

EFFECTS OF DEAFENING ON SONG DEVELOPMENT IN TWO SPECIES OF JUNCOS

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The development of bird song has been studied in several passerine species by rearing birds in acoustic isolation (for example, Thorpe, 1961; Sauer, 1954; Messmer and Messmer, 1956). The results of these experiments vary with the species used. The development of normal vocalization without any external source of reference implies that there is an internal and inherited source of reference. There may be an inherited mechanism in the central nervous system which is responsible for "patterned" vocal motor output without any sensory feedback. Or the central nervous system may have an inherited mechanism to recognize normal vocalization as it is registered by the ear or by the pattern of proprioceptive or other nonauditory feedback. The isolation experiment alone does not discriminate between these possibilities. It is the purpose of the present work to investigate the role of audition in the development of song, using audio-spectrographic analyses of the sound.

MATERIAL AND METHODS

Oregon Juncos (*Junco oreganus*), collected in Berkeley, California, and Mexican Juncos (*Junco phaeonotus*), obtained from the Rustler Park area in the Chiricahua Mountains, Arizona, were used. Except for two Oregon Juncos, acquired at approximately 14 and 80 days of age, respectively, all birds were collected as five- to eight-day-old nestlings and were then hand-reared. They were operated on at ages ranging from 47 to 90 days after the estimated time of hatching. In all cases they were deafened before the onset of song or subsong (table 1). During the interval between collection and operation the birds were kept in soundproof chambers.

Deafening technique.—Schwartzkopff (1949) developed a method for deafening small passerine birds by extirpation of the cochlea. Except for some minor points his method was followed closely in the present work. This method will be described as it applies to passerine birds in general. Birds are anesthetized with Nembutal (50 mg. per cc., Abbot Laboratories, North Chicago). The range of safe and effective dosage varies not only with weight and health of the individual bird but also varies significantly from species to species. Some examples are given in table 2. Great care must be taken with the original commercial concentration to avoid mortality due to overdosage. Another anesthetic, "Equithesin" (Jensen-Salsbery Laboratories, Kansas City, Missouri), is recommended for small passerine species. Although no systematic study of the dosage-weight relationship of this drug was made, it appears to have a much wider range of safe and effective dosage than does Nembutal.

The first step of the operation is to pluck the feathers in the rear part of the head from behind the ears to the median line, either on one side or on both sides. The bird is then mounted on a homemade operating table which can rotate in all directions and is equipped with a harness to hold the head still during operation. The harness is so orientated as to expose the rear part of the head (fig. 1a). Schwartzkopff used a different device to hold the head. An incision in the skin is made from behind the ear to the median line of the head in order to expose the neck muscles. There is a strip of connective and adipose tissue which marks the median line where the muscles of the contralateral sides meet one another.

The neck muscles must be displaced from the median line toward the ear on the side to be operated on in order to expose the skull surface underlying it. The part of the

TABLE 1
HISTORY OF THE EXPERIMENTAL BIRDS

Bird	Date collected (1961)	Date cochlea removed		Age in days when taken
		Left	Right	
Oregon Junco				
1	May 3	July 22	July 23	ca. 14
2	June 15	23	28	5-8
3	April 28	21	28	5-8
4	Aug. 14	Aug. 26	Aug. 26	ca. 80
OF1	April 28	July 23	July 28	5-8
OF2	28	21	28	5-8
OF3	28	22	28	5-8
Mexican Junco				
Y	June 26	Aug. 5	Aug. 12	5-8
Z	26	7	12	5-8
AF1	26	7	12	5-8
AF2	26	7	12	5-8

skull surface underlying the end of the elastic extension of the tongue bone, which lies on top of the neck muscles, must be exposed. After this is done, the point at which the posterior and the external semicircular canals cross each other is located under the somewhat transparent skull surface (fig. 1*b*). This cross divides the region of the skull surface overlying it into four sections. One of the quadrants is located near the ear on the operating side and is partly surrounded by a large venous sinus which runs parallel to the external canal for some distance. A window about half the size of this quadrant is cut close to the crossing point of the canals. It is then possible to see through this window various bony structures housing different parts of the labyrinth (fig. 1*c, d*). With the aid of a binocular dissecting microscope equipped with a vertical illuminator, the topography of this area must be thoroughly examined to determine the proper orientation. Individual and species variations in the topography of this region are considerable. In species with a small auditory bulla, the stalk of the columella that extends into the oval window will be seen without difficulty. It was found helpful to use the columella as one of the points of reference for the next step of the operation. However, in species with a large auditory bulla, it may be difficult to find the columella.

There are four dome-shaped bony prominences in this area, rostrally the ampulla of the external canal, caudally the ampulla of the posterior canal, and between these

TABLE 2
EXAMPLES OF NEMBUTAL DOSAGE-WEIGHT RELATIONSHIPS FOR JUVENAL PASSERINE BIRDS

Species	Weight range (gm.)	Dosage range (units)*
Oregon Junco (<i>Junco oreganus</i>)	19.0-21.5	2.0-2.5
House Finch (<i>Carpodacus mexicanus</i>)	19.9	2.0
White-crowned Sparrow (<i>Zonotrichia leucophrys</i>)	26.8-33.0	2.5-3.0
Rufous-sided Towhee (<i>Pipilo erythrophthalmus</i>)	39.0-46.1	4.5-6.0
Stellar Jay (<i>Cyanocitta stelleri</i>)	94.0-95.2	7.0

* 1 unit = 1/200 cc.

