Department of Zoology, Duke University, Durham, and
Department of Zoology, University of California, Davis

Is the Tonal Quality of Birdsong Learned? Evidence from Song Sparrows

STEPHEN NOWICKI, PETER MARLER, ALICIA MAYNARD & SUSAN PETERS

Abstract

Song sparrow (*Melospiza melodia*) songs are composed largely of pure-tonal sounds. This paper investigates the role that learning plays in the development of the tonal structure of song sparrow songs, as well as the role that tonal quality plays in determining the suitability of songs as models for learning. 20 birds were trained with both normal pure-tonal songs and modified songs that included harmonic overtones. The harmonic-modified songs were obtained from birds singing in a helium atmosphere, the result of which is to perturb vocal tract resonances and thus alter a song's tonal quality. Subjects learned equally well from normal and harmonic models. Birds that learned material from harmonic models reproduced some of this material with harmonic overtones, but the majority of notes learned from harmonic models were subsequently reproduced as pure-tonal copies. Thus, the tonal structure of songs does not influence young song sparrows in their selection of song models, but there is a strong tendency to reproduce songs in a pure-tonal fashion, even if learned from harmonic models.

Corresponding author: Stephen NOWICKI, Department of Zoology, Duke University, Durham, NC 27706, U.S.A.

Introduction

The tonal quality of sound refers to the presence, distribution and amplitude of overtones above a fundamental frequency (BENADE 1976). In human speech, changes in tonal quality are related to our perception of different vowel sounds and thus are essential for encoding information in language (MOORE 1989). The tonal quality of musical sounds, or timbre, is an important factor in our recognition of different musical instruments (SEASHORE 1938). The importance of tonal quality in animal acoustic communication signals, such as birdsong, is less well-understood.

Many songbird songs are characterized by a predominance of pure-tonal or "whistle-like" sounds (GREENEWALT 1968; MARLER 1969), with most of their acoustic energy concentrated at a single frequency. Several studies have shown that birds are perceptually sensitive to the pure-tonal quality of their songs in natural contexts (FALLS 1963; BRÉMOND 1976; NOWICKI et al. 1989), and narrow bandwidth has been implicated as a factor in the efficiency of signal production and transmission (MORTON 1975; WILEY & RICHARDS 1982; NOWICKI & MARLER 1988). But the functional significance of pure-tonal sound in birdsong is otherwise largely unexplored.

Because the use of pure-tonal sounds in birdsong is phylogenetically widespread (GREENEWALT 1968; MARLER 1977), one might assume that it occurs simply as a physiological consequence of how birds make sound. The fact that some birds do not produce pure-tonal songs, and that others can produce both pure-tonal and broad-band sounds, however, argues against this view (NOWICKI & MARLER 1988), as do experiments that demonstrate the importance of active vocal tract coordination in the production of pure-tonal sounds (NOWICKI 1987). What, then, is the functional origin of the pure-tonal quality of birdsong? Is it the case, as with many species-typical features of songs, that the tonal quality of birdsong is learned?

Pure-tonal notes predominate in the songs of song sparrows (*Melospiza melodia*) (e.g., Fig. 1 A, B), and even the highly modulated "buzzes" and frequency sweeps produced by this species lack harmonic overtones of significant amplitude. Studies of vocal ontogeny in song sparrows suggest that the pure-tonal quality of their songs is not an inherent feature of production and that learning plays a role in its development. Like many songbirds, male song sparrows learn their songs by imitating models heard during a sensitive phase in the first several months of life (KROODSMA 1977; MARLER & PETERS 1987). Laboratory-trained birds, however, are often observed to produce notes that are not copied from any model (MARLER & PETERS 1982). These "inventions" often include strong harmonic overtones such as are rarely observed in the songs of wild song sparrows. Furthermore, song sparrows raised in isolation and deprived of any song models produce highly atypical songs, one characteristic of which is an unusually large number of notes that have strong harmonic overtones (MARLER & SHERMAN 1985). Thus, song elements that are not learned in a normal fashion tend to depart from typical pure-tonal structure.

The fact that unlearned song elements often have abnormal tonal qualities does not by itself prove that normal tonal properties are learned. To test this idea, we trained young male song sparrows during their sensitive phase for song acquisition with songs that were normal in every respect except that they included strong harmonic overtones. If birds learn from these harmonic model songs and faithfully reproduce them with harmonic overtones, we can conclude that learning plays a role in mediating the tonal quality of songs.

