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INFLUENCE OF AUDITORY STIMULATION ON THE DEVELOPMENT OF SYNTACTICAL AND TEMPORAL FEATURES IN EUROPEAN STARLING SONG

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ABSTRACT.—We investigated how European Starlings (*Sturnus vulgaris*) were influenced during song learning by acoustic patterns lacking certain syntactical and temporal features of the species-specific song. Hand-reared males were exposed to a sequence of heterospecific song patterns (song types of Common Nightingales, *Luscinia megarhynchos*) which, in contrast to normal starling song, were not reiterated, were evenly separated by breaks throughout the entire tutor sequence, and did not show an increase in maximum frequency from the beginning to the end of the sequence. The experimental males acquired none or only a few of the song patterns from the training tape and developed songs with aspects of normal syntax (sequential order of low- and high-frequency motif types) and temporal organization (more breaks between motifs at beginning than at end of song). These features are missing in the songs of males reared in complete acoustic isolation (Chaiken et al. 1993). Therefore, we conclude that European Starlings have a predetermined knowledge of some syntactical and temporal song features, but need an acoustic input from the environment to convert such information into a corresponding vocal output. The results show that acoustic patterns effective in stimulating such a development do not need to contain specific features of starling song. *Received 14 June 1995, accepted 20 August 1995.*

SONGBIRDS MUST LEARN the species-typical song pattern during ontogeny. If young birds are deprived of acoustic models or are exposed to heterospecific songs or inadequate learning conditions, they will develop song patterns which differ from the species-specific one (review in Kroodsma 1982). Provided the individual history of the respective bird is known, the analysis of such abnormal acoustic patterns can reveal how predispositions and the acquisition of external stimuli contribute to behavioral development (e.g. Marler 1987, Ten Cate 1994).

Song patterns are characterized by different levels of organization. Elements or notes, the basic units of production, have a specific acoustic morphology (phonological organization) and usually are arranged in a sequence according to species-typical rules (syntactical organization). The duration and distribution of silent intervals between elements or element groups determines the speed and rhythm of performance (temporal organization). Several studies using heterospecific or artificially arranged song patterns as learning stimuli indicate that the different levels of organization play different roles during song learning. For example, heterospecific elements or short-element groups can be copied quite accurately, even in species that normally do not mimic alien songs, while the typical song syntax of the own species is usually preserved (Greenfinch, *Chloris chloris* [Güttinger 1980]; Zebra Finch, *Taeniopygia guttata*, and Bengalese Finch, *Lonchura striata* [Clayton 1989]; but see Hultsch [1991] for Common Nightingales, *Luscinia megarhynchos*). In Swamp Sparrows (*Melospiza georgiana*) and Song Sparrows (*M. melodia*), song syntax can serve as a guideline in the selection of song elements to be learned (Marler 1987, Marler and Peters 1988).

In a study on the influence of social factors during song learning in European Starlings (*Sturnus vulgaris*), tape-tutored males developed songs deviating in several aspects from the species-specific pattern as developed by starlings exposed to a live conspecific tutor (Chaiken et al. 1993). The characteristics of those deficiencies strongly suggested that the acquisition of phonological and syntactical information are two different processes in starlings, which sing long songs of up to 40 s with a complex syntactical and temporal organization (Adret-Hausberger and Jenkins 1988, Eens et al. 1989, 1991, Böhner et al. 1990, Böhner 1993, Chaiken et al. 1993).

The aim of our study was to investigate how syntactical and temporal song features are acquired by young male starlings. For that purpose, song patterns differing from starling song in several measures were arranged on tape and presented by a "social tutor" (i.e. a person familiar to the birds). This method of social tutoring has proven to be effective in Common Nightingales (Hultsch and Todt 1989), which fail to acquire songs presented from tape alone during early ontogeny (Todt et al. 1979, Todt and Böhner 1994). Here we report that European Starlings did not acquire many song patterns from the training tape, but were clearly influenced by the exposure to auditory stimuli. They developed songs with aspects of conspecific syntax and temporal organization absent in the songs of starlings reared in complete acoustic isolation (Chaiken et al. 1993).

METHODS

Subjects and housing conditions.—Six European Starling males were taken from the field in April 1990 at four to nine days of age and hand-reared in the laboratory. After reaching independence at about 35 days, they were kept as visually isolated groups of three birds each in cages (120 × 40 × 50 cm) in the same room. The light schedule was adjusted weekly to the natural photoperiod of Berlin, Germany (52°N) throughout the entire experiment.

