

# Origins of music in credible signaling

Samuel A. Mehr<sup>a,b,c,\*</sup> [sam@wjh.harvard.edu](mailto:sam@wjh.harvard.edu) <https://mehr.cz>  
Max M. Krasnow<sup>a,\*</sup> [krasnow@fas.harvard.edu](mailto:krasnow@fas.harvard.edu) <https://projects.iq.harvard.edu/epl>  
Gregory A. Bryant<sup>d,e,\*</sup> [gabryant@ucla.edu](mailto:gabryant@ucla.edu) <https://gabryant.bol.ucla.edu>  
Edward H. Hagen<sup>f,\*</sup> [edhagen@wsu.edu](mailto:edhagen@wsu.edu) <https://anthro.vancouver.wsu.edu/people/hagen>

<sup>a</sup>Department of Psychology, Harvard University, Cambridge MA 02138, USA

<sup>b</sup>Data Science Initiative, Harvard University, Cambridge MA 02138, USA

<sup>c</sup>School of Psychology, Victoria University of Wellington, Wellington 6012, New Zealand

<sup>d</sup>Department of Communication, University of California Los Angeles, Los Angeles CA 90095, USA

<sup>e</sup>Center for Behavior, Evolution, & Culture, University of California Los Angeles, Los Angeles CA 90095, USA

<sup>f</sup>Department of Anthropology, Washington State University, Vancouver WA 98686 USA

\*All authors contributed to this paper and are listed in order of reverse seniority.

## 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 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.

## Word counts

Short abstract: 93

Long abstract: 197

Main text: 11355

References: 7348

Entire document: 19192

# 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

48 reproduction. Conversely, a pumping function best explains why the heart has the structure it has, instead  
49 of other tissues in other arrangements, reliably and efficiently solving an adaptive problem (Darwin 1859;  
50 Williams 1966).

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

57 A key issue when investigating the evolution of a trait — one central to questions of the evolution of music, as  
58 we will discuss — is the distinction between *proximate* and *ultimate*-level explanations (Mayr 1961; Tinbergen  
59 1963). Proximate-level questions ask how a trait develops over ontogeny and what causal relationships it  
60 has with other parts of the organism. Ultimate-level questions, on the other hand, ask why a trait came to  
61 be and require identifying the phylogenetic history of the trait across ancestral and extant species, and the  
62 causal role it played, if any, in the reproduction of genes coding for it (discussion: Dickins & Barton 2013;  
63 Laland *et al.* 2011; Scott-Phillips *et al.* 2011).

64 A proximate-level explanation for bitter taste, for instance, is that certain chemicals bind to bitter taste  
65 receptor proteins on the tongue, increasing intracellular calcium in the taste receptor cell, thereby stimulating  
66 a sensory afferent neuron, and so on. An ultimate-level explanation accounts for the presence of bitter taste  
67 receptor genes across vertebrates, and their expression in the oral cavity and other tissues, as part of a  
68 neurophysiological system to detect and avoid dietary toxins, which, if ingested, could reduce inclusive  
69 fitness (Roper & Chaudhari 2017). Proximate-level explanation can also be applied to dysfunctions (such  
70 as cancer) and non-functions (such as the beating sound of the heart); they do not imply that a trait is an  
71 adaptation.

72 Ultimate-level analyses also do not presuppose adaptation. Adaptationist claims are onerous; there are  
73 infinitely many ways a phenotype can be carved into traits, most of which are unrelated to a genetic lineage’s  
74 reproductive fitness. Supporting a claim of adaptation therefore requires evidence for design: evidence that a  
75 trait is improbably well-organized to efficiently, effectively, and reliably solve an adaptive problem (Williams  
76 1966).

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

### 79 **3 Two claims regarding the origins of music are unconvincing**

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

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

90 We appreciate the focus on gene-culture co-evolution, a phenomenon we do not explore in detail in this  
91 paper, but which dovetails nicely with our concluding ideas concerning cultural evolution. Nevertheless, the  
92 two approaches differ substantially. The theoretical justification for music as a social bonding mechanism  
93 relies primarily on the work of Robin Dunbar and colleagues, who argued that grooming serves this function  
94 in smaller groups of non-human primates, but that larger human groups required more efficient mechanisms,

95 namely laughter and music. On this idea, social bonds are created by the effects of joint musical performances  
96 on the neurobiology of the performers, rather than from information encoded in music. The costs of music  
97 production do not enter into this account, and Savage *et al.* (2020) mostly avoid theoretical or phylogenetic  
98 connections between human musicality and similar phenomena in other species (though they do offer some  
99 predictions concerning musicality in other species).

