Preprints, 12th IFAC Workshop on Time Delay Systems
June 28-30, 2015. Ann Arbor, MI, USA

Phase models and clustering in networks of oscillators with delayed, all-to-all coupling

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Abstract: We consider a general model for a network of all-to-all coupled oscillators with time delayed connections. We reduce the system of delay differential equations to a phase model where the time delay enters as a phase shift. By analyzing the phase model, we study the existence and stability of cluster solutions. These are solutions where the oscillators divide into groups; oscillators within a group are synchronized, while oscillators in different groups are phase-locked with a fixed phase difference. We show that the time delay can lead to the multistability between different cluster states. Analytical results are compared with numerical studies of the full system of delay differential equations.

Keywords: Time delay, neural network, oscillators, synchronization, stability.

1. INTRODUCTION

Many biological and physical systems can be studied using coupled oscillator models, for example neural networks (Hansel et al., 1993), laser arrays (Winful and Wang, 1988), flashing of fireflies (Mirollo and Strogatz, 1990), and movement of a slime mold (Takamatsu et al., 2000). A fundamental question about these systems is whether the elements 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 subgroups. Each subgroup consists of fully synchronized oscillators, and different subgroups oscillate with a fixed phase difference. Symmetric clustering refers to the situation when all the subgroups are the same size while non-symmetric clustering means the subgroups have different sizes.

Phase models have been used to study the behaviour of networks of coupled oscillators beginning with the work of Kuramoto (1984). While they have been used to study a variety of phenomena, especially in neural networks (Ermentrout and Kopell, 1984, 1991; Ermentrout, 1996; Galán, 2009; Hansel et al., 1993), Okuda (1993) was the first to study clustering behaviour using this tool. Considering a phase model for a network of arbitrary size with all-to-all coupling, Okuda (1993) established general criteral for the stability of all possible symmetric cluster solutions as well as some non-symmetric cluster solutions. He showed that these results gave a good prediction of stability for a variety of model networks. Recently, similar results have been obtained for networks with nearest-neighbour coupling (Miller et al., 2015). Phase model analysis has been extensively used to study phase-locking in pairs of model (Kopell and Ermentrout, 2002; Saraga et al., 2006) and experimental (Mancilla et al., 2007) neurons. More recently it has been used to study clustering in model (Kilpatrick and Ermentrout, 2011) and experimental (Galán et al., 2006) neural networks.

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 there is a delay due to conduction of electrical activity along an axon or a dendrite and due to processing time at the synapse(Crook et al., 1997; Kopell and Ermentrout, 2002). While much work has been devoted to the study of the effect of time delays in neural networks, the majority of this work has focussed on systems where the neurons are excitatory not oscillatory, (e.g., Burić et al. (2005); Dahlem et al. (2009); Panchuk et al. (2013)), pairs of oscillators (e.g., Campbell and Kobelevskiy (2012); Kopell and Ermentrout (2002); Schuster and Wagner (1989)) or synchronization (e.g., Crook et al. (1997); Orosz (2012, 2014a)). We note that extensive work has been done on networks of Stuart-Landau oscillators with delayed coupling (e.g., Choe et al. (2010); Dahms et al. (2012)) where the model for the individual oscillators is the normal form for a Hopf bifurcation and thus the system is often amenable to direct analysis. Recent work has developed new approaches to determine the Floquet multipliers, and hence stability, of cluster solutions in delayed neural oscillator networks Orosz (2014a,b). There is also a vast literature on time delays in artificial neural networks which we do not attempt to cite here.

In this paper, we investigate the effect of time delays in the coupling on the clustering behavior of networks of all-to-all coupled identical oscillators, using the phase model approach. The advantage of this approach over Floquet analysis is that one can often draw conclusions which are independent of the particular oscillator model and the size of the network. The disadvantage is that phase model analysis requires weak coupling.

The plan for our article is as follows. In section 2, we review how to reduce the differential equation model for our network to a phase model. In section 3, we analyze the phase model to investigate the existence and stability of symmetric cluster states and draw some conclusions which depend only on the connectivity structure of the network. In section 4, we apply our results to a specific example: a network of all-to-all coupled Morris-Lecar oscillators with delayed synaptic coupling. A comparison of numerical results for the full model and the phase model analysis is given. In section 5, we discuss some biological implications of our results and directions for further investigation.

