MODULATION IN BIRD SOUNDS

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IN describing variation both within and between individuals and species of birds the complexities in vocal pattern have caused many problems. Yet these complexities are useful not only in the study of the patterns themselves, but also for interpreting the functional anatomy of the sound producing structures, the nature of the message, and the relationships among the birds involved. This paper analyzes several bird vocalizations and interprets their patterns as the product of individual and interacting oscillators and sound modifying structures; it also suggests a model for the operation of the syrinx during sound production.

To determine some of the variation and complexity in bird vocalizations I made sound spectrograms and oscillograms of song phrases sampled from the records produced by Kellogg and Allen (1959, 1962). These spectrograms indicated that the most complex fundamentals were similar to electronically produced modulations. Such modulations are easily recognized by their audible "buzzy" quality.

On the spectrograms time is indicated on the horizontal axis, frequency on the vertical one. The horizontal line on some spectrograms indicates that portion of the signal shown on the corresponding oscillogram.

On oscillograms time is indicated on the horizontal axis and the instantaneous relative amplitude of the sound wave on the vertical one.

SOUND STRUCTURE

Some bird vocalizations are simple, in that their fundamentals are analogous to signals produced electronically by a single sine-wave oscillator. Up-slurs and down-slurs are simple changes in frequency. Other sounds are mixtures of two such independent signals. The most complex sounds discussed in this paper are amplitude-modulated (AM) and frequency-modulated (FM) signals, particular interactions between two independent oscillations and analogous to radio broadcasting waves. Explanations of the nature of such waves may be found in the *Radio amateur's handbook* (Amateur Radio Relay League, 1960).

In essence, AM and FM are complex waves, the shapes of which are controlled by three independent variables: (1) the carrier frequency (CF) which is high and normally sinusoidal; (2) the modulating frequency (MF) which is low and may be of any shape; and (3) the amplitudes of these frequencies relative to one another. The last of these is correlated to the per cent of modulation in AM and the modulation index in FM.

On a spectrogram the first variable determines the vertical position of

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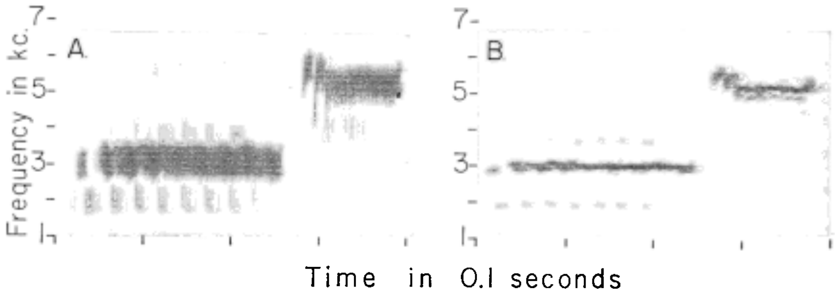

Figure 1. Song of a Loggerhead Shrike. A, wide band spectrogram; B, narrow band spectrogram.

the trace, the second determines the pattern along the time axis, and the third determines the light to dark contrast (in AM) or the vertical spread of the trace (in FM). Each of the two forms of modulation has an equivalent pattern, a carrier with sidebands, which occurs when the MF is high relative to the width of the filter used in making the spectrogram.

On an oscillogram the CF determines the wavelength within the envelope of the AM signal, the MF determines the pattern of the envelope, and the percentage of modulation determines the vertical displacement of the envelope. In FM the CF determines the average wavelength of the signal; the MF determines the pattern of distribution of the different wavelengths, and the modulation index determines the amount of deviation from the average wavelength. In undistorted FM the amplitude of the wave does not vary.

Unfortunately a biologically produced modulation does not have the steady state characteristic of an ideal signal. Nevertheless by allowing for changes in the independent variables, such sounds can be explained.

The occurrence and relationships among these variables in bird sounds are shown by example.

Amplitude modulation.—Examples of undistorted or predominant amplitude modulated sounds seem to be uncommon among birds. Most if not all FM sounds also show the presence of AM. The amplitude changes of the AM are regularly correlated to the pattern of frequency variation in FM, but the correlation may differ from one signal to the next.

