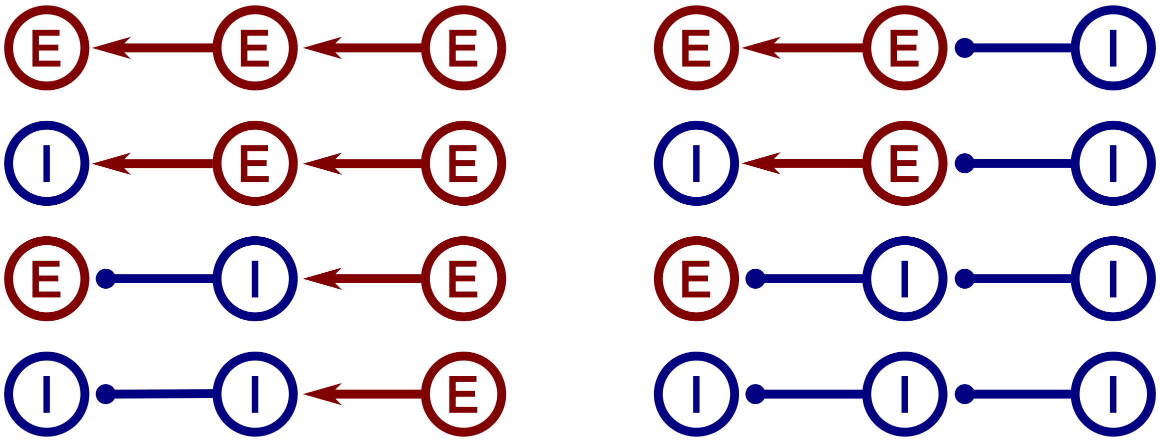


Conclusion: Yes, but chains dramatically change the mean-field equations.

Eight types of chains

Each of three neurons in chain could be E or I
$\Rightarrow$ 8 types of chains



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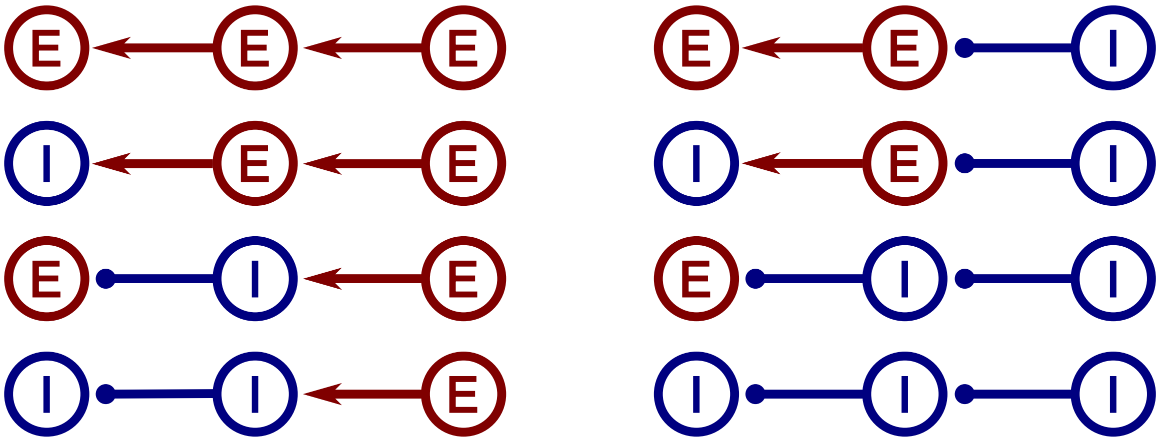
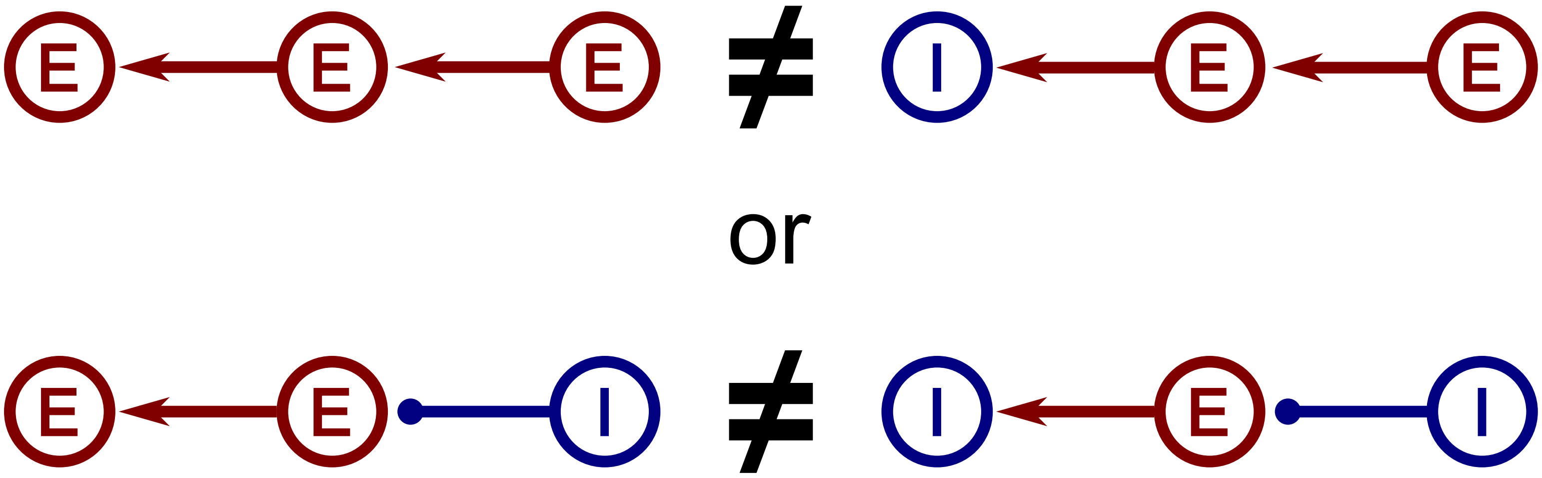


