



The Evolution of Music in Comparative Perspective

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ABSTRACT: In this paper, I briefly review some comparative data that provide an empirical basis for research on the evolution of music making in humans. First, a brief comparison of music and language leads to discussion of design features of music, suggesting a deep connection between the biology of music and language. I then selectively review data on animal “music.” Examining sound production in animals, we find examples of repeated convergent evolution or analogy (the evolution of vocal learning of complex songs in birds, whales, and seals). A fascinating but overlooked potential homology to instrumental music is provided by manual percussion in African apes. Such comparative behavioral data, combined with neuroscientific and developmental data, provide an important starting point for any hypothesis about how or why human music evolved. Regarding these functional and phylogenetic questions, I discuss some previously proposed functions of music, including Pinker’s “cheesecake” hypothesis; Darwin’s and others’ sexual selection model; Dunbar’s group “grooming” hypothesis; and Trehub’s caregiving model. I conclude that only the last hypothesis receives strong support from currently available data. I end with a brief synopsis of Darwin’s model of a songlike musical “protolanguage,” concluding that Darwin’s model is consistent with much of the available evidence concerning the evolution of both music and language. There is a rich future for empirical investigations of the evolution of music, both in investigations of individual differences among humans, and in interspecific investigations of musical abilities in other animals, especially those of our ape cousins, about which we know little.

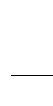
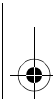
KEYWORDS: biomusicology; evolution of music; design features of music; comparative data; birdsong; whalesong; ape drumming

INTRODUCTION

After a long hiatus, there has recently been a surge of interest in the biology and evolution of music.¹⁻⁴ From a biologist’s perspective, a logical starting place to begin a discussion of the biology and evolution of human music is provided by the study of the evolution of communication in animals. In particular, a comparative approach, using empirical data from living organisms, rather than speculations based on fossils, provides a rich source of empirical data to ground hypotheses and test predictions. The purpose of this review is to introduce the reader to some core questions

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in evolutionary musicology (biomusicology), to discuss some comparative ethological data relevant to these questions, and to highlight some key topics for future empirical research. I argue for an empirical, multicomponent perspective, breaking music down into several different subcomponents for further study. Two obvious components, song and instrumental music, provide a framework for the current review. Each of these phenomena, and the biological capacities underlying them (e.g., vocal learning and entrainment, respectively), might have a different evolutionary function and history. Indeed, I will argue that the comparative data available necessitate rather different approaches to the evolution of song versus the evolution of instrumental music.

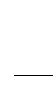
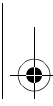
The comparative approach to music has at least three different component: a cross-cultural component (comparative musicology and ethnomusicology); the intraspecific comparison with other human cognitive functions, especially language; and finally the interspecific comparison with the music of other species. I will discuss the first two here, before turning to my main focus on the comparisons with animals. Because I have recently reviewed the biology and evolution of music from a multicomponent comparative perspective in more detail elsewhere,⁵ I will remain brief here and focus citations on reviews, when available. Several recent multi-authored volumes provide detailed consideration of some of the relevant ethological data,^{1,6} so I highlight some topics that previous commentators appear to have overlooked (e.g., female birdsong or ape drumming). Because music perception has been well reviewed recently by others,^{7,8} my focus in this review is mainly on musical production, rather than perception: music-making results in behavior that can be recorded and analyzed and is the focus of most ethological investigation. Thus, our comparative data are richest for this topic.

MUSIC AND LANGUAGE: SIMILARITIES AND DIFFERENCES

There are a number of deep similarities between human music and language, and the comparison between these two faculties provides a persistent leitmotif in musicology. I agree with the opinion of Lerdahl and Jackendoff^{9,10} that music should be studied empirically as an independent cognitive domain from language (not assumed to be parasitic upon, or derivative of, language, e.g., as presented in Ref. 11). However, it seems likely that the results of this empirical endeavor will have important implications for language,¹² just as the study of language has already had a significant impact on the study of music cognition.^{9,13,14} Both the core similarities, and a few crucial differences, between music and language are relevant to much of the work on the biology of music, particularly when they are viewed from the perspective of animal communication systems.

Although linguists and musicologists often focus attention on the differences between music and language, from a biologist's perspective the similarities appear more striking. At a superficial level, both music and language use the auditory/vocal domain preferentially. Each faculty has, in addition, closely related nonvocal domains of expression (signed languages, instrumental music and dance), and both can be written or notated successfully. At a deeper cognitive level, there are significant formal similarities in musical and linguistic cognition, both in phonology (e.g., metrical phonology and rhythm¹⁵) and at higher organizational levels (e.g., the





existence of hierarchical phrase structure in both domains¹⁰). Most importantly, however, both music and language represent human universals, found in all human cultures, and both seem to rely on innate biological proclivities that are quite unusual in the animal kingdom. This biological basis is reflected both in very early biases and predispositions in human infants (e.g., the preference for processing relative rather than absolute pitch, already observable at six months of age⁸) and in a considerable overlap of the brain regions involved in processing musical and linguistic stimuli.¹⁶ These similarities seem unlikely to result from chance, suggesting that the study of the biology and evolution of language will have interesting implications for the evolution of music, and vice versa.

