Three Models of Song Learning: Evidence from Behavior

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ABSTRACT: Research on avian song learning has traditionally been based on an instructional model, as exemplified by the sensorimotor model of song development. Several large-scale, species-wide field studies of learned birdsongs have revealed that variation is narrowly restricted to certain aspects of song structure. Other aspects are sufficiently stereotyped and so widely shared by species' members that they qualify as species-specific universals. The limitations on natural song variation are difficult to reconcile with a fully open, instructive model of song learning. An alternative model based on memorization by selection postulates a system of innate neural templates that facilitate the recognition and rapid memorization of conspecific song patterns. Behavioral evidence compatible with this model includes learning preferences, rapid conspecific song learning, and

INTRODUCTION

Studies of the physiological basis of song learning in birds have traditionally been dominated by what is essentially an instructive model. This is the socalled "sensorimotor model" of vocal learning, with song acquisition followed after some interval by retrieval and production of memorized songs, all proceeding with relatively few constraints aside from the obvious physical limitations on sensory processing and sound production. Over the past decade, however, students of song variation under natural conditions have become increasingly concerned widespread ocurrence of species-specific song universals that are recognized innately but fail to develop in songs of social isolates. A third model combines instruction, in the memorization phase, with selection during song production. An overproduced repertoire of plastic songs previously memorized by instruction is winnowed by selection imposed during social interactions at the time of adult song crystallization. Selection during production is well established as a factor in the song development of several species, in the form of action-based learning. The possible role of selective processes in song memorization meritsfurther neurobiological investigation. © 1997 John Wiley & Sons, Inc. J Neurobiol 33: 501–516, 1997

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with a contradiction that threatens to undermine the principles upon which many current investigations are based. The nature and extent of variation in some natural birdsongs proves to be quite limited, to a degree that it is hardly compatible with viewing song learning as an open process.

The basic case for the dependence of oscine song development on learning remains unchallenged. Species after species of songbird has been shown to develop abnormal song when deprived of the opportunity while young to learn from older birds (Kroodsma and Miller, 1982, 1996; Catchpole and Slater, 1995). The ubiquity of geographical song traditions, often so restricted and so well defined that we do not hesitate to identify them as local dialects, speaks to the pervasive role of learning in avian vocal development (Baptista, 1976; Baptista and King, 1980; Baker and Cunningham, 1985).

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Learned bird songs are highly individualistic, so that with experience birds and bird watchers alike use them for personal identification. The fact that an individual can readily be taught to sing a nonnatal dialect given tutoring at the appropriate phase of development (e.g., Petrinovitch, 1985), and even songs of other species in some cases (e.g., Baptista and Morton, 1981), favors a view of song learning as relatively free of constraints.

The importance of learning in songbird vocal development is thus unquestioned, and the findings of a large and burgeoning body of researchers on many aspects of the neural basis of vocal plasticity attest to the validity of this conclusion. But now comes the paradox. As ornithologists have painstakingly documented geographic variation in the songs of different oscines throughout the species range, first impressions of almost endless variability in acoustic morphology have proved to be deceptive. Careful analysis has repeatedly revealed a limited repertoire of notes, syllables, and patterns from which all songs of a given species are constructed. Each species has its own distinctive set of relatively stable core attributes. The attributes that qualify as universals vary with the taxon, focused sometimes in phonology, sometimes in syntax. In birdsongs in which the major species universals are phonological, variability is greater in such features as the order in which different syllable or note types are sequenced, the intonation with which they are uttered, the subset of the note type lexicon used, or aspects of syntax, rather than in the basic, categorical structure of the phonological core elements. Where the dominant universals lie in the syntactical domain there are more degrees of freedom in song phonology, as is well illustrated by birds that mimic other species, such as members of the mockingbird family.

Thus, far from displaying the almost unlimited variability often assumed, variation in certain aspects of learned bird songs as heard in nature is highly constrained. These limitations are at odds with the traditional sensorimotor view of song learning. Given the uncertainties of copy error, the likelihood of drift as song patterns are passed from generation to generation, and perturbations of the transmission process by intergenerational changes in the acoustic environment in which songs are learned, it is unlikely that any aspects of song structure would remain uniform over time throughout an entire species range if song learning were a fully open process. Yet, the existence of species-specific core features in learned bird songs is now well-enough documented to suggest that it may be a universal phenomenon. This may require us to reexamine the principles upon which theories of song learning are based. It is in this spirit that the following speculative review of three alternative models of the songlearning process is cast: one based on instruction, the second on selection, and the third a hybrid model incorporating elements of both.

MODEL 1: LEARNING BY INSTRUCTION: THE SENSORIMOTOR MODEL

The widely used sensorimotor model, primarily instructive in nature (e.g., Konishi, 1965, 1985; Bottjer and Arnold, 1986; Nottebohm, 1993), originated with studies of local dialects and effects of deafening on song learning in the white-crowned sparrow (Marler and Tamura, 1962, 1964; Konishi, 1965). The songs that males develop when raised in social isolation are abnormal, lacking any trace of the home dialect. Any dialect, natal or alien, can be instated by playing tape recordings to a male during the sensitive period for song acquisition, originally defined in this species as between 10 and 50 days of age. Recent work shows that the sensitive period usually begins later than originally thought, around 20 days, and peaks in the next 30 days, with some acquisition possible later, up to 100 or 150 days. Tape and live tutoring yield similar results (Marler, 1970; Baptista and Petrinovitch, 1986; Nelson, 1997). The timing of the peak can vary by up to a month in different populations (Nelson et al., 1995).

