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Mechanism for the Production of Echolocating Clicks by the Grey Swiftlet, *Collocalia spodiopygia*

Roderick A. Suthers and Dwight H. Hector
Indiana University School of Medicine, Bloomington, Indiana 47405, USA

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Summary. 1. Orientation sounds of the echolocating swiftlet, *Collocalia spodiopygia* (family Apodidae) consist of two clicks, each having a duration of a few milliseconds, separated from each other by a silent interval lasting about 20 ms (Fig. 1). Most of the acoustic energy is between 2 and 8 kHz.

2. These clicks are generated in the syrinx and require syringeal airflow.

3. The first member of the double click is initiated by contraction of the sternotrachealis muscles (Fig. 3) which reduces tension on the syrinx by pulling the trachea caudad (Fig. 2). This causes the first bronchial ring to rotate inward (Fig. 10), reducing the syringeal aperture. As the external tympaniform membrane approaches the internal tympaniform membrane, the subsyringeal (= sternal air sac) pressure rises with increasing syringeal resistance and expiratory tracheal airflow peaks at about 6.1 ml/s (Figs. 6, 7, Table 1). Bernoulli forces cause the internal tympaniform membranes to vibrate, producing the first member of the double click (Fig. 9b).

4. The syrinx is closed during the silent intraclick interval by apposition of the syringeal membranes (Figs. 9c, 10). Subsyringeal pressure peaks at about 17 cm H_2O during this interval (Fig. 6), which is terminated by contraction of the tracheolateralis muscles (Fig. 3) that moves the syrinx craniad and causes the first bronchial ring to rotate outward, thus abducting the external tympaniform membranes and opening the syringeal lumen (Fig. 9d).

5. The second member of the double click occurs as the internal and external tympaniform membranes begin to separate, allowing expiratory airflow to resume (Fig. 9d). Tracheal airflow peaks at about 10 ml/s during this click as syringeal resistance and subsyringeal pressure drop (Figs. 6, 7, Table 1). The second click is terminated by further abduction of the external tympaniform membranes to their resting position (Fig. 9a).

6. The ability of swiftlets to transform a longer duration squeak-like vocalization into two brief clicks by momentarily closing the syrinx probably represents an important adaptation for acoustic orientation. By generating brief clicks they have created a sonar signal with a greater bandwidth and having abrupt rise-decay times that should improve target range determination based on measurement of the pulse-echo interval.

Introduction

Paleotropical swiftlets (genus *Collocalia*[1] in the family Apodidae) and neotropical oilbirds (Genus *Steatornis,* in the family Steatornithidae) are unique among birds in possessing an ability to orient acoustically in darkness by echolocation. Although swiftlets are diurnal insectivores and oilbirds are nocturnal frugivores, both groups nest in caves and when flying in darkness produce echolocative signals consisting of broad band clicks which are distinctively different from most other avian vocalizations. A knowledge of how these sounds are produced, in addition to being of general bioacoustical interest, is of special importance for a better understanding of avian sonar systems. In this paper we describe the mechanism by which the grey (or white-rumped) swiftlet, *Collocalia spodiopygia,* generates and controls its echolocative signals.

Abbreviation: EMG electromyogram

1 Brooke (1970, 1972) proposed placing echolocating swiftlets in the genus *Aerodramus.* Since this revision has not yet been adopted by the International Commission on Zoological Nomenclature we do not use it here

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Echolocation by swiftlets was recently reviewed by Medway and Pye (1977) and Pye (1980). All but two species, which restrict their breeding to partially lighted caves, appear to utilize echolocation. Echolocative clicks are also sometimes emitted during daytime flight outside the breeding cave, suggesting that they also play a role in social communication (Harrisson 1966).

Swiftlet echolocation has been studied by various authors (e.g., Medway 1967; Griffin and Suthers 1970; Fenton 1975; Smyth 1979). The use of echolocation by *C. spodiopygia* was established experimentally by Roberts et al. (1976) who also described the structure of the echolocative clicks. Two recent experiments have attempted to measure the sensitivity of echolocation in *C. spodiopygia*. Griffin and Thompson (1982) obtained evidence that these birds can acoustically detect and avoid wires having a diameter as small as 6.3 mm stretched across their flight space. Smyth and Roberts (in press) using a different experimental design obtained data which they believe indicates a detection threshold for wire diameters between 10 and 20 mm. Insect capture is presumably accomplished without the aid of echolocation, however.

The means by which swiftlets produce their clicks has been the subject of much conjecture. Harrisson (1966) suggested click production was in some way dependent on wing movement, but we have observed that birds resting quietly in cloth bags can emit clicks. Medway and Pye (1977) postulated that the sonar clicks of *Collocalia* are produced by action of the tongue against the palate, perhaps in a manner analogous to that by which the megachiropteran fruit bat, *Rousettus,* produces its orientation clicks (Kulzer 1960). They pointed out that the fact that swiftlets which echolocate carry nesting material in their feet, while those that do not echolocate carry it in their mouth, suggests involvement of the mouth in echolocation. However, they believed that the nature of the sounds and the variability in their frequency spectrum militated against a syringeal origin. Smyth (1979) conducted a series of experiments on the mechanism of click production by *C. spodiopygia*. His results were somewhat contradictory, however, and led him to conclude that both the syrinx and the glottis participate in click production, but that the primary sound source was probably further down the air way, possibly involving the air sacs.

Materials and Methods

Adult grey swiftlets, *Collocalia spodiopygia,* weighing about 10 g, were collected in mist nets stretched across the entrance to their breeding caves in the vicinity of Chillagoe in north Queensland, Australia. Experiments were conducted early in the breeding season in order to minimize their effect on reproduction. The birds were usually collected as they left the cave at dawn and held individually in cloth bags in our laboratory in Chillagoe for use in experiments on the same day.

A series of clicks to be used as control vocalizations were recorded from each bird before an experiment. Since *Collocalia* only reliably produce echolocating clicks while flying in the dark, a small dark recording chamber, measuring about 1.4 m on each side by 2.4 m high, was constructed. Clicks were tape recorded (Racal model 4 DS) while the bird hovered in front of a calibrated 1/2 inch (12.7 mm) condenser microphone (Brüel and Kjaer, model 4133) mounted inside this chamber. Relatively anechoic recordings were achieved by lining the portion of the chamber around the microphone where the bird hovered with fiberglass insulation. The complete sound recording system had a flat frequency response from 100 Hz to either 37 or 75 kHz, depending on the tape speed used. Occasionally, flight tests were also conducted in a large dark flight chamber measuring 9 m long, 3 m wide and 2.4 m high.

All surgery was performed under methoxyflurane anesthesia and with the aid of a dissecting microscope. After the swiftlet had fully recovered from the anesthetic, its vocalizations were again recorded inside the dark chamber, usually in conjunction with some of the physiological data described below, as it hovered on a tether several cm in front of the microphone.

The electrical activity of the tracheal muscles was recorded by inserting a pair of teflon coated platinum iridium wires, 0.025 mm (1 mil) in diameter, into the body of the muscle. The insulation was removed from the portion of the wire in the muscle and the electrodes were held in place by applying a very small amount of histoacryl blue tissue cement (B. Braun Melsungen, Federal Republic of Germany) to the wire where it penetrated the muscle. There is considerable movement of these muscles relative to other nearby structures, so great care was taken to avoid cementing any portion of the wire or muscle to adjacent tissues. A loop of slack wire was left near the muscle as a further precaution against limiting the muscles' mobility. After exiting from the ventral neck region, the electrode wires were soldered to shielded flexible copper leads which were attached to the sternum with cyanoacrylate glue and to the base of the rectrices with adhesive tape. The shield was connected to an indifferent silver wire electrode placed under the skin of the back. The leads were then connected differentially to the input of a preamplifier (Princeton Applied Research model, 113) with a band pass of 300 Hz to 3 kHz. Where they left the tail they formed a tether by which the bird was held while it hovered in front of the microphone in the dark recording chamber. The amplified EMG was recorded in the FM mode on one channel of the Racal tape recorder.

