Spatially localized cluster solutions in inhibitory neural networks

Hwayeon Ryu^{a,*}, Jennifer Miller^{b,**}, Zeynep Teymuroglu^c, Xueying Wang^d,
Victoria Booth^e, Sue Ann Campbell^f

^a*Department of Mathematics and Statistics, Elon University, Elon, NC, USA*

^b*Mathematics Department, Bellarmine University, Louisville, KY, USA*

^c*Department of Mathematics and Computer Science, Rollins College, Winter Park, FL, USA*

^d*Department of Mathematics and Statistics, Washington State University, Pullman, WA, USA*

^e*Departments of Mathematics and Anesthesiology, University of Michigan, Ann Arbor, MI USA*

^f*Department of Applied Mathematics and Centre for Theoretical Neuroscience, University of Waterloo, Waterloo ON, Canada*

Abstract

Neurons in the inhibitory network of the striatum display cell assembly firing patterns which recent results suggest may consist of spatially compact neural clusters. Previous computational modeling of striatal neural networks has indicated that non-monotonic, distance-dependent coupling may promote spatially localized cluster firing. Here, we identify conditions for the existence and stability of cluster firing solutions in which clusters consist of spatially adjacent neurons in inhibitory neural networks. We consider simple non-monotonic, distance-dependent connectivity schemes in weakly coupled 1-D networks where cells make strong connections with their k^{th} nearest neighbors on each side. Using the phase model reduction of the network system, we prove the existence of cluster solutions where neurons that are spatially close together are also synchronized in the same cluster, and find stability conditions for these solutions. Our analysis predicts the long-term behavior for networks of neurons, and we confirm our results by numerical simulations of biophysical neuron network models. Additionally, we add weaker coupling between closer neighbors as a perturbation to our network connectivity. We analyze the existence and stability of cluster solutions of the perturbed network and validate our results with numerical simulations. Our results demonstrate that an inhibitory network with non-monotonic, distance-dependent connectivity can exhibit cluster

*Corresponding author

**Co-first author

Email addresses: hryu@elon.edu (Hwayeon Ryu), jmiller@bellarmine.edu (Jennifer Miller), zteymuroglu@rollins.edu (Zeynep Teymuroglu), xueying.wang@wsu.edu (Xueying Wang), vbooth@med.umich.edu (Victoria Booth), sacampbell@uwaterloo.ca (Sue Ann Campbell)

solutions where adjacent cells fire together.

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1. Introduction

Many types of brain activity are characterized by coordinated activity of neural assemblies, in which neuron firing is synchronized within an individual assembly but not between different assemblies [18, 27, 19, 11, 32, 6]. Neural assemblies have been observed between neurons in different cortical columns [18], within regions of the hippocampus [19, 11], the dentate gyrus [32] and between cells in the striatum [6, 9, 2] and the olfactory bulb [27]. Neural assemblies may involve neurons which are widespread across one or more brain regions [18, 19] or may involve spatially localized neurons [32, 6]. Understanding the dynamics and formation of neuronal assemblies within larger neural networks has gained increasing importance in neuroscience [12] and has been studied both experimentally [27, 19, 15, 32, 6] and using computational modeling [16, 28, 17, 8, 1, 22, 3, 34].

In neural network models, the formation of neural assemblies has been analyzed by identifying cluster solutions in networks of intrinsically oscillating neurons [16, 17, 28, 15, 22, 31, 7]. Clustering defines a type of solution where the network of oscillators breaks into subgroups. Within each subgroup, the phases of the oscillators are the same, while oscillators in different subgroups are phase-locked with some nonzero phase difference. A useful mathematical framework for studying cluster solutions is the phase model reduction [21, 37]. This framework has been used to study synchronization and clustering in a variety of coupled oscillator networks [5, 33, 25, 36, 29].

In previous work [31, 7], we used the phase model approach to determine existence and stability conditions of cluster solutions of networks with neurons arranged in a 1-dimensional ring, of arbitrary size, with various connectivity schemes. As in many other studies [5, 33], our work focused on cluster solutions where the phase difference between any two adjacent neurons in the network is the same. Thus, other than the case of homogeneous all-to-all coupling, cells in the same cluster were dispersed throughout the network.

Neural assembly firing has been identified in the striatum, a sparsely connected, inhibitory network that is part of the basal ganglia circuit [30, 9, 2, 6, 23]. Recent experimental imaging of inhibitory medium spiny neuron firing in the striatum has suggested that assemblies can be spatially compact [6]. While computational modeling of inhibitory striatal networks has primarily investigated the formation of neural assemblies in which the assembly cells are spatially dispersed in the network [34, 3], a recent study found that spatially compact cluster firing patterns can result from non-monotonic, distance-dependent connectivity in which cells made stronger synaptic connections with their more spatially distant neighbors compared to their nearest neighbors [38]. This result suggests

40 that in inhibitory networks neurons located near one another should be able to be a part of the same cluster when they are more strongly connected to neighbors farther away.

In this work, motivated by the results in [38], we study 1-D ring, inhibitory networks with simple non-monotonic, distance-dependent connectivity schemes. Specifically, we consider networks in which neurons are connected to only their 45 k^{th} nearest neighbors and identify conditions for the existence and stability of solutions which exhibit spatially localized cluster firing. We additionally consider connectivity schemes with connections between the first to $(k-1)^{th}$ nearest neighbors that are weaker than connections to k^{th} nearest neighbors, and analyze how this additional local coupling between cells affects the existence and 50 stability of spatially localized cluster solutions. We employ a phase model reduction of the network to obtain analytical conditions and then test the conditions with numerical simulations of biophysical neural network models.

Our paper is structured as follows: Section 2 provides the description of the methodology we employ, including the phase model reduction (Sec. 2.1) for 55 analysis and the biophysical neuron model (Sec. 2.2) for numerical simulations. Section 3 describes our analysis and numerical results for the case of only k^{th} nearest neighbor coupling. Section 4 presents results for the case of additional coupling(s) between the first k nearest neighbors. We conclude with a discussion 60 of our results in Section 5.

2. Methodology

We begin by reviewing the phase reduction method that reduces a weakly coupled neural network model to a phase model. This phase model is used to conduct our analysis. We then introduce the specific neural network model 65 that we use for numerical simulations and include the parameter values for our simulations.

2.1. Phase reduction method

Consider a general network model consisting of N identical, weakly coupled oscillators on a ring with circulant coupling

$$\frac{dX_i}{dt} = F(X_i(t)) + \epsilon \sum_{j=1}^N g_{ij} G(X_i, X_j), \quad X_i \in \mathbb{R}^n, \quad 1 \leq i \leq N, \quad (1)$$

where ϵ is the coupling strength with $0 < \epsilon \ll 1$, F is the vector field of the isolated neuron, G is the coupling function and $W = (g_{ij})$ is the coupling matrix 70 with $g_{ij} = g_{j-i \pmod{N}}$ and $g_{ii} = 0$ for $i, j = 1, 2, \dots, N$.

We assume that when isolated from the network each neuron exhibits an exponentially asymptotically stable T -periodic orbit, denoted as $\hat{X}(t)$, for $0 \leq t \leq T = \frac{2\pi}{\Omega}$, which is a solution of

$$\frac{dX}{dt} = F(X(t)), \quad X \in \mathbb{R}^n. \quad (2)$$

Applying the theory of weakly coupled oscillators [14, 21, 37], the complete state of each neuron in the network can be approximated by its phase on its T -periodic limit cycle, $\theta_i(t) = \Omega t + \varphi_i(t) \in [0, 2\pi)$, where $\varphi_i(t)$ is the relative phase of the i^{th} neuron. Hence, this theory enables us to significantly reduce
75 the number of equations that describe a neuronal network from n equations to one per neuron.

