Globally Attracting Synchrony in a Network of Oscillators with Strong Inhibitory Pulse Coupling

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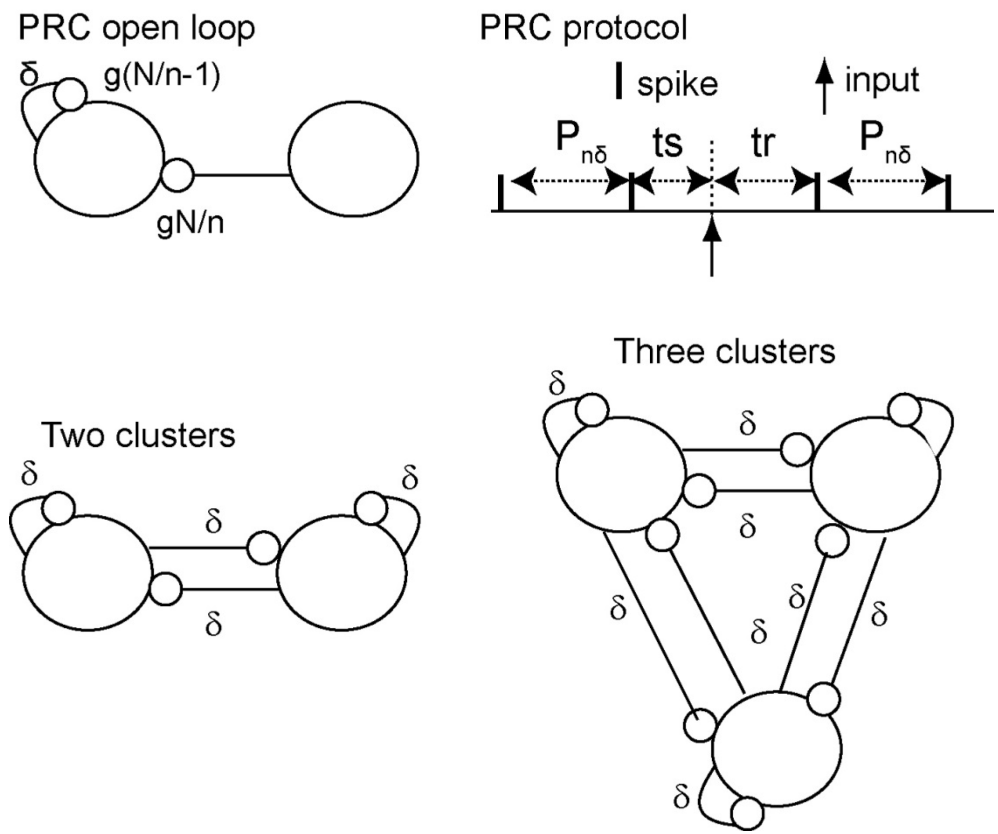
Hybrid Discrete/Continuous Pulse Coupled All to all Network of Oscillators

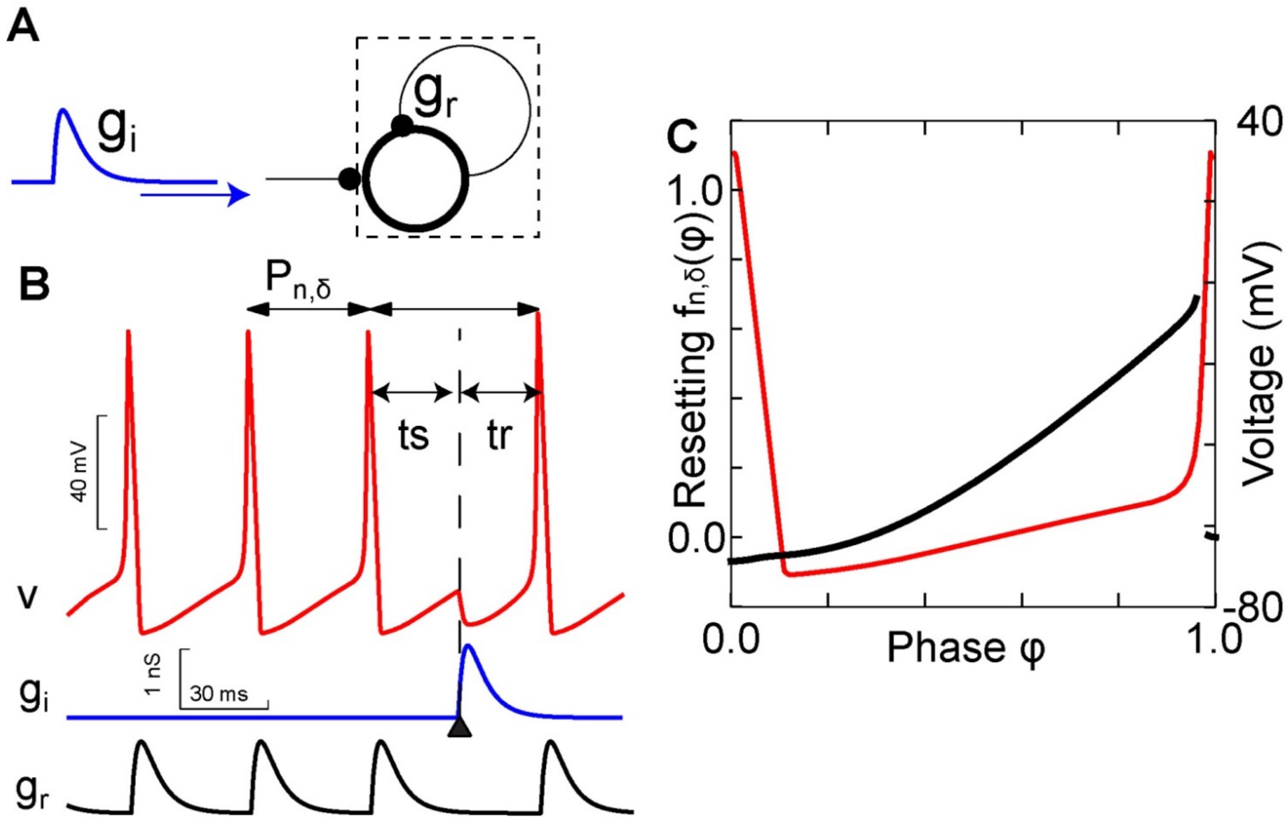
$$\frac{d\varphi_i}{dt} = 1 - \sum_{j=1}^{j=N-1,\, j\neq i} f(\varphi_i)\delta(t - t_j - \delta)$$

When the phase of oscillator j reaches 1, it is reset to zero and a pulse is emitted at time t_j. The pulsatile nature of the coupling is indicated by the Dirac delta function. The pulse reaches the target oscillators after a conduction delay.