However, within this context of shared properties, there are several striking differences between music and language as well. Perhaps the most obvious is the significant disparity in the type of meaning attached to linguistic and musical stimuli. Although language can be used musically (in the sense of poetry or song, where the form of the utterances themselves become a focus of attention), the prototypical linguistic utterance is propositional: it expresses a specific meaning that can be either true or false. Linguistic semantics is largely focused upon meaning as intentional, propositional messages. Such meaning is largely absent in human music (with some relatively peripheral exceptions, e.g., flute trills signifying birdsong). Certainly, a musical phrase is not easily judged as true or false. Although it would be incorrect to say that music lacks meaning entirely, *musical meaning* is notoriously hard to pinpoint, suggesting that its very openness and ambiguity are perhaps one of its virtues. Despite many attempts to define musical meaning, and a widespread conviction that music is well suited to expressing mood and emotion, there is no widely accepted characterization of musical meaning. Ian Cross, focussing on the social functions of musical meaning, has suggested the term *floating intentionality*.¹⁷ Cross points out that music seems to “absorb” *aboutness* from whatever context it appears in (evoking strong associations to that context on later hearings), while simultaneously providing aboutness to that context, in the sense of enriching our sense of the meaningfulness of a given context (hence the close association of music with ritual in all of the world’s cultures). A rather different formulation is due to Manfred Bierwisch,¹⁸ who coined the apt term *gestural form* to describe the mapping between musical structure and musical interpretation, connoting our ability to make an analogical mapping between the acoustic form of music and either the affective trajectory of emotional experience, or the motor trajectory of dance. In short, however one attempts to characterize musical meaning, the meaning of music and that of language are clearly distinct, and this difference is crucial to understanding these two related faculties.

DESIGN FEATURES OF MUSIC: A MULTICOMPONENT APPROACH

As already suggested, a profitable comparison of music and language or of human and animal musics requires that we break music down into its various component abilities rather than treating music as an indivisible whole. Achieving an apt analysis is obviously far from a trivial task, and “carving nature at the joints” may require many cycles of theorization and test. However, certain very basic distinctions are already quite clear. The first is between production (music making) and perception: while the former is quite variable among individuals, the latter seems to be

TABLE 1. Hockett's²² Design Features of Language

Language Design Feature	Music		
	Instrumental	Vocal Innate Calls	
1. Vocal auditory channel	No	Yes	Yes
2. Broadcast transmission	Yes	Yes	Yes
3. Rapid fading	Yes	Yes	Yes
4. Interchangeability	No	Yes	Yes
5. Total feedback	Yes	Yes	Yes
6. Specialization	Yes	Yes	Yes
7. Semanticity	No	No	No
8. Arbitrariness	No	No	No
9. Displacement	No	No	No
10. Duality of patterning	No	No	No
11. Productivity	Yes	Yes	No
12. Discreteness	Yes	Yes	No
13. Cultural transmission	Yes	Yes	No

NOTE: Innate Calls refers to vocalizations of nonhuman primates along with laughter or screams in humans. Brief explanations of nonobvious terms (see Hockett²² for detailed description, and Fitch⁵ for discussion): 4. interchangeability (anyone can say anything they can understand) vs. males alone singing; 5. total feedback (you hear what you're saying); 6. specialization (speech "triggers" desired results with negligible direct energy expenditure, unlike forcing someone manually); 7. semanticity (words associated with things); 9. discreteness (digital vs. analog); 10. displacement (capacity to refer to nonpresent objects or events); 11. productivity (novelty, counterfactuality); 12. duality of patterning (meaningless elements combine for large number of meaningful elements).

much more universally shared, even among self-professed "unmusical" individuals.¹⁹ We might also profitably subdivide musical mechanisms along more traditional lines of rhythm, melody, and harmony, as is implicit in much of the experimental literature on music psychology.²⁰ A third prominent subdivision is that between song and instrumental music. Scholars have long hypothesized different origins for these two subcomponents,²¹ and this will form a core distinction in the current review.

My starting point⁵ for this analysis of the music faculty and comparison with language will be a characterization of design features of human language offered by the linguist Charles Hockett. Hockett provided a list of relevant features of language that have been quite influential in the subsequent study of animal communication,²² providing a widely discussed and well-known decomposition of linguistic abilities that also allows a specific comparison with human music. Hockett himself discussed instrumental music in this context but did not discuss song (which is arguably more biologically basic, and certainly shares more with speech). I present Hockett's features for language, as compared to song, in TABLE 1. This table shows that most of the features Hockett singled out as particularly relevant for human spoken language are shared by song. The exceptions all tie in to the basic distinction between musical and linguistic meaning discussed above. Thus, from a linguistic perspective, we see that the two domains share physical and physiological features (dependence on the

TABLE 2. Design Features of Music

Design Feature	Spoken Language	Innate Calls
1. Complexity	Yes	No
2. Generative	Yes	No
3. Culturally transmitted	Yes	No
4. Discrete pitches	No	No
5. Isochronic	No	No
6. Transposability	Yes	?
7. Performative context	No	No
8. Repeatable	No	No
9. A-referentially expressive	No	Yes

AU:
“A-referentially expressive” okay in table 2?

NOTE: See Fitch⁵ for detailed explanation and discussion.

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auditory channel, and vocalization) as well as deeper formal similarities at the phonological and syntactic levels, but that music lacks propositional meaning. From this perspective one might say, as a first approximation, that music is halfway to language.

Of course, from a musicologist’s perspective, characterizing music as language minus meaning seems both limiting and somewhat derogatory. Turning the analysis the other way around, we may ask what special characteristics music possesses and then compare language with these. As a step in this direction I have proposed some design features of music, asking whether these are shared by language.⁵ A summary of this analysis is presented in TABLE 2. I make no claims that this is the best breakdown, but the proposed features are often cited by scholars as potential universal characteristics of the musics of the world.^{23, 24} Here we find, again, a mixed pattern of shared and disparate elements. Despite the first three shared features, music has a number of specific features that are lacking in language, three of them formal or perceptual and three of them social and intentional. Taking these features as provisionally “special” to music, we may thus turn to comparative data to see which of the shared ensemble of musical and linguistic design features might be shared between humans and other species. See Ref. 5 for a more detailed discussion.

