

Mechanisms of vocal production in budgerigars (*Melopsittacus undulatus*)

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Songbirds vocalizing in helium show a change in the spectral quality of their vocalizations. This effect is due to an increase in the speed of sound in helium that in turn alters the resonance properties of the vocal tract. Here, this approach is extended to a psittacine, the budgerigar (*Melopsittacus undulatus*), whose syringeal anatomy and innervation differ from that of a songbird. Contact calls from birds vocalizing in heliox (70/30 helium/oxygen environment) showed an overall increase in the amount of energy at frequencies above the fundamental, slight changes in the frequency of the fundamental and harmonics, and some change in the level of harmonics. Calls produced by a syringeally denervated bird showed more dramatic changes. Recordings from live birds were compared with sounds produced by various simple "artificial" tracheal and syringeal models. Results suggest that budgerigars produce contact calls using the syringeal membranes as a unitary sound source which produces acoustic energy in a narrow frequency band whose fundamental frequency is matched to the resonant frequency of the trachea. The syrinx is not normally coupled to the tracheal resonator, and resonances probably play only a minor role in shaping the spectrum of contact calls. © 1997 Acoustical Society of America.

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INTRODUCTION

Sound production in birds has historically been viewed as different from that of humans and other mammals. Humans produce speech beginning with an interruption of air flow across the vocal cords (i.e., vibration of the vocal cords). The filtering properties of the vocal tract, which can be modified both by constrictions of the tract and by movement of the tongue and lips, shape the resulting sound spectrum (e.g., Rossing, 1989). The rate of vibration of the vocal cords is determined primarily by their mass and tension and normally undergoes little change during speech production. In humans, the vibrations of the vocal cords act independently of the resonant cavities of the vocal tract. The human vocal tract can be modeled fairly effectively by a single tube extending from the vocal cords to the lips. The resonant frequencies of such a tube, closed at one end by the glottis and open at the lips, are its odd harmonics. The fundamental frequency of a human voice in helium gas does not change significantly because helium does not affect the vibration frequency of the vocal cords (Beil, 1962). However, helium does affect the speed of sound thus altering the bandpass or resonance characteristics of the vocal tract. Speech produced in helium compared to air contains more energy at higher harmonics and less energy at lower harmonics with no change in frequency of the fundamental. This set of results is taken as evidence that in humans the vocal cords (the source) and the trachea (resonator) are uncoupled during speech pro-

duction. Here, we test whether a similar relation holds for the budgerigar (*Melopsittacus undulatus*) syrinx and trachea.

Birds have syringes that contain specialized tympaniform membranes (TMs) that act as acoustic sources when caused to vibrate by air flow across their surface through the Bernoulli effect (Fletcher, 1992). Whether vocal tract resonances influence the characteristics of bird vocalizations has been a long standing debate in the study of bird song. For instance, analogies have often been drawn between bird phonation and sound production by woodwind instruments. These theories assume that the resonator (the trachea) is coupled to the source (syringeal membranes) as with woodwind musical instruments (e.g., Nowicki, 1987; Nowicki and Marler, 1988). Still other research has suggested a closer parallel between bird phonation and human sound production (Nowicki, 1987). In at least some songbirds, the syrinx and trachea appear to be uncoupled with the resonant properties of the vocal tract affecting the harmonic spectrum of vocalizations but not the fundamental (Nowicki, 1987; Westneat *et al.*, 1993).

Most of the previous work on bird vocalizations has been concerned with how birds produce tonal signals such as the contact calls of budgerigars which are tonal, frequency modulated signals falling in the spectral region of 2–4 kHz (Dooling, 1986). A review of the literature suggests there are essentially three classes of models about how the avian syrinx and trachea produce tonal vocalizations. The first model suggests that pure-tone whistles are obtained from harmonic

signals generated by the syringeal source (this source can be either a whistle or a vibrating membrane) with vocal tract resonances acting to filter out all but a single dominant frequency (i.e., the fundamental or sometimes the second harmonic) (e.g., Nowicki, 1987; Nowicki and Marler, 1988; Westneat *et al.*, 1993). As in human speech production, the source and the resonant tube appear to act in an uncoupled fashion in this model so that tracheal resonances have little or no effect on the behavior of the source. In this model, a bird may be able to influence the output level, but probably not the frequency, of the fundamental by changing its tracheal resonances. It can potentially do this by increasing tracheal length, partially obstructing the trachea with the tongue, or flaring the beak (Podos *et al.*, 1995; Westneat *et al.*, 1993).

A second model suggests that vocal tract resonances directly influence vibrational characteristics of syringeal membranes by constraining them to vibrate in a more nearly sinusoidal fashion and at a particular frequency. In this model, the bird controls the tonal properties of the sounds it produces by actively controlling the resonant properties of the tracheal filter by the same mechanisms described above—all of which can potentially influence the pattern of vibration of the syringeal membranes. The defining characteristics of this model are that the behavior of the syringeal membranes can be modified by tracheal resonances, and the syringeal source must be strongly coupled to the trachea.

Finally, there is a logical third possibility that, like the first model, does not require that the syringeal source and the trachea be strongly coupled. In this model, a bird first changes the spectral quality of the sounds it produces by altering the vibration pattern of the syringeal source through neuromuscular control of membrane location and/or tension. The bird then adjusts its tracheal resonances to actively “track” these new vibration frequencies (Nowicki, 1987). In this model, the syringeal source and the trachea are either uncoupled or weakly coupled so that they act in an independent but coordinated fashion.

What makes this issue interesting is that there is tremendous variation in vocal production among species of birds, and it is unlikely that there is one mechanism that accounts for all avian vocalizations or even that only one mechanism operates exclusively in a single species. Songbirds, for instance, have a bronchiosyrinx with one “syrinx” in each bronchus (four membranes), which are separately innervated, while psittacines have a tracheosyrinx consisting of two membranes at the bronchotracheal junction and a hemidesussate innervation pattern (Gaunt, 1983). Taken together, the models described above touch on a number of unresolved issues in the study of vocal production in birds including: (1) whether the trachea acts as an acoustic filter that enhances and/or suppresses part of the spectrum of the vocalizations; (2) whether the trachea functions as a tube that has both ends opened (at the syrinx and the beak), both ends closed, or only one end open (beak); (3) whether the resonances of the avian vocal tract are passive characteristics of the tube or actively manipulated by the bird; (4) whether the syringeal membranes (the vibrating sources) are coupled to the trachea (the resonator); and finally, (5) whether the two syringeal mem-

branes act as independently vibrating sources if they are physically coupled to a same trachea.

It is worth noting that recent accounts of sound production in birds have concentrated on the effects of the tracheal tube on sound produced by the vibrating syringeal membranes (see, for example, Fletcher, 1992; Nowicki and Marler, 1988; Suthers, 1994; Westneat *et al.*, 1993). The band-pass or resonant properties of the passive trachea depend on its length and shape. Both the resonant frequency and the width of the resonance filter can affect the shape of the output spectrum. As far as we know, the resonant properties of the passive trachea have not been directly measured in birds but arguments based on indirect evidence, from analyses of songbird vocalizations, strongly point to an important role in vocal production at least in some species (see, for example, Myers, 1917; Nowicki, 1987; Sutherland and McChesney, 1965; Suthers, 1990, 1994).

