

SYNCHRONIZATION OF PULSE-COUPLED OSCILLATORS¹

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Abstract

I have studied the synchronization of pulse-interacting oscillators, coupled in a network. Undisturbed, an oscillator will fire a pulse at regular intervals. When receiving a pulse, the time until the next firing is delayed according to phase dependant activation potential which is strictly increasing and concave down. Assuming that the oscillators have the same intrinsic firing frequency, and that the total input to each is equal, there exists a synchronized state where all oscillators fire at the same time. By introducing a perturbation of this state, and constructing a linearized map for the perturbation, the synchronized state is showed to be stable. Numerically, the perturbation is shown to approach the synchronized state in different networks.

Oppsummering

Jeg har studert synkroniseringen av pulskoblede oscillatorer i nettverk. Når en oscillator står uforstyrret, sender den ut pulssignaler med jevne mellomrom. Når oscillatoren mottar en puls, blir tiden til neste pulsavfiring forsinket avhengig av et aktiveringspotensial som er strengt økende og konkavt ned. Dersom man antar at oscillatorene har samme egenfrekvens, og at den totale koblingsstyrken inn til hver av oscillatorene er den samme, eksisterer det en synkronisert tilstand hvor alle oscillatorer sender ut pulser samtidig. Ved å introdusere en pertubasjon av denne tilstanden, og konstruere en lineær iterativ funksjon for pertubasjonen, blir det vist at den synkroniserte tilstanden er stabil. Pertubasjonen blir vist numerisk å gå mot den synkroniserte tilstanden i forskjellige nettverk.

At the heart of the universe is a steady, insistent beat: the sound of cycles in sync. It pervades nature at every scale from the nucleus to the cosmos. Every night along the tidal rivers of Malaysia, thousands of fireflies congregate in the mangroves and flash in unison, without any leader or cue from the environment. Trillions of electrons march in lockstep in a superconductor, enabling electricity to flow through it with zero resistance. In the solar system, gravitational synchrony can eject huge boulders out of the asteroid belt and toward earth; the cataclysmic impact of one such meteor is thought to have killed the dinosaurs. Even our bodies are symphonies of rhythm, kept alive by the relentless, coordinated firing of thousands of pacemaker cells in our hearts. In every case, these feats of synchrony occur spontaneously, almost as if nature has an eerie yearning of order.

Steven Strogatz in the preamble of Sync[20]

Contents

1	Introduction	1
1.1	Self-organizing oscillators	1
1.2	A mathematical model for spontaneous order	3
1.3	The Kuramoto model	4
1.4	Pulse coupled oscillators	4
1.5	Networks	5
1.5.1	The adjacency matrix	6
1.5.2	Direction	6
1.5.3	Weight	6
1.5.4	Degree	6
1.5.5	Connectivity	7
2	A model for pulse-coupled oscillators	8
2.1	The synchronous state	9
2.2	A perturbation and its stroboscopic map	10
2.3	A first order approximation	11
2.4	Stability analysis	12
2.4.1	Properties of the transition matrix	12
2.4.2	Stability for strongly connected networks	14
2.4.3	Using a leaky fire-and-integrate potential	15
3	Numerical analysis	16
3.1	Zachary	16
3.2	Erdős-Rényi networks	21
3.3	AS network	25
4	Discussion and conclusions	28
A	Program listing	A-1

Chapter 1

Introduction

How can thousands of fireflies along the tidal rivers of Malaysia flash in perfect synchrony? For many years, the notion that thousands of insects could be capable of coordinating their flashing and synchronize, was hard to believe. Often discarded as tall tales or optical illusions. One observer, Phillip Laurent, wrote in 1917

Some twenty years ago I saw, or thought I saw, a synchronal or simultaneous flashing of fireflies (*Lampyridse*). I could hardly believe my eyes, for such a thing to occur among insects is certainly contrary to all natural laws. However, I soon solved the enigma. The apparent phenomenon was caused by the twitching or sudden lowering and raising of my eyelids. The insects had nothing whatsoever to do with it.[11]

Other explanations varied from synchrony by accident, fireflies having a *sense* of rythm, sensitivity of changes in airpressure or a single pacemaker fly setting the pace of the rest[5, 18].

1.1 Self-organizing oscillators

In 1961, the mathematician Norbert Wiener wrote in his second edition of his book *Cybernetics*[24] about the alpha rhythm of the brain. The alpha rhythm is a 8 – 12 Hz wave pattern commonly detected by electroencephalography¹. Wiener was theorising that the alpha rythm was the clock of the brain, beating like a sentral drummer, coordinating the communication much like the clock in a computer. As one neuron alone hardly could serve this purpose, being too imprecise to function as a clock, Wiener instead proposed that the alpha rythm was the result of many cooperating neurons.

¹The recording of electrical activity along the scalp produced by the firing of neurons within the brain.

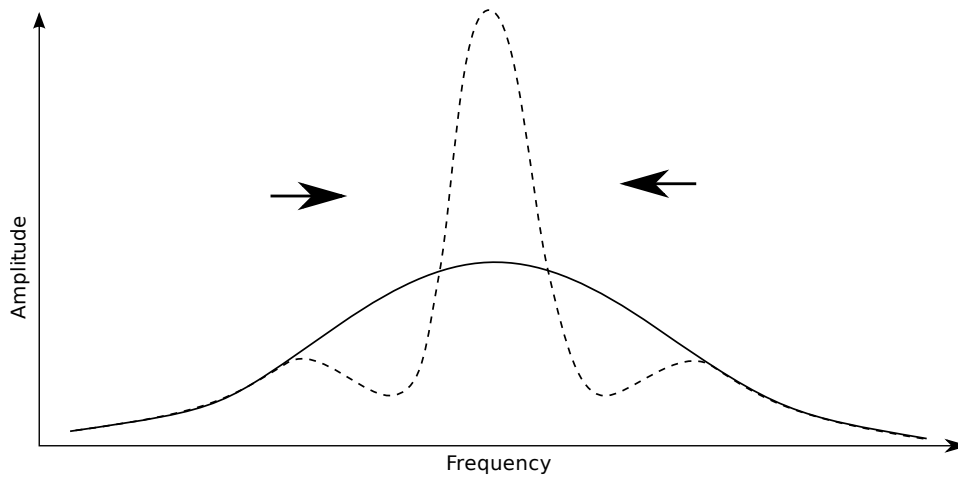


Figure 1.1: Wiener's proposed signature for frequency pulling between oscillators whose frequency is distributed in a bell shape. The solid line illustrates the spectrum when the oscillators are not communicating, and the stippled line illustrates a spectrum where the oscillators pull each other's frequencies into the middle, creating a hole on either side of the peak.

Wiener observed the fact that the alpha waves could be modified by flicking light into the eyes about ten times every second, creating a strong component in the spectrum with the same frequency as the flicking [23]. In other words, an oscillator receiving impulses in a frequency close to its own can be pulled towards the frequency of the external impulses. If each of the neurons are oscillators having their own firing frequency in the area around 10 Hz, while pulling each other's frequencies by sending their pulses to each other, the frequencies - and phases - of the neurons are likely to pull together into "one or more little clumps" [24] in the spectrum.

Wiener proposed a telltale signature for this process. Suppose that the oscillators are distributed around a central frequency in a bell-shaped spectrum. When the oscillators start communicating, the oscillators slow relative to the rest will be stimulated to speed up, while the oscillators running fast relative to the rest will be slowed down. As most oscillators already are in the middle of the spectrum, the oscillators on either side will be drawn into the middle. As the consensus in the middle grows stronger, more oscillators on the flanks are drawn in. However, some oscillators are too far away from the center to be influenced, creating shoulders on either side of the peak. See figure 1.1.

With his theory of frequency pulling, Wiener suggested how many imprecise oscillators could self-organize to make one precise, as if they were possessed by a central governor. To validate his theory, Wiener proposed to

study the synchronous flashing of fireflies or similar phenomena in nature like the synchronous chirping of crickets. He contended that the synchronous flashing of many Asian fireflies was too marked to be put down to human optical illusion, and urged biologists to perform a precise study of fireflies, looking for his signature spectrum.