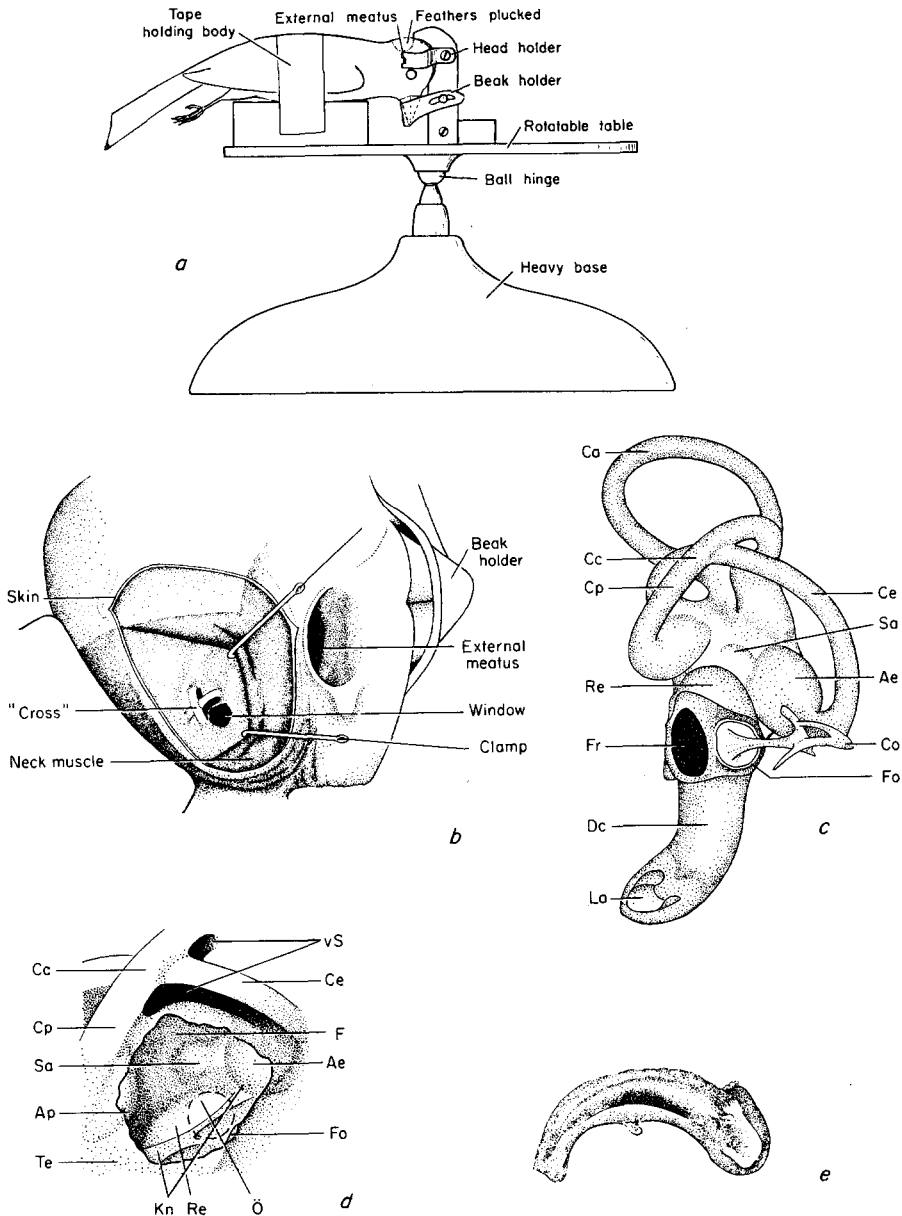


Fig. 1. *a*, operating table; *b*, the neck muscles are displaced from the median line so that the point of crossing between the two semicircular canals becomes visible through somewhat transparent skull bone (slightly modified from Schwartzkopff, 1949); *c*, the entire labyrinth and *d*, its various structures as seen through the window opened on the skull. (Ae) ampulla of external canal, (Ap) ampulla of posterior canal, (Cc) cross of two canals, (Ce) external canal, (Co) columella, (Cp) posterior canal, (Dc) ductus cochlearis, (F) window opened on skull, (Fr) round window, (Fo) oval window, (Kn) bony ridge, (La) lagena, (ö) opening for removal of cochlea, (Re) fourth dome-shaped prominence (see text), (Sa) macula neglecta, (Te) skull surface, (vS) venous sinus. *e*, extirpated cochlea marked by the presence of the lagena at its distal end. The latter appears as a convoluted sack. (*c* and *d* are from Schwartzkopff, 1949.)

there is a somewhat whitish and smaller dome, the *Macula neglecta*. The columella stalk points toward the fourth dome which is located lateral to the *Macula neglecta*. This dome is the upper end of the bony canal encasing the cochlea. A small window is cut in the top of this dome (fig. 1*d*:ö) that is just large enough to permit the passage of the cochlea and lagena without being broken. To remove the cochlea and lagena a fine wire with a hooked end is introduced through this window to grasp the cochlea. Schwartzkopff extends the hook down into the end of the canal to reach the lagena, but I found it possible to catch hold of the upper end of the cochlea near the ductus reunis to remove it in its entirety, including the lagena. There is little danger of breaking the cochlea short by this procedure. When the cochlea is pulled out, it is easily identified by the presence of the lagena at its end (fig. 1*e*).

After extirpation of the cochlea, the first window on the outer skull bone is usually closed with the bony flap that was left partly attached. If for some reason the flap was removed, the window can be left open. The neck muscles are now returned to the original position and the skin incision is closed by sewing. During the period of effective anesthesia, which is from 45 to 60 minutes, both sides can be operated, although a slight complication (such as bleeding resulting from inexperience in performing the operation) may prolong the operating time so that only one side can be finished at a time. During the operation the neck muscles tend to dry up due to illumination. This can be prevented by applying a piece of cotton soaked with physiological saline for warm-blooded animals.

The above method is applicable to birds ranging in size from the Song Sparrow (*Melospiza melodia*) to the American Robin (*Turdus migratorius*). Schleidt (1961) successfully applied the same method to turkey chicks.

As Schwartzkopff (1949) and Messmer and Messmer (1956) state, removal of the lagena causes several types of vestibular disturbance. The operated birds often, if not always, hold the head back, a behavior called "opisthotonus." They also tend to have difficulty in flight in a vertical direction, which is perhaps caused by the abnormal head position. They show erratic flights, colliding with stationary objects and failing to alight properly. All these abnormal acts disappear in a short time. But they recur whenever the birds are placed in a new environment or are frightened. After a short time in a new environment, they learn to coordinate muscular activities by using visual cues in the environment. When the visual cues are removed or altered, therefore, the birds again lose coordination. Nevertheless, in their living cages the operated birds perform all kinds of aerial maneuvers common among intact caged birds. They take a water bath in an entirely normal manner. They also assume the typical singing posture. It may be added that mortality directly due to the deafening operation is almost nonexistent.

All the deaf juncos were kept together in the same location, but each was put in a separate cage. In the first year (1961) they were maintained in a penthouse on the roof of the Life Sciences Building on the campus of the University of California. Autopsies were conducted on birds that died accidentally to check whether the cochlea had been removed completely. In no case was there a trace of this structure in the bony canal, which often contained some liquid and connective tissue material.

Sound recording and analysis.—All sound recordings taken during the first year were made in the penthouse and all recordings in the second year were taken in soundproof chambers. The recordings were made with a Wollensak T1500 tape recorder with an Altec 633-A microphone at a tape speed of $7\frac{1}{2}$ or $3\frac{3}{4}$ inches per second. The latter speed was mainly used for long-term recordings. The recorded tapes were played back with the same tape recorder to transfer the recordings onto an audiospectrograph (Kay

Electric Company Sonagraph). Audiospectrograms were made with the "high-shape" circuits and a "wide band" filter setting. Measurements were made on the audiospectrograms with the clipboard designed by Marler and Isaac (1960). The measurements of inter-song intervals were taken from oscillograms made with a Sanborn single-channel recorder 151-100A (see Fish, 1954).

DEVELOPMENT OF THE BASIC FORM OF JUNCO SONGS

Oregon Juncos.—I have studied both qualitative and quantitative aspects of the song of a wild population of Oregon Juncos (Konishi, in press). The basic form of the song of the wild individual is the so-called "trill" in which the same unit of sound, a "syllable," is repeated with a constant interval. The syllable unit is defined as the first level of temporal grouping of "notes," which are defined as any continuous markings on the audiospectrogram. A syllable may consist of a single note (fig. 2).

