

our studies, receivers eventually learned the mapping that senders used in a game. However, more relevant from the point of view of the target article is evidence of convergent evolution. Small transmission errors, likely driven by individual biases, accumulated in the musical code. Each transmission chain developed its own “musical culture” based on patterns of melodic and rhythmic structure. Thus, we demonstrated experimentally that individual biases, brought out by intergenerational signaling, can lead to convergence toward attested musical patterns.

Modifications of the signaling games paradigm could be useful to test other hypotheses from the target article. One is the cumulative increase in the complexity and diversity of signals, particularly in groups where signalers have conflicting interests (sect. 5.2). Signaling games are flexible enough to accommodate several network structures – from simple dyads to games with many senders and receivers – and payoff structures – from shared to conflicting interests between signalers. To address the former hypothesis, one could organize senders and receivers into “microsocieties” (Baum, Richerson, Efferson, & Paciotti, 2004) of several interacting individuals, where player payoffs would either differ (experimental groups) or not (control groups). The generational progression would be recreated by replacing the longest-standing members of the groups with naive players. Finally, the complexity and diversity of signals could be quantified (Miton & Charbonneau, 2018) and compared between groups and across generations.

Importantly, some of our experimental results diverge from a core proposal by Mehr et al.: the music-specificity of cultural attractors (sect. 3.1). In two studies (Lumaca & Baggio, 2016; Lumaca et al., 2018), we used signaling games in combination with electroencephalogram (EEG) to test the idea that music adapts to auditory perception mechanisms (Trainor, 2015). We recorded participants’ brain responses in an auditory oddball task, which evoked an ERP signature of auditory scene analysis (ASA): the mismatch negativity (MMN) (Näätänen, Gaillard, & Mäntysalo, 1978). Another day, participants played in one signaling game as receivers and in a subsequent game as senders of a musical code. We showed that individual MMN latencies, which reflect ASA efficiency, predict the degree of melodic (Lumaca & Baggio, 2016) and rhythmic structures (Lumaca et al., 2018) introduced in the code. These findings trace the origins of core musical structures to neural mechanisms of ASA, which are arguably phylogenetically older than human musicality and are fairly widely conserved across species.

We argue that Mehr et al. could take advantage of the signaling games model to refine, constrain, and empirically test their hypothesis on the origins of music as a credible signal. Our experiments are a highly simplified model of signaling behavior and music transmission, yet they tap into the essential mechanisms which we suspect are at work in the emergence and evolution of music as a cultural symbolic system. Ultimately, the study of music’s origins demands a joint effort across different disciplines and methods, including behavior and neuroscience. But, a unification of methods and results is unlikely to happen in the absence of a model and paradigm that can guide research. Signaling games can take on such a unifying role, especially if we accept the idea that human symbolic systems, including music, are systems of culturally transmitted credible signals.

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Why don't cockatoos have war songs?

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Abstract

We suggest that the accounts offered by the target articles could be strengthened by acknowledging the role of group selection and cultural niche construction in shaping the evolutionary trajectory of human music. We argue that group level traits and highly variable cultural niches can explain the diversity of human song, but the target articles' accounts are insufficient to explain such diversity.

It is rare (but not uncommon) that music is performed alone or specifically for oneself. Most functional accounts of music evolution, therefore, rightfully place group functions such as bonding and coordination at the forefront of their hypotheses. The target articles by Savage et al. and Mehr et al. excel at providing functional group accounts for their hypotheses using phylogenetic and comparative accounts of animal vocal behavior. But, a question remains regarding the differentiation of human musicality from the music-like behaviors of animals. We want to ask not what features human music has *in common* with animal vocalizations, but ask instead, “why is human music *unique*?” That is, why do we see an increase in the diversity and flexibility of form–function links in human song compared to birds and nonhuman primates? We propose a simple answer to the dilemma by noting that it is not just human music which is unique, but human sociality, which may have had a fundamental role in the evolution of music. In short, the uniqueness and diversity of human music could be the result of the manner in which human songs are nested within complex and highly variable social and cultural environments.

