DYNAMICS OF A FULLY STOCHASTIC DISCRETIZED NEURONAL MODEL WITH EXCITATORY AND INHIBITORY NEURONS

BY

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DISSERTATION

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Abstract

We consider here an extension and generalization of the stochastic neuronal network model developed by DeVille et al.; their model corresponded to an all-to-all network of discretized integrate-and-fire excitatory neurons where synapses are failure-prone. It was shown that this model exhibits different metastable phases of asynchronous and synchronous behavior, since the model limits on a mean-field deterministic system with multiple attractors. Our work investigates adding inhibition into the model. The new model exhibits the same metastable phases, but also exhibits new non-monotonic behavior that was not seen in the DeVille et al. model. The techniques used by DeVille et al. for finding the mean-field limit are not suitable for this new model. We explore early attempts at obtaining a new mean-field deterministic system that would give us an understanding of the behavior seen in the new model. After redefining the process we do find a mean-field deterministic system that the model limits on, and we investigate the behavior of the new model studying the mean-field system.

To my wife and son.

Acknowledgments

This project would not have been possible without the support of many people. First and foremost, I give much thanks to my advisor, Lee DeVille, who propelled me through this project and whose guidance and support allowed me to work through the numerous difficulties. I also thank my committee members Kay Kirkpatrick, Zoi Rapti, and Vadim Zharnitsky for their advice and guidance. Thanks to the National Science Foundation for support throughout this project from grant DMS 08-38434 EMSW21-MCTP: Research Experience for Graduate Students. Thanks to State Farm for awarding me the State Farm Foundation Fellowship which gave me the financial means necessary to complete this project. Thanks to my parents for without their love and guidance, I would not be where I am today. And finally, I would like to thank my wife for through her immense support and love I was able to complete this long process.

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Preface

1.1 Background

In neuroscience, studying the dynamics of pulse-coupled nonlinear oscillators is of great interest. This is due to neurons having a natural characterization as such oscillators: since there is only one particular phase of a neuron's cycle in which it has the ability to effect other neurons to which it is coupled. In particular, neurons interact with each other through electrical signals. Signals are received through the dendrites of a neuron, and neurons send out signals through their axon terminals (see Figure 1.1). The structure in which the signal goes from the axon terminal of one neuron to the dendrite of another is called a synapse. Once the signal crosses the synapse and reaches another neuron it can either excite the membrane potential of the other neuron increasing its electrical charge, or inhibit the membrane potential decreasing its electrical charge. If the electrical charge of a neuron increases and hits a threshold, it causes an action potential in which the neuron sends an electrical signal from its nucleus down its axon and through synapses to other neurons to which it is coupled. After an action potential (which we call "firing"), the membrane potential will reset back to its resting potential after a refractory period in which the neuron is not able to be excited.

The majority of work with pulse-coupled oscillators is done with leaky integrate-and-fire neurons. An example of a leaky integrate-and-fire neuron is one in which the membrane potential takes values in the range $[V_0, V_T]$, where V_T is the voltage threshold that once the potential reaches the neuron fires, and V_0 is the potential the neuron is reset to after firing and the proceeding refractory period. The neuron is "leaky" in that in the absence of external input the membrane potential relaxes exponentially fast toward the reset level V_0.

Peskin in [5, p. 268–278] considered two "slightly leaky" integrate-and-fire neurons and showed under the assumption that the firing of one neuron causes a small increase in the state of the other neuron, that the neurons synchronize. This was generalized by Mirollo and Strogatz to any number of neurons in [6] where they also clarified the role of a generalized notion of "leakiness" in synchronization. A further generalization

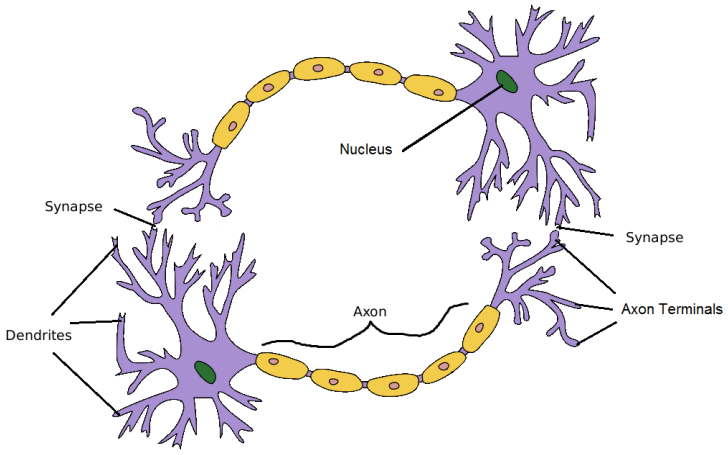


Figure 1.1: Image of two neurons coupled to each other. For the bottom neuron, its dendrites are on the left around its nucleus and its axon terminals are on the right. For the top neuron the dendrites are on the right around its nucleus and its axon terminals are on the left. Two synapses are labeled in which the neurons are making connections to each other. Original image retrieved from `https://upload.wikimedia.org/wikipedia/commons/b/be/Derived_Neuron_schema_with_no_labels.svg` an adaptation of Image:Neuron.svg by Actam. Used under the license CC BY-SA 3.0 at `http://creativecommons.org/licenses/by-sa/3.0/`

to the synchronization of non-identical pulse-coupled oscillators, but without leakiness, was made by Senn and Urbanczik [7].

Instead of using a model of deterministic continuous-state integrate-and-fire neurons, DeVille and Peskin [2] replaced it with a discrete-state neural model. Their model displayed three regimes. In the first regime the network displayed synchrony in which there was almost periodic (in time and size) large bursts of size $O(N)$ interspersed with many small busts of size $O(1)$. The second regime was asynchronous in which the network did not have any recognizable pattern of behavior. In the third regime the network would make random shifts between synchrony and asynchrony. DeVille, Peskin, and Spencer [1] showed that in the limit of network size going to infinity, the dynamics are given by a hybrid system, specifically a continuous ODE on the state space coupled with a map. This mean-field limit of the model has multiple attractors and a bistable region which provides an explanation and understanding for the behavior of their model.

1.2 Introduction and Motivation

We begin with motivation for replacing the deterministic continuous-state integrate-and-fire neuron by a fully stochastic, discrete-state neuron which was initially done by DeVille et al. in [1]. We simply give the motivation from [1] restated in the context of the model used here. The physiological motivation comes from

the stochastic nature of synaptic transmissions. When an action potential reaches a pre-synaptic terminal, with some probability synaptic vesicles from the pre-synaptic neuron release neurotransmitters into the synaptic cleft. We assume here the simplest case when the number of vesicles is either 0 or 1, the individual events of vesicles releasing neurotransmitters are mutually independent, and the probability of a vesicle releasing neurotransmitters is constant. Hence, for this model there are no inhomogeneities in time and the synaptic strength between neurons is constant. Also we assume for the post-synaptic neuron that the release of neurotransmitters into the synaptic cleft either increases (excites) or decreases (inhibits) its membrane potential by a fixed amount ΔV, and the membrane potential remains constant between the releasing events.

These assumptions let us only consider aspects of synchronization that are independent of membrane leakiness, and allow us to only consider the discrete states $V \in \{V_0, V_0 + \Delta V, V_0 + 2\Delta V, ..., V_T\}$ in the model of the neuron used, where V is the membrane potential, V_0 is the potential to which neurons are reset after firing, and V_T is the threshold potential at which neurons fire. In [1] it was also assumed the number of events of a vesicle releasing neurotransmitters that are needed for a post-synaptic neuron to go from V_0 to V_T is given by some integer K. Here, the releasing event may inhibit the membrane potential and so K would be the net number of releases that excite the membrane potential. Hence here we also have $V_T - V_0 = K\Delta V$. Once a neuron advances to V_T it fires and is subsequently reset back to V_0.

In between bursting events there are events of vesicles releasing neurotransmitters onto neurons increasing their membrane potential. These vesicle releases, which happen at a rate ρ per neuron, are thought of as coming from outside the network and is what turns our neuron model into an oscillator. In particular there is a probability per time unit ρ that the membrane potential of any neuron can increase one unit giving us the mean time between firing events as K/ρ.

To create the network in the model we assume each neuron makes exactly one synapse on every other neuron in the population. When a neuron fires there is then a probability that every other neuron in the population is affected. We also assume that there are only two types of neurons. There are excitatory neurons where the synapses it makes are exclusively excitatory only causing increases in membrane potential, and there are inhibitory neurons where the synapses it makes are exclusively inhibitory only causing decreases in membrane potential. The effect of firing for an excitatory neuron will cause the membrane potential of the post-synaptic neuron to increase by ΔV, and for an inhibitory neuron will cause the membrane potential to decrease by ΔV. When a neuron is promoted it may bring the membrane potential to V_T in which case that neuron fires leading to the possibility, if the firing neuron is excitatory, of other neurons reaching the firing threshold and firing. Those neurons in turn may cause other neurons to reach the threshold and fire and so

on. Such a chain reaction we will call a bursting event and is restricted by the rules that, for simplicity, no neuron can be demoted below state V_0 and that no neuron can fire twice during the event. The latter rule reflects the physiological phenomenon of refractoriness discussed above which restricts the firing rate of a neuron from being arbitrarily high. Our refractoriness occurs only during the bursting event which we have idealized as having zero duration. With this idealization we do not need to introduce a parameter for the duration of the refractory period. We quickly note that the only difference between the model here and the model of DeVille et al. in [1] is that their model consisted only of purely excitatory neurons. We thus refer to the model here as the inhibitory model and the model in [1] as the excitatory model.

The inhibitory model can exhibit both synchronous and asynchronous behavior. In particular, the inhibitory model shared the same surprising behavior as the excitatory model in that there is a range of parameters in which the system abruptly switches from synchronous to asynchronous behavior, and vice versa. This rich behavior is not seen in the continuous state models that are most commonly worked with. The inhibitory model also showed a counter-intuitive, "non-monotonic" behavior when looking at the proportion of bursts that were larger than 25% of the network that was not seen in the excitatory model.

We take the viewpoint of DeVille et al. in [1] that our system should be viewed as a perturbation of an underlying deterministic mean-field system. As in their excitatory model, in the large N limit K is held fixed. That is, the voltage change remains the same order of magnitude in the limit. This differs from earlier mean-field models of populations of neurons which provides the motivation for the mean-field system of the excitatory model (e.g. [4, p. 21-27]) . In these earlier models K becomes asymptotically small.

In the large N limit, we also have the synaptic strength p scaling like $1/N$. This scaling of p results in p being quite small compared to the probability of a vesicle release due to an action potential in a real brain. For example, as seen from [9], the average probability that a action potential causes a kick in the post-synaptic neuron in local cortical circuits of a rat brain is much higher at around 20%. In order for a kick to happen, neurotransmitters had to have been released from vesicles into the synapse and be taken up by the post-synaptic neuron. Hence what we call the synaptic strength would be higher than 20%. This incongruency is due to a degree/probability offset. The scaling of p, in fact, is actually $1/d$ where d is the average degree of each neuron. For our network, $d = N$. A true neural network is not all-to-all. Drachman [13] states there are approximately 20 billion neocortical neurons in the human brain, with an average of 7,000 synaptic connections each. We see then that the degree is several magnitudes smaller than the number of neurons resulting in the connectivity being much lower than in our model. Therefore, for a more realistic sparse network, the scaling of p would be much higher than in the mean-field limit we are

seeking.

It should be noted, that in the process of modeling real life systems and phenomena, the system is typically too complex and difficult to construct an exact model representing the system. So we begin with idealizations. Once we have a good understanding of this idealization, we add more and more complexity to the model in an attempt to build up to the exact model. DeVille et al. had an idealized model that exhibited rich behavior. Adding inhibition to the model adds another level of complexity that is closer to an exact model of a true neural network. This model, even with an all-to-all network, again exhibits rich behavior that is difficult to understand and analyze. After a good analysis is complete, studying the effect of network topology on the model would be the next step. Until then, to off-set the idealization of the all-to-all network, we have the synaptic strength p quite small and scaling like $1/N$.

1.3 Overview of Thesis

In Chapter 2 we give a description and the definition of the inhibitory model as well as discuss the model behavior. Chapter 3 discusses our first attempts in finding a mean-field model to approximate the inhibitory model. In our first attempts we came up with a completely continuous mean field system for the excitatory model with the idea of extending this model to the inhibitory model. We then took a generational approach to finding a mean field system and came up with some partial results. Proceeding this we finally arrive at what we titled the counting model. Chapter 4 discusses our first investigations of the bursting dynamics of the counting model with $K = 2$. In Chapter 5 we give the complete definition of the counting model and show that this stochastic process is equivalent to the inhibitory model. After this in Chapter 6 we define the mean-field system for the counting model and prove the mean field limit. Next in Chapter 7 we discuss the mean field analysis and the non-monotonic behavior. We finally discuss our conclusions and future work in Chapter 8.

Chapter 2

Inhibitory Model

2.1 Model Description and Definition

As stated, the inhibitory model used in this paper is a variation of the excitatory model of the fully stochastic neuronal network developed in [2], where the modification comes from having inhibitory neurons instead of all excitatory neurons. Hence our definition follows precisely the definition of the excitatory model except for a modification in the bursting configuration. The inhibitory model has five parameters: $N, E, K \in \mathbb{Z}^+, 0 \leq E \leq N, p \in (0,1), \rho \in \mathbb{R}^+$. The network consists of N neurons, and each neuron can be at any of the levels $\{0, 1, ..., K-1\}$. Of the N neurons, we have E excitatory with the rest being inhibitory (we denote $I = N - E$ as the number of inhibitory neurons.) ρ is the rate at which exogenous input from neurons outside the network are promoting neurons one level at a time. That is, for any small time Δt, there is a probability $\rho\Delta t + O(\Delta t^2)$ for each neuron to be spontaneously promoted one level. With the occurrence of a promotion an event begins. Thus the distribution of the successive differences between the times of these events is exponential with mean $(\rho N)^{-1}$. If the neuron promoted was at any level other than $K-1$, then the event stops. If the neuron was at level $K-1$ prior to being promoted, then we say that this neuron "fires", and this is the start of a "burst". When a neuron fires in the excitatory model it kicks every other neuron not already in state K up one state with probability p. In the inhibitory model, this kicking only occurs if the neuron is excitatory. If the firing neuron is instead inhibitory, then it demotes every other neuron not already in state K or in state 0 down one state with probability p. This computation is continued until the effect of each neuron which fired during the burst is computed. No neuron fires more than once in a burst, and at the end of the burst, all neurons that have fired are set to level 0.

To give a precise definition of the inhibitory model used, we define the state space of our system as the set $(\{0, 1, ..., K-1\})^N$; picking a point in this space specifies the level of each neuron. To compute the bursting events below, we will find it convenient to append two states at levels K and $K+1$ (we think of K as the level where a neuron is "firing", and $K+1$ is the level where a neuron which has already fired remains until

the end of the burst). Now consider an initial (perhaps random) vector $X_0 \in (\{0, 1, ..., K-1\})^N$. Since the network is all-to-all, it does not affect how we choose which neurons are excitatory and which are inhibitory (q.v. Section 5.2). So for simplicity, we pick the first E neurons of the vector to be excitatory and the remaining $I = N - E$ to be inhibitory. We next define a cadlag process on the evolution of X_t as follows. Let $0 = t_0 < t_1 < ...$ be a sequence of event times such that $t_{i+1} - t_i$ is exponentially distributed with mean $(\rho N)^{-1}$, and define X_t to be constant on $[t_i, t_{i+1})$. At each event time, pick an index $n \in \{1, ..., N\}$ uniformly and compute the following:

- If $X_{t_i,n} < K-1$, then $X_{t_{i+1},n} = X_{t_i,n} + 1$, and $X_{t-i+1,j} = X_{t_i,j}$ for all $j \neq n$, i.e. promote only neuron n by one level, at which point the event ends.

- If $X_{t_i,n} = K-1$, then define a temporary vector $Y^{(0)}$ with $Y^{(0)}_j = X_{t_i,j}$ for all $j \neq n$ and $Y^{(0)}_n = K$.

  We recursively define $Y^{(r)}$ for $r \geq 1$. For each $r = 1, 2, ...$, if there is no m with $Y^{(r-1)}_m = K$, then we say $Y^{(r)} = Y^{(r-1)}$, i.e. there is no neuron firing for $Y^{(r-1)}$, so $Y^{(r)}$ remains the same as $Y^{(r-1)}$.

  Otherwise, some neuron is firing, so we set

  $$A^{(r)} = \{n \in \{1, ..., N\} : Y^{(r-1)}_n = K\},$$

  to be the set of all firing neurons of $Y^{(r-1)}$. Choose m uniformly out of $A^{(r)}$. If $m \leq E$ (m excitatory), define $Z \in (\{0, 1\})^N$ as the random vector with $Z_m = 1$, $Z_j = 0$ for all j such that $Y^{(r-1)}_j \in \{K, K+1\}$, and all other entries of Z as independent realizations of the Bernoulli random variable which is 1 with probability p and 0 with probability $1 - p$.

  If $m > E$ (m inhibitory), define $Z \in (\{0, 1\})^N$ as the random vector with $Z_m = 1$, $Z_j = 0$ for all j such that $Y^{(r-1)}_j \in \{0, K, K+1\}$, and all other entries of Z as independent realizations of the Bernoulli random variable which is -1 with probability p and 0 with probability $1 - p$.

  We, then define $Y^{(r)} = Y^{(r-1)} + Z$. Finally, define

  $$k^* = \min_{k>0}(Y^{(k)}_n \neq K \text{ for all } n)$$

  and

  $$X_{t_{k+1},n} = \begin{cases} Y^{k^*}_n & \text{if } Y^{k^*}_n \neq K+1; \\ 0 & \text{if } Y^{k^*}_n = K+1. \end{cases}$$

k^* is the first $k = 1, 2, ...$, such that $Y^{(k)}$ has no firing neurons. At this point, we update the process and the burst ends. The appended state K we can think of as the "queue", i.e. neurons awaiting processing, and $K + 1$ as neurons which have been processed.

The above process can be summarized as follows. Whenever we promote a neuron, if it is not at level $K-1$, then no burst occurs. If it is, however, we move it to the queue. We then iterate the following algorithm until the queue is empty: pick a certain neuron at random from the queue. If the neuron is of index $\leq E$, promote each neuron in the network which has not yet reached the queue by one level independently with probability p. If the neuron is of index $> E$, demote each neuron in the network which has not reached the queue and is not at level 0 by one level independently with probability p. Leave the neurons which are already in the queue, or have been processed, where they are, and then move the neuron we picked from the queue into the processed bin.

As defined above, $Y^{(r)}$ is defined for all $r \in \mathbb{N}$, but in practice we only need consider Y until such time as the queue is empty. However, $k^* < N$, so for any burst, we need only compute a finite set of $Y^{(r)}$. Notice since all the excitatory neurons are equivalent, and all the inhibitory neurons are equivalent, we only need to keep track of the number of excitatory neurons and the number of inhibitory neurons at each level. (This equivalency is what leads to the equivalency of the inhibitory model and the counting model defined later.) This would of course not be true in a network whose structure was inhomogeneous. Finally, a quick note about ρ: changing ρ does not qualitatively change anything about the stochastic process, and amounts only to a (deterministic) time change. We will set $\rho = 1$ below. Also, it is important to note that the model definition just given for $E = N$, that is in the absence of inhibitory neurons, is the exact model definition for the excitatory model of DeVille et al.

2.2 Model Behavior

As stated, the inhibitory model has three regimes as in the excitatory model: one of synchrony, one of asynchrony, and one where the network switches between synchrony and asynchrony. Specifically, for many N and K we have the following. If p is chosen sufficiently large, the network settles into a nearly periodic pattern in which large bursts (of size $O(N)$) are separated by many small bursts (of size $O(1)$). If p is sufficiently small, we have the opposite behavior: there is no discernible pattern in time. Thus, as one increases p, there is a transition from asynchrony to synchrony. (Realizations of this behavior can be seen in Figure 2.1. Panels (a) and (b) are of synchrony and asynchrony, respectively, for the excitatory model,

and panels (c) and (d) are of synchrony and asynchrony, respectively, for the inhibitory model.) And for an intermediate range of p, the network can exhibit both synchronous and asynchronous behavior. For p in this range, any realization of this network will actually switch back and forth between synchrony and asynchrony, suggesting that these two states are each metastable and that the system makes stochastic transitions between them. (Realizations of this behavior can be seen in Figure 2.2 (a), for the excitatory model, and in Figure 2.2 (b), for the inhibitory model.)

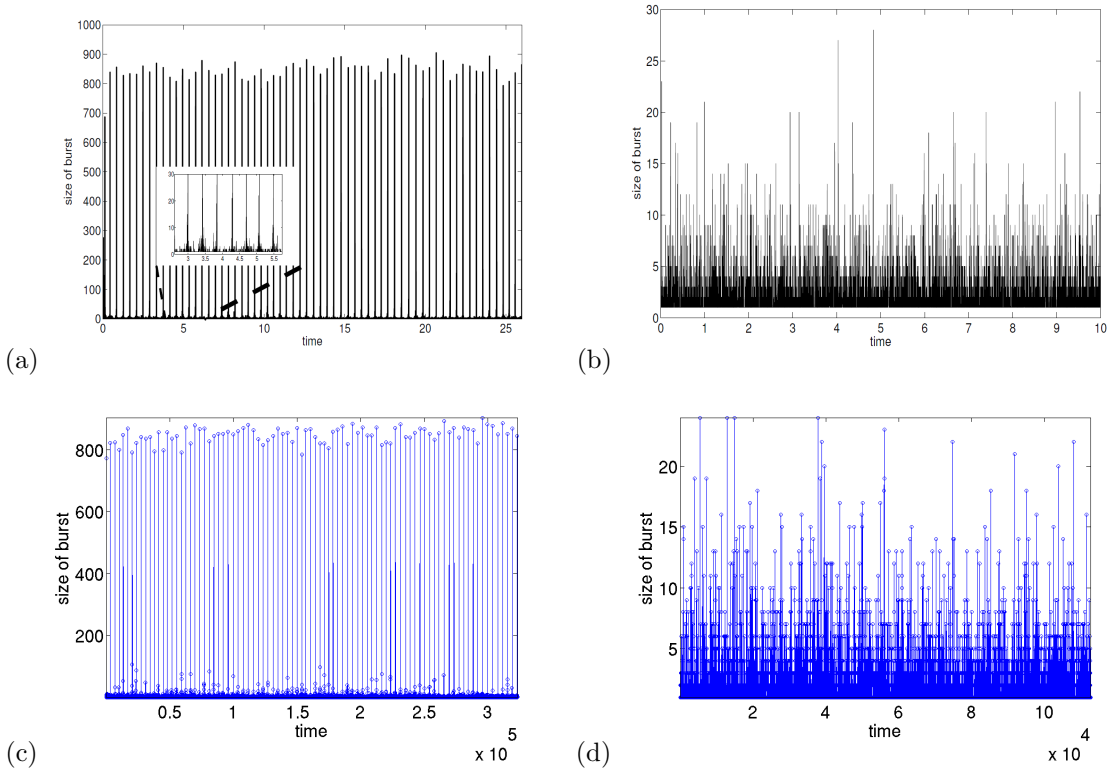
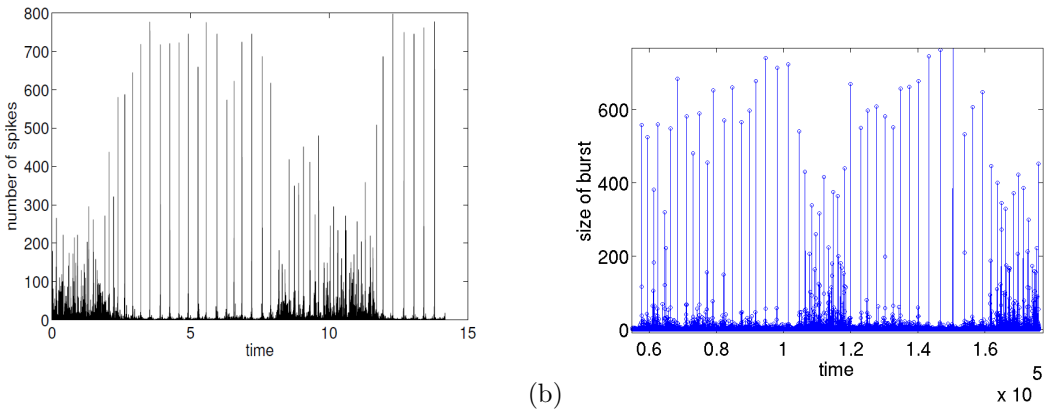


Figure 2.1: Simulations with $N = 1000$, $K = 10$. The top two panels are the excitatory model, where in (a) $p = .01$, and in (b) $p = .005$. The bottom two panels are the inhibitory model with $E = 800$ and in (c) $p = .0175$, and in (d) $p = .007$. The panels on the left show synchrony and the panels on the right show asynchrony.

