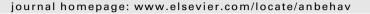
Animal Behaviour 84 (2012) 309-313

Contents lists available at SciVerse ScienceDirect

Animal Behaviour



Is birdsong music? Evaluating harmonic intervals in songs of a Neotropical songbird

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ARTICLE INFO

Article history: Received 4 December 2011 Initial acceptance 15 February 2012 Final acceptance 25 April 2012 Available online 6 June 2012 MS. number: A11-00965R

Keywords: biomusicology birdsong harmonic interval *Microcerculus philomela* music musical scale nightingale wren

Signals in animal communication are commonly judged as aesthetically appealing by human standards. This is particularly common for birdsong, often equated to musical compositions. No formal test, however, has analysed the harmonic properties of bird vocalizations. Musical intervals are based on the same physical characteristics of sound that underlie animal vocal signals. Thus, animals may use these intervals as rules to organize their vocalizations in a similar way as music. I tested a prediction derived from this hypothesis, that frequency ratios of adjacent notes in birdsong are closer to harmonic intervals than expected by chance. I determined to what degree the intervals created by adjacent notes of the song of nightingale wrens, Microcerculus philomela, conform to harmonic intervals. I analysed songs from 81 birds across the entire distribution range of the species, comparing the intervals formed by adjacent notes to three musical scales: chromatic, major diatonic and major pentatonic. Comparisons were made based on null model distributions. From 243 comparisons, only six ($\sim 2\%$) were significantly close to harmonic intervals, suggesting no consistent use of harmonic intervals. The frequency of the notes is the most varying song parameter in this species. If the frequencies are not determined by harmonic intervals in this species, it seems less likely that it happens in other birds with more complex song elements. Documented musical properties in birds might be caused by cultural biases of the listener or misunderstanding of the physics of musical compositions.

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Since ancient times, humans have judged animal signals by human standards of beauty (Darwin 1871: Grammer et al. 2003). This is particularly recurrent in the appreciation of birdsongs. because of their resemblance to musical composition (Darwin 1871; Scholes 1938; Hartshorne 1958; Saunders 1959; Hall-Craggs 1969; Dobson & Lemon 1977; West & King 1990; West et al. 2004; Baptista & Keister 2005; Tierney et al. 2011). The resemblance is due to the use of specific tonal qualities, pitch relationships and phrase duration and rhythm in birdsongs (Marler 1969; Baptista 2004). The parallel between birdsong and music has inspired many researchers and naturalists to equate the variation in frequency found in birdsongs to their counterparts in musical scales. For instance, Baptista & Keister (2005, page 432) in their paper 'why birdsong is sometimes like music' wrote: 'Some birdsong is pitched to the same scale as Western music, which is one possible reason for human attraction to these sounds'. Many other examples can be found in ornithological literature: Saunders (1959) suggested that white-throated sparrows, Zonotrichia albicollis, have

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a perfect fourth (musical interval) between the first and second notes, Borror & Reese (1956, page 182) suggested that the songs of the wood thrush, *Hylocichla mustelina*, 'are so pitched that they follow our musical scale very accurately', Hartshorne (1973), that the canyon wren, *Catherpes mexicanus*, sings in the chromatic scale (musical scale with 12 pitches per octave), and Wing (1951), that the hermit thrush, *Catharus guttatus*, sings in the pentatonic scale (musical scale with five pitches per octave).

Although the aforementioned accounts may be useful for describing the pitch variation among song elements in birdsongs, they imply that birds use discrete sound intervals, instead of a continuous range of sounds, to organize their songs. If true, this would have important implications for understanding the patterns of song ontogeny and evolution in animal signals. However, that hypothesis has not been properly tested for any bird species. To my knowledge, the only study on this matter was made by Dobson & Lemon (1977), who qualitatively compared the songs of white-throated sparrows, *Z. albicollis*, and African boubou shrikes (*Laniarius* sp.) with the most common Western musical scales. Unfortunately, no statistical test was made and no clear insight was provided on the harmonic properties of birdsongs.

