Synchronization, Multistability and Clustering: How Useful are Predictions from Phase Models?

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Motivation

- Phase models have mostly been used to give *qualitative* predictions about the behaviour of a system. E.g. *What possible oscillation patterns can occur?*
- Many people study phase models in isolation *without making a direct connection to the biophysical model* although this is possible.
- Our goal - determine of how much *quantitative* information can be gained from phase models which are derived directly from a given biophysical neural model.

Biophysical Neural Model

X.J. Wang and G. Busaki (1996)
J. Neurosci., 16: 6402-6413

$$\frac{dV_i}{dt} = -g_{Na}m_\infty^3(V_i)h_i(V_i - V_{Na}) - g_K n_i^4(V_i - V_K)$$
$$-g_L(V_i - V_L) + I_{\mu,i} + \frac{g_{syn}}{n-1}(V_i - V_{syn})\sum_{j=1,\, j\neq i}^{n} s_{ij}$$
$$\frac{dh_i}{dt} = \phi[\alpha_h(V_i)(1-h_i) - \beta_h(V_i)h_i]$$
$$\frac{dn_i}{dt} = \phi[\alpha_n(V_i)(1-n_i) - \beta_n(V_i)n_i]$$
$$\frac{ds_{ij}}{dt} = \alpha T(V_j)(1-s_{ij}) - \frac{s_{ij}}{\tau_{syn}}$$

$$m_\infty(V) = \frac{\alpha_m(V)}{\alpha_m(V)+\beta_m(V)}$$
$$\alpha_m(V) = -0.1\frac{V+35}{e^{-0.1(V+35)}-1}, \quad \beta_m(V) = 4e^{-(V+60)/18}$$
$$\alpha_h(V) = 0.07e^{-(V+58)/20}, \quad \beta_h(V) = \frac{1.0}{e^{-0.1(V+28)}+1}$$
$$\alpha_n(V) = -0.01\frac{V+34}{e^{-0.1(V+34)}-1}, \quad \beta_n(V) = 0.125e^{-(V+44)/80}$$

g_{Na}	35 mS/cm^2	V_{Na}	55 mV
g_K	9 mS/cm^2	V_K	-90 mV
g_L	0.1 mS/cm^2	V_L	-65 mV
ϕ	5	I_μ	1
g_{syn}	0.1 mS/cm^2	V_{syn}	-75 mV
α	6.25 ms^{-1}	τ_{syn}	$1-10$

Heterogeneity introduced through applied current:
$$I_{\mu,1} = I_\mu + \epsilon, \qquad I_{\mu,2} = I_\mu - \epsilon$$

Phase Model Reduction

F.C. Hoppensteadt and E.M. Izhikevich (1997)
Weakly connected neural networks

If couping strength (g_{syn}) is small enough, each neuron may be represented by a single phase variable θ_i.
Effect of coupling is given by interaction function H.

G.B. Ermentrout (2002) *Simulating, Analyzing and Animating Dynamical Systems: A Guide to XPPAUT for Researchers and Students.*

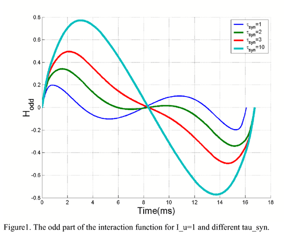
Interaction function can be computed numerically.

Homogeneous Two Cell Network

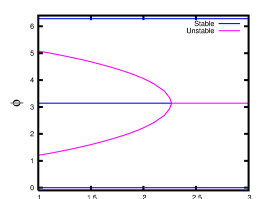
Phase Model

$$\frac{d\phi}{dt} = -2g_{syn}H_{odd}(\phi)$$

where $\phi = \theta_2 - \theta_1$ is the phase difference.



