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PERSPECTIVE

On the biological basis of musicality

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In recent years, music and musicality have been the focus of an increasing amount of research effort. This has led to a growing role and visibility of the contribution of (bio)musicology to the field of neuroscience and cognitive sciences at large. While it has been widely acknowledged that there are commonalities between speech, language, and musicality, several researchers explain this by considering musicality as an epiphenomenon of language. However, an alternative hypothesis is that musicality is an innate and widely shared capacity for music that can be seen as a natural, spontaneously developing set of traits based on and constrained by our cognitive abilities and their underlying biology. A comparative study of musicality in humans and well-known animal models (monkeys, birds, pinnipeds) will further our insights on which features of musicality are exclusive to humans and which are shared between humans and nonhuman animals, contribute to an understanding of the musical phenotype, and further constrain existing evolutionary theories of music and musicality.

Keywords: music; musicality; comparative research

Introduction

Musical activity can be observed in all cultures, from the oldest civilizations of Africa, China, and the Middle East to the countless cultures of today's world.[1] No culture has yet been found that does not have music. Music supports many social and cultural activities, from rituals and concerts to dance parties and funerals. It unites, consoles, and, simply, gives listening pleasure.[2,3] However, some music researchers are skeptical about the biological foundations of musicality. In their opinion, every form of music in every culture is unique and is determined by human, social, and cultural conventions. If this is true, then music and musicality have little to do with our biology.[a]

The literature supporting the idea of music as a cultural artifact[4,5] usually restricts itself to music from Western culture, where music is generally the domain of professional musicians with years of study behind them. Such a position does not do justice to the presence of music in all cultures in all periods.[6] A broad range of research shows that all people, not just highly trained musicians, have a predisposition for music in the form of musicality.[7–9]

Over the past few years, more and more systematic research has been conducted on the similarities and differences in music from around the world. But might there be limits on what is heard, experienced, appreciated, and passed on to future generations as music? The avant-garde composer Anton Webern (1883–1945) thought it was only a matter of time before postmen would be whistling his atonal melodies. Though postmen seem to be slowly disappearing, one might wonder whether the same applies to certain melodic and rhythmic patterns. Observing all music cultures around the world, is it possible to say that certain musical structures occur more often than others, which either never or seldom occur?

Savage *et al.* recently analyzed hundreds of music recordings from different musical traditions

[a] *Musicality* is defined here as a natural, spontaneously developing set of traits based on and constrained by our cognitive abilities and their underlying biology. *Music* is defined as a social and cultural construct based on that very musicality.[53]

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from North and South America; Europe; Africa; the Middle East; South, East, and Southeast Asia; and Oceania.[1] The study, based on classifying music fragments according to a long list of features drawn up earlier by ethnomusicologists, such as Alan Lomax and Bruno Nettl, revealed huge differences.[10,11] Surprisingly—and this constituted the major contribution of this research—the analyses also demonstrated uniformity; specific structural features of music were found in nearly all of the recordings. Melodies are usually made up of a limited set of discrete pitches (seven or fewer), which form part of a scale that is divided into unequal and relatively small intervals. Most music also has a regular pulse (an isochronous beat), usually with two or three subdivisions, and a limited set of rhythmic patterns.[1]

In a certain sense, these universals are counterintuitive; one would expect to find considerably more variation in such a large collection of music, certainly based on the continuum of possibilities that tone and rhythm allow for in theory. A scale can be subdivided in an infinite number of ways. It would appear that dividing this continuum into a limited number of discrete units—specific tones with a specific duration—has, cognitively speaking, a particular appeal for humans. A limited number of pitches and rhythms can be easily remembered but also combined in an endless number of ways.[8] These characteristics ensure that the resulting melodies can be learned with relative ease and passed on to a subsequent generation.[12] In addition, a regular beat facilitates anticipating the rhythm and tempo of the music, a prerequisite for being able to dance and make music together.[13]

These are exciting insights when it comes to analyzing the structure of music and the underlying similarities, but, most likely, they tell us little about the biological foundations of musicality. This is because the method is indirect: the object of study is music—the result of musicality—rather than musicality itself. Comparative research is therefore a powerful tool in studying the evolutionary origins of musicality.[14] Furthermore, it is difficult to distinguish between the individual contributions of culture and biology. For example, it is not clear whether dividing a scale into small and unequal intervals in a particular music culture is the result of a widespread music theory doctrine or a music perception ability or preference.

