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Fast and robust estimation of spectro-temporal receptive fields using stochastic approximations

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HIGHLIGHTS

- We apply stochastic approximations to receptive field (RF) estimation.
- Reliable reconstruction of RFs from responses to highly non-Gaussian stimuli.
- Stochastic approximations preserve predictive power and tuning properties.
- Estimation time is reduced by about 90% compared to the full solution.
- On-line monitoring of RF parameters for more than 30 neurons on a single computer.

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ABSTRACT

Background: The receptive field (RF) represents the signal preferences of sensory neurons and is the primary analysis method for understanding sensory coding. While it is essential to estimate a neuron's RF, finding numerical solutions to increasingly complex RF models can become computationally intensive, in particular for high-dimensional stimuli or when many neurons are involved.
New method: Here we propose an optimization scheme based on stochastic approximations that facilitate this task. The basic idea is to derive solutions on a random subset rather than computing the full solution on the available data set. To test this, we applied different optimization schemes based on stochastic gradient descent (SGD) to both the generalized linear model (GLM) and a recently developed classification-based RF estimation approach.
Results and comparison with existing method: Using simulated and recorded responses, we demonstrate that RF parameter optimization based on state-of-the-art SGD algorithms produces robust estimates of the spectro-temporal receptive field (STRF). Results on recordings from the auditory midbrain demonstrate that stochastic approximations preserve both predictive power and tuning properties of STRFs. A correlation of 0.93 with the STRF derived from the full solution may be obtained in less than 10% of the full solution's estimation time. We also present an on-line algorithm that allows simultaneous monitoring of STRF properties of more than 30 neurons on a single computer.
Conclusions: The proposed approach may not only prove helpful for large-scale recordings but also provides a more comprehensive characterization of neural tuning in experiments than standard tuning curves.

1. Introduction

Understanding what makes a neuron fire is a central question in neuroscience (Bialek et al., 1991; Rieke et al., 1997; Dayan and Abbott, 2005). In sensory systems, this implies creating a model that can predict the neural responses not only to learned but also to novel stimuli. The primary model to study neural encoding of sensory stimuli is the receptive field (RF; for a review see Simoncelli et al., 2004; Wu et al., 2006; Sharpee, 2013). The RF describes how a sensory neuron integrates stimulus features and is defined as

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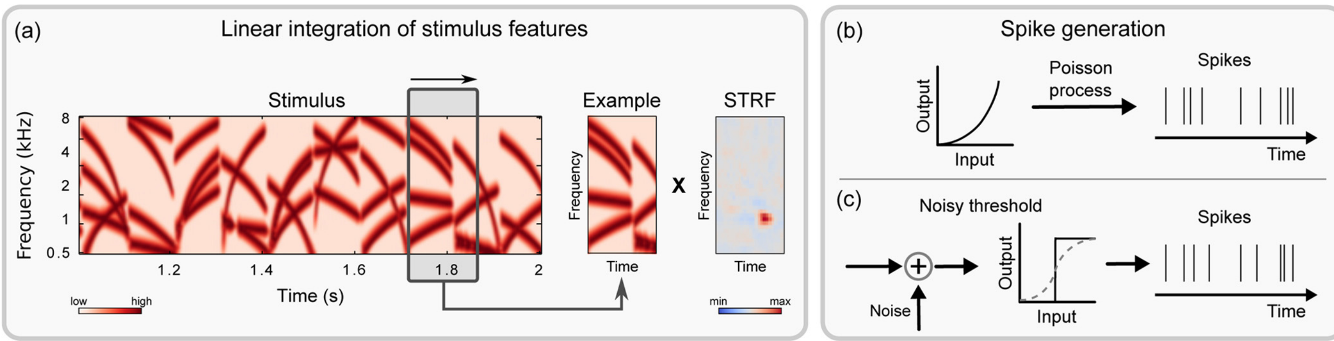

Fig. 1. Model of neural response generation. (a) The linear stage describes integration of stimulus features by a linear filter, the receptive field (RF). In the auditory system, stimulus examples are sampled from the stimulus spectrogram by considering the spectro-temporal density preceding the response. The extracted instantaneous spectro-temporal patch is filtered using the spectro-temporal receptive field (STRF) of the neuron. (b) The linear-nonlinear Poisson (LNP) model assumes that spikes are generated from the output of the linear stage by a static neural nonlinearity with subsequent Poisson spike generation. Parameters of the LNP are typically estimated using a generalized linear model (GLM). (c) An alternative approach, classification-based RF (CbRF) estimation, is based on the assumption of a noisy threshold operation that produces a probabilistic binary spike train. The average nonlinear response can be described by the cumulative distribution function of the noise around the threshold as indicated by the dashed gray line.

the linear part in a linear-nonlinear (LN) cascade model (deBoer and Kuyper, 1968; Chichilnisky, 2001). The LN model conceptually separates how the neuron processes stimuli (filtering through the RF) from the details of how its response is generated (nonlinearity and subsequent spike generation). The linear RF stage maps the high-dimensional stimulus to a scalar value by correlating the stimulus with the stimulus pattern maximally driving that neuron, namely the RF (Fig. 1(a)). The higher the correlation between stimulus and RF, the more likely a spike is elicited. The relation between correlation and spiking probability is described by the neural nonlinearity, which transforms the filtered stimuli into a spike rate (Fig. 1(b)).