Each Cluster with its Internal Conduction Delays Is a “Black Box” Oscillator for PRC analysis



Definition of Phase Resetting: Open Loop with No Feedback



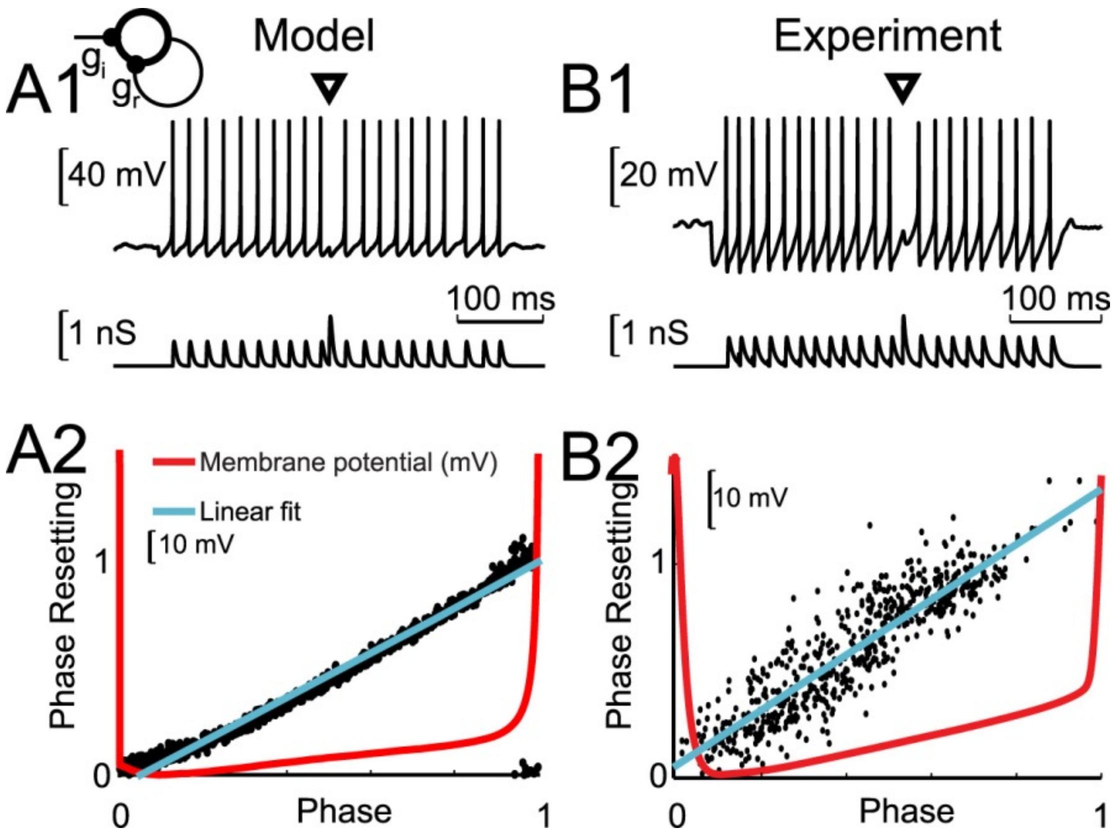
$$ts = P_{n,\delta}\varphi$$

$$f_{n,\delta}(\varphi) = (ts + tr - P_{n,\delta}) / P_{n,\delta}$$

PRC is parameterized by number of clusters and by internal conduction delays

Tikidji-Hamburyan and Canavier, in preparation

Focus on Monotonically Increasing PRC -> Implies a Discontinuity
Actual Quasi Linear Phase Response Curve (PRC) of a Self-Connected Interneuron



Izhikevitch Type 2

Entorhinal PV+ basket cell

Tikidji-Hamburyan, Martinez, White and Canavier, J. Neurosci. 2015

Existence and Stability Criteria Global Synchrony and Two Cluster Modes

synchrony at k=2: $$-1 < 1 - f'(\varphi) - f'(\varphi) < 1$$
$$\varphi = \delta / P$$

Exception: with no delay k=1 $$-1 < (1 - f'(0^{+})(1 - f'(1^{-}) < 1$$
$$\varphi = 0,1$$

k is the integer number of cycles it takes for the effect of a spike in one neuron
To affect the firing of the same neuron via feedback through the network

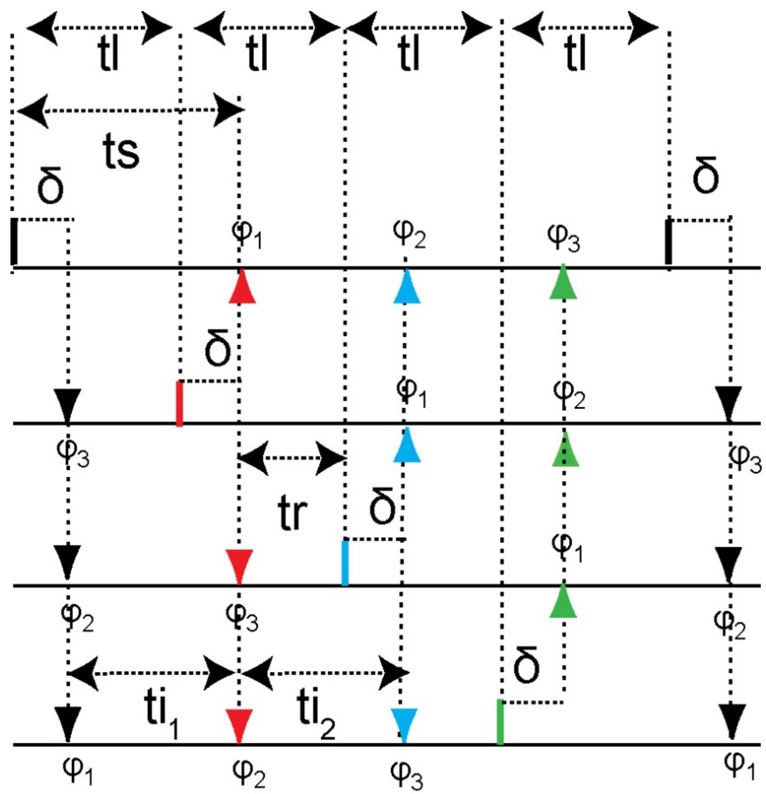
Note that f'(1^{-}) is undefined due to the discontinuity,
but the "virtual" infinite negative slope is destabilizing

Antiphase at k=1: $$-1 < \left(1 - f'(\varphi_{AP})\right)\left(1 - f'(\varphi_{AP})\right) < 1$$
$$\varphi_{AP} = 0.5 + 0.5 f(\varphi_{AP}) + \delta / P$$

Positive (in our convention) PRC slopes *f'(φ)* tend to make the absolute value of the eigenvalues <1 and therefore ensure stability.

Woodman and Canavier, *J Computational Neurosci* 2011
Canavier et al. , *Frontiers in Computational Neuroscience*, 2013

Firing Pattern for Splay Mode with Equal Time Lags



Define intervals in the closed loop using the open loop PRC:

time lag

$$tl = ts - \delta = ti_i = tr + \delta$$

stimulus interval

$$ts = P_{n,\delta}\varphi_1$$

recovery interval

$$tr = P_{n,\delta}\{1 - \varphi_{n-1} + f_{n,\delta}(\varphi_{n-1})\}$$

intermediate intervals

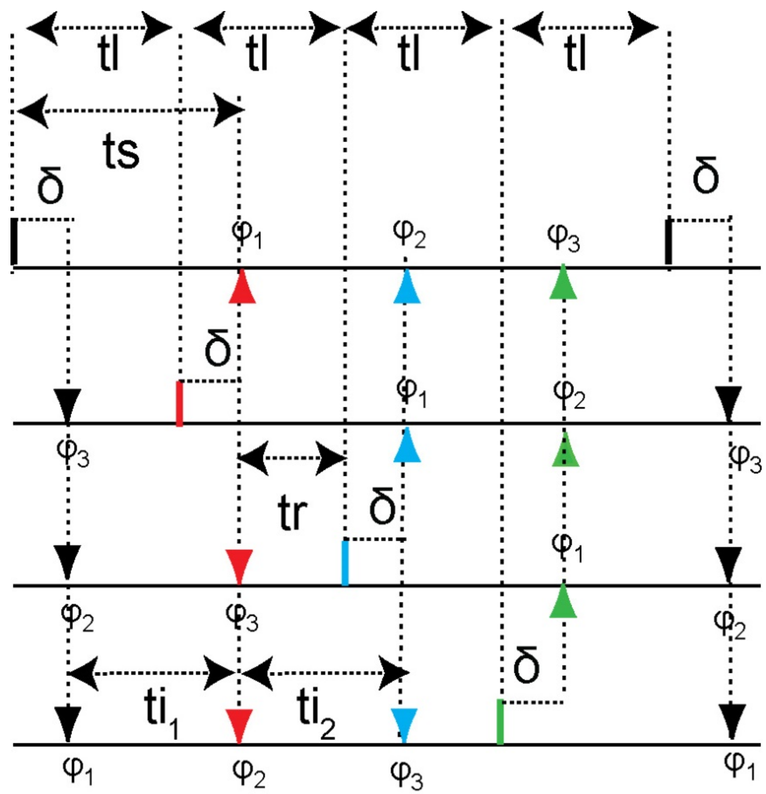
$$ti_i = P_{n,\delta}\{\varphi_{i+1} - \varphi_i + f_{n,\delta}(\varphi_i)\}$$

