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Spatio-Temporal Feedback in Stochastic Neural Networks

By
Connie Sutherland

Thesis submitted to
the Faculty of Graduate and Postdoctoral Studies
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Abstract

The mechanisms by which groups of neurons interact is an important facet to understanding how the brain functions. Here we study stochastic neural networks with delayed feedback. The first part of our study looks at how feedback and noise affect the mean firing rate of the network. Secondly we look at how the spatial profile of the feedback affects the behavior of the network.

Our numerical and theoretical results show that negative (inhibitory) feedback linearizes the frequency vs input current (f-I) curve via the divisive gain effect it has on the network. The interaction of the inhibitory feedback and the input bias is what produces the divisive decrease in the slope (known as the gain) of the f-I curve. Our work predicts that an increase in noise is required along with increase in inhibitory feedback to attain a divisive and subtractive shift of the gain as seen in experiments [1].

Our results also show that, although the spatial profile of the feedback does not effect the mean activity of the network, it does influence the overall dynamics of the network. Local feedback generates a network oscillation, which is more robust against disruption by noise or uncorrelated input or

network heterogeneity, than that for the global feedback (all-to-all coupling) case. For example uncorrelated input completely disrupts the network oscillation generated by global feedback, but only diminishes the network oscillation due to local feedback. This is characterized by 1st and 2nd order spike train statistics. Further, our theory agrees well with numerical simulations of network dynamics.

Résumé

Les mécanismes par lesquels les groupes de neurones interagissent sont un aspect important dans la compréhension du fonctionnement du cerveau. Dans cet essai, nous étudions les réseaux neuronaux avec délai rétroactif. La première partie de cette étude se concentre sur comment la rétroaction et le bruit affectent le taux de décharge moyen du réseau. Deuxièmement, nous nous penchons sur l'effet qu'a le profil spatial de la rétroaction sur le comportement général du réseau.

Les résultats numériques et théoriques montrent que la rétroaction inhibitrice linéarise la courbe de la fréquence en fonction du courant d'entrée ($f-I$) via l'effet qu'a le gain diviseur sur le réseau. L'enchevêtrement de la rétroaction inhibitrice et la perturbation du signal d'entrée sont les causes de la réduction de la pente (nommée gain) de la courbe $f-I$. Un bruit additionnel est requis, de même qu'une rétroaction inhibitrice, afin de parvenir à un décalage du gain, tel qu'observé dans diverses expériences [1].

Nos résultats montrent aussi que même si le profil spatial de la rétroaction n'affecte pas l'activité moyenne du réseau, elle en influence la dynamique globale. Comparé à la rétroaction globale, la rétroaction locale génère une

oscillation qui est plus robuste face à la disruption du bruit ou encore les hétérogénéités présente dans le réseau. En guise d' exemple, un signal d' entrée non corrélé anéantit complètement l' oscillation engendrée par la rétroaction globale, mais ne fait que diminuer cette oscillation lorsque celle-ci est causée par une rétroaction locale. Ceci est caractérisé par la statistique des séries de potentiels d'action du premier et second ordre. Aussi, la théorie développée correspond bien aux résultats numériques.

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Glossary

Terminology:

Bias	Average input bias to the network
Activity	Mean firing rate of the network
Gain	Slope of the f-I curve

Acronyms:

ELL	Electrosensory Lateral Line Lobe
LIF	Leaky Integrate and Fire Neuron Model
ISI	interspike interval
PCI	Percentage Correlated Input
GCI	Gaussian Correlated Input

Symbols:

v	Membrane potential
v_{th}	Threshold potential
v_r	Reset potential
τ_m	Membrane time constant
τ_R	Refractory period
$I(t)$	Input to the network
$I_{ext}(t)$	External input to the network
μ	Average input bias to the network
$\eta(t)$	Noise
D_{int}	Strength of internal noise
D	Strength of internal + external noise
σ	External noise intensity
c	Correlation of PCI
$C(\frac{x-x'}{\lambda})$	Spatial correlation of GCI
λ	Correlation length of GCI
$\xi(t)$	Gaussian white noise
$x(t)$	Spike train
$\delta(t)$	Dirac's delta function
x	Space

N	Number of neurons in the network
$f_{i,j}(t)$	Connectivity function of the network
τ_d	Time delay of feedback
g	Feedback strength
$K_{\tau_d}(t)$	Feedback kernel (alpha function)
α	Spread of feedback kernel
$p(i - j)$	Profile of feedback (Gaussian)
σ_g	Spread of feedback
r	Mean firing rate of the network
$S(\omega)$	Power Spectral Density
$S_0(\omega)$	Unperturbed Power Spectral Density
$A(\omega)$	Linear response function
$\mathcal{D}_a(z)$	Parabolic cylinder function
$\Gamma(f_2 - f_1)$	Total Power over a frequency range in the Power Spectrum

Chapter 1

Introduction

On a macroscopic level computers function the same way the human brain does. Input from the outside world is attained through peripheral devices: keyboard, mouse, eyes, ears, nose, tongue and skin. The information is then processed in the central processing unit or brain and then the system responds in terms of output via the screen, printer, motor neurons, and vocal cords. However, the processing on a microscopic level is much more complex in a human brain than the binary processing of a computer, unless the electric signal with which brain cells communicate does represent a one or a zero. The ambiguity of the computational intricacies of the brain make it a prime field of interest in scientific research. There are many unanswered

questions about how the brain processes and stores information. A key component to answering these questions is to understand how brain cells interact. Modelling biological neural networks is one way to investigate how neurons communicate. When modelling neural networks it is important to encompass the pertinent features of real biological neural networks.

1.1 Neural Networks

Two features we focus on, which are commonly found in biological neural networks, are feedback and noise.

Feedback is ubiquitous in the brain and thus much effort has been devoted to modelling neural networks with feedback. Many models also take into account the finite processing and transmission time of the return signal, by including a delay of the feedback in the model. Most studies focus on global feedback, otherwise known as all-to-all coupling ([2], [3], [4] and subsequent references therein), but a few have focused on more localized feedback [5], [6], [7], [8].

Noise is another common concept in neural network research. It is often included in modelling to mimic the myriad of inputs that come from different

areas of the brain, as well as physical fluctuations in the stimuli that drive sensory neurons. It can also represent the efficiency of signal transmission between neurons, and the randomness of activation of ion channels in individual neurons (neuron conductance) [9]. Stochastics are commonly studied not only in neural networks, but many other areas of research as well (for a review see [10], [11]).

Of interest is how feedback and noise effect the dynamics of neural networks.

1.2 Feedback Effects on Neural Networks

Two important aspects of network dynamics we look at are f-I curves and network oscillations.

One way to look at information processing in neurons is to describe the output of the neuron as a function of the input to the neuron. The f-I curve is a plot of the average firing rate of the network (or neuron) f as a function of the input current I , which increases as the input current increases (see Chapter 4). In neuroscience the f-I curve is useful to study the range of response of a network (or neuron) given a range of input signal (“stimulus”) values.

The gain, which is the slope of the f-I curve, indicates the responsiveness of the neuron (or network). Most neurons adapt to input by altering their f-I curves; this is called gain modulation. Gain modulation has been shown to be an important computational tool in the central nervous system of various animals ([12], [13] and subsequent references therein). It is well known that the presence of feedback OR noise in a neural network can linearize its highly nonlinear f-I curve, which is one form of gain modulation. However, the combination of feedback AND noise studied in this thesis is not well understood. The linearization of f-I curves is also useful for neural modelers as it allows the use of linear response theory, which requires a linear transfer function in order to accurately predict the dynamics of the network response to stimuli.

Another way to look at information processing is to look at dynamics across the network. Collective oscillations in the firing pattern of groups of neurons are commonly found in many parts of the brain and may be a signalling mechanism to/from higher brain centres (for example [14], [15], [4] and [16]). There is evidence that oscillations can be important for biasing input selection, altering the connection strength between neurons and temporarily linking neurons to assemblies [15]. Feedback from higher brain centres is one way oscillations can be produced in a neural network [17], [18],

[4].

1.3 Scope of Thesis

The general focus of this thesis is on delayed feedback in stochastic neural networks. Although much work has been done on feedback in neural networks, a comparison of the precise differences of network dynamics due to local and global delayed feedback has not been addressed. We use simulation and theory to look at how spatially localized delayed feedback affects the dynamics of a stochastic neural network in comparison with globally delayed feedback. As a convenient initial investigation we look at gain modulation in a network with globally delayed feedback.

1.4 Biological Motivation

Studying neural networks theoretically and computationally allows us to look at more complex processing occurring in networks of brain cells, but it is not trivial to precisely model the entire detailed physiology of a nervous system. Thus, many studies consider a finite group of ideal neurons with specific connections unique to the architecture of a particular part of the nervous system

of interest. The specific biological motivation for the network studied here is the weakly electric fish known as the brown ghost knife fish (*Apteronotus leptorhynchus*). It is one of many animals that have stochastic neural networks with delayed feedback as part of their nervous system. The weakly electric fish is ideal for studying the role of noise and feedback in sensory information processing since it has a far simpler neural network than many mammals commonly used in neuroscience studies, such as rats, cats and monkeys. The particular biological network of interest in the weakly electric fish is the electrosensory lateral line lobe (ELL). The ELL is the second neural processing layer of the weakly electric fish. It receives electrosensory inputs from receptor cells in the skin and sends its output (“feeds forward”) to various higher brain centres, which in turn feedback to the ELL via direct and indirect pathways. The higher brain centre known as the Np feeds directly back to the ELL via two different pathways, one which provides spatially diffuse feedback to the ELL, and another which provides spatially localized feedback (for anatomical reviews see [19], [20]). Previous theoretical studies [18], [21] modelled the spatially diffuse feedback pathway using global delayed feedback in a stochastic neural network. It was found that network oscillations in such a global feedback network are important to the weakly

electric fish to correctly detect stimuli. In this study we look at how local delayed feedback affects oscillations in the network.

1.5 Layout of Thesis

The layout of the thesis is as follows. Relevant background information on neural networks and mathematical tools used to study them are presented in Chapter 2. Chapter 3 details the model used in simulations. In Chapter 4 we discuss how noise and feedback linearize the f-I curve of a neural network. Chapter 5 compares the effect of spatially diffuse (global) feedback and spatially focused (local) feedback on the output of a stochastic neural network with respect to two differently spatially correlated inputs outlined in Chapter 3. The first spatial correlation type has been used in previous studies with global feedback and is used here for continuity. The other is a more physically relevant form of spatial correlation. Chapter 6 analyses further the differences found between global and local feedback, with the two different types of correlated input, by focussing on the individual effects of noise and regime (superthreshold or subthreshold) of the individual neurons. In the final chapter we summarize our results and indicate possible further

investigation into neural network information processing.

Chapter 2

Background

To understand the motivation for modelling neural networks, it is instructive to know some of the biology of real neural networks and how models approximate this biology. This background section gives a brief overview of biological neurons, the leaky integrate-and-fire (LIF) neuron model, leaky integrate-and-fire neural network models, and measures that characterize the behaviour of such models.

2.1 Neurons

Neurons are the main processing subunits of the brain. These wonderfully complex cells form numerous connections with each other, allowing us to

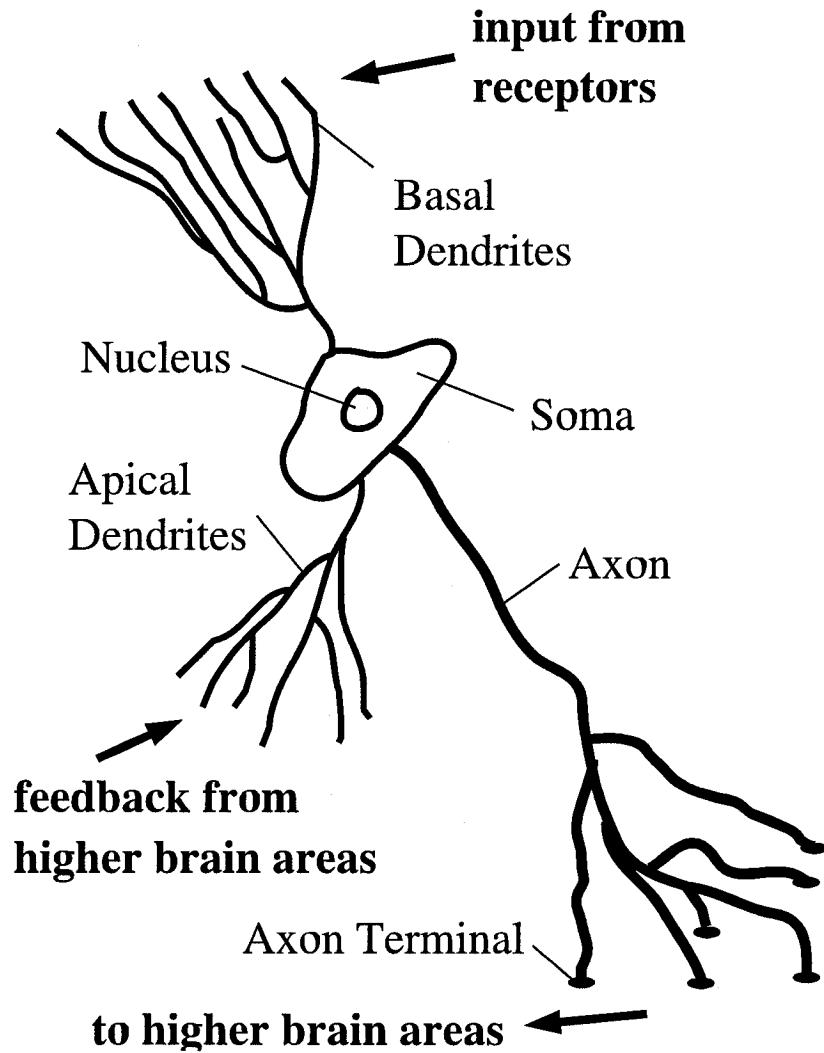


Figure 2.1: Neuron schematic of a typical pyramidal cell found in the electrosensory lateral line lobe (ELL) of the weakly electric fish.

process complex input coming from our surrounding environment and form appropriate responses. These cells have an interior of mainly potassium ions, which create approximately a -65mV potential across the cell membrane [9] (the interior being negative with respect to the exterior). While neurons vary widely in shape and size most contain three common structural components: dendrites, soma (or cell body), and axons (Figure 2.1). Dendrites branch off the soma in a bush-like fashion and receive most of the input coming from other cells. This input is then transferred to the soma, which is the main processing centre of the neuron. The soma receives information from the dendrites as well as direct inputs from other neurons. These inputs come in the form of electrical signals called post-synaptic potentials and act to either depolarize the cell body (i.e. raise the potential across the membrane of the soma towards more positive values) or hyperpolarize it (i.e. make it more negative). When input to the soma creates a depolarization of the membrane potential beyond threshold potential (generally $20 - 30\text{mV}$ above resting membrane potential [9]), a large and brief electric signal is generated at the base of the axon where it connects to the soma. This electric pulse, called an action potential, propagates along the axon in the form of a soliton wave towards synapses that innervate other neurons. The axon branches off

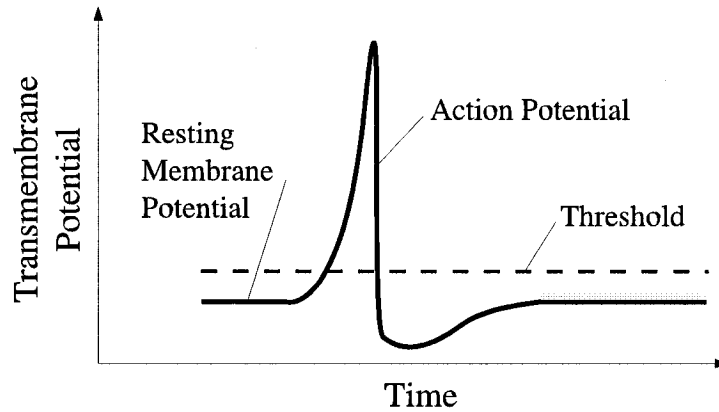


Figure 2.2: Action Potential Schematic: If the input causes the membrane potential to increase (depolarize) past some threshold, an excursion of the membrane potential occurs. Then the voltage decreases again, re-polarizing past the resting membrane potential, becoming hyperpolarized. The voltage slowly rises again to the resting membrane potential and then the process can repeat.

of the soma in a tree-like fashion into multiple end terminals, which synapse onto target neurons. Figure 2.1 shows a schematic diagram of a typical pyramidal neuron.

Action potentials have a typical amplitude of 100 mV and duration of 1-2 ms [9] (schematic shown in Figure 2.2) and do not vary much in shape or duration. They consist of a large excursion in membrane potential (or

depolarization) and then a quick decrease in membrane potential, dropping below the resting membrane potential. The dip below resting membrane potential is called an after hyperpolarization. During the period when the cell is hyperpolarized, it takes a stronger input to create another action potential and thus the cell is less likely to fire. The rigidity of the action potential suggests that it carries little information to the next processing layer; rather, the timing of the action potential event itself is thought to be the important feature for communication between cells. Simple neuron models such as the Leaky Integrate-and-Fire (LIF) neuron model, which only focus on the timing of the action potentials and not their shape or duration, are based on this assumption.

2.2 Deterministic LIF Neuron Model

The LIF neuron model is a simplistic representation of a neuron, which reduces it to a soma with no spatial extent. Superthreshold dynamics are ignored and the subthreshold response of the soma to input is modelled by a RC circuit (Figure 2.3).

$I(t)$ represents the input current coming into the soma. The membrane in fact acts as a capacitor in parallel with a resistor, allowing charge to build

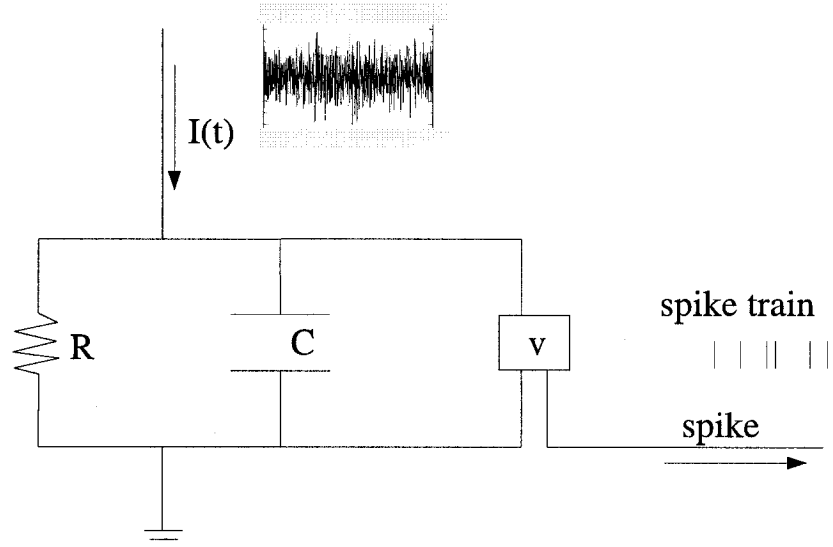


Figure 2.3: A circuit diagram representation of the LIF neuron model.

up inside the soma as input comes in. The resistor can be thought of as a leak channel out of the soma, so that only some of the incoming current will contribute to the potential across the membrane. When the potential across the capacitor reaches the threshold membrane potential, v_{th} , a spike is generated representing the action potential as Dirac's delta function at the time of threshold crossing. The membrane potential is reset to a membrane potential v_r , and the process repeats.

The LIF model can be mathematically expressed by Equation 2.1, which can be derived from the circuit diagram in Figure 2.3 using simple circuit

theory:

$$\tau_m \frac{dv(t)}{dt} = -v(t) + RI(t). \quad (2.1)$$

In terms of the LIF model $\tau_m = RC$ represents the membrane time constant of the soma, v represents the potential across the membrane, and R represents the resistance of the membrane to incoming current I or the portion of the input current that leaks out of the soma.

Equation 2.1 can be converted to standard form by changing the voltage variable to a dimensionless variable $v' = \frac{v-v_r}{v_{th}-v_r}$, time to units of the membrane time constant $t' = \frac{t}{\tau_m}$ and without loss of generality set $R = 1$ [22]. Removing the prime notation Equation 2.1 becomes

$$\frac{dv}{dt} = -v + I(t) \quad (2.2)$$

where we choose $v_r = 0 < v < v_{th} = 1$ and $I(t)$ differs only by a scale factor from Equation 2.1. Once v reaches v_{th} the potential is reset to v_r and the integration begins again. From this model one obtains a series of spikes for the neuron, called a spike train:

$$x(t) = \sum_i^m \delta(t - t_i) \quad (2.3)$$

where $\delta()$ is Dirac's delta function and $t_i, i = (0 \dots m)$ are the spike times generated by the model.

In the special case where the input is constant, $I(t) = I_0$, and the initial condition for the membrane potential is $v(0) = v_0 = 0$, the solution of Equation 2.2 is $v = I_0(1 - e^{-t})$. For $I_0 < 1$, $v(t)$ never reaches v_{th} and the neuron does not fire; the neuron is said to be operating in the *subthreshold* regime. For $I_0 > 1$, $v(t)$ does reach v_{th} in some finite period T and the neuron is said to be operating in the *superthreshold* regime. In such a deterministic superthreshold neuron the firing rate can be easily calculated by setting $t = T$, where $v(T) = v_{th}$, and solving for the period, T [9]:

$$T = \ln \left[\frac{I_0}{I_0 - v_{th}} \right]. \quad (2.4)$$

The firing rate is then just $r = \frac{1}{T}$.

The LIF model we have developed so far ignores not only the duration of the action potential but also the after-hyperpolarization of the neuron. To amend this an absolute refractory period, i.e. an interval of time for which the neuron cannot produce another spike, can be introduced immediately after a spike is generated. The firing rate then becomes

$$r = \left\{ \tau_R + \ln \left[\frac{I}{I - v_{th}} \right] \right\}^{-1} \quad (2.5)$$

where τ_R represents the refractory period. Figure 2.4 shows a sample evolution of the voltage as a function of time and the corresponding spike train

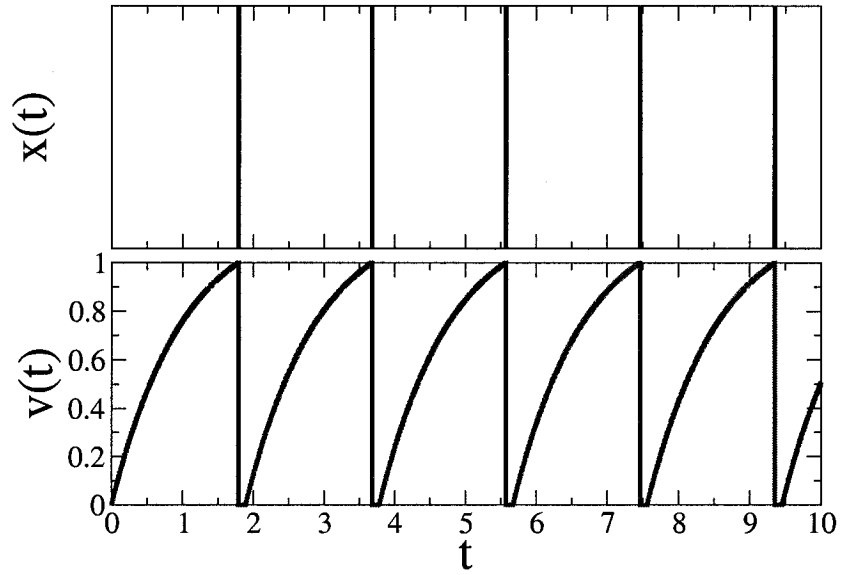


Figure 2.4: The evolution of the voltage as a function of time for a deterministic LIF neuron model (bottom) is shown along with the spike train generated by the same voltage trace (top). The y-axis scale on the top plot is absent, since these lines are supposed to represent a series of delta functions.

for such a deterministic network. The LIF model can be extended to a more realistic type of neuron that contains internal noise and/or a time-dependent input.

2.3 Stochastic LIF Neuron Model

The addition of noise makes a neuron model more realistic, as it mimics fluctuations in a real neuron. These fluctuations arise from various sources, the main one being the continuous arrival of small synaptic inputs.

Adding internal noise, the deterministic LIF neuron model, Equation 2.2, can be extended to a stochastic LIF neuron model:

$$\frac{dv}{dt} = -v + \eta + I. \quad (2.6)$$

where η , which is a function of t , represents additive noise. This is known as a Langevin equation, which has a more general form [23]:

$$\frac{dv}{dt} = l(v, t) + m(v, t)\eta(t) \quad (2.7)$$

where $l(v, t)$ and $m(v, t)$ are known functions. Langevin assumed that random motion could be described by an ordinary differential equation with a rapidly and irregularly fluctuating force (the noise term in this case, $\eta(t)$, which will later be identified with Gaussian white noise).

The noise term is characterized by its distribution and autocorrelation function. The distribution is the probability density function, p , of the stochastic process $\eta(t)$. The autocorrelation of the stochastic process is defined mathematically as

$$E \{ \eta(t) \eta(t') \} = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \eta(t) \eta(t') p(\eta(t), \eta(t')) d\eta(t) d\eta(t'). \quad (2.8)$$

For a stationary stochastic process we can set $t' = t + \tau$ and the autocorrelation becomes

$$E \{ \eta(t) \eta(t') \} = E \{ \eta(t) \eta(t + \tau) \} \quad (2.9)$$

and can be numerically estimated by taking the time average:

$$\langle \eta(t) \eta(t') \rangle = \lim_{T \rightarrow \infty} \frac{1}{T} \int_{-T}^T \eta(t) \eta(t + \tau) d\tau \quad (2.10)$$

where $\langle \rangle$ represents an ensemble average of realizations of the stochastic process, due to ergodicity.

$\eta(t)$ is often modelled as Gaussian white noise, which is formally defined as the temporal derivative of the Wiener process, $W(t)$, [24]:

$$\eta = \frac{dW}{dt} \quad (2.11)$$

The Wiener process, $W(t)$, describes Brownian motion, which is historically the random motion of pollen particles suspended in a fluid. It is a Gaussian

random process with a Gaussian probability distribution of zero mean, and autocorrelation:

$$\langle W(t)W(t') \rangle = 2D_{int} \min(t, t') \quad (2.12)$$

where D_{int} controls the rate of increase of the variance of the process, which represents the diffusion coefficient in the case of Brownian motion. The Wiener process itself is not stationary, but its increments, ΔW , are. The increments of the Wiener process form a stationary Gaussian random process with zero mean and autocorrelation [24]:

$$\langle (W(t) - W(t'))^2 \rangle = 2D_{int}(t - t') \quad (2.13)$$

The derivative of the Wiener process is also a Gaussian random process with zero mean and autocorrelation:

$$\langle (\eta(t)\eta(t')) \rangle = 2D_{int}\delta(t - t') \quad (2.14)$$

where in terms of Gaussian white noise D_{int} can be considered the strength or “intensity” of the noise.

