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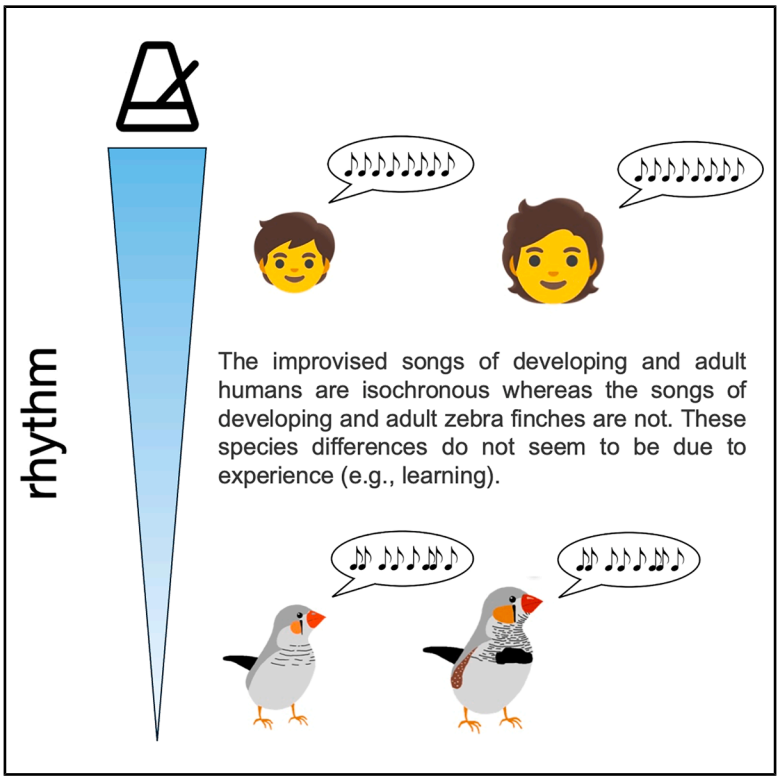
Humans, but not zebra finches, produce spontaneously isochronous song through the lifespan

Graphical abstract



Highlights

- Children and non-musician adults produced improvised songs with isochronous rhythm
- Juvenile and adult zebra finches' songs demonstrated less isochrony than chance
- We found little support for substantive learning of rhythm production in finches
- Our data suggest stable species differences in the degree of isochrony production

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In brief

Natural sciences; Biological sciences; Evolutionary biology

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Humans, but not zebra finches, produce spontaneously isochronous song through the lifespan

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SUMMARY

Isochrony—the regular beat of a metronome—is cross-culturally ubiquitous in music. Is this ubiquity due to a widespread biological inclination for isochrony in acoustic communication? If so, it should be present in lesser-studied vocal music, in the absence of musical training and early in development, and in comparable non-human species' vocalizations. We quantified isochrony in improvised songs from non-musician adults (n = 15, 24–82 years old) and children (n = 38, 3–10 years old), and in songs from juvenile and adult zebra finches (n = 77, ~50 and >120 days post-hatch). Isochrony was expressed in Western non-musician and children's improvised songs to a comparable degree. In contrast, both juvenile and adult zebra finches produced songs with less isochrony than chance, with no evidence for the learning of isochrony. These data show that spontaneous isochrony in learned vocalizations appears differently in two species. We propose that species variation in chorusing behaviors may explain why.

INTRODUCTION

Rhythm is one of the basic building blocks of human musicality.[1] In its simplest form, the use of a regular pulse—like the clicking of a metronome, referred to as *isochrony*—is extremely widespread among music traditions.[2,3] Musicians from Mali, Bulgaria, and Germany all finger-tap to reliably mimic small integer ratio rhythms, where durations of adjacent notes have small integer ratio relationships, such as 1:1 and 1:2; they also show a tendency to simplify complex rhythms (e.g., to 1:1, isochrony).[4] This ubiquity suggests the behavior has some shared, biological basis. Indeed, the ability to clap in time to a perceived isochronous pulse has an identifiable polygenetic basis in humans.[5] The presence of isochrony in the vocalizations of distantly related non-human animal species—non-human primates,[6–9] birds,[10–12] frogs,[13] and pinnipeds[14–16]—further indicate some biological basis to this behavior. To date, however, we have little data concerning whether isochrony is expressed in an ancient and universal musical form—singing—and whether there are comparable expressions of isochrony in non-human species capable of combinatorial, learned vocalizations (as opposed to simple, repeated, innate ones). Here, we present a developmental and comparative analysis of isochrony in human improvised songs, and spontaneous song from a non-human animal capable of learned, complex songs: the zebra finch.

Isochrony production is widespread and consistent in human percussive musical behaviors. Musicianship is not a prerequisite: non-musicians' accuracy in tapping synchronously to isochronous stimuli is on par with that of amateur musicians.[17] When musicians and non-musicians from 15 countries were tasked with reproducing an auditory rhythm by tapping along to it, their "errors" systematically favored isochrony even when it was not originally present in the stimulus.[3] Percussive isochrony emerges early in human development; by 2–4 years old, children's manual tapping spontaneously show regular rates,[18] and they show full-body rhythmic movements in response to music, though inconsistently synchronized to it.[19] By 6–7 years old, the ability to synchronize to an isochronous stimulus is almost at adult-level accuracy,[20] and this accuracy is well-preserved through aging.[21]

If isochrony is as fundamental to human musicality as the above findings suggest, we should also see this rhythm in untrained vocal song. Singing is a universal[22] and spontaneous behavior in humans, and its perception is associated with

