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# The Role of Auditory Feedback in the Maintenance of Song in Adult Male Bengalese Finches *Lonchura striata* var. *domestica*

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**ABSTRACT**—Young songbirds use auditory feedback to match their own vocalizations with a memorized tutor's song in order to develop their songs normally. After learning, songs of adult birds are stereotyped and remain stable. Recent studies showed that auditory feedback is necessary for maintaining the stability of adult bird song in some species including Bengalese finches. We deprived adult male Bengalese finches of auditory input by removing their cochleae and acoustically analyzed the songs of the deafened birds. After the operation, song patterns altered within a week and remained unstable for approximately a month. The post-operative songs were finally stabilized within 60 days after the operation, although their patterns were different from those of the pre-operative songs. Compared with the pre-operative songs, syllables with higher fundamental frequencies decreased and those with lower fundamental frequencies increased in the stabilized post-operative songs of all the birds examined. These results suggest that adult male Bengalese finches need auditory feedback in order to maintain their normal songs and that this feedback is involved in retaining the syllables of higher fundamental frequencies. They also suggest that the stabilized post-operative songs consisting of syllables with lower fundamental frequencies may be maintained by other sensory feedback systems.

## INTRODUCTION

Male songbirds learn species-specific song during sensitive periods of development. Young birds first listen to a tutor's song to memorize it and then reproduce the memorized song as they mature. It has been demonstrated that the young birds which were deafened after memorizing the song failed to develop a copy of it (Konishi, 1965; Nottebohm, 1968; Marler and Waser, 1977; Price, 1979). These data suggested that young birds use auditory feedback in practicing their own vocalizations to match the memorized song.

Songs of adult birds after the song learning period are stereotyped and remain stable. The necessity of auditory feedback for maintaining adult bird song has also been examined in some species. In zebra finches, white-crowned sparrow, and chaffinches, which maintain their songs throughout adult life, the songs of adult birds deafened by bilateral cochlear removal did not alter (Konishi, 1965; Nottebohm, 1968; Price, 1979; Bottjer and Arnold, 1984). The song of a deafened canary, however, which renews its song every year, did deteriorate even after the completion of song learning (Nottebohm *et al.*, 1976). Thus it was reasoned that auditory feedback is necessary to maintain normal songs in adult bird species such as canary which learn new songs by using continuous auditory input in adulthood. Recent results, however, appear to contradict these previous studies. Nordeen and Nordeen (1992) showed that the songs of zebra finches gradually altered after the birds were deafened, as did those of Bengalese finches (Okanoya and Yamaguchi, 1997; Woolley and Rubel, 1997), whose songs are also normally stable throughout adult life. These observations provide evidence that even species whose songs do not alter throughout adult life after they are learned need auditory feedback to maintain their songs.

In this study, we deprived adult Bengalese finches of auditory input by removing both cochleae and analyzed the structure of the deafened birds' song. By observing alterations of the post-operative song and its acoustical characteristics, we suggest the possible role of auditory feedback and assess the contribution of non-auditory feedback in maintaining adult bird song.

## MATERIALS AND METHODS

### Subjects

Twenty-one adult male Bengalese finches (*Lonchura striata* var. *domestica*), over 4 months old, were used in this study. All birds were purchased from commercial resources except 4 which were hatched and raised in our laboratory. Birds were caged in a group of 10-12 (cage size: 34 × 39 × 43 cm) before cochlear removal. After the operation, the birds were individually housed in small cages (cage size:

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30 × 15 × 19 cm) which were placed in the same room to prevent physical, but not visual, contact. Throughout the experimental period, the birds were kept in an air-conditioned room (25 ± 2°C) under a 14:10 hr light/dark cycle. They were fed food, water, and crushed shell in the cage every day.

**Surgical deafening**

To deprive them completely of auditory input, the birds were deafened by removing both cochleae. The birds were anesthetized with a mixture of ketamine (35 mg/kg body weight, Ketalar 10, Sankyo) and xylazine (6 mg/kg body weight, Sigma), and the cochleae were removed according to procedure described by Konishi (1963) using a fine hooked wire (Elgiloy, Rocky Mountain). The skin incision was then sealed with cyanoacrylate (Aron Alpha A, Sankyo). The excised cochleae were then examined microscopically for the presence of lagenae at their digital ends to verify complete removal.

