Effects of deafening on the calls and warble song of adult budgerigars (*Melopsittacus undulatus*)

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Budgerigars are small Australian parrots that learn new vocalizations throughout adulthood. Earlier work has shown that an external acoustic model and auditory feedback are necessary for the development of normal contact calls in this species. Here, the role of auditory feedback in the maintenance of species-typical contact calls and warble song in adult budgerigars is documented. Deafened adult birds (five male, one female) vocalized less frequently and showed both suprasegmental and segmental changes in their contact calls and warble song. Contact calls of all adult-deafened budgerigars showed abnormalities in acoustic structure within days to a few weeks following surgery. Within 6 months of surgery, nearly all contact calls produced by deafened birds were strikingly abnormal, showing highly variable patterns of frequency modulation and duration. The warble song of deafened male budgerigars also differed significantly from that of normal budgerigars on several acoustic measures. These results show that auditory feedback is necessary for the maintenance of a normal, species-typical vocal repertoire in budgerigars. © *1999 Acoustical Society of America.* [S0001-4966(99)03702-9]

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INTRODUCTION

It is well known that auditory feedback is critical for normal vocal development and vocal learning in young songbirds. Much less is known about the role of auditory feedback in the maintenance of normal vocal repertoires in adulthood. For the songbird species that have been investigated to date, deafening has a profound effect on the development of learned vocalizations (e.g., Brenowitz and Kroodsma, 1996; Konishi, 1965a, 1965b; Marler, 1991; Nottebohm, 1968), while deafening later in life often yields more complicated and sometimes more subtle effects. Some oscine songbirds such as white-crowned sparrows (*Zonotrichia leucophrys*) and chaffinches (*Fringilla coelebs*) can maintain their vocal repertoire for years if deafened in adulthood after song crystallization (Konishi, 1965a; Konishi and Nottebohm, 1969). The stability of song syntax and phonology in the absence of auditory feedback for these species may be related to the fact that they are closed-ended learners and normally do not change their song-syllable repertoires as adults. Consistent with this notion is the observation that canaries (*Serinus canaria*), who add and delete song notes seasonally throughout adulthood (open-ended learners), show signs of song disruption within a week of deafening, and profound deterioration within a month (Nottebohm *et al.*, 1976; Nottebohm, personal communication, 1997).

More recent experiments with Australian zebra finches (*Taeniopygia guttata*) and Bengalese finches (*Lonchura striata* var. *domestica*) have challenged the simple dichotomy that open-ended learners require auditory feedback for song maintenance and closed-ended learners do not. While both finches are closed-ended learners, zebra finches show signs of song disruption within 1–2 months of deafening, and profound deterioration in song over a period of several months (Nordeen and Nordeen, 1992). Bengalese finches, on the other hand, show marked changes in song structure even within a few days of deafening, followed by deterioration of song phonology similar to that of zebra finches over a matter of months (Okanoya and Yamaguchi, 1997; Watanabe and Aoki, 1996; Wooley and Rubel, 1996). The difference in time course and pattern of vocal degradation between these two species may be related to differences in the flexibility of adulthood song structure (Okanoya and Yamaguchi, 1997). Although neither species normally changes its adult syllable repertoire, zebra finches produce song syllables in a highly stereotyped order, whereas Bengalese finches demonstrate plasticity in syllable ordering or syntax. This suggests that the dependence on auditory feedback for song maintenance in adulthood may be related not only to plasticity of segmental vocal features (e.g., the pitch, amplitude, and duration of syllables), but also to flexibility in suprasegmental features (e.g., the syntax and rate of syllables).

While the requirement for auditory feedback in the development and maintenance of vocal behavior is most conspicuous in humans and songbirds, deafening does affect vocal behavior to a lesser degree in a wide variety of animals. For instance, kittens deafened early in life produce louder calls than normal-hearing kittens even in adulthood (Romand and Ehret, 1984; Shipley *et al.*, 1988). Moreover, the calls of deafened kittens are abnormal in other ways including an elevation of fundamental frequency, an increase in low-frequency harmonics, and a delay in the acquisition of rapid frequency and amplitude modulations (Romand and Ehret, 1984; Shipley *et al.*, 1988). Deafening also has a small but demonstrable effect on both suprasegmental and segmental aspects of many species-typical vocal signals of nonpasserine birds that do not learn their vocalizations (Konishi, 1963; Nottebohm and Nottebohm, 1971).

There is remarkably little information on the effects of

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deafening on vocal output in adult animals that have acquired their species-specific adult repertoire. Studies in humans show that hearing-impaired children use high-pitched vocalizations and show abnormal variations in fundamental frequency and abnormal stress patterns (Martony, 1968; Monsen, 1978a, 1978b, 1979; Smith, 1975). It is also well established that the characteristics of vocal output disintegrate following profound hearing loss in postlingually deafened children (Binnie *et al.*, 1982) and adults (Waldstein, 1990). Recent experiments show that the speech of cochlear-implant patients immediately undergoes specific changes when the implant is turned off (Tobey, 1993).

The present study investigated the effects of deafening on the maintenance of normal calls and songs in a small Australian parrot, the budgerigar (*Melopsittacus undulatus*). Budgerigars are well known for their vocal plasticity and for their ability to learn and imitate a wide variety of complex sounds throughout adulthood (see, for example, Dooling, 1986; Farabaugh *et al.*, 1992; Farabaugh *et al.*, 1994). Since vocal learning is believed to have evolved independently in psittacines and passerines (Nottebohm, 1972), it is of interest to know whether the effects of adult deafening in psittacines are similar to that observed in passerines. As far as we know, there have been no studies of the effects of adult deafening in parrots in spite of the fact that vocal learning appears to be widespread among psittacines (Farabaugh and Dooling, 1996).

Previous studies have shown that budgerigars deafened early in life, or reared in acoustic isolation, fail to develop normal contact calls (Dooling *et al.*, 1987; Dooling *et al.* 1990). The present experiments extend the effect of deafening on the maintenance of learned contact calls and warble song to adult budgerigars. Given that adult parrots show exceptional plasticity in both segmental and suprasegmental vocal features, we expected that budgerigars would demonstrate a high degree of dependence on auditory feedback for the maintenance of normal calls and song.

