Ontogeny of Bird Song

Different strategies in vocal development are reflected in learning stages, critical periods, and neural lateralization.

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The study of avian vocalizations has been almost exclusively the concern of ethologists. Recent advances in this area may be of interest to psychologists (*1*), neuroscientists, and students of evolution.

Man is not the only species with ability to acquire new sounds from the environment, although no other terrestrial mammal, including the primates, is known to possess this talent (*2*). Vocal imitation is more common among birds (*3–5*), even if the total number of species so endowed is, in all likelihood, only a small fraction of all members of the class.

Linguists, comparative psychologists, and neuroanatomists continue to ponder the uniqueness of man. To a large extent their attention has been focused on language phenomena. Functional lateralization of language performance in the human brain has understandably drawn much of this interest (*6*). Evidence presented here suggests that lateralization of neural vocal control is not restricted to man. A review of the development of avian vocalizations points to some phenomena that may be typical of a particular task, rather than of a particular species.

Studies on the evolution of behavior may concentrate on a group of closely related species and focus on the phylogeny of a particular trait. In this situation a given behavior is seen as evolving from another closely related one, or from an inferred common ancestral pattern. Alternatively, we may ask what are the correlates—anatomical, social, or ecological—that accompany the manifestation of particular behavior patterns. An analysis of this kind, covering a host of related and unrelated taxa, has a good chance of teasing apart casual and causal correlations. Whereas the strictly phylogenetic approach addresses itself to genetic evolution, the broader analysis of behavioral similarities evaluates the evolutionary interactions between genotypes and natural selective forces. These two approaches are particularly helpful when one is trying to understand the various strategies followed by birds in their development of complex vocal patterns.

Vocal Performance in Birds

Avian vocalizations are produced by the flow of air past the elastic membranes of the syrinx. Rapid changes in the tension of these membranes determine changes in pitch. A complex set of muscles controls the performance of the syrinx. Although anatomy, acoustics, and physiology are distinctly different for the syrinx and the human larynx, it is useful to think of these two structures as subserving a similar role.

As motor organs, the syrinx and the larynx are well buffered from environmental variables. This makes them particularly good subjects for study of the ontogeny of behavior. In birds the interclavicular air sac which surrounds the syrinx on all sides is a predictable milieu completely under the control of the organism. Vocal patterns can develop without interaction between effector organ and environmental substrate. This eliminates one source of feedback information which the organism could use to control its motor performance. The fitness of a particular vocal act is not measured by its immediate success in coping with external challenge: a priori, there are no right or wrong patterns, which is not the case for many motor tasks, such as locomotion or feeding. Consequently, a study of vocal development involves control over only a small number of variables. This does not mean that the operation of the vocal system is free from constraints. The characteristics of its innervation (*7*), musculature (*8*), membranes and resonators (*9*) impose a limit on what can be done, and its functioning must incorporate the priority of respiratory needs. Also, vocal patterns may be programmed by properties of the nervous system.

Development of a Complex Motor Pattern

The wild chaffinch, *Fringilla coelebs*, a European passerine, has to learn its song from adult conspecifics (*10, 11*). This song consists of two or three phrases and ends in a more complex set of notes. The overall range of fundamental frequencies lies between 3 and 6 khz; the entire song lasts some 2 seconds (Fig. 1). Song variations on successive renderings are restricted to the number of times an element is repeated in each phrase of the song. Once song is fully developed during the first year of life, it remains very stable. Song patterns vary among individuals, and the same bird may have as many as six different song themes in its repertoire. The songs of birds reared in auditory isolation are of normal duration and pitch, but they show no phrasing and lack a complex ending. These songs of "isolates" are composed of rather simple frequency modulations (Fig. 1).

Chaffinches deafened at 3 months of age produce adult patterns very different from the isolate type (*12*). Their songs include elements of an extremely abnormal structure; some of these elements are reminiscent of the food-begging calls of fledglings of this species. These songs are stable only at a rather gross level; phrasing and complex endings are absent. The song of one of these birds was a continuous screech from beginning to end (Fig. 2). This is the extent of the motor skill the bird has to rely on when it is deprived of auditory feedback at an early age and given no access to external models. The prior vocal experience of birds deafened at 3 months of age includes little more than the food-begging calls they gave as juveniles.