In the last half of the 1960s, the biologist John Buck and his wife Elisabeth systematically studied fireflies in Thailand. Releasing fireflies—*Pteroptyx malacca*—into a dark room, they watched how local groups of up to a dozen flies gradually started to synchronize until they flashed in perfect synchrony[4]. Subjecting fireflies to artificial flashing light, they found that individual fireflies will shift their rhythm in a predictable manner depending on the phase difference between the firefly and the light. They suggested a mechanism for synchronization were each individual firefly adjust their rhythm according signals received from their neighbours while at the same time sending signals stimulating their neighbours

1.2 A mathematical model for spontaneous order

Wiener never developed a mathematical theory for his hypothesis. But in 1965, the college student Art Winfree found a feasible approach to describe the process mathematically[25]. In his model, Winfree described each oscillator with a sensitivity and an influence function. As their names imply, the influence function describes the influence of an oscillator on the rest, while the sensitivity function describes the oscillators sensitivity for signals from other oscillators.

These functions depend on the phase of the oscillator. For a firefly, the influence function would reflect the light the firefly emits, spiking for each lightpulse, being zero in periods of darkness. The sensitivity of the firefly might be a little more subtle, but one would expect it to reflect how the firefly is influenced by signals around its own frequency. Perhaps by being more sensitive close to its own firing, and less sensitive further away.

With a large number of non-linear functions describing the behavior of the oscillators, Winfree did not develop explicit solutions. But by conducting numeric experiments², Winfree could observe how some combinations of sensitivity and influence functions resulted in chaos while other combinations resulted in synchronization no matter where the individual phases started relative to each other.

Through numerical experiments Winfree also observed that, for the oscillators to synchronize, the frequencies needed to be fairly homogenous. Winfree discovered that, as soon as the spread in frequency came beneath a certain threshold, the oscillators locked their frequencies to each other and synchronized.[20].

²Using an IBM 7094[25].

1.3 The Kuramoto model

In the 1970s, a Japanese physicist by the name Yoshiki Kuramoto was trying to penetrate the hard shell of multiple coupled non-linear equations which governed the problem of group synchronization. Following a strong intuition, Kuramoto proposed an all-to-all sinusoidal coupling for the oscillators[10, 1, 20].

Faced with a set of infinite, non-linear, coupled equations, Kuramoto devised a macroscopic parameter which measured the phase coherence of the oscillator population. With this parameter, Kuromoto was able to replace the all-to-all coupling with mean field quantities: the phase coherence parameter, and the mean phase.

With the mean field approach, Kuramoto could not only see the same threshold for synchronization that Winfree observed in his numerics, he could derive a formula for it.

The Kuromoto modell opened up a new world of research on synchronization, with applications ranging from biology to finance. A recent review, [1], gives a good overview over many such applications.

1.4 Pulse coupled oscillators

In the Kuramoto modell, the interactions between the oscillators are smooth and continous. However, in some cases of self-organization, the interactions take the form of pulses. Some biological systems, like fireflies or neurons, communicate by firing sudden impulses[4, 8].

The interaction in these cases take place in an instant compared to the period of the oscillators. So how does the firefly incorporate these interactions to adjust its own firing closer to the firing signals it receives? How can the *Pteroptyx malaccae* synchronize with a precision in the order of 16 ms, when the reaction time of a firefly is known to be in the order of 50 ms for visual stimuli[4]?

In 1975, C.S. Peskin proposed a model for the self-synchronization of the neurons in the sinustrial node, the pacemaker of the heart[16]. Peskin modelled the pacemaker as a weakly interacting population of "pacemaker" neurons, each with a potential variable x_i , governed by

$$\dot{x}_i = S_0 - \gamma x_i. \tag{1.1}$$

When the potential reached $x_i = 1$, it fired and reset to $x_i = 0$. The firing of one neuron affects the potentials of all the other neurons by bringing them up an amount ε .

Peskin conjectured that this system approaches a state where the neurons fire synchronously, and that this remains true even when the oscillators

are not quite identical. With his model, Peskin was able to show the synchronization of two identical oscillators with small coupling ε and dissipation γ .

In 1990, Mirollo and Strogatz released a paper inspired by Peskin's model [14]. They introduced a more general phase-dependent potential function,

$$x = f(\phi), \tag{1.2}$$

where f is a monotonically increasing and concave down function, and the phase has a constant speed. When an oscillator reaches the firing threshold $x = 1$, it fires and pulls the potential of the other oscillators up an amount ε , as before, but now with an accompanying change in phase.

Starting with two oscillators, they developed a return map for the phase of an oscillator, describing the phase of the oscillator as a function of the phase in the subsequent period. Using the monotonically increasing and concave down properties, they showed that two oscillators would synchronize. Finally, using a technique of absorbing states, where already synchronized oscillators act as one, they showed that the system of N identical oscillators would synchronize for almost any initial conditions.

With this model, Mirollo and Strogatz showed how a population of oscillators could synchronize with simple pulse interactions.

1.5 Networks

The models presented above have all assumed all-to-all connections. In many applications, however, there are limits as to how many other oscillators an oscillator can see or influence. For fireflies, there might be leaves and branches blocking the view. But this does not seem to stop the fireflies from synchronizing through whole trees [5]. As long as a firefly can see one other fly, and this fly can see other flies, the first firefly only needs to synchronize with the firefly it sees, while this fly synchronizes with the other fireflies. They are all connected in a *network*.

A network, in essence, is a number of entities connected to each other. In mathematical literature, the model of a network is called a *graph*. In a graph, the connected entities are *vertices* and the connections *edges*. In physical literature the vertices are often called *nodes*, while the edges are called *links*. The terms *network* and *graph* are often used to describe the same thing, and the difference between them is not always obvious. But often, the term *graph* refers to a purely mathematical object, while *network* refers to a real, naturally evolving system [17].³

A wide variety of systems are networks, and can be abstracted as a graph. Transport systems, social networks and the synchronizing fireflies are all

³Partial reuse of the corresponding section in [9].

examples of networks. In transport systems, the edges are roads, and the vertices are roadjunctions. In social networks, the vertices are people, and the connections between them are friendships or acquaintances. In our case of the fireflies, each vertex is a firefly, and if they see each others signals, they are connected by an edge—a line of sight.

1.5.1 The adjacency matrix

To describe a network mathematically, the vertices are arranged in a matrix: A network with N vertices is described by an $N \times N$ *adjacency matrix* A , where each entry a_{ij} represents the edge—if any—from vertex j to i . If there is no edge from j to i , then $a_{ij} = 0$. If there is such a connection, then $a_{ij} \neq 0$.

1.5.2 Direction

Notice that a_{ij} describes the edge from j to i . The edges are in general directed, reflecting that—for example—if firefly i sees firefly j , it does not necessarily mean that j can see i . In the case that i sees j , but j does not see i , $a_{ij} \neq 0$ and $a_{ji} = 0$. The convention here is that the column index labels the sender, while the row index labels the receiver: i sees j and receives its light signals.

In many cases, all connections in a network go both ways. If the firefly can see in all directions from where it is sitting, then a clear line of sight from i to j means they both see each other. In that case, the network is *undirected*, and $a_{ij} = a_{ji}$. That is, the adjacency matrix of an undirected network is symmetric.

1.5.3 Weight

So far, we have only been interested in whether there is a connection or not. In the case where it only matters whether there is a connection or not, the convention is to use $a_{ij} = 1$ if there is a connection, and $a_{ij} = 0$ otherwise. But in many cases, we are also interested in the strength, width or *weight* of a connection. This weight might be the width of the road, or the strength of a friendship. In that case, the non-zero elements of the adjacency matrix has a value reflecting the weight of the connection, and the network is *weighted*. Weighted networks are undirected if the weight is the same both ways.

1.5.4 Degree

A much used term in network theory, is the *degree*. The *in-degree* of a vertex is the number of incoming edges to the vertex. While the *out-degree* is the number of outgoing edges from the vertex.

In the case of weighted networks, the degree can sometimes label the total outgoing or incoming weight of a vertex[15]. In this report we will use the term *degree* about the number of in- or outgoing edges.

1.5.5 Connectivity

In the example where one firefly only saw one other firefly, it could still indirectly synchronize with the rest of the network because the firefly it synchronized with, also synchronized with other fireflies it could see. In the network of fireflies, there was a *path* between the first firefly and the rest of the network, so it could indirectly *reach* any other firefly.

However, mapping the connections between fireflies in a tree, one might find that there are several separate groups which does not communicate with each other. In that case, each group is a *component* of the total network in the tree. A *connected component*, is a part of the network—a subnetwork—where all vertices can reach each other. An undirected network consisting of one component is said to be *connected*.

For the case of the directed network, connectivity has a little wider spectrum of possibilities: Imagine a directed network consisting of two connected components, with only one directed link between them. If the network had been undirected, it would have been connected. We call this network *weakly connected*. The term *weakly connected*, applies to any directed network where not every vertex can be reached from every vertex, but the corresponding undirected graph is connected.

