Second Order Networks with spatial structure

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Abstract

Synchronization of spiking activity across neurons plays a role in many processes in the brain. Using the framework of Second Order Networks (SONETs) paired with a global ring structure, we looked at the relationships between the connectivity statistics and two key eigenvalue quantities related to the synchrony of the network - the largest eigenvalue of the connectivity matrix and the variance of the eigenvalues of the Laplacian. Previously, Zhao et al. [1] examined these relationships in the case of homogeneous SONETs, in which there is no spatial variation in the network. In this work, we broaden our view to SONETs where we allow the connection probabilities to depend on the spatial structure of the network. First, we develop an algorithm to generate SONETs which allows us to specify both the global and local geometry of the network. We then randomly generated a wide range of SONETs to examine the relationships between the connectivity statistics and the eigenvalue quantities of the resulting networks. We find that two of the second order statistics, namely those corresponding to the frequency of convergent connections and to the frequency of chain connections, primarily influence the values of the two eigenvalue quantities. Our results are remarkably similar to those of the homogeneous case, indicating that the qualitative relationship we see between synchrony and second order statstics should extend to a larger class of networks. We also find that for the networks we considered, the parameters used to describe the overall geometry of the network had a minimal influence on the two key eigenvalue quantities.

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Chapter 1

Introduction

The brain is a vast network of connections among neurons. Understanding the underlying network structure can provide insight into the dynamics of the network. For example, a recent study by Perin and Markram has provided evidence of a synaptic organizing principle among groups of pyramidal neurons in the neocortex that accurately predicts both connection probabilities and synaptic weights [2]. In this vein, the Human Connectome Project aims to provide a comprehensive map of neural connections in the brain. However, the only completed wiring diagram is that of the nematode worm *C. elegans*, containing 302 neurons [3]. This took 12 years to complete, and there still does not exist a complete mapping of the synaptic weights for this network. Because of this, great focus has been devoted to developing functional models which display statistics similar to those found in brain networks.

Describing the connectivity of a complex network requires a large number of dimensions. It is important to have low-dimensional models which are easier to work with but still retain useful information about the network. Zhao, Beverlin, Netoff, and Nykamp proposed a model which characterizes networks based on key second order connectivity statistics [1]. They refer to this framework as second order networks, or SONETs. Their model is low-dimensional (for homogeneous SONETs, where there is only one first order statistic, the model is five-dimensional), but still captures important features of real neural networks and is useful for investigating how network structure affects certain processes in the brain. They then used this framework to investigate how changes in network topology affect the synchrony of the network [1]. In this thesis, we look at the relationship between network topology and synchrony for SONETs in which we allow the connections to depend on the spatial structure of the network.

This thesis is divided into two main sections. In Chapter 2, after reviewing the framework of SONETs, we discuss the relevant results from the work by Zhao et al. mentioned above. They found that two of the second order connectivity statistics influence the synchrony of the network: the frequency of convergent connections and the frequency of chain connections. This was predicted based on the relationships between these statistics and two key eigenvalue quantities of the adjacency matrix W.

In Chapter 3, we consider SONETs where we allow for spatial variation in the connection probabilities. First, we describe the algorithm we developed to generate second order networks. Then we look at the relationship between the connectivity statistics and the eigenvalue quantities of the resulting networks, and compare these results to the homogeneous case.

Chapter 2

Background: Homogeneous Second Order Networks

2.1 Second Order Networks

A common technique used to model neural networks is to randomly and independently generate connections between neurons given a small probability of connection between neurons; this probability may depend on things like neuron identity and location. This model is referred to as the independent random network model. The special case where the probability of any connection is the same value p is called the Erdős-Rényi random network. The independent random network model is the natural model that results from only specifying the connection probabilities, as it adds minimal additional structure beyond what is required by the connection probabilities [1]. In this model, all higher order statistics are set to zero.

However, the independent model does not capture the network structure exhibited by neural networks. For example, Erdős-Rényi random networks have binomial degree distributions, while the degree distributions of neural networks have a heavy tail and are better modeled by a power-law distribution. Thus, we need to specify additional structure to better capture the properties seen in real-world networks.

One approach, developed by Zhao et al. [1],[4], is to allow nonzero second-order network statistics; these statistics determine the covariance among edges. An equivalent way to think of this is that we specify not only the connection probabilities, but also the frequency of pairs of edges which share at least one common node. There are four distinct patterns of two connections sharing a common node, which we will refer to as reciprocal, convergent, divergent, and chain motifs (pictured in Figure 2.1). Zhao et al. refer to such networks as second order networks, abbreviated as SONETs.

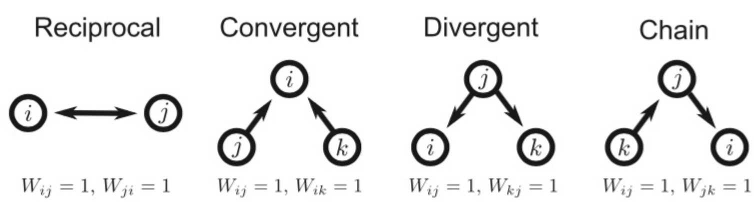

Figure 2.1: The four second order connection motifs [1]

In a given network, the connectivity or adjacency matrix W defines the connectivity among the N neurons. Each component W_{ij} is either 0 or 1, indicating that a connection from neuron j to neuron i is absent or present, respectively. We do not allow self-coupling, so $W_{ii} = 0$.

In their paper, Zhao et al. considered only homogeneous SONETs, meaning that each possible edge has the same probability p. Thus for every pair of neurons i and j,

$$\mathrm{P}(W_{ij} = 1) = p \tag{2.1}$$

If the edges were independent of one another, the probability of any two-edge motif would be p^2. The second order statistics $\alpha^{\mathrm{recip}}, \alpha^{\mathrm{conv}}, \alpha^{\mathrm{div}}$, and α^{chain}, which measure deviations from independence of the frequency of the four two-edge motifs, are defined as follows:

$$\mathrm{P}(W_{ij} = 1, W_{ji} = 1) = p^2(1 + \alpha^{\mathrm{recip}}) \tag{2.2a}$$

$$\mathrm{P}(W_{ij} = 1, W_{ik} = 1) = p^2(1 + \alpha^{\mathrm{conv}}) \tag{2.2b}$$

$$\mathrm{P}(W_{ij} = 1, W_{kj} = 1) = p^2(1 + \alpha^{\mathrm{div}}) \tag{2.2c}$$

$$\mathrm{P}(W_{ij} = 1, W_{jk} = 1) = p^2(1 + \alpha^{\mathrm{chain}}) \tag{2.2d}$$

for any triplet of distinct neurons i, j, and k. All pairs of edges that do not share a common node have probability p^2. As the network is homogeneous, the second order statistics are independent of neuron label. This class of SONETs is a natural generalization of the Erdős-Rényi random network model, and reduces to this model when all α's are zero.

A SONET is determined by specifying the probability of connection p and the four α's. The SONET model is a five-dimensional probability distribution for the network connectivity matrix W that satisfies conditions (2.1) and (2.2), and adds minimal structure (i.e. higher order correlations) beyond these constraints [1].

Zhao et al. used dichotomized Gaussian random variables to generate SONETs [1]. They used a Gaussian random variable because, in the continuous case, the Gaussian distribution has the highest entropy of all probability distributions with a specified covariance. (We wish to maximize entropy so that the resulting probability distribution adds minimal structure beyond the prescribed constraints.) In the discrete case, the entropy of the dichotomized Gaussian is near the maximum possible value. To generate SONETs using the dichotomized Gaussian method, we first sample an $N \times N$ matrix of joint Gaussian random variables with appropriate covariance matrix Σ such that after dichotomizing, we get a network with first and second order statistics as defined in equations (2.1) and (2.2). We then threshold them into Bernoulli random variables W_{ij}. We will examine this method in further detail in Chapter 3.

