International Journal of Comparative Psychology

Title

Behavioural Factors Governing Song Complexity in Bengalese Finches

Journal
International Journal of Comparative Psychology, 25(1)

ISSN
0889-3675

Author
Okanoya, Kazuo

Publication Date
2012

DOI
10.46867/ijcp.2012.25.01.02

International Journal of Comparative Psychology, 2012, 25, 44-59.

Behavioural Factors Governing Song Complexity in Bengalese Finches

Kazuo Okanoya
The University of Tokyo, Japan

Bengalese finches are the domesticated strain of the wild white-rumped munias. Bengalese finches had been domesticated for over 250 years from the wild strain white-rumped munias and during this period the courtship song became phonologically and syntactically complex. The purpose of this study is to understand proximate and ultimate causes for song complexity in Bengalese finches. Field observation of white-rumped munias in Taiwan suggests that populations of munias show a gradient of song syntactical complexity: when the population has more sympatric species, the population showed less syntactical complexity, suggesting that syntactical complexity does not develop under the pressure for species recognition. Laboratory study of cross-fostering between the two strains revealed that white-rumped munias are more specialized in accurately learning own-strain phonology while Bengalese finches learned equally but less accurately learned phonology of both strains suggesting that Bengalese finches lost species-specific bias to accurately learn own phonology. By a nest-building assay, we found that females work more when stimulated with complex songs but not with simple songs. Taken these evidences together, we suggest that phonological and syntactical complexity in Bengalese finch songs evolved first because domestication freed them from pressure for species recognition based on song characteristics and then sexual selection advanced the complexity. This is enabled by longer song learning period in Bengalese finches. Neural and molecular studies also support the notion that Bengalese finches keep more song plasticity as adult. In conclusion, song complexity in Bengalese finches provides a unique opportunity for integrative study of animal communication.

Birdsong is a learned behavior that is culturally transmitted within a set of biological constraints. Birdsong can serve as an important biological model to study interactions between environment and heredity. This study examined the differences between a wild and a domesticated strain of white-rumped munia (*Lonchura striata*) in terms of their songs. The comparison between the two strains revealed evolutionary factors affecting the acoustical and syntactical morphology of species-specific songs.

Wild white-rumped munias were originally imported from Zhapu port in Zhejiang Province, China, to Nagasaki, Japan, by a federal king of the Kyusyu prefecture in 1763 (Washio, 1996). Since that time, they have frequently been imported from China to Japan, particularly during 1804-1829, when aviculture flourished in Japan. The white-rumped munia is generally brown with a white patch on the rump, as its name implies (Restall, 1996). However, in 1856, birds with totally white plumage were distinguished from white-rumped munias and called *Juushimatsu*, society finches. Although these birds were actually imported from China, European aviculturists believed that they came from India, and domesticated white-rumped munias imported from Japan to Europe were referred to as Bengalese finches (Buchan, 1976). In what follows, the Japanese strain of wild white-rumped munias will be referred to as Bengalese finches. Figure 1 presents a photograph of a wild white-rumped munia and a domesticated Bengalese finch along with a drawing of a Bengalese finch during Edo era (ca.

Correspondence regarding this article should be addressed to Kazuo Okanoya, Laboratory for Biolinguistics, RIKEN Brain Science Institute, Saitama, 351-0198, Japan. (okanoya@brain.riken.jp)

1850). The drawing suggests that the Bengalese finches are domesticated strain of the white-rumed munia.

Bengalese finches were domesticated for their reproductive efficiency and their ability to foster other bird species, as well as their plumage (Taka-Tsukasa, 1917). During the approximately 250 years of their domestication, however, song characteristics have changed substantially from those observed in the wild strain, and the purpose of this paper is to discuss the possible behavioral and evolutionary reasons behind these differences.

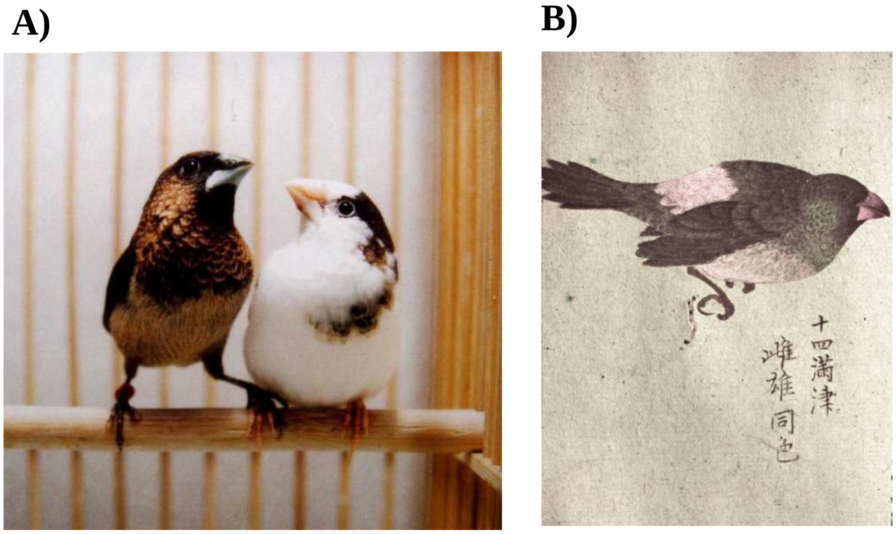

Figure 1. **A)** A white-rumped munia (left) and a Bengalese finch (right). Photo by Maki Ikebuchi. **B)** A drawing of a Bengalese finch during Edo period (ca. 1850). The artist for this drawing is not known.