Songs are memorized at this time, and production of imitations usually begins some weeks or months later. Exposure to song is unnecessary at this time; song development is guided by memory, proceeding by reference to an acquired auditory template (Konishi, 1965; Marler, 1976). The work of Konishi on effects of deafening on song development demonstrated the crucial role of auditory feedback for conversion of memorized song into produced song. Early-deafened males of a variety of species produced highly abnormal songs (e.g., Konishi, 1964, 1965; Dittus and Lemon, 1970; Price, 1979; Marler and Waser, 1977; Marler and Sherman, 1985), and in the white-crowned sparrow, males deafened when young produced the same highly degraded song whether they were deafened before song training or after song training but before song production (Konishi, 1965). As production proceeds, auditory feedback becomes less important for the maintenance of song structure after a certain degree of proficiency has been accomplished (Nottebohm, 1966, 1968). Late deafening had less effect on the song of mature males, although recent studies may require some revision of this judgment (Nordeen and Nordeen, 1992). The effects of deafening and the separation in time of memorization and production (Marler and Tamura, 1964; Konishi, 1965) lead to the widely accepted "sensorimotor model" of song learning.

An issue that is unaddressed by this model, and by most behavioral and neurobiological studies that have been guided by it, is the degree to which songbirds possess foreknowledge about the song of their species. Despite the existence of learning preferences in young male songbirds, especially as embodied in so-called "innate song templates" (Konishi, 1965; Marler and Sherman, 1983), the most common view is that the songbird brain will participate in learning and reproducing virtually any song that the bird can be persuaded to memorize, within the limitations of its vocal apparatus. This view is reinforced by the ease with which birds that are mimics can imitate a huge variety of animate and inanimate sounds, and the fact that even nonhabitual mimics will memorize and reproduce songs of other species under certain conditions. In practice, the sensorimotor model has usually been viewed as instructive in nature, with the underlying assumption, either explicit or implicit, that birds know little or nothing about their species song until appropriate auditory instructions have been received.

MODEL 2: LEARNING BASED ON SELECTION

An alternative to the common assumption that prior to auditory experience of song, oscine brains are relatively uninformed about the structure of their species song, is to assume that the naive songbird brain has extensive foreknowledge about the natural song patterns of its species. Instead of modeling the process of song acquisition as if it were based on instruction, an alternative is to invoke a process of selection, operating on preexisting circuitry. Efforts to develop a model of this nature, proceeding through several iterations (e.g., Marler, 1984), most recently by Marler and Nelson (1992), have placed primary emphasis on the existence of species-specific universals in natural birdsongs and on the failure of many of these universals to develop in songs of birds raised in social isolation.

The concept of selective learning mechanisms is well entrenched in neurobiological theory (e.g.,

Jerne, 1967; Changeux et al., 1984) and especially championed in a series of important publications by Edelman (1978, 1981, 1987). Selective learning has already been invoked as a factor in song development, imposed at a late stage during the winnowing of imitations of songs acquired in an earlier, instructive phase (Marler and Peters, 1982; Nelson, 1992; Marler and Nelson, 1993; Nelson and Marler, 1994). The present model extends the notion of selection to earlier stages of the learning process and assumes that extensive pre-encoding of information about species-specific song structure embodied in innately specified brain circuitry provides the basis for the initial process of song memorization. Auditory experience is assumed to operate on this preordained circuitry in a selective fashion, either directly or indirectly, so that some subset of the innate knowledge that it encodes becomes committed to the future guidance of motor development by auditory feedback.

The key component in the model is a set of auditory mechanisms that collectively display highly selective responsiveness to sounds heard during the sensitive period for song memorization. These mechanisms are viewed as operating in parallel to the auditory pathways normally used for receiving and processing sound which are not normally employed in song learning although they can be under certain conditions, as when an alien song is learned. Instead, song memorization is viewed as normally engaging a song-specific pathway especially dedicated to the detection and recognition of conspecific song and preferential commitment of the songs heard to memory. As conceptualized, two kinds of functionally distinct mechanisms operate in this song-specific pathway, with rather different roles in development. Both are defined as templates, serving initially for the selective filtration of incoming auditory stimuli, emphasizing some sounds over others, and ensuring that they receive the subjects' full attention. The templates encode sufficient information to detect conspecific songs and distinguish them from other sounds with which they might be confused in nature, especially other birdsongs. The properties of this song recognition circuitry are innately pre-encoded, serving to detect the set of acoustic universals that characterizes the normal singing behavior of each species. Some of these characteristics are panspecific, such as the controlled tonality that is characteristic of so many birdsongs. Others are species specific, defining the set of features that is unique to and shared by all species members. These include such features as spectral structure and the patterns of amplitude and frequency modulation that collectively define song phonology, and the temporal features that make up the typical syntactical patterns of the species song.

Templates of two developmental forms are postulated: latent templates and preactive templates, distinguished by the spontaneity of their activation. The initial patterns of selective responsiveness of both are under genetic control. Preactive templates become available at a certain stage of development for the bird's use by auditory feedback, activated as a function of normal processes of growth and development. If, for example, a bird is raised in isolation with no song stimulation, preactive templates will guide its song development. They will specify certain phonological and/or syntactical features of the species song, becoming available to guide the motor development of song. They thus coincide with what were previously defined as innate song templates (Konishi, 1965). How these templates become preactive is not clear. They may be activated endogenously in the course of maturation, or early self-stimulation may be required, as by the bird's own nestling or fledgling calls. The diagnostic feature of preactive templates is that stimulation by another individual is not required for them to participate in the motor development of song by auditory feedback.

