

AN HYPOTHESIS CONCERNING THE RELATIONSHIP OF SYRINGEAL STRUCTURE TO VOCAL ABILITIES

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ABSTRACT.—Neither the possession of large vocabularies or repertoires nor the ability to learn phonations can be precisely correlated with the structural complexity of a syrinx. Hence, some recent investigators have suggested that avian vocal plasticity arises solely from a neurological shift. A simple syrinx, i.e. one with only extrinsic musculature, is subject to certain constraints, however. Its configuration changes as a unit, and the factors responsible for modulating sounds cannot be independently varied. Thus, the temporal characteristics of sound patterns can be varied easily, but rapid juxtaposition of different modulatory patterns is difficult. Intrinsic musculature permits isolation and independent control of syringeal components and thereby simplifies control of modulations. Syringeal complexity may not be an adaptation (i.e. did not evolve under selection) for plastic vocal behavior, but it is permissive of and probably prerequisite for such behavior. *Received 17 November 1982, accepted 16 May 1983.*

BOTH the vocal behaviors and vocal organs (syringes) of birds range from very simple to very complex. The extremes of both coincide. Complex syringes have evolved independently at least three times, in the psittacids, trochilids, and passerines. Each of these lines contains species capable of complex vocal behavior, and such behavior is virtually confined to these lines. These coincidences suggest a close (causal?) linkage between the two phenomena. The intent of this paper is to examine the possible nature of that linkage.

Before continuing, I will define my use of several terms. By "vocabulary," I mean the set of sounds and modulations a bird can make. Essentially any sound recognizable as a specific figure in a sonogram is an element of a vocabulary (Fig. 1). A "song" is a repeated pattern of vocabulary elements (= phrase, song or song-type of others). Sequences of vocabulary events of different rhythm, tempo, or emphasis, or containing different numbers of repeated elements are considered versions of the same song, but any change in the sequence of elements constitutes a new song. A "repertoire" is the number of calls and songs used by an individual bird.

A fourth term, "intrinsic muscles" of the syrinx, is somewhat more difficult to define. In most present usages, it refers to a series of short muscles with cranial attachments on or immediately cranial of the syrinx and caudal attach-

ments invariably on a syringeal element, usually a bronchial bar. Ames (1971) limited the term to those muscles arising entirely within the syrinx, but that characteristic is not easily determined by gross dissection of preserved specimens. Further, in a rather diverse group of birds, the tracheolateralis extends caudad onto the syrinx (Yarrell 1833, Wunderlich 1884, Beddard 1898). In doves, only the caudal portion of the tracheolateralis is well developed, and it extends from the insertion of the extrinsic sternotrachealis caudad onto the lateral tympanic membranes (Warner 1972). Many authors have treated such extensions of the tracheolateralis as intrinsic muscles. This practice has led to some rather elaborate and confusing categorizations (Gadow 1896). I consider a muscle to be intrinsic if it can affect the syringeal configuration by some means other than adjusting the position of the caudal end of the trachea. This definition eliminates those extensions of the tracheolateralis that insert cranial to the membranes but includes extensions past the tympanum onto the bronchial rings, a situation existing in many of the sub-oscine passerines (see also Fig. 4 for the condition in oscines). If, as is generally supposed, intrinsic muscles are derived from the tracheolateralis, then such ambiguities should be expected.

"Simple vocal behavior" is an ambiguous term that has been used to refer to small vocabularies, small repertoires, or stereotyped

