Neuronal Correlations Depend on Second Order Motifs

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Introduction

Central Questions:

1. How do neuronal correlations depend on the frequency of second order graphical motifs?
2. Can we use linear response theory to uncover an explicit approximation of this dependency?

Setup

We consider a network of spiking model neurons driven by independent biased Gaussian noise processes. Cells in the network are connected "weakly" according to a coupling matrix $\mathbf{W}$, and the shape of the interactions is general.

Example: Exponential integrate-and-fire (EIF) model neuron with current-based, delayed α-shaped coupling and arbitrary synaptic time constants.

$$\tau_i \dot{v}_i = -(v_i + E_{L,i}) + \psi(v_i) + E_i + \sqrt{\sigma_i^2 \tau_i}\xi_i(t) + f_i(t)$$

$$f_i(t) = \sum_j (\mathbf{J}_{ij} * y_j) \quad \mathbf{J}_{ij}(t) = \begin{cases} \mathbf{W}_{ij}\alpha_j(t - \tau_{D,j}) & t \geq \tau_{D,j} \\ 0 & t < \tau_{D,j} \end{cases}$$

where $\psi(v) = \Delta_T \exp[(v - v_T)/\Delta_T]$. Applying a threshold and reset to the membrane potential of cell i yields an output spike train y_i.

Cross correlation function - Describes how the outputs of a pair of cells in the network covary at a given time offset

$$\mathbf{C}_{ij}(\tau) = \mathrm{cov}(y_i(t+\tau), y_j(t))$$

Cross spectrum - Describes how the output of a pair of cells share power at a given frequency

$$\tilde{\mathbf{C}}_{ij}(\omega) = \mathbf{E}\left[\tilde{y}_i \tilde{y}_j^*\right] \quad \text{where} \quad \tilde{y}_i(\omega) = \frac{1}{\sqrt{T}}\int_0^T dt\, e^{i\omega t}(y_i(t) - r_0)$$

Correlation coefficient - Defining $N_{y_i}(t_1, t_2) = \int_{t_1}^{t_2} y_i(s)ds$ and

$$\boldsymbol{\rho}_{ij}(T) = \frac{\mathrm{cov}(N_{y_i}(t, t+T), N_{y_j}(t, t+T))}{\sqrt{\mathrm{var}(N_{y_i}(t, t+T))\mathrm{var}(N_{y_j}(t, t+T))}}$$

to be the spike count correlation coefficient over windows of length T. We will make use of the "long-window correlation coefficient" $\boldsymbol{\rho}_{ij}(\infty) = \lim_{T\to\infty} \boldsymbol{\rho}_{ij}(T)$ to quantify dependencies over all timescales.

Linear response theory

Firing rate response: Suppose that a noisy IF neuron receives a zero-mean input $\epsilon X(t)$. Linear response theory yields the firing rate to linear order in ϵ:

$$r(t) = r_0 + (A * \epsilon X)(t)$$

where $A(t)$ is the linear response function. $A(t)$ is equal to a rescaling of the STA to first order in ϵ. $A(t)$ depends on model parameters (and is particularly sensitive to the mean potential $E_{L,i} + E_i$ and noise variance σ_i^2), but is independent of the stimulus $X(t)$ for small ϵ.

Linear response theory in networks: We generalize the approach of Lindner et al[1], and make the approximation

$$y(t) \approx y^0(t) + (A * \epsilon X)(t).$$

where $y^0(t)$ may be thought of as a realization of the output of the IF cell with $\epsilon = 0$.

Accounting for the full architecture: Set $\epsilon X(t) = f_i(t) - \mathbf{E}[f_i]$. Define $\mathbf{K}_{ij}(t) = (A_i * \mathbf{J}_{ij})(t)$. The full network structure can be accounted for in an approximation to correlations by

$$\boxed{\tilde{\mathbf{C}}(\omega) \approx (\mathbf{I} - \tilde{\mathbf{K}}(\omega))^{-1}\tilde{\mathbf{C}}^0(\omega)(\mathbf{I} - \tilde{\mathbf{K}}^*(\omega))^{-1}}$$

when $\Psi(\tilde{\mathbf{K}}) < 1$. By expanding these matrix inverses as power series in $\tilde{\mathbf{K}}$, cross-correlations can be expressed in terms of motifs (chain and diverging) involving arbitrary numbers of connections. For example, the term

$$\tilde{\mathbf{K}}^n \tilde{\mathbf{C}}^0 \tilde{\mathbf{K}}^{m*}$$

represents the correlating effects of diverging motifs featuring n connections along one branch and m along the other. For more details, see [2].