Sternal air sac pressure was recorded with a temperature compensated miniature piezoresistive pressure transducer (Endevco model 8507-5), having a flat response from DC to 13 kHz and a resonant frequency of 65 kHz. This transducer was fitted onto the end of a 15 mm long cannula of PE 50 tubing (ID = 0.58 mm), the other end of which was inserted into the sternal air sac and sealed in place with cyanoacrylate glue. The transducer's excitation and output voltages were transmitted through flexible wires that were taped to the rectrices and which also formed part of the tether on which the bird hovered. The output voltage was amplified and recorded in the FM mode on a channel of the Racal tape recorder. The frequency response of this system was either 0.03 Hz or 5 Hz to 5 kHz, depending on the amplifier used.

Tracheal pressure was monitored by a similar piezoresistive transducer attached to the side arm of a T-cannula inserted

through a ventral slit in the trachea that did not disturb the tracheolateralis muscles or hypoglossal nerve. The barrel of this T-cannula was constructed of 16 gauge stainless steel tubing. The side arm was made of an 8 mm length of 18 gauge hypodermic needle extending from a hub into which the pressure transducer was mounted. The total volume of the T-cannula dead space was about 8.8 µl.

The tracheal T-cannula also contained a flow probe consisting of two microbead thermistors (Veco 32A 402C) mounted less than 0.5 mm apart opposite the side arm and centered on the axis of the barrel. These thermistors were heated and maintained at a constant temperature by feedback circuity. The sum of the currents through the thermistors was non-linearly proportional to the airflow rate through the tracheal T-cannula. The non-linear output voltage of the flow meter circuit was empirically calibrated against flow rate (ml/s) using water saturated air at body temperature. The response time of the flow meter was 90% of full scale in 6 ms. The non-linear voltage output was tape recorded in the FM mode which had a flat frequency response from DC to 5 kHz. The recorded signal was then played back through a third order linearizing circuit, the coefficients of which were determined by a least squares fit of the non-linear calibration data to a straight line. The linearized output was a voltage linearly proportional to the airflow rate and was integrated to give breath volume. The technique was modeled after that of Bernstein and Schmidt-Nielsen (1974).

Leads from the flow probe and pressure transducer in the T-cannula were attached to the rectrices and formed a part of the tether used to restrain the bird while it hovered in front of the microphone.

In order to study their microscopic anatomy, some syringes were embedded in paraffin, serially sectioned at 6 µm and stained with hematoxylin and eosin.

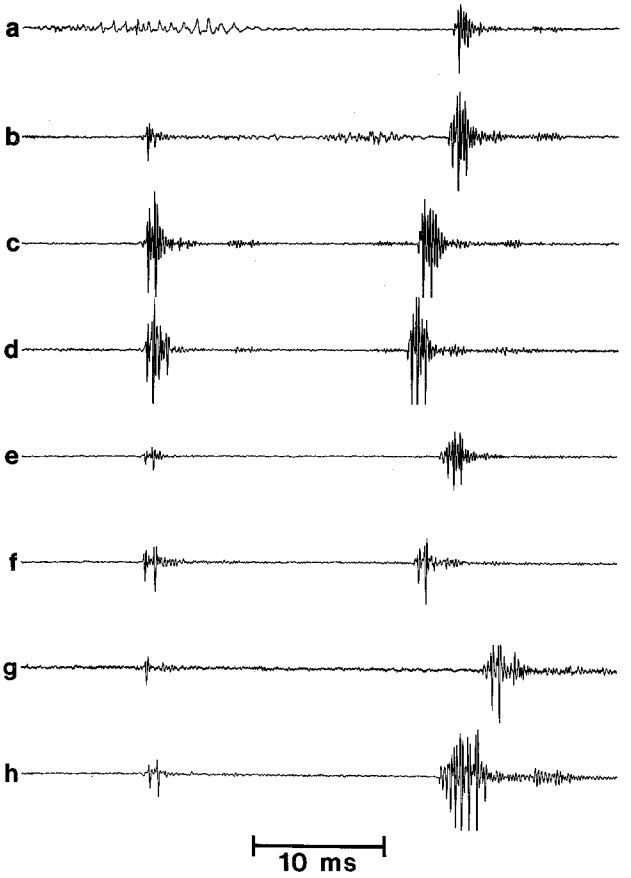

Fig. 1a–h. Clicks emitted by intact swiftlets while hovering in front of a microphone in a dark chamber. Each line shows one double click. **a–d** Variation in double clicks emitted by bird 20. **e–h** Double clicks emitted by 4 other swiftlets. Note variation in the silent intraclick interval and in relative amplitude of the 1st and 2nd members of the double click. The 1st click in line a has an unusually low amplitude and long duration

Results

Normal Echolocative Clicks

A series of clicks emitted by several freshly captured intact swiftlets while hovering in the flight chamber is shown in Fig. 1. The first four clicks (Fig. 1 a–d) indicate the range of variability present in the clicks emitted by an individual bird during a single recording session. The remaining four clicks (Fig. 1 e–h) are single examples from four other swiftlets and give some indication of the extent of interindividual variation. Sound spectrographs of a series of clicks from yet another intact bird can be seen in Fig. 5 a.

Each of these examples consist of two successive clicks, referred to as a double click, having a broad frequency spectrum and separated by a silent period, the intraclick interval, lasting roughly 25 ms. Most of the energy lies between 2 and 8 kHz. It is clear from Fig. 1 that there is variation in the intraclick interval, even for an individual bird; typical values range from about 18 to 25 ms. The low amplitude oscillation, visible in some of the recordings (e.g., Fig. 1 c and d), which starts about 4 or 5 ms after each click is probably an echo.

The first member of the double click is usually at a lower amplitude and of shorter duration than the second member. The first click may consist of as little as one cycle (e.g., Fig. 1 g), but usually contains several cycles. An unusual variant having a long duration is illustrated in Fig. 1 a. Occasionally only one member of the double click is detectable, even under good recording conditions at a short range. Sometimes, on the other hand, both members of the double click are about equal in amplitude (Fig. 1 c and d) and rarely the first click is much more intense then the second.

Where are the Echolocative Clicks Generated?

Although the vocal organ of birds is the syrinx, it was theoretically possible that *Collocalia* might generate these sounds with its tongue as does the bat, *Rousettus* (Kulzer 1960), or its glottis. Our first