I. METHODS

A. Subjects

The subjects deafened in these experiments were five adult male and one adult female budgerigars. Four additional adult budgerigars (two male, two female) were used in the behavioral observation experiments. In addition, warble song was analyzed for one adult male budgerigar which was deafened at three weeks of age (Dooling *et al.*, 1987), one adult male budgerigar which was deafened at 9 days of age (Heaton and Brauth, 1996), and two adult male budgerigars which were isolated as nestlings (Farabaugh *et al.*, 1992). These latter birds had been individually isolated from approximately 3 weeks to 8 months of age, but had been living in a large aviary with 50–100 other budgerigars for several months prior to vocal recording. All adult budgerigars had been in our possession for at least one year prior to experimentation; however, since many were purchased from commercial vendors, their exact ages were unknown. The birds were housed and fed in aviaries at the University of Maryland and kept on a normal photoperiod correlated with the season. All procedures were conducted under the auspices of protocols approved by the campus Animal Care and Use Committee.

B. Deafening

The birds were deafened by bilateral extirpation of the cochlea using the procedures described by Konishi (1963) for deafening domestic fowl. Briefly, the deafening procedure involved first anesthetizing each subject with a mixture of ketamine hydrochloride (40 mg/kg, IM) and xylazine hydrochloride (10 mg/kg, IM). Next the tympanic membrane was excised, and the columella and columellar footplate were pulled from the vestibular window with a pair of curved forceps. Finally, using a fine-hooked tungsten wire, the entire basilar papilla and lagena were pulled from the bony labyrinth. The subject's ears were then filled with an antibacterial ointment (Neosporin), and it was given an intramuscular injection of the xylazine-reversing agent yohimbine hydrochloride (0.275 mg/kg; Heaton and Brauth, 1992; Kilander and Williams, 1992). The recovering bird was placed in a humidity- and temperature-controlled incubation chamber until it perched. It was then returned to the vivarium and periodically monitored for signs of discomfort and for complications arising from surgery. Subjects were killed 1–2 years after deafening for postmortem examination of each middle ear to confirm complete extirpation of the cochlea.

C. Recording

Samples of each bird's vocal repertoire were recorded both before and after surgery in a sound-attenuated chamber lined with acoustic foam wedges. The front and top of the chambers were made of clear acrylic (Plexiglas) so that we could elicit vocalizations from subjects by providing visual contact with their cagemates. Calls and song were recorded through an Electro-Voice (model PL50N/D) microphone connected to a Digitech digital-delay system (model RDS4000). Real-time output from the delay board was fed to a Uher Akustomat F411 sound-activated relay switch that turned on a Marantz PMD 221 cassette recorder. This apparatus allowed time-delayed output (1-s delay) of the bird's vocalization to reach the recorder after the tape was at full speed. Approximately 200 contact calls were collected during presurgical recording sessions for each bird. By contrast, birds typically vocalized less frequently after deafening, so some recording sessions lasted for days in order to acquire multiple contact calls. Warble song was particularly rare after deafening and was obtained from only two of the six deafened adult subjects. Warble song was recorded with either a Marantz PMD 221 cassette recorder or a Sony D7 digital-audiotape recorder.

D. Call analysis

Recorded contact calls were digitized with a Kay DSP 5500 sona-graph and stored as computer files (20 480 samples/s). Calls were then analyzed and compared using a commercial digital-signal-processing software package (SIGNAL, Engineering Design, Belmont, MA). A sample of 50 consecutive pre-surgical contact calls was digitized for each subject. Each of the 50 calls recorded before deafening was compared to every other call in the sample (50 calls generated 1225 unique pairwise comparisons) with a spectrogram cross-correlation routine, generating a half matrix of correlation coefficients (similarity scores) ranging from 0 to 1 (Clark, Marler, and Beeman, 1987). Each half matrix of similarity scores for pre-surgical calls was then analyzed with multidimensional scaling (MDS) and average-linkage cluster analysis. Contact-call types (clusters) were identified by examination of both MDS plots and cluster results. The average pair-wise intercorrelations of calls in the call-type groupings that emerged from the cluster analysis were in all cases above 0.70. We then calculated the average similarity (i.e., mean intercorrelation) of each call to the other calls of the same type and ranked them based on these similarity scores. The five calls with the highest intercorrelation were taken as representative exemplars for that contact call type to compare with post-surgical calls, since, by definition, they had the highest average intercorrelation with all other calls of the same type (see Heaton *et al.*, 1995).

Calls recorded after deafening for each subject were compared to each other and to the five exemplar calls of each subject's pre-deafening call type(s) by spectrogram cross correlation. A post-deafening call was considered to be of a particular call type if the average similarity of that call to the five exemplars of any of the pre-surgical dominant types was greater than or equal to a criterion level of 0.65. This criterion level for assignment was intentionally chosen to be lower (by 0.05) than the average similarity of pre-deafening calls of each type to the five best exemplars. This more conservative criterion ensured that we would err on the side of including rather than excluding post-deafening calls that closely resembled a pre-deafening call type. The correlation matrices were then analyzed by MDS to produce a spatial map of the acoustic similarity among pre-surgical and post-surgical contact calls, and spectrograms of these digitized calls were produced with a Kay DSP 5500 sona-graph and a Raytheon TDU-850 gray-scale printer.

To objectively define the number of contact-call types and the average within-type call-similarity scores of normal adult budgerigars, 40 contact calls were digitized for each of five male and five female budgerigars and compared using spectrogram cross correlation. Calls examined for each subject were produced consecutively during either one or two recording sessions occurring no greater than 3 days apart, and recording sessions were conducted at various dates over a 2-year period. Call-similarity scores were analyzed for each subject with both MDS and cluster analysis in order to identify call-type groupings as described previously.