Song Differences in two Strains

Representative sonograms from a Bengalese finch and a white-rumped munia are shown in Figure 2. Brief inspection of the sonograms suggested that these two songs are very different in acoustical morphology and the order of elements. In general, the songs of the wild strain were noise-like and the notes were ordered simply and in stereotyped fashion, whereas the songs of the domesticated strain were more narrow-banded and had complex note-to-note transition patterns. We initially confirmed these impressions with acoustical analyses of song notes and then by transition analysis of note sequences (Honda & Okanoya, 1999).

Acoustical analyses revealed that the frequency of the maximum amplitude was higher in Bengalese finches than in white-rumped munias, and bandwidths 15dB below the maximum amplitude were wider in white-rumped munias than in Bengalese finches. Furthermore, the sound density (root mean square value of 5 s of continuous singing) was, on average, 14dB higher in Bengalese finches than in white-rumped munias when recordings were made with identical settings. However, no differences in the number of types of song elements were found between Bengalese finches (average 9.3) and white-rumped munias (average 8.4). Thus, Bengalese finch songs were higher pitched, more narrow-banded, and louder than were white-rumped munia songs, but the strains did not differ with regard to repertoire size.

The sequential complexity of the songs was evaluated with the linearity index (Scharff & Nottebohm, 1991), which is the number obtained by dividing the number of unique types of song notes by the number of observed transition patterns from one note type to another. This index is 1.0 (when N is the number of note types, then this will be $N/N = 1$) when the element sequence in the song is always identical, and it will approach 0 ($N/N^2 = 1/N$) when the element sequence is completely random. Results of this analysis showed that the average linearity index was significantly lower, signifying greater complexity, in Bengalese finches (0.33) than in white-rumped munias (0.61). Representative transition diagrams from both strains are shown in Figure 3.

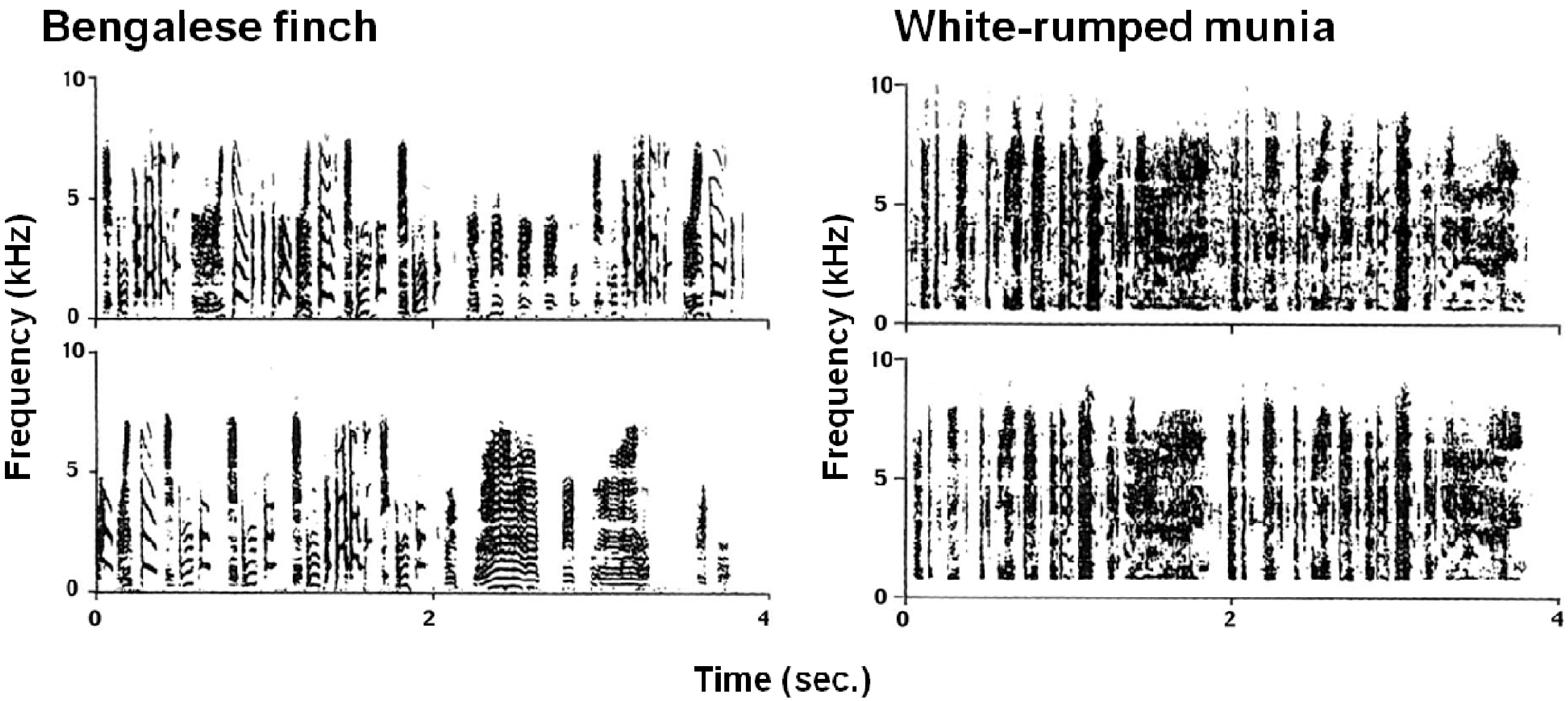

Figure 2. Sonogram of a Bengalese finch song (left) and a white-rumped munia song (right).