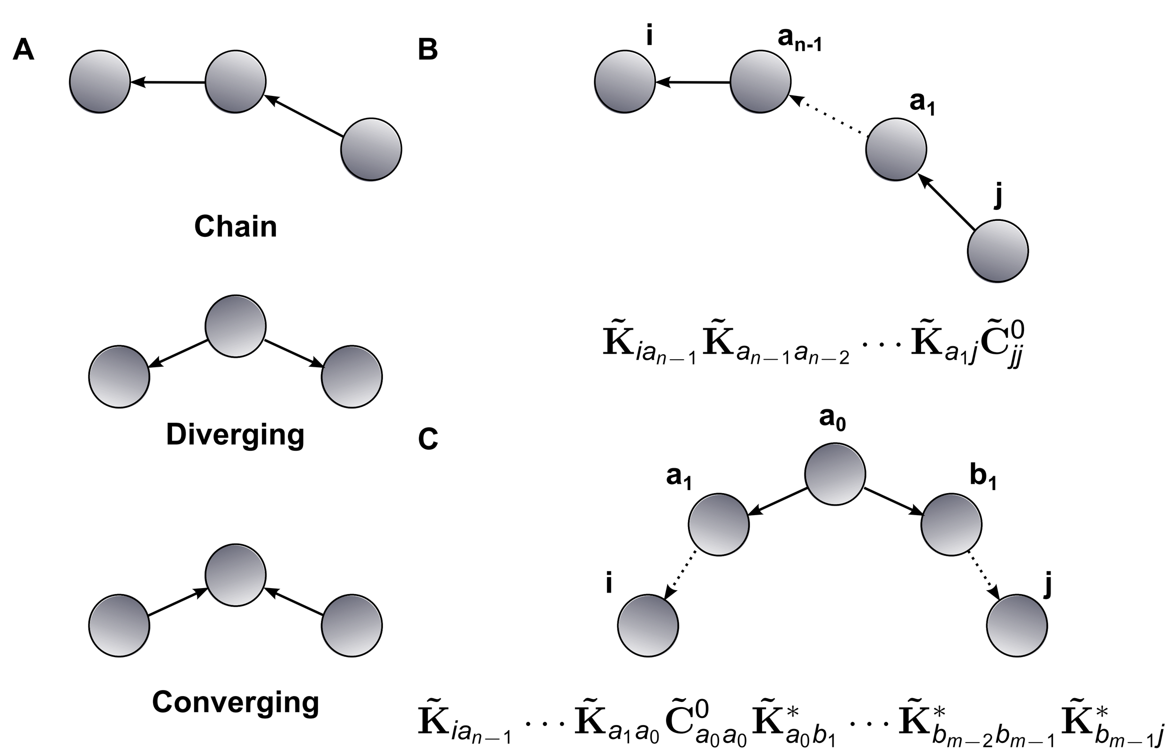

Figure 1: Visualizing network motifs. **A.** Second order motifs. **B.** An order n chain motif. **C.** An order $n+m$ diverging motif.

Second Order Motifs

Let $\mathbf{L} = \frac{1}{N}\mathbf{1}_{N,1}$, where $\mathbf{1}_{N,M}$ is the $N \times M$ matrix of all ones. The vector $\mathbf{L}$ is defined so that for a matrix $\mathbf{X}$,

$$\langle \mathbf{X} \rangle = \mathbf{L}^T \mathbf{X} \mathbf{L},$$

where $\langle \mathbf{X} \rangle$ is the average across all entries of $\mathbf{X}$.

Network definition: N recurrently-coupled excitatory cells with connection weight w and adjacency matrix $\mathbf{W}^0$ (so $\mathbf{W} = w\mathbf{W}^0$).

Empirical connection probability p:

$$p = \mathbf{L}^T \mathbf{W}^0 \mathbf{L}.$$

Second order motif frequencies (exceeding Erdös-Rényi chance):

$$q_{\mathrm{div}} = \frac{1}{N}\mathbf{L}^T\mathbf{W}^0\mathbf{W}^{0T}\mathbf{L} - p^2, \quad q_{\mathrm{con}} = \frac{1}{N}\mathbf{L}^T\mathbf{W}^{0T}\mathbf{W}\mathbf{L} - p^2,$$
$$q_{\mathrm{ch}} = \frac{1}{N}\mathbf{L}^T\mathbf{W}^0\mathbf{W}^0\mathbf{L} - p^2.$$

Average correlation expansion:

$$\langle \tilde{\mathbf{C}}^\infty \rangle = \tilde{C}^0 \sum_{i,j=0}^{\infty} (\tilde{A}w)^{i+j}\mathbf{L}^T\left(\mathbf{W}^0\right)^i\left(\mathbf{W}^{0T}\right)^j\mathbf{L}.$$

All spectral quantities are evaluated at $\omega = 0$ (approximating *total covariance*).