The dynamics of the relative phase of the i^{th} neuronal oscillator is slowly varying and governed by the equation

$$\frac{d\varphi_i}{dt} = \epsilon \sum_{j=1}^N g_{ij} H(\theta_j(t) - \theta_i(t)). \quad (3)$$

Here H is known as the interaction function and is given by

$$H(\theta_j - \theta_i) = \frac{1}{T} \int_0^T Z(t) G[\hat{X}(t), \hat{X}(t + (\theta_j - \theta_i)/\Omega)] dt. \quad (4)$$

H captures the modulation of the instantaneous phase of the i^{th} oscillator due to the coupling. Z is referred to as the phase response curve of the unperturbed oscillator, which is the unique periodic solution of the linearized adjoint system

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

subject to the normalization condition

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

Thus, the corresponding phase model is given by

$$\frac{d\theta_i}{dt} = \Omega + \epsilon \sum_{j=1}^N g_{ij} H(\theta_j(t) - \theta_i(t)), \quad 1 \leq i \leq N. \quad (5)$$

In view of circulant coupling ($g_{ij} = g_{j-i \pmod N}$ for $1 \leq i, j \leq N$) and no self-coupling ($g_{ii} = g_0 = 0$, $1 \leq i \leq N$), the phase model (5) can be written as

$$\frac{d\theta_i}{dt} = \Omega + \epsilon \sum_{k=1}^{N-1} g_k H(\theta_{(i+k) \pmod N} - \theta_i), \quad 1 \leq i \leq N. \quad (6)$$

We will use this phase model to determine the existence and stability of certain cluster solutions and how this depends on the connections g_k , focusing on results that can be applied to any neural model (1). We then use these
80 results to predict which cluster solutions will be stable in the neural network model described below.

2.2. Neural network model

To verify our analysis results, we numerically simulate networks of neurons modeled by the conductance-based Wang and Buzsáki inhibitory interneuron model [41]. This model uses the classic Hodgkin-Huxley formalism [20] with parameters adjusted to match the action potential shape and spiking properties of fast-spiking interneurons. The membrane voltage V of each individual neuron is governed by the following equations:

$$\begin{aligned} C \frac{dV}{dt} &= I_{app} - g_{Na} m_{\infty}^3(V) h(V - V_{Na}) - g_K n^4(V - V_K) - g_L(V - V_L) \\ &= I_{app} - I_{ion}(V, h, n) = f^V(V, h, n), \\ \frac{dh}{dt} &= \phi(\alpha_h(V)(1 - h) - \beta_h(V)h) = f^h(V, h), \\ \frac{dn}{dt} &= \phi(\alpha_n(V)(1 - n) - \beta_n(V)n) = f^n(V, n), \end{aligned} \quad (7)$$

where t is time in ms and V is the cell membrane potential in mV. The variables h and n are, respectively, the inactivation gating of the sodium current and the activation gating of the potassium current. The sodium current is assumed to instantaneously activate according to the steady state activation function $m_{\infty}(V) = \alpha_m(V)/(\alpha_m(V) + \beta_m(V))$, where $\alpha_m(V) = -0.1(V + 35)/(\exp(-0.1(V + 35)) - 1)$, $\beta_m(V) = 4 \exp(-(V + 60)/18)$ are the voltage dependent reaction rates associated with the activation gate with units ms^{-1} . The reaction rates for the inactivation of the sodium channel and activation of the potassium channel are given by: $\alpha_h(V) = 0.07 \exp(-(V + 58)/20)$, $\beta_h(V) = 1/(\exp(-0.1(V + 28)) + 1)$, $\alpha_n(V) = -0.01(V + 34)/(\exp(-0.1(V + 34)) - 1)$, $\beta_n(V) = 0.125 \exp(-(V + 44)/80)$. We model the situation where each neuron is intrinsically firing at a biologically reasonable rate of less than 60 Hz [41, 26] by setting $I_{app} < 1 \mu\text{A}/\text{cm}^2$.

In the network, neurons are coupled with fast inhibitory synapses that are modeled using first order kinetics following [10]:

$$\begin{aligned} C \frac{dV_i}{dt} &= f^V(V_i, h_i, n_i) - g_{syn}(V_i - V_{syn}) \sum_{j=1}^N g_{ij} s_j, \\ \frac{dh_i}{dt} &= f^h(V_i, h_i), \\ \frac{dn_i}{dt} &= f^n(V_i, n_i), \\ \frac{ds_i}{dt} &= -\frac{s_i}{\tau_{inh}} + \alpha_{inh}(V_i)(1 - s_i) = f^s(V_i, s_i), \end{aligned} \quad (8)$$

where g_{syn} is the maximal synaptic strength and g_{ij} scales the strength of the synaptic current from cell j to cell i . The synaptic gating variable s_i for presynaptic cell i depends on membrane voltage V_i according to

$$\alpha_{inh}(V) = \alpha_0/(1 + \exp(-V/5)).$$

Descriptions of the parameters and values used in our numerical simulations are given in Table 1.

Parameter	Description	Value
ϕ	adjusts reaction rates for temperature	5
g_{Na}	maximal sodium conductance	35 mS/cm ²
g_K	maximal potassium conductance	9 mS/cm ²
g_L	maximal leak conductance	0.1 mS/cm ²
V_{Na}	sodium reversal potential	55 mV
V_K	potassium reversal potential	−90 mV
V_L	leak reversal potential	−65 mV
C	membrane capacitance	1 μF/cm ²
I_{app}	applied current	0.4 μA/cm ²
V_{syn}	synapse reversal potential	−75 mV
g_{syn}	maximal synaptic conductance	0.05 mS/cm ²
α_0	synaptic maximal activation rate	4 ms ^{−1}
τ_{inh}	synaptic inactivation time constant	2 ms

Table 1: Description of parameters and the values used for the neuron model in (8).

Comparison of numerical results of this interneuron network model with the predictions given by the phase reduction model requires the interaction function H in Eq. (6). The model (8) can be put in the form given in (1) if we identify $\epsilon = g_{syn}$, $X_i = (V_i, h_i, n_i, s_i)^T$, $F = (f^V, f^h, f^n, f^s)^T$ and $G(X_i, X_j) = ((V_{syn} - V_i)s_j, 0, 0, 0)^T$. Then the function H can be computed from (4). For any neural network, H rarely has a closed-form expression and one usually has to resort to numerical evaluation. In this paper, we use XPPAUT [13] to numerically compute H for the Wang-Buzsáki inhibitory network (8).

3. The First Case: k^{th} Nearest Neighbor Coupling Only

In this section, we first study the cluster solutions of an N -cell network with k^{th} nearest neighbor coupling only; i.e., $g_k > 0$, $g_{N-k} > 0$, and $g_i = 0$ otherwise. We look for solutions with m clusters. We assume that $N = mkp$ for some $1 \leq p \leq N$. We show two examples of this type of network solution with $N = 12$ in Figure 1. In Fig. 1(a), there are $m = 2$ clusters (cells represented by circular nodes all fire together as one cluster and those represented by rectangular nodes fire together as the second). The cells have reciprocal, second nearest neighbor coupling, $k = 2$ (e.g., cell 1 is coupled to cells 3 and 11). There are $p = 3$ subgroups in each cluster (e.g., the cluster of cells represented by circular nodes contains three spatially separated subgroups: 1 & 2, 5 & 6, and 9 & 10). The second nearest neighbor coupling causes the network to have two disjoint subnetworks, shown on the right, i.e., odd-numbered vs. even-numbered cells.