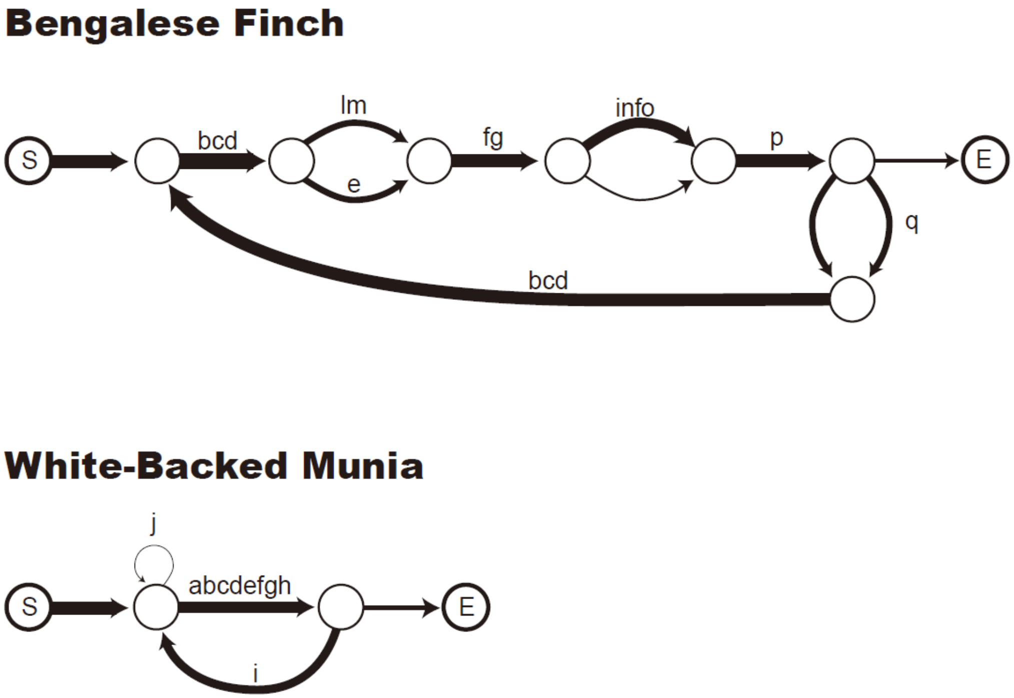

Figure 3. Transition diagram of a Bengalese finch song (upper; linearity = 0.45) and a white-rumped munia song (lower; linearity = 0.81). “S” inidicates the start of the song and “E” indicates the end of the song.

Effect of Domestication: Insight from a Field Study

We assumed that songs were kept simple in wild white-rumped munias because of specific pressures in the wild. Singing loud, complex songs in the wild is costly for at least three reasons. First, such songs may easily attract predators. Second, they draw on cognitive resources necessary for reacting to dangers, including predations. Third, the evolution and maintenance of the brain mechanisms underlying complex songs are costly. We began our fieldwork in Taiwan to examine these hypotheses. However, the observation of predation in the wild is very rare to allow the quantitative assessment of the hypotheses.

We examined the factors that might have accounted for the loss of the innate bias in Bengalese finches with regard to learning songs. One reason for this bias might involve an important function served by songs in the wild. Before a song can function as a mating signal to attract conspecific females, the singer must be identified as conspecific by the female. Toward this end, the song should possess species-specific characteristics. This function as an identifying mechanism might degenerate in a domestic environment because birds are paired by humans in these settings and thus do not need to seek mates on their own.

Several field studies might support this hypothesis. In the wild, white-rumped munias coexist with various sympatric species, including spotted munias (*Lonchura punctulata*). A strong innate bias toward conspecific phonology should be adaptive for species of munia in avoiding futile attempts at hybridization. In contrast, Bengalese finches are domesticated and have been subject to controlled breeding. In such an environment, a species-specific bias would be neutral and might degenerate rapidly, perhaps allowing Bengalese finches to gain a more general ability to learn a wide-ranging phonology.

We have preliminary data on the relationship between the degree of colony mixing (with spotted munia) and song linearity in wild populations of white-rumped munia (Kagawa et al., 2012). When the level of heterogeneity in the colony was higher, songs of white-rumped munia were more linear (Figure 4) and exhibited less variable phonology. This might indicate that when more sympatric birds are present, species of munia must exaggerate their species-specific characteristics in their songs.