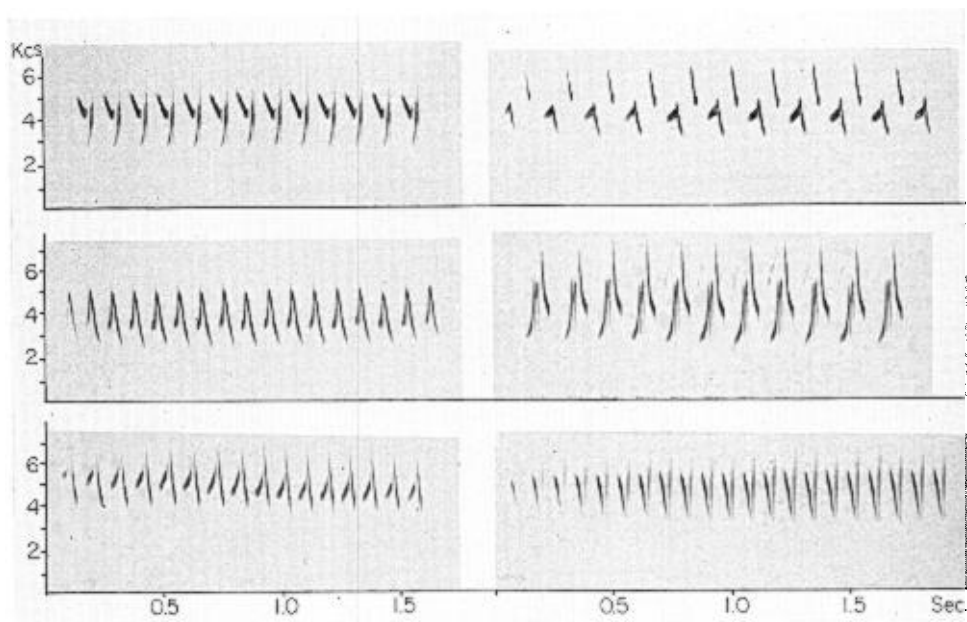


Fig. 2. Audiospectrograms of the typical simple trill-type songs of wild Oregon Juncos.

Except for one song (2B in fig. 3) the trill form of song developed in all the deaf Oregon Juncos, including three females which were induced to sing by testosterone implantation, 10 to 15 mg. subcutaneously (figs. 3, 4). Comparison of seven measurable properties that roughly characterize a song was made between wild and deaf birds (table 3). It is seen that the ranges of the values of all seven characteristics in the sample from the deaf birds are not radically different from those in the sample of the wild birds.

However, the averages of four properties of song in the deaf group are significantly different statistically from those of the wild group. The deaf birds produce songs with fewer syllables, and their songs tend to have higher maximum and minimum frequencies on the average. However, the two groups are not significantly different in frequency spread. The mean of inter-syllable intervals is also significantly larger in the deaf group,

TABLE 3
 VARIABILITY IN SEVEN CHARACTERISTICS OF SONG IN WILD AND DEAF OREGON JUNCOS¹

	WILD ²		DEAF ³	
	Mean and standard deviation	Range	Mean and standard deviation	Range
Number of syllables	14.1 ± 4.38	8-20	11.1 ± 3.85 ⁴	5-20
Song duration (sec.)	1.490 ± 0.203	1.152- 1.945	1.253 ± 0.190	0.746- 1.550
Inter-syllable interval (sec.)	0.036 ± 0.0092	0.020- 0.060	0.048 ± 0.015 ¹	0.026- 0.076
Syllable duration (sec.)	0.080 ± 0.0293	0.165- 0.028	0.077 ± 0.026	0.034- 0.141
Maximum frequency (kc.)	6.53 ± 0.648	7.50 - 4.60	6.87 ± 0.643 ⁴	8.3 - 6.0
Minimum frequency (kc.)	2.98 ± 0.120	3.80 - 2.10	3.47 ± 0.460 ⁴	2.8 - 4.3
Frequency spread (kc.)	3.52 ± 0.659	2.30 - 4.70	3.40 ± 0.767	1.8 - 5.0

¹ Artificially induced songs of female juncos and abnormal song 2B excluded from statistical analysis.

² Based on a sample of 77 songs from 64 birds.

³ Based on a sample of 19 different song types produced in two years.

⁴ Denotes that the means have been shown to be different between the two groups at the 5 per cent level of significance.

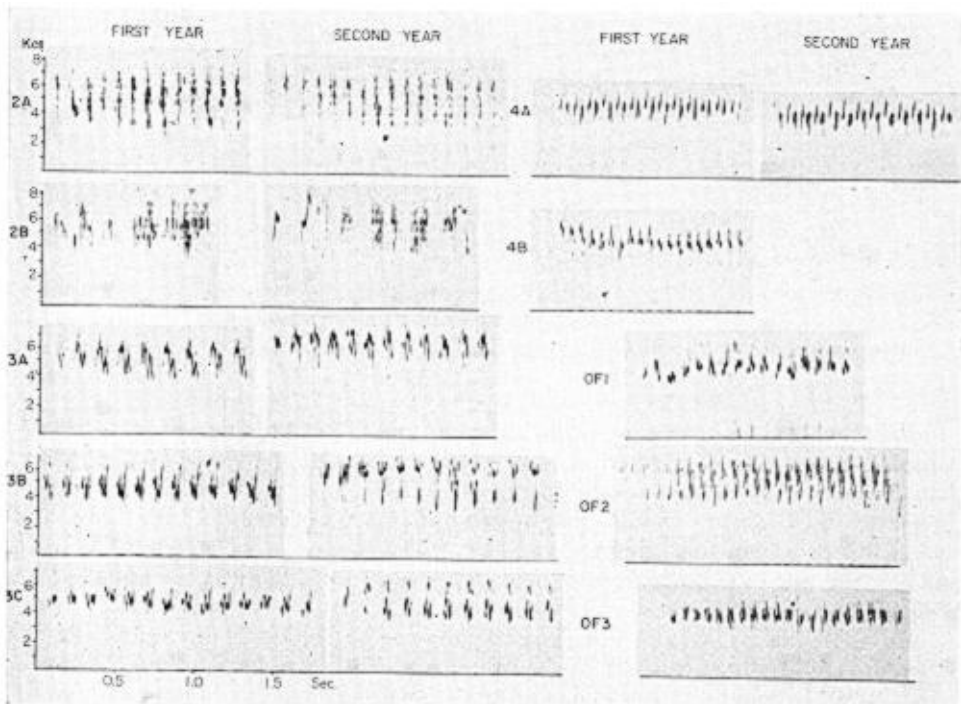


Fig. 3. Audiospectrograms of the songs of three deaf male Oregon Juncos 2, 3, and 4, and three deaf females (OF 1, 2, 3) which were induced to sing by testosterone implantation. A, B, and C denote three song types from one bird.

and variation in the intervals is much greater. In the wild group, the latter is one of the least variable characteristics. The means of the rest of the properties measured are not significantly different between the wild and deaf groups.