Both articles compellingly point to comparative examples of music-like behaviors in other species in order to show continuity between nonhuman and human musicality. In the case of Mehr et al., phylogenetic examples from the primate kingdom are highlighted to emphasize the role that territorial calls may have had in shaping group songs. In Savage et al., examples from primates, whales, and birds are used to show that coordination of melodic, harmonic, and complex rhythmic patterns is less developed in these social species. Meanwhile, these coordinated actions serve as a sort of glue for the role of *communitas* in human sociality. Despite this difference, they also note that some birds demonstrate human-like beat perception and rhythmic abilities. One notable example of such a bird is Snowball, a sulfur-crested cockatoo who can famously entrain to a musical beat (Patel, Iversen, Bregman, & Schulz, 2009) and has recently showcased a diversity of spontaneous dance movements in response to music (Keehn, Iversen, Schulz, & Patel, 2019). Additionally, thrush nightingales, like humans, demonstrate cultural evolution of categorical rhythms (Roeske, Tchernichovski, Poepfel, & Jacoby, 2020). These nightingales also produce isochronous rhythms, a pattern important for synchronous coordination in human music and dance (however, nightingale rhythmic coordination is notably different from that of human music-making, Roeske et al., 2020). There is now some evidence of similar coordinated rhythmic abilities in primates (Gamba et al., 2016). In sum, both humans and nonhuman animals share similar, yet not identical, capacities for rhythm and synchrony, both fundamental features of human musicality.

If we share so many important music-like features with primates and birds, as in the case of Snowball, why is it that our *repertoire* is so much more diverse? A general musical toolbox

as proposed in Savage et al.'s hypothesis is insufficient for explaining musical diversity, as the authors note themselves, stating, “Each feature may have been initially based on behavioral innovations ... each innovation opened a new cognitive/musical niche selecting for independent specialization of relevant neural circuitry.” Similarly, the more *specific* territorial defense feature of our primate ancestors as proposed by Mehr et al. is insufficient to explain the plethora of form–function links that are the hallmark of their theoretical approach. In both articles, the role that group selection plays in shaping form–functionality is largely downplayed. This approach is limiting, as group selection is essential when we begin to ask questions such as, “why don't cockatoos have war songs?”

This is where integrating an understanding of selection for group-level traits is critical (Richerson et al., 2016; Smaldino, 2014; Zefferman & Mathew, 2015). Cockatoos lack war songs because cockatoos lack *war* (see Hobson, 2020 on the individualistic nature of bird fights). Unlike the examples from both birds and primates, humans occupy a unique social niche characterized by both its productivity and recombination (cultural evolution) and its ability to create new problems and avenues for these processes (cultural niche construction). Although many birds indeed exhibit cultural evolution of their songs and material culture, as in the case of bowerbirds, and possess the same hallmarks as human song's “unique” features such as its incremental change, learned elements, and social preferences, the application of these features is largely tied to singular and highly specific functions such as mate choice or predator evasion. In the case of humans, form–function links in song are highly varied precisely because our “functions” vary along an extremely diverse social dimension.

Smaldino (2014) refers to many of these unique traits as emergent “group-level traits,” which are those traits which “are properly defined only at the level of group organization.” A timeline of the evolution of human music should certainly take into account the evolution of group-level traits, all the way from our basal primate origins to what Turchin (2016) has coined our “ultrasociety.” Unlike primate and avian societies, human societies exhibit group structures that are both hierarchical and multidimensional, with differentiation within and between levels, and traits distinguishing these structures and levels (Moffett, 2019; Smaldino, 2019). The adaptive significance of these traits almost certainly had an effect on the evolution of human music diversity (related proposals have been suggested for the evolution of language – see Thompson, Kirby, & Smith, 2016). It is not unlikely that as human social life expanded the importance of culture in shaping human behavior did as well, with vocal plasticity both in the forms of speech and music finding its way into our social niches.

We believe that the accounts by both articles greatly expand our understanding of human music evolution and are a long awaited start to a serious conversation on the origins of music. However, both approaches would be enriched by granular attention to the unique social evolution of our species, particularly the way our complex social structure has shaped the cultural evolution of behavior – from kinship, to occupations, to social differentiation. The complex and highly variable social and cultural environments associated with human ultrasociality almost certainly had a functional effect on music evolution.