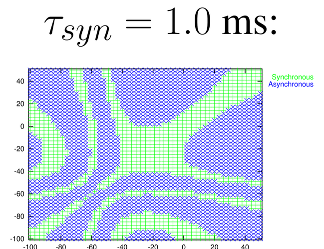
Predictions of phase model



Stable synchronous solution exists for all τ_{syn}
Stable asynchronous (antiphase) solution exists for $\tau_{syn} < 2.3$
Size of basins of attraction easily found from bifurcation diagram

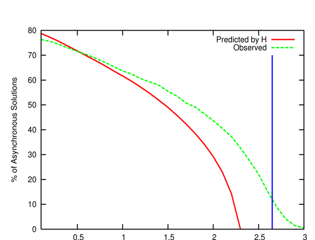
Results from biophysical model

Stable synchronous solution exists for all τ_{syn}
Stable asynchronous (antiphase) solution exists for $\tau_{syn} < 2.65$
Size of basins of attraction were determined by running *many* numerical simulations.
Example: Basins of attraction in V_1, V_2 space for $\tau_{syn} = 1.0$ ms:



Initial Conditions: V_1, V_2 as shown, all other variables 0.
Numerical simluations varying initial conditions for all variables yielded similar results.

Comparison of Basins of Attraction



Blue line shows cut-off for antiphase solutions at $\tau \approx 2.65$. Discrepency likely due to transients.

Heterogeneous Two Cell Network

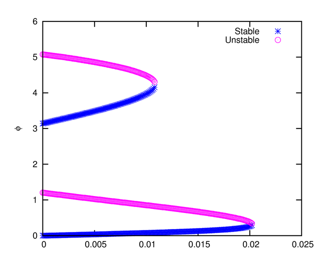
Phase Model

$$\frac{d\phi}{dt} = \omega_2(\epsilon) - \omega_1(\epsilon) - 2g_{syn}H_{odd}(\phi)$$

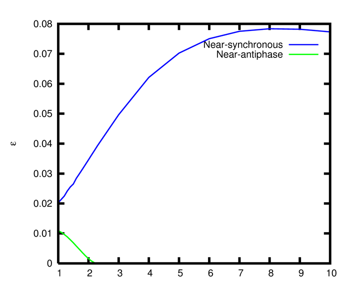
where ω_i is the frequency of neuron i.

Predictions of Phase Model

Heterogeneity can destroy both near-synchronous and antiphase oscillations.
Bifurcation plot of ϕ vs ϵ for $\tau_{syn} = 1.0$ ms:



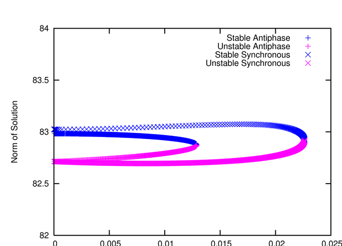
ϵ values where near-synchronous and antiphase oscillations are lost as a function of τ_{syn}:



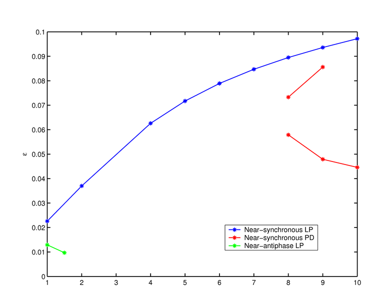
Since antiphase solution only persists for small ϵ, basins of attraction are basically unchanged.

Results from biophysical model

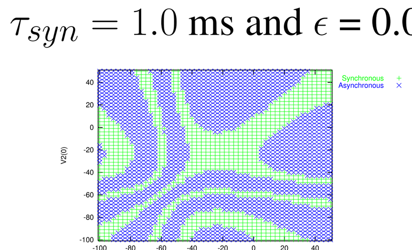
Bifurcation plot of ϕ vs ϵ for $\tau_{syn} = 1.0$ ms:



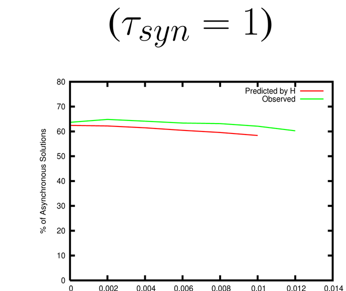
ϵ values where near-synchronous and antiphase oscillations are lost as a function of τ_{syn}:



Basins of attraction in V_1, V_2 space for $\tau_{syn} = 1.0$ ms and $\epsilon = 0.01$:



Comparison of Basins of Attraction
($\tau_{syn} = 1$)



Homogeneous n Cell Network

Phase Model

$$\frac{d\phi_i}{dt} = f_i(\phi_1, \ldots, \phi_{n-1})$$

where $\phi_i = \theta_{i+1} - \theta_i$ are the phase differences.

