BURSTING IN INTEGRATE-AND-FIRE NEURONAL NETWORKS

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September 4, 2010

Abstract

The basic integrate-and-fire model for neuronal networks does not support bursting, when all of the neurons rapidly fire. For high coupling strengths, the basic model will climb into a run-away state where the neurons recursively excite each other and spike. We explore two additions to the model to shut down the bursting: 1) increasing the synaptic failure exponentially with the number of times a given neuron has spiked in the burst; and 2) exponentially decreasing the spike felt with the number of times a given neuron has spiked in the burst. For simplicity, we use the current-based, delta-spike, all-to-all coupled integrate-and-fire model. In this report, we detail our progress with both models using constant current and poisson-driven input.

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Part I

Introduction

1 Integrate-and-Fire Networks

1.1 Introduction to Bursting

The dynamics of a neuron are governed by the voltage V_i across its membrane.[1] Although there are various types of neurons, many are modelled by a leaky integrate-and-fire network. This means that each neuron's voltage decays, or leaks, with time, and that the neurons receive current from other neurons which increases their membrane potential. When the voltage reaches some threshold, it *spikes*, releasing an action potential to other neurons in the network, and its membrane potential is instantly reset to some reset value. The action potential sent to other cells causes their voltage to increase in the same manner. These networks often exhibit a pattern called bursting: the cells rarely spike during a *quiescent phase*; then spike several times in the shorter, *active* or *burst phase.* Figure 1 is an experimental example from a developing chick's spinal column at embryonic day 7.5 (Vladimirski et al., 2008).

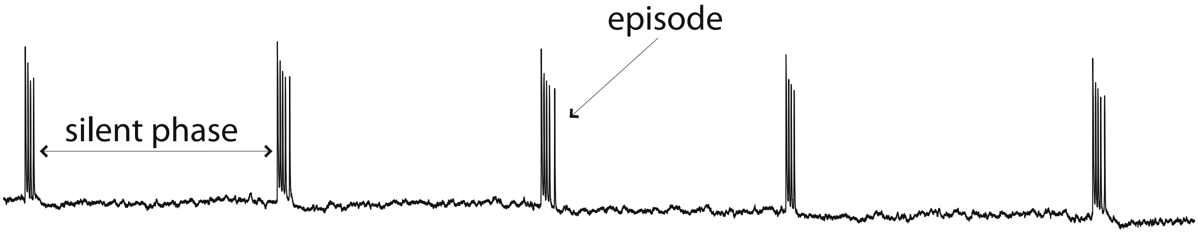

Figure 1: Reprinted from Vladimirski et. al.

Many simple models do not incorporate bursting. Our goal is to include bursting in the simple integrate-and-fire model using the common approximation that spikes are instantaneous, which is reasonable because they operate on a shorter timescale than the voltage decay. We take this a step further and approximate each burst as instantaneous, since they too are on a shorter timescale than the quiescent phase. More formally, this can be justified as a perturbation expansion where the length of a burst is a small parameter.

1.2 The Differential Equation

Suppose that we have a network of N neurons, each with voltage V_i across their membrane. We study the dynamics of this system using the standard leaky, all-to-all coupled, current-based integrate-and-fire model. The voltages are governed by the following system of differential equations:

$$C\frac{dV_i}{dt'} = -g_{leak}\left(V_i - V_R\right) + \tilde{I}_i(t') + \tilde{E}_i(t'). \tag{1}$$

Here C is the capacitance, g_{leak} the conductance, V_R the reset potential, $\tilde{I}_i$ the incoming current from outside the network, and $\tilde{E}_i$ the incoming current from other neurons within the network. We will nondimensionalize this to remove some of the parameters. For now we make no assumptions on the behaviour of $\tilde{I}_i$, and note that it may be stochastic.

Whenever a voltage V_i reaches the threshold potential V_T, we say that the neuron spikes; then V_i is instantaneously reset to V_R, and a signal is sent to all other neurons. This temporarily increases all other $\tilde{E}_i$, causing the voltages of the other neurons to rise. More formally, for some spike function E_{sp},

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[1] There are more biologically detailed models that track ion channels inside a cell (Koch, 2004).

we can say that $\tilde{E}_i = \Sigma_{k=0}^{\infty} E_{sp}(t' - t_{ik})$, where the t_{ik} are the times neuron i recieves a spike. Since $E_{sp}(t - t_0)$ represents the signal sent from other neurons, we insist that $E_{sp}(t - t_0) = 0$ for $t < t_0$, and that E_{sp} decays to 0 as t increases.

We now nondimensionalize the system. Let $v_i = \frac{V_i - V_R}{V_T - V_R}$, $t = \frac{g_{leak}}{C} t'$, $I_i = \frac{\tilde{I}_i}{g_{leak}}$ and $E_i = \frac{\tilde{E}_i}{g_{leak}}$. The governing differential equations become

$$\frac{dv_i}{dt} = -v_i + I_i(t) + E_i(t) \tag{2}$$

and a neuron spikes when v_i reaches 1, resetting v_i to 0.

1.3 Internal and External Spikes: $E_i(t)$ and $I_i(t)$

We said in the previous section that $E_i(t) = \Sigma_{k=0}^{\infty} E_{sp}(t - t_{ik})$ for some spike functions E_{sp}. We use a scaled Dirac Delta, $E_{sp}(t) = \frac{S}{N}\delta(t)$, for simplicity. This causes v_i to jump instantaneously by S/N whenever another neuron spikes. Although this is a standard approximation (see, for example, Newhall et. al.), whenever a neuron spikes it actually takes some finite amount of time for E_i to rise and fall.

The external input is very similar. We take it to be of the form $I_i(t) = f\Sigma_{k=0}^{\infty}\delta(t - T_{ik})$ where T_{ik} is a Poisson Train with frequency ν. The Poisson Trains for different neurons are identically distributed and independent. In theory, these spikes would come from other neurons not modeled in our network, which fire tonically when isolated (van Vreeswijk & Hansel, 2001). See Figure 8 for graphs of voltage versus time using such external spikes.

1.4 Mean-Field Approximation

If ν is large and $f\nu$ is above threshold, we can approximate the effect of frequent external spikes as constant current. The net strength is $I = f\nu$ for all neurons (see Figure 9).

In a regime where no neurons fire,[2] we can solve the equation $v' = -v + I$ analytically: $v(t) = I + ce - t$ for some constant c. Checking initial conditions $v(t_o) = v_o$, we see that

$$v(t) = I + (v_o - I)e^{-t}.$$

This asymptotes towards I, so assuming that v_o is between reset ($v = 0$) and threshold ($v = 1$), the neurons will only spike if $I > 1$. Hence we restrict ourselves to this case. The time t_{IB} until the next spike depends only on the maximum initial voltage v_{max}. In particular,

$$t_{IB} = \log\left(\frac{I - v_{max}}{I - 1}\right).$$

We can therefore plot the maximum voltage after a burst in order to get information about the time until the next spike.

Although using the constant current approximation gives similar behavior in the case of $I = f\nu > 1$, in the case of $f\nu \leq 1$ a constant current provides no spiking. Using Poisson inputs, however, a small fluctuation can cause network spiking. This is sometimes called *subthreshold forcing*, because the mean input is below threshold. It is also known as the fluctuation-driven regime because only the fluctuations in input can cause spiking. See Figure 10.

1.5 Bursts

The behaviour of the system can be summarized:

- The voltage v_i decays exponentially when no other neurons spike.

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[2] Each neuron is independent, so we drop the indices.

- If $v_i(t)$ reaches 1, we reset it to $v_i(t) = 0$ and we say that neuron i spikes.
- The voltage v_i jumps instantaneously by S/N whenever another neuron spikes.
- The voltage v_i jumps instantaneously by f at random times, independent of the other neurons.

