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MECHANICS AND ENERGETICS OF SOUND PRODUCTION IN BIRDS

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Introduction. Sounds in birds, as in mammals and amphibians, are produced by the respiratory system. Contraction of the respiratory muscles produces airstreams which are capable, in appropriate conditions, of triggering the sound production mechanism in the voice box. Sound production is dependent not only on the generation of aerodynamic forces of sufficient intensity but also on the activation of the vocal muscles. The present paper is concerned primarily with the mechanical aspects of vocalization and the reader is referred elsewhere (Ref. 5) for a review of the control of the vocal muscles.

Structure of the Syrinx. The voice-box or syrinx lies at the base of the neck, where the trachea divides into the two main bronchial connections to the lungs (Fig. 1). The avian lung, unlike that of a mammal, is inexpansible and air is driven into and out of the respiratory system by the bellows-like action of a series of air sacs. The air sacs are in 3 or 4 pairs, one of each pair connecting to each lung, except for the clavicular air sac which is unpaired, connects to both lungs and encloses the base of the trachea, including the syrinx. In song birds the syrinx contains two thin, but relatively inelastic membranes, the tension of which can be altered by the vocal muscles (Fig. 2). When the vocal muscles are relaxed, elsatic forces in the trachea and main bronchi hold the membranes taut. Contraction of the vocal muscles brings about a shortening of the longitudinal axis of the syrinx and the membranes are free to bulge into the syringeal lumen.

Aeromechanics of the Syrinx. In all species that have been examined experimentally, spontaneous sound is produced only during the expiratory or positive pressure phase of respiration. Electrical activity in the vocal muscles coincides with that in the expiratory muscles during most of the vocal cycle (Refs 8-10, 12). Simultaneously there is an increase in air sac pressure and respiratory air flow (Fig. 3). The relaxed tympaniform membranes become drawn into the syringeal lumen partly under the influence of pressure from within the clavicular air sac and partly from suction forces created by the air flowing through the syrinx. It is possible to produce sound artificially, even though the vocal muscles are not activated, by blowing air into the air sacs but this requires inordinately large increases in air sac pressure and air flow. Consequently, the activity of the vocal muscles may be regarded as lowering the threshold at which the membranes can be drawn into the lumen.

Since the earliest work of Miskimen (Ref. 11) most authors have agreed that sound is produced directly by the tympaniform membranes which are made to vibrate in a drum-like manner by the air flowing through the syrinx. The pitch and intensity of the sound can be varied by the membrane tension and airflow velocity respectively. In turn, the membrane tension can be adjusted by the vocal muscles. The critical aerodynamic conditions for the production of a sustained membrane vibration have been discussed in Reference 4.

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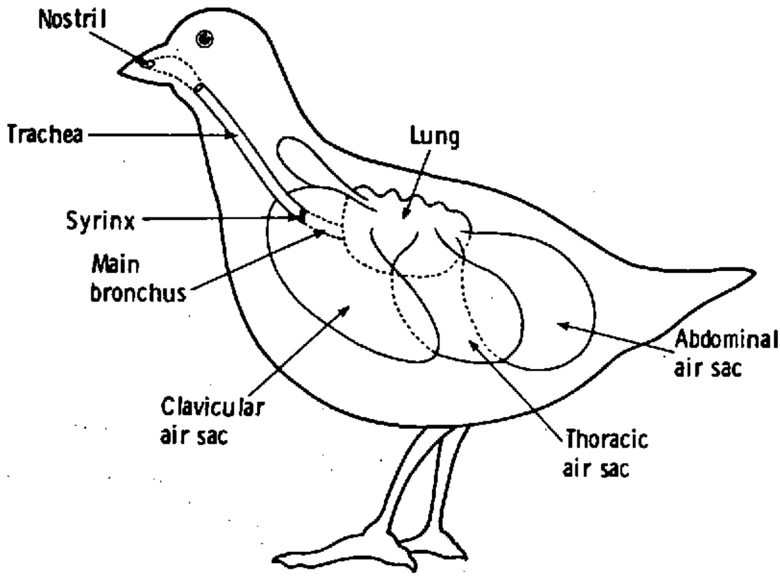

Fig. 1. Lung air sac system of songbird.

There is recent evidence that some types of sound may be produced by a different kind of mechanism in which the membranes do not act as the primary source of sound. This model, which is due to Gaunt et al. (Ref. 9), stems from the observation that although many bird calls consist of single tones or whistles, it is not possible for a conventional model of the syrinx based on an edge-clamped, freely-oscillating membrane to generate sounds that are free from overtones. However, a whistle mechanism, based on the formation of eddies or vortices as air is forced though the slit made by the infolded tympaniform membrane and the lateral wall of the main bronchus (Figs. 2, 4) would be capable of producing pure tones.