Under natural conditions chaffinches acquire a stable song pattern at 10 months of age. This full song is pre-

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ceded by development of a rather soft and rambling vocalization known as subsong. Subsong progresses through various stages of increasing complexity, until it finally grades into "plastic song"; the latter includes most of the characteristics of full song but lacks well defined phrases and overall stability. Birds exposed to wild-type song and deafened at these various stages of vocal ontogeny develop a song the quality of which is well correlated with their presumed vocal experience prior to being deafened (*12*). The more limited this experience, the more rudimentary the song developed (Fig. 2). In the chaffinches deafened at 3 months of age, subsong and most of the calls are abnormal too.

Whether a chaffinch is reared in auditory contact with wild conspecifics or in auditory isolation, and whether or not it can hear its own vocalizations, an end to song development is invariably achieved. It is easy to see how a bird imitating a song model will cease its own vocal development when the matching of model and output has been accomplished. Similarly, in the case of the hand-reared isolate, one can argue that vocal development proceeds until the song matches a built-in template. It is harder to understand why deafened individuals with varying amounts of vocal experience before deafening also settle for an end pattern in the development of their abnormal songs. One is forced to conclude that the achievement of a relatively stable and predictable song does not imply the existence of a preconceived or acquired goal. This is a point of some importance to the ontogeny of fixed-action patterns.

Marler *et al.* hand-reared two groups of Oregon juncos (*Junco oreganus*) (*13*). The birds in one group were isolated individually in soundproof boxes; birds in the other group were placed where they could hear each other's vocalizations as well as the sounds of other species kept in the laboratory. Juncos in both groups developed stable song patterns. However, the birds raised in the rich auditory environment had more song types that included more elaborate elements, derived not from imitations but presumably from unspecific stimulation to "improvise" (*13*). The strategies of vocal development vary from species to species (*14*). The ontogeny of song in some birds may integrate the vocal experience of each developmental stage with elements derived from the auditory environment at large. The type of

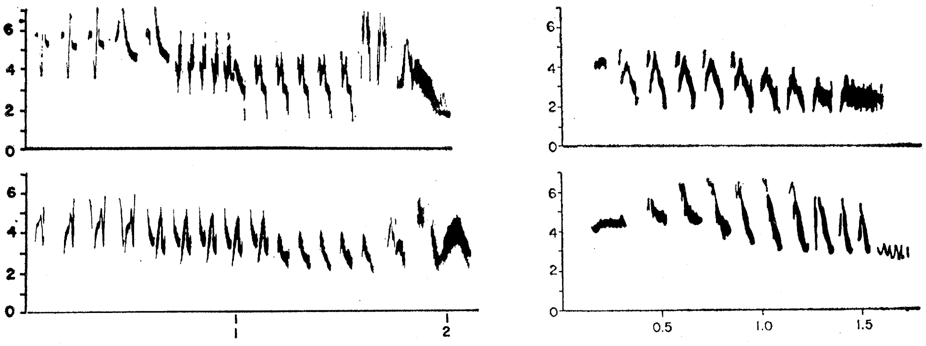

Fig. 1. The two songs to the left are part of the repertoire of an adult wild-caught male chaffinch. Those to the right were sung, respectively, by two males reared in auditory isolation. Values on the ordinate, frequency (in kilohertz); those on the abscissa, time (in seconds).