Firing order remains constant if we assume

$$0 < f'_{n,\delta}(\varphi_i) < 1, \varphi_i \in [0,1)$$

Canavier and Tikidji-Hamburyan Physical Review E 95(3):032215, 2017.

Firing Pattern for Splay Mode with Equal Time Lags



Caveat: All proofs assume that the conduction delays are short enough that the order of spike and Inputs events is unchanged.

Constant firing order eliminates chaotic solutions and complex period ones (eg 2P)

Canavier and Tikidji-Hamburyan Physical Review E 95(3):032215, 2017.

Existence Criteria for Splay Mode with Equal Time Lags

Use the constraint that all time lags are equal and the definition of the intervals

Using the PRC to write existence criteria in terms of the phase of the last input received

n=2

$$f_{2,\delta}(\varphi_1) = 2(\varphi_1 - \frac{\delta}{P_{2,\delta}}) - 1$$

n=3

$$2f_{3,\delta}(\varphi_2) - f_{3,\delta}(1-\varphi_2 + f_{3,\delta}(\varphi_2) + \frac{2\delta}{P_{3,\delta}}) = 3(\varphi_2 - \frac{\delta}{P_{3,\delta}}) - 2$$

n=4

$$3f_{4,\delta}(\varphi_3) - f_{4,\delta}(1-\varphi_3 + f_{4,\delta}(\varphi_3) + \frac{2\delta}{P_{n,\delta}}) - f_{4,\delta}(2 + \frac{3\delta}{P_{4,\delta}} - 2\varphi_3 + 2f_{4,\delta}(\varphi_3) -$$

$$f_{4,\delta}(1-\varphi_3 + f_{4,\delta}(\varphi_3) + \frac{2\delta}{P_{4,\delta}})) = 4(\varphi_3 - \frac{\delta}{P_{4,\delta}}) - 3$$

Note right hand side is always a line

Canavier and Tikidji-Hamburyan Physical Review E 95(3):032215, 2017.

Generalized Existence Criteria for Splay Mode with Equal Time Lags

The left hand side can be written in terms of the phase resetting:

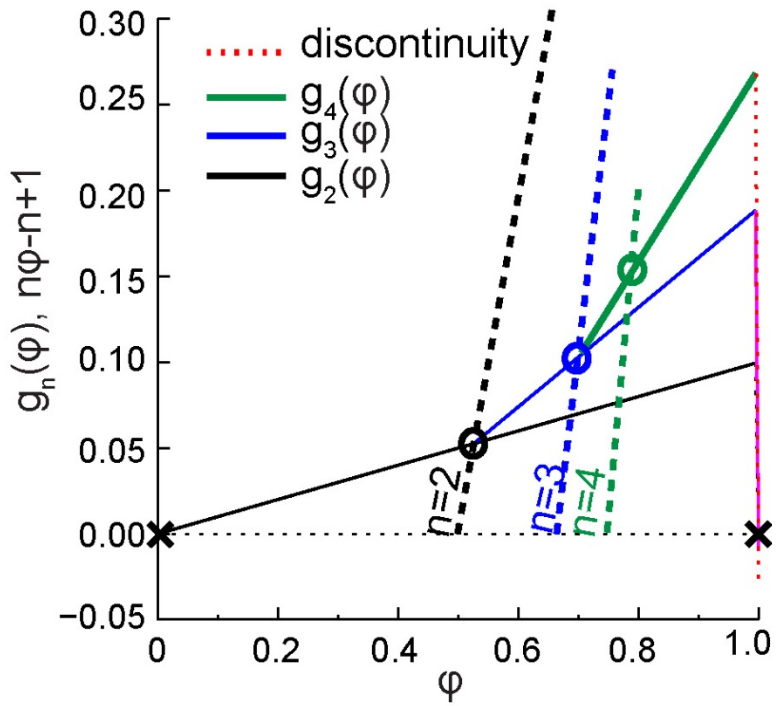
$$g_{n,\delta}(\varphi_{n-1}) = (n-1) f_{n,\delta}(\varphi_{n-1}) - \sum_{i=2}^{n-2} f_{n,\delta}(\varphi_i)$$

When the right hand side (function of PRC) is equal to the line on the left hand side , you obtain at the intersection the value of the phase at the time the last input is received in the cluster mode

$$g_{n,\delta_j,j}(\varphi^*_{n-1,j}) = n\varphi^*_{n-1,j} - n + 1 - \frac{n\delta}{P_{n,\delta_j}}$$

Canavier and Tikidji-Hamburyan Physical Review E 95(3):032215, 2017.

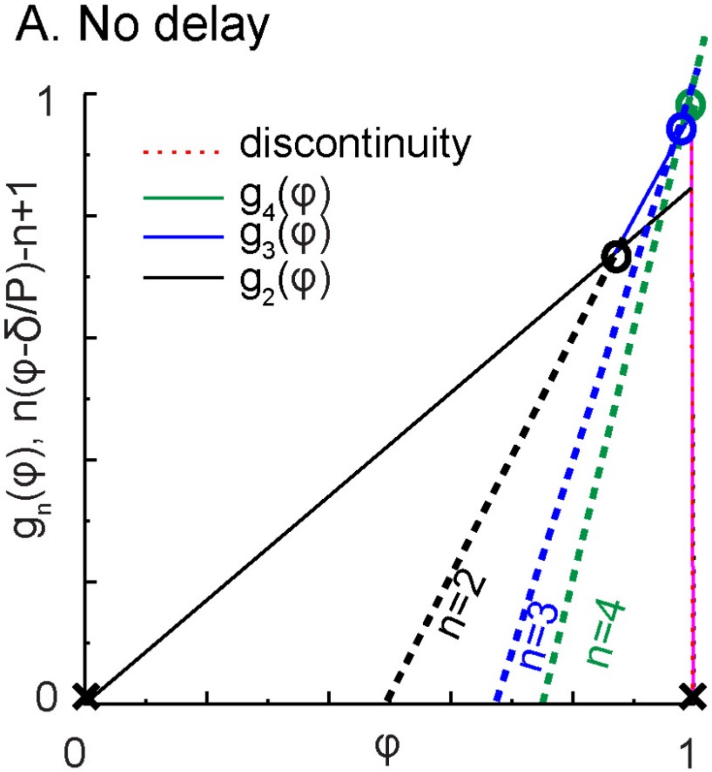
Cluster Analysis for Weak Linear PRC



The results for a rather weak PRC are intuitive: phase of last input for n=2 is around 1/2, for n=3 around 2/3and for n=4 around ¾. The problem is that individual clusters cannot synchronize without a small delay.