Tutoring regime and program.—All subjects were exposed to a set of tutor songs for six weeks at 90 days of age, when starlings acquire songs very easily (Chaiken et al. 1994). Tutor songs were presented six times in the morning, with a 2-min break between single presentations, on six successive days per week.

Tutor songs were played from a tape recorder (Uher 4400 Report) through a loudspeaker (Aiwa SC-A5), which was positioned on a table about 2 m from the subjects' cages. The person who hand-raised the birds was sitting close to the loudspeaker with visual contact to all males (social tutor; cf. Todt et al. 1979, Todt and Böhner 1994).

We used a set of 42 different Common Nightingale song types as heterospecific tutor patterns. The song types had a mean duration of 3.4 ± SD of 1.0 s (Fig. 1; for detailed description of nightingale song, see Hultsch 1980) and were arranged in one sequence in which each song type occurred only once. The order of song types was determined by chance, and all song types were evenly separated by breaks (silent intervals) of, on average, 4.1 ± 0.8 s. Therefore, the tutor sequence differed from typical starling song, which is also a sequence of different stereotyped song patterns (called motifs in this study and by Adret-Hausberger and Jenkins 1988, Böhner and Veit 1993, Chaiken et al. 1993, 1994; phrases by Mountjoy and Lemon 1995; song types by Eens et al. 1989, 1991, 1992) in the following parameters (for sonagrams of normal starling song see Eens et al. 1989, Böhner and Veit 1993, Chaiken et al. 1993): (1) Tutor song patterns were longer than starling motifs, of which the species-typical duration is 0.5 to 1.0 s. (2) Tutor patterns were presented with "immediate variety" (abcde . . .) and not as repetitive units (aabbccc . . .). (3) Breaks between the tutor patterns were equally distributed (i.e. there was no increase in speed, as is the case in normal starling song, where the number of breaks between motifs decreases as the song progresses). (4) Unlike in starling song, there was no increase in frequency from the beginning to the end of the tutor sequence. The average maximum frequency of song patterns in the first and the last half of the sequence was 6.4 ± 1.1 kHz and 6.4 ± 1.0 kHz, respectively (Mann-Whitney U-test, $P = 0.87$). There was also no difference when only the first and the last five song patterns were taken into account, a period of time more similar to the respective periods of different frequencies in normal starling song as measured by Chaiken et al. (1993): 6.9 ± 1.2 kHz versus 6.8 ± 0.6 kHz (Mann-Whitney U-test, $P = 0.92$).

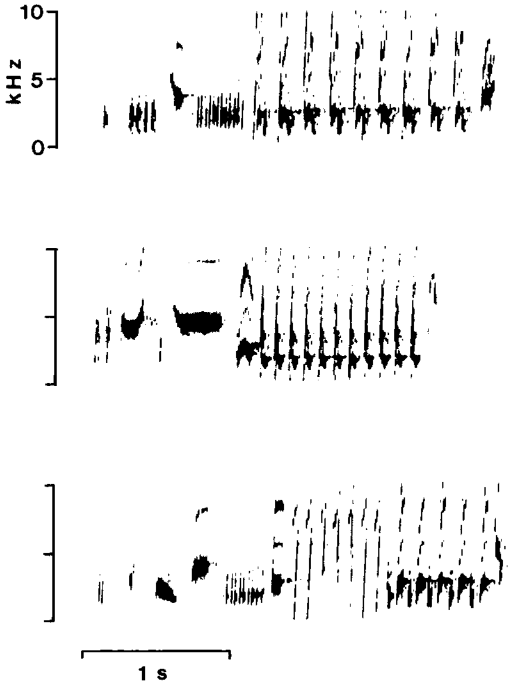

Fig. 1. Examples of heterospecific tutor patterns used for training tape (song types of Common Nightingales).

Recordings and analysis.—After tutoring, all males were individually kept in acoustic isolation. Song output was monitored every other week (Uher 4400 Report tape recorder and Sennheiser ME 80 microphone) to check progress in song development. Songs had fully crystallized in February when the birds were about nine months old, and recordings for a detailed analysis were made at that time.

