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Selection-based learning in bird song development

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ABSTRACT Bird song is a model system for study of the neurobiology, development, and functions of learned vocal communication signals. Research on avian song learning has been dominated by an instructive model of learning—the sensorimotor model. Developmental plasticity is assumed to be based on the incorporation of novel material into the song repertoire. Experimental evidence now indicates an alternative form of plasticity operating in harmony with sensorimotor learning, based on principles of selection, rather than instruction. Song dialects, a common consequence of vocal learning, can be achieved by overproduction of previously memorized songs and selective attrition of those that fail to match the dialect of interacting males. These distinct processes of learning have important implications for study of the neural substrates underlying song production and perception and for efforts to interpret patterns of geographic variation in song.

Learning is generally thought to provide the behavioral flexibility advantageous in an uncertain environment. Two general models of learning mechanisms may be termed instructive and selective (1–4). In the class of instructive models, environmental stimulation adds information not previously present either latent in the brain or already realized in the behavioral repertoire. For example, a young bird is instructed when it memorizes a novel song. In contrast, a selective model posits that the organism already possesses the information prior to stimulation by the environment. Learning consists of the selection of certain behaviors and their underlying neural substrates as a function of experience and usage.

The existence of vocal dialects in birds first suggested that bird songs are learned. Adult male white-crowned sparrows (*Zonotrichia leucophrys*) typically sing one song type, and those at one location sing similar songs, which differ from those at other localities (5, 6). Young males raised in acoustic isolation develop abnormal songs, but naive young males can learn any tape-recorded dialect (7). Thus, experience with adult song models is necessary for normal vocal development.

The sensorimotor model of song learning includes two stages: a sensory (instructive) phase in which songs are memorized, and a sensorimotor phase in which the bird compares its own song, via auditory feedback, to the memory trace acquired earlier (8). In sparrows, most songs are memorized prior to 50 days of age but are not produced until some weeks or months later (7).

If one postulates that vocal plasticity in birds is mediated solely by instructive mechanisms, then song-matching dialects could arise in two ways. In sedentary populations, such as those of Nuttall's white-crowned sparrow, *Z. l. nuttalli*, dialects will result when males settle and breed as adults in the same area where they acquired their song. In migratory populations, such as those of the Montane white-crowned sparrow, *Z. l. oriantha*, where dispersal distances from natal

to breeding site are large, then an instructive model requires that the ability to acquire novel songs must persist into a bird's first spring when he learns songs from his neighbors as he settles upon a breeding territory (9).

We present here an experimental test of the hypothesis (10, 11) that song matching is achieved not by instruction, but by a selective attrition process, occurring at a phase of the life cycle when novel songs can no longer be acquired. This hypothesized process, also termed action-based learning (11), derives from several observations. When young males of the swamp sparrow (*Melospiza georgiana*), closely related to the white-crowned sparrow, are learning to sing, they produce many more song types in the plastic stage of song development than are required to form a mature repertoire (10). Plastic song, beginning at approximately 6–9 months of age in young male sparrows, is the stage where imitations of previously memorized tutor songs first appear. Songs are then lost from the young males' overproduced repertoire of 12 or so types until, in the sexually matured swamp sparrow, approximately 3 song types remain (10). Similarly, wild young male field sparrows (*Spizella pusilla*) and white-crowned sparrows often sing multiple song types when first establishing territories. Apart from rare exceptions (2% of field sparrows, ref. 12; 3% of white-crowned sparrows, refs. 6, 13, and 14), males then selectively retain only the song type that best matches one of their neighboring rival's songs (12, 15).

We tested the selective attrition hypothesis by tutoring hand-reared male white-crowned sparrows with multiple song types in the first months of life. When the birds began to sing imitations of tutor songs in their first spring, we played back to some birds a tutor song that matched one of the song types in their overproduced plastic song repertoires. This experimental design mimics the matched counter-singing between rivals that occurs when yearlings first establish their territories. Control birds heard a novel song type, never heard or produced before. If dialects arise by a process of selection, then experimental birds should retain and crystallize their matching type and discard the nonmatching type; the control birds should not acquire the novel type, but instead crystallize one of their previously memorized and produced plastic songs. If, on the other hand, song-sharing results from the instructive acquisition of new songs from territorial rivals as yearlings, then control birds should acquire the novel type.

METHODS

Subjects. We collected 10 male white-crowned sparrows in 1990 (2 *Z. l. nuttalli* and 4 *Z. l. oriantha*) and 1991 (4 *oriantha*) as 3- to 10-day-old nestlings and handreared them to independence. *Z. l. nuttalli* were collected at the Bodega Marine Lab Reserve, Sonoma County, California, and the *Z. l. oriantha* were collected in Lee Vining Canyon near Tioga Pass, Mono County, California.