E. Warble song analysis

Budgerigar warble song consists of long sequences of both broadband and tonal syllables that are diverse in structure, ranging from simple clicks to multinote, frequency-modulated tonal syllables (Farabaugh *et al.*, 1992). These syllables are delivered at a variable tempo and variable loudness depending on a variety of social factors, presumably having to do with the animal's level of arousal and reproductive state. Males at some times deliver soft warble in a non-directed fashion while sitting alone on a perch, and at other times deliver much louder warble directed at female birds with great fervor during courtship bouts (Brockway, 1964, 1969; Farabaugh *et al.*, 1992; Nespor *et al.*, 1996). Because of the acoustic complexity of warble, the fact that many of the syllables are not stereotyped, and the high level of variation in temporal delivery, we analyzed the warble syllables reported here on four rather basic characteristics: peak frequency, bandwidth, duration, and the duration of interelement interval. We used these relatively straightforward measures to characterize the warble of six normal adult male budgerigars, and compare these results to the warble of adult birds isolated as juveniles $(n=2)$, deafened as nestlings $(n=2)$, or deafened as adults $(n=2)$ (see Sec. I A).

Recorded streams of warble song were digitized with a Kay DSP 5500 sona-graph and stored as computer files (20 480 samples/s). Measurements from 500 warble elements were made for each subject using a Kay Elemetrics DSP sonograph (model 5500). The dependent variables included peak frequency, 20-dB down bandwidth, interelement interval, and element duration. Settings for the sona-graph in the spectropgraphic analysis mode, were frequency range: 8 kHz, time axis: 1 s/screen, and analysis filter: 300 Hz. Two adjacent sounds greater than 10-ms duration were treated as part of the same syllable if the interval between them was less than 10 ms. For each of the four dependent variables, an average frequency-of-occurrence histogram was obtained for the six intact adult males. Histograms for each of the experimental birds were compared to average histograms of the normal adults using Kolmogorov–Smirnov (KS) tests.

F. Behavioral observations

Nine budgerigars (six males and three females) were housed together in a large cage (60 × 36 × 24 in.) and observed for the occurrence of behaviors which fell into five broad categories: inactive (e.g., sleeping, sitting quietly), maintenance (e.g., eating, preening), vocalizing, aggressive, and affiliative (e.g., nonaggressive interactions). Of these nine birds, four males had been deafened one year earlier. One male and one female budgerigar were observed both before and 1–3 weeks after deafening. Using a procedure of focal animal sampling, the experimenter observed the birds in daily 1/2-h sessions and recorded the total time a bird spent in each of several pre-defined behavioral categories. A total of two and one-half h of behavioral observations was conducted on each bird. Behavior was coded such that a subject was in one of the five categories at all times. Total time spent in each behavioral category was combined for the hearing males $(n=2)$, hearing females $(n=2)$, and deaf males $(n=5)$, and differences in group means were tested with t-tests. Mean times spent in each category measured before and after deafening for one male and one female subject were likewise compared with t-tests.

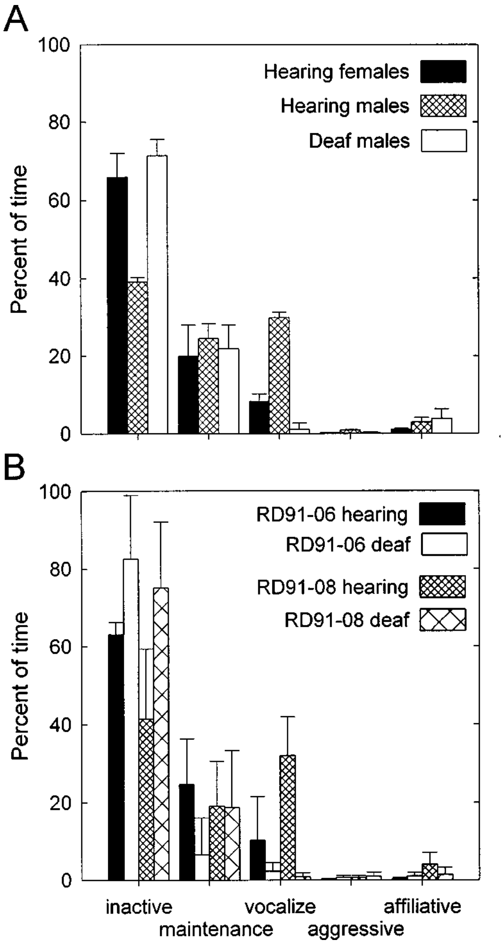

FIG. 1. Histograms (a) showing the percent of time spent in five behavioral categories for hearing females ($n=2$), hearing males ($n=5$), and deaf males ($n=5$), and (b) for a pair-bonded female (RD91-06) and male (RD91-08) budgerigar before and 1–3 weeks after deafening.

II. RESULTS

A. Behavioral observations

The percentage of time that hearing females ($n=2$), hearing males ($n=2$), and deaf males ($n=5$) spent in each of the five behavioral categories is shown in Fig. 1(a). Deafened males were less active than hearing males ($p<0.01$) and vocalized less frequently than hearing birds ($p<0.01$). Hearing females were less active than hearing males ($p<0.01$) but not significantly different from deaf males on this measure. Hearing females also vocalized less than hearing males ($p<0.01$) but vocalized more frequently than deaf males ($p<0.01$). The two birds observed both before and after deafening [Fig. 1(b)] showed similar, significant changes in their behavior in that they both became less active and less vocal after deafening ($p<0.01$).

B. Contact calls

Post-surgical audio-recording sessions were initiated for all six deafened adult budgerigars within 24 h after recovery from anesthesia. Birds were either temporarily housed in the recording chambers or placed there 4–10 h a day for the first 5–7 days after surgery. Recording sessions, each lasting 4–48 h were then conducted 1–2 times per week for 2 months, and then 1–2 times per month for a year. In spite of this fairly intensive recording schedule, two of the six budgerigars failed to produce a sufficient amount of warble song or contact calls to analyze, and thus they were dropped from further consideration. A somewhat intermediate response was observed in subject Red Three, who did not vocalize in the recording chambers for the first 8 weeks after surgery but did produce a sufficient number of calls thereafter. By contrast, numerous contact calls were obtained from the other three budgerigars during the first 1–2 weeks after deafening. Thus, in terms of the frequency of vocalizing, there was considerable variation in response to cochlear removal, from a near-total lack of calling to only a slight reduction in calling rate. The reduction in calling rate following deafening was both significant and unusual, since pre-surgical recording sessions for these and other birds typically yielded hundreds of calls within a matter of hours. These results were entirely consistent with the overall reduction of vocal behavior of deafened birds noted in our behavioral observation experiments.