Latent templates, on the other hand, require activation by specific auditory stimuli before exerting an influence on motor development. The process of activation by sounds matched to their own set of innate phonological and/or syntactical specifications also facilitates the commitment of those same sounds to memory. Thus, both preactive and latent templates contribute to the process of song memorization and later, to motor development. Once activated by auditory stimulation that satisfies their input criteria, latent templates acquire the potential that preactive templates already possess to influence subsequent motor development by auditory feedback. Without effective stimulation, latent templates may never exert an overt effect on behavior, or they may participate in the perceptual processing of the songs of others.

Functions of the Template System

From a behavioral point of view, song templates as conceptualized serve three primary functions. First, they sensitize the young bird to certain patterns of auditory stimulation from the environment, providing a basis for selective responsiveness in the face of the enormous variety of audible but biologically irrelevant sounds that the young organism hears in its natural environment. They sensitize the bird to the subset of sounds most important to it from the viewpoint of song development: namely, the song patterns of its own species. Other sounds are less potent in capturing the bird's attention but are not excluded from its awareness. In certain circumstances, as is typical of mimics such as mockingbirds and starlings, sounds of other species may bypass or override the song-specific pathway, as will be discussed later. Most songbirds do not mimic in nature, however, focusing their song-learning abilities preferentially on members of their own species. The template system is viewed as the primary mechanism for achieving that focus. In special situations, as when raised without access to conspecific song or with a heterospecific live tutor, even birds that do not customarily mimic will learn songs of other species, and there are records of this occurring even when conspecific song is accessible, especially under conditions of very high arousal. In these cases, it is postulated that processing will be mediated by general auditory mechanisms, and not by the song-specific pathway. The second function of the template system is to participate in the commitment of songs to memory. Once memorized, the information is of value in later life in many ways: not only in guidance of the bird's own song development but also in the perceptual processing of the songs of others. The third function that the template system serves is to guide the motor development of the bird's own song repertoire.

Behavioral Evidence Supportive of a Neuroselective Model

Four main lines of behavioral evidence are consistent with the hypothesis that selective processes play a role in the normal process of conspecific song learning. First is the fact that remarkably few auditory experiences of song are sufficient for the memorization of conspecific song to occur. Second, there are learning preferences, typically with a bias favoring conspecific songs. Third, large-scale analyses of song variation have repeatedly revealed the existence of acoustic universals. These recur in the natural singing behavior of all species members, often unique to a species within a given songbird community. The fourth and final point is that many of these universals fail to develop in males reared in social isolation, and even more are lacking from the songs of early-deafened birds. These various lines of circumstantial evidence are consistent with a neuroselective model of song memorization.

A Few Experiences Are Often Adequate for Learning

In the field it is impossible to determine the number of heard songs necessary for normal development. In laboratory studies, it is common to expose birds to hundreds or even thousands of repetitions of song models, either from tape recordings or from live tutors. Such experiments are designed to optimize the likelihood that learning will take place and do not usually specify how few song stimuli are sufficient. But in some cases, we have evidence of the minimum number of experiences of a song type necessary for its memorization and imitation, and the number is sometimes surprisingly small. A male white-crowned sparrow learned from 120 repetitions of a song type over a 20-day period (Petrinovich, 1985). Three European blackbirds (Turdus merula) each learned one song motif from a range of 12-50 presentations on a single day (Thielcke-Poltz and Thielcke, 1960). At the peak of his sensitive period for acquiring tape-recorded songs, a male song sparrow learned parts of a taped song from 30 exposures in 5 min on a single day (Peters et al., 1992). The most remarkable case comes from studies of song learning in the nightingale (Luscinia megarhynchos) (Hultsch and Todt, 1989; Todt et al., 1979). Four males faithfully copied a string of 12 different song types presented once per day for 15 days. In another group, one male acquired 90% of a string of 21 song types presented twice per day for 5 days. Thus, each song type was heard only 10 times. In another experiment, one male learned an entire string of 60 song types heard only once per day for 20 days. This bird not only memorized the 60 song types, but also acquired much information about the order in which they were presented in the training program.

There are indications from the avicultural literature that rapid and precise memorization of a few song stimuli is a special feature of conspecific song learning. Lore among bird fanciers has it that a bird raised in a mixed-species aviary in isolation from members of its species, normally destined to learn eventually from its companions, requires only brief exposure to conspecific song for it to be learned to the exclusion of other species (see Huxley, 1942, for examples). Again, few experiences are often sufficient. These remarkable feats of rapid memorization of complex sound patterns hint at special auditory processing brought to bear on the task of song learning. Song stimuli matching the specifications of both preactive and latent templates may be memorized especially quickly and accurately, as well as being given priority in guiding subsequent song development.

Learning Preferences

W. H. Thorpe (1958, 1961) was one of the first to deduce that song learning preferences must exist. If songbirds learn to sing, and yet for the most part rarely copy sounds of other species, mechanisms must exist to impose selectivity on the learning process. Thorpe demonstrated that captive chaffinches, Fringilla coelebs, failed to learn several kinds of artificial songs and tape recordings. It is hard to be sure whether this failure resulted from active rejection or from deficiencies in the training paradigm. Learning of other, more acceptable models offered in a choice situation would have ratified the training procedure. Also, as in most other songlearning studies, because evidence for or against acquisition was drawn from analyses of the songs, a role for motor constraints in selectivity cannot be excluded. There are hints from some of Thorpe's classic experiments that motor limitations may indeed play a role, as though the vocal apparatus can cope more easily with conspecific songs than with other sounds. One male chaffinch that learned elements of a tree pipit song (Anthus trivialis), chosen because it bears some resemblance to chaffinch song, eventually discarded them and reverted to "a modified version of its innate or Kaspar Hauser song" (Thorpe, 1958). Similarly, one male chaffinch exposed to canary song when young produced canary imitations in its plastic song, but discontinued them at the time of song crystallization (Thorpe, 1958). Thorpe invoked sensory predispositions as an explanation, but it is equally possible that production constraints were responsible for this rejection of heterospecific material late in the process of motor development.