It is called white noise because it contains equal power at all frequencies, like white light. Figure 2.5 shows a sample of simulated Gaussian white noise, the distribution of the generated noise, and its power spectrum. The variance of the distribution in Figure 2.5 is one, but these numbers are scaled

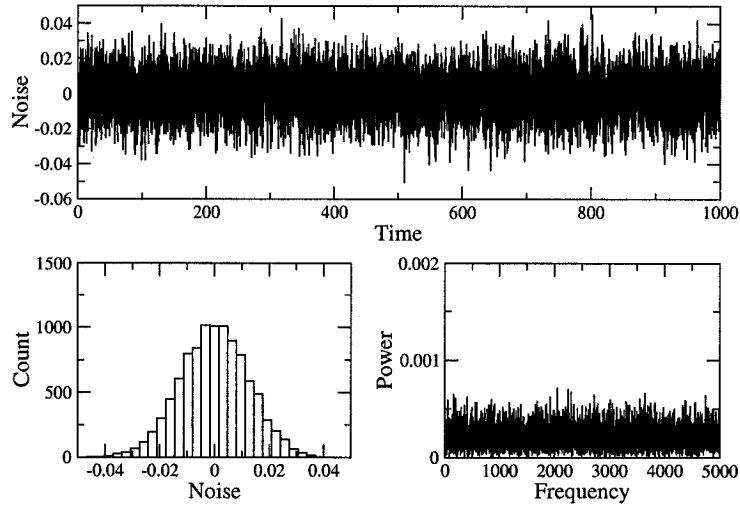


Figure 2.5: Simulated Gaussian White Noise (top). The histogram of the simulated data (bottom left) forms a Gaussian distribution and the power spectrum (bottom right) is flat like that of white light.

by $\sqrt{2D_{int}\Delta t}$ when integrating to create Gaussian white noise of intensity D_{int} and discrete time step Δt . Gaussian white noise is an approximation of real noise, and has simple statistical properties, that make it ideal for analytical study [24]. In particular it allows an analytical form for the mean firing rate of a neuron, which is discussed below.

The firing rate for a stochastic neuron model is slightly more complicated to calculate, since with the addition of noise $v(t)$ is now a stochastic process. For a stochastic process there is no mathematical way to determine the

exact value of the membrane potential, but only a probability of it having a given value in some interval. Thus, the state of the system is described by a probability density function, $p(v, t)$, which in the diffusion limit evolves according to the Fokker-Planck Equation. The Fokker-Planck Equation has the form [23]

$$\frac{\partial p(v, t)}{\partial t} = -\frac{\partial}{\partial v} [l(v, t)p(v, t)] + \frac{\partial^2}{\partial v^2} \left[\frac{m(v, t)^2}{2} p(v, t) \right] \quad (2.15)$$

where $l(v, t)$ represents a drift coefficient and $m(v, t)$ represents a diffusion coefficient (These are the same functions as in Equation 2.7). The Fokker-Planck Equation describes the random process, $v(t)$, which is continuous (In our case $v(t)$ is continuous between v_r and v_{th}). The Langevin Equation is equivalent to the Fokker-Planck Equation in the description of $v(t)$ and can be used to determine the coefficients $l(v, t)$ and $m(v, t)$ [24]. For the stochastic LIF neuron model, Equation 2.6, the Fokker-Planck equation is [9]

$$\frac{\partial p(v, t)}{\partial t} = -\frac{\partial}{\partial v} [(I - v)p(v, t)] + D \frac{\partial^2}{\partial v^2} p(v, t) \quad (2.16)$$

with boundary condition

$$p(v_{th}, t) = 0 \quad (2.17)$$

and initial condition

$$p(v, 0) = \delta(v - v_r). \quad (2.18)$$

The first term in Equation 2.16 is a drift term and the second term is a diffusion term. It should be noted that v_r and v_{th} are used in the boundary conditions here merely for clarification purposes and that the above equation actually requires $v_r = 0$ and $v_{th} = 1$.

The average firing rate of the neuron can be calculated [9] by using the Fokker-Planck equation to solve for the density, p , and the mean first passage time given by [23]

$$\langle T \rangle = - \int_0^\infty t \frac{\partial}{\partial t} P(v_r, t) dt \quad (2.19)$$

where

$$P(v_r, t) = \int_{-\infty}^{v_{th}} p(v, t | v_r, 0) dv \quad (2.20)$$

is the probability that $T \geq t$ and $p(v, t | v_r, 0)$ is the conditional probability density function. The mean firing rate is the refractory period plus the solution to the mean first passage time problem [9]:

$$r = \left[\tau_R + \sqrt{\pi} \int_b^a e^{\mu'^2} \text{erfc}(\mu') d\mu' \right]^{-1} \quad (2.21)$$

where

$$a = \frac{\mu - v_{th}}{\sqrt{2D_{int}}} \quad (2.22)$$

and

$$b = \frac{\mu - v_r}{\sqrt{2D_{int}}}. \quad (2.23)$$

Here μ represents a constant input I_0 , D_{int} is the strength of the internal noise and $\text{erfc}(\mu')$ is the complementary error function. A derivation of this equation, known as the Siegert formula, is beyond the scope of this thesis, but can be found in Siegert 1951, Ricciardi 1977, and a book by Tuckwell 1988.

The average firing rate can also be estimated using simulations. The voltage trajectory will evolve differently each time the voltage is reset to v_r due to the noise in the system as shown in Figure 2.6. Each different voltage path traced from the same initial condition is called a realization of the membrane potential. To estimate the firing rate of the neuron, the period, also known as the interspike interval (ISI), of the neuron is averaged over many realizations:

$$r = \frac{1}{\langle T \rangle}. \quad (2.24)$$

There are many other neuron models, which are more complex and model more precisely neuronal dynamics, such as the Hodgkin-Huxley model, which includes voltage gated conductances, and various compartmental models, which include the spatial extent of the neuron [9]. Two other simple neuron models similar to the LIF model are the Spike Response Model and the Quadratic Leaky Integrate and Fire Model [9]. These can also be used in studying neural networks, but the former also lacks an accurate description of

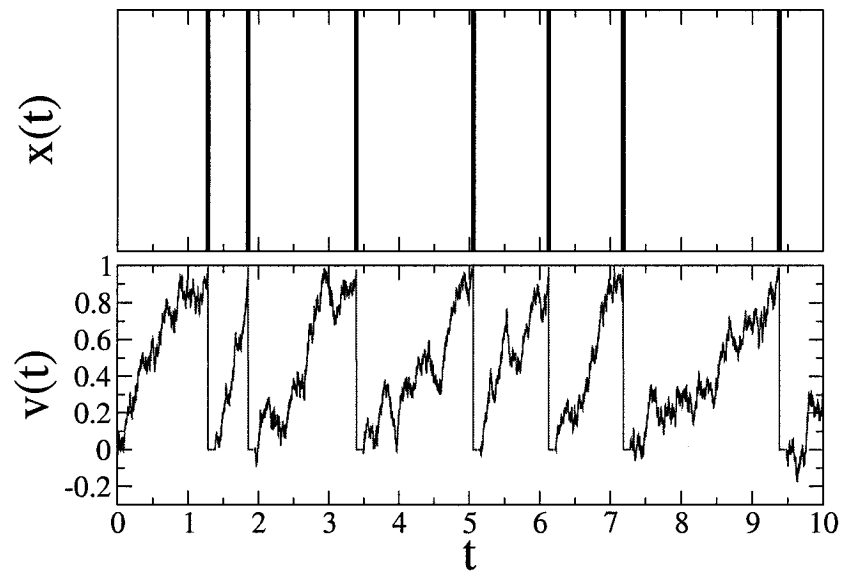


Figure 2.6: The evolution of the voltage as a function of time for a stochastic LIF neuron model (bottom) is shown. The spike train generated by the same voltage trace can be seen above it. Again the y-axis scale on the top plot is absent, since these lines are supposed to represent a series of delta functions.

the effect of noise, and the latter is less analytically tractable than the LIF neuron model, two factors that become important when considering large stochastic neural networks.

2.4 LIF Network Models

The simplicity of the LIF model makes it ideal for network modelling. Not only is it more analytically tractable than most models, it also has a simple integration algorithm, which is ideal when computational time constraints are present. For a homogeneous network of N independent, deterministic LIF neurons, the dynamics of the network reduces to

$$\dot{v}_i = -v_i + I_i(t) \quad (2.25)$$

where the subscript i represents the i^{th} neuron in the network ($i = 1 \dots N$). In the case of a network, $I_i(t)$ includes both external input, $I_{ext,i}(t)$, as well as input from other areas of the network, $f_{i,j}(t)$, where the j subscript represents input from the j^{th} neuron to the i^{th} neuron. Hence $I_i(t)$ becomes

$$I_i(t) = \mu + I_{ext,i}(t) + \sum_{j=1}^N f_{i,j}(t). \quad (2.26)$$

Here μ represents the time independent part of the external input (referred to in the rest of the thesis as the input bias), which is common to all neurons

in the network, and $I_{ext,i}(t)$ represents only the time dependent part of the input (i.e. the average of $I_{ext,i}(t) = 0$).

This model can also be extended to model a stochastic neural network by including internal noise, $\eta(t)$. Equation 2.25 becomes

$$\dot{v}_i = -v_i + \eta_i(t) + \mu + I_{ext,i}(t) + \sum_{j=1}^N f_{i,j}(t). \quad (2.27)$$

The noise sources, η_i , are uncorrelated with each other. This is the base model used in [18] and [21]. The model we use has the same base equation, but the functions $I_{ext,i}$ and $f_{i,j}$ are slightly different.

Equation 2.27 can be integrated numerically by approximating it with a difference equation [25]:

$$v_{i,n+1} = v_{i,n} + \Delta t(-v_{i,n} + \mu + I_{i,n} + \sum_{j=1}^N f_{i,j,n}) + \sqrt{2D_{int}\Delta t}\xi_{i,n} \quad (2.28)$$

where $v_{i,n} = v_i(n\Delta t)$, $I_{i,n} = I_i(n\Delta t)$, $f_{i,j,n} = f_{i,j}(n\Delta t)$ and $\xi_{i,n}$ are Gaussian distributed with unit variance and zero mean. The above equation is integrated until the potential difference across the membrane, v_i , reaches threshold, v_{th} ; this gives an estimate of the firing period. The membrane potential is reset to v_r , and then the process is repeated many times to obtain a sufficiently accurate measure of the mean firing period or mean interspike interval (ISI). 10^6 realizations of the ISI gives an accurate approximation of

the actual mean and variance of the ISI [25]. Simulations showed that 10^4 realizations was also sufficient for first-order statistics. For both deterministic [26] and stochastic [25] simulations a time step of 0.001 is sufficient to get an accurate estimate of spike train statistics. The choice of a classically more accurate integration method doesn't reduce the uncertainty in firing times for the LIF neuron, since the discontinuity at threshold introduces an error on the order of the time step [26]. The time step is the main limiting factor in these simulations. It limits the resolution with which one can estimate the firing time of the neuron for both deterministic and stochastic networks. It is even more crucial in stochastic networks, as not only is the firing time uncertain between $v_n < v_{th}$ and $v_{n+1} > v_{th}$, but there is also a possibility, due to the stochastic nature of the network, that the neuron has fired in between $v_n < v_{th}$ and $v_{n+1} < v_{th}$. In this case the neuron's potential crosses threshold and then comes back below threshold; if the time step is too coarse, this crossing is not detected. This additional problem causes an overestimation of the ISI on the order of $\sqrt{\Delta t}$ [25]. Nevertheless, these errors are acceptable for the investigation of gain modulation and spatially profiled feedback.

2.5 Network Measures

There are currently two main theories on how actions potentials are processed. If a higher brain centre is paying attention to the rate at which it receives input then we speak of “rate coding”; if the higher brain centre is paying attention to the pattern of inputs, then we speak of “temporal coding” or “spike coding”. There is much controversy over which of these are actually occurring in real neural networks [9]. Recent studies have hinted towards both types of processing being utilized [27].

In this study we look at both types of coding by using various spike train statistics to analyze the output of a simulated LIF network. The mean firing rate (activity), interspike interval (ISI) histograms, and power spectrum are first-order and second-order spike train statistics that are used to detect rate codes. To detect potential spike coding, we look at raster plots, synchrony and clustering of the network spike trains.

One of the first-order statistical measures of interest is the activity of the network, that is, the average firing rate of the network, which is the “f” in the f-I curve. It can be calculated from simulations using

$$r = \frac{\sum_{i=0}^N n_i}{N t_{max}} \quad (2.29)$$

where n_i represents the number of spikes in the i^{th} spike train, which is summed over the entire network and then divided by the number of neurons in the network, N , and the run time of the simulation, t_{max} . The activity for the network used in this study can be theoretically calculated, as discussed in Chapter 3.

Another measure that is important from a probabilistic point of view is the ISI histogram. An ISI, T_i , is the time between two adjacent spikes:

$$T_i = t_{i+1} - t_i. \quad (2.30)$$

Creating a histogram of the ISI's from a long spike train, one can obtain a good approximation of the probability density of the ISI. This gives an indication of the probability of a spike occurring within a given time interval. Since we do not have an explicit analytical function for the probability density, we are often interested in the information that can be obtained from a numerically generated ISI histogram at a glance. The shape of the ISI histogram may indeed look like a well-know distribution and be quantified as such, but often this is not the case. It should be noted here that, even though the analytical form for the ISI density is not know, its mean can still be analytically found, as in Equation 3.12.

Two qualitative features we will take advantage of are sharp peaks in the

ISI histogram and the presence of bimodality. Sharp peaks in the distribution indicate that there may exist an oscillation in the network, which may be an important indicator for higher brain centres. Bimodality in a ISI histogram is an indication that there may be clusters of spikes or “bursting” present in the spike train, which might also be important for signalling higher brain centres.

Higher order statistics such as the power spectrum of individual spike trains are a clearer indicator of network oscillations. The power spectrum is a measure of the power at various frequencies in the spike train. A peak in the power spectrum indicates that there is a particularly strong presence of this frequency in the spike train, which implies that the spike train is roughly periodic, or that there is an oscillation in the neuron firing rate at that frequency. If this frequency is prominent in all network spike trains, then there is likely an oscillation in the network.

The power spectrum from simulations is calculated using Equation 7 from [21]

$$S(\omega) = \langle \tilde{x}(\omega)^* \tilde{x}(\omega) \rangle \quad (2.31)$$

where $\tilde{x}(\omega)$ is the Fourier transform of the spike train and $*$ denotes the complex conjugate. Since x is stochastic in nature, a single realization of the

power spectrum is very noisy. Thus, many realizations are averaged over to obtain a clear picture of power spectral features.

As discussed above, bimodality in the ISI distribution suggests that bursts may be present in the spike train. To confirm the presence of bursts, an ISI return map, which is a plot of the $i^{th} + 1$ ISI as a function of the i^{th} ISI, is useful. Bursts in the spike train are apparent in the ISI return map as a pattern. This pattern consists of dense regions along the x and y axis, indicating long ISIs followed by short ISIs, as well as a dense region near the origin, which indicates short ISIs followed by short ISIs, and sparse everywhere else (see Figure 6.8(b), top right plot on page 102).

With the exception of the ISI return map, the properties discussed so far are averaged over the network and over many realizations. The next few measures take a more in-depth look at the output of the network directly, which may reveal patterns generated across the network. The simplest way to do this is to look at a plot of the output spike trains of the entire network. Such a plot is called a raster plot, with the position of the neuron in the network plotted on the y-axis, time on the x-axis, and a dot indicating that the neuron has fired. However, patterns present in the raster plots are not always apparent and are better quantified by measures such as synchrony

and clustering.

Synchrony is a measure of how closely in time the neurons of the network fire. It is calculated using the following equation [28]:

$$Syn(t) = \left\| \frac{1}{N} \sum_{j=1}^N e^{2\pi i \phi_j(t)} \right\| \quad (2.32)$$

where $\| \cdot \|$ denotes magnitude, $\phi_j(t)$ is the phase of the j^{th} neuron at time t and i represents $\sqrt{-1}$. To estimate the phase of a stochastic neuron the time between firing is normalized to one [28]:

$$\phi_j(t) = \frac{t_n - t}{t_n - t_p} \quad (2.33)$$

where t_n represents the next firing time of the neuron, t_p represents the previous firing time of the neuron and t represents the time at which we are calculating the synchrony. The more coherent the firing times of the individual neurons are with each other, the higher synchrony value of the network.

Clustering measures a somewhat coarser synchrony. It is very similar to a raster plot, but in this case a dot appears in the cluster plot if 4 out of 7 nearest neighbour neurons have fired within the last 100 time steps (or 10% of the membrane time constant).

With these tools in hand we can hope to decipher how feedback controls

the mean firing rate and the presence of oscillations in the network.

Chapter 3

Network Model

The following chapters contain results from simulating neural networks. Here we give details of the simulated network and theory that describes it.

The specific network model used in this study follows Equation 2.27, where the time-dependent part of the input to the network, $I_{i,ext}(t)$, takes on two different forms and the connectivity function of the network, $f_{i,j}(t)$, is in the form of spatially profiled feedback.

As in [18], network simulations were performed using a standard Euler-Maruyama integration method, simulating 100 neurons, for 30 seconds, with a time step of $6 * 10^{-6}$ s. Each neuron in the network had a threshold $v_{th} = 1$, a reset $v_r = 0$, and a refractory period $\tau_R = 0.6$ ms. The feedback to the network is delayed by an amount $\tau_d = 6$ ms and has a parameter $\alpha = 3$,

which is part of the feedback kernel:

$$K_{\tau_d}(t) = \alpha^2(t - \tau_d)e^{-\alpha(t - \tau_d)} \quad (3.1)$$

that controls the temporal spread of the feedback, which is explained later on in this chapter. These parameters were chosen for their biological relevance to the weakly electric fish [18], [17] and various experimental studies cited therein. One hundred neurons were selected for comparison purposes with the previous global feedback studies done in [18], and [21]. Other parameters are as specified in the results.

3.1 Input

The two different time-dependent inputs that were simulated are percentage correlated input (PCI) and Gaussian correlated input (GCI), which differ spatially, yet are both temporally uncorrelated (“white”). A sample of either input as a function of time is shown in Figure 3.1.

Initially PCI was used as the time-dependent input to the network. It is the same time-dependent input used in [18] and has the form

$$I_{ext,j}(t) = \sigma(\sqrt{c}\xi(t) + \sqrt{1-c}\xi_j(t)) \quad (3.2)$$

A fraction c of the input, which is Gaussian white noise generated using a Box-Muller algorithm [29], is spatially correlated (i.e. the same for each

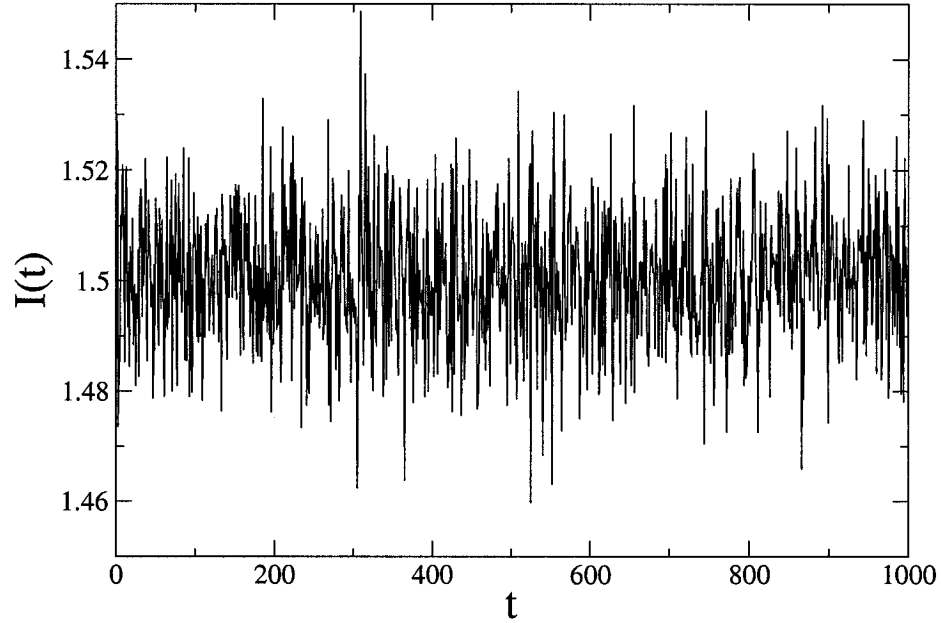


Figure 3.1: Sample input to a neuron as a function of time. The input to the network was white in time for all simulations.

neuron) and a fraction $1 - c$ is spatially uncorrelated (i.e. unique to each neuron). This allows the input intensity σ to remain constant regardless of the value of c . The top row of Figure 3.2 shows a sample of the percentage correlated input for three different values of c , at one instant in time. PCI is meant to represent external input with varying levels of spatially correlated input [18].

Simulations were also done with Gaussian correlated input because it is

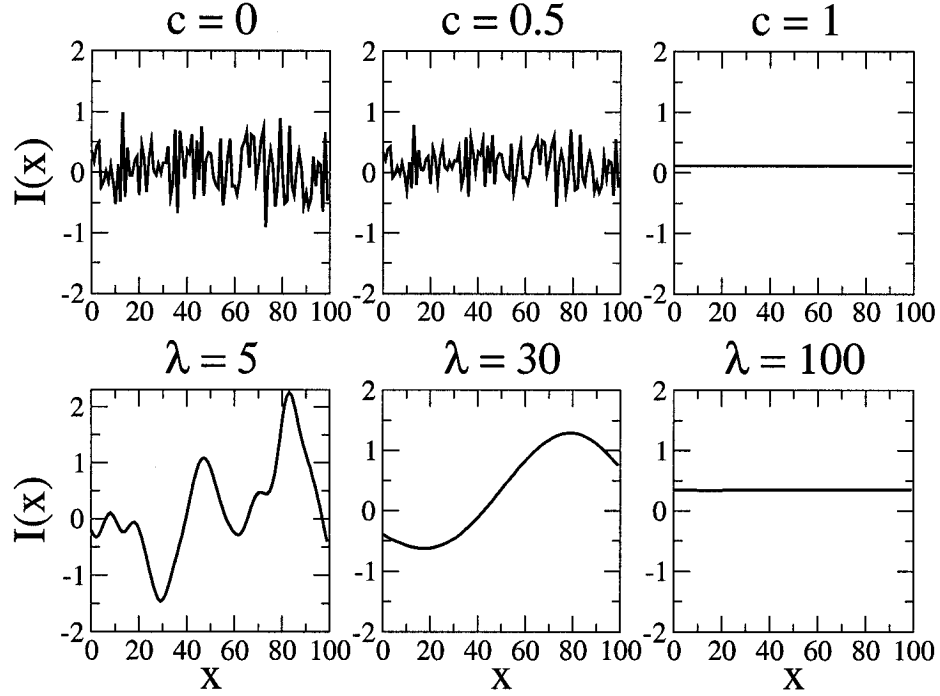


Figure 3.2: Example of external stochastic input as a function of neuron number, i.e. the spatial extent of the network. These graphs correspond to a snapshot in time of the input noise across the network. The top row shows an example of the spatial correlation of PCI for various values of c (Equation 3.2). The bottom row shows a sample of the spatial correlation of GCI for three different values of λ (Equation 3.3)

slightly more representative of what a fish might receive spatially as input in the ELL. It has the form

$$I_{ext}(x, t) = \sigma \eta(x, t) \quad (3.3)$$

where σ is the strength of the input and $\eta(x, t)$ has a correlation length given by [11]:

$$\langle \eta(x, t) \eta(x', t') \rangle = 2C \left(\frac{x - x'}{\lambda} \right) \delta(t - t') \quad (3.4)$$

where

$$C \left(\frac{x - x'}{\lambda} \right) = \frac{\epsilon}{\sqrt{2\pi}\lambda} \exp \left\{ -\frac{|x - x'|^2}{2\lambda^2} \right\}. \quad (3.5)$$

The spatial correlation here has a Gaussian form, characterized by the correlation length λ . As λ goes to zero $\eta(x, t)$ becomes white in space with intensity ϵ . Sample input for different values of λ are shown in the bottom row of Figure 3.2. As λ increases the signal becomes smoother indicating a longer spatial correlation length. Figure 3.3 shows the spatial correlation length of simulated GCI input for two different values of λ . This input is generated numerically in Fourier space [11]:

$$\eta(k, t) = \sqrt{C(k)} \alpha(k, t) \quad (3.6)$$

$$\sqrt{C(k)} = \sqrt{\epsilon} \exp \left\{ -\frac{k^2 \lambda^2}{4} \right\} \quad (3.7)$$

$$\alpha(k, t) = a + ib \quad (3.8)$$

where $\eta(k, t)$ is the Fourier transform of $\eta(x, t)$, $C(k)$ is the Fourier transform of $C(x)$, $k = \frac{2\pi i}{N}$ and $\alpha(k, t)$ are Gaussian random numbers with zero mean and correlated according to

$$\langle \alpha(k, t) \alpha(k', t') \rangle = 2\delta(t - t')\delta(k + k') \quad (3.9)$$

This correlation is generated by 3.8, where i represents $\sqrt{-1}$ and a and b are Gaussian random numbers with zero mean and 0.5 variance, except at $k = 0$ and $k = N/2$, where the variance of a is 1 and the variance of b is 0 ([11] Appendix B).

An array of 128 α values are generated to calculate the inverse Fourier transform into the time domain via the Fast Fourier Transform method [29], which is much quicker than the Discrete Fourier Transform method. Only 100 of the 128 time domain values are used as input in the simulation since there are only 100 neurons in the network. The intensity of the input is scaled such that it is constant with respect to λ , so that comparisons can be made between simulation results for spatially correlated inputs with different values of λ . Figure 3.4 shows the average intensity over time for Gaussian correlated input for a few different values of λ .

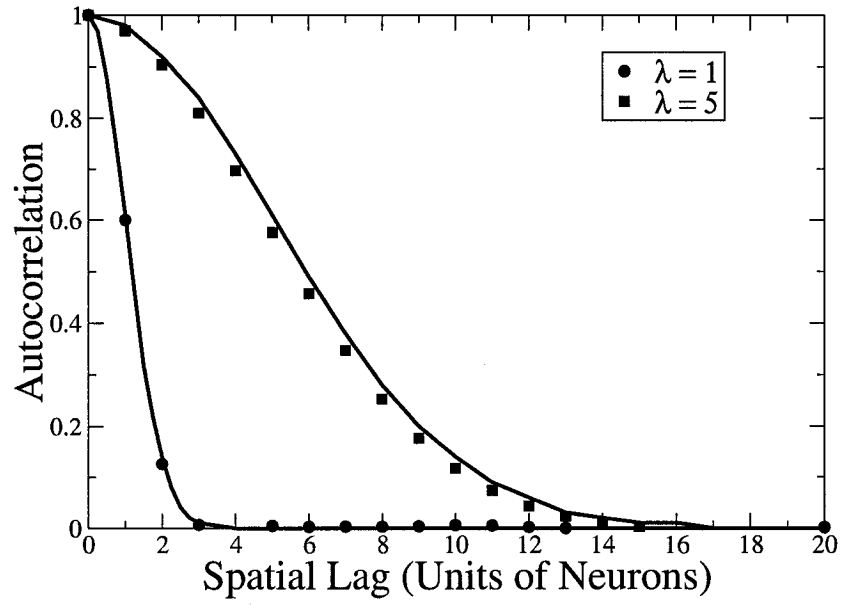


Figure 3.3: Spatial correlation length of the Gaussian correlated input for two different values of λ . Symbols represent spatial correlation of numerically simulated GCI and solid lines represent theory (Equation 3.5).