THE COMPARATIVE APPROACH TO MUSIC EVOLUTION

Turning from the comparison between music and language to interspecific comparisons, various behaviors in nonhuman animals can be considered analogues of human music making. The most obvious of these is birdsong, already termed *song* by Aristotle.²⁵ More recently, biologists have learned that several other animal groups, including two independent orders of marine mammals, whales and seals, have evolved learned, complex vocal displays termed song (for reviews, see Ref. 1). Besides song, however, there are other animal displays that may deserve comparisons with human music that are less well known. In particular, I suggest below that African ape percussive behavior or “drumming” may represent a homologue and thus indicate a potential precursor of human instrumental music.

The comparative method, which involves using data from living organisms to draw inferences about extinct ancestors and/or past selective forces, is one of the most powerful tools available to the biologist. Experimentation in evolutionary biology is limited by the great time spans required for evolution, so (in contrast to physics and chemistry, but in common with meteorology, cosmology, or geology) biology relies heavily on the careful observation, collation, and comparison of “experiments of nature.” Each living species can be considered a separate data point, each having its own independent evolutionary history since its divergence from other related species. By gathering data from living organisms and organizing them phylogenetically, we gain access to a huge body of information relevant to understanding evolution. There are two basic types of inferences one can draw from comparative data, which derive from two fundamentally different ways in which organisms can come to resemble one another.

One common form of similarity results from two different lineages independently evolving a similar solution to the same problem. Following a long tradition in comparative biology, starting with Richard Owen, such convergently evolved traits can be termed *analogues* (in contrast to *homologues*, which result from common ancestry, see below). Examples include the independent evolution of flapping wings for flight in insects, birds, and bats; of streamlined form in fast swimming vertebrates such as dolphins, ichthyosaurs, and sharks; or of short, powerful arms adapted for digging in placental and marsupial moles.^{26,27} In many cases, striking resemblances in form have arisen in organisms whose ancestors looked very different from one another (e.g., birds arose from a bipedal dinosaur, while bats evolved from a quadrupedal mammal). In such cases, similar lineages clearly represent independent data points, with quite separate evolutionary histories. Here, convergent evolution provides one of the most powerful clues to adaptation, because we can exclude potential confounds such as phylogenetic inertia (the tendency for closely related species to remain similar after their divergence for reasons of history rather than adaptation). Thus, when we observe convergent evolution in nature, we are immediately led to postulate an adaptation to the task at hand²⁸ (see Ref. 29, however).

The other pervasive form of similarity was termed *homology* by Owen. In current usage, this term indicates similarities in two or more species that are derived from their common ancestor. Thus a homologous trait is one that was present, though perhaps in a somewhat different form or with different function, in the common ancestor of the lineages possessing the homologue. Homology plays a key role in evolutionary biology, because homologous traits allow us to build and test phylogenetic hypotheses.³⁰ More importantly in the present context, homologous traits allow us to reconstruct the traits of extinct ancestors, even in the absence of fossil evidence, by examining shared characteristics of their living descendents. Summarizing, both homologous and analogous traits provide useful insights into the evolutionary past,³¹ and in this review I will offer potential examples of each.

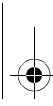
Convergent Evolution: Vocal Learning and Song in Nonhuman Animals

The analogy between birdsong and human music has been recognized since ancient times, and birdsong receives ever-increasing scientific attention as the most sophisticated vocal communication system in the animal kingdom besides human song and language.^{32–34} More recently, with the invention of the hydrophone, song-

like vocalizations have been discovered in two independent lineages of marine mammal, the cetaceans (whales and dolphins) and the pinnipeds (seals and sea lions).^{35,36} Darwin knew that songbirds required exposure to conspecific song in order to sing “properly.” This ability to imitate novel sounds, termed *vocal learning*, has since been demonstrated in marine mammals and thus appears to represent a core component of “animal song,” as this term is currently used. Because vocal learning is critical in language, many authors have noted the importance of vocal learning in animals as a critical analogue of human language acquisition;^{37–39} it is less often noted that it is just as relevant to cultural transmission of musical song.⁴⁰ Indeed, I join⁴¹ in suggesting contra,⁷ that comparison of the deep similarities between human and animal song is highly relevant to the evolution of music, possibly more so than the traditional comparison between animal song and human language. From this perspective, a long tradition of research on vocal learning in nonhuman animals has interesting implications for the evolution of both song and speech in humans.

By considering only animal vocal displays that are both learned and complex enough to deserve the appellation *song*, I exclude such phenomena as frog or cricket song that, although pleasant to listen to, are neither complex nor learned (for more discussion, see Ref. 5). More controversially, this restriction excludes vocalizations classically termed song in gibbons or suboscine birds, which is complex but not learned.^{34,42} Such vocalizations may serve a similar adaptive function to songbird or human song but seem to rely on different neural mechanisms. Vocal learning of novel sounds is not possible for our nearest cousins, the apes, or apparently other nonhuman primates.⁴³ Despite some limited vocal learning,⁴⁴ nothing like the human (or songbird) ability to learn complex, novel vocalizations from the environment has been demonstrated in any nonhuman primate, despite repeated strenuous efforts.⁴⁵ Despite some similarities in form and function (for an excellent review, see Ref. 42), and clear homology at the level of the vocal production system, the lack of extensibility of primate calls renders them categorically different from human music and speech. This difference between humans and other primates appears to be underlain by fundamental differences in the neural control of vocalization.⁴⁶ I thus concur with Marler⁴¹ that primate calls are a poor choice for comparison to human song (for a different viewpoint, see Ref. 42).

