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Sue Ann Campbell, Zhen Wang



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Phase models and clustering in networks of oscillators with delayed coupling

Sue Ann Campbell^a, Zhen Wang^b

^a*Department of Applied Mathematics and Centre for Theoretical Neuroscience,
University of Waterloo Waterloo ON N2L 3G1 Canada (e-mail:
sacampbell@uwaterloo.ca).*

^b*Department of Applied Mathematics, University of Waterloo Waterloo ON N2L 3G1
Canada (e-mail: z377wang@uwaterloo.ca).*

Abstract

We consider a general model for a network of oscillators with time delayed coupling where the coupling matrix is circulant. We use the theory of weakly coupled oscillators to reduce the system of delay differential equations to a phase model where the time delay enters as a phase shift. We use the phase model to determine model independent existence and stability results for symmetric cluster solutions. Our results extend previous work to systems with time delay and a more general coupling matrix. We show that the presence of the time delay can lead to the coexistence of multiple stable clustering solutions. We apply our analytical results to a network of Morris Lecar neurons and compare these results with numerical continuation and simulation studies.

Keywords: Time delay, neural network, oscillators, clustering solutions, stability

1. Introduction

Coupled oscillator models have been used to study many biological and physical systems, for example neural networks [1, 2], laser arrays [3, 4], flashing of fireflies [5], and movement of a slime mold [6]. A basic question explored with such models is whether the elements in the system will phase-lock, i.e., oscillate with some fixed phase difference, and how the physical parameters affect the answer to this question. Clustering is a type of phase locking behavior where the oscillators in a network separate into groups.

Each group consists of fully synchronized oscillators, and different groups are phase-locked with nonzero phase difference. Symmetric clustering refers to the situation when all the groups are the same size while non-symmetric clustering means the groups have different sizes.

A phase model represents each oscillator with a single variable. A differential equation for each phase variable indicates how the phase of the oscillator changes in time:

$$\frac{d\theta_i}{dt} = \Omega_i + H_i(\theta_1, \theta_2, \dots, \theta_N)$$

Here Ω_i is the intrinsic frequency of the i^{th} oscillator and the functions H_i described how the coupling between oscillators influences the phases. Phase models have been used to study the behaviour of networks of coupled oscillators beginning with the work of [7]. Phase models are sometimes *posed* as models for coupled oscillators [5, 7, 8, 9]. When the coupling between oscillators is sufficiently weak, however, a phase model representation of a system can be *derived* from a higher dimensional differential equation model, such as one obtained from a physical or biological description of the system [10, 11, 12, 13]. The low dimensional phase model can then be used to predict behaviour in the original high dimensional physical model. This approach has proved useful in studying synchronization properties of many different neural models [1, 14, 15, 16, 17, 18, 19, 20]. Phase models can be linked to experimentally derived phase resetting curves [10, 13], thus this approach has also been used to make predictions about synchronization properties of experimental preparations [19].

[21, 8] were the first to use phase models to study clustering behaviour. Using the theory of equivariant differential equations [21] studied a general network of identical oscillators of arbitrary size with symmetric, weak coupling, corresponding to the symmetry groups S_n , Z_n , and D_n . They determined which type of solutions are forced to exist by the symmetry in each case. For the case of S_n symmetry they gave conditions for the stability of several types of solutions, including symmetric cluster solutions, and determined which bifurcations are forced by symmetry to occur. They also studied the existence of heteroclinic cycles and tori for some special cases. By direct analysis of the phase model, [8] studied a network with global homogeneous coupling, (S_n symmetry). He established general criteria for the stability of all possible symmetric cluster solutions as well as some nonsymmetric cluster solutions. Using numerical simulations, [8] further showed that these results

give a good prediction of stability for a variety of model networks. More recently, [22] considered the existence and stability of cluster solutions and fixed tori for phase models corresponding to networks with global homogeneous coupling. They also considered the effect of additional absolute-phase product coupling. Using a similar approach as [8] stability results have been obtained for inhibitory neural networks with nearest-neighbour coupling [23]. Phase model analysis has also been extensively used to study phase-locking in pairs of model and experimental neurons [12, 25, 19]. More recently it has been used to study clustering in larger neural networks [26, 27]. A more comprehensive review of the analysis of phase models and their application to the study of synchronization is given in [24].

In many systems there are time delays in the connections between the oscillators due to the time for a signal to propagate from one element to the other. In neural networks this delay is attributed to the conduction of electrical activity along an axon or a dendrite [15, 12]. Much work has been devoted to the study of the effect of time delays in neural networks. However, the majority of this work has focussed on systems where the neurons are excitable not oscillatory, (e.g., [28, 29, 30, 31, 32, 33]), the networks have only a few neurons (e.g., [9, 34, 12, 35, 36]) or focussed exclusively on synchronization (e.g., [15, 37, 38, 39, 32]). Extensive work has been done on networks of Stuart-Landau oscillators with delayed diffusive coupling (e.g., [40, 41] where the model for the individual oscillators is the normal form for a Hopf bifurcation and thus the system is often amenable to theoretical analysis. Numerical approaches to study the stability of cluster solutions in delayed neural oscillator networks have also been developed [39, 42]. We note that there is a vast literature on time delays in artificial neural networks which we do not attempt to cite here.

Initial studies of phase models for systems with delayed coupling considered models where the delay occurs in the argument of the phases [36, 37, 43, 44, 45]. However, it has been shown [12, 46, 47] that for small enough time delays it is more appropriate to include the time delay as phase shift in the argument of the coupling function. Crook et al. [15] use this type of model to study a continuum of cortical oscillators with spatially decaying coupling and axonal delay. Bressloff and Coombes [14, 48] study phase locking in chains and rings of pulse coupled neurons with distributed delays and show that distributed delays result in phase models with a distribution of phase shifts. They consider phase models derived from integrate and fire neurons and the Kuramoto phase model.

In this paper, we investigate the effect of time delayed coupling on the clustering behavior of oscillator networks. The plan for our article are as follows. In the next section we will review how a general network model with delayed coupling may be reduced to a phase model. In section 3 we use the phase model to determine conditions for existence and stability of symmetric cluster solutions in a network with a circulant coupling matrix, extending some prior results [21, 8, 23] to systems with time delays and more general coupling. In section 4 we consider a particular application: a network of Morris-Lecar oscillators. We derive the particular phase model for this system and compare the predictions of the phase model theory to numerical continuation and simulation studies to determine when the weak coupling assumption breaks down. We show that the time delay can induce multistability between different cluster solutions and explore how changing the coupling matrix affects this. In section 5 we explore the effects of breaking the symmetry of the connection matrix and introducing multiple time delays on our results. In section 6 we discuss our work.

2. Reduction to a phase model

In this section, we review how to reduce a general model for a network of all-to-all coupled oscillators with time-delayed connections to a phase model. We assume the model for a single oscillator

$$\frac{dX}{dt} = F(X(t)), \quad (1)$$

admits an exponentially asymptotically stable periodic orbit, denoted by $\hat{X}(t)$, with period T . Further, we denote by $Z = \hat{Z}(t)$ the unique periodic solution of the system adjoint to the linearization of (1) about $\hat{X}(t)$ satisfying the normalization condition:

$$\frac{1}{T} \int_0^T \hat{Z}(t) \cdot F(\hat{X}(t)) dt = 1.$$

Now consider the following network of identical oscillators with all-to-all, time-delayed coupling

$$\frac{dX_i}{dt} = F(X_i(t)) + \epsilon \sum_{j=1}^N w_{ij} G(X_i(t), X_j(t - \tau_{ij})), \quad i = 1, \dots, N. \quad (2)$$

Here $G : \mathbb{R}^n \times \mathbb{R}^n \rightarrow \mathbb{R}^n$ describes the coupling between two oscillators, ϵ is referred to as the coupling strength, and $W = [w_{ij}]$ is the coupling matrix. We assume $w_{ij} \geq 0$.