100 The theory we will describe differs substantially from this view. We propose that music has deep evolutionary  
101 roots in primate vocalizations, especially contact calls and territorial advertisements that were likely present  
102 in the last common ancestor of all primates, approximately 55 to 85 million years ago. We see music as  
103 a credible signal conveying information to listeners with whom signalers might have conflicts of interest,  
104 in a fashion similar to most work on non-human vocalizations. We draw theoretical and phylogenetic  
105 connections between human music and similar phenomena in other primate and non-primate species. We  
106 argue that unique aspects of human lifestyle, including multilevel social organization and high levels of  
107 parental investment (including from alloparents), selected for especially elaborate vocal signaling relative to  
108 most other species. Finally, we propose that the key features of musicality arising from adaptations in the  
109 proper domain of credible signaling serve as building blocks for cultural evolution, which shapes music into  
110 its actual domain.

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

### 113 3.1 The byproduct hypothesis fails in light of six lines of evidence

114 The null hypothesis against which hypotheses for adaptation are tested claims that music has no evolved  
115 function, and instead is a byproduct of other adaptations that evolved for other functions unrelated to  
116 music. The *byproduct hypothesis* dates at least to William James, who wrote that music “is a pure incident  
117 of having a hearing organ” (James 1890 p. 627); this view echoed other scholars of his time and before  
118 (Darwin 1871; Monboddo 1774; Rousseau 1781; Spencer 1902), and is common in the literature. Music has  
119 been proposed to be a byproduct of linguistic or emotive communication (Bryant 2013; Cattell 1891; Cross &  
120 Woodruff 2009; Jackendoff 2009; Panksepp 2009; Patel 2008; Pinker 1997; Schulkin 2013; Sievers *et al.* 2013);  
121 auditory scene analysis and habitat selection (Pinker 1997; Trainor 2015); signaling vocalizations (Bryant  
122 2013; Livingstone 1973; Mithen 2005; Pinker 1997; Richman 1993); mimicry of other animals’ vocalizations  
123 (Benzon 2001; Krause 2012); physical or motor abilities (Geist 1978; Larsson 2014; Panksepp 2009; Tierney  
124 *et al.* 2011); theory of mind (Livingstone & Thompson 2009); or general cognitive capacities (Cross 2012;  
125 Honing & Ploeger 2012; Jackendoff & Lerdahl 2006; Justus & Hutsler 2005; Marcus 2012).

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

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

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

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<sup>1</sup>The 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).

140 Third, music shows evidence for complex design, including grammar-like structures analogous to those of  
141 language (Lerdahl & Jackendoff 1983), some of which may be universal (Jacoby *et al.* 2019; Mehr *et al.*  
142 2019). Moreover, music perception is computationally complex, such that artificial intelligence is currently  
143 at pains to emulate it (Benetos *et al.* 2013). Music is unlikely to occur as a result of random chance.

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

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

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

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

### 157 **3.2 The social bonding hypothesis fails in light of three theoretical issues**

158 The best-known evolutionary hypothesis for music is that it evolved to create and maintain “social bonds.”  
159 Juan Roederer (1984), for example, argued that music established “behavioral coherency in masses of people”  
160 to meet the demands of “coherent, collective actions on the part of groups of human society” (p. 356). Steven  
161 Brown (2000b) asserted that “music-making has all the hallmarks of a group adaptation and functions as  
162 a device for promoting group identity, coordination, action, cognition, and emotional expression” (p. 296).  
163 These and similar claims (Barrow 2005; Benzon 2001; Brown 2000a; Conard *et al.* 2009; Cross & Morley  
164 2009; Dissanayake 2000, 2008, 2009; Dunbar 1998, 2012a; Freeman 2000; Fritz *et al.* 2013; Geissmann  
165 2000; Huron 2001; Jourdain 1997; Kirschner & Tomasello 2009, 2010; Koelsch & Siebel 2005; Kogan 1994;  
166 Launay *et al.* 2016; Loersch & Arbuckle 2013; McNeill 1995; Merker *et al.* 2009; Morley 2012; Pearce *et al.*  
167 2015; Reddish *et al.* 2013; Richman 1993; Schulkin 2013; Schulkin & Raglan 2014; Weinstein *et al.* 2016;  
168 Wiltermuth & Heath 2009) together form the *social bonding hypothesis*.