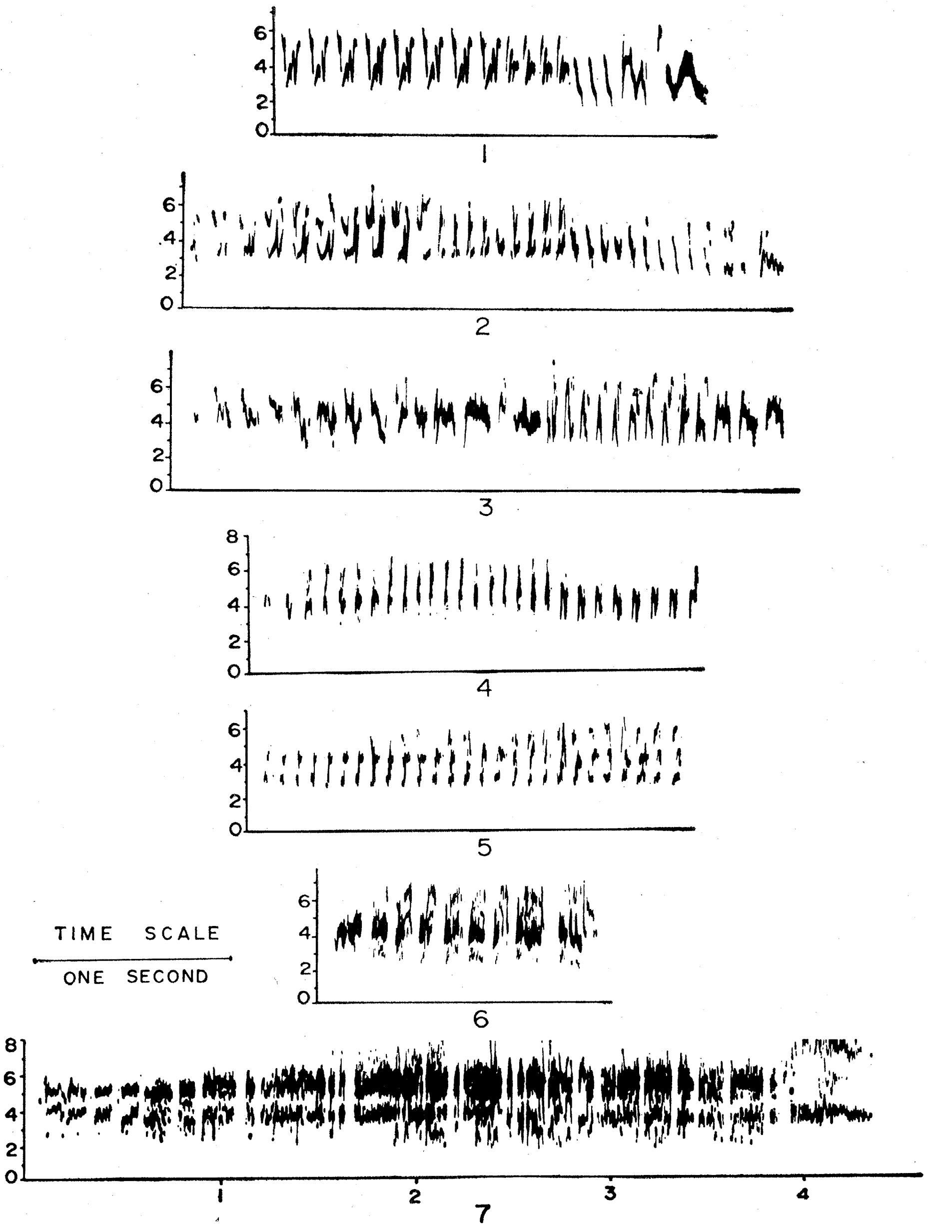

Fig. 2. Songs of male chaffinches deafened at different stages of vocal development. 1, Bird deafened as adult, after it had developed stable song; 2, 3, and 4, birds deafened in their first spring after they had been in "plastic" song stage for 12, 2, and 1 days, respectively; 5, bird deafened in the middle of its first winter, when 7 months old; 6, bird deafened at 107 days of age; 7, bird deafened at 88 days.

song developed under various experimental conditions seems to be fairly predictable. Thus, the relation between successive stages of vocal development must follow preset guidelines.

Establishment of a Song Memory

During its first 4 months of life—that is, during its first spring and summer—a wild chaffinch hears the song of adult conspecifics. If such a bird is trapped in the fall and kept in auditory isolation, in the following spring it will develop a close replica of a song pattern present in the area where it was born (*11*).

The imitation of a song model consists of two processes: (i) establishment of the memory of an auditory template; (ii) its conversion to a motor pattern. If the auditory template is to be matched by song development, hearing must remain intact (*15*).

Adult male chaffinches deafened after at least one full season of singing experience retain their song pattern with great fidelity. By contrast, the song patterns of a year-old male deafened when it had almost perfected its two song themes were not retained, but regressed in quality (*12*). This suggests that there are two stages in the development and stabilization of song—a transient memory, requiring auditory feedback for its maintenance, and later a permanent memory retained even in the absence of auditory feedback. Whether these memories are just an efferent program or an integration of output and proprioceptive feedback is not known.

Critical Period for Song Learning

The restriction of song learning to a certain period in the bird's life has already been described for several species. Some authors (*11*, *16*) have likened the "critical period" for song learning to the processes that occur during imprinting—the song is learned during a sensitive period; after the end of this sensitive period further acoustic stimuli do not alter the bird's repertoire.

It is not always clear, however, what *kind* of learning is restricted to the critical period. In at least two cases (*11*, *17*), the evidence presented only refers to an end in the observed capacity to acquire new motor patterns of song. In two other cases (*4*, *18*), the critical period refers specifically to the bird's ability to acquire the auditory information after which it will shape its own song.