Additional effect of chains
If the frequencies of the chain types differ, the mean-field dynamics can become intrinsically four-dimensional.

Chains can increase mean-field dimension

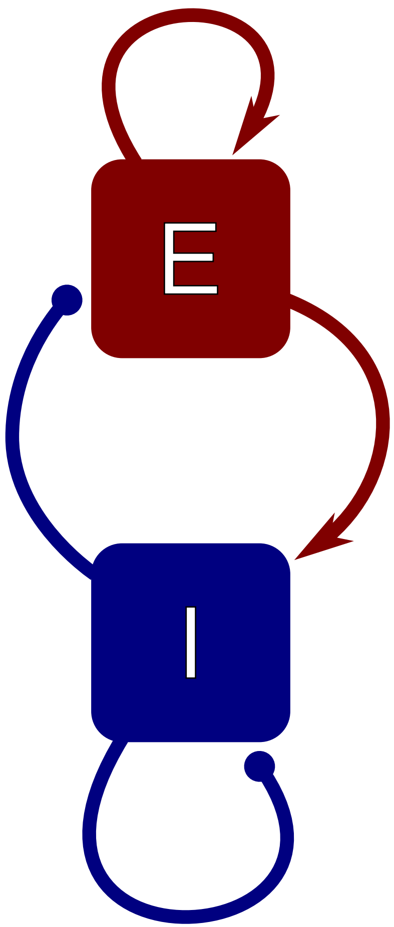
If chains centered on E depend on last neuron's population



then excitatory input onto E could have different dynamics than excitatory input onto I.

Need separate equations for synaptic drives $S_{ee}(t)$ and $S_{ie}(t)$.

