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TEMPORAL RELATIONSHIPS IN WHITE-THROATED SPARROW SONG

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Bird song has been likened to human music for centuries (e.g., Anonymous 1717, Hartshorne 1973). The analogy between bird song and music is perpetrated to some degree by the use of musical terms to describe avian vocalizations: individual sound elements are called "notes," and strings of notes are called "songs." In most modern studies of song this analogy has fallen out of favor (e.g., Dobson and Lemon 1977). However, recent studies have shown that fixed relationships between the frequencies of adjacent notes, a defining feature of human music, occur in the songs of several species, and the birds seem to use this feature to recognize their songs (e.g., see Weary et al. 1991).

The aim of the present study was to determine if there are other predictable relationships between notes. In particular we investigated whether the duration of song notes sung by White-throated Sparrows (*Zonotrichia albicollis*) are correlated. When an individual produces a relatively long first note, do the subsequent notes tend to be longer? These temporal relationships between notes are termed rhythm when describing music. The familiar tune is still recognized when it is sped up or slowed down (changes in tempo), because the temporal relationships between the notes (and internote intervals) are maintained.

The only formal study of rhythm perception in nonhuman animals was done in the laboratory on European Starlings (*Sturnus vulgaris*) (Hulse et al. 1984). This study showed that birds can learn to discriminate rhythmic from arrhythmic sound patterns, and can generalize this discrimination over changes in tempo. How important are the temporal relationships among sounds in nature? For birds, there is some evidence that these relationships are important. Becker's (1982) review pointed to several temporal features of song that are important in species recognition. For example, the manipulation of the intervals between notes in a song affects recognition in several species, including White-throated Sparrows (Falls 1963). Also, interspecific comparisons have demonstrated that birds which sing longer songs also tend to use greater intervals to separate them (Dobson and Lemon 1975, Weary and Lemon 1988). Thus, certain aspects of timing do seem important in bird song.

Other evidence is harder to interpret. For example, Lambrechts and Dhondt (1987) found that during the course of a song, Great Tits (*Parus major*) tend to sing with progressively longer intervals between notes. The rhythmic aspect of this behavior is that when Great Tits produce longer inter-note intervals, they also produce longer inter-phrase intervals (phrases consist of groups of notes). The arrhythmic aspect is that there is no corresponding increase in the duration of the notes themselves. Thus, in one respect Great Tits maintain rhythm over a change in tempo, but in another they do not.

METHODS

White-throated Sparrows sing two types of songs, each composed of, on average, five notes (Fig. 1). Most common is the ascending song in which there is an increase in frequency between the first and second notes. Less common is the descending song where the major change in frequency is a decrease between the second and third notes (Borror and Gunn 1965). Each of the songs we considered fell unambiguously into one of these two categories. For ascending (56 birds) and descending (20 birds) songs, we measured the duration of the first three notes, as well as the duration of the silent interval between the first and second notes and between the second and third notes. Because some subjects sang songs composed of only three notes, this was the maximum number which we could consider in our analysis. Three songs were recorded from each bird. Values from the three songs per bird were averaged, and this mean value was then used in all analyses. Birds were recorded

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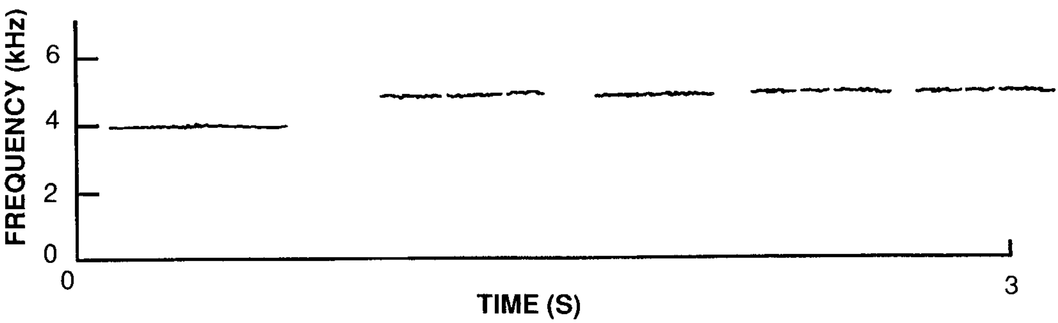

FIGURE 1. An example of an ascending White-throated Sparrow song. We measured the durations of the first three notes and the intervals between the first and second notes, and the second and third notes.

in Algonquin Park, Ontario during May and June 1987 and 1988 using a Sony WM-D6C cassette recorder and Sennheiser M-816 microphone. Songs were digitized and measured using MacSpeech Lab software and a Macintosh computer. The measurement error of this system is approximately 6 msec.