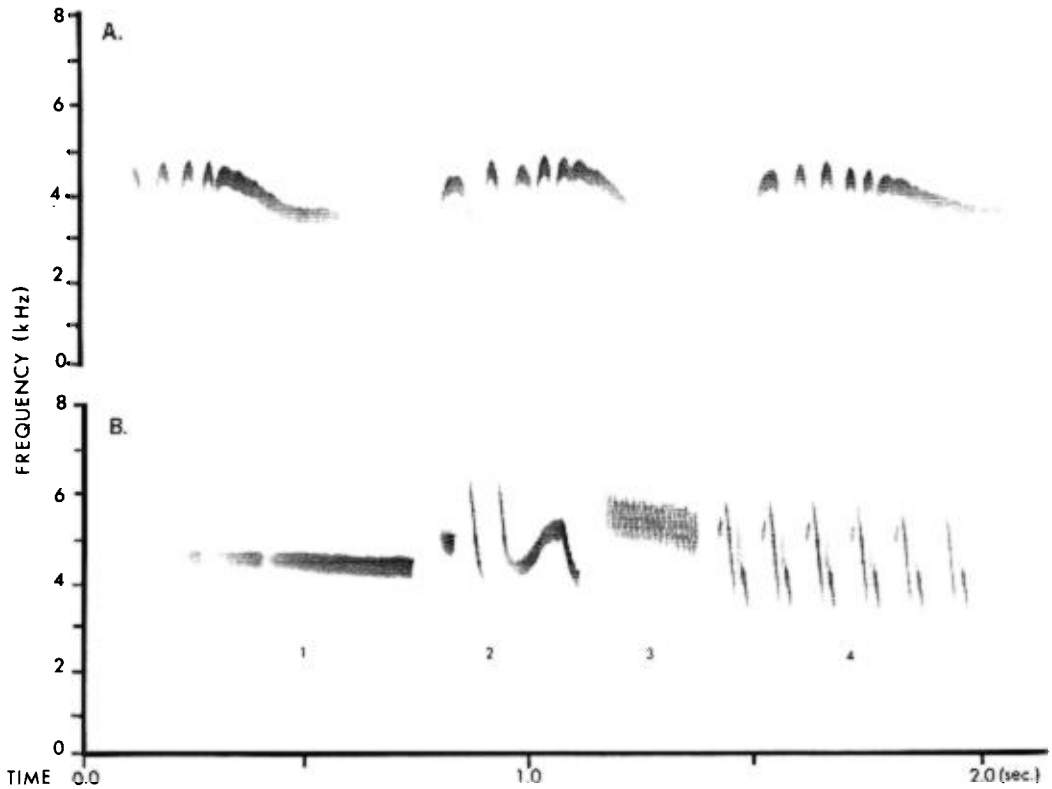


Fig. 1. Wideband sonograms of simple and complex vocalizations. A. Calls of a Killdeer (*Charadrius vociferus*), a species with a simple syrinx. This vocalization shows some frequency modulation but is composed essentially of a single, simple vocabulary element that is prolonged at the end of the call. B. Song of a White-crowned Sparrow (*Zonotrichia leucophrys*). This species has unusually complex, short songs that dramatically demonstrate the ability of a complex syrinx to utter quite different sounds in rapid sequence. The example contains at least four different vocabulary elements, of which the second could be further subdivided.

repertoires. Clearly, these restrictions are, to some degree, interdependent. My use of the term incorporates them all but emphasizes the lack of plasticity, whether that be an inability to produce or to learn vocabulary elements. In those species with simple behavior, geographic variation occurs at the subspecific level (Smythies 1960, Armstrong 1973, van der Weyden 1973, Hand 1981), but I have found no report of culturally maintained, local variants (dialects).

Complex vocal behavior is characterized by plasticity of both vocabulary and repertoire. Acquisition of a normal repertoire depends to some degree on learning (Nottebohm 1970, Lemon 1975). In some species, the repertoire may be modified during an individual's life

(Nottebohm and Nottebohm 1978). Dialects are common. Vocabularies and repertoires may be extensive, with hundreds of songs reported for some species, over a thousand for a few (Verner 1975; Kroodsma 1975, 1978; Kroodsma and Parker 1977). Such abilities are widely distributed among oscines.

