

Dynamics of a network of Hodgkin-Huxley neurons under a constant external current

C.V.Leena (2007B4A4394G) under the guidance of Dr Gaurav Dar

May 7, 2011

Dynamics of a network of Hodgkin-Huxley neurons under a constant external current
submitted in partial fulfilment of the requirements of
Computer Projects Course BITS C331

by

C.V.Leena

ID No- 2007B4A4394G

Under the supervision of

Dr Gaurav Dar

Associate Professor



BIRLA INSTITUTE OF TECHNOLOGY AND SCIENCE, PILANI
K K BIRLA GOA CAMPUS

May, 2011

Abstract

In this project we have studied single neurons, two coupled neurons, network of neurons connected in a ring, and a network of neurons with all neurons connected to each other. We have modelled the neurons using the HH equations and taken neurons to be coupled electrically with the coupling strength being inversely proportional to the resistance of the synapse. In our simulations, we have studied the dynamics of the neurons in response to an external current fed into one of them. We find that for low values of current none of the neurons spike. We have also carried out a linear stability analysis to investigate the fixed point stability. For higher values of currents and for high coupling strength, all neurons show spiking behaviour which vanishes quite suddenly beyond some value of current with the neurons settling down to a low amplitude limit cycle. The value of external current at which this transition takes place reduced with decrease in coupling strength. However, for smaller coupling strength the amplitude of spikes reduce gradually with increasing current.

Acknowledgements

This project could not have been completed without Dr. Gaurav Dar, my project guide who had been extremely great at guiding me. Neurosciences is a field where I was a novice and Dr. Dar helped me in understanding the subject extremely well. In spite of his completely packed up schedule he could find time to help me and guide me whenever it was essential. I am really thankful to him for that. I am grateful and thankful to my parents, without them I would have never been doing this project. Lastly I thank all my friends at BITS for staying by my side throughout as it is not exactly an easy task to bear with me. I also thank each and every one who has helped me in making this project successful.

Contents

1	Introduction	3
2	The Hodgkin Huxley Model	5
2.1	Ionic Currents	5
3	Dynamics of a single Hodgkin-Huxley neuron	7
3.1	Numerical results	7
3.2	Stability Analysis of fixed points	7
4	Dynamics of two electrically coupled Hodgkin-Huxley neurons	10
5	Dynamics of a ring of six Hodgkin-Huxley neurons	12
5.1	Nearest neighbour connectivity	12
5.1.1	Bifurcation Diagrams	12
5.2	Detailed analysis at the transition region	14
5.2.1	Different behavior observed in the simulations	16
5.2.2	Phase space plots	17
5.3	Ring of neurons(all of them connected)	17
5.4	Stability Analysis of fixed points for a ring of neurons	18
5.5	Conclusion	19
6	Transitions to a limit cycle	20
6.1	Neuronal networks	20
6.2	A 2-d system with a ghost limit cycle	21
7	Discussions and Results	23

Chapter 1

Introduction

Brain is the most sophisticated and intricate organ the nature has ever devised. But the basic strategy in unraveling the structure and function of the brain still remains the same. So we need to begin with the basic cell of the brain and the nervous system, study them individually and then assemble them together to see how they function and work together. So we begin with the neuron, the basic cells of the nervous system.

Structure of neuron: Axon and dendrites are the feature differentiating the neuron from the other cells. Axon begins with a region “Axon Hillock” and terminates with the axon terminal. Terminal is the site where axon comes into contact with the other Neurons. The point of contact is called the synapse and transmission of electrical signals from one neuron to the other is termed as synaptic transmission.

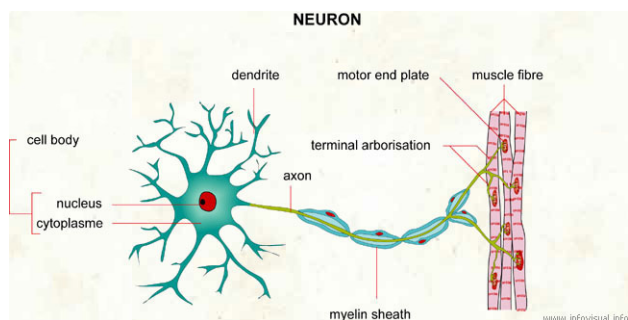


Figure 1.1: The biological neuron

The cell membrane is a phospholipid bi layer separating the intracellular and the extra cellular fluids. It is about 5nm thick and is studded with proteins. Some of the protein molecules together form channels with selective permeability to different ions to flow through them and some of them form pumps that pump ions from inside to outside of the cell against the concentration gradient. Neuronal membrane endows neuron with remarkable ability to transfer electrical signals throughout the brain and the body.

Electrical charge in axon is carried by ions and not through electrons. So the conduction is much slower in the axon. It is also not well insulated as the extracellular fluid conducts electricity. The axonal membrane has properties that would enable it to transmit special type of signals called “The Action Potentials” . They are signals of fixed size and duration.

Membrane Potential The cell membrane of the neuron is associated with potential difference due to a concentration gradient that exists across the cell. The intracellular fluid (ICF) and the extracellular fluid (ECF) have different concentrations of ions. ECF has sodium ions in abundance whereas the ICF has large concentrations of potassium ions. The cellular membrane has selective permeability and ionic channels regulate the permeability of the membrane to different ionic species.

Equilibrium Potential To explain this let us consider the case where the ICF has large concentrations of potassium ions and ECF has lesser concentrations of the potassium ions and the ion channels are selectively permeable to potassium ions. When

ionic channels open up initially diffusion rules allowing potassium ions to travel through the membrane but the corresponding anions are left behind and the cell begins to accumulate net negative charge inside the cell and an electrical potential difference is established across the membrane. As the inside fluid acquires more and more negative charge potassium ions are pulled back into the cell thus creating an electrical force. Equilibrium state is reached when the diffusion current counterbalances the ionic current and the net movement of ions ceases. The electrical potential difference that exactly balances an ionic concentration gradient is called the ionic equilibrium potential.

Rest Membrane Potential When a cell with excitable membrane is not generating signals then it is said to be at rest. In a resting neuron the inside of cell is (-) vely charged with respect to outside of the cell and the potential difference across the mebrane is the rest membrane potential. The rest membrane potential is typically -65mV. Inside of the cell has larger concentrations of $[K^+]$ ions and the outside of the cell have larger concentrations of $[Na^+]$ ions.

Action Potential The action potential results from a rapid change in the permeability of the neuronal membrane to sodium and potassium. The permeability changes as voltage-gated ion channels open and close. Initially the cell membrane potential is at a negative potential. An action potential is a brief reversal of of this situation. The membrane potential briefly becomes positive.

The action potential has certain identifiable parts The first part called a rising phase, is characterized by a rapid depolarization of the membrane. The change in membrane potential continues until V_m where it reaches a peak values of about 40mV. The part of action potential where the inside of neuron is negatively chrged compared to the outside is called the overshoot. The falling phase of the action potential is a rapid depolarization until the Voltage across the membrane is actually more negative than the resting potential. The last part of the falling phase is called the undershoot.

