Musicality without humanity

Marco Gamba, Valeria Torti

Abstract

After years in which the study of musical abilities in species other than humans occurred sporadically, the investigation of these building blocks (e.g., rhythm, frequency variation) received a new impetus. Using the comparative approach, recent studies have shown how the investigation of rhythm in the vocal displays of primate species can yield surprising results that help us to shed light on the factors that may have acted as selective pressures throughout the evolution of the primate tree. This contribution aims to review the studies conducted in the last decade on primates and understand how these can be useful in reconstructing a phylogeny of some of the abilities that enable humans to make music.

Keywords: Singing; Vocalization; Communication; Territorial Advertising; Turn-Taking.

Sommario

Dopo anni in cui lo studio delle abilità musicali in specie diverse dall'uomo è stato sporadico, l'indagine su questi elementi costitutivi (ad esempio, ritmo, variazione di frequenza) ha ricevuto un nuovo impulso. Utilizzando l'approccio comparativo, gli studi degli ultimi anni hanno dimostrato come l'indagine sul ritmo nelle manifestazioni vocali delle specie di primati possa dare risultati sorprendenti che ci aiutano a far luce sui fattori che possono aver agito come pressioni selettive nel corso dell'evoluzione dell'albero dei primati. Questo contributo si propone di passare in rassegna gli studi condotti nell'ultimo decennio sui primati e di capire come questi possano essere utili per ricostruire una filogenesi di alcune delle abilità che permettono all'uomo di fare musica.

Parole chiave: Canto; Vocalizzazione; Comunicazione; Advertising territoriale; Turn-Taking.

1. Musicality vs Music

Studying the behaviour and communication of non-human primates is fundamental to unveiling our species' language and musical abilities, especially since fossil remains are scarcely informative when it comes to reconstructing the evolution of our ancestors' communicative skills. Parallel to the study of the evolution of language, which has engaged scholars from many disciplines for decades, a new framework for the study of the communicative capacities of other animal species has emerged, inspired mainly by the concept of Musicality, that set of mental and peripheral capacities that underlie musical production.

The idea behind the definition of Musicality contrasts that of Music, a cultural artifact that is undoubtedly uniquely human. We owe much to those who initiated the studies on Musicality, among whom we would like to

mention Patel and Honing. To them, we owe the modern and lucid dichotomy between the definitions of Music and Musicality and a new impetus to studying Musicality in the animal world. With his multi-component view of Musicality (Honing, 2018), the study of the phylogeny of the traits underlying the production of Music has taken on scientific terms and initiated a fascinating field of investigation, in which other authors, such as Ravignani, Jacobi, and Savage, have entered by contributing comparative studies of the highest scientific profile.

2. Singing in a comparative perspective

The human voice is the musical instrument par excellence. It finds its prominent expression in singing, but to the surprise of many, we must point out that humans are not the only primates that sing. Not only are vocal expression and vocal perception fundamental aspects of primate vocal communication (Seyfarth & Cheney, 2003; Egnor et al., 2004; Carlson et al., 2020) but there are singing displays in which individuals perform alone, in duets and choruses. This is even though the very definition of singing has been repeatedly revised. Thorpe (1961) defined birdsong as a sequence of notes of various types produced in succession, forming a pattern of sequences over time. Geissmann (2002) and Haimoff (1986) adopted Thorpe's (1961) definition when referring to gibbon songs. This definition is particularly apt, as it focuses on the spectral and temporal characteristics of the utterance rather than its function and ontogeny (Logue & Krupp, 2016; Catchpole & Slater, 1995). Thorpe's criteria would easily separate songs from loud calls: the roars of Black and White Colobus Monkey (Colobus guereza), for example, are composed of harsh emissions in which melodic features are absent (Harris et al., 2006). In De Gregorio et al. 2021, we proposed that songs are series of units of different types, emitted following a hierarchical structure (Fee & Long, 2013) and characterised by frequency modulation. Singing can occur with varying degrees of interaction with conspecifics. We can, therefore, recognise solos in which only one singer is involved (Seddon,

2002), duets that represent a dyadic interaction (de Reus et al., 2021), and choruses that include multiple singers (e.g. birds, Seddon 2002; primates, Raemaerkers et al. 1984).

