Stephen Davies, Philosophy, University of Auckland

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Evolution

Abstract and Key Words

Making or listening to music is pan-cultural, nearly universal, and highly valued. Musical behaviors probably appeared between 500,000 and 60,000 years ago. The more recent date captures the era when *H. sapiens* spread globally from Africa. The older date corresponds with a time when song might have produced individual or social benefits and the physiological and cognitive conditions for its production were present (in our predecessor, *H. heidelbergensis*). Music is so multi-functional, however, that it is not clear if it was an evolutionary adaptation (as opposed to a byproduct or non-biological technology) or, if so, what it was an adaptation for.

Musicality, evolution, fitness, adaptation, spandrel, technology, song, language, sound processing

Evolution

When and why did music making first originate? We do not know. Music can be made without the use of artefacts that would persist in the archaeological record And it can be made with items that do persist, such as resonant stalagmites (Montelle 2004), that are not usually recognizable for their musical adoption (but see Dams 1985 on when this recognition is possible). For these reasons, music could have been practiced for millennia in prehistory without this being evident now. As a result, the discussion of music's origins and evolutionary significance must be speculative. This speculation need not be entirely idle, however, when considered against the backdrop of a number of relevant issues.

The issue of music's origins and functions is not directly philosophical, I allow. But applied philosophy is concerned with the critical evaluation of arguments and of the bearing of complex bodies of evidence, especially where the theories involved tend to outstrip the available empirical support. So the writings on this topic, which come from a wide spread of disciplines, are fair game for philosophical discussion.

The first task is to consider evidence for the view that musicality has ancient, biological roots. Is music making pan-cultural? Do all and only humans make music? Despite their manifest differences, are there any features common to the musics of the world?

Considering possible connections between our music behaviors and our evolved human nature involves delving into the conditions under which musicality originated and first developed. It also involves trying to distinguish modes of auditory processing and vocalization that are primarily musical from those that are primarily linguistic (assuming this can be done in a manner that is not ethnocentrically question-begging, as is doubted in Wachsmann 1971; Robertson-DeCarbo 1976). And it also requires separating both of these from the auditory processing with which we generally make sense of our noisy world.

There are two overall strategies that can be adopted in trying to argue that music originally served as an evolutionary adaptation by improving the reproductive success of those who were biologically inclined toward making it over those who were not, with the eventual outcome that there was selection for musicality and music making.

The first approach is to look at the development of the physiological conditions that were necessary for musicality and that probably marked the emergence of musical behaviors. Of special importance here would be the existence of inherited neural circuits dedicated to musical functions and the timing of their appearance. But, as we will see, there is not agreement about whether these exist or about whether their non-existence shows that music is not an adaptation. One complicating factor is the brain's inherent plasticity. Musical practice or exposure can change it considerably, so it is not always easy to distinguish inherited from acquired structures. A second major complication concerns the fact that both language and music share many parts of the brain and we are not certain which came first.

The second approach considers the evolutionarily valuable functions music might have served at the time when first it appeared. For instance, did it create a mutual bond between mothers and their helpless, highly dependent babies? Or was the musician more sexually desirable than his non-musical lookalike? (I write "his" deliberately; according to the common version of this second theory, music is a form of male courtship display.) Or did music cement the group and confirm its common values? Or was some combination of effects involved? One problem with this second approach is that music is so multi-functional, sometimes in conflicting ways—it can be used both to include others and to exclude them, for example—that it is difficult to identify what was initially beneficial to the fecundity of its possessors.

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Is music apparent in every known culture and do many members of the culture engage with it?

If music is not only pan-cultural but also practiced universally, and if the world's many musics share crucial features and parameters, this would suggest, at the very least, that it is an ancient practice and that, most likely, it was subject to selection by evolutionary forces. This is not to deny cultural influence and wide differences between musics, or the effects of self-reflection and historical change on music of any given place, but is to look past these to seek some underlying core.

No culture has been discovered without music (Brown 1991; Nettl 2000). The music of a culture is usually distinctive to some degree and there is no evidence that music was spread originally through cultural contact from a primary source. Moreover, though one culture might favor rhythmic complexity where another features rich harmony, the music of all cultures is highly developed and is often accompanied by music-theoretic terms and notions. Music everywhere is valued. Skilled performers and composers are esteemed. (Even in cultures in which new songs are dreamed and come as gifts of the gods, those who dream the better songs are recognized for doing so.) Not only is music pan-cultural, engagement with it is virtually universal (Blacking 1973). Whether made in groups, pairs, or singly, in hunter-forager cultures everyone participates. They sing melodically, beat out rhythms, or dance in time. Even in the modern West, where amateurs are distinguished from professionals and listening is more common than performing, most people sing along with their favorite tunes where this is socially acceptable, join in with the national anthem, and so on.

Despite their many, manifest differences, do the musics of the world's cultures share any universal features that are not a consequence of the domination of any one culture or of cultural transmission?

A number of structural principles are regularly put forward as more or less universal. Octaves are treated as equivalent (that is, as the same note, but higher or lower); scales are organized with 5-7 notes, a centering tone, some uneven intervals, and usually a perfect fifth or fourth; simultaneously sounded notes with low, simple ratios are perceived as more stable and less tense than ones with high, complex ratios. Moreover, all listeners seek pattern and continuity according to standard Gestalt principles that track repetition, sequence, and closure. (Representative references are Nettl 2000; Justus and Hutsler 2005; McDermott and Hauser 2005; Higgins 2006; Stevens and Byron 2009; Stevens 2012; Brown and Jordania 2013. For an apparent exception to the preference for simple harmonic ratios, see McDermott et al. 2016.) Some aspects of temporal processing in music appear to be universal (Drake and Bertrand 2003) as do proportional tempo-keeping (Epstein 1988), perhaps mirroring the pace of physiological processes.

