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Origins of music in credible signaling

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Short abstract

How did music evolve? We show that prevailing views on the evolution of music — that music is a byproduct of other evolved faculties, that music evolved for social bonding, and that music evolved to signal mate quality — are incomplete or wrong. We argue instead that music evolved as a credible signal in at least two contexts: coalitional interactions and infant care. We suggest that basic features of music, including melody and rhythm, result from adaptations in the proper domain of human music, providing a foundation that cultural evolution shapes into its actual domain.

Long abstract

Music comprises a diverse category of cognitive phenomena that likely represent both the effects of psychological adaptations that are specific to music (e.g., rhythmic entrainment) and the effects of adaptations for non-musical functions (e.g., auditory scene analysis). How did music evolve? Here, we show that prevailing views on the evolution of music — that music is a byproduct of other evolved faculties, evolved for social bonding, or evolved to signal mate quality — are incomplete or wrong. We argue instead that music evolved as a credible signal in at least two contexts: coalitional interactions and infant care. Specifically, we propose that (1) the production and reception of coordinated, entrained rhythmic displays is a co-evolved system for credibly signaling coalition strength, size, and coordination ability; and (2) the production and reception of infant-directed song is a co-evolved system for credibly signaling parental attention to secondarily altricial infants. These proposals, supported by interdisciplinary evidence, suggest that basic features of music, such as melody and rhythm, result from adaptations in the proper domain

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Conflicts of interest

None.

of human music. The adaptations provide a foundation for the cultural evolution of music in its actual domain, yielding the diversity of musical forms and musical behaviors found worldwide.

1 Introduction

Thirty years ago, Steven Pinker and Paul Bloom made the “incredibly boring” (1990 p. 708) argument that language is the product of natural selection, resulting from adaptations for communication. This was, in fact, controversial: despite the facts that language is universally used to communicate information essential to survival and reproduction; that all people typically acquire language easily in infancy; that languages have deep computational structure unrelated to technological or societal progress; that neural injuries cause specific language impairments; and that specialized neuroanatomy enables speech production — many believed that language arose from byproducts of adaptations for cognition, not communication (e.g., Chomsky 1968). The question of how language evolved is far from settled but it continues to generate testable hypotheses and productive results (e.g., Atkinson *et al.* 2008; Christiansen & Chater 2008; Fitch 2017; Searcy 2019).

Music shares many of the above facts with language but its contributions to survival and reproduction, if any, are less evident than those of language. As such, there is no consensus surrounding why humans make and listen to music; why music has its particular features and not others; or how music evolved. Three views on the evolution of music are prominent: a byproduct view, where music developed as a result of non-musical adaptations; an adaptationist view, where music evolved to create and maintain social bonds; and a second adaptationist view, where music evolved to signal mate quality.

We will argue that these views are incomplete or incorrect, proposing instead that the human psychology of music is built on adaptations for at least two categories of vocal signals common across species: territorial advertisements and contact calls. In these contexts, music can communicate overt information about covert properties of the human mind, functioning as a *credible signal*. This account explains some basic musical phenomena and the limited scope of music’s proper domain, laying a foundation for cultural-evolutionary processes that shape the diversity of music worldwide.

2 What constitutes evidence for adaptation by natural selection?

Since antiquity, it has been recognized that unlike abiotic natural phenomena, the existence and form of many biological traits must be explained in reference to their “purpose”. Rain does not fall in order to make corn grow, Aristotle wrote, but of necessity: “What is drawn up must cool, and what has been cooled must become water and descend, the result of this being that the corn grows.” (Physics II, part 8). Teeth, in contrast, are “admirably constructed for their general office, the front ones being sharp, so as to cut the food into bits, and the hinder ones broad and flat, so as to grind it to a pulp.” (Parts of Animals III, part 1). Human teeth universally grow this way, so this relation of means to ends cannot be due to chance, Aristotle argued; instead, these parts of animals can only be explained by their purpose, which benefits the animal itself (Ariew 2002).

Two millennia later, William Paley described the organism as an intricate machine, “a cluster of contrivances” whose physical structures are best comprehended in relation to the useful functions they provide the organism (Paley 1803 p. 185). He recognized that these contrivances must be understood in relation to their environments: “Can it be doubted, whether the wings of birds bear a relation to air, and the fins of fish to water?” (Paley 1803 p. 291). Whereas Paley, arguing by exclusion, took evidence of design to be evidence for God, Darwin instead proposed that design evolved via heritable variation and differential reproduction, i.e., adaptation by natural selection (Darwin 1859).

Hypotheses for adaptation can be evaluated using criteria not so different from those of Aristotle, Darwin, or even Paley. Adaptations are generally characteristics of an entire species recognizable from a tight relation of means to ends: a fit between the features of the proposed adaptation and the features of the adaptive problem that it putatively solved. This constitutes evidence of *design* (Williams 1966).

The human heart must be an adaptation to pump blood, for example, because it develops universally with properties that efficiently and reliably cause blood to circulate (e.g., muscles that compress chambers; valves; inlet and outlet ports; connections to the circulatory system), an outcome essential to survival and reproduction. Conversely, a pumping function best explains why the heart has the structure it has, instead of other tissues in other arrangements, reliably and efficiently solving an adaptive problem (Darwin 1859; Williams 1966).

There are important differences between pre- and post-Darwinian conceptions of design, however. Selection among heritable variants generally optimized traits to increase *inclusive fitness*, the reproduction of self or close relatives (Hamilton 1964), contra, e.g., “well-being” or “longevity”; and did so in ancestral environments but not necessarily modern ones. In Williams’s words, “the degree to which an organism actually achieves reproductive survival” is “rather trivial... The central biological problem is not survival as such, but design for survival” (Williams 1966 p. 159).

A key issue when investigating the evolution of a trait — one central to questions of the evolution of music, as we will discuss — is the distinction between *proximate* and *ultimate*-level explanations (Mayr 1961; Tinbergen 1963). Proximate-level questions ask how a trait develops over ontogeny and what causal relationships it has with other parts of the organism. Ultimate-level questions, on the other hand, ask why a trait came to be and require identifying the phylogenetic history of the trait across ancestral and extant species, and the causal role it played, if any, in the reproduction of genes coding for it (discussion: Dickins & Barton 2013; Laland *et al.* 2011; Scott-Phillips *et al.* 2011).

A proximate-level explanation for bitter taste, for instance, is that certain chemicals bind to bitter taste receptor proteins on the tongue, increasing intracellular calcium in the taste receptor cell, thereby stimulating a sensory afferent neuron, and so on. An ultimate-level explanation accounts for the presence of bitter taste receptor genes across vertebrates, and their expression in the oral cavity and other tissues, as part of a neurophysiological system to detect and avoid dietary toxins, which, if ingested, could reduce inclusive fitness (Roper &

Chaudhari 2017). Proximate-level explanation can also be applied to dysfunctions (such as cancer) and non-functions (such as the beating sound of the heart); they do not imply that a trait is an adaptation.

Ultimate-level analyses also do not presuppose adaptation. Adaptationist claims are onerous; there are infinitely many ways a phenotype can be carved into traits, most of which are unrelated to a genetic lineage's reproductive fitness. Supporting a claim of adaptation therefore requires evidence for design: evidence that a trait is improbably well-organized to efficiently, effectively, and reliably solve an adaptive problem (Williams 1966).

Here we evaluate claims about the evolution of music using the approach outlined above, with particular attention to the psychological design of music.

3 Two claims regarding the origins of music are unconvincing

A successful account of music must provide evidence for design of its principal features. Music is an auditory display built from melodies and rhythms. It can involve loud, elaborate, coordinated performances with voices and musical instruments, with many listeners; it also can involve quiet, simple lullabies between parents and infants. It appears in many behavioral contexts, across the sexes and across the lifespan, as a common element of daily life.

Before we proceed, readers should note a companion *BBS* target article, "Music as a coevolved system for social bonding" (Savage *et al.* 2020), which presents an alternate evolutionary scenario for the origins of music. Savage and colleagues propose that musicality arose fairly recently in human ancestry as a cultural invention to enhance social bonding, and was then elaborated via gene-culture evolution over tens of thousands of years (see also Podlipniak 2017).