Furthermore, no cogent rationale for the use of similar intervals in music and birdsong has been proposed. Why should a bird use





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the same intervals as musicians? Musicians use specific intervals because of the consonance produced by the combination of their sounds. This consonance comes from the physical properties of instruments and human vocal tracts (Benson 2008). Stringed and wind instruments and human vocal tracts produce a spectrum of overtones along with a fundamental frequency for each note. In both instruments and vocal tracts these overtones are harmonics. which are defined as exact integer multiples of the fundamental frequency (Benson 2008; Gill & Purves 2009). Different pitch notes for which the frequencies are proportionally related share most of their harmonics, which generates the consonance of their interval (Benson 2008). In other words, musical intervals are formed by sounds with a higher similarity in the frequencies of their harmonic spectrum compared to nonmusical intervals. Thus, musical intervals are based not in human conventional arrays of frequencies but in the physical characteristics of the sounds. The preference in humans may have evolved through a sensory bias towards intervals reflecting the spectral characteristics of conspecific vocalizations (Gill & Purves 2009) or as a honest signal of cognitive abilities favoured by sexual selection (Miller 2001). Similar hypotheses may explain the evolution of analogous preferences in other animals with comparable spectral complexity (see below). Several other hypotheses have been proposed for the evolution of music in humans and the present list is not exhaustive (Patel 2010).

Many species of birds, as well as mammals and amphibians, generate harmonics proportionally related to the fundamental frequency in their vocalizations in the same way as the musical instruments we use (Bradbury & Vehrencamp 1998). In addition, birds seem to have the necessary auditory and neural capacity to relate harmonically linked sounds. Birds can perceive the harmonic structure of single elements in their songs (Cynx et al. 1990; Lohr & Dooling 1998; Dooling et al. 2002) and in some cases use it to encode biologically relevant information (Morgan & Howse 1973; Aubin &

Bremond 1992). Some bird species even show relative pitch discrimination as humans do and can discriminate pairs of notes by their frequency ratios (Weary & Weisman 1991; Weisman et al. 1994; Bottoni et al. 2003). Overall, the available evidence suggests that birds have the necessary abilities required to relate and organize different song elements by the consonance of their frequencies, or in other words, to conform songs to harmonic intervals.

Even though birdsongs might conform to harmonic scales, the often complex and frequency-modulated structure of the song elements has made the testing of this hypothesis difficult, basically because it complicates the selection of a single frequency value as representative of a particular element. Only a few bird species seem to have the adequate element structure and pitch variation between elements to allow detailed analysis (Dobson & Lemon 1977). An ideal birdsong for analysis in terms of harmonic intervals should have sounds of sustained and almost pure pitch elements, a variety of frequencies among adjacent elements, and clear harmonic structure to its elements. The nightingale wren, Microcerculus philomela, represents an excellent opportunity to test these ideas. Its song consists of a single stereotyped series of nearly pure-tone notes at different pitches. The notes show clear harmonic structure with roughly no pitch repetition among consecutive notes (Fig. 1). This species also shows microgeographical song variation with several dialects in an area of just a few kilometres (M. Araya-Salas, T. F. Wright & G. Barrantes, unpublished data). The geographical variation is due to different arrays of notes rather than to variation in the structure of the composing elements (M. Arava-Salas, T. F. Wright & G. Barrantes, unpublished data). This type of variation allows us to test the existence of harmonic intervals in several different arrays of notes. For this study, I tested the prediction derived from the harmonic birdsong hypothesis, that the frequency ratio of adjacent notes would be closer to harmonic intervals than expected by chance. For this I use 'just intonation'

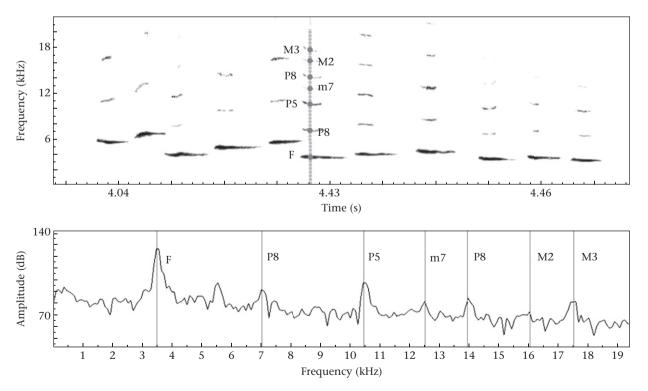


Figure 1. Spectrogram of a segment of the song of a nightingale wren from La Selva Biological Station, Costa Rica. The spectrogram shows the harmonic structure of the different notes. Below is a spectrogram slice corresponding to the dotted line in the spectrogram view indicating the fundamental pitch and the associated harmonics according to the nomenclature of Western music (F: fundamental; P8: perfect octave; P5: perfect fifth; M2: major second; 3M: major third). Points over the dotted line indicate the fundamental frequency (lowest point) and the associated harmonics in the spectrogram slice. Frequencies of the harmonics are exact integer multiples of the fundamental frequency.

intervals, a particular type of musical interval formed by pairs of notes related by small integer ratios. Similar integer ratios are produced between a fundamental note and its harmonics and in animal vocalizations. Hence, these scales represent the most intuitive pattern in which birds might base their songs.