The inhibitory model also displays new behavior not in the excitatory model in what is called the S_{25} curve. Let $S_n(p)$ be, for a given p, the proportion of the total number of bursts in a simulation with size greater than or equal to $n\%$ of the network. It would naturally seem that $S_n(p)$ would be a monotone increasing function of p. That is, as you in increase the synaptic strength p, the number of bursts of size $(n/100)N$ would monotonically increase. This was not observed as seen in the left plot of Figure 2.3. This behavior was not limited to the case with $N = 1000$ and $E = 800$. For $N = 10000$ there were several choices of E where this behavior was seen as well. Moreover, for $N = 10000$, the behavior was exaggerated for



(a) (b)

Figure 2.2: Simulations with $N = 1000$, $K = 10$. (a) is a simulation of the excitatory model with $p = .00945$. (b) is a simulation of the inhibitory model with $E = 800$ and $p = .0156$.

$E = 6000$ as seen in Figure 2.4. The right plot of Figure 2.3 shows that this behavior was not seen in the excitatory model.

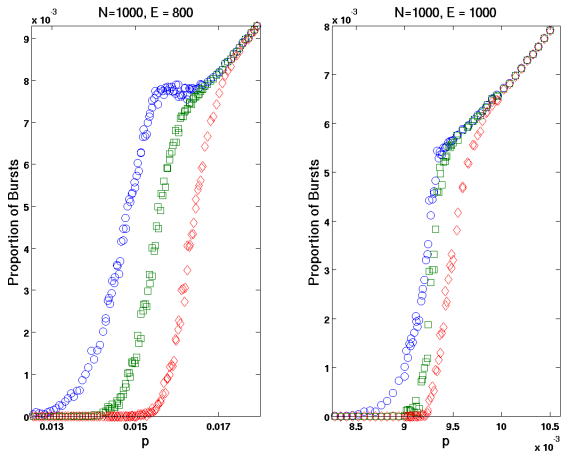


Figure 2.3: Plots of the S_{25} (blue circles), S_{50} (green squares), and S_{75} (red diamonds) curves for simulations of the inhibitory processes with $N = 1000$, $K = 10$. The plot on the left are the S_n curves for $E = 800$, and the plot on the right are the S_n curves for $E = 1000$.

This interesting non-monotonic behavior of the inhibitory model is also seen in the model of Singh et al. in [8]. They were looking at dynamics on random graphs $\mathcal{G}(n, p)$, where n is the number of nodes in the graph, and p is the probability of an edge existing between any two nodes. For a large number of input parameters for their model, they found that the fraction of initial conditions that tend to a periodic solution, as a function of p, was non-monotonic. We investigate the non-monotonic behavior of our model in Section 7.2.

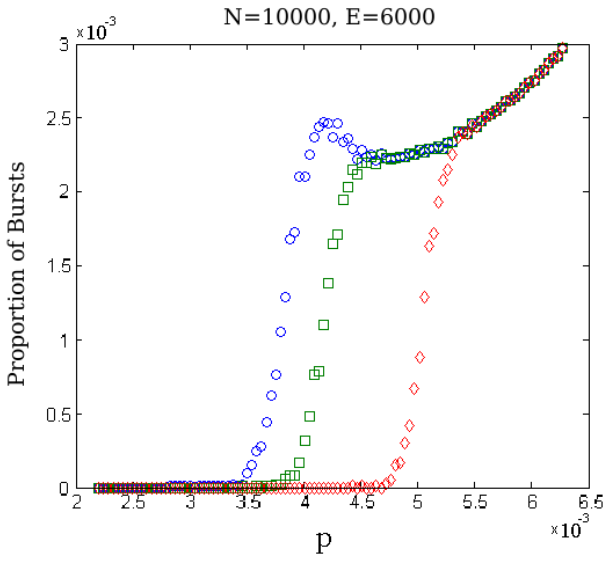


Figure 2.4: Plot of the S_{25} (blue circles), S_{50} (green squares), and S_{75} (red diamonds) curves for simulations of the inhibitory process with $N = 10000$, $K = 10$, and $E = 6000$.

Chapter 3

First Attempts at Mean-Field System

DeVille et al. in [2] took the viewpoint that the excitatory model should be viewed as a perturbation of an underlying deterministic system. This underlying system for some range of parameters should be able to support two different types of dynamical behavior. Adding noise to the system would cause random shifts between these two types of dynamics. In this context, it makes sense to think of noise being small as $N \to \infty$. Moreover, in some specific limit as $N \to \infty$ where we hold pN fixed, the stochastic system should then be a perturbation in some sense of a particular underlying deterministic system. These ideas lay the approach to finding a mean-field limit for the inhibitory model.

3.1 Excitatory Mean-Field Model

We begin with discussing the mean-field limit of the excitatory model. This mean field limit, as stated earlier, is a continuous ODE on the state space coupled with a map. The precise definition of the mean field limit does not concern us here (for such a precise definition see [1]). Here we are merely interested in that the mean field limit is a deterministic approximation of the excitatory model, and that the mean field limit has multiple attractors with a bistable region. Theorem 1 of [1] shows that the times at which the excitatory stochastic model has big bursts are close to the times predicted by the mean field and that the stochastic process is pathwise convergent to the mean field. In the mean-field limit $\beta = pN$ remains constant and is the characterizing parameter for the dynamics.

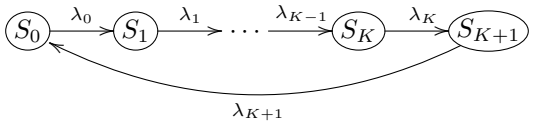
DeVille et al. showed three results for the mean field system. One, for β small enough, the mean field had an attracting fixed point. That is, no big bursts occur. Two, for β large enough, the mean field has infinitely many big bursts. And three, for an intermediate region of β, some initial conditions lead to infinitely many big bursts, while others went to the fixed point. Hence, the mean-field system had a bistable region with two attractors. Adding noise to the system while in this region, would cause jumps between these two attractors. This explains the switching behavior observed in the excitatory model.

As mentioned, we cannot use the techniques of [1] in finding a mean-field limit for the inhibitory model since the ordering of the firing of neurons matters in the inhibitory model. A complication that came up in finding a mean-field limit for the excitatory model came from the "discontinuity" of the model. There are two regimes in the model, the non-bursting regime, and the bursting regime. After a burst, everything that fired is reset to state zero and the non-bursting regime resumes. This resetting to zero is a "discontinuity" in the process. The ODE in the mean-field system for the excitatory case is the approximation for the non-bursting regime. The "discontinuity" of resetting all the fired neurons to zero is approximated by the map coupled to the ODE. The map sends the process to the state at which the system is at after firing. i.e it is approximating the state of the system after firing.

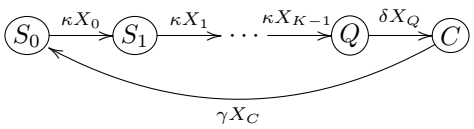
We revamped the model as a continuous time Markov chain to overcome this "discontinuity". With a CTMC, the mean-field system would be a system of continuous ODEs not coupled with a map and would be avoiding the discontinuity. We refer to this model as the continuous excitatory model. Our plan was to extend this mean-field system to the inhibitory model. However, taking the mean-field limit of this model lead to a stiff non-linear ODE. In hind-sight, this should be expected given we are approximating the discontinuity with a continuous process.

3.2 Continuous Excitatory Model

The model has five input parameters: $N, K \in \mathbb{Z}^+$, $p \in (0,1)$, $\rho, \delta, T \in \mathbb{R}^+$. N is the number of neurons, K is the number of in-active states, p again is thought of as the synaptic strength, ρ is the rate of promotion due to exogenous input, δ is thought of as the rate at which a firing neuron actually fires, and T is the total time the Markov chain is ran. Note that the Markov chain will have $K+2$ states. Let the states be S_i for $i = 0, 1, ..., K+1$. We think of $S_K = Q$ as the firing state and $S_{K+1} = C$ as the cool down state. Define for $i = 0, 1, ..., K-1$, $X_i(t) := |S_i|_t$ to be the number of neurons in state S_i at time t. Also define $\gamma := \frac{\sqrt{\delta}}{2}$ and $\kappa(t) := p\delta X_K(t) + \rho$. The transition rates of our Markov chain are then given by $\lambda_i(t) = \kappa(t)X_i(t)$, for $i = 0, 1, ..., K-1$, $\lambda_K(t) = \delta X_K(t)$, and $\lambda_{K+1}(t) = \gamma X_{K+1}(t)$, where for $i = 0, 1, ..., K$, $\lambda_i(t)$ is the transition rate from $S_i \to S_{i+1}$, and $\lambda_{K+1}(t)$ is the transition rate from $S_{K+1} \to S_0$. Notice that the rates are functions of time. For convenience we drop the notational (t). Our model is then illustrated by the following Markov chain:



or rewritten



which is run for a total of time T. In this model, a burst begins when Q becomes non-empty, and ends when Q becomes empty again. The size of the burst would be the number of neurons to transition through Q during this period.

For δ large, this model displayed the same qualitative behavior as the excitatory model. For many N and K and for δ sufficiently large, it is found for p sufficiently large the network synchronizes, for p sufficiently small the network fires asynchronously, and for an intermediate range of p, the network switches between synchrony and asynchrony (see Figure 3.1). In the excitatory model, the characterization of a burst can be thought of as the rate of promotion for neurons increasing. We take δ large to mimic this characterization. Also, the model was set up with the goal that in the limit as $\delta \to \infty$, the continuous excitatory model $X(t)$ will limit on the process in the excitatory model.

Taking $N \to \infty$ and scaling p like $1/N$, we use Kurtz's Theorem [12, Theorem 5.3] to obtain the mean-field limit $x(t)$ which satisfies the ODE:

$$\begin{aligned}
\dot{x}_0 &= \gamma x_{K+1} - (\beta\delta x_K + \rho)x_0 \\
\dot{x}_i &= (\beta\delta x_K + \rho)(x_{i-1} - x_i) \\
\dot{x}_K &= (\beta\delta x_K + \rho)x_{K-1} - \delta x_K \\
\dot{x}_{K+1} &= \delta x_K - \gamma x_{K+1}
\end{aligned}$$

where i in the second line goes from 1 to $K-1$, x_j is viewed as the proportion of neurons in state S_j, for $j = 0, ..., K+1$, and $\beta = pN$. This is a non-linear ODE. Also, since we are only considering the case when δ is large, the ODE is stiff. In other words, this mean-field limit is difficult to work with. It seems in trying to eliminate one difficulty, we encountered another.

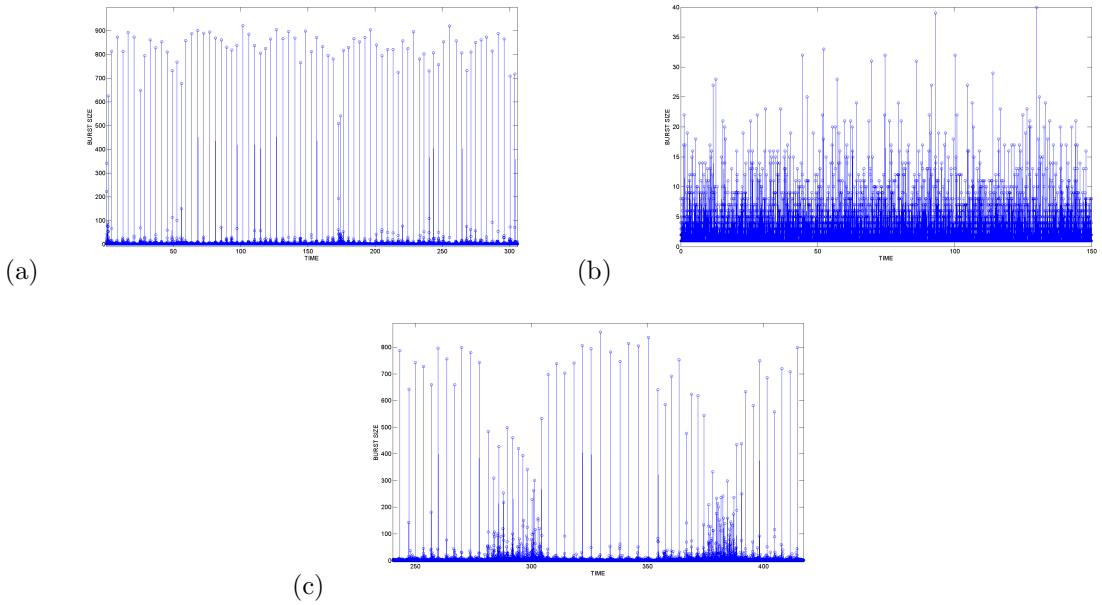


Figure 3.1: Simulations of the continuous excitatory model with $N = 1000$, $K = 10$. In (a) $p = .01$ and we see synchrony. In (b) $p = .005$ and we see asynchrony. In (c) $p = .00945$ and we see the switching behavior.

Another difficulty mentioned with the inhibitory model is the ordering of the neurons firing. To overcome this obstacle, we redefined the bursting dynamics as a generational process. That is, every neuron in the firing queue would fire at once and the cumulative effect of this firing for each neuron was calculated. The number of neurons that would reach the firing queue after determining the cumulative effect would be the next generation. This lead to a branching-like process definition of the bursting dynamics for the inhibitory model.

3.3 Branching-Like Process

We redefine the bursting configuration for the inhibitory model. For simplicity, we start with the case where $K = 1$. For this model we have six states, three excitatory states, $S_0^{\mathcal{E}}$, $Q^{\mathcal{E}}$, and $P^{\mathcal{E}}$ and three inhibitory states, $S_0^{\mathcal{I}}$, $Q^{\mathcal{I}}$, and $P^{\mathcal{I}}$. Excitatory neurons only move through the excitatory states and the inhibitory neurons only move through the inhibitory states. For both types of neurons, S_0 is the inactive state, Q is the firing state and P is the fired state. We begin this approach assuming replacement in the $(K-1)^{st} = 0^{th}$. The parameters N, E, and p are as before in the inhibitory model definition.

We have two generational processes Z_k and Y_k, $k = 0, 1, 2, ...$, where Z_k is the number of firing excitatory neurons at generation k, and Y_k is the number of firing inhibitory neurons at generation k. A neuron will be

promoted to state Q if the difference of two binomials A_k and B_k, is positive, where $A_k \sim \text{Binomial}(Z_k, p)$ and $B_k \sim \text{Binomial}(Y_k, p)$. If the first neuron to fire is an inhibitory neuron, no more neurons will fire during this burst, and, subsequently, we immediately go back to the non-bursting regime. Hence we are only interested in when the first neuron to fire is excitatory. Naturally then, we set $Z_0 = 1$ and $Y_0 = 0$. To define the rest of the process, we must define a series of random variables.

Let $X_{\mathcal{E}} = S^{\mathcal{E}}_{K-1}$ and $X_{\mathcal{I}} = S^{\mathcal{I}}_{K-1}$. For $1 \leq j \leq X_{\mathcal{E}} + X_{\mathcal{I}}$, we define the series of Binomial random variables

$$A^j_k \sim \text{Binomial}(Z_{k-1}, p), \quad B^j_k \sim \text{Binomial}(Y_{k-1}, p).$$

We think of A^j_k as the number of excitatory neurons that kicked neuron v_j at generation k and B^j_k as the number of inhibitory neurons that demoted neuron v_j at generation k.

Now we can define Z_k, Y_k for $k \geq 1$. Recall that a neuron in state $X_{\mathcal{E}}$ or $X_{\mathcal{I}}$ gets promoted to the firing state if and only if the difference of two binomial random variables is positive. The distribution of these two random variables is exactly the distributions of A^j_k and B^j_k respectively. In particular we have a promotion for neuron v_j if and only if $A^j_k > B^j_k$. Recalling we are assuming replacement, the number of neurons firing at generation k would then be

$$Z_k = \sum_{j=1}^{X_{\mathcal{E}}} \mathbf{1}(A^j_k > B^j_k), \quad Y_k = \sum_{j=X_{\mathcal{E}}+1}^{X_{\mathcal{E}}+X_{\mathcal{I}}} \mathbf{1}(A^j_k > B^j_k).$$

We are interested in the expected total number of neurons fired. That is, we want to know the value $C = \mathbb{E}\left[\sum_{k\geq 0} Z_k + Y_k\right]$. To investigate this number, it is natural to start by investigating $\mathbb{E}[Z_k]$ and $\lim_{k\to\infty} \mathbb{E}[Z_k]$.

3.3.1 $\mathbb{E}[Z_k]$

We are first interested in $\mathbb{E}[Z_k]$ as a function of p and studying its limit as $k \to \infty$. Clearly $\mathbb{E}[Z_k] = X_{\mathcal{E}}\ \mathbb{P}(A^j_k > B^j_k)$ since A^j_k, B^j_k are independent with respect to the index j. So we study $\mathbb{P}(A^j_k > B^j_k)$. Now the events $\{A^j_k > B^j_k\}$ are i.i.d. This allows us to define $P_k(p) := \mathbb{P}(A_k > B_k)$ where the j is dropped. We then define $\Psi_p : [0,1] \to [0,1]$ by

$$\Psi_p(x) = \sum_{s=1}^{X_{\mathcal{E}}} \sum_{t=0}^{X_{\mathcal{I}}} \alpha_{s,t}(p) \binom{X_{\mathcal{E}}}{s} \binom{X_{\mathcal{I}}}{t} x^{s+t} (1-x)^{X_{\mathcal{E}}+X_{\mathcal{I}}-s-t},$$

where $\alpha_{s,t}(p) := \mathbb{P}(A_k^j > B_k^j \mid Z_{k-1} = s, Y_{k-1} = t)$. Notice $\Psi_p(x)$ is actually a function of $x, p, X_\mathcal{E}$, and $X_\mathcal{I}$, but we suppress the notation for $X_\mathcal{E}$ and $X_\mathcal{I}$ and assume they are fixed. We are now ready for our first theorem.

Theorem 3.3.1. $\mathbb{E}[Z_k] = X_\mathcal{E}\Psi_p^{k-1}(p)$

Proof. Z_k being a sum of independent indicators gives us that its expected value is simply the sum of the probabilities of the events of the indicators. These indicators are $\mathbf{1}(A_{k-1}^j > B_{k-1}^j)$ with events $\{A_{k-1}^j > B_{k-1}^j\}$ which are i.i.d. with $\mathbb{P}\{A_{k-1}^j > B_{k-1}^j\} = P_k(p)$. This give us that

$$\mathbb{E}[Z_k] = \sum_{j=1}^{X_\mathcal{E}} P_k(p) = X_\mathcal{E} P_k(p)$$

Let us now consider $\alpha_{s,t}(p)$, the probability of the event $\{A_k^j > B_k^j\}$ conditioned on $Z_{k-1} = s$ and $Y_{k-1} = t$. This is

$$\alpha_{s,t}(p) = \sum_{j=1}^{s} \sum_{r=0}^{s-j\wedge t} \binom{s}{r+j}\binom{t}{r} p^{2r+j}(1-p)^{s+t-2r-j}.$$

To see why this is the form of $\alpha_{s,t}(p)$, recall that we need A_k^j to be at least one more than B_k^j. The index j is then $A_k^j - B_k^j$, and the index r is B_k^j. So $A_k^j = r + j$. The largest A_k^j can be is $Z_{k-1} = s$ and the largest B_k^j can be is the minimum of $Z_{k-1} - j$ and Y_{k-1}. Noting that both A_k^j and B_k^j are both binomial random variables with parameters (s, p) and (t, p) respectively, the probability that $A_k^j = r + j$ is then $\binom{s}{r+j}p^{r+j}(1-p)^{s-r-j}$, and the probability that $B_k^j = r$ is $\binom{t}{r}p^r(1-p)^{t-r}$. Combining all of this gives the form for $\alpha_{s,t}(p)$.

Using the law of total probability we get

$$P_k(p) = \sum_{s=1}^{X_\mathcal{E}} \sum_{t=0}^{X_\mathcal{I}} \alpha_{s,t}(p)\mathbb{P}(Z_{k-1} = s)\mathbb{P}(Y_{k-1} = t). \tag{3.1}$$

Notice the first sum begins at $s = 1$ since if $Z_{k-1} = 0$, we must have $A_k^j \leq B_k^j$. Now in order for $Z_{k-1} = s$, s of the $X_\mathcal{E}$ possibilities in the sum $\sum_{j=1}^{X_\mathcal{E}} \mathbf{1}(A_{k-1}^j > B_{k-1}^j)$ must be 1. Each term is 1 with probability $P_{k-1}(p)$. Likewise for $Y_{k-1} = t$. Hence both $\mathbb{P}(Z_{k-1} = s)$ and $\mathbb{P}(Y_{k-1} = t)$ are binomial random variables with parameters $(X_\mathcal{E}, P_{k-1}(p))$ and $(X_\mathcal{I}, P_{k-1}(p))$ respectively. Therefore, we have $\mathbb{P}(Z_{k-1} = s) = \binom{X_\mathcal{E}}{s}P_{k-1}(p)^s(1 - P_{k-1}(p))^{X_\mathcal{E}-s}$ and $\mathbb{P}(Y_{k-1} = t) = \binom{X_\mathcal{I}}{t}P_{k-1}(p)^t(1 - P_{k-1}(p))^{X_\mathcal{I}-t}$. Com-

bining everything (3.1) becomes

$$P_k(p) = \sum_{s=1}^{X_\mathcal{E}} \sum_{t=0}^{X_\mathcal{I}} \alpha_{s,t}(p) \binom{X_\mathcal{E}}{s} \binom{X_\mathcal{I}}{t} P_{k-1}(p)^{s+t} (1 - P_{k-1}(p))^{X_\mathcal{E}+X_\mathcal{I}-s-t},$$

or rewritten, $P_k = \Psi_p(P_{k-1})$.