We appreciate the focus on gene-culture co-evolution, a phenomenon we do not explore in detail in this paper, but which dovetails nicely with our concluding ideas concerning cultural evolution. Nevertheless, the two approaches differ substantially. The theoretical justification for music as a social bonding mechanism relies primarily on the work of Robin Dunbar and colleagues, who argued that grooming serves this function in smaller groups of non-human primates, but that larger human groups required more efficient mechanisms, namely laughter and music. On this idea, social bonds are created by the effects of joint musical performances on the neurobiology of the performers, rather than from information encoded in music. The costs of music production do not enter into this account, and Savage *et al.* (2020) mostly avoid theoretical or phylogenetic connections between human musicality and similar phenomena in other species (though they do offer some predictions concerning musicality in other species).

The theory we will describe differs substantially from this view. We propose that music has deep evolutionary roots in primate vocalizations, especially contact calls and territorial advertisements that were likely present in the last common ancestor of all primates, approximately 55 to 85 million years ago. We see music as a credible signal conveying information to listeners with whom signalers might have conflicts of interest, in a fashion

similar to most work on non-human vocalizations. We draw theoretical and phylogenetic connections between human music and similar phenomena in other primate and non-primate species. We argue that unique aspects of human lifestyle, including multilevel social organization and high levels of parental investment (including from alloparents), selected for especially elaborate vocal signaling relative to most other species. Finally, we propose that the key features of musicality arising from adaptations in the proper domain of credible signaling serve as building blocks for cultural evolution, which shapes music into its actual domain.

To begin, we review two popular ideas about the origins of music, and ask whether they explain the core properties of music.

3.1 The byproduct hypothesis fails in light of six lines of evidence

The null hypothesis against which hypotheses for adaptation are tested claims that music has no evolved function, and instead is a byproduct of other adaptations that evolved for other functions unrelated to music. The *byproduct hypothesis* dates at least to William James, who wrote that music “is a pure incident of having a hearing organ” (James 1890 p. 627); this view echoed other scholars of his time and before (Darwin 1871; Monboddo 1774; Rousseau 1781; Spencer 1902), and is common in the literature. Music has been proposed to be a byproduct of linguistic or emotive communication (Bryant 2013; Cattell 1891; Cross & Woodruff 2009; Jackendoff 2009; Panksepp 2009; Patel 2008; Pinker 1997; Schulkin 2013; Sievers *et al.* 2013); auditory scene analysis and habitat selection (Pinker 1997; Trainor 2015); signaling vocalizations (Bryant 2013; Livingstone 1973; Mithen 2005; Pinker 1997; Richman 1993); mimicry of other animals’ vocalizations (Benzon 2001; Krause 2012); physical or motor abilities (Geist 1978; Larsson 2014; Panksepp 2009; Tierney *et al.* 2011); theory of mind (Livingstone & Thompson 2009); or general cognitive capacities (Cross 2012; Honing & Ploeger 2012; Jackendoff & Lerdahl 2006; Justus & Hutsler 2005; Marcus 2012).

Pinker’s (1997) framing is the best-known: “I suspect that music is auditory cheesecake, an exquisite confection crafted to tickle the sensitive spots of ... our mental faculties” (p. 534). Six lines of evidence, taken together, call the byproduct hypothesis into question, however, and motivate theories of specific adaptations for music.

First, complex, song-like vocalizations have evolved convergently across distantly-related animals, including multiple clades of birds, marine mammals, primates, and insects; and provide important benefits related to mating and territorial defense (Coen *et al.* 2016). In many cases these are socially learned, like music (Schachner *et al.* 2009). Moreover, at least some explicitly musical behaviors, such as entrainment to a beat, appear in many species (Phillips-Silver *et al.* 2010; Wilson & Cook 2016). Music-like adaptations can therefore evolve, in principle.¹

¹The degree to which music-like behaviors in non-human species are homologous to music is up for debate (see Honing *et al.* 2018; Bertolo *et al.* 2020; McDermott & Hauser 2005), especially given surprising differences in auditory cognition and auditory preferences across species (Bregman *et al.* 2016; McDermott & Hauser 2004, 2007). For discussion, see Kotz *et al.* (2018) and Patel (2017).

Second, music is a human universal: it appears throughout a representative sample of human societies (Mehr *et al.* 2019); plays an essential role in important activities, such as rituals and ceremonies (Nettl 2015); and demonstrates cross-cultural links between form and function (Bainbridge *et al.* 2020; Mehr *et al.* 2019, 2018; Trehub *et al.* 1993a). Music is not a byproduct of traits present in only some cultures.

Third, music shows evidence for complex design, including grammar-like structures analogous to those of language (Lerdahl & Jackendoff 1983), some of which may be universal (Jacoby *et al.* 2019; Mehr *et al.* 2019). Moreover, music perception is computationally complex, such that artificial intelligence is currently at pains to emulate it (Benetos *et al.* 2013). Music is unlikely to occur as a result of random chance.

Fourth, the motivation and ability to perceive music appear early in ontogeny: neonates are sensitive to rhythms (Winkler *et al.* 2009) and melodies (Granier-Deferre *et al.* 2011) and infant music cognition is precocial (e.g., infants have detailed long-term memory for music; Mehr *et al.* 2016; Mehr & Spelke 2017; Trainor *et al.* 2004; reviews: Trehub 2001; Hannon & Trainor 2007). Music perception develops naturally, does not require extensive training, and is not a byproduct of traits specific to adults.

Fifth, music perception displays evidence for neural specialization (Norman-Haignere *et al.* 2015, 2019) and is impaired in specific deficits, such as tone-deafness (Peretz *et al.* 2002; Peretz & Vuvan 2017). Music is unlikely to be a byproduct of other neural systems.

Last, music is ancient: flutes are at least 40,000 years old (Conard *et al.* 2009) and the human auditory and vocal production systems are far older (Fitch 2006; Martínez *et al.* 2004; Quam *et al.* 2013). Music is not a recent cultural invention.

While no one of these pieces of evidence is a sufficient condition for rejecting the byproduct hypothesis, taken together, they motivate a search for an alternative.

3.2 The social bonding hypothesis fails in light of three theoretical issues

The best-known evolutionary hypothesis for music is that it evolved to create and maintain “social bonds.” Juan Roederer (1984), for example, argued that music established “behavioral coherency in masses of people” to meet the demands of “coherent, collective actions on the part of groups of human society” (p. 356). Steven Brown (2000b) asserted that “music-making has all the hallmarks of a group adaptation and functions as a device for promoting group identity, coordination, action, cognition, and emotional expression” (p. 296). These and similar claims (Barrow 2005; Benzoni 2001; Brown 2000a; Conard *et al.* 2009; Cross & Morley 2009; Dissanayake 2000, 2008, 2009; Dunbar 1998, 2012a; Freeman 2000; Fritz *et al.* 2013; Geissmann 2000; Huron 2001; Jourdain 1997; Kirschner & Tomasello 2009, 2010; Koelsch & Siebel 2005; Kogan 1994; Launay *et al.* 2016; Loersch & Arbuckle 2013; McNeill 1995; Merker *et al.* 2009; Morley 2012; Pearce *et al.* 2015; Reddish *et al.* 2013; Richman 1993; Schulkin 2013; Schulkin & Raglan 2014; Weinstein *et al.* 2016; Wiltermuth & Heath 2009) together form the *social bonding hypothesis*.

This view was popularized in part by Robin Dunbar’s proposal of a role for social bonding in the evolution of many human social traits (Dunbar 1991): he argued that

in primates, manual grooming serves a social bonding function; as group size increased in the hominin lineage, manual grooming became prohibitively time-consuming, creating a selection pressure for a less costly bonding mechanism; and, as a consequence, new bonding mechanisms evolved. These mechanisms were first proposed to be language and gossiping, which could be broadcast to multiple individuals while doing other tasks, replacing grooming as the primary means of social bonding in humans (Dunbar 1998). Later, Dunbar and colleagues revised this position (Dunbar & Lehmann 2013), arguing that musical chorusing and laughter evolved instead (Dunbar 2012a; Dunbar & Dunbar 2004; Dunbar *et al.* 2012; Pearce *et al.* 2015, 2017, 2016; Tarr *et al.* 2015, 2014, 2016).