The configuration of a simple syrinx is usually determined by the actions of two pairs of extrinsic muscles, the aforementioned sternotrachealis and tracheolateralis, but in a few species the extrinsic cleidotrachealis also helps (Youngren et al. 1974, Lockner and Youngren 1976, Gaunt and Gaunt 1977, Gaunt et al. 1982, Suthers and Hector 1982). The configurations of complex syringes are controlled by more than two pairs of muscles, at least one pair of which

is intrinsic. The very complex syringes of oscines contain 4-9 (depending on what you choose to count) pairs of intrinsic muscles (Ames 1971, Dürrwang 1974) in addition to the sternotrachealis and tracheolateralis.

THE PROBLEM

The fact that the most complex syringes are found in the oscines, a group containing many species noted for their vocal abilities, leads to the easy supposition of a cause-and-effect relationship. The notion that there is a direct correlation between syringeal complexity and vocal virtuosity is commonly expressed in popular literature and some recent textbooks (Welty 1975: 118) and, indeed, finds support in some critical analyses (Miskimen 1951; *N.B.*: Ames was unable to confirm the myological differences reported by Miskimen). Yet ornithologists have long recognized (e.g. Beddard 1898) that the relationship is hardly precise. Contrary evidence may be gathered from several observations.

First, vocal plasticity is not absolutely linked to the number of intrinsic muscles. Parrots have only two pairs of intrinsic muscles (Nottebohm 1976). Among passerines noted for their mimetic abilities, the Lyre Bird (*Menura novaehollandiae*) has three pairs of intrinsic muscles, but the Indian Hill Myna (*Gracula religiosa*) and Mockingbird (*Mimus polyglottos*) have at least four (Ames 1971). Second, although all oscines have complex syringes, some have only a single song (Bertram 1970). Third, closely related species may have quite different abilities. Within Emberizinae, different species of *Aimophila* have as many as 200 songs (Groschupf and Mills 1982) or as few as 12 (Groschupf *in litt.*). In the genus *Zonotrichia*, males usually have one song, but that song is culturally transmitted and divided into many dialects (Marler and Tamura 1964, Lemon and Harris 1974, Baptista 1977). Fourth, song complexity and repertoire size can vary geographically within a single species, e.g. the Winter Wren (*Troglodytes troglodytes*; Kroodsma 1980). Finally, Greenewalt (1968: 180) stated that if complexity is equated with elaborate modulations, then numerous nonoscines have complex calls. Of his examples, however, the songs of only the two tyrant flycatchers show both amplitude (AM) and frequency (FM) modulations. The

syrinx of tyrant flycatchers contains several intrinsic muscles and is "simple" only in comparison with an oscine syrinx. The calls of his nonpasserine examples are all rich in AM but show little or no FM. Although AM can be traced directly to the activity of intrinsic syringeal muscles (Gaunt and Gaunt 1982), the use of extrinsic muscles for this purpose has not been demonstrated with certainty. Moreover, complex patterns of AM can be produced by changes of the driving pressure or by flow-driven oscillations of syringeal components (Gaunt et al. 1982). Greenewalt specifically distinguished between complex modulations and variety of modulations. He observed that oscines do have a wider frequency range and more varied kinds of modulation.

These observations have led to an impression that vocal behavior is not limited by the morphology of vocal structures, but rather is regulated and restricted by neurology. Ames (1971) summarized a discussion of syringeal vs. vocal complexity with the statement, "Evidently the major factor in vocal diversification in the oscines has been changes in the nervous system, rather than syringeal structure." Similarly, Lemon (1975) stated, "My point is that the apparent innateness in the calls of fowl and doves may reflect a much simpler situation than in oscines where normally the song elements require a much higher level of neuromuscular control." But this supposition leads to something of a conundrum. Nottebohm (1972a) wrote that, as commonly accepted advantages for the evolution of complex behavior "may be expected to be of broad occurrence, we are left to wonder why some birds evolved vocal learning while others did not." In neither the extensive discussion of 1972 nor in a list of physiological constraints on vocalization appearing in a later (1975) review did he even allude to the possibility that morphology per se might be limiting.

