Analysis, classification, and coding of multielectrode spike trains with hidden Markov models

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Abstract. It is shown that hidden Markov models (HMMs) are a powerful tool in the analysis of multielectrode data. This is demonstrated for a 30-electrode measurement of neuronal spike activity in the monkey's visual cortex during the application of different visual stimuli. HMMs with optimized parameters code the information contained in the spatiotemporal discharge patterns as a probabilistic function of a Markov process and thus provide abstract dynamical models of the pattern-generating process. We compare HMMs obtained from vector-quantized data with models in which parametrized output processes such as multivariate Poisson or binomial distributions are assumed. In the latter cases the visual stimuli are recognized at rates of more than 90% from the neuronal spike patterns. An analysis of the models obtained reveals important aspects of the coding of information in the brain. For example, we identify relevant time scales and characterize the degree and nature of the spatiotemporal variations on these scales.

1 Introduction

The analysis of multielectrode data and the extraction of information about the coding principles in the brain are difficult tasks. This is mainly due to the following characteristics of the measured data: The observed processes are in general nonstationary, and they exhibit large variations, which usually cannot be explained by simple noise but may show systematic fluctuations that may have hidden meanings. In addition, the data are high-dimensional. For instance, we have to deal with 30 degrees of freedom corresponding to a measurement with 30 electrodes.

The experimental data treated in this work consist of simultaneous recordings of spike trains with 30 microelectrodes from the visual cortex of an anesthetized and paralyzed monkey (Krüger and Aiple 1988). We are interested in the neuronal responses recorded during the application of various visual stimuli. In this work, we investigate the responses to bars moving in different directions. This gives rise to corresponding classes of neuronal activity at the electrode array, which are in some sense characteristic for the applied stimuli. It turned out (Krüger and Becker 1991) that the 30 mean firing rates or the spike counts at each electrode during the relevant response intervals contain little information about the currently applied stimulus. Instead, this information was found in the recorded spatiotemporal discharge patterns. This is in accordance with results from other experiments (Richmond et al. 1987). Thus, our goal consisted in analyzing and characterizing such spatiotemporal excitation patterns.

As a first step in this direction, one has to evaluate, whether or not one can assign the corresponding visual stimulus to an observed spike pattern. Or, in other words, can one recognize the visual stimulus from the elicited neuronal discharges? It should be borne in mind that it is in this way that the animal makes use of neuronal excitations. This problem is basically a pattern recognition task which can be tackled with classical methods. For our data one can successfully apply linear classifiers (Krüger and Becker 1991) or non-linear classifiers such as artificial neural networks. A result of these investigations is that the spatio-temporal patterns contain relevant information about the applied stimulus. These methods, however, do not take into account that the patterns are generated dynamically. Furthermore, it is difficult to infer which properties of the patterns led to the discrimination, to what extent they are of a statistical nature, and what are the characteristics of the various stochastic components of the patterns.

Possible approaches for the solution of these questions could combine spectral methods like principle component analysis, as used, e.g., in Richmond et al. (1987), and classical pattern recognition techniques. Here
we present results based on the use of hidden Markov models (HMMs) and corresponding parameter estimation techniques (Baum et al. 1970). These models, which are otherwise known as stochastic automata (Paz 1971) or probabilistic functions of Markov chains (Baum et al. 1970), have been very successfully applied in various speech recognition tasks (for reviews see, e.g., Rabiner 1989; Bahl et al. 1983; Huang et al. 1990). In these applications, the data, energies in the time-frequency domain, show a similar degree of complexity, non-stationarity, and large variability as in our case. This led us to investigate whether HMMs are equally well suited for the classification and analysis of our multielectrode data (Radons et al. 1992). The idea of modeling spike data with HMMs was independently developed by two other groups. In Pawelzik et al. (1993), the experimentally observed oscillatory neuronal responses in the cat’s visual cortex (Gray et al. 1989) are explained in terms of an HMM, while in Gat and Tishby (1993), two behavioral modes of monkeys are identified with the aid of HMMs. In contrast, our work treats the problem of modeling and distinguishing the neuronal responses to many external stimuli, which implies that, similar to speech recognition problems, we have to work with an ensemble of different HMMs. Another biophysical problem in which HMMs were applied successfully is the analysis of ion currents through channels of cell membranes (Chung et al. 1990, 1991; Fredkin and Rice 1992; Becker et al. 1994).