Iterating this function Ψ_p, we have that $P_k = \Psi_p^{k-1}(P_1)$. Now $P_1 = \mathbb{P}(A_1 > B_1) = p$ simply due to the fact that $Y_0 = 0$ which makes $B_1 = 0$. Hence $\mathbb{E}[Z_k] = X_\mathcal{E} \Psi_p^{k-1}(p)$ as desired.

□

At this stage, since we know $\mathbb{E}[Z_k] = X_\mathcal{E} \Psi_p^{k-1}(p)$, if we can determine the behavior of $\Psi_p(x)$ as a discrete dynamical system, then we can largely determine the limit of $\mathbb{E}[Z_k]$ as $k \to \infty$ since $X_\mathcal{E}$ is a fixed value. We proceed with a lemma.

Lemma 3.3.2. $\Psi_p'(0) = X_\mathcal{E}\ p$

Proof. Taking the derivative of $\Psi_p(x)$ with respect to x gives

$$\Psi_p'(x) = \sum_{s=1}^{X_\mathcal{E}} \sum_{t=0}^{X_\mathcal{I}} \alpha_{s,t}(p) \binom{X_\mathcal{E}}{s} \binom{X_\mathcal{I}}{t} (s+t)(x^{s+t-1}(1-x)^{X_\mathcal{E}+X_\mathcal{I}-s-t} - (X_\mathcal{E}+X_\mathcal{I}-s-t)x^{s+t}(1-x)^{X_\mathcal{E}+X_\mathcal{I}-s-t-1}).$$

Plugging in $x = 0$ we see that the only term to survive is when $s + t = 1$, which only occurs when $s = 1$ and $t = 0$. This term evaluates to $\Psi_p'(0) = X_\mathcal{E}\ \alpha_{1,0}(p) = X_\mathcal{E}\ p$ □

This leads us to three conjectures:

1. If $\Psi_p'(0) = X_\mathcal{E} p \leq 1$, then Ψ_p has only 0 has a fixed point and $\lim_{k\to\infty} \Psi_p^k(x) = 0$ for all $x \in (0, 1]$
2. If $X_\mathcal{E} p > 1$, then Ψ_p has a unique positive fixed point $x^* > 0$ and $\lim_{k\to\infty} \Psi_p^k(x) = x^*$ for all $x \in (0, 1]$
3. $\dfrac{\partial x^*}{\partial X_\mathcal{E}} > 0$ and $\dfrac{\partial x^*}{\partial X_\mathcal{I}} < 0$.

Proving these conjectures will give us what we need to know about $\mathbb{E}[Z_k]$. Moreover, it will also determine the extinction probability of Z_k as seen in the next section.

3.3.2 Probability of Extinction

The probability of extinction is another quantity critical in understanding the behavior of Z_k. We will denote this value by θ_k. We proceed similarly as in the previous section. Let us define $Q_k(p) = \mathbb{P}(A_k \leq B_k) = 1 - P_k(p)$,

where again the j is dropped due to the events $\{A_k^j < B_k^j\}$ being i.i.d. We then define $\Lambda_p : [0,1] \to [0,1]$ by

$$\Lambda_p(x) = \sum_{s=0}^{X_\mathcal{E}} \sum_{t=0}^{X_\mathcal{I}} \omega_{s,t}(p) \binom{X_\mathcal{E}}{s} \binom{X_\mathcal{I}}{t} (1-x)^{s+t} x^{X_\mathcal{E}+X_\mathcal{I}-s-t},$$

where $\omega_{s,t}(p) = \mathbb{P}(A_k^j \leq B_k^j \mid Z_{k-1} = s, Y_{k-1} = t) = 1 - \alpha_{s,t}(p)$. Similar to $\Psi_p(x)$, $\Lambda_p(x)$ is actually a function of $x, p, X_\mathcal{E}$, and $X_\mathcal{I}$, but we we suppress the notation for $X_\mathcal{E}$ and $X_\mathcal{I}$ and assume they are fixed.

For extinction to occur, we would need $A_k^j < B_k^j$ for every $1 \leq j \leq X^\mathcal{E}$. That is, every neuron in $S_0^\mathcal{E}$ receives more depressions than kicks. Hence, the probability of extinction at generation k is $\theta_k = \mathbb{P}(A_k < B_k)^{X^\mathcal{E}} = Q_k(p)^{X^\mathcal{E}}$ Our goal is to show $Q_k(p) = \Lambda_p^{k-1}(1-p)$. We first begin with a lemma.

Lemma 3.3.3. $\Lambda_p(x) = 1 - \Psi_p(1-x)$

Proof. The proof is simple algebra:

$$\begin{aligned}
\Lambda_p(x) &= \sum_{s=0}^{X_\mathcal{E}} \sum_{t=0}^{X_\mathcal{I}} \omega_{s,t}(p) \binom{X_\mathcal{E}}{s} \binom{X_\mathcal{I}}{t} (1-x)^{s+t} x^{X_\mathcal{E}+X_\mathcal{I}-s-t} \\
&= \sum_{s=0}^{X_\mathcal{E}} \sum_{t=0}^{X_\mathcal{I}} (1-\alpha_{s,t}(p)) \binom{X_\mathcal{E}}{s} \binom{X_\mathcal{I}}{t} (1-x)^{s+t} x^{X_\mathcal{E}+X_\mathcal{I}-s-t} \\
&= \sum_{s=0}^{X_\mathcal{E}} \sum_{t=0}^{X_\mathcal{I}} \binom{X_\mathcal{E}}{s} \binom{X_\mathcal{I}}{t} (1-x)^{s+t} x^{X_\mathcal{E}+X_\mathcal{I}-s-t} - \sum_{s=0}^{X_\mathcal{E}} \sum_{t=0}^{X_\mathcal{I}} \alpha_{s,t}(p) \binom{X_\mathcal{E}}{s} \binom{X_\mathcal{I}}{t} (1-x)^{s+t} x^{X_\mathcal{E}+X_\mathcal{I}-s-t} \\
&= 1 - \sum_{s=1}^{X_\mathcal{E}} \sum_{t=0}^{X_\mathcal{I}} \alpha_{s,t}(p) \binom{X_\mathcal{E}}{s} \binom{X_\mathcal{I}}{t} (1-x)^{s+t} x^{X_\mathcal{E}+X_\mathcal{I}-s-t} = 1 - \Psi_p(1-x),
\end{aligned}$$

where the second last equality comes from the first term being two complete binomial sums and the second term being equal to 0 when $s = t = 0$. □

We now proceed with showing $Q_k(p) = \Lambda_p^{k-1}(1-p)$.

Theorem 3.3.4. $Q_k(p) = \Lambda_p^{k-1}(1-p)$

Proof. We have $Q_k(p) = 1 - P_k(p)$. From the proof of Theorem 6.1, we know $P_k(p) = \Psi_p^{k-1}(p)$. It can be seen that

$$\Lambda_p^{k+1}(x) = \Lambda_p(\Lambda_p^k(x)) = 1 - \Psi_p(1 - \Lambda_p^k(x)).$$

With Lemma 6.3 as the base case, we can proceed by induction to conclude that $\Lambda_p^k(x) = 1 - \Psi_p^k(1-x)$ for

every $k \geq 1$. Putting everything together we get:

$$Q_k(p) = 1 - P_k(p) = 1 - \Psi_p^{k-1}(p) = \Lambda_p^{k-1}(1-p)$$

□

From Theorem 3.3.4 we can conclude that the probability of extinction is $\theta_k = (\Lambda_p^{k-1}(p))^{X^{\mathcal{E}}}$. Lemma 3.3.3 shows us that understanding the function $\Psi_p(x)$ as an iterated function, will give us the same understanding for $\Lambda_p(x)$. That is, proving the conjectures at the end of Section 3.3.1 will prove the analogous conjectures for $\Lambda_p(x)$, and hence allow us to determine the probability of extinction of Z_k as stated at the end of the previous section.

Knowing the expected size of each generation, $\mathbb{E}[Z_k]$ and the probability of extinction, θ_k, would give us what we need to know about the behavior of this branching type process. However, it is important to note, that proving the conjectures at the end of Section 3.3.1 is a difficult task given that $\Psi_p(x)$ is a quadruple sum of binomial coefficients. Replacing the binomial coefficients with their Poisson approximation does not improve the picture much either, we are still left with a difficult expression. Moreover the processes Z_k and Y_k are only for when $K = 1$ and we have replacement in the $(K-1)^{st}$ state. So we again seem to be running into what can be called the conservation of misery.

The model used for the mean-field limit came about trying to resolve the issues from the generational approach while still eliminating the problems from ordering. We call this model the counting model in which we look at the ratio of excitatory neurons to inhibitory neurons in the firing queue.

Chapter 4

Counting Model with K = 2

Our investigation began with trying to get a sense of the behavior of this model in the bursting configuration, i.e. when a burst occurs, what is the expected size of the burst. We again redefine the bursting configuration for the inhibitory model, and similarly for simplicity, we start with the case where $K = 2$.

For this model we have eight states, four excitatory states, $S_0^{\mathcal{E}}(t)$, $S_1^{\mathcal{E}}(t)$, $Q^{\mathcal{E}}(t)$, and $P^{\mathcal{E}}(t)$ and four inhibitory states, $S_0^{\mathcal{I}}(t)$, $S_1^{\mathcal{I}}(t)$, $Q^{\mathcal{I}}(t)$, and $P^{\mathcal{I}}(t)$. Excitatory neurons only move through the excitatory states and the inhibitory neurons only move through the inhibitory states. For both types of neurons, S_0 and S_1 are the inactive states, Q is the firing state, and P is the fired state. The parameters N, E, and p are as before in the inhibitory model definition. States S_0 and P are absorbing states. Neurons in state S_1 can transition to Q or S_0 depending on if they are kicked or depressed respectively. Neurons in state Q can only transition to state P.

Again for the same reasons as in the branching-like process, we only consider the case when the first neuron to fire is excitatory. We also assume for simplicity that no neurons are in state S_0 and no neurons can transition out of state S_0. (This last assumption will eventually be dropped.) So we begin with the following setup: $S_1^{\mathcal{E}}(0) = E - 1$, $S_1^{\mathcal{I}}(0) = I$, $Q^{\mathcal{E}}(0) = 1$, and $S_0^{\mathcal{E}}(0) = S_0^{\mathcal{I}}(0) = Q^{\mathcal{I}}(0) = 0$. The process proceeds one firing neuron at a time. That is, we process one firing neuron at each time step, update the system, and then process the next firing neuron at the next time step. This give us the following definition for this process. The initial state at time $t = 0$ is as above. At time $t = 1$ we have $Q^{\mathcal{E}}(1) \sim \text{Binomial}(E-1, p)-1$, $Q^{\mathcal{I}}(1) \sim \text{Binomial}(I, p)$. For $t \geq 2$, we define the Bernoulli random variable N_t to be 1 if the firing neuron is excitatory, or 0 if the firing neuron is inhibitory. The probability that an excitatory neuron was processed is precisely the ratio of the number of excitatory neurons firing to the total number of neurons firing. Likewise for the probability that an inhibitory neuron was processed. Therefore,

$$N_t = \begin{cases} 1 & \text{with probability } \frac{Q^{\mathcal{E}}(t-1)}{Q^{\mathcal{E}}(t-1)+Q^{\mathcal{I}}(t-1)}; \\ 0 & \text{with probability } \frac{Q^{\mathcal{I}}(t-1)}{Q^{\mathcal{E}}(t-1)+Q^{\mathcal{I}}(t-1)}. \end{cases}$$

Still having $t \geq 2$ we define the random variables A_t, B_t, C_t, and D_t by

$$A_t \sim N_t \times \text{Binomial}(S_1^{\mathcal{E}}(t-1), p), \qquad C_t \sim (1-N_t) \times \text{Binomial}(S_1^{\mathcal{E}}(t-1), p),$$
$$B_t \sim N_t \times \text{Binomial}(S_1^{\mathcal{I}}(t-1), p), \qquad D_t \sim (1-N_t) \times \text{Binomial}(S_1^{\mathcal{I}}(t-1), p).$$

A_t and B_t are the number of excitatory neurons and inhibitory neurons kicked, respectively, and C_t and D_t are the number of excitatory neurons and inhibitory neurons depressed, respectively, after processing the neuron at time step $t-1$. So we have for $t \geq 2$

$$\begin{aligned}
S_0^{\mathcal{E}}(t) &= S_0^{\mathcal{E}}(t-1) + C_t & S_0^{\mathcal{I}}(t) &= S_0^{\mathcal{I}}(t-1) + D_t \\
S_1^{\mathcal{E}}(t) &= S_1^{\mathcal{E}}(t-1) - A_t - C_t & S_1^{\mathcal{I}}(t) &= S_1^{\mathcal{I}}(t-1) - B_t - D_t \\
Q^{\mathcal{E}}(t) &= Q^{\mathcal{E}}(t-1) + A_t - N_t & Q^{\mathcal{I}}(t) &= Q^{\mathcal{I}}(t-1) + B_t - (1-N_t) \\
P^{\mathcal{E}}(t) &= P^{\mathcal{E}}(t) + N_t & P^{\mathcal{I}}(t) &= P^{\mathcal{I}}(t) + (1-N_t)
\end{aligned}$$

This setup for the bursting configuration of the counting model avoids the complications of keeping tract of the ordering of firing neurons and any complications from taking a generational approach. This should allow us to define the mean-field model and carry out the analysis with less difficulty than what was seen in the other attempts of obtaining a deterministic model.

The model can be seen as a discrete time Markov chain with state space $\mathcal{S}$ a subset of $\{0, 1, ..., E\}^4 \times \{0, 1, ..., I\}^4$. Notice that the transition probabilities are state dependent. This makes dealing with this discrete time Markov chain difficult. Therefore we will study the mean behavior of this Markov chain and treat it as an ODE. The proof that the following ODE is the correct mean-field model for the bursting configuration will follow from Theorem 6.2.1.

The ODE will be a system of eight variables $x_0, x_1, x_2, x_3, y_0, y_1, y_2, y_3$, where the x variables correspond to the excitatory states, and the y variables correspond to the inhibitory states. We also need to define the indicator function $\mathbf{1} := \mathbf{1}\{x_2 \neq 0 \vee y_2 \neq 0\}$. Our ODE is then given by

$$
\begin{aligned}
\dot{x}_0 &= \mathbf{1}\frac{y_2}{x_2+y_2}\beta x_1 & \dot{y}_0 &= \mathbf{1}\frac{y_2}{x_2+y_2}\beta y_1 \\
\dot{x}_1 &= -\mathbf{1}\beta x_1 & \dot{y}_1 &= -\mathbf{1}\beta y_1 \\
\dot{x}_2 &= \mathbf{1}\frac{x_2}{x_2+y_2}(\beta x_1 - 1) & \dot{y}_2 &= \mathbf{1}\left(\frac{x_2}{x_2+y_2}\beta x_1 - \frac{y_2}{x_2+y_2}\right) \\
\dot{x}_3 &= \mathbf{1}\frac{x_2}{x_2+y_2} & \dot{y}_3 &= \mathbf{1}\frac{y_2}{x_2+y_2}
\end{aligned}
\tag{4.1}
$$

Now we take notice that the set of fixed points $\mathcal{F} = \{(x,y) \in \mathcal{S} | x_2 = 0 \wedge y_2 = 0\}$ for this ODE is a whole subspace of the state space $\mathcal{S}$. A quick study of the ODE will show that if we ever perturb any point in $\mathcal{F}$, we will eventually comeback to another point in $\mathcal{F}$. Recall the discrete time Markov chain has initial state $(0, E-1, 1, 0, 0, I, 0, 0)$. This would correspond to a small perturbation by some $\epsilon > 0$ of the fixed point $(0, E, 0, 0, 0, I, 0, 0)$ in the direction $v = (0, -1, 1, 0, 0, 0, 0, 0)$. As stated, after this perturbation, we will eventually come back to another fixed point in $\mathcal{F}$ which we will call $(x,y)^{\epsilon v}$. The question we want to then answer is, what is $x_3^{\epsilon v} + y_3^{\epsilon v}$, which can be seen as the size of the burst.

4.1 Numerical Simulations

In approaching this problem through numerical simulations, when perturbing the fixed point $(0, E, 0, 0, 0, I, 0, 0)$ by ϵv, we concentrated on when x_2 first returns to 0. Hence we run a simulation starting with initial condition $(0, E, 0, 0, 0, I, 0, 0) + \epsilon v = (0, E(1-\epsilon), \epsilon E, 0, 0, I, 0, 0)$ and we are interested in the time $\tau = \inf\{t > 0 | x_2(t) = 0\}$. In particular we want to know $x_3(\tau) + y_3(\tau)$. We begin by focusing on determining what $x_3(\tau)$ will be. If we can determine this, we can then apply the methods used to determine $y_3(\tau)$.

We ran numerical simulations of the ODE with initial condition

$$(x(0), y(0)) = (0, E(1-\epsilon), \epsilon E, 0, 0, I, 0, 0)$$

for various choices of $0 < \epsilon \ll 1$ and for $1 \leq \beta \leq 2$. We plotted $x_3(\tau)$ for each β. Figure 4.1 shows the resulting plots for $\epsilon = 1e^{-2}, 1e^{-4}$, and, $1e^{-8}$. Notice as ϵ gets smaller, the jump becomes more sharp. This suggests there is a critical β at which there is a transition from a small burst to a large burst. That is, this

β is the critical β at which we transition to big burst activity. Let us define

$$\beta_c = \inf\{\beta > 0 : \frac{\partial}{\partial \beta} x_3(\tau) > 0\}$$

to be this critical β.

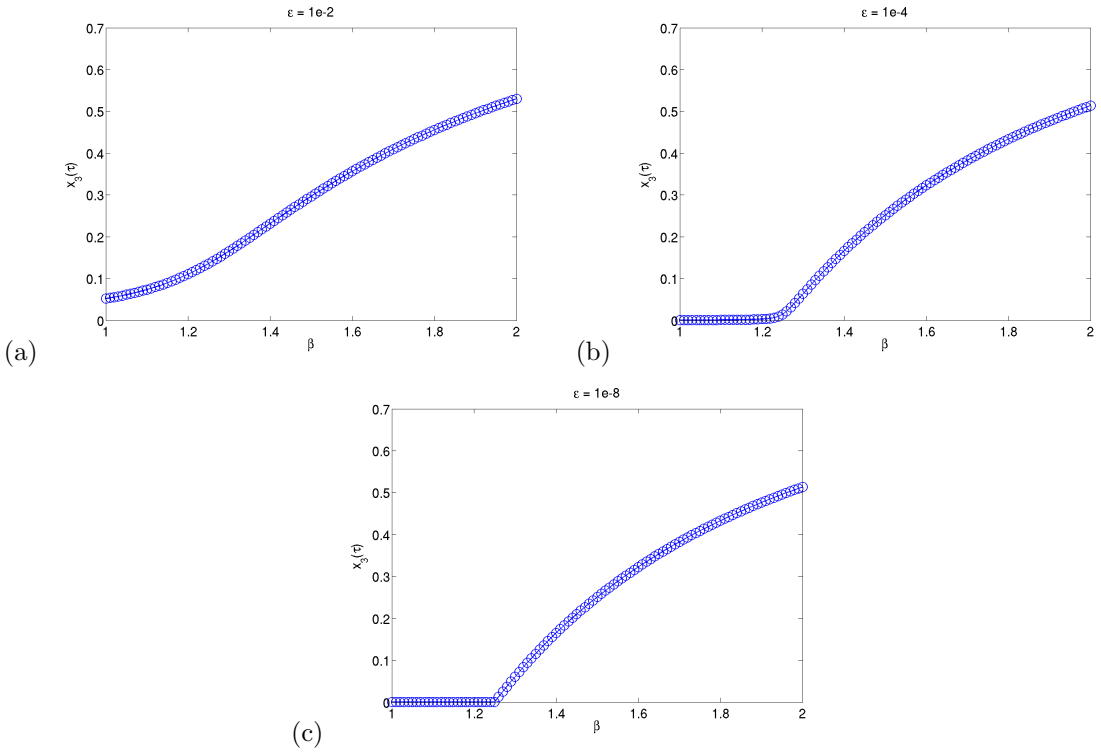


Figure 4.1: Simulations of the ODE from equations (4.1) with initial condition $(0, 0.8(1-\epsilon), 0.8\epsilon, 0, 0, 0.2, 0, 0)$ and $1 \leq \beta \leq 2$. (a) $\epsilon = 1e^{-2}$, (b) $\epsilon = 1e^{-4}$, and (c) $\epsilon = 1e^{-8}$.

4.2 Taylor Approximation

We now attempt a Taylor expansion to asymptotically determine β_c. In particular, we use a Taylor approximation of x_2 with ϵ fixed. For notational purposes, we denote $T_{i,\epsilon}x_2(t)$ to be the $o(t^i)$ Taylor approximation of x_2 with a perturbation by ϵ. We successively look at the Taylor approximations $T_{i,\epsilon}x_2$ and determine $\hat{\beta}_{c,i}(\epsilon) = \inf\{\beta > 0 : \forall t > 0 \;\; T_{i,\epsilon}x_2(t) > 0\}$. Sending $i \to \infty$ we should obtain $\lim_{i\to\infty} \hat{\beta}_{c,i}(\epsilon) = \beta_c(\epsilon)$. We then hope by sending $\epsilon \to 0$ we would obtain $\beta_c(\epsilon) \to \beta_c$.