The phrase of the Loggerhead Shrike, *Lanius ludovicianus,* shown in Figure 1 has two syllables. The first syllable, with its slight zigzag in the lower trace, appears to have some FM (Figure 1A). The corresponding narrow band trace (Figure 1B) shows the variation to be slight, and periodic at about 65 per second. This frequency is too low for the modulation to be resolved into its sideband form. The second syllable, about an octave in frequency higher, shows vertical beat lines. This indicates

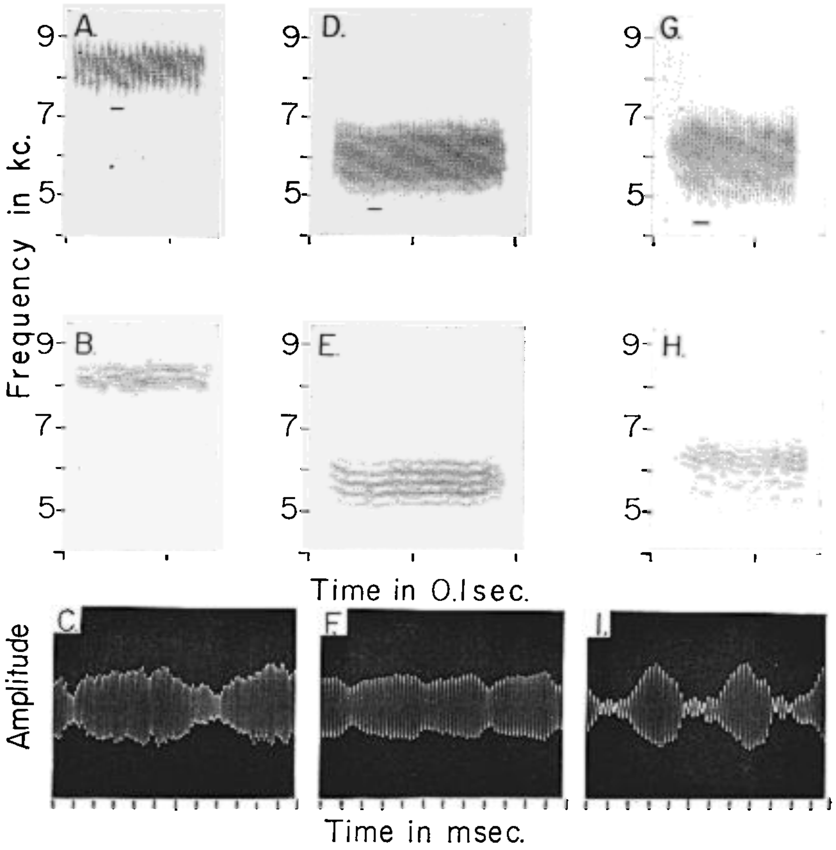

Figure 2. Spectrograms and oscillograms of portions of the songs of warblers, showing frequency modulation. A–C, Golden-winged Warbler; D–F, Prairie Warbler; G–I, Black-throated Blue Warbler.

the presence of separate simultaneous signals, and the periodicity of the beats is a function of the difference between such frequencies. In this example the frequency is about 200 per second. This same syllable in Figure 1B shows a dark (middle) carrier frequency with a weaker lower sideband and a still weaker upper one parallel to it. The difference between the carrier and the sidebands is about 200 cps, as was suggested by Figure 1A.

Frequency modulation.—In none of the bird sounds studied was the amplitude constant, i.e. where the upper and lower limits of the oscilloscope trace were parallel. Instead, these traces indicated that each bird sound had at least 30% AM. Among the birds studied, those with 30% to 70% amplitude variation were considered moderate in this character;

