THE ORIGINS OF MUSIC: INNATENESS, UNIQUENESS, AND EVOLUTION

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THE ORIGINS and adaptive significance of music, long an elusive target, are now active topics of empirical study, with many interesting developments over the past few years. This article reviews research in anthropology, ethnomusicology, developmental and comparative psychology, neuropsychology, and neurophysiology that bears on questions concerning the origins and evolution of music. We focus on the hypothesis that music perception is constrained by innate, possibly human- and music-specific principles of organization, as these are candidates for evolutionary explanations. We begin by discussing the distinct roles of different fields of inquiry in constraining claims about innateness and adaptation, and then proceed to review the available evidence. Although research on many of these topics is still in its infancy, at present there is converging evidence that a few basic features of music (relative pitch, the importance of the octave, intervals with simple ratios, tonality, and perhaps elementary musical preferences) are determined in part by innate constraints. At present, it is unclear how many of these constraints are uniquely human and specific to music. Many, however, are unlikely to be adaptations for music, but rather are probably side effects of more general-purpose mechanisms. We conclude by reiterating the significance of identifying processes that are innate, unique to humans, and specific to music, and highlight several possible directions for future research.

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FROM THE PERSPECTIVE of cognitive science, music ranks among the most bizarre and fascinating features of human culture. Music is apparently universal, being found in every known human culture, past and present. It is incorporated into a vast array of cultural events, including weddings and funerals, religious services, dances, and sporting events, as well as solitary listening sessions. It can make people feel happy or sad, so much so that music is central to modern advertising campaigns. And people throughout the world spend billions of dollars annually on the music and clubbing industries. Despite this central role in human culture, the origins and adaptive function of music remain virtually a complete mystery. Music stands in sharp contrast to most other enjoyable human behaviors (eating, sleeping, talking, sex) in that it yields no obvious benefits to those who partake of it. The evolutionary origins of music have thus puzzled scientists and philosophers alike since the time of Darwin (1871).

Theories about the evolution of music abound. Many have suggested that music might be a biological adaptation, with functions ranging from courtship to social cohesion in group activities such as religion and war (e.g., Darwin, 1871; Merker, 2000; Miller, 2001; Cross, 2001; Huron, 2001; Hagen & Bryant, 2003). Still others have suggested that music is not an adaptation but rather a side effect of properties of the auditory system that evolved for other purposes (Pinker, 1997). These hypotheses need not be mutually exclusive; it may well turn out that some aspects of music are the result of general purpose auditory mechanisms, and others the result of music-specific adaptations. In any case, at present there is relatively little evidence to distinguish the various hypotheses. We suggest that rather than beginning with a debate about putative adaptive functions of music, a more reasonable goal for cognitive science, and a necessary first step for evolutionary psychology, is to establish whether any aspects of music are innate and thus potential targets of natural selection. Many if not most aspects of music might simply be acquired by general learning mechanisms through exposure to a culture, which would preclude an evolutionary story about music. Indeed, much of twentieth-century music theory is based on the notion that musical preferences are mostly an arbitrary result of history (Boulez, 1971). Schoenberg famously contended that given enough exposure, atonal music would become just as popular as tonal music, reflecting the popular view that musical

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preferences are largely a function of one's cultural upbringing (Schoenberg, 1984). And yet certain key features of music suggest the signature of an innate mechanism. Every culture in the world has some form of music, and most cultures have apparently developed music independently from each other. At the very least, therefore, there seems to be some innate machinery motivating the production and appreciation of music. A detailed account of the innate mechanisms underlying music and how they interface with cultural experience will place strong constraints on evolutionary explanations of music. This review, therefore, focuses on the various strands of evidence related to the innate mechanisms underlying music perception, with a key goal being to identify properties that are both unique to humans and unique to music as a specialized domain.

Theoretical Background

Having set out to discuss the origins of music, it might seem sensible to begin by defining what we mean by music. However, defining music is notoriously problematic given the diversity of musical phenomena that are found across the world (Nettl, 1983). Music is often said to involve combinations of tones, for instance, and yet pitch is a rather tangential component of many African musics, which rely more heavily on rhythm (Chernoff, 1979). In our view a definition of music is not particularly important at this stage as long as it is approximately clear what we refer to with the term. This might best be established ostensively over the course of the article, but there are a few features of music that seem worth noting here at the outset. First, by music we denote structured sounds produced directly or indirectly by humans. These sounds often vary in pitch, timbre, and/or rhythm. Second, these sounds are often made to convey emotions and to produce enjoyment, though not always. Thirdly, they often have complex structure, though not always. It follows from the heterogeneity of music that any hypothetical innate constraints on music might apply only to some subset of musical phenomena, however they may be defined. That said, there are aspects of music that are likely to be universal or at least quite widespread across cultures, as we will discuss shortly. Understanding the origins of these musical features will be important even if there are musical phenomena to which they do not fully apply.

We think an explanation of the origins and evolution of music will eventually benefit from framing discussion with some of the same questions that directed thinking on the origins and structure of the language faculty (Chomsky, 1986; Lerdahl & Jackendoff, 1983; Hauser, Chomsky, & Fitch, 2002; Hauser & McDermott, 2003). Given that music perception, like linguistic competence, may be the product of innate constraints shaped by environmental stimulation, a complete explanation will include characterizations of (a) the innate state of musical predispositions prior to experience with music, (b) how this initial state is transformed by the relevant experience into the mature state of musical knowledge, and (c) the evolutionary history of the initial state and of the acquisition processes that guide the development of musical knowledge. At present we know little about any of these. In this article, therefore, we focus on characterizing the initial, innate state.

Most of the kinds of evidence we will discuss do not directly demonstrate anything about the initial state of an organism, simply because it is difficult to study organisms in the absence of any experience. We will nonetheless speak of innate traits in the discussion that follows, following conventional usage of the term to denote traits determined by factors present in an individual from birth, even though the traits in question may not emerge until later in development. Our interest is in determining whether any features of music are the product of innate constraints, as it is these constraints that are the product of natural selection. The difficulty, of course, lies in the fact that the role of innate constraints is generally confounded with the role of the environment, i.e., exposure to music. All of the kinds of evidence we will discuss function in various ways to suggest that musical experience cannot account for certain characteristics of music perception. For instance, developmental studies can show that infants perceive music in many of the same ways as fully enculturated adults, even though infants have had minimal exposure to music; cross-cultural studies point to universals in the presence of dramatically different musical traditions, implying that musical exposure is not responsible for the shared features. Because the logic behind each source of evidence is somewhat distinct, we will begin by detailing the inferential role of the different sorts of evidence we will discuss.

Developmental Evidence

Perhaps the most obvious way to study whether any aspects of music perception are innate is to study infants, who lack the cultural exposure that all adults have been subject to. Developmental psychology has been a particularly rich source of studies relevant to the origins of music, due in part to the development of powerful tools to probe infants' minds. (See Trehub

[2003] for a review.) Developmental studies can also be difficult to interpret, as infants never completely lack exposure to music, especially if one considers in utero experience during the third trimester of pregnancy, when the fetus can hear.

Infants pose an experimental challenge because unlike an adult subject, they cannot verbally report on their experiences. Instead, developmental psychologists make use of the fact that changes that are salient to an infant attract its attention, which can be measured via nonverbal behavioral responses. Although the behavioral assays vary, the fundamental logic underlying the method is the same: Exemplars from one category are repeatedly presented until the infant's response—sucking a non-nutritive pacifier for neonates, looking or orienting to a stimulus presentation for older infants—habituates, at which point exemplars from either the same or a different category are presented. In a classic setup, a sample of music is played repeatedly from a speaker. Once the orienting response to the music habituates, the experimenter conducts test trials, some of which introduce some change to the music sample, such as a change in key or a rearrangement of the notes. If the infant is sensitive to the change that is made, then they will tend to look longer at the speaker following the trials containing the change.

This kind of developmental approach has the virtue that it allows for tests of musical sensitivity well before infants have the capacity to speak, sing, or act on the world. Nonetheless, the approach suffers from the fact that from the third trimester on, infants are exposed to an uncontrollable range of auditory experiences, some of which inevitably involve exposure to music (James, Spencer, & Stepsis, 2002). It is thus difficult to assess to what extent musical competence reflects early exposure followed by rapid learning or tuning, as opposed to innate capacities. Broadly comparative studies involving different cultures and different populations within cultures can help: Convergence across these populations, in the face of significant differences in auditory experience, would provide significant evidence of an innate signature. Such cross-cultural developmental studies are understandably rare, however.

Comparative Evidence

Another way to limit musical exposure and its effects is to study animals, whose musical experience can be carefully controlled. There have been relatively few studies of music-related phenomena in other species (although see below for discussions of early work by Hulse, D'Amato, and others), but we think the comparative approach is particularly powerful, as it can also provide constraints on evolutionary origins and adaptive specialization that are difficult to obtain in other ways.

Like a human infant, an animal cannot verbally report on its experiences, what it likes or does not like, what it considers the same, what it anticipates, and so on. In parallel with studies of human infants, however, animal studies have implemented a battery of tests to understand what animals think, perceive, and feel. Some of these tests are the same as those reported for infants, using the subject's spontaneous ability to orient or look longer at an unfamiliar or impossible event (Hauser & Carey, 1998). Other techniques involve training animals to detect or discriminate different classes of stimuli (e.g., Wegener, 1964). Once trained, the animals can be tested for generalization to new stimuli, the results of which can reveal the nature of their mental representations. For instance, such methods have been used to investigate whether transformations that preserve the identity of a melody in humans will also do so in animals (D'Amato, 1988; Wright, Rivera, Hulse, Shyan, & Neiworth, 2000).