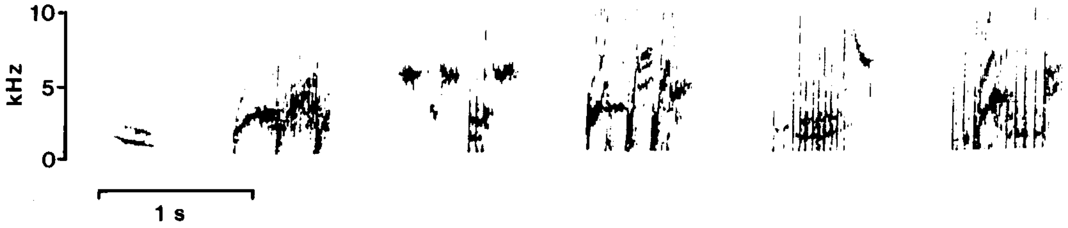

Fig. 2. Examples of motif types developed by one of experimental males.

Each male was recorded for 1 h, which resulted in 14 to 17 min of continuous singing or, on average, 19 complete songs (i.e. songs longer than 15 s). This amount of song has been shown to be sufficient for the identification of the entire repertoire of motif types of a starling male (Chaiken et al. 1993; see also Adret-Hausberger and Jenkins 1988, Eens et al. 1991).

Sonagrams of the males' songs were made using a Nicolet UA-500A spectrum analyzer, a PM 3230 oscilloscope, and a Recordine K-696 camera. The songs were then compared with the training songs to check whether any tutor song patterns had been acquired. In addition, the following measurements were taken from the songs of all males, following criteria developed by Chaiken et al. (1993) to characterize the syntactical and temporal organization of starling song: (1) repertoire size, the number of different motif types; (2) number of motif types of repertoire that were immediately reiterated during singing; (3) distribution of breaks between motifs as an indicator for speed of performance (i.e. number of breaks of 0.5 to 5.0 s measured in first and last 7.5 s of each song); (4) maximum frequency attained within first and last 5 s of each song.

Control males.—Starlings do not learn as well from tape as from live tutors (Chaiken et al. 1993). To distinguish between possible effects of the chosen tutoring design and of the heterospecific acoustic morphology of the tutor song patterns, three additional males were reared, kept, tutored, and recorded on the same developmental schedule as the experimental subjects, with the exception of one male which was tutored for three weeks only. However, instead of being exposed to the sequence of heterospecific tutor song patterns, the control males heard a sequence of 10 starling songs recorded from an adult bird at the peak of the breeding season. These songs contained 73 different motif types, which is a typical adult male's repertoire, and displayed all the syntactical and temporal features of normal starling song: 60% of the motif types were reiterated; there were more breaks at the beginning (on average 2.4 ± 0.8) than at the end (none) of a song; and there was a pronounced increase in average maximum frequency from the beginning (4.7 ± 1.6 kHz) to the end (9.0 ± 0.9 kHz) of a song.

RESULTS

Repertoire size.—The six males of the experimental group developed repertoires averaging

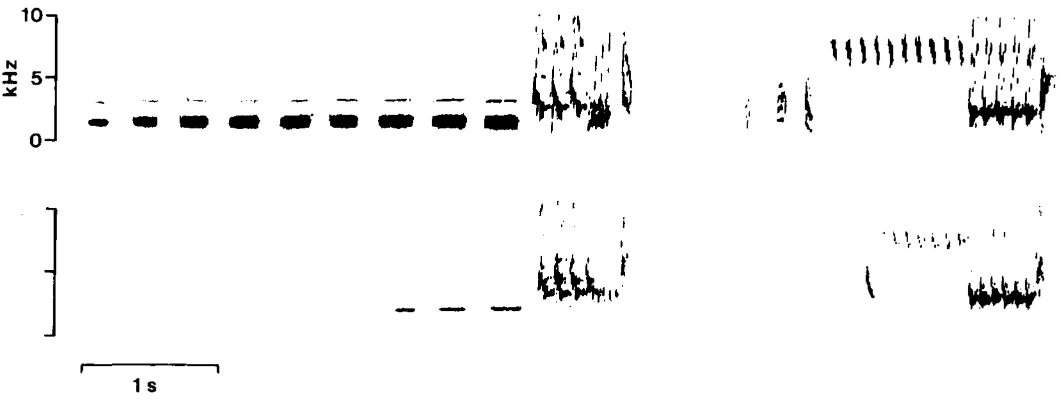

Fig. 3. Examples of the few song patterns copied from training tape. Tutor patterns are shown on top, and respective imitations on bottom. Copies match most of phonological details of tutor patterns, but usually are shorter.