Even if song sparrows are capable of learning harmonic song elements, they may still select against them as models to be copied if they also are exposed to pure-tonal songs, much as they might select against heterospecific song models in the wild. To evaluate this possibility, we also exposed birds to normal, pure-tonal

song sparrow songs as well as to harmonic songs, thus offering a choice of models from which to learn. We included in our training program both normal and harmonic songs of the swamp sparrow (*M. georgiana*). Song sparrows preferentially learn from conspecific songs (MARLER & PETERS 1988), but imitation of heterospecific songs, such as those of the swamp sparrow, does occur both in the field and in the laboratory (EBERHARDT & BAPTISTA 1977; MARLER & PETERS 1989). Thus, training with swamp sparrow song provides another reference point from which we can evaluate the influence of tonal quality on learning. Lastly, we compared the tonal properties of invented notes between birds in this experiment and two other groups from previous experiments as a means of evaluating how early exposure to song models with different tonal qualities might generally influence tonal quality in later song production.

Methods

Subjects and Song Training

Subjects were 16 male song sparrows collected from the wild when 3—10 d old. We divided birds into two groups, each exposed to different training conditions during their sensitive phase for song learning (Table 1). All birds heard both normal and harmonic-modified songs. We trained Group I with separate programs of conspecific and heterospecific (swamp sparrow) songs. We presented only the conspecific song program to Group II. In both the conspecific and heterospecific training programs, the birds heard a total of 18 different songtypes over a 4-wk period. 15 of these were normal songs (e.g., Fig. 1A, B); three were harmonic-modified songs (e.g., Fig. 1C, D). We trained birds with an excess of normal songs out of concern that birds would not learn well without a sufficient number of songs known to be acceptable as models, although our results (below) suggest that this concern was unfounded. Details of training procedures are found in MARLER & PETERS (1987). The 4-wk long conspecific and heterospecific training programs were presented in sequence to Group I, with 5 birds hearing the conspecific program first and 6 hearing the heterospecific program first. We counterbalanced the order of presentation this way in order to encourage heterospecific learning in some birds (MARLER & PETERS 1989).

Harmonic training songs were recorded from wild birds singing in a helium-oxygen atmosphere, the effect of which is to reveal harmonic overtones because of a perturbation of the bird's vocal

Table 1: Experimental groups, sample sizes, and training

Group	n	Training songs heard[1])
I	11	15 normal conspecific
		3 harmonic conspecific
		15 normal heterospecific
		3 harmonic heterospecific
II	5	15 normal conspecific
		3 harmonic conspecific

[1]) For Group I, the conspecific and heterospecific training programs were presented in sequence. 5 birds heard the conspecific program first, 6 heard the heterospecific program first. This pattern of song presentation was intended to promote heterospecific learning by depriving some birds of conspecific models early in the sensitive phase (MARLER & PETERS 1987, 1989).