Communication using vocalisations among primates encompasses many diverse acoustic emissions and intricate vocal performances such as songs (e.g., indris and gibbons—Geissmann 2000). Solos, duets, and choruses also appear in primate songs, with differential occurrences in different species. Singing behaviour is a distinct form of primate vocal communication observed in species referred to as singing primates: members of the Pitheciidae, Hylobatidae, Tarsiidae, and Indriidae families. These primates produce complex, coordinated vocalisations involving two or more individuals. Recent research has emphasised the ability of primate songs, such as those of gibbons, tarsiers, indris, and titi monkeys, to exhibit vocal plasticity and flexibility in their characteristics (gibbons, Terleph et al. 2018; tarsiers, Clink et al. 2020; indris, De Gregorio et al. 2019; titi monkeys, Clink et al., 2019).

3. The songs of the indris

Over the last 15 years, despite its geographical distribution being limited to rainforests and Madagascar's remoteness, indri (Indri indri) has become a model for the study of animal singing. In the indris, singing takes the form of a chorus in which all adults and sub-adults in a group emit their contributions precisely and coordinatedly (Gamba et al., 2016). The function of vocalising a song may vary depending on the situation and facilitates communication within and between groups (Baker-Médard et al., 2013; Torti et al., 2013; Spezie et al., 2022). Additionally, vocalisations likely convey information about group composition and play a role in forming new groups (Gamba et al., 2016; Torti et al., 2017; Zanoli et al., 2020). There are differences between the sexes in the vocalisations of this species, with males producing longer notes, although the overall vocal investment is similar for males and females (Giacoma et al., 2010; Torti et al., 2018). This sexual difference in vocal units

and organisation is evident in adults (De Gregorio et al., 2019; Valente et al., 2021) and differs from how it occurs during individuals' development (De Gregorio et al., 2021a). Although the variation in frequency parameters during growth is similar between the sexes, temporal characteristics show distinct developmental patterns between males and females. Specifically, males exhibit a decrease in vocalisation during development, while utterances duration is longer in females (De Gregorio et al., 2021a).

The indris' vocalisations consist of a series of vocal units organised into phrases (Thalmann et al., 1993; Gamba et al., 2011). The vocal sequence begins with different group members' simultaneous emission of roars. The roars are followed by long notes, mainly emitted by males, and then by a prolonged series of frequency-modulated units organised into descending phrases (Pollock, 1986; Sorrentino et al., 2013; Zanoli et al., 2020). The descending phrases start with a high fundamental frequency unit, followed by one or more additional units (up to five) with progressively lower initial frequencies. Depending on the season, once a day, every couple of days or several times per day, two or more individuals coordinate the timing of their descending phrases to achieve a stable duet pattern (Ferrario et al., 2024). Adult pairs lead in vocalising, while younger individuals may only partially contribute. Dominant males and females influence the timing of the start of the chorus sequence, with the dominant male and female of a group overlapping more frequently than non-dominant males (Gamba et al., 2016). This 2016 study inaugurated a series of investigations into the temporal structure of songs in indri and other singing primates, showing how temporal structuring plays a crucial role in animal communication (Filippi et al. 2019) and human behaviour (Stivers et al. 2009). Rhythmic patterns are a valuable tool for species discrimination (de Oliveira David et al. 2003; Ravignani et al. 2019) and may play a critical role in mate choice and individual recognition (Norton & Scharff 2016; André 2000; Mathevon et al. 2017). In these temporally structured series of sounds, we can observe that single

elements may be organised in smaller homogeneous groups, generating a metric structure showing different hierarchical levels (Kotz et al. 2018).

4. Singing primates and the evolution of rhythm

Extending the study to other singing primates seemed the most obvious way to begin investigating rhythms in primates. Singing in primates is certainly the vocal performance that, from a structural point of view, exhibits the greatest complexity and, from an exquisitely spectral point of view, often shows a more pronounced frequency variation than we can observe in other vocal repertoire emissions. However, researchers have identified singing primates in definite taxa that are not closely related to each other (Haimoff, 1986). The fact that different species of song primates may have very distinctive phylogenetic distances enriches this picture: selective pressures may also have played a role in the evolution of different rhythmic categories. For example, the last common ancestor between the lar gibbon (Hylobates lar) and humans is dated 15 million years ago (Kumar et al. 2017). Beyond primate singing, a system governed at least in part by similar rules is that of loud calling, of which orangutans (Pongo pygmaeus awurmbii) are a prime example. Orangutans' evolutionary history separated from humans around 9 million years ago.