2.2 Estimating Connectivity Statistics

The first and second order connectivity statistics are determined by a probability distribution for the connectivity matrix W. We can estimate these statistics directly from a given connectivity matrix W. We denote these estimates $\hat{p}$ and $\hat{\alpha}$.

The average connectivity $\hat{p}$ is the number of connections N_{conn} present in W divided by the number of possible connections:

$$\hat{p} = \frac{N_{\text{conn}}}{N(N-1)},$$

where $N_{\text{conn}} = \|W\|_1 = \sum_{i,j} |W_{ij}|$. Similarly, the average second order connectivity statistics are determined by the total number of corresponding second order motifs in the network, divided by the total possible:

$$\hat{p}^2(1+\hat{\alpha}^{\text{recip}}) = \frac{N_{\text{recip}}}{N(N-1)/2}$$
$$\hat{p}^2(1+\hat{\alpha}^{\text{conv}}) = \frac{N_{\text{conv}}}{N(N-1)(N-2)/2}$$
$$\hat{p}^2(1+\hat{\alpha}^{\text{div}}) = \frac{N_{\text{div}}}{N(N-1)(N-2)/2}$$
$$\hat{p}^2(1+\hat{\alpha}^{\text{chain}}) = \frac{N_{\text{chain}}}{N(N-1)(N-2)}.$$

The values $N_{\text{recip}}, N_{\text{conv}}, N_{\text{div}}, N_{\text{chain}}$ refer to the number of corresponding second order motifs present in the network. These values can be determined from W using the equations $N_{\text{recip}} = \text{Tr}(W^2)/2$, $N_{\text{conv}} = (\left\|W^T W\right\|_1 - \|W\|_1)/2$, $N_{\text{div}} = (\left\|W W^T\right\|_1 - \|W\|_1)/2$, and $N_{\text{chain}} = \left\|W^2\right\|_1 - \text{Tr}(W^2)$.

In our network simulations, we compare the measured $\hat{\alpha}$ to the network synchrony even when we know the parameters α. Because these networks are generated probabilistically, the actual $\hat{\alpha}$ varies slightly from α. We find that of the two, $\hat{\alpha}$ is better at predicting synchrony.

2.3 Relating Second Order Connectivity Statistics to Degree Distribution

Next, we look at the connection between the second order connectivity statistics and the degree distribution of the network. The in-degree of neuron i is the total number of connections directed toward neuron i, $d^i_{\text{in}} = \sum_j W_{ij}$. Similarly, the out-degree of neuron i is the total number of connections directed away from neuron i, $d^i_{\text{out}} = \sum_j W_{ji}$. The mean in-degree and mean out-degree are equal; we will call this value the mean degree, $d = \frac{1}{N}\sum_{i,j} W_{ij}$.

Zhao et al. [1] derived the following relationships between second order connectivity statistics and the degree distribution, which hold for large network size N:

$$\alpha^{\text{conv}} \approx \frac{\text{var}(d^i_{\text{in}}) - E(d)}{E(d)^2} \tag{2.3a}$$

$$\alpha^{\text{div}} \approx \frac{\text{var}(d^i_{\text{out}}) - E(d)}{E(d)^2} \tag{2.3b}$$

$$\alpha^{\text{chain}} \approx \frac{\text{cov}(d^i_{\text{in}}, d^i_{\text{out}})}{E(d)^2} \tag{2.3c}$$

Thus, we see that α^{conv} and α^{div} are nearly equal to the variance of the in-degree and out-degree distributions, normalized by the mean degree squared (with small offset $1/\text{E}(d)$). α^{chain} is nearly equal to the covariance between the in-degree and the out-degree, again normalized by the mean degree squared. These relationships will give us an intuitive idea of the effect of the connectivity statistics on properties of the network, particularly the synchrony of the network.

2.4 Synchrony and Second Order Connectivity Statistics

Synchronization of spiking activity across neurons plays a role in many processes in the brain. Neural synchrony is important to certain processes involved in memory formation [5], while excessive synchrony is associated with seizure activity in epilepsy [6] and with tremors associated with Parkinson's disease [7]. There are many factors which influence the tendency of a network to synchronize, such as individual neuron dynamics and the topology of the network. In their paper *Synchronization from second order connectivity statistics* [1], Zhao et al. focused on how network structure affects the synchronizability of a network, using the framework of SONETs. They found that two of the second order statistics should have an influence on the synchrony of the network: α^{conv} and α^{chain}.

2.4.1 Influence of Convergent Connections

By looking at the stability of the completely synchronous state, one of the two extreme cases of synchrony, Zhao et al. found that changes in network structure that decrease the spread of the eigenvalues of the Laplacian will increase the tendency of a network to synchronize. One measure of eigenvalue spread for asymmetric matrices [8] is the variance σ_μ^2 of the eigenvalues normalized by the mean degree squared,

$$\sigma_\mu^2 = \frac{1}{d^2(N-1)} \sum_{i=2}^{N} |\mu_i - \bar{\mu}|^2,$$

where $\bar{\mu} = \frac{1}{N-1} \sum_{i=2}^{N} \mu_i$ is the mean of the eigenvalues. This variance ignores the zero eigenvalue $\mu_1 = 0$ present in every Laplacian matrix. The connection to second order connectivity statistics is that α^{conv} and σ_μ^2 are approximately equal [1]:

$$\alpha^{\text{conv}} \approx \sigma_\mu^2 - \frac{1}{d} \tag{2.4}$$

Given this relationship, we expect that a higher value of α^{conv} will decrease synchrony. The intuitive idea behind this is that since α^{conv} is correlated with the variance of the in-degree distribution, networks with high frequencies of convergent motifs will have in-degree distributions with a large spread. This leads to significant differences in the firing rates of neurons across the network, which will decrease synchrony. This does not completely explain the effect of convergent connections on synchrony, but is a good heuristic explanation.

2.4.2 Influence of Chain Connections

By examining the stability of the asynchronous state, Zhao et al. find another measure that influences synchrony: the largest eigenvalue $\lambda_{\max}$ of the connectivity matrix W. We expect an increase in $\lambda_{\max}$ will increase synchrony, since $\lambda_{\max}$ is a measure of the effective coupling strength of the network. Restrepo et al. [9] give an approximate expression for $\lambda_{\max}$ based on the degree distribution: $\lambda_{\max} \approx E(d_{\text{in}}^i d_{\text{out}}^i)/E(d)$. Using relationship (2.3c), we can rewrite this in terms of α^{chain}:

$$\lambda_{\max} \approx \frac{\text{cov}(d_{\text{in}}^i, d_{\text{out}}^i) + E(d)^2}{E(d)} = (\alpha^{\text{chain}} + 1)E(d) \tag{2.5}$$

In this approximation $\lambda_{\max}$ increases linearly with α^{chain}, so we expect that an increase in the frequency of the chain motif will increase $\lambda_{\max}$. This means that an increase in α^{chain} should increase the effective coupling strength of the network, which would increase synchrony. The intuition is that with an increase in the frequency of the chain motif, nodes with large in-degree are likely to also have large out-degree (neurons that are good listeners are also good talkers), so neurons in the network are able to more effectively communicate with one another.

2.4.3 Experimental Results

Zhao et al. examined these predicted relationships between network structure and synchrony by generating 186 SONETs with N=3000 neurons and 10% connectivity ($p = 0.1$). One of these networks was a standard Erdős-Rényi random network, where all α's are zero; for the rest of the networks, the second order connectivity statistics were randomly sampled from the ranges $\alpha^{\text{recip}} \in [-1, 4]$, $\alpha^{\text{conv}} \in [-0, 1]$, $\alpha^{\text{div}} \in [0, 1]$, and $\alpha^{\text{chain}} \in [-1, 1]$.

Their results demonstrated that $\lambda_{\max}$ increased with α^{chain}, and that only α^{conv} affected the spread of the eigenvalues of the Laplacian L, as predicted. They found that both the relationship between σ_μ^2 and α^{conv} and the relationship between $\lambda_{\max}$ and α^{chain} closely resembled the expected relationships (2.4) and (2.5).