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Sex and drugs and rock and roll

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Abstract

This article is extraordinarily rigorous and rich, although there are reasons to be skeptical of its theory that music originated to signal group quality and infant solicitude. These include the lack of any signature of the centrality of these functions in the distribution or experience of music; of a role for the pleasure taken in music; and of its connections with language.

As someone who accidentally kicked off two decades of theorizing about the evolution of music with a few pages of discussion in one book (Pinker, 1997), I've long been nonplussed at the fervor with which theoreticians have striven to show that music is a Darwinian adaptation. I had included that discussion partly to sharpen readers' conceptions of the criteria for an adaptation. After 500 pages that had argued for the adaptive basis of many psychological faculties – stereo vision, the recency effect, disgust, jealousy, and revenge – I wanted to show that not *everything* is an adaptation. Any rigorous adaptationist hypothesis had to go beyond a trait merely being commonplace and lay out independent signs of engineering design for attaining some goal that was a subgoal of inclusive fitness. Whereas, it's easy to reverse-engineer, say, language, stereo vision, or fear, the function of music is far from obvious. If the concept of adaptation is not to

apply to everything, and hence to nothing, we must entertain the possibility that music instead is a pleasure technology: an application of human ingenuity to the evolutionarily dubious but proximately compelling goal of activating our pleasure circuits. In the case of music, these circuits might belong to language, auditory scene analysis, habitat selection, emotional calls, motor control, and perhaps some non-adaptive features of the auditory brain, such as proximity to other systems and their entrainment by the periodicity in auditory signals.

And yet while many scholars despise the idea that psychological traits are adaptations, blowing it off as a bunch of after-the-fact just-so stories, they are equally offended by the idea that music is *not* an adaptation, and so have offered hypotheses that are dead on arrival, such as that music evolved to bond the group or attract females. The reason for the discrepancy, I suspect, is that adaptation is not conceived of as a testable hypothesis from evolutionary biology but as an affirmation of how we value, deplore, or frame features of human nature. To say that music is an adaptation is to exalt its value; to say it is a by-product is a philistine denigration.

For these reasons, it's a pleasure to see Mehr et al. transcend all this wooliness in their superb article. After performing masterful necropsies on the bond-the-group and woo-the-ladies hypotheses, and raising reasonable criticisms of the by-product possibility, they propose a two-part hypothesis – credible signaling of coalition quality and of attention to infants – that satisfies the criteria for an adaptation and has impressive support from phylogenetic, ethnographic, genetic, and behavioral evidence. Maybe the theory is even true, although I think that it has some shortcomings.

First, it's not easy to see how these two very specific functions can be reconciled with the broad range of forms and contexts in which music is produced and enjoyed. If coalition quality and infant care are the two pillars, and everything else a set of cultural embellishments and extensions, we should see signs that those two functions are particularly robust, universal, archetypal, pervasive, and salient in the panoply of musical experience. But, that is exactly what was *not* found in Mehr et al.'s (2019) mammoth cross-cultural survey. It was not the case that music exemplifying the two proposed cores, such as war songs and lullabies, were universal, whereas the supposed extensions, such as love songs, healing songs, dance music, and other genres, were distributed more patchily, followed paths of historical influence rather than species-wide universality, or had less reliable acoustic signatures. Our major conclusion was that the four kinds of music spotlighted in the paper, together with 16 other genres were pretty much equally robust, distinctive, and universal: “Music is not a fixed biological response with a single prototypical adaptive function: It is produced worldwide in diverse behavioral contexts”

In a similar vein, the contemporary phenomenology of music shows no signs of the core-plus-periphery structure their theory implies. I see no evidence that group-advertising genres such as anthems and team songs, together with lullabies, are the most popular or accessible musical genres, that listeners backslide to pondering formidable cliques or calm babies when they experience other kinds of music, or any other sign of centrality. Both the ethnography and the psychology imply that music involves a broad mapping between acoustic structures and human experience, with no obvious common reaction or instrumental benefit. We enjoy a diversity of musical forms equally, and with no characteristic outcome other than the pleasure we get as we listen.

This leads to my second reservation about the theory. The most blazingly obvious feature of music – people enjoy it – plays no role