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SYNCHRONY AND DESYNCHRONY IN NEURAL OSCILLATORS

DISSERTATION

Presented in Partial Fulfillment of the Requirements for
the Degree Doctor of Philosophy in the Graduate
School of The Ohio State University

By

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1997

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Theoreticians have proposed that correlations in the firing times of groups of neurons may be an efficient representational framework for information processing and the feature binding problem. In the last decade, many observations of synchronous oscillations in the brain have given support to the above proposal and have created much interest in understanding how synchrony arises. We analyze locally coupled networks of neurobiologically based oscillators in order to understand how synchrony and desynchrony arise, and we propose several oscillator networks for perceptual organization and feature binding.

We examine locally coupled networks of integrate-and-fire oscillators and find that they synchronize at times proportional to the logarithm of the system size. We create a means of desynchronization and propose a network for image segmentation. The abilities of this network are demonstrated using real images.

We examine locally coupled networks of relaxation oscillators. These neurobiologically based oscillators exhibit properties of fast synchronization and we derive conditions necessary to ensure synchrony occurs. Several types of desynchronous solutions are also examined.

We examine how the interaction between oscillators affects the time to synchrony. Our data indicate that a discontinuous interaction results in better properties of synchronization than networks with smooth interactions, regardless of whether the oscillators are of
relaxation or sinusoidal type.

Also studied are relaxation oscillators with time delay coupling, a more biologically realistic model of neuronal behavior. Our analysis shows that a pair of oscillators can achieve loose synchrony for a wide range of initial conditions and time delays. We present simulations for larger networks.

In locally coupled networks of Wilson-Cowan oscillators a mechanism is shown for achieving fast synchrony (in one cycle) and we prove that networks of these oscillators after linear approximation can synchronize given a sufficient coupling strength. We also demonstrate a technique for desynchronizing multiple groups of oscillators.

A major theme of this work is examining how the rate at which oscillator networks synchronize is related to their size. We examine several different types of oscillators and find evidence for four different scaling relations, thus indicating one means of categorizing these systems.
To my family
I came to graduate school with the rather broad goal of doing original and interesting research. I had trouble finding funding in the Physics department, but fortunately, I met Dr. DeLiang Wang in the Computer and Information Science department. His research deals with complex dynamical systems - a rich and mathematically challenging topic. Beyond that, Dr. Wang’s research is based on the brain, which is one of the most interesting mysteries on Earth.

Not only were the topics interesting, but Prof. Wang provided an inspiring and supportive atmosphere. He encouraged me to learn the basics and gave insightful guidance when I was struggling with confusing research problems. He is devoted to science and his students. I also appreciate the efforts of Prof. Jayaprakash, my physics adviser, who supported my somewhat unusual route to a Ph.D., and who also gave me invaluable advice as to how to approach problems. Both advisers deserve thanks for improving the quality of my research and of my writing. Special thanks go to Prof. Wang for his relentless correction of the logical, grammatical, and other errors that occurred in my writing.

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46 Loose synchrony in a two dimensional grid of oscillators. This figure displays the temporal activities of every oscillator from a $10 \times 10$ network. Each oscillator is coupled with its four nearest neighbors. The network achieves stability by the third cycle, and for all neighboring oscillators $i$ and $j$, $|\Gamma(y_i(t), y_j(t))| \leq \tau$. The parameter values used are the same as in Figure 45.

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48 Desynchronous solutions in a chain of relaxation oscillators. If the coupling strength is below the lower bound specified in (4.15), desynchronous solutions can arise. In this simulation, $\alpha_R = 1$, which is below the lower bound specified in (4.15), and all other parameters are as listed in the caption of Figure 44. Oscillators 12 and 13 had initial conditions such that they are able to remain in a desynchronous relationship. All other neighboring oscillators are loosely synchronous.

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The histograms of $\gamma^k$ for two dimensional networks. These histograms are based on simulations with initial conditions as described in the caption of Figure 50. The data was taken during the 11th cycle. The average time needed to achieve stability was approximately 3 cycles. (A) and (B) are the results for $5 \times 5$ and $10 \times 10$ oscillator networks respectively. The data for $\gamma^k$ in (A) and (B) are based on 2530 and 1320 simulations respectively. The parameter values used are the same as in the caption of Figure 45.

A plot of the evolution of the maximum time difference for 1980 trials. The trials are arranged in order from largest to smallest to emphasize that most of the trials resulted in a decrease in $\gamma^k$. The thick line is a plot of $\gamma^2 - \gamma^1$ and $\gamma^3 - \gamma^2$ is indicated by the thin line. The network is almost stable by the third cycle and the change in $\gamma^3 - \gamma^2$ is not nearly as great as for $\gamma^2 - \gamma^1$. The dotted line displays $\gamma^7 - \gamma^6$. The parameters used are the same as in the caption of Figure 42 with the exceptions that $\lambda = 7$ and $\tau = 0.04T$.

Basic architecture of the model. The oscillators are arranged in a 2-D grid, where each square on the grid represents an oscillator. The connections between oscillators are local. Three representative situations are shown in the figure, where an oscillator located at a black site is connected only to oscillators on adjacent striped squares. Note that we do not use periodic boundary conditions. The global inhibitor (GI) is pictured at the top and is coupled with all oscillators in the network.

A diagram showing the connections that each excitatory and inhibitory unit has within an oscillator. Triangles represent excitatory connections, and circles represent inhibitory connections.

The y nullcline (small dashes), x nullcline (large dashes), and trajectory (solid) for a single oscillator are displayed. The parameters are $a = 10.0$, $b = 7.0$, $\phi_x = 4.075$, $c = 10.0$, $d = 10.2129$, $\phi_y = 7.0$, $\sigma = 2.1$, $\eta = 7.0$, and $D = 0$. 

\( \varepsilon = 0.025 \)
56 Input used for the network. Black squares denote oscillators that receive input. Starting clockwise from the upper left hand corner, we name the objects as follows: a helicopter, a thick addition sign, a tree, a truck, and a house. .......................... 167

57 A diagram showing the interactions between the excitatory and inhibitory units in a chain of oscillators. See the caption of Figure 54 for the meaning of the notations. ................................................................................................................................. 168

58 An enlarged diagram of the upper left hand corner of Figure 55 that displays the nullclines of two interacting oscillators. The two dashed curves are the nullclines for the leading oscillator, and the black filled circle represents the position of the leading oscillator. The interaction term causes the y-nullcline (short dashed curve) of the leading oscillator to be perturbed to the left so that it intersects the x-nullcline (long dashed curve). This creates an attracting fixed point, and a saddle fixed point. The interaction term does not impede the motion of the trailing oscillator (open circle), which will approximately follow the path given by the solid curve. The leading oscillator will be trapped at the attracting fixed point until the distance between the oscillators is very small. ................................................................................................. 177

59 This graph displays the combined $x$ values of 34 oscillators with respect to time. An accurate synchrony is achieved within the first cycle. The random initial conditions used were restricted to the range of the limit cycle, i.e. $0.0 \leq x \leq 0.5$ and $0.0 \leq y \leq 1.0$. Parameters $\alpha_w = 90$ and $\sigma = 0$. ...................... 179

60 A close look of the triggering region (black filled triangle), the $x$ nullcline (short dashed curve), and the $y$ nullcline (long dashed curve). The value $\mu = 0.048$ was used in the simulations, but other nearby values result in desynchronization also. The other parameters were $U = 2.9$ and $v = 2.0$. ......................... 182

61 The activities of two oscillators and the global separator are plotted with respect to time. The two oscillators are desynchronized during the second cycle. The shape of the first oscillator is significantly altered because its speed is increased by GI. All parameters are the same as those listed in Figure 55 and Figure 60. .................. 183

62 Each picture represents network activity at a time step in the numerical simulation. The size of the circle is proportional to the $x$ activity of the corresponding oscillator. (A) The oscillators have random positions on the phase plane at the first time step. (B)-(F) Successive time steps that correspond to the maximal activities for each group of oscillators. $\alpha_w = 10.0$ in this simulation. The other parameters are as specified in the captions of Figure 55 and Figure 60. The random initial conditions used were restricted to the range of the limit cycle, namely, $0.0 \leq x \leq 0.5$ and $0.0 \leq y \leq 1.0$. .................................................. 185

63 The plot labeled “GI” displays the activity of the global separator with respect to

xx
time. The other five plots display the combined $x$ activities of all the oscillators stimulated by the corresponding object. Each of the five oscillator groups is synchronized within the first cycle, and by the second cycle is desynchronized from the other oscillator groups.

A diagram showing the qualitative direction of motion for system (A.1). The two curves represent the $x$- and $y$-nullclines.

(A) The limit (thick curve) cycle for (A.1) with $\varepsilon = 1.0$. The $x$- and $y$-nullclines are the thinner curves. (B) The temporal evolution of the $x$-variable and the $y$-variable.

Three different limit cycles and their respective plots as a function of time are shown for three different values of $\varepsilon$. (A) $\varepsilon = 0.33$. (B) $\varepsilon = 0.1$. (C) $\varepsilon = 0.01$.

A plot of the nullclines and the synchronous limit cycle of a relaxation oscillator defined in (A.2). The dotted cubics are the excited and unexcited $x$-nullclines, and the dash-dot curve is the $y$-nullcline. The thick solid curve represents the synchronous limit cycle for a pair of oscillators, which is the result of numerical calculation. The parameters used are $\alpha_R = 2$, $\theta = -0.5$, $\kappa = 5000$, $\lambda = 8$, $\gamma = 12$, $\varepsilon = 0.005$, and $\beta = 1000$.

The trajectories of the three cases that lead to synchrony in a pair of coupled oscillators. In (A), (B), and (C) the first oscillator to jump is given by the dotted line and the second is denoted by the solid line. (A), (B) and (C) display the evolution of the system in $x$-$y$ space. (D), (E), and (F) display the $x$-activities of both oscillators as a function of time. The parameters used are the same as in Figure 67.

An example of a desynchronous solution that arises because the coupling strength is not large enough. The first oscillator to jump is given by the dotted line and the second is denoted by the solid line. (A) displays the evolution of the system in $x$-$y$ space, and (B) displays the $x$-activities of both oscillators as a function of time. The parameter $\alpha_R = 0.8$ was used with the other parameters as in Figure 67.
CHAPTER 1

INTRODUCTION

1.1 Coupled Oscillators

In 1665, Christiaan Huygens [Huygens, 1673] noted "When we suspended two clocks so constructed from two hooks imbedded in the same wooden beam, the motions of each pendulum on opposite swings were so much in agreement that they never receded the least bit from each other and the sound of each was always heard simultaneously. Further, if this agreement was disturbed by some interference, it reestablished itself in a short time. For a long time I was amazed at this unexpected result, but after a careful examination finally found that the cause of this is due to the motion of the beam, even though this is hardly perceptible. The cause is that the oscillations of the pendula, in proportion to their weight, communicate some motion to the clocks. This motion, impressed onto the beam, necessarily has the effect of making the pendula come to a state of exactly contrary swings if it happened that they moved otherwise at first, and from this finally the motion of the beam completely ceases." The study of coupled oscillators has since become an active branch of mathematics, with applications in physics, biology, and chemistry. In physics, one encounters coupled oscillators in arrays of Josephson junctions [Chung et al., 1989, Blackburn et al., 1994], in modelling molecules [Sage, 1994], and in coupled lasers..."
[Dente et al., 1990]. Coupled oscillators are also prevalent in biological systems. Most organisms appear to be coupled to various periodicities extant in our surroundings, such as the rotation of the earth about the sun, the alternation of night and day, or the tides. Not only do organisms exhibit periodicities due to their environment, but they also exhibit innate periodic behavior. Breathing, pumping blood, chewing, and galloping are examples of rhythmic patterns of motion.

One of our main concerns is understanding how synchrony is achieved in locally interacting populations of oscillators, where synchrony means that oscillators have the same frequency and phase. Some examples of biological synchrony occur between organisms, such as the synchronous flashing of fireflies in Southeast Asia [Smith, 1935], and the synchronous chirping of crickets [Walker, 1969]. Other types of biological synchronization occur between cells, such as the synchronous firing of the pacemaker cells of the heart [Peskin, 1975] and the synchronous neural activity seen in many different regions of the brain [Singer and Gray, 1995].

Our work is motivated specifically by synchronous neural activity observed in the brain. Synchrony in neural activity has been observed in several mammals [Singer and Gray, 1995], as well as in amphibians [Prechtl, 1994] and insects [MacLeod and Laurent, 1996]. Synchronous neural activity has been measured across 14 mm in the monkey motor cortex [Murthy and Fetz, 1992] and across different hemispheres of the brain in the visual cortices of cats [Engel et al., 1991]. The wide range of brain regions which exhibit synchronous activity, and the diversity of organisms in which synchrony is observed, suggest that neural synchronization may be fundamental to biological information processing.
To illustrate the phrase neural synchrony, we display data from Steriade [Steriade, 1994] in Figure 1, which shows several different recordings from three different brain regions of a cat. The top three graphs represent the firing times of neurons in cortical area 5, cortical area 7, and the thalamus. A simultaneously recorded electroencephalogram (EEG) is the fourth graph in the figure and the bottom row of graphs display the cross-correlations between the firing times of the neurons from the three different brain regions. The cross-correlation has a peak near zero indicating near perfect synchrony in the firing times of these cells. The peaks in this cross-correlation decrease to zero within a few periods, indicating that the period is not fixed. This figure demonstrates synchrony of the slow rhythm (approximately 0.6 Hz) which occurs during sleep.

Figure 1. Synchronization in cortical and thalamic cells. The first three graphs are simultaneous extracellular recordings of neurons from cortical areas 5, 7, and the thalamus. The fourth plot is of the simultaneously measured EEG. The three plots at the bottom are cross-correlations of the firing times of pairs of the three different recordings of neurons.
The dynamical systems we study are based on simplified models of neuronal oscillators. While these oscillator networks have relations to neurophysiology, their links to physics are less straightforward. The concepts of energy and temperature in these networks resist definition and these systems are at best classified as non-equilibrium systems. Also, we study noiseless systems, and the mathematical techniques of equilibrium statistical mechanics are difficult to apply. However, many concepts useful in describing and understanding equilibrium systems, like spin systems, are useful in attempting to understand these non-equilibrium biological networks.

1.2 The Feature Binding Problem

Theoreticians have proposed that the temporal correlation of neural groups may be an efficient representation for feature binding [Milner, 1974, von der Malsburg, 1981]. In order to fully describe the feature binding problem, the following background is provided. First, neurons in the visual cortex appear to be functionally specialized. For example, some neurons respond best to stimuli of a certain orientation and speed, while other neurons respond best to certain color combinations [Zeki, 1993]. In later stages of the visual hierarchy, there appear to be entire cortical regions which are also functionally specialized, i.e. they are devoted to the perception of specific visual features such as color, motion, or depth [Zeki, 1993, Kandel et al., 1991]. Several clinical cases also offer convincing support for the functional specialization of the cortex. Reports exist of injuries causing loss of color vision [Zeki, 1993], while the perceptions of depth and motion remain. There is also one striking case of an injury resulting in motion blindness [Zihl et al., 1983]. The patient had difficulty perceiving motion. She had trouble crossing roads because a car that appeared far away would suddenly be nearby. The patient's perception
of color, texture, depth, and her ability to recognize shapes were unimpaired. Within this framework, it becomes nontrivial to understand how these features, which are "processed" by different neurons in different cortical areas, are linked to form the perception of a coherent whole; this is the feature binding problem. Given that many objects exist in a typical natural scene, and that each object can have different features, such as texture, brightness, orientation, color, motion, depth, etc., it becomes obvious that there are a combinatorial number of linkages between features and objects.

There are two primary and competing approaches to bind the features of an object together. The first approach assumes that it is the average firing rate of a neuron which conveys information, which is the traditional assumption [Zeki, 1993, Singer, 1993]. Since the individual firing times of neurons do not encode any information, then the neurons in these separate regions of the visual cortex must be grouped and segregated by some other mechanism. It has been proposed that neurons become more selective as one proceeds from lower to higher visual brain areas [Barlow, 1972]. Instead of responding preferentially to a direction and velocity, a neuron may respond best to a single object. This is called the grandmother-cell representation. One would expect a large region of the brain to be devoted to this task given the large number of objects humans can recognize, but currently, evidence does not strongly favor this proposal. There are cortical areas that appear to be selective to classes of patterns [Fujita et al., 1992] (faces and hands for example [Desimone et al., 1984, Perrett et al., 1987]), but these are not object-specific cells. Another problem with this proposal is that objects must be recognized in order to be deemed as objects, which makes the categorization of an object as "unfamiliar" problematic. Also, the features of an object can be bound together preattentively, suggesting that feature binding and segregation occur without recognition, and therefore without the aid
of grandmother-cells. The second approach uses temporal correlation in the firing times of neurons to create linkages. Here the precise firing times of neurons are important. Both grouping and segregation can be encoded by the firing times of groups of neurons; and other, more complex mechanisms need not be proposed. Using temporal correlation as a framework in which to represent feature binding appears elegant. Furthermore, it appears to be possible given the known physiology of the brain.

Several experiments have been proposed to test the hypothesis that correlations in the firing times of neural groups may have a role in information processing. Gray et al. [Gray et al., 1989] moved a single long bar of optimal orientation, velocity, and preferred direction through the receptive field of recorded neurons in the primary visual cortex of an anesthetized cat. A typical response to this stimulus is shown in Figure 2, (reproduced from Gray and Singer [Gray and Singer, 1989]). The local field potential is shown in the top graph, and the multiunit activity is shown in the second graph. The third and fourth plots are portions of the first two plots with an expanded time scale. The local field potential indicates the combined activity of many neurons (100’s or 1000’s). The multiunit activity indicates the firing times of a few neurons in the immediate vicinity of an electrode. The neurons generating these spikes fire at nearly the same time, although their activity is not rigidly periodic. This synchronous activity has an average frequency of approximately 40Hz and ranges from 35-50Hz. Gray and Singer found that the neural response to the stimulus exhibited synchronous neural activity over a distance of 7mm in the cortex and that synchrony occurred 25-50 ms after stimulus onset. When two separate and smaller bars moving in the same direction passed through the cat’s visual field, there was a decrease in the synchrony between the neural responses to the separate bars. When two separate bars moved through the cat’s visual field in opposite directions, there was no
Figure 2. The local field potential (first graph) and the multi-unit activity (second graph) in response to a moving bar. The third and fourth graphs are portions of the first two graphs with an expanded time scale.

correlation in the neural responses between the two bars. This suggests that an object may be encoded by the synchronous firing times of neurons responsive to that object, and that the firing times of these neurons are uncorrelated with the firing times of the neurons responsive to different objects. The animals in these experiments were unconscious, which suggests that neural synchrony in the visual cortex may be a process that is not governed by recognition or attention. Also, in this area of the cat visual cortex the longest reported connection between neurons is approximately 4mm [Hirsch and Gilbert, 1991], thus implying that synchrony is achieved through local interactions.
Based on the above experiments, one can conjecture that a single object is represented by many neurons, each of which is firing in synchrony. Different objects may be represented by different groups of neurons which have different firing times. A simple implementation of this would be to represent each feature (or pixel) in an image with an oscillator. An example of this is shown Figure 3A. Here, each grid of the array consists of an oscillator coupled with its four nearest neighbors. The oscillators receiving stimulus (black squares) begin to oscillate, while the oscillators that do not receive stimulus (white squares) remain inactive. All active oscillators have the same frequency. The oscillators comprising a single object begin to oscillate in synchrony, while the oscillators representing different objects have distinct phases of oscillation. This form of temporal correlation is called oscillatory correlation by Wang and Terman [Wang and Terman, 1995]. These authors have proposed a network that performs oscillatory correlation and the temporal activity of their network is shown in Figure 3B using Figure 3A as the input. The temporal
correlation of the oscillators (in this case synchrony) allows the features (pixels) of a single object to be bound together, while allowing different objects to be segregated. The network can be said to represent the three objects simultaneously.

1.3 Relation to Computer Vision

In our work, the primary goal of performing synchronization and desynchronization is for visual processing (although feature binding through oscillatory correlation can be used in other sensory perceptions [Baird, 1986, Wang, 1996b]). The stage of visual information processing that these networks most clearly correspond to is that of segmentation. Segmentation is typically labelled as a "low-level" processing task [Pavlidis, 1973, Brad-dick and Atkinson, 1982]. In Figure 3 for example, the oscillator network segments the three objects from the background, and also from one another. In segmentation, the pixels of an image are grouped together using some basic visual features such as intensity, color, or texture [Haralick and Shapiro, 1985, Sarkar and Boyer, 1993]. After segmentation, the image is then suitably prepared for "higher-level" tasks, such as pattern recognition. The reason for this is that it should be more efficient to perform recognition after the image has been broken into big chunks, or objects. Performing recognition at the pixel level would require much more computation. Scene segmentation is largely regarded as unsolved [Pal and Pal, 1993]. Despite decades of research (for reviews see [Zucker, 1976, Haralick and Shapiro, 1985, Pal and Pal, 1993]), it remains a computation roadblock for the computer vision community.

We present some real images which have been segmented using an oscillator network in Chapter 2. These results are obtained using procedures nearly identical to those developed in Wang and Terman [Wang and Terman, 1997]. Although our segmentation
results are arguably no better or worse than other conventional computer vision approaches, our networks offer some advantages that traditional algorithms lack. The first advantage is that our networks are based on the brain, which offers the only working image processing paradigm. Our networks are related to the neurophysiology of the brain, and they make use of local computations. Many of the techniques from computer vision make use of global computations, such as averages [Pavlidis, 1977] or clustering [Jain and Dubes, 1988]. Experiments from visual psychophysics and neurophysiology indicate that global information is not always necessary to segment images [Nothdurft, 1994]. Our networks perform local computations, which is neurophysiologically supported, and further, more suitable for VLSI implementation.

1.4 Neural Network Approaches

The classification abilities of neural networks have been used to perform segmentation based upon pixel classification [Kohonen, 1995, Koh et al., 1995, Raghu et al., 1995]. However, these classification schemes require that the number of clusters be specified a priori. This requirement is a drawback since segmentation should reveal how many objects are in a given image. Also, all of these networks must be trained, but, as noted previously, scene segmentation does not require recognition. Further, these networks do not have the ability to represent multiple objects simultaneously - a serious drawback since most natural scenes contain many objects.

Temporal correlation offers an elegant means of representing multiple objects simultaneously. The discovery of synchronous oscillations in the visual cortex has created a flurry of activity in attempts to apply oscillator networks to the problems of scene segmentation. Oscillator neural network models simulating the experimental results have been
proposed [Schuster and Wagner, 1990, König and Schillen, 1991, Grossberg and Somers, 1991, Sompolinsky et al., 1991, Chawanya et al., 1993, Grannan et al., 1993, Wang, 1993a], and have been used to explore the ability of oscillatory correlation to solve the problems of pattern segmentation and feature binding [Sporns et al., 1989, Baldi and Meir, 1990, Horn et al., 1991, Hummel and Biederman, 1992, von der Malsburg and Buhmann, 1992, Murata and Shimizu, 1993, Schillen and König, 1994, Terman and Wang, 1995, Hopfield and Herz, 1995]. To be used as a solution for the feature binding problem an oscillatory network must be able to perform synchronization and desynchronization. Of the models proposed, only Terman and Wang [Terman and Wang, 1995] prove that their network can achieve synchrony. The others demonstrate the behavior of their networks through computer simulations. Also, the authors (excepting [Terman and Wang, 1995]) do not examine how the time needed to achieve synchrony scales with the network size. This is an important issue because in the models proposed, no real images were segmented; only results for toy problems, as in Figure 3, were shown. How their networks can be utilized for image processing remains unknown unless the behavior of their networks at larger scales (say $256 \times 256$) are known. To the best of our knowledge, only Wang and Terman [Wang and Terman, 1997] segment real images with an oscillatory neural network. Also, most of these models do not address the task of desynchronization. Several authors consider this issue [von der Malsburg and Buhmann, 1992, König and Schillen, 1991], but they only demonstrate desynchronization between two different groups of oscillators. Terman and Wang [Terman and Wang, 1995] and Campbell and Wang [Campbell and Wang, 1996] provide two networks that are able to segment more than two objects.
1.5 Statement of Main Goal, and Related Issues

One of the main goals of this study is to understand how synchrony arises in finite, locally connected networks of neural oscillators. Because of the complexity of the problem, the networks we study are simplified as much as possible. The connections are only between nearest neighbors, and all the oscillators are identical. The interactions between oscillators are also identical, although not always symmetrical. Noise is not analyzed, although it is used in simulations to test the robustness of these networks.

Local connections are examined not only because of their basis in neurophysiology [Kandel et al., 1991, Hirsch and Gilbert, 1991], but also because they may be required for scene segmentation [Sporns et al., 1991, Wang, 1993b]. Specifically, in a two dimensional array of oscillators, where each oscillator represents an element in a sensory field, all to all couplings indiscriminately connect multiple objects. All pertinent geometrical information about each object, and about the spatial relationships between objects is lost. Because this spatial information is necessary for object recognition and segmentation, it must be preserved as effectively and as simply as possible. The use of local couplings is one method of maintaining such spatial relationships.

We are not only interested in the property of synchrony, but in how fast it is attained. The neurophysiological data indicate that the neural response to visual stimuli synchronizes quickly, in 25-50 ms, or 1-2 periods of oscillation assuming a 40 Hz frequency [Gray et al., 1989]. Thus, in the brain some form of self-organization occurs within a relatively short time. As previously noted, the features of an object are bound together before recognition occurs. If feature binding is necessary for recognition, then recognition can only occur after feature binding. Psychophysics experiments [Biederman and Ju, 1988] indicate that recognition can take place within 50-100 ms after stimulus presentation. Though this
does not support temporal correlation as a means of feature binding, this evidence does not refute it either. If synchrony underlies such basic cognitive processes as scene analysis and object recognition, then intuitively it must occur quickly to be useful in a rapidly changing environment.

Desynchronization is another topic we study. In order for different objects to be represented simultaneously, different groups of oscillators must be desynchronized while synchrony within each group of oscillators is maintained. In the networks studied here, in which there is only a single frequency, this corresponds to separating the phases of different objects. This is an important task. If two or more groups of oscillators happen to have the same phase, then they will be mistakenly grouped together. This probability of accidental synchrony [Hummel and Biederman, 1992] can be substantial when one considers that the effects of noise and the time needed to achieve synchrony require that a tolerance of phase differences be allowed. Also, as the number of groups increases, the possibility of accidental synchrony increases significantly. Some form of desynchronization is necessary to avoid this problem. In two of the networks we examine, mechanisms which perform desynchronization are demonstrated.

Another topic of interest is that of time delays in the interactions between oscillators. The speed of neural signal conduction is relatively slow, around 1 m/s in unmyelinated axons [Kandel et al., 1991, Traub et al., 1996]. For two neurons that are separated by 1 mm, the time delay is approximately 4% of the period of oscillation (assuming a 40 Hz frequency). How neural synchrony is achieved in the presence of significant time delays is an important question. We will examine time delays in a pair of neural oscillators in which an analytic solution can be found. Simulations are then used to help understand how time delays affect synchrony in larger populations of oscillators.
1.6 Background Knowledge

Achieving synchrony in locally coupled populations of oscillators has not been a widely studied topic. There are no general classifications describing the forms of interactions necessary for synchrony using a given type of oscillator. Below, we briefly review a few of the papers relevant to synchrony in networks of oscillators. This is not meant to be a comprehensive review, as more papers will be cited when relevant in later Chapters.

Much of the work done on populations of oscillators deals with the simplest description of limit cycle behavior, the phase oscillator,

$$\dot{\phi}_i = \omega_i + \sum_j J_{ij} G(\phi_i, \phi_j) \tag{1.1}$$

where the rate of change in the phase of oscillator $i$ is given by its intrinsic frequency $\omega_i$, and its interaction with its neighbors. The coupling strength and the extent of the coupling are given by $J_{ij}$. The interaction between two oscillators is defined by $G(\phi_i, \phi_j)$. Much work with phase oscillators has been done in globally connected oscillator networks in which each oscillator is coupled with every other oscillator (see [Kuramoto, 1984, Daido, 1993a, Strogatz and Mirollo, 1988] for example).

Niebur et al. [Niebur et al., 1991b] have derived results for locally coupled phase oscillators with a diffusive interaction, $G(\phi_i, \phi_j) = (\phi_i - \phi_j)$, in the presence of noise and with a distribution of intrinsic frequencies; both noise and disorder result in the absence of synchrony. If all the phase oscillators have identical frequencies and there is no noise, then diffusive coupling leads to perfect synchronization [Niebur et al., 1991b].
Another type of oscillator that has been frequently examined is the integrate-and-fire oscillator [Peskin, 1975], (see Section 2.2 for a description). The following authors report that synchrony occurs in locally coupled networks of integrate-and-fire oscillators [Mirollo and Strogatz, 1990, Corral et al., 1995b, Hopfield and Herz, 1995]. Hopfield and Herz [Hopfield and Herz, 1995] report that synchrony occurs, but that it occurs on slow time scales (several hundred periods). In Chapter 2 we reproduce their results and indicate how to adjust parameters to achieve fast synchrony. We also provide numerical evidence that synchrony occurs at times proportional to the logarithm of the network size for one- and two-dimensional systems.

Relaxation oscillators are two variable systems with limit cycle oscillations and they are also frequently studied (see Appendix A for an introduction). Relaxation oscillators are directly related to models of neurons [Fitzhugh, 1961, Morris and Lecar, 1981] and because of their biological relevance, they have a long history as models of biological oscillations (starting perhaps with [van der Pol and van der Mark, 1928]). Somers and Kopell [Somers and Kopell, 1993] and independently Wang [Wang, 1993a] indicated that networks of locally connected networks of relaxation oscillators, strongly coupled with a Heaviside type interaction, have fast properties of synchronization relative to sinusoidal type oscillators. Terman and Wang [Terman and Wang, 1995] further showed that a locally connected network of relaxation oscillators, with certain restrictions on the initial conditions, can synchronize at an exponential rate independent of the size of the network. With more general initial conditions the rate of synchrony alters drastically. In Chapter 3 we provide numerical evidence that the time to synchrony increases as a power law of the size of the network for one-dimensional systems.
Work has also been done on desynchronization in locally coupled oscillator networks [Schillen and König, 1991, von der Malsburg and Buhmann, 1992, Schillen and König, 1994], but none of these authors demonstrate an ability to robustly desynchronize more than two groups of oscillators. Terman and Wang [Terman and Wang, 1995] are the only authors we know of to have performed a rigorous analysis detailing how desynchronization occurs. We present two novel methods for desynchronization of multiple groups of oscillators in Chapter 2 and Chapter 5.

1.7 Outline of Dissertation

Synchrony is investigated in three types of neurally derived oscillators. In Chapter 2 we examine the simplest model of neural behavior, the integrate-and-fire oscillator [Peskin, 1975]. One- and two-dimensional locally coupled networks without noise are examined and we observe that synchrony is always achieved. Furthermore, our data suggest that the average time to synchrony increases logarithmically with the size of the system. We present some heuristic arguments for this behavior. Numerical results are shown that indicate error-correction also occurs on a time scale proportional to the logarithm of the size of the error. Using integrate-and-fire oscillators we are able to desynchronize groups of oscillators without destroying synchrony within each group of oscillators. We then create an oscillator network which is able to segment real images using oscillatory correlation.

In Chapter 3, we perform a similar computational analysis for another, more complex model of neural dynamics, the relaxation oscillator [Fitzhugh, 1961, Morris and Lecar, 1981]. We first examine relaxation oscillators in the singular limit, and our numerical evidence suggest that the time to synchrony scales as a power law of the system size.
for one-dimensional networks without noise. There is a parameter regime for which the
time to synchrony increases as the logarithm of the system size and we characterize the
parameters required to observe this scaling relation. Relaxation oscillators are typically
believed to share some properties with integrate-and-fire oscillators. The results of this
chapter show that there are qualitative difference between these two models and we indi­
cate where these differences originate. We also explore how the type of interaction affects
the time to synchrony in networks of oscillators and find that a discontinuous interaction
results in better properties of synchrony when compared to a smooth interaction. We
believe that this statement might apply to many classes of oscillators and interactions.

In Chapter 4 time delays are introduced into the coupling between relaxation oscilla­
tors. In the specific relaxation oscillator we use, we are able to analyze the behavior of a
pair of oscillators for a broad range of initial conditions and time delays. The time delays
results in a phase relationship we call loose synchrony. We introduce a new measure of
synchrony and use simulations to help understand the behavior of networks of relaxation
oscillators with time delays in one- and two-dimensions. We also describe a range of ini­
tial conditions in which the degree of synchrony does not degrade as the network evolves.

We investigate synchrony and desynchrony in the Wilson-Cowan oscillator in Chap­
ter 5. The Wilson-Cowan oscillator is derived from interacting populations of excitatory
and inhibitory neurons [Wilson and Cowan, 1972]. We create a Lyapunov function for the
piecewise linear approximation to this oscillator, and it is shown that synchrony is
achieved if the coupling strength is large enough. Also, a mechanism is presented for
achieving synchrony within one cycle for a finite number of oscillators. This mechanism
uses strong coupling and is based on an interaction that dynamically creates and destroys

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fixed points in a fashion that assists synchronization. Also shown for this specific model is a means of achieving desynchronization for a small number of objects. Chapter 6 concludes the dissertation.
CHAPTER 2

INTEGRATE-AND-FIRE OSCILLATORS

2.1 Introduction

The integrate-and-fire oscillator is possibly the simplest model of neuronal behavior. A variable associated with the membrane voltage of a neuron is allowed to increase from zero until a threshold is reached. Once the threshold is attained, the oscillator is said to "fire". This variable is instantaneously reset to zero and the process repeats. Although a gross approximation of neural activity, the integrate-and-fire model has been of heuristic value to neurobiology. Peskin [Peskin, 1975] created a network of globally connected integrate-and-fire oscillators to generate synchronous periodic activity; his purpose was to model the sinoatrial node - the group of synchronous neurons which generate the heart beat. Networks of integrate-and-fire neurons have been examined by physicists and mathematicians [Mirollo and Strogatz, 1990, Kuramoto, 1991, Bottani, 1995]. The neural network community has used these oscillators to model neural activity [Eckhorn et al., 1990, Chawanya et al., 1993]. Also, some types of integrate-and-fire oscillators are identical to
the driven elements used in earthquake models, as noted by Corral et al. [Corral et al., 1995a]. Thus, these networks have direct links to studies of earthquake, avalanche, and forest fire models.

We examine only locally coupled networks. Local couplings are more neurobiologically realistic and it has been argued they allow for more powerful and flexible properties of information processing in Section 1.5. In simulations with locally coupled networks of integrate-and-fire oscillators, several authors have observed that they exhibit synchrony, i.e. all oscillators fire at the same time. [Mirollo and Strogatz, 1990, Corral et al., 1995a, Hopfield and Herz, 1995]. Mirollo and Strogatz [Mirollo and Strogatz, 1990] speculated that, a system of such oscillators would “end up firing in unison for almost all initial conditions, no matter how the oscillators were interconnected.” Rigorous mathematical proof indicating that synchrony occurs in these systems remains undiscovered. The answers to many questions about synchronization in integrate-and-fire oscillators are unknown, such as “What is the rate of synchronization?”, “How robust is synchronization in the presence of disorder?”, “How does the rate of synchronization change in the presence of disorder?”, “How do the behaviors of the network change as the dimension of the system changes?”, etc. In this Chapter, we examine the rate of synchronization in locally coupled networks. We provide numerical evidence and a heuristic explanation indicating that the time to synchrony increases with the logarithm of the system size for one- and two-dimensional networks of identical oscillators without noise.
Integrate-and-fire oscillators have been used in the neural network community to perform computational tasks [Hopfield and Herz, 1995], as have pulse-coupled neural networks [Johnson, 1994], a similar type of oscillator. Hopfield and Herz [Hopfield and Herz, 1995] indicate that in locally connected networks of integrate-and-fire oscillators, synchrony occurs on long time scales (more than a hundred periods in a 40 × 40 network). Based on this observation, they view synchrony as biologically irrelevant because computational decisions must be made rapidly by an animal. They then construct a network of integrate-and-fire oscillators which uses local synchrony to perform image segmentation. Local synchrony is a behavior in which clusters of oscillators fire in unison, but the entire network is not synchronous. In their network (as in Figure 3) each pixel of an image is associated with an oscillator. The potential of an oscillator is determined by the grey-level of its corresponding pixel. When one oscillator fires, it can induce its neighbor to fire if the potentials of the oscillators are similar. Different groups of oscillators corresponding to different homogeneous grey-level regions in the image fire at different times. One drawback of this network is that a region of smoothly varying grey-level intensities can be arbitrarily broken into smaller regions. Another drawback is that two different regions with the same intensity would fire at the same time and would thus be improperly grouped together. This occurs because their network does not have a mechanism which actively desynchronizes different oscillator groups.

In our examination of integrate-and-fire oscillators, we have duplicated the results of Hopfield and Herz [Hopfield and Herz, 1995] and further, we have found that synchrony can occur quickly (within a few periods) in these networks by appropriate adjustment of
parameters. We use this property of fast synchrony to create a network for image segmentation (Section 2.9) that does not have the flaws of the network proposed by Hopfield and Herz [Hopfield and Herz, 1995]. Our network actively desynchronizes different oscillator groups so that only a single region fires at a time. Also, because our network achieves synchrony (as opposed to local synchrony), regions with smoothly varying grey-levels are not arbitrarily broken apart. The network architecture we use is directly based on that of Terman and Wang [Terman and Wang, 1995]. Because of the computational efficiency with which integrate-and-fire oscillators can be numerically integrated, we apply our network to real images and segmentation results for two such images are shown.

One of our purposes is to compare how different types of oscillators synchronize when locally connected. In Chapter 3 we study relaxation oscillators (see Appendix A for a quick review of relaxation oscillators). Relaxation oscillators and integrate-and-fire oscillators are frequently assumed to have similar properties. Both models have two time scales and both models are typically examined with an asymmetric, discontinuous coupling [Mirollo and Strogatz, 1990, Somers and Kopell, 1993, Terman and Wang, 1995, Ernst et al., 1995]. However, the two models have significant differences. For example, integrate-and-fire oscillators have an instantaneous interaction, while that between relaxation oscillators is of finite duration. Furthermore, integrate-and-fire oscillators contain only one variable and are computationally simpler. On the other hand, they cannot exhibit amplitude variations as seen in relaxation oscillators. In Chapter 3 we examine relaxation oscillators and observe that in one-dimensional networks the time to synchrony is a power
law in relation to the size of the network. In Section 3.7 we attempt to explain where these qualitative differences between relaxation oscillators and integrate-and-fire oscillators originate.