Why study the animal mind if you are only interested in humans? Studies of animals can often shed light on the evolution of human traits, for instance, by helping to test if the trait in question is unique to humans and specialized for the function in question. If the trait is not uniquely human, tests in multiple species can reveal whether it evolved as a *homology* (i.e., inherited from a common ancestor that expressed the trait) or a *homoplasy* (i.e., shared across two distinct lineages lacking a common ancestor with the trait). Studies of animals can also help to establish whether the trait in question evolved as an adaptation to a particular problem. For example, although the descent of the larynx played an important role in shaping the sounds we use during speech production, a descended larynx has been found in other species, leading to the suggestion that its original function was for size exaggeration as opposed to speech (Fitch, 2000). Even uniquely human characteristics such as mathematics, moral rules, navigating subway systems, and so on are likely built on biologically ancient precursors, and comparative studies can help to reveal what they are and why they evolved.

Comparative studies are particularly powerful tools for investigating the evolution of music for at least two reasons (Hauser & McDermott, 2003). First, because so much of the debate surrounding the evolution of music concerns the role of learning through exposure, it is useful to be able to precisely control an organism's musical experience. Although practical and ethical concerns preclude such an approach in humans, animals in a laboratory can be deprived of exposure to music and then tested, using the methods described above, to see if they exhibit various perceptual effects found in humans. Under such conditions, music-related perceptual biases cannot be attributed to musical exposure and must be the result of the innate structure of the auditory system, perhaps in conjunction with nonmusical acoustic input.

Second, because nonhuman animals do not naturally produce music (as we define it; see below for discussions of animal song), any perceptual effect found in a nonhuman species cannot be part of an adaptation for music. If the perceptual phenomenon in question is determined to be homologous to that found in humans, it must have evolved for some purpose other than that of making and perceiving music, only to be co-opted for use in music. Comparative studies can thus provide insights into the evolution of music that are difficult to obtain with other methods.

Cross-Cultural Evidence

Other evidence comes from studies of music perception in different cultures (Nettl, 1956, 1983; Malm, 1996). Because different cultures have different musical traditions that in many cases developed independently of each other, common features provide evidence of innate constraints on what people are predisposed to perceptually discriminate, remember, and enjoy. As we shall see, these commonalities can either be features of the music itself or of the patterns of perceptual judgments subjects from different cultures make. Similar insights can be gained from investigations of what music was like in ancient cultures. Again, given the large window of time separating ancient and modern cultures, similarities between musical styles from different periods might indicate that there are innate constraints on the music cultures are likely to produce. Here there is some risk that common features might have been simply passed down across the ages and are not indications of anything built into the brain. Many features of music have, however, clearly undergone significant change over time. Those that have not most likely represent musical features that are stable given the brain's tendencies or constraints.

Neural Evidence

Genetic constraints on music might also be indicated by the existence of brain circuitry dedicated to music, i.e., circuitry that is used primarily during music perception or production. Such circuitry would be a candidate for an adaptation for music, just as the hypothesized functionally dedicated brain circuitry in other domains (motion perception: Newsome, Wurtz, Dursteler, & Mikami, 1985; face recognition: Kanwisher, McDermott, & Chun, 1997; theory of mind: Baron-Cohen, 1997; language: Caplan, 1995) are candidates for adaptations for those functions. Studies of patients with brain damage aim to show music-specific deficits—patients with problems recognizing melodies, for instance, who have otherwise normal hearing and unimpaired cognitive function (Peretz & Coltheart, 2003). Such patients provide evidence that the damaged brain area is specialized for music perception, perhaps as part of a music-related adaptation. However, damage in such cases, which often results from stroke, is typically diffuse, making it hard to pinpoint specific regions as the source of the problem. A larger issue is that even if there is evidence that part of the brain functions specifically for music perception, it is difficult to rule out the possibility that the music-specific structures in question emerged through a lifetime of musical experience rather than being the product of innate constraints.

We next turn to a more detailed discussion of these various findings, attempting to synthesize the core results as they bear on the innateness of music. We begin by discussing evidence for universal features of music and then turn to evidence for innate sensitivities to musical structure. From there we turn to experiments relevant to the origins of musical preferences and of the emotional responses to music. We conclude by discussing evidence for neural circuitry dedicated to music.

Universal Features of Music

Pitch

Although rhythm is arguably just as important, if not more so, to many cultures' music, pitch has received far more attention in the literature we will review. This is likely due to its importance in Western music and the resultant theoretical ideas about how pitch functions in music. By comparison, there are fewer frameworks available to Western scholars through which to view and discuss rhythm, and perhaps for this reason it remains less well studied and documented. There are surely many revealing cross-cultural observations that could be made with regard to rhythmic properties of music, but given the current state of music research, we will confine ourselves predominantly to discussions of pitch.

In music, the relationships between pitches are generally more important than the absolute values of the pitches that are used. A melody will be recognized effortlessly even if it is transposed up or down by a fixed amount, a manipulation that alters the absolute pitch but preserves the relative pitch distances. As far as we know, relative pitch is fundamental to how music is perceived in every known culture, so much so that it is rarely cited as a universal. However, the centrality of relative pitch suggests a role for an innately specified auditory mechanism for encoding stimuli in terms of the distances between pitches. As we will see, the ability to hear relative pitch is nontrivial and may not be shared by nonhuman animals. Of particular importance are the relationships between pitches separated by an octave, which are generally heard as having the same pitch chroma. Every developed musical system known to Western scholars is thought to be based in part on the similarity relations the octave defines among pitches (Burns & Ward, 1982). The role of the octave in turn is thought to be partially due to the mechanisms for perceiving pitch (Terhardt, 1974), which are likely to be shared by all mammals.

Several other features of human music that seem to be universal, or nearly so, concern the structure of scales, i.e., the sets of pitches used in music. For instance, nearly every known musical culture appears to produce music from a discrete set of five to seven pitches arranged within an octave range, such as the pentatonic and diatonic scales (Burns & Ward, 1982). Many have noted that the tendency to use a small set of discrete notes might be the product of well-known constraints on short-term memory and categorization (Miller, 1956).

Most scales found in music around the world also share the property of having pitches separated by unequal steps, e.g., one and two semitones in the case of the diatonic scale or two and three semitones in the pentatonic scales common to many forms of indigenous music. Various explanations have been proposed for the ubiquitous presence of unequal interval scales. Most involve the fact that unequal intervals result in each note of the scale having a unique set of interval relations with the other notes of the scale (Balzano, 1980, 1982; Shepard, 1982). This makes it possible to assign different functions to different notes (e.g., the tonic) and to have a listener easily recognize which note serves each functional role in a given melody (a functional assignment which will change depending on the key). Thus, for music theoretic reasons, such unequal-step scales are perhaps more desirable, and it is possible that they have culturally evolved among many different societies for this reason. It is also possible that melodies whose notes are taken from unequal interval scales are for some reason encoded more easily by the auditory system, an idea that we will return to in a later section.

Most musical systems also feature intervals (note pairs) whose ratios approximate simple fractions. Although memory constraints are typically invoked to explain the five or seven pitches that are usually used in musical compositions, this number of discrete pitches, as well as perhaps their spacing, could also originate in a sensory or computational bias to have intervals that approximate simple integer ratios (Dowling & Harwood, 1986). Even musical systems that sound relatively foreign to the Western ear, such as those of Java and Thailand, are said to feature an interval that approximates a perfect fifth. Interestingly, although intervals with simple ratios (such as the fifth and the octave) often have structural importance in melodies, their occurrence is relatively rare, at least if one considers the intervals between successive notes. In cultures all over the world, small intervals (one and two semitones) occur most often; the frequency of use drops exponentially with interval size above two semitones (Dowling & Harwood, 1986; Vos & Troost, 1989). Fifths and other intervals with simple ratios can be readily found in melodies, but they are usually reached via intermediate, smaller steps.

Thus despite the heterogeneity of music across the world, several common features are evident in the sets of pitches used in indigenous popular music. The focus on these aspects of pitch may reflect Western-centric biases, and their importance in music may vary from culture to culture, but their presence nonetheless suggests that music is shaped by constraints that are built into the brain. These common features will be further discussed below in the context of other methods of inquiry.

Lullabies

Lullabies—songs composed and performed for infants—are a particularly striking musical phenomenon found in cultures across the world and appear to represent a true music universal. Lullabies are recognizable as such regardless of the culture (Trehub, Unyk, & Trainor, 1993), even when verbal cues are obscured by low-pass filtering (Unyk, Trehub, Trainor, & Schellenberg, 1992). This suggests that there are at least some invariant musical features that characterize infant-directed music; this aspect of music directly parallels studies in language of infant-directed speech (Fernald, 1992). Lullabies are generally slow in tempo, are often characterized as simple and repetitive by adult listeners, and may feature more descending intervals than other melodies (Unyk et al., 1992). Both adults and children perform lullabies in a distinctive manner when singing to infants; listeners can pick out the version of a melody that was actually sung in the presence of an infant. Infant-directed singing tends to have a higher pitch and slower tempo than regular singing and carries a particular timbre, jitter, and shimmer (Trehub, Hill, & Kamenetsky, 1997b).

The characteristics of lullabies, as well as the particular acoustic properties that adults and children imbue them with when sung to infants, appear to be tailored to what infants like. When infants are played both lullabies and adult songs under similar conditions, adults who watch them on videotape judge the infants to be happier when played the lullabies than when played adult songs (Trehub, 2000). The fact that the preferred characteristics of lullabies are culturally universal suggests that infant preferences for lullabies are indeed innate. Further, because no other animal parent vocalizes to its offspring in anything resembling motherese or a lullaby, this style of musical expression also appears to be uniquely human. At this point the origin of lullabies and their particular features remain unknown, but their existence suggests that at least one major genre of music is predominantly innate in origin and uniquely human.