Figure 4.2 shows a series of plots of $T_{i,.001}x_2(t)$ for $i = 1, 2, 3, 4$ and for $1.8 \leq \beta \leq 3$. We can see from these plots that there appears to be a critical β for which x_2 shoots off and does not cross the t-axis. This

should correspond to β_c. Proceeding as explained above, we first set $T_i x_2 = 0$ and solve for t to find an approximation for τ. For $T_{1,\epsilon} x_2$, we find $\tau \approx \frac{e\epsilon}{1+e\beta(\epsilon-1)}$. This approximation of τ has a vertical asymptote at $\beta = \frac{1}{e(\epsilon-1)}$ which corresponds to an approximation of $\beta_c(\epsilon)$. To get a better approximation we solve for $T_3 x_2 = 0$. In proceeding, we found there is an issue with the Taylor expansions. For any $n > 1$, the $o(t^n)$

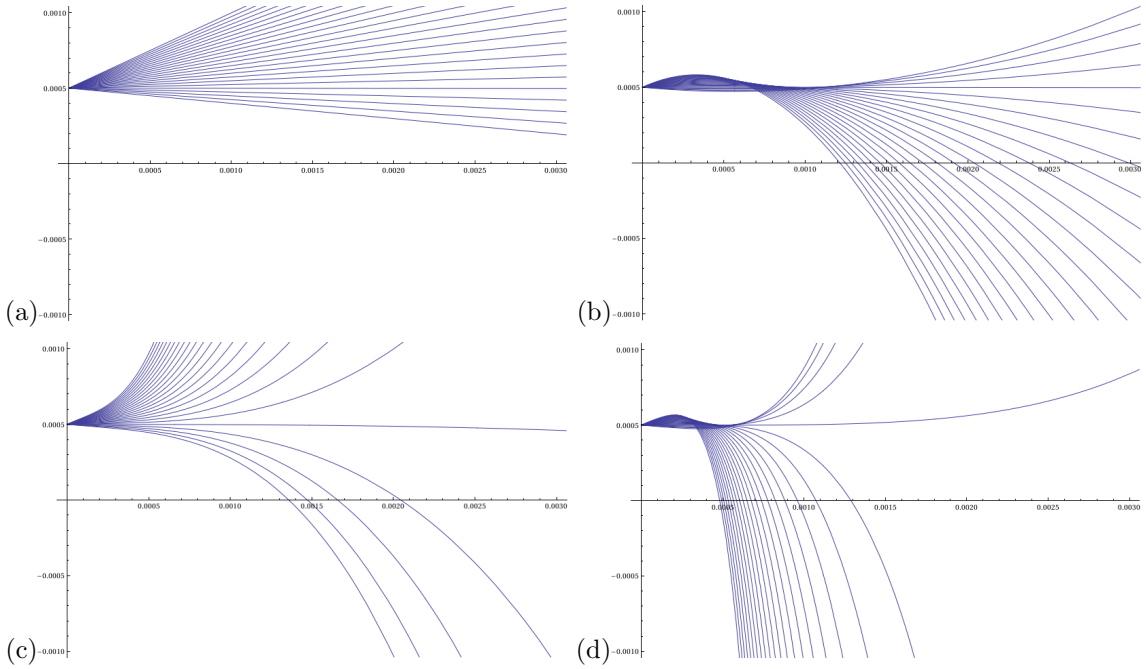


Figure 4.2: Plots of the Taylor expansion with initial condition $(0, 0.8(1-\epsilon), 0.8\epsilon, 0, 0, 0.2, 0, 0)$ and $1 \leq \beta \leq 2$. (a) $o(t)$ approximation, (b) $o(t^2)$ approximation, (c) $o(t^3)$ approximation, and (d) $o(t^4)$ approximation.

Taylor approximation is of order $O(\epsilon^{-(n-1)})$. Since we are interested in the critical β as $\epsilon \to 0$, this is a problem. We continued on with another approach.

4.3 Excitatory Mean Behavior

Let us consider setting $E = 1$ to study the bursting configuration of the excitatory counting model with the goal of developing insight that we can extend to the analysis of the bursting configuration of the inhibitory model. The bursting configuration of the excitatory model is given by the ODE

$$\begin{aligned} \dot{x}_0 &= 0 & \dot{x}_2 &= \mathbf{1}(\beta x_1 - 1) \\ \dot{x}_1 &= -\mathbf{1}\beta x_1 & \dot{x}_3 &= \mathbf{1} \end{aligned} \tag{4.2}$$

with initial condition $(0, (1-\epsilon), \epsilon, 0)$. Solving this ODE we obtain

$$\begin{aligned} x_{0,\epsilon} &= 0 & x_{2,\epsilon} &= 1 - t - e^{-t\beta}(1-\epsilon) \\ x_{1,\epsilon} &= e^{-t\beta}(1-\epsilon) & x_{3,\epsilon} &= t \end{aligned} \tag{4.3}$$

assuming that once $x_{2,\epsilon} = 0$ the system becomes constant. We want to know the size of a burst as a function of the parameter β. This will simply be given by the value of $x_{3,\epsilon}$ when $x_{2,\epsilon}$ first becomes zero. To this end we define $\tau_\epsilon(\beta) = \inf\{t > 0 : x_{2,\epsilon}(t) \leq 0\}$ to be the time when $x_{2,\epsilon}$ first becomes non-positive, and we define $\Omega_\epsilon(\beta) = x_{3,\epsilon}(\tau_\epsilon(\beta))$ to be the size of the burst. By (4.3), $\Omega_\epsilon(\beta) = \tau_\epsilon(\beta)$, and will be a solution of $1 - t - e^{-t\beta}(1-\epsilon) = 0$.

We are interested in the limit as $\epsilon \to 0$. Hence we want to know $\Omega_0(\beta)$, which will be a root of

$$x_{2,0}(t) = 1 - t - e^{-t\beta} = 0. \tag{4.4}$$

Solving for this root in (4.4) we have

$$\Omega_0(\beta) = 1 + \frac{w}{\beta},$$

where w satisfies $we^w = -\beta e^{-\beta}$. Plugging in $t = \Omega_0(\beta)$ back into (4.4) we see that w must be a root of the function

$$\varphi_\beta(x) = -\frac{x}{\beta} - e^{-(x+\beta)}. \tag{4.5}$$

Lemma 4.3.1. *$\varphi_\beta(x)$ has exactly one real root for $\beta = 1$ and exactly two real roots for every other $\beta > 0$.*

Proof. We assume $\beta > 0$ and observe we always have $x = -\beta$ as a root of $\varphi(x)$. Note that $\lim_{x\to\infty} \varphi(x) = \lim_{x\to-\infty} \varphi(x) = -\infty$. We also have that $\varphi'(x) = -\frac{1}{\beta} + e^{-(x+\beta)}$ has exactly one root at $x^* = \beta + \ln(\frac{1}{\beta})$. When $\beta = 1$, $x^* = \beta$ and we have $\varphi'(-\beta) = \varphi(-\beta) = 0$. Hence $-\beta$ is the only real root.

Let us now suppose that $\beta \neq 1$. Then $\varphi(-\beta) > 0$, in which case there must be another root since $\varphi(x) \to -\infty$ as $x \to \pm\infty$ and $\varphi'(x)$ has only one real root. □

Lemma 4.3.2. *The size of the burst $\Omega_0(\beta) = 0$ if and only if $\dot{x}_{2,0}(0) \leq 0$.*

Proof. ($\Rightarrow$) We do a proof by contradiction. Suppose $\dot{x}_{2,0}(0) > 0$. We want $\Omega_0(\beta) > 0$. Noticing $x_{2,0}(0) = 0$, there must be some $T > 0$ such that for every $0 < \epsilon \leq T$, $x_{2,0}(\epsilon) > 0$. That is, for some positive amount of time after $t = 0$, $x_{2,0}$ must be positive. Hence, $\tau_0(\beta) = \inf\{t > 0 : x_{2,0}(t) \leq 0\} > 0$. Therefore, $\Omega_0(\beta) = \tau_0(\beta) > 0$ and we have our contradiction.

($\Leftarrow$) Suppose $\dot{x}_{2,0}(0) \leq 0$. Looking at the second derivative of $x_{2,0}$, we see that $\ddot{x}_{2,0}(t) = -\beta^2 e^{-\beta t}$ which is negative for all $t \geq 0$. Hence $\dot{x}_{2,0}$ is decreasing for all $t \geq 0$. Therefore, since we know $\dot{x}_{2,0}(0) \leq 0$ and $x_{2,0}(0) = 0$, we must have that $x_{2,0}(t) \leq 0$ for all $t \geq 0$. Hence, $\Omega_0(\beta) = \tau_0(\beta) = \inf\{t > 0 : x_{2,0}(t) \leq 0\} = 0$. □

Theorem 4.3.3. *w is the unique solution to $\varphi(x) = 0$ in the interval $(-1, 0)$.*

Proof. If $\beta > 1$, then $\dot{x}_{2,0}(0) = -1 + \beta > 0$. By Lemma 4.3.2 we have that $\Omega_0(\beta) = 1 + \frac{w}{\beta} > 0$, and hence we must have $w \neq -\beta$. Notice $\varphi(-1) > 0$ and $\varphi(0) < 0$. So by the Mean Value Theorem, there must be a root of $\varphi(x)$ in the interval $(-1, 0)$. By Lemma 4.3.1, this root must be w. If $\beta \leq 1$, then $\dot{x}_{2,0}(0) = -1 + \beta \leq 0$, and by Lemma 4.3.2, $\Omega_0(\beta) = 1 + \frac{w}{\beta} = 0$. Therefore, we must have $w = -\beta \in (-1, 0)$. □

4.4 Inhibitory Asymptotics

In this section we consider the inhibitory model setting $E < 1$ in an attempt to extend the analysis of the previous section to this model. Equation (4.1) gives us the ODE we are considering and we redisplay it here for quick reference:

$$\begin{aligned}
\dot{x}_0 &= \mathbf{1}\frac{y_2}{x_2 + y_2}\beta x_1 & \dot{y}_0 &= \mathbf{1}\frac{y_2}{x_2 + y_2}\beta y_1 \\
\dot{x}_1 &= -\mathbf{1}\beta x_1 & \dot{y}_1 &= -\mathbf{1}\beta y_1 \\
\dot{x}_2 &= \mathbf{1}\frac{x_2}{x_2 + y_2}(\beta x_1 - 1) & \dot{y}_2 &= \mathbf{1}\left(\frac{x_2}{x_2 + y_2}\beta x_1 - \frac{y_2}{x_2 + y_2}\right) \\
\dot{x}_3 &= \mathbf{1}\frac{x_2}{x_2 + y_2} & \dot{y}_3 &= \mathbf{1}\frac{y_2}{x_2 + y_2}
\end{aligned}$$

with initial condition $(0, E(1-\epsilon), E\epsilon, 0, 0, (1-E), 0)$, where the first four coordinates correspond to the x variables and the last four correspond to the y variables. We are again interested in when x_2 first becomes non-positive. To aid this analysis, we introduce a new variable $z = \frac{x_2}{x_2 + y_2}$. Observe in the given ODE that x_1 is easily solved for and seen to be $x_1 = E(1-\epsilon)e^{-\beta t}$. Then $\dot{x_2}$ is simply an equation of z. One can easily solve for $\dot{z}$ and arrive at the coupled system

$$\dot{z} = \frac{1}{x_2}\beta e^{-\beta t}(E(1-\epsilon)z^2 - (1 - E\epsilon)z^3) \tag{4.6a}$$

$$\dot{x}_2 = z(E(1-\epsilon)\beta e^{-\beta t} - 1), \tag{4.6b}$$

with initial condition $(z(0), x_2(0)) = (1, \epsilon)$. Studying the equilibrium point in equation (4.6a), we see that $z = \frac{E(1-\epsilon)}{1-E\epsilon}$ is an attracting fixed point. Observe that $\dot{z}$ has $\frac{1}{x_2}$ as a factor and that $x_2(0) = \epsilon$. Therefore, z near zero is quite fast and should become very near its equilibrium quickly. Following this through, we view the coupled system in equation (4.6) as a perturbation of the solution of the system when z is at equilibrium:

$$z = z_0 + \delta z_1 \qquad x_2 = x_{2,0} + \delta x_{2,1}, \tag{4.7}$$

where $z_0 = R(\epsilon) = \frac{E(1-\epsilon)}{1-E\epsilon}$ is z at equilibrium, and $x_{2,0}$ is the solution to equation (4.6b) with z at equilibrium given by

$$x_{2,0} = R(\epsilon)(E(1-\epsilon)(1-e^{-\beta t}) - t) + \epsilon.$$

We are able to solve for when $x_{2,0} = 0$. Our goal is then to derive upper and lower bounds on when $x_2 = 0$ through finding a supremum for $|x_{2,1}|$. It is easy to see that $\dot{x}_{2,1} = z_1(E(1-\epsilon)\beta e^{-\beta t} - 1)$. Therefore, we turn our attention to finding bounds for z_1 in order to find a supremum for $|x_{2,1}|$. We replace the occurrences of z in the equation for $\dot{z}_1$ with $z = R(\epsilon) + \delta z_1$ and simplify to obtain:

$$\dot{z}_1 = \frac{1}{x_2}\beta e^{-\beta t}\left[-R(\epsilon)E(1-\epsilon)z_1 - \delta\left(2E(1-\epsilon)z_1^2\right) - \delta^2\left((1-E\epsilon)z_1^3\right)\right].$$

Using a taylor expansion for the function $\frac{1}{x}$, and that $x_2 = x_{2,0} + \delta x_{2,1}$ we get $\frac{1}{x_2} = \frac{1}{x_{2,0}} + \mathcal{O}(\delta)$. We can combine this with the above equation to obtain the first order approximation of $\dot{z}_1$ in δ as

$$\dot{z}_1 = \frac{1}{x_{2,0}}\beta e^{-\beta t}\left[-R(\epsilon)E(1-\epsilon)z_1\right] + \mathcal{O}(\delta). \tag{4.8}$$

Recall $x_{2,0}(0) = \epsilon$ giving us a $\frac{1}{\epsilon}$ term in our equation for $\dot{z}_1$. We resolve this issue by rescaling $x_{2,0}$ and time by $1/\epsilon$. We define the new variable $Y(t) = x_{2,0}/\epsilon$ and a new time variable τ by $\tau = t/\epsilon$, and hence $\epsilon d\tau = dt$. Therefore, we have $x_{2,0} = \epsilon Y$ and $\frac{d}{dt} = \frac{1}{\epsilon}\frac{d}{d\tau}$, and plugging this into equation (4.8) gives us

$$\frac{d}{d\tau}z_1 = \frac{1}{Y}\beta e^{-\beta\epsilon\tau}\left[-R(\epsilon)E(1-\epsilon)z_1\right] + \mathcal{O}(\delta). \tag{4.9}$$

Our goal was to show that z_1 decays in $O(\frac{1}{\epsilon})$ time in t and to use this result to get a bound on $x_{2,1}$. However, this analysis relied heavily on being able to solve for x_1 which is quite easy here since $\dot{x}_1 = -\mathbf{1}\beta x_1$. In the full model however, $\dot{x}$ does not have a simple form leaving this asymptotic analysis difficult to extend. We proceed then with extending the definition of the counting model to a continuous time stochastic process.

Chapter 5

Counting Model - Fully Defined

5.1 Model Definition

The counting model has five parameters as in the inhibitory model: $N, E, K \in \mathbb{Z}^+, 0 \leq E \leq N$, $p \in (0,1)$, $\rho \in \mathbb{R}^+$. The model again consists of N neurons, E of which are excitatory and $I = N - E$ are inhibitory. For each of the excitatory and each of the inhibitory neurons there are K resting levels, $0, ..., K-1$, a firing level K, and an already fired level $K+1$. We keep track of the number of neurons in each state. We denote the number of excitatory neurons and the number of inhibitory neurons at level k for $0 \leq k \leq K-1$ by $S_k^{\mathcal{E}} \in \{0, 1, ..., E\}$ and $S_k^{\mathcal{I}} \in \{0, 1, ..., I\}$, respectively. (The firing and already fired states are only considered in the bursting regime.) Our state space is then defined by

$$M^K := \left\{ S = (S^{\mathcal{E}}, S^{\mathcal{I}}) \in (\{0, 1, ..., E\} \times \{0, 1, ..., I\})^K : \sum_{k=0}^{K-1} S_k^{\mathcal{E}} = E, \ \sum_{k=0}^{K-1} S_k^{\mathcal{I}} = I \right\}$$

Now pick any initial (perhaps random) vector $S \in M^K$. Indices $0, ..., K-1$ of S are the excitatory states, and indices $K, ..., 2K-1$ of S are the inhibitory states. We will find it convenient when talking about excitatory neurons exclusively to label the states $0, ..., K-1$ and denote the levels by $S_k^{\mathcal{E}}$, or similarly, if we are talking about inhibitory neurons exclusively, to label the states $0, ..., K-1$ and denote the levels by $S_k^{\mathcal{I}}$, i.e. $S = (S^{\mathcal{E}}, S^{\mathcal{I}})$. Analogous to the inhibitory model we define a cadlag process on the evolution of $S(t)$ as follows. Let $0 = t_0 < t_1 < ...$ be a sequence of event times such that $t_{i+1} - t_i$ is exponentially distributed with mean $(\rho N)^{-1}$, and define $S(t)$ to be constant on $[t_i, t_{i+1})$. At each event time t_i, pick an index $n \in \{0, 1, ..., 2K-1\}$ randomly where the probability of state n being chosen is given by $S_n(t_i)/(\sum_{k=0}^{2K-1} S_k(t_i))$ and compute the following:

- If $0 \leq n < K-1$ or $K \leq n < 2K-1$, then $S_n(t_{i+1}) = S_n(t_i) - 1$, $S_{n+1}(t_{i+1}) = S_{n+1}(t_i) + 1$, and $S_j(t_{i+1}) = S_j(t_i)$ for all $j \neq n, n+1$, i.e. promote only a neuron from state n by one level, at which point the event ends.

- If $n = K-1$ or $n = 2K-1$, then we define a temporary vector $Y(0) = (Y^{\mathcal{E}}, Y^{\mathcal{I}}) \in M^K$ with $Y_j(0) = S_j(t_i)$ for all $j \neq n$ and $Y_n = S_n(t_i) - 1$. If $n = K-1$ define $Q^{\mathcal{E}}(0) = 1$, and $Q^{\mathcal{I}}(0) = P^{\mathcal{E}}(0) = P^{\mathcal{I}}(0) = 0$. If $n = 2K-1$ define $Q^{\mathcal{I}}(0) = 1$, and $Q^{\mathcal{E}}(0) = P^{\mathcal{E}}(0) = P^{\mathcal{I}}(0) = 0$.

  To define the evolution on these new variables for $r > 0$, we define the following random variable

$$N_r = \begin{cases} 1 & \text{with probability } \frac{Q^{\mathcal{E}}(r-1)}{Q^{\mathcal{E}}(r-1)+Q^{\mathcal{I}}(t-1)}; \\ 0 & \text{with probability } \frac{Q^{\mathcal{I}}(r-1)}{Q^{\mathcal{E}}(r-1)+Q^{\mathcal{I}}(r-1)} \end{cases}$$

  and the random variables A_r^k, B_r^k, C_r^k, and D_r^k by

$$A_r^k \sim N_r \times \text{Binomial}(Y_k^{\mathcal{E}}(t-1), p), \quad C_r^k \sim (1-N_r) \times \text{Binomial}(Y_k^{\mathcal{E}}(t-1), p),$$
$$B_r^k \sim N_r \times \text{Binomial}(Y_k^{\mathcal{I}}(t-1), p), \quad D_r^k \sim (1-N_r) \times \text{Binomial}(Y_k^{\mathcal{I}}(t-1), p)$$

  $N_r = 1$ indicates that an excitatory neuron is firing, and $N_r = 0$ indicates that an inhibitory neuron is firing. A_r^k and B_r^k are the number of excitatory and inhibitory neurons that are promoted from level k, respectively, if an excitatory neuron fires. C_r^k and D_r^k are the number of excitatory and inhibitory neurons that are demoted from level k, respectively, if an inhibitory neuron fires. With these random variables we can proceed to define the $2K+4$ states for $r > 0$.

$$\begin{aligned} Y_0^{\mathcal{E}}(r) &= Y_0^{\mathcal{E}}(r-1) + C_r^1 - A_r^0, \\ Y_k^{\mathcal{E}}(r) &= Y_k^{\mathcal{E}}(r-1) + A_r^{k-1} + C_r^{k+1} - (A_r^k + C_r^k), \\ Y_{K-1}^{\mathcal{E}}(r) &= Y_{K-1}^{\mathcal{E}}(r-1) + A_r^{K-2} - (A_r^{K-1} + C_r^{K-1}), \\ Q^{\mathcal{E}}(r) &= Q^{\mathcal{E}}(r-1) + A_r^{K-1} - N_r, \\ P^{\mathcal{E}}(r) &= P^{\mathcal{E}}(r-1) + N_r, \end{aligned}$$

$$\begin{aligned} Y_0^{\mathcal{I}}(r) &= Y_0^{\mathcal{I}}(r-1) + D_r^1 - B_r^0, \\ Y_k^{\mathcal{I}}(r) &= Y_k^{\mathcal{I}}(r-1) + B_r^{k-1} + D_r^{k+1} - (B_r^k + D_r^k), \\ Y_{K-1}^{\mathcal{I}}(r) &= Y_{K-1}^{\mathcal{I}}(r-1) + B_r^{K-2} - (B_r^{K-1} + D_r^{K-1}), \\ Q^{\mathcal{I}}(r) &= Q^{\mathcal{I}}(r-1) + B_r^{K-1} - (1-N_r), \\ P^{\mathcal{I}}(r) &= P^{\mathcal{I}}(r-1) + (1-N_r), \end{aligned}$$

where $0 \leq k \leq K-2$.

We then define

$$r^* = \min_{r>0}(Q^{\mathcal{E}}(r) + Q^{\mathcal{I}}(r) = 0)$$

and

$$S_n(t_{i+1}) = \begin{cases} Y_n(r^*) & \text{if } n \in [2K-1] \setminus \{0, K\}; \\ Y_0(r^*) + P^{\mathcal{E}}(r^*) & \text{if } n = 0; \\ Y_K(r^*) + P^{\mathcal{I}}(r^*) & \text{if } n = K. \end{cases}$$

r^* is the first $r = 1, 2, ...$ such that $Q^{\mathcal{E}}$ and $Q^{\mathcal{I}}$ are both empty and hence there are no more neurons waiting to fire. At this point the burst ends and we update the process. The two appended states $Q^{\mathcal{E}}$ and $Q^{\mathcal{I}}$ we think of as the firing neurons, and the two appended states $P^{\mathcal{E}}$ and $P^{\mathcal{I}}$ we think of as the already fired neurons.

We summarize the above process as follows: We pick some state n to promote a neuron from. If n is not level $K-1$ for either the excitatory or inhibitory states, then no burst occurs. If however $n = K-1$ for either the excitatory states or inhibitory states, we iterate the following algorithm until both firing states are empty: pick whether the firing neuron is an excitatory or an inhibitory neuron where the probability of choosing one over the other is given by the respective sizes of the firing queues. If the neuron chosen to fire is excitatory, for each state $0 \leq k \leq K-1$ promote m neurons from state k to state $k+1$, where m is chosen from the binomial(M, p) distribution with M being the number of neurons in state k and p the given parameter of the system, and promote one neuron from the excitatory firing state to the excitatory already fired state. If the neuron chosen to fire is inhibitory, for each state $1 \leq k \leq K-1$ demote m neurons from state k to state $k-1$, where m is chosen from the binomial(M, p) distribution with M again being the number of neurons in state k and p the given parameter of the system, and promote one neuron from the inhibitory firing state to the inhibitory already fired state.

As before we have defined $Y(r)$ for all $r \in \mathbb{N}$, but we only need to consider Y until both firing queues are empty. Since $r^* < N$, for any burst we only need to compute a finite number of $Y(r)$.

5.2 Equivalency of Counting Model and Inhibitory Model

We show below that the process defined by the counting model and the process defined by the inhibitory model are the same. To achieve this we need to set up some machinery. We begin by showing the process defined in the inhibitory model and the process defined in the counting model are both Markovian.

Lemma 5.2.1. *The process defined in the inhibitory model definition is a Markov process.*

Proof. Let $X_0 \in (\{0, 1, ..., K-1\})^N$ and X_{t_i} be the process defined in the inhibitory model with initial condition X_0. Recall that the sequence of event times $t_0, t_1, t_2, ...$ are chosen so that for each $j > 0$, $t_j - t_{j-1}$ is exponentially distributed with mean $(\rho N)^{-1}$. Hence we only need to show for every $t_i,\ i > 0$, and any $A \subseteq (\{0, 1, ..., K-1\})^N$ we have

$$\mathbb{P}(X_{t_i} \in A | X_{t_j},\ 0 \leq j < i) = \mathbb{P}(X_{t_i} \in A | X_{t_{i-1}}).$$

So say $X_{t_j},\ 0 \leq j < i$, is given. In order to determine what X_{t_i} will be we pick an index $n \in \{1, ..., N\}$ uniformly and compute some rules to determine X_{t_i}. In terms of $X_{t_j},\ 0 \leq j < i$, the things computed rely only on $X_{t_{i-1}}$, as can be seen by looking at the definition of the inhibitory model. Hence knowing $X_{t_j},\ 0 \leq j < i$, gives no more information than knowing $X_{t_{i-1}}$ giving us our desired result.