Predictions of phase model

Synchronous solution
Condition for stability exactly the same as for two cell network

Antiphase solution - n even
Network separates into two clusters of $\frac{n}{2}$ neurons each
Within cluster neurons are synchronous.
Phase difference between clusters is π.
Condition for stability exactly the same as for two cell network

Antiphase solution - n odd
Network separates into two clusters of $\frac{n+1}{2}$ neurons and $\frac{n-1}{2}$ neurons
Within cluster neurons are synchronous.
Phase difference between clusters is $\bar{\phi}(n, \tau_{syn})$
For large n, $\bar{\phi} \to \pi$ and stability condition approaches that for two cell network.

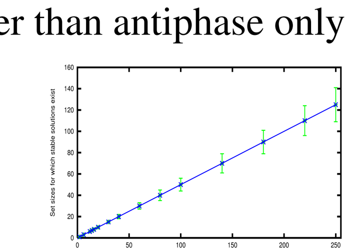
Existence and Stability

τ_{syn} / n	5	7	9	11	17	25	55	105	155	205
0.5	•	•	•	•	•	•	•	•	•	•
1.0	×	×	•	•	•	•	•	•	•	•
1.5	×	×	×	×	•	•	•	•	•	•
1.7	×	×	×	×	×	•	•	•	•	•
1.9	×	×	×	×	×	×	•	•	•	•
2.0	×	×	×	×	×	×	×	•	•	•
2.1	×	×	×	×	×	×	×	×	•	•
2.2	×	×	×	×	×	×	×	×	×	×

• = stable, × = unstable or non-existent

Other Symmetric Clusters
Network separates into N clusters of n/N neurons each.
Many choices of clusters.
Within cluster neurons are synchronous.
Phase difference between clusters is $\frac{2\pi}{N}$
Stable clusters only occur for $N = 3$, $\tau_{syn} \leq 0.7$

Other Asymmetric Clusters
Network separates into two clusters of k neurons and $n - k$ neurons
Within cluster neurons are synchronous.
Phase difference between clusters is $\bar{\phi}(n, \tau_{syn})$
Solutions other than antiphase only occur if $n > 15$.



Sizes of cell groups with stable solutions vs. n for $\tau_{syn} = 1.0$

Homogeneous n Cell Network

Results from biophysical model

All types of predicted solutions are observed
Solutions other than synchronous and antiphase only occur for $n > 16$

Example: $n = 7$
Only antiphase $(4/3)$ solution occurs.
Comparision of cluster phase difference:

τ_{syn}	Predicted $\bar{\phi}$	Observed $\bar{\phi}$
0.2	3.91069	3.88080
0.4	3.91442	3.90873
0.6	3.94507	3.93602
0.8	4.02303	3.99840
1.0	-	4.09466

Example: $n = 24$

τ_{syn}	Solution type	Number of solutions
1.0	synchronous solution	2146
1.0	antiphase solution (12/12)	207
1.0	2 clusters (11/13)	423
1.0	2 clusters (10/14)	129
1.0	3 clusters (8/8/8)	1
1.5	synchronized solution	1345
1.5	antiphase solution (12/12)	55
1.5	2 clusters (11/13)	98
2.0	synchronized solutions	1488
2.0	antiphase solution (12/12)	12

Conclusions

Homogeneous Two cell network

- Phase model gives reasonable prediction of existence, stability and basins of attraction of synchronous and antiphase solutions

Heterogeneous Two cell network

- Phase model gives reasonable prediction of existence of near-synchronous and near-antiphase solutions.
- Stability/basin of attraction predictions are accurate for τ_{syn} small enough.
- Phase model cannot predict period doubling bifurcations which cause loss of stability at higher τ_{syn}

Homogeneous n cell network

- All solution types predicted to occur by phase model are observed in biophysical model.
- Phase model predicts that stability of synchronous solution, antiphase solution (n even or n odd and large) are determined by two cell network. Results from biophysical model are consistent with this.
- Phase model gives reasonable prediction of existence and stability of clusters and of phase difference between clusters.

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