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BIRDSONG: FROM BEHAVIOR TO NEURON

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INTRODUCTION

The study of birdsong has made significant contributions to the development of modern ethology. Concepts such as species-specificity in animal signals, innate predisposition in learning, and sensory templates for motor development were put forth first in birdsong research (Marler 1957, 1964, Konishi 1965b, Hinde 1982). Also, it was the study of song development that elevated the much debated issue of instinct versus learning from the realm of semantic discourse and confusion to an experimentally tractable subject (Marler 1983).

The recent discovery of neural substrates for song has introduced a new dimension to the study of birdsong, making integration of behavioral and neurobiological studies feasible (Nottebohm et al 1976). Neurobiological concepts and methods are now directly applicable to this field. This integrated approach can address not only some of the outstanding issues that arose in behavioral studies and that are refractory to further behavioral analysis, but it also makes birdsong an attractive subject for the study of such basic issues as neural coding, learning, memory, developmental plasticity, and sensorimotor coordination. In this review I shall examine critically the major current issues and ideas in this field, placing special emphasis on the topics related to the development, learning, and neural control of song. Because extensive listings and reviews of recent literature on birdsongs are available (Kroodsma & Miller 1982a,b), the references cited are limited to those essential for the discussion of facts and theories on selected topics.

THE ETHOLOGY OF BIRDSONG

What is a Song?

A song is different from a call. Although the common usage "birdcall" includes song in nontechnical and old descriptions, the two types of vocalization are

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clearly distinguished in ornithological and ethological literature. The song is usually the longest and most elaborate of the vocalizations produced by a bird. In many species only sexually mature males sing during breeding season, but in some species females sing also. Song duration varies from about 2 sec, as in many species, to tens of seconds, as in those which deliver a series of brief sounds in bouts of seconds. The delivery of songs is periodic, especially in species with short songs. Many birds can sing as frequently as one song every 7 sec. Singing can occur spontaneously; an isolated bird starts and stops singing without any external stimulus. Songbirds usually choose fixed locations such as high perches in their territories for singing. A particular body posture accompanies singing.

All of the above attributes are lacking in calls. These are usually brief, simple sounds and occur neither spontaneously nor periodically but in response to a particular stimulus, such as the presence of predators and filial members. Calls involve neither the use of specific perches nor typical body posture.

Although crowing of roosters and cooing of doves are perhaps functionally equivalent to the song of songbirds, the term, "birdsong," is reserved for the song of passerine (perching) birds. This review deals mainly with the study of passerine songs, for most of the interesting issues and ideas in this field concern them.

Acoustic Structure and Terminology of Song

Song consists of a series of sounds with silent intervals between them (Figure 1). The most elementary unit of song appears as a continuous marking on a soundspectrogram. This is called a "note" or an "element." The acoustic structure of a note can vary from a steady narrow-band sound to a complex frequency- and amplitude-modulated sound. Two or more notes may group together to form a "syllable." In some cases notes and syllables are identical, i.e. one-note syllables, which are classified as syllables because they are spaced

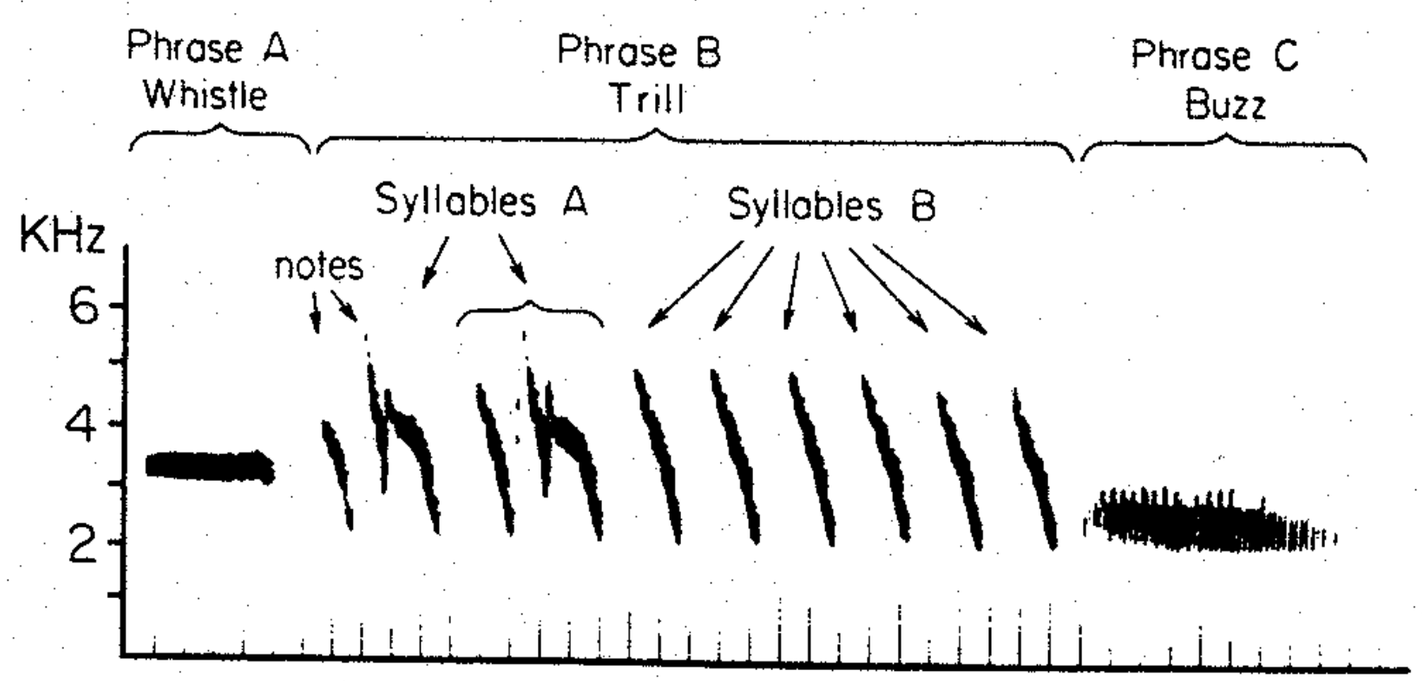


Figure 1 The terminology of birdsong. The time-frequency soundspectrogram of a white-crowned sparrow's song shows how its component sounds and their groupings are named. The ordinate and abscissa are frequency in kilohertz and time in 50 msec per division, respectively.

like multinote syllables. The component notes and their spacing characterize the structure of a syllable. Syllables are often grouped together to form a "phrase," which may contain a series of identical or different syllables. Phrases consisting of one syllable or note also occur and are identified as such by their positions in the temporal structure of song. Many birds deliver several different phrases in a fixed sequence as a unit, which is the song. Birds like mockingbirds and thrushes produce syllables in groups and in fixed or variable sequences. Completely random sequencing of phrases and syllables seldom occurs. The rules of timing and sequencing of phrases and syllables are called the syntactical rules and are usually unique to a species.

Song Repertoire

The whole set of different song types sung by a bird is called its song repertoire. Its size ranges from one, as in the white-crowned sparrow (*Zonotrichia leucophrys*), to several hundreds, as in the winter wren (*Troglodytes troglodytes*) (Kroodsma 1980). The term, "syllable repertoire," applies to those birds which deliver syllables in a continuous series instead of in a short song. Good singers usually have large syllable repertoires; for example, a brown thrasher (*Toxostomia rufum*) may have as many as 2000 syllables (Kroodsma & Parker 1977).

Species-Specificity, Dialects, and Individual Differences

Each species of bird has a unique song or songs. This rule applies both to birds with a single song type and to those with a large song repertoire (Figure 2). In many species, songs are so specific that naturalists can use them to identify birds of a single species from widely separate areas such as the East and West coasts of North America. Song sparrows (*Zonotrichia melodia*), mockingbirds (*Mimus polyglottos*), American robins (*Turdus migratorius*), and chipping sparrows (*Spizella passerina*), to name a few, can be identified by their songs anywhere in North America. However, in addition to universal features, many songs show distinct geographical variations, known as "song dialects" (Figure 3) (Marler & Tamura 1962, Baptista 1975, Mundinger 1982). These dialects are transmitted culturally: Young birds or even adult birds of some species copy the songs of their birthplace or neighbors. Song dialects are usually stable: In one of the most carefully studied species, dialects unique to small restricted areas persisted for at least 12–15 years, well beyond the life span of marked individuals (Payne et al 1981).

Birdsongs show individual differences as well as universal and local features. For example, in Oregon juncos (*Junco oreganus*) and swamp sparrows (*Zonotrichia georgiana*), all songs consist of a trill, hence a universal feature, but the syllables making up the trill vary among individuals (cf Figure 7) (Konishi 1964, Marler & Peters 1982c).

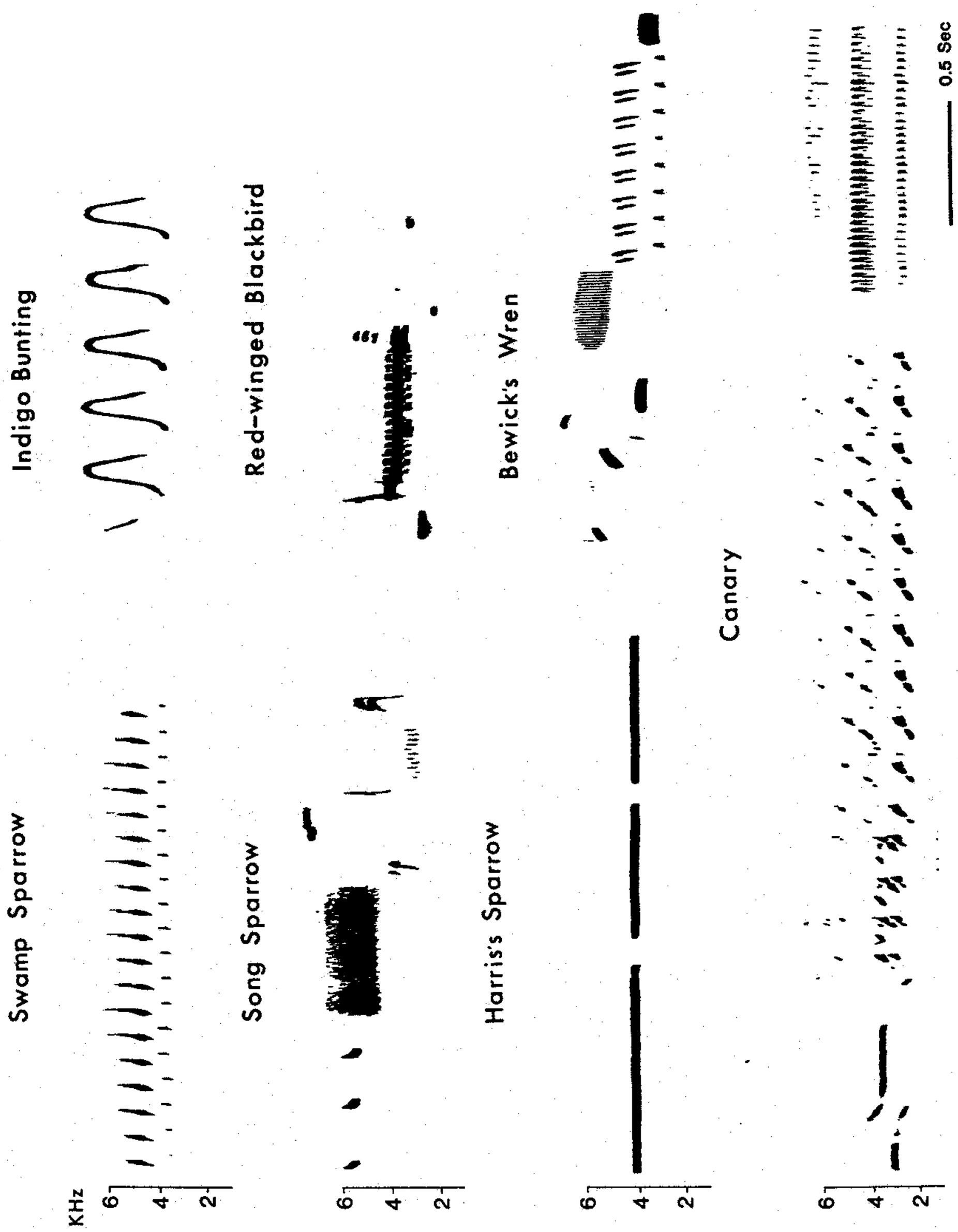


Figure 2 The diversity of birdsong. Each species has a unique song or songs. The number of songs or syllables per individual varies greatly from species to species. Most of the species in this figure sing more than one song type. Some birds sing short songs and others long series of syllables. The canary belongs to the latter group and a short segment of its song is shown here.

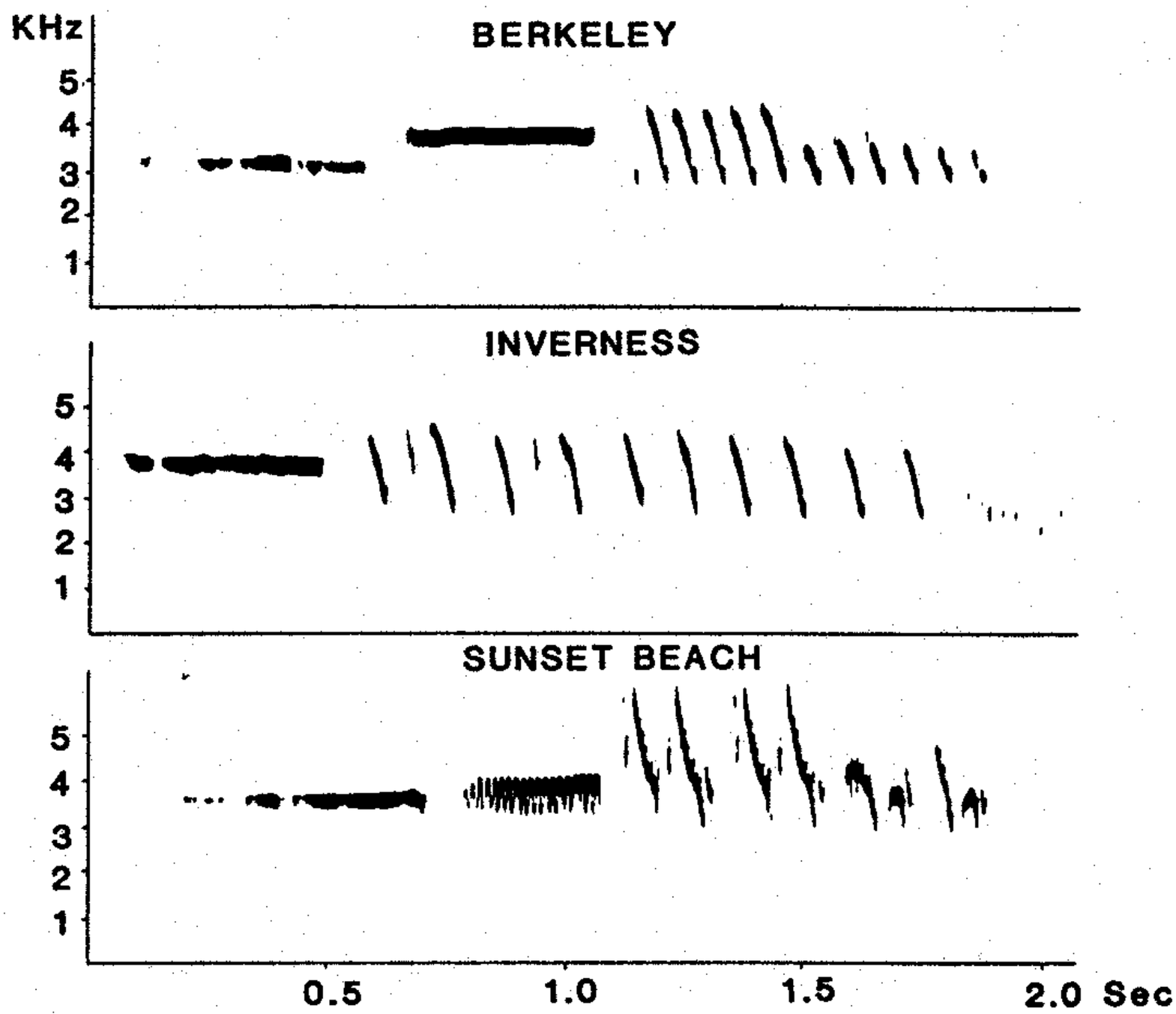


Figure 3 Song dialects. Songs of white-crowned sparrows from three different locations in coastal California. Song dialects are transmitted culturally from generation to generation and they persist for many years (from Konishi 1965b).

Songs as Social Signals

Birds sing to communicate. To a female the song may signal the presence of a potential mate, his species and individual identity, his location, his ownership of territory, his readiness to breed, and perhaps his potential as a provider for his offspring. To a male the song may convey different information, such as "neighbor" versus "stranger," in addition to species and other messages (Marler 1961).

