The effects of within-neuron degree correlations in networks of spiking neurons

Carlo R. Laing   Christian Bläsche

Abstract We consider the effects of correlations between the in- and out-degrees of individual neurons on the dynamics of a network of neurons. By using theta neurons, we can derive a set of coupled differential equations for the expected dynamics of neurons with the same in-degree. A Gaussian copula is used to introduce correlations between a neuron's in- and out-degree and numerical bifurcation analysis is used determine the effects of these correlations on the network's dynamics. For excitatory coupling we find that inducing positive correlations has a similar effect to increasing the coupling strength between neurons, while for inhibitory coupling it has the opposite effect. We also determine the propensity of various two- and three-neuron motifs to occur as correlations are varied and give a plausible

relations. They showed that once correlations were included, the dynamics are effectively four-dimensional, in contrast to the two-dimensional dynamics expected from a standard rate-based excitatory/inhibitory network. They also related the degree distributions to cortical motifs. Experimental evidence for within-neuron degree correlations is given in [31].

The structure of the paper is as follows. In Sec. 2 we present the model network and summarise the analysis of [1] showing that under certain assumptions, the network can be described by a coupled set of ordinary differential equations, one for the dynamics associated with each distinct in-degree. In Sec. 3 we discuss how to generate correlated in- and out-degrees using a Gaussian copula. Our model involves sums over all distinct in-degrees, and in Sec. 4 we present a computationally efficient method for evaluating these sums, in analogy with Gaussian quadrature. Our main results are in Sec. 5 and we show in Sec. 6 that they also occur in networks of more realistic Morris-Lecar spiking neurons. We discuss motifs in Sec. 7 and conclude in Sec. 8.

2 Model

We consider the same model of pulse-coupled theta neurons as in [1]. The governing equations are

$$\frac{d\theta_i}{dt} = 1 - \cos\theta_i + (1 + \cos\theta_i)(\eta_i + I_i) \tag{1}$$

for $i = 1, 2 \ldots N$, where the phase angle θ_i characterises the state of neuron i, which fires an action potential as θ_i increases through π,

$$I_i = \frac{K}{\langle k \rangle} \sum_{j=1}^{N} A_{ij} P_n(\theta_j); \tag{2}$$

K is the strength of connections within the network, $A_{ij} = 1$ if there is a connection from neuron j to neuron i and $A_{ij} = 0$ otherwise, $\langle k \rangle$ is the average degree, $\sum_{i,j} A_{ij} = N$, and $P_n(\theta) = a_n(1 - \cos\theta)^n$ where a_n is chosen such that $\int_0^{2\pi} P_n(\theta)d\theta = 1$. The function $P_n(\theta_j)$ models the pulse of current emitted by neuron j when it fires and can be made arbitrarily "spike-like" and localised around $\theta_j = \pi$ by increasing n. The parameter η_i is the input current to neuron i in the absence of coupling and the η_i are independently and randomly chosen from a Lorentzian distribution

$$g(\eta) = \frac{\Delta/\pi}{(\eta - \eta_0)^2 + \Delta^2} \tag{3}$$

Chandra et al. [1] considered the limit of large N and assumed that the network can be characterised by two functions. Firstly a degree distribution $P(\mathbf{k})$, normalised so that $\sum_{\mathbf{k}} P(\mathbf{k}) = N$, where $\mathbf{k} = (k_{in}, k_{out})$ and k_{in} and k_{out} are the in- and out-degrees, respectively of a neuron with degree $\mathbf{k}$. Secondly, an assortativity function $a(\mathbf{k}' \to \mathbf{k})$ giving the probability of a connection from a neuron with degree $\mathbf{k}'$ to one with degree $\mathbf{k}$, given that such neurons exist. Whereas [1] investigated the effects of varying $a(\mathbf{k}' \to \mathbf{k})$, here we consider the default value for this function (i.e. its value expected by chance, see (11)) and investigate the effects of varying correlations between k_{in} and k_{out} as specified by the degree distribution $P(\mathbf{k})$. We emphasise that we are

