

Inspiratory Muscle Activity during Bird Song

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ABSTRACT: The apparently continuous flow of bird song is in reality punctuated by brief periods of silence during which there are short inspirations called minibreaths. To determine whether these minibreaths are accompanied, and thus perhaps caused, by activity in inspiratory muscles, electromyographic (EMG) activity was recorded in *M. scalenus* in zebra finches and in *M. scalenus* and *Mm. levatores costarum* in cowbirds, together with EMGs from the abdominal expiratory muscles, air sac pressure and tracheal airflow. EMG activity in *Mm. scalenus* and *levatores costarum* consistently preceded the onset of negative air sac pressure by ~11 ms during both quiet respiration and singing in both species. The electrical activity of these two muscles was very similar. Compared with during quiet respiration, the amplitude of inspiratory muscle EMG during singing was increased

between five- and 12-fold and its duration was decreased from >200 ms to on average 41 ms during minibreaths, again for both species, but inspiratory muscle activity did not overlap with that of the expiratory muscles. Thus, there was no indication that the inspiratory muscles acted either to shorten the duration of expiration or to reduce the expiratory effort as might occur if both expiratory and inspiratory muscles were simultaneously active. Inspiratory and expiratory muscle activities were highly stereotyped during song to the extent that together, they defined the temporal pattern of the songs and song types of individual birds. © 1998 John Wiley & Sons, Inc. *J Neurobiol* 36: 441–453, 1998

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Bird song, like human speech and song, involves the intricate coordination of various groups of muscles belonging to the vocal, respiratory, and articulatory (supravocal) systems (Wild, 1997; Suthers, 1997). The vocal (syringeal) and respiratory muscles in particular work in extremely close concert to produce the more or less complicated syllabic pattern that characterizes the species typical song (Hartley, 1990; Vicario, 1991a,b; Suthers et al., 1994; Goller and Suthers, 1996a; Suthers and Goller, 1996). In songbirds, the vocal system consists of four or five

pairs of intrinsic and two pairs of extrinsic syringeal muscles (King, 1989), their innervation by neurons in the hypoglossal nucleus, and a host of brain stem and forebrain nuclei that are involved in the control of vocal production and vocal learning (Brenowitz et al., 1997a; Wild, 1997). The respiratory system consists of a pair of largely nonexpanding lungs coupled to a set of mostly paired air sacs, the volume of which is under the partial control of inspiratory and expiratory muscles which function in both normal respiration and during vocalization (Fedde, 1987; Brackenbury, 1987; Hartley, 1990; Wild, 1993a; Goller and Suthers, 1996a).

During quiet respiration, the duration of inspiratory and expiratory phases are roughly equal. During song, which for many species characteristically lasts far longer than the respiratory cycle, the ventilatory pattern changes dramatically (e.g., Suthers, 1997). In canaries, for example, there is a sudden

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increase in tempo and a marked shortening of the inspiratory phase accompanied by large fluctuations in rates of airflow and subsyringeal pressure. Phonatory periods consisting of single notes, syllables, or note clusters, are correlated with marked increases in electromyographic activity in abdominal expiratory muscles and large concomitant increases in positive (i.e., supra-atmospheric) air sac pressure. Punctuating the phonatory periods are brief (as short as 15-ms) periods of silence, which are correlated with high rates of tracheal airflow combined with negative (i.e., subatmospheric) air sac pressures, indicative of inspirations known as minibreaths (Calder, 1970; Hartley and Suthers, 1989; Hartley, 1990). The physiological basis of these brief inspirations during song, however, is uncertain. That is, it is not clear whether during song inspiration is actively controlled by an inspiratory motor program or passively determined by changing balances between the force of expiratory muscles and the opposing forces of elastic recoil of the body wall. Thus, although inspiratory muscle activity might be assumed to accompany, and possibly cause, the minibreaths that have now been demonstrated to occur in the songs of several oscine species (Hartley and Suthers, 1989; Allan and Suthers, 1994; Goller and Suthers, 1996b,c), negative air sac pressures and inspiratory airflow could, in principle, result solely from elastic recoil of the compressed thoracic and abdominal cavities following expiration. The present investigation therefore set out to determine whether minibreaths are generated actively by motor programs to the inspiratory muscles or passively by recoil forces reflecting the motor pattern of expiratory muscles. An abstract of the results has been presented (Wild et al., 1997).

MATERIALS AND METHODS

The subjects were five male zebra finches (*Taeniopygia guttata*) and five male brown-headed cowbirds (*Molothrus ater*). Each was anesthetized with isoflurane gas, and into a cranial thoracic air sac a flexible cannula (Silastic tubing) was inserted through a small hole made in the abdominal wall for the measurement of subsyringeal pressure. The cannula was secured to the caudal end of the rib cage with suture and tissue adhesive, and its distal end connected to a piezoresistive pressure transducer (Fujikura model FPM-02PG) mounted on a backpack on the bird's back by means of a Velcro tab affixed to an elastic belt worn around the chest in front of the wings.

Each bird was also implanted with one or more pairs of fine stainless-steel wires (0.025 mm, insulated except at the tip) to measure electromyographic (EMG) activity

in inspiratory and expiratory muscles. The inspiratory muscles chosen were the M. scalenus and, in two of the cowbirds, the Mm. levatores costarum. Birds lack a muscular diaphragm, and it is technically difficult to measure EMG activity in the intercostal muscles of small songbirds (Hartley, 1990). The cranial and caudal portions of M. scalenus attach the transverse processes of lower cervical vertebrae to the first and second ribs, respectively; while the several slips of Mm. levatores costarum attach thoracic vertebrae to caudally adjacent ribs in similar fashion (Fedde, 1987). The M. scalenus was approached by dissecting the muscles attaching the medial border of the scapula to the vertebrae and separating the underlying air sac from the surface of the more ventrally situated M. scalenus. One of the slips of Mm. levatores costarum was approached more caudally, but in a similar fashion. These two muscles are known to be principal inspiratory muscles in birds (Fedde, 1987) and have been used as the focus of neuroanatomical experiments aimed at determining the location of their motoneurons and premotor neurons as part of an ongoing program designed to elucidate respiratory-vocal control mechanisms in birds (Reinke and Wild, 1997, 1998).