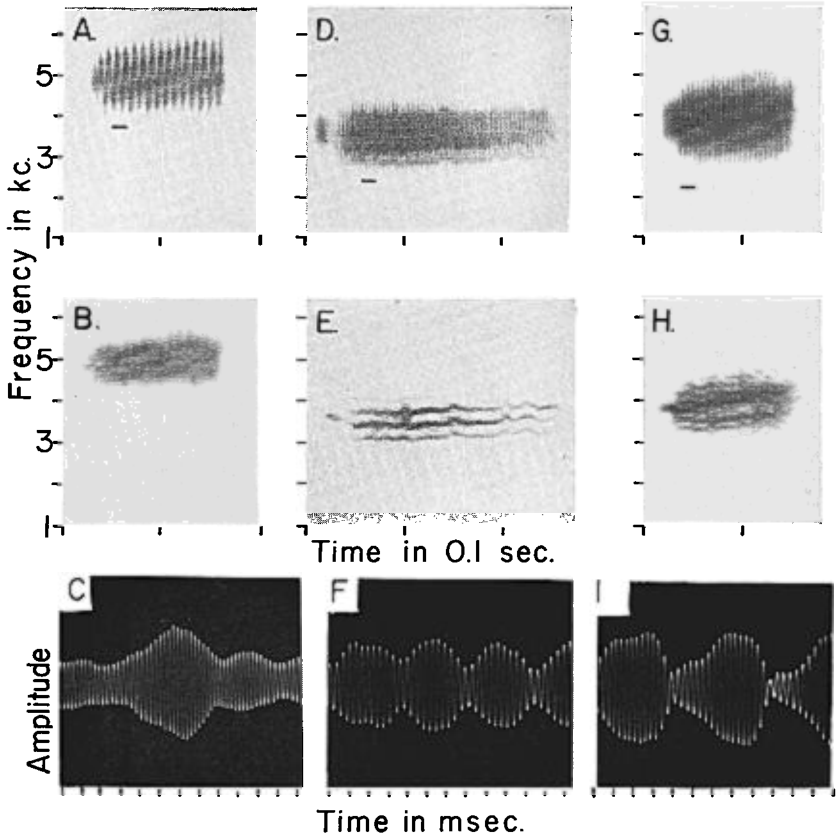

Figure 3. Spectrograms and oscillograms of portions of the songs of sparrows, showing frequency modulation. A–C, White-crowned Sparrow; D–F, Song Sparrow; G–I, Chestnut-collared Longspur.

those with over 70% were considered extreme. Of the parameters controlling the FM, the MF was usually stable. The carrier was either constant, with allowances for flutter, or was slurred. The modulation index normally was constant, especially after one or two modulating cycles at the beginning of a sound.

The first group of sounds shown in Figures 2 and 3 have moderate AM and fairly constant FM. The group includes parts of the songs of the Golden-winged (*Vermivora chrysoptera*), Prairie (*Dendroica discolor*), and Black-throated Blue (*D. caerulescens*) warblers, and in Figure 3 the White-crowned (*Zonotrichia leucophrys*) and Song (*Melospiza melodia*) sparrows, and the Chestnut-collared Longspur (*Calcarius ornatus*). Table 1 gives the parameters for the modulations in these sounds. In these six

TABLE 1
PARAMETERS OF MODULATIONS IN BIRD SONGS WITH LESS THAN 70 PER CENT AMPLITUDE MODULATION

Species	*Carrier frequency (kc)*	*Modulating frequency (cy/sec)*	*Deviation (kc)*	*Modulation index*
Golden-winged Warbler	8.4	140	0.7	5
Black-throated Blue Warbler	6.1	220	1.4	7
Prairie Warbler	5.4	280	0.9	3+
White-crowned Sparrow	4.9	110	0.8	7+
Song Sparrow	3.2	300	0.7	2+
Chestnut-collared Longspur	3.6	190	0.9	4+

species the carrier frequency was between 3.2 and 8.4 kc, the modulating frequency between 100 and 300 cps, and the modulation index between 2 and 7.

The second group, illustrated in Figure 4, include sounds with extreme amplitude modulation. They are portions of the songs of the Golden-cheeked (*Dendroica chrysoparia*), Black-throated Blue (*D. caerulescens*), Blue-winged (*Vermivora pinus*), Bachman's (*V. bachmanii*) and Parula (*Parula americana*) warblers, the Rock Wren (*Salpinctes obsoletus*), Clay-colored Sparrow (*Spizella pallida*), and the Yellow-bellied Flycatcher (*Empidonax flaviventris*). The data from these individual sounds are included in Table 2. Spectrograms of many of these show low frequency attenuation (i.e. the traces fade at their lowest frequencies). The Yellow-bellied Flycatcher spectrogram shows high frequency attenuation. Four oscillograms in Figure 4 show different degrees of intermittent sound, i.e. where the amplitude is periodically so low that the trace becomes discontinuous. Davis (1964*b*) has described variation in the modulations of the Clay-colored Sparrow in more detail.

The Black-throated Green Warbler (*Dendroica virens*) can produce two frequency modulations simultaneously. This is shown in Figure 5A

TABLE 2
PARAMETERS OF MODULATIONS IN BIRD SONGS WITH MORE THAN 70 PER CENT AMPLITUDE MODULATION

Species	*Carrier frequency (kc)*	*Modulating frequency (cy/sec)*	*Deviation (kc)*	*Modulation index*
Golden-cheeked Warbler	3.4–4.4	120	1.1	9
Blue-winged Warbler	6.7–7.2	2.5	1.1	5
Bachman's Warbler	7.0	140	1.5	11–
Parula Warbler	5.2–5.7	90	1.2	13+
Clay-colored Sparrow	3.9	150	1.1	7+
Yellow-bellied Flycatcher	5.2	150	1.7	11+