RESULTS

In addition to the major difference in the frequency characteristics between the ascending and descending songs, there are also differences in the timing of the notes and intervals (Table 1). Almost all notes of ascending songs are longer than the corresponding notes in descending songs, and this difference is statistically significant for both the second note and the second inter-note interval ($t = 4.19$, $P < 0.0001$, and $t = 4.72$, $P < 0.0001$ respectively). Because of these differences, we analyzed the temporal relationships between the notes separately for the two types of songs.

We tested the hypothesis that White-throated Sparrows maintain a species typical rhythm, with the different individuals singing at different tempos. This hypothesis predicts that when an individual sings a long first note, all other aspects of his song will tend to be longer. We thus expected a positive correlation between the durations of all elements (i.e., notes and inter-note intervals) in both ascending and descending songs.

TABLE 1. The mean, standard deviation and coefficient of variation of the duration(s) of each of the first three notes and two inter-note intervals for (a) ascending songs (56 subjects) and (b) descending songs (20 subjects).

Element	Mean	SD	CV
(a) Ascending songs			
1st note	0.76	0.15	19
Interval	0.20	0.06	27
2nd note	0.62	0.11	17
Interval	0.17	0.04	24
3rd note	0.43	0.05	12
(b) Descending songs			
1st note	0.70	0.11	15
Interval	0.18	0.05	25
2nd note	0.51	0.06	12
Interval	0.12	0.03	28
3rd note	0.44	0.04	08

As predicted, there are certain positive temporal relationships among the notes of songs sung by White-throated Sparrows. Among singers of the ascending songs, individuals that sang long introductory notes tended to sing longer second notes (Fig. 2: $r = +0.646$, $P < 0.0001$), and longer third notes ($r = +0.595$, $P < 0.0001$). There was no independent relationship between the second and third notes (partial $r = +0.173$, $P > 0.2$). Birds which paused for relatively long periods between the first and second notes also tended to produce a long silent interval between the second and third notes ($r = +0.507$, $P < 0.0001$). However, none of the relationships between the durations of the three notes and the two intervals were significant (in all cases $P > 0.1$).

Among the singers of descending songs the pattern was somewhat different. The durations of the first and second notes were not significantly related ($r = +0.273$, $P > 0.2$), and, contrary to our prediction, singers of relatively long introductory notes actually tended to sing shorter third notes ($r = -0.545$, $P < 0.05$). In agreement with the prediction of consistent rhythm, and as observed in the ascending songs, birds which produced a long inter-note interval between the first and second notes were more likely to use long intervals between the second and third notes ($r = +0.728$, $P < 0.0005$). Once again, none of the relationships between the durations of the three notes and the two intervals were significant (in all cases $P > 0.1$).

DISCUSSION

Our results indicate that White-throated Sparrows produce some consistent relationships between the duration of notes and inter-note intervals in their songs. These findings are important for at least two reasons: (1) the relationships can help account for the variability in duration of this complex signal, and (2) the birds may be using the relationships to identify songs. The latter can be tested in playback experiments where songs with normal and altered temporal relationships are played to territorial males.