Vocal learning represents a clear case of analogy: neither the ancestral mammal, nor the ancestral bird, nor the common ancestor of birds and mammals, possessed vocal learning or song. Complex vocal learning has arisen independently in at least three clades of birds (oscine passerines or “songbirds,” hummingbirds, and parrots) and three clades of mammals (cetaceans, pinnipeds, and hominids), and this list is probably not exhaustive.^{35,47} Thus, any similarities in these convergently evolved vocal learning systems may represent adaptations, evolved to solve particular functional problems. A suggestive example is provided by babbling. Both young songbirds and human children go through a stage of private vocal experimentation termed *babbling* in humans and *subsong* in birds, widely believed to allow the youngster to calibrate its vocal apparatus and auditory system, and providing the arena in which it can learn to successively approximate the vocalizations of adult models.⁴⁸ A pre-adult babbling stage that closes the auditory/vocal loop seems to be a prerequisite for vocal learning and is something that both young birds and humans do avidly, without external reinforcement. Babbling/subsong may thus be a key mechanistic component of the innate capacity for complex vocal learning that underlies both



human and animal song, as well as human language. This is a testable hypothesis: To my knowledge, no one has yet documented a babbling stage in nonhuman mammalian vocal learners, and if more detailed studies of singing whales or seals revealed no such stage, we could reject this “vocal learning entails babbling” hypothesis.

In terms of function (the adaptive problem “solved” by song), the repeated convergent evolution of learned song in the animal kingdom provides a rich source of data. Darwin recognized that, with some exceptions, it is mostly male birds who sing and that they do so most commonly in the mating season. He thus saw sexual selection for mate choice as a critical factor in the evolution of bird song.⁴⁹ Among marine mammals, it appears that only male whales produce complex song, and song is mostly restricted to male seals (although vocal learning is present in bottlenosed dolphins of both sexes); again, song is common only during the mating season. Partly by analogy with birdsong, these displays are thus widely believed to function as sexual displays.^{50,51}

However, it is important to note that the preponderance of male song is only a first approximation and that two deviations from this rule are commonly observed in birds. In the first, both males and females contribute to “duets:” complex songs with different, often tightly interlocking, male and female parts.^{52,53} These are particularly common in nonmigratory tropical birds, and for historical reasons duetting is less well known than the male song typical of birds from temperate climates. Second, with the rise of detailed studies on identified, sexed birds, it has become increasingly clear that female birds, even in temperate regions, may sing independently of males.^{54,55} For example, in robins (*Erithacus rubecula*) the male alone sings during the spring mating season, but in the autumn females establish separate winter territories that they sing to protect⁵⁶—an example of natural, not sexual, selection. There has been a recent surge of interest in female bird song, but our understanding of it is still limited at present.⁵⁵ Given the lack of any clear sex differences in singing ability in our own species, where both women and men have highly developed singing abilities, song in female birds is clearly relevant to the evolution of human song. Thus, caution is warranted regarding extrapolation from male-specific bird or whalesong to the sexually egalitarian song of human beings, at least regarding the adaptive function of these vocalizations.

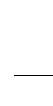
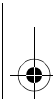
Ape Drumming as a Potential Homologue to Instrumental Music

Turning from analogy to homology, we find a number of plausible perceptual homologies between auditory perception in humans and other vertebrates.⁷ At the level of basic pitch and timbre perception, important components of music perception appear to be widely shared. For instance, goldfish and pigeons can both learn to identify musical styles (e.g., blues vs. baroque music) and extrapolate to new pieces outside the training set.^{57,58} However, regarding music making, we must turn to our own mammalian order to find behaviors that represent plausible homologues. With regard to the anatomical basis for song, there are no fundamental differences between humans and most other mammals.⁵⁹ To go beyond this very basic, and very deep, set of homologies, we must thus look to the way this system is used, particularly at the level of its neural control. Here it is the human ability to imitate novel sounds (vocal learning) that seems the most critical aspect of our vocal behavior, and

as already discussed, this ability is not shared by other primates. If gibbon “song” or chimpanzee long calls are not homologous to human singing, are there any aspects of primate behavior that are potential homologues to human music making? I believe that the answer is yes and that the percussive behavior commonly observed in great apes, often called “drumming,” represents a plausible but heretofore overlooked homologue to human instrumental music making.

Bimanual percussion on resonant objects (drumming) is a common, easily observed behavior in African great apes (chimpanzees, bonobos, and gorillas). Behaviors analogous to drumming or other instrumental music are quite rare in animals, the most prominent other examples being palm cockatoos (which use sticks to drum on hollow trees⁶⁰), many species of woodpecker (who seek out resonant trees for display drumming),^{61,62} or various desert rodent species who “drum” with their hind feet on the ground.⁶³ Great ape drumming has been the topic of surprisingly little research and has been largely overlooked in recent discussions of the evolution of music. In gorillas, drumming behavior is prototypically seen in the agonistic displays of adult male silverbacks, where a vocal “hoo” display is commonly combined with bimanual beating on the chest (and the inflated vocal air sacs, increasing the resonance of drumming).⁶⁴ However, gorilla drumming is also observed in females and young, often in a contagious, playful, and unsteretyped fashion, and young gorillas beat on many surfaces (including their bellies, the bodies of other gorillas, the floor, and on hollow objects, Fitch & Gomez, unpublished video data). This more playful and creative context is much more suggestively similar to much of human music. In chimpanzees and bonobos, drumming is typically observed on resonant structures in the environment (rather than their own bodies), often as part of the climax of the male dominance display.^{65–67} Wild chimpanzees seek out particular tree buttresses and in zoo contexts sometimes discover and drum upon resonant structures (e.g., hollow walls, J. Call, personal communication). Finally, bonobos have a variety of clapping and drumming displays,⁶⁸ and enculturated bonobos, such as the language-trained Kanzi, produce and apparently enjoy drumming on resonant objects bimanually in a highly coordinated fashion (S. Savage-Rumbaugh, personal communication).

