NEUROCOMPUTING

Neurocomputing 44–46 (2002) 373–379

www.elsevier.com/locate/neucom

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

Alexander G. Dimitrov[a,*], John P. Miller[a], Zane Aldworth[a], Albert E. Parker[b]

[a] Center for Computational Biology, Montana State University, Bozeman, MT 59717, USA
[b] Department of Mathematical Sciences, Montana State University, Bozeman, MT 59717, USA

Abstract

We apply the recently developed information distortion method (Comput. Neural Systems 12 (4) (2001) 441) 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.

Keywords: 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 [4] 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

☆ Research supported in part by NIH Grants MH12159 (AGD) and MH57179 (JPM, ZA), and NSF grants DGE9972824(ZA,AEP) and MRI9871191.

* Corresponding author. Tel.: +1-406-994-6494; fax: +1-406-994-7438.

E-mail addresses: alex@cns.montana.edu (A.G. Dimitrov), jpm@cns.montana.edu (J.P. Miller), zane@cns.montana.edu (Z. Aldworth), parker@math.montana.edu (A.E. Parker).

PII: S0925-2312(02)00384-3

that in this context a coding 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 [4] to the analysis of coding by single neurons in the cricket cercal sensory system. We consider this encoding process within a probabilistic framework [1,6]. In this framework we model a neuron or a group of neurons as a communication channel [2]. 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 [4] 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:

$$\max_{q(y_N|y)} H(Y_N|Y) \quad \text{constrained by}$$

$$D_I(q(y_N|y)) \leqslant D_0, \quad \sum_{y_N} q(y_N|y) = 1 \quad \text{and} \quad q(y_N|y) \geqslant 0 \quad \forall y \in Y, \tag{2}$$

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 $N \leqslant N_c \approx 2^{I(X;Y)}$ and $D_I \approx const$ for $N \geqslant N_c$ [4]. Since we in general do not 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 $0 \leqslant D_I \leqslant \tilde{D}_I$. 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 [3]

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

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 [3,5]. 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 [8]. The method of linear stimulus reconstruction was applied to the analysis of this system. The results are presented in Fig. 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 25 ms long sequences of the air velocity stimulus.

We applied the information distortion method to this system. The results are presented in Fig. 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).

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, $\cdots$), 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

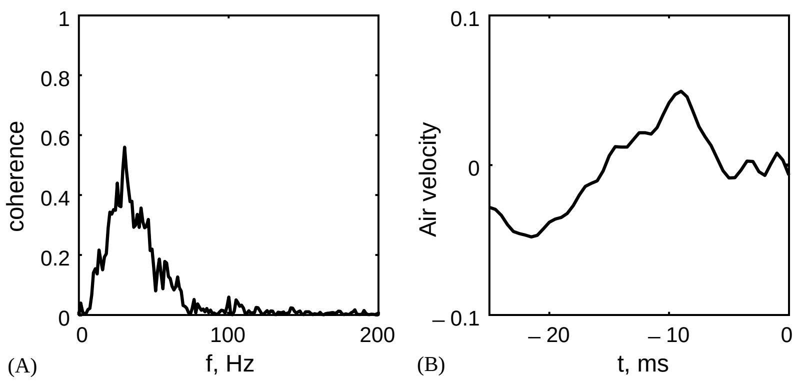

Fig. 1. The linear reconstruction method. The system is fully characterized by its coherence (A). It's response to stimuli is governed by its impulse response properties (B), shown in [7] to be the spike conditioned stimulus mean in this case.