The expiratory muscles monitored were the abdominal expiratory group, principally the M. obliquus externus abdominis (two zebra finches and three cowbirds), which was approached behind the leg, with the bird lying on its side. Stabilization of the EMG wires within both inspiratory and expiratory muscles was achieved by a fishhook arrangement of the electrode tips and by a small drop of *N*-butyl cyanoacrylate adhesive (Nexaband; Veterinary Products Laboratories). The wires from each muscle were coiled two or three times under the overlying skin, to lend them flexibility during body movements, and were then routed subcutaneously to the region of the backpack. EMG signals were differentially amplified and bandpass-filtered (200–3000 Hz) (Princeton Applied Research; model 113 or Dagan Ex4-400).

In two of the zebra finches and two of the cowbirds, tracheal airflow was also measured by implanting a microbead thermistor (Thermometrics; BB05JA202) in the lumen of the distal end of the trachea via a small hole made between adjacent tracheal rings (Suthers et al., 1994). Wires to the bead were anchored to the outer surface of the trachea with tissue adhesive and were then routed subcutaneously to the backpack. Wires from the connector on the backpack provided the excitation voltage for the pressure transducer and transmitted the pressure, airflow, and EMG signals through the top of the bird's cage to appropriate signal conditioning circuits before being recorded on separate channels of a rotary data recorder (Metrum Information Storage; model RSR512). Voltage responses of the pressure transducers are linear within the range of pressures measured in this study. The frequency response of pressure transducers (>10 kHz) and thermistors (~4 kHz) is adequate for accurate determination of rapid pressure and flow-reversal points.

Following surgery, the birds were returned immedi-

ately to their cages, where they quickly recovered. In some instances, the cowbirds began singing within minutes; the zebra finches, however, took longer to begin singing, but usually they did so within 1 or 2 days.

Song and other vocalizations were recorded with a microphone (Sennheiser MKH 416 TU-3) placed 20 cm in front of the bird. Because of the extensive dynamic range of the cowbird song, the voltage signal was recorded with different gains on two separate channels of the rotary recorder. Scores of songs, often elicited by presenting a female of the appropriate species in a nearby cage, were recorded from each bird over a 3- to 5-day postoperative period.

For data analysis, all parameters were digitized using half-speed playback for a real-time digitization rate of 50 kHz (Data Translation 2821-G) and subsequently analyzed using Signal software with appropriate time and frequency corrections for the reduced tape speed (Engineering Design, v. 3.0). At least 15 songs from each zebra finch and between 25 and 30 songs from each cowbird were used for quantitative analysis. The EMG signals were rectified (time constant 0.1 ms using the ENV procedure in Signal) for measurements, and for illustrations they were also integrated (time constant 2 ms using the SM procedure in Signal). In this article, we use the term "inspiratory pressure" to describe the difference between the air sac pressure and ambient pressure during inspiration. Therefore, an increase in inspiratory pressure represents a decrease in the air sac pressure.

RESULTS

The overall pattern of the temporal structure and phonetic morphology of the songs or song types of both species were generally highly stereotyped. As described by Sossinka and Böhner (1980), the song of the zebra finch is characterized by a number of introductory notes followed by one or more repetitions of a stereotyped series of temporally discrete syllables (motifs), with the fundamental frequency centered typically between 500 and 700 Hz (Williams et al., 1989) (Figs. 1 and 7). The song of cowbirds is generally characterized by its wide dynamic range, beginning with extremely low-frequency notes of low amplitude, followed by a series of note clusters that increase in pitch and amplitude. The song is usually terminated by a very high pitched "whistle" (Figs. 2 and 8). The repertoire of individuals usually consists of a number of different song types, each of which is produced with high stereotypy (Allan and Suthers, 1994). Cowbird song is also remarkable in that it is frequently accompanied by a visual display, consisting of the bird raising its head and neck feathers, spreading its wings, and "bowing." Although the song and

the display are clearly correlated in time, the exact temporal relationship between their individual components is unknown.

Figures 1 and 2 present spectrograms of zebra finch and cowbird song, respectively, accompanied by records of air sac pressure and EMGs from respiratory muscles. Prior to the song of the zebra finch a period of quiet respiration occurs during which small increases of positive and negative air sac pressure (i.e., above and below ambient pressure) alternate with roughly equal duration. Periods with sub-atmospheric pressure (i.e., inspirations) were accompanied by discrete, small amplitude EMGs from *M. scalenus*. Although not shown in Figure 2, similar small amplitude EMGs from *M. scalenus* and from *M. levator costarum* were also observed to accompany small increases in inspiratory pressure during quiet respiration in the cowbird. However, this was not the case for the 1- to 2-s period immediately preceding the cowbird song; this is discussed below. These observations suggest that *M. scalenus* and *Mm. levatores costarum* are inspiratory muscles normally active during quiet respiration.

In the zebra finch, song was immediately preceded by a marked increase in inspiratory pressure, i.e., a deep inspiration similar to a minibreath but appended to the end of a normal inspiratory cycle (Figs. 1 and 7). During the song, the introductory notes and the syllables of the motif alternated with silent intervals during which there were increases of sudden onset in negative air sac pressure (i.e., inspiratory minibreaths) accompanied by large amplitude EMGs from *M. scalenus*. The duration of these inspiratory minibreaths [mean \pm 1 standard deviation (SD) = 41.4 ± 18.9 ; range 17.3–125.2 ms; $n = 130$], however, was up to 20-fold less than that during the inspiratory phase of quiet respiration (mean = 215.7 ± 27.3 ; $n = 75$). In the cowbird, song was not immediately preceded by a sudden, deep inspiration as it was in the zebra finch, but three brief inspiratory episodes (mean = 41.5 ± 10.1 ; range 30.2–89.9; $n = 126$; mean duration of quiet respiration = 271.1 ± 55.7 ms; $n = 83$) nevertheless separated the note clusters, and these were accompanied by discrete, large-amplitude EMGs from *M. scalenus* and from *M. levator costarum* (Figs. 2 and 8). For both zebra finch and cowbird song, inspiratory muscle EMGs always preceded the onset of the negative pressure cycle by ~ 11 ms (mean = 11.1 ± 3.8 ms; $n = 127$ in zebra finches, and 11.6 ± 2.9 ms; $n = 72$ in cowbirds). Also for both species, shorter inspirations and greater inspiratory pressure were accompanied by larger amplitude EMGs (Figs. 1–3), although there