Ancient Instruments

Additional evidence for universal musical tendencies comes from archaeological discoveries of musical instruments and scores from thousands of years ago. If music were purely a cultural invention, one might expect ancient music to be dramatically different from modern music, given the huge cultural differences between then and now. Similarities between ancient and modern music provide a potential signature of innate constraints.

At present the earliest example of what may be a musical instrument is a bone "flute" that dates to approximately 50,000 years ago, during the middle Paleolithic (Kunej & Turk, 2000). Found in a Neanderthal campsite in Slovenia, the supposed flute was made from the femur of a bear cub and has four visible holes (Figure 1). Fink (Anonymous, 1997) has noted that the distance between the second and third holes of the flute is twice that between the third and fourth holes, which is consistent with the whole and half-tones of the diatonic scale. Kunej and Turk (2000) constructed replicas of the fossilized flute, however, and found that although they could produce tones consistent with a diatonic scale, it was possible to produce a continuum of other tones depending on finger placement and other details of how the flute was played. There is also controversy surrounding whether this fossil was in fact used for music, as puncture holes are occasionally made in bones by carnivores in pursuit of the marrow inside, and there is no clear evidence that the holes in the fossil were made by hominids.

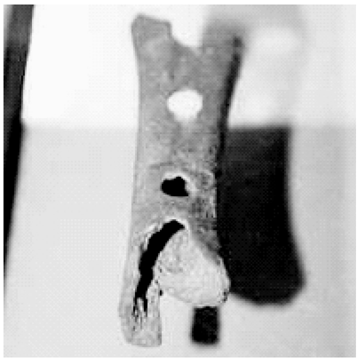

FIG 1. The oldest known putative musical instrument, from a Neanderthal campsite.

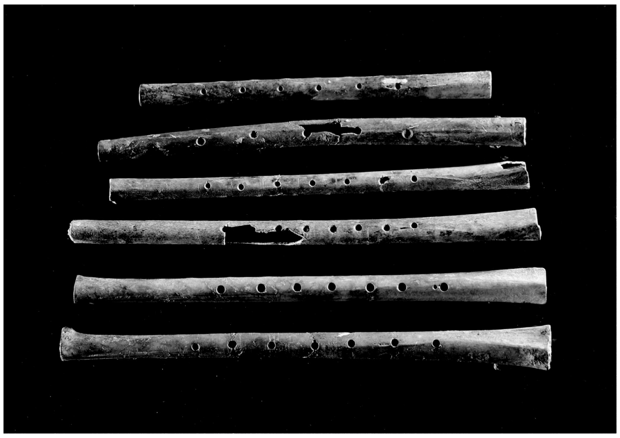

FIG 2. Ancient Chinese flutes.

The earliest well-preserved musical instruments were recently found at a Neolithic site in China and date to between 7000 BC and 5700 BC (Zhang, Harbottle, Wang, & Kong, 1999). These instruments are clearly flutes (some have as many as eight holes) and were made from crane bone (Figure 2). The best preserved of the flutes was played several times for the purposes of tonal analysis. As with the Neanderthal flute, the tones produced depend on how the instrument is played, but it was easy for a flute player to produce a diatonic scale. Although we are limited in the conclusions that can be drawn from known ancient musical instruments, their physical designs and apparent function are consistent with the notion that humans have long been predisposed to use particular sets of musical intervals.

The earliest known musical score is Sumerian, dating to approximately 1400 BC. The score was unearthed and decoded in the 1970s and first performed by modern musicians in 1974. The scholars who decoded the piece are fairly confident that the notes largely conform to the diatonic scale (Kilmer et al., 1976). The score appears to represent notes via their interval distances from a tonic, and there is a conspicuous absence of tritone intervals. The recording made of the scholars' decoded score is reminiscent of a folk song or lullaby and sounds more familiar than exotic. This again suggests that some central features of Western music, including the importance of a tonic note, and perhaps the prevalence of particular musical intervals, were present even before formal "Western music" existed.

The available cross-cultural and anthropological data thus suggest that at least some features of music are universal, shared across cultures and historical eras. We now turn to studies suggesting that some aspects of sensitivity to musical structure are universal and arise in the absence of extensive exposure to music. Many of these studies are inspired by observations of apparent musical universals.

Innate Sensitivity to Musical Structure

Another way to reveal innate constraints on music perception is to show that certain musical stimuli are represented or remembered more accurately than others, independent of experience. Often the structures that human subjects perceive most accurately are those that are prevalent in music across the globe, suggesting a common cause or perhaps a causal link. These sensitivity effects have the added virtue of providing measures that are well suited to experiments in human infants and animals.

Developmental Evidence

Many of the most interesting sensitivity effects come from studies of young infants with minimal musical experience. Over the past two decades Sandra Trehub and her colleagues have conducted a series of pioneering studies suggesting that even very young infants possess rudimentary musical sensitivities. Much of the developmental work begins with prevalent features of Western and non-Western music (candidates for universals) and tests for sensitivity to them in infants. At the most basic level, infants as young as 8 months seem to perceive melodic pitch contours much as adults do, treating a transposed version of a melody as the same even though the tones composing the melody are different (Chang & Trehub, 1977; Trehub, Bull, & Thorpe, 1984). In contrast, if the tones are reordered, altering the melody, infants treat the second tone sequence as new, directing their gaze toward the speaker through which it is played. Apparently relative pitch changes are highly salient to infants, just as they are to adults. Infants are also capable of generalizing across tempo changes (Trehub & Thorpe, 1989), again demonstrating the ability to abstract melodic information from a tone sequence just as adults can. Thus some of the basic auditory perceptual abilities needed for music perception seem to be present in infants with minimal exposure to music. It remains to be seen whether these perceptual abilities are general-purpose features of the mammalian auditory system or whether they are unique to humans and perhaps evolved for music and/or speech perception; see below for discussion of related comparative studies.

Other candidate universals have also been the focus of much developmental work. We first turn to "natural" musical intervals; given the long history of interest in their possible universality and innateness, it is no surprise that they have been the subject of developmental research. Inspired no doubt by well-known Greek theories of aesthetics, Pythagoras first observed that pairs of vibrating strings whose lengths were related by simple integer ratios produced tones that sounded better together than did tones of strings with complex ratios. Centuries later, Helmholtz (1885/1954) famously proposed an explanation of consonance in terms of critical bands in the cochlea, claiming that dissonance is the result of "beating" between overtones of two simultaneously played sounds. Subsequent physiological investigations have shown that consonance and dissonance are indeed distinguished by these peripheral differences (Tramo, Cariani, Delgutte, & Braida, 2001). Further sensitivity to simple harmonic intervals, in which the two tones are played simultaneously, could result from the physical structure of natural sounds, whose overtones tend to be harmonic, and therefore related by simple ratios. Notably, however, simple intervals are still musically important when the notes are played in succession and peripheral interactions do not distinguish the different interval classes. Tritones (which have ratios of 32:45), for example, are rarely used in melodies (and were in fact banned from early Western music due to how difficult they were to sing), whereas simple intervals such as the fifth (2:3) are more common and often play critical roles in the structure of melodies. The reason for the "naturalness" of simple intervals in melodies is a matter of some debate, but the prevailing view is arguably that it is largely due to experience, tuned by the local culture (e.g., Schoenberg, 1984; Dowling & Harwood, 1986).

Trehub and colleagues have tested this view with a series of experiments exploring how human infants perceive musical intervals. In one early study, Trehub, Thorpe, and Trainor (1990) compared short melodies containing simple intervals to "atonal" melodies that were not in any single key and had fewer simple melodic intervals. They found that infants were more sensitive to perturbations made to the typical Western melodies than they were to perturbations in "atonal" melodies. Such results suggest that infants are somehow atuned to the structure of typical Western melodies, perhaps because they contain simple intervals. To isolate individual intervals, Schellenberg and Trehub (1996) measured infants' sensitivity to changes made to a pair of tones when the tones were related either by simple (e.g., a perfect fifth or fourth) or complex ratios (e.g., a tritone). In one experiment the two notes of each interval were played simultaneously, while in another they were played one after the other. Critically, the notes composing each interval were pure tones. As a result, none of the stimuli, not even those in the simultaneous case, produced significant amounts of beating, which if present might have been used to detect the changes. Despite this, the authors found that infants much more readily detected changes made to simple intervals than to complex, both for simultaneously played and sequentially played tone pairs.

For the simultaneous case, the stimulus design precludes explanations in terms of beating, but the results might nonetheless be predicted if one supposes that the auditory system is attuned to harmonicity, for instance, for the purpose of extracting pitch (Terhardt, 1974). The frequencies of the fifth and fourth are produced simultaneously by any harmonic complex tone—the second and third harmonics are related by a fifth, and the third and fourth harmonics by a fourth. In contrast the frequencies of a tritone are in practice not present in complex tones, being that they are related by a 32:45 ratio. Harmonic amplitudes generally drop off with increasing frequency, and due to the limited resolution of cochlear filters, only the first 8–12 harmonics of a complex are resolved to begin with. Thus one explanation of the result with simultaneous intervals is that any tendency of the auditory system to respond to harmonically related tones might produce responses to simple, and not complex, ratio intervals. These responses, if built into the mammalian auditory system or acquired via exposure to harmonic sounds, could be used by infants and adults alike to detect changes to simple harmonic intervals and might explain the superior performance compared to that for the tritone. They might also make simple intervals easier to remember and could conceivably help to account for the prevalence of such intervals in human music.

