AUDITORY PERCEPTION OF LEARNED VOCALIZATIONS IN BENGALESE FINCHES: DISCREPANCY BETWEEN BEHAVIORAL AND PHYSIOLOGICAL MEASURES

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ABSTRACT

Auditory neurons in the songbird central vocal control system responds preferentially to the learned song, suggesting special perceptual process for the birds' own song. The Bengalese finch is a species of songbirds that sings complex song. We prepared modified songs as stimuli and compared the results of electrophysiological experiments and operant discrimination tasks. Response properties of the HVc neurons describe only small part of auditory perception. To understand the perception at the level of individual would require an integration of physiological data recorded from several sites of the auditory vocal system.

INTRODUCTION

Male songbirds sing songs to defend territory and to attract females [1]. The song consists of hierarchically organized sound elements. These complex, ordered motor programs are controlled mainly by the following three telencephalic nuclei: the HVc, RA, and the NIf. From lesion experiments and electro-physiological experiments in these nuclei, the functions of these have been speculated. RA encodes each song note, HVc then controls the temporal sequences of the song notes, and NIf produces the higher pattern of song notes sequences [2].

Previous neurophysiological studies have shown that neurons in these nuclei selectively

respond to the bird's own song (BOS). In zebra finch (*Taeniopygia guttata*) neurons in HVc responded only to the correct temporal order of the bird's own song [3, 4], but whether or not this selectivity at neuronal level is related with song perception of individual birds.

In this study, we collected the holistic neural activity in the HVc of six Bengalese finches in response to self-produced or conspecific songs edited in several ways. Furthermore, we trained additional birds in an operant task to discriminate between forward and reversed songs and tested their perception of edited songs. We thus obtained behavioral and physiological data with an identical set of stimuli.

MATERIALS AND METHODS

Animals, Song Recordings, and Sound Stimuli

In total, fourteen adult male Bengalese finches, six of which for electrophysiological experiment and eight of them for behavioral experiment, were used. For the analysis of song transition patterns, ten to twenty song bouts were collected for each individual bird. Sonagrams were obtained by a sound analyses software (Avisoft SAS Lab. Version 3.0). Song notes were classified into several categories based on spectro-temporal patterns. Each song note category was encoded with different alphabet, and the song was expressed as a string of alphabets.

For behavioral and electrophysiological experiments, each bird was presented with five sound stimuli, 1) forward song of their own song (BOS), 2) reversed song (REV), 3) each song element reversed, but the order of song elements retained (local-reversed song, abbreviated as LREV), 4) order of song elements reversed, but the local feature of the element retained (order-reversed song, abbreviated as OREV), and 5) a conspecific song (CON). The duration of each song stimuli was about 2.8 sec. This generally included two main phrases. By using these song stimuli, we could ask whether birds were paying attention to the local features of each song element or the global features of spectro-temporal compositions of self- or other- produced songs.

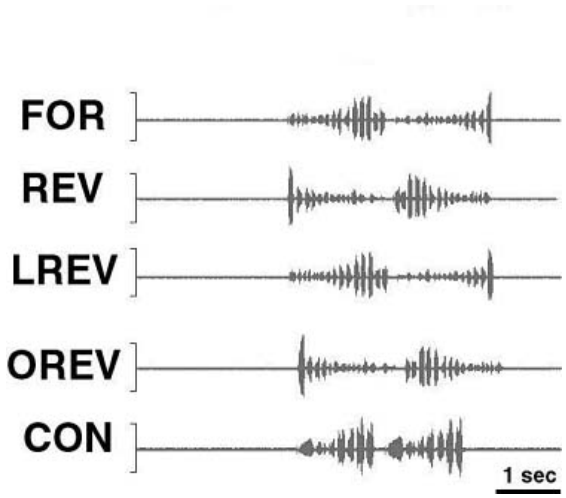

Fig. 1. Song stimuli used in this experiment.

FOR: Forward, bird's own song. REV: Reversal of his own song. LREV: Each song note was locally reversed but global position of each song note was retained. OREV: The global order of the song note was reversed but each note retained its phonological features. CON: Conspecific songs.

Electrophysiological Experiment

Recording experiments were carried out under a neuroleptic anesthesia while the bird was held by a head post to the stereotaxic apparatus. In a recording session, the bird was presented with the above five song stimuli. Since each song stimulus was presented 20 times in a random order, 100 trials per one recording site were conducted. The duration of inter trail interval was 5 sec. The obtained digitized waveform data were rectified and the spike number per 20 msec bins for each song stimulus was counted.

The handling of the spike count data was referenced with the data analysis methods used by Volman [5]. Specifically, we adopted the "relative response index" to investigate the selectivity response toward BOS at each recording site. In this study, we also calculated the two types of the relative response index. The first index was referred to as "relative response percentage" (RRP) which was expressed as percentage figures by dividing the number of the spike count rate for each song stimulus by the sum of spike count rate for all 5-song stimuli. The second index was referred to " selectivity index" (*SI*). Song selectivity index was expresses as the selectivity response toward autogenous song.

