The Role of Learned Acoustic Structure in the Song of the Budgerigar, *Melopsittacus undulatus*

Hiroko Eda-Fujiwara^{*1)}, Aiko Watanabe* and Takeji Kimura*

Abstract. We examined the functional significance of learned acoustic structure in Budgerigars, a species of Psittaciformes in which vocal learning is common. We compared the acoustic structure of normal song to the song of males deafened early in life. The 'deaf song' differed from normal song in the structure of its component sounds. In playback experiments, normal male song elicited more song from male subjects than did the deaf song. The results are discussed in terms of the possible roles that learned acoustic structure plays in male-male communication among Budgerigars.

Key words: Deafening, *Melopsittacus undulatus*, Vocal learning.

キーワード: 聴覚遮断, セキセイインコ, 音声学習.

Introduction

In birds, vocal learning has been observed among parrots (Psittaciformes), hummingbirds (Apodiformes), and songbirds (Oscines, Passeriformes), while it is not known in several bird species of other taxonomic groups (Catchpole & Slater 1995). Konishi (1985) mentioned in his review article that the use of auditory feedback control in the song development of birds resembles learning by trial and error; he referred to song development by auditory feedback control as "song learning". Thus, vocal learning is not evident in birds that can develop normal vocalizations without auditory feedback.

What is the functional significance of vocal learning? This question has been addressed mainly for oscine songbirds (Slater 1989). Some playback experiments have provided evidence that learning increases the potency of song in male-male and/or male-female communication (Searcy *et al.* 1985, Searcy & Marler 1987). When adult Song Sparrows (*Melospiza melodia*) are exposed to songs of conspecific males that have been reared in acoustic isolation or have been deafened early in life, territorial males respond more aggressively to playback of songs of isolated males than to songs of deafened males (Searcy & Marler 1987). Another study showed that male territory owners responded more to conspecific natural songs than to 'isolate' songs (Searcy *et al.* 1985). However, in non-oscine birds, there is no evidence related to vocal learning.

In this study, we addressed the question: what is the functional significance of learned acoustic structure in male-male interactions among Budgerigars? Budgerigars produce long complex vocalizations known as the warble song. Both sexes vocalize warble songs, although males warble more frequently than females (Brockway 1969). Warble song is

Received 1 February 2002, Revised 23 May 2002, Accepted 12 June 2002.

* Department of Chemical and Biological Sciences, Japan Women's University, Mejirodai, Bunkyo-ku, Tokyo 112-8681, Japan.

¹⁾ E-mail: hirofujiwa@fc.jwu.ac.jp

comprised of a sequence of elements with silent intervals between them. The spectral structure of warble elements greatly changes through learning (Eda-Fujiwara & Okumura 1992, Farabaugh *et al.* 1992, Eda-Fujiwara *et al.* 1995). The warble song plays a crucial role in the reproduction of this colonial species; hearing the warble song stimulates females to occupy nest boxes (Brockway 1969). The warble song of others stimulates warbling in males, which in turn adds to the social vocal stimulation of the group (Brockway 1968). Social facilitation by this vocal behavior is salient to reproduction in colonial Budgerigars, since the warble song promotes the attainment of full gonadal activity in both sexes (Brockway 1969).

Budgerigars deafened early in life produce abnormal warble songs (Eda-Fujiwara *et al.* 1995). In the first part of this study, we conducted a more detailed acoustic analysis, compared to a previous study, and show quantitative differences between the normal song and the song of males deafened early in life. We then attempted to resolve the question posed above by means of playback experiments. A functional song is one that elicits warble songs from other males in a colony. Therefore, we expected that the song of males that were deafened early in life might induce less singing in normal males. We made comparisons between male responses to the song of normal males and male responses to the song of deafened males.

Methods

Song analysis

Two sets of song recordings were used for song analysis: normal warble songs from six male Budgerigars and deaf songs from three males. All males were obtained from a local pet supplier, and three of them were deafened bilaterally by extirpation of the cochlea at about 28 days of age, following the procedure described by Konishi (1963) under Nembutal anesthesia. Cochlea removals were confirmed by examination of the extirpated basilar papillae.