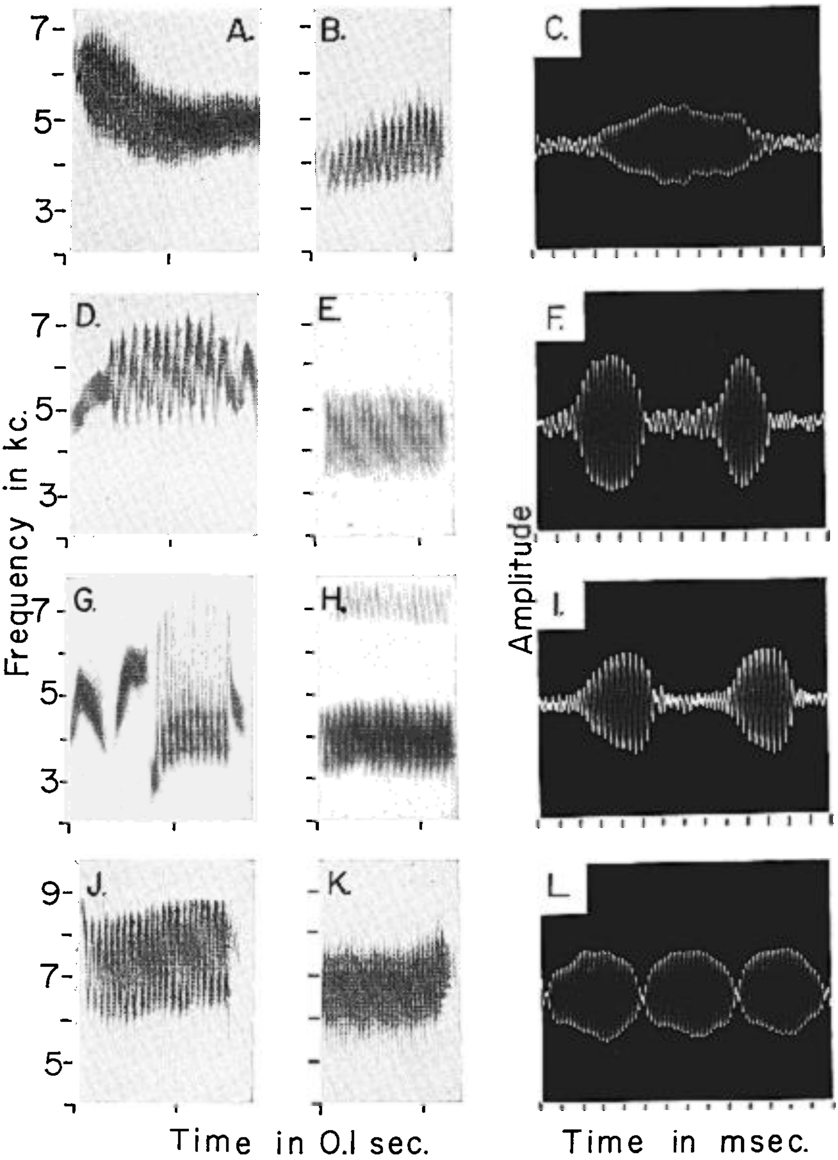

Figure 4. Spectrograms and oscillograms of portions of songs showing frequency modulation and more than 70 per cent amplitude variation. A, Black-throated Blue Warbler; B, Golden-cheeked Warbler; C, D, Parula Warbler; E, F, Clay-colored Sparrow; G, Yellow-bellied Flycatcher; H, Rock Wren; I, Yellow-bellied Flycatcher; J, Bachman's Warbler; K, L, Blue-winged Warbler.

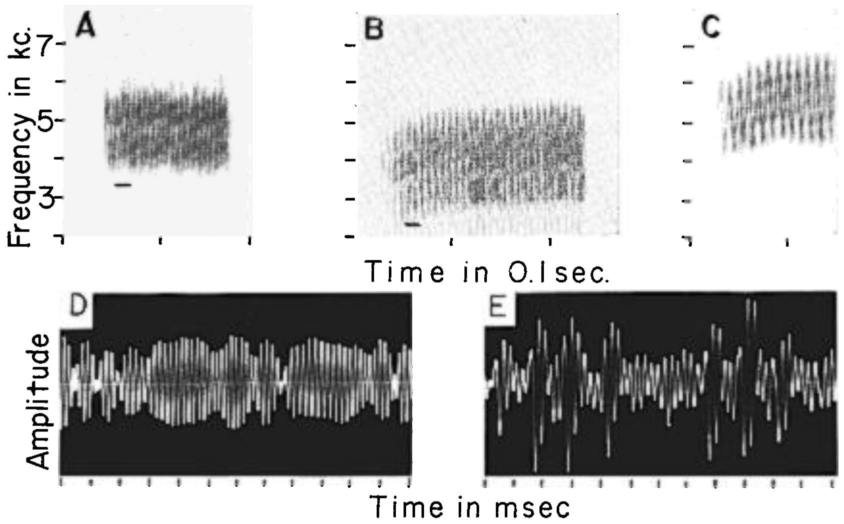

Figure 5. Spectrograms and oscillograms of portions of songs showing two simultaneous frequency modulations. A, D, Black-throated Green Warbler; B, E, Varied Thrush; C, Cerulean Warbler.