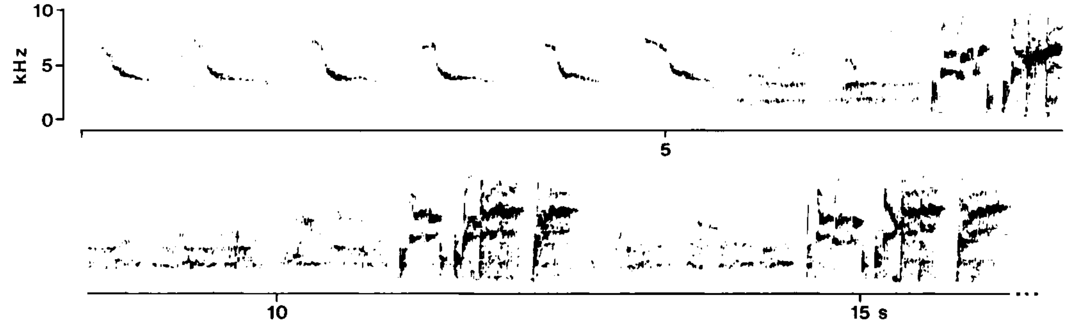

Fig. 4. Section of song of one of experimental males.

17.0 ± 5.8 different motif types (range 11-24). The three control males sang 19, 13, and 24 motif types, respectively. Examples of developed motif types are shown in Figure 2.

Song material acquired from training tape.—Only two of the experimental males developed a number of motif types (1 and 4, respectively) that clearly matched tutor song patterns. A few additional motif types were developed that displayed some general features of the tutor patterns (e.g. the species-typical repetition rate of short elements or element combinations of nightingale song types; cf. Hultsch 1980). In these cases, however, it was not possible to identify any specific tutor pattern that might have served as model. If those motif types with general characteristics of nightingale song types are also counted as acquired from the training tape, three males copied 5, 4, and 2 tutor song patterns, respectively.

In the few cases when tutor song patterns clearly had been acquired, the developed copies matched most of the phonological details of the tutor patterns, but were usually shortened to a duration between 1 and 1.5 s (Fig. 3). The low acquisition success also was evident in the three control males which learned only 2, 2, and 6 starling motifs, respectively, from the training tape.

Syntactical features.—All males sang their motifs in long sequences, as typical for normal starling song (Fig. 4). Motif types that were immediately reiterated accounted for an average of 67 ± 10% of the entire repertoire in the six experimental males. The respective values for the three control males were 63, 75, and 100%.

All males of the experimental group preferentially sang low-frequency motif types at the beginning and high-frequency motif types at the end of a motif sequence. The average maximum frequency reached within the first 5 s was 5.0 ± 0.5 kHz, and in the last 5 s was 6.4 ± 0.8 kHz (Wilcoxon test, $P < 0.05$). The respective values for the three control males were 5.1, 4.3, and 5.9 kHz for the beginning, and 7.9, 6.7, and 7.8 kHz for the end of a song.

Temporal features.—In all experimental males, songs were performed with increasing speed, as indicated by the uneven distribution of breaks between motifs. On average, 3.5 ± 0.6 breaks were found within the first 7.5 s, and only 2.0 ± 0.6 breaks within the last 7.5 s of a song, a significant difference ($P < 0.05$, Wilcoxon test). The control males' songs contained an average of 2.0, 1.7, and 2.4 breaks, respectively, at the beginning, and 1.0, 0.5, and 1.5 breaks at the end.

DISCUSSION

Acquisition success.—The experimental males developed a surprisingly small repertoire averaging 17 different motif types. Such a repertoire size is comparable to that of starlings reared in complete acoustic isolation (16 motif types; Chaiken et al. 1993) and is significantly smaller than the average repertoire size of one-year-old males kept with a live conspecific tutor (37 motif types; Chaiken et al. 1993). Furthermore, most motif types developed by the experimental males were not acquired from the training tape. Because the three control males, exposed to conspecific song, also copied only a few tutor patterns from the training tape, we conclude that the low acquisition success was not due to the acoustic morphology of the heterospecific song patterns presented to the experimental males.

Numerous studies have shown that European Starlings are able to memorize and produce complex heterospecific acoustic patterns (Hindmarsh 1984, Hausberger et al. 1991, Eens et al. 1992, Böhner 1993), which is also indicated by those few tutor patterns copied by two of the experimental males. Social factors play an important role during song learning in starlings as demonstrated by Chaiken et al. (1993); in their study, young males learned a high number of motif types from live conspecific tutors, but acquired only little from songs played from tape (see also West et al. 1983). Possible reasons for the failure of young starlings to learn a significant number of motif types from tape alone are discussed by Chaiken et al. (1993), some of which (e.g. no interaction between tutor and pupil) also may account for the low acquisition success of the males in our study.