We first define our integrate-and-fire model in Section 2.2 and examine the behavior of a pair of coupled oscillators in Section 2.3. In Section 2.4 we present our data on the time to synchrony for locally coupled one-dimensional systems of integrate-and-fire oscillators. In Section 2.5 we present similar data for two-dimensional systems of locally coupled integrate-and-fire oscillators. We heuristically explain how the time to synchrony scales as the size of the system in Section 2.6. Our integrate-and-fire oscillator system contains only two parameters and in Section 2.7 we examine how these two parameters are related to the rate of synchronization. In Section 2.8 we examine how quickly synchrony is attained when errors of various sizes are introduced into a two-dimensional synchronized system. Section 2.9 demonstrates how to achieve desynchronization between different groups of integrate-and-fire oscillators while maintaining synchrony within each group. We use this ability of synchrony and desynchrony to perform a temporal labelling task related to image processing in Section 2.10. We discuss our results in Section 2.11.

2.2 Model definition

A network of integrate-and-fire oscillators is defined as follows,

\[ \dot{x}_i = -x_i + I_0 + \sum_{j \in N(i)} J_{ij} P_j(t), \quad i = 1, \ldots, n \]  

(2.1)
Figure 4. A diagram of a pair of integrate-and-fire oscillators with pulsatile coupling. The solid curves represent the potentials of the two coupled oscillators and the dashed lines represent the threshold. The initial potentials of the oscillators are chosen randomly. The oscillator labeled $x_2$ fires first and the potential of $x_1$ increases at that time. Similarly, when $x_1$ fires, the potential of $x_2$ increases. The phase shifts caused by the pulsatile interaction causes the oscillators to fire synchronously by the second cycle. The spikes shown when an oscillator fires are for illustration only.

where the sum is over the oscillators in a neighborhood, $\mathcal{N}(i)$, about oscillator $i$. The variable $x_i$ represents some voltage-like state and we refer to this as the potential of oscillator $i$. The parameter $I_0$ controls the period of an uncoupled oscillator. The threshold of an oscillator is 1. When $x_i = 1$ the oscillator is said to "fire". Its potential is instantly reset to 0 and it sends excitation to its neighbors. The interaction between oscillators, $P_j(t)$, is defined as follows,

$$P_j(t) = \sum_m \delta(t - t_j^m)$$  \hspace{1cm} (2.2)

where $t_j^m$ represents the $m$ firing times of oscillator $j$ and $\delta(t)$ is the Dirac Delta function. When oscillator $j$ fires at time $t$, oscillator $i$ receives an instantaneous pulse. This pulse increases $x_i$ by $J_{ij}$. If $x_i$ is increased above the threshold, then it will fire. Note that information is transmitted between oscillators instantaneously, thus the propagation speed is infinite. Figure 4 displays the temporal activity of a pair of integrate-and-fire oscillators. The oscillators initially have different potentials, but the interaction quickly adjusts their
trajectories so that they eventually fire in unison. When two or more oscillators fire at the same time we call them synchronous. The spikes shown in Figure 4 when an oscillator reaches the threshold are for illustrative purposes only.

The coupling is between nearest neighbors, i.e. an oscillator interacts with two neighbors in one-dimension and four neighbors in two-dimensions. The connection strength from oscillator $j$ to oscillator $i$ is normalized as follows

$$J_{ij} = \frac{a_j}{Z_i}$$

where $Z_i$ is the number of nearest neighbors that oscillator $i$ has, e.g. $Z_i = 2$ for an oscillator $i$ at the corner of a two-dimensional system. The constant $a_j$ is the coupling strength and the subscript $I$ is used to denote that this parameter is used for integrate-and-fire oscillators. The normalization ensures that all oscillators receive the same amount of stimulus, and therefore, have the same trajectory in phase space when synchronous [Wang, 1995].

Note that there are only two parameters in system (2.1), the coupling strength $a_j$ and $I_0$. When oscillator $i$ reaches its threshold, it will fire, and its value will be reset to zero. Oscillator $i$ then sends an instantaneous impulse to neighboring oscillator $j$. If oscillator $j$ is induced to fire, then its value is reset in the following manner,

$$x_j(t^+) = x_j(t^-) + J_{ji} - 1$$

Since oscillator $j$ fires, immediately oscillator $i$ receives excitation and thus $x_i(t^+) = J_{ij}$. Because of this, the period of the synchronous system is shorter than the period of a single uncoupled oscillator. The synchronous period of the system is given by

$$\log\left(\frac{S - \varepsilon}{S - 1}\right)$$
There are many reset rules to choose from and we choose (2.4) because it appears to have
the greatest similarity to the system of relaxation oscillators studied in Chapter 3. This
particular realization of a network of integrate-and-fire oscillators was called "Model A"
by Hopfield and Herz [Hopfield and Herz, 1995].

2.3 A pair of integrate-and-fire oscillators

We now describe the behavior of a pair of integrate-and-fire oscillators. This section is
a short summary of some of the results derived by Mirollo and Strogatz [Mirollo and
Strogatz, 1990]. The trajectory of a single oscillator can be solved analytically, i.e.
\[ x(\phi) = f(\phi) = I_0(1 - \exp(-\phi)), \]
where \( \phi \) can be thought of as a phase, or a local time variable. Note that the function \( f(\phi) \) increases monotonically, \( f'(\phi) > 0 \), and is concave
down, \( f''(\phi) < 0 \). Using \( f(\phi) \) and its inverse, \( g(x) \), one can calculate the return map (Figure
5A) for a pair of pulse coupled integrate-and-fire oscillators. A line of slope 1 is also
shown in Figure 5A for comparison. The horizontal axis represents the initial phase differ­
ence between the two oscillators and the vertical axis represents the phase difference
between the two oscillators after they have both fired once. There are three different
regions in the return map. The first region is in the range of initial conditions \( \phi_1 \in [0, \phi_L] \),
where \( \phi_L = 1 - g(1 - \alpha) \). In this region, the oscillators are near enough so that when one
oscillator fires, the second oscillator is induced to fire as well. We call this the jumping
region, and it has a direct analog in a pair of relaxation oscillators. Once the two oscilla­
tors are in the jumping region, the oscillators always fire at the same time and it can be
shown that their phase difference always decreases. The same is true for the analogous
jumping region in a pair of relaxation oscillators [Terman and Wang, 1995]. The second
region is in the range of initial conditions from \( [\phi_L, \phi_U] \), where \( \phi_U = 1 - g(f(\phi_L) - \alpha) \).
Figure 5. (A) The return map for two pulse coupled integrate-and-fire oscillators. The phase difference between the oscillators before they have jumped ($\phi_1$, horizontal axis) and after they have jumped ($\phi_2$, vertical axis). (B) A plot of the number of cycles needed, $C_J$, before the two oscillators are synchronous as a function of $\phi_1$. Both plots use $I_0 = 1.11$ and $\alpha_I = 0.2$.

For these initial conditions, when the first oscillator fires, the other oscillator receives excitation, but is not induced to fire at the same time (as in the first firing of the second oscillator in Figure 4). Similarly, when the second oscillator fires, the relative phase between the two oscillators again changes, but the two oscillators do not fire in unison. In this region there is an unstable fixed point for which the phase between the oscillators does not change. In the third region, the first oscillator fires and the second oscillator receives excitation, but does not fire immediately. When the second oscillator fires, the first oscillator receives excitation and is induced to fire a second time. We consider this third region as part of the jumping region. In summary, this return map contains a range of initial conditions for which the two oscillators fire together, and another set of initial conditions for which it may take several cycles before both oscillators begin firing together.
In Figure 5B we display the number of cycles needed before the two oscillators are in the jumping region. The horizontal axis in Figure 5B indicates the initial phase separation between the two integrate-and-fire oscillators and the vertical axis indicates the number of cycles needed until the two oscillators are in the jumping region. As expected, initial conditions near the unstable fixed point require more cycles before synchrony occurs.

2.4 Synchrony in One-Dimensional Chains

We observe that synchrony occurs in all locally coupled networks of integrate-and-fire oscillators with positive coupling, with \( f'(\phi) > 0 \), and \( f''(\phi) < 0 \) for all initial conditions tested. This is consistent with the observations of several authors [Mirollo and Strogatz, 1990, Corral et al., 1995a, Hopfield and Herz, 1995]. They each observed that locally coupled networks of integrate-and-fire oscillators always synchronized.

The oscillators in (2.1) can be numerically integrated with an event driven algorithm. In all simulations we use the following procedure.

1. The potentials are chosen from the range [0,1].
2. Calculate the local time, or phase variable, for all oscillators.
3. Find the oscillator nearest to the threshold. The amount of time it needs to fire is calculated and all the oscillators are advanced using this amount of time.
4. The oscillator at the threshold fires. The potential of this oscillator is reset to zero and the potentials of its neighboring oscillators are increased using (2.3).
5. Check if any of the oscillators that have received excitation are above the threshold. If any oscillators are above the threshold, they are reset according to (2.4) and excitation is sent to their neighbors. Repeat this step until no oscillators are above the threshold.
6. Return to step 2.

All trials with locally coupled networks of integrate-and-fire oscillators have resulted in synchrony. Over $10^5$ trials in which the initial conditions were chosen randomly and uniformly in the range $[0, 1]$ have been recorded. These networks were also tested with other, more correlated initial conditions. Networks in which the initial conditions were spin waves also achieved synchrony. The speed with which networks with spin wave type initial conditions attained synchrony was, on average, faster than the time to synchrony using random initial conditions. For long wavelength spin waves, the potentials of the oscillators are near to each other and one oscillator can cause many of its neighbors to fire. Several large groups, or blocks, of oscillators form and fire synchronously during the first cycle. For short wavelengths that are integer multiples of the lattice size, the oscillators also synchronize more quickly than with random initial conditions. Small blocks of synchronous oscillators form, and since these blocks are formed based on repeating patterns of initial conditions the blocks have a spatially repeating pattern. This process repeats until synchrony occurs. This implies that incommensurate wavelengths may take longer to synchronize because spatially repeating patterns of blocks do not form and their interactions with one another would not be uniform. This intuition does appear to be correct; incommensurate wavelengths tend to have longer synchronization times. However, we could not find any initial conditions whose resultant time to synchrony was an order of magnitude larger than the average time to synchrony with random initial conditions (over $10^4$ incommensurate frequencies were tested). Similar tests in two-dimensional networks yield similar results. There are a few solutions which are not synchronous, e.g. initial conditions in which the phase difference between pairs of oscillators is at the unstable fixed point shown in Figure 5A. In numerical tests with these initial conditions, floating point
errors eventually cause small perturbations away from this unstable solution and synchrony quickly results. Furthermore, in trials with periodic boundary conditions (a ring topology), solutions with travelling waves were never observed. Based on these observations, it is our belief that locally coupled networks of integrate-and-fire oscillators always synchronize. Although all of our data has been gathered using one or two specific integrate-and-fire oscillators, we claim that our results generalize to the class of integrate-and-fire oscillators with positive coupling, $f'(\phi) > 0$, and $f''(\phi) < 0$.

We display the temporal evolution of a one-dimensional network in Figure 6. In this graph we display the firing times of all the oscillators in a network of 400 oscillators. Time is shown along the vertical axis and the horizontal axis represents the index of the oscillators. Each dot represents the firing time of one oscillator and each line represents the firing time of a block of oscillators. Near the bottom of the graph, there are many single dots and
small lines. These represent the fact that the oscillators have random initial conditions and initially have distinct firing times. But quickly, by the time $t = 5$, blocks of various sizes have formed. Just after time $t = 5$, at the lower left of Figure 6, oscillators 1-20 fire simultaneously. This block formed from three smaller blocks. Near $t = 30$ there is a single solid line shown, indicating that all the oscillators fired at the same time. Underneath this line, there are two separate blocks of oscillators. One might at first wonder why these two large blocks have merged in just one cycle. This represents the fact that the system has an instantaneous propagation speed. When the oscillator at the border of the left block receives excitation, it is induced to fire. When this oscillator fires it sends excitation to its left neighbor, which is also induced to fire, and this process repeats throughout the length of the left block. In the algorithm we use, the firing and reset of an oscillator are instantaneous, as are the excitatory pulses sent to neighboring oscillators. This results in an infinite propagation speed. Thus, no matter how large a block is, it can merge with a neighboring block in one cycle. The most striking feature of Figure 6 is that it is impossible to find a block that decreases in size. In Section 2.4.1 we prove that in a one-dimensional network, it is not possible for the interaction to break apart a block of oscillators.

In Figure 7 we display data indicating that the average time needed to synchronize a chain of size $n$ increases in proportion to $\log_{10}(n)$. The averages are based on several hundred trials with random initial conditions. The averages appear to lie on a straight line for each of the three parameter pairs tested. Although only three data sets are displayed, our tests with other parameters only yield a change in the slope of the resulting line. The inset in this Figure is shown with error bars to indicate the standard deviation of the averages. The standard deviation for the other data sets are similar in that they remain nearly con-
Figure 7. The average time needed for a chain of $n$ oscillators to synchronize as a function of $\log_{10}(n)$. Three different symbols represent different parameters: black diamonds, $\alpha_i = 0.25, I_0 = 5.5$, open diamonds $\alpha_i = 0.025, I_0 = 1.1$, and small diamonds $\alpha_i = 0.2, I_0 = 1.11$. The data is based on approximately 300 trials with random initial conditions. The inset displays the data for $\alpha_i = 0.2, I_0 = 1.11$ along with the standard deviation of the averages.

stant after the chain length becomes larger than 20. We tested various combinations of $\alpha_i$ and $I_0$ in the ranges $\alpha_i \in [0.0025, 0.96]$ and $I_0 \in [1.01, 20]$. In Section 2.7 we discuss how these two parameters relate to the slopes of the lines shown in Figure 7.

Only several hundred trials were needed to compute the averages because simulations indicated that the distribution of the synchronization times did not appear to have a long tail. In Figure 8 we display the distribution of the synchronization times for a chain of 500 oscillators for 20000 trials with random initial conditions. The data however, is not sufficient enough to determine whether the tail is an exponential decay with an exponent between 1 and 2, or a an algebraic decay with an exponent of 5 or greater.
2.4.1 Block Size Only Increases

We now show that in one-dimensional networks, blocks of synchronous oscillators do not decrease in size. The first necessary step in arguing that blocks of oscillators do not break is to define a block of oscillators. A block of oscillators is a connected group of oscillators that has previously fired in unison. In Figure 9 we give an example of a block of oscillators. In Figure 9A one oscillator is at the threshold and when it fires, all of its neighboring oscillators are able to fire at the same time because they have a potential greater than $1-\varepsilon/2$, or equivalently, the maximum phase difference between any two neighboring oscillators is less than

$$\zeta = g(1) - g(1 - \varepsilon/2)$$ (2.6)

Figure 8. A histogram of the synchronization times for a one-dimensional chain of 500 oscillators. This data is based on 20000 trials with random initial conditions. The parameters used are $\alpha_f = 0.2$, $I_0 = 1.11$. 
We are using the notation given in Section 2.3 where the potential of an oscillator is given by $x = f(\phi)$, where $\phi$ represents the phase of an oscillator, and the inverse is $\phi = g(x)$.

After these oscillators have fired their values are reset using (2.4). Figure 9B shows the potentials of the oscillators immediately after the block has fired. Most of the oscillators in the block have two neighbors that also fire, and thus receive two pulses weighted by $\varepsilon/2$. The oscillators that receive two pulses cannot have a potential less than $\varepsilon/2$ after firing and these oscillators are the black filled circles in Figure 9B. The two oscillators at the ends of the block receive excitation from only one neighbor. These oscillator are distinguished by unfilled circles in Figure 9B and cannot have a value greater than $\varepsilon/2$. For all the oscillators in the bulk, the potential difference between them is maintained immediately before and after the jump. It is obvious that these oscillators will again jump together because the maximum difference between their potentials is less than $\varepsilon/2$. However, it is uncertain whether or not the two border oscillators will again fire with the block.
We examine how the two oscillators on the block boundary are altered when their neighbors which are not part of the block jump. Let us denote the oscillator on a border of a block as $O_B$, and let its neighbor which is not part of the block be $O_C$. We do not assume anything about $O_C$, but it must fire some time $t^e$ in the range $t^e \in [0, g(1) - g(\varepsilon)]$ (we also assume that Figure 9B represents $t = 0$). The question that needs to be answered is, after $O_C$ fires, can $O_B$ still fire in unison with the block it originally fired with. There are only two cases that need to be examined. The first case occurs when $O_B$ receives excitation from $O_C$ and the resultant potential of $O_B$ is greater than that of any oscillator in the block. We examine the worst case, when the greatest potential of any oscillator in the block has a value of just greater than $\varepsilon/2$ (the case of a block of size 2), and the potential of the other oscillator is just less than $\varepsilon/2$. We need to test the following relation,

$$g(f(t^e) + \varepsilon/2) - t^e < \zeta$$  \hspace{1cm} (2.7)

The LHS of this relation yields the phase difference between the bordering oscillator and oscillator with potential $\varepsilon/2$ after a time $t^e$ has passed. The bordering oscillator receives excitation at time $t^e$. We first note that the derivative of the LHS is given by

$$g'(f(t^e) + \varepsilon/2)f'(t^e) - 1$$

since $g'(f(t))f'(t) = 1$ we rewrite (2.8) as

$$g'(f(t^e) + \varepsilon/2)/g'(f(t^e)) - 1$$ \hspace{1cm} (2.9)

Since $g'(f(t^e)) = 1/f'(t)$ we know $g'(f(t^e)) > 0$ and also $g''(f(t^e)) > 0$, which shows that (2.9) must be positive. This implies that the largest value of the LHS of (2.7) is given by $t^e = g(1 - \varepsilon/2)$ which yields $\zeta$. Since the actual value of $t^e$ must be less than $g(1 - \varepsilon/2)$ (otherwise it implies that $O_C$ had the same firing time as the block) the inequality of (2.7) is satisfied. Since the derivative is positive, the maximum value is given by
this upper bound, which implies that the inequality is met for all \( t^e \) less than \( g(1 - \epsilon/2) \).

The second case that must be examined is when the separation between oscillator in the bulk with the largest potential and \( O_B \) is at its maximum. In this case it might be possible for the block to fire without the bordering oscillator. We examine the following inequality

\[
\begin{align*}
  g(\epsilon) + t^e - g(f(t^e) + \epsilon/2) &< \zeta \\
  (2.10)
\end{align*}
\]

The LHS represents the phase separation from the oscillator nearest to the threshold and the bordering oscillator. Again, we start with the derivative of the LHS, which is

\[
1 - \frac{g'(f(t^e) + \epsilon/2)}{g'(f(t^e))} < 0 \\
(2.11)
\]

so the largest value of the LHS of (2.10) is given by \( t^e = 0 \), which yields \( g(\epsilon) - g(\epsilon/2) \). This value is less than \( \zeta \) because \( g(x) \) is an increasing function of \( x \), therefore the bordering oscillator still fires with the block.

We have shown that the bordering oscillators continue to fire with the block they originally fired with, regardless of the influences of its other neighbor. The potentials of the other oscillators in the block never change their respective ordering, although the relative distance between the oscillators within the block decreases because of the compression that occurs each period. Thus in one-dimension, blocks never break apart, and can only increase in size by merging with other blocks.

2.5 Two-dimensional systems of oscillators

We now present data indicating that the time to synchrony in two-dimensional networks of locally coupled integrate-and-fire oscillators increases as the logarithm of the system size. As mentioned previously, all trials with two-dimensional networks resulted in synchrony. We tested various size spin waves in the two directions with similar results to
Figure 10. The average times for an $L \times L$ network of oscillators to synchronize are plotted as a function of $\log_{10}(2L - 1)$. The solid diamonds are for the parameters $\alpha = 0.2, I_0 = 2.0$ and the open diamonds are for $\alpha = 0.2, I_0 = 1.11$. Each average is computed from approximately one hundred trials with random initial conditions. The inset indicates the standard deviation for one set of data.

those in one-dimensional systems, namely synchrony was achieved regardless of the initial conditions. Travelling waves were never observed, even with periodic boundary conditions.

We display the average synchronization time for a two-dimensional system as a function of $\log_{10}(2L - 1)$ in Figure 10. In this two-dimensional system, each oscillator is coupled to its four nearest neighbors and the longest distance between any two oscillators (in terms of lattice sites) is $2L-1$. The data indicate that the average time to synchronize scales logarithmically with the system size. We have tested more parameters than shown in Figure 10 and all tested parameters yield an identical scaling relation.

As we examine two-dimensional systems, a natural question is “How does the rate of synchronization vary as the dimension of the system changes?” We first define the rate of synchrony as follows. The data indicate that $\langle T_s \rangle \sim \frac{1}{r_s \log(n)}$, where $\frac{1}{r_s}$ corresponds to the
slope of a line from Figure 7. We refer to $r_s$ as the rate of synchronization. In tests where the value of $\alpha_l$ is held constant, but the dimension of the system changes from 1 to 2, we find that the rate of synchrony halves. When the individual coupling strengths between oscillators are maintained, i.e. $\alpha_l$ doubles, we find that the rate of synchronization remains approximately the same as the dimension of the system increases from 1 to 2. This indicates that the rate of synchrony is controlled by the individual connection weights between oscillators and not the total input to each oscillator.

### 2.5.1 Disorder in Integrate-and-Fire Oscillators

We have also tested this system with disorder in the form of different intrinsic frequencies, $\omega_i$, of oscillators. The intrinsic frequencies are allowed to vary within a range $\omega_0 - \Delta < \omega_i < \omega_0 + \Delta$ (plus or minus 5 percent for example). With this type of disorder synchrony is still achieved in both one- and two-dimensional networks. Imagine that all the oscillators are initially given an potential of zero. The oscillator with the highest frequency reaches the threshold first and the rest of the oscillators have a smaller potential, but are still near the threshold. If the coupling strength is large enough, then the entire network can be induced to fire. So oscillators can repeatedly fire at the same time as long as their frequency difference is not too large. However, if one allows the intrinsic frequencies to have a Gaussian distribution, then the system behaves differently. If the width of the distribution is not too large then small one-dimensional systems can synchronize completely. As the system size becomes larger, then synchrony occurs less often. The system
typically has several large synchronized clusters. Tests with two-dimensional systems yields a similar qualitative behavior. Unfortunately, we have not quantized any of the above observations and this remains a subject of study.

2.6 Heuristic argument for exponential block growth

Here we present an argument for the exponential increase in the block size as a function of time. We have not been able to directly relate the time to synchrony to the system size using equations (2.1)-(2.4). However, we are able to make the following heuristic arguments based on the two following assumptions; a block never decreases in size and its probability of merging with another block is independent of block size.

For mathematical simplicity we make the following arguments based on the breaking of blocks, which can be thought of as the time reversal of the synchronization process. We begin with a single block that is the size of the system, where \( S \) is the number of sites in the system. We use the following assumptions; a block never increases in size, a block can only break into two smaller blocks, when a block breaks into two pieces, there is no preference for the sizes of the resultant pieces. The probability of a block not breaking is given by \( 1 - \lambda \) and is independent of block size. Let \( N_m(t) \) represent the number of blocks of size \( m \) at time \( t \). With the above assumptions and notations, we write the following,

\[
N_m(t + 1) = (1 - \lambda) N_m(t) + \sum_{j > m}^S P_{jm} N_m(t)
\]

(2.12)

where \( P_{jm} \) is the probability that a block of size \( j \) breaks into block of size \( m \) and \( j - m \).

We write (2.12) as a continuous function of time

\[
\frac{d}{dt}(N_m(t)) = -\lambda N_m(t) + \sum_{j > m}^S P_{jm} N_m(t)
\]

(2.13)
Note that (2.12) and (2.13) are only valid for \( m > 1 \). For \( m = 1 \), the first term on the RHS of (2.13) disappears because blocks of size 1 cannot be broken. There is a conservation of the total number of sites, which can be written as

\[
\frac{d}{dt} \left( \sum_{m=1}^{\infty} mN_m(t) \right) = \frac{d}{dt} (S) = 0
\]  

(2.14)

Using (2.13) we rewrite (2.14) as

\[
\frac{d}{dt} \left( \sum_{m=1}^{S} mN_m(t) \right) = -\lambda \sum_{m=2}^{S} mN_m(t) + \sum_{m=1}^{S} m \sum_{j>m}^{S} P_{jm}N_j(t) = 0
\]

(2.15)

In matrix form this becomes

\[
\lambda \sum_{m=2}^{S} mN_m(t) = \begin{bmatrix}
\ldots & P_{21}N_2 & P_{31}N_3 & P_{41}N_4 & \ldots \\
2P_{32}N_3 & 2P_{42}N_4 & 2P_{52}N_5 & 2P_{62}N_6 \\
3P_{43}N_4 & 3P_{53}N_5 & 3P_{63}N_6 \\
4P_{54}N_5 & 4P_{64}N_6 \\
5P_{65}N_6 \\
\ldots
\end{bmatrix}
\]

(2.16)

We set the individual terms \( N_k \) equal, yielding

\[
\lambda kN_k(t) = \sum_{i=1}^{k-1} iP_{ki}N_k(t)
\]  

(2.17)

for \( k > 1 \). As mentioned previously, we assume that the probability of a block breaking into two pieces is independent of the size of the two smaller pieces (with the exception being the probability of block with an even numbered size breaking into two equal size pieces). Because of this difference we compute the simplest case first, that of a block with an odd numbered size. In this case we assume \( P_{km} = c_k \) where \( c_k \) is independent of \( m \).

With this assumption, (2.17) becomes
\[ \lambda_k = \sum_{i=1}^{k-1} iP_{ki} = c_k \sum_{i=1}^{k-1} i = c_k k (k-1)/2 \]  

(2.18)

which leads to probabilities \( c_k = 2\lambda / (k - 1) \). For a block with an even numbered size, we assume that \( P_{km} = d_k, m \neq k/2 \) and \( P_{k(k/2)} = d_k/2 \). Substituting these assumptions into (2.17) yields \( d_k = 2\lambda / (k - 3/2) \). Now that the probabilities are known, we calculate other quantities. Of interest is how the average block size changes in time. Let \( \mu \) be the average block size, or

\[ \mu = \frac{\sum_{m=1}^{S} mN_m(t)}{\sum_{m=1}^{S} N_m(t)} = \frac{S}{\sum_{m=1}^{S} N_m(t)} \]  

(2.19)

The derivative of \( \mu \) with respect to time is

\[ \frac{d\mu}{dt} = -\frac{S}{\sum_{m=1}^{S} N_m(t)} \left[ \frac{d}{dt} \left( \sum_{m=1}^{S} N_m(t) \right) \right] = -\mu \left[ \frac{\sum_{m=1}^{S} P_{jm}N_m(t)}{\sum_{m=1}^{S} N_m(t)} \right] \]  

(2.20)

We solve for the derivative of the total number of blocks by using (2.13), which results in

\[ \frac{d}{dt} \sum_{m=1}^{S} N_m(t) = -\lambda \sum_{m=2}^{S} N_m(t) + \sum_{m=1}^{S} \sum_{j>m}^{S} P_{jm}N_m(t) \]  

(2.21)

Using the appropriate probability values derived above, and performing the sum of the second term on the RHS of (2.21) yields

\[ \frac{d}{dt} \sum_{m=1}^{S} N_m(t) = -\lambda \sum_{m=2}^{S} N_m(t) + 2\lambda \sum_{m=2}^{S} N_m(t) = \lambda \sum_{m=2}^{S} N_m(t) \]  

(2.22)

Substituting this in (2.20) yields
\[
\frac{d \mu}{dt} = -\lambda \mu \left[ \sum_{m=2}^{S} \frac{N_m(t)}{\sum_{m=1}^{S} N_m(t)} \right]
\]  

(2.23)

There are three cases to consider for this equation. The first case is if there are no blocks of size one, or \( N_1(t) = 0 \), then the bracketed term in (2.23) is equal to one and the average block size decreases exponentially. The second case occurs if there are some blocks of size one, then the bracketed term in (2.23) is less than one, and the rate of change of the average blocks size is an exponential modified by a constant. The third case is when all the blocks are of size 1, then the bracketed term is zero and the average block size does not change. This last case makes sense because if all the blocks are of size one, then there can be no further changes in the average block size.

For the set of assumptions used, we obtain an exponential decrease in the block size until the smallest block size is attained. Since our equations describe the breaking of blocks, the inverse time evolution of the system is the merging of blocks and yields an exponential growth in the average block size. The linkage between this argument and integrate-and-fire systems is relatively weak. The above argument contains no topology and can be seen as a mean field model because there is no correlation between blocks.

In two-dimensional networks numerical simulations indicate that blocks can break apart. This seemingly qualitative change in behavior does not appear to alter the logarithmic relation between the time to synchrony and the system size. Attempts to incorporate this dynamic into (2.12) have not been fruitful. The addition of a positive nonlinear term
to the RHS of (2.12) (implying that the block size can increase) yields equations that are
not readily solved. However, the terms leading to exponential decay are still present and
they might dominate the behavior of the average block size.

2.7 The Rate of Synchrony in Integrate-and-Fire Oscillators

We present data indicating that the rate of synchrony is approximately proportional to
\( \alpha_f/(I_0 - 1) \) for a specified range of parameter values. Remember that we have defined
the measured rate of synchronization as the inverse of the slope of a line from Figure 7.
We first consider the qualitatively consider the coupling strength, \( \alpha_f \), for a pair of oscilla-
tors. As the coupling strength goes to zero, the average time to synchrony must become
infinite and \( r_s \) approaches zero. Also, with \( \alpha_f = 0 \) the return map is straight line with
slope 1. A first guess is that the coupling strength is proportional to the rate of synchrony.
Note that this cannot be true for large values of the coupling strength. As \( \alpha_f \) nears 1, the
period approaches 0; the oscillators fire frequently, but only slowly change their relative
phase. As \( \alpha_f \) nears 1 the time to synchrony must become infinite. At \( \alpha_f = 1 \) system (2.1)
is meaningless because the oscillators are constantly firing and resetting. Now we examine
\( I_0 \), which essentially controls the period and is related to the curvature of the potential
curve, which is given by \( I_0 e^{-\alpha_f(1+I_0^2e^{-2t})} \). For values of \( I_0 > 10 \) the potential of the oscilla-
tor rises quickly to the threshold and the potential curve is nearly linear. For smaller values
of \( I_0 \), the potential curve become more nonlinear (see Figure 4 for example). A perfectly
linear slope would yield a return map with a slope of 1 (except for the jumping regions)
and a pair of oscillators would have a constant phase difference. As \( I_0 \) approaches 1, the
curvature becomes highly nonlinear and yields a larger compression of the phase differ-
cence for each period. Our first guess is that the rate of synchrony is inversely proportional
We display the inverse of the measured rate of synchrony as a function of \((I_0 - 1)/\alpha_I\). Most of the 140 different parameter pairs are near a straight line. An examination indicates that those points not near the line have values of \(\alpha_I > 0.8\) and/or values of \(I_0 < 1.05\). Each point represents the average time to synchrony calculated from 250 trials with random initial conditions.

to \(I_0 - 1\). We mention that Hopfield and Herz [Hopfield and Herz, 1995] used a value of \(I_0 = 10\) in their simulations and this is the reason that they saw rather slow convergence times to synchrony. Both Peskin [Peskin, 1975] and Mirollo and Strogatz [Mirollo and Strogatz, 1990] note that the coupling strength and the degree of nonlinearity in the potential curve are important to the rate of synchronization.

In order to examine how the rate of synchrony varies with these two parameters, we performed trials with several different size chains, with randomly chosen values of \(\alpha_I \in (0, 1)\) and \(I_0 \in (1, 11)\). The size of the chains varied from 100 to 1000. In Figure 11 we display the inverse of the measured rate of synchrony as a function of \((I_0 - 1)/\alpha_I\). The data lie near a line, indicating that this simple first guess is not a bad approximation. An examination of the points not on the line indicates that they have values of \(\alpha_I > 0.8\) and/or \(I_0 < 1.05\).
Figure 12. A plot of the measured rate of synchrony as a function of the coupling strength. The linear relationship between the coupling strength and the time to synchrony is maintained for $\alpha_f < 0.8$. A value of $I_0 = 5.0$ was used. The inset indicates the rate of synchrony predicted from the return map for two oscillators. We used a chain length of 500 oscillators. Each point represents the average over several hundred trials with random initial conditions.

A more direct evaluation of how the coupling strength alters the rate of synchrony is shown in Figure 12 where we vary only the coupling strength. The rate of synchrony is approximately proportional to the coupling strength for $\alpha_f < 0.8$. Similar tests in which $I_0$ alone is varied yield synchronization rates that vary approximately inversely with $I_0 - 1$. Figure 13 displays this relationship for two different values of the coupling strength.

We also attempted to determine how the values of the parameters relate to the rate of synchronization. We reasoned that the return map Figure 5 between two oscillators give one some idea of how fast two oscillators might synchronize. If the coupling strength is zero, then the return map is a straight line of slope one and synchrony never occurs - also, the area under the return map, $A_f$, is equal to 0.5. As the coupling strength increases, $A_f$ becomes less than 0.5 and the two oscillators synchronize. At a qualitative level, there is some link between $A_f$ and the rate of synchrony, $r_s$. In the inset shown in Figure 12, we
plot $1/A_f - 2.0$ as a function of the coupling strength. This theoretical curve does share several things in common with the numerically obtained data in that the endpoints are correct and there is only a single maximum. However, the location of this maximum is significantly different from the maximum given by the numerical data, indicating that this approach to deriving $r_s$ is flawed. For completeness we also calculate $A_f$ as a function of $I_0$ and display this graph in the inset of Figure 13. These graphs exhibit a much different shape and given further indication that this is not the correct route for analytically deriving the rate of synchrony. The area under the return map, $A_f$, cannot be calculated analytically for the particular equations we use (see Section 2.3), although one can derive a power series expansion for the area, which results in

Figure 13. The inverse of the measured rate of synchrony (times $\alpha_f$) is plotted as a function of $I_0$. The filled diamonds are for $\alpha_f = 0.25$ and the plus symbols are for $\alpha_f = 0.8$. The data is from a chain of 1000 oscillators using 100 trials with random initial conditions. The inset represents the rate of synchrony predicted from the return map for two oscillators.
\[ A_I = -\phi_L \log (I_0 - \alpha_I) + \mathcal{S}(1 - \alpha_p (I_0 - 1) \exp (\phi_L)) + \mathcal{S}(1 - \alpha_p (I_0 - 1)) - \]
\[ \left( \alpha_I - \phi_L \right) \log (I_0) - \mathcal{S}(I_0 (I_0 - 1) - \alpha_I^2, \alpha_I (I_0 - 1) \exp (\phi_I)) + \]
\[ \mathcal{S}(I_0 (I_0 - 1) - \alpha_I^2, \alpha_I (I_0 - 1) \exp (\phi_I)) + \mathcal{S}(\alpha_p, \alpha_I (1 - I_0) \exp (\phi_I)) - \]
\[ \mathcal{S}(\alpha_p, \alpha_I (1 - I_0) \exp (\phi_I)) - (P - \phi_I) \log ((I_0 - \alpha_I) + ) \]
\[ \mathcal{S}((1 - \alpha_I) \alpha_I + I_0 (1 - I_0), (1 - \alpha_I) (I_0 - 1) \exp (P)) - \]
\[ \mathcal{S}((1 - \alpha_I) \alpha_I + I_0 (1 - I_0), (1 - \alpha_I) (I_0 - 1) \exp (\phi_I)) - \]
\[ \mathcal{S}(\alpha_p, (1 - I_0) \exp (P)) + \mathcal{S}(\alpha_p, (1 - I_0) \exp (\phi_I)) \quad (2.24) \]

where

\[ \mathcal{S}(a, x) = \log (a) \log (x) + \frac{x}{a} - \frac{x^2}{2 a^2} + \frac{x^3}{3 a^3} - \frac{x^4}{4 a^4} \ldots \quad [x^2 < a^2] \]

\[ = \left( \frac{\log (x)}{2} \right)^2 - \frac{a}{x} + \frac{a^2}{2 x^2} - \frac{a^3}{3 x^3} + \frac{a^4}{4 x^4} \ldots \quad [x^2 > a^2] \quad (2.25) \]

2.8 Error Correction

We now examine how errors are corrected in noiseless, locally coupled two-dimensional networks of identical integrate-and-fire oscillators. We start with initial conditions for a two-dimensional network such that a small central region of oscillators has random potentials and the oscillators in the larger surrounding area are given the same potential. The small region within the larger synchronized block of oscillators is considered the "error." This error will take some amount of time to synchronize with the larger block and we call this the correction time. This particular form of error was found to take the longest time to correct. A rectangular block of oscillators in the center of the system with initial conditions such that its phase relationship with the rest of the network is near the unstable fixed point, shown in Figure 5A, results in synchronization on the same time scale as just
Figure 14. The time needed to correct a given size error in a two-dimensional network of integrate-and-fire oscillators. The error is a right isosceles triangle region that contains oscillators with random initial conditions. B represents the size of the base of the triangle.

two oscillators with the same phase relationship. This occurs because all the blocks in the error have the same potential and changes that occur on the boundary can propagate through the entire region in an instant. Other types of errors (spin waves) were also found to be quickly corrected, so a central block of random potentials was deemed the most difficult generic error to correct.

We now examine the average time needed to correct a central block of oscillators with random potentials. Numerical simulations indicate that the error is corrected at times that increase linearly with the logarithm of the perimeter of the smallest bounding rectangle. In Figure 14 we display the time needed to synchronize a triangular error (random potentials of oscillators surrounded by a synchronous grid of oscillators) as a function of the logarithm of the smallest square enclosing the error. The data indicate an error correction time that scales as the logarithm of the error size. This indicates that the system is robust with respect to errors.
Given the rigid lattice structure of this system, each oscillator is coupled to its four nearest neighbors, it is possible that differently shaped regions of error may exhibit different correction times. In tests with circular and triangular regions of error, we noted that these regions typically expanded in size until to the smallest rectangle enclosing the original error.

2.9 Desynchronization in Integrate-and-Fire Oscillator Networks

The integrate-and-fire networks examined so far have the property that synchrony is quickly achieved. But a system that only achieves synchrony is not very useful for information processing, since such a system is dissipative and almost all information is lost. In order to perform computations, some other mechanisms must exist that can store or represent information. In oscillatory correlation, the different phases of oscillators encode binding and segregation information.

