

The evolution of the music faculty: a comparative perspective

Marc D Hauser^{1,2} & Josh McDermott^{2,3}

We propose a theoretical framework for exploring the evolution of the music faculty from a comparative perspective. This framework addresses questions of phylogeny, adaptive function, innate biases and perceptual mechanisms. We argue that comparative studies can make two unique contributions to investigations of the origins of music. First, musical exposure can be controlled and manipulated to an extent not possible in humans. Second, any features of music perception found in nonhuman animals must not be part of an adaptation for music, and must rather be side effects of more general features of perception or cognition. We review studies that use animal research to target specific aspects of music perception (such as octave generalization), as well as studies that investigate more general and shared systems of the mind/brain that may be relevant to music (such as rhythm perception and emotional encoding). Finally, we suggest several directions for future work, following the lead of comparative studies on the language faculty.

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 among the most mysterious with which he is endowed. –Charles Darwin¹, p. 878

Throughout human history, on every part of the globe, in every extinct and extant culture, individuals have played and enjoyed music. Music is a fascinating topic for cognitive scientists because it raises important questions about perception, cognition, emotion, learning and memory. But perhaps the most intriguing question about the music faculty concerns its evolutionary origins: given its omnipresence in human culture, why is there no clear-cut adaptive function? Unlike language, which allows us to communicate our thoughts to others through sounds or signs, music has no readily apparent functional consequence. The origins and adaptive significance of music thus remain deeply mysterious^{2–4}.

In the present review, we provide a framework for studying the evolution of the music faculty. We begin by laying out what we consider to be the relevant theoretical issues for such an investigation, then we review what is currently known about the evolution of music from a comparative perspective^{4–6}, and finally we highlight new methods and studies that will bear most directly on the theoretical framework we favor.

A theoretical perspective on the music faculty

The theoretical perspective we favor is in part inspired by Noam Chomsky's analysis of language⁷. Although analogies between music and language are commonplace in cognitive science^{3,8–10}, we suggest

that the questions and distinctions that have been central to understanding language have been lost or inadequately addressed in discussions of the evolution of music. We therefore begin by sketching out some of these questions and distinctions as they apply to music.

Decades ago, Chomsky set out to explain how all mature speakers of a language can both generate and interpret a limitless number of sentences. He drew attention in particular to the problem of grammaticality: for any given language, certain sentences seem grammatical to nearly all speakers of a language, whereas other sentences seem ungrammatical. The fact that all speakers of a language can make this distinction, independent of their education, suggests that language processing involves the operation of principles that define sentence structure within a given language. He used the phrase “knowledge of language” to refer to these unconscious and potentially inaccessible principles that guide grammaticality judgments as well as sentence comprehension and production. The principles shared by all humans constitute our universal grammar, and the specific settings of such principles constitute the grammar of any given language. Chomsky's framework for understanding language is devoted to understanding what these principles are and how they come to be instantiated in the brain through the combination of genetic constraints and linguistic experience.

Music is at least superficially similar to language in that certain acoustic stimuli are recognized as music by most members of a given culture, even if these sounds have never been heard before. Conversely, there are other stimuli that nearly everyone recognizes as unmusical (such as a ‘sour’ note in a melody). It thus seems meaningful to speak of ‘knowledge of music’ just as Chomsky spoke of knowledge of language. Such knowledge differs fundamentally from the kind of knowl-

Department of Psychology and Program in Neurosciences¹ and Primate Cognitive Neuroscience Lab², Harvard University, 33 Kirkland Street, Cambridge, Massachusetts 02138, USA. ³Department of Brain and Cognitive Sciences, Massachusetts Institute of Technology, 77 Massachusetts Avenue, Cambridge, Massachusetts 02139, USA. Correspondence should be addressed to M.D.H. (mdhauser@wjh.harvard.edu) or J.M. (jhm@mit.edu).