The claim about universality might be questioned. The intervals of the Javanese slendro scale are all approximately equal (though the differences are not neglible (Perlman and Krumhansl 1996)). And modernist Western classical music might use all 12 notes of the equal-tempered scale, avoid treating any as a centering tone, shun metric regularity, repetition, and closure, and eschew harmonies with simple ratios (such as fifths and fourths). What is probably true is that at least one of the musical kinds in any culture conforms to the stereotype. The Javanese pelog scale has unequal intervals and most popular Western music is based on the major scale, a regular meter, and easily followed patterns.

One musical type with a claim to universality is the lullaby. Typically, lullabies have descending melodic contours and soothing, smooth, expressive qualities (Fernald 1992; Unyk et al. 1992; Trehub et al. 1993a, 1993b). The expressive effect of lullabies is quite likely a result of their elaboration of the prosodic features of infant-directed speech—a highly expressive and inflected mode of vocalization adopted by parents in all cultures when they interact vocally with newborns. In that case, the universal effects are not specific to the fact that lullabies are music, but depend rather on musical aspects of a vocal form. Infant-directed speech would not normally be regarded as music. It is musical, however, to the extent that it highlights pitch differences and rhythmic repetition, even if it does not possess the full range of features (tonality, regular tempo, metre, rhythm, balanced phrasing) that are characteristic of music's most familiar and basic forms. But as is discussed below, it is a possible precursor both of music and of language.

Cross-cultural agreement on the expression of some basic emotions in music has been presented as indicating a universal basis for such recognitions (Fritz et al. 2009). (For a more sober assessment of the cross-cultural evidence, see Thompson and Balkwill 2010, and for criticism of a number of published studies, see Davies 2011.) It seems unlikely that the expressive character of all foreign music is universally accessible, however, since some such music can be very difficult for foreigners to follow and anticipate successfully. But the relevant universal might be this: to those at home with its given type, music is experienced as expressive of emotion and among such listeners there is high agreement at a general level about what is expressed.

Staying with the cross-cultural, even if we cannot always recognize the expressive tone of foreign music or appreciate its intricacies, it is perhaps noteworthy that foreign music almost always is recognizable as music (just as foreign languages are almost always recognizable as languages). And through exposure, we can bootstrap our way into foreign music (Huron 2006:47–55; Higgins 2012:ch. 5) and, over time, grasp its conventions and principles. Just as a listener can move with ease from one musical style to another—from blues to jazz to medieval church music to nineteenth-century Romantic classical music—so she might grasp Chinese opera, Japanese kabuki, and African thumb-piano music.

How do infants respond to music?

If babies displayed an innate understanding of music, that would surely suggest that it is a hard-wired capacity. The evidence for this is equivocal or negative, however.

Babies respond differently to "good" and "bad" melodies, to "concords" and "discords" and it is sometimes said that their reactions have an emotionally valenced character (according to the frontal hemisphere in which the response is processed, the one being associated with positive evaluations or experiences and the other with negative ones) (Trehub et al. 1990; Trainor and Trehub 1994; Trehub 2003a).

It is not at all straightforward to identify these reactions to musical stimuli as evidence of innate musical predispositions, however. Even newborns might not be musical innocents; they hear music when in the womb. And the experiments tend to be performed on babies of 6-9 months, who have already been exposed to music. Besides, the studies show that babies pay more (positive) attention to some musical sounds than to others, but this does not show that these reactions are to music as such, as opposed to relying on processing directed to the general environment or anticipating the comprehension of language. (Reservations along these lines are expressed in Justus and Hutsler 2005, McDermott and Hauser 2005, and Patel 2008:377–86. These authors similarly object to studies that infer from individuals whose musicality is affected by neural deficits to what is innate and music-specific in undamaged people.)

Nevertheless, babies as young as eighteen months make up melodies structured more in terms of contour than pitch (Ball 2010) and pitch-structured, metrically regular vocalizing is in place before a child is 5 years of age (Trehub 2003a, 2003b). Compared to their acquisition of reading and writing, music behaviors emerge spontaneously in young children.

How do non-human animals respond to music?

Plainly many non-human animals can hear music, but it is not clear how they cognize it (Wallaschek 1891). For instance, cotton-top tamarins do not show a preference for consonance over dissonance (McDermott and Hauser 2005).

The experience of notes at the octave being the same is crucial to how humans hear music. Apparently octave equivalence is experienced also by a number of non-human animals. When trained to respond (e.g., by salivating in anticipation of food) to a note of a given pitch, a number of animals respond more (e.g., salivate more) to the octave than to any other "wrong" note (Lerdahl and Jackendoff 1983). Rhesus monkeys identify 6- to 7-note musical passages as the same when they are transposed to the octave or double octave, but not when transposed to the fifth or twelfth (Wright 2000), but it is not clear how to interpret this result. (Or what is the influence of their living in labs with piped music or TVs, see McDermott and Hauser 2005.) A number of bird species have absolute pitch (Weiseman et al. 2006), as do a (small) minority of humans.

The relevant behaviors and discriminations fall far short of the human reaction to and following of music. (For instance, we recognize melodies transformed and transposed in many ways, and absolute pitch is not necessary for this capacity.) And dogs and monkeys do not act in musical ways outside the experimental situation. Rather than providing evidence of animal musicality, these data are better interpreted as implying that many of the pitch recognitions and experiences crucial to human's musical experience first evolved in other, older species as part of general auditory processing.