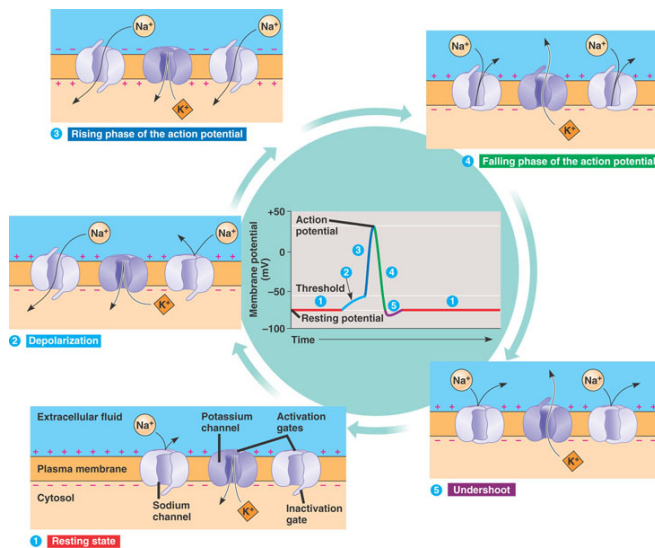


Figure 1.2: Action Potential

when an external stimulus acts sodium channels open. Because of the large concentration gradient, Na^+ ions enter the fiber through channels. The entry of Na^+ depolarizes the membrane. If the depolarization achieves a critical level, the mebrane will generate a action potential. The critical level of the depolarization that must be crossed in order to generate an action potential is called threshold. The rising phase of the action potential could be explained as follows. If the membrane is depolarized beyond threshold, sodium channels open and this would allow Na^+ to enter the neuron, causing a massive depolarization until membrane potential approached the equilibrium potential of Soidum. When sodium channels close and potassium channels open, the membrane ion permeability switches back from Na^+ to K^+ . Then K^+ would flow out of the cell. The rising phase of action potential is explained by an inward sodium current, and the falling phase is explained by an outward potassium current.

Chapter 2

The Hodgkin Huxley Model

Hodgkin Huxley model is a mathematical model that describes the behavior of a neuron under the action of an external stimulus. It is a set of non linear differential equations that describe how action potentials are generated and propagated.

They have conducted their experiments on a giant squid axon and they came up with a model that describes the generation and propagation of action potentials in a neuron.

2.1 Ionic Currents

Different ionic currents as defined by the Hodgkin Huxley model are given as follows.

$$Sodiumcurrent = G'_{Na}(V, t)(V - V_{Na}) \quad (2.1)$$

Where

$$G'_{Na} = G_{Na}m^3h \quad (2.2)$$

$$Potassiumcurrent = G'_K(V, t)(V - V_K) \quad (2.3)$$

$$G'_K = G_Kn^4 \quad (2.4)$$

V , V_{Na} and V_K are values measured with respect to V_R - the rest potential. Through experimentation Hodgkin and Huxley found that dependence of ion currents on voltage.

Thus the total ionic current per unit area across the membrane is expressed as

$$J_{ion} = G_{Na}m^3h(V - V_{Na}) + G_Kn^4(V - V_K) + G_L(V - V_L) \quad (2.5)$$

Where G_L term corresponds to the leakage term.

Below is a table of parameter values measured by Hodgkin-Huxley for the giant squid axon.

Parameter	Mean	Range	Standard	Units
C	0.91	(0.8-1.5)	1.0	$\mu F/cm^2$
G_{Na}	120	(65-260)	120	mmhos/ cm^2
G_K	34	(26-49)	36	mmhos/ cm^2
G_L	0.26	(0.13-0.5)	0.3	mmhos/ cm^2
V_{Na}	+109	(95-119)	+115	mV
V_K	-11	(9-14)	-12	mV
V_L	+11	(4-22)	+10.5995	mV

Table 2.1: Parameter values measured by H-H in a giant squid axon

When current is injected into the neuron, the membrane potential rises till it reaches a threshold value, when the sodium gates open up and allow the sodium ion current to flow into the axon. The m variable is termed as the sodium turn on variable and n variable is termed as potassium turn on variable. When membran voltage increases sodium channels open up and (m tends to 1). When the membrane potential approaches the equilibrium potential of sodium potassium channels open up and n variable tends to 1 and sodium channels close and the sodium turn off variable tend to 0. Then the potassium ions flow back rapidly out of the neuron and brings the voltage back to the rest value.

The system of H-H equations is given below.

$$C \frac{dV}{dt} = I_{ext} - G_{Na} m^3 h (V - V_{Na}) - G_K n^4 (V - V_K) - G_L (V - V_L) \quad (2.6)$$

$$\frac{dm}{dt} = \alpha_m (1 - m) - \beta_m m \quad (2.7)$$

$$\frac{dh}{dt} = \alpha_h (1 - h) - \beta_h h \quad (2.8)$$

$$\frac{dn}{dt} = \alpha_n (1 - h) - \beta_n h \quad (2.9)$$

where

$$\alpha_m = \frac{0.1(25 - V)}{\exp[\frac{25-V}{10}] - 1} \quad (2.10)$$

$$\beta_m = 4 \exp(\frac{-V}{18}) \quad (2.11)$$

$$\alpha_h = 0.07 \exp(\frac{-V}{20}) \quad (2.12)$$

$$\beta_h = \frac{1}{\exp[\frac{30-V}{10}] + 1} \quad (2.13)$$

$$\alpha_n = \frac{0.01(10 - V)}{\exp[\frac{10-V}{10}] - 1} \quad (2.14)$$

$$\beta_n = 0.125 \exp(\frac{-V}{80}) \quad (2.15)$$

In this project, we have numerically solved the above equations using the Runge Kutta Methods and various results were produced for several chosen parameters.

Chapter 3

Dynamics of a single Hodgkin-Huxley neuron

In this chapter we have studied the dynamics of a single Hodgkin-Huxley neuron for various values of external current. The bifurcation diagram below conveys this dynamics.

3.1 Numerical results

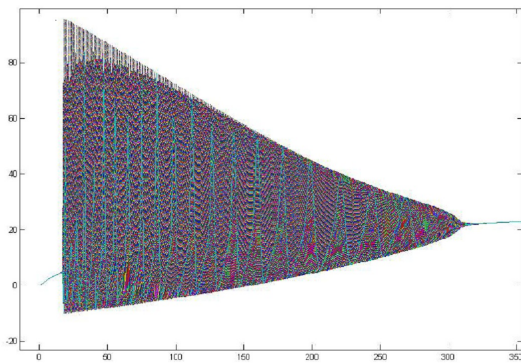


Figure 3.1: Bifurcation diagram of a single neuron V vs I_{ext}

We find that the system approaches a fixed point at low values of current and at high values of current. Between these two values the system approaches a limit cycle. A bifurcation occurs at two points in the above bifurcation diagram. At the first bifurcation point the fixed point loses stability (as we will show later by means of fixed point analysis) giving rise to a stable limit cycle through a Hopf bifurcation (which has been shown in other references). At the second bifurcation point the fixed point again becomes stable. Another point of interest is to note that the amplitude of the limit cycle reduces with increasing value of external current.

The phase space plot between the Voltage and the m variable are shown below. The first figure shows the entire dynamics of the system and the second one shows the stable limit cycle that the system approaches for $I_{ext} = 100$, $R = 10$.

3.2 Stability Analysis of fixed points

The HH model of a neuron has been numerically as well as analytically solved to obtain the fixed points and the results were in close agreement with each other. The nullclines of the system were plotted and the fixed points were obtained from the nullclines. The equations were also solved using Runge Kutta methods to obtain the fixed points.

The stability of the fixed points was determined by linearizing the system around the fixed point and performing a stability analysis by computing the Jacobian Matrix and finding out the Eigen values.

