

## S01-3 Neuro-ecology of song complexity in Bengalese finches

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**Abstract** The Bengalese finch, *Lonchura striata* var. *domestica*, a strain derived from the wild white-rumped munia, *Lonchura striata*, has been under domestication in Japan for 240 years. We compared song syntax of these two strains and found that the domesticated strain developed highly complex, conspicuous songs, whereas the wild strain sang very stereotyped songs. To identify a possible neural substrate responsible for this difference in song behavior, we performed a lesion study. In Bengalese finches, lesions of the NIf, a higher order song control nucleus, resulted in simplification of complex song syntax. We then compared the levels of serum estradiol in female birds that were stimulated with complex or simple song. Estradiol levels were significantly higher in the females stimulated by complex songs. Based on these data, we hypothesize that a mutation in the song control nucleus occurred in the domestic strain that enabled the development of complex song syntax, and that this mutation became fixed in the domestic population through sexual selection.

**Key words** Estrildid finches, Domestication, Song complexity, Neuro-ecology

### 1 Introduction

Tinbergen's four questions (1963), the pillars of classical ethology, have been divided into two major areas of ethological inquiry, namely neuroethology and behavioral ecology (Wilson, 1975). Adherence to this approach has led to the neglect of the relationship between ecological adaptation and associated changes in central nervous system. The comparative study of birdsong presents an opportunity to integrate ethological science in such a way as to simultaneously address proximate and ultimate causes of behavior (Baptista and Gaunt, 1994).

Luis Baptista was interested in our behavioral studies of the domesticated Bengalese finch (Okanoya, 1997; Okanoya and Yamaguchi, 1997), partly because they addressed the importance of auditory feedback in adulthood (Brainard and Doupe, 2000), and partly because of his enthusiasm for aviculture (e.g. Baptista, 1995). He encouraged us to compare Bengalese finches, which are all white, and white-rumped munias, which are pigmented, because the latter are considered to be the source stock of Bengalese finches (Buchan, 1976). Molecular techniques have established that these finches, indeed, are the same species (Yodogawa et al., unpublished).

We began by making field observations of wild white-rumped munias (Okanoya et al., 1995) and found that their distance calls were the same as those of Bengalese finches. We then imported white-rumped munias and compared their songs with those of Bengalese finches (Honda and Okanoya, 1999). This comparison suggested a process of behavioral evolution, the study of which would be tractable from a

neuro-ethological perspective and provide us with a unique opportunity for truly fruitful "neuro-ecology" (Bolhuis and Macphail, 2001).

To that end we performed three studies in our laboratory. First, we compared syntactical complexity in domesticated and wild strains of white-rumped munias (Honda and Okanoya, 1999). Next, we undertook a lesion study, to find that a higher-order song control nucleus is responsible for song complexity in Bengalese finches (Hosino and Okanoya, 2000). Finally, we assessed the levels of estradiol in females exposed to simple and complex finch songs, finding that song complexity is an important parameter for females when selecting potential mates (Takashima et al., unpublished). These three studies are reviewed here.