16*

tract resonances (NOWICKI 1987; NOWICKI & MARLER 1988). These songs preserve all details of the time-varying frequency and amplitude characteristics of normal songs, and differ only by the addition of harmonic overtones.
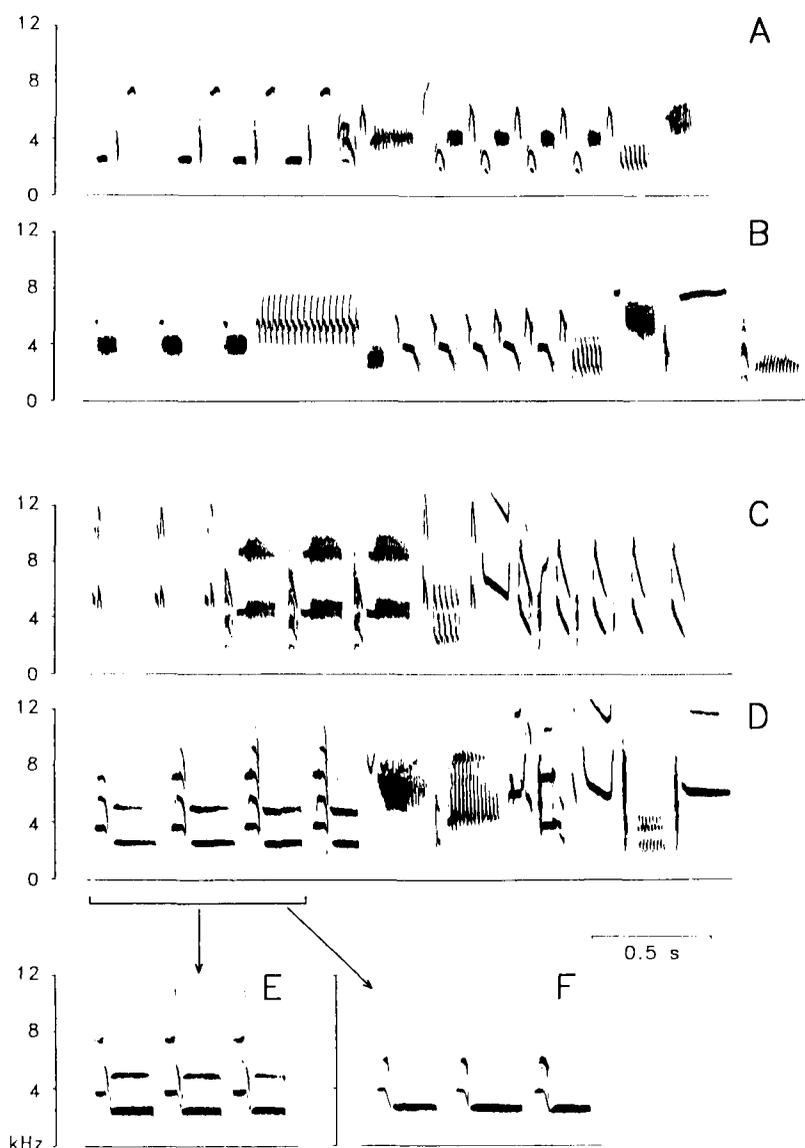

Fig. 1: A, B. Examples of normal song sparrow training songs. C, D. Examples of harmonic song sparrow training songs, recorded in an atmosphere of 80 % helium : 20 % oxygen. Note the presence of harmonic overtones for elements that appear as pure tones in normal air. E. Example of a learned song segment copied from the training song in D (bracket), and reproduced with a harmonic structure similar to the training model. F. Example of a learned song element copied from the same part of the training song in D, but reproduced by the pupil in a pure-tonal fashion. Frequency resolution 300 Hz

To compare the spectral characteristics of invented notes produced by birds that have had different experience with tonal quality during their sensitive phase, we analyzed the songs of two groups of birds from previous studies. The first group included 7 birds (control birds in MARLER et al. 1988) trained with conspecific and heterospecific song as in the present experiment, but with normal song models only, and that learned from these songs. The second group included 5 birds (isolate birds in MARLER & SHERMAN 1985) raised from the egg without ever hearing any song models. Because the isolate birds had no opportunity to copy songs, all of their song elements qualify as inventions by our definition. We compared the percentage of pure-tonal inventions of these groups with that of the 13 birds in the present experiment that were exposed to both harmonic and pure-tonal models and copied conspecific songs.

Recording and Analysis

We recorded about 400 songs from each subject at 1 yr of age ($\overline{X} \pm SE = 421 \pm 22$ songs), using either a Marantz PMD 221 cassette recorder or a Tandberg series 15 reel-to-reel recorder, with a Panasonic WM-2298 microphone. Because of the limited high frequency response of these systems (about 12 kHz), we made additional recordings using a SONY TC-D5M recorder and a Sennheiser ME20 microphone to verify the presence or absence of higher harmonics in songs (up to about 15 kHz).

Using a Kay model 5500 DSP Sona-Graph, we visually compared songs of trained birds to the models they heard to determine which models had been copied (WASER & MARLER 1977; MARLER & PETERS 1988). To quantify harmonic content, songs were digitized ("SIGNAL" software, BEEMAN 1989) at 37.5 kpts/s (analysis bandwidth 0—15 kHz) and amplitude spectra (512 pt Fourier transform, frequency resolution = 73 Hz) were calculated from individual notes.