A directed network where any vertex is reachable from any vertex is said to be *strongly connected*. In terms of the adjacency matrix, A , the network is strongly connected if for any i and j , there exists a natural number q such that $a_{ij}^{(q)} \neq 0$, where $a_{ij}^{(q)}$ is the (i, j) element of A^q . This means that the adjacency matrix for a strongly connected network is irreducible[3].

Chapter 2

A modell for pulse-coupled oscillators

We will present a mathematical modell of pulse-coupled oscillators based on the Mirollo-Strogatz[14] representation of each oscillator with a phase-variable changed by a concave-down potential function. The model presented is found in papers [22, 21] by Timme, Wolf and Geisel.

Consider a system of N oscillators connected in a directed network. Each oscillator interacts with its neighbours in the network by receiving pulses along its incoming connections and sending pulses along outgoing connections. We will refer to oscillators having input to oscillator i as the *presynaptic* oscillators of i , $\text{Pre}(i)$. Oscillators receiving output from oscillator i will be referred to as the *postsynaptic* oscillators of i , $\text{Post}(i)$

The state of each oscillator i is described by a phase-like variable $\phi_i \in (-\infty, 1]$. As long as no pulses are received by oscillator i , its phase increases uniformly in time,

$$\frac{d\phi_i}{dt} = 1. \quad (2.1)$$

When the phase reaches a firing threshold, defined as $\phi_i(t_{fire}) \geq 1$, the phase is reset to zero, $\phi_i(t_{fire}^+) = 0$, and a pulse is fired along the outgoing connections of i , giving the oscillator an intrinsic period $T_{int} = 1$.

Due to a finite propagation speed of the pulse, the postsynaptic oscillators of i receives the pulse a time τ later. The pulse induces a phasechange in the oscillators $j \in \text{Post}(i)$,

$$\phi_j((t_{fire} + \tau)^+) = U^{-1}(U(\phi_j(t_{fire} + \tau)) + \varepsilon_{ji}). \quad (2.2)$$

Here, ε_{ji} is the coupling strenght from i to j . The activation potential, $U(\phi)$, encodes the effect of the pulse and its dependence on the current phase $\phi_j(t_{fire} + \tau)$. The potential we will consider here, is a twice differentiable, monotonically increasing and concave down function. That is,

$$U'(\phi) > 0 \text{ and } U''(\phi) < 0. \quad (2.3)$$

For simplicity, the function is also normalized,

$$U(0) = 0 \text{ and } U(1) = 1. \quad (2.4)$$

The coupling strength between any pair of oscillators i and j , ε_{ji} , can be both positive and negative. Because U is monotonically increasing, a positive coupling strength ε_{ji} corresponds to an *excitatory* coupling. Meaning that a pulse from i to j will advance, or excite, the phase of j such that

$$\phi_j((t_{fire} + \tau)^+) > \phi_j(t_{fire} + \tau). \quad (2.5)$$

A negative coupling strength corresponds to an *inhibitory* coupling,

$$\phi_j((t_{fire} + \tau)^+) < \phi_j(t_{fire} + \tau). \quad (2.6)$$

In this paper, we will look at inhibitorically coupled oscillators, so receiving pulses delays the time to the next firing.

2.1 The synchronous state

Assuming that the coupling strengths in the network are normalized,

$$\sum_{j \in \text{Pre}(i)} \varepsilon_{ij} = \varepsilon \quad \text{for all } i, \quad (2.7)$$

there exists a synchronous state

$$\phi_i(t) = \phi_0(t) \quad \text{for all } i, \quad (2.8)$$

where ϕ_0 is a periodic function, $\phi_0(t + T) = \phi_0(t)$.

With a sufficiently small delay, $\tau < 1$, all oscillators will receive a pulse from all their presynaptic neighbours a time τ after their last firing. As $\partial_t \phi_i = 1$, the phase is at this point $\phi_0 = \tau$. Assuming inhibitory couplings, $\varepsilon < 0$, the total input is guaranteed to be subthreshold, $U(\tau) + \varepsilon < 1$. And so, the phase right after the pulse is received is

$$\alpha := \phi_0(\tau^+) = U^{-1}(U(\tau) + \varepsilon). \quad (2.9)$$

After a time $1 - \alpha$, all oscillators will fire again. In total, the period of this synchronous state is

$$T = \tau + 1 - \alpha. \quad (2.10)$$

2.2 A perturbation and its stroboscopic map

To determine the stability of the synchronous state, we introduce a perturbation to the phases,

$$\boldsymbol{\delta}(0) := \boldsymbol{\delta} = (\delta_1, \dots, \delta_N)^\top, \quad (2.11)$$

where

$$\delta_i = \phi_i(0) - \phi_0(0). \quad (2.12)$$

We assume that the initial perturbations are small, in the sense that

$$\max_i \delta_i - \min_i \delta_i < \tau. \quad (2.13)$$

In other words, all oscillators will fire within a time window smaller than the time it takes for a pulse to reach its postsynaptic oscillators.

Now, to determine how this perturbation evolves, a stroboscopic period- T map of the perturbations will be constructed.

For each oscillator i , the perturbations of its presynaptic neighbours, δ_j where $j \in \text{Pre}(i)$, is labeled according to their size,

$$\Delta_{i,1} \geq \Delta_{i,2} \geq \dots \geq \Delta_{i,k_i}, \quad (2.14)$$

where $k_i = |\text{Pre}(i)|$ is the number of presynaptic oscillators—the incoming degree—for i . The index, $n \in \{1, \dots, k_i\}$, will by this labeling count the order in which signals arrive to oscillator i . So, if $j_n := j_n(i) \in \text{Pre}(i)$ labels the oscillator from which oscillator i receives its n^{th} signal, then

$$\Delta_{i,n} = \delta_{j_n}. \quad (2.15)$$

The perturbation of i itself will be labeled

$$\Delta_{i,0} := \delta_i. \quad (2.16)$$

Using the phase shift function

$$h(\phi, \varepsilon) = U^{-1}(U(\phi) + \varepsilon), \quad (2.17)$$

the time evolution of an arbitrary perturbation satisfying (2.13), starting near $\phi_0(0) = 0$, is calculated according to the scheme in table 2.1.

Starting out with its initial perturbation $\Delta_{i,0}$, the time to threshold for oscillator i is given in the last row of table 2.1,

$$T_i^{(0)} = \tau - \Delta_{i,k_i} + 1 - \beta_{i,k_i}. \quad (2.18)$$

The difference between this time and the period of the synchronized state will offset the phase ϕ_i relative to ϕ_0 in the next period, and so the perturbation of i in the next period is given by

$$\delta_i(T) = T - T_i^{(0)} = \Delta_{i,k_i} + \beta_{i,k_i} - \alpha. \quad (2.19)$$

Table 2.1: Evolution of the phasevariable of oscillator i , ϕ_i , starting at time $t = 0$ with $\phi_0(0) = 0$. The phase ϕ_i is found in the right column at different times t , given in the left column. ϕ_i starts out with its initial perturbation $\phi_i = \phi_0 + \Delta_{i,0} = \Delta_{i,0}$. After a time $\tau - \Delta_{i,1}$, i starts receiving pulse signals from its presynaptic oscillators. The phase after the j^{th} pulse is received is labeled $\beta_{i,j}$. The last time in the table is the time to threshold for oscillator i , $T_i^{(0)} = \tau - \Delta_{i,k_i} + 1 - \beta_{i,k_i}$. The difference between this time and the period of the synchronized state will be the perturbation of i in the next period, $\delta_i(T)$, as $\partial_t \phi_i = 1$ for all i .

t	$\phi_i(t)$
0	$\delta_i =: \Delta_{i,0}$
$\tau - \Delta_{i,1}$	$h(\Delta_{i,0} + \tau - \Delta_{i,1}, \varepsilon_{ij_1}) =: \beta_{i,1}$
$\tau - \Delta_{i,2}$	$h(\beta_{i,1} + \Delta_{i,1} - \Delta_{i,2}, \varepsilon_{ij_2}) =: \beta_{i,2}$
\vdots	\vdots
$\tau - \Delta_{i,k_i}$	$h(\beta_{i,k_i-1} + \Delta_{i,k_i-1} - \Delta_{i,k_i}, \varepsilon_{ij_{k_i}}) =: \beta_{i,k_i}$
$\tau - \Delta_{i,k_i} + 1 - \beta_{i,k_i}$	fire: $1 \mapsto 0$

Where, β_{i,k_i} , is recursively related to $\delta_i(0) = \Delta_{i,0}$ by

$$\beta_{i,m} = h(\beta_{i,m-1} + \Delta_{i,m-1} - \Delta_{i,m}, \varepsilon_{ij_m}), \quad (2.20)$$

with $\beta_{i,0} := \tau$.