SYRINGEAL MECHANICS

To seek a solution to this problem, we must begin by considering how syringes make sounds. Either or both of two major mechanisms, vibrating membranes or vortex series, may form the sound source (Gaunt et al. 1982). The former may be responsible for complex tones, often (and sometimes erroneously) called

harmonic tones, in which energy is simultaneously distributed into several frequencies; the latter usually produces pure tones. The two mechanisms can interact, and sometimes determining which is dominant is difficult. In both cases, sound is modulated at the source; tracheal resonance plays little or no role (Hersh 1966, Greenewalt 1968, Abs 1980).

The classic hypothesis states that sound is produced by vibrations of the membranous portions of the syrinx. The sound's pitch is determined by the tension of the membrane, loudness by the amplitude of the oscillation. As a first step, the taut membranes are relaxed. Compression of the airsacs by the bodywall musculature creates a pressure head to drive air through the trachea. Flow induces a Bernoulli effect as air passes the membranes. Because the syrinx is suspended in the interclavicular airsac, a substantial pressure differential may develop across the membranes, drawing them into the lumen until tensile forces balance the pressure differential. The final tension is determined by the elastic properties of the membrane, the action of the syringeal muscles, the rate of airflow through the syrinx, and the pressure in the interclavicular airsac (Gaunt and Wells 1973). The latter two parameters will also affect the loudness of the sound. Finally, the average diameter of the bore of the lumen opposite the membrane will influence airflow and limit the oscillation of the membrane. In some cases, especially where they are directly opposite each other, the membranes may completely occlude the lumen and act more like mammalian vocal cords.

The whistling model supposes that the initial changes in syringeal configuration form one or more slots through which the airstream is forced (Gaunt et al. 1982). Shearing forces at the slot establish a vortex series that constitutes the sound source. How frequency is modulated has not been established with certainty. In many mechanical whistles, the configuration of the slot is important (Wilson et al. 1971). In any configuration, the frequency of a whistle tends to increase only slightly as airflow increases to some critical rate at which the frequency jumps abruptly to a new stable value, usually an octave higher. Both real and modelled dove syringes show this pattern (Abs 1980). Many whistles used by humans as musical instruments are controlled by coupling them to reso-

nators, the properties of which are easily changed. If the membranes of the syrinx act as resonators, then pitch may again be determined by membrane tension. In complex tones, increased airflow may shift the energy distribution toward the higher frequencies, thus raising the pitch.

Loudness is regulated similarly in both membrane and vortex systems. Of the several factors that may affect loudness, the pressure differential through the syrinx, which is determined by a combination of the driving pressure and the resistance of the passageway, is the most important (i.e. to sing louder, blow harder). The driving pressure is controlled by the bodywall musculature; resistance can be adjusted by changing the position of the flexible portions of the syrinx, which alters its average cross-sectional area. As previously discussed, however, position of the membranes is determined by a complex interaction of airflow, interclavicular airsac pressure, and activity in syringeal muscles. A second factor regulating loudness is the presence of devices that augment or inhibit the sound once it has been produced. Many species possess throat pouches of one or another kind, and these may contribute to the dissemination of sound (Chapin 1922, Gross 1932). The acoustics of these pouches have not been well studied, however. Another possibility for augmentation is a resonant relationship between a membrane and a whistle in which the vortices stimulate the membrane's oscillations. Sound will be loudest at the natural frequency of the membrane and will drop off to either side. This common relationship could explain the coupling of AM and FM described by Greenewalt (Gaunt and Wells 1973, Klatt and Stefanski 1974). Brackenbury (1979a) has proposed a somewhat different interaction of airflow and membrane vibration that also leads to augmentation of the elicited sound. The most probable muffling structures are the lateral and medial labia or, where labia are absent, lateral tympaniform membranes. These structures are set into oscillation by the same airstream that activates the sound source and would occlude the sound passageway in a pattern depending on their vibratory properties. Finally, many birds can activate sources in both right and left bronchi simultaneously. Species with appropriate musculature can produce completely different sounds from the two sides,

