# 鳴禽類におけるシンタックス構造の神経内コード様式

# Neural coding of syntactic structure in learned vocalizations in songbirds

藤本 久貴 (Hisataka Fujimoto), 渡邉 大 (Dai Watanabe)

京都大学・医・生体情報 (Department of Biological Sciences, Faculty of Medicine, Kyoto, Japan)

脳PRO NEUROSCIENCE 2011

## Abstract

As a fundamental interface for communication, vocal signals convey information in their acoustic and sequence patterns. While vocal signals, including human languages, are composed of a finite set of acoustic elements, syntactic rules expand the diversity of sequence patterns. To enable such syntactic vocal communication, neural systems must extract the sequence patterns from auditory information and establish syntactic rules to generate motor commands for vocal organs. However, the neural processing of syntax for learned vocal signals remains largely unknown. We found that the basal ganglia projecting premotor neurons ($HVC_X$ neurons) in Bengalese finches represent syntactic rules. These songbirds assemble a fixed number of vocal elements called syllables based upon a finite-state type of syntax, which defines "alternative transitions" to or from syllables. When vocalizing such an alternative transition segment between different syllables, activities of $HVC_X$ neurons represent a specific syllable type and a specific transition direction among the alternative trajectories. When vocalizing a variable repetition sequence of the same syllable, $HVC_X$ neurons signal the initiation and termination of the repetition sequence and the progress and state-of-completeness of the repetition, in addition to the identity of repeated syllables. These different types of syntactic information are frequently integrated within the activity of single $HVC_X$ neurons, suggesting that syntactic attributes of the individual $HVC_X$ neurons are not determined as a basic cellular subtype in advance but acquired in the course of vocal learning and maturation. Furthermore, some auditory-vocal mirroring type $HVC_X$ neurons display transition selectivity in the auditory phase just as they do in the vocal phase, suggesting that these songbirds may extract syntactic rules from auditory experience and apply them to form their own vocal behaviors.

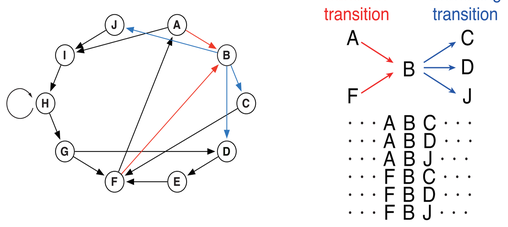
## Background

In human languages, complex vocal patterns can be created from combinations of acoustic elements, linked together by syntactic rules.

Human acquire language through imitative learning.

However, the neural basis of syntactic processing of learned vocal signals remains largely unknown.

Bengalese finches establish variable songs through imitative learning, and assemble a fixed number of vocal elements called syllables into variable sequences.

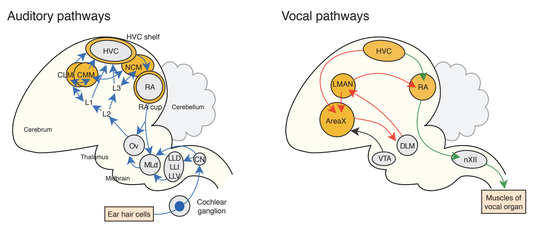



Alternative transitions between syllables generate song variations.

In the songbird brain, telencephalic premotor nucleus HVC functions in both sensory and motor processing of songs.

A subpopulation of basal ganglia projecting HVC neurons ($HVC_X$ neurons) exhibits both motor-related activity and auditory response to the individual bird' s own song (BOS) playback (Prather et al., 2008), suggesting that $HVC_X$ neurons function as a primary sensorimotor integration site for vocal signals.

To explore the neural representation of syntax, we focused on $HVC_X$ neurons.




HVC is involved in both auditory and vocal pathway.

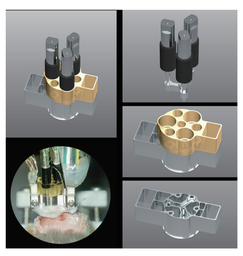
## Methods

9 adult male Bengalese finches and zebra finches were used.

