Dynamics of the Fitzhugh-Nagumo Neuron Model

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Abstract

In this paper, the dynamical behavior of the Fitzhugh-Nagumo model is examined. The relationship between neuron input current and the firing frequency of the neuron is characterized. Various coupling schemes are also examined, and their effects on the dynamics of the system is discussed. The phenomenon of stochastic resonance is studied for a single uncoupled Fitzhugh-Nagumo neuron.

Introduction

What is it that makes humans unique among the many different species that inhabit this planet? What is the defining characteristic that has put our species at the top of the food chain when our physical adaptations should have left us behind in terms of physical predation advantages? While a case can be argued from many vantage points, the strongest case is that it is intelligence that has made humans the dominant form of life on Earth. But where does intelligence come from?

The easy answer to give is that humanity's intelligence advantage stems from the fact that our brains are more developed than those of other species. However, for the most part the brain has just been treated as gray matter that lights up with electrical pulses that drive neural activity in its many incarnations. This led some ancient Greeks to the conclusion that the brain wasnt nearly as important to human existence as the heart.

This lack of fundamental understanding of neural systems has led humanity to apply its intelligence to the problem of where intelligence comes from in the last century and with the advent of computers much progress has been made. During the 1950s two scientists by the names of Hodgkin and Huxley began experimenting with the giant squid axon in order to come up with a set of differential equations that govern the physics of neural activity. Their point neuron model is made up of four coupled differential equations and four variable functions and it has become the bellwether for physically accurate simulations in the field of computational neuroscience. For this project I will be exploring a simplified version of the Hodgkin-Huxley (HH) model, the Fitzhugh-Nagumo (FN) model in the context of nonlinear dynamical systems and bifurcations with the variation of the key parameter for neuron dynamics, namely the input current.

The FN model is useful for becoming acquainted with the mathematical modeling of physically accurate point neurons. This paper describes a method by which MATLAB is used to numerically approximate the solutions to the two coupled nonlinear differential equations that make up the FN model. Various coupling schemes are briefly examined and others can be implemented using the MATLAB code provided in Appendix I. In addition, varying amounts of noise was added to the input of a single neuron to study stochastic resonance effects. Stochastic resonance is a phenomenon where the addition of an optimal amount of noise to the subthreshold input signal of a single uncoupled point neuron makes the conditions more favorable for a neuron to fire. The improved signal response is found using the signal to noise ratio of the power spectrum of the neuron output signal as the noise amplitude is increased.

Experimental Design

For all of the numerical simulations performed in this project, the specific mathematical model that is used is the primary feature of the analysis of FN model dynamics. The variation of the model used for all simulations performed in this paper comes from a modification to the van der Pol oscillator, named the Bonhoeffer van der Pol oscillator by Fitzhugh in his original paper [1]. The proof that verifies the modification to the van der Pol oscillator that is required to obtain the Fitzhugh-Nagumo model is provided in Appendix II. The FN model is expressed as

$$\dot{v} = c\left(v - \frac{1}{3}v^3 + r + I\right), \tag{1}$$

$$\dot{r} = -\frac{1}{c}\left(v - a + br\right), \tag{2}$$

where v is the rate of change of the neuron membrane potential with respect to time, a, b and c are constants and r is the recovery variable for the neuron membrane potential having to do with fast and slow diffusive ion currents in the neuron [2]. This is a system of two first order coupled nonlinear ordinary differential equations and possible solutions to the equations can be found given certain values of the constant parameters and the input current. To find the solutions to a set of differential equations MATLAB has an ode45 numerical solver package that will approximate the solutions using an algorithm based on the fourth and fifth order Runge-Kutta method. For all of the simulations in this paper however, a custom fourth and fifth order Runge-Kutta algorithm is implemented for numerical solution of the system.

Neurons commonly exhibit a relaxation time after firing that prevents them from firing for a short time. They also experience a threshold phenomenon where the neuron doesn't fire until a threshold for the input current is reached. Qualitatively, before the input threshold is reached our neurons exhibit a stable spiral in phase space down to some fixed point dependent on the model being studied. When the input current I reaches a certain stimulus threshold however, the system undergoes a supercritical Hopf bifurcation where the stable fixed point in the system makes a transition to an unstable fixed point surrounded by a stable limit cycle. The limit cycle of the neuron in phase space describes the periodic signal of the neuron membrane potential as it evolves in time.

In Strogatz's book [3], he presents a method shown by Guckenheimer and Holmes through which we can more rigorously determine the type of Hopf bifurcation that is occurring in our system using

$$16a = f_{xxx} + f_{xyy} + g_{xxy} + g_{yyy} + \frac{1}{\omega}\left(f_{xy}\left(f_{xx} + f_{yy}\right) - g_{xy}\left(g_{xx} + g_{yy}\right) - f_{xx}g_{xx} + f_{yy}g_{yy}\right), \tag{3}$$

and determining the sign of a. If a <0 the system undergoes a supercritical Hopf bifurcation and if a >0 then the system undergoes a subcritical Hopf bifurcation. This is all assuming that the system can be written as

$$\dot{x} = -\omega y + f(x, y), \tag{4}$$

$$\dot{y} = \omega x + g(x, y). \tag{5}$$

By rearranging terms in the FN model we find that it can be written as

$$
\begin{aligned}
f(v,r) &= cv - \frac{c}{3}v^3 \\
g(v,r) &= \frac{br}{c}, \qquad \text{therefore using (3)} \\
16a &= -2c + 0 + 0 + 0 + \frac{1}{\omega}\left(0 - 0 - 0 - 0\right).
\end{aligned}
$$

This means that for our system a = -c/8, where the constant c = 3 because this is the range of physical system behavior for the model. Since a = -3/8, a < 0 and it has now been shown that the system undergoes a supercritical Hopf bifurcation when the neuron membrane input current reaches the threshold required for the neuron to begin firing.

As the constant input current in the model is increased from zero, the firing frequency of the neuron is examined using MATLAB. The reason that the firing frequency is of interest is because it is presently thought that information is encoded in neurons by the frequency at which they are firing. The frequency response is studied by increasing the input current I, from the value at which the supercritical Hopf bifurcation occurs up until the neuron becomes overstimulated. Beyond that point the system goes from its limit cycle behavior back to critically damped behavior, where it again settles to a fixed point. By measuring the firing frequency as a function of the input membrane current, the relationship between input current and neuron firing frequency is determined.

Multiple FN units can be coupled together through various methods by adding a coupling term to each point neuron. This is a method for simulating networks of FN neurons. By examining the system behavior and dynamics with the variation of the system parameters for coupled neurons the behavior of large networks of these neurons can be studied. By comparing the dynamics of networks of these FN neurons with the experimental observations, agreement between experiment and the theory of the FN model can be determined. We will examine a network of four linearly coupled neurons given by

$$
\begin{aligned}
\dot{v_1} &= c\left(v - \frac{1}{3}v^3 + r + I + k(\dot{v_2} - \dot{v_1})\right), \\
\dot{r_1} &= -\frac{1}{c}\left(v - a + br\right), \\
\dot{v_2} &= c\left(v - \frac{1}{3}v^3 + r + k(\dot{v_1} - \dot{v_2}) + k(\dot{v_3} - \dot{v_2})\right), \\
\dot{r_2} &= -\frac{1}{c}\left(v - a + br\right), \\
\dot{v_3} &= c\left(v - \frac{1}{3}v^3 + r + k(\dot{v_2} - \dot{v_3}) + k(\dot{v_4} - \dot{v_3})\right), \\
\dot{r_3} &= -\frac{1}{c}\left(v - a + br\right), \\
\dot{v_4} &= c\left(v - \frac{1}{3}v^3 + r + k(\dot{v_3} - \dot{v_4})\right), \\
\dot{r_4} &= -\frac{1}{c}\left(v - a + br\right).
\end{aligned}
$$

These equations represent four individual FN neurons, coupled via the coupling constant k multiplied by the difference of the membrane potentials of the nearest neighbors, influencing the membrane potential of the given neuron. Since the example shown is a linear coupling, we expect the first and last neuron in the coupled network to have fewer coupling terms and this is the case. To establish circular coupling, a second coupling term would be added to both the first and last neuron in the coupled network which would make the membrane potential of each of the end neurons depend upon each other.

