Spike pattern-based coding schemes in the cricket cercal sensory system ⋆

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Abstract

We apply the recently developed information distortion method [1] to the analysis of coding by single neurons in the cricket cercal sensory system. This technique allows simultaneous identification of stimulus features and corresponding neural responses. The best approximation of a coding scheme that we obtained suggests that significant information is encoded in spike patterns. We compare this method to the linear stimulus reconstruction approach. Our coarsest nontrivial reproduction completely recovers the stimulus reconstruction results. Further refinements uncover additional structure, not present in the stimulus reconstruction results.

Key words: neural coding, information theory, quantization, cricket

1 INTRODUCTION

The general goals of the research reported here were to extend a recent analytical approach for studying the neural code, and to apply that more powerful approach to the analysis of neural coding in a simple sensory system. We recently used tools from information theory [1] to achieve two goals towards characterizing the neural coding scheme of a simple sensory system. First, we modeled the functioning of a neural system as a communication channel. Although this model is stochastic, we demonstrated that in this context a coding

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scheme consists of classes of stimulus/response pairs which form a structure akin to a dictionary: each class consists of a stimulus set and a response set, which are synonymous. The classes themselves are almost independent, with few intersecting members. The number of distinguishable classes is related to the mutual information between stimulus and response. Next, we developed a method to find high quality approximations of such a coding scheme. To do this, we quantized the neural responses to a small reproduction set and minimized an information-based distortion function to obtain an optimal quantization. Fixing the size of the reproduction produces an approximation of the coding scheme described above. The approximation can be refined by increasing the size of the reproduction. For the model described above, there is a critical size, beyond which further refinements do not significantly decrease the distortion. We choose the optimal quantization at this size to represent the coding scheme.

We applied this method to several synthetic test cases where the joint probability, describing the stimulus/response relation, was known. Here we present an extension to the analysis to physiological recordings from the cricket cercal sensory system, where in general the probability is not known. We extend the method to cases involving complex, high dimensional input stimuli, similar to the natural sensory environment of the animal. The approach we take is to model the stimulus/response relation in a way that gives us an upper bound of the information distortion cost function. In this way, minimizing an upper bound of the distortion also decreases the actual distortion and produces good approximations of the coding scheme. It also gives us a quantitative method to evaluate the quality of different models. We consider a model to be better if the minimum distortion it provides is smaller than that of other models. We further provide an example of a model which satisfies the upper bound requirements and use it to investigate coding properties of neurons in the cricket cercal sensory system.

2 PRELIMINARIES

We apply the recently developed information distortion method [1] to the analysis of coding by single neurons in the cricket cercal sensory system. We consider this encoding process within a probabilistic framework [2,3]. In this framework we model a neuron or a group of neurons as a communication channel [4]. Results from information theory can be applied almost directly to this model for insights into the operation of a neural sensory system. Although the model is stochastic, an almost deterministic relation emerges naturally on the level of clusters of stimulus/response pairs. Given this model of neural function, we want to recover the codebook. The approach we used in [1] was to quantize (cluster) the response space Y to a small reproduction space,

Y_N, of finitely many abstract classes. Since the mutual information plays an important role in our model of a coding scheme, we measure the quality of a quantization with the *information distortion function*

$$D_I(Y, Y_N) = I(X;Y) - I(X;Y_N). \tag{1}$$

We formulated the problem for finding a good quantizer as a maximum entropy [5], constrained optimization problem:

$$\max_{q(y_N|y)} H(Y_N|Y) \quad \text{constrained by} \tag{2}$$
$$D_I(q(y_N|y)) \leq D_0, \quad \sum_{y_N} q(y_N|y) = 1 \quad \text{and} \quad q(y_N|y) \geq 0 \quad \forall y \in Y$$

A related formulation can be found in [9]. The optimal quantizer ${}^*q(y_N|y)$ induces a coding scheme from $X \to Y_N$: $p(y_N|x) = \sum_y {}^*q(y_N|y)p(y|x)$ is the most informative approximation of the original relation $p(x|y)$ for a fixed size N of the reproduction Y_N. Increasing N produces a refinement of the approximation, which is more informative (has lower distortion and thus preserves more of the original mutual information I(X;Y)). The model of a coding scheme we use suggests that $D_I \propto -\log N$ for $N \leq N_c \approx 2^{I(X;Y)}$ and $D_I \approx$ *const* for $N \geq N_c$ [1]. Since we in general don't know $I(X;Y)$, we empirically choose N_c at which the rate of change of D_I with N decreases dramatically. This method allows us to study coarse but highly informative models of a coding scheme, and then to automatically refine them when more data becomes available.