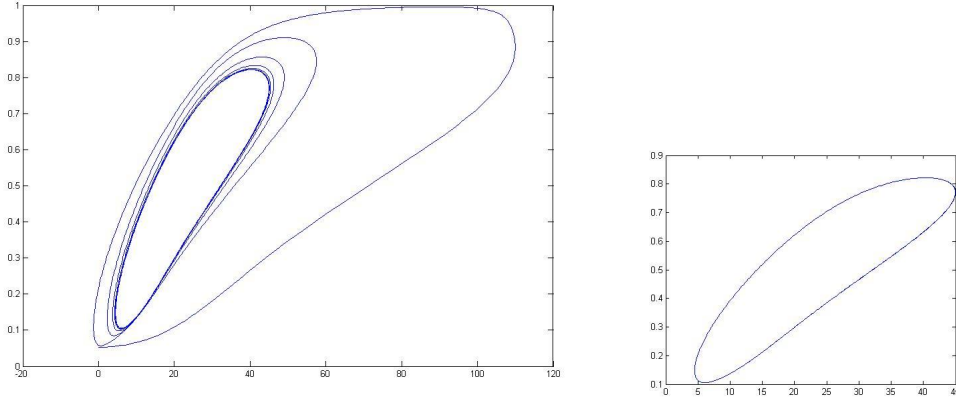


Figure 3.2: a)Phase space (V,m) plot for a single neuron b)Final stable limit cycle (for $I_{ext} = 100$).

S.no	I_{ext}	Fixed Point (V,m,h,n)	Eigen values	Stability
1	5	(3.26,0.07702,0.4775,0.3687)	-4.5910,-0.1008+0.5216i,-0.1008,- 0.5216i -0.1291	Stable
2	10	(5.43,0.09819,0.4038,0.4031)	-4.7764,0.0054+0.5879i,0.0054-0.5879i,-0.1389	Unstable
3	100	(18.46,0.3304,0.1038,0.59950)	-8.2421,0.2233+0.9055i,0.2233-0.9055i,-0.2617	Unstable
4	400	(31.3,0.6563,0.02664,0.741)	-12.6546,-0.9290+1.1046i,-0.9290-1.1046i,-0.4687	Stable

Table 3.1: Stability of fixed points for a single neuron R,10 for different values of external currents

The results obtained in the bifurcation diagram(Fig 2.1) for a single neuron show that the system finally reaches a stable fixed point for low values of current and then the stability of the fixed point seems to change and the system reaches a limit cycle for a certain range of currents and then the fixed point becomes stable again. The computed eigen values also predict the same behavior. For $I_{ext} = 5$, the fixed point is stable, is unstable for $I_{ext} = 10, 100$ and then the fixed point becomes stable again. The system has a single fixed point as the nullclines intersected at a single point in the space. The system also has a single stable limit cycle which was observed by doing the following.

The above simulations and analysis was all carried out for a single initial condition. It is conceivable that the system has multiple limit cycle and approaches the limit cycle of our simulations for this chosen initial condition. We wanted to explore the existence of any other limit cycles. To do this we generated a large number of random initial conditions. For each of these we carried out the simulation and found the the average voltage values after a certain period of time. For a system possessing multiple limit cycles we would expect the average voltages to have a number of distinct values equal to the number of stable limit cycles. However, as seen in the plot below we found only a single value indicating the presence of only one stable limit cycle.

Plot of average voltage values for various initial conditions for a particular value of external current. The average value oscillates with a very less amplitude compared to the values of voltages the system usually takes which indicates the existence of a single stable limit cycle in the system.

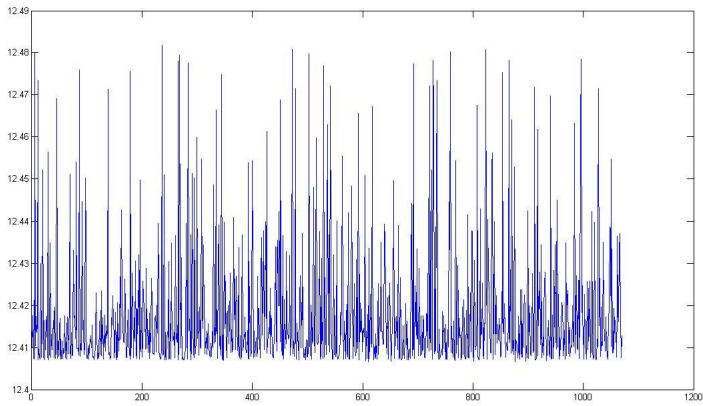


Figure 3.3: V_{avg} on the y-axis plotted for different initial conditions indicated by numbers 1,2,3,... on the x-axis. Initial conditions were chosen randomly. The voltage values were averaged over a fixed number of iterations after throwing away the transients.

Chapter 4

Dynamics of two electrically coupled Hodgkin-Huxley neurons

We connect two neurons and supply external current to only one of the two neurons. The synapses are electrical and they are associated with synaptic strength which is the resistance term. Charge flows from one neuron to other due a potential difference that is generated due to the external current that is supplied to the first neuron. Here we report the different types of behaviour observed in the two neurons.

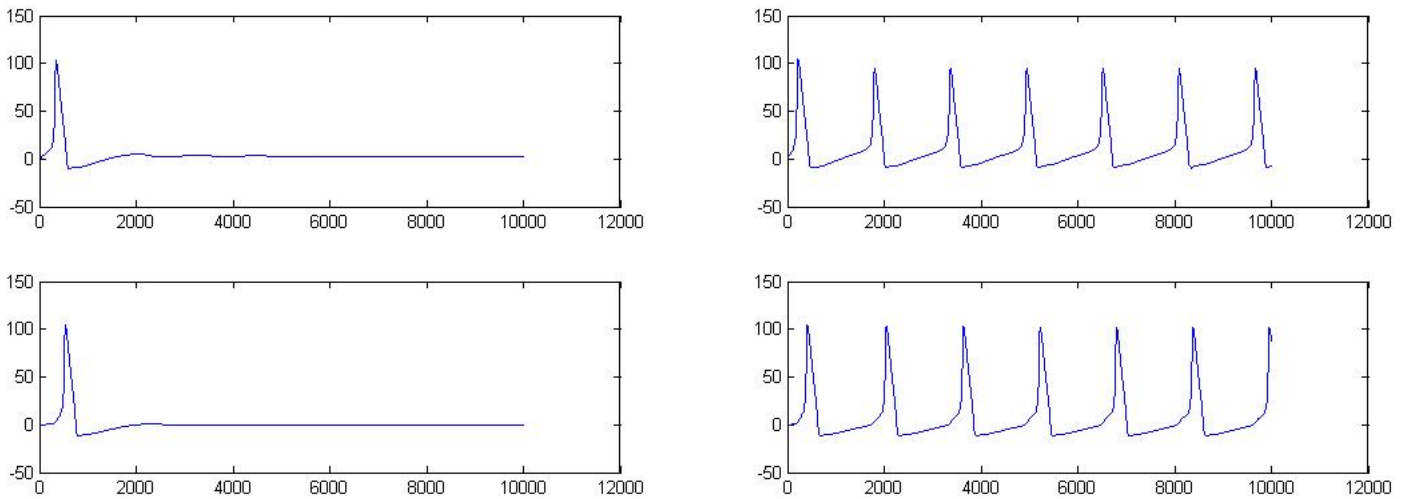


Figure 4.1: a) Voltage vs time $I_{ext} = 5$, $R = 10$ b) Voltage vs time $I_{ext} = 10$, $R = 10$. The upper plot is for neuron '1' into which an external current is fed.

The behaviour depicted by the system of electrically coupled neurons was found to be qualitatively similar to that exhibited by a ring of neurons. For low values of currents the system reaches a fixed point, as I_{ext} increases the fixed point is unstable and the system reaches a limit cycle. For very high values of current the system again reaches a fixed point. We also observe that the width of the limit cycle (height of the peak) decreases with increasing value of external current. We also observe the sudden transition behavior between a ghost limit cycle and the stable limit cycle of the system (see the last chapter).