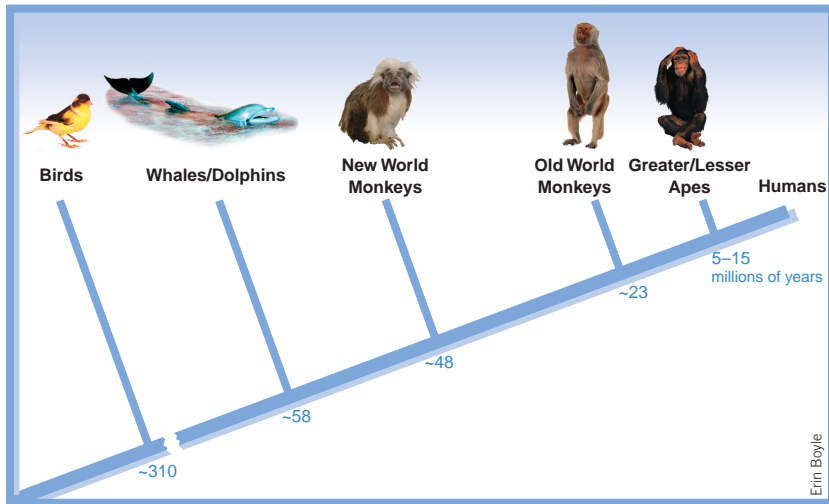


Figure 1 Phylogeny of some of the relevant taxonomic groups used in studies of the origins and evolution of music; divergence times based on recent molecular data are presented at the nodes.

existence demonstrates that some features of music may be innate. A thorough characterization of the aspects of musical knowledge that are independent of musical experience will place strong constraints on possible evolutionary explanations.

The second question concerns how the initial state of knowledge is transformed into the mature state of music perception that characterizes adult humans within a culture. This is a question about both musical experience as well as the development of other domains of cognition and perception that interface with music. Some subordinate questions concerning innateness arise: Is

edge one gains by studying music theory or by learning to perform a piano piece by Bach. Instead, it is acquired through normal exposure to music within a culture, without training, just as linguistic knowledge is acquired through normal exposure to language, independent of formal education. By drawing an analogy with language, we do not mean to imply that the notion of a universal grammar, with its constituent principles, is directly applicable to music. Indeed, with the exception of work by Lerdahl and Jackendoff⁸, there are few proposals for what the principles underlying the mature state of musical knowledge might be. Instead, we suggest that the questions that have guided research on the evolutionary and developmental origins of language may be a useful place to begin understanding the origins of music. In particular, there are three main questions—similar to those posed by Chomsky—that we think should guide research and discussion about the origins of this musical knowledge:

1. What is the initial, innate state of knowledge of music prior to experience with music?
2. How is this initial state transformed by relevant experience into the mature state of music knowledge?
3. What is the evolutionary history of the initial state and the acquisition processes that guide the development of musical knowledge?

In contrast with language and other cognitive systems that have been examined from an evolutionary perspective (such as mathematics, vision and morality)^{3,11,12} we have few answers to these questions for music. It is therefore important at this stage to be clear about what each question entails and what it demands in terms of empirical tests.

The first question concerns whether there are any initial constraints on music perception, independent of musical experience within a culture. Before we can reasonably entertain hypotheses concerning the evolution of the music faculty, we must first determine which, if any, features of music are innate and are therefore candidates for evolutionary explanation. Cross-cultural data suggest that there are indeed innate constraints on music, as evidenced by the universality of particular features of music across cultures with fundamentally different musical genres or styles (for example, the widespread use of scales based around the octave, with 5–7 pitches per octave). These constraints may well not be specific to music, and could instead be reflections of general features of perception and/or memory; however, their

there a critical period for music perception and comprehension during which a child must be exposed to music in order to develop normal, music-specific perceptual abilities? Is there a ‘poverty of the stimulus’ problem as there is in language, whereby musically relevant data are sparse enough to lead us to invoke innate principles in explaining the development of normal music perception? In addition, do apparent cross-cultural variations in musical expression coexist with universal, homogeneous principles or organization? Here the absence of accepted theories of the principles underlying mature knowledge of music may make its investigation fundamentally different from that of language. For example, without evidence of a clear set of principles underlying music perception, and with little understanding of the relevant musical data that are available to the developing child, we can only guess whether there is a poverty of the stimulus problem.