2. REDUCTION TO 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 begin by considering the model for a single oscillator. This is a system of ordinary differential equations

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

which admits an exponentially asymptotically stable periodic orbit, denoted by $\hat{X}(t)$, with period $T = \frac{2\pi}{\Omega}$. Linearizing the model (1) about the periodic solution $\hat{X}(t)$ we obtain

$$\frac{dX}{dt} = DF(\hat{X}(t))X, \tag{2}$$

and its adjoint system

$$\frac{dZ}{dt} = -[DF(\hat{X}(t))]^T Z. \tag{3}$$

Here $DF(\hat{X}(t))$ represents the Jacobian matrix of F with respect to X, evaluated at $\hat{X}(t)$. Denote by $Z = \hat{Z}(t)$ the unique periodic solution of the adjoint system (3) 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

$$\frac{dX_i}{dt} = F(X_i(t)) + \epsilon \sum_{j=1, j\neq i}^{N} G(X_i(t), X_j(t-\tau)),\ i = 1, \cdots, N. \tag{4}$$

Here G describes the coupling behavior and ϵ is referred to as the coupling strength. When ϵ is sufficiently small, we can apply the theory of weakly coupled oscillators to reduce (4) to a phase model (Ermentrout and Terman, 2010; Hoppensteadt and Izhikevich, 1997). While there are no general results on how small ϵ should be, it can been quantified for particular models. See section 4.2.

How the time delay enters into the phase model depends on the size of the delay relative to other time constants in the model. It has been shown (Ermentrout, 1994; Izhikevich, 1998; Kopell and Ermentrout, 2002) that if the delay is such that $\Omega\tau = O(1)$ with respect to the coupling strength ϵ then the appropriate model is

$$\frac{d\phi_i}{dt} = \Omega + \epsilon \sum_{j=1, j\neq i}^{N} H(\phi_j - \phi_i - \eta),\ i = 1, 2, \cdots, N, \tag{5}$$

where $\eta = \Omega\tau$. That is, the delay enters as a phase lag. The interaction function H is a 2π-periodic function which satisfies

$$H(\phi) = \frac{1}{T}\int_0^T \hat{Z}(s)G(\hat{X}(s+\phi))ds.$$

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

We have focussed on the case with no self-coupling, which leads to the $j \neq i$ condition in the sum above. However, the model (5) is included in the more general model

$$\frac{d\phi_i}{dt} = \tilde{\Omega} + \epsilon \sum_{j=1}^{N} H(\phi_j - \phi_i - \eta),\ i = 1, 2, \cdots, N. \tag{6}$$

For the model with no self-coupling, $\tilde{\Omega} = \Omega - H(-\eta)$, while for the model with self-coupling $\tilde{\Omega} = \Omega$. We will work with (6) in the following. Note that this model has S_N symmetry, that is, one can make any permutation of the indices of phases and the equations are left unchanged.

Finally, we note that when the delay is long enough ($\eta \sim O(1/\epsilon)$), the delay enters into the model not as phase shift, but in the argument of the oscillators, $\phi_j(t) - \phi_i(t-\tau)$ (Izhikevich, 1998). This type of model has been the subject of several studies (Kim et al., 1997; Niebur et al., 1991; Schuster and Wagner, 1989; Sethia et al., 2011; Yeung and Strogatz, 1999).

2.1 Phase difference model

Noting that the right hand side of (6) depends only on the differences between the phases, we define the variables $\theta_i = \phi_i - \phi_{i+1}$, $i = 1, 2, \ldots, N-1$. Assuming $\epsilon > 0$ and introducing the slow time $u = \epsilon t$, then gives rise to the following equations

$$\frac{d\theta_i}{du} = \sum_{j=1}^{N} \big(H(\phi_j - \phi_i - \eta) - H(\phi_j - \phi_{i+1} - \eta)\big). \tag{7}$$

Now when $j < i$, we have

$$\phi_j - \phi_i = \theta_j + \theta_{j+1} + \cdots + \theta_{i-1},$$

while, when $j > i$, we have

$$\phi_j - \phi_i = -(\theta_i + \theta_{i+1} + \cdots + \theta_{j-1}).$$

Thus, we can write (7) in the following form

$$\begin{aligned}\frac{d\theta_i}{du} = &\sum_{j=1}^{i-1} H(\sum_{k=j}^{i-1}\theta_k - \eta) + \sum_{j=i}^{N-1} H(-\sum_{k=i}^{j}\theta_k - \eta)\\ &- \sum_{j=1}^{i} H(\sum_{k=j}^{i}\theta_k - \eta) - \sum_{j=i+1}^{N-1} H(-\sum_{k=i+1}^{j}\theta_k - \eta)\end{aligned} \tag{8}$$

The phase difference model (8) reduces the dimension of the model from N to $N-1$. However, it also has less symmetry than the phase model system. We will find that both models are useful in our study of cluster states.

