The Bengalese Finch

A Window on the Behavioral Neurobiology of Birdsong Syntax

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ABSTRACT: The Bengalese finch \textit{Lonchura striata} var. \textit{domestica} is a domesticated strain of a wild species, the white-rumped munia \textit{Lonchura striata} of Southeast Asia. Bengalese finches have been domesticated in Japan for 240 years. Comparing their song syntax with that of their wild ancestors, we found that the domesticated strain has highly complex, conspicuous songs with finite-state syntax, while the wild ancestor sang very stereotyped linear songs. To examine the functional utility of the song complexity, we compared serum levels of estradiol and measured the amount of nesting materials carried into the nest by female birds that were stimulated with either the complex “domesticated” song or the simple wild-type song. In the females stimulated with complex songs the estradiol levels were significantly higher and the amount of nesting material carried was significantly greater. We then performed brain lesions in the song system to identify the neural substrates that are responsible for these differences in song behavior. In Bengalese finches lesions of NIf, a higher order song control nucleus, resulted in simplification of the complex song syntax. That is, the complex “domesticated” syntax changed into the simple wild-type syntax. Based on these data, we hypothesize that mutations in the song control nuclei have occurred that enabled complex song syntax and became fixed into the population of domesticated Bengalese finches through a process of indirect sexual selection.

KEYWORDS: estrildid finches; domestication: song complexity; finite-state syntax; female choice; neuro-ecology

INTRODUCTION: BIRDSONG AND FOUR QUESTIONS

Tinbergen’s four questions\textsuperscript{1} define the ideal aims of classical ethology. He pointed out that when studying behavior, we should ask questions from mechanistic, developmental, functional, and evolutionary viewpoints. However, as ethological study advanced, the four questions were divided into two major areas of inquiry, namely,
neuroethology and behavioral ecology. One consequence of this trend has been the neglect of important questions about the relationship between ecological adaptation and associated changes in the central nervous system. However, the study of birdsong has made a more integrative approach possible, simultaneously addressing proximate and ultimate causes of behavior. Here we present an example of such integration.

**SEQUENTIAL AND SYNTACTICAL CONTROLS**

Birdsong has been regarded as a biological model of human language, especially because of the similarity in developmental processes. Birdsong shares another exciting aspect with human language: its syntactical organization. Human language is an hierarchically organized syntactical behavior. Phonemes are formed into a word, words into a sentence, and sentences into a speech. When each word is integrated into a sentence, a mental grammar combines them into a syntactical organization. By this combinatory action, a finite word set can generate an infinite number of meanings. Such combinatory productivity of new meanings is lacking in birdsong: birdsong functions in mate attraction and/or territorial defense, but changing the order of song notes does not change the meaning.

Syntactical control of birdsong should nevertheless provide important insights into neural control of syntactical behavior and the evolutionary emergence of syntax. However, most studies dealing with birdsong syntax actually deal with sequential control of song elements. Sequential control is a part of syntactical control, but it lacks the interesting feature of syntax, namely, the rule-based production of new sequences. I suggest that Bengalese finch songs can provide a new perspective on the study of birdsong.

We may divide birdsongs into two types. When one song note is followed by another song note in deterministic fashion in a single song, or the order of song notes are fixed in each song of a multirepertoire bird, such songs may be identified as "linear" song. The most widely used oscine song system models (the zebra finch, white-crowned sparrow, song sparrow, and swamp sparrow) could all be identified as having linear song syntax. When there are some variations introduced in the ordering of song notes, such a song should be called as a non-deterministic song. Species with non-deterministic song repertoires include the nightingale, starling, willow warbler, and Bengalese finch.

Among these species, Bengalese finches are unique in that their songs are characterized by finite-state syntax. Finite-state syntax refers to a simple form of syntax in which finite numbers of state are interconnected by arrows and a string of letters is produced when state transition occurs. In Bengalese finches, 2 to 5 song notes are chunked together, each of these chunks are emitted at a particular state transition, and the pattern of chunk production follows finite-state syntax. More simply, finite-state syntax can be expressed as a Markov model of note-to-note transitions, in which transition probabilities of certain combinations of notes are high, while that between some note and others are low, reflecting chunking, recursive loop, and complex state transitions of the song production. Given such complexity Bengalese finch song may be useful to answer questions about both proximate and ultimate aspects of behavior.
PROXIMATE AND ULTIMATE VALUE OF BENGALESE FINCH SONG SYNTAX