When ϵ is sufficiently small and the w_{ij} are of order 1 with respect to ϵ , we can apply the theory of weakly coupled oscillators to reduce (2) to a phase model [10, 11, 12]. The way in which the time delays enter into the phase model depends on the size of the delays relative to other time constants in the model. Let $\Omega = 2\pi/T$. It has been shown [12, 46, 47] that if the delays satisfy $\Omega\tau_{ij} = O(1)$ with respect to the coupling strength ϵ , then the appropriate model is

$$\frac{d\theta_i}{dt} = \Omega + \epsilon \sum_{j=1}^N W_{ij} H(\theta_j - \theta_i - \eta_{ij}) + O(\epsilon^2), \quad i = 1, 2, \dots, N, \quad (3)$$

where $\eta_{ij} = \Omega\tau_{ij}$. That is, the delays enter as phase lags. The interaction function H is a 2π -periodic function which satisfies

$$H(\theta) = \frac{1}{T} \int_0^T \hat{Z}(s) \cdot G(\hat{X}(s), \hat{X}(s + \theta/\Omega)) ds.$$

with \hat{X}, \hat{Z} as defined above.

To study cluster solutions we will make two simplifications. First, we assume that all the delays are equal:

$$\tau_{ij} = \tau, \quad \text{i.e., } \eta_{ij} = \eta. \quad (4)$$

Second, we will assume the network has some symmetry. In particular, we will consider the coupling matrix to be in circulant form:

$$W = \text{circ}(w_0, w_1, w_2, \dots, w_{N-1}), \quad \text{equivalently, } W_{ij} = w_{j-i \pmod{N}}. \quad (5)$$

Following [23], we will say the network has connectivity radius r , if $w_k > 0$ for all $k \leq r$, and $w_k = 0$ for all $k > r$. For example, a network with nearest neighbor coupling has connectivity radius $r = 1$. Our results will be derived with the coupling matrix (5), but can be applied to coupling with any connectivity radius by setting the appropriate $w_k = 0$.

We will also assume there is no self coupling, $w_0 = 0$, as this generally the case in applications. The results are essentially unchanged if we include it [50]. These simplifications will apply for the next two sections. In section 5, we will return to the general model (3).

3. Existence and stability of cluster solutions

Rewriting (3) using the simplifications (4)-(5) and dropping the higher order terms in ϵ we have

$$\frac{d\theta_i}{dt} = \Omega + \epsilon \sum_{j=1, j \neq i}^N w_{j-i \pmod{N}} H(\theta_j - \theta_i - \eta), \quad i = 1, 2, \dots, N. \quad (6)$$

Now the right hand sides of equation (6) depend only on the difference of phases. Thus, introducing the phase difference variables:

$$\phi_i = \theta_{i+1} - \theta_i, \quad i = 1, \dots, N, \quad (7)$$

we can transform the phase equation (6), to the following system

$$\frac{d\phi_i}{dt} = \epsilon \sum_{k=1}^{N-1} w_k \left(H\left(\sum_{s=0}^{k-1} \phi_{i+s+1} \pmod{N} - \eta\right) - H\left(\sum_{s=0}^{k-1} \phi_{i+s} \pmod{N} - \eta\right) \right) \quad (8)$$

for $i = 1, 2, \dots, N$.

Note that the N phase difference variables are not independent but satisfy the relation

$$\sum_{i=1}^N \phi_i = 0 \pmod{2\pi}. \quad (9)$$

Thus, the N -dimensional system (8) could be reduced to system of dimension $N - 1$. However, to take advantage of the symmetry, we choose instead to work with the full set of N equations and apply the constraint (9).

As discussed above, a cluster solution of the DDE model (2) is one where all the oscillators have the same waveform, but they separate into different groups or clusters. Oscillators within a cluster are synchronized, while oscillators in different clusters are phase-locked with some fixed phase difference. It follows that in a cluster solution the difference between the phases of any two oscillators are fixed. Using (6) we can show that, to order ϵ , these solutions correspond to the lines

$$\theta_i = (\Omega + \epsilon\omega)t + \theta_{i0}. \quad (10)$$

See [8] for details of this calculation in the case that $\eta = 0$ and $w_k = w$. The case we are considering is completely analogous. Further, from the definition (7), it is clear that cluster solutions correspond to equilibrium points

of the phase difference equation (8). Therefore, by studying the existence of the equilibrium points of the phase difference model (8), we can obtain the existence of the corresponding cluster solutions of the original DDE model.

We can now state our first result.

Theorem 1 (Existence of cluster solutions). *For any values of H and the w_k , the phase difference model (8) admits N equilibrium points of the form $\phi_i = \psi$, $i = 1, \dots, N$:*

- (i) $\psi = 0$ corresponds to the 1-cluster or fully synchronized solution.
- (ii) $\psi = \frac{2p\pi}{N}$ where p, N are relatively prime corresponds to an N -cluster solution, also called a splay or rotating wave solution.
- (iii) $\psi = \frac{2m\pi}{n}$ where $N = nk$ for some positive integers $n, k > 1$, $1 \leq m < n$, and m, n are relatively prime corresponds to a symmetric n -cluster solution.

If ψ is a solution then so is $2\pi - \psi$ and they have the same number of clusters. The ordering of the clusters of the $2\pi - \psi$ solution is the reverse of the ψ solution. For generic weights, these are the only model independent equilibrium points.

Proof. It is clear from eq. (8) that, for any H and w_k , there are equilibrium points given by $\phi_i = \psi$, $i = 1, \dots, N$, subject to the constraint

$$N\psi = 0 \pmod{2\pi}. \quad (11)$$

Analysis of this constraint determine the possible values for ψ . Using these values in the solution (10) determines the number and ordering of clusters in the solution. The details of this analysis are similar to those in [23], which considers the case of no delays ($\eta = 0$), hence we omit them.

In the case of generic weights, i.e., no further symmetry in the connection matrix, model-independent equilibrium points exist if and only if there are constant values of the ϕ_i satisfying

$$\phi_{i+k} - \phi_i = 0 \pmod{2\pi}, \quad i = 1, \dots, N, \quad k = 1, \dots, N - i.$$

Analysis of these equations shows that the only possible solutions are in the form $\phi_i = \psi$, $i = 1, \dots, N$. □

Note that different values of ψ can have the same number of clusters with different oscillators in the clusters and/or a different ordering of the clusters in the solution. We shall see some examples of this in section 4.

We next analyze the stability of the equilibrium points $\phi_i = \psi$.

Theorem 2 (Stability of cluster solutions). *Let $\epsilon > 0$ and define*

$$\mu_j = \sum_{k=1}^{N-1} w_k H'(k\psi - \eta) (1 - \cos(2\pi k j / N)). \quad (12)$$

The equilibrium point $\psi = \frac{2\pi k}{N}$, $k \in \{0, \dots, N-1\}$, and the corresponding cluster solution is asymptotically stable when $\mu_j > 0$ for $j = 1, \dots, \lfloor \frac{N}{2} \rfloor$, and unstable if at least one $\mu_j < 0$.

Proof. The Jacobian matrix of the linearization of (8) about the equilibrium point $\phi_i = \psi$, $i = 1, \dots, N$, is the circulant matrix $\epsilon J = \text{circ}(c_0, c_1, \dots, c_{N-1})$ with $c_0 = -\sum_{s=1}^{N-1} w_s H'(s\psi - \eta)$ and $c_k = w_k H'(k\psi - \eta)$, $k = 1, \dots, N-1$. A standard result for circulant matrices [49] shows that the eigenvalues of J are $\epsilon \lambda_j$, $j = 0, 1, \dots, N$ where

$$\lambda_j = -\sum_{k=1}^{N-1} w_k H'(k\psi - \eta) (1 - e^{\frac{2\pi i}{N} k j}).$$

Thus there is always one zero eigenvalue, corresponding to λ_0 . This is because the phase differences in (8) are not all independent. It can be verified that if the constraint (9) is used to reduce the phase difference model (8) to $N-1$ equations then the linearization yields only the eigenvalues $\epsilon \lambda_j$, $j = 1, \dots, N-1$. A simple calculation shows that $\lambda_{N-j} = \overline{\lambda_j}$, $j = 1, \dots, \lfloor \frac{N}{2} \rfloor$ and $\text{Re}(\lambda_j) = \mu_j$. The result follows. \square

Recall that a cluster solution corresponds to a line in the phase model (6). The zero eigenvalue corresponds to the motion along this line.