The third question turns to evolution, and in particular, to both questions of adaptation and phylogeny. Supposing that there are non-trivial innate constraints on music, where do they come from? More specifically, we must address whether music can properly be considered an adaptation and if so, what kind of problem it was designed to solve, when, and by which species. Some argue, following Darwin, that music evolved as a sexually selected system, designed to attract mates and signal mate quality^{1,2}. Others think that music functions to coordinate coalitions, and thus serves a more group-oriented function¹³. And still others believe that music serves no adaptive function, and is simply a fortuitous side effect of various perceptual and cognitive mechanisms that serve other functions³. At present, we lack the empirical evidence needed to test these ideas, so there is little basis on which to choose between the various hypotheses. For this reason, we focus this review on comparative data from nonhuman animals (Fig. 1) that bear on the extent to which different features of music perception are shared across species; this is the kind of evidence that we believe should constrain evolutionary hypotheses concerning music. Such data have been slowly accumulating over the past 15 or so years, and new methods have recently been developed that are likely to increase the range of problems addressed. Thus, a rich comparative data set will enable us to (i) document patterns of evolution (for example, distinguish between homoplasies—traits that are similar because of the evolutionary convergence of two distinct lineages—and homologies, which are traits that descend from a common ancestor), (ii) identify adaptations and (iii) more fully understand the innate principles that underlie music perception. Such evidence will, in turn, help focus studies at the neurophysiological level.

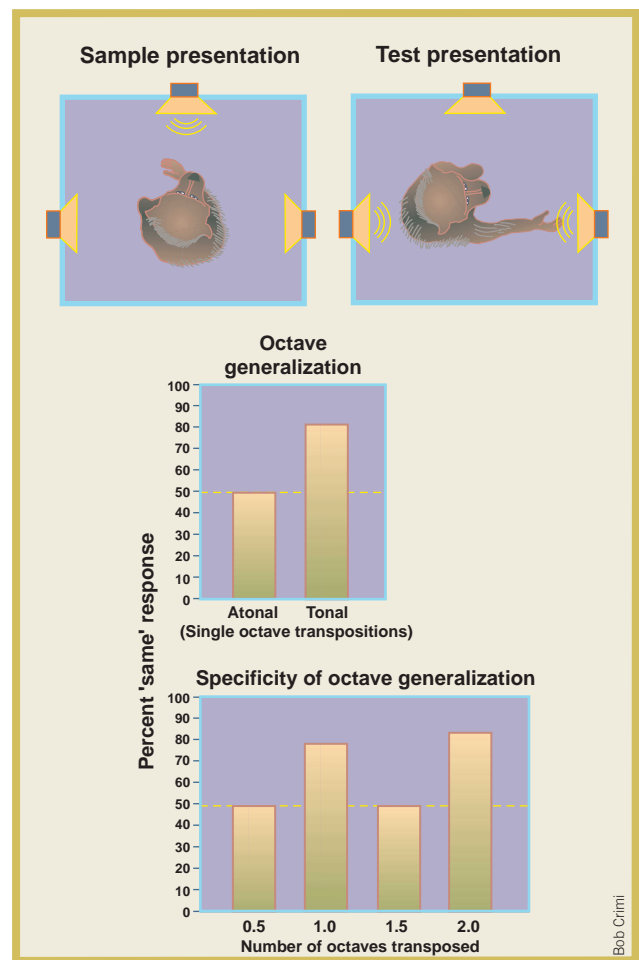
Figure 2 Rhesus monkeys show octave generalization. Top, experimental task. Subject is presented with a sample sound from the center speaker. In the test presentation, one sound is presented simultaneously from both of the lateral speakers. Subjects respond by touching one of the lateral speakers if the test and sample are the same, and the other if they are different. Middle, subjects' 'same' responses when presented with a tonal or atonal sequence of notes in the sample that has been transposed one octave in the test phase. Bottom, subjects' 'same' responses when presented with tonal sequences that have been transposed at 0.5-octave intervals. Modified from ref. 19.