can be regarded as a complex-valued "order parameter" for neurons with degree $\mathbf{k}$ at time t. The function $G(\mathbf{k}'; t)$ can be regarded as the output current from neurons with degree $\mathbf{k}'$, and its form results from rewriting the pulse function $P_n(\ )$ in terms of $b(\mathbf{k}'; t)$. [For general n, $G(\mathbf{k}'; t)$ is the sum of a degree-n polynomial in $b(\mathbf{k}'; t)$ and one in

human brain is given in [4], for example.) So the probability distribution function of either in- or out-degree k is

$$p(k) = \begin{cases} \frac{2a^2b^2}{b^2-a^2}k^{-3} & a \le k \le b \\ 0 & \text{otherwise} \end{cases} \tag{16}$$

where the normalisation factor results from approximating the sum from a to b by an integral. (The approximation improves as a and b are both increased.) We want to introduce correlations between the in- and out-degree of a neuron, while retaining these marginal distributions. We do this using a Gaussian copula [18]. The correlated bivariate normal distribution with zero mean is

$$f(x, y; \rho) = \frac{1}{2\pi\sqrt{|\Sigma|}}e^{-(\mathbf{x}^T \Sigma^{-1}\mathbf{x})/2}$$

$$= \frac{1}{2\pi\sqrt{1-\rho^2}}e^{-(x^2-2\rho xy+y^2)/[2(1-\rho^2)]} \tag{17}$$

where

$$\Sigma \begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} 1 & \rho \\ \rho & 1 \end{pmatrix} \tag{18}$$

and $\rho \in 2(-1, 1)$ is the correlation between x and y. The variables x and y have no physical meaning and we use the copula just as a way of deriving an analytic expression for $P(k_{in}^\ell, k_{out}^\ell; \rho)$ for which the correlations between k_{in}^ℓ and k_{out}^ℓ can be varied systematically.

The marginal distributions for x and y are the same:

$$p(x) = \frac{1}{\sqrt{2\pi}} \qquad x \text{ and } y$$

In practice, to find the roots of q_n we use the Golub-Welsch algorithm. Form the tridiagonal matrix

$$J = \begin{pmatrix} \\ \\ \\ \\ \\ \\ \end{pmatrix}$$

Fig. 5 Mean frequency, f, versus ofor (left to right) $=0.5,0$ and 0.5. Solid: stable, dashed: unstable. Parameters: $a=100$; $b=400$; $K=1.5$; $=0.05$.

where

$$m_1(V) = 0.5(1 + \tanh[(V - V_1)/V_2]) \qquad (47)$$

$$w_1(V) = 0.5(1 + \tanh[(V - V_3)/V_4]) \qquad (48)$$

$$_n(V) = \frac{1}{\cosh[(V - V_3)/(2V_4)]} \qquad (49)$$

Parameters are $V_1 = -1.2$; $V_2 = 18$; $V_3 = 12$; $V_4 = 17.4$; $_0 = 1/15 msec^{-1}$; $g_L = 2$; $g_K = 8$; $g_{Ca} = 4$; $V_L = -60$; $V_{Ca} = 120$; $V_K = -80$; $C = 20 F/cm^2$; $= 100$; $V_{ex} = 120$; $= 5 mS/cm^2$. Voltages are in mV, conductances are in mS/cm^2, time is measured in milliseconds, and currents in A/cm^2. In the absence of coupling and heterogeneity a neuron undergoes a SNIC bifurcation as I_0 is increased through 40. We have used synaptic coupling of the form in [6], but on a timescale rather than instantaneous as in that paper. The I_i are randomly chosen from a Lorentzian distribution with mean zero and half-width at half-maximum 0.05.