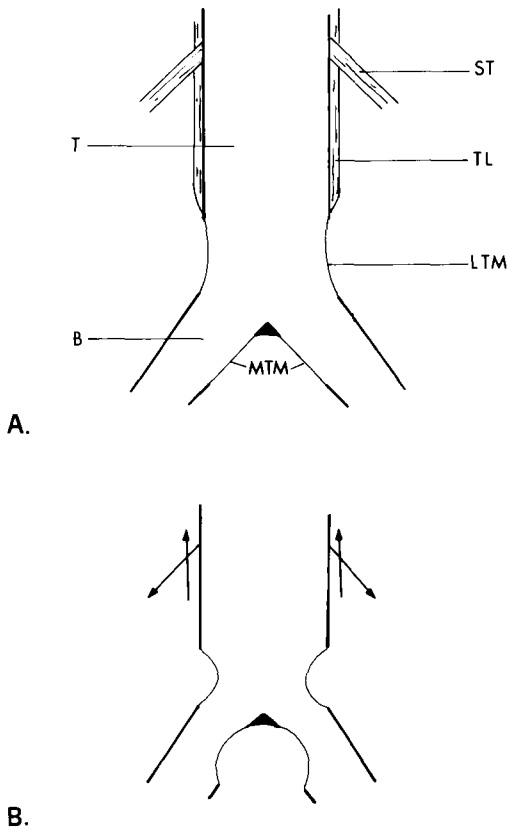


Fig. 2. Frontal sections of an idealized, simple syrinx. A. Relaxed position. B. Vocalizing configuration. Note that the forces (arrows) produced by contraction of the extrinsic sternotrachealis (ST) and tracheolateralis (TL) muscles must affect the position and tension of both the lateral and medial tympanic membranes (LTM and MTM) simultaneously. B, bronchus; T, trachea.

an ability termed the "two-voice" phenomenon (Greenewalt 1968; Nottebohm 1971, 1972b). Seemingly, various combinations of mechanical and aerodynamic vibrations should allow even a simple syrinx to produce a wide variety of sounds. The exact kinds would be determined by three factors: the rate of airflow, the diameter of the lumen opposite flexible portions of the syrinx, and the elastic properties of those flexible portions. What, then, limits the vocabularies and repertoires of species with simple syringes?

The constraints of a simple syrinx become apparent when one considers how it modulates

sounds. Suppose that the sound is produced in the vicinity of the median tympaniform membranes (Fig. 2) and that a pattern of AM is imposed on that sound by oscillations of the lateral tympaniform membrane. The simplest way to change the modulating pattern would be to change the position and tension of that membrane, presumably by adjusting the activity of the syringeal muscles. Because both pairs of controlling muscles insert craniad of all membranous portions, any change in muscular activity will also affect the position and tension of the medial membranes and the diameter of the lumen opposite them, thus changing the sound source. Moreover, both pairs of membranes must relax or stiffen together, though not necessarily to the same extent. Neither individual nor divergent changes seem possible. Nor is this the only linkage in the system. The tension on the membranes is determined by a complex interaction of airflow, interclavicular airsac pressure, and activity of the syringeal muscles. If the new setting alters the diameter of the syringeal bore, the resistance to flow and airsac pressure will change, thereby changing the tension on and the local turbulence patterns near the membranes. Because the syrinx changes shape as a unit, the components of the system are not independent, and even apparently minor changes of its configuration may have unpredicted consequences.

This is not to say that no changes are possible, for many require no adjustments in syringeal configuration. For instance, distinctly different patterns can be obtained by changing the tempo, rhythm, accent, or number of elements. The latter is especially effective if elements are repeated. A major shift in frequency can be achieved by overblowing, a technique that may be exploited in producing a gull's Long Call. All kinds of FM, continuous, stepped, oscillatory, or patterned, are found in the vocabularies of different species with simple syringes. The range of sounds uttered by different species with simple syringes suggests that any specific acoustic effect can be achieved by some combination of simple structure and neuromuscular activity. What is not achieved is the production of diverse effects from any one simple structure. Therefore, the rapid juxtaposition of different vocabulary elements, especially those involving FM, is rare in the calls of such species.