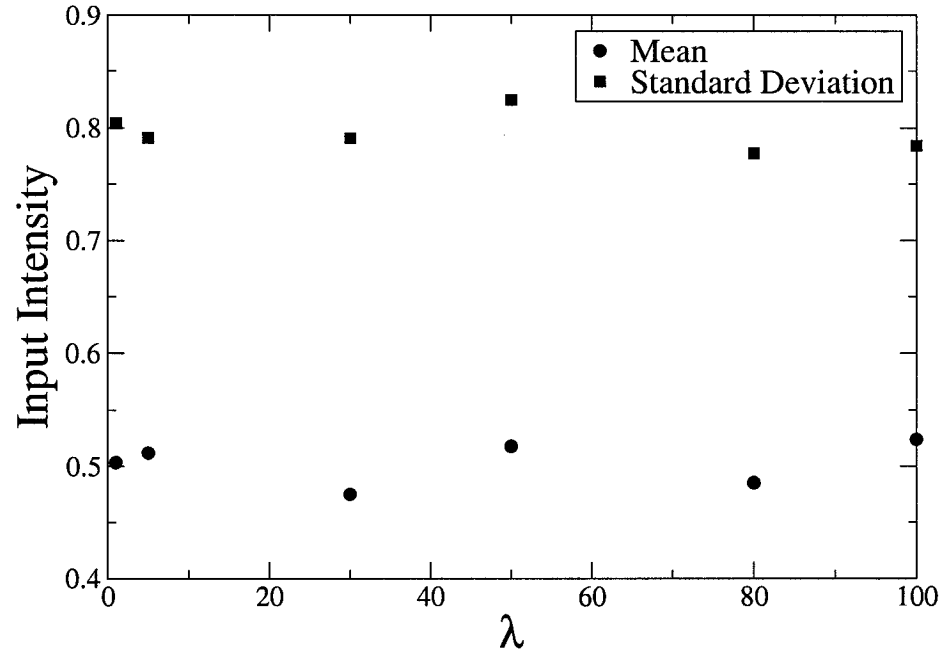


Figure 3.4: Sample input intensity for various values of λ . The input was scaled so that the input intensity did not change for different values of λ , except for statistical fluctuations.

3.2 Feedback

The connectivity function, $\sum_{j=1}^N f_{i,j}$, has the form

$$\sum_{j=1}^N f_{i,j}(t) = \frac{g}{N} \sum_{j=1}^N p(i-j) \int_{\tau_d}^{\infty} x_j(t-\tau) \alpha^2(\tau-\tau_d) e^{-\alpha(\tau-\tau_d)} d\tau \quad (3.10)$$

where g represents the strength of the feedback and N represents the number of neurons in the network. The convolution of the feedback kernel (Equation 3.1) with the sum over all spike trains represents feedback from a higher brain centre to the network. The feedback is different from [21] by the spatially connectivity function $p(i-j)$, which alters the spatial profile of the feedback in the following manner:

$$p(i-j) = \frac{1}{\sqrt{2\pi\sigma_g^2}} \exp\left(-\frac{|i-j|^2}{2\sigma_g^2}\right). \quad (3.11)$$

The spatial connectivity function used in this study is a Gaussian, with standard deviation σ_g . Figure 3.5 shows the feedback from a single neuron ($i = 50$) to the rest of the network for three different values of σ_g . As σ_g increases the feedback spreads to more of the network.

A complete schematic of the network is shown in Figure 3.6, along with a sample of the two main types of spatial feedback profiles used in simulations. In addition to simulations, theory was also developed for spatially profiled feedback.

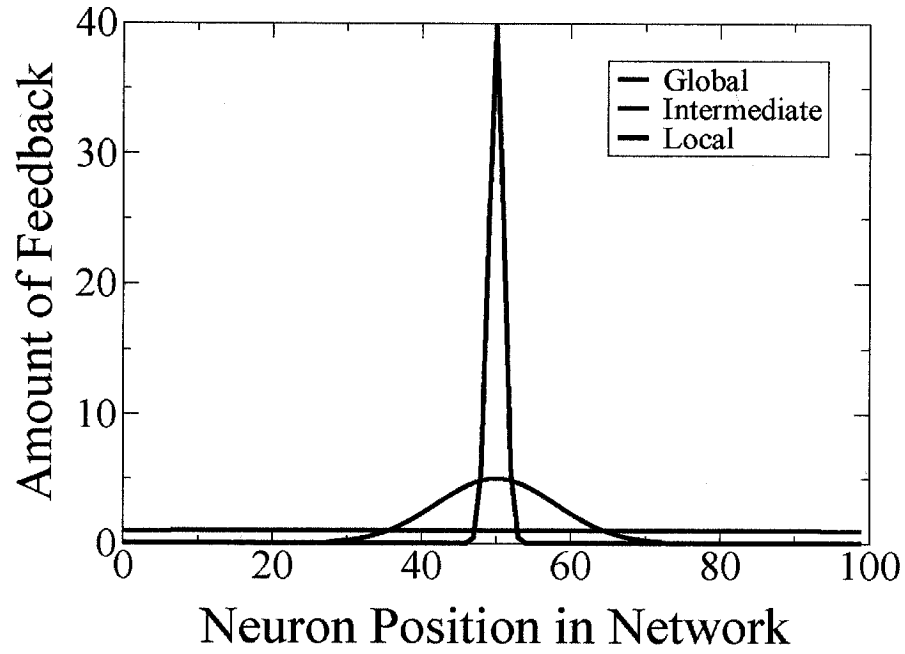


Figure 3.5: Spatial feedback profiles for three different values of σ_g . σ_g is 1, 9, and 100 for “local”, “intermediate” and “global” feedback respectively. The connectivity strength to its neighbours is shown here only for neuron $i = 50$.

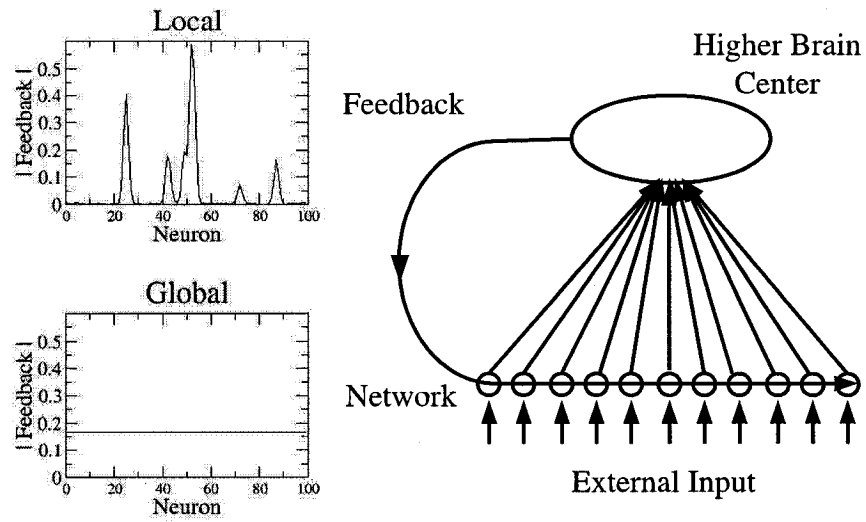


Figure 3.6: Network schematic (right) with a snapshot in time of the two different spatial feedback profiles (left) that are typical of those found in simulations for local (top) and global (bottom) feedback.

3.3 Theory

Theoretically the activity of a LIF network with delayed global feedback can be determined self-consistently using the rate equation for a stochastic LIF neuron (Equation 2.21), by substituting μ with μ_{eff} (Equation 3.16) and D_{int} with D (Equation 3.15) [18]:

$$r = \left[\tau_R + \sqrt{(\pi)} \int_b^a e^{\mu'^2} \text{erfc}(\mu') d\mu' \right]^{-1} \quad (3.12)$$

where

$$a = \frac{\mu_{eff} - v_{th}}{\sqrt{2D}} \quad (3.13)$$

$$b = \frac{\mu_{eff} - v_r}{\sqrt{2D}} \quad (3.14)$$

$$D = D_{int} + \frac{\sigma^2}{2} \quad (3.15)$$

and

$$\mu_{eff} = \mu + gr(\mu_{eff}). \quad (3.16)$$

Here Equation 3.16 represents the average input, or input bias, adjusted to account for the average feedback and D represents the total noise strength, which accounts for the internal noise of the neuron plus the external noise due to the input signal. These equations are also valid for spatially profiled feedback networks, if the total amount of feedback is held fixed, independent

of the spatial profile. Simulation and theoretical calculations of network activity are compared in Chapter 4.

For a noise driven stochastic LIF network model with delayed feedback the power spectrum of an individual spike train can be calculated theoretically using a linear ansatz [18] borrowed from linear response theory:

$$\tilde{x}_i(\omega) = \tilde{x}_{0,i}(\omega) + A(\omega)[\tilde{I}_{ext,i}(\omega) + \frac{g}{N}\tilde{K}_{\tau_d}(\omega)\sum_j^N p_{i,j}\tilde{x}_j(\omega)] \quad (3.17)$$

where the term $p_{i,j}$ has been added to include profiled feedback in the network. Thus, $p_{i,j} = 1$ corresponds to the global feedback case studied previously. Here $\tilde{x}_i(\omega)$ and $\tilde{x}_{0,i}(\omega)$ are the Fourier transform of the individual spike trains with external input and feedback and without external input and feedback, respectively. Thus, $\tilde{x}_{0,i}(\omega)$ represents the Fourier transform of the spontaneous activity of an isolated neuron. $A(\omega)$ represents the Fourier transform of the transfer function (also known as the susceptibility) which multiplies the perturbation terms: $\tilde{I}_{ext,i}(\omega)$, the Fourier transform of the external input, and $\tilde{K}_{\tau_d}(\omega) = \frac{e^{i\omega\tau_d}}{(1-i\omega\alpha^{-1})^2}$, the Fourier transform of the feedback kernel. This linear approximation is good for small inputs and sufficient noise intensity (see Chapter 4).

In this thesis, these expressions are elaborated to include a spatially profiled feedback. Specifically, the linear ansatz can be written in matrix form

as

$$\tilde{\mathbf{x}}(\omega) = \tilde{\mathbf{x}}_0(\omega) + A(\omega)[\tilde{\mathbf{I}}_{\text{ext}}(\omega) + \frac{g}{N}\tilde{K}_{\tau_d}(\omega)\mathbf{P} \cdot \tilde{\mathbf{x}}(\omega)] \quad (3.18)$$

where $\tilde{\mathbf{x}}(\omega)$ represents a vector of all the neuron spike trains in the Fourier domain, $\tilde{\mathbf{I}}_{\text{ext}}$ represents the corresponding external inputs, and $\mathbf{P}$ represents the spatial connectivity matrix.

The average power spectrum of individual spike trains can be calculated by

$$S = \frac{\langle \tilde{\mathbf{x}}^{*T} \tilde{\mathbf{x}} \rangle}{N} \quad (3.19)$$

where T denotes the transpose. Rearranging for $\tilde{\mathbf{x}}$, 3.18 becomes

$$\tilde{\mathbf{x}} = [\mathbf{I} - \frac{Ag\tilde{K}_{\tau_d}}{N}\mathbf{P}]^{-1}[\tilde{\mathbf{x}}_0(\omega) + A(\omega)\tilde{\mathbf{I}}_{\text{ext}}(\omega)] \quad (3.20)$$

where $\mathbf{I}$ is the identity matrix. Substituting Equation 3.20 into 3.19 we have

$$S = \frac{1}{N} \langle [\tilde{\mathbf{x}}_0(\omega) + A(\omega)\tilde{\mathbf{I}}_{\text{ext}}(\omega)]^{*T} \mathbf{Q} [\tilde{\mathbf{x}}_0(\omega) + A(\omega)\tilde{\mathbf{I}}_{\text{ext}}(\omega)] \rangle \quad (3.21)$$

where

$$\mathbf{Q} = [\mathbf{I} - \frac{Ag\tilde{K}_{\tau_d}}{N}\mathbf{P}]^{-1} [\mathbf{I} - \frac{Ag\tilde{K}_{\tau_d}}{N}\mathbf{P}]^{*T} \quad (3.22)$$

and the general solution for the i^{th} individual spike train power spectrum is

$$S_i = \langle (x_{0,i} + AI_{\text{ext},i})^* Q_{i,i} (x_{0,i} + AI_{\text{ext},i}) + \sum_{j=1, j \neq i}^{N-1} (x_{0,i} + AI_{\text{ext},i})^* Q_{i,j} (x_{0,j} + AI_{\text{ext},j}) \rangle. \quad (3.23)$$

The power spectrum of the individual spike train for percentage correlated input can be calculated with the following two assumptions. One, the spike trains generated by a network without input or feedback, $\tilde{x}_{0,i}$, are uncorrelated

$$\langle \tilde{x}_{0,i}(\omega)^*, \tilde{x}_{0,j}(\omega) \rangle = 0, \quad i \neq j \quad (3.24)$$

and two, $\tilde{I}_{ext,i}$ is uncorrelated with $\tilde{x}_{0,i}$

$$\langle \tilde{I}_{ext,i}(\omega)^*, \tilde{x}_{0,j}(\omega) \rangle = 0. \quad (3.25)$$

With these assumptions the i^{th} individual spike train power spectrum becomes

$$S_i = Q_{i,i}(S_0 + |A|^2 S_{st}) + c|A|^2 S_{st} \sum_{j \neq i}^{N-1} Q_{i,j}, \quad (3.26)$$

where $S_0 = \langle \tilde{x}_0 * \tilde{x}_0 \rangle$ represents the power spectrum of the spike train without input or feedback and $S_{st} = \langle \eta * \eta \rangle$ represents the power spectrum of the external input noise. In the case of percentage correlated input $S_{st} = \sigma^2$ [18].

Analytical expressions for the unperturbed power spectrum, S_0 , and the susceptibility, $A(w)$, have been calculated for a single stochastic LIF neuron with additive noise [30].

$$S_0(\omega) = r \frac{\left| \mathcal{D}_{i\omega} \left(\frac{\mu_{eff} - v_{th}}{\sqrt{D}} \right) \right|^2 - e^{2\delta} \left| \mathcal{D}_{i\omega} \left(\frac{\mu_{eff} - v_r}{\sqrt{D}} \right) \right|^2}{\left| \mathcal{D}_{i\omega} \left(\frac{\mu_{eff} - v_{th}}{\sqrt{D}} \right) - e^{\delta} e^{i\omega\tau} \mathcal{D}_{i\omega} \left(\frac{\mu_{eff} - v_r}{\sqrt{D}} \right) \right|^2} \quad (3.27)$$

where

$$\delta = \frac{v_r^2 - v_{th}^2 + 2\mu_{eff}(v_{th} - v_r)}{4D} \quad (3.28)$$

and [31].

$$A(\omega) = \frac{ri\omega}{\sqrt{D}(i\omega - 1)} \frac{\mathcal{D}_{i\omega-1}\left(\frac{\mu-v_{th}}{\sqrt{D}}\right) - e^\delta \mathcal{D}_{i\omega-1}\left(\frac{\mu-v_r}{\sqrt{D}}\right)}{\mathcal{D}_{i\omega}\left(\frac{\mu-v_{th}}{\sqrt{D}}\right) - e^\delta e^{i\omega\tau} \mathcal{D}_{i\omega}\left(\frac{\mu-v_r}{\sqrt{D}}\right)}. \quad (3.29)$$

Here $\mathcal{D}_a(z)$ represents the parabolic cylinder function, D represents the total noise contributed by the cell and the input (refer to Equation 3.15) and r is the activity of the neuron (refer to Equation 3.12).

In the limit of global feedback, $\mathbf{P}$ is a N by N matrix with $P_{ij} = 1$ and we obtain

$$S_i = S_0 + |A|^2 S_{st} + c|A|^2 S_{st} \frac{2\text{Re}(AgK) - |AgK|^2}{|1 - AgK|^2} + \frac{1}{N} [S_0 + (1 - c)|A|^2 S_{st}] \frac{2\text{Re}(AgK) - |AgK|^2}{|1 - AgK|^2} \quad (3.30)$$

which is the exact equation from [21] for a finite network with global feedback.

So in the limit of global feedback we recover the finite network spectral equation from [21]. Details of the derivation of Equation 3.30 are given in Appendix A.

Maple was used to calculate some theoretical results (network activity in Chapter 4 and power spectral density in Chapter 5), which are later compared to simulation data presented in Chapters 4 and 5.

Chapter 4

Linearization of f-I Curves

4.1 Introduction

If rate coding is important to higher brain centres, then the activity of the network and mechanisms that alter network activity are of interest. In this chapter we analyze f-I curves, which look at the network activity as a function of input strength.

For a deterministic LIF network the f-I curve is highly non-linear, going from a slope of zero to an infinite slope at the onset of firing (this can be seen in Figure 4.1, solid curve). One way network activity changes is by the linearization of the f-I curve, which can be caused by noise, feedback, or both.

Initially simulations with no feedback were done to demonstrate linearization of f-I curves by the addition of noise to a neural network; the analysis is

done for internal, external, and both internal and external noise. Simulations of a deterministic network with feedback were then done to demonstrate the linearization of f-I curves due to inhibitory feedback in the network. Further simulations with feedback and progressively increasing noise were done to get a clear picture of linearization effects with both noise and feedback in a neural network. All simulations presented in this chapter were done with global feedback.

4.2 Noise

Noise in a neural network causes linearization of the f-I curve. Figure 4.1 shows that adding noise to a deterministic LIF network with no feedback causes the network to fire before the input bias (μ in Equation 2.27) of the network reaches threshold. This is a case of noise-induced firing, where a network which would otherwise not fire, now with the addition of noise shows its underlying dynamics. As more noise is added to the network the neurons are able to fire at lower and lower bias levels. This effectively linearizes the f-I curve and increases the overall activity of the network. However, for moderate amounts of noise the gain (or slope) of the f-I curve increases only for input biases below threshold and decreases for input biases just above

threshold.

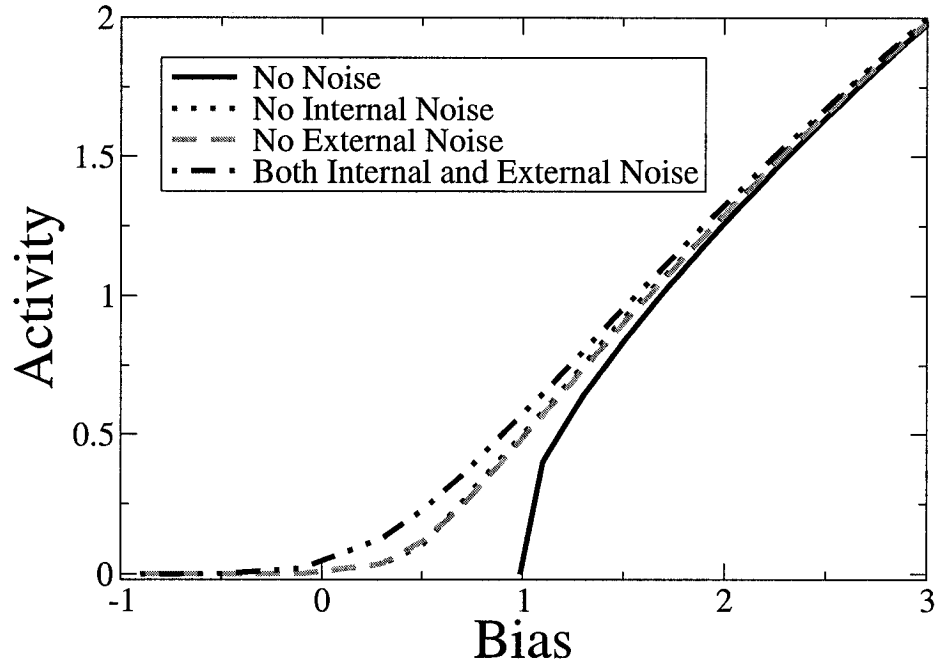


Figure 4.1: f-I curves for increasing amounts of noise in a LIF neural network without feedback. For “no noise” (solid line), $\sigma^2 = 0$ and $D_{int} = 0$. For “no internal noise” (dotted line), $\sigma^2 = 0.16$ and $D_{int} = 0$. For “no external noise” (dashed line), $\sigma^2 = 0$ and $D_{int} = 0.08$. With both internal and external noise, $\sigma^2 = 0.16$ and $D_{int} = 0.08$. Other parameters used for these simulations were $\mu = 1.5$, $g = 0$, $\sigma_g = 100$, and $c = 1$. As the amount of noise in the system increases the f-I curve becomes more linear (i.e. the $\ln$ function in Equation 2.5 becomes smoothed out). The linearization is due to the ability of the neurons in the network to reach threshold without a superthreshold input bias, with the help of the noise.

4.3 Gain

The gain of the f-I curve can change in two ways. The simplest is a shift of the f-I curve to the right or left, known as a subtractive gain shift. The other way is by a change in slope of the f-I curve, which is known as a divisive shift of the gain. Here we focus on the later.

In vivo studies in the weakly electric fish have shown that feedback can divisively shift the gain to reduce the frequency response range of the ELL [1] and in this way adapt to stimuli. Many subsequent studies ([32], [33], [34], [35], [13]) have also shown that inhibitory input causes divisive gain shifts, yet the biophysical mechanism of divisive gain shift is poorly understood. Several mechanisms have been proposed and many studies suggest descending (feedback) pathways as a possible cause. Another theoretical study of deterministic neurons showed that inhibitory feedback linearizes a nonlinear f-I curve near the onset of firing [36]. Here we link these two concepts together. Linearization of f-I curves due to feedback comes from the divisive gain effect caused by inhibitory feedback.

Indeed, for a completely deterministic network with inhibitory feedback, linearization is seen in the f-I curve, Figure 4.2, even though the network responds only for input above threshold. The top curve (solid line) shows

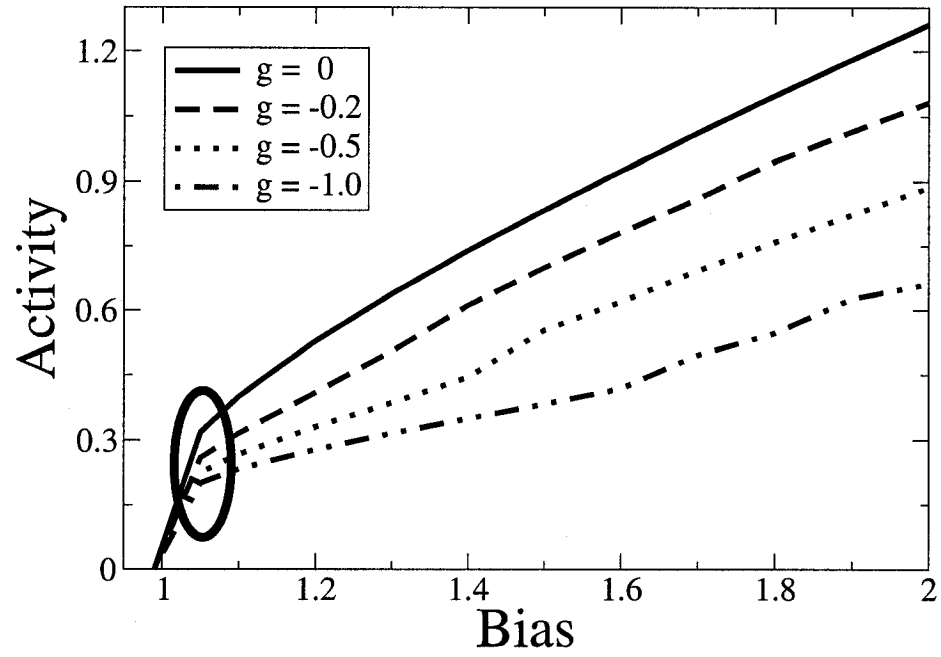


Figure 4.2: f-I curves with increasing inhibitory feedback strength for a network with no internal or external noise. The other parameters used in the simulation are the same as in Figure 4.1. As the strength of inhibitory feedback is increased the gain divisively shifts down, causing the f-I curve to become more linear near the onset of firing (encircled area).

the standard f-I curve for a deterministic LIF network without feedback. As inhibitory feedback is added, the f-I curve divisively shifts downward (the lower curves representing different strengths of inhibitory feedback in the network), while becoming more linear just beyond the onset of firing (circled area in Figure 4.2).

To understand the mechanism behind the divisive gain shift seen in Figure 4.2 we look at network raster plots and voltage traces for various feedback strengths and input biases (Figures 4.3 - 4.8). Comparing Figures 4.6 and 4.3, and Figures 4.7 and 4.4, we see that the stronger the inhibitory feedback, the slower the firing rate. The decrease of the firing rate is due to the hyperpolarizing effect of the delayed inhibitory feedback on the membrane potential of the neurons in the network. The decrease in membrane potential delays the next firing time of the neurons (as long as the delay, τ_d , is not too large). In other words, the inhibition causes the membrane potential to take longer to reach threshold. For stronger inhibitory feedback, neurons fire at even later times, and thus as inhibitory feedback strength is increased, the firing rate of the network decreases.

There is a multiplicative effect between the inhibition and the input bias that causes the divisive gain shift. The inhibition is less effective for a low

input bias compared to a high input bias, due to the fact that the feedback is a function of firing rate which depends on the input bias. As the strength of feedback increases, it will have a greater affect on lowering the firing rate, and this decrease in the firing rate is greater for higher input bias, due again to the dependence of feedback on input bias. The multiplicative effect can be seen by comparing the shift in firing rate between Figures 4.3 and 4.6 and the shift in firing rate between Figures 4.4 and 4.7.

Figure 4.2 also shows that the smoothness of the f-I curve disappears when inhibitory feedback is present in the network (i.e. there are small bumps seen in the f-I curves with inhibitory feedback), despite the absence of noise. As the input bias is increased for a constant, nonzero feedback strength, the depolarization of the membrane occurs quicker and the inhibitory feedback affects it at a later stage in its rise time and with a smaller amplitude (compare Figures 4.3 and 4.4). If the input bias is large enough, the neuron may even fire before the inhibitory feedback has a chance to affect it, due to the time delay of the feedback τ_d (Figure 4.5). This causes different firing patterns for different input bias strengths. For input bias values near the transition phase from one firing pattern (Figure 4.4) to the next (Figure 4.5) the phase locking of neurons in the network becomes destabilized as in Fig-

ure 4.8. Consequently the f-I curves with inhibitory feedback are not smooth like the f-I curve for no feedback, even though the network is not stochastic (i.e. there are no statistical fluctuations in the network). This particular phenomenon is also seen in [37] and [13].

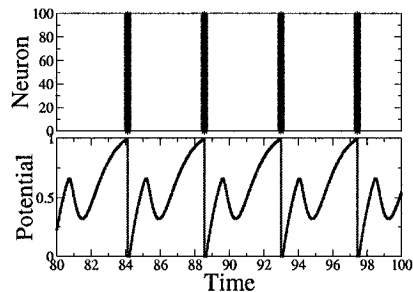


Figure 4.3: Raster plot and voltage curve for $\mu = 1.1$ and $g = -1.2$.

