Heterogeneous firing rates modeled in densely connected recurrent neural networks

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Background

Instead of examining spike trains produced by neurons as isolated events, we are exploring the significance of the heterogeneity in spike patterns across an entire neural network. Understanding the heterogeneity in neural activity will help develop theories in neural dynamics and coding - how sensory information is encoded via spike times and patterns. A natural cause of heterogeneity in a network arises from the non-regular connectivity between neurons. We created random networks of both purely excitatory and mixed inhibitory-excitatory (IE) networks and observed the neural activity of each neuron once the network had converged to steady state. We recorded the steady-state for each network at different connection strengths and linearly approximated the steady-states with respect to connection strengths. We then tested the ability to predict levels of heterogeneity from a fundamental feature of network connectivity: the mean and variance of connection counts arriving at each cell.

Modeling neurons and firing rates

- Leaky integrate and fire differential equation:

$$\tau\dot{v} = -(v - E_L) + \mu + \sqrt{\sigma^2\tau}\xi(t) + i_{ext}(t)$$

- We adopted the leaky integrate and fire model for the dynamics of each cell in our network model.
- Firing rate function averages spike counts given an average input current. Firing rates saturate for large values of input current.

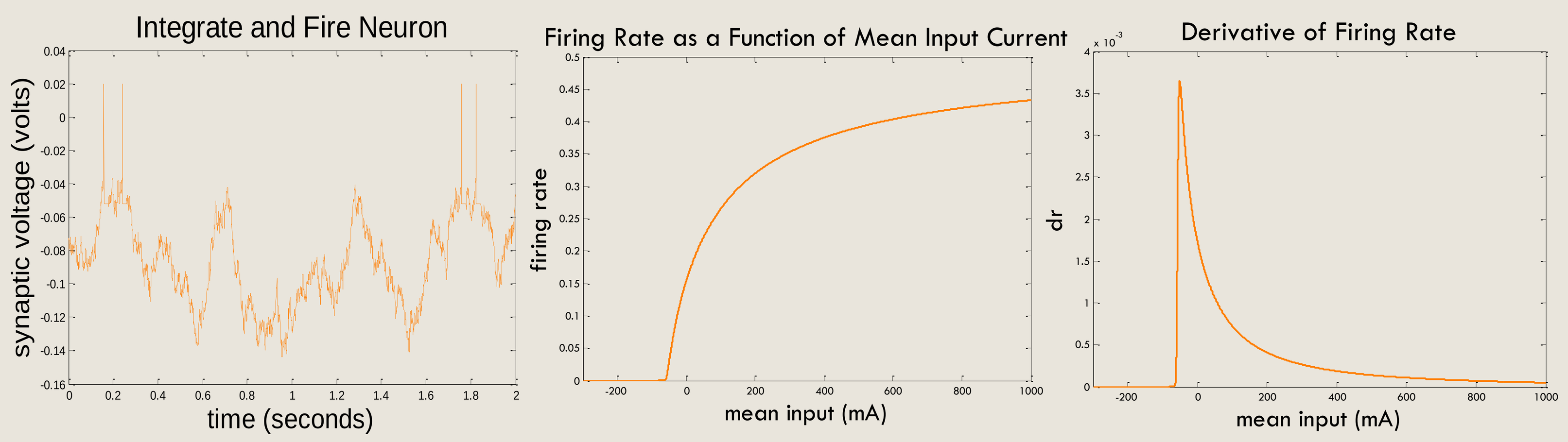
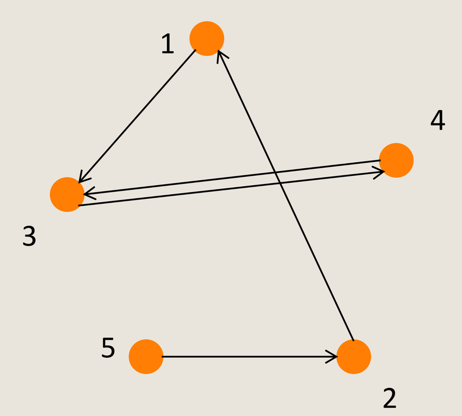


Figure 1: (**Left**): Voltage plot for standard integrate and fire neuron with spiking mechanism. (**Center**) Plot of neuron's firing rate as a function of average current input. (**Right**) Plot of the derivative of the firing rate.