Much of the previous work on the mechanisms of avian sound production has been conducted on songbirds, and some of the logic that arises from these studies is the following. In songbirds, if the two syringeal membranes can *simultaneously* produce two, harmonically unrelated tones of about the same intensity, then the bandwidth of the tracheal filter must be quite broad or only low pass with a relatively high cutoff frequency (Greenewalt, 1968). The *nonsimultaneous* production of two harmonically unrelated tones, on the other hand, could result from a trachea which acts as either a broad filter, only a low-pass filter, or as a variable filter that is capable of rapid adjustments either in frequency or bandwidth (Nowicki, 1987; Suthers, 1990). Gaunt *et al.* (1982) have shown that active frequency modulations can be entirely source generated from adjustments of the syringeal configuration through the action of the syringeal musculature.

So at least for songbirds then, the data show that some aspects of the mechanism(s) by which the bird produces tonal sounds can be teased apart from experiments with birds vocalizing in a mixture of air and helium (heliox). A songbird whose syringeal membranes and trachea are uncoupled should show no change in the frequency of the fundamental but a decrease in its relative amplitude when vocalizing in heliox. Depending on the harmonic content generated by syringeal vibration, a vocalization produced in heliox may also show an increase in amplitude of specific harmonics and an attenuation of others. Some previous work (see Nowicki and Marler, 1988 for review) has shown that the tonal quality of some bird vocalizations bears a strong resemblance to sounds produced by wind instruments—implying that the characteristics of a bird’s vocal tract can affect the fundamental frequency of the song it produces (Nowicki, 1987; Nowicki and Marler, 1988). A wind instrument, such as a trombone, provides a standard model for such effects. The tube component of a trombone (which has certain bandpass or resonance properties) is coupled to the sound source (the lips). When a resonator is strongly coupled to a source, the source is forced to match its vibrations to the harmonic spectrum of the resonator (e.g., Greenewalt, 1968). Because of this coupling, the spectrum of a sound played by a trombone in helium shows an increase in the fundamental frequency in

the same proportion as the increase in the resonances of the corresponding tube. Thus, a bird whose syringeal membranes and trachea are coupled, should show the same effects as those shown by a trombone—changes in tracheal resonances should alter the vibrational pattern of the syringeal membranes thereby increasing the frequency of the fundamental.

Data from songbirds vocalizing in heliox also address the issue of whether vocalizations are solely source generated or modified by the resonances of the vocal tract (Nowicki, 1987; Nowicki and Marler, 1988; Nowicki *et al.*, 1989). Constant frequency song elements produced in air have no overtones, while the same constant frequency song elements produced in heliox show increased energy at harmonic overtones of the fundamental. These results suggest a potential role for vocal tract resonances in avian sound production. Harmonic overtones appearing in vocalizations produced in heliox, but not in air, would obtain if the bird's vocal tract normally acts as a narrow acoustic filter centered on the fundamental frequency (Nowicki, 1987).

Suthers (1994) recently extended work on acoustic resonance in avian sound production to a nonsongbird, the oilbird (*Steatornis caripensis*). In this species, anatomical differences between the left and right bronchus lead to differences in filtering properties that are realized as different formants in the oilbirds' social vocalizations. The effect of structural changes in vocal tract parameters on vocalizations in birds, in general, has not been well studied. Interestingly, others have recently reported a positive correlation between beak gape and sound frequency in the song of two species of sparrows (*Zonotrichia albicollis* and *Melospiza georgiana*) (Westneat *et al.*, 1993). This is an interesting approach since it could reveal the mechanisms by which birds might alter the resonant properties of the vocal tract and affect the spectral quality of vocal output.

In the following experiments, we sought to learn the extent to which resonances of the vocal tract influence vocalizations produced by a psittacine species, the budgerigar. The budgerigar represents an interesting addition to previous studies for several reasons. First, this species has an unusually complex vocal repertoire consisting of both tonal and broadband sounds (Dooling, 1986; Farabaugh *et al.*, 1992). Second, the budgerigars' syringeal anatomy and innervation differ considerably from that of songbirds and other nonpsittacines (see Gaunt, 1983; Heaton *et al.*, 1995; Manogue and Nottebohm, 1982; Nottebohm, 1976). Third, budgerigars learn their contact calls throughout life (Dooling, 1986; Farabaugh *et al.*, 1994). The calls are tonal, frequency modulated vocalizations that average about 150–200 ms in duration, with energy concentrated in the frequency region of 2–4 kHz (Dooling, 1986; Dooling *et al.*, 1987). Contact calls also show no apparent sexual dimorphism and yet have patterns of frequency modulation that can differ dramatically between birds. Each individual bird generally produces one to several call types, but the pattern of frequency modulation within each call type is highly stereotyped from one rendition to another (Brockway, 1969; Dooling, 1986; Wyndham, 1980). Birds typically produce contact calls when they are separated from flock mates, in flight, or preparing for the evening roost (Wyndham, 1980).

To summarize, budgerigars may control the spectral content of contact calls by at least two general mechanisms. They could produce a broadband harmonic signal at the source (syrinx) which the trachea (resonator) subsequently filters to produce a narrowband output. Moreover, the syrx and the trachea could function in an acoustically coupled or uncoupled fashion. Alternatively, budgerigars could produce a narrow-band acoustic signal at the source which is matched to the resonant properties of the trachea. This system could also operate in an acoustically coupled or uncoupled fashion. In each case, the trachea alone could act as a tube opened at both ends, closed at both ends, or closed at one end (syrinx) and open at the other (beak). These mechanisms lead to different predictions as to the effect of heliox on the production of contact calls.

In the following experiments, we placed birds in an environment consisting of 70% helium and 30% oxygen (heliox) and examined the acoustic characteristics of contact calls in this gas mixture. We also examined the effect of heliox on simple sound producing whistles and tubes loosely modeled after the budgerigar syrx in order to better understand the possible mechanisms budgerigars use to produce vocalizations.

I. METHODS

A. Subjects

A total of eight adult budgerigars (seven males, one female) served as subjects in this experiment. We housed the birds in an avian vivarium at the University of Maryland and kept them on a photoperiod correlated with the season. As a test of whether the vocal tract resonances are actively controlled, one subject underwent bilateral tracheosyringeal (ts) nerve resections to denervate its syrx. Briefly, we anesthetized the bird with an intramuscular injection of ketamine hydrochloride (40 mg/kg) and xylazine hydrochloride (10 mg/kg) mixed in a 0.7% saline vehicle. We resected at least 1 cm of its ts nerve bilaterally through a small incision in the plucked skin of the neck and closed the incision with Nexaband S/C liquid.