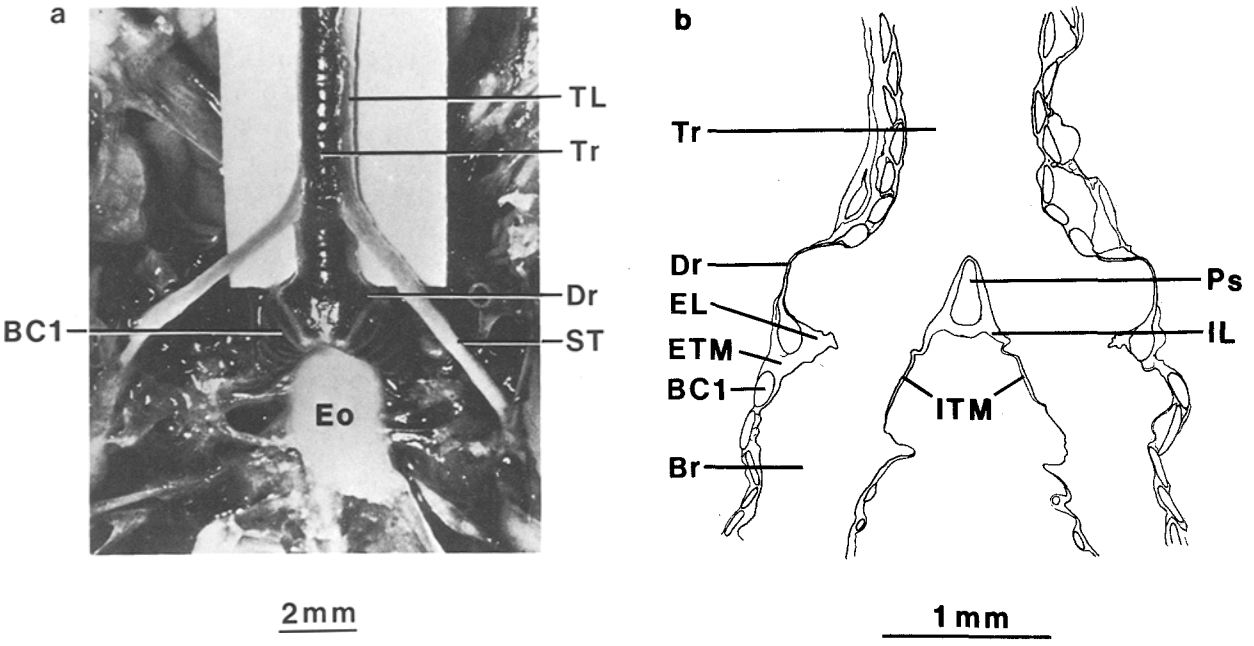

Fig. 2. a Ventral view of syrinx of *Collocalia spodiopygia,* showing bronchi, trachea and tracheal muscles. **b** Drawing of histological section through the syrinx showing details of its anatomy. *BC 1* first bronchial cartilage; *Br* bronchus; *Dr* cartilaginous drum of syrinx; *Eo* esophagus; *EL* external labium; *ETM* external tympaniform membrane; *IL* internal labium, *ITM* internal tympaniform membrane; *Ps* pessulus; *St* sternotrachealis muscle; *TL* tracheolateralis muscle; *Tr* trachea. The interclavicular air sac completely surrounds the syrinx and is traversed by the sternotrachealis muscles and trachea. Note: BC 1 in this paper is designated as the second bronchial cartilage by Smyth (1979) who retains the term first bronchial cartilage for the bronchial cartilage which fuses with a tracheal cartilage to form the drum of the syrinx

experiments were therefore designed to determine the site where the clicks are produced.

Immobilization of the Tongue. The possibility that the clicks might be generated by the tongue was tested by gluing the tongue to the floor of the mouth with tissue cement. This procedure did not impair the bird's ability to click. Our result thus confirms that of Smyth (1979) who conducted a similar experiment.

Sealing the Glottis. A tracheostomy was performed on a second bird, after which its glottis was sealed shut with tissue cement. This bird continued to emit normal clicks through its tracheal cannula when it was flown in a dark room.

Elimination of Syringeal Airflow. A cannula of PE 190 tubing a few centimeters long was inserted into the sternal air sac of a third *Collocalia.* Following this procedure this bird produced clicks while flying in the dark, but these vocalizations sounded much fainter than normal and consisted of only single, rather than double, clicks. When a reversible plug was placed in the air sac cannula double clicks were again emitted at a normal intensity.

The air sac cannula reduces the subsyringeal air pressure and reduces, but does not eliminate, the volume of air flowing through the syrinx. In order to eliminate syringeal airflow we reopened the sternal air sac cannula and sealed the glottis with tissue cement. When flown in total darkness no sounds of any kind were produced and the bird behaved as if it could not detect the walls of the flight chamber or other objects in its flight path.

Anatomy of the Vocal Apparatus

The lungs and air sacs of *C. spodiopygia* appear similar to those of Oscines (song birds) (see Duncker 1971). The vocal apparatus is structurally simple (Fig. 2). The trachea divides at the syrinx into two primary bronchi. Two pairs of muscles, the sternotrachealis and tracheolateralis, attach to the trachea but there are no intrinsic syringeal muscles. The tracheohyoideus (= cleidotrachealis) muscle also appears to be absent. The trachea is about 22 mm long, and 1.5 mm in diameter in its upper 5 mm. It narrows to slightly over 1 mm in its lower 17 mm and has complete overlapping hyaline cartilage rings along its entire length. The tracheolateralis muscles form 0.5 mm wide bands of skeletal muscle which run along the lateral aspects

of the trachea from the larynx to the drum of the syrinx and are firmly attached along the entire length. Between 2 and 3 mm (6–10 rings) above the syrinx they are joined by the sternotrachealis muscles which are nearly cylindrical muscles about 0.5 mm in diameter by 8 mm long that traverse the interclavicular air sacs and are attached posteriolaterally to the first vertebral rib and to the pulmonary aponeurosis at the lateral margin of the lung. The sternotrachealis muscles in most other birds that have been studied extensively (e.g., song birds, chickens, ducks) are attached to the sternum. The syrinx of *C. spodiopygia* is suspended in the interclavicular air sac by the trachea, tracheal muscles and bronchi and is composed of fused rings of cartilage forming the barrel and pessulus where the airway divides. The syrinx at the junction with the primary bronchi is flattened laterally. Incomplete cartilaginous rings (7 extrapulmonary) support the bronchi but are open on the medial aspect of the bronchi. This portion of the bronchus is closed only by a thin membrane which appears slightly thickened in its anterior 0.5 mm. This forms the internal tympaniform membrane and is attached to the pessulus at the internal labium. Opposite the internal tympaniform membrane and suspended on the posterior aspect of the barrel is the external labium which supports the external tympaniform membrane between the barrel and the first bronchial cartilage. The labia and tympaniform membranes are lined with a non-ciliated, flattened epithelium while the remainder of the trachea, syrinx and primary bronchi have a ciliated epithelium. This indicates that mechanical vibration associated with sound production probably involves the labia and tympaniform membranes.

Activity of the Tracheal Muscles

Since the swiftlet syrinx has no intrinsic muscles, syringeal motion is controlled by tracheal muscles: the tracheolateralis and sternotrachealis. These muscles act on the syrinx by lengthening or shortening the trachea and primary bronchi, thus altering the tension across the syrinx. This in turn controls the aperture of the syringeal lumen and makes sound production possible. Movement of the head and neck can also affect the syrinx by varying the tension on the trachea. The activity pattern of the tracheal muscles may be altered during such activity.

We attempted to record the EMGs of these muscles in 5 birds during flight. We were able to obtain good recordings from the sternotrachealis muscle in two of these animals and from the tracheolateralis muscle in one animal. A second bird yielded marginal recordings from the tracheolateralis muscle which appeared to be consistent with the much better recordings obtained from the first animal.

M. sternotrachealis. Bilateral contraction of the sternotrachealis muscles lengthens the trachea and moves the syrinx caudad, reducing the tension across the syrinx and allowing the airway to narrow.

Electromyographic recordings show that these muscles become active about 17 to 20 ms before the onset of a click (Fig. 3a). The amplitude of the electrical activity continues at a high level for about 25 ms and then usually declines to the background noise level within 30 to 40 ms after the onset of the EMG. Insertion of the recording electrodes into this muscle interferes slightly with the tracheal movement and converts the normal double click into a longer duration sound which continues during what is normally the intraclick interval. This vocalization begins and ends when the first and second members of the double click, respectively, normally occur. The high amplitude portion of the EMG terminates during the time corresponding to the intraclick interval, but lower amplitude electrical activity may continue for several ms after the end of the vocalization.

M. tracheolateralis. Contraction of the tracheolateralis muscles shortens the trachea and its primary action is to pull the syrinx craniad, thus increasing the tension across the syrinx and opening the airway.

Recording electrodes in this muscle also restrict its movement enough to convert the double clicks into continuous pulses, as in the case of the sternotrachealis. Nevertheless, it is clear that the electrical activity of the tracheolateralis muscles normally begins 10 to 15 ms after the onset of the double click, i.e., in about the middle of the intraclick interval when the EMG of sternotrachealis muscles becomes attenuated or terminates (Fig. 3b). The tracheolateralis EMG continues during the second member of the click pair, ending 12 to 20 ms after it began.

Effect of Surgical Intervention with Tracheal Muscles

Further information on the role of the tracheal muscles in producing clicks was obtained by observing the effect on sound production of their paralysis or ablation.