In most cases, the presence or absence of harmonics in a note copy was obvious and digital spectra only confirmed what was seen on sonagrams (Fig. 2). Based on a subsample, typical pure-tonal (narrow-band) notes in normal song sparrow songs used as training models had second harmonics that were −30.1 ± 3.5 dB below the amplitude of the fundamental frequency ($\overline{X} \pm SE$; n = 12). By contrast, the second harmonic amplitudes of training songs recorded in helium were only −4.2 ± 1.3 dB relative to the fundamental. Comparable measurements from learned songs were −33.9 ± 2.9 dB for narrow-band notes (n = 12) vs. −10.1 ± 2.3 dB for notes with harmonics (n = 10). The presence of a second harmonic with an amplitude greater than −20 dB relative to the fundamental was used as a criterion for the few cases where the presence of harmonics was ambiguous.
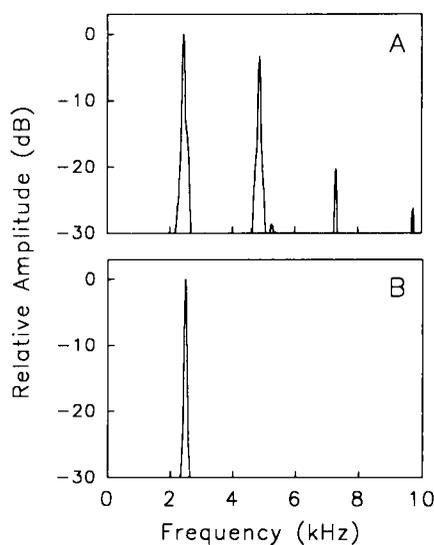
Fig. 2: A. Amplitude spectrum of the unmodulated tonal note at 2.4 kHz shown in Fig. 1E. This note was copied from a harmonic training song (Fig. 1D) and it includes the harmonic overtones of the model. B. Amplitude spectrum of a copy of the same note, but reproduced by a different bird as a pure tone, as shown in Fig. 1F. Both spectra are digital FFTs, see text for details

Results

Conspecific and Heterospecific Song Learning

10 of 11 males in Group I learned from training models, and the number of males learning conspecific versus heterospecific songs did not differ significantly. 4 males copied from both conspecific and heterospecific songs, thus showing no absolute preference for either species' songs, while 6 copied either from conspecific or heterospecific songs only (binomial test, $p = 0.377$). 5 of the 6 males that showed a preference copied only from conspecific songs and one copied only from heterospecific songs (binomial test, $p = 0.109$).

Another means of determining learning preferences is to compare the percentage of conspecific versus heterospecific song models learned by each male. The 10 males who learned copied from an average of $31 \pm 8 \%$ ($\overline{X} \pm SE$) of the conspecific song models to which they were exposed as compared to $4 \pm 2 \%$ heterospecific song models (Fig. 3 A; Wilcoxon test, $p = 0.036$). Thus, significantly more conspecific songs were acquired as models, in agreement with results from previous studies (MARLER & PETERS 1988, 1989).
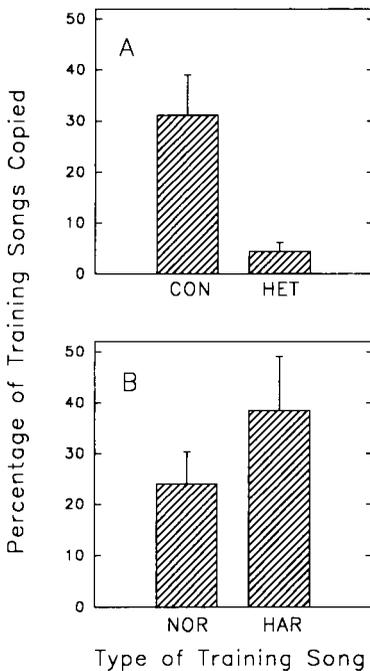

Fig. 3: A. Percentage of conspecific (CON) vs. heterospecific (HET) training songs copied by the 10 birds in Group I that learned (Wilcoxon test, $p = 0.036$). B. Percentage of normal (NOR) vs. harmonic (HAR) training songs copied by the 13 birds in Groups I & II that learned from conspecific songs (Wilcoxon test, $p = 0.141$). Shown are means and SE of the mean

Preferences for Learning from Normal and Helium Models

Combining data from Groups I and II, there were 13 birds total that learned from conspecific song models. Of these, 8 birds copied at least some material from harmonic training songs. By contrast, none of the 5 birds that learned from heterospecific models in Group I copied anything from harmonic versions of

these songs. Thus, song sparrows will accept harmonic renditions of conspecific song as models for learning, but swamp sparrow songs become significantly less acceptable as models if presented with harmonics (Fisher exact probability, p = 0.03).