and 5D. Here the two modulations have similar parameters, but are about 180° apart in phase. The beats produced by the mixture of the two FM signals mask the effects of AM, such that the percentage of modulation cannot be determined. These beats are responsible for the irregular duration of amplitude peaks in the oscillogram. The beats are longest when the instantaneous frequencies of the two modulations are most similar, i.e. where they cross each other on a spectrogram, and are shortest where the maximum of one and the minimum of the other occur simultaneously.

Two FM signals seem to occur in the sound from the Varied Thrush (*Ixoreus naevius*) shown in Figure 5B and 5E, and in the sound from the Cerulean Warbler (*Dendroica caerulea*) shown in Figure 5C. In the latter case the loud part of the signal, represented by the dark trace, has a CF between 5.6 and 6.0 kc, an MF at about 95 cps, and a modulation index of about 12. The weaker signal, barely discernable in the spectrogram, may be another FM signal out of phase.

The sound of the White-crowned Sparrow shown in Figure 6 appears to be a series of beats. However, when I slowed down the signal, in addition to the beats shown there, fainter beats of higher frequency appeared. This suggests the presence of a second weaker signal. The dark beats, too, no longer appeared to be vertical. These observations suggest that the dark "beats" are parts of two frequency modulations with attenuation

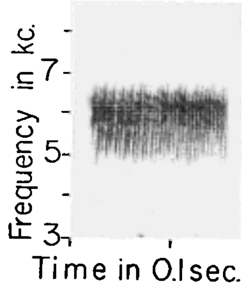

Figure 6. Wide band spectrogram of part of a White-crowned Sparrow song.

of all but the lowest frequencies, so that only a small part of the modulation had enough energy to cause a trace on the spectrogram.

The flight call of the Common Nighthawk (*Chordeiles minor*) shown in Figure 7 shows a change in the modulation index. In this call the CF of the latter half is lower than that of the first half, but the MF stays constant throughout. The modulation index decreases from about 7 to 5 during a single modulating cycle.

MECHANISM FOR MODULATION

The fundamentals of all of the above sounds can be produced by two simultaneous, independently operating frequency modulators. Each frequency modulator needs two oscillators, one for the carrier and one for the modulating frequency.

The carrier frequency found in these bird sounds varied from about 3.2 to 8.4 kc. This is the frequency range characteristic of the fundamental of the songs of many oscines. These frequencies are sufficiently high that the only likely explanation requires an oscillator vibrating at its natural frequency. Variations in frequency can be produced by changing the tension upon the oscillator, thus altering its natural frequency.

The modulating frequencies observed varied from 90 to 300 cps. Such frequencies could be generated by an oscillating structure with greater mass or less rigidity than that which produces the carrier, or by a structure similar to that which produces the CF, but with less tension upon it. Of the three, I believe the first is the most likely.

Another possibility for the MF is a periodic change in the tension on the CF oscillator. To interpret whether this or an explanation from the previous paragraph is more likely, the duration of muscle contraction–relaxation cycles was estimated. The fastest time for this cycle in the skeletal muscles of mammals (e.g. the cat) is 7.5 to 10 milliseconds (Prosser and Brown, 1961: 418 ff.). In no vertebrate muscle listed was the half-relaxation time less than the contraction time. Therefore the