Fig. 1(b) shows a network solution with the same number of cells but with different connectivity. Each neuron is only coupled to its third nearest neighbor ($k = 3$) on each side and the network of $N = 12$ decomposes into 3 disjoint sub-

Figure 1: (a) Top: the full network for $N = 12$, $m = 2$, $k = 2$, $p = 3$, which can be decomposed into the two disjoint networks of 6 cells each, i.e., odd-numbered vs. even-numbered cells; (b) Bottom: the network of $N = 12$, $m = 2$, $k = 3$, $p = 2$.

networks, each containing 4 neurons. In general, k^{th} nearest neighbor coupling results in k disjoint subnetworks with mp neurons in each subnetwork.

3.1. Cluster Solutions

125 This subsection begins by showing the existence of the m -cluster solutions with this specific network structure and finding stability conditions. Next, we apply the results to make predictions for the behavior of examples with $N = 8, 12, 18$. Finally, we compare these predictions to numerical simulations of the example networks.

130 3.1.1. Existence and stability

Define the phase difference $\phi_i = \theta_{(i+1) \bmod N} - \theta_i$, $i = 1, \dots, N$. We prove the following theorem which shows that, for networks with the structure described above, certain m -cluster solutions of the type shown in Figure 1 always exist.

Further, the stability of these solutions depends on the phase difference between the clusters.

Theorem 3.1. *For any given network structure with $N = mkp$ neurons and $g_k > 0$, $g_{N-k} > 0$ and $g_i = 0$ otherwise, there exists an m -cluster solution of the following form:*

$$\begin{aligned} \phi_{kq+1} &= \phi_{kq+2} = \dots = \phi_{kq+(k-1)} = 0, \quad q = 0, 1, \dots, mp-1, \\ \phi_{kq+k} &= \frac{2\pi l}{m} := \psi_{m,l} := \psi_m, \end{aligned} \quad (9)$$

with $\gcd(l, m) = 1$ and $l < m$. Moreover, the m -cluster solution (9) is stable if

$$g_k H'(\psi_m) + g_{N-k} H'(-\psi_m) > 0. \quad (10)$$

In particular, if $g_k = g_{N-k}$, then this m -cluster solution is stable if $H'_{\text{odd}}(\psi_m) > 0$.

Proof. Existence: We look for the solution of the form $\bar{\theta}_i = (\Omega + \epsilon\omega)t + \theta_{i0}$ where $\theta_{10} = 0$ and $\theta_{i0} = \sum_{j=1}^{i-1} \phi_j$ for $2 \leq i \leq N$. If $\bar{\theta}_i(t)$ is a solution of (6), then

$$\begin{aligned} \frac{d\bar{\theta}_i}{dt} &= \Omega + \epsilon\omega = \Omega + \epsilon(g_k H(\theta_{i+k,0} - \theta_{i0}) + g_{N-k} H(\theta_{i+N-k,0} - \theta_{i0})) \\ &= \Omega + \epsilon(g_k H(\psi_m) + g_{N-k} H(2\pi j - \psi_m)) \\ &= \Omega + \epsilon(g_k H(\psi_m) + g_{N-k} H(-\psi_m)). \end{aligned}$$

Thus, $\omega = g_k H(\psi_m) + g_{N-k} H(-\psi_m)$. It is clear that, in (9), $\sum_{i=1}^N \phi_i = m\psi_m = 0 \bmod 2\pi$, which leads to an m -cluster solution in the network of size $N = mkp$.

Stability: Let $\theta_i(t) = \bar{\theta}_i(t) + u_i(t)$. Then

$$\begin{aligned} \frac{du_i}{dt} &= \epsilon \left(g_k [H'(\psi_m)(-u_i) + H'(\psi_m)u_{(i+k) \bmod N}] \right. \\ &\quad \left. + g_{N-k} [H'(-\psi_m)(-u_i) + H'(-\psi_m)u_{(i+N-k) \bmod N}] \right) \\ &= \epsilon \left[(g_k H'(\psi_m) + g_{N-k} H'(-\psi_m))(-u_i) \right. \\ &\quad \left. + g_k H'(\psi_m)u_{(i+k) \bmod N} + g_{N-k} H'(-\psi_m)u_{(i-k) \bmod N} \right]. \end{aligned} \quad (11)$$

Let $A = \text{circ}(a_1, a_2, \dots, a_N)$ for which

$$\begin{aligned} a_1 &= -(g_k H'(\psi_m) + g_{N-k} H'(-\psi_m)), & a_{k+1} &= g_k H'(\psi_m), \\ a_{N-k+1} &= g_{N-k} H'(-\psi_m), & a_i &= 0 \quad \text{otherwise.} \end{aligned}$$

Rewriting (11) in vector form, we have

$$\frac{d\vec{u}}{dt} = \epsilon A \vec{u},$$

where $\vec{u} = (u_1, u_2, \dots, u_N)^T$. The stability of this vector equation is determined by the real part of the eigenvalues of the Jacobian matrix A . Let $\rho_j = e^{2\pi j\sqrt{-1}/N}$ for $1 \leq j \leq N$. Because A is circulant and $\rho^N = 1$, the eigenvalues of A are given by

$$\begin{aligned}\lambda_j^A &= a_1 + a_{k+1}\rho_j^k + a_{N-k+1}\rho_j^{N-k} \\ &= -(g_k H'(\psi_m) + g_{N-k} H'(-\psi_m)) + g_k H'(\psi_m)\rho_j^k + g_{N-k} H'(-\psi_m)\rho_j^{-k}.\end{aligned}$$

Hence, the real part of the eigenvalues is

$$\Re(\lambda_j^A) = -(g_k H'(\psi_m) + g_{N-k} H'(-\psi_m)) \left(1 - \cos \frac{2\pi k j}{N}\right), \quad 1 \leq j \leq N.$$

Note that $\Re(\lambda_j^A) = 0$ whenever $\frac{kj}{N}$ is an integer. Thus there are k zero eigenvalues. When $g_k = g_{N-k}$, then

$$\Re(\lambda_j^A) = -2g_k H'_{\text{odd}}(\psi_m) \left(1 - \cos \frac{2\pi k j}{N}\right), \quad 1 \leq j \leq N.$$

Therefore, the m -cluster solution is stable if

$$g_k H'(\psi_m) + g_{N-k} H'(-\psi_m) > 0.$$

140 Additionally, when $g_k = g_{N-k}$, then this m -cluster solution is stable if $H'_{\text{odd}}(\psi_m) > 0$. $\square$

We note that the existence of m -cluster solutions is determined only by the network structure. Additionally, given symmetric connection weights, the stability of the solutions is independent of the network size. Due to the zero
145 eigenvalues, we can obtain stability but not asymptotic stability of these solutions when $k > 1$. We will discuss these zero eigenvalues further in Sec. 3.2.1. When $k = 1$, however, there is only one zero eigenvalue which corresponds to motion along the solutions [7]. Thus for $k = 1$ the condition (10) does give asymptotic stability. This is consistent with the stability result in [31] where we
150 showed that an m -cluster solution is asymptotically stable if $H'_{\text{odd}}(\psi_m) > 0$, in the case of symmetric connectivity with only first nearest neighbor coupling.

3.1.2. Specific network examples

To clarify our results and for comparison with the numerical simulations in the next section, we now apply the phase model results to some examples
155 for specific values of the total number of neurons N , with $N = mkp$ for some integers m, k, p with $m > 1$.

Given N and k , from Theorem 3.1, the stability condition for any appropriate m is $g_k H'(\psi_m) + g_{N-k} H'(-\psi_m) > 0$ where ψ_m is the phase difference between clusters as defined in the theorem. In the numerical simulations below
160 we use symmetric coupling, $g_k = g_{N-k} > 0$, so the stability condition reduces to $H'_{\text{odd}}(\psi_m) > 0$, where H_{odd} is the odd part of H . Hence for a given interaction

function H , stability depends only on the phase difference and not the coupling strengths. Thus to find the stability of an m -cluster solution, we need only calculate ψ_m and determine the sign of $H'_{odd}(\psi_m)$.