Experimental and comparative observations are used for the study of the message contents of songs. In the experimental approach the receiver's response is the only clue to the messages conveyed by a song. If a song can carry more than one message, whether or not the receiver's response allows discrimination between different messages is a crucial question. Species identity is the message that can be most easily recognized in a song. Breeding male songbirds stake out and defend an area against male intruders of their own species. Song is one of the clues they use to recognize other males and it is thought to advertise the ownership of territories. Territorial males react to playback of recorded songs by counter-singing, aggressive display, and approach or avoidance of the speaker. Although many experiments demonstrate the bird's ability to discriminate between conspecific and alien songs, they do not prove the

advertising role of songs. However, recent studies seem to demonstrate this role: Broadcasting recorded song prevents new males from trespassing and occupying vacant territories, which would otherwise be rapidly claimed (Krebs et al 1978, Yasukawa 1981).

Although the effects of male vocal signals on the behavior and reproductive physiology of female birds are well documented in some birds (e.g. Brockway 1969), what a song means to a female songbird is not well understood. In contrast to territorial males, female birds seldom show any overt response to song playback. However, as in female frogs, female indigobirds (*Vidua chalybeata*) in breeding condition approach a loudspeaker emitting the song of their own species (Payne 1973). Breeding condition brought about by manipulation of photoperiod or by injection of estrogen induces female birds to show precopulatory behavior in response to the conspecific song in white-crowned sparrows (*Zonotrichia leucophrys*) (Baker et al 1981), cowbirds (*Molothrus ater*) (West et al 1979), and swamp sparrows (Searcy et al 1981). Thus, female songbirds are selective for the songs of their own species.

The capacity for multiple song types is one of the most intriguing attributes of birds (Krebs & Kroodsma 1980). Are the songs redundant or do they have different functions? When a bird has 300 song types, as does the winter wren, their functional separation would seem unrealistic. For birds with smaller repertoires there is some indication that different song types serve different purposes, such as territorial advertisement and mate attraction (Catchpole 1983). However, such functional separation seems to be rare, although the lack of methods sensitive enough to detect it may be the main reason for this rarity. If several song types of a bird serve the same function, say, territorial advertisement, the advantage of such a scheme is an interesting issue for sociobiologists. One imaginative explanation is the Beau Geste hypothesis, which assumes, first, that territorial settlers avoid an area occupied by many individuals and, second, that many songs from an individual deceive intruders in their assessment of population density (Krebs 1977). Experiments in which small or large song repertoires were broadcast in vacant territories showed that large repertoires were more effective than small repertoires in preventing potential intruders from trespassing the territories (Krebs et al 1978, Yasukawa 1981). Despite these observations, there is no reason to believe that birds avoid a high density area or remain deceived by multiple song types for any length of time, although any deterrent effects of song that increases a bird's inclusive fitness can make a difference in evolutionary time.

Another explanation for a large song repertoire uses the concept of sexual selection: If males with larger song repertoires leave more offspring than those with smaller repertoires, the frequency of genes for large repertoires should increase. The effects of sexual selection should be much more pronounced in polygynous (many females for one male) species than in monogamous species.

This prediction seems to be true of some cases but not of others; among North American wrens, polygynous species tend to have larger song repertoires than monogamous species (Kroodsma 1977b). On the other hand, many monogamous species sing more than one song type. One of the problems in the comparative approach is its inability to distinguish cause and effect from indirect correlations. For example, in indigobirds the amount of singing, and not song repertoire, is positively correlated with mating success (Payne & Payne 1977). In the great tit (*Parus major*), although song repertoires do not influence the female's choice of mates, males with intermediate or large repertoires "are more likely to father offspring which survive to breed than males with fewer song types." Also, "males with larger repertoires produce heavier fledglings, and this may be related to territory quality" (McGregor et al 1981). The significance of song repertoires was also studied in a laboratory experiment, which avoided the difficulty of establishing a direct correlation in the field. Two groups of virgin female canaries were exposed either to a tape-recorded song made of five syllable types chosen from normal canary songs or to one made of 35 syllable types. The group that heard the more elaborate song built nests faster and laid more eggs than the other group. One interpretation of these results is that the elaborate song stimulated the females reproductive behavior more than the less elaborate song. Another interpretation is that the females responded better to the more familiar song consisting of 35 syllable types, as in the normal song, than to an unusual song containing only 5 syllable types (Kroodsma 1976). A control for the familiarity problem would be to use females that have never heard normal canary songs.

How Songs Encode Species-Specificity

A song contains many potential acoustic cues for encoding messages. Because the response of males to their species song is easy to observe and measure, most studies have addressed the encoding of species-specificity in the territorial context. The methods consisted mainly of comparing birds' responses to songs in which various properties were deleted, added, or altered. A few obvious generalizations follow from these studies:

1. Song properties common to all individuals serve in species recognition, but not all common properties are used by the birds for species recognition.
2. A small number (two to three) of song properties are usually sufficient for species recognition.
3. Different cues may be additive or redundant.
4. Different species may use different aspects of song for species recognition.

The physical properties of songs should allow certain predictions to be made about the potential cues available to the birds. Many birdsongs are composed of tonal sounds containing energy in discrete frequency bands, although noises

occur in the songs of some species (cf Figure 2). In tonal songs, changes in frequency or amplitude as a function of time are potential cues. Frequency and amplitude modulations occur together or separately both within and between phrases, syllables, or notes. Syllable or note structure is important for species recognition in birds with simple trill type songs in which frequency modulation occurs only within the syllable or note; examples are swamp sparrows (Peters et al 1980), indigo buntings (*Passerina cyanea*) (Shiovitz 1975), and firecrests (*Regulus ignicapillus*) (Becker 1976). Many species sing songs in which the frequency changes between phrases or syllables. This feature is important for species recognition in European robins (*Erithacus rubecula*) (Bremond 1968), white-throated sparrows (*Zonotrichia albicollis*) (Falls 1963), and goldcrests (*Regulus regulus*) (Becker 1976), for example. The alternating pattern of sounds and silent intervals, a type of amplitude modulation, is used by some birds for species recognition, for example, ovenbirds (*Seiurus aurocapillus*) (Falls 1963), indigo buntings (Emlen 1972), song sparrows (Peters et al 1980), and red-winged blackbirds (*Agelaius phoeniceus*) (Brenowitz 1983). However, when a song contains all of the above properties, it is difficult to predict which of the properties encodes species-specificity.

Despite studies such as those cited above, the acoustical properties of song that encode species-specificity are much better defined in frogs and orthopterans than in songbirds (e.g. Capranica 1966, Gerhardt 1978, von Helversen 1971, Walker 1957). The use of purely synthetic songs in playback experiments is largely responsible for the success in the frog and insect studies. The development of methods to analyze, synthesize, and modify birdsongs rapidly will promise to elevate the level of analysis from simple rearrangement of natural song components to the testing of synthetic songs with precisely defined acoustical properties (cf Margoliash 1983). This approach, in turn, may lead to the discovery of general principles of coding.

Another problem that confounds the study of song recognition is learning; unlike frogs and insects, birds learn not only to sing but also to recognize their species song. In the species studied so far, the abnormal songs of birds raised in isolation elicited no response in territorial males (Shiovitz 1975). Also, birds can recognize different dialects and the songs of different individuals (Emlen 1971, Brooks & Falls 1975). These facts point to the importance of learning in song recognition by adult birds. If different individuals learn to use different sets of cues, finding common cues becomes difficult. Thus, the apparent lack of general rules of coding may well be due to learning.

THE ONTOGENY OF SONG

An animal's ability to select a complex stimulus or to produce a specific movement does not appear suddenly in adulthood but develops gradually. How

it develops has been one of the central issues in ethology and psychology. The plasticity of song development has been known since ancient times in the Orient. The Japanese zoologist Tamiji Kawamura (1947) wrote, in his book *Science of Birdsong,* how well bird fanciers in old Japan knew about the characteristics of song development. Such properties as the impressionable phase of song learning, the effects of tutoring, subsong, imitation, song dialects, and species differences in these attributes were well known to them. Kawamura pointed out that birdsongs would offer unique opportunities to address psychological issues, particularly behavioral development. Otto Koehler (1951) in Freiburg, Germany and William Thorpe (1954, 1961) in Cambridge, England were the first to study song development under controlled laboratory conditions. Thorpe was the first to use the tape recorder and soundspectrograph in the study of song development. The questions he asked and the methods he used were adopted by many subsequent workers in this field.

Stages of Song Development

Few behaviors show developmental changes more graphically than birdsongs. The stereotyped song of an adult bird, which is called "full song," develops in several stages. The methods of study involve tracking distinct acoustic patterns in the full song from earlier stages of song development. Song development may begin with the calls of the nestling, but an objective study of this stage has not been made. There may be a long period of reduced vocal activity between the fledgling and juvenile stages. Juvenile birds start vocalizing more frequently and persistently in their first autumn when they are three to four months of age. They do not yet assume the typical singing posture of the adult, and their vocalization, termed "subsong," consists of a rambling series of sounds. Subsong tends to be longer and more variable, and its frequency range is wider and more variable, than those of full song. Some of the sounds of subsong gradually become discrete and recurrent as the birds begin to vocalize more loudly and assume the typical singing posture more frequently. The basic organization of the species song is clearly recognizable at this stage, although the syllables and song duration may still be somewhat variable. The transition from the plastic song to the full song stage usually occurs rapidly. The structure of syllables, the sequence of phrases, and the duration of song all become fixed or "crystallize" to the level of full song. Once a song is crystallized, it recurs unchanged in subsequent years in most birds.

Overproduction and Attrition of Syllables

Song development, at least in some species, is not a steady progression from precursor sounds to crystallized syllables. For example, young swamp sparrows, during their plastic song stage, produce syllable types that are never used in their final songs. These syllables simply disappear before the final

stage of song crystallization (Marler & Peters 1982a,b). Although the phenomenon of overproduction and attrition of syllables has been studied closely only in one species, it may be universal (e.g. red-winged blackbirds, Marler et al. 1972, white-crowned sparrows, Marler 1970; nightingales, Todt & Hultsch 1985). Kawamura (1947) described "attrition" and "unused songs" during song development in white-eyes (*Zosteropus palpebosa*) and Japanese meadow buntings (*Emberiza cioides*). Birds tutored with alien songs sometimes produce good copies of the alien syllables during the subsong or plastic song stage, but abandon or modify the sounds by the time of song crystallization (Thorpe 1961, M. Konishi and E. Akutagawa, unpublished).

Why do birds overproduce syllables? It may be a method by which birds review and calibrate their vocal repertoires, because they cannot know what sounds they can produce before they vocalize. Birds must first try to produce various sound patterns and select those which satisfy the criteria set by genetical and experiential influences. Birds seem to develop song by modifying and selecting sounds as they produce them. Instructional and selectional processes appear to occur in series as well as in parallel at several levels of song organization. This strategy is largely responsible for the plasticity of song development.

Theory of Song Learning: An Overview

The synonymous use of "song learning" and "song development" has caused some confusion in birdsong research. A bird's use of auditory feedback in song development resembles learning by trial and error; the bird corrects errors in vocal output until it matches the intended pattern. Because feedback control of voice is essential for song development with or without a tutor model, song development inevitably contains some element of learning. However, it is useful to distinguish development from learning, because some normal features of song develop without auditory feedback in some species (Guettinger 1981, Konishi 1965a, Marler & Sherman 1982). For this reason I shall refer to copying of song as "song imitation" instead of "song learning." The term "song learning" refers explicitly to song development by auditory feedback control of voice. "Song development" will be used only in a descriptive sense.

Song imitation consists of sensory and sensorimotor stages. Birds are predisposed to learn the song of their own species. They must hear an acceptable song during a period in their youth, and they commit the song to memory without vocally reproducing it. This period will be referred to as the "impressionable phase." During the sensorimotor stage birds must hear themselves vocalize in order to match vocal output with the memory trace of the tutor song. Thus, the song memory is used like a template (cf Figure 12). When birds develop song without any song tutor, they use an innate template or an internal reference for the control of voice by auditory feedback. The innate

template explains the differences between the songs of birds raised in acoustic isolation and those of birds deafened in youth (Konishi 1965b).

What is an Innate Song?

All songbirds studied so far, when raised in acoustic isolation, develop songs lacking some or most of the characteristics of their wild-type song (Figure 4). These birds are called "isolates" and their songs "isolate songs." Isolate songs are sometimes referred to as "innate songs." Interspecific differences in isolate songs are likely to be due to genetic differences between species. The source of instruction for isolate songs must be internal, because the bird hears no song to copy. These reasons justify the definition of an innate song as above. However, this practice of naming innate songs creates an interesting logical dilemma, when one considers how song learning is defined. As pointed out above, auditory feedback control of voice is regarded as learning. Because the development of innate songs requires auditory feedback, the innate songs are learned! By this logic only the sound patterns that develop without auditory feedback can be called innate.

Normal songs seldom develop in acoustic isolation, but some aspects of the song develop more normally than others. The frequency range, tonal quality, and duration of song tend to be least affected by isolation. The first two attributes are perhaps due to the properties of the vocal organ, the syrinx, itself. Also, syntactical rules of song seem less affected by isolation, because some of them are evident in isolate songs of many species. Moreover, in some species the syntactical rules resist tutoring and even interspecific hybridiza-

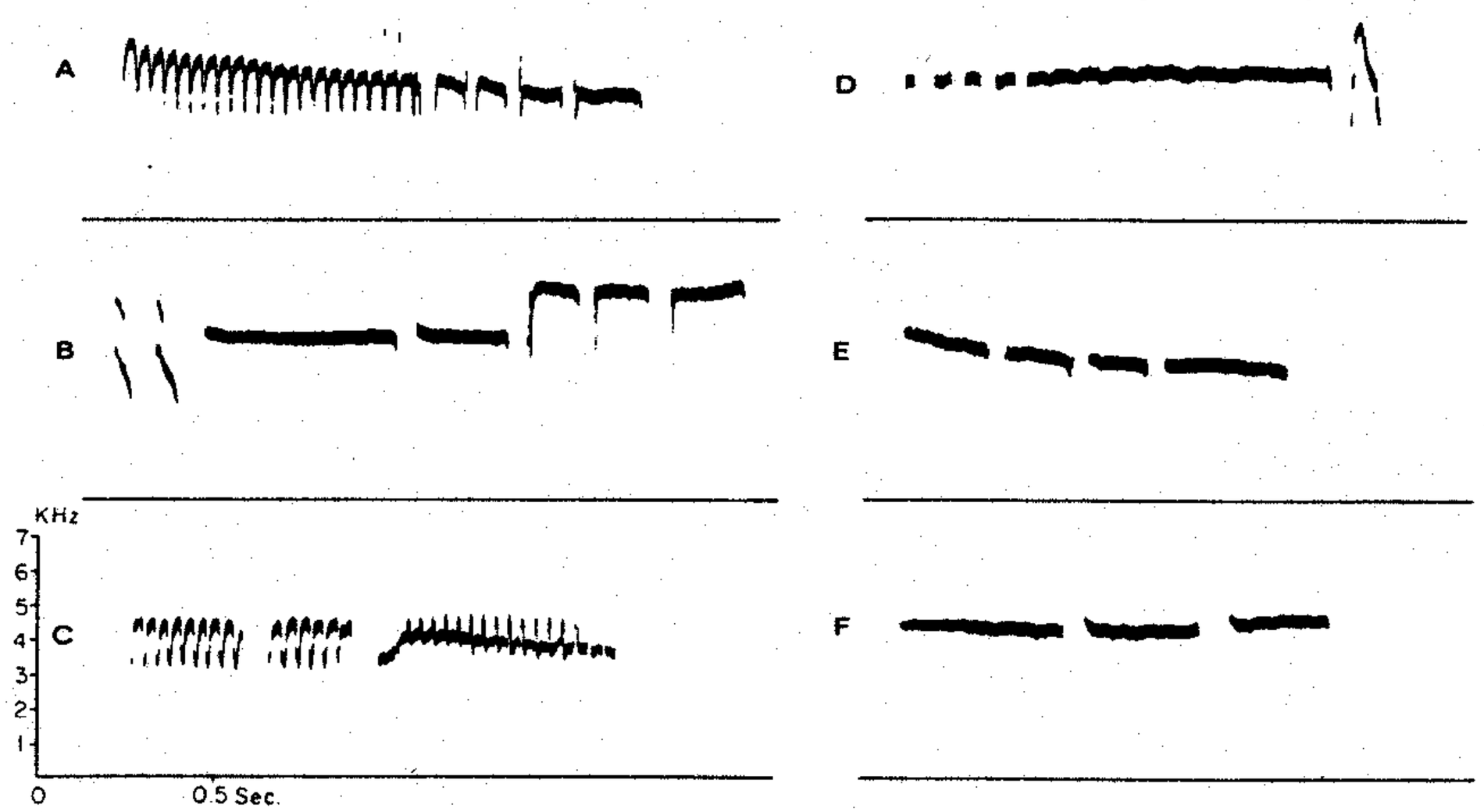


Figure 4 Isolate songs. Normal songs seldom develop in birds raised in acoustic isolation. Their songs lack some or most of the features typical of the wild-type song, as exemplified here by the songs of two white-crowned sparrows that grew up in acoustic isolation from the egg (*A*,*B*). Also, birds that failed to copy a tutor song develop isolate-like songs (*C*–*F*) (from Konishi 1978).

tion. For example, in cross-fostering experiments, a greenfinch (*Chloris chloris*) raised by canaries sang canary syllables, not by the canary rules, but by the greenfinch rules (Guettinger 1979). Hybrids between canaries and greenfinches sang syllables by the rules of the maternal species, which they could not copy from their nonsinging mothers (Guettinger et al 1978). On the other hand, isolate syllables generally contain simpler patterns of frequency modulation than those found in the wild-type song.