Chains transform to four dimensions

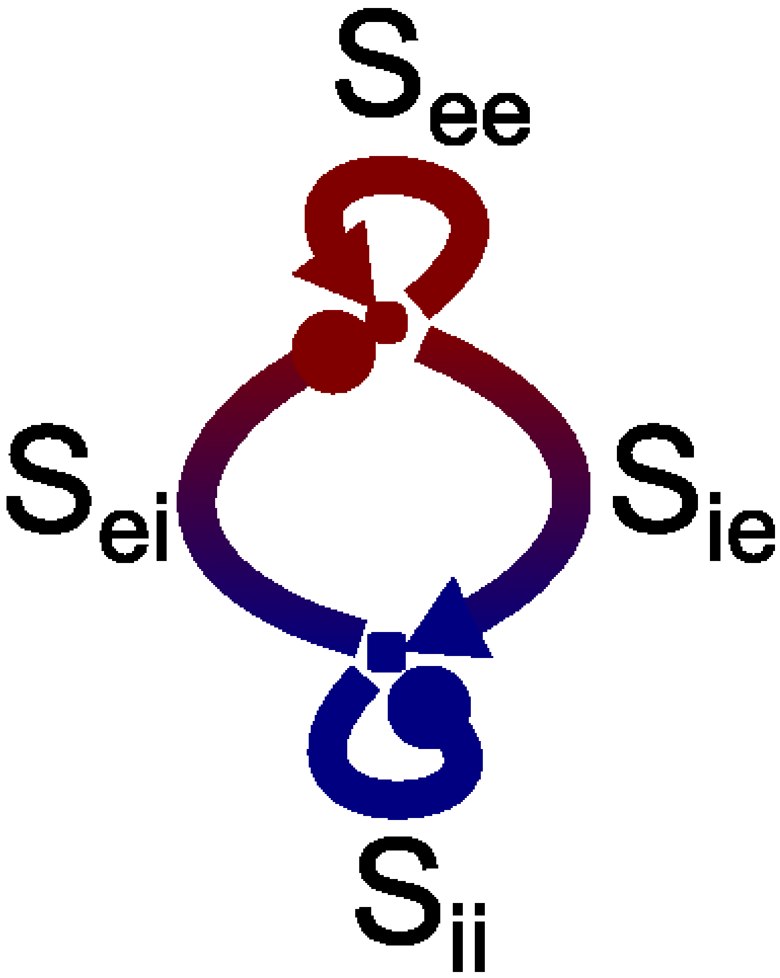


In mean field, have separate equations for the four synaptic drives S_{ee}, S_{ie}, S_{ei} and S_{ii}.

Each edge of graph is separate dynamic variable that interact with each other.

Obtain equations similar to four interacting populations.

Chains transform to four dimensions



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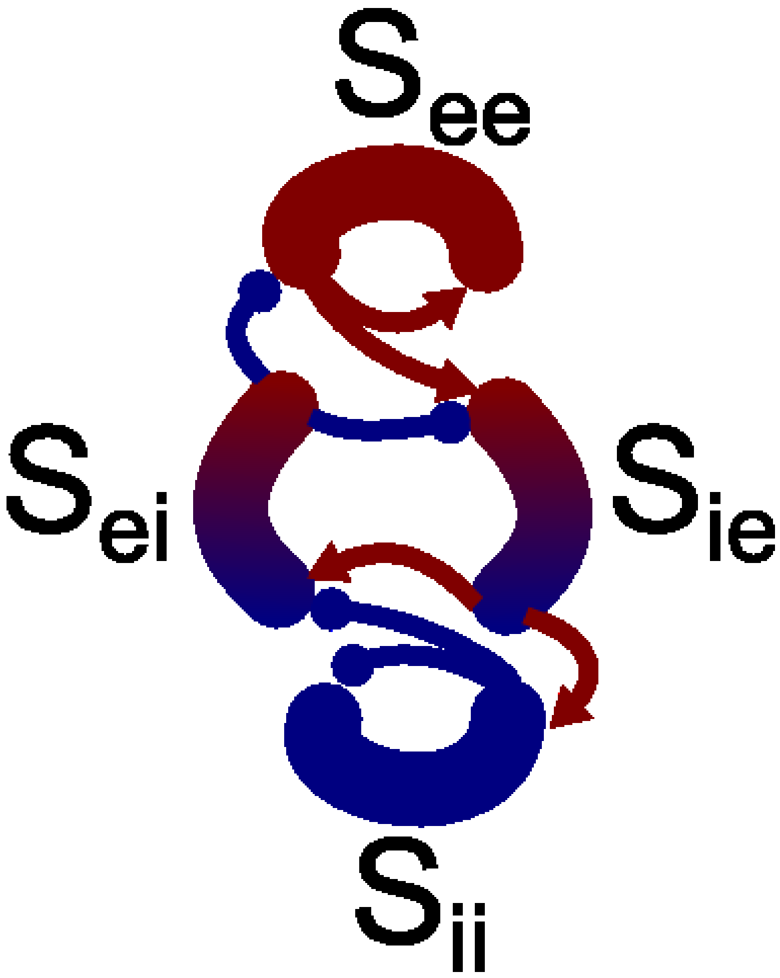