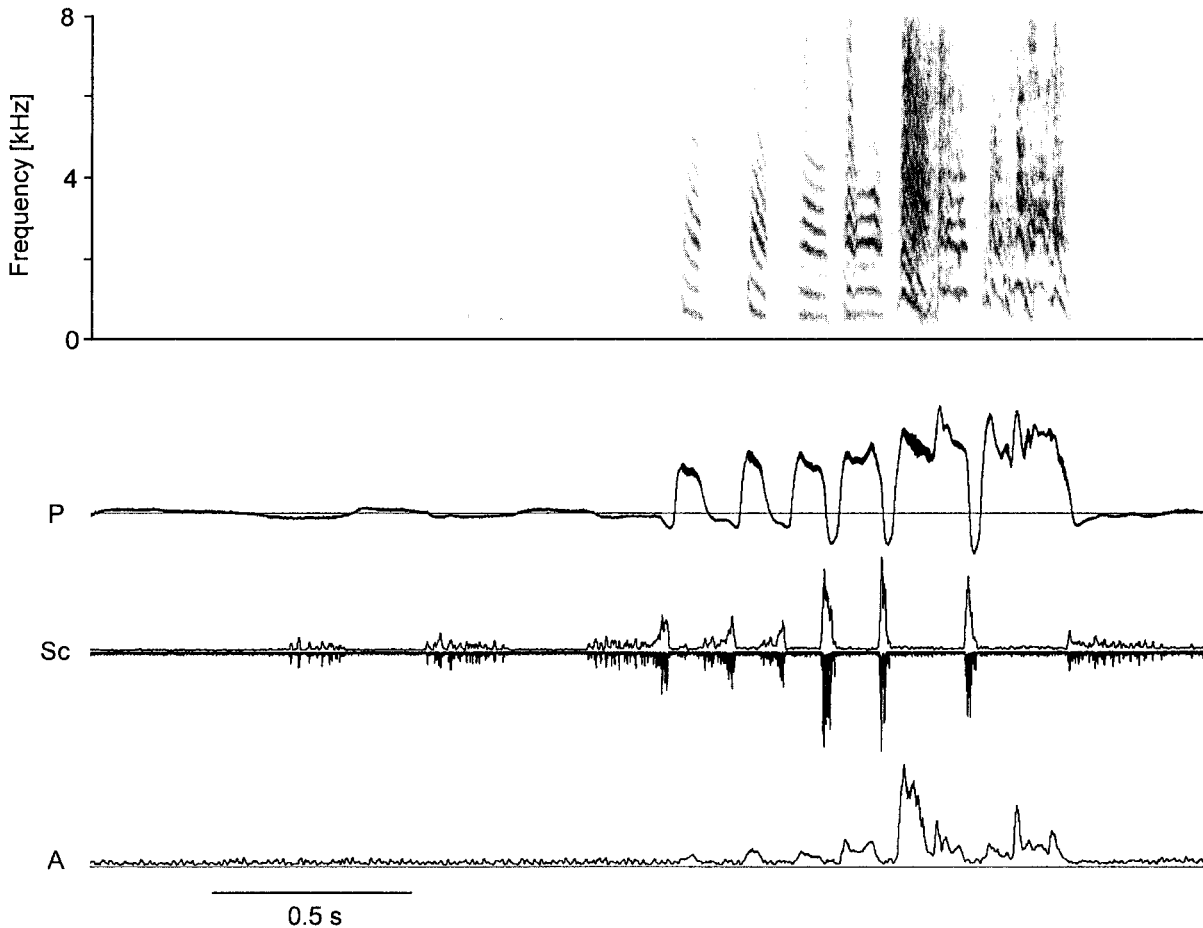


Figure 1 Quiet respiratory activity followed by song in a zebra finch. (Top) Spectrogram of song; P = subsyringeal air sac pressure (horizontal line indicates ambient pressure); Sc = EMG activity in *M. scalenus* (integrated record upward, time constant 5 ms; rectified original EMG recording downward); A = sound amplitude represented as rectified and integrated (time constant 2 ms).

was considerable variability in the relationship between air sac pressure and EMG amplitude. The reason(s) for this variability is obscure, but it may be related to differences in posture. In contrast, there was a high correlation between the duration of the negative pressure cycle and the duration of the inspiratory muscle EMG (Fig. 4). During song, average EMG activity generally increased with decreasing duration of the minibreath, indicating that shorter inspirations tended to be deeper (Fig. 5). This was particularly striking for the song of the zebra finch, which contained a wider range of duration of minibreaths than cowbird song (see above).

As mentioned above with respect to Figure 2, cowbird song was not immediately preceded by a respiratory pattern characteristic of quiet respiration. Instead, it was preceded by a period of maintained activity in inspiratory muscles such as *M.*

scalenus (Fig. 2) and *Mm. levatores costarum* (see Fig. 8—only the end of the visual display is illustrated, marked with arrows), the actions of which during cowbird song appear to be very similar in both their temporal pattern and amplitude (see Fig. 8). The duration of this maintained activity varied between about 0.8 and 2 s, and its magnitude was significantly greater than that of the activity of these muscles during quiet respiration ($p < .001$ in each of the three birds) (Figs. 2 and 6). Despite this activity, air sac pressure was slightly less negative than during quiet respiration (Figs. 2 and 6), and inspiratory airflow was markedly lower than during minibreaths (see Fig. 8, beginning of records, marked by arrow). This curious pattern of activity was correlated with the beginning of the visual display, during which the feathers on the head and neck are raised prior to the commencement of the