By changing the value of the coupling constant k, the strength of the coupling between the neurons is controlled. If desired, different coupling constants can be used for the different connections between the neurons to examine the effects on the network dynamics that a variable coupling would have. The methods for coupling examined here are just two of the many that are available for implementation using the FN model. Linear and circular coupling are simple to understand and provide a good introduction to coupling FN neurons. However, actual coupling between neurons in the brain is not so uniform or well-structured. A more complex coupling method known as small worlds coupling [4], randomly couples the neurons within the network.

Important aspects of examining the dynamics of coupled neurons is to examine how the addition of more FN neurons to the system effects the overall system dynamics. This means that the inputsignal threshold for firing may change with the coupling of more neurons together. The firing frequency of the coupled network as a function of the input signal may also undergo different behaviors as the coupling characteristics are changed. If analyzed as a nonlinear dynamical system, bifurcations for the system can be studied as the strength and type of coupling is modified.

Nonlinear systems like that of the FN model are also a testing ground for the phenomenon of stochastic resonance. Stochastic resonance (SR) is a tendency of some nonlinear systems to exhibit more favorable signal response with the addition of an optimal amount of noise to the signal [5]. In the context of the present discussion of the FN model, the nonlinear system is the coupled FN nonlinear system of equations. By adding noise to the input parameter of a single uncoupled neuron, the effects of SR are studied. However, SR cannot generally be characterized and there is much debate about how to quantify SR's effects. The most agreed upon method is to use the signal-to-noise (SNR) ratio which is what is used for the findings of this paper.

In order to study SR in the FN model, we start out simply. By studying one uncoupled neuron, the signal transmission characteristics of the FN neuron as a function of noise amplitude can be measured in isolation from an entire network. After gaining more knowledge about the general characteristics and dynamics of SR as a phenomenon, then a more developed and complete understanding of the effects of SR on an FN network can be achieved.

To introduce noise to the input parameter of a FN neuron we use MATLAB's randn function, that generates random numbers with a Gaussian distribution, and add it to the input parameter of (1) to get

$$\dot{v} = c\left(v - \frac{1}{3}v^3 + r + I + NA. * randn\right), \tag{6}$$

$$\dot{r} = -\frac{1}{c}\left(v - a + br\right), \tag{7}$$

where the final term inside the parenthesis of (6) is the added noise. By setting the input parameter I to a value that is subthreshold, ie below the firing threshold of the neuron, without the noise we have a neuron that doesn't fire. However, with the addition of noise to the input parameter the neuron may be excited above its threshold and fire. By varying NA, the noise amplitude, and measuring the SNR of the output membrane potential signal of the FN neuron, a general relationship between the noise amplitude and the SNR showing positive effects of noise can be found.

Analysis

First we'll acquaint ourselves with the membrane potential of an FN neuron both as a function of time and the phase space trajectory of the system without noise. Figure 1 shows the membrane potential of one FN neuron without an input, I = 0. Figure 2 shows the phase space trajectory of a single uncoupled neuron, I = 0. As the magnitude of the input parameter is increased from zero we see the phase space trajectory make the transition from a spiral to a stable fixed point for the system to a stable limit cycle. This transition indicates a supercritical

Hopf bifurcation. Figure 3 shows the neuron membrane potential with respect to time as the magnitude of the input parameter is increased to some value above zero. Figure 4 shows the phase space trajectory of the neuron for the same neuron as Figure 3. The spiral down to a fixed point becomes stretched with the increased input parameter until it makes the transition to a limit cycle. An important side note is that for this particular FN model, the input parameter is negative in order for the system to exhibit physical behavior. Figure 5 shows the membrane potential for a single uncoupled FN neuron after the input parameter has surpassed the firing threshold for the neuron. The phase space trajectory corresponding to this behavior is shown in Figure 6 and shows a limit cycle.

After the general dynamics of a single FN neuron have been examined and verified with theoretical expectations the task at hand is to couple two Fitzhugh-Nagumo neurons. Figure 7 shows the first and second neuron's behavior without any initial input current. Figures 8 shows the first and second neurons with an input current equal to the critical value associated with the supercritical Hopf bifurcation normally undergone by a single uncoupled neuron. Since these two figures don't show limit cycle behavior normally associated with supercritical Hopf bifurcations yet, we know that the coupling of the second neuron that does not receive the same input signal, changes the value of the supercritical Hopf bifurcation for first neuron as we would expect. Figure 9 and 10 show the behavior of both neuron 1 and neuron 2 as the input current is increased. Figure 10 shows the neurons exhibiting limit cycle behavior common to a system that has undergone a supercritical Hopf bifurcation.

After two neurons have been successfully coupled within the RK45 solver and observed to behave as we would expect coupled oscillators to behave theoretically, the effects of coupling between multiple neurons with various different coupling schemes can be studied. Once this examination of coupling schemes has been performed and the more realistic coupling scheme has been selected, more subtle dynamical behaviors of the system such as SR are studied. However, before moving on to studying SR there are other basics of coupled FN system behavior that must be developed.

To begin with, the relationship between the neuron firing frequency and the magnitude of the input current is simulated. Figure 11 shows that as the input current is increased, the firing frequency of the neuron also increases, leveling off around I = 0.9, as we would expect from theory. Figure 8 shows the neuron with input in blue and the neuron that is only coupled without an input current in red. The membrane potential offset is a result of the fact that the coupled neuron has no input and so lacks stimuli that the driver neuron has as a result of direct input.

For a more in depth analysis of the coupled system dynamics for 2 linearly coupled neurons using the RK4 algorithm, the coupling constant is varied with a changing input signal. The first goal was to apply an input current so that the driving neuron fires regularly with the coupling constant k = 0. After this was accomplished we began increasing the coupling constant between the driving neuron and the coupled neuron. Figure 12 shows the driving neuron with k = 0 and with the driving neuron firing regularly. As we increase the coupling constant up to k = 0.1 we see from 13 that the coupled neuron is more responsive to the driving neuron at this stronger coupling as we would expect.

When we reach a coupling strength of k = 0.104 our coupled neuron undergoes more exotic firing behavior as shown in Figure 14. As we increase the coupling strength still further we find that at a coupling strength of k = 0.11 we can see from Figure 15 that both the driving neuron and the coupled neuron are experiencing period tripled behavior. Increasing the coupling to k = 0.112 gives us the behavior shown in Figure 16 where both the driving and coupled neuron seem to be experiencing something that looks like period quadrupling. Since increasing the coupling constant is providing interesting behavior for both the driving and coupled neurons we want to find the next realm of coupling strength where both neurons are firing regularly.

This occurs when the coupling strength is k = 0.12. Figure 17 shows both the driving neuron and the coupled neuron firing regularly. Both neurons are firing at an almost identical frequency, the same as the uncoupled neuron for the same input, and as we would expect from the physical characteristics of our system the coupled neuron's response lags the driving neuron slightly but as previously mentioned both neurons are firing at the same frequency.

Now our objective is to see what effect noise has on the firing characteristics of the coupled neuron at an originally sub-threshold coupling strength when the driving neuron is firing regularly. In order to study, in the simplest way, the response of the coupled neuron in the presence of noise, we consider a single unit receiving a sub-threshold, periodic input signal and additive noise. The sub-threshold periodic signal represents the input received via the coupling term when the driving neuron is firing.

Finally, the signal to noise ratio as a function of the input noise amplitude for a neuron receiving sub-threshold periodic signal is examined. At each noise amplitude NA, the expected frequency peak is found by observation to be f = 79.43 Hz. After subtracting this peak region from the power spectrum data, I averaged the relative power of the remaining frequencies present in the power spectrum due to noise. By doing this I had generated an average relative power in the noise for the neuron membrane potential signal, for a given NA. For a particular numerical example the relative power in the noise was found for NA = 3 to be NRP = $1.0749 \text{x} 10^4$. After this I determined the relative intensity of the neuron membrane potential signal at the expected firing frequency. This was determined, for NA = 3, to be SRP = $1.13 \text{x} 10^6$. After both of these values were determined, they're plugged into the formula

$$SNR = 10 * log_{10}\left(\frac{SRP}{NRP}\right), \tag{8}$$

to find a signal-to-noise ratio of SNR = 20.31 for NA = 3.