Song Imitation

Bird fanciers in old Japan paid fees to have young birds tutored by prize-winning singers. Both captive and wild birds served as tutors. A person would erect a small hut near a skylark singing "good" song, in order to charge admission for tutoring. If older pupils started to chirp while younger pupils were listening quietly, the chirpers were immediately removed for fear that younger pupils would learn bad sounds (Kawamura 1947). Although vocal mimicry by some wild birds such as mockingbirds and starlings (*Sturnus vulgaris*) was well known, imitation of the species' own song as a method for normal song development was not widely appreciated by professional ornithologists. Sharing of songs or syllables among birds living in close proximity, i.e. a song dialect, was considered a sign of imitation. Isolation experiments suggested the need for imitation in normal song development, but more rigorous evidence came from tests with song playback (Thorpe 1958, 1961). When young birds heard normal songs broadcast to their isolation chambers, they developed normal songs as adults, indicating that exposure to appropriate song alone can sustain normal song development.

Although many birds can imitate all characteristics of a tutor song, some rules seem to govern song imitation. As mentioned above, the syntactical rules tend to be refractory to modification by imitation. Notes in a syllable or syllables in a phrase are theoretically separable entities, yet birds usually copy a syllable or phrase as a unit. During the plastic song stage, song sparrows and swamp sparrows rearrange copied syllables without breaking them up into their component notes (Marler & Peters 1982a). Nightingales combine syllables and phrases from different tutor songs to produce new songs in addition to straight copying (Todt & Hultsch 1985).

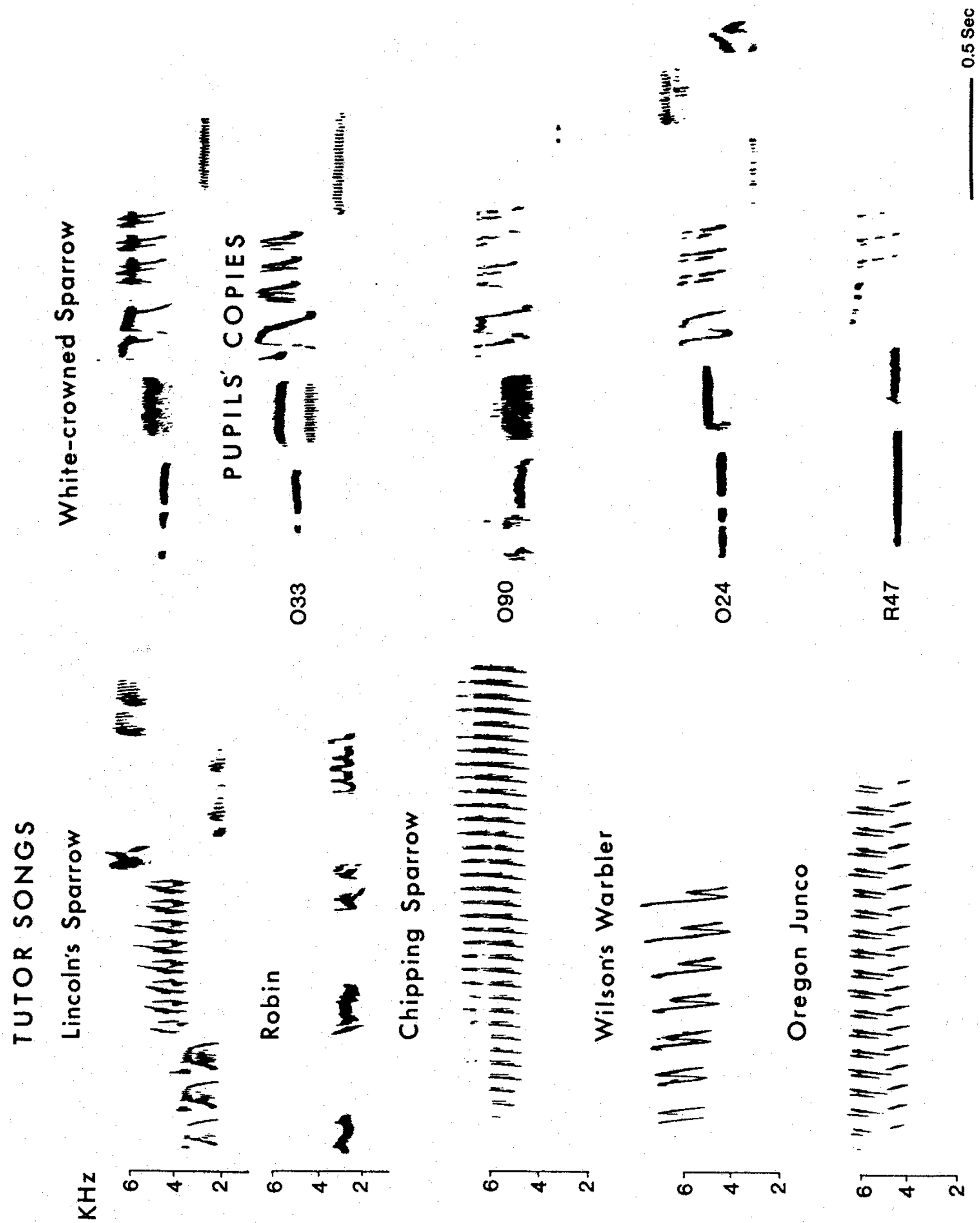
The amount of playback necessary for copying a tutor song has not been systematically studied. It may be surprisingly small, as in the following examples. Nightingales copied a sequence of 60 different songs broadcast once per day for 20 days from a loudspeaker placed next to a silent nightingale (Todt & Hultsch 1985). Two white-crowned sparrows imitated a recorded song after exposure to it for 20 and 21 days, respectively (Marler 1970). Similarly, young swamp sparrows tutored with a recorded song for ten days reproduced the song as adults (cited in Kroodsma 1982).

The methods and conditions of tutoring greatly affect the outcome of an experiment. Training birds singly or in a group, the choice of live or tape-recorded tutors, social relationship between tutors and pupils, different photoperiods, and daily rhythm affect the success of tutoring. Birds that seldom copy even conspecific songs from playback are said to imitate live tutors (Baptista & Petrinovich 1984, Kroodsma 1982, Rice & Thompson 1968, Payne 1981). The nightingale experiment cited above shows clearly that visual cues provided by a live bird are an important factor in song imitation. The young birds that could see the caged bird during tape playback copied the tutor songs more accurately than did those prevented from seeing the live bird (Todt & Hultsch 1985). Thus, live tutors can have profound effects on various aspects of song imitation, including song preference, the accuracy of copying, the impressionable phase, and the rate of song development. The effects of live tutors on these aspects are reviewed in appropriate sections below.

Innate Preference for the Species' Own Song

Bird fanciers in old Japan looked down upon birds that incorporated the songs of other species during a singing competition (Kawamura 1947). Most species studied so far copy the song of their own species in a choice situation. Tape playback allows song preference to be tested under standardized conditions. The rate, duration, and intensity of playback can be made equal or similar for different songs to be presented. Thorpe (1958, 1961), using the chaffinch (*Fringilla coelebs*), was the first to show song preference by the tape playback method. Most experiments in this field used birds collected in the wild as nestlings that had presumably heard their fathers and other adults sing. Although five- to ten-day-old nestlings do not copy songs, hearing them might have general effects on the birds such that it biases the future choice of songs. This uncertainty was overcome by the use of canaries as foster parents to raise wild birds from the egg. Swamp sparrows raised in this manner copied the songs of their own species when tutored with both swamp and song sparrow songs (Marler & Peters 1977). White-crowned sparrows also show a preference for their own species' song. However, contrary to the earlier conclusion that white-crowned sparrows reject alien songs whether these are presented alone or with a conspecific song (Marler 1970), birds raised from the egg in isolation imitated alien songs or produced modified versions of them, either in addition to copying the conspecific song in a choice situation or in a no-choice situation involving only alien songs (Figure 5B). Nevertheless, in a choice situation, birds always copied the conspecific song, and when they imitated alien songs in addition, the imitations were seldom as complete and accurate as those of the conspecific model (Figure 5A) (M. Konishi and E. Akutagawa, unpublished).

These and other experiments indicate that young birds must be able to recognize the song of their own species solely by the particular acoustical


TUTOR SONGS
Lincoln's Sparrow
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Chipping Sparrow
Wilson's Warbler
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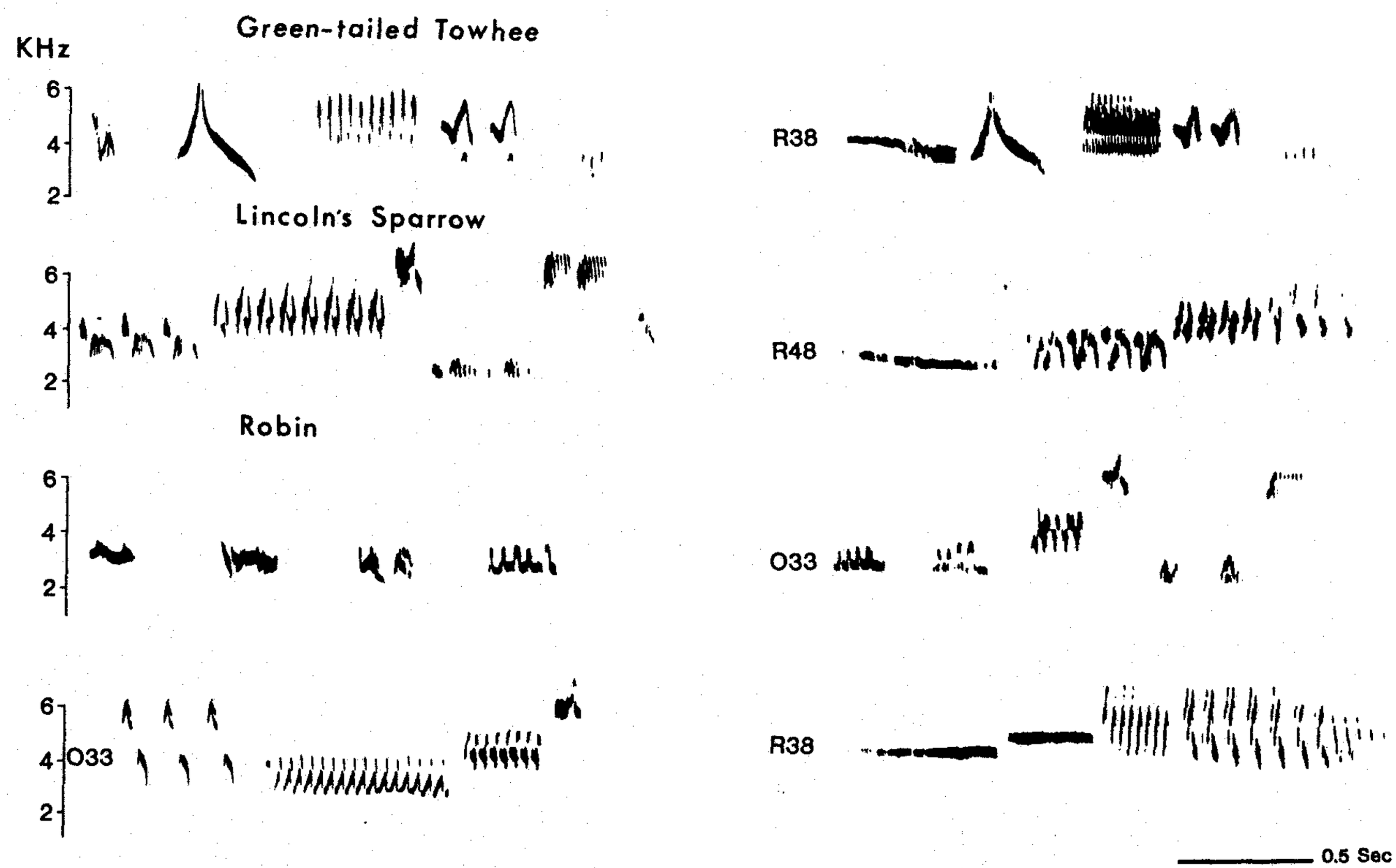

Figure 5 *A:* An innate predisposition in song imitation. All four white-crowned sparrows raised in acoustic isolation from the egg selected the song of their own species over the songs of five sympatric species. *B:* Two other birds (R38 and R48) that were given only the five alien songs produced songs resembling one of the tutor songs, Lincoln's sparrow song in the case of R48 and green-tailed towhee song (used as a substitute for Lincoln's sparrow song) in the case of R38. Unlike wild white-crowned sparrows, some of the hand-raised birds sang more than one song type, for example, O33 produced two different song types in addition to a copy of the conspecific model and R38 sang two types. The copies of alien songs are less accurate than those of the conspecific song, because white-crowns tend to produce songs conforming to the species' syntactical rules by adding to or modifying alien sounds. Notice that the songs of R38 and R48 contain an introductory whistle, which the birds could not have copied from any of the tutor songs. Unlike isolates, tutored white-crowns compose new song types by copying, improvising, and inventing, especially when they are exposed to more than one tutor song (e.g. O33 *right* and *left bottom* and R38 *right bottom*).

cues contained in it. The existing data allow few generalizations to be made about cues in song imitation; they seem to be present at all levels of song organization. In theory, a song may be acceptable because it contains particular sound patterns or because it lacks unacceptable sounds. Some parts of the song may be more important than others and different cues may play different roles in song recognition in the context of song imitation. For instance, a particular sound may promote the copying of other sounds that accompany it (Marler 1984).

Rearrangement of natural song components has been the main method used for the study of selective song imitation. Swamp and song sparrows sing different types of song often within earshot of each other (cf Figure 2). When young birds of these species were tutored with songs containing combinations of features of the two species, the young swamp sparrows selectively copied songs containing syllables from their own species' songs irrespective of their temporal arrangement (Marler & Peters 1977, 1982a). Interestingly, swamp sparrows would copy song sparrow notes and syllables, if these were embedded in a series of swamp sparrow syllables, indicating that a certain cue can induce the birds to copy normally unacceptable sounds. For young song sparrows, either the syllabic structure or the temporal pattern of song seems to serve as a cue for the recognition of the species song. Thus, young song sparrows copied a song composed of swamp sparrow syllables that were arranged in the song sparrow's temporal pattern. They would also copy a song containing song sparrow syllables arranged in the temporal pattern of the swamp sparrow song, but not a song in which swamp sparrow syllables were arranged in the swamp sparrow's temporal pattern.

A bird's ability to select its own species' song led to the hypothesis that each species has a "blueprint" of its song (Thorpe 1961). This concept became equated with that of an innate template, which was developed in another context, as discussed below. The blueprint concept implies a perceptual device. Song selectivity may be due to one such central mechanism or it may be attributable to a combination of different factors, such as auditory and motor constraints, that may be present both in the periphery and in the brain. Because a bird can produce a wide range of sound patterns, song selectivity due to motor constraints is considered unlikely. However, these factors cannot be completely excluded, because, for instance, when white-crowned sparrows copy synthetic songs that sound mechanical to the human ear, they do not sing in mechanical voice but in the voice of their normal song (M. Konishi and E. Akutagawa, unpublished). This is one aspect of motor constraints contributing to the outcome of song imitation. Other constraints might be operative at other levels of song organization. Another problem is the question of which pattern is easier or harder to sing; this cannot be easily answered. Song imitation is assessed by motor performance; i.e. imitation is said to have occurred if the

bird produces a copy of the tutor song. If the bird does not produce a copy, it is difficult to assess at which stage of song imitation and why the failure occurred. Therefore, tests that do not involve singing would be useful for assessing song selectivity. One such method measures changes in heart rate: Young swamp sparrows show greater changes in heart rate when a swamp sparrow song is broadcast than when a song sparrow song is played back (Dooling & Searcy 1980).

Tutoring with recorded songs tests a bird's ability to select conspecific songs by sound alone. Live tutors can affect song selectivity. For example, young zebra finches (*Poephila guttata*) that were raised by Bengalese finches (*Lonchura striata*) copied the song of the Bengalese foster father even when they could hear adult zebra finches sing nearby. However, this result does not negate the existence of an innate preference for the species song in zebra finches. Young zebra finches raised by two female Bengalese finches, which do not sing, developed songs composed of syllables from different adult zebra finches in the room (Immelmann 1969). The white-crowned sparrow has served as a model for selective learning. Even in this species live tutors can override the innate predisposition: Young white-crowned sparrows copied the song of a strawberry finch (*Amandava amandava*) both in choice and in no-choice situations, the choice being between white-crown and finch songs (Baptista & Petrinovich 1984). Because the strawberry finch song is somewhat like an isolate song of the white-crown, its acceptance by the white-crowns is not surprising. However, in earlier tape-playback experiments young white-crowns selected their species song over the song of the Harris' sparrow (*Zonotrichia querula*), which also resembles white-crown isolate songs (Figure 2). Similarly, white-crowned sparrows did not copy the song of a song sparrow whether it was presented alone or with a white-crown song (Marler 1970). However, in another experimental paradigm in which live tutors were used, young white-crowns selected the song of a song sparrow serving as a visible tutor over conspecific songs sung by hidden white-crown tutors (L. F. Baptista and L. Petrinovich, in preparation). These findings show that a live tutor can override the white-crown's innate predisposition for the conspecific song. In nature live tutors always sing the species-specific song to which the pupils are predisposed. The innate selectivity may be part of a multifaceted system that ensures normal song development in nature.