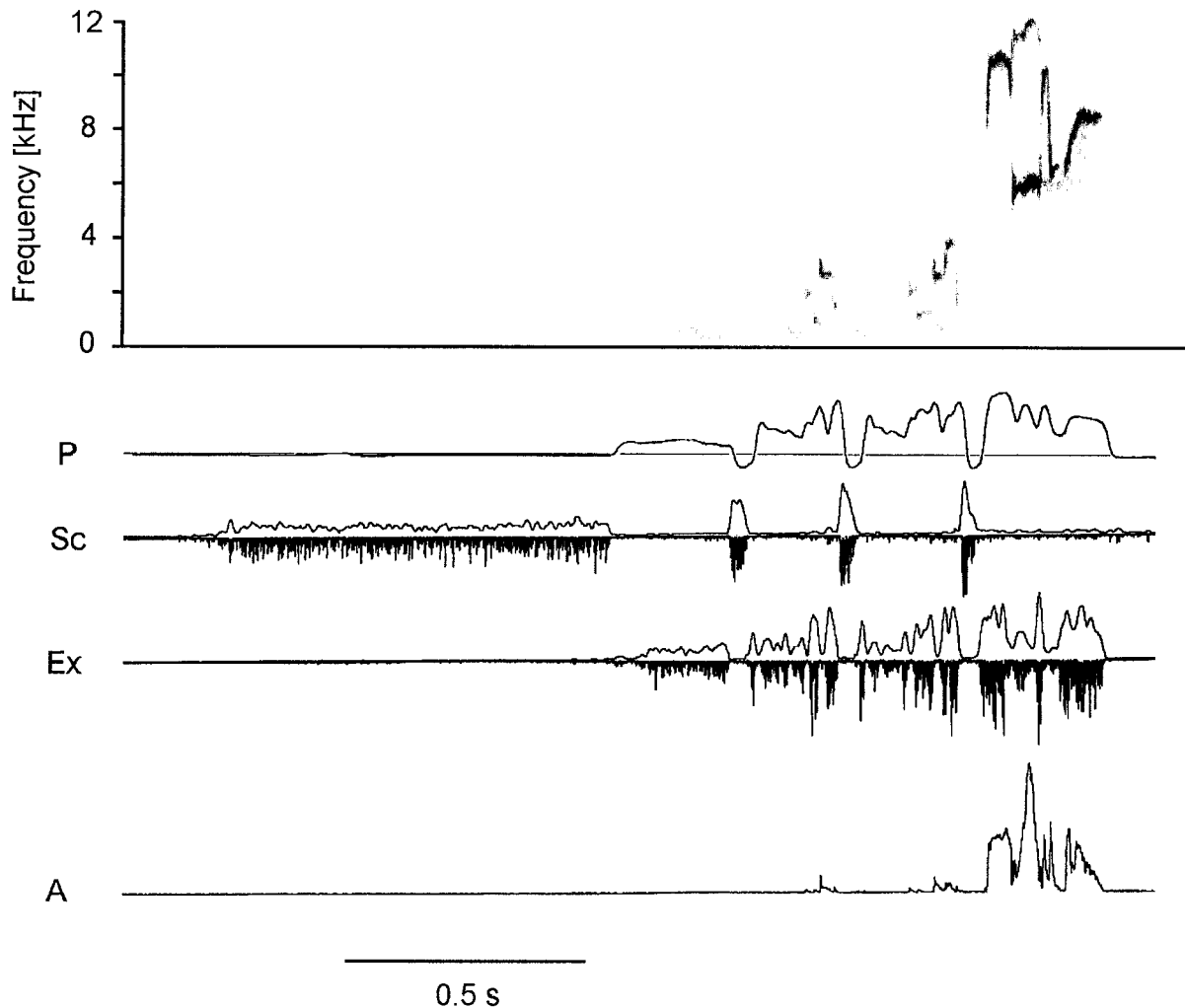


Figure 2 Representative cowbird song. (Top) Sonogram of song; Exp = EMG activity in abdominal expiratory muscles; other abbreviations as in Figure 1. Note activity in *M. scalenus* before the song, which coincides with the raising of head and neck feathers at the beginning of the visual display.

song. Although this might suggest that the activity in *M. scalenus* and *Mm. levatores costarum* was related to movement in some way during this pre-visual period, there was no similar maintained activity in either muscle during any other, more vigorous part of the visual display, such as during wing spreading or bowing. These inspiratory muscles were not activated during any other movements unrelated to song. Moreover, the beginning of the visual display, defined by head and neck feather raising, was always accompanied by maintained EMG activity in both inspiratory muscles whether or not it was followed by song, and whether or not it was followed by other components of the visual display, e.g., wing spreading and bowing.

In the songs of both zebra finch and cowbird, as

in quiet respiration, there was no overlap of EMG activity in inspiratory and abdominal expiratory muscles (Figs. 2 and 7); activity in one alternated without a pause, with activity in the other in an extremely temporally precise fashion. Moreover, the pattern of expiratory and inspiratory activities was remarkably stereotyped in the songs of individual members of both species. Figure 9 shows, for instance, the means and very small SDs of the duration of expiratory and inspiratory pulses during 10 motifs of the song of a zebra finch. Occasionally, somewhat higher variability was found in the duration of expirations and subsequent inspirations for the first syllable when the motif was repeated a second time within one song (note larger SD for syllable 1 in Fig. 9). Cowbird song was likewise

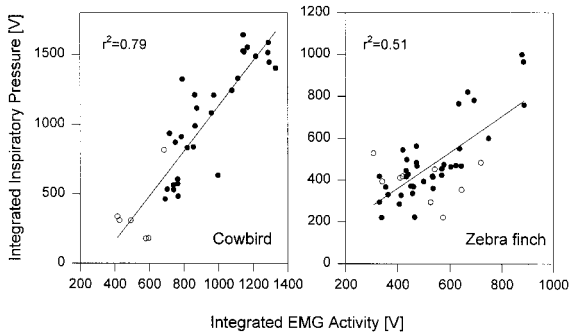


Figure 3 Inspiratory pressure generally increases with increasing EMG activity in inspiratory muscles (*M. scalenus*). For a definition of inspiratory pressure, see Methods. Both variables were measured as integrated voltages over the entire duration of one inspiratory episode and the associated EMG burst. Substantial variability exists in both species. Closed symbols represent intersyllable inspirations; open symbols, “quiet” respiration prior to song in zebra finches and prior to the visual display in cowbirds.

characterized by stereotypy of expiratory (see quantitative data in Allan and Suthers, 1994) and inspiratory patterning. The patterns of expiratory and inspiratory pulses differed between different song types produced by the same bird (Figs. 10 and 11).

DISCUSSION

This study confirms that in these species, *M. scalenus* and *Mm. levatores costarum* are inspiratory muscles active during quiet respiration (Fedde,

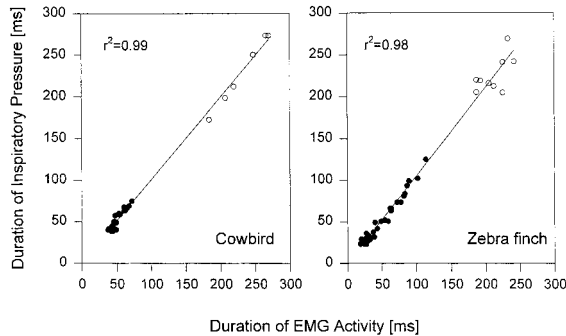


Figure 4 Correlation of duration of inspiratory pressure with EMG bursts in *M. scalenus* in zebra finches and cowbirds. Closed symbols represent correlations during song; open symbols, during “quiet” respiration. Duration of inspirations during song is more variable in zebra finches than in cowbirds, especially between introductory notes.