Most empirical tests of the hypothesis examine music's impact on prosociality and its hormonal mediators in laboratory experiments: participants are randomized into groups that engage in synchronized musical behavior (treatment) or another activity (control). The general finding is greater levels of prosociality and cooperation in the music/dancing conditions relative to controls² (Anshel & Kipper 1988; Cirelli *et al.* 2014; Kirschner & Tomasello 2009, 2010; Pearce *et al.* 2015, 2017, 2016; Reddish *et al.* 2013; Schellenberg & Habashi 2015; Tarr *et al.* 2015).

The social bonding hypothesis has at least three key issues, however.

3.2.1 A “stress-reducing” social bonding mechanism is superfluous—The ultimate-level problem of sociality is that it imposes difficult-to-overcome inclusive fitness costs: increased competition with conspecifics for essential, limited resources; inbreeding depression; and increased exposure to pathogens (Alexander 1974). Living with and cooperating with conspecifics requires that the inclusive fitness benefits of sociality outweigh its fitness costs. Often they do not: dispersal and solitary living are ubiquitous across species (Benton *et al.* 2017; Bowler & Benton 2005; Duputié & Massol 2013).

In primates, diurnal social living evolved about 52 million years ago (Shultz *et al.* 2011). Because diurnal foraging increases predation risk, the joint evolution of diurnality and sociality supports the long-standing idea that primate sociality evolved as a defense against predators (Silk & Kappeler 2017; Van Schaik 1983). Advocates of the social bonding hypothesis claim that social living creates psychological stresses that threaten the cohesion of the group, necessitating a “bonding mechanism” (in non-human primates, grooming; in humans, music) that reduces stress:

Since living in groups of any kind creates stresses that would normally result in the group disbanding, species that live in stable social groups have to circumvent this problem if they are to prevent group size collapsing.

(Dunbar 2012a p. 1838)

This idea is superficially appealing because it draws attention to the fitness costs of social living, presenting them as proximate-level stresses, and implying a need for a behavioral response to relieve the stress.

²We leave aside a serious issue: most studies of prosocial effects of music-making are vulnerable to participant expectancy effects, which may account for the literature's poor reproducibility (Atwood et al. 2020).

But an ultimate-level analysis must consider alternative strategies. The alternative to sociality is solitary living, seen in ~70% of mammal species (Wilson & Reeder 2005). On the hypothesis that sociality solves the adaptive problem of defense against predators, the *net* fitness benefits of sociality exceed those of solitary life (with its attendant high risk of predation). The stress-related benefits of a “social bonding mechanism” are superfluous.

For an analogy, consider a group of friends walking close together in a dangerous neighborhood at night. There are costs to this sociality: they bump into each other; they don't fit on the sidewalk, forcing some to risk injury from oncoming cars; it's harder for them to converse, and so on. An ultimate-level analysis recognizes that the benefits of their sociality — defense against getting mugged — outweigh the costs, and no bonding mechanism, such as grooming or singing, is required to keep them together.

Grooming does provide hygienic benefits to primates, such as removal of ectoparasites (Barton 1985); perhaps with social functions beyond hygiene (McKenna 1978; Seyfarth 1977; Seyfarth & Cheney 1984), because across species the proportion of time spent grooming is positively correlated with group size (Dunbar 1991). But this association, core empirical finding underlying the social bonding hypothesis, is poorly evidenced: its strength is modest, and, when adjusting for terrestriality and other ecological factors, is not distinguishable from zero (Jaeggi *et al.* 2017). This may be because primate group size is confounded with terrestriality; if so, increased grooming time could instead be explained by some property of a terrestrial niche, such as increased parasite load (Grueter *et al.* 2013; Jaeggi *et al.* 2017; cf. Dunbar & Lehmann 2013).

Whatever evolved social functions grooming might have, it is unlikely that they include stress reduction. Predation risk, not grooming, is the ultimate-level “bonding force” that likely explains primate sociality, and the additional benefits of cooperative endeavors such as hunting, parenting, and territorial defense likely explain human sociality.

3.2.2 The social bonding hypothesis conflates proximate- and ultimate-level reasoning—Might grooming solve other problems of sociality? Defense against predators, territory defense, hunting, and parenting are compelling examples of cooperation whose benefits could offset sociality's costs. They raise profound theoretical challenges, however, involving free-riders: agents that receive benefits from others but do not provide any. Without countermeasures, free-riding is favored by natural selection (Nowak 2006), so forming cooperative relationships with arbitrary individuals is untenable. Instead, these relationships must be targeted at specific categories of individuals, such as kin, neighbors, or those likely to reciprocate, and adjusted to local socio-ecological conditions (Markham *et al.* 2015) such that long-run benefits are provided only when they exceed long-run costs to the donor (Nowak 2006).

Proponents of the social bonding hypothesis offer a proximate-level explanation, wherein the neurohormonal effects of music are a solution to the impediments to sociality and cooperation described above:

My proposal is that music arose originally because it allows individuals to become more group-oriented. Music seems to achieve this through a capacity to produce endorphins which have a positive effect on our attitudes towards others.

(Dunbar 2012b p. 208)

We propose that synchrony might act as direct means to encourage group cohesion by causing the release of neurohormones that influence social bonding.

(Launay et al. 2016 p. 779)

There are two problems with these claims. First, evidence that X causes Y is weak evidence that X evolved to cause Y . Recall Aristotle: rain causes corn to grow without implying any “purpose” for rain. Rain shows little evidence of special design for solving corn’s hydration problem, it has many other, unrelated effects, and so on. By analogy, a proximate-level analysis shows that petting animals reduces human anxiety via hormonal and physiological effects (Beetz *et al.* 2012), but animal-petting did not evolve to reduce anxiety or the threats that trigger it, of course.

Second, proximate mechanisms, such as release of neurohormones, are themselves subject to selection, and therefore cannot serve as ultimate-level explanations for the genetic evolution of a social bonding strategy. In order for a social strategy to evolve, it must outperform conceivable mutant strategies (a well-recognized criterion for claims of adaptation, the evolutionarily stable strategy; Smith & Price 1973). A mutation that prevented music from increasing endorphins and/or reduced endorphins’ effects on prosociality would have allowed humans with that mutation to free-ride: they could gain from the prosocial behavior of others (becoming more bonded with the group) without being prosocial themselves. Such a free-rider mutation would be selected for (Nowak 2006).

How can an unconditional social bonding mechanism like music be stabilized against free-riders? Confusion between proximate- and ultimate-level analyses in the social bonding hypothesis leaves this question unanswered.

3.2.3 Music is poorly designed to coordinate groups—Another version of the social bonding hypothesis proposes that music evolved by genetic group selection to enable humans to act as coordinated superorganisms: music increased group fitness by promoting group identity, cognition, coordination, and catharsis. These within-group functions are proposed to increase the ability of groups to compete with other groups (Brown 2000a).

While music does play a universal role in rituals (e.g., shamanistic trance; Singh 2018; Mehr *et al.* 2019), the problem with this view is that it equates proximate social “functions” or “effects” with adaptations shaped by natural selection³. Because any behavior has effects, and some of those effects may be incidentally “useful” (e.g., animal-petting reduces anxiety), the proper criterion is that music be well-designed for the proposed within-group function.

³We leave aside intense debates over whether or not genetic group selection is tenable; see Pinker (2012) and commentaries.

The superorganism model is based on an explicit analogy with multicellular organisms, where energy and time are sharply constrained resources. Within-organism signaling, cognition, and coordination evolved to be as efficient as possible, to maximize between-organism competitiveness. In neural signaling, for example, time and energy trade off: higher information rates use more energy, so at all levels of neural organization, strategies evolved to reduce energy consumption by filtering out predictable inputs, reducing the amount of redundant encoding (Laughlin 2001; Niven 2016; Niven & Laughlin 2008).