Evidently a simple structure imposes severe limitations on the ease of compiling and re-arranging series of different kinds of vocabulary elements. Hence, we may suppose that neurological programming to elicit a series of different specific effects from a single structure is either impossible or impractical, i.e. sufficiently difficult to override the advantages of plasticity. Yet the use of an organ that can produce diverse effects but is extremely difficult to control need not yield cacophony. A syrinx of a given structure and size, activated by muscular contractions of a given intensity and with a given airflow, will produce certain sounds more readily than others. Selection should act on both the structure and the flow pattern to produce species-specific sounds appropriate to a given environment. The ease with which the ventilatory musculature can control airflow should encourage the development of a second approach, the use of simple codes, e.g. loud sounds vs. soft sounds, high vs. low pitch, or modulated vs. constant tones. Some variables might be continuous, e.g. repetition rate or duration. Even these simple codes, however, use more than a single syringeal setting. Hence, sufficient control to insure at least minimal predictability would be required.

The genetic inheritance of at least a basic neuromuscular pattern insures both that a behavior can be performed and that it will be appropriately performed. Species with stereotyped vocal behavior can be expected to produce the correct sound pattern when first presented with the correct stimulus (assuming appropriate age and hormonal state). This, indeed, is the case for two species, chickens (Konishi 1963) and doves (Nottebohm and Nottebohm 1971), that have been tested. Stereotypy is also typical of the calls of all birds. In contrast to songs, calls often convey information that must be correctly sent and received with no practice.

AN HYPOTHESIS

If the foregoing analysis is correct, then complex vocal behavior depends on the ability to control sound production precisely. Control of sound production would be eased by any arrangement that dissociates acoustic linkages and isolates the effects of structural components. I hypothesize that intrinsic muscles provide the

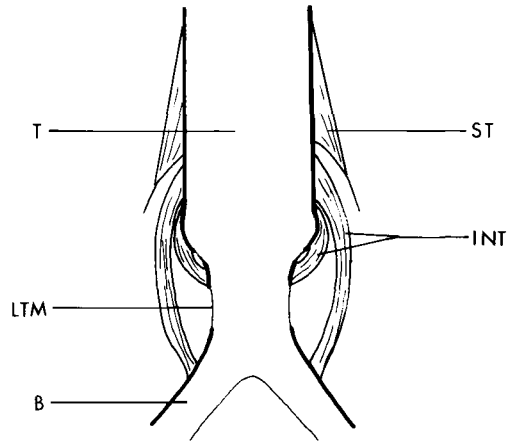


Fig. 3. Frontal section of an idealized, psittacid syrinx. The extrinsic sternotrachealis passes directly over the body of the syrinx and inserts onto the oblique septum rather than to the sternum. The tracheolateralis is absent. INT, intrinsic muscles.

potential for such a dissociation and, thus, their presence is a necessary, structural prerequisite to the evolution of vocal plasticity.

DISCUSSION

Precision of control in a parrot's syrinx is increased by two means (Fig. 3). First, the number of components is reduced. As the syrinx is tracheal rather than bronchial, it is not bilaterally divided, and parrots cannot speak with two voices. It also contains but one pair of membranes, thereby eliminating the potential for interactions between two simultaneously adjusted oscillators. Such an elimination of components is not unique to parrots, but it is rare, and few of the other species that show it are noted for their vocal virtuosity. Second, two of the three pairs of muscles controlling a parrot's syrinx are intrinsic, and one, the tracheobronchialis, spans the membranes. Its contraction rotates a set of fused bronchial bars to constrict the syringeal lumen regardless of the position of the trachea. This change in arrangement, not the addition of another pair of muscles, is critical. The syringeus muscle arises from the syringeal tympanum and inserts on a highly modified tracheal bar imbedded in the lateral membrane. The action of the syringeus opposes that of the tracheobronchialis and provides for an extremely precise regulation of