We now describe a network of integrate-and-fire oscillators which can desynchronize different groups of synchronous oscillators. In order to create a network of integrate-and-fire oscillators for oscillatory correlation, we need a mechanism which desynchronizes different oscillator groups. This mechanism will be connected with every oscillators since the phases of different oscillator groups need to be desynchronous regardless of their position in the network. This unit is called the global inhibitor and the architecture of this network is identical to the locally excitatory globally inhibitory oscillator networks (LEGION) proposed by Terman and Wang [Terman and Wang, 1995]. Figure 15A displays a diagram of the LEGION architecture.
We now define a LEGION network which uses integrate-and-fire oscillators as its basic units. The activity of each oscillator in the network is described by

\[ \dot{x}_i = -x_i + I_i + \sum_{j \in N(i)} J_{ij} P_j(t) - G(t), \quad i = 1, \ldots, n \]  

(2.26)

where \( n \) is the number of oscillators. \( N(i) \) represents the four nearest neighbors of oscillators \( i \). The parameter, \( I_i \), is now dependent on the input image; we refer to this parameter as the stimulus given to an oscillator. In this section we segment a toy image that consists of binary pixels. The respective stimulus for each oscillator is either \( I_i > 1 \) or \( I_i = 0 \). If \( I_i > 1 \) we call oscillator \( i \) stimulated. If an oscillator does not receive stimulus, \( I_i = 0 \), its potential decays exponentially towards zero. As before the threshold for each oscillator is 1. The interaction term, \( P_j(t) \), is the same as in (2.2). Only neighboring oscillators that both receive stimulus have a nonzero coupling strength. Thus, image information is contained in the connection weights between oscillators. Only oscillators that are part of the same connected image region can be coupled. This is also an implicit encoding of the Gestalt principle of connectedness [Rock and Palmer, 1990]. The connection strengths are normalized so that all stimulated oscillators receive the same sum of connection input and have the same frequency. However, we use a slightly modified version of (2.3) to reflect that the input to oscillator \( i \) is now normalized by the number of stimulated neighbors coupled with \( i \).

The global inhibitor, \( G(t) \), sends an instantaneous inhibitory pulse to the entire network when any oscillator in the network fires. It is defined as

\[ G(t) = \Gamma \delta(t - t^m_j), \quad \forall j, m \]  

(2.27)
where \( r_{jm} \) represent the \( m \) firing times of the \( j^{th} \) oscillator. The constant \( \Gamma \) is less than the smallest coupling strength. When an oscillator fires, the global inhibitor serves to lower the potential of all oscillators, but because this impulse is not as large as the excitatory signal between neighboring oscillators, it does not destroy the synchronizing effect of the local couplings (see [Terman and Wang, 1995]). In this fashion, a connected region of oscillators receiving input synchronizes as the system evolves in time. This region of oscillators has no direct excitatory connections with other spatially separate oscillators. It will however, interact with other groups of oscillators through the global inhibitor. This interaction inhibits other blocks of oscillators from firing at the same time and ensures that there is a finite amount of time between firings of synchronous groups of oscillators.

We now demonstrate the ability of this network to perform oscillatory correlation. In Figure 15B we display an input image and in Figure 15C we display the network response. The four graphs in Figure 15C display the combined potentials of every oscillator comprising each of the four objects. The oscillators have random initial conditions varying uniformly from 0 to 1. Initially, many oscillators fire and the effect of the global inhibitor can be seen in the jitter, or lack of smoothness, in the potentials of the oscillators during this time. As the system evolves, clusters of oscillators begin to form and the curves become smoother because the global inhibitor does not send inhibitory impulses as often. By the third cycle each group of oscillators comprising a distinct object is almost perfectly synchronous and the different oscillator groups have distinct phases. Oscillators that do not receive excitation (not shown) experience an exponential decay towards zero and are periodically perturbed by the small inhibitory signals from the global inhibitor.
Figure 15. (A) A diagram of the network architecture. Each unit has local excitatory connections. The global inhibitor is coupled with every unit in the network and serves to desynchronize different groups of oscillators. (B) The input we use to demonstrate the behavior of our network. The black squares represent those units which receive stimulus and the units corresponding to the unfilled squares receive no stimulus. (C) We display the temporal activities of all units comprising each of the four objects in (B). The parameters used are $I_i = 1.05$ for those oscillators receiving stimulus, $\alpha_i = 0.2$, and $\Gamma = 0.01$. 

rectangle

"u" shape

triangle

square
In this network, there is an unlimited number of oscillator groups that can be segmented. In other words, the segmentation capacity is infinite. Imagine two groups of oscillators that have nearly the same phase. When the first group fires, the potential of the second group of oscillators decreases by $\Gamma$. Thus, the second group needs to traverse this distance $\Gamma$ before it can fire. This implies that there is a finite amount of time between the firings of two consecutive groups. This also implies that as the number of groups increases, the period of the system increases. Simulations support the above statements and we have segmented more than 100 groups of oscillators.

### 2.10 Image Segmentation Using Integrate-and-Fire Oscillators

In the previous Section, we segmented four black objects on a white background in a small $20 \times 20$ image. Since numerical evidence suggests that there is a logarithmic scaling relation between the time to synchrony and the network size, we should be able to use this same network to quickly (in a few periods) perform image processing tasks with real images.

In order to segment gray-level images, we alter how the connection weights and values of $I_i$ are chosen. The alterations made are variations of methods proposed in Wang and Terman [Wang and Terman, 1997]. Let the intensity of pixel $i$ be denoted by $p_i$. If $|p_i - p_j|$ is less than a given threshold, then the two pixels are said to satisfy the pixel difference test. Two oscillators have a nonzero coupling strength only if they are neighbors (we now use the eight nearest neighbors of $i$) and if their corresponding pixel values satisfy the pixel difference test. The weights of the connection strengths are determined using (2.3), except that $Z_i$ now represents the number of neighboring pixels of $i$ that pass the
pixel difference test. The stimulus $I_i$ for each oscillator is chosen in the following manner. We examine a region $Q(i)$ centered on pixel $i$. $Q(i)$ is a neighborhood about oscillator $i$ that contains more pixels than $N(i)$. If half of the pixels in $Q(i)$ satisfy the pixel difference test, then pixel $i$ is possibly within a homogeneous region and we set the stimulus, $I_i$, to a value $I_L$ which is greater than 1. Such an oscillator is called a leader [Wang and Terman, 1997] and is able to oscillate. If the region about pixel $i$ contains no pixels that satisfy the pixel difference test, then we assume that this region is noisy, or contains high intensity variations. The corresponding oscillator $i$, receives no stimulus, and does not oscillate. If pixel $i$ is not a leader, but its surrounding region contains one or more pixels that satisfy the pixel difference test, oscillator $i$ is given a stimulus $I_N$, which is less than, but near 1, and is said to be a near threshold oscillator. A near threshold oscillator is able to fire only through interactions with other oscillators. In this fashion, only regions of sufficient size, and with smoothly varying intensities will contain oscillators which are leaders. These leaders will oscillate, and can induce neighboring oscillators that are near threshold to oscillate. The border of a region will consist of pixels whose neighboring pixels have sufficiently different grey-levels that they do not pass the pixel difference test and are not connected. Only sizeable regions of smoothly varying intensities will be connected and oscillatory. Regions with high intensity variations will not exhibit oscillatory activity and are referred to as the background.

The rules for the connection weights and oscillator stimuli described above have been implemented in an integrate-and-fire oscillator network and we display the segmentation results for two real images in Figure 16. Figure 16A displays an aerial photograph.
In Figure 16B we display the segmentation results of our network. Each group of synchronous oscillators is represented by a single grey-level intensity. Inactive oscillators comprising the background are colored black. There are 29 regions shown, although it is not easy to discern every different grey-level. We also segment a CT (computerized tomography) image of a slice of a human head. The original grey-level image is shown in Figure 16C. The bright areas indicate bone structure. Our segmentation result is shown in Figure 16D and contains 25 different regions. The different bones are segmented, except for two of the smaller bones which do not contain many pixels. Regions of soft tissue are also segmented. These results are comparable with those in [Wang and Terman, 1997, Shareef et al., 1997], which used similar methods and images in their oscillator networks. Shareef et al. [Shareef et al., 1997] used a similar CT image and obtained almost three times as many different regions as we did; many of their regions were small however. Through appropriate parameter choices, we could also obtain more and smaller regions.

This segmentation process has conceptual relations to region growing algorithms in computer vision. In region growing, a region is grown outward from some chosen seed. Pixels on the border of a region are merged with that region if their grey-level intensities satisfy some conditions based on the existing region, i.e. the pixel intensity is within some threshold based on the average pixel intensity of the region. Some of these techniques (in particular [Adams and Bischof, 1994]) are similar to our network if one removes the dynamical aspects of oscillatory correlation and replaces it with an algorithmic labelling procedure. Many different segmentation algorithms exist. They all suffer from the same problems in that the segmentation results are parameter sensitive and judgement of the
Figure 16. (A) An aerial image with $128 \times 128$ pixels and (B) the segmentation results for (A). The network produced 29 different synchronized groups. Each synchronized group is represented by a single grey-level. Black pixels represent those oscillators that do not exhibit periodic activity. The threshold for the pixel difference test is 19, $Q(i)$ is a region of size $7 \times 7$, with $I_i = 1.025$, $I_N = 0.99$, $\alpha_I = 0.2$, and $\Gamma = 0.01$. (C) A $128 \times 128$ CT image of a slice of a human head (the bright regions indicate bone). (D) The segmentation results for (C). The network produced 25 different groups of synchronized oscillators. Each synchronized group is represented by a single grey-level. Black pixels represent those oscillators that do not exhibit periodic activity. The threshold for the pixel difference test is 15 and $Q(i)$ is a region of size $9 \times 9$ and the other parameters are as listed above.
results is subjective. The advantage that our image segmentation network has over others is in its neurobiological basis and in the parallel and distributed nature of computation. The oscillators all operate in parallel and segmentation computations are made on a local basis (the global inhibitor does not make any decisions regarding which pixel belongs to which region, it merely assists in labelling the regions). This allows for comparisons with the distributed perceptual processes of the brain, and it also allows for VLSI implementation.

2.11 Discussion

Our investigation of locally coupled networks of identical integrate-and-fire oscillators has revealed a number of interesting properties which may have significant computational implications. Among the most interesting is that the time needed to achieve synchronization appears to scale logarithmically with the size of the system for one- and two-dimensional noiseless systems. Other properties of the system also appear to scale similarly. When an error is introduced into a synchronized system, in the form of a small region of oscillators with randomly chosen potentials, numerical results indicate that synchrony is attained at times proportional to the logarithm of the perimeter of the smallest square enclosing the error. This indicates a quick correction of faults and makes this oscillator appealing for use in networks where synchronization is a desirable feature.

If we introduce disorder in the form of different intrinsic frequencies, \( \omega_i \), of oscillators, and the distribution of the frequencies is \( \omega_0 - \Delta < \omega_i < \omega_0 + \Delta \), then synchrony is still possible. This is quite different from a network of phase oscillators with diffusive coupling, in which synchrony is not possible using the same distribution of intrinsic frequencies.
It is interesting to note that slightly different versions of this network can yield drastically different behaviors. Corral et al. [Corral et al., 1995a] examine an almost identical oscillator network and derive parameter regimes in which three different behaviors arise, self organized criticality, periodic with a few clusters of oscillators, or globally synchronous. If we do not normalize the connection strengths, the oscillators along the borders have different periods from oscillators in the bulk. It appears that these different frequencies cause different dynamics to arise in these networks [Middleton and Tang, 1995, Corral et al., 1995a].

Hopfield and Herz [Hopfield and Herz, 1995] numerically examined several different types of integrate-and-fire oscillators and found that they attained synchrony on long time scales (100's of periods). Because of this, they discount synchrony as too slow to be useful in biological computations and instead use a network capable of local synchrony to perform image segmentation. Their network suffers from several problems. Because they rely on local synchrony, large homogeneous grey-level regions can be arbitrarily broken into several regions. Another problem is that they ignore the issue of desynchronization, and as a result different objects can have the same firing time and thus are incorrectly grouped.

In our investigation of integrate-and-fire oscillator networks, we duplicated the results of Hopfield and Herz [Hopfield and Herz, 1995] and found that by modifying the parameters, we can obtain synchrony on short time scales (a few periods). Because locally coupled networks of integrate-and-fire oscillators are able to achieve synchrony quickly, we examined their potential as a feature binding network. We found that using the LEGION architecture [Terman and Wang, 1995] we are able to create an oscillator network for image segmentation. Our network is able to synchronize a large homogeneous region of smoothly varying grey-levels without breaking it into small regions. The LEGION archi-
tecture contains a global inhibitor, which serves the purpose of desynchronizing different groups of oscillators, while maintaining synchrony within each group of oscillators. This ensures that different oscillator groups have distinct firing times. This property allows for a temporal labelling of perceptually distinct objects as proposed by theoreticians [Milner, 1974, von der Malsburg, 1981] and we think that this is a promising framework for representing the results of feature binding.

There are differences between the network proposed here, and the network studied in [Terman and Wang, 1995]. A major difference is the segmentation capacity, or the number of different objects which can be desynchronized. Their network has a finite limit on the number of groups that can be desynchronized. In our integrate-and-fire network the period increases as the number of oscillator groups increases. Since there is no consequence of lengthening the period, there appears to be no limitation on the number of groups that can be desynchronized. This may be computationally more desirable, but is not psychophysically plausible, since the number of objects that can be attended to is generally considered to be small, 7 plus or minus 2 [Miller, 1956].

Our results indicate that the form of the interaction between oscillators results in significantly different behaviors. We observe that with a pulsatile interaction integrate-and-fire oscillators synchronize at times proportional the logarithm of the network size (in one- and two-dimensions). If the coupling is a continuous function of the phase variables (diffusive for example) then the time to synchrony exhibits a completely different relation with the size of the network [Niebur et al., 1991b]. Also, the discontinuity in the interaction is partially responsible for the ability of the network to achieve synchrony in the presence of some forms of disorder. These results are in agreement with two other papers indicating that oscillator networks with discontinuous interactions have fundamentally
different properties of synchronization than equivalent networks with continuous interactions. Daido [Daido, 1993b] achieves partial synchronization in a globally coupled network of phase oscillators with a normal distribution of frequencies using a step-like interaction. This same network with a continuous interaction achieves partial phase-locking (the oscillators have the same frequency but maintain a constant phase difference), but not synchronization. Somers and Kopell [Somers and Kopell, 1993] reported that a Heaviside type coupling in locally coupled networks of relaxation oscillators resulted in fast synchrony and they conjectured that the time to synchrony scales linearly with the size of the system. In Chapter 3 we further indicating that sinusoidal type oscillators also synchronize at times proportional to the network size with a Heaviside type interaction. This information not only indicates some generic classifications of the interactions in oscillator networks, but it may have possible practical applications as well. Several devices (Josephson junctions and resonance tunneling diodes [Young et al., 1988]) oscillate at megahertz frequencies. However, the output current of both of these devices is very small. There is interest in creating devices that can oscillate at these high frequencies and have a substantial current output as well. At the moment, it is unknown how to synchronize the outputs of locally coupled arrays of these devices. Even a partial understanding of how to achieve quick synchrony in the presence of disorder and noise would be highly valuable.
CHAPTER 3

SYNCHRONY IN RELAXATION OSCILLATORS

3.1 Introduction

The phrase "relaxation oscillations" was coined by van der Pol in 1926 in his analysis of a triode circuit [van der Pol, 1926]. A relaxation oscillator has two distinct time scales; a slow time scale which reflects the charging of a capacitor and a fast time scale which describes a quick discharge. The period of oscillation can be approximated by the time needed to charge the capacitor, hence the name relaxation oscillations. See Appendix A for a more detailed discussion of relaxation oscillators and their relation to sinusoidal type oscillators.

Relaxation oscillators were immediately recognized as having similarities to biological oscillators. Van der Pol and van der Mark may have been the first to use relaxation oscillators to model biological phenomena [van der Pol and van der Mark, 1928]. In 1952 Hodgkin and Huxley gave a mathematical model of the membrane potential and ionic conductances of a nerve cell using a four variable system of differential equations [Hodgkin and Huxley, 1952]. This famous system of equations was later simplified to a two variable system of equations that is essentially a relaxation oscillator [Fitzhugh, 1961, Nagumo et al., 1962]. Later, Mayeri [Mayeri, 1973] derived the van der Pol relaxation
oscillator as a quantitative description of his experiments with the cardiac ganglion cells of the lobster. Morris and Lecar [Morris and Lecar, 1981] also derived a two variable relaxation type oscillator in their study of the conductances and currents in the barnacle giant muscle fiber. Due to these direct links to neurophysiology, relaxation oscillators have been frequently examined as models of neural behavior [Grasman and Jansen, 1979, Plant, 1981, Grossberg and Somers, 1991, Somers and Kopell, 1993, Terman and Wang, 1995].

Synchrony in networks of relaxation oscillators has been studied previously. Somers and Kopell [Somers and Kopell, 1993] and independently Wang [Wang, 1993a] both noted that synchrony occurs more rapidly in locally coupled networks of identical relaxation oscillators than in networks of locally coupled sinusoidal oscillators. Terman and Wang [Terman and Wang, 1995] proved that a network of locally coupled identical relaxation oscillators with a Heaviside type interaction can achieve synchrony at an exponential rate independent of the number of oscillators or the dimension of the network. However, this rate of synchronization is possible only when the oscillators are initially on a specific portion of the limit cycle.

We examine the rate of synchrony in such networks in which the oscillators can be placed anywhere on the limit cycle. This results in a fundamental change in average time needed to achieve synchrony. For one-dimensional noiseless networks in the singular limit ($\varepsilon = 0$, also see Section 3.3.1 and Appendix A), we find that the average time to synchrony, $\langle T_s \rangle$, is proportional to $n^p$, where $n$ is the size of the system and $p$ is a numerically obtained value that is less than 0.5 and is dependent on system parameters. For two-
dimensional networks of relaxation oscillators, our results are not conclusive, but for appropriate parameter choices we observe that \( \langle T_S \rangle \) increases logarithmically with the system size.

One-dimensional networks of locally coupled identical relaxation oscillators exhibit other behaviors besides synchrony. There are two types of desynchronous solutions, fractured synchrony and travelling waves. We derive explicit conditions needed for the formation of fractured synchrony and we provide a detailed explanation of the conditions necessary for the formation of travelling waves. In two dimensional networks, additional spatiotemporal patterns arise, including rotating waves. We give examples of some spatiotemporal patterns and describe initial conditions and parameters which can inhibit or enhance their formation.

Relaxation oscillators also share some similarities with the integrate-and-fire oscillators discussed in Chapter 2. Both types of oscillators have two distinct time scales and both are typically studied with a nonlinear, asymmetric interaction. Because of these similarities, integrate-and-fire oscillators and relaxation oscillators are thought to share many properties. But, there are differences. For example, relaxation oscillators have interactions of finite duration. Our analysis of relaxation oscillators indicates how to modify parameters so that relaxation oscillators have properties associated with integrate-and-fire type oscillators.

For one-dimensional networks of identical relaxation oscillators with \( \epsilon > 0 \) and a Heaviside type interaction, Somers and Kopell [Somers and Kopell, 1993] suggested that the average time to synchrony increases linearly with \( n \). However, it is not known whether this scaling relation is due to the fact that the oscillators are relaxation type, or because the interaction is discontinuous. We present numerical evidence suggesting that the interac-
tion can result in this scaling relation, independent of the type of oscillator used. This provides further evidence [see Chapter 2, Daido, 1993b] that a discontinuous interactions can qualitatively change the properties of synchronization in oscillator networks when compared with smooth, continuous interactions.

This Chapter is organized as follows. In Section 3.2 we briefly describe a single relaxation oscillator. We then describe a pair of interacting relaxation oscillators and detail how we perform analysis in the singular limit ($\varepsilon = 0$) in Section 3.3. We discuss desynchrony in one-dimensional chains of oscillators in Section 3.4, which contains a detailed examination of fractured synchrony and travelling waves. In Section 3.5 we discuss our data on synchrony in one-dimensional networks of relaxation oscillators. We attempt to explain the observed scaling relationship and we also examine the sensitivity of these systems to spin wave type initial conditions. Section 3.6 displays our data on synchrony and spatiotemporal pattern formation in two-dimensional networks. In Section 3.7 we compare the average time to synchrony in one-dimensional networks of integrate-and-fire oscillators with that of networks of relaxation oscillators. In Section 3.8 we present data for the average time to synchrony in one-dimensional networks of relaxation oscillators that are not in the singular limit ($\varepsilon > 0$) using both smooth and discontinuous interactions. Section 3.9 concludes the Chapter.

3.2 A Single Relaxation Oscillator

The relaxation oscillators we use are equivalent to the Terman-Wang relaxation oscillator [Terman and Wang, 1995]. This oscillator is closely related to the model of neuronal oscillation derived by Morris and Lecar [Morris and Lecar, 1981], but is considerably sim-
Figure 17. A plot of the nullclines and limit cycle of a relaxation oscillator. The dotted curve is the $x$-nullcline and the dash-dot curve is the $y$-nullcline. The limit cycle is given by the thick dark curve. The abbreviations are described in the text. The parameters used are $\lambda = 8$, $\gamma = 12$, $\epsilon = 0.005$, and $\beta = 1000$.

A single relaxation oscillator is defined as

$$\dot{x} = 3x - x^3 - y$$

$$\dot{y} = \epsilon (\lambda + \gamma \tanh(\beta x) - y)$$

The limit cycle and nullclines for this oscillator are shown in Figure 17. The $x$-nullcline, $\dot{x} = 0$, is a cubic function. Two important values of this cubic are the $y$-values of the local extrema, denoted by $RK$ (right knee) and $LK$ (left knee). The $y$-nullcline, $\dot{y} = 0$, is a sigmoid and is assumed to be below the left branch (LB) and above the right branch (RB) of the cubic as shown in Figure 17. The parameter $\beta$ controls the steepness of the sigmoid and we use $\beta \gg 1$. The value $\epsilon$ is chosen to be small, $0 < \epsilon \ll 1$, so that motion in the $x$-direction is fast in comparison to motion in the $y$-direction. The oscillator thus defined is a typical relaxation oscillator. The limit cycle is made up of four pieces: two slowly changing pieces along the left and right branches of the cubic and two fast pieces that connect
the left and right solutions. The parameters $\lambda$ and $\gamma$ are used to modify the amount of time an oscillator spends on the left and right branches. We assume that the amount of time an oscillator needs to traverse the left branch is larger than the amount of time it needs to traverse the right branch. The left and right branches are referred to as the silent and active phases of the limit cycle.

### 3.3 A Pair of Relaxation Oscillators

We now examine two coupled relaxation oscillators, defined as

$$\dot{x}_1 = 3x_1 - x_1^3 - y_1 + \alpha_R S(x_2)$$

(3.2.a)

$$\dot{y}_1 = \varepsilon \left( \lambda + \gamma \tanh(\beta x_1) - y_1 \right)$$

(3.2.b)

$$\dot{x}_2 = 3x_2 - x_2^3 - y_2 + \alpha_R S(x_1)$$

(3.2.c)

$$\dot{y}_2 = \varepsilon \left( \lambda + \gamma \tanh(\beta x_2) - y_2 \right)$$

(3.2.d)

$$S(x) = \left[ 1 + \exp(\kappa (\Theta - x)) \right]^{-1}$$

(3.2.e)

The parameter $\alpha_R$ is the coupling strength and is assumed to be positive. The subscript $R$ denotes that this is the coupling strength between relaxation oscillators. The interaction term is a sigmoid, mimicking excitatory chemical synapses. Increasing the value of $\alpha_R S(x)$ elevates the $x$-nullcline, $\dot{x}_i = 0$. This is a property seen in several descriptions of neural behavior [Hodgkin and Huxley, 1952, Fitzhugh, 1961, Wilson and Cowan, 1972, Morris and Lecar, 1981]. Because the parameter $\kappa \approx 1$, the interaction is approximately a binary function. The threshold of the interaction term, $\Theta$, is placed between the left and right branches of the $x$-nullcline, thus the interaction term is either on or off depending on whether or not an oscillator is on the active or silent phase of the limit cycle. When one oscillator, $O_1$, is on the right branch, the other oscillator, $O_2$, is said to receive excitation.
This excitation raises the $x$-nullcline of $O_2$, now called the excited, or upper nullcline, and $O_2$ now exhibits dynamics based on its modified phase space. The three nullclines for this system and the limit cycle of the synchronous solution are shown in Figure 18. The pertinent values of the $x$-nullclines are the $y$-values of their local extrema. For the particular equations we use in (3.2), the $x$-nullcline shifts upward in direct proportion to $\alpha_R S(x)$. The four local extrema are denoted by the lower left knee ($LLK$) and the lower right knee ($LRK$) for the unexcited $x$-nullcline, and the upper left knee ($ULK$) and the upper right knee ($URK$) for the excited nullcline. The values of the extrema for the $x$-nullclines given in (3.2) are

$$LLK = (LLK_x, LLK_y) = (-1, -2)$$
$$LRK = (LRK_x, LRK_y) = (1, 2)$$
$$ULK = (ULK_x,ULK_y + \alpha_R)$$
$$URK = (URK_x,URK_y + \alpha_R)$$
The synchronous solution for a pair of oscillators is shown in Figure 18. Because of the interaction, the oscillators travel a larger distance along the cubics than when uncoupled and therefore the synchronous solution has a longer period than a single uncoupled oscillator. When an oscillator is on either of the left branches, we say that it is in the silent phase and when an oscillator is on either of the right branches, we say that it is in the active phase.

In Figure 19 we display an example of the trajectories for two coupled oscillators, as well as the excited and unexcited x-nullclines; both oscillators are initially placed on the lower left branch. The trajectory of $O_1$ is shown by the thin curve and that of $O_2$ is shown by the thick curve. $O_1$ travels until it reaches the lower left knee. When it reaches this knee, it begins to move in the positive x-direction. Motion in the x-direction occurs quickly in relation to motion in the y-direction (or instantly if $\varepsilon = 0$). This motion is referred to as a “jump up” from the silent to the active phase. As $O_1$ jumps up, its x-value crosses the threshold of the interaction, $\theta$, and $O_2$ receives excitation. The interaction term elevates the x-nullcline of $O_2$ by $\alpha R$. When its x-nullcline rises, $O_2$ is suddenly below the upper left knee and is induced to jump up. The range of initial conditions for which this can occur is called the jumping region, and this jumping region is analogous to the jumping region described for integrate-and-fire oscillators (see Section 2.2). Note that when the two oscillators jump up together, the y-distance between them does not change. Because of this, we use the reset rule for integrate-and-fire oscillators given in (2.4), which does not alter the Euclidean distance between two integrate-and-fire oscillators when they fire synchronously. It has been shown that a locally coupled network of relaxation oscillators, with initial conditions such that all oscillators can jump up together, synchronizes at a geometric rate [Terman and Wang, 1995].
Figure 19. An example of the trajectories for a pair of coupled relaxation oscillators. The thin solid curve represents the first oscillator to jump and the thick solid curve represents the oscillator that receives excitation. The two dotted curves are the excited and unexcited cubics. The parameters are the same as in Figure 18 with $\alpha_R = 6.0$.

Figure 19 diagrams just one class of trajectories that a pair of coupled relaxation oscillators can exhibit. There are other trajectories for the two relaxation oscillators dependent on their initial conditions. For example, $O_2$ can have an initial condition such that it is not able to jump immediately when it receives excitation and instead "hops" from the lower left branch to the upper left branch. Somers and Kopell [Somers and Kopell, 1993] originally described several classes of these trajectories (shown in Appendix A2). For the particular relaxation oscillator we study, these classes of trajectories have been analyzed by Campbell and Wang [Campbell and Wang, in press]. Although we examined time delays, the results they obtained are valid for zero time delay and are derived in Appendix B. If there is no time delay in the interaction, then synchrony is the asymptotically approached solution for all initial conditions in which both oscillators start on the lower left branch of the limit cycle and if coupling strength satisfies (B.35). In Section 3.3.1 we describe how to analytically examine the trajectories of a pair of relaxation oscillators in the singular limit.
If the coupling strength is not large enough, then a pair of relaxation oscillators can have stable desynchronous solutions [Kopell and Somers, 1995]. We explicitly derive the minimum coupling strength needed for synchrony in a pair of coupled Terman-Wang oscillators in Appendix B. When dealing with one-dimensional networks of relaxation oscillators, another constraint on the coupling strength arises. We explain this constraint and explicitly derive the minimum coupling strength needed to prohibit these desynchronous solutions in Section 3.4.1. For all synchronization results in this paper, we use a coupling strength that always results in synchrony. Note that a pair of pulse-coupled integrate-and-fire oscillators become synchronous with any positive coupling strength [Mirollo and Strogatz, 1990].

3.3.1 Relaxation Oscillators in the Singular Limit

We now describe how the trajectories for coupled relaxation oscillators can be analytically computed. In the singular limit, when $\varepsilon = 0$, the motion of an oscillator can be determined by a single variable and the knowledge of which branch the oscillator is on (see [Terman and Wang, 1995]). We derive these statements below.

We examine the two oscillators defined in (3.2),

\begin{align}
\dot{x}_1 &= 3x_1 - x_1^2 - y_1 + \alpha_R S(x_2) \\
\dot{y}_1 &= \varepsilon (\lambda + \gamma \tanh(\beta x_1) - y_1) \\
\dot{x}_2 &= 3x_2 - x_2^3 - y_2 + \alpha_R S(x_1) \\
\dot{y}_2 &= \varepsilon (\lambda + \gamma \tanh(\beta x_2) - y_2) \\
S(x) &= \left[ 1 + \exp(\kappa (\theta - x)) \right]^{-1}
\end{align}

The fast system of (3.3) is obtained by setting $\varepsilon = 0$. This results in

70
\[
\dot{x}_i = 3x_i - x_i^3 - y_i + \alpha R S(x_j(t)) \quad (3.4.a)
\]
\[
\dot{y}_i = 0 \quad (3.4.b)
\]

where \( i = 1, 2 \) and \( j = 3 - i \). The slow system for (3.3) is derived by introducing a slow time scale \( t' = \varepsilon t \) and then setting \( \varepsilon = 0 \). The slow system for the lower left branch is

\[
x_i = h(y_i) \quad (3.5.a)
\]
\[
\dot{y}_i = \lambda + \gamma \tanh[\beta h(y_i)] - y_i \quad (3.5.b)
\]

where \( x = h(y) \) describes the lower left branch of (3.3). System (3.5) determines the slow evolution of an oscillator on the lower left branch. Because \( \beta \gg 1 \) and \( h(y) \leq -1 \), we rewrite (3.5.b) as

\[
\dot{y}_i = \lambda - \gamma - y_i \quad (3.6)
\]

For an oscillator on the upper left branch, (3.6) will again result because \( h_u(y) \leq -1 \), where \( x = h_u(y) \) defines the upper left branch. Thus, because the \( y \)-nullcline is step-like, an oscillator has the same velocity in the \( y \)-direction along either of the left branches. For the right branches, these same steps result in the following analogous equation,

\[
\dot{y}_i = \lambda + \gamma - y_i \quad (3.7)
\]

The velocity in the \( y \)-direction of an oscillator along either of the right branches is given by (3.7). This type of analysis can be done for other relaxation oscillators as well. In more generalized versions of relaxation oscillators, the speed along different cubics may be different.
In the singular limit, $\varepsilon = 0$, system (3.3) reduces to two variables. The exact form of the x-nullcline is not important as long as a general cubic shape is maintained. The evolution of the system is determined through the knowledge of the location of the local extrema and by solving (3.6) and (3.7). The equation describing $y_i(t)$ along either of the left branches is

$$y_i(t) = (y_i(0) - \lambda + \gamma) e^{-t} + \lambda - \gamma$$

(3.8)

The y-position of an oscillator along either of the right branches is given by

$$y_i(t) = (y_i(0) - \lambda - \gamma) e^{-t} + \lambda + \gamma$$

(3.9)

We compute the total period of oscillation, $P_T$, for the synchronous solution using (3.8) and (3.9). The time it takes to travel from $LLK_y$ to $LRK_y + \alpha_R$, along the upper right branch, is given by

$$\tau_{URB} = \log \left( \frac{LLK_y - \gamma - \lambda}{LRK_y + \alpha_R - \gamma - \lambda} \right)$$

(3.10)

The time needed to travel from $LRK_y + \alpha_R$ to $LLK_y$, along the lower left branch, is given by

$$\tau_{LLB} = \log \left( \frac{LRK_y + \alpha_R + \gamma - \lambda}{LLK_y + \gamma - \lambda} \right)$$

(3.11)

Thus, we have $P_T = \tau_{URB} + \tau_{LLB}$. The period of the synchronous solution for two coupled oscillators is greater than the period of a single uncoupled oscillator, because the coupling always has an effect even if the oscillators are perfectly synchronous. Thus the synchronous period is a function of the coupling strength. As mentioned previously, the amount of time an oscillator spends in the silent phase is larger it does in the active phase.
This will become an important consideration in later sections. We define the branch ratio, \( B_r \), as the time an oscillator spends on the lower left branch divided by the time it spends on the upper right branch,

\[
B_r = \frac{\tau_{LLB}}{\tau_{URB}}
\]  

(3.12)

The branch ratio also gives a qualitative measure of how the speeds along the left and right branches differ since both branches have the same length in the \( y \)-direction.

Our analyses in this Chapter and in Appendix B are derived at the singular limit, i.e. \( \epsilon = 0 \). We have not carried out a perturbation analysis, but we note that Terman and Wang [Terman and Wang, 1995] have carried out an analysis of networks of relaxation oscillators in the singular limit and extended their analysis from \( \epsilon = 0 \) to small positive \( \epsilon \). Our networks do not differ from theirs, so our results should also be valid for small positive \( \epsilon \). We have confirmed this with substantial simulations using various values of \( \epsilon \). Our results indicate that values of \( 0 < \epsilon \ll 1 \) do not significantly alter any of the trajectories discussed for a pair of oscillators. However, a finite value of \( \epsilon \) does change the scaling relation between the time to synchrony and the size of the system. We discuss this issue in Section 3.8.

In studying relaxation oscillators, it is useful to have some measure of the distance between them. We characterize the separation between the two oscillators by using the time difference between them, \( \Gamma(y_1, y_2) \), which is defined as

\[
\Gamma(y_1, y_2) = \begin{cases} 
\log \left( \frac{y_2 - \lambda + \gamma}{y_1 - \lambda + \gamma} \right) & \text{if both oscillators on left branch} \\
\log \left( \frac{y_2 - \lambda - \gamma}{y_1 - \lambda - \gamma} \right) & \text{if both oscillators on right branch}
\end{cases}
\]  

(3.13)
where $y_i$ is the $y$-value of $O_i$. This function represents the time needed for $y_2$ to travel to the position of $y_1$. This function is valid only if both oscillators are on the silent (or active) phase of the limit cycle and is undefined otherwise. We use the time difference between the two oscillators as a description of their relationship because this quantity is invariant when the two oscillators are on the same branch of the system [LoFaro, 1994, Terman and Wang, 1995].

We use the equations derived in Appendix B to calculate a return map (Figure 20A) for a pair of oscillators initially placed on the lower left branch. The initial time difference between the two oscillators is represented on the horizontal axis. The vertical axis displays the time difference between the two oscillators the next time they are both on the lower left branch. This return map ignores changes in ordering which occur. We note several features of this return map. The jumping region is given by the first 70% of the initial conditions. Just beyond the jumping region, there is an initial time difference, $t_{PS}$, which results in perfect synchrony between the two oscillators. Somers and Kopell [Somers and

Figure 20. (A) The return map for two relaxation oscillators. The horizontal axis represents the initial time difference, $t_I$, between the two oscillators on the lower left branch and the vertical axis represents the time difference between the two oscillators when they are next on the lower left branch, $t_2$. (B) A plot of the number of periods needed before both oscillators are in the jumping region, $C_f$, as a function of the initial time difference between the two oscillators, $t_I$. The parameters used are given in the Figure 18 caption.
Kopell, 1993] called the region near this time difference “supercompressed”, because large initial time differences are mapped, or compressed, into very small time differences in just one period. For larger initial time differences, the first oscillator can jump up, and traverse the lower right branch before the other oscillator can jump up. For the parameters we use, this trajectory also results in a significant reduction in the time difference. In Figure 20B we display the number of periods that are needed before the two oscillators are in the jumping region as a function of their initial time difference. The maximum number of cycles needed before both oscillators jump up together is one.

Although we have performed analysis only for initial conditions such that both oscillators start on the lower left branch, all of our computer simulations indicate that synchrony is achieved in a pair of oscillators even if both oscillators are randomly distributed on both branches of the limit cycle (if the coupling strength is large enough). This observation has also been made by Somers and Kopell [Somers and Kopell, 1993, Terman and Wang, 1995].

We now describe another aspect of a pair of relaxation oscillators. For two oscillators we define the compression ratio, \( C_R \). This term is a multiplicative factor that is less than one and describes how the time difference between the two oscillators changes when they jump up and down together. The largest value of \( C_R \) for system (3.3) is given by the following quantity,

\[
C_R = \frac{\log \left( \frac{c_4}{c_8} \right) \log \left( \frac{c_5}{c_1} \right)}{\log \left( \frac{c_2}{c_6} \right) \log \left( \frac{c_7}{c_3} \right)}
\]

(3.14)

where the values of \( c_i \) are given by
\[ c_1 = LLK_y - \lambda - \gamma \quad c_5 = LLK_y + \alpha_R - \lambda - \gamma \]
\[ c_2 = LLK_y - \lambda + \gamma \quad c_6 = LLK_y + \alpha_R - \lambda + \gamma \]
\[ c_3 = LRK_y - \lambda - \gamma \quad c_7 = LRK_y + \alpha_R - \lambda - \gamma \]
\[ c_4 = LRK_y - \lambda + \gamma \quad c_8 = LRK_y + \alpha_R - \lambda + \gamma \]

It can be shown that (3.14) has its minimum value when \( B_r = 1 \), i.e. when the amount of time an oscillator spends in the active phase is equal to the amount of time it spends in the silent phase. When \( B_r = 1 \) a pair of oscillators has the smallest value of \( C_R \). Both \( B_r \) and \( C_R \) will play a role in the rate of synchronization in one-dimensional chains of relaxation oscillators.

In summary, we described the dynamics of a pair of relaxation oscillators with a Heaviside type coupling. We have shown how analysis is performed in the singular limit and we have shown that synchrony is the asymptotically approached solution for a broad range of initial conditions. We have also described that desynchronous solutions exist if the coupling strength is not large enough.

### 3.4 Desynchrony in One-Dimensional Networks

In a pair of relaxation oscillators, there are two types of behaviors, a synchronous solution that arises if the coupling strength is large enough, and a desynchronous solution that can occur otherwise. One-dimensional networks of oscillators exhibit two analogous behaviors and a third dynamic which is a travelling wave. A network of relaxation oscillators is called synchronous if all the oscillators jump up (or down) at the same time. It is described as exhibiting fractured synchrony (following the terminology of Kopell and Somers [Kopell and Somers, 1995]) if groups of oscillators exist that have desynchronous relations with each other because the coupling strength is not large enough. We examine
fractured synchrony in Section 3.4.1. The third behavior, travelling waves, only occur in networks of oscillators with a ring topology and we examine this behavior in Section 3.4.2.