These temporal relationships between the notes are

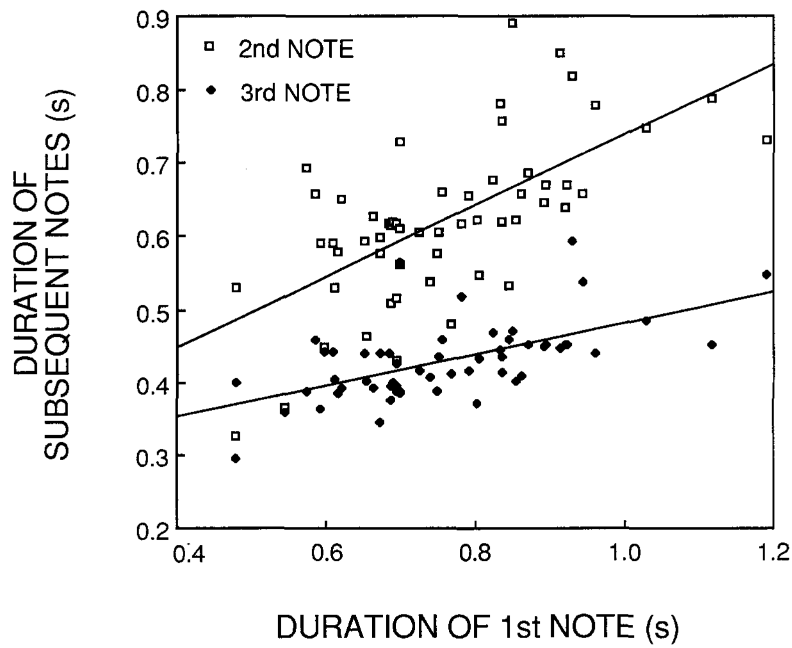

FIGURE 2. The relationships between the duration of the first note and that of the second note (open squares) and third note (closed diamonds) for the 56 ascending songs.

less robust than many of the frequency relationships that have been described in this species and others (Hurly et al. 1991, Weary et al. 1991, Weisman et al. 1990). There are at least two reasons why this should be the case. One is that temporal information in sounds is much more susceptible to degradation during transmission through the environment. Even though our recordings were of high quality, it is likely that some of the temporal measures were flawed.

A second reason is that birds are less able to accurately measure duration than frequency. Song birds are able to detect changes in frequency of less than 1%, as compared to changes of over 10% for duration (Dooling 1982). Perhaps because of this difference in sensitivity, birds tend to rely more on frequency than duration in recognizing songs (Nelson 1988, Weary 1990). Their limited ability to perceive differences in the duration of notes may result in a relaxed selection pressure on the precision of note duration during production. Also, the production and perception of song in birds might be intimately associated (e.g., they may involve similar areas of the brain). Therefore, the variability in production may be the result of the same mechanism that produces error in perception.

Do the temporal relationships which we have described actually indicate that White-throated Sparrows are maintaining some sort of species typical rhythm, with the different individuals singing at different tempos? The prediction of positive correlations between all elements was not upheld. However, there are some significant positive relationships which do indicate some degree of rhythm. These relationships are based on variation between individual. It is possible that similar relationships also exist for the variation among songs sung by a single individual. In order to detect such within-individual relationships, individuals must produce their songs with adequate variability. A larger sample of songs from each subject is required to examine this problem.

European Starlings use both the duration of the notes and the duration of the inter-note intervals to recognize rhythm (Hulse et al. 1984). When either of these features were made arrhythmic, discrimination performance was reduced. However, both had to be made arrhythmic for discrimination to disappear. In the present study, we found that while the durations of the notes are correlated, and the duration of the inter-note intervals are correlated, the duration of the notes are not correlated with those of the intervals. This evidence suggests that there may be a rhythm of note durations, and a different rhythm of intervals, but no overall rhythm to the song.

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SONG SPARROWS LEARN FROM LIMITED EXPOSURE TO SONG MODELS[1]

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Key words: Song; song learning; sensitive periods; Song Sparrow, Melospiza melodia.

In many songbirds, song learning is characterized by a distinct separation between an early "sensitive phase" when an individual hears and is thought to acquire song models, and a later "sensorimotor phase" when the bird practices and reproduces the songs it has learned (Marler and Peters 1982, Slater 1983, Marler 1991). This separation demonstrates that birds store song models in memory before using them as prototypes for motor output. Here we address the question of how much exposure to song is necessary to allow acquisition, storage and retrieval from memory of particular models in the Song Sparrow, *Melospiza melodia.*

Laboratory song learning experiments typically expose test subjects to hundreds or even thousands of repetitions of tape-recorded song models over the course of training. This extensive exposure is presumed to maximize an individual's opportunity to copy song material (e.g., Kroodsma and Pickert 1984, Marler and Peters 1987). Acquisition from limited exposure to training songs has also been reported, however. A White-crowned Sparrow (*Zonotrichia leucophrys*) exposed to 120 repetitions of a song type over 20 days reproduced a good copy of that model (Petrinovitch 1985). Each of three European Blackbirds (*Turdus merula*) learned one song motif from a range of 12–50 presentations on a single day (Thielcke-Poltz and Thielcke 1960). The most impressive cases reported of learning from limited exposure involve the Nightingale (*Luscinia megarhynchos*). Four of five males faithfully copied a string of 12 song types presented once per day for 15 days. One male from another group that heard a string of 21 song types presented twice per day for five days acquired 90% of that string (Hultsch and Todt 1989a). In another experiment, one male learned an entire string

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