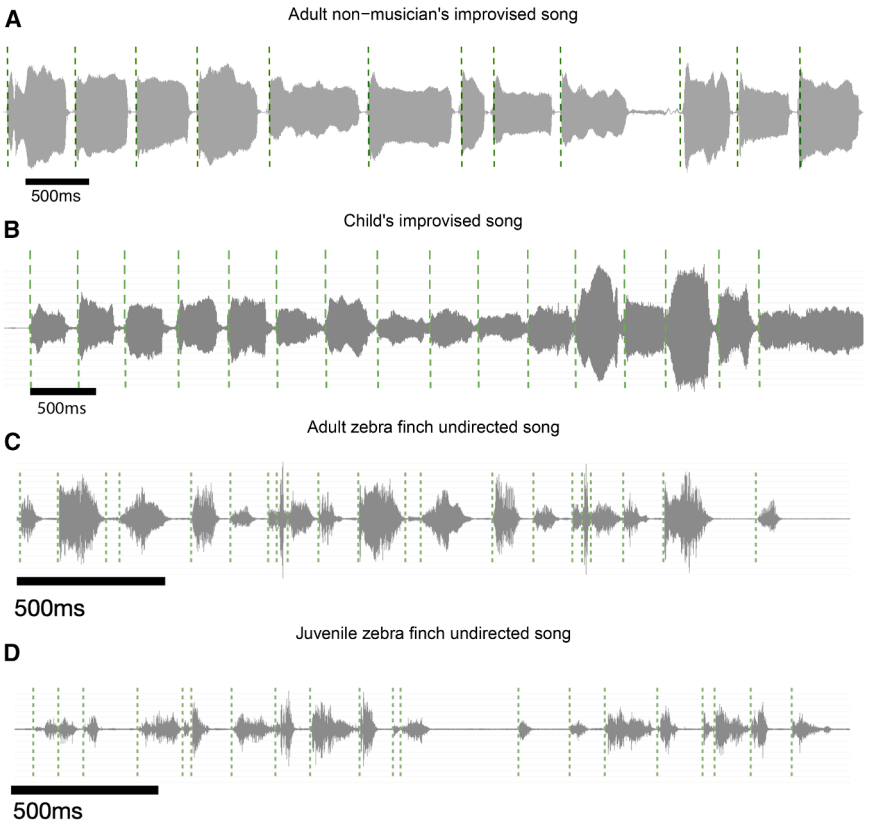

Figure 1. Example sound waveforms

Waveforms of (A) an adult non-musician's song, (B) a child's improvised song, (C) an adult zebra finch's song, and (D) song from that same zebra finch as a juvenile. Visually, the intervals between the onsets (green dashed lines) of adjacent notes/syllables are roughly equivalent in human songs—indicating isochronous organization, and more variable in the zebra finch song. We used the dyadic interval ratio to quantify isochrony in the song recordings of human children and adults, and zebra finch juveniles and adults. This is the ratio for any two adjacent inter-onset intervals $\frac{IOI_n}{IOI_n+IOI_{n+1}}$, where a highly regular signal such as a metronome with identical IOIs would only result in ratios of 0.5. Each panel's scale bar indicates 500 ms.

specific neural networks.[23] Young children create new tunes and adapt familiar ones,[24,25] and this practice of real-time improvisation is found across many of the world's musical traditions.[26] Improvisational singing, furthermore, is a methodologically useful tool in that it can be intuitively performed by people with little to no formal musical training, through the lifespan. Western non-musicians' improvised songs remarkably show pitch use that is consistent with the conventions of Western music.[27] Previous findings of isochrony in corpora that include both instrumental and vocal music[2] suggest that isochrony is likely also present in song, but such corpora include music that is the product of explicit musical training. Instead, the study of non-musicians' improvised song—in the absence of explicit training or mimicry—can better characterize how spontaneously isochrony may arise in human musical production. We expect that non-musicians' improvised songs should show isochrony in line with their percussive musical behaviors. Similarly, this trait should emerge around the age of 6 or 7 in children's improvised songs.

Sung improvisation, which by design imposes very little constraints on participants, also allows for more direct cross-species comparisons. Very few non-human species "improvise"; many species' vocalizations consist of innate calls that are repeated at consistent and stereotyped intervals[13,28] creating, by definition, isochronous sequences. By contrast, vocalizations that combine and sequence many different sound elements do not necessarily result in an isochronous rhythm; we know much less about whether isochrony is also the prevailing rhythmic organization in the combinatorial vocalizations of non-human animals.

Songbirds like the zebra finch are ideal for investigating isochrony in learned vocalizations that are combinatorial in nature. Zebra finches learn their song by memorizing and imitating a tutor's song, and mechanisms underlying the perception, acquisition, and performance of these songs have been extensively studied.[29] Juvenile zebra finches' songs are more temporally variable than mature song[30,31]; through development, they learn the sequencing and timing of song elements ("syllables"),[29,32] affording them a level of temporal control that in principle could be used to give their complex vocalizations rhythmic structure similar to human song. Timing is ecologically relevant for these songbirds; they coordinate their song with body and head movements,[33,34] and show inter-individual coordinated timing,[35] but notably they do not sing synchronously. Zebra finches are also able to perceptually discriminate between isochronous and non-isochronous stimuli with some degree of tempo flexibility.[11]

Here, we provide a developmental and comparative analysis of isochrony in humans and songbirds, focusing on spontaneous/improvised songs in each species. We tested for the presence of isochrony in the improvised songs of children and adult non-musicians, and in the spontaneous songs of juvenile and adult zebra finches. While two previous studies have reported isochrony in adult zebra finch song,[10,36] no study to date has examined developmental changes in isochrony, analyzed the contribution of learning to isochrony, and directly compared isochrony in zebra finch song to isochrony in human vocal music. This comparative study of isochrony will provide a more detailed account of the degree of similarity between human and songbird vocal rhythms, which will help evaluate candidate theories for the origins of rhythm, including the vocal learning hypothesis for beat perception and synchronization,[37] the gradual audiomotor evolution hypothesis,[38] and the origins of rhythm production in group dancing[39] or other group behaviors.[40,41]