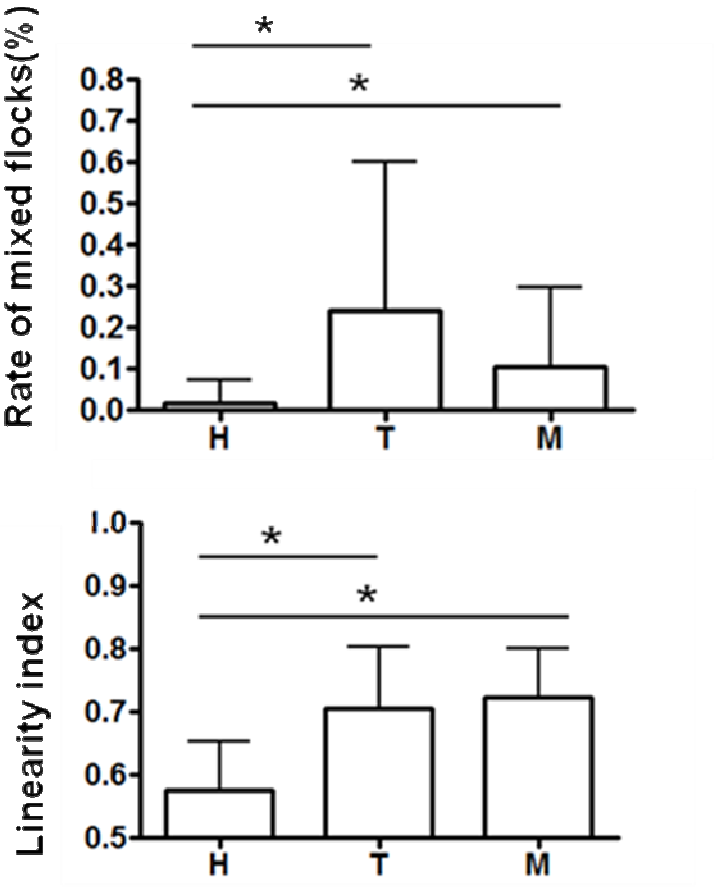

Figure 4. The rate of hetero-specific mixed colonies (upper) corresponds with the song simplicity (lower). H (Huben), T (Taipei), M (Martaian) are the different geographical populations in Taiwan.

Learnability: A Cross-fostering Study

Bengalese finch songs are sequentially and phonologically complex, whereas white-rumped munia songs are simpler. To elucidate the degree to which environmental and genetic factors contributed to these differences in song structure, we cross-fostered white-rumped munia and Bengalese finch chicks. We used seven pairs of Bengalese finches and four pairs of white-rumped munia and exchanged some of the eggs during incubation (Takahasi & Okanoya, 2010). As a result, we obtained seven Bengalese finch-reared male white-rumped munias and seven white-rumped munia-reared male Bengalese finches. For comparison, we also examined 12 normally reared male Bengalese finches and 14 normally reared male white-rumped munias. When the chicks had fully matured, their songs were recorded, and phonological and syntactical comparisons were performed. Inspection of sonograms revealed that munia-fostered Bengalese finches were able to learn most of the songs sung by fostering fathers but Bengalese-fostered munias had some difficulty in learning the songs sung by fostering fathers (Figure 5).

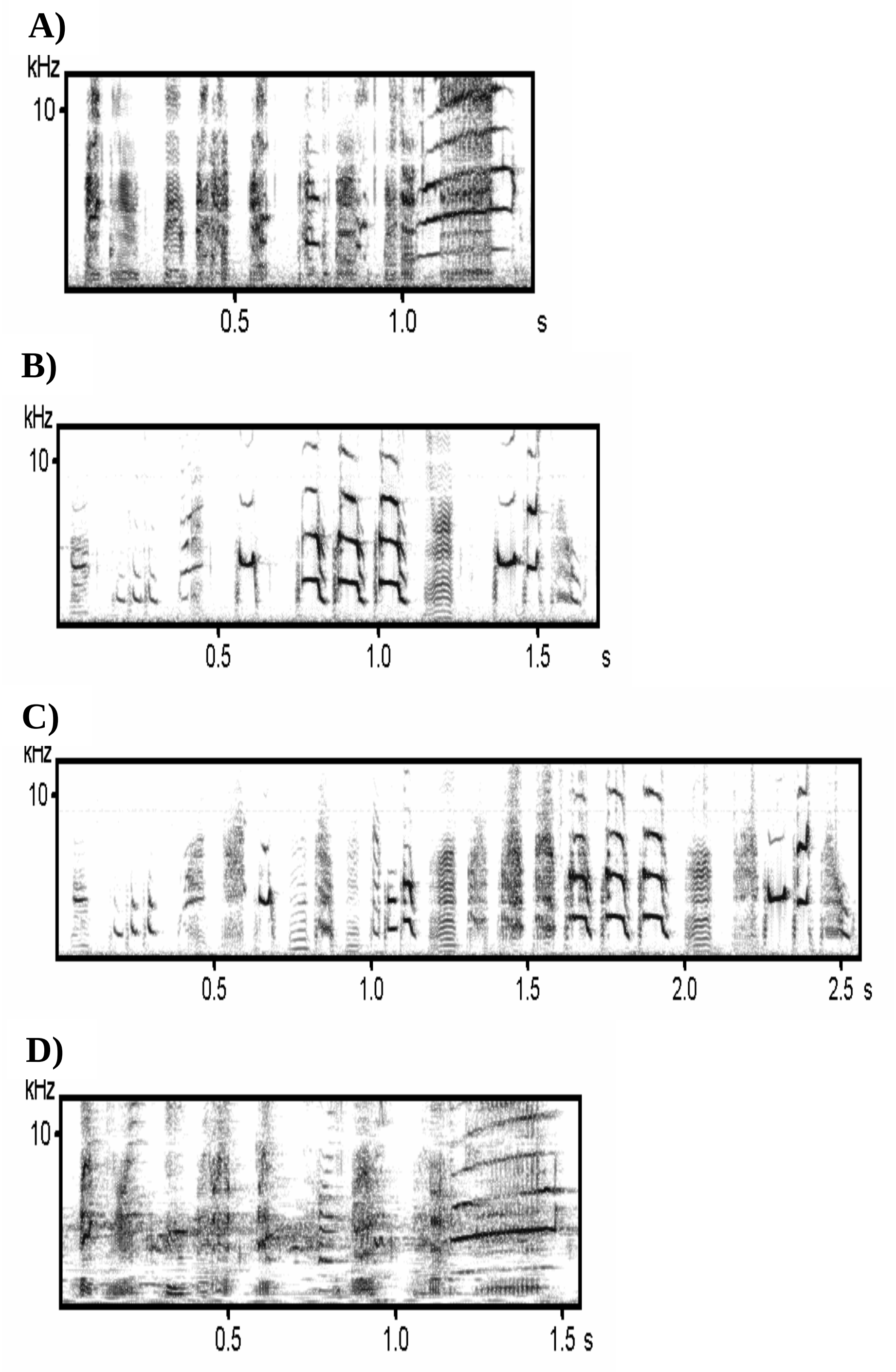

Figure 5. Results of cross-fostering experiment. A munia chick **(B)** fostered by a Bengalese finch father **(A)** did not learn a part of the song, but a Bengalese finch chick **(D)** fostered by a munia father **(C)** had no apparent difficulty learning the song.