The network is created as follows, using the Gaussian copula of Sec. 3. For each $i \in \{1, \ldots, N\}$ let x_1 and x_2 be independently chosen from a unit normal distribution. Then x_1 and $y_1 = {}^\wedge x_1 + \sqrt{1 - {}^{\wedge 2}} x_2$ both have unit normal distributions and covariance $^\wedge$, i.e. are realisations of x and y in (17). We then set $k_{in}^i = C_k^{-1}(C(x_1))$ and $k_{out}^i = C_k^{-1}(C(y_1))$. These degrees each have distribution $p(k)$ but have correlation coefficient $, where $ is determined by the value of $^\wedge$ as shown in Fig. 2. We then create the connection from neuron j to neuron i (i.e. set $A_{ij} = 1$) with probability

$$k_{in}^i k_{out}^j$$

motif statistics and ring rate, as observed here, seems yet to be developed.

We chose a Lorentzian distribution of the $_i$ in (1), as many others have done [22], in order to analytically evaluate an integral and derive (6). However, we repeated the calculations shown in Figs. 5, 7, 9 and 10 using a Gaussian distribution of the $_i$ and found the same qualitative behaviour (not shown). Regarding the parameter n governing the sharpness of the function $P_n(\ )$, we repeated the calculations shown in Figs. 5 and 7 for $n = 5; 7$ and obtained qualitatively the same results (not shown). We used a Gaussian copula to correlate in- and out-degrees due to its analytical form, but numerically investigated the scenarios shown in Figs. 5 and 7 for t copulas and Archimedean Clayton, Frank and Gumbel copulas and found the same qualitative behaviour (also not shown).

For simplicity we used the same truncated power law distribution for both in- and out-degrees. However, the use of a Gaussian copula for inducing correlations between degrees does not require them to be the same, so one could use the framework presented here to investigate the e ects of varying degree distributions [26], correlated or not.

We also only considered either excitatory or inhibitory networks, but it would be straightforward to generalise the techniques used here to the case of both types of neuron, with within-neuron degree correlations for either or both populations, though at the expense of increasing the number of parameters to investigate.

Con ict of interest

The authors declare that they have no con ict of interest.

References

1. Chandra, S., Hathcock, D., Crain, K., Antonsen, T.M., Girvan, M., Ott, E.: Modeling the network dynamics of pulse-coupled neurons. Chaos **27**(3), 033102 (2017). DOI 10.1063/1.4977514
2. Chung, F., Lu, L.: Connected components in random graphs with given expected degree sequences. Annals of combinatorics **6**(2), 125{145 (2002)
3. Coombes, S., Byrne, A.: Next generation neural mass models. In: Nonlinear Dynamics in Computational Neuroscience, pp. 1{16. Springer (2019)
4. Egu luz, V.M., Chialvo, D.R., Cecchi, G.A., Baliki, M., Apkarian, A.V.: Scale-free brain func-

23. Ott, E., Antonsen, T.: Long time evolution of phase oscillator systems. Chaos **19**, 023117 (2009)
24. Perin, R., Berger, T.K., Markram, H.: A synaptic organizing principle for cortical neuronal groups. Proceedings of the National Academy of Sciences **108**(13), 5419{5424 (2011). DOI 10.1073/pnas.1016051108. URL https://www.pnas.org/content/108/13/5419
25. Restrepo, J.G., Ott, E.: Mean- eld theory of assortative networks of phase oscillators. Europhysics Letters **107**(6), 60006 (2014)
26. Roxin, A.: The role of degree distribution in shaping the dynamics in networks of sparsely connected spiking neurons. Frontiers in Computational Neuroscience **5**, 8 (2011)
27. Schmeltzer, C., Kihara, A.H., Sokolov, I.M., Rüdiger, S.: Degree correlations optimize neuronal network sensitivity to sub-threshold stimuli. PloS One **10**, e0121794 (2015)
28. Song, S., Sjöström, P.J., Reigl, M., Nelson, S., Chklovskii, D.B.: Highly nonrandom features of synaptic connectivity in local cortical circuits. PLoS biology **3**(3), e68 (2005)
29. Tsumoto, K., Kitajima, H., Yoshinaga, T., Aihara, K., Kawakami, H.: Bifurcations in morris{lecar neuron model. Neurocomputing **69**