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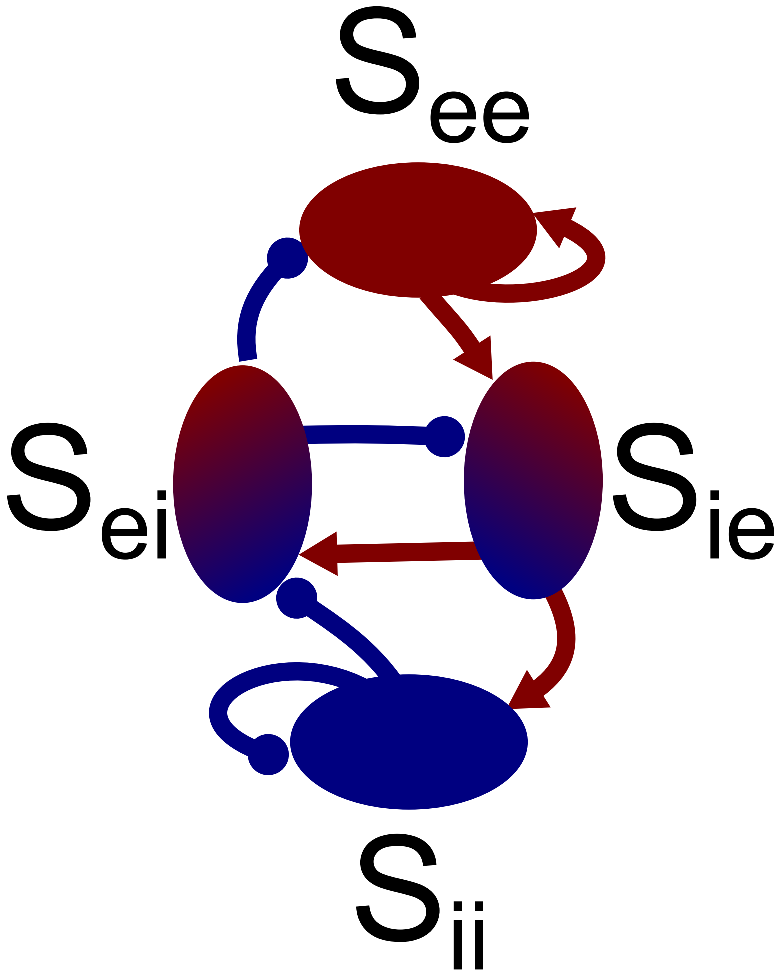