The Impressionable Phase of Song Imitation

Another process that facilitates the selective copying of a conspecific song by young birds involves the timing of the impressionable phase of song imitation, which coincides with the period when young birds are most likely to hear their father or other adults sing. Although anecdotal accounts abound, the number of species that have been carefully studied in regard to this phenomenon is

small. The white-crowned sparrow provides a classical example. Two white-crowned sparrows were tutored, one with the dialect of its birthplace, the other with an alien dialect, from post-hatching day 8 to day 28 and from day 35 to day 56, respectively. Both birds developed an approximate copy of the tutor song as adults. Two other birds that were tutored from 50 to 71 days of age did not copy the tutor song at all. Five other birds collected as fledglings of 30–100 days of age did not copy the tutor song but developed songs resembling their home dialect. Playback tutoring of a nestling and a first-year adult did not have any specific effect on their song development. These results led to the conclusion that the impressionable phase of song imitation in the white-crowned sparrow is between 10 and 50 days of age (Marler 1970). However, a recent study with live tutors disputes the above conclusion (Baptista & Petrinovich 1984). Ten white-crowned sparrows aged 50 to 54 days were exposed to visible live tutors for 50 days. All of them copied the tutor song, including a strawberry finch song sung either by a strawberry finch or by a white-crowned sparrow that had copied it earlier from the finch. Although these results indicate that a bird's age is not the sole determinant of the impressionable phase, they do not disprove the presence of such a phase. A better experiment would be to test whether the young birds that have been exposed to one live tutor before 50 days of age would copy a second live tutor after 50 days of age.

What terminates the impressionable phase? The duration of this phase does not seem to be rigidly fixed by age alone. It is becoming increasingly evident that the nature of sensory experience is an important determinant in ending the impressionable phase of song imitation.

An excellent study of the impressionable phase using live tutors was carried out with the zebra finch. Because the song of the Bengalese finch is distinctly different from that of the zebra finch, the time and extent of song copying can be conveniently studied by removing the young from their foster parents at different stages of song imitation. Young zebra finches memorize the patterns of component sounds in the song of their foster father by 40 days of age. As they start singing juvenile song at about 40 days of age and continue to develop song up to about 80 days of age, they copy the length and sequence of the component sounds as well as the overall temporal pattern of song from the same tutor. These zebra finches do not imitate conspecific songs after about the eightieth day of life, even when they are brought into close social contact with singing conspecifics for as long as four months (Immelmann 1969, Boehner 1983).

Furthermore, young zebra finches raised by their own parents for the first 35–40 days of life did not imitate the songs of other adults, but reproduced the song of their father as accurately as birds that were allowed to hear their

father until the hundredth day of life. In contrast, young zebra finches reproduced the song of their Bengalese foster father less accurately when removed from the father before the fortieth day of life than when removed between the fortieth and sixtieth day (J. Boehner, in preparation). These findings suggest that the impressionable phase of song imitation ends much earlier when young birds copy a conspecific song than when they copy an alien song. It is also well known among students of song development that isolates and birds tutored with alien songs take a much longer time to crystallize song than birds tutored with their species' songs.

Some birds can copy new songs even after song crystallization in the first singing season. Red-winged blackbirds (Yasukawa et al 1981), indigo buntings (Payne 1982), saddlebacks (*Creadion carunculatus*) (Jenkins 1977), indigobirds (Payne & Payne 1977), and Bewick's wrens (*Thrymanes bewickii*) (Kroodsma 1974) copy territorial neighbors when they move to a new area.

Finally, a word of caution is in order. The results of tutoring reported by different authors differ from one another even for the same species. As mentioned above, many factors affect song imitation, and few attempts have been made to standardize the methods and conditions of tutoring. If such seemingly unimportant conditions as early social relationships, tutoring before or after feeding, and the time of day affect song imitation (Todt & Hultsch 1985), different results obtained by different methods and authors may be caused by variations in any number of experimental conditions. There are also species and individual differences in responses to tutoring. Also, the number of birds used in these experiments tends to be small, for obvious reasons. These considerations call for careful scrutiny of claims in this field.

Improvisation and Invention

Most birds do not indiscriminantly copy every feature of the tutor song, especially in playback tutoring, rather they incorporate individual styles in their final songs. Two processes contribute to the development of individual styles: A bird "improvises" a variation on the theme provided by the tutor song (cf Figure 5B). A bird also "invents" a sound pattern that is neither a copy of the tutor model nor an example of isolate sound patterns (Marler et al 1962, Marler & Peters 1982c). Song properties susceptible to improvisation and invention seem to vary among species. In white-crowned sparrows (Marler 1970, Konishi 1978), some isolate Oregon juncos (Marler et al 1962), and red-winged blackbirds (Marler et al 1972) the overall song temporal pattern as well as syllables are subject to improvisation and invention, whereas in hand-reared swamp sparrows (Marler & Peters 1982a,b) only syllable structure is varied. Improvisation and invention are perhaps another manifestation of the instructional and selectional processes operating in an integrated manner.

Memory in Song Imitation

Young birds do not imitate songs immediately like school children learning melodies from their music teacher. Birds listen to and memorize a song first and vocally reproduce it later. The interval between these two events can be as long as several months, during which the bird need neither hear nor rehearse the song. Thus, birds can remember complex acoustical patterns for a long time. In some species the two periods overlap with each other such that the bird continues to copy new sounds after the sensorimotor stage has started. The absence of rehearsal is technically difficult to demonstrate because of the number of recordings that must be examined. Swamp sparrows that had been tutored during the first 60 days of life did not sing at all or sang too infrequently to be recorded during weekly sample monitoring until about 240 days after the last tutoring session (Marler & Peters 1981).

Song Templates

When a bird learns to sing from memory, he must hear himself vocalize. Although this is expected, we must exclude the possibility that the song memory is internally translated into the corresponding vocal motor pattern. Surgical removal of the cochleae makes a bird totally deaf. When a bird becomes deaf before the onset of subsong, he can no longer vocally reproduce the tutor song (Konishi 1965b). Thus, the vocal control system can use the song memory only via the route linking vocal organ, voice, ear, auditory system, and vocal motor system: i.e. the auditory feedback loop (cf Figure 12). All songbirds studied so far develop highly abnormal songs when deafened before the onset of subsong (Konishi & Nottebohm 1969) (Figure 6). The most extreme effect of deafening is the disappearance of all the recognizable structural entities of song; notes, syllables, and phrases may be lacking in the songs of deaf birds. If deaf birds produce distinct notes and syllables at all, these tend to contain abnormal patterns of frequency modulation. Notes and syllables produced by deaf birds usually appear irregular and fuzzy on a soundspectrogram (cf Figure 7). In sharp contrast with the songs of intact birds, the notes and syllables of deaf birds are not repeated in exactly the same form either from song to song or within a song, even though their general patterns are maintained. Despite this short-term instability, deaf birds can maintain to a considerable extent the individual characteristics of their songs in successive years.

If deafness renders the song memory unusable for song development, how does it affect song development when there is no song memory, i.e. without a tutor song? If a bird raised in isolation is deafened, he develops a song different from the song of an intact isolate. The deaf bird's song typically contains significantly fewer normal characteristics than the isolate song. Thus if a bird can hear himself sing, he knows how to produce some of the normal

song properties. Furthermore, the effects of deafening on song development are the same between tutored and untutored birds. Birds use hearing to prevent the developing song from deviating from the intended pattern. In other words, birds use auditory feedback to match their voice with the intended pattern serving as a template. The template can be acquired either by learning, as in tutoring, or by inheritance, as in rearing in isolation. This was how the concept of templates was formulated (Konishi 1965b, Marler 1964).

If isolates use an innate template, why should they not develop uniform song patterns? In some species, isolates show large individual differences in song (cf Figure 4) (Konishi 1978). Perhaps, the innate template only crudely defines the species song, leaving considerable freedom for imitation, improvisation, and invention. Another question about the innate template is whether it is good enough to guide the development of a normal song in any species. As mentioned before, isolates do develop some properties of the normal song in some species, but no bird produces completely normal songs in isolation. Although song sparrow isolates had been thought to develop normal songs (Mulligan 1966), a subsequent study did not support this claim (Kroodsma 1977a). The effects of deafening show large species differences; again, deaf white-crowned sparrows fail to develop most of the normal song properties,

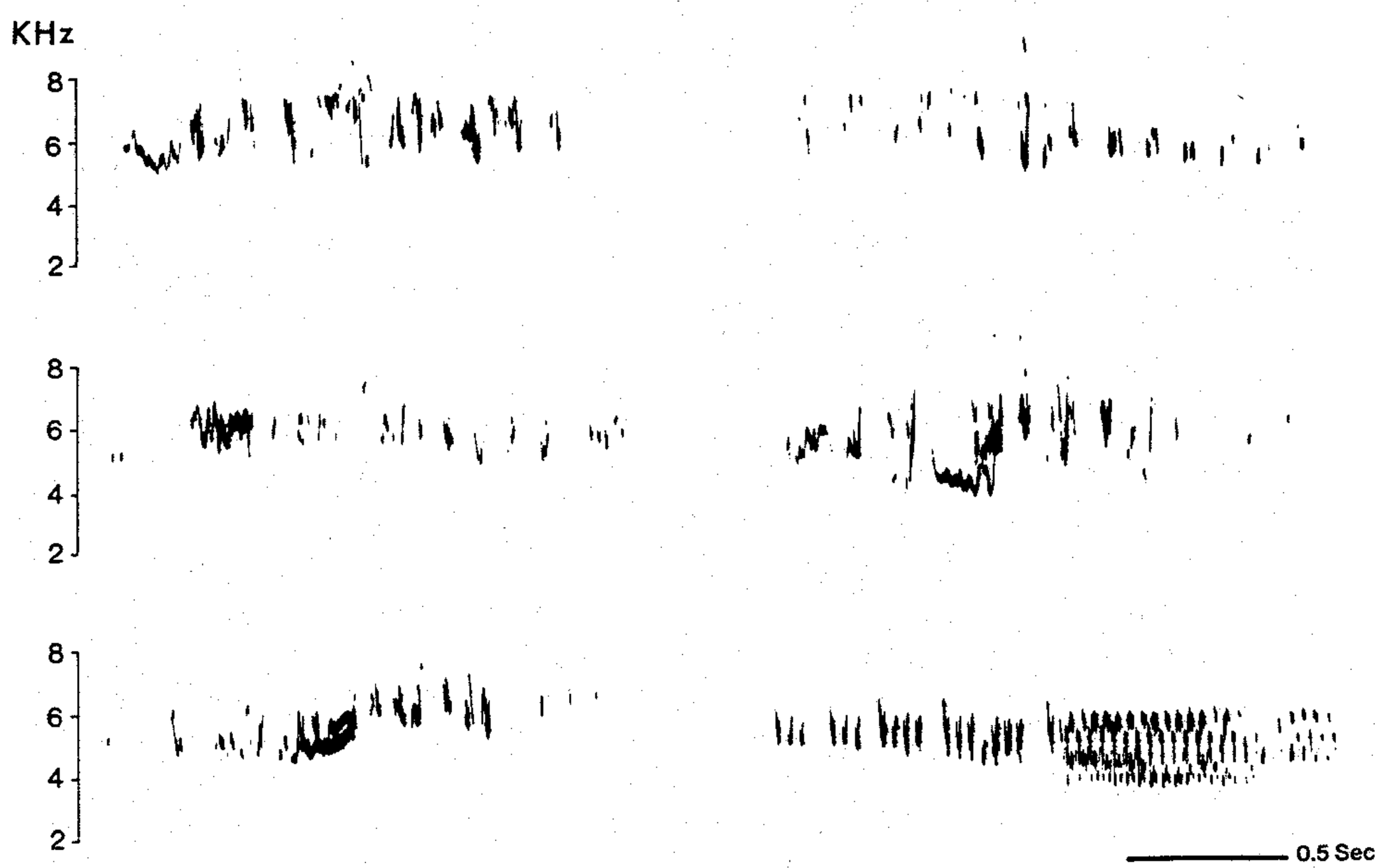

Figure 6 Songs of deaf birds. Hearing a bird's own voice is essential for normal song development in all songbirds studied so far. Deaf birds sing, but their songs are abnormal. In extreme cases none of the structural units of song, i.e. note, syllable, and phrase, develops, as exemplified here by the songs of six white-crowned sparrows. Notice that they differ from both the wild-type songs of Figure 3 and the isolate songs of Figure 4.

whereas deaf canaries (Marler & Waser 1977, Guettinger 1981) and Oregon juncos develop some of the normal syntactical rules of the species song (cf Figure 7). An Oregon junco normally has a repertoire of about four songs. Deaf Oregon juncos produced repertoires and delivered different song types in bouts like intact birds (Konishi 1964, 1965a).

Misunderstood Templates

The same innate template might underlie both the recognition of the species' song and the control of vocal development in isolation. Although there is no evidence for this dual role, the template concept came to be used in both contexts (Marler 1976). This dual usage has confused the authors of some recent publications. For example, one of them contains the following statement (Baptista & Petrinovich 1984):

> These templates are considered to guide the development of motor behavior and to explain some of the complexities of vocal learning. Studies of song development in the white-crowned sparrow have provided some of the key elements of support in attempts to understand how the template operates. Exposure to song between 10 and 50 days of age is considered to create an "engram" if the song has the characteristics of the species. If the song is not appropriate, the stimulus is rendered ineffective by a sensory gating mechanism. Thus, alien song is rejected, the mechanism is closed after 50 days of age, and the crystallized song is the result of matching vocal output to the dictates of the auditory template. Although the above explanation seems adequate with tape tutoring, our evidence suggests that it is inadequate with social tutoring unless the idea of the template is broadened considerably.

The work of these authors concerns the innate predisposition and impressionable phase of song imitation, but it has nothing directly to do with the role of templates in motor development. The concept of templates is largely a short-hand description of observed facts. All it says is that a bird memorizes a song and reproduces it from memory. The only hypothetical aspect of this theory is about the manner in which auditory feedback is used. Control of voice by auditory feedback requires a criterion by which errors in vocal output are corrected. Abnormal songs result when the errors are not corrected. The template simply refers to that criterion.

Song Maintenance Without Auditory Feedback

In several species, auditory feedback is essential for song development but not for its maintenance once crystallization has occurred (Konishi 1965b, Nottebohm 1968). The maintenance must be due either to nonauditory feedback or to the fixation of the output pattern within the central generator. Birds monitor auditory and nonauditory feedback simultaneously so as to learn the pattern of nonauditory feedback for a given sound. After this stage, the hypothetical nonauditory feedback alone becomes sufficient for the birds to evaluate the performance of their vocal organ. This possibility is difficult to exclude,

because nonauditory feedback can come from many parts of the body that move during singing. Nonetheless, it is hard to imagine that fine control of membrane vibration in the syrinx can be precisely monitored by sense organs other than those in the syrinx or syringeal musculature itself. Although the tracheosyringealis nerve bundle is said to contain an afferent nerve, neither the target of its innervation nor its physiological role in the control of song is known (Bottjer & Arnold 1982). If nonauditory feedback can be excluded, we are left with the intriguing alternative that the central song generator uses auditory feedback to establish its output pattern, which later becomes independent of hearing. Does this method of establishing a central motor program exist elsewhere? Central rhythm generators are known in many animals; they were demonstrated mostly in adult animals. In only few of these cases have attempts been made to investigate whether they develop without rhythmic sensory input. For example, the basic pattern of muscular contraction underlying the song and flight of crickets develops before the wings grow, indicating that sensory feedback from wing movement is not necessary for the development of the pattern (Bentley & Hoy 1970). Similarly, the basic sequence of forelimb movement during grooming develops in mice whose forelimbs were amputated shortly after birth (Fentress 1973).