□

Lemma 5.2.2. *The process defined in the counting model definition is a Markov process.*

Proof. Let $S_0 \in M^K$ and $S(t_i)$ be the process defined in the counting model with initial condition S_0. The sequence of event times $t_0, t_1, t_2, ...$ are chosen in the same way as in the inhibitory model leaving us only needing to show that for every $t_i,\ i > 0$, and any $A \subseteq M^K$ we have

$$\mathbb{P}(S(t_i) \in A | S(t_j),\ 0 \leq j < i) = \mathbb{P}(S(t_i) \in A | S(t_{i-1})).$$

Say $S(t_j),\ 0 \leq j < i$, is given. In order to determine what $S(t_i)$ will be we pick a state $n \in \{0, 1, ..., 2K-1\}$ where the probability of state n being chosen is given by $S_n(t_{i-1})/(\sum_{k=0}^{2K-1} S_k(t_{i-1}))$. We then compute some rules defined on the values of $S(t_{i-1})$ to determine $S(t_i)$. Hence knowing $S(t_j),\ 0 \leq j < i$, gives no more information than knowing $S(t_{i-1})$ giving us our desired result.

□

For the following we let Ω_1 and Ω_2 be the probability spaces associated with the processes defined in the inhibitory model and counting model, respectively. These process being Markovian allows us to define the maps

$$f : (\{0, 1, ..., K-1\})^N \times \Omega_1 \to (\{0, 1, ..., K-1\})^N$$
$$g : M^K \times \Omega_2 \to M^K$$

to be the rules by which the defined stochastic processes progress. That is for f, if we let $X_0 \in (\{0, 1, ..., K-1\})^N$ and define X_{t_i} for $i \geq 0$ to be a realization of the process defined by the inhibitory model given by some choices of $\omega_i \in \Omega_1$ with initial condition X_0, then $X_{t_i} = f(X_{t_{i-1}}, \omega_i)$ for every $i > 0$. For g, if we let $S_0 \in (\{0, 1, ..., K-1\})^N$ and define $S(t_j)$ for $j \geq 0$ to be a realization of the process defined by the counting model given by some choices of $\omega_j \in \Omega_2$ with initial condition $S(0) = S_0$, then $S(t_j) = g(S(t_{j-1}), \omega_j)$ for every $j > 0$.

We now set up a map between our two models. Recall the state space of the inhibitory model is $(\{0, 1, ..., K-1\})^N$ where picking a point in this space specifies the level of each of the N neurons. For any vector of neurons $X \in (\{0, 1, ..., K-1\})^N$ let us define for $0 \leq k \leq K-1$ the following map $H = (H^{\mathcal{E}}, H^{\mathcal{I}}) : (\{0, 1, ..., K-1\})^N \to M^K$:

$$H_k^{\mathcal{E}}(X) := \sum_{j=1}^{E} \mathbf{1}(X_j = k), \quad \text{and} \quad H_k^{\mathcal{I}}(X) = \sum_{j=E+1}^{N} \mathbf{1}(X_j = k).$$

For any vector of neurons X, $H_k^{\mathcal{E}}(X)$ is the number of excitatory neurons at level k, and $H_k^{\mathcal{I}}(X)$ is the number of inhibitory neurons at level k.

The map H gives us the following equivalence relation.

Definition 1. *For $X, \hat{X} \in (\{0, 1, ..., K-1\})^N$, we say $X \sim \hat{X}$ if $H(X) = H(\hat{X})$.*

Let us take a closer look at the structure of Ω_1. Pick any $\omega \in \Omega_1$. $\omega = (n, A)$, where n is the index of the neuron chosen to be promoted and A indicates what to do if the neuron promoted fires. If the neuron does not fire, we ignore A. If the neuron does fire, the columns of A indicate which neurons to promote at each particular step in the burst. Since at most N neurons can burst, there can be at most N steps in the burst. If we ever stop bursting at say step $n < N$, we do not use the remaining columns of A. Provided the above we can write $\Omega_1 = [N] \times \{0, 1\}^{N^2}$. Given any $\omega \in \Omega_1$, $f(\cdot, \omega)$ is a deterministic function.

We similarly take a closer look at the structure of Ω_2. For a given $S \in M^K$ we write out a sequence in

$[K-1]^N$ where the first S_0 elements are 0, the next S_1 elements are 1,..., and the next S_{2K-1} elements are $2K-1$. For example if $K=2$ and $S=(2,3,6,1)$ then the sequence S is mapped to is $S \mapsto (001112222223)$. Note this map, if we mod out the sequences by the symmetric group $\mathcal{S}_{2K}$, is a bijection which allows us to map any sequence back to M^k.

Now for any $\omega \in \Omega_2$, we have $\omega = (k, A)$, where k is the level to promote a neuron from, and A provides the same information as in Ω_1 used on the sequence an element S is mapped to. Looking at the definition of the process, $\mathbb{P}(k = l) = S_l/N$. Again, if no burst occurs, we ignore A. If a burst does occur, after we use A we map the resulting sequence back to an element of M_K. Provided the above we can write $\Omega_2 = [2K-1] \times \{0,1\}^{N^2}$. Given any $\omega \in \Omega_2$, $g(\cdot, \omega)$ is a deterministic function.

We can now define a map $\alpha : \Omega_1 \to \Omega_2$ where for $\omega = (n, A) \in \Omega_1$, $\alpha(n, A) = (X_n, A)$. We now show that α is measure preserving. For the following lemma, $\mathbb{P}_1$ and $\mathbb{P}_2$ are the provided measures of Ω_1 and Ω_2, respectively.

Lemma 5.2.3. *The map $\alpha : \Omega_1 \to \Omega_2$ is measure preserving. That is for any $\omega \in \Omega_2$*

$$\mathbb{P}_2(\omega) = \mathbb{P}_1(\alpha^{-1}(\omega)).$$

Proof. First note that the second coordinate of α is the identity map. Looking at the definition of the inhibitory model it is easy to see that if we setup the process in the terminology of the counting model, we get the burst process of the counting model. That is the rule which determines A for both models is the same, i.e. $\mathbb{P}_1(A) = \mathbb{P}_2(A)$.

Now pick any $\omega = (k, A) \in \Omega_2$. The preimage under α is given by $\alpha^{-1}(\omega) = \{(n, A) \in \Omega_1 : X_n = k\}$. We have $\mathbb{P}(\{(n, A) \in \Omega_1 : X_n = k\}|A) = H(X)_k/N$, that is the ratio of the total number of neurons at level k to the total number of neurons. Similarly, $\mathbb{P}(\omega = (k, A)|A) = S_k/N$, the ratio of the total number of neurons at level k to the total number of neurons. Putting everything together we get

$$\mathbb{P}_1(\alpha^{-1}(\omega)) = \mathbb{P}_1(\alpha^{-1}(\omega)|A)\mathbb{P}_1(A) = \mathbb{P}_2(\omega = (k, A)|A)\mathbb{P}_2(A) = \mathbb{P}_2(\omega).$$

□

An important property is that any two elements of an equivalence class both proceed with the same distribution under the process of the Inhibitory model. That is for $X \sim \hat{X}$ and for any $\omega \in \Omega_1$, $f(X, \omega) \sim f(\hat{X}, \omega)$. To prove this property we begin by showing for any composition σ of a permutation on the first E indices of

$[N]$ and a permutation of the last I indices of $[N]$, f is equivariant under σ, i.e. $\sigma^{-1}f\sigma = f$. For the following, we let P be the set of all compositions of a permutation on the first E indices of $[N]$ and a permutation of the last I indices of $[N]$. Also for any $\sigma \in P$ and $A \in \{0,1\}^{N^2}$, we denote by $\sigma(A)$ the permutation of the rows of A, by σ, i.e. if $\sigma(i) = j$, then row i of A becomes row j of $\sigma(A)$.

Lemma 5.2.4. *Given any permutation $\sigma \in P$, $\sigma^{-1}f\sigma = f$. That is for every $X \in (\{0,1,...,K-1\})^N$ and any choice of $(n,A) \in \Omega_1$, $f(\sigma(X),(\sigma(n),\sigma(A))) = \sigma(f(X,(n,A)))$.*

Proof. When we apply $f(\cdot,(n,A))$ to X, the neuron at index n is promoted and either no burst occurs, $X_n < K-1$, or a burst does occur, $X_n = K-1$. Assume no burst occurs. Then all that occurs in the application of $f(\cdot,(n,A))$ is the promotion of X_n while all other indices of X are unchanged. In applying $f(\cdot,(\sigma(n),\sigma(A)))$ to $\sigma(X)$, the neuron at index $\sigma(n)$ is promoted. The value of the neuron is $\sigma(X)_{\sigma(n)} = X_n < K-1$. So again no burst occurs and all that happens is $\sigma(X)_{\sigma(n)}$ is promoted and all other indices of X are unchanged. Hence applying σ to $f(X,(n,A))$ will give us $f(\sigma(X),(\sigma(n),\sigma(A)))$.

Let us recall the columns of A tell us which neurons to promote at each step. Let us define the operation A_rX as applying the first r rows of A to X. Clearly this operation is invariant under permutations in P, i.e. $\sigma(A)_r\sigma(X) = \sigma(A_rX)$. For i,j with either $1 \le i,j \le E$ or $E+1 \le i,j \le N$, if we permute row i and j of A, then promote X_j according to row j, this is the same as promoting X_i according to row i and then permuting. As a result of this if we start with the same number of neurons at each state, the number of neurons at level K for any step for A and $\sigma(A)$ is the same. Hence the burst will end on the same step for both A and $\sigma(A)$ provided we start with same number of neurons at every state.

Now let us assume a burst does occur when applying $f(\cdot,(n,A))$ to X, i.e. $X_n = K-1$. As before $\sigma(X)_{\sigma(n)} = X_n = K-1$, so applying $f(\cdot,(\sigma(n),\sigma(A)))$ to $\sigma(X)$ also leads to a burst. Note that the number of neurons at each state is the same for both X and $\sigma(X)$. By the previous paragraph the number of steps in these two bursts is the same, say r, and $\sigma(A)_r\sigma(X) = \sigma(A_rX)$. Hence $f(\sigma(X),(\sigma(n),\sigma(A))) = \sigma(f(X,(n,A)))$.

□

The property of equivalence classes proceeding with the same distribution then follows from the following lemma which is also needed to achieve the desired result of this section.

Lemma 5.2.5. *Let $X \in (\{0,1,...,K-1\})^N$ and $(n,A) \in \Omega_1$. Then for every $X_1 \in (\{0,1,...,K-1\})^N$,*

$X_1 \sim X$ if and only if there exists a permutation $\sigma \in P$ such that $X_1 = \sigma(X)$. Moreover,

$$H(f(X,(n,A))) = H(f(\sigma(X),(\sigma(n),\sigma(A)))).$$

Proof. By definition $H(X_1) = H(X)$ which means the number of excitatory and inhibitory neurons in at each level for both X_1 and X is the same. Permuting the indices of the excitatory neurons and separately for the inhibitory neurons of an element in $(\{0,1,...,K-1\})^N$ does not change the number of neurons at any level for each of the two types of neurons. Hence $H(\sigma(X)) = H(X)$. For the reverse direction, we just need a permutation that for each $1 \leq n_1 \leq E$ sends n_1 to an m_1 such that $X_{n_1} = X_{m_1}$ and $1 \leq m_1 \leq E$ and for each $E+1 \leq n_2 \leq N$ sends n_2 to an m_2 such that $X_{n_2} = X_{m_2}$ and $1 \leq m_2 \leq E$. We are able to find such a permutation precisely because the number of neurons at each level for both X and X_1 is the same. For the second part, we have from Lemma 5.2.5 that $f(\sigma(X),(\sigma(n),\sigma(A))) = \sigma(f(X,(n,A)))$, and we just showed that $H(\sigma(f(X,(n,A)))) = H(f(X,(n,A)))$. So we have our result $H(f(X,(n,A))) = H(f(\sigma(X),(\sigma(n),\sigma(A))))$. □

We can now state and prove the following crucial lemma.

Lemma 5.2.6. *Pick any $X_0 \in (\{0,1,...,K-1\})^N$ and let X_{t_i} be the process defined in the inhibitory model with initial condition X_0. Then for any choice of $\omega \in \Omega_1$ and any $t_i,\ i \geq 0$, the following diagram is commutative:*

$$\begin{array}{ccc} X_{t_i} & \xrightarrow{f(\cdot,\omega)} & X_{t_{i+1}} \\ {\scriptstyle H}\downarrow & & \downarrow{\scriptstyle H} \\ S(t_i) & \xrightarrow{g(\cdot,\alpha(\omega))} & S(t_{i+1}) \end{array}$$

and $\mathbb{P}(f(X_{t_i},\omega) \sim X) = \mathbb{P}(g(H(X_{t_i}),\alpha(\omega)) = H(X))$.

Proof. We first show the diagram is commutative. Pick any $\omega \in \Omega_1$ and any $t_i,\ i \geq 0$. We show

$$H(f(X_{t_i},\omega)) = g(H(X_{t_i}),\alpha(\omega)).$$

In our discussion of the setup of Ω_2 as $[2K-1] \times \{0,1\}^{N^2}$ we have that in applying $g(\cdot,(k,A))$ to $H(X)$, k indicates from which level to promote, and A indicates which neurons to promote at each step. Promoting neuron n in X_{t_i} will leave us with the same number of neurons in each state as promoting a neuron from level $X_{t_i,n}$. Since $\sigma(A)\sigma(X) = AX$, applying A to $H(X)$ will leave us with the same number of neurons in each level as applying A to X. In particular then $H(f(X,(n,A))) = g(H(X),(X_n,A))$.

For the second part, by definition $\mathbb{P}(f(X_{t_i},\omega) \sim X) = \mathbb{P}(H(f(X_{t_i},\omega)) = H(X))$. From the first part we know $H(f(X_{t_i},\omega) = g(H(X_{t_i}),\alpha(\omega))$. Knowing that α is measure preserving from Lemma 5.2.3 gives us $\mathbb{P}(H(f(X_{t_i},\omega)) = H(X)) = \mathbb{P}(g(H(X_{t_i}),\alpha(\omega)) = H(X))$. Putting all the equalities together gives us our result. □

We are now able to conclude our desired result.

Theorem 5.2.7. *The process in the inhibitory model and the process in the counting model are the same. That is for any $X_0 \in (\{0,1,...,K-1\})^N$ if we let X_{t_i} be the process defined in the inhibitory model with initial condition X_0, and let $S(t_i)$ be the process defined in the counting model with initial condition $S_0 = H(X_{t_i})$, then for any $i \geq 0$ and any $X \in (\{0,1,...,K-1\})^N$, $\mathbb{P}(X_{t_i} \sim X) = \mathbb{P}(S(t_i) = H(X))$.*

Proof. The proof follows immediately from inductively applying Lemma 5.2.6. □

Chapter 6

Mean-Field Model

We now proceed with defining and proving the mean-field limit.

6.1 Mean Field Definition

The mean-field system must model the two different non-bursting and bursting regimes the stochastic system has. To this end, we have the non-bursting state space for modeling the non-bursting regime and the bursting state space for modeling the bursting regime. The setup follows the notation used in [2]. The model has three parameters: $K \in \mathbb{Z}^+$, $e \in [0,1]$, and $\beta \in \mathbb{R}^+$. We think of e as giving us the proportion of the system that is excitatory (think $e = E/N$ where E, N come from the counting model).

To define the non-bursting state space, we define the following sets:

$$\mathcal{E}_K = \left\{ x \in \mathbb{R}^K : 0 \leq x_k \leq e, \sum_{k=0}^{K-1} x_k = e \right\},$$

$$\mathcal{I}_K = \left\{ y \in \mathbb{R}^K : 0 \leq y_k \leq 1-e, \sum_{k=0}^{K-1} y_k = 1-e \right\}.$$

We think of $\mathcal{E}_K$ has the state space for the excitatory neurons and $\mathcal{I}_K$ as the state space for the inhibitory neurons. The non-bursting state space is then given by

$$S_K = \mathcal{E}_K \times \mathcal{I}_K, \tag{6.1}$$

with elements of the form $v = (x, y)$ with the first K elements as the excitatory neurons and the last K elements as inhibitory neurons.

We define the "big-burst domain" as

$$D_{\beta,K} := \{ v \in S_K : \beta x_{K-1} > 1, R x_{K-2} > x_{K-1} \}, \tag{6.2}$$

where R is defined in the next section. This will be the critical region of the system.

The bursting state space is the same as the non-bursting state space with four additional states appended on, the firing and cool-down states for both the excitatory and inhibitory neurons. So we can define the bursting state space by

$$B_K = \mathcal{E}_{K+2} \times \mathcal{I}_{K+2}, \tag{6.3}$$

with elements of the form $b = (x, y)$ with the first $K + 2$ elements as the excitatory neurons and the last $K + 2$ elements as inhibitory neurons. For notational purposes, we denote the states representing the firing queues, $b_K = x_K$ and $b_{2K+2} = y_K$, by x_Q and y_Q respectively, and we denote the states representing the cool-down states, $b_{K+1} = x_{K+1}$ and $b_{2K+3} = y_{K+1}$, by x_P and y_P respectively.

To describe the system, we begin by defining three functions

$$f : S_K \setminus D_{\beta,K} \to \mathbb{R}^{2K} \qquad g_1 : B_K \to \mathbb{R}^{2K+4} \qquad g_2 : B_K \to \mathbb{R}^{2K+4}.$$

The exact form of these functions will be given in the next section. Define ϕ, γ_1, γ_2 as the flows generated by f, g_1, and g_2 respectively. In particular, $\phi(\xi, \tau) := v(\tau)$, $\gamma_1(\xi, \tau) := b_1(\tau)$, $\gamma_2(\xi, \tau) := b_2(\tau)$, where v, b_1, b_2 satisfy the ODEs given by

$$\frac{d}{dt}v(t) = f(v(t)), \quad v(0) = \xi$$

$$\frac{d}{dt}b_1(t) = g_1(b_1(t)), \quad b_1(0) = \xi$$

$$\frac{d}{dt}b_2(t) = g_2(b_1(t)), \quad b_2(0) = \xi.$$

ϕ is the flow of the system on the non-bursting state space, γ_1 is the flow of the system on the bursting state space when $x_Q > 0$, and γ_2 is the flow of the system on the bursting state space when $x_Q = 0$.

Define $s^* : S_K \setminus D_{\beta,K} \to \mathbb{R} \cup \{\infty\}$ by

$$s^*(v) = \inf\{\tau > 0 : \phi(v, \tau) \in D_{\beta,K}\}.$$

Given a point v not in the big-burst domain, $s^*(v)$ gives the time that $\phi(v, t)$ first hits the big-burst domain. If $s^*(v) < \infty$ define

$$F_{\beta,K}(v) = \phi(v, s^*(v))$$

as the state of the system when it hits the big-burst domain. The domain of $F_{\beta,K}$ is then

$$D(F_{\beta,K}) = \{v \in S_K \setminus D_{\beta,K} : s^*(v) < \infty\}$$

To describe the non-bursting system we need an additional function

$$M_K : D_{\beta,K} \to B_K$$

which is the map from the non-bursting state space to the bursting state space. The exact form of M_K can be easily defined as

$$M_K(v) = M_K((x,y)) = (x_0, ..., x_{K-1}, 0, 0, y_0, ..., y_{K-1}, 0, 0).$$

We have two flows on the bursting state space, one when the excitatory firing queue is non-empty, and one when it is empty. To describe the switch between these flows we need to define a few more functions. Define $\omega_1^* : B_K \to \mathbb{R}$ by

$$\omega_1^*(b) = \inf\{\tau > 0 : \gamma_{1,K}(b,\tau) = x_Q(\tau) = 0\}.$$

After defining g_1 explicitly we will prove that ω_1^* is bounded. Hence, the domain of ω_1^* is all of B_K. Define $D(R_1) = \{b \in B_K : b_K = x_Q = 0\}$ and $R_1 : D(R_1) \to B_K$ by

$$R_1(x_0, x_1, ..., x_{K-1}, 0, x_P, y) = (x_0 + x_P, x_1, ..., x_{K-1}, 0, 0, y).$$

R_1 resets the contents in the excitatory cool down state to the the initial state x_0. Define

$$G_{1,\beta,K}(b) = \gamma_1(b, \omega_1^*(b)),$$

the state of the system once $x_Q = 0$.

Define $\omega_2^* : B_K \to \mathbb{R}$ by

$$\omega_2^*(b) = \inf\{\tau > 0 : \gamma_{2,2K+2}(b,\tau) = y_Q(\tau) = 0\}.$$

Again after defining g_2 explicitly we will prove that ω_2^* is bounded. Define $D(R_2) = \{b \in B_K : b_{2K+2} = y_Q = 0\}$

and $R_2 : D(R_2) \to S_K$ by

$$R_2(x_0, ..., x_{K-1}, 0, 0, y_0, y_1, ..., y_{K-1}, 0, y_P) = (x_0, ..., x_{K-1}, y_0 + y_P, y_1, ..., y_{K-1}).$$

R_2 resets the contents in the inhibitory cool down state to the the initial state y_0 and eliminates the firing and cool-down states which are now all zero. We will show later that the image of R_2 is $S_K \setminus D_{\beta,K}$. Define

$$G_{2,\beta,K}(b) = \gamma_2(b, \omega_2^*(b))$$

to be the state of the system once $y_Q = 0$.

We are now set to define our dynamical system. Pick any initial condition in the non-bursting state space not in the big-burst domain $\xi_0 \in S_K \setminus D_{\beta,K}$ and define

$$\xi(t) = \phi(\xi_0, t), \quad 0 \leq t < s^*(\xi_0).$$

If $s^*(\xi_0) < \infty$, then we define

$$b_0 = M_K(F_{\beta,K}(\xi_0)), \quad \tau_1^* = \omega_1^*(b_0), \quad b_1 = R_1(G_{1,\beta,K}(b_0)), \text{ and } \tau_2^* = \omega_2^*(b_1). \tag{6.4}$$

From these we define

$$\xi(s^*(\xi_0)) = R_2(G_{2,\beta,K}(b_1)).$$

In summary, we flow under ϕ until we hit the big-burst domain, at which point we are mapped to the big burst state space. We then flow under γ_1 until x_Q becomes empty and we reset the states using R_1. We then flow until y_Q becomes empty and we reset the states and are mapped back into the non-bursting state space under R_2. It should be noted that with the definitions we choose for g_1 and g_2, letting $b_1 = G_{1,\beta,K}(b_0)$ and letting $\xi(s^*(\xi_0)) = R_2(R_1(G_{2,\beta,K}(b_1))$ does not change the dynamics of the system, i.e. they are equivalent definitions.