3.4.1 Fractured Synchrony in Chains of Relaxation Oscillators

We first define a network of $n$ relaxation oscillators as follows,

\[
\begin{align*}
\dot{x}_i &= 3x_i - x_i^3 - y_i + \sum_{j \in N(i)} J_{ij} S(x_j) \quad (3.16.a) \\
\dot{y}_i &= \varepsilon (\lambda + \gamma \tanh(\beta x_i) - y_i) \quad (3.16.b) \\
S(x) &= \left[ 1 + \exp(\kappa (\Theta - x)) \right]^{-1} \quad (3.16.c)
\end{align*}
\]

The sum is over all the nearest neighbors, $N(i)$, of oscillator $i$. As in networks of integrate-and-fire oscillators, the coupling strengths are normalized using

\[
J_{ij} = \frac{\alpha_R}{Z_i} \quad (3.17)
\]

where $Z_i$ is the number of nearest neighbors that oscillator $i$ has. This normalization ensures that all the oscillators have the same trajectory in phase space when synchronous regardless of how many neighbors they have [Wang, 1995].

As mentioned previously, a pair of oscillators do not achieve synchrony for all initial conditions on the lower left branch if the coupling strength is not large enough [Kopell and Somers, 1995]. For system (3.3) we derive this condition in Appendix B. When dealing with a one-dimensional chain of oscillators a similar constraint arises; desynchronous solutions can arise if the coupling strength is not large enough.
In a one-dimensional chain of oscillators there are three pertinent \( x \)-nullclines that an oscillator may lie on, dependent on whether it receives excitation from zero, one, or two of its neighboring oscillators. In Figure 21A we display a portion of the trajectories of two neighboring oscillators which have a desynchronous relation in a chain of oscillators. One oscillator, \( O_1 \), receives excitation and jumps up to the right middle branch. It quickly travels the length of this branch and jumps down to the middle left branch. When \( O_1 \) sends excitation to \( O_2 \), \( O_2 \) hops to the middle left branch. \( O_2 \) receives excitation only for a time \( \tau_C \) and it hops back down to the lower left branch when it ceases to receive excitation. This process repeats if \( O_2 \) is able to travel down to the lower left knee, a minimum time of \( \tau_A \), and traverse the right middle branch, a time of \( \tau_C \), before \( O_1 \) can traverse the length of the left middle branch, which takes a time \( \tau_B \). The portions of the nullclines that correspond to these constants \((\tau_A, \tau_B, \tau_C)\) are shown in Figure 21B. In order to prevent desynchronous solutions, the following condition must hold

\[
\tau_A + \tau_C > \tau_B
\]  

(3.18)

Figure 21. (A) The trajectories of two neighboring oscillators that have a desynchronous relation in a chain of oscillators. (B) The three pertinent portions of the \( x \)-nullclines which play a role in the desynchronous solutions. The symbols \( \tau_A, \tau_B, \) and \( \tau_C \) represent the time needed to traverse the indicated portions of the cubics.
For system (3.16) (with \( e = 0 \)) these time constants can be found explicitly as shown in the Section 3.3.1. Condition (3.18) becomes

\[
\frac{c_3c_7}{c_6c_1} < \frac{c_6}{c_8}
\]  

(3.19)

where the values of \( c_i \) are given in (3.15). Condition (3.19) can be rewritten as a function of \( \alpha_R \).

\[
\alpha_R^2 (c_2 - c_1) + \alpha_R (c_2c_3 + c_2c_4 - 2c_1c_2) + c_2c_3c_4 - c_1c_2^2 < 0
\]  

(3.20)

This results in the following relationship between \( \alpha_R \) and the other system parameters,

\[
\alpha_R > \frac{- (c_2c_3 + c_2c_4 - 2c_1c_2)}{2(c_2 - c_1)} + \sqrt{\frac{(c_2c_3 + c_2c_4 - 2c_1c_2)^2 - 4(c_2 - c_1) (c_2c_3c_4 - c_1c_2^2)}{2(c_2 - c_1)}}
\]  

(3.21)

If condition (3.21) is satisfied then these desynchronous solutions do not occur in one-dimensional networks. Numerical tests verify the above condition on the coupling strength. Let us denote the minimum coupling strength needed to satisfy (3.21) as the critical coupling strength, \( \alpha_R^c \). If \( \alpha_R \) is less than \( \alpha_R^c \), then some range of initial conditions exist in which neighboring oscillators can have a desynchronous relationship. For each initial condition within this range, there is a corresponding trajectory for a desynchronous solution. Thus these solutions are neutrally stable. This neutral stability results from the fact that the speed of motion in the y-direction is the same along all of the left branches. If the speed of motion in the y-direction is different for the different branches (a more general case) then an analysis similar to that by Kopell and Somers [Kopell and Somers, 1995] can indicate how the stability of desynchronous solutions is related to the
different speeds of motion along the different branches. Because these desynchronous oscillators do not travel along the same path as the synchronous solutions, their frequency is different. The frequency of these desynchronous solutions is

\[ P_D = \log \left( \frac{c_1}{c_3 + \alpha_R^2} \right) + \log \left( \frac{c_4 + \alpha_R^2}{c_2} \right) \] (3.22)

and this has been confirmed by simulations.

If the coupling strength does not satisfy condition (3.21) then two oscillators in a chain can have a desynchronous relation. This requires that the two oscillators have a specific spatiotemporal relationship on the limit cycle and further, that this relationship is maintained as the two desynchronous neighboring oscillators interact with their other neighbors. Thus, even if the coupling is less than the critical coupling strength, it is possible that a chain of oscillators with random initial conditions can exhibit synchrony. It is also possible that, occasionally, two oscillators will be desynchronous and create a boundary between two clusters, or blocks, of synchronous oscillators. Kopell and Somers refer to this formation of blocks of synchronous oscillators as fractured synchrony [Kopell and Somers, 1995].

Fractured synchrony arises only when the coupling strength is small enough and when two neighboring oscillators in the network have the correct relative positions on the \( x \)-nullclines to remain in a desynchronous relationship. As \( \alpha_R \) increases, the range of initial conditions which result in desynchronous solutions decreases and one expects that the average block size must increase. How the average block size increases in relation to the coupling strength is an intriguing question. In Figure 22 we display our numerical data on how the average block size increases as a function of \( \alpha_R \) for networks of different sizes. The data indicate that the average block size (for blocks of size less than 10) forms inde-
Figure 22. The average block size as a function of the coupling strength for several chains of length $n$. The parameters used are $\lambda = 9$ and $\gamma = 12$. The critical coupling strength is $\alpha_R^c = 2.3786$ using (3.18). Each point represents the average block size calculated from several hundred trials with random initial conditions.

dependent of the system size. For larger values of the coupling strength, the average block size becomes dependent on the size of the system, which is expected because the block size is limited by the size of the system. For an infinite system, the function describing the relationship between the average block size and $\alpha_R$ must diverge at the critical coupling strength, $\alpha_R^c$. One can fit the lower portion of the curves in Figure 22 well with a function of the form

$$\frac{e^{3\alpha_R}}{(\alpha_R^c - \alpha_R)^{-3}}$$

(3.23)

This function diverges at the critical coupling strength but we have no theoretical understanding of how (3.23) arises. Also, we have not been able to accurately estimate the functional form for finite size systems.
All data were obtained for relaxation oscillators in the singular limit ($\varepsilon = 0$). The trajectories of the oscillators were computed numerically using the algorithm developed by Linsay and Wang called the singular limit method [Linsay and Wang, 1996], which is much faster than traditional methods of numerical integration.

3.4.2 Travelling Waves in Rings of Relaxation Oscillators

In the previous section we derived a condition that prohibits fractured synchrony in one-dimensional networks of relaxation oscillators. This is not a sufficient condition for synchrony and we find that other behaviors arise besides synchrony. Travelling waves may develop if the network is a ring instead of a chain of oscillators (also observed by [Somers and Kopell, 1993]). We graphically describe these travelling waves for one-dimensional systems below and this analysis allows us to derive their frequency as well as approximate the minimum number of oscillators necessary to form a travelling wave.

In Figure 23 we display a few snapshots in time of a travelling wave. The x- and y-positions of 16 oscillators are shown, as well as the three nullclines that each oscillator can lie on. The initial conditions are specifically chosen so that a travelling wave results. Oscillator B is coupled to oscillators A and C. Oscillator C is coupled with oscillators B and D and each oscillator on the left branches is coupled to its nearest neighbors. Some of the oscillators have synchronized and their dots overlap. The speed of motion along the left and right branches are quite different, i.e. $B_r = 5.14$. Thus, even though the Euclidean distance between two oscillators on the active phase is greater than that between two oscillators on the silent phase, their time differences are very similar. Figure 23A shows the locations of the oscillators just before oscillator B jumps up and Figure 23B shows the system just after oscillator B jumps up. Oscillator B sends excitation to both oscillators C
and A. As a result oscillator C hops from the middle right branch to the upper right branch and oscillator A hops from the lower left branch to the middle left branch. Figure 23C shows the positions of the oscillators when oscillator D has just jumped down to the lower middle branch. As a result, oscillator E hops down from the middle left branch to the lower left branch and oscillator C hops down from the upper right branch to the middle right branch. For a few moments in time there are only two oscillators on the right branches and then oscillator A jumps up. This configuration is shown in Figure 23D, which is nearly identical to Figure 23B. Because the oscillators have appropriate spatial locations, the sequence of events shown in Figure 23 is able to repeat.

An important point about travelling waves is that the time difference between oscillators does not change. Figure 23A represents the oscillators just before oscillator B jumps up; there is some y-distance between oscillator A and the middle left knee (the position of oscillator B). When oscillator B jumps up, oscillator A is induced to hop to the middle left branch and must traverse this same y-distance before it can jump up. Because the oscillators traverse the same y-distance, their time difference does not change. The time differences between all oscillators in this travelling wave are maintained and thus the travelling wave cycles endlessly.

The period of this travelling wave is different from the synchronous period because the oscillators never traverse the entire length of the outer branches. They only traverse the length of the middle left and right branches and this period is given by

\[ P_M = \tau_B + \tau_C = \log\left(\frac{c_1 + \alpha_R/2}{c_2 + \alpha_R/2}\right) + \log\left(\frac{c_1 + \alpha_R/2}{c_3 + \alpha_R/2}\right) \]  

(3.24)
Figure 23. The positions of 16 oscillators in a travelling wave are shown at four different instants in time. The time slices are shown in consecutive order in (A), (B), (C), and (D). The network is a one-dimensional ring. The parameters are $\lambda = 9$, $\gamma = 12$, and $\alpha_R = 4$.

where the constants $c_i$ are given in (3.15). This period matches that observed in simulations. This travelling wave is a neutrally stable solution and in simulations, noise eventually perturbs the system into a synchronous solution, which is asymptotically stable.

In order to form a travelling wave, there is a minimum number of oscillators required. This minimum number of oscillators arises from the fact that no two neighboring oscillators can have a time difference larger than the amount of time spent on the middle right branch, $\tau_C$. If there are two neighboring oscillators such that $\Gamma(y_i, y_{i+1}) > \tau_C$, then there will be an instant in time when no oscillators are on the active phase. As a result, one
oscillator can travel to the lower left knee and the trajectories seen in Figure 23 cannot be maintained. As a conservative estimate, let us say that the time difference between every neighboring oscillator can be no greater than $\tau_C/2$ if travelling waves are to occur. This implies that the number of oscillators necessary to form a travelling wave, $n_w$, is approximately

$$n_w \approx \frac{2P_M}{\tau_C}$$

(3.25)

This approximation appears valid for all tested parameters. Thus, if $\tau_C$ is small in comparison to $P_M$, then the travelling wave will consist of a large number of oscillators arranged in a specific spatial order. If we go to the other extreme and $\tau_C = \tau_B$, which also implies that $B_r = 1$, then only four oscillators (or groups of oscillators) are needed to form a travelling wave. If the initial conditions of the oscillators are randomly chosen, then the probability of forming a travelling wave should be greatest when $\tau_C = \tau_B$. If $\tau_C \ll P_M$, then a travelling wave will require the specific spatial arrangement of a large number of oscillators, which becomes a low probability event using random initial conditions. Our numerical studies support these statements.

It is interesting to consider a limiting case of relaxation oscillators in which the amount of time spent on the right branches goes to zero, $\tau_{URB} \rightarrow 0$. As the active phase becomes instantaneous, $\tau_C \rightarrow 0$ and approximation (3.25) indicates that the number of oscillators required to form a travelling wave becomes infinite. Therefore travelling waves should not be possible in this limiting case of a relaxation oscillator. Also, as $\tau_{URB} \rightarrow 0$, the traversal of the right branch can be thought of as an instant reset to the left branch and the relaxation oscillators become qualitatively similar to integrate-and-fire oscillators, although the pulsatile interaction and the reset rule are different from those specified in
Section 2.2. So as an individual relaxation oscillator becomes similar to an integrate-and-fire oscillator, networks of these relaxation oscillators take on properties observed in networks of integrate-and-fire oscillators, namely that travelling waves do not occur (see Chapter 2).

We argue that the travelling waves described here are necessarily a result of the topology of the network. If we use a chain instead of a ring of oscillators, then travelling waves are never observed and logically it does not appear possible for travelling waves to exist. For a travelling wave to exist, it would need to change directions (reflect) at the ends of the chain, and for a travelling wave to reverse directions it appears to require a complete reversal of the spatial ordering of at least $n_w$ oscillators. We are not aware of a mechanism through which this reordering of $n_w$ oscillators can occur.

In summary, we have graphically described travelling waves. Based on this analysis we have derived the period of a travelling wave and created an approximation for the minimum number of oscillators needed to form a travelling wave. Our understanding of how travelling waves form allows us to choose parameters to either increase or decrease their probability of occurrence when initial conditions are randomly chosen. We have also described why reflections are not possible and therefore that these travelling waves cannot exist in one-dimensional chains of oscillators. We have also formed a link between one limiting case of relaxation oscillators (when $B_r$ becomes infinite) and integrate-and-fire oscillators. In this limiting case, the interactions between relaxation oscillators become instantaneous (as is the interaction between integrate-and-fire oscillators) and the number of oscillators needed to form a travelling wave goes to infinity. Since integrate-and-fire oscillator networks do not exhibit travelling waves, we have further justification for linking relaxation oscillators as $B_r \to \infty$ and integrate-and-fire oscillators.
3.5 Synchrony in One-Dimensional Chains

In the previous Section we described two ways in which synchrony does not occur in one-dimensional networks of relaxation oscillators. In Section 3.4.1 we indicated how fractured synchrony could arise if coupling strength is small enough and in Section 3.4.2 we described how travelling waves can arise in a ring of oscillators. We now examine synchrony one-dimensional chains of locally coupled relaxation oscillators.

In order to ensure that synchrony occurs in chains of relaxation oscillators, we use a coupling strength large enough so that fractured synchrony does not occur, i.e. condition (3.21) is satisfied. We do not worry about travelling waves in chains of oscillators because they should not occur without periodic boundary conditions. For a travelling wave to reverse directions would require a complete reversal of the spatial ordering of at least $n_w$ oscillators. Due to this logic, we are convinced that travelling waves do not exist in chains of identical relaxation oscillators. Our data also support this statement.

Section 3.5.1 displays our data indicating that the average time to synchrony $\langle T_s \rangle$ scales as $n^p$, where $n$ is the length of the chain and $p$ is an experimentally obtained quantity which is less than 0.5 for all of our data. We then attempt to explain why $\langle T_s \rangle \sim n^p$ in Section 3.5.2. In Section 3.5.3 we examine the sensitivity of the system to the initial conditions. This section will offer some support for our claims in Section 3.5.2 regarding the scaling relation $\langle T_s \rangle \sim n^p$. We summarize our results in Section 3.5.4. All data in this Section have been obtained in the singular limit ($\epsilon = 0$) using the singular limit method of Linsay and Wang [Linsay and Wang, 1996].
3.5.1 Synchrony in One-Dimensional Networks

We now display our numerical data on synchrony in chains of locally coupled identical relaxation oscillators. Figure 24 displays the average time to synchrony for a chain of \( n \) relaxation oscillators as a function of \( \log_{10}(n) \), with parameters such that the branch ratio is large, i.e. \( B_r = 1190 \). For large values of \( B_r \), an oscillator spends very little time on the active phase and sends excitation to its neighbors for a very short amount of time. In this respect it is similar to the integrate-and-fire oscillators used in Chapter 2. The resultant qualitative synchronization behavior of these relaxation oscillator networks is the same as that seen for integrate-and-fire oscillator networks, i.e. the average time to synchrony increases with the logarithm of the system size.
As an oscillator spends more and more time on the right branch of the limit cycle, it becomes intuitively less and less similar to an integrate-and-fire oscillator. We examine whether decreasing \( B_r \) results in a qualitative change in the average time to synchrony. In Figure 25 we display the average time to synchrony as a function of \( \log_{10}(n) \) for several choices of \( B_r \) (\( B_r = 1190, B_r = 19.2, B_r = 8.87, \) and \( B_r = 7.15 \)). The data indicate that chains with \( n < 20 \) have the same average synchronization time. For larger chain lengths, networks with different parameters exhibit different times to synchrony. The diamonds (\( B_r = 1190 \)), plus signs (\( B_r = 19.2 \)), and squares (\( B_r = 8.87 \)) all appear to lie on a straight line for values of \( n > 100 \). The slopes of these lines decrease as the oscillator spends more time on the right branch. We believe that this can be qualitatively explained by noting that the compression ratio, \( C_R \), decreases as \( B_r \rightarrow 1 \) (a decrease in \( C_R \) increases the rate of synchronization for a pair of oscillators). The fourth set of data (shown by the “crosses”) is for relaxation oscillators with \( B_r = 7.15 \) and \( \langle T_2 \rangle \) is no longer linear on this semi-log plot. The compression ratio is smallest for these relaxation oscillators indicating that some other phenomenon occurs which increases \( \langle T_2 \rangle \) as \( B_r \) becomes smaller.

The parameters were chosen specifically to decrease the amount of time an oscillator spends on the right branch without significantly altering other quantities. The other quantities we are interested in maintaining are the size of the jumping region relative to the period, and the coupling strength. By keeping these two quantities similar while widely varying \( B_r \), we hoped to observe changes in \( \langle T_2 \rangle \) that resulted only from varying \( B_r \).

We explore synchrony for smaller values of \( B_r \). In Figure 26 the trend that started in Figure 25 becomes more pronounced. The average time to synchrony increases significantly as \( B_r \) decreases. In Figure 27 we display the same data as shown in Figure 26 except that the data is plotted on a log-log scale. We do not show all of the data from
Figure 25. The average time to synchrony for chains of \( n \) relaxation oscillators as a function of \( \log_{10}(n) \). The four different symbols represent four different branch ratios, also indicated are the four different percentages for the amount of time an oscillator spends in the silent phase as compared to the total period. The initial conditions were randomly distributed on the limit cycle.
Figure 26. The average time to synchronize a chain of $n$ relaxation oscillators as a function of $\log_{10}(n)$ for five different values of $B_r$. The averages are based on several hundred trials. The initial conditions were randomly distributed on the limit cycle.
Figure 27. A log-log plot of the time to synchrony as a function of the system size for several different parameters. The inset is the log-log plot for $B_r = 7.15$ and is shown to indicate the standard deviations associated with each average. Each point corresponds to the average computed from several hundred trials with initial conditions uniformly and randomly distributed throughout the entire limit cycle.
Figure 26 because the average times to synchrony for $n < 100$ do not yield straight lines and we assume that the data for small system sizes does not reflect the asymptotic behavior of the system. For system sizes from $10^2 - 10^4$, our data indicate that $\langle T_s \rangle \sim n^p$. It is not highly noticeable, but in Figure 27 one can see that the slopes of the lines are slightly different, the points are closer together at the bottom of the graph than at the top of the graph. The slopes of the lines shown in Figure 27 are listed in the table below the figure and vary from a high of 0.46 ($B_r = 1.19$) to a low of 0.14 ($B_r = 7.15$). The data in Figure 27 are somewhat misleading because they give the impression that $p$ is directly related to $B_r$.

While it is true in general that $p$ increases as $B_r$ decreases (all of our data support this statement), it is not true that $B_r$ is the only factor controlling the rate of synchrony. Different parameter sets can yield identical values for $B_r$, but the resultant scaling relation between $\langle T_s \rangle$ and $n$ can be quite different. Using the parameters listed at the bottom of the table in Figure 27, results in an average time to synchrony that scales logarithmically with the size of the system, even though $B_r = 3.07$, a value nearly identical to one of the parameter sets shown. We do not have a detailed understanding of how and which parameters are related to $p$, other than the general statement that $p$ increases as $B_r$ decreases. We give some theoretical insight into why this general statement should be correct in the following subsection.

3.5.2 Attempt to Explain the Scaling Relation for Relaxation Oscillators

Now that we have this data indicating that $\langle T_s \rangle \sim n^p$ and a rough estimate of how $p$ varies with $B_r$, the task remains of how to explain it. We begin by examining if there are any immediately obvious difference between the behavior of a network with $B_r \gg 1$ and networks with parameters such that $B_r = 1$. 

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Figure 28. The temporal evolution of a chain of 400 relaxation oscillators with $B_r = 102$. The thin (thick) lines represent the time each oscillator jumps up (down), but these lines are too close together to distinguish. The rectangle highlights an area where some oscillators fire with different blocks. The parameters used are $\alpha_R = 3.5$, $\lambda = 179$, and $\gamma = 182$. The oscillators were randomly distributed on the limit cycle.

We begin this examination graphically. In Figure 28 we display the temporal evolution of a one-dimensional network of relaxation oscillators with $B_r = 102$ (an oscillator spends 99% of its period on the left branch). Each line represents the time an oscillator jumps up. Because the jump down occurs so quickly after the jump up, the lines representing these events are not visible in Figure 28 due to the thickness of the lines. The oscillators quickly merge and form sizeable blocks within the first cycle. These blocks merge to form larger blocks. However, some oscillators can switch from one block to another. The rectangle shown in Figure 28 highlights a region in which one can see a number of oscillators which fire with one block, shortly after $t = 2$; these oscillators then fire with a different block shortly before $t = 4$. This is different from one-dimensional networks of integrate-and-fire
oscillators in which blocks do not break. However, this breaking of blocks is not prominent enough to destroy the overall dynamics that lead to synchronization of the network. Some blocks may become smaller, but the average block size still increases.

We now examine a relaxation oscillator network with $B_r = 1$. The temporal evolution of a network of 400 relaxation oscillators with $B_r = 1$ is shown in Figure 29. Both the jumps up (thin lines) and the jumps down (thick lines) are now visible because the oscillators spend a significant percentage of their period (50%) on the active phase. Figure 29 is different from Figure 28 in several ways. One of these differences is that the borders between blocks are no longer sharp. The borders between blocks appear to be of some thickness and they are not corrected, or do not merge with neighboring blocks quickly. Another noticeable feature of Figure 29 is that there are two different frequencies in the system. The synchronous period (about 4 time units) can be seen at the top of the graph when all of the oscillators fire in unison. Another frequency is seen at the ends of the chain (oscillators 300-400 from time 0-10 and elsewhere). From this graph we refer to two types of defects in relaxation oscillator networks. The first defect we call “small defects” and these small defects are rather quickly corrected as blocks of oscillators form. We suggest that nearly all the small defects are corrected by time $t = 4$. The other defect we refer to as “frequency defects” because they cause the regions of higher frequency. For comparison, Figure 28 contains no frequency defects.

We conjecture that this power law behavior $\langle T_x \rangle \sim n^p$, arises from the frequency defects and that these frequency defects arise from the same types of initial conditions that lead to travelling waves. In support of this conclusion are several facts. The first fact is that the frequency defects have the same frequency as that of the travelling waves. The second fact is that the frequency defects appear to occur most frequently in systems with
Figure 29. The temporal evolution of a system of 400 relaxation oscillators is displayed. Each thin (thick) dot, or line, represents the time each oscillator (or block of oscillators) jumps up (down). The parameters used are $\alpha_R = 3.5$, $\lambda = 1.75$, and $\gamma = 4.75$, with initial conditions randomly distributed on the entire limit cycle.

If $B_r = 1$, then the number of oscillators (or oscillator groups) necessary to create a travelling wave is 4 (using (3.25)). This is the minimum number of oscillators needed to create a travelling wave. Thus, given random initial conditions one would expect frequency defects to occur most often in systems with $B_r = 1$. These facts lead us to believe that frequency defects are the cause of the scaling relation $\langle T_S \rangle \sim n^p$.

How the frequency defects are related to the scaling relation $\langle T_S \rangle \sim n^p$ is as yet unknown. From Figure 29 one can see that frequency defects appear to be corrected when they interact with oscillators that have the synchronous frequency. Where these regions of the synchronous frequency occur and how many of them occur are currently unknown. Since there can be several regions that exhibit the synchronous frequency, the frequency defects can be corrected in many ways. We will later create initial conditions such that there is only one region of oscillators which has the synchronous frequency. This region is
located at one end of the chain, thus only one defect at a time can be corrected. Experiments show that for this arrangement, the time needed to synchronize the network is linearly dependent on the number of frequency defects. This supports our conjecture that it is the number of regions with synchronous frequencies and their resultant interactions with frequency defects that controls the rate at which a network synchronizes.

We have attempted to come up with other explanations for this power law. So far no evidence supports other possibilities. For example, one can view these defects as boundaries between blocks of oscillators. If the size of the boundaries changed over time, or if the size of the boundaries increased as the size of the system increased, then we could examine this change as a means through which the scaling relation $\langle T_S \rangle \sim n^p$ might arise. However, as one can see in Figure 29, once a defect (or a boundary) exists, there does not seem to be any noticeable change in this boundary until it interacts with a block that has the synchronous frequency. A more careful examination of the boundaries with differently sized networks yields the same conclusion: that the boundary layer does not change in time, or with the size of the system. The fact that these boundaries do not change in time gives support to our conjecture that these frequency defects are related to travelling waves. This is because the time differences between oscillators in a travelling wave are maintained (as discussed in Section 3.4.2).

3.5.3 Sensitivity of Relaxation Oscillator Networks to Initial Conditions

In the previous section we indicated that the scaling relation $\langle T_S \rangle \sim n^p$ may arise from frequency defects and their interaction with regions of the synchronous frequency, both of which arise from the initial conditions. This leads us to examine the issue of how sensitive these networks are to initial conditions.
Figure 30. The time to synchrony as a function of the wave number of spin wave type initial conditions in a one-dimensional network of 500 relaxation oscillators. The oscillators were evenly distributed (temporally) on the limit cycle of the travelling wave. The parameters used are $\alpha_I = 5.5$, $\lambda = 2.75$, and $\gamma = 5.75$.

As indicated in Section 3.4.2, one needs a specific spatial relationship between several oscillators to create a travelling wave. Merely shifting the position of a single oscillator in Figure 23 can destroy the travelling wave and the system becomes synchronous. Similarly, shifting the initial position of a single oscillator in Figure 29 can remove one of the frequency defects. If we were to remove the frequency defect near oscillator 225, then one can imagine that oscillators 50-300 become synchronous by time $t = 4$. Because of this change, the entire system could synchronize by time $t = 8$. In tests we have cut the synchronization time of a network in half by altering the initial condition of a single oscillator.

Similarly, one can increase the synchronization time of a network by the creation of frequency defects. Due to the cyclic nature of the travelling waves on the limit cycle, spin wave type initial conditions can create frequency defects. For example, if the wavelength of the spin wave is the size of the system, then there is one frequency defect. If the wavelength is half of the system size then there are two frequency defects, etc. Also, since there
is a minimum number, $n_w$, of oscillators needed to create a travelling wave, we infer that there is a similar number of oscillators needed to create a frequency defect. Thus, there should be a maximum number of defects that any one network can contain. When $B_r = 1$ then $n_w \sim 4$ and there can be at most $n/4$ frequency defects in a chain of length $n$. In Figure 30 we plot the time to synchrony for a chain of 500 oscillators (with $B_r = 1$) as a function of the wave number (inverse wavelength). Due to memory constraints, this diagram is a schematic representation of the actual data and the right half of the graph in particular is a caricature of the actual data. We focus on the left half of this graph, which indicates a linear increase in the time to synchrony as the wave number increases. In these trials, one end of the chain begins oscillating at the synchronous frequency of the system, $P_r$. All the other frequency defects are interacting with other frequency defects and are not corrected. This is shown in Figure 31. Since only one frequency defect is corrected at
a time, the time to synchrony should increase linearly with the number of defects. The data in Figure 30 support this statement. The maximum time to synchrony occurs at a wave number of 0.25 (wavelength 4), which is as expected since the maximum number of frequency defects is created at this wave number. For larger value of the wave number, the spin wave type initial conditions do not generate frequency defects in a simple fashion and the graph becomes correspondingly more complex.

3.5.4 Summary

In summary we have presented numerical data indicated that $\langle T_S \rangle \sim n^p$ in one-dimensional chains of identical relaxation oscillators without noise. Our data indicate that $p$ increases as $B_r$ decreases. We have examined networks of oscillators in order to find the origin of this scaling relation and in doing so, we have discovered frequency defects. We have shown how these frequency defects can be created and this gives us theoretical insight as to why $p$ should increase as $B_r$ decreases. We have proposed that frequency defects are corrected when they interact with blocks of oscillators that have the synchronous frequency and we have shown some simple cases in which we can control the creation of frequency defects and predict their rates of correction. However, for random initial conditions, the creation of frequency defects and the creation of blocks of oscillators with the synchronous frequency occur unpredictably and we do not know how to accurately estimate even their average quantities. Also, we do not have a complete understanding of how they interact, which we conjecture results in the scaling relation $\langle T_S \rangle \sim n^p$. 

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3.6 Two-dimensional Networks of Relaxation Oscillators

In two-dimensional networks of relaxation oscillators, we again find the three basic behaviors seen in one-dimensional networks; fractured synchrony, travelling waves, and synchrony. With random initial conditions, synchrony is the most frequently observed final state of the system. We also find more complex dynamics than in one-dimensional systems. With periodic boundary conditions (the network is a torus) travelling waves move across the network (up, down, right, and left) and other, more complex spatiotemporal patterns occur. Using normalization (3.17), rotating waves are observed.

In Section 3.6.1 we describe synchronization in two-dimensional networks of relaxation oscillators with parameters such that \( B_r \gg 1 \). In this limit, the networks exhibit a scaling relation \( \langle T_s \rangle \sim \log_{10}(n) \). We describe how the initial conditions can be restricted so that spatiotemporal patterns are never observed. We then graphically describe several types of spatiotemporal patterns in two-dimensional systems in Section 3.6.2.

3.6.1 Synchrony in Two-Dimensional Relaxation Oscillators

We now display some of our numerical data on the synchronization time in two-dimensional networks of relaxation oscillators. We first display our data for networks of oscillators in which \( B_r = 47.7 \) in Figure 32A. For the parameters used, we did not observe rotating waves and synchrony was the final state of the system for all trials. The time to synchrony yields a straight line on the semi-log plot, indicating that \( \langle T_s \rangle \sim \log_{10}(n) \). Rotating waves are possible however, but we believe that they are an extremely low probability event given random initial conditions, using the same arguments presented in Section 3.4.2, namely that a large number of oscillators must have the correct spatial ordering on the limit cycle to form a rotating wave when \( B_r \gg 1 \).
Figure 32. The average time to synchrony in an $L \times L$ network of relaxation oscillators as a function of $\log_{10}(2L-1)$. (A) A network with parameters such that $B_r = 47.7$ ($\alpha_R = 8$, $\lambda = 112$, and $\gamma = 115$) and the initial conditions were chosen randomly and uniformly from the entire limit cycle. (B) A network with parameters such that $B_r = 3.03$ ($\alpha_R = 8$, $\lambda = 8$, and $\gamma = 11$). The averages are based on several hundred trials and the initial conditions were chosen randomly and uniformly on the lower left branch of the limit cycle.

In Figure 32B we plot a similar graph with parameters chosen such that $B_r = 3.03$. Also, the initial conditions were restricted to lie only on the left branch. With these restrictions on the initial conditions, we have always observed synchrony as the final state of the system. However, even though synchrony is always achieved, there is no longer any apparent scaling behavior. The curve is non-monotonic and non-intuitive. We have no theoretical understanding of how this curve arises. Our data suggest that with initial conditions on the lower left branch, synchronization is bounded above by a quantity proportional to $\log_{10}(2L-1)$ in an $L \times L$ network. If one allows some oscillators to lie on the right branch, then it is possible for spatiotemporal patterns to form.

3.6.2 Spatiotemporal Pattern Formation

Synchrony is not always attained in two-dimensional networks. As in the one-dimensional case, spatiotemporal patterns require a specific set of initial conditions before travelling waves or other periodic behavior form. In one-dimensional systems, at least one
Figure 33. One type of spatiotemporal pattern observed in a network of relaxation oscillators with periodic boundary conditions. The smaller circles represent those oscillators which have recently jumped up to the right branch. The larger circles represent oscillators which are on the right branch of the limit cycle. The parameters used to create this diagram are $\alpha_R = 3.5$, $\lambda = 1.75$, and $\gamma = 4.75$.

An oscillator must be on the active phase of the limit cycle at any one time. Also, a travelling wave can consist of blocks of oscillators, or single oscillators. In two-dimensional systems similar logic applies. We display a pattern that appeared in a $4 \times 4$ network of oscillators with periodic boundary conditions in Figure 33. In larger networks, $10 \times 10$ for example, we saw many different types of patterns. Categorizing these patterns remains a topic of interest. The period of these patterns is different from the synchronous frequency of the individual oscillators, and it is also different from the frequency travelling waves seen in one-dimensional systems. In a two-dimensional network with periodic boundary conditions, there are five $x$-nullclines that an oscillator can lie on dependent on how many oscillators it receives excitation from. The patterns were characterized by one common feature: each group of oscillators was configured such that each oscillator in the group had three nearest neighbors. From this, we surmise that these oscillators travel on the next to the lowest left branch, and the next to the highest right branch, giving a period of
Figure 34. One type of spatiotemporal pattern observed in a network of relaxation oscillators with a grid topology and with connection weights normalized using (3.17). The filled circles represent oscillators which are on the right branch of the limit cycle. The parameters used are the same as in Figure 33.

$$P_3 = \tau_{L1} + \tau_{R3} = \log \left( \frac{c_4 + 3\alpha_R/4}{c_2 + \alpha_R/4} \right) + \log \left( \frac{c_1 + \alpha_R/4}{c_3 + 3\alpha_R/4} \right)$$

(3.26)

This period matches that observed numerically. We do not know if this is the only period possible in two-dimensional spatiotemporal patterns.

In two-dimensional networks with a grid topology, normalized using (3.17), slightly different types of travelling waves occur. In these systems, we do not see the variety of patterns seen in networks with periodic boundary conditions. We observe only rotating waves. These rotating waves do not have the same period as those in networks with periodic boundary conditions. This is because there are now seven x-nullclines in the system because the weights have more than just a single given value. This period can be described analytically, but we do not get into this detail here. As before, we display a 4 x 4 network of oscillators with a highly symmetric rotating wave. In larger systems, rotating waves have the same general pattern, but they may consist of more than four blocks and the center of rotation does not need to be in the center of the network. The waves rotate either clockwise or counter-clockwise. These spatiotemporal patterns are neutrally stable and noise will perturb the system into the synchronous state, which is asymptotically stable.
These patterns do not occur with a high probability when the initial conditions are randomly chosen. When $B_r = 1$, spatiotemporal patterns appear approximately 1/100 trials with random initial conditions. If $B_r = 3$, then a desynchronous solution might result once in $10^4$ trials. If we limit the initial conditions so that the oscillators are only on the lower left branch of the limit cycle, then we observe only synchronous solutions.

We mention these patterns because they might be useful for information processing. Each of the many patterns could represent a stored memory for example. Also, with a more general type of relaxation oscillator in which the speeds along the different branches are different, these spatiotemporal patterns might be stable, as is the desynchronous solutions of a pair of relaxation oscillators [Kopell and Somers, 1995], also see [Terman and Lee, 1997].

3.7 Comparison with Integrate-and-Fire Oscillators

Relaxation oscillators are typically thought to have much in common with integrate-and-fire oscillators. Both oscillators used to model neuronal behavior and both are typically examined with a discontinuous interaction. When one relaxation oscillator fires, it can induce its neighbor to fire as well, a dynamic which is similar to that of integrate-and-fire neurons. However, in relaxation oscillators, the interaction is of finite duration, unlike the instantaneous interaction between integrate-and-fire oscillators. Further, in relaxation oscillators the oscillator receiving excitation does not necessarily change its position in phase space, unlike integrate-and-fire oscillators with pulsatile coupling - the oscillator receiving the pulse instantly changes its position in phase space.
Our data indicate that of the differences mentioned, the duration of the interaction is of crucial importance. If the amount of time an oscillator spends on the right branch becomes infinitesimal, or \( B_r \to \infty \), then the interaction becomes pulsatile. When an oscillator jumps to the active phase, it makes an instantaneous traversal of the right branch and returns to the top of the left branch. This is similar to the reset mechanism of integrate-and-fire oscillators. However, the interaction is still quite different from that of the integrate-and-fire oscillators. In integrate-and-fire oscillators, the pulse causes an immediate and finite change in the phase of the oscillator receiving the pulse. For relaxation oscillators with \( B_r \to \infty \), the interaction either causes an oscillator to jump, or it does not alter its position.

In Figure 35 we display the average time to synchrony for these two oscillator networks as a function of \( \log_{10}(n) \), where \( n \) is the length of the chain. The data indicate that both types of oscillator networks synchronize at times proportional to \( \log_{10}(n) \).
comparison of integrate-and-fire oscillator networks and relaxation oscillator networks, we have tried to compare oscillators that exhibit the greatest similarity. We have created an algorithm in which the amount of time spent travelling the right branches is actually zero and we chose parameters so that the size of the jumping region is approximately 70% of the limit cycle for both oscillators. Also, in tests with periodic boundary conditions, travelling waves were not seen in relaxation oscillator networks. This is similar to networks of integrate-and-fire oscillators, in which travelling waves were never seen.