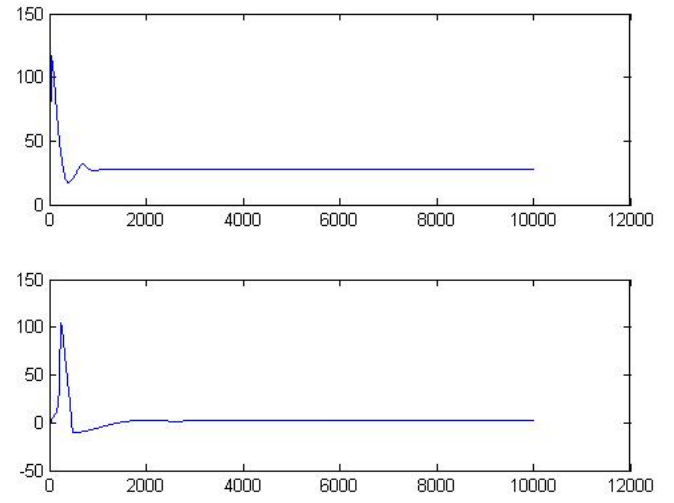
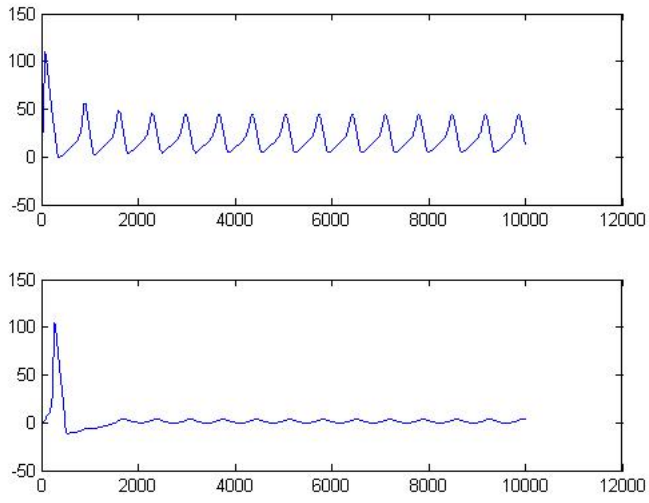


Figure 4.2: a) Voltage vs time $I_{ext} = 100$, $R = 10$ b) Voltage vs time $I_{ext} = 300$, $R = 10$. The upper plot is for neuron '1' into which an external current is fed.

Chapter 5

Dynamics of a ring of six Hodgkin-Huxley neurons

To further our understanding of the effect of coupling neurons we have considered a ring of neurons. Within this ring we first considered nearest neighbour coupling and then allowed all the neurons to be coupled to each other. The coupling strength (R) between each neuron pair is taken to be equal in all our simulations. Similar to the case where we coupled two neurons here also we feed an external current only into one neuron within the ring. The results of our simulation and analysis for varying values of external current and coupling strength (resistance) in this chapter.

5.1 Nearest neighbour connectivity

5.1.1 Bifurcation Diagrams

Bifurcation diagrams for various values of synaptic strengths in a ring of neurons

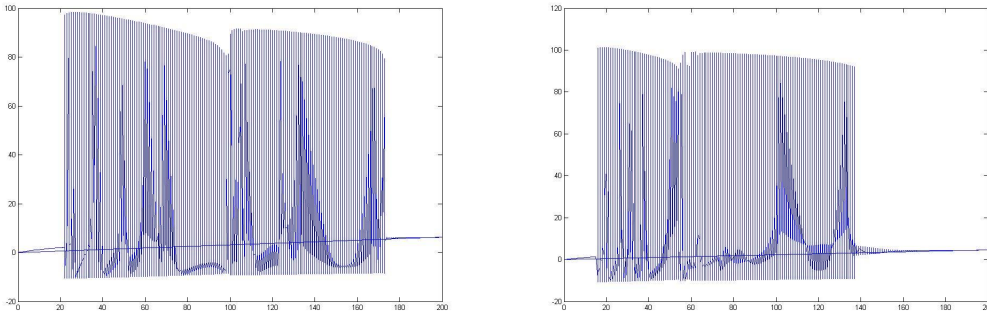


Figure 5.1: a) $R = 1$, Bifurcation diagram V vs I_{ext} for the 2nd Neuron, b) $R = 2$, Bifurcation diagram V vs I_{ext} for the 2nd Neuron

These bifurcation diagrams corresponding to $R = 1$ and $R = 2$ show that the system reaches a fixed point for low values of external current and undergoes a bifurcation and the fixed point becomes unstable, and the system evolves into a stable limit cycle for some period of time and the height of the peak slowly decreases in some region and then it increases again at a single point and then it gradually reduces with I_{ext} and then it undergoes a sudden transition from a limit cycle to what appears to be a limit cycle of lower amplitude. We have carried out, in the next section, a finer simulation to investigate the transition between the two limit cycles to check whether a bifurcation has occurred or has the amplitude of the limit cycle merely reduced rapidly with I_{ext} .

At $R=6$ there is an anomaly that we do not see for other coupling values. In midst of limit cycles of low amplitude a limit cycle of much greater amplitude grows sharply close to one value of I_{ext} .

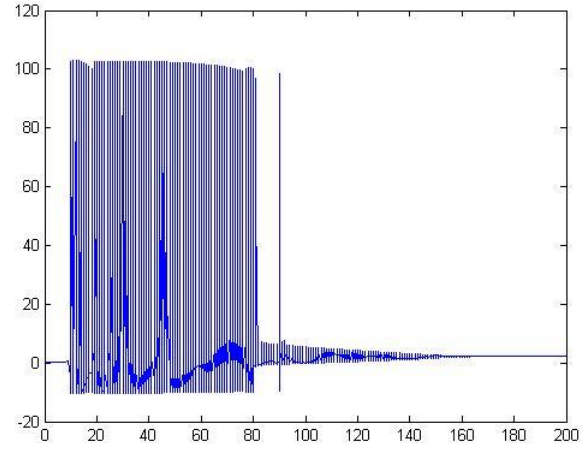
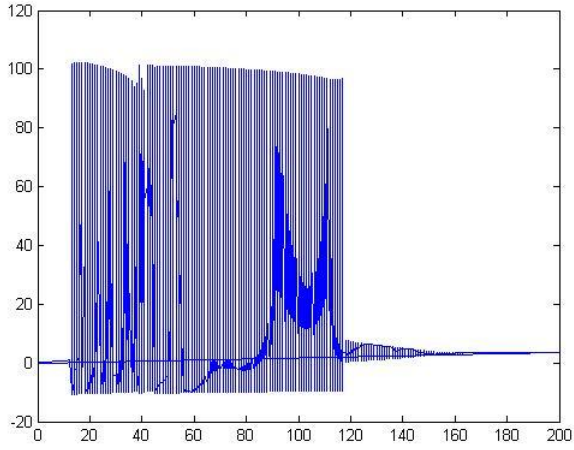


Figure 5.2: a) $R = 3$, Bifurcation diagram V vs I_{ext} for the 2nd Neuron, b) $R = 6$, Bifurcation diagram V vs I_{ext} for the 2nd Neuron