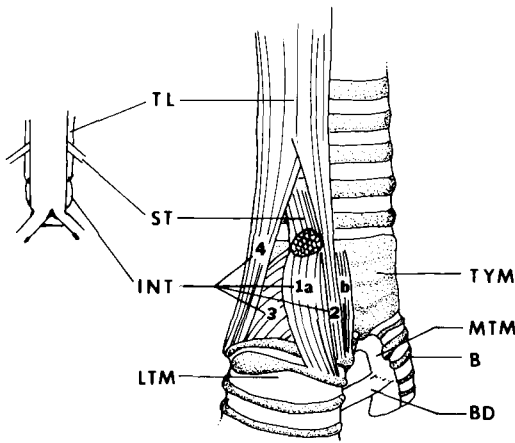


Fig. 4. Frontal section and lateral view of an idealized, oscine syrinx. Muscles of the left side are not shown. The presumed intrinsic muscles have been numbered. Many authors consider 1a and b separate muscles, but they seem to be portions of a single mass of tissue. Similarly, 2 and 4 are universally considered as intrinsic muscles, but do seem to be direct extensions of TL. B, bronchial bar; BD, bronchidesmus; TYM, tympanum.

both the syringeal bore and the tension on the medial ends of the rotating bronchial bars. Nottebohm (1976) has suggested that the determination of whether the syrinx will produce a harsh tone or a whistle depends on the action of the syringeus muscle. Although this has not yet been demonstrated, both the intrinsic muscles show considerably different electromyographic patterns from the extrinsic sternotrachealis (Gaunt and Gaunt 1982, in prep.). Contraction of the sternotrachealis relaxes the caudal end of the trachea and permits a free interplay of the two intrinsic muscles.

The structure of a songbird's syrinx is quite different (Fig. 4). Its most obvious feature is a proliferation of intrinsic muscles. The seven to nine pairs listed by some authors, often on the basis of supposed functions, are certainly too many. Ames (1971) recognized four pairs, one divided into medial and lateral portions. He states, "Until more is known about the operation of the syrinx, it seems unwise to name the muscles on a functional basis or employ functional groupings of muscle fasciculi." Yet, recognition of at least four functional units seems justified.

Each intrinsic muscle seems to affect the membranous portions of the syrinx in a differ-

ent manner by adjusting the position of bronchial bars (Chamberlain et al. 1968). The lateral labium encloses one bronchial bar. Rotation of the bar moves the labium into the lumen where it determines the configuration of the airway. That configuration may cause the airflow to vibrate a membrane, form a vortex-shedding slot (Gaunt et al. 1982), or induce the formation of harmonic tones (Greenewalt 1968). The labium may also act as an oscillator of relatively slow period (Stein 1968). According to Chamberlain's analysis, the position of the labial bar and the tension of the overlying tissues are determined by the interactions of several muscles and can be adjusted independently. Control of the tension of the internal membrane appears to be far less precise, but it involves the position of another bronchial bar and another combination of muscles.

The isolation of the flexible portions and the specialization of muscular function permit an extremely fine control of the oscine syrinx. That control does not enable oscines to produce new kinds of sounds, but it does simplify the conversion from one to another. Here a proliferation of components has simplified control, and with that simplification vocal plasticity and large repertoires become practical.

Although psittacids and oscines may seem to have quite different syrinxes, the key innovation permitting vocal plasticity in both is the acquisition of muscles that directly alter syringeal configuration, which becomes independent of the position of the trachea. Thus, the independence of syringeal components from each other is greatly increased.

I have been able to find accounts of only a few cases of presumed vocal learning in birds other than psittacids or passerines (see also Krebs and Kroodsma 1980). The first is in the Emerald Toucanet (*Anulacorhynchus prasinus*), which is reported to mimic local species in its immediate presence (Wagner 1944). All the supposed mimicked calls consisted of loud, two-pulsed sounds, e.g. "yow-yow," "rayg-rayg," "dir-rit," etc. The quality of the mimicry was unsubstantiated by spectrographic analysis. I have examined the syrinxes of two Emerald Toucanets and found no evidence of intrinsic muscles. Indeed, the musculature is remarkably simple. The sternotrachealis is unusually large and closely approaches the cranial end of the syrinx. The tracheolateralis is absent or severely reduced.