Searching for regularity of rhythmic patterns in the indris, it was more than surprising to find out that a species that diverged from the human clade between 61 and 78 million years ago showed the three most common rhythms corresponding to small integer ratios (1:1, 1:2, 2:1; De Gregorio et al. 2021a; 2024; Savage et al. 2015; Ravignani et al. 2018; Roeske et al. 2020). Although research into rhythmic categories in non-human primate species and animals, in general, is still at an embryonic stage, investigations now cover several species of lesser apes and at least one orangutan and have not shown the same level of rhythmic diversity (De Gregorio et al. 2024; Ma et al. 2024, Lameira et al. 2024). Lar gibbons (Hylobates lar) studied in Thailand showed a single prominent rhythmic category corresponding to 1:1 (isochrony), as did five out

of six crested gibbons. The study of orangutans showed that these monkeys exhibit nested degrees of isochrony during their long calls. One species of crested gibbon also indicates a tendency towards another rhythmic category.
This is an exciting result in several respects. The first of these aspects is that it is surprising to observe a species phylogenetically distant from our own that presents three rhythmic categories. The second key aspect is that when analysing the vocal behaviour of these animals, we observed that the three rhythmic categories corresponding to the small integer ratios only occur in songs (De Gregorio et al. 2024). Therefore, the marked rhythmic diversity of indri does not happen during alarm signals, which show no regularity or isochrony. Still, it manifests itself when these animals sing with other members of their family group. It is certainly too early to say, but it is fascinating to think that the need or habit of singing along with others played an important role during evolution in determining the emergence of individual rhythmic capacities. It is also peculiar if we consider that, unlike in many gibbon species, indri very rarely sings alone, and the vast majority of its songs are choruses in which the presence and participation of the other individuals in the group are one of the critical factors (Torti et al. 2013; 2018).
The work of De Gregorio and colleagues (2021b) has also shown that although there are sexually dimorphic intervals between the emissions of male and female Indri, the rhythmic structure is common to individuals of both sexes. Isochrony and other forms of rhythmic regularity may have evolved convergently between songbird species such as songbirds, indris, and humans. They may have played a key role in coordinating and processing vocal signals during evolution.

References

ANDRÉ M., KAMMINGA C. (2000), Rhythmic dimension in the echolocation click trains of sperm whales: A possible function of identification and communication, «Journal of the Marine Biological Association of the United Kingdom», 80, pp.163-169.

BAKER-MÉDARD M.S.A., BAKER M.C., LOGUE D. M. (2013), Chorus song of the indri (Indri indri: Primates, Lemuridae): group differences and analysis of within-group vocal interactions, «International Journal of Comparative Psychology», 26, pp. 241-255.

CARLSON N.V., GREENE E., TEMPLETON C.N. (2020), Nuthatches vary their alarm calls based upon the source of the eavesdropped signals, «Nature Communications», 11, pp. 526.

CATCHPOLE C.K., SLATER P.J.B. (1995), Bird song: biological themes and variations, Cambridge University Press, Cambridge, U.K.

CLINK D.J., TASIRIN J.S., KLINCK H. (2020), Vocal individuality and rhythm in male and female duet contributions of a nonhuman primate, «Current Zoology», 66, pp. 173-186.

CLINK D.J., LAU A.R., BALES K.L. (2019), Age-related changes and vocal convergence in titi monkey duet pulses, «Behaviour», 156, 5, pp. 1471-1494.

DE OLIVEIRA DAVID J.A., ZEFA E., FONTANETTI C.S. (2003), Cryptic species of Gryllus in the light of bioacoustic (Orthoptera: Gryllidae), «Neotropical Entomology», 32, 75-80.

DE GREGORIO C., ZANOLI A., VALENTE D., TORTI V., BONADONNA G., RANDRIANARISON R.M., GIACOMA C., GAMBA M. (2019), Female indris determine the rhythmic structure of the song and sustain a higher cost when the chorus size increases, «Current Zoology», 65, pp. 89-97.

DE GREGORIO C., VALENTE D., RAIMONDI T., TORTI V., MIARETSOA L., FRIARD O., GIACOMA C., RAVIGNANI A.,

GAMBA M. (2021a), Categorical rhythms in a singing primate, «Current Biology», 31, pp. 1379-1380.

DE GREGORIO C., CARUGATI F., ESTIENNE V., VALENTE D., RAIMONDI T., TORTI V., MIARETSOA L., RATSIMBAZAFY J.H., GAMBA M., GIACOMA C. (2021b), Born to sing! Song development in a singing primate, «Current Zoology», 67, 6, 597–608.

DE GREGORIO C., VALENTE D., FERRARIO V., CARUGATI F., CRISTIANO W., RAIMONDI T., TORTI V., GIACOMA C., GAMBA M. (2024), Who you live with and what you duet for: a review of the function of primate duets in relation to their social organization, «Journal of Comparative Physiology», 210, pp. 281–294.