After this was completed the SNR is calculated in the same way as already described for the remainder of the noise amplitudes. Figures 18 through 21 show examples of the neuron membrane potential signals and their corresponding power spectra for the noise amplitudes of NA = 0.6 , and NA = 0.8. Figure 22 shows the relationship between the SNR and NA for this study. However, further investigations are required in order to characterize this relationship with more certainty. The code provided in Appendix I provides the details of how the average relative power in the noise and the SNR for each power spectrum is determined.

Conclusion

This paper has explored some of the details of the dynamics of the FN model. Coupling between neurons is found to have a large effect on the overall dynamics of the system by increasing the dimensionality of the system through the coupling term. The increase in the input parameter is also found to have the effect of increasing the firing frequency of the individual neurons simulated in the FN model. Stochastic resonance for a single neuron is also examined and the noise amplitude is found to have an optimal range for enhancing system signal transmission as expected from theory.

To continue the analysis presented herein, SR could be studied for systems of coupled neurons. This would provide the opportunity to study large networks of coupled FN neurons and compare the results with the reality of empirical data on neural dynamics. Studying the dynamics for large networks of coupled neurons could also provide insights into the way in which information is encoded in large scale neuron networks. This in turn would have profound impacts on the human understanding of how the brain works from the fundamental level up to a network the size of an animals brain. For an advanced mathematical analysis, delay differential equations could also be introduced into the model to additionally simulate the fact that membrane potential signals take time to propagate through the system. It is very likely that incorporating such a delay into the model would also alter the system dynamics in ways previously unknown.

Figures

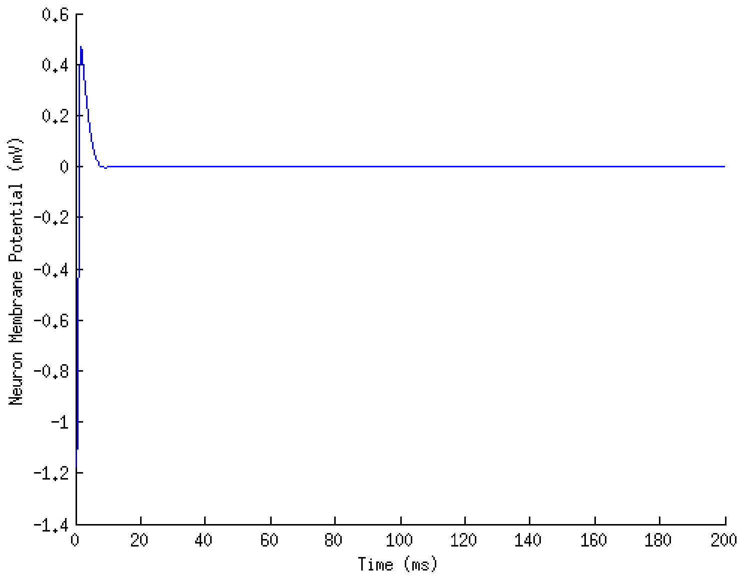

Figure 1: I = 0, zero input neuron membrane potential over time, no noise.

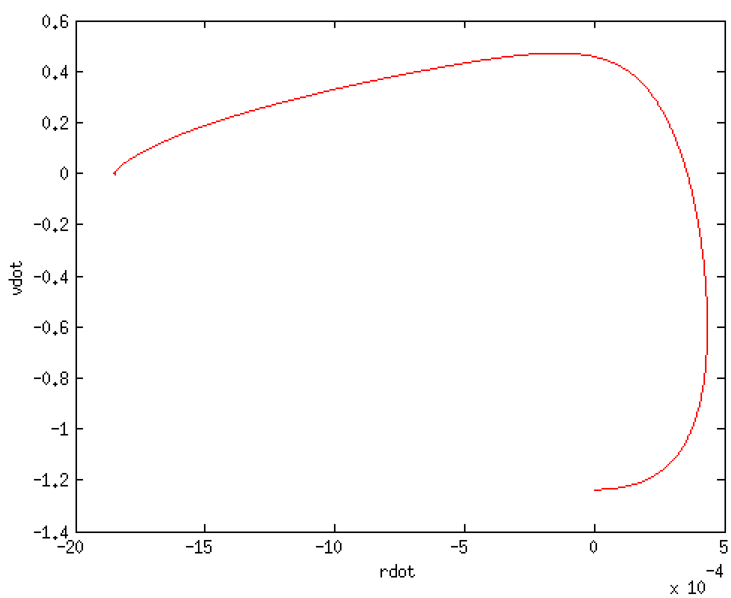

Figure 2: Phase plot of I = 0 FN neuron, no noise.

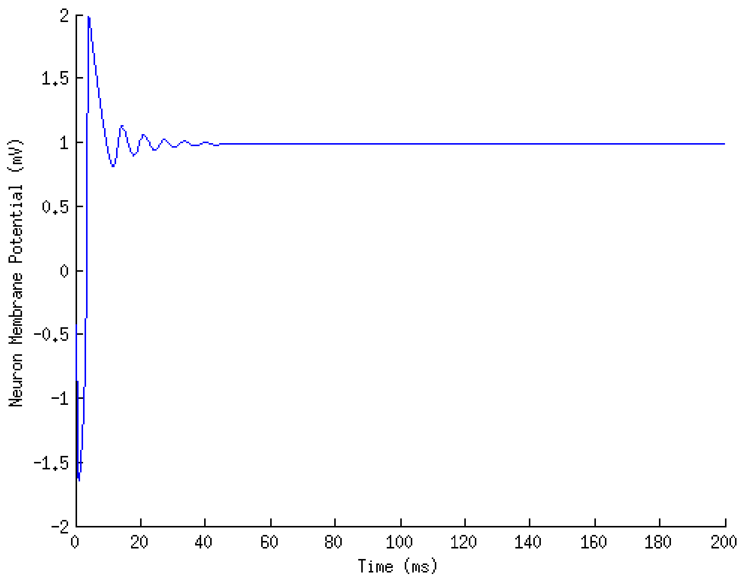

Figure 3: Non-zero subthreshold input neuron membrane potential over time, no noise.

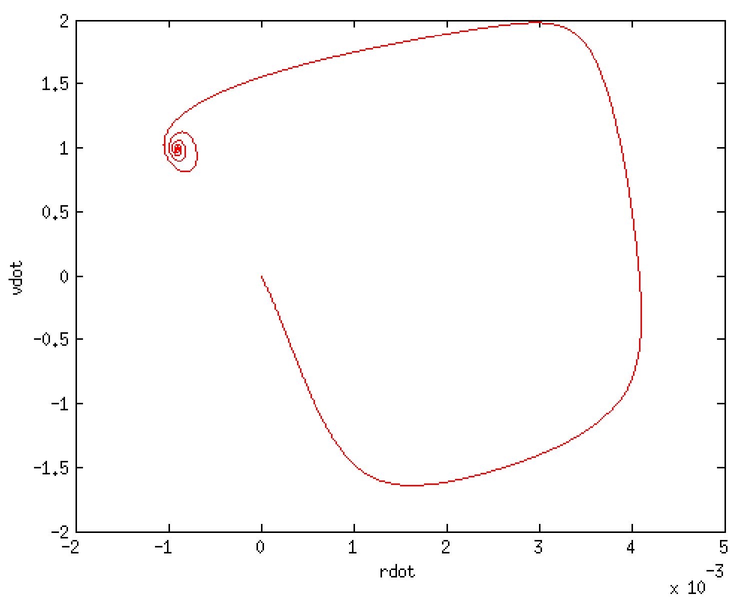

Figure 4: Phase plot of non-zero subthreshold input FN neuron, no noise.