Central Song Generators

The acoustical patterns of isolate songs may be due both to the innate template and to central vocal motor generators. In most species studied so far, some deaf individuals produce noise-like songs lacking apparently all the species-specific properties. This observation led to the conclusion that the song motor control system cannot by itself generate any song-like patterns of output, meaning that the motor system needs instruction from the sensory template (Nottebohm 1968, Nottebohm et al 1976, Marler 1976, 1981, Konishi 1978, Bentley & Konishi 1978). There are species and individuals that produce some of the sound patterns of the normal song without auditory feedback, although the sounds are always abnormal. Singing different syllables in separate phrases is one of the properties of the canary song, and it is present in the songs of deaf canaries (Guettinger 1981). Similarly, the species-typical phrase structure is evident in the songs of some deaf song sparrows (Marler & Sherman 1982). Some deaf Oregon juncos (Konishi 1965a) also produced songs consisting of a simple trill typical of their normal songs (Figure 7). The most intriguing aspect of these observations is the individual differences. Different individuals mature at different rates, which may result in different rates of vocal development. Vocal patterns that developed before deafening tend to survive the operation. Therefore, if birds are deafened at different stages of song development, individual differences in songs can occur. It is important to monitor vocal development in each bird closely before it is deafened. Nevertheless,

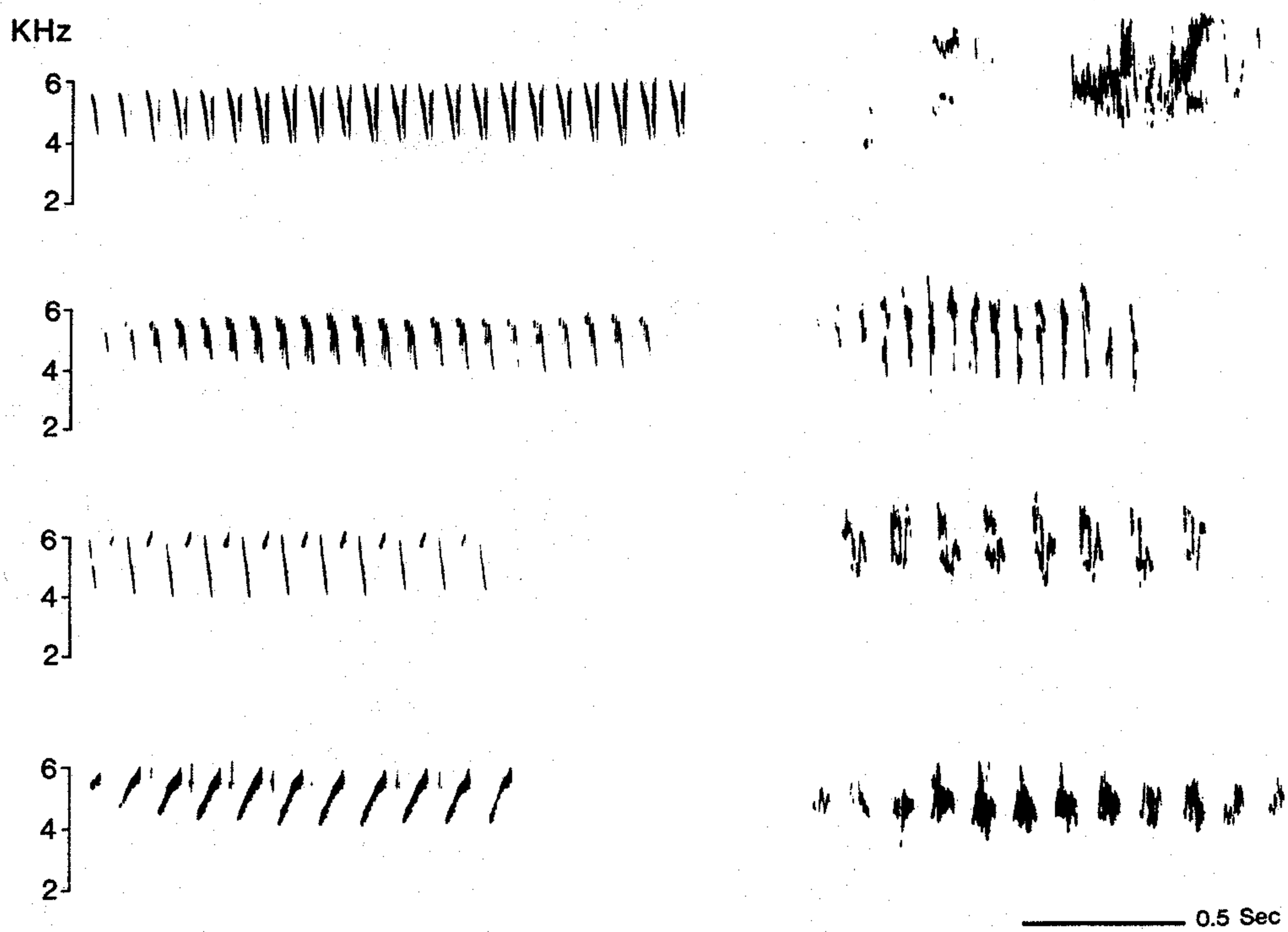

Figure 7 Normal features in deaf birds' songs. Some of the species' typical properties of song occur in deaf individuals of several species studied. The Oregon junco is an example; its song is a simple trill consisting of identical syllables (*left column*). Deaf Oregon juncos developed trill-type songs (except one song of one bird as shown at *top* in *right column*), although their syllables were abnormal.

there appear to be distinct species differences in the number of normal features that appear in the song of a deaf bird. Canaries born and raised in an ear-damaging noise and subsequently deafened before the onset of singing produced songs containing some of the normal aspects of song organization. These birds perhaps never heard themselves verbalize either before or during song development (Marler & Waser 1977).

The observation that songs of deaf birds contain normal features does not require changes in the template concept (cf Marler & Sherman 1982). The central generators for song indicate only that the postulated innate song template is not the only means to govern song development in isolation. The innate template was invoked for the explanation of the differences between the isolate and deaf songs. The theory of central generators can only account for the presence of some normal sound patterns in the songs of deaf birds, but it cannot explain why the songs of intact isolates differ from those of deaf ones.

NEURAL SUBSTRATES FOR SONG

The deafening experiment introduced a new way of thinking about song development, i.e. in terms of central generators and auditory feedback. An obvious question is where the central generator resides and how auditory feedback modulates its output. A discrete brain pathway controls song and it occupies a relatively large volume of the brain, particularly the forebrain. It consists of five nuclei in the forebrain, one in the thalamus, one in the midbrain, and one in the hindbrain (Nottebohm et al 1976, Nottebohm et al 1982, Gurney 1981). The last nucleus, the tracheosyringealis part of the hypoglossal nucleus, innervates the musculature of the vocal organ, the syrinx. The results of anatomical tracing of the vocal control system are summarized in Figure 8. The tracheosyringealis nucleus (X11ts) receives input from the robust nucleus of the archistriatum (RA) both directly and indirectly via the dorsomedial nucleus (DM) of the midbrain. RA receives input from the nucleus hyperstriatum ventrale, pars caudale (HVc) and the magnocellular nucleus of the anterior neostriatum (MAN). HVc is located just under the ependymal layer of the lateral ventricle opposite the hippocampus, which is on the dorsomedial surface of the forebrain. There is some uncertainty about the brain layer to which HVc belongs, both because it is unclear whether the hyperstriatum in songbirds extends posteriorly to encompass HVc and because this nucleus, despite its name, occurs in the neostriatum in the parakeet brain. HVc projects to RA

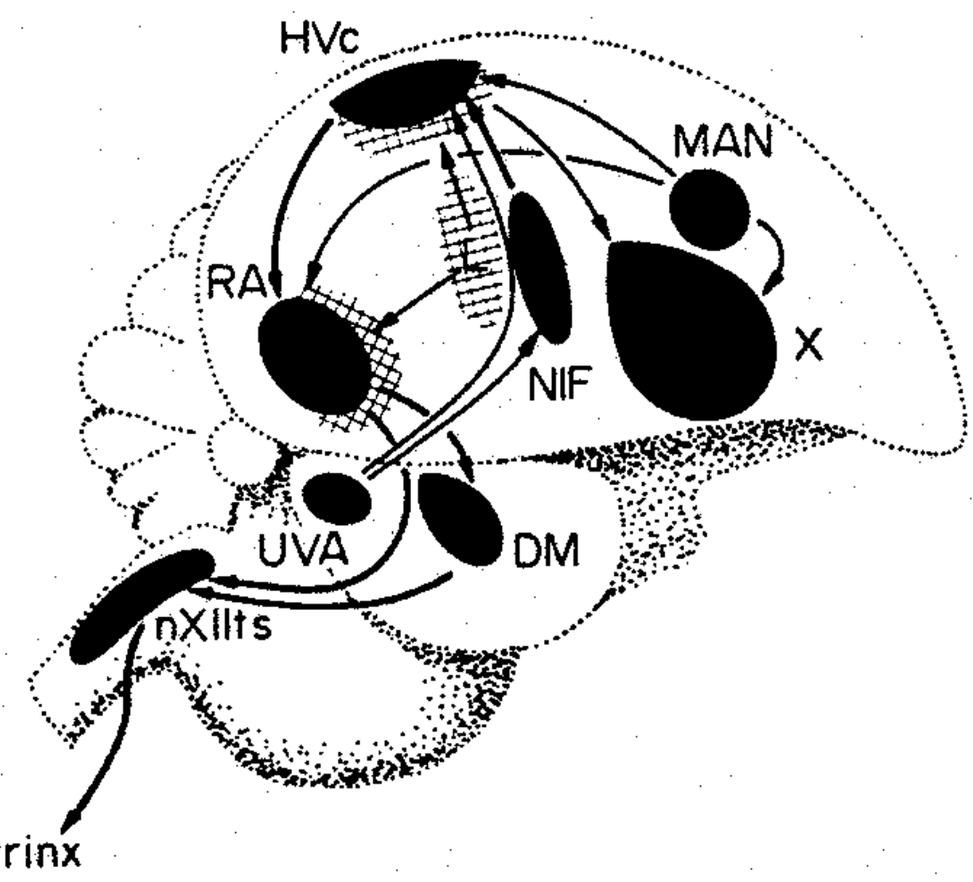

Figure 8 The vocal control system. This diagram shows most of the known nuclei and connections of the vocal control system. All *arrows* indicate anterograde connections. Neural signals for song originate in NIF (Nucleus interface) and descend the pathway to the syrinx via HVc (nucleus hyperstriatum ventrale, pars caudale), RA (nucleus robustus archistriatalis), DM (dorsomedial nucleus of nucleus intercollicularis), and X11ts (nucleus hypoglossus, pars tracheosyringealis) in that order as shown by the *thick arrows*. Other nuclei are inactive during song in adult birds. *Hatched areas* indicate the known projection zones of the telencephalic auditory area, Field L.

and area X of the parolfactory lobe and is innervated by fibers from MAN, nucleus interface (NIF) and the thalamic nucleus, nucleus uva (UVA). NIF also receives input from UVA. The forebrain auditory area, Field L, projects to the vicinity, the so-called shelf area, of both HVc and RA (Kelley & Nottebohm 1979). Intracellular recording shows that a class of neurons in HVc and RA receives auditory input, although its exact source is unknown. Furthermore, many of these auditory neurons of HVc send their axons to area X (Katz & Gurney 1981, Katz 1982).

The conclusion that the pathway controls song is supported by two types of evidence. Lesions of HVc, RA, or the hypoglossal nerve cause deterioration in the adult song. Control lesions placed elsewhere do not affect the song (Nottebohm et al 1976). Recording of neural activity from the singing bird indicates that NIF, HVc, and RA show periods of activity and inactivity corresponding, respectively, to the sounds and silent intervals of song (McCasland 1983). Furthermore, the latency between the onset of neural discharge and sound is longest in NIF, shorter in HVc, and shortest in RA, indicating the sequence of signal transmission within the forebrain nuclei. So far, a neural signal for song has not been detected before NIF in the descending pathway, and furthermore, bilateral lesions of UVA, the sole source of inputs to NIF, do not affect song. Also, UVA, MAN, and area X show no song-related neural activity at all. These nuclei are considered to be parts of the vocal control system because of their anatomical connections with it. The vocal control system regulates predominantly the ipsilateral syringeal musculature; no anatomical connection between the two sides has been found so far.

Lateralization of Song Control

Birdsongs share some attributes with development of human speech. One of them is thought to be hemispheric lateralization. In the canary, lesions of the left hypoglossal nerve or left HVc cause greater losses or more severe deterioration of syllables than similar lesions on the right side. These observations led to the hypothesis that each hemisphere independently controls the ipsilateral half of the syrinx and that the left hemisphere controls more syllables than the right one (Nottebohm et al 1976, Nottebohm & Nottebohm 1976). This hypothesis also derives support from the so-called two-voice phenomenon, which refers to the simultaneous occurrence of two harmonically unrelated frequencies in some birdsongs (Greenewalt 1968, Stein 1968). Although the two-voice theory may be correct, there are two important issues to consider. One concerns the mechanism of generating harmonically unrelated frequencies. A circular membrane, for example a drumhead, produces a family of frequencies formally described by Bessell functions. Furthermore, sounds may be produced by vortex effects as air flows through a narrow slot. Vortex-

and membrane-generated sounds can interact, resulting in a complex distribution of frequencies (Gaunt 1983). The other problem is how to produce one voice with two sound sources. Many birdsongs contain one-voice syllables. There are two mutually exclusive alternatives: One voice comes from only one side and the other side is silent, or both sides contribute to the same voice. When a canary sings with its left bronchus plugged, its song contains many of the original syllables, including the two-voice ones. This finding indicates that the right and left syringeal halves produce the same syllables (McCasland 1983).

Another important aspect of the hypothesis is the site of lateralization. The sites of effective lesions are not necessarily the loci of lateralization; direct and indirect effects of lesioning must be distinguished. Because the vocal system controls predominantly the ipsilateral syringeal musculature, a lesion of any part of the descending pathway may disable the musculature of that side. If the left half of the syrinx plays a more dominant role in song control than does the right half, then cutting the hypoglossal nerve or lesioning the HVc simply exposes the syringeal asymmetry. It does not discriminate between hemispheric and peripheral lateralization. Such a peripheral asymmetry does exist in the canary's syrinx. The syringeal musculature on the left is clearly more voluminous than that on the right (Nottebohm 1980a). Consistent with this asymmetry, the left bronchus working alone can produce a larger number of normal syllables than the right one working alone, although the right one contributes to all syllables (McCasland 1983). Some HVc-lesioned canaries showed fewer changes in their songs than hypoglossus-lesioned birds (Nottebohm 1980a, Nottebohm et al 1976, Nottebohm & Nottebohm 1976). This difference may be due to the fact that a peripheral nerve can be lesioned more cleanly than a brain nucleus. Also, the hypoglossal nerve contains neurons that cause the syringeal muscles to contract in synchrony with the respiratory rhythm (Manogue & Paton 1982). Cutting these fibers may disrupt the coordination between respiration and vocalization, whereas a lesion of HVc does not affect this aspect of vocal control. Furthermore, if the size of HVc can serve as the index of song learning, one would expect left-right anatomical differences in the vocal control nuclei. No such differences are present in any of the vocal control nuclei except the hypoglossal nucleus, where the left side is said to be larger than the right by 6% (Nottebohm & Arnold 1976). Even a detailed analysis of neuronal morphology of RA, which demonstrated clear male-female differences, did not find any left-right bias (DeVoogd & Nottebohm 1981). Recordings from the HVc of the singing canary show that both sides are active during all syllables. This observation is consistent with the result of bronchus-plugging mentioned above, but it is difficult to explain, if HVc is the site of lateralization (McCasland 1983).

How the muscular asymmetry develops in the ontogeny of an individual is an unanswered question. Some unknown central asymmetry may drive the two sides differently, or it may develop in response to differential loading by the periphery. In the adult canary, lesions of the left hypoglossus result in a shift of song control to the right side (Nottebohm et al 1979). However, this shift parallels a shift in the muscular asymmetry to the right side. Why lateralized control of song evolved is another unanswered question. There does not seem to be any correlation between the ability to imitate song and the degree of lateralization. Deaf canaries, which are not supposed to "learn" song, are left-dominant (Nottebohm et al 1976). An asymmetry is barely noticeable in the song of the zebra finch, which imitates song well (Price 1977). Thus, the analogy of song lateralization with lateralization of human speech should be viewed with caution.

Neural Theory of Song Learning

Comparative brain anatomy and neuroendocrinological studies have recently uncovered several new facts that are thought to link the vocal control system with song learning.

CROSS-TAXA COMPARISONS The forebrain nuclei HVc, RA, X, and perhaps also MAN and NIF occur only in birds capable of vocal imitation, such as songbirds, and are apparently absent in birds that lack this capability. Species in which isolates develop abnormal songs have the nuclei and those in which isolates develop normal songs, such as tyrannid flycatchers, do not (Nottebohm 1980a, Kroodsma 1984). If auditory inputs of HVc, RA, and X are necessary for the control of vocal development by auditory feedback, deafening should affect vocal development only in birds with the nuclei. This prediction is borne out within the range of species studied so far. The nuclei are present in birds that develop abnormal vocalizations when deafened and are absent in species that suffer no ill effects from deafening, such as chickens (*Gallus domesticus*) (Konishi 1963) and ring doves (*Streptopelia risoria*) (Nottebohm & Nottebohm 1971).

Interestingly, the dichotomies mentioned above seem to reflect partly taxonomic divisions. Passerines (Order Passeriformes) include oscine songbirds, such as sparrows, canaries, and starlings, and suboscine songbirds, such as tyrannid flycatchers. The forebrain nuclei occur in oscines, but not in suboscines (Nottebohm 1980a). Birds of nonpasserine orders, such as Galliformes (chickens, turkeys, etc) and Columbiformes (pigeons and doves), generally lack the forebrain nuclei. The parakeet of Order Psittaciformes (parrots) and the hermit hummingbird (*Phaethornis longuemareus*) of Order Apodiformes (swifts and hummingbirds) may be exceptions to the above rule, first, because they are the only well-documented nonpasserines that imitate sounds (Snow

1968, Wiley 1971), and, second, because structures analogous or homologous to HVc and RA are present in the parakeet's brain (Paton et al 1981). Whether or not the forebrain song nuclei evolved independently in oscine songbirds and parrots to accommodate vocal imitation is an unanswered question. The brain of the hummingbird has not been examined for the presence of the forebrain nuclei.