**Song recording**

Songs were recorded on a digital audio tape recorder (TDC D-10, Sony) through a microphone (ECM 959DT, Sony) placed constantly at the same distance from the cage. "Undirected" song (sung toward no particular object) was recorded while each bird was placed individually in a sound-attenuated chamber. For each recording date, 5-7 bouts (defined below) of undirected song was recorded from each bird.

Prior to cochlear removal, the songs were recorded for a period of 63.7 days on average (8 days for the shortest, 205 days for the longest) at more than 3 timepoints. Cochlear removal was performed within 3 days after the last pre-operative recording. Post-operative songs were recorded every day for the first 7 days, twice a week up to 30 days, and at least once a week up to 60 days (90 days in 11 birds) after surgery.

**Song analysis**

All acoustical analyses were performed with a sound spectrograph (DSP Sona-Graph Model 5500, Kay Elemetrics Corp.).

*Description and terminology of song.* The song of Bengalese finches occurs in bout of approximately 10-20 sec, defined as a sequence of one repeated phrase initiated by single syllables with harmonics of low fundamental frequency ("introductory notes") and surrounded by at least 2 sec of silence. A phrase consists of several distinct types of syllables which usually appear in a fixed sequential order. In this study, syllables were defined as continuous, morphologically discrete traces on a sound spectrogram, separated by intervals of at least 10 msec.

*Classification of syllables.* Syllables in pre-operative songs were classified by phonological structure observed on a sound spectrogram and a power spectrum display of the sound spectrograph, and assigned successive numbers. Each syllable in the post-operative songs was then assigned to the pre-operative syllable type which it