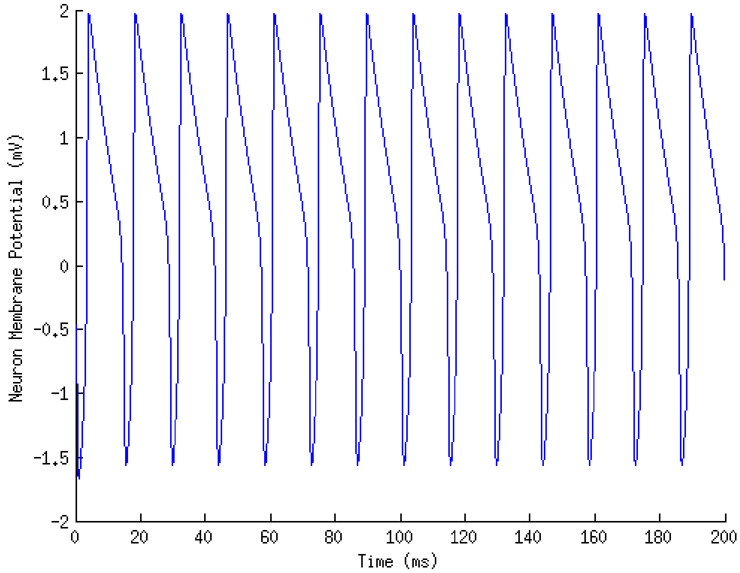

Figure 5: I = -0.39, membrane potential, no noise.

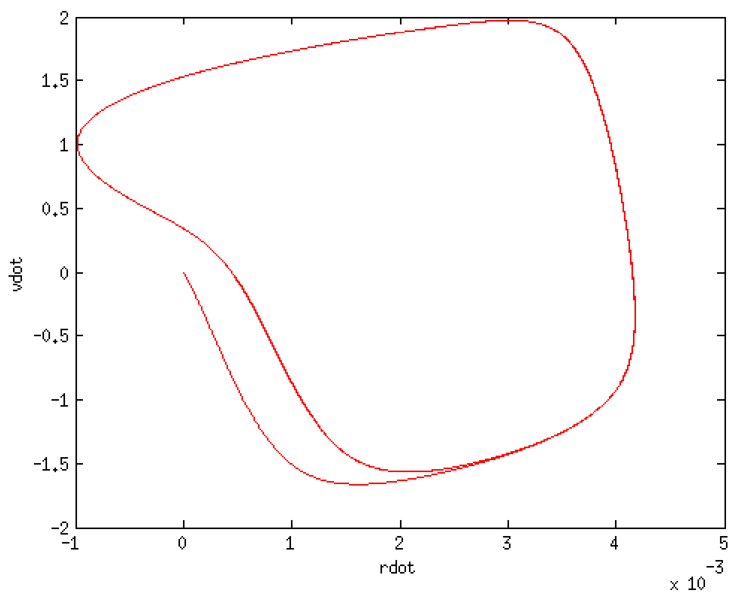

Figure 6: I = -0.39, limit cycle in phase space, no noise.

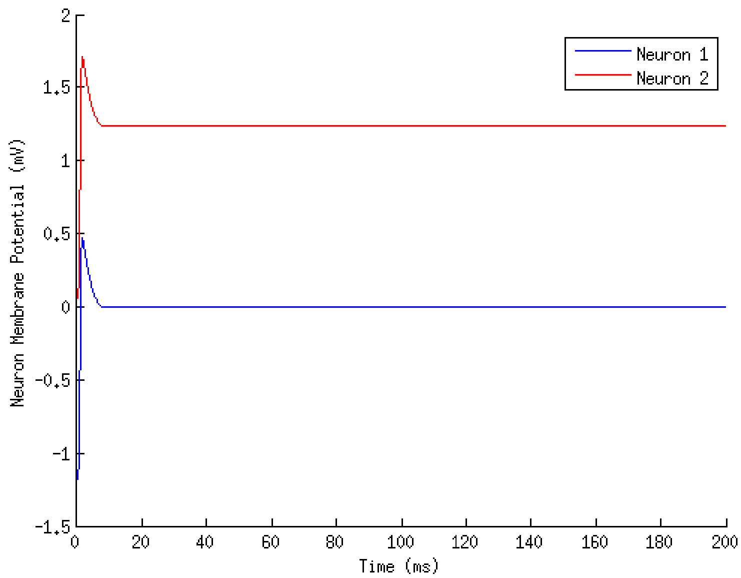

Figure 7: I = 0, two linearly coupled FN units, no noise.

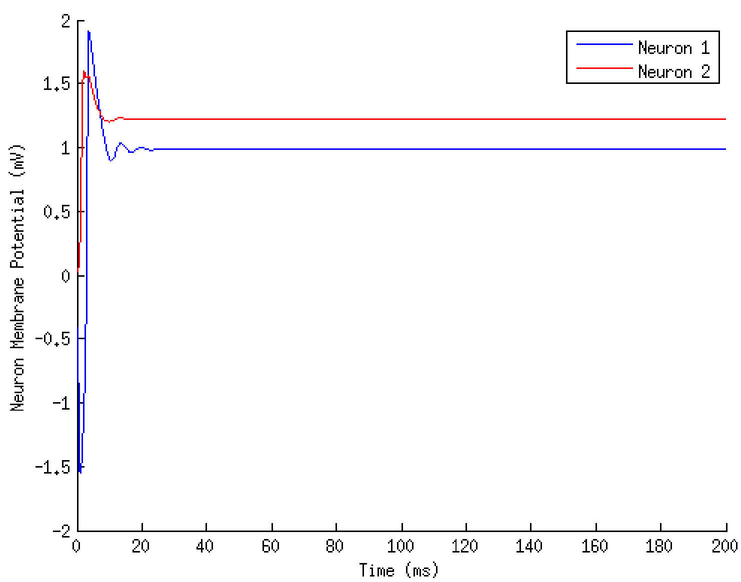

Figure 8: I = -0.39, two linearly coupled FN units, no noise.

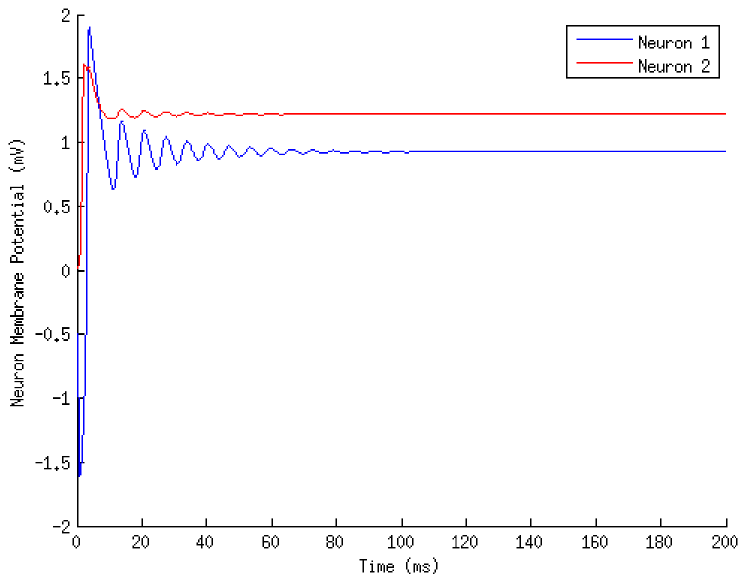

Figure 9: I > -0.39, two linearly coupled FN units, no noise.

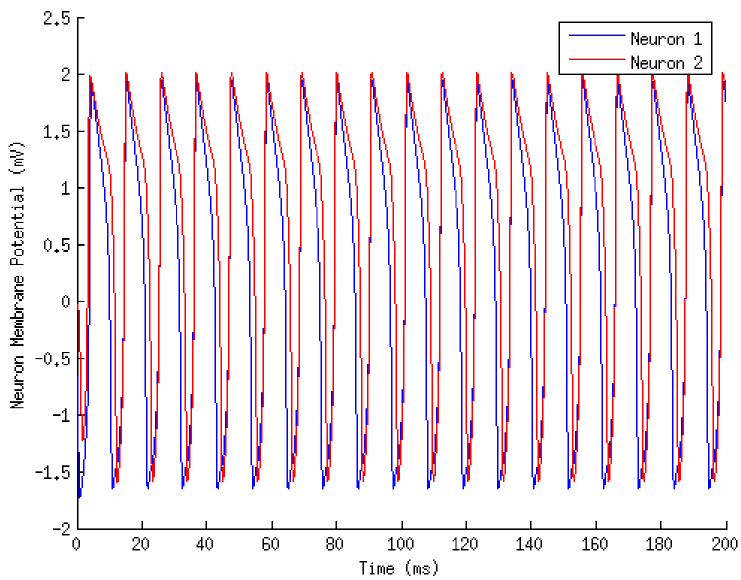

Figure 10: I > threshold, two linearly coupled FN units, no noise.