In interpreting these results some reservations must be made, for 50 per cent of the sample from the deaf birds consists of the songs from one bird (O.J. 1), which had a tendency to produce songs of a very similar temporal pattern (see fig. 4). Nevertheless, it is reasonable to say that the deaf birds produced types of songs which very closely approximate the basic form of the species song.

While the song of an Oregon Junco is, in general, highly stereotyped, the songs of the deaf birds generally appear to be less stereotyped (see fig. 6). While the qualitative aspect of this instability will be discussed later, table 4 gives some idea of the variability in four measurable properties in a sample of 20 consecutively recorded songs. As comparison of the coefficients of variation indicates, the songs of the deaf birds are

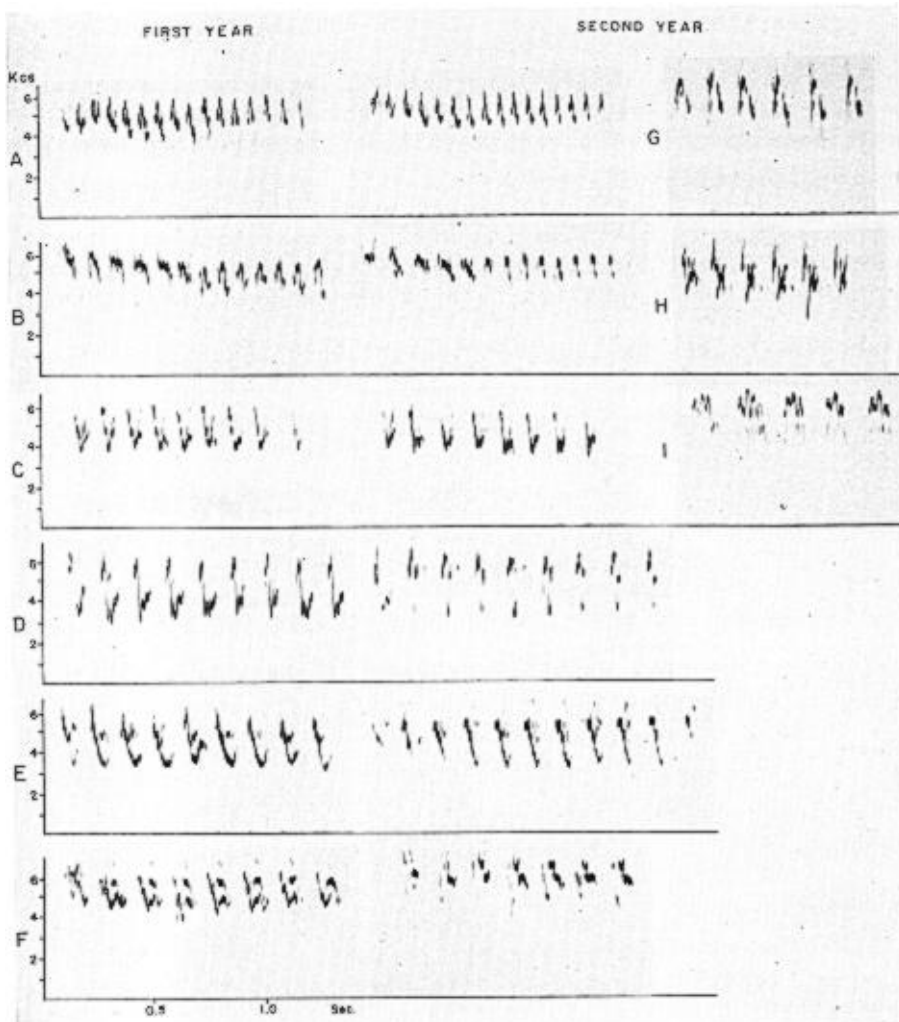


Fig. 4. Audiospectrograms of the first- and second-year songs of a deaf Oregon Junco, O.J. 1.

TABLE 4
VARIABILITY IN FOUR CHARACTERISTICS OF SONG IN WILD AND DEAF OREGON JUNCOS

	Maximum frequency (kc.)	Minimum frequency (kc.)	Number of syllables ³	Song duration (sec.)
Wild bird 1	5.66 ± 0.31 ² (5.48) ⁴	2.47 ± 0.0019 (0.077)	15-17 ³	1.44 ± 0.065 (4.51)
Wild bird 2	6.53 ± 0.061 (0.93)	2.58 ± 0.052 (2.02)	9-14	1.64 ± 0.17 (10.4)
Deaf O.J. 1F	6.37 ± 0.149 (2.30)	4.21 ± 0.191 (4.50)	7-9	1.183 ± 0.105 (8.90)
Deaf O.J. 3A	8.15 ± 0.342 (4.20)	3.94 ± 0.426 (10.80)	10-12	1.228 ± 0.308 (25.1)

¹ The minimum and maximum frequencies were measured on the syllable in the middle of a song.

² Mean and standard deviation.

³ Range.

⁴ Coefficient of variation.

more variable than those of wild birds in most features studied (table 4). A similar comparison was made for inter-syllable intervals (table 5). Syllable duration and inter-syllable interval are the parameters that determine the overall temporal pattern of a song. It appears that in these temporal characteristics the songs of the deaf birds fluctuate more widely than those of wild birds.

Mexican Juncos.—According to Marler and Isaac (1961), who studied song variation in a population of Mexican Juncos in Durango, México, the simple trill-type song was completely absent in the birds studied there. The song of the Mexican Junco generally consists of three or more parts, including trills and phrases (top row in fig. 5).

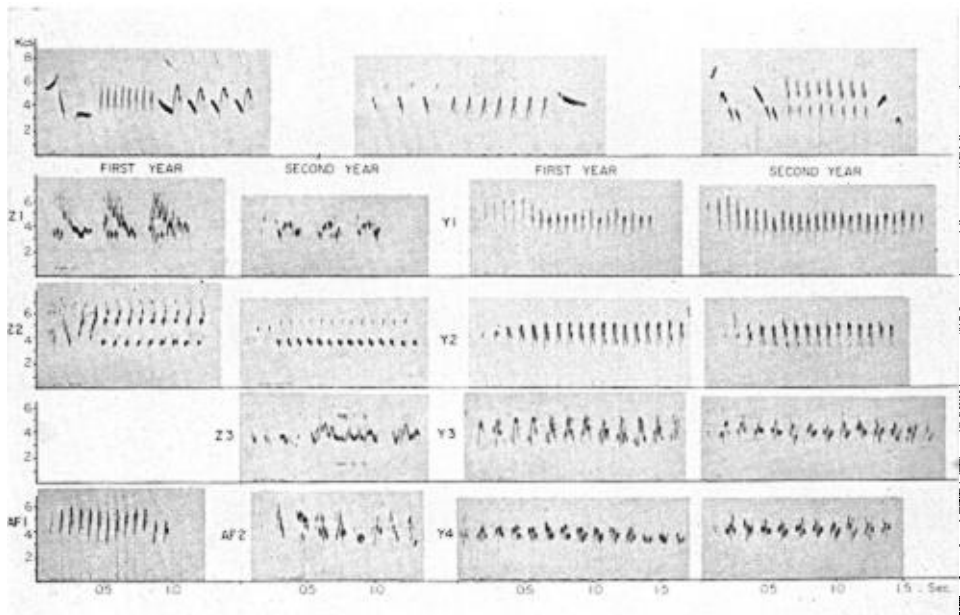


Fig. 5. Audiospectrograms of three songs of wild Mexican Juncos (top row) and the first- and second-year songs of four deaf Mexican Juncos, including two females (AF 1 and 2) which were induced to sing by testosterone implantation.