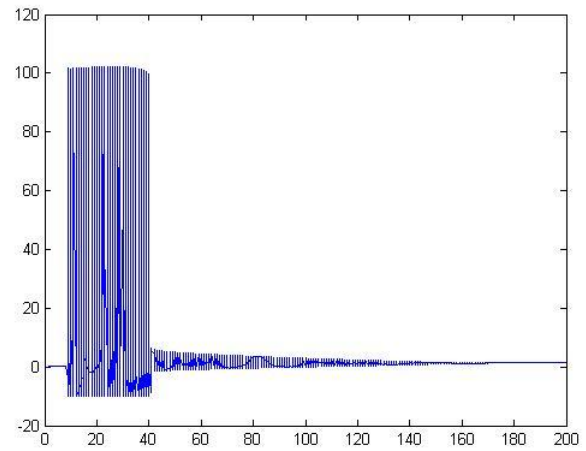
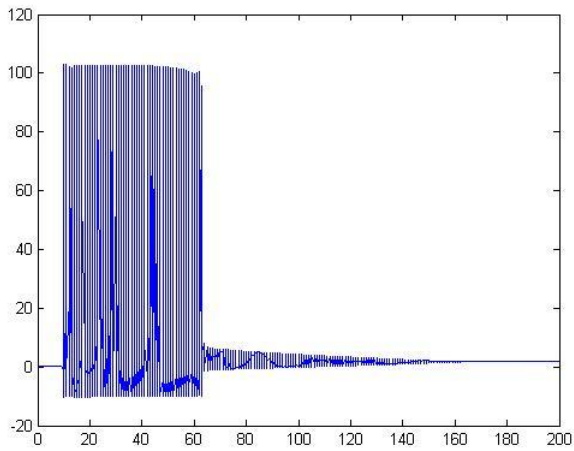


Figure 5.3: a) $R = 8$, Bifurcation diagram V vs I_{ext} for the 2nd Neuron, b) $R = 12$, Bifurcation diagram V vs I_{ext} for the 2nd Neuron

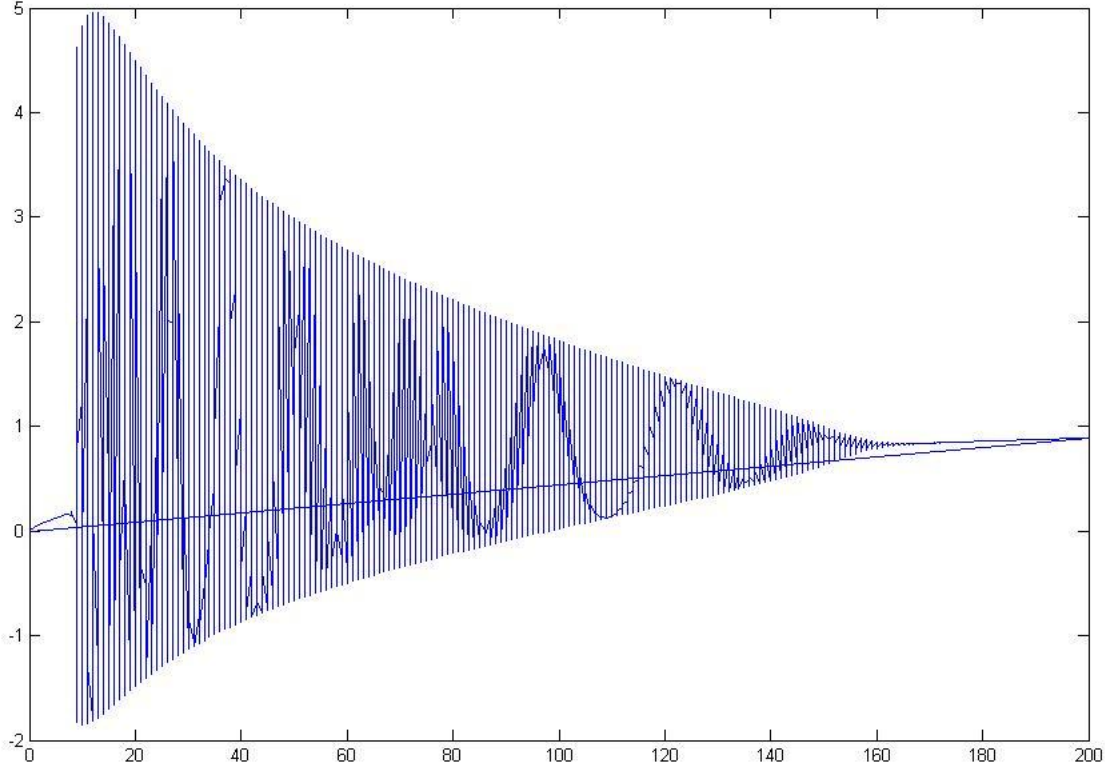


Figure 5.4: $R = 20$, Bifurcation diagram V vs I_{ext} for the 2nd Neuron

For value of $R = 20$, we observed that the transition behaviour between a limit cycle and a fixed point is not sudden, its rather gradual, qualitatively similar to the bifurcation diagram of a single neuron.

We have observed that for changing synaptic strength the set of parameters for which the limit cycle is observed is gradually decreasing with increase in the synaptic strength and the transition is sudden. We need to isolate the region of transition and perform a careful analysis in order to see the kind of bifurcation the system is undergoing. This behavior is seen for a certain range of resistance values and then the transition is gradual as seen in that of a single neuron case.

5.2 Detailed analysis at the transition region

We carried out a detailed analysis at the point of bifurcation in a ring of neurons as the transition between two limit cycles in the bifurcation figure sharp and a detailed analysis is needed for us to know whether a bifurcation has taken place at the transition region or the limit cycles have just diminished in size gradually which we have not been able to observe due to limitations in carrying out numerical Analysis. In order to investigate this we have performed a detailed analysis of the transition region. The results are shown below. The circled regions in each figure show the transition region which is blown up in the figure following it.

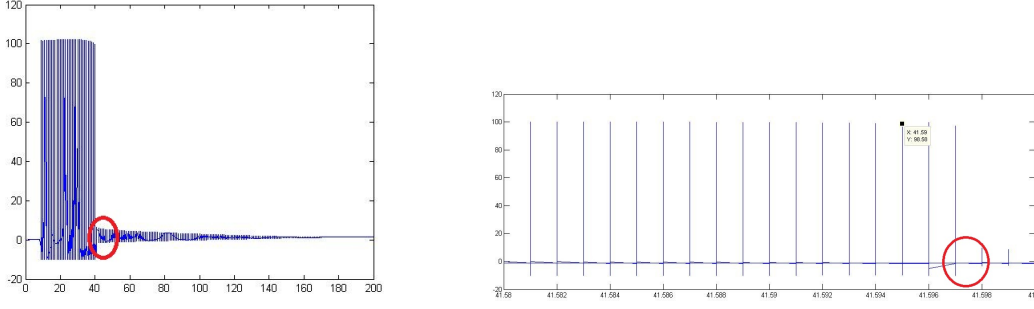


Figure 5.5: a)Bifurcation diagram of the 2nd neuron in a ring of neurons with nearest neighbour connectivity for $R = 12$ between $I_{ext} = 0$ to 200 in 201 stepsb)Bifurcation diagram of the 2nd neuron in a ring of neurons with nearest neighbour connectivity for $R = 12$ between $I_{ext} = 41.58$ to 41.59 in 201 steps

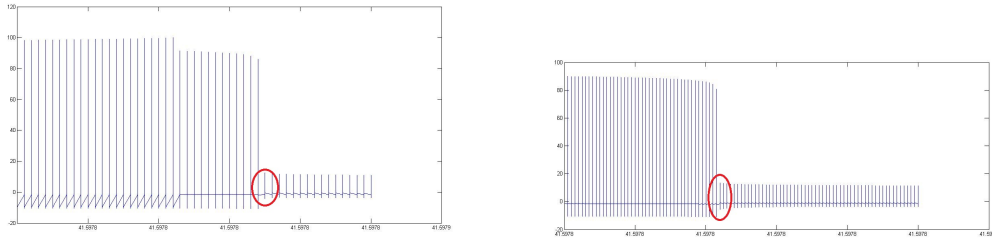


Figure 5.6: a)Bifurcation diagram of the 2nd neuron in a ring of neurons with nearest neighbour connectivity for $R = 12$ between 41.59780 to 41.59785 in 21 stepsb)Bifurcation diagram of the 2nd neuron in a ring of neurons with nearest neighbour connectivity for $R = 12$ between 41.59783 to 41.59785 in 21 steps

In the simulation we have checked for values of currents upto an accuracy of 10^{-5} and the results have been shown above. The level of accuracy needed to be improved in order to answer the question to a satisfactory level. We could do an analytical analysis in order to find whether a bifurcation is actually taking place at the point.