On the proximate side, we have found that Bengalese finches are critically dependent on auditory input for real-time control of songs and show complex finite-state syntax in their singing patterns. Furthermore, Bengalese finches adjust sound pressure level of ongoing singing to the background noise level. When exposed to helium air that changes the velocity of sound and alters resonating property of vocal apparatus, Bengalese finches change finite-state syntax during and after such treatment. These data suggest that Bengalese finches are actively listening their own vocalizations while singing and branching patterns of finite-state syntax is also con-
trolled by the real-time auditory feedback. Bengalese finches are therefore of interest as a model system in which to study neural mechanisms of feedback control. On the ultimate side, behavioral comparisons between Bengalese finches and white-rumped munias (Fig. 1) are of interest because this bird, considered to be the ancestor of Bengalese finches, sings linear songs without finite-state syntax. White-rumped munia of southeast Asia were imported to Japan 240 years ago and then domesticated in Japan. Several factors might have affected the song syntax of white-rumped munias under natural conditions and under the domesticated environment. Thus, from such comparisons we hope to define evolutionary forces that transformed linear syntax into finite-state syntax. We pursued this aim in a series of field and laboratory studies.

NEURO-ECOLOGY OF BIRDSONG SYNTAX

We first made field observations of white-rumped munias and found that contact calls of white-rumped munias were the same as those of Bengalese finches. We then imported some white-rumped munias to Japan and began comparing their songs with those of Bengalese finches. Recently, by using molecular techniques, we have established that the white-rumped munia and the Bengalese finch are indeed the same species (Yodogawa and colleagues, unpublished data). Through these studies, we hoped that the comparison between wild and domesticated strains might reveal a process of behavioral evolution that is also tractable from a neuroethological perspective. It may provide us with a unique opportunity for truly fruitful “neuro-ecology.”

The results of our laboratory studies are summarized below. First, we compared syntactical complexity in domesticated and wild strains of white-rumped munias. Next, we showed that song complexity is an important parameter for females when selecting a potential mate. Finally, we used a lesion study to implicate a higher-order song control nucleus in the generation of song complexity in Bengalese finches.

EXPERIMENTAL STUDIES

Comparisons of Song Parameters

Bengalese finches Lonchura striata var. domestica are the domesticated strain of the wild white-rumped munia Lonchura striata, a species imported into Japan about 240 years ago, and subsequently domesticated. Japanese aviculturists selected white-rumped munias for their parental abilities and for white mutations, but there are no records in the avicultural literature indicating that Bengalese finches were selected for their songs. Casual interviews with modern aviculturists in Japan and in Europe also supported this notion. It is unlikely that songs of Bengalese finches experienced artificial selection.

To begin asking evolutionary questions about song complexity we first compared song syntax of the white-rumped munia and the Bengalese finch. Figure 2 shows examples of transition diagrams obtained from a white-rumped munia (upper) and a
Bengalese finch song (lower). While the average number of notes used in a song by white-rumped munias and Bengalese finches was not significantly different, the average song linearity, an index of song simplicity, was significantly lower in Bengalese finches (0.33) than in white-rumped munias (0.61). The overall amplitude of songs is also significantly higher for the Bengalese finches. Bengalese finches were singing, on average, 14 dB louder than the white-rumped munias.

Thus, Bengalese finch song has become much louder and much more complex than white-rumped munias during the past 240 years, an interval roughly equivalent to 500 generations for Bengalese finches. We suspect the song characteristics (amplitude and complexity) enhanced in Bengalese finches are both traits that can be a
handicap in the wild. That is, louder song would be easier to be located by predators and elaborated song syntax would require more cognitive cost, which would also result in predation. These possibilities should be tested in the wild. Whether or not the differences between wild and domesticated strains may be attributed to cultural or genetic factors could be clarified by cross-fostering experiments.

Function of Song Complexity

Bengalese finches have been bred under domesticated environment. Under such conditions, sexual selection should only function indirectly, because birds are paired artificially. Although active choice on female’s side might not function directly, indirect female choice will result in reproductive efficiency in the female who was coupled with desirable mate. Since white-rumped munias were selected mainly for their parenting behavior, reproductively efficient pairs might be the pair in which the male was singing a complex syntactical song.