These taxonomic correlations are partly due to the fact that the structure of the syrinx, which is an important key in avian classification, is one of the determinants of vocal plasticity. Obviously, the vocal organ and its neural substrates must coevolve. The syrinx of nonpasserine birds, like chickens, turkeys, and ring doves, have two pairs of extrinsic muscles that cause the displacement and rotation of the whole syrinx for the production of sounds. The complex syrinx of oscine songbirds is equipped not only with extrinsic musculature but also with four to nine pairs of intrinsic muscles for the independent control of different parts of the organ (Figure 9). Intrinsic muscles also occur in the syringes of parrots and hummingbirds. Thus intrinsic muscles seem to be a necessary condition for plastic vocal development (Gaunt 1983, and personal communication). However, the converse is not always true; for instance, acoustic isolation does not affect song development in suboscine

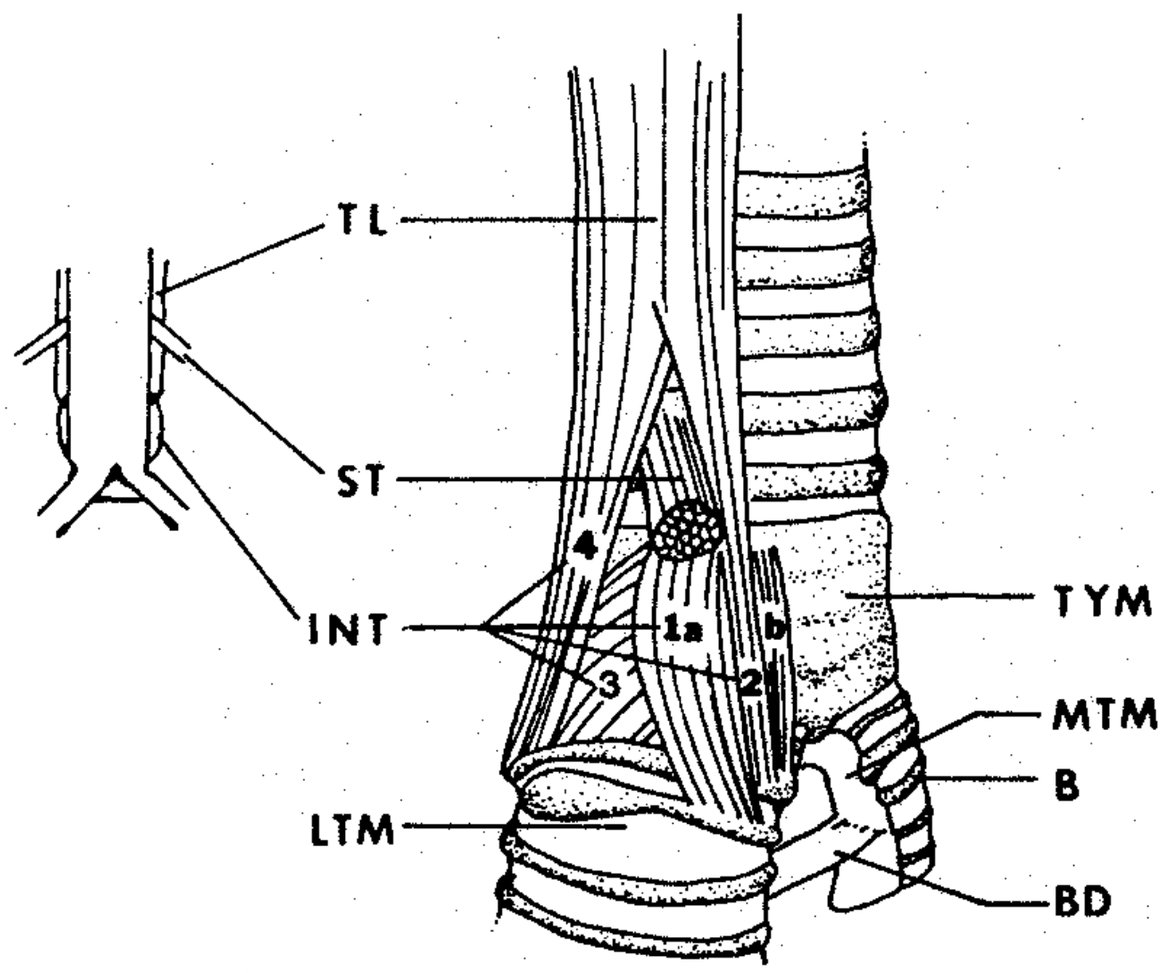

Figure 9 The syrinx of oscine songbirds. This sketch shows a frontal section and right lateral view of an idealized, oscine syrinx. The numbers indicate the presumed intrinsic muscles (INT). Muscles 1a and 1b are considered separate despite their appearance as a single mass. Muscles 2 and 4, which seem to be extensions of the tracheolateralis muscle (TL), are regarded as intrinsic muscles. B, bronchial bar; BD, bronchidesmus; TYM, tympanum; MTM, medial or internal tympanic membrane; LTM, lateral tympanic membrane; and ST, sternotrachealis muscle. TL and ST are the extrinsic muscles (from Gaunt 1983).

flycatchers that have a simple syrinx with several intrinsic muscles (Gaunt 1983).

Although the complexity of the syrinx is thought to be correlated with the complexity of vocalizations, the number of intrinsic muscles is not directly correlated with either repertoire size or imitative ability (Gaunt 1983). For example, the well known vocal mimics such as lyre birds (*Menura novaehollandiae*), Indian Hill mynahs (*Gracula religiosa*), and mockingbirds have three or four intrinsic muscles, whereas some oscines with more complex syringes can sing only a single song. Also, song repertoire size varies greatly among closely related species with similar syringeal anatomy. For example, the song sparrow with 20 song types and the white-crowned sparrow with one song type are now considered to belong to the same genus *Zonotrichia*. Thus, these differences are due perhaps to differences in the brain vocal control system (Gaunt 1983).

BRAIN ANATOMY AND SONG LEARNING Comparisons of different individuals or populations of the same species have uncovered a correlation between the size of song system nuclei and song learning. Western populations of long-billed marsh wrens (*Cistohorus palustris*) with large song repertoires have larger HVcs than Eastern populations with small repertoires (cited in Kroodsma 1982). Canaries produce a long, continuous series of syllables in their songs and the number of different syllables used by an individual can vary from about 20 to 50. Canaries with larger numbers of syllables tend to have larger HVcs and RAs than those with smaller numbers of syllables, although it is a statistically weak correlation (Nottebohm et al 1981). Also, female canaries that sing in response to testosterone administration have five to seven syllables in comparison with about 30 in the male. These females have HVcs and RAs that are less than 50% of their male counterparts' in volume (Nottebohm 1980b). However, according to a recent report (Pesch 1983), female canaries sing spontaneously after the breeding season or when isolated from other birds, and the number of syllables is about the same as that of the male.

Young canaries develop syllables by imitating their fathers and other adults and by improvising (Waser & Marler 1977). In contrast with many species that do not change their songs after the first singing season, canaries "change their song repertoires each year by adding, dropping, or modifying components" (Nottebohm & Nottebohm 1978). Canaries deafened after their first singing season fail to maintain or increase their syllable repertoires in subsequent singing seasons (Nottebohm et al 1976). Therefore, the process by which new and modified syllables are created is regarded as learning, and the number of syllables in the repertoire can serve as the index of song learning (Nottebohm 1980a). Why does the nuclear size correlation exist? The size of a brain area can vary for various reasons: In addition to neuronal components, non-

neuronal components like glia, capillaries, and intercellular matrix can contribute to a size difference. It will be important to determine the ratio of neuronal and nonneuronal contributions in any such comparison. A more serious question here is how to derive cause and effect relationships from correlations. If the number of different syllables is correlated with any other variables, then it will be necessary to determine which variable is causally related with the size of HVc and RA. For example, a reasonable hypothesis is that the direct relationship is between the total amount of sound energy in the songs and the nuclear size. If this is true, then the size of a nucleus would have nothing directly to do with learning. Although canaries deafened after their first singing season produce abnormal songs, the total amount of sound energy in their songs is measurable. It would be of interest to compare the HVcs and RAs of deaf canaries that use different amounts of sound energy in singing. If there is a size correlation, then it may be due to differential usage instead of learning.

The plasticity of canary song predicts the existence of modifiable neural substrates. Testosterone, which stimulates singing in young birds, females, and castrated males, causes growth in the somata and dendrites of RA and HVc neurons (DeVoogd & Nottebohm 1981, Nottebohm 1980b). In the male canary the size of HVc and RA fluctuates in parallel with the seasonal variation in circulating testosterone. They are larger in the spring singing season than in the fall and winter (Nottebohm 1981). The growth and shrinkage of dendrites presumably contribute to this fluctuation. An increase in synaptic sites probably accompanies growth in dendrites. The view that learning necessarily involves the formation of new synapses is not generally accepted (Kandel 1979), although there is physiological evidence that in some cases it does, such as the new synapses formed in the cat's red nucleus during readjustment of forelimb coordination following cross-innervation of flexor and extensor muscles (Tsukahara 1981).

The hypothesis that the seasonal fluctuation in HVc and RA volume indicates learning and forgetting of song requires careful scrutiny (Nottebohm 1981). There is a real possibility that HVc and RA undergo seasonal volume changes in deaf canaries, because their singing fluctuates seasonally, as in intact birds. If this is true, then the significance of this phenomenon for song learning is doubtful. The normal temporal pattern of song that develops in deaf canaries is likely to be due to central pattern generator circuits, as mentioned above. Because it develops by the first singing season without auditory feedback, it would not be surprising if some of its generator circuits are annually "reformed" even in deaf birds. Therefore, the distinction between the anatomical and physiological changes associated with feedback controlled modification of song on one hand and those related to central reorganization and use-disuse phenomena on the other will be important.

A SINGLE-NEURON APPROACH TO BIRDSONG

Although some of the correlations mentioned above may link brain anatomy to song learning, the ultimate proof for it requires an understanding of the neural codes involved. How memorized songs, auditory feedback, and song motor programs are encoded is an important question that calls for physiological analysis at the cellular level.

Many studies show that special neuronal circuits generate rhythmic patterns in invertebrates (Bentley & Konishi 1978). Evidence also suggests that the spinal cord and brainstem of vertebrates contain generator circuits for locomotor coordination (Grillner 1975, Stein 1978), but little is known about the control of complex movements. The discrete nuclei and pathway of the vocal control system are convenient for the analysis of neuronal mechanisms underlying complex movements.

Multi-unit activity in the HVc of singing birds shows a unique pattern of discharge occurring before a syllable, and a quiescent period before a silent interval in the bird's song. Thus, a neural equivalent of the song manifests itself in the HVc. This nucleus precedes the hypoglossal nucleus by at least three synapses. HVc receives input from NIF and UVA, and NIF shows a similar song-related discharge pattern. Because the areas around NIF and UVA show no song-related discharge, NIF may be the source of the song pattern. An intriguing possibility is that the motor program for a copied song might reside in NIF.

Single units recorded from the HVc of mockingbirds show neuronal specializations for the generation of the song pattern (McCasland 1983). Many neurons fire for all syllables, some neurons fire long (500 msec) before the onset of song, and a few neurons produce highly stereotyped bursts of spikes for only a few syllable types. Some of these neurons (motor-specific neurons) fire selectively for one syllable type and do not fire for other very similar syllables (Figure 10).

Specializations related to the song are also evident among HVc auditory neurons. In the canary and white-crowned sparrow, the bird's own song is the most effective stimulus for eliciting multi-unit responses in HVc. Furthermore, the bird's own song broadcast backward is much less effective than when it is delivered in the normal direction, suggesting that the sequence of the component sounds is an important cue for these neurons (McCasland & Konishi 1981).

The stimulus requirements of single HVc neurons substantiates the above suggestion about stimulus cues. In the white-crowned sparrow, some HVc neurons respond selectively to a particular set of acoustic cues in the bird's own song (song-specific neurons) (Margoliash 1983). All song-specific neurons that were thoroughly studied require two consecutive sounds (phrases or parts

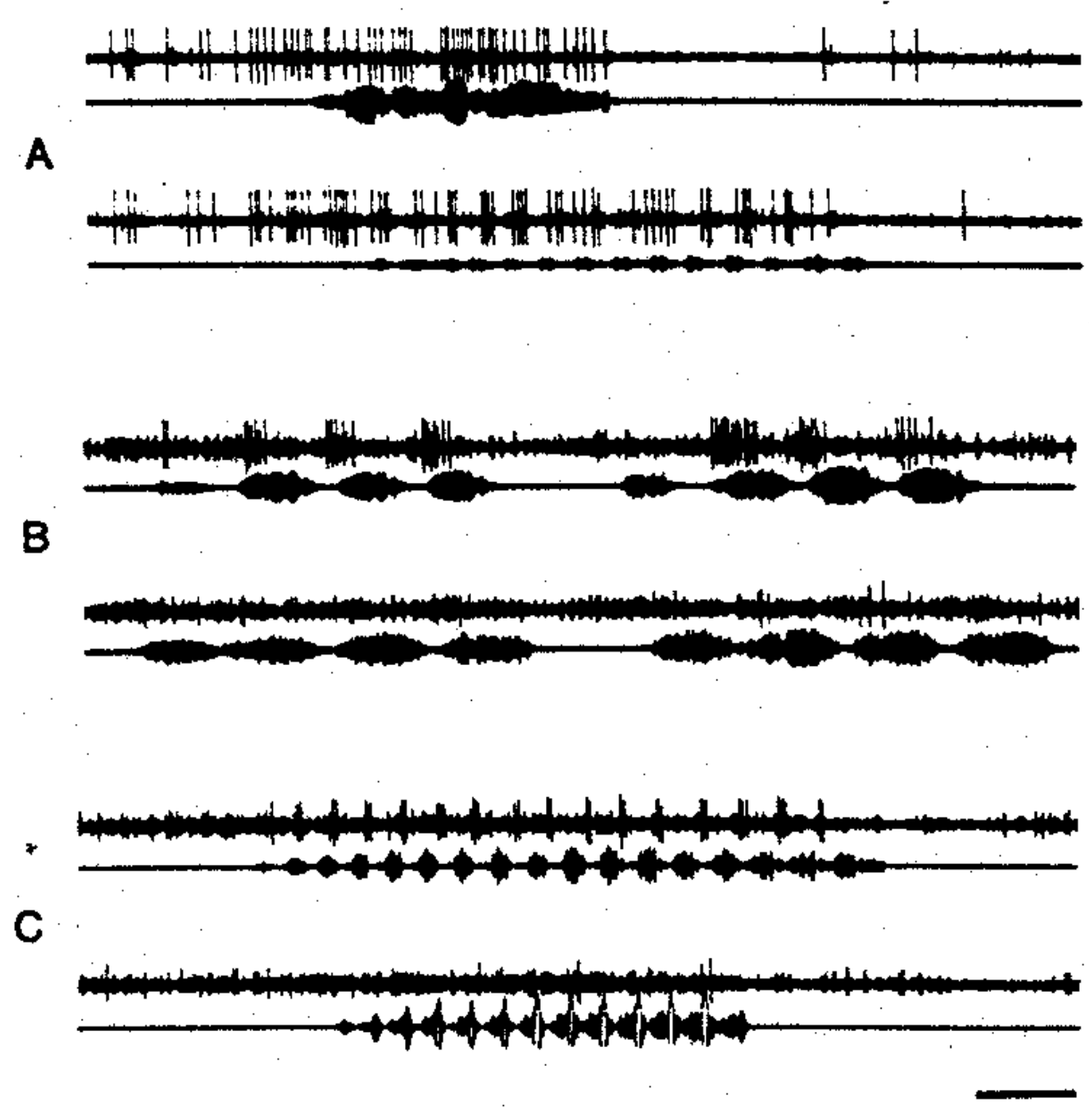

Figure 10 Neuronal specializations for song motor control. *A*, *B*, and *C* show segments of simultaneous recordings of neuronal HVc discharge and song syllables from a mockingbird. *A* fired before and during all syllables. *B* and *C* are motor-specific neurons, which fired only before and during a specific syllable (*upper pair of traces* in each group); they remained inactive before and during syllables (*lower pair of traces*) similar to the specific one. Scale bar indicates 100 msec.

of a phrase) of the song, each of which alone elicits little or no response (Figure 11). They detect particular acoustic cues such as changes in frequency and a silent gap between the two sounds. A bird's song-specific neurons may respond to the songs of some other individuals from the same dialect area and typically fail to respond to the songs of birds from other dialect areas. This selectivity is predictable when the relevant acoustic features in the bird's own song are compared with the corresponding features in the other songs. Song-specific neurons in birds singing abnormal songs, due to early isolation, respond selectively to these abnormal songs and fail to respond to wild-type songs of the species. When a bird's own song differs from its early tutor song, its song-specific neurons are selective not for the tutor song but for the song sung by the bird.