5.2.1 Different behavior observed in the simulations

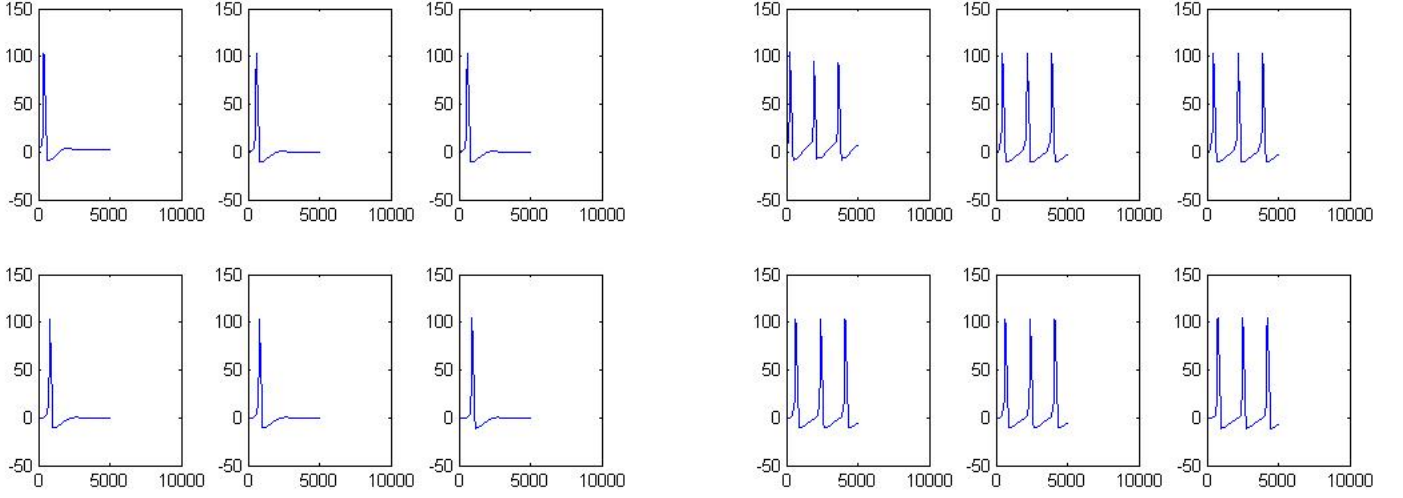


Figure 5.7: a) V vs t for all the 6 neurons when $I_{ext} = 5$, $R = 10$ b) V vs t for all the 6 neurons when $I_{ext} = 10$, $R = 10$. Simulation was carried out only for 5000 time steps

When $I_{ext} = 5$, all the neurons just give 1 spike and then the voltage does not change with time. When $I_{ext} = 10$ all the neurons exhibit spiking behaviour (the action potentials propagate through out the network without diminishing in size).

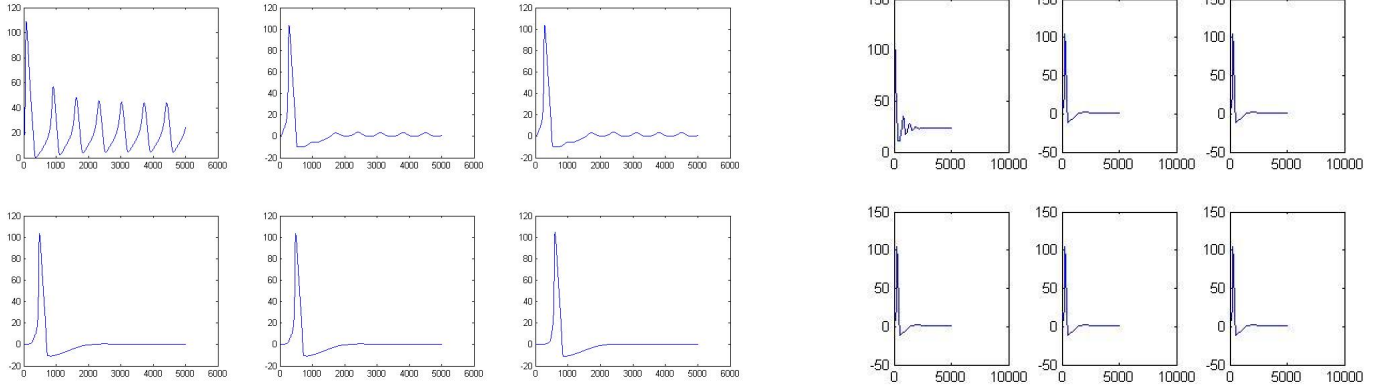


Figure 5.8: a) V vs t for all the 6 neurons when $I_{ext} = 100$, $R = 10$ b) V vs t for all the 6 neurons when $I_{ext} = 200$, $R = 10$

When $I_{ext} = 100$, All the neurons show some oscillatory behaviour. The first neuron shows some sharp changes in voltages. We distinguish this behaviour from the spiking behaviour as the signal is not propagated through out the network with out any loss of information. When $I_{ext} = 200$, all the neurons just give a single spike and then signal does not propagate.

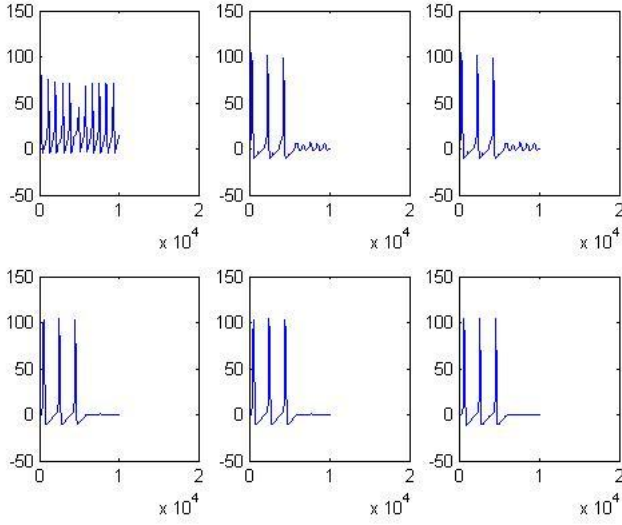


Figure 5.9: a) V vs t for all neurons for $I_{ext} = 51$, $R = 10$

For $I_{ext} = 51$, initially the signal propagates and all the neurons seem to fire action potentials, but it suddenly undergoes a transition and the signal propagates with certain loss of information associated with it.

We observe different kinds of behaviour where the system reaches a fixed point or goes to a limit cycle. For low values of current the system reaches a fixed point and then for a certain range of values all the neurons show spiking behaviour (generate action potentials), and then for a certain range of values all the neurons show oscillatory behaviour, where the action potentials are not generated but there is some lossy information that is being propagated through the network, and then for higher values of external current the system reaches a stable fixed point.