This prompts the question: suppose that a neuron spikes and causes another neuron to spike, which in turn causes another neuron to spike, and so on. This could cause the first neuron to spike again, possibly creating an infinite chain if $S \geq 1$. We need some mechanism to shut down the burst. The standard solution (Newhall et al., 2009) is to take any neuron that has already spiked in a timestep offline; it sits at $v_i = 0$ even if other neurons spike at the same time. Instead, we propose two solutions.

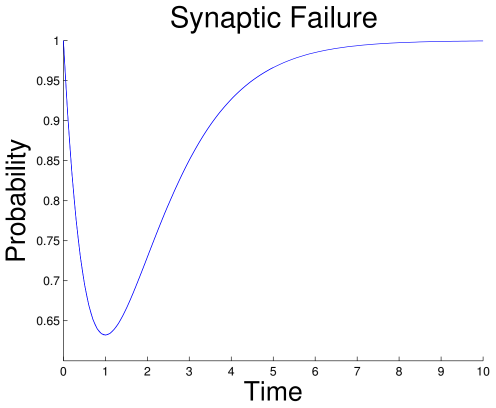

Figure 2: Qualitative graph of probability of spike transmission versus time since the latest spike. The probability will not necessarily approach 1, and time is in some non-dimensional system.

First, we make each neuron have a chance $P(n_i) = e^{-n_i}$ of ignoring a spike, where n_i is the number of times neuron i has spiked in the current timestep.[3] According to Koch, a neuron's chance of ignoring received spikes increases with the number of times it has recently spiked (Figure 2). The standard assumption is that the probability of transmitting a spike is $P(t) = 0$ on some short timescale and $P(t) = 1$ on a long timescale. We instead assume that $P(t) = P_0 = 1/e$ on some short timescale and $P(t) = 1$ on the longer timescale. If there are multiple spikes within a short time, the effect is compounded; for n spikes, the probability is e^{-n}.

We show graphs of these possible $P(n)$ as simple step functions (Figure 11), although perturbation theory justifies this with broader assumptions; however, this requires that the timescale on which P decreases is much faster than the timescale on which it approaches the asymptote. The graphs in Koch make it appear that this is not a trivial assumption.

The second solution is to have the coupling strength decay exponentially with the number of times the neuron has spiked: $S(n_i) = S_0 e^{-n_i}$. This is mathematically equivalent to a model in which the threshold increases when the neuron has spiked recently (Koch, 2004).

Part II

Model

2 Synaptic Failure Increase

If a neuron has spiked n times and another neuron spikes, suppose that is has a probability $P_{fail}(n) = 1 - e^{-n}$ of synaptic failure (ignoring the next spike). Notice that this does not depend on the sending neuron, only the receiving one. We would like to ask how the system behaves – how many times each neuron spikes in a burst and how often the network bursts. We have two main tools which we use in the coming sections. First, our simplest visualization of a simulation is the raster plot. We graph time versus neuron index, putting a point when each neuron fires. Since this model collapses each burst, it is possible to have one neuron fire multiple times instantaneously. We color code the points to convey this information. We also use histograms to display the voltages of the neurons before or after a burst.

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[3] Technically, n_i needs to be a function of t too. However, we will often omit even the i for brevity.

2.1 Inside Each Burst

Given some initial distribution of voltages, we wish to examine the voltages after a burst. We do not have a solution, but we have several observations.

- After a neuron has fired, it has finitely many possible voltages; namely 0, S/N, $2S/N$, and so on.
- We can reduce this to a countable-state, discrete-time Markov Chain. We do this below by replacing the voltages v with discrete variables x. This is countable-state but not finite-state because we also need to know how many times each neuron has fired.

Let $M = \lceil \frac{N}{S} \rceil$ and $x(v) = \lfloor vM \rfloor$. Then M is the number of spikes needed to take a neuron from reset to threshold, and $M - x(v)$ is the number of spikes a neuron at (nondimensionalized) potential v needs to reach threshold. Notice also that every time a neuron receives a spike, $x(v)$ increases by 1. Hence we can characterize the dynamics entirely in terms of x to turn the normally continuous problem into a discrete one. In particular, if a neuron has already spiked, we only need to know x – the number of spikes it has received since it was reset – to know what v is: it is $\frac{Sx}{N}$. We conclude that after a burst, only finitely many voltages are possible – namely $\left\{0, \frac{S}{N}, \frac{2S}{N}, \cdots, \frac{(M-1)S}{N}\right\}$. Therefore we don't speak of the probability distribution function after a burst, but instead the probability of getting some specific x, or equivalent v, value. Additionally, the exact S value is unimportant; it only determines M.[4]

2.2 Conditions for a Burst

For the purposes of this paper, a *burst* is an event where all neurons fire instantaneously, even if they each fire only once. We wish to examine the conditions for a burst to occur. These are exactly analagous to those in Newhall et. al. First, there must be some neuron at or above threshold, $x = M$. For a second spike in the network to occur, there must be another neuron at $x = M - 1$ or higher; so together, we need two neurons at or above $x = M - 1$. Continuing by induction, for k spikes to occur we need one neuron at $x = M$; two at $x = M - 1$ or higher; and k neurons at or above $x = M - k + 1$. This condition is both necessary and sufficient. Once M neurons have fired, we know that a burst will occur since that alone is good enough to move any neuron from reset to threshold. The condition is therefore that we have k neurons at $x = M - k + 1$, for all integers $k \in [0, M]$.

These conditions are independent of the condition that P decays exponentially; however, if neurons that have not yet spiked have some chance of synaptic failure, then this is necessary but not sufficient.

2.3 Raster Plots

A raster plot is a graph of time versus neuron index, with a dot to indicate a spike. Since it is possible in our model for a neuron to spike more than once at the same time, we color-code the dots. See Figure 12. We can tell how frequent the bursts are, how many times each neuron fires per burst, and how random the inter-burst interval t_{IB} is. Indirectly, this tells us what the maximum voltage after a burst is, but doesn't give us any clues to the distribution of voltages.

Observe that the number of spikes per burst increases with S but is relatively constant with N, and that the interval between bursts becomes more regular as N gets large. Compared to the plots in Newhall et. al, we have more frequent bursts.[5] Our model is the same outside of bursts, but the voltages are not reset to 0 after a total firing event.

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[4] That is, that it does not affect the dynamics inside a burst. Since it *does* affect the final voltages, it certainly changes statistics outside a burst, and potentially even the initial x-values for the next burst.

[5] Technically, there are no bursts in Newhall et. al. We mean to say that our bursts occur more frequently than total firing events in the model presented in Newhall et. al.

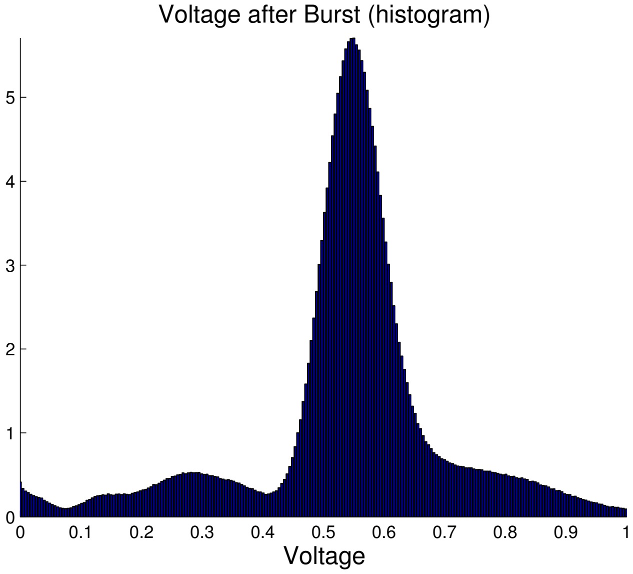

Figure 3: Histogram of the voltage after a burst for $N = 2500$, $S = 11$ and $I = 1.1$ after 1000 bursts. We use one bin for every possible voltage aftera a burst.