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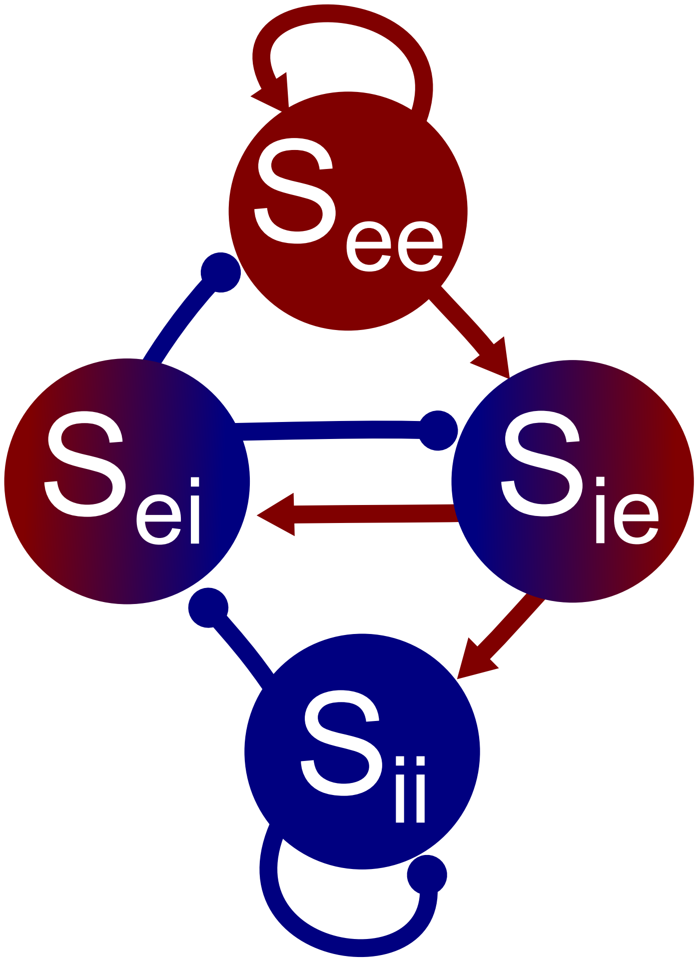

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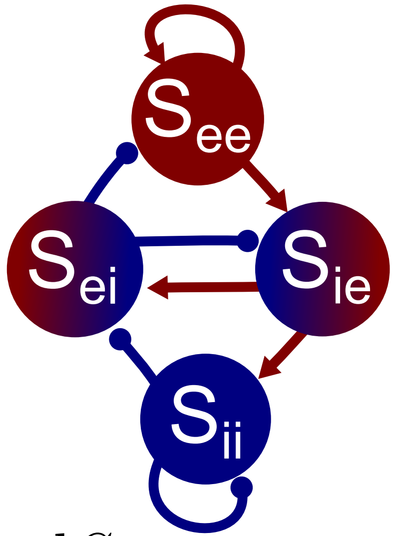
Obtain equations similar to four interacting populations.

Four dimensional mean-field equations



Mean-field equations for the S_{jk} are of same form as the one population case.

$$\frac{\mathrm{d}S_{ee}}{\mathrm{d}t}+S_{ee}=\int \mu_{ee}(x_{ee},x_{ei})\rho_e(x_{ee},x_{ei})\Phi_e(J_{ee}x_{ee}S_{ee}-J_{ei}x_{ei}S_{ei}+I_e)dx_{ee}dx_{ei}$$

$$\frac{\mathrm{d}S_{ie}}{\mathrm{d}t}+S_{ie}=\int \mu_{ie}(x_{ee},x_{ei})\rho_e(x_{ee},x_{ei})\Phi_e(J_{ee}x_{ee}S_{ee}-J_{ei}x_{ei}S_{ei}+I_e)dx_{ee}dx_{ei}$$

$$\tau\frac{\mathrm{d}S_{ei}}{\mathrm{d}t}+S_{ei}=\int \mu_{ei}(x_{ie},x_{ii})\rho_i(x_{ie},x_{ii})\Phi_i(J_{ie}x_{ie}S_{ie}-J_{ii}x_{ii}S_{ii}+I_i)dx_{ie}dx_{ii}$$

$$\tau\frac{\mathrm{d}S_{ii}}{\mathrm{d}t}+S_{ii}=\int \mu_{ii}(x_{ie},x_{ii})\rho_i(x_{ie},x_{ii})\Phi_i(J_{ie}x_{ie}S_{ie}-J_{ii}x_{ii}S_{ii}+I_i)dx_{ie}dx_{ii}$$

