

Lab 6

February 13, 2009

Attention: Controlling Synchrony

In Lab 5, we studied many interconnected inhibitory neurons and determined that synaptic rise-time sets the network period. In this lab we study the onset of synchrony, exploring the effect of increasing inhibitory strength.

We will drive a population of 256 interneurons with constant input current and have them inhibit each other; the strength of inhibition determines whether or not synchrony occurs. We will model the neurons in the network as phase-coupled oscillators (a method introduced by Kuramoto). When coupling is weak, the oscillators run at their natural frequencies. When coupling is strong, as would happen when attention is present, the network synchronizes.

6.1 Reading

- B. Daniels. Synchronization of Globally Coupled Nonlinear Oscillators: the Rich Behavior of the Kuramoto Model. *Ohio Wesleyan Physics Dept., Essay*, pp. 7-20, 2005.

6.2 Prelab

1. Phase-Coupled Oscillators

Modeling each neuron as an oscillator, we can describe the rate at which the k th oscillator's phase changes by:

$$\dot{\theta}_k = \omega_k + \frac{K}{N} \sum_{n=1}^N \sin(\theta_n - \theta_k) \quad (6.1)$$

where ω_k is its natural frequency, K is the degree of coupling, and N is the number of oscillators.

- (a) Show that this equation can be rewritten as:

$$\dot{\theta}_k = \omega_k + Kr \sin(\psi - \theta_k) \quad (6.2)$$

Where ψ and r are defined by:

$$r e^{i\psi} = \frac{1}{N} \sum_{n=1}^N e^{i\theta_n} \quad (6.3)$$

The identity $2i \sin x = e^{ix} - e^{-ix}$ may be helpful.

- (b) Sketch the relationship between ω_k and θ_k in steady state ($\dot{\theta}_k = 0$) on the range $0 < \theta_k < 2\pi$.

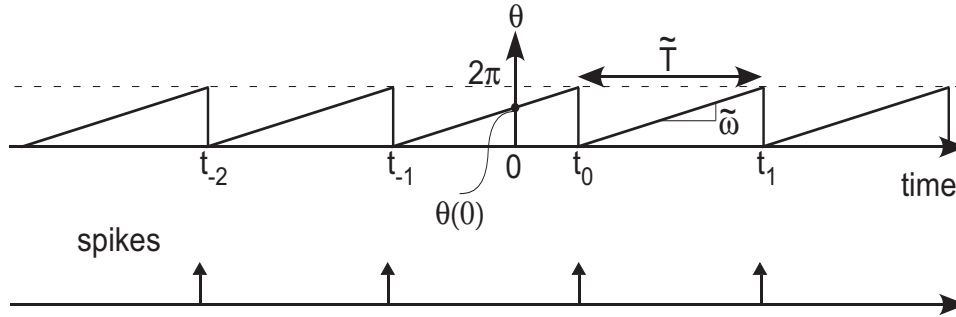


Figure 6.1: The phase of a spiking neuron over time.

2. Dealing with Spiking Neurons

The analysis in Question 1 assigned each oscillator a phase based on where it was in its cycle. The phase of a single oscillator is related to its frequency as:

$$\theta(t) = (\theta(0) + \tilde{\omega}t) \bmod 2\pi \quad (6.4)$$

See Figure 6.1 for a pictorial description.

- (a) By expressing $\theta(0)$ and $\tilde{\omega}$ as functions of t_0 and \tilde{T} , show that this can be rewritten as:

$$\theta(t) = 2\pi \left(\frac{(t - t_0) \bmod \tilde{T}}{\tilde{T}} \right) \quad (6.5)$$

- (b) When using neurons, we assign a phase based on the time at which the spike arrives, relative to the other spikes. A neuron spike occurs when $\theta(t) = 2\pi$. Solve for spike times, t_n , using Equation 6.5. The solution obtained holds when a neuron's period is perfectly stable. With a real system we average the phase over several cycles.
- (c) We take a single point in time, t_ψ , and calculate each neuron's phase by using the time of its spike within the period prior to t_ψ . In a synchronized network the period for each neuron is the same ($\tilde{T}_n = T$). Find the n th neuron's phase at t_ψ . At this point take the average of the phaser over all N neurons, $\langle e^{i\theta_n(t_\psi)} \rangle$. Show that this can be simplified to:

$$b = e^{i\psi} \frac{1}{N} \sum_{n=1}^N e^{-i\theta_n(0)} \quad (6.6)$$

where $\psi = \frac{2\pi t_\psi}{T}$ is the network phase at this time and $\theta_n(0) = \frac{2\pi t_{n0}}{T}$. Vector strength is equivalent to $\frac{1}{b}$. At this point, Equation 6.3 holds true for our neurons. What is the relationship between vector strength and r ?