3. EXISTENCE AND STABILITY OF SYMMETRIC CLUSTER STATES

To begin let us consider any arbitrary phase-locked solution of the full model (4). This corresponds to a solution of the phase model (6) where any two phase variables maintain a fixed difference. Any such solution can be written as

$$\phi_j - \phi_{j+1} = \bar{\theta}_j, \ j = 1, 2, \dots N-1, \tag{9}$$

for some constants $\bar{\theta}_j$. Note that such solutions are one dimensional lines in the N dimensional phase space of the phase model (6), while they are just equilibrium points of the phase difference model (8). From the symmetry of the model (6), if the system admits a phase-locked solution of the form (9) then any permutation of the constant phase differences is also a phase-locked solution of the system and it has the same stability.

Cluster states are special phase-locked solutions, where oscillators in the same group/cluster are phase-locked with zero phase difference (i.e., they are synchronized) while those in different clusters have non-zero phase-difference. We focus on symmetric cluster states, where there are the same number of oscillators in each cluster.

Let n be an integer that divides N. Then there exist symmetric cluster states with n clusters and N/n oscillators per cluster. To see this, let Φ_k be the phase of cluster k, $k = 0, 1, \dots, n-1$. As discussed above, the symmetry of the equations implies that if one such a solution exists, there is a whole family: the oscillators can be arranged in any way such that N/n distinct oscillators are in each cluster. Without loss of generality, we will focus on the solution where the oscillators cluster in order of their indices, i.e., $\phi_i = \Phi_k, \ i = k \cdot \frac{N}{n} + 1, \dots, (k+1) \cdot \frac{N}{n}, \ k = 0, \dots, n-1$. From the phase equation (6), the cluster phase differences satisfy the following equations

$$\frac{d\Phi_k}{dt} = \tilde{\Omega} + \epsilon \frac{N}{n} \sum_{l=0}^{n-1} H(\Phi_l - \Phi_k - \eta). \tag{10}$$

Assume that

$$\Phi_k = (\tilde{\Omega} + \omega^{(n)})t + \frac{2\pi k}{n}, \tag{11}$$

which means that the n clusters are equally separated in phase. Substituting (11) into (10), and using the fact that H is a 2π-periodic function, shows that such a solution exists with $\omega^{(n)}$ given by

$$\omega^{(n)} = \epsilon \frac{N}{n} \sum_{m=0}^{n-1} H(\frac{2\pi m}{n} - \eta). \tag{12}$$

The symmetric cluster state (11) of (6) corresponds to the equilibrium, θ^*, of (8), where $\theta^* = (\theta_1^*, \theta_2^*, \dots, \theta_{N-1}^*)$ with $\theta_i^* = 0$, if $i \neq \frac{kN}{n}$, and $\theta^*_{\frac{kN}{n}} = \frac{2\pi}{n}$, for $k = 1, 2, \dots, n-1$.

To analyze the stability of θ^*, we consider the linearization of system (8) at θ^*:

$$\frac{d\theta}{du} = A\theta, \tag{13}$$

where A is the Jacobian matrix. Moving the $(k\frac{N}{n})^{th}$ $(k = 1, 2, \dots, n-1)$ rows of A to be the last $n-1$ rows, results in the following matrix which is equivalent to A

$$\tilde{A} = \begin{pmatrix} -\alpha I_{(N-n)\times(N-n)} & 0_{(N-n)\times(n-1)} \\ X_{(n-1)\times(N-n)} & B_{(n-1)\times(n-1)} \end{pmatrix}.$$

Here $I_{(N-n)\times(N-n)}$ is the $(N-n)\times(N-n)$ identity matrix, and

$$B_{ij} = \begin{cases} -\alpha + \gamma_0 - \gamma_i & \text{if } i = j \\ \gamma_{(i-j) \bmod n} - \gamma_i & \text{if } i \neq j \end{cases}$$

with $\alpha = \sum_{k=0}^{n-1} \gamma_k$ where

$$\gamma_k = \frac{N}{n} H'(\frac{2\pi k}{n} - \eta), \ k = 0, 1, \dots, n-1$$

From the expression for $\tilde{A}$, $N-n$ eigenvalues of A are:

$$\lambda_0^{(n)} = -\alpha, \ \text{multiplicity } N-n. \tag{14}$$

The other $n-1$ eigenvalues are just the eigenvalues of B:

$$\lambda_p^{(n)} = -\alpha + \sum_{k=0}^{n-1} \gamma_k e^{i2\pi kp/n}, \ p = 1, \cdots, n-1. \tag{15}$$