A similar result was obtained with the swamp sparrow (*Melospiza georgiana*) (Marler and Peters, 1977, 1982). Male swamp sparrows normally reject song sparrow songs as models for vocal learning, but by experimenting with synthetic songs in which phonological and syntactical cues were independently varied (review in Marler and Peters, 1989), swamp sparrows were induced to learn some song sparrow material. By following song development closely, it was possible to capture the first efforts at imitation in plastic song of 34 swamp sparrows exposed to simple repetitive swamp-sparrow-like trills that consisted either of swamp sparrow (474) or song sparrow syllables (458). At this stage, they sang 116 imitations of swamp sparrow syllables and 34 imitations of song sparrow syllables, but when their overproduced plastic song repertoires crystallized, they still discarded more of the song sparrow syllables (91%) than of the swamp sparrow syllables (59%). Again, rejection of heterospecific song material in late stages of motor development suggests that the vocal circuitry and apparatus of these swamp sparrows were more comfortable reproducing conspecific than heterospecific songs.

Thorpe may also have been premature in concluding from his chaffinch experiments that "the chaffinch has the inborn blueprint conferring on it a tendency to learn to pay attention to certain kinds of sounds and certain types of phrase only" (Thorpe, 1958, p. 84). In addition to the confounding of sensory and motor constraints, early experience was not adequately controlled. Several of Thorpe's experimental subjects were not raised by hand but were captured after fledging at an age of several weeks, providing them with ample opportunity to learn attributes of chaffinch song prior to being brought into the laboratory.

Experimental controls of early experience were more complete in later studies on learning preferences of North American sparrows. Hand-reared white-crowned sparrows given a choice of tape-recorded songs of white-crowned and song sparrows favored their own species (Marler and Tamura, 1964; Marler, 1970). However, early developmental stages of song production were only casually studied, so once again a role for motor constraints could not be excluded. More exhaustive analyses of learning preferences were conducted with two other members of the same family, the swamp sparrow (Melospiza georgiana) and the song sparrow (Melospiza melodia) (reviewed in Marler and Peters, 1989). Males taken as nestlings and raised by hand in the laboratory were presented with a choice of learning equal numbers of tape-recorded songs of both species. Isolated males displayed a highly significant preference for learning their own species' song. Despite evidence that song learning does not take place in nestling songbirds (Slater, 1983; Marler and Peters, 1987), there remained a lingering doubt that song experience in the nest might influence later behavior as in some precocial birds. Although this seemed unlikely in an altricial species, hatched at a much earlier developmental stage, in a second study, birds were taken as eggs from nests in the wild and raised in the laboratory. Choice experiments with them yielded the same results, showing that early nestling experience is not responsible for the learning preferences that the birds display (Marler and Peters, 1987, 1988, 1989). Evidently, song-learning preferences are innate. As already indicated, however, analyses of the attrition and crystallization of plastic songs suggests that motor constraints may contribute to the favoring of conspecific song. Thus, final proof of purely sensory contributions to song recognition and memorization as a basis for selective learning remained elusive.

The need for learning preference tests that are independent of the production of imitations led to several new approaches. Dooling and Searcy (1980) developed a cardiac measure of the responsiveness of newly fledged sparrows to tape-recorded songs. The results indicated preferential responsiveness to conspecific song, stronger in swamp than in song sparrows, as early as 3 weeks of age. The procedure was demanding, however, and only five subjects were used—three males and two females—undermining the significance of the results but also serving as an important reminder that selective song responsiveness in females is a valid subject for study.

Resolution of this methodological dilemma came when Nelson quantified the calling behavior of young sparrows in the laboratory in response to playback of tape-recorded songs, showing that newly fledged white-crowned sparrows of both sexes call more to conspecific than to heterospecific (song sparrow) song (Nelson and Marler, 1993). Whaling et al. (1995) went on to replicate this result and to demonstrate strong responsiveness in young, naive subjects not only to complete white-crown songs but also to artificial songs consisting of repetitions of single song elements, including whistles, buzzes, and complex and simple trill syllables.

There is thus unequivocal evidence of selective responsiveness to conspecific song stimulation prior to any song production, including subsong. Evidently sensory mechanisms exist that enable the young songbird to discriminate between conspecific and heterospecific song. The innate knowledge about their species song that young sparrows display is based not on a single sign stimulus, but on multiple characters, suggesting that they possess remarkably complete internal representations of the normal singing patterns of their species. The physiological means by which this is accomplished is unknown. Until recently, it has not been the subject of detailed investigation (Whaling et al., 1995). Yet, innate selective responsiveness may conceivably hold the key to understanding the memorization phase of the

process of learning to sing, perhaps as represented in this neuroselective model of song development.