There have been reports of auditory neurons selectively responding to bird vocalizations. In the starling a few Field L neurons responded to a single call out of many calls presented as stimuli (Leppelsack & Vogt 1976). This finding certainly suggests the presence of selective neuronal responses. However, it does not show neuronal specificity for the call. When a neuron requires a set of physically definable acoustic properties that are unique to a call, the neuron can be named a "call-specific neuron." Song-specific neurons are "tuned" to specific acoustical parameters that are unique to the bird's own song. "Selective" neurons are those which prefer one call to other calls. Call-selective

neurons are obviously more common than call-specific neurons. A match between a neuron's frequency sensitivity and a call's spectrum alone can account for the responses of call-selective neurons in some cases (Scheich et al 1979). Song-specific neurons show the importance of the temporal pattern of the stimulus in neural coding of the complex sound, an aspect that has been studied

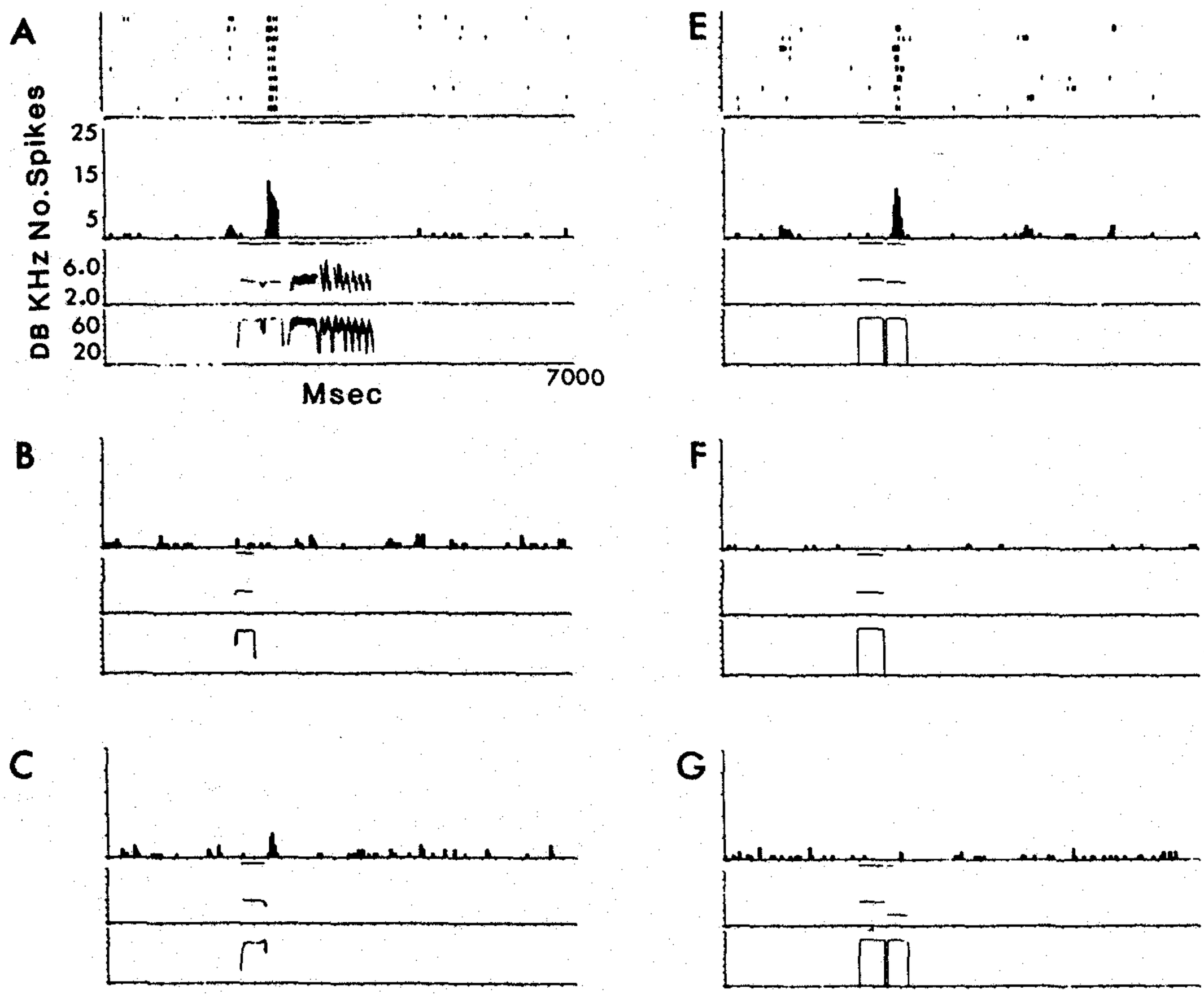

Figure 11 A song-specific neuron from the HVc of a white-crowned sparrow. Some HVc neurons respond selectively to a particular acoustic cue in the bird's own song. The pattern of transition in frequency between two consecutive phrases constitutes the cue for all song-specific neurons found in this species. In each section (*A*, *B*, etc), the top graph is a raster representation of unit response. Each *vertical* tick represents one spike; each row is marked on the ordinate by a horizontal tick and represents one stimulus presentation. The *middle graph* is a histogram of spike numbers. The *bottom graph* shows the pattern of frequency (*upper trace*) and amplitude (*lower trace*) modulation in the stimulus. This unit responded selectively to the bird's own song (*A*). It required the first and second parts of the introductory whistle, the first (*B*) or second (*C*) part alone eliciting little or no response. Two consecutive tones could mimic the natural trigger feature (*E*), again one tone alone having no stimulatory effect (*F*). The neuron was insensitive to variation in the interval between the two tones, but it was sensitive to differences in frequency between them (*G*) (from Margoliash 1983).

very little in auditory physiology (Suga 1982). This attribute of song-specific neurons cannot be explained by simple peripheral mechanisms such as frequency tuning and two-tone inhibition.

Whether song-specific neurons are involved in some aspect of the template matching processes is not known, although their specificities are appropriate for that which is required of the template. Because the template is established by early auditory exposure, its neural representation should be present before the onset of singing. So far, song-specific neurons have not been found in presinging birds (D. Margoliash, unpublished results). Our current hypothesis about the origin of song-specific neurons is as follows. Song-specific neurons acquire their specificity during song development; their properties become matched to the final form of song as it is shaped. A similar argument would apply to the motor-specific neurons mentioned above; their specificity may also develop during the sensorimotor phase of song learning.

Why do motor and auditory neurons occur, apparently completely mixed, within the same nucleus? The need for auditory feedback for song development indicates that the vocal control system is directly or indirectly linked to the auditory system. HVc is one of the sites of this linkage. Although the auditory and motor neurons have clearly different cell forms, the nature of anatomical connections between them is not known (Katz & Gurney 1981). However, multiunit recordings from HVc show that auditory neurons are inhibited while motor neurons are firing during song (McCasland & Konishi 1981). This inhibition perhaps occurs in HVc itself, because Field L neurons are generally not inhibited during song (McCasland 1983). Although Field L projects to the vicinity of HVc, the immediate source of auditory input to HVc is not known. Also, the properties of auditory neurons in area X and RA have not yet been studied.

A NEURAL MODEL OF SONG LEARNING: A SUMMARY

The template theory offered a simple model of song learning without any reference to brain anatomy and physiology. A slightly more realistic model that incorporates the known anatomical and physiological attributes into its design is now feasible (Figure 12). This model assigns song generator function to the forebrain nuclei, NIF, HVc, and RA, of which the last two contain sensorimotor circuits for auditory-vocal interaction. These circuits use error signals derived from matching auditory feedback with the template to regulate the output of the song generator. There must be a reciprocal relationship between the song generator and sensorimotor circuits, for these are developmentally plastic and become "fixed" as the output of the song generator crystallizes.

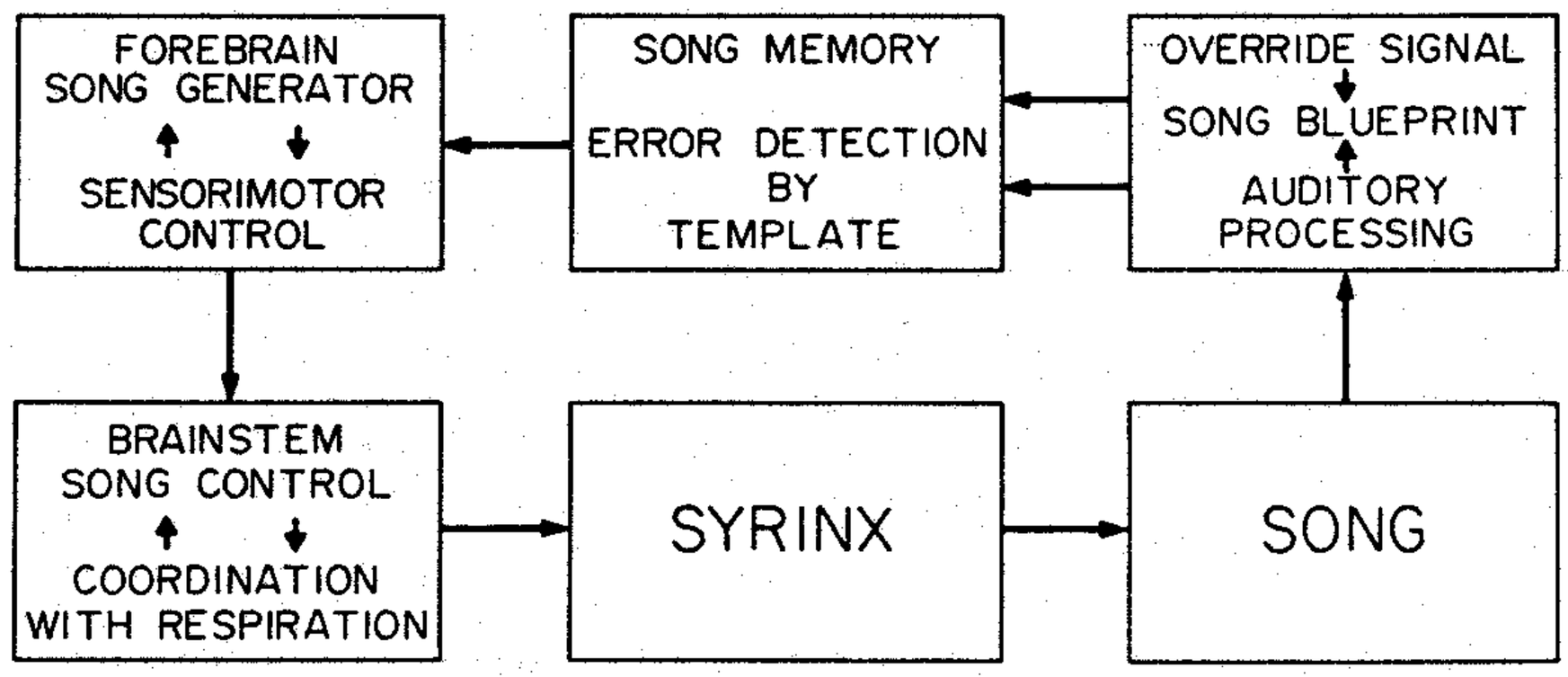

Figure 12 A neural model of song learning. This model is an attempt to integrate anatomical, physiological, and behavioral facts for the explanation of song learning (see text for discussion).

The motor-specific and song-specific neurons may be part of the circuit and result from the fixation process.

The output of the song generator exits the forebrain from RA. The brainstem song control pathway perhaps coordinates vocalization and respiration. The relationship between the two must be reciprocal: The extent to which vocal patterns can modify the respiratory rhythm must be limited; conversely, respiration certainly does not dictate patterned vocalizations. Whether respiratory control is exerted directly on the forebrain song generator is not known, but it can be accomplished automatically, for the respiratory system rejects, mechanically and metabolically, unrealizable vocal patterns, leaving those realizable for control by auditory feedback.

This model identifies unresolved issues of importance: the site and nature of the template, what constitutes the blueprint, and how visual cues override the blueprint. Finally, the coordination between the two brain hemispheres remains one of the most intriguing problems.

SEX HORMONES AND THE VOCAL CONTROL SYSTEM

Affinity for Androgens

Steroid autoradiography shows that most of the adult vocal control nuclei contain neurons that selectively absorb androgens such as testosterone and dihydrotestosterone (DHT) (Arnold et al 1976). It is not known whether NIF and UVA neurons accumulate the hormones. Although in area X, steroid autoradiography does not show a higher grain density, systemically implanted testosterone or DHT induces or increases protein synthesis, suggesting that this nucleus also contains androgen accumulating neurons (Konishi & Akutagawa 1981). The affinity for testosterone is not restricted to higher-order

brain cells, but it occurs as well in the motor neurons of the tracheosyringealis part of the hypoglossal nucleus and in the syringeal musculature. Castration causes a decrease in choline acetyltransferase and acetylcholinesterase activity in this musculature, and administration of testosterone restores their activity (Luine et al 1980).

So far as tests show, the vocal control nuclei do not seem to contain neurons that accumulate estrogen (Konishi & Akutagawa 1981). On the other hand, biochemical assays show that the brain of an adult zebra finch contains both androgen and estrogen receptors. There are sex differences in the number of androgen and estrogen receptor sites; the male brain contains more androgen than estrogen receptors and the converse is true of the female brain (Siegel et al 1983). Also, neurons of the male zebra finch HVc and MAN accumulate more radioactive androgen than those of the female counterparts (Arnold & Saltiel 1979, Arnold 1980).

Anatomical Sex Differences in the Vocal Control System

In many songbirds, the male sings and the female does not. This behavioral dichotomy is due to sexual dimorphism in the vocal control system. HVc and RA in the female canary are half as large as their counterparts in the male. These differences are most pronounced in species such as the zebra finch and the Bengalese finch, in which the female does not sing even under the influence of exogenous testosterone, which induces singing in the female of many species (Nottebohm & Arnold 1976; a recent review in Arnold & Gorski 1984). In the female zebra finch, HVc, RA, MAN, NIF, and area X are either rudimentary or unrecognizable. Comparison of Golgi-stained neurons of RA shows that their somata are much smaller and their dendrites are shorter in the female than in the male. Also HVc and RA contain fewer neurons in the female than in the male. Interestingly, DM and the hypoglossal nucleus show much smaller sex differences than any of the forebrain nuclei (Gurney 1981).

Hormonal Control of Sexual Differentiation

Behavioral effects of early hormone treatment led to the theory that sex hormones exert organizing and activating effects on the nervous system; they control in youth anatomical differentiation of the brain neural circuits for sexual behavior, and they induce in adulthood sexual behavior by activating the existing neural circuits (Phoenix et al 1959). The sexual dimorphism of the brain has been thought to support the theory under the assumption that sex hormones are the cause of the dimorphism. The distinction between the two types of effects depends on the level of analysis, if morphological criteria are the only means of discriminating between the two. Sex hormones can "activate" by inducing morphological changes no matter how small they may be. Testosterone induces dendritic growth in the adult canary's RA. This effect is

presumably reversible. The grown dendrites are assumed to shrink, because the dendrites of RA neurons are shorter when testosterone titer is low (DeVoogd & Nottebohm 1981). Therefore, reversibility or irreversibility should be the criterion for distinguishing one type of effect from the other. Irreversible morphological and physiological changes in the nervous system are organizing effects and reversible changes are activating effects. Because the soma size of neurons in the forebrain nuclei clearly separate the male and female zebra finch, the effects of sex hormones on the sexual differentiation of the vocal control system can be studied at the cellular level.

A subcutaneous implant of estrogen or testosterone in a newly hatched female chick induces a masculine-like differentiation of neurons in her forebrain nuclei, particularly in HVc, RA, X, and MAN (Gurney 1981, 1982, Gurney & Konishi 1980, Konishi & Gurney 1982). The somata of RA neurons in an estrogen-treated female are intermediate in size between male and normal

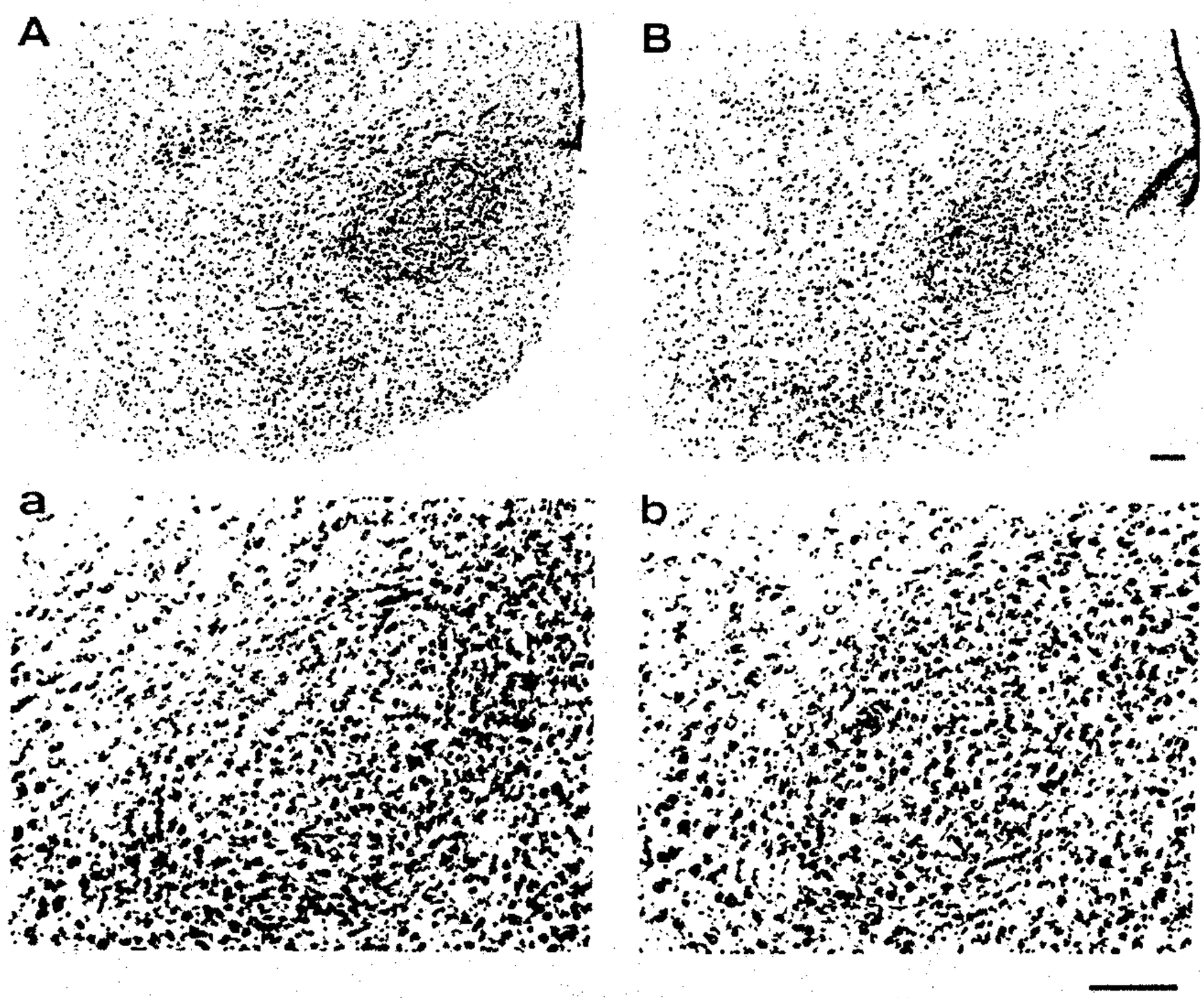

Figure 13 Brain sex differences are absent in young zebra finches. At 15 days of age, male (*A*) and female (*B*) finches show little or no sex differences in the volume and cell size of RA. *A* and *B* are low-power photomicrographs of crysl violet stained RA, and *a* and *b* are their high-power versions, respectively. Both scale bars show 100 μm.

female RA neurons. If such a bird receives an implant of testosterone or dihydrotestosterone in adulthood, RA neurons grow more and the bird sings spontaneously. Because the same treatment, estrogen followed by testosterone, induces neither cell growth nor singing in adult females, the masculinizing effect of estrogen is restricted to a specific period in development.