To examine the functional implications of song complexity we manipulated song complexity directly. Song recordings obtained from a male Bengalese finch were analyzed, and four distinctive song phrases were identified. In this bird’s song, these four phrases were organized so that phrases A or B were repeated several times, and phrases C or D followed this repetition, but these phrases were never repeated consecutively. After C or D was sung once, phrases A or B were again repeated. We wrote software that produced either this sequence of song phrases (the complex syntax song), or only repeated phrase B (the simple syntax song). Phrase B included most of the song notes that made up phrases A, C, and D.

Three groups of female Bengalese finches were studied. Each group consisted of four finches, separately caged, and kept together in a sound isolation box. In each cage, one hundred nesting strings were presented every day in a string dispenser. The

FIGURE 3. Median number of strings carried by each of the complex, simple, and control groups.
first group was stimulated with the complex syntax song, the second group with the simple syntax song, and the third group was not stimulated. The levels of serum estradiol adjusted by the level prior to the experiment were compared among the groups and the number of strings carried into the pot nest was counted.

Estradiol level was twice as high in the females stimulated with the complex song, but only minimally higher in the females stimulated with the simple song. The maximum number of strings carried into the nest was significantly higher in the complex song group than in the non-stimulated (control) group and the number of days required to reach the maximum number of strings was also significantly smaller in the complex song group than in the simple song group (Fig. 3). Thus, the complex song was more effective in stimulating female Bengalese finches to come into reproductive condition. Artificial pairing under domesticated environment could result in enhancement of particular male trait through indirect selection. To prove this is in fact the case, we will need to gather evidence from broader measures of reproductive behavior.

**Mechanism of Song Complexity**

What mechanisms make the complex song of Bengalese finches possible? Central and peripheral mechanisms for birdsong production have been well studied. Song is produced by the combined activity of respiratory and syringeal mechanisms, and a resonating apparatus consisting of the trachea, the tongue, and the beak. The neural pathway that directly controls syringeal activity is well described and sometimes called the posterior pathway. The syringeal muscles are directly controlled by the tracheo-syringeal branch of the hypoglossal nerve NXIIIts. This nucleus is innervated both by the telencephalic motor nucleus (RA) and by a mesencephalic motor nucleus, the dorsomedialis (DM). Going upstream, RA is then innervated by the telencephalic sensory/motor integration nucleus (HVC). This nucleus receives auditory input from the primary auditory center, Field L, and from surrounding higher auditory structures. Among them, NIf sends auditory/motor input to HVC.

Since NIf is a higher order nucleus than HVC, we hypothesized that it was mediating a song feature of more complexity—such as organization of the song syntax. However, bilateral lesions of NIf in zebra finches produced no detectable effects, other than some transient deterioration of song structure. It is possible that zebra finch song, which involves a repeated sequence of syllable types in an identical order, might be too simple to display NIf lesion effects. If NIf is in fact governing a higher order aspect of song organization, its function might be evident only in songs with a syntactical organization higher than the level of song phrase.

We therefore repeated NIf lesion studies on Bengalese finch song, which consists of several different phrases organized into variable sequences. The effects proved to be a joint function of song complexity and the bilateral extent of the lesion. Unilateral lesions or those of adjacent structures had no effects on song syntax. Of the three cases of complete bilateral lesion, however, effects upon song were seen only in two birds that were singing complex, multi-phrased songs. In these birds, bilateral NIf lesion eliminated phrase level complexity, reducing the multi-phrased organization of the song to a single phrase (Fig. 4). In the remaining bird, which was singing a simple single-phrase song, there were no effects of bilateral NIf lesions. Thus we conclude that NIf is responsible for phrase-to-phrase transitions.
Moreover, we noticed that the post-operative song of the bilaterally lesioned bird is more like that of a white-rumped munia than a Bengalese finch. Most of the recursive loops and song element repetitions were eliminated by this operation and the syntax was very linear. NIf is thus responsible of the unique feature of Bengalese finch song syntax. Whether white-rumped munias do not have a recursive program in their NIf or they simply did not have such structures in their song culture should be identified in a future research. Ongoing cross-fostering experiments in fact suggest that there may be several syntactical and phonological aspects of Bengalese finch songs that white-rumped munias are not adapted to learn well (Takahashi and Okanoya, unpublished data).