Canavier and Tikidji-Hamburyan Physical Review E 95(3):032215, 2017.

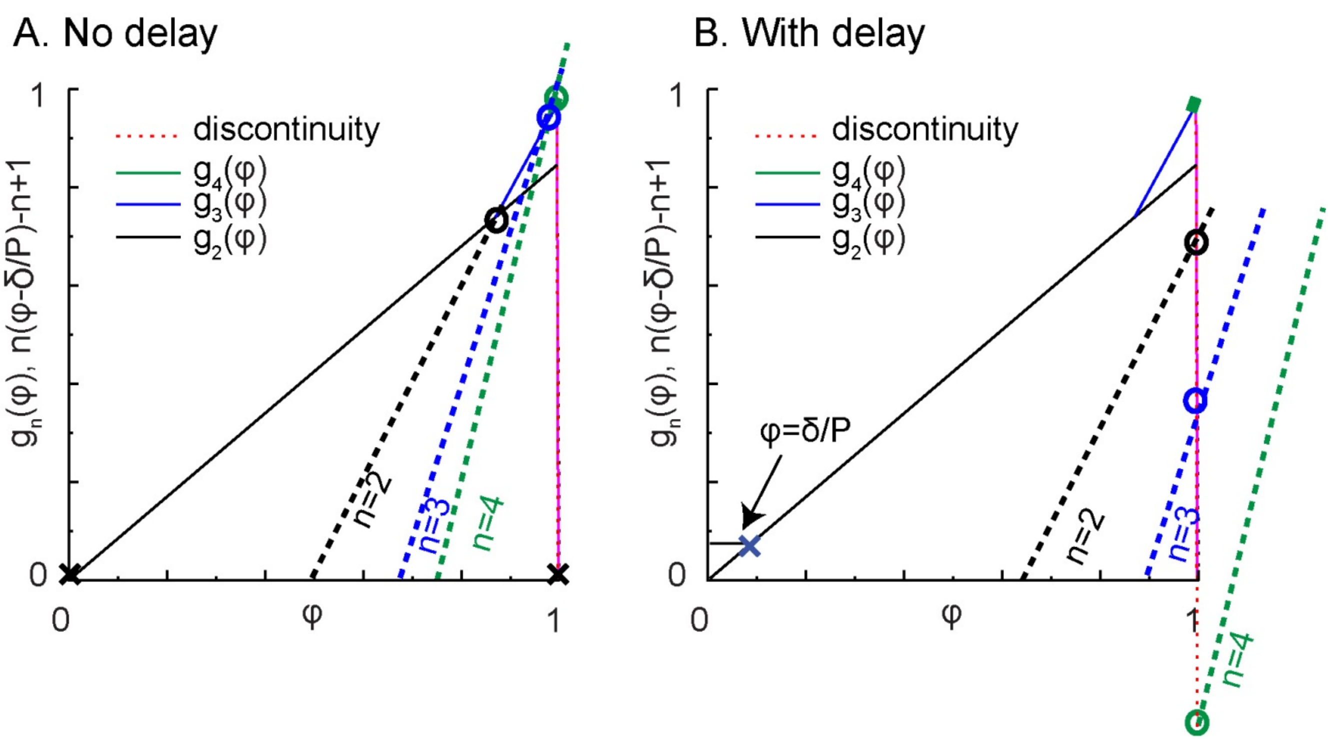
Cluster Analysis for Strong Linear PRC



Clusters are pushed to much later phases for a much stronger PRC but the problem with f'(-1) remains.

Canavier and Tikidji-Hamburyan Physical Review E 95(3):032215, 2017.

Effect of Delay on Cluster Analysis



Delays serve two functions: first they eliminate the contribution of f'(-1), allowing within cluster synchrony. Second they can eliminate cluster modes.

Canavier and Tikidji-Hamburyan Physical Review E 95(3):032215, 2017.

Prove lack of existence of two cluster solution Implies no equal time lag cluster modes exist

Assume PRC saturated and independent of cluster size: thus all clusters no longer have to be the same size.

$$f_{n,\delta}(\varphi) = f_{n-1,\delta}(\varphi)$$

Fires next so it has to be the largest

$g_{n,\delta}(\varphi_{n-1}) = f_{\delta}(\varphi_{n-1}) + \sum_{i=1}^{n-2}\{f_{\delta}(\varphi_{n-1}) - (f_{\delta}(\varphi_i)\}$ and $\varphi_{n-1} > \varphi_i$ and $0 < f'_{n,\delta}(\varphi_i) < 1, \varphi_i \in [0,1)$

imply $g_{n,\delta}(\varphi) > g_{2,\delta}(\varphi)$

If no two cluster equal time lag mode exists then $2\varphi - 1 < g_{2,0}(\varphi), \varphi \in [0,1)$

For $\varphi < 1$ then $(\varphi - 1) < 0$ implies $n(\varphi - 1) < 2(\varphi - 1)$

For no delay $n\varphi - n + 1 < 2\varphi - 1 < g_{2,0}(\varphi) < g_{n,0}(\varphi), \varphi \in [0,1)$