2.4 Voltage Distributions

We plot a histogram of the voltages after a burst in Figure 3. This is normalized to have an integral of 1 since we would like to think of it as a probability density function. Two things challenge this interpretation. First, the voltages after a burst could be dependent, or could change with time. Second, only finitely many voltages are possible after a burst, so we should really use a discrete random variable, not a continuous one.

We can easily see if the membrane potential is evolving with time by taking histograms of the voltage after sequential bursts. In particular, we would like to know if it approaching a stable distribution. It appears that the histograms do not approach any stable distribution after around 1000 bursts. Refering to Figure 13, we see that the voltage is approximately normally distributed around about $v = 0.55$ after two of the four bursts shown (Figure 13(b) and Figure 13(d)) and has a large peak there in Figure 13(a) . Since the histogram combining all the bursts, Figure 3, has a large peak at $v = 0.55$ this is expected. We should also note that the two distributions with peaks not at $v = 0.55$ have some neurons very near threshold. It is possible that the randomness here is significant: that if one neuron had spiked, all the neuorns near threshold would have gone over. This would have shifted the center mode right slightly in Figure 13(a), leaving it at about $v = 0.55$; however, in Figure 13(c), many other neurons could go over threshold, pushing the peak near $v = 0.32$ right substantially. Since most of the neurons in this simulation have spiked three times, we assume that all of them in the $v = 0.32$ peak have $n = 3$. $L = 986$ new neurons would pass threshold, pushing the $v = 0.32$ peak up by $\Delta v \approx Se^{-3}\frac{L}{N} = 11e^{-3}\frac{986}{2500} \approx 0.22$. This would put the peak very close to the common $v = 0.55$ value.

We would like to explain why the $v = 0.55$ value is so important in this network. Consider the following scenario. Each neuron has spiked twice and is near threshold. A very small number, say L, cross threshold, pushing the rest over in one wave. On average, each of the L neurons first crossing threshold feel $(N - 1)e^{-3}$ spikes, compared to $(N - 1 - L)e^{-3}$ felt by the other $N - L$ neurons. Since L is small, each neuron's voltage is about $v = Se^{-3} \approx 0.548$. Notice that if each neuron has spiked twice, they would be at about $v = Se^{-2} \approx 1.489$ – well over the threshold of $v = 1$ – which is why we expect them to spike three times. It is not immediately clear how much large L disrupts this argument or what happens when the neurons go over in more than two waves. Neurons that went over later would probably receive fewer spikes on average, making them typically have $v < 0.55$. This could explain the presence of lower modes. In order to test how closely the graph in Figure 13(d) agrees with a binomial distribution with $P = e{-}3$, $N = 2500$ we compute statistical values. The sample mean and deviation are about 0.549

and 0.0466, respectively. The figures from a binomial distribution are very similar: 0.548 and 0.0479.

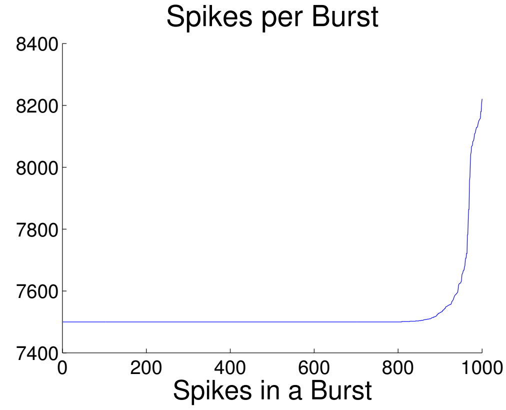

Figure 4: $N = 2500$. The minimum value is 7500, or three spikes per neuron in a burst, which 808 of the 1000 bursts had, and 900 had 7530 spikes per burst or more. This maximum is 8221.

In this discussion, we made a couple statements about how many times each neuron has fired, but not showed any data or graphs. We sort the number of spikes in each burst, then plot them versus some dummy index. We can see that there are usually exactly three spikes per neuron (averaged over a burst), and never less than that. This means that the peaks above $v = 0.55$ in Figure 13(a) and Figure 13(c) probably have neurons that already fired three times. The discussion about the peak at $v = 0.55$ apparently contradicts this; we have a peak of neurons that have fired three times substantially above Se^{-3} (or the expected deviation), meaning that each neuron must have received more than N spikes without spiking in between. This is the only way that a neuron can spike more than 3 times per burst, without receiving far more than the expected $Ne-n$ spikes. It is not too rare to see a burst with more than 7500 spikes (over 5% of bursts have an extra 100 spikes or more), this effect is probably significant.

Let us now ask if there is any connection between the histograms and the number of times each neuron has fired. On the surface, it certainly appears like there is; of the *eleven* graphs, and their histograms are approximately a normal distribution if and only if there are 7500 spikes per burst. To test this more widely and systematically, we need some algorithm to identify the peaks in a histogram and to screen out random noise. Unfortunately, there is very much noise and the naive algorithms we've tried work fine for histograms with more data,[6] but choke on these. Such an algorithm would allow us to test the hypotheses in this section on a much wider scale, and also to track the correlation between two consecutive bursts. This brings us to a broad and unanswered question: what causes some bursts to behave differently? It seems, from Figures 13(b) and 13(c) that the randomness inside a burst could be significant: if a few neurons had barely passed threshold rather than barely missing it, they could have pushed others over threshold. On the other hand, the voltages coming into the burst could cause the heterogeneity. Given some better way of classifying the different histograms, we could investigate that by finding (via simulations) conditional probabilities.

2.4.1 Correlation

The histograms from the last section may be interpreted as a probability density function for v. However, this interpretation is not so nice if the voltages are dependent. We compute the Sample (Pearson) Correlation Coefficient between two arbitrary neurons for several different values of N. Since the neurons are identical, the choice of neurons should be arbitrary. Additionally, after each burst we reset the voltages to some uniform distribution. This avoids the potential pitfall that a cell may maintain some memory of the previous bursts. Suppose, for instance, that a neuron that ends a burst with a high voltage will tend to have a high voltage after the next burst, too. Then the correlation coefficients between two high neurons could be different than those between high and low-voltage neurons. In principle, we could test this by measuring the correlation between every two neurons.

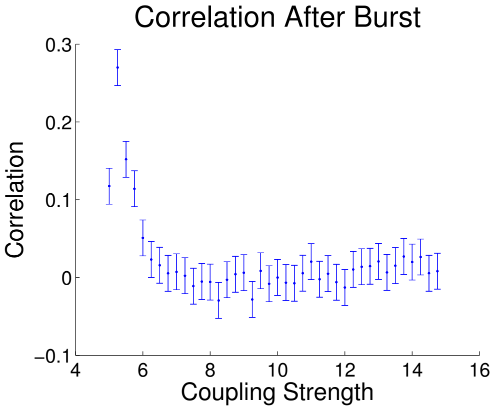

Figure 5: Correlations between neuron voltages after a simulation with 7500 bursts. Each point corresponds to one simulation. The horizontal axis is S. Other parameters: $I = 1.1$, $N = 100$. Same formula for error bars as in Figure 14.

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[6] Actually, I can't prove that they work as advertised even under good conditions.

From Figure 14(b), it looks like the correlation is 0 for $S = 10$, even for relatively small values of N (the smallest network size tested here is 100). However, the correlation does not necessarily shrink as N gets large; see Figure 14(a).

We now change S and see how this affects the system. In Figure 5, we see that the correlation decays as S increases. It also looks oscillatory, although the error is large enough that this might be coincidence. Assuming that the patterns in Figure 14 hold, whether or not the correlation is near 0 should be independent of N for fairly large networks.

A much more extensive search of the parameter space is computationally lengthy but not impossible. These results should be treated as educated guesses until such a search is conducted. In particular, we should check larger N and run the simulations longer, and most importantly use a square grid of S and N values. It is probably not necessary to check parameters closer together, except perhaps for small S.