**FIGURE 4.** Changes in song syntax of a Bengalese finch following NIf lesion. Pre-operatively, song had a complex transition pattern as in most Bengalese finches (upper) while post-operative song lost complex transitions (lower). The post-operative song syntax is more similar to that of white-rumped munias. Re-plotted from Hosino and Okanoya.\(^{20}\) Diagrams constructed by third-order Markovian model optimized by a genetic algorithm.

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**GENERAL DISCUSSION**

*Song Complexity and Female Choice*

The most remarkable difference we found between the white-rumped munia and its domesticated strain, the Bengalese finch, is that the domesticated strain sang songs with more complex note-to-note transitions than the wild strain. Previous studies had shown that female Bengalese finches gave more copulation displays to the playback of a six-element song over a four-element song.\(^{40}\) Similarly, female Bengalese finches perch-hopped more often when stimulated with a song with more elements rather than a song with a few elements.\(^{41}\) These results suggested that females might favor more variety in the number of song element types. However, we did not find significant differences in the number of song elements between wild and domes-
tic birds. In the study by Clayton and Prove, the degree of complexity of the stimulus songs in the temporal domain was not reported, as was the case with the study by Nakamura and colleagues. Since these authors were using tape-recorded songs, temporal-domain dynamics were not introduced. Thus until now, how song complexity in the temporal domain might influence female birds in Bengalese finches was not known. Although there are several studies relating “song complexity” and female choice, most of these studies viewed variations in note type as “complexity.”

In our present research, song complexity in Bengalese finches was introduced as dynamic variations in time series rather than variations in note types. We found that in females stimulated with complex song E2 levels were elevated twice as much compared to the basal level and these birds carried more strings to the nest than other groups. Song complexity thus brought females into reproductive condition more quickly (see Nowicki and Searcy, this volume).

**Neural Control of Song Complexity**

We showed that lesions of the higher vocal-auditory integration nucleus NIf disrupted phrase-level variability in those Bengalese finches that sang multistate songs. When the same operation was performed on birds whose song was simpler, we did not find any effects on song syntax. The results on the simpler Bengalese singers are reminiscent of negative results reported by Vu and colleagues on zebra finches. Based on this limited data set, we postulate that NIf may control higher-order or phrase-to-phrase song transition. In addition, NIf-lesioned birds did not change the pattern of note-to-note transitions within their song phrases, suggesting that NIf is responsible only for phrase level transitions and not for note level transitions.

When HVC was partially lesioned in Bengalese finches, there are very small, but reproducible effects on note-to-note transitions within song phrases. Taken together, these observations suggest that NIf may govern phrase-to-phrase (or chunk-to-chunk) transitions while HVC may govern element chunking in Bengalese finch songs. Finite-state syntax in Bengalese finches thus may involve contributions from both NIf and HVC.

**Evolutionary Schema for Finite-State Syntax in Bengalese Finches**

Based on these discussions, we propose the following scenario to explain ultimate and proximate causes of song complexity in Bengalese finches. We assume that there is some rate of mutation occurring in NIf that enables finite-state song syntax in white-rumped munias. However, syntactically complex songs impose a greater cognitive load and singing such songs might increase predation in a natural environment. Upon domestication, however, such mutation is not eliminated from the population because cognitively demanding song would do no harm. Rather, since the females’ perceptual system evolved under such predation pressure, females would prefer song complexity because an individual’s ability to sing a complex song yet survive in a harsh environment would guarantee that individuals with these songs should have a reproductive advantage.

We suggest that a female bias to prefer syntactical complexity led to selection for this mutation in the population of domesticated Bengalese finches. When female preference in a natural environment guides the direction of evolution and then do-
mestication eliminates natural constraints, the directed feature will continued to evolve until certain limits and that is what we see in domesticated Bengalese finches.

CONCLUSION

Obviously, further work is necessary to prove this scenario. One obvious question is the influence of genetic factors in determining song complexity. This should be sorted out by cross-fostering experiments between Bengalese finches and white-rumped munias. A second question is: Why does NIf seem to be critical only in Bengalese finches with complex song syntax? For what functions has NIf evolved in the male songbird brain? Although it is one of the most conspicuous sex-linked brain structures on oscine brain, we know too little about the physiology and anatomy of this nucleus to answer questions about its function. Finally, a more comprehensive analysis of female song preferences in this species should be carried out in a semi-natural environment. Nevertheless, even this brief review suggests that proximate and ultimate analyses of song syntax in Bengalese finches should provide a worthwhile and rewarding task for integrative behavioral neurobiology.

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