The advantage of using HMMs for the analysis of multielectrode data is threefold: Beyond being a pattern recognition and classification tool, it provides us with probabilistic dynamical models of the pattern-generating process. This implies the possibility of reproducing the data with a reduced set of parameters, and thus serves as a data compression method; on the other hand, it preserves the possibility to extract, e.g., various correlational functions or correlograms. The third point is that the extracted models, although of abstract nature, are amenable to an analysis in terms of subprocesses, if present, which contribute to the pattern-generating process as a whole.

In Sect. 2 we briefly describe the nature of the data to be analyzed, and we introduce the principles of HMMs and the variants tested in this work. Section 3 is devoted to the presentation of results, where we compare the performances of the various models in terms of recognition rates and demonstrate the quality in reproducing the original data. In Sect. 4, the results are discussed. The Appendix consists of a collection of formulas used in the parameter estimation procedures.

2 General aspects

2.1 The data

The data were recorded with 30 microelecrodes in layer VI of the striate cortex of a paralyzed and anesthetized monkey. Electrodes were arranged in a 5 × 6 array with a spacing of 160 μm. Thus, the electrodes were located in an area of 0.64 × 0.8 mm². They were labelled A–E (columns) and 1–6 (rows). Figure 1 shows two typical recordings of the neuronal response to the same stimulus. Note the large variability of the spike patterns. The spikes were recorded at a sampling rate of 1 ms. For about half of the electrodes, the recorded signals stem from one cell. At the remaining electrodes, contributions from more cells cannot be excluded, although typically spikes from one cell are dominant. The stimuli were monocularly presented bright bars on a dark background. The bars were 7 min of arc wide and moved at 1 min of arc per 10 ms. One trial lasting 40 s consisted of a sequential presentation of the bar moving in sixteen equally spaced directions. The experiment was repeated 21 times, and therefore the data consist of 21 trials, i.e., repetitions of 16 stimuli. Responses to different stimuli are well separated in time.

A more detailed description of the measurement can be found in Krüger and Aiple (1988).

2.2 Principles of HMMs and their application to multidimensional spike trains

In the following, we briefly survey the general principles of HMMs and their application to spike data. In Sect. 2.2.1 we describe how a given HMM is used as a probabilistic generator of symbol sequences. The meaning of the symbols varies from application to application and is described for spike data in Sect. 2.2.4. Section 2.2.2 reviews how an ensemble of HMMs may serve as a classifier or pattern recognition tool. Such an application presupposes optimized models which can be found by ‘learning’ procedures also described in this section. How such optimized HMMs can be analyzed is explained in Sect. 2.2.3.

2.2.1 HMMs as probabilistic dynamic models. An HMM is an abstract object consisting of a given number of states i, i = 1, . . . , N and transitions between these states. Transitions occur with probabilities aij, i.e., aij is the conditional probability p(i | j) for making a transition to state j, if the system is in state i. The aij have the property \( \sum_{j=1}^{N} a_{ij} = 1 \) for all i, which means that some transition occurs with probability 1. Therefore, they can be considered as elements of a stochastic matrix A, the transition matrix.

So far, this defines a simple Markov process, because the probability for the next state j depends only on the current state i. HMMs are characterized by the additional ingredient that for every state i one defines a probability distribution bi(S) for emitting a symbol S of some alphabet {S} of length |S|. The alphabet may also consist of infinitely many symbols |S| = ∞. Some symbol is generated with certainty in every state i, which means that \( \sum_{j=0}^{b} b_{i}(S) = 1 \) for every i. The bi(S) are, in general, different functions depending on i. The meaning of the symbols is application-dependent and is introduced for our problem in Sect. 2.2.4 below. The above definitions explain why HMMs are often called probabilistic functions of Markov processes.

In order to generate symbol sequences with such models, one also has to specify an initial probability distribution \( \pi = (\pi_1, \ldots, \pi_N) \) over the states i. A symbol