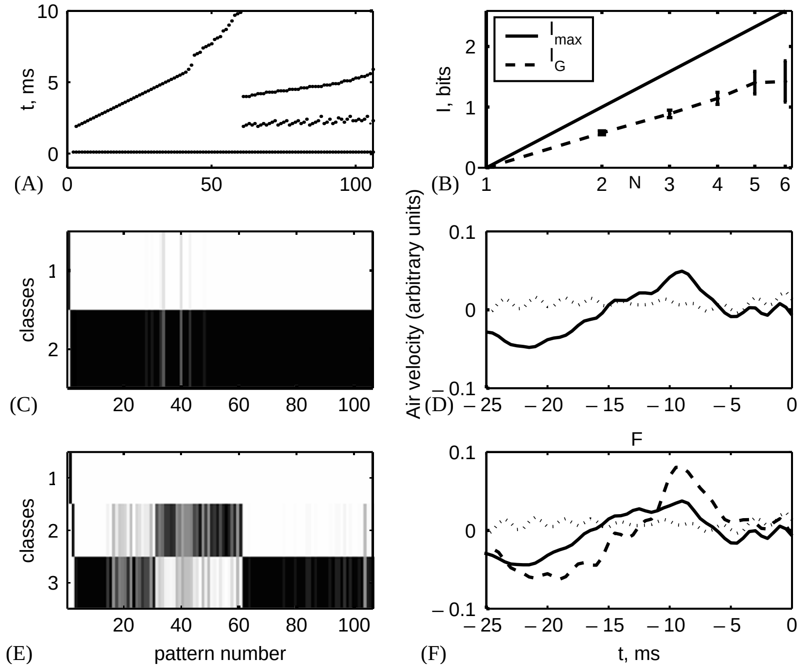

Fig. 2. Results from the information distortion method. (A) All the response spike patterns that were analyzed. Each dot represents the occurrence of a single spike. Each column of dots represents a distinct sequence of spikes. The y-axis is the time in ms after the occurrence of the first spike in the 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 ($\cdots$) or 2 (–). (E) The optimal quantizer for $N = 3$ classes. (F) The means, conditioned on the occurrence of class 1 ($\cdots$), 2 (–) or 3 (- -).

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 $ISI > 5$ ms, and class 3, which contains all doublets with $ISI < 2$ ms and all triplets. We interpret class 2 as a class representing a single spike. The observed doublets with $ISI > 5$ ms 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 $I(X;Y_N)$ (Fig. 2B). 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 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.

References

[1] H.B. Barlow, Possible principlpes underlying the transformation of sensory messages, in: W.A. Rosenblith (Ed.), Sensory Communications, MIT Press, Cambridge, MA, 1961.

[2] T. Cover, J. Thomas, Elements of Information Theory, Wiley Series in Communication, New York, 1991.

[3] A.G. Dimitrov, J.P. Miller, Natural time scales for neural encoding, Neurocomputing 32–33 (2000) 1027–1034.

[4] A.G. Dimitrov, J.P. Miller, Neural coding and decoding: communication channels and quantization, Network: Comput. Neural Systems 12 (4) (2001) 441–472.

[5] E.T. Jaynes, On the rationale of maximum-entropy methods, Proc. IEEE 70 (1982) 939–952.

[6] T.W. Kjaer, J.A. Hertz, B.J. Richmond, Decoding cortical neuronal signals: network models, information estimation and spatial tuning, J. Comput. Neurosci. 1 (1–2) (1994) 109–139.

[7] F. Rieke, D. Warland, R.R. de Ruyter van Steveninck, W. Bialek, Spikes: Exploring the Neural Code, MIT Press, Cambridge, 1997.

[8] F. Theunissen, J.C. Roddey, S. Stufflebeam, H. Clague, J.P. Miller, Information theoretic analysis of dynamical encoding by four primary sensory interneurons in the cricket cercal system, J. Neurophysiol 75 (1996) 1345–1359.

Alexander Dimitrov is a research assistant professor at the Center for Computational Biology at Montana State University in Bozeman, Montana. He majored in Physics at St. Kliment Ohridski University of Sofia, Bulgaria. He proceeded with his graduate studies at the University of Chicago, where he received his M.Sc. in Physics in 1993 and Ph.D. in Applied Mathematics in 1998, under the guidance of Dr. Jack D. Cowan. He continued with postdoctoral training with Dr. John Miller under a personal training grant from the NIMH. Dr. Dimitrov's main interests are in computational neuroscience and problems of neural coding.

John P. Miller is Professor of Biology, and the Director of the Center for Computational Biology at Montana State University, in Bozeman. He received his B.A. in Physics at the University of California, Berkeley, in 1972, and his Ph.D. in Biology at the University of California, San Diego, 1980. He did postdoctoral research at NIH in Bethesda, M.D., with Dr. Wilfrid Rall and Dr. John Rinzel. Dr. Miller was a faculty member at U.C. Berkeley until 1997, when he moved to become the founding director of the Center for Computational Biology at MSU. His research interests include neural encoding, mechanisms of synaptic integration and system-level function. He was one of 6 founding editors of the Journal of Computational Neuroscience. Along with Jim Bower of Cal Tech, Dr. Miller also established and co-organized the annual

Computational Neuroscience (CNS) Meetings from 1992 until 1997. He currently serves as a member of the President's Information Technology Advisory Committee (PITAC).

Zane Aldworth is a graduate student of Dr. John Miller in the Center for Computational Biology at Montana State University, Bozeman, Montana. Zane has a B.S. in Physics from the University of Puget Sound in Tacoma, WA, and a B.S. in Biology from MSU, Bozeman. He is pursuing graduate studies as part of the NSF-sponsored IGERT program in Complex Biological Systems, with an emphasis in the neural basis of information processing.

Al Parker is a graduate student in the Department of Mathematical Science at Montana State Univeristy. He is pursuing graduate studies as part of the NSF-sponsored IGERT program in Complex Biological Systems. Al holds M.Sc. in Mathematics from the University of Vermont and B.Sc. in Mathematics/Computer Science from Bridgewater State College. His current interests include applied dynamical systems, mathematical modeling, problems in neural coding, numerical optimization, and bayesian data analysis.