Plots of synchrony as a function of pairs of connectivity statistics showed that synchrony was a function of only the second order statistics α^{conv} and α^{chain}. Synchrony varied smoothly in the (α^{conv}, α^{chain}) projection, even though the other statistics α^{div} and α^{recip} were taking on a wide range of values. Furthermore, for a given value of α^{conv}, there was threshold value of α^{chain} where the synchrony dramatically increased. Similarly, for a given value of α^{chain}, there was a value α^{conv} where the synchrony jumped down significantly.

To summarize, by using the SONET model to describe network structure, Zhao et al. found that the frequencies of convergent and chain motifs are the key network statistics that influence synchrony. This was predicted based on the relationships betweetn these connectivity statistics and two key eigenvalue quantities - the largest eigenvalue of the connectivity matrix and the variance of the eigenvalues of the Laplacian. A natural next step would be to investigate whether these results hold for more general SONETs where the connection probabilities are allowed to vary. In the next chapter, we will examine the relationship between the connectivity statistics and the eigenvalue quantities in this more general case.

Chapter 3

Second Order Networks with spatial structure

In the rest of this paper, we will consider second order networks where we allow for spatial variation in the connection probabilities. These SONETs are a generalization of the independent random network model. Hence, the probability of connection depends on neuron label:

$$\mathrm{P}(W_{ij} = 1) = p_{ij} \tag{3.1}$$

However, to keep the problem of generating such networks tractable, we will assume that the deviations from independence or the four two-edge motifs are independent of neuron label:

$$\mathrm{P}(W_{ij} = 1, W_{ji} = 1) = p_{ij}p_{ji}(1 + \alpha^{\mathrm{recip}}) \tag{3.2a}$$
$$\mathrm{P}(W_{ij} = 1, W_{ik} = 1) = p_{ij}p_{ik}(1 + \alpha^{\mathrm{conv}}) \tag{3.2b}$$
$$\mathrm{P}(W_{ij} = 1, W_{kj} = 1) = p_{ij}p_{kj}(1 + \alpha^{\mathrm{div}}) \tag{3.2c}$$
$$\mathrm{P}(W_{ij} = 1, W_{jk} = 1) = p_{ij}p_{jk}(1 + \alpha^{\mathrm{chain}}) \tag{3.2d}$$

Based on current knowledge about the brain, it is reasonable to assume the second order statistics are identical for the entire population. We know that the connection probabilities in neuronal networks vary based on distance and location [11], but do not have any similar information about the second order statistics.

A motivating example we looked at is a ring model with the neurons labeled consecutively from 1 to the total number of neurons N, where p_{ij} is determined by shortest distance d_{ij} from neuron j to neuron i around ring. More specifically, in our ring model we defined p_{ij} using an exponential function, $p_{ij} = p_{\max}(\ell)\exp\left(\frac{-d_{ij}}{\ell}\right)$, where $p_{\max}(\ell)$ specifies the maximum possible value for any p_{ij}. The parameter ℓ specifies the spatial scale of connections; if ℓ is small, then there are primarily only local connections, whereas if ℓ is large, there are more global connections. In the limiting case where $\ell = \infty$, we are back in the case of homogenous SONETs as described in Chapter 2.

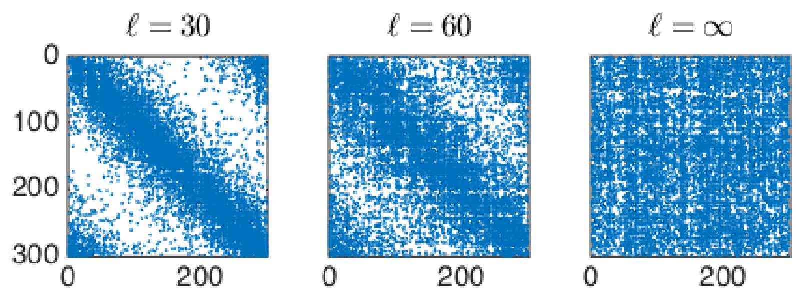

Figure 3.1: Sample connection matrices corresponding to the ring model with $N = 300$ neurons and 10% average connectivity for different values of ℓ. The second order statistics are $\alpha_{\text{conv}} = 0.3$, $\alpha_{\text{div}} = 0.3$, $\alpha_{\text{chain}} = -0.2$, $\alpha_{\text{recip}} = -0.2$.

In the remaining sections of this chapter, we will demonstrate how to generate such networks using dichotomized Gaussian random variables. Then, after generating some networks, we will examine the relationship between α^{chain} and $\lambda_{\max}$ and the relationship between α^{conv} and σ_μ^2, and see how these relationships compare to what we saw for the homogeneous case in Chapter 2.

3.1 Generating Networks

3.1.1 Overview

As mentioned in Chapter 2, to generate SONETs we will use dichotomized Gaussian random variables so as to minimize all higher order statistics. To do this, we first generate Gaussian random variables Z_{ij} with appropriate covariance matrix Σ such that after dichotomizing, we get a network with first and second order connectivity statistics as prescribed in equations (3.1) and (3.2). We then threshold them to Bernoulli random variables to create an adjacency matrix W. To generate the Gaussian random variables, we first compute a square root S of Σ and then compute $Z = SX$ where X is an $N \times N$ matrix of independent standard normal random variables; the resultant Z is a multivariate normal random variable with covariance matrix Σ.

The main challenge with this method is that if we want to model a network with a realistic number of neurons N (or even a relatively small number of neurons, e.g. N=1000), we cannot compute SX directly, as S is a $N^2 \times N^2$ matrix. Instead, we will exploit the structure of Σ to calculate an approximate form for S in terms of a small number of parameters, which we will then use to calculate the matrix multiplication efficiently by hand.

To summarize, our method to generate SONETs will be as follows:

- Calculate the covariance matrix Σ of the corresponding Gaussian random variables
- Compute an approximate square root S of Σ
- Generate the desired Gaussian random variable via $Z = SX$, where X is a $N \times N$ matrix (viewed as an $N^2 \times 1$ vector) with entries independently drawn from the standard normal distribution
- Threshold Z to a Bernoulli random variable W, where $W_{ij} = 1$ if $Z_{ij} > 1$ and $W_{ij} = 0$ otherwise

3.1.2 Calculating the covariance matrix

Here, we will determine what the entries of Σ should be so that when we threshold the Gaussian random variables, we get a network with desired first and second order connectivity statistics (3.1) and (3.2).

Let σ_{ij} denote the standard deviation of Z_{ij}. The correlation coefficients wil be denoted as follows: $\rho^{\text{recip}}_{ij} = \rho^{\text{recip}}_{ji}$ corresponds to the reciprocal motif, $\rho^{\text{conv}}_{ijk} = \rho^{\text{conv}}_{ikj}$ corresponds to convergent motif, $\rho^{\text{div}}_{ikj} = \rho^{\text{div}}_{kij}$ correspond to the divergent motif, and $\rho^{\text{chain}}_{ijk}$ corresponds to chain motif. (When we refer to a value of ρ without knowing the motif type, we will denote it as $\rho^v_{ij\tilde{i}\tilde{j}}$, where $v \in \{\text{recip}, \text{conv}, \text{div}, \text{chain}\}$.) Then we have that the nonzero entries of Σ are

$$
\begin{aligned}
\Sigma_{(i,j),(i,j)} &= \mathrm{Var}(Z_{ij}) = \sigma_{ij}^2 \\
\Sigma_{(i,j),(j,i)} &= \mathrm{Cov}(Z_{ij}, Z_{ji}) = \sigma_{ij}\sigma_{ji}\rho_{ij}^{\text{recip}} \\
\Sigma_{(i,j),(i,k)} &= \mathrm{Cov}(Z_{ij}, Z_{ik}) = \sigma_{ij}\sigma_{ik}\rho_{ijk}^{\text{conv}} \\
\Sigma_{(i,j),(k,j)} &= \mathrm{Cov}(Z_{ij}, Z_{kj}) = \sigma_{ij}\sigma_{kj}\rho_{ikj}^{\text{div}} \\
\Sigma_{(i,j),(j,k)} &= \mathrm{Cov}(Z_{ij}, Z_{jk}) = \sigma_{ij}\sigma_{jk}\rho_{ijk}^{\text{chain}},
\end{aligned}
$$

and the rest of the entries of Σ are all zero. We determine the nonzero entries of Σ from the first and second order connectivity statistics of the network. The p_{ij} and σ_{ij} are related by the following equation:

$$
\begin{aligned}
p_{ij} &= \mathrm{P}(W_{ij} = 1) \\
&= \mathrm{P}(Z_{ij} > 1) \\
&= \int_1^\infty \frac{1}{\sqrt{2\pi}\sigma_{ij}} e^{-\frac{Z_{ij}^2}{2\sigma_{ij}^2}}\, dZ_{ij}.
\end{aligned}
$$