Behavioral Experiment

Eight adult male Bengalese finches were trained by operant techniques to discriminate between two songs, GO songs and NOGO songs. Four of these were first trained with own songs: forward song (BOS) and reversed song (REV). The remaining four birds were trained with other bird's song (CON) and the reversal of that song (CREV). Upon completing the training, probe stimuli were inserted in addition to GO and NOGO stimuli. Probe stimuli included OREV and LREV of the bird's own song or other bird's song, depending on which stimulus set the bird was trained. After completing one set of testing, the stimulus set was switched, i.e., those birds trained with their own song were now trained with other birds' song and vise versa [6].

RESULTS

Electrophysiology

Multi-unit responses of the HVc neurons were strongest for the BOS stimuli, followed by OREV, CON, LREV, and REV. Features retained in BOS, OREV, and CON were the general phonological structures of Bengalese finch songs, thus HVc neurons preferentially responded those local, phonological features.

However, the degree of selectivity for the OREV stimuli (element order reversed but local phonological features retained) differed among individuals. Birds with higher degree of song syntactical plasticity showed stronger response to the OREV of his own song but birds with stereotyped, fixed song element sequence showed very week response to the OREV. Thus, the HVc neurons of the fixed order song singers were very strict to the order of song elements (Fig. 2).

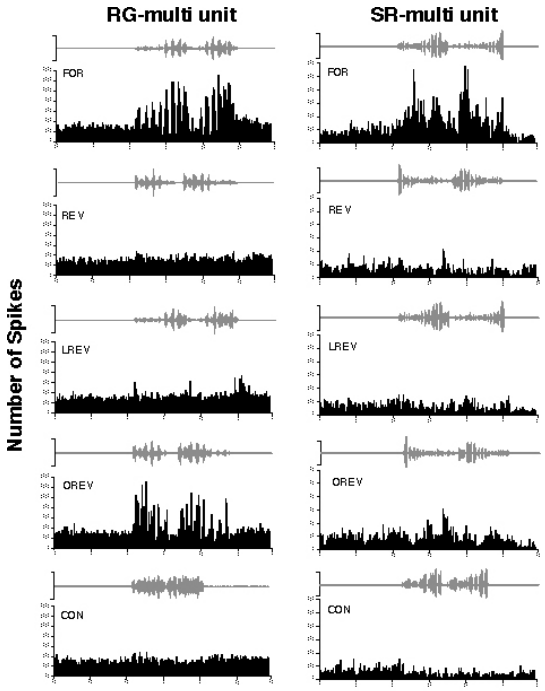

Fig 1. Multi-unit responses of the HVc neurons.

Bird RG sang complex song with multiple possible note-to-note transitions. HVc of this bird responded strongly to the OREV song. Bird SR sang highly stereotyped, simple song. HVc of this bird did not respond to the OREV as much as bird RG, the complex song singer.

Behaviour Response to probe stimuli differed when the bird was trained with his own song and when he was trained by other bird's song. When trained to peck for his own song and not to peck for the reversal of his own song, the bird treated the LREV (locally reversed) song more as his own. When trained with other bird's song, however, the bird pecked more for the OREV (order reversed) song (Fig. 3).

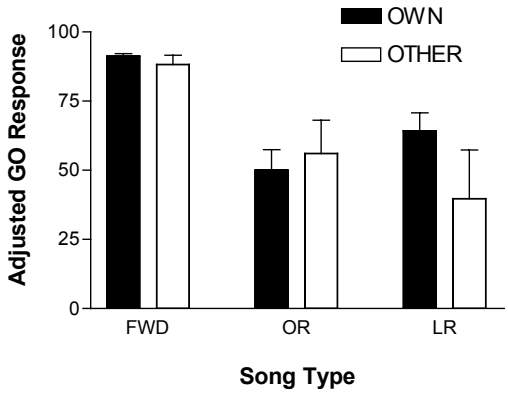

Fig. 3 Response to probe stimuli.

OWN: Bird's own song, OTHER: Other bird's song. When trained with own song, the bird treated LREV song more as his own song than OREV song, but when trained with other bird's song, this tendency reversed.

DISCUSSION

In a previous study, Lewicki and Arthur [4] presented the song stimuli that were edited in similar fashion as in this study to the zebra finches to investigate the selectivity properties of the HVc neurons. Their results showed that some HVc neurons responded to OREV as well as to BOS. Temporal combination sensitive neurons were found in the zebra finch HVc nucleus [3,4] that responded only to the correct order song note sequences. Our results are unique in that we described personalized auditory selectivity.

In our study, the individuals with the higher song stereotypy may include the same neural properties as in the zebra finches. On the other hand, it is possible that the individuals with lower song stereotypy might involve different mechanisms. One possibility is that these individuals have only small numbers of combination sensitive neurons in the HVc and responses occurred to each isolated song note. Another possibility is such individuals might have many kinds of combination selective neurons.

Individual bird responded differently from the HVc neurons. Birds treated LREV song more like his own song, but regarded OREV song more like other bird's song. This response tendency could be interpreted as that birds paid much attention to global feature (i.e., syntax and envelope) of the song when listening to his own song, but paid more attention to the local features, such as the directions of frequency modulation when listening to other birds' song.

This context dependency was not detected in the electrophysiological experiment. Basically, the HVc neurons responded preferentially to the bird's own song and not at all to the LREV song that was regarded to being similar by behaving birds. The OREV song was treated being similar to his own song by complex song singers but not so by simple song singers. Such behavioral difference was not observed in the operant experiment.

ACKNOWLEDGEMENT

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