B. Apparatus

We recorded the birds in a small wire mesh cage (11×7×8.5 in.³) which was placed within an airtight Plexiglas box (27×14×17.5 in.³). The Plexiglas box could then be filled with heliox (a gas mixture consisting of 70% helium and 30% oxygen, Matheson Gas, Inc., New Jersey) which was released from a pressurized tank fitted with a regulator. The heliox entered the Plexiglas box through a 1-in.-diam hole in the floor of the box. Due to properties of lighter gases, the heliox rose to the top of the box and in effect pushed the air, the more dense gas, toward the bottom of the tank where it escaped through a small opening.

The interior of the Plexiglas box contained a perch, and the box was insulated on four sides with 1-in. acoustic foam (Sonex) to reduce sound reflection. A window (3 in.²) was cut in the foam on one side to allow the test bird to view other birds. An omnidirectional Realistic electret tie pin mi-

crophone (frequency response 50–15 000 Hz), connected to a reel-to-reel Teac A-3440 four-track tape recorder, was used to record the test birds' calls. This microphone was mounted directly above the wire cage that housed the test bird. We positioned a second microphone and a high-frequency click generator at approximately the same height as the head of the bird and about 10 cm apart, to measure the velocity of sound. This second 1/2-in. microphone was connected by a 3-m extension cable to a precision sound level meter (SLM) (General Radio model 1982), and the ac output of this SLM was displayed on an oscilloscope (Hitachi, V-212). The click generator consisted of a custom built driver and a high-frequency condenser speaker (Machmerth *et al.*, 1975). The click generator produced 50- μ s duration clicks delivered at the rate of 200 Hz. To measure propagation time, a trigger pulse from this driver also initiated the oscilloscope sweep trace. We monitored the temperature and calculated the velocity of sound in air according to the following formula:

$$\text{Velocity}_{\text{air}} = 331.4(1 + (t/273))^{1/2}$$

with t = temperature in °C (Weast *et al.*, 1987, p. F-108). The velocity of sound in the heliox mixture was derived from the change in propagation time of the click (a halving of the propagation time means a doubling of sound velocity).

In addition to taking recordings from live birds, we also constructed several "artificial" syringes consisting either of toy plastic whistles of different lengths or small diameter plastic tubes of roughly the diameter and length of the budgerigar trachea. For one model, vibrating "membranes" constructed from small, stretched pieces of latex cut from a rubber condom were used as the source. The acoustic output from these simple sound-producing instruments were measured in air and heliox and, in the case of the tube plus latex membrane, the vibration of the latex membranes were measured simultaneously. Spectra were calculated by placing the microphone of the sound level meter at the end of the tube and passing the ac output to a Stanford Research Systems FFT spectrum analyzer (model SR760) or a Bruel & Kjaer model 4181 probe microphone, amplifier (B&K type 2609) and signal analyzer (HP 3562A). The vibrations of the latex membranes were measured with a Dantec type 41X60 laser Doppler vibrometer (Klump and Larsen, 1992). These measures were compared to calls produced by live birds to gain insight into the possible mechanisms of sound production in budgerigars.

C. Procedure and analysis

1. Recording

Each bird was placed in the small wire mesh cage after being isolated from all other birds for at least 1–2 h. The Plexiglas box was placed over the smaller cage, and it was sealed with vaseline to reduce leaks. We calculated the speed of sound in air from the ambient temperature. Once a recording session began, a cage containing several other budgerigars was placed within view of the bird in the Plexiglas box. At least 10–20 contact calls were elicited from the test bird in the normal air environment. When the bird produced the selected number of calls, the other birds were placed out of

sight of the test bird. The regulator to the heliox tank was then set to release heliox into the Plexiglas box slowly. The click generator was then turned on and changes in the speed of sound with increasing concentrations of helium were calculated from the oscilloscope trace every 15 min. Once sound velocity remained unchanged for at least 15 min, the cage containing the other budgerigars was again placed in view of the test bird, and the bird's calls were recorded in heliox. On average, this steady-state concentration of heliox was reached in 50 min.

Theoretically, the velocity of sound at 0 °C should increase from 331 m/s to 506 m/s when air is replaced by a mixture of 70% helium and 30% oxygen (Weast *et al.*, 1987, p. F-104). This increase in velocity should cause the resonant frequencies of a simple tube to increase by 52.9% at 0 °C.

2. Analysis

Nine calls from each bird in air and heliox were sampled at a rate of 40 960 Hz by a Kay 5500 real time analyzer and stored as files on a microcomputer. The Kay real time analyzer was set to compute spectra from 0 to 16 kHz. In addition, we converted each call to a pattern of spectro-temporal values using a fast Fourier transform (FFT) based commercial software package called SIGNAL (Version 2.20; Beeman, 1992). These calls ($n=18$) for each subject were analyzed for similarity using a spectrogram cross-correlation technique (Clark *et al.*, 1987) to determine the variance in call production. Power spectra were calculated using a 8192-pt FFT resulting in a spectral line every 5 Hz. To reduce the number of data points for each call, the spectral lines were averaged over bandwidths of 100 Hz to produce final power spectra consisting of 91 intensity values from 0.1 to 10.0 kHz in steps of 100 Hz.

Budgerigars produce contact calls that are quite stereotyped but the intensity can vary from call to call, especially if the bird changes position relative to the microphone. To minimize the effect of intensity variation among calls produced in each condition, the spectrum for each call was normalized to its peak frequency (the fundamental). Using the measured increase in the speed of sound in heliox as an index, the hypothesized shift in fundamental frequency was calculated. The dependent variable in this experiment was taken as the total energy in the $\frac{1}{4}$ octave frequency band around this frequency for each call produced in air and in heliox. The amount of energy in this band for calls produced in air versus calls produced in heliox was compared using a two way repeated measures ANOVA. We expected that an upward shift of tracheal resonances would lead to an increase in energy in the band of frequencies above the fundamental. A paired t test was used to test resonance effects in the one test nerve resected bird.

Several additional steps were taken to characterize the effect of tracheal resonances further. First, Nowicki and Marler (Nowicki, 1987; Nowicki and Marler, 1988) have shown in songbirds that within the production of a single song, some constant frequency portions of the song will show evidence of harmonics appearing in heliox while other adjacent portions will not. One interpretation of these results is that some birds may be capable of rapidly (i.e., on a note by note

basis) adjusting their tracheal filter. Unfortunately, budgerigar contact calls do not lend themselves well to such an analysis since the entire call is only about 200 ms in duration and they tend to be frequency modulated. Usually there are one to a few “constant frequency” segments in each call but these are rarely adjacent. Nonetheless, we extracted these portions from each call and analyzed them by a spectral analysis and by zero crossing analysis (constancy of intonation according to Greenewalt, 1968) to look for overtones.

Second, as a way of separating the effects of tube resonances from other contributions to vocal output, we measured the acoustic output from 2 mm in diameter soft plastic tubes with lengths of 3.5, 5.5, 6.5, and 7.5 cm in air and in heliox. These lengths bracket the length of the typical budgerigar trachea plus buccal cavity. Broadband noise or a swept pure tone was presented through a small speaker (2P20A, 8 Ω) mounted in the large end of an infant otoscopic speculum. The small end of the speculum was inserted in the plastic tube 1.5 cm from one end. We also measured the acoustic output of a 5-cm whistle in air and heliox which was attached to a turkey baster. Squeezing the hollow, pliable rubber bulb of the baster produced rather uniform air flow through the whistle for 300–500 ms as evidenced by a relatively constant pitch.