Having $R_2(G_{2,\beta,K}(b_1)) \in S_K \setminus D_{\beta,K}$, still to be shown, allows us to extend this mean-field definition in the same way as in [2]. Given $\xi_0 \in S_K \setminus D_{\beta,K}$, define

$$0 = \tau_0 < \tau_1 < \cdots < \tau_n < \cdots$$

by $\tau_n - \tau_{n-1} = s^*(\xi(\tau_{n-1}))$, define

$$\xi(t) = \phi(\xi(\tau_{n-1}), t - \tau_{n-1}), \text{ for } t \in [\tau_{n-1}, \tau_n),$$

and

$$\xi(\tau_n) = R_2\left(G_{2,\beta,K}\left(R_1\left(G_{1,\beta,K}\left(M\left(F_{\beta,K}\left(\xi\left(\tau_{n-1}\right)\right)\right)\right)\right)\right)\right).$$

The τ_j are the times of the big bursts. We denote the size of the burst by

$$B_j := B(\tau_j) = G_{1,\beta,K,K+1}(M(F_{\beta,K}(\xi\left(\tau_{n-1}\right)))) + G_{2,\beta,K,2K+3}(R_1(G_{1,\beta,K}(M(F_{\beta,K}(\xi\left(\tau_{n-1}\right)))))). \quad (6.5)$$

We will be able to deduce from the definitions of the flows γ_1 and γ_2 that exact form of the sum of the coordinates x_{K+1} and x_{2K+3} is given by $x_{K+1} + x_{2K+3} = t$. Hence for $\xi \in D_{\beta_K}$, if we let $t^*(\xi) = \tau_1^* + \tau_2^*$ where τ_1^*, τ_2^* are defined in the equations (6.4), then $B_j = t^*(\xi(\tau_j))$.

For ease of notation in the analysis of the mean field system, we define the map $\mathscr{G}_{\beta,K} : D_{\beta,K} \to S_K \setminus D_{\beta,K}$ by

$$\mathscr{G}_{\beta,K}(\xi) = R_2\left(G_{2,\beta,K}\left(R_1\left(G_{1,\beta,K}\left(M\left(F_{\beta,K}\left(\xi\right)\right)\right)\right)\right)\right).$$

6.1.1 Definition of Flows

We now explicitly define the function f on the non-bursting state space and the functions g_1 and g_2 on the bursting state space that generate the flows of the system. The definition of f follows that of the corresponding f in [2]. We define a $2K \times 2K$ matrix L by

$$L_{i,j} = \begin{cases} -1 & \text{if } i = j; \\ 1 & \text{if } i = j + 1 \mod K; \\ 0 & \text{otherwise.} \end{cases}$$

f is then given by

$$\frac{d}{dt}x = f(x) := Lx.$$

We define g_1 with the following ODE:

$$\begin{aligned}
\dot{x}_0 &= (1-R)\beta x_1 - R\beta x_0 & \dot{y}_0 &= (1-R)\beta y_1 - R\beta y_0 \\
\dot{x}_k &= (1-R)\beta x_{k+1} + R\beta x_{k-1} - \beta x_k & \dot{y}_k &= (1-R)\beta y_{k+1} + R\beta y_{k-1} - \beta y_k \\
\dot{x}_{K-1} &= R\beta x_{K-2} - \beta x_{K-1} & \dot{y}_{K-1} &= R\beta y_{K-2} - \beta y_{K-1} \\
\dot{x}_Q &= R(\beta x_{K-1} - 1) & \dot{y}_Q &= R\beta y_{K-1} - (1-R) \\
\dot{x}_P &= R & \dot{y}_P &= 1-R,
\end{aligned}$$

where k goes from 1 to $K-2$ and

$$R(t) = \frac{x_Q(t)}{x_Q(t) + y_Q(t)}.$$

$R(t)$ gives us the ratio of the size of the excitatory firing queue to the sizes of both queues. Note that we begin flowing under γ_1, the flow generated by g_1, when $x_Q = y_Q = 0$. To resolve this, we define

$$R(0) = \frac{x_{K-1}(0)}{x_{K-1}(0) + y_{K-1}(0)}.$$

We will show later that this definition of $R(t)$ is continuous for any initial condition $b(t)$ and for $0 \le t \le \omega_1^*(b)$.

When we are flowing according to g_2, $x_Q = 0$ and $y_Q \ge 0$, and we flow until $y_Q = 0$. g_2 is defined with the ODE:

$$\begin{aligned}
\dot{x}_0 &= \beta x_1 & \dot{y}_0 &= \beta y_1 \\
\dot{x}_k &= \beta x_{k+1} - \beta x_k & \dot{y}_k &= \beta y_{k+1} - \beta y_k \\
\dot{x}_{K-1} &= -\beta x_{K-1} & \dot{y}_{K-1} &= -\beta y_{K-1} \\
\dot{x}_Q &= 0 & \dot{y}_Q &= -1 \\
\dot{x}_P &= 0 & \dot{y}_P &= 1,
\end{aligned}$$

where k goes from 1 to $K-2$.

6.1.2 Validity of Model Definition

The validity of the model definition relies on ω_1^* and ω_2^* both being bounded, the image of $\mathscr{G}_{\beta,K}(\xi)$ being in $S_K \setminus D_{\beta,K}$ and not being in the big-burst domain, and $R(t)$ being a continuous function for $0 \le t \le \omega_1^*$. We now prove these three key statements.

Theorem 6.1.1. *For every $b \in B_K$,*

$$\omega_1^*(b) = \inf\{\tau > 0 : \gamma_{1,K}(b,\tau) = x_Q(\tau) = 0\}$$

and

$$\omega_2^*(b) = \inf\{\tau > 0 : \gamma_{2,2K+2}(b,\tau) = y_Q(\tau) = 0\}$$

are both bounded.

Proof. First note that the flows generated by both g_1 and g_2 are conserved, i.e. $\sum_k \dot{x}_k = \sum_k \dot{y}_k = 0$ where the sums range over $k = 0, ..., K-1, Q, P$. Secondly note that for both flows and any $k = 0, ..., K-1, P$, if $x_k = 0$ then $\dot{x}_k \geq 0$, and if $y_k = 0$ then $\dot{y}_k \geq 0$. Hence $x_k, y_k \geq 0$ for all time since $x_k(0), y_k(0) \geq 0$. Also note that by definition of our mean-field system that x_Q, y_Q can never become negative. Finally recall that $\sum_k x_k(0) + y_k(0) = 1$.

Pick any $b \in B_K$. If we set $Z(t) = x_P(t) + y_P(t)$, then $\dot{Z} = \dot{x}_P + \dot{y}_P = 1$ and hence $Z(t) = t$. This is true for both the flows generated by g_1 and g_2. Hence $x_Q(1) = y_Q(1) = 0$ by the positivity of all the variables and the conservation in the two systems. Therefore $\omega_1^*(b), \omega_1^*(b) \leq 1$. □

Theorem 6.1.2. *The image of the map $\mathscr{G}_{\beta,K}(\xi) = R_2(G_{2,\beta,K}(R_1(G_{1,\beta,K}(M(F_{\beta,K}(\xi))))))$ is indeed $S_K \setminus D_{\beta,K}$. In particular, the image of $G_{2,\beta,K}(R_1(G_{1,\beta,K}(M(F_{\beta,K}(\xi)))))$ under the map $R_2 : D(R_2) \to S_K$ is $S_K \setminus D_{\beta,K}$.*

Proof. Choose $\xi \in D_{\beta,K}$ and let $b = M(F_{\beta,K}(\xi))$. Recall $G_{1,\beta,K}(b) = \gamma_1(b, \omega_1^*(b))$ and that $\omega_1^*(b) = \inf\{\tau > 0 : \gamma_{1,K}(b,\tau) = x_Q(\tau) = 0\}$. By definition, for all $0 \leq t < \omega_1^*(b)$, $x_Q(t) > 0$ and g_1 is continuous. Hence $x_Q(t)$ is continuous and differentiable for this time. Hence $\dot{x}_Q(\omega_1^*(b)-) < 0$ from which it follows from the definition of $\dot{x}_Q$ that under g_1, $\beta x_{K-1} \leq 1$ when the map R_1 is applied. Notice under γ_2, $\dot{x}_{K-1} = -\beta x_{K-1}$, so all x_{K-1} can do if we do flow under γ_2 is decrease. So when we apply the map R_2, we still must have that $\beta x_{K-1} \leq 1$ giving us that $R_2(G_{2,\beta,K}(R_1(G_{1,\beta,K}(b))))$ is indeed $S_K \setminus D_{\beta,K}$. □

Theorem 6.1.3. *$R(t)$ is continuous for any initial condition $b(t) \in Im(M_k)$ and for $0 \leq t \leq \omega_1^*(b)$.*

Proof. Pick any initial condition $b(0) \in Im(M_k)$. For $0 < t \leq \omega_1^*(b)$, $R(t) = \frac{x_Q(t)}{x_Q(t)+y_Q(t)}$, where x_Q and y_Q solve the corresponding components of the ODE given by g_1. In particular, if we rewrite the derivatives of

x_Q and y_Q with R replaced by its definition, we get

$$\dot{x}_Q = \frac{x_Q}{x_Q + y_Q}(\beta x_{K-1} - 1) \text{ and } \dot{y}_Q = \frac{x_Q}{x_Q + y_Q}\beta y_{K-1} - 1 + \frac{x_Q}{x_Q + y_Q}.$$

These derivatives do not exist only if $x_Q + y_Q = 0$. Recalling that $\omega_1^*(b) = \inf\{\tau > 0 : \gamma_{1,K}(b, \tau) = x_Q(\tau) = 0\}$, this only occurs at $t = 0$. So for $0 < t \leq \omega_1^*(t)$, $x_q + y_Q \neq 0$, the derivatives exist and hence x_Q, y_Q are continuous, and therefore $R(t) = \frac{x_Q(t)}{x_Q(t)+y_Q(t)}$ is continuous.

This leaves us with showing $R(t)$ being right continuous at $t = 0$. In particular we need to show

$$\lim_{t\to 0^+} R(t) = R(0).$$

At $t = 0$, $x_Q = 0$ and $y_Q = 0$. Hence $R = \frac{x_Q}{x_Q+y_Q}$ is of an indeterminate form and we use L'Hôpitals rule to get

$$\lim_{t\to 0^+} \frac{x_Q(t)}{x_Q(t) + y_Q(t)} = \lim_{t\to 0^+} \frac{R(\beta x_{K-1} - 1)}{R(\beta x_{K-1} - 1) + R\beta y_{K-1} - 1 + R}.$$

To show the desired result, if we set $R = \frac{R(\beta x_{K-1}-1)}{R(\beta x_{K-1}-1)+R\beta y_{K-1}-1+R}$ and solve for R, we get $R = \frac{x_{K-1}}{x_{K-1}+y_{K-1}}$. Hence if we take $R(0) = \frac{x_{K-1}(0)}{x_{K-1}(0)+y_{K-1}(0)}$, which we have by definition, we get

$$\lim_{t\to 0^+} R(t) = \lim_{t\to 0^+} \frac{x_Q(t)}{x_Q(t) + y_Q(t)} = \lim_{t\to 0^+} \frac{R(t)(\beta x_{K-1}(t) - 1)}{R(t)(\beta x_{K-1}(t) - 1) + R(t)\beta y_{K-1}(t) - 1 + R(t)}$$
$$\lim_{t\to 0^+} \frac{x_{K-1}(t)}{x_{K-1}(t) + y_{K-1}(t)} = \frac{x_{K-1}(0)}{x_{K-1}(0) + y_{K-1}(0)} = R(0).$$

To complete the proof we only need to note that at $t = 0$, by definition of the big-burst domain, the domain of the map M_K, $x_{K-1} \neq 0$. □

6.2 Mean Field Limit

We now show that in the limit as $N \to \infty$, our mean-field model approximates the counting model quite well. As in [2] we show the following:

- the times at which "big bursts" occur for the counting model are close to the burst times of the mean field model,
- the sizes of these big bursts are close to the sizes of the predicted bursts in the mean-field model,
- between big bursts, the counting model stays close to the non-bursting regime of the mean-field model.

These will be shown through the following theorem.

Theorem 6.2.1. *Consider any $v = (x, y) \in S_k \cap \mathbb{Q}^{2K}$. For N sufficiently large, $Nv \in \mathbb{Z}^{2K}$ and we can define $S(t)^{(N)}$ to be the process defined by the counting model in Section 5.1 with initial condition $S(0)^{(N)} = Nv$.*

Choose and fix $\epsilon, h, T > 0$. Let $\xi(t)$ be the solution of the mean-field model with initial condition $\xi(0) = v$. Then there exists a sequence of times $\tau_1, \tau_2, ...$ at which they system has a big burst. Let $b_{min}(T) = min\{B(\tau_k) : \tau_k < T\}$ be the smallest big burst which occurs before time T, and let the number of big bursts in $[0, T]$ be $m(T) = arg\ max_k\ \tau_k < T$.

Pick any $\alpha < b_{min}(T)$. Consider the counting process $S(t)^{(N)}$ and denote by $T_k^{(N)}$ the times at which the $S(t)^{(N)}$ has a big burst of size larger than αN. Then there exists constants $C_{0,1}(\epsilon)$ such that for N sufficiently large,

$$\mathbb{P}\left(\sup_{j=1}^{m(T)} \left|T_j^{(N)} - \tau_j\right| > \epsilon\right) \leq C_0(\epsilon)N\ \exp(-C_1(\epsilon)N^{\psi(K)}), \tag{6.6}$$

and

$$\mathbb{P}\left(\sup_{j=1}^{m(T)} \sup_{t\in[\tau_j,(\tau_{j+1}\wedge T_{j+1}^{(N)})-\epsilon]} \left|S(t)^{(N)} - \xi(t - (T_j^{(N)} - \tau_j))\right| > \epsilon\right) \leq C_0(\epsilon)N\ \exp(-C_1(\epsilon)N^{\psi(K)}), \tag{6.7}$$

where $\psi(K) = O(1/K)$.

The proof will be broken up into Lemmas 6.2.2, 6.2.3, 6.2.4 below. Let us quickly discuss what the theorem give us. The first estimate given in (6.6) tells us that the the times at which the counting process has a big burst is close to the burst times of the mean-field process. The second estimate given in (6.7) tells us that if we make the appropriate time shift so that the the interburst times begin at the same time for both processes, then the counting process is pathwise convergent to the mean-field process. Notice that as $N \to \infty$, the number of separate events that can occur in the Markov chain in the counting model grows $O(N)$ since we can have a burst of size N. This is why the error estimate in both cases are not quite exponential, i.e. $\psi(K) < 1$.

Throughout the following we denote $\gamma_1 = \beta x_{K-1}$, $\gamma_2 = 1 - (Rx_{K-2} - x_{K-1})$, and set $\gamma = \gamma_1 \wedge \gamma_2$, where $R = x_{K-1}/(x_{K-1} + y_{K-1})$. Clearly, if $\gamma < 1$ then $v = (x, y) \notin D_{\beta,K}$, and if $\gamma > 1$ then $v \in D_{\beta,K}$. We characterize the burst size in the case when $\gamma < 1$, $\gamma > 1$ (we do not need to consider the critical case $\gamma = 1$ here). For any $v = (x, y) \in S_k \cap \mathbb{Q}^{2K}$, for N sufficiently large, $vN \in \mathbb{Z}^{2K}$. Define $B^{(N)}(v)$ as the random

variable which is the burst size given that we start the system in state

$$(x_0N, x_1N, ..., x_{K-1}N - 1, 1, 0, y_0N, y_1N, ...y_{K-1}N, 0, 0).$$

Lemma 6.2.2. *Let v be such that $\gamma < 1$. Then for any $b \geq 1$ and $\gamma < \gamma' < 1$, we have*

$$\lim_{b\to\infty} \lim_{N\to\infty} \mathbb{P}(B^{(N)}(v) > b) = 0.$$

Equivalently: let $\mu > \gamma e^{1-\gamma}$ (μ can be chosen in $(0,1)$ if $\gamma \in (0,1)$). Then for b sufficiently large,

$$\mathbb{P}(B^{(N)}(v) > b) < \mu^b.$$

Finally,

$$\lim_{N\to\infty} \mathbb{E}(B^{(N)}(v) > b) = \frac{1}{1-\gamma},$$

and in particular is finite for $\gamma \in [0,1)$.

Lemma 6.2.3. *Consider v with $\gamma > 1$. Then there is a $p(\gamma) \in (0,1)$ such that*

$$\lim_{b\to\infty} \lim_{N\to\infty} \mathbb{P}(B^{(N)}(v) > b) = p(\gamma).$$

From this it follows that there exists a $\eta' > 0$ such that

$$\lim_{N\to\infty} \mathbb{P}(B^{(N)}(v) > \eta' N) > 0.$$

In fact, we can be more precise: $p(\gamma) = \tilde{\gamma}/\gamma$, where $\tilde{\gamma}$ is the unique solution in $(0,1)$ of

$$\gamma e^{1-\gamma} = \tilde{\gamma} e^{1-\tilde{\gamma}}.$$

As in equation (6.5) let us define $B(\tau_1)$ to be the size of the first burst of $\xi(t)$ where $\xi(0) = v$. Then for all $\eta > 0$, there exists $C_{0,1}(\eta) > 0$ such that for N sufficiently large,

$$\mathbb{P}\left(\left|B^{(N)}(v) - B(\tau_1)N\right| > \eta N | B^{(N)}(v) > \eta' N\right) \leq C_0(\eta)\, \exp(-C_1(\eta)N).$$

Lemma 6.2.4. *Choose $v, S(t)^{(N)}, T = \tau_1, T_1^{(N)}$ as in Theorem 6.2.1, where we also require that $v \notin D_{\beta,K}$.*

By definition, for $t < \tau_1$, the solution of $\xi(t)$ to the mean-field model has no big bursts, and in particular $(\beta\xi_{K-1}) \wedge (1 - (R\xi_{K-2} - \xi_{K-1})) < 1$ during this time. Define the events

$$A_1^\epsilon := \left\{\omega : \left|T_1^{(N)} - \tau_1\right| > \epsilon\right\}, \tag{6.8}$$

$$A_2^\epsilon := \left\{\omega : \sup_{t\in[0,(\tau_1\wedge T_1^{(N)})-\epsilon]} \left|\xi(t) - N^{-1}S(t)^{(N)}\right| > \epsilon\right\}, \tag{6.9}$$

$$A_3^\epsilon := \left\{\omega : \left|B(T_1^{(N)}) - B(\tau_1)N\right| > \epsilon N\right\}. \tag{6.10}$$

Then for all $\epsilon > 0$, there are $C_{0,1}(\epsilon) > 0$ so that for N sufficiently large,

$$\mathbb{P}(A_1^\epsilon \cup A_2^\epsilon \cup A_3^\epsilon) \leq C_0(\epsilon)N\ \exp(-C_1(\epsilon)N^{\psi(K)}),$$

where $\psi(K) = O(1/K)$.

The proofs of these lemmas follows the proofs of Lemmas $2, 3, 4$ in [2]. The proof of Theorem 6.2.1 then, is almost verbatim the proof of Theorem 1 in [2]. The content of these lemmas are the same as Lemmas $2, 3, 4$ in [2]. Lemma 6.2.2 tells us if $\gamma < 1$, then the probability of a big burst is exponentially small in N for large N due to the probability of a burst of size b decaying exponentially in b. It also gives us that the expected size of a burst is bounded for any $\gamma < 1$ and as $\gamma \to 1$, the expected size does not blow up too badly. Lemma 6.2.3 tells us that if $\gamma > 1$, we do get big burst with some positive probability and that whenever we do get a big burst, the probability that its size is close to the expected size given by $B(\tau_1)$ is exponentially close to 1.

Lemma 6.2.4 states that the probability of each of the three events $A_1^\epsilon, A_2^\epsilon, A_3^\epsilon$ occurring goes to zero exponentially fast as $N \to \infty$. Event A_1^ϵ being unlikely to occur means the times of the first big burst for both the counting process and the mean field process are close. Event A_2^ϵ being unlikely indicates that the the stochastic process is likely close to the mean-field process for the time given. A_2^ϵ does not cover all of the time before the first big burst due to the non-uniformity of the process. Event A_3^ϵ being unlikely gives us that the size of the first big burst in the stochastic process is close to the size of the big burst in the deterministic process.

Chapter 7

Analysis of Behavior

7.1 Mean Field Analysis

We are interested in using the mean-field model to analyze the bistability and non-monotonic behavior seen in the inhibitory model. The setup of the analysis of the bistability closely follows that seen in [2]. We want to investigate what points in the state space S_K go to the fixed point of the flow under the ODE f, where f is defined in Section 6.1.1, and what points have infinitely many bursts.

In the limit where we obtain the mean-field model, $N \to \infty$, $p \to \beta/N$, $\rho = 1$ and $e = E/N, K$ are fixed. Hence our model only depends on β, K, e. Define $T_0 = D_{\beta,K}$ and $U^0_{\beta,K,e}$ as the subset of $S_K \setminus D_{\beta,K}$ that flows into $D_{\beta,K}$ under the ODE f. For each $k > 0$, define $T^k = \mathscr{G}^{-1}_{\beta,K}(U^{k-1}_{\beta,K,e})$ and $U^k_{\beta,K,e}$ as the subset of $S_K \setminus D_{\beta,K}$ which flows into T^k. The set of initial conditions that have at least k bursts is then precisely the set $U^k_{\beta,K,e}$. We finally define the set of initial conditions which have infinitely many bursts by $U^\infty_{\beta,K,e} = \cap_{k\geq 0} U^k_{\beta,K,e}$.

We are most interested when K is fixed and studying for various values of e the set $U^\infty_{\beta,K,e}$ as β changes. Numerically we see that for all e, for β small enough, no initial conditions give rise to infinitely many bursts, and for some e, for β sufficiently large, some initial conditions do have infinitely many bursts. Only for $e = 1$ was it observed for β sufficiently large, that all initial conditions have infinitely many big bursts. This leads to two critical β values as seen in [2]

$$\beta_{c,1}(K, e) = \inf\{\beta : U^\infty_{\beta,K,e} \neq \emptyset\}, \quad \beta_{c,2}(K, e) = \sup\{\beta : U^\infty_{\beta,K,e} = S_K\}. \tag{7.1}$$

If $\beta > \beta_{c,1}$ then the system does undergo infinitely many bursts for some initial conditions. If $\beta < \beta_{c,2}$ then the system does not undergo infinitely many bursts for some initial conditions. Therefore if $\beta_{c,1} < \beta < \beta_{c,2}$ then the system can express to qualitatively different types of behavior, one in which the system goes to a fixed point, and the other where the system goes to a "periodic" orbit.

Numerically, it appears for $e = .5, .6, ..., 1$, that $\beta_{c,1}$ is finite; there is a value of β where the periodic

orbits arise. However, only for $e = 1$ does $\beta_{c,2}$ appear to be finite. (Both of these results can be seen in Figure 7.1.) In fact, we can show for $e < 1$ that $\beta_{c,2} = \infty$.

