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THE COMMUNICATIVE SIGNIFICANCE OF TONALITY IN BIRDSONG: RESPONSES TO SONGS PRODUCED IN HELIUM

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ABSTRACT

"Pure tones" are a distinctive acoustic feature of many birdsongs. Recent research on songbird vocal physiology suggests that such tonal sounds result from a coordinated interaction between the syrinx and a vocal filter, as demonstrated by the emergence of harmonic overtones when a bird sings in helium. To investigate the communicative significance of vocal tract filtration in the production of birdsong, we used field playback experiments to compare the responses of male swamp sparrows *Melospiza georgiana* to normal songs and those same songs recorded in helium. We also measured responses to pure tone songs that had been shifted upward in frequency to match the average spectra of those songs with added harmonics. Male sparrows were significantly more responsive to the playback of normal songs than to either helium songs with added harmonics or frequency-shifted pure tone songs. Songs with harmonics retained a high degree of salience, however. We conclude that explanations for the occurrence of tonal sounds in birdsongs must consider perceptual attributes of songs as communicative signals, as well as problems of song production and transmission.

INTRODUCTION

One of the most notable acoustic features of oscine birdsong is the presence of narrow band frequency components, often termed "whistles" or "pure tones," which appear on a sound spectrogram as single, well-defined narrow traces (Greenewalt 1968, Marler 1977). Recent work on songbird vocal physiology demonstrates that the production of these pure tone sounds is not an inherent property of the operation of the bird's vocal organ, or syrinx, as was previously assumed. Instead such sounds are achieved through coordination of several elements of the vocal system, especially involving the acoustic configuration of a vocal tract filter (Nowicki and Capranica 1986, Nowicki 1987). In this paper, we explore the communicative significance of vocal tract filtration in the production of oscine birdsong through the use of field playbacks of normal songs and songs of birds whose vocal filter has been experimentally manipulated.

The discovery that acoustic resonances of the songbird's vocal tract play a key role in vocal production was made by comparing songs recorded under normal conditions to songs recorded in an atmosphere in which the nitrogen was replaced by the less dense gas helium. The physical effect of this manipulation is to increase the speed of sound, and thus to raise the frequencies of any acoustic resonances by a proportional amount (Rayleigh 1894, Beranek 1949). In singing birds, the result is the appearance of one or more harmonics above each note that originally appeared as a pure tone in normal air (Nowicki 1987). These results argue that the bird's vocal tract is acting as an acoustic filter, shaping the spectral properties of the emitted song in a manner analogous to the way the human vocal tract modifies the harmonic signal generated by the larynx (Fant 1970, Nowicki 1987, Nowicki and Marler 1988). By this interpretation, the pure tones commonly observed in song are in fact harmonic sounds, the overtones of which are normally suppressed by a band-pass filter centered around the fundamental frequency. In helium, the resonances of the vocal tract shift upward, modifying the frequency response of the vocal filter, and allowing the appearance of the otherwise attenuated higher harmonics.

In human speech, the attributes of the vocal filter play an essential role in communication, especially with regard to the production of different vowel sounds (Fant 1970, Flanagan 1972). Whether or not the properties of an oscine bird's vocal filter might be significant for communication is not as clear. To investigate this question, we compared the responses of territorial male swamp sparrows, *Melospiza georgiana*, to playback of normal songs and those same songs obtained by placing the singer in helium. Normal swamp sparrow songs are composed entirely of pure tone notes (Figure 1, Marler and Pickert 1984), while their helium counterparts reveal one or more harmonic overtones due to the shifted vocal filter. To control for the effects of the upward shift in the average frequency distribution in helium, as opposed to variations in overtone structure, comparisons were also made with songs with synthetically elevated fundamental frequencies. These frequency-shifted songs retained their pure tone nature, but had average frequency distributions that matched those seen in helium songs.