DE REUS K., SOMA M., ANICHINI M., GAMBA M., DE HEER K.M., LENSE M., BRUNO J.H., TRAINOR L., RAVIGNANI A. (2021), Rhythm in dyadic interactions, «Philosophical Transactions of the Royal Society B», 376, 20200337.

EGNOR S.E.R., MILLER C., HAUSER M.D. (2004), Nonhuman primate communication, in K. Brown (ed.), Encyclopedia of Language and Linguistics, Elsevier Academic Press, Amsterdam, pp. 659–668

FEE M.S., LONG M.A. (2013), Neural mechanisms underlying the generation of birdsong: a modular sequential behavior, in R. C., Berwick, N. Chomsky (eds), Birdsong, speech, and language: exploring the evolution of mind and brain, MIT Press, Cambridge

FERRARIO V., RAIMONDI T., DEGREGORIO C., CARUGATI F., CRISTIANO W., TORTI V., LEWIS R.N., VALENTE D., WILLIAMS L.J., RAISIN C., GAMBA M., VON HARDENBERG A., GIACOMA C. (2024), Singing in the rain! Climate constraints on the occurrence of indri's song, «American Journal of Primatology», 86, e23673.

FILIPPI P., HOESCHELE M., SPIERINGS M., BOWLING D.L. (2019), Temporal modulation in speech, music, and animal vocal communication: evidence of conserved function, «Annals of the New York Academy of Science», 1453, pp. 99-113.

GAMBA M., FAVARO L., TORTI V., SORRENTINO V., GIACOMA C. (2011), Vocal tract flexibility and variation in the vocal output in wild indris, «Bioacoustics», 20, 3, pp. 251-26.

GAMBA M., TORTI V., ESTIENNE V., RANDRIANARISON R.M., VALENTE D., ROVARA P., BONADONNA G., FRIARD O., GIACOMA C. (2016), The indris have got rhythm! Timing and pitch variation of a primate song examined between sexes and age classes, «Frontiers in Neuroscience», 10, 249.

GEISSMANN T. (2000), Duet songs of the siamang, Hylobates syndactylus: I. Structure and organization, «Primate Reports», 56, pp. 33-60.

GEISSMANN T. (2002), Duet-splitting and the evolution of gibbon songs, «Biological Reviews», 77, pp. 57–76.

GIACOMA C., SORRENTINO V., RABARIVOLA C., GAMBA M. (2010), Sex differences in the song of Indri indri, «International Journal of Primatology», 31, pp. 539-551.

HAIMOFF E.H. (1986), Convergence in the duetting of monogamous Old World primates, «Journal of Human Evolution», 15, 1, pp. 51-59.

HARRIS T.R., FITCH W.T., GOLDSTEIN L.M., FASHING P.J. (2006), Black and White Colobus Monkey (Colobus guereza) Roars as a Source of Both Honest and Exaggerated Information About Body Mass, «Ethology», 112, pp. 911-920.

HONING H. (2018), On the biological basis of musicality, «Annals of the New York Academy of Science», 1423, pp. 51-56.

KOTZ S.A., RAVIGNANI A., FITCH W.T. (2018), The Evolution of Rhythm Processing. «Trends in Cognitive Sciences», 22, 10, pp. 896-910.

KUMAR S., STECHER G., SULESKI M., HEDGES S.B. (2017), TimeTree: A resource for timelines, timetrees, and divergence times, «Molecular Biology and Evolution», 34, 7, pp. 1812–1819.

LAMEIRA A.R., HARDUS M.E., RAVIGNANI A., RAIMONDI T., GAMBA M. (2024), Recursive self-embedded vocal motifs in wild orangutans, «ELife», 12, RP88348.

LOGUE D.M., KRUPP D.M. (2016), Duetting as a Collective Behavior, «Frontiers in Ecology and Evolution», 4, 7.

MA H., WANG Z., HAN P., FAN P., CHAPMAN C.A., GARBER P.A., FAN P. (2024), Small apes adjust rhythms to facilitate song coordination, «Current Biology», 34, 5, pp. 935-945.

MATHEVON N., CASEY C., REICHMUTH C., CHARRIER I. (2017), Northern Elephant Seals Memorize the Rhythm and Timbre of Their Rivals' Voices, «Current Biology», 27, 15, pp. 2352-2356.

NORTON P., SCHARFF C. (2016), Bird Song Metronomics: Isochronous Organization of Zebra Finch Song Rhythm, «Frontiers in Neuroscience», 10.

POLLOCK J.I. (1986), The song of the indris (Indri indri); Primates; Lemuroidea: natural history form and function, «International Journal of Primatology», 7, pp. 225–264.