169 This view was popularized in part by Robin Dunbar’s proposal of a role for social bonding in the evolution  
170 of many human social traits (Dunbar 1991): he argued that in primates, manual grooming serves a social  
171 bonding function; as group size increased in the hominin lineage, manual grooming became prohibitively  
172 time-consuming, creating a selection pressure for a less costly bonding mechanism; and, as a consequence,  
173 new bonding mechanisms evolved. These mechanisms were first proposed to be language and gossiping,  
174 which could be broadcast to multiple individuals while doing other tasks, replacing grooming as the primary  
175 means of social bonding in humans (Dunbar 1998). Later, Dunbar and colleagues revised this position  
176 (Dunbar & Lehmann 2013), arguing that musical chorusing and laughter evolved instead (Dunbar 2012a;  
177 Dunbar & Dunbar 2004; Dunbar *et al.* 2012; Pearce *et al.* 2015, 2017, 2016; Tarr *et al.* 2015, 2014, 2016).

178 Most empirical tests of the hypothesis examine music’s impact on prosociality and its hormonal mediators  
179 in laboratory experiments: participants are randomized into groups that engage in synchronized musical  
180 behavior (treatment) or another activity (control). The general finding is greater levels of prosociality and  
181 cooperation in the music/dancing conditions relative to controls<sup>2</sup> (Anshel & Kipper 1988; Cirelli *et al.* 2014;  
182 Kirschner & Tomasello 2009, 2010; Pearce *et al.* 2015, 2017, 2016; Reddish *et al.* 2013; Schellenberg &  
183 Habashi 2015; Tarr *et al.* 2015).

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

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<sup>2</sup>We 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).

### 185 3.2.1 A “stress-reducing” social bonding mechanism is superfluous

186 The ultimate-level problem of sociality is that it imposes difficult-to-overcome inclusive fitness costs: in-  
187 creased competition with conspecifics for essential, limited resources; inbreeding depression; and increased  
188 exposure to pathogens (Alexander 1974). Living with and cooperating with conspecifics requires that the  
189 inclusive fitness benefits of sociality outweigh its fitness costs. Often they do not: dispersal and solitary  
190 living are ubiquitous across species (Benton *et al.* 2017; Bowler & Benton 2005; Duputié & Massol 2013).

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

197 *Since living in groups of any kind creates stresses that would normally result in the group disbanding, species*  
198 *that live in stable social groups have to circumvent this problem if they are to prevent group size collapsing.*  
199 *(Dunbar 2012a p. 1838)*

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

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

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

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

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

### 224 3.2.2 The social bonding hypothesis conflates proximate- and ultimate-level reasoning

225 Might grooming solve other problems of sociality? Defense against predators, territory defense, hunting, and  
226 parenting are compelling examples of cooperation whose benefits could offset sociality’s costs. They raise  
227 profound theoretical challenges, however, involving free-riders: agents that receive benefits from others but  
228 do not provide any. Without countermeasures, free-riding is favored by natural selection (Nowak 2006), so  
229 forming cooperative relationships with arbitrary individuals is untenable. Instead, these relationships must  
230 be targeted at specific categories of individuals, such as kin, neighbors, or those likely to reciprocate, and

231 adjusted to local socio-ecological conditions (Markham *et al.* 2015) such that long-run benefits are provided  
232 only when they exceed long-run costs to the donor (Nowak 2006).

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

235 *My proposal is that music arose originally because it allows individuals to become more group-oriented. Music*  
236 *seems to achieve this through a capacity to produce endorphins which have a positive effect on our attitudes*  
237 *towards others. (Dunbar 2012b p. 208)*

238 *We propose that synchrony might act as direct means to encourage group cohesion by causing the release of*  
239 *neurohormones that influence social bonding. (Launay *et al.* 2016 p. 779)*

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

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

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

### 257 **3.2.3 Music is poorly designed to coordinate groups**

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

262 While music does play a universal role in rituals (e.g., shamanistic trance; Singh 2018; Mehr *et al.* 2019), the  
263 problem with this view is that it equates proximate social “functions” or “effects” with adaptations shaped by  
264 natural selection<sup>3</sup>. Because any behavior has effects, and some of those effects may be incidentally “useful”  
265 (e.g., animal-petting reduces anxiety), the proper criterion is that music be well-designed for the proposed  
266 within-group function.

