Chapter 1

Introduction: Scope of the study

Over the past few decades, mathematical analysis has become an important tool to understand the working of the brain. As an approach to understand brain mechanisms, one could consider a network of biological neurons (henceforth referred to as a neuron network) as a dynamical system of (partial) differential equations. Typically, such a system comprises of coupled oscillators where an oscillator represents a neuron. Mathematicians interested in biological applications study such systems because they provide insights into the underlying mechanisms of neural information processing. Alternatively, one could conceive simple formulas based on certain properties of a set of neurons and eventually use them to mimic several functions of the brain. The latter approach is preferred by scientists in applied areas since it is easier to understand and use a simple formula than a dynamical system consisting of differential equations for an application. In the study presented here, we use both of these approaches to understand different brain phenomena.

From a broader perspective, we address two important questions, viz., (a) What kind of mechanism would enable a neuron network to switch between various tasks or stored patterns? (b) What are the properties of neurons that are used by the visual system in early motion detection? To address (a) we model neuron networks as coupled oscillator systems and analyze their dynamics to construct a possible mechanism that can explain switching between tasks/stored patterns. This question is addressed under the heading ‘attractor switching in neuron networks’. The question in (b) is answered by studying spatiotemporal filters for motion detection and subsequent surround inhibition mechanisms under the heading 'spatiotemporal filters for motion processing'. The purpose of this chapter is to motivate and introduce the reader to these problems.

1.1 Attractor switching in neuron networks

Many physical systems exhibit oscillatory activity. Examples include orbital motion of planets, oscillating chemical reactions, electromagnetic waves, heart beats, circadian rhythms and menstrual cycle among women (see for example, (Gonzalez-Miranda 2004, Strogatz 2003)). Typically, an oscillator does not operate as a single unit. Instead, it works as a part of a coupled system comprising of several oscillators. In such a coupled system,
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Figure 1.1: Oscillatory activity exhibited by a spiking neuron: When the membrane potential function \( f(x) \) reaches a particular threshold \( f_{\text{max}} \), the neuron fires and the potential is reset to a lower value.

the nature of the interactions can vary from being continuous to episodic. The following references provide a great deal of material on coupled oscillators and their dynamics (Winfree 2001, Strogatz 1994, Strogatz 2003).

A part of this study is devoted to understanding the dynamics of a pulse-coupled oscillator network inspired by the function of networks of spiking neurons. In a pulse-coupled oscillator system, the interactions are episodic or occurs only at discrete times. Such systems, among other things, are also used to model earthquakes, synchronous flashing of fireflies, pacemaker cells and riots (Herz and Hopfield 1995, Buck and Buck 1976, Buck 1988, Peskin 1984, Strogatz 2003, Timme 2002).

In the case of spiking neurons, an oscillator represents a single neuron and the membrane potential of the neuron is related to the phase of the oscillator. When the potential reaches a particular threshold, the neuron fires and the potential is reset to a lower value (see Figure 1.1). As a consequence of firing, a pulse is sent to several other neurons. The pulse relays a positive or negative charge to the neurons and this transfer of charge defines the coupling in the system. In this manner, a neuron network can be modeled as a dynamical system of pulse-coupled oscillators.

In analyzing a dynamical system it is important to understand its asymptotic behavior by identifying the attractors and their basins. In theory, an attractor can be a fixed point or a periodic orbit or even a complicated set with a fractal structure known as strange attractor (Guckenheimer and Holmes 1990, Strogatz 1994, Broer and Takens 2008 (to appear)). In the case of a coupled oscillator system, an attractor may correspond to a state in which all oscillators become synchronous (with zero phase difference) (Mirollo and Strogatz 1990, Chen 1994, Senn and Urbanczik 2001) or form several groups or clusters in
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which oscillators within a group are synchronized but maintain a constant nonzero phase difference from those that do not belong the same group (Ernst et al. 1995, Ernst et al. 1998, Timme 2002, Timme et al. 2002b, Timme et al. 2002c). In addition, asynchronous states and traveling waves are other asymptotics that can occur (Abbott and van Vreeswijk 1993, Bressloff and Coombes 1998, Timme 2002). In general, the long term behavior depends on the arithmetical properties of the frequencies of the individual oscillators. If the frequencies are rationally independent quasi-periodic (or non-resonant) dynamics would be observed (Ciocci et al. 2005). Furthermore, the presence of delays and network connectivity also influence the asymptotic behavior of the system. For example, when interactions between oscillators have a certain (non-zero) time delay, it can cause oscillator death (Reddy et al. 1998, Strogatz 1998) or can cause a (unique) global attractor to make way for several attractors (Ernst et al. 1995, Timme et al. 2002b). Complex connectivity can produce chaotic dynamics, where irregular firing of single neurons is observed (van Vreeswijk and Sompolinsky 1996, van Vreeswijk and Sompolinsky 1998, Timme et al. 2002a, Timme 2002).