In the chaffinch, the critical period for song learning is within the first 10 months of a potential lifespan of 5 or more years (*11*). After song is established in its final stereotyped pattern it will not change in subsequent years, nor will new themes be added to the repertoire. We know that this is not strictly age-dependent in the chaffinch. If onset of song, which depends on testosterone levels (*19*), is delayed by castration, the termination of the critical period for song learning is postponed. A 2-year-old bird which has had no singing experience, under the influence of testosterone will develop a good imitation of a tutor model (*20*). It is not known whether the end of song learning results from the establishment of a stable motor pattern, or whether it is determined by the accompanying high testosterone levels.

In other species (*4*, *18*) the end of the critical learning period occurs before the actual incidence of full song. Motor learning in these cases cannot be invoked as the immediate cause for the observed end of the critical period. It is conceivable, however, that even in these species postponement of the motor learning of song would result in recurrence of a "critical period" in successive years, under normally recurring hormonal conditions. Since acquisition of an auditory template and motor learning are distinct phenomena it seems possible that loss of plasticity of either of them would be determined by different variables.

A loss of the ability to acquire new vocalizations with increasing age is not an inescapable limitation of avian vocal systems. I had a gray African parrot, *Psittacus erithacus,* which at an age of 20 years was recorded, over a period of 1 year, producing over 100 different and recurrent vocalizations, which included imitations of other species, words, phrases, tunes, and mechanical sounds. At that age it was adding still new elements to its repertoire. Some cardueline birds (*21*) will modify on successive years their calls so as to match those of their mate or members of a flock.

Lateralization of Vocal Control

Over a century ago Hughlings Jackson introduced the idea of a leading hemisphere. "The two brains," he wrote, "cannot be mere duplicates if damage to one alone can make a man speechless. For those processes [of speech], of which there are none higher, there must surely be one side which is leading" (*22*). Lenneberg (*23*) adds that "only man has hemispheric dominance with lateralization of function and marked preference with respect to side in the use of limbs and sensory organs." The mention of sensory organs here refers to the superior recognition of words arriving at the right ear over conflicting stimuli presented to the left ear during dichotic tests (*24*). The fact that central lateralization of a behavioral performance was discovered in the human brain may have overshadowed the more general implications of this phenomenon. Recent work on the control of avian vocalizations is relevant here (*25*).

The syrinx is innervated bilaterally by the ramus descendens superior of the hypoglossus nerve and by a much smaller branch of the vagus (*7*). The hypoglossus provides motor input to the syrinx, as can be seen by stimulating this nerve after its central connections are severed. It probably also includes sensory fibers that carry proprioceptive information. Unfortunately there is no detailed account of the functional innervation of the syrinx.

Experimental evidence on the lateralization of vocal control in some birds is of the following nature. The roots of the hypoglossus nerve are cut unilaterally in adult chaffinches that have already established a stable song pattern, and the effects of this operation on singing performance are observed. When only the left hypoglossus is severed, either (i) the majority of song elements (for example, nine out of 12) disappears, so that their corresponding place in the song sequence is now vacant, while the remaining elements retain their structure and position within the song, or (ii) all components of song are highly modified so that their structure becomes that of short bursts of noise or very simple modulations (Fig. 3). If the operation is performed on the right hypoglossus, either the structure of song is not affected at all, or two or three of its simpler elements are lost (Fig. 4). These experiments involved 12 chaffinches, seven operated on the right side, five on the left. In each group there was a bird that had been deafened as an adult, before the hypoglossal operation; the deaf birds performed no differently from the others.

Up to 1 year after the hypoglossal operation, recovery of lost song elements had not occurred.