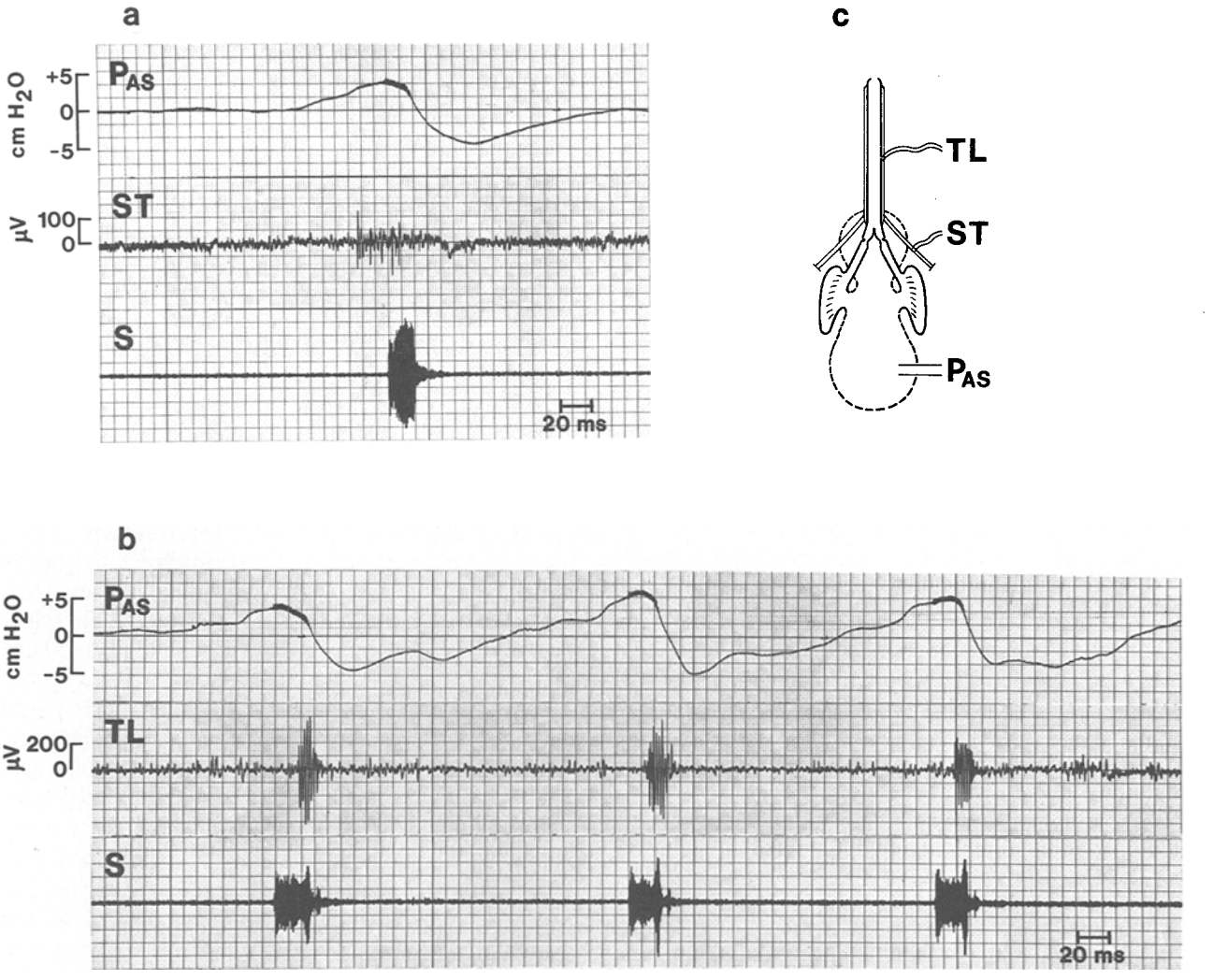

Fig. 3a–c. Electrical activity of tracheal muscles and sternal air sac pressure during click production by bird 25. **a** Sternotrachealis muscles; **b** Tracheolateralis muscle. **c** Schematic anatomical diagram of respiratory system showing position of recording electrodes in muscles and sternal air sac cannula. End of cannula was sealed with pressure transducer. Electrical activity occurs first in sternotrachealis muscle then in tracheolateralis muscle. The slight mechanical interference of recording electrodes converts the double click into a continuous sound having a duration similar to that of the complete double click. P_{AS} sternal air sac pressure; *ST* m. sternotrachealis; *TL* m. tracheolateralis; *S* sound

Denervation of Tracheal Muscles. Both the tracheolateralis and sternotrachealis muscles are innervated by cranial nerve XII, the hypoglossal nerve. This nerve runs down the trachea, sending multiple branches to the tracheolateralis, until it reaches the caudal end of the trachea where twigs leave the trachea and innervate the sternotrachealis. Section of these twigs paralyzes the sternotrachealis muscles but not the tracheolateralis muscles, whereas section of the nerve at the cranial end of the trachea paralyzes both the sternotrachealis and the tracheolateralis. Bilateral denervation of only the sternotrachealis converts the normal double click (Fig. 4a) into a single vocalization (Fig. 4b) having a squeaky quality with a duration considerably longer than either member of the normal double click. The sound spectrographs in Fig. 5 show that the broad energy spectrum of the normal brief clicks (Fig. 5a) is converted into a series of harmonics having a fundamental at about 2 kHz (Fig. 5b). Similar squeaks or chirps are emitted if cranial nerve XII is then sectioned bilaterally at the cranial end of the trachea, paralyzing both pairs of tracheal muscles. In this case there is a tendency toward frequency modulation at the beginning and end of most vocalizations (Figs. 4c and 5c) in bird 5, or even a continuous downward FM sweep in bird 6 (Fig. 5d). In a third swiftlet (bird 4) only the left hypoglossal nerve was cut at the cranial end of the trachea. The pulses emitted after unilateral neur-

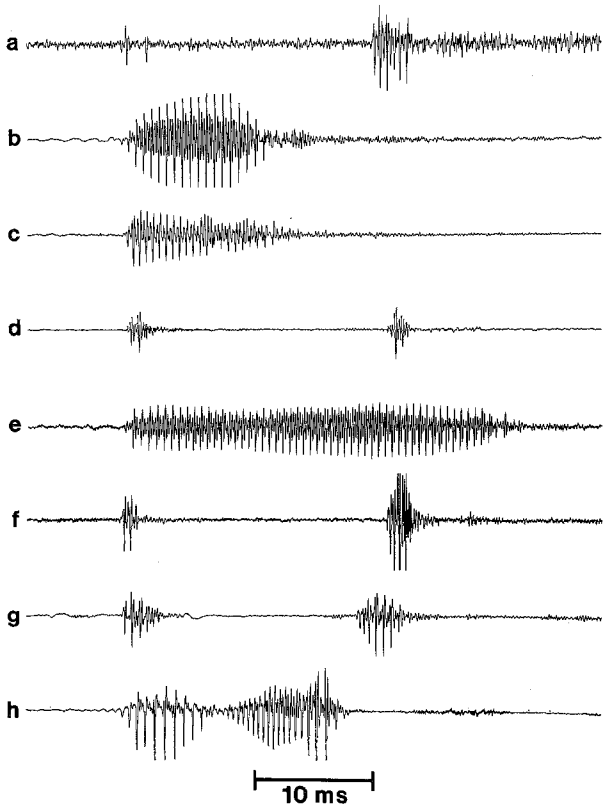

Fig. 4a–h. Effect of various surgical procedures on the echolocative clicks of swiftlets. **a–c** Bird 5: **a** normal double click before surgery; **b** after paralysis of both sternotrachealis muscles by bilateral section of hypoglossal nerves near caudal end of trachea; **c** after paralysis of both sternotrachealis and tracheolateralis muscles by bilateral section of hypoglossal nerves near cranial end of trachea. **d–e** Bird 7: **d** normal double click before surgery; **e** squeak-like vocalization produced when bird attempted to click after surgical removal of both tracheolateralis muscles and denervation of the sternotrachealis muscles. **f–h** Bird 21: **f** normal double click before surgery; **g, h** modified clicks emitted after tissue cement was placed on external surface of both external tympaniform membranes in order to reduce their mobility

otomy were similar, however, to those emitted following bilateral neurotomy. Unlike birds 5 and 7, this bird produced no vocalizations after the right hypoglossal nerve was also sectioned.