Remark 1. *Due to the periodicity of H , the stability of the cluster solutions is 2π -periodic in the parameter η . Recall that $\eta = 2\pi\tau/T$ where τ is the time delay in the coupling and T is the intrinsic period of the uncoupled oscillators. Thus the stability is T -periodic in τ . That is, if a given solution is asymptotically stable (unstable) for $\tau = \tau_0$ then it is asymptotically stable (unstable) for $\tau = \tau_0 + kT$, $k = 1, 2, \dots$. This will carry over to the original delay differential equation model so long as τ is sufficiently small that the phase model is a valid approximation, i.e., $\frac{2\pi\tau}{T} = O(1)$ with respect to ϵ .*

From the two theorems above we can obtain some general results about certain common solutions.

Corollary 1 (Synchronized solution). *The phase difference model (8) always admits the 1-cluster solution, $\psi = 0$, corresponding to the solution where all the oscillators are synchronized. The stability of this solution is independent of the size of the network and coupling between oscillators (w_k). In particular, the synchronized solution is asymptotically stable when $H'(-\eta) > 0$, and unstable when $H'(-\eta) < 0$.*

Corollary 2 (Anti-phase solution). *If N is even the phase difference model (8) admits 2-cluster solution, $\psi = \pi$, which corresponds to the anti-phase solution where adjacent oscillators are out of phase by one half period. The stability of this solution is independent of the coupling. For $N = 2$ it is asymptotically stable (unstable) if $H'(\pi - \eta) > 0$ (< 0). For all $N > 2$ this solution is asymptotically stable if $H'(-\eta) > 0$ and $H'(\pi - \eta) > 0$ and unstable if $H'(\pi - \eta) < 0$.*

Remark 2. *In the above stability results, we assume $\epsilon > 0$. If $\epsilon < 0$, the stability of asymptotically stable solutions and totally unstable solutions will be reversed, and the saddle type solutions will remain of saddle type.*

3.1. Stability analysis for bi-directional, distance dependent coupling

In this section, we consider a special case where the coupling strength is distance-dependent and bi-directional. In real neural networks, coupling strength is not necessarily determined by the physical distance. However, the “distance” here can be generalized to include functional distance [9]: the degree of correlation in the activity of coupled neurons. Therefore, we consider a coupling matrix that satisfies

$$W = \text{circ}(0, w_1, w_2, \dots, w_{N/2}, \dots, w_2, w_1) \quad (13)$$

if N is even, and

$$W = \text{circ}(0, w_1, w_2, \dots, w_{(N-1)/2}, w_{(N-1)/2}, \dots, w_2, w_1) \quad (14)$$

if N is odd. Applying Theorem 2 to this system leads to the following.

Corollary 3. Consider (8) with bi-directional, distance dependent coupling. Define

$$\mu_j = \sum_{k=1}^{\frac{N-1}{2}} w_k [H'(k\psi - \eta) + H'(-k\psi - \eta)] (1 - \cos(2\pi kj/N))$$

for N odd and

$$\mu_j = w_m H'(m\psi - \eta) (1 - (-1)^j) + \sum_{k=1}^{m-1} w_k [H'(k\psi - \eta) + H'(-k\psi - \eta)] (1 - \cos(2\pi kj/N))$$

for $N = 2m$, even. The equilibrium point $\psi = \frac{2\pi k}{N}$, $k \in \{0, \dots, N-1\}$, and the corresponding cluster solution is asymptotically stable when $\mu_j > 0$ for $j = 1, \dots, \lfloor \frac{N}{2} \rfloor$, and unstable if at least one $\mu_j < 0$.

Recall that ψ and $2\pi - \psi$ correspond to the same type of cluster solution. For a network with bi-directional coupling, these solutions have a stronger relationship.

Corollary 4. For the phase model with coupling matrix given by (13) or (14), the solutions $\phi_i = \psi$ and $\phi_i = 2\pi - \psi$ have the same stability.

Proof. This follows by replacing ψ by $2\pi - \psi$ in the expressions for μ_j in Corollary 3 and using the 2π -periodicity of H . \square

A special case of bi-directional coupling is when the only nonzero coupling coefficient is w_1 . This is commonly called nearest-neighbour coupling. In this case the stability of any symmetric cluster solution is easily determined.

Corollary 5. For the phase model with coupling matrix given by (13) or (14) with $w_1 \neq 0$ and $w_j = 0$, $j = 2, \dots, N$, the symmetric cluster solution with $\phi_i = \psi$ is asymptotically stable if $H'(\psi - \eta) + H'(-\psi - \eta) > 0$ and unstable if $H'(\psi - \eta) + H'(-\psi - \eta) < 0$.

Proof. In this case we have

$$\mu_j = -w_1 [H'(\psi - \eta) + H'(-\psi - \eta)] (1 - \cos(2\pi j/N)).$$

The result follows. \square

This extends the result in [23, Section 3.2] to systems with time delayed coupling.

3.2. Stability analysis for global homogeneous coupling

We next consider a special case: $W_2 = \text{circ}(0, 1, \dots, 1)$. That is, all the coupling weights are the same. A straightforward calculation shows that, in this case, for a symmetric n -cluster solution we have

$$\begin{aligned} \lambda_0 &= 0, \\ \lambda_0^{(n)} &= -\frac{N}{n} \sum_{k=0}^{n-1} H'\left(\frac{2\pi k}{n} - \eta\right), \text{ multiplicity } N - n, \\ \lambda_j^{(n)} &= -\frac{N}{n} \sum_{k=0}^{n-1} H'\left(\frac{2\pi k}{n} - \eta\right)(1 - e^{i2\pi kj/n}), \quad p = 1, \dots, n - 1. \end{aligned} \quad (15)$$

where λ_j is as defined in the proof of Theorem 2.

This recovers the result of [50], which was an extension to systems with time delayed coupling of results in [21, Section 6.1], [8, Section 2]. In [50] they made the following observation. The stability of an n -cluster solution (with $n < N$) depends on the number of clusters and the phase differences, not the size of the network. For example, any network with $N = 3m$ (m a positive integer) has a 3-cluster solution with $\psi = 2\pi/3$. The stability of this solution is the same for all networks with $m > 1$.

As discussed in [50, 21], since networks with global homogeneous coupling are unchanged by any rearrangement of the indices, there are many more cluster solutions. For example, consider a network where $N > 2$ is even. When the connection matrix is circulant with different w_k , there is one 2-cluster solution with oscillators $1, 3, 5, \dots, N - 1$ forming one cluster and oscillators $2, 4, \dots, N$ forming the second cluster. For a network with global homogeneous coupling, *any* division of the oscillators into two groups of $N/2$ oscillators is an admissible 2-cluster solution with stability described by (15) with $n = 2$.

3.3. Other types of cluster solutions

If more conditions are put on the coupling matrix then different cluster solutions may occur. For example, consider a 2-cluster solution where the phase differences between adjacent elements is not the same, but is described by

$$\phi_1 = \phi_3 = \dots = \phi_{N-1} = 0, \text{ and } \phi_2 = \phi_4 = \dots = \phi_N = \pi, \quad (16)$$

or

$$\phi_1 = \phi_3 = \dots = \phi_{N-1} = \pi, \text{ and } \phi_2 = \phi_4 = \dots = \phi_N = 0. \quad (17)$$

In this situation the elements group into pairs, so that each element is synchronized with one of its nearest neighbours and one-half period out of phase with its other nearest neighbour. As shown by the next result, these solutions exist under appropriate conditions on the connectivity matrix.

Theorem 3. *For a network with a circulant connectivity matrix, the system (8) admits solutions of the form (16) and (17) if $N = 4p$ for some integer p , and $\sum_{k=0}^{p-1} w_{4k+1} = \sum_{k=0}^{p-1} w_{4k+3}$. These two solutions have the same stability.*

Proof. Applying the constraint condition (9) to (16) or (17), we have that, for some integer p ,

$$\frac{N}{2} \cdot \pi = 2p\pi.$$

Therefore, $N = 4p$, for some integer p .

Substituting solution (16) or (17) into the system (8), we have that

$$\sum_{k=0}^{p-1} w_{4k+1} (H(\pi - \eta) - H(-\eta)) = \sum_{k=0}^{p-1} w_{4k+3} (H(\pi - \eta) - H(-\eta)).$$

To satisfy this for any H , we must have $\sum_{k=0}^{p-1} w_{4k+1} = \sum_{k=0}^{p-1} w_{4k+3}$.