The acoustic spectrum of the sound emanating from these tubes and whistles was calculated with the spectrum analyzer. The final spectrum consisted of an average of 500 spectra for each condition for each tube length, in air and in heliox, and with these tubes open at both ends or closed at the end nearest to the insertion of the speculum. The resonance spectra were obtained by subtracting the spectrum taken at the speculum (without a tube attached) from the spectrum obtained from the speculum plus the tube. These tests were conducted in a foam-lined Plexiglas box (20.5 × 11 × 13 in.³) similar but smaller than that used to record the birds. The change in the speed of sound provided a direct measure of the exact concentration of helium.

For the more realistic psittacine syrinx, we also used stretched latex over two holes on opposite surfaces of a 2 mm in diameter plastic tube. The length of the tube from the membranes to the tip was 5.5 cm. Changing the tension on the latex membrane changed the frequency of vibration of the membranes. For a fixed tension that produced a fundamental frequency of vibration around 3 kHz, we concurrently measured the vibration of one membrane with a Dantec laser Doppler vibrometer and the acoustic output at the end of the tube with a Bruel & Kjaer 4181 probe microphone under various conditions. Briefly, we placed small reflecting spheres (Scotchlite, 30–50 μm diameter, weight < 1 μg) on the membrane to improve signal-to-noise ratio. The laser was focused on the sphere and vibration measured in the manner described by Klump and Larsen (1992) for tympanum vibration in live birds. We compared acoustic output and membrane vibration for conditions including changes in tube length, flaring of the distal end of the tube (mimicking the effects of beak opening), partial obstructions of the distal end of the tube at different locations (mimicking the effect of different tongue placements), and other manipulations (e.g.,

TABLE I. Velocity of sound in air and heliox for each bird.

| Bird | Air velocity (m/s) | Heliox velocity (m/s) | % Shift |
|--------|--------------------|-----------------------|---------|
| 93-20 | 343 | 485 | 41 |
| 93-14 | 345 | 495 | 44 |
| 92-02 | 346 | 485 | 40 |
| 92-06 | 347 | 490 | 41 |
| 91-10 | 345 | 449 | 30 |
| 91-12 | 345 | 487 | 41 |
| 93-06 | 346 | 489 | 41 |
| 90-03* | 348 | 500 | 44 |

loading with rubber cement, tearing, reducing tension) to only the contralateral of the two membranes.

II. RESULTS

A. Recordings from live birds

Spectrogram cross correlations generated by SIGNAL provided a quantitative check that each bird always produced the same call type in air as in heliox. The nine renditions of dominant call types from the seven normally innervated birds showed an average correlation of 0.80 in air and 0.83 in heliox, with intensities ranging 73–88 A-weighted sound level in dB in air and 60–82 dB in heliox. The overall correlations for the calls produced by the ts nerve resected bird were 0.75 in air and 0.66 in heliox and intensities ranged from 63 to 77 dB in air and were constant at 68 dB in heliox.

Peaks in the total power spectrum of budgerigar contact calls appear at both odd and even harmonics. This suggests that the trachea acts predominantly as a tube open, or closed, at both ends creating resonances appropriate to $\frac{1}{2}$ the tube length, $f_n = (nv)/(2l)$. An adult budgerigar’s trachea measures approximately 5 cm from the glottis to the bottom of the syrinx. Using this length in the formula above, the fundamental ($H1$) should theoretically occur at 3310 Hz, the second harmonic ($H2$) at 6620 Hz, and the third ($H3$) at 9930 Hz. The average frequency value of the fundamental and harmonics across birds was 3413 ± 439 Hz for the fundamental, 6842 ± 861 Hz for the second harmonic, and $10\,257 \pm 1293$ Hz for the third harmonic. This is a difference of 3.1%, 3.1%, and 3.3%, respectively. From the speed of sound and the fundamental frequency of each bird’s call, we estimated the effective length of a tube, open at both ends, having a resonance centered at the bird’s fundamental frequency to be about 5 cm, which is identical to the length of the actual tracheal taken from a dead budgerigar.

The average sound velocities calculated from the clicks produced in air and heliox for the eight subjects were 345.5 ± 1.5 m/s and 485 ± 14.4 m/s, respectively. This change in sound velocity results in an increase of 40% in the resonant frequencies of a simple tube and corresponds to an average steady-state concentration of helium in the Plexiglas box of $67 \pm 2\%$. This is very close to the maximum attainable concentration of 70%. The velocity of sound in air and heliox and the relative percent increase between air and heliox for each bird are given in Table I.

Figure 1 shows the sonagrams of one token dominant contact call type, from four birds, recorded in air and heliox.

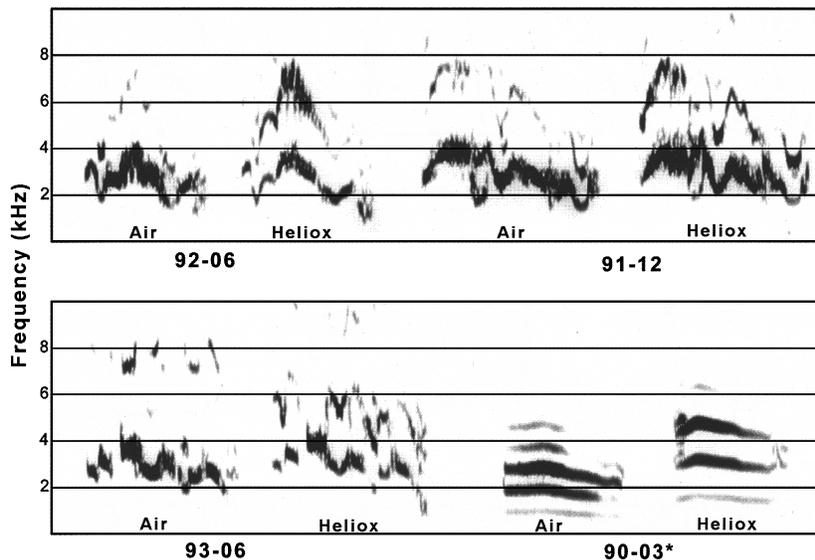


FIG. 1. Sonograms of contact calls produced in normal air and in heliox (10-kHz analysis range, 300-Hz analysis bandwidth) for three budgerigars with normally innervated syrinxes and one ts nerve resected budgerigar (90-03*).

Three sonograms were from normally innervated birds and one from the ts nerve resected bird. In the sonograms of calls produced by normal birds in heliox, energy appeared at harmonic frequencies around 5–6 kHz that was not present in calls produced in air. The sonograms of calls produced by the ts nerve resected bird (90-03*) showed more complex effects. For this bird, the fundamental frequency increased significantly as reflected by the greater separation between the harmonics in calls produced in heliox compared with those produced in air (Fig. 1).