Both the normal and deafened birds began to vocalize warble songs at two to three months of age. In contrast to oscine songbirds, the song development of Budgerigars does not undergo several stages such as the subsong, the plastic song, and, after crystallization, the full song. Hence the recording sessions were interspersed over a period of several months between five and ten months of age for both the normal and deafened birds, because deafened birds tended to warble more frequently during this period than in later periods. In each recording session, the warble song was recorded with a cassette recorder (Sony TC-D5 PRO) through a condenser microphone (Sony ECM-150T) in a quiet room. During recording, the bird was isolated in an individual wire cage. The deafened birds were housed individually, like the normal birds, and vocalized the warble song without facing another bird.

There is no fixed length for a warble song, and a bout of warble song can last from a few seconds to several minutes. When a Budgerigar stopped vocalizing for 1 s or more, we considered the song to have ended. Farabaugh *et al.* (1992) provided a sonographic description and a classification of the constituent syllables of the Budgerigar warble song.

Fig. 1. Sonograms of portions of representative warble song bouts from a normal bird (upper) and a deafened bird (lower). Asterisks above the sonograms indicate 'contact' syllables.

They proposed that a silent interval greater than or equal to 65 ms separates one syllable from another, and we adopted this syllable definition in our study. We sampled and analyzed at least 90 s of song bouts, an average of 275 syllables (range=150–597) recorded from each individual with a Kay Elemetrics DSP Sonagraph model 5500, using a 300-Hz analysis bandwidth.

Farabaugh *et al.* (1992) identified 42 warble-syllable classes. The 'contact'-syllable class was the most commonly produced (Fig. 1). Therefore, we calculated the proportion of contact syllables in song samples. Of a total of 2478 syllables, 360 were examined by three observers, two of whom were not familiar with the predictions of the analysis. The observers were given sonograms of representative examples of contact syllables (Fig. 3 in Farabaugh *et al.* 1992). They were also given sonograms of 14 contact calls recorded from different Budgerigars (Fig. 1 in Brown *et al.* 1988), because both contact calls and contact syllables are narrowband sounds with a duration of 100–300 ms and are strongly frequency modulated, primarily within the range of 2–4 kHz. Observers were asked to select contact syllables from among three song bouts of three normal males and from three song bouts of three deaf males. Of the 182 syllables made by the three deafened birds, no syllable was placed in the contact syllable class by any of the three observers. Of the 178 syllables made by the three normal birds, 66 syllables were placed in the contact syllable class by at least two of the observers; of these, 59 were placed in the contact syllable class by all three observers. We considered that deaf song could reliably be compared to normal song by the one observer who was familiar with the predictions of the analysis. Thus, this observer examined the remaining 2118 syllables, and these results are described below. We used a two-tailed Fisher's exact probability test for the comparison between normal and deafened males.

Playback Experiment

The playback song was chosen from the recordings used in the song analysis. Song was digitized with a 16-bit resolution at a 32-kHz sampling rate, using a computer-based system (Canopus Sound Master) and a computer (Epson PC286-US). The duration of a song bout is usually too long for repeated presentation in playback experiments. We

therefore selected a segment about 10 s long (song segment) from a song bout. Song segments were edited and then recorded at equal amplitudes from the computer D/A onto the recorder.

We used 10 adult male Budgerigars obtained from a local pet supplier and held in a penthouse with each bird caged singly. We conducted the experiment from 13 May to 10 July 1998. Each bird was used only once within an experiment. We performed the experiment using a within-subjects design and compared the responses of the subjects to two kinds of song-segment stimuli (normal and deaf song segments).

Trials were conducted using a single speaker. Responses of each bird to alternating playback of two different stimuli were compared. Birds were isolated individually in a sound attenuation chamber. Each male was acclimated to the chamber for at least 15 h before each trial. During each trial, the playback tapes were played through the digital cassette recorder and speaker (Kenwood AS-5). The peak value of the playback stimuli, measured 20 cm away from the speaker, was 90 dB SPL (Rion Sound Level Meter model NA-14, A-weighting, slow response). Ferrell & Baptista (1982) suggested that most warbling activity by Budgerigars is confined to the morning hours. Two different stimuli alternated for 2 h, from 0800 to 1000. The first song segment was assigned randomly before the 2 h of playback trial to control for order effects. We used the same sound attenuation chamber throughout this study, thus setting all birds visually in the same condition.