The Jacobian matrix of the linearization of system (8) at (16) is in the

$$\text{form} \quad (L)_{ij} = \begin{cases} (L_1)_{ij}, & \text{if } i \text{ is even,} \\ (L_2)_{ij}, & \text{if } i \text{ is odd.} \end{cases} \quad (18)$$

with $L_1 = \text{circ}(\alpha_0, \dots, \alpha_{N-1})$, and $L_2 = \text{circ}(\beta_0, \dots, \beta_{N-1})$, with $\alpha_k, \beta_k, k = 0, \dots, N-1$ can be explicitly expressed in terms of $w_1, \dots, w_{N-1}, H'(\pi - \eta)$ and $H'(-\eta)$.

The Jacobian matrix of the linearization of system (8) at (17) is in the

$$\text{form} \quad (\hat{L})_{ij} = \begin{cases} (L_2)_{ij}, & \text{if } i \text{ is even,} \\ (L_1)_{ij}, & \text{if } i \text{ is odd.} \end{cases} \quad (19)$$

which is equivalent to L . \square

Remark 3. *Note that, for networks with bi-directional coupling or global homogeneous coupling, the second condition, $\sum_{k=0}^{p-1} w_{4k+1} = \sum_{k=0}^{p-1} w_{4k+3}$, is automatically satisfied if $N = 4p$.*

We were not able to obtain general results about the eigenvalues of L and \hat{L} . Thus, we are not able to make any general conclusions about the stability of solutions (16) and (17). However, we have general expressions for the α_k, β_k :

$$\alpha_0 = \beta_0 = -H'(-\eta) \left(\sum_{k=0}^{p-1} w_{4k+1} + \sum_{k=1}^{p-1} w_{4k} \right) - H'(\pi - \eta) \sum_{k=0}^{p-1} (w_{4k+2} + w_{4k+3}),$$

and, for $k = 1, \dots, N - 1$ and appropriate s values

$$\alpha_k = \begin{cases} w_k H'(\pi - \eta) + B_1(s) (H'(\pi - \eta) - H'(-\eta)), & k = 4s + 1, 4s + 2 \\ w_k H'(-\eta) + B_2(s) (H'(\pi - \eta) - H'(-\eta)), & k = 4s + 3, 4s \end{cases}$$

$$\beta_k = \begin{cases} w_k H'(-\eta) - B_2(s) (H'(\pi - \eta) - H'(-\eta)), & k = 4s + 1, \\ w_k H'(\pi - \eta) - B_2(s) (H'(\pi - \eta) - H'(-\eta)), & k = 4s + 2, \\ w_k H'(\pi - \eta) - B_1(s) (H'(\pi - \eta) - H'(-\eta)), & k = 4s + 3 \\ w_k H'(-\eta) - B_1(s) (H'(\pi - \eta) - H'(-\eta)), & k = 4s \end{cases}$$

where

$$B_1(s) = \left(\sum_{j=s+1}^{p-1} w_{4j+1} - \sum_{j=s+1}^{p-1} w_{4j+3} \right), \quad B_2(s) = \left(\sum_{j=s+1}^{p-1} w_{4j+1} - \sum_{j=s}^{p-1} w_{4j+3} \right).$$

These can be used to calculate the eigenvalues calculated numerically for particular cases. We will do this for the example in the next section.

4. Application to networks of Morris-Lecar oscillators with global synaptic coupling

In this section, we apply our results to a specific network: globally coupled Morris-Lecar oscillators. Since the nondimensional form of Morris-Lecar equation is more convenient to work with, we adopt the dimensionless Morris-Lecar model which is formulated by Rinzel and Ermentrout in [51]. Considering N identical Morris-Lecar oscillators with delayed synaptic coupling, we have the following model

$$\begin{aligned} v_i' &= I_{app} - g_{Ca} m_\infty(v_i) (v_i - v_{Ca}) - g_K w_i (v_i - v_K) \\ &\quad - g_L (v_i - v_L) - \frac{g_{syn}}{N-1} \sum_{j=1, j \neq i}^N s(v_j(t-\tau)) (v_i(t) - E_{syn}), \\ w_i' &= \varphi \lambda(v_i) (w_\infty(v_i) - w_i), \end{aligned} \quad (20)$$

where $i = 1, \dots, N$ and

$$m_\infty(v) = \frac{1}{2}(1 + \tanh((v - \nu_1)/\nu_2)), \lambda(v) = \cosh((v - \nu_3)/2\nu_4),$$

$$w_\infty(v) = \frac{1}{2}(1 + \tanh((v - \nu_3)/\nu_4)), s(v) = \frac{1}{2}(1 + \tanh(10v)).$$

Using the parameter set I from [34, Table 1], when there is no coupling in the network each oscillator has a unique exponentially asymptotically stable limit cycle with period $T \approx 23.87$ corresponding to $\Omega = 0.2632$.

Parameter	Name	value
v_{Ca}	Calcium equilibrium potential	1
v_K	Potassium equilibrium potential	-0.7
v_L	Leak equilibrium potential	-0.5
g_K	Potassium ionic conductance	2
g_L	Leak ionic conductance	0.5
φ	Potassium rate constant	$\frac{1}{3}$
ν_1	Calcium activation potential	-0.01
ν_2	Calcium reciprocal slope	0.15
ν_3	Potassium activation potential	0.1
ν_4	Potassium reciprocal slope	0.145
g_{Ca}	Calcium potential conductance	1
I_{app}	Applied current	0.09

Table 1: Parameters used in system (20) [34, Table 1]

4.1. Phase model analysis

The calculation of the phase model interaction function, H , described in section 2, may be carried out numerically. We used the numerical simulation package XPPAUT [52] to do this for model (20) with $\tau = 0$, and to calculate a finite number of terms in the Fourier series approximation for H . This gives an explicit approximation for H :

$$H(\phi) \approx a_0 + \sum_{k=1}^K (a_k \cos(k\phi) + b_k \sin(k\phi)). \quad (21)$$

The first nine terms of Fourier coefficients are shown in Table 2. Figure 1 shows the plot of the interaction function (red solid), H , together with the

approximations using one (black solid) and 20 terms (green dashed) of Fourier Series. Obviously, the one term approximation is not enough to explain the behavior of H . However, the 20-term approximation is indistinguishable with the numerically calculated H . Therefore, we adopt the 20-term approximation for subsequent calculations.

k	a_k	b_k	k	a_k	b_k
0	-2.0214064	0	5	-0.01054942	0.010251001
1	1.994447	-0.93897837	6	-0.002131111	0.0046384884
2	0.010604496	0.27575842	7	9.9814584e-05	0.0013808256
3	-0.051657807	0.042355601	8	0.00015646126	7.391713e-05
4	-0.029127343	0.01801952	9	-8.1846403e-05	-0.00024995379

Table 2: Fourier coefficients of the interaction function for model (20).

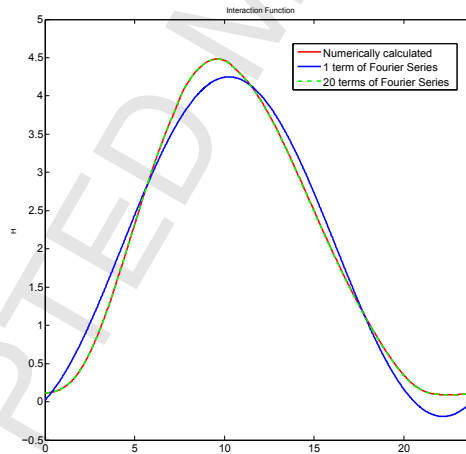


Figure 1: Interaction function for model (20) and the approximations using 1 and 20 terms of Fourier Series

With the explicit approximation for H (21) and the value of the coefficients a_j, b_j , we can determine the asymptotic stability of any possible

symmetric cluster states for any N using the eigenvalues calculated in the last section. In this section, we consider two coupling matrices

$$W_1 = \text{circ}(0, 1, \frac{1}{2}, \frac{1}{3}, \dots, \frac{1}{2}, 1), \text{ bi-directional, distance dependent} \quad (22)$$

$$W_2 = \text{circ}(0, 1, 1, \dots, 1), \text{ global homogeneous.} \quad (23)$$

With the coupling matrices W_1 and W_2 , various values of ϵ and the time delay τ , we used our phase model results above to predict the stability of all possible symmetric cluster solutions for $N = 2, \dots, 10$. The results are shown in Tables 3 and 4. Note that, in all cases, for $\tau = 0$ only the synchronous (1-cluster) solution is asymptotically stable. However, increasing τ may destabilize this solution and/or stabilize other cluster solutions. In particular, for some values of τ multistability between different cluster solutions occurs. Further, changing the coupling matrix from W_1 (bi-directional, distance dependent coupling) to W_2 (global homogeneous coupling) can cause significant changes in stability. For example, when N is a prime number, the only clustered states are splay states (rotating waves). With W_2 all the splay states for a given N have the same stability (Table 4), while with W_1 splay states corresponding to different ψ can have quite different stabilities (Table 3).