But music takes considerable time and energy to produce. People who produce music incur opportunity costs (Mehr & Krasnow 2017) and expend energy that could be used for other activities that directly increase reproductive success, such as food production (Hagen & Bryant 2003). Music is also often loud, and could attract predators or allow competing groups to eavesdrop. These costs also accrue to the variants of the social bonding hypothesis discussed earlier. Indeed, while music and other synchronous, ritualistic behaviors are often argued to be unambiguously beneficial for groups, the “neglected dark side of synchrony” (p. 3) shows that synchrony increases conformity and groupthink while reducing creativity and productive dissent (Gelfand *et al.* 2020).

Because natural selection shapes traits to perform specific functions by selecting among alternatives, a criterion for claiming adaptation is that a trait is uniquely suited to causing certain effects, relative to feasible alternatives. In the case of the social bonding hypothesis, an obvious alternative to music that serves the same proposed within-group functions is language, a low-cost signaling system that efficiently facilitates the coordination of collective action and other social behaviors (Pinker & Bloom 1990). Consider that the coxswain, whose job is to maintain the coordination of rowers, does not sing, nor does the crew; the efficient vocalization “row!” minimizes the energy required for within-group coordination, while maximizing the rowers’ ability to win a race⁴. Moreover, in a sample of six small-scale human societies, *conversation* time was close to the expected grooming time for a terrestrial primate with recent ape ancestry (Jaeggi *et al.* 2017), suggesting that language adequately provides whatever social functions grooming may have. As a social coordination or bonding mechanism, music thus appears to have no advantages over language and many disadvantages.

The weak case for music as an adaptation for social bonding does not mean that music has no evolved social functions. In the rest of this paper, we outline an alternative social hypothesis for the origins of music.

4 Origins of music in credible signaling

The social bonding hypothesis proposes that the fitness benefit of music arises from the neurophysiological effects of music production on music-makers themselves. Signaling hypotheses, in contrast, propose that fitness benefits arise from the information communicated by music-makers, via their music, to various categories of listeners.

⁴We thank anonymous Reviewer 5 for this example.

Acoustic communication has evolved repeatedly and independently in many clades of tetrapods. It appeared 200 million years ago in therian mammals and is found in ~95% of mammal species (Chen & Wiens 2020). If music is an adaptation, it likely evolved from ancestral vocalizations, an idea foreshadowed by Lucretius two millennia ago:

To imitate the liquid notes of birds
Was earlier far 'mongst men than power to
make, By measured song, melodious verse and give Delight to ears.

(De Rerum Natura, Book V)⁵

In non-human animals, most vocal adaptations evolve to send *signals*, which are defined as “any act or structure which alters the behaviour of other organisms, which evolved because of that effect, and which is effective because the receiver’s response has also evolved” (Maynard Smith & Harper 2003 p. 3).⁶ On average, receivers benefit from responding to the signal, and signalers benefit from the receivers’ response.⁷ Cues, in contrast, convey information about one organism to another but did not evolve to do so (e.g., bleeding is a cue of injury but did not evolve to signal injury). Common functions of signals include species identification in mate choice; individual recognition in interactions among conspecifics, such as territoriality, dominance, and cooperation; and conveying information on formidability, health, or behavioral type (Tibbetts *et al.* 2017).

Why do animals believe the vocal signals they hear? What maintains their credibility? If the interests of signaler and receiver are aligned, as in cells in an organism or agents in a superorganism, then selection for dishonesty is absent and signals evolve to be as efficient as possible (Maynard Smith & Harper 2003). If not, then selection can drive signalers to deceive and receivers to be vigilant against manipulation.

Some signals are necessarily credible because they are causally related to the quality being signaled. A wolf howl credibly indicates that a wolf is present, for example, and the number of distinct, simultaneous wolf howls credibly indicates a lower bound on the size of the pack (an “index”; Maynard Smith & Harper 2003). *Costly* signals, in contrast, are credible because to send them imposes a fitness cost that is lower for individuals with the quality than those without it: faking the signal is more costly than it is worth⁸ (Spence 1973; Zahavi 1975).

In addition to credibility, multiple selection pressures can shape signals, including biases in the sensory systems of receivers; receiver abilities to discriminate signals; the structure of the environment; social challenges; and arms races between signalers and receivers (Krebs & Dawkins 1984), where signalers are selected to produce the signal at lower cost and receivers are selected to better discriminate the quality of signalers (Bradbury & Vehrencamp 1998; Cummings & Endler 2018; Doorn & Weissing 2006; Hill 1994; Lindsay *et al.* 2019; McCoy & Haig 2020).

⁵We thank Cody Moser for suggesting this quotation.

⁶A fascinating exception is the phenomenon of echolocation, wherein the sender and receiver of a vocal signal are the same organism.

⁷We leave aside deceptive signals, which benefit the signaler at the expense of the receiver.

⁸For discussion of cues, indices, costly signals, and their relationships, see Biernaskie *et al.* (2018) and references therein.

Here, we emphasize the importance of conflicts of interest between music producers and the audience, private information, and the features of music that underlie its ability to overtly signal covert information about the minds of those producing it.

4.1 The mate quality hypothesis is poorly supported

An early theory of music, first proposed by Darwin (1871) and endorsed by many others (Barrow 2005; Charlton 2014; Dutton 2009; Merker 2000a; Miller 2000a, 2000b; Miranda *et al.* 2003; Orians 2014; Sluming & Manning 2000; Todd 2000; Todd & Werner 1999; van den Broek & Todd 2009) is that male musical abilities and female musical preferences coevolved, with music functioning as a credible signal of male mate quality.

If musical production requires a brain and body relatively unperturbed by genetic mutation, infection, or developmental instability, plus time to cultivate one's talent (properties that are difficult to perceive directly), the *mate quality hypothesis* argues that mates who prefer music-producers will benefit. This increases selection for music-producers to generate more impressive, complex, or interesting music (so as to improve the chance of being chosen as a mate). Given the sex difference in the amount of investment required of human parents for an offspring to be reproductively viable (Trivers 1972), signal production should be accentuated in the sex with lower obligate parental investment (males) and choosiness should be accentuated in the sex with the higher obligate parental investment (females).

Sexually dimorphic signals of mate quality are common across species (e.g., coloration, ornaments) and they play key roles in mate attraction (Andersson 1994; Dale *et al.* 2015; O'Brien *et al.* 2018); for example, male birdsong functions in part to attract mates (Catchpole & Slater 2018). Some mammals show this pattern too. In sac-winged bats, males produce complex songs that females may use in mating decisions (Behr *et al.* 2006). Adult house mice produce sexually dimorphic ultrasonic vocalizations with song-like features in response to the presence of novel female urine, but not the scents of immature females or other males (Musolf *et al.* 2010). If human music evolved in the context of signaling mate quality, it should have retained similar, signature features of a sexually selected adaptation⁹.

Ironically, the mate quality hypothesis is easy to refute precisely because it is so well-specified. Music is tenuously linked to mate quality. While love/courtship songs are common across cultures, they are only weakly identifiable as such relative to other forms of song (Mehr *et al.* 2019, 2018). A large twin study found inconsistent relations between measures of reproductive success or sociosexuality and measures of music production or music perception abilities (Mosing *et al.* 2015); the few positive relations reported were weak, and no stronger in men than in women. In another study, music performance quality was positively associated with indices of mate quality and attractiveness, but the effects and sample size were small and did not differ by sex (Madison *et al.* 2018). Musical preferences can vary across the menstrual cycle (Charlton 2014), perhaps indicating a role in mating, but this effect has failed to replicate¹⁰ (Charlton *et al.* 2012).

⁹This is true even of adaptations that subsequently change; bird feathers served as insulation before supporting flight but they retain features revealing their original function (see Persons & Currie 2019 and your duvet).