We used XPPAUT [13] to numerically compute the functions H and H_{odd} for the model (8) with parameters given in Table 1. The results are shown in Figure 2. Careful inspection of the results shows that $H'_{odd}(\phi)$ is positive for $\phi \in [0, 0.11\pi) \cup (0.62\pi, 1.38\pi) \cup (1.89\pi, 2\pi]$ and negative everywhere else.

Figure 2: Profile information of the interaction function H for the neural model (8) with parameter values given in Table 1.

In [7] it is shown that the synchronous (1-cluster) solution exists for all values of N and any circulant coupling matrix, and that this solution is asymptotically stable if $H'(0) > 0$. Thus from Figure 2 we predict that the synchronous solution is asymptotically stable for the specific neural model we consider, given in Eq. (8), with any circulant coupling matrix.

Now consider any N , with k th nearest neighbor coupling. For $m = 2$, $\psi_m = \pi$ and $H'_{odd}(\pi) > 0$ so the 2-cluster solution is predicted to be stable. For $m = 4$, $\psi_m = \pi/2$ or $\psi_m = 3\pi/2$. Since $H'_{odd}(\pi/2) < 0$ and $H'_{odd}(3\pi/2) < 0$ the 4-cluster solution is predicted to be unstable. Now with $N = 8$ and $k = 2$ one may have $m = 2$ or $m = 4$. Thus for $N = 8$ with second nearest neighbor coupling the prediction is that only the synchronous and 2-cluster solutions are stable. We summarize the predictions for other values of N in Table 2.

3.1.3. Numerical results

We numerically simulate networks of N neurons (where N is even) with only k^{th} nearest neighbor coupling to validate the existence and stability of m -cluster solutions, as discussed in Sec. 3.1.1. For all simulations, we use the model in (8) and the parameter values given in Table 1, including synaptic coupling strength g_{syn} , implemented in Matlab. Only the number of cells in the network N and the connectivity pattern (second or third nearest neighbor coupling) are varied.

N	k	m	p	ψ_m	Prediction
8	2	2	2	π	stable
		4	1	$\pi/2, 3\pi/2$	unstable
	4	2	1	π	stable
12	2	2	3	π	stable
		3	2	$2\pi/3, 4\pi/3$	stable
		6	1	$\pi/3, 5\pi/3$	unstable
	3	2	2	π	stable
		4	1	$\pi/2, 3\pi/2$	unstable
		6	1	π	stable
18	2	3	3	$2\pi/3, 4\pi/3$	stable
		9	1	$2\pi/9, 4\pi/9, 14\pi/9, 16\pi/9$	unstable
		9	1	$8\pi/9, 10\pi/9$	stable
	3	2	3	π	stable
		3	2	$2\pi/3, 4\pi/3$	stable
		6	1	$\pi/3, 5\pi/3$	unstable

Table 2: Stability predictions from phase model analysis for the network (8).

We first consider the case for second nearest neighbor coupling only, i.e., $k = 2$. We use random initial conditions and simulate at least up to $t = 3 \cdot 10^3$ to obtain the corresponding steady-state solutions. Various m -cluster solutions and their respective raster plots for different values of the network size N are given in Figure 3. Fig. 3(a) shows the 2-cluster solution in the network of $N = 8$, for which $m = 2, k = 2, p = 2$. In Fig. 3(b), we obtain the 1-cluster solution resulting in the synchronized behavior of all neurons in the network of $N = 12$. Also, the 2-cluster solution with $m = 2, k = 2, p = 3$ for $N = 12$ is shown in Fig. 3(c), matching the schematic diagram in Fig. 1(a). Finally, Fig. 3(d) shows the 9-cluster solution for $N = 18$, i.e., $m = 9, k = 2, p = 1$.

We also explore the network where each neuron is connected to its third nearest neighbor only, i.e., $k = 3$. The 2-cluster solutions for $N = 12$ and $N = 18$ are demonstrated in Figs. 4(a) and 4(b), respectively. The former solution has $m = 2, k = 3, p = 2$ and the latter has $m = 2, k = 3, p = 3$.

3.2. Non-Zero Time-Shifted Solutions

The networks considered so far have connections between every k^{th} nearest neighbor such that each cell is not connected to its $1^{st}, 2^{nd}, \dots, (k-1)^{th}$ nearest neighbors. This means that the network decomposes into k disjoint subnetworks (Figs. 1(a) and (b) for $N = 12$ with $k = 2$ and $k = 3$, respectively). The solutions discussed above in Sec. 3.1 focus on the case where the k disjoint subnetworks are synchronized, namely when cells within each cluster have the same phases (or spike at the same time) or, equivalently, have a zero time shift between them. However, other solutions, where the disjoint subnetworks are not synchronized, may exist. Such solutions would have phase differences

$$\phi_{kq+1}, \phi_{kq+2}, \dots, \phi_{kq+(k-1)}, \phi_{kq+k} \geq 0, \quad q = 0, 1, \dots, mp - 1. \quad (12)$$

Figure 3: Time series (left) and its raster plot (right) for different cluster solutions with second nearest coupling only in the network for different N values.

In this section, we consider these non-zero time-shifted solutions.

Figure 4: Time series (left) and its raster plot (right) for 2-cluster solutions with third nearest neighbor coupling ($k = 3$) only; (a) the network for $N = 12$ and (b) $N = 18$.

3.2.1. Existence and stability

In the stability analysis in Sec. 3.1.1, we noted that some real parts of the eigenvalues of the circulant Jacobian matrix A are equal to zero. In fact, $\Re(\lambda_j^A) = 0$ whenever $j - 1$ is a multiple of mp . Since $1 \leq j \leq N$ and $N = mkp$, there are k values of j that make the real part of the eigenvalue zero: $j = 1, mp + 1, 2mp + 1, \dots, (k - 1)mp + 1$.

This is related to our statement in Sec. 3.1.1 that the phase-shifts ϕ_i are not independent, but satisfy the constraint $\sum_{i=1}^N \phi_i = m\psi_m = 0 \bmod 2\pi$. This could be used to reduce the system to fewer equations with a loss of symmetry in our system. Since our network of N neurons decomposes into k disjoint subnetworks, each with mp neurons, this means that $\sum_{i \equiv \beta \bmod k} \phi_i = m\psi_m = 0 \bmod 2\pi$ where $\beta = 0, \dots, k - 1$. In other words, we have k constraints on our system. We could reduce the system to $N - k$ equations, but we choose not to in order to leverage the symmetry. The result is that the system will have k eigenvalues equal to 0 due to the k disjoint subnetworks. These zero eigenvalues are directly related to the existence of non-zero time-shifted solutions.

Now we show the existence of the non-zero time-shifted solution between k disjoint subnetworks for a network of $N = mkp$ cells with only k^{th} nearest neighbor coupling. The phase model for the network is described by (6) with the circulant coupling matrix

$$\text{circ}[0, g_1, g_2, \dots, g_k, 0, \dots, 0, g_{N-k}, \dots, g_{N-2}, g_{N-1}], \quad (13)$$

with the additional assumptions of symmetric connectivity ($g_{N-i} = g_i$), $g_i = 0$ for $i < k$, and $g_k = O(1)$ with respect to ϵ . Taking the phase difference $\phi_i = \theta_{i+1} - \theta_i$ as in Sec. 3.1.1 ($1 \leq i \leq N$ and i is modulo N), we get the following system from (6) for the evolution of phase differences:

$$\begin{aligned} \frac{d\phi_i}{dt} = & \epsilon g_k \left[H \left(\sum_{s=0}^{k-1} \phi_{i+s+1} \right) - H \left(\sum_{s=0}^{k-1} \phi_{i+s} \right) \right. \\ & \left. + H \left(-\sum_{s=0}^{k-1} \phi_{i-s} \right) - H \left(-\sum_{s=0}^{k-1} \phi_{i-s-1} \right) \right]. \end{aligned} \quad (14)$$

Recall that the phase differences are not independent but satisfy the constraint

$$\sum_{i=1}^N \phi_i = 0 \bmod 2\pi. \quad (15)$$

For analysis simplicity, we focus on the case of second nearest neighbor coupling ($k = 2$) only. In this case, (14) reduces to

$$\begin{aligned} \frac{d\phi_i}{dt} = & \epsilon g_2 [H(\phi_{i+1} + \phi_{i+2}) - H(\phi_i + \phi_{i+1}) + H(-\phi_i - \phi_{i-1}) \\ & - H(-\phi_{i-1} - \phi_{i-2})], \end{aligned} \quad (16)$$

220 for $1 \leq i \leq N$.