Although the discovery of tool use by wild chimpanzees⁶⁵ generated an uproar, dethroning humans from their sole status of “toolmakers,” the existence of drumming in apes has remained largely unnoticed by musicologists. It has long been speculated that vocal and instrumental music have independent origins and evolutionary histories,²¹ and the sharp difference between ape drumming (with its similarities to human instrumental music) and ape vocal capabilities (which show no evidence of the vocal learning and control required for song) provide strong support for this hypothesis. In my opinion, ape drumming represents a striking parallel to human percussive behavior, and its appearance in our closest living relatives (but not, apparently, among orangutans or other primates) strongly suggests the possibility of an overlooked and important homology for human instrumental music making. Unfortunately, there has been little empirical research on great ape drumming, and we are currently unable to answer even very basic questions that would help evaluate this hypothesis. In particular, despite very questionable statements in the popular literature,⁶⁹ it remains unclear whether apes can entrain their drumming to a regular, externally given beat. Vocally, gibbons may be able to entrain their calling to a metronome (see Ref. 42), and bonobos may entrain their group calling,⁶⁸ but here too



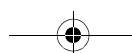
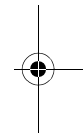
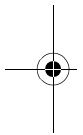
the data are inadequate at present. Since both entrainment and isochrony have been proposed as design features of music and are thought by some researchers to be uniquely human capabilities, this is an open question that critically needs empirical resolution. Thus, the hypothesis that ape drumming is homologous to human instrumental music remains a tantalizing possibility that cries out for controlled experimental study.

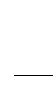
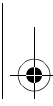
Concluding, even this rather cursory exploration of the comparative database demands that we move beyond simplistic models of music, considered as an undifferentiated whole unique to our species. Once we begin breaking the human music faculty into its component parts, such as song and drumming, we find abundant parallels in the animal world, including very deep and basic homologies (e.g., at the level of vocal production or basic auditory perception) and fascinating analogies (e.g., vocal learning in birds or seals). Further empirical research may well reveal a residue of musical traits that are unusual or possibly unique to our own species (e.g., isochronous entrainment).⁴⁰ Of course, the only way to discover such uniquely human characters is to first carefully investigate all potentially relevant animal behaviors. Both the psychology and anthropology literatures are replete with cautionary tales in the form of claims of uniquely human characters that were later falsified by comparative data.^{70,71} Thus, the study of animal musics is a fascinating and rewarding field in its own right, but it is also a logical prerequisite to any claims about uniquely human musical capabilities.

THE ADAPTIVE FUNCTIONS OF MUSIC: BEYOND SEXUAL SELECTION

The adaptive function(s) of music represents an area of considerable discussion in the contemporary literature.^{1,11,72,73} In my opinion, this issue has been overemphasized, because a specification of the adaptive function(s) of music is neither necessary nor sufficient for a rich understanding of the biology and evolution of music. Several classes of question asked by evolutionary and behavioral biologists are independent of one another and represent complements to one another (rather than alternatives).⁷⁴ These include mechanistic questions about how the behavior is implemented genetically, physiologically, and neurally (e.g., the wealth of current research on the mechanisms of birdsong), ontogenetic questions about how it develops (e.g., the parallels between babbling and subsong), phylogenetic questions about the origin and subsequent evolutionary pathway of the behavior, and finally functional question about the adaptive value (or values) that the behavior served or serves. Answers to such functional questions must ultimately be framed in terms of increased survival and reproductive success. Although functional questions are undeniably interesting, they are notoriously difficult to answer, and represent neither the only, nor the primary, questions that biologists ask about evolved traits. Thus, I do not see the question, Is music an adaptation? to be central to biomusicology. I suggest that debate on this topic has shed more heat than light and should not continue to occupy center stage in this young field.

A key difficulty for functional hypotheses is the ever-present possibility of change of function. Although careful observation and experiments can provide empirical information about the current adaptive function of a trait, we must be quite



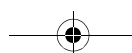
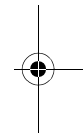
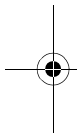


cautious about extrapolating from such findings to the past ancestral function(s) of the trait. For example, regarding morphological data (where we do have clear fossil evidence), evolutionary history is full of systems that have changed their function. To choose three examples directly relevant to music, the mammalian middle ear bones started as jaw supports (for feeding) but now function as an impedance-matching system for audition. The vertebrate larynx started out as gill supports for underwater respiration in our aquatic ancestors but now is adapted to sound production in terrestrial vertebrates. Finally, our lungs are used in aerial respiration, and drive vocalization, but are homologous to the swim bladder in fish, which serves in underwater posture maintenance and floatation. Clearly, over evolutionary time, we cannot expect current function to flawlessly predict past function or assume that the function of music in today's world is identical with that of our long-extinct ancestors. Indeed, such functional lability has led some theorists to advocate ignoring past function entirely in discussions of adaptation,⁷⁵ although this suggestion has not been widely adopted. We should keep this possibility in mind as we evaluate current hypotheses concerning musical function.