2.3 A first order approximation

To determine the local stability, we look at a first order approximation of the map in equation (2.19). Expanding β_{i,k_i} to the first order, with $\Delta_{i,n-1} - \Delta_{i,n} \ll 1$, it can be shown by induction that¹[22]

$$\beta_{i,k_i} \doteq \alpha + \sum_{n=1}^{k_i} p_{i,n-1} (\Delta_{i,n-1} - \Delta_{i,n}), \quad (2.21)$$

where

$$p_{i,n} := \frac{U'(U^{-1}(U(\tau) + \sum_{m=1}^n \varepsilon_{i,j_m}))}{U'(U^{-1}(U(\tau) + \varepsilon))} \quad (2.22)$$

Inserting into equation (2.19), this yields

$$\delta(T) \doteq \Delta_{i,k_i} + \sum_{n=1}^{k_i} p_{i,n-1} (\Delta_{i,n-1} - \Delta_{i,n}), \quad (2.23)$$

¹Using the notation $x \doteq y$ meaning $x = y + \mathcal{O}((\Delta_{i,n-1} - \Delta_{i,n})^2)$

which can be rewritten

$$\delta(T) \doteq p_{i,0}\Delta_{i,0} + \sum_{n=1}^{k_i} (p_{i,n} - p_{i,n-1})\Delta_{i,n}. \quad (2.24)$$

Using $\Delta_{i,n} = \delta_{j_n(i)}$ and $\Delta_{i,0} = \delta_i$, this results in the first order map

$$\delta(T) \doteq A\delta, \quad (2.25)$$

where

$$A_{ij} = \begin{cases} p_{i,n} - p_{i,n-1} & \text{if } j = j_n \in \text{Pre}(i) \\ p_{i,0} & \text{if } j = i \\ 0 & \text{if } j \notin \text{Pre}(i) \cup i \end{cases} \quad (2.26)$$

We will here term the matrix A as the transition matrix, as it transfers the perturbation vector to the next period. The transition matrix is closely related to the adjacency matrix of the underlying network, having (off-diagonal) elements describing the effect of a pulse from j to i where the adjacency matrix has the coupling strength ε_{ij}

Notice that the matrix elements encoding the change in the phase of i due to input from oscillators $j \in \text{Pre}(i)$ will depend on the order in which the pulses from oscillators j arrive to oscillator i . Since the order of arrival in general is different for each iteration of the map (2.25), the stability analysis using this first-order map is a multi-operator problem. That is, the matrix A might change from one iteration to another if the order of the pulses change.

2.4 Stability analysis

Although the transition matrix introduced above describes a deterministic process, in many applications the transition matrix describes transition probabilities between possible states of the system. For these processes, the transition matrix is a stochastic matrix. A stochastic matrix, not to be confused with a random matrix, is a matrix which consists of non-negative real numbers and where the row or column sums are equal to one. A matrix with row sums equal to one is a row stochastic matrix, often just referred to as a stochastic matrix, see for example [3] or [13] for additional details.

2.4.1 Properties of the transition matrix

The row-sum of the transition matrix (2.26) is

$$\sum_{j=1}^N A_{ij} = p_{i,0} + \sum_{n=1}^{k_i} (p_{i,n} - p_{i,n-1}) = p_{i,k_i}. \quad (2.27)$$

Now, looking at equation (2.22), using the normalized coupling strength (2.7),

$$p_{i,k_i} = \frac{U'(U^{-1}(U(\tau) + \sum_{m=1}^{k_i} \varepsilon_{i,j_m}))}{U'(U^{-1}(U(\tau) + \varepsilon))} = 1. \quad (2.28)$$

Because U is a strictly rising and concave down function (2.3),

$$U'(U^{-1}(x_1)) > U'(U^{-1}(x_2)) \quad \text{for all } x_1 < x_2, \quad (2.29)$$

and because all coupling strengths are inhibitory, $\varepsilon_{ij} \leq 0$,

$$p_{i,n-1} < p_{i,n}. \quad (2.30)$$

The strictly rising property furthermore ensures that $p_{i,n} > 0$. Together with $p_{i,k_i} = 1$, this yields

$$0 < p_{i,n \neq 0} \leq 1. \quad (2.31)$$

Looking at the equations (2.30) and (2.31), the nonzero off-diagonal elements of the matrix (2.26) are positive and bounded above by one. The diagonal elements

$$A_{ii} = p_{i,0} = \frac{U'(\tau)}{U'(U^{-1}(U(\tau) + \varepsilon))}, \quad (2.32)$$

are equal for all i . And again, because U is monotonically rising and concave down, they satisfy

$$0 < A_{ii} < 1. \quad (2.33)$$

In total, all transition matrices A are row stochastic matrices. By the Perron-Frobenius theorem, there is therefore a maximum eigenvalue of one, and all other eigenvalues are confined within the unit circle in the complex plane. If furthermore the matrix is irreducible, this maximum eigenvalue is simple[3]. So, for strongly connected networks, the maximum eigenvalue is simple since the corresponding adjacency matrix—and therefore the transition matrix—is irreducible[3]. It is easy to see that the maximum eigenvalue corresponds to a synchronized state where $\delta = c(1, 1, \dots, 1)^\top$, since all rows sum to one. The synchronized state is therefore a fixed state of the linear stroboscopic map, and for strongly connected networks, it is the only fixed state.

With all eigenvalues except the one corresponding to the synchronized state having an absolute value less than one, it should be easy to show through eigendecomposition² that the synchronized state is stable. The transition matrices are however, not symmetric, and does not in general satisfy the spectral theorem, which guarantees that such a decomposition can be done[2]. The stability of a perturbation is therefore determined without the use of spectral decomposition.

²Diagonalizing the transfermatrix with a basis of eigenvectors.

2.4.2 Stability for strongly connected networks

We start by assuming that the perturbation δ is not a synchronous state. We can without loss of generality assume that all the components δ_i are non-negative, because otherwise a phaseshift proportional to the synchronized state $\theta = c(1, 1, \dots, 1)^\top$ can be added to eliminate any negativity. Starting non-negative, the perturbation will stay non-negative for all times as the transition matrix is a non-negative matrix.

We label the maximal component of the perturbation $\delta_M := \max_i \delta_i$, and the second largest $\delta_m := \max_i \{\delta_i \mid \delta_i < \delta_M\}$. We also define the set of maximal components

$$\mathbb{M} := \{j \in \{1, \dots, N\} \mid \delta_j = \delta_M\} \quad (2.34)$$

Using these definitions, we find[22]

$$\delta_i(T) = \sum_{j=1}^N A_{ij} \delta_j \quad (2.35)$$

$$= \sum_{j \in \mathbb{M}} A_{ij} \delta_j + \sum_{j \notin \mathbb{M}} A_{ij} \delta_j \quad (2.36)$$

$$\leq \sum_{j \in \mathbb{M}} A_{ij} \delta_M + \sum_{j \notin \mathbb{M}} A_{ij} \delta_m + \sum_{j \notin \mathbb{M}} A_{ij} \delta_M - \sum_{j \notin \mathbb{M}} A_{ij} \delta_M \quad (2.37)$$

$$= \delta_M \sum_{j=1}^N A_{ij} - (\delta_M - \delta_m) \sum_{j \notin \mathbb{M}} A_{ij} \quad (2.38)$$

$$= \delta_M - (\delta_M - \delta_m) \sum_{j \notin \mathbb{M}} A_{ij}. \quad (2.39)$$

Observe that the maximal component in the next period is going to be smaller than the current if $\sum_{j \notin \mathbb{M}} A_{ij} > 0$,

$$\max_i \delta_i(T) < \delta_M. \quad (2.40)$$

However, if there exist an oscillator k only receiving input from oscillators with maximum components, and which itself has the maximum component, then

$$\delta_k(T) = \max_i \delta_i(T) = \delta_M. \quad (2.41)$$

In the next period, if at least one of the presynaptic oscillators of k no longer has the maximum component, then the condition is no longer fulfilled, and the maximum component of the perturbation will decrease. The only way the presynaptic oscillators of k , can keep the maximum value is if all their presynaptic oscillators also have maximum components. It can be shown[22], that the maximum component will decrease after a maximum

of l periods if all oscillators j , connected to k with a sequence of l or less connections, have components $\delta_j = \delta_M$.

In a strongly connected network, all oscillators are connected with a finite sequence of directed connections, so the maximum component will eventually decrease unless all oscillators have the same value, which corresponds to a synchronized state. Thus, in a strongly connected network, the synchronized state is stable.