Evolutionary and developmental approaches

Many developmental studies on music perception in human infants (see accompanying review by Trehub¹⁴ in this issue) suggest that particular abilities or capacities are innate, as they appear early in development and in the absence of relevant experience. Experiments in infants are generally plagued by a common problem, however: it is nearly impossible to control for the level of early exposure to music, especially because the fetus can hear a filtered version of sounds in the external environment by the third trimester of pregnancy^{15,16}. In addition, developmental studies typically only test infants from Western cultures, and therefore cannot determine whether exposure to different kinds of input can alter early musical preferences and perceptual discriminations. It is thus difficult to rule out the possibility that many of the seemingly innate traits found in infants actually result from early exposure to music. Herein lies one of the key contributions of comparative research: studies of nonhuman animals can precisely control what individuals do and do not hear, and thus can more readily address the question of whether particular capacities depend on particular experiences. If animals reared without exposure to music develop features of human music perception, there is good reason to assume that they are innate features of the brain.

Moreover, since nonhuman animals do not normally make or experience music themselves, any features of music perception found in animals cannot be part of an adaptation for music, but must instead represent a capacity that evolved for more general auditory analysis. This second key role of comparative data is most evident in recent studies on language¹⁷. It is now clear that many, if not most, of the mechanisms underlying speech perception are shared with other animals, the implication being that it is unlikely that these mechanisms evolved for the specific purpose of perceiving speech. Rather, a more parsimonious explanation is that the mechanisms represent more general solutions to problems of auditory perception that, over evolutionary time, were co-opted for speech perception in humans. Although many perceptual mechanisms may be shared across primate species, the infinite generative capacity of humans (in language or number, for example) may be unique to our species (but see ref. 18 for a possible exception).

Comparative data also hold promise for understanding the evolution of music. The two contributions of comparative data are perhaps best illustrated with an example, for which we turn to a recent study on rhesus monkeys. Wright and colleagues¹⁹ trained two monkeys to make same/different judgments on successively presented auditory stimuli (various natural and environmental sounds such as animal calls, car horns, and so on), and then substituted short melodies as stimuli to see whether the monkeys would judge melodies to be the same, even if the comparison melody was transposed (moved up or down in pitch) with respect to the original (Fig. 2). Previous studies with other non-primate animals did not find evidence of generalization across transposition (for review, see refs. 5,6). Wright and colleagues find that like humans, the rhesus monkeys showed octave generalization—they tended to judge two melodies to be the same



when transposed by one or even two octaves. The octave was found to hold a privileged status, however: the monkeys failed to generalize if the melodies were transposed by 0.5 or 1.5 octaves, leaving the notes physically closer to the originals but changing the key. Most interestingly, octave generalization occurred only for melodies taken from the diatonic scale. When the monkeys were tested on atonal melodies whose notes were chosen randomly from all 12 tones of the chromatic scale, there was no evidence of octave generalization. This difference could arise either because the monkeys were unable to remember atonal melodies, or because atonal melodies were remembered but not represented in a manner that permitted them to be matched to transposed versions. One explanation is that the monkeys encode tonal melodies relative to their key and use this encoding to do the task; this would facilitate their capacity to recall the melody and respond with the correct match. Either way, the results¹⁹ indicate that tonal melodies have special status even in nonhuman primates.