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

273 But music takes considerable time and energy to produce. People who produce music incur opportunity costs  
274 (Mehr & Krasnow 2017) and expend energy that could be used for other activities that directly increase  
275 reproductive success, such as food production (Hagen & Bryant 2003). Music is also often loud, and could  
276 attract predators or allow competing groups to eavesdrop. These costs also accrue to the variants of the

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

277 social bonding hypothesis discussed earlier. Indeed, while music and other synchronous, ritualistic behaviors  
278 are often argued to be unambiguously beneficial for groups, the “neglected dark side of synchrony” (p. 3)  
279 shows that synchrony increases conformity and groupthink while reducing creativity and productive dissent  
280 (Gelfand *et al.* 2020).

281 Because natural selection shapes traits to perform specific functions by selecting among alternatives, a  
282 criterion for claiming adaptation is that a trait is uniquely suited to causing certain effects, relative to  
283 feasible alternatives. In the case of the social bonding hypothesis, an obvious alternative to music that  
284 serves the same proposed within-group functions is language, a low-cost signaling system that efficiently  
285 facilitates the coordination of collective action and other social behaviors (Pinker & Bloom 1990). Consider  
286 that the coxswain, whose job is to maintain the coordination of rowers, does not sing, nor does the crew; the  
287 efficient vocalization “row!” minimizes the energy required for within-group coordination, while maximizing  
288 the rowers’ ability to win a race<sup>4</sup>. Moreover, in a sample of six small-scale human societies, *conversation*  
289 time was close to the expected grooming time for a terrestrial primate with recent ape ancestry (Jaeggi *et*  
290 *al.* 2017), suggesting that language adequately provides whatever social functions grooming may have. As  
291 a social coordination or bonding mechanism, music thus appears to have no advantages over language and  
292 many disadvantages.

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

## 295 4 Origins of music in credible signaling

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

300 Acoustic communication has evolved repeatedly and independently in many clades of tetrapods. It appeared  
301 200 million years ago in therian mammals and is found in ~95% of mammal species (Chen & Wiens 2020).  
302 If music is an adaptation, it likely evolved from ancestral vocalizations, an idea foreshadowed by Lucretius  
303 two millennia ago:

304 *To imitate the liquid notes of birds*  
305 *Was earlier far ’mongst men than power to make,*  
306 *By measured song, melodious verse and give*  
307 *Delight to ears. (De Rerum Natura, Book V)<sup>5</sup>*

308 In non-human animals, most vocal adaptations evolve to send *signals*, which are defined as “any act or  
309 structure which alters the behaviour of other organisms, which evolved because of that effect, and which is  
310 effective because the receiver’s response has also evolved” (Maynard Smith & Harper 2003 p. 3).<sup>6</sup> On average,  
311 receivers benefit from responding to the signal, and signalers benefit from the receivers’ response.<sup>7</sup> Cues, in  
312 contrast, convey information about one organism to another but did not evolve to do so (e.g., bleeding is a  
313 cue of injury but did not evolve to signal injury). Common functions of signals include species identification  
314 in mate choice; individual recognition in interactions among conspecifics, such as territoriality, dominance,  
315 and cooperation; and conveying information on formidability, health, or behavioral type (Tibbetts *et al.*  
316 2017).

317 Why do animals believe the vocal signals they hear? What maintains their credibility? If the interests of  
318 signaler and receiver are aligned, as in cells in an organism or agents in a superorganism, then selection for

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<sup>4</sup>We thank anonymous Reviewer 5 for this example.

<sup>5</sup>We thank Cody Moser for suggesting this quotation.

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

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

319 dishonesty is absent and signals evolve to be as efficient as possible (Maynard Smith & Harper 2003). If not,  
320 then selection can drive signalers to deceive and receivers to be vigilant against manipulation.

321 Some signals are necessarily credible because they are causally related to the quality being signaled. A  
322 wolf howl credibly indicates that a wolf is present, for example, and the number of distinct, simultaneous  
323 wolf howls credibly indicates a lower bound on the size of the pack (an “index”; Maynard Smith & Harper  
324 2003). *Costly* signals, in contrast, are credible because to send them imposes a fitness cost that is lower for  
325 individuals with the quality than those without it: faking the signal is more costly than it is worth<sup>8</sup> (Spence  
326 1973; Zahavi 1975).