Equilibrium solutions must satisfy

$$\begin{aligned} 0 = & \epsilon g_2 [H(\phi_{i+1} + \phi_{i+2}) - H(\phi_i + \phi_{i+1}) + H(-\phi_i - \phi_{i-1}) \\ & - H(-\phi_{i-1} - \phi_{i-2})]. \end{aligned} \quad (17)$$

We consider solutions such that each subnetwork exhibits two clusters. In this case, cells within the same subnetwork fire in anti-phase, i.e., $\theta_{i+2} - \theta_i = \pi$. Let $\phi_{kq+1} = \theta_{kq+2} - \theta_{kq+1} = \alpha$ and $\phi_{kq+2} = \theta_{kq+3} - \theta_{kq+2} = \pi - \alpha$ for $q = 0, 1, \dots, mp - 1$. This gives the following phase differences for arbitrary i :

$$\begin{aligned} \phi_i &= \phi_{i+2} = \dots = \phi_{i+(N-2)}, \\ \phi_i + \phi_{i+1} &= \pi, \end{aligned}$$

for $1 \leq i \leq N$. Applying the above properties of ϕ_i satisfies (17) as follows:

$$0 = \epsilon g_2 [H(\pi) - H(\pi) + H(-\pi) - H(-\pi)], \quad 1 \leq i \leq N. \quad (18)$$

This proves the existence of non-zero time-shifted solutions for the case $k = 2$.

Note that we can easily generalize this argument to arbitrary k . Then, the network consists of k disjoint subnetworks with each subnetwork exhibiting 2-cluster firing so that $\theta_{i+k} - \theta_i = \pi$. This leads to the following relationships for the phase differences

$$\begin{aligned} \phi_i &= \phi_{i+k} = \dots = \phi_{i+(N-k)}, \\ \phi_i + \phi_{i+1} + \dots + \phi_{i+k-1} &= \pi, \end{aligned}$$

which will satisfy equilibrium solutions of (14).

Stability of these solutions stems from the stability of 2-cluster solutions in each of the disjoint subnetworks consisting of mp cells where $m = 2$. In this case, we can apply the stability conditions in Theorem 3.1 with $k = 1$. For example, consider the network shown in Fig. 2(a) with $N = 12$ neurons connected with their second nearest neighbors ($k = 2$) that breaks into two subnetworks of $N_{sub} = 6$ neurons each. For the subnetwork of odd-numbered cells $\{1, 3, 5, 7, 9, 11\}$, we consider the stability of the 2-cluster solution: $C_0 = \{1, 5, 9\}$ and $C_1 = \{3, 7, 11\}$ where $k_{sub} = 1$ and $p_{sub} = 3$. Theorem 3.1 with the assumption of symmetric weights can be applied to conclude that the 2-cluster solution is locally asymptotically stable within the subnetwork with $H'_{odd}(\pi) > 0$.

3.2.2. Numerical results

Based on the analysis results, numerical simulations in Matlab were conducted to validate the existence and stability of non-zero time-shifted solutions using (8) and the model parameter values provided in Table 1. We simulate networks of different N values with second ($k = 2$) or third ($k = 3$) nearest neighbor coupling only.

We first consider the case of $k = 2$ where the network consists of two disjoint subnetworks. If the time shift between these subnetworks is nonzero, 4-cluster solutions will arise. Figure 5 demonstrates three different non-zero time-shifted solutions and their respective raster plots for the network of $N = 8$.

We also explore the network where each neuron is connected to its third nearest neighbors only, i.e., $k = 3$ for $N = 18$. In this case, the whole network consists of three subnetworks that are disjoint from each other. Each subnetwork exhibits a 2-cluster solution in which the clusters fire in anti-phase to each other. If two subnetworks fire together but the third subnetwork spikes at a different time, a 4-cluster solution arises, as shown in Fig. 6(a). On the other hand, if each of the three disjoint subnetworks fire at different times, a 6-cluster solution is found, as shown in Fig. 6(b).

4. The Second Case: k^{th} Neighbor Coupling with Additional Couplings

In this section, we will study the effect of additional network connections on solutions studied in the previous section. The most general circulant coupling matrix with no self-coupling for the model (8) is given by

$$\text{circ}[0, g_1, g_2, \dots, g_k, \dots, g_{N-k}, \dots, g_{N-1}]. \quad (19)$$

We will consider how the additional coupling terms affect the results from the previous section. We will use the phase model (6) to formulate mathematical conditions for the existence and stability of cluster solutions in the next subsection. In the following subsection we verify our analysis through numerical simulations of the model (8).

Figure 5: Time series (left) and its raster plot (right) for non-zero time-shifted (or 4-cluster) solutions in the network of $N = 8$ with second nearest coupling ($k = 2$) only and varying nonzero time shifts between the two disjoint subnetworks.

4.1. Phase Model Analysis

260 4.1.1. Existence and stability of zero time-shifted solutions.

Here we consider the m -cluster solutions described in Section 3.1.1. We consider different possible relative strengths of the k^{th} nearest neighbour coupling g_k, g_{N-k} and the additional couplings.

265 The simplest situation is when $g_k, g_{N-k} = O(1)$ with respect to ϵ but the rest of the coupling strengths are $O(\epsilon)$. In this case all terms involving these g_j come in at higher powers of ϵ in Eqs. (6) and (11). Thus we expect all the results of Theorem 3.1 to hold.

Now consider the case when all connections which exist are of equal strength, i.e., $O(1)$ with respect to ϵ . Then we have the following.

Theorem 4.1. Consider the system (6) with $N = mkp$ and coupling matrix defined by

$$\text{circ}[0, g_1, g_2, \dots, g_k, 0, \dots, 0, g_{N-k}, \dots, g_{N-1}], \quad (20)$$

Figure 6: Time series (left) and its raster plot (right) for different non-zero time-shifted (or cluster) solutions in the network of $N = 18$ with third nearest neighbor coupling ($k = 3$) only.

where $g_j = O(1)$ with respect to ϵ . There are only two types of model-independent phase-locked solutions with adjacent neurons synchronized. The synchronous (1-cluster) solution exists for any choice of coupling strengths. The 2-cluster solution exists if N is even and the coupling strengths satisfy

$$g_{k-j} = g_{N-j}, \quad j = 1, \dots, k-1. \quad (21)$$

Proof. Using the same setup as in Section 3.1.1, define the phase difference $\phi_i = \theta_{i+1} - \theta_i$, $i = 1, \dots, N$. We look for solution of the form $\bar{\theta}_i = (\Omega + \epsilon\omega)t + \theta_{i0}$ where $\theta_{10} = 0$ and $\theta_{i0} = \sum_{k=1}^{i-1} \phi_k$ for $2 \leq i \leq N$. We assume $N = mkp$ and that coupling occurs between all neighbours from nearest to k^{th} , i.e., the coupling matrix is defined by (20).