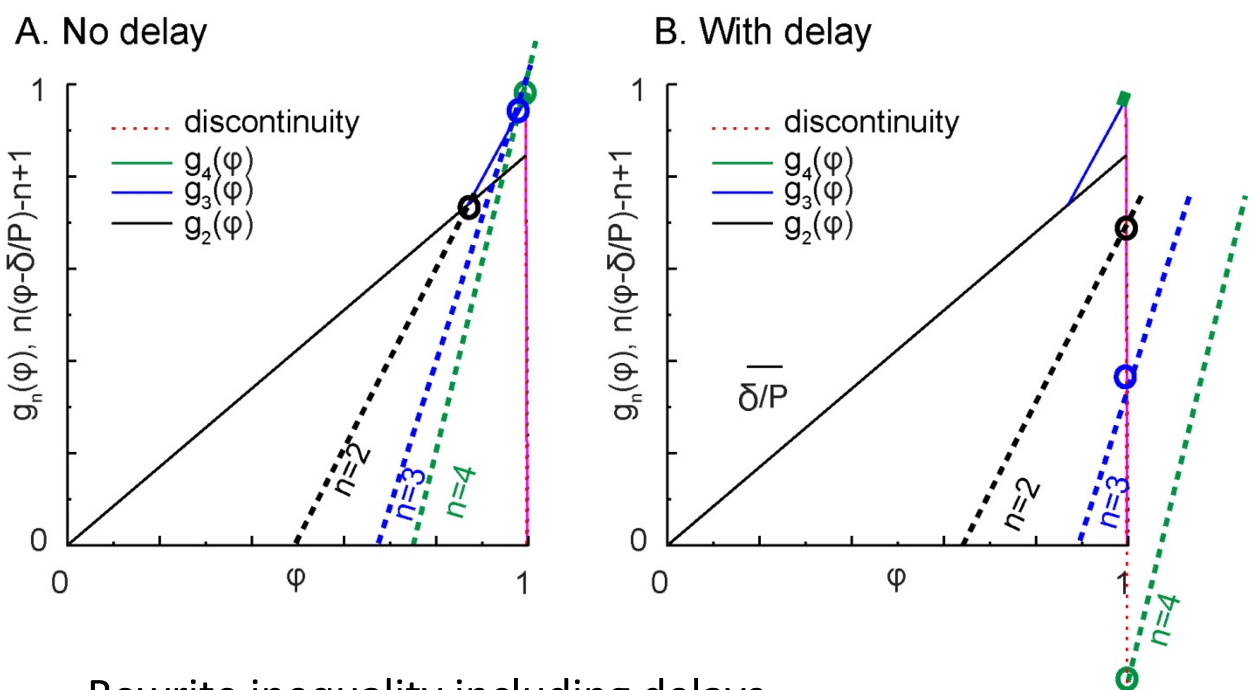
Line for n-cluster mode

Line for 2-cluster mode

PRC for 2-cluster mode

PRC function for n-cluster mode

No intersection for n=2 implies no line will intersect

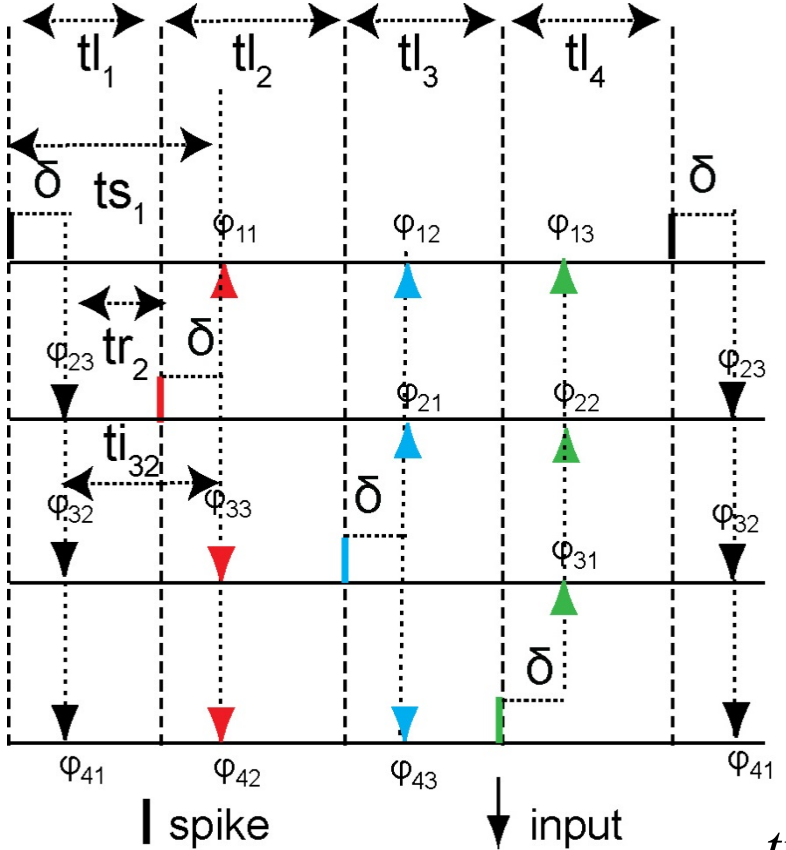


Rewrite inequality including delays

$$n\left(\varphi-\frac{\delta}{P_{n,\delta}}\right)-(n-1)<2\left(\varphi-\frac{\delta}{P_{2,\delta}}\right)-1<g_{2,\delta}(\varphi)<g_{n,\delta}(\varphi)$$

Canavier and Tikidji-Hamburyan Physical Review E 95(3):032215, 2017.

Firing Pattern for Splay Mode with Unequal Time Lags



time lag

$$tl_1 = ts_1 - \delta = ti_{n-1,n-2} = tr_2 + \delta$$

stimulus interval

$$ts_1 = P_{n,\delta}\varphi_{11}$$

recovery interval

$$tr_2 = P_{n,\delta}\{1 - \varphi_{n-1} + f_{n,\delta}(\varphi_{n-1})\}$$

intermediate intervals

$$ti_{n-1,n-2} = P_{n,\delta}\{\varphi_{n-1} - \varphi_{n-2} + f_{n,\delta}(\varphi_{n-2})\}$$

Canavier and Tikidji-Hamburyan Physical Review E 95(3):032215, 2017.

Assume one time lag tl_j in the unequal time lags case is shorter than the time lag tl in the corresponding equal time lag n-cluster mode

From definition of stimulus intervals: $\varphi_{11}^{*} < \varphi_{1}^{*}$

$$tl_1 = ts_1 - \delta = tr_2 + \delta \qquad ts_1 - 2\delta = tr_2$$

$$\varphi_1 = 1 - \varphi_{n-1} + f_{n,\delta}(\varphi_{n-1}) + 2\delta / P_{n,\delta}$$

equal $$\varphi_{n-1}^{*} - f(\varphi_{n-1}^{*}) = 1 - \varphi_{1}^{*} + 2\delta / P_{n\delta}$$

unequal $$\varphi_{2,n-1}^{*} - f(\varphi_{2,n-1}^{*}) = 1 - \varphi_{11}^{*} + 2\delta / P_{n\delta}$$

$0 < f_{n,\delta}^{'}(\varphi_i) < 1, \varphi_i \in [0,1)$ implies $\varphi_{2,n-1}^{*} > \varphi_{n-1}^{*}$

Then the phase at which the last input received by one oscillator in the unequal time lags mode is greater than the phase at which the last input is received in the equal time lag mode.

Contradiction proves that always one time lag in the unequal time lag mode is always shorter than the lags in the equal time lag mode

1) Assume the stimulus interval for oscillator j is greater in the unequal lag mode. Then by the same logic of previous slide using stimulus and recovery interval definitions:

$$\varphi_{j1} - \delta / P_{\mathrm{n},\delta} > \varphi_1 - \delta / P_{\mathrm{n},\delta} \quad \text{implies} \quad \varphi_{j1} > \varphi_1 \quad \text{implies} \quad \boxed{\varphi_{j+1,n-1} < \varphi_{n-1}}$$

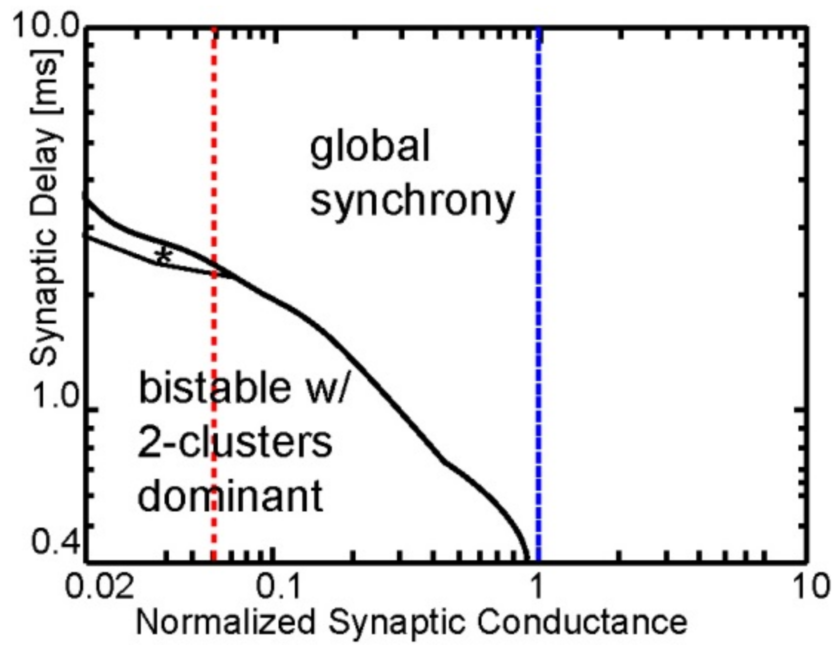
2) Assume all intermediate intervals for oscillator j are greater in the unequal lag mode

$$\varphi_{j,i+1} - \varphi_{ji} + f_{n,\delta}(\varphi_{ji}) > \varphi_{i+1} - \varphi_i + f_{n,\delta}(\varphi_i) \quad \text{implies} \quad \varphi_{j,i+1} > \varphi_{i+1}$$

$$\text{provided} \quad \varphi_{j,i} > \varphi_i \quad \text{thus} \quad \varphi_{j1} > \varphi_1 \quad \text{implies} \quad \boxed{\varphi_{j+1,n-1} > \varphi_{n-1}}$$

Therefore if the phase at which the last input is received falls in the discontinuity for an n-cluster equal time lag mode, at least one last input in any n-cluster unequal time lag mode will also fall in the discontinuity.