In our work, we focus on the effects of interaction delays to the dynamics of the system. To this end, we consider a simple pulse-coupled oscillator network in which each neuron is connected to every other neuron thus leading to a global network with non-zero interaction delay. We establish that such systems containing three or more oscillators possess attractors that are unstable. Such attractors are saddle points (of a suitably defined Poincaré map) whose basin has a non-empty interior in the whole state space. Therefore, almost all initial states in an open neighborhood of the attractor leave that neighborhood in finite time. A formal definition will be provided in Chapter 3. In Figure 1.2 we provide an example of unstable attractor in the case of one-dimensional maps. The unstable attracting fixed point $x = 1/2$ could be considered as an attractor in the sense of Milnor (Milnor 1985).

Figure 1.2: Unstable attractors in one-dimensional maps. One-dimensional map $f : [0, 1] \rightarrow [0, 1]$ have an unstable attracting fixed point at $x = 1/2$. The presence of the ‘flat piece’ is the reason that $x = 1/2$ could be considered as an attractor in the sense of Milnor (Milnor 1985).
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Figure 1.3: Attractor switching through heteroclinic orbits: Each attractor $A_j$ lies in the interior of the closure of the basin of $A_{j+1}$. When the orbit of an initial state reaches a particular unstable attractor, say $A_j$, one can make the system switch to a different attractor $A_{j+1}$ by introducing a small noise (cf. (Ashwin and Timme 2005a)).

Point $x = 1/2$ is an attractor in the sense of Milnor (Milnor 1985) because there exists an open set in the state space (the 'flat piece' in the graph of $f$) for which $f(x) = 1/2$.

Further, in the case of four oscillators, we also prove that such systems have heteroclinic orbits/cycles between unstable attractors. These heteroclinic connections pave the way for attractor switching in neuron networks (Ashwin and Timme 2005a). For instance, consider the case where the system has $N$ unstable attractors $A_1, \ldots, A_N$ such that the attractor $A_j$ is contained in the interior of the closure of $B(A_{j+1})$ which is the basin of $A_{j+1}$ and $A_N$ is contained in the interior of the closure of $B(A_1)$. When the orbit of an initial state reaches a particular unstable attractor, say $A_j$, one can make the system switch to a different attractor ($A_{j+1}$, in this case) by adding a small perturbation such as noise (Timme et al. 2002c). In this way, heteroclinic connections together with some external noise can make the system switch from one attractor to another (see Figure 1.3).

Such switching between attractors/fixed points through heteroclinic connections is relevant in many physical systems. For instance, heteroclinic orbits are used in spacecraft missions to compute trajectories that consume less fuel (Koon et al. 2000, Taubes 1999). These heteroclinic orbits are created by gravitational forces between celestial bodies. In climatology, transitions in regimes are often thought to occur through heteroclinic connections (Crommelin 2003, Stewart 2003). A regime is a kind of atmospheric circulation pattern which lasts for a few weeks. After this period, a change in circulation pattern happens through heteroclinic connections giving rise to a new regime.

In the context of a neuron network, dynamics along heteroclinic connections is hypoth-
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esized as an efficient way to process neural information (Rabinovich et al. 2001, Huerta et al. 2004, Huerta and Rabinovich 2004, Hansel et al. 1993, Kori and Kuramoto 2001, Ashwin and Timme 2005b). A fixed point or an attractor, for a biological neuronal network could represent a task performed by the network or a stored pattern of memory. The presence of heteroclinic connections would mean that the network can switch between various tasks or stored patterns without much effort. The conclusions and implications of such studies serve as motivation for our work.

