Preface

Why Data Analysis of Parallel Spike Trains is Needed

The brain is composed of billions of neurons, the elementary units of neuronal information processing. The neocortex, which is critical to most higher brain functions, is a highly complex network of neurons each of which receives signals from thousands of other neurons and projects its own spikes to thousands of other neurons. In order to observe neuronal activity in the active brain, a large variety of recording techniques are being employed: intra-cellular recordings of the membrane potentials of individual neurons, extra-cellular spike recordings from one or more individual neurons, and recordings of signals that measure the activity of populations of neurons either locally as the local field potential, or from larger brain regions via the EEG, MEG, or fMRI. Any particular choice of the recording technique reflects the hypothesis the researcher has in mind about the mechanisms of neuronal processing.

The focus on spike recordings from individual neurons imposed on this book implies that one strives to understand the elementary units of neuronal processing. Early electro-physiological experiments were bound to record from single neurons only. The resulting insights are now the basis for the "classical" view of sensory coding: firing rates are modulated in a feed-forward hierarchy of processing steps. Signals from sensory epithelia are assumed to eventually converge to cortical detectors for certain combinations of stimulus features. Highly specific percepts would be represented by the elevated firing of a single nerve cell or a small group of neurons. Due to a number of conceptual shortcomings, however, it has been seriously questioned whether such a scheme qualifies as a universal method for representation in the brain.

It was Donald Hebb (1949) who first demonstrated the conceptual power of a brain theory based on cell assemblies. Inspired by Hebb's influential writings, and driven by more recent physiological and anatomical evidence in favor of a distributed network hypothesis, brain theorists constructed models that rely on groups of neurons, rather than single nerve cells, as the *functional* building blocks for representation and processing of information. Despite conceptual similarities, such concepts of neuronal cooperativity differ in their detailed assumptions with respect to the spatio-temporal organization of the neuronal activity.

To understand the principles of coordinated neuronal activity and its spatio-temporal scales, it is obligatory to observe the activity of multiple single-neurons simultaneously. Due to recent technological developments in recording methodology, this can easily and regularly be done. Coordinated activity of neurons is only visible in (wide-sense) correlations of their respective spike trains, which typically admit no simple interpretation in terms of fixed synaptic wiring diagrams. Rather, it became evident that the correlation dynamics apparent in time-resolved multiple-channel measurements reflect variable and context-dependent coalitions among neurons and groups of neurons. Thus, the analysis of simultaneously recorded spike trains allows us to relate concerted activity of ensembles of neurons to behavior and cognition. Different analysis approaches are thereby relevant to distinguish different or even complementary spatio-temporal scales. Analysis of parallel spike trains is the logical next step to improve our understanding of the neuronal mechanisms underlying information processing in the brain.

Purpose of the Book

Solid data analysis is the most important basis for the meaningful evaluation and reliable interpretation of experiments. Although the technology of parallel spike train recording using multielectrode arrangements has been available for decades now, it only recently gained wide popularity among electro-physiologists. However, the relevant literature for the analysis of cooperative phenomena in parallel spike trains is unfortunately scattered across many journal publications, and we know of the pain to compile a useful reader for our students. Reinforced by the considerable interest in courses and schools on data analysis on these issues (offered by us and other colleagues), the idea came up to collect the knowledge on spike train analysis that is available in the literature in a single book.

This first textbook on spike train analysis concentrates on the analysis of *parallel* spike trains. The focus is on concepts and methods of correlation analysis (synchrony, patterns, rate covariance), combined with a solid introduction into approaches for single spike trains, that represent the basis of correlation analysis. Any specific method of analysis must make assumptions about the nature of the data it operates on. It happens that those who apply any particular analysis procedure are not well informed about the underlying assumptions, because they are only implicit or not discussed at all in the literature. Many traditional analysis methods are based on firing rates obtained by trial-averaging, and some of the assumptions for such procedures to work can indeed be ignored without serious consequences.

The situation is different for correlation analysis, the result of which may be considerably distorted if certain critical assumptions for the method to work are violated by the data. Therefore, we have put efforts in stating explicitly the underlying assumptions of the various methods, and giving methods at hand allowing to test if the assumptions are indeed fulfilled. In addition, we supply the reader also with stochastic modeling tools and numerical methods to test if the analysis method chosen serves the intended purpose. In the still ongoing discussion on the relevance of temporal coordination of spikes it is even more important to be aware of prerequisites and pitfalls to avoid potentially wrong interpretations of data due to violations of critical assumptions.