4.2. Numerical studies

Numerical continuation studies of the full model (20) were carried out in DDE-BIFTOOL [53] in MATLAB. This package allows one to compute branches of periodic orbits and their stability as a parameter is varied. Using the delay as a continuation parameter, we used this package to compute the stability of all possible symmetric cluster solutions for $N = 2, 3, \dots, 10$ with the two different coupling matrices W_1, W_2 and four different values of ϵ , $\epsilon = 0.001, 0.01, 0.05, 0.1$. These results indicated that the phase model prediction is accurate up to $\epsilon = 0.01$. The results for $\epsilon = 0.01, 0.05$ are shown in Tables 3 and 4. In particular we observe that the synchronous solution is stable for approximately the same τ -interval in all networks (cf. Corollary 1) and the 2-cluster solution is stable for approximately the same τ -interval in all networks with $N > 2$ and even (cf. Corollary 2).

Using dde23 in MATLAB, we are able to numerically simulate the solution for larger sizes of networks. In the following, we show several numerical simulations that verify the predictions of the phase model for the case of a network with $N = 140$ oscillators. This network admits 1-cluster, 2-cluster,

N	n	ψ	Phase model prediction	Full model	
				$\epsilon = 0.01$	$\epsilon = 0.05$
4	1	0	$(0, 1.53) \cup (14.28, 23.87)$ $(2.47, 10.46)$	$(0, 1.44) \cup (12.75, 23.87)$	$(0, 1.62) \cup (8.83, 23.87)$ $(1.68, 9.32) \cup (17.47, 23.87)$ $(0.226) \cup (6.86, 12.36)$
	4	π	$(0.57, 3.22) \cup (8.69, 14.69)$	$(0.296) \cup (8.36, 14.16)$	
	5	0	$(0, 1.53) \cup (14.28, 23.87)$ $(1.26, 2.48) \cup (10.84, 13.46)$ $(1.66, 3.66) \cup (4.26, 13.09)$	$(0, 1.41) \cup (12.51, 23.87)$ $(0.2, 2.21) \cup (10.31, 12.71)$ $(1.513, 12.61)$	$(0, 1.67) \cup (8.19, 23.87)$ $(0, 1.51) \cup (8.71, 10.81)$ $(0.70, 11.49)$
6	1	0	$(0, 1.53) \cup (14.28, 23.87)$ $(2.64, 9.45)$ $(0.41, 12.91)$	$(0, 1.41) \cup (12.31, 23.87)$ $(2.30, 9.10)$	$(0, 1.70) \cup (7.82, 23.87)$ $(1.58, 7.79) \cup (16.59, 27.31)$
	3	π	$(0.58, 0.87) \cup (12.32, 14.10)$	$(0, 4.19) \cup (5.30, 11.40) \cup (17.41, 20.9) \cup (22.31, 23.87)$ $(0, 1.51) \cup (12.01, 13.11)$	
	6	$\frac{4\pi}{3}$	$(0, 1.53) \cup (14.28, 23.87)$ $(12.82, 13.86)$	$(0, 1.49) \cup (12.19, 23.87)$ $(0, 1.21) \cup (12.11, 12.81)$	$(0, 1.11) \cup (9.21, 10.31)$ $(0, 1.68) \cup (7.52, 23.87)$ $(0, 1.10) \cup (8.82, 9.82)$
7	1	0	$(2.33, 4.37) \cup (7.59, 13.83)$ $(2.51, 3.45) \cup (4.04, 4.93) \cup (5.48, 5.96) \cup (7.47, 13.13)$	$(0.51, 3.91) \cup (7.21, 13.11)$ $(2.51, 4.91) \cup (6.91, 12.11)$	$(0, 2.71) \cup (5.81, 11.11)$ $(1.70, 3.81) \cup (5.70, 10.82)$
	7	$\frac{2\pi}{7}$	$(0, 1.53) \cup (14.28, 23.87)$ $(2.63, 9.53)$	$(0, 1.44) \cup (12.04, 23.87)$ $(2.25, 9.05)$	$(0, 1.74) \cup (7.27, 23.87)$ $(1.55, 7.45) \cup (15.73, 23.87)$
	8	π	$(1.71, 3.22) \cup (8.09, 14.57)$ $(13.34, 13.95)$ $(3.96, 13.13)$	$(0.31, 2.81) \cup (8.11, 13.71)$ $(0, 1.01) \cup (12.31, 12.71)$ $(3.41, 12.41)$	$(0, 1.80) \cup (6.21, 11.20)$ $(0, 1.00) \cup (8.52, 9.42)$ $(0.11, 0.71) \cup (2.61, 10.82)$
9	1	0	$(0, 1.53) \cup (14.28, 23.87)$ $(0.41, 5.04) \cup (8.08, 12.93)$	$(0, 1.66) \cup (11.93, 23.87)$ $(0.41, 4.61) \cup (7.71, 12.41)$	$(0, 1.73) \cup (7.06, 23.87)$ $(0, 3.30) \cup (5.80, 10.60) \cup (16.61, 19.31)$
	3	$\frac{4\pi}{9}$	$(13.46, 14.01)$		
	9	$\frac{2\pi}{9}$	$(2.50, 2.57) \cup (9.81, 13.94)$ $(2.90, 3.77) \cup (8.08, 11.38)$	$(0.41, 2.61) \cup (9.11, 13.01)$ $(2.61, 4.01) \cup (7.51, 11.01)$	$(0, 1.71) \cup (6.51, 10.41)$ $(1.60, 3.12) \cup (5.92, 8.81)$

Table 3: Comparison of phase model prediction of τ -intervals of asymptotic stability for n -cluster solution with numerical of the full model. The coupling matrix is W_1 . Other parameter values are given in Table 1.

N	n	Phase model prediction	Full model	
			$\epsilon = 0.01$	$\epsilon = 0.05$
2	1	$(0, 1.53) \cup (14.28, 23.87)$	$(0, 1.46) \cup (13.56, 23.87)$	$(0, 1.43) \cup (11.53, 23.87)$
	2	$(2.35, 13.46)$	$(2.23, 13.43)$	$(1.92, 13.32)$
3	1	$(0, 1.53) \cup (14.28, 23.87)$	$(0, 1.48) \cup (13.09, 23.87)$	$(0, 1.52) \cup (9.53, 23.87)$
	3	$(0.41, 13.74)$	$(0.50, 13.40)$	$(0, 12.6)$
	1	$(0, 1.53) \cup (14.28, 23.87)$	$(0, 1.47) \cup (12.57, 23.87)$	$(0, 1.70) \cup (8.11, 23.87)$
4	2	$(2.73, 9.19)$	$(2.41, 8.91)$	$(1.71, 7.71) \cup (17.53, 23.87)$
	4	$(1.93, 3.22) \cup (8.69, 14.47)$	$(0.97, 2.87) \cup (8.47, 13.97)$	$(0, 1.96) \cup (6.97, 12.27)$
5	1	$(0, 1.53) \cup (14.28, 23.87)$	$(0, 1.49) \cup (11.99, 23.87)$	$(0, 1.79) \cup (7.22, 23.87)$
	5	$(1.57, 2.69) \cup (9.76, 13.20)$	$(0.93, 2.23) \cup (9.13, 12.43)$	$(0, 1.32) \cup (6.13, 10.42)$
6	1	$(0, 1.53) \cup (14.28, 23.87)$	$(0, 1.46) \cup (11.56, 23.87)$	
	2	$(2.73, 9.19)$	$(2.30, 8.51)$	$(1.48, 6.29) \cup (15.0, 23.19)$
	3	$(0.41, 4.83) \cup (8.29, 12.79)$	$(0.28, 4.18) \cup (7.98, 11.98)$	$(0, 3.03) \cup (5.54, 9.83) \cup (15.94, 18.44)$
7	6	$(12.26, 13.86)$	$(11.96, 12.72)$	$(0, 0.91) \cup (9.21, 9.91)$
	1	$(0, 1.53) \cup (14.28, 23.87)$	$(0, 1.49) \cup (11.01, 23.87)$	$(0, 1.94) \cup (6.10, 23.87)$
8	7	$(12.47, 13.54)$	$(11.92, 12.32)$	$(0, 0.92) \cup (8.52, 9.32)$
	1	$(0, 1.53) \cup (14.28, 23.87)$	$(0, 1.50) \cup (10.70, 23.87)$	$(0, 2.00) \cup (5.70, 23.87)$
9	2	$(2.73, 9.19)$	$(2.22, 8.22)$	$(1.34, 5.44) \cup (13.24, 20.34)$
	4	$(1.94, 3.22) \cup (8.69, 9.35) \cup (12.37, 14.47)$	$(0.53, 2.63) \cup (7.53, 8.43) \cup (11.13, 13.03) \cup (22.63, 23.23)$	$(0, 1.33) \cup (5.13, 6.03) \cup (7.33, 9.14) \cup (19.04, 20.34) \cup (20.94, 21.64)$
	8	All unstable	$(0, 1.35) \cup (6.15, 6.95) \cup (16.36, 17.56)$	$(0, 0.95) \cup (7.95, 8.75)$
9	1	$(0, 1.53) \cup (14.28, 23.87)$	$(0, 1.48) \cup (10.22, 23.87)$	$(0, 2.08) \cup (5.40, 23.87)$
	3	$(0.41, 4.83) \cup (8.29, 12.79)$	$(0.19, 4.00) \cup (7.49, 11.29) \cup (21.39, 23.87)$	$(0, 2.78) \cup (5.00, 8.29) \cup (14.39, 15.80) \cup (17.50, 22.40)$
9	9	$(13.30, 13.65)$	$(0.56, 1.16) \cup (11.36, 11.96)$	$(0, 0.96) \cup (7.56, 8.37)$