TABLE 5

VARIABILITY IN DURATION OF INTER-SYLLABLE INTERVALS WITHIN A SONG¹

Interval no.	Wild bird	Deaf O.J. 1F	Deaf O.J. 3A
1	0.0300 ± 0.00239 ² (8.0) ³	0.0615 ± 0.0064 (10.04)	0.0645 ± 0.00582 (9.0)
2	0.281 ± 0.00211 (7.5)	0.0590 ± 0.0054 (10.5)	0.0566 ± 0.0038 (6.7)
3	0.0287 ± 0.00185 (6.4)	0.0470 ± 0.0058 (12.3)	0.0539 ± 0.0045 (8.3)
4	0.0286 ± 0.00131 (4.6)	0.047 ± 0.0060 (12.7)	0.0538 ± 0.0032 (5.9)
5	0.0306 ± 0.00184 (6.0)	0.045 ± 0.0080 (11.1)	0.0536 ± 0.0045 (8.3)
6	0.0317 ± 0.00215 (6.8)	0.049 ± 0.0057 (11.6)	0.0538 ± 0.0012 (2.2)
7	0.0328 ± 0.00209 (6.4)	0.0544 ± 0.00465 (8.5)

¹ Expressed in seconds.² Mean and standard deviation.³ Coefficient of variation.

Marler and Isaac (1961:197) state that "each song always includes one or more trills . . . there is also a diversity of syllable types in each song. . . each song always has at least two syllable types." However, "the trills make up the greater proportion of each song."

A deaf Mexican Junco (A.J. Z) produced two extremely abnormal song types (Z1 and Z3) and one type (Z2) suggesting a three-part structure. Another deaf Mexican Junco (A.J. Y) produced four more or less simple trill-type songs resembling the song

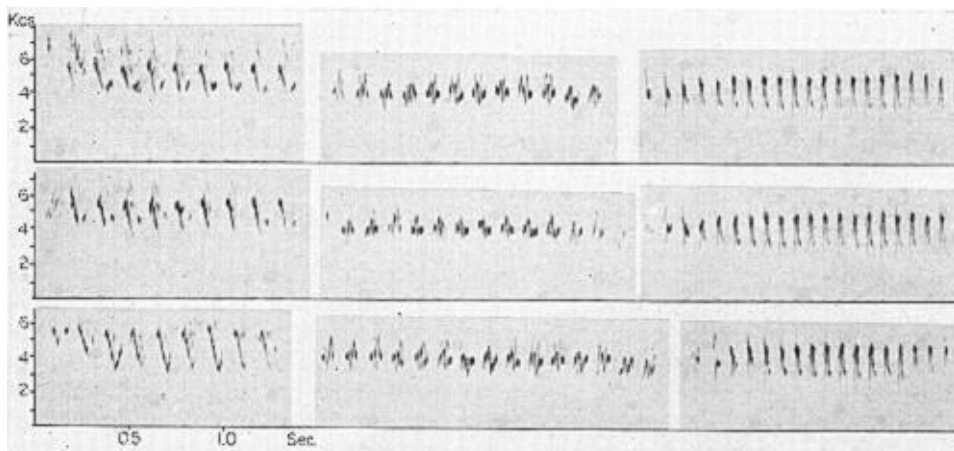


Fig. 6. Instability in syllable structure within a song and from song to song. First column, Song E of O.J. 1 in which not only the form of syllable but also the range of the minimum and maximum frequencies fluctuate. Second and third columns, songs Y4 and Y2 of A.J. Y, respectively, illustrating that a structurally complex syllable fluctuates more than a simpler one.

of the Oregon Junco. However, there is an indication of a two-part trill structure in song Y1. One of two deaf female Mexican Juncos which were induced to sing by testosterone implantation produced a simple trill-type song (AF 1); the other had a rather irregular song type (AF 2).

There is, however, no song type that has the pronounced multi-part structure characteristic of the song of wild birds. According to Marler and Tamura (personal communication), the songs of wild birds can be classified into several categories by the types of parts, such as phrases and trills, of which the songs are composed. Birds raised as a group in acoustic isolation produced predominantly multi-parted songs. Furthermore, when classified by the same criteria, the frequency distribution of different categories showed a similar trend. There was, however, one simple trill-type song among them. The single trill-type song may not be completely absent from the Arizona population from which the experimental birds were obtained. In a recent field trip to the Chiricahua Mountains, Arizona, we heard a couple of simple trill songs from wild birds there. Because of the small sample of deaf birds studied, it is not safe to conclude that deafening always obscures or eliminates the many-parted structure of the song of the Mexican Junco.

OTHER NORMAL ASPECTS IN SONGS OF DEAF BIRDS

There are several rules that govern the structural organization of the songs of a wild population of Oregon Juncos. For instance, there is an inverse correlation between the duration of syllable and the number of syllables contained in a song or in a unit of time. The longer the syllable the smaller the number of syllables. On the other hand, the total duration of song is for the most part constant, it being relatively independent of variations in syllable duration, inter-syllable interval, and in the number of syllables in a song or per unit of time.

These correlations seem to hold in the songs of deaf birds. For example, song A of O.J. 1 has a short syllable and a correspondingly greater number of syllables, whereas some of the other songs of the same bird have longer syllables with fewer syllables.

In contrast, with such species as the White-crowned Sparrow (*Zonotrichia leucophrys*) in which an individual bird usually possesses only one song type, the juncos tend to have more than one song type, even though it is difficult to collect all the songs a junco in the field is capable of singing. All of the deaf birds produced more than one song type.

SOME CONSISTENT ABNORMALITIES IN THE SONGS OF THE DEAF BIRDS

Despite the fact that the basic overall pattern of the song of the species developed in the deaf birds, there are some distinct and consistent abnormalities in their songs. They are as follows:

1. *Abnormal syllable structure.*—The frequency-time spectrogram of syllables and notes in the songs of wild juncos generally has distinct and regular outlines. When there are rapid frequency modulations in a note, they appear regularly (cf. fig. 2). With few exceptions, the spectrograms of syllables in the songs of the deaf birds have irregular outlines. Compared with the songs of wild birds, there are not only a greater number of frequency inflections within a syllable but also the patterns of the modulations are highly irregular. It is true, however, that some of the songs of the deaf juncos have rather normal syllables, especially among the songs of the deaf Mexican Juncos (for example, Y1 and Y2 in fig. 5).