Though biologically inspired, the work presented in this part of the work is predominantly mathematical. To make the mathematical analysis tractable we make some idealizations in the model. For example, we assume that all the oscillators in a given population are strictly identical and they are connected in an all-to-all fashion. Indeed, such assumptions guarantee a certain symmetry which is used to prove the presence of heteroclinic cycles. An analysis on such idealized models is important because even simple systems can have different types of attractors and exhibit novel dynamics. In addition, often such studies shed light into the working of complex systems.

1.2 Spatiotemporal filters for motion perception

One of the important tasks of our visual system is to perceive motion. Even simple tasks such as filling a kettle or crossing a road involve motion perception (Snowden and Freeman 2004). Cue from motion is important in variety of tasks ranging from tracking of moving objects to segmenting a scene into its constituents by detecting boundaries between regions of different motions. Consequently, over the years, many physiological, psychophysical and computational studies have been carried out to understand motion perception. Among these, the work of Werner Reichardt is considered to be pioneering (Reichardt 1961). The main hypothesis of his work was that to perceive motion, the visual system combines the output from different neurons by incorporating time delays (Spillmann and Werner 1990). In Figure 1.4, we illustrate a simple Reichardt detector that prefers left to right motion. A stimulus traveling rightwards at a given speed elicits a certain response in receptor (neuron) $R_a$ at time $t$ which reaches the multiplier $M$ after some delay $\delta$. The unit as a whole responds maximally if the stimulus evokes a response in $R_b$ at time $t + \delta$. Many computational models in motion perception that exist today have their origin in Reichardt’s original model. The essence of Reichardt’s model is that, to perceive motion, information has to be integrated over space and time. And filters that combine information over space and time are called spatiotemporal filters.

The spatiotemporal filters that we study in the current work are inspired by the properties of simple and complex cells found in area V1 of the visual cortex. These cells respond to a line or an edge of a certain spatial orientation moving with a particular velocity (speed
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Figure 1.4: Reichardt detector that prefers left to right motion: A stimulus traveling rightwards at a given speed elicits a certain response in receptor \( R_a \) at time \( t \) which reaches the multiplier \( M \) after some delay \( \delta \). The unit as a whole responds maximally if the stimulus evokes a response in \( R_b \) at time \( t + \delta \). The amount of delay specifies the preferred speed of motion. Further, if the delay is associated with the response from receptor \( R_b \) instead of \( R_a \) then the unit would prefer leftward motion. This basic scheme can be extended to make use of \( n \) receptor units instead of just two (cf. (Spillmann and Werner 1990)).

and direction) in a given position of the visual field. The receptive field (RF) profiles of these cells are inseparable functions of space and time, and the specific structure of alternating elongated excitatory and inhibitory regions which are tilted in space-time underlie the orientation, speed and direction selectivity of these cells (DeAngelis et al. 1993a, DeAngelis et al. 1993b, DeAngelis et al. 1995). An intuitive understanding to this idea was provided in (Adelson and Bergen 1985) where the authors consider a a bar that is moving rightwards with a certain speed as shown in Figure 1.5(a). Since the dimension of the bar along the \( y \)-direction does not change, one can disregard that dimension and visualize the moving bar in the \( x - t \) space as in Figure 1.5(b). Evidently, the orientation of the moving bar in the \( x - t \) domain codifies the velocity of motion. Hence, motion can be thought of as orientation in space-time and filters whose receptive field profiles have a certain spatiotemporal orientation (see Figure 1.5(c)) are suitable for motion analysis.

When applied to digital image sequences, these filters, depending upon their receptive field duration, combine information over a large number of past frames to compute the output at current time. Such an approach to motion analysis has several advantages over classical methods that involve computing image/optic flow. First, they do not match fea-
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Figure 1.5: Motion as orientation in space-time. (a) A bar moving rightwards. (b) $x - t$ plot of the moving bar (time axis is discrete). (c) A spatiotemporal filter with suitable orientation. The '+' and '-' signs refers to the excitatory and inhibitory lobes of the filter respectively. The orientation of the bar in space-time codifies the velocity of motion and a filter with an appropriate orientation in space-time would respond maximally to the moving bar (cf. (Adelson and Bergen 1985)).