Table 4: Comparison of phase model prediction of τ -intervals of asymptotic stability for n -cluster solution with numerical of the full model. The coupling matrix is W_2 . Other parameter values are given in Table 1.

n	ψ	Stability w.r.t. τ	
		W_1	W_2
1	0	$(0, 1.52) \cup (14.28, 23.87)$	$(0, 1.52) \cup (14.28, 23.87)$
2	π	$(2.73, 9.19)$	$(2.73, 9.19)$
5	$\frac{2\pi}{5}, \frac{8\pi}{5}$ $\frac{4\pi}{5}, \frac{6\pi}{5}$	$(1.52, 2.61) \cup (10.78, 12.55)$ $(1.61, 2.81) \cup (6.21, 7.77) \cup (10.03, 12.55)$	$(1.57, 2.69) \cup (10.03, 12.54)$
7	$\frac{2\pi}{7}, \frac{12\pi}{7}$ $\frac{4\pi}{7}, \frac{10\pi}{7}$ $\frac{6\pi}{7}, \frac{8\pi}{7}$	$(12.77, 13.29)$ $(8.13, 9.81) \cup (11.12, 13.28)$ $(8.45, 9.88) \cup (11.11, 13.13)$	$(12.47, 13.28)$
10	$\frac{\pi}{5}, \frac{9\pi}{5}$ $\frac{3\pi}{5}, \frac{7\pi}{5}$	All unstable $(7.85, 7.86) \cup (11.80, 12.62)$	All unstable

Table 5: Phase model prediction of intervals of τ where stable 1-, 2-, 5-, 7-, and 10-cluster solutions exist. The network has 140 oscillators and the coupling matrix W_1 or W_2 .

5-cluster, 7-cluster, 10-cluster, 14-cluster, 35-cluster, 70-cluster, and 140-cluster solutions. From the phase model analysis, we are able to predict the stability regions for all the cluster states. Table 5 summarize the stability intervals with respect to τ for the first five cluster types.

The phase model predicts that, for bidirectional coupling, there should be four stable 5-cluster solutions when $\tau = 12$ corresponding to $\psi = \frac{k\pi}{5}$, $k = 1, 2, 3, 4$. In these 5-cluster solutions, the clusters are the same and given by

$$\begin{aligned}
 C_1 &= \{1, 6, 11, \dots, 136\}, \\
 C_2 &= \{2, 7, 12, \dots, 137\}, \\
 &\vdots \\
 C_5 &= \{5, 10, 15, \dots, 140\}.
 \end{aligned}$$

but each solution has a different cluster ordering. The ordering is $C_1 - C_2 - C_3 - C_4 - C_5$ with $\psi = 2\pi/5$ (see Figure 2 (a)), $C_1 - C_4 - C_2 - C_5 - C_3$ with $\psi = 4\pi/5$ (see Figure 2 (b)), $C_1 - C_3 - C_5 - C_2 - C_4$ with $\psi = 6\pi/5$ (see Figure 2 (c)) and $C_1 - C_5 - C_4 - C_3 - C_2$ with $\psi = 8\pi/5$ (see Figure 2 (d)). Note that in Figure 2 we reorder the indices so that oscillators that belong to the same cluster are plotted together.

Now consider the 7-cluster solution with connection matrix W_1 . The phase model predicts that when $\tau = 13$ there exist six stable 7-cluster solu-

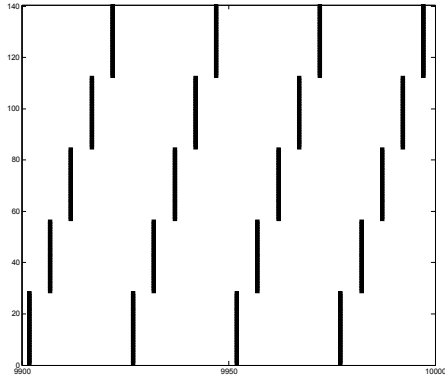
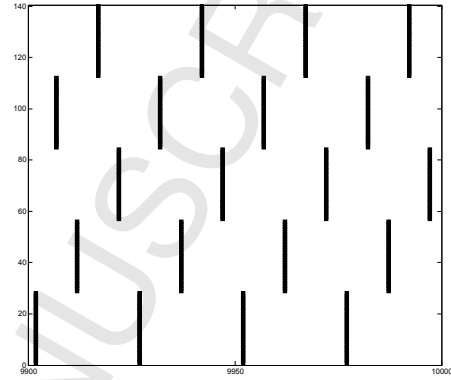
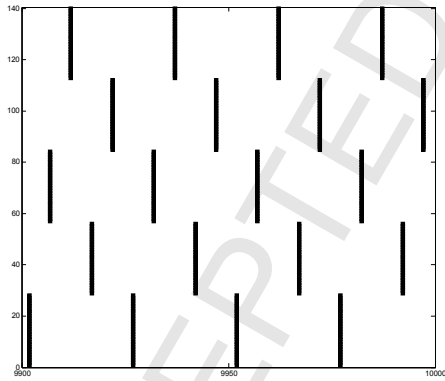
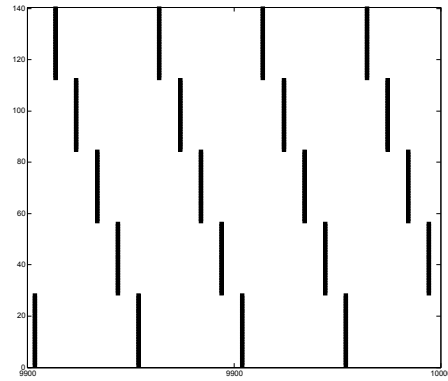
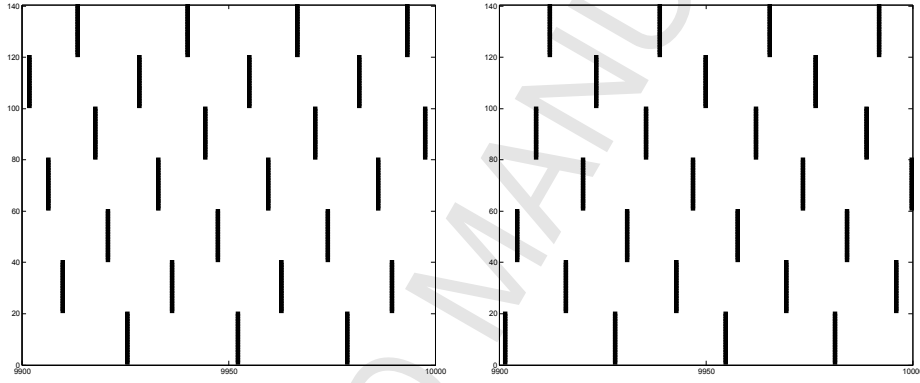
(a) $\psi = 2\pi/5$ (b) $\psi = 4\pi/5$ (c) $\psi = 6\pi/5$ (d) $\psi = 8\pi/5$