Contact calls recorded during the first 2 months after surgery for subjects Red Four, Orange Nine, and RD91-08 showed a dramatic change in call stereotypy compared with pre-surgical calls. These changes were evident both by inspection of spectrograms and by quantitative analyses by MDS. MDS plots of spectrogram similarity scores for calls produced by two of these birds before deafening are shown in Fig. 2(a). Figure 2(b) shows spectrograms of five call exemplars from each call category (cluster) shown in Fig. 2(a). Of the three deafened birds that vocalized most frequently, subject Orange Nine showed relatively less initial vocal disruption, whereas contact calls from the other two birds, as well as the first calls recorded from subject Red Three at 2–6 months after deafening, showed little resemblance to their pre-surgical call patterns. To illustrate this difference in pre- versus post-surgical contact-call production between birds, MDS plots of spectrogram-similarity scores are compared in Fig. 3 for a bird from each pattern of disruption: Orange Nine (less initial, more gradual disruption) and Red Four (more rapid call disruption). Since each MDS plot is calculated independently from the others, the salient point across time periods is that calls produced after deafening are scattered and no (Red Four) or only a few (Orange Nine) post-deafening calls fall near the tight clusters of pre-deafening calls. Spectrograms of these aberrant calls for each bird are shown in Fig. 4.

Due to the variability in timing of successful post-surgical recording sessions, contact calls were grouped for analysis into three broad post-surgical time frames: 0–7 weeks, 2–9 months, and greater than 1 year. Although calls recorded in the first time frame were obtained over several recording sessions, sometimes separated by several weeks, there was no clear relationship (either between or within subjects) between time from surgery and degree of vocal disruption. This was based on both spectrogram cross-correlation analysis with pre-surgical exemplars (see Sec. I) and visual inspection of spectrograms. Across the three time periods after deafening, however, phonological changes were evident in the spectrograms of each subject's contact calls (shown in

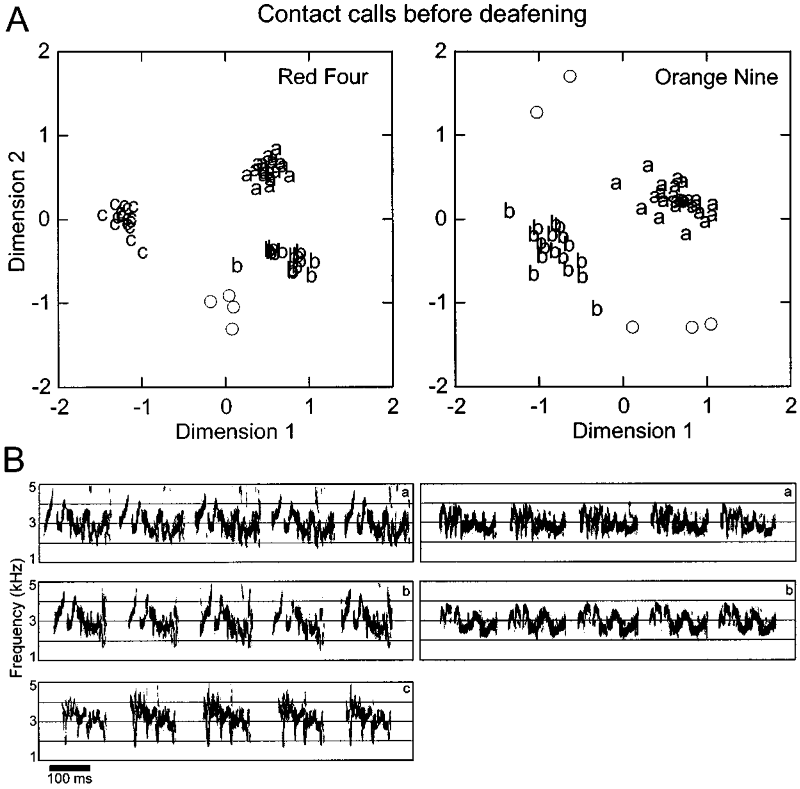

FIG. 2. Contact calls before deafening for subjects Red Four and Orange Nine. (a) MDS solutions depicting call similarity for 50 pre-deafening contact calls each from subjects Red Four and Orange Nine. Subject Red Four had three distinct call types (a), (b), and (c), with average similarities of 0.78 (±0.02), 0.78 (±0.04), and 0.82 (±0.04), respectively. Subject Orange Nine had two call types (a) and (b), with average similarities of 0.77 (±0.04) and 0.73 (±0.06), respectively. Each bird had 4–5 calls which did not fall into a particular call type (open circles). (b) Spectrograms depict the five exemplar calls of each dominant call type. These calls had the highest average intercorrelation with all other calls of the same type.

Figs. 3 and 4). Along with a continued lack of stereotypy, contact calls from all four subjects showed a drop in frequency across the length of each call. Thus, spectrograms of these calls showed an overall downward-sweeping pattern even 1 year after deafening. This was evident not only in randomly selected post-surgical contact calls from subjects Orange Nine and Red Four, but also in the post-surgical calls from Orange Nine which were the most similar to his pre-surgical call patterns (Fig. 5).

Previous work has shown that both male and female adult budgerigars typically have one to several dominant contact-call types in their repertoires (Farabaugh *et al.*, 1994). The subjects in this experiment had four (Red Three), three (Red Four), two (Orange Nine), and one (RD91-08) dominant call types prior to deafening as determined by spectrogram cross-correlation values (see Sec. I). Only 2%–16% of the pre-deafening contact calls for these birds failed to fall into a particular call type (see, for example, open circles in Fig. 2). Within a year of deafening the reverse was true, with only 0%–6% of post-deafening contact calls for each bird meeting the criterion for inclusion into a pre-deafening call type. The few calls of deafened birds that did match a pre-surgical call type always matched the bird's most frequently produced call type prior to deafening.