Music as Cheesecake

The logical starting point for any discussion of the adaptive value of a trait is that it is not an adaptation at all. This is the null hypothesis to be rejected first in any empirical investigation of adaptation. There are many reasons that any particular trait might be nonadaptive or even maladaptive.⁷⁶ The trait might be an automatic by-product of some bona fide adaptation, generated by developmental or architectural constraints (such traits are often termed *spandrels*, following the discussion of Gould and Lewontin⁷⁷). It has been suggested that music is an automatic by-product of language in this way,¹¹ much as cheesecake is nonadaptive but fulfills a desire for sugars and fat that is (or was) adaptive. Alternatively, a trait may be a "hangover" like the appendix, leftover from a past time when it did serve an adaptive function (phylogenetic inertia). This notion of music as a phylogenetic hangover from the communication system of earlier hominids is implicit in Darwin's hypothesis of a music-like "protolanguage" (see below).

Finally, a supposed trait might actually be an artifact of our way of carving up an organism, but not itself under genetic control or subject to past selection. To take an uncontroversial example, a chess grand master may spend all of his time playing chess, relying on his chess skills for both survival and increased mating success, and scientists can even study the genetics and neurology of chess.⁷⁸ Such demonstrable utility obviously does not make "chess" an adaptation. Although various components of chess-playing ability might be properly considered adaptations (e.g., the ability to form complex perceptual and symbolic representations, encode rules, and plan ahead strategically), it would be silly to reify the "chess faculty" as an adaptation in its own right. Of course, music is historically much older than chess, is found in all human cultures, and appears to entail perceptual specializations that are either innate or very early developing, and for all these reasons the human music capacity seems a much more promising candidate as a Darwinian adaptation than chess. However, we should treat this reification of music as very provisional: the term *music* is a recent one in English and is absent in many languages.⁴⁰ Cross-culturally, perhaps the relevant adaptative complex is music + dance. In any case, the first goal of a





scholar interested in the adaptive value of music should be to reject the null hypothesis—that music lacks any biologically adaptive value—by demonstrating some systematic, widespread, and plausibly ancient current function of music. Even with regard to the current function of human music, potentially a topic of empirical research, hard data is surprisingly scarce and vastly outweighed by the theoretical speculation on this topic. This lack of solid data represents a clear and easily filled lacuna in our current understanding of music evolution, as I will stress below.

Music and Sexual Selection

Perhaps the most widespread hypothesis for the adaptive function of music dates back to Darwin, who suggested, by analogy with birdsong, that “musical notes and rhythm were first acquired by the male or female progenitors of mankind for the sake of charming the opposite sex.”⁴⁹ Combined with the contemporary prominence of love songs, the idea that music (either song or instrumental music) functions in mate choice, and sexual selection more generally, seems intuitive and is often repeated.^{79,80} This makes it surprising that there is, to my knowledge, no clear evidence supporting this supposition for humans, and its wide appeal seems to rest mainly upon intuition. We might expect, for example, demonstrations that skilled musicians, across cultures, have greater reproductive success than nonmusicians (or less-skilled musicians). Experiments involving attractiveness ratings of videos, using musical skill as a controlled variable, could easily be performed. Results from Web-based surveys querying large numbers of musicians about their sex habits, although demanding circumspection, would also provide a valuable initial source of data. Even statistical data showing that famous Western musicians have significantly more offspring (or better offspring survival) than others would be worthwhile. For every Bach who spawned a large family, however, there may be a Beethoven who died childless. Despite there being no obvious hurdles in the way, data supporting the sexual selection hypothesis, is to my knowledge currently unavailable, and we must look to animals for relevant empirical data.

The comparative database on animal song, at first glance, offers little support for a primary role of sexual selection in the evolution of human singing or vocal learning. In the vast majority of well-studied species, song is the exclusive province of males and occurs mainly during the mating season after the attainment of sexual maturity. Human singing, by contrast, is done equally well by males and females, in many different behavioral contexts. However, as discussed above, there is a growing literature on female bird song, that weakens the impact of this particular criticism. Among primates, duetting species tend to be monogamous,⁸¹ and monogamy is an extremely rare mating system among mammals (less than 5% of species). The human tendency (admittedly imperfect) toward long-term mating partnerships and male parental care makes this analogy particularly interesting. A much more telling difficulty for the sexual selection hypothesis, in my opinion, is the very early maturation of music perception and singing behavior in human infants, and the universal use of song between mothers and their infants.⁸² Such early maturation is quite atypical of sexually selected traits in the animal kingdom, which typically appear in their mature form only upon sexual maturity, when they are needed. Thus, despite an intuitive appeal, there is currently little data supporting the role of sexual selection and mate choice as the sole or primary selective force underlying the specific human

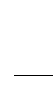
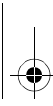
capacity for song and vocal learning, or other subcomponents of the music faculty, and skepticism seems warranted until such data have been gathered.