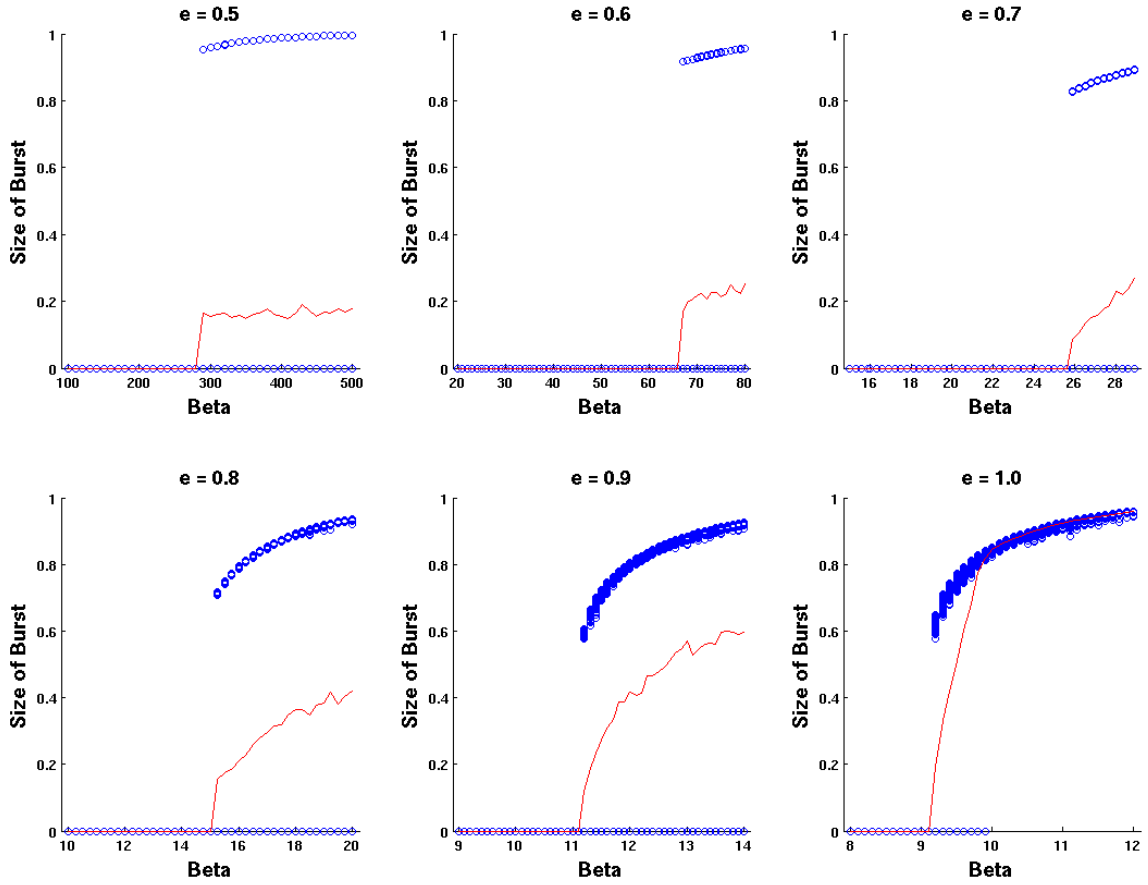


Figure 7.1: Plot of simulations of the mean-field model for $K = 10, e = 0.5, 0.6, 0.7, 0.8, 0.9, 1.0$ where the initial conditions were randomly chosen. For the given series of β in each plot, we ran 1000 simulations and plotted the average burst size if the simulation went to the periodic orbit, or zero if the simulation went to the fixed point. The red line indicates the average value of the points at that β, i.e. it gives the average burst size over all initial conditions both going to the periodic orbit and to the fixed point.

Using the arguments in Section 5 of [2], the ODE defined by f has an attracting fixed point given by $(e/K, ..., e/K, (1-e)/K, ..., (1-e)/K)$, where the switch from e to $(e-1)$ occurs at the $(K-1)^{st}$ and K^{th} coordinates (where we maintain the first coordinate is the 0th coordinate). In Figure 7.2 we have plots of the big-burst domain $D_{\beta,K}$ projected onto the the x_{K-2}, x_{K-1}-plane for the excitatory model $e = 1$, left panel, and the inhibitory model $e < 1$, right panel. For $e = 1$, the big-burst domain is given by

$$D_{\beta,K} := \{v \in S_K : \beta x_{K-1} > 1, x_{K-2} > x_{K-1}\}.$$

The values of x_{K-2} and x_{K-1} at the fixed point are both given by $1/K$. In the x_{K-2}, x_{K-1}-plane this is on the line $x_{K-2} = x_{K-1}$ which forms part of the boundary of the big-burst domain (as seen in the left panel of Figure 7.2). We see if $\beta > K$, then the fixed point is on the boundary of $D_{\beta,K}$, and so there are arbitrarily small perturbation that move the point into $D_{\beta,K}$. Hence, the fixed point is unstable for $\beta > K$.

However, for the inhibitory model the fixed point never loses stability. For $e < 1$, the values of x_{K-2} and x_{K-1} at the fixed point are both given by e/K, which in the x_{K-2}, x_{K-1}-plane is still on the line $x_{K-2} = x_{K-1}$. The big-burst domain is given by $D_{\beta,K} := \{v \in S_K : \beta x_{K-1} > 1, R x_{K-2} > x_{K-1}\}$, where $R = x_{K-1}/(x_{K-1} + y_{K-1})$. Rewriting we get

$$D_{\beta,K} := \{v \in S_K : \beta x_{K-1} > 1, x_{K-2} > x_{K-1} + y_{K-1}\}.$$

Hence the boundary of $D_{\beta,K}$ is some positive distance away from the line $x_{K-2} = x_{K-1}$ (as seen in the right panel of Figure 7.2). Therefore, for any $e < 1, \beta > 0$, there is some $\varepsilon > 0$ we can perturb the fixed point by and not move into the big-burst domain $D_{\beta,K}$. Hence the fixed point never loses stability.

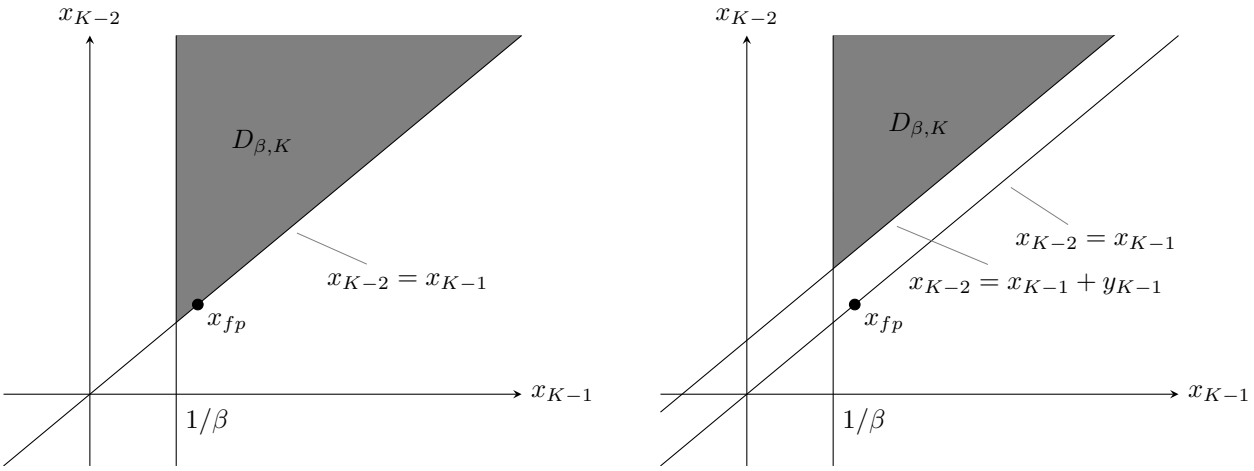


Figure 7.2: Plots of the big burst domain $D_{\beta,K}$ in the x_{K-1}, x_{K-2}-plane. Left is the domain when $e = 1$, and right is the domain when $e < 1$. The point x_{fp} is the fixed point for each system assuming $\beta > K$. Notice left x_{fp} is on the boundary of $D_{\beta,K}$ reflecting it being unstable for $e = 1$, and right x_{fp} is a positive distance away from $D_{\beta,K}$ reflecting it being stable for $e < 1$.

From the above arguments we can conclude the following theorem.

Theorem 7.1.1. *In the mean-field system defined in Section 6.1, and for $\beta_{c,2}$ defined above, if $e < 1$ then $\beta_{c,2} = \infty$.*

We also point out that once the periodic orbits arise the size of the bursts between these orbits are quite close, as seen in Figure 7.1. That is, there is not a scale separation between the burst sizes as seen in the

stochastic system. This suggests that the non-monotonic behavior seen in the inhibitory model arises only for finite N. In the next section we explore this behavior more.

7.2 Non-Monotonic Behavior

We now investigate the non-monotonic behavior seen in the Inhibitory model. For $p_i \in (0,1)$, $i = 1, 2, ...$, let X_{t,p_i} be a realization of the process in the inhibitory model with the parameter p in the model set to p_i. For a given X_{t,p_i}, recall our definition of $S_n(p)$ as the proportion of the total number of bursts of X_{t,p_i} with size greater than or equal to $n\%$ of the network. As seen in Figures 2.3 and 2.4, the S_{25} curve in simulations is non-monotonic for some choices of N, E. Notice this non-monotonicity occurs only when the curves S_n, $n = 25, 50$, are not equal. In the mean-field system, numerically we see that the analogous two curves are always equal as seen in Figure 7.1. That is, if there is a burst, the size of the burst is at least half the size of the system. This suggests that this non-monotonic behavior is a finite N effect.

We define two critical values of the parameter p,

$$p_{c,1} = \inf\{p \in (0,1) : \mathbb{E}(S_{25}) \neq \mathbb{E}(S_{50})\} \tag{7.2}$$

$$p_{c,2} = \sup\{p \in (0,1) : \mathbb{E}(S_{25}) \neq \mathbb{E}(S_{50})\}. \tag{7.3}$$

As stated, our numerical results strongly suggest that the non-monotonicity occurs only for $p \in (p_{c,1}, p_{c,2})$. This and the behavior being a finite N effect would hold from the following conjecture:

Conjecture 7.2.1. *The non-monotonicity behavior only occurs for $p \in (p_{c,1}, p_{c,2})$, and as N blows up this behavior ceases. In particular, the following holds for the length of the interval $(p_{c,1}, p_{c,2})$ scaled by N:*

$$\lim_{N\to\infty} N\,|p_{c,2} - p_{c,1}| = 0.$$

Looking at Figures 2.3 and 2.4 gives strong evidence for the first part of this conjecture. The absence of the non-monotonicity in the mean-field model indicates validity of the second part of this conjecture. Numerically we also computed the scaled length of $(p_{c,1}, p_{c,2})$ for $N = 100, 1000, 10000, 100000$ and for $e = E/N = .8$ and obtained approximate scaled lengths of $11, 4.2, 1.2, 1$, respectively giving more evidence for our conjecture (see Figure 7.3).

Moving on to investigating the cause of the non-monotonic behavior. When we plot the burst sizes vs time for $p \in (p_{c,1}, p_{c,2})$, we see that there are a series of groupings of medium sized bursts, and these

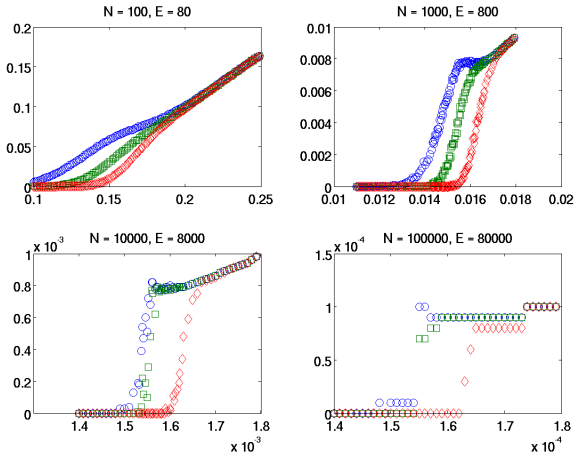


Figure 7.3: Plot of the S_{25} (blue circles), S_{50} (green squares), and S_{75} (red diamonds) curves for simulations of the inhibitory model with $K = 10$, $e = E/N = 0.8$, and top left $N = 100$, top right $N = 1000$, bottom left $N = 10000$, bottom right $N = 100000$.

groupings decrease as p increases, as seen in Figure 7.4. This suggests that when we have a medium sized burst, the system remains near critical after the burst and another medium sized burst occurs soon after. As E/N is increased, numerically these groupings become much less prevalent. Let us make these statements more precise.

For the following we fix $p \in (0, 1)$ and let $X_{t,p}$ be a realization of the process in the inhibitory model with the parameter p. Define T_i, $i = 1, 2, ...$, to be the times at which a burst of any size occurs for $X_{t,p}$, and let $B(T_i)$ be the size of the burst. For T_i and $0 \leq q \leq 1$, we define the time to the next burst of size greater than qN to be

$$T_q^*(T_i, p) = \min_{j>i}\{T_j - T_i : B(T_j) \geq qN\},$$

and the size of the burst at that time to be

$$b_q(T_i, p) = B(T_q^*(T_i, p)).$$

We use these to define two useful expectations. Define for $q, r \in [0, 1]$

$$\tau_{q,r}(T_i, p) = \mathbb{E}[T_q^*(T_i, p)|B(T_i) \geq rN]$$

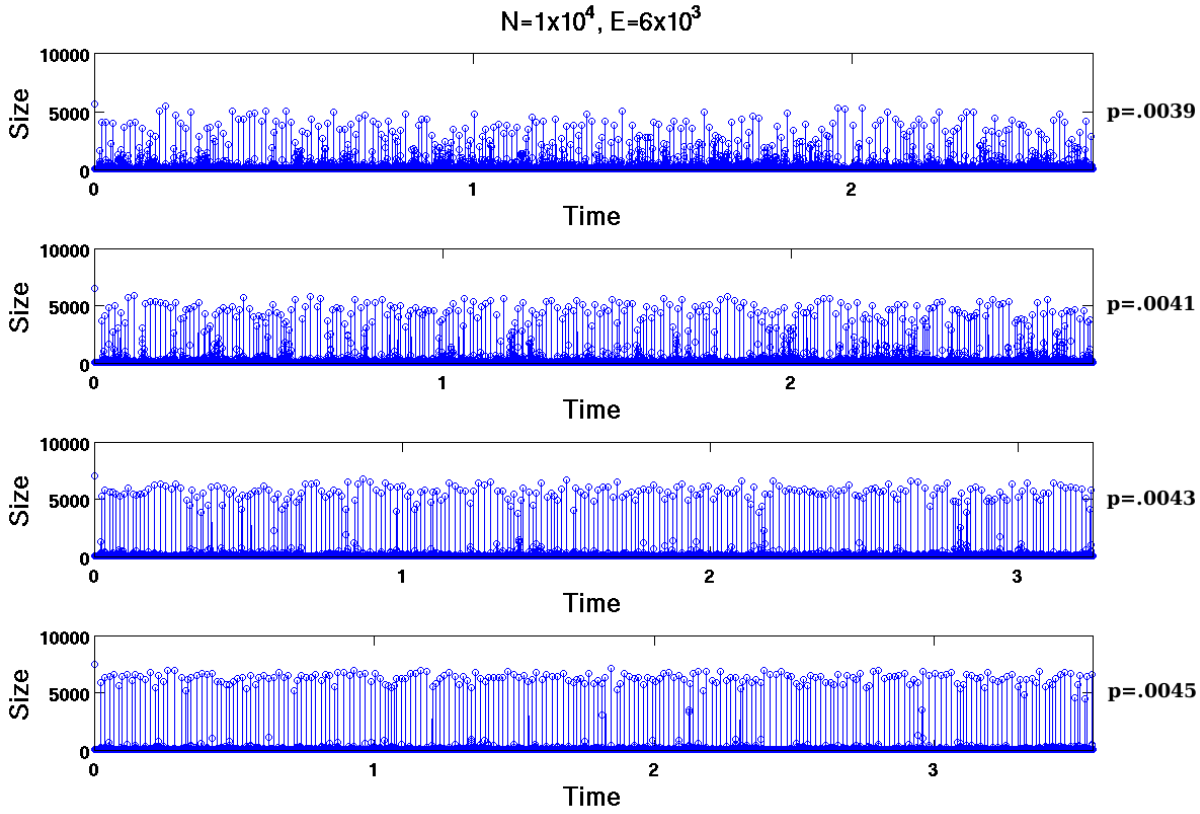


Figure 7.4: Simulations of the inhibitory model for $N = 10000, K = 10, E = 6000$ for $p = 0.0039$, 0.0041, 0.0043, 0.0045, where we plot the size of each burst vs time.

to be the expected time to the next burst of size $\geq qN$ given that the current burst is of size $\geq rN$, and

$$\nu_{q,r}(T_i, p) = \mathbb{E}[b_q(T_i, p)|B(T_i) \geq rN]$$

to be the expected size of the next burst of size $\geq qN$ given that the current burst is of size $\geq rN$. Now our hypothesis can be stated in the following two conjectures.

Conjecture 7.2.2. *For a burst of size qN, $q \geq .25$, the expected amount of time until the next burst of size $\geq .25N$ increases as q increases, and the rate of this increase decreases as E/N is increased. More precisely, taking expectation over $p \in (p_{c,1}, p_{c,2})$, $\mathbb{E}(\tau_{.25,r}(T_i, p))$ is an increasing function of r, there exits some $\lambda_1, \lambda_2 > 0$ such that*

$$\mathbb{E}[\tau_{.25,.25}(T_i, p)] < \lambda_1 < \lambda_2 < \mathbb{E}[\tau_{.25,.75}(T_i, p)],$$

and $\mathbb{E}[\tau_{.25,.75}(T_i, p)] - \mathbb{E}[\tau_{.25,.25}(T_i, p)]$ decreases as a function of E/N.

Conjecture 7.2.3. *For $E/N < 1$ and a burst of size qN, $q \geq .25$, the expected size of the next burst of size $\geq .25N$ increases as q increases in a "smooth" fashion, unlike when $E/N = 1$. More precisely, taking expectation over $p \in (p_{c,1}, p_{c,2})$, $\mathbb{E}(\nu_{.25,r}(T_i, p))$ is a smooth (possibly C_1) increasing function of r. Moreover, there exits some $\lambda_1, \lambda_2 > 0$ such that*

$$\mathbb{E}[\nu_{.25,.25}(T_i, p)] < \lambda_1 < \lambda_2 < \mathbb{E}[\nu_{.25,.75}(T_i, p)].$$

Observe in Figure 7.5 that the histogram of the time until the next burst of size $\geq .25N$ moves to the right as we increase the size of the burst we are considering. Also, in Figure 7.6 the histogram of the size of the next burst of size $\geq .25N$ also moves to the right in the same fashion supporting our conjectures.

In Figure 7.7 we plot the histogram of the size of a burst and the time until the next medium sized burst for various $p \in (p_{c,1}, p_{c,2})$. In panel (a) we have $N = 10000, E = 6000$, and there appears to be a strong linear relationship between burst size and time until next medium sized burst. In panel (b) we have $N = 1000, E = 1000$ and see this linear relationship is not as strong for smaller p in the critical range. Also the time until the next medium sized burst is much smaller for when the linear relationship is strong. This suggests that the time until this burst increases as function of the size of the burst we are considering for each $p \in (p_{c,1}, p_{c,2})$, and moreover, the rate of this increase is much slower for the excitatory model. This gives support to Conjecture 7.2.2.

In Figure 7.8 we plot the histogram of the size of a burst and the size of the next medium sized burst for various $p \in (p_{c,1}, p_{c,2})$. In panel (a) we have $N = 10000, E = 6000$ and see the cloud of points moves up and to the right as p is increased in a continuous fashion. In panel (b) we have $N = 1000, E = 1000$ and see that the cloud of points does not move in a continuous fashion, but rather there appears to be a sudden onset of larger bursts reflecting the expected behavior of the excitatory model. This suggest that the size of the next medium sized burst increases as a function of the size of the burst we are considering for each $p \in (p_{c,1}, p_{c,2})$. Moreover, for $E/N < 1$ there is a "smooth" transition from medium sized bursts to large bursts not seen for the excitatory model. This gives evidence for Conjecture 7.2.3.

In our hypothesis we also state that after a medium sized burst the system remains near critical. Numerically we see that for medium size bursts of size $\leq .5N$, the system remains close to or above critical, as seen in Figure 7.9 (a), and as we look at larger and larger sized bursts, we move farther away from criticality. In panel (b) we see that for the excitatory model, more neurons are depleted out of states x_{K-2} and x_{K-1} than in panel (a). This suggests the system does not remain critical after medium sized bursts. It would seem

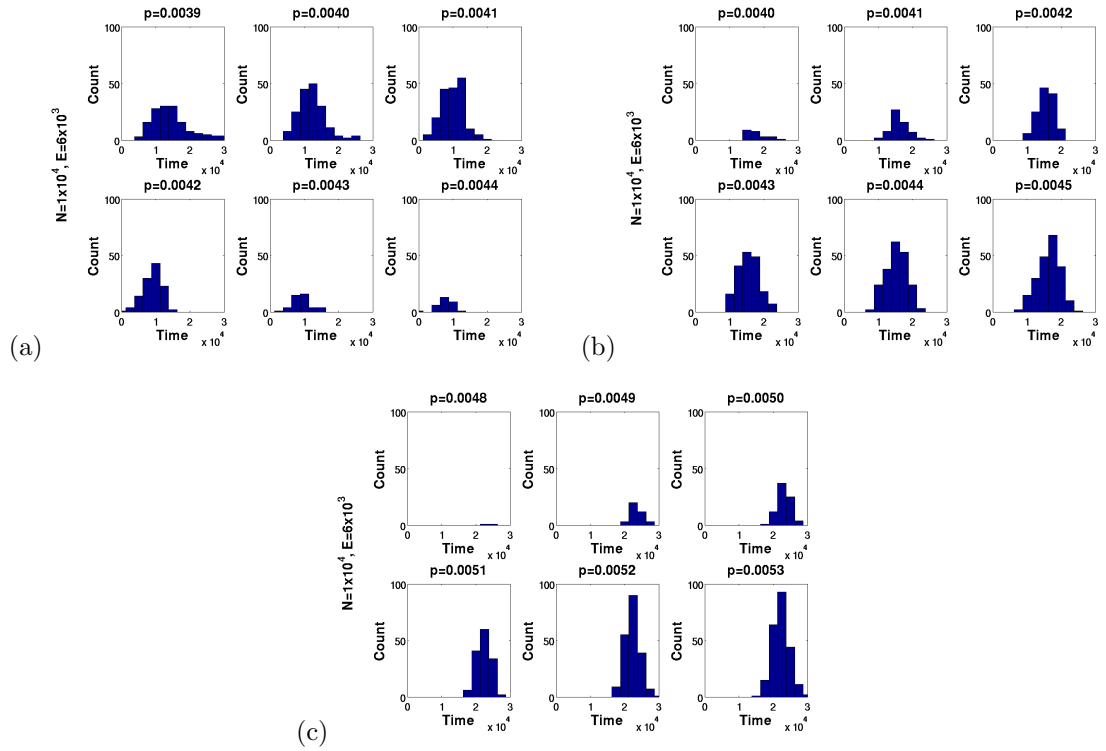


Figure 7.5: Histograms for particular burst sizes of the time until the next medium sized burst for simulations of the inhibitory model with $N = 10000, K = 10, E = 6000$ and for various p. We only consider for (a) burst sizes in the range $[.25N, .5N)$, for (b) burst sizes in the range $[.5N, .75N)$, and for (c) burst sizes in the range $[.75N, N]$.

then in the inhibitory model, that the inhibition is killing off a burst before it can deplete the $(K-2)^{nd}$ and $(K-1)^{st}$ state to a non-critical size. Here critical is when x_{K-1}, the number of excitatory neurons in state $K-1$, is above $1/p$ and when $Rx_{k-2} > x_{K-1}$ ($R = x_{K-1}/(x_{K-1} + y_{K-1})$), which in the mean-field limit would lead to our two conditions for the big-burst domain. (The line $y = 1/p$, and $y = x_{K-1}/R$ is drawn in each of the histograms in Figure 7.9.) This supports Conjecture 7.2.2 that another medium burst will occur shortly after. Also notice in Figure 7.10, that the state of the system after a medium sized burst of size $\leq .5N$ does not look like the state of the system before bursts of larger size. This suggests that if the system does burst soon after, the size of the burst will remain medium which supports Conjecture 7.2.3.