This study by Wright and colleagues¹⁹ aptly illustrates the two ways in which comparative data constrain our answers to the questions raised above. Barring the possibility that incidental music exposure affected the monkeys' performance, these results are the strongest evidence yet that there are innate constraints on music perception. Because monkeys do not produce music on their own, the fact that they possess musical sensitivity suggests that at least some aspects of music perception are determined by general properties of the auditory system. Specifically, these results indicate that there are fundamental differences in the way that tonal and atonal melodies are encoded by

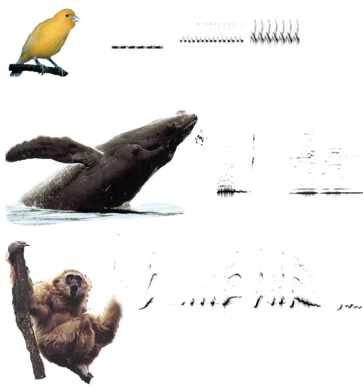


Figure 3 The primary classes of animals that sing. Sound spectrograms are shown for a canary (photo by Stefan Leitner), humpback whale (photo by Peter Tyack) and white-handed gibbon (photo by Thomas Geissmann).

the brain²⁰, independent of the role they play in music perception and production in humans. Moreover, the fact that monkeys, but not songbirds, have the capacity for melody transpositions, suggests that this capacity evolved after the divergence of birds and mammals. Whether this particular capacity represents a homology or homoplasy remains an open question, as similar studies have yet to be carried out in other Old World monkeys or, more importantly, in any of the apes.

It should be emphasized, though, that the strength of these conclusions depends critically on whether the monkeys had exposure to Western music before the experiments. It is common for monkey facilities to have a television set for the monkeys to watch, and the monkeys could have been exposed to a considerable amount of music this way, the potential effect of which is difficult to assess. It would therefore be ideal to repeat the experiments using animals that had been carefully shielded from any musical exposure, or to titrate the level of musical experience and assess whether it impacts performance. Furthermore, although the results have some intuitive plausibility, they do not fit with findings in humans as well as one might hope. First, there is some reason to doubt that musical key is automatically extracted by the auditory system, as infants seem to lack much of the sensitivity to key structure that is found in adults²¹. Second, key distance effects in adult humans performing music recognition tasks are usually weak and are only found under specific experimental conditions^{22,23}; adult listeners are generally quite good at recognizing melodies independent of the key they are played in^{24,25}. Monkeys in the Wright *et al.* study, by contrast, almost never categorized two melodies as the same if they were played in different keys. Third, any similarities that exist at the behavioral level need not reflect similar neural mechanisms²⁶. There may thus be important differences in how macaques and humans encode melodies, and there is clearly a need for additional research on this topic. However, the Wright *et al.* study alone amply shows how powerful comparative data can be.

A second study addressing music perception in animals involves neurophysiological recordings of responses to consonant and dissonant chords in macaques and human patients suffering from epileptic seizures. It has long been suggested that consonance and dissonance might be distinguished by the amplitude modulation, or beating, that occurs in dissonant chords due to the interactions of overtones at the level of the cochlea. Fishman and colleagues²⁷ sought to characterize how consonant and dissonant stimuli are represented in the cortex. Recordings were collected from the primary auditory cortex of awake rhesus monkeys during the presentation of chords created from two

simultaneously presented, harmonic, complex tones; dissonant chords consisted of minor and major seconds, whereas consonant chords consisted of octaves and perfect fifths. Results show clear differences in neural responses, with the magnitude of the oscillatory phase-locked activity highly correlated with the extent of dissonance. Specifically, when dissonant chords were played, neural activity was phase-locked to the difference frequencies (that is, the frequency of the beating); consonant chords showed no phase-locked activity, consistent with the relative absence of amplitude modulations in such stimuli. Virtually identical neural signatures were observed in the patient recordings, albeit only from electrodes placed in Heschl's gyrus as opposed to those placed in the planum temporale. Thus, in both humans and rhesus, synchronous, phase-locked activity of neurons in primary auditory cortex signal the degree of sensory dissonance, consistent with the Helmholtzian notion that differences in the peripheral encoding of consonant and dissonant stimuli are perceptually important. It remains to be seen whether consonant and dissonant stimuli will produce different degrees of pleasure/aversive responses in animals, as they do in humans. For example, studies of human infants indicate that by 16 weeks of age, babies turn away from a speaker playing dissonant chords and often fuss and cry; in contrast, they look toward the speaker playing consonant chords and often smile^{28–30}. Preliminary data from our lab suggest that the cotton-top tamarin has no such preference for consonant over dissonant stimuli, but it will be important to explore the issue in other species as well.