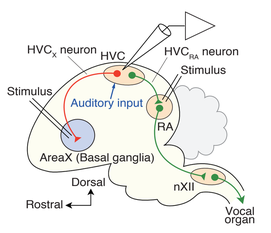
A motorized microdrive were implanted into HVC and stimulus electrodes were implanted into Area X and RA.

The microdrive system included three motorized positioners and a headstage preamplifier.

Electrophysiological recordings from $HVC_X$ neurons were performed during singing, and during hearing auditory stimuli including BOS.

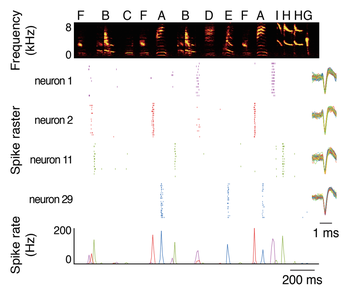


Microdrive system for chronic neural recording in freely behaving animal.

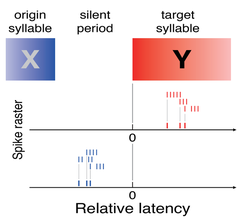



Single-unit recordings were made in HVC. $HVC_X$ neurons were identified by antidromic stimulation in area X and RA.

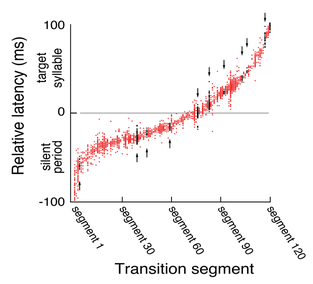
## Results




Activity of 4 $HVC_X$ neurons recorded from one bird.

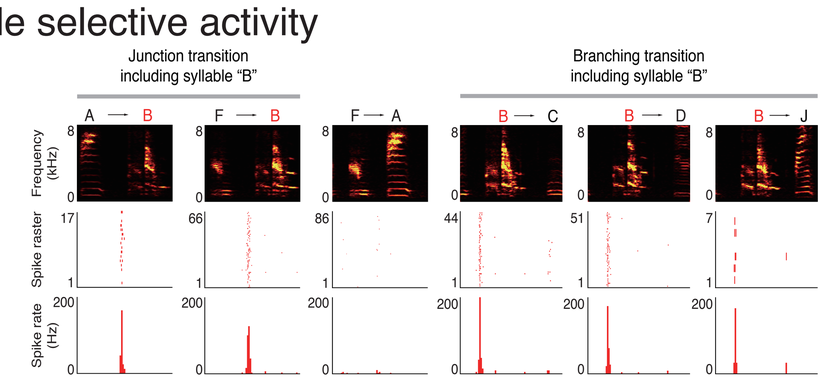



The relative latency of a burst event was measured from the onset of the target syllable (Y) to the onset of the burst.



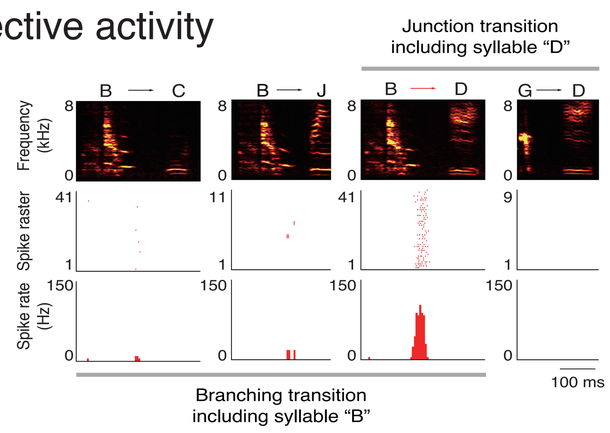

The relative latencies of bursts to target syllable.

### Syllable selective activity



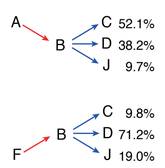

This neuron preserved the identical spike pattern with the same relative latency to the onset of syllable B independently of the adjacent syllable types.