RAEMAEKERS J.J., RAEMAEKERS P.M., HAIMOFF E.H. (1984), Loud calls of the gibbon (Hylobates lar): repertoire, organisation and context, «Behaviour», 91, pp. 146-189.

RAVIGNANI A., THOMPSON B., LUMACA M., GRUBE M. (2018), Why do durations in musical rhythms conform to small integer ratios, «Frontiers in Computational Neuroscience», 12, 86.

RAVIGNANI A., DALLA BELLA S., FALK S., KELLO C.T., NORIEGA F., KOTZ S.A. (2019), Rhythm in speech and animal vocalizations: A cross-species perspective, «Annals of the New York Academy of Sciences», 1453, 1, pp. 79-98.

ROESKE T.C., TCHERNICHOVSKI O., POEPPEL D., JACOBY N. (2020), Categorical Rhythms Are Shared between Songbirds and Humans, «Current Biology», 30, 18, pp. 3544-3555.

SAVAGE P.E., BROWN S., SAKAI E., CURRIE T.E. (2015), Statistical universals reveal the structures and functions of human music, «Proceedings of the National Academy of Sciences of the United States of America», 112, 29, pp. 8987-92.

SEDDON N. (2002), The structure, context and possible function of solos, duets and choruses in the subdesert mesite (Monias benschi), «Behaviour», 139, pp. 645-676.

SEYFARTH R.M., CHENEY D.L. (2003), Signalers and receivers in animal communication, «Annual review of psychology», 54, pp. 145-73.

SORRENTINO V., GAMBA M., GIACOMA C. (2013), A quantitative description of the vocal types emitted in the indri's song, in J.C. Masters, M. Gamba, F. Genin (eds.), Leaping ahead: Advances in prosimian biology, Springer, New York, pp. 315-322.

SPEZIE G., TORTI V., BONADONNA G., DE GREGORIO C., VALENTE D., GIACOMA C., GAMBA M. (2022), Evidence for acoustic discrimination in lemurs: a playback experiment in wild indris (Indri indri), «Current Zoology», 69, 1, pp. 41–49.

STIVERS T., ENFIELD N.J., BROWN P., ENGLERT C., HAYASHI M., HEINEMANN T., HOYMANN G., ROSSANO F., DE RUITER J.P., YOON K-E., LEVINSON S.C. (2009), Universals and cultural variation in turn-taking in conversation, «PNAS», 106, 26, pp. 10587-10592.

TERLEPH T.A., MALAIVIJITNOND S., REICHARD, U.H. (2018), An analysis of white-handed gibbon male song reveals speech-like phrases, «American Journal of Physical Anthropology», 166, 3, 649-660.

THALMANN U., GEISSMANN T., SIMONA A., MUTSCHLER T. (1993), The indris of Anjanaharibe-Sud, northeastern Madagascar, «International Journal of Primatology», 14, pp. 357-381.

THORPE W.H. (1961), Bird-song: the biology of vocal communication and expression in birds, University Press.

TORTI V., GAMBA M., RABEMANANJARA Z.H., GIACOMA C. (2023), The songs of the indris (Mammalia: Primates: Indridae): contextual variation in the long-distance calls of a lemur, «Italian Journal of Zoology», 80, pp. 596-607.

TORTI V., BONADONNA G., DE GREGORIO C., VALENTE D., RANDRIANARISON R.M., FRIARD O., POZZI L., GAMBA M.,

GIACOMA C. (2017), An intrapopulation analysis of the indris' song dissimilarity in the light of genetic distance. «Scientific Reports», 7, 10140.

TORTI V., VALENTE D., DE GREGORIO C., COMAZZI C., MIARETSOA L., RATSIMBAZAFY J., GIACOMA C., GAMBA M. (2018), Call and be counted! Can we reliably estimate the number of callers in the indri's (Indri indri) song?, «PLoS ONE», 13, e0201664.

VALENTE D., DE GREGORIO C., FAVARO L., FRIARD O., MIARETSOA L., RAIMONDI T., RATSIMBAZAFY J., TORTI V., ZANOLI A., GIACOMA C., GAMBA M. (2021), Linguistic laws of brevity: conformity in Indri indri, «Animal Cognition», 24, pp.897–906.

ZANOLI A., DE GREGORIO C., VALENTE D., TORTI V., BONADONNA G., RANDRIANARISON R.M., GIACOMA C., GAMBA M. (2020), Sexually dimorphic phrase organization in the song of the indris (Indri indri), «American Journal of Primatology», 82, e23132.