At present, there are few other comparative studies directly related to music that address the sorts of questions raised above. However, as in current comparative work on language¹⁷, we can also ask whether some general mechanisms that might be used by our music faculty during perception are present in other animals. Here we highlight a few key examples to illustrate how one might go about fleshing out the comparative research program that we champion.

It is commonly claimed that the adaptive function of music is to regulate or at least influence our emotions. Indeed, the emotional effects of music are central to people's enjoyment of it, but the fact that particular acoustic patterns influence our emotional states is not unique to music or to humans. We have known since Darwin's time that animal vocalizations are shaped by natural selection to convey specific information about the caller's emotional state. For example, many submissive or affiliative calls tend to be harmonically structured, often quite richly so; attention-getting signals often have rising frequency contours; aggressive calls are often short, staccato bursts; and so on. Interestingly, many of these patterns appear in human vocalizations, including our purely emotive sounds (laughter, crying), the paralinguistic signals that ride *atop* our linguistic utterances, infant-directed speech (commonly known as motherese)^{10,31–33} and even the sounds we use to train animals^{34,35}. Human and nonhuman animals thus encode emotional information in their vocalizations and have perceptual systems that are designed to respond appropriately to such signals. Given its evolutionary ancestry, our music faculty may well have co-opted this mechanism for use in music, even if it did not evolve for this function. One recent cross-cultural study examined whether Westerners perceive the same emotions in North Indian ragas as do native Indians³⁶. They found that Westerners and native Indians often make very similar judgments of emotion, suggesting that at least some of the cues to emotion in music (most obviously tempo, but also perhaps characteristic pitch changes and/or modes) are shared across cultures, providing further evidence that there may be innate mechanisms for perceiving emotion in music that composers and musicians aim to engage. It remains to be seen whether these emotional mechanisms bear any relation to the vocal and perceptual mech-

anisms that we apparently inherited from our nonhuman ancestors.

As in music, languages have different rhythmic properties, although the precise definition of rhythm differs between these domains, with music placing more emphasis on beat or timing of particular musical notes and language focusing on the overall frequency contours and durations of particular phonemic clusters. Ramus and colleagues³⁷, in particular, propose an empirical measure of rhythm in language defined as the proportion of time occupied by vowels; this measure provides an excellent fit with classical taxonomies of language using more subjective notions of rhythmic class^{38,39}. Developmental studies in humans show that at an early age, infants can discriminate sentences from two non-native languages in different rhythmic classes if the sentences are played in their normal, forward direction. Discrimination fails if the sentences are played backwards^{40,41}, presumably because onset cues are critical to hearing the rhythmic differences; we know from several neurophysiological studies in primates that onset cues are particularly salient⁴². This capacity, appearing as it does early in development, raises specific questions about whether it is in fact innate, unique to humans, and due to the rhythmic properties of language. To address these issues, a comparative study of newborn human infants and cotton-top tamarin monkeys was initiated using the same stimuli and spontaneous, non-training methods⁴³. In particular, both species were habituated to sentences from one language group and then tested with sentences from a different group; the focal languages, representing different rhythmic classes, were Dutch and Japanese. Although the dependent measure was sucking in newborns and an orienting response in tamarins, all other aspects of the methods were the same. Results showed that both species can discriminate sentences from these two languages, but only if played in their normal, forward direction. These results suggest that like human newborns, tamarins have the capacity to discriminate languages based on their rhythmic cues, and that similar acoustic features (namely, the abrupt onsets provided by sounds such as consonants) may be critical to how rhythms are represented in both species. These findings allow us to draw an important comparative point: although human infants may be equipped with a capacity to discriminate languages on the basis of rhythmic cues, the presence of this capacity in nonhuman primates that lack language suggests that it evolved for more general auditory purposes. This, in turn, suggests that some aspects of rhythm perception for music may be tapping domain-general auditory mechanisms that may well have been in place before our species began producing music. Further experiments comparing human and primate rhythmic discrimination with nonlinguistic stimuli could help to bolster this claim.