2D Bifurcation Diagram for 300 HH Model Neurons with Inhibitory Coupling



Tikidji-Hamburyan and Canavier, in preparation

Existence and Stability Criteria Global Synchrony and Two Cluster Modes

synchrony at k=2: $-1 < 1 - f'(\varphi) - f'(\varphi) < 1$

$$\varphi = \delta / P$$

Exception: with no delay k=1 $-1 < 1 - f'(0^+))(1 - f'(1^-) < 1$

$$\varphi = 0,1$$

Antiphase at k=1: $-1 < \left(1 - f'(\varphi_{AP})\right)\left(1 - f'(\varphi_{AP})\right) < 1$

$$\varphi_{AP} = 0.5 + 0.5 f(\varphi_{AP}) + \delta / P$$

unequal time lags at k=1: $f(\varphi_R) = f(\varphi_L)$ (impossible for monotonically Increasing PRC)

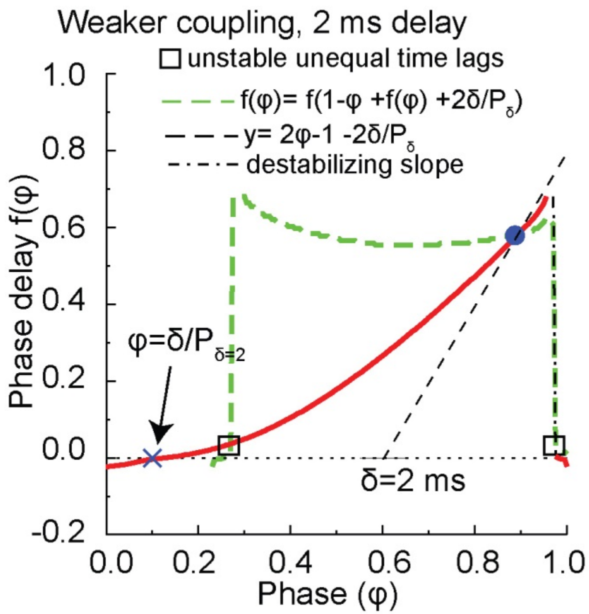
$$-1 < \left(1 - f'(\varphi_R)\right)\left(1 - f'(\varphi_L)\right) < 1$$

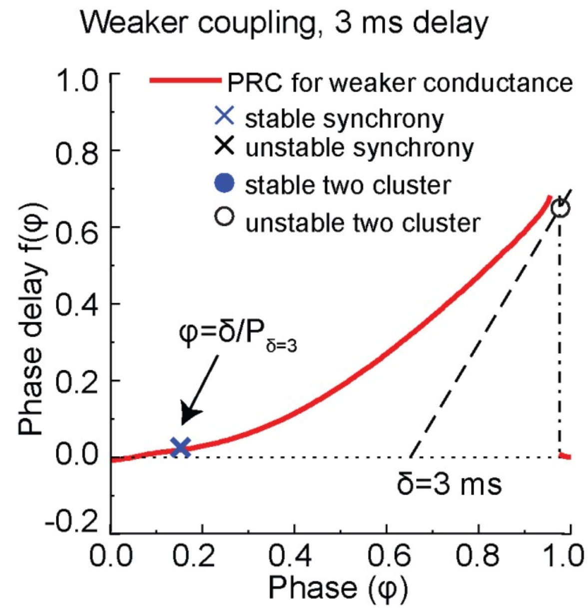
Closed form only possible for n=2 unequal lags mode $f(\varphi_i) = f(1 - \varphi_i + f(\varphi_i) + 2\delta / P)$

Negative PRC slopes *f′(φ)* tend to make the absolute value >1

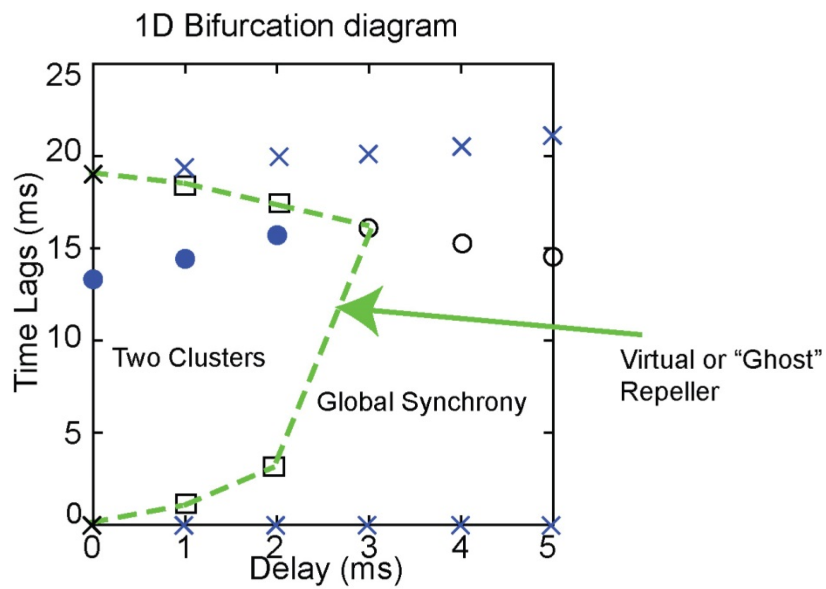
Woodman and Canavier, *J Computational Neurosci* 2011
Canavier et al. , *Frontiers in Computational Neuroscience*, 2013

PRC Analysis Explains 1D Bifurcation Diagrams for Weaker Inhibitory Coupling



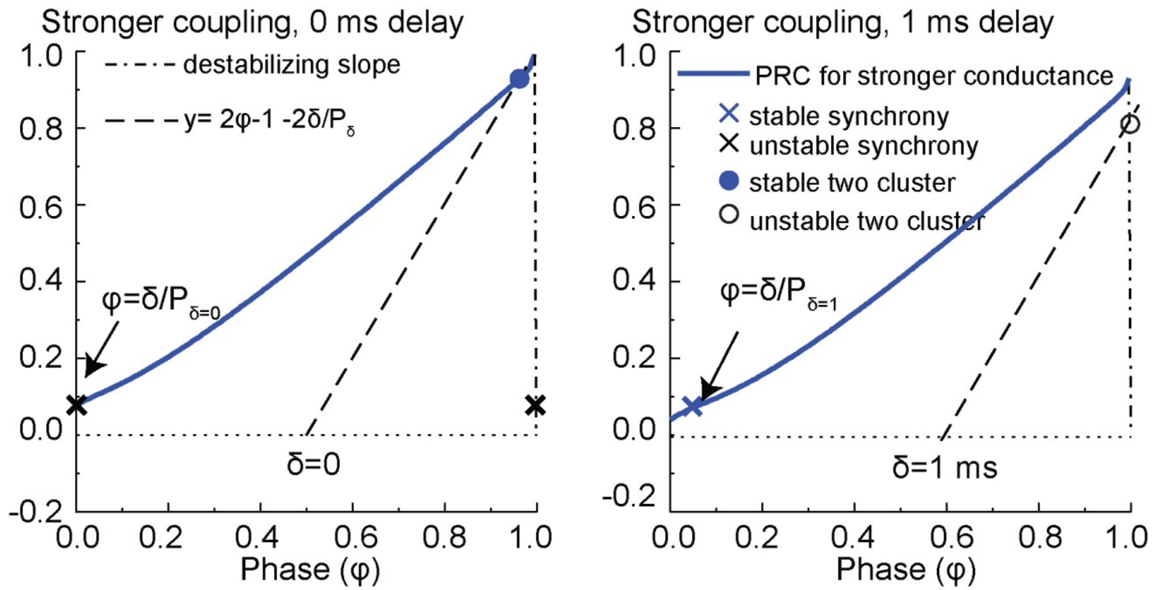


Global synchrony becomes globally attracting when the black dashed line for n=2 falls everywhere to the right of the PRC