Species Universals in Learned Songs and Their Failure to Develop in Isolates

Learned birdsongs are incredibly variable. In addition to the widespread occurrence of local dialects, songs of no two individuals are precisely identical, and as already noted, birds rely on the individual differences that are always present in learned songs to identify one another personally (review in Falls, 1982). It was therefore unexpected when several efforts to characterize the song patterns of an entire species revealed that variation in the natural song patterns of some birds is more constrained than anticipated. Along with the song characteristics that vary between individuals and populations, there are always others that are shared, and a surprising number of natural song features proved to be species specific. Occurrence of these species universals, sufficient in some cases to describe the major features of all known natural song variants, contradicts previous impressions of almost unlimited variability in the culturally transmitted patterns of birdsong, casting doubt on the very concept of instructive models of learning unconstrained by special predispositions. With a neuroselective model of song learning, however, the existence of species universals in song would be predicted. Here are a few examples.

Universals in Swamp Sparrow Song

The simple trilled song of the male swamp sparrow is stereotyped in overall structure and variable in the construction of the repeated syllables that make up the 2-s song. Swamp sparrow songs develop abnormally in social isolates and are highly degraded in birds deafened early in life (Marler and Sherman, 1983, 1985). In addition to individual differences in the syllables from which swamp sparrow songs are constructed, there are also learned dialects, each thought to cover some hundreds of square miles. Learning early in life determines which local dialect a male sings, and also the dialect to which females are most responsive (Balaban, 1988). Thus, swamp sparrow song satisfies the criteria for a culturally transmitted behavior. If purely instructive processes were responsible, there should be a tendency for the song patterns present in a population to drift over time, as songs are transmitted over generations, as birds invade new habitats, with new acoustic environments, and as transmission errors accumulate from generation to generation. Under such circumstances, the boundaries around the song patterns of a given species should be fuzzy and changing, with a high degree of variability. Descriptive analysis of the typology of swamp sparrow song revealed a different picture (Marler and Pickert, 1984). Any known natural swamp sparrow song can be described by reference to a lexicon of six note types, defined on the basis of such basic characteristics as duration, bandwidth, and the pattern of frequency modulation. Much the same typology results if it is derived from sound spectrograms by eye (Marler and Pickert, 1984) or by statistical procedures such as multidimensional scaling (Clark et al., 1987; Nelson and Marler, 1989). There is a certain order to the way in which these note types are assembled into a song syllable, with rules that vary from one locality to another. For example, a New York song syllable typically begins with a type I note and closes with a type VI note, with one or more notes of some other category in between. The Minnesota dialect has an opposite rule, with song syllables typically beginning with a type VI note and ending with a type I note. Males and females will learn either dialect depending on individual experience. In females, the experience appears to determine the song type that they find most stimulating sexually, presumably one that they will favor in a mate, when they reach reproductive maturity (Balaban, 1988).

Thus, instead of the expected unmanageable degree of variability, a highly ordered system was found with predictable rules operating on a surprisingly limited number of basic acoustic patterns. Superimposed on the basic typology, there is a significant degree of within-category variation in note morphology from bird to bird. This variation, together with the many different ways in which note types can be combined to create a syllable, leaves ample room for dialects and individual variability, so that no two individuals even in the same population have exactly identical songs. Territorial males are, in fact, highly responsive to individual differences as a basis for neighbor-stranger discrimination (Searcy et al., 1981a, 1982). Species recognition, on the other hand, in both sexes appears to be based on those song features that are species universals (Searcy et al., 1981b,c).

Universals in Songs of Canaries, Buntings, and Other Species

Songs of male domestic canaries, *Serinus canaria*, a traditional subject for research on the neural basis of vocal learning, can be defined on the basis of

about 10 distinct syllable types, each with some degree of within-category variation. The presence of these "tours" in all canary songs has been known by generations of fanciers who breed and display certain strains competitively for their prowess as singers (Guttinger, 1985, 1979). Canary songs are learned by acquiring particular sets of note categories and particular sequences of note types (Waser and Marler, 1977). Obvious copying occurs in sequencing and at the level of subtypes within the 10 major categories, varying in subtle aspects of pitch or modulation rate. Male canaries raised in auditory isolation have an abnormal song, lacking several of those features that are universal in the song of canaries with normal social experience (Guttinger, 1979; Marler and Waser, 1977; Waser and Marler, 1977). As in the swamp sparrow, so in the domestic canary we can speak of universals in note typology that are generally distributed but lacking in birds raised in isolation.

Universals are also present in songs of the indigo bunting, famous from the research of Thompson (1970, 1976), Shiovitz and Thompson (1970), Shiovitz (1975), Emlen (1971, 1972), Payne et al. (1981), and Margoliash et al. (1991), but on a different scale. Here there is a specieswide syllable repertoire of something over 100 types. The same catalog, first developed by Thompson, has been used for nearly 30 years to describe thousands of indigo bunting songs in all parts of the species' range. Individuals and populations differ in song structure, and there are local dialects (Payne, 1983) based on which subset of the specieswide syllable repertoire is used and the ordering of the syllables within the song. Baker and Boylan (1995) recently updated the species-universal catalog, now totaling 127 syllable types for the indigo bunting, Passerina cyanea, and 122 syllable types for the closely related lazuli bunting, Passerina amoena (cf. Thompson, 1968), all recurring "at similar frequencies of abundance in different populations at different times." Again, song develops abnormally in isolation (Rice and Thompson, 1968), and normal song patterns are learned and transmitted by cultural transmission (Payne et al., 1981; Payne and Payne, 1993).

The Zebra Finch

It is the subject of scores of studies of song learning and its neural basis, but little effort has been directed to descriptive studies of zebra finch song structure. Nevertheless, inspection of published analyses always seems to reveal the same four or so basic note types, some with considerable within-category variation, others with relatively little (Sossinki and Bohner, 1980; Bohner, 1983; Williams, 1990). Learning determines which variants are used and their sequencing (Price, 1979). Of special interest is the finding by Clayton (1990a,b) that songs of an island subspecies on Timor have a structure rather different from those in Australia. Thus, species universals in song structure vary not only between species, but also from one subspecies to another. These song universals have survived many generations of breeding in captivity. Once again, songs are abnormal if males are raised in isolation and even more degraded in deaf birds (Price, 1979; Williams et al., 1993).