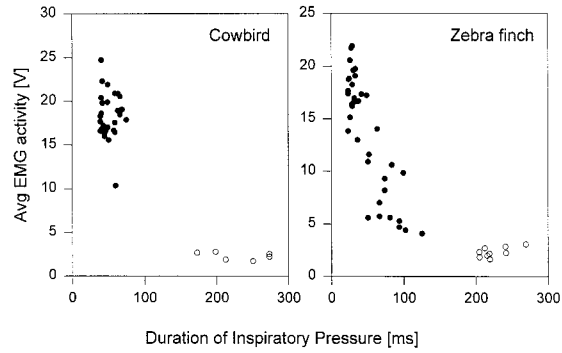


Figure 5 Average EMG activity (mean voltage, V) as a function of the duration of inspiratory air sac pressure. Closed symbols represent values during song; open symbols, during “quiet” respiration.

1987). The present study has also shown that both *M. scalenus* and *M. levator costarum* are actively involved in vocalization, particularly during song. The fact that the activity of these two muscles always preceded the onset of the inspiratory pressure cycle by a relatively fixed duration of ~11 ms strongly suggests that they actively contribute to the inspiratory effort required to produce the mini-breath, although other muscles such as the external intercostals may also contribute. It is also clear from these observations that several different muscles play a part in inspiration during vocalization, which might account for the less than expected level of activity in the external intercostals that Peek et al.

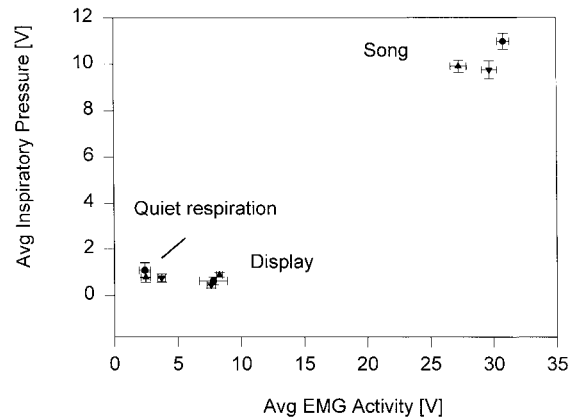


Figure 6 Means (± 1 standard error) of average inspiratory pressure (V) and average EMG activity (V) in *M. scalenus* for “quiet” respiration, the beginning of the visual display before song, and song in three individual cowbirds (different symbols). Although the mean air sac pressure is about the same for display and quiet respiration, EMG activity during the display is significantly greater (*t* test; $p < .001$ for all three individuals).

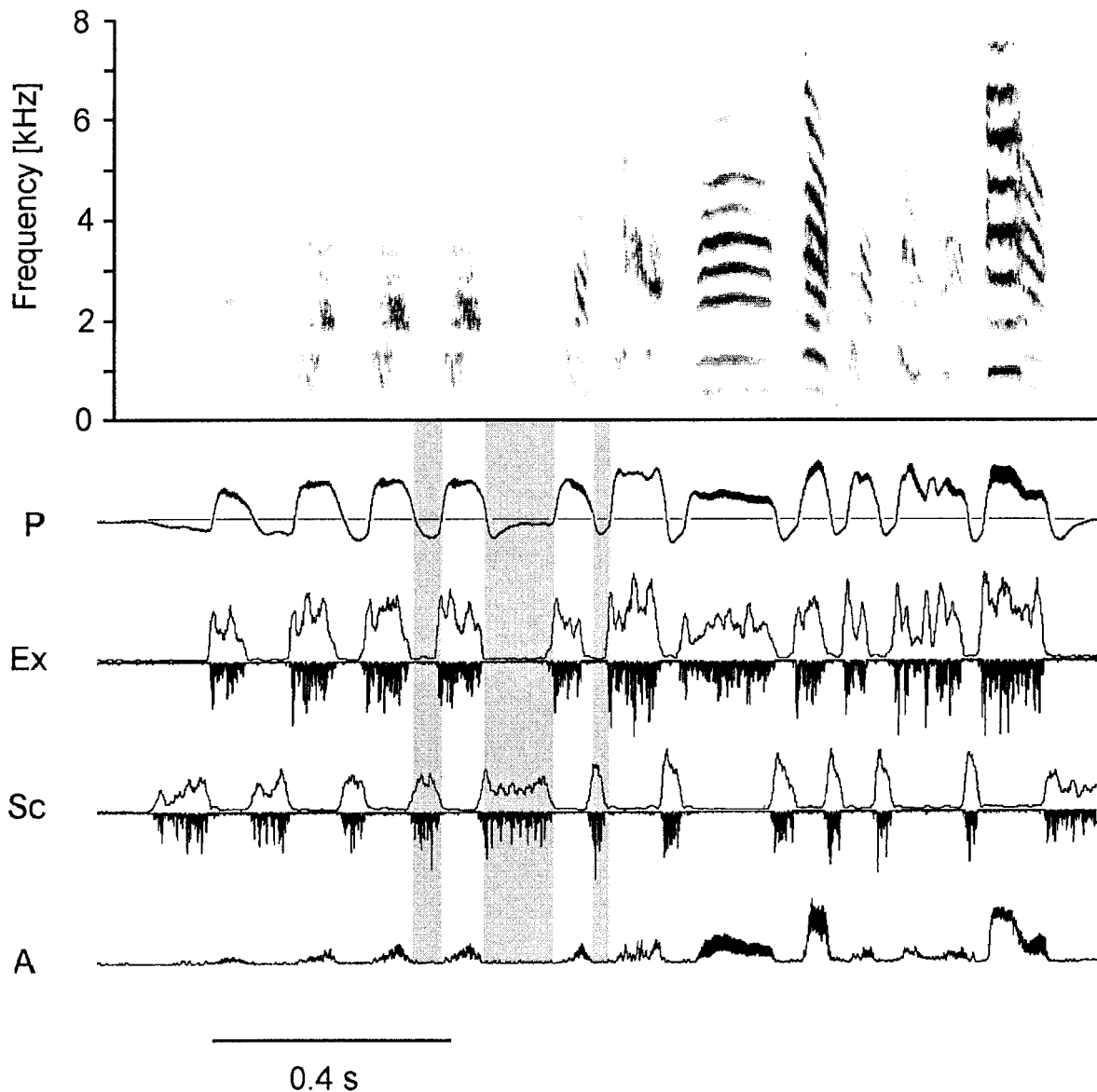


Figure 7 Zebra finch song with inspiratory and expiratory EMGs showing that EMG activity is restricted to inspiration and does not overlap with EMGs from abdominal expiratory muscles. Abbreviations as in previous figures. Shaded areas mark three inspirations of varying duration.