¹⁰Cycle effects on mate preferences, in general, have been questioned by recent studies (Gangestad *et al.* 2016; Jones *et al.* 2018).

Sexually-selected traits that function for display and choice in mating contexts are often developmentally and contextually calibrated to mating (Kokko 1997). In humans, for instance, puberty coordinates the developmental timing of physical and psychological traits that support mating: menarche and spermarche coincide with the development of secondary sexual characteristics and the relative onset of mating psychological systems (Kaplan & Gangestad 2005). But humans of all ages produce and listen to music; no part of the music faculty emerges at or around puberty¹¹. Young children enjoy the music of sexually mature conspecifics, and vice versa, a pattern contrasting with that of sexual attraction, which begins in late childhood (Herdt & McClintock 2000). While mating-related behaviors tend to be produced only in mating-relevant contexts, music is produced and consumed in multifarious contexts, universally, that are completely unrelated to mating (e.g., work, healing, greeting visitors, mourning; Mehr *et al.* 2019).

Last, many mating-related traits in humans are sexually dimorphic, such as male biases for traits useful in physical competition (Puts 2010; Sell *et al.* 2008) and female biases for traits useful in discerning investment potential (Buss 1989; Conroy-Beam *et al.* 2015; Kenrick & Keefe 1992). If music evolved to signal mate quality, then adaptations for music production should be more developed in men and adaptations for music perception should be more developed in women.

Little evidence supports this pattern. Dimorphisms in human vocalizations and vocal anatomy — lower voices in males, signaling threat potential (Puts *et al.* 2011), and higher voices in females, signaling fecundity (Apicella & Feinberg 2009) — appear beginning at puberty (McDermott 2012), but are neither more exaggerated nor more honestly signaled via song rather than via speech (cf. Keller *et al.* 2017). Auditory perception skills are comparable in males and females, with only small and inconsistent sex differences (Müllensiefen *et al.* 2014; Shuter-Dyson & Gabriel 1981). Musical disorders, such as specific musical anhedonia and congenital amusia, are found just as frequently in males as in females (Mas-Herrero *et al.* 2014; Peretz & Vuvan 2017). A lone report of sex differences in the frequency of music performance across human societies (Savage *et al.* 2015) is likely the result of sampling bias (discussion: Mehr *et al.* 2018, 2019). If anything, female musicians produce more novel songs than their male peers (Askin *et al.* 2020).

The pervasiveness of music across the sexes is evident in daily life: both males and females seek out and enjoy the performances of both male and female musicians (Hagen & Bryant 2003), and some evidence suggests that musical preferences are biased toward performers of the same sex as the listener (Greenberg *et al.* 2020). Male and female performers are both well-represented, historically, on the Billboard Top 100, albeit with an advantage toward males (LaFrance *et al.* 2011). While many of the highest-grossing musical artists of all time are male, sex differences in success as a musician likely have little to do with biology — a half-century ago, virtually all professional orchestral musicians were male, for example, whereas now the world's top orchestras are approaching gender parity (Sergeant & Himonides 2019).

¹¹Musical preferences change modestly during middle childhood (e.g., Hargreaves *et al.* 1995) but whether the *frequency* of musical behaviors also changes is unknown.

This pattern of evidence has contributed to a growing consensus that links between music and mate quality are weak (Mosing *et al.* 2015; Ravignani 2018).

4.2 Music as a credible signal of cooperative intent

We agree with proponents of the mate quality hypothesis that music is a credible signal. But song-like vocalizations in non-human animals often signal much more than mate quality. Even in songbirds, the poster-species for the sexual selection of male song, singing can serve other functions, such as territorial advertisements (Tobias *et al.* 2016).

We also agree with proponents of the social bonding hypothesis that musical abilities evolved because musical performances played an important role in cooperative sociality. But given the issues described above, we find it more likely that music evolved to credibly signal decisions to cooperate that were already reached by other means, not to determine them. Cooperation often fails, making it useful to have a credible signal indicating that, by various (non-musical) means, one or more agents have decided to cooperate. Credible signals of cooperative intent, in turn, can produce decisions by signal receivers that benefit the signalers.

We will discuss two behavioral contexts where complex vocal signals have evolved in numerous other species; where unique characteristics of the human species created selection pressures for an elaborate credible signal; and where music universally appears.

First, in the context of territorial advertisements, we consider pressures of coordinated territorial defense across coalitions and in the context of cooperative alliances with other groups. We propose that music could function as a credible signal of coalition strength, size, and coordination ability.

Second, in the context of contact calls, we consider pressures of helpless infants requiring substantial parental investment, relative to other primates; and multiple dependent siblings competing for parental investment. We propose that music could function as a credible signal of parental attention.

4.2.1 Synchronous coordinated music as a credible signal of coalition strength, size, and cooperation ability—In mammals, loud auditory signals are frequently agonistic, and territorial advertisements are a prime example (Gustison & Townsend 2015). Territoriality is common in taxa ranging from bacteria to vertebrates (Maher & Lott 2000; Smith & Dworkin 1994), including primates (Willems & van Schaik 2015). Territory owners have a consistent advantage over intruders, often retaining their territory without a fight (Kokko *et al.* 2006). It is thus in the interest of owners to advertise their residence in a territory to deter intruders and avoid a fight.

Territorial calls, which credibly signal that a territory is occupied, are found in many species, including birds, primates, and other mammals (Bates 1970; Gustison & Townsend 2015; Ladich & Winkler 2017; Wich & Nunn 2002). Loud primate calls are a plausible evolutionary precursor to human music (Geissmann 2000) because they appear to have existed in the last common ancestor of all primates and are often produced by both sexes

and directed at both sexes (Wich & Nunn 2002). Some African apes display drumming-like behaviors as part of territorial signals (Goodall 1986; Hagen & Hammerstein 2009). In humans, vocal and instrumental music are reliably associated with war, procession, and ritual across a representative sample of societies (Mehr *et al.* 2019, Table 1); appears in political and military contexts with analogues to territorial signaling (Hagen & Bryant 2003; Hagen & Hammerstein 2009); is generally not sexually differentiated (see above); and, of course, is often loud.

Social species that collectively defend territory, such as chimpanzees and several species of social carnivores (e.g., lions, wolves) produce coordinated vocal territorial advertisements (e.g., roars, howls), which credibly signal group size to potential intruders (Harrington 1989; Harrington & Mech 1979; Krebs 1977; McComb *et al.* 1994; Wilson *et al.* 2001). In a study of nearly 10,000 bird species, the presence of communal signaling was associated with territoriality, typically in conjunction with stable social bonds (Tobias *et al.* 2016). Moreover, the effect of territoriality was more than twice the size of that of social bonds, and territoriality was a crucial precursor to communal signaling, suggesting that long-term social bonds might evolve after communal signaling.

Some coordinated vocal signals, like bird duets, involve complex, temporally synchronized displays. A high level of synchronous coordination among signalers requires considerable effort to achieve, and thus credibly signals a willingness and ability to cooperate over time, thereby serving as an index of the quality of the coalition defending the territory, above and beyond coalition size (critical information otherwise not apparent to intruders; Hagen & Bryant 2003; Hall & Magrath 2007; Wiley & Wiley 1977). If synchronous coordination is a signal of coalition quality, selection should push receivers to better discriminate differences in degrees of coordination, and signalers to produce more complex coordinated signals, leading to signal elaboration.

Several primate species also produce highly synchronized song-like duets. As in birds, song-like calls are characteristic of species living in small, monogamous groups (Schruth *et al.* 2019). Although duetting and coordinated vocalizations might have some role in pair-bond formation and strengthening in a few monogamous species, such as gibbons and titi monkeys, most evidence suggests these calls primarily function to exclude intruders and maintain spacing: they are territorial advertisements (Snowdon 2017). Experimental evidence suggests that higher levels of coordination in such signals indicate higher coalition quality. Duetting magpie-larks that had been paired for a longer time were more likely to produce highly coordinated displays, and in an experimental loudspeaker study on natural territories, playbacks of highly coordinated duets, which simulated territorial intrusions, evoked significantly higher song rates by resident males than poorly coordinated duets (indicating that the highly coordinated duets were perceived as more threatening; Hall & Magrath 2007).