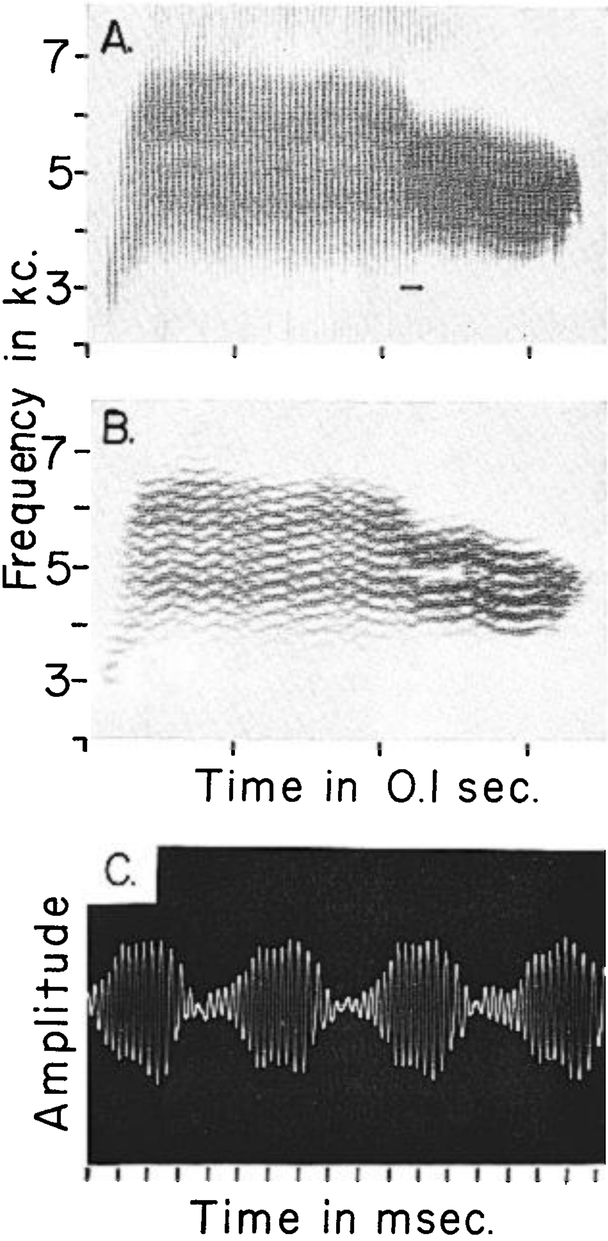

Figure 7. "Peent" call of a Common Nighthawk. A, wide band spectrogram; B, narrow band spectrogram; C, oscillogram of portion where index of modulation changes.

duration of a contraction (half-relaxation) cycle in vertebrate muscle presumably cannot be less than 15 to 20 msec, or occur at a maximum frequency much over 50 to 60 cps. Prosser and Brown (1961: 419) give the rate of the wing beat of a hummingbird "standing still" in air as 55 per second. Greenewalt (1960: table facing p. 214) gives the wing beat rates of hummingbirds from 24 to 80 per second. These data suggest that any frequency in a bird sound that is noticeably over 70 cps is most likely the result of an oscillator driven at its natural frequency rather than from the active contraction–relaxation cycle of a muscle, *if* energy is supplied at each cycle. As it is possible to supply energy at some other rate (e.g. only on every second cycle) muscle contraction might be involved in higher modulation frequencies. However in a damped system, such as occurs in these animal tissues, the deviation of the peaks of a frequency modulation would show a progressive decrease between applications of energy. As this is not apparent in the oscilloscope traces studied, it seems that energy must be supplied during each modulating cycle, or by muscle contraction tuning the natural frequency of a driven oscillator. The latter is more likely true.

The song of the Black-throated Green Warbler requires the presence of two independent modulators, the outputs of which must be mixed acoustically before they leave the vocal tract. When only a single fundamental or modulated signal is present, these modulators must either operate in perfect synchrony or one must be inactivated. The mixture of a modulated and unmodulated sound, as has been observed in the Song Sparrow among others, requires that the modulating frequency of one modulator be inactivated.

The fact that amplitude changes are correlated to the FM might suggest that the AM and FM systems are connected in some way.

SYRINGEAL STRUCTURE

The basic structure of the syrinx of the Red-winged Blackbird (*Agelaius phoeniceus*) is shown in Figure 8. This species was chosen as an example because it contains the maximum number of syringeal muscles, the trill of its "song" contains modulation, and its syrinx is relatively large for a passerine bird. The figure was drawn from the projection of a 10 μ-thick frontal section. The figure is similar to the thrush syrinx illustrated by Häcker (1900).

Miller (1934, 1947) implied in owls, and Miskimen (1951) demonstrated experimentally with House Sparrows (*Passer domesticus*), that the internal tympaniform membrane (ITM) is the vibratile one. The thinnest portion of the ITM vibrates most during the production of a sound. This thin portion should have the highest natural frequency of any oscillating structure in the syrinx. The thicker portions probably