Constraints in Phonological Learning

The accuracy of song-note learning was measured as the percentage of song elements shared between the chick and the father. Detailed phonological analyses revealed that the accuracy of song-note learning was highest in white-rumped munia chicks reared by white-rumped munias (98%) and lowest in white-rumped munia chicks cross-fostered by Bengalese finches (82%). In contrast, Bengalese finch chicks exhibited an intermediate degree of learning accuracy, irrespective of whether they were reared by white-rumped munias (92%) or conspecifics (94%). A two-way ANOVA detected a significant interaction between genetic background and rearing environment, indicating that white-rumped munias were sensitive to their rearing environments, whereas Bengalese finches were not ($p < 0.04$). These results suggest that white-rumped munias are highly specialized for learning the phonology of their own songs but are less adaptable to learning the phonology of Bengalese finch songs. In contrast, Bengalese finches are less specialized for learning the phonology of their own strain and more able to generalize their capacities to learn the songs sung by white-rumped munias. These findings suggested an innate bias toward species-specific phonology in white-rumped munias that might have been lost in Bengalese finches during domestication (Takahasi & Okanoya, 2010).

Constraints in Syntax Learning

We used the same data set to test for a learning bias for song syntax. Similarities between the two types of song syntax were evaluated by first expressing the two songs under study as Markovian transition matrices (Takahasi & Okanoya, 2010). In constructing these matrices, we considered the song notes shared by the songs of both tutor and pupil, as well as the song notes in songs sung only by tutors or only by pupils. The correlation coefficient calculated from the nonzero elements of the two matrices was used as an index for syntactical similarity. Using this method, we calculated average similarities between the songs of tutor and pupil in the four cross-fostered groups (Bengalese finches tutored by Bengalese finches, white-rumped munias tutored by white-rumped munias, Bengalese finches tutored by white-rumped munias, and white-rumped munias tutored by Bengalese finches).

Consistent with the results of the phonological learning experiment, the similarity between the songs of tutors and pupils was highest for white-rumped munias tutored by white-rumped munias (0.91) and lowest for white-rumped munias tutored by Bengalese finches (0.70). The similarities of Bengalese finches tutored by Bengalese finches (0.82) or by white-rumped munias (0.75) were intermediate in comparison with the two more extreme cases. Thus, when learning to sequence song elements, white-rumped munias were biased toward learning the linear syntax associated with their own strain and were far less adept at learning the complex syntax associated with Bengalese finches. These results supported our previous conclusion that white-rumped munias might have an innate bias for learning species-specific syntax and that this bias might have disappeared in Bengalese finches during domestication.

Learnability and Brain Plasticity

These behavioral results suggest that Bengalese finches might have a wider range of song learnability than white-rumped munias. Encouraged by this finding, we extended our research into differences in proximate mechanisms.

First, we compared between volumes of the brain nuclei that are considered to be related with song learning and control. Birds were perfused by phosphate-buffered solution containing formaldehyde through the heart after deep anesthesia and brains were post fixed. 40-micro-meter-thick slices were cut and these were stained by Nissle solution. Volume of song control nuclei was measured by a computer-connected microscope system. Since Bengalese and Munias has difference in body weight and overall brain volume, a brain muclei considered to be unrelated with song control, a thalamic relay nucleus was used as reference on which volume of each of the song control nuclei was indicated (Figure 6). Song nuclei are overall larger in Bengalese finches than in white-rumped munias (Takahasi, unpublished data).

We then examined gene-expression profiles on the brain of the two strains. We especially focused on genes that are related with synaptic plasticity including neuro-tropic factors, calcium regulations, and glutamate receptors. Although research is still in progress, we found that overall Bengalese finch brain shows higher degree of plasticity-related gene expressions (Kato & Okanoya, 2010).

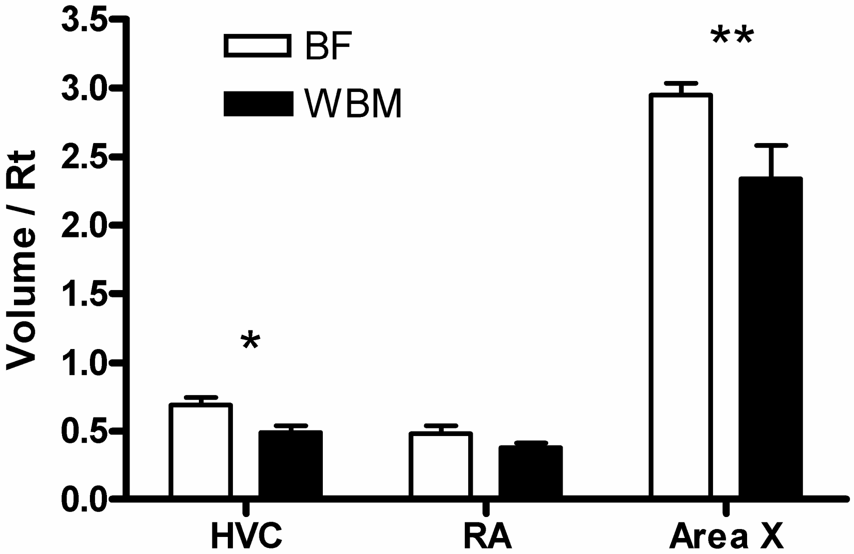

Figure 6. Volumetric comparisons among song control nuclei in Bengalese finches and white-rumped munias. Bengalese has larger song control nuclei than munias. $*p < 0.05$, $**p < 0.01$.