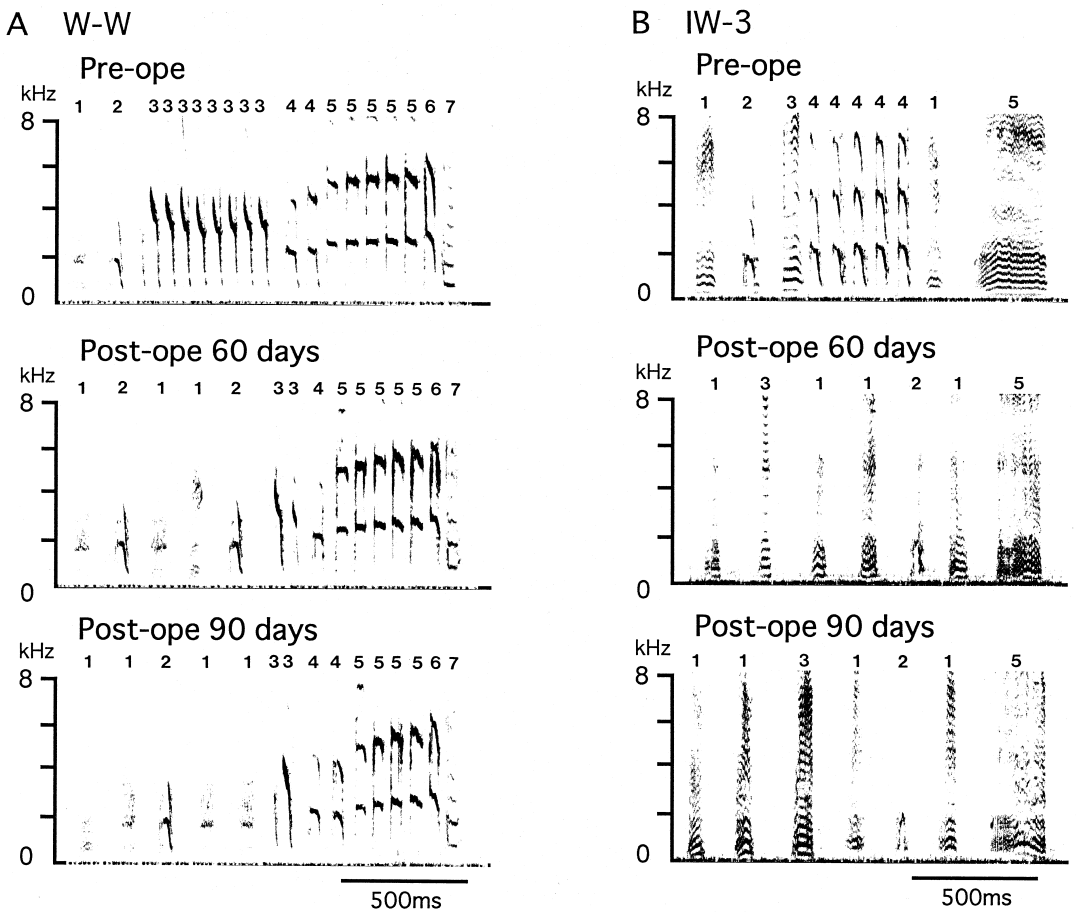


**Fig. 1.** Sound spectrograms of one song phrase from two birds before and after cochlear removal. Syllables comprising the phrase are classified into types and denoted by successive numbers (shown above syllables). In post-operative songs of both birds, some syllable types are dropping or decreasing in number. (**A**) Song of bird W-W with 7 syllable types recorded 1 day before the operation (upper), 60 days (middle), and 90 days after the operation (lower). (**B**) Song of bird IW-3 with 5 syllable types recorded on 1 day before the operation (upper), 60 days (middle) and 90 days after the operation (lower).

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most closely resembled phonologically.

*Number of syllables*. The numbers of syllables of each type per 20 sec were calculated from the sum of the number of syllables contained in 3 bouts of song (27.0-65.8 sec) which were randomly selected from each recording date. For statistical comparisons, the Wilcoxon signed rank test (two-tailed) was used.

*Fundamental frequency (FF) of the pre-operative syllables*. Since most of the syllables in the songs of Bengalese finches were composed of harmonically related tones, we measured the fundamental frequency (FF; the first harmonic frequency) of each syllable type in the pre-operative songs. To determine the FF more precisely, the frequency difference between the first and second harmonics was also measured, and then these two values were averaged. When a syllable was composed of modulated frequency, the FF was determined from the highest peak of amplitude on the power spectrum. In a few cases where a syllable contained both harmonics and another harmonically unrelated tone, the FF was determined from the component showing the highest amplitude on the sound spectrogram. For estimating the FF of each syllable type, FFs of more than 5 syllables contained in at least 3 different bouts from the two different pre-operative timepoints were randomly sampled and averaged.

## RESULTS

Figure 1 shows an example of the songs from two adult Bengalese finches (W-W, IW-3) before and after surgical deafening. The song phrase consisted of 4-11 distinct types of syllables, some of which were repeated within one phrase. Phrases of the pre-operative songs (Fig. 1, top panel) were stable; that is, the sequences of syllables and the number of