3 DEALING WITH COMPLEX STIMULI

To successfully apply this method, we need to estimate the information distortion D_I, which in turn depends on the joint stimulus/response probability $p(x,y)$. For this work we choose to model the stimulus/response relationship. The formulation as an optimization problem suggests certain classes of models which are better suited for this approach. We shall look for models that give us strict upper bounds $\tilde{D}_I$ of the information distortion function. In this case, when we minimize the upper bound, the actual value of D_I is also decreased, since $0 \leq D_I \leq \tilde{D}_I$. This also gives us a quantitative measure of the quality of a model: a model with smaller $\tilde{D}_I$ is better.

We start the modeling process by noting that D_I can be expressed as $D_I(Y, Y_N; X) = H(X) - H(X|Y) - (H(X) - H(X|Y_N))$. The only term here that depends on the quantizer $q(y_N|y)$ is $H(X|Y_N)$. We can further express $H(X|Y_N)$ as [6]

$$H(X|Y_N) = \sum_{y_N} p(y_N) H(X|y_N), \tag{3}$$

where each term $H(X|y_N)$ is the entropy of X conditioned on y_N being the observed response class. One way to produce a bound to (3) is by constructing a maximum entropy model [6,5]. We can estimate the class conditioned mean x_{y_N} and covariance matrix $C_{X|y_N}$ of the stimulus from data. The maximum entropy model under such constraints is a Gaussian with the estimated mean and covariance. We use this model to obtain an upper bound $\tilde{D}_I$ to the cost function (1). This yields an explicit formula for the upper bound of the distortion which can be used in place of D_I in the optimization scheme (2).

4 RESULTS

We apply the method to intracellular recordings from an identified interneuron in the cricket cercal sensory system. During the course of the physiological recording, the system was stimulated with air current stimuli, drawn from a band-limited (5-500Hz) Gaussian white noise (GWN) source [7]. The method of linear stimulus reconstruction was applied to the analysis of this system. The results are presented in figure 1. Here and later, the conditioned stimuli are presented as time series relative to the occurrence of an event (spike or a sequence of spikes). The input space X consists of digitized $25ms$ long sequences of the air velocity stimulus.

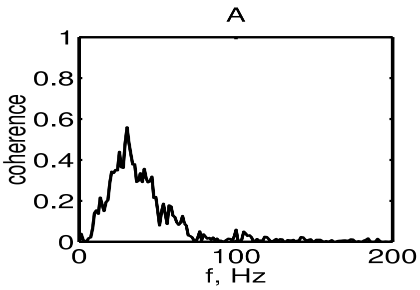

Fig. 1. The linear reconstruction method. The system is fully characterized by its coherence (A). It's response to stimuli is governed by its impulse response properties (B), shown in [8] to be the spike conditioned stimulus mean in this case.

We applied the information distortion method to this system. The results are presented in figure 2. All patterns except the first one in panel A were obtained by choosing 10 ms sequences from the recording which started with a spike (at time 0 here). Sequences, in which the initial spike was preceded by another spike closer than 10 ms were excluded. Pattern 2 contains a single spike, then follows a set of about 50 doublets, then a set of several triplets. Pattern one is a well isolated empty codeword (occurrences were chosen to be relatively far from the other patterns). Each pattern was observed multiple times (histogram not shown).