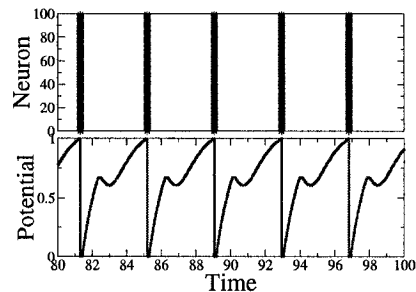


Figure 4.6: Raster plot and voltage curve for $\mu = 1.1$ and $g = -0.6$.

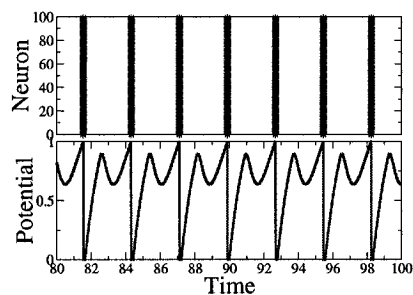


Figure 4.4: Raster plot and voltage curve for $\mu = 1.5$ and $g = -1.2$.

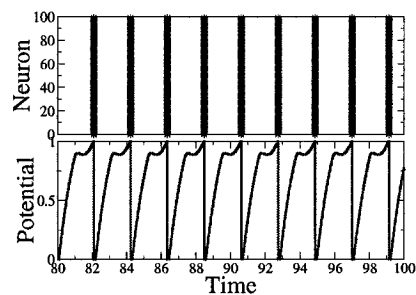


Figure 4.7: Raster plot and voltage curve for $\mu = 1.5$ and $g = -0.6$.

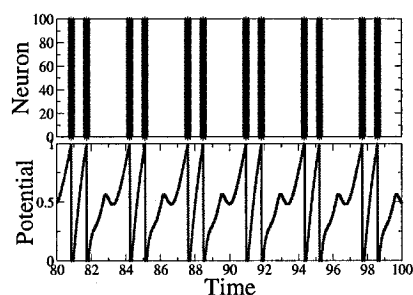


Figure 4.5: Raster plot and voltage curve for $\mu = 1.9$ and $g = -1.2$.

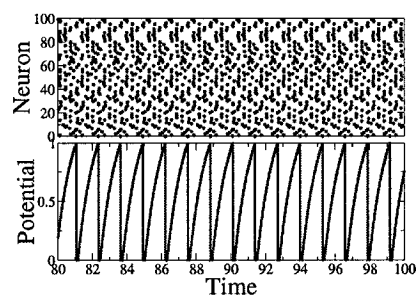


Figure 4.8: Raster plot and voltage curve for $\mu = 1.9$ and $g = -0.6$.

In 1998 Ermentrout theoretically predicted that instantaneous feedback linearizes non-linear f-I curves in deterministic neurons (just above threshold for the LIF neuron model) [36]. Here we do a similar calculation as in [36] for a LIF neuron, with the goal of extending it to stochastic neurons with delayed feedback. The effect can be understood by looking at a single neuron with feedback onto itself.

The firing rate for a deterministic LIF neuron is given by

$$r = \left[\ln \left(\frac{I}{I - v_{th}} \right) \right]^{-1} \quad (4.1)$$

Modelling inhibitory feedback as an input current shift proportional to the gain and the firing rate [36], the input current becomes

$$I = I_0 + g\beta r \quad (4.2)$$

where β is a constant. Substituting Equation 4.2 into Equation 4.1 yields:

$$I_0 + g\beta r - v_{th} = e^{-\frac{1}{r}}(I_0 + g\beta r). \quad (4.3)$$

Differentiating implicitly with respect to I_0 Equation 4.3 becomes

$$1 + g\beta r' = \frac{r'}{r^2} e^{-\frac{1}{r}}(I_0 + g\beta r) + e^{-\frac{1}{r}}(1 + g\beta r') \quad (4.4)$$

where r' represents the derivative of r with respect to I_0 . Solving for r' we

have

$$r' = \frac{1 - e^{-\frac{1}{r}}}{\frac{I_0}{r^2}e^{-\frac{1}{r}} + \frac{g\beta}{r}e^{-\frac{1}{r}} + g\beta e^{-\frac{1}{r}} - g\beta}. \quad (4.5)$$

For large r , $1/r$ is small, which implies that $e^{-\frac{1}{r}}$ is significantly larger than zero; however, since r is positive, $e^{-\frac{1}{r}} < 1$. Therefore the first two terms in the denominator will be negligible for large r and we can approximate r' by

$$r' \simeq -\frac{1 - e^{-\frac{1}{r}}}{g\beta(1 - e^{-\frac{1}{r}})}, \quad (4.6)$$

which reduces to

$$\frac{dr}{dI_0} = -\frac{1}{g\beta}. \quad (4.7)$$

This is also the case for small r . When r is small, $\frac{1}{r}$ is large and $e^{-\frac{1}{r}}$ goes to zero. Thus the first three terms in the denominator of Equation 4.5 vanish and we get Equation 4.7 for extremely small r . This implies that inhibitory feedback causes the activity to become linear with respect to the input just above threshold (when r is very small) as well as when r is large [36].

4.4 Noise and Gain

Numerical and theoretical studies later showed that divisive gain can be achieved through simultaneously increasing the mean and variance of background inhibitory synaptic input in the absence of feedback [33], [34]. An in

vitro study of rat somatosensory cortex [38] was done around the same time which confirmed the results found in [33] and indicated as well, with supporting simulation results, that balanced excitatory and inhibitory inputs allow divisive gain to occur for higher firing rates. Further theoretical studies were done to show that nonlinear gain modulation can occur without feedback for balanced excitatory and inhibitory input [35]. Here we show that these divisive gain shifts can also be accounted for by the combination of noise and inhibitory feedback, via closed loop simulations of a LIF network.

Introducing noise into a network with inhibitory feedback further linearizes the f-I curve. Figure 4.9 shows a comparison of a completely deterministic network and three stochastic networks with varying levels of noise. The divisive shift in the gain due to feedback that is seen in the deterministic network (Figure 4.9 a)) is also present in Figures 4.9 b), 4.9 c), and 4.9 d), which have both feedback and noise.

The addition of noise smooths out the f-I curve and acts to linearize it mainly in the subthreshold regime as seen in Figure 4.1. It is also apparent from Figures 4.9 b), c), and d) that, while the noise linearizes the f-I curve in the subthreshold regime, it also allows linearization due to feedback in this regime, which is not possible in Figure 4.9 a) because the deterministic

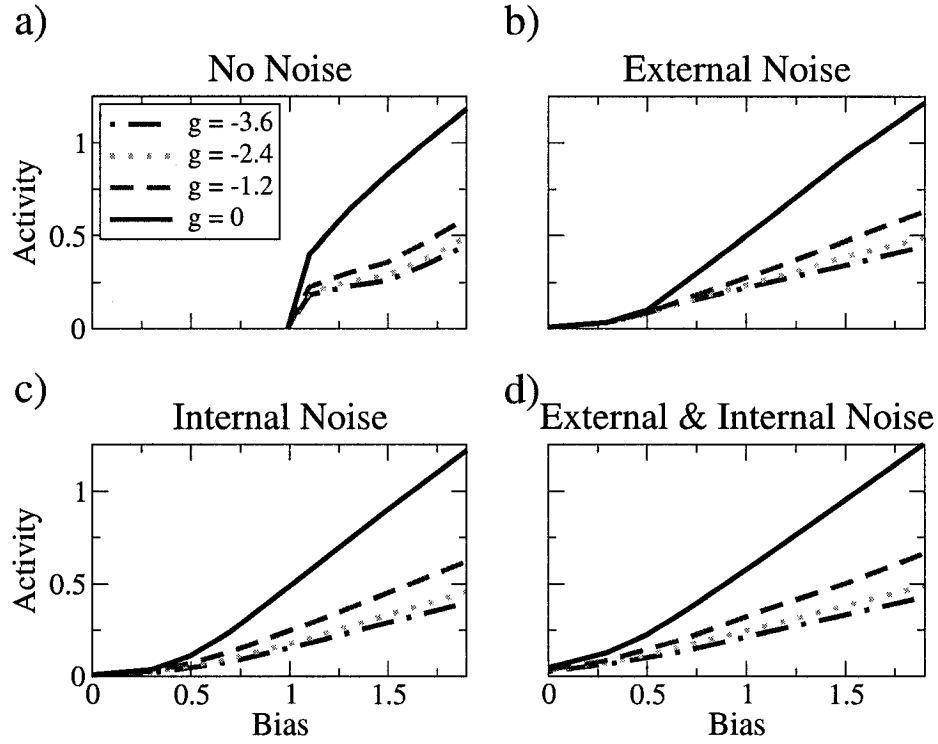


Figure 4.9: f-I curves with increasing inhibitory feedback strength for a) a network with no noise, b) a network with external noise, c) a network with internal noise and d) a network with both internal and external noise. Parameters are the same as those in Figure 4.1. As the strength of inhibitory feedback is increased, the gain divisively shifts down causing the f-I curve to become more linear. Linearization of the f-I curve is also seen in the transition from a) to d) as more noise is added.

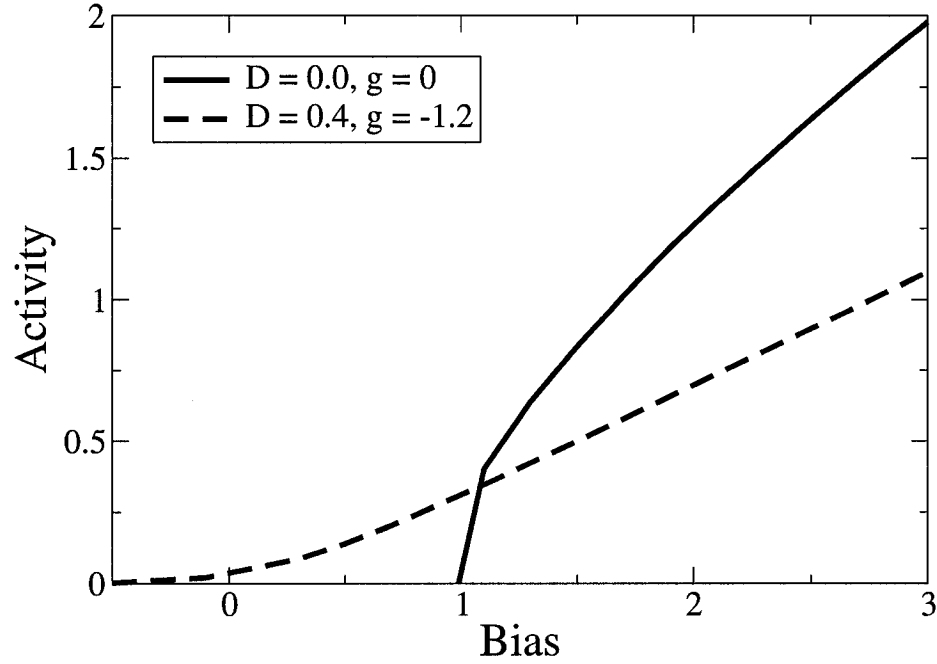


Figure 4.10: F-I curve for a network with no feedback and no noise, solid line, compared to the f-I curve for a network with feedback ($g = -1.2$) and noise ($D = 0.16$).

network does not fire below threshold.

The combination of the two linearizing effects could possibly produce a gain shift similar to the one seen in the weakly electric fish [1] and rat cortex [38] for unbalanced inhibition and excitation. These experimental studies showed not only a divisive gain shift, but a subtractive gain shift as well. Figure 4.10 shows a overlay of the solid line of Figure 4.9 a) and the dashed

line of Figure 4.9 d). It is clear from the overlay that the combination of the two linearization effects can produce a leftward shift and a multiplicative decrease in the gain.

For a network with both internal and external noise the linearization due to feedback indicated in [36] still applies. The theoretical firing rate of the network is given by Equations 3.12 - 3.16:

$$r = \left[\tau_R + \sqrt{(\pi)} \int_b^a e^{\mu'^2} \text{erfc}(\mu u') d\mu u' \right]^{-1} \quad (4.8)$$

where

$$a = \frac{\mu_{eff} - v_t}{\sqrt{2D}}, \quad (4.9)$$

$$b = \frac{\mu_{eff} - v_r}{\sqrt{2D}}, \quad (4.10)$$

and

$$\mu_{eff} = \mu + gr(\mu_{eff}). \quad (4.11)$$

Differentiating with respect to μ we obtain

$$\frac{dr}{d\mu} = \frac{dr}{d\mu_{eff}} \frac{d\mu_{eff}}{d\mu} \quad (4.12)$$

where

$$\frac{d\mu_{eff}}{d\mu} = 1 + g \frac{dr}{d\mu}. \quad (4.13)$$

Substituting Equation 4.13 back into 4.12 we get

$$\frac{dr}{d\mu} = \frac{dr}{d\mu_{eff}} \left(1 + g \frac{dr}{d\mu}\right). \quad (4.14)$$

Rearranging we obtain:

$$\frac{dr}{d\mu} = \frac{\frac{dr}{d\mu_{eff}}}{1 - g \frac{dr}{d\mu_{eff}}}. \quad (4.15)$$

Now

$$\frac{dr}{d\mu_{eff}} = r^2 \sqrt{\frac{\pi}{2D}} \left[e^{a^2} \text{erfc}(a) - e^{b^2} \text{erfc}(b) \right] \quad (4.16)$$

which is exactly $\frac{dr}{d\mu}$ for Equation 2.21 if we replace D_{int} by D . This means that

$$\frac{dr(g)}{d\mu_{eff}} \simeq \frac{dr(g=0)}{d\mu} \quad (4.17)$$

i.e. $\frac{dr}{d\mu_{eff}}$ is approximately equal to the open loop (no feedback) slope $\frac{dr(g=0)}{d\mu}$.

By looking at the curve for $g = 0$ in Figure 4.11 we see that the slope is constant for sufficiently large μ . This will depend on the parameter D of the system, which also affects the firing rate. In this case, $D = 0.16$, $\mu > 0.3$ would be sufficient.

For constant $\frac{dr(g=0)}{d\mu}$ Equation 4.15 becomes

$$\frac{dr(g)}{d\mu} \simeq \frac{\gamma}{1 - g\gamma} \quad (4.18)$$

where $\gamma \equiv \frac{dr}{d\mu_{eff}}$ is a positive constant. This is the same form as Equation 4.7, indicating that inhibitory feedback linearizes a non-linear f-I curve.

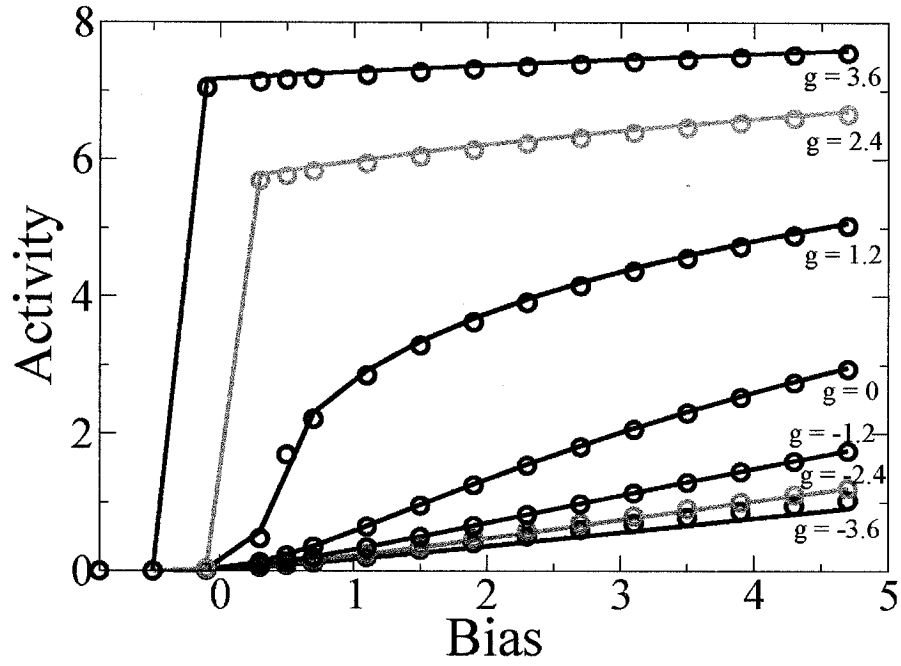


Figure 4.11: Network activity as a function of the input bias (μ) for various inhibitory (red, orange, blue) and excitatory (green, brown, violet) feedback strengths. The black line represents the activity of a network with no feedback. Parameters used for these simulations were $\sigma^2 = 0.16$, $\sigma_g = 100$, and $c = 1$. The theoretical (solid lines) activity of the network, Equation 4.8, matches numerical simulations (open circles).

So far we have looked at inhibitory feedback, but excitatory feedback also divisively shifts the gain of the f-I curves. Figure 4.11 shows how network activity varies with increasing input current bias (the time independent part of the input, μ) for both excitatory and inhibitory feedback in a network with internal and external noise. As expected, input current bias increases cause higher activity in the network and increasing inhibitory feedback strength in the network causes lower activity in the network (as shown above). For excitatory feedback, increasing the strength causes the activity of the network to increase and near the onset of firing shows a divisive increase in the gain of the f-I curve.

There are some other interesting features of the divisive shift in the gain at different values of feedback strength. The divisive shift decreases at large input bias, as inhibitory feedback strength, g , becomes very strong, showing a limitation of the network to modify its firing frequency at this extreme. At the other extreme, for strong excitatory input, there is a nearly instantaneous jump to a fast firing rate and the network no longer has a divisive gain increase, but a decrease. The further increase in bias has less effect at such extreme high firing rates.

Examining Equation 4.18, we can predict simulation results for values of

input bias larger than approximately 0.3. For $1 - g\gamma > \gamma$ the slope of the f-I curve will be small and positive. This occurs for all negative values of g . This can be seen in Figure 4.11 for all values of μ . For $\gamma > 1 - g\gamma$ the slope of the f-I curve will be large and positive. This occurs for a small range of positive g values. This is seen in Figure 4.11 for sufficiently small values of μ . Thus in general the theory can predict simulation results for values of μ around one, where the slope of the f-I curve increases, as g goes from negative to small positive values.

Separating the input into a time dependent and time independent part also allows us to look at the effect of the signal noise intensity (external noise intensity) on the activity of the network independent of the average input (input bias). The activity of the network for a constant input bias and increasing signal noise strength, as seen in Figure 4.12, is similar to that of increasing input bias and constant noise strength. As the signal noise strength increases, so does the activity of the network. Increasing the inhibitory feedback strength of the network lowers the overall activity in a divisive manner, as before. Increasing the positive feedback strength of the network increases the network activity in a divisive manner (This is true increasing g from 0 to 1.2, but is not quite visible in Figure 4.12).

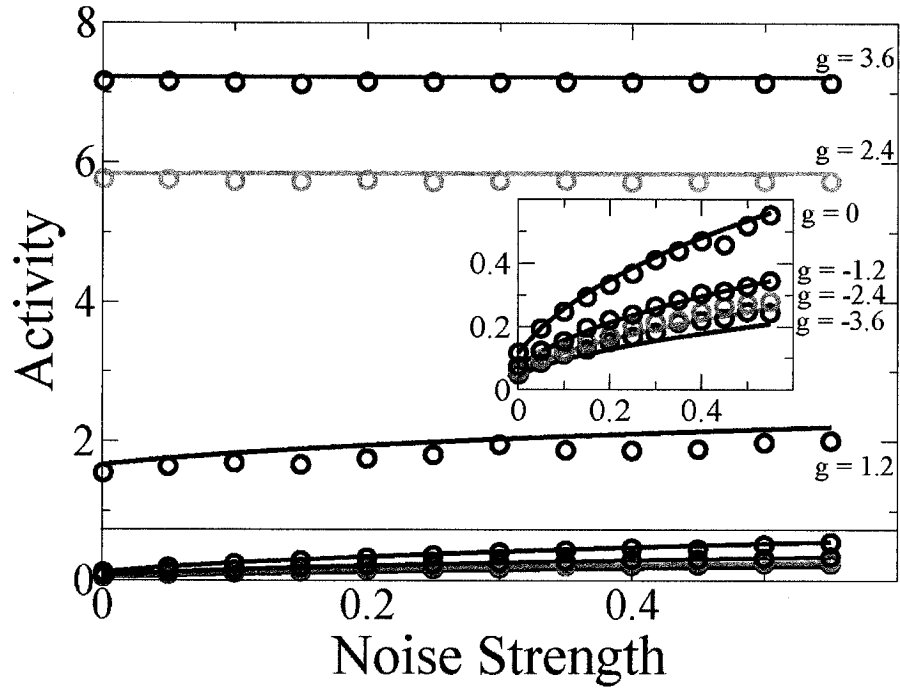


Figure 4.12: Network activity as a function of input noise strength (σ) for various amounts of inhibitory (red, orange, blue) and excitatory (green, brown, violet) feedback. The black line represents the activity of a network with no feedback. Parameters used for these simulations were $\mu = 0.5$, $\sigma_g = 100$, and $c = 1$. The theoretical (solid lines) activity of the network, Equation 4.8, matches numerical simulations (open circles).

However, signal noise strength affects the gain of the network, at extremely large magnitudes of feedback strength, in a slightly different way. It similarly shows that increasing the inhibitory feedback strength, at already large negative values of g , causes the network to become less and less able to change its rate. However, at the other extreme, large positive values of g , increasing signal noise strength has no effect on the network activity. In general, for a network with low activity, increasing the input noise strength increases the activity of the network (see inset of Figure 4.12), but networks with high activity are virtually unaffected by increasing the input noise strength. These results agree with those found in [33] and [38]. Theoretical activities were also plotted in Figures 4.11 and 4.12 to show that Equation 4.8 predicts the activity of the network fairly well.

4.5 Summary

The addition of noise to a deterministic LIF network linearizes the f-I curve of the network. Feedback can also linearize the f-I curve of the network and this comes from the coupling of the feedback strength to the bias in a closed loop simulation. The coupling of feedback strength to input bias due to a single feedback pathway is suggested in [32], but is not shown to be a

useful mechanism to adjust the gain divisively. The combination of the two linearization effects can reproduce the gain shift seen from open loop to close loop in the weakly electric fish [1].

The theoretical rate equation for the stochastic LIF network, which takes into account the mean level of activity of the feedback, Equation 4.8, predicts simulation results fairly accurately, even though the variance of the feedback is not taken into account. The feedback variance, or feedback noise, does not have much effect on the onset of activity of the network, due to the fact that it is only present after the network is already firing. As we see from Figure 4.1, in the superthreshold regime any noise does not have much effect on the mean firing rate. Thus, approximating the change in the activity due to feedback, by the mean feedback is sufficient.

Chapter 5

Effects of local feedback

5.1 Introduction

In order to explore the effects of localized delayed feedback, found in many areas of the brain, a comparison is made between local and global feedback. Figure 5.1 shows the specific difference between a global feedback network, Figure 5.1 a) and a local feedback network, Figure 5.1 b). These network schematics depict the feedback profile and pathway, due to the firing of the middle neuron in the schematic. The feedback pathway indicates the connectivity of the feedback and the profile indicates the feedback strength as a function of distance from a reference neuron. For both global and local feedback networks the feedback pathway includes a time delay, τ_d .

In this chapter we compare simulation results of the two different networks, first with percentage correlated input (PCI), and then with Gaussian

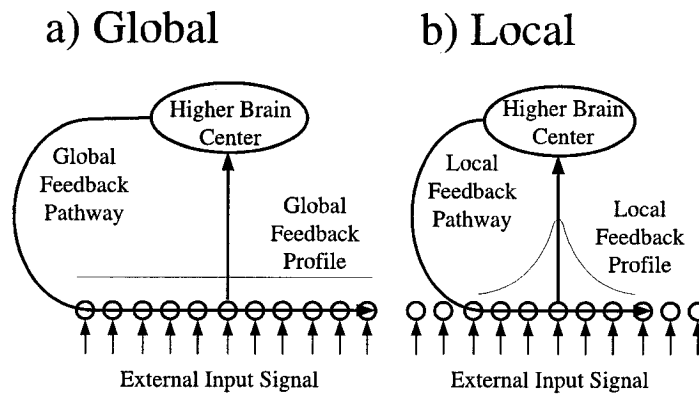


Figure 5.1: Two different types of network architectures used in simulations. Panel a) shows the global feedback profile and b) shows the local feedback profile from a single neuron in the network onto its neighbours.

correlated input (GCI), using network activity, raster plots and power spectra. The survey done in this chapter identifies the main differences between the two types of networks and their response to each input. A more detailed analysis, which includes the use of other network measures, is done in Chapter 6.

5.2 Percentage Correlated Input

Percentage correlated input is used in [18] and is studied here for comparison purposes. As in the previous chapter, we begin by examining f-I curves to look at the mean firing rate of the network.

Independent of spatial profile, both inhibitory and excitatory feedback simulations showed similar f-I curves for increasing input bias, μ , (Figure 5.2). Small differences seen between global and local feedback f-I curves in Figure 5.2 imply that the mean firing rate of the network appears to be independent of the spatial profile of the feedback, and to only depend on the average amount of feedback to the network. This is expected intuitively since the total amount of feedback coming back to the network was held fixed regardless of spatial profile (i.e. the area under the curve in Figure 3.5 was held fixed).

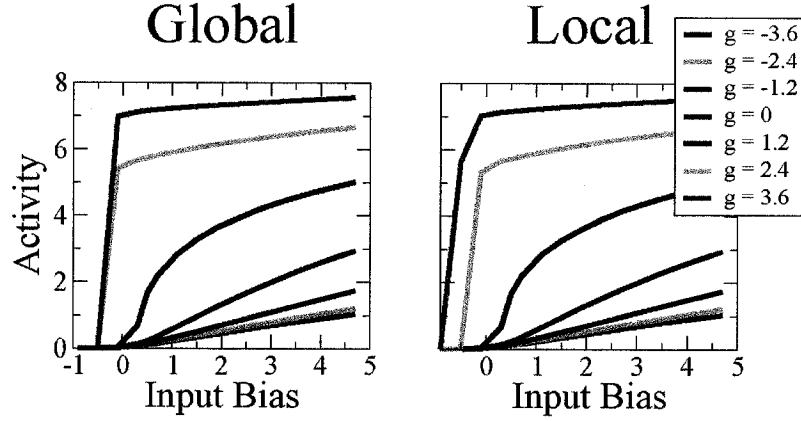


Figure 5.2: F-I curves for local ($\sigma_g = 1$) and global ($\sigma_g = 100$) feedback. Activity as a function of input bias with increasing levels of feedback strength. The input parameters used for these simulations are $c = 1$, and $\sigma^2 = 0.16$.

The same trend can be seen in the case of the “input noise strength”, (Figure 5.3), regardless of feedback profile. Again, small discrepancies between local and global f-I curves appear to be due to statistical error. Even though this first-order statistic shows quantitative similar results for local and global feedback, the network dynamics do depend on the spatial feedback profile, as we will see.