(1975) attributed to elastic recoil of the respiratory apparatus following the cessation of crowing in the chicken. The present evidence in songbirds does not exclude the possibility that chest wall recoil plays a part in reversing the direction of tracheal airflow following end expiration, but if it does, its inspiratory effect is strongly augmented by the action of inspiratory muscles such as *M. scalenus* and *Mm. levatores costarum*. The commencement of EMG activity in these muscles is coincident with the end of EMG activity in the abdominal expiratory muscles, inspiratory EMGs precede the onset of nega-

tive air sac pressure, and their amplitude and duration are positively correlated with the depth and duration of minibreaths. These observations strongly suggest that inspiratory muscle activities are the principal means of minibreath production. Thus, in birds, both inspiration and expiration are active processes during both quiet respiration and vocalization.

It has been suggested that the function of mini-breathing in songbirds is to replenish air expelled during phonation, to allow them to sing for longer periods of time than their vital capacities would

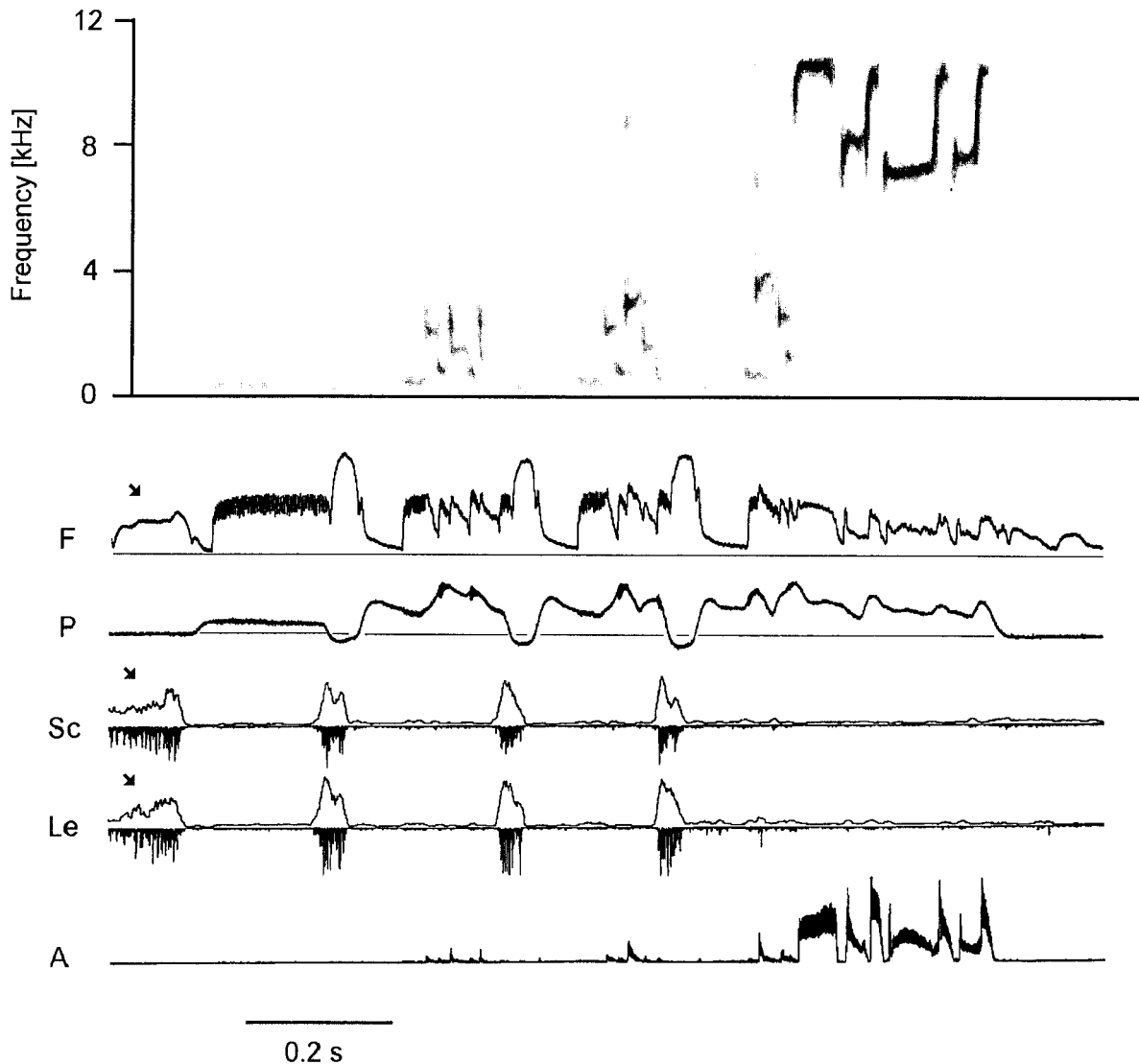


Figure 8 Cowbird song showing EMG activity in *M. scalenus* and *M. levator costarum*, and tracheal airflow (F). Note the similarity of EMG activity in the two muscles. The rate of airflow is greater during inspiration than expiration indicating a lower syringeal resistance; inspiratory air sac pressure is also of lower absolute amplitude than expiratory pressure.

otherwise allow (Calder, 1970; Hartley and Suthers, 1989; Suthers and Goller, 1997). Direct evidence for this was provided in singing canaries by determining the volume of expired and inspired air from calibrated data on the rate of tracheal airflow (Hartley and Suthers, 1989). In all measured syllables, inspiratory volume during minibreaths equaled the volume of air expelled during phonation. Syllables of long duration were followed by longer minibreaths than short syllables, but inspiratory flow rate also varied substantially between different syllable types (at least a twofold difference). This positive correlation between the duration of the expiratory

phase and that of the inspiratory phase may not exist in all species, however. In the present study of zebra finch and cowbird song, for instance, there was no convincing evidence that longer minibreaths consistently followed longer notes or syllables, at least within individual songs (e.g., Fig. 9). The minibreaths of the zebra finch did vary in duration over the course of a song, but in one case (e.g., Fig. 1) shorter minibreaths were associated with the longer syllables of the motif, rather than with the shorter introductory notes. These shorter minibreaths tended to be deeper and were accompanied by greater amplitude EMGs, indicating that expelled

