Culturally Transmitted Patterns of Vocal Behavior in Sparrows

Although there had been some efforts to understand whether animal behaviour could be learnt culturally, that is, by social influences from members of one’s species, Marler and Tamura’s paper completely revolutionized our understanding of these behaviours. Following the finding that white-crowned sparrows in California possessed distinct regional “dialects”, they performed a careful series of laboratory experiments involving the tutoring of hand-reared birds, a method still widely used today. Firstly, they found that white-crowned sparrows learned their songs during a “sensitive period” of development. During this period, birds from one region could learn a “foreign” dialect if tutored with a loudspeaker. This demonstrated that cultural transmission could dramatically affect the entire motor pattern used to produce the song. This paper helped establish a legacy that spans neuroscience, ecology, and evolutionary biology and remains a fertile ground for cross-disciplinary research to this day.

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Abstract. Male white-crowned sparrows have song "dialects," acquired in about the first 100 days of life by learning from older males. In the laboratory an alien white-crowned sparrow dialect can be taught. Once the song is established further acoustical experience does not change the pattern. White-crowned sparrows do not copy recorded songs of other sparrow species presented under similar conditions.

The white-crowned sparrow, Zonotrichia leucophrys, is a small song bird with an extensive breeding distribution in all but the southern and eastern parts of North America (1). Ornithologists have long remarked upon the geographical variability of its song. Physical analysis of field recordings of the several vocalizations of the Pacific Coast subspecies Z. l. nuttalli reveals that while most of the seven or so sounds which make up the adult repertoire vary little from one population to another, the song patterns of the male show striking variation (see 2).

Each adult male has a single basic song pattern which, with minor variations of omission or repetition, is repeated throughout the season. Within a population small differences separate the songs of individual males but they all share certain salient characteristics of the song. In each discrete population there is one predominant pattern which differs in certain consistent re-
spects from the patterns found in neighboring populations (Fig. 1). The term "dialect" seems appropriate for the properties of the song patterns that characterize each separate population of breeding birds. The detailed structure of syllables in the second part of the song is the most reliable indicator. Such dialects are known in other song birds (3).

The white-crowned sparrow is remarkable for the homogeneity of song patterns in one area. As a result, the differences in song patterns between populations are ideal subjects for study of the developmental basis of behavior. If young male birds are taken from a given area, an accurate prediction can be made about several properties of the songs that would have developed if they had been left in their natural environment. Thus there is a firm frame of reference with which to compare vocal patterns developing under experimental conditions. Since 1959 we have raised some 88 white-crowned sparrows in various types of acoustical environments and observed the effects upon their vocal behavior. Here we report on the adult song patterns of 35 such experimental male birds. The several types of acoustical chamber in which they were raised will be described elsewhere.

In nature a young male white-crown begins singing from its father and neighbors from 20 to about 100 days after fledgling. Then the adults stop during the summer molt and during the fall. Singing is resumed again in late winter and early spring, when the young males of the previous year begin to participate. Young males captured between the ages of 30 and 100 days, and raised in pairs in divided acoustical chambers, developed song patterns in the following spring which matched the dialect of their home area closely. If males were taken as nestlings or fledglings when 3 to 50 days of age and kept as a group in a large soundproof room, the process of song development was very different. Figure 2 shows sound spectrograms of the songs of nine males taken from three different locations and raised in a soundproof room. The patterns lack the characteristics of the home dialect. Moreover, some birds developed strikingly similar patterns (A3, B2, and C4 in Fig. 2). Only when the males taken at the same age and individually isolated also developed songs which lacked the dialect characteristics (Fig. 3). Although the dialect properties are absent in such birds isolated in groups or individually, the songs do have some of the species-specific characteristics. The sustained tone in the introduction is generally, though not always, followed by a repetitive series of shorter sounds, with or without a sustained tone at the end. An ornithologist would identify such songs as utterances of a Zonotrichia species.