Sexual Selection

What are the functions of song complexity in the Bengalese finch? Although this species is domesticated, we hypothesized that function evolved in part as a result of sexual selection by females (Anderson & Iwasa, 1996; Okanoya, 2002). Because the Japanese avicultural literature does not contain evidence that songs were artificially selected by breeders (Washio, 1996), we assumed that breeders selected only successful pairs and that this indirectly resulted in the selection of good singers. Therefore, we further hypothesized that males and females differed with regard to song perception and that song complexity efficiently stimulated sexual behavior in females. We evaluated the former hypothesis using heart-rate measurements and the latter using several assays that supplemented one another (Searcy, 1992). We first measured the reinforcing properties of a complex song using an operant task involving perch selection. Next, we measured the degree of nest building behavior by female Bengalese finches as a function of stimulus songs. In addition, we measured the serum estradiol levels in females stimulated with complex versus simple songs.

Heart Rate Response to Song Novelty

Birdsong might be assessed and processed differently by each sex because its production and functional use are often sexually dimorphic. However, straightforward examination of this hypothesis has been difficult because different behavioral measures have been used to describe the process of song assessment in the two sexes. We analyzed changes in heart rate as an index of song assessment in the Bengalese finch (Ikebuchi & Okanoya, 2003). In this species, only males sing, and song is used exclusively for mate attraction. Bengalese finches are not territorial, and the songs are not used in aggressive contexts. When a song stimulus was presented for the first time, the heart rate of the study participants increased. The duration of this increase in heart rate was defined as the period in which the heart rate increased by two standard deviations above that measured in the baseline interval, which was 10 s before song presentation. In both sexes, the repeated presentation of one song resulted in a reduction in the heart-rate response. The presentation of heterospecific (zebra finch) songs did not increase the heart rate of Bengalese finches. When a novel conspecific song was presented, the heart rate increased only in female and not in male birds with each presentation of the stimulus. These findings confirmed the differential responses to songs by each sex in this species: males ignored the songs of other birds, whereas females were attentive. These patterns were not due to sex differences in memory capacity; operant conditioning studies have demonstrated that males and females do not differ in their memory capacity for songs (Ikebuchi & Okanoya, 2000). The results suggested that syntactically complex songs might be more potent than simple songs in maintaining arousal in females.

Reinforcing Properties of Complexity

To examine the preferences of female Bengalese finches with regard to song complexity, we employed an operant conditioning technique using the song as a reinforcer (Morisaka, Katahira, & Okanoya, 2008). The protocol and apparatus used by Gentner and Hulse (2000) to test song preference in female European starlings were modified for Bengalese finches. We prepared a large metal cage and placed pot-shaped nests in two upper corners. We also placed small speakers for song playback inside the nests and fastened a perch in front of each of the nest pots. A natural song sung by a male Bengalese finch was used to prepare a simple (order of song notes fixed) and a complex (order of song notes varied according to a finite-state rule) song, both of which were played back from the relevant speaker when the bird sat on the perch. A female bird was placed inside this apparatus. Four of the eight birds tested chose the complex song, one chose the simple song, and the remaining three birds chose both songs at random. These results suggested that the song preferences of female Bengalese finches varied depending on the individual, although more tended to prefer complex to simple songs. Because only one type of song was used in the experiment, the results should be interpreted with caution. Nevertheless, such female preferences could potentially contribute to sexual selection that facilitates the evolution of complex songs in male Bengalese finches (Morisaka et al., 2008).

Nest Building Behavior

To further demonstrate the function of song complexity, we examined the nest building behaviors of females (Eisner, 1961) in response to songs with complex or simple syntax (Okanoya & Takashima, 1997) using an approach first developed by Hinde and Steel (1976) and Kroodsma (1976). Hinde and Steel (1976) demonstrated that female domesticated canaries engaged in more transportation of nest material when stimulated with conspecific songs than with songs of other species. Kroodsma (1976) found that female canaries performed more nest building and laid more eggs when stimulated with large compared to small repertoire songs.

We analyzed the song recordings of a male Bengalese finch and identified four distinctive song phrases (Okanoya & Takashima, 1997). The four phrases in this bird's song were organized such that phrases A or B were repeated several times and phrases C or D followed this repetition, but phrases C and D were never repeated. After phrase C or D was sung once, phrase A or B was repeated. We designed a computer program to produce this sequence of song phrases (complex syntax song) or one that repeated only phrase B (simple syntax song). Phrase B contained most of the song notes that occurred in phrases A, C, and D.

We examined three groups of four female Bengalese finches; each finch was kept in a separate cage and they were kept together in a sound isolation box. The first group was stimulated with the song characterized by the complex syntax, the second group with the song characterized by the simple syntax, and the third group (control) was not stimulated with any song. The number of nesting items carried each day was counted and compared among the groups. Females stimulated with complex songs carried more nesting material than when stimulated with simple songs or no songs (Figure 7). We further examined whether randomly generated note sequences were more effective than were syntactically synthesized ones. Females who were stimulated with random note sequences were less responsive and carried comparable numbers of nest items compared to females stimulated with the simple sequence (data not shown). Although random sequences resulted in complex orderings of song notes, randomness did not generate the same female response as did complexity produced by syntax (Okanoya, 2004).