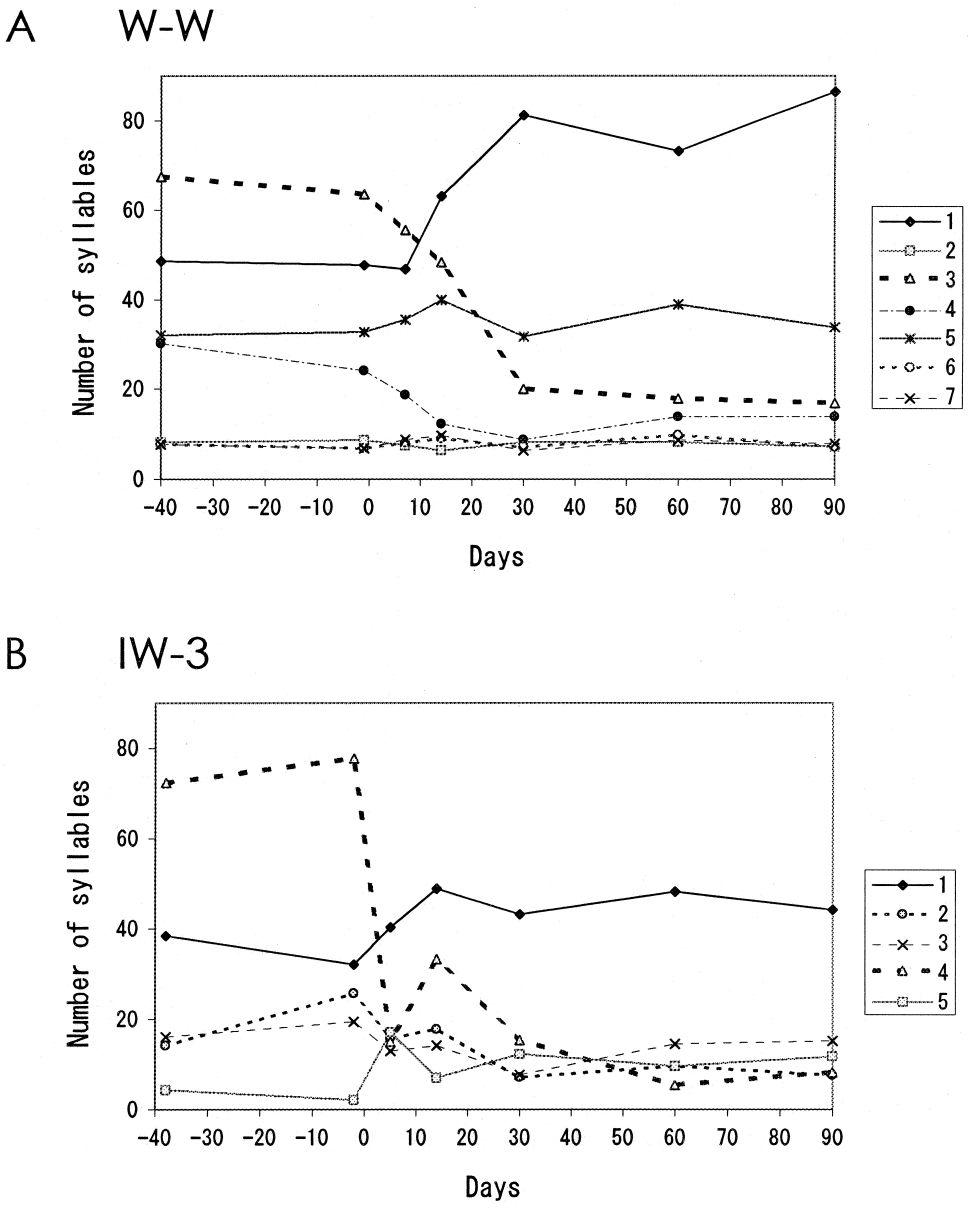


**Fig. 2.** Changes in numbers of syllables of each type contained in 20 sec of song before and after cochlear removal. Numbers in the figure denote each syllable type. Horizontal axis shows days since cochlear removal, which is day 0. (**A**) An example of W-W. (**B**) The other example of IW-3.

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syllables of each type remained almost unaltered during the pre-operative recording period of 63.7 days on average (8 days for the shortest, 205 days for the longest). After cochlear removal, the song patterns became quite unstable and kept altering for approximately a month after the operation; that is, sound spectrograms during this period showed that both the sequences of syllables and the number of syllables of each type altered from day to day (sound spectrograms not shown). Although the songs were finally well stabilized within 60 days after the operation, they were considerably different from the pre-operative songs (see Fig. 1, middle and bottom panels for 60 days and 90 days after the operation, respectively). Sound spectrograms of the post-operative songs clearly demonstrated that in all of the 21 birds examined, syllables of one or more types disappeared or remarkably decreased in number. For example, syllable 3 in bird W-W decreased. On the other hand, syllables 1 and 2 increased and placed around where syllable 3 had occupied (Fig. 1A), and syllable 4 in bird IW-3 almost disappeared (Fig. 1B). In bird IW-3 and 6 other birds, alterations in the sequence of syllables and prolongation of inter-syllable intervals were also observed (for example, bird IW-3 in Fig. 1B). Phonological structures of some syllables were altered to some extent in bird IW-3 (see syllable 2 and 5 in Fig. 1B) and 5 other birds, but each of these syllables was similar to one of the pre-operative syllable types.

The time course of post-operative song alteration indicated by sound spectrograms was supported by every type of syllable alteration in all 21 birds examined (data from two birds, W-W and IW-3, are shown in Fig. 2A and B respectively). The numbers of syllables of all types remained considerably stable before the cochlear removal. Then for approximately 30 days after the operation, the numbers of syllables of some types dramatically decreased (syllable 3 in Fig. 2A and syllable 4 in Fig. 2B) or increased (syllable 1 in Fig. 2A). The numbers of syllables of all types became stable after about 30 post-operative days, reflecting stabilization of the song.