Comparing the raster plots for global (Figure 5.4 a)) and local (Figure 5.4 b)) feedback, qualitatively we see that the networks behave differently. Network firing times for global feedback are slightly more arbitrary than the network firing times for local feedback, which appear to cluster more. Success-

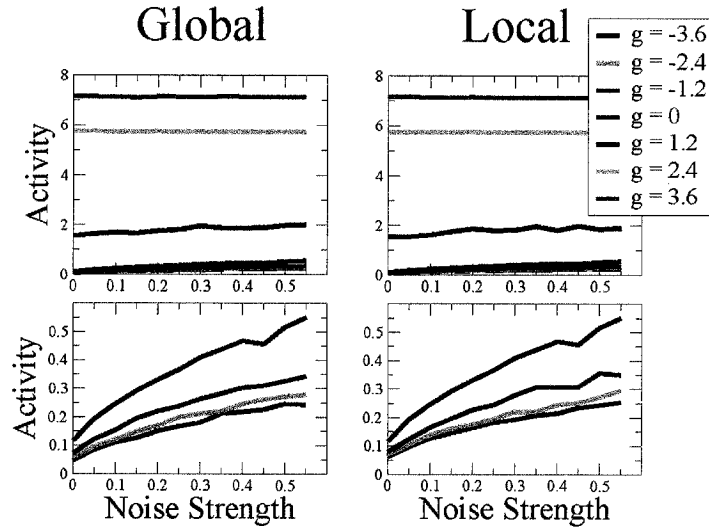


Figure 5.3: Activity vs input noise strength curves for local and global feedback for increasing levels of feedback strength. The lower two graphs expand the vertical scale of the graph above them. The input parameters used for these simulations were $c = 1$, and $\mu = 0.5$.

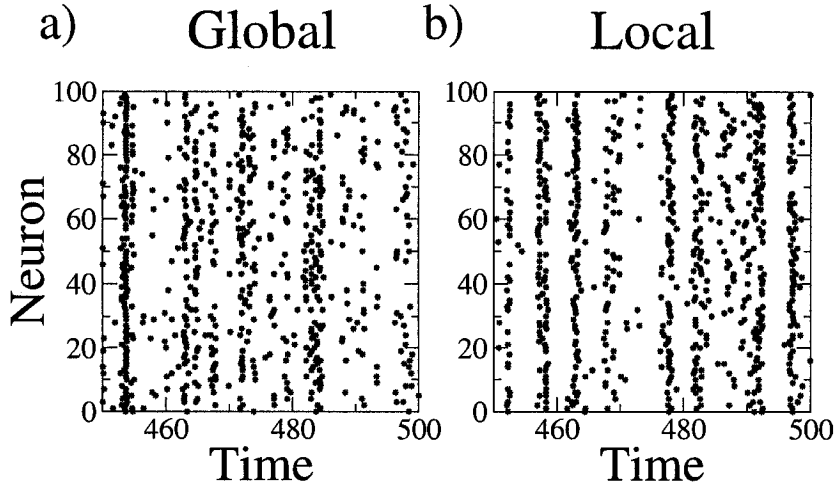


Figure 5.4: Raster plots for a) global and b) local feedback profiles. Each star (or dot if you like) represents a firing time (x-axis) of a neuron (y-axis). The alignment of firing times in the local feedback raster plot indicates synchrony across the network. This is less visible in the global feedback raster plot. The parameters for these simulations were $g = -1.2$, $\mu = 0.5$, $c = 1.0$, and $\sigma^2 = 0.16$.

sive waves of firing and non-firing are also apparent in the temporal domain of the local feedback raster plot. This may indicate that the local feedback is attempting to entrain less neurons in the network than the global feedback. As a result the local feedback network can more effectively produce an oscillation in the network. This effect can be seen quantitatively by looking at the power spectrum of the individual spike trains for each network in Figure 5.5.

The power spectrum of the global feedback network (Figure 5.5 a) with

spatially correlated input, $c = 1$, contains a peak in the spectrum at approximately 50 Hz and no peak for spatially uncorrelated input, $c = 0$. This indicates that there is a network oscillation at approximately 50 Hz for correlated input and no network oscillation for uncorrelated input in the case of global feedback. These results agree well with theory (Equation 3.30) and qualitatively with simulation results presented in [18]. Quantitative agreement was also obtained by using the same feedback strength ($g = -1.2$) as in [18]. It should be noted here that the frequency at which the peak in the power spectra occurs is dependant on the time delay of the feedback [21]. In this case the peak in each network appears at the same frequency due to the common feedback delay time. The effects of changing delay time are discussed in [21] and are beyond the scope of this thesis.

The power spectra of the local feedback network, Figure 5.5 b), have peaks for correlated input as well as uncorrelated input at approximately 50 Hz. The peak present in the local feedback network is more pronounced for correlated input than for uncorrelated input, indicating that the network oscillation for correlated input is more prominent than for uncorrelated input.

Comparing the power spectra of the local and global feedback networks we see that, for correlated input, the local feedback network contains a stronger

network oscillation than the global feedback network. In the case of uncorrelated input, the local network not only shows a peak in the power spectra where the global feedback network does not, but the peak is also stronger than the peak in the global feedback network for correlated input. This indicates that uncorrelated input in a local feedback network produces a oscillation in the network, which is even stronger than the oscillation produced by correlated input in a global feedback network.

Theoretical predictions from Equation 3.23 agree with simulation results for both global and local feedback networks as shown in Figure 5.5, where dashed lines represent correlated input and solid lines represent uncorrelated input. Small discrepancies between theory and simulation are most likely due to the underestimation of the firing rate in the Euler integration scheme (as discussed in Section 2.4).

Theoretical results for stronger inhibitory feedback show a larger discrepancy with numerics in the local feedback case. The reasons for this are not well understood, but it is perhaps due to the linear approximations used in theory, which are less valid. Because g is scaling feedback spikes in the local feedback case, the feedback may no longer be small enough to apply only linear response theory; at this point higher order terms in the response

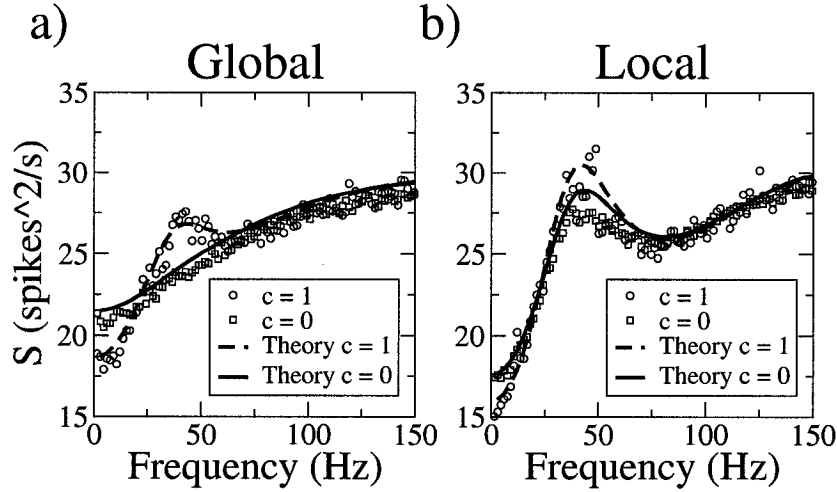


Figure 5.5: Individual spike train power spectrum averaged over 10^4 realizations a) for global feedback and b) local feedback. Circles and dashed lines represent the simulations and theory (Equation 3.23) respectively for a network with correlated input ($c = 1$). The squares and solid lines represent the simulations and theory for the uncorrelated input case ($c = 0$). The parameters used for simulations were $g = -0.6$, $\mu = 0.5$, $c = 1.0$, and $\sigma^2 = 0.16$. The axes have been scaled such that the membrane time constant τ_m is 6 ms. The global feedback profile produces qualitatively similar results as those obtained in [18] and [21]. The interesting feature is that the individual power spectra for local feedback show a network oscillation already for uncorrelated input ($c = 0$), whereas the global feedback case for $c = 0$ shows no oscillation.

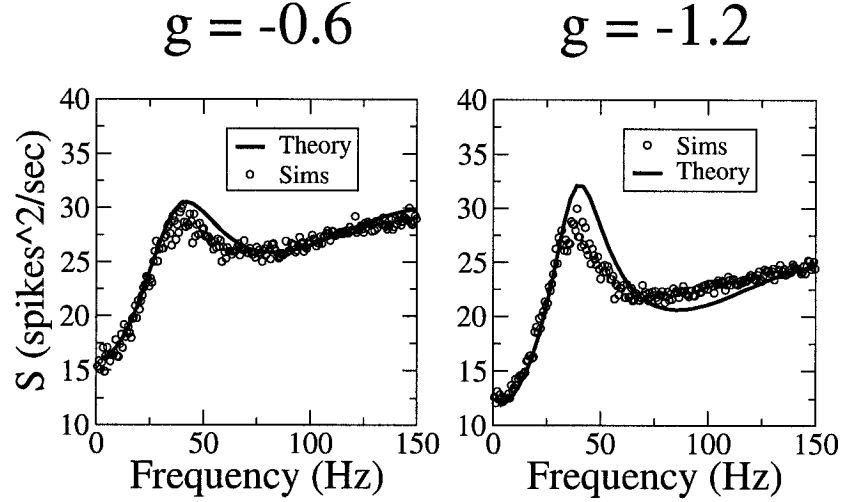


Figure 5.6: Power spectra of a local feedback network for two different values of feedback strength. Comparing the weak feedback (left) to stronger feedback (right), the discrepancy between theory (solid line) and simulation results (circles) becomes larger for increased feedback strength. Input and feedback parameters used in these simulations were $\mu = 0.5$, $c = 1$, $\sigma^2 = 0.16$, and $\sigma_g = 1$.

function can no longer be ignored. While it is not our goal to examine this nonlinear regime of the local feedback network, it is interesting to note that the non-linearity found in the local feedback network, for stronger inhibitory feedback, strengthens the network oscillation (Figure 5.6).

Simulations of a network with a square feedback profile (rather than Gaussian) were also explored. Power spectra results for a square feedback profile shape are shown in Figure 5.7. We see again that the height of the peak in

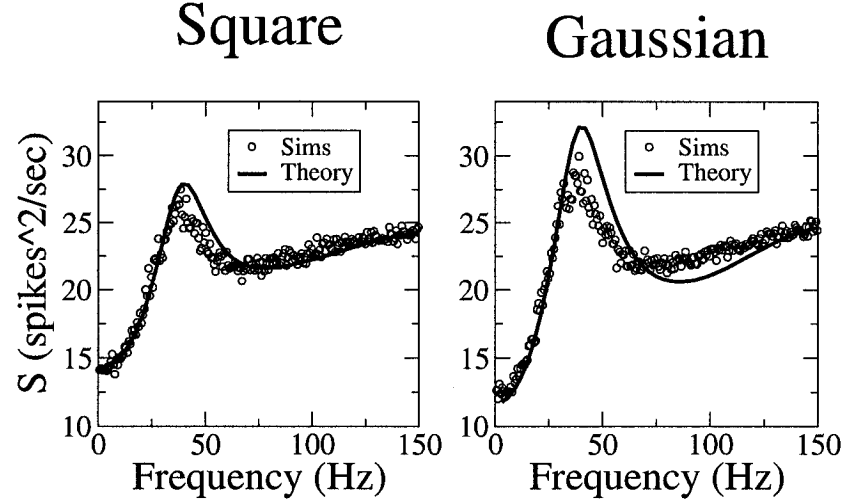


Figure 5.7: Power spectra of a local feedback network with a square feedback profile (left) compared to a local feedback network with a Gaussian feedback profile (right). There is a noticeable decrease in the height of the peak at 50 Hz for the square feedback profile in the simulations (circles), which is predicted by theory (solid line). The input and feedback parameters used in these simulations are the same as those indicated in Figure 5.6, with $g = -1.2$.

the power spectrum depends not only on the extent of the feedback profile, but also on the shape. It should be also noted here that theory (adjusted for this case) matches fairly well with simulations for the square feedback profile, indicating that the theory is not limited to a specifically Gaussian feedback profile. The precise effects of this square feedback profile shape on network dynamics is beyond the scope of this thesis.

These simulation results indicate that although the activity of the network

is not strongly affected by a change in spatial profile of the feedback, the robustness of a network oscillation is susceptible to the connectivity and shape of the spatial feedback profile. The same trends in oscillation strength for the local and global feedback networks are also seen for higher values of input bias (μ), including the superthreshold regime, $\mu > v_{th}$, (results shown in Chapter 6).

5.3 Gaussian Correlated Input

With the above results the question now becomes: how is this locally induced oscillation important for the weakly electric fish? This can be addressed by studying a more relevant input for the weakly electric fish. Here, we consider a Gaussian spatially correlated time dependent input, which is more appropriate for input signals with a finite spatial extent, such as prey signals.

Gaussian correlated input (GCI), described in chapter 3, is coloured in space and white in time, with spatial correlation parameter λ . So now λ controls the spatial correlation of the input instead of c . Here we give a brief overview of the similarities and differences between simulation results for GCI and PCI. For more details on GCI and PCI simulation results see Chapter 6.

The simulation results for GCI are similar to PCI results. Power spectra results, Figure 5.8, show the same types of trends for both inputs. A network with local feedback shows a peak in the power spectrum for uncorrelated input ($c = 0$) and for input with a short correlation length (eg. $\lambda = 1$). But there is a difference between PCI and GCI. The differences between the two types of input are apparent in the increase of the peak in the power spectra generated in each case. A linear increase in peak height is observed for percentage correlated input, Figure 5.8 top row, as c increases from 0 (no correlation) to 1 (complete correlation). However, for Gaussian correlated input, Figure 5.8 bottom row, the peak in the power spectra increases with increasing spatial input correlation length until the correlation length of the input matches or exceeds that of the feedback, at which point it tapers off.

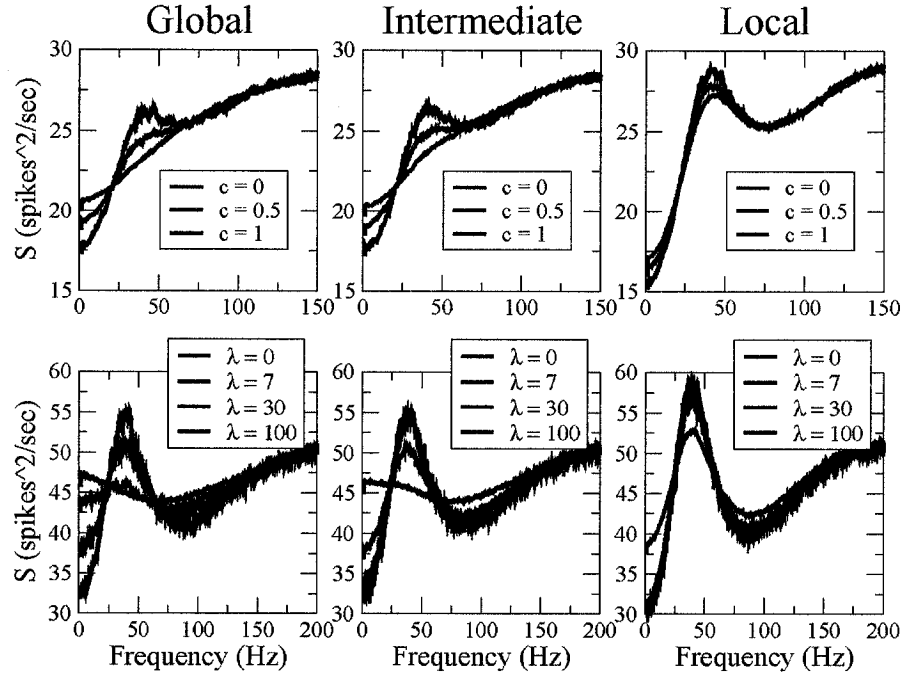


Figure 5.8: Power spectra of a stochastic LIF network driven by percentage correlated input, top row, and Gaussian correlated input, bottom row, for global feedback ($\sigma_g = 100$), first column, intermediate feedback ($\sigma_g = 9$), second column, and local feedback ($\sigma_g = 1$), third column. Other parameters used in these simulations were $\mu = 0.5$, $g = -0.6$, and $\sigma^2 = 0.16$.

This difference is more apparent looking at the peak power, which can be calculated using the “ Γ ” measure [18], $\Gamma(f_2 - f_1)$, which integrates the total power between two frequencies in the power spectra. Figure 5.9 shows the total power in the peak of the power spectrum (frequency range 40 Hz - 60 Hz), and the total power in the dip of the power spectrum (frequency range 2 Hz - 22 Hz), as a function of the spatial correlation parameter.

As in [18] this measure is an indicator of the strength of oscillation found in the network. That is, the area under the peak indicates the strength of the oscillation. The area under the dip decreasing correspondingly indicates a transfer of power from lower frequency to higher frequencies (i.e. the graphs in Figure 5.9 are symmetric about the point of inflection of the peak).

The differences between PCI and GCI become much more apparent looking at Figure 5.9. For a network with PCI (Figure 5.9 a)) Γ is plotted as a function of c , the portion of the input common to all neurons in the network. Here we see a steady increase in the oscillation strength of the network as c increases for both global, intermediate, and local inhibitory feedback profiles. The Γ results for the global inhibitory feedback network agree with those found in Figure 3 a) of [18]. The local inhibitory feedback network oscillation strength increases linearly as well, but is shifted to higher power

due to the network oscillation being stronger for local feedback, as discussed in the previous section.

For a network with Gaussian correlated input (Figure 5.9 b)) Γ is plotted as a function of λ , the spatial correlation length of the input. The local feedback network shows an increasing oscillation strength, which levels off for spatial correlations larger than the spread of the feedback. The same trend is seen for a intermediate feedback profile. The oscillation strength stops increasing after the input correlation has exceeded the spread of the feedback. In the case of global feedback, the network produces no oscillation for small spatial correlations, but only after a finite amount of spatial correlation is present in the input does the oscillation appear and continually increase.

In summary a stochastic LIF network with local feedback displays a network oscillation whether driven by percentage correlated input or Gaussian correlated input. The former type of input causes a linear increase in network oscillation strength as the amount of correlation in the input increases. The latter input shows a novel effect where a linear increase in network oscillation strength as the correlation length of the input increases until the input correlation length reaches the correlation length of the feedback and plateaus thereafter. In the next chapter we take a more in depth look at GCI and

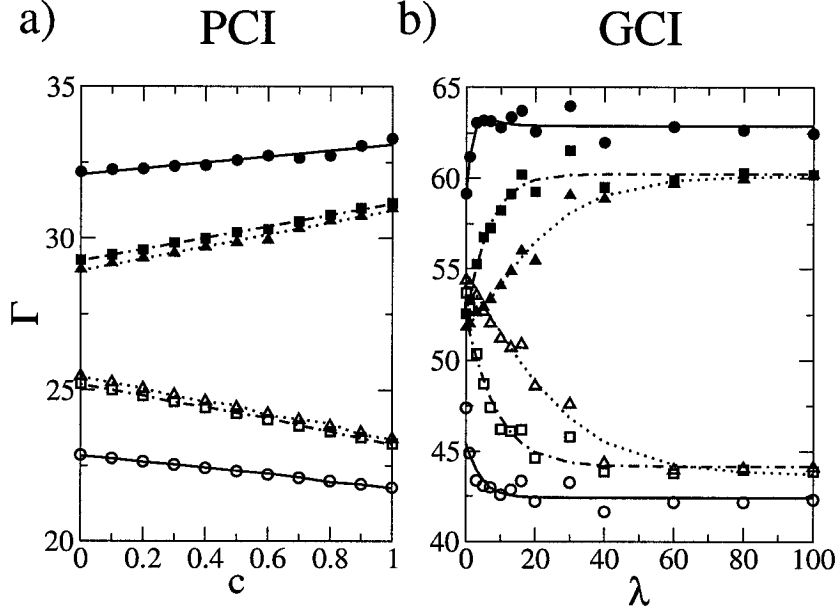


Figure 5.9: Power over a range of frequencies in the power spectrum, $\Gamma(f_2 - f_1)$, as a function of spatial correlation for a) PCI ($c = 0$ to $c = 1$) and b) GCI ($\lambda = 0$ to $\lambda = 100$). In both panels solid symbols represent the power found in the peak of the individual spike train spectra ($\Gamma(40Hz - 20Hz)$), open symbols represent the power in the preceding trough ($\Gamma(22Hz - 2Hz)$), triangles represent a global feedback ($\sigma_g = 100$) network, and circles represent a local feedback ($\sigma_g = 1$) network. The solid symbols are an indication of the network oscillation strength. In the PCI network, panel a), as c increases the oscillation strength increases proportionally. Lines in a) represent a linear fit to data. In the GCI network, panel b), as λ increases the oscillation strength increases until it matches the spatial extent of the feedback. The oscillation strength plateaus after $\lambda = \sigma_g$. Lines in b) represent an exponential fit to data. An additional feedback profile in between local and global is also included (squares) to show that these trends also occur for local feedback profiles with intermediate spatial extent, $\sigma_g = 9$. These results are for $\mu = 0.5$, $g = -0.6$, and $\sigma^2 = 0.16$.

PCI inputs for both global and local feedback.

Chapter 6

Simulation Results

6.1 Introduction

To understand how local feedback affects the network differently than global feedback it is instructive to reduce the model to its most basic form and build on this. Here we start with a simple deterministic LIF model and build up to the fully stochastic LIF model with spatially profiled delayed feedback. Various measures discussed in Chapter 2, such as raster plots, ISI histograms and synchrony, are used to gain further insight into the results obtained thus far.

Parameters used in simulation results shown in this chapter are $g = 0$ (no feedback), $g = -1.2$ (global and local inhibitory feedback), $\sigma_g = 100$ (global feedback), $\sigma_g = 1$ (local feedback), $\mu = 1.5$ (superthreshold), and $\mu = 0.5$ (subthreshold). As specified in Chapter 3, $v_{th} = 1$, $v_r = 0$, $\tau_R = 0.1$, $\sigma = 3$,

$\tau_d = 1.0$, and $\Delta t = 0.001$. Other parameters, D_{int} , σ^2 , and c (PCI input) or λ (GCI input) are specified below.

6.2 Deterministic LIF Network

First we look at raster plot simulation results for a basic deterministic LIF network ($D_{int} = 0.0$ and $\sigma^2 = 0.0$) with various feedback profiles. With no feedback (Figure 6.1(a)) each cell in the network is a self-oscillator and thus the firing pattern attained in Figure 6.1(a) is asynchronous. The specific pattern obtained in the no-feedback network is dependent on the initial conditions of the individual neurons in the network (which are randomly generated in these simulations). That is, if the initial state is synchronous (i.e. identical for all cells) then the future states of the network will be synchronous, but if the initial state is asynchronous, so will future states of the network. As in [4] we will call the oscillation period of the individual neurons the neuron period, which has an associated frequency f_{neuron} .

Global feedback (Figure 6.1(b)) causes the individual oscillators to synchronize and oscillate with a longer period, which is called the network period and has an associated frequency f_{net} [4]. Local feedback (Figure 6.1(c)) also causes the individual LIFs to oscillate with the same network period as global

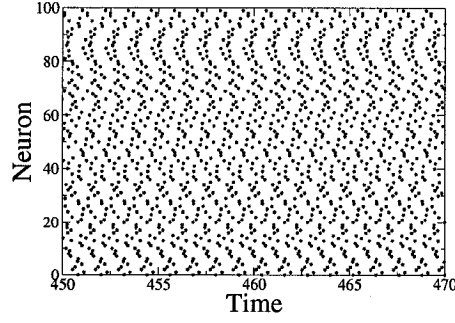
feedback, but the network is no longer synchronous. This longer period is caused by the feedback delay [4], which is the same for both network architectures.

The difference between local and global feedback in the deterministic LIF network is that local feedback does not cause the individual oscillators to synchronize, but produces a standing wave across the network. The term standing wave is used here to indicate that the wave shape is preserved over time. Zoom-in's of Figures 6.1(b) and 6.1(c) are overlayed in Figure 6.1(d) to show the complete synchronization in the case of global feedback and the standing wave in the case of local feedback. The shape of the standing wave will be highly dependent on initial conditions due to the fact that, with local feedback, there persists a memory of the initial conditions in the shape of the firing pattern.

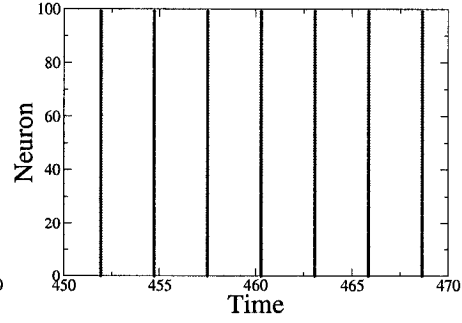
A more quantitative measure of the period of oscillation can be found by looking at the ISI histograms of the network. The ISI histograms (Figure 6.2(a)) for the three different types of architectures mentioned above show the two different periods of oscillation, with $f_{neuron} \sim 130Hz$ for the network with no feedback and $f_{net} \sim 50Hz$ for the networks with inhibitory feedback.

Figure 6.2(b) shows the synchrony (Equation 2.32) created by the three

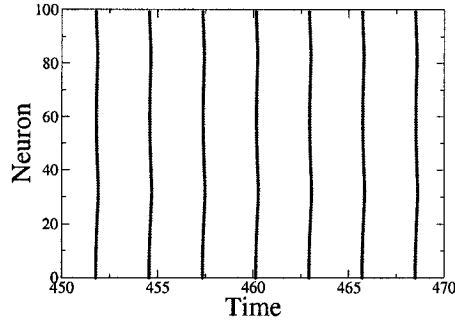
different types of network architecture. Global feedback synchronizes the population rapidly. The local feedback also appears to synchronize the network, but in fact local feedback actually synchronizes the network into standing waves (Figure 6.1(d)). The slow increase of synchrony seen for the local feedback architecture indicates that the standing wave of synchrony is generated more slowly than the complete synchrony in the global feedback architecture. The synchrony of the network with no feedback depends on the initial state of the network, as discussed above.



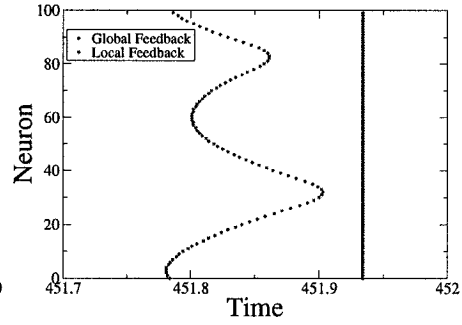
(a) Raster plot of a deterministic LIF network without feedback.



(b) Raster plot of a deterministic LIF network with global feedback.

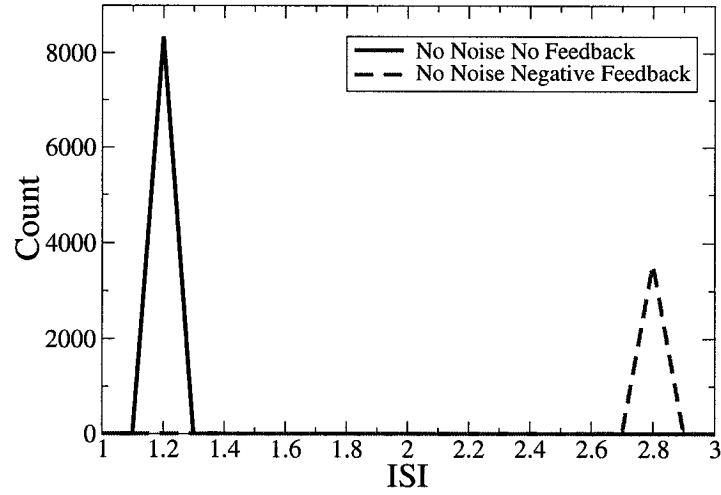


(c) Raster plot of a deterministic LIF network with local feedback.