Humans are both primates and social hunters, so we expect human ancestors to have advertised territory ownership in a similar fashion: using loud, coordinated vocalizations, perhaps with drumming. We propose that such territorial vocalizations are an evolutionary precursor to music, especially rhythmic music (Hagen & Bryant 2003; Hagen &

Hammerstein 2009; cf. Merker 2000b). Signatures of this function might persist in modern humans in coordinated group dances that are universal across cultures (Mehr *et al.* 2019; Nettl 2015; e.g., the M ori *haka*; Best 1924). The group music of Aka Congo Basin hunter-gatherers, for instance, is audible to groups living some distance away.¹²

Complex forms of social organization likely set the stage for the evolution of complex credible signals, including synchronized and coordinated vocalizations. Sometime after diverging from other apes, the human lineage underwent a major transition to a multilevel society. In multilevel societies, small family units regularly aggregate with other family units, forming a higher-level unit, which in some species aggregate to form an even higher-level unit. This societal structure occurs in some other primate species (e.g., hamadryas baboons; Swedell & Plummer 2019), and some evidence suggests that higher degrees of social complexity are correlated with increased vocal diversity and flexibility (e.g., in macaques; Rebut *et al.* 2020).

A notable attribute of some multilevel-society species is that, in addition to the agonism or tolerance exhibited between units, units also cooperate. *Homo sapiens* exhibits particularly rich cooperative behavior between units: cooperative families are nested within cooperative residential groups that often form cooperative alliances with other residential groups to obtain food, buffer resource variation, raise children, defend territory, and so on (Chapais 2013; Hamilton *et al.* 2007; Pisor & Surbeck 2019; Rodseth *et al.* 1991; Swedell & Plummer 2019).

Between-group cooperation likely created many new selection pressures. In particular, if human groups varied in the benefits they could provide other groups as allies, and the number of alliances a group could maintain was limited, a biological market would have arisen (Hammerstein & Noë 2016), wherein groups evaluated the coalition quality of potential allies by assessing their size, cooperation ability, and willingness to cooperate, and potential allies had incentives to exaggerate these qualities (Hagen & Bryant 2003; Hagen & Hammerstein 2009). Common properties of music, especially those found in rhythmic, coordinated performances, provide a close fit to the necessary criteria for a credible signal of such otherwise difficult-to-observe group-level features. The time needed to create and practice group complex musical performances and achieve complex synchrony necessarily corresponds to a dimension of the underlying quality of the coalition: the amount of time coalition members have cooperated with one another.

In summary, we propose that music evolved, in part, as a means for groups to credibly show off their qualities to other groups.

There is substantial ethnographic, historical, and archaeological evidence of credible signaling of coalition quality among human groups, typically in the context of *feasting*. In feasting, two or more individuals share special types or quantities of foods, for a special purpose or event (Hayden 2014). In addition to food, feasting often includes special clothing, ornaments and other artifacts — and music and dance. Feasting has

¹²This statement is supported by personal interviews in E.H.'s fieldwork.

been documented in societies of all levels of social complexity, ranging from band-level hunter-gatherers to nation-states, including at archaeological sites throughout the Holocene (reviewed in Hayden & Villeneuve 2011; Hayden 2014). While many functions of feasting have been proposed (Hayden 2014; Wiessner & Schiefenhövel 1998), there is widespread agreement that feasts play a critical role in the formation of alliances between groups (reviewed in Hayden & Villeneuve 2011; Hayden 2014). As Sosis (2000) observed, the goal of ritualized foraging and feasting and other forms of food distribution is often to enhance the reputation of an entire group by displaying its productivity.

It is notable, then, that music and dance co-occur with feasting frequently in the ethnographic record.¹³ For example, Congo Basin hunter-gatherers are renowned for their music, which they perform in many social contexts, including at spirit plays and large inter-community dances following big game kills (Fürniss 2017; Lewis 2013, 2017), as in the Mbendjele BaYaka:

Sharing [food] between camps is less frequent, but will occur when big game is killed and during massana forest spirit performances. When an elephant is killed, Mbendjele in the area go rapidly to where the carcass is lying. Large camps grow, and feasting and dancing go on until the elephant has been consumed.

(Lewis 2017 p. 227)

It is plausible that similar events regularly occurred during human evolution because there is archaeological evidence for domestic spaces, large game hunting, mass kills, cooking, large aggregations, burials, ornaments, use of pigments, and musical instruments throughout the Upper Pleistocene, with some evidence appearing earlier (Barham 2002; Conard *et al.* 2009; Kuhn 2014; Kuhn & Stiner 2019; Maher & Conkey 2019; Stiner 2019, 2013, 2017).

A function of music in the context of alliance formation may also help to explain why music is often produced for and enjoyed by strangers, as in modern recorded music and live concerts. The selective dynamics of “social foraging” in the hominin niche, where strangers have an uncertain but non-zero possibility of becoming lucrative social partners, frame strangers as the appropriate targets of social foraging tactics (Delton *et al.* 2011; Delton & Robertson 2012; Rand *et al.* 2014). Moreover, some data shows that observers can infer coalition quality and fighting ability from observations of musical performances and other coordinated behaviors. People who listened to a musical performance with instruments mixed either in-sync, consistently out-of-sync, or scrambled rated coalition quality higher in the in-sync vs. out-of-sync (but not scrambled) conditions (Hagen & Bryant 2003). When listening to people marching asynchronously or synchronously, judges rated the synchronous groups as more formidable, better able to coordinate a physical attack, and higher in social closeness; judgments of formidability were mediated by judgments of coordination, not bonding (Fessler & Holbrook 2016).

On this view, music is clearly rooted in sociality. In contrast to the social bonding hypothesis, however, we predict that music does not *directly* cause social cohesion: rather, it

¹³Whereas evidence of feasting is abundant in agricultural and complex hunter-gatherer societies throughout the Holocene, it is less well-documented in simple hunter-gatherer societies, with some exceptions (Hayden 2014; Wallis & Blessing 2015).

signals existing social cohesion that was obtained by other means (Hagen & Bryant 2003 p. 30).

We do not think this is the only social context in which music can act as a credible signal. Within groups, musical performances might also create common knowledge of decisions to cooperate, which could serve group coordination and cooperation (Chwe 2001; Freitas *et al.* 2019; see Hagen & Bryant 2003 for other possibilities); credibly signal qualities guiding same-sex partner choice in a biological market (Hammerstein & Noë 2016), and perhaps informing mate choice by *both* sexes; and as a group analog of emotional expression (Hagen & Bryant 2003; Hagen & Hammerstein 2009). Producing music that is specific to a group might also credibly signal membership in that group (Mehr *et al.* 2016; Mehr & Spelke 2017) in a fashion similar to food preferences and dialects (see Liberman *et al.* 2016; Kinzler *et al.* 2007).

Next, we examine a case where we believe within-group rather than between-group credible signaling has shaped music.

4.2.2 Infant-directed song as a co-evolved system for negotiating parental investment of attention—Contact calls are a common vocalization across many species, distinct from territorial signals. In primates, these include loud calls between separated group members, and frequent quiet calls during heightened risk of separation (e.g., in dense vegetation). Contact calls rank among the most diverse and complex call types across species (Bouchet *et al.* 2013; Leighton 2017), enabling individuals to recognize, estimate distance to, and maintain contact with their social partners (Kondo & Watanabe 2009; Rendall *et al.* 2000).

One important class of contact calls are those between parents and offspring. These serve functions of mutual interest to parents and offspring, for example, enabling parents to be available to solve problems their offspring are ill-suited to solve on their own. Chacma baboon barks, for example, range from tonal, harmonically rich variants that are used for contact calls, to barks with a noisier, harsher structure that are used for alarm calls. By the age of six months, infants learn to discriminate call types and to discriminate their mothers' contact barks from those of unrelated females (Fischer *et al.* 2000); and mothers recognize their infants' contact calls (Rendall *et al.* 2000).