Our data indicate that both types of oscillator networks synchronize at times proportional to \(\log_{10}(n)\). However, relaxation oscillator networks achieve synchrony faster than integrate-and-fire oscillator networks. We suggest that this difference may be qualitatively explained by referring to the return maps for two relaxation oscillators (Figure 20A) and the return map for integrate-and-fire oscillators (Figure 5A). The return map for the relaxation oscillators in Figure 20A is not significantly different from the return map for a pair of relaxation oscillators with \(B_r \to \infty\). The return map for relaxation oscillators indicates a larger compression per period (in general) and the number of cycles needed before both oscillators can jump together is only one (Figure 20B), while the number of cycles needed for two integrate-and-fire oscillators to fire synchronously can be greater than one (Figure 5B). Based on these return maps alone, one might expect that the time needed to synchronize a chain of relaxation oscillator would be less than the time needed to synchronize a chain of integrate-and-fire oscillators.
3.8 Relaxation Oscillators with $\varepsilon > 0$

In the previous sections of this Chapter, the relaxation oscillators were in the singular limit and no time was needed to jump (or hop) from branch to branch. We now investigate relaxation oscillators with $\varepsilon > 0$. There is now a finite amount of time needed for an oscillator to jump from branch to branch. This change immediately causes a fundamental increase in the average time needed to synchronize a network of oscillators. The time needed for one oscillator to induce another oscillator to jump up is finite and information can only propagate from one end of the chain to the other at times proportional to $n$. This was suggested by Somers and Kopell [Somers and Kopell, 1993]. They emphasized the role of relaxation oscillators in obtaining fast synchrony when compared to sinusoidal oscillators. They suggested that when relaxation oscillators are in “the sinusoidal regime, that general invariant manifold theory suggests that phase-pulling mechanisms dominate the behavior.” They further noted that in networks of phase oscillators coupled through their phase differences, “the approach to synchrony occurs on the time-scale $O(n^2)$, which is much slower than the time scale suggested above for the relaxation case.” Somers and Kopell are clear in their emphasis that sinusoidal oscillators do not synchronize as quickly as relaxation oscillators. However, they are not clear on whether the scaling relation between the time to synchrony and the network size is dependent on the form of the interaction, or the type of oscillator used. In this Section we provide numerical evidence indicating that the type of interaction used can change the scaling relation between the time to synchrony and the size of the system.

We present data indicating that relaxation oscillators with a smoothly varying interaction (3.16.c) with $\kappa = 1$ results in an average time to synchrony proportional to $n^2$. When the coupling is highly nonlinear ($\kappa = 5000$) we observe an average time to synchrony pro-
portional to $n$ regardless of whether or not the oscillations are sinusoidal or relaxation like. For $\varepsilon > 0$, it is not possible to use the singular limit method [Linsay and Wang, 1996] and we must use more traditional numerical methods to evolve a network of oscillators. This limits the size of the networks we can examine as well as the number of trials with different initial conditions.

In the singular limit, we defined a network as synchronous when the oscillators all jumped at the same time. For $\varepsilon > 0$, we now need to use a more conventional definition of synchrony. We define a network as synchronous when the average Euclidean distance squared between the oscillators is less than 0.01,

$$0.01 > \frac{2}{n(n-1)} \sum_{i,j<i} (x_i - x_j)^2 + (y_i - y_j)^2$$

The limit cycle of the oscillator varies in both the $x$- and $y$-directions by roughly $O(1)$, thus the threshold chosen in (3.27) indicates that the oscillators are relatively close to each other. We tested several other measures of synchrony and we did not notice any discernible difference in our results.

We used an adaptive fifth order Runge-Kutta method from [Press et al., 1992]. This method was tested against the fourth order Runge-Kutta method with fixed step-size and we found that it was best to modify the adaptive method by placing an upper bound on the step-size. If there is not an upper bound on the step-size, the adaptive method would sometimes take large step-sizes when on the smoothly varying portions of the limit cycle and these large step-sizes could result in unacceptable errors when the oscillators begin to move through the quickly varying portions of the limit cycle. We also compared the results of these numerical methods to results obtained with the Bulirsch-Stoer method of
integration, which uses a fundamentally different technique for integration than the Runge-Kutta method. All three methods yield similar numerical results, thus we are confident that our data do not contain significant errors from our numerical procedures.

We present our data in the form of histograms of the time to synchrony for one-dimensional networks. These histograms are based on several thousand trials with the initial conditions randomly distributed on the lower left branch of cubic. All trials resulted in synchrony. We use parameters so that the speed of motion along the limit cycle is as uniform as possible when $\varepsilon$ is $O(1)$. The parameter $\kappa$ controls the steepness of the slope of the sigmoidal interaction. The parameter $\varepsilon$ is used to vary the oscillator from sinusoidal to relaxation type. We vary $\varepsilon$, $\kappa$, and $n$, in order to determine whether it is the interaction, or the type of oscillator that controls the scaling relationship between $\langle T_S \rangle$ and $n$.

Figure 36A displays scaled histograms of the time to synchrony for a network of oscillators with $\varepsilon = 1$ and $\kappa = 1$, for networks of sizes $n = 25$ and $n = 50$. The histograms have been scaled by $n^2$ and it is evident that this scaling is appropriate. Although the histograms are extremely noisy and the variance of the average time to synchrony is quite large, the scaled histograms exhibit a good qualitative match in their general shape and their extent. Figure 36B displays similar histograms except that $\varepsilon = 0.1$ and the oscillators are more relaxation like. This data also indicate that scaling by $n^2$ is appropriate for this interaction.

We also display histograms for $\varepsilon = 0.01$ in Figure 36C. Here there seems to be a discrepancy in that the scaled histogram for $n = 50$ does not line up precisely with the histogram for $n = 25$. Scaling by $n^2$ overestimates the time to synchrony. This is as expected because for small $\varepsilon$, the jumps between branches occur quickly and as such the interaction also
Figure 36. The histograms of the time to synchrony for chains of length $n = 25$ (thin) and $n = 50$ (thick). The histograms are scaled by $n^2$. All histograms are based on more than 1000 trials. (A) The scaled histograms for $\varepsilon = 1.0$, (B) $\varepsilon = 0.1$, and (C) $\varepsilon = 0.01$. The other parameters used are $\alpha_R = 6$, $\lambda = 3$, $\gamma = 42$, $\theta = -0.5$, and $\beta = 1000$.

changes quickly and it behaves like a Heaviside function. We do not yet have enough data to estimate a value of $\varepsilon$ that would yield synchronization times proportional $n$ for an interaction with $\kappa = 1$.

We now display similar histograms with an interaction term that is virtually discontinuous, i.e. $\kappa = 5000$. The histograms are scaled by $n$ in Figure 37. The scaled histograms give good qualitative evidence that $\langle T_s \rangle$ scales linearly with the size of the network, even if the oscillator is sinusoidal. See Appendix A to view the limit cycle and waveform of the oscillator with $\varepsilon = 1$.  

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Our data confirm the results of Somers and Kopell [Somers and Kopell, 1993] in that relaxation oscillators do exhibit faster synchronization than sinusoidal oscillators. For all values of κ tested, the average time to synchrony decreases as ε decreases, or as the oscillators become more relaxation like (data shown in Figure 38). The data also indicate that

<table>
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<table>
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<tr>
<td>ε = 0.1</td>
<td>7.76</td>
<td>18.0</td>
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Figure 38. We display the average time to synchrony (in units of periods) for different values of n, ε, and κ. (A) is our data for κ = 1.0 and (B) is our data for κ = 5000. The data indicate an increase in the time to synchrony as n^2 for κ = 1.0 and as n for κ = 5000. The data also suggest that the time to synchrony is proportional to ε^{2/3} for both cases.
the time to synchrony is proportional to $\varepsilon^{2/3}$. This is in agreement with perturbation theory for relaxation oscillators, in which an expansion in $\varepsilon$ gives a first term of order $\varepsilon^{2/3}$ [Bender and Orszag, 1978].

Based on this data we conjecture that a discontinuous interaction has better properties of synchronization than a smooth interaction for many classes of oscillators. This is a bold generalization based on a specific model of oscillation with a specific type of interaction. Our data may include large errors due to boundary effects, or the effects of correlations that are larger than the size of the system used. In spite of these possibilities, we have good reasons to believe in our data. One reason is that the histograms for different $n$ have very similar shapes, indicating that these shapes result from the system parameters and not the size of the network. Also, our data indicate an expected proportionality to $\varepsilon^{2/3}$, and this proportionality might not have been evident if boundary effects were significant.

This conjecture is in agreement with the work of Daido [Daido, 1993b] which indicates that a step-like interaction can perfectly synchronize a portion of the oscillators in a globally coupled network of oscillators with a normal distribution of intrinsic frequencies (whereas a smooth coupling cannot). In Chapter 2 we presented numerical evidence that a network of pulse coupled integrate-and-fire oscillators synchronizes at times proportional to $\log_{10}(n)$ for one- and two-dimensional networks. When integrate-and-fire oscillators are coupled with a smoothly varying function, the scaling relation changes completely. Both Daido's work and the data presented here and in Chapter 2 indicate that a discontinuous interaction induces better properties of synchronization in networks of oscillators than a smooth interaction. We do not yet have compelling explanations for why this should be true and we hope that our work encourages further study of this issue.
3.9 Discussion

We have thoroughly examined locally coupled networks of identical relaxation oscillators with a Heaviside type interaction. The motivation for studying relaxation oscillators with this form of interaction comes directly from neurobiology. Relaxation oscillators have been derived directly from models of neuronal activity [Fitzhugh, 1961, Nagumo et al., 1962] and the Heaviside coupling mimics chemical excitatory synaptic coupling between neurons. We have examined locally coupled networks because they are more neurobiologically plausible and because theoretically, more interesting computations can be carried out in such networks (see Section 1.5 for a more detailed explanation).

The relaxation oscillators we examine are the Terman-Wang oscillators [Terman and Wang, 1995] that are based on the Morris-Lecar model of neural behavior [Morris and Lecar, 1981]. Networks of these relaxation oscillators contain seven parameters. The most basic of these is $\varepsilon$, the parameter that controls the two different time scales that define relaxation oscillators. If $\varepsilon$ is of $O(1)$, then the oscillator is said to be in the sinusoidal regime because it can have a nearly uniform speed of motion along its limit cycle. As $\varepsilon$ becomes small, the oscillator begins to exhibit two distinct time scales and there is a smooth transition from sinusoidal oscillations to relaxation oscillations. At $\varepsilon = 0$, the relaxation oscillators are said to be in the singular limit, and the two different time scales have an infinite ratio. In the singular limit, one can vary other parameters so that relaxation oscillators begin to take on characteristics of integrate-and-fire oscillators. Common relaxation oscillators, relaxation oscillators in the singular limit, and relaxation oscillators in the pulsatile limit can all approach synchronous solutions and they each have different time scales for this approach.
We have performed analysis in the singular limit indicating that a pair of identical relation oscillators can synchronize given specific initial conditions and if the coupling strength is large enough. We explicitly derived the coupling strength needed for two oscillators to synchronize. We then extended this analysis to indicate what conditions are necessary in order for a one-dimensional chain of oscillators to synchronize. Using this knowledge we then studied the rate of synchronization in one-dimensional networks of relaxation oscillators (also in the singular limit). Our simulations indicate that the average time needed to synchronize increases as $n^p$, where $n$ is the length of the chain and $p$ is an experimentally determined constant that depends on network parameters. Our data indicate that $p$ is related to the branch ratio, $B_r$, of the oscillators, defined as the amount of time an oscillator spends on the lower left branch divided by the amount of time an oscillators spends on the upper right branch. Our data indicates that $p$ increases as $B_r$ decreases (with the minimum value of $B_r$ being 1 and the maximum observed value of $p$ being 0.46).

We have made a great deal of progress in understanding the system and we have discussed what we believe to be the underlying causes of this power law, but we have not explicitly derived the scaling relation $\langle T_0 \rangle \sim n^p$.

If the amount of time an oscillator spends on the right branch is very small, i.e. $B_r$ is much greater than one, then the oscillator becomes intuitively similar to the integrate-and-fire oscillators studied in Chapter 2. Our numerical studies indicate that as $B_r$ becomes large, the average time to synchrony increase logarithmically with the size of the system, or $p$ in the power law becomes small which makes it appear like a logarithmic increase for the system sizes we are able to examine numerically. This result indicates that by varying the appropriate parameters, networks of relaxation oscillators can exhibit synchronization properties similar to networks of integrate-and-fire oscillators.
Our results reveal the extreme versatility of relaxation oscillators, which, through appropriate parameter choices, can in one extreme appear similar to sinusoidal oscillators, and at another extreme exhibit qualities and behaviors of integrate-and-fire oscillators. Each of these two extremes exhibit different properties from relaxation oscillators in the singular limit, which have their own independent properties of synchronization.

Synchrony in two-dimensional networks of relaxation oscillators is not so easily quantified. If $B_r$ is large, these networks again have synchronization times that scale logarithmically with the system size. If $B_r$ is $O(1)$ then we must constrain the initial conditions appropriately so that rotating waves do not occur. We are unable to characterize the rate of synchronization. From our data, we guess that the rate of synchronization in two-dimensional networks is bounded from above by a logarithmic relation to the size of the network. Parameters can be chosen so that two-dimensional networks synchronize extremely fast, e.g. a $1000 \times 1000$ network can synchronize in less than two periods.

Networks of relaxation oscillators exhibit a wide variety of behaviors - synchrony is not the only final state of the network. In a network with periodic boundaries, we have characterized travelling waves and understood the conditions necessary for their creation. These travelling waves have their own frequency and we can explicitly derive this frequency as a function of system parameters. In two dimensional networks, rotating waves can occur. They can exist in a wide variety of distinct states and this might be useful for information processing. With periodic boundaries, we observe other types of spatiotemporal patterns.

We have also examined networks of identical locally coupled relaxation oscillators using a Heaviside interaction and with finite values of $\varepsilon$. This is a distinctly different regime and networks of oscillators with finite $\varepsilon$ appear to synchronize at times directly
proportional to $n$. Somers and Kopell [Somers and Kopell, 1993] suggested this synchronization rate and compared it to sinusoidal oscillators, which typically exhibit synchronization times that are proportional to $n^2$. They noted that relaxation oscillators synchronize more quickly than sinusoidal oscillators but they did not clarify whether or not the scaling relation was dependent on the type of interaction, the nature of the oscillations, or some combination of the two. We have performed numerical experiments indicating that it is the nature of the interaction that determines the scaling relation between the time to synchrony and the size of the network. Based on these results, we conjecture that discontinuous interactions can qualitatively improve the synchronization properties of oscillator networks when compared to smooth interactions. Our conclusion is in agreement with Chapter 2 and with the work of Daido [Daido, 1993b] who indicated that a step-like function could perfectly synchronize a significant fraction of the oscillators in a globally coupled network of phase oscillators with a normal distribution of intrinsic frequencies. Our conjecture may have practical applications besides image processing. Several devices (Josephson junctions and resonance tunneling diodes [Young et al., 1988]) oscillate at megahertz frequencies. However, the output current of both of these devices is very small and there is a need to create devices that can yield a high output current at these frequencies. At the moment, it is unknown how to quickly synchronize the outputs of locally coupled arrays of these devices. Even a partial understanding of how to achieve quick synchrony in the presence of noise and disorder would be valuable. This form of interaction may also be useful in the synchronization of chaotic dynamical systems.
CHAPTER 4

RELAXATION OSCILLATORS WITH TIME DELAY COUPLING

4.1 Introduction

Thus far we have studied synchronization in networks of locally coupled neurobiologically based oscillator models. One additional detail that would make these models more realistic is time delays in the interaction. Time delays in signal transmission are inevitable in both the brain and physical systems. In unmyelinated axons, the speed of signal conduction is approximately 1 mm/ms [Kandel et al., 1991]. Connected neurons which are 1 mm apart may have a time delay of approximately 4% of the period of oscillation (assuming 40 Hz oscillations). How synchronization is achieved in the presence of significant time delays is an important question. Furthermore, in any physical implementation (such as analog VLSI) of an oscillator network, transmission delays are unavoidable. Since even small delays may alter the dynamics of differential equations with time delays [Kuang, 1993], it is necessary to understand how conduction delays change the behavior of oscillator networks.
The inclusion of time delays in a differential equation immediately causes the dimensionality of the system to become infinite because the system is now dependent on an infinite set of initial conditions. To illustrate the effects time delays may have, we discuss the following equation,

\[ \dot{x}(t) + 2x(t) = -x(t) \]

The above equation has an asymptotically stable fixed point at zero. A trajectory for the above equation is the thick curve displayed in Figure 39. If one introduces a time delay,

\[ \dot{x}(t) + 2x(t - \tau) = -x(t) \]

then the trivial solution becomes unstable for any positive delay \( \tau \) [Kuang, 1993]. One such trajectory for this time delay differential equation is the thin curve in Figure 39.

In this Chapter we study relaxation oscillators with time delay coupling. We choose to study time delays in relaxation oscillators for several reasons. They are based on neurobiology [Fitzhugh, 1961, Nagumo et al., 1962]. They exhibit better properties of synchrony.
when compared to non-relaxation type, such as sinusoidal oscillators [Somers and Kopell, 1993, Wang, 1993a, Terman and Wang, 1995, Somers and Kopell, 1995, also see Chapter 3]. Also, relaxation oscillators have been analytically shown to have robust properties of desynchronization [Terman and Wang, 1995] and have been used for feature binding tasks [Wang, 1996b, Wang and Terman, 1997]. Furthermore, they can exhibit properties of both sinusoidal and integrate-and-fire type oscillators by proper adjustment of parameters. Studying time delays in relaxation oscillators might result in understanding time delays in networks consisting of these other types of oscillators. Due to these unique properties, we have chosen to examine the effects of time delays in relaxation oscillators.

To our knowledge, time delays in networks of relaxation oscillators have not been extensively studied. In Grasman and Jansen [Grasman and Jansen, 1979], a perturbation analysis was carried out for coupled relaxation oscillators with time delays. The coupling was assumed to be small and the interaction term was not based on excitatory chemical synapses, as is ours. Due to the differences in the coupling term, it is not surprising their results do not agree with ours. Studies of time delays in other oscillator networks have revealed a diverse and interesting range of behaviors. For example, in a network of identical phase oscillators with local coupling, the inclusion of a time delay in the interactions decreases the frequency [Niebur et al., 1991a]. See [Plant, 1981, Schuster and Wagner, 1989, MacDonald, 1989, Ernst et al., 1995, Luzyanina, 1995, Foss et al., 1996, Gerstner, 1996] for other examples of delays in differential equations.

In this Chapter, the dynamics of relaxation oscillators without time delay coupling is first described in Section 4.2. In Section 4.3 we present analysis for a pair of relaxation oscillators with time delay coupling. We show that the oscillators always become loosely synchronous (approach each other so that their time difference is less than or equal to the
time delay) for a wide range of initial conditions and time delays. In Section 4.4 we describe that the dynamics of one- and two-dimensional oscillator networks is similar to that of a pair of oscillators. Here we define our measure of synchrony for networks of oscillators. We also show a simulation of LEGION with time delay coupling between oscillators, and suggest that its properties of grouping oscillators together and desynchronizing different oscillator groups are maintained. In Section 4.5 we study our measure of synchrony for one and two dimensional networks of oscillators. A particular case of initial conditions is discussed, where the degree of synchrony does not degrade as the network evolves. Section 4.6 concludes the Chapter.\(^1\)

4.2 Basic Dynamics of Neural Oscillators

Before treating the dynamics of relaxation oscillators coupled with time delays, it is useful to describe their dynamics without time delays. We examine a specific oscillator model. A more general description of a pair of coupled relaxation oscillators can be found in [Somers and Kopell, 1993]. The oscillator we study is defined as

\[
\begin{align*}
\dot{x} &= 3x - x^3 - y \\
\dot{y} &= \varepsilon (\lambda + \gamma \tanh(\beta x) - y)
\end{align*}
\]

These functions are equivalent to those used in [Terman and Wang, 1995]. The x-nullcline, \(\dot{x} = 0\), is a cubic function. Two important values of this cubic are the y-values of the local extrema. In Figure 40 the extrema are denoted by \(RK\) (right knee) and \(LK\) (left knee). The y-nullcline, \(\dot{y} = 0\), is a sigmoid and is assumed to be below the left branch (LB) and above the right branch (RB) of the cubic as shown in Figure 40. The parameter \(\beta\) controls the steepness of the sigmoid and we use \(\beta \approx 1\). The value \(\varepsilon\) is chosen to be

\(^1\) Most of the contents of this Chapter are based on material that is to appear in Physica D.
small, $0 < \varepsilon \ll 1$, so $x$ is a fast variable and $y$ is a slow variable. The oscillator thus defined is a typical relaxation oscillator. The limit cycle is made up of four pieces: two slowly changing pieces along the left branch and right branch, and two fast pieces that connect the left and right solutions. The parameters $\lambda$ and $\gamma$ are used to modify the amount of time an oscillator spends on the left and right branches. The trajectory and nullclines for this oscillator are shown in Figure 40.

To illustrate the coupling, we examine two oscillators, defined as

\begin{align*}
\dot{x}_1 &= 3x_1 - x_1^3 - y_1 + \alpha_R S(x_2) \\
\dot{y}_1 &= \varepsilon (\lambda + \gamma \tanh(\beta x_1) - y_1) \\
\dot{x}_2 &= 3x_2 - x_2^3 - y_2 + \alpha_R S(x_1) \\
\dot{y}_2 &= \varepsilon (\lambda + \gamma \tanh(\beta x_2) - y_2) \\
S(x) &= [1 + \exp(\kappa(\Theta - x))]^{-1}
\end{align*}

\begin{align*}
\lambda &= 8, \quad \gamma = 12, \quad \varepsilon = 0.005, \quad \beta = 1000.
\end{align*}
The value \( \alpha_R \) is the coupling strength, and the interaction term is a sigmoid, mimicking excitatory synaptic coupling. The value of \( \kappa \) modifies the steepness of this sigmoid and we use \( \kappa \gg 1 \). Increasing the value of \( \alpha_R S(x) \) results in a raise of the \( x \)-nullcline, \( \dot{x} = 0 \). This is a property seen in several descriptions of neural behavior [Hodgkin and Huxley, 1952, Fitzhugh, 1961, Wilson and Cowan, 1972, Morris and Lecar, 1981]. In the limit, \( \varepsilon \to 0 \), with the threshold of the interaction term, \( \theta \), between the outer branches of the cubic, the system behaves as if \( S(x) \) is a step function. Thus the interaction is either nonexistent, or excitatory. When an oscillator travels from a left branch to a right branch, the other oscillator receives excitation. The excitation raises the \( x \)-nullcline of the oscillator. The excited oscillator then exhibits dynamics based on its modified phase space, a mechanism referred to as fast threshold modulation [Somers and Kopell, 1993]. The three pertinent nullclines for this system are pictured in Figure 41. As before, the pertinent values of the \( x \)-nullclines are the \( y \)-values of their local extrema. For the particular equations we use in (4.2), the \( x \)-nullcline shifts upward in direct proportion with a change in \( \alpha_R S(x) \).
The local extrema are denoted by the lower left knee \((LLK)\) and the lower right knee \((LRK)\) for the unexcited \(x\)-nullcline, and the upper left knee \((ULK)\) and the upper right knee \((URK)\) for the excited nullcline. The values of the extrema are

\[
\begin{align*}
LLK & = (LLK_x, LLK_y) = (-1, -2) \\
LRK & = (LRK_x, LRK_y) = (1, 2) \\
ULK & = (LLK_x, LLK_y + \alpha_R) \\
URK & = (LRK_x, LRK_y + \alpha_R)
\end{align*}
\]

The term ‘jump’ is used when an oscillator moves from either of the left branches to either of the right branches, or vice versa. The term ‘hop’ is used to describe the relatively smaller movements when an oscillator moves from an upper to a lower branch, or vice versa. Also, when an oscillator is on either of the left branches, we say that it is in the silent phase and when an oscillator is on either of the right branches, we say that it is in the active phase.

A basic description of the behavior of (4.2) now follows. Let the oscillators be denoted by \(O_1\) and \(O_2\). Let both oscillators begin on the lower left branch (LLB), with \(y_2 > y_1\). We assume that the time an oscillator spends traveling along LLB is longer than the time an oscillator spends on the upper right branch (URB). Because the motion is counter-clockwise along the limit cycle, \(O_1\) leads \(O_2\). The leading oscillator, \(O_1\), will reach \(LLK_y\) first, and jump up to the lower right branch (LRB). There are four basic trajectories that can arise based on the position of \(O_2\) at the time \(O_1\) jumps up. Somers and Kopell [Somers and Kopell, 1993] have described similar trajectories, so we give only a brief summary here. If \(O_2\) is below \(LLK_y + \alpha_R\) it will jump up to URB. When \(O_2\) crosses the interaction threshold, \(O_1\) will hop from LRB to URB. The order of the oscillators is reversed for this case. If, however, \(O_2\) is above \(LLK_y + \alpha_R\) when \(O_1\) jumps up, \(O_2\) will hop to the upper
left branch (ULB). Its motion will continue along ULB until it reaches \( LLK_y + \alpha_R \), at which time it will jump up to URB. There are two possibilities for the relative positions of the oscillators on the active phase: the order may be reversed or not. This accounts for two more cases. The fourth trajectory occurs when \( O_1 \) jumps up, and \( O_2 \) is above \( LLK_y + \alpha_R \) by such an amount that it is possible for \( O_1 \) to traverse the active phase, and return to the silent phase before \( O_2 \) can jump up. Parameters can be found so that each case results in a significant phase contraction between the two oscillators. Terman and Wang [Terman and Wang, 1995] showed that rapid synchrony is achieved in a network of locally coupled relaxation oscillators. This fast synchrony is independent of the dimension, or the size of the network.

4.3 Dynamics Including Time Delay

4.3.1 Singular Solutions

We now introduce a time delay in the interactions. The equations are

\[
\begin{align*}
\dot{x}_1 &= 3x_1 - x_1^3 - y_1 + \alpha_R S(x_2(t - \tau)) \\
\dot{y}_1 &= \varepsilon(\lambda + \gamma \tanh(\beta x_1) - y_1) \\
\dot{x}_2 &= 3x_2 - x_2^3 - y_2 + \alpha_R S(x_1(t - \tau)) \\
\dot{y}_2 &= \varepsilon(\lambda + \gamma \tanh(\beta x_2) - y_2)
\end{align*}
\]

The time delay is only in the interaction between the \( x \) variables. The fast system of (4.3) is obtained by setting \( \varepsilon = 0 \). This results in

\[
\begin{align*}
\dot{x}_i &= 3x_i - x_i^3 - y_i + \alpha_R S(x_j(t - \tau)) \\
\dot{y}_i &= 0
\end{align*}
\]
where \( i = 1, 2 \) and \( j = 3 - i \). The slow system for (4.3) is derived by introducing a slow time scale \( t' = \varepsilon t \) and then setting \( \varepsilon = 0 \). The slow system for the lower left branch is

\[
x_i = h(y_i) \tag{4.5.a}
\]

\[
y_i' = \lambda + \gamma \tanh[\beta h(y_i)] - y_i \tag{4.5.b}
\]

where \( x = h(y) \) describes the lower left branch of (4.3). System (4.5) determines the slow evolution of an oscillator on the lower left branch. Because \( \beta \gg 1 \) and \( h(y) \leq -1 \), we rewrite (4.5.b) as

\[
y_i' = \lambda - \gamma - y_i \tag{4.6}
\]

For an oscillator on the upper left branch, (4.6) will again result because \( h_i(y) \leq -1 \), where \( x = h_i(y) \) defines the upper left branch. Thus an oscillator has the same velocity in the \( y \)-direction along either of the left branches. For the right branches, these same steps result in the following analogous equation,

\[
y_i' = \lambda + \gamma - y_i \tag{4.7}
\]

The velocity in the \( y \)-direction of an oscillator along either of the right branches is given by (4.7). Because of this, the hops that occur along the upper and lower cubics do not affect the time difference between the two oscillators. Only the jumps from a left branch to a right branch and vice versa can result in changes in the time difference between the two oscillators. In more generalized versions of relaxation oscillators, the speed along different cubics may be different. We briefly address this issue in Section 4.3.4.

In the singular limit, \( \varepsilon = 0 \), system (4.3) reduces to two variables. The exact form of the \( x \)-nullcline is not important as long as a general cubic shape is maintained. The evolution of the system is determined by solving (4.6) and (4.7). The equation describing \( y_i(t) \) along either of the left branches is
The $y$-position of an oscillator along either of the right branches is given by

$$y_i(t) = (y_i(0) - \lambda + \gamma) e^{-t} + \lambda - \gamma$$  \hspace{1cm} (4.8)$$

We compute the total period of oscillation, $T_r$, for the synchronous solution using (4.8) and (4.9). The time it takes to travel from $LLK_y$ to $LRK_y + \alpha_R$, along the upper right branch, is given by

$$\tau_{URB} = \log\left(\frac{LLK_y - \gamma - \lambda}{LRK_y + \alpha_R - \gamma - \lambda}\right)$$  \hspace{1cm} (4.10)$$

The time needed to travel from $LRK_y - \alpha_R$ to $LLK_y$, along the lower left branch, is given by

$$\tau_{LLB} = \log\left(\frac{LRK_y + \alpha_R + \gamma - \lambda}{LLK_y + \gamma - \lambda}\right)$$  \hspace{1cm} (4.11)$$

Thus, we have $P_T = \tau_{URB} + \tau_{LLB}$. The evolution (4.3) can be solved with knowledge of the initial conditions, the branches the oscillators are on, and the times at which the oscillators receive excitation. This can become somewhat complicated in this time delay system, especially for larger delays, but some general classes of trajectories can be analyzed easily.

Our analysis in this section and Section 4.3.2 is derived at the singular limit ($\varepsilon = 0$). We have not carried out a perturbation analysis. We note, however, that Terman and Wang [Terman and Wang, 1995] have carried out an analysis of networks of relaxation oscillators in the singular limit and extended their analysis from $\varepsilon = 0$ to small positive $\varepsilon$. Our networks differ from theirs in the inclusion of time delays between the oscillators, but it
may be possible that a singular perturbation analysis can be carried out similarly. We have done substantial testing with various values of $\varepsilon$. Our results indicate that values of $0 < \varepsilon \ll 1$ do not significantly alter any of the dynamics discussed.

4.3.2 Loosely Synchronous Solutions

As part of our analysis, we need a measure of the distance between the two oscillators. The Euclidean measure of distance does not yield intuitive results because of the constantly changing speed of motion along the limit cycle. We instead use the time difference between the two oscillators, $\Gamma(y_1, y_2)$ [LoFaro, 1994, Terman and Wang, 1995], defined as

$$
\Gamma(y_1, y_2) = \begin{cases} 
\log \left( \frac{y_2 - \lambda + \gamma}{y_1 - \lambda + \gamma} \right) & \text{if both oscillators on left branch} \\
\log \left( \frac{y_2 - \lambda - \gamma}{y_1 - \lambda - \gamma} \right) & \text{if both oscillators on right branch}
\end{cases}
$$

(4.12)

where $y_i$ represents the $y$-value of $O_i$. This function measures the time it takes an oscillator at $y_2$ to travel to $y_1$ and is only valid if both oscillators are on the same branch of the limit cycle. Two oscillators are defined to be loosely synchronous if the time difference between them is less than or equal to the time delay, or $\Gamma(y_1, y_2) \leq \tau$.

We describe various solutions for (4.3) in the singular limit, but only for a set of specific initial conditions and a limited range of time delays. We assume that both oscillators lie on LLB so that they are on the limit cycle during the time $[-\tau, 0]$, with $y_2 > y_1$. This assumption bounds the maximum initial time difference by $\tau_{LLB} - \tau$. By restricting the initial conditions in this manner, the behavior of the system is determined by two parameters; the initial time difference between the two oscillators and the time delay. In broad
regions of this parameter space we find distinct classes of trajectories. For some of these classes we are able to calculate the time difference between the two oscillators. For other regions we rely on numerical simulations to indicate the final state of the system. In Figure 42 we summarize five regions of the parameter space that we have examined. In regions I-IV we show that loosely synchronous solutions arise provided that the coupling strength is appropriately bounded. Numerical simulations in region V indicate that antiphase solutions of high frequency can result. We examine time delays in the range 0 to $\tau_{RM}$. The value $\tau_{RM}$ (the subscript $RM$ stands for right minimum) is the time needed to traverse the fastest branch in the system, which in our system is LRB, and is given by

$$\tau_{RM} = \log \left( \frac{LLK_y - \lambda - \gamma}{LRK_y - \lambda - \gamma} \right)$$

This value can be a significant portion of the period of oscillation and we present analytic results within this range. Numerical simulations indicate that for $\tau > \tau_{RM}$, loose synchrony is not commonly achieved.

We first describe region I of Figure 42. Here the oscillators have an initial time difference of less than or equal to $\tau$, or $\Gamma(y_1(0), y_2(0)) \leq \tau$. In this situation, $O_2$ will jump up to LRB before receiving excitation. Thus, the only effect of the interaction is to cause $O_2$ to hop from LRB to URB. Since this hop does not affect the speed of an oscillator in the $y$-direction, or its $y$-value, it has no effect on the time difference between the two oscillators. In this region the oscillators have simple periodic motion and maintain a constant time difference. Any small perturbation within this region changes the time difference; thus region I is neutrally stable. Solutions in region I are always loosely synchronous. Typical trajectories for a pair of oscillators in region I are shown in Figure 43A. There are two boundaries for region I, and the first is given simply by $\Gamma(y_1(0), y_2(0)) \leq \tau$ for $0 \leq \tau < \tau_{RM}/2$.
Figure 42. A diagram in parameter space indicating regions of distinct behaviors. Regions I-IV are distinguished by specific classes of trajectories and these regions result in loosely synchronous solutions. Numerical simulations indicate that much of region V consists of desynchronous solutions. The unlabeled region is not analyzed because it contains initial conditions which do not lie on the limit cycle for a given value of the time delay. The axes do not have the same scale. The equations specifying the boundaries of regions I-IV are given in Section 4.3.2 and also in Appendix B.
Figure 43. Plots of trajectories in $x$ and $y$ space for various classes of initial conditions. All trajectories are numerically calculated using parameters listed in the captions of Figure 40 and Figure 41 with a time delay of $\tau = 0.03T$ and $\alpha_R = 2$. The thin solid curve represents the trajectory of $O_1$, which is always the first oscillator to jump up in (A), (B), (C), and (D). $O_1$ is also the first oscillator to jump down in (E) and (F). The thick dashed curve represents the trajectory for $O_2$. (A) This graph displays typical trajectories for a pair of oscillators whose initial time difference is in region I of Figure 42. (B) Trajectories for a pair of oscillators whose initial time difference is in region II. (C) Trajectories for region III. (D) Trajectories for region IV. In (E) and (F) we display the two classes of trajectories arising when two oscillators jump down from the active phase to the silent phase of the limit cycle. (E) This graph displays the trajectories region II of Figure 42. (F) This graph displays the trajectories analogous to region III of Figure 42.
For time delays larger than $\tau_{RM}/2$, there is a different relation between the initial separation and the time delay. In order for loose synchrony to occur, we must ensure that $O_1$ does not traverse LRB and jump down to LLB before receiving excitation. This condition results in $\Gamma(y_1(0), y_2(0)) + \tau < \tau_{RM}$ for $\tau_{RM}/2 \leq \tau < \tau_{RM}$. If $\Gamma(y_1(0), y_2(0)) + \tau \geq \tau_{RM}$, then $O_1$ receives excitation after it has jumped down to LLB. For this case, one oscillator is in the silent phase, and the other oscillator is in the active phase. Numerical simulations indicate that desynchronous solutions typically result from this type of trajectory.

Region II of Figure 42 contains trajectories such that when $O_2$ receives excitation, it is able to immediately jump up to URB, and $O_1$ receives excitation at time $2\tau$. If $\tau > \tau_{RM}/2$, then $O_1$ jumps down to LRB and one oscillators is in the silent phase and the other oscillator is in the active phase. As previously noted, desynchronous solutions typically result from this type of trajectory. However, if the time delay satisfies $0 \leq \tau < \tau_{RM}/2$, then $O_1$ hops from LRB to URB when it receives excitation and both oscillators are on URB. The evolution of the system can then readily be calculated. Region II is thus defined for time delays $0 \leq \tau < \tau_{RM}/2$. Typical trajectories for a pair of oscillators in this region are shown in Fig. 5B. The initial time difference is bounded by $\tau < \Gamma(y_1(0), y_2(0)) \leq \tau_1 + \tau$, where $\tau_1$ is given by

$$\tau_1 = \log \left( \frac{LLK_y + \alpha_R - \lambda + \gamma}{LLK_y - \lambda + \gamma} \right)$$

(4.14)

This is the time of travel from $LLK_y + \alpha_R$ to $LLK_y$ on the lower left branch. With zero time delay, the $y$-distance between the two oscillators remains the same before and after the jump up, but the time difference between them changes. If the ratio of the initial time difference on LLB to the time difference after the jump (on URB) is less than one, then there is compression [Somers and Kopell, 1993], and oscillators synchronize at a geomet-
ric rate. With time delay, the y-distance between the two oscillators changes before they are both on URB. From Figure 43B, one can see that $O_1$ travels upward on LRB, while $O_2$ travels downward on LLB until receiving excitation. Depending on the initial conditions, the y-distance between the two oscillators can shrink, or increase. When the y-distance decreases, the time difference decreases by a factor greater than the compression ratio alone. When the y-distance increases, the time difference is less than or equal to the time delay. In Appendix B, we derive the time difference between the two oscillators after one period, and show that it decreases.

The initial conditions of region III of Figure 42 are bounded by $\tau_1 + \tau < \Gamma(y_1(0), y_2(0)) < \tau_1 + \tau_{RM} - \tau$. In region III, $O_2$ receives excitation, hops to ULB, and jumps up to URB before $O_1$ jumps down to LLB. Typical trajectories for a pair of oscillators in region III are shown in Figure 43C. For this class of trajectories, it is shown in Appendix B that after one cycle, the time difference between the two oscillators decreases.

Region IV of Figure 42 is bounded by $\tau_1 + \tau_{RM} + \tau < \Gamma(y_1(0), y_2(0)) \leq \tau_{LLB} - \tau$. If the initial separation of the oscillators is larger than the upper bound, then the oscillators cannot be on the limit cycle and on the lower left branch during the time $[-\tau, 0]$, and we do not examine initial time differences beyond this range. In region IV, $O_2$ receives excitation and hops to ULB. However, $O_2$ does not receive excitation long enough to reach $LLK_y + \alpha$ and hops back to LLB after $O_1$ has traversed LRB. Typical trajectories for a pair of oscillators in region IV are shown in Figure 43D. In Appendix B we show that the time difference between the two oscillators decreases if the coupling strength is sufficiently large, i.e. satisfies condition (B35). We also show that if that condition is met, then
the oscillators whose initial conditions are in region IV do not map into region V, but instead map to regions I, II, or III. If condition (B35) is not satisfied then desynchronous solutions can occur for some initial conditions.