Is there a preference for copying normal or harmonic conspecific models? Of the 13 males that learned from conspecific models, 7 males learned both from normal and harmonic models (binomial test, p = 0.500). 5 of the 6 birds that showed an absolute preference for either normal or harmonic models learned only from normal models (binomial test, p = 0.109). This lack of a significant difference is especially notable given that the birds heard 5 times more normal songtypes than they did harmonic songtypes (Table 1).

Taking the percentage of songtypes copied by individuals as an alternative measure of song selectivity, the 13 males who learned from conspecific models copied from an average of 24 ± 6 % ($\overline{X}$ ± SE) of the normal song models to which they were exposed as compared to 38 ± 11 % harmonic song models, showing no significant preference for either type of model (Fig. 3 B; Wilcoxon test, p = 0.141).

Production of Learned Songs with or without Harmonics

Of the 8 birds that learned from harmonic models, one bird reproduced all the material it learned as pure-tonal copies without including the harmonics of the model (e.g., Fig. 1 F vs. E). The other 7 birds reproduced some of the harmonic song material they learned with harmonics, and the rest of it as pure-tonal copies. Thus, birds that learned from harmonic models did not necessarily later reproduce that material with harmonics. There appears to be no intrinsic difficulty, however, that prevents males from reproducing song material with harmonics, because most of the males learning from helium models later produced at least some of this material with harmonic overtones.

To explore this issue further, we considered the individual notes that were learned from training songs instead of entire songs. This approach is useful because song sparrows often learn pieces of model songs, instead of entire songs, which they later incorporate into their adult repertoire (MARLER & PETERS 1987). As a group, the 8 males who learned from harmonic models produced 141 notes that were copied from harmonic training songs. Only 20 (14.2 %) of these notes were reproduced with harmonics. Although we here pool data across all birds, the results are descriptive of all individuals and are not due to a few abnormal birds. Of 346 notes learned from normal models, all were reproduced later as pure-tonal copies. The bias towards production of pure-tonal copies from both harmonic and pure-tonal models is highly significant (χ^2 = 47.64, p < 0.001).

"Invented" Notes

Does exposure to harmonic models during training affect the extent to which harmonics are expressed in inventions? There was significant heterogeneity in the proportion of inventions produced as pure tones among the three experimental groups we compared (Fig. 4; Kruskal-Wallis test, p = 0.004). Pairwise compari-

sons revealed no difference between birds exposed only to normal songs and those exposed to both normal and helium songs. By contrast, the isolate group produced significantly fewer pure-tonal inventions than either of these two groups (CONOVER 1980, p < 0.05 for both).
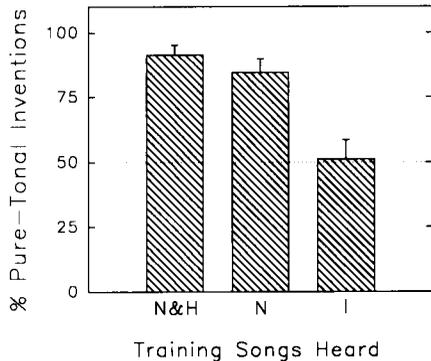

Fig. 4: Percentage of pure-tonal inventions produced by three groups that had different exposure to tonal quality during their sensitive phase for learning. N & H: 13 birds trained with both normal and harmonic songs in the present study, N: 7 birds trained with normal songs only (MARLER et al. 1988), I: 5 birds that were raised in isolation from any song models (MARLER & SHERMAN 1985). Dotted line at 50 %: proportion at which no preference is evident for producing either pure-tonal or harmonic inventions. There is significant heterogeneity among the three groups (see text for details). Shown are means and SE of the mean

Discussion

Tonal properties influence the song sparrow's selection of heterospecific song models when learning. Although significantly fewer heterospecific than conspecific songs were used as models (Fig. 3 A), half of the birds in Group I copied some heterospecific song. All of the heterospecific songs copied were pure-tonal, however, and heterospecific songs that included harmonics appeared to be completely unacceptable as models. This result demonstrates that young song sparrows are attentive to the tonal properties of the song models they hear, and that tonal properties can influence learning selectivity. Thus, it is significant that the tonal quality of songs has little or no influence on a song sparrow's selection of conspecific models from which to learn. Even though the model songs we recorded in helium differ radically from any song sparrow song that would be heard in nature (e.g., Fig. 1 A, B vs. 1 C, D), young birds learned from them as readily as they did from normal songs under comparable conditions (Fig. 3 B). This was true even though the majority of songs to which birds were exposed had normal tonal properties.