Future directions

As comparative work on music is still in its infancy, there is much left to be done. We will conclude by highlighting a few of the most promising directions for future research.

First, much can be learned from simply attempting to replicate many of the human developmental studies in animals, using some of the same spontaneous techniques that have proved effective in studies of language perception¹⁷. Research by Trehub and others has revealed a host of intriguing musical sensitivities in young infants (reviewed in this issue¹⁴). Infants are better at discriminating changes to 'natural' musical intervals (those defined by simple integer ratios between the frequencies of the two tones) such as fifths and octaves than to 'unnatural', complex ones such as tritones or minor seconds⁴⁴. Discrimination is also better for tonal melodies than for atonal ones⁴⁵, although this may in part derive from the fact that tonal melodies tend to contain more natural intervals than do atonal melodies. It is impressive that these effects can be found in infants as young as six months,

but it is nonetheless quite possible that some or all of the effects result from prior exposure to Western music; we have no way of knowing whether the exposure to music is sufficient to account for the musical competences observed. Analogous studies in animals completely deprived of music would help to settle the matter decisively and would also shed light on the extent to which these effects represent music-specific adaptations.

Comparative work could also inform investigations into how music exposure alters knowledge of music. Although the developmental literature has revealed numerous musical sensitivities and preferences in infants, there are also several documented instances where infants lack sensitivities found in adults. For instance, although adults respond very differently to melody perturbations that violate key compared to those that don't, infants are equally sensitive to the two sorts of changes, suggesting that key structure may be learned from musical exposure²¹. One can again ask whether the acquisition mechanisms at work are general features of the auditory system or specific adaptations for music. If comparable key sensitivity can be elicited in animals through controlled exposure to music, the most parsimonious account would favor a general auditory mechanism.

A third promising line of research concerns analyses of animal vocalizations. Throughout this review, we have not discussed animal songs, which are perhaps the most obvious animal phenomenon relevant to music (Fig. 3). It is relatively clear that animal songs are neither homologous nor analogous with human music. With respect to homology, none of the other great apes sing, indicating that our last common ancestor did not sing. With respect to analogy, though other species sing, the context for singing is extremely limited and defined by its role in the adaptive context of territory defense and mate attraction^{46,47}. Moreover, although animal song may modulate the emotions of its listeners, its sole function is communicative, with no evidence of solo performances, practice or productions for entertainment. Human singing, though clearly communicative, is notably different in that it is characteristically produced for pure enjoyment. Another difference is that in most nonhuman singing species, singing is predominantly a male behavior, which is not true for humans. Animal song thus likely has little to do with human music. Although animal songs are unlikely to be analogs of human song, and thus their evolution unrelated to the evolution of human music, there may be insights to be gained from their analysis. Supposing that there are general auditory constraints imposed on the structure of human music by the brain, such constraints are likely present in animals as well, and may influence their vocalizations. If animal vocalizations evolved to be easy to remember or encode⁴⁸, and constraints on what is easy to remember or encode have shaped the nature of human music, then one might expect to find structural similarities between human music and animal calls/songs. It would thus be of interest to examine, for instance, the intervals separating pitches in animal songs, to see if they tend to approximate our 'natural' musical intervals.

In conclusion, we have argued that a productive way forward in understanding music as a biological phenomenon is to anchor it in a framework similar to that laid out by Chomsky for language, and to raise questions concerning its evolutionary ancestry. By documenting patterns of convergence and divergence with music capacities in other animals, we will emerge with a clear picture of the uniquely human aspects of the music faculty as well as the building blocks that provided the foundation for its evolution.

ACKNOWLEDGMENTS

For comments on the paper, we thank R. Jackendoff and A. Patel. For support during the writing of this paper, M.H. acknowledges the McDonnell Foundation.

COMPETING INTERESTS STATEMENT

The authors declare that they have no competing financial interests.

Received 14 March; accepted 18 May 2003

Published online 25 June 2003; doi:10.1038/nn1080

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