The calls of these four subjects 1 year or longer after deafening were extremely variable, phonetically degraded, and typically bore little resemblance to the contact calls of intact birds. Although the calls of deafened birds showed the characteristic overall downward-sweeping pattern in frequency, they also continued to show variable patterns of frequency modulation. Consequently, new call types or clusters were not clearly identifiable either visually (by inspection of spectrograms) or quantitatively from post-surgical recording sessions (see Fig. 3)—something which is unusual since budgerigars typically maintain highly stereotyped contact-call patterns even when learning new calls as adults (cf. Farabaugh *et al.*, 1994; Trillmich, 1976a, 1976b). For example, the contact-call repertoires of ten normal adult budgerigars contained an average of 2.4 call types (s.d.$=$1.07), and calls within each type had an average similarity of 0.74 (s.d. $=$0.076). Most notably, of the 40 calls examined for each normal subject, only 0%–17.5% ($x = 7.75\%$, s.d.$=$5.71%) failed to fall within a call type, whereas 94%–100% of the deafened birds' calls failed to fall into call types 1–2 years after deafening. Figure 6 shows the percent of sampled calls that fell into call types both before and after deafening for all four subjects.

Calls produced by Orange Nine were initially less affected by deafening than were the calls of the other birds. Post-mortem examination of the bony labyrinths from all of the deafened subjects, with special attention paid to those of Orange Nine, showed that the basilar papillae of these birds had been completely extirpated during surgery.

C. Warble song

The warble song of adult subjects either deafened or isolated as juveniles, or deafened as adults, sounded abnormal to the human ear. The warble song of deafened subjects, in particular, sounded extremely monotonous, with relatively little variation in frequency and temporal patterning. Figure 7 shows brief streams of warble from two normal adult males, two birds deafened as adults, and one bird deafened at 3 weeks of age. As can be seen, the warble of deafened birds lacks the temporal and spectral complexity evident in the song of intact birds.

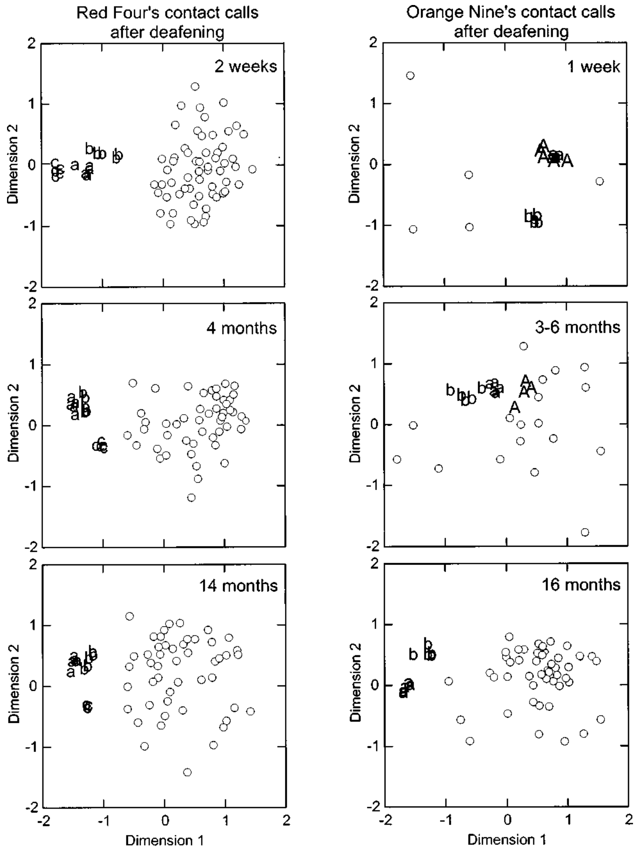

FIG. 3. MDS solutions for spectrogram cross-correlation scores of call similarity for post-deafening contact calls at three time points after deafening with the five exemplars from each pre-deafening call type for birds Red Four and Orange Nine (shown in Fig. 2). Lower-case letters indicate the exemplar calls themselves, upper-case letters indicate calls that met criterion for similarity to the exemplars, and open circles indicate calls that did not reach criterion for similarity to any of the pre-deafening call types. (Left) Red Four did not produce any calls which met the criterion for similarity to a pre-surgical call type. (Right) Five contact calls (top panel) recorded from Orange Nine during the first week after deafening met the criterion for similarity to call type (a) and five calls were not similar to the pre-deafening calls or to each other. Seven calls out of 22 recorded 3–6 months after deafening met the criterion for similarity to call type (a) and at 16 months no calls met criterion out of 49 calls measured from one recording session.

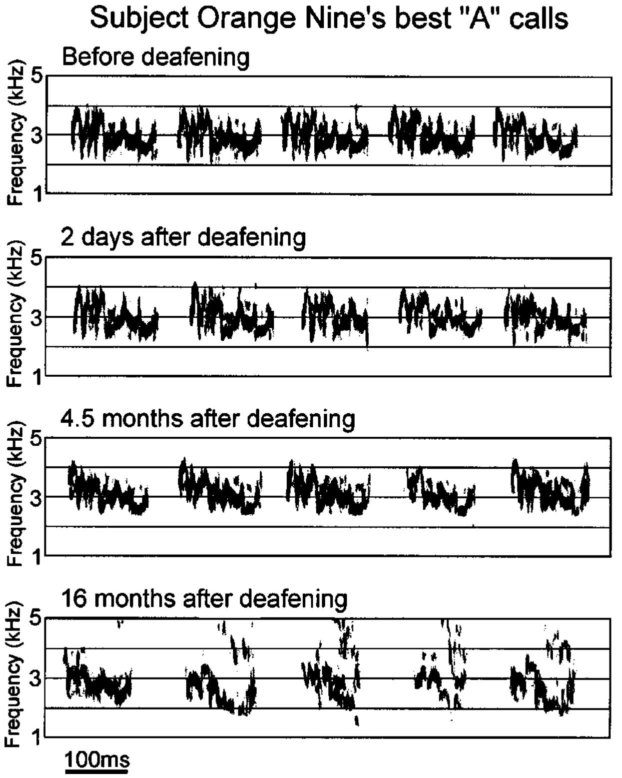

FIG. 5. Spectrograms of the five best type (a) contact calls from before deafening, and the five calls that were most similar to these calls during each of three time periods after deafening for subject Orange Nine, who showed the most gradual deterioration. At 2 days after deafening the calls still looked very similar to pre-deafening (a) calls. Four months after deafening, this bird's calls were beginning to show change from the pre-deafening. By 16 months after deafening the calls retained little of the original spectral characters of the pre-deafening type (a) calls and also began to show an overall drop in frequency of the call.