Tutoring. Birds were individually housed in sound isolation chambers and tutored daily with tape-recorded natural songs of both subspecies. Tutor songs were chosen from acousti-

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cally distinct geographic song dialects. Tutoring began the day after collection. The 6 birds in 1990 heard 28 pairs of different song types over the first year of life, with new pairs introduced every 10 days, or, in winter, every 30 days. Each pair consisted of one *nutalli* and one *oriantha* song type. Each song type in the pair was presented 80 times per day in the morning. The 4 subjects in 1991 were tutored with two sets of 16 song types: one set from approximately 10 to 50 days of age, and the next from 50 to 90 days. When this cohort began plastic song at the age of 260 days, tutoring resumed with a set of 4 different song types presented for 40 days. Each song type was repeated 36 times per day for the 1991 cohort. In both cohorts, after we identified tutor imitations in plastic song, these tutoring procedures were replaced with the experimental procedures described below. Different tutoring regimes were used because the subjects were part of other experiments.

Song Analysis. Singing was recorded monthly during fall and winter and at least weekly once plastic song began. Vocalizations were analyzed by real-time sound spectrography (16) to identify imitations of tutor songs. Imitations were identified by visual comparison to the library of tutor songs that the birds were exposed to previously.

Imitation Accuracy. To compare the instructive effects of early (first summer and fall) versus late (spring) tutoring, we made quantitative comparisons of the similarity between subjects' imitations and specific tutor songs. Ten crystallized songs from each subject were digitized (25-kHz sampling rate, 12-bit precision) and stored as computer files. Each song was "cut" into separate files, each containing one song phrase: a whistle, buzz, syllable, or note complex. One example of each imitated tutor song was treated similarly. We then performed digital spectrogram cross-correlation analyses (17, 18) to measure the acoustic similarity between

subjects' imitations and the tutor songs. The mean ($n = 10$) cross-correlation between each phrase imitation and the corresponding tutor phrase was calculated, and the mean song cross-correlation was calculated across the number of phrases in the song (three or four phrases per song).

Experimental Procedure. Pairs of birds, matched for subspecies and stage of song development, were divided at random into two groups: experimental (matching second tutor playback) and control (novel second tutor playback). For experimental subjects, one of two equally common song types in their plastic song repertoires was chosen at random, and the tutor song type resembling it was played back. Birds in the novel condition were played a song type never heard before. The six birds in the 1990 cohort heard 160 repetitions per day for 10 days, and the four in the 1991 cohort heard 576. These presentation rates are 2 and 16 times higher, respectively, than the rates used for early tutoring that resulted in acquisition. To avoid pseudoreplication, different song types were used for each subject in plastic song (19).

RESULTS

As youngsters the males each produced two plastic song types, sung approximately equally often (Fig. 1). The four males from 1991 also sang partial or complete imitations of 4–7 other tutor songs in early plastic song but stopped singing them as plastic song progressed. The age of song acquisition was estimated most accurately from the 1990 cohort: median age = 36 days, $n = 12$ song types. In the 1991 cohort, 11/14 (79%) song types were acquired from the first block of 16 types, at the end of which birds were at most 46 days old. Plastic song emerged at an average of 275 days of age. We then played to five birds a song that matched one of their