This lack of preference by young song sparrows contrasts with evidence from other species demonstrating the importance of tonal structure in conspecific song perception by adults. The addition of overtones to pure-tonal songs greatly reduces responsiveness in field playback tests with white-throated sparrows (*Zonotrichia albicollis,* FALLS 1963) and Bonelli's warblers (*Phylloscopus bonelli,* BRÉMOND 1976). A significant reduction in response was also observed in adult swamp sparrows when the harmonic overtones added to song were the result of a manipulation of vocal tract characteristics with helium, as in the present experiment (NOWICKI et al. 1989). If song sparrow adult males also are shown to be responsive to changes in tonal structure, as seems likely, then it might be that

perceptual preferences for tonal quality shift during ontogeny and are themselves influenced by learning.

Although there is no preference for tonal quality during song acquisition, there is a strong tendency for birds to reproduce songs without harmonics, regardless of whether they are learned from pure-tonal or harmonic models. This bias is not simply the result of physiological limitations on the birds' ability to reproduce harmonic sounds. Most of the birds that learned from harmonic models reproduced at least some of this material with harmonics. The reproductions of helium-induced harmonics were quite accurate — the average difference in amplitudes of second harmonics between normal and harmonic training songs was 25.9 dB, as compared to a 23.8 dB difference between pure-tonal and harmonic reproductions by the trained birds. This result shows that song sparrows are capable of achieving a vocal configuration that results in the production of harmonics comparable to those induced by perturbation of the vocal tract with helium.

Is, then, the production bias for pure-tonal sounds learned? That is, would birds still favor pure-tonal notes in song production if they did not hear pure-tonal models during their sensitive phase for learning? All the birds in our experiment were exposed to both normal and harmonic songs, so our data do not directly answer this question, but the analysis of invented notes provides us with some insight. Because inventions are not copies of specific song elements, we might expect them to reveal any general influence due to the tonal quality of training songs. We found, however, that birds trained with harmonic and normal songs exhibited the same proportion of harmonic inventions in their songs as did birds trained with normal song models alone (Fig. 4). This result supports the idea that exposure to harmonic models does not have a general influence on the degree to which harmonic sounds are subsequently produced, although we cannot rule out the possibility that exposure to a higher proportion of harmonic models might still reveal an effect.

Comparisons with the songs of isolate birds are more illuminating. The proportion of pure-tonal inventions produced by isolates is significantly less than that produced either by birds trained with only normal songs or by birds trained with both normal and harmonic songs (Fig. 4). Furthermore, the relative numbers of pure-tonal and harmonic notes produced by isolates are approximately equal. Thus, early experience does appear to influence later production biases for pure-tonal quality, at least in the sense that the lack of exposure to pure-tonal models eliminates this bias in the tonal characteristics of inventions. An experiment in which birds are trained predominantly or exclusively with harmonic song models will be needed to verify this result, and also to test whether production biases can be reversed and caused to favor the production of harmonic sounds.

Like predispositions for acquiring other specific attributes of conspecific song, the song sparrow's production bias for pure-tonal sounds might represent a feature of a song "template" that must be activated by exposure to external models in order to be expressed (MARLER 1984). If so, then we predict that exclusive exposure to harmonic song models during learning would only suppress, but not reverse, the bias for producing pure-tonal sounds. If the preference

for pure-tonal sounds is associated with a song template, however, it differs from other template features by not influencing the selection of song models, and instead only becoming evident in their subsequent reproduction.

The fact that song sparrows learn from harmonic songs and reproduce them precisely, but without the harmonic overtones of the original, also suggests that the ontogenetic processing of tonal quality is not necessarily coupled to the processing underlying other aspects of vocal imitation. The harmonic overtones produced by adult birds in a helium atmosphere result from the modification of vocal tract resonances and a resulting lack of coordination between the activity of the syringeal vocal source and the motor systems controlling vocal tract resonances (NOWICKI & MARLER 1988). An important outcome of the early motor development of song is likely to be the attainment of this coordination. Possibly, the young bird learns the correct motor relationship not as a specific property of any model song it is duplicating, but instead as a general feature that is influenced by learning from a set of models, and then generalized to other learned material. The significance of pure-tonal sounds in song sparrow songs, as in the songs of many birds, becomes even more intriguing given that it is neither a necessary feature of the physiology of song production nor an inevitable consequence of learning from specific models.

