

PRIMATE RHYTHMIC CATEGORIES ANALYZED ON AN INDIVIDUAL BASIS

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Rhythm is a fundamental feature characterizing communicative displays, and recent studies showed that primate songs encompass categorical rhythms falling on small integer ratios observed in humans. We individually assessed the presence and sexual dimorphism of rhythmic categories, analyzing songs emitted by 39 wild indris. Considering the intervals between the units given during each song, we extracted 13556 interval ratios and found three peaks (at around 0.33, 0.47, and 0.70). Two peaks indicated rhythmic categories corresponding to small integer ratios (1:1, 2:1). All individuals showed a peak at 0.70, and most showed those at 0.47 and 0.33. In addition, we found sex differences in the peak at 0.47 only, with males showing lower values than females. This work investigates the presence of individual rhythmic categories in a non-human species; further research may highlight the significance of rhythmicity and untie selective pressures that guided its evolution across species, including humans.

1. Introduction

Rhythm is a fundamental feature of human communicative displays and characteristically permeates the musical performances of our species (Hausen et al. 2013, Savage et al. 2015). When we think of a typical human communicative display, such as conversation, we realize that numerous factors play a critical role in the temporality of exchanges between interlocutors (Pouw & Holler 2022). Among these features is rhythm, which is often contextually adapted to align semantic and syntactic processes (Himberg et al. 2015).

Moreover, we know that complex rhythms characterize communication in human and non-human animals (Pouw et al. 2021; Ravignani et al. 2019). Recent research also indicated comparable features in the temporal structure

characterizing human speech, music, and non-human animal vocalizations (Kello et al. 2017; Pouw et al. 2021). Complex rhythms are typical of interactions between two or more conspecifics, emitting a series of signals and taking turns (Gamba et al. 2011; 2016). It is difficult to imagine that we will be able to discern the cognitive processes involved in turn-taking for a large number of species, but finding similarities across extant primates could help us to understand the selective pressures that may have played a role during the evolution of human language (Levinson 2016).

Indeed, rhythmic displays can provide important information about the communicative features of other species, in particular concerning the contextual variation and temporal characteristics that permeate long sequences of emissions (Clink et al. 2017). Specifically, recent research has shown that the study of primate songs may indicate the presence of rhythmic categories that fall on small integer ratios which at least partially overlap with those we can observe in human music (De Gregorio et al. 2021).

A question remains unanswered: to what extent rhythmic patterns are stable across the individuals of a particular species and whether all individuals share a certain rhythmic category more often than others. In order to shed light on this aspect, we investigated the acoustic emissions of a singing primate that has already been the subject of studies on rhythmic categories, *Indri indri*. Indri is a primate species with an evolutionary history parted from humans by around 74 million years (Hedges et al. 2015). Our first hypothesis is that adult individuals of this species present at least two rhythmic categories in their songs. We, therefore, expect that the density distributions of all studied indris show two or three peaks around human typical small integer ratios of 1:2 (0.33), 1:1 (0.50), and 2:1 (0.67), following the results of previous work (De Gregorio et al. 2021). The second hypothesis, alternative to the previous one, is that rhythmic categories appear at least consistently within one of the sexes, in line with the fact that, in the indri, many of the vocal features are distinctly dimorphic between males and females (Giacoma et al. 2010; Gamba et al. 2016; De Gregorio et al. 2019; Zanoli et al. 2020, Valente et al. 2021).

2. Materials and Methods

2.1. Study subjects and recordings

We recorded songs produced by 39 reproductive indris of 20 different groups. As indri groups usually comprise a reproductive pair and their offspring, by doing so we included in the analyses a number of individuals comparable for each of the sampled group. These indris lived in various forest sites in Madagascar: Analamazaotra Reserve (Andasibe-Mantadia

National Park), Mantadia (Andasibe-Mantadia National Park), Mitsinjo Station Forestière, Maromizaha Forest.

We collected data between 2005 and 2016 using solid-state recorders (SoundDevices 702, Olympus S100 and LS05, and Tascam DR-100, DR-40, and DR-05) equipped with Sennheiser (ME 66 and ME 67) or AKG (CK 98) microphones. We set a sampling rate of 44.1 kHz and 16-bit amplitude resolution for all recording sessions. The distance ranged from 2 to 20 meters when recording the animals, with the microphone aimed at the focal singing animal.

2.2. Acoustic and statistical analyses

We tracked inter onset intervals between the units given during each song using Praat TextGrids, where we assigned each singer to a particular TextGrid tier. After extracting interval duration to a text file (Gamba et al. 2016), we obtained 13556 interval ratios using the Roeske et al. (2020) formula. Interval ratios r_k were calculated by dividing a particular inter-onset interval t_k for itself + the following inter-onset interval ($r_k = t_k / (t_k + t_{k+1})$).

3. Results

The distribution of the peaks in the r_k density graphs showed three different patterns (Fig. 1A). A first pattern, occurring in 56% of the individuals, showed the presence of three peaks means at 0.33 ± 0.02 , 0.47 ± 0.02 , 0.70 ± 0.02 . All individuals had a peak at around 0.70 (Fig. 1B). In 26% of the indris, the peak at around 0.33 was missing, while 18% did not show the peak at around 0.47 (Fig. 1B).