We consider an m -cluster solution as described by equation (9). Substituting

this into equation (6) with the coupling matrix (20) gives

$$\begin{aligned}
 \omega &= g_1 H(\theta_{i+1,0} - \theta_{i0}) + g_2 H(\theta_{i+2,0} - \theta_{i0}) + \cdots + g_k H(\theta_{i+k,0} - \theta_{i0}) \\
 &\quad + g_{N-k} H(\theta_{i+N-k,0} - \theta_{i0}) + \cdots + g_{N-2} H(\theta_{i+N-2,0} - \theta_{i0}) \\
 &\quad + g_{N-1} H(\theta_{i+N-1,0} - \theta_{i0}) \\
 &= g_1 H(\phi_i) + g_2 H(\phi_{i+1} + \phi_i) + \cdots + g_k H\left(\sum_{j=0}^{k-1} \phi_{i+j}\right) \\
 &\quad + g_{N-k} H\left(-\sum_{j=1}^k \phi_{i-j}\right) + \cdots + g_{N-2} H(-(\phi_{i-2} + \phi_{i-1})) + g_{N-1} H(-\phi_{i-1}).
 \end{aligned}$$

There are k cases to consider for the values of ϕ_i , corresponding to $i = kq + 1, kq + 2, \dots, kq + k$. All must yield the same value of ω for the solution to exist. Thus we have

$$\begin{aligned}
 \omega &= g_1 H(0) + \cdots + g_{k-1} H(0) + g_k H(\psi_m) + g_{N-k} H(-\psi_m) \\
 &\quad + g_{N-k+1} H(-\psi_m) + \cdots + g_{N-1} H(-\psi_m) \tag{22}
 \end{aligned}$$

$$\begin{aligned}
 &= g_1 H(0) + \cdots + g_{k-2} H(0) + g_{k-1} H(\psi_m) + g_k H(\psi_m) + g_{N-k} H(-\psi_m) \\
 &\quad + g_{N-k+1} H(-\psi_m) + \cdots + g_{N-2} H(-\psi_m) + g_{N-1} H(0) \tag{23}
 \end{aligned}$$

$\vdots$

$$\begin{aligned}
 &= g_1 H(\psi_m) + \cdots + g_{k-1} H(\psi_m) + g_k H(\psi_m) + g_{N-k} H(-\psi_m) \\
 &\quad + g_{N-k+1} H(0) + \cdots + g_{N-1} H(0). \tag{24}
 \end{aligned}$$

280 We see immediately that these equations are all satisfied for any H and any g_j if $\psi_m = 0$. Thus we conclude that the 1-cluster (totally synchronized) solution always exists. This is consistent with results for systems with first and second nearest neighbour coupling [31].

To proceed further, take the difference of equations (22)–(23) to find the condition

$$[H(0) - H(\psi_m)]g_{k-1} + [H(-\psi_m) - H(0)]g_{N-1} = 0.$$

This will be satisfied for any H if

$$\psi_m = \pi \text{ and } g_{k-1} = g_{N-1}.$$

285 Repeating this with other pairs of equations leads to the same constraint on ψ_m and the conditions (21). The result follows. $\square$

Remark 4.1. *It follows from the proof of Theorem 4.1 that under the conditions (21) the m -cluster solution will exist if $H_{\text{odd}}(\psi_m) = 0$. Thus, we do not expect any m -cluster solution with $m > 2$ to exist for every H ; however, solutions for specific m may exist for a particular H . Further, other model-dependent solutions may exist under different conditions on the connection weights.*

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Figure 7: (a) Left: The network of $N = 8$ with additional coupling (in dashed lines) between nearest neighbors; (b) Right: The network of $N = 12$ with additional coupling between nearest neighbors.

The stability of the 2-cluster solution described in this theorem is difficult to describe for general N ; thus we consider an in-between case, where the additional connections are weaker than g_k and g_{N-k} . We need to be careful that the weaker connections are not so weak that they are of similar strength to the neglected terms. Keeping in mind the conditions for existence of solutions derived above, we consider 2-cluster solutions ($m = 2$, $\psi_m = \pi$) and assume the coupling matrix defined by (20) satisfies the additional condition $g_1, \dots, g_{k-1}, g_{N-k+1}, \dots, g_{N-1} = s\delta$, while $g_k, g_{N-k} = O(1)$ with respect to ϵ and $0 < \epsilon \ll \delta \ll 1$. We show two examples in Figure 7: $N = 8$ with $k = 2$ (Fig. 7(a)) and $N = 12$ with $k = 2$ (Fig. 7(b)). For the example with $N = 12$, the $O(1)$ couplings are the same as in Fig. 1(a) (represented by solid lines) with weaker couplings between nearest neighbors (represented by dashed lines).

We have the following result.

Theorem 4.2. Consider the model (6) with $N = 2kp$. Suppose the coupling matrix is defined by

$$\text{circ}[0, \delta s, \dots, \delta s, g_k, 0, \dots, 0, g_{N-k}, \delta s, \dots, \delta s], \quad (25)$$

where s, g_j are positive, $g_k, g_{N-k} = O(1)$ with respect to ϵ and $s = O(1)$ with respect to δ and $0 < \epsilon \ll \delta \ll 1$. Then there is a 2-cluster solution where each cluster consists of p subgroups of k neurons. Each subgroup is synchronized and adjacent groups are π out of phase with each other. This solution is locally asymptotically stable if and only if $H'(\pi) > 0$ and $H'(0) + H'(\pi) > 0$.

Proof. Existence. The existence of solutions follows from Theorem 4.1 since the given N and coupling strengths satisfy the conditions of that theorem.

Stability. A simple calculation shows that the Jacobian matrix for the linearization of the model (6) with the coupling matrix (25) can be written as

$$\epsilon(A + s\delta B),$$

where A is the Jacobian matrix for the situation with no additional coupling ($\delta = 0$). It follows from the analysis in Section 3.1.1 and the discussion in Section 3.2.1 that A has k zero eigenvalues and the rest of the eigenvalues are proportional (with positive constant) to $-H'(\pi)$. Further, the eigenvalue 0 has geometric multiplicity k with linearly independent eigenvectors $\mathbf{v}_0, \dots, \mathbf{v}_{k-1}$. We take $\mathbf{v}_0 = [1, 1, \dots, 1]^T$.

Consideration of Eq. (6) shows that each row sum of $A + s\delta B$ is 0. Thus, when $\delta \neq 0$, one zero eigenvalue persists since $[A + s\delta B]\mathbf{v}_0 = \mathbf{0}$.

Now let λ_j be a nonzero eigenvalue of A with eigenvector $\mathbf{v}_j$. Then

$$(A + s\delta B)\mathbf{v}_j = \lambda_j \mathbf{v}_j + s\delta B\mathbf{v}_j = \lambda_j \mathbf{v}_j + O(\delta).$$

Thus, to order δ , λ_j remains an eigenvalue for the solution. If $\lambda_j = 0$, however, we have

$$[A + s\delta B]\mathbf{v}_j = s\delta B\mathbf{v}_j, \quad j = 1, \dots, k-1.$$

Thus the other zero eigenvalues may not persist.

For simplicity, in the rest of the proof we will take $k = 2$. The proof for other values of k is similar. In this case

$$A = \text{circ}[-(g_2 + g_{N-2})H'(\pi), 0, g_2H'(\pi), 0, \dots, 0, g_{N-2}H'(\pi), 0]$$

and a second, linearly independent eigenvector of the eigenvalue 0 of A is $\mathbf{v}_1 = [1, -1, 1, -1, \dots, 1, -1]^T$. Further, B is a banded matrix with $B_{ii} = -(H'(0) + H'(\pi))$ and

$$\begin{aligned} B_{i,(i-1) \bmod N} &= H'(\pi), \quad B_{i,(i+1) \bmod N} = H'(0), \quad \text{if } i \text{ even,} \\ B_{i,(i-1) \bmod N} &= H'(0), \quad B_{i,(i+1) \bmod N} = H'(\pi), \quad \text{if } i \text{ odd.} \end{aligned}$$

It then follows that with $\delta > 0$ the second zero eigenvalue becomes $-2s\delta[H'(0) + H'(\pi)]$ since $[A + s\delta B]\mathbf{v}_1 = s\delta B\mathbf{v}_1 = -2s\delta[H'(0) + H'(\pi)]\mathbf{v}_1$.