2. *Lack of separation between notes within a syllable.*—In the songs of wild Oregon

Juncos, few syllables are composed of only one note. Moreover, notes forming a syllable unit are clearly separated from one another along the time axis, or the frequency axis, or both, on the audiospectrogram. The majority of the songs of the deaf birds has one-note syllables by the definition of note. This fact combined with the abnormal syllable structures just mentioned suggests that these songs lack a clear separation between notes within a syllable.

3. *Instability in the form of a syllable.*—In contrast with the songs of wild birds, the syllable unit in most of the songs of the deaf birds is not repeated in exactly the same form either from song to song or within a song, even though the overall form of the syllable is maintained. The quantitative aspect of the instability was discussed earlier, and examples of it are shown in figure 6. This type of instability is never present among wild juncos. However, some of the songs of the deaf birds are relatively stable (for example, 1A, 4A, Z2, and Y2). It appears that the simpler a syllable structure the more stable it is both within a song and from song to song. For instance, in song Y2 except for the introductory part, the syllable is repeated without much variation, whereas the syllable unit of song Y4 from the same bird shows a greater fluctuation. Also the syllable structures that are more or less normal in the songs of the deaf Mexican Juncos tend to be repeated without much fluctuation in form both within a song and from song to song.

4. *Similar overall temporal patterns with different syllable structures among the songs of a deaf bird.*—It is generally true that when a junco has several song types, they are different not only in syllable structure but also in the overall temporal pattern. Among nine song types produced by O.J. 1, there are four patterns corresponding to the following groups: D, E, and F; G, H, and I; A and B; and C (see fig. 4). Within each of these groups the songs are similar in the overall temporal pattern. Nevertheless, the similar types are not variants of one song type due to the instability mentioned previously. They are different and recurrent types. As mentioned later in detail, the junco delivers different song types in separate clusters, which enables us to distinguish distinct types from mere variants of one type. However, developmentally this peculiar phenomenon may be due to the fixation of variant or deviant song forms which are caused by this instability. There are more examples of this phenomenon among the other deaf birds used in this study.

LONG-TERM STABILITY OF SONG TYPES IN DEAF BIRDS

The form of a song of an intact junco is generally quite constant year after year. Other than variations due to the short-term instability in syllable structure mentioned earlier, most of the songs of the deaf juncos continued on in the second year without gross changes, although some song types appear to have undergone changes in their syllables by the second year. Clear examples are D and F of O.J. 1 (see fig. 4) and Z2 of A.J. Z (see fig. 5). However, it was often difficult to discriminate between changes that occurred in the first-year song types and songs that appeared for the first time in the second year, especially when a bird produced several types of songs which were similar in the overall temporal pattern (for example, 3B and 3C in fig. 3). On the other hand, if the form of the syllable or note remains unchanged, modification in other features is easy to detect. A rare type of change in which the entire frequency range shifted without altering the form of the syllable was observed in song 3A (fig. 3).

Marler, Kreith, and Tamura (1962) report that in hand-reared Oregon Juncos, some song types disappeared by the second year, while new song types were added in the same year. Similar cases were observed in the deaf juncos (for example, Z3 and 4B).

STAGES OF SONG DEVELOPMENT IN THE DEAF BIRDS

It is the consensus of those who have studied the development of passerine song that there is a gradual transition from the so-called "subsung" to the full song by elimination of the irregular frequency and temporal features of utterances in the subsung. Such a process is called "crystallization" (Thorpe, 1961). Marler, Kreith, and Tamura (1962) report a similar course of song development in hand-reared Oregon Juncos. It would be interesting to know if deaf birds can accomplish crystallization.

Figure 7 shows two examples of song development. In both cases at the initial stage (January 9 and November 28), vocal utterances tend to have a wide frequency range, and irregular temporal pattern and forms of notes, which are characteristics of subsung. In the next stage, the frequency range gradually becomes more restricted as a more regular temporal pattern becomes evident. In O.J. 1 the form of the song first recorded

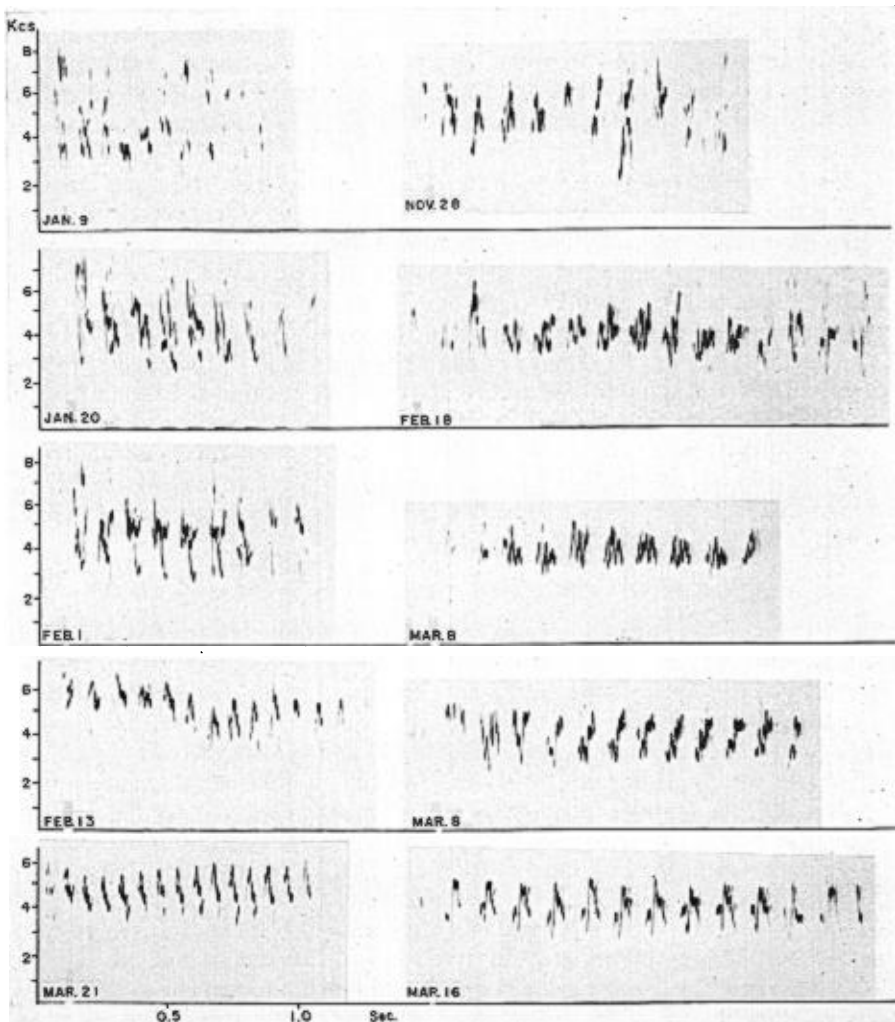


Fig. 7. Stages of song development. First column, Oregon Junco 1. Second column, Mexican Junco, A.J. Y.

on February 13 later came to be recognized as song B with some modification. This bird produced subsequently a similar type, song A. A.J. Y already had two types on March 8, one of them approximating in form to Y3 by March 16 and the other subsequently became Y4. However, as pointed out before, the form of the syllable tends to remain unstable even after the overall pattern is recognizable as a distinct song type.