The analysis of regions II-IV of Figure 42 requires that we calculate the change in the time difference between the two oscillators when they jump down from the active to the silent phase as well. We do this in Appendix B. The cases examined are analogous to regions II and III and are called region II_R and III_R. In Figure 43E we display trajectories for a pair of oscillators in region II_R. The leading oscillator in this region jumps down and the other oscillator is able to jump down from URB to LLB when it no longer receives excitation. In region III_R the leading oscillator jumps down and the other oscillator hops from URB to LRB when it no longer receives excitation and then jumps to LLB. Typical trajectories for a pair of oscillators in region III_R are shown in Figure 43F. We assume that LRB is the fastest branch in the system. This places a limit on the size of \( \alpha_R \), and also limits the number of trajectories that can arise from the right branches. The resulting restriction on \( \alpha_R \) is given in (B14). Both restrictions, (B35) and (B14), on the coupling strength are summarized to

\[
\frac{c_2 c_3 c_4}{c_1} e^{-\tau} - c_2 < \alpha_R < \frac{c_1 c_2 - c_3 c_4}{c_3 - c_1} \tag{4.15}
\]

where the values of \( c_i \) are given by

\[
\begin{align*}
    c_1 &= LLK_y - \lambda - \gamma & c_5 &= LLK_y + \alpha_R - \lambda - \gamma \\
    c_2 &= LLK_y - \lambda + \gamma & c_6 &= LLK_y + \alpha_R - \lambda + \gamma \\
    c_3 &= LRK_y - \lambda - \gamma & c_7 &= LRK_y + \alpha_R - \lambda - \gamma \\
    c_4 &= LRK_y - \lambda + \gamma & c_8 &= LRK_y + \alpha_R - \lambda + \gamma
\end{align*}
\tag{4.16}
\]
For the parameters listed in the Figure 45 caption, for example, the coupling strength must be within the following values $1.1334 < \alpha_R < 16$ according to (4.15). Note that in the case of zero time delay, the conditions in (4.15) must still be satisfied in order for loose synchrony (in this case perfect synchrony) to occur.

Within the bounds specified in (4.15), and given initial conditions in regions II-IV of Figure 42, the time difference between the two oscillators will always decrease. As the system evolves, the time difference will decrease until it becomes less than the time delay. The oscillators will then be loosely synchronous.

Note that the diagram obtained in Figure 42 is not completely generic for all parameter values. One can modify parameters, $\alpha_R, \gamma, \lambda, LRK_y,$ and $LLK_y,$ so that the value of $\tau_{LBB}$ changes. This is the value that controls the height of the thick line in Figure 42. By shifting this line up or down one can change the relative sizes of the regions or even remove region IV. But, since we have assumed that $\tau_{LBB} > \tau_{URB}$ the value of $\tau_{LBB}$ cannot be altered so that regions II or III are removed, i.e. $\tau_{LBB} > \tau_1 + \tau_{RM}$. Thus regions II and III always exist. If $\tau_{LBB}$ is made larger, then region IV becomes larger, but no new regions are created in this manner.

4.3.3 Desynchronous Solutions

If $\alpha_R$ is larger than the upper bound in (4.15), numerical simulations indicate that loose synchrony is still possible. If $\alpha_R$ is less than the lower bound in (4.15), then our analysis shows that neutrally stable desynchronous solutions of period less than $P_T$ arise for some initial conditions in region IV of Figure 42. The period is less than the period of the loosely synchronous solution in part because the oscillators traverse LRB, instead of the longer URB. This desynchronous solution is analogous to a case of antiphase behavior as
discussed by Kopell and Somers [Kopell and Somers, 1995]. In [Kopell and Somers, 1995] it was stated that antiphase solutions can arise given a coupling strength between relaxation oscillators that is not too large, with limit cycles such that the time spent on the active and silent phases are sufficiently unequal. Our results for region IV are in agreement with these statements. Region IV exists only when the time spent on the silent phase is sufficiently larger than the time spent on the active phase, i.e. $\tau_{LLB} > \tau_1 + \tau_{RM} > \tau_{URB}$, and desynchronous solutions can arise in this region only if the coupling strength is below the lower bound of (4.15). Because the speed of an oscillator is identical on both upper and lower cubics, these desynchronous solutions are neutrally stable, that is, any small perturbation moves the oscillators into another nearby desynchronous solution. This possibility is also noted in [Kopell and Somers, 1995]. The range of possible desynchronous solutions does not cover the entire area of region IV. We do not delve further into these particular desynchronous solutions.

In regions I, II, and III of Figure 42, $O_1$ always receives excitation before jumping down, and both oscillators are on $URB$ for some amount of time. This situation does not occur in region V and this is the reason why loosely synchronous solutions exhibited in regions I, II, and III, generally disappear in region V. In this region, with time delays larger than $\tau_{RM}/2$, $O_1$ traverses $LRB$ and jumps down to $LLB$ before receiving excitation. Meanwhile, $O_2$ receives excitation and jumps up to $URB$. One oscillator is in the silent phase, and the other oscillator is in the active phase, or the oscillators are on the opposite sides of the limit cycle. From these initial conditions, numerical simulations indicate that desynchronous solutions typically arise. They can quickly become perfectly antiphase, with one oscillator receiving excitation and traveling upward along $URB$, while the other oscillator is not receiving excitation and is traveling downward along $LLB$. After a time
Figure 44. A plot of antiphase behavior arising in region V of Figure 42. The parameter values used are listed in the captions of Figure 40 and Figure 41 with $\tau = 7$, $\alpha_R = 6$, and $\epsilon = 0.025$.

equal to the time delay, the oscillator on the active phase ceases to receive excitation and jumps down to LLB, while the oscillator on the silent phase begins to receive excitation, and jumps up to URB. This solution has period $2\tau$. The behavior just described is one of many desynchronous solutions that can exist in region V dependent on the location of the knees and the coupling strength. We have obtained some analytic results for a few small convex areas within region V. Our results are not shown here because they do not cover a significant portion of region V. Also, the derivations are quite lengthy. The areas we have examined analytically in region V have desynchronous or antiphase solutions of period less than $P_\tau$. Numerical simulations suggest that region V consists mostly of solutions in which the oscillators are nearly antiphase and have a period less than $P_\tau$. In Figure 44 we display an example of antiphase behavior in region V. The period of oscillation measured in this figure is approximately $2\tau$. 

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4.3.4 Time Delays in Other Relaxation Oscillators

For the oscillator model we use, the speed of an oscillator depends only on its y-value, or in other words, the speed of an oscillator is the same no matter which cubic it is on. This condition allows for exact solutions, but is not very general. As noted in Kopell and Somers [Kopell and Somers, 1995], different speeds of motion along different cubics can give rise to different behaviors. We have tested this scenario by using the Morris-Lecar equations [Morris and Lecar, 1981] and other relaxation oscillators that exhibit different speeds along different cubics, and our results from numerical simulations indicate that the predominant behavior of loose synchrony is still observed. A pair of oscillators quickly converges to a solution in which the time difference between the two oscillators is less than or equal to the time delay. However, the loosely synchronous solutions are no longer neutrally stable. We observe several possible stable solutions for two oscillators, stable synchronous solutions, and a stable solution such that the oscillators whose time difference is equal to the time delay. There may be other possible states as well. We have not yet performed an analysis of these systems. For all tested systems, we observe that loose synchrony persists under analogous conditions to those given in Section 4.3.2.

We find that for initial conditions analogous to region IV of Figure 42, several desynchronous solutions can exist for small coupling strengths. These solutions are analogous to those described by Kopell and Somers [Kopell and Somers, 1995], in their analysis of a pair of relaxation oscillators without time delay coupling.
For time delays larger than half the amount of time spent on the fastest branch of the system, we find equivalent behaviors to those observed in region V of Figure 42. The oscillators frequently exhibit nearly antiphase relations with periods of approximately $2\tau$, thus conforming to earlier results when the speed of motion is the same for the upper and lower cubics.

In summary, we have analyzed a pair of relaxation oscillators in the singular limit, with initial conditions such that the oscillators are on the silent phase of the limit cycle during the time $[-\tau, 0]$, and with time delays of less than $\tau_{RM}$. Given the appropriate upper and lower bounds on the coupling strength, as specified in (4.15), loosely synchronous solutions arise for regions I-IV of Figure 42. For coupling strengths less than the lower bound in (4.15) and initial conditions such that the time difference between the two oscillators is in region IV, desynchronous solutions can occur. Extensive numerical simulations in region V indicate that loosely synchronous solutions occur, as do antiphase and desynchronous solutions with periods less than $P_T$. In numerical studies with Morris-Lecar oscillators and other relaxation oscillators, in which the speed along different cubics is not identical, we find similar results.

4.4 Networks of Oscillators

4.4.1 Relationship with Pairs of Oscillators

Analysis of more than two locally coupled oscillators quickly becomes infeasible because the number of possible initial configurations and their resultant possible trajectories increases dramatically with the number of oscillators. The rest of the Chapter is based on numerical simulations of oscillator networks. The connection strengths are normalized so that the sum of the weights is the same for every oscillator [Wang, 1995]. For example,
in a chain of oscillators, an oscillator at one end receives input from only one oscillator. This connection weight is twice the amount of the connection weight to an oscillator in the center of the chain, which receives input from its two nearest neighbors. Initially, oscillators are randomly placed on the lower left branch of the limit cycle so that the time difference between every pair of oscillators is in regions I-III of Figure 42. These simulations reveal that the behavior of a network has similarities to that of two oscillators. The most pertinent similarity is that after the network has settled into a stable periodic solution, any two neighboring oscillators \( i \) and \( j \) have a time difference as follows,

\[
|\Gamma(y_i(t), y_j(t))| \leq \tau
\]  
(4.17)

In Figure 45 we demonstrate this behavior by displaying the \( x \)-values of a chain of 50 oscillators with nearest neighbor coupling and \( \tau = 0.03T \). We use the term loosely synchronous to describe networks of oscillators in which condition (4.17) is met because each oscillator is still loosely synchronized with its neighbors. In Figure 45 it appears that the network has stabilized by the 3\( ^{rd} \) or 4\( ^{th} \) cycle. In our numerical simulation, we call a network stable if the changes in time difference between neighboring oscillators remains below a threshold for more than two periods. This threshold is set to 0.0075\( T \). With this measure, the network in Figure 45 meets our criteria of stability by the 3\( ^{rd} \) cycle.

We have also examined networks in which the connection weights are not normalized, thus the two oscillators at the ends of the chain receive only half as much input as the other oscillators. We find that loose synchrony is achieved so long as the coupling strength to the end oscillators are still within the bounds specified in (4.15). Also, in tests where 10\% variation is added to the coupling strengths and with no normalization, we find that loose synchrony can still be achieved. The oscillators quickly attain solutions such that they are within region I or II with respect to their neighbors, and are thus able to jump when they
Figure 45. Loose synchrony in a chain of relaxation oscillators. The temporal activities of 50 oscillators with nearest neighbor coupling are shown. Numerical calculations indicate that this network achieves stability by the 3rd cycle and that all neighboring oscillators satisfy the condition $|\Gamma(y_i(t), y_{i+1}(t))| \leq \tau$. The parameter values used are $\lambda = 8$, $\gamma = 12$, $\beta = 1000$, $\kappa = 500$, $\tau = 0.03T$, $\alpha_R = 6$, $\theta = -0.5$, and $\epsilon = 0.025$. 
receive excitation. If the conditions in (4.15) are not satisfied, then desynchronous solutions can arise. We also note that similar behaviors hold in networks of relaxation oscillators in which the speed of motion is different for different cubics. Loose synchrony is quickly achieved, but, as in the case for two oscillators, loose synchrony is no longer neutrally stable.

We find through extensive simulations that two dimensional locally coupled networks also display loose synchrony. In these simulations, all oscillators are randomly distributed on the lower left branch so that the time difference between every pair of oscillators is within regions I-III of Figure 42. After the network has achieved stability, using the same criteria of stability mentioned previously, the time differences between any oscillator and its nearest neighbors are always less than or equal to the time delay. Thus two dimensional networks also exhibit loose synchrony, similar to a pair of oscillators or a chain. In Figure 46 we display an example of loose synchrony in a $10 \times 10$ network of oscillators. We have combined the $x$-values of all 100 oscillators in the figure to facilitate the comparison between phases. The network in Figure 46 meets our criteria of stability by the third cycle.

In region V of Figure 42, a pair of oscillators typically exhibits antiphase behavior of high frequency. This behavior can also been seen in networks of oscillators. In Figure 47 we display an example of antiphase behavior in a chain of 15 oscillators. The oscillators are randomly placed on the lower left branch of the limit cycle so that the time difference between every pair of oscillators is in region V with $\tau > \tau_{RM}/2$. In this simulation oscillators quickly achieve nearly antiphase relations with their neighbors and the period of each oscillator approaches $2\tau$. 

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Figure 48. Desynchronous solutions in a chain of relaxation oscillators. If the coupling strength is below the lower bound specified in (4.15), desynchronous solutions can arise. In this simulation, \( \alpha_R = 1 \), which is below the lower bound specified in (4.15), and all other parameters are as listed in the caption of Figure 44. Oscillators 12 and 13 had initial conditions such that they are able to remain in a desynchronous relationship. All other neighboring oscillators are loosely synchronous.

example of desynchronous behavior arising from region IV in a chain of 15 oscillators. The initial conditions are chosen so that the time difference between every pair of oscillators is randomly distributed in regions I-IV. In Figure 48 several oscillators initially begin with desynchronous relationships, but become loosely synchronous through interactions with their neighbors. Oscillators 12 and 13, however, remain in a desynchronous relationship, and exhibit the same period of oscillation as the loosely synchronous solutions. This behavior corresponds to fractured synchrony as described in Kopell and Somers [Kopell and Somers, 1995]. The correspondence, however, is not exact. Time delays were not studied in [Kopell and Somers, 1995]. A one dimensional ring of relaxation oscillators in their system exhibited two distinct groups of oscillators. Each group achieved perfect synchrony and was approximately antiphase with the other group. In our simulation, two
groups of oscillators exist in a one dimensional chain of oscillators. Each group exhibits loose synchrony, and an approximately antiphase relationship exists between the two oscillators on the single border between the two groups.

For time delays and initial conditions in region V of Figure 42, there is not a clear relation between pairs of oscillators and networks of oscillators. In pairs of oscillators region V consists mostly of antiphase relations. For networks of oscillators loosely synchronous, antiphase, and other solutions arise dependent on the initial conditions and the coupling strength. For the rest of the Chapter we will focus on the initial conditions and time delays which lead to loose synchrony between neighboring oscillators.

4.4.2 The Maximum Time Difference

Although simulations indicate that neighboring oscillators are loosely synchronous, loose synchrony does not indicate the degree of global synchrony in an entire network. Obviously, a measure of global synchrony is important, and there are many ways of determining synchrony in an oscillatory system, see Pinsky and Rinzel [Pinsky and Rinzel, 1995] for examples. We could convert positions of oscillators on the limit cycle into phase variables, \( \phi_j \), but due to the large amplitude variations during the hops and jumps, defining a phase is problematic. One could also base a measure on Euclidean distance, and find the average separation between oscillators. However, during the jumps, much distance is covered in a short time. A measure based on Euclidean distance can vary during a single cycle. We instead examine the maximum time difference between any two oscillators in the network. The maximum time difference is defined as follows. Let \( t_i^k \) denote the time at which the \( i^{th} \) oscillator, \( O_i \), jumps up during the \( k^{th} \) period. Let \( \tau_{ij}^k = |t_i^k - t_j^k| \) and
\[ \Upsilon^k = \max(\Upsilon^k_{ij}), \quad (i, j = 1, \ldots, N) \]  

Thus, \( \Upsilon^k \) is the maximum time difference between any two oscillators during the \( k^{th} \) period. Each period of an oscillator can be delineated by the time it jumps up. The initial conditions we use, with the time difference between every pair of oscillators in regions I-III of Figure 42, allow for this simple definition of the period (see Figure 45). This measure offers direct comparison with other pertinent quantities such as the period of oscillation, and the amount of time spent on the active and silent phases. Also, the maximum time difference becomes a constant when the oscillator network achieves stability.

4.4.3 LEGION with Time Delay Coupling

We first describe LEGION and then, based on numerical simulations, describe how the dynamics of LEGION changes when time delays are included in the interaction between oscillators. The architecture of LEGION is a two dimensional array of locally coupled relaxation oscillators. In addition, each of the oscillators is coupled with a unit called a Global Inhibitor (GI). Desynchronization is accomplished by GI. Oscillators receiving stimulus become oscillatory and those that do not remain inactive. The connections weights between oscillators are dynamic. The connections between stimulated neighboring oscillators increase to a constant, while connections with unstimulated oscillators decrease to zero. Thus, only stimulated neighboring oscillators are connected. Let us assume that all the oscillators are on the silent phase of the limit cycle. When one oscillator jumps up to the active phase, GI becomes active on the fast time scale and sends inhibition to all oscillators. This inhibition serves to lower the x-nullcline of every oscillator. The x-nullclines of unexcited oscillators are lowered so that they intersect their y-nullclines and the oscillators are attracted to the newly created fixed points. The inhibition
from GI, however, is not enough to prevent oscillators receiving excitation from jumping up to the active phase. Thus the oscillator that has jumped up to the active phase, can recruit its stimulated neighboring oscillators. These oscillators jump up to the active phase and recruit their stimulated neighbors and so on. Since each jump decreases the distance between coupled oscillators, a group of stimulated neighboring oscillators quickly synchronizes. Following [Terman and Wang, 1995], we refer to a group of stimulated and connected oscillators as a block. A block will jump up to the active phase, while other blocks continue to travel along the silent phase, approaching the attracting fixed points. This mechanism is called selective gating [Terman and Wang, 1995]. When a block of oscillators jumps down, GI quickly releases its inhibition to the network on a fast time scale. The x-nullclines of all oscillators will then rise so that the attracting fixed points disappear. Other blocks can then jump up to the active phase and the aforementioned process repeats.

Assuming a block of oscillators is perfectly synchronous, the number of blocks that can be desynchronized is related to the ratio of the time an oscillator block spends on the active and silent phases [Terman and Wang, 1995]. If, however, a block of oscillators is not perfectly synchronous, the amount of time a block spends in the active phase increases. The amount of time a block spends in the active phase is thus an important measure for the network.

In Figure 49 we present the output of a network equivalent to LEGION, with the inclusion of time delays between oscillators. Even though all oscillators receive stimulation, we set both the connection weights between oscillators 20 and 21, and between those of oscillators 40 and 41, to zero in order to create three groups of oscillators. The network is able to group and segregate the three blocks, but the individual blocks no longer attain perfect
Figure 49. An example of LEGION dynamics with time delays in the coupling between oscillators. The temporal activity is displayed for 60 oscillators and GI. The activity of GI is displayed beneath the oscillators. The following parameter values are used: $\gamma = 6$, $\lambda = 3.95$, $\alpha_R = 2$, $\tau = 1$, $\kappa = 500$, $\beta = 1000$, $\theta = -0.5$, and $\varepsilon = 0.025$. 
synchrony; loose synchrony is achieved within each block. Neighboring oscillators are loosely synchronous according to (4.17). Because perfect synchrony is no longer achieved, the amount of time that a block of oscillators spends on the active phase is no longer simply determined by that of a single oscillator. The additional amount of time a block spends on the active phase, in comparison with the time a perfectly synchronous block spends on the active phase, is given by the maximum time difference within a block of oscillators. If the maximum time difference for a block is near $\tau_{LLB}$, then the other blocks on the silent phase of the limit cycle become stuck at the attracting fixed points and further segregating them becomes problematic. If, however, the maximum time difference is still relatively small in comparison with $\tau_{LLB}$, then other blocks of oscillators can be separated, and the number of distinct blocks LEGION can segregate does not decrease drastically.

4.5 Maximum Time Difference in Oscillator Networks

4.5.1 One and Two Dimensional Networks

We examine the maximum time difference for one dimensional networks of oscillators. Since the times at which the oscillators jump up are intrinsically determined by the initial conditions of the network, we cannot determine analytically the value that $\Upsilon^k$ will take. Of course, in a chain of $n$ oscillators, the maximum possible value of $\Upsilon^k$ is given by $(n - 1) \tau$, but in simulations, we rarely see values of even half of this. We are thus led to examine the distribution of $\Upsilon^k$ over a number of trials.

In Figure 50A and Figure 50B we display histograms of $\Upsilon^k$ for networks of size 50 and 100 oscillators. The oscillators are placed on LLB so that the initial time difference between every pair of oscillators is randomly distributed in regions I-III of Figure 42. The
Figure 50. The histograms of $\gamma^k$ for one dimensional networks. The histograms $\gamma^k$ are based on simulations whose initial conditions were restricted to the lower left branch of the limit cycle so that the time difference between any two oscillators were in regions I-III of Figure 42. The horizontal axis represents the maximum difference attained, and the vertical axis represent the number of times it was attained. The data was taken after the system had evolved for 11 cycles. The average time needed to achieve stability was approximately 3 cycles. (A) and (B) are the results for 50 and 100 oscillators respectively. The data for $\gamma^k$ in (A) and (B) are based on 2250 and 2160 simulations respectively. The parameters used are given in the caption of Figure 45.

The largest value $\gamma^1$ can have is 21 in the dimensionless units of Figure 50A and Figure 50B. After the network has achieved stability, most of the trials have values of $\gamma^k (k > 1)$ that are less than 21. A small percentage (4%) of the trials resulted in $\gamma^k$ increasing significantly larger than $\gamma^1$, in some cases almost doubling. Other histograms generated with different parameter values display similar distributions. By similar we mean that there is a marked tendency for a majority of the trials to remain within the maximum time difference of the initial bounds, or $\gamma^k < \gamma^1$. In addition, there is a small but noticeable peak on the tail of the distribution in Figure 50A and Figure 50B. This suggests that there are a few initial conditions which result in large values of the maximum time difference, but we do not know what initial configurations cause this.
We also find in other simulations that the distribution $\Psi^k$ is sensitive to initial conditions. For initial conditions such that 10% of the oscillators are randomly distributed on URB, the distribution $\Psi^k$ becomes much broader and the average maximum time difference almost doubles (data not shown).

Because the oscillators are constrained to be within a certain time difference of one another, but are otherwise not constrained whether or not they fire at time $\tau$ ahead of their neighbors, or at time $\tau$ behind their numbers, the firing times of the oscillators in the chain appear like the steps in a random walk. The time measure we use, the maximum time difference between any two oscillators in the chain, is equivalent to the finding the range of a random walk. Daniels [Daniels, 1941] solved for the range of a random walk using Bernoulli trials, and Feller [Feller, 1951] later generalized this to the range of a random walk with steps that are independently distributed with a Gaussian distribution. Both yield similar results for the average value and variance of the range. The average value of the range increases as $n^{0.5}$ and the standard deviation also increases as $n^{0.5}$, where $n$ is the number of steps in the random walk. Our data for the maximum time difference as a function of $n$ is not extensive enough to accurately determine whether or not the maximum time difference in a chain of oscillators increases with $n^{0.5}$, where $n$ is the number of oscillators. We speculate that the initial conditions of the system are too constrained to allow $\Psi^k$ to increase indefinitely, and that there is some finite maximum value for $\Psi^k$.

We now discuss our simulations of two dimensional networks, in which oscillators are coupled with their four nearest neighbors. The initial conditions are as before, with every oscillator randomly positioned on LLB so that the initial time difference between every pair of oscillators is in regions I-III of Figure 42. Our simulations indicate that after the network achieves stability, neighboring oscillators have time differences that are less than
Figure 51. The histograms of $\gamma^k$ for two dimensional networks. These histograms are based on simulations with initial conditions as described in the caption of Figure 50. The data was taken during the $11^{th}$ cycle. The average time needed to achieve stability was approximately 3 cycles. (A) and (B) are the results for $5 \times 5$ and $10 \times 10$ oscillator networks respectively. The data for $\gamma^k$ in (A) and (B) are based on 2530 and 1320 simulations respectively. The parameter values used are the same as in the caption of Figure 45.

We note that, although the network sizes are not large, the above simulations are computationally expensive. Each of the histograms shown in Figure 50 and Figure 51 requires a large number of data points. To collect the data we made use of several hundred high-performance workstations, located in various computer laboratories in The Ohio State University Department of Computer and Information Science.
4.5.2 Bounding the Maximum Time Difference

As noted previously, $Y^k$ can increase as the network evolves. Numerical simulations indicate that in most cases $Y^k$ decreases as $k$ increases, but for some initial conditions $Y^k$ increases with $k$. We want to know if there is some range of initial conditions along LLB such that $Y^k$ does not increase with time. This would be useful in determining the amount of time a block of oscillators spends in the active phase, and thus would play an important role in determining network parameters. If there were such a constraint, then one could always begin the oscillators within this range and know for certain that $Y^k$ will not increase as the system evolves, in spite of coupling delays between neighboring oscillators.

Specifically, we explore whether there exists some range of initial conditions, which we call $\Omega$, such that if $N$ oscillators are randomly distributed within $\Omega$, then,

$$ Y^1 \geq Y^k $$

Let $\Omega$ be a range of initial conditions on the lower left branch defined as $\Omega = [\Omega_B, \Omega_T]$, so that $\Omega_T - \Omega_B$ is the time it takes to traverse $\Omega$. If $\Omega_T - \Omega_B \leq \tau$, then the time difference between every pair of oscillators in the network satisfies $\Gamma(y_i(0), y_j(0)) \leq \tau$ and the interaction term does not cause any oscillators to jump up or down. Since the interaction does not change the time difference between any oscillators, the maximum time difference does not change, or $Y^1 = Y^k$. We conjecture a larger range,

$$ \Omega_C = [0, t_{ps}] $$

where

$$ t_{ps} = \log \left( \frac{c_1 + 2 \gamma e^\tau}{c_2} \right) $$

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The value of $t_{ps}$ originates from analysis of two oscillators. It is the time difference resulting in perfect synchronization for a pair of oscillators. Simulations of oscillator networks, with random initial conditions in the range $\Omega_C$, support this conjecture. In Figure 52 we plot values of $\gamma^2 - \gamma^1$ (thick solid line) for 1980 trials of a chain of 75 oscillators randomly positioned so that the initial time difference between every pair of oscillators is within $\Omega_C$. The values of $\gamma^2 - \gamma^1$ have been plotted in order from largest to smallest for simplicity. By far, the majority of trials yield a negative result for $\gamma^2 - \gamma^1$, indicating that the value of $\gamma^k$ decreases from the first to second period. Approximately 4% of the trials did, however, yield positive values for $\gamma^2 - \gamma^1$. The largest positive change had a value of 0.1905. The numerical method used was an adaptive Runge-Kutta method modified from

Figure 52. A plot of the evolution of the maximum time difference for 1980 trials. The trials are arranged in order from largest to smallest to emphasize that most of the trials resulted in a decrease in $\gamma^k$. The thick line is a plot of $\gamma^2 - \gamma^1$ and $\gamma^3 - \gamma^2$ is indicated by the thin line. The network is almost stable by the third cycle and the change in $\gamma^3 - \gamma^2$ is not nearly as great as for $\gamma^2 - \gamma^1$. The dotted line displays $\gamma^7 - \gamma^6$. The parameters used are the same as in the caption of Figure 42 with the exceptions that $\lambda = 7$ and $\tau = 0.04T$. 

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[Press et al., 1992] for time delay differential equations. The resulting average step size of the method was 0.1305. Errors in computing the $\gamma^k$ are on the order of the average step size. The small percentage of trials that resulted in small positive values of $\gamma^2 - \gamma^1$ are very likely to have resulted from numerical inaccuracy. In Figure 52, $\gamma^3 - \gamma^2$ is given by the thin solid line. Note that there is less of a change from the second to third cycle because the network achieves stability quickly. The average number of cycles needed to achieve stability is 4, so the values of $\gamma^7 - \gamma^6$ should be near zero. In Figure 52 the dotted line represents $\gamma^7 - \gamma^6$, and although near zero, it has noticeable deviations. The deviations from zero are again on the order of the average step size. This provides further evidence that numerical errors cause the deviations seen in both $\gamma^7 - \gamma^6$ and $\gamma^2 - \gamma^1$. We have tested this result with networks of 25, 50, and 100 oscillators as well, and display only one graph because the others are extremely similar and little additional information is revealed. We have also tested this algorithm with a fourth order Runge-Kutta algorithm with fixed step size. Similar results were obtained. Approximately 5% of the trials resulted in small positive increases in $\gamma^2 - \gamma^1$. Using this numerical algorithm, the maximum increase was $15h$, with step-size $h = 0.005$. We attribute these small increases to the fact that our conjecture is based on the singular limit $\varepsilon \to 0$, while in simulations, the value used was $\varepsilon = 0.025$.

In summary, our extensive simulations support our conjecture that $\Omega_c$ is a range of initial conditions which satisfies condition (4.19). Further examination of this conjecture also lends support. For ranges larger than $\Omega_c$, a significant percentage of trials result in $\gamma^2 - \gamma^1 > 1$. For ranges smaller than $\Omega_c$ there are specific initial conditions in which
(4.19) is violated. But these conditions do not cause an increase when the range becomes as large as $\Omega_c$. We note that parameters can be chosen so that the range $\Omega_c$ is a significant percentage of the period.

4.6 Concluding Remarks

We have presented analysis describing the dynamics of a pair of relaxation oscillators with time delay coupling. We have proven that loosely synchronous solutions exist dependent on the initial conditions, the time delay, and the strength of the coupling. We have provided explicit statements regarding appropriate initial conditions, time delays, and coupling strengths which result in loose synchrony. Analysis and numerical simulations indicate that there is a critical time delay, $\tau_{RM}/2$, beyond which antiphase solutions of period less than $P_T$ commonly arise. Although the analysis for multiple oscillators has not been carried out, numerical simulations indicate that locally coupled networks of oscillators also display similar behaviors as seen in a pair of oscillators. In particular, loose synchrony exists between neighboring oscillators.

The behaviors analyzed and simulated in this Chapter are in terms of a specific set of relaxation oscillators. However, the behaviors we examined should also exist in other relaxation oscillators. In preliminary investigations of locally coupled networks of Morris-Lecar oscillators [Morris and Lecar, 1981], Bonhoeffer-van der Pol oscillators [Fitzhugh, 1961], and other relaxation type oscillators, we find that loose synchrony is quickly attained for time delays less than the time spent on the fastest branch of the system. Both the Morris-Lecar and Bonhoeffer-van der Pol are related to the class of excitable-oscillatory systems including the Hodgkin-Huxley model of neuronal activity [Hodgkin and Huxley, 1952], and some of the behaviors seen here may carry over to this
more complex model. Furthermore, by appropriate adjustment of parameters, relaxation oscillators can be made to vary from sinusoidal type oscillators, to integrate-and-fire type oscillators. Our work here might have relations to the behaviors of time delays in other types of oscillator networks. Preliminary investigations of integrate-and-fire oscillator with time delay coupling indicates that similar behavior occurs in that the time difference between oscillators is at most $\tau$.

To characterize the degree of synchrony in the network as a whole, we have introduced a measure of synchrony, the maximum time difference between any two oscillators in the network. The maximum time difference of a network depends on the initial conditions of the oscillators. In order to study the maximum time difference, we have given histograms of this measure using random initial conditions for several networks. Our results indicate that the maximum time difference typically decreases as the system evolves, and rarely reaches its maximum possible value, $(N - 1) \tau$. This observation holds even for small networks, where the initial time difference between oscillators can be greater than $(N - 1) \tau$. But our results indicate that some initial conditions exist which cause relatively large increases in the maximum time difference. In an effort to bound the maximum time difference we have postulated a range of initial conditions in which the maximum time difference does not increase. This range arises naturally from the analysis of a pair of oscillators and our extensive numerical experiments support this conjecture.

Below a certain connection strength, a pair of oscillators can exhibit neutrally stable desynchronous solutions. This result is in agreement with the results of [Kopell and Somers, 1995]. With this result we found an analogous behavior to that of fractured synchrony described in [Somers and Kopell, 1995]. Above the critical time delay, a pair of oscillators typically displays antiphase behavior with a frequency that can be significantly
higher than the frequency of the synchronous solution. In networks of oscillators, with \( \tau > \tau_{RM}/2 \), antiphase, loosely synchronous, and other more complex behaviors are seen in numerical simulations.

We have tested a network equivalent to LEGION with time delays in the coupling between neighboring oscillators, and found that groups of oscillators can be desynchronized. However, the number of groups that can be segmented by LEGION decreases when time delays are introduced. This is because oscillator groups are no longer perfectly synchronous. The ability of LEGION to segment oscillator groups is related to the maximum time difference within each group. With our knowledge of a range of initial conditions in which the maximum time difference does not increase, we can choose appropriate parameters and initial conditions so that the properties of oscillatory correlation in LEGION are maintained.

Because relaxation oscillators capture some basic neuronal properties and time delays are inevitable in neuronal signal transmission, our results should have implications to understanding oscillations in the nervous system. Our study suggests that in the presence of time delays local connections alone may be incapable of supporting precise synchronization over large neuronal populations. This may explain why synchrony is not seen across distances of more than 7 mm in the cat visual cortex, where lateral connections within the cortex are assumed to give rise to the observed synchronization [Singer and Gray, 1995]. Also, measurements of synchrony in neural activities indicate that synchrony is not perfect [Singer and Gray, 1995]. This imperfect synchronization might indicate the existence of loose synchrony because lateral connections always have time delays.
CHAPTER 5

SYNCHRONY AND DESYNCHRONY IN NETWORKS OF LOCALLY COUPLED WILSON-COWAN OSCILLATORS

5.1 Introduction

In this Chapter, we study networks of locally coupled Wilson-Cowan (W-C) oscillators [Wilson and Cowan, 1972]. The W-C oscillator is a two variable system of ordinary differential equations and represents an interacting population of excitatory and inhibitory neurons. The amplitudes of the variables symbolize the proportion of each population of neurons that is active. We study these equations because they represent neuronal groups, which may be the basic processing units in the brain [Edelman, 1987]. The W-C equations have a large number of parameters, which allow for a wide range of dynamics. These equations have been used widely in modelling various brain processes [Feldman and Cowan, 1975, König and Schillen, 1991, Borisuyk et al., 1993], in creating oscillatory recall networks [Wang et al., 1990], and in exploring the binding problem [Horn et al., 1991, von der Malsburg and Buhmann, 1992, Wang, 1995]. Because of the neurophysiological importance of the W-C equations, several authors have examined their mathematical properties [Ermentrout and Cowan, 1979, Kawahara et al., 1983,
Baird, 1986, Sakaguchi, 1988, Ermentrout, 1990, Cairns et al., 1993]. Of particular relevance is a study by Cairns et al. [Cairns et al., 1993], which indicates that synchronization is possible with these equations. Despite extensive studies on W-C oscillators, it remains unclear to whether or not a locally coupled network can exhibit synchrony. It is also unknown how desynchronization can be achieved in such a network.

We study locally coupled networks because globally coupled networks lack topological mappings [Sporns et al., 1989, Chawanya et al., 1993]. Specifically, in a two-dimensional network of oscillators, all-to-all couplings indiscriminately connects multiple objects. All pertinent geometrical information about each object, and about its relationships with other objects is lost. This information should be preserved if the network is to be used for segmentation and object recognition. Local couplings simply and efficiently preserve these spatial relationships.

We study W-C oscillator networks with diffusive coupling. This coupling arises naturally from the equations, but, as mentioned in Chapter 3, oscillator networks with diffusive couplings typically achieve synchrony at times proportional to $n^2$ (see also [Kopell and Ermentrout, 1986, Niebur et al., 1991b]). In order to achieve fast synchrony (in one cycle), we adjust parameters so that the system is near a bifurcation. This causes the interaction to create and destroy fixed points in such a manner that synchrony is quickly attained.

The two main aspects of the theory of oscillatory correlation (described in Section 1.2) are synchronization within an object, and desynchronization between objects. In our model desynchronization of multiple objects is accomplished with a global inhibitor (GI), which receives input from the entire network, and feeds back to all oscillators.
The global connections serve to adjust the relative phases between oscillator groups, wherever they may be on the network. The model we present uses short range coupling to achieve synchrony, while global couplings with GI give rise to desynchronization.

The model is described in the following section. In Section 5.3, it is proven that synchrony is the globally stable solution for a line of oscillators given sufficient coupling strength, and a technique for fast entrainment is presented. GI and the dynamics of desynchronization are described in Section 5.4. Computer simulations of a two dimensional network with five objects are shown in Section 5.5. In Section 5.6 we discuss possible extensions to our model.¹

5.2 Model Definition

The basic architecture of the model is shown in Figure 53. GI is connected to the entire network. The connections between oscillators are local. An oscillator located on a black square can only be coupled with oscillators on adjacent diagonally striped squares. The topology of the network is a rectangle, not a torus. The coupling strengths are dynamically changed on a fast time scale compared to the period of the oscillations (further discussion below). The dynamic couplings serve to increase the coupling strength between units that are active, to decrease the coupling strength between excited units and inactive units, and to decrease the connection strength between two silent units, all rapidly and temporarily.

¹. The majority of this work has been published in Campbell and Wang, 1996.
Figure 53. Basic architecture of the model. The oscillators are arranged in a 2-D grid, where each square on the grid represents an oscillator. The connections between oscillators are local. Three representative situations are shown in the figure, where an oscillator located at a black site is connected only to oscillators on adjacent striped squares. Note that we do not use periodic boundary conditions. The global inhibitor (GI) is pictured at the top and is coupled with all oscillators in the network.

Each functional element on the grid is a simplified W-C oscillator defined as,

\[
\begin{align*}
\dot{x}_i &= -x_i + H(ax_i - by_i - \phi_x + \sigma z + I_i + \rho_i(t)) + \alpha_w S_{x_i} \\
\dot{y}_i &= \eta (-y_i + H(cx_i + dy_i - \phi_y)) + \alpha_w S_{y_i}
\end{align*}
\] (5.1.a, 5.1.b)

\[
H(v) = \frac{1}{1 + exp(-v)}
\] (5.1.c)

The parameters have the following meanings: \(a\) and \(d\) are the values of self excitation in the \(x\) and \(y\) units respectively. \(b\) is the strength of the coupling from the inhibitory unit, \(y\), to the excitatory unit, \(x\). The corresponding coupling strength from \(x\) to \(y\) is given by \(c\). \(\phi_x\) and \(\phi_y\) are the biases, or thresholds. Figure 54 shows the connections for single oscillator. The \(x\) and \(y\) variables are interpreted as the average activity of the population of exci-
tatory and inhibitory neurons respectively. \( \eta \) modifies the rate of change of the \( y \) unit. The coupling strength between oscillators is given by \( \alpha_w \). \( \rho(t) \) is a noise term. The noise is assumed to be Gaussian with statistical property

\[
\langle \rho_i(t) \rangle = 0 \tag{5.2.a}
\]

\[
\langle \rho_i(t)\rho_j(t') \rangle = 2D \delta_{ij} \delta(t-t') \tag{5.2.b}
\]

where \( D \) is the amplitude of the noise, \( \delta(t-t') \) is the Dirac delta function, and \( \delta_{ij} = 1 \) if \( i = j \) and 0 otherwise. The \( i^{th} \) oscillator receives a binary input \( I_i \). A value of \( I_i = 1 \) corresponds to those parts of the sensory field that are stimulated and drives the oscillator into a periodic regime. Oscillators that do not receive input, namely \( I_i = 0 \), remain silent.