Males of different ages were exposed to recorded sounds played into the acoustical chambers through loudspeakers. One male given an alien dialect (8 minutes of singing per day) from the 3rd to 8th day after hatching, and individually isolated, showed no effects of the training. Thus the early experience as a nestling probably has no long-term specific effect. One of the group-raised males was removed at about 1 year of age and given 10 weeks of daily training with an alien dialect in an open cage in the laboratory. His song pattern was unaffected. In general, acoustical experience seems to have no effect on the song pattern after males reach adulthood. Birds taken as fledglings aged from 30 to 100 days were given an alien dialect for a 3-week period, some at about 100 days of age, some at 200, and some at 300 days of age. Only the training at the age of 100 days had a slight effect upon the adult song. The other groups developed accurate versions of the home dialect. Attention is thus focused on the effects of training between the ages of about 10 and 100 days. Two males were placed in individual isolation at 5 and 10 days of age, respectively, and were exposed alternately to the songs of a normal white-crowned sparrow and a bird of a different species. One male was exposed at 6 to 28 days, the other...
at 35 to 56 days. Both developed faint copies of the training song which was the home dialect for one and an alien dialect for the other. Although the renditions of the training song are not perfect, it establishes that the dialect patterns of the male song develop through learning from older birds in the first month or two of life. Experiments are in progress to determine whether further training periods are necessary for perfect copying of the training pattern.

The training song of the white-crowned sparrow was alternated in one case with the song of a song sparrow, *Melospiza melodia*, a common bird in the areas where the white-crows were taken, and in the other case with a song of a Harris’s sparrow, *Zonotrichia querula*. Neither song seemed to have any effect on the adult patterns of the experimental birds. To pursue this issue further, three males were individually isolated at 5 days of age and trained with song-sparrow song alone from about the 5th to 30th days. The adult songs of these birds bore no resemblance to the training patterns and resembled those of naive birds (Fig. 3). There is thus a predisposition to learn white-crowned sparrow songs in preference to those of other species.

The songs of white-crowned sparrows in isolation have some normal characteristics. Recent work by Konishi (O) has shown that a young male must be able to hear his own voice if these properties are to appear. Deafening in youth by removal of the cochlea causes development of quite different songs, with a variable broken pattern and a sibilant tone, lacking the pure whistles of the intact, isolated birds. Furthermore, there is a resemblance between the songs of male white-crowned sparrows isolated in youth and those of another species, *Hesperospiza longipes*, subjected to similar treatment. The songs of intact junco and white-crows are quite different. Konishi also finds that males which have been exposed to the dialect of their birthplace during the sensitive period need to hear themselves before the memory trace can be translated into motor activity. Males deafened after exposure to their home dialects during the sensitive period, but before they start to sing themselves, develop songs like those of a deafened naive bird. However, once the adult pattern of species has become established then deafening has little or no effect upon it. Konishi finds that in the course of

Fig. 3. Songs of 12 males raised under various experimental conditions. A1 and A2, Birds raised in individual isolation. B, Male from Sunset Beach trained with Moltz song (see Fig. 1) from the 3rd to the 8th day of age. C1 to C4, Moltz birds brought into the laboratory at the age of 20 to 100 days. C1, Untrained. C2 to C4, Trained with Sunset Beach songs; C2 at about 100 days of age, C3 at 200 days, C4 at 300 days. D1, Wolf from Sunset Beach trained with Moltz white-crowned sparrow song and a Harris’s sparrow song (see G) from the age of 15 to 36 days. D2, Moltz bird trained with Moltz white-crowned sparrow song and a song-sparrow song (see F) from the age of 6 to 28 days. E1 to E3, Two birds from Sunset Beach and one from Berkeley trained with song-sparrow song from the age of 7 to 28 days. F1, A song-sparrow training song for D2 and E3 up to E3. G, A Harris’s sparrow training song for D1.
crystallization of the motor pattern some control mechanism other than auditory feedback takes over and becomes adequate to maintain its organization. There are thus several pathways impinging upon the development of song patterns in the white-crowned sparrow, including acoustical influences from the external environment, acoustical feedback from the bird's own vocalizations, and perhaps nonauditory feedback as well.

Cultural transmission is known to play a role in the development of several types of animal behavior (5). However, most examples consist of the reorientation through experience of motor patterns, the basic organization of which remains little changed. In the development of vocal behavior in the white-crowned sparrow and certain other species of song birds, we find a rare case of drastic reorganization of whole patterns of motor activity through cultural influence (6). The process of acquisition in the white-crowned sparrow is interesting in that, unlike that of some birds (7), it requires no social bond between the young bird and the emitter of the copied sound, such as is postulated as a prerequisite for speech learning in human children (8). The reinforcement process underlying the acquisition of sound patterns transmitted through a loudspeaker is obscure.

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References and Notes

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1486