EXPERIMENTAL BIRDS

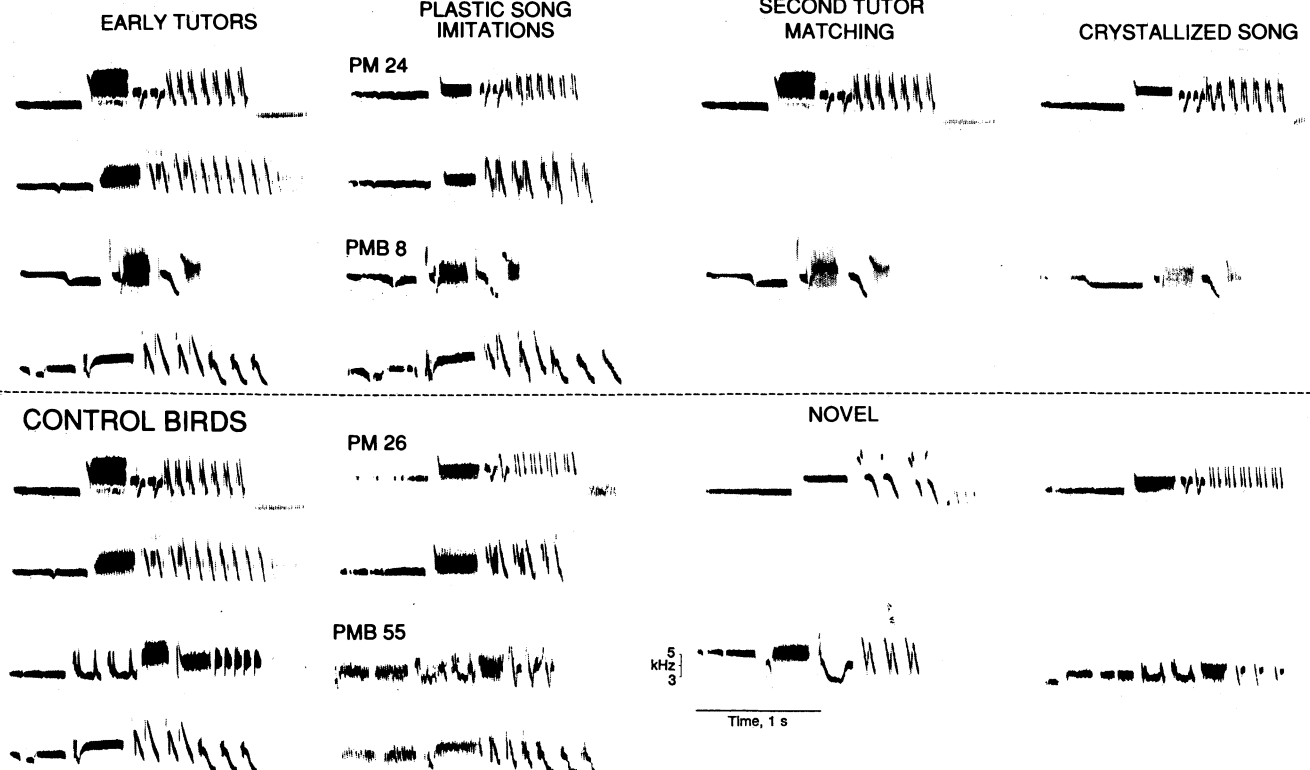


FIG. 1. Audiospectrograms of white-crowned sparrow songs: early tutor songs, subjects' plastic song imitations of early tutor songs recorded 1 or 2 days prior to initiation of playback, second tutor songs (matching or novel), and subjects' crystallized songs. The top two birds (PM24 and PMB8) heard playback of a song that matched one of their plastic songs; the bottom two birds (PM26 and PMB55) are their matched controls who heard a novel song type.

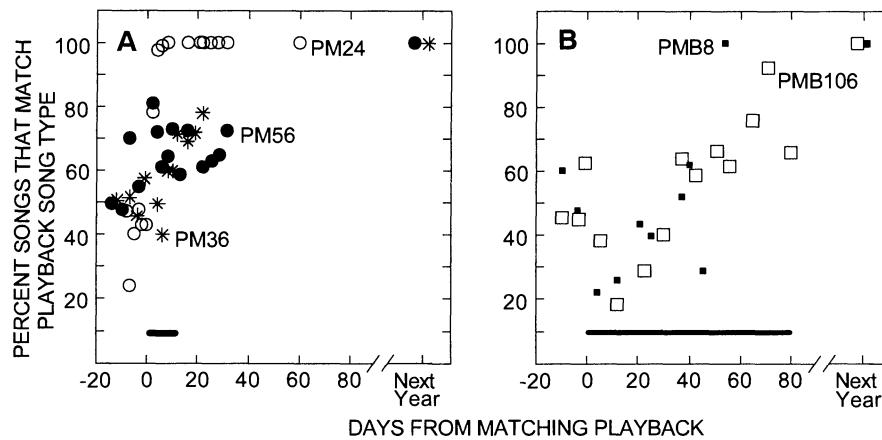


FIG. 2. Progression of song crystallization in the five birds that heard matching second tutor song playback during plastic song, showing increased performance of the matched song type. Birds are identified by different symbols. (A) Experimental birds 1990. (B) Experimental birds 1991. The duration of matching playback in 1990 and 1991 is indicated by the horizontal black bars, beginning at day 0. The ordinate is the number of songs performed that matched the playback type, divided by the total number of songs performed that day (based on 22–769 songs per point, mean = 169 ± 16 songs).

plastic song types (Fig. 1), and five controls heard a novel song.

All five matching birds crystallized the matching type ($P = 0.03$, binomial test, Fig. 2). None of the control birds reproduced the novel type, despite having heard more of it than the tutor songs acquired earlier. Instead, they crystallized a plastic song they already possessed when novel playback began. The results parallel those of other experiments in which we have tutored 64 birds both in infancy and again as yearlings during plastic song. Only one bird modified song material after plastic song began.