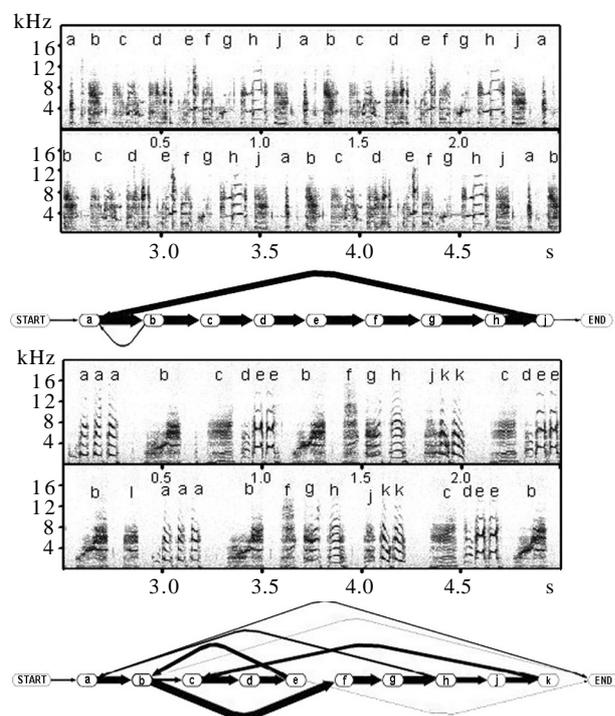
### 2 Comparisons of song parameters

#### 2.1 Rationale

When white-rumped munias were imported into Japan, aviculturists selected birds for parental ability and white mutations. There are no records in the avicultural literature indicating that the resulting Bengalese finches were selected for song. To begin asking evolutionary questions on the complexity of songs, we first compared song morphology in white-rumped munias and Bengalese finches (Honda and Okanoya, 1999).

#### 2.2 Methods

Eight Bengalese finch songs and five white-rumped munia songs were randomly sampled from a library of recordings in our laboratory, and spectrograms made. Fig. 1



**Fig. 1** Sonograms and song note transition diagrams of a white-rumped munia song (upper) and a Bengalese finch song (lower)

Re-plotted from Honda and Okanoya (1999).

shows phrase transition diagrams from each finch strain.

### 2.3 Results

The average number of song notes used by white-rumped munias (average 8.40, range 7–10) and Bengalese finches (average = 9.25, range = 6–15) was similar ( $P=0.64$ ). However, the average song linearity, an index of song simplicity (Scharff and Nottebohm, 1991), was significantly lower ( $P<0.001$ ) in Bengalese finches (average 0.33, range 0.24–0.43) than in white-rumped munias (average 0.61, range 0.41–0.69). In other words, Bengalese finches sang songs with more note-to-note transitions.

Song complexity in Bengalese finches must have evolved in the past 240 years of domestication, which seems a short time, but translates to 500–1 000 generations and corresponds roughly to 20 000 human years. Though it might be attributed to cultural drift, genetic constraints could also be involved (Okanoya, 2002).

## 3 Mechanism of song complexity

### 3.1 Rationale

What mechanisms make the more complex song of Bengalese finches possible? Central and peripheral mechanisms for birdsong production have been well studied (Margoliash, 1997; Suthers, 1997). To describe the brain areas used in them, we use acronyms as proper names because the acronyms were originally based on many neuroanatomical terms that have since proved incorrect or inappropriate. Song is produced physically by the com-

bined activity of respiratory, syringeal, and resonating apparatus (trachea, tongue, and beak). Control of song production is governed by a set of discrete brain nuclei.

Syringeal activity is controlled by what is sometimes called the posterior pathway (Margoliash, 1997). 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, the RA, and by the mesencephalic motor nucleus, the DM. The RA is in turn innervated by the telencephalic sensory/motor integration nucleus, the HVC. This nucleus receives auditory input from the primary auditory center, the Field L, and from surrounding higher auditory structures, including the Nif nucleus which sends auditory/motor input to the HVC.

Because the Nif is at a higher order than the HVC, the former nucleus was thought to govern a higher organization of song syntax (Margoliash, 1997). Bilateral lesion of the Nif was attempted in zebra finches (*Taeniopygia guttata*), but lesion effects were not detectable on song, except for some transient deterioration that lasted about two weeks post-surgery (Vu et al., 1995). We suspected that the zebra finch songs might be too simple for detecting the effects of nucleus Nif lesion, because their songs are composed usually of repeated sequences of the same syllable order (Zann, 1997). If the Nif does in fact govern higher order song organization, the song should have higher order syntactical organization than the level of one song phrase. In Bengalese finches, song is organized into several different phrases by following different paths, so we predicted that lesion effects might be detectable in these song paths (Fig. 1).

### 3.2 Methods

Accordingly, we attempted to make lesions to the Nif nuclei of 12 Bengalese finches. Of these, only three were successful bilateral Nif lesions. Of the remainder, two were unilateral and the rest misplaced. All successful lesions completely eliminated the Nif nucleus.