METHODS

Recording, analysis and synthesis of playback signals

We recorded two song types from a wild-caught male swamp sparrow *Melospiza georgiana*, both in normal atmosphere (roughly 80% nitrogen, 20% oxygen) and in heliox (80% helium, 20% oxygen). Two exemplars were used to minimize the chance that a single idiosyncratic stimulus would influence the results. The resulting song types are referred to as normal

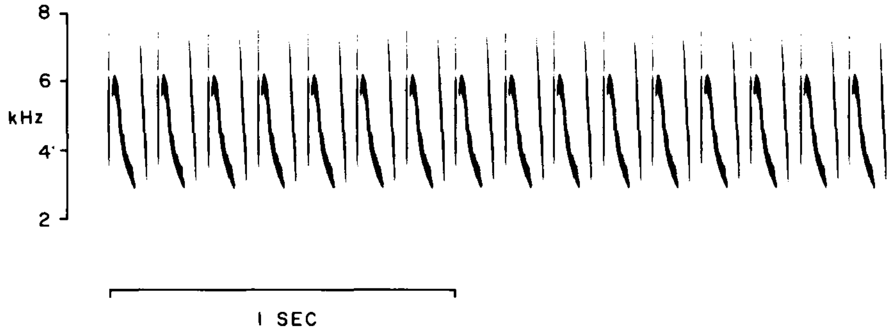

Figure 1. Sonagram of an entire swamp sparrow song, illustrating the arrangement of repeating syllables to form a trill. This song is composed of normal syllable type B (N-B) used in the playback experiments. Analysis range = 0–8 kHz, frequency resolution = 300 Hz (Kay Elemetric Digital Sonagraph model 7800).

type A (N-A), normal type B (N-B), helium type A (H-A) and helium type B (H-B) (Figures 1, 2A, B, D, E). Recordings were made in a gas-sealed acoustic chamber, using a B&K 4145 calibrated microphone, a B&K 2604 amplifier (flat weighting), and a Nagra 4.2L tape recorder (19 cm/s). The flat frequency response of this system was 30–16000 Hz.

We digitized the songs using a PDP-11/23 computer, sampling with 12-bit precision at a rate of 41667 Hz for an effective FFT bandwidth of 16667 Hz (Beeman 1987). We determined spectral characteristics of each of the four song types (N-A, N-B, H-A, H-B) by calculating a single FFT (8192 points, 197 ms, frequency resolution = 5 Hz) over the duration of one entire syllable (Figure 3). After averaging results obtained from two examples of each song, we determined the bandwidth at -20 dB below the spectral component of maximum amplitude, and the center frequency of this band of maximum amplitude.

We created control songs for playback by digitally copying and concatenating one exemplar of each normal syllable type (N-A, N-B) to produce two trilled songs that were 16 syllables long (frequency resolution = 163 Hz; temporal resolution = 6 ms). Inter-syllable intervals were matched to those observed in normal songs. Frequency-shifted songs (FS-A, FS-B) were produced by raising the fundamental frequencies of control songs in integral multiples of 163 Hz to achieve the desired shift (Zoloth et al. 1980, Clark et al. 1983), as determined by the difference in the center frequencies of the normal and helium songs (see Results below). We created the helium playback songs (H-A, H-B) by concatenating helium syllables using the same digital procedures as above, but without frequency shifts. Amplitudes of all test stimuli were equalized during D/A conversion.

Subjects and playback procedures

We conducted all playbacks between 0630 and 1000 hours, from 7 May to 3 June 1987, at study sites in Dutchess County, New York. Subjects were 30 territorial male swamp sparrows. We performed three experiments, comparing the birds' responses to two kinds of stimulus songs in each experiment: 1) normal versus helium, 2) normal versus frequency-shifted, and 3) helium versus frequency-shifted. Each experiment included ten trials for a total of 30 trials. To avoid habituation or potentiation of response, each subject was used in only a single playback trial. Half the trials in each experiment used song type A (e.g., N-A, H-A, or FS-A) while the other half used song type B. No difference in response to the two song types was discerned. The particular experiment and trial in which any individual was tested was randomized.