Chains modulate effective connection strength

Jacobian of system of four equations for S_{jk} is of the form:

$$\begin{pmatrix} -1 + J_{ee}C_{eee}\Phi'_e & 0 & -J_{ei}C_{eei}\Phi'_e & 0 \\ J_{ee}C_{iee}\Phi'_e & -1 & -J_{ei}C_{iei}\Phi'_e & 0 \\ 0 & J_{ie}C_{eie}\Phi'_i/\tau & -1/\tau & -J_{ii}C_{eii}\Phi'_i/\tau \\ 0 & J_{ie}C_{iie}\Phi'_i/\tau & 0 & -1/\tau - J_{ii}C_{iii}\Phi'_i/\tau \end{pmatrix}$$

where $C_{jkl} = 1 + \alpha_{jkl}^{\text{chain}}$.

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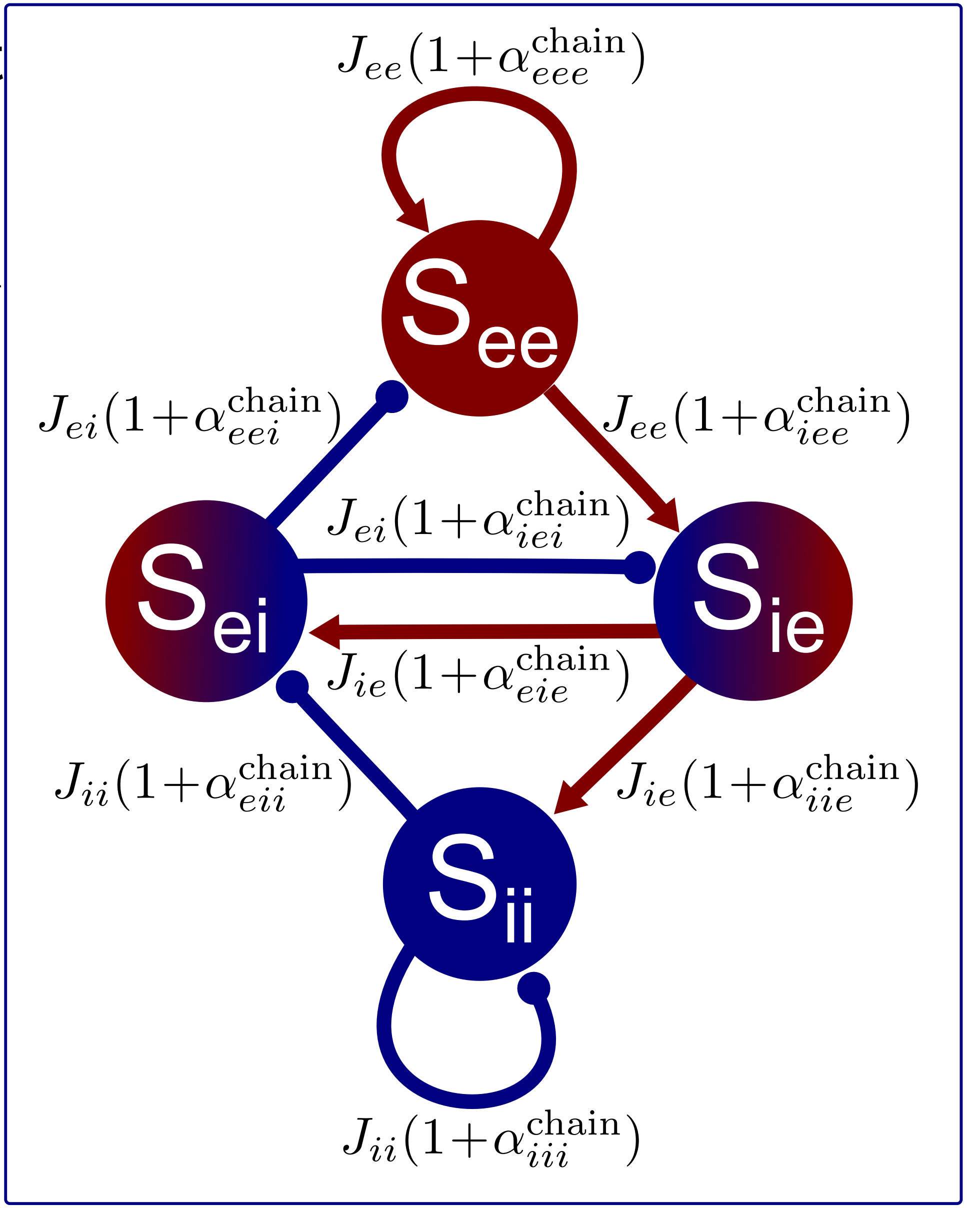
Effective strengths of the eight connections among the S_{jk} depend on the corresponding α^{chain}.

