Encoding of communication sounds of Mongolian gerbil in the auditory cortical neurons

Hiroshi Riquimaroux and Atsushi Nakagawa.

Department of Knowledge Engineering & Computer Sciences, Faculty of Engineering, Doshisha University, 1-3 Miyakodani, Tataru, Kyotanabe, Kyoto 610-0321, Japan

hrkimar@mail.doshisha.ac.jp

Abstract

In this research, we investigated how communication sounds of Mongolian gerbil were encoded in the auditory cortex. Artificial communication sounds were synthesized based upon recorded gerbil communication sounds, which were composed of combination of harmonically structured rising and falling FM sweeps. The sounds where temporal or spectral structures were modified were monaurally presented to anesthetized animals. We recorded single unit activities of neurons in the contra-lateral auditory cortex responding to these sounds. Results indicated that encoding of communication sounds was not linearly structured and that preceding stimuli changed responses to the following stimuli. In other words, data suggested that the neurons encoded a temporal combination or a temporal sequence of communication sounds. The present results indicated that response properties of the auditory cortex in Mongolian gerbil were complex and a longer time window was needed for recordings than those used in previous works.

1. Introduction

We may observe tonotopic organization in the primary auditory cortex (AI) when sound stimuli are at threshold level. However, a simple tonotopic organization cannot be easily found when sound stimuli are above threshold at 60 or 70 dB SPL. In other words, AI neurons respond to different frequencies with totally different temporal response patterns. This evidence was at least observed in Japanese monkeys and Mongolian gerbils. Even the temporal response pattern of AI neurons to simple tone bursts was found not to be a simple ON response but a complicated multiple peaked one (Riquimaroux et al., 1994, Sumida and Riquimaroux, 2002). As a matter of fact, natural inputs, such as environmental sounds and vocalization sounds for communication, are not simple tone bursts but temporally and spectrally complex sounds. How these communication sounds are encoded into the auditory system is interesting and important for understanding speech-processing system. Recent studies have shown that AI neurons of Marmoset respond to their forward species specific communication calls more strongly than to reversed calls. However, when the Marmoset calls were presented to cats, AI neurons showed no preference to forward or reversed playbacks (Wang et al., 2000; Wang et al., 2001). Different from bat biosonar systems (Suga, 1984; Riquimaroux et al., 1991), how acoustical component of communication sounds contribute to the specific response has not been studied in details. The present study will investigate how AI neurons respond to synthesized communication sounds of Mongolian gerbils and try to understand how temporal and spectral structures of their communication sounds are encoded in the central auditory system.

2. Methods

2.1. Stimuli

Male Mongolian gerbils (Meriones unguiculatus) about a month old were used for recording communication vocalization. Three animals were put in a cage where a microphone (SONY, MDR-EX70SL) was placed at the ceiling. Their communication sounds were recorded in a temperature controlled (25 degree centigrade) sound attenuated chamber by a digital audio tape-recorder (Pioneer, D-C88) with 44.1 kHz sampling rate and 16-bit resolution between 9 and 11 PM. We analyzed the entire set of vocalization and found three major types (A, B and C shown in Fig. 1). Type A was the most frequent. The duration of the call was between 120 and 150 ms. We named Type A call, the “Original call”. Based upon Type A call, we synthesized artificial calls (Matlab, Math Works), where frequency gradually declined, and then rose to some extent. We synthesized 6 kinds of calls with 3 harmonics (the fundamental, the second and the third); ordinary (A), ordinary fall or the first FM component (B), ordinary rise or the second FM component (C), temporally reversed (D), spectrally upside-down or each FM part temporally reversed (E), and reversed and upside-down or order reversed (F) (Fig. 2). For each synthesized call, the fundamental frequency (f0) alone (b) and the second harmonic alone (c) were added to three-harmonic complex (a). Therefore, there were 3 variations in each call type, making total number of calls eighteen. Simple complex tone bursts with 3 harmonics (G-a) were also synthesized with the f0 of 4000, 5000 and 6000 Hz. For each complex tone burst, the f0 alone (b) and the second harmonic alone (c) were also added as stimuli. Then, there were 3 different subtypes for each f0, making total number of tone bursts...
nine. A band-pass noise burst whose bandwidth (2~19 kHz) was similar to the Original call was also synthesized and named “Noise” (H). We provided totally 29 stimuli; eighteen synthesized calls, nine tone bursts, one band-pass noise burst and the Original call. Duration of stimulus was 130 ms including 5 ms rise/fall times except for tone bursts where stimulus duration was 75 ms including 5 ms rise/fall times. For the ordinary call, the first part of 100 ms was downward FM, while the second part of 30 ms was upward FM (A-a). Sound pressure level was 55 dB SPL measured inside the external auditory meatus. The sound system was calibrated by a probe microphone (Etymotic Research, ER-7C). Inter-stimulus interval was set at 1.5 sec. The order of stimulus presentation was randomized. Each stimulus was presented at least 15 times.