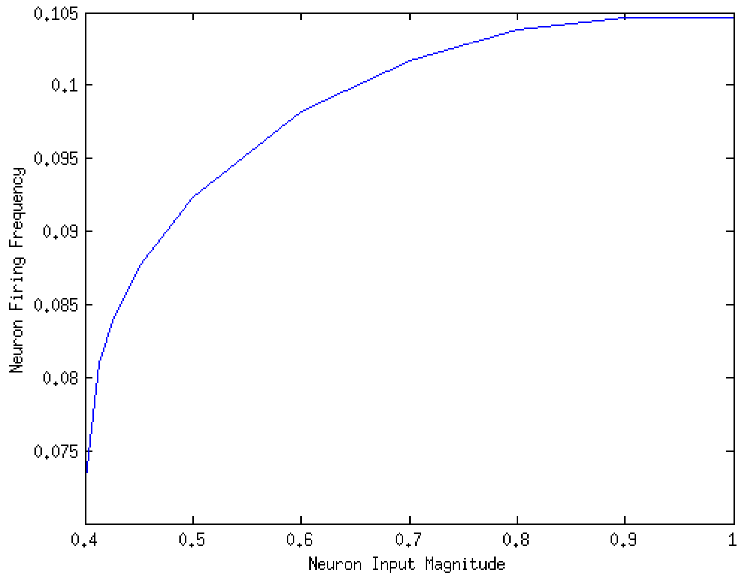

Figure 11: Neuron membrane potential firing frequency (kHz) as a function of input signal magnitude (mV).

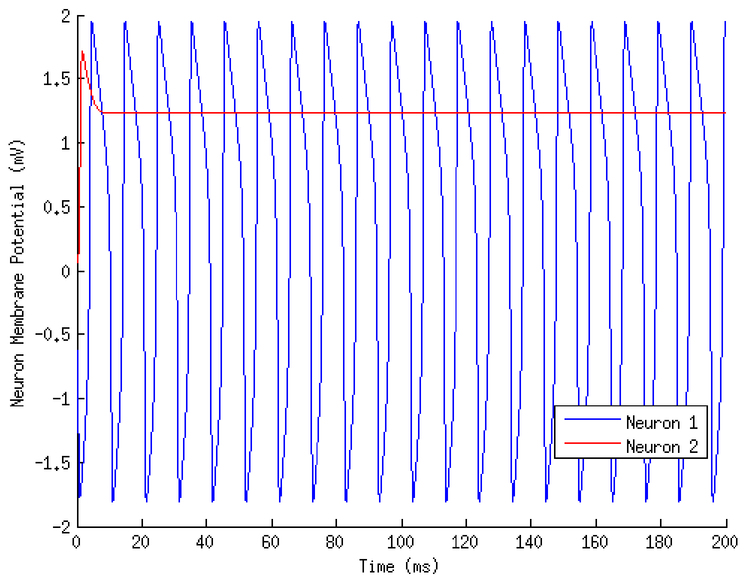

Figure 12: I = -0.58, k = 0, two linearly coupled neurons with initial conditions all set to zero. This is the RK4 solution. As we can see, the driving neuron is firing regularly while the coupled neuron is not.

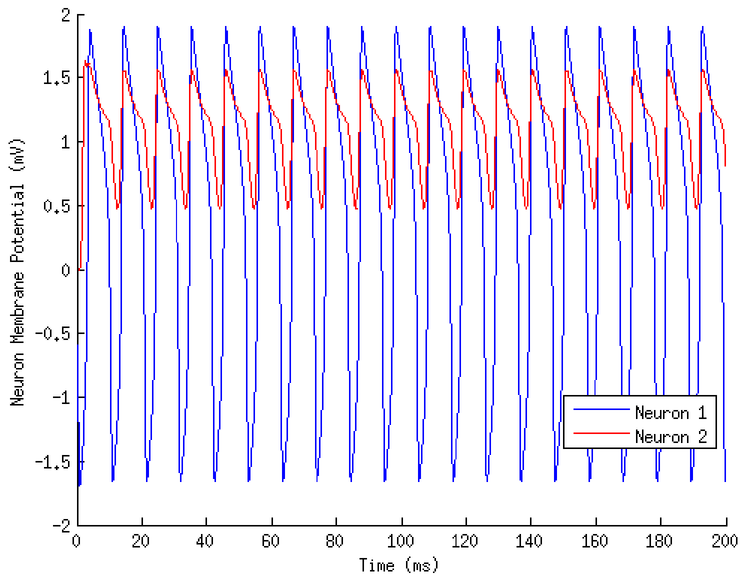

Figure 13: I = -0.58, k = 0.1, two linearly coupled neurons with initial conditions all set to zero. This is the RK4 solution. As we can see, the driving neuron is firing regularly while the coupled neuron is showing more of a response to the driving neuron.

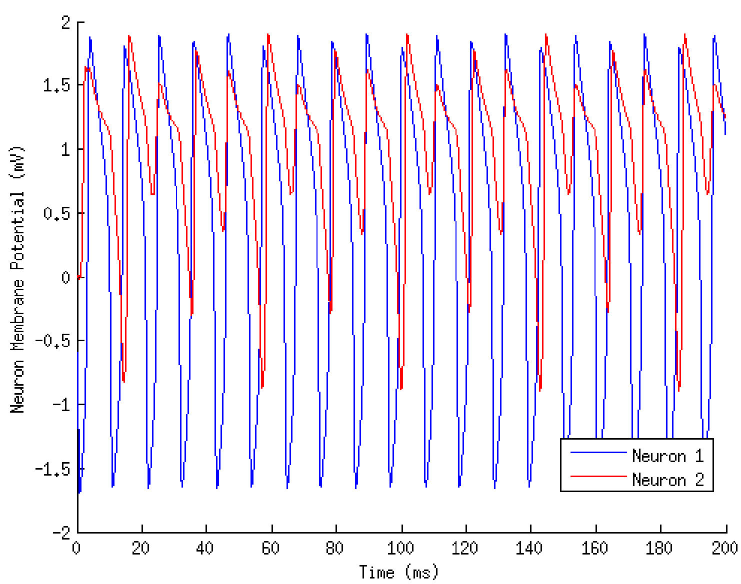

Figure 14: I = -0.58, k = 0.104, two linearly coupled neurons with initial conditions all set to zero. This is the RK4 solution. As we can see, the driving neuron firing regularly while the coupled neuron is experiencing more exotic firing behavior.

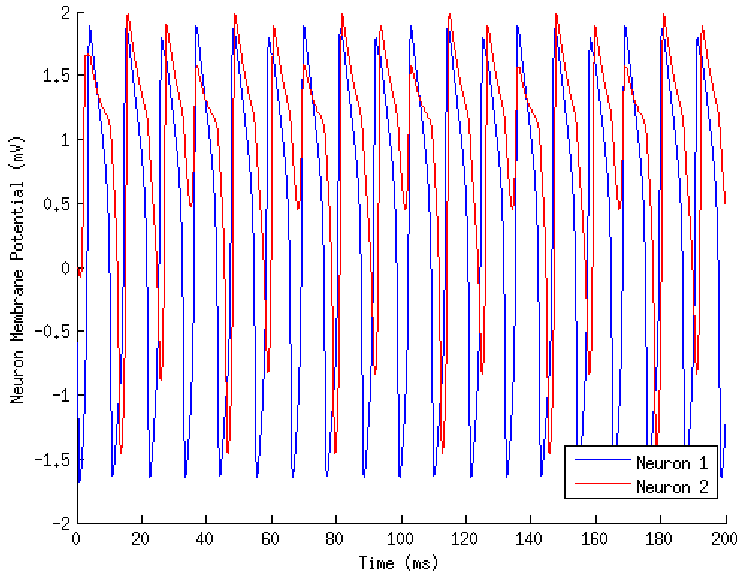

Figure 15: I = -0.58, k = 0.11, two linearly coupled neurons with initial conditions all set to zero. This is the RK4 solution. As we can see, at this coupling strength both the driving neuron and the coupled neuron are undergoing period tripled behavior.