To examine the acoustic properties of the altered syllable types, we measured the fundamental frequencies (FFs) of all syllable types contained in the pre-operative songs of all 21 birds. According to the FF, all syllables could be roughly classified into three groups (Fig. 3): Low (0-1000 Hz), Middle (1000-3000 Hz) and High (more than 3000 Hz). Fourteen of the 21 birds had syllables of all groups in their songs. Figure 4 shows the effect of deafening in these 14 birds on the number of syllables of each group (mean ± SEM). After the operation, syllables of the Middle and High groups significantly decreased ($p < 0.05$ and $p < 0.001$, respectively), and syllables of the Low group increased ($p < 0.01$). Of the remaining 7 birds, six had syllables of the Low and Middle groups but not of the High group, and one had only syllables of the Low group. In these 6 birds, syllables of the Middle group decreased significantly ($p < 0.05$) after the operation, while syllables of Low group tended to increase (Fig. 5). In the remaining bird, the total number of Low group syllables per 20 sec decreased after the operation from 99.5 to 65.5, but no statistical analysis could be performed because of the small sample size ($n = 1$). All

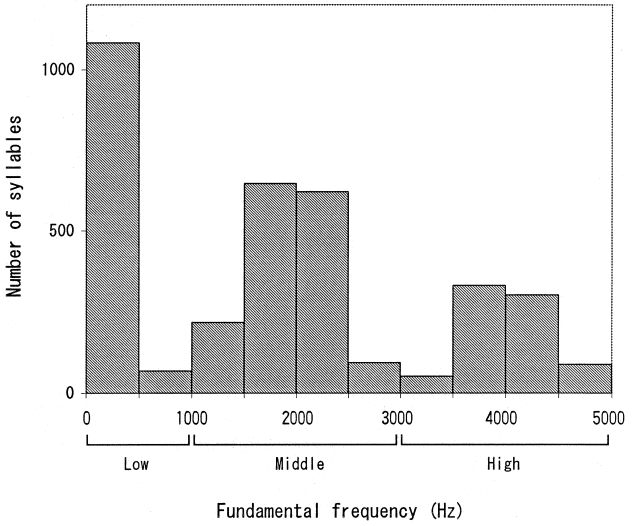


**Fig. 3.** Distribution of fundamental frequencies (FFs) of the syllables contained in the pre-operative songs (recorded within 3 days before surgery) of the 21 birds. Vertical axis shows total number of the syllables in 20 sec. Three peaks depict "Low group" (0-1000 Hz), "Middle group" (1000-3000 Hz), and "High group" (over 3000 Hz).

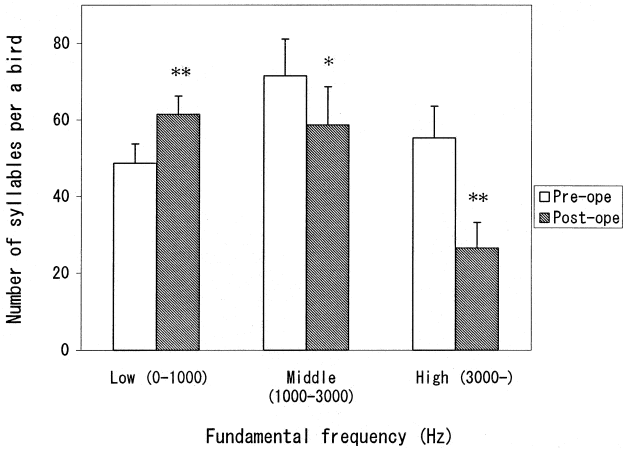


**Fig. 4.** Numbers of syllables in pre- and post-operative songs of 14 birds which had syllables of all (Low, Middle, and High) groups. In each column, left bar shows mean number of syllables in 20 sec of the pre-operative song (recorded within 3 days before surgery), and right bar shows that of 60-day post-operative song. Error bars indicate SEM. Asterisks indicate that syllables increase or decrease significantly after the operation (*, $p < 0.05$; **, $p < 0.01$; Wilcoxon signed rank test).

syllable types of this bird were grouped in the Low group, but a syllable type with the highest FF (424.0 Hz) among them was remarkably decreased.