One distinctive aspect of the human response to music is entrainment—matching movement to the pulse of the music (and perhaps also matching mood to its expressive character). No other species are known to entrain in this way in the wild. However, individual parrots have been known to "dance" in time with music (Fitch 2009; Patel et al. 2009). When a Californian sea lion was trained to bob in time with music (Cook et al. 2013), this unusual phenomenon was widely reported in popular news media.

Do any non-human animals make music?

There can be no denying that some creatures—most notably, birds—make attractive musical sounds. Those who would claim songbirds as musicians (for example, Hartshorne 1973) rightly point out that species' songs are inherited only in outline and learning is involved in perfecting them, with the result that song dialects are common (Whaling 2000). But I would expect more for music: a freedom of invention or rendition that results in generativity or creative development. Change in birdsong is not of this kind, but looks instead to be random and accidental (Davies 2012, but see Merker 2012; for more general arguments and reference to other animals, see Mâche 2000; Marler 2000). By contrast with birdsong, something like generativity occurs in Humpback whale song, with the "song" changing significantly each season (Payne 2000; Merker 2012).

We can leave the issue undecided, because it is plain that our species is the most emphatically musical and that songbirds and whales are not the ancestors from whom we inherited our musicianship. About six million years ago we shared an ancestor in common with the great apes; one branch led from it to them and another to us. Singing evolved on several different occasions in the primate lineage (Geisseman 2000) but it is not apparent in the line from our common ancestor to the apes, whose vocalizations give vent to feelings but lack musical control or complexity. Accordingly, we should anticipate that musicality arose either with us or with an earlier species on our (the hominin) evolutionary branch.

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The point of the questions so far asked was to establish if all and only humans make music and if there is evidence of a music-specific, biologically inherited component to our doing so. The data are inconclusive, but they are sufficiently suggestive to encourage us to dig more deeply.

The ethologist Ellen Dissanayake (1988) suggests that, if a pattern of behavior is *universal*, *ancient*, and *intrinsically pleasurable*, this provides strong evidence that the behavior was selected by evolutionary forces in the past. Indeed, she thinks these three qualities are the hallmarks of evolutionary adaptations. (This last claim might go too far—see Davies 2012:186–7—though evolutionary explanations will be appropriate to many behaviors with these features.)

Music apparently meets these conditions. As has been argued already, music is pan-cultural and universal, as well as being highly valued because, among other things, it is a source of pleasure (Brattico et al. 2009). Musical behaviors are rewarding to the extent of often being self-motivating. Is music making also ancient? The earliest surviving musical instruments crafted for their musical function are about 40,000 years old (Conard et al. 2009). But these are sophisticated artefacts and the improvisational use of what came to hand as beaters and rattles is likely much older and older still, surely, is the use of the voice as a musical instrument (Gamble 2012; Morley 2013).

In addition, we might reason as follows: given that sophisticated but different forms of music are found in *every* culture and people, though the groups concerned have often been isolated for a very long time; and given also that our species originated in Africa and later spread to other parts of the globe; then sophisticated forms of music must have existed earlier in Africa. Given its ubiquity and complexity, music left Africa with *Homo sapiens* emigrants, rather than being invented subsequently in every isolated community. (A similar argument has been applied to the history of syntactically complex languages (Gibson 2007; Collins 2013).) So, when did members of our species leave Africa? After an earlier visit by *Homo sapiens* to the Middle East and perhaps further, the current consensus puts the global spread of our species as initiated from Africa about 60,000 years ago (Wells 2002; Finlayson 2009). By the earlier reasoning, sophisticated forms of music must have pre-dated that.

This conclusion is disputed by Gary Tomlinson (2015), who dates discrete-pitch, metered music to 40–20 thousand years ago, which was a period when widely dispersed, small groups of *Homo sapiens* occupied much of Europe and Asia, as well as Africa. He suggests that this form of music was invented independently in many places and cultures. I find the previous argument more persuasive than this alternative, however. And we shall shortly get to further, indirect evidence of music's antiquity.

The approach we turn to next considers the physiological (and social) underpinnings of musical production and appreciation.

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At what stage of human evolution were the physiological, cognitive, and social resources necessary for music production and appreciation (that is, musicality) in place?

Extended musical vocalization in hominins requires fine breath and tongue control, a descended larynx, and the capacities to control pitch, to generate beat-structured rhythmic patterns, and to recognize and remember occurrences of these. Relevant physiological evidence takes several forms: fine tongue control requires an enlarged hypoglossal canal and breath control demands extensive thoracic nerve structures. Hearing should be sensitive to the pitch-bands that are most prominent in speech and the environment. The relevant cognitive resources can be suggested by the external shape of the brain as reflected by the inner cranium and by brain size more generally. The social circumstances conducive to the production of music would be ones in which members of groups interacted and communicated extensively and in which coordination and cooperation were vital. Entraining with the beat of the music and with the movements of others also would be crucial to marry music with dance.