We note that, when $\eta = 0$, the eigenvalues found above for the phase difference model are exactly the same as those found by Okuda (1993) using the phase model (6), except that Okuda had an additional eigenvalue which was always zero. Recall that a phase-locked solution is a line in the phase model. It is easy to check that the zero eigenvalue corresponds to motion along this line. It follows that the cluster solution of the phase model is asymptotically stable when the equilibrium solution θ^* of the phase difference model is asymptotically stable. Thus when the $N-1$ eigenvalues described above have negative real parts, the symmetric cluster state is asymptotically stable.

Based on this analysis we can make the following general conclusions about symmetric cluster solutions. If $n < N$ and n is an integer that divides N then symmetric cluster solutions with n clusters exist. Their stability is determined by n eigenvalues and depends on number of clusters and phase differences, not on the size of the network. In particular, for any N, the 1-cluster (synchronized) solution always exists and is asymptotically stable if $H'(-\eta) > 0$. If $N > 2$ is even, 2-cluster solutions always exists and are asymptotically stable if $H'(\pi - \eta) > 0$ and $H'(\pi - \eta) + H'(-\eta) > 0$. The presence of self-coupling does not influence the stability, only the frequency of the solution.

We assumed $\epsilon > 0$. If $\epsilon < 0$ then the stability of asymptotically stable solutions and totally unstable solutions will be reversed, while saddle type solutions remain of saddle type.

4. APPLICATION TO A NETWORK OF MORRIS-LECAR OSCILLATORS

In this section, we apply our results to a specific network: one with Morris-Lecar neurons (Morris and Lecar, 1981). For convenience, we adopt the dimensionless Morris-Lecar model formulated by Rinzel and Ermentrout (1989). Considering N identical Morris-Lecar oscillators with delayed synaptic coupling, we have the following model

$$
\begin{aligned}
v_i' &= I_{app} - g_{Ca} m_\infty(v_i)(v_i - v_{Ca}) - g_K w_i (v_i - v_K) \qquad (16)\\
&-g_L(v_i - v_L) - \frac{g_{syn}}{N-1} \sum_{j=1, j\neq i}^{N} s(v_j(t-\tau))(v_i(t) - E_{syn}),\\
w_i' &= \varphi \lambda(v_i)(w_\infty(v_i) - w_i),
\end{aligned}
$$

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

$$
\begin{aligned}
m_\infty(v) &= \frac{1}{2}(1 + \tanh((v - \nu_1)/\nu_2)),\\
w_\infty(v) &= \frac{1}{2}(1 + \tanh((v - \nu_3)/\nu_4)),\\
\lambda(v) &= \cosh((v - \nu_3)/2\nu_4), s(v) = \frac{1}{2}(1 + \tanh(10v)).
\end{aligned}
$$

Using the parameter set I in (Campbell and Kobelevskiy, 2012, 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 $\Omega = 0.2632$. We have used the common convention to scale the input to each oscillator by the number of inputs, thus we define $\epsilon = \frac{g_{syn}}{N-1}$. If we did not do this scaling then we would have $\epsilon = g_{syn}$.

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 (16).

4.1 Phase model analysis

We used the package XPPAUT (Ermentrout, 2002) to calculate the interaction functions, H, for model (16) using a numerical implementation of the method described in section 2. This package can also be used to calculate a finite number of coefficients of the Fourier series for H. This gives an explicit, closed form approximation for H:

$$
H(\phi) \approx a_0 + \sum_{k=1}^{K} (a_k \cos(k\phi) + b_k \sin(k\phi)), \qquad (17)
$$

(and hence $H'(\phi)$) where the a_k and b_k are known to numerical accuracy. Figure 1 shows the plot of the numerically computed interaction function (red solid), H, together with the approximations using one (blue solid) and twenty terms (green dashed) of Fourier Series. The twenty term approximation is used in the stability calculations below as it gives a good balance of accuracy and complexity.