2.4.3 Using a leaky fire-and-integrate potential

We have so far used a general description of the potential function, only assuming that the potential function is monotonically increasing, concave down and normalized. We will now consider the leaky integrate-and-fire function

$$U(\phi) = U_{IF}(\phi) = I(1 - e^{-\phi T_{IF}}). \quad (2.42)$$

with $I > 1$ and $T_{IF} = \ln(I/(I - 1))$ to satisfy the normalization. Using a suitably chosen coupling strength,

$$\varepsilon_{ij} = \frac{\varepsilon}{k_i}, \quad (2.43)$$

this function interestingly turns out to result in a single degenerate³ transition matrix with off-diagonal non-zero elements[21]

$$A_{ij} = \frac{1}{Ie^{-\tau T_{IF}} - \varepsilon} \frac{\varepsilon}{k_i}. \quad (2.44)$$

So, choosing the leaky fire-and-integrate function, instead of dealing with multiple transition matrices, we now have a single transition matrix describing the evolution of a perturbation.

Using a similarity transform modelled after [19], the eigenvalues of this transition matrix can be shown to be real if all links are two-way. The matrix A is similar to

$$S = KAK^{-1}, \quad (2.45)$$

with $K_{ij} = \delta_{ij}\sqrt{k_i}$. Performing the multiplications, S has off-diagonal non-zero elements

$$S_{ij} = \frac{1}{Ie^{-\tau T_{IF}} - \varepsilon} \frac{\varepsilon}{\sqrt{k_i k_j}}. \quad (2.46)$$

As can be seen, this matrix is symmetric provided that any linked oscillators are linked both ways, that is $A_{ij} \neq 0$ implies $A_{ji} \neq 0$.⁴ In that case, the transition matrix is similar to a symmetric matrix, and its eigenvalues can be guaranteed to be real.

³With respect to the pulseorder. I.e. only dependant of underlying network topology.

⁴Note that this does not imply that the network is undirected, because the coupling strength might not be the same both ways.

Chapter 3

Numerical analysis

Using a perturbation with uniformly distributed components we will iterate the map (2.25) on different networks. We will use the leaky fire-and-integrate function (2.42) as the activation potential, and normalize the coupling according to (2.43).

3.1 Zachary

A classic illustrative network is the Zachary network, shown in figure 3.1. The network is a mapping of the communications in a 34 member karate-club done by the sociologist Wayne Zachary in the 70s[27]. By just mapping the communication in the club, Zachary could observe an evolving conflict between the trainer and the administrator: In the communication map, he saw how the club gradually divided into two distinct clusters centered around the two.

In the context of pulse-coupled oscillators, one might think of the members of the karate-club as fireflies: Exchanging the verbal communication with flashing, and the two clusters with two loosely separated firefly communities, much like the ones that settled in Buchs ceiling[4]. We assume that all connections in this network are two-way, so any connection between two fireflies mean they both see each others flashing.

Using coupling strengths (2.43), the amount any firefly—being of a species we here freely describe—will adjust its phase to respond to a flash depends on how many other fireflies it can see. The total normalized coupling strength $\varepsilon = \sum_j \varepsilon_{ij}$ is set to $\varepsilon = -0.2$ for all fireflies. The time delay for a flash to affect the phase is set to $\tau = 0.05$, or five percent of the fireflies intrinsic period, $T_{int} = 1$. The time delay reflects the fireflies reaction time, from it sees a flash until the phase is adjusted. For the activation potential, we use the fire-and-integrate function (2.42), with $I = 1.1$.

The phases of the fireflies are shifted from a synchronized state $\phi_i = \phi_0$ by a perturbation with components uniformly distributed between 0 and

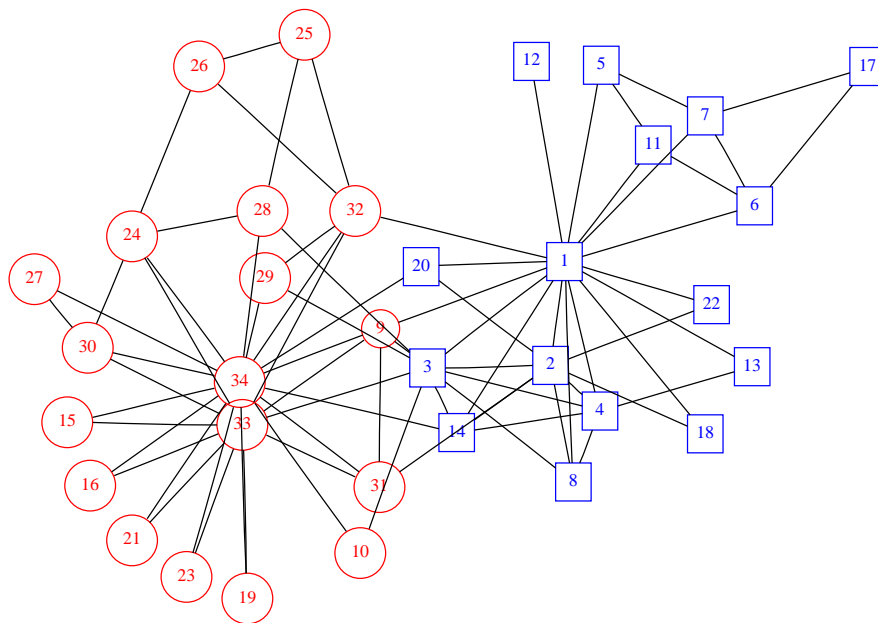


Figure 3.1: The Zachary network, a mapping of the communication in a 34 member karateclub done by the sociologist W.W. Zachary. A conflict in the club divided it in two distinct clusters centered around the administrator (node 34) and the trainer (node 1). The data for the network can be found at [26]. The figure, found in [19], was provided by Simonsen.

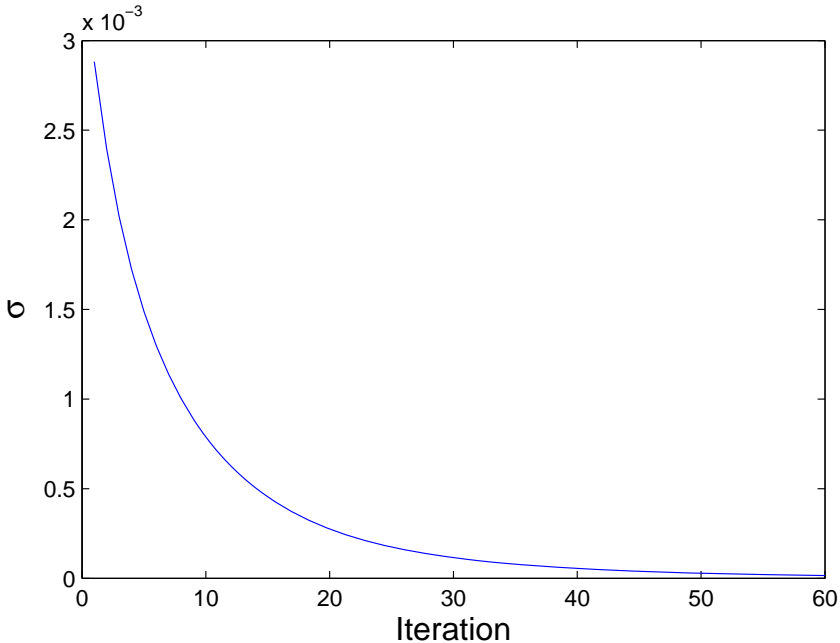


Figure 3.2: The evolution of standard deviation in the phases of pulse-oscillators in the Zachary network, using the map (2.25). The phases are originally shifted by a perturbation uniformly distributed between 0 and 0.01. The standard deviation asymptotically moves towards zero as the oscillators synchronize.

0.01. Evolving the map (2.25), the standard deviation of the fireflies phases, $\sigma = \sqrt{\frac{1}{N} \sum_i (\delta_i - \bar{\delta})^2}$, is plotted in figure 3.2. As can be seen, the standard deviation asymptotically moves towards zero, and the fireflies synchronize.

In figure 3.3, we have plotted the eigenvalues of the transition matrix corresponding to the initial perturbed state of the Zachary network. As expected, the eigenvalues are real. We expect the second largest eigenvalue to determine the speed of convergence towards the synchronous state, as it corresponds to the slowest decaying eigendirection.