In this case the syrinx would function like the lips of a person whistling. It is possible according to this model, that the tympaniform membranes, although not producing the sound directly, could be secondarily excited by the vibrating air column in the trachea. This presents considerable interpretational difficulties since at first sight it would be impossible to decide whether the vibrating membrane was producing the sound or merely reacting to it.

Importance of the Clavicular Air Sac. Experimental rupture of the clavicular air sac and exposure of the syrinx to the atmosphere prevented spontaneous sound production in chickens (Ref. 12) and Mallard ducks (Ref. 10) even after

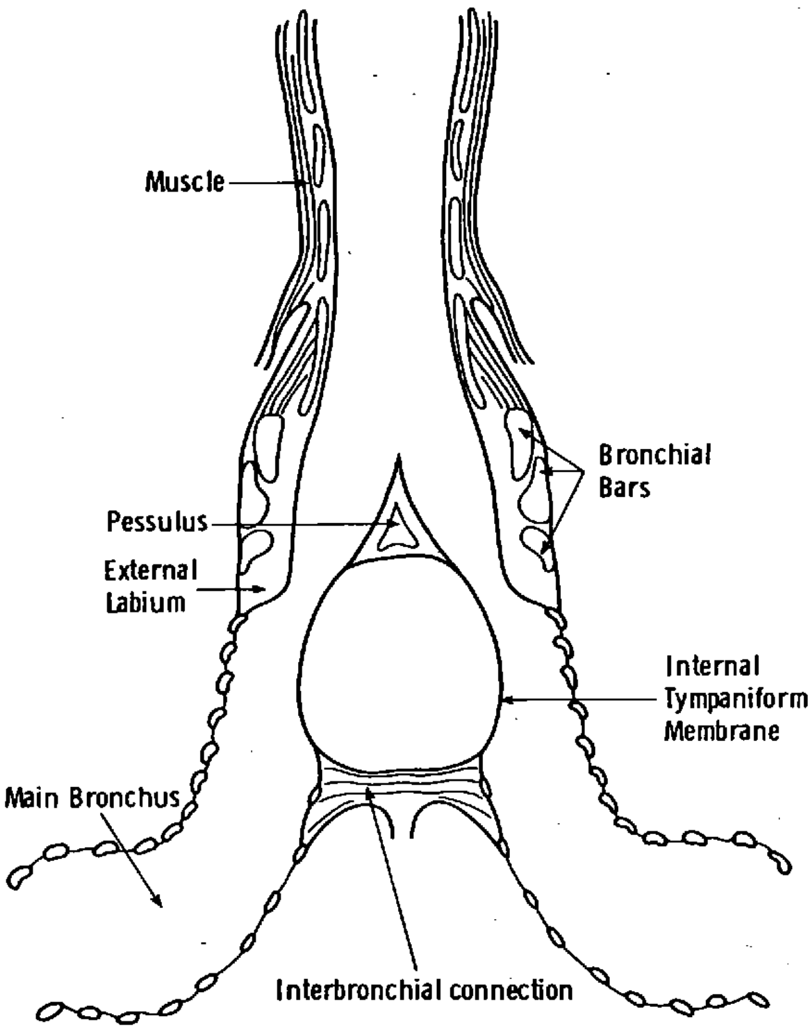

Fig. 2. Longitudinal section through songbird syrinx.

the connections between the air sac and the lung had been blocked in order to ensure that all the expired air passed through the syrinx. These experiments showed that in order for the syrinx to be able to produce sound the clavicular

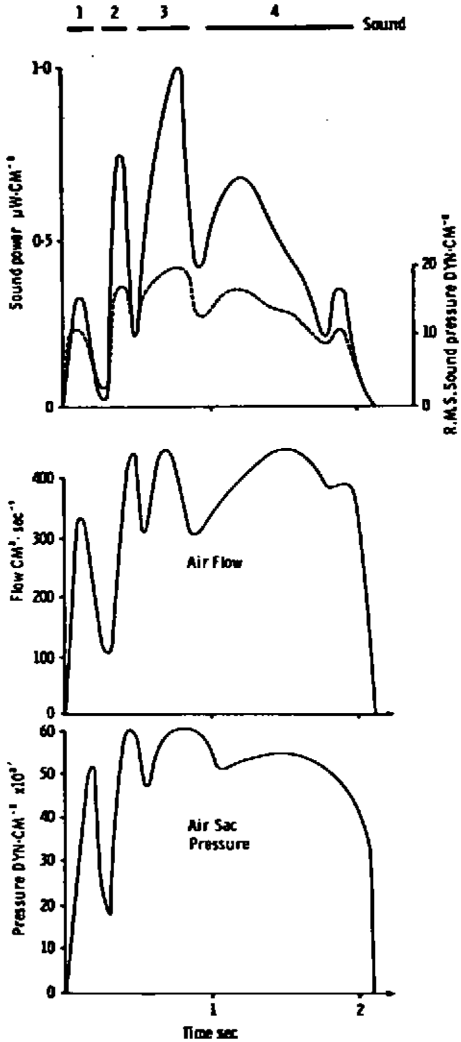

Fig. 3. Air sac pressure, respiratory air flow and sound output during cock-crow.