Sensitivity to simple melodic intervals is more difficult to explain, because the frequencies composing the intervals do not overlap in time and thus presumably would not coactivate harmonicity detectors. Because the changes made to each interval were a whole semitone in magnitude (vs. only a quarter-semitone in the simultaneous case), on change trials the fifth (seven semitones) was changed into a tritone (six semitones), the tritone was changed into a fourth (five semitones), and the fourth was changed into a major third (four semitones). The results can thus be restated as showing that infants more readily detect a change from a simple interval to a more complex one than vice versa. This pattern of results has been replicated by Trainor (1997), who showed that both infants and adults were better at detecting changes from "natural" sequential intervals with simple integer ratios (the fifth and the octave) to "unnatural" intervals (tritone, minor sixth, major seventh, minor ninth) than the reverse. Related asymmetries have also been demonstrated in adults. Schellenberg (2002) found that observers were better at detecting an interval going out of tune than they were a mistuned interval becoming more in tune, even though the magnitude of the change was the same in both cases. The effect was found in both trained and untrained listeners. Perceptual asymmetries of this sort are often observed for categorical prototypes in many domains (Rosch, 1975). The Schellenberg and Trehub (1996) results can thus perhaps be best summarized by postulating that "natural" musical intervals serve as perceptual prototypes in young infants, with many of the concomitant behavioral effects, whereas unnatural intervals do not.

Schellenberg and Trehub argue that their results suggest an innate biological basis for the prevalence of particular intervals in human music. Setting aside the issue of how the sensitivity differences they measured might be causally linked to the prevalence of certain intervals in music, we can consider the claim that the sensitivity differences are innate. Many if not most prototypes are learned, so learning could certainly have played a role in the observed effects. Clearly the infants tested had far less musical exposure than normal adult humans, but it is hard to assess how much exposure they received and what its effect might be. It is clear that infants begin to learn the specific characteristics of the music of their culture within the first year of life (e.g., Lynch & Eilers, 1992), and so their musical exposure could play a role in the interval effects. Suppose that infants hear more instances of certain intervals than others over the course of their auditory experience, due perhaps to their prevalence in the native music environment. One might then expect infants to dishabituate less to such intervals in experimental trials compared to more novel intervals such as the tritone—which they might never have heard. The asymmetries could therefore be due to a tendency to dishabituate more to novel stimuli rather than to any innate biases. One reason to question this kind of account is that "natural" melodic intervals, though functionally important in music, are not the most commonly used in melodies. As mentioned earlier, most common melodies traverse intervals such as the fifth and fourth via a series of smaller steps, rendering one and two semitone steps (minor seconds and major seconds, respectively) the most common (Dowling & Harwood, 1986; Vos & Troost, 1989). On the basis of this observation, one might expect sensitivity to be greatest to these smaller intervals even though the ratios that define them are more complex (15:16 and 8:9, respectively), a prediction which is inconsistent with the reported results (although to our knowledge it has not been tested explicitly). It would thus seem unlikely that the effects result purely from the infants' limited exposure to music, although it is hard to know for sure what effect this might have.

An alternative explanation is that natural musical intervals are granted their prototype status by some built-in feature of the brain. One possibility is that there are frequency ratio detectors that are tuned to certain intervals and not others, perhaps due to mechanisms for estimating pitch (Terhardt, 1974); see below for further discussion of this possibility. Burns and Ward (1982) point out that although musically trained listeners often exhibit categorical perception of musical intervals, untrained listeners do not. They take this as evidence that such frequency ratio detectors are not present in the auditory system, at least not without musical training. However, categorical perception is often found only under particular circumstances even in trained listeners (Burns and Ward, 1978), so it is unclear how to interpret its absence in untrained subjects.

In sum, we regard the current evidence on the biological basis of "natural" musical intervals to be equivocal. Comparative studies on this topic would be of great interest, because the exposure to different kinds of intervals could be completely controlled.

Another series of experiments was inspired by the apparent universality of scales with unequal intervals. Trehub and colleagues (Trehub, Schellenberg, & Kamenetsky, 1999) studied the perception of melodies composed of pitches taken from various kinds of scales to see if scales similar to those used in indigenous musics would exhibit any perceptual advantages. They played stimuli to young infant and adult human subjects and tested their ability to detect 1.5 semitone perturbations made to one of the notes of the melodies. In one set of conditions the pitches were drawn from the diatonic scale, in another from an unfamiliar scale with unequal intervals, and in another from an unfamiliar scale with equal intervals. The unfamiliar scales had eight notes spanning an octave, just like the diatonic scale. Remarkably, the authors reported that the infant subjects were able to detect the perturbations made to the melodies taken from both the diatonic and unfamiliar unequal interval scale but not to the melodies taken from the equal interval scale. Apparently there is something about unequal interval scales that makes melodies easier to perceive and remember. The adult subjects showed a different pattern of results. They were able to detect the changes made to melodies whose pitches came from the diatonic scale but not the changes made to melodies taken from either of the unfamiliar scales. Evidently the exposure to music that occurs during human development renders adults insensitive to unfamiliar musical structures, paralleling the case for language acquisition. The effect seen in infants nonetheless requires explanation, as it is hard to see how it could be the product of incidental exposure, an explanation to which the interval results are more vulnerable.

As discussed earlier, the standard explanations for unequal interval scales are music theoretic in nature, involving the assignment of functional roles to different pitches, which is easier for unequal than equal interval scales (Balzano, 1980, 1982; Shepard, 1982). These explanations suppose that unequal interval scales have arisen in many different cultures because they enable certain properties of music, properties that are by hypothesis desirable to the cultures in question. However, the results of Trehub, Schellenberg, and Kamenetsky (1999) show that unfamiliar unequal scales are encoded more accurately than equal interval scales, suggesting an alternative reason for their prevalence. Apparently, melodies from equal interval scales are harder to remember. It is unclear what might cause this effect, but it clearly merits further study. The effect could be an incidental side effect of some pre-existing property of the auditory system, in which case one might expect to find it in a nonhuman animal. Alternatively, if uniquely human it would be a candidate for a music-specific adaptation, which could conceivably be driven in part by the music theoretic considerations discussed previously.

The studies we have discussed thus far concern sensitivity to musical structure that can be found in the absence of extensive musical experience. Although infants display an impressive array of such sensitivities, many aspects of music perception seem to require more time or exposure to develop. Several other divergent results between adults and infants support this idea. Lynch and colleagues found that American infants were equally sensitive to perturbations in Western and Javanese melodies, whereas American adults were better at detecting changes to Western melodies (Lynch, Eilers, Oller, & Urbano, 1990). This again suggests that just as is the case with language, infants are sensitive to many different types of musical structures and lose their sensitivity to some of them with exposure to a particular kind or genre of music. Lynch and Eilers (1992) found evidence that this process of acculturation can begin to have effects by a year of age and possibly much earlier.

Several other studies have examined the development of the tonal hierarchy—the system of expectations that endows the different notes of a scale with different degrees of "stability," i.e., appropriateness (Krumhansl, 1990). For instance, in Western popular music the tonic note within a key is the most stable, in that it occurs most frequently, often with longer durations than other notes, and is expected to occur at the end of a piece. These systems of expectations, which normal listeners acquire through incidental exposure to music, are critical to the perception of tension and resolution within a piece of music (Lerdahl & Jackendoff, 1983; Lerdahl, 2001). Tonal hierarchies are culture-specific in that different cultures use different scales (sets of pitches/intervals chosen within an octave) but have been demonstrated in Western and non-Western cultures alike (Castellano, Bharucha, & Krumhansl, 1984; Kessler, Hansen, & Shepard, 1984). The formation of tonal hierarchies likely involves the acquisition of culture-specific musical parameters, perhaps modulating innate principles as is thought to occur in language acquisition (Chomsky, 1986). Listeners probably monitor statistical regularities from musical pieces (most obviously, the number of occurrences of various notes and their duration) that provide cues to the structure of the hierarchy. To investigate the timecourse of this acquisition, Krumhansl and Keil (1982) made a detailed assessment of tonal expectations in children of elementary school age. They found that by first grade, children hear the difference between in-key and out-of-key notes and consider the in-key notes to be more appropriate when played in melodies. The tonal hierarchy becomes increasingly elaborated as children age; older children distinguish between notes of the tonic triad and other notes within a key just as adults do. However, even fifth- and sixth-graders do not evidence the full hierarchy expressed in adults. It is unclear to what extent the gradual onset is due to the maturation of the brain as opposed to the gradual accumulation of musical exposure, but the culture-specificity of the tonal hierarchy (Castellano et al., 1984) suggests that brain maturation is not the only contributing factor. Further to these findings, Trainor and Trehub (1992) have found that while adults are much better at detecting changes to melodies when the changes violate key structure, 8-month-old infants are just as good at detecting in-key and out-of-key changes. This again suggests that at least some aspects of diatonic key structure are learned from exposure to music and depend on the maturation of the brain. Trainor and Trehub (1994) also found that sensitivity to implied harmony is absent in 5 year olds but present in 7 year olds, suggesting that it may be learned over time. The exposure to music that occurs after infancy thus clearly has substantial effects, and the mechanisms that allow for learning from this exposure will hopefully be one target of future research in this area.

Although infants clearly have not learned as much from their limited exposure to music as adults have from a lifetime of listening, it is nonetheless difficult to account for the effects of the exposure that occurs both in the womb and in the first few months of life. A skeptic could always argue that this exposure could endow infants with the sensitivities that are measured in some of these experiments, particularly given the myriad examples of rapid learning in human infants. In utero recordings in sheep reveal that environmental sounds are rather faithfully transmitted from the environment through the uterine wall (Lecanuet, 1996), and recent studies of human infants before and after birth suggest that musical stimuli played prior to birth can be learned by the baby and recalled after birth (James et al., 2002). Thus any music in the environment of a pregnant mother could conceivably have some effect on the developing fetus. Even brief experience following birth could be sufficient for rapid learning of musical structure (although it might be argued that a music-specific learning mechanism might be involved). Many results from the developmental literature are thus suggestive but inconclusive because it is impossible to control for the amount of exposure to music.