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

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

#### 336 4.1 The mate quality hypothesis is poorly supported

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

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

350 Sexually dimorphic signals of mate quality are common across species (e.g., coloration, ornaments) and they  
351 play key roles in mate attraction (Andersson 1994; Dale *et al.* 2015; O’Brien *et al.* 2018); for example, male  
352 birdsong functions in part to attract mates (Catchpole & Slater 2018). Some mammals show this pattern  
353 too. In sac-winged bats, males produce complex songs that females may use in mating decisions (Behr *et*  
354 *al.* 2006). Adult house mice produce sexually dimorphic ultrasonic vocalizations with song-like features in  
355 response to the presence of novel female urine, but not the scents of immature females or other males (Musolf  
356 *et al.* 2010). If human music evolved in the context of signaling mate quality, it should have retained similar,  
357 signature features of a sexually selected adaptation<sup>9</sup>.

358 Ironically, the mate quality hypothesis is easy to refute precisely because it is so well-specified. Music is  
359 tenuously linked to mate quality. While love/courtship songs are common across cultures, they are only  
360 weakly identifiable as such relative to other forms of song (Mehr *et al.* 2019, 2018). A large twin study  
361 found inconsistent relations between measures of reproductive success or sociosexuality and measures of  
362 music production or music perception abilities (Mosing *et al.* 2015); the few positive relations reported were  
363 weak, and no stronger in men than in women. In another study, music performance quality was positively

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

<sup>9</sup>This 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).

364 associated with indices of mate quality and attractiveness, but the effects and sample size were small and did  
365 not differ by sex (Madison *et al.* 2018). Musical preferences can vary across the menstrual cycle (Charlton  
366 2014), perhaps indicating a role in mating, but this effect has failed to replicate<sup>10</sup> (Charlton *et al.* 2012).

367 Sexually-selected traits that function for display and choice in mating contexts are often developmentally and  
368 contextually calibrated to mating (Kokko 1997). In humans, for instance, puberty coordinates the develop-  
369 mental timing of physical and psychological traits that support mating: menarche and spermatarche coincide  
370 with the development of secondary sexual characteristics and the relative onset of mating psychological sys-  
371 tems (Kaplan & Gangestad 2005). But humans of all ages produce and listen to music; no part of the music  
372 faculty emerges at or around puberty<sup>11</sup>. Young children enjoy the music of sexually mature conspecifics,  
373 and vice versa, a pattern contrasting with that of sexual attraction, which begins in late childhood (Herd  
374 & McClintock 2000). While mating-related behaviors tend to be produced only in mating-relevant con-  
375 texts, music is produced and consumed in multifarious contexts, universally, that are completely unrelated  
376 to mating (e.g., work, healing, greeting visitors, mourning; Mehr *et al.* 2019).

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

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

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

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

## 402 **4.2 Music as a credible signal of cooperative intent**

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

407 We also agree with proponents of the social bonding hypothesis that musical abilities evolved because musical  
408 performances played an important role in cooperative sociality. But given the issues described above, we

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

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

409 find it more likely that music evolved to credibly signal decisions to cooperate that were already reached  
410 by other means, not to determine them. Cooperation often fails, making it useful to have a credible signal  
411 indicating that, by various (non-musical) means, one or more agents have decided to cooperate. Credible  
412 signals of cooperative intent, in turn, can produce decisions by signal receivers that benefit the signalers.

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

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

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

#### 422 **4.2.1 Synchronous coordinated music as a credible signal of coalition strength, size, and** 423 **cooperation ability**

424 In mammals, loud auditory signals are frequently agonistic, and territorial advertisements are a prime ex-  
425 ample (Gustison & Townsend 2015). Territoriality is common in taxa ranging from bacteria to vertebrates  
426 (Maher & Lott 2000; Smith & Dworkin 1994), including primates (Willems & van Schaik 2015). Territory  
427 owners have a consistent advantage over intruders, often retaining their territory without a fight (Kokko *et*  
428 *al.* 2006). It is thus in the interest of owners to advertise their residence in a territory to deter intruders  
429 and avoid a fight.

430 Territorial calls, which credibly signal that a territory is occupied, are found in many species, including birds,  
431 primates, and other mammals (Bates 1970; Gustison & Townsend 2015; Ladich & Winkler 2017; Wich &  
432 Nunn 2002). Loud primate calls are a plausible evolutionary precursor to human music (Geissmann 2000)  
433 because they appear to have existed in the last common ancestor of all primates and are often produced  
434 by both sexes and directed at both sexes (Wich & Nunn 2002). Some African apes display drumming-like  
435 behaviors as part of territorial signals (Goodall 1986; Hagen & Hammerstein 2009). In humans, vocal and  
436 instrumental music are reliably associated with war, procession, and ritual across a representative sample of  
437 societies (Mehr *et al.* 2019, Table 1); appears in political and military contexts with analogues to territorial  
438 signaling (Hagen & Bryant 2003; Hagen & Hammerstein 2009); is generally not sexually differentiated (see  
439 above); and, of course, is often loud.