Songs of the wood thrush, Hylocichla mustelina, are among the most beautiful of all to human ears. They have three parts, a, b, and c, of which bis especially influenced by learning (Whitney and Miller, 1985; Whitney, 1989). Inspection of hundreds of songs led to the conclusion that all natural *b*-phrases, wherever they occur in the species range, fall into about 20 rough categories, each with a degree of within-category variation. These bphrases develop abnormally in isolation (Lanyon, 1979; Whitney and Miller, 1987). Songs of wood warblers, such as the chestnut-sided warbler, Dendroica pensylvanica, which has two distinct song types, are learned, and develop abnormally in isolation (Byers and Kroodsma, 1992). One song type of this species has proved to be remarkably uniform throughout the species range (Byers, 1996). The prothonotary warbler, Protonotaria citrea, is a similar case (Bryan et al., 1987), with similar song patterns recurring in different parts of the species range. Baker and Boylan (1995) reviewed other examples. There can be no doubt that specieswide song universals are a frequent feature of learned birdsongs, a predictable correlate of a selectionbased learning process.

Summary of Evidence and Replay of the Selection-Based Model

The four lines of evidence reviewed suggest that a selective model of song learning is worthy of further investigation. The ease and precision with which a few exposures suffice for conspecific songs to be memorized and reproduced by a naive subject are notable, consistent with a neural system especially dedicated to the tasks of song recognition and commitment to memory. Other models cannot be excluded on this basis, however. More direct and compelling is the evidence for learning preferences, im-

plying neural mechanisms that focus the young bird's attention selectively on conspecific song patterns. Most striking are the demonstrations of species-specific universals in the structure of learned songs, many of which fail to develop in birds raised in isolation. These birds behave as though they possess extensive innate knowledge about their species song, but cannot transform that knowledge into produced song without the experience of matched sounds in the songs of others. Such behavior is consistent with a selection-based model of the song memorization.

The essential postulate of this model is that species-specific song universals are pre-encoded in the brain, and that every young male of a species has the potential to produce all universals. A plausible model also has to take account of the all-pervasiveness of developmental plasticity, the impact of auditory experience, and the effects of deafening. With the exception of a small but interesting minority (see Marler and Nelson, 1992), most song universals fail to develop normally in isolation. Even fewer develop in birds deafened early in life as illustrated by the swamp sparrow (Marler and Sherman, 1983, 1985). Any theory of song development must somehow deal with the highly degraded songs of early deafened birds and the more structured songs of birds raised in isolation with their hearing intact. The memorization by selection model attributes the song structure present in hearing isolates to preactive auditory templates that become active in development whether or not conspecific song has been experienced. Latent auditory templates cannot exert an influence on motor development before activation by auditory stimuli that match their acoustic specifications. Stimulation of templates is also presumed to aid in memorization of song stimuli. During memorization, stimulus-triggered events in different parts of the template system will become similarly coordinated in time in memory, thus matching the pattern of the stimulus song. Also, sound stimuli that engage templates will be committed to memory more rapidly and precisely than others that do not, such as songs of other species. It is presumed that material memorized after interaction with the template system will be dedicated specifically to the processing of song stimuli and to guidance of the bird's own song production.

Qualifications of the Model

Any song-specific template mechanisms that exist must operate in parallel with brain mechanisms that support generalized auditory learning, presumed to be capable of sustaining song learning in some circumstances. Even highly selective song learners can be persuaded to learn alien songs if those of their own species are withheld. Especially when highly aroused by social stimulation, this can occur in the presence of conspecific song stimulation, bypassing the template system. It is presumed that this will take more time and effort than learning own-species songs, which as we have seen can be very rapid and precise. All birds can be taught to give an arbitrary response to alien songs, but interestingly, sensitivity to individual differences is typically greater with conspecific songs than with those of other species, consistent with the idea that template-based acquisition would confer greater sensitivity to acoustic detail (Dooling, 1989; Sinnott, 1989). However, involvement of the template system in song memorization is not obligatory, as when a nonmimic learns the song of another species.

Template systems could be involved directly or indirectly in memorization. They could serve to flag song components and other associated stimuli especially worthy of attention and memorization by the general auditory system. Consistent with this idea is the success Soha (1996) achieved in persuading birds to learn songs they would otherwise spurn by embedding within them rudiments of the birds' own species song. It remains for neurobiologists to determine where in the oscine brain these different functions are served and the degree to which the template system, if it exists, achieves its functional ends by intrinsic mechanisms, or more indirectly, by priming other parts of the brain that serve more general functions of sound memorization, to pay special attention to conspecific song.

MODEL 3: MEMORIZATION BY INSTRUCTION FOLLOWED BY SELECTION IN PRODUCTION

A model of song learning incorporating both memorization by instruction and selection during production originated with a shift of focus from the memorization phase of song development to the production phase. A new form of vocal plasticity termed ''action-based learning'' was revealed (Marler, 1991; Marler and Nelson, 1993; Nelson and Marler, 1994). Once songs have been memorized by a young sparrow, it begins after some interval to produce imitations, often supplemented in plastic song by inventions and improvisations. With practice, the motor patterns stabilize and the adult song repertoire crystallizes. After closure of the sensitive period for memorization of new songs, and prior to crystallization, it seems to be common for songbirds to produce more songs than they will need. The overproduced repertoire is winnowed as crystallization approaches, and social factors exert an influence on which songs are kept and which are discarded. This is the context for action-based learning.