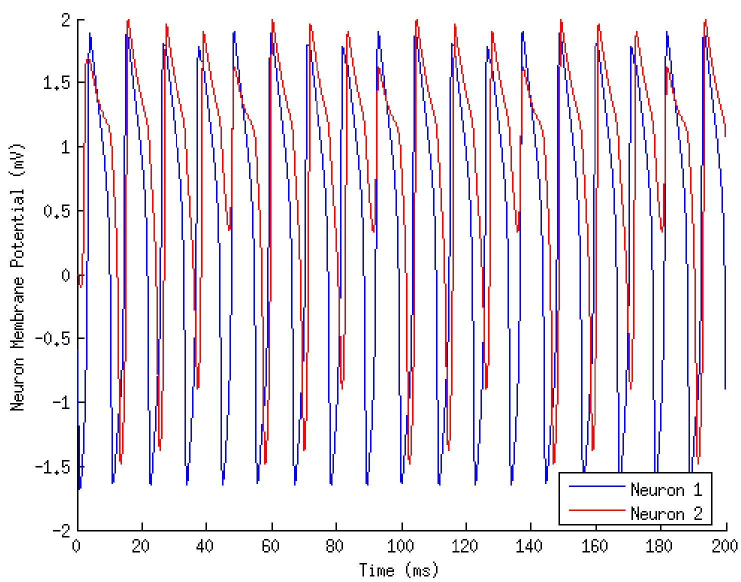

Figure 16: I = -0.58, k = 0.112, two linearly coupled neurons with initial conditions all set to zero. This is the RK4 solution. As we can see, both the driving and the coupled neuron are experiencing period quadrupled behavior.

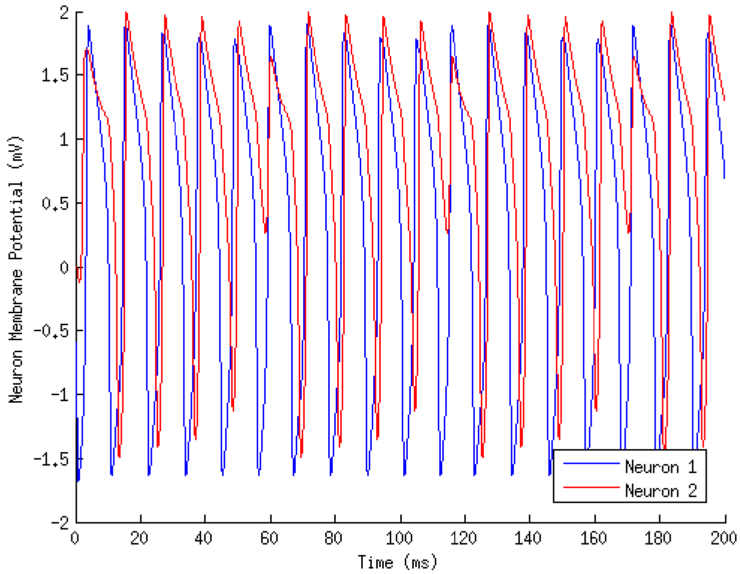

Figure 17: I = -0.58, k = 0.113, two linearly coupled neurons with initial conditions all set to zero, no noise.

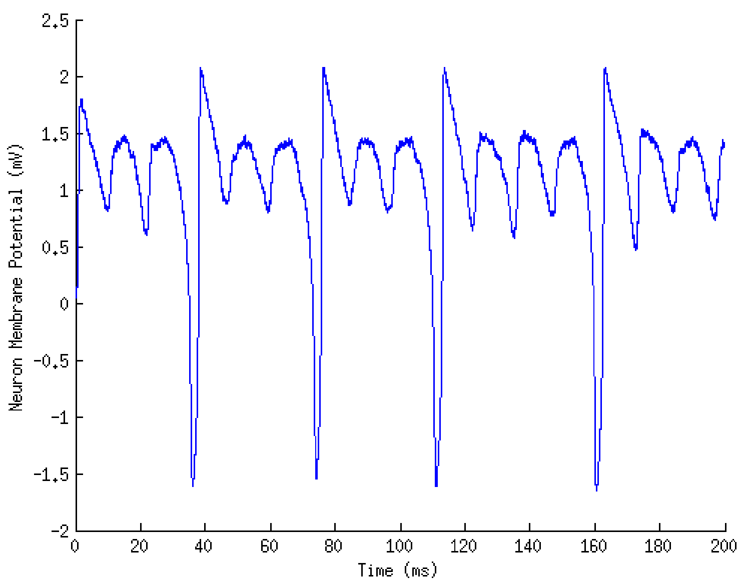

Figure 18: Subthreshold neuron membrane potential signal with respect to time for NA = 0.6.

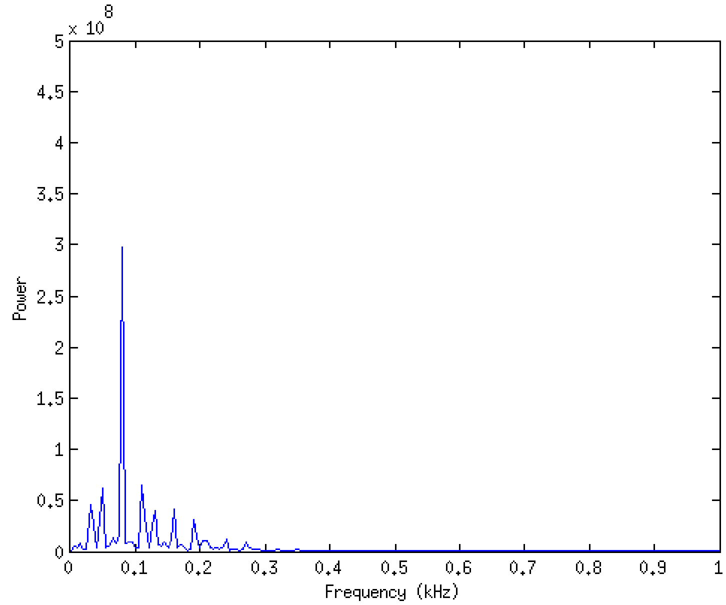

Figure 19: Power spectrum of the neuron membrane potential signal for NA = 0.6.

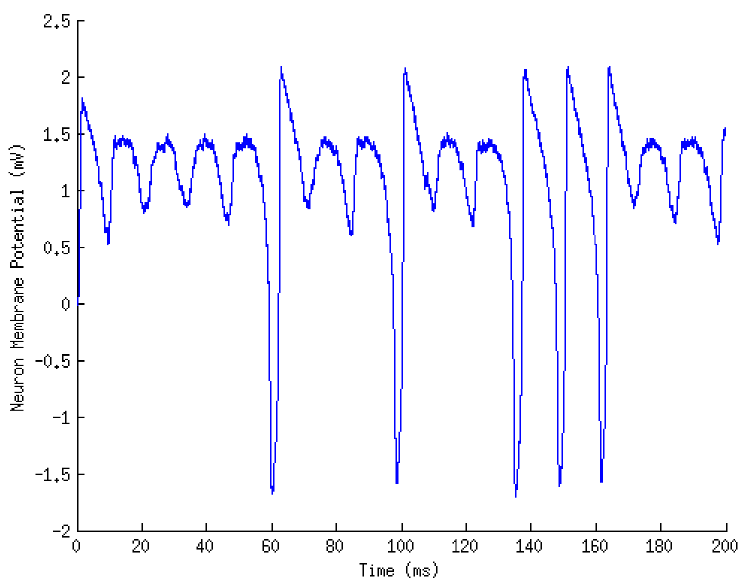

Figure 20: Subthreshold neuron membrane potential signal with respect to time for NA = 0.8.