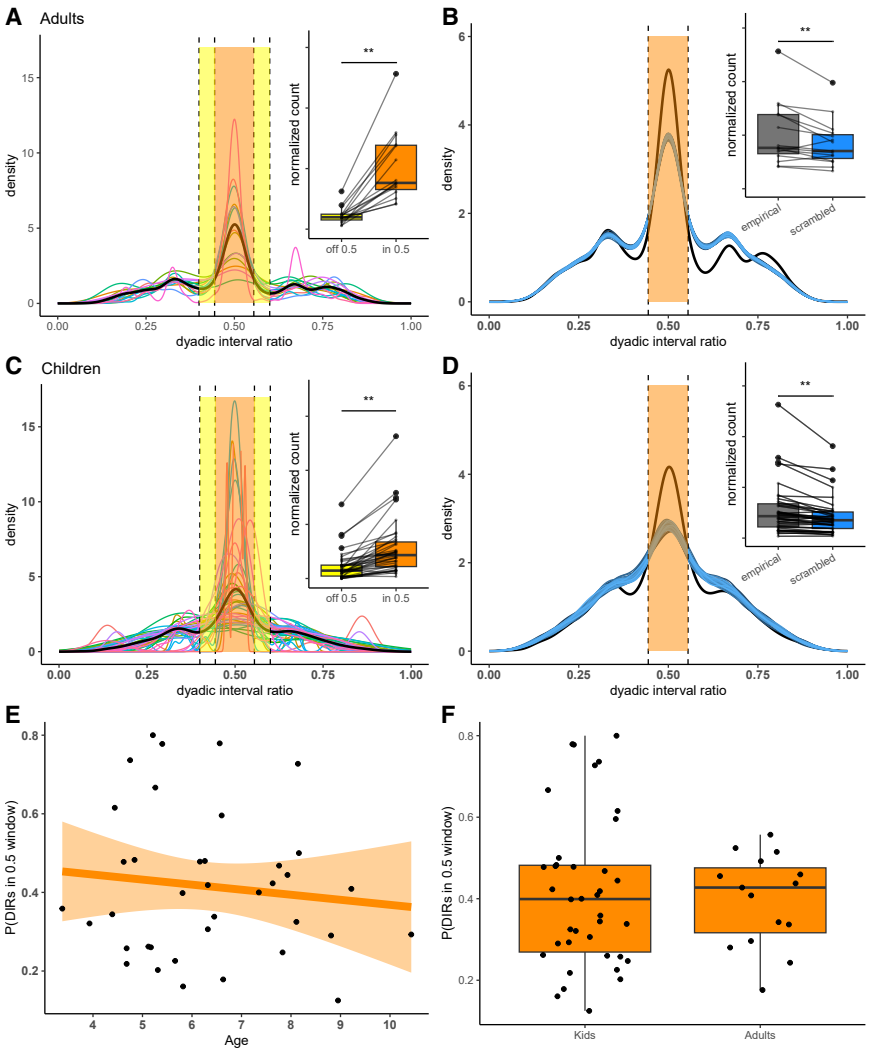

Figure 2. Non-musician adult and children's improvised songs show isochrony

Distributions of dyadic interval ratios of (A) adult non-musicians' songs show more ratios in the isochrony window ("in 0.5", window highlighted in in orange) than outside of it ("off 0.5", window highlighted in yellow). Each colored line is an individual participant's distribution; the thicker black line is the population average. The inset shows each of the 15 adults' difference in how many ratios fell in 0.5 vs. off 0.5; this is quantified as a normalized count, which is the number of ratios that fell in each window, divided by the width of the windows. Plotted are individual data points and boxplots depicting the median and quartile of the distributions.

(B) Adults' songs show more ratios inside this window than chance. Each blue line plots the distribution of dyadic intervals in one of the 50 scrambled datasets; each point in the boxplot is a participant's normalized count of ratios in the isochrony window, in the empirical data or averaged in the scrambled data. The inset plots the normalized empirical (observed) and scrambled (chance) counts for each individual. Plotted are individual data points and boxplots.

(C and D) Children's (n = 38) improvised songs show the same pattern as adults. One child's distribution of ratios is not plotted for clarity (the peak height would visually distort the rest of the graph; see Figure S1). Insets are similar to those plotted in (A) and (B).

(E) There is no significant linear relationship between the children's age and amount of isochrony in their song. Plotted is the regression line with the shaded region indicating the standard error of the estimate.

(F) There is no significant difference between children and adults in the amount of isochrony in their song. Plotted are individual data points as well as boxplots depicting the median and quartiles of the distributions. *p < 0.05, **p < 0.01.

RESULTS

Songs were semi-automatically segmented to timestamp the onsets of notes (in human song) and syllables (in zebra finch song; Figure 1), and dyadic interval ratios were computed based on inter-onset intervals (see STAR Methods).

Adult non-musicians' improvised songs display isochrony

Adult non-musicians' improvised songs showed significantly more dyadic interval ratios in the isochrony window than the off window (Figure 2A; n = 15; V = 120, p < 0.001). Additionally, the degree of isochrony in these songs was greater than one would observe by chance (Figure 2B; V = 103, p = 0.012). There was no linear relationship between adults' ages and proportion of ratios in the isochrony window (β = −0.0001, $SE[\beta]$ = 0.0058, z = −0.018, p = 0.986).

Children's improvised songs also display isochrony

Similar to adults, children aged 3–10 years old spontaneously produced isochrony in their improvised songs (Figure 2C; n = 38; V = 736, p < 0.001), at a higher-than-chance rate (Figure 2D; V = 686, p < 0.001). Additionally, there was no evidence for an influence of age on the degree of isochrony expressed: there was no linear relationship between children's age and proportion of ratios that fell in the isochrony window (Figure 2E; β = −0.0512, $SE[\beta]$ = 0.0711, z = −0.721, p = 0.471), and no significant difference between children and adults in proportion of ratios in the isochrony window (Figure 2F; β = −0.045, $SE[\beta]$ = 0.144, z = −0.312, p = 0.755).