Nelson demonstrated that a process of selection lies at the heart of action-based learning (1992a,b; Nelson and Marler, 1994). Overproduction was first demonstrated in the swamp sparrow, Melospiza georgiana (Marler and Peters, 1982). In plastic song, beginning at about 6-9 months of age, imitations of previously memorized tutor songs first appear. Young males produce more plastic song types than needed for a mature repertoire. The overproduced repertoire of 12 or so song types suffers gradual attrition until it has shrunk to about three song types, the typical adult male repertoire. Crystallization then occurs. Similarly, wild young male field sparrows, Spizella pusilla, and white-crowned sparrows, Zonotrichia leucophrys, often sing several song types when first establishing territories. They then select one, usually choosing to retain that which best matches one of a neighboring rival's songs, at the site where the young male is establishing his first territory, often somewhat remote from the birthplace (Nelson, 1992). This takes place after closure of the sensitive period for memorization of new songs in these species (e.g., Nelson and Marler, 1994). The retention of a matched song has sometimes given the mistaken impression that young males were imitating new neighbor songs at this stage. In fact, a process of selection from within a pre-established repertoire is responsible.

In experimental verification of this process, hand-reared male white-crowned sparrows were tutored with a number of song types early in life. When they began to produce imitations in plastic song the following spring, other songs were played to them that matched one item in their overproduced plastic song repertoire, simulating the matched countersinging between rivals that occurs in nature when yearlings first establish their territories. In addition, birds heard a novel song type never encountered or produced before. Although these birds were incapable of acquiring new songs at this stage, they retained and crystallized the song type that most closely matched the tutor and discarded nonmatching types. This process of selective retention and attrition was imposed on a repertoire acquired at 5-6 weeks, more than 200 days previously (Nelson and Marler, 1994).

This sequence of events can be modeled as a

combination of instructive and selective processes. The sensorimotor model for song memorization assumes that the young bird memorizes new songs by instruction, committing to memory more than will be needed for a normal adult repertoire. These memorized songs, together with invented and improvised material, emerge at a later stage when memorization by instruction is no longer possible, as the overproduced repertoire of plastic songs. A process of selection now intrudes, mediated by patterns of social interaction in which the young male engages as the overproduced repertoire is winnowed. In intermale countersinging, responding with a song type that matches the competing rival is especially effective in territorial establishment, even if the matching is only approximate. This interactive potency may contribute to the process of selective retention.

The process of selection appears to proceed independently from memorization by instruction. The two kinds of process proceed on different timetables and must engage different neural mechanisms despite the fact that the behavioral consequences are somewhat similar: Both result in a degree of experientially dependent matching of songs produced with songs heard. Further evidence that instruction and selection are independent processes is provided by the parallel case of the brown-headed cowbird, Molothrus ater, in which the male's choice of which overproduced song types to retain is guided not by male-male interactions, but by interactions with females. Males retain those song types that elicit a distinctive "wing stroke" display from females (West and King, 1988). In this case, visual signals rather than auditory exchanges are responsible for the development of male vocal behavior. As studies proceed, it is likely that action-based learning as a form of selection-based developmental plasticity occuring during motor development, will prove to be widespread and that depending on the species, a range of interactive processes can control which items in an overproduced repertoire are retained and which are set aside.

DISCUSSION

Of the three models of vocal learning reviewed, the one based on concepts of memorization by selection is most radical. The lines of behavioral evidence with the strongest bearing on the tenability of this model are: (a) the existence of learning preferences in naive birds, leading them in the very first step of the learning process in which songs are memorized, to favor conspecific songs over those of other species. In some cases, innate knowledge of a wide array of species-specific song attributes has been demonstrated prior to any song production of a wide array of species-specific song attributes. (b) Another line of evidence is the failure of much of this innate knowledge to be realized in the songs of birds raised in social isolation. Certain aspects of the normal song of the species do develop in social isolates, however, provided that their hearing is intact. In birds deafened prior to singing, even these few normal features of isolate songs fail to develop other than a few basic attributes such as song duration and some elements of phrase structure, perhaps controlled by respiratory motor programs (Marler and Sherman, 1983). As Konishi (1965) demonstrated in his classic studies, auditory feedback is critical for normal song development. (c) Harder to interpret, but perhaps ultimately a more valuable source of new insights, is the discovery that variation in the patterning of natural bird songs is often highly constrained and that learned often songs display species-specific universals in many aspects of their structure. Those aspects that do vary can be permuted in many different combinations, providing ample acoustic vehicles for local dialects and individual differences. Other aspects of song structure, many more than previously realized, are shared by all species members, each individual employing some fraction of the universal lexicon.

None of these lines of evidence is compatible with a simple instructive model of song learning, the essence of which is taken to be that the process is basically open and unconstrained. In fact, the version of the sensorimotor model presented here (Fig. 1, Model 1) is probably something of a caricature, although it serves a purpose by heightening the contrast with other models in which constraints on the learning process are more evident and pervasive. All three lines of evidence sit more comfortably with a model based on selection, but a neuroselective model of song learning is hardly likely to be taken seriously until direct neurobiological support is forthcoming. Thus, both of the first two models set forth, one briefly, the other in more detail, remain speculative.