The required physiological capacities and social conditions for music making may have been in existence some 500,000 years ago (Mithen 2005; Gamble 2012; Morley 2013). Our species, *Homo sapiens*, is about 190,000 years old. We descended from a previous species, *Homo heidelbergensis*, which also gave rise to the Neanderthals (*Homo neanderthalensis*) in Europe about 300,000 years ago. Our species overlapped with Neanderthals in Europe from about 40–30,000 years ago, when they became extinct. So, if we extrapolate from the capacities to the behaviors, it may be that the first musicians were an ancestral form of humans. (For reservations about just this kind of extrapolation, see Dubreuil 2011.) *H. heidelbergensis* had large brains, was highly social, and traded goods over hundreds of kilometers (Stringer 2011). Intellectually and physically, they had what it takes to make and enjoy listening to music. Meanwhile, when we met our cousins, the Neanderthals, it is possible that they sang. (There is no evidence of Neanderthal musical instruments, however, while our species was making them at the time.)

It might be objected, as does Tomlinson (2015), that these ancestral species did not have the cognitive sophistication to produce what we would recognize as music. He reasons that music requires combinatorial and hierarchical modes of cognition, and considers as evidence for when these arose the much later emergence of multi-part tools and the like. In fact, though, there is evidence of composite (multi-part) tools as long as 285 thousand years ago (McBrearty 2007). And in hunter-forager rituals, children standardly join the group's singing and dancing long before they master abstract modes of thinking. Moreover, the human capacity for combinatorial and hierarchical modes of cognition, rather than being foundationally abstract and symbolic, may be better interpreted as a consequence of the emergence of a much older capacity for motor rehearsal (see Stout and Chaminade 2012). So Tomlinson's criteria for music making might be inappropriate.

Debates about the dating in our species of the emergence of "symbolic thinking" (aka psychological or behavioral modernity) are too complex to consider here, but it is often associated in the literature with religion and art, including music, the adoption of insignia and decorations, burial with grave goods, and so forth. There is no unambiguous archaeological evidence of such behaviors in *H. heidelbergensis*. And while it is now widely agreed that Neanderthals were unfairly disparaged in the past, only a comparatively few signs of such behaviors became apparent in them, and then mainly after their contact with us (Finlayson 2009).

In response to this concern, Iain Morley (2013) makes the reasonable case that music making of a quite developed kind can be more about emotional expression and group coordination and entrainment than about abstract thinking. Individuals with mental deficits can be highly musical. And as just noted, even young children can be drawn to participate fully in the group's dancing and singing. Music making is a practical skill that calls for "know how" but need not require "knowing that, " the capacity verbally to cognize and articulate what is done (Davies 2004). What matters, then, is not whether *H. heidelbergensis* was a great thinker but whether she was inclined to vocalize her feelings in a musical fashion, perhaps while interacting with her baby or while cooperating with her fellows. If her group celebrated their successes and mourned their losses, these ancients could have found applications for the musical potentials that they possessed.

So we have a timeframe for music's origins: some time after about 500,000 years ago and before about 60,000 years ago. This is consistent with more general work on the development of communication (see Levinson and Holler 2014).

Are there any music-specific neural circuits? Is there a unique combination of neural circuits dedicated to making and processing music?

If some neural-circuits were exclusive to music making or appreciation, this would provide strong evidence that such behaviors are the product of evolutionary selection. Unfortunately, there is no agreement on the matter (see Rebuschat et al. 2012). Some think there are such circuits. (For example, S.

Brown 2000a; Huron 2003; Peretz and Coltheart 2003; Feist 2007). Others do not. (For example, Justus and Hutsler 2005; Patel 2008; Ball 2010). The evidence is inconclusive (McDermott and Hauser 2005). Morley (2013) suggests that what might be distinctive to music is the *combination* of different neural regions that it activates.

One difficulty lies in distinguishing acquired neural circuits from innate ones (McDermott and Hauser 2005); the brain is very plastic. Another problem is that music might piggyback on neural structures evolved originally for processing the wider soundscape. A third is the huge overlap in brain regions used both by language and by music (Justus and Hutsler 2005; Patel 2008; Koelsch 2012; Rebuschat et al. 2012, pt. 4; Arbib 2013, pt. 4). Moreover, both music and language are neurally processed in similar ways (Patel 2008; Fenk-Oczlon and Fenk 2009; Koelsch 2012). What look like modules for processing rhythmic strings, for example, might have evolved to service language, not music. And because we are not sure whether or not music preceded language or if they shared a common ancestor, as is discussed further below, we cannot be sure which had first claim, as it were, on the brain.

What in music draws on processes evolved for parsing the regular soundscape?

As we have already seen, recognition of octave equivalence is present to some degree in the auditory experience of some other animals, so that particular aspect of *Homo* auditory perception could easily pre-date musical behaviors. And we seek regularity and pattern in the environment at large, so our detection of metric regularity and rhythmic pattern and of tonal regularity and melodic organization are probably grounded in more general auditory capacities (Wallaschek 1891; Janata and Grafton 2003). Our tendency to segment the soundscape into streams (Bregman 1990) also finds obvious application in following music. An interest in the timbral qualities of sounds must have been present in precursor species, because timbre provides crucial evidence of how a sound is produced and what makes it. More generally, the tendency to hear sounds in connection with sound-makers must be ancient. We hear in and through sounds the actions—beating, sawing, chopping, filing—that go into their making. The pitch of a sound also provides evidence of the size of the creature or thing that made it, as does its amplitude, at least sometimes. As well, imitative learning is a deeply rooted *Homo* disposition (Sterelny 2012), so vocal imitation of other people and of natural sounds most likely came prior to music as such.

What in music draws on processes evolved for speech, including its prosodic features?