The RF has successfully been used to study processing in sensory neurons in different brain areas, e.g., the visual cortex (David et al., 2004; Sharpee et al., 2006), the auditory midbrain (Escabi et al., 2003; Lesica and Grothe, 2008), and the auditory cortex (deCharms et al., 1998; Fritz et al., 2003; Rabinowitz et al., 2011). However, much of our current understanding about the function of sensory areas has been obtained using parametric stimuli, such as random dots and sinusoidal gratings in vision (Ringach et al., 1997; Dayan and Abbott, 2005), and random chords and ripple combinations in audition (deCharms et al., 1998; Escabi and Schreiner, 2002; Klein et al., 2006). The use of parametric stimuli has its own advantage as it may significantly simplify estimation of the parameters of the LN model. E.g., the spike-triggered average (STA), a linear estimator of the LN model, provides for unbiased estimation of RF parameters if the stimulus ensemble exhibits a Gaussian distribution (Chichilnisky, 2001; Paninski, 2003; Sharpee et al., 2004). Recent evidence, however, suggests that sensory cortical areas are sensitive to structural features of natural stimuli rather than to simple stimuli (Nelken et al., 1999; Chechik and Nelken, 2012; Freeman et al., 2013). In particular, natural stimuli are encoded more efficiently than artificial stimuli (Sharpee et al., 2006; Escabi et al., 2003; Vinje and Gallant, 2000) and model-based predictions based on responses to simple artificial stimuli are not sufficient to predict neural responses to natural stimuli (David et al., 2004; Theunissen et al., 2000).

Natural stimuli, however, exhibit a statistically more complex structure than parametric stimuli (Sharpee et al., 2004; Ruderman and Bialek, 1994). Thus, to characterize the feature selectivity with natural stimuli and other stimuli with non-Gaussian correlations, the presence of higher-order stimulus correlations in such stimulus ensembles must be taken into account (Paninski, 2003, 2004; Sharpee et al., 2004; Truccolo et al., 2005; Meyer et al., 2014a). Estimators that allow estimation of the parameters of the LN model under natural stimulation typically come at the expense of elaborated optimization schemes, e.g., maximum information dimensions (MID), which generalize the STA to non-Gaussian stimulus ensembles and arbitrary neural nonlinearities (Sharpee et al., 2006, 2004). However, the need for computationally efficient methods is twofold. First, progress in neural recording techniques motivated the development of models that include a large number of neurons (Pillow et al., 2008). While these model provide a more accurate description of neural responses, computational complexity scales linearly (no interactions) or quadratic (pair-wise interactions) with the number of neurons. Second, characterization of neural responses during experiments becomes increasingly important, e.g., adjusting experimental parameters based on extracted frequency profiles (Rabinowitz et al., 2011), stimulation of neurons with preferred stimulus patterns (Touryan et al., 2002), and (on-line) closed-loop experiments (Benda et al., 2007; Lewi et al., 2009; Park and Pillow, 2012).

Our goal in this study is to employ stochastic approximations to the task of RF estimation to reduce computational complexity. The approximation scheme proposed here, stochastic gradient descend (SGD), has received much attention in the field of machine learning (see, e.g., (Bottou, 2010; Bottou and Bousquet, 2011), for a recent overview). However, while SGD has been successfully applied in engineering applications, it remains unclear if SGD allows robust and computationally efficient estimation of RF parameters. In particular, the complex statistical structure of natural stimulus ensembles may limit its use. To test this, we apply SGD-based optimization schemes to both the generalized linear model (GLM, Nelder and Wedderburn, 1972; Paninski, 2004; Truccolo et al., 2005), a flexible framework that allows to include interactions between multiple neurons (Pillow et al., 2008), and a previously developed classification-based RF estimation method (CbRF, Meyer et al., 2014a). Both methods have successfully been used to characterize responses of auditory midbrain neurons used in this study (Meyer et al., 2014a).

We present three key results: first, using simulated responses, we demonstrate that optimization of RF parameters using SGD produces extremely robust RF estimates, even for highly non-Gaussian stimulus ensembles such as human speech and natural images. The same stimuli lead to biased RF estimation when derived using standard linear estimators (Sharpee et al., 2006, 2004; Christianson et al., 2008). Second, we apply the method to recordings from the auditory midbrain in anesthetized Mongolian gerbils. We show that stochastic approximations preserve tuning properties and predictive power of the spectro-temporal receptive field (STRF). Furthermore, the time to obtain an approximate STRF estimate takes only a fraction of the experimental time. Third,