TEMPORAL PATTERN OF SINGING IN DEAF BIRDS

In the previous sections the effects of deafening upon the form of song were described. This part of the investigation was made to determine whether the pattern of song delivery is affected by deafening. From field observations it is found that a junco delivers songs in clusters. This can be demonstrated by obtaining the frequency distribution of inter-song interval lengths. Such a distribution indicates the presence of a dominant interval for each individual. It implies that a junco tends to deliver songs at a particular rate. An intact junco that was isolated in a sound-proof chamber showed the same tendency. It is seen that the temporal pattern of singing in the deaf juncos is not different from that of the intact junco. In a wild population of Oregon Juncos, there is a wide variation in the dominant interval between individuals. This is also evident in the deaf juncos (fig. 8).

The number of songs delivered during a given period of time varies widely both within and between individuals. It appears that deafening has no appreciable effect upon the frequency of singing. For instance, O.J. 1 sang 1274 songs during a period of $3\frac{1}{2}$ hours. During this period the bird was kept in a soundproof chamber with a deaf female Oregon Junco caged next to it. Other than this it had no source of visual stimulation. On the other hand, this same bird sang only 194 songs during the same length of time in the absence of another bird. This may indicate that visual stimuli alone can affect the frequency of singing. As may be judged from the numbers of inter-song intervals in the figure, some of the other deaf juncos also delivered large numbers of songs per unit of time.

All juncos tend to have more than one song type. The different song types are usually delivered in separate clusters such as AAAAAA BBBBBB, and so on. Also juncos usually repeat one type of song many times before switching to another type. The deaf juncos are no exception in these respects. For example, O.J. 1 which had nine song types in the second year delivered them in the following sequence and frequencies during a period of $3\frac{1}{2}$ hours:

E(43) - D(16) - A(154) - C(120) - A(2) - C(11) - B(1) - C(1) - B(1) - C(1) - B(1) - C(1) - B(65) - I(47) - F(11) - G(33) - H(33) - B(1) - G(35) - D(509) - G(107) - E(81).

The letters indicate the song types and the numbers are frequencies. Thus, some types occur more often than others. Even with a record of this length, it is difficult to determine whether there is any definite order in which different song types are delivered, because the number of transitions from one type to another is not sufficient for a statistical test. It can be noted, however, that at one point in the preceding record, B and C were given in alternation.

Judging from the temporal pattern of singing, the many song types produced by O.J. 1 are distinct types even though some of them are similar in the overall temporal pattern. It is interesting to note that even when songs are extremely abnormal, such as 2B, Z1 and Z3, the pattern of their delivery is not different from that in more normal songs, indicating that these abnormal types are distinct songs.

It also may be pointed out that this pattern of singing gradually becomes evident with the development of the full song. Therefore, even when a song is extremely abnor-

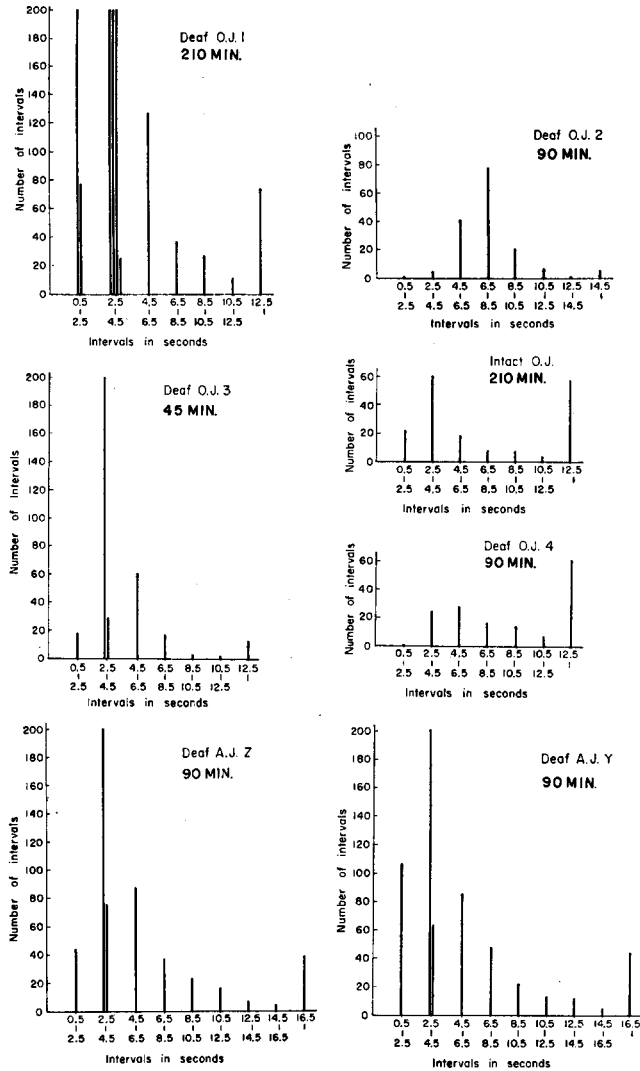


Fig. 8. Frequency distribution of inter-song intervals. Time in each graph is the period of recording.

mal, it can be identified as a song early in its development, although the typical posture assumed during singing is the most reliable criterion for distinguishing a song from other utterances.

DISCUSSION

The results reported in the previous sections indicate that the effects of deafening on song development vary with different properties of song and to some extent from species to species. The song patterns and singing behavior of deaf Oregon Juncos exhibited a number of normal features. This implies, first, that normal properties of the species song do not require external auditory reference for their development; in other words, for their establishment the bird need not hear the song from other birds or any

external source. Second, it implies that auditory feedback is not necessary in order for these features to develop; in other words, the bird can produce them even without hearing its own song. As mentioned in the introduction, the central nervous system may pattern the vocal motor output without any sensory feedback. Deafening experiments, however, do not exclude the possibility that proprioceptive feedback may be responsible for the development of the normal features. Nor do the experiments exclude the possibility of a simultaneous operation of these two methods. In whichever case, it is true that there is an inherited mechanism to ensure the development of the normal properties, for deafening excludes their acquisition from any external source. Similar results were reported for the domestic chicken (Konishi, 1963). In this species, the basic forms of several different calls developed normally in birds deafened at an early age.