For the ten subjects we used five song segments from five normal males and five song segments from two deaf males. Each of the subjects had had auditory experience with, but no visual and tactile experience with, both of the birds used for the paired stimulus. In 2 h of a playback trial, 2-min blocks of each of the paired segments alternated with succeeding blocks separated by 1 min of silence. A song segment was broadcast every 20 s, for six repetitions per block. In normal warble song segments, the elements (the smallest units of song) are produced at characteristically short intervals (Eda-Fujiwara *et al.* 1995). All segments showed the temporal pattern characteristic of warble song. We made the number of elements per segment constant across each stimulus pair.

For each playback trial, vocal behaviors of subjects were recorded for 2 h. We counted the number of 10-s intervals in which at least one song was produced, not the number of songs, as the response for each of the two paired stimuli. We used two-tailed Wilcoxon's matched-pairs tests for the comparison of responses by males to normal and deaf songs.

Results

More of the normal males (6/6) vocalized song that included contact syllables than did deafened males (0/3; Fisher's exact probability test, $p < 0.02$). In normal song bouts, the percentage of 'contact' syllables for each bird ranged from 15–46%, with an average percentage of 31%.

Males vocalized more warble song in response to normal song segments than to deaf song segments when these two stimuli were paired (Table 1, $t = 7.5$, $n = 10$, $p < 0.05$). This result suggests that male Budgerigars are more responsive to normal than to deaf song.

Table 1. The warble song score given by male Budgerigars in response to the playback of normal and deafened song segments.

Individual	Response to	
	Normal	Deaf
6MG	67	73
6SE	21	4
6SB	3	1
8JA	29	14
5MB	10	3
8FD	22	18
7AA	2	0
6MJ	0	1
6SC	1	0
6MI	144	117

Discussion

In this acoustic analysis, we compared song bouts of normal males to those of males deafened early in life. 'Contact' syllables are the most common syllable type produced in the normal warble song (Farabaugh *et al.* 1992). Deaf birds, however, produced song bouts that contained no contact syllables.

There are two main vocal states in the Budgerigar, the warble state (WS) and the chedelee state (CS; Eda-Fujiwara *et al.* 1995). WS and CS have respective characteristic temporal patterns, a feature that appears in longer continuous acoustic samples (18 sec). In the CS, birds usually repeat chedeleees, which have also been referred to as contact calls by other researchers (Dooling *et al.* 1987, Brown *et al.* 1988). Budgerigars use contact calls as warble song syllables, termed 'contact syllables' by Farabaugh *et al.* (1992). In birds deafened early in life, two main vocal states are observed, and WS and CS have the same respective temporal patterns as those of normal Budgerigars. However, calls vocalized in the CS of early-deafened birds lack the rapid prominent frequency modulation characteristic of contact calls in the CS of normal birds. (Dooling *et al.* 1987). In our acoustic analysis, we found few contact syllables in deaf warble songs, possibly because the birds were unable to learn the characteristic frequency modulations.

Male Budgerigars vocalized more warble song in response to normal song segments than to deaf segments. This result suggests that learned acoustic structure increases the adaptive value of song in male-male communication. The 'contact'-class syllable is a possible reason for the stronger response to normal song segments. On the other hand, deaf song has the same characteristic temporal pattern as the normal song at the level of overall song organization (Eda-Fujiwara *et al.* 1995). The temporal pattern may be responsible for the response evoked by deaf song segments.

Sharing acoustic characteristics with particular conspecifics is thought to serve in the integration and cohesion of a pair or a flock (Farabaugh *et al.* 1994). Male Budgerigars share a significantly greater percentage of their warble syllable-class repertoire with males

of the same social group than with males of different groups (Farabaugh *et al.* 1992). Such vocal convergence is achieved in contact calls through mutual vocal imitation of social companions (Farabaugh *et al.* 1994). Contact calls are produced when birds are separated from flock mates, in flight or when preparing for the evening roost (Wyndham 1980). Farabaugh *et al.* (1994) suggested that shared contact calls might aid in synchronizing and coordinating the movements and activities of flock members. Coupled with the results from our study, this indicates that learned acoustic characteristics may increase the survival value of vocalizations in the Budgerigar.