Chains modulate effective connection strength

Jacobian of system of four equat

$$\begin{pmatrix} -1 + J_{ee}C_{eee}\Phi'_e & 0 & - \\ J_{ee}C_{iee}\Phi'_e & -1 & - \\ 0 & J_{ie}C_{eie}\Phi'_i/\tau & \\ 0 & J_{ie}C_{iie}\Phi'_i/\tau & \end{pmatrix}$$



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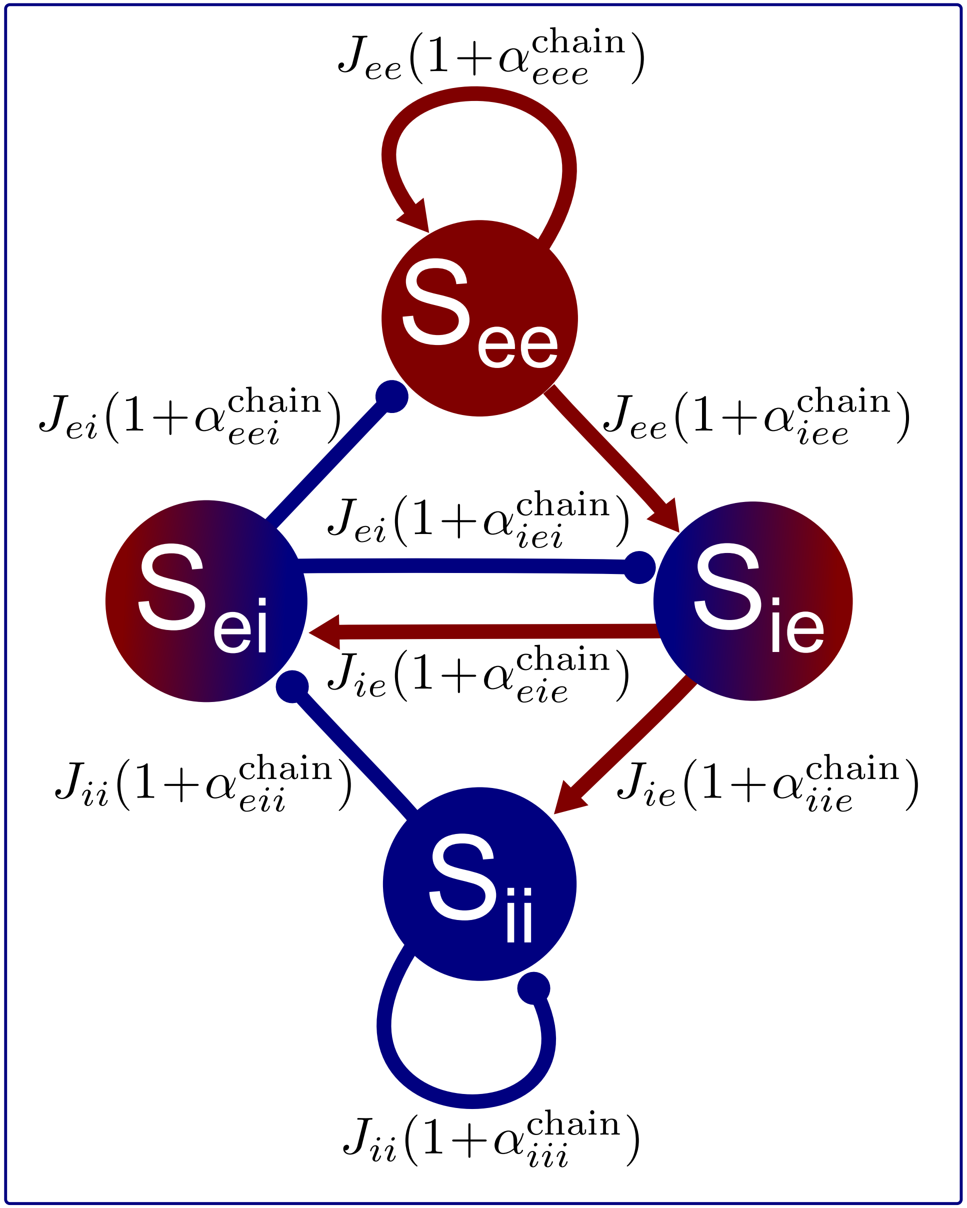
Transformation to effective dynamics