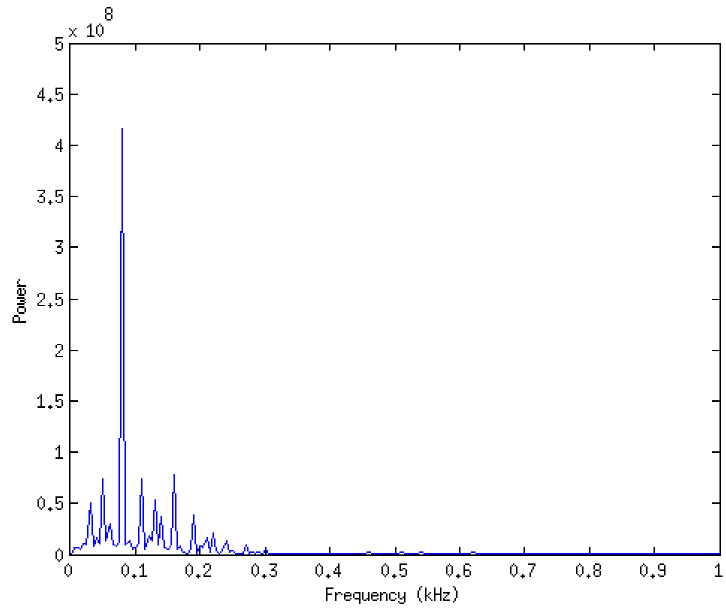

Figure 21: Power spectrum of the neuron membrane potential signal for NA = 0.8.

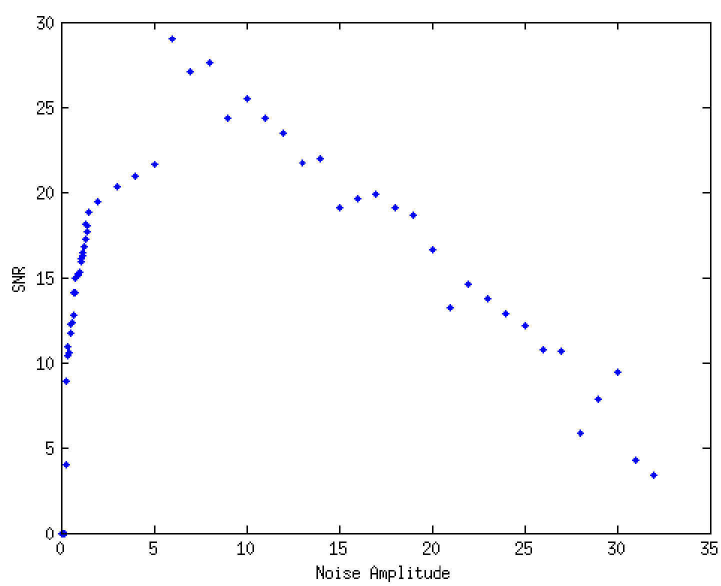

Figure 22: Relationship between SNR and NA for a single subthreshold uncoupled FN neuron.

Appendix I

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%% PHYS-463 & 464: Senior Project
% Studying dynamics in the Fitzhugh-Nagumo
% neuron model.

%% Runge-Kutte ODE Approximation
% This cell provides an alternative ode solving option using a Runge-Kutte
% solver algorithm

clear all; clc;

% want a timestep of around 3.0447e-5

h = 3.0447e-3;       % this is the timestep for the solving algorithm
t0 = 0;              % initial time for solver
tf = 200;            % final time for solver

B = 0.4;             % input signal amplitude, 0.2265 is around the region of system Hopf bifurcat
f = 0.08;              % input signal frequency
omega = 2*pi*f;      % input signal angular frequency
sigtime = t0:h:tf;   % this is the time vector for the input signal
sig = B.*sin(omega.*sigtime);  % input signal

tic                  % begin timing the run time of the program

N = tf/h;            % number of time steps for the solver

xnot = [0 0 0 0];          % initial conditions vector
xdash = xnot';             % transpose of the initial conditions vector

k1x = zeros(2,1);    %
k2x = zeros(2,1);    %
k3x = zeros(2,1);    %
k4x = zeros(2,1);    %
xn1 = zeros(2,1);    %
xn2 = zeros(2,1);    %
xn3 = zeros(2,1);    %

xn(:,1) = xdash;         %

for i = 1:N-1

k1x = h*fitznaglc(i*h,xdash); % ,sig(i)
xn1 = xdash + k1x/2;

k2x = h*fitznaglc((i+1/2)*h,xn1);
xn2 = xdash + k2x/2;

k3x = h*fitznaglc((i+1/2)*h,xn2);
xn3 = xdash + k3x;

k4x = h*fitznaglc((i+1)*h,xn3);
xn(:,i+1) = xdash + k1x/6 + k2x/3 + k3x/3 + k4x/6;
```

```
xdash = xn(:,i+1);

end

toc

xn(2,:) = xn(2,:).*h;

figure(1); hold on
plot(xn(1,:),'b')
plot(xn(3,:),'r')
% plot(xn(6,:),'g')
% plot(xn(8,:),'m')
xlabel('Time (ms)')
ylabel('Neuron Membrane Potential (mV)')
legend(['Neuron 1' ; 'Neuron 2'])

figure(3)
plot(xn(2,:) , xn(1,:),'r')
%title('Neuron Phase Portrait (Fitzhugh-Nagumo) RK4')
xlabel('rdot')
ylabel('vdot')

%legend(['ode45'' ; 'RK4'])

DCoffset = mean(xn(1,:));
xn(1,:) = xn(1,:) - DCoffset;

% Dr. Sungar's method

freq1 = 0:(1/200):(1/200)*(length(xn(1,:))-1);

ps = fft(xn(1,:));
ps1 = ps.*conj(ps);
%
% figure(2)
% plot(freq1(1:length(ps1)/2),ps1(1:length(ps1)/2))
% xlabel('Frequency (mHz)')
% ylabel('Power')
% axis([0 1 0 20e8])

% % Dr. Jasbinsek's method
%
% Fs = 1/h;
% [X,freq] = centeredFFT(xn(1,:),Fs);
% ps2 = X;
% ps3 = ps2.*conj(ps2);

% figure(3)
% plot(freq,ps3)
% xlabel('Frequency (Hz)')
% ylabel('Power')
% axis([0 1 0 5e8])
```

```
%% Characterizing the Signal to Noise Ratio

NAps1 = mean(ps1(1:16));                % calculated average noise amplitudes
NAps2 = mean(ps1(18:65687));
NAps = (mean(NAps1) + mean(NAps2))/2;

NA = mean(NAps);

SA = 0.234e8;                           % calculated signal amplitude

SNR = 10*log10(SA/NA)    % SNR

NA = [0.01 0.05 0.1 0.15 0.2 0.25 0.3 0.35 0.4 0.45 0.5 0.55 0.6 0.65 0.7 0.75 0.8 0.85 0.9 0.95 1
SNRfinal = [0 0 0 0 0 3.98 8.88 10.91 10.43 10.55 11.73 12.24 12.29 12.75 14.06 14.06 14.98 15.07

figure(11)
plot(NA,SNRfinal,'.')
xlabel('Noise Amplitude')
ylabel('SNR')

%% Effect of firing frequency dependence on I input
% This cell contains an averaging procedure for determining the frequency
% at which the spikes of the neuron are occuring. Individual data points
% were determined using the ode45 solver method.