If the above conjectures hold to be true, then it is necessary for non-monotinicity that the expected size of a burst increases as a function of p. That is as p increases, we get larger and larger bursts. Larger bursts have larger gaps in time between their occurrences, so for a given time interval, there will be less large bursts compared to if the bursts were medium sized, see Figure 7.11. Thus there will be a decrease in the number of medium or greater sized bursts as one transitions from medium to large bursts.

The conjectures above holding do not necessarily guarantee non-monotonicity. The difference seen in

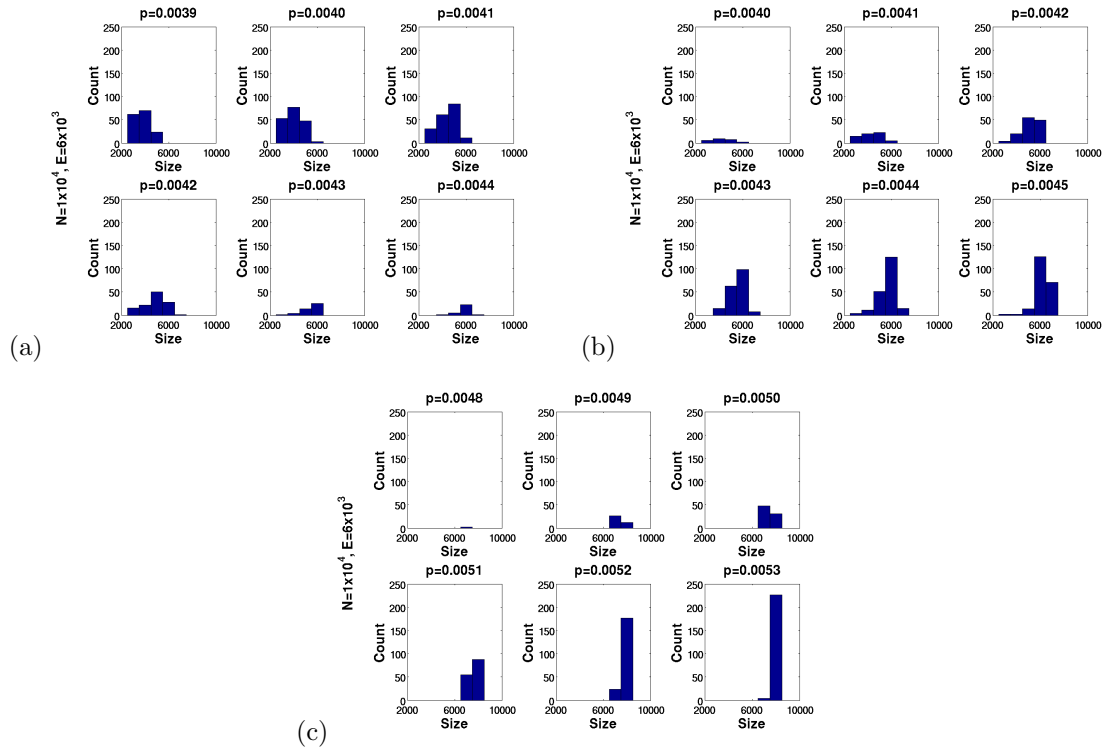
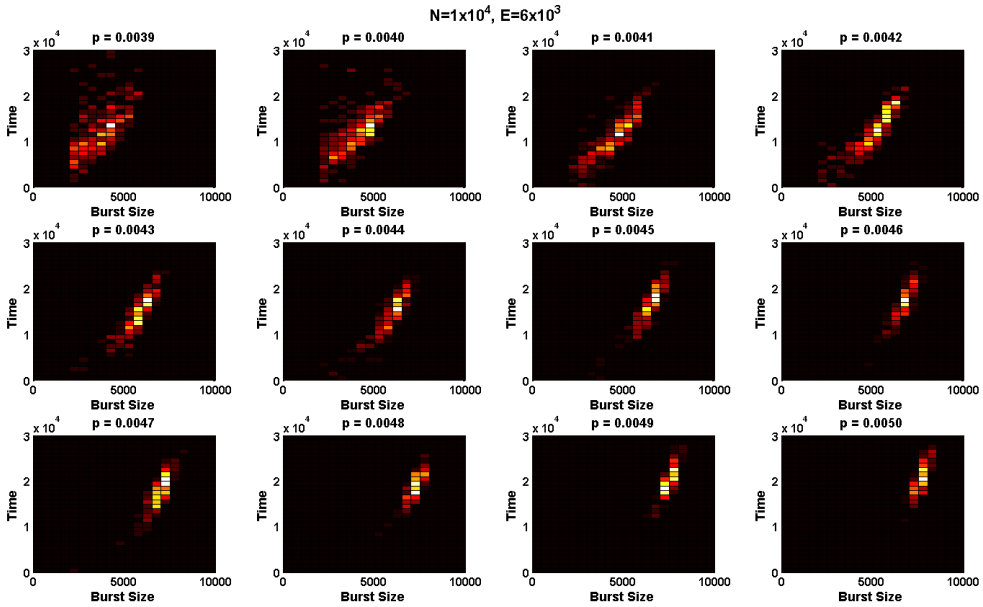
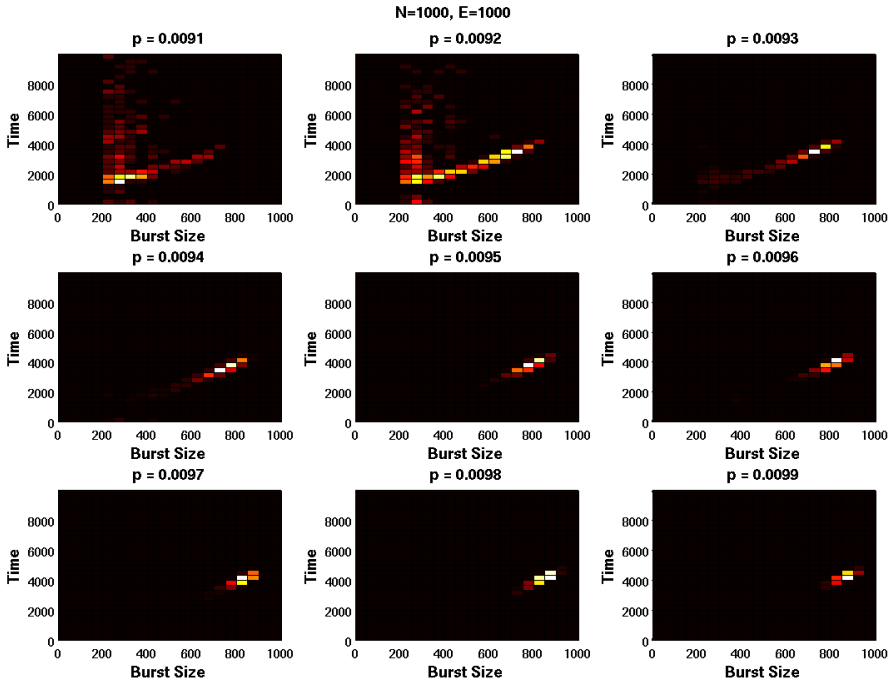


Figure 7.6: Here we have histograms for particular burst sizes of the size of the next medium sized burst for simulations of the inhibitory model with $N = 10000, K = 10, E = 6000$ and for various p. We only consider for (a) burst sizes in the range $[.25N, .5N)$, for (b) burst sizes in the range $[.5N, .75N)$, and for (c) burst sizes in the range $[.75N, .N]$.

the above analysis between the excitatory model and inhibitory model appears to be necessary for the appearance of the non-monotonicity seen in the inhibitory model, but what is sufficient? The non-monotone behavior would appear if the number of medium sized bursts would go down before the number of larger bursts increase. If these were to happen at the same time, then we would not get the behavior. The adding of inhibition to the system is causing a gap between the occurrence of these two events. Future work is planned to further explore these ideas and conjectures.

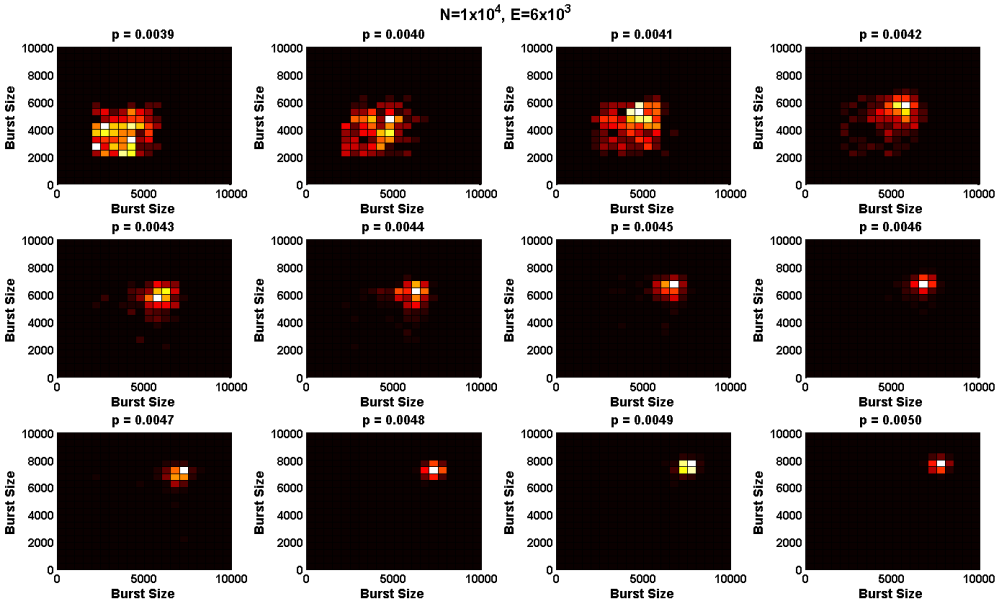


(a)

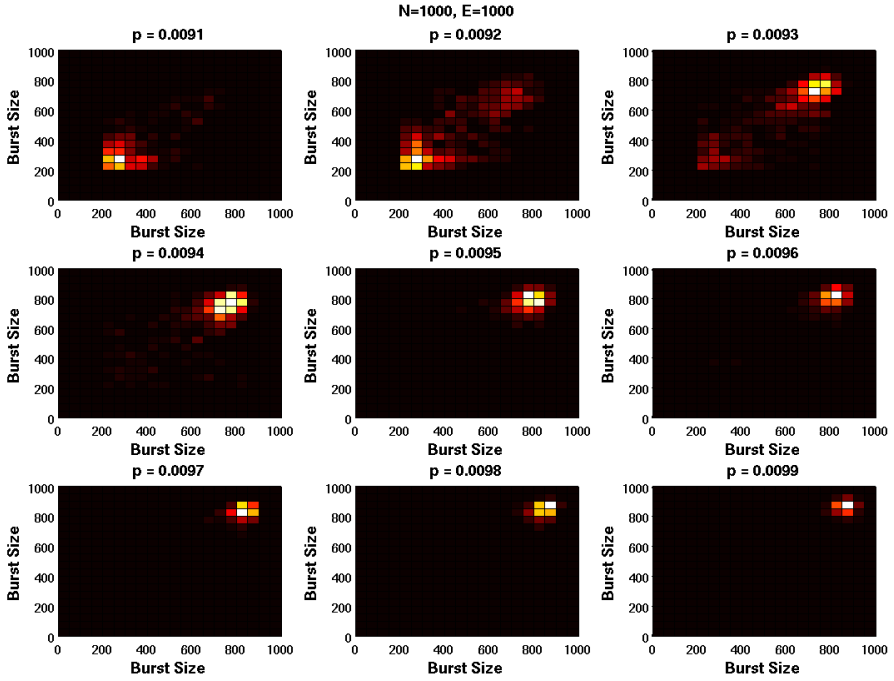


(b)

Figure 7.7: Histograms of the time until a next medium sized burst vs the size of the burst we are considering for simulations of the inhibitory model for various $p \in (p_{c,1}, p_{c,1})$ where we only consider bursts of size greater than $.2N$. (a) $N = 10000, K = 10, E = 6000$, (b) $N = 1000, K = 10, E = 1000$.

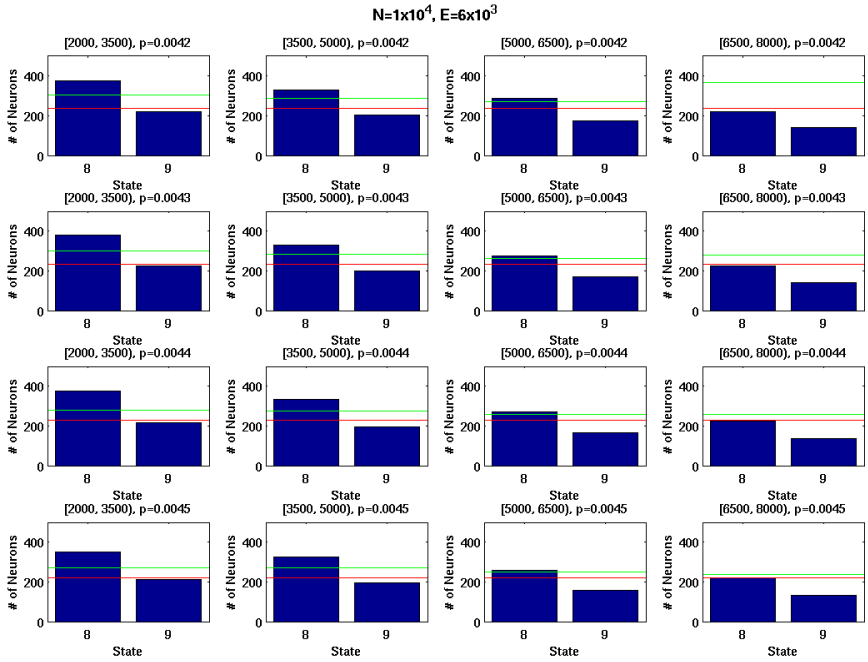


(a)

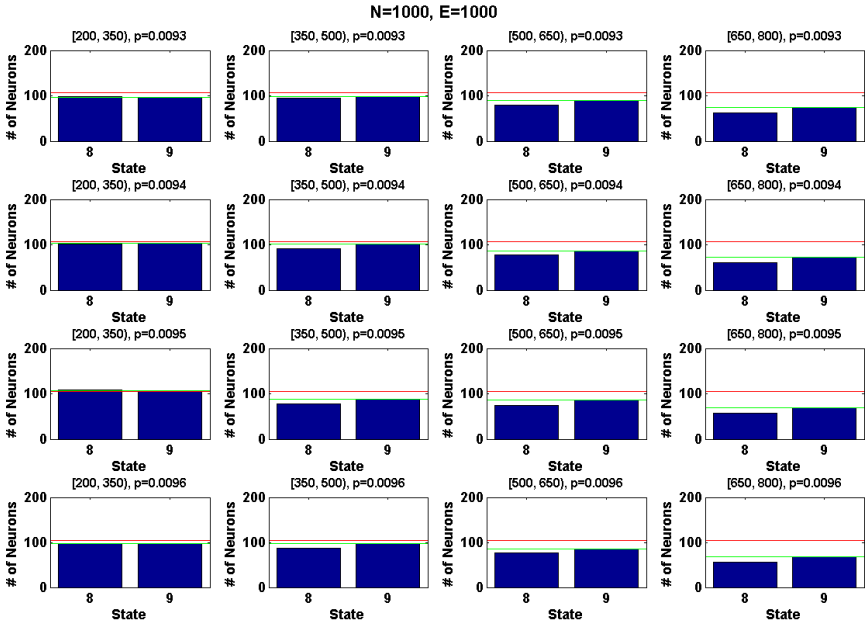


(b)

Figure 7.8: Histograms of the size of the next medium sized burst vs the size of the current burst for simulations of the inhibitory model for various $p \in (p_{c,1}, p_{c,1})$ where we only consider bursts of size greater than $.2N$. (a) $N = 10000, K = 10, E = 6000$, (b) $N = 1000, K = 10, E = 1000$.



(a)



(b)

Figure 7.9: Histograms of the number of neurons in states x_{K-1}, x_{K-2} after a burst of size specified by the interval for simulations of the inhibitory model for various $p \in (p_{c,1}, p_{c,1})$. (a) $N = 10000, K = 10, E = 6000$, (b) $N = 1000, K = 10, E = 1000$. The red line is $y = 1/p$ which is the line x_{K-1} needs to be above for crticality, and the green line is $y = x_{K-1}/R$, $R = x_{K-1}/(x_{K-1} + y_{K-1})$, which is the line x_{K-2} needs to be above for criticality. That is if both $x_{K-1} > 1/p$ and $x_{K-2} > x_{K-1}/R$, then in the mean-field limit, the system will be in the big-burst domain.

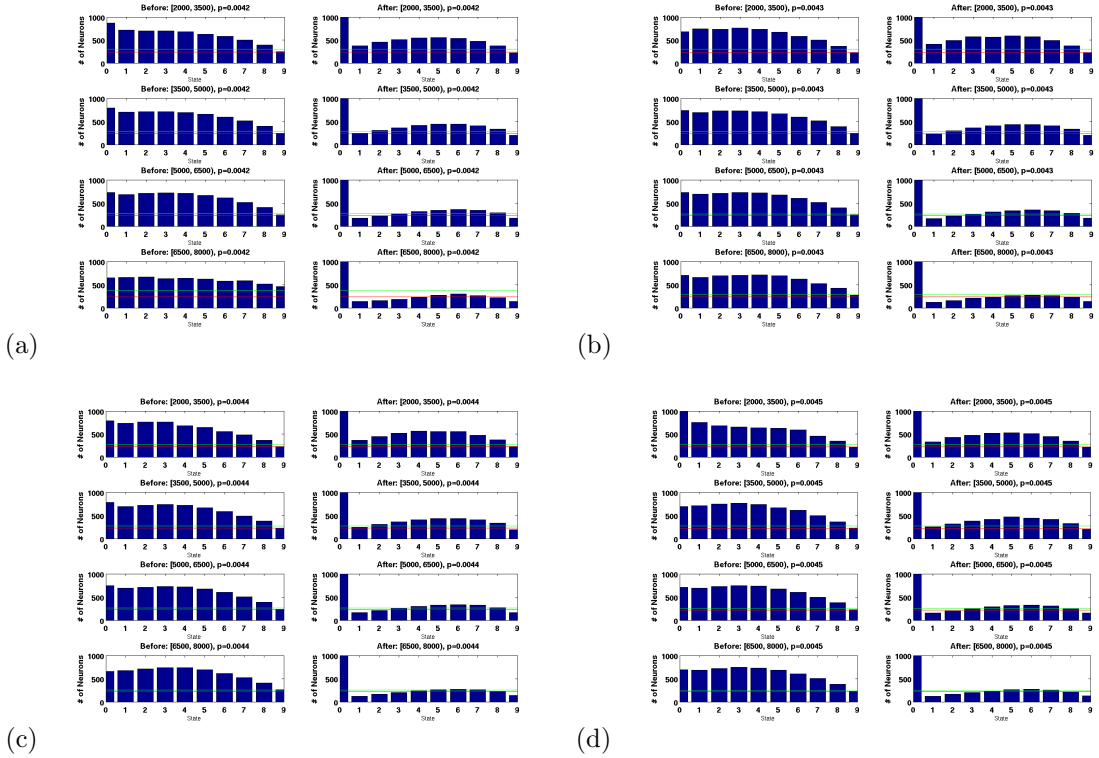


Figure 7.10: Histograms of the distribution of neurons over the excitatory states for before and after a burst of size specified by the interval. This is for simulations of the inhibitory model with $N = 10000, K = 10, E = 6000$ and for various p. The red line is $y = 1/p$ which is the line x_{K-1} needs to be above for crticality, and the green line is $y = x_{K-1}/R$, $R = x_{K-1}/(x_{K-1} + y_{K-1})$.

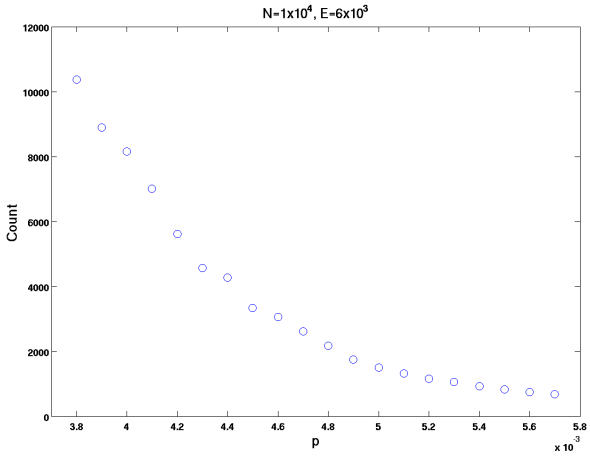


Figure 7.11: Plot for simulations of the inhibitory model with $N = 10000, K = 10, E = 6000$. We fix a time interval and plot for various p the number of bursts of size greater than $.2N$

Chapter 8

Conclusions

There are several open questions unresolved for this model. We have shown for $e < 1$, $\beta_{c,2} = \infty$. A next step would be to try and characterize the stable manifold for the fixed-point of the mean-field system and determine how it changes as a function of e and β. Also we see numerically that $\beta_{c,1}$ is finite for e large enough. Can we determine analytically $\beta_{c,1}$ for a given e?

It is still unclear from our analysis how exactly the inhibition is causing the non-monotonicity seen in the stochastic model. Numerically, it is clear that the conjectures in Section 7.2 are necessary, but what is sufficient? A more indepth investigation of the state of the system before and after a burst and exploring how it depends on E may lead to an answer.

In [3] DeVille et al. studied the effects of topology on the excitatory model. They found that uniform and small-world graphs behave quite similarly to all-to-all networks and their fine structure does not matter a great deal. However, scale-free networks exhibit a rich behavior and do not behave like all-to-all networks, and the fine details of these scale-free networks are quite important to the dynamics. It would be interesting to do the same type of analysis with the inhibitory model.

Changing the topology of the network in the inhibitory model adds another level of complexity to the model and would be moving us closer to a real-life model of a true neuronal network. Hopefully the ideas explored in the analysis of the model in this thesis can be extended and used to explain the rich behavior seen in more complicated networks that are closer models to real-life phenomena.

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