Fractal-like neural representation in the songbird forebrain

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Abstract– Song of birds is excellent model of human language in terms of syntactical property, especially in Bengalese finches whose song obey finite state grammar. In the present paper, we executed an electrophysiological experiment to clear the neural representation of song element sequence in forebrain nucleus HVc. The results show that most of neurons in HVc responded not only the sequence included in their own song but also the sequence not included. Thus, Each neuron have each response distribution toward the whole element sequence. From this result, we think that many neurons with different response distribution to each sequence represent whole song sequence as a neural ensemble, that is, population coding of song element sequence. From the dynamical systems point of view, this sequence representation in HVc of songbirds might have fractallike structure with hierarchical structure.

1. Introduction

Dynamics of neural activity has been considered as a key to understand the information processing in the brain. One of most complex behavior in animals is observed in songbirds. Their songs are composed of various song elements which have typical frequency modulation, and each element aligned in own sequential rule. Especially in Bengalese finches (*Lonchura striata var. domestica*), the sequential rule obeys finite state grammar [3], and it is focused what neural mechanism enables such a complex sequential rule. In order to learn and maintain their own song, they have auditory neural representation of their own song in the forebrain area HVc. Although there are neurons selectively respond to a typical element sequence included in their own song [4,5], it is

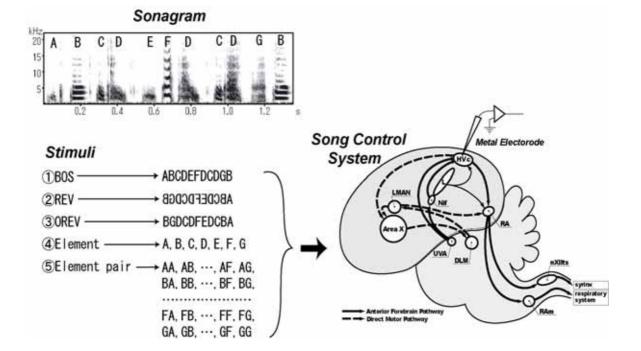


Figure 1: A sonagaram of a Bengalese finch's song, list of auditory stimuli, and HVc in the song control system.

known that such a neuron is hardly founded because of their rarity. From a theoretical point of view [1,2,6], it is more natural that the state of many neurons in HVc represent the sequential information as a fractal-like structure. In the present paper, we executed an electrophysiological experiment, and record the activities of HVc neurons driven by song element pair stimuli.

2. Materials and Methods

Five adult male Bengalese finches were prepared for this experiment. The birds were at least one year old at the time of the experiment, and weighed 12.6-18.5g.

Undirected songs were recorded in a quiet soundproof room using a condenser microphone connected to a digital audio tape recorder with a sampling rate 44.1kHz with 16-bit resolution. A birdsong consists of a series of discrete sound elements with silent intervals. Song elements were divided into distinct types by visual inspection of spectro-temporal structure of each sonagram. Each type of song elements was encoded using different letters and a song was expressed as a string of letters. (See the left upper panel of Fig. 1)

In this experiment, each bird was presented with five sound stimuli: 1) a forward recording of their own song (BOS; Bird's Own Song), 2) a reversed song (REV), 3) a modified song in which the song the order of the song elements was reversed, but the spectro-temporal composition of each song element was retained (OREV), 4) each single element (Element), 5) all element pair we can make from the elements of song (Element pair). Left bottom description shows a schematic diagram of these stimuli. These auditory stimuli were modified by the sound analysis software SAS Lab (Avisoft, Germany) and Matlab (Mathworks, USA).

Before the electrophysiological recording session, birds were anesthetized with 10% urethane 0.04ml each, 4 doses at 30min intervals to attach a head post made of dental cement. Then, we fix the bird to the sereotaxic device (David Kopf, USA). The setting was placed in a magnetic-shielded sound-proof chamber. A hydraulic micro positioner (David Kopf, USA) was used to lower a parylene-coated tungsten electrode (A-M Systems, USA, Impedance 2-5M) through a small opening just above the nucleus HVc (see right panel of Fig.1).

In a recording session, the birds were presented with the five song stimuli at a peak sound pressure of 70dB. Each song stimulus was presented 20 times in a random order with an interstimulus interval of 3-5s. Both the single-unit response data and the sound stimulus data were recorded simultaneously as digitized data using the analysis software Spike2 (Cambridge Electronic Design, UK). The signals from the electrode were amplified (gain10,000) and filtered (100Hz to 10kHz bandpass) using an extracellular recording amplifier (Cygnus Technology, USA) digitized at 20kHz with 16-bit resolution by Micro1401 (Cambridge Electronic Design), and save on a computer disk for off-line analyses.