Zebra finch song is less isochronous than chance through the lifespan

Songs from our large colony sample of semi-naturalistically reared adult zebra finches (n = 61) tended to show more dyadic interval ratios in the isochrony window than in the "off" window, but this comparison was not statistically significant (Figure 3A; V = 1158, p = 0.074). Further analysis revealed that the magnitude of this peak in the isochrony window was significantly lower than would be expected by chance (Figure 3B; V = 191, p < 0.001).

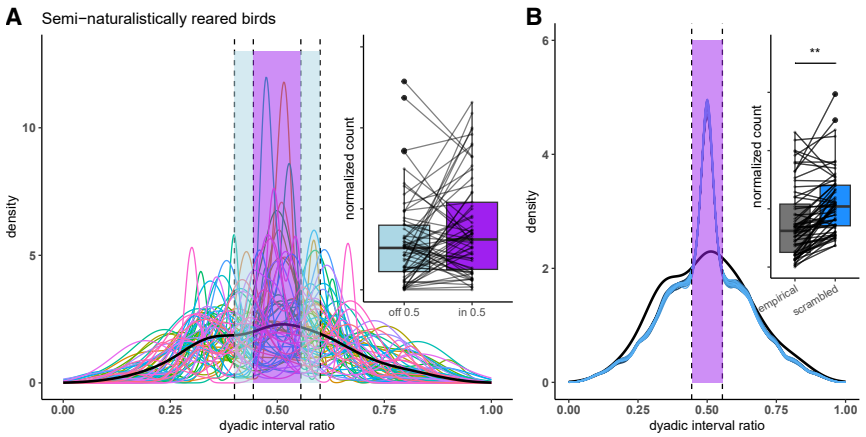

Figure 3. Adult zebra finch song is less isochronous than chance

(A) Each colored line represents the distribution of dyadic interval ratios of an individual adult zebra finch. The thicker black line indicates the population average distribution of dyadic interval ratios. There are not significantly more ratios within the isochrony window ("in 0.5") than outside it ("off 0.5"). Plotted in the inset are the normalized counts for in 0.5 vs. off 0.5 for each bird (see also Figure 2). Boxplot summarize the median and quartiles of the distributions.

(B) The degree of isochrony in zebra finch song was significantly lower than expected by chance. The thicker black line is the same population average as in (A), and each blue line is the distribution of dyadic interval ratios by chance, as reconstructed from each of the 50 scrambles of these same birds' data. Plotted in the inset are normalized empirical (observed) and scrambled (chance) counts for each bird. Normalized counts are computed by taking the number of ratios observed in a window ("in 0.5" or "off 0.5") and dividing that by the width of the window. Chance degrees of isochrony are computed from iterations of scrambling the order of each bird's inter-onset intervals and recomputing DIRs. Boxplot depicts median and quartiles. *$p < 0.05$; **$p < 0.01$.

In the longitudinally recorded birds (n = 16), zebra finches showed significantly more ratios in the isochrony window than in the off window when they were adults but not when they were juveniles (Figures 4A and 4B; juveniles, t[15] = 1.781, p = 0.095; adults, V = 117, p = 0.009). While in isolation this could be indicative of a developmental trend for the emergence of isochronous rhythm, further analysis shows a pattern similar to the colony bird population: this incidence of ratios in the isochrony window was significantly lower than would be observed by chance when birds were both juveniles (t[15] = −2.289, p = 0.037) and adults (V = 20, p = 0.011; Figure 4). There was no overall effect of age on the incidence of isochrony production (β = −0.08, $SE[\beta]$ = 0.215, z = −0.392, p = 0.695).

Zebra finches do not appear to learn isochrony naturally

We found no evidence for the learning of isochrony: the amount of isochrony (even if below chance) in the songs of tutor birds was not significantly predictive of the amount of isochrony in their pupils' songs (Figure 5; β = 1.27, $SE[\beta]$ = 0.9, z = 1.48 p = 0.138).

DISCUSSION

We studied rhythm in naturalistic, spontaneous vocalizations from humans and zebra finches. While both species are precocious singers and dependent on social and sensory experiences to learn their songs, only humans' songs were isochronous, and this species difference persisted through development (in the age ranges considered here). These findings for improvised human song expand on the ecological validity of corpus[2] and tapping[3] studies that indicate how common isochrony is in human musicality. Our findings also replicated a report that zebra finch song shows a high density of dyadic interval ratios around 0.5.[10] However, subsequent analyses indicated that the magnitude of this peak was significantly lower than expected by chance, in both juvenile and adult birds' songs; consequently, zebra finch song are not isochronous in a way that is analogous to human song.

What underlies this species difference is unknown. It is possible that humans, but not songbirds, produced isochrony due to their greater experience with this rhythm, but two of our findings weigh against this possibility. First, if more isochrony exposure in humans led to more isochrony production, we would have observed a developmental increase in isochrony production: this was not the case in our data, with isochrony production being rather constant over the 3–10 years age range, and between children and adults. If isochrony production is experience dependent, this effect might be acting only very early in development. While these participants had minimal musical training, future cross-cultural work may determine how passive musical exposure may influence isochrony production. Second, if isochrony production were a function of exposure, we would have observed that prevalence of isochrony in a zebra finch pupil's song would mirror that of its tutor's. This also was not borne out in the data. The lack of correlation in the degree of isochrony between tutor and pupil songs suggests a minimal contribution of learning and is surprising given previous studies of temporal learning. This may be due to birds prioritizing the reproduction of low-level temporal features (i.e., syllable structure and gap durations) over global rhythmic structures (as previously suggested in some studies[42–44]). We observed instances where tutors and pupils showed generally similar sequencing of sounds, but where pupils merged or split syllables from their tutor's song,[45] leading to altered inter-onset intervals and, consequently, dyadic interval ratios. Any isochrony observed in zebra finch song might therefore be incidental to their reproduction of low-level temporal features; this is in contrast to human musical rhythms where the production of an isochronous rhythm is persistent through variation in low-level features like average inter-onset interval (see Figure S2).