We can solve this equation for σ_{ij} using the Gaussian error function, denoted erf:

$$
\sigma_{ij} = \begin{cases} \dfrac{1}{\sqrt{2}\mathrm{erf}^{-1}(1 - 2p_{ij})} & \text{for } p_{ij} \in (0,1) \\ 0 & \text{otherwise.} \end{cases}
$$

The $\rho^v_{ij\tilde{i}\tilde{j}}$ depend on both the p_{ij} and α^v via the equations

$$
\begin{aligned}
p_{ij}p_{\tilde{i}\tilde{j}}(1 + \alpha^v) &= \mathrm{P}(W_{ij} = 1, W_{\tilde{i}\tilde{j}} = 1) \\
&= \mathrm{P}(Z_{ij} > 1, Z_{\tilde{i}\tilde{j}} > 1) \\
&= \int_1^\infty \int_1^\infty \frac{e^{-\frac{1}{2(1-(\rho^v_{ij\tilde{i}\tilde{j}})^2)}\left(\frac{Z_{ij}^2}{\sigma_{ij}^2} + \frac{Z_{ji}^2}{\sigma_{\tilde{i}\tilde{j}}^2} - \frac{2\rho^v_{ij\tilde{i}\tilde{j}} Z_{ij} Z_{ji}}{\sigma_{ij}\sigma_{\tilde{i}\tilde{j}}}\right)}}{2\pi\sigma_{ij}\sigma_{\tilde{i}\tilde{j}}\sqrt{1 - (\rho^v_{ij\tilde{i}\tilde{j}})^2}}\, dZ_{ij}\, dZ_{ji}.
\end{aligned}
$$

For example, the relationship between α^{recip} and ρ_{ij}^{recip} is that

$$\begin{aligned} p_{ij}p_{ji}(1+\alpha^{\text{recip}}) &= \mathrm{P}(W_{ij}=1, W_{ji}=1) \\ &= \mathrm{P}(Z_{ij}>1, Z_{ji}>1) \\ &= \int_1^\infty \int_1^\infty \frac{e^{-\frac{1}{2(1-(\rho_{ij}^{\text{recip}})^2)}\left(\frac{Z_{ij}^2}{\sigma_{ij}^2}+\frac{Z_{ji}^2}{\sigma_{ji}^2}-\frac{2\rho_{ij}^{\text{recip}}Z_{ij}Z_{ji}}{\sigma_{ij}\sigma_{ji}}\right)}}{2\pi\sigma_{ij}\sigma_{ji}\sqrt{1-(\rho_{ij}^{\text{recip}})^2}}\, dZ_{ij}\, dZ_{ji}. \end{aligned}$$

One can solve these equations numerically for the $\rho_{ij\tilde{i}\tilde{j}}^v$.

At this point, solving for S will be intractable because we will have too many equations to solve, as the $\rho_{ij\tilde{i}\tilde{j}}^v$ depend on neuron label. For this reason, we looked for a simple relation between $\rho_{ij\tilde{i}\tilde{j}}^v$ and α^v so that we could express the entries of Σ in terms of the α^v, which are independent of neuron label. Using a nonlinear least-squares fit in the parameter ranges $0 \le p_{ij} \le 0.25$ and $0 \le \alpha^v \le 1$, we found that $\rho_{ij\tilde{i}\tilde{j}}^v$ is approximately related to p_{ij} and α^v in the following way:

$$\rho_{ij\tilde{i}\tilde{j}}^v = c_1(p_{ij}+c_2)(p_{ji}+c_2)(\alpha^v+c_3) \tag{3.3}$$

where $c_1 = 1.9531, c_2 = 0.2658$, and $c_3 = 0.047$ (mean-squared error 9.0837 e-06).

As desired, we can rewrite the entries of Σ using relationship (3.3). For example, the reciprocal entries become

$$\begin{aligned} \sigma_{ij}\sigma_{ji}\rho_{ij}^{\text{recip}} &= \sigma_{ij}\sigma_{ji}c_1(p_{ij}+c_2)(p_{ji}+c_2)(\alpha^{\text{recip}}+c_3) \\ &= c_1\sigma_{ij}(p_{ij}+c_2)\sigma_{ji}(p_{ji}+c_2)(\alpha^{\text{recip}}+c_3) \\ &= c_1\tilde{\sigma}_{ij}\tilde{\sigma}_{ji}(\alpha^{\text{recip}}+c_3), \end{aligned}$$

where we define

$$\tilde{\sigma}_{ij} = \sigma_{ij}(p_{ij}+c_2).$$

We can now rewrite the entries of Σ as follows:

$$
\begin{aligned}
\Sigma_{(i,j),(i,j)} &= \mathrm{Var}(Z_{ij}) = \sigma_{ij}^2 \\
\Sigma_{(i,j),(j,i)} &= \mathrm{Cov}(Z_{ij}, Z_{ji}) = c_1 \widetilde{\sigma}_{ij} \widetilde{\sigma}_{ji} (\alpha^{\mathrm{recip}} + c_3) \\
\Sigma_{(i,j),(i,k)} &= \mathrm{Cov}(Z_{ij}, Z_{ik}) = c_1 \widetilde{\sigma}_{ij} \widetilde{\sigma}_{ik} (\alpha^{\mathrm{conv}} + c_3) \\
\Sigma_{(i,j),(k,j)} &= \mathrm{Cov}(Z_{ij}, Z_{kj}) = c_1 \widetilde{\sigma}_{ik} \widetilde{\sigma}_{jk} (\alpha^{\mathrm{div}} + c_3) \\
\Sigma_{(i,j),(j,k)} &= \mathrm{Cov}(Z_{ij}, Z_{jk}) = c_1 \widetilde{\sigma}_{ij} \widetilde{\sigma}_{jk} (\alpha^{\mathrm{chain}} + c_3).
\end{aligned}
$$

3.1.3 Equations that determine the square root S

Let S be a square root of Σ, the covariance matrix for the Gaussian random variable Z. We hope to find a square root S that has the same structure as that of Σ. Let a_{ij} be the diagonal entry of the square root corresponding to W_{ij}. Let $b_{ij} = b_{ji}$ correspond to reciprocal connection $W_{ij}W_{ji}$. Let $c_{ijk} = c_{ikj}$ correspond to convergent connection $W_{ij}W_{ik}$. Let $d_{ijk} = d_{jik}$ correspond to divergent connection $W_{ik}W_{jk}$. Let e_{ijk} correspond to chain connection $W_{ij}W_{jk}$. We set other entries of the square root to be zero, ignoring the fact that this leads to nonzero entries in other entries of the covariance matrix. These nonzero entries are small for large N.

