



RHYTHMIC CATEGORIES ACROSS PRIMATE VOCAL DISPLAYS

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ABSTRACT

The last few years have revealed that several species may share the building blocks of Musicality with humans. The recognition of these building blocks (e.g., rhythm, frequency variation) was a necessary impetus for a new round of studies investigating rhythmic variation in animal vocal displays. Singing primates are a small group of primate species that produce modulated songs ranging from tens to thousands of vocal units. Previous studies showed that the indri, the only singing lemur, is currently the only known species that perform duet and choruses showing multiple rhythmic categories, as seen in human music. Rhythmic categories occur when temporal intervals between note onsets are not uniformly distributed, and rhythms with a small integer ratio between these intervals are typical of human music. Besides indris, white-handed gibbons and three crested gibbon species showed a prominent rhythmic category corresponding to a single small integer ratio, isochrony. This study reviews previous evidence on the co-occurrence of rhythmic categories in primates and focuses on the prospects for a comparative, multimodal study of rhythmicity in this clade.

Keywords: *singing, vocalization, communication, territorial advertising, turn-taking.*

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1. INTRODUCTION

The study of non-human primates, their behaviour and communication skills, and peculiar features is a crucial element in the study of our language and, in particular, its evolution [1]. Removing the study of non-human primates from the language mosaic would greatly impoverish our ability to understand what selective pressures have led to communication characteristics shared with other species [2] and other remarkably different ones [3]. In recent years, the study of rhythmic categories has become a robust framework of analysis within which we can compare the characteristics of vocal displays of different species, from prosimians to great apes [4]. Several studies evaluated factors that may shape rhythmic regularities across primate behaviours while keeping it clear that we are referring to observational analyses, which, contrary to what we can do with human studies, do not have an equally transparent and established neuro-cognitive counterpart. Unfortunately, studies on the perceptual component of rhythm in primates have several limitations dictated by laboratory conditions, investigative procedures and the small number of animals that can be tested [5]. Recent research primarily focused on investigating the occurrence of rhythmic categories towards the simplest small-integer ratios such as 1:1 (isochrony), 1:2, and 2:1. Categories corresponding to small-integer ratios are critical building blocks of human musical displays, but it is possible that further research could identify different recurring regularities in animal species. And, although the presence of rhythmic categories in speech is debated, we know that rhythm in speech perception and production has a critical role [6].

The study of singing primates seemed to be one of the most obvious options to begin the investigation of small-ratio rhythms in primates. Singing in primates is certainly the vocal display that, from a structural point of view, shows the greatest complexity [7] and also, from an exquisitely spectral point of view, often presents a more pronounced frequency variation than we can observe in the other emissions of the vocal repertoire [8]. However, scholars identified singing primates in a few taxa that are not closely related to each other [9]. The fact that different species of singing primates may have very different phylogenetic distances enriches this picture with an essential element to consider from the perspective of selective pressures that may have played a role in the evolution of different rhythmic categories. For instance, the last common ancestor between the lar gibbon (*Hylobates lar*) and humans has dated 15 MYA [10], while indris (*Indri indri*) have an evolutionary history separated from humans by about 61 MYA [11]. Moving beyond singing primates, a system governed at least in part by comparable rules is that of loud calling, for which orangutans (*Pongo pygmaeus wurmbii*) are paradigmatic examples. The evolutionary history of orangutans separated from humans around 9 MYA [12]. This study reviews the evidence for rhythmic categories in primates and looks at the prospect of a comparative study of rhythmicity in this clade, possibly from a multimodal perspective.

2. SMALL-RATIO RHYTHMS ACROSS PRIMATES

First, we must clarify that of the 70 singing primate species identified in a recent review [9], 21 are data deficient, and we only possess data on small-integer ratios for two species. A previous study showed that the indris (*Indri indri*) display multiple rhythmic categories, similar to what we can observe in-Western human music [13]. The occurrence of categories corresponding to 1:2 and 1:1 is significant in comparing on-peak and off-peak values (see Fig. 1 in [13]). Thus individual indris are consistently emitting towards 1:2 and 1:1. Although there is individual variability, this pattern appeared consistent across the sexes. Lar gibbons (*Hylobates lar*) studied in Thailand showed a single prominent rhythmic category corresponding to 1:1 (isochrony) [14]. The study of orangutans showed how these apes exhibited nested degrees of isochrony during their long calls [15].

3. DISCUSSION

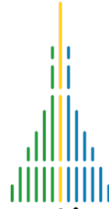
The study of rhythmic categories in animals, and in particular in the vocal signals of animals, is becoming increasingly important. For example, studies on male hyraxes have shown that males that vocalise with a more regular isochronous pattern and for longer periods have greater reproductive success and generate offspring that tend to survive longer [16].

The complexity of primates' singing behaviour has long gathered the attention of researchers interested in understanding the selective pressures underpinning the evolution of complex vocal sequences [17] [18] [19]. In this sense, rhythmic categories are a great addition to the traits we can compare and possibly one of the most easily accessible to researchers. However, the question that remains unanswered is what factors might have favoured the evolution of a song showing three rhythmic categories in Indri [20], two of which correspond significantly with the small integer ratios 1:2 and 1:1. This question takes on the particular force concerning the evidence that seems to show that in a small ape like the white-handed gibbon, there is only one peak, corresponding to isochrony.

Previous work has shown us three distinctive features of indri that could contribute to this debate. The first aspect is related to the organisation of the chorus and the overlapping of individuals. Studies on indri have shown evidence for the presence of three types of singing (i.e., serving territorial advertisement, group cohesion, and mediating vocal fights during territorial encounters), but that singing is always a collective behaviour, rarely emitted by a single individual and potentially as an unanswered duet attempt [21] [22]. This aspect seems to be an essential element in distinguishing indri from other singing primates. On the other hand, solo singing is common in several species of gibbons, especially in males.

Moreover, non-reproductive individuals within a group (i.e., offspring of the pair-bonded adults) may overlap with the pair [23] but tend to minimize the overlapping with their parents' singing [24]. Chorusing in the indris seems to adhere to fine organizational rules where the female's singing template guides the offspring's participation in the song [25].

We can speculate that this regular alternation of singers in the song and that they take turns but overlap non-randomly [25] may have played a role in the evolution of complex rhythmic abilities. However, further investigations are needed to understand whether isochrony in small apes and apes is consistent (e.g., across lar and crested gibbons species). Also, broadening our view on different aspects of vocal communication, such as alarm calls and contact calls,



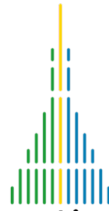
may reveal whether multiple rhythmic categories may be confined to particular interactions or widespread across contexts.

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