Future studies among denizens of different musical cultures would help characterize whether the present results are species-typical of humans. The method used here—of recording children's songs online, supervised by their parents—is a scalable alternative to in-lab methods. This scalability, in addition

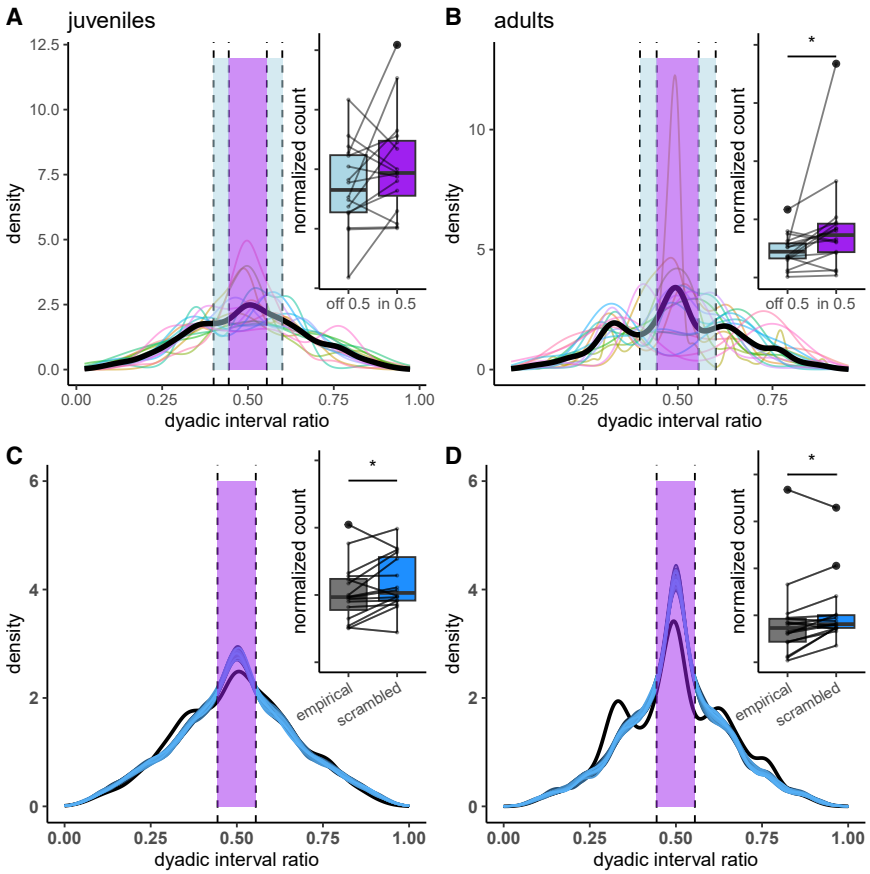

Figure 4. Zebra finch song is less isochronous than chance through the lifespan

(A and B) Distributions of dyadic interval ratios from recordings of the same birds when they were (A) juveniles and (B) adults. Zebra finches showed a significantly higher number of ratios in the isochrony window ("in 0.5") than outside it ("off 0.5") when they were adults but not when they were juveniles (see Figure 3 for description of insets).

(C and D) Both the juvenile and adult songs of these birds showed less isochrony than would be expected by chance (see Figure 3 for description of insets).

*$p < 0.05$.

to this method's requirement for minimal participant instruction, lends itself to facilitating cross-cultural study. If humans have no predisposed rhythm inclinations and isochrony production is purely experience-dependent, we might see, for instance, Malian children's improvised songs would show a prevalence of isochronous and non-isochronous rhythms in accordance with their prevalence in jembe music.[46] Replications of this work would also reveal whether the lack of an age effect persists in other samples. We found no evidence for an increase in spontaneous isochrony production with age, which was surprising given that body movements to music[19] and manual tapping[20] become more accurate through the age range of ~2–7 years old. If replicated, the vocal production of isochrony may be more precocious than previously expected.

In addition to the note/syllable level isochrony considered here, isochrony may occur at different time scales across species. For example, the Australian pied butcherbird's song shows isochrony not at the syllable but at the phrase level, with interphrase-onset intervals being of consistent duration.[47] We used a prevalent, semi-automated syllable-based segmentation for zebra finch song, where adjacent elements are delineated with brief silences. This is the same method used in prior investigations of isochrony in birdsong[10,11] as well as countless other analyses of zebra finch song. Alternatively, one could consider that syllables in bird song can consist of several "gestures," where gesture onsets have been reported to align with isochronous events more than would be expected by chance[36] (though this study also reports isochrony at the syllable level) and to contain some signature of learning.[48] Future work can make explicit at what level (gestures, notes, phrases) we expect to observe isochronous organization, in which species, and why. If isochrony's function, as a perfectly predictable rhythm, is to serve inter-individual coordination or synchronization,[49] naturalistic interactions between individuals should show coordination at the levels of segmentation considered. This interpretation is aligned with findings that isochrony is a defining feature of vocalizations that we chorus in, like song, and less so of turn-taking vocalizations like speech[41,50] or zebra finch song, where these birds do not chorus, and in fact deliberately avoid overlapping with an interlocutor.[42]

This species difference has broader implications about the biological basis of musicality. Much ongoing work seeks to determine which species produce rhythmic vocalizations, and why. One popularly evoked condition is vocal learning.[6,14,51,52] The vocal learning hypothesis[37] suggests that vocal learning neural circuitry is necessary for beat perception and synchronization, and many have tested whether vocal learner species also *produce* rhythmic vocalizations. For example, a recent study documents that the warble songs of budgerigar, a species of parrots, contain significant isochrony (compared to chance).[12] Our data suggest that vocal learning might not be strongly linked to the production of isochronous rhythms in learned vocalizations across species. Future work testing what other features selectively covary with rhythmic vocalizations may elucidate whether music's rhythms may be attributable to higher vocal learning capacities, or other, yet untheorized species traits.