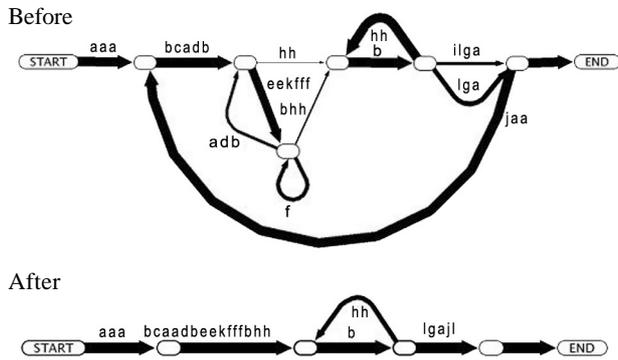
### 3.3 Results

Unilateral and misplaced lesions produced no change in song syntax. For bilateral lesions, moreover, the result depended upon the degree of song complexity demonstrated by the bird prior to surgery. In two birds that sang complex, multi-phrased songs, bilateral Nif lesion eliminated phrase level complexity; the multi-phrased organization of the song was reduced into single phrase song (Fig. 2). The third bird had initially sung a simple, single-phrase song, and it showed no effect from bilateral Nif lesion. Thus we conclude that the Nif is responsible for phrase-to-phrase transitions in song (Hosino and Okanoya, 2000).

## 4 Function of song complexity

### 4.1 Rationale

Given that song syntax differs between Bengalese



**Fig. 2** Changes in song syntax of a NIf lesioned Bengalese finch

Pre-operative song (upper) has a complex transition pattern as in most Bengalese finches, while post-operative song (lower) lost complex transitions. Post-operative song syntax is similar to that of white-rumped munias (Fig. 1). Re-plotted from Hosino and Okanoya (2000).

finches and white-rumped munias, and that its complexity is controlled by the auditory-motor interface nucleus, the NIf, our next step was to examine its functional implications. For this, we chose to examine the hormonal state of females stimulated by either complex or simple syntax songs (Takashima, Otsuka, Wada and Okanoya, pers. obs.).

#### 4.2 Methods

Song recordings obtained from a male Bengalese finch were analyzed, and four distinctive song phrases identified. In the song, the four phrases were organized in such a way that phrases A or B were repeated several times, then phrases C or D followed but without repeat; and after phrase C or D was sung once, phrases A or B were again repeated. We wrote computer software that produced (1) this sequence of song phrases (complex syntax song) and (2) a sequence that repeated only phrase B (simple syntax song). It should be noted that phrase B includes most of the song notes used in phrases A, C, and D.

Three groups of female Bengalese finches were used. Each group consisted of four finches, separately caged, and kept together in a sound isolation box. The first group was stimulated with the complex syntax song, the second group with the simple syntax song, and the third group, as the control, received no playback songs. The levels of serum estradiol were compared among groups both prior to and after the experiment so that baseline level differences could be taken into account.

#### 4.3 Results

Estradiol levels were on average 2.23 times (range 1.58–3.65) higher than baseline in the females stimulated with complex song, 1.08 times (range 0.91–1.45) higher in the females stimulated with the simple song, and 1.12 times (range 0.81–1.43) in control females. Thus complex song was more effective in stimulating female Bengalese finches into reproductive condition ( $P < 0.05$ , by post-hoc tests).

## 5 Discussion

In our comparison of the syntactical characteristics of songs in the white-rumped munia, and its domesticated strain, the Bengalese finch, we expected to find simplified traits that would be favored in a domesticated environment. Yet the most remarkable difference that appeared was the more complex song of the domesticated strain, with more note-to-note transitions than in the wild form.

In previous studies, female Bengalese finches performed more copulation displays to the playback of a 6-element song than a 4-element song (Clayton and Prove, 1989). Female Bengalese finches also perch-hopped more often when stimulated by songs with more rather than few elements (Nakamura et al., 1985). These results suggest that female choice might favor more variety in song element types. However, we did not find significant differences in the number of song element types between the strains. In the studies by Clayton and Prove (1989) and Nakamura et al. (1985), the degree of complexity in the temporal domain of the stimulus songs was not reported, and these authors did not introduce temporal-domain dynamics into their playback regimes. Thus, how song complexity in that domain might cause different effects on female Bengalese finches is unknown. Although several studies address “song complexity” and female choice (Kroodsma, 1976; Clayton and Prove, 1989; Eens et al., 1991; Catchpole and Leisler, 1996), most of them treat variations in note type as “complexity.”