Trials were conducted using a two-speaker paradigm (Lanyon 1978, Peters et al. 1980, Nelson 1988), in which we compared the responses of each bird to concurrent playback of two different stimulus songs. Thus, any bird might hear one of six possible combinations: N-A versus H-A, N-A versus FS-A, H-A versus FS-A, N-B versus H-B, N-B versus FS-B, or H-B versus FS-B. In each trial two Nagra DSM speakers covered with brown cloth were placed 16 m apart near the center of the bird's territory. Poles at 4 m intervals between the speakers facilitated the measurement of distances. The two songs presented in any trial were recorded at equal amplitude on separate tracks of a SONY TC-D5M stereo tape recorder such that they alternated between the two speakers at 5 s intervals. Songs were produced at 96 dB SPL measured at 1 m from the source (Realistic Sound Level Meter model 33-2050, A-weighting, slow response). A trial consisted of two 120-s playback blocks separated by 120 s of silence, with each block containing ten repetitions of each of two songs. Two coin flips before each trial determined which speaker played which song, and which song was played first in the first block. In the second block, speaker cables and the order of presentation of songs were reversed.

Response measure and statistical tests

For each trial, an average approach distance to each song was calculated by determining the bird's position relative to each speaker at 5 s intervals during the two playback blocks (Peters et al. 1980, Searcy et al. 1981). Approach distances (x) were divided into six categories: $x \leqslant 2$ (mean = 1 m), $2 < x \leqslant 4$ (3 m); $4 < x \leqslant 8$ (6 m), $8 < x \leqslant 14$ (11 m), $14 < x \leqslant 18$ (16 m), and $x > 18$ (24 m). The differences between mean approach distance to paired stimulus songs were compared statistically for each experiment using two-tailed Wilcoxon's matched-pairs signed-ranks tests (Siegel 1956). This test allowed us to evaluate whether responses to the two stimulus songs in an experiment differed significantly. In order to evaluate differences in the *magnitude* of differential responsiveness to songs among the three experiments, we compared the differences in mean approach distances to songs in each trial, using the Kruskal-Wallis non-parametric one-way analysis of variance with pairwise comparisons (Conover 1980).

RESULTS

Signal characteristics

The phonological consequence of the helium atmosphere was the appearance of one or more harmonic overtones above each acoustic element that originally appeared as a pure tone in normal air (compare Figures 2A & B, 2D & E). By comparing the average amplitude spectra of

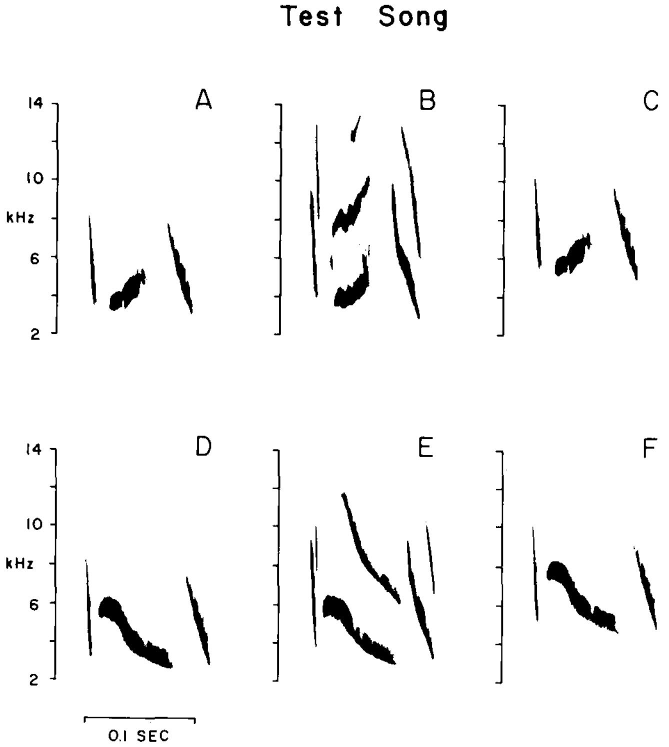

Figure 2. Sonagrams of the six syllable types used to construct playback songs. **A**, normal syllable type A (N-A); **B**, syllable type A produced in a helium atmosphere (H-A); **C**, syllable type A after an upward frequency shift of 2 kHz (FS-A); **D**, normal syllable type B (N-B); **E**, syllable type B produced in a helium atmosphere (H-B); **F**, syllable type B after an upward frequency shift of 2 kHz (FS-B). In helium, harmonics appear above each note produced as a pure tone in normal atmosphere. Analysis range = 0–16 kHz, frequency resolution = 600 Hz (note that the expanded analysis range causes the syllables to appear compressed in frequency as compared to Fig. 1).