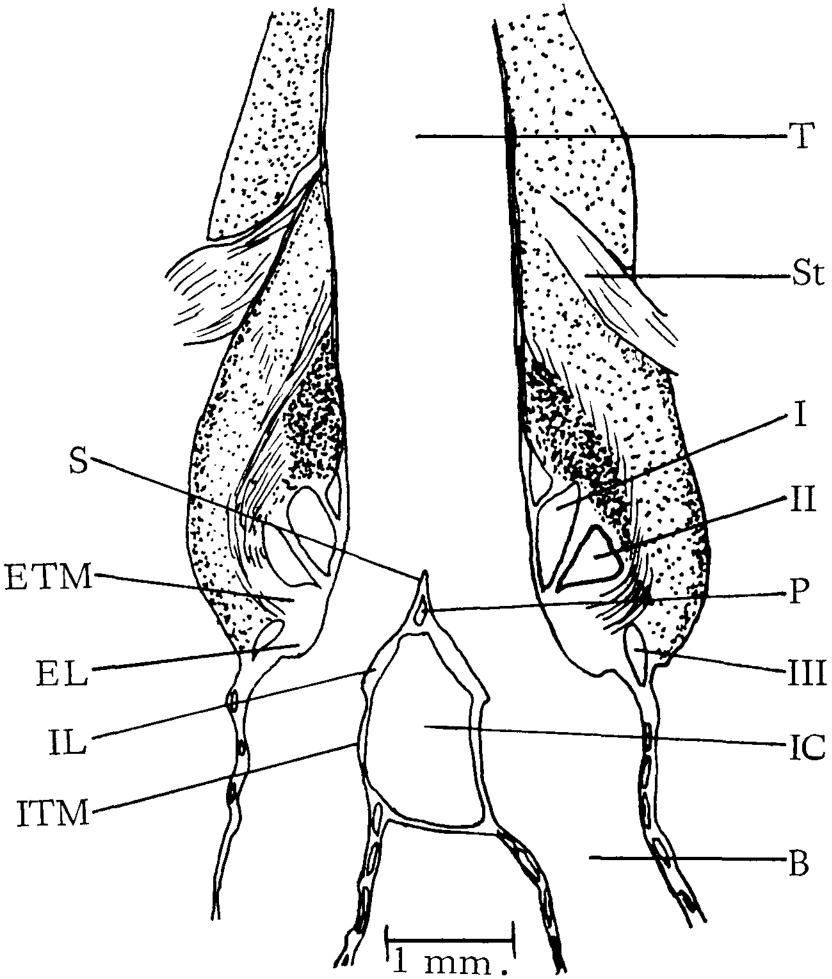

Figure 8. Longitudinal section through the tracheobronchial syrinx of the Red-winged Blackbird, *Agelaius phoeniceus*. Key: B, lumen of bronchus; EL, external labium; ETM, external tympaniform membrane; IC, interclavicular air sac; I, II, III, bronchial bars; IL, internal labium; ITM, internal tympaniform membrane; P, pessulus; S, semilunar membrane; St, sternotrachealis muscle; T, lumen of trachea.

act more as supporting structures, and aid in distributing tension evenly over the thin surface. This portion, then, probably produces the high frequency fundamental of a bird song, or the carrier frequency of a modulated one. As most passerines have two ITM's separated by the pessulus, two independent fundamentals could be produced. Because of the basic symmetry of these membranes, the two fundamentals should be similar most of the time, and conceivably could even be synchronized.

The tension on the ITM controls the frequency at which it vibrates most efficiently. This tension is controlled by contraction of syringeal muscles attached to the bronchial bars which support the membrane. Setterwall (1901: 67) particularly mentions the *laryngosyringeus dorsalis* (= *bronchotrachealis posticus*). In addition to stretching the ITM, contraction of this muscle also changes the form of the inner vocal cord (= internal labium) and the form and size of the sound fissure (= lumen of bronchus).

Miskimen (1951) demonstrated that the ITM is set into vibration by the excurrent flow of air. This occurs during the active phase of respiration. Control of the pressure of air entering the bronchi and passing over the membranes may regulate the amplitude of the signal. Some control of pressure may come from regulating the size of the lumina of the bronchi (e.g. by the labia) or the trachea. In any case, increased differences in pressure in the vocal tract as opposed to that in the interclavicular air sac (on the other side of the ITM) are responsible for setting the membrane into vibration.

The modulating frequency is most likely produced by vibration of the labia driven by the same air stream. The internal labia are essentially a part of the ITM (see above) and may be too intimately connected to it to allow for independent operation. Several factors suggest that the external labium (EL) and the external tympaniform membrane (ETM) are a more logical source of the modulating frequency:

(1) The mass of the EL is considerably greater than that of the other vibrating parts of the syrinx. It would thus have a much lower natural frequency.

(2) There is an EL in each bronchus. This allows for the possibility of two simultaneous modulations, or just one. While this factor does not eliminate the IL as the source of the MF, it does eliminate the semilunar membrane.