Now, the phase model for (16) is

$$
\frac{d\phi_i}{dt} = \Omega - \epsilon \sum_{j=1, j\neq i}^{N} H(\phi_j - \phi_i - \eta),\ i = 1, \ldots, N. \ (18)
$$

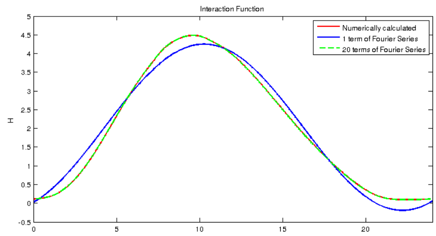

Fig. 1. Interaction function for model (16) and the approximations using 1 and 20 terms of Fourier Series

With the explicit expression for H, (17), we can determine the asymptotic stability of any possible symmetric cluster states for any N by studying the eigenvalues derived in the previous section. We study the network with $N = 6$ in more detail in the following. With $N = 6$, there are four possible symmetric cluster states: 1-cluster (synchronous oscillation), 2-clusters, 3-clusters, and 6-clusters. Following equations (15) and (14), we can explicitly express the eigenvalues for each case with respect to H.

Defining $\beta_k = H'(\frac{k}{3}\pi - \eta)$, we have the following expressions for the eigenvalues:

- 1-cluster solution (all oscillators synchronized)
$$\lambda_0^{(1)} = -6\beta_0, \text{ multiplicity } 5.$$
- 2-cluster solution
$$
\begin{aligned}
\lambda_0^{(2)} &= -\frac{3}{2}\big(\beta_0 + \beta_3\big), \text{ multiplicity } 4,\\
\lambda_1^{(2)} &= -6\beta_3.
\end{aligned}
$$
- 3-cluster solution
$$
\begin{aligned}
\lambda_0^{(3)} &= -2\big(\beta_0 + \beta_2 + \beta_4\big), \text{ multiplicity } 3\\
\lambda_1^{(3)} &= -3(\beta_2 + \beta_4) + i\sqrt{3}(\beta_4 - \beta_2)\\
\lambda_2^{(3)} &= \overline{\lambda_1^{(3)}}
\end{aligned}
$$
- 6-cluster solution (splay state/travelling wave)
$$
\begin{aligned}
\lambda_1^{(6)} = \overline{\lambda_5^{(6)}} &= -2\beta_3 - \frac{1}{2}\left(3(\beta_2 + \beta_4) + \beta_1 + \beta_5\right)\\
&\quad + i\frac{\sqrt{3}}{2}\left(\beta_4 + \beta_5 - \beta_1 - \beta_2\right)\\
\lambda_2^{(6)} = \overline{\lambda_4^{(6)}} &= -\frac{3}{2}(\beta_1 + \beta_2 + \beta_4 + \beta_5)\\
&\quad + i\frac{\sqrt{3}}{2}\left(\beta_2 + \beta_5 - \beta_1 - \beta_4\right)\\
\lambda_3^{(6)} &= -2(\beta_1 + \beta_3 + \beta_5)
\end{aligned}
$$

Figure 2 shows a summary of the stable regions for all the symmetric cluster solutions and indicates that there are several regions of multistability. Note that the stability result for the 1-cluster solution is valid for **any** size of network, for the 2-cluster (3-cluster) solution for any network with $N > 2$ even ($N = 3p$, $p > 1$). The result for the 6-cluster solution applies only for $N = 6$.

4.2 Numerical study

We carried out a numerical continuation study of the full delay differential equation model (16) using the package

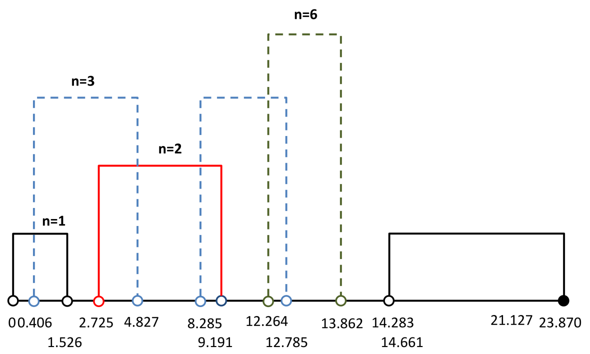

Fig. 2. Phase model prediction of τ intervals where symmetric n-cluster solutions are asymptotically stable.