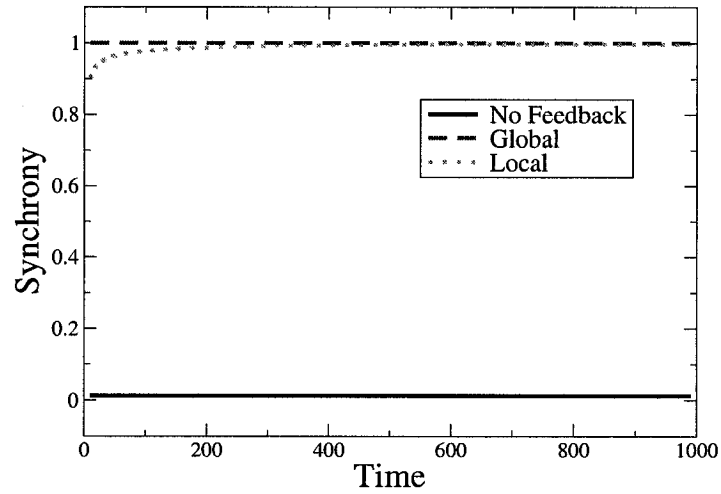


(d) Overlay of (b) and (c), local feedback on the left and global feedback on the right.

Figure 6.1: Simulation results for a deterministic LIF network with no external noise in the superthreshold regime.



(a) ISI histogram of a deterministic LIF network.



(b) Synchrony of a deterministic LIF network.

Figure 6.2: Simulation results for a deterministic LIF network with no external noise in the superthreshold regime.

6.3 Stochastic LIF Network

The addition of internal noise ($D_{int} = 0.08$, $\sigma^2 = 0.0$) to a deterministic network causes the network to behave stochastically. In such a stochastic LIF network, action potentials can be seen even with a subthreshold base current (or input bias, μ) due to noise-induced crossings of the threshold, whereas in the deterministic network we need to provide a superthreshold base current to generate action potentials. For comparison purposes we discuss a stochastic network with a superthreshold base current and then compare these results to the ones obtained with a subthreshold base current.

Superthreshold Regime

The addition of internal noise to the network disrupts both the network oscillation and the individual neuron oscillation. However, in the case of local feedback not all of the network oscillation is wiped out. A bit more oscillatory structure can be seen in the local feedback raster plot (Figure 6.3(c)) compared to the global feedback raster plot (Figure 6.3(b)) and the no-feedback raster plot (Figure 6.3(a)), which both fire stochastically. One possible reason for this is that the local feedback network only entrains a small local portion of the network to oscillate and indeed Figure 6.3(d) shows

the clustering in the local feedback network is greater than in the global feedback network. However, the average synchrony in the network (Figure 6.4(a)) shows that the global feedback network is more synchronous than the local feedback network. Although not obvious, these two results are not contradictory, they both support the idea that the global feedback network attempts to entrain all the neurons in the network into an oscillation and that the local feedback network only tries to entrain a few nearby, thus making the overall synchrony across the network less for local feedback.

The difference between local and global feedback is also prominent in the ISI histograms (Figure 6.4(c)). The global feedback has a wide spread of ISI's peaked near the self-oscillation period, whereas the local feedback ISI distribution is bimodal with a peak near the self-oscillation period and another peak at the network oscillation period. Both global feedback and no feedback ISI histograms resemble Poisson distributions, further indicating that these two networks are firing stochastically. The bimodal histogram seen in the local feedback case is an indicator of oscillatory activity in the network and bursting in the spike trains of the network (as discussed in Chapter 2). The power spectrum (Figure 6.4(d)) clearly indicates that there is indeed an oscillation in the local feedback network at the network oscillation frequency

and not for the other two network architectures. The pattern of the ISI return map (Figure 6.4(b)) indicates that there indeed are bursts of spikes in the spike trains of the local feedback network and much fewer in the other two networks.

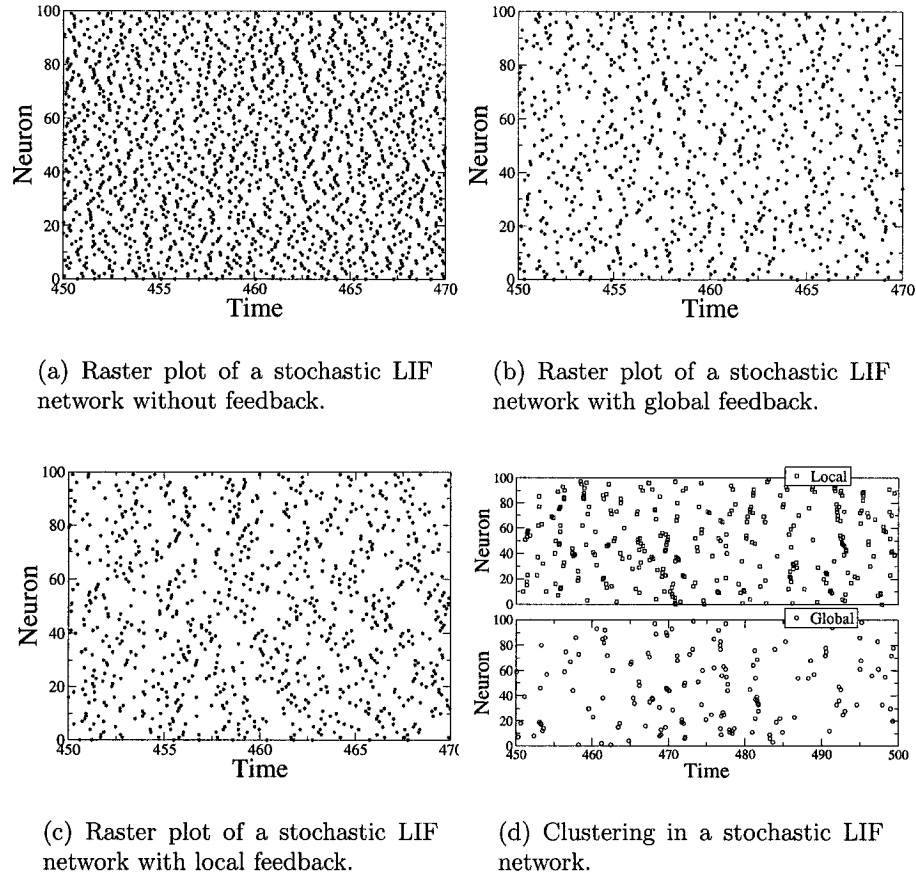
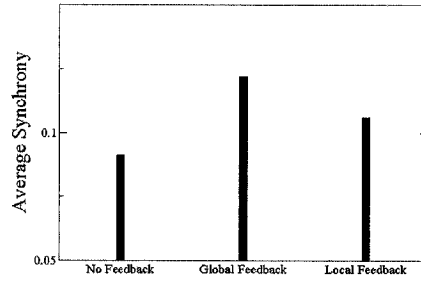
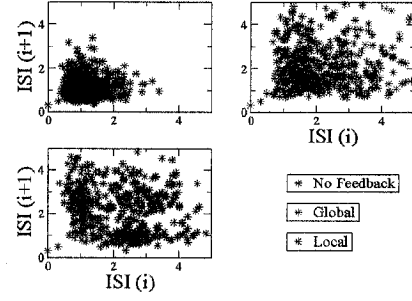


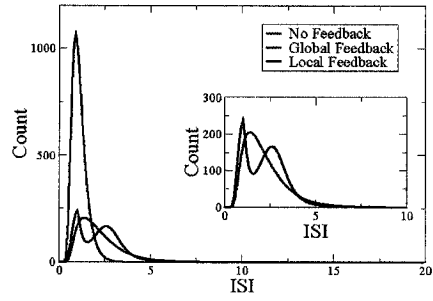
Figure 6.3: Simulation results for a stochastic LIF network with no external noise in the superthreshold regime.



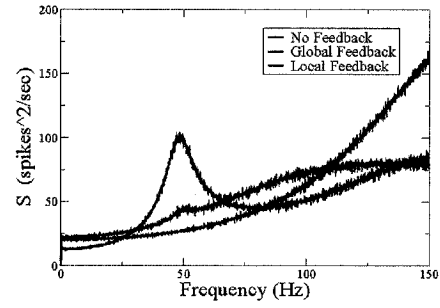
(a) Synchrony of a stochastic LIF network.



(b) Return Map of a stochastic LIF network.



(c) ISI histogram of a stochastic LIF network.



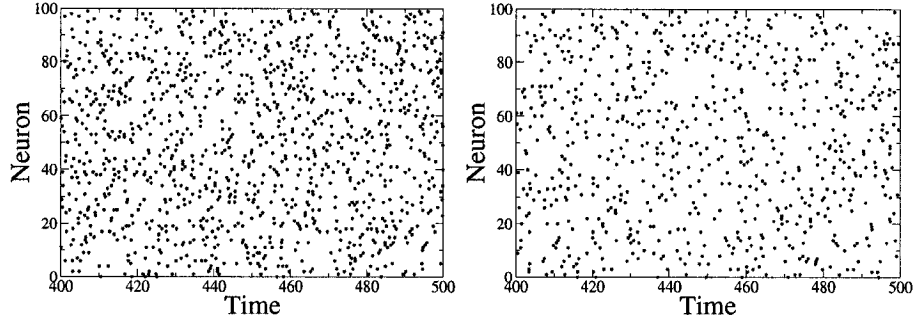
(d) Power Spectrum of a stochastic LIF network.

Figure 6.4: Simulation results for a stochastic LIF network with no external noise in the superthreshold regime.

Subthreshold Regime

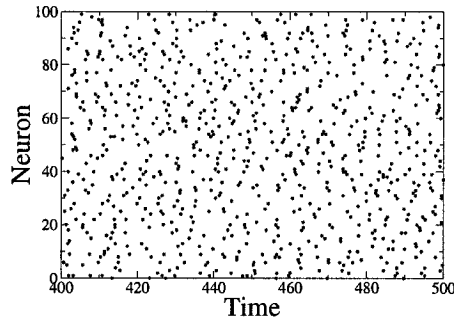
With a subthreshold base current, the cells in the network fire much more sparsely and the difference between local and global feedback networks becomes less noticeable. No noticeable pattern can be discerned in the local feedback raster plot (Figure 6.5(c)), the global feedback raster plot (Figure 6.5(b)) nor the raster plot for the network without any feedback (Figure 6.5(a)). The difference between the three different architectures in the subthreshold regime only becomes evident when looking at the ISI histograms (Figure 6.6(c)) and power spectra (Figure 6.6(d)). The ISI histogram becomes broader for global feedback and develops a small bimodality for local feedback. The power spectrum confirms a weak oscillation for the case of local feedback. The ISI return map (6.6(b)) reveals no information about the firing patterns of the spike trains in the subthreshold regime; this is also due to the sparseness of the firing. Interestingly the average synchrony (Figure 6.6(a)) in the subthreshold network is the opposite of the superthreshold case. Global feedback is slightly less synchronous than local feedback. The weak firing in the subthreshold regime reduces the synchrony for global feedback much more dramatically than local feedback, because it is trying to entrain the whole network when it is scarcely firing. The sparse firing has

less effect on the local feedback network's ability to entrain small sections of the network.



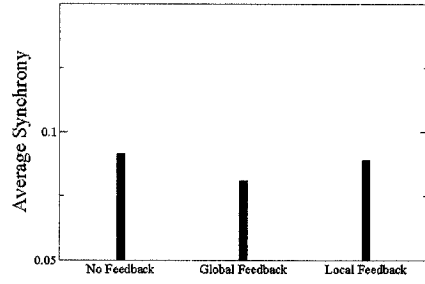
(a) Raster plot of a stochastic LIF network without feedback.

(b) Raster plot of a stochastic LIF network with global feedback.

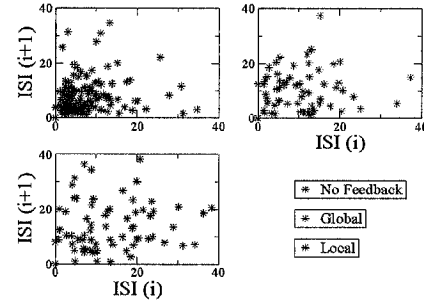


(c) Raster plot of a stochastic LIF network with local feedback.

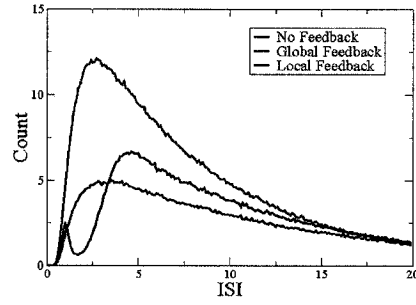
Figure 6.5: Simulation results for a stochastic LIF network with no external noise in the subthreshold regime.



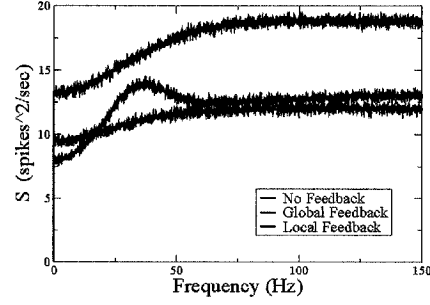
(a) Synchrony of a stochastic LIF network.



(b) Return Map of a stochastic LIF network.



(c) ISI histogram of a stochastic LIF network.



(d) Power Spectrum of a stochastic LIF network.

Figure 6.6: Simulation results for a stochastic LIF network with no external noise in the subthreshold regime.

6.4 Stimulus Driven LIF Network

6.4.1 Percentage Correlated Input ($c = 1$) in a Deterministic LIF Network

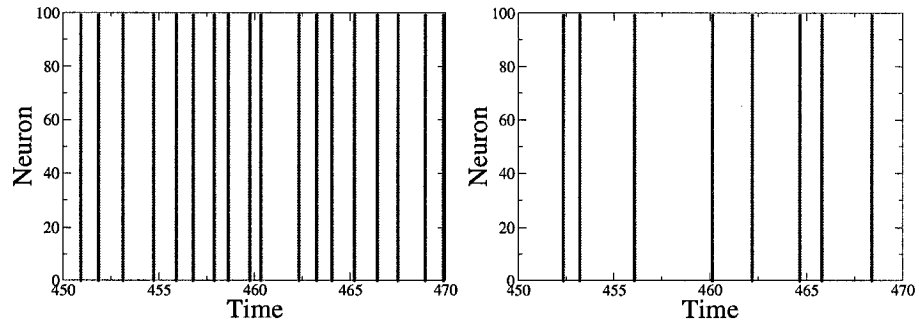
Adding a stochastic spatially correlated input signal (Equation 3.2, $c = 1$, $\sigma^2 = 0.16$) to the deterministic LIF network ($D_{int} = 0$) causes the network population to fire synchronously.

Superthreshold Regime

This synchrony can be seen in all three network raster plots (Figure 6.7(a), 6.7(b), and 6.7(c)). The neurons in the network fire synchronously in an attempt to follow the input. In the network with no feedback the neurons fire synchronously, no longer oscillating independently as in the non-driven network, with periods distributed about f_{neuron} (see Figure 6.7(a)). Similarly networks with inhibitory feedback fire synchronously, but with periods that actually jump back and forth from being distributed around f_{net} and f_{neuron} (Figure 6.7(b) and 6.7(c)). In this case the network oscillation is broken up by the external input. Additionally, in the local inhibitory feedback case, the standing wave seen in Figure 6.1(d) also disappears due to the synchronizing effect of the correlated input. The average synchrony is slightly lower in the local feedback case (see Figure 6.8(a)) due to the longer relaxation time of

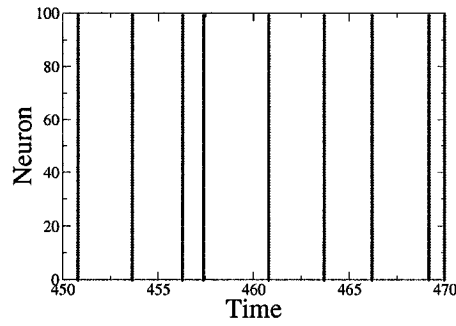
the local feedback network compared to the global feedback network, which can also be seen in the non-driven deterministic network (Figure 6.2(b)).

The ISI histograms also show that in a deterministic network, with an external stochastic driving signal, there is little difference, apart from statistical fluctuations, between local and global feedback (see Figure 6.8(c)). The bimodality of the ISI histogram and the pattern of the ISI return map (Figure 6.8(b)) indicate that the spike trains contain bursts, which are an attribute of the inhibitory feedback in the network. The power spectra (Figure 6.8(d)) show that both inhibitory feedback networks produce a pronounced oscillation at the network frequency. Compared with the power spectra for the non-driven stochastic network (Figure 6.4(d)), a larger peak is present in the power spectrum for the driven deterministic network. Thus, internal noise reduces the strength of the network oscillation at f_{net} .



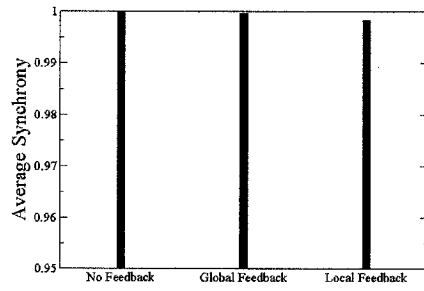
(a) Raster plot of a PCI driven deterministic LIF network with no feedback.

(b) Raster plot of a PCI driven deterministic LIF network with global feedback.

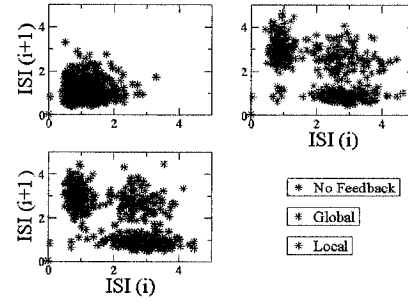


(c) Raster plot of a PCI driven deterministic LIF network with local feedback.

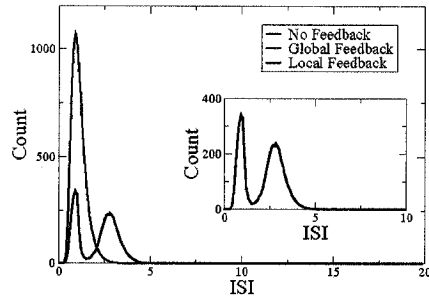
Figure 6.7: Simulation results for a deterministic LIF network with PCI ($c = 1$), in the superthreshold regime.



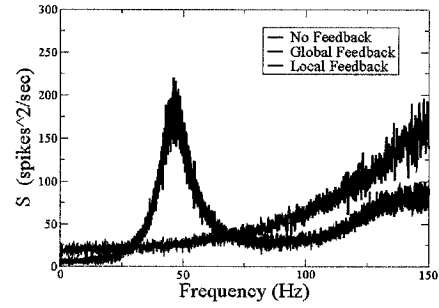
(a) Synchrony of a PCI driven deterministic LIF network.



(b) Return Map of a PCI driven deterministic LIF network.



(c) ISI histogram of a PCI driven deterministic LIF network.



(d) Power Spectrum of a PCI driven deterministic LIF network.

Figure 6.8: Simulation results for a deterministic LIF network with PCI ($c = 1$), in the superthreshold regime.

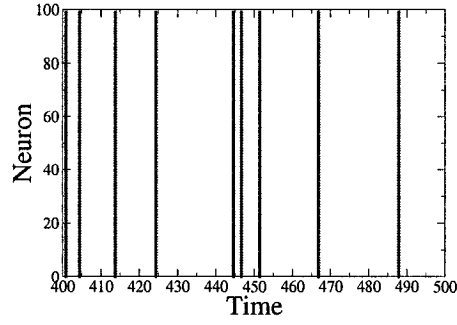
Subthreshold Regime

In the subthreshold regime the networks with inhibitory feedback behave synchronously as well and in this case the raster plots have become identical (Figures 6.9(b), and 6.9(c)), showing that the feedback profile is unimportant for a driven deterministic LIF network in the subthreshold regime. The network can only fire for sufficiently large stimulus and hence it follows the large positive excursions of the input. The average synchrony amongst the different network architectures is fairly even, as seen in Figure 6.10(a). Comparing with Figure 6.8(a) we see that all three architectures are synchronizing the system at the same rate, indicating that the network is indeed following the input.

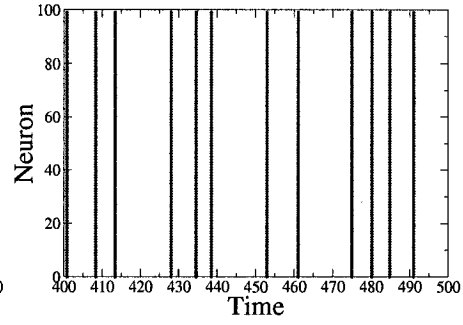
The ISI histograms (Figure 6.10(c) right) and return maps (Figure 6.10(b)) indicate that there is only a small amount of bursting occurring in the inhibitory feedback networks. Accordingly the power spectra (Figure 6.10(d)) show that a small oscillation still exists in the networks with inhibitory feedback.

To summarize, a deterministic LIF network, driven by a stochastic input that is homogeneous across the network, synchronizes to follow the driving input. In the subthreshold regime the network cannot fire without stimuli

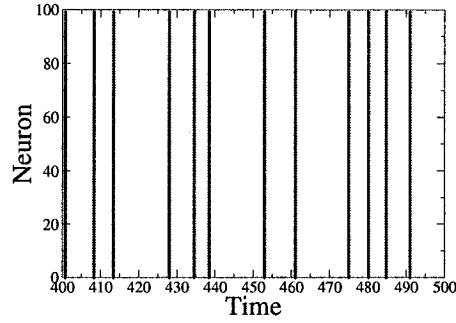
and thus follows the stimulus more closely. Inhibitory feedback, regardless of its profile, has the same effect on the network, creating a strong network oscillation with bursts in the superthreshold regime and a weaker network oscillation with few bursts in the subthreshold regime.



(a) Raster plot of a PCI driven deterministic LIF network with no feedback.

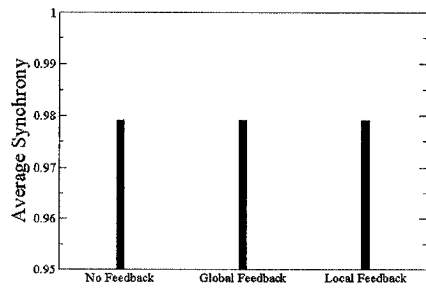


(b) Raster plot of a PCI driven deterministic LIF network with global feedback.

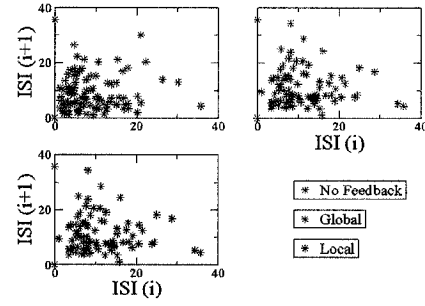


(c) Raster plot of a PCI driven deterministic LIF network with local feedback.

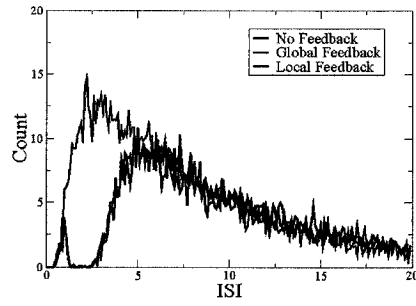
Figure 6.9: Simulation results for a deterministic LIF network with PCI ($c = 1$), in the subthreshold regime.



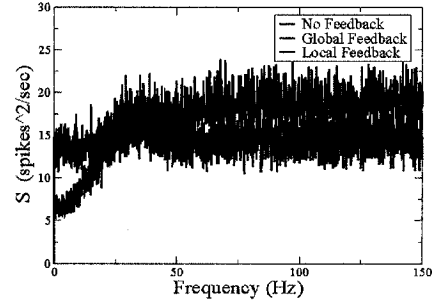
(a) Synchrony of a PCI driven deterministic LIF network.



(b) Return Map of a PCI driven deterministic LIF network.



(c) ISI histogram of a PCI driven deterministic LIF network.



(d) Power Spectrum of a PCI driven deterministic LIF network.

Figure 6.10: Simulation results for a deterministic LIF network with PCI ($c = 1$), in the subthreshold regime.

6.4.2 Percentage Correlated Input ($c = 1$) in a Stochastic LIF Network

Adding internal noise to the network we now look at simulation results of a driven stochastic neural network ($D_{int} = 0.08$, $\sigma^2 = 0.16$).

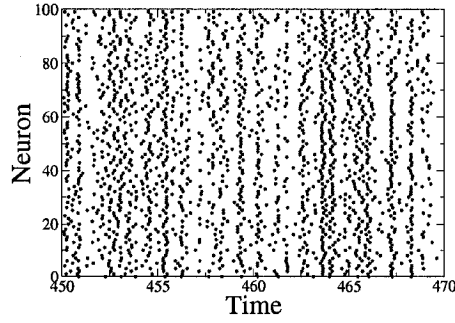
Superthreshold Regime

It is apparent from the raster plots (Figures 6.11(a), 6.11(b) and 6.11(c)), as for the driven deterministic network, that the network with no feedback follows the individual neuron oscillation frequency, and that the network with either local or global inhibitory feedback follows a combination of the two times scales of the network.

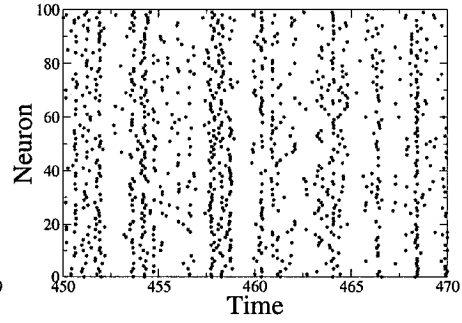
As in the non-driven stochastic network case, the addition of internal noise allows differences between local and global feedback, with the local feedback network being able to maintain a network oscillation more effectively than the global feedback network. This is not apparent in the raster plots, but can be seen in the cluster diagram (Figure 6.11(d)). Local feedback appears to have more aligned clusters spaced at the network period than global feedback.

This can be quantitatively seen by looking at the ISI histogram (Figure 6.12(c)) as well as the power spectra (Figure 6.12(d)). The ISI histogram shows a stronger bimodality in the local feedback case and the power spec-

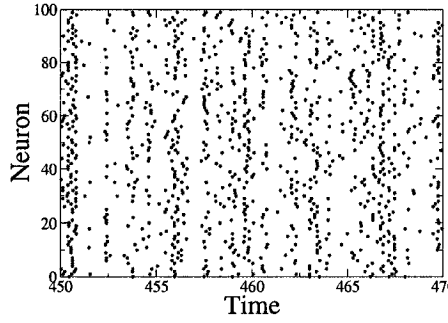
trum has a higher peak for local feedback than global. Both indicate a stronger oscillation in the local feedback network. This difference arises due to the global feedback network attempting to entrain the entire network of neurons, while the local feedback network only tries to entrain a small cluster of neighbouring neurons. While it is evident that the local feedback network fires more in local clusters and oscillates more strongly at f_{net} , Figure 6.12(a) shows that the global feedback network is more synchronous. Again this is not a contradiction, but supports the idea that global feedback works to entrain more neurons in the network. The ISI return map (Figure 6.12(b)) has no visible bursting pattern for global feedback, but shows a slight resemblance to a burst pattern for local feedback.