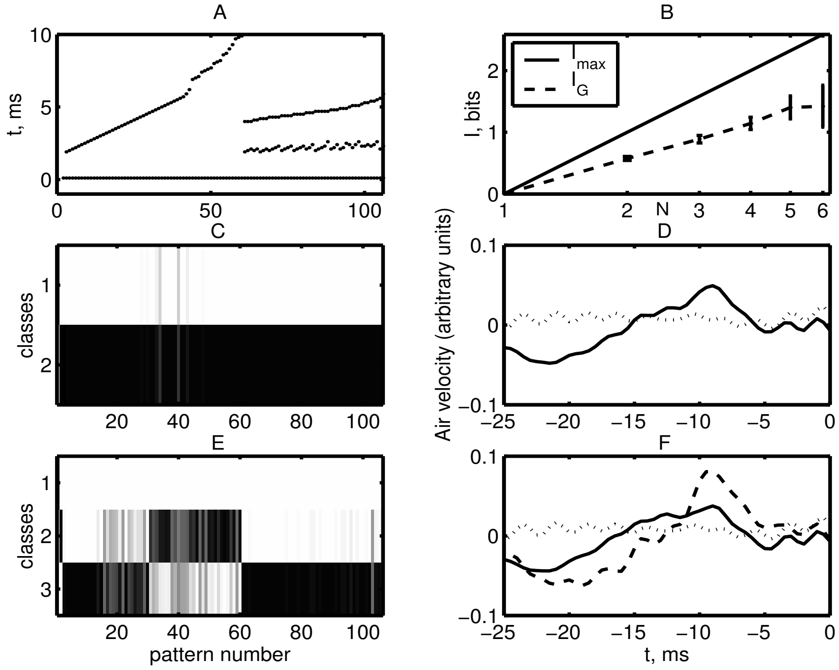

Fig. 2. *Results from the information distortion method. A) All the response spike patterns that were analyzed. Each dot represents the occurrence of a single spike. Each column of dots represents a distinct sequence of spikes. The y axis is the time in ms after the occurrence of the first spike in the pattern. The x axis here and below is an arbitrary number, assigned to each pattern. B) The lower bound of the I (- -) obtained through the Gaussian model can be compared to the absolute upper bound $I = \log_2 N$ for an N class reproduction (–). C) The optimal quantizer for $N = 2$ classes. This is the conditional probability $q(y_N|y)$ of a pattern number y from A) (horizontal axis) belonging to class y_N (vertical axis). White represents zero, black – one, and intermediate values are represented by levels of gray. D) The means, conditioned on the occurrence of class 1 (...) or 2 (–). E) The optimal quantizer for $N = 3$ classes. F) The means, conditioned on the occurrence of class 1 (...), 2 (–) or 3 (- -).*

Panels (C–F) show the results of applying the information distortion approach to this dataset. The optimal quantizer for the $N = 2$ reproduction is shown in panel (C). It isolates the empty codeword in one class (class 1) and all other patterns in another class (class 2). The mean, associated with the zero codeword (D, ...), does not significantly deviate from zero. The second class effectively reproduces the linear reconstruction kernel, since the class does not discriminate between any patterns that start with a spike. The mean, associated with class 2 (D, –), is similar to the linear reconstruction mean.

Panels E and F show the results of extending the analysis to a reproduction of $N = 3$ classes. It uncovers structure not present in the linear reconstruction method. The zero codeword remained in class 1. Class 2 in C was split in two separate classes here: class 2, which contains the single spike codeword and codewords with an interspike interval $ISI > 5ms$, and class 3, which contains all doublets with $ISI < 2ms$ and all triplets. We interpret class 2 as a class representing a single spike. The observed doublets with $ISI > 5ms$ are probably the start of the next codeword. The mean in (D, –) was split in two separate class conditioned means (F, – and - -).

To test the significance of this split we examine the lower bound of the mutual information $I(X; Y_N)$ (figure 2 B). All errorbars were obtained by bootstrap. $I(X; Y_N)$ increases significantly until the transition from 4 to 5 classes, but remains essentially the same for the next transition ($5 \to 6$, quantizer not shown), while the uncertainty of the estimate increases significantly. We conclude that the refinements $2 \to 5$ were significant, while subsequent refinements were not, so this particular dataset supports 5 codeword classes.

5 CONCLUSIONS

We apply the information distortion method to the analysis of single neurons in the cricket cercal sensory system. To cope with the high dimensional input space, we model the relationship between stimulus and reproduction with a maximum entropy model. Such a model produces an upper bound to the information distortion $D_I(Y; Y_N)$. We compared the performance of the method to the linear stimulus reconstruction approach. A 2 class reproduction completely recovers the stimulus reconstruction result. A 3 class reproduction uncovered additional structure, not present in the stimulus reconstruction result. The particular dataset we analyzed allowed refinements of the reproduction space of up to 5 classes.

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