Figure 2: Raster plots showing a stable 5-cluster solutions in a network with $N = 140$ neurons and bi-directional coupling (connectivity matrix W_1). $\tau = 12$ and $\epsilon = 0.001$ all other parameters values are given in Table 1. (a) $\psi = 2\pi/5$, cluster ordering $C_1 - C_2 - C_3 - C_4 - C_5$ (b) $\psi = 4\pi/5$, cluster ordering $C_1 - C_4 - C_2 - C_5 - C_3$ (c) $\psi = 6\pi/5$, cluster ordering $C_1 - C_3 - C_5 - C_2 - C_4$ (d) $\psi = 8\pi/5$, cluster ordering $C_1 - C_5 - C_4 - C_3 - C_2$

tions with clusters:

$$\begin{aligned} C_1 &= \{1, 8, 15, \dots, 134\}, \\ C_2 &= \{2, 9, 16, \dots, 135\}, \\ &\vdots \\ C_7 &= \{7, 14, 21, \dots, 140\}. \end{aligned}$$



(a) $\psi = 8\pi/7$

(b) $\psi = 6\pi/7$

Figure 3: Raster plots showing stable 7-cluster solutions with $\tau = 13$, $\epsilon = 0.01$ in a network with $N = 140$ neurons and bi-directional coupling (connectivity matrix W_1). (a) $\psi = \frac{6\pi}{7}$, cluster ordering $C_1 - C_6 - C_4 - C_7 - C_5 - C_3$. (b) $\psi = \frac{8\pi}{7}$, cluster ordering $C_1 - C_3 - C_5 - C_7 - C_2 - C_4 - C_6$.

For $\psi = \frac{6\pi}{7}$, the cluster ordering is $C_1 - C_6 - C_4 - C_2 - C_7 - C_5 - C_3$ (see Figure 3(a)), while for $\psi = \frac{8\pi}{7}$, the cluster ordering is $C_1 - C_3 - C_5 - C_7 - C_2 - C_4 - C_6$ (see Figure 3(b)). In Figure 3, we reorder the oscillator indices so that oscillators that belong to the same cluster are plotted together. We were unable to find the other 7-cluster solutions numerically.

Remark 4. We have observed other types of stable cluster solutions. For example, Figure 4 shows solutions of the type (16) and (17) which appear to

be stable. With $N = 8$ and bidirectional coupling in (22), the phase model predicts that the solutions of the type (16) and (17) are unstable for all τ when $\epsilon > 0$, and stable for $\tau \in (1.5, 2.0] \cup (13.8, 14.1)$ when $\epsilon < 0$. This prediction is consistent the numerically observed solution which occurs for $\epsilon = -0.01$, and $\tau = 2$.

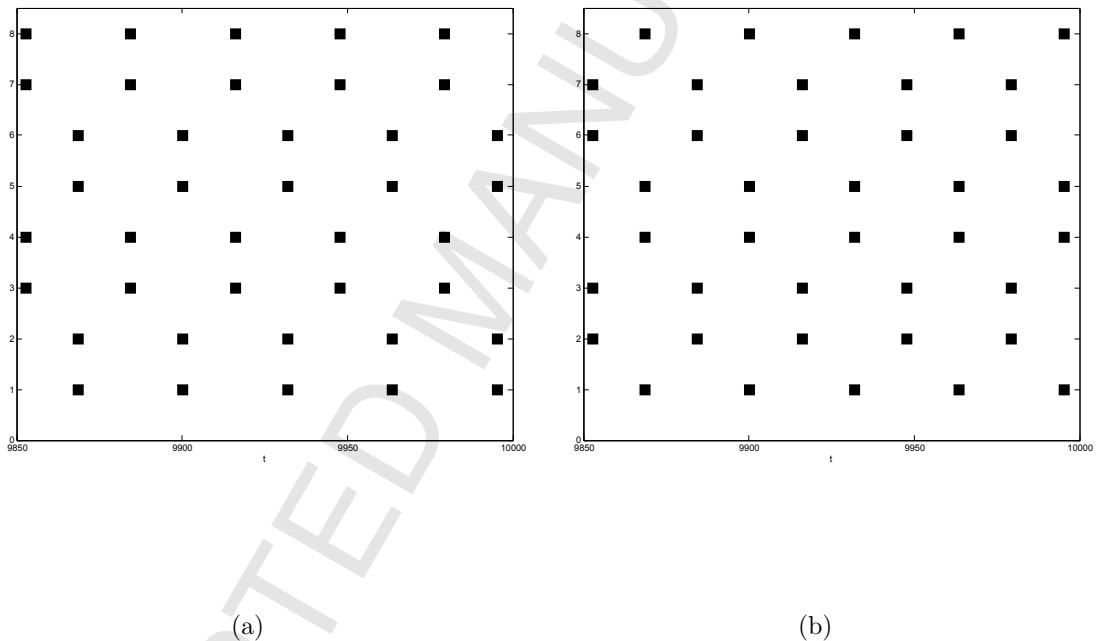


Figure 4: 2-cluster solutions of the form (16) (a) and (17) (b) for $N = 8$, $\epsilon = -0.01$, $\tau = 2$ and connectivity matrix W_1 .

From Tables 3 and 4 it is clear that the system exhibits multistability for a large range of τ values. To further investigate the multistability, we carried out numerical simulations of the model (20) with $N = 6$ and coupling matrix W_1 using XPPAUT [52]. We start with constant initial conditions ($v_i(t) = v_{i0}$, $w_i(t) = w_{i0}$, $-\tau \leq t \leq 0$), and apply a small perturbation to the input current of one or more neurons during the simulation. The perturbations could cause switching between two different cluster types or

between different realizations of the same cluster type. Figure 5 show two examples, where the dark bars indicate when a particular neuron spikes. When $\tau = 8$, both the 2-cluster solutions and 3-cluster solutions are stable. Figure 5 (a) shows that when $\tau = 8$, a perturbation to neurons 1, 2, 3, 4 and 6 for $600 \leq t \leq 650$ switches the networks from a 3-cluster solution (with clusters (1, 4), (2, 5) and (3, 6)) to a 2-cluster solution (with clusters (1, 3, 5), and (2, 4, 6)). Figure 5 (b) shows when $\tau = 8$, a perturbation to neuron 2, 4, 5, and 6 for $600 \leq t \leq 650$ switches the network from a 3-cluster solution with clusters ordering (1, 4)-(3, 6)-(2, 5) to a 3-cluster solution with clusters ordering (1, 4)-(2, 5)-(3, 6).

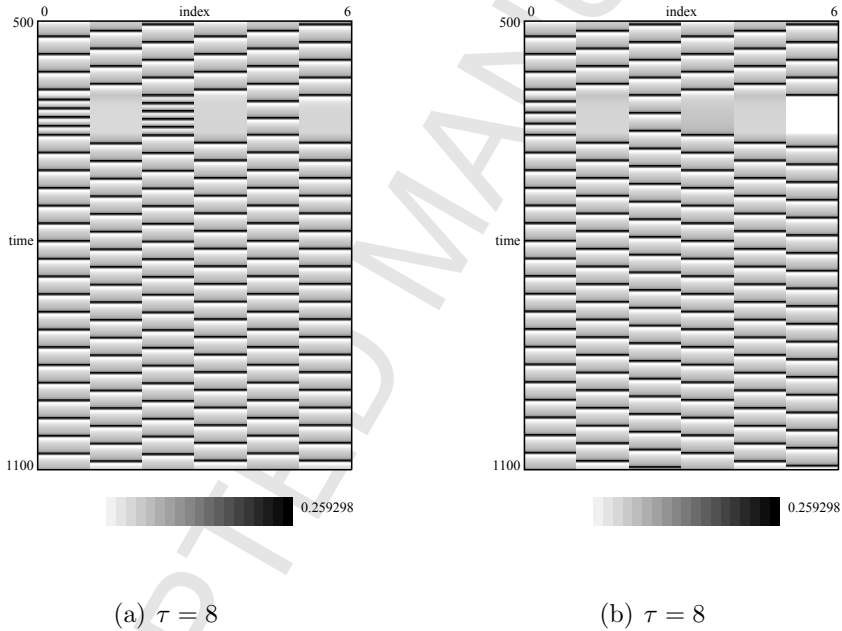


Figure 5: Numerical simulations showing multistability in a 6 neuron network with bidirectional coupling (22). (a) Switching from a 3-cluster solution to a 2-cluster solution. (b) Switching from a 3-cluster solution to a 3-cluster solution. $\tau = 8$ and $\epsilon = 0.001$. All other parameters are given in Table 1.