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

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

455 Several primate species also produce highly synchronized song-like duets. As in birds, song-like calls are  
456 characteristic of species living in small, monogamous groups (Schruth *et al.* 2019). Although duetting

457 and coordinated vocalizations might have some role in pair-bond formation and strengthening in a few  
458 monogamous species, such as gibbons and titi monkeys, most evidence suggests these calls primarily function  
459 to exclude intruders and maintain spacing: they are territorial advertisements (Snowdon 2017). Experimental  
460 evidence suggests that higher levels of coordination in such signals indicate higher coalition quality. Duetting  
461 magpie-larks that had been paired for a longer time were more likely to produce highly coordinated displays,  
462 and in an experimental loudspeaker study on natural territories, playbacks of highly coordinated duets,  
463 which simulated territorial intrusions, evoked significantly higher song rates by resident males than poorly  
464 coordinated duets (indicating that the highly coordinated duets were perceived as more threatening; Hall &  
465 Magrath 2007).

466 Humans are both primates and social hunters, so we expect human ancestors to have advertised territory  
467 ownership in a similar fashion: using loud, coordinated vocalizations, perhaps with drumming. We propose  
468 that such territorial vocalizations are an evolutionary precursor to music, especially rhythmic music (Hagen  
469 & Bryant 2003; Hagen & Hammerstein 2009; cf. Merker 2000b). Signatures of this function might persist  
470 in modern humans in coordinated group dances that are universal across cultures (Mehr *et al.* 2019; Nettl  
471 2015; e.g., the Māori *haka*; Best 1924). The group music of Aka Congo Basin hunter-gatherers, for instance,  
472 is audible to groups living some distance away.<sup>12</sup>

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

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

486 Between-group cooperation likely created many new selection pressures. In particular, if human groups varied  
487 in the benefits they could provide other groups as allies, and the number of alliances a group could maintain  
488 was limited, a biological market would have arisen (Hammerstein & Noë 2016), wherein groups evaluated the  
489 coalition quality of potential allies by assessing their size, cooperation ability, and willingness to cooperate,  
490 and potential allies had incentives to exaggerate these qualities (Hagen & Bryant 2003; Hagen & Hammerstein  
491 2009). Common properties of music, especially those found in rhythmic, coordinated performances, provide  
492 a close fit to the necessary criteria for a credible signal of such otherwise difficult-to-observe group-level  
493 features. The time needed to create and practice group complex musical performances and achieve complex  
494 synchrony necessarily corresponds to a dimension of the underlying quality of the coalition: the amount of  
495 time coalition members have cooperated with one another.

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

498 There is substantial ethnographic, historical, and archaeological evidence of credible signaling of coalition  
499 quality among human groups, typically in the context of *feasting*. In feasting, two or more individuals share  
500 special types or quantities of foods, for a special purpose or event (Hayden 2014). In addition to food,  
501 feasting often includes special clothing, ornaments and other artifacts — and music and dance. Feasting has  
502 been documented in societies of all levels of social complexity, ranging from band-level hunter-gatherers to  
503 nation-states, including at archaeological sites throughout the Holocene (reviewed in Hayden & Villeneuve  
504 2011; Hayden 2014). While many functions of feasting have been proposed (Hayden 2014; Wiessner &  
505 Schiefelhövel 1998), there is widespread agreement that feasts play a critical role in the formation of alliances  
506 between groups (reviewed in Hayden & Villeneuve 2011; Hayden 2014). As Sosis (2000) observed, the goal

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<sup>12</sup>This statement is supported by personal interviews in E.H.'s fieldwork.

507 of ritualized foraging and feasting and other forms of food distribution is often to enhance the reputation of  
508 an entire group by displaying its productivity.

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

513 *Sharing [food] between camps is less frequent, but will occur when big game is killed and during massana forest*  
514 *spirit performances. When an elephant is killed, Mbendjele in the area go rapidly to where the carcass is lying.*  
515 *Large camps grow, and feasting and dancing go on until the elephant has been consumed. (Lewis 2017 p. 227)*

516 It is plausible that similar events regularly occurred during human evolution because there is archaeological  
517 evidence for domestic spaces, large game hunting, mass kills, cooking, large aggregations, burials, ornaments,  
518 use of pigments, and musical instruments throughout the Upper Pleistocene, with some evidence appearing  
519 earlier (Barham 2002; Conard *et al.* 2009; Kuhn 2014; Kuhn & Stiner 2019; Maher & Conkey 2019; Stiner  
520 2019, 2013, 2017).

