

Correspondence

Categorical rhythms
in a singing primate

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What are the origins of musical rhythm? One approach to the biology and evolution of music consists in finding common musical traits across species. These similarities allow biologists to infer when and how musical traits appeared in our species¹. A parallel approach to the biology and evolution of music focuses on finding statistical universals in human music². These include rhythmic features that appear above chance across musical cultures. One such universal is the production of categorical rhythms³, defined as those where temporal intervals between note onsets are distributed categorically rather than uniformly^{2,4,5}. Prominent rhythm categories include those with intervals related by small integer ratios, such as 1:1 (isochrony) and 1:2, which translates as some notes being twice as long as their adjacent ones. In humans, universals are often defined in relation to the beat, a top-down cognitive process of inferring a temporal regularity from a complex musical scene¹. Without assuming the presence of the beat in other animals, one can still investigate its downstream products, namely rhythmic categories with small integer ratios detected in recorded signals. Here we combine the comparative and statistical universals approaches, testing the hypothesis that rhythmic categories and small integer ratios should appear in species showing coordinated group singing³. We find that a lemur species displays, in its coordinated songs, the isochronous and 1:2 rhythm categories seen in human music, showing that such categories are not, among mammals, unique to humans³.

Beyond melodic features (Figure 1A), individual animal vocalizations have onsets (blue lines in Figure 1C). Two onsets delimit an inter-onset interval

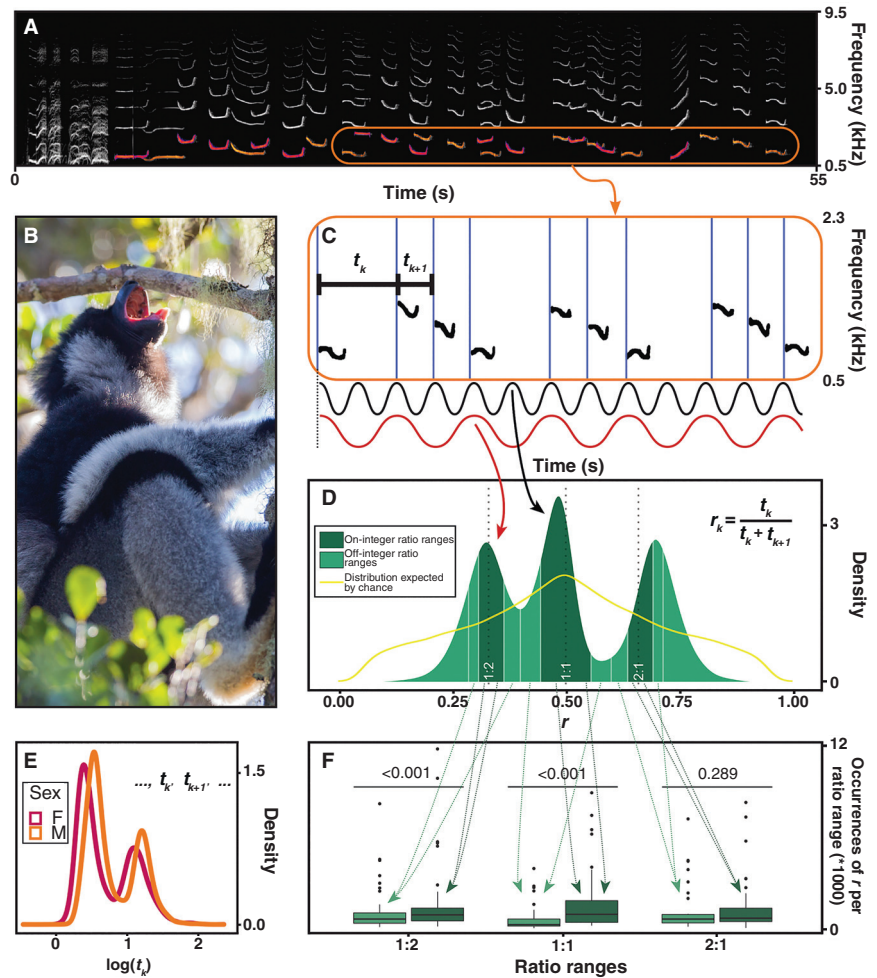


Figure 1. Indris' songs: Extracting individual inter-onset intervals and rhythm ratios from group choruses.

(A) Spectrogram of the indris' song, highlighting the fundamental frequencies of male (orange) and female (pink) notes (iZotope RX). The orange inset highlights the male song portion detailed in C. (B) Adult male indri singing in the Maromizaha New Protected Area, Madagascar (credit: Filippo Carugati). (C) Schematic representation of onsets (solid blue lines) in a male indri song. Pairs of onsets define inter-onset intervals t_k , marked by solid black lines. Sine waves (bottom) exemplify which purported oscillatory processes might generate the rhythmic categories found in the data: 1:1 ratio in black, 1:2 ratio in red. (D) Probability density function of rhythm ratios (r_k), which we calculated across 39 adult indris and 636 individual contributions to songs. On-integer (dark green) and off-integer (light green) ratio ranges are highlighted. The yellow line depicts a null distribution, showing how the ratios would be distributed in the absence of rhythmic categories, i.e. if the underlying intervals were uniformly distributed (see Supplemental information). The empirical ratio distribution significantly differs from this null distribution (2-sample Kolmogorov-Smirnov tests: $0.109 < D < 0.127$, $p < 0.001$). The central peak being slightly to the left of the 1:1 ratio may be diagnostic of a 'ritardando'³. (E) Probability density function of the logarithm of inter-onset intervals (t_k), which significantly differs from a uniform distribution with the same boundaries (2-sample Kolmogorov-Smirnov test: $D = 0.656$, $p < 0.001$) and shows sexual dimorphism (i.e. a statistically significant sex difference; see Supplemental information). (F) Boxplots of adjusted r_k occurrence for on-integer (dark green) and off-integer (light green) ratio ranges. The ratio counts for individual indris constitute the data points for the analysis, and counts are normalized by bin size (see Supplemental information). Indris significantly produce more on-integer than off-integer ratios for the 1:2 (Wilcoxon signed-rank test, $V = 81$, p-values in figure) and the isochronous 1:1 categories ($V = 0$) but not for the 2:1 category ($V = 313$).

