

Filippi, P., Hoeschele, M., Spierings, M., & Bowling, D. L. (2019). Temporal modulation in speech, music, and animal vocal communication: Evidence of conserved function. *Annals of the New York Academy of Sciences*, *1453*, 99–113. <https://doi.org/10.1111/nyas.14228>.

Gould, S. J. (1991). Exaptation: A crucial tool for an evolutionary psychology. *Journal of Social Issues*, *47*(3), 43–65. <https://doi.org/10.1111/j.1540-4560.1991.tb01822.x>.

Hoeschele, M. (2017). Animal pitch perception: Melodies and harmonies. *Comparative Cognition & Behavior Reviews*, *12*, 5–18. <https://doi.org/10.3819/CCBR.2017.120002>.

Hooper, P. L., & Miller, G. F. (2008). Mutual mate choice can drive costly signaling even under perfect monogamy. *Adaptive Behavior*, *16*(1), 53–70. <https://doi.org/10.1177/1059712307087283>.

Jones, A. G., & Ratterman, N. L. (2009). Mate choice and sexual selection: What have we learned since Darwin? *In The Light of Evolution*, *3*, 169–190. <https://doi.org/10.17226/12692>.

Machin, A., & Dunbar, R. (2011). The brain opioid theory of social attachment: A review of the evidence. *Behaviour*, *148*(9), 985–1025. <https://doi.org/10.1163/000579511X596624>.

Mehr, S. A., Krasnow, M. M., Bryant, G. A., & Hagan, E. H. (2020). Origins of music in credible signaling. *Brain and Behavioral Sciences*.

Miller, G. (2000). Evolution of human music through sexual selection. In S. Brown, B. Merker & C. Wallin (Eds.), *The origins of music* (pp. 329–360). The MIT Press.

North, A. C., & Hargreaves, D. J. (1999). Music and adolescent identity. *Music Education Research*, *1*(1), 75–92. <https://doi.org/10.1080/1461380990010107>.

Puts, D. A., Hill, A. K., Bailey, D. H., Walker, R. S., Rendall, D., Wheatley, J. R., ... Ramos-Fernandez, G. (2016). Sexual selection on male vocal fundamental frequency in humans and other anthropoids. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1829), 1–7. <https://doi.org/10.1098/rspb.2015.2830>.

Savage, P. E., Loui, P., Tarr, B., Schachner, A., Glowacki, L., Mithen, S., & Fitch, W. T. (2020). *Behavioral and Brain Sciences*. <https://doi.org/https://doi.org/10.1017/S0140525X20000333>.

Tarr, B., Launay, J., & Dunbar, R. (2014). Music and social bonding: “self-other” merging and neurohormonal mechanisms. *Frontiers in Psychology*, *5*, 1096.

Titze, I. R. (2000). *Principles of voice production*. National Center for Voice and Speech.

Williams, G. C. (1966). *Adaptation and natural selection: A critique of some current evolutionary thought*. Princeton University Press.

Q42 Q43  
Q44

## The evolution of music: One trait, many ultimate-level explanations

Edgar Dubourg<sup>a</sup>, Jean-Baptiste André<sup>a,b,c</sup> and Nicolas Baumard<sup>a,b,c</sup> 

Q1

<sup>a</sup>ENS-PSL, Paris, France; <sup>b</sup>CNRS, Paris, France and <sup>c</sup>EHESS, Paris, France.  
06 32 43 37 51  
[edgar.dubourg@gmail.com](mailto:edgar.dubourg@gmail.com),  
[jeanbaptisteandre@gmail.com](mailto:jeanbaptisteandre@gmail.com) [nbaumard@gmail.com](mailto:nbaumard@gmail.com)

doi:10.1017/S0140525X20001156, e0

### Abstract

We propose an approach reconciling the ultimate-level explanations proposed by Savage et al. and Mehr et al. as to why music evolved. We also question the current adaptationist view of culture, which too often fails to disentangle distinct fitness benefits.

Savage et al. focus on the social functions of music-related behaviors, but they don’t explain why musicality, and not music is often preferred to other things such as food, perfume, and painting, to increase social bonding in humans. Similarly, Mehr et al.’s article focuses on the adaptive nature of musicality, which might well be rooted in credible signaling for coalition strength, but they don’t expand on how and why music develops new social functions beyond coalition signaling. We argue that both hypotheses need each other to provide a comprehensive and consistent

evolutionary understanding of music. We aim at showing why this is the case by disentangling three evolutionary steps.

