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Journal of Neuroscience Methods 169 (2008) 391–404

JOURNAL OF
NEUROSCIENCE
METHODS

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Responses of neurons in the inferior colliculus to binaural disparities: Insights from the use of Fisher information and mutual information

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Received 31 July 2007; received in revised form 4 November 2007; accepted 10 November 2007

Abstract

The minimal change in a stimulus property that is detectable by neurons has been often quantified using the receiver operating characteristic (ROC) curve, but recent studies introduced the use of the related Fisher information (FI). Whereas ROC analysis and FI quantify the information available for discriminating between two stimuli, global aspects of the information carried by a neuron are quantified by the mutual information (MI) between stimuli and responses. FI and MI have been shown to be related to each other when FI is large. Here the responses of neurons recorded in the inferior colliculus of anesthetized guinea pigs in response to ensembles of sounds differing in their interaural time differences (ITDs) or binaural correlation (BC) were analyzed. Although the FI is not uniformly large, there are strong relationships between MI and FI. Information-theoretic measures are used to demonstrate the importance of the non-Poisson statistics of these responses. These neurons may reflect the maximization of the MI between stimuli and responses under constraints on the coded stimulus range and the range of firing rates. Remarkably, whereas the maximization of MI, in conjunction with the non-Poisson statistics of the spike trains, is enough to create neurons whose ITD discrimination capabilities are close to the behavioral limits, the same rule does not achieve single-neuron BC discrimination that is as close to behavioral performance.

Keywords: Auditory system; Binaural disparities; Inferior colliculus; Guinea pig; Fisher information; Mutual information

1. Introduction

Developing the appropriate tools for the quantification of neural responses to sensory stimuli is an important goal in neuroscience. Throughout the modern history of neuroscience, the availability of the right quantifiers of stimulus–response relationships has been crucial for scientific advances. Thus, the study of auditory sensory coding cannot be imagined today without tools such as the peristimulus time histogram introduced by Gerstein (1960), reverse correlation techniques initially introduced by De Boer (1968,1969), or the concept of the spectro-temporal receptive field (Aertsen and Johannesma, 1980, 1981; Aertsen et al., 1981).

While all of the quantifiers above are important for understanding how a stimulus affects neuronal responses, a separate toolkit has been developed in order to study the reverse question—how can the nervous system use neuronal responses in order to extract information about the environment. Typically, such studies start with a set of relevant stimuli (e.g. broadband noise presented from many different directions in space, Middlebrooks et al., 1994). To evaluate the discrimination based on single trials, a classifier is trained to use the response recorded in single trials in order to identify the stimulus that gave rise to the response.

A large number of different classifiers have been used for the general problem of classifying neuronal responses. However, this approach is inherently *ad hoc*: there may always be yet another, better classifier that will achieve a higher discrimination performance based on the same responses. It turns out that the performance of all classifiers on a given set of responses can in fact be uniformly bounded. For this purpose, the performance of a classifier is quantified by the so-called transmitted information.

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doi:10.1016/j.jneumeth.2007.11.005

The transmitted information is computed from the confusion matrix, which estimates how many times a response to a given stimulus was classified as resulting from the presentation of any of the other stimuli. The transmitted information of any classifier is bounded by the mutual information (MI) between stimuli and responses, a measure that can be computed without any reference to a specific classifier. Thus, the MI is an absolute bound on the performance of any classifier (see the review in Nelken et al., 2005).

One important special case occurs often in the literature. In case the set of relevant stimuli consists of only two stimuli, the classifier becomes a discriminator whose goal is to identify which of the two stimuli was presented given single trial responses. In the context of the auditory system, this approach has been extensively applied to the case in which the two stimuli are close to each other along some sensory scale, leading to estimates of the sensory resolution of single trial responses. The tool that has been traditionally used for quantifying the discrimination between pairs of stimuli is the receiver operating characteristic (ROC) curve. This curve can be used to estimate the best possible performance in a 2-alternative, 2-interval forced choice task (Green and Swets, 1966).