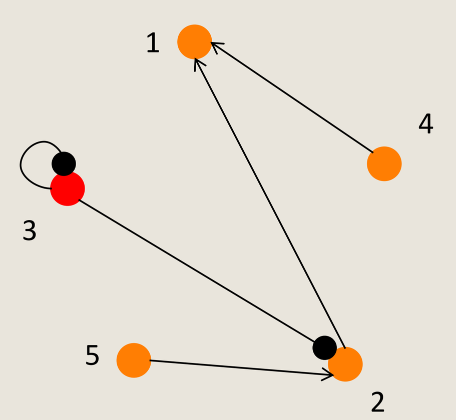
Creating neural networks

- We represent a neural network as a directed graph
- We used the Erdos-Renyi (n,p) model for our first order networks.
- The network architecture is stored in a connection matrix W where W_{ij} represents the connection strength from the jth neuron to the ith neuron.



0	1	0	0	0
0	0	0	0	1
1	0	0	1	0
0	0	1	0	0
0	0	0	0	0

Figure 2a: Graphical representation (**left**) and adjacency matrix (**right**) of a purely excitatory (E) network.



0	1	0	1	0
0	0	-1	0	1
0	0	-1	1	0
0	0	0	0	0
0	0	0	0	0

Figure 2b: Graphical representation (**left**) and adjacency matrix (**right**) of a mixed IE network

$$E_i^{n+1} = E_0 + \sum_j W_{ij} r\left(E_j^n\right)$$

Equation Key:

- $\boldsymbol{E_m^n}$ is the average input current into the mth neuron at the nth step
- $\boldsymbol{E_0}$ is average current due to white noise
- W_{ij} is the connection from the ith neuron to the $j$the neuron
- $\boldsymbol{r(E)}$ is the average firing rate of a neuron given the average input current

Equation 1 [1]: Discreet dynamics used to govern changes in the average current distribution in a neural network. We are interested in observing network activity of networks in steady-state.

Steady-states: analytically

- Banach's fixed-point theorem: every contraction mapping has a unique fixed point, which means for f a contraction, there exists an x^* so all infinite iterations of any initial value will converge to x^*, or

$$f(x_n) = x_{n+1}, \lim_{n\to\infty} f(x_n) \to f(x^*).$$

- Definition for contraction mapping:

$$d\big(f(x), f(y)\big) \le kd(x,y), k < 1.$$

- Mean value theorem for $f: R^n \to R^n$:

$$\vec{f}(\vec{x}) - \vec{f}\left(\overline{x+h}\right) = \int_0^1 Df\left(\overline{x+th}\right)dt \cdot h.$$

- Using an upper bound approximation for integrals and Hölder's inequality,

$$\left|\vec{f}(\vec{x}) - \vec{f}\left(\overline{x+h}\right)\right| \le \max Df \cdot |h|.$$

- The Jacobian is defined as $Df_{ij} = W_{ij} * dr\left(E_j\right)$ which means

$$\max Df = \max dr\,|W|.$$

Steady-states: numerically

To find steady-states (fixed points) numerically we used an iteration method. We iterated the function starting with a random initial value until it converged to a fixed point. Then we tested several dozen more initial values and compared the fixed points to check for uniqueness.