(3) The ETM, while not normally thin enough to vibrate in a manner similar to the ITM, may act in association with the EL by allowing for additional flexibility in the movement of the latter. In this way the ETM would function like the conjunctiva between the sclerites of the exoskeleton of insects. According to Peter Ames (pers. comm.) the ETM is not always present in oscines. Whether such oscines produce modulations is a question that has not been investigated.

(4) The *laryngosyringeus ventralis* (= *bronchotrachealis anticus*) is a muscle regularly associated with the EL and ETM. Setterwall (1901: 62) emphasized the importance of this muscle as a regulator of the form and size of the outer vocal cord (= EL). He stated that the ETM and its

muscle (and also the muscle to the ventral end of the third arch) might be regarded as regulators of form and size of the outer vocal cord, and by this the width of the sound fissure.

Amplitude modulation.—Amplitude modulation can be produced by having the labia set into vibration at their natural frequency while they are projecting into the lumina of the bronchi. Such periodic changing of the cross-sectional area of the lumina can be compared to the production of tremolo in an organ pipe, or the trills produced by a man blowing through his lips. Both of these are familiar forms of mechanically produced amplitude modulation.

As there is a mechanical connection between the EL and the bronchial bars that support the periphery of the ITM, interaction between them can be expected. This is the first possible explanation for the presence and correlation of amplitude changes in FM signals. The ITM, acting without the influence of the EL, could produce the CF. This would be analogous to a DC bias introduced into a voltage-controlled oscillator. Periodic variation in tension on the ITM, the result of vibration of the EL, would be analogous to an AC signal introduced into the same oscillator. Under such conditions the output would be an FM signal.

The second possible source of amplitude variation involves only the operation of the ITM. This membrane, or pair of membranes, has a natural frequency range within which it vibrates most efficiently, i.e. to the greatest extent with the least expenditure of energy. Within this range the instantaneous frequency can be changed by altering the tension on the membrane. However as the limits of this range are approached, efficiency decreases. In FM therefore whenever the frequency approaches one of these limits, attenuation will occur. When the limits are exceeded, the membrane will cease to vibrate.

A third possibility involves the resonant frequency of the trachea, a tube. Such tubes may act as band-pass filters, allowing certain frequencies to pass through them with relatively little loss of amplitude. Rüppel (1933) suggested that tracheal resonance is important in the production of sounds by more primitive birds. Sutherland and McChesney (1965) have demonstrated this in the calls of geese. As the length of the trachea is variable, and length is one of the main factors in determining the resonant frequency of a tube, such changes might account for differences in attenuation of the same frequency at different times. The position of the mouth and the degree to which it is open may also affect the characteristics or effective length of the tube system.

In all probability the contribution of each of these three, and possibly other different means of attenuation, varies with the species and even among different sounds of a single species.

Pessulus and semilunar membrane.—The possible role of the pessulus in the physical support of the syrinx and in isolating the action of the two ITM's has already been suggested. The semilunar membrane, an extension of the pessulus anteriorly into the lumen of the trachea, may function to isolate the air coming from the bronchi so that mixing of the two different sounds can occur without disturbing the sources of vibration.

Intrinsic syringeal muscles.—No particular function relative to sound production can be assigned to the individual syringeal muscles yet, aside from the few mentioned earlier. Ames (1967) suggests that in passerines more variation in syringeal anatomy exists than has formerly been suspected. Among oscines, where song variation is particularly great, syringeal anatomy has been considered to be fairly constant. This suggests that much of the variation in sound may be more dependent upon neuromuscular control than on syringeal structure. The study of the effects of individual muscle action upon sound production is an important, but unexplored aspect of syringeal knowledge. The detailed investigation of syringeal anatomy and its correlation to sound throughout the oscines should not only provide an understanding of the action of the syringeal components, but also provide a better understanding of the taxonomic usefulness of syringeal anatomy.

SUMMARY

The first part of this paper shows the kinds of variation in the two forms of modulation in the song phrases of birds. Portions of these phrases are used to demonstrate the variation in the parameters of amplitude modulation and frequency modulation. Evidence supporting the dual-oscillator hypothesis, i.e. that oscine birds have two independent oscillator systems that may be operated independently or simultaneously, is presented. Three possible explanations for the presence of amplitude changes in FM signals are presented.

The second part hypothesizes how certain details of sound structure may be related to specific structures in the vocal tract, particularly the internal and external tympaniform membranes, the internal and external labia, the pessulus and semilunar membrane, and certain intrinsic muscles.

In passerines, sound and syringeal anatomy have been utilized in behavioral, anatomical, and systematic studies. The usefulness and applicability of these two can only be strengthened by establishing their interrelationship more precisely.

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