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Quantifying higher-order correlations in a neuronal pool

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HIGHLIGHTS

- Population of neurons has shown significant amount of higher-order correlations.
- We account for beyond second order inputs correlations seen by each neuron.
- We obtain an exact analytical expression for the joint distribution of firing.
- This method allows us to characterize higher-order correlations in a neuronal pool.
- Input nonlinearities can enhance coding performance by neural populations.

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ABSTRACT

Recent experiments involving a relatively large population of neurons have shown a very significant amount of higher-order correlations. However, little is known of how these affect the integration and firing behavior of a population of neurons beyond the second order statistics. To investigate how higher-order inputs statistics can shape beyond pairwise spike correlations and affect information coding in the brain, we consider a neuronal pool where each neuron fires stochastically. We develop a simple mathematically tractable model that makes it feasible to account for higher-order spike correlations in a neuronal pool with highly interconnected common inputs beyond second order statistics. In our model, correlations between neurons appear from q-Gaussian inputs into threshold neurons. The approach constitutes the natural extension of the Dichotomized Gaussian model, where the inputs to the model are just Gaussian distributed and therefore have no input interactions beyond second order. We obtain an exact analytical expression for the joint distribution of firing, quantifying the degree of higher-order spike correlations, truly emphasizing the functional aspects of higher-order statistics, as we account for beyond second order inputs correlations seen by each neuron within the pool. We determine how higher-order correlations depend on the interaction structure of the input, showing that the joint distribution of firing is skewed as the parameter q increases inducing larger excursions of synchronized spikes. We show how input nonlinearities can shape higher-order correlations and enhance coding performance by neural populations.

1. Introduction

Neurons in the cortex receive 3000–10,000 synaptic inputs, 85% of which are excitatory. Nearly half of the excitatory inputs to any one neuron come from nearby neurons that fall within a cylinder of 100–200 μm radius, arranged as a column, sometimes termed a mini-column [1–4]. This suggests that cortical neurons receive abundant excitatory inputs and

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are embedded in a network of highly convergent signals. These networks have a recurrent nature, thus it is likely that those neurons receive similar inputs and emit spikes under similar conditions. This means that the conditions that lead to a response of any one neuron in the mini-column are likely to involve considerable activity from a large number of its inputs beyond second order statistics. It is therefore reasonable to expect that many spike inputs will arrive in synchrony within a very small time window.

The integration of features into gestalt entities [5–8] is one the most important challenges in cognition. It has been proposed that correlated activity within the millisecond time range may be the signature of neuronal assembly formation. If this is the case, it may be essential in the context of multiple object encoding. According to the temporal binding hypothesis of von der Malsburg, cells belonging to the same assembly fire action potentials synchronously with a precision of a few milliseconds, and cells belonging to different assemblies fire asynchronously. This hypothesis requires cortical neurons to act as coincidence detectors [9–11]. In agreement with the latter, the major causes of correlated firing in neural networks are common presynaptic input. Behavior then stems from the emergent properties of a large set of neurons with overlapping neural circuits that share common dynamical inputs. A primary challenge in theoretical neuroscience is to gain further understanding of circuit dynamics incorporating the neuronal activity at a variety of spatial and temporal scales. Moreover, temporal dynamics and plasticity encode information about the outside world. Identification of relevant neural ensembles underlying cognitive behavior thus requires new modeling techniques and theoretical frameworks. Approaches that may help to link the multiple spatial, temporal, and organizational scales of neuronal assemblies could provide important insights into the emergent properties of the neural network, as they may lead to new discoveries concerning neural circuitry that could eventually shape the biophysical bases of behavior.

Information processing in the brain is usually encoded in the activity of large and highly interconnected neural populations. It has been proposed that synapses between neurons that fire synchronously are strengthened, forming cell assemblies and phase sequences. At short scales, it is expected that cell assemblies would affect information processing while at longer scales they could shape behavior and perception. Neuronal cells synchronize through correlated input, and spike synchronization between neurons emerges as a result of transient activity. Approaches using binary maximum entropy models at a pairwise level have been developed considering a very large number of neurons on short time scales [12–14]. These models can capture essential structures of the neural population activity, however, due to their pairwise nature their generality has been subject to debate [15–17]. In particular, E. Ohiorhenuan and J. D. Victor have shown the importance of triplets of spikes to characterize scale dependence in cortical networks [17,18]. That is to say, although models accounting for pairwise interactions have proved able to capture some of the most important features of population activity at the level of the retina [12,13], pairwise models are not enough to provide reliable descriptions of neural systems in general, as experiments considering a relatively large population of neurons have displayed a very significant amount of higher-order correlations ('HOCs') [15–19].

More specifically, neurophysiological research has shown that pairwise models fail to explain the responses of spatially localized triplets of cells [17–20], along with describing the activity of large neuronal populations responding to natural stimuli [19]. Deviations from the Maximum Entropy model indicate that HOCs have to be taken into account for modeling the population statistics [21–24]. Thus, the intricacy of the neurophysiological data highlights the need to develop a theoretical framework accounting for the statistical complexity of synchronous activity patterns. Pattern probabilities for the so-called Dichotomized Gaussian ('DG') model [20–24] were estimated using the cumulative distribution of multivariate Gaussians showing high precision fitting of the experimental data.

In this paper, we provide a simple mathematically tractable model able to account for HOCs in the joint firing distribution of a neuronal population. In our model, correlations between neurons arise from q-Gaussian inputs into threshold neurons. It is therefore an extension of the DG model proposed by Amari [21], where the inputs to the model are Gaussian distributed and therefore have no interactions beyond second order. Our current theoretical formalism relies on recent progress made on the Extended Central Limit Theorem ('ECLT'), and thus using mathematical tools of non-extensive statistical mechanics [25–33], we provide an approach that quantifies the degree of HOCs. We present the exact analytical solution of the joint distribution of firing including neural correlation patterns of all orders across a population. That is, we estimate by means of an analytically solvable model the amount of correlations of order higher than two in a neuronal pool through direct application of a q-Gaussian distribution of common synaptic inputs providing the expression of the joint distribution, Tsallis Relative Entropy and Fisher Information. We test the robustness of our approach using a set of simulated independent and correlated neurons. Using our model, we investigate different analytical solutions when considering three typical distributions: concentrated, widely spread, and bimodal. We study the emergent properties of the Fisher information in a large neural population, and show their impact on the efficiency of population coding. Our approach allows us to investigate how input nonlinearities can shape HOCs and improve information transmission. This could be a useful tool for understanding how groups of neurons could integrate into unique functional cell assemblies.

2. Methodology

2.1. Higher order interactions in the pooled model

We represent the neuronal firing in a population of size N by a binary vector $\mathbf{x} = (x_1, \ldots, x_N)$, where $x_i = 0$ if neuron i is silent in some time window ΔT and $x_i = 1$ if it is firing a spike. We consider the probability distribution of those binary