### Transition selective activity

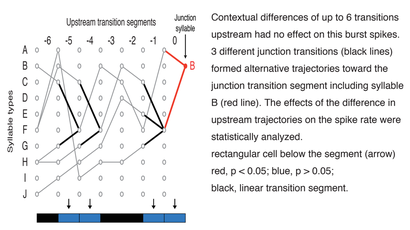



This neuron displayed burst spikes only while taking the trajectory from syllable B to D.

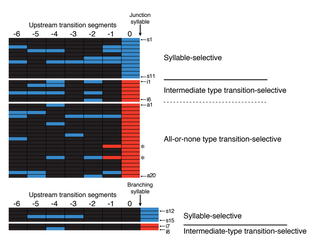
### Selectivity from distant syllable




The probability distribution of syllable transitions is altered depending on the sequence history.




Contextual differences of up to 6 transitions upstream had no effect on this burst spikes. 3 different junction transitions (black lines) formed alternative trajectories toward the junction transition segment including syllable B (red line). The effects of the difference in upstream trajectories on the spike rate were statistically analyzed.
rectangular cell below the segment (arrow)
red, $p < 0.05$; blue, $p > 0.05$;
black, linear transition segment.

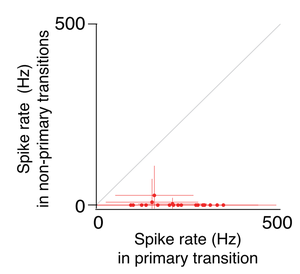



Alternative paths in remote segments had no effect on the firing properties.

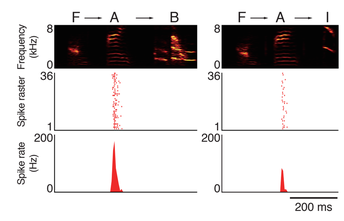
## Abstract

As a fundamental interface for communication, vocal signals convey information in their acoustic and sequence patterns. While vocal signals, including human languages, are composed of a finite set of acoustic elements, syntactic rules expand the diversity of sequence patterns. To enable such syntactic vocal communication, neural systems must extract the sequence patterns from auditory information and establish syntactic rules to generate motor commands for vocal organs. However, the neural processing of syntax for learned vocal signals remains largely unknown. We found that the basal ganglia projecting premotor neurons ($HVC_X$ neurons) in Bengalese finches represent syntactic rules. These songbirds assemble a fixed number of vocal elements called syllables based upon a finite-state type of syntax, which defines "alternative transitions" to or from syllables. When vocalizing such an alternative transition segment between different syllables, activities of $HVC_X$ neurons represent a specific syllable type and a specific transition direction among the alternative trajectories. When vocalizing a variable repetition sequence of the same syllable, $HVC_X$ neurons signal the initiation and termination of the repetition sequence and the progress and state-of-completeness of the repetition, in addition to the identity of repeated syllables. These different types of syntactic information are frequently integrated within the activity of single $HVC_X$ neurons, suggesting that syntactic attributes of the individual $HVC_X$ neurons are not determined as a basic cellular subtype in advance but acquired in the course of vocal learning and maturation. Furthermore, some auditory-vocal mirroring type $HVC_X$ neurons display transition selectivity in the auditory phase just as they do in the vocal phase, suggesting that these songbirds may extract syntactic rules from auditory experience and apply them to form their own vocal behaviors.

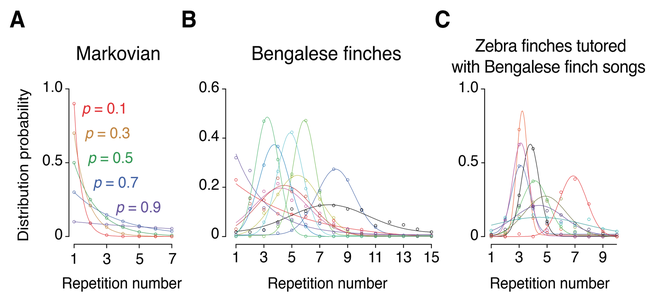
### All-or-non type transition selectivity