3 Coupling Strength Decrease

The second method we use to shut down a burst event is to exponentially decrease the individual coupling strength between the neurons based on the number of times a neuron has fired. Let the coupling strength between the neurons be $S = S_0 e^{-n}$, where n denotes the number of times a given neuron has fired and S_0 the initial coupling strength. We define the 'level' of a burst to be the number of times the neuron has spiked in the burst: a neuron is on the first level of the burst if it has spiked once. We will focus on the number of spikes per neuron in a burst and the voltages of the neurons post-burst.

For finite N, the allowable voltages post-burst are discrete, being $\frac{S}{Ne^n}, \frac{2S}{Ne^n}, \ldots$. Although the neurons may end in different levels of the burst with differing n values, we have primarily observed all neurons ending on the same level.

3.1 Constant Current Input

For simplicity, we first analyze the model using a constant current input.

$$\frac{dV}{dt} = -\left(V - V_R\right) + I \tag{3}$$

Using the constant current and a non-probabilistic shut-off mechanism, we note that this model is deterministic with the only possible randomness present in the initial conditions of the network.

Also, because the time between a spike within the network is given as the minimum value of

$$-log\left(\frac{V_T - V_R - I}{v_0 - V_R - I}\right)$$

between the neurons, with v_0 being the voltage after the previous spike event, it is required that $I > 1$ to allow spiking. In the figures shown, we use $I = 1.02$. The external current plays no role within the bursting and primarily controls the time between bursts.

3.1.1 End Voltages

The distribution of voltages post-burst shows discrete 'modes'. After a sufficient number of bursts, the voltages fall into and remain in 2-3 prominent modes. When a neuron releases an action potential to the other neurons, it may push multiple neurons, say y neurons, over threshold, causing each of their voltages to jump to $\frac{S_0(y-1)}{Ne}$. These y neurons simultaneously also send their action potentials to all other neurons, potentially pushing a larger group of neurons over at once, creating a new mode. Thus the spiking of such modes effectively creates more modes. This causes an unrealistic staggered stacking effect of the neuron voltages (Figure 15) due to the determinism inherent to the model. All neurons receive the same signal after every spike and are therefore never able to separate themselves from the modes.

We now look at how long it takes for the neurons to reach such a state. This depends on the initial distribution of voltages as well as the current which controls time between burst. Higher values of S cause neurons to group together faster by pushing more neurons over threshold at one instant. Lower coupling strengths give neurons a longer time before the first burst to synchronize; when the neurons are spread out, they are unable to start a burst and thus must attain a clustered state before able to enact a burst. After the first burst, the voltages are usually discretized into 4-8 modes; however, after the second burst, the neuron voltages are fully synchronized into their final state of 2-3 prominent modes (Figure 15). We classify a mode as 'prominent' if it contains at least 2.5% of the total neurons. In most cases, the non-prominent modes contain only $1 - 10$ neurons.

We started by testing the following intial distributions: a uniform distribution; a randomly generated gaussian using the Box-Muller Transformation; and a point distribution with all voltages intialized to zero.

With the trivial point distribution, the neurons remained in the same group the entire simulation. Using the uniform distribution, the neurons form 2-3 modes, with only 2 prominent modes.

Using the gaussian distributions, we varied the mean over $[0.3, 0.7]$ and the standard deviation over $[0.01, 0.1]$. The neurons formed one to six modes, although only one to three prominent modes. The simulations with lower S and higher mean and higher standard deviation resulted in more modes. As the voltages go toward V_T, the difference between voltages decreases. This is due to the $-v$ term in (3). A higher mean allows the neurons to start closer to V_T and thus provides less time for the voltages to cluster together, allowing for more modes to exist due to a greater spread in voltages going into the burst. Figure 6 shows that most of these simulations yeilded one or two prominent modes. With one mode, the model acts as with the trivial point distribution. In order to study the case with two prominent modes more in-depth, we created an initial distribution with two modes.

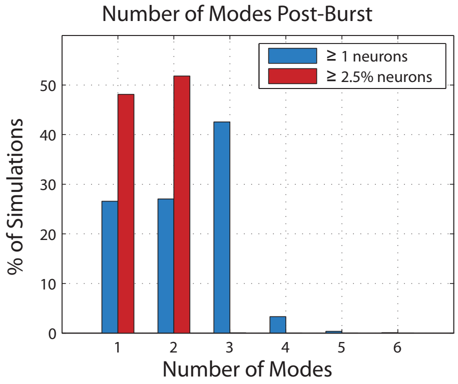

Figure 6: Count of the number of modes post-burst 200 containing 1 to N neurons in red and at least $0.025N$ neurons in blue. Simulations used $N = 500, \mu \in [.3, .7], \sigma \in [0.01, 0.1], S \in [0.1, 2]$. One to two prominent modes is usual, with all other modes containing only a few neurons (most frequently only one neuron).

3.1.2 Investigating Modes

For easier analysis of the voltages of the prominent modes, we created a new initial distribution with two modes, one at voltage x with m neurons and the other at voltage $V_R = 0$ with $N - m$ neurons. Note that x only affects the possibility of clustering into a single mode in the first burst.

Varying m and S and x, we note the distinct trends of the post-burst voltages in Table 1 (see Figure 16 for 3-D visual). The expected voltages are: $\frac{S(N-1)}{Ne^n}$ for one mode, which recieves spikes from both modes; and either $\frac{S(N-m-1)}{Ne^n}$, if the group of m neurons leads the burst, or $\frac{S(m-1)}{Ne^n}$, in the other case. Note the voltages of the basic top mode of neurons follow a voltage of approximately S/e, jumping to S/e^2 at e (Figure 17).

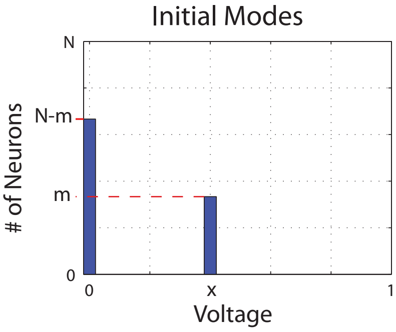

Figure 7: Initial mode distribution with m neurons in the "first" mode, $N - m$ in the second mode, and an initial spacing of $x \in (0, 1]$.

For clustering of the two modes into a single mode, we would expect a single mode of voltage $\frac{S(N-1)}{Ne^n}$. This can occur during any $n \geq 1$ level of the burst. On this level, mode 1 spikes, then mode 2. The spiking of mode 2 provides enough voltage to push both modes over V_T, causing them to merge. Thus, the clustering conditions are

$$\frac{S\,(N - m - 1)}{Ne^n} \geq 1 \text{ and } \frac{S\,(m - 1)}{Ne^n} < 1.$$

The first condition is that the spiking of mode 2 provides a strong enough signal to push itself over threshold again. The second requirement is that both modes are on the same level of the burst before clustering occurs. Note that mode 1 and mode 2 may switch ordering if mode 2 initiates the burst.

Table 1 shows a few regions which do not match up with the expected trends. For example, consider the case where $N = 1000$, $m = 800$, $S = 4$ (see Figure 18 for visual). The first mode spikes and is on the first level of the burst. This provides enough current to push both modes over V_T, because $\frac{S(m-1)}{N} \geq 1$ and $\frac{S(m-1)}{Ne} \geq 1$. Then the spiking of both modes provides enough to push the second mode over V_T, $\frac{S(N-1)}{Ne} \geq 1$, and leave the first mode at $\frac{S(N-1)}{Ne^2}$, the expected top voltage. Finally, the spiking of the second mode pushes itself to the expected bottom mode, $\frac{S(N-m-1)}{Ne^2}$, and pushes the first mode up to $\frac{S(N-1+(N-m))}{Ne^2}$.

3.1.3 Number of Spikes

Within a burst using this method, there will exist a neuron with highest voltage $\frac{S(N-1)}{N}e^{-n} \approx Se^{-n}$ where n is the level of the burst the neurons are on. The spiking of the network will end when $\frac{S(N-1)}{N}e^{-n} < 1$, given that the neuron with highest voltage will be unable to reach threshold, or $n > log\left(\frac{S(N-1)}{N}\right) \approx log\left(S\right)$. This ignores the artifact of the model mentioned above; however, it will also hold for the fluctuation-driven regime as the spiking within bursts is unaffected by outside current due to being instantaneous.