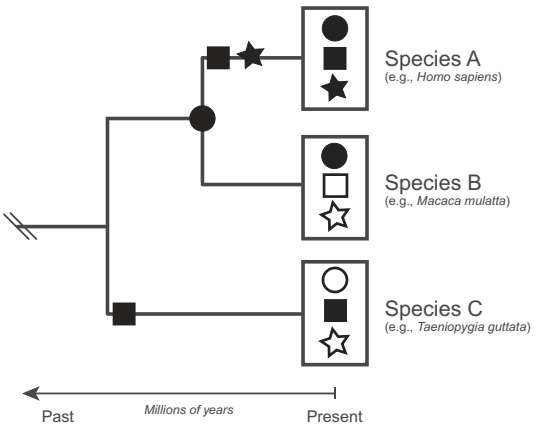

Figure 1. **Multicomponent perspective on musicality. Diagrammatic representation of the structure and evolutionary history of musicality, depicted as a phylogenetic tree with different shapes marking presence (solid) or absence (unfilled) of a particular trait at different points in evolutionary history. These traits could be speculated to be isochrony perception (circle), beat perception (square), or relative pitch (star). The positions of shapes on the tree stand for the hypothesized dates of origin of those traits. Adapted from Ref. 53.**

Here, I introduce a research program about the structure of musicality, not the structure of music.

Studying musicality using a multicomponent approach

As with people, the components of musicality have a genealogy that branches out across the globe and goes far back in time. As well as being a cultural artifact, musicality probably also has a biological basis.[14–16,49] But, unfortunately, since neither musical sounds nor our musical brain fossilize, no physical evidence about the history of musicality can be found.[17,18] Comparative biological research, however, does allow for mapping out the genealogy of musicality.[19,49] By studying whether a certain musical trait appears in related or unrelated animals, one can say something about their common biological history (Fig. 1). Potential candidates for the basic components of musicality that have been proposed in the recent literature are relative pitch (e.g., contour and interval analysis),[20] regularity and beat perception,[13,21] tonal encoding of pitch,[22,23] and metrical encoding of rhythm.[24,25] Some of these musical traits may be common to humans and other species, and others might be uniquely human.

The *multicomponent approach* is based on the neo-Darwinian assumption that if closely related

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species (e.g., humans and apes or walruses and sea lions) exhibit similar solutions to similar problems, they are probably engaging similar mechanisms. If two related species share a particular trait, their common ancestor would probably have had that trait as well. This is how we date the origins of a specific musical characteristic. If two unrelated species share a characteristic, this may say something about the underlying mechanism and the natural selection pressure that might have led to that characteristic. Comparative research is therefore a powerful method for learning more about human musical ability, despite the absence of fossils from a distant past.

Darwin assumed that all animals perceive and appreciate rhythm and melody simply because they have comparable nervous systems.[26] He therefore had no doubt that human musicality had a biological basis. He also suggested that sensitivity to music must be a very old trait, much older than language. He viewed musicality as the source of both music and language, an ability that humans and animals owe to the evolutionary mechanism of sexual selection. Darwin wrote,[26] "With all those animals, namely insects, amphibians, and birds, the males of which during the season of courtship incessantly produce musical notes or mere rhythmical sounds, we must believe that the females are able to appreciate them, and are thus excited or charmed; otherwise the incessant efforts of the males and the complex structures often possessed exclusively by them would be useless" (p. 403).

One way to map out the biological foundations of musicality is to conduct comparative research on animal species that share a specific musical trait with humans, a trait that is fundamental to experiencing music. It is wise to begin with model animals, animals we already know a lot about owing to substantial research during past decades. For research on the auditory system, *Macaca mulatta*, better known as the rhesus macaque, is relevant, along with *Taeniopygia guttata*, the zebra finch. Using these animals, we continue to improve our knowledge about hearing, speech, and the brain in general. In genetic terms, rhesus macaques are closely related to humans, and their brains have a similar structure to ours. As a result, this species of monkey is a much-used animal model for neurobiological research into, for example, the cause and treatment of hearing and movement disorders in humans. Much of what we know about brain function can be attributed to biomedical research on rhesus macaques.[27,28]

Zebra finches, on the other hand, are far removed from us genetically, with bird brains having a totally different structure than primate brains. Despite this, however, certain songbirds have traits comparable with those of human musicality. They can, for example, learn new songs. Through research into songbirds, we are learning more and more about the role of genetics, environment, and the evolution of their musical abilities.[29–31]

An example

While Charles Darwin suggested that the perception of rhythm was common to all animals, experimental research has only recently begun to support this claim.[32,33] However, rather than all