Warble-song elements were analyzed along four basic characteristics: peak frequency, bandwidth, duration, and duration of interelement interval. The average frequency distributions of warble-element values were compared for experimental-versus-control subject groups using multiple KS tests (see Table I). Comparisons with the frequency distributions from control birds were made individually for the two subjects deafened as adults, since warble-element parameters were differentially affected for these two birds (see Sec. III). Values for the pairs of subjects in the other experimental conditions were grouped for comparisons with control birds, since deafening or isolation affected these birds similarly. Warble-element parameters which differed signifi-

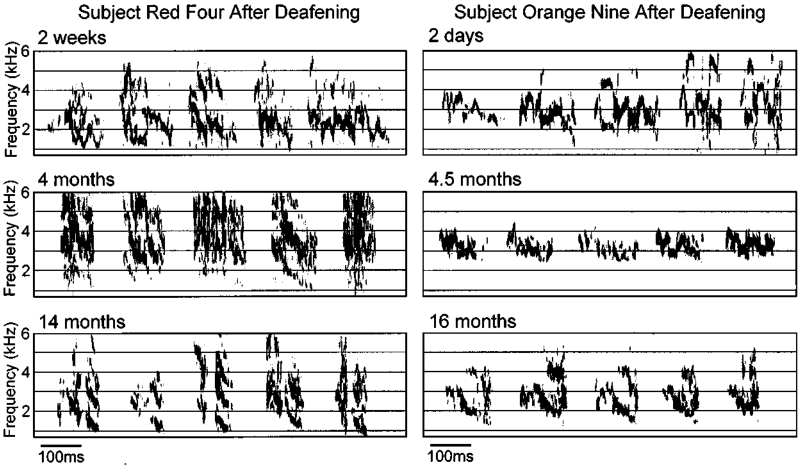

FIG. 4. Spectrograms of randomly selected calls from birds Red Four (left) and Orange Nine (right) at the three post-deafening time periods described in Fig. 3.

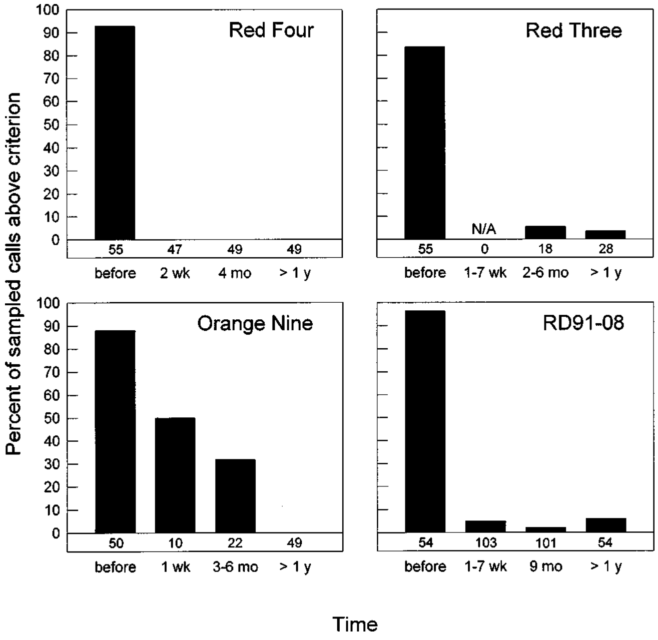

FIG. 6. Histograms of the percentage of sampled contact calls which met criterion for inclusion in a predeafening call type for four subjects. The number of calls analyzed for each time period is given below the histogram bar.

cantly from controls ($p < 0.05$) are presented in bold text in Table I.

As an example, the average frequency distributions for two adult subjects deafened as juveniles are compared with the values from six normal control subjects in Fig. 8. In this example, warble element-value distributions for the deafened birds appeared notably different from those of normal subjects on three of the four element characteristics, which was-consistent with the statistical findings of the KS tests. The two subjects deafened as juveniles showed the greatest disruption of warble-song features compared to birds deafened as adults or isolated as juveniles.

III. DISCUSSION

Budgerigars can learn new contact calls throughout adulthood. At any given time a bird may produce one to several dominant call types, and birds caged together in the laboratory typically come to share call patterns within a matter of weeks (Dooling, 1986; Farabaugh *et al.*, 1994). Despite this proclivity for vocal learning in adulthood, dominant call types remain highly stereotyped over time and are produced with considerable precision even as new call types are learned (Farabaugh *et al.*, 1994; Trillmich, 1976a, 1976b). In this study, we show that the maintenance of normal contact-call and warble-song repertoires in budgerigars is dependent on auditory feedback.

Adult budgerigars deafened by cochlear removal exhibited dramatic instability in contact-call frequency-modulated patterns. In some birds, these changes were evident in the calls recorded even a few days after deafening and were noticeable in all birds a few months after deafening. The calls of deafened budgerigars were abnormal by spectro-