By comparing entries of S^2 and Σ, we get the following equations that define the entries of S:

$$\sigma_{ij}^2 = a_{ij}^2 + b_{ij}^2 + \sum_{k \notin \{i,j\}} (c_{ijk}^2 + d_{ikj}^2 + e_{ijk}^2 + e_{kij}^2) \tag{3.4a}$$

$$c_1 \widetilde{\sigma}_{ij} \widetilde{\sigma}_{ji} (\alpha^{\text{recip}} + c_3) = (a_{ij} + a_{ji}) b_{ij} + \sum_{k \notin \{i,j\}} (c_{ijk} e_{jik} + c_{jik} e_{ijk} + d_{ikj} e_{kji} + d_{jki} e_{kij}) \tag{3.4b}$$

$$\begin{aligned} c_1 \widetilde{\sigma}_{ij} \widetilde{\sigma}_{ik} (\alpha^{\text{conv}} + c_3) = &(a_{ij} + a_{ik}) c_{ijk} + b_{ij} e_{jik} + b_{ik} e_{kij} + d_{ikj} e_{ikj} + d_{ijk} e_{ijk} \\ &+ \sum_{l \notin \{i,j,k\}} (c_{ijl} c_{ikl} + e_{lij} e_{lik}) \end{aligned} \tag{3.4c}$$

$$\begin{aligned} c_1 \widetilde{\sigma}_{ik} \widetilde{\sigma}_{jk} (\alpha^{\text{div}} + c_3) = &(a_{ik} + a_{jk}) d_{ijk} + b_{ik} e_{jki} + b_{kj} e_{ikj} + c_{ikj} e_{ijk} + c_{jki} e_{jik} \\ &+ \sum_{l \notin \{i,j,k\}} (d_{ilk} d_{jlk} + e_{ikl} e_{jkl}) \end{aligned} \tag{3.4d}$$

$$\begin{aligned} c_1 \widetilde{\sigma}_{ij} \widetilde{\sigma}_{jk} (\alpha^{\text{chain}} + c_3) = &(a_{ij} + a_{jk}) e_{ijk} + b_{ij} c_{jik} + b_{jk} d_{ikj} + c_{ijk} d_{ijk} + e_{kij} e_{jki} \\ &+ \sum_{l \notin \{i,j,k\}} (c_{jkl} e_{ijl} + d_{ilj} e_{ljk}) \end{aligned} \tag{3.4e}$$

The only terms that depend on indicies on the left-hand side are the σ_{ij}'s and the $\tilde{\sigma}_{ij}$'s. This form of the equations will allow us to do some nice cancellation in what follows and to ultimately find a solution to (3.4).

We now have $O(N^3)$ equations in $O(N^3)$ unknowns. We could go through and numerically solve these equations, but this would be numerically intractable. Instead, we will solve for an approximate solution to these equations.

3.1.4 Solving for convergent, divergent, and chain entries of S

To find an approximate square root S, we'll start by examining equations (3.4c)-(3.4e). For each of these equations, we assume that compared to the entire sum on the right-hand side, the first five terms are negligible. After neglecting these terms, these equations are now only in terms of c_{ijk}, d_{ijk}, and e_{ijk}:

$$c_1\widetilde{\sigma}_{ij}\widetilde{\sigma}_{ik}(\alpha^{\text{conv}} + c_3) = \sum_{l \notin \{i,j,k\}} (c_{ijl}c_{ikl} + e_{lij}e_{lik})$$
$$c_1\widetilde{\sigma}_{ik}\widetilde{\sigma}_{jk}(\alpha^{\text{div}} + c_3) = \sum_{l \notin \{i,j,k\}} (d_{ilk}d_{jlk} + e_{ikl}e_{jkl})$$
$$c_1\widetilde{\sigma}_{ij}\widetilde{\sigma}_{jk}(\alpha^{\text{chain}} + c_3) = \sum_{l \notin \{i,j,k\}} (c_{jkl}e_{ijl} + d_{ilj}e_{ljk}).$$

At this point, we have a lot of unknown parameters to solve for: all of the c_{ijk}, d_{ijk}, and e_{ijk}. However, given our above approximations, it turns out we can solve these equations by assuming a simple form for these parameters. Namely, we assume that there are constants c, d, and e such that for all i, j, and k, $c_{ijk} = c\widetilde{\sigma}_{ij}\widetilde{\sigma}_{ik}, d_{ijk} = d\widetilde{\sigma}_{ij}\widetilde{\sigma}_{kj}$, and $e_{ijk} = e\widetilde{\sigma}_{ij}\widetilde{\sigma}_{jk}$. Now, we just need to solve for the three parameters c, d, and e. Under this assumption, and after some nice cancellation, these equations become

$$c_1(\alpha^{\text{conv}} + c_3) = \Big(\sum_{l \notin \{i,j,k\}} \widetilde{\sigma}_{il}^2\Big)c^2 + \Big(\sum_{l \notin \{i,j,k\}} \widetilde{\sigma}_{li}^2\Big)e^2 \tag{3.5a}$$
$$c_1(\alpha^{\text{div}} + c_3) = \Big(\sum_{l \notin \{i,j,k\}} \widetilde{\sigma}_{lk}^2\Big)d^2 + \Big(\sum_{l \notin \{i,j,k\}} \widetilde{\sigma}_{kl}^2\Big)e^2 \tag{3.5b}$$
$$c_1(\alpha^{\text{chain}} + c_3) = \Big(\sum_{l \notin \{i,j,k\}} \widetilde{\sigma}_{jl}^2\Big)ce + \Big(\sum_{l \notin \{i,j,k\}} \widetilde{\sigma}_{lj}^2\Big)de. \tag{3.5c}$$

Now we have a system of inconsistent equations, since the left-hand sides of these equations do not depend on i, j, or k, while the right-hand sides do. Our next assumption will allow us to eliminate these inconsistencies. Let M be an $N \times N$ matrix such that $M_{ij} = \widetilde{\sigma}_{ij}^2$. We'll make the assumption that all of the row-sums and column-sums of M are equal to the same value, which we'll call m. All of the coefficients on the right-hand side of equations (3.5a)-(3.5c) are almost equal to m. We assume that for each of these sums, the two nonzero missing terms are negligible in comparison to m.

Under this assumption, the system of equations (3.5) becomes

$$\begin{aligned} c_1(\alpha^{\text{conv}} + c_3) &= mc^2 + me^2 \\ c_1(\alpha^{\text{div}} + c_3) &= md^2 + me^2 \\ c_1(\alpha^{\text{chain}} + c_3) &= mce + mde. \end{aligned}$$

Solving this system of equations is the same as solving the matrix equation

$$AA^T = E \tag{3.6}$$

where

$$E = c_1 \begin{bmatrix} \alpha^{\text{conv}} + c_3 & \alpha^{\text{chain}} + c_3 \\ \alpha^{\text{chain}} + c_3 & \alpha^{\text{div}} + c_3 \end{bmatrix} \qquad \text{and} \qquad A = \begin{bmatrix} c\sqrt{m} & e\sqrt{m} \\ e\sqrt{m} & d\sqrt{m} \end{bmatrix}.$$

Both E and A are real symmetric matrices, so we can find eigenvalue decompositions $E = VDV^{-1}$ and $A = UBU^{-1}$ where V and U are unitary, i.e. $V^{-1} = V^T$ and $U^{-1} = U^T$. Then $AA^T = (UBU^{-1})(UBU^{-1}) = UB^2U^{-1}$, so setting $U = V$ and $B^2 = D$ satisfies equation (3.6). We solve for the diagonal matrix B that satistfies $B^2 = D$ by letting $B(i,i) = \sqrt{D(i,i)}$. (Note that this makes it easy to see when we won't get a solution for B - i.e. when there is at least one negative eigenvalue for E.) Then $A = VBV^{-1}$ is a solution to (3.6). We can then solve for the values of c, d, and e:

$$c = \frac{A_{11}}{\sqrt{m}}, \quad d = \frac{A_{22}}{\sqrt{m}}, \quad e = \frac{A_{12}}{\sqrt{m}}.$$