5.2.2 Phase space plots

Phase space plots for a ring of neurons

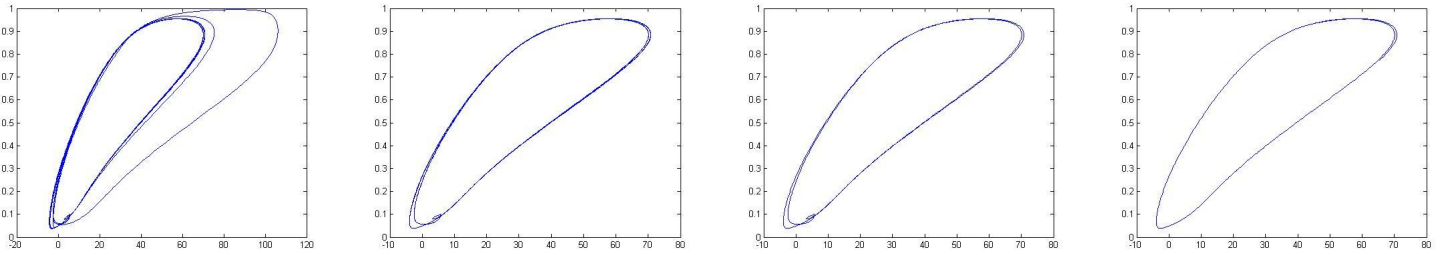


Figure 5.10: a) Phase space V vs m for time 0:10000, b) Phase space V vs m for $t = 5000:10000$, c) Phase space V vs m for $t = 8000:10000$, d) Phase Space V vs t for $t = 9000:10000$

The figures show that the system evolves slowly into a stable limit cycle when we start off with some initial conditions. The corresponding V vs time plots are shown below.

5.3 Ring of neurons(all of them connected)

All the neurons except the first one would be at a same level in that case. As expected all the plots for neurons 2 to 6 are similar. The figures show that the system evolves slowly into a stable limit cycle when we start off with some initial conditions.

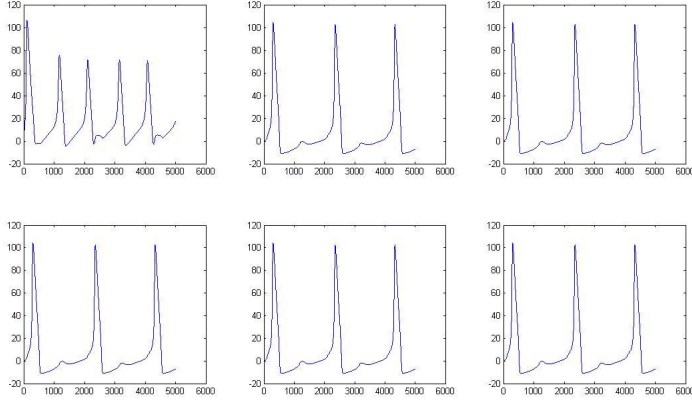


Figure 5.11: V vs t plot for al the 6 neurons I = 50, R = 10

5.4 Stability Analysis of fixed points for a ring of neurons

We have found out the nullclines of the system using analytical methods(by setting $dV1/dt$, $dV2/dt$ and $dV4/dt$ equal to zero and then solving the equations using algebraic methods. This is a system of 24 dimensional non linear ordinary differential equations, as there are six neurons and each neuron is associated with (V,m,h,n) variables.). We find out the jacobian of this system and find out the eigen values of the system. The results obtained for various values of external currents and resistance values are tabulated below.

-4.5454	-4.6349	-4.6494	-4.6591	-4.6328	-.021+.4604i	-.021-.4605i	-.031+.3625i
-.031-.3625i	-.191+.387i	-.191-.3871i	-.1166+.4012i	-.1166-.4012i	-.648+.3728i	-.648-.3728i	-.155+.3882i
-.1550-.3882i	-0.1284	-0.1207	-0.1213	-0.1211	-0.1213	-0.1209	-4.6724

Table 5.1: Eigen values corresponding to $I_{ext} = 5$ in a ring of neurons with nearest neighbour connectivity, R = 10,

-4.6143	-4.6887	-4.6764	-4.6211	-4.6474	.0626+.5368i	.0626-.5368i	-.1900+.3844i
-.19-.3844i	-.033+.3601i	-.033-.3601i	-.110+.3949i	-.110-.3949i	-0.1372	-.1530+.3911i	-.1530-.3911i
-.063+.3761i	-.063-.3761i	-.1206	-0.1215	-0.1210	-0.1215	-0.1209	-4.6586

Table 5.2: Eigen values corresponding to $I_{ext} = 10$ in a ring of neurons with nearest neighbour connectivity, R = 10,

-8.0211	.2758+.8764i	.2758-.8764i	-4.7271	-4.6521	-4.5690	-4.6537	-0.0424+0.359i
-.0424-.359i	-.0905+.409i	-.0905-.409i	-.1859+.3754i	-.1859-.3754i	-0.2583	-.0587+.4003i	-.0587-.4003i
-.1367+.4031i	-.1367-.4031i	-0.1200	-0.1210	-0.1233	-0.1210	-0.1233	-4.5687

Table 5.3: Eigen values corresponding to $I_{ext} = 100$ in a ring of neurons with nearest neighbour connectivity, R = 10,

-9.9473	-4.6736	-4.5547	-4.6414	-.162+1.1374i	-.162-1.1374i	-4.5550	-4.6479
-0.3426	-.0365+.3691i	-.0365-.3691i	-.0793+.425i	-.0793-.425i	-.1821+.388i	-.1821-.388i	-.0557+.413i
-.0557-.413i	-.1287+.4063i	-.1287-.4063i	-.1241	-0.1207	-0.1212	-0.1241	-0.1211

Table 5.4: Eigen values corresponding to $I_{ext} = 200$ in a ring of neurons with nearest neighbour connectivity, R = 10,

5.5 Conclusion

In this chapter we have studied different behaviour exhibited by a ring of neurons under the action of an external stimulus. We have done a fixed point analysis to validate our results. We observed that the numerical results obtained using Runge Kutta methods are in agreement with analytical results obtained by finding out the nullclines using algebraic methods and solving them. The fixed point as expected is stable for lower values of currents and then it loses stability for a while before it becomes stable again and there fore there are two bifurcations between a fixed point and a limit cycle and then form a limit cycle behaviour to a fixed point.

Chapter 6

Transitions to a limit cycle

Here we find an interesting way in which the system suddenly transits from what appears to be a limit cycle to the true limit cycle of the system