peaks04 = [((3.31+3.26)/2); ((17.13+17.07)/2); ((30.93+30.86)/2); 44.62; ((58.51+58.27)/2); 72.26;
          ((86.13+86.1)/2); 99.85; ((113.8+113.7)/2); 127.5; 141.3; 155; 168.9; 182.7; 196.5];
T04 = [13.815 13.795 13.625 13.77 13.87 13.855 13.735 13.9 13.75 13.7 13.7 13.9 13.8 13.8];
T04 = mean(T04); % do this for all of the data series

peaks1 = [4.587; 14.14; 23.62; 33.21; 42.84; 52.46; 61.9; 71.43; 81.02; 90.61; 100.1;...
          109.8; 119.3; 128.9; 138.4; 148; 157.5; 167.1; 176.6; 186.3; 195.8];
T1 = [9.553 9.48 9.59 9.63 9.62 9.44 9.53 9.59 9.59 9.49 9.7 9.5 9.6 9.5 9.6 9.5 9.6 9.5 9.7 9.5];
T1 = mean(T1);

f = [1/T04 1/T0425 1/T045 1/T05 1/T06 1/T07 1/T08 1/T09 1/T1 ]; % firing frequency
I = [-0.4 -0.425 -0.45 -0.5 -0.6 -0.7 -0.8 -0.9 -1];            % input current
I = abs(I);                                                      % magnitude of the current

figure(1)
plot(I,f)
xlabel('Neuron Input')
ylabel('Neuron Firing Frequency')

function [ soln ] = fitznaglc( t , x  )
% Fitzhugh-Nagumo model with linear coupling
%   Detailed explanation goes here


a = 0.75;  % 0.75
b = 0.8;   % 0.8
c = 3.0;   % 3.0

I = -0.58;  % -0.39947 with constant,
```

```
k = 0.113;   % coupling constant
%NA = 32;      % noise amplitude, 0.15 stocres starts NA.*randn

soln = [c*(x(1) - (1/3)*x(1)^3 + x(2) + I + k*(x(3) - x(1))); ...
        (-1/c)*(x(1) - a + b*x(2));
        c*(x(3) - (1/3)*x(3)^3 + x(4) + k*(x(1) - x(3))); ...
        (-1/c)*(x(3) - a + b*x(4))];     %; ...
%         c*(x(5) - (1/3)*x(5)^3 + x(6) + k*(x(3) - x(5))) + k*(x(7) - x(5)); ...
%         (-1/c)*(x(5) - a + b*x(6)); ...
%         c*(x(7) - (1/3)*x(7)^3 + x(8) + k*(x(5) - x(7))); ...
%         (-1/c)*(x(7) - a + b*x(8))];

end
```

Appendix II

If we start with the van der Pol oscillator from Strogatz, pg. 198 and 212 we have

$$\ddot{x} + \mu \left(x^2 - 1\right) \dot{x} + x = 0, \qquad \text{we can re-write this as:} \tag{9}$$

$$\ddot{x} + \mu \dot{x} \left(x^2 - 1\right) = \frac{d}{dt} \left(\dot{x} + \mu \left(\frac{1}{3} x^3 - x \right) \right), \tag{10}$$

Here all we're doing is factoring a time derivative out of the whole thing. From this point, if we let:

$$F(x) = \frac{1}{3} x^3 - x, \qquad \text{and} \tag{11}$$

$$w = \dot{x} + \mu F(x). \tag{12}$$

taking the time derivative of w, we get:

$$\dot{w} = \frac{d}{dt} \left(\dot{x} + \mu F(x) \right) = \ddot{x} + \mu \frac{d}{dt} F(x) \tag{13}$$

Since we know from the van der Pol equation (10) that:

$$\ddot{x} = -\mu \left(x^2 - 1\right) \dot{x} - x, \qquad \text{we know that} \tag{14}$$

$$\dot{w} = -\mu \left(x^2 - 1\right) \dot{x} - x + \mu \left(x^2 - 1\right) \dot{x} \tag{15}$$

$$\dot{w} = -x. \tag{16}$$

Once we know this we can set up the van der Pol oscillator as a system of equations by changing (13) to the form:

$$\dot{x} = w - \mu F(x), \qquad \text{and also using} \tag{17}$$

$$\dot{w} = -x. \tag{18}$$

one more change of variables is needed to make this into a form closer to that used in the MATLAB for neuroscientists book:

$$\begin{aligned} y &= \frac{w}{\mu} \\ w &= y\mu \\ \dot{w} &= \dot{y}\mu \\ \dot{w} &= \dot{y}\mu = -x \\ \dot{y} &= \frac{-1}{\mu} x, \end{aligned}$$

doing a similar thing to (18):

$$\begin{aligned} \dot{x} &= y\mu - \mu F(x) = \mu \left(y - F(x) \right) \\ \dot{x} &= \mu \left(y - F(x) \right) = \mu \left(y - \frac{1}{3} x^3 + x \right) \\ \dot{y} &= \frac{-1}{\mu} x. \end{aligned}$$

Now we need to switch our variable convention to match that of the Matlab for Neuroscientists book. Let's set:

$$\begin{aligned}
\dot{x} &= \dot{v} \qquad \text{and} \qquad \dot{y} = \dot{r}, \text{we get} \\
\dot{v} &= \mu\left(r - \frac{1}{3}v^3 + v\right) \\
\dot{r} &= \frac{-1}{\mu}v.
\end{aligned}$$

One more change of variable convention gets us extremely close to the form used in the book [2], so we say that

$$\mu = c, \qquad \text{and get:} \tag{19}$$

$$\dot{v} = c\left(v - \frac{1}{3}v^3 + r\right) \tag{20}$$

$$\dot{r} = \frac{-1}{c}v. \tag{21}$$

comparing this with the system for the FN model in the neuroscience book, we see that:

$$\dot{v} = c\left(v - \frac{1}{3}v^3 + r + I\right) \tag{22}$$

$$\dot{r} = \frac{-1}{c}\left(v - a + br\right), \tag{23}$$

the only difference between (20) and (22) is the added input current inside the parenthesis of (22). The difference between (21) and (23) is that inside the parenthesis of (23) the additional quantity (br - a) is added. On page three of Fitzhugh's 1961 paper he provides the following set of equations

$$\begin{aligned}
\dot{x} &= c\left(x - \frac{1}{3}x^3 + y\right) \qquad \text{is equal to} \qquad \dot{v} = c\left(v - \frac{1}{3}v^3 + r\right) \\
\dot{y} &= \frac{-1}{c}x, \qquad \text{is equal to} \qquad \dot{r} = \frac{-1}{c}v
\end{aligned}$$

then Fitzhugh says "The BVP (Bonhoeffer-van der Pol model) is obtained by adding terms to these equations as follows:

$$\begin{aligned}
\dot{x} &= c\left(x - \frac{1}{3}x^3 + y + z\right) \qquad \text{is equal to} \qquad \dot{v} = c\left(v - \frac{1}{3}v^3 + r + I\right) \\
\dot{y} &= \frac{-1}{c}\left(x - a + by\right), \qquad \text{is equal to} \qquad \dot{r} = \frac{-1}{c}\left(v - a + br\right)
\end{aligned}$$

where: 1 - 2b/3 $<$ a $<$ 1, b$<$c^2. Both a and b are constants. Z is the stimulus intensity, a variable corresponding to membrane current I in the HH equations."

References

1. FitzHugh R. (1961) Impulses and physiological states in theoretical models of nerve membrane. Biophysical J. 1:445466

2. Wallisch, Pascal, Michael E. Lusignan, Marc D. Benayoun, Tanya I. Baker, Adam S. Dickey, and Nicholas G. Hatsopoulos. "MATLAB for Neuroscientists: An Introduction to Scientific Computing in MATLAB [Hardcover]." 9780123745514: Amazon.com: Books. N.p., n.d. Web. 16 June 2013.

3. Strogatz, Steven H. "Nonlinear Dynamics And Chaos: With Applications To Physics, Biology, Chemistry, And Engineering (Studies in Nonlinearity) [Paperback]. 9780738204536: Amazon.com: Books. N.p., n.d. Web. 16 June 2013.

4. Perc, Matjaz. "Effects of Small-world Connectivity on Noise-induced Temporal and Spatial Order in Neural Media." Matjazperc.com. Matjazperc.com, n.d. Web. 16 June 2013.

5. McDonnel, Mark D., Nigel G. Stocks, Charles EM Pearce, and Derek Abbott. "Stochastic Resonance: From Suprathreshold Stochastic Resonance to Stochastic Signal Quantization [Paperback]." 9781107411326: Amazon.com: Books. N.p., n.d. Web. 16 June 2013.