\( z \) represents the activity of GI and will be specified in detail in Section 5.4. Though it may seem unusual to denote the position of an oscillator in a 2-D array with only one index, we do so to avoid using four indices to label the connections between oscillators. Figure 55 displays the nullclines, the curves along which the values of \( x \) or \( y \) are zero, and the trajectory of a point near the limit cycle. The caption of Figure 55 lists values for the parameters \( a, b, c, \sigma, \eta, d, \phi_x, \phi_y \) and \( D \).
Figure 55. The $y$ nullcline (small dashes), $x$ nullcline (large dashes), and trajectory (solid) for a single oscillator are displayed. The parameters are $a = 10.0$, $b = 7.0$, $\phi_x = 4.075$, $c = 10.0$, $d = 10.2129$, $\phi_y = 7.0$, $\sigma = 2.1$, $\eta = 7.0$, and $D = 0$.

The interaction terms are given by

$$S_{xi} = -\kappa_i x_i + \sum_j J_{ij} x_j$$  \hspace{1cm} (5.3.a)

$$S_{yi} = -\kappa_i y_i + \sum_j J_{ij} y_j$$  \hspace{1cm} (5.3.b)

where the sum is over $j \in N(i)$, and $N(i)$ is the set of neighbors that element $i$ has. We call this form of coupling scalar diffusive coupling following the terminology of Aronson et al. [Aronson et al., 1990]. The terms $\kappa_i(t)$ and $J_{ij}(t)$ are specified below.

The connections between the oscillators are allowed to change on a fast time scale, as first suggested by von der Malsburg [von der Malsburg, 1981, von der Malsburg and Schneider, 1986]. They obey the following Hebbian rule: the connections between excited oscillators increase to a maximum, the connections between excited and unstimulated oscillators decrease to zero, and the connections between unstimulated oscillators decrease to zero. This rule uses of a pair of connection weights. The permanent links $T_{ij}$'s denote existence of connections between $i$ and $j$, and reflect the architecture of the net-
work (locally connected 2-D grid, see Figure 53). The dynamic links \( J_{ij} \)'s change on a fast time scale compared to the period of oscillation, and represent the efficacy of the permanent links. The idea of fast synaptic modulation is introduced on the basis of its computational advantages and neurobiological plausibility [von der Malsburg, 1981, von der Malsburg and Schneider, 1986]. The permanent links are given by \( T_{ij} = 1 \) if \( i, j \) are neighbors and \( T_{ij} = 0 \) otherwise. The dynamic links are computed as follows

\[
J_{ij} = T_{ij} h(\langle x_i \rangle) h(\langle x_j \rangle)
\]

(5.4)

where \( h(\langle x_i \rangle) \) is a measure of the activity of oscillator \( i \). It is defined as \( h(\langle x_i \rangle) = \Theta(\langle x_i \rangle - \varphi) \), where \( \varphi \) is some threshold, and \( \Theta \) is the Heaviside step function. Namely \( h(\langle x_i \rangle) = 1 \) if the temporal average of activity, \( \langle x_i \rangle \), is greater than the threshold, or \( h(\langle x_i \rangle) = 0 \) if otherwise. With (5.4) in place, only neighboring excited oscillators will be effectively coupled. This is an implicit encoding of the Gestalt principle of connectedness [Rock and Palmer, 1990].

With scalar diffusive coupling, the Hebbian rule defined above would destabilize the synchronous solution. To understand how the instability arises, consider three excited oscillators arranged in a row, and each with the same values of activities, i.e. \( x_1 = x_2 = x_3 \), and \( y_1 = y_2 = y_3 \). Because of the Hebbian coupling rule, the middle oscillator has the following interaction term \(-\kappa_2 x_2 + x_1 + x_3 = (2 - \kappa_2) x_1\), while the first and third oscillators have the interaction terms \(-\kappa_1 x_1 + x_2 = (1 - \kappa_1) x_1\) and \(-\kappa_3 x_3 + x_2 = (1 - \kappa_3) x_1\) respectively. These interaction terms are different, and cause the trajectories of the oscillators to be different. An exact synchrony is not possible. An obvious solution is to change \( \kappa_i(t) \) so that it equals the number of excited neighbors that oscillator \( i \) is coupled with. We set
\[ \kappa_i(t) = \sum_j J_{ij}(t) \]  

so that the interaction terms will be zero when the oscillators are synchronized. All the oscillators will now have the same trajectory and remain synchronous. The effect of (5.5) is similar to the dynamic normalization introduced by Wang [Wang, 1993a, Wang, 1995]. The original form of dynamic normalization served to normalize the connection strengths between oscillators. In this model we do not normalize connection strengths, but instead alter the multiplicative constant on the scalar diffusive coupling term. Either formulation would have the same results with these equations, but we choose to normalize the multiplicative constant because it is more direct. The effect of dynamic normalization is to maintain a balanced interaction term so that coupled oscillators remain synchronous independent of the number of connections that they have.

The architecture of this network allows us to implement the basic aspects of oscillatory correlation, synchrony and desynchrony. To illustrate, assume that the network receives input as shown in Figure 56. The black squares represent units that receive stimulation, and these units then produce oscillatory behavior. The dynamic couplings will disconnect excited units from unexcited units, and group connected units together. For the five objects pictured in the input, there will be five corresponding groups of oscillators. Connected oscillators synchronize, and GI ensures that no two spatially separated objects have the same phase.
Figure 56. Input used for the network. Black squares denote oscillators that receive input. Starting clockwise from the upper left hand corner, we name the objects as follows: a helicopter, a thick addition sign, a tree, a truck, and a house.

5.3 Synchronization

Much work has been done with coupled phase oscillators [Kuramoto and Nishikawa, 1987, Daido, 1988, Strogatz and Mirollo, 1988, Ermentrout, 1990, Ermentrout and Kopell, 1990, Sompolinsky et al., 1991] because the phase model is the simplest description of a smooth limit cycle. Phase oscillators are generally defined as

$$\dot{\phi}_i = \omega_i + \sum_j J_{ij} G(\phi_i, \phi_j)$$

(5.6)

where $\phi_i$ is the phase of the $i^{th}$ oscillator, $\omega_i$ is its intrinsic frequency. $J_{ij}$ is the coupling strength between the $i^{th}$ and the $j^{th}$ oscillators. For phase oscillators with local diffusive coupling, and identical intrinsic frequencies, the in-phase solution is asymptotically stable [Cohen et al., 1982]. But the phase model does not exhibit the rich variety of behaviors that other, more complex nonlinear oscillators, have when locally coupled (for example [Schreiber and Marek, 1982, Ashkenazi and Othmer, 1978, Han et al., 1995]. Because the system of W-C oscillators that we use differs significantly from those mentioned above,
we examine the properties of the following approximation to the W-C oscillator in detail. We show that with a sufficiently large coupling strength synchrony occurs for a finite number of oscillators, independent of their initial conditions.

Using basic matrix stability analysis, we show that a line of oscillators can achieve synchrony. The equations we analyze are a bit different from those shown in (5.1). We do not include parameter $\eta$, $D = 0$, and we do not consider the effects of GI. We have also dropped the $S$ notation because the interaction terms can be explicitly included. A diagram of the connections between units, arranged in a line, is given in Figure 57. Note that the two ends are not connected with one another. Thus we are analyzing a line, not a ring, of $n$ oscillators. The equations are

\begin{align*}
\dot{x}_1 &= -x_1 + P(ax_1 - by_1 - \varphi_x) + \alpha_w (x_2 - x_1) \\
\dot{y}_1 &= -y_1 + P(cx_1 + dy_1 - \varphi_y) + \alpha_w (y_2 - y_1) \\
\ldots \\
\dot{x}_i &= -x_i + P(ax_i - by_i - \varphi_x) + \alpha_w (x_{i+1} + x_{i-1} - 2x_i) \\
\dot{y}_i &= -y_i + P(cx_i + dy_i - \varphi_y) + \alpha_w (y_{i+1} + y_{i-1} - 2y_i)
\end{align*}
where the sigmoid function $H(v)$ has been approximated with

$$P(v) = \begin{cases} 
0 & \text{if } v < -\epsilon \\
\frac{v}{2\epsilon} + \frac{1}{2} & \text{if } -\epsilon < v \leq \epsilon \\
1 & \text{if } v > \epsilon 
\end{cases} \quad (5.8)$$

The constants $a, b, c, d, \phi_x$, and $\phi_y$ are positive values, $\log(\epsilon) = 1$, and $\alpha_w$ is the coupling strength. We now state our major analytical result as the following theorem.

**Theorem** For the system of coupled oscillators defined in (5.7) and (5.8), the coupling strength $\alpha_w$ can be chosen such that synchrony is asymptotically stable.

**Proof:** First, let $a^2 + b^2 > c^2 + d^2$, and let us define the following notations

$$\hat{r}_i = (x_i - x_{i+1}, y_i - y_{i+1}) \quad r_i^2 = (x_i - x_{i+1})^2 + (y_i - y_{i+1})^2 \quad (5.9)$$

$$\cos(\theta_i) = \frac{x_i - x_{i+1}}{r_i}, \quad \sin(\theta_i) = \frac{y_i - y_{i+1}}{r_i} \quad (5.10)$$

$$f_i = P(ax_i - by_i - \phi_x) - P(ax_{i+1} - by_{i+1} - \phi_x) \quad (5.11.a)$$

$$g_i = P(cx_i + dy_i - \phi_y) - P(cx_{i+1} + dy_{i+1} - \phi_y) \quad (5.11.b)$$

Note that $\hat{r}_i$ is a two element vector, and $r_i$ is the positive square root of $r_i^2$. The time derivative of the distance between two oscillators can be written as

$$\frac{1}{2} \frac{d}{dt} r_i^2 = \hat{r}_i \cdot \dot{\hat{r}}_i = r_i \hat{r}_i \quad (5.12)$$

We will use the "dot" above a variable to denote its first order time derivative. According to (5.7) we can write
\[ r_i \dot{r}_i = - (1 + 2\alpha_w) r_i^2 + (r_i \cos (\theta_i) f_i + r_i \sin (\theta_i) g_i) \]
\[ + \alpha_w (\tilde{r}_i \cdot \tilde{r}_{i-1} + \tilde{r}_i \cdot \tilde{r}_{i+1}) \]  

(5.13)

In the above equation 1 ≤ i ≤ n - 1, and let the values of the undefined variables \( r_0 = r_n = 0 \). The functions \( f_i \) and \( g_i \) are bounded by

\[-1 \leq f_i \leq 1, \quad -1 \leq g_i \leq 1 \]  

(5.14)

Thus, the second term on the RHS of is bounded by

\[-\sqrt{2} r_i \leq r_i \cos (\theta_i) f_i + r_i \sin (\theta_i) g_i \leq \sqrt{2} r_i \]  

(5.15)

The last term on the RHS of is bounded by

\[-\alpha_w r_i (r_{i-1} + r_{i+1}) \leq \alpha (\tilde{r}_i \cdot \tilde{r}_{i-1} + \tilde{r}_i \cdot \tilde{r}_{i+1}) \leq \alpha_w r_i (r_{i-1} + r_{i+1}) \]  

(5.16)

Using (5.15) and (5.16), an upper bound and a lower bound on \( r_i \) can be written as

\[-(1 + 2\alpha_w) r_i^2 - \sqrt{2} r_i - \alpha_w r_i (r_{i-1} + r_{i+1}) \leq r_i \dot{r}_i \leq -(1 + 2\alpha_w) r_i^2 + \sqrt{2} r_i + \alpha_w r_i (r_{i-1} + r_{i+1}) \]  

(5.17)

which now places a finite bound on \( r_i \) as a function of \( \alpha \) and \( n \). If \( \alpha = 0 \), and we divide both sides by \( r_i \), then (5.17) becomes

\[-r_i - \sqrt{2} \leq \dot{r}_i \leq -r_i + \sqrt{2} \]  

(5.18)

which implies that \( \dot{r} \leq 0 \) if \( r_i > \sqrt{2} \). Consequently, the bounds will reach an equilibrium such that \( r_{max} \), the maximum distance between any two connected oscillators, is less than, or equal to \( \sqrt{2} \). Thus, without any coupling whatsoever, there is a finite bound on \( r_{max} \).

Because the interaction terms are designed to give rise to synchrony, one would expect that they would have the effect of reducing \( r_{max} \). We now show that we can control the size of \( r_{max} \) by an appropriate choice of \( \alpha_w \). We divide (5.17) by \( r_i \) and examine only the upper bound, which we rewrite as a matrix equation.
\[ q = \alpha_w \begin{pmatrix} -1/\alpha_w & 1 \\ 1 & -1/\alpha_w & 1 \\ & \ddots & \ddots & \ddots \\ & & 1 & -1/\alpha_w & 1 \\ & & & 1 & -1/\alpha_w \\ & & & & 1 \end{pmatrix} q + \sqrt{2}k \] (5.19)

where \( q = (q_1, q_2, \ldots, q_{n-1})^t \) and \( k \) is a \((n-1) \times 1\) column vector of all 1's. Let \( A \) be the matrix in (5.19). We will use the convention of denoting vectors with lower case bold letters, and matrices with upper case bold letters. The superscript "t" denotes the transpose. The eigenvalues of \( A \) are all negative, thus (5.19) approaches an equilibrium value at an exponential rate. The equilibrium values of the elements in \( q \), which we denote with \( q^{eq} \), are defined by

\[ q^{eq} = \frac{\sqrt{2}}{\alpha_w} A^{-1} k \] (5.20)

We multiply each side of (5.20) by \( k^t \) to obtain

\[ \sum_{i=1}^{n-1} q_i^{eq} = \frac{\sqrt{2}}{\alpha_w} \sum_{i,j=1}^{n-1} (A^{-1})_{ij} \] (5.21)

For \( \alpha_w \gg 1 \) we can approximate \( A \) with \( B \), where

\[ B = \begin{pmatrix} -2 & 1 \\ 1 & -2 & 1 \\ & \ddots & \ddots & \ddots \\ & & 1 & -2 & 1 \\ & & & 1 & -2 \end{pmatrix} \] (5.22)

The inverse of this matrix follows a regular pattern and we can explicitly write

\[ -\sum_{i,j=1}^{n-1} (B^{-1})_{ij} = \frac{1}{2} + \frac{11}{12} (n-1) + \frac{1}{2} (n-1)^2 + \frac{1}{12} (n-1)^3 \] (5.23)
Because the elements of $A^{-1}$ change continuously and monotonically with $\alpha_w$ (see [Bellman, 1970]), and also because $A$ remains invertible in the range $0 \leq \alpha_w < \infty$, we can use (5.23) as an upper bound on the sum of all the elements in $A^{-1}$, i.e.

$$- \sum_{i,j=1}^{n-1} (A^{-1})_{ij} < - \sum_{i,j=1}^{n-1} (B^{-1})_{ij} \quad (5.24)$$

We use (5.23) and (5.24) to bound (5.21) as

$$\sum_{i=1}^{n-1} q_i^{eq} < \frac{\sqrt{2}}{\alpha_w} \left[ \frac{1}{2} + \frac{11}{12} (n-1) + \frac{1}{2} (n-1)^2 + \frac{1}{12} (n-1)^3 \right] \quad (5.25)$$

It can be shown that the elements of matrix $A^{-1}$ are all negative. Given that the elements of $k$ are all 1's, (5.20) implies that all the elements of $q^{eq}$ are greater than zero. With this we can write the following inequality

$$q_{eq}^{\max} \leq \sum_{i=1}^{n-1} q_i^{eq} \quad (5.26)$$

where $q_{eq}^{\max}$ is the maximum of the $q_i^{eq}$'s. (5.26) and (5.25) give the following inequality

$$q_{eq}^{\max} < \frac{\sqrt{2}}{\alpha_w} \left[ \frac{1}{2} + \frac{11}{12} (n-1) + \frac{1}{2} (n-1)^2 + \frac{1}{12} (n-1)^3 \right] \quad (5.27)$$

Assume that both systems of $r$ and $q$ start with the same initial conditions, i.e. $r(0) = q(0)$. Given that $r \leq Ar + \sqrt{2}k$ and $q = Aq + \sqrt{2}k$, it is known that $r(t) \leq q(t)$ for $t \geq 0$ [Golomb and Shanks, 1965]. Thus, after some time, (5.18) will reach equilibrium, and we can use (5.27) and that $r_{eq}^{max} \leq q_{eq}^{max}$ to write

$$r_{eq}^{max} \leq \frac{\sqrt{2}}{\alpha_w} \left[ \frac{1}{2} + \frac{11}{12} (n-1) + \frac{1}{2} (n-1)^2 + \frac{1}{12} (n-1)^3 \right] \quad (5.28)$$
(5.28) shows that for fixed \( n \), \( r_{\text{max}} \) is bounded by a quantity that is inversely proportional to \( \alpha_w \). In essence, we can decrease \( r_{\text{max}} \) by increasing \( \alpha_w \). We use this control to further constrain the upper bound of (5.15), because once \( r_{\text{max}} \) is smaller than a certain value,

\[
    r_f = \frac{2e}{\left(\frac{a^2 + b^2}{2e}\right)^{1/2}} \quad (5.29)
\]

the maximal values for \( f_i \) and \( g_i \) are no longer equal to 1. According to (5.8) and (5.11), if \( f_i = 1 \) then one oscillator is at a location on the plane such that \( ax_1 - by_1 - \phi_x > e \), and the other oscillator must satisfy \( ax_2 - by_2 - \phi_x < -e \). In other words, the oscillators lie on opposite sides of the piece-wise linear function \( P(\nu) \), and do not lie on the intermediate sloped line. \( r_f \) is the minimum distance between two oscillators such that \( f_i = 1 \). If the distance between two oscillators is less than \( r_f \), then the two oscillators lie on the same, or adjacent, pieces of function \( P(\nu) \) and thus \( f_i < 1 \). There is also a corresponding value \( r_g \) for the function \( g_i \), but \( r_f < r_g \) due to the constraint \( a^2 + b^2 > c^2 + d^2 \) previously mentioned. If \( r_{\text{max}} < r_f \) then automatically \( r_{\text{max}} < r_g \) which implies that \( g_i < 1 \). Thus we want to choose \( \alpha_w \) such that

\[
    \alpha_w > \left(\frac{a^2 + b^2}{2e}\right)^{1/2} \left[ \frac{1}{2} + \frac{11}{12} (n-1) + \frac{1}{2} (n-1)^2 + \frac{1}{12} (n-1)^3 \right] \quad (5.30)
\]

If the inequality in (5.30) is satisfied, then \( r_{\text{max}} \) is less than \( r_f \) and, using (5.8) and (5.11), the functions \( f_i \) and \( g_i \) will have the following bounds

\[
    -\frac{r_i}{2e} (a \cos (\theta_i) - b \sin (\theta_i)) \leq f_i \leq \frac{r_i}{2e} (a \cos (\theta_i) - b \sin (\theta_i)) \quad (5.31.a)
\]

\[
    -\frac{r_i}{2e} (c \cos (\theta_i) + d \sin (\theta_i)) \leq g_i \leq \frac{r_i}{2e} (c \cos (\theta_i) + d \sin (\theta_i)) \quad (5.31.b)
\]

which simplify to

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\[
-\frac{r_i}{2e} \sqrt{a^2 + b^2} \leq f_i \leq \frac{r_i}{2e} \sqrt{a^2 + b^2} \tag{5.32.a}
\]
\[
-\frac{r_i}{2e} \sqrt{c^2 + d^2} \leq g_i \leq \frac{r_i}{2e} \sqrt{c^2 + d^2} \tag{5.32.b}
\]

In the terms involving \(f_i\) and \(g_i\) are multiplicative. Hence, \([r_i \cos (\theta_i) f_i + r_i \sin (\theta_i) g_i]\) is the function that must be examined. If \(r_{\text{max}} \leq r_f\) we can use (5.32) to write
\[
r_i \cos (\theta_i) f_i + r_i \sin (\theta_i) g_i \leq \frac{r_i^2}{2e} \sqrt{a^2 + b^2 + c^2 + d^2} \tag{5.33}
\]

For convenience let
\[
M = \frac{1}{2e} \sqrt{a^2 + b^2 + c^2 + d^2} \tag{5.34}
\]

Using (5.34) and (5.16) an upper bound of \(\frac{1}{2}^e\) can be written as
\[
r_i \dot{r}_i \leq - (1 + 2\alpha_w) r_i^2 + M r_i^2 + \alpha_w r_i \left( r_{i-1} + r_{i+1} \right) \tag{5.35}
\]

which simplifies to
\[
\dot{r}_i \leq - (1 + 2\alpha_w) r_i + M r_i + \alpha_w \left( r_{i-1} + r_{i+1} \right) \tag{5.36}
\]

Letting \(\beta = M - 1\) and
\[
W = \begin{bmatrix}
\beta - 2\alpha_w & \alpha_w \\
\alpha_w & \beta - 2\alpha_w & \alpha_w \\
\alpha_w & \beta - 2\alpha_w & \alpha_w \\
\vdots & \alpha_w & \beta - 2\alpha_w \\
\alpha_w & \beta - 2\alpha_w & \alpha_w \\
\alpha_w & \beta - 2\alpha_w
\end{bmatrix}
\tag{5.37}
\]

we rewrite (5.36) as
\[
\dot{r} \leq W r \tag{5.38}
\]

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Using the same logic which leads to (5.19), let

\[ \dot{p} = Wp \]  

(5.39)

and assume that the initial conditions for both systems are identical, i.e. \( p(0) = r(0) \), then \( r(t) \leq p(t) \) for \( t > 0 \). If all the eigenvalues of \( W \) are negative, then the matrix is stable. If the matrix is stable all the elements of \( p \) approach zero, which forces all the elements of \( r \) to approach zero. We now examine the eigenvalues of \( W \) to find under what conditions they become negative. The eigenvalues of \( W \) are given by

\[ \lambda_k = (\beta - 2\alpha_w) - 2\alpha_w \cos \left( \frac{k\pi}{n} \right) \]  

(5.40)

where \( k = 1, 2, \ldots n - 1 \) and \( n \geq 3 \). The condition for all eigenvalues to be negative can be written as

\[ \alpha_w > \frac{\beta}{4\sin^2(\pi/2n)} \]  

(5.41)

For \( n \gg 1 \) this becomes

\[ \alpha_w > \frac{\beta n^2}{\pi^2} \]  

(5.42)

In summary, synchrony will be asymptotically stable for the chain of coupled oscillators defined in (5.7) if \( \alpha_w \) is chosen such that the inequalities in (5.30) and (5.41) are satisfied. This concludes the proof.

The reported time for a human subject to identify a single object is estimated to be less than 100 ms. [Biederman, 1987]. If oscillatory correlation is used by the brain, synchrony must be achieved before identification takes place. Experimental evidence from the cat visual cortex shows that synchrony is achieved quickly, within 25-50 ms., or 1-2 cycles in 40 Hz oscillations [Gray et al., 1991]. These experimental results emphasize the
importance of fast synchrony. From practical considerations synchrony must also be achieved quickly in order to deal with a rapidly changing environment. In this model we can control the rate of synchrony by increasing the coupling strength. But that would lead to unreasonably large values for $\alpha_w$. This problem can be avoided by careful adjustment of the nullclines, and we now describe a method by which a chain of several hundred W-C oscillators, as defined in (5.1), but arranged as a one dimensional chain, can be entrained within the first cycle.

Our method of fast synchrony requires that there exist one region in the phase plane where the $x$ and $y$ nullclines of the oscillator are very near to one another. More specifically, in the system of (5.1), the parameters were chosen so that this occurs in the upper left hand corner, as seen in Figure 55. The oscillators travel slowly through this region because, close to the nullclines, the values of $\dot{x}$ and $\dot{y}$ are near zero. Note that this need not be true in general, but it is true in the smoothly varying W-C equations that we use. The $x$ and $y$ nullclines are so near each other that only a small perturbation is needed to push the $y$ nullcline to the left, and cause it to intersect the $x$ nullcline (we will use the coupling term to create this perturbation). When the nullclines intersect, two new fixed points are created. One of these fixed points is attracting, and will stop periodic motion. We neglect the case when the nullclines just touch, as the single bifurcation point exists only momentarily, and does not significantly affect the dynamics.

Let us examine the case of two coupled oscillators in detail. Specifically, we examine two oscillators that are near to one another and approaching the upper left hand corner of the unit square from the right, i.e. rotating counterclockwise. Figure 58 displays an enlarged picture of this region. The interaction term will cause the $x$ and $y$ nullclines of the leading oscillator to intersect, effectively trapping it at the newly created fixed point.
Figure 58. An enlarged diagram of the upper left hand corner of Figure 55 that displays the nullclines of two interacting oscillators. The two dashed curves are the nullclines for the leading oscillator, and the black filled circle represents the position of the leading oscillator. The interaction term causes the $y$ nullcline (short dashed curve) of the leading oscillator to be perturbed to the left so that it intersects the $x$ nullcline (long dashed curve). This creates an attracting fixed point, and a saddle fixed point. The interaction term does not impede the motion of the trailing oscillator (open circle), which will approximately follow the path given by the solid curve. The leading oscillator will be trapped at the attracting fixed point until the distance between the oscillators is very small.

In Figure 58 the leading oscillator (black filled circle) is shown trapped at the attracting fixed point, which is the top intersection of the $x$ nullcline and the $y$ nullcline. The other oscillator is represented by an unfilled circle, and its movement along the limit cycle is not impeded. As the oscillators come closer the interaction term decreases, and the $y$ nullcline of the leading oscillator moves to the right. When the oscillators are close enough, the $x$ and $y$ nullclines of the leading oscillator will separate, releasing the leading oscillator from the fixed point and allowing its motion along the limit cycle to continue. We have ignored the motion of the $x$ nullcline because it moves up and down only a small amount during this process. Since the $x$ nullcline is almost completely vertical in this region, mov-
ing it by a small amount has a negligible effect. In summary, our method of fast synchrony
requires that there be a region such that the parameters are near a saddle bifurcation, and
that the interaction terms be organized to alter the behavior of an oscillator in this region
appropriately as described above.

The distance between the oscillators can be controlled precisely in this manner. It
depends solely on the original separation of nullclines, and the size of $\alpha_w$. To be more
precise, for the parameters specified in the caption of Figure 55, a $y$ interaction term
greater than 0.0003 will cause the nullclines to intersect. Thus, the distance between the
oscillators in the $y$ direction, $(y_2 - y_1)$, will have to be less than $(0.0003/\alpha_w)$ before peri-
odic motion resumes. Because the oscillators are almost directly above one another,
$x_2 = x_1$, and the distance between the oscillators can be approximated by $(0.0003/\alpha_w)$.
This distance is orders of magnitude smaller than the size of the limit cycle, so we can
safely call the oscillators separated by this distance synchronized. However, this phase
adjustment only occurs in the upper left hand corner of the limit cycle. One must ensure
that both oscillators are in this region and not on opposite sides of the limit cycle. We
increase the value of $\alpha_w$ to make sure the oscillators approach each other before moving
to the limit cycle. This behavior can be explained by examining only the interaction terms
in (5.1), and ignoring the oscillatory terms. We find that the scalar diffusive coupling
terms converge asymptotically to a single stable point. Thus, if $\alpha_w$ is sufficiently large, the
interaction terms will dominate over the oscillatory terms, and cause the oscillators
approach each other. As the oscillators come together, the interaction terms decrease, and
the oscillatory terms start to contribute to the dynamics. So, with a sufficiently large $\alpha_w$, the
oscillators will be loosely synchronized before oscillatory motion starts. The oscilla-
tors will then approach the upper left hand corner of the limit cycle. If the distance
Figure 59. This graph displays the combined $x$ values of 34 oscillators with respect to time. An accurate synchrony is achieved within the first cycle. The random initial conditions used were restricted to the range of the limit cycle, i.e. $0.0 \leq x \leq 0.5$ and $0.0 \leq y \leq 1.0$. Parameters $\alpha_w = 90$ and $\sigma = 0$.

Between the two oscillators is larger than $(0.0003/\alpha_w)$, then the interaction term will cause the nullclines of the leading oscillator to intersect. An attracting point will be created and the leading oscillator will be trapped at this point until the second oscillator moves to within a distance of $(0.0003/\alpha_w)$. In summary, $\alpha_w$ is used to loosely group the oscillators together. The oscillators then travel along the limit cycle to the upper left hand corner, where they become tightly synchronized.

By controlling $\alpha_w$ and the position of the nullclines, we can reduce the distance between the two oscillators to an arbitrarily small value. Using these same techniques, we can control the overall entrainment of a chain of oscillators. Figure 59 shows the $x$ activities of 34 oscillators plotted on the same graph. The oscillators are those defined in (5.1), but they are arranged in a chain, and are not connected to GI. The strong interaction terms cause the oscillators to approach each other rapidly, creating a thick conglomeration of curves, instead of 34 completely random curves. These loosely synchronized oscillators will then approach the upper left hand corner of the limit cycle, where they become tightly synchronized. By the next peak, one can see that only a single thin curve is exhibited, as
all the oscillators are at virtually the same $x$ value at the same time. We make no claims that an infinite number of oscillators can be entrained using this method. Large line lengths ($n > 500$) could require excessively large coupling strengths. We are interested in finite systems, and have tested this method with chain lengths up to several hundred oscillators. We conjecture that the behavior for a matrix of $256 \times 256$ locally coupled oscillators would be similar in terms of their synchronization.

The method described above can group many oscillators to within a small distance of one another, and therefore within a small distance of the in-phase solution. Because we have not shown that the actual W-C oscillators synchronize, a variational analysis [Minorsky, 1962] is appropriate. In this analysis all the variables are perturbed by a small amount from a known solution, in this case, the synchronous solution. The perturbations are assumed to be sufficiently small so that their first order approximations are valid. The properties of the resulting system of linear equations can then be examined. We assume the existence of a smooth stable limit cycle, and do not consider the effects of noise or GI. Our analysis has shown that the in-phase solution is locally stable. We omit the details of this straightforward procedure of the analysis.

In summary, we have shown that the piece-wise linear form of the W-C oscillator will synchronize if the coupling strength meets a certain criteria, and we have presented a method for rapid synchrony. In our simulations, we have used both the piece-wise linear approximation of the oscillator (5.7) and the actual W-C oscillators (5.1), and observed that any positive coupling strength will give rise to synchrony, even if it does not satisfy the conditions previously specified. Therefore we conclude that synchrony can be achieved in populations of neural oscillators with local connections.
5.4 Desynchronzation

As discussed previously, a method of desynchronization is necessary for minimizing the possibility of accidental synchrony. Several models [Schillen and König, 1991, von der Malsburg and Buhmann, 1992] have methods of desynchronization, but it is not clear how these models perform with more than two objects. In Hansel and Sompolinsky [Hansel and Sompolinsky, 1992], noise in a chaotic system is used to desynchronize objects, but this can also synchronize objects. Hence this is not a reliable method of distinguishing multiple objects.

In order to reliably desynchronize multiple objects, independent oscillations in an oscillator network cannot be permitted. Thus we globally connect GI to and from every oscillator in the network so that no two oscillators act fully independently. These connections serve to adjust phase relationships between oscillator groups representing different objects. GI has a minimum value of zero, and is defined as

\[ \dot{z} = U(1 - z) Tr - \nu z \]  

(5.43)

\( Tr \) is a binary value, which is turned on (set to one) if any oscillator lies within a small region near the origin; it is defined as

\[ Tr = \begin{cases} 
1 & \text{if } (x_i + y_i) < \mu, \quad 1 < i < N \\
0 & \text{if otherwise} 
\end{cases} \]  

(5.44)

The positive parameters \( U \) and \( \nu \) control the rate of growth and decay of \( z \). We call this area near the origin the *triggering region* because when an oscillator enters this region, \( Tr = 1 \), and the value of GI starts to increase. \( \mu \) controls the size of the triggering region. As seen in (5.1), the value of GI is fed into the \( x \) unit of every oscillator. This manipulation has the simple effect of raising or lowering the \( x \) nullcline of every oscillator. Figure
Figure 60. A close look of the triggering region (black filled triangle), the $x$ nullcline (short dashed curve), and the $y$ nullcline (long dashed curve). The value $\mu = 0.048$ was used in the simulations, but other nearby values result in desynchronization also. The other parameters were $U = 2.9$ and $v = 2.0$.

60 displays the triggering region and its position relative to the nullclines. Just to the right of the triggering region there is another slow region, because the $x$ and $y$ nullclines are relatively close. All oscillators rotate counterclockwise, so an oscillator will enter the triggering region, and then pass through the slow region between the nullclines.

GI can only take on positive values, enabling it to raise nullclines or return them to their original positions. An oscillator in the triggering region will cause the $x$ nullcline of every oscillator to rise, and will produce a marked increase the speed of those oscillators in the slow area. Because the triggering region and the slow region are adjacent, any two oscillators with nearby phases will be separated when the trailing oscillator enters the triggering region. The movement of the $x$ nullclines will affect oscillators elsewhere on the limit cycle, but the change in their speed of motion will be negligible compared to the increase in speed received by an oscillator in the slow area.
Figure 61 displays the ability of GI to separate two oscillators. The first two plots display the $x$ activity of two oscillators in time. The third plot is the activity of GI with respect to time. The oscillators are almost in phase in the first cycle, but a major shift occurs during the second cycle. This occurs when oscillator 2, which trails oscillator 1, enters the triggering region and thus excites GI, which then increases the speed of oscillator 1. The sharp change in the characteristic shape of oscillator 1 during the second cycle demonstrates the increase in speed induced by GI while oscillator 1 was within the slow region. Afterward, GI continues to cause minor phase shifts during every cycle. These small phase shifts slowly decrease as the relative phase difference increases. Eventually, an equilibrium is attained. The equilibrium, however, does not ensure an antiphase relationship between the two oscillators, but suffices to clearly distinguish their phases.
Naturally, the desynchronization of objects by this method acts in direct opposition to the necessity of achieving synchrony within groups of oscillators. We resolve this problem by increasing the coupling strength. Increased coupling maintains synchrony within groups of connected oscillators, but does not alter the performance of GI because it does not change the shape of the limit cycle.

5.5 Simulation Results

We now discuss the simulation results of this model using the input displayed in Figure 56. Figure 62A-F display network activity at specific time steps during numerical integration. Figure 62A represents the initial activity of the network. The sizes of the circles are directly proportional to the \( x \) values of the corresponding oscillators. The random sizes of the circles in Figure 62A represent the random initial conditions of the oscillators. Figure 62B is a later time step when the object that resembles a house is at its highest activation. Figure 62C displays the time step after Figure 62B when the object resembling a helicopter is maximally active. Figure 62D corresponds to the time step after Figure 62C when the highest activation for the tree-like object is attained. This object was specifically selected to emphasize that any connected region will synchronize, whether it is concave or convex. Figure 62E shows a later time step when the truck shaped object is maximally activated. The object resembling a thick addition symbol is also weakly activated at this time step. Finally, Figure 62F shows the time step when the thick addition sign is at its highest activation. The objects clearly "pop out" once every cycle.
Figure 62. Each picture represents network activity at a time step in the numerical simulation. The size of the circle is proportional to the $x$ activity of the corresponding oscillator. (A) The oscillators have random positions on the phase plane at the first time step. (B)-(F) Successive time steps that correspond to the maximal activities for each group of oscillators. $\alpha_w = 10.0$ in this simulation. The other parameters are as specified in the captions of Figure 55 and Figure 60. The random initial conditions used were restricted to the range of the limit cycle, namely, $0.0 \leq x \leq 0.5$ and $0.0 \leq y \leq 1.0$. 
Figure 63. The plot labeled "GI" displays the activity of the global separator with respect to time. The other five plots display the combined \( x \) activities of all the oscillators stimulated by the corresponding object. Each of the five oscillator groups is synchronized within the first cycle, and by the second cycle is desynchronized from the other oscillator groups.

In Figure 63, we display the activities of GI and the \( x \) activities of all stimulated oscillators for the first few cycles. The first five plots display the combined \( x \) activities of all oscillators that are stimulated by the five objects. Each of the properties we have described in previous sections are shown in this graph. Initially the interaction terms dominate and cause the oscillators to loosely synchronize. Loose synchrony is seen on the graph by observing that each of plots quickly merge into a thick line. By the second peak, the oscillators have been synchronized to such a degree that only a thin single curve is exhibited. Desynchronization most noticeably occurs during the fourth activation of GI. The phase difference between the oscillator groups representing the house and the addition sign is significantly altered at this time. This shift in phase is signaled by the change
in the characteristic shape of the oscillator group representing the addition sign. The activity of GI is displayed on the last frame of Figure 63. GI is activated when any oscillator, or oscillator group passes through the triggering region. When the oscillators are well separated, GI will be active five times per cycle, signaling successive “pop outs” of the five objects. Only the first three cycles are depicted in this graph, but as we have tested, synchrony within the oscillator groups, as well as desynchrony between the groups is maintained afterwards without degradation.

We can reliably separate up to at least 9 objects (results not shown). Separating the phases of more objects becomes increasingly difficult for this system. The finite time required for an oscillator to travel through the triggering region, and the finite area affected by GI, constrain the number of objects that can be separated. This limitation seems consistent with the well-known psychological result that humans have a fundamental bound on the number of objects that can be held in their attentional span [Miller, 1956].

Even though noise was not used in the simulations presented here, we have tested the network with various amounts of noise. As expected, the system is robust for small amounts of noise, but cannot tolerate very large quantities. This is because noise by itself can cause the nullclines to intersect and thus interfere with the mechanism we use to synchronize oscillators. The amount of noise the system can tolerate increases with the size of the coupling strength.

We used the numerical ODE solvers found in [Press et al., 1992] to conduct the above simulations. An adaptive Runge-Kutta method was used for most of the simulations reported. The Bulirsch-Stoer method was later used to confirm the numerical results. The network had the same dynamics with either of the integration methods. So it is very unlikely that numerical errors played any significant role in our simulation results.
5.6 Discussion

Our analysis of the W-C oscillator network demonstrates that it contains the basic features necessary to achieve oscillatory correlation. This includes: dynamic couplings, local excitatory connections to synchronize oscillators, and global excitatory connections to desynchronize groups of oscillators. With this simple architecture, we have used the theory of oscillatory correlation, together with the Gestalt principle of connectedness to illustrate sensory segmentation. The model retains information of spatial relationships through local coupling, and does not suffer from the problems of accidental synchrony through the use of a global separator to segregate objects.