Matching playback might have had an instructive effect if a plastic song that approximately matched came to match the model even more closely. If this were true, crystallized songs in the matching group should then resemble the matching tutor more closely than songs in the control group did, which were sung from memory acquired 200 days earlier. Digital spectrogram cross-correlation analyses showed that the five matching birds resembled their second tutor models no more closely than the five control birds resembled their original early models, indicating that sensorimotor instruction had no detectable effects during plastic song (Fig. 3; Mann–Whitney $U = 19$, $P = 0.18$).

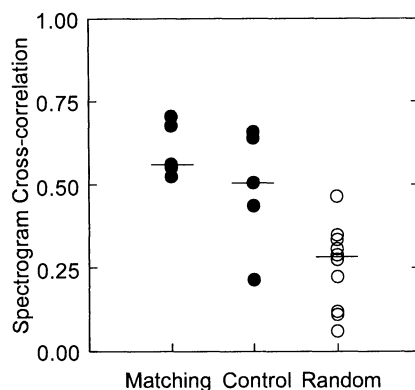


FIG. 3. Mean spectrogram cross-correlations between subjects' imitations and their models and between imitations and one tutor chosen at random for each subject. Short horizontal bars are sample medians. Experimental birds did neither better nor worse in matching their second tutor than control birds did in matching their original tutor models, memorized 200 days earlier. Both groups' songs resembled their tutors' songs significantly more than songs chosen at random (Wilcoxon matched-pairs signed-ranks tests, $z = 2.80$, $P < 0.01$), showing that the method is sensitive to song differences.

DISCUSSION

We conclude that song-matching dialects in birds can originate by means other than the instructive process of sensorimotor learning. Young white-crowned sparrows appear to acquire novel songs originally by instruction but lose this ability as they approach sexual maturity. Males wander after fledging (20, 21) and may memorize a variety of songs and then selectively retain the one that matches the dialect of neighbors where they settle to breed (15, 22). We suggest that these two forms of learning have been confused in the past and that it is a mistake to assume that all instances of song plasticity late in life are the result of instructive processes.

There is some evidence that tutoring with live birds extends the sensitive phase for song acquisition in white-crowned sparrows beyond 50 days of age (23, 24), but these experiments are difficult to interpret. In the studies purporting to demonstrate this effect subjects were kept with a living tutor from the age of 51 days until they crystallized their songs the next spring (200+ days of tutoring). It cannot be determined when after 51 days of age these birds learned. When subjected to this treatment, significantly fewer subjects learned from a live tutor after 51 days than before this age (ref. 24, p. 971) and none learned when tutoring began on day 100. Thus the existing evidence all supports the conclusion that the sensitive period for song acquisition in white-crowned sparrows, whether live- or tape-tutored, begins to decline around 30–50 days of age (25). Instances of song “change” in wild *Z. l. nuttalli* after 50 days of age involve overproduction of songs and selective attrition resulting in song sharing with neighbors (15). It is important to emphasize that such descriptions of song change in wild birds do not provide evidence of instruction occurring at that time and place (see below). We conclude that experimental live tutoring has demonstrated a modest effect of extending the sensitive period for song acquisition, certainly to no more than 100 days of age.

We found no evidence that tutoring in a bird's first spring had instructive effects (Fig. 3). This result agrees with detailed, quantitative comparison of the songs of territory neighbors in wild populations of *Z. l. nuttalli* (26, 27). Territory neighbors do not have more similar songs than do non-neighbors. These results indicate that instruction does not routinely occur after settling on a breeding territory and that instruction and selection proceed as independent processes in vocal learning. Further evidence that instruction and selection are independent processes is provided by

Table 1. Differences between sensorimotor (Instructive) and action-based (Selective) models of vocal plasticity in birds

Process	Learning	
	Instructive	Selective
Learning	Precedes performance	Follows performance
Timing	Defined by acquisition schedule	Defined by performance schedule
"Reinforcement"*	Unnecessary	Necessary

*The precise nature of the reinforcement process has yet to be identified, other than the close temporal relationship between the learning stimulus and the behavioral change.

studies on the brown-headed cowbird (*Molothrus ater*). In this species, males overproduce song types but then selectively retain those that elicit a "wing stroke" display from females (28). In this example, selection of acoustic signals is exerted via a different modality—vision.

The distinction between instructive and selective mechanisms of developmental plasticity has implications for the nature of the underlying neural mechanisms (29). Selective learning of the form we have described is necessarily subject to different behavioral and physiological contingencies and with different operational timetables than instructive learning (Table 1). In the present case, selection operates on patterns of behavior produced in overabundance as a consequence of learning earlier in life. It has been hypothesized, however, that even early song acquisition may be selective, rather than instructive, with experience serving to winnow innate brain circuitry that preencodes specifications for normal song (4). As Jerne (1) has indicated, even plasticity that appears to be instructive at the behavioral level may involve selection at the neural level.

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