Comparative Evidence

Animals represent a complementary experimental population to human infants and adults, since their musical exposure is minimal or nonexistent and can be rigorously controlled in an experimental setting. Evidence of music-related perceptual abilities in animals is additionally important because such abilities cannot be attributed to music-specific adaptations, if such exist. This unique inferential role of comparative data relies on the claim that nonhuman animals do not normally make or experience music, which might seem at odds with singing behavior in animals ranging from birds to gibbons and whales. We therefore begin with a discussion of animal song before proceeding to investigations of music perception in animals.

For the purposes of this article we define music on the basis of what humans do, as that is the phenomenon we are interested in explaining. Although the boundaries of what counts as music are nebulous and ill-defined, there are several key features of interest to virtually everything that we would categorize as music. First, like language, music consists of combinations of sounds organized into a hierarchical structure that allows for massive variation. Second, although many might describe music as conveying a message, it is not referentially precise in the way that language is, and its medium of expression is primarily emotional. Perhaps for this reason, music is commonly produced and listened to for enjoyment rather than for communicative purposes. In some instances music is used to convey a mood to a group of people, as in wartime, sporting events, carnivals, and so forth, but individuals often listen to music on their own (in Western cultures, at least, this is clearly the dominant mode of listening), in which case there is not even the most rudimentary of communicative functions. Finally, anyone can perceive and enjoy music without training (although the lifetime of exposure to music that each person in a culture receives clearly has a profound influence on their comprehension and enjoyment of music).

Birds (Catchpole & Slater, 1995), gibbons (Geissmann, 2000), and whales (Payne, 2000), among others, produce song-like structures, and these might seem plausible candidates for homologies of human music. Closer inspection reveals a host of key differences, and we think there is good reason to think that human and animal songs are neither homologous nor homoplasic and thus have little to do with each other. (See Fitch [in press] for an alternative perspective.) The fact that some animal songs sound musical to our ear is likely a coincidence, as they function as communication signals to the animals that produce them and are produced only under highly restricted contexts. As Darwin pointed out, when animals sing, they do so almost exclusively in the context of courtship or territorial defense. If one were to eliminate song from the vocal repertoire of animals that sing, one would effectively cut out one of the major sources of communication critical for survival and reproduction. Although animal songs may in some sense alter the emotions of animal listeners, no animal sings for the pure enjoyment of others or for its own enjoyment, at least not as far as we know. When individuals sing, the structure of song is typically quite stereotyped, even though some species alter song from season to season. In most singing species, except for those that duet (e.g., neotropical wrens, gibbons), only males sing and show unique neural adaptations for song.

On a structural level, there are admittedly some parallels with human music, more so in some species than in others. Song in birds and whales seems to be generated by a rule-based system for stringing together notes into phrases, and phrases into larger themes. Within a given species, there are innate constraints on the kinds of notes used and even on some of the ways in which they are sequenced. However, there is also a degree of variation within these constraints, although arguably much less than with human music. There is further evidence of dialects, showing that some aspects of song are learned in both songbirds and whales. One could perhaps argue that the mechanisms for producing animal songs might have been passed down to form human musical abilities, except that numerous other species more closely related to humans (e.g., chimpanzees, gorillas, orangutans) lack song. It thus seems unlikely that any resemblance between some elements of human and animal song is due to a homology. One interesting possibility is that animal song and human music were shaped by common perceptual constraints, for instance, on what sorts of acoustic structures are easy to encode or remember (Hauser & McDermott, 2003). In general, though, we do not regard animal song as the most productive avenue for comparative research.

Investigations of the perception of human musical structure in animals are potentially more relevant to the evolution of human musical abilities, because the perceptual systems of animals and humans are better candidates for homologies than are the systems for producing songs. Studies of music perception in animals are few and far between, but we hope this article will help to inspire more of them. Most studies have involved training animals to associate some musical stimulus with a reward followed by tests of generalization.

Studies in both birds and monkeys have used such methods to study the perception of consonance and dissonance. These studies tested whether the perceptual distinction between consonance and dissonance is apparent to nonhuman animals, without regard to whether one is preferred over the other. Izumi (2000) trained Japanese monkeys to discriminate changes from octave intervals (consonant) to major sevenths (dissonant), and then tested for generalization to other consonant and dissonant intervals; complex tones were used to generate the stimuli. The three monkeys used in the study acquired this discrimination rather quickly (between four and 16 sessions of approximately 100 trials) and were then run in transfer test sessions in which different consonant and dissonant intervals were used. Izumi found that the animals reliably detected changes from consonant intervals to dissonant ones but not the reverse. This suggests that the animals had learned to respond to the general class of dissonant stimuli, even though their prior training had been almost exclusively with one particular dissonant interval. The results thus support the notion that the beating present in dissonant stimuli is readily apparent to animals as well as humans. The speed with which the animals acquired the discrimination is further consistent with this conclusion, as is physiological evidence from macaques that beating remains salient at the level of the auditory cortex (Fishman et al., 2001). The results of the Izumi study are also at least superficially similar to the asymmetries observed in human adults and infants: Their Japanese macaque subjects detect a change from a consonant interval to a dissonant one but not the reverse. In this case, though, the effect is likely an artifact of the training procedure, in that the monkeys were trained to detect changes from consonance to dissonance but not the reverse (as noted by the authors).

There is also some evidence that birds can be trained to discriminate consonant and dissonant chords (Hulse, Bernard, & Braaten, 1995), again consistent with the notion that beating is likely present in their cochlea as it is in ours. As with monkeys, there is no reason to suppose that birds perceive consonant chords as pleasant or less aversive than dissonant chords, but the timbral distinctions appear to be readily apparent to both species.

Hulse, Cynx, and colleagues have also used operant methods in songbirds to study how they represent melodies. When exposed to a melody, humans generally extract and remember the sequence of relative pitch changes from note to note. This sequence of pitch changes, often termed the melodic contour, identifies a melody independent of the absolute pitch range in which it is played. The fact that we can easily recognize melodies and speech intonation patterns across different keys and speakers illustrates the importance of the melodic contour, and, as noted above, even very young infants seem to hear and remember the sequence of relative pitch changes produced by a series of notes (Trehub et al., 1984). The extraction of relative pitch changes is something that might be a basic built-in capacity of the auditory system, shared by nonhuman animals, but it might also have evolved in humans to enable speech and music perception.

Relative pitch has some importance in birdsong recognition, at least in some species in which songs are defined by specific frequency ratios between the “notes” composing the song (Hurly, Weisman, Ratcliffe, & Johnsrude, 1991; Weary, Weisman, Lemon, Chin & Mongrain, 1991; Weisman, Ratcliffe, Johnsrude, & Hurly, 1990). Typically, individuals sing at fixed frequencies that vary from bird to bird, but the ratios between frequencies is fixed for a particular species. Artificially altering the pitch intervals of a conspecific’s song produces a less aggressive response, suggesting that the pitch intervals play a role in song recognition (Hurly, Ratcliffe, Weary & Weisman, 1992; Shackleton, Ratcliffe, & Weary, 1992). There is thus some reason to expect that birds might be able to represent musical stimuli in terms of relative pitch, although the possibility remains that song recognition relies on modular acoustic analysis that might not apply to arbitrary stimuli or that relative pitch perception is present only in those species that use it as a song cue.

To test whether birds extract relative pitch from melodies as humans do, starlings were trained to respond to falling but not rising melodies, a task they can master given enough training (Hulse, Cynx, & Humpal, 1984). The rising and falling melodies used were composed of pure tone notes and typically spanned an octave range of frequencies. After mastering the discrimination, the birds were able to generalize to novel rising and falling melodies whose notes were taken from the same frequency range. However, the pattern of responses suggested that they had memorized the absolute frequency of many of the notes of the training exemplars and were relying on this in addition to the relative pitch changes across notes. More strikingly, the birds were unable to generalize the discrimination to novel melodies transposed up or down by an octave and whose pitches, as a result, fell outside the range in which they had been trained (Hulse & Cynx, 1985; Cynx, Hulse, & Polyzois, 1986; see MacDougall-Shackleton & Hulse, 1996, for an exception). This result has been replicated several times in various species of birds, including some nonsongbirds (Cynx, 1995). The failure to generalize occurs even when the birds are trained on melodies in a high and low range of pitches, separated by an octave, and then tested on the intermediate octave (Hulse & Cynx, 1985). Moreover, when absolute pitch is fully removed as a cue to discrimination, birds seem unable to acquire the discrimination at all (Page, Hulse, & Cynx, 1989). Apparently birds do not readily perceive relative pitch. This would appear to be at odds with the behavior of adult and infant humans, who readily recognize melodies across large transpositions, especially octave transpositions.

One caveat is that most of the studies on this topic were conducted with rising and falling melodies whose notes were separated by constant intervals (usually two semitones, forming whole-tone scales). Such melodies are quite atypical of those used in indigenous human music and would be considered atonal (in reference to the fact that none of the notes of such a scale has a unique set of interval relationships with the other notes). Humans recognize transpositions of novel atonal melodies less readily than transpositions of other sorts of melodies (e.g., Cuddy, Cohen, & Mewhort, 1981; Dowling, Kwak, & Andrews, 1995). Although the reason for this effect is unclear, such stimuli arguably do not provide the strongest test of melody perception. That said, one would think that with the thousands of exposures that the birds have in these studies, humans would learn the pitch contour in great detail and have no trouble recognizing transpositions. There thus seems to be a legitimate species difference.