(t_k), i.e. the time between the onset of a note and the next one^{5,6}. Ratios between these intervals are calculated

by dividing an interval by itself plus its adjacent one³. Patterns in these ratios may emerge: for instance, two identical



intervals generate a 1:1 ratio, and an interval followed by another twice its duration generates a 1:2 ratio. This approach has successfully highlighted rhythmic similarities between birdsong and human music³. In particular, for the first time in a non-human species, it was recently demonstrated that songs of thrush nightingales show a significant isochronous rhythmic category (1:1 ratio) and a potential bias towards 1:2 categories³. Apart from songbirds, singing mammals are promising species to look for musical universals, offering the advantage of phylogenetic proximity to humans.

We focused on one of the few singing primates, the lemur *Indri indri* (Figure 1B), sampling approximately 1% of all living individuals from this critically endangered species (for details, see Supplemental information, published with this article online). All members of a family group sing in temporally coordinated duets and choruses (see: <https://youtu.be/wxVYsAodZ6U>)^{7,8}. Over 12 years, we recorded songs from 20 indri groups (39 individuals) living in their natural habitat, the rainforest of Madagascar. We extracted temporal features of indris' songs, analyzing inter-onset intervals (Figure 1E) and their ratios (Figure 1D).

First, we find that intervals between note onsets are not uniformly distributed (Figure 1E), and their ratios appear to form three clusters (green density function in Figure 1D). In other words, the intervals between notes are not sampled with the same probability among all possible values (yellow line in Figure 1D), similarly to the discretely sampled note durations found in human music^{3,4}. Note that finding these clusters does not imply that they match specific integer ratios⁵.

Second, we find that ratios match two rhythmic categories: 1:1, isochronous, similar to the pace of a metronome, and 1:2, a fundamentally small integer ratio. We ask whether ratios produced by each individual fall more frequently on-integer, i.e. in the vicinity of a small integer ratio, than off-integer, i.e. in the vicinity of its adjacent non-integer ratio (Figure 1D and Supplemental information)³. By pairing the number of on-integer to off-integer ratios produced by each indri, we find that the empirical rhythmic ratios from songs fall statistically more

often on small integer ratios than off integer ratios (Figure 1F). In particular, and similarly to songbirds³, indri songs have a strong, above chance, isochronous component with some tempo flexibility; indris sing at a slightly decreasing isochronous tempo, similar to musical 'ritardando' (Figure 1D). While songbirds do not produce 1:2 categories above chance³, indris' empirical ratios do statistically match the theoretical 1:2 category (Figure 1F). This provides direct evidence for one musical universal, categorical rhythms^{2,5}. The small integer ratios, falling at 1:1 and 1:2, are exactly those expected for beat production and binary, metrical subdivisions⁶; both of these are aspects of human musicality rare in other species¹. The 1:1 and 1:2 integer ratios we witness are not direct evidence of beat or meter, though they may hint at similar nested periodic processes (bottom of Figure 1C).

Third, we find that in males and females the absolute interval lengths are different (Figures 1E and S1F) but the 1:1 ratios are the same (see Supplemental information). This may be relevant to selective hypotheses for music, hypothesizing a role of sexual selection, social bonding, etc. on rhythm origins⁹. Productive inference on how rhythm evolved requires multicomponent thinking^{1,6,9}: rhythm as a whole is a mystery but some of its defining features may be present in other species, as we show here. Male and female indris may produce different singing tempi and interval durations, but 1:1 ratios are the same between sexes. This suggests that sexual selection should not affect the evolution of isochrony in indris; it might, however, play a role in single interval timing and in non-isochronous rhythmic categories¹.

Why should another primate, apart from humans, produce categorical rhythms? As the last common ancestor between humans and indris lived 77.5 MYA, common ancestry of categorical rhythms is unlikely; instead, this ability may have convergently evolved among singing species, such as songbirds, indris, and humans¹⁰. As in songbirds, isochrony and rhythmic categories in indris may facilitate song coordination, processing, and potentially learning^{1,3,6,7}. The mechanisms supporting rhythmic

categories in indri are unknown; cognitive or not, they might still constitute a foundational phenomenon for beat-related behaviors in our and other species. We encourage comparative work on indri and other endangered species to gain more data before it is too late to witness their breath-taking singing displays.

SUPPLEMENTAL INFORMATION

Supplemental information contains one figure, one table, experimental procedures, results and can be found with this article online at <https://doi.org/10.1016/j.cub.2021.09.032>.

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