3.2 Poisson-Driven Input

When using Poisson-driven input, the neuron voltages post-burst remain discretized. Here, although the neuron voltages still cluster into modes during a bursting event, the intermittent time between bursts allow the voltages to separate given the Poisson inputs to random neurons (Figure 19). Thus, although the voltages are clustered post-burst, the neurons may switch modes between bursts.

3.3 Exponential Adaptation

To reduce clustering, we add randomness to the coupling strength of internal spikes. Generating an exponentially distributed random number, x, we use

$$S = xS_0e^{-n}.$$

This allows for strictly positive coupling strengths with average value S_0e^{-n}. Discreteness is eliminated and the post-burst voltages cluster with greater spread (Figure 20).

Analytically, we may treat the incoming spikes to a neuron as a Poisson train, which may prove helpful in further analysis of the model.

Part III

Comparison to Other Models

4 Adaptation Current

We compare our results to a much more complicated model from Van Vreeswick et. al. The dynamics are still governed by differential equations for the voltage v_i, with reset $V_R = 0$ and threshold $V_T = 1$. After one neuron spikes, it depresses the voltages of the other neurons to make it harder for them to spike. For the voltage to decrease, there must be some current A_i flowing out of the neuron, called the adaptation current. The differential equation describing this system is:

$$\tau \frac{dv_i}{dt} = I_i - v_i + E_i - A_i \tag{4}$$

This looks very similar to equation (2), with the addition of A_i; however, there is another timescale τ that we nondimensionalized out. For now, $I_i(t)$ is some arbitrary external input, but unlike our model $E_i(t)$ doesn't use Dirac Delta functions, so v_i takes some finite time to rise with each spike. In particular,

$$E_i(t) = \frac{\sigma}{\tau_1 - \tau_2} \sum_{j,k} \left(\exp\left(-\frac{t - t_{jk}}{\tau_1} \right) - \exp\left(-\frac{t - t_{jk}}{\tau_2} \right) \right) = \sum_{j,k} f_E(t - t_{jk}) \tag{5}$$

where the sum runs over all other neurons j and all spike times $t_{jk} < t$. Here τ_1 is the timescale on which E_i decays back down to 0, and τ_2 is the timescale on which E_i rises. The adaptation current is similar, except that it rises instantaneously and falls on a timescale τ_A. In particular, it is

$$A_i(t) = \frac{\alpha}{\tau_A} \sum_{j,k} \exp\left(-\frac{t - t_{jk}}{\tau_A} \right) = \sum_{j,k} f_A(t - t_{jk}). \tag{6}$$

Notice that E_i and A_i both depend on an arbitrary weight σ or α[7]. The factors $\frac{\sigma}{\tau_1 - \tau_2}$ and $\frac{\alpha}{\tau_A}$ also depend on the timescales so that $\int_0^\infty f_E(t)dt$ is independent of τ_1 and τ_2. A similar statement for f_A and τ_A holds. Since the change in v_i depends on the integral, this means that the timescales only change how fast v_i changes from each spike, but not how much.

The fact that A_i scales with $1/\tau_A$ has unrealistic consequences. In the large-τ_A limit, the bursts and the inter-burst intervals are both order τ_A. However, as we discussed, and as shown in the experimental data in fig 1, the bursts should be short compared to the time between bursts. Van Vreeswick et. al. show a simulation (Figure 2 in their paper) with realistic parameters in which the burst length and inter-burst similar.[8]

The adaptation current model differs from our scheme in the following ways:

- v_i does not rise instantaneously.
- A neuron spiking makes it more difficult for other neurons to spike, but does not affect itself. This is the exact opposite of our model, although ours could be easily modified to mimic this.
- Bursts are not instantaneous. In fact, they take a relatively large time.
- There are many more timescales, but no functions like $P(n)$.
- The voltage changes are controlled by current accross the membrane. We do this when not in a burst, but abandon this approach inside a burst.

Part IV

Conclusion

We first considered the scenario where each neuron has synaptic failure $P(n) = e^{-n}$, where n is the number of times that neuron has spiked in one burst. To examine this, we tracked the distribution of

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[7] σ correpsonds roughly to S/N in our model.

[8] One possible cause is in equation 4. We would like to say that τ is the timescale on which v_i decays, but that isn't all it does: it's actually the timescale on which v_i changes from any source, decay or not. We could easily nondimensionalize the equation differently to get $\frac{dv_i}{dt} = I_i - \frac{1}{\tau_D} V_i + E_i - A_i$. Holding τ_D fixed might be different than holding τ fixed. Alternately, we could look at limit where $\tau_1 \ll \tau_A \ll \tau_D$, which from Van Vreeswick's choice of parameters in his Figure 2 appears to make more sense. This is the closest approximation to our model.

voltages after a burst. These graphs typically resemble a sum of normal distributions, but they do not always approach a limit with large time. Although we do not know exactly where the peaks are, we examined a specific case in which we could determine about how many times we expect the neurons to fire, and where the largest peak should be. We would like to examine the effects of S and N on these conclusions, but we need some algorithm to identify peaks in order to do this. It is possible to look at some statistics, such as the correlation between neuron voltages, over different simulations to give us some idea how the parameters effect the system. It appears that small N systems have highly correlated neuron voltages.

By exponentially decreasing the coupling strength, we successfully shut down the bursting and can easily solve for the post-burst voltages given initial conditions and the model parameters; however, this simplistic addition creates unrealistic behavior of neurons grouping eternally. Further, although the Poisson-driven input separates the voltages from their modes between bursts, the neurons still group together within the bursts. When randomizing the coupling strength around the exponentially decreasing coupling strength, the neurons voltages are not fully determined but show a more realistic spread. It is possible that we will be able to use the simplistic behavior of the first idea to help illustrate what is happening in this more complex proposal.

Part V

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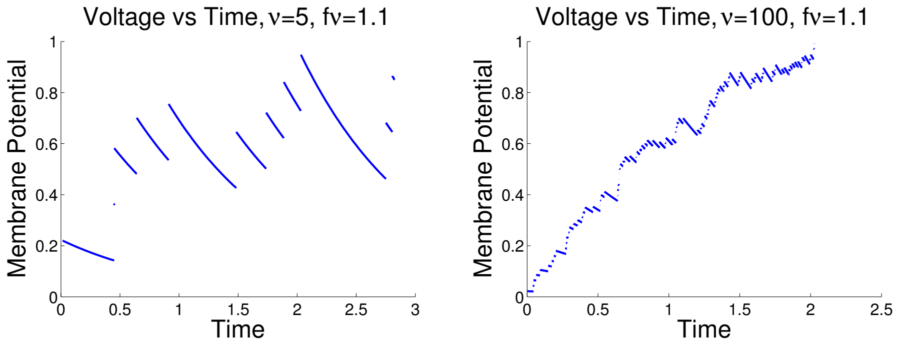
Part VI