The possibility can be excluded that auditory experience acquired by the juncos prior to the deafening operation might have been responsible for the development of the normal features. In the White-crowned Sparrow it has been demonstrated that any acoustic experience acquired prior to deafening is completely erased by the operation, provided that it has not been translated into the corresponding vocal form. Therefore, the birds must be deafened before the onset of singing in order to study the effects of deafening on the development of song (Konishi, MS, Univ. Calif.).

Explanations must also be found for the abnormalities in the songs of the deaf birds. There are two ways to explain the instability in syllable structure. One possibility is that auditory feedback plays an important role in maintaining stability in the form of a syllable. This possibility is unlikely, because in the White-crowned Sparrow it has been shown that the pre-established form of song remained unchanged for a long period of time after deafening even when it was originally learned through the ear. The other possibility is that the songs of the deaf birds have never reached the terminal point of crystallization. One of the important elements in the process of crystallization is the establishment of the terminal and stable pattern of syllable and note units. Insofar as the overall form of song is concerned, crystallization proceeds without auditory feedback, as demonstrated here. In addition to instability, the irregular patterns and greater numbers of frequency modulations found in the syllables produced by the deaf birds give an indication of the role of hearing in the process of song crystallization.

The significance of deafening experiments can be evaluated only by comparing their results with those of isolation experiments. The ear has a doublefold function. It is the means of access not only to the external source of reference but also to the internal one when this is present. The central nervous system may have an inherited source of reference for the species song which can be used only through the ear. Marler, Kreith, and Tamura (1962) demonstrated that Oregon Juncos raised from the nestling stage in acoustic isolation could develop the typical wild-type songs. In the syllables of these songs, none of the abnormalities mentioned earlier is found. This means that if the bird can hear itself, it can produce the normal form of syllable. A corollary of this is that the vocal motor output established without auditory feedback is insufficient to produce the normal form of syllable. It suggests also, as mentioned earlier, that the central nervous system may have an inherited mechanism that recognizes the normal form of the species song as it is registered by the ear.

Marler, Kreith, and Tamura (1962) also demonstrated that hand-reared Oregon Juncos could learn the songs of other species when exposed to them. However, in a wild population, no syllable is shared between birds. In those species where song learning is reported there is usually considerable sharing of syllable types between birds (Messmer and Messmer, 1956; Marler and Tamura, 1962). There are several possible causes

for the diversity in syllables. It may directly reflect the genetic diversity of the population. Young juncos may copy songs from adult birds in their birthplace but move out of the area to join different populations in which they subsequently sing. They may also copy songs only partly, as is known to occur in the European Blackbird, *Turdus merula* (Messmer and Messmer, 1956). In fact, the forms of notes in the songs of wild juncos can be classified into a few general categories of frequency-time patterns, suggesting that copying of the general forms may occur. However, it was demonstrated here that a diversity of syllable types was produced in the deaf birds, even though they tended to be abnormal. Genetic diversity in the wild population may, therefore, be directly responsible for the diversity in syllable structures.

Another factor that may be responsible for the syllable diversity is "improvisation." The hand-reared Oregon Juncos not only showed an ability to produce wild type songs and to copy, but they also showed an ability to produce types of song that were neither present in wild populations nor heard by the birds. This phenomenon has been called improvisation (Marler, Kreith, and Tamura, 1962). According to these authors, in an environment rich in auditory stimulation there was a greater degree of improvisation than in an acoustically simple one. Improvisation typically enhances diversity in syllable structures and in the overall temporal pattern of song. Except for one bird, O.J. 1, the deaf birds of both species produced much smaller numbers of song types than their conspecifics raised in group isolation. Furthermore, in contrast with the Oregon Juncos raised in group isolation which tended to produce more complex song types, including multi-parted songs, the songs of the deaf Oregon Juncos did not depart from the basic simple trill-type apart from one exception. The above results combined with the uniformity in the overall temporal pattern in the song of wild Oregon Juncos suggest that improvisation does not seem to play an important role in establishing the temporal pattern of the song among wild Oregon Juncos.

While the possible causes for the diversity in syllable structure have been discussed above, variations in the other features of the songs of the deaf birds must be explained. The contribution of the acoustic variables in the environment to the variations was excluded by deafening. However, as Lorenz (1961) points out, unless two animals have the same genotype, it is logically impossible to attribute differences in behavior between them to variation in environmental factors: The genetic diversity of the experimental birds may have been responsible for the variations. Also variation in interaction between the genotypes and the nonacoustic aspects of the environment may have caused them. In this study, only the acoustic variables of the environment were controlled.

The failure of deaf Mexican Juncos to produce the typical many-part song of wild conspecifics may indicate that these birds have an inherited template of that structure which cannot be used without auditory feedback. Or, on the other hand, such may be due to intensive improvisation among wild birds. A definite conclusion can be reached only by using a larger number of deaf birds and also by rearing birds systematically in various auditory environments, including complete individual isolation.

The normal pattern of singing behavior exhibited by the deaf birds gives certain hints on the role of auditory feedback in singing. Both species of *Junco* used in this study deliver songs in clusters. When there is more than one song type in the repertoire of a junco, the different types are delivered in separate clusters. Within a cluster, songs are spaced more or less regularly in time. Hinde (1958) described a similar pattern of singing in the Chaffinch (*Fringilla coelebs*). In order to explain this type of song delivery, he postulates that the motor performance of singing a song and/or its sensory feedback causes an inhibitory effect which is responsible for a silent period that follows

the song. Hinde found that on the average there were longer pauses between songs of different types than between those of the same type. He also assumes that singing a song of one type facilitates the consecutive delivery of a song of that type. Thus, "the alternation between sequences [clusters, M.K.] would be then due to a difference between the time constants of the decay of the facilitative and inhibitory effects" (p. 217).

The cluster formation and alternation between types in the deaf juncos indicate that these can be performed without auditory feedback. Hence, the inhibitory and facilitative effects are not obligatorily dependent on auditory feedback. As Hinde mentions, they can be under the control of the central nervous system and/or proprioceptive feedback. However, it does not necessarily mean that either auditory feedback or external acoustic stimuli may not be involved in regulating the temporal pattern of singing. Hinde has demonstrated that the playing back of songs of one type facilitated the delivery of songs of that type. Whether the regulation of song delivery is central or peripheral cannot be determined without investigating the proprioceptive feedback pathways.

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SUMMARY

The effects of deafening on song development in two species of *Junco* were studied. Audiospectrographic analyses of the songs of deaf birds indicate that some aspects of song developed normally without auditory feedback, while some other aspects are abnormal. The basic overall form of the song of the wild Oregon Junco developed in deafened Oregon Juncos. The typical multi-parted structure in the song of the wild Mexican Junco failed to develop in deaf Mexican Juncos. The songs of deaf female birds that were induced to sing by testosterone implantation were similar to those of the deaf males. In general, the most distinct features in the songs of the deaf birds were the abnormality and instability in the form of syllables within a song and from song to song. This is due to the lack of complete crystallization of song in the absence of auditory feedback. The temporal pattern of singing in the deaf birds was quite normal and the frequency of songs delivered in a unit of time did not appear to be affected by deafness.

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