Data were analyzed off-line using spike-sorting software Spike2 (Cambridge Electronic Design, UK). Extracellular wave forms were detected, and sorted to remove non-spiking noises using the template matching procedure. The obtained data were rectified and the spike number per 5ms bin was counted for each song stimulus. Peri-stimulus time histograms (PSTHs) were produced for each stimulus from 20 trials.

After the final recording session, electric lesions were made to mark the position of the electrode in each bird $1\mu A$ (DC for 10s). The birds were then deeply anesthetized with an overdose of sodium pentobarbital and perfused through the heart with saline, followed by 4% formaldehyde to fix the brain. The brains were cut into 50 μ m sections and stained with cresyl violet. These stained sections were used to localize the recording sites.

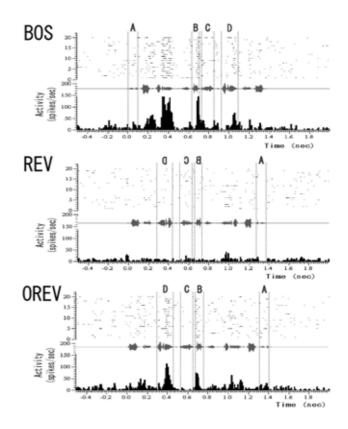


Figure 2: A typical example of neural activities responding to BOS, REV, and OREV.

3. Results

Figure 2 shows an typical example of a neuron in the nucleus HVc. Each panel shows raster plot and PSTHs for BOS, REV, and OREV with the oscillogram of the stimuli. The neural activity for BOS is greater than that for REV. Thus, the activity is affected by the time

modulation of the song. The activity for BOS differ from that for OREV. This result shows that the activity is affected by the sequence of song elements.

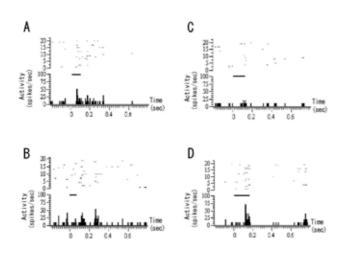


Figure 3: A typical example of neural activities responding to each single element A, B, C, and D.

Figure 3 shows the neural activities responding to each single element A, B, C, and D, while Fig. 4 shows the response to each song element pair AA, AB, AC, ..., DB, DC, DD. Two solid lines show the duration of first element and that of second element. Let us focus on the responses in the second duration because it is the response toward the element sequence. This neuron responds not only to the song element pair contained in BOS (See solid squares in Fig. 4), but also to the pair not contained (See dotted squares as same). This type of neural response was recorded in 4 neurons out of 8 neurons of 5 birds. The results imply that neurons in HVc have individual response distribution to each song element sequence.

4. Discussion

We recorded the neural activity of HVc in Bengalese finches with all element pair stimuli. The results show that each neuron has own response distribution to the sequence of song element, and there are various response distribution in same individual. This result implies that an ensemble of many neurons with various response distribution represent the sequence of song element as

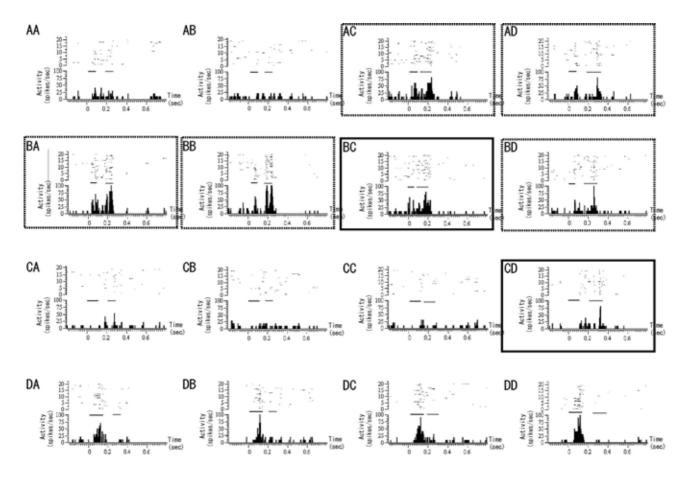


Figure 4: A typical example of neural activities responding to whole element sequences. Dotted squares show the case of same sequences to BOS, while dotted squares show the case of not contained sequence in BOS.

population coding. Figure 5 shows a schematic diagram of this idea. We think that this representation may affect the song grammar of songbirds.

We are planning to execute multi-unit recording with same stimuli, and it may be revealed to show the self similarity of fractal-like internal representation in HVC of songbirds.

Population Coding in HVC

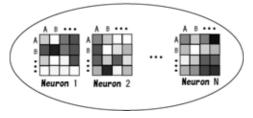


Figure 5: A schematic diagram of population coding for song element sequence in HVc.

Acknowledgments

This work was supported by a grant from PRESTO, Japan Science and Technology Agency (JST) and by a Grant in aid for Scientific Research # 16011208.

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