Detection of non-stationary higher-order spike correlation

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Abstract

Classical studies in neurophysiology are based on the idea that stimulus information is encoded in the firing rates of single neurons. Alternatively, precise spike coordination is discussed as an indication of coordinated network activity and may be expressed by higher-order correlation between the simultaneous spiking activities of neurons. As shown in earlier studies [1], correlation between neurons may modulating in time in relation to the behavioral demand.

Here, we simultaneously estimate the time-dependent rate and correlation underlying multiple-neuron spiking activities by means of state-space analysis [2,3]. We model discretized parallel spike trains by a conditionally independent multivariate Bernoulli process using a log-linear link function [4-8]. A nonlinear recursive filtering formula is derived from a log-quadratic approximation to the posterior distribution of the state. Together with a fixed-interval smoothing algorithm, time-dependent log-linear parameters are estimated. The smoothed estimates are optimized via EM-algorithm such that their prior covariance matrix maximizes the expected complete data log-likelihood. In addition, we perform model selection on the hierarchical log-linear models to avoid over-fitting. Application of the method to simultaneously recorded neuronal spike sequences is expected to contribute to uncover dynamic cooperative activities of neurons in relation to behavior.

Introduction

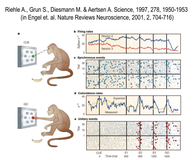
To study cooperative neural network activity, we develop state-space method to estimate the time-dependent correlation structures embedded in parallel spike trains.

Hypothetical Dynamic Cooperative Activity of Neurons

Precise spike coordination may appear due to the coordinated network activity. Composition of the spike coordination may dynamically change.

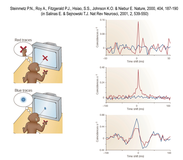
Evidence of Dynamical Correlation

Riehle A., Grün S., Diesmann M. & Aertsen A. Science, 1997, 278, 1950-1953 (in Engel et. al. Nature Reviews Neuroscience, 2001, 2, 704-716)



Excess synchrony appeared with expectation.

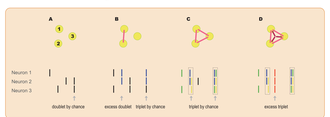
Steinmetz P.N., Roy A., Fitzgerald P.J., Hsiao, S.S., Johnson K.O. & Niebur E. Nature, 2000, 404, 187-190 (in Salinas E. & Sejnowski T.J. Nat Rev Neurosci, 2001, 2, 539-550)



Excess synchrony appeared with attention.

It has been shown that spike correlation with ms precision i) is modulated in time and ii) occurs at behaviorally relevant instances.

What is the Higher Order Correlation?



A Neurons are independent. Synchrony may appear by chance.

B Neuron 1 and 2 are positively correlated. Triplets may appear by chance.

C Three neurons are connected with pairwise correlations. Triplets may appear by chance.

D A triplewise correlation is added. Eoess triplets are generated.

Positive higher order correlation (HOC) indicates excess synchrony that can not be *explained* by the lower order correlations.

Log-linear model

The log-linear model provides a well-defined measure of higher-order correlation based on information geometry [5].

The Log-linear model of two binary variables

$\log p(x_1,x_2) = -\psi + \theta_1 x_1 + \theta_2 x_2 + \theta_{12} x_1 x_2$ $\quad \psi(\boldsymbol{\theta})$: cumulant generating function

x_1	x_2
0	0
1	0
0	1
1	1

P-coordinate: p_{00}, p_{10}, p_{01}, p_{11}

θ-coordinate: $\log p_{00} = -\psi$; $\log p_{10} = -\psi + \theta_1$; $\log p_{01} = -\psi + \theta_2$; $\log p_{11} = -\psi + \theta_1 + \theta_2 + \theta_{12}$

η-coordinate: $\eta_1 = E[x_1] = p_{10} + p_{11}$; $\eta_2 = E[x_2] = p_{01} + p_{11}$; $\eta_{12} = E[x_1 x_2] = p_{11}$

The mixed coordinate $(\eta_1, \eta_2, \theta_{12})$ is an orthogonal coordinate.

Amari, IEEE Trans. Inf. Theory, 2001

The last parameter of the log-linear model provides the higher-order correlation.

3 Neurons: $\log p(\mathbf{x}|\boldsymbol{\theta}) = -\psi + \sum_i \theta_i x_i + \sum_{i<j} \theta_{ij} x_i x_j + \theta_{123} x_1 x_2 x_3$ (Tripplewise correlation)

N Neurons: $\log p(\mathbf{x}|\boldsymbol{\theta}) = -\psi + \sum_i \theta_i x_i + \sum_{i<j} \theta_{ij} x_i x_j + \cdots + \theta_{12\cdots N} x_1 x_2 x_3 \cdots x_N$ (N-th order correlation)

To *N-tuple* parallel spike sequences, one can fit the sub-model with up to r-th order correlations:

Rate model (Independent model): $\log p(\mathbf{x}|\boldsymbol{\theta}) = -\psi + \sum_i \theta_i x_i$

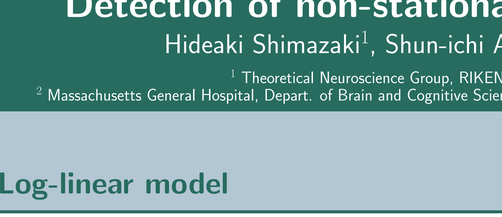
Pairwise-correlation model: $\log p(\mathbf{x}|\boldsymbol{\theta}) = -\psi + \sum_i \theta_i x_i + \sum_{i<j} \theta_{ij} x_i x_j$

Tripplewise-correlation model: $\log p(\mathbf{x}|\boldsymbol{\theta}) = -\psi + \sum_i \theta_i x_i + \sum_{i<j} \theta_{ij} x_i x_j + \sum_{i<j<k} \theta_{ijk} x_i x_j x_k$

State-space Analysis

A state-space framework allows regression of a time-dependent system to spike data.