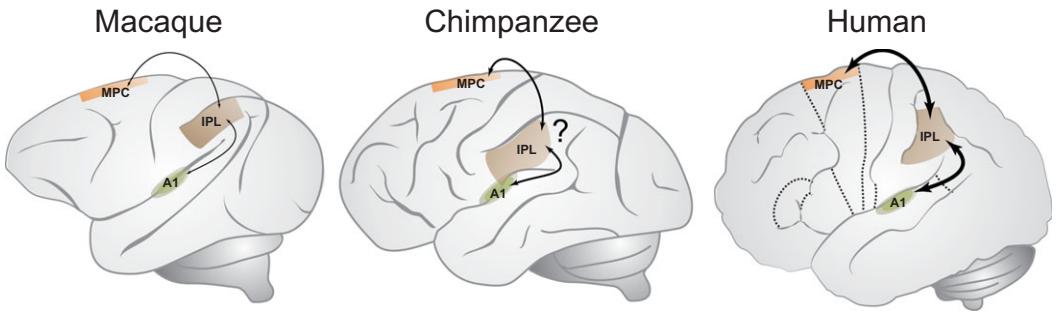

Figure 2. **The gradual audiomotor evolution (GAE) hypothesis. This hypothesis suggests that connections between the medial premotor cortex (MPC), inferior parietal lobe (IPL), and primary auditory area (A1) are stronger in humans than in other primates (marked with solid lines), suggesting that beat-based timing gradually evolved over evolutionary history. Line thickness indicates the hypothesized connection strength (strong for humans, weak for chimpanzees, and absent for macaques); the question mark indicates absence of evidence. Adapted from Ref. 49.**

species having a similar rhythmic ability, there are also aspects of rhythm cognition that appear to be species specific,[24] such as the capability to perceive a regular pulse in a varying rhythm (i.e., one level of a metrical structure) and consequently being able to synchronize to it (i.e., rhythmic entrainment), referred to here as *beat-based timing*.[34]

Beat-based timing in humans is a complex neurocognitive phenomenon that depends on a dynamic interaction between auditory and motor systems in the brain.[35–39] This dynamic interaction is hypothesized to be facilitated by bidirectional and potentially causal links between the auditory and motor areas in the brain (Fig. 2), including the motor cortico–basal ganglia–thalamo–cortical (mCBGT) circuit, that appear to be more developed in humans compared with nonhuman primates and related species.[32,37,40–42]

Recently, Honing *et al.*[43] found that, contrary to what was observed in human adults and infants,[44,45] there were no significant differences in the mismatch negativity (an informative component of the event-related potential measured on the skull)[46] in response to omissions in beat positions versus offbeat positions. This lead to the conclusion that rhesus monkeys are unable to sense a beat. Despite some drawbacks in the experimental design[47] (that are currently being addressed[49]), the former study lead to the *gradual audiomotor evolution* hypothesis,[34] which suggests that beat-based timing developed gradually in primates over evolutionary history. As such, beat perception is a common trait in humans, while it might only be marginally present in apes and possibly absent in monkeys. This is in contrast to interval-based timing, which appears to be present in both humans and nonhuman primates.

With regard to rhythmic cognition in avian species, the literature remains partial and divided. Initially, a causal link between vocal learning and beat perception and synchronization was proposed. Vocal learning underlies our ability to learn news sounds via imitation and produce relatively complex vocalizations. It is shared with a diverse set of bird and mammal species (but is not found in any nonhuman primate).[48] Patel suggested that beat perception in humans is a result of evolutionary modifications to the basal ganglia that play key roles in mediating a link between auditory input and motor output during learning.[50]

More recent studies have questioned an explicit link between vocal learning and beat perception[32,51] or have suggested at least a graded scale in avian species.[21] Some bird species appear to attend more strongly to specific local features of the individual stimuli (e.g., the interval between two onsets) rather than the overall regularity (or isochrony) of the stimuli, a main feature attended to by human listeners.[52] These findings seem to call for a reexamination of the nature and mechanisms underlying rhythmic cognition and its core components, such as isochrony and beat perception.

Conclusions

Here, I have introduced some aspects of a novel research program on musicality (discussed in more detail in Refs. 53 and 54) that combines functional, developmental, phylogenetic, and mechanistic approaches in order to generate an integrated theory of musicality. The main strategy is to focus on the constituent capacities underlying the musicality phenotype and find ways to effectively probe these traits in humans and animal models. Inspired by the four explanatory levels that Tinbergen[14,55] posited, describing the mechanisms, functions, phylogeny, and developmental course of musicality in a variety of animals and cultures, and with input from anthropological, neuroscientific and genetic sources, it will hopefully enhance understanding of both the cultural and biological factors that contribute to music and musicality and how they might have evolved.

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This paper contains (translated) fragments of a book that will appear in Dutch in 2018, Honing, H. Aap slaat maat. *Op zoek naar de oorsprong van muzikaliteit bij mens en dier*. Amsterdam: Nieuw Amsterdam.

Competing interests

The author declares no competing interests.

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