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Discrimination of behaviorally relevant signals by auditory receptor neurons

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Abstract

In hearing insects, discrimination of auditory signals is vital to mate selection. We tested the capability of single auditory receptor neurons to discriminate calling songs from different individual grasshoppers of the same species. Spike trains elicited from different songs were studied using the metric-space analysis of Victor and Purpura (Networks: Comput. Neural Syst. 8 (1997) 127–164). Our data show that the natural songs can be distinguished perfectly after a mere 100 msec if spike trains are evaluated on time scales of about 10 msec. This time scale is well matched to the temporal structure of the grasshopper songs.

Keywords: Stimulus discrimination; Neural code; Auditory receptor; Metric-space analysis

1. Introduction

Rapid discrimination of natural stimuli is of central importance for many animals. This capability should manifest itself in the neural responses at all levels of the sensory pathway. Here we analyze neural responses with emphasis on the following questions: How much time is required to discriminate natural stimuli and how does this correlate with behavioral time scales? How many spikes are available for computation during that time? Of what relevance is the timing of spikes for discrimination?

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A simple system that allows to correlate neurophysiology and behavior is the grasshopper auditory system. Grasshoppers must detect and discriminate the calling songs of potential mates. For instance, male grasshoppers of the species *Chorthippus biguttulus* rhythmically generate songs of 2–4 sec duration that consist of many repetitions of a basic pattern, termed "syllable" (Fig. 1). Every syllable, in turn, is composed of six elementary sound pulses which normally are fused. Among individual grasshoppers of this species, syllables vary considerably in their length (60–120 msec), their more or less pulsed substructure, and their frequency content. Behavioral experiments show that female grasshoppers prefer certain male songs over others, even when the sound intensities of the songs are the same (R. Balakrishnan, personal communication). While it is not known which of the song differences are most relevant in the female's decision, the grasshopper's ability to discriminate between different songs should be visible in the neural responses. Focusing on the auditory periphery, we analyzed how well different stimuli can be distinguished from the spike trains of single auditory receptor neurons.

2. Methods

Eight different songs were repeatedly presented to a grasshopper while keeping the peak sound intensity constant. Spike trains were recorded intracellularly from an auditory receptor of *Locusta migratoria*, an established model system for *Chorthippus biguttulus* [2]. The experimental methods are described elsewhere [2]. The initial rising phase of the songs (usually the first second) was neglected to make the results comparable with behavioral experiments that employ model songs. The resulting spike trains were analyzed using the metric-space analysis introduced by Victor and Purpura [3].

The metric-space analysis consists of two steps: (1) A distance is calculated between every two spike trains by a stepwise transformation of one spike train into the other.

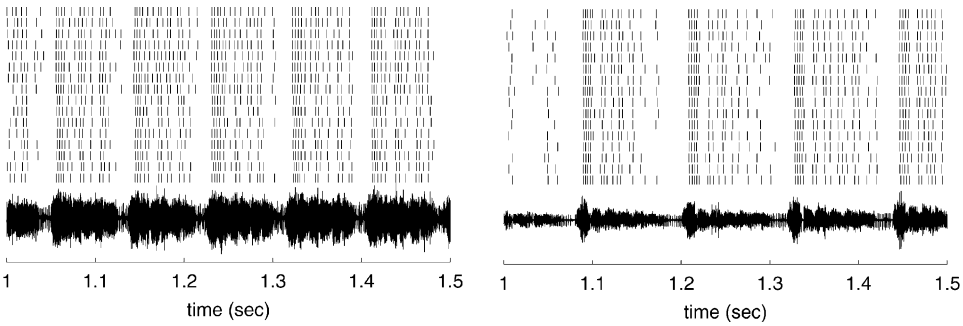

Fig. 1. Sections of two grasshopper songs (sound pressure level versus time) and 16 spike trains recorded from a single auditory receptor neuron while repeating the respective stimulus.