The first step should account for the fitness benefits of producing music-like sounds in the first place. Mehr et al. provide evidence that contact calls and territorial advertisements may have been the evolutionary precursors of music-related cognitive processes and behavior in humans. Coordinated rhythm, according to Mehr et al., enhanced fitness in local environments when humans evolved because it credibly signaled high level of inter-individual coordination. Their hypothesis is seducing because it explains both how music could emerge by natural selection (because it provides a unique way to signal coalition that food or smell cannot provide) and the cognitive constraints such an evolution would have put on all future music-related inventions (they need a least some rhythm). This hypothesis explains why humans evolved cognitive mechanisms to detect and enjoy music-like inputs, at the proximate level. However, it doesn’t explain why music evolved culturally with much variability and extend beyond situations of coalitional signaling.

This is the second step. In many species, once a behavioral or phenotypic trait has emerged, it can be co-opted for new adaptive functions. This is very often the case, in particular for traits involved in signaling, as signaling evolves by recycling traits that have first evolved for other functions (Krebs & Dawkins, 1978; Lorenz, 1966). For instance, the female frog *Physalaemus pustulosus* had pre-existing preferences for lower-frequency chuck sounds, and then males evolved the ability to produce such sounds to exploit this sensory preference (Ryan, Fox, Wilczynski, & Rand, 1990). In nonhuman animals, this recycling usually emerges by natural selection.

But, it can also emerge by cultural evolution. Humans are very plastic. Thanks to their cognitive flexibility, they can recycle existing behaviors and preferences and use evolved preferences (e.g., for sugar, sex, social information, and musicality) to shape sophisticated cultural things (e.g., cheesecakes, pornography, stories, and music) that other people enjoy consuming. As many have noted, musicians, singers, and dancers honestly signal skills and qualities through their performances and this leads to sexual, reputational, or material benefits (André, Baumard, & Boyer, 2020; Miller, 2001). Even in modern industrialized societies, musicians and singers take advantage of their productions with economic benefits. We suggest this underlies the producers’ motivation to craft such cultural items in the first place.

This second step crucially explains why music appeared in human culture: because (1) humans had evolved a preference for music-like sounds and (2) people adaptively used this preference to do other things. However, it does not explain why, according to many empirical studies reported by Savage et al., music promotes social bonding.

The third step implies that signaling is not necessarily selfish. At least in small-scale societies, consumers should have fitness benefits too. The most obvious one is the acquisition of the information about the musicians, inferred from their music. A similar phenomenon is well described in the nonhuman animal literature: Peacocks impress peahens with their large and beautiful tails, but the peahens are adaptively drawn to them because the size of the tails honestly signal the genetic quality of the peacocks, leading to a more informative sexual partner choice (Petrie, 1994; Petrie, Tim, & Carolyn, 1991; Zahavi, 1975). Similarly, in small-scale societies, consumers know how skilled producers of music are merely by listening to their music, and they can arguably better choose skilled cooperative agents or mating partners. In large-

1244  
1245  
1246  
1247  
1248  
1249  
1250  
1251  
1252  
1253  
1254  
1255  
1256  
1257  
1258  
1259  
1260  
1261  
1262  
1263  
1264  
1265  
1266  
1267  
1268  
1269  
1270  
1271  
1272  
1273  
1274  
1275  
1276  
1277  
1278  
1279  
1280  
1281  
Q45  
1282  
1283  
1284  
1285  
1286  
1287  
1288  
1289  
1290  
1291  
1292  
1293  
1294  
1295  
1296  
1297  
1298  
1299  
1300  
1301  
1302  
1303  
1304  
1305

**Table 1.** Fitness costs and benefits of music-related behavior on both producers and consumers of music, with the framework from social evolution theory (André et al., 2020; Hamilton, 1964)

		Effect on recipients	
		Positive	Negative
Effect on actor	Positive	<p><i>Mutualism</i></p> <p>(1) Producing artificial signal of coordination to send and receive signals of personal quality</p> <p>(2) Producing artificial signals of coordination to create bonding for mutual benefit (e.g., sport)</p>	<p><i>Selfishness</i></p> <p>(1) Producing artificial signal of coordination to send and receive false signals of personal quality</p> <p>(2) Producing artificial signals of coordination to create bonding for manipulation (e.g., supermarket)</p>
	Negative	<p><i>Altruism</i></p> <p>(1) Producing artificial signals of coordination in the form of lullabies to provide social support to children</p>	<p><i>Spite</i></p>

scale societies, consumers can take advantage of the fact that other people are also attracted by music to signal preferences, skills, and qualities of their own to other people (Bourdieu, 1979; Veblen, 1899).