A more substantial report is that of the presence of learned songs in populations of Little Hermit Hummingbirds (*Phaethornis longuemareus*; Snow 1968). Each portion of a breeding lek of this species has its peculiar song. Young birds entering the lek adopt the song of their neighbors. The report contained sound spectrographs of unique groups. Wiley (1971) extended Snow's observations and confirmed the similarity of songs within a song-group with an additional spectrographic analysis. Significantly, hummingbirds are one of the few non-passerine groups to possess intrinsic muscles (Müller 1847, Zusi pers. comm., pers. obs.).

A third case, deserving close examination, is that of the Greater Prairie Chicken (*Tympanuchus cupido*), Sharp-tailed Grouse (*Tympanuchus phasianellus*), and their hybrids. Sparling (1979) reported that wild male Greater Prairie Chickens adopted a three-note call uttered by hybrids. The mimicry may have been accomplished by modifying the "number of notes per bout, mean note duration, strongest frequency and . . . form of frequency modulation" of the Prairie Chicken's "Whine." Sonograms showed the mimicked calls to be close but not perfect copies of the model.

In a second example, a hybrid responded to either Prairie Chickens or Sharp-tailed Grouse with appropriate calls. Vocal learning is not certain here, although the hybrid may have learned which response was appropriate.

Finally, Sparling showed that a Sharp-tailed Grouse was able to mimic playbacks of altered calls "so faithfully that his calls could not be distinguished from recorded ones," even by spectrographic analysis. Of great interest is the fact that, again, the calls were altered by changing the duration of notes and internote intervals. Similarly, the learned, covey-specific "hoy" and "hoy-poo" calls of Northern Bobwhite (*Colinus virginianus*) differ in temporal components (Baily and Baker 1982). Both the number of elements in a call and their temporal properties are more easily derived from patterns of airsac compression than from changes in syringeal configuration (Gaunt et al. 1973, 1976, 1982). Such variations may be common among species with simple syringes, and much of the subspecific diversity in the vocalizations of species with simple syringes consists of changes in numerical or temporal properties (Smythies 1960, Armstrong 1973).

The evolution of complex vocal behavior ev-

idently requires two sets of modifications: a syringeal structure that permits the isolation and individual control of elements and a neurological shift that can exploit the potential of that structure. Although I judge the development of intrinsic musculature to be the key innovation permitting vocal plasticity, I do not wish to imply that it is an adaptation for that function. Many of the suboscine passerines that possess intrinsic muscles, and even some oscines, have small repertoires and stereotypic vocal behavior. Evidently, a complex syrinx only permits plastic vocal behavior. Aside from the fact that a syrinx is part of a respiratory system and may have functions associated with airflow, intrinsic musculature may provide other advantages to a vocal system. It may permit a bird to sing louder or longer for a given amount of air (Gaunt et al. 1973) or energy (Brackenbury 1977). Brackenbury (1979b) has also suggested that the passerine syrinx may have evolved under pressure from allometric constraints. According to his calculations, a small bird might have difficulty producing a significant sound with a simple syrinx. If so, then the independent evolution of complex syringes in hummingbirds is less surprising.

Having evolved, for whatever reason, intrinsic musculature has the potential to release the constraints of a simple syrinx. Now Ames' previously quoted statement may be appreciated in a somewhat different manner. The proper emphasis is on "oscines" rather than on "diversification," for the oscines possess a structure with functional potentials that could be exploited for an appropriate change in the nervous system.

I have neither the intent nor expertise to discuss the presumed neurological shift or the selective factors favoring it. The aforementioned studies of Bailey and Baker, Sparling, and Wagner suggest that some modifications of vocal performance, perhaps even crude forms of mimicry, are possible even for species with simple syringes. Parrots, though they may learn to imitate human speech, are not noted mimics in the wild. Latent, genetic potential for a neurological shift may be widespread. Given an appropriate release from structural constraints, such a proclivity could be exploited.

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