Section of m. sternotrachealis. The tracheolateralis and sternotrachealis muscles have antagonistic actions in that they pull the trachea in opposite directions. Even after paralysis, the flaccid intact muscles will provide a passive resistance to the action of the antagonistic muscle pair.

We therefore sectioned the sternotrachealis muscle of bird 9 bilaterally near its attachment to the trachea, leaving the tracheolateralis muscle and its innervation intact. This bird, which clicked normally before this operation, was totally silent after it. Intact, if flaccid, sternotrachealis muscles are apparently necessary for click production.

Removal of m. tracheolateralis. Since the tracheolateralis muscle is attached to the trachea along its entire length, making a transverse cut through it does not eliminate its passive mechanical effect. We therefore surgically removed the tracheolateralis from both sides of the trachea of one bird. This operation, which also denervated both sternotrachealis muscles, changed the typical double click (Fig. 4d) into a long duration squeak or chirp containing a number of harmonics beginning with a rising FM and terminating with descending FM (Figs. 4e and 5e).

Nature of the Syringeal Generator

The external and internal tympaniform membranes are the structures in the syrinx which are most likely to act as sound generators. Each of these membranes is present in both sides of the syrinx, where Bernoulli forces created by syringeal airflow may cause them to vibrate if they approach each other in the syringeal lumen (see Fig. 2b).

Although an otherwise intact swiftlet is still capable of emitting apparently normal double clicks after the mobility of both external tympaniform membranes is greatly reduced by the application of tissue cement to their outer surface (Fig. 4f and g; Fig. 5f, first 5 clicks), a large proportion of the orientation sounds are abnormal after this treatment and consist of a single click with an unusually long duration. Unfortunately, we cannot be sure that the external tympaniform membranes were completely immobilized by the tissue cement. The abnormally long sounds are sometimes attenuated in the middle so that they give the appearance of a double click which has been fused together by elimination of the intraclick interval (Figs. 4h and 5f, last 4 clicks). In any case, vibration of the external tympaniform membranes is apparently not essential for click production. At least under these experimental conditions, the syringeal waveform is probably generated by vibration of the internal tympaniform membranes alone. Unfortunately, their inaccessible position prevented us from selectively immobilizing them without affecting the external tympaniform membranes.

Does Each Half of the Syrinx Contribute One Member of the Double Click?

In order to test the possibility that the first and second members of the double click might be

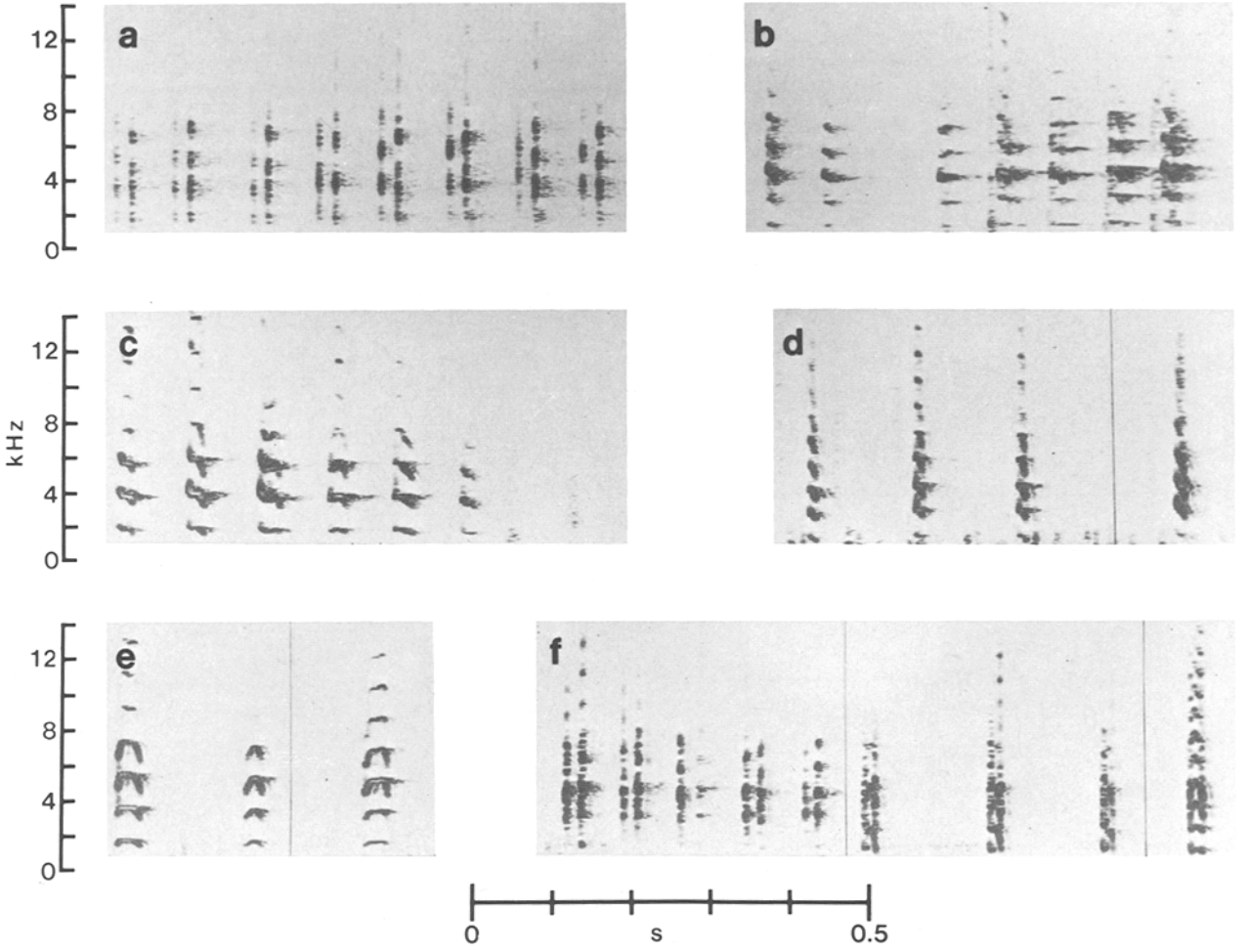

Fig. 5a–f. Sonagrams of normal and of experimentally modified clicks. **a** Control clicks of bird 5; **b** modified clicks after bilateral section of hypoglossal nerves near caudal end of trachea, thus denervating the sternotrachealis muscles of bird 5; **c** modified clicks after bilateral section of hypoglossal nerves near cranial end of trachea, thus denervating both the tracheolateralis and sternotrachealis muscles of bird 5; **d** same treatment as in **c**, bird 6; **e** modified clicks emitted one day after bilateral removal of tracheolateralis muscles in bird 7. This treatment also denervated the sternotrachealis muscles. **f** Modified clicks emitted by bird 21 after applying tissue cement to external surface of each of the external tympaniform membranes in order to reduce their mobility

produced in opposite sides of the syrinx, we plugged either the left bronchus or the right bronchus of different birds by injecting a droplet of tissue cement into the lumen through the external tympaniform membrane. These birds continued to produce essentially normal double clicks even though one side of their syrinx was completely plugged, as verified during autopsy. Under normal conditions, both sides of the syrinx must therefore operate together and contribute to each member of the click pair. This requires precise coordination of both sides of the syrinx. The numerous interconnections visible between the left and right hypoglossal nerves as they travel down the trachea suggest that each muscle receives motor innervation from both nerve trunks. This bilateral innervation may play a role in synchronizing the contraction of the left and right tracheal muscles, thus ensuring that the two sides of the syrinx operate in unison.