### Intermediate type transition selectivity




## Transition dynamics in syllable repetition



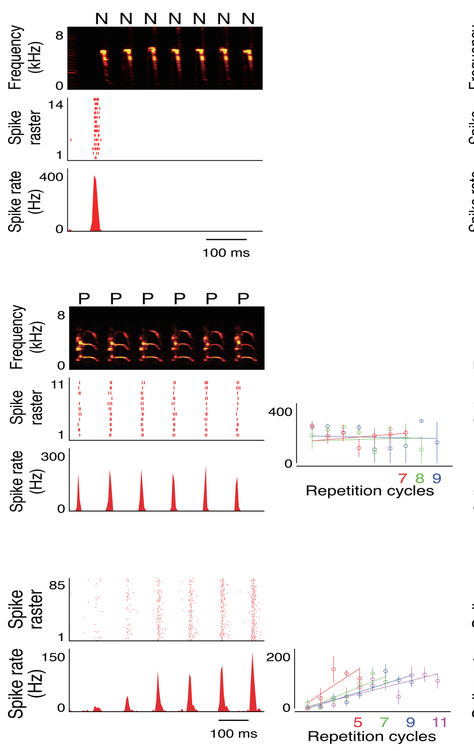

Non-Markovian transition dynamics in consecutive repetition.

A, Theoretical probability distribution expected for a random process, in which transition probability between the same syllable is constant with a value of p.

B, Actual probability distribution of syllable repeats in Bengalese finches (n = 11 syllables from 8 birds).

C, Probability distribution of syllable repeats in 9 zebra finches that successfully learned the repetitive phrases of a Bengalese finch song.

## Syntax-related activity in syllable repetition

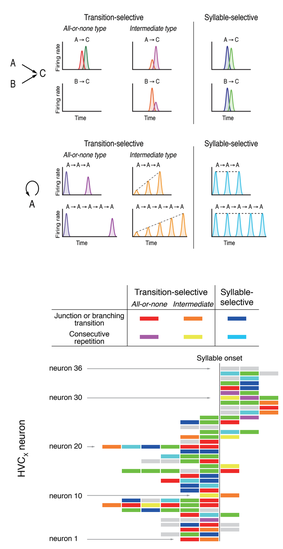



These neurons signal the initiation or termination of the syllable repetition.

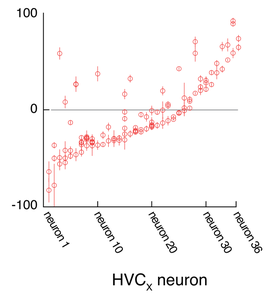
These neurons encode the type of syllable.

These neurons encode progress and state-of-completeness of variable repetition.

## Selectivity are intermingled, but have similar temporal structure in single neuron

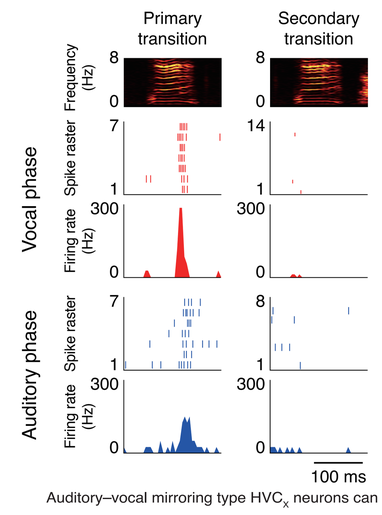



$HVC_X$ neurons cannot be classified from their functional relationship to syntax.




$HVC_X$ neuron generated bursts at a similar latency to syllables with different phonological profiles.

## Syntax-related sensory-motor corespondence




Auditory–vocal mirroring type $HVC_X$ neurons can display transition selectivity in response to the auditory presentation of syntacticsong sequences, just as they do in the vocal phase.

## Conclusion

1. Basal ganglia projecting premotor neurons ($HVC_X$ neurons) represent syntactic rules.
2. Different types of syntactic information are integrated within single neurons.
3. Auditory–vocal mirroring type $HVC_X$ neurons display transition selectivity also in the auditory phase.

## References

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