In summary, all eigenvalues except the one zero eigenvalue that persists satisfy $\Re(\lambda_j) < 0$ if and only if $H'(\pi) > 0$ and $H'(0) + H'(\pi) > 0$.

Recall that the solutions we study are of the form $\bar{\theta}_i = (\Omega + \epsilon\omega)t + \theta_{i0}$. Thus the solutions correspond to lines

$$\theta_{(i+1) \bmod N} - \theta_i = \phi_i$$

with ϕ_i given by (9). The zero eigenvalue that persists corresponds to motion along these lines and hence does not affect the stability of the solutions. The result follows. $\square$

Remark 4.2. It follows from Remark 4.1, that under the conditions of Theorem 4.2 other cluster solutions may exist for particular models. The proof of Theorem 4.2 shows that if these solutions are unstable for the case $\delta = 0$, then they will be unstable for the case $\delta > 0$.

4.1.2. Application to the model network

For comparison with the numerical simulations below, we now consider what this analysis predicts for the model network (8) with parameters as in Table 1 and symmetric coupling matrix defined by

$$\text{circ}[0, g_1, g_2, \dots, g_k, 0, \dots, 0, g_k, \dots, g_1]. \quad (26)$$

335 We assume that $g_k = O(1)$ with respect to ϵ .

Recall that Section 3.1.2 and specifically Table 2 gives the existence and stability for some specific values of the total number of neurons N , with $N = mkp$ for some integers m, k, p , in the case that all couplings except g_k are zero. As discussed above, if the additional couplings $g_1, \dots, g_{k-1} = O(\epsilon)$ then these results will still hold.

340 Now consider the case where the additional couplings are equal and of order δ , $g_1 = g_2 = \dots = g_{k-1} = s\delta$, where δ and s are as in Theorem 4.2. (See Figure 7 for examples with $N = 8$ or $N = 12$ and $k = 2$.) As discussed in Section 3.1.2, the synchronous solution will exist and will be asymptotically stable since $H'(0) > 0$ (see Figure 2). Further, it follows from Theorem 4.2 if $N = 2kp$ the 2-cluster solution with k nearest neighbours synchronized will exist and will be stable since $H'(\pi) > 0$ and $H'(0) > 0$ from Figure 2. Finally, note that in Figure 2 we have $H_{\text{odd}}(\phi) = 0$ at $\phi \approx \pi/3, 5\pi/3$. Thus from Remark 4.1, we predict that the 6-cluster solution may exist if $N = 6kp$ but no other m -cluster solutions as described in Section 3.1.1 exist. Since this solution is unstable for the case with no additional couplings (see Table 2), from Remark 4.2 we expect that it will be unstable with the additional couplings.

4.1.3. Existence of non-zero time-shifted solution

In this section, we consider the existence of time-shifted solutions as described in Sec. 3.2.1 with phase differences satisfying (12) in networks with $g_1, g_2, \dots, g_k \neq 0$. With non-zero coupling to the first k nearest neighbors, the evolution equation for the phase differences ϕ_i derived from (6) becomes

$$\begin{aligned} \frac{d\phi_i}{dt} = & \epsilon \sum_{j=1}^k g_j \left[H \left(\sum_{s=0}^{j-1} \phi_{i+s+1} \right) - H \left(\sum_{s=0}^{j-1} \phi_{i+s} \right) \right. \\ & \left. + H \left(-\sum_{s=0}^{j-1} \phi_{i-s} \right) - H \left(-\sum_{s=0}^{j-1} \phi_{i-s-1} \right) \right]. \end{aligned} \quad (27)$$

For simplicity, we consider the case $k = 2$. In this case, any equilibrium solution must satisfy the following equation:

$$\begin{aligned} 0 = & \epsilon g_1 [H(\phi_{i+1}) - H(\phi_i) + H(-\phi_i) - H(-\phi_{i-1})] \\ & + \epsilon g_2 [H(\phi_{i+1} + \phi_{i+2}) - H(\phi_i + \phi_{i+1}) + H(-\phi_i - \phi_{i-1}) - H(-\phi_{i-1} - \phi_{i-2})], \end{aligned}$$

where $1 \leq i \leq N$. From (18), we know the second term on the right-hand side is zero. Thus, for existence, the first term must be zero. Using the properties

of the phase differences ϕ_i given in Sec. 3.2.1 yields

$$\begin{aligned} 0 &= \epsilon g_1 [H(\pi - \alpha) - H(\alpha) + H(-\alpha) - H(-(\pi - \alpha))], \quad i = 2q + 1, \\ 0 &= \epsilon g_1 [H(\alpha) - H(\pi - \alpha) + H(-(\pi - \alpha)) - H(-\alpha)], \quad i = 2q + 2, \end{aligned} \quad (28)$$

for $q = 0, 1, \dots, mp - 1$. These equations are satisfied for two conditions: i) for any time shift α if the function H is even; and ii) for $\alpha = \pi/2$ for any H . For most neural network models, H is not an even function suggesting that the only time-shifted solution that may exist has an $\alpha = \pi/2$ shift between cells $2q + 1$ and $2q + 2$ ($q = 0, 1, \dots, mp - 1$) resulting in a 4-cluster solution with $\phi_i = \pi/2$ for all i . This is a cluster solution of the type studied by [31, 7] where the neurons in a given cluster are not adjacent. Results in those papers show that this solution will be stable if and only if

$$g_1 H'_{odd}(\pi/2) + 2g_2 H'_{odd}(\pi)(1 + \cos(2j\pi/N)) > 0, \quad j = 1, 2, \dots, N/2. \quad (29)$$

Finally, we note that since we always consider circulant coupling matrices, the system with k^{th} nearest neighbour and additional coupling will admit m -cluster solutions of the type studied by [31, 7]. Conditions for the stability of these solutions can be found in those papers.

4.2. Numerical Results

Here, we numerically explore the existence and stability of non-zero time-shifted solutions in networks with k nearest neighbor coupling and additional “weak” coupling between first to $(k - 1)^{st}$ nearest neighbors. To make the additional coupling(s) weaker than the primary coupling strength, g_{syn} in (8), we use the scaling factor of $g_{ij} = 0.1$ for $|i - j| \leq k - 1, i \neq j$.

In Fig. 8(a), we simulate a network of $N = 8$ neurons with second nearest coupling ($k = 2$) and weak first nearest neighbor coupling. Fig. 7(a) shows the schematic diagram of network connectivity. The network is initialized in the non-zero time-shifted solution displayed in Fig. 5(a) in which there is a time shift in firing between the two disjoint subnetworks ($\phi_{2q+1} \neq 0, q = 0, 1, 2, 3$) which results in a 4-cluster solution. To test its existence and stability in the presence of additional coupling(s), we set the scaling factor for the first nearest neighbor coupling strength to zero until $t = 1, 500$ ms (Fig. 8(a), top row) then set its value to 0.1 to turn on the weak additional coupling. Our results show that the non-zero time-shifted solution eventually transitions to the stable 2-cluster solution with zero time-shift ($\phi_{2q+1} = 0, q = 0, 1, 2, 3$) (bottom row). The initial solution is close to the time-shifted solution with $\phi_{2q+1} = \alpha = \pi/2$. The above analysis in Sec. 4.1.3 indicates that the $\phi_{2q+1} = \alpha = \pi/2$ solution exists with first and second nearest neighbor coupling but based on Eq. (29) is unstable since $H'_{odd}(\pi/2) < 0$ (specifically, (29) is not satisfied for $j = 4$) which agrees with our simulations.