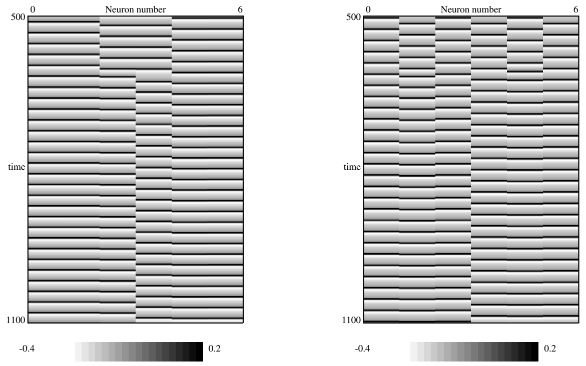

Fig. 3. Numerical simulations showing bistability. A dark bar indicates when a neuron has a spike. Left: Switching between 3-cluster solution and 2-cluster solution. Right: Switching between two 2-cluster solutions.

DDE-BIFTOOL(Engelborghs et al., 2001). With parameter values as given in Table 1, various values of g_{syn} and using $\tau \in [0, 23.9]$ as the continuation parameter, we verified that the phase model stability predictions found in the previous section hold for $\epsilon \leq 0.002$. See Table 2. To investigate the bistability further, we carried

n	$g_{syn} = 0.01$ ($\epsilon = 0.002$)	$g_{syn} = 0.1$ ($\epsilon = 0.02$)
1	$[0, 1.6) \cup (13.4, 23.9]$	$[0, 1.7) \cup (9.4, 23.9]$
2	$(2.4, 9.1)$	$(1.9, 8.0) \cup (20.2, 23.9]$
3	$(0.6, 4.9) \cup (8.5, 12.8)$	$(0.1, 3.9) \cup (7.2, 11.2) \cup (20.2, 23.3)$
6	$(12.4, 13.7)$	$(0.2, 1.0) \cup (11.0, 12.0)$

Table 2. Numerical continuation results: τ intervals where symmetric n-cluster solutions are asymptotically stable.

out numerical simulations of the model (16) using XPPAUT (Ermentrout, 2002). Constant initial conditions, $v_i(t) = v_{i0}$, $w_i(t) = w_{i0}$, $-\tau \leq t \leq 0$, were used and a small perturbation was applied to the input current of one or more neurons during the course of the simulation. The perturbations could cause switching between two different cluster types and between different realizations of the same cluster type. Fig. 3 shows two examples. When $\tau = 3$ both the 2-cluster solutions and 3-cluster solutions are stable. A perturbation to neurons 3 and 4 for $600 \leq t \leq 620$ switches the network from a 3-cluster solution to a 2-cluster solution. When $\tau = 8$ the 2-cluster solutions are the only stable solutions. A perturbation to neurons 2 and 5 for $600 \leq t \leq 620$ switches the network from a 2-cluster solution with clusters $1, 3, 5$ and $2, 4, 6$ to one with clusters $1, 2, 3$ and $4, 5, 6$.

5. DISCUSSION AND FUTURE WORK

One possible application of our work is to understand the formation of neural assemblies. A neural assembly is a group of neurons which transiently act together to achieve a particular purpose. It has been proposed that neural assemblies are formed not just due to external inputs to the system, but also due to the intrinsic dynamics of the network (Engel et al., 2001). Mathematically, the intrinsic dynamics of the network should support solutions with multiple different grouping of neurons, with different neurons able to participate in multiple groupings. Further, switching between different groupings should be able to be acheived by changing the input to the network. Clustering behaviour seems a good candidate for this intrinsic dynamics and hence it has been linked to the formation of neural assemblies (Galán et al., 2006).

Our work gives further support to this hypothesis. In particular, the numerical simulations in the last section show how small perturbations can be used to change the clusters in the system, which would be akin to switching the neural assemblies. We note that this change could be switching between the same or different types of clusters. In the former case the network averaged frequency would be the same or similar. In the latter it could change.

There are many ways our work could be extended. We have focussed on all-to-all coupling, but other types of connectivity with symmetry could be analyzed in a similar manner (e.g. Miller et al. (2015) studied nearest neighbour coupling without delay). Our work is restricted to phase locked solutions, symmetric clusters and weak coupling. Relaxing these these restrictions will require other approaches, such as the use of equivariant bifurcation theory Wu (1998) or matrix analysis Orosz (2014b).

ACKNOWLEDGEMENTS

This work has benefitted from the support of the NSERC and the Faculty of Mathematics, University of Waterloo.

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