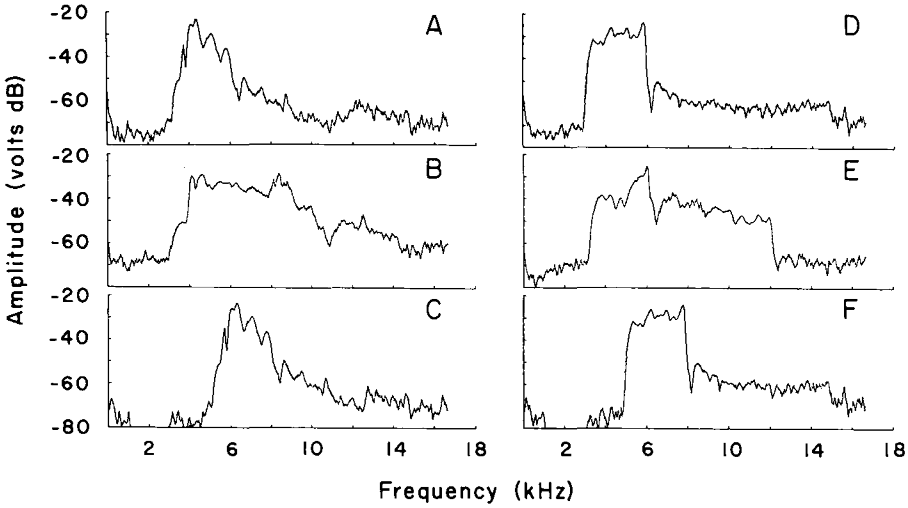

Figure 3. Amplitude spectra of the six syllable types illustrated in Fig. 2. **A**, syllable N-A; **B**, syllable H-A; **C**, syllable FS-A; **D**, syllable N-B; **E**, syllable H-B; **F**, syllable FS-B. See text for details of analysis, bandwidth, and resolution.

syllables produced in normal atmosphere to those same syllables produced in helium, we determined that the helium caused an upward shift of approximately 2100 Hz in the center frequency of the band of maximum amplitude for song-type A (Figures 3A & B) and an upward shift of 1800 Hz for song-type B (Figures 3D & E). Note that the center frequency did not necessarily coincide with the frequency component of maximum amplitude, and that the bandwidths of helium songs were approximately double those of normal songs, as is expected given the emergence of a harmonic in helium (Nowicki 1987). On the basis of these results, we raised the frequency of the pure tone fundamentals of both song-types by 1956 Hz (12 multiples of 163 Hz, see Methods above) to create frequency-shifted songs that were comparable in the central tendency of their frequency distributions to those observed in helium (Figures 2C & F, 3C & F). This modification represented a 43% increase in frequency for song-type A and a 34% increase for song-type B.

Playback tests

During playback trials, territorial male swamp sparrows approached normal songs more closely than songs sung in helium (Figure 4A, P = 0.01) and also approached normal songs more closely than songs whose fundamental frequency had been digitally shifted upward in frequency