The above findings led to the conclusion that estrogen induces neuronal growth in both HVc and RA. However, a subsequent study suggests that the small HVc, RA, and MAN of the female are not due just to failure to grow, but to cellular atrophy. At post-hatching day 5, HVc and RA show little sex difference. By day 12, HVc has already undergone atrophy in the female, whereas both RA and MAN remain large and show little sex difference (Figure 13). Then, RA and MAN undergo atrophy in the female between days 25 and

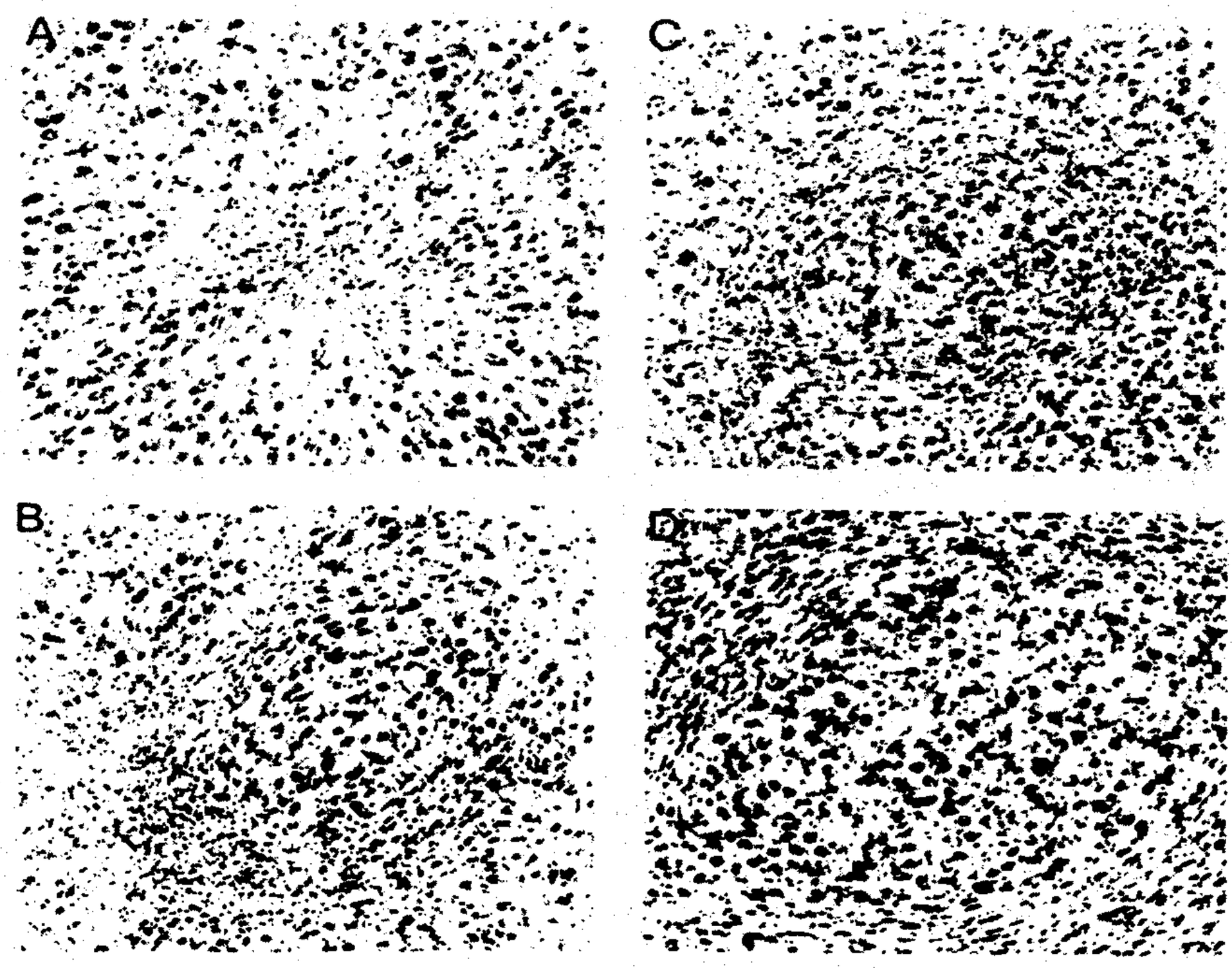

Figure 14 Hormone-induced differentiation of RA. In normal female zebra finches (*A*), RA contains only small neurons, which are not due to retarded growth but to atrophy. A central core of large neurons surrounded by a rim of small neurons characterizes a partially masculinized RA as shown in *B* and *C*, which resulted from estrogen implantation for the first 7 and 12 posthatching days, respectively. A fully masculinized RA contains only large neurons as in *D*. Administration of testosterone in adulthood to birds with *B*, *C*, or *D* condition induced singing. Scale bar 100 μm.

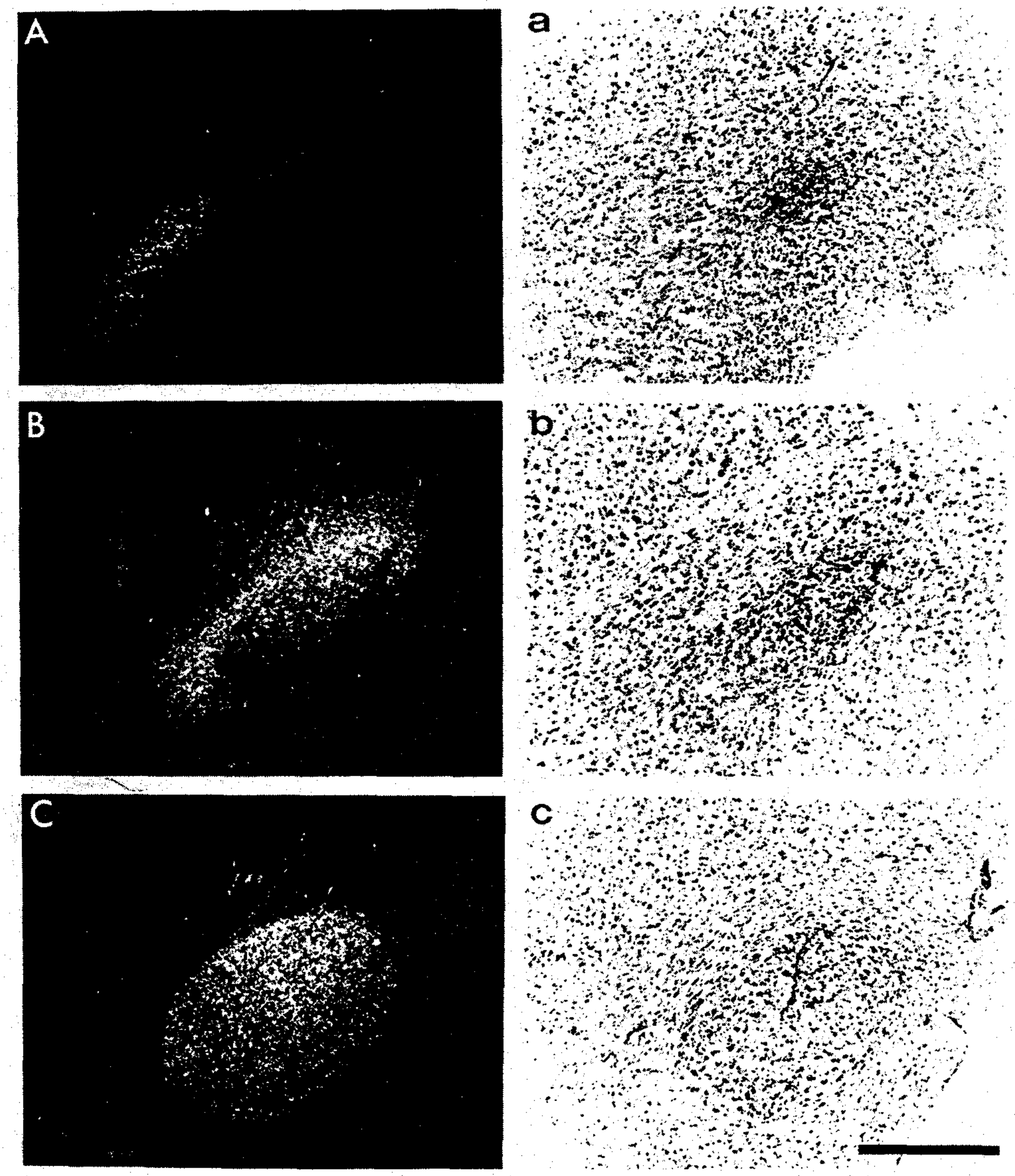

Figure 15-1 Innervation of RA in normal and hormone-treated female zebra finches. Projection of HVc axons to RA shown by amino acid autoradiography compared with the distribution of small and large cells in RA. In normal females (*A* = dark field, *a* = crysl), the axons do not terminate in RA but remain outside it. In partially masculinized females (*B*,) some of the axons appear to enter RA, but a large part of the nucleus still remains uninnervated. Notice that the crysl-violet-stained section (*b*) shows RA populated mostly by small neurons. In fully masculinized females (*C*, *c*), RA contains only large neurons and is completely innervated by HVc axons. Scale 500 μm.

35; their volume and cells become progressively smaller. Thus, sexual differentiation of the forebrain nuclei in the zebra finch vocal control system seems to involve programmed cell death with different time courses for different nuclei. How estrogen prevents cell death is an intriguing question for study.

A fully masculinized RA contains uniformly large cell bodies, whereas a partially masculinized one shows a central core of large cell bodies surrounded by a rim of small cells (Gurney 1982, M. Konishi and E. Akutagawa, unpublished) (Figure 14). The size of the central core is a function of the duration of estrogen release. Anterograde transport of tritiated amino acid and HRP shows that the axon terminals of HVc neurons innervate only these large cells, although the small uninnervated cells in the rim clearly belong to RA. The RA of an adult female does not seem to be innervated by HVc neurons; their axon terminals remain outside the well-demarcated boundaries of RA (Figure 15) (M. Konishi and E. Akutagawa, unpublished).

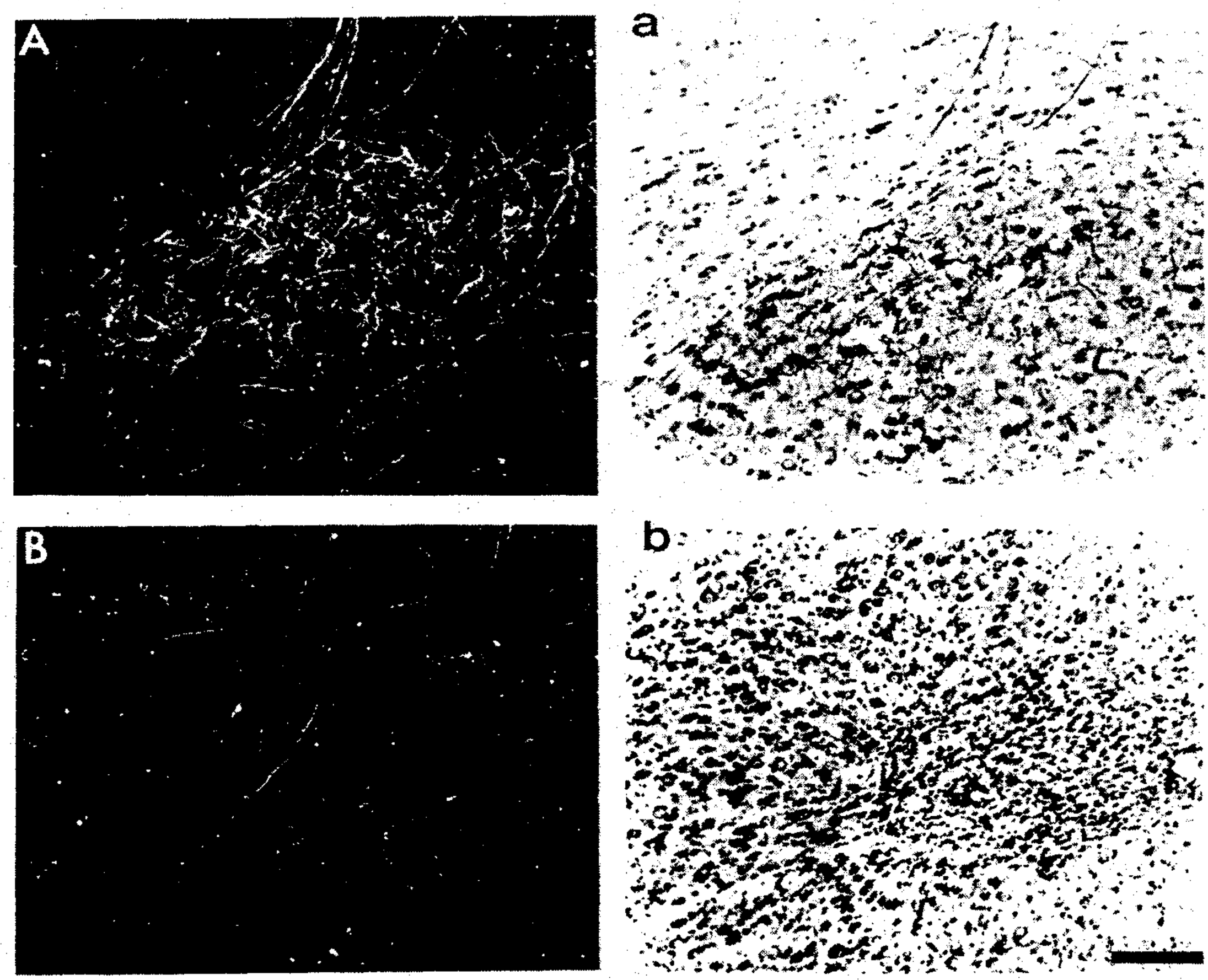

Figure 15-II Axon terminals stained with HRP + cobalt n the RA of a fully masculinized (*A*) and a normal (*B*) female. *A* and *B* are dark field pictures and the corresponding crysl violet stained sections are shown in *a* and *b*. Scale 100 μm.

What hormone controls normal differentiation in the male zebra finch is unknown. Both estrogen and testosterone, but not dihydrotestosterone, masculinize the female vocal system. This result suggests that testosterone acts on the vocal system by being converted to estrogen. However, a recent study shows that a large amount of estrogen is present in the blood of male zebra finch chicks. Therefore, there is no need to postulate the conversion of testosterone to estrogen in the male zebra finch (R. E. Hutchison, J. Wingfield, and J. B. Hutchison, personal communication).

CONCLUDING REMARKS

The ultimate goal of neurobiology is to explain behavior in terms of connections and signals between neurons. Cellular and molecular studies investigate how the connections and signals are made and how they work in intercellular communication. However, their roles in the whole organism can be understood only with reference to its behavior. Behavioral relevance is usually an undefined variable in neurobiological studies. On the other hand, purely behavioral approaches can quickly reach the point where the problems become intractable. The discovery of the vocal control system established a bridge between the cellular and behavioral approaches to birdsong. The results of recent attempts to bring the two approaches together in various studies reviewed above are encouraging. Many of the phenomena associated with birdsong and its neural substrates bear on major issues in neurobiology. Thus, we can address important problems in neurobiology by studying the beautiful songs of birds!

ACKNOWLEDGMENT

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