Results

Terms in the expansion may be expressed linearly in the second-order frequencies q modulo higher order terms. Define the orthogonal projection matrices

$$\mathbf{H} = N\mathbf{L}\mathbf{L}^T, \quad \mathbf{\Theta} = \mathbf{I} - \mathbf{H}.$$

Then we may write, for example,

$$q_{\mathrm{div}} = \frac{1}{N}\mathbf{L}^T\mathbf{W}^0\mathbf{\Theta}\mathbf{W}^{0T}\mathbf{L}.$$

Example: Term corresponding to length three chains:

$$\mathbf{L}^T\left(\mathbf{W}^0\right)^3\mathbf{L} = \mathbf{L}^T\left[\mathbf{W}^0(\mathbf{H} + \mathbf{\Theta})\right]^2\mathbf{W}^0\mathbf{L}$$
$$\approx N^2(p^3 + 2pq_{\mathrm{ch}}).$$

Linear contributions of second order motifs:

$$\langle \tilde{\mathbf{C}}^\infty \rangle \approx \frac{1}{N(1 - N\tilde{A}wp)^2} + \frac{N(\tilde{A}w)^2}{(1 - N\tilde{A}wp)^2}q_{\mathrm{div}} + \frac{2N(\tilde{A}w)^2}{(1 - N\tilde{A}wp)^3}q_{\mathrm{ch}}.$$

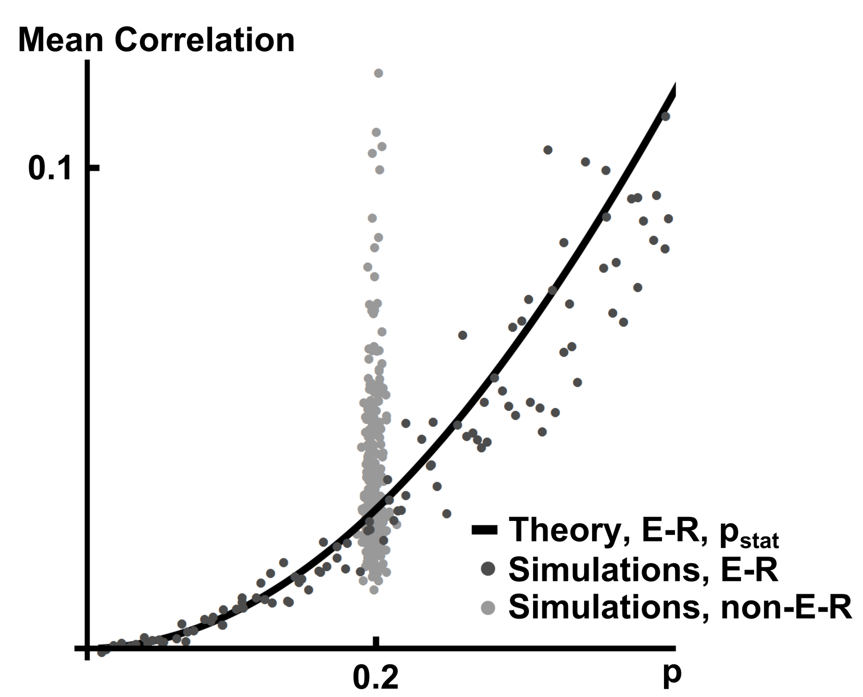

Figure 2: Connection probability and second order motifs affect mean correlation.

Nonlinear contributions of second order motifs:

$$\langle \tilde{\mathbf{C}}^\infty \rangle \approx \frac{1}{N}\frac{1 + \left(N\tilde{A}w\right)^2 q_{\mathrm{div}}}{\left[1 - \left(N\tilde{A}w\right)p - \left(N\tilde{A}w\right)^2 q_{\mathrm{ch}}\right]^2}.$$