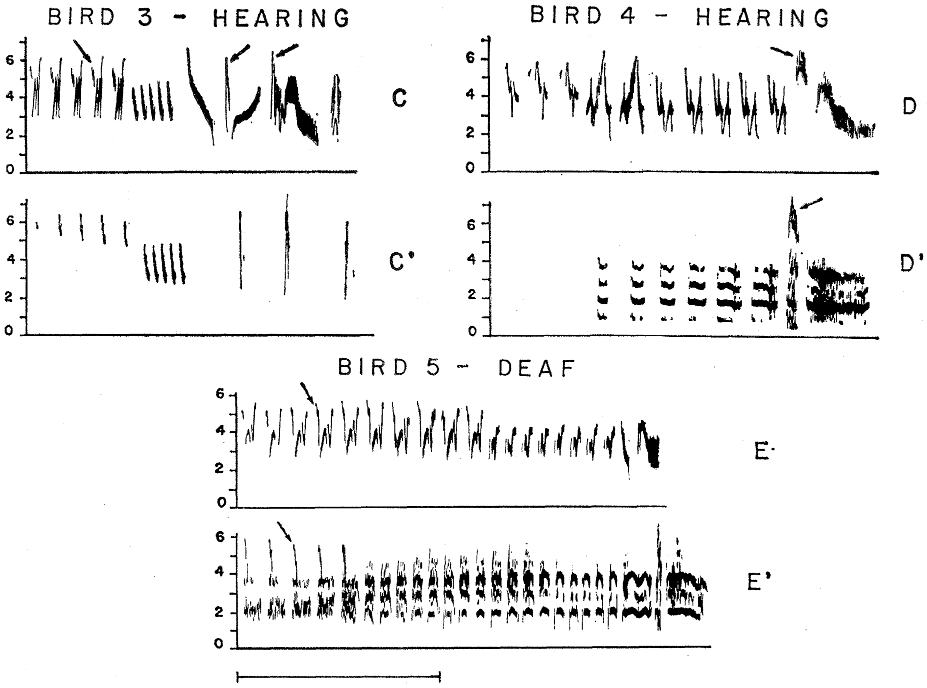

Fig. 3. Songs of three different birds which had had the left hypoglossus nerve severed. For each is shown its rendering of a particular theme (top) before and (bottom) after the operation. Arrows indicate elements retained intact after operation, when this is not obvious. One of these birds, No. 5, was deafened (song E) before its left hypoglossus was cut. Values on the ordinate indicate frequency (in kilohertz); the horizontal bar corresponds to 1 second.

The behavioral outcome of unilateral section of the hypoglossus in chaffinches is very different if the operation is performed before the bird has ever sung. Such a bird can develop the complete patern of a model song with only its left or its right hypoglossus intact (*26*). Clearly, hypoglossal lateralization over song control is not determined by peripheral restrictions.

These observations indicate that song learning in the chaffinch is lateralized at the hypoglossus. This lateral commitment occurs at the time song is learned as a motor skill. Before this learning takes place, lateral control can be shifted from what is usually the dominant side to the other side. We do not know to what extent, if at all, this lateralization is represented at higher centers of control.

If we assume that lateral dominance as described in the chaffinch extends to the cerebral hemispheres, we note some similarities between this phenomenon and its occurrence in humans (*23*). In adult humans a lesion to the speech area of the dominant hemisphere results in deterioration of vocal performance. However, if this lesion occurs early in life, the usually nondominant hemisphere is still capable of carrying on speech functions.

Reason for Lateralization

Kupfermann and Kandel (*27*) described the defensive-withdrawal reflex in *Aplysia*. This response involves the simultaneous participation of three organs and is controlled by five cells. These cells are always located in the left half of the abdominal ganglion of this mollusk.

Perhaps many kinds of integrated behaviors are under lateralized control. A behavioral sequence has to commence, and, unless it is rigidly programmed, it must incorporate a continuous decision-making process. Control of the commencement of behavior and decision making might be inefficient under equipotent and simultaneous bilateral representation. Yet, one may wonder why advanced nervous systems have not evolved medially placed decision-making structures, a position occupied by such neurosecretory tissues as the pineal and hypophysial glands. It may be fruitful to seek out functional asymmetries in nervous systems which, macroscopically at least, seem to be symmetrical. Even gross anatomical asymmetries of the temporal cortex and occipital horns have been described in the human brain (*28*). Perhaps the challenge is to find what kinds of tasks are under lateralized control. The few examples known from vertebrates all involve complex learned behaviors.

Adult Song: Feedback and Plasticity Reevaluated

To evaluate the correlation between the end of the critical period for song learning and the onset of irreversible lateralized dominance of vocal control, we must carefully question what vocal plasticity the bird retains after that time. Consider the following evidence.

Marler (*29*) noted that when territorial chaffinches engage in countersinging, those themes shared with other neighbors are the ones most frequently sung. Hinde (*30*) repeated this observation under experimental conditions. This suggests that, even after they have developed their full song, adult male chaffinches retain an auditory memory of what these patterns sound like, so that a particular stimulus affects the pattern that resembles it most.

We know that a chaffinch is capable of producing complete and normal songs with only right or left hypoglossal innervation to the syrinx. The fact that an adult male is unable to reintroduce song elements lost following destruction of its left or right hypoglossus cannot be attributed to mechanical inadequacy of the part of the vocal system that remains intact. Since we can assume that the auditory template remains unaltered and available, the adult bird's inability to reconstitute its own song after the operation may be attributed to a loss of motivation or to an end of motor plasticity for song learning.