Edges of original graph
$\rightarrow$ nodes of effective graph

Chains of original graph
$\rightarrow$ edges of effective graph

Effective strengths of the eight connections among the S_{jk} depend on the corresponding α^{chain}.



Conclusions

Simulations and mean-field analysis of SONETs reveals:

1. For single population
   (a) Common input (divergence) alone has little influence on synchrony.
   (b) Chains multiply coupling strength so that Hopf bifurcation leading to synchrony occurs earlier.
2. For excitatory-inhibitory network
   (a) Chains can increase the dimension of the intrinsic dynamics of the activity.
   (b) Resulting range of behavior still needs to be explored.

Thanks

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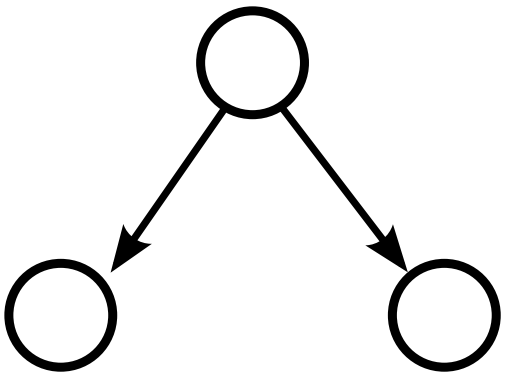

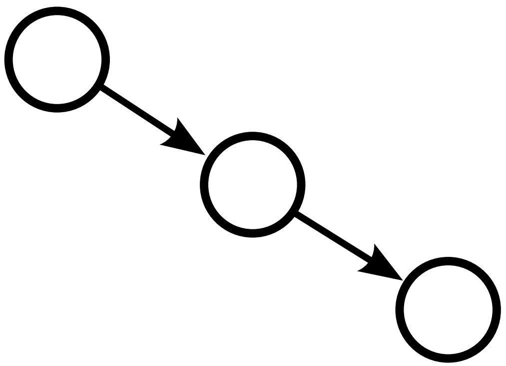

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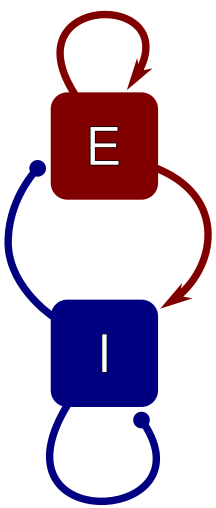

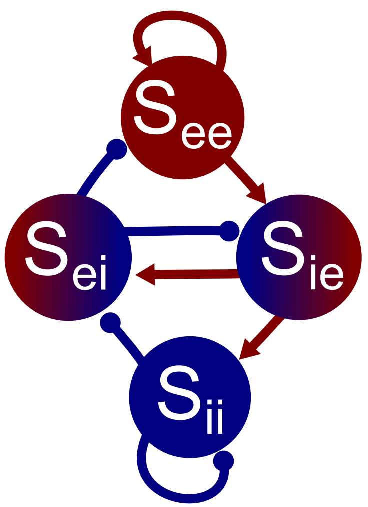

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