Figure 2 shows the average total power spectra of the nine calls for four birds whose contact calls are shown in Fig. 1. There is a shift of energy to frequencies above the fundamental in the three normally innervated birds but little change in the fundamental. There is significantly more energy in the $\frac{1}{4}$ octave band above the fundamental in calls produced in heliox as compared to air [$F(1,6)=10.26$; $p<0.05$]. The average shift in spectra for all calls produced in air compared to heliox by normally innervated birds is shown in Fig. 3. By contrast, the bird that received bilateral ts nerve resection produced calls in heliox showing a large increase in the frequency of the fundamental and its harmonics compared to calls produced in air ($t=-3.73$; $p<0.05$). The fundamental frequency ($H1$) increased 61% and the harmonics ($H2$, $H3$, and $H4$) increased 59%, 61%, and 46%, respectively.

To obtain a more precise estimate of shifts in frequency and amplitude of vocalizations produced in heliox, we selected a relatively constant frequency portion from each contact call produced in air and heliox and analyzed only these pieces. For normally innervated birds, the frequency content of these call portions was analyzed by a zero crossing analysis followed by average frequency plots of the zero crossings for each call. The period (frequency) with the highest count for calls was correlated with the peak in the power spectrum of these constant frequency portions and there was no significant difference in peak frequency of the fundamental for

calls produced in air compared to those produced in heliox [$F(1,6)=2.31$; $p>0.05$]. Figure 4 shows the average frequency plots for calls produced in air compared with calls produced in heliox normalized to the predominate frequency. The shape of these distributions confirms what was obtained by computing the power spectra—these call portions are relatively narrow band, show little evidence of side bands, and show an upward shift in frequency in heliox. For comparison, a frequency distribution from a zero crossing analysis of a 200-Hz band of noise is also shown. The intensity of

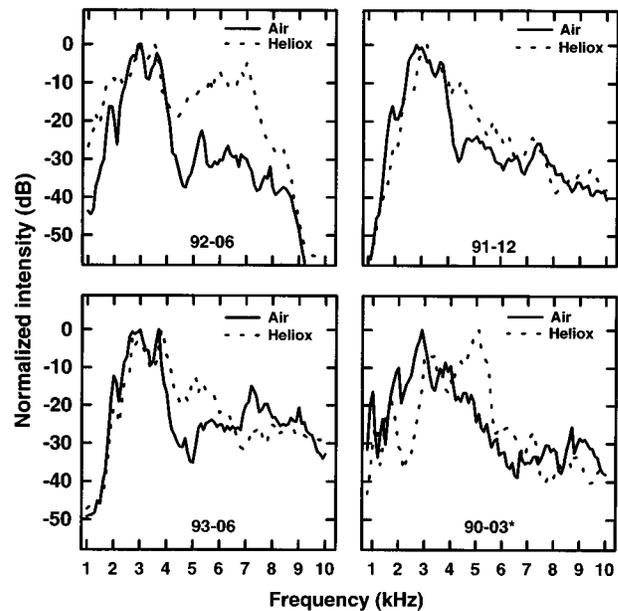


FIG. 2. Average power spectrum (40-kHz sampling rate, 10-kHz analysis range, 8192-pt FFT, yielding a frequency resolution of 5 Hz) for the nine contact calls presented in sonographic form in Fig. 1. In heliox, energy is decreased in the 2–4 kHz range and increased in the 4–7 kHz range (dotted line). Intensity was normalized relative to the peak in the power spectrum.

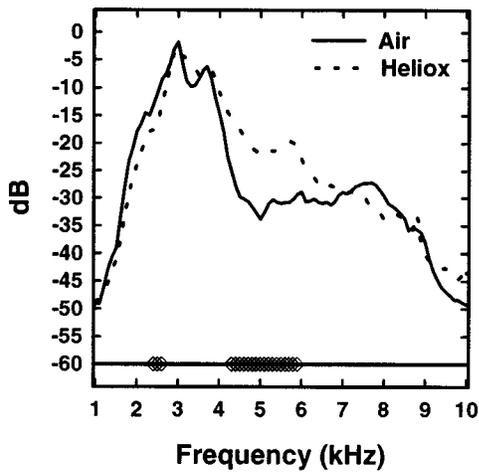


FIG. 3. Paired t-tests were performed on each spectral line throughout these average spectra and the symbols at the bottom show which of these spectral lines were different between calls produced in air and in heliox. On average, calls produced in heliox show less energy at 2.4–2.6 kHz (below the fundamental) and more energy at 4.3–5.9 kHz (above the fundamental) compared to calls produced in air.

the fundamental relative to the intensity of the second harmonic when birds were vocalizing in air compared to heliox were also not significantly different [$F(1,6)=0.09$; $p>0.05$] by a power spectral analysis.

Of the six normally innervated birds, one bird (92-02) was somewhat unusual in showing four relatively constant frequency portions in its contact call. This provided the opportunity to examine several constant frequency portions in the same call in air and in heliox. Figure 5 shows the power spectra from four constant frequency portions within this bird's contact call produced in air and in heliox. Overall these spectra show more energy at higher frequencies in calls produced in heliox, but there were only slight shifts in the frequency and intensity of the fundamental and harmonics, and these shifts are not in a consistent direction.

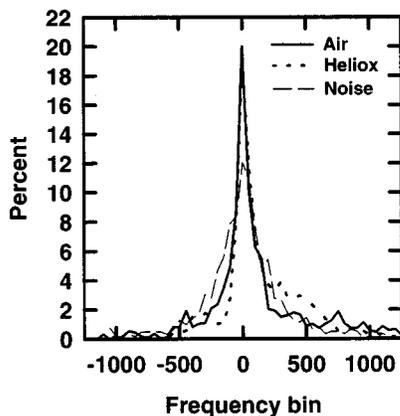


FIG. 4. Frequency plots for calls produced in air (solid line) and heliox (dotted line) along with the frequency distribution resulting from a zero crossing analysis of a 200-Hz band of noise (dashed line) are shown.

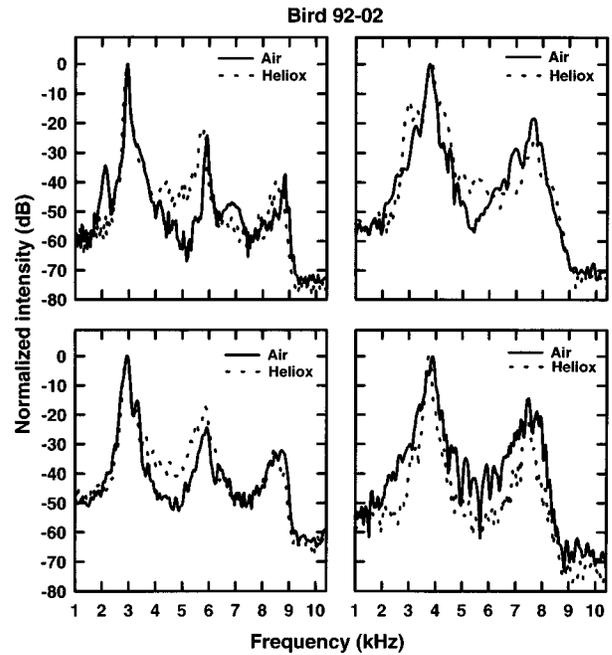


FIG. 5. Total power spectra for four flat segments within a single bird's (92-02) call. Other than an overall shift of energy to higher frequencies, these spectra are noteworthy for their lack of consistent changes from air to heliox. Intensity was normalized relative to the peak in the power spectrum.