This is a trick question, of course. It should be reversed if music came before language. But we should say this much. Both provide semantic and expressive content, but to very different degrees. Music without accompanying words can be suggestive of mood, motion, and of distinctive sound-makers, and, as a result of conditioning or its prior association with significant occasions, it can bring other things or events to mind. But in general, music is poor as a medium for communicating information when compared to language, except with respect to its expressiveness. Meanwhile, the power of language to impart meaning is in part gestural and prosodic (Corballis 2003; Davies 2014). Musical features with the same qualities as prosodic aspects of expressive speech express the emotions conveyed in such speech (Juslin and Laukka 2003; but on differences between speech and musical prosody, see Sunderberg 2012).

Which came first, music or language, or did both share a common predecessor (known as protolanguage or musilanguage)?

The short answer is that we are not sure. It was suggested previously that the earliest musical behaviors might date to 500,000 years ago. But almost all the physiological capacities essential to musicality are also essential for language and speech. Moreover, the *Homo sapiens* variant of the FOXP2 gene, which seems to be essential in the mastery of speech (Enard et al. 2002), was shared with Neanderthals (Krause et al. 2007; Green 2010), which implies that it was also possessed by our common ancestor, *H. heidelbergensis*. Broca's area, a part of the brain that deals importantly with language (along with the right hand and music), was well-developed in both *H. heidelbergensis* and *H. neanderthalensis*. So some form of language could also date to 500,000 years ago (Wells 2010; Collins 2013).

Some theorists regard music as a by-product of the evolution of language. (For example, Spencer 1966, vol. 14 [1857]; Pinker 1999; Barrow 2005; De Smedt and De Cruz 2010.) Others see it as originating out of pre-linguistic vocalizing and hence, as prior to language. (For instance, Darwin 1880, pt. 3, ch. 19:572; Brown 2000a; Merker 2005; Mithen 2005; Fenk-Oczlon and Fenk 2009; Gamble 2012.) A more specific version of this last theory identifies infant directed speech as the precursor to music. (See Dissanayake 1999, 2000a, 2000b, 2006, 2008; Trehub 2003a, 2003b; Koelsch and Siebel 2005; Panksepp 2009.) As alternatives, Parncutt (2009) identifies sounds experienced by the fetus in utero as the source of music and Wermke and Mende (2009) suggest that babies' crying is the source of music.

The view according to which infant-directed speech was a precursor to music could be a special instance of the more general thesis according to which both music and language shared a common, ancestral form of vocalization, known either as "protolanguage" or "musilanguage." According to the general thesis, proto/musilanguage was not confined to interactions with infants but was employed as part of a more general form of communication between all members of the group.

Of course, our hominin predecessors vocalized, as do much older species. They issued alarm and contact calls; perhaps they defended their territory or attracted mates by vocalizing; they cooed and clucked at their babies; they vented their rage, despair, and grief vocally. It has been suggested that what distinguished the vocalizations of hominins from ancestors we share with the apes was their adoption of synchronous chorusing (Merker 2000; Brown 2007). The development of language would have been gradual but inexorable, given the selective advantage of detailed, accurate communication between members of the group. Ostension and gesture linked sounds to individuals, things, or events; holophrasistic utterances (that could not be broken, tensed, or declined) took on significance; these might then be conjoined; increasingly complex syntactic structures came into use. (For discussion, see Brown 2000a, 2003; Corballis 2003; Fitch 2010; Collins 2013.) Whether it came earlier or not, a similar path of development presumably could be traced for music. Expressive slides and glides, fragmentary melodic phrases, beats and rhythms were combined, repeated, and developed until something recognizable as music emerged (Brown 2000a). This all would have been gradual. But at some stage our predecessors had both music and language.

According to the proto/musilanguage view, on which we will focus here, both music and language could be traced to more or less the same earlier modes of vocalizing (Molino 2000; Davies 2014). Tomlinson (2015) agrees that some form of protodiscourse came first, but he also emphasizes the distinctness of music and language and regards their subsequent development as parallel but independent.

Two leading exponents of the proto/musilanguage view are Steven Brown (2000a) and Steven Mithen (2005, 2007). They differ to some extent in their accounts of the precursor to music and language. Whereas Brown thinks musilanguage conjoined basic lexical units according to primitive grammatical rules, Mithen thinks that the protolanguage was primarily holophrasistic. His term for the protolanguage is "**Hmmmmm,**" because it was **H**olistic, **m**anipulative (in calling for shared attention and response), **m**ulti-modal (that is, including mime and gesture), **m**usical , and **m**imetic (that is, imitating natural sounds) (2005:172). But these contrasting perspectives need not be fundamentally opposed. The protolanguage could have changed over time, starting as primarily gestural and holophrasistic and later becoming more segmented, or it could have been mixed from the beginning in terms of the structures it employed.

Brown holds that the protolanguage emerged some time in the last five million years. And Mithen holds that musicality goes back to the early hominins. While Brown does not commit himself to a date for the emergence of full-blooded language from the protolanguage, Mithen holds that this happened only with our species, *Homo sapiens*. He thinks (2005, 2007) Neanderthals communicated in the protolanguage. But as indicated above, recent work has discussed the possibility that *Homo heidelbergensis*, our common ancestor with Neanderthals, was chatty, in which case the Neanderthals encountered by our Cro-Magnon predecessors in Europe were likely speakers too.