5. Persistence under symmetry breaking.

By the weakly connected theory, the phase model analysis should persist under ϵ -perturbation of the original model. From the steps of phase model

reduction, we can see that if we perturb the connectivity matrix $W = (w_{ij})$ as $\tilde{W} = w_{ij}(1 + \epsilon m_{ij})$, the ϵ -perturbation term will finally add to $O(\epsilon^2)$ term in the phase model (6). A similar conclusion is obtained if we perturb the time delay τ as $\tau_{ij} = \tau(1 + \epsilon \sigma_{ij})$. Here $M = (m_{ij})$, and $S = (\sigma_{ij})$ are $N \times N$ matrices with elements which are $O(1)$ with respect to ϵ . τ_{ij} represents transmission time from the j th oscillator to the i th oscillator. Note that, after the perturbation, system (2) no longer possesses any symmetry. To $O(\epsilon)$ the symmetry persists, however. We thus expect that, for ϵ sufficiently small, the analysis of section 3 should still predict the behaviour of the system.

In order to investigate the effect of the ϵ -perturbation on the connectivity matrix and time delay, we carried out sets of numerical simulations. For each set, we compare the original model with W and τ , to a model with \tilde{W} and τ , and a model with W and τ_{ij} . Take $N = 6$, $W = circ\{0, 1, 1/2, 1/3, 1/2, 1\}$, and m_{ij}, σ_{ij} to be random numbers between 0 and 1. We simulate the original model and two perturbed models with $\tau = 1, \dots, 15$, and $\epsilon = 0.001, 0.01, 0.05, 0.1$, respectively. From the simulation results, we see that for $\epsilon = 0.001, 0.01, 0.05$ the behavior of the perturbed models are the same as the unperturbed one for large time t . More accurately, the perturbed models take longer to settle at steady states than the original model. For $\epsilon = 0.1$, the behavior of unperturbed model almost captures the behavior of the perturbed ones. However, the system is sensitive to the τ values where steady states switch stability. Therefore, we conclude that for a network with 6 oscillators, the analysis of the original model is valid under perturbation with ϵ up to 0.05. Furthermore, for a network with N oscillators, the analysis of the system (2) should persist under sufficiently small ϵ -perturbation.

6. Conclusions and future work

In this paper, we studied a general system of identical oscillators with global circulant, time-delayed coupling and showed that clustering behavior is a quite prevalent pattern of solution. We classified different clusters by the phase differences between neighboring oscillators, and investigated the existence and linear stability of clustering solutions. We focussed on symmetric cluster solutions, where the same number of oscillators belong to each cluster. In particular, we showed that certain symmetric cluster solutions exist for any type of oscillator and any value of the delay – their existence depends only on the presence of circulant coupling. We gave a complete analysis of the linear stability of these cluster solutions. In the case of global

τ	PMP	$\epsilon = 0.001$			$\epsilon = 0.01$			$\epsilon = 0.05$			$\epsilon = 0.1$		
		original	\bar{W}	$\bar{\tau}$	original	\bar{W}	$\bar{\tau}$	original	\bar{W}	$\bar{\tau}$	original	\bar{W}	$\bar{\tau}$
1	1C/3C	1C	1C	1C	NC	NC	NC	NC	NC	NC	6C	NC	NC
2	3C	6C	6C	6C	3C	3C	3C	2C	2C	2C	2C	2C	2C
3	2C/3C	2C	2C	2C	3C	3C	3C	2C	2C	2C	2C	2C	2C
4	2C/3C	2C	2C	2C	2C	2C	2C	2C	2C	2C	2C	2C	2C
5	2C/3C	3C	3C	3C	2C	2C	2C	2C	2C	2C	2C	2C	2C
6	2C/3C	2C	2C	2C	2C	2C	2C	2C	2C	2C	2C	2C	NC
7	2C/3C	2C	2C	2C	2C	2C	2C	2C	2C	2C	1C	1C	1C
8	2C/3C	2C	2C	2C	2C	2C	2C	3C	3C	NC	1C	1C	1C
9	2C/3C	3C	3C	3C	2C	2C	2C	NC	1C	1C	1C	1C	1C
10	3C	3C	3C	3C	1C	1C	1C	1C	1C	1C	1C	1C	1C
11	3C	NC	NC	NC	NC	NC	NC	1C	1C	1C	1C	1C	1C
12	3C	NC	NC	NC	NC	NC	NC	1C	1C	1C	1C	1C	1C
13	3C/6C	6C	6C	6C	1C	1C	1C	1C	1C	1C	1C	1C	1C
14	6C	6C	6C	6C	1C	1C	1C	1C	1C	1C	1C	1C	1C
15	1C	1C	1C	1C	1C	1C	1C	1C	1C	1C	1C	2C	NC

Table 6: Comparison of the original model and the two perturbed models for $\tau = 1, 2, \dots, 15$ with $N = 6$. The first column shows the stable cluster solutions predicted by the phase model for each τ .

bidirectional coupling and global homogeneous coupling, more details about how the stability changes with parameters could be obtained using the symmetry. Our results extend some previous work [21, Section 6.1], [8, Section 2], [23, Section 3.2] to the case with time delayed and more general circulant coupling.

Further exploration was done through numerical continuation and numerical simulation studies of a specific example: circulantly coupled Morris-Lecar oscillators. We considered both small ($N = 6, 8$) and large ($N = 140$) networks and two types of coupling: homogeneous and bi-directional, distance dependent. As expected, the numerical studies agree with the theoretical predictions of the phase model, so long as the strength of the coupling (ϵ) was sufficiently small. For the parameters we explored this was $\epsilon \lesssim 0.05$. In all cases we explored, the 1-cluster (synchronous) solution was the only asymptotically stable solution when there was no delay in the system. For non-zero delay, this solution could become unstable and other cluster solutions became stable. We found ranges of the delay for which the system exhibits a high degree of multistability. The multistability persisted even under perturbations of the coupling matrix (W), and time delay (τ) which break the symmetry of the model. The perturbed model agreed with the phase model prediction for $\epsilon \lesssim 0.01$.

Delay-induced multistability has been observed in Hopfield neural networks (e.g., [54, 55]), in networks of spiking neurons [56, 57, 58], and even in experimental systems [59], where it has been postulated as a potential mechanism for memory storage. The multistability we observe has similar potential. It also provides the network with a simple way to respond differently to different inputs, without changing synaptic weights. Switching between solutions with a different number of clusters changes the network average frequency, which could then change how the network affects downstream neurons.

Multistability between different cluster solutions also has potential connections with the concept of neural assemblies. A neural assembly is a group of neurons which transiently act together to achieve a particular purpose [60, 61, 62]. A network with multiple stable cluster solutions provides a basic model for such behaviour. As the system switches between different cluster solutions different neurons become synchronized with each other. As we have shown, it is possible for a network to possess multiple stable solutions with the same number of clusters but with different groupings of the neurons.

In the future, it would be interesting to pursue a variety of the directions suggested by our results. The switching of stability of the cluster solutions as the delay is varied should be associated with bifurcations in the model. In the case of a system with two neurons it has been shown that delay induced stability changes of the 1- and 2- cluster solutions are associated with pitchfork and saddle-node bifurcations in the phase model and sometimes involve other phase-locked solutions [34]. It would be interesting to explore the delay induced bifurcations that occur in our network model. Preliminary numerical investigations of the phase model (not shown) indicate a quite complex bifurcation structure. It would also be interesting to compute the bifurcation structure of the cluster solutions in the (τ, ϵ) parameter plane to get a better understanding of the limits of the validity of the phase model.

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