Birds have also been trained to discriminate complex classes of musical stimuli. Porter and Neuringer (1984) trained pigeons to discriminate music by Bach from that of Stravinsky by rewarding responses to one of the two classes of stimuli. They found that birds who were rewarded for responding to Bach and not Stravinsky generalized to Buxtehude and Scarlatti (two other classical composers), while those trained to respond to Stravinsky generalized to Carter and Piston (two other modern composers). Similarly, Watanabe and Sato (1999) trained Java sparrows to discriminate Bach from Schoenberg. They found that the birds trained to respond to Bach generalized to Vivaldi, while those trained to respond to Schoenberg generalized to Carter. It is unclear what acoustic features of the musical pieces the birds in these studies were using to make their discrimination, but the results suggest that they can acquire sensitivity to some of the acoustic dimensions along which musical genres differ. It would be interesting to test birds on more controlled stimuli that differ along specific dimensions (conformity to a particular key, for instance, which is one way in which classical and "difficult" modern music differ), to get a better idea of what musical features they can learn.

Auditory operant procedures have also been employed in nonhuman primates, so far with mixed results. Interestingly, it is generally held that it is much harder to train nonhuman primates in operant conditioning paradigms with auditory stimuli than with visual stimuli, for reasons that are not well understood (Wegener, 1964; D'Amato, 1988). In contrast to songbirds and humans, nonhuman primates show weak evidence of vocal learning for their own, species-specific calls (Egnor & Hauser, 2004), which may be related to the difficulty they have with general auditory tasks. No such modality difference exists in humans to our knowledge. Perhaps for this reason there are only a handful of primate studies involving musical structures.

D'Amato and colleagues (reviewed in D'Amato [1988]) conducted a series of studies in which they trained capuchin monkeys to respond to one of two melodies to get a food reward. They then presented the animals with octave transpositions of the training stimuli to test whether they had learned the melodic contour. As was the case with the birds tested in the studies described above, the capuchin monkeys performed at chance levels when transferred to these octave-transposed stimuli, demonstrating that they had not extracted a representation of the melodic contour. It is worth noting that in all cases, the animals were trained on pairs of melodies that could be differentiated on the basis of simple and often local cues, such as the absolute frequency of one or two of the notes. Further experiments by D'Amato and colleagues confirmed that the monkeys were indeed attending to these local cues rather than the global pattern of the melodies. It would be of interest to see whether nonhuman primates can learn to discriminate melodies when local cues are eliminated, thereby forcing them to learn something about the global pattern. Nonetheless, the monkeys' behavior is quite different from what one would expect from a human in a similar task. The monkeys seem to readily learn the absolute frequencies of the notes of a melodic stimulus, whereas humans would surely find it easier to remember the melodic contour. Moreover, in an additional experiment D'Amato and colleagues repeated the Hulse and Cynx (1985) experiment in which an animal is trained to discriminate rising and falling melodies in both a high and a low range of pitches, and is then tested in the intermediate octave. Like the birds, the monkeys show no generalization to melodies with the same contour drawn from this intermediate octave.

As with the bird experiments on melodic contour, D'Amato and colleagues used melodic stimuli whose intervals differ notably from typical indigenous human music, in some cases being taken from whole-tone scales. It would again be of interest to test the animals with typical tonal melodies drawn from a diatonic scale. However, the experiments suggest that, like birds, monkeys represent melodies differently than humans do—they do not appear to represent a melody's contour in discrimination tasks as long as other means are available to do the tasks. One recent study by Brosch and colleagues (2004) demonstrates that macaque monkeys can be trained, with great effort, to discriminate the direction of pitch changes when all other cues to a discrimination task are eliminated. The results are consistent with those of D'Amato in that the animals initially adopted various strategies to rely on absolute pitch rather than relative pitch changes, learning the relative pitch discrimination only when absolute pitch was removed as a cue. Moreover, the monkeys were never forced to discriminate pitch changes below half an octave in magnitude. As mentioned before, the most common melodic intervals in human music are one and two semitones, and it would be of interest to test for generalization to pitch changes this small, which normal, untrained humans readily hear.

Ohl and colleagues (Wetzel, Wagner, Ohl, & Scheich, 1998; Ohl, Scheich & Freeman, 2001) trained gerbils to discriminate rising from falling FM sweeps. They found that the gerbils could learn to respond to rising FM sweeps independent of the absolute frequency range covered by the sweep. The sweeps used were quite large (typically an octave) and fast (250 ms or less in duration), which is rather far from the one or two semitone jumps found most commonly in human music. Moreover, they found that performance declined in test sessions where the sweep range was reduced to half an octave, which is still far greater than typical musical intervals. FM sensitive neurons in the auditory cortex of various species have been well documented (Mendelson, Schreiner, Sutter, & Grasse, 1993; Tian & Rauschecker, 1994; Tian & Rauschecker, 2004). Unfortunately, such neurons are also typically tested with quite large FM sweeps, as the interest is mainly in their selectivity for direction and speed. As such it is unclear whether they are relevant to the representation of musical stimuli. Experiments with smaller sweeps and with stimuli consisting of successive discrete notes would help to clarify their role. Interestingly, a lesion study by Ohl and colleagues (Wetzel, Ohl, Wagner, & Scheich, 1998) found that lesions to the right hemisphere greatly impaired the discrimination of rising and falling FM sweeps, whereas similar lesions to the left hemisphere had no significant effect. As will be discussed below, this has an intriguing parallel in the human literature (Johnsrude, Penhune, & Zatorre, 2000) that suggests that the human mechanisms for relative pitch may have evolved from related mechanisms in nonhumans, even if these mechanisms have much poorer resolution in nonhumans.

Taken together, these studies suggest that animals can learn to discriminate coarse pitch changes independent of absolute frequency if they are trained on enough transposed versions of the stimuli. Although further studies testing fine pitch changes (on the order of typical musical intervals) would be useful, on the basis of these studies it does not seem that animals represent these pitch changes anywhere near as readily as humans do. They require extensive training to extract them and do not generalize in a way that suggests any sort of primacy for the melodic contour as a form of representation. Rather, they seem to most naturally encode musical stimuli in terms of either absolute pitch or the absolute frequency content. In contrast, human infants with no training per se appear to readily perceive and encode the relative pitch changes in melodies, suggesting that it is a representation mode that comes naturally to humans.

The comparative results reviewed thus far largely underscore the notion that animals perceive musical structures quite differently from humans. The one exception to this in the comparative literature is a recent study on rhesus monkeys (Wright et al., 2000). In contrast to other studies of melody perception in monkeys and birds, which have used go/no-go tasks in which responses to specific classes of stimuli were rewarded, Wright and colleagues trained two monkeys to make same/different judgments on successively presented nonmusical sounds and then substituted short melodies as stimuli. As with other studies, they were interested in whether the monkeys would identify melodies as the same even if the second melody was transposed upward or downward so that the tones in the two instances were physically different. Their results differ markedly from the other studies in birds and monkeys in showing that, like humans, monkeys display octave generalization—they tend to identify two melodies as the same if they are transposed by one or even two octaves. Octave generalization was not found for individual pitches, suggesting that it was a function of the pitch contour of the melodies. Moreover, the octave was found to have a privileged status. No generalization was obtained if the melodies were transposed by 0.5 or 1.5 octaves, leaving the notes physically closer to the originals but changing the chroma of the notes and the key of the melody. Most intriguingly, 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 the full 12 tones of the chromatic scale, they responded as though the melodies an octave apart sounded different.

There are thus two key results to the study: the octave specificity of transposition recognition in tonal melodies and the failure to recognize octave transpositions of atonal melodies. The octave specificity effect is unlikely to be the mere product of octave equivalence of the pitches composing the melodies, because no effect was found for individual pitches. It thus seems likely that the animals were recognizing the preserved melodic contour rather than transpositions of individual pitches. The failure to recognize tritone transpositions as the same could indicate that the animals were nonetheless using pitch chroma as an additional cue or that they were somehow encoding tonal melodies relative to their key (both chroma and key change for tritone but not octave transpositions). As for the failure to recognize atonal transpositions, one possibility is that the monkeys had difficulty remembering atonal melodies. Alternatively, the atonal melodies could have been remembered but not represented in a manner that permitted them to be matched to transposed versions (e.g., in terms of absolute rather than relative pitch). Either way, the results suggest two key conclusions: first, that the rhesus monkeys used in the study reliably encoded the relative pitch changes in the tonal melodies, and second, that tonal melodies have special status even in nonhuman primates.

Clearly, the results are quite different from what would be expected on the basis of the other studies of melody perception in birds and nonhuman primates. There are several differences in Wright's protocol that may have been key to the animals' apparent ability to extract the global features of the melodies. First, Wright's monkeys were trained to perform a same-different judgment with arbitrary stimuli, whereas all the other studies we have discussed trained animals to associate a particular stimulus or class of stimuli with reward. Wright's monkeys were thus tested on many different melodic stimuli, each of which they heard a few times at most. In contrast, the animal subjects of all the other studies reviewed here heard the rewarded melodic stimuli many times more, often completing thousands of trials in the course of learning the discrimination. Wright's animals completed many trials during the course of training as well, but with unrelated stimuli, as they were learning to make same-different judgments. This difference is substantial and could be important—as mentioned earlier, humans seem to retain fairly accurate information about the absolute pitch of highly overlearned melodies (Levitin, 1994; Schellenberg & Trehub, 2003). Of course, humans are also better at recognizing transpositions of highly overlearned melodies, so it would be surprising if exposing an animal to the same melody thousands of times in a row somehow rendered the melodic contour inaccessible. But the difference in exposure could conceivably play a role in the differing results.

The differing paradigms also place different demands on memory that could be important. To complete a trial, Wright's animals presumably had to store the first of two melody stimuli in short-term memory and then make a comparison between that stored representation and the second stimulus. In contrast, the animal subjects in the other studies reviewed here presumably acquired a representation of the rewarded stimuli in long-term memory and then compared novel stimuli to that stored representation. Thus differences between short- and long-term memory could also be relevant to the pattern of results.