Acoustical stimulation and development of syntactical and temporal song features.—The songs of the experimental males clearly displayed a number of species-typical characteristics. Motifs were arranged in long sequences in which certain motif types were reiterated. Furthermore, the songs showed an uneven distribution of breaks, resulting in an increase in singing speed, and a shift from low to high frequencies as the song progresses. Because the sequence of the tutor song patterns did not display any of these features, we conclude that young starlings have a predetermined knowledge of these song characteristics (i.e. that no experience with the respective acoustic pattern is necessary). Chaiken et al. (1993) reared, kept, and recorded young starling males under the same experimental conditions as those in our study, but did not expose the birds to any tutor songs. These males in complete acoustic isolation also developed crystallized songs, consisting of sequences of different motif types of which only a certain percentage was reiterated. The songs of such isolates, however, differed significantly in two parameters from the songs of the males of our study, which indicates that the tutor songs heard actually had an influence on the ontogenetic development of some song features:

(1) Isolate starlings' songs display a completely even distribution of breaks and, therefore, lack any increase in speed of performance (Chaiken et al. 1993). The experimental males, exposed to a tutor sequence with an entirely even distribution of breaks, clearly sang songs with increasing speed, due to more breaks at the beginning than at the end of a song.

(2) The songs of starling isolates show only a slight, albeit significant, shift in frequency from low to high of, on average, 0.5 kHz (Chaiken et al. 1993). This value is significantly smaller than the observed frequency shift of 1.4 kHz in the songs of the experimental males of the present study (Mann-Whitney U-test, $P < 0.05$).

The differences between the songs of starlings reared in complete acoustic isolation and the songs of the experimental males thus strongly indicate that acoustic stimulation from the environment was necessary for the development of certain syntactical and temporal song features. Because the tutor songs did not display these features, some kind of general acoustic input is probably sufficient for the development of a specific (i.e. species-typical) acoustic pattern. It is not clear how unspecific such a stimulus can be. Experiments are planned to investigate whether any acoustic stimulation will also do (e.g. white noise) or whether an auditory stimulus must exhibit some kind of temporal organization or frequency shift. The influence of general and specific stimulation on ontogenetic development and learning has been discussed for song learning by several authors (e.g. Marler 1987, Ten Cate 1989, 1994). However, they have focussed mainly on preferences and perceptual mechanisms for the acquisition and memorization of acoustic patterns (see also Hultsch 1993). The results of our study demonstrate that external acoustic stimuli can have a general but necessary influence on the development of vocal motor patterns, which are not acquired from the acoustic environment.

In a recent model of song learning, Marler and Nelson (1994) suggested that extensive information about species-specific song features is already encoded in a young bird's brain. They propose two kinds of templates to account for the fact that birds reared in acoustic isolation fail to develop certain species-specific song features: (1) "pre-active" templates, which require no external auditory stimulation to guide the development of those species-typical features found in the songs of isolates; and (2) "latent" templates, requiring specific auditory input (i.e. experience with acoustic patterns that match the information encoded in the respective template). Such specific stimulation is thought to activate the template, which then controls the motor development of those song features absent in the songs of isolates. The fact that our starlings developed song features not present in the tutor songs heard and absent in the songs of males reared in complete acoustic isolation suggests that "no auditory stimulation" and, as postulated by Marler and Nelson (1994), "specific auditory stimulation" by the environment may be just two extreme forms and that intermediate stages exist. For the development of some song features, like the increase in speed of performance and a pronounced shift in frequency in starling song, at least an "unspecific auditory stimulation"—but no auditory experience with that specific song features—is necessary.

The role of song syntax in vocal development and learning has been investigated in other species. Several syntactical features in the songs of Song Sparrows developed normally in males reared in complete acoustic isolation (Marler and Sherman 1985). Swamp Sparrows, without the possibility to listen to external model songs, developed song patterns that consist of an immediate repetition of elements or element groups, as typical for normal Swamp Sparrow song (Marler and Sherman 1985). Similar results have been reported for Common Nightingales (Wistel-Wozniak and Hultsch 1992). In some species, like the Greenfinch and the Zebra Finch, song elements or groups of elements were copied accurately from heterospecific songs, which also differ in song syntax. These song units, however, were then sung in a syntactical arrangement typical for the own species (Güttinger 1980, Clayton 1989). Therefore, there is accumulating evidence that, like in European Starlings, several aspects of the syntactical organization are rather inflexible and largely predetermined song features. The degree to which unspecific acoustic stimulation can trigger the development of additional features of normal song syntax in other species, however, still needs to be determined.

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