Spike timing and the coding of naturalistic sounds in a central auditory area of songbirds

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Abstract

In nature, animals encounter high dimensional sensory stimuli that have complex statistical and dynamical structure. Attempts to study the neural coding of these natural signals face challenges both in the selection of the signal ensemble and in the analysis of the resulting neural responses. For zebra finches, naturalistic stimuli can be defined as sounds that they encounter in a colony of conspecific birds. We assembled an ensemble of these sounds by recording groups of 10-40 zebra finches, and then analyzed the response of single neurons in the songbird central auditory area (field L) to continuous playback of long segments from this ensemble. Following methods developed in the fly visual system, we measured the information that spike trains provide about the acoustic stimulus without any assumptions about which features of the stimulus are relevant. Preliminary results indicate that large amounts of information are carried by spike timing, with roughly half of the information accessible only at time resolutions better than 10 ms; additional information is still being revealed as time resolution is improved to 2 ms. Information can be decomposed into that carried by the locking of individual spikes to the stimulus (or modulations of spike rate) vs. that carried by timing in spike patterns. Initial results show that in field L, temporal patterns give at least ~ 20% extra information. Thus, single central auditory neurons can provide an informative representation of naturalistic sounds, in which spike timing may play a significant role.

1 Introduction

Nearly fifty years ago, Barlow [1] and Attnave [2] suggested that the brain may construct a neural code that provides an efficient representation for the sensory stimuli that occur in the natural world. Slightly earlier, MacKay and McCulloch [3] emphasized that neurons that could make use of spike timing—rather than a coarser “rate code”—would have available a vastly larger capacity to convey information, although they left open the question of whether this capacity is used efficiently. Theories for timing codes and efficient
representation have been discussed extensively, but the evidence for these attractive ideas remains tenuous. A real attack on these issues requires (at least) that we actually measure the information content and efficiency of the neural code under stimulus conditions that approximate the natural ones. In practice, constructing an ensemble of “natural” stimuli inevitably involves compromises, and the responses to such complex dynamic signals can be very difficult to analyze.

At present the clearest evidence on efficiency and timing in the coding of naturalistic stimuli comes from central invertebrate neurons [4, 5] and from the sensory periphery [6, 7] and thalamus [8, 9] of vertebrates. The situation for central vertebrate brain areas is much less clear. Here we use the songbird auditory system as an accessible test case for these ideas. The set of songbird telencephalic auditory areas known as the field L complex is analogous to mammalian auditory cortex and contains neurons that are strongly driven by natural sounds, including the songs of birds of the same species (conspecifics) [10, 11, 12, 13]. We record from the zebra finch field L, using naturalistic stimuli that consist of recordings from groups of 10-40 conspecific birds. We find that single neurons in field L show robust and well modulated responses to playback of long segments from this song ensemble, and that we are able to maintain recordings of sufficient stability to collect the large data sets that are required for a model independent information theoretic analysis. Here we give a preliminary account of our experiments.

2 A naturalistic ensemble

Auditory processing of complex sounds is critical for perception and communication in many species, including humans, but surprisingly little is known about how high level brain areas accomplish this task. Songbirds provide a useful model for tackling this issue, because each bird within a species produces a complex individualized acoustic signal known as a song, which reflects some innate information about the species’ song as well as information learned from a “tutor” in early life. In addition to learning their own song, birds use the acoustic information in songs of others to identify mates and group members, to discriminate neighbors from intruders, and to control their living space [14]. Consistent with how ethologically critical these functions are, songbirds have a large number of forebrain auditory areas with strong and increasingly specialized responses to songs [11, 15, 16]. The combination of a rich set of behaviorally relevant stimuli and a series of high-level auditory areas responsive to those sounds provides an opportunity to reveal general principles of central neural encoding of complex sensory stimuli. Many prior studies have chosen to study neural responses to individual songs or altered versions thereof. In order to make the sounds studied increasingly complex and natural, we have made recordings of the sounds encountered by birds in our colony of zebra finches. To generate the sound ensemble that was used in this study we first created long records of the vocalizations of groups of 10-40 zebra finches in a soundproof acoustic chamber with a directional microphone above the bird cages. The group of birds generated a wide variety of vocalizations including songs and a variety of different types of calls. Segments of these sounds were then joined to create the sounds presented in the experiment. One of the segments that was presented (~ 30 sec) was repeated in alternation with different segments.

We recorded the neural responses in field L of one of the birds from the group to the ensemble of natural sounds played back through a speaker, at an intensity approximately equal to that in the colony recording. This bird was lightly anesthetized with urethane. We used a single electrode to record the neural response waveforms and sorted single units offline. Further details concerning experimental techniques can be found in Ref. [13].