3.1.5 Finding the remaining entries of S

Now that we have the values of c, d, and e, we can go back and solve for the values of a_{ij}, a_{ji}, and $b_{ij} = b_{ji}$. From equations (3.4a) and (3.4b) we have that

$$\begin{aligned}
\sigma_{ij}^2 &= a_{ij}^2 + b_{ij}^2 + \widetilde{\sigma}_{ij}^2 \sum_{k\notin\{i,j\}} (c^2\widetilde{\sigma}_{ik}^2 + d^2\widetilde{\sigma}_{kj}^2 + e^2\widetilde{\sigma}_{jk}^2 + e^2\widetilde{\sigma}_{ki}^2) \\
\sigma_{ji}^2 &= a_{ji}^2 + b_{ij}^2 + \widetilde{\sigma}_{ji}^2 \sum_{k\notin\{i,j\}} (c^2\widetilde{\sigma}_{jk}^2 + d^2\widetilde{\sigma}_{ki}^2 + e^2\widetilde{\sigma}_{ik}^2 + e^2\widetilde{\sigma}_{kj}^2) \\
c_1\widetilde{\sigma}_{ij}\widetilde{\sigma}_{ji}(\alpha^{\text{recip}} + c_3) &= (a_{ij} + a_{ji})b_{ij} + \widetilde{\sigma}_{ij}\widetilde{\sigma}_{ji} \sum_{k\notin\{i,j\}} (ce\widetilde{\sigma}_{ik}^2 + ce\widetilde{\sigma}_{jk}^2 + de\widetilde{\sigma}_{kj}^2 + de\widetilde{\sigma}_{ki}^2).
\end{aligned}$$

These equations can be written in the form

$$a_{ij}^2 + b_{ij}^2 = f_{ij} \tag{3.7a}$$

$$a_{ji}^2 + b_{ij}^2 = g_{ij} \tag{3.7b}$$

$$(a_{ij} + a_{ji})b_{ij} = h_{ij} \tag{3.7c}$$

where

$$\begin{aligned}
f_{ij} &= \sigma_{ij}^2 - \widetilde{\sigma}_{ij}^2 \sum_{k\notin\{i,j\}} (c^2\widetilde{\sigma}_{ik}^2 + d^2\widetilde{\sigma}_{kj}^2 + e^2\widetilde{\sigma}_{jk}^2 + e^2\widetilde{\sigma}_{ki}^2) \\
g_{ij} &= \sigma_{ji}^2 - \widetilde{\sigma}_{ji}^2 \sum_{k\notin\{i,j\}} (c^2\widetilde{\sigma}_{jk}^2 + d^2\widetilde{\sigma}_{ki}^2 + e^2\widetilde{\sigma}_{ik}^2 + e^2\widetilde{\sigma}_{kj}^2) \\
h_{ij} &= c_1\widetilde{\sigma}_{ij}\widetilde{\sigma}_{ji}(\alpha^{\text{recip}} + c_3) - \widetilde{\sigma}_{ij}\widetilde{\sigma}_{ji} \sum_{k\notin\{i,j\}} (ce\widetilde{\sigma}_{ik}^2 + ce\widetilde{\sigma}_{jk}^2 + de\widetilde{\sigma}_{kj}^2 + de\widetilde{\sigma}_{ki}^2).
\end{aligned}$$

Note that these equations requre that $f_{ij} \geq 0$ and $g_{ij} \geq 0$ for solutions to exist. If $f_{ij} > 0$ and $g_{ij} > 0$, we can solve these equations in the following manner. First, we use equation (3.7c) to rewrite equations (3.7a) and (3.7b) in terms of a_{ij} and a_{ji}:

$$a_{ij}^2 + \frac{h_{ij}^2}{(a_{ij} + a_{ji})^2} = f_{ij} \tag{3.8a}$$

$$a_{ji}^2 + \frac{h_{ij}^2}{(a_{ij} + a_{ji})^2} = g_{ij} \tag{3.8b}$$

Next, we solve equation (3.8a) for a_{ji}:

$$a_{ji} = \frac{\pm h_{ij}}{\sqrt{f_{ij} - a_{ij}^2}} - a_{ij} \tag{3.9}$$

Then we plug this into equation (3.8b) and solve for a_{ij}:

$$\begin{aligned}
\left(\frac{\pm h_{ij}}{\sqrt{f_{ij} - a_{ij}^2}} - a_{ij}\right)^2 + f_{ij} - a_{ij}^2 &= g_{ij} \\
\frac{h_{ij}^2}{f_{ij} - a_{ij}^2} - 2a_{ij}\frac{\pm h_{ij}}{\sqrt{f_{ij} - a_{ij}^2}} + f_{ij} &= g_{ij} \\
\frac{h_{ij}^2}{f_{ij} - a_{ij}^2} + f_{ij} - g_{ij} &= 2a_{ij}\frac{\pm h_{ij}}{\sqrt{f_{ij} - a_{ij}^2}} \\
\frac{h_{ij}^4}{(f_{ij} - a_{ij}^2)^2} + 2\frac{h_{ij}^2}{f_{ij} - a_{ij}^2}(f_{ij} - g_{ij}) + (f_{ij} - g_{ij})^2 &= 4a_{ij}^2\frac{h_{ij}^2}{f_{ij} - a_{ij}^2} \\
h_{ij}^4 + 2h_{ij}^2(f - a_{ij}^2)(f_{ij} - g_{ij}) + (f_{ij} - a_{ij}^2)^2(f_{ij} - g_{ij})^2 &= 4a_{ij}^2h_{ij}^2(f_{ij} - a_{ij}^2)
\end{aligned}$$

$$\begin{aligned}
[(f_{ij} - g_{ij})^2 + 4h_{ij}^2]a_{ij}^4 - [2h_{ij}^2(f_{ij} - g_{ij}) + 2f_{ij}(f_{ij} - g_{ij})^2 + 4h_{ij}^2 f_{ij}]a_{ij}^2 \\
+[h_{ij}^2 + f_{ij}(f_{ij} - g_{ij})]^2 = 0
\end{aligned}$$

We solve this last equation for a_{ij}^2, looking for a positive solution using the quadratic formula. If a position solution exists, then we can solve for a_{ij}. We will take a_{ij} to have positive sign.

We then calculate a_{ji} using equation (3.9), but we need to know which sign of the $\pm$ to use. We need to use the sign so that the above equations are satisfied before the squaring that got rid of the sign. This is the sign of

$$\left[\frac{h_{ij}^2}{f_{ij} - a_{ij}^2} + f_{ij} - g_{ij}\right] \Big/ \left[2a_{ij}\frac{h_{ij}}{\sqrt{f_{ij} - a_{ij}^2}}\right],$$

which should be either 1 or -1 (within numerical error). Then we can go back and solve for b_{ij}.

3.1.6 Generating the corresponding second order network

Now that we have solved for S, our approximate square root of Σ, we can use it to generate a second order network with prescribed first and second order statistics. Let X be a $N \times N$ matrix with entries independently drawn from the standard normal distribution. Then $Z = SX$ is a correlated Gaussian with covariance matrix equal to S^2, which is approximately equal to Σ. We can easily find the entries of Z given S, since most entries of S are equal to zero:

$$\begin{aligned}
Z_{ij} = &\sum_{m,n=1}^{N} S_{((i,j),(m,n))} X_{mn} \\
=& a_{ij} X_{ij} + b_{ij} X_{ji} + \sum_{n \notin \{i,j\}} c_{ijn} X_{in} + \sum_{m \notin \{i,j\}} d_{imj} X_{mj} + \sum_{n \notin \{i,j\}} e_{ijn} X_{jn} \\
&+ \sum_{m \notin \{i,j\}} e_{mij} X_{mi}.
\end{aligned}$$

Then we dichotomize Z to get a Bernoulli random variable W:

$$W_{ij} = \begin{cases} 1 & \text{if } Z_{ij} > 1 \\ 0 & \text{otherwise} \end{cases}$$

The matrix W forms the adjacency matrix of the resulting SONET. The adjacency matricies of a few sample networks are shown in Figure 3.2. They provide a nice visualization of the global structure of the ring juxtaposed with the microstructure due to the second order connection motifs. In the convergent network, the horizontal banding reflects the correlation between α_{conv} and $\text{var}(d^i_{\text{in}})$. Likewise, the vertical banding in the divergent network reflects the correlation between α_{div} and $\text{var}(d^i_{\text{out}})$. Compared to a network with negative α_{chain} (not shown), we see greater symmetry between the horizontal and vertical banding in the chain network, indicating that high (low) in-degree corresponds to high (low) out-degree.

