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Gibbon vocal communication provides insights into the origin and evolution of human music and language

Humans across cultures convey feelings and thoughts through music. Despite its ubiquity, the origins and evolution of music remain enigmatic. Archaeological evidence has traced the history of music back at least 40 000 years ago based on prehistoric bone flutes (Fitch, 2006). Comparative studies have also explored earlier histories by identifying common musical features between animals and humans (Fitch, 2006). For example, songbirds exhibit categorical rhythms similar to human music (Roeske et al., 2020), and humans can recognize emotional arousal in signals across all classes of terrestrial vertebrates (Filippi et al., 2017). These findings, while surprising, align with the longstanding human perception of animal signals as music (Gray et al., 2001). The universality of music and its features intensifies the fundamental question posed by Darwin (1871): how has a behavior that is energetically costly and seemingly non-adaptive evolved to become so widespread? This question can be further divided into two sub-questions (Savage et al., 2021): (1) how do musical features contribute to the production or expressive power of music (i.e., mechanisms), and (2) how does music benefit performers in terms of survival, reproductions, or other aspects (i.e., functions).

For over a century, theoretical and empirical studies have suggested that the primary selective pressure for music is its role in social interactions (Savage et al., 2021). Darwin (1871) proposed that music can profoundly influence emotions, such as anger or love, serving as a challenge to rivals or an attraction to mates. This often-cited hypothesis is supported by animal models, particularly songbirds (Fitch, 2006), as well as by some recent empirical research in humans (Ravignani, 2018). In larger social groups, music often unites individuals, diffusing tension and promoting cooperation, or the dynamic coordination of music and dance may deter potential external aggression (Fitch, 2006). Moreover, universal music features such as discrete pitches and categorical rhythms are hypothesized to facilitate coordination by providing unified signals (Savage et al., 2021). Despite various documented group-based functions of coordinated music in both human and animal models (Fitch, 2006; Savage et al., 2021), the underlying mechanisms remain largely unexplored. Developing an animal model that systematically addresses the mechanisms and functions of music coordination should greatly improve our understanding of the origins of music.

Gibbons (family Hylobatidae) are excellent candidates for comparative studies on the evolution of music. As the closest sister group to the family Hominidae (humans and great apes), these small arboreal apes share vocal mechanisms and even soprano capabilities similar to humans (Koda, 2016). Gibbons uniquely structure a series of notes, phrases, or sequences into long song bouts, a feature not observed in other non-human primates (Geissmann, 2000). Typically, adult males and females of all species, except *Hylobates klossii* and *H. moloch*, coordinate their sex-specific vocalizations to create coordinated song bouts (Koda, 2016). In addition to similarities in song structure with human music (Geissmann, 2000), categorical rhythms have been documented in several gibbon species (De Gregorio et al., 2023). Gibbons live in small family groups with high territoriality; their loud songs travel beyond the range of neighbor groups and serve various social functions (Ma et al., 2022). Song coordination can maintain and strengthen socio-sexual bonds within a family group, while advertising these bonds to outsiders can potentially aid in territory defense and prevent replacement.

A recent study, involving long-term habituation and monitoring, revealed an intriguing mechanism of song coordination in three crested gibbon (genus *Nomascus*) species (Ma et al., 2024), including the Cao-vit gibbon (*Nomascus nasutus*), Hainan gibbon (*N. hainanus*), and western black-crested gibbon (*N. concolor*). These gibbons, unlike their tropical relatives that typically live in monogamous groups, often reside in stable polygynous groups comprising one adult male and two adult females (Guan et al., 2018). Both sexes contribute their unique vocalizations, creating a coordinated triadic song. Notably, male gibbons in these species achieve successful song coordination by producing more isochronous rhythms and faster tempos, rather than adjusting the fundamental frequency. This adaptation appears to enhance the synchronization of their songs. Moreover, interspecies comparisons indicate that species with less variation in rhythm experience higher rates of coordination failure, highlighting the importance of both rhythmic consistency and variability. Isochrony, characterized by equal time divisions, has long been hypothesized to facilitate song coordination due to its universality and regularity (Roeske et al., 2020). This study not only provides the first empirical cross-species evidence supporting this hypothesis but also offers a comprehensive understanding of the role of rhythms in song coordination using a gibbon model.

The potential functions of song coordination have been

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explored previously. Notably, based on a six-year field study of Cao-vit gibbon behavior, Ma et al. (2022) reported that socio-sexual bonds remain relatively stable and are correlated with song coordination intensity and proficiency, but not with short-term coordination. Consequently, song coordination in Cao-vit gibbons primarily functions to signal and reinforce existing socio-sexual bonds, aiding in deterring potential intruders and preventing replacement. This prevention is crucial as replacement deprives individuals of reproductive opportunities and resources and reduces inclusive fitness through increased risk of infanticide (Ma et al., 2019). Replacement risk has also driven the evolution of precise rhythmic signals, providing crucial timing information for effective song coordination (Ma et al., 2024). Gibbons adjust the rhythms of *aa* notes, staccato and repetitive notes within a narrow frequency band, thus contributing to compression (Huang et al., 2020) and suggesting potential energetic efficiency in rhythmic signals. The complexity of coordinating songs in a polygynous social structure may further enhance the precision of male-female song coordination and rhythmic signals. Future studies exploring different social and ecological characteristics may provide deeper insights into why some species produce weaker rhythmic signals.