References

- Brockway, B. F. 1968. Influences of sex hormones on the loud and soft warbles of male Budgerigars. *Animal Behaviour* **16**: 5–12.
- Brockway, B. F. 1969. Roles of Budgerigar vocalization in the integration of breeding behaviour. In *Bird vocalizations* (ed. R. A. Hinde), pp. 131–158. Cambridge Univ. Press.
- Brown, S. D., Dooling, R. J. & O'Grady, K. 1988. Perceptual organization of acoustic stimuli by Budgerigars (*Melopsittacus undulatus*): III. Contact calls. *Journal of Comparative Psychology* **102**: 236–247.
- Catchpole, C. K. & Slater, P. J. B. 1995. *Bird song. Biological themes and variations*. Cambridge Univ. Press.
- Dooling, R. J., Gephart, B. F., Price, P. H., McHale, C. & Brauth, S. E. 1987. Effects of deafening on the contact call of the Budgerigar (*Melopsittacus undulatus*). *Animal Behaviour* **35**: 1264–1266.
- Eda-Fujiwara, H. & Okumura, H. 1992. The temporal pattern of vocalizations in the Budgerigar, *Melopsittacus undulatus*. *Journal of Yamashina Institute for Ornithology* **24**: 18–31.
- Eda-Fujiwara, H., Watanabe, A. & Okumura, H. 1995. Effects of deafening on the temporal pattern of vocalizations in the Budgerigar *Melopsittacus undulatus*. *Journal of Ethology* **13**: 145–152.
- Ferrell, R. & Baptista, L. F. 1982. Diurnal rhythms in the vocalizations of Budgerigars. *Condor* **84**: 123–124.
- Farabaugh, S. M., Brown, E. D. & Dooling, R. J. 1992. Analysis of warble song of the Budgerigar *Melopsittacus undulatus*. *Bioacoustics* **4**: 111–130.
- Farabaugh, S. M., Linzenbold, A. & Dooling, R. J. 1994. Vocal plasticity in Budgerigars (*Melopsittacus undulatus*): evidence for social factors in the learning of contact calls. *Journal of Comparative Psychology* **108**: 81–92.
- Konishi, M. 1963. The role of auditory feedback in the vocal behavior of the domestic fowl. *Zeitschrift für Tierpsychologie* **20**: 349–367.
- Konishi, M. 1985. Birdsong: from behavior to neuron. *Annual Review of Neuroscience* **8**: 125–170.
- Searcy, W. A. & Marler, P. 1987. Response of sparrows to songs of deaf and isolation-reared males: further evidence for innate auditory templates. *Developmental Psychobiology* **20**: 509–519.
- Searcy, W. A., Marler, P. & Peters, S. S. 1985. Songs of isolation-reared sparrows function in communication, but are significantly less effective than learned songs. *Behavioral Ecology and Sociobiology* **17**: 223–229.
- Slater, P. J. B. 1989. Bird song learning: causes and consequences. *Ethology Ecology and Evolution* **1**: 19–46.
- Wyndham, E. 1980. Diurnal cycle, behaviour and social organization of the Budgerigar *Melopsittacus undulatus*. *Emu* **80**: 25–33.

セキセイインコ *Melopsittacus undulatus* のさえずりにおける学習の役割

セキセイインコは学習によってさえずりを発達させる。本研究では、正常個体が音声学習によって獲得する音響的構造の重要性を検討した。まず、正常個体と幼鳥時に蝸牛管除去された個体（聴覚遮断個体）からさえずりを録音し、音声解析を行った。聴覚遮断個体のさえずりは、各構成要素の音響的構造に異常が見られた。次に、録音されたさえずりを雄セキセイインコに聞かせて反応を比較した。聴覚遮断個体よりも正常個体のさえずりの方が有意に強い発声反応を誘発した。学習によって得られた音響的構造がセキセイインコ雄間のコミュニケーションにおいて果たす役割に関して、本研究の結果を議論する。

藤原宏子*・渡辺愛子・木村武二：日本女子大学理学部物質生物科学科。〒112-8681 東京都文京区目白台 2-8-1.

* E-mail: hirofujiwa@fc.jwu.ac.jp