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

533 On this view, music is clearly rooted in sociality. In contrast to the social bonding hypothesis, however, we  
534 predict that music does not *directly* cause social cohesion: rather, it signals existing social cohesion that was  
535 obtained by other means (Hagen & Bryant 2003 p. 30).

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

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

#### 546 **4.2.2 Infant-directed song as a co-evolved system for negotiating parental investment of at-** 547 **tention**

548 Contact calls are a common vocalization across many species, distinct from territorial signals. In primates,  
549 these include loud calls between separated group members, and frequent quiet calls during heightened risk  
550 of separation (e.g., in dense vegetation). Contact calls rank among the most diverse and complex call types  
551 across species (Bouchet *et al.* 2013; Leighton 2017), enabling individuals to recognize, estimate distance to,  
552 and maintain contact with their social partners (Kondo & Watanabe 2009; Rendall *et al.* 2000).

<sup>13</sup>Whereas 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).

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

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

569 Some aspects of human reproduction suggest that selection pressures for complex contact calls have increased  
570 relative to those in apes. First, human brain size is about triple that of other apes (Schoenemann 2006) and  
571 most brain growth occurs postnatally, implying that human infants are born helpless and have a very long  
572 juvenile period. Second, human forager interbirth intervals are about half those of chimpanzees (Marlowe  
573 2005; Thompson 2013), requiring ancestral human mothers to simultaneously care for multiple dependent  
574 offspring (in contrast to chimpanzee mothers, who typically care for a single dependent offspring). Third, un-  
575 like other great apes, humans rely heavily on alloparenting in a multilevel society, requiring ancestral human  
576 infants to establish relationships with multiple caregivers and vice versa (Hrdy 2009); unlike chimpanzee  
577 infants, ancestral human infants typically competed with multiple juveniles for the attention of multiple  
578 caregivers.

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

584 How does this conflict of interests play out? Infants have bargaining power to extract parental investment  
585 (in the form of material investment, like nursing, or parental attention); they demand attention by crying  
586 (for discussion of evolutionary scenarios, see Soltis 2004 and commentaries). Parents lack perfect access to  
587 their infant's internal state, so crying provides information about when investment can be provided. Care-  
588 eliciting infant vocalizations (e.g., distress calls, separation calls) are common across mammals (Newman  
589 2007), including humans, and mothers reliably respond to these vocalizations by providing care (Bornstein  
590 *et al.* 2017).

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

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

603 Here again we expect an evolutionary arms race, driven by partially conflicting fitness interests between

604 senders and receivers, producing an elaborated signal. We propose that this process could lead to key  
605 features of music: in particular, contrasting with the rhythmic features developing from territorial signals,  
606 we expect the rather more subdued context of soothing parent-infant contact calls to give rise to melodic  
607 features, tokens of which are the lullabies we sing to infants today (Mehr & Krasnow 2017).

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

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

630 Genomic imprinting disorders, where genetic dysregulation is differentiated by parent-of-origin, provide a  
631 unique test of the relation between a trait and its putative link to parental investment (Haig & Wharton  
632 2003). Angelman and Prader-Willi syndromes result from opposing dysregulation at the same genetic region  
633 (15q11-13), with a loss of genes expressing maternal interest resulting in Angelman syndrome, and the reverse,  
634 a relative loss of genes expressing paternal interest resulting in Prader-Willi syndrome. The behavioral  
635 phenotypes reflect the different effects of maternally vs. paternally inherited genes: infants with Angelman  
636 syndrome have a voracious appetite while nursing, are awake for more hours of the day than typically  
637 developing infants, and attract more attention via smiling than do typically developing children (Ubeda  
638 2008; Williams *et al.* 2006), increasing investment demands on the mother. Infants with Prader-Willi  
639 syndrome, in contrast, are born with low birth weight, sleep more than typically developing infants, and  
640 often lack a suckle reflex (Cassidy & Driscoll 2008; Holm *et al.* 1993; Peters 2014), with the opposite effect  
641 (decreasing investment demands on the mother).