Limitations of the study

We used automated procedures that are established and routinely used in the fields to segment human and finch songs. However, the algorithms differ slightly across the species, with pitch information taken into consideration for human but not finch song. We do not believe that this impacts the conclusions of our

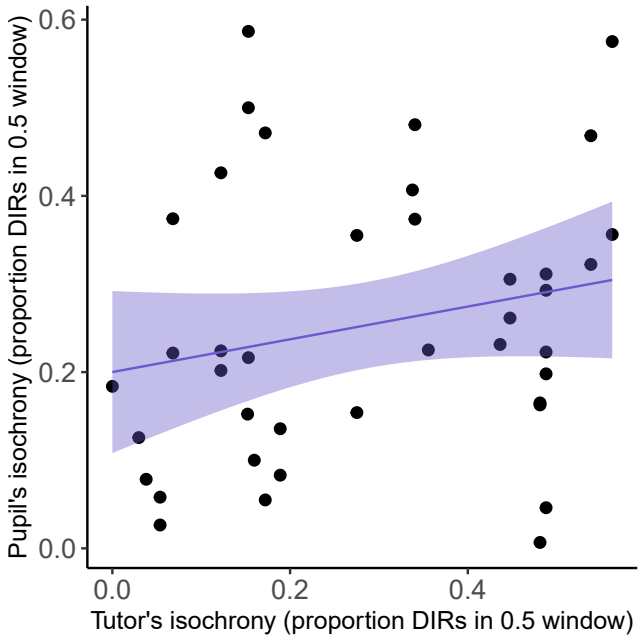

Figure 5. No significant relationship between isochrony in a tutor and its pupil's song in the colony sample of zebra finches

The amount of isochrony in a tutor's song is not significantly related to the amount of isochrony in its pupil's song, suggesting that zebra finches do not learn to produce this rhythm. Plotted are data for individual tutor-pupil pairs, with the line and shaded region indicating, respectively, the regression line and the standard error of that estimate.

study because segmenting human songs based purely on amplitude led to similar conclusions about isochrony (Figure S3). Attempts to segment zebra finch song using the software for segmenting human songs were unsuccessful (which is likely due to the substantive differences in acoustic properties of vocal units across species). Other studies have manually segmented zebra finch song into notes (i.e., gestures) and documented evidence of isochrony and learning of temporal patterns,[36,48] and this segmentation difference, as well as different analysis approaches for the quantification of rhythm, could lead to different conclusions to ours. Dyadic interval ratios are one of a number of different measures of rhythm, and it is possible that we would find stronger evidence of rhythm learning in finches using other metrics. A greater range of children and a global population of individuals with less musical training could improve our understanding of the biological foundations (e.g., innateness) of rhythm production in humans.

RESOURCE AVAILABILITY

Lead contact

Requests for further information and resources should be directed to and will be fulfilled by the lead contact, Jon T. Sakata (jon.sakata@mcgill.ca).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- Data are available as supplementary materials, and publicly archived at OSF: https://doi.org/10.17605/OSF.IO/FN2MX.
- Code is also publicly archived at OSF: https://doi.org/10.17605/OSF.IO/FN2MX.
- Any additional information required to reanalyze the data reported in this study is available from the lead contact upon request.

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AUTHOR CONTRIBUTIONS

Conceptualization, M.B., M.W.W., I.P., and J.T.S.; experimental design and implementation, M.W.W. and J.T.S.; data processing, M.B., M.W.W., and D.S.; analysis and visualization, M.B.; writing, M.B. J.T.S., and I.P.; editing, M.B., M.W.W., I.P., and J.T.S.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.isci.2026.116751.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Repository of primary data and analysis code	N/A	https://osf.io/fn2mx
Experimental models: Organisms/strains		
Zebra finch *Taeniopygia guttata*	Lab reared	N/A
Software and algorithms		
MATLAB	MathWorks	https://www.mathworks.com/
R (Version 2026.01.1)	The R Project for Statistical Computing	https://cran.r-project.org/
TONY	Mauch et al.[53]	https://sonicvisualiser.org/tony/

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

We tested for the presence of isochrony in the following three datasets

1. **Human, cross-sectional:** We analyzed recordings of spontaneous, improvised songs from adults (n = 15, ages 24–82 years old) and children (n = 38, ages 3–10 years old). Procedures for adult and children song recordings were approved by the Comité d'éthique de la recherche en éducation et en psychologie (CEREP), University of Montreal (2021–2839, CEREP-21-003-D for adult song recordings, 2019–2616, CEREP-19-061-D for children song recordings).

Adults: 15 non-musician adults were recorded as part of a prior study.[27] To summarise, these participants (*M* = 58.6 years, *SD* = 21.3 years; 10 female, 5 male) resided in Quebec, Canada. Those who requested information were told that the task involved singing. They did not have specific music deficits associated with congenital amusia using the Montreal Protocol for Identification of Amusia,[54] and were considered ''non-musicians'' in that they had 5 or fewer years of music training. 5 years is a somewhat arbitrary threshold, but useful because people with more than 6 years of training start showing neural sensorimotor changes associated with playing an instrument.[55] As reported in the prior study[27] participants had minimal music lessons (0.4 ± 1.2 years of lessons (mean ± SD), range: 0–5). Participants provided informed consent and were paid for their participation.