As another example, we consider a network of $N = 12$ neurons with third nearest neighbor coupling ($k = 3$) and weaker first and second nearest neighbor coupling that is initialized in a time-shifted, 6-cluster solution (Fig. 8(b), top row). Before $t = 1, 500$ ms, the scaling factor for the weaker first and second

(a) Transition from 4-cluster (top; Fig. 5(a)) to 2-cluster solution (bottom; Fig. 3(a)) for $N = 8$

(b) Transition from 6-cluster (top) to 2-cluster solution (bottom; Fig. 4(a)) for $N = 12$

(c) Transition from 9-cluster (top; Fig. 3(d)) to 18-cluster solution (bottom) for $N = 18$

Figure 8: (a) and (b): Time series (left) and its raster plot (right) to show a transition from non-zero time-shifted solution to 2-cluster solution with additional coupling(s); (c): a transition from zero to non-zero time-shifted solutions with additional first nearest coupling. Additional coupling(s) were applied at $t = 1500$.

nearest coupling is zero, and then it is set to 0.1. Results show that the solution transitions to the 2-cluster solution with zero time-shift ($\phi_{3q+1} = \phi_{3q+2} = 0$, $q = 0, 1, 2, 3$) that is shown to be stable in Theorem 4.2.

Finally we show simulations that suggest that the 9-cluster solution for $N = 18$ which exists with only second nearest coupling ($k = 2$), shown in the top row of Fig. 8(c) (same as Fig. 3(d)), no longer exists when the weak first nearest neighbor coupling is added. After $t = 1,500$ ms, when the weaker first nearest coupling is turned on, the 9-cluster solution transitions to the 18-cluster solution with equal phase difference between adjacent cells ($\phi_i = \pi/18$, for $i = 1, \dots, 18$, bottom row of Fig. 8(c)). These simulation results agree with the result of Theorem 4.1, which states that the only m -cluster solution, with adjacent neurons synchronized, that can exist with additional nearest neighbor coupling is that for $m = 2$. Since for $N = 18$ and $k = 2$ the 2-cluster solution is never possible, no m -cluster solution with adjacent neurons synchronized can occur. The network thus evolves to another solution type, namely the 18-cluster solution of the type studied in [31] with equal phase differences between adjacent neurons. We have verified that this solution is predicted to be stable by the phase model analysis [31, 7].

5. Discussion

In this paper, we study 1-D, weakly coupled inhibitory neuron networks to investigate the existence and stability of m -cluster solutions, in which clusters consist of groups of adjacent cells in the network that fire together. To simply describe non-monotonic, distance-dependent connectivity [38], we first consider k^{th} nearest neighbor symmetric coupling such that each neuron in the 1-D ring is connected with its k^{th} nearest neighbors only. This connectivity scheme results in the decomposition of the network into k disjoint subnetworks.

Our analysis for the k^{th} nearest coupling only case shows that spatially localized, m -cluster solutions exist and can be stable. The existence of the solutions relies on the network structure rather than the network size N . The stability depends on the interaction function H and the strength of connections between cells. We use our phase model results to predict the behavior of several specific values of N and k . In particular, we can predict the number of clusters generated in the network and their stability. These results are confirmed by numerical simulations illustrating various m -cluster solutions for different network sizes as well as k values.

To study more generalized coupling, we consider the case where the network has coupling between the first to k^{th} nearest neighbours. We show if the additional coupling (first to $(k - 1)^{th}$) strength is sufficiently weaker than that of the k^{th} neighbor coupling then the results with no additional coupling persist. For slightly stronger additional coupling, only two of the m -cluster solutions are guaranteed to persist for any model network. The synchronous (1-cluster) solution exists for any size of network and the 2-cluster solution exists if the network has an even number of neurons. We provide stability conditions for these two solutions. These results are confirmed with numerical simulations.

With only k^{th} nearest neighbor coupling, in addition to the spatially localized, m -cluster solutions, our results demonstrate that solutions with more clusters exist but cells in the same cluster are spatially dispersed in the network. These solutions correspond to non-zero time-shifted solutions that emerge due to the decomposition of the network into disjoint subnetworks. In these solutions, the disjoint subnetworks are not synchronized but their cells fire with a non-zero time shift. However, when the additional coupling(s) are introduced to the network, the previously disjoint subnetworks become connected and, consequently, all but one of the non-zero time-shifted solutions no longer exist, as shown in Figure 8. The solution that retains existence displays clusters with the same phase shift between all pairs of adjacent neurons and cells in the same cluster dispersed throughout the network.

This study extends our previous work [31] in that the existence and stability conditions of m -cluster solutions include k^{th} nearest neighbor coupling with asymmetric weights. Previously, we only worked with a symmetric connectivity matrix for neurons that are coupled to their first and/or second nearest neighbors on both sides. Here, we also perform a perturbation analysis to discuss the existence and stability conditions with additional coupling(s) to the k^{th} nearest coupling. Moreover, we extend our previous work by considering nonuniform phase differences between nearest neighbors.

Model limitations and future directions. Despite the richness of our analytical and numerical results, our results are based on the phase model reduction of an inhibitory network which explicitly assumes that neurons are weakly coupled to each other. Phase models have limitations even for studying networks of oscillatory neurons [42, 4].

Synchronization in inhibitory networks can also be obtained by mechanisms known as Interneuron Network Gamma (ING) or Pyramidal Interneuron Network Gamma (PING) [43, 24, 39, 40, 35]. In these mechanisms, synchronization of inhibitory neurons results due to gating of the timing of firing by synaptic inhibition such that cells are suppressed while inhibitory synaptic currents are active and are able to fire when synaptic currents decay. Thus, this mechanism assumes sufficiently strong synaptic coupling between cells so as to prevent firing. Our results apply to the case of weak coupling in the inhibitory network where synaptic interactions perturb the timing of cell firing without suppression of firing.

Our results focus on 1-D networks whereas the recent study [38] on non-monotonic distance-dependent connectivity considered a 2-D network. Thus, our future study would extend the 1-D network model to investigate the 2-D network behaviors. In the 2-D setting, the diagonal neighbor coupling is a feature which could not be considered in our 1-D model. Thus we will consider its effects on cluster formation in 2-D inhibitory networks in conjunction with non-monotonic distance-dependent network connectivity.

Conclusions. Our work may help understand cluster formation in the striatum [6, 23]. Note that the striatum has sparse, weak, unidirectional coupling [3]. Our results show that spatially localized clusters can occur when there are very few connections in the network. There has been some dispute as to

whether clusters in the striatum are truly spatially compact, that is, involve only
 475 nearby neurons [23]. Our work shows that spatially compact clusters may occur,
 but that clusters which involve multiple groups of nearby neurons may also
 occur. Such solutions could correspond to clusters that involve both localized
 and longer range correlations between neurons as observed in [23]. Here we use
 reciprocal coupling in our simulations, but the mathematical results would apply
 480 to unidirectional coupling by setting some connections to zero. For example
 Theorem 3.1 is valid if $g_k > 0$ and $g_{N-k} = 0$. Since we use a general interaction
 function H , the mathematical results also apply to excitatory neurons so could
 be used to study cluster formation in the dentate gyrus [32].

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7. CRediT Author Statement

490 All authors contributed to conceptualization, methodology, writing the original
 draft, reviewing and editing the final manuscript. SAC, JM, ZT and XW
 conducted the phase model analyses. VB and HR implemented and conducted
 numerical simulations.

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