But, there is another social use of music that relates to the first adaptive function of musicality. Coordinated rhythm evolved to be perceived as a credible signal of coalitional bond. Thus, when we listen to coordinated rhythm outside an agonistic context, we cannot help but analyze this signal as a cue that, somehow, we are part of a well-coordinated coalition. Hence, we feel the pleasure of having social support. This would explain why, by default, music makes people cheerful: it mimics the signal that we have coalitional allies (exactly like pornography is arousing because it mimics the signal that we have an opportunity to reproduce). Humans will thus use music in all cases when they need to artificially create social bonding, with actual fitness consequences (Table 1). We propose that most of the findings reported by Savage et al. are best understood in light of this adaptive recycling.

In sum, we believe evolutionary approaches of cultural items such as music should carefully distinguish fitness costs and benefits from separate evolutionary steps. In that sense, we believe that the publication of these two articles as a pair is an exciting event in the field, if we prevent ourselves from setting them against each other.

**Financial support.** This study is supported by FrontCog ANR-17-EURE-0017.

**Conflict of interest.** None.

## References

- André, J.-B., Baumard, N., & Boyer, P. (2020). *The Mystery of Symbolic Culture: What fitness costs? What fitness benefits?* 18. <https://osf.io/kdh7t/download?format=pdf>.
- Bourdieu, P. (1979). *La distinction: Critique sociale du jugement*. Éditions de Minuit.
- Krebs, J. R., & Dawkins, R. (1978). Animal signals: Mind reading and manipulation. In *Behavioral ecology: An evolutionary approach*. Blackwell Scientific Publications.
- Lorenz, K. Z. (1966). Evolution of ritualization in the biological and cultural spheres. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 251(772), 273–284.

- Petrie, M. (1994). Improved growth and survival of offspring of peacocks with more elaborate trains. *Nature*, 371(6498), 598–599. <https://doi.org/10.1038/371598a0>.
- Petrie, M., Tim, H., & Carolyn, S. (1991). Peahens prefer peacocks with elaborate trains. *Animal Behaviour*, 41(2), 323–331. [https://doi.org/10.1016/S0003-3472\(05\)80484-1](https://doi.org/10.1016/S0003-3472(05)80484-1).
- Pinker, S. (1997). *How the mind works (Norton pbk)*. Norton.
- Ryan, M. J., Fox, J. H., Wilczynski, W., & Rand, A. S. (1990). Sexual selection for sensory exploitation in the frog *Physalaemus pustulosus*. *Nature*, 343(6253), 66–67. <https://doi.org/10.1038/343066a0>.
- Veblen, T. (1899). *Theory of the leisure class* (New ed.).
- Zahavi, A. (1975). Mate selection – A selection for a handicap. *Journal of Theoretical Biology*, 53(1), 205–214. [https://doi.org/10.1016/0022-5193\(75\)90111-3](https://doi.org/10.1016/0022-5193(75)90111-3).

## Human evolution of gestural messaging and its critical role in the human development of music

Martin F. Gardiner 

Brown University, Providence, RI 02912.

[martin\\_gardiner@brown.edu](mailto:martin_gardiner@brown.edu)

doi:10.1017/S0140525X20001697, e0

### Abstract

By fostering bonding (Savage et al., 2020), music illustrates marvelously its ability to induce emotional experience. But, music can induce emotion more generally as well. To help to explain how music fosters bonding and induces other emotion, I propose that music derives this power from the evolution of what I term “gestural messaging.”

The subjective experience music provides (Dewey, 1934) is what fosters bonding (Savage et al., 2020). Music builds bonding by inducing joint emotional experience, but also, as I now discuss, induces emotional experience more broadly.

Often neglected by psychology and brain research, brain development of subjective awareness and its functional significance is