In figure 3.4, we have plotted the difference between the largest and smallest element of the perturbation. After some time, the slowest decaying eigendirection seems to dominate, with the slope corresponding to a multiplier of 0.9778, close to the second largest eigenvalue $\lambda_2 = 0.9775$

Taking a closer look at individual nodes, or fireflies, in the Zachary network, the phase of node 3, 10 and 34 is plotted in figure 3.5. As can be seen in figure 3.1, firefly 10 can only see firefly 3 and 34. The phase of fly 10 starts a distance away from the phases of 3 and 34. Instead of uniformly converging towards the final synchronized state, node 10 first moves quickly

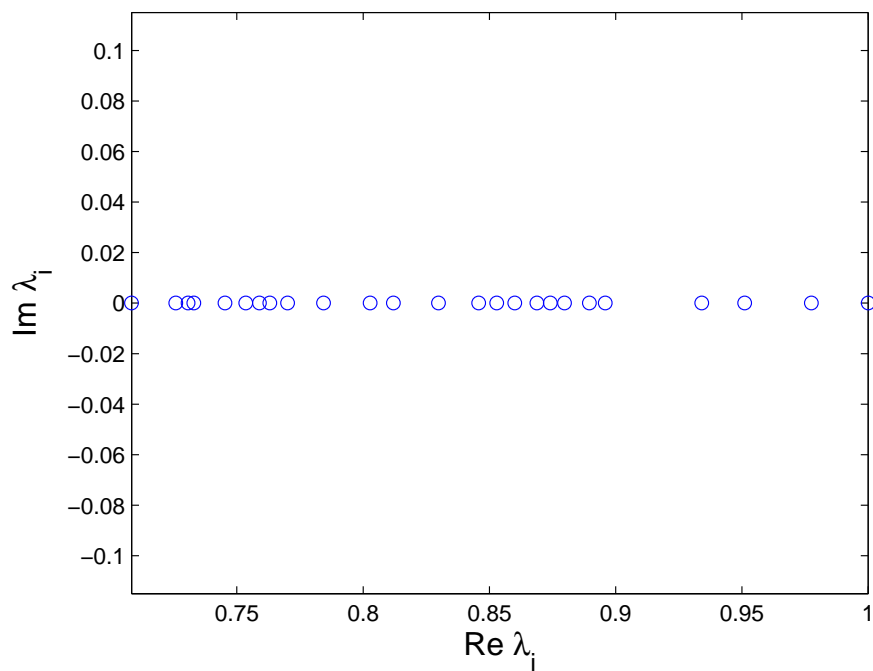


Figure 3.3: Eigenvalues of the transition matrix in the Zachary network. All eigenvalues are real, as expected for a network with two-way connections. As can be seen, there is a maximum eigenvalue $\lambda_1 = 1$. All other eigenvalues are less than one, so their corresponding eigendirections will decay with the iterations of (2.25).

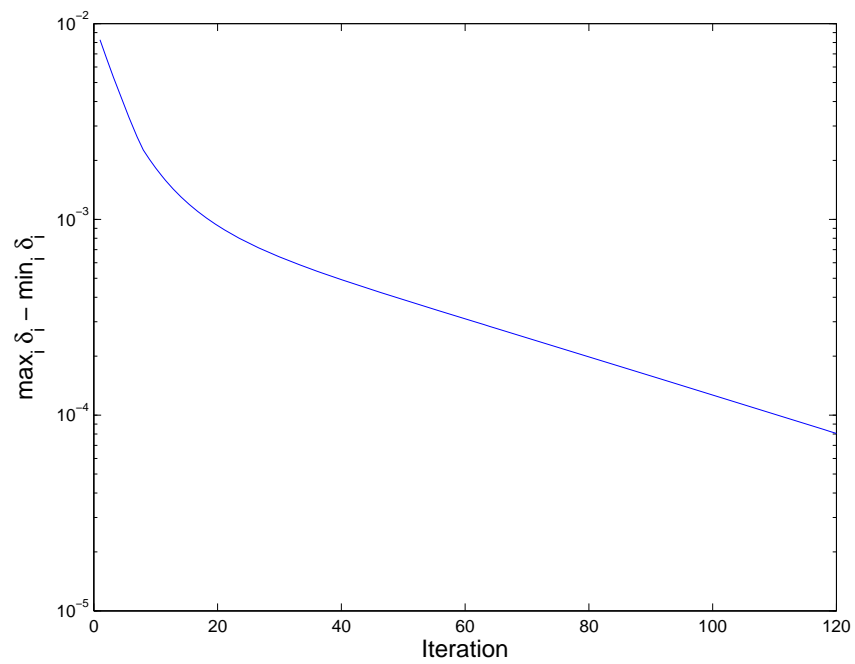


Figure 3.4: The difference between the largest and smallest perturbation in the Zachary network as the map (2.25) is iterated. After 40 iterations, the slowest decaying eigendirection seems to dominate, with the slope corresponding to a multiplier close to the second largest eigenvalue.

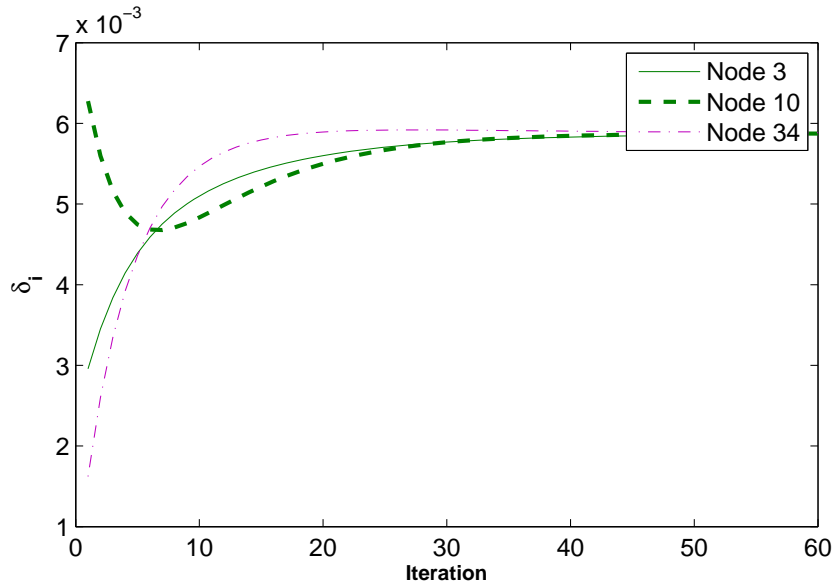


Figure 3.5: Caption

to meet the phases of the only other fireflies it sees. But before 10 reach the phases of 34 and 3 they have already adjusted their phase towards 10 and the other fireflies they see, now a little ahead of 10. Finally as 34 and 3 are drawn towards the consensus, they drag 10 with them.

Notice that, the longer the phase of 10 is ahead of the other fireflies, the quicker the phase is adjusted towards them. This arises from the concavity of the activation potential, $U(\phi)$. The longer into its period the firefly receives a pulse, the more the pulse delays the phase of the firefly.

3.2 Erdős-Rényi networks

We now turn our attention to Erdős-Rényi networks, which we will abbreviate as ER-networks. ER-networks are random networks where the probability for a connection from i to j is constant[6]. In figures 3.6, 3.7 and 3.8 we have plotted the eigenvalues of transition matrices of ER-networks with different connection probabilities, using the integrate-and-fire potential (2.42).

As can be seen, the eigenvalues of the generated ER-networks are not purely real: As the connections in general are not two-way, the transition matrices are not similar with a symmetric matrix, as was the case for the Zachary network.