We propose that in the human lineage, maternal contact calls evolved to encode credible information beyond identity and distance, namely attention to the infant. There are few relationships where inclusive fitness interests overlap as much as they do between parents and offspring — but even these are not perfectly aligned. Because of the mechanics of diploid sexual reproduction, a parent is equally related to all her offspring, whereas each offspring is twice and four times as related to itself as it is to each of its full and half siblings, respectively. A strategy that optimizes the parent's inclusive fitness (e.g., equal food distribution across offspring) does not necessarily optimize an offspring's inclusive fitness, and vice versa. This possibility, parent-offspring conflict (Trivers 1974), implies differences in the interests of supply genes in the parent and demand genes in the offspring (Bossan *et al.* 2013).

Some aspects of human reproduction suggest that selection pressures for complex contact calls have increased relative to those in apes. First, human brain size is about triple that of other apes (Schoenemann 2006) and most brain growth occurs postnatally, implying that human infants are born helpless and have a very long juvenile period. Second, human forager interbirth intervals are about half those of chimpanzees (Marlowe 2005; Thompson 2013), requiring ancestral human mothers to simultaneously care for multiple dependent offspring (in contrast to chimpanzee mothers, who typically care for a single dependent offspring). Third, unlike other great apes, humans rely heavily on alloparenting in a multilevel society, requiring ancestral human infants to establish relationships with multiple caregivers and vice versa (Hrdy 2009); unlike chimpanzee infants, ancestral human infants typically competed with multiple juveniles for the attention of multiple caregivers.

Human parents increase their offspring's fitness by attending to them and protecting them from harm. Attention is a limited resource, however; many other challenges require attention, and solving those may benefit the parent more than the infant (relative to the provisioning of attention to maintain infant safety). The interests of infants and their parents conflict, in terms of the optimal provisioning of attention: infants often "prefer" more attention than a parent would "prefer" to provide.

How does this conflict of interests play out? Infants have bargaining power to extract parental investment (in the form of material investment, like nursing, or parental attention); they demand attention by crying (for discussion of evolutionary scenarios, see Soltis 2004 and commentaries). Parents lack perfect access to their infant's internal state, so crying provides information about when investment can be provided. Care-eliciting infant vocalizations (e.g., distress calls, separation calls) are common across mammals (Newman 2007), including humans, and mothers reliably respond to these vocalizations by providing care (Bornstein *et al.* 2017).

Whereas infants can easily detect when material investment has been provisioned, attention is a covert property of the parent's mind, with unreliable cues. Infants can infer that parents are attending to them from estimating the parent's gaze direction, but this only provides partial information (the parent could be concentrating on something else). Touch is also a good cue that a parent is nearby; but the parent could be asleep, or attending to something else.

Better than these cues would be a credible signal from the parent, reliably indicating that the infant has their attention (Mehr & Krasnow 2017). A vocal signal is a good candidate because its acoustic properties allow the proximity of the producer of the signal to be reliably inferred by the target. To the extent that the signal monopolizes the vocal apparatus, producing it is incompatible with other activities (such as speaking to another adult) that could co-opt the parent's attention. And aspects of the vocal signal can be modulated in real time, in response to the infant's state and behavior, which cannot be done without attending to the infant.

Here again we expect an evolutionary arms race, driven by partially conflicting fitness interests between senders and receivers, producing an elaborated signal. We propose that

this process could lead to key features of music: in particular, contrasting with the rhythmic features developing from territorial signals, we expect the rather more subdued context of soothing parent-infant contact calls to give rise to melodic features, tokens of which are the lullabies we sing to infants today (Mehr & Krasnow 2017).

Three sets of results support this idea. First, if adaptations support the production of song in parents and alloparents, and the appetite for and ability to perceive song in infants, then music should appear universally in the context of infant care and infant-directed songs should share features worldwide. These predictions, long discussed in the music cognition literature (Hannon & Trainor 2007; Peretz 2006; Trehub & Nakata 2001–2002), are well-evidenced. In an analysis of high-quality ethnography from a representative sample of human societies, text concerning vocal music was significantly associated with infant care and children, over and above base rates of reporting (this finding replicates both with expert annotations of the ethnography and automated text analysis; Mehr *et al.* 2019). Moreover, infant-directed songs are found in 100% of a pseudorandom sample of field recordings in mostly-small-scale societies; and naïve listeners, who are unfamiliar with the languages or cultures involved, reliably recognize them as infant-directed, with remarkable consistency (Mehr *et al.* 2019, 2018). This finding replicates prior cross-cultural work (Trehub *et al.* 1993b, 1993a).

Second, the genetic architecture of musical perception and motivation should be regulated, in part, by parent-of-origin epigenetic mechanisms, such as genomic imprinting. Humans are sexually reproducing but not obligately monogamous, which differentiates the conflict of interest between parents and offspring by parental sex: because maternity certainty is greater than paternity certainty, genes of maternal origin are more likely to be found in an offspring's siblings than genes of paternal origin (Haig & Wilkins 2000). Genes of maternal origin are thus under selection to bias the tradeoff in demand for parental investment in the direction of the offspring's siblings and away from the offspring; on average, maternally inherited genes should reduce investment demands on mothers, and vice versa. This prediction is confirmed by the fact that genes with parent-of-origin effects tend to affect demands for parental investment, such as intrauterine growth (Haig 1993).

Genomic imprinting disorders, where genetic dysregulation is differentiated by parent-of-origin, provide a unique test of the relation between a trait and its putative link to parental investment (Haig & Wharton 2003). Angelman and Prader-Willi syndromes result from opposing dysregulation at the same genetic region (15q11–13), with a loss of genes expressing maternal interest resulting in Angelman syndrome, and the reverse, a relative loss of genes expressing paternal interest resulting in Prader-Willi syndrome. The behavioral phenotypes reflect the different effects of maternally vs. paternally inherited genes: infants with Angelman syndrome have a voracious appetite while nursing, are awake for more hours of the day than typically developing infants, and attract more attention via smiling than do typically developing children (Ubeda 2008; Williams *et al.* 2006), increasing investment demands on the mother. Infants with Prader-Willi syndrome, in contrast, are born with low birth weight, sleep more than typically developing infants, and often lack a suckle reflex (Cassidy & Driscoll 2008; Holm *et al.* 1993; Peters 2014), with the opposite effect (decreasing investment demands on the mother).

Recent findings show that these effects extend to the domain of music, demonstrating a genetic link between music perception and parental investment. People with Angelman syndrome have a suppressed relaxation response to music (Kotler *et al.* 2019); while people with Prader-Willi syndrome have a potentiated relaxation response to music, along with pitch perception deficits (Mehr *et al.* 2017). These results support the idea that music signals attention: suppressed relaxation in Angelman syndrome implies increased maternal demands, while potentiated relaxation in Prader-Willi syndrome implies reduced maternal demands, in line with other findings concerning parental investment demands in genomic imprinting disorders.

Last, we also expect relationships between the acoustic features of non-human primate contact calls and human infant-directed song. While few data exist with which to test these relationships, preliminary findings suggest that similarities do exist. For example, baboon contact calls are harmonically rich, whereas alarm calls are harsh and noisy (Fischer *et al.* 2000); in a vocalization corpus from 21 human societies, infant-directed song was acoustically distinct from infant-directed speech across many pitch, rhythmic, phonetic, and timbral attributes (Moser *et al.* 2020), with a similar pattern of results to the acoustic differences between baboon contact calls and alarm calls. Moreover, several acoustic features driving these effects were related to vocal exertion (e.g., temporal modulation, pitch rate, vowel rate), perhaps honestly signaling additional costs incurred by the signaler.

5 Discussion

A comprehensive understanding of music requires that proximate-level explanations are distinguished from ultimate-level explanations uniquely linked to music; that proposed adaptations explain the core features of music that are putatively shaped by natural selection, and distinguish them from features that are byproducts of other adaptations; and finally, that the results of evolutionary analyses provide a foundation on which cultural-evolutionary processes can plausibly act.