3. Synchrony Onset

The Kuramoto model predicts a critical level of coupling strength which must be exceeded to achieve synchrony. That is:

$$r = \sqrt{1 - \frac{K_c}{K}} \quad (6.7)$$

where K_c is the critical coupling. To test this prediction, we need to determine the amount of coupling, K , between the neurons in our network. To the first order, we

can estimate K as a linear function of the inhibition strength in the network. This approximation is complicated by the fact that as inhibition increases, fewer neurons spike. Which neurons will drop out first, those with a high or low base rate? Will this have any effect on the amount of delay in the system? Does this complication act to (increase/decrease/not change) the network period?

6.3 Setup

As in previous labs, there will be a folder on the Desktop; this one is named **Attention Lab**. This folder contains the instrument control program to acquire and view the interneuron membrane potential and spikes in real-time. The TA will instruct you on the use of the software.

Before each test edit the contents of *parameters.txt*. In this lab, the parameters of interest are:

- Input current (I_{IN})
- Leak conductance (G_{lk})
- Inhibitory rise-time (T_r)
- Inhibitory spread (λ_I)
- Inhibitory conductance amplitude (G_I)

As you increase the input current, leak conductance, rise-time, and spread biases, I_{IN} , G_{lk} , T_r , and λ_I increase exponentially. As the inhibitory conductance amplitude bias is increased, G_I decreases exponentially. Other biases can be changed dynamically while running the program (press the $F1$ key for help). These can be used to further explore synchrony, but they are not required in the lab.

6.4 Experiments

In the first experiment, we will explore the amount of inhibition necessary to synchronize a population of inhibitory interneurons. In the second experiment, we will examine the phase of the individual neurons within the population. Specifically, we will study how the natural frequency of each neuron affects its synchronized phase.

Experiment 1: Synchrony Onset

In this experiment, we will

- Observe the amount of inhibition required for the network to synchronize

Disconnect the interneurons from each other by setting the inhibitory spread to 0.750V. Leave the other biases at default levels ($G_{lk} = 0.0$; $T_r = 2.286$, $G_I = 1.97$). Adjust I_{IN}

to get a mean network frequency of about 40 Hz. Note this level of I_{IN} and use it for subsequent experiments.

Globally connect the interneurons by setting the inhibitory spread bias to 1.750V. Vary the inhibitory synapse's strength (20-30 values). Be sure that synchrony is not seen at the highest voltage, but is seen at the smallest. The total range should be about 300 mV. For each strength, take data for about one second.

As was done in Lab 5, compute the vector strength (VS) for the entire network at each G_I value. In addition, measure the total number of active neurons, N_f , and the average firing rate, μ_f , at each G_I value. We approximate the coupling between the neurons as:

$$K_{\text{approx}} = \alpha_c N_f \mu_f (5.0 \times 10^{-9}) e^{0.7(2.5 - V_B)/0.0256} \quad (6.8)$$

where V_B is the G_I voltage bias value and α_c is a proportionality constant. Set $\alpha_c = 1$ for this experiment. Plot the calculated VS vs the K_{approx} value. Fit Equation 6.7 to your data. What value of K_c did you find?

Experiment 2: Frequency–Phase Relationship

In this experiment, we will

- Establish how the phases of individual neurons relate to their natural frequencies

Using your data from Experiment 1, pick a G_I value with a high VS and a relatively large number of active neurons (those with a frequency greater than 4 Hz). For this value, find the phase of each neuron and plot it against that neuron's natural frequency, measured at a G_I value with a low VS (pick a point just before the estimated K_c point to closely match the average frequency of the neurons when they are synchronous). When plotting, choose your axes to allow a linear fit of the steady state relationship obtained in the prelab. Only fit neurons that are not drifting (use the VS of each neuron to determine whether or not it can be included). From the fit determine the value of K . During long experiments the network period can change; to avoid this effect in these calculations use only the first 200ms of data.

Using the measured K value and Equation 6.8 find a corrected value of α_c such that $K_{\text{approx}} = K$. Report the value of α_c found.

We would like to relate the value of K_c to an intrinsic network property. A calculation using the Kuramoto model finds the relationship $K_c = 2\gamma$, where γ is the width of the distribution of oscillator natural frequencies. We can approximate γ with the standard deviation of the neuron natural frequencies. Measure the standard deviation of the natural frequencies. Calculate a K_c value. How close is this calculated value to the number derived from you fit? Can you think of any reasons for the deviation?

Experiment 3: Full K Measurement (Extra Credit)

Using the same method described above, calculate K values for all G_I values. Plot this vs the K_{approx} values and fit a linear equation to the data. Is the data linear as assumed? How close was the calculated α_c value to the slope of the fit? On a new figure, plot VS

against K , and fit this using Equation 6.7. How do the new plot and K_c value compare to the previous results?