Comparing the eigenvalues at different connection probabilities, as the connection probability go up, the spread of the non-trivial eigenvalues de-

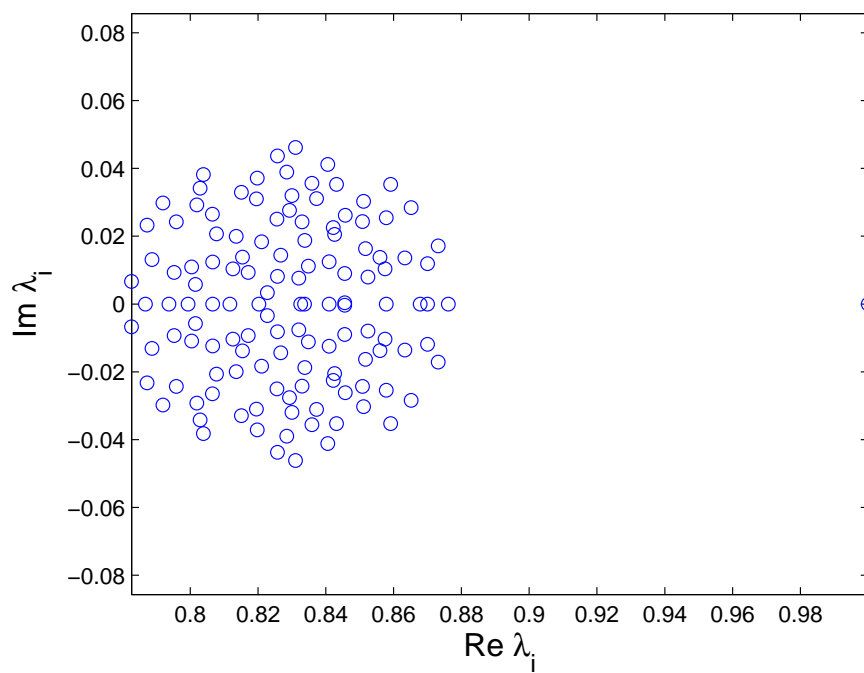


Figure 3.6: Eigenvalues of the transition matrix for a 128 node ER-network with connection probability $p = 0.1$. The activation potential is the integrate-and-fire function (2.42), with $I = 1.1$. The pulse delay is set to $\tau = 0.05$, and the total coupling strength is $\varepsilon = -0.2$.

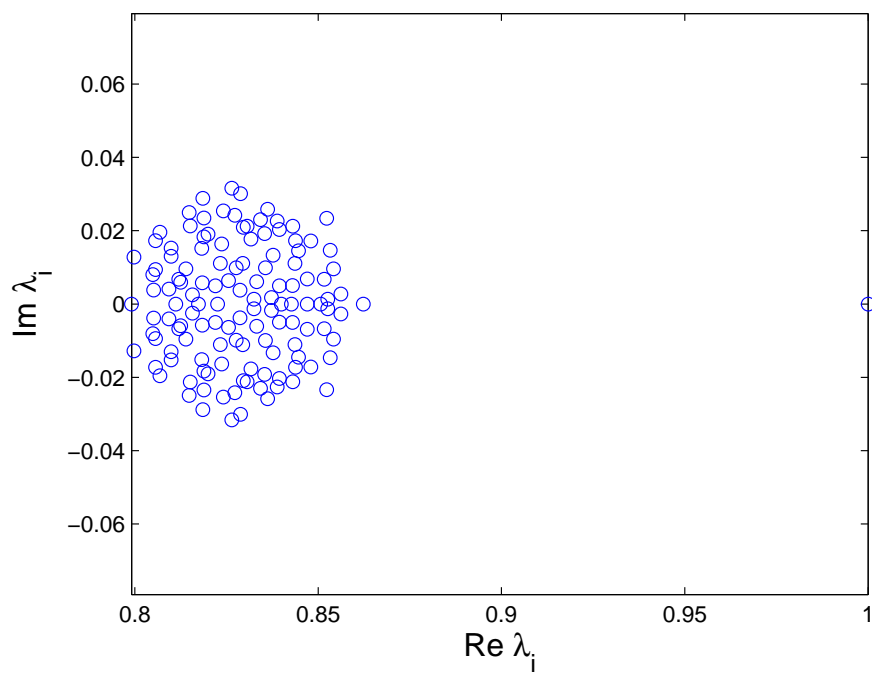


Figure 3.7: Eigenvalues of the transition matrix for a 128 node ER-network with connection probability $p = 0.2$. The activation potential is the integrate-and-fire function (2.42), with $I = 1.1$. The pulse delay is set to $\tau = 0.05$, and the total coupling strength is $\varepsilon = -0.2$.

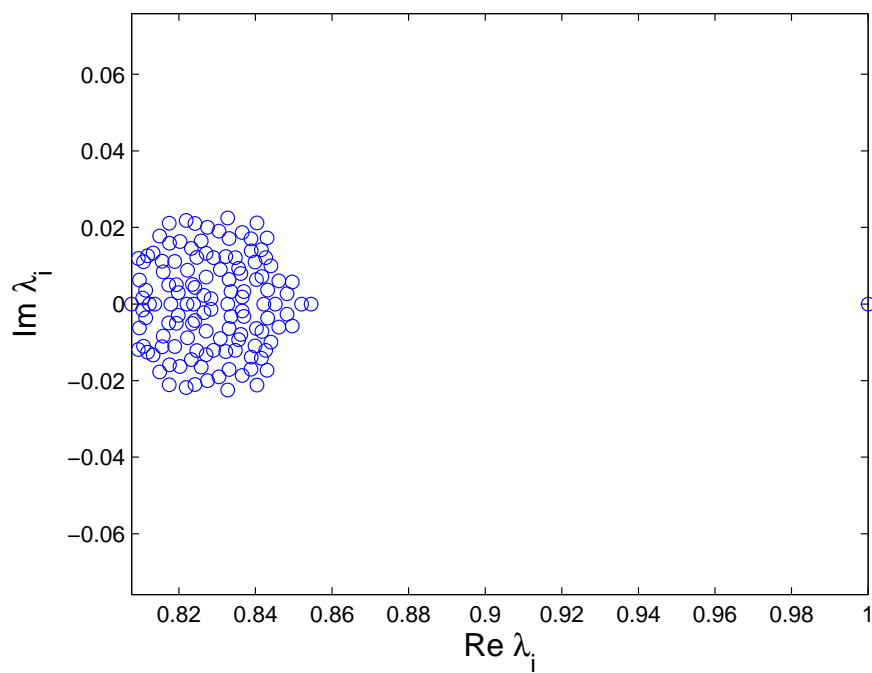


Figure 3.8: Eigenvalues of the transition matrix for a 128 node ER-network with connection probability $p = 0.3$. The activation potential is the integrate-and-fire function (2.42), with $I = 1.1$. The pulse delay is set to $\tau = 0.05$, and the total coupling strength is $\varepsilon = -0.2$.

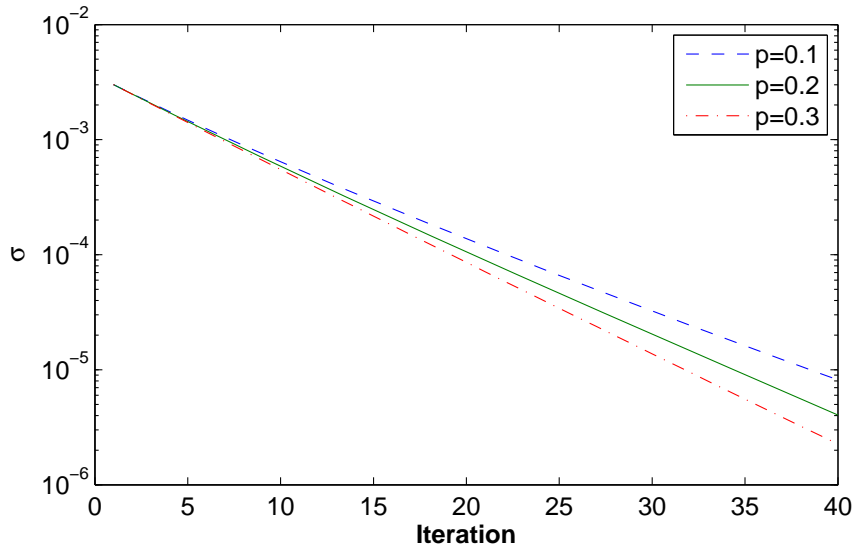


Figure 3.9: The evolution of the standard deviation of the perturbation in Erdős-Rényi networks with different connection probabilities. The networks has $N = 128$ nodes, coupling strengths $\varepsilon_{ij} = \frac{-0.2}{k_i}$ and pulse delay $\tau = 0.05$.

crease, and the second largest eigenvalue is a little smaller. In figure 3.9 the speed of convergence is compared for the different probabilities. As one would expect, more densely connected networks synchronize faster.

3.3 AS network

The last network we do analysis on is the autonomous systems network, abbreviated as the AS network. The network describe the routing tables of 6474 big hubs of the internet at a certain time[7, 12]. In figure, the 20 largest eigenvalues are plotted. As the connections in this network is two-way, the eigenvalues are real.

The slowest decaying eigendirection in the AS network has an eigenvalue closer to 1 than any network we have looked at so far. In figure we have compared the decline of the standard deviation of the AS network with the Zachary network and an ER network with 128 noded and connection probability $p = 0.2$.