Appendix

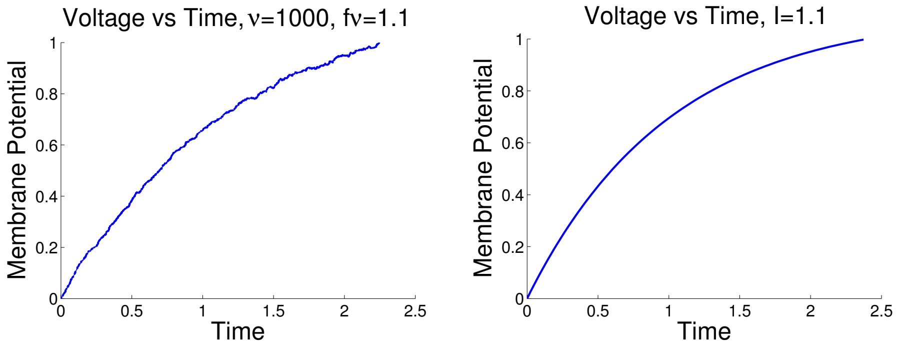
5 Figures



(a) $\nu = 5$

(b) $\nu = 50$

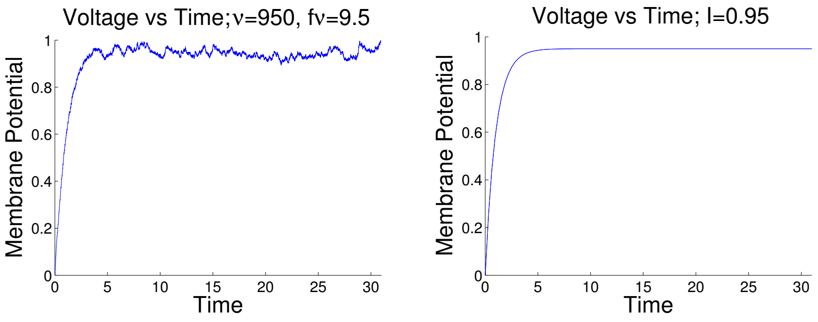
Figure 8: Graphs of v versus t until the first spike, with $f\nu = 1.1$. See figure 9 for an example with larger ν.



(a) $\nu = 1000$

(b) $I = 1.1$

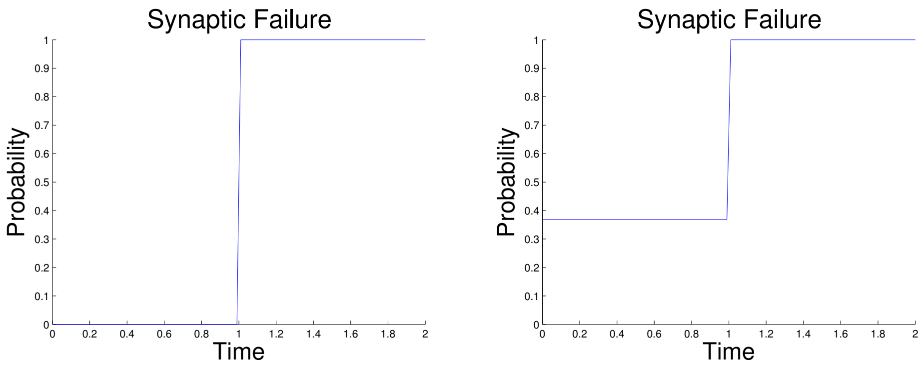
Figure 9: Graphs of v versus t until the first spike, with $f\nu = I = 1.1$.



(a) $f = 0.001$

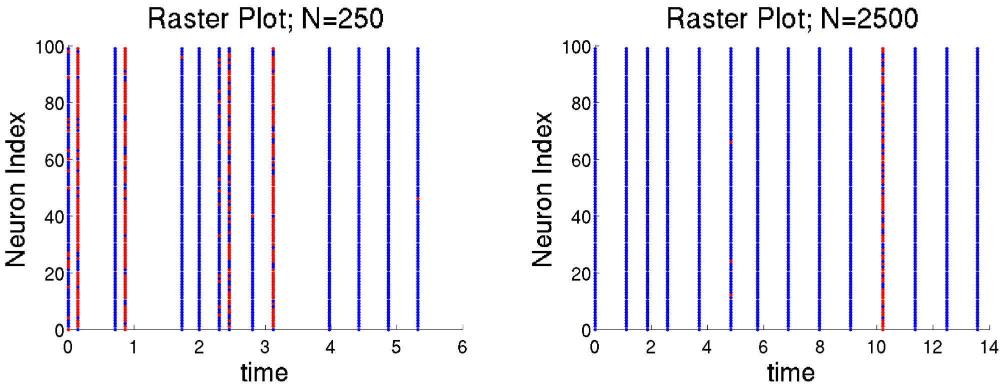
(b) $I = 0.95$

Figure 10: Graphs of v versus t until the time of the first spike using random input.

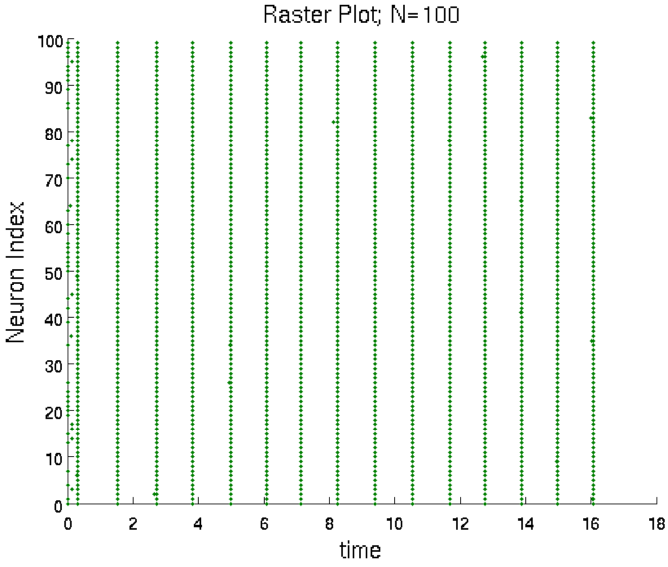


(a) Standard Model (b) Our Model

Figure 11: Assumptions on probability of transmitting a spike on short and long timescales presented as a step function.

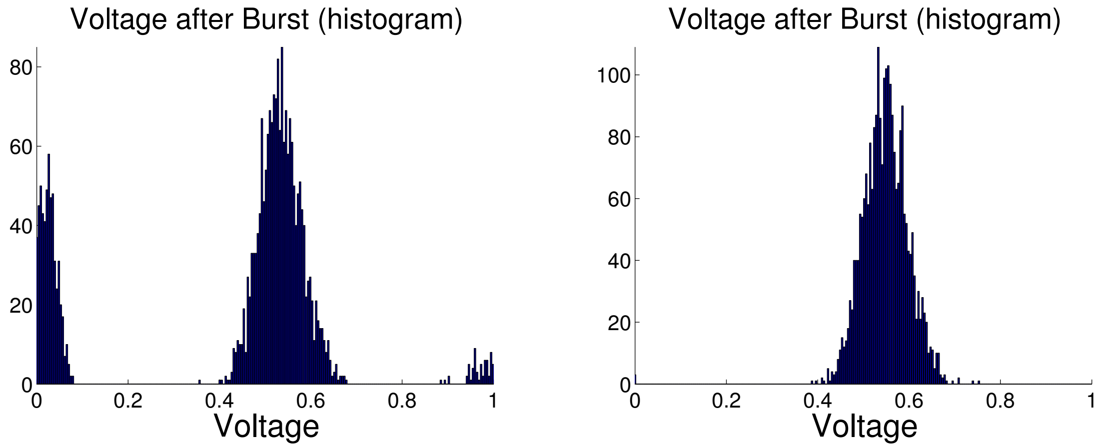


(a) $N = 250$ (b) $N = 2500$



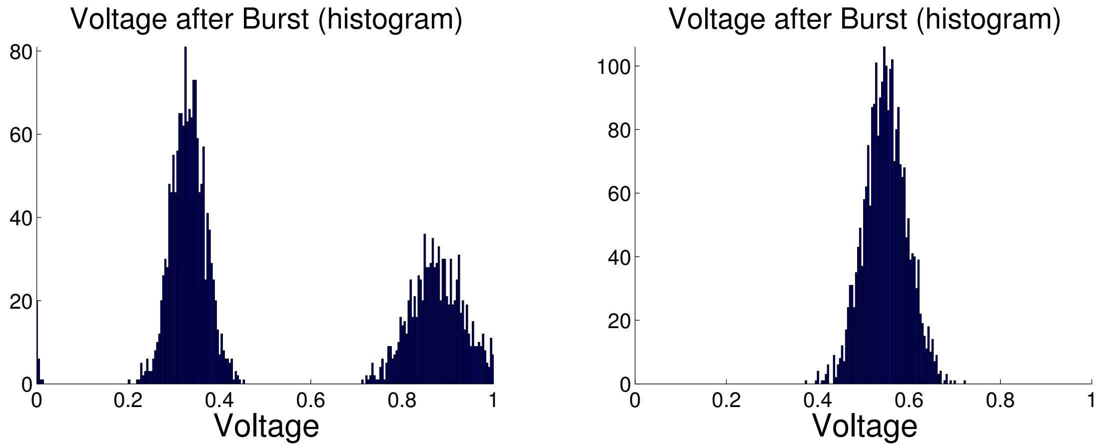
(c) $N = 100$

Figure 12: Green: One spike; Blue: Two spikes; Red: Three spikes.
Simulation parameters: for first two plots, $S = 5$ and $I = 1.1$. For the third, $f = 0.002$, $\nu = 600$, $S = 1.001$. Only the first hundred neurons are shown.