Each step consists of inserting, deleting, or shifting a spike and is associated with a cost. Insertion and deletion cost one unit each, while a shift in time of length Δt costs $q\Delta t$ units, where q is a free parameter that determines how important the precise timing of spikes is. The distance between two spike trains is defined as the minimal cost of transforming one train into the other. (2) A supervised clustering algorithm is applied, sorting spike trains close to each other into one group. The resulting groups are then compared with groups of spike trains generated by the same stimulus, allowing us to calculate the mutual information between the two sets, one sorted by metric distance, the other by stimulus. For eight songs the maximum information, indicating perfect discrimination, is 3 bits since $2^3 = 8$. The complete analysis depends on the parameter q; the value of q that results in optimal stimulus discrimination describes the precision with which spike times should be evaluated.

3. Results

3.1. Time needed for discrimination

To investigate how the available time interval influences distinguishability, only the first T milliseconds of each spike train were taken into account, where T was varied from 0–500 msec (see also Fig. 2, legend). An analysis varying both T and q yields the contours shown in Fig. 2, outlining the regions in (T, q) space that have a mutual information of at least 1, 1.5, 2, 2.5, or 3 bits.

Initially, the ability to discriminate the eight songs grows with the inclusion of ever longer time windows T. Unexpectedly, however, beyond the first 100–200 msec window, longer samples of the spike trains improve discrimination ability only marginally, as can be seen by the nearly horizontal contours in Fig. 2. This effect can be attributed to the repetitive structure of these songs. After a certain amount of time, additional syllables do not significantly aid in song discrimination.

To distinguish the songs perfectly, one needs to observe a little more than one hundred milliseconds of each spike train when a cost factor of $q \approx 100\ \text{sec}^{-1}$ is used, as can be observed from the 3 bit contour. Within this time, only one to two syllables of each song have been played back to the grasshopper. Therefore, under the given conditions, all songs can be perfectly discriminated taking only two syllables into account. In other experiments, perfect discrimination also took longer (200 msec) or a few spike trains were not assigned to the correct song.

3.2. Number of spikes needed

The relative importance of spikes can be inferred from the number of spikes that are needed for a correct stimulus discrimination. The central panel of Fig. 2 depicts for every window length the average number of spikes as well as the minimum and maximum number of spikes available in that particular time window. After 100 msec when all songs can be discriminated perfectly, the spike count varies between 3–20 spikes with an average of 10 spikes.