Intended Audience

This book is, on the one hand, written for the practitioners of data analysis, irrespective of whether they use available software packages or whether they implement the procedures themselves. On the other hand, some parts of the book feature abstract mathematical background necessary for a deeper understanding of the formal foundations of point processes that underlie most discussed analysis methods. Thus, the book is directed to research neurophysiologists, data analysts, and theoretical neuroscientists, but also to graduate and postgraduate students in systems neuroscience, computational neuroscience, and related neuroscience schools and courses.

Organization of the Book

There are *very* many different approaches to the analysis of parallel spike trains, and the field is far from having agreed upon a set of canonical tools everybody knows and everybody uses in the lab. In fact, almost every major publication written since the seminal papers by George Gerstein and his colleagues in the 1960s featured a new variant of multiple spike train analysis, matched to the specific experimental design and associated data format, and catering to the particular question their authors had in mind. Doing justice to all of them would require an encyclopedic work, not necessarily helpful in providing guidance for the inexperienced. Instead we concentrate here on a selection of methods that we consider most sound and also most inspiring with respect to their actual purpose: elucidating some aspect of brain function on the level of individual neurons and their interactions.

Part I of the book first gives an introduction to stochastic point processes which is the appropriate mathematical object to represent a spike train, or a statistical ensemble of spike trains, to be precise (Chap. 1). In this framework, estimating the firing rate of a neuron becomes a well-defined statistical procedure (Chap. 2). Second-order properties of spike trains associated with irregularity in time or variability across trials can also be dealt with consistently if embedded into point process theory (Chap. 3). Peculiarities of signals obtained in a periodic setting are then dealt with separately (Chap. 4).

Part II concentrates on the pairwise comparison of spike trains and first introduces classical cross-correlation techniques, both in the time domain and in the frequency domain (Chap. 5). Time scale issues of correlation analysis are the topic of a separate article (Chap. 6). A general framework for the comparison of spike trains in terms of abstract distance functions is then developed (Chap. 7). Finally, a method is described that can, based on pairwise comparisons, identify clusters of similar spike trains in larger populations (Chap. 8).

Part III focuses on multineuron spike configurations and first describes the concept of precise spatio-temporal firing patterns (Chap. 9). Patterns of near-simultaneous spikes are then discussed, along with statistical issues associated with their detection (Chap. 10). An information-geometric perspective on spike patterns in discrete time (Chap. 11) is finally complemented by a continuous-time framework to deal with correlations of higher order in parallel spike trains (Chap. 12).

Part IV introduces population-based analyses and gives first an introduction to the classical theory of Shannon information (Chap. 13). Encoding and decoding of neuronal population activity is then discussed in the light of information theory (Chap. 14). Finally, different types of multivariate point process models are employed to characterize neuronal ensemble spike trains (Chap. 15).

Part V deals with practical issues that are critical for neuronal data analysis. Methods to numerically simulate stochastic point processes with well-defined statistical properties are first explained (Chap. 16). Alternatively, data recorded from real neurons can be manipulated to obtain surrogate spike trains that preserve some properties and destroy others (Chap. 17). For testing complex hypotheses about neuronal spike trains, the bootstrap method can be effectively employed (Chap. 18). For numerical simulation, manipulation of recorded data, or bootstrap procedures, the availability of high-quality pseudo-random numbers is of great importance (Chap. 19). The last contribution in the book deals with the effective use of parallel and distributed computing facilities for data analysis in a neuroscience laboratory (Chap. 20).

How to Read This Book

The book can be read at two levels. Researchers whose main interest is in applications should read enough of each chapter to understand purpose and scope of the method presented and to be able to explore their own data with the software provided by the authors (see below). The theoretically oriented reader will find some mathematical details in most chapters, and in all cases pointers are given to the primary literature on the subject.

Software Download

For supplying the reader with the analysis software kindly provided by various authors of this book, we set up a website http://www.apst.spiketrain-analysis.org that links to all the websites of the various contributors. This has the advantage—in contrast to supplying the readers with the software on CD—that the software can stay at the original websites of the respective authors, and can there be updated as needed. Also links can easily be changed if necessary. If you are also willing to provide your software to the public, please let us know, and we add the links.

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