Children: 38 children (M = 6.3 years old, range 3.4–10.4; 22 female, 16 male) were recruited using social media to diffuse an advertisement for an online study on children's improvised singing, with the incentive that participating families could be entered in a raffle to earn a $50 gift card to the bookstore of their choice. These children were mostly Canadian residents (*n* = 35), one resided in Vietnam, one in the United States, and one did not report country of residence. By following the hyperlink in the ad, parents were directed to an online study hosted on https://brams.org/, run on jspsych.[56]

Like the adults in our study, the children had less than 5 years of music training (12 had musical instrument lessons: 0.8 ± 1.4 years of lessons, range = 0–5; 2 had voice lessons: *m* = 0.2 ± 0.9 years, range 0–5; both of the two children with voice lessons also had instrument lessons).

2. **Zebra finch colony population**: 61 male zebra finches were semi-naturally raised in a breeding colony at McGill University. These birds were raised by their parents and learned their song from their father. They remained with their parents until they were ∼60 days post-hatch (dph) and then were socially housed in same-sex group cages. Only male zebra finches produce songs, so only males were analyzed here. All these birds were recorded when they were developmentally mature (i.e., >120 dph), and none were of what would be considered advanced age for this species; although small changes to syllable structure and timing are observed in adult finches,[57–59] overall zebra finch song is stable in adulthood, and we do not expect substantial variation in the degree of isochrony over the age range of adults studied here. Average age at date of recording was 135 ± 12.8 days (where data were available; some dates were lost during the process of recoding file names to mask IDs and dates). 40 of the birds in the dataset were raised by 21 different fathers (on average, each father raised and tutored 1.9 pupils; range 1–5 pupils per tutor). Four of these 61 birds were also represented in the longitudinal dataset (see below), with only their adult recordings included in this population dataset. All procedures were approved by the McGill University Animal Care and Use Committee (protocol #7149) in accordance with the guidelines of the Canadian Council on Animal Care.
3. **Zebra finch, longitudinal**: The 16 birds in this analysis were raised by both parents and were able to physically and acoustically interact with other birds. Male juveniles were individually housed in a sound-attenuating chamber for a few days for song recording (see below) starting at 44–51 days post-hatch (dph). The birds were then housed with other males until they

reached adulthood (~120 dph), at which point they were moved back into a sound-attenuating chamber for song recording for a few days, and then returned to a group cage.

METHOD DETAILS

Adults: The participants were instructed to "make up a new melody" for each improvisation trial, that should not be a repetition of a melody they had heard before, or a repetition of a melody they produced in a previous trial. They were told to improvise using the syllable "da" instead of using words, and to sing for as long as felt appropriate. Each participant completed 28 improvisations; 8 in response to verbal prompts (lullaby, dance, healing, and love songs; 2 happy, 2 sad songs), 16 prompted with short melodic stems (3–4 notes), 2 prompted with longer melodic stems (10 notes), and 2 periods of free improvisation. Participants were tested while seated in a sound-attenuating booth, where melodic prompts were presented to them via headphones (DT-770 Pro, Beyerdynamic, Inc.) through Audition (Adobe, Inc.). Verbal prompts were communicated to them by the experimenter, who was outside the booth and able to communicate with the participant through the participant's headphones. Their improvisations were recorded via a Neumann TLM-103 microphone.

Children: After a parent provided informed consent and answered demographic questions, the game provided audio instructions for musical games for the child. An onscreen character ("Bunny" in English, "Lapinou" in French) narrated instructions for the child to sing back songs that they played (these warm-up trials were not included in analysis), and then to make up a song *"without any words, like "da da da", and try to sing something totally new that you've never heard before!"*. This prompt for made-up songs was repeated 6 times, and after each of these trials, a text prompt addressed to the parent asked whether the song was truly improvised, or whether it was familiar to them; only songs that the parent marked as improvised were retained for analysis. Children produced an average of 2.4 songs (range 1–5), with an average of 83.9 ± 78.3 notes per trial. The total study ran for approximately 10 min.

Zebra finches: All birds were housed on a 14 L:10 D light cycle and provided food and water *ad libitum*. For all bird recordings, zebra finches were recorded whilst housed individually in a sound-attenuating chamber (TRA Acoustics, Ontario, Canada) via an omnidirectional microphone (Countryman Associates, Inc, Menlo Park, CA). A continuously recording system (Sound Analysis Pro (SAP) 2011) was set to save audio as triggered by the detection of sound (digitized at 44.1 kHz). Like humans, zebra finches produce songs even without audiences,[60] and all songs recorded for this study were taken while the birds were housed individually; all these songs are therefore spontaneous ("undirected") song.

QUANTIFICATION AND STATISTICAL ANALYSIS

For all datasets, onsets of notes (in humans) and "syllables" (in birdsong) were semi-automatically timestamped. Human recording audio files were processed in TONY.[53] The automatically generated note onsets and offsets were manually checked, and corrected where necessary (e.g., erroneous boundaries placed by the algorithm). For each zebra finch, 10 recordings per bird were semi-automatically annotated using custom software in MATLAB (evsonganaly) and manually checked for accuracy. Adult zebra finch songs are highly stereotyped, with the timing and sequencing of syllables being highly consistent across renditions; as such, the rhythm of a bird's song can be readily captured with few song examples. Similar to many published studies (e.g.,[32]), segmentation parameters were determined per bird (i.e., amplitude threshold above which one would consider there to be a sound; the signal had to be above this threshold for at least 20 ms to mark a syllable, and below this threshold for at least 5 ms to mark a gap). This use of amplitude thresholds to segment non-human species' calls is the same method used in much previous work that reports on rhythm in non-human species' vocalizations[6–8,10–12,14] though other methods exist.[36,48] Audio files can contain both songs and calls; all segmented sounds were manually annotated in order to retain only song syllables for subsequent analysis. All vocalizations within songs (i.e., introductory notes and song syllables) were annotated for analysis. We used a threshold of 1 s of silence as the delineator between separate bouts.