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The "physiological" approach to the prehistory of music does not produce a decisive result, largely due to our uncertainty about the historical relation between music and language, and about the neural and other physiological structures that subserve them. But I think there are reasons for betting that music came before language. A person does not need to be able to speak in order to make music and, and given its importance in communicating emotion, in coordinating dance and work, and in bonding both with infants and with fellow group members, powerful selective pressures would have supported its adoption and development. Music making does not depend on the highly sophisticated cognitive attributes and skills that are required for precise, clear linguistic communication. Admittedly, the hunting and trade practices of hominins like *H. heidelbergensis* must have required effective means of information exchange, but protolanguage may have been up to that task

(Marwick 2003; Tomlinson 2015). So, on balance, I am inclined to side with those who see language as a special case of music (Morley 2013), which is a view for which there is some neurological evidence (Koelsch and Siebel 2005; Brandt et al. 2012), rather than with those who see syntactically rich forms of language as coming first. Note that "tone" languages, such as Mandarin, in which semantic meaning depends on relative pitch location as well as sound, presume a developed sense of subtle pitch discrimination.

The first of the strategies for connecting music to our evolutionary history is not entirely successful, then. What about the second? This seeks functions that music might have served, where these functions improved the biological fitness of those who made and appreciated music. Biological fitness is measured in terms of a person's (potential) success in passing their genes to future generations. So, this approach considers musical effects that might have produced such an outcome. If they are located, it is plausible to argue that musical behaviors are evolutionary adaptations. The conclusion that music is an evolutionary adaptation alleges a close, positive connection between music and survival.

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The first step is to outline the functions music might have served for its earliest makers. In fact, there are many.

Music can be used to soothe infants and to bond with them. (See references for infant-directed speech as the precursor to music.) An extension of this view suggests that music primes the baby for its future mental life and for speech (Tooby and Cosmides 1989; Trehub 2003a, 2003b; Merker 2006).

Various positive effects on children and/or older individuals have been suggested for music. It might play a role in cross-domain cognitive development (Cross 2009, 2012, but for a skeptical response, see Davies 2012). Or in evoking affectively charged memories (Schubert 2009), or, more generally, in forging a sense of self-identity in adolescence (Patel 2010). As a result, it contributes to effecting the social differentiation of individuals (Ralevski 2000; Grewe et al. 2009).

A common theme emphasizes the role of music in male competition (Boyd 2005) and sexual display (Darwin 1880; Brown 2000b; Miller 2000a, 2000b; Dutton 2009; Dunbar 2012).

More often, it is the way that music benefits the group that is stressed. One suggestion is that it was used originally to establish and defend the group's territory (Brown 2000a; Hagen and Hammerstein 2009). Other proposed benefits remain apparent today. It is used to incite effort (Aristides Quintilianus 1983; Brown 2000b; Huron 2003; Boyd 2005) and to ensure group bonding, identity, synchrony, coordination, entrainment, and emotional catharsis (Dissanayake 1988, 1995a; S. Brown 2000a, 2000b; Merker 2000; Cross 2009, 2012; Dunbar 2003, 2012; Koelsch and Siebel 2005; Mithen 2005; Gamble 2012; Morley 2013). The underlying mechanism here might involve its suppressing testosterone and stimulating endorphins (Fukui and Yamashita 1998; Fukui 2001; Dunbar 2012). It has been suggested that music serves as a form of vocal grooming at a distance (Dunbar 2003, 2012) and that it can contribute to conflict resolution (Fukui 2001; Huron 2003; Bown and Wiggins 2009).

Did music enhance the fitness (reproductive potential) of those who first engaged in it? That is, was it adaptive in the evolutionary sense? If so, how? What were its evolution-relevant functions?

What are we to make of this rich array of proposals? The first point to note is that music certainly is multi-functional and perhaps always was so. When the music of present-day hunter-foragers is examined, there is no one function that dominates in all (Morley 2013). Of course, the music that defines one's distinctively personal identity cannot be identical to that which defines groups and subgroups to which one belongs. And the music that goes with competitive male display is unlikely to be the same as that which unites the group and reduces conflict. But some music might perform the one function and other music the other.

The issue, though, is not about the range of uses to which music can be put but about its alleged evolutionary function. That music is useful in signaling when a home run has been struck in baseball plainly does not entail that music is an evolved adaptation to this end. Nevertheless, in the vast majority of cases, the proposals listed above each *do* claim to identify music's primary adaptive function: musical behaviors were selected because they improved the relative reproductive success of those who had them by benefitting their reproduction *in the specified way*; that is, by attracting more sexual partners, resolving conflict, defending group territory, or whatever other function is highlighted. Such behaviors are now universal, it is suggested, because, over time, the relevant traits spread genetically through the wider population. (High levels of musical talent are only weakly heritable—Pratt 1977, Howe et al. 1998—but appropriate low-level musical skills now are universal and emerge with normal development—Davies 2012, but for doubt, see Patel 2008.)

Taken as claims about music's primary adaptive function, these various proposals are in direct conflict. For instance, in evolutionary terms, music's purpose cannot be to unite the group if its primary evolutionary function is as a competitive form of male display (Boyd 2005; Pinker 2007; Dutton 2009).

It is not easy to judge among the many alternative proposals and I will not attempt to do so in detail here. Nevertheless, I find it difficult to believe that the original, primary function of music was as a competitive male courtship display targeting potential female sexual partners. The sexes are equally musical, most music occurs outside of courtship situations, and the musical ties between a mother and her baby seem more prominent than those between mutually attracted adults. Undoubtedly, music can be enlisted as a prop for seduction, but it is hard to believe that we can describe its evolutionary origins along these lines. (For further critical discussion of the idea that music is a product of sexual selection, see Dissanayake 1999a, 2000a; Cross and Morley 2009; Ball 2010; Davies 2012.)