The song of chaffinches deafened after they acquired their full song remains unchanged in its detailed structure even 3 years after the operation. Konishi (*15*) speculates that during song learning the bird may convert its auditory template into a proprioceptive template. This then could explain the accurate retention of song patterns in deaf adults. However, the persistence of some song elements while others are irreversibly lost after unilateral denervation of the syrinx suggests that song is not controlled by a dynamic relation between output and peripheral feedback involving the entirety of the song pattern. Alterations of auditory and proprioceptive feedback such as follow omission or distortion of some song elements (*31*) do not affect the remainder of song. These observations suggest that the chaffinch song may be laid down as a central pattern, its performance becoming independent of its own peripheral feedback.

Each spring, adult male chaffinches go through a series of stages—subsong, plastic song, full song—which is highly reminiscent of the performance of a 1-year-old bird learning to sing. One might be tempted to conclude that this recapitulation constitutes a relearning, so that the organism reverts to a plastic stage that allows it to acquire once more the song patterns of the previous year. Available evidence suggests this is not the case. Chaffinches deafened as adults go through these stages, once more to sing the themes they had acquired before they were deafened. Birds which in the previous year experienced unilateral denervation of the syrinx also traverse these stages, but are not able to recover elements lost as a result of the operation. Thus, this apparent recapitulation of ontogeny is not a reversal to an earlier plastic condition, but merely a reflection of increasing hormonal levels. The transition from subsong to full song can be elicited in adult chaffinches in midwinter by administration of exogenous testosterone. We may expect to find such processes of apparent learning in the vocal ontogeny of other species.

Phylogeny of Vocal Learning in Birds

The adults of most avian species produce rather predictable and stereotyped vocalizations. The way these patterns develop varies markedly among species. At least one other bird, the white-crowned sparrow, *Zonotrichia leucophrys*, acquires its song as the chaffinch does. Access to an external song model and to auditory feedback is necessary if the species-specific song is to develop (*1, 4, 15*). Conversely, the domestic fowl *Gallus domesticus* (*32*) and ring doves, *Streptopelia risoria* (*25*), develop all their typical calls even if they are deafened during their first days of life. Between these two extremes is the song sparrow, *Melospiza melodia* (*33*), which achieves normal song when reared in auditory isolation, though it needs auditory feedback to do this. Song sparrows can imitate in a facultative manner the song of conspecifics; domestic chickens and ring doves cannot.

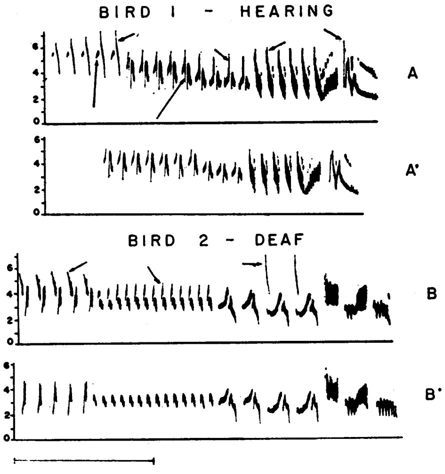

Fig. 4. Songs of two birds which had had the right hypoglossus nerve severed. For each bird is shown its rendering of a particular theme (top) before and (bottom) after the operation. Arrows indicate elements lost after the operation. Song B of bird 2 was sung after this bird had been deafened. Values on the ordinate indicate frequency (in kilohertz); the horizontal bar corresponds to 1 second.

Avian taxonomists consider that galliformes and columbiformes are closer in morphology and possibly in behavior to their ancestral stocks than are groups such as passeriformes and psittaciformes. If this is so, then vocal development in birds seems to show a phylogenetic trend from self-centered strategies to more open and environmentally dependent vocal ontogenies (*34*). In avian evolution this trend may have manifested itself at least three times, in passeriformes, psittaciformes, and hummingbirds. The evidence for the latter case comes from one species, Longuemare's hermit, *Phaethornis longyamarius,* and is still indirect. As reported by Snow (*35*), neighboring males on a display ground sing very close replicas of one theme, though there is considerable variability in the song of this species when sampled over a broad area. The suggestion is that, as young males occupy perches on the communal display ground, they adopt the song of other males displaying nearby.

Significance of Dialects

In the chaffinch (*36*), the white-crowned sparrow (*1, 4*), and a parrot species, *Amazona amazonica* (*25*), vocal learning has given rise to dialects. These known cases and preliminary data from another sparrow, *Zonotrichia capensis* (*37*), suggest that the shift from self-centered to environmentally dependent vocal ontogenies may have accompanied the quick expansion of new avian groups into varied and contiguous habitats. Advantages inherent in the formation of vocal dialects may have encouraged the overhaul of the genetic constraints on vocal development. This is suggested by the following example.