Although we have not attempted to simulate the experimental findings of Gray et al. [Gray et al., 1989], the network is neurally plausible. The W-C equations represent the activities of neural groups, and local excitatory connections are consistent with lateral connections widely seen in the brain [Kandel et al., 1991]. The global separator may be viewed as part of an attentional mechanism. Experiments conducted by Treisman and Gelade [Treisman and Gelade, 1980] suggest that if an object has several features, a correct conjunction of those features relies on attention. Thus, if feature binding is achieved through oscillatory correlation, the attentive mechanism may serve to synchronize features into a coherent object, as well as segment different objects. In performing desynchronization, GI may accomplish a task that is fundamental to attention. GI also has structural similarities to a proposed neural attentional mechanism. Crick [Crick, 1984] suggested that the reticular complex of the thalamus may control attention, in part because it has connections both to and from many regions of the cortex. Thus, the reticular complex of the thal-
amus may have influence over widely separated sensory processing regions. With its wide range couplings, GI may have structural, as well as functional, relations to the proposed attentional mechanisms.

We have shown that synchrony can occur in locally coupled oscillators if the coupling is sufficiently large. This is proven using the piece-wise linear approximation to the W-C oscillators. Numerically we observe that synchrony occurs, with local coupling, in the actual W-C oscillators (5.1), as well as our approximation to them (5.7), with any positive coupling strength. This implies that synchrony in such oscillator networks is possible with local connections only. We have also demonstrated a method that can synchronize large numbers of oscillators within the first cycle. The method is based on choosing parameters such that the system is near a bifurcation. This technique is not specific to W-C oscillators, or even scalar diffusive coupling. It should be applicable to other types of oscillators as well. We do not know yet have an estimate for how the rate of synchrony changes with the size of the system.

We also present a mechanism for desynchronization, which can segment up to 9 spatially separate objects. Our mechanism requires only a basic control of speed through a single region of the limit cycle, so it can be transferred to other oscillator models (see also [Wang and Terman, 1995] and [Terman and Wang, 1995]).

The matrix analysis we have done for a chain of oscillators can be extended to analyze higher dimensional oscillator lattices. We conjecture that synchrony can also be achieved in more than two dimensions, with only a positive coupling strength. This is based on simulations that we have done with two dimensional grids that exhibit the same phase locking behavior as we have seen in one dimensional chains. Also, this analysis can be done with lateral connections farther than nearest neighbor connections. In fact, numer-
ical simulations (data not shown) in one and two dimensions show that longer range connections facilitate synchronization. We speculate that analysis with longer range connections would indicate a decrease in the connection strength required to achieve synchrony.

In our model, spatial relationships are preserved through local excitatory coupling. The information contained in these relationships allows us to define objects using the Gestalt principles of proximity and connectedness. Thus any spatially separate object can be segmented, independent of its similarity to other objects in other features. That spatial segmentation is fundamental to perceptual processes is supported by the work of Keele et al. [Keele et al., 1988], who show that spatial location is a basic cue for feature binding.

Aside from explaining what may occur in the brain, oscillatory correlation offers a unique approach to the engineering of pattern segmentation, figure/ground segregation, and feature binding. Due to the nature of the oscillations, only a single object is active at any given time, and multiple objects are sequentially activated. The model can be used as a framework upon which more sophisticated methods of segmentation can be built. For example, the network can be extended to handle gray level input also. Dynamic couplings between excited neighboring oscillators could then be based on the contrast in the gray level of the stimulus. Regions with smoothly changing input would be grouped together, and segmented from regions with boundaries of sharp changes in gray level (see Chapter 2 for an implementation of this).

A unique advantage of using oscillatory correlation for perceptual organization is that the architecture is inherently parallel. Each oscillator operates simultaneously with all the others, and computations are based only on connections and oscillations, both of which are particularly feasible for VLSI chip implementation (for an actual chip imple-
mentation exploring phase locking see [Andreou and Edwards, 1994]). It also provides an
elegant representation for real time processing. Given the enormous amount of informa-
tion processing required by sensory processing, a parallel architecture and the potential for
VLSI implementation are both very desirable qualities.

Perceptual tasks involving neural oscillations have also been observed in audition
and olfaction [Freeman, 1978]. Oscillations have also been explored in associative recall
properties plus the support of biological evidence, this model may offer a general
approach to pattern segmentation and figure/ground segregation.
CHAPTER 6

SUMMARY AND FUTURE WORK

6.1 Summary

Synchronous neural activity has been observed in many brain regions [Singer and Gray, 1995] and understanding this phenomena may be fundamental to understanding the brain. In order to understand synchronous neural activity we have explored the dynamics of locally coupled populations of neural oscillators. We have been interested specifically in synchrony and desynchrony, and we have studied these topics in the context of how they may be used for information processing.

We first examined integrate-and-fire oscillators [Peskin, 1975], a one variable oscillator and perhaps the simplest model of neuronal behavior. Our numerical data indicate that one- and two-dimensional noiseless networks of identical oscillators synchronize at times proportional to the logarithm of the system size. We gave a heuristic explanation for this behavior. We also demonstrated a neurally plausible network of integrate-and-fire oscillators that performs oscillatory correlation, i.e. groups of oscillators that are desynchronized from each other, while synchrony is maintained within each group. We used this oscillator network to perform image segmentation with real images.
We also examined networks of relaxation oscillators, a more complicated, two-variable system of equations that model neuronal behavior [Fitzhugh, 1961, Nagumo et al., 1962, Morris and Lecar, 1981]. Through appropriate parameter choices, these oscillators can exhibit either sinusoidal type, relaxation type, or integrate-and-fire type oscillations. By studying relaxation oscillators, we revealed their intrinsic links to these two other classes of oscillators. In one-dimensional noiseless networks of identical relaxation oscillators we have examined synchrony, fractured synchrony, and travelling waves. Our analysis has yielded conditions necessary for formation of each of these three behaviors. Note that the basin of attraction for synchrony is much larger than the other two types of solutions when random initial conditions are used. Our numerical evidence indicates that the time to synchrony increases as $n^p$, where $n$ is the system size and $p$ is calculated from the data. We have suggested what the causes of this scaling relationship might be. For two-dimensional networks there exist parameter regimes in which the time to synchrony scales as $\log_{10}(n)$, and we have shown other, more complex relationships between the time to synchrony and the system size. Rotating waves and other types of patterns can exist in two-dimensional networks and we have suggested parameters regimes and initial conditions which hinder their formation.

We have examined how the time to synchrony is affected by the type of oscillator and the type of interaction used. Our data suggest that a discontinuous Heaviside type interaction leads to synchronization times proportional to $n$, independent of whether the oscillations are sinusoidal or relaxation like. When a smooth interaction is used, the time to synchrony scales as $n^2$. We conjecture that discontinuous interactions in general have better properties of synchronization in networks of oscillators than smooth interactions. In support of this conjecture is the work in Chapter 2, in which a discontinuous interaction
leads to much faster rate of synchrony than a diffusive interaction. Also in support of this conjecture is the work of Daido [Daido, 1993b], who noted that a discontinuous interaction resulted in the synchronization of a significant fraction of oscillators in a globally coupled network of phase oscillators with a normal distribution of frequencies. If a smooth interaction was used, this same network would not exhibit any synchronization. This conjecture may have practical applications in synchronizing chaotic systems, or arrays of Josephson junctions.

We also examined relaxation oscillators with time delays in the interaction. We analytically derived results for a pair of oscillators indicating that perfect synchrony was no longer attained, but that the oscillators asymptotically approached a solution such that their time difference was less than or equal to the time delay - a solution we called loose synchrony. In one- and two-dimensional networks of locally coupled oscillators, simulations revealed similar behaviors. We suggested a measure of synchrony for networks of such oscillators and presented evidence indicating how this measure increases as the network size increases. A range of initial conditions was proposed in which the degree of synchrony does not degrade as the system evolves. If the time delay becomes larger than the critical time delay, we find desynchronous solutions of high frequency form in both pairs and networks of oscillators.

Finally, we examined networks of Wilson-Cowan oscillators. These oscillators are based on populations of interacting excitatory and inhibitory neurons [Wilson and Cowan, 1972]. We proved that one-dimensional networks consisting of piece-wise linear approximation to Wilson-Cowan oscillators achieved synchrony if the coupling strength was large enough. In order to achieve synchrony quickly (in one or two cycles), we used a diffusive type coupling and chose parameters so that the system was near a bifurcation
point. Because of this, the interaction resulted in the formation and destruction of fixed points that occurred in such a fashion that synchrony was facilitated. Also, we created a mechanism for desynchronization in these networks. Up to nine different groups of oscillators could be desynchronized without destroying synchrony within each group. To our knowledge this is one of a few networks in which desynchronization of more than two oscillator groups can be achieved. Two other networks are described in Chapter 2 and in [Terman and Wang, 1995].

In summary we have investigated several classes of oscillators and how locally coupled networks of these oscillators synchronize with respect to $n$, the size of the network. We have observed four different scaling relationships between the average time to synchrony and $n$: $\langle T_s \rangle \sim \log_{10}(n)$, $\langle T_s \rangle \sim n^p$ with $p < 0.5$, $\langle T_s \rangle \sim n$, and $\langle T_s \rangle \sim n^2$. To the best of our knowledge, the first two relationships are new to the literature of coupled oscillators. Also, we have used numerical simulations to explore how the interaction alters the rate of synchronization. Our data indicate that the scaling relation $\langle T_s \rangle \sim n$ arises when a discontinuous interaction is used, and is independent of whether the oscillator is relaxation or sinusoidal type. Our work has also demonstrated the versatility of relaxation oscillator networks, which through proper alteration of parameters can exhibit all four scaling relationships.
6.2 Future Work

While we have understood and characterized synchrony and desynchrony in several types of oscillator networks, there are many questions which remain unanswered. Foremost among these questions is "What are the fundamental causes of the four different scaling relationships we observed in the time to synchrony as a function of the system size?" We list Chapter by Chapter some more specific directions for future work.

In Chapter 2 we examined integrate-and-fire oscillators with a specific reset rule and a specific type of interaction. How much can one alter these rule and these interactions and still observe the scaling relation \( T_s \sim \log_{10}(n) \)? Networks of these oscillators achieve synchrony in the presence of some forms of noise. This raises several questions. How much noise can these systems tolerate? What kind of noise can these systems tolerate? How does the rate of synchrony change in the presence of noise?

In Chapter 3 we examined relaxation oscillators and found a variety of phenomena. In one-dimensional networks that exhibit fractured synchrony, it is unknown how the block size is related to the coupling strength. The formation of fractured synchrony in two-dimensional systems is also of interest. Preliminary work indicates that the average block size approaches the system size at much smaller coupling strengths than in one-dimensional networks. Many similar questions can also be asked about travelling waves. Given random initial conditions, and a network with periodic boundary conditions, how frequently do travelling waves form? What is the average block size within the travelling waves? These are two specific questions that are part of the same general question that arises when several basins of attraction exist between units in an interacting system. A detailed understanding of these questions may provide some insight for similar questions in other dynamical systems.
Spatiotemporal pattern formation is also an interesting topic in these relaxation oscillator networks. One of the first questions that should be examined is whether or not these patterns are stable in other types of relaxation oscillators (the specific model we studied resulted in patterns that were neutrally stable). If these patterns are stable, then each separate pattern has a basin of attraction and estimating the stability and the number of patterns then becomes an interesting issue. If many stable patterns can form, then this system might be useful as an associative memory.

In two-dimensional networks of relaxation oscillators we have even more questions. We have suggested that restricting the initial conditions to the lower left branch prevents spatiotemporal pattern formation, but we have not proven this. Also, we have noticed an unusual phenomenon in the synchronization time for two-dimensional networks; a non-monotonic relationships between the systems size and the time to synchrony. This is counter-intuitive and we do not yet have an understanding of its cause.

In relaxation oscillators with time delays (Chapter 4) there are many unresolved issues. One of these issues is the speed with which the network attains the loosely synchronous solution. Is the time needed to achieve a loosely synchronous solution related to the time to synchrony in networks without time delays? It appears that all the behaviors seen in relaxation oscillator networks without time delays also arise in networks with time delays. It would be interesting to see if the properties of fractured synchrony, travelling waves, and spatiotemporal pattern formation observed in networks without time delays, have similar properties when time delays are included. Also, numerical simulations indicate that with small alterations in the defining equations, the synchronous solution becomes stable. Investigating this phenomena might reveal general properties of how to maintain synchrony in the presence of time delays.
In networks Wilson-Cowan oscillators (Chapter 5) we used diffusive coupling and chose parameters such that the system was near a bifurcation point. We do not know how the time to synchrony scales as a function of the system size. On a different note, König and Schillen [König and Schillen, 1991] showed that synchrony arises in a network of Wilson-Cowan type oscillators with time delay coupling. It would be interesting to understand how synchrony in these networks is related to synchrony in relaxation oscillator systems with time delays.

In this work we have described some properties of locally coupled networks for a few types of oscillators. However, these systems have not been fully examined with global coupling. It would be most interesting to see what similarities and differences arise as the nature of the coupling changes. As we begin to understand the differences between locally coupled systems and globally coupled systems, then one may gain substantial insight into how to modify the analytical tools that have been created for globally coupled networks so that they can be used in locally coupled systems.
APPENDIX A

RELAXATION OSCILLATORS

A1 Introduction

Relaxation oscillators are a generic type of oscillators. They are continuous but highly nonlinear and are typically thought to represent a class of oscillators different from the familiar harmonic, or sinusoidal oscillators. A reader unfamiliar with concepts such as nullclines, limit cycles, sinusoidal oscillators, and relaxation oscillators may find this Appendix useful. We also graphically describe the transition from sinusoidal to relaxation type oscillations. In Section A2 we describe four types of trajectories that arise in a pair of coupled oscillators.

The relaxation oscillators we examine are the Terman-Wang oscillators [Terman and Wang, 1995] that are based on the Morris-Lecar model of neural behavior [Morris and Lecar, 1981]. The relaxation oscillator used here is the same as that used in Chapter 3. All but one of the parameters have been fixed for simplicity,

\[
\frac{dx}{dt} = \dot{x} = 3x - x^3 - y \quad (A.1.a)
\]

\[
\frac{dy}{dt} = \dot{y} = \varepsilon (3 + 42 \tanh (10x) - y) \quad (A.1.b)
\]
This is a pair of coupled first order nonlinear differential equations. A starting point for understanding this system is to examine its nullclines, which are shown in Figure 64. The cubic shaped curve represents the x-nullcline, or the curve along which \( \dot{x} = 0 \). This is given by \( \dot{x} = 3x - x^3 - y = 0 \), or \( y = 3x - x^3 \). We will frequently refer to the cubic as consisting of three different "branches"; the middle branch, which passes through the point \((0,0)\) and connects the two local extrema, and the left and right branches, which extend from the local extrema to \(+\infty\) and \(-\infty\) respectively. The y-nullcline, \( \dot{y} = 0 \), is given by \( y = 3 + 42\tanh(10x) \). This hyperbolic tangent results in a sigmoid shaped curve, but because the argument of the hyperbolic tangent is multiplied by 10, the function looks more like a step function. The nullclines divide the x-y plane into four portions. Above the x-nullcline, the x-velocity is negative, thus all values of \( x \) in that region of the plane will result in a negative x-velocity (as indicated by the arrows in Figure 64). Below the x-nullcline, the x-velocity is positive, thus motion is in the positive x-direction. Analogous statements can be made for the y-nullcline. From these qualitative directions of motion one can see how a periodic trajectory might arise. However, there are several further requirements needed for oscillatory behavior to exist and one can find the details in [Minorsky, 1962].

The parameter \( \varepsilon \) describes the two different time scales that define relaxation oscillators. If \( \varepsilon \) is of \( O(1) \), then the oscillators is said to be in the sinusoidal regime because it can have a nearly uniform speed of motion along its limit cycle. For small \( \varepsilon \), the oscillator begins to exhibit two distinct time scales, or it has two different speeds of motion along disparate portions of its limit cycle. As one varies \( \varepsilon \), the equations change smoothly from sinusoidal oscillators to relaxation oscillators. Figure 65A displays the limit cycle for \( \varepsilon = 1 \) for (A.1) and one can see that it does appear qualitatively sinusoidal, as do the temporal
Figure 64. A diagram showing the qualitative direction of motion for system (A.1). The two curves represent the x- and y-nullclines.

Figure 65. (A) The limit (thick curve) cycle for (A.1) with $\varepsilon = 1.0$. The x- and y-nullclines are the thinner curves. (B) The temporal evolution of the x-variable and the y-variable.
evolution of both variables in Figure 65B. In Figure 66A, B, and C we display limit cycles and temporal evolution of the variables for progressively smaller values of $\varepsilon$ ($\varepsilon = 0.33$, $\varepsilon = 0.1$, $\varepsilon = 0.01$). As $\varepsilon$ becomes smaller, the velocity in the y-direction becomes smaller, and comparatively, motion in the x-direction becomes faster. In Figure 66C, $\varepsilon = 0.01$ and motion from the left branch to the right branch (and vice-versa) occurs quickly. Motion along the cubic (in the y-direction) is dominated by the slow parameter and occurs approximately 100 times slower than motion between the branches.

The term relaxation oscillator was first coined by van der Pol in 1926 [van der Pol, 1926]. The transition from a sinusoidal oscillator (as one might classify the limit cycle shown in Figure 65) to a relaxation oscillator (the limit cycle in Figure 66C) is smooth, and not clearly defined to our knowledge, but the distinction is an important qualitative one. Study still continues in understanding the differences between sinusoidal and relaxation oscillators.

When $\varepsilon = 0$ an oscillator is said to be in the singular limit and the relative speed of motion in the x-direction is infinitely fast in comparison with the speed of motion along the outer branches. The transition between the left and right branches thus occurs instantaneously, with no change in the y-variable. In the singular limit, and if the form of (A.1) is sufficiently simple, the speed of motion can be found analytically for y-variable and the speed of motion for the x-variable can be ignored, since it is instantaneous during the jumps. For small values of $\varepsilon$, a perturbation analysis can be performed [Bender and Orszag, 1978].
Figure 66. Three different limit cycles and their respective plots as a function of time are shown for three different values of $\varepsilon$. (A) $\varepsilon = 0.33$. (B) $\varepsilon = 0.1$. (C) $\varepsilon = 0.01$. 

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A2 A Pair of Relaxation Oscillators

A pair of coupled relaxation oscillators is defined as follows,

\[ \begin{align*}
\dot{x}_1 &= 3x_1 - x_1^3 - y_1 + \alpha_R S(x_2) \\
\dot{y}_1 &= \varepsilon (\lambda + \gamma \tanh(\beta x_1) - y_1) \\
\dot{x}_2 &= 3x_2 - x_2^3 - y_2 + \alpha_R S(x_1) \\
\dot{y}_2 &= \varepsilon (\lambda + \gamma \tanh(\beta x_2) - y_2) \\
S(x) &= \left[ 1 + \exp(\kappa (\theta - x)) \right]^{-1}
\end{align*} \]

The value \( \alpha_R \) is the coupling strength and the interaction term is a sigmoid that mimics excitatory synaptic coupling. The value of \( \kappa \) modifies the steepness of this sigmoid and we use \( \kappa \gg 1 \). Increasing the value of \( \alpha_R S(x) \) results in a raise of the x-nullcline, \( \dot{x}_i = 0 \).

For small values of \( \varepsilon \), motion in the x-direction occurs quickly and an oscillator is said to "jump" between the left and right branches of the cubic. When an oscillator jumps up from the left to the right branch, it crosses the threshold of the interaction term, \( \theta \), and sends "excitation" to the other oscillator. Thus the interaction is either on or off depending on the positions of the oscillator. When an oscillator receives excitation, its x-nullcline rises by an amount \( \alpha_R \). This excited oscillator then exhibits dynamics based on its modified phase space. The three pertinent nullclines for this system are pictured in Figure 67.

The pertinent values of the x-nullclines are the y-values of their local extrema, which are denoted by the lower left knee (LLK) and the lower right knee (LRK) for the unexcited x-nullcline, and the upper left knee (ULK) and the upper right knee (URK) for the excited nullcline. The values of the extrema for the x-nullclines given in (A.2) are

\[ LLK = (LLK_x, LLK_y) = (-1, -2) \]
Figure 67. A plot of the nullclines and the synchronous limit cycle of a relaxation oscillator defined in (A.2). The dotted cubics are the excited and unexcited x-nullclines, and the dash-dot curve is the y-nullcline. The thick solid curve represents the synchronous limit cycle for a pair of oscillators, which is the result of numerical calculation. The parameters used are $\alpha_R = 2$, $\theta = -0.5$, $\kappa = 5000$, $\lambda = 8$, $\gamma = 12$, $\varepsilon = 0.005$, and $\beta = 1000$.

\[
\begin{align*}
LRK &= (LRK_x', LRK_y) = (1, 2) \\
ULK &= (LLK_x', LLK_y + \alpha_R) \\
URK &= (LLK_x', LLK_y + \alpha_R)
\end{align*}
\]

A basic description of the behavior of (A.2) now follows. Let the oscillators be denoted by $O_1$ and $O_2$. Let both oscillators begin on the lower left branch (LLB), with $y_2 > y_1$. We assume that the time an oscillator spends travelling along LLB is longer than the time an oscillator spends on the upper right branch (URB). Because the motion is counter-clockwise along the limit cycle, $O_1$ leads $O_2$. The leading oscillator, $O_1$, will reach $LLK_y$ first, and jump up to the lower right branch (LRB). Since $O_1$ has crossed the threshold, $\theta$, of the interaction term, $O_2$ will now receive excitation. There are three main classes of trajectories that arise dependent on the position of $O_2$ on LLB. If $O_2$ is below $LLK_y + \alpha_R$ it will jump up to URB. When $O_2$ crosses the interaction threshold, $O_1$ will
hop from LRB to URB. This trajectory is shown in Figure 68A and Figure 68B. This leads to a contraction in the time difference between the two oscillators. It can be shown that the time difference between the two oscillators on the left branch is greater than the time difference between the oscillators after they have jumped to the right branch. Therefore, the interaction has caused the time difference between the oscillator to shrink. Somers and Kopell [Somers and Kopell, 1993] refer to this as a compression. This compression occurs twice during each period, once for the jump up and again during the jump down, and leads to a geometric decrease in the time difference between the two oscillators.

If, however, $O_2$ is above $LLK_y + \alpha_R$ when $O_1$ jumps up, $O_2$ will hop to the upper left branch (ULB). Its motion will continue along ULB until it reaches $LLK_y + \alpha_R$, at which time it will jump up to URB. This case is shown in Figure 68C and Figure 68D. It can be shown that this trajectory also results in a decrease in the time difference between the two oscillators.

There is a third class of trajectories that is shown in Figure 68E and Figure 68F. Here, $O_2$ is above $LLK_y + \alpha_R$ so that $O_1$ jumps up and traverses LRB before $O_2$ reaches ULK. $O_2$ hops from LLB to ULB and then back to LLB while $O_1$ traverses LRB. For this class of trajectories the time difference between the oscillators decreases only if the coupling strength is above a critical value. Figure 68F indicates that the oscillators become synchronous. Figure 69A displays a trajectory for initial conditions similar to Figure 68D, but with a coupling strength less than the critical coupling strength. A desynchronous solution results.
Figure 68. The trajectories of the three cases that lead to synchrony in a pair of coupled oscillators. In (A), (B), and (C) the first oscillator to jump is given by the dotted line and the second is denoted by the solid line. (A), (B) and (C) display the evolution of the system in x-y space. (D), (E), and (F) display the x-activities of both oscillators as a function of time. The parameters used are the same as in Figure 67.
Figure 69. An example of a desynchronous solution that arises because the coupling strength is not large enough. The first oscillator to jump is given by the dotted line and the second is denoted by the solid line. (A) displays the evolution of the system in x-y space, and (B) displays the x-activities of both oscillators as a function of time. The coupling strength used was $\alpha_R = 0.8$ with the other parameters as in Figure 67.
APPENDIX B

ANALYSIS OF A PAIR OF RELAXATION OSCILLATORS WITH TIME DELAYS

For regions II and III in Figure 42, we show, in the singular limit, that as system (4.3) evolves, the time difference between the oscillators decreases. In region IV, we find that the time difference between the oscillators decreases only if the coupling strength is above a certain value, which we derive. Calculating how the time difference between the oscillators changes involves both 'jump-up' and 'jump-down' cases. The jump-up case is analyzed in Section B1, while the jump-down case is analyzed in Section B2. Analysis in both Appendices is for time delays $0 \leq \tau < \tau_{RM}/2$.

B1 Left Branch

Region II

In Region II, $O_1$ jumps up, and the initial position of $O_2$ is such that when it receives excitation at time $\tau$ later, it jumps up directly to URB. This activity is displayed in Figure 43B. This region is bounded by $\tau < t_0 \leq \tau_1 + \tau$, where we use $t_0$ to denote the initial time difference between the two oscillators. Assuming that $O_1$ jumps up at time $t = 0$, and using (4.8) and (4.9), the positions of $O_1$ and $O_2$ at time $\tau$ are given by
\[ y_1(\tau) = (LLK_y - \lambda - \gamma) e^{-\tau} + \lambda + \gamma = c_1 e^{-\tau} + \lambda + \gamma \quad \text{(B.1)} \]

\[ y_2(\tau) = (y_2(0) - \lambda + \gamma) e^{-\tau} + \lambda - \gamma \quad \text{(B.2)} \]

We rewrite \( y_2(0) \) in terms of \( t_0 \), yielding

\[ (LLK_y - \lambda + \gamma) e^{t_0} = c_2 e^{t_0} = (y_2(0) - \lambda + \gamma) \quad \text{(B.3)} \]

Using (B.3), we rewrite (B.2) as

\[ y_2(\tau) = c_2 e^{t_0 - \tau} + \lambda - \gamma \quad \text{(B.4)} \]

To find the time difference between the oscillators after they have jumped up to the active phase, \( t_1 \), we use (4.9) to write

\[ y_2(\tau) = (y_1(\tau) - \lambda - \gamma) e^{-\tau_1} + \lambda + \gamma \quad \text{(B.5)} \]

substituting (B.1) and (B.4) into (B.5) yields

\[ c_2 e^{t_0 - \tau} - 2\gamma = c_1 e^{-\tau - t_1} \quad \text{(B.6)} \]

We use (B.6) to write \( t_1 \) as a function of the initial time difference, \( t_0 \),

\[ t_1 = \log \left[ \frac{c_1 e^{-\tau}}{c_2 e^{t_0 - \tau} - 2\gamma} \right] = g(t_0) \quad \text{(B.7)} \]

This equation arises when the order of the oscillators has been switched, i.e. \( O_2 \) leads \( O_1 \). Only in this case can the time difference between the oscillators become larger than \( \tau \). It can be shown that initial conditions in region II always map into the analogous region on the upper right branch, called region \( \Pi_R \). The equation for determining the time difference between the oscillators after the jump-down to the silent phase is given in (B.44). Using both (B.7) and (B.44) we can explicitly write the time difference between the oscillators after they return to the silent phase, \( t_2 \), as a function of the initial time difference, \( t_0 \).
After some tedious algebra it can be shown that $t_0 > t_2$ for all values of $t_0 > 0$ in region II.

**Region III**

We now examine region III, which is defined by

$$\tau_1 + \tau < t_0 < \tau_1 + \tau_{RM} - \tau$$  \hspace{1cm} (B.9)

where $\tau_{RM}$ is given in (4.13) and $\tau_1$ is given in (4.14). In this region, $O_1$ jumps up at time $t = 0$ and $O_2$ receives excitation at a time $\tau$ later. $O_2$ is far up enough on LLB such that it hops to ULB before jumping up to URB. Typical trajectories for a pair of oscillators in this region are displayed in Figure 43C. In this case we calculate the positions of the oscillators as follows,

$$y_1(t_0 - \tau_1) = (LLK_y - \lambda - \gamma)e^{\tau_1 - t_0} + \lambda + \gamma = c_1 e^{\tau_1 - t_0} + \lambda + \gamma$$  \hspace{1cm} (B.10)

$$y_2(t_0 - \tau_1) = LLK_y + \alpha_R$$  \hspace{1cm} (B.11)

To find the time difference between the oscillators on the active phase, $t_1$, we use (4.9) to write

$$c_1 e^{\tau_1 - t_0} = (LLK_y + \alpha_R - \lambda - \gamma)e^{-\tau_1} = c_5 e^{-\tau_1}$$  \hspace{1cm} (B.12)

We use (B.12) to write $t_1$ as a function of the initial time difference, $t_0$,

$$t_1 = t_0 - \tau_1 - \tau_s$$  \hspace{1cm} (B.13)

where

$$\tau_s = \log\left(\frac{c_1}{c_5}\right)$$  \hspace{1cm} (B.14)
In this case it can be shown that the values of $t_1$ can be in both regions $II_R$ and $III_R$. We do not examine region $II_R$ as these time differences can be shown to always map to region $II$, and then the time difference between the oscillators always decreases as discussed previously. When now examine the time difference between the oscillators when they map from region $II$ to region $III_R$. Using (B.13) and (B.49) we write the time difference between the oscillators after they have both returned to the silent phase, $t_2$, as

$$t_2 = t_0 - \tau_1 - \tau_5 - \tau_2 - \tau_4$$

(B.15)

The values of $\tau_2$ and $\tau_4$ arise from the analysis of the jump-down and are given in (B.41) and (B.50) respectively. We examine what values of $t_0$ result in a value of $t_1$ that is in region $III_R$, or

$$t_1 > \tau_2 + \tau$$

(B.16)

$$t_0 - \tau_1 - \tau_5 > \tau_2 + \tau$$

(B.17)

$$t_0 > \tau_1 + \tau_5 + \tau_2 + \tau$$

(B.18)

If $t_2$ is positive, then (B.15) shows that the time difference between the oscillators after a single period has decreased. However, if $t_2$ is negative, we must test if it is possible for $|t_2| > t_0$. We examine the following inequality,

$$t_2 = t_0 - \tau_1 - \tau_5 - \tau_2 - \tau_4 > -t_0$$

(B.19)

$$2t_0 > \tau_1 + \tau_5 + \tau_2 + \tau_4$$

(B.20)

Using (B.20) and the minimum value of $t_0$, from (B.18), results in

$$2(\tau_1 + \tau_5 + \tau_2 + \tau) > \tau_1 + \tau_5 + \tau_2 + \tau_4$$

(B.21)

$$\tau_1 + \tau_5 + \tau_2 + 2\tau > \tau_4$$

(B.22)
Since $\tau_1 > \tau_4$, (B.22) is always true, and therefore $|t_2| < t_0$. Thus, the oscillators in region III always experience a decrease in the absolute value of their time difference after jumping up and down.

**Region IV**

We now examine region IV. The last case we examine on LLB is for initial conditions such that $O_1$ jumps up to URB and down to LLB, while $O_2$ remains on the silent phase (see Figure 43D). This region is defined by the following bounds,

$$\tau_1 + \tau_{RM} + \tau < t_0 \leq \tau_{LLB} - \tau$$  \hspace{1cm} (B.23)

where $\tau_{LLB}$ is given in (4.11). The leading oscillator, $O_1$, jumps up at time $t = 0$, and the positions of the oscillators after $O_1$ traverses LRB are

$$y_1(\tau_{RM}) = LRK_y$$  \hspace{1cm} (B.24)

$$y_2(\tau_{RM}) = c_2 e^{t_0 - \tau_{RM}} + \lambda - \gamma$$  \hspace{1cm} (B.25)

To find the time difference between the oscillators when they are both on the silent phase, $t_2$, we use (4.8) to write

$$LRK_y = c_2 e^{t_0 - \tau_{RM} - t_2} + \lambda - \gamma$$  \hspace{1cm} (B.26)

We use (B.26) to write $t_2$ as a function of $t_0$,

$$t_2 = t_0 - \tau_6 - \tau_{RM}$$  \hspace{1cm} (B.27)

with

$$\tau_6 = \log\left(\frac{c_4}{c_2}\right)$$  \hspace{1cm} (B.28)
If $t_2$ is positive, then a decrease in the time difference between the oscillators occurs. However, if $t_2$ is negative, then $O_2$ leads $O_1$, and we must check if $|t_2| > t_0$. We examine the following equation

$$
\tau_6 + \tau_{RM} - t_0 < t_0 \quad (B.29)
$$

$$
t_0 > \frac{\tau_6 + \tau_{RM}}{2} \quad (B.30)
$$

Using the minimum value of $t_0$ in region IV, the constraint (B.30) becomes

$$
2(\tau_1 + \tau_{RM} + \tau) > \tau_6 + \tau_{RM} \quad (B.31)
$$

or,

$$
\tau_6 < 2\tau_1 + \tau_{RM} + 2\tau \quad (B.32)
$$

$$
\frac{c_4}{c_2} < \left( \frac{c_6}{c_2} \right)^2 \frac{c_4}{c_3} e^{2\tau} \quad (B.33)
$$

$$
c_6^2 = (c_2 + \alpha_R)^2 > \frac{c_2 c_3 c_4}{c_1} e^{-2\tau} \quad (B.34)
$$

We rewrite (B.34) as a restriction on the coupling strength,

$$
\alpha_R > \sqrt[\sqrt[\sqrt{\frac{c_2 c_3 c_4}{c_1}} e^{-\tau} - c_2} \quad (B.35)
$$

The above condition puts a limiting value on the minimum value of $\alpha_R$. Below this value for the connection weight it is possible for $|t_2| > t_0$ and neutrally stable desynchronous solutions can result.
There is a part of region V that juts between region IV and region III. In region V, it is possible for antiphase solutions to arise dependent on the initial conditions, the time delay, and the coupling strength. We examine whether a pair of oscillators with initial conditions in region IV will automatically map to region III, without entering region V. To test this we make the following statement,

\[ t_2 = \tau_6 + \tau_{RM} - t_0 < \tau_1 + \tau_{RM} - \tau \]  (B.36)

\[ \tau_6 - \tau_1 + \tau < t_0 \]  (B.37)

Using (B.37) with the smallest value that \( t_0 \) can take in region IV, we write

\[ \tau_6 - \tau_1 + \tau < \tau_1 + \tau_{RM} + \tau \]  (B.38)

\[ \tau_6 - \tau_{RM} < 2\tau_1 \]  (B.39)

\[ \alpha_R > \sqrt{\frac{c_4c_3}{c_1}} - c_2 \]  (B.40)

If condition (B.40) is satisfied then the oscillators whose initial conditions are in region IV will not map into region V. We note that if condition (B.35) is satisfied, then automatically, (B.40) is satisfied. Thus for coupling strengths that result in loose synchrony, a pair of oscillators in region IV will never map to region V. Also, we note that it is not possible for \( O_1 \) to make two traversals of LRB because the maximum possible \( y \)-value for \( O_2 \) is \( LRK_y + \alpha_R \).

If constraints (B.35) and the constraint derived in Appendix B, (B.44), are satisfied then the oscillators whose initial time difference is in regions II-IV of Figure 42, will eventually have a time difference of less than or equal to the time delay, i.e. they will be loosely synchronous.
B2 Right Branch

We calculate how the time difference between the oscillators changes as they jump down from the active phase to the silent phase. We label the two regions II\(_R\) and III\(_R\) because of their correspondence to regions II and III of Figure 42. No other trajectories are possible since we have assumed that the fastest branch of the system is LRB.

We assume that \(O_1\) jumps down first, at time \(t = 0\), then \(O_2\) ceases to receive excitation at time \(\tau\) and jumps down to LLB (Figure 43E). The time difference between the oscillators in region II\(_R\) is bounded by \(\tau < t_1 \leq \tau_2 + \tau\), where

\[
\tau_2 = \log \left( \frac{c_3}{c_7} \right) \tag{B.41}
\]

The positions of the oscillators immediately after the jump-down are given by

\[
y_1(\tau) = c_8 e^{-\tau} + \lambda - \gamma \tag{B.42}
\]

\[
y_2(\tau) = c_7 e^{t_1 - \tau} + \lambda + \gamma \tag{B.43}
\]

The time difference between the oscillators after they are both on the silent phase, \(t_2\), is given by

\[
t_2 = \log \left[ \frac{c_8 e^{-\tau}}{c_7 e^{t_1 - \tau} + 2\gamma} \right] = f(t_1) \tag{B.44}
\]

It can be shown that the oscillators whose initial conditions are in region II\(_R\) always map to region II of Figure 42.

Region III\(_R\)

The second case to examine is the region

\[
\tau_2 + \tau < t_1 \leq \tau_2 + \tau_{RM} - \tau \tag{B.45}
\]
where $\tau_{RM}$ is defined in (4.13). In this region, $O_1$ jumps down, and the initial separation between the oscillators is such that $O_2$ hops to LRB before jumping down to LLB. Trajectories for a pair of oscillators in this region are shown in Figure 43F. The positions of the oscillators when they are both on LLB are given by

$$ y_1(t_1 - \tau_2) = (LRK_y + \alpha_R - \lambda + \gamma) e^{\tau_2 - \tau_1} + \lambda - \gamma = c_8 e^{\tau_2 - \tau_1} + \lambda - \gamma $$  \hspace{1cm} (B.46)

$$ y_2(t_1 - \tau_2) = LRK_y $$  \hspace{1cm} (B.47)

To find the time difference between the oscillators when they are both on the silent phase, $t_2$, we use (4.8) to write

$$ c_8 e^{\tau_2 - \tau_1} = c_4 e^{-t_2} $$  \hspace{1cm} (B.48)

resulting in

$$ t_2 = t_1 - \tau_2 - \tau_4 $$  \hspace{1cm} (B.49)

where

$$ \tau_4 = \log \left( \frac{c_8}{c_4} \right) $$  \hspace{1cm} (B.50)

Other trajectories can arise during the jump-down, but not with the assumptions that LRB is the fastest branch in the system. This assumption implies that the following condition must be true,

$$ \tau_{RM} < \tau_9 $$  \hspace{1cm} (B.51)

where

$$ \tau_9 = \log \left( \frac{c_8}{c_6} \right) $$  \hspace{1cm} (B.52)
From condition (B.51) we derive the following bound on the coupling strength,

\[
\frac{c_1}{c_3} < \frac{c_4 + \alpha_R}{c_2 + \alpha_R} \tag{B.53}
\]

\[
\alpha_R < \frac{c_1 c_2 - c_3 c_4}{c_3 - c_1} \tag{B.54}
\]
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