## DISCUSSION

Our results, as well as two other recent studies (Okanoya and Yamaguchi, 1997; Woolley and Rubel, 1997), showed that the song pattern of adult Bengalese finches is altered after deafening by bilateral cochlear removal. This observa-

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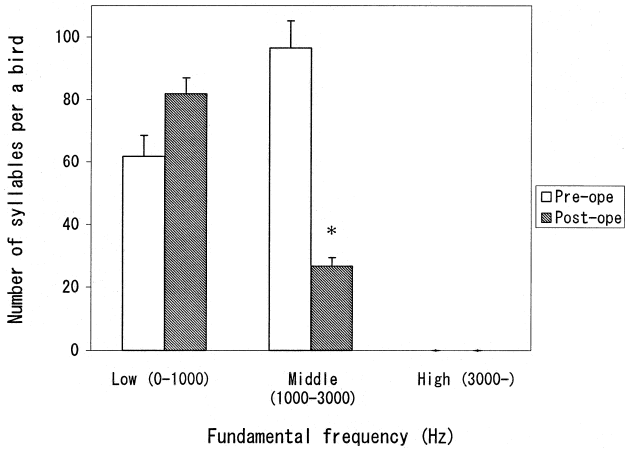


**Fig. 5.** Numbers of syllables in pre- and post-operative songs for 6 birds which had syllables of the Low and Middle groups. All other details are as in Fig. 4.

tion resembled the results of Nordeen and Nordeen (1992) in zebra finches which showed that auditory input is needed to produce the stereotyped adult bird song. These data strongly suggest that adult birds which have already acquired a stable song pattern still need auditory feedback to maintain their stable songs after a sensitive period of song learning.

Deafening of Bengalese finches noticeably disrupted the pre-operative song and finally produced stable post-operative song. Although the song patterns remained alterable for approximately a month after the operation, they were stabilized thereafter in all the deafened birds. The production of the stable post-operative song may occur somewhat differently among individuals (Fig. 1), but in every bird this process was accompanied by remarkable loss of syllables with higher FFs from the pre-operative song. In contrast, syllables with lower FFs increased in the post-operative song, implying that the absence of syllables with higher FFs was compensated by those with lower FFs. Thus, our results suggest that auditory feedback plays an important role in maintaining adult bird song by retaining the syllables with higher FFs.

The deafened birds' ability to maintain stable post-operative songs raises a possibility that their motor system can reproduce the post-operative songs autonomously without any sensory feedback. However, it is possible that the deafened birds maintain their songs using non-auditory feedback. Schwartzkopff (1949) reported that deafened bullfinches discriminated vibratory stimuli by mechanoreceptors called Herpst corpuscles. The vibration of the syrinx as they sing may thus be propagated through their bodies. Because lower-frequency vibration is generally harder to attenuate than that with higher frequency, syllables with lower frequencies should be more easily received by the somatic sensory system as vibratory stimuli. Considering that the post-operative songs consist mainly of the syllables with lower FFs, it is likely that birds maintained their post-operative songs using somatosensory feedback from vibration of the syrinx.

Proprioceptive feedback may provide another form of non-auditory feedback to maintain the post-operative song (Konishi, 1965). Histological study revealed the existence of afferent neurons in the hypoglossal nerve originating in the syringeal muscles (Bottjer and Arnold, 1982). Thus, birds may also receive proprioceptive feedback from the syrinx when they sing, although it cannot explain why deafened birds retain syllables of a particular frequency. However, Bottjer and Arnold (1984) demonstrated that eliminating proprioceptive feedback from the syrinx by cutting the hypoglossal afferent fibers did not affect the songs of deafened adult zebra finches.

In conclusion, our results demonstrated that for a month after deafening, the songs of all birds altered, showing a decreased number of syllables with higher FFs, and stayed stable thereafter. Our findings suggest that adult Bengalese finches use auditory feedback to retain syllables with higher FFs in their normal song and that syllables with lower FFs can be retained without auditory feedback. Further experiments are needed to identify other sensory mechanisms which may play a role in maintaining adult bird song.

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