B. Recordings from artificial sources

The control experiments with plastic tubes, whistles, and “artificial” syringes illustrated the effects of passive tube resonances and several expected effects are shown in Fig. 6(a)–(d). Opening and closing a 5.5-cm tube [Fig. 6(a)] driven by a broadband white noise showed a shift in resonance frequencies from both odd and even harmonics to only odd harmonics. Changing the tube length also shifted resonance frequencies as expected [Fig. 6(b)] and the resonance shifts for the tubes open at both ends more closely matched the peaks expected by the calculations (see Table II) than did those of the tubes closed at one end. The upward shift in the spectra of the noise emanating from a 5.5-cm tube open at both ends in air and in heliox shown in Fig. 6(c) is also predictable from the concentration of helium in the environment. In air, the fundamental resonance of this tube is at 3062 Hz, the second harmonic at 5969 Hz, and the third harmonic at 8500 Hz. In heliox, the three peaks are shifted upward an average of 35% so that the fundamental was located at 4188 Hz, the second harmonic at 7938 Hz, and the third harmonic at 11 563 Hz. Very similar effects occurred when the sound source was changed from a small speaker producing white noise to a 5-cm plastic whistle. The effect of replacing air with heliox on the spectra obtained from the plastic whistle is shown in Fig. 6(d).

In aggregate, the effects shown in Fig. 6 with plastic tubes and whistles can be explained by simple physical principles involving a broadband or harmonic source, changes in the speed of sound in air and heliox, and the resonances of a simple tube. In these simple syringeal models, the source and the resonating tube are clearly not coupled. The more realistic syringeal model constructed from a 5-cm tube and two

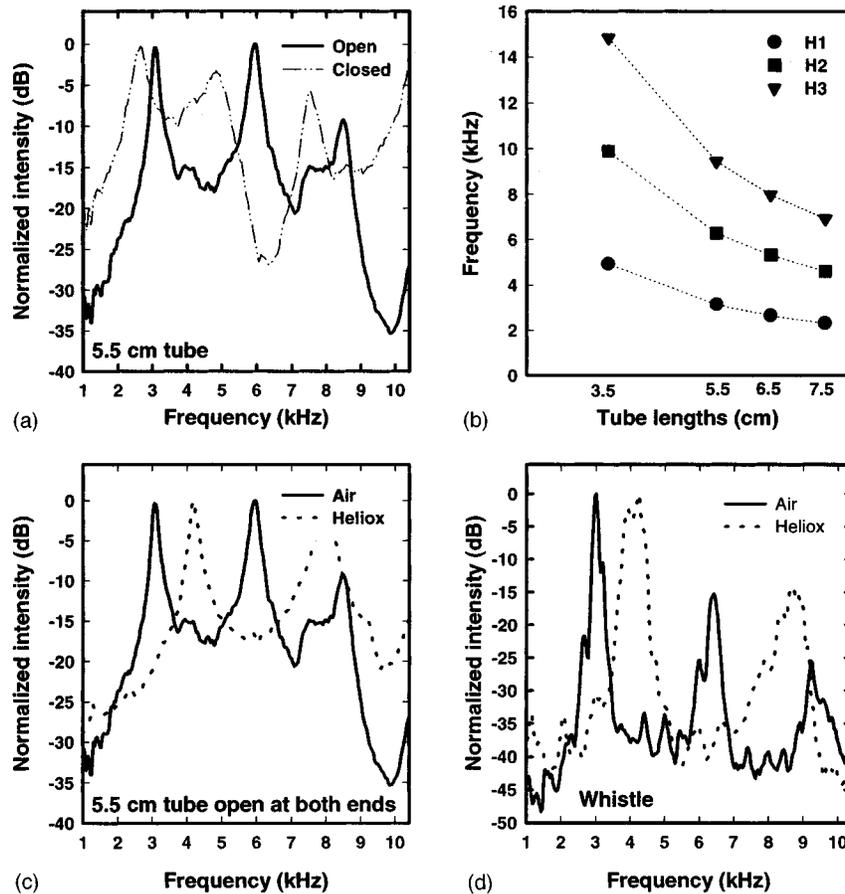


FIG. 6. (a) Total power spectra from a 5.5-cm tube open at both ends (solid line) and open at one end and closed at the other (dashed line). (b) Change in frequency of the fundamental and harmonics as a function of tube length. (c) Total power spectra from a 5.5-cm tube open at both ends in air (solid line) and heliox (dotted line). (d) Total power spectra from a whistle played in air (solid line) and heliox (dotted line).

vibrating latex membranes driven by moving air from a turkey baster (the pressure source) showed different effects. These changes from air to heliox were similar to those seen in the calls of a normally innervated bird. Figure 7(a) shows the effect of replacing air with heliox on the output from a model syrinx with vibrating latex membranes. For comparison, Fig. 7(b) shows the effect of replacing air with heliox on the constant frequency portion of the contact call produced by a live budgerigar. In both cases, there is only a small upward shift in the frequency of the fundamental with little or no change in its amplitude—an effect that could be due to the decreased load on the vibrating membranes from the lighter gas, heliox. In both cases, there is also an overall shift in energy to higher frequencies above the fundamental.

Figure 8 shows the relation between one of the vibrating rubber membranes and the spectrum of the acoustic output at

the end of the 5-cm tube. Peaks in the vibration spectrum and the acoustic spectrum are at exactly the same frequency. We repeated these measures with different tube lengths (mimicking putative tracheal changes when a bird stretches its neck), partial occlusion of the tube opening (as might occur from occlusion by the tongue), and flaring of the tube (loosely modeling the effects of opening the beak). None of these manipulations had any effect on the relation between the spectrum of the vibrating membrane and the acoustic spec-

TABLE II. Predicted and actual measures for resonance frequencies from a 5.5-cm tube.

| | Predicted | | Actual | |
|----|-----------|---------|---------|---------|
| | Open | Closed | Open | Closed |
| H1 | 3145 | H1 1573 | H1 3063 | H1 2656 |
| H2 | 6290 | H3 4718 | H2 5969 | H3 4844 |
| H3 | 9435 | H5 7863 | H3 8500 | H5 7531 |

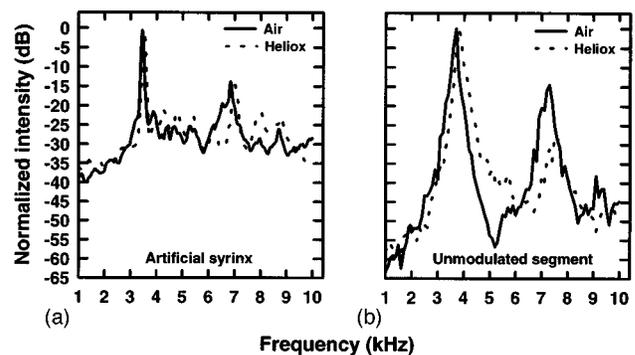


FIG. 7. Example of the total power spectrum for the artificial syrinx compared to the power spectrum of an unmodulated segment of a contact call for bird 93-06. Intensity was normalized relative to the peak in the power spectrum.