In our study, song complexity in Bengalese finches involves dynamics in time series, i.e. temporal domain, rather than variations in note types. In this context, our results on estradiol measurements are of interest. Females stimulated with complex song had estradiol levels elevated to twice the height of base levels. Song complexity, as opposed to note complexity, thus, stimulated female reproductive condition.

Lesions of the NIf also disrupted phrase-level variability in Bengalese finches that sang multi-phrase songs. When the same operation was performed on birds with simpler song, it had no discernible effect on song syntax. Based on our limited data, we postulate that the NIf nucleus may control higher-order song transition or phrase-to-phrase transition. In addition, the finding that NIf-lesioned birds did not change the pattern of note-to-note transition within a phrase suggests that NIf is responsible only for phrase level transition and not for note level transition.

These findings taken together lead us to propose the following scenario to explain song complexity in the Bengalese finch. A mutation involving the NIf nucleus enabled the development of syntactically complex song during the process of domestication. Female bias for syntactical complexity then selected this mutation in domesticated populations. Further work is necessary to test this prediction, as well as to address the more fundamental question: what is the genetic component determining observed song complexity?

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## References

- Baptista LF, 1995. A guide to the study of estrildids. *The Estrildian* 3: 13–24.
- Baptista LF, Gaunt SLL, 1994. Advances in studies of avian sound communication. *Condor* 96: 817–830.
- Bolhuis JJ, Macphail EM, 2001. A critique of the neuroecology of learning and memory. *Trends Cog. Sci.* 5: 426–433.
- Brainard MS, Doupe AJ, 2000. Auditory feedback in learning and maintenance of vocal behaviour. *Nature Rev. Neurosci.* 1: 31–40.
- Buchan J, 1976. *The Bengalese finch*. Bristol: Isles d'Avon.
- Catchpole CK, Leisler B, 1996. Female aquatic warblers *Acrocephalus paludicola* are attracted by playback of longer and more complicated songs. *Behav.* 133: 1153–1164.
- Clayton NS, Prove E, 1989. Song discrimination in female zebra finches and Bengalese finches. *Anim. Behav.* 38: 352–362.
- Eens M, Pinxten R, Verheyen RF, 1991. Male song as a cue for mate choice in the European starling. *Behav.* 116: 211–238.
- 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*. *Zool. Sci.* 16: 319–326.
- Hosino T, Okanoya K, 2000. Lesion of a higher-order song nucleus disrupts phrase level complexity in Bengalese finches. *Neuro. Report* 11: 2 091–2 095.
- Kroodsma DE, 1976. Reproductive development in a female songbird: differential stimulation by quality of male song. *Science* 192: 574–575.
- Margoliash D, 1997. Functional organization of forebrain pathways for song production and perception. *J. Neurobiol.* 33: 671–693.
- Nakamura T, Matsuno K, Suga S, 1985. Reproductive response of female common finches to the different quality of male songs. *Yamanashi Univ. Res. Rep.* 35: 66–70.
- Okanoya K, 1997. Voco-auditory behavior in the Bengalese finch: A comparison with the zebra finch. *Biomed. Res. Tokyo* 18: 53–70.
- Okanoya K, 2002. Sexual selection as a vehicle of syntax. In: Wray A ed. *The Transitions to Language*. Oxford: Oxford University Press.
- Okanoya K, Yoneda T, Iseki S, 1995. Distance calls of the wild white-backed munia in Kijoka, Okinawa, Japan. *J. Ornithol.* 44: 231–233.
- Okanoya K, Yamaguchi A, 1997. Adult Bengalese finches require real-time auditory feedback to produce normal song syntax. *J. Neurobiol.* 33: 343–356.
- 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. *J. Neurosci.* 11: 2 896–2 913.
- Suthers RA, 1997. Peripheral control and lateralization of birdsong. *J. Neurobiol.* 33: 632–652.
- Tinbergen N, 1963. On aims and methods of ethology. *Z. Tierpsychol.* 20: 410–433.
- Vu ET, Mazurek ME, Kuo YC, 1995. Hierarchical organization of brain areas mediating zebra finch learned vocalizations. Abstract. Neuroscience Society.
- Wilson EO, 1975. *Sociobiology: The New Synthesis*. Cambridge, MA: Harvard University Press.
- Zann RA, 1997. *Zebra finches*. Oxford: Oxford University Press.