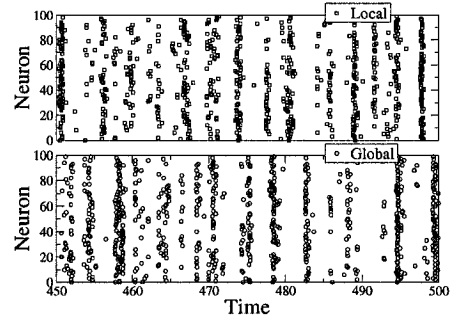
(a) Raster plot of a PCI driven stochastic LIF network with no feedback.



(b) Raster plot of a PCI driven stochastic LIF network with global feedback.

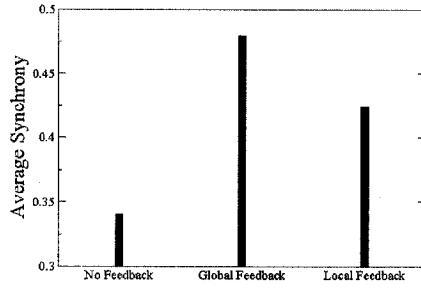


(c) Raster plot of a PCI driven stochastic LIF network with local feedback.

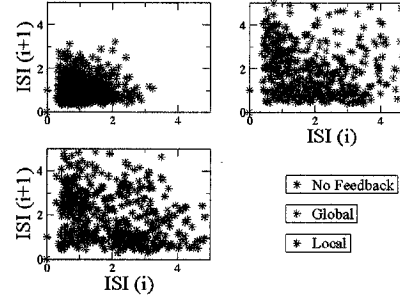


(d) Clustering in a PCI driven stochastic LIF network.

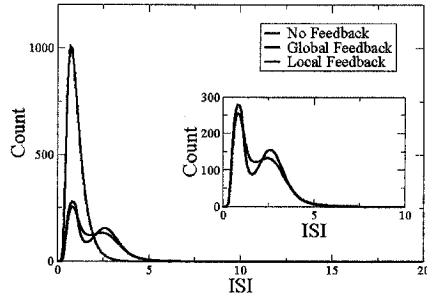
Figure 6.11: Simulation results for a stochastic LIF network with PCI ($c = 1$), in the superthreshold regime.



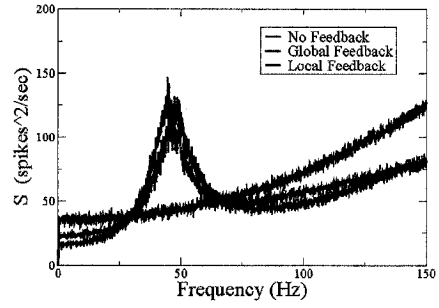
(a) Synchrony of a PCI driven stochastic LIF network.



(b) Return Map of a PCI driven stochastic LIF network.



(c) ISI histogram of a PCI driven stochastic LIF network.



(d) Power Spectrum of a PCI driven stochastic LIF network.

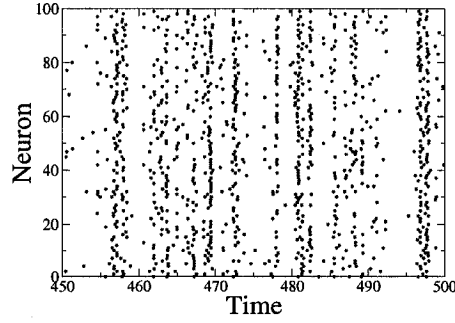
Figure 6.12: Simulation results for a stochastic LIF network with PCI ($c = 1$), in the superthreshold regime.

Subthreshold Regime

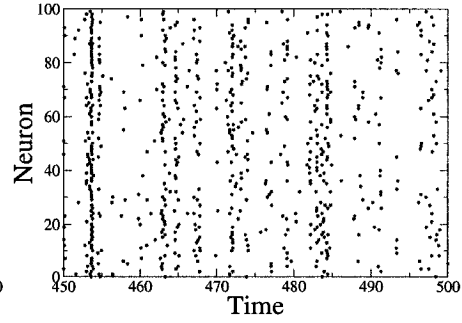
In the subthreshold regime the addition of internal noise allows the network to fire more than with only external noise, and thus, better expresses the characteristics of the network. The network with no feedback is able to fire more synchronously (comparing Figures 6.12(a) and 6.14(a)) in the subthreshold regime and thus follows the stimulus slightly better. This is also visible comparing the two raster plots (Figures 6.11(a) and 6.13(a)). The tendency of each neuron to oscillate independently is more prominent in the superthreshold regime. For the networks with inhibitory feedback, the raster plots (Figures 6.13(b) and 6.13(c) respectively) reveal a slightly stronger network oscillation in the local feedback network compared to the global feedback network. The same trends are seen in the ISI histograms (Figure 6.14(c)) and the power spectra (Figure 6.14(d)), as seen in the superthreshold regime. Due to the sparse firing of the network in the subthreshold regime the local feedback network appears more synchronous than the global feedback network (Figure 6.14(a)). The global feedback network is inefficient at entraining the entire network under such sparse firing conditions. This can be seen by comparing raster plots (Figures 6.13(b) and 6.13(c)) and in the cluster diagram (Figure 6.13(d)). The ISI return maps give no indication of

bursting in the subthreshold regime (Figure 6.14(b)).

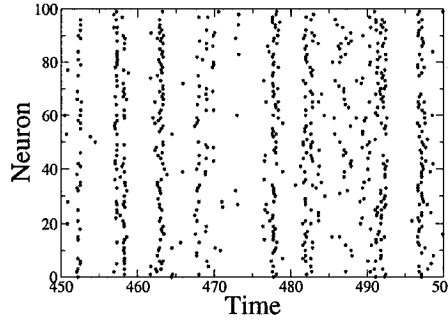
In summary, a driven stochastic LIF network is less synchronous than a driven deterministic LIF network. In the PCI driven deterministic LIF network there is no apparent difference between feedback profiles, but a difference becomes apparent in the PCI driven stochastic LIF network. Local inhibitory feedback produces a stronger oscillation than global inhibitory feedback. The local feedback profile only affects a few neighbouring neurons in the network and is able to maintain the network oscillation in small clusters of the network. In doing so it is more effective at producing a network oscillation amongst all the neurons in the network.



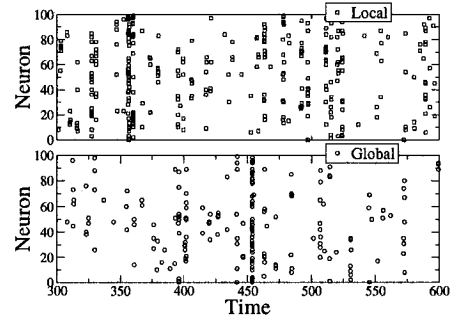
(a) Raster plot of a PCI driven stochastic LIF network with no feedback.



(b) Raster plot of a PCI driven stochastic LIF network with global feedback.

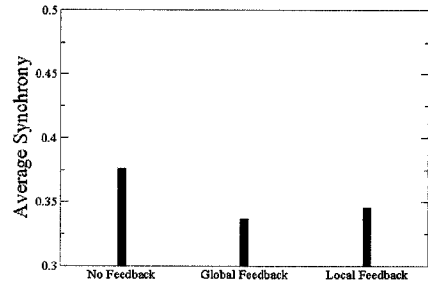


(c) Raster plot of a PCI driven stochastic LIF network with local feedback.

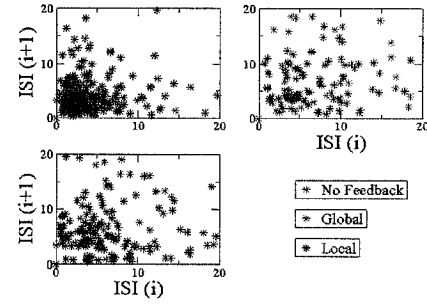


(d) Clustering in a PCI driven stochastic LIF network.

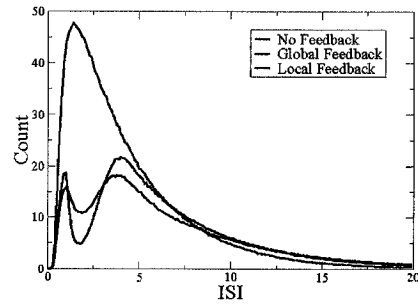
Figure 6.13: Simulation results for a stochastic LIF network with PCI ($c = 1$), in the subthreshold regime.



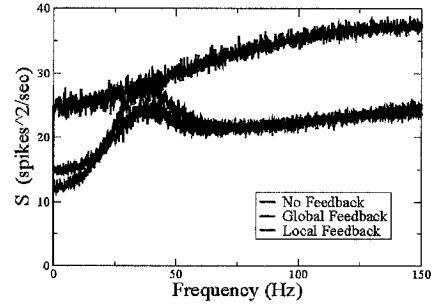
(a) Synchrony of a PCI driven stochastic LIF network.



(b) Return Map of a PCI driven stochastic LIF network.



(c) ISI histogram of a PCI driven stochastic LIF network.

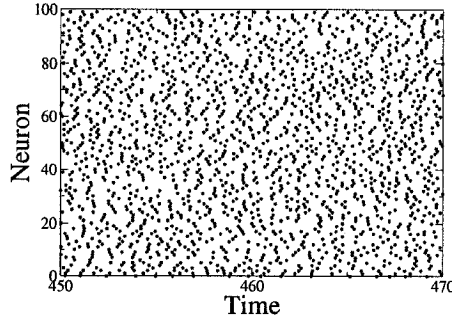


(d) Power Spectrum of a PCI driven stochastic LIF network.

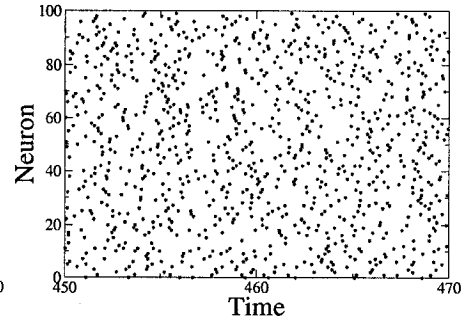
Figure 6.14: Simulation results for a stochastic LIF network with PCI ($c = 1$), in the subthreshold regime.

6.4.3 Percentage Correlated Input ($c = 0$) in a Stochastic LIF Network

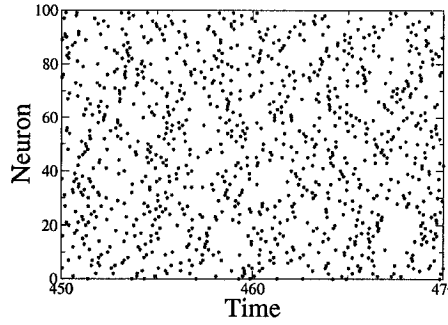
The driving input in the previous graphs has been completely spatially correlated. Here we look at the noise driven stochastic model ($D_{int} = 0.08, \sigma^2 = 0.16$) with spatially uncorrelated input, $c = 0$. The uncorrelated input adds enough noise to the network to completely destroy the network oscillation of the global inhibitory feedback network, whereas the local network still produces a network oscillation, though weaker than for correlated input. This is also true for the subthreshold regime (not shown).



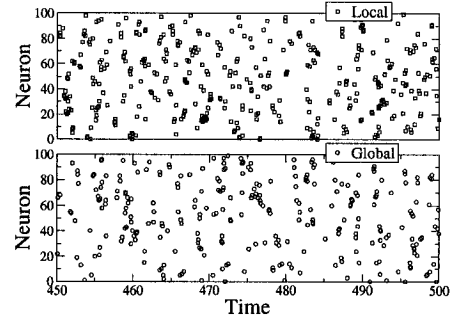
(a) Raster plot of a PCI driven stochastic LIF network with no feedback.



(b) Raster plot of a PCI driven stochastic LIF network with global feedback.

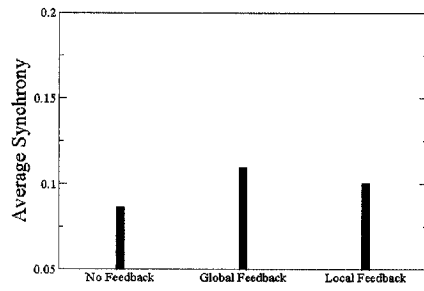


(c) Raster plot of a PCI driven stochastic LIF network with local feedback.

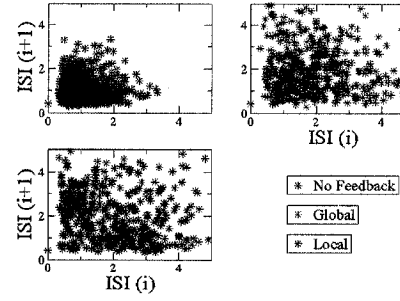


(d) Clustering in a PCI driven stochastic LIF network.

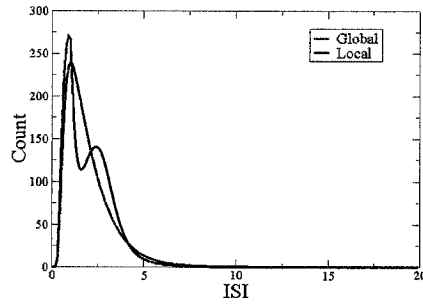
Figure 6.15: Simulation results for a stochastic LIF network with PCI ($c = 0$), in the superthreshold regime.



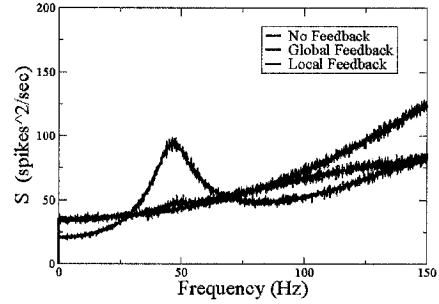
(a) Synchrony of a PCI driven stochastic LIF network.



(b) Return Map of a PCI driven stochastic LIF network.



(c) ISI histogram of a PCI driven stochastic LIF network.



(d) Power Spectrum of a PCI driven stochastic LIF network.

Figure 6.16: Simulation results for a stochastic LIF network with PCI ($c = 0$), in the superthreshold regime.

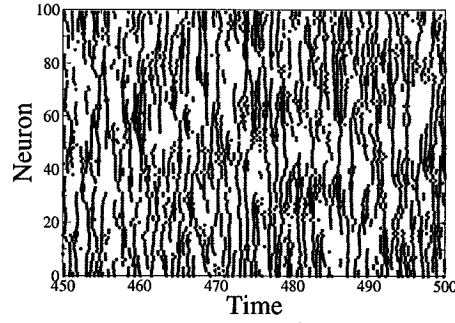
6.4.4 Gaussian Correlated Input ($\lambda = 5$) in a Deterministic LIF Network

Driving a deterministic LIF network ($D_{int} = 0$) with Gaussian correlated input (Equation 3.3, $\lambda = 5.0$, $\sigma^2 = 0.16$), rather than PCI, causes the network to fire in wave fragments (localized stretches of points in spacetime).

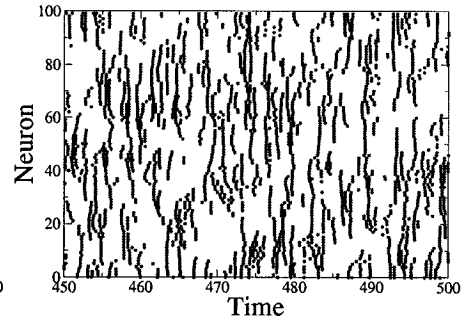
Superthreshold Regime

The wave fragment firing pattern can be seen in the raster plots of all three networks (Figures 6.17(a), 6.17(b), and 6.17(c)), which indicates in general that the stimulus is being followed by the network. The network without feedback has more densely packed wave fragments than both inhibitory feedback networks, which is expected from a network with a higher average firing rate. The cluster diagram (Figure 6.17(d)) shows a visible network oscillation in the case of local feedback, but not in the case of global feedback. This can also be seen somewhat in the raster plots (comparing Figures 6.17(b) and 6.17(c)). While synchrony in all three networks is rather low (Figure 6.18(a)), it is slightly higher for the network with global feedback than the network with local feedback or no feedback. This may indicate that the global feedback network has more vertical wave segments in the raster plot than the other two networks. The ISI histogram (Figure 6.18(c)) is bimodal

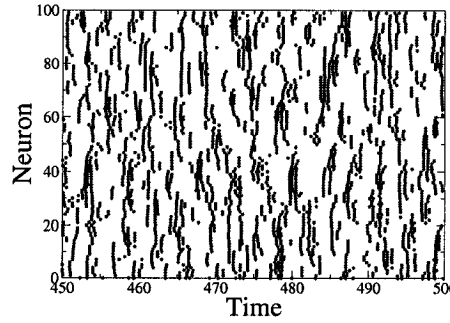
for local feedback and unimodal for global feedback indicating that there exists an oscillation in the network for locally profiled feedback and none for globally profiled feedback. However, the power spectra (Figure 6.18(d)) actually show a small peak at the network oscillation frequency for the global feedback network, showing that the ISI histogram isn't always a perfect indicator of network oscillations. The bimodality of the ISI histogram for the local feedback network also reveals the presence of bursts, which is confirmed by the dense regions along the axes of the ISI return map (Figure 6.18(b)).



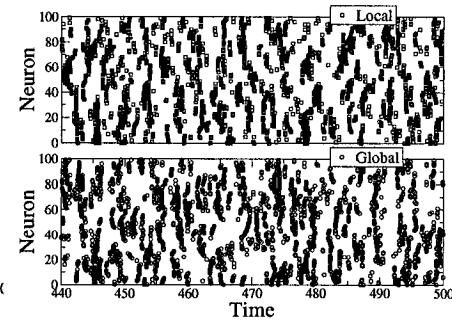
(a) Raster plot of a GCI driven deterministic LIF network with no feedback.



(b) Raster plot of a GCI driven deterministic LIF network with global feedback.

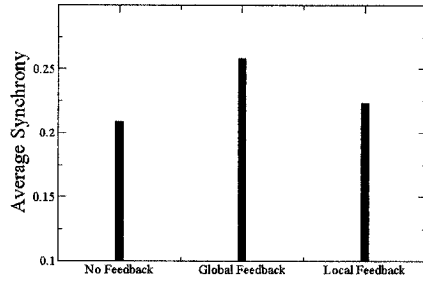


(c) Raster plot of a GCI driven deterministic LIF network with local feedback.

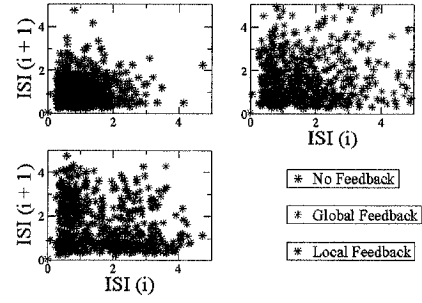


(d) Clustering in a GCI driven deterministic LIF network.

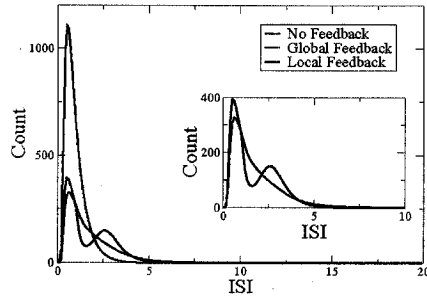
Figure 6.17: Simulation results for a deterministic LIF network with GCI ($\lambda = 5$), in the superthreshold regime.



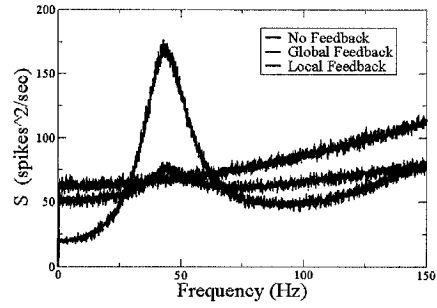
(a) Synchrony of a GCI driven deterministic LIF network.



(b) Return Map of a GCI driven deterministic LIF network.



(c) ISI histogram of a GCI driven deterministic LIF network.

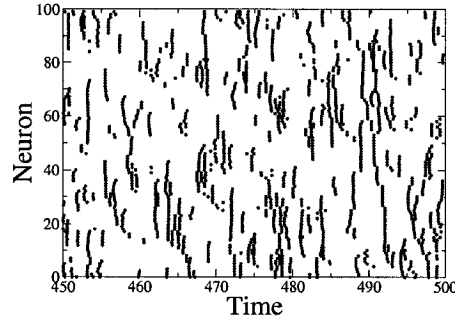


(d) Power Spectrum of a GCI driven deterministic LIF network.

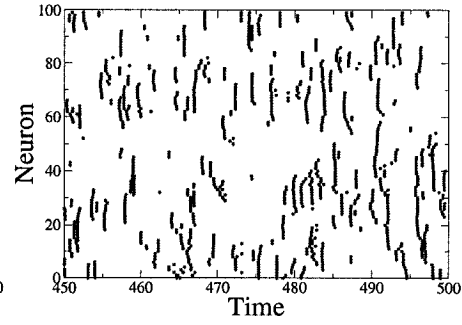
Figure 6.18: Simulation results for a deterministic LIF network with GCI ($\lambda = 5$), in the superthreshold regime.

Subthreshold Regime

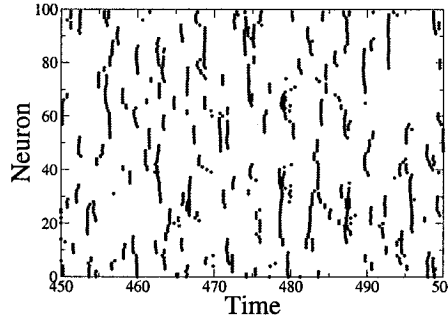
In the subthreshold regime the raster plots show that the network fires much more sparsely (Figures 6.19(a), 6.19(b) and 6.19(c)). The wave fragment firing pattern is visible in all three indicating that the firing is following the input signal (since there is no internal noise). The cluster diagram (Figure 6.19(d)) shows that there are more clusters of neurons firing for the local feedback network than the global feedback network, but no cross network wave is visible in either. Again, as in the PCI case, the sparse firing affects the global feedback network most in decreasing its average synchrony (Figure 6.20(a)). The ISI histogram (Figure 6.20(c)) shows a strong bimodality for local feedback and a very weak bimodality for global feedback indicating a potential oscillation and bursts in the network. The power spectra (Figure 6.20(d)) show a pronounced oscillation for local feedback and a weak oscillation for global feedback. According to the ISI return maps (Figure 6.20(b)) bursts appear to be present in the local feedback spike trains, but not the global feedback spike trains.



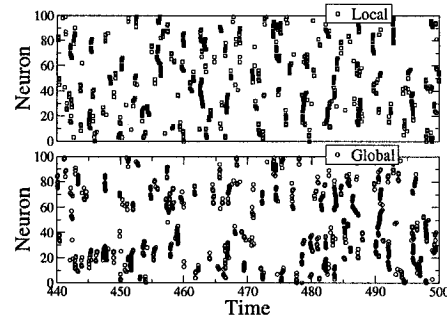
(a) Raster plot of a GCI driven deterministic LIF network with no feedback.



(b) Raster plot of a GCI driven deterministic LIF network with global feedback.

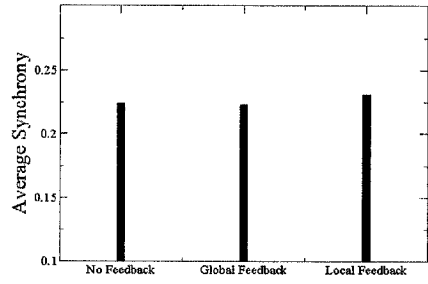


(c) Raster plot of a GCI driven deterministic LIF network with local feedback.

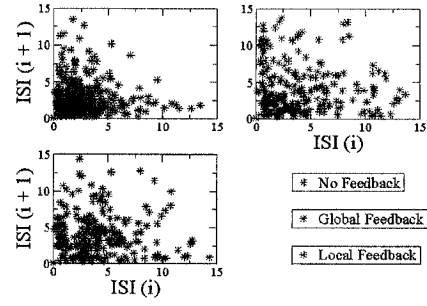


(d) Clustering in a GCI driven deterministic LIF network.

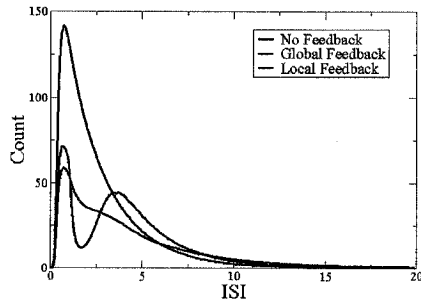
Figure 6.19: Simulation results for a deterministic LIF network with GCI ($\lambda = 5$), in the subthreshold regime.



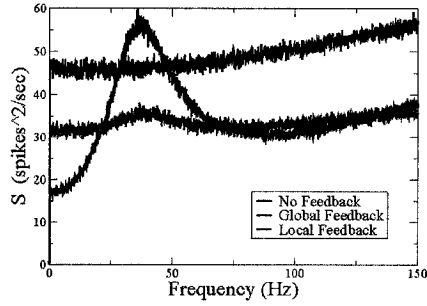
(a) Synchrony of a GCI driven deterministic LIF network.



(b) Return Map of a GCI driven deterministic LIF network.



(c) ISI histogram of a GCI driven deterministic LIF network.



(d) Power Spectrum of a GCI driven deterministic LIF network.

Figure 6.20: Simulation results for a deterministic LIF network with GCI ($\lambda = 5$), in the subthreshold regime.

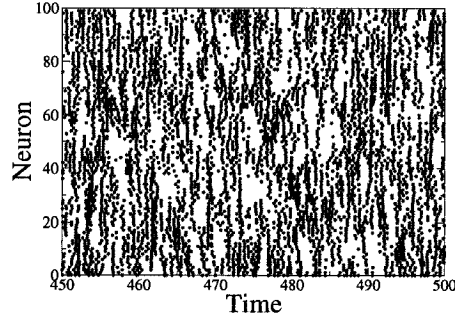
6.4.5 Gaussian Correlated Input ($\lambda = 5$) in a Stochastic LIF Network

Adding noise ($D_{int} = 0.08$) to a network driven by Gaussian correlated input doesn't have as much affect as adding noise to a network driven by percentage correlated input. The noise acts to reduce oscillations found in the global and local feedback networks.