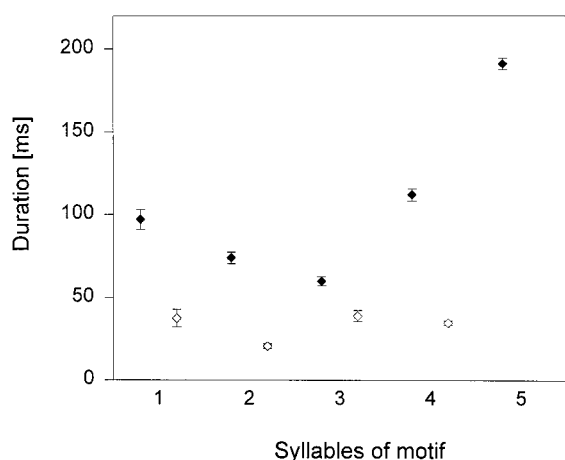


Figure 9 Representative example of mean duration (± 1 SD) of expiratory (solid circles) and inspiratory (open circles) pressure cycles during 10 repeated motifs of the song of one zebra finch. Note the low variability in both inspiration and expiration.

air is replenished by increasing the rate of airflow rather than the duration of the inspiratory period. In cowbird song, silent periods between note clusters are not entirely for inspiration, but consist of a minibreath and a significant period of expiratory pressure (50 ms) during which both sides of the syrinx are closed to airflow, and thus do not produce sound (Allan and Suthers, 1989) (Fig. 8). Zebra finches and cowbirds may not be as constrained by the need to replenish air as are canaries because of the high syllable repetition rates and long song duration of the latter. In canaries, airflow during minibreaths may be maximal; therefore, additional increases in inspiratory volume can be achieved only by increasing inspiratory duration.

Inspiratory activity could in principle also contribute to the fine control of expiratory effort by counteracting (braking) either the natural tendency of the rib cage to contract under relaxation pressures, or the forces of expiratory muscles, as proposed for human speech and singing (e.g., Draper et al., 1959). However, neither during quiet respiration nor in song was there an overlap of EMG activity in inspiratory and expiratory muscles. Although EMG recordings from intercostal muscles are not available for songbirds, a similar lack of overlap in inspiratory intercostal and abdominal expiratory muscles was found in the vocalizing chicken (Peek et al., 1975). An important implication of this pattern of activity is that expiration during song is not controlled (braked) by the action of inspiratory muscles, at least by the muscles studied here. In birds, unlike the case in mammals, active expiration

commences at the end of inspiration, and does not, as in some mammals, come into play only when passive elastic forces cease to provide sufficient chest wall compression. For reasons that are not entirely clear, braking by inspiratory muscles may be more meaningful when it counteracts passive elastic forces, rather than active contractile forces of expiratory muscles. Thus, in songbirds, airflow during phonation appears to be regulated not by simultaneous activity of inspiratory and expiratory muscles, but by a very close coordination of expiratory and syringeal muscles. The intricate coordination of these latter motor systems is necessary for the generation of appropriate pressure and flow conditions for phonation and to cater for the demands of syllabic construction and vocal intensity (Goller and Suthers, 1996b; Suthers et al., 1997).

In addition to their ventilatory role during singing, minibreaths, by their very presence, may be thought of as having another role in defining (punctuating) the temporal structure of song by regulating, together with expiratory control, the internote or intersyllable intervals. Intersyllable intervals are generally equal to the duration of the inspiration (Suthers et al., 1994; Goller and Suthers, 1996b; this study). Notable exceptions to this general observation are the silent periods between introductory note clusters in cowbirds, which are composed of the minibreath and the first part of the expiration (Allan and Suthers, 1994) (Fig. 8), and some syllables in canaries, during which two notes separated by a silent period are generated during one expiratory pulse (Hartley and Suthers, 1989). However minibreaths are viewed, they are clearly integral to the stereotypical pattern that defines the temporal structure of both the species typical song and song type. Such silent intervals are known to be perceptually salient, at least for some species (Becker, 1982), and zebra finches are sensitive to experimental changes in their duration (Nespor and Dooling, 1997).

One significant difference between the inspiratory muscle activity of cowbirds and zebra finches was the maintained activity that precedes song in the former. As noted, this activity is correlated in time with the first part of the visual display in which the head and neck feathers are raised, but not with other more dynamic components of the display. During this period, there is inspiratory airflow, as indicated by slightly negative air sac pressure, comparable to quiet respiration, but much higher EMG activity. It is possible that both *M. scalenus* and *Mm. levatores costarum* are, in addition to their inspiratory role, also involved in movements that