Another potentially important difference between the Wright et al. study and the other comparative studies of melody perception is that Wright made use of "tonal" melodies, drawn from the diatonic scale, whereas all other studies have used "atonal" melodies, the tones of which were drawn from whole-tone or other scales atypical of human music. Indeed, Wright found that tonality was the critical variable determining whether his monkeys could recognize octave transpositions. This parallels results in humans, who are generally worse at recognizing transpositions of atonal compared to tonal melodies (Cuddy et al., 1981). This result in adult humans is readily explained by the greater exposure to tonal than atonal music, but the Wright result suggests there might be a biological basis for some of this effect. At any rate, this difference in stimuli between the Wright et al. study and those that preceded it could be important.

It is also possible that the observed patterns of results are due to species differences in auditory perception, with the Old World monkey macaques having evolved different perceptual abilities from the New World monkey capuchins and birds. However, the Brosch et al. (2004) study used macaques as subjects and found, as D'Amato had with capuchins, that they had great difficulty learning to recognize pitch changes. A species difference thus seems unlikely to account for the divergent results.

An additional caveat is in order as well, in that the monkeys' behavior is not completely consistent with human behavior in similar tasks. Key distance effects, exhibited in Wright's monkeys by the smaller number of "same" responses to tritone-transposed tonal melodies than to octave-transposed tonal melodies, are generally weak in humans and only found in rather specific experimental circumstances (Cuddy, Cohen, & Miller, 1979; Bartlett & Dowling, 1980; Cuddy et al., 1981; Dowling, 1991; van Egmond, Povel, & Maris, 1996). Adult humans can generally recognize a transposed tonal melody as the same, regardless of the key it is played in (Attneave & Olson, 1971; Dowling & Bartlett, 1981); subjects are only somewhat worse for unfamiliar melodies transposed to "far" keys (Trainor & Trehub, 1993). The monkeys in the Wright et al. study, in contrast, almost never categorized two melodies as the same if they were played in different keys, and the magnitude of this effect is surprising given human perception. This difference could be related to the fact that Wright's monkeys had been trained to match exact replications of the same sound rather than transposed melodies, but the results are nonetheless surprising given how humans hear melodic stimuli.

Although fully reconciling the Wright results with previous work in humans and animals will, in our view, require further research, the study is significant because it is the first suggestion that animals are naturally sensitive to some signature features of human musical structure. It also raises two significant points with respect to the role of comparative data in illuminating the psychological design features of music. First, assuming the effects cannot be attributed to incidental exposure the monkeys may have had to music, the Wright study provides evidence that there are innate constraints on music perception, since the monkeys certainly did not acquire their melodic sensitivity through cultural exposure. Second, because monkeys—especially the rhesus monkeys investigated—do not produce or experience music on their own, the fact that they apparently possess musical sensitivity suggests that at least some aspects of music perception are determined by pre-existing structures in the auditory nervous system. The monkeys clearly did not evolve musical sensitivity for the purpose of listening to or producing music, which means that their sensitivity must be the byproduct of a mechanism evolved for some other purpose. This study thus provides an intriguing demonstration of the power of comparative data.

In summary, at present there are relatively few studies of musical sensitivity effects in nonhuman animals, and those that exist do not paint a completely consistent picture. Most studies suggest that animals have trouble representing the pitch contour of a melody, a representation that is key to human music perception. The Wright et al. study suggests that at least one species of monkey can recognize transpositions and therefore extract the melodic contour, but only for "tonal" melodies taken from the diatonic scale. It remains to be seen how crucial a role tonality plays in other species and paradigms.

Musical Preferences

The studies reviewed in the previous sections all describe sensitivity to musical structure present either across cultures or in the absence of extensive experience, suggesting that such sensitivities may be built into the way the auditory system works. Sensitivity to musical structure does not, however, explain why we like it. Clearly, many aspects of musical preferences are learned, as exhibited by the liking most humans take to the music of their own culture. Nonetheless certain elementary preferences might be innate and could be evidenced by the prevalence of some musical features across cultures. Other explanations of such features are, however, equally viable (e.g., prevalent features might be those that make the resulting music easier to remember), and the innate presence of such preferences thus requires direct experimental tests.

Debate over whether particular musical structures are inherently pleasing dates back at least to the time of the Greeks and the interest in consonant and dissonant intervals. Although there are differences in how consonant and dissonant pairs of tones excite the peripheral auditory system, as mentioned earlier (Helmholtz, 1885/1954; Tramo et al., 2001), this does not explain the most important feature of the phenomenon—that, in isolation, consonance sounds good and dissonance bad. Functional imaging studies suggest that consonant and dissonant musical stimuli activate some of the same brain regions that are found to be active for other pleasant and unpleasant stimuli (Blood, Zatorre, Bermudez, & Evans, 1999) but do not explain the origins of the pleasant and unpleasant nature of the stimuli. The aesthetic responses to consonance and dissonance could themselves be acquired through cultural exposure. Perhaps surprisingly, there is relatively little cross-cultural data on the perception of consonance and dissonance. In one study, Butler and Daston (1968) found that consonance judgments were largely similar across American and Japanese subjects. Maher (1976) compared judgments from Indian and Canadian subjects, finding the Indian subjects to be more tolerant of dissonant intervals. To our knowledge these are the only two studies that have compared consonance perception across different cultures. This is clearly an area that would benefit from more research, because it will be important to determine to what extent the preference for consonance that is widespread among Western listeners is universal (and therefore probably innate).

Infant studies provide another way to look at innateness. Schellenberg and Trehub's (1996) experiments with infants suggest that consonant musical intervals seem to be more discriminable than dissonant ones even in the absence of extensive experience with such sounds. But do the infants hear the different intervals as pleasant and aversive just as adults do? Zentner and Kagan (1996, 1998) asked just this question, playing 4-month-old infants melodies composed of consonant or dissonant intervals (major thirds and minor seconds, respectively) and recording their facial and orienting reactions. Infants spent more time looking at the music source and made fewer movements to consonant melodies than to dissonant melodies, suggesting that they preferred the consonant melodies. The infant subjects also showed signs of distress (as judged by observers blind to the condition) when listening to the dissonant versions. Similar results were obtained by Trainor and Heinmiller (1998) and earlier by Crowder and colleagues (Crowder, Reznick, & Rosenkrantz, 1991). Trainor and colleagues also replicated their results in 2-month-old infants (Trainor, Tsang, & Cheung, 2002). The authors suggest that the preference for consonant melodies is innate, emerging independent of experience.

As with some of the sensitivity effects, it is conceivable that the preferences found in infants are due to early exposure. It is well-known that adults and infants tend to prefer stimuli to which they have had prior exposure, all other things being equal (Zajonc, 1968). So if the infants had heard consonant musical stimuli more than dissonant ones, which seems likely given their relative prevalence in music and given the nature of the music typically played to infants and children in Western cultures, this could conceivably have produced the observed preferences. Even if the experiential account is wrong, and the preference is innate, it is unclear whether the mechanism is part of a music-specific adaptation or some other, domain-general mechanism.

To address these issues, we have recently examined whether similar preferences can be found in nonhuman primates with no prior exposure to music (McDermott & Hauser, 2004). Our task involved a Y-shaped maze in which subjects—cotton-top tamarins—freely moved about. At the beginning of a trial, we placed a subject at the stem of the maze and then released it. As soon as the subject entered one branch of the maze, a concealed speaker played one particular sound, while movement into the other branch triggered a different sound. Since the task did not entail a food reward, a bias to spend more time in one branch as opposed to the other was taken as evidence for a sound preference. As proof that the method worked, we first compared a low-amplitude white noise signal to a very loud white noise signal and found that tamarins preferred to stay inside the branch delivering the softer stimulus. They also preferred to stay on the side playing back species-specific food chirps (a sound that presumably has positive emotional connotations, if any) as opposed to species-specific fear screams (which presumably have negative emotional connotations), again suggesting that the method provides an appropriate assay for exploring un-trained acoustic preferences. When given a choice between consonant intervals and dissonant intervals, however, tamarins showed no preference, spending equal amounts of time on each side of the maze. Most surprisingly, when we contrasted a screeching noise similar to the sound of fingernails scratching on a blackboard—a sound that nearly all humans find aversive—with amplitude-matched white noise, tamarins again failed to show any preference. Tamarins thus appear to lack the preferences for different kinds of sounds that are present in both adult and infant humans. Although we are currently in the process of exploring other contrasts in the same and other species, it is possible that such preferences are unique to humans.

Consonance and dissonance in harmonic intervals is only one (and one of the most basic) of the aesthetic contrasts that are ubiquitous in music. Also of interest is the perception of melodic intervals. Generally speaking, the intervals that are consonant and dissonant when the component tones are played simultaneously also sound more and less natural, respectively, when played sequentially, even though there is no obvious physiological correlate to distinguish them, as the notes are separated in time. The origins of basic phenomena such as this as well as more complicated aspects of what make melodies sound good and bad remain largely unstudied. The prevailing view is arguably that the aesthetic judgments for melodies are largely a function of experience, tuned by the local culture (e.g., Dowling & Harwood, 1986). This hypothesis has yet to be tested, and will require a richer cross-cultural sample.