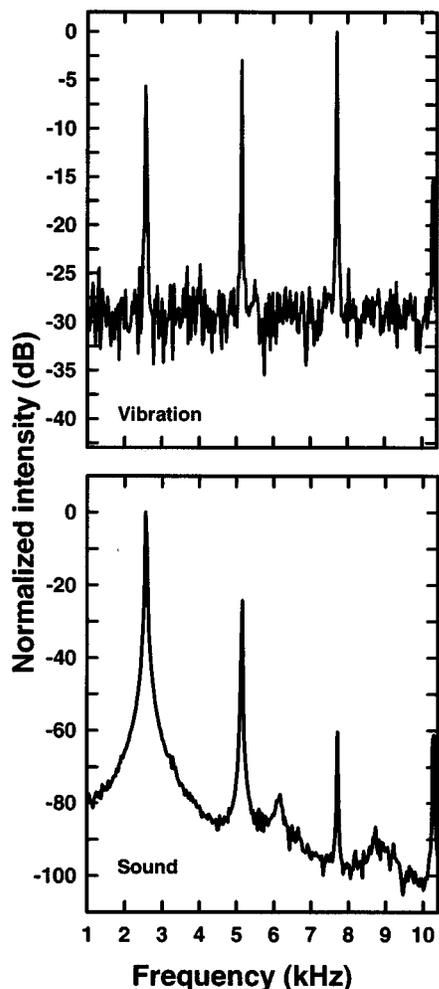


FIG. 8. Power spectra for the vibration of the latex membrane and the acoustic output of the artificial syrinx. Intensity was normalized relative to the peak in the power spectrum.

trum measured at the output of the tube. Decreasing tension on the opposite latex membrane, puncturing it, or loading it with rubber cement resulted in a decrease in fundamental frequency.

III. DISCUSSION

These experiments have attempted to elucidate the mechanical processes involved in the production of vocalizations by budgerigars. To return to the questions posed earlier:

Can the trachea act as an acoustic filter which modifies the spectrum of vocalizations?

The resonant frequencies of the trachea depend on the length, diameter, and stiffness of the tissues. A wealth of correlational evidence argues that the dominant frequencies in the calls of birds are those syringeal membrane frequencies that most nearly approach the tracheal resonant frequencies (see, for example, Sutherland and McChesney, 1965). The strong suggestion here is that the trachea (and probably other air chambers) can act to enhance or dampen certain harmonic overtones that provide timbre to a bird's voice. But

there may be other possibilities as well. Zebra finches, for example, can emphasize and suppress particular harmonics in their calls and song syllables, and these patterns can be learned (Williams *et al.*, 1989). Syringeally denervated zebra finches presumably lack such timbre control suggesting that some of the harmonic suppression found in normal zebra finch song is accomplished by the syrinx and not the trachea (Williams *et al.*, 1989).

The tonal, frequency modulated contact calls of budgerigars have fundamental frequencies that fall between 2 and 4 kHz. Comparing the total power spectrum of the contact calls produced in heliox with those produced in air shows an increase at high frequencies, consistent with the notion that energy in frequencies above the fundamental in air are normally attenuated by a tracheal filter centered around 3 kHz. These results suggest that the trachea might be acting as a broad, bandpass acoustic filter that shifts upward in frequency in heliox, thereby slightly attenuating low-frequency spectral components and simultaneously enhancing high-frequency components of the vocalization spectrum.

Interestingly, a closer examination of brief, constant frequency portions of contact calls, however, failed to show either a consistent reduction in amplitude of the fundamental or other changes in amplitudes of the other harmonics of calls produced in heliox as compared with those produced in air. This is in contrast to that reported by Nowicki (1987) for the songbird. In theory, a filter centered over the fundamental (and approximating the width of those shown for our plastic tubes), when shifted upward in heliox, should cause a decrease in amplitude of the fundamental and an increase in amplitude of the second and perhaps the third harmonic over calls produced in air. Instead, the frequency and amplitude of the fundamental changed very little in calls produced in air compared to those produced in heliox, and the amplitude of the second harmonic showed no consistent change relative to the amplitude of the fundamental.

In general, the findings in live birds are similar to results from sounds produced in air and heliox by an artificial syrinx consisting of vibrating membranes attached to a small diameter tube approximating the length of the budgerigar trachea. These results suggest that tracheal resonances do have a slight effect but do not normally play a very large role in determining the spectral content of contact calls.

Does the trachea function as a tube that is open at both ends (syrinx and beak), closed at both ends or closed at one end (syrinx)?

The preponderance of evidence both from the vocalizations of normally innervated birds, the syringeally denervated bird, as well as from simple models of the avian syrinx strongly suggests that the budgerigar syrinx can best be modeled as a tube open at both ends. But others (Nottebohm, 1976; Westneat *et al.*, 1993) have suggested that the open end (glottal end) can be constricted, thus changing the surface area of the opening so that the trachea can act more like a tube that is closed at both ends. Since we could find both odd and even harmonics in budgerigar contact calls, and the fundamental of budgerigar contact calls is more closely approximated by the formula $f_n = (nv)/(2l)$ given a vocal tract

length of 5 cm, we conclude that the trachea is functioning most of the time as a tube either open or closed at both ends rather than a tube open at one end and closed at the other.

Can the resonances of the budgerigar vocal tract be actively manipulated by the bird?

Even though tracheal resonances may play only a minor role in shaping the spectral characteristics of budgerigar vocalizations, recent work has suggested that acoustic resonances can be altered in the avian vocal production system in at least three ways: (1) lengthening or shortening the tube; (2) partially occluding the open end of the resonating tube or changing its size; or (3) flaring the open end of the tube (Nowicki and Marler, 1988; Westneat *et al.*, 1993). There is ample correlational and anecdotal evidence for a relationship between vocal tract length and vocal pitch. Birds with longer and wider tracheas tend to have deeper voices (e.g., Whooping crane and Trumpeter swan, Portmann, 1950) while birds with narrower and shorter tracheas tend to have higher pitched voices (nestling calls in passerines and budgerigars, Popp and Ficken, 1991; Brittan-Powell *et al.*, in press).

Westneat *et al.* (1993) proposed that beak gape can alter the resonance properties of a bird's trachea in at least two ways: by effectively shortening the distal portion of the tube (thereby increasing the resonant frequency) or by altering the impedance at the anterior end of the vocal tract by occluding the open end of the tube. These investigators conclude that beak motion is functionally related to sound production in songbirds but the evidence is largely correlational.