METHODS

Study Species and Sites

The nightingale wren is a resident of the understory of mature forests from southern Mexico to northern Costa Rica (AOU 1998). I recorded eight individuals from La Tirimbina Biological Station (10°24'40.87"N; 84° 6'48.40"W) with a Sony TCM-2000DV recorder and a Sennheiser ME66 directional microphone. In addition, I obtained 73 recordings from bioacoustics archives from eight sites (Supplementary Table S1). These recordings belong to nine populations from the Caribbean Slope of Costa Rica and eight populations from other locations in Central America and Mexico (Supplementary Fig. S1). Thus, the recordings fairly represent the song variation across the entire geographical distribution of the species.

I digitalized recordings from La Tirimbina at a sampling rate of 48 kHz. All other recordings were digitalized at a sampling rate of 44.1 kHz. I analysed the songs using Raven 1.2 software (Charif et al. 2004). For spectrogram analysis, I used the Hann window function, a frame length of 202 samples, a filter bandwidth of 314 Hz, and the 'Gray scale' colour scheme option. I measured the fundamental frequency (the lowest frequency in a harmonic series) of each note. Based on this variable I calculated the interval formed by adjacent notes from the same song, dividing the fundamental frequency of the second note of the interval by the fundamental frequency of the first note (Fig. 2). Thus, the intervals were expressed as ratios of values between one and two. Ratios higher than two were divided by integer multiples of two. This calculation allowed me to simplify the analysis, keeping all the ratios in the same range without changing the harmonic relation between notes (e.g. a ratio of 3 and a ratio of 1.5 are harmonically the same: a perfect fifth). Intervals formed by repeated notes (notes with equal frequency; e.g. introductory notes) were omitted from the analysis. These notes create harmonic intervals as a by-product of note repetition.

Data Analysis

For each bird, I tested the harmony of the entire number of intervals (the intervals from all the songs). To carry out the analysis I first calculated for each frequency interval the distance to the closest harmonic interval. The distance was considered as the absolute difference between the observed interval ratio and the closest harmonic interval ratio. For instance, two intervals with values of 1.53 and 1.47 would have the same distance of 0.03 to the

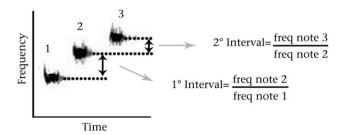


Figure 2. Spectrogram of three notes of the nightingale wren showing the calculation of interval ratios between adjacent notes. Dotted lines indicate the fundamental frequency of the notes (frequency with the highest energy). Interval ratios were defined as the ratio of the fundamental frequency of the second note to the first note of the interval.

closest harmonic interval (1.5; a perfect fifth). In the harmonic scales (described below), the range between harmonic intervals is related to the magnitude of the intervals: the higher the magnitude of the harmonic interval, the higher the range among subsequent intervals. To account for this, I standardized the distance to the closest harmonic interval by converting distances to percentages, with 100% representing the closest distance (or an exact harmonic interval) and 0% the furthest distance (exactly in the middle of two harmonic intervals).