Given the parallels between music and language in terms of form and cognition, gibbon songs may also provide an excellent model for investigating language evolution (Fitch, 2006). Recent studies have uncovered considerable similarities between human language and gibbon songs. For example, the songs of Cao-vit and western black-crested gibbons conform to two linguistic principles: Zipf's law of brevity and Menzerath's law (Huang et al., 2020). However, the evolutionary questions surrounding language differ from those of music because the communicative functions of language are concrete and obvious. In contrast, fundamental abilities related to language use and production, such as intention and learning, are highly sophisticated and have rarely been documented in animals, including non-human primates (Fitch, 2020). Any definitive evidence of these abilities in animal vocal communication would significantly advance our understanding of language evolution. The evolutionary questions and empirical studies highlighted here (Figure 1) suggest that while novel computational tools have greatly facilitated comparative research in identifying statistical universals, long-term field observations remain critical for investigating and understanding animal models.

Gibbon songs will continue to provide an instructive model for comparative studies on the evolution of music and language. However, gibbons are on the precipice of extinction, primarily due to poaching and habitat loss. According to the International Union for Conservation of Nature (IUCN) Red List of Threatened Species, all but one gibbon species (*Hoolock leuconedys*, classified as Vulnerable) are listed as either Endangered (14 species) or Critically Endangered (five species). Research on gibbon vocal communications also provides valuable information for developing acoustic-based conservation strategies. Integrating conservation efforts with scientific inquiry is crucial to fully reveal the unique music and language capacities of gibbons. Without such efforts, we risk permanently losing key insights into the evolutionary history of these traits in our own species.

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

P.F.F. conceived the idea. Z.D.W. wrote the draft and generated the figure. P.F.F. and H.G.M. revised and edited the draft. All authors read and approved the final version of the manuscript.

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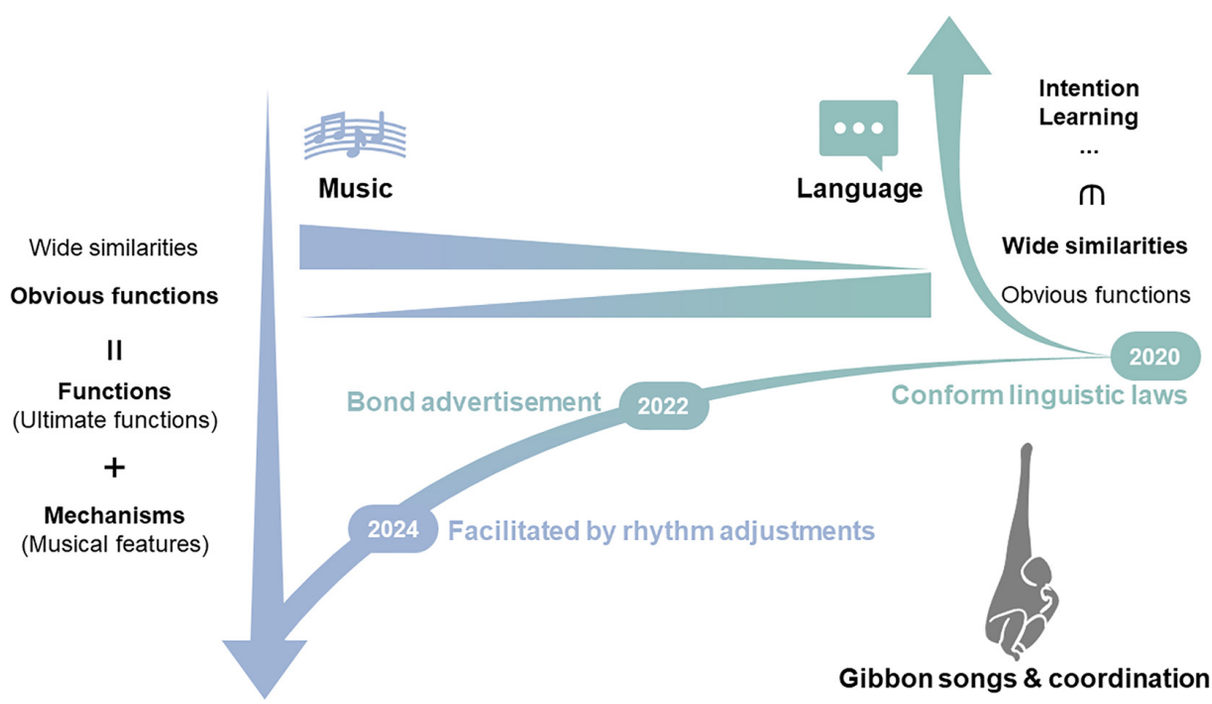

Figure 1 Evolutionary questions regarding music and language, with recent and future comparative studies of gibbon songs and song coordination

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