sac must be pressurized, and the pressure on the outer side of the tympaniform membranes must exceed that on the inner or luminal side. The driving pressure generated by the expiratory effort is virtually identical in all the air sacs, including the clavicular. There is a small loss in pressure head

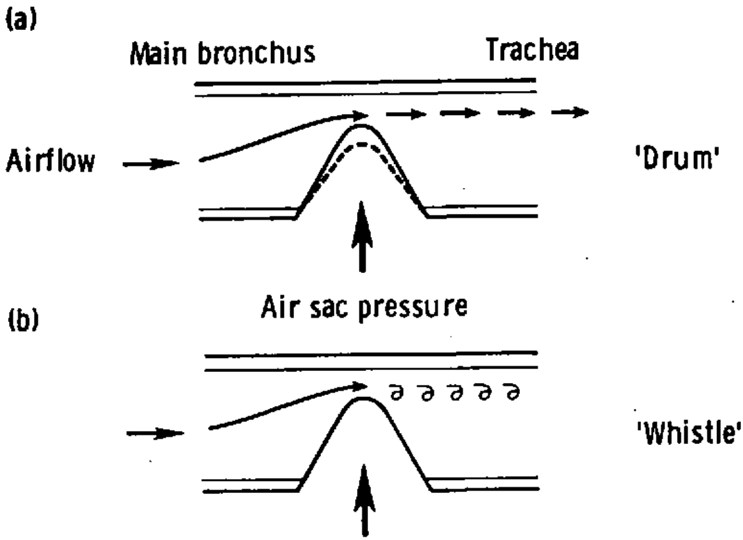

Fig. 4. Models of syringeal action. In (a) the tympaniform membrane vibrates like a drum; in (b) the membrane does not vibrate but produces vortices in the exhalant air stream.

during the passage of air along the main bronchus so that the hydrostatic pressure within the syrinx is slightly less than that of the clavicular air sac. Consequently this assists the initial bulging of the tympaniform membranes into the syringeal lumen when the vocal muscles contract, and this invasion is further assisted by the Bernovilli effect as air accelerates through the constricted lumen. It is noteworthy that when air is drawn through the syrinx in the reverse direction by applying negative pressure to the air sacs, the same mechanical arguments suggest that the pressure in the clavicular sac would be more negative than that in the syrinx, with the result that the membranes would be drawn out of, not into, the lumen. This may explain why birds do not appear to be able to produce sounds during inspiration.

Power Relationships. The pressures generated within the lung air sac system during spontaneous vocalization vary in size over a large range depending on the quality and intensity of the sounds produced. The maximum pressure that has been measured is ca. 6×10^3 N. m^{-2} and occurs during cockcrow (Refs. 1-3, 7, 8). At the same time the pressure in the trachea downstream of the syrinx is only ca. 1×10^3 N. m^{-2} indicating that ca. 85% of the fluid power generated during cock crow is lost in the main bronchi and syrinx. Whereas air sac pressure during cock crow increases ca. 100 times compared to peak pressure during normal breathing, respiratory air flow increases by only 15 times. Consequently, the airway resistance must increase by 6-7 times, presumably as a result of the constriction caused by the infolded membranes.

Despite the very obvious physical effort that goes into cock crow, and although the maximum sound pressure level reaches 100 dB, the *efficiency* of the process is disappointingly low. The aeroacoustic conversion efficiency can be estimated by comparing the amount of fluid energy injected into the respiratory tract during vocalization with the amount of acoustic energy generated. Instantaneous fluid power is equivalent to air sac pressure X airflow rate (Fig. 3). Sound power can be estimated by assuming that the sound is radiated over a hemisphere in front of the bird (Refs. 1, 2). Such calculations show that the mean sound power output during cockcrow is 27 mW compared to a mean fluid power input of 1.75 W, resulting in a conversion efficiency of 1.5%

Not all birds appear to be as profligate in their use of air as cockerels. Starlings use only a little more air when producing sounds as when respiring normally (Ref. 6) and songbirds in general seem to make more effective use of the gas exhausted. This may result from the more effective coupling between airflow and internal tympaniform membranes made possible by the presence of additional vocal muscles. These muscles appear to be able to protrude the lateral wall of the syrinx, the so-called external labium (Fig. 2), into the bronchial lumen thereby producing the necessary constriction that eventually leads to engagement of the tympaniform membranes.

Although birds such as chicken and duck require a large volume of air to operate the syrinx, the very size of the airflow may enable them to gain additional sound output by a process of convective amplification. Since the enhancement due to this process is proportional to (air flow velocity/sound velocity)^2 it is clear that only those species capable of producing very high expiratory flow rates could benefit from the effect (Ref. 4)

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