Airway Dynamics and the Production of Clicks

An understanding of the role of the tracheal muscles in click production is greatly facilitated by knowledge of the concurrent changes in respiratory air pressure and flow. The subsyringeal air pressure provides the driving force for click production. This pressure is essentially identical to that in the lungs and air sacs (Brackenbury 1972) and can be most conveniently monitored via a cannula inserted into the sternal air sac. Since the syrinx is suspended in the interclavicular air sac, the pressure differential between the syringeal lumen and the interclavicular

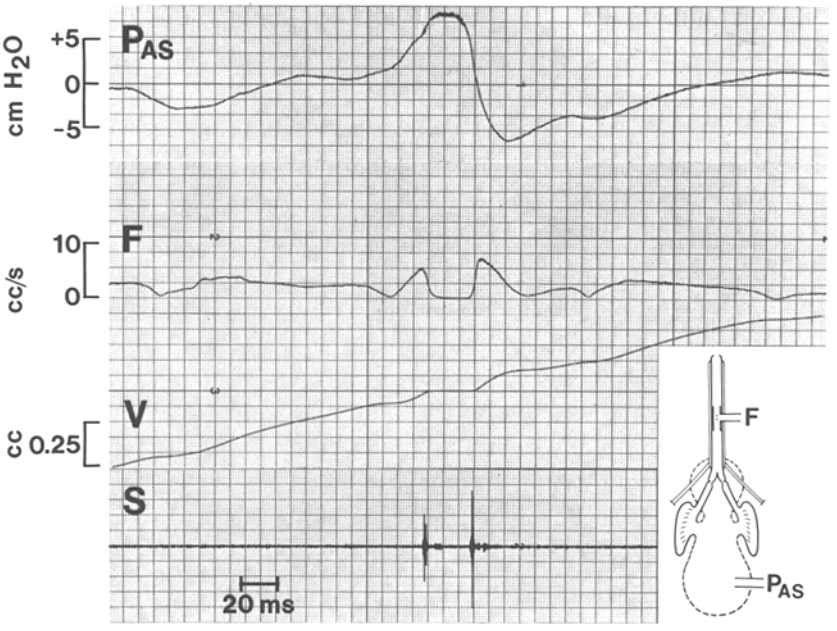

Fig. 6. Sternal air sac pressure (P_{AS}), rate of tracheal airflow (F) and expiratory volume (V) during the generation of a typical double click (S) by bird 24 while hovering. Schematic diagram of the respiratory system shows the location of the flow probe in the trachea and pressure cannula in the sternal air sac. Sidearm of tracheal T-cannula and air sac cannula were sealed with pressure transducers. During low frequency silent respiration the zero crossings of air sac pressure do not coincide with zero tracheal flow. We believe this is an artifact due to movement of the trachea. Note that this artifact is not present during the higher frequency fluctuations associated with the click. Inertia of the moving column of air may also contribute to the disparity in zero crossings. These same factors apply to the relationship between tracheal pressure and flow in Fig. 7

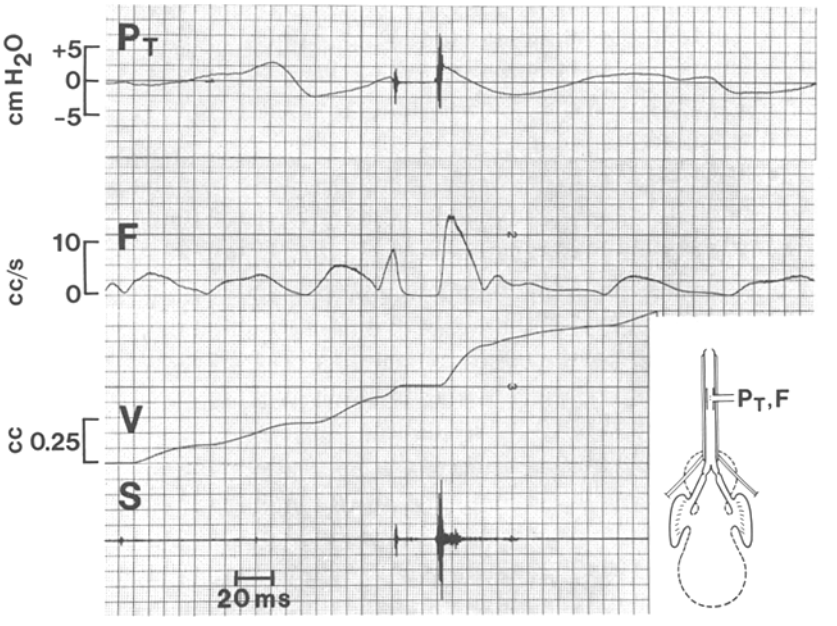

Fig. 7. Tracheal pressure (P_T), rate of tracheal airflow (F) and expiratory volume (V) during a typical double click emitted by bird 24 while hovering. (See legend of Fig. 6)

sac (i.e., across the tympaniform membranes) is negligible in the absence of Bernoulli forces generated by rapid airflow through the syrinx.

The sternal air sac pressure, tracheal airflow and expiratory volume during a typical double click are shown in Fig. 6. Tracheal pressure, flow and expiratory volume are shown in Fig. 7. The mean peak values of pressure and rate of airflow during silent respiration and vocalization are summarized in Table 1. Just prior to sound emission the bird increases its expiratory effort, causing sternal air sac pressure to rise. Tracheal pressure and airflow also begin to increase about 10 to 20 ms before the click. Tracheal airflow peaks at the onset of the first click and oscillates with the acoustic waveform during the sound (Fig. 7). Air sac pressure remains high during the intraclick interval, but both tracheal pressure and flow drop abruptly during the first member of the click pair and remain at zero during the intraclick interval, indicating that the syrinx is

Table 1. Swiftlet respiratory pressures and rates of airflow while hovering in tethered flight[a]

	Sternal air sac pressure (cm H_2O)	Tracheal pressure (cm H_2O)	Tracheal flow (ml/s)
Silent inspiration	-1.9 ± 0.2	-0.07 ± 0.01	1.0 ± 0.04
Silent expiration	1.5 ± 0.1	0.10 ± 0.02	0.8 ± 0.04
During 1st member of double click		0.09 ± 0.02	6.1 ± 0.3
	16.7 ± 0.4[b]		
During 2nd member of double click		0.08 ± 0.02	10.1 ± 0.5
n	≧26	≧22	≧18

[a] Mean peak values ± standard error. Transient oscillation of tracheal pressure during click is not included

[b] Peak sternal air sac pressure occurs during silent intraclick interval

closed. The more gradual decay of flow, compared to pressure, after the first click represents the response time of the flow meter.

At the end of the intraclick interval, which averages about 25 ms, the syrinx opens. Tracheal flow and pressure increase abruptly as the second click is produced, typically reaching values greater than those attained during the first click and again oscillating with the acoustic waveform. The peak to peak amplitude of this oscillation often reaches 10 cm H_2O. Air sac pressure begins to drop before the second member of the double click is emitted (Fig. 6). After this click tracheal flow and pressure decline. Although the tracheal pressure reaches zero about 20 ms after the click, and then becomes negative, expiratory flow continues for another 4 or 5 ms before inspiratory flow begins (Fig. 7). We believe this brief lag of flow behind the pressure gradient is probably due to movement of the trachea and perhaps also to the inertia of the moving column of tracheal air.

Discussion

Summary of Click Mechanism

We can now formulate a coherent hypothesis of the mechanism of click production by *Collocalia*. The tracheal muscle activity and airway dynamics associated with a typical double click are schematically summarized in Fig. 8.