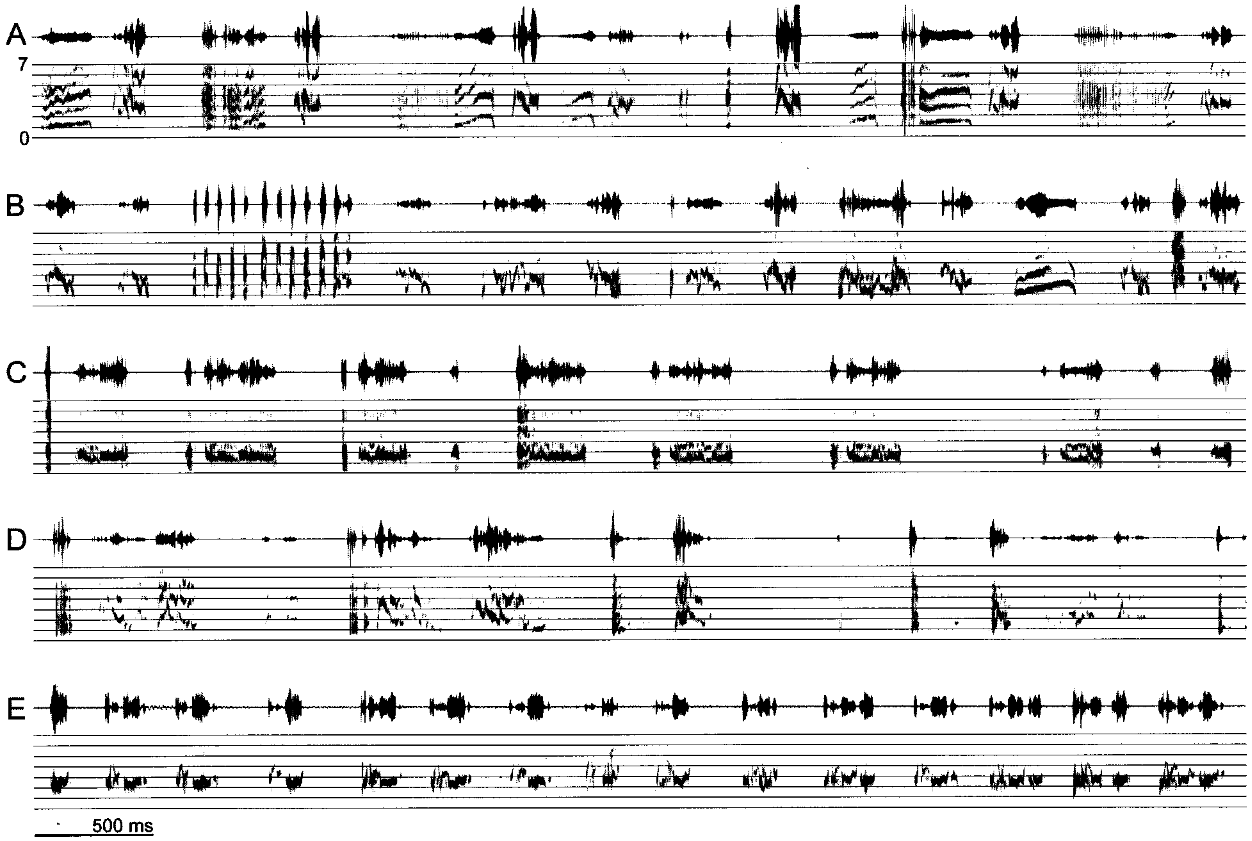

FIG. 7. Streams of warble from two normal adult males (A and B), two birds deafened as adults (C and D), and one bird deafened at 3 weeks of age (E).

TABLE I. Kolmogorov–Smirnov nonparametric two-sided probability tests of warble-element distributions. Probability values indicating statistical significance are shown in bold.

Subjects and condition	Disrupted element parameters	Bandwidth	Peak frequency	Element duration	Interval duration
Deafened as nestlings					
95-48 and Q-DJ	3/4	**0.001**	**0.001**	**0.034**	0.130
Deafened in adulthood					
Orange	2/4	**0.001**	**0.001**	0.228	0.564
RD91-08	1/4	0.604	0.260	**0.016**	0.373
Isolated as nestlings					
ISO-1 and ISO-2	2/4	**0.001**	**0.044**	0.373	0.937

graphic inspection and by objective, quantitative methods. Calls of deafened budgerigars did not resemble pre-surgical call exemplars and showed high variability from rendition to rendition. Long-term changes in the patterns of frequency modulation included a decrease in tonal quality and an increase in bandwidth, even in calls for subject Orange Nine who showed less initial disruption in contact-call repertoire. This pattern of results resembles the long-term effects of deafening on song production in adult Bengalese finches, zebra finches, and canaries (Okanoya and Yamaguchi, 1997; Nordeen and Nordeen, 1992; Nottebohm *et al.*, 1976, respectively). Moreover, two of the three budgerigars recorded within 2 months of deafening showed a dramatic increase in call variety (e.g., loss of identifiable call types), which is similar to the effects on contact-call production demonstrated by budgerigars sustaining a profound but temporary auditory-threshold shift from acoustic overexposure or ototoxic drugs (Dooling, Manabe, and Ryals, 1996; Dooling, Ryals, and Manabe, 1997).

A. Species differences in the role of auditory feedback in adulthood

As far as we know, the effects of deafening on call structure in adult budgerigars have not been described in songbirds, where the focus has been more on song. While comparing the effect of deafening on *call* production in budgerigars with *song* production in songbirds is tenuous, the present results suggest that the effects of deafening on call production in budgerigars differ from the effect of deafening on song production in songbirds both in its time course and in the immediate increase in variety of frequency-modulated patterns.

Closed-ended song learners with stable song syntax in adulthood such as white-crowned sparrows (Konishi, 1965a), chaffinches (Konishi and Nottebohm, 1969), and zebra finches (Nordeen and Nordeen, 1992; Price, 1979) seem to suffer few initial effects of deafening, and sometimes few long-term effects. Open-ended or seasonal vocal learners such as canaries, in addition to traditional closed-ended learners that have variable song syntax as adults such as Bengalese finches (Okanoya and Yamaguchi, 1997), demonstrate marked changes in suprasegmental song features (e.g., syntax) within days of deafening, and phonetic deterioration over weeks and months. Canaries seem particularly vulnerable to vocal disruption from deafening, not only demonstrating changes in song structure within 1 week, but also suffering prominent spectral changes of syllables within a month. Within a year of deafening, an adult canary will *eventually* come to sing like deafened juveniles that never had access to their own auditory feedback (Marler *et al.*,