Music and Social Groups

A second possibility for the function of song derives from its potential role in increasing group solidarity, consistent with the apparent role of music in defusing tension and cementing individual and group relationships in today's world. This argument has been presented in detailed form by Robin Dunbar,^{83,84} who suggested that an increase in group size over the course of human evolution necessitated ever-more-sophisticated mechanisms for maintaining group harmony. In most primates, the social bonds underlying group solidarity are maintained by grooming (via its physiological concomitants, such as endorphin release). By this hypothesis, the intensive, one-on-one nature of the grooming relationship became inadequate once group size increased beyond a certain limit and was replaced by "vocal grooming" that allowed a single vocalizer to simultaneously service multiple listeners, and thus cement multiple relationships simultaneously. Given the centrality of individual relationships and group membership in chimpanzees, and the apparently increasing importance of group solidarity later in hominid evolution, the notion that some novel mechanism helped maintain group cohesion during human evolution is plausible, and Dunbar's hypothesis is consistent with a considerable mass of comparative, neural, and archaeological data. Although Dunbar situates his hypothesis in the context of the evolution of language rather than music, he makes clear that in the early stages of his hypothetical phylogeny, vocal grooming was devoid of propositional meaning and thus more akin to song than to speech. Thus, this group cohesion function is consistent with Darwin's notion of a music-like protolanguage (see below). Again, however, I know of no empirical data clearly demonstrating a specific role for music in enhancing group harmony or coordination in the scientific literature, providing another promising topic for empirical research.

Music and Caregiving

A third possible function of music, specifically song, concerns its role in parent-offspring communication and, in particular, the mother's song to regulate infant arousal.⁸⁵⁻⁸⁷ The mother-infant relationship represents a specific, intense social bond, rendered particularly important in humans (and apes) by our long childhood and lengthy interbirth interval, making each child an unusually valuable investment. The use of lullabies to quite effectively soothe infants to sleep is apparently a human universal, practiced in all cultures.⁸² Given the potential detrimental effects of crying or upset infants throughout our evolutionary history, the success of parents in achieving the goal of keeping their children quiet could be of considerable adaptive relevance to the evolution of song. Similarly, the use of play songs to arouse infants, focus their attention, and strengthen the mother-infant bond is both widespread and potentially adaptively relevant. Thus the considerable data supporting the effects of music on mood and arousal are compatible with this hypothesis.^{88,89} The extremely early development of music perceptual abilities, while incompatible with sexual selection, is obviously nicely explained by the caregiving hypothesis. A documented infant preference for song over speech provides an argument against the null hypoth-



esis that song is simply a nonadaptive by-product of speech. Finally, the childcare hypothesis is compatible with Dunbar's vocal grooming hypothesis, as well as related arguments for the evolutionary significance of motherese.^{90,91} The efficacy of song in general social bonding might derive evolutionarily from its prior development in mother–infant communication (much as many courtship displays are evolutionarily derived from parent–offspring displays, e.g., begging displays). Thus, many of the arguments for vocal grooming and group cohesion can be applied, *mutatis mutandis*, to the caregiving hypothesis. I conclude that the childcare hypothesis represents the account of the adaptive function of music currently most firmly grounded in data.

Summarizing this section, debates about the adaptive function(s) of music will remain difficult to resolve. Certainty about the past adaptive function of music will be hard to achieve, because it is likely that the function(s) of music has changed over evolutionary time, or that music has served (or continues to serve) multiple adaptive functions sequentially or simultaneously. Despite its interest, the question, Is music an adaptation? is thus not necessarily the most productive focus for discussions of the biology and evolution of music. In striking contrast to the amount of published speculation, empirical data on function are scarce, but a wide variety of data could potentially inform the issue, and might readily be collected. Thus, this topic provides clear opportunities for future empirical study, and the adaptive hypotheses already on offer will hopefully spur a new crop of experimental and comparative studies rather than further speculation.

THE PHYLOGENY OF MUSICAL ABILITIES

For behavioral traits, questions concerning phylogenetic history are often the most difficult to answer, and the phylogeny of human musical abilities is no exception. The lack of relevant fossils for most behavioral traits puts strict limits on what we can know with certainty about past history of a trait. There are few fossil cues that are relevant to the evolution of singing. The most convincing possibility so far is due to MacLarnon and Hewitt,⁹² who examined the size of the thoracic intervertebral canal in extant primates and various fossil hominids. Because some of the motor neurons involved in the fine control of breathing are housed in the thoracic canal, these authors proposed that the enlargement of this bony space during the evolution of the genus *Homo* indicates an increase in the fine respiratory motor control involved in vocalization. Based on the fossil data, this occurred at some point after *Homo ergaster*, an early member of our own genus. Although the authors situated their arguments in the context of speech evolution, they are equally (if not more) relevant to singing.⁵⁹ Singing requires both greater respiratory capacity (both in terms of air volume and subglottal pressures) and finer control than that necessary for normal conversational speech.⁹³ Thus, these data can be reinterpreted, perhaps more convincingly, as pushing the onset of singing back to before the split between Neanderthals and modern humans.

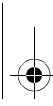
Regarding instrumental music, we are on firmer archaeological ground.⁹⁴ A wide variety of fossil musical instruments have been discovered (incidentally making our material evidence for instrumental music far stronger, and far older, than fossil evidence for language). The oldest indubitable musical instrument is a fine bone flute

found in Geissenklösterle in Germany, associated with modern human remains, reliably dated to 36,000 years ago.⁹⁵ More tantalizing, but far more controversial, is a multiply pierced cave bear bone found associated with Neanderthal remains in Divje Baba, Slovenia, and considered by its discoverers to be a flute. Although not much older than the Geissenklösterle flute (the Divje Baba artifact is dated to 40,000 years ago), its association with Neanderthals would push the evolution of instrumental music to before the split between Neanderthals and modern *Homo sapiens* (at least 200,000, and more likely 500,000 years ago).⁹⁶ According to some scholars, this split predates the evolution of spoken language, and a Neanderthal flute would then provide quite strong evidence that music preceded language in our evolutionary history. Unfortunately, both pieces of evidence are controversial. First, the fossil evidence for the evolution of human speech is very tenuous,³⁷ and the timing of the origin of spoken language remains highly controversial. Furthermore, critics of the Divje Baba find⁹⁷ claim that it represents not a hominid artifact, but a bone pierced by carnivore teeth (for discussion and further references, see Ref. 98). Thus, the currently available paleontological data do not strongly constrain hypotheses about the origin and phylogenetic history of human music.