Clicks are generated in the syrinx where their production is controlled by the action of the sternotrachealis and tracheolateralis muscles. The

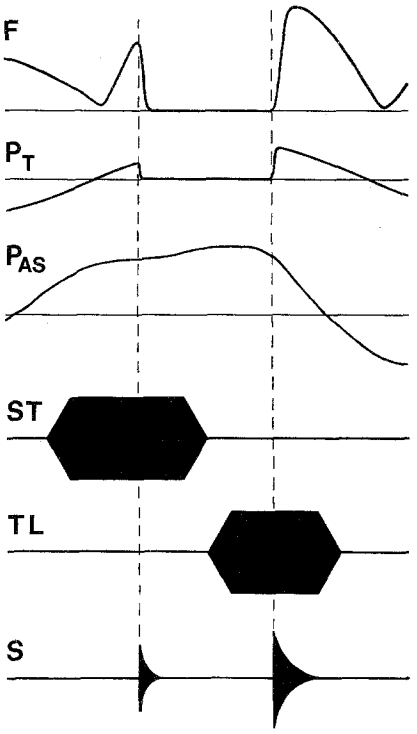

Fig. 8. Schematic summary of temporal relationships between events during a normal double click. *F* rate of tracheal airflow; P_T tracheal pressure; P_{AS} sternal air sac pressure; *ST* EMG of m. sternotrachealis; *TL* EMG of m. tracheolateralis; *S* double click

cycle of events responsible for each double click is summarized in Fig. 9. During silent respiration the syrinx is open and the tracheal muscles are relaxed (Fig. 9a). The sternotrachealis initiates the first part of the click by drawing the syrinx caudad and allowing the first bronchial half ring to rotate inward. This moves the external tympaniform membrane into the syringeal lumen and obstructs the airway (Fig. 9b). The mechanism by which this closure occurs is shown in more detail in Fig. 10 and can be mimicked in an anesthetized bird by manually increasing and decreasing the tension exerted on the syrinx by the trachea. Just before the airway is occluded, the velocity of the expiratory air peaks and we believe the associated Bernoulli forces cause the internal tympaniform membranes to vibrate. This vibration, which constitutes the first member of the click pair, lasts about 3 ms and is terminated when the two membranes make contact with each other (Fig. 9c). At this time tracheal airflow and pressure go to zero. The tracheolateralis muscle then becomes active, pulling the syrinx craniad, and causing the first bronchial half ring to rotate outward. As air begins to flow through the restricted opening, the internal tympaniform membranes are set into vibration once again,

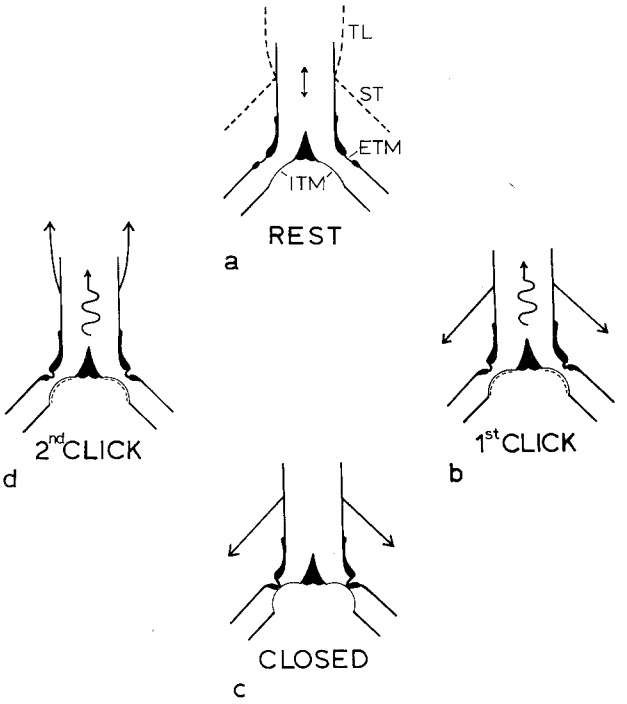

Fig. 9. Diagram of syrinx and tracheal muscles of *Collocalia spodiopygia* showing cycle of events responsible for production of a double click. Action of the tracheal muscles is indicated by arrows from tracheal wall. Airflow is indicated by *arrow* in trachea. See text for explanation. *ETM* external tympaniform membrane; *ITM* internal tympaniform membrane

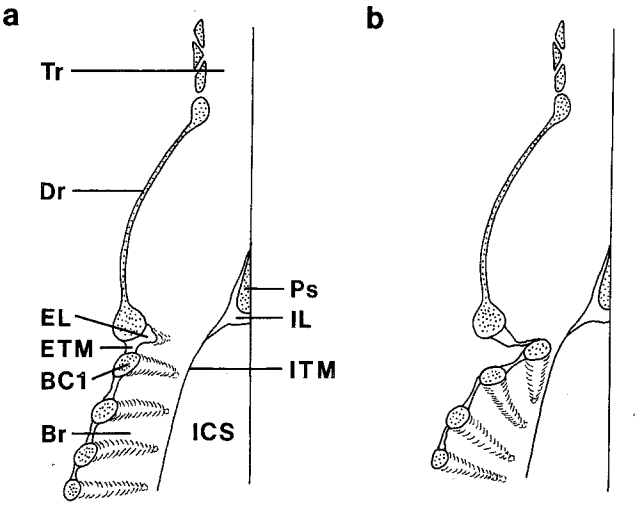

Fig. 10a, b. Ventral view of longitudinal section through right half of syrinx showing inward rotation of first bronchial cartilage. **a** Resting position with bronchus open as during silent respiration. **b** Inward rotation of first bronchial cartilage when tension across the syrinx is relaxed by contraction of sternotrachealis muscles during click production. The C-shaped cartilage rotates on an axis through its open ends. External labium may act as latch holding the first bronchial cartilage in lumen until syrinx moves cranially. *BC 1* first bronchial cartilage (see note in legend of Fig. 2); *BR* bronchus; *Dr* cartilaginous drum of syrinx; *EL* external labium; *ETM* external tympaniform membrane; *Ps* pessulus; *Tr* trachea

producing the second member of the click pair (Fig. 9d). This second click is terminated by the continued abduction of the external tympaniform membranes. As the syringeal aperture increases, the air velocity past the internal tympaniform membranes decreases and their vibration is damped. The syrinx thus returns to its resting condition and the tracheolateralis muscle relaxes (Fig. 9a). During each cycle of adduction followed by abduction, the syringeal membranes must twice pass through an intermediate position where the airflow causes the internal tympaniform membranes to vibrate. In an intact bird each of these periods of vibration is very brief; together they produce the double click. We believe that these very brief broadband clicks are most likely the result of vibrating membranes, as described above, rather than arising from vortexes at the constriction of the syringeal lumen as in the case of an aerodynamic whistle, which seems better suited for producing tones. This latter possibility cannot be totally excluded, however, and it is conceivable that both of these mechanisms may contribute to click production.

Membrane vibration during the second member of the click pair, unlike the first, can damp out more gradually since it is not terminated by physical contact with the opposite membrane. This difference may explain the longer and more variable duration of the second click, compared with the first. The second click is also usually at a greater intensity than the first, probably due to the fact that subsyringeal pressure continues to rise during the intraclick interval and thus provides a greater driving force during the second member of the click pair.

Occasionally swiftlets emit a single click, or one in which the first member of the click pair is barely detectable even when the bird is hovering several centimeters in front of the microphone. In all cases that we have examined, the tracheal pressure recording clearly indicates that single clicks are the result of failure of the first member of the click pair, which is absent because the syrinx closes before there is adequate expiratory airflow to generate this first member of the double click.

Even very mild interference with the action of the tracheal muscles – such as insertion of the nearly invisible wires which we used as recording electrodes – is enough to hinder their movement and convert the normal double click into a continuous tone burst or squeak. Tracheal airflow continues during a squeak, indicating that squeaks result from

the bird's inability to rapidly and precisely close the syrinx by fully adducting the syringeal membranes which therefore remain longer in a partially adducted vibratory position. The fundamental frequency of the squeak is about 2 kHz which presumably represents the resonant frequency of the syringeal membranes.

Relationship to Other Avian Vocalizations

The physiology and acoustics of avian social vocalizations have been studied in relatively few species and are not completely understood (Gaunt and Wells 1973). Comparison of swiftlet clicks with vocalizations by other species is also complicated by the fact that syringeal anatomy varies considerably among different taxa. Many birds for example, have several pairs of intrinsic syringeal muscles and additional tracheal muscles which are not present in swiftlets. Nevertheless, the mechanism by which swiftlets produce their echolocating clicks appears to have much in common with that responsible for many other avian vocalizations.

In other birds, as in the case of swiftlets, the external tympaniform membrane and/or the closely associated external labium act as valves regulating the syringeal airflow by varying the bronchial aperture. Sound production by the crow (*Corvus brachyrhynchos*), for example, is thought to be dependent on the inward rotation of the fourth bronchial ring by contraction of certain intrinsic muscles which thus reduce the syringeal lumen and increase syringeal resistance by bringing the external tympaniform membrane closer to the internal tympaniform membrane while also adjusting membrane tension (Chamberlain et al. 1968). A similar valve-like action of the external labium or external tympaniform membrane has been suggested for other species (Stein 1968; Gaunt et al. 1973). The presence of this syringeal resistance is responsible for the fact that in starlings (*Sturnus vulgaris*) (Gaunt et al. 1973) and in chickens (*Gallus gallus*) (Gaunt et al. 1976), as well as in swiftlets, tracheal pressure is typically well below bronchial pressure during vocalization.

