



Domestication changes innate constraints for birdsong learning



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ABSTRACT

Birdsongs are acquired by imitating the sounds produced by conspecifics. Within a species, songs diverge by cultural transmission, but the range of species-specific features is restricted by innate constraints. Bengalese finches (*Lonchura striata* var. *domestica*) are a domesticated strain of the wild White-rumped munia (*Lonchura striata*). The songs of the domesticated strain have more tonal sounds and more variable sequences than those of the wild strain. We compared the features of songs that were produced by normal birds, isolation-reared birds, and cross-fostered birds in both White-rumped munias and Bengalese finches to identify differences in the genetic and environmental factors of their songs. Factor analyses were conducted based on 17 song measurements. We found that isolated songs differed from normal and cross-fostered songs, especially in unstable prosodic features. In addition, there were significant differences in sound property of mean frequency between the two strains regardless of the rearing conditions. Thus, innate constraints that partially determine birdsong phenotypes may be altered through domestication.

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1. Introduction

Songbirds learn their songs from parents and neighbors (Beecher and Brenowitz, 2005). This learning process increases song diversity within a species (Catchpole and Slater, 1995; Podos and Warren, 2007). Song diversity is affected by temporary changes in the local environment, such as surrounding noises, species, and vegetation, or through the process of miscopying of songs from parents to offspring (Slabbekoorn and Smith, 2002; Podos et al., 2004a). Songs are modified from generation to generation (Derryberry, 2010). As a result, song dialects and geographic variations in songs exist in most songbird species. Birdsong provides a good example of a culturally evolving system, which depends on social transmission of information.

Cultural transmission is coevolved with innate predispositions (Lachlan and Feldman, 2003), and changes in these innate predispositions may enlarge or alter the range of species-specific song features. Song learning in birds is affected by innate predispositions that guide juveniles so that they can learn what to sing and how (reviewed in Adret, 2004). Juveniles have innate biases toward choosing and producing conspecific song features even when they are untutored, or tutored by other species or artificial sounds (Marler and Peters, 1977; Nelson and Marler, 1993; Mundinger, 1995; Whaling et al., 1997; Braaten and Reynolds, 1999; Nelson, 2000; Hauber et al., 2001; Podos et al., 2004b; Gardner et al., 2005). Recent reports have shown that innate predispositions may guide birds to produce species-specific songs across generations even when an appropriate song model is unavailable (Belzner et al., 2009; Feher et al., 2009). Thus, the range of song diversity may be controlled by innate predispositions and altered via gene-culture co-evolution (Byers et al., 2010).

Bengalese finches were domesticated from White-rumped munias about 250 years ago (Okanoya, 2004). Songs of Bengalese finches changed through domestication: Bengalese finch songs contain more tonal sounds and complex note-to-note transitions than those produced by White-rumped munias (Honda and Okanoya, 1999). Cross-fostering experiments suggest that the accuracy of song learning is different between the two strains. White-rumped munias can learn song phonology more accurately

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from their own strain than from the other strain (Takahasi and Okanoya, 2010). On the other hand, Bengalese finches learn songs equally, but less accurately, from both strains. This experiment reveals that the innate bias for learning species-specific songs could differ between the two strains. Thus, domestication could alter not only song features but also innate predispositions of song learning between the strains. The songs of domestic strains have changed over time, and now differ from the songs of the wild finches as a result of relaxed natural selection due to changes in their environment (Okanoya, 2004; Kagawa et al., 2012).

In addition to results from cross-fostering experiments, song features of isolation-raised birds enable us to examine the genetic and environmental factors involved in song learning. Juveniles that are isolated from conspecific songs develop atypical songs that differ from those of juveniles raised under normal conditions. However, the songs of isolated birds often retain crude species-specific features (Marler and Sherman, 1985). We compared songs by birds isolated from conspecifics in the two strains to examine the innate aspects of song learning. Then songs of normal birds in both strains were analyzed to examine the song features formed by environmental factors. In addition, we compared cross-fostered birds to test whether the song features retained in isolation-reared birds are constant when they learn songs from the other strain (e.g., White-rumped munias learning Bengalese finches' songs, and *vice versa*). Thus, this paper presents a discussion on song features between the two strains, and whether these features are innately constrained or varied by the environment.