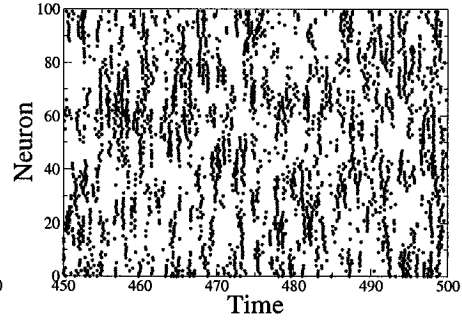
Superthreshold Regime

The raster plots (Figures 6.21(a), 6.21(b) and 6.21(c)) show that the randomness of the firing patterns in the network has increased with the addition of the internal noise. Clustering is still more prominent in the local feedback network than the global feedback network, see the cluster diagram (Figure 6.21(d)). Almost continuous waves across most of the network can be seen in the local feedback cluster plot, but not many can be seen in the global feedback cluster plot. These large waves, which spread across most of the network indicate that the wave fragments in the network overlap, forming almost a standing wave firing pattern. These waves are also somewhat visible in the raster plot, Figure 6.21(c). However, the global feedback network still displays the most synchrony (Figure 6.22(a)). Again this probably indicates that global feedback has more straight line segments in the raster plot, when

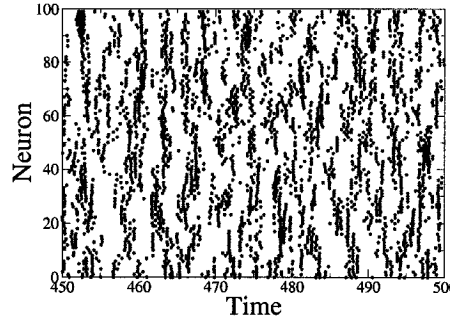
averaging over time. Since the input is already less correlated than the PCI ($c = 1$), the addition of noise to the network only slightly diminishes the small network oscillation seen for the global feedback network (this is seen in the ISI histogram (Figure 6.22(c)) and power spectra (Figure 6.22(d))). The local feedback network also shows a slightly weaker oscillation than for the deterministic network, but bursting is still present (see Figure 6.22(b)).



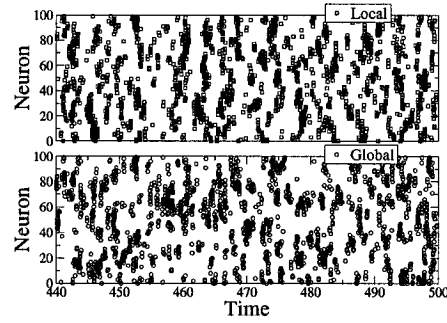
(a) Raster plot of a GCI driven stochastic LIF network with no feedback.



(b) Raster plot of a GCI driven stochastic LIF network with global feedback.

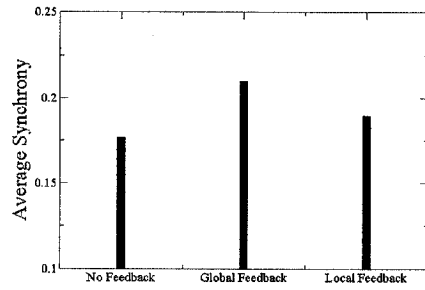


(c) Raster plot of a GCI driven stochastic LIF network with local feedback.

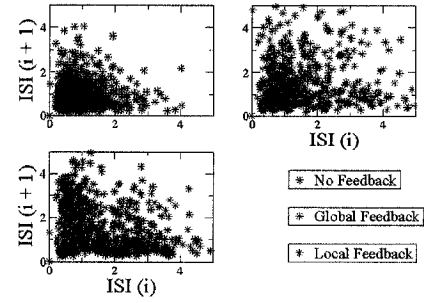


(d) Clustering in a GCI driven stochastic LIF network.

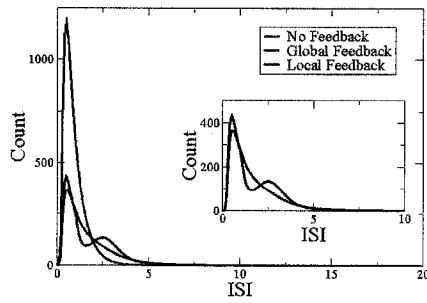
Figure 6.21: Simulation results for a stochastic LIF network with GCI ($\lambda = 5$), in the superthreshold regime.



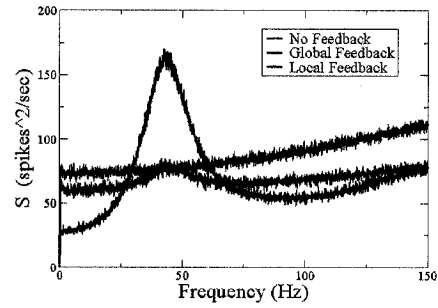
(a) Synchrony of a GCI driven stochastic LIF network.



(b) Return Map of a GCI driven stochastic LIF network.



(c) ISI histogram of a GCI driven stochastic LIF network.



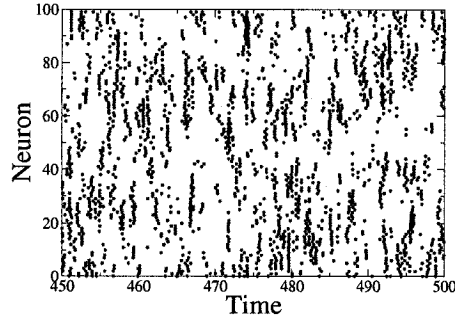
(d) Power Spectrum of a GCI driven stochastic LIF network.

Figure 6.22: Simulation results for a stochastic LIF network with GCI ($\lambda = 5$), in the superthreshold regime.

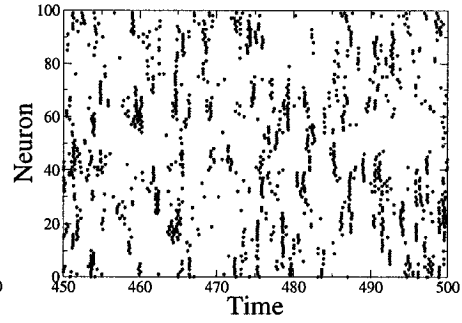
Subthreshold Regime

In the subthreshold regime the raster plots (Figures 6.23(a), 6.23(b), and 6.23(c)) also show that the firing times have become more arbitrary. The cluster diagram, Figure 6.23(d), shows that there are more clusters present with local feedback than global feedback, but here we don't see the full wave pattern as in the superthreshold case. Instead we see much shorter wave segments in the cluster plot, which may indicate that parts of the local feedback network are oscillating. In this case the synchrony of the local feedback appears higher than the other two network architectures, generally supporting this idea (Figure 6.24(a)). A strong peak in the power spectrum and a bimodal ISI histogram implies that there is an oscillation in the local feedback network, Figures 6.24(c) and 6.24(d) respectively. Along with the oscillation of the local feedback network there are also bursts of spikes in the spike train as indicated by the bimodality in the ISI histogram and the denser regions along the axis of the ISI return map (Figure 6.24(b)). While the ISI histogram is unimodal for the global feedback network, a small peak in the power spectrum indicates an extremely small oscillation in the network. Similar to the case without noise, and consistent with the ISI histogram, there is no obvious burst pattern in the ISI return map for global feedback. It is

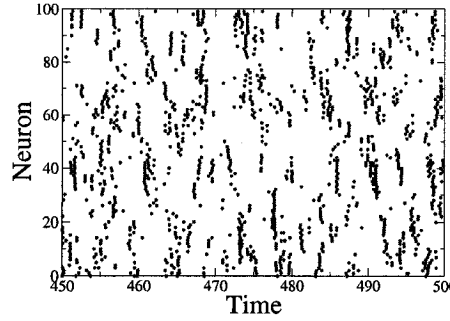
worth noting, for comparison purposes, that the curves of the power spectra are shifted up compared to the power spectra curves of the deterministic networks in the subthreshold regime. This is because the additional noise for a subthreshold network increases the overall firing rate of the network. This effect is also seen in the superthreshold case, but only for low frequencies.



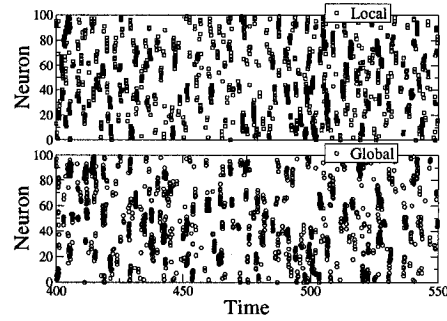
(a) Raster plot of a GCI driven stochastic LIF network with no feedback.



(b) Raster plot of a GCI driven stochastic LIF network with global feedback.

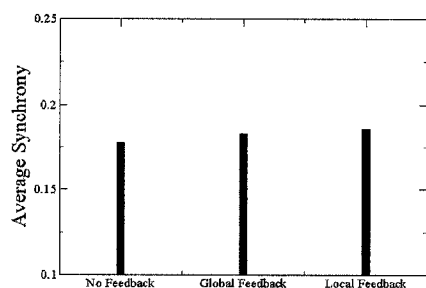


(c) Raster plot of a GCI driven stochastic LIF network with local feedback.

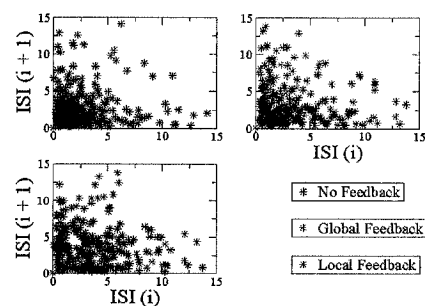


(d) Clustering in a GCI driven stochastic LIF network.

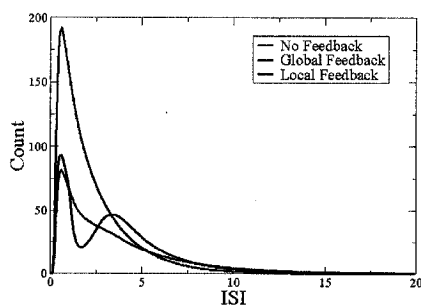
Figure 6.23: Simulation results for a stochastic LIF network with GCI ($\lambda = 5$), in the subthreshold regime.



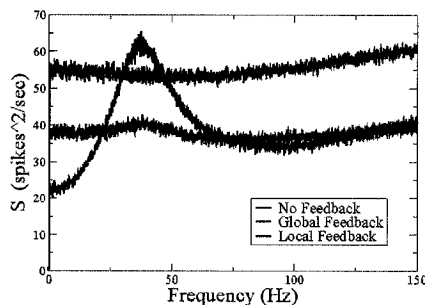
(a) Synchrony of a GCI driven stochastic LIF network.



(b) Return Map of a GCI driven stochastic LIF network.



(c) ISI histogram of a GCI driven stochastic LIF network.



(d) Power Spectrum of a GCI driven stochastic LIF network.

Figure 6.24: Simulation results for a stochastic LIF network with GCI ($\lambda = 5$), in the subthreshold regime.

6.5 Summary

The following tables summarize the results obtained in this chapter. The first table is a summary of the deterministic network results. In the non-driven network (i.e. no external input signal noise) each different type of feedback causes a different network output. The network without feedback provides no information to the other neurons about their neighbours and thus they fire independent of each other, oscillating on their own at f_{neuron} . Global feedback forces the network into a synchronous oscillation at f_{net} , whereas local feedback causes the network to form a standing wave oscillation at f_{net} .

Driving the network with a common input (PCI, $c = 1$), not surprisingly, causes the network to fire synchronously regardless of feedback type. The feedback in this case causes a bursty oscillation across the network, in the superthreshold regime. In the subthreshold regime the feedback only causes a weak oscillation at f_{net} , with no apparent burst pattern. However, driving the network with a spatially profiled input (GCI, $\lambda = 5$) causes the network to fire in small segments of synchrony. Thus, the overall synchrony in the network appears quite low. Without the common input the global feedback network only fires with a very weak oscillation at f_{net} , but the local feedback network still displays a strong bursty network oscillation. This trend is present in

both superthreshold and subthreshold regimes.

The second table summarizes the stochastic network results (i.e. the results with independent internal noise sources for each neuron). In the non-driven stochastic network the internal noise destroys the synchronous oscillations present in the non-driven deterministic network. However, the noise is not completely successful at destroying the network oscillation for local feedback, as a weak oscillation is still present.

Driving the system with PCI ($c=1$) causes the global feedback network to oscillate and the oscillation of the local feedback network to become stronger. The synchrony and oscillation strength are considerably less for both local and global feedback in the stochastic PCI driven network, than for the deterministic PCI driven network, with the exception of the network oscillation strength in the subthreshold regime. Since noise in the subthreshold regime increases the network activity it is not surprising that the oscillation strength would also increase. Adding spatial noise on top of the already stochastic input signal (PCI, $c = 0$), the PCI driven network sees its global oscillation wiped out completely, and weakens considerably the local oscillation. GCI driven stochastic networks behave similarly to the deterministic GCI driven network, with the noise merely creating less synchrony, as for PCI. Surpris-

ingly the increase in internal noise does not affect the oscillation strength in the network as much in the superthreshold regime. This can be explained by considering the different amounts of noise in the two different inputs. The GCI input is already spatially quite noisy, whereas the PCI ($c = 1$) has no spatial noise. Thus, the addition of internal noise to the network with GCI doesn't have much affect on the oscillation strength in the superthreshold regime. Similar to the PCI case, the network oscillation strength in the subthreshold regime increases upon going from a deterministic GCI driven network to a stochastic GCI driven network, due to the higher average firing rate of the stochastic network.

Network Type	Feedback	Raster Plot	Cluster Count	Synchrony	ISI Histogram	Power Spectrum	Peak Power	ISI Return Map
Deterministic Network								
Superthreshold	None	Ind. Osc.	none*	100% wave	spike spike	peak at f_{neuron} peak at f_{net} peak at f_{net}		
	Global	Net. Osc.						
Local	Net. Osc.							
Driven Deterministic Network with Percentage Correlated Input ($c = 1$)								
Superthreshold	None	rapid synch. firing		100%	unimodal	no peak	174	no pattern
	Global	slow synch. firing						
Subthreshold	Local	slow synch. firing		99.96%	bimodal	peak at f_{net}	174	burst pattern
	None	synch. firing						
	Global	synch. firing		97.92%	unimodal	no peak	18	no pattern
	None	synch. firing						
Local	synch. firing							
Driven Deterministic Network with Gaussian Correlated Input ($\lambda = 5$)								
Superthreshold	None	rapid seg. firing	39459	20.87%	unimodal	no peak	76	no pattern
	Global	slow seg. firing						
Subthreshold	Local	slow seg. firing	39866	22.33%	bimodal	small peak at f_{net}	168	burst pattern
	None	seg. firing						
	Global	seg. firing	14623	22.31%	weakly bimodal	small peak at f_{net}	35	no pattern
	Local	seg. firing						
	Global	seg. firing	15166	23.08%	bimodal	peak at f_{net}	56	burst pattern
	Local	seg. firing						

Table 6.1: Summary of deterministic network simulation results. The first column indicates the type of network. The second column indicates the type of feedback. The third column gives a qualitative description of the raster plot results. The number of clusters detected in the network is shown in the fourth column. The percentage of network synchrony is given in the fifth column, where the synchrony (“spike” means that there is only one ISI for the network). Column six indicates the shape of the ISI histogram (“spike” means that there is only one ISI for the network). Peaks in the power spectra are indicated in column seven and the peak power is given in column eight, with units of $\text{spikes}^2/\text{sec}$. The last column indicates any burst patterns in the ISI return map.

Network Type	Feedback	Raster Plot	Cluster Count	Synchrony	ISI Histogram	Power Spectrum	Peak Power	ISI Return Map
Stochastic Network								
Suprathreshold	None	no pattern	3670	9.12%	unimodal	no peak	47	no pattern
	Global	no pattern		12.22%	unimodal	small peak at f_{net}		no pattern
	Local	weak pattern	5421	10.61%	bimodal	large peak at f_{net}	97	burst pattern
Subthreshold	None	no pattern		9.14%	unimodal	no peak		no pattern
	Global	no pattern		8.11%	unimodal	no peak		no pattern
	Local	no pattern		8.92%	bimodal	peak at f_{net}	14	no pattern
Driven Stochastic Network with Percentage Correlated Input ($c = 1$)								
Suprathreshold	None	weak Ind. Osc.		34.08%	unimodal	no peak		no pattern
	Global	weak Net. Osc.	16103	47.93%	bimodal	peak at f_{net}	105	no pattern
	Local	weak Net. Osc.	15636	42.43%	bimodal	peak at f_{net}	121	burst pattern
Subthreshold	None	weak Ind. Osc.		37.63%	unimodal	no peak		no pattern
	Global	weak Net. Osc.	1143	33.66%	bimodal	peak at f_{net}	25	no pattern
	Local	weak Net. Osc.	1283	34.54%	bimodal	peak at f_{net}	28	no pattern
Driven Stochastic Network with Percentage Correlated Input ($c = 0$)								
Suprathreshold	None	no pattern		8.67%	unimodal	no peak		no pattern
	Global	no pattern	5135	10.99%	unimodal	no peak		no pattern
	Local	weak pattern	6837	10.07%	bimodal	peak at f_{net}	92	burst pattern
Driven Stochastic Network with Gaussian Correlated Input ($\lambda = 5$)								
Suprathreshold	None	noisy rapid seg. firing		17.62%	unimodal	no peak		no pattern
	Global	noisy slow seg. firing	28696	21.00%	unimodal	small peak at f_{net}	79	no pattern
	Local	weak Net. Osc.	31416	18.95%	bimodal	peak at f_{net}	162	burst pattern
Subthreshold	None	noisy seg. firing		17.77%	unimodal	no peak		no pattern
	Global	noisy seg. firing	8287	18.32%	weakly bimodal	tiny peak at f_{net}	40	no pattern
	Local	noisy seg. firing	9122	18.58%	bimodal	peak at f_{net}	62	burst pattern

Table 6.2: Summary of stochastic network simulation results. The format is the same as in Table 6.1.

Chapter 7

Discussion

In this thesis we have studied two problems using a combination of theory and numerical simulations. Mechanisms for gain modulation were researched to understand how neural networks can adapt to incoming input signals. Our novel results show that inhibitory feedback alone can cause a divisive gain shift, but that to attain both a divisive gain shift and a subtractive gain shift, an increase in noise and inhibition was required.

The second problem we looked into was delayed feedback profiles and how different profiles affect the network dynamics. Both theory and simulations predict a network oscillation for a localized feedback network with small spatial correlations in the input. This novel result indicates that local feedback networks may be useful for tracking stimuli with small spatial correlations.

The results obtained in this thesis apply not only to the weakly electric

fish, but may be useful in many different biological neural networks with similar architecture. The simplicity of the neuron model and network architecture lends itself to broad application. The parameters used here are the main specialization of the model to the weakly electric fish. This model may be extended to biological networks of other animals merely by the appropriate choice of parameters.

In this chapter we review the main conclusions from chapters 3-5 and discuss the implications of these results. Finally, we suggest a few questions that could be addressed in future research.

7.1 Linearization of F-I Curves

The network gain has important implications for rate coding. Both noise and inhibitory feedback linearize the f-i curve of the network. Additive noise allows the neuron with a subthreshold bias to become active and in doing so linearizes the f-i curve, whereas feedback can only linearize the f-i curve if the neuron is already in the superthreshold regime. Inhibitory feedback linearizes the f-i curve because it divisively reduces the gain of the network. Our theory is that the divisiveness appears due to the functional relation between the inhibitory feedback and the input bias.

The combination of noise linearization and feedback linearization allows an effective subtractive and divisive gain shift as is seen in the weakly electric fish [1]. The combination of these effects predict that to get a divisive gain shift in parallel with a subtractive shift, both an increase in the average inhibitory input and the variance of the input is needed [33], [34]. In this way noise and feedback can alter the f-I curve and thus the rate seen by the next higher brain centre. This mechanism is most likely applicable in many other biological networks where similar gain modulations are found.

7.2 Spatially Profiled Feedback

The functionality of different architectures within neural circuits is important for understanding neural processing. The comparison of local and global feedback profiles was thus investigated. While the mean activity of the network remains unaffected by a change in spatial profile of the feedback, the underlying dynamics of the network depend on the shape and spatial extent of the feedback profile.

As in [18], the global feedback network with uncorrelated input showed no signs of network oscillation, but with correlated input produced a network oscillation of approximately 50 Hz. In contrast, spatially local feedback caused

a network oscillation for uncorrelated input, which was even stronger than the global feedback oscillation for correlated input. The oscillation strength for local feedback only increased in the case of correlated input. These differences suggest that the global feedback and local feedback may play different rolls in neuronal processing.

Differences between two different types of correlated input were also investigated. The percentage correlated input mimics perhaps more of a combination of input signals, while Gaussian correlated input mimics more the spatial extent of a specific input, with a given spatial correlation length. As the PCI increased from $c = 0$ to $c = 1$, the network oscillation strength increased linearly for both local and global feedback networks. The spatially Gaussian correlated input showed an interesting result for different feedback profiles. The oscillation strength increased as λ (the spatial correlation length of the input) increased to match the spread of the feedback profile and then levelled off for spatial correlation lengths broader than the feedback. We comment on the significance of these results in the next section.

7.3 Simulation Results

With a look at more simplistic network models, the precise differences between local and global feedback architecture effects on network performance were determined. Uncorrelated input, which can also be interpreted as noise or inhomogeneity amongst neurons in the network, is the source of the differences seen between local and global feedback. The local feedback architecture is less susceptible to noise than the global feedback architecture; it allows the network oscillation to persist in the presence of more noise than the global feedback architecture. The local feedback network is able to maintain the oscillation because it is only attempting to entrain a small portion of the network whereas the global feedback network tries to recruit the entire network.

One possible implication for the weakly electric fish, which has both local and global feedback pathways, is that local stimuli are detected via the local feedback pathway and global stimuli are detected via the global feedback pathway. This theory is also supported by the greater drop in power at low frequencies for the local feedback network, which may lead to better detection of weak, low frequency signals, such as prey signals seen by the weakly electric fish. It could also be that the local stimuli and global stimuli are differentiated by oscillation strength itself, if both feedback pathways are

active at the same time. A further study combining the two types of feedback in the same network would be an interesting avenue for future work.

7.4 Future Work

In general the next step in simulations will be to include both feedback pathways in the network architecture at once. This could possibly alight to even more interesting processing features of neural networks. Another facet of the simulation which could be improved and possibly reveal more details of network dynamics is the neuron model. A neuron model that better describes biological neurons may reveal more processing details of the network. The next theoretical step would be to calculate dynamical predictions for the neural network with Gaussian correlated input and compare these to simulations. Only two different types of input have been investigated here and further work could be done studying various other types of input to the network, such as input which is correlated spatially and temporally, this being a more realistic input. Finally, a combination of both positive and negative feedback to the network would be an interesting avenue to investigate. This would be a more realistic representation of the network architecture of the ELL in the weakly electric fish, but could also be extended to different

biological networks with similar architecture.

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Appendix A

Here we give a detailed derivation of the individual spike train power spectra for a global feedback network with PCI. The general solution for the power spectra of an individual spike train is given by Equation 3.26:

$$S_i = Q_{i,i}(S_0 + |A|^2 S_{st}) + c|A|^2 S_{st} \sum_{j \neq i}^{N-1} Q_{i,j} \quad (7.1)$$

which, for global feedback, can be rewritten as

$$S_0 = Q_{0,0}(S_0 + |A|^2 S_{st}) + c|A|^2 S_{st}(N-1)Q_{0,1}. \quad (7.2)$$

Recall

$$\mathbf{Q} = [\mathbf{I} - \frac{Ag\tilde{K}_{\tau_d}}{N}\mathbf{P}]^{-1}{}^{*T} [\mathbf{I} - \frac{Ag\tilde{K}_{\tau_d}}{N}\mathbf{P}]^{-1}. \quad (7.3)$$

In the case of global feedback $\mathbf{P}$ is a $N \times N$ matrix of 1's

$$\mathbf{P} = \begin{pmatrix} 1 & 1 & . & . & . \\ 1 & 1 & & & \\ . & & . & & \\ . & & & . & \\ . & & & & . \end{pmatrix} \quad (7.4)$$

and $\mathbf{Q}$ becomes

$$\mathbf{Q} = \mathbf{B}^{-1*T}\mathbf{B}^{-1} \quad (7.5)$$

where

$$\mathbf{B} = \begin{pmatrix} 1 - \frac{AgK}{N} & -\frac{AgK}{N} & \cdot & \cdot & \cdot \\ -\frac{AgK}{N} & 1 - \frac{AgK}{N} & & & \\ \cdot & & \cdot & & \\ \cdot & & & \cdot & \\ \cdot & & & & \cdot \end{pmatrix}. \quad (7.6)$$

Using maple we can determine that

$$\mathbf{B}^{-1} = \begin{pmatrix} \frac{(N-1)\frac{AgK}{N}-1}{1-AgK} & -\frac{\frac{AgK}{N}}{1-AgK} & \cdot & \cdot & \cdot \\ -\frac{\frac{AgK}{N}}{1-AgK} & \frac{(N-1)\frac{AgK}{N}-1}{1-AgK} & & & \\ \cdot & & \cdot & & \\ \cdot & & & \cdot & \\ \cdot & & & & \cdot \end{pmatrix}. \quad (7.7)$$

Since B is symmetric

$$\mathbf{Q} = \mathbf{B}^{-1*}\mathbf{B}^{-1}. \quad (7.8)$$

Substituting Equation 7.7 into Equation 7.8 we get

$$\mathbf{Q} = \begin{pmatrix} \frac{(N-1)\frac{AgK}{N}-1}{1-AgK} & -\frac{\frac{AgK}{N}}{1-AgK} & \cdot & \cdot & \cdot \\ -\frac{\frac{AgK}{N}}{1-AgK} & \frac{(N-1)\frac{AgK}{N}-1}{1-AgK} & & & \\ \cdot & & \cdot & & \\ \cdot & & & \cdot & \\ \cdot & & & & \cdot \end{pmatrix}^* \begin{pmatrix} \frac{(N-1)\frac{AgK}{N}-1}{1-AgK} & -\frac{\frac{AgK}{N}}{1-AgK} & \cdot & \cdot & \cdot \\ -\frac{\frac{AgK}{N}}{1-AgK} & \frac{(N-1)\frac{AgK}{N}-1}{1-AgK} & & & \\ \cdot & & \cdot & & \\ \cdot & & & \cdot & \\ \cdot & & & & \cdot \end{pmatrix} \quad (7.9)$$

which simplifies to

$$\mathbf{Q} = \begin{pmatrix} 1 + \frac{2\text{Re}(AgK)-|AgK|^2}{N|1-AgK|^2} & \frac{2\text{Re}(AgK)-|AgK|^2}{N|1-AgK|^2} & \cdot & \cdot & \cdot \\ \frac{2\text{Re}(AgK)-|AgK|^2}{N|1-AgK|^2} & 1 + \frac{2\text{Re}(AgK)-|AgK|^2}{N|1-AgK|^2} & & & \\ \cdot & & \cdot & & \\ \cdot & & & \cdot & \\ \cdot & & & & \cdot \end{pmatrix}. \quad (7.10)$$

Substituting Equation 7.10 into 7.2 we get

$$S_0 = S_0 + |A|^2 S_{st} + \frac{2\operatorname{Re}(AgK) - |AgK|^2}{N|1 - AgK|^2} (S_0 + |A|^2 S_{st}) + c|A|^2 S_{st} (N-1) \frac{2\operatorname{Re}(Agk) - |AgK|^2}{N|1 - AgK|^2} \quad (7.11)$$

which is exactly

$$S_0 = S_0 + |A|^2 S_{st} + c|A|^2 S_{st} \frac{2\operatorname{Re}(AgK) - |AgK|^2}{|1 - AgK|^2} + \frac{1}{N} [S_0 + (1-c)|A|^2 S_{st}] \frac{2\operatorname{Re}(Agk) - |AgK|^2}{|1 - AgK|^2} \quad (7.12)$$

QED.