The credible signaling account meets these criteria, whereas other accounts of the origins of music do not.

5.1 Credible signaling may explain some basic features of music

Early in this paper we noted some properties of human music that need explanation. While we find it implausible that any one theory can explain all of them, two core features of music are directly related to the ideas presented here.

An evolved system for quickly and reliably signaling coalition quality, which might otherwise be difficult to perceive, especially during territorial advertisements, agonistic intergroup encounters (e.g., war songs, dances), and alliance-forging feasts, provides a functional explanation for rhythm: selection pressures toward synchronized isochronous sounds, with complex internal design. An evolved system for credibly signaling parental attention to infants provides a functional explanation for melody: selection pressures toward manipulating affective prosody in vocalizations, constrained by the physics of the vocal production system and inherent features of the auditory world.

These “building blocks” appear universally in music (Mehr *et al.* 2019; Nettl 2015; Savage *et al.* 2015), like “building blocks” of language (e.g., Baker 2001). They provide a grammar-like, combinatorially generative interface through which musical content can be created, improvised, and elaborated upon, through hierarchical organization of meter and tonality¹⁴ (Krumhansl 2001; Lerdahl & Jackendoff 1983), in fashions that themselves have universal signatures (Jacoby & McDermott 2017; Jacoby *et al.* 2019; Mehr *et al.* 2019).

The importance of rhythm and pitch in human music perception — and the degree to which these features of music are unique to human vocalizations — may be directly tied to their evolutionary history.

5.2 Music is culturally evolved but cultural evolution has to start somewhere

We understand culture as information that affects individuals’ behavior and that is acquired from conspecifics through teaching, imitation, and other types of social transmission (Boyd & Richerson 2004; Tooby & Cosmides 1992). Because information is transmitted with some degree of fidelity through non-genetic means (e.g., memory, learning), information is cumulative. Some cultural information is passed on with greater frequency and higher regularity than other information. For example, social learners tend to pay attention to information sources that have established prestige more than sources that do not (Henrich & Boyd 2002). Similarly, some information is easier to learn than other information; children exhibit interest about information associated with danger and retain it with greater fidelity and over longer periods than related information unassociated with danger (Barrett *et al.* 2016; Wertz 2019).

One characteristic of cumulative culture is ritualization (Lorenz 1966), analogous to co-evolutionary processes underlying animal communication systems (Krebs & Dawkins 1984). Cultural signals can develop extravagant physical features resulting from arms race dynamics, particularly in cases when there is a conflict of interest between senders and receivers. Examples from modern environments include conspicuously branded luxury goods, which can signal wealth (Han *et al.* 2010); or businesses that engage in one-upmanship by incorporating exaggerated sensory features in competitive advertisements (Dunham 2011).

Such cultural ritualization is likely at play in the musical domain, especially given the increasingly important role of elaborate feasting in the cultural evolution of social complexity across the globe throughout the Holocene (Hayden 2014), and given the highly variable musical features that continually unfold over time across compositional styles, instrumentation and orchestration, improvisatory motifs, setting lyrics to music, and so on. Music must be shaped by culture in all contexts, however, not only those of coalition signaling and parental care.

We propose that the adaptations proposed here provide a foundation for cultural-evolutionary processes. These traits — particular grammar-like structures, for instance,

¹⁴Here, Temperley’s (2004) discussion of communicative structure in the evolution of musical style may have surprising parallels in the biological evolution of music.

such as tonalities and meters — gravitate towards certain forms, or “attractors”, and away from others (Sperber 1996; Sperber & Hirschfeld 2004). These attractors will interact with evolved capacities for nonmusical traits resulting in sensitivity and attraction to features in communicative acts that trigger them (e.g., musical phenomena that evoke the sound of an emotional voice), increasing variability in music.

As this process repeats within and across cultures, the diversity of music increases, while underlaid by universals that can be traced back to music’s adaptive functions in credible signaling. This pattern of universality and diversity is exactly what is observed in systematic analyses of music across cultures (Mehr *et al.* 2019) and, we believe, is what continues to shape music, worldwide, today.

Understanding this variability has been a longstanding interest of ethnomusicologists, who document musical traditions as they are shaped by social environments, politics, and ethnolinguistic history (Blacking 1973; Feld 1984; Nettl 2015), but it has strong parallels in the study of cultural evolution and social transmission. In particular, the prevalence of specific musical features (a particular scale, musical instrument, ornament, vocal practice, and so on) in a given society’s music is likely to be shaped by that society’s relation to other societies, just as the presence or absence of linguistic features is predictable by lineage (Dunn *et al.* 2011).

We expect that studying the cultural evolution of musical features will be a productive endeavor (with promising first steps already underway; e.g., Savage *et al.* 2015). We predict, however, that those features least likely to be shaped by culture are those core features predicted by the evolutionary account described here. For example, whereas we expect few musical systems worldwide to *lack* melody and rhythm as core features, we expect many to have rather different *instantiations* of those features. This is uncontroversial: while scales commonly used in music differ across cultures, they nevertheless are mutually intelligible, implying shared psychological mechanisms for music perception surrounding the interpretation of melodies (Castellano *et al.* 1984; Krumhansl *et al.* 2000; Mehr *et al.* 2019).

5.3 Auditory cheesecake: not wrong, but not right either

A key difficulty of studying the evolution of music, to which we alluded throughout this paper, is that the present environment has diverged from the environment in which humans evolved. In this context, Pinker’s (1997) “auditory cheesecake” analogy for a byproduct account of music is neither surprising nor controversial. We should expect *many* human behaviors to have cheesecake-like features. Just as the world’s great writers have stretched the bounds of human language far beyond language’s original adaptive functions, the boundless creativity of composers and performers have created an actual domain of music that, we believe, is quite far from its proper domain.

In this sense, we agree with Pinker that many musical inventions are byproducts, plain and simple: auditory cheesecake is not wrong. But in light of the adaptations proposed here, auditory cheesecake isn’t right either: as we have argued, in at least two contexts, music

exhibits design features consistent with adaptations for credible signaling, which give rise to a universal human psychology of music.

6 Conclusions

Why study the origins of music, language, or any other human behavior? It's unlikely that anyone will ever explain the full extent to which a particular behavior is accounted for by one or more adaptations because, given its complexity, human behavior cannot be exhaustively measured.

Nevertheless, we think that inching toward a functional understanding of complex behavior helps determine what the phenomena in question are, exactly, by isolating the core psychological representations and cultural processes underlying the phenomena from those that are merely associated with them. In the case of music, the analyses presented here lay out a roadmap for understanding the phenomenon of human musicality.

Music-like behaviors occur in a broad swath of species, including our ape relatives, and increasing evidence indicates that these serve important credible signaling functions among agents with conflicts of interest, such as territorial advertisements and mate attraction. In humans, across cultures, music is associated with social behaviors that directly involve credible signaling private information among agents with conflicts of interest, especially coalitional interactions and infant care, but perhaps others too. Accordingly, the psychological mechanisms for processing and producing features of music that are implied by those contexts, such as melody and rhythm, should also be universal; all of this is proposed to constitute music's proper domain. In music's actual domain, in contrast, we should expect the engine of cultural evolution to develop and expand these features, producing a diverse set of musical manifestations worldwide that retain some key features of their evolved functions.

Additional mechanisms likely interact with these core features. These may include psychological mechanisms that enable the perception of higher-level features of music, such as implied harmony or musical emotions; linguistic mechanisms that shape the ways in which language and music are intertwined; cultural mechanisms that drive musical traditions and are shaped historically as cultures mix and combine to form new cultures; technological mechanisms that directly alter the feature space of musicality, including musical inventions, such as instruments and music production software, or new musical forms, such as microtonal music; and, not least, aesthetic mechanisms that drive the preferences and interests of those who make and listen to music worldwide.

Understanding these mechanisms in isolation and as they interact with each other to produce the phenomenon of human musicality is a key challenge for the field — a challenge that will be served well by a clear explanation for the origins of music, which can then be built upon using the interdisciplinary toolkit of modern science.

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