(a) $t = 100$

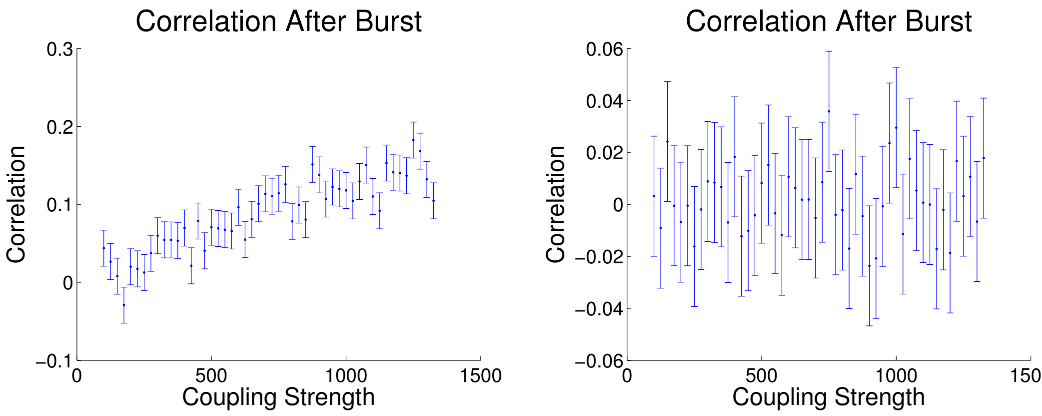
(b) $t = 200$



(c) $t = 700$

(d) $t = 1000$

Figure 13: The data is collected at the first burst exceeding the specified time. In each, the error in time is less than 2. There was almost exactly one burst per unit time (the thousandth burst occured at $t = 1013.16$). These examples were selected to show different patterns. It appears that most bursts follow the gaussian shape of the right two histograms, with the same center. Parameters are the same as in Figure 3.



(a) $S = 6.5$

(b) $S = 10$

Figure 14: Correlations between neuron voltages after a simulation with 7500 bursts. Each point corresponds to one simulation. The horizontal axis is N, the size of the network for that simulation. These use the mean-field approximation with $I = 1.1$. Error bars use the standard formula $\sigma_C = \frac{2}{\sqrt{(B)}}$, where σ_C is the standard (sample) deviation of the correlation coefficient, and B is the number of bursts. More generally, this is the number of samples used to calculate the correlation coefficient.

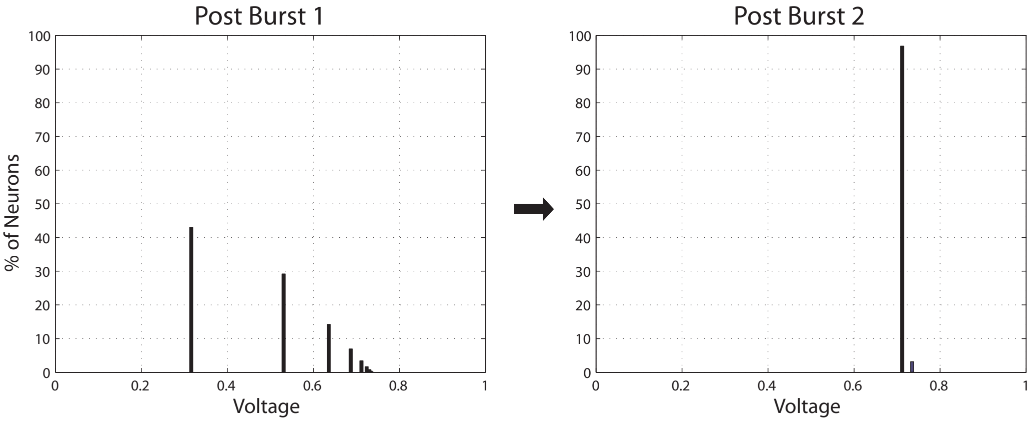
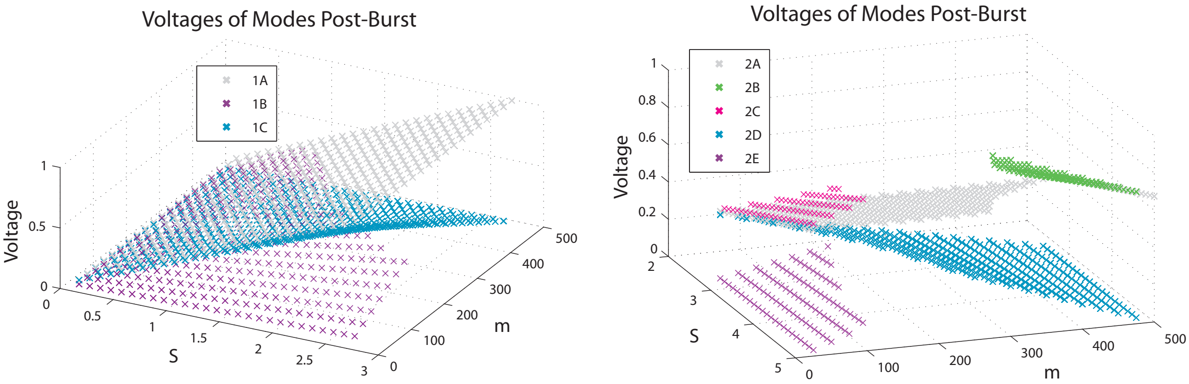


Figure 15: Example of stacking effect and how the voltages fully group into their long-term modes by the end of burst two. Simulation parameters $S = 2$, $N = 2000$, $I = 1.002$, and uniform initial distribution.



(a) Network spikes once.

(b) Network spikes twice.

Figure 16: Post-burst voltages in two-mode initial distribution. Grey points are expected top-mode voltages and blue points are expected bottom-mode voltages. See Table 1 for more details.

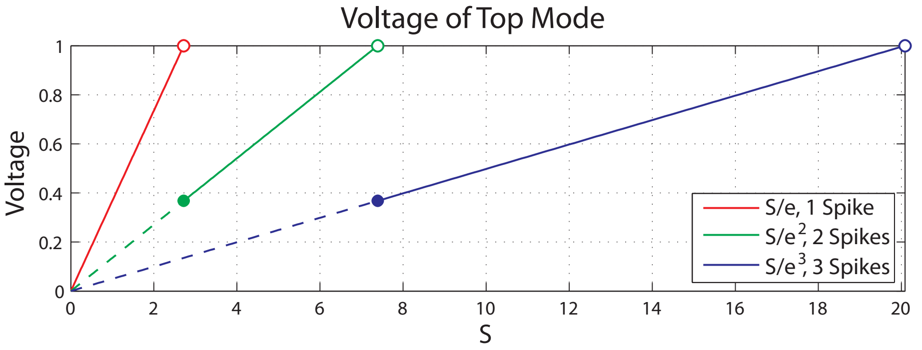


Figure 17: Showing expected top-mode voltages, $\frac{S(N-1)}{Ne^n} \approx Se^{-n}$, post-burst. As $\frac{S(N-1)}{Ne^n}$ reaches V_T, n is incremented and causing the expected voltage to be discontinuous.