I used three musical scales derived from 'just intonation' intervals to test the conformity of the songs to harmonic intervals (Fig. 3a-c): chromatic scale (12 notes), major diatonic scale (seven notes) and major pentatonic scale (five notes). The chromatic scale has the 12 intervals used in Western music, including consonant and dissonant intervals (Fig. 3a). The other two scales (diatonic and pentatonic) are subsets of the chromatic scale containing only the intervals with the smallest integer ratios (called consonant intervals). These intervals are formed by notes that share most of their harmonics. The pentatonic scale contains the fundamental (or octave), major second, major third, perfect fifth and major sixth (Fig. 3c), which are the intervals derived from the first five harmonics. These are also the harmonics that are emphasized in the nightingale wren whistles (Fig. 1). The diatonic scale contains, additionally, the perfect fourth and major seventh (Fig. 3b), which are derived from the sixth and seventh harmonics, respectively. The chromatic scale also contains another type of interval created by the secondary relationship between consonant intervals: these intervals are called dissonant. For instance, if a tonic note is played. followed by a major third, and then a major sixth is played from that major third, the interval created by the last note and the tonic note is a minor second, a dissonant interval. Hence the chromatic scale would occur only if the notes have a harmonic relation to notes two or more positions away in the song. Diatonic and pentatonic scales would occur if the birds build harmonic intervals only between immediately consecutive notes. Therefore, the scales were selected under the criteria of assessing two levels of consonance (pentatonic and diatonic scales) and evaluating the possible harmonic relation among nonconsecutive notes (chromatic scale). Although other subsets of intervals from the chromatic scale might be formed, they would occlude some consonant intervals or mix consonant and dissonant intervals with no clear criteria.

I used a null model to compare the observed intervals (represented by the percentage of the distance to the closest harmonic interval) to expected nonharmonic values. Intervals from nonharmonic songs are expected to be uniformly distributed around harmonic interval values. Hence, for each individual, I randomly created a uniformly distributed variable of 10 000 values between 0 and 100. I then took 1000 subsets from the generated variable



Figure 3. Musical notation of three scales used to assess the conformity of the songs to harmonic intervals: (a) chromatic scale (12 notes), (b) major diatonic scale (seven notes) and (c) major pentatonic scale (five notes). F: fundamental; m: minor; M: major; P: perfect; A: augmented. Numbers represent the ordinal position of the note (e.g. M2 = major second).

(with replacement), each one having a sample size equal to the number of intervals of the individual to be compared. Each subset was compared to the observed set of values with a Student's *t* test. The proportion of the 1000 tests in which the observed values were not significantly different from the uniform distribution was used as the associated statistical probability. These analyses were carried out in R version 2.9.0 (R Development Core Team 2009).

In addition, I analysed the melodies of musical compositions to validate my method for detecting harmonic structure in acoustic signals. I analysed songs from continuous pitch instruments. Unlike instruments such as piano and flute, continuous pitch instruments are not constrained to play notes at discrete intervals, allowing the production of any possible interval in an octave, similar to an avian syrinx and a human vocal tract. Hence, the intervals produced by continuous pitch instruments represent an actual selection of specific intervals by the musicians. Musical compositions were obtained from commercial recordings or solo performances freely available online (Supplementary Table S2). Compositions belong to three musical styles: classical, jazz and popular music. A minimum of 40 notes per song were included in the analysis. Intervals formed by notes of equal frequency were discarded. Melodies were analysed in the same way as bird recordings.

Ethical Note

This research involved recording from nightingale wrens in the wild. No birds were captured, and no behavioural experiments were implemented. The study was conducted in compliance with regulations of the Department of Environment and Energy of the government of Costa Rica.

RESULTS

A total of 81 birds were used in the analysis. These birds belonged to 16 song type populations: eight in Northern Costa Rica and the rest from other sites across the species' distribution range (see Supplementary Fig. S1). I carried out 243 comparisons (81 for each of the three scales). A mean of 96 (range 15–970) intervals were used in each test. Only five birds (~6%) had intervals that were significantly closer to harmonic intervals than the expected random distribution (2.5% of the 243 comparisons). In three cases the intervals conformed to the pentatonic scale (MG8: P = 0.013; TO5: P = 0.002; OC1: P = 0.037). One of these birds also conformed to the diatonic scale (OC1 = 0.044). Two other birds conformed to