Another issue addressed in this context is related to surround interactions. The surround is a region that is present outside the classical receptive field (CRF) of a neuron. Physiological studies have revealed that once a cell is activated by a stimulus in its CRF, additional stimuli placed in the surround can strongly affect the cell response (Blakemore and Tobin 1972, Knierim and van Essen 1992, Nothdurft et al. 1999, Allman et al. 1985, Born and Bradley 2005). This is known in neurophysiology as center-surround interactions. When these interactions are inhibitive the phenomenon is known as surround suppression.
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Figure 1.6: Importance of surround mechanisms in the spatiotemporal domain: The pixels in the central region (the inner circle) belong to the foreground while the rest represents background. The arrows denote the direction of motion. The task of the observer is to identify the shape of the moving object. The boundary of the inner-circle would ‘pop out’ only when the motion inside the circle is significantly different from the motion in the background (cf. Tadin 2004).

This modulatory effect has important consequences in purely spatial and spatiotemporal domains. The implications in the spatial domain contributed to the development of a contour detector based on the contextual information present in the image (Petkov and Westenberg 2003, Grigorescu et al. 2003, Grigorescu 2004). The current study, however, explores the effects of center-surround interactions in the spatiotemporal domain. A simple psychophysical experiment shown in Figure 1.6 exemplifies the role of center-surround interactions in the spatiotemporal domain, wherein, the task of the observer is to identify the boundary of the moving object. One can recognize the outliers of the moving object only when the motion inside the object is significantly different from the motion in the background (Tadin 2004). Such experiments exemplify the role of center-surround interactions in enabling the visual system to detect motion discontinuities and segregate figure from background.

In this part of the study, we describe a computational model to process visual motion and augment it with a surround suppression term to qualitatively reproduce the center-surround behavior of motion sensitive neurons. The proposed model is also used to highlight several benefits of spatiotemporal filters to motion perception.

1.3 Overview of the study

This chapter presents a short introduction to the topics addressed in this work, viz., (a) attractor switching in neuron networks through heteroclinic orbits, (b) spatiotemporal filters with surround inhibition for motion processing. Chapters 2, 3 and 4 deal with the dynamics of a pulse coupled neuron networks while chapter 5 presents the benefits of using
spatiotemporal filters with surround inhibition for motion processing.

Chapter 2 outlines the mathematical details of a pulse coupled oscillator system. It describes the state space of the system, the evolution operator and a metric for the state space. Furthermore, a symbolic representation of the dynamics, called event representation, is described which is used in later chapters to prove several results. Some general properties of the metric are also discussed in the appendix of the chapter.

Chapter 3 uses the formalism provided in chapter 2 to prove the existence of unstable attractors for an oscillator network consisting of three or more oscillators for an open region in the parameter space. The chapter also provides numerical results on a system of three oscillators in order to demonstrate the global behavior of the system, the occurrence of unstable attractors and the local dynamics around them.

Chapter 4 provides the proof for the existence of heteroclinic cycles for a network of four oscillators in an open region of the parameter space. Numerical results are shown to demonstrate that such cycles also exist in systems containing more than four oscillators.

Chapter 5 deals with the spatiotemporal filters for motion processing. Gabor filters defined in the space-time domain are used to model the V1 cells in primate visual cortex. A spatiotemporal surround suppression stage is augmented to study the inhibitory effect of stimuli outside the classical receptive field. Illustrations are shown to suggest that spatiotemporal integration and surround suppression reduces the noise in the output considerably. An effective and straightforward motion detection computation is proposed that uses the population code of a set of motion energy filters tuned to different velocities. In addition, it is shown that surround inhibition leads to suppression of noise and texture and thus improves the visibility of object contours and facilitates the recognition and detection of objects.

A brief summary and outlook are presented in chapter 6. The results presented in this study are based on the following articles.


2. Henk Broer, Konstantinos Efstathiou and Easwar Subramanian, Heteroclinic cycles between unstable attractors, Nonlinearity (Submitted).

3. Nicolai Petkov and Easwar Subramanian, Motion detection, noise reduction, texture suppression and contour enhancement by spatiotemporal Gabor filters with surround inhibition, Biological Cybernetics, (Accepted), doi: 10.1007/s00422-007-0182-0.