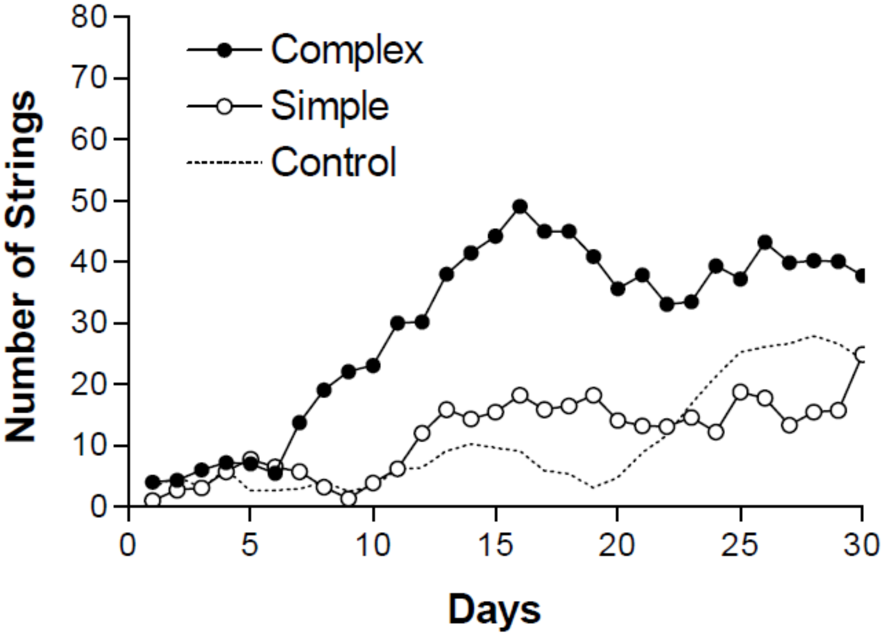

Figure 7. Results of nest building assay in female Bengalese finches. Complex song effectively stimulated nest carrying behaviour than simple song or no song (control).

Estradiol Levels

Three groups of female Bengalese finches were used in this experiment; each group consisted of four separately caged females kept together in a sound isolation box (Okanoya, 2004). The first group was stimulated with the song characterized by complex syntax, the second group with the song characterized by simple syntax, and the third group received no song stimulation. The levels of serum estradiol were compared among the groups before and after the experiment in order to consider baseline differences. Serum estradiol levels before and after the experiment were, on average, 0.37 and 0.76 ng mg^{-1}, respectively, in females stimulated with the complex song; 0.55 and 0.67 ng mg^{-1}, respectively, in females stimulated with the simple song, and 0.46 and 0.52 ng mg^{-1}, respectively, in females who heard a blank tape. Therefore, the complex song was more effective in stimulating female Bengalese finches into the reproductive condition.

Discussion

We described acoustical and syntactical differences between wild white-rumped munias and Bengalese finches, female responses to song complexity, effects of cross-fostering, and fieldwork to identify geographic variations in songs. Integrating these findings, we can now suggest a testable scenario for song evolution in Bengalese finches.

Domestication and Sexual Selection

The cross-fostering study revealed that white-rumped munias had a narrowly tuned learning mechanism for strain-specific phonology, whereas Bengalese finches had a more broadly tuned but less accurate learning mechanism. This finding should be considered in light of the results of fieldwork that showed that higher sympatric ratios were associated with lower levels of song complexity.

Birdsong must initially operate as a species-identifier, and then it can function for sexual selection. In this regard, songs do not need to function as species markers in the absence of sympatric, closely related species. In environments characterized by the latter, however, songs should serve a sexual purpose. Domestication represents a special case in which no sympatric species exists. Because Bengalese finches no longer need to identify their species, they might have gradually lost the bias toward learning and producing species-specific characteristics in their songs. As a result of broadening the species-specific filter, Bengalese finches might have developed the ability to produce phonologically and syntactically complex songs. In this sense, song complexity might have arisen from a loss of species-specific bias rather than representing a gain in general learnability. Once constraints are weakened, female preferences might reinforce this tendency towards more complex songs. Indeed, male songs can be complex in syntactical and phonological domains to satisfy females' preference for variations.

The Evolution of Song Complexity

Based on the experimental results reviewed in this chapter, we suggest several steps that might underlie the evolution of complex song syntax in the Bengalese finch. In most estrildid finches, songs are used solely for the purpose of mating and not in male–male interactions. Thus, sexual selection is likely to have enhanced those song properties on which females base their choices, resulting in traits that are handicaps in the wild environment (Darwin, 1871; Zahavi, 1975). The following is one possible scenario that might explain the emergence of finite-state syntax in the Bengalese finch.

Complexity in song-note transitions became a sexually selected trait in white-rumped munias and was subject to individual variations due to genetic differences in neural capabilities and cultural differences in song traditions. However, the wild environment restricted the degree of possible song complexity in white-rumped munias due to the various costs associated with the maintenance of such traits, possibly including predation costs, foraging time, immunological costs associated with the production of testosterone, and a metabolic cost associated with maintaining sufficient brain capacity to underpin the song system. Furthermore, songs needed to identify species in the wild, requiring that songs avoid phonological and syntactical complexity. Thus, mutations leading to greater song complexity would not have become fixed in a population of wild white-rumped munias, especially when sympatric species were living near them.