The tension of the syringeal membranes in several passerine and non-passerine species is controlled primarily by the antagonistic interaction of the sternotrachealis and tracheolateralis muscles (Miskimen 1951; Youngren et al. 1974; Gaunt and Gaunt 1977) such as it is in swiftlets. Lockner and Youngren (1976) showed that in mallard ducks (*Anas platyrhynchos*), induced to vocalize by brain stimulation, the electrical activity of the sternotrachealis muscles immediately precedes that of the tracheolateralis muscles and coincides with that of the external abdominal oblique muscles which are responsible for developing expiratory pressures in the air sacs. Miskimen (1951) reported that excision of the sternotrachealis muscles abolished song in cardinals (*Richmondea cardinalis*) and Nottebohm (1971) found that bilateral denervation of the chaffinch (*Fringilla coelebs*) syrinx rendered the bird almost aphonic. Smith (1977) however found that the species typical songs of rock pigeons (*Columba livia*) and several passerines returned to normal within about two weeks after these muscles were cut and attributed this recovery of normal song to healing of the interclavicular air sac. Phillips and Youngren (1981) report that denervation or section of the sternotrachealis muscles of chicks eliminated their low intensity calls and reduced the high frequency components of other vocalizations.

It thus seems likely that these two pairs of tracheal muscles perform a qualitatively similar function during vocalization in a variety of other birds as they do in echolocating swiftlets. The sternotrachealis muscles allowing the first bronchial cartilage to initiate sound production by restricting the syringeal lumen; the tracheolateralis muscles terminating vocalization by increasing the tension across the syrinx and drawing the first bronchial cartilage out of the air stream. Brackenbury (1978), in fact, postulated that the rapid pulses in the rhythmic songs of two British warblers (*Locustella naevia* and *Acrocephalus schoenobaenus*) might be produced by alternate contraction of these two pairs of antagonistic tracheal muscles, functioning in a manner almost identical to that which we have found experimentally in swiftlets. Brackenbury further suggested that, in these passerines, amplitude modulation of low frequency pulses (less than about 100 Hz) to produce higher frequency pulses or "ripples" may depend on the intrinsic syringeal muscles which, because of their smaller mass, should have a higher resonant frequency than the tracheal muscles.

Evolution of the Double Click

Although the production of social vocalizations has not been studied in swiftlets, it is likely that their ability to produce echolocative double clicks required relatively minor modifications of existing motor patterns.

The squeak which results when movement of the tracheal muscles is restricted is similar to simple vocalizations of many non-echolocating birds. One may speculate that echolocating clicks in swiftlets evolved from such a vocalization. By shutting off

the syrinx in the middle of the squeak and thus converting it into a pair of clicks, swiftlets have evolved a sonar signal with an abrupt onset and greater bandwidth. These changes should significantly improve the bird's ability to measure the time interval between the emitted signal and returning echo and to determine the range and position of a target.

One can easily imagine primitive avian sonar signals representing stages in the gradual transformation of squeaks into clicks as the neural control and properties of the tracheal muscles were modified for click production. Many squeaks emitted by our experimental animals were greatly attenuated in the middle, making them suggestive of the beginnings of a double click. It would be interesting to determine if *C. spodiopygia* can obtain any useful information from the echoes of such squeaks.

All but three swiftlets produce echolocative clicks very similar to those of *C. spodiopygia* (see review by Medway and Pye 1977). Two of these three (*Collocalia gigas* and *C. esculenta*) apparently do not echolocate and the third (*C. maxima*) produces single instead of double clicks. Recordings of *C. vanikorensis* mostly contained double pulses but occasionally showed one which appeared to have a third high amplitude peak (Griffin and Suthers 1970). These recordings contain many more echoes than do ours of *C. spodiopygia* and it is desirable to further investigate the possible occurrence of triple clicks under more nearly anechoic conditions.

Differences in syringeal anatomy between *C. spodiopygia* and the non-echolocating species, *C. esculenta,* are particularly interesting in the light of our proposed mechanism of click production by the former. The external labia of *C. spodiopygia,* which we believe generate the double click by opening and closing the airway, are about twice as thick as those of *C. esculenta* and possess supporting fiberous connective tissue that is lacking in *C. esculenta.* The internal tympaniform membranes are also thinner in *C. spodiopygia,* possessing only a single layer of connective tissue plus a lining of epithelial cells, and the first bronchial and tracheal cartilages are fused ventrally into a thin bony sheet, instead of remaining discrete elements as in *C. esculenta* (Smyth 1979). Another echolocating species, *C. fuciphaga,* is also reported to have a much more prominent external labium than does *C. esculenta* (Hollander 1971).

Compatibility with Previous Experimental Data

The only other experimental investigation of the production of echolocating clicks by swiftlets is that of Smyth (1979) who also studied *C. spodiopygia.* Smyth showed that immobilizing the tongue with cyanoacrylate adhesive, applying topical anesthetic to the tongue, palate, floor of mouth and glottis or preventing the beak from closing did not affect the bird's ability to fly or echolocate. A bird in which the beak was sealed shut flew in the light but refused to fly in the dark and emitted no clicks. Our experiments confirm Smyth's results in ruling out the tongue and beak as the source of the clicks.

Smyth also reported that syringeal denervation by section of the left hypoglossal nerve in one bird or of both hypoglossal nerves in a second bird did not interfere with normal click production. After tracheostomy, however, which included section of both tracheolateralis muscles as well as both hypoglossal nerves, the clicks were converted into squeaks having a longer duration than clicks and lacking their double character. Smyth interpreted this to indicate either a non-syringeal sound source or at least that the hypoglossal nerves were unimportant in click production.

We found that bilateral denervation of either the sternotrachealis or of both the sternotrachealis and tracheolateralis muscles (it is not possible to denervate only the tracheolateralis) caused one bird to produce squeaks similar to those described by Smyth after tracheostomy, and made a second bird totally aphonic. This, together with the fact that electrical activity in these muscles is correlated with click production, convinces us that they play an essential role in generating normal clicks. We suspect that Smyth may have missed some of the numerous very small twigs which appear to communicate between the two hypoglossal nerves along the length of the trachea when he cut the main nerve trunks and that the tracheal muscles were not completely denervated. The ability of one of our bilaterally denervated birds to squeak was probably dependent on neck movements which stretched the trachea and caused it to pull against the passive resistance of the paralyzed sternotrachealis muscles, thus putting the syringeal membranes in a vibratory position. This interpretation is supported by our finding that bilateral section of the sternotrachealis muscles renders the swiftlet aphonic even though the tracheolateralis muscles and their innervation remain intact.

Another point on which Smyth's data led him to a conclusion different from our own has to do with the role of the glottis. Smyth found that holding the glottis open, by inserting of a 1 mm diameter catheter into it, stopped the bird from clicking. Nevertheless, birds with a tracheostomy produced squeaks at the click rate and these squeaks were

unaffected by the presence of a glottal cannula. This led Smyth to conclude that although the glottis was not the primary sound source – which he postulated might be in the syrinx or air sacs – it was responsible for transforming the whistle or squeak from the primary generator into a double click. We have shown, however, that tightly sealing the glottis shut with a drop of tissue cement and allowing the bird to breath through the open sidearm of a T-cannula inserted into the trachea without disturbing either the tracheal muscles or their nerve supply, has no effect on the swiftlet's ability to produce normal double clicks. This experiment conclusively rules out an essential role for the glottis in the generation of double clicks. Furthermore, it is not necessary to postulate major changes in glottal resistance during click production to explain the airway dynamics as monitored in the air sacs and trachea. We believe that the refusal of Smyth's birds to produce sounds with a glottal cannula in place was probably due to the strong sensory stimulation and probable discomfort such a cannula must elicit.

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