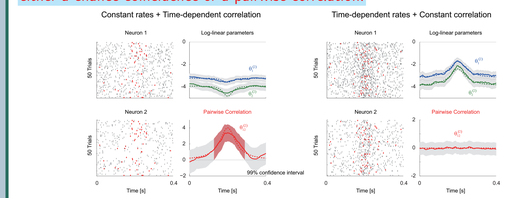
State-Space Model of Parallel Spike Trains



Filtering/smoothing and hyper-parameter optimization

2 Neurons

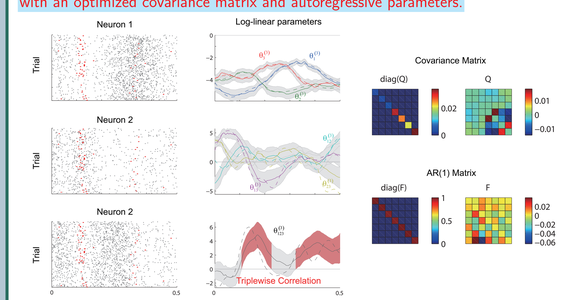
Synchrony between two neurons were appropriately attributed to either a chance coincidence or a pairwise correlation.



[First column] 50 trials of simulated parallel spike trains. Each pattern of spikes was counted with 1[ms] resolution. Red dots indicate synchronous spikes (doublets). **[Second column]** Log-linear parameters. Shaded area indicates 99% confidence interval.

3 Neurons

Time-dependence of triplewise correlation was estimated with an optimized covariance matrix and autoregressive parameters.



[First column] 100 trials of simulated parallel spike train. Each pattern of spikes was counted with 1[ms] resolution. Red dots indicate synchronous spikes (triplets). **[Second column]** Log-linear parameters. Shaded area indicates 99% confidence interval. **[Third column]** Optimized hyper-parameters.

Model Selection

To validate that the inclusion of the triplewise correlation improves the goodness-of-fit, we computed ABICs for the hierarchical state-space models.

The Akaike Bayesian information criterion (ABIC) is computed as

$$\mathrm{ABIC} = -2\log p(\mathbf{y}_{1:T}|\mathbf{w}) + 2\dim \mathbf{w},$$

where $\log p(\mathbf{y}_{1:T}|\mathbf{w}) = \sum_{t=1}^{T} \log p(\mathbf{y}_t|\mathbf{y}_{1:t-1}, \mathbf{w}) \sim n \sum_{t=1}^{T} (\mathbf{y}_t' \boldsymbol{\theta}_{t|t-1} - \psi_{t|t-1})$.

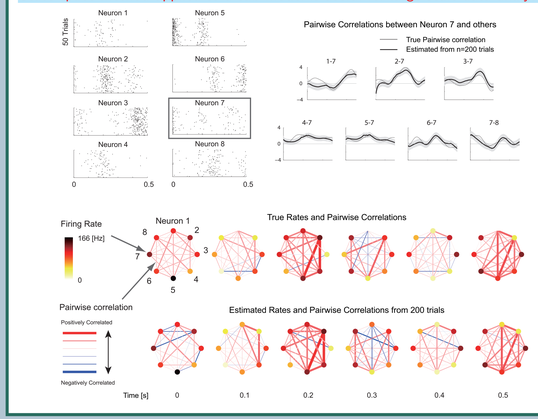
Note that the marginal likelihood takes account of the parameter uncertainty only (its approximation is known as BIC).

	Rate model	Pair-corr. model	Triple-corr. model
	$r=1$	$r=2$	$r=3$
$n=5$	2085*	2097	2144
$n=20$	7913	7698*	7728
$n=50$	19263	18542	18540*
$n=100$	38478	36811	36781*
$n=200$	76683	73330	73238*

The complexity of the model needs to be selected based on the sample size and the prominence of higher-order structure.

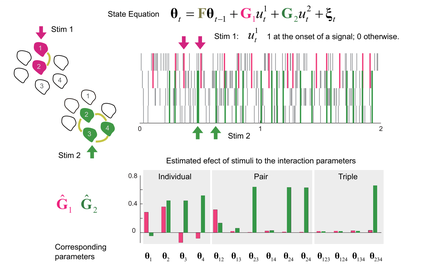
8 Neurons

State-space method applied to a sub-model is useful for large-scale data analysis.



Modeling external signals' effects

Incorporation of the cue signals into the model may be useful for detecting assemblies related to behavior.



Summary and Outlook

We developed a method for estimating time-varying rate and higher-order correlation structure in parallel spike sequences. To our knowledge, it is the first method that can resolve the time-dependent spike rates and 'well-defined' spike correlation measures simultaneously. The method is thus applicable to simultaneously recorded neuronal spike sequences recorded from an awake behaving animal. Such an application is expected to provide us with new insights into dynamic assembly activities, their compositions, and behavioral relevance.

The presented method will be summarized in

Shimazaki H., Amari S., Brown E. N., and Grün S. "State-space Analysis on Time-varying Correlations in Parallel Spike Sequences", *Proc. IEEE ICASSP2009 in press*

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