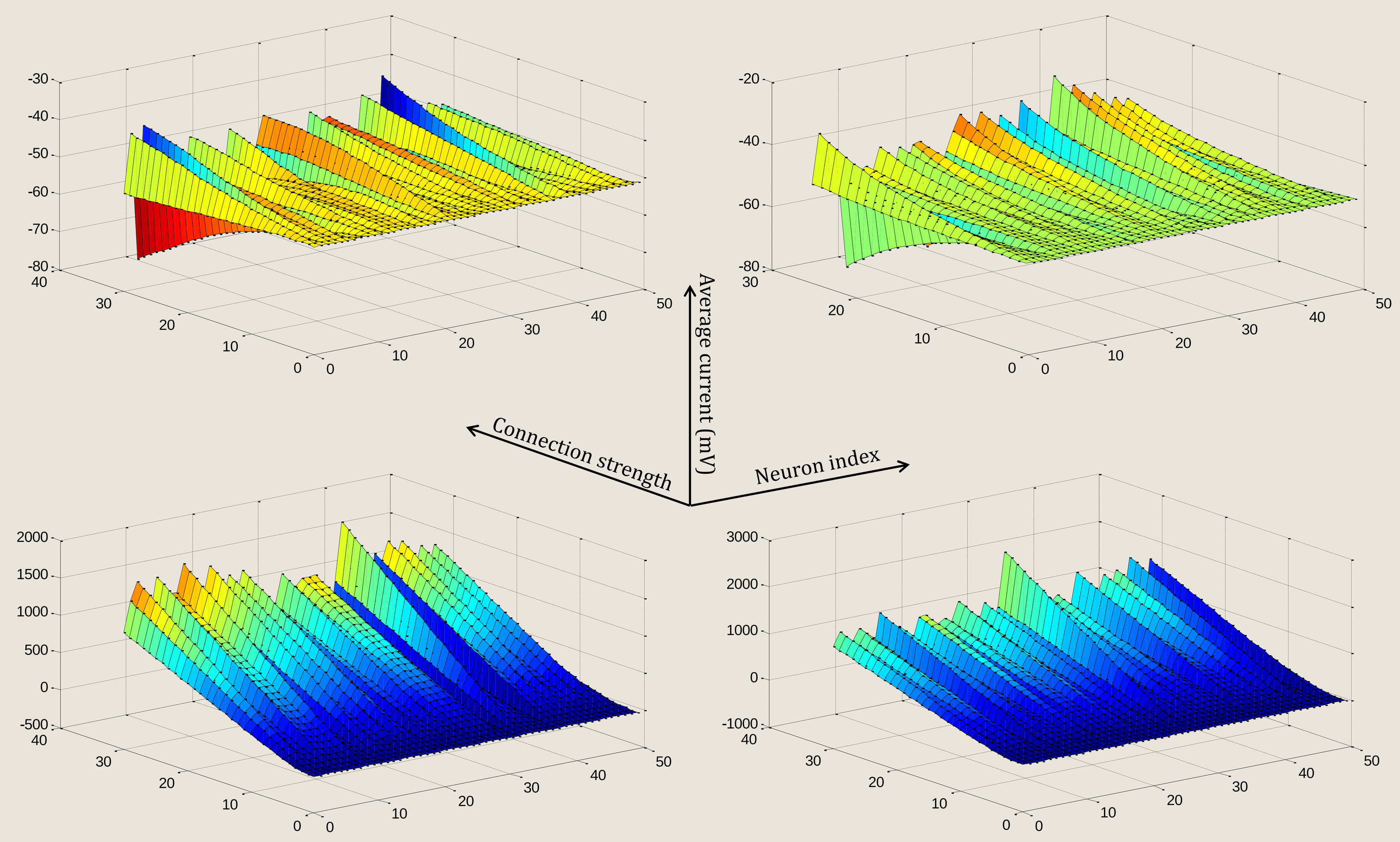


Figure 3: Plots of fixed points in neural activity for different connection strengths. (**Top left**): Mixed IE network, fully convergent. (**Top right**): Mixed IE network, stops converging for larger connection strengths. (**Bottom**): Two purely excitatory networks.

Preliminary Results

- We tested 100 50-neuron and 100 100-neuron Erdos-Renyi networks as well as 100 50-neuron and 100-neuron second-order networks (SONETs). For purely excitatory networks, the relationship between fixed points and connection strengths is very linear and unbounded, that is for arbitrarily large connection strengths, we could obtain arbitrarily large mean current input.
- Due to the balanced input of the mixed IE networks, convergence was not observed for all networks. Furthermore, the relationship between fixed points and connection strengths was much less linear.
- Larger network sizes increased the rate of change of fixed points with respect to connection strengths.

Future Work

We are testing relationships between the second order moments of the fixed points in each network with second order moments of two quantifiable architecture properties:

- In-degree – the number of connections into each neuron
- Frequencies of three-cell motifs:

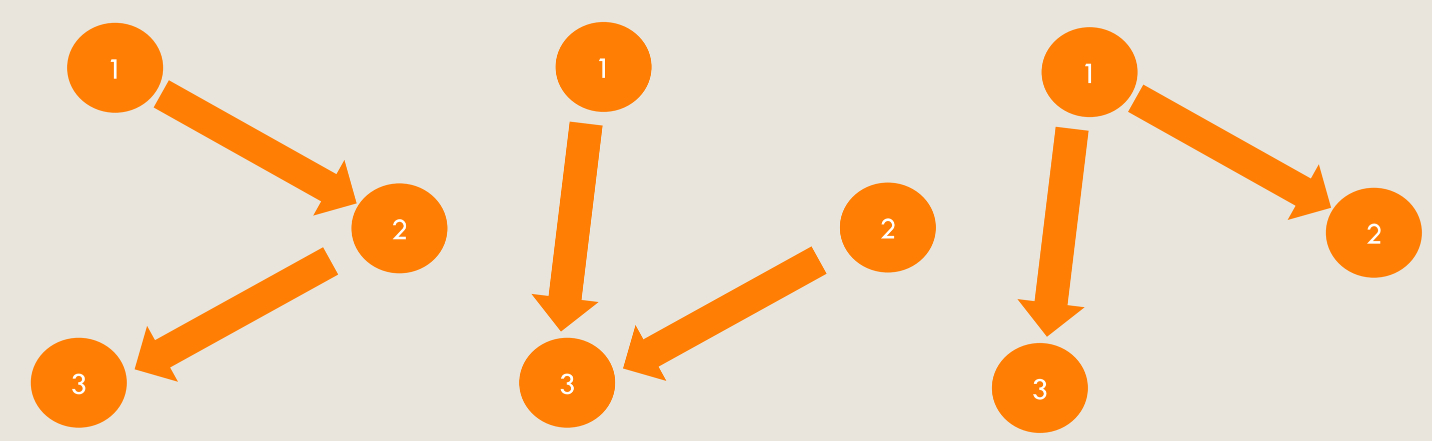


Figure 4a: Graphical representation of (**left**) chain, (**center**) convergent and (**right**) divergent motifs.

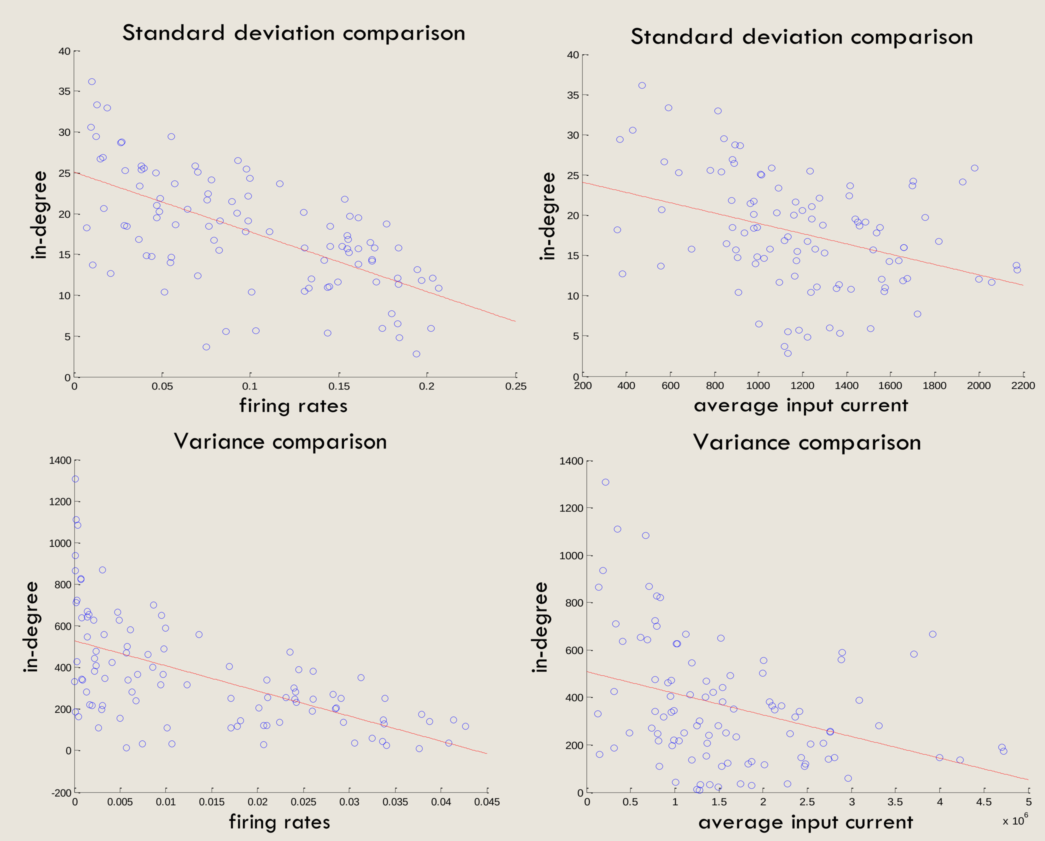


Figure 4b: Preliminary scatter plots comparing the (**top**) standard deviations and (**bottom**) variances of the in-degrees of the network and both the (**left**) firing rates and (**right**) average input current. Data shown for connection strength of 190 for all 100 ER networks with 100 neurons.

References

[1] J. Trousdale, Y. Hu, E. Shea-Brown, K. Josic. Impact of Network Structure and Cellular Response on Spike Time Correlations. PLOS Computational Biology, volume 8, issue 3, pg 14.

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