![Fig. 1. Types of gerbil calls. Type A is the most major.](image)

2.2. Procedure

Adult males (age: about 4 months) were used. Animals were anesthetized with Ketamin (50 mg/kg, i.m.) and Xylazin (10 mg/kg, i.m.) and put on a stage in a sound attenuated and electrically shielded chamber. The animals were immobilized with a metal rod glued to the skull. Sounds were presented to the animal’s left ear through an earphone (Sony, MDR-EX70SL), which was tightly attached to the external meatus. Action potentials were extracellularly picked up from the right primary auditory cortex (AI) by glass-coated Elgiloy electrodes, amplified (WPI, DAM-80), band-pass filtered (from 300 Hz to 3 kHz) and isolated by a window discriminator. The output of the window discriminator was sent to a PC and PST (post stimulus time) histograms were constructed.

3. Results

Fifteen units were obtained. Some neurons showed a sustained response to the ordinary vocalization (A-a), while others produced an onset response to the same stimulus. A sketchy description about one typical neuron will be given below (Fig. 3).

The present neuron responded to all types of stimuli and all subtypes of stimuli used. A complete set of stimulus with 3 harmonics produced the largest responses, followed by the f0 only, and then the second harmonic alone. Basically, responses to the complete set and the f0 alone were quite similar but the second harmonic produced simpler ON responses. Responses to the first part of slowly declining FM were almost the same as those to the complete stimulus. Responses to upward FM followed by downward FM, spectrally upside-down and temporally reversed with spectrally upside-down, appeared to be inhibited by responses to downward FM. Late firings after an inhibitory period were observed in responses to upward FM alone, temporally reversed, spectrally upside-down, upward FM alone and noise bursts. Particularly, the upward FM alone condition produced pronounced firings followed by a strong inhibition.

4. Discussion

Recent works on Marmoset showed that responses to species-specific vocalization were stronger than responses to the reversed playback sounds (Wang, 2000; Wang and Kandia, 2001). In the present study neurons in the auditory cortex of Mongolian gerbils showed totally different responses to the ordinary and reversed playbacks. Data indicate direction sensitivities and combination sensitivities in the auditory cortex of Mongolian gerbils. Previous works on the gerbil and monkey auditory cortical neurons illustrated that single neurons respond to different frequencies with totally different temporal firing patterns (Riquimaroux et al., 1994, Sumida and Riquimaroux, 2002). These data strongly support the present findings.
Fig. 2. Synthesized calls, tone bursts and noise burst used in the experiment. A: ordinary call, B: ordinary fall, C: ordinary rise, D: temporally reversed, E: spectrally upside-down, F: reversed and upside-down, G: tone burst, H: noise burst (2–19 kHz). a: three harmonics, b: fundamental frequency alone, c: second harmonic alone. For tone bursts, three fundamental frequencies were used (4, 5, and 6 kHz).
5. Summary

Data indicate that the f0 appears to be important. Responses to the ordinary stimulus (A-a) resembled to those to downward FM or the first part of f0 (B-b). So, the essential portion of the ordinary stimulus is the first part of f0. When the temporal order of the ordinary stimulus was reversed, the response appeared to be squeezed but fundamentally similar to the response to the ordinary stimulus. When we used the temporally reversed with spectrally upside-down stimulus, the temporal order of responses to the ordinary stimulus was switched.

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7. References