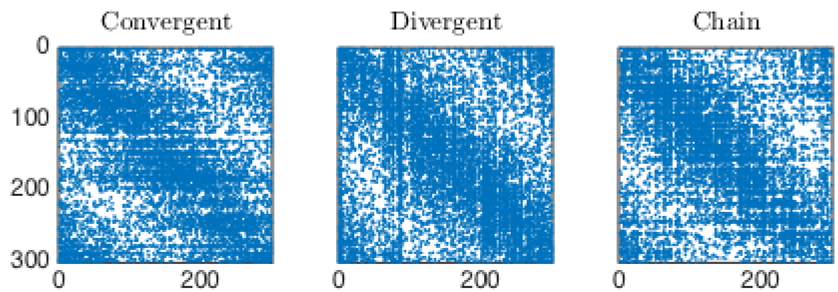

Figure 3.2: Connection matricies for a few sample networks with $N = 300$ neurons. The connection probabilities are determined by the ring model, with $\ell = 75$ and with 10% average connectivity. For all networks, $\alpha_{\text{recip}} = 1$. Convergent network: $\alpha_{\text{conv}} = 0.5$, $\alpha_{\text{div}} = 0$, $\alpha_{\text{chain}} = 0$. Divergent network: $\alpha_{\text{conv}} = 0$, $\alpha_{\text{div}} = 0.5$, $\alpha_{\text{chain}} = 0$. Chain network: $\alpha_{\text{conv}} = 0.5$, $\alpha_{\text{div}} = 0.5$, $\alpha_{\text{chain}} = 0.4$.

3.2 Relationship to eigenvalue measures

3.2.1 Results

We examine the predicted relationships between network structure and key eigenvalue quantities by generating 190 SONETs with N=1000 neurons and 10% average connectivity. We use latin hypercube sampling to choose the second order statistics, where the ranges for the second order connectivity statistics are $\alpha^{\text{recip}} \in [-1, 4]$, $\alpha^{\text{conv}} \in [0, 1]$, $\alpha^{\text{div}} \in [0, 1]$, and $\alpha^{\text{chain}} \in [-0.5, 1]$. We use the ring model from the beginning of this chapter to generate connection probabilities, with $\ln(\ell)$ randomly sampled (as part of the hypercube sampling) from the range $[\ln(50), \ln(500)]$. For each network, we assign $p_{\max}$ based on the value of ℓ so that the average connection probability remains at approximately $p = 0.1$. To find $p_{\max}$ as a function of ℓ, we performed a least-squares fit (with $N = 1000$ neurons and for data where the average connectivity was kept at approximately 10%) and found that these parameters were related by a power law, $p_{\max} \approx 90.63\ell^{-1.174} + 0.09644$. After plotting ℓ against $\lambda_{\max}$ and σ_{μ}^2, we find that ℓ does not have an influence on either of these statistics (graphs not shown).

Even though we know the underlying probability distribution, meaning we know the parameters α, we compare the network synchrony to the measured values of $\hat{\alpha}$. Because these networks are generated probabilistically, $\hat{\alpha}$ will vary slightly from α. We find that of the two, $\hat{\alpha}$ is the better predictor of synchrony.

Figure 3.3 shows $\lambda_{\max}$ plotted as a function of pairs of connectivity statistics. From this, we can see that $\lambda_{\max}$ appears to primarily be determined by α^{chain}, as $\lambda_{\max}$ varies smoothly with α^{chain} even though all the other second order statistics and the value of l are varying significantly. Similarly, Figure 3.4 demonstrates that σ_μ^2 seems to be determined primarily by α^{conv}.

In both of these figures, we see that the valid range of α^{chain} seems to depend on the other three statistics. The valid range of α^{chain} increases as both α^{conv} and α^{div} increase, due to how these three statistics relate to the degree distribution. We also see that α^{chain} values depend on $\alpha^{\text{reciprocal}}$ values and vice versa, which is not surprising, as a reciprocal connection is like a chain connection but with the same starting and ending neuron.

Sample spectrum from a few connectivity matrices W are plotted in Figure 3.5. We see that $\lambda_{\max}$ increases with α^{chain} (middle plot), and that only α^{conv} affects the spread of the eigenvalues of the Laplacian L (right). These results are nearly identical to what Zhao et al saw in the homogeneous case ([1], Figure 7).

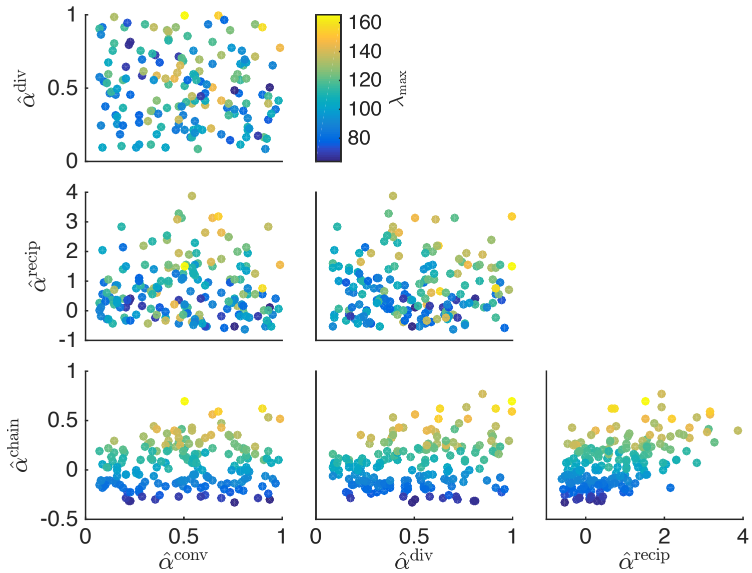

Figure 3.3: λ_{max} plotted as a function of pairs of connectivity statistics. Each dot represents one network, and color indicates the largest eigenvalue λ_{max} of the network.

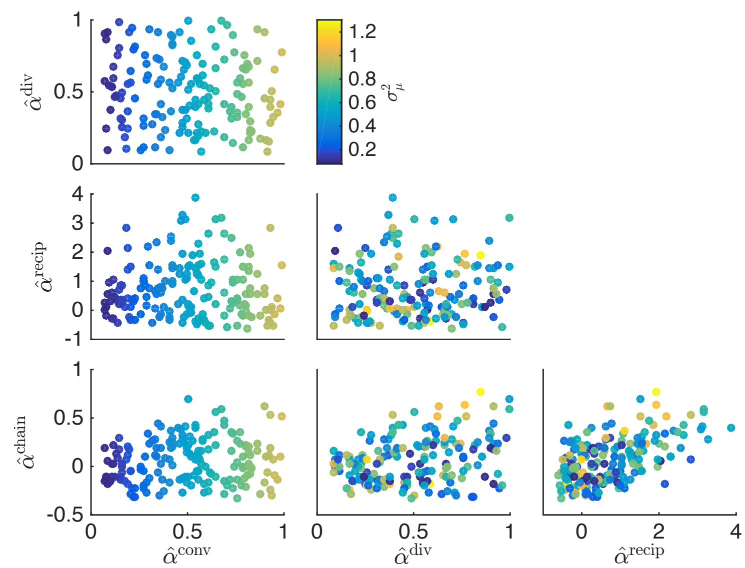

Figure 3.4: σ^2_μ plotted as a function of pairs of connectivity statistics. Each dot represents one network, and color indicates the normalized variance of the Laplacian, σ^2_μ.