Given this, it is unsurprising that speculative hypotheses fill the literature on this topic. This older literature is well reviewed,⁹⁹ with a brief synopsis in English.¹⁰⁰ Rather than review these many hypotheses here, I will end by reviewing a phylogenetic hypothesis that seems, to me, quite plausible, and which more importantly illustrates the value of incorporating comparative principles—a fitting end for the current review. This is Darwin's hypothesis of a music-like protolanguage.⁴⁹ Although Darwin's comments on this topic were brief, they concisely lay out the idea (often rediscovered or rehearsed without attribution by modern scholars¹⁰¹) that an intermediate stage of human evolution, before the evolution of language, was characterized by a vocal communication system more similar to modern song than to modern speech.

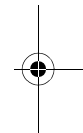
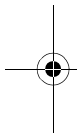
Recognizing that music is a human universal “present...in men of all races, even the most savage,” Darwin clearly felt that human musical ability warranted an evolutionary explanation. However, he concluded that “as neither the enjoyment nor the capacity of producing musical notes are faculties of the 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.” After briefly discussing the comparative evidence regarding learned birdsong and gibbon vocalizations, Darwin concluded that “primeval man, or rather some early progenitor of man, probably first used his voice in producing true musical cadences, that is in singing.” Regarding function, and again drawing on the comparative data, Darwin suggested, based on “widely-spread analogy, that this power would have been especially exerted during the courtship of the sexes, would have expressed various emotions, such as love, jealousy, triumph, and would have served as a challenge to rivals.” Finally, Darwin contrasts his theory to that of Spencer and Diderot that music is derived from speech. Thus, Darwin's musical protolanguage hypothesis holds that a music-like communication system, based crucially on vocal learning and lacking propositional meaning, predates true language.

Darwin's hypothesis has much to recommend it,¹² and many biologically oriented researchers find it plausible.^{5,40,41} First, the frequent convergent evolution of song-like communication systems in many vertebrate lineages suggests that, given the proper conditions, complex, learned song evolves relatively easily. This is in



sharp contrast to spoken language per se that, as a vehicle for conveying discrete propositional meaning, appears to be uniquely human. The many similarities between music and language mean that, as an evolutionary intermediate, music really would be halfway to language, and would provide a suitable intermediate scaffold for the evolution of intentionally meaningful speech. Darwin's hypothesis is compatible with the paleontological data reviewed above and with the observation of considerable, but not total, overlap in the brain mechanisms underlying music and language.²⁻⁴

The hypothesis also makes some testable predictions: Darwin's hypothesis predicts a correlation of individuals' skills in components shared by music and language (e.g., phonetic and phonological skills), but deviation in those that are not shared (e.g., semantic interpretative abilities). This can easily be tested, for instance by examining individual variability among modern humans in particular subcomponents of the musical versus linguistic faculties. As more genetic data becomes available, and our understanding of the genetic bases for music and language improves, we can further predict a partial overlap of genetic determinants of the two traits. Furthermore, to the extent that different genes are involved in the two domains, the stamp of selection, as estimated via techniques like those applied to language,¹⁰² should be much older in genes underlying music than those involved in speech, and we would expect to see indicators of relaxed selection pressures on musical capabilities during recent postlinguistic human evolution. Regardless of the ultimate fate of Darwin's hypothesis, such data would represent a useful integration between biolinguistics and biomusicology, as well as valuable steps forward in our mechanistic understanding of the biology and evolution of music. Indeed, phylogenetic hypotheses are perhaps most valuable as sources of clear empirical predictions that spur the collection of relevant data.



CONCLUSION

In summary, I have argued that the comparative approach has great promise to enrich our understanding of the biology of music and that data from animal behavior provide both inspiration for, and constraints on, theories of the evolution of music. More importantly, a more detailed exploration of the neural mechanisms and ontogenetic development of musical behaviors in other species potentially offers important insights into the analogous human capabilities. Data on birdsong have already provided an extremely fruitful source of insights into the genetics, endocrinology, physiology, and neural control of the most complex vocalization system known outside of human language and music. In sharp contrast, the potentially fascinating homology between great ape drumming and human instrumental music has been largely overlooked, but may offer equally useful insights into another major component of human musical behavior. The intraspecific comparative approach between music and other cognitive faculties seems equally promising, especially with language (though by no means excluding other arts, especially dance). Theories about the adaptive value and phylogenetic history of music have much in common with those for language, and there appears to be considerable room for mutual constraint and cross-pollination in discussing the evolution of music and language together. In this vein, Darwin's hypothesis of a music-like protolanguage holds considerable ap-



peal and appears to be consistent with much of the available comparative and neural data. The study of the biology and evolution of music (biomusicology) and language (biolinguistics) are cognate fields, with substantial potential for cross-fertilization and integration. Thus, the budding field of biological and evolutionary musicology seems to hold considerable promise, both for understanding music itself and for a deeper understanding of other aspects of complex, biologically based, but culturally contingent human cognition.

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