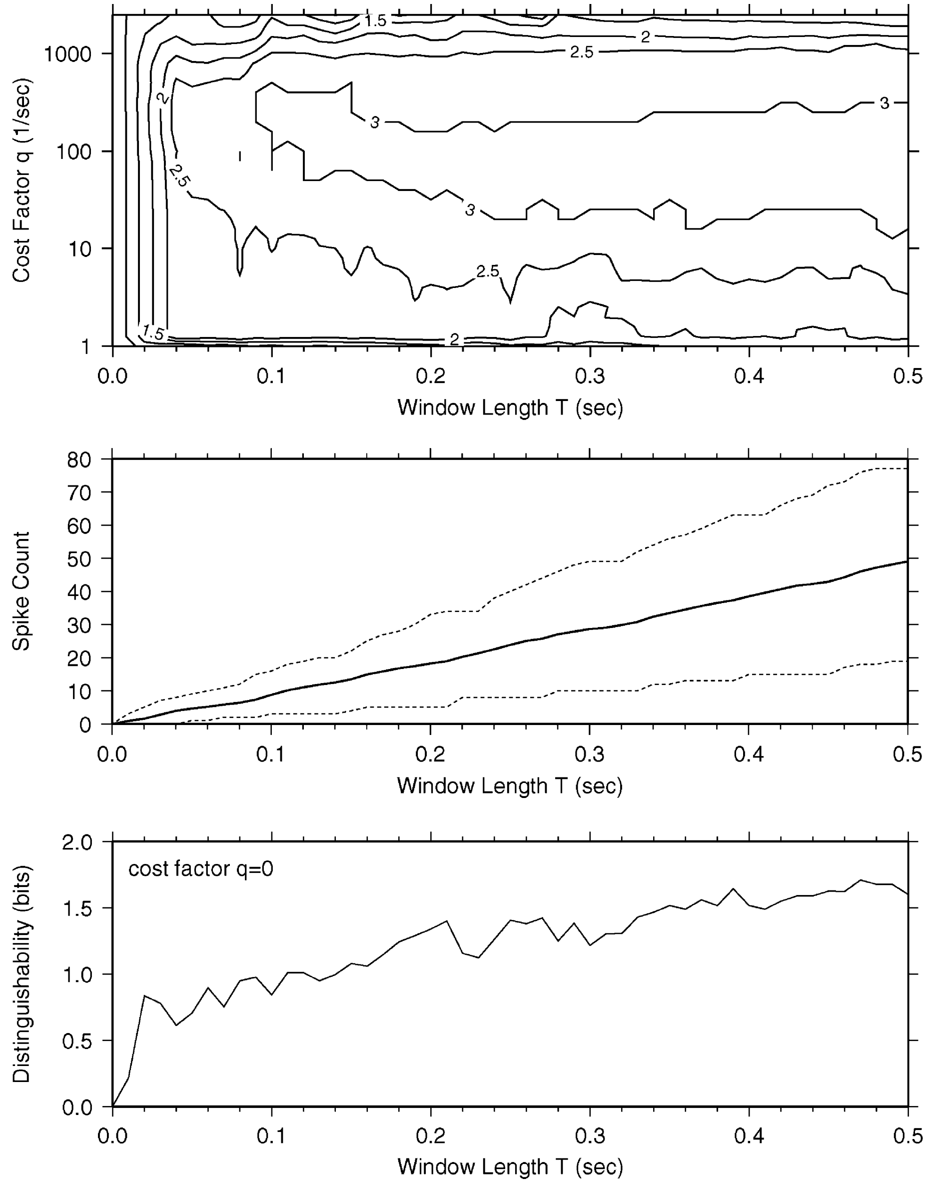

Fig. 2. (top) Contour plot of distinguishability (measured in terms of the mutual information) as a function of window length T and cost factor q. Here, T denotes the length of the spike trains after the first second has been cut off. (center) Average spike count (solid line) as well as minimum and maximum number of spikes (dashed lines) available for a given time window. (bottom) Distinguishability as a function of window length for a cost factor $q = 0$.

3.3. Spike timing required

We have already seen that the best discrimination results are obtained for a cost factor of $q \approx 100\ \text{sec}^{-1}$ (Fig. 2). This factor corresponds to comparing spike trains at a time scale of about 10 msec, a scale which matches that of the substructure of each syllable (six pulses of length 10–20 msec). We conclude, therefore, that the substructure plays a vital role in discrimination.

Although cost factors that are associated with a much higher or lower spike timing precision do not allow full discrimination, it is instructive to further investigate the case $q = 0$, when the distance between two spike trains corresponds to the difference in the number of spikes. In this case we obtain a distinguishability of about 1 bit after 100 msec (Fig. 2, bottom panel), suggesting that the spike trains fall into two groups. This is indeed the case, as three of the songs tested had considerably less power in the preferred frequency band (~ 5 kHz) of the auditory receptor, thus evoking spike trains with lower firing rates than the other songs.

4. Conclusion

This study demonstrates that the information present in the songs, namely the syllable length and syllable substructure, is well preserved in the spike trains of the receptor neurons. Spike trains of only 100 msec duration, corresponding to 10 spikes on average, suffice to perfectly discriminate all stimuli. How grasshoppers make use of this information, however, cannot be decided at this stage. It remains a subject of further investigation to determine the limits to the ability of single auditory receptors to discriminate natural stimuli. Note also that with a population of thirty to forty auditory receptors per ear, the discrimination ability of the animal as a whole will be even greater.

Interestingly, under ideal conditions male grasshoppers can perfectly distinguish calling songs of males and females after only 2–3 syllables [1]. Our study shows that this achievement can already be explained at the level of single auditory receptor neurons. Whether further syllable repetitions are needed in noisy environments is an open question and calls for more experiments in both behavior and physiology.

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