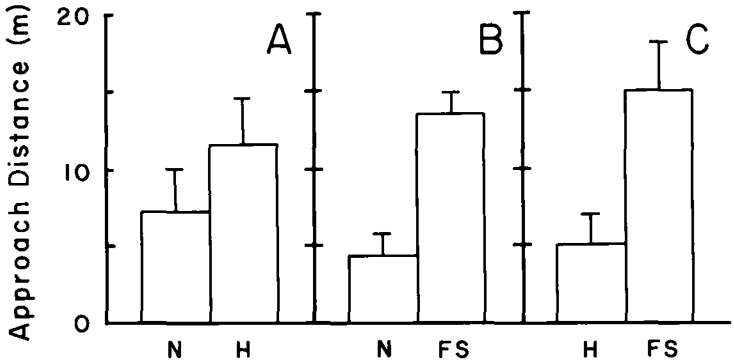

Figure 4. Responses of male swamp sparrows to playback songs. Mean approach distances are shown; error bars indicate one standard deviation from the mean. N = normal songs; H = helium songs; FS = frequency-shifted songs. Differences between the average approach distances to songs in each of the three experiments were **A**, N vs. H = 4.3; **B**, N vs. FS = 9.3; **C**, H vs. FS = 10.0.

(Figure 4B, P = 0.01). When given the choice between helium songs and frequency-shifted songs, males approached significantly closer to helium songs (Figure 4C, P = 0.01).

Average differences between approach distances to songs showed significant heterogeneity among the three experiments (P = 0.001). That is, the response differential between paired test stimuli, as measured by the differences in their distances to approach each song, varied among the three experiments. Pairwise comparisons revealed that the average difference between approach distances to normal versus helium songs (4.3 m) was significantly less than those differences in experiments using normal versus frequency-shifted songs (9.3 m), and helium versus frequency-shifted songs (10.0 m; P = 0.01 for both). By contrast, the average approach distance differences between playbacks involving normal versus frequency-shifted songs did not differ from the value between playbacks of helium versus frequency-shifted songs (P>0.05). This trend was apparent to the observers. Although birds stayed closer on average to normal signals in normal versus helium trials, the subjects often spent much of the test flitting back and forth, from one speaker to the other, as the two signals alternated. In normal versus frequency-shifted trials and, to a lesser extent, helium versus frequency-shifted trials, the subject's behavior was clearly centered around the speaker playing the normal song or helium song, respectively. Subjects did not often sing during the playback period, but did give aggressive displays, such as waving one wing over the back while perched.

DISCUSSION

The acoustic attributes of a songbird's vocal tract filter clearly influence the perceptual salience of conspecific song. Given a choice between normal songs composed of pure tones and helium songs in which the filter has been manipulated so as to reveal higher harmonics, swamp sparrows were significantly more responsive to the normal songs (Figure 4A). Typical swamp sparrow songs never display harmonics (Marler and Pickert 1984), and the spectral structure of helium songs is quite unlike that of their corresponding normal songs (compare Figures 2A & B, D & E; Figures 3A & B, D & E). The frequency-shifted songs, which also elicited a significantly weaker response than normal songs, exhibited a pure tone phonology identical to that of normal songs, but with frequency ranges that fell well beyond the species norm (Marler and Pickert 1984). Previous playback studies with other species have demonstrated that frequency shifts in excess of 20% produce a drastic reduction in the salience of a test song (Falls 1963, G. Schubert 1971, M. Schubert 1971, Bremond 1976, Dabelsteen and Pedersen 1985, Nelson 1988). In the present case, frequency shifts were of the order of 40% for song-type A and 30% for song-type B.

It is more surprising that the helium songs retained as much salience as they did, as evidenced by the strong preference for helium songs over frequency-shifted songs. Consider the statistical comparison of differences in playback responses among the three experiments. Comparing the normal versus frequency-shifted and helium versus frequency-shifted experiments, the average differences in response did not differ statistically, but both of these experiments resulted in significantly greater differences in approach distances than those observed in the normal versus helium experiment (Figure 4). This result suggests that the difference in salience between normal and helium songs, although significant, is not as extreme as the difference between normal and frequency-shifted songs or even the difference between helium and frequency-shifted songs.

Manipulation of the bird's vocal filter with helium results in two main differences in phonology: 1) a change in spectral organization from pure tones to sounds with harmonic overtones, and 2) an upward shift in average frequency distribution, which is a necessary correlate of the addition of harmonics. We used frequency-shifted songs as a control for this second feature, creating a change in average frequency distribution without changing tonal structure. Despite their retention of pure tone phonology, frequency-shifted songs almost completely lost their salience (Figure 4), as expected. Helium songs, however, retained significantly greater salience, even though their average frequency distributions were as high as frequency-shifted songs. We conclude from this comparison that the higher frequencies represented in both the helium and frequency-shifted signals are not in themselves solely responsible for inhibition of responsiveness. If the presence of energy in a particular frequency range were simply inhibitory, as has been demonstrated, for example, with frog mating calls (Capranica 1965, 1966), then responses to helium songs should be much lower.