When testing the sensory resolution, so that the two stimuli to be discriminated are very similar to each other, there is an alternative measure of performance: the Fisher information (FI). FI is a sensitivity measure: it measures the extent by which the response of the neuron changes when the sensory parameter is changed by a small amount (Schervish, 1995). Clearly, when the response is a sensitive function of the sensory parameter, it will be easier to discriminate between nearby values of that parameter. The main importance of FI is the fact that it can be used to extrapolate single-neuron discrimination capabilities to large populations, which is difficult to do with ROC analysis. Thus, when they make sense and can be estimated, FI and MI are in fact appealing quantifiers of neural responses. FI in various guises has been used for a long time (e.g. Siebert, 1965), but its explicit use in auditory research is to the best of our knowledge only rather recent (Harper and McAlpine, 2004; Heinz et al., 2001a,b; Jenison, 2000; Jenison and Reale, 2003).

Since ROC curves, FI and MI are different measures of the information that is available in single neuronal responses, it is natural to ask what the relationships between them are. The theoretical relationships will be discussed in Section 2. The first purpose of this paper is to compare these relationships with actual measured responses. The data consist of a previously collected, unique set of responses of inferior colliculus (IC) neurons in guinea pigs (Shackleton et al., 2003, 2005; Skottun et al., 2001) to two types of binaural disparities: interaural time differences (ITDs) and various levels of binaural correlation (BC).

The neurons were studied with an extremely high-resolution of the sensory continua, and each ITD or BC value was tested ≥ 100 times. This makes the dataset large enough to stably estimate all three information measures.

The second purpose of this paper is to illustrate the importance of information-theoretic measures for understanding the ‘design features’ of neurons. Information-theoretic measures are used to demonstrate the importance of the non-Poisson statistics of the responses of these neurons, and to suggest that these neurons optimize the MI between stimuli and responses under constraints on the range of the encoded parameters and the range of firing rates.

2. Methods

2.1. Electrophysiology

The paper is based on the data from Shackleton et al. (2005). Detailed methods are described in the above paper. In short, responses of well-separated single neurons were collected in the inferior colliculus (IC) of urethane-anesthetized guinea pigs. All experiments were carried out in accordance with the UK Animal (Scientific Procedures) Act of 1986.

Stimuli were delivered to each ear through sealed acoustic systems comprising custom-modified Radioshack 40-1377 tweeters joined via a conical section to a damped 2.5-mm-diameter, 34-mm-long tube (M. Ravicz, Eaton Peabody Laboratory, Boston, MA, USA), which fitted into the hollow speculum. The output was calibrated a few millimeters from the tympanic membrane using a Brüel and Kjær 4134 microphone fitted with a calibrated 1-mm probe tube.

All stimuli were digitally synthesized (System II, Tucker-Davies Technologies) at sampling rates between 100 and 200 kHz and were output through a waveform reconstruction filter set at one fourth the sampling rate (135 dB/octave elliptic: Kemo 1608/500/01 modules supported by custom electronics). Stimuli were of 50-ms duration at 20 dB above the threshold for that stimulus, switched on and off simultaneously in the two ears with cosine-squared gates with 2 ms rise/fall times (10–90%). Since gating was applied simultaneously in both ears, there were only ongoing interaural phase differences (IPDs) in the stimulus and no onset ITD.

The stimuli consisted of narrow noise bands around the best frequency of each neuron (one equivalent rectangular band for the guinea pig, about $6.477f^{0.56}$ at center frequency f kHz). The stimuli were presented with varying ITD or varying binaural correlation (BC). For the ITD responses, 16–31 ITD values were selected at a typical resolution of 0.01 cycles covering the dynamic range of the neuron. For BC variation only noise stimuli were used. The stimuli were presented at the best ITD of the neuron. BC varied from -1 to 1 in steps of 0.1 (21 values in all). Examples of stimuli with different BC are displayed in Fig. 1A.

Data was acquired only from neurons with good modulation of the rate by interaural delay and a spike signal-to-noise ratio that was judged likely to be sufficient for a recording of 2–3 h. The noise stimuli were ‘frozen’ (the same stimulus token was presented for all presentations of each ITD or BC value). Data was sometimes collected for a number of different frozen tokens of the noise stimuli. Only in a few cases differential sensitivity to the noise tokens was found, and therefore the responses to all tokens were superimposed in the analyses below.