One issue to consider is how the claims about group benefits might be reconciled with the classical evolutionary model, according to which it is the individual (or, more precisely, their genes) that is the target of evolutionary selection. A first possibility is that benefits to the group are not evenly distributed among its members, so that some individuals benefit comparatively more than others. Under this scenario, overall group benefits are compatible with selection among individuals. A few authors explicitly subscribe to some such view (for example, Dissanayake 1988, 1995; Dunbar 2012; Morley 2013).

The alternative would be to accept multilevel selection theory and claim that groups, not only individuals, can be subject to evolutionary selection (Richerson and Boyd 2005; Wilson 2007; Bowles and Gintis 2011). In this case, transmission of the desirable characteristics could be exclusively cultural and not genetic beyond what is necessary for ordinary sound processing. The idea then would be that music-rich groups outcompeted music-impoverished groups because of the group strengths garnered from music, with the relevant musical behaviors passed on within the group via teaching and imitation.

The status of multilevel selection within the philosophy of biology has been questioned (Okasha 2006; Hampton 2010) and there is doubt about its applicability in this kind of case (Pinker 2007). If it is to be invoked, it then is necessary to demonstrate that the relevant intergroup pressures were more significant or powerful than selective forces operating via intra-group competition between each group's individual members. Typically, those who claim that music's group benefits were adaptive and who seem to commit to group-level selection, do not address this issue.

We might agree with Dissanayake (1988) that the fact that music is universal, ancient, and intrinsically rewarding suggests a probability that it was evolutionarily adaptive for our forerunners, even if we cannot be sure which of its potential uses was fitness-enhancing in the past and led to its later proliferation. But before endorsing this view, there are alternatives to be considered.

Or rather, was music a happy by-product of auditory capacities and biological interests with no fitness-enhancing features of its own?

Darwin himself noted that music is apparently not adaptive in its own right: "As neither the enjoyment nor the capacity of producing musical notes are faculties of the least use to man in reference to his daily habits of life, they must be ranked amongst the most mysterious with which he is endowed" (1880, pt. 3, ch. 19:569–70).

I have already cited a number of people who regard music as a by-product of language, including Darwin's contemporary, Herbert Spencer (1966, vol. 14 [1857]). Another evolutionist of that period, Alfred Russel Wallace (1989), held that music and dancing are by-products of our brainpower and excessive vitality. (For a modern version of the view, see Feist 2007.) Other suggestions are that music is an offshoot of ancient socio-affective systems (Panksepp 2009) or that it builds on the capacity, known as "theory of mind," to understand others as intentional agents with beliefs, desires, and emotions (Livingstone and Thompson 2009).

In a passage that was to become notorious, the evolutionary psychologist, Steven Pinker, compared music in its effects to recreational drugs. "I suspect that music is auditory cheesecake, an exquisite confection crafted to tickle the sensitive spots of at least six of our mental faculties . . ." (1999:534), these being language (when the music has lyrics), auditory scene analysis, emotional calls, habitat selection (as expressed in musical tone picturing of the sea, weather, etc.), motor control (when music leads to dancing), and "something else that makes the whole more than the sum of the parts" (1999:538). In other words, senses and capacities evolved for nonmusical purposes are stimulated by music in a fashion that we find pleasurable, though not to any evolutionary purpose. (For discussion of Pinker's choice of the cheesecake metaphor, see Davies 2012:139–42.)

The by-product thesis might be able to account for music's ubiquity. And it is true that we highly value many things that are not evolutionarily adaptive. Still, I wonder whether this theory can explain the passion with which music is pursued and the very high value placed on it. And most versions of the theory do not, as they should, clearly identify the adaptation from which music derives and the route of its derivation. If the musical whole is more than the sum of its derived parts, as Pinker allows, that is a reason for thinking it is not merely an accidental side-effect of nonmusical adaptations.

Or is it so distantly related to only very general characteristics (such as intelligence, curiosity, emotionality, sociality, and identity) that it is better regarded as a cultural technology than as either an adaptation or a by-product?

Aniruddh D. Patel (2008, 2010) has described music as a transformative technology that is not directly a product of evolution. It is transformative in terms of its many valuable effects, but it comes to us as part of our cultural, not biological, endowment. In this it can be compared to the control of fire, which is an ancient, universal, and highly valuable capacity that is taught, rather than being genetically inherited. Or the comparison could be made with writing and reading, which draw on evolved capacities for manual control and shape recognition but apply them to a quite specific, highly valuable end in a fashion that must be taught.

How strong are these analogies, though? The spontaneous emergence of musical behaviors in the course of normal development might not be so robust as linguistic behaviors, but they are surely much more so than is the case for fire-making and reading and writing, which suggests they involve an important genetic component. And whereas fire and literacy are highly valued, this is because they are *means* to effects that we value highly: heat, light, cooked food, dry clothes; the reliable transmission of information over distance and time, the creation of entertaining fictions. Exposure to music may produce desirable effects, but most of the time we engage with it primarily for its own sake and we treat it as intrinsically valuable. And it is not as if we think just any music, so long as there is a sufficient quantity of it, is always as good or potent as any other music. These are all reasons for interrogating the analogy on which Patel's argument relies. (For more detailed discussion, see Davies 2012:ch. 10.)

Supposing music was originally adaptive, does it retain that evolutionary function still? Has music taken on some new evolutionary function?

It is not clear how to answer this question if we do not know what music's original adaptive function was. But we do know that evolution builds adaptations on earlier, different adaptations, rather than starting afresh. Feathers that helped regulate temperature, with some modifications later facilitated flight. So, the possibility that music's evolutionary function has altered is a real one.