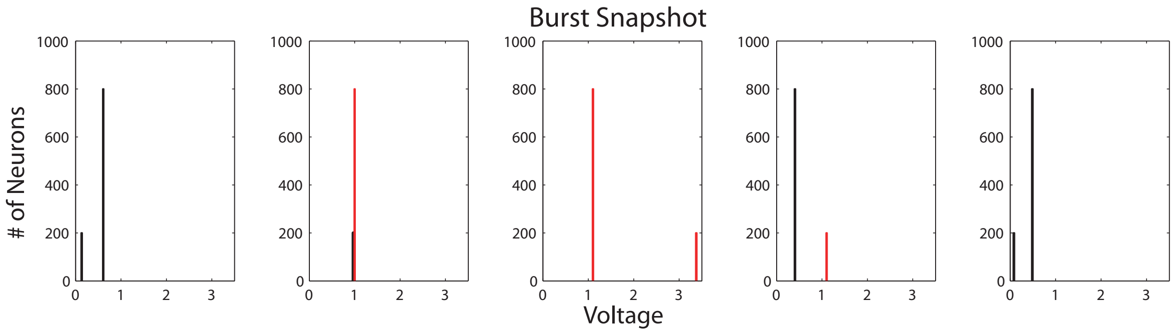


Figure 18: Snapshot of bursting with two modes where N=1000, m=800, S=4.

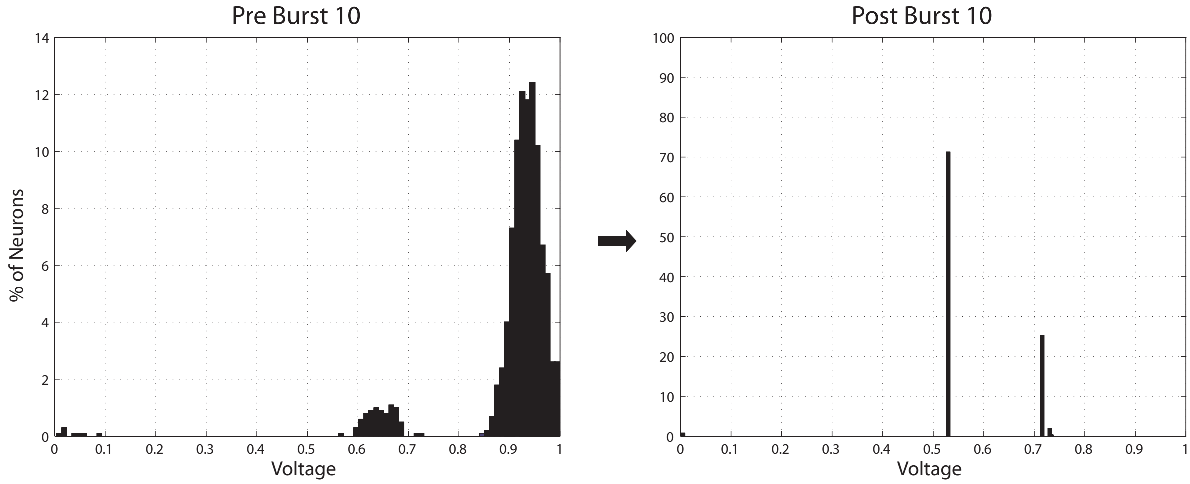


Figure 19: Example of voltage spread between bursts and clustering of voltages post-burst using $f = 0.002$, $\nu = 600$ with the Poisson-driven input.

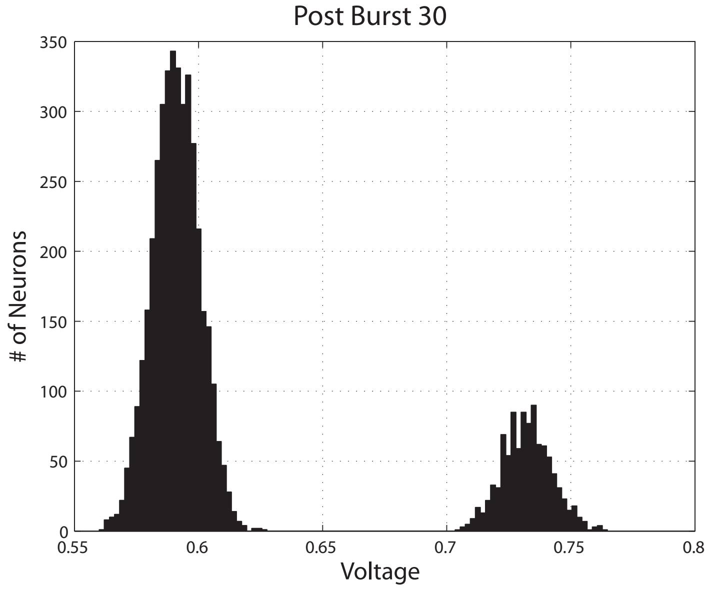


Figure 20: An example of the voltage distribution post-burst 30 using the SE mode with parameters $N = 5000$, $S = 2$, and uniform initial distribution.

6 Tables

Table 1: Post-burst voltages of modes of neurons using decreasing coupling-strength, mean-field.
Layer refers to whether mode has top or bottom mode (higher or lower voltage). See Figure 16 for visual. Mode 0 contains m neurons.

Mode	Layer	Mode #	Voltage	Description
1A	Top	0,1	$\frac{S\,(N-1)}{Ne}$	Typical top mode. Mode 0 spans whole plane. Mode 1 spans most; corresponds to mode 0 in 1B.
1B	Bottom	0	$\frac{S\,(m-1)}{Ne}$	Typical bottom mode value. Mode 0 provides insufficient current to start burst; mode 1 is burst leader and starts on top. Corresponds to mode 0 in 1A. Boundary where $\frac{Sm}{N} < 1$, only with large separation values x. On boundary, $x = 1$.
1C	Bottom	1	$\frac{S\,(N-m-1)}{Ne}$	Typical bottom mode. Crosses with 1B at $m = N/2$. Different sloping lines (because voltage relies on S and m).
2A	Top	0,1	$\frac{S\,(N-1)}{Ne^2}$	Typical top mode with two spikes per mode. Mode 0 usually on top because large S values allow easy bursting. Mode 1 on top only for small S, m. Mode 1 appears on top when $\frac{Sm}{N} < 1$.
2B	Top	0	$\frac{S\,(2N-1-m)}{Ne^2}$	Above typical top mode. Mode 0 feels mode 1 twice. High m values. Boundary where $\frac{Sm}{Ne} \geq 1$. Causes bottom mode 1 to spike twice. Largest affect for small m (feels more from other mode). Downward slope toward normal plane. Joins normal plane at $m = N = 500$.
2C	Top	1	$\frac{S\,(N-1+m)}{Ne^2}$	Above typical top mode. Mode 1 feels mode 0 twice. Low m values. Lower boundary where $\frac{S(N-m)}{Ne} \geq 1$. Causes bottom mode 0 to spike twice. Largest affect for larger m (feels more from other mode). Downward slope toward normal plane. Joins normal plane at $m = 0$. Upper boundary (high m side) where $\frac{Sm}{N} < 1$ (same as 2A boundary) allowing mode 1 to be on top.
2D	Bottom	1	$\frac{S\,(N-m-1)}{Ne^2}$	Typical bottom mode with two spikes per mode. Boundary where $\frac{S(N-m-1)}{Ne} \geq 1$. All above this cluster into one, top mode (mode 0 into 2A). Note low m, high $N-m$.
2E	Bottom	0	$\frac{S\,(m-1)}{Ne^2}$	Typical bottom mode with mode 1 on top. See 2C and mode 1 on 2A for top mode. Perfect overlay. Boundary where $\frac{Sm}{N} < 1$.