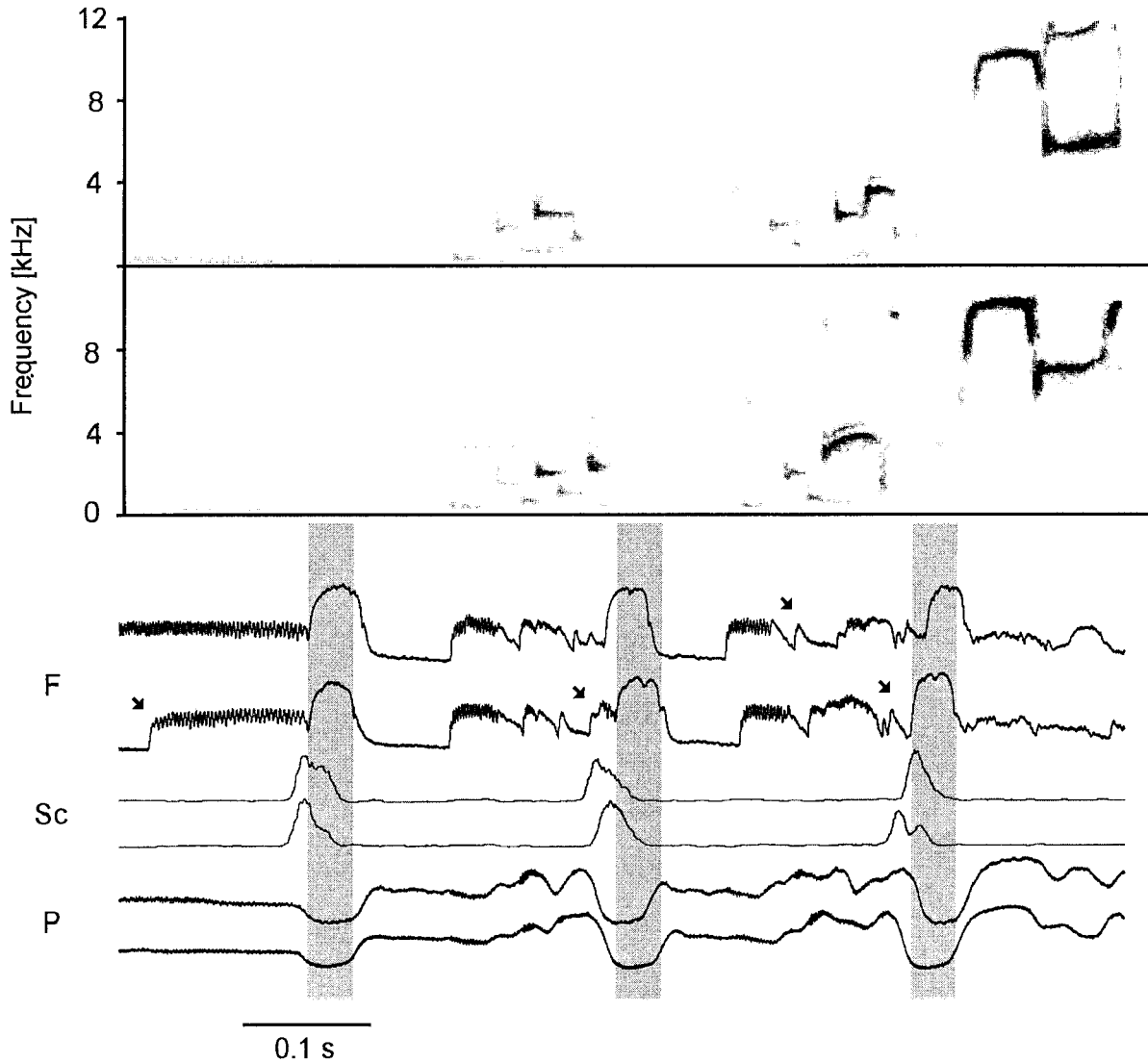


Figure 10 A segment of two cowbird song types (one above the other) overlaid on the same time scale and aligned at the first inspiration. Note the subtle differences in the duration of inspirations and how inspirations become more and more offset in time over the course of the song owing to varying duration of expiration and inspiration combined. Arrows point to the most marked differences in expiratory air flow between the two song types. Differences in motor correlates of song are also expressed in the acoustic output of the song as seen in the spectrogram (top).

help effect a raising of the head and neck feathers. However, the potential mechanical mechanisms by which such movements might be accomplished are unknown.

Neural Control of Respiratory Pattern during Singing

The stereotypical nature and precise temporal patterning of expiratory and inspiratory phases during

singing suggest the presence of a highly coordinated neural control system that integrates the sequence and timing of respiratory muscle activation with that of the syringeal muscles (Vicario, 1991a,b; Suthers, 1997; Wild, 1997). Some of the brain stem and spinal neuronal circuitry that is likely to be involved in this control has been delineated (Wild, 1993a; Reinke and Wild, 1997, 1998), and in songbirds, it is conceivable that the whole respiratory-vocal pattern is controlled via the output of the telence-

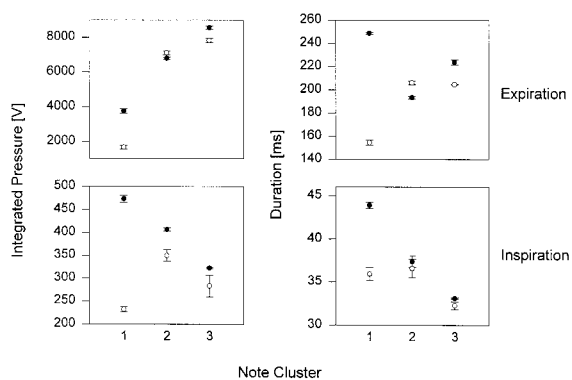


Figure 11 Example of stereotypy within, and difference between, two song types of a cowbird (different symbols). The top two panels show mean (± 1 SD) air sac pressure and duration of expirations generating note clusters 1–3, and the lower panels show mean amplitude and duration of inspiratory pressure cycles between note clusters. Inspiratory as well as expiratory patterns are characteristic of song types.

phalic nucleus robustus archistriatalis (RA) (Vicario, 1991c, 1993; Wild, 1993b, 1997).

Comparative Aspects

The avian respiratory apparatus is different from that of mammals in that there is no muscular diaphragm that functions as a principal inspiratory muscle, the lungs are largely static, and they are separated from the ventilatory pump made up of the air sacs and the muscles that act upon them. Many of these muscles nevertheless appear to be homologous with those that are involved in either respiration and/or vocalization in other vertebrates, irrespective of the presence/absence of a diaphragm. For instance, the levator costae have been shown to be active during normal inspiration in the garter snake and in the cat (Rosenberg, 1973; Hilaire et al., 1983). Somewhat surprisingly, however, there is little information on the role of the various abdominal and thoracic muscles during vocalization in non-human animals, even in mammals, where the placement of recording electrodes in deeper muscles of the body wall can be effected under visual control at surgery. The study of Jürgens and Schriever (1991) in the squirrel monkey is the most extensive in terms of the number of muscles sampled, and here, the vocalizations were elicited by midbrain electrical stimulation in anesthetized animals which were lying in either the prone or supine position. In these situations, scalenus medius was found not to be involved in vocalization, unlike scalenus caudalis

in the present study, and the internal and external intercostal muscles were simultaneously active during phonation—that is, at the same time as the abdominal expiratory muscles. Jürgens and Schriever concluded, therefore, that the intercostal muscles are not concerned with moving air during vocalization, but serve to stabilize the thorax, against which the abdominal expiratory muscles can act. In humans, the external intercostal muscles, which are generally thought to be inspiratory muscles, have been found to be active during vocalization in some studies (Draper et al., 1959; Hoshiko, 1960; Hoshiko and Berger, 1965; Sears and Newsom Davis, 1968), but not in others (Taylor, 1960). Draper et al. (1959) and Sears and Newsom Davis (1968) showed they were active only at the beginning of vocalizations that were preceded by a deep inspiration, the implication being that these muscles helped control the rate of air loss during speech by counteracting relaxation pressures. We have already noted that such was not the case for the inspiratory muscles recorded in the present study.

Despite some obvious differences in the ventilatory patterns during vocalization in birds and mammals, birds may constitute a useful model system in which to study the neurophysiological mechanisms involved in the coordination of respiration and vocalization, such coordination being the sine qua non of effective vocal communication (Davis et al., 1993; Zocchi et al., 1990; Metz and Schiavetti, 1995; Wild, 1997). In no other animal are some of the factors involved in vocal learning and vocal control better known than in songbirds or the respiratory-vocal control pathways better delineated (see Brenowitz et al., 1997b). Furthermore, birds are the only terrestrial vertebrates other than humans that are known to learn complex vocalizations involved in intraspecies and possibly interspecies communication (Kroodsma and Miller, 1996).

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