2. Material and methods

2.1. Normal and isolated birds

We used a total of 32 male subjects, half of which were Bengalese finches and the rest were White-rumped munias. These two groups were further differentiated into 8 isolated birds and 8 normal birds in each group (Appendix 1). Normal male Bengalese finches were purchased from pet breeders or bred in our laboratory. Normal male White-rumped munias were kept for more than 1 year after being captured from the wild in Taiwan, or were bred in our laboratory from the captured birds. They were kept in large metal cages with either related or nonrelated individuals. The age of all normal birds was older than 120 days post-hatch, which is an age following the conclusion of the normal song-learning process (Takahasi and Okanoya, 2010). Isolated subjects were raised only by their mothers from about day 7 post-hatch in a soundproof chamber to isolate them from conspecific songs. From day 36 post-hatch, they were kept alone in a plastic cage (150 mm × 305 mm × 220 mm) placed in a soundproof chamber. Songs were recorded when birds were older than 120 days post-hatch. All birds were fed three types of millet, calcium supplements, green leaves, and freely available vitamin-enhanced water. Their environment was maintained with a controlled temperature below 25 °C, humidity of less than 60%, and 13 h of daytime. This experiment complied with the Animal Care and Use Committee of RIKEN (#H20-2-231 and #H22-2-217) and National Institutes of Health Guidelines.

2.2. Song recording

Songs were recorded in a soundproof chamber. We recorded undirected songs, sung for practice and maintenance (*i.e.*, not used to address females). We used a microphone (AT3031, Audio-technica, Tokyo, Japan) connected to a PC (T3400, Dell, Austin, TX, USA) with an amplifier (SP-828, Studioproject, Gardena, CA, USA). The sampling frequency was 44.1 kHz and the resolution was 16 bits. The microphone was set 10 cm from the cage.

2.3. Songs of cross-fostered birds

We analyzed songs of cross-fostered birds that were recorded in a previous study (Takahasi and Okanoya, 2010). We chose a total of 11 cross-fostered males (seven fostered-Bengalese finches and four fostered-White-rumped munias), based on the recording condition of their songs (Appendix 1). The fostered birds and their foster parents were not genetically related to our isolated and normal subjects. Cross-fostered offspring were reared with foster parents of the opposite strain before they hatched. Songs of the birds at 150 days post-hatch were recorded in a soundproof chamber (640 mm × 1295 mm × 1720 mm, Science cabin) using a DAT recorder (Sony ZA5ES, Tokyo, Japan) or a laptop computer with a microphone (Sony ECMMS957). Details of rearing conditions and recording methods are provided in the previous study (Takahasi and Okanoya, 2010).

2.4. Song analysis

Songs were passed through a band-pass filter between 1 and 12 kHz and normalized for dynamic range. We measured song structure using Sound Analysis Pro software (Tchernichovski et al., 2004) and SASLab Pro (Avisoft Bioacoustics, Berlin, Germany). We used a singing duration of 20 s to analyze phonological features from isolated, normal and cross-fostered birds. This amount of songs was shown to be sufficient for the present purpose according to a study on the songs of untutored Zebra finches (Feher et al., 2009). We measured the features using 10 ms windows using Sound Analysis Pro. A total of seven values, entropy, frequency modulation (FM), pitch which is fundamental frequency estimated by the YIN method (de Cheveigné and Kawahara, 2002), goodness of pitch, mean frequency, peak frequency and mean frequency amplitude (Table 1), were computed. We recorded and analyzed 30 song bouts per individual in isolated and normal birds to evaluate two temporal features, note duration and note-to-note interval using SASLab (Table 1). The number of songs in cross-fostered birds used for temporal analysis was an average of 18 bouts (mean 18.3 ± 8.5, max: 32, min: 11), due to the fact that the number of songs recorded in previous study (Takahasi and Okanoya, 2010) was smaller than that in this study. The recorded songs were analyzed and transformed into sonograms (spectrogram resolution of 94 Hz, 2.667 ms, 75% overlap, FFT size 512, Hamming window). For each song measurement, we calculated the median and coefficient of variation (CV) from each individual's song. Because scales were different among the song features, we used CVs instead of standard deviations to compare variation of the song features in each individual. Median of amplitude was excluded from the statistical analysis because the recording environment was not rigorously controlled to measure amplitude.

2.5. Statistical analysis

We used maximum likelihood factor analysis (FA) using promax rotation to detect the structure of the relationship between variables so that they could be categorized. Each variable was centered and transformed into *z*-scores. We tested sampling adequacy for FA using the Bartlett sphericity test and the Kaiser–Meyer–Olkin (KMO). A total of 17 variables and 43 samples were used for the analysis (Bartlett sphericity test, $\chi^2 = 1620.13$, $df = 136$, $p \ll 0.001$, $KMO = 0.57$). We extracted factors with eigenvalues > 1 following the Kaiser criterion. We picked song variables that contributed to each factor component based on loading values greater than 0.5 (Sergey, 2010). The factorial scores were computed using a regression method to compare song features among conditions (normal, isolated and cross-fostered) in Bengalese finches and White-rumped munias. Using a two-way ANOVA, we examined

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