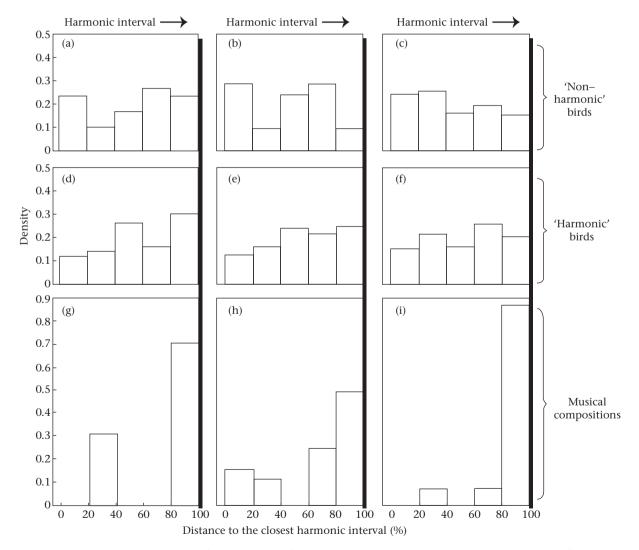


Figure 4. Distance to harmonic intervals (chromatic scale) of adjacent note ratios from three nightingale wrens whose adjacent note ratios were nonsignificantly close to harmonic intervals (a–c, 'nonharmonic birds'), three birds whose adjacent note ratios were significantly close to harmonic intervals (d–f, 'harmonic birds') and three musical compositions (g–i). Distances are shown as percentages. In the histograms, 100% represents the closest distance (a perfect harmonic interval; thick lines) and 0% represents the furthest distance (exactly in the middle of two harmonic intervals).

the chromatic scale (LS8: P = 0.016; LS10: P = 0.032). Only two birds belonged to the same population.

In contrast, my method successfully detected the harmonic structure in musical compositions. From the 24 melodies analysed, all were significantly close to intervals from the chromatic scale (P < 0.003 in all cases), and 21 were also significantly close to intervals of both pentatonic and diatonic scales. Differences in the distribution of frequency ratios in songs of nightingale wrens and musical compositions are graphically shown in Fig. 4.

DISCUSSION

Nightingale wren songs are not organized by the same rules used in musical composition. Overall, the frequency relation between adjacent notes did not fit with harmonic intervals, nor was there any consistency in the particular scale used in the few cases (2.5% of all examined) where harmonic scales were detected. The few songs that conformed to musical scales are probably an unintended matching to harmony, which can be expected based on the large sample size (81 birds, 243 comparisons). Given the uncommon use of harmonic intervals in this species, my results strongly suggest that it is not an intentional feature of these birdsongs.

My method was successful in detecting harmonic intervals in human musical compositions. All the melodies conformed to harmonic intervals. My results, however, did not show a perfect match to all three harmonic scales. The mismatch between some melodies and the pentatonic and diatonic scales is most likely due to the use of intervals not included in these scales but included in the chromatic scale.

Nightingale wren song is unusual among birdsongs in the extent to which frequency alone, rather than duration or patterns of frequency modulation, is the dominant difference among notes. Thus, variation in note frequencies is the primary way to generate song complexity (otherwise the song would be a series of equally pitched whistles). This variation creates different note arrays, which constitute the variation among song types (M. Araya-Salas, T. F. Wright & G. Barrantes, unpublished data). If the harmonic relationship between notes is not used as a rule to organize notes in the song of this species, it seems even less likely that this occurs in other birds with more complex song elements, in which song variability seems to be emphasized in the production and combination of different types of elements (e.g. ascending or descending whistles, broad-bandwidth elements, trills, etc.). Nevertheless, the harmonic birdsong hypothesis remains to be tested in species with more complex song elements.

This work represents the first quantitative analysis for testing whether the frequency shifts in a songbird's vocalizations conforms to the harmonic intervals associated with human music and provides no support for a significant role of harmonic intervals in the organization of the songs. This pattern might also occur in other bird species where versatility is not based on tonal variation between repeated elements. The documented musical properties in other species may be caused by a cultural bias of the human listener towards recognizing the occasional harmonic interval or by a simple misunderstanding of the physics of music composition, rather than an actual characteristic of the songs. This study should help bioacoustics researchers to clarify some notions about the acoustic structure of music and to recognize the implicit assumptions when equating music and birdsong.

Acknowledgments

I thank Eduardo Chacon, Erick Fuchs, Federico Bolaños and Gilbert Barrantes for stimulating discussion of ideas on early stages of this manuscript, and Elizabeth Hobson, Timothy Wright, Johel Chaves, Sean Ehlman and anonymous referees for comments on the manuscript. I am also grateful to Borror Laboratory of Bioacoustics, Bioacoustics Laboratory of Universidad de Costa Rica, Florida Museum of Natural History, Macaulay Library, Alex Villegas, David Bradley, Gerardo Obando and Julio Sanchez for access to recordings and the Organization for Tropical Studies and Tirimbina Biological Reserve for logistic support. Finally, I thank Evelyn Cubillo for help and support during the development of this manuscript.

Supplementary Material

Supplementary material for this article is available, in the online version, at doi:10.1016/j.anbehav.2012.04.038.

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