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

649 Last, we also expect relationships between the acoustic features of non-human primate contact calls and  
650 human infant-directed song. While few data exist with which to test these relationships, preliminary findings  
651 suggest that similarities do exist. For example, baboon contact calls are harmonically rich, whereas alarm  
652 calls are harsh and noisy (Fischer *et al.* 2000); in a vocalization corpus from 21 human societies, infant-  
653 directed song was acoustically distinct from infant-directed speech across many pitch, rhythmic, phonetic,  
654 and timbral attributes (Moser *et al.* 2020), with a similar pattern of results to the acoustic differences  
655 between baboon contact calls and alarm calls. Moreover, several acoustic features driving these effects were

656 related to vocal exertion (e.g., temporal modulation, pitch rate, vowel rate), perhaps honestly signaling  
657 additional costs incurred by the signaler.

## 658 5 Discussion

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

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

### 665 5.1 Credible signaling may explain some basic features of music

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

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

676 These “building blocks” appear universally in music (Mehr *et al.* 2019; Nettl 2015; Savage *et al.* 2015), like  
677 “building blocks” of language (e.g., Baker 2001). They provide a grammar-like, combinatorially generative  
678 interface through which musical content can be created, improvised, and elaborated upon, through hierar-  
679 chical organization of meter and tonality<sup>14</sup> (Krumhansl 2001; Lerdahl & Jackendoff 1983), in fashions that  
680 themselves have universal signatures (Jacoby & McDermott 2017; Jacoby *et al.* 2019; Mehr *et al.* 2019).

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

### 683 5.2 Music is culturally evolved but cultural evolution has to start somewhere

684 We understand culture as information that affects individuals’ behavior and that is acquired from conspecifics  
685 through teaching, imitation, and other types of social transmission (Boyd & Richerson 2004; Tooby &  
686 Cosmides 1992). Because information is transmitted with some degree of fidelity through non-genetic means  
687 (e.g., memory, learning), information is cumulative. Some cultural information is passed on with greater  
688 frequency and higher regularity than other information. For example, social learners tend to pay attention  
689 to information sources that have established prestige more than sources that do not (Henrich & Boyd  
690 2002). Similarly, some information is easier to learn than other information; children exhibit interest about  
691 information associated with danger and retain it with greater fidelity and over longer periods than related  
692 information unassociated with danger (Barrett *et al.* 2016; Wertz 2019).

693 One characteristic of cumulative culture is ritualization (Lorenz 1966), analogous to co-evolutionary processes  
694 underlying animal communication systems (Krebs & Dawkins 1984). Cultural signals can develop extrava-  
695 gant physical features resulting from arms race dynamics, particularly in cases when there is a conflict of

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

696 interest between senders and receivers. Examples from modern environments include conspicuously branded  
697 luxury goods, which can signal wealth (Han *et al.* 2010); or businesses that engage in one-upmanship by  
698 incorporating exaggerated sensory features in competitive advertisements (Dunham 2011).

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

705 We propose that the adaptations proposed here provide a foundation for cultural-evolutionary processes.  
706 These traits — particular grammar-like structures, for instance, such as tonalities and meters — gravitate  
707 towards certain forms, or “attractors”, and away from others (Sperber 1996; Sperber & Hirschfeld 2004).  
708 These attractors will interact with evolved capacities for nonmusical traits resulting in sensitivity and at-  
709 traction to features in communicative acts that trigger them (e.g., musical phenomena that evoke the sound  
710 of an emotional voice), increasing variability in music.

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

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

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

### 729 **5.3 Auditory cheesecake: not wrong, but not right either**

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

737 In this sense, we agree with Pinker that many musical inventions are byproducts, plain and simple: auditory  
738 cheesecake is not wrong. But in light of the adaptations proposed here, auditory cheesecake isn’t right either:  
739 as we have argued, in at least two contexts, music exhibits design features consistent with adaptations for  
740 credible signaling, which give rise to a universal human psychology of music.

## 741 **6 Conclusions**

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

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

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

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

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

## 770 **Acknowledgments**

771 We thank Paul Seabright, the Institute for Advanced Study in Toulouse, and the Fondation Royaumont,  
772 whose meeting “Origins of music in non-state societies” sparked the idea for this paper; and Mila Bertolo,  
773 Courtney Hilton, Cody Moser, and Manvir Singh for feedback on the manuscript.

## 774 **Funding statement**

775 The “Origins of music in non-state societies” meeting was supported by the Agence Nationale de la Recherche  
776 (Investissements d’Avenir ANR-17-EURE-0010). S.A.M. is supported by the Harvard Data Science Initiative  
777 and the National Institutes of Health Director’s Early Independence Award DP5OD024566.

## 778 **Conflicts of interest**

779 None.

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