The third model, combining elements of instruction and selection (Fig. 1, Model 3), has greater substance. The role of social processes in selecting songs for crystallization from overproduced plastic song repertoires is well established and likely to be widespread. The basic underlying process is straightforward. At a certain stage of development, a wide array of motor patterns is produced and subsequently winnowed down to a smaller and more enduring repertoire (review in Nelson, 1992b; Marler and Nelson, 1993). The timing of this stage of highly unstable motor activity will vary widely from species to species. In some, such as the male swamp sparrow, it is brief and occurs once as the young male approaches sexual maturity. In others, such as the field sparrow and the indigo bunting, it is more extensive, encompassing a significant part of a male's first breeding season. The developmental window for action-based learning may recur periodically on a seasonal basis in some species. The canary may prove to be such a case (Nottebohm et al., 1986, 1987). There is also likely to be variation between species in the social mechanism that controls the winnowing process. Two versions have already been described involving male-to-male territorial countersinging in sparrows and a form of sexual reinforcement by females in the brownheaded cowbird (West and King, 1988). Thus, action-based learning is well established as a component in the development of learned bird songs and may have parallels in other contexts, such as the transition from play to adult behavior. Less clear is the source of the overproduced repertoire upon which action-based learning operates. If in the face of further research instructive models of song memorization prevail, then a mixed model will be vindicated. On the other hand, if a selection-based model of song memorization proves to be closer to the truth, then a fourth model must be contemplated in which instruction in the pure sense plays little role (Fig. 1, Model 4). It would be premature to try to forecast which of these alternatives is valid or whether some mechanism will emerge, as yet unanticipated, that provides the basis for song memorization as a first step in the learning process.

Where might song template processing occur in the oscine brain? As a direct consequence of the discovery of the song system in the oscine brain (Nottebohm et al., 1976; Kelley and Nottebohm, 1979), we have a more complete picture of the underlying circuitry for song learning than for any other learned behavior. Many functional questions remain, however. One of the most challenging is the role of the so-called "recursive" or "anterior forebrain circuit," consisting of the chain of nuclei HVc-Area X-DLM-IMAN-RA, in the process of song development. Lesioning seems to have no immediate effect on adult singing behavior, but greatly disrupts song ontogeny (Bottjer et al., 1984; Sohrabji et al., 1990). If the naive songbirds' brain is in fact innately equipped with an array of auditory templates for song, the recursive song circuit is a likely place for them to be found. This circuit is in

1. Memorization by instruction: sensorimotor learning





Figure 1 Diagrams of the three models described in detail in the text (Models 1-3) plus a fourth that combines elements of Models 2 and 3.

place and functional early in life, prior to establishment of the motor circuit; and the functional timetable of at least one of its components, IMAN, agrees well with the timing of song acquisition, both in canaries and in zebra finches. Auditory neurons can be found in HVc and throughout the recursive circuit, and some have the remarkable property discovered by Margoliash (1983, 1986) and Margoliash and Konishi (1985) that in adults, they are maximally responsive to the male's own song. Highly selective song responsiveness in adulthood is especially characteristic of IMAN, an obvious place to look early in life for sensitivity to the species-specific universals to which we know songbirds are behaviorally responsive. Responsiveness to a male's own song develops only late as song performance matures (Volman, 1993). Prior to that, song responsiveness is less specific (Doupe and Konishi, 1992; Doupe, 1997). Only recently has exploration begun of the possibility that there is species-specific song responsiveness in the song system at early stages of development (Whaling et al., 1995). If the selection-based model of song memorization has any validity, then song-selective circuitry must exist somewhere in the naive songbird brain. The selective model of learning predicts that activation of this circuitry will play a critical role in the process of song memorization, with an influence on the processing not only of the bird's own species songs (see Mooney, 1992), but perhaps for those of other species as well. The search may embrace other pathways than the song system sensu stricto including subareas of the forebrain auditory projection area Field L, where neurons that selectively respond to complex sounds, including songs and calls, have been identified (Leppelsack, 1983; Scheich et al.,

1979). Other sound-processing areas may also be involved, and are only now being identified (Clayton, 1997), as in recent efforts to establish directly the role of gene activation in the process of song learning.

Mello et al. (1992) broke new ground with their demonstration of the activation of an immediate early gene, zenk in adult canary and zebra finch brains in response to song stimulation after being deprived of song access. Heterospecific song had a weaker effect, and tone bursts none at all. The increases occurred in several unexpected areas, and were most marked in NCM in the neostriatum (caudo-medial neostriatum). This area had not previously been identified as part of the song system, although it is nearby and close to Field L, the auditory forebrain projection area. Most surprising was the lack of *zenk* induction by song in the general song system. It may be that much of the critical processing of song stimuli by the template system, such as is postulated, is in fact completed prior to the arrival of auditory information in the song control system. Significant support for the memorization by selection model would result if gene activation is demonstrated in young males hearing song for the first time. The method may be sensitive enough to reveal what aspects of song are responded to, as the use of artificial songs is known to be behaviorally effective in young naive birds. The zenk response can discriminate between conspecific song types. After habituation to one type, the response resumes if another is substituted (Mello et al., 1997). Localization in the brain appears to be sufficiently precise to pinpoint whether and where special perceptual processing of song stimuli is taking place at different stages of development, in relation to the classical oscine system about which we now know so much. We may even be on the brink of a new era of research on genetic mechanisms that sustain learning, not just as it occurs in song development, but in other types of learning as well, thus spanning the full spectrum from genes to behavior. Genetic contributions to behavioral development, long emphasized in classical ethology, may come once again to receive full and proper acknowledgment. We may even have a prospect of achieving complete solutions to some of the nature-nurture conundrums that have exercised students of both animal and human behavior for so long. Song-learning studies are well placed for a leading role in this development.

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