Analysis of Neuronal Spike Trains, Deconstructed.

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Abstract:

This excellent review announces that theoretical and computational neuroscience has come of age. The authors have, wisely, confined themselves to a small corner of an ever-growing field – the methods that are used to connect sensory or motor system variables to the spike trains of single neurons or neural networks. Historically, an early method was the spike-triggered average (STA) – the average sensory stimulus that precedes a spike. This method is intuitively appealing but its naïve simplicity masks the underlying assumptions that may restrict its applicability. The analytic framework of this review clearly sets out the assumptions of the STA and its more sophisticated derivation – spike triggered covariance (STC). The analytic framework of this review places these methods in the rigorous mathematical framework of linear algebra: STA computes the one dimensional “feature” that best predicts the occurrence of a spike while STC computes multiple independent vectors (features) whose linear combination best predicts spike occurrence. With this framework, it becomes natural to introduce other methods using an information theory based approach such as maximal noise entropy (MNE). A very nice pedagogical approach of this paper is that it combines a mathematically sophisticated presentation of these methods with exemplars that illustrate how they work in practice. The data sets used as exemplars are very nicely chosen. The simplest is the response of retinal ganglion cells to a white noise stimulus – these data have driven several generations of predictive coding models and it helps the reader understand in a concrete manner what STA and STC methods extract from the data. The other two data sets represent the direction in which this field is moving: (a) spiking responses of thalamic neurons to input generated by freely whisking vibrissae input and (b) recordings from monkey motor cortex as it manipulates a joy stick. These more natural behavioral settings introduce serious theoretical and practical challenges to the STA, and STC and MNE methods and these are carefully delineated in this review.

The STA, STC and MNE methods all assume that the high-dimensional stimulus entirely determines the spike output of a neuron; the intrinsic dynamics of neurons and their interaction within, e.g., cortical networks, are neglected. The authors cover an approach that can better deal with the messy details of neurobiology – the generalized linear model (GLM). With the GLM, the experimenter can take into account neuron dynamics, e.g., the neuron’s spiking history that can increase or decrease the probability of firing following each spike. The GLM framework can even be extended to account for synaptic input from neurons within a local network. The power of the GLM approach comes with its own set of problems and this paper very carefully addresses the complex issues that arise in fitting a GLM model to data that arises from cells sensing or controlling self-motion.

This review is not an easy read. The explanatory boxes and superbly crafted figures do a fine job in introducing the mathematical concepts to readers. I suspect, however, that some background in linear algebra and probability theory would be essential for any experimenter wanting to make use of the code provided by the authors and to use these methods to help design and analyze their own experiments. We now have the capability of recording from many neurons far from the periphery (e.g., cortex or hippocampus) as the animal engages in some natural task (e.g., making decisions, learning, etc.). Simply summarizing the firing rates of the recorded neuron ensemble is clearly no longer sufficient to connect the animal’s behavior to the population discharge pattern. Close collaboration between systems neuroscientists and theoreticians is now becoming standard and, for such collaborations to work, there will have to be a common “language” for designing experiments and analyzing the results. This article provides such a common language for a restricted set of problems in systems neuroscience and does so in an exemplary manner.

This review is confined to only this facet of theoretical neuroscience – connecting the external world to the spike trains of single neurons and neuronal ensembles. It will be most useful to those working on brain regions close to the external world, e.g., retina to visual cortex or motor cortex to spinal cord. It is not clear at all whether it will be useful for, e.g., recordings of a population of premotor cortex neurons discharging while the animal utilizes working memory to learn a complex task. Two outstanding recent books [1,2] will introduce interested readers to the burgeoning wider field of theoretical neuroscience and to methods that apply to a wider range of interesting but very difficult questions.

References

2. Neuronal Dynamics.

Disclosures
None declared
As information flows through the brain, neuronal firing progresses from encoding the world as sensed by the animal to driving the motor output of subsequent behavior. One of the more tractable goals of quantitative neuroscience is to develop predictive models that relate the sensory or motor streams with neuronal firing. Here we review and contrast analytical tools used to accomplish this task. We focus on classes of models in which the external variable is compared with one or more feature vectors to extract a low-dimensional representation, the history of spiking and other variables are potentially incorporated, and these factors are nonlinearly transformed to predict the occurrences of spikes. We illustrate these techniques in application to datasets of different degrees of complexity. In particular, we address the fitting of models in the presence of strong correlations in the external variable, as occurs in natural sensory stimuli and in movement. Spectral correlation between predicted and measured spike trains is introduced to contrast the relative success of different methods.

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