The song of *Zonotrichia capensis* remains relatively homogeneous over vast areas of pampas country in Argentina. Climatic changes over distance occur only very gradually in these monotonous flatlands. However, in places where the terrain rises a hundred meters or more, on mountainsides, or in the vast marshes of the Paraná delta, distinct dialects can be recognized by the unaided ear. Neighboring populations established on habitats with different climatic, edaphic, and vegetational characteristics sing in a different manner.

The possible evolutionary significance of these dialects is illustrated in white-crowned sparrows, *Zonotrichia leucophrys.* Males and females learn their dialect markers at an early age, before they have wandered far from their birthplace (*1, 4, 15*). This is so even though females of this species do not normally sing. If dialects play a role in an assortative mating system, as some evidence suggests (*38*), the flow of genes across the boundary between two dialect populations would be significantly reduced. This prediction, which is basic to the argument presented here, has yet to be tested. If dialects afford some degree of genetic isolation, they will encourage the emergence of locally adaptive traits, such as thresholds of tolerance to temperature, humidity, altitude, food items, diseases, and so forth. The role of avian dialects in microevolutionary processes would thus be considerable.

Is this a very roundabout way of ensuring genetic isolation? Would it be easier and more efficient to evolve isolating mechanisms under more strict genetic control? Probably not. The crowing patterns of inbred strains of *Gallus domesticus* show considerable variability (*39*). It is true that these strains were not selected for crowing performance. Yet, the suggestion is that even in rather homogeneous genetic stocks complex behavioral patterns vary significantly. The learning of a tradition would seem to offer a quicker way to achieve distinct and highly stereotyped song patterns.

An isolating mechanism transmitted by learning may permit the evolution of physiological step clines (*37*, *40*) without any necessary irrevocable commitment to actual speciation and subspeciation, although it also may lead to these extreme end products. In an environment of habitat mosaics subject to temporal and spatial fluctuation, it might be advantageous for any one population to avoid irreversible separation from its neighbors. Whereas genetic isolation of small populations may lead to high rates of extinction and even possibly to excessive inbreeding, differences in vocalizations are probably rarely insuperable barriers to breeding, and thus the microevolutionary process is kept more flexible and open.

Other Circumstances Favoring Plastic Vocal Ontogenies

Clearly, birds can achieve some degree of genetic isolation between populations by means other than the hypothetical role here attributed to dialects. Successive generations of a local population may show a very low dispersal rate (*41*), or a species may restrict its occurrence to a very narrowly defined niche. In either case dialects would seem to be redundant. Conversely, the formation of dialects need not be the only reason for the evolutionary trend from self-centered to environmentally dependent vocal ontogenies. Extreme developments of imitative ability may occur in tropical birds in which the main function of the song is to provide for social recognition and cohesion rather than territorial advertisement (*42*). Examples of this theory might be found in the shama bird, *Copsychus malabaricus* (*43*), in African shrikes of the genus *Laniarius* (*42*), and in the parrot *Amazona amazonica* (*25*). In all these species members of a pair engage in antiphonal duets. According to Thorpe and North (*42*), the evolution of imitative talents in these birds would have taken place to facilitate recognition between members of a pair. It is difficult to see why such a phenomenon should be restricted to the tropics. At least one of these species, *Amazona amazonica*, also has dialects. It is not known whether the other species also have dialects, and thus in their case the balance of selective forces leading toward vocal plasticity remains unclear.

What is clear is that a shift toward plastic vocal development in birds can occur even though the nature of the message conveyed by the vocalization itself is not radically new. The songs of *Zonotrichia leucophrys* and of *Gallus gallus* (*44*) are both used in territorial advertisement. Yet in the former the message is learned from conspecifics, whereas in the latter it develops without exposure to external models. Though the nature of the message is similar in these two species, in the case of the sparrow it conveys more information since it denotes the affiliation of the singer with a particular population.

Whatever the evolutionary pathway may have been, we should be aware that the change from a self-centered to an environmentally dependent vocal ontogeny must have taken place, presumably avoiding the confusion and information loss that might follow the loosening of genetic control over information patterns. Hopefully, a study of extant avian species will tell us how this transition occurred.

Of Birds and Primates: Questions We May Ask

A review of this kind raises more questions than it answers. It also suggests comparisons with other organisms, so that research strategies fruitfully employed with birds may yield relevant information elsewhere.

