Unilateral and Bilateral Oscillation in the Excised Squirrel Monkey Larynx

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Recent studies of squirrel monkey phonation have shown that the larynx may exhibit either unilateral oscillation or bilateral oscillation. In the case of unilateral oscillation, airflow is nearly ineffective in inducing vibration in the right vocal fold though the left vocal fold oscillates readily. The converse of this has not been observed. In the case of bilateral oscillation, the left and right vocal folds both vibrate and the oscillation may be coordinated so that the left and right vocal folds oscillate synchronously in phase, or uncoordinated so that the two folds oscillate out of phase or at different fundamental frequencies. In the present study we manipulated subglottal pressure, adduction, and vocal fold elongation and recorded the pattern of oscillation and the frequency distribution of the acoustic signal produced by voicing.

Excised squirrel monkey larynges were obtained from the Squirrel Monkey Breeding and Research Resource, University of South Alabama. The larynges of nine monkeys were harvested from animals that suffered a natural spontaneous death. No monkeys were killed for the purpose of conducting this research. Each larynx was dissected and trimmed, and the false vocal folds were removed. The tracheal tissue and larynx was mounted on a pseudotracheal tapered rigid tube (3mm average diameter), positioned on a laboratory bench, and the tracheal axis was oriented in the vertical position, exposing the glottis to a camera and recording apparatus. The pseudotracheal tube was supplied with compressed air heated to 37^{o} C, and humidified to approximately 100% relative humidity. The top view of the larynx and vocal folds was videotaped, and a stroboscope was employed to slow down the motion of the vocal folds. Audio recordings of the signal were obtained with a microphone positioned 10 cm away from the glottis, the analog signals were recorded on Digital Audio Tape (DAT) recorder, and the audio records were subsequently analyzed on a personal computer using MATLAB or TFR signal processing software.

The following patterns were observed: In the absence of adduction or elongation, vocal fold oscillation tended to be restricted to the left vocal fold. Under these conditions changes in subglottal pressure were insufficient to induce bilateral oscillation. Furthermore, changes in adduction and subglottal pressure were also ineffective in changing the pattern of oscillation from unilateral to bilateral. Elongation of the vocal folds was required to establish bilateral oscillation. At moderate levels of elongation, moderate levels of adduction and subglottal pressure were necessary to produce bilateral oscillation of the left and right vocal folds. At increased levels of elongation all combinations of adduction and subglottal pressure tended to produce bilateral oscillation. The amplitude of the vocal signal was dependent upon changes in subglottal pressure, and appeared to be only weakly influenced by the mode of oscillation (unilateral or bilateral). In virtually all samples of unilateral oscillation the amplitude of the upper harmonics strongly exceeded that of the fundamental. In the case of unilateral oscillation, the fundamental frequency was typically in the region of 800 to 1,200 Hz, and the highest amplitude component of the signal varied between 6 and 9 kHz. Close examination of the frequencies of the harmonics indicated that in some cases one fundamental frequency was apparent and each harmonic was an exact interger multiple of the fundamental frequency. In other cases, however, evidence of two or more frequencies was observed. The two frequency components could be close in frequency. For example, the frequency difference between successive harmonics could alternate between 818 Hz and 861 Hz (818, 1679, 2497, and so forth). In other cases, the two frequency components may be more distantly spaced.

In the majority of samples of bilateral oscillation, the amplitude of the upper harmonics exceeded the amplitude of the fundamental as was observed for the case of unilateral oscillation. However, in about thirty percent of the samples the fundamental frequency was the highest amplitude component, and each successive harmonic decreased in amplitude 3-6 dB per octave approximating the source features of spoken vowels.

These findings suggest that in a single vocal fold the pattern of oscillation may be complicated such that airflow through the glottis may induce different portions of the mucosa to vibrate at different frequencies. Berry and his associates have observed cases where the horizontal and vertical motion of the vocal fold may oscillate at different frequencies, and this may be occurring in the squirrel monkey under certain conditions (Berry, Herzel, Titze, and Krischer, 1994, J. Acoust, Soc, Am., 15, 3595-3604). The vocal repertoire of squirrel monkeys includes many calls in which the peak amplitude of the call is in the region of 5-9 kHz, and the peak frequencies of many of the samples observed here, particularly some of those produced by nearly unilateral oscillation of the left vocal fold, may underlie the production of these calls. The squirrel monkey displays a very rich vocal repertoire with some calls exhibiting a vowel-like source (a descending harmonic series), and other calls exhibiting biphonation or even staccato phonation. Because squirrel monkeys appear to intentionally shift between several different regimes of phonation an evolutionary premium must have been placed on the high precision neuromuscular control of the laryngeal complex and associated structures.