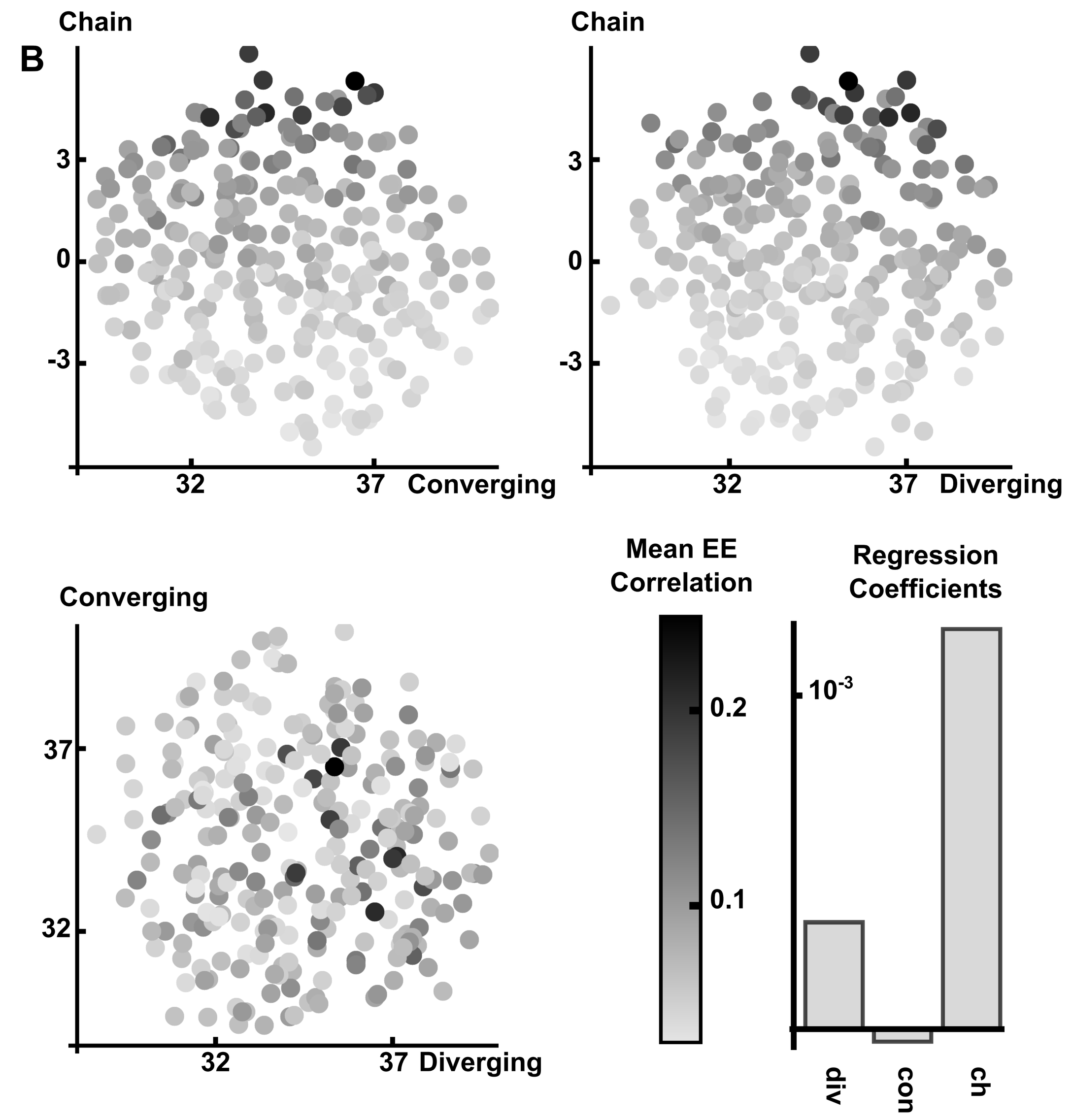

Figure 3: Chain (and to a lesser extent diverging) motifs are central in determining the mean correlation in noisy neuronal networks.

Distance-dependent networks

The theory works well for networks with a large amount of spatial structure. We consider a 1-D ring network and a 2-D torus network with "boxcar" connectivity.

Network type	Simulation	Full Theory	S.O. Motifs
Circular boxcar ($N = 100$)	0.0332 ± 0.0903	0.0346 ± 0.1022	0.0477
Random ($N = 100$)	0.0402 ± 0.0252	0.0481 ± 0.0240	0.0494
Planar boxcar ($N = 1000$)	0.0061 ± 0.0415	0.0082 ± 0.0439	0.0084
Random ($N = 1000$)	0.0066 ± 0.0068	0.0072 ± 0.0060	0.0073

Table 1: Mean and standard deviation of the distribution of EE correlations in structured and random networks. The approximations based on second order motifs give only an estimate of mean correlation.

Conclusions

- Diverging and especially chain motifs are a strong determing factor for mean correlation in noisy neuronal networks.
- Mean correlation will often be low in balanced networks because q_{ch} is generally small in such networks.
- **Question:** Can a similar theory offer an approximation of the variance of correlations?

[1] Lindner, B., Doiron, B., and Longtin, A. (2005) Theory of oscillatory firing induced by spatially correlated noise and delayed inhibitory feedback. *Phys. Rev. E* 72, 061919.

[2] Trousdale, J., Hu, Y., Shea-Brown, E., and Josić, K. (2012) Impact of network structure and cellular response on spike time correlations. *PLoS Comput Biol* 8(3).

[3] Hu, Y., Trousdale, J., Josić, K. and Shea-Brown, E. Motif statistics and spike correlations in neuronal networks. *In preparation.*