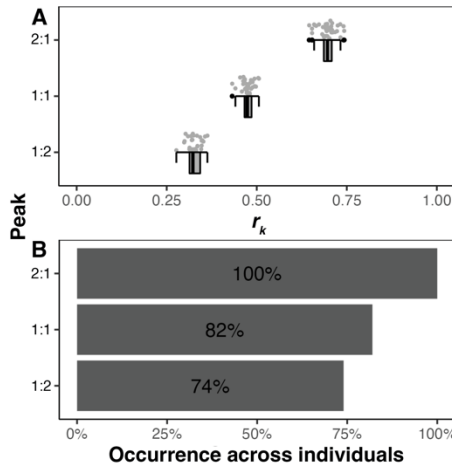


Figure 1. Variation of the rhythm ratios (r_k) across individual indris for each peak of their density plot (A, see also Fig. 2). Grey points denote individual rhythm ratios for a particular peak, black points denote outliers. Percentage distribution of rhythm ratios across individuals for the three peaks (B, see also Fig. 2).

The coefficient of variation of the peak around 0.33 was 6.1%, while the other two showed lower values, 3.5% and 3.4%, respectively (Fig. 1A, Fig. 2). We analysed the occurrence of peaks across the sexes and found no statistical difference for the peak at 0.70 (Mann-Whitney test, $W = 213$, p -value = 0.5315). The peak at 0.33 showed marginal significance, but small effect size ($W = 57$, p -value = 0.0476, $r = -0.44$), whereas the peak at around 0.47 showed significant difference ($W = 188$, p -value = 0.02195, $r = 0.47$). Males showed an average peak of 0.47 ± 0.02 , while females showed values at 0.48 ± 0.01 .

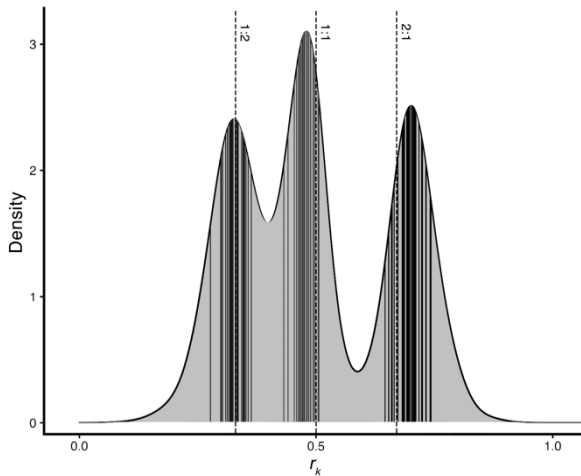


Figure 2. Probability density function of rhythm ratios (r_k), which we calculated across 39 adult indris and 636 individual contributions to songs. Solid lines denote peaks of each individual indri for each group of peaks. Dotted lines denote 1:2 (0.33), 1:1 (0.50), and 2:1 (0.67) ratios.

4. Discussion

In agreement with the De Gregorio and colleagues (2021) study, we observed that most indri part of our sample showed three distinct peaks representing as many rhythmic categories. The location of the peaks is in agreement with the two rhythmic categories, significantly corresponding to small integer ratios in De Gregorio and colleagues (2021). The peak at 2:1 (0.67) was not statistically significant in the previously cited work because points around 0.67 were not dense enough. Although the methodology used here is slightly different, we see the same trend, showing a well-identified and consistent peak at 0.70 ± 0.02 in most animals studied. In most individuals, we observe three peaks; however, the 44% of indris shows only two peaks, distributed over two of the three categories mentioned above. Indeed, the presence of two and not three rhythmic categories is not easily attributable to the sex of the individuals. Interestingly, the absence of the third peak does not alter the

consistency of the remainder concerning the species-specific characteristics that emerged in this study and De Gregorio and colleagues (2021).

De Gregorio and colleagues' (2021) findings concerning male and female absolute interval lengths are different, but the 1:1 ratios are the same and appear consistent with our overall results. However, by analyzing individual peaks, a slight difference emerges for values below 1:1 (i.e., isochrony).

Indri groups are often small, include a pair and their offspring, and communicate in a very extensive network of other conspecific groups. Unlike what has been suggested for birdsong, which undergoes a vocal learning process, we do not know what role learning plays in primate songs. Historically, it has been assumed that singing has a strong genetic component, but recent studies point to plasticity that is difficult to explain by factors that do not involve some degree of learning.

This work is the first to analyze rhythmic categories at the individual level because previous investigations have focused on a species-specific pattern rather than an individual pattern (Roeske et al. 2020; De Gregorio et al., 2021). Given the hierarchical organization of natural systems, expanding the levels of analyses can provide insight regarding the evolutionary levels on which selection mechanisms may act. Our results suggest new insights for subsequent research, which may be aimed at understanding whether the presence of rhythmic categories varies with the age of individuals, or is a trait that becomes fixed early and then does not change during ontogeny, or whether it varies dynamically over time. Our study also shows that most indris studied exhibit rhythmic categories that correspond to small integer ratios. Unfortunately, our findings concerning the production of categorical rhythmic patterns in the indris cannot be paralleled by pieces of evidence about the perception of these lemurs. However, it appears challenging to study whether the indris' perceptual abilities are biased towards the same categories in the wild.

Acknowledgements

This research was supported by Università degli Studi di Torino and the African, Caribbean, and Pacific (ACP) Science and Technology Programme of the ACP Group of States, with the financial assistance of the European Union and by grants from the Parco Natura Viva—Centro Tutela Specie Minacciate. We are grateful

to GERP (Groupe d'Etude et des Recherche sur les Primates) and Dr. Jonah Ratsimbazafy. We thank Dr. Cesare Avesani Zaborra and Dr. Caterina Spiezio for helping us with the organization of the field station in Maromizaha. We are grateful to the researchers and the research guides, to Mamatin and all our Malagasy collaborators in the forest, for their help and logistical support. The contents of this document are the sole responsibility of the authors and can under no circumstances be regarded as reflecting the position of the European Union. We have received permits for all the research activities from “Direction des Eaux et Forêts” and “Madagascar National Parks” (formerly ANGAP).

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