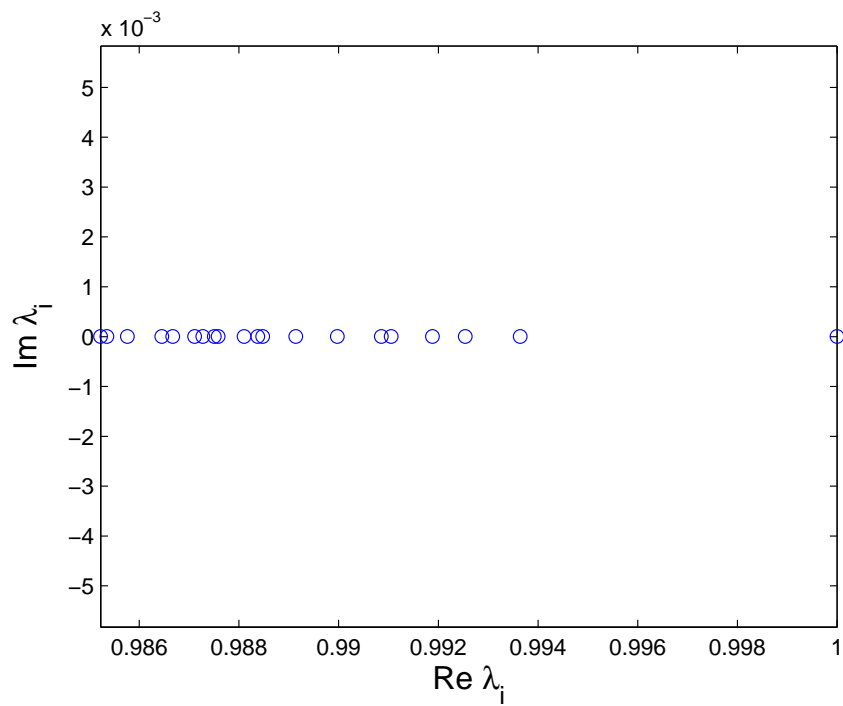


Figure 3.10: 20 largest eigenvalues of the transition matrix for the AS network. The activation potential is the integrate-and-fire function (2.42), with $I = 1.1$. The pulse delay is set to $\tau = 0.05$, and the total coupling strength is $\varepsilon = -0.2$.

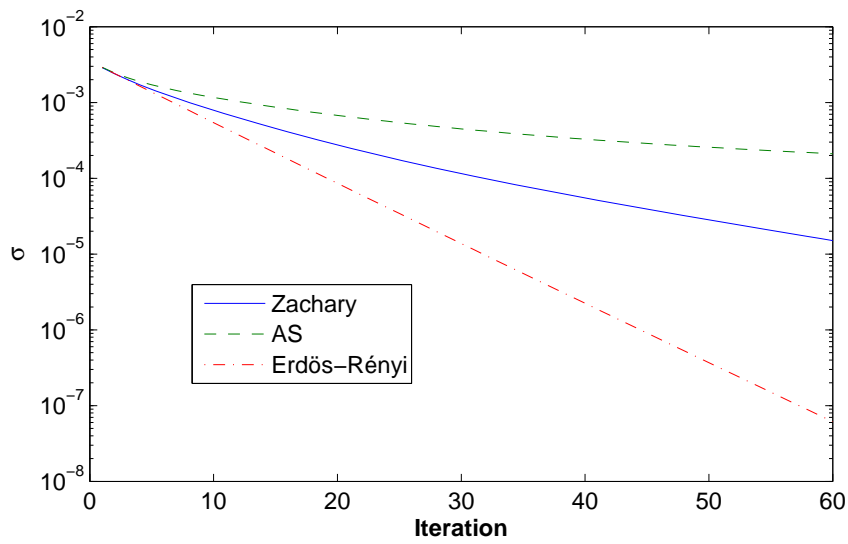


Figure 3.11: The evolution of the standard deviation of the perturbation in the AS network, the Zachary network and an ER network with $N = 128$ nodes and $p = 0.2$. The coupling strengths are $\varepsilon_{ij} = \frac{-0.2}{k_i}$ and the pulse delay $\tau = 0.05$ for all networks.

Chapter 4

Discussion and conclusions

We have studied synchronization of inhibitorically pulse-coupled oscillators connected in a network. Assuming that all oscillators have the same intrinsic frequency, and monotonically increasing, concave down activation potentials, the stability of the synchronized state is analysed. Analytically we have seen that for strongly connected networks, the synchronized state is a stable fixed state. We have seen numerically that even over large networks with several thousand vertices, the phases approach the synchronized state.

Similar to the original Mirollo-Strogatz model[14] the concave down property of the activation potential is a key for the synchronization. If the activation potential would have been linear, then, looking at equations (2.22) and (2.26), the transition matrix would have reduced to the identity matrix, propagating any perturbation indefinitely.

Interestingly, the leaky fire-and-integrate function simplifies the problem, resulting in a constant transition matrix instead of potentially many different depending on the order in which the pulses arrive. This is the function Peskin originally used[16] when he modeled the pacemaker neurons in the heart.

In the analysis, two quite restrictive assumptions are made: (i) that the oscillators have the same intrinsic frequency and that (ii) the total incoming coupling strength is constant over all oscillators. For many oscillator populations in nature, the assumption of identical frequencies is not realistic. But if the distribution of frequencies is narrow enough compared to the total period, this assumption might be a fair approximation[14]. Further research should seek to explore the scenarios where there might be a frequency distribution, and where the total incoming coupling strengths are not constant.

However, the model provides some insights into how synchronization can occur in a network of oscillators with simple pulse-interactions, without any central organization, external input or extraordinary response time. A century ago, the amazing displays of fireflies synchronizing was such a

mystery, some people did not believe their own eyes. This mystery is now unraveling.

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Appendix A

Program listing

```
function A = make_netw_randdir(N, p, eps)
%make random directed network with fixed connection propability p and
%flat normalized total incoming coupling strength eps. Output is the adjacency m
%A of the network

A = zeros(N,N);
k=0;
for i=1:N
    k=0;
    for j=1:N
        if rand<=p && j~=i
            A(i,j) = 1;
            k=k+1;
        end
    end
    for j=1:N
        if A(i,j)~=0
            A(i,j)=eps/k;
        end
    end
end

end

function A = make_transferm(adjm,tau,delta,I_in)
%make_transferm(adjm,tau,delta,I_in)
%make transfermatrix with input adjacency matrix of network with
%coupling strength eps and delay tau. Based on perturbation delta and
%IF-model parameter I
global I T_IF

I=I_in;
```

```

N = size(adjm,1);
if size(delta)~= [N,1]
    disp('Wrong dimension: \delta ');
    return
end

adjm = double(adjm);
eps = sum(adjm(1,:),2);

% for i=2:N
%     if sum(adjm(i,:),2)~=eps
%         disp('Coupling (eps) not normalized ');
%         return
%     end
% end

T_IF = log(I/(I-1));

p_in = zeros(2,1);
A = zeros(N,N);

denomi = dU_IF(U_IF_inv(U_IF(tau)+eps));
A_0 = dU_IF(tau)/denomi;

for i=1:N
    eps_sum=0;
    neigind = find(adjm(i,:));
    neigind = neigind.';
    sortvec = [neigind delta(neigind)];
    sortvec = sortrows(sortvec,-2);
    p_in(1)=A_0;
    for n=1:size(sortvec)
        eps_sum = eps_sum+adjm(i,sortvec(n));
        p_in(2) = dU_IF(U_IF_inv(U_IF(tau)+eps_sum))/denomi;
        A(i,sortvec(n))=p_in(2)-p_in(1);
        p_in(1)=p_in(2);
    end
    A(i,i)=A_0;
end

end

end

function U=dU_IF(phi)
global I T_IF
U=I*T_IF*exp(-phi*T_IF);
end

function U = U_IF_inv(y)
global I T_IF

```



```

U = -(1/T_IF)*log(1-y/I);
end

function U = U_IF(phi)
global I T_IF
U=I*(1-exp(-phi*T_IF));
end

function [deltas sigma] = evolve_delta(adjm,tau,init_delta,I_in,steps)
%evolve_delta(adjm,tau,init_delta,I_in,steps)
%Evolve the perturbation delta in the oscillator network adjm (so far) using
%integrate-and-fire functions for potential

deltas=zeros(size(init_delta,1),steps);
deltas(:,1)=init_delta;

for i=2:steps
    T = make_transferm(adjm,tau,deltas(:,i-1),I_in);
    deltas(:,i)=T*deltas(:,i-1);
end

sigma = zeros(steps,1);
for i=1:steps
    sigma(i) = std(deltas(:,i));
end

figure
plot(sigma);
xlabel('Iteration','fontsize',14);
ylabel('\sigma','fontsize',14);
end

```