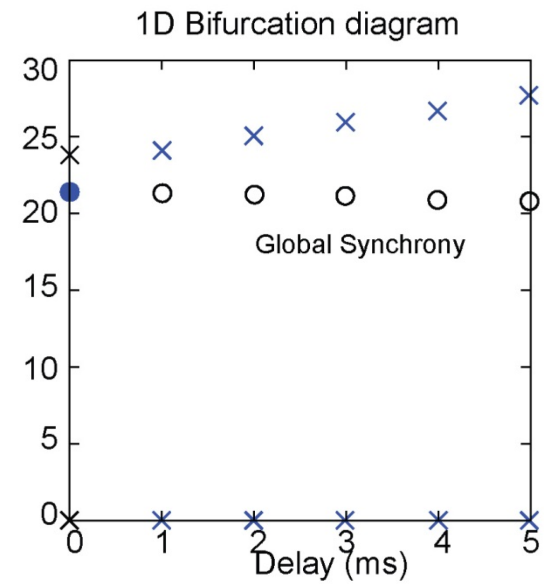


Tikidji-Hamburyan and Canavier, in preparation

PRC Analysis Explains 1D Bifurcation Diagrams for Weaker Inhibitory Coupling

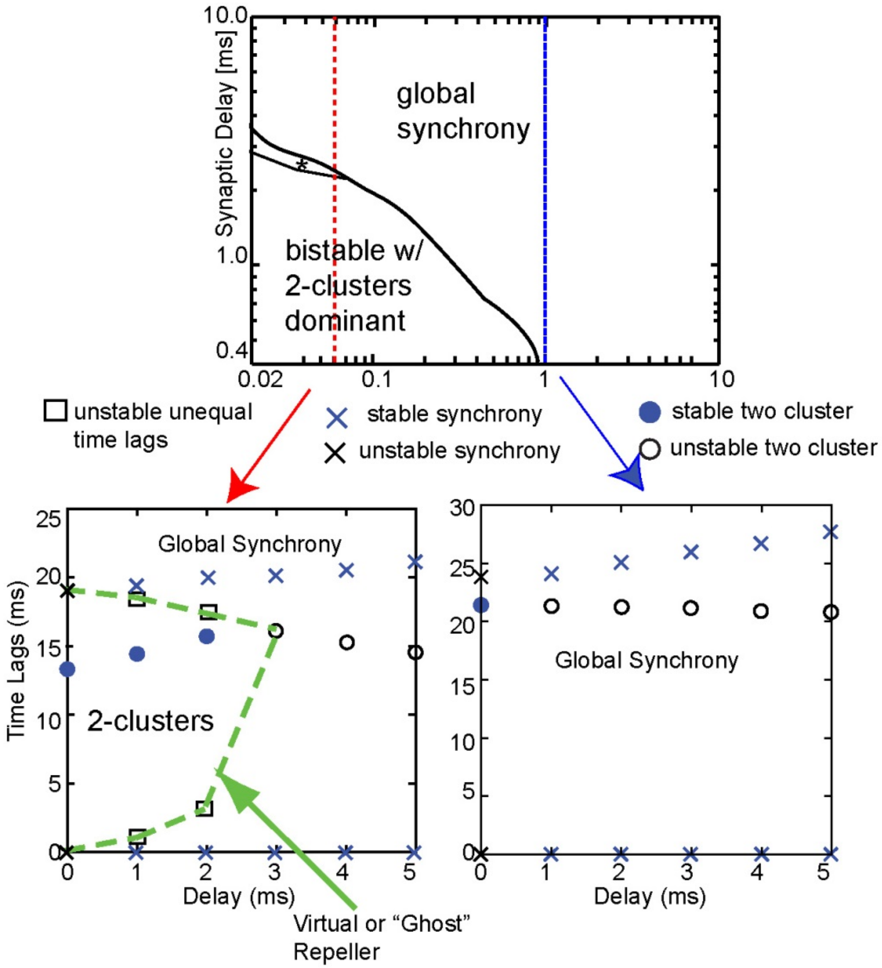


Global synchrony becomes globally attracting when the black dashed line for n=2 falls everywhere to the right of the PRC



Tikidji-Hamburyan and Canavier, in preparation

Bifurcation Diagrams for 300 HH Model Neurons with Inhibitory Coupling



Note that the results hold despite:

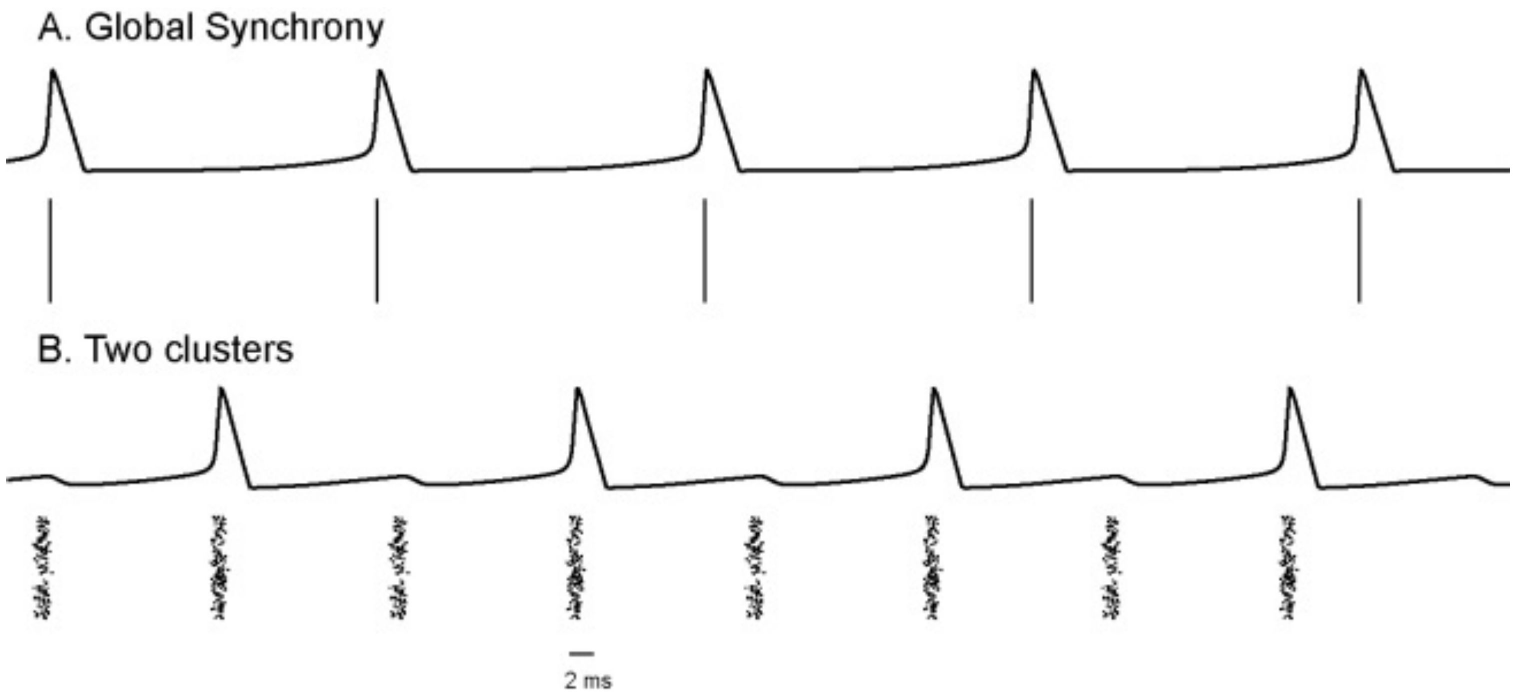
$$f_{n,\delta}(\varphi) \neq f_{n-1,\delta}(\varphi)$$