If the original adaptive function was territory maintenance, then it is no longer primary now. But given the energy and dedication we put into music, either the original function is retained, or some new one has taken over, or some new one sits alongside the original one. I doubted that music originated in sexual display or that this is now its primary function, but it could be a subsidiary yet adaptive function that (popular) music is put to by some of its makers.

Has music transcended its biological origins as a result of becoming universal?

Music may have given those committed to it higher fitness and hence an evolutionary advantage over their amusical contemporaries. Music could still confer some such advantage, even when it becomes universal, if it is practiced to different degrees by different individuals and if those who are comparatively less musical do not make up for this in other ways (such as by being painters, say). But it is possible that musicality is shared equally enough that it does not provide a selective advantage now, though it did so in the past. (As an example, think of bipedalism.) In that sense it could transcend its original biological function(s).

There is another way music could easily cut its ties with biology. There should be no denying the importance of culture and tradition in musical behaviors, even if they have biological drivers and components. As the culture's music develops (and progressively repudiates its musical ancestors), the avant-garde might take it to a point where it would be no longer capable of carrying out biological agendas it served previously. Its composers might abandon tonality and serialize every parameter, or create a twenty-note piece with a tempo that has it last 500 years, or specify it as for performance in the soundless vacuum of space, or include only pitches that are beyond the range of the indicated instruments. Many cultures have esoteric, sophisticated modes of art that are accessible only to connoisseurs and cognoscenti because of the degree to which they have been refined and become conceptual and self-referential. When music becomes like that, it dispenses with any ties to evolution its ancestral forms possessed.

There is no reason to think that that result is to be condemned. But notice this: however specialized some modes of art become, they rarely replace more quotidian, accessible forms. Lullabies remain the same and popular music tends to be conservative and conventional where it aspires to a mass audience, even if 12-tone operas or isorhythmic motets get added to the tradition.

Are the key notions employed here—adaptation, by-product, non-biological technology—the ones best suited to understanding the place of music in human evolution?

Tomlinson argues against the usefulness of arguing that music has any particular adaptive function on the grounds that music's emergence was piecemeal, incremental, and various, and involved the coalescence of many different capacities. He criticizes adaptationist hypotheses for seeking a "unilateral explanation for a manifold phenomenon" (2015:33).

There are more general reasons why we should question the explanatory power of these evolutionary categories to our species' development, as I now outline.

While some creatures, such as beavers, construct aspects of the environment in which they prefer to live, we humans are unique in the extent to which we do this (Odling-Smee et al. 2003). The earliest members of our species buffered themselves against raw nature. They wore clothes, made tools, created weapons, occupied heated shelters, cooked their food, used natural medicines and supernatural rituals to protect against injury and illness, and so on. Some ten thousand years ago, when most of us progressively abandoned the hunter-forager existence in favor of towns, agriculture, and the domestication of animals, we took yet more control over the construction of our environment. Nowadays, the trend is even more marked. Many of us eat meat and vegetables without ever killing an animal or pulling up a plant. We live in a humanly created environment that is the product of culture and technology. And with us, just as our biological nature places constraints on the form that culture takes—unassisted flying is not an Olympic sport—culture modifies our biology—the dentition and guts (and perhaps even brain size, see Wrangham 2009) of our ancestors changed as a consequence of their move to cooked foods. As a result, there are feedback loops in both directions between human culture and human biology, so these cannot be regarded as isolated, mutually exclusive domains in which we exist (Richerson and Boyd 2005).

Originally, individual fitness was proposed as the measure of an organism's adaptedness to its environment. That was later changed to potential fecundity, because creatures will take on physical handicaps for the sake of reproductive success. But once we include the other sex as an aspect of the environment, the two accounts come back into line. However, as just observed, both the physical and the socio-cultural environment are in our species largely self-created. This makes the standard biological notion of adaptedness difficult to apply. There is no easy way to distinguish adaptations from by-products and technologies, and little explanatory value in doing so. Rather than debating which of these categories applies to music, it might be more meaningful to track the way we construct and populate the musical niche (Fitch 2006; Killin 2013; Menary 2014).

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What is the upshot of this analysis?

We are the only species capable of creating and presenting music that melds melody, tonality, and rhythmic articulation set against a regular pulse and meter, to name some central elements characteristic of music as such. Extinct hominin species may have preceded us, however. Music making may be as old as 500,000 years and most likely is more than 60,000 years. Not only is it pan-cultural, a modest but respectable level of musical competence is near universal (Davies 2012). We value music highly and often intrinsically, though it is also a means to incidental benefits. Together, these facts suggest that it may have been evolutionarily adaptive for our predecessors and is universal now because they out-reproduced their tone deaf conspecifics.

Whether music was adaptive is not settled by the neurological evidence, especially given our uncertainty about the timing of its emergence relative to that of language and given the possibility that other, proto-musical forms of communication might have foreshadowed both music and language. And while many adaptive benefits of the adoption of music have been claimed, there is conflict between them and a lack of consensus about which are the more plausible. Other possibilities—that music is a by-product that is not adaptive in itself, or that it is better regarded as a cultural technology far removed from our biological endowment—have also been presented.

Adjudicating between these various options might become easier when we learn more about prehistory or the brain. But on the other hand, framing the debate in terms of these familiar categories might be unhelpful, even distorting, given the extent of mutual influence and feedbacks between genetics and culture in the development of our species. And even if we could clear these hurdles, it would remain to work out if music has taken on new evolutionary functions and what these might be, or, alternatively, if it has become so culturally arcane that it has transcended and made irrelevant its biological roots in our evolutionary past.

Stephen Davies,
University of Auckland.

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