However, domestication eliminated many of these potential costs, especially those associated with predation and foraging time. Thus, domestication relaxed the restrictions imposed on the evolution of song complexity (Okanoya, 2002; Ritchie & Kirby, 2007). Furthermore, it reduced the necessity for identifying members of the species via song. Therefore, mutations leading to song complexity through the loss of a rigid song structure were not fixed in the natural environment and were not eliminated in the domesticated environment. Changes in brain structure then allowed more elaborate songs to be learned and gave rise to the improvisation of song syntax. Genes that allowed for the learning of complex songs were selected because of the preferences of females.

Implication

Through the study of song complexity in Bengalese finches, we learned that the combination of domestication and sexual selection could promote the evolution of signal complexity. Domestication functions in the direction to free the animal from some of selection pressures in the wild, and sexual selection functions to exaggerate a particular trait preferred by females in the absence of the selection pressures in the wild. This is an example of relaxed selection (Deacon, 2010). Similar processes could function, for example, in the evolution of plastic traits including language in humans. Thus, the study of signal evolution in Bengalese finches may promote understanding of language evolution in humans by providing framework for hypothesis formation (Okanoya, 2002).

References

Anderson, M., & Iwasa, Y. (1996). Sexual selection. *Trends in Ecology & Evolution, 11*, 53-58.

Buchan, J. (1976). *The Bengalese Finch*. Isles d`Avon.

Deacon, T. W. (2010). Colloquium Paper: A role for relaxed selection in the evolution of the language capacity. *Proceedings of the National Academy of Sciences, 107*, 9000-9006.

Darwin, C. (1871). *The descent of man*. London: J Murray.

Eisner, E. (1961). The behaviour of the Bengalese finch in the nest. *Ardea, 49*, 51-69.

Gentner, T. Q., & Hulse, S. H. (2000). Female European starling preference and choice for variation in conspecific male song. *Animal Behaviour, 59*, 443-458.

Hinde, R., & Steel, E. (1976). The effect of male song on an estrogen-dependent behavior pattern in the female canary (*Serinus canarius*). *Hormones & Behavior, 7*, 293-304.

Honda, E., & Okanoya, K. (1999). Acoustical and syntactical comparisons between songs of the white-backed Munia (*Lonchura striata*) and its domesticated strain, the Bengalese finch (*Lonchura striata* var. *domestica*). *Zoological Science, 16*, 319-326.

Ikebuchi, M., & Okanoya, K. (2000). Limited auditory memory for conspecific songs in a non-territorial songbird. *Neuroreport, 11*, 3915-3919.

Ikebuchi, M., & Okanoya, K. (2003). Sex differences in song perception in Bengalese finches measured by the cardiac response. *Animal Behaviour, 65*, 123-130.

Kagawa, H., Yamada, H., Lin, R.-S., Mizuta, T., Hasegawa, T., & Okanoya, K. (2012). Ecological correlates of song complexity in white-rumped munias: The implication of relaxation of selection as a cause for signal variation in birdsong. *Interaction Studies* (in press).

Kato, M., & Okanoya, K. (2010). Molecular characterization of the song control nucleus HVC in Bengalese finch brain. *Brain Research, 1360*, 56-76.

Kroodsma, D. (1976). Reproductive development in a female songbird: differential stimulation by quality of male song. *Science, 192*, 574-575.

Morisaka, T., Katahira, K., & Okanoya, K. (2008). Variability in preference for conspecific songs with syntactical complexity in female Bengalese finches: Towards an understanding of song evolution. *Ornithological Science*, *7*, 75-84.

Okanoya, K. (2002). Sexual display as a syntactical vehicle: The evolution of syntax in birdsong and human language through sexual selection. In A. Wray (Ed.), *The transition to language* (pp. 46-63). Oxford, UK: Oxford University Press.

Okanoya, K., & Takashima, A. (1997). Auditory preference of the female as a factor directing the evolution of Bengalese finch songs. *Transaction of Technical Communications in Psychoogical and Physiological Acoustics, 27*, 1-6.

Okanoya, K. (2004). Song syntax in Bengalese finches: proximate and ultimate analyses. *Advances in the Study of Behaviour*, *34*, 297-346.

Restall, R. (1996). *Munias and mannikins*: Pica Press.

Ritchie, G., & Kirby, S. (2007). A possible role for selective masking in the evolution of complex, learned communication systems. In C. Lyon, C. Nehaniv & A. Cangelosi (Eds.), *Emergence of Communication and Language* (pp. 387-401). London: Springer.

Scharff, C., & Nottebohm, F. (1991). A comparative study of the behavioral deficits following lesions of various parts of the zebra finch song system: Implications for vocal learning. *Journal of Neuroscience, 11*, 2896-2913.

Searcy, W. (1992). Song repertoire and mate choice in birds. *Integrative and Comparative Biology, 32*, 71.

Taka-Tsukasa. (1917). *Companion birds* (in Japanese). Tokyo: Shoka-bo.

Takahasi, M., & Okanoya, K. (2010). Song learning in wild and domesticated strains of White-rumped munia, *Lonchura striata*, compared by cross-fostering procedures: Domestication increases song variability by decreasing strain-specific bias. *Ethology, 116*, 396-405.

Washio, K. (1996). *Enigma of Bengalese finches* (in Japanese). Tokyo: Kindai-Bungei-Sha.

Zahavi, A. (1975). Mate selection — a selection for a handicap. *Journal of Theoretical Biology, 53*, 205-214.