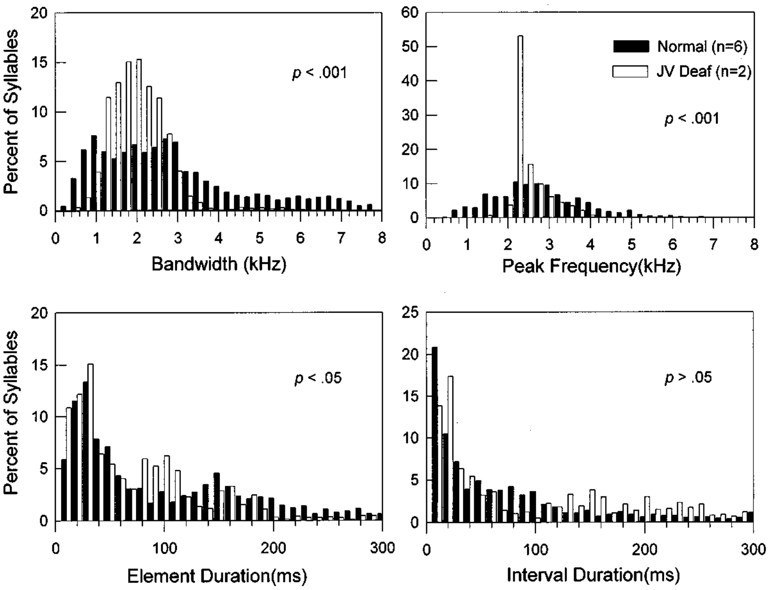

FIG. 8. The average frequency distributions for warble-element bandwidth, peak frequency, duration, and the duration of interelement interval for six normal-hearing budgerigars are compared with those of two adult budgerigars deafened within the first 3 weeks of life. The warble song of these deaf subjects significantly differed from normal control subjects on three of the four warble-element characteristics (see the ''*p*'' values).

1973; Nottebohm *et al.*, 1976). Thus, the relative importance of auditory feedback in maintaining learned vocalizations may be tied to the nature and degree of plasticity in vocal production throughout life. Adult flexibility and versatility in either song structure or song-syllable phonology may carry with it a necessary dependence on auditory feedback. Moreover, maintaining flexibility in both may require the most auditory supervision of vocal output. The results reported here are consistent with this hypothesis, since adult budgerigars have exceptional plasticity in both segmental and suprasegmental vocal features, and show dependence on auditory feedback of both of these aspects of normal species-typical calls and song.

B. Parallels with human speech and deafness

It is common knowledge that postlingually deaf humans exhibit distortions in all classes of speech sounds, with the degree of impairment in speech somewhat dependent upon the age at onset of deafness (Waldstein, 1990). In general, the same appears to hold true for birds that learn their vocalizations, including our budgerigars. The effects of deafening and isolation on warble song in budgerigars include both segmental and suprasegmental effects, with the degree of impairment related to the age of deafening. Budgerigars isolated from conspecifics beginning several weeks after hatching show abnormal vocal repertoires as adults (Dooling *et al.*, 1990). Here and elsewhere (Brittan Powell *et al.*, 1997; Dooling *et al.*, 1987), we show that budgerigars deafened early in vocal development generally produce more abnormal calls and warble than those deafened as adults, as is sometimes the case for normal adult song in songbirds. Chaffinches, for instance, deafened earlier in song development produce more abnormal vocalizations than those deafened later in development (Nottebohm, 1968).

In humans, the exact role of auditory feedback after the acquisition of adult speech and language is surprisingly unclear. Certain experimental conditions such as delayed auditory feedback (Fairbanks, 1955) and the introduction of loud background noise cause immediate and significant changes in speech output such as stuttering and the Lombard effect (for a review, see Lane and Tranel, 1971). This suggests that auditory feedback plays an important role in the moment-to-moment guidance of the motor gestures resulting in speech. However, because it can be demonstrated that much of auditory feedback is processed after the speech gestures it is supposed to correct, others argue that auditory feedback serves more as a calibrator for other sensory feedback such as proprioception (Borden, 1979; Cowie and Douglas-Cowie, 1983). Most likely, auditory feedback is used for both ongoing speech production and for comparing phonetic output with phonemic intention for parametric control of future speech movements (Lane and Webster, 1991; Perkell *et al.*, 1992).

One compelling argument for auditory feedback serving as a calibrator for other feedback mechanisms is the common observation that the speech of postlingually deafened adults systematically deteriorates but is not completely eliminated. It is interesting in this regard that while all four adult-deafened budgerigars in our sample showed extensive deterioration of their contact calls with time, two of the birds showed an immediate and dramatic increase in the number of different contact-call patterns they produced—an effect not usually reported in the literature on human hearing loss. We also know from recent work that budgerigars show a strong Lombard effect (Manabe, Sadr, and Dooling, 1998). These results taken together are most consistent with the idea that auditory feedback plays an active, primary role in guiding contact-call production in budgerigars and that when these birds vocalize, they are matching (through auditory feedback) a stored auditory memory (template) of their contact call.

Finally, to extend the parallels between the effects of deafening in budgerigars with what is known in humans, we examined behavioral measures of social interaction in budgerigars before and after deafening. It is well known that acquired deafness in humans often is accompanied by a host of psychological problems including social withdrawal, depression, and interpersonal anxiety (Darbyshire, 1984; Stein and Bienenfield, 1992; Weinstein and Ventry, 1982). Behavioral observations in budgerigars following deafening also point to broad effects, including an increase in the amount of time spent alone and a decrease in the amount of time spent vocalizing. This significant reduction in vocal production was evident in the infrequent post-surgical recordings of calls and song, particularly in the two birds which had to be excluded from further acoustic analysis of vocalizations. The decrease in social interaction of deafened birds is a complex issue, likely relating to multiple factors. It is unlikely to be due solely to the deaf bird's abnormal vocal repertoire. We know from other work that budgerigars sustaining profound disruption in call structure after syringeal denervation show little effect on their social interactions with intact birds (Shea *et al.*, 1997) and are able to attract and maintain breeding mates and raise young (personal observation).

IV. CONCLUSIONS

The notion of possible parallels between speech and language in humans and vocal behavior in birds is not new (Marler, 1970). Taken together, the present results extend some of these parallels to a psittacine species. The present results also reveal some differences between the role of auditory feedback in the maintenance of human speech and language, and the maintenance of learned avian vocalizations in a highly plastic avian species, the budgerigar. Future investigations of vocal production in budgerigars might use delayed auditory feedback, high levels of background noise, or temporary threshold shift to further extend the parallels between auditory feedback and call production in these birds and the production of speech in humans.

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