In the case of budgerigars, there are vocal tract resonances that are passive consequences of tube characteristics (shown dramatically by the denervated bird) but it is unlikely that these are actively manipulated by the bird. Casual observation of budgerigars and more formal observation in other psittacines such as the African Grey Parrot (Patterson and Pepperberg, 1994) show that tongue movement and beak opening is correlated with sound production. Both species, however, are also able to produce species-typical vocalizations with the beak nearly completely closed. Moreover, recent work on denervation of multi-cranio-motor systems including the tongue, pharynx, and larynx do not alter contact call patterns appreciably (Brauth *et al.*, in press).

The present results from measurements with simple plastic tubes are illuminating. For a tube the length of the budgerigar trachea, the fundamental falls around 3300 Hz and the average peak in the power spectrum of budgerigar contact calls was about 3400 Hz. Moreover, as in the bird with the denervated syrinx, the frequency of the fundamental and the harmonics obtained from a plastic tube shifted upward in frequency in heliox with the levels of the fundamental changing appropriately, effects completely expected with a source coupled to a resonating tube. This effect was distinctly not observed in normal budgerigars. Together with the fact that manipulations of tube length, partial obstructions, and flaring—all suggested as mechanisms for actively manipulating tracheal resonances—have virtually no effect on either the vibration of the membranes in our artificial syrinx or on the acoustic output at end of the tube, we conclude that active changes in tracheal resonances by the bud-

gerigar are probably not required for normal vocal production. Instead, it is likely that normally innervated budgerigars probably override the passive resonance characteristics of their trachea.

Are the vibrating sources in the budgerigar syrinx coupled to the trachea?

Similar arguments can be brought to bear on the question of whether the syringeal membranes of budgerigars are coupled to the trachea. The fact that the fundamental frequency (nor the harmonics for that matter) of contact calls produced in heliox by normally innervated budgerigars does not significantly increase suggests, at best, a very loose coupling between the syringeal membranes and the trachea. In this regard, the source-filter theory of vocal production as proposed for human speech production is probably an appropriate model for the call production in budgerigars.

The findings from the denervated bird provide important support for this conclusion. Bilateral resection of the ts nerves have numerous consequences (e.g., denervation of the extrinsic tracheal and the intrinsic and extrinsic syringeal muscles among other effects) that can affect the mechanical properties of the vocal system in a dramatic way. Contact calls in air and heliox produced by the syringeally denervated bird differed significantly from those produced by normally innervated birds. In this bird, the harmonic frequencies increased by the amount expected from a shift in tracheal resonances due to changes in the speed of sound in heliox. Moreover, the fundamental frequency in this bird's contact calls increased by a proportional amount suggesting the syringeal membranes were now coupled to the trachea. For this bird, a more appropriate model for vocal production might indeed be a woodwind or brass instrument (Benade, 1976) where the fundamental frequency of such an instrument played in helium increases in the same proportion as the resonances of the corresponding tube (Nowicki and Marler, 1988). These are important data since they show that tracheal resonances *can* have a very pronounced effect on the spectral distribution of energy in contact calls exactly as predicted by the resonance properties of tracheal-length tubes in heliox but only when the syringeal musculature is denervated. Such effects could occur with a coupled source-resonator model but not with a uncoupled source-filter model of vocal production.

Do the two syringeal membranes act as independently vibrating sound sources?

As early as 1947, researchers have suggested that birds might have independent control of their two sound sources (Potter *et al.*, 1947). However, it was not until 1968 that Greenewalt, through a zero crossing analysis of the songs of many songbird species, provided the first evidence that birds have "two voices." He concluded that the two sides of the songbird syrinx may operate independently and produce harmonically unrelated tones simultaneously. Later denervation experiments provided more evidence that the two sides of the syrinx can act independently (Nottebohm, 1971; Lemon, 1973; Nottebohm and Nottebohm, 1976; Seller, 1979). The specific elements deleted from songs of birds with unilateral syringeal denervation were presumably those generated by

the disabled side of the organ. The situation is not completely clear cut, however, since Nowicki and Capranica (1986) clearly showed that, at least in the chickadee, the two syringeal sources behave as if they are coupled in some manner. Using grey catbirds (*Dumetella carolinensis*) and brown thrashers (*Toxostoma rufum*), Suthers (1990) provided more direct and refined evidence of a two-voice theory. He showed that the two sides of the syrinx can act in three ways: both sides may contribute simultaneously to a note or syllable, both may generate the same sound, or each side may produce a different sound. Taken together, these studies show that the two sides of the syrinx are not limited to the production of different sounds but can, in fact, produce combinations of identical or very similar sounds. Thus, the original two-voice theory (at least in its simple form) probably underestimates the true capabilities of the avian syrinx.

In the songbird syrinx, the internal tympaniform membranes (ITMs), located on the medial walls of the primary bronchi just caudal to the syringeal lumen, vibrate to generate sound. Since the tension of the right and left ITMs can be independently manipulated and are driven by potentially independent columns of air, the two syringeal halves can produce harmonically unrelated sounds. In the parrot syrinx, on the other hand, the external tympaniform membranes (ETMs) located within the syringeal lumen are driven by a single column of air, and therefore cannot be "two voiced" in the same sense as in the songbird syrinx. Moreover, while hypoglossal innervation of the syrinx is ipsilateral in songbirds, it hemidecussates in parrots through an anastomosis zone distal to the syrinx.

In theory, then, either the left or right hypoglossal nucleus could support normal vocalizations in budgerigars; a point supported by the fact that resections of the right or left ts nerve below the anastomosis do not seem to dramatically affect budgerigar contact calls (Heaton *et al.*, 1995). It is interesting that although the syrinx of the Orange-Winged Amazon parrot is structurally similar to that of the budgerigar, unilateral syringeal denervation just caudal to the anastomosis (disrupting control of the ipsilateral half of the syrinx) markedly affects the long call in this species. This suggests, at least for this psittacine, the behavior of one syringeal membrane during vocal production is dependent on the behavior of the other (Nottebohm, 1976). We observed a similar result with our "artificial" syrinx consisting of a 5-cm plastic tube and two latex rubber membranes when one was "deactivated" by either reducing tension, puncturing the membrane, or loading the membrane with rubber cement—these manipulations all lowered the fundamental frequency of the acoustic output of the tube. Neither spectral analyses nor zero crossing analyses of constant frequency portions of contact calls in air and in heliox showed any evidence of two sources ("voices") operating independently when budgerigars produced contact calls.

IV. CONCLUSION

Taken together, these results from budgerigars producing contact calls in air and heliox and from various "artificial" syringes and tracheas suggest that budgerigars use their syringeal membranes as a unitary sound source that produces

acoustic energy in a relatively narrow frequency band with fairly shallow skirts especially on the low-frequency side of the filter. The fundamental frequency is matched to the resonant frequency of the trachea. The syrinx is not normally coupled to the tracheal resonator, and tube resonances play only a minor role in shaping the overall spectral profile of contact calls.

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