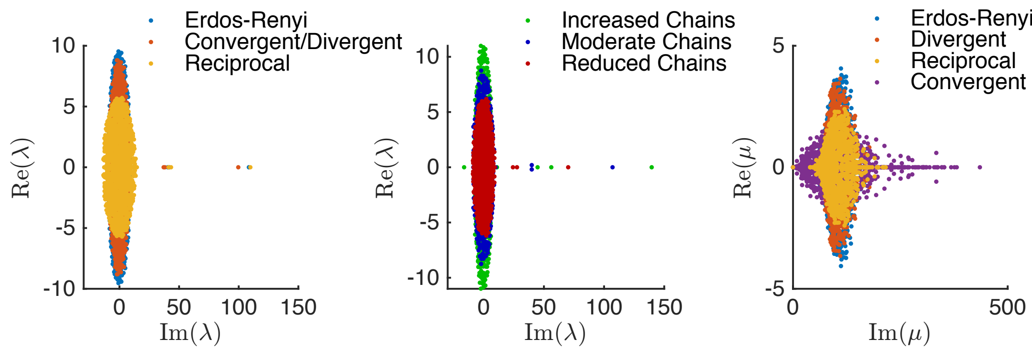

Figure 3.5: Spectra of connectivity matrices and Laplacian matricies for sample networks. All α's not mentioned are zero. **Left**: Non-zero parameters $\alpha^{\text{conv}} = 0.5$ (convergent), $\alpha^{\text{div}} = 0.5$ (divergent), $\alpha^{\text{recip}} = 2$ (reciprocal). Eigenvalues for convergent and divergent networks were identical. **Middle**: Largest eigenvalue λ_{max} increases linearly with α^{chain}. All three networks have substantial convergence and divergence ($\alpha^{\text{conv}} = \alpha^{\text{conv}} = 0.5$) to allow for large values of α^{chain}. Parameters: $\alpha^{\text{chain}} = 0.4$ (increased chains), $\alpha^{\text{chain}} = 0$ (moderate chains), $\alpha^{\text{chain}} = -0.4$ (reduced chains). **Right**: Eigenvalues of the Laplacian for the networks from the left panel. Only α^{conv} significantly moderates the variance of the eigenvalues. Changing the value of α^{chain} did not affect the variance (not shown).

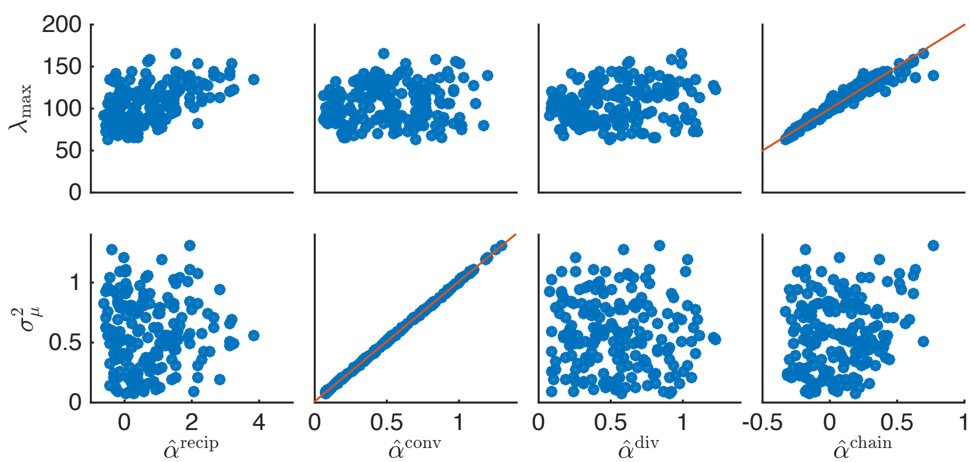

Figure 3.6: The relationship between the two key eigenvalue quantities and the connectivity statistics for the 186 sampled SONETs. In each panel, each dot corresponds to one of the networks. Red line in the top right panel is relationship (2.5) between λ_{max} and α^{chain}. Red line in the second panel of the bottom row is relationship (2.4) between σ^2_μ and α^{conv}.

Figure 3.6 shows the connectivity statistics plotted against both λ_{max} and σ_μ^2. In the top right panel, the red line is the predicted relationship (2.5) between λ_{max} and α^{chain}, which fits the data well. In the second panel of the bottom row, the red line is the predicted relationship (2.4) between σ_μ^2 and α^{conv}, which fits the data almost identically. These plots show the same general trends as in the homogeneous case ([1], Figure 8).

3.2.2 Discussion

Using the framework of SONETs paired with a global ring structure, we looked at the relationship between the connectivity statistics and two key eigenvalue quantities related to the synchrony of the network - the largest eigenvalue of the connectivity matrix and the variance of the eigenvalues of the Laplacian. The results we saw were remarkably similar to those of the homogeneous case, with σ_μ^2 approximately equal to α_{conv} and with λ_{max} increasing linearly with α_{chain}. This indicates that this qualitative relationship between synchrony and second order statstics should extend to a larger class of networks. We also found that for the networks we considered, the eigenvalues do not depend on the specific parameters used to describe the overall geometry of the network (although this will not always be the case for other networks).

One important feature about our new approach is the ability to specify not only the microstructure of the local network but also how the connectivity varies at a larger scale. The brain is organized geometrically [10] and distance is known to play an important role in connections [11]. The homoegeneous model lacks any ability to specify the macrostructure, as the connectivity statistics of any pair or triplet of neurons are identical. In our approach, we can allow the connectivity to depend on neuron index, so we can work with a variety of neural networks. For example, we could make the connectivity depend on the underlying geometry of the network, which could be one-dimensional (as in the ring example) or two-dimensional. This model is also computationally efficient for a continuous description or a fine discretization of the network. To give a continuous description using the homogeneous model, we would need to discretize the network into many different populations and specify different p's and α's for every pair or triplet of populations. The computations needed increases rapidly with the number of populations, so it would be difficult to represent a continuous description of the network, such as one depending on the geometry of the network. With this new model, we do not need create subpopulations in order to give a continuous description of the network.

A major condition that made our algorithm computationally efficient was that the α's did not depend on neuron index. This is quite restrictive, as it requires the second order statistics to not depend on factors like distance or location of neurons. We'd like to be able to relax this condition so that we could have more complicated underlying geometries. However, this does seem to be a difficult problem, as we would have many more parameters to deal with. Another restrictive assumption was that the sum of the $\tilde{\sigma}_{ij}^2$'s over i or over j did not depend on neuronal index, which allowed us to reduce the number of equations and unknowns that determined S. This assumption also narrows the field of possible networks we can examine with this model, so we'd like to find some way to relax this condition. This seems more straightforward, but would require developing an approach to solve the larger system of equations efficiently.

A future possibility is to combine this model with a feedforward architecture. In this case, we wouldn't be able to use the eigenvalues of W to predict the synchrony of the network, since the eigenvalue analysis of feedforward and functionally feedforward matrices does not predict the persistent activity seen in the corresponding networks [12]. Instead, we would need to analyze these networks via a Schur decomposition, which identifies a different set of activity patterns that better predict the network activity. It's possible that we could determine network statistics rising from the Schur decomposition that are related to the synchrony of the network.

A different approach to combine microstructure with macrostructure is referred to as the "replace and rewire" method [13], which can be used to generate large networks with patterned structure. This method is based explicitly on a concept of populations of neurons and utilizes the Kronecker product of adjacency matrices. Each network is determined by three matrices - one specifies which populations are connected, one gives the intraconnectivity between the neurons of different populations, and one gives the interconnectivity within each population. It would be interesting to determine how these two approaches are related or how we might combine these two methods.

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