6.1 Neuronal networks

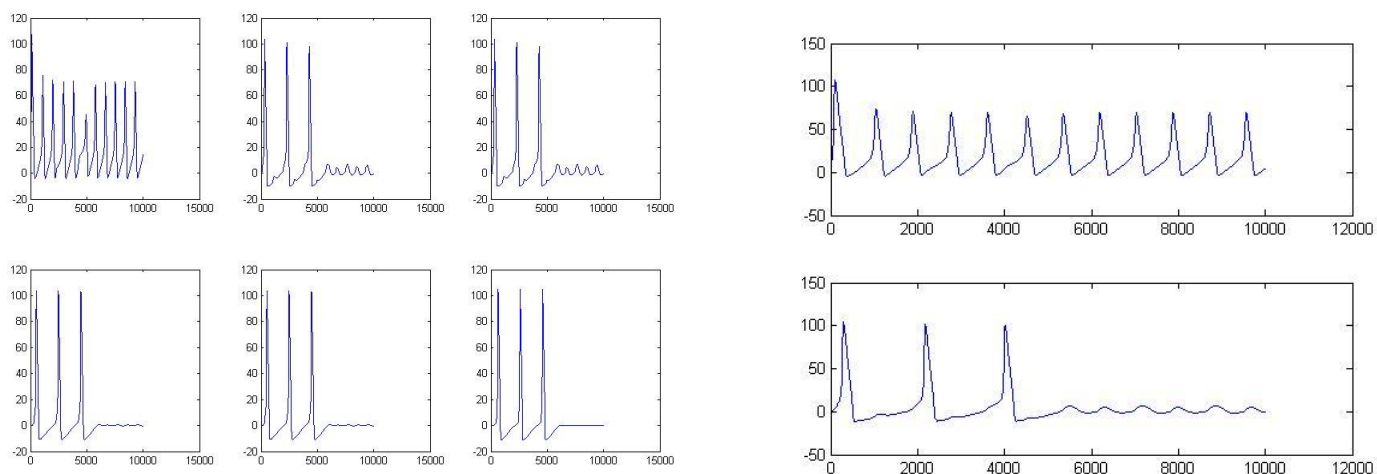


Figure 6.1: a) V vs time plot for a ring of 6 neurons, $I_{ext} = 51$, $R = 10$ b) V vs t for a 2 neuron network, $I_{ext} = 53$, $R = 10$. In both cases we see spiking behaviour that suddenly undergoes a transition to another smaller limit cycle. The spiking behaviour is like a 'ghost' limit cycle.

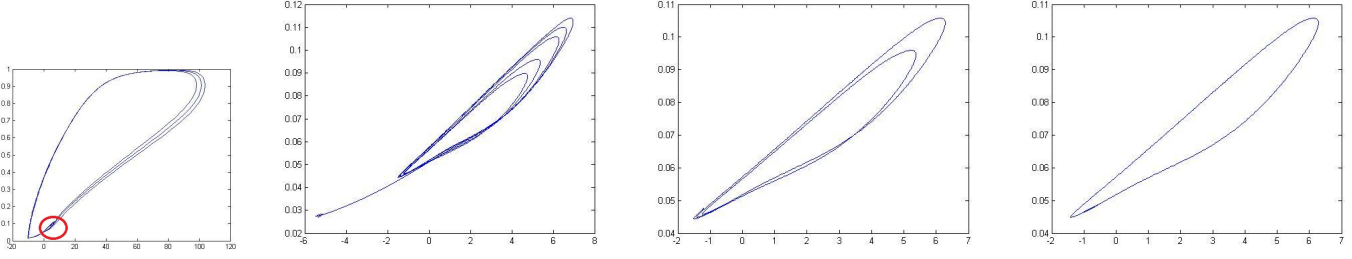


Figure 6.2: a)Phase space V vs m for the second neuron in a ring of six neurons for time 0:10000, b) Phase space V vs m for t = 6000:10000, c) Phase space V vs m for t = 8000:10000, d) Phase Space V vs t for t = 9000:10000

The different phase space plots shown in the figure above show a sudden transition behavior between some kind of a ghost limit cycle and the stable limit cycle the system finally lands in. The encircled region in figure (a) is blown up in figure (b). The trajectory goes around and it appears as though it is approaching a limit cycle at a particular region in space it suddely undergoes a transition and it finally reaches a stable limit cycle.

6.2 A 2-d system with a ghost limit cycle

We have formulated a mathematical expression to understand the sudden transition behavior from a ghost limit cycle to the limit cycle as exhibited by the network of neurons. We constructed the following 2-d system

$$\frac{dx}{dt} = y \quad (6.1)$$

$$\frac{dy}{dt} = -\exp\left[-\frac{(\text{sqrt}(x^2 + y^2 - 1))^2}{10}\right] + \exp\left[\frac{-(x^2 + y^2)}{10}\right] + \exp\left[\frac{-\text{sqrt}(x^2 + y^2) - 2)^2}{10}\right]) * (-y) * (x^2 - 1/3) * y) - x^5; \quad (6.2)$$

It can be seen in the phase plot that the trajectories starting at some distance from the stable limit cycle appear as though they approach a limit cycle but they undergo a sudden transition and they finally reach the smaller stable limit cycle. The phase space plots were constructed using Pplane8.

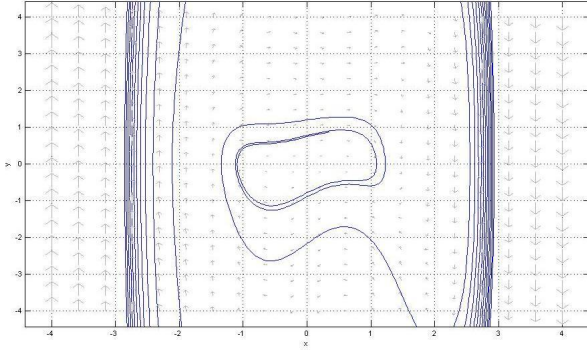


Figure 6.3: Phase space x vs y for the given mathematical model

Using Runge Kutta method we have numerically solve the system of equations and the y vs t plot for the system is shown below.

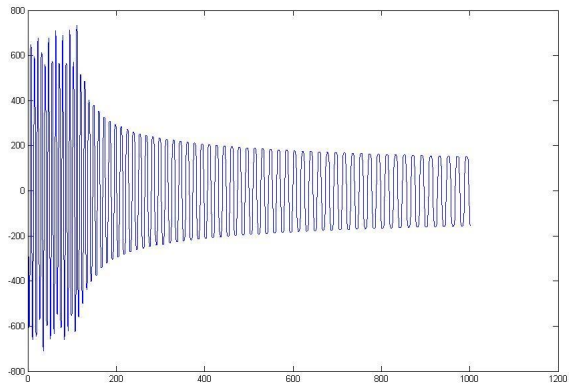


Figure 6.4: Y vs t plot for the above mathematical model

Y vs t plot for the 2D system is shown above.

Chapter 7

Discussions and Results

We had started off with a 2 dimensional HH model in order to validate our results and then we have carried out simulation of H-H equations for a single neuron by feeding a constant amount of external current into the neuron.

For single neurons, we observed that the system of equations undergoes a bifurcation from a fixed point to a limit cycle and then another bifurcation from limit cycle behaviour to a fixed point. When a constant amount of current is fed into the system, for low values of currents the system shows a fixed point behaviour. As the parameter I_{ext} increases the system finally lands up in a limit cycle where the neuron shows spiking/oscillatory behaviour. Then for high values of external current, the system reaches a fixed point again.

We also studied the dynamics of two neurons coupled electrically and pumped current into only one of the neurons. We had also connected 6 electrically coupled HH neurons in a ring with nearest neighbour connectivity and observed a qualitatively similar behaviour for both the systems. Here we summarize the results of our simulations

- For low values of currents both the systems showed a fixed point behaviour and the signals do not propagate through the network.
- As we keep increasing the external current all the neurons show spiking behaviour (action potentials). When spikes generated by one neuron propagate through the network without diminishing in size we refer to it as spiking behaviour. The spikes generated are propagated through out the network without loss of information.
- Then as we increase the amount of external current into the neuron the neurons show oscillatory behaviour where the neuron into which current is pumped shows sharp changes in voltages and the rest of the neurons show oscillatory behaviour with small amplitudes.
- For higher values of current all the neurons land up in stable fixed points. The behaviour is qualitatively same in both the networks that we have built.
- We also tried to find out if there were any other attractors in the phase space of these systems by starting off with random initial conditions and we found out that the limit cycles/ the fixed points the system finally reaches is the only stable attractor in the phase space.
- We have also observed some sudden transition behaviours between a ghost limit cycle and a stable limit cycle of the system in a network of neurons. We have made a 2 dimensional mathematical model that helps us to understand the underlying origin of this sudden transition.
- We have also found out that once action potentials start propagating, even if we connect a large number of neurons in a network the signals propagate through out the network with no loss of information.