The salience retained by helium songs is likely due to the fact that normal and helium songs share the same fundamental frequency components. The decreased salience of helium songs as compared to their normal counterparts demonstrates that the correct tuning of a vocal filter also contributes to the perceptual salience of a bird's song. In the case of tonal songs, such as those of the swamp sparrow, shifting the vocal filter reveals harmonic overtones. Because the vocal filter is no longer centered around the frequency of the fundamental, however, this shift also results in a reduction in the absolute amplitude of the fundamental frequency (Nowicki 1987). It is conceivable, then, that the reduced responsiveness to helium songs simply reflected an intensity reduction in a single frequency component of interest (i.e., the fundamental).

Field measurements revealed that the fundamental frequency components of helium songs were only about 8 dB lower than those of the normal songs. Amplitude variations of this magnitude commonly occur in singing due to local differences in vegetation, wind, elevation, and other natural sources of excess attentuation (Morton 1975, Marten and Marler 1977, Wiley and Richards 1982, Michelsen 1983), suggesting that the lower response to helium songs was not simply due to their weaker fundamentals. Furthermore, it is difficult to compare the *perceptual* difference (in terms of loudness) between a pure tone of a given amplitude and a single frequency component that is part of a more complex frequency distribution, such as a harmonic series. What is likely to be of greater perceptual salience is the difference in the *relative* amplitudes of frequency components within the signal, which varies directly with the tuning of the vocal filter.

We conclude that male swamp sparrows discriminate between normal and helium songs on the basis of differences in overtone structure. This suggestion is supported by other studies. Most relevant is the pioneering work of Falls (1963), who added harmonics to artificially generated white-throated sparrow, *Zonotrichia albicollis*, songs and observed an intermediate reduction in response during playback. The addition of a non-harmonic overtone caused a more severe reduction. Bremond (1976) added non-harmonic overtones and undertones to Bonelli's warbler, *Phylloscopus bonelli*, songs and found that these added tones severely reduced responsiveness in playback tests. In these studies, the added frequencies and their amplitudes were not designed to reflect perturbations of vocal production as in the present case, but the results suggest that selective responsiveness to narrow band tonal signals may be common in songbirds.

Pure tonal songs are widely distributed among oscine birds. Any adaptive significance attributable to the perception of vocal tract characteristics or narrow band phonology is thus likely to be more global than that associated with the more idiosyncratic acoustic features involved in species recognition. Studies of frequency-dependent attentuation, for example, suggest that narrow band signals may optimize transmission (Morton 1975, Wiley and Richards 1982, Michelsen 1983). Signals do not need to be limited to a single pure tone, however, to conform to a transmission "sound window." On the other hand, if a bird can achieve a higher amplitude sound at the source by concentrating all of the signal's energy into a single frequency component, then pure tone phonology might be selected to promote maximal transmission (Morton 1975, Wiley and Richards 1982, Brenowitz 1986).

An important caveat here is that no advantage is gained if the vocal tract acts as a passive band-pass filter, simply attentuating frequencies produced at the source. An increase in production efficiency will only be achieved if there is a source-filter interaction such that the resonance properties of the vocal tract can influence the vibration characteristics of the acoustic source in the syrinx. Interestingly, an interaction of this sort has recently been shown to occur in the human soprano voice, when the lowest resonance frequency (or formant) of the singer's vocal tract coincides with the fundamental frequency produced at the glottis (Rothenberg 1987). While this overlap between the source's fundamental and the filter's resonance frequency may be unique to sopranos in human phonation, it is likely to be the norm during the production of birdsong. More detailed studies are needed to determine whether such source-tract interactions occur in birds, and how features of production influence perception or vice versa.

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