As an example, the existence of human dialects has been acknowledged over a broad spectrum of populations. The tendency has been to treat these dialects as concomitants of the social systems within which they evolved (*23*, *45*). Is it possible that they have played an active role in human evolution? As suggested for birds, might human dialects have influenced the emergence of local physiological adaptations? This possibility could be tested in extant primitive societies that, until recently, lived in ecological balance with their environment. That gene pools and dialects can be coextensive is suggested by observations on Australian aborigines. Birdsell (*45*) indicates that in these populations dialect tribes are the breeding unit. If his observations are confirmed and generalized, human dialects may emerge as forceful instruments in an assortative mating system.

Lenneberg (*23*) notes that the "incidence of 'language-learning-blocks' rapidly increases after puberty." This results in a "critical period" for the learning of language in humans which corresponds roughly to that of maximum familial dependence. With the onset of puberty and self-reliance, when the chances of an individual's wandering beyond the limits of its community are greatest, the ability to acquire new languages has diminished significantly. This is contrary to other expectations; one might argue that, at that age, man's vocal abilities have reached high proficiency. Might this be a cue to a hitherto unsuspected function of language—namely, that of hindering communication between communities that speak different languages or dialects?

Current speculation on the origin of human language associates its early beginnings with complex tools, complex societies, and the need to say novel things (*46*). We are ignorant about the early stages of human language, yet it is pertinent that, in other animals, plastic vocal ontogenies have arisen free from any association with such specific human needs. Quite obviously, the subsequent development of language, made possible by whichever circumstances determined the overhaul of prior genetic constraints, need bear no similarities to avian phenomena.

Avian data suggest that plastic vocal ontogenies evolved so that a bird could specifically address its mate or members of its community. One of the functions of these vocalizations is to bring individuals together. By contrast, there is no suggestion that the calls of monkeys and apes are given to attract females. No calls have been described that might be instrumental in establishing selective mating patterns, or that may determine who joins a social grouping (*47*). Perhaps this is one reason why the strategies of vocal ontogeny developed by some birds and by nonhuman primates are so different. The social and ecological contexts which have favored the evolution of plastic vocal ontogenies in birds have not acted upon the vocalizations of nonhuman primates. These apparent differences need confirmation by studies of the vocal ontogeny of hearing and deaf monkeys and apes.

Passeriformes (*3*) and parrots (*25*) traverse during their ontogeny a vocal state in which vocalizations of low volume and highly variable structure are rendered in rambling sequences. This stage has been labeled "subsong" (*48*). Human infants undergo a similar stage which has been called "babbling" (*23*). In both cases the sounds produced are spontaneous and seem to have no contextual significance. Marler (*1*) suggests that this kind of behavior constitutes an important step in the acquisition of the vocal practice which precedes vocal imitation.

Similar behavior is not reported for nonhuman primates, nor is it present in avian species such as domestic chicken and doves which do not exhibit auditorily guided vocal learning. In the chaffinch (*12*) normal subsong depends on auditory feedback, but deaf infants are credited with producing normal babbling sounds (*23*). However, the latter report is not based on analysis of sound spectrograms. It will be interesting to see if the occurrence of an early vocal stage such as subsong or babbling is in all cases associated with vocal learning. Can vocal learning occur in species which do not traverse such a stage, or in individuals where this stage is blocked?

Perspective

Present knowledge of avian ontogenies indicates that a shift from self-centered to environmentally dependent strategies occurred at least three times during avian evolution. Circumstantial evidence suggests that a strong selective force favoring this shift is an advantage associated with the formation of song dialects, though other social pressures that may have influenced this trend are not excluded. The very fact that self-centered vocal ontogenies gave rise to environmentally dependent ones suggests that physiologically these two strategies have more in common than one may surmise on the basis of available evidence. Some species, like the song sparrow, which need auditory feedback but do not require external models to establish normal song may possess characteristics of both kinds of development and thus may hold the key to the solution of this evolutionary riddle.

If dialects are to fulfill their role as population markers, indicating the affiliation of the individual with a particular gene pool, they must be acquired while the individual is still residing near its birthplace and in close association with members of its own population. This requires a "critical period" for vocal learning, at least insofar as it affects the acquisition of dialect characteristics.

Once the song dialect is learned, the position of the syrinx sets it free from interactions with environmental variables. Not only does the bird lose the ability to acquire new song patterns; it also loses the capacity to correct for auditory and proprioceptive distortions conveyed by its own pathways for sensory feedback. This is so for the chaffinch. Other species may retain their vocal plasticity through different stages of their life in accord with their social and ecological characteristics.

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