We computed inter-onset intervals (*IOI* s) from the recordings' timestamped onsets of notes and syllables. We quantified the presence of isochrony using the ***dyadic interval ratio*** (as in[6,10,15,47]): for any given dyad i.e., two adjacent inter-onset intervals, this is the ratio resulting from the duration of the first IOI divided by the sum of the whole dyad's IOIs: $\frac{IOI_n}{IOI_n+IOI_{n+1}}$. For a recording of a ticking clock, for example, where all IOIs are identical, one would only observe the ratio 0.5. For a recording of any signal that is more temporally variable than a ticking clock, one would observe a distribution of dyadic interval ratios between the bounds [0, 1], where the density of ratios around 0.5 may be taken as indicative of how isochronous this signal is. As in prior research,[6] we accepted a small window of ratio values around 0.5 as indicative of isochrony (ratio values in the window [0.444, 0.555]; henceforth referred to as the *isochrony window*), and a small range of values symmetrical around this window as being "off" isochrony (windows [0.400–0.444] and [0.555–0.600]). When comparing the density of ratio values that fall "in" isochrony relative to "off", we normalized the number of ratios by dividing this count by the width of the window they are observed in (also consistent with[6,9]). This is a characterization of isochronous organization of a recording's notes/syllables' IOIs, so we note that this is different than a study of a "beat" which could refer to a perceived, latent isochronous pulse; a beat can be perceived from a stimulus that does not have acoustic events at every beat and has extra acoustic events in between beats.

The above approach that compares the density of ratios in the isochrony window to the density of ratios outside of it tests the observed data against an implicit, relatively weak null distribution that arises from randomly generated interval lengths.[61] We sought

to additionally test a stricter null hypothesis, that accounts for there being production constraints and biases on interval lengths. In order to quantify whether observed isochrony is higher than would be expected by chance, we simulated 50 datasets in which the order of IOIs was scrambled for each individual, and distributions of dyadic interval ratios re-computed for these data. For the human adult data where the improvised songs were elicited by a number of different prompts (i.e., lullaby, sad song, dance song, etc.), we scrambled per individual *and* per song type: initial analyses revealed that song types differed in average IOIs (Figure S4), so scrambling across song types could have plausibly led to scrambled songs with unusually wide IOI variances. This method yielded results that were identical to those obtained when data were scrambled per individual (as we did for zebra finches; see Figure S5). These simulated datasets are therefore biologically plausible in that they retain each participant/bird's propensity to produce IOIs of certain durations, but reduces any rhythmic structure to only what may be observed by chance from randomly sequenced vocalizations.

This empirical-vs-scramble analysis fails in certain fringe cases where the underlying distribution of IOIs is very tight. Scrambling a metronome, for instance, results in a chance level of isochrony that is indistinguishable to the empirical level of isochrony. The present data demonstrate substantial variation in IOIs and do not fall in this fringe case (see IOI distributions in Figure S6). Moreover, for this fringe case, there is a chance of erroneously failing to detect that a real signal is more isochronous than the scrambled signal; this property of this empirical-vs-scramble test, however, cannot explain instances where a real signal is found to be *less* isochronous than scrambled signal.

We tested for the presence of isochrony in each population (children, adults, zebra finch juveniles, zebra finch adults) first by applying paired t-tests or Wilcoxon signed-rank tests (depending on the distribution of underlying data) to determine whether the normalized count of dyadic interval ratios was greater inside the isochrony window than "off" this window. In order to test whether each population showed more isochrony than chance, we applied paired t-tests or Wilcoxon signed-ranks test comparing each participant's number of ratios in the isochrony window in actual data vs. the average incidence in their scrambled data.

To test whether, in either species, there were developmental differences in the incidence of isochrony, we summarised each participant's data into a proportion of how many observed ratios fell in the isochrony window. Because proportions are a measure bounded [0,1] and therefore best modeled with a beta distribution, we fit beta regressions for each species (package *glmmTMB*) predicting this outcome variable *proportion*, using a fixed effect for age group (juvenile/children vs. adults), and random intercepts for ID in the longitudinal bird data (where data is grouped by ID). We fit another beta regression to test whether human children's ages correlated with the proportion of ratios that fell in the isochrony window (fixed effect for children's ages).

Zebra finches learn many temporal aspects of their song, including duration of syllables and gaps, and the sequencing of syllables.[29,32] We therefore tested whether the degree of isochrony in their song also appeared to be learned. We tested this by running a beta regression modeling the proportion of a pupil's ratios in the isochrony window, as predicted by a fixed effect of the tutor's proportion of ratios in isochrony window, with a random intercept for tutor ID (as some tutors had more than one pupil).

We additionally computed descriptive statistics for the human data to contextualise how similar our recordings of improvised song are to previous studies of song and instrumental music. This included average speed (the inverse of IOI length) per group, and coefficient of variation (see Table S1). We tested whether adults' lullaby vs. dance songs differed in speed by fitting a mixed model testing mean IOI as predicted from the fixed effect prompt type (lullaby or dance song) and random intercept for participant ID. We used t-tests to test whether children and adults' songs differed in speed; and a Pearson correlation to test whether children's ages correlated with speed. These analyses indicated that our samples of improvised songs bore similarities to prior studies of musical behaviors, in that children had faster spontaneous production rates than adults, and that improvised lullabies were slower than improvised dance songs (see Table S1; Figure S4). These samples of improvised song therefore appear to be ecologically valid samples that are comparable with musical behaviors reported elsewhere, on these basic dimensions.