Acknowledgements

Literature Cited

BEEMAN, K. 1989: "SIGNAL" Software Manual. Engineering Design, Belmont.
BENADE, A. H. 1976: Fundamentals of Musical Acoustics. Oxford Univ. Press, New York.
BRÉMOND, J.-C. 1976: Specific recognition of the song of Bonelli's warbler. Behaviour 58, 99—116.
CONOVER, W. J. 1980: Practical Nonparametric Statistics. Wiley & Sons, New York.
EBERHARDT, C. & BAPTISTA, L. F. 1977: Intra- and inter-specific song mimesis in the song sparrow, Melospiza melodia. Bird Banding 48, 193—205.
FALLS, J. B. 1963: Properties of bird song eliciting responses from territorial males. Proc. Int. Orn. Congr. 13, 259—271.
GREENEWALT, C. H. 1968: Bird Song: Acoustics and Physiology. Smithsonian, Washington, D.C.
KROODSMA, D. E. 1977: A re-evaluation of song development in the song sparrow. Anim. Behav. 25, 390—399.
MARLER, P. 1969: Tonal quality of bird sounds. In: Bird Vocalizations. (HINDE, R. A., ed.) Cambridge Univ. Press, Cambridge, pp. 5—18.
— — 1977: The structure of animal communication sounds. In: Recognition of Complex Acoustic Signals. (BULLOCK, T. H., ed.) Dahlem Konf., Berlin, pp. 17—35.
— — 1984: Song learning: Innate species differences in the learning process. In: The Biology of Learning. (MARLER, P. & TERRACE, H. S., eds.) Dahlem Konf., Berlin, pp. 289—310.
— — & PETERS, S. 1982: Subsong and plastic song: Their role in the vocal learning process. In: Acoustic Communication in Birds. Vol. 2. (KROODSMA, D. E. & MILLER, E. H., eds.) Acad. Press, New York, pp. 25—50.
— — & — — 1987: A sensitive period for song acquisition in the song sparrow, Melospiza melodia: A case of age-limited learning. Ethology 76, 89—100.

— — & — — 1988: The role of song phonology and syntax in vocal learning preferences in the song sparrow, *Melospiza melodia*. Ethology **77**, 125—149.

— — & — — 1989: Species differences in auditory responsiveness in early vocal learning. In: The Comparative Psychology of Audition: Perceiving Complex Sounds. (DOOLING, R. J. & HULSE, S. H., eds.) Lawrence Erlbaum Assoc., Hillsdale, pp. 243—273.

— —, — —, BALL, G. F., DUFTY, A. M. & WINGFIELD, J. C. 1988: The role of sex steroids in the acquisition and production of birdsong. Nature **336**, 770—772.

— — & SHERMAN, V. 1985: Innate differences in singing behaviour of sparrows reared in isolation from adult conspecific song. Anim. Behav. **33**, 57—71.

MOORE, B. C. J. 1989: An Introduction to the Psychology of Hearing. 3rd ed. Acad. Press, London, San Diego.

MORTON, E. S. 1975: Ecological sources of selection on avian sounds. Am. Nat. **109**, 17—34.

NOWICKI, S. 1987: Vocal tract resonance in oscine bird sound production: Evidence from birdsongs in a helium atmosphere. Nature **325**, 53—55.

— — & MARLER, P. 1988: How do birds sing? Music Percep. **5**, 391—426.

— —, MITANI, J. C., NELSON, D. A. & MARLER, P. 1989: The communicative significance of tonality in birdsong: Responses to songs produced in helium. Bioacoustics **2**, 35—46.

SEASHORE, C. E. 1938: Psychology of Music (reprinted ed. 1967). Dover, New York.

WASER, M. S. & MARLER, P. 1977: Song learning in canaries. J. Comp. Physiol. Psychol. **91**, 1—7.

WILEY, R. H. & D. H. RICHARDS, 1982: Adaptations for acoustic communication in birds: Sound transmission and signal detection. In: Acoustic Communication in Birds. Vol. 1. (KROODSMA, D. E. & MILLER, E. H., eds.) Acad. Press, New York, pp. 131—181.