All you need is $g_{n,\delta}(\varphi) > g_{2,\delta}(\varphi)$

$$g_{n,\delta}(\varphi_{n-1}) = f_{\delta}(\varphi_{n-1}) + \sum_{i=1}^{n-2} \{ f_{\delta}(\varphi_{n-1}) - (f_{\delta}(\varphi_i) \}$$

Tikidji-Hamburyan and Canavier, in preparation

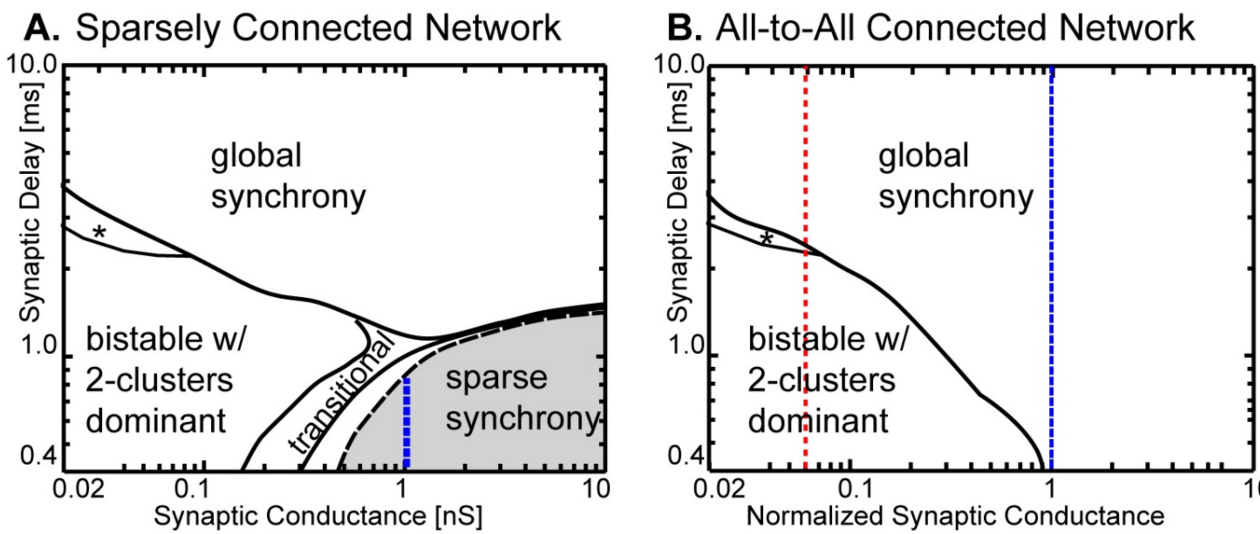
Sparse Connectivity Introduces Jitter in Two Cluster Mode
(40 each in 300 neuron network)



Two cluster solution is robust to jitter because the destabilizing discontinuity is not sampled

Tikidji-Hamburyan and Canavier, in preparation

Bifurcation Diagram is Largely Preserved With Sparse Connectivity
(40 each in 300 neuron network)



Jitter (vertical dashed line) samples the destabilizing discontinuity

Tikidji-Hamburyan and Canavier, in preparation

Conclusions

- By assuming a monotonically increasing PRC and invariance of the PRC to cluster size, we can prove that synchrony is globally attracting if no equal time lag two cluster solution exists (PRC is everywhere to the left of 2ϕ-1) for small but nonzero conduction delays.
- The discontinuity due to a monotonically increasing PRC is destabilizing.
- Delays allow the system to avoid the destabilizing effect of the discontinuity.
- The discontinuity can produce a virtual or ghost repeller.
- Analysis can be extended to sparse connectivity with caveats.

Stability of Splay Mode

$$\Delta\varphi_i[\mathrm{k}] = \varphi_i[\mathrm{k}] - \varphi_i^*$$

$$\Delta[k] = [\Delta\varphi_{n-1}[\mathrm{k}], \Delta\varphi_{n-2}[\mathrm{k}], \cdots, \Delta\varphi_2[\mathrm{k}], \Delta\varphi_1[\mathrm{k}]]^T$$

$$\Delta[k+1] = A\Delta[k]$$

$$\boldsymbol{A} = \begin{pmatrix} f'_{n,\delta}\left(\varphi^*_{n-1}\right) - 1 & 1 - f'_{n,\delta}\left(\varphi^*_{n-2}\right) & 0 & \cdots & 0 \\ f'_{n,\delta}\left(\varphi^*_{n-1}\right) - 1 & 0 & 1 - f'_{n,\delta}\left(\varphi^*_{n-3}\right) & \cdots & 0 \\ \vdots & \vdots & \vdots & \cdots & \vdots \\ \vdots & \vdots & \vdots & \cdots & 1 - f'_{n,\delta}\left(\varphi^*_1\right) \\ f'_{n,\delta}\left(\varphi^*_{n-1}\right) - 1 & 0 & 0 & \cdots & 0 \end{pmatrix}$$

If the time lags are unequal, the matrix is different for each distinct value

Achuthan and Canavier J Neurosci. 2009 Apr 22;29(16):5218-33

$$
\begin{pmatrix}
f'_{n,\delta}\left(\varphi^*_{n-1}\right)-1 & 1-f'_{n,\delta}\left(\varphi^*_{n-2}\right) & 0 & \mathrm{L} & 0 \\
f'_{n,\delta}\left(\varphi^*_{n-1}\right)-1 & 0 & 1-f'_{n,\delta}\left(\varphi^*_{n-3}\right) & \mathrm{L} & 0 \\
\mathrm{M} & \mathrm{M} & \mathrm{M} & \mathrm{L} & \mathrm{M} \\
\mathrm{M} & \mathrm{M} & \mathrm{M} & \mathrm{L} & 1-f'_{n,\delta}\left(\varphi^*_{1}\right) \\
f'_{n,\delta}\left(\varphi^*_{n-1}\right)-1 & 0 & 0 & \mathrm{L} & 0
\end{pmatrix}
$$

The last term in the characteristic equation for this matrix is $\prod_{i}^{n}\left(1-f'_{n,\delta}\left(\varphi^*_{n-i}\right)\right)$

which is also the product of the eigenvectors. Clearly, any infinitely large negative slope will produce an infinitely large product, so one of the eigenvalues must also be infinitely large and therefore maximally unstable.