In the one other study to our knowledge that has tested for musical preferences in nonhuman animals, Watanabe and Nemoto (1998) recently reported experiments on java sparrows, using a paradigm similar to that of McDermott and Hauser (2004). The birds were placed in a room with three perches, rigged such that the perch they chose to rest on determined which of two kinds of music, or silence, they heard. They measured the amount of time the birds spent on each perch, with the assumption that the time on a perch would be related to the relative preferences for the associated auditory stimulus. In the first experiment, one perch triggered a piece by Bach, one triggered silence, and the other triggered a piece by Schoenberg. The authors found that two of their four subjects spent more time on the Bach perch than on the Schoenberg perch (the other two showed no difference). These subjects also spent more time listening to Bach than to silence. The effect replicated in the same two subjects in a second experiment with different pieces by Bach and Schoenberg. In a third experiment, the same two birds also spent more time listening to a piece by Vivaldi than to one by Carter. Evidently there is some property of music by Bach and Vivaldi that causes some Java sparrows to prefer it to the modern classical music of Carter and Schoenberg. One possibility is that there is some resemblance between the songs the birds produce themselves and some kinds of classical music. We have speculated (Hauser and McDermott, 2003) that animal vocalizations and human music might be shaped by similar constraints on auditory perception or memory, and it is possible that some features of tonal music ("natural" intervals, for instance) might be found in animal vocalizations for this reason. Perhaps some similarity for this or other reasons drives the reported preferences, although Java sparrow songs to our ears bear little resemblance to any sort of human music. The individual differences between birds are also hard to explain. However, the results are intriguing and further research of this sort would be valuable. It would be of great interest, for instance, to know whether the birds that prefer Bach to Schoenberg would also prefer consonant intervals to dissonant ones.

Additional developmental experiments on preferences also suggest themselves. It would be particularly interesting to check for preferences for tonal over atonal music in infants (again, by tonal we refer to melodies whose notes come from the diatonic scale, and by atonal to melodies whose notes come from chromatic or whole-tone scales and thus are not in any particular key). Although infants are reported to be more sensitive to changes to tonal melodies than to atonal ones (Trehub et al., 1990), it is unclear if this would translate to a preference for one over the other. In general, the relationship between the sensitivity differences often seen in infants and the musical preferences that are the most salient effect in adults merits further exploration. (See the next section for further discussion.)

Emotional Responses to Music

Music produces strong emotional responses in those who listen to it. At least among members of a particular culture, certain pieces of music sound happy, others sad, others contemplative, and so forth. This is remarkable given the often abstract, nonrepresentational nature of music. How is it that a simple sequence of tones can evoke a particular emotion? In our view there are three key questions. First, what are the acoustic cues to emotion in music? Second, are the responses to these cues innate? And, third, why do these cues signal particular emotions? With respect to the last question, it is of particular interest to know whether associations between acoustic cues and emotion derive from nonmusical contexts or whether they are specific to music.

In Western music, happy and sad emotions are often conveyed with fast tempos and major keys, and slow tempos and minor keys, respectively. At present, the origins of these cues remain unclear. One obvious approach would be to test whether major and minor keys have similar effects on individuals from foreign cultures who have little to no prior exposure to Western music. Unfortunately, individuals with little exposure to Western music are in practice hard to come by, as Western music has by now permeated most of the globe. Balkwill and Thompson (1999) therefore adopted the opposite approach. They took excerpts of North Indian ragas performed with different emotional connotations and played them to Westerners to see if the Westerners would perceive the intended emotion. More often than not their Western subjects perceived the intended emotion, suggesting that at least some of the cues to emotion are shared across cultures. Tempo may be primarily responsible for their results, but other variables, such as melodic and rhythmic complexity as well as pitch range, also seem to be implicated.

Developmental research has also addressed these questions. In Western music, one of the primary acoustic cues to emotion is the sort of scale from which the notes of a piece are drawn. All other things being equal, to a first approximation, pieces in major keys typically sound happy, while those in minor keys sound sad (Hevner, 1935). The major/minor distinction has been of interest to researchers for some time, and several studies suggest that children below the age of 6 years do not readily associate major and minor keys with a mood (Gerardi & Gerken, 1995; Gregory, Worrall, & Sarge, 1996; see also Kastner & Crowder, 1990). To separate the contributions of tempo and mode to emotional judgments in music, Peretz and colleagues manipulated the two cues independently in a recent developmental study (Dalla Bella, Peretz, Rousseau, & Gosselin, 2001). Children of different ages were played excerpts of classical music, some happy, some sad. Happy selections were played at the same fast tempo and were written in a major key; sad selections were played at the same slow tempo and written in a minor key. To test the role of mode and tempo in perceived affect, each selection was shifted to the other tempo in one set of trials, transposed to the other mode in another set of trials, and shifted in both tempo and mode in yet another. Subjects were asked to judge whether a given stimulus sounded happy or sad. Peretz and colleagues report that the judgments of children 6–8 years old resembled those of adults in being affected both by tempo and mode changes. Five-year-olds, however, although responding to tempo changes, did not associate changes from major to minor keys with changes in affective content. Three- and 4-year-old children were at chance in all conditions.

The results are consistent with the idea that emotional sensitivity to mode may depend more on learning than emotional sensitivity to tempo and might be taken to suggest that the emotional connotations of major and minor keys are not intrinsic to the key, but rather are arbitrarily acquired. As the authors note, it is also possible that the classical excerpts that were used were too complicated for the young children to comprehend. It is well-known that childhood songs ("Old MacDonald," etc.) and lullabies tend to be among the most repetitive of songs (Unyk et al., 1992), and perhaps this is because children have trouble representing or remembering musical structures that are more complex. But supposing the emotional connotations of music are acquired through learning, how might this occur? Simple associative learning is a candidate. If enough examples of happy and sad events co-occur with major- and minor-key music, for instance, through weddings, funerals, movies, plays, television, etc., one might eventually come to automatically hear minor keys as sad and major keys as happy. Even if emotional connotations are learned rather than innate, there is still something about music that demands explanation, which is the ease with which it acquires emotional associations. Such associations are arguably more potent in music than in any other art form, and one can only speculate as to why.

Although future developmental work with simpler pieces of music will certainly help to further illuminate the role of learning in music and emotion, cross cultural studies would also be of great value. It would obviously be of interest to know to what extent the contributions of tempo and mode are culturally invariant. The predominance of major and minor modes is specific to Western music, and it remains to be seen whether other cultures will have the same emotional associations that Westerners do.

Dedicated Brain Mechanisms for Music?

Given speculations that certain aspects of music are innate, neuroscientists have naturally been interested in whether there is dedicated neural circuitry for music perception (Peretz & Zatorre, 2003). Neuropsychology is perhaps most relevant to this issue, as it is only by removing or inactivating part of the brain that one can show that it is necessary for a particular capacity, such as music perception. However, the recent advent of functional imaging techniques has provided another tool with which to investigate these issues and in time will presumably yield a wealth of data about the brain networks active during music perception and production. Music perception involves many different kinds of processes, including basic perceptual analysis of pitch and rhythm information, the extraction of music-specific structures such as the tonal hierarchy in Western music, the interpretation of this structure in terms of emotions and meaning, and the interaction of these representations with memory. Neuropsychology and neuroimaging studies have targeted many of these various levels of processing, and we will discuss them in turn. We will predominantly focus on studies of individuals who have not had extensive musical training. There is an extensive literature on the effects of musical training on the brain (e.g., Gaser & Schlaug, 2003; Stewart et al., 2003), but for the most part it does not bear on the issues that are central to this article, as training is not needed for normal human listeners to develop music comprehension skills. Studies of untrained listeners are therefore more relevant to understanding the evolutionary origins of these skills, the development of which merely requires exposure to music rather than training.

Pitch Perception

Music is typically described in terms of pitch and rhythm. A myriad of perceptual processes are no doubt involved in both, but thus far more attention has been devoted to pitch (although see, for example, Liégeois-Chauvel, Peretz, Babai, Laguitton, & Chauvel [1998] for a patient with meter perception deficits, Sakai et al. [1999] for a neuroimaging study on meter perception, and Alcock, Wade, Anslow, & Passingham [2000] for dissociations between impairments in melody and rhythm in the singing of brain-damaged patients). Although the neural code for pitch remains a controversial issue in auditory neuroscience, nonprimary regions of auditory cortex appear to be involved (Patterson, Uppenkamp, Johnsrude, & Griffiths, 2002; Tramo, Shah, & Braida, 2002; Penagos, Melcher, & Oxenham, 2004; Bendor & Wang, 2005), and the right auditory cortex seems to be particularly important (Zatorre, 1988), with lesions therein leading to pitch perception deficits. In melodies, the relative pitch between notes is arguably more important than the absolute pitch values. It is conventional to distinguish between contour information (whether the pitch goes up or down from one note to the next) and interval information (the precise amount by which the pitch changes, which differentiates a fifth from a tritone, for instance). Both cues are generally used to discriminate melodies in normal adults.

Several studies suggest that the right temporal lobe is critical to the perception of the melodic contour. Zatorre (1985) found that melody discrimination was particularly impaired by damage to right anterolateral temporal lobe regions, and although the task used did not specifically isolate melodic contour cues, the results are consistent with a role for right temporal regions in extracting the melodic contour. Johnsrude, Penhune, and Zatorre (2000) compared pitch discrimination and pitch direction discrimination in normal controls and patients with temporal lobe excisions. Subjects were presented with two tones in succession and had to judge whether the two tones were different or whether the pitch increased or decreased from the first tone to the second. The authors found that thresholds for pitch discrimination and pitch direction discrimination were comparable in normal controls and in patients with left hemisphere excisions but that pitch direction thresholds were markedly worse in patients with right hemisphere excisions. Thresholds in such patients were approximately two semitones on average (compared to well under a semitone for normals), meaning that without the right auditory cortex, the most common note-to-note pitch changes in melodies would be imperceptible. Consistent with these results, Brechmann and Scheich (2005) found in an fMRI study that a pitch direction discrimination task activated the right auditory cortex more than the left, whereas a duration judgment task had the opposite effect. There are thus several strands of evidence suggesting that in humans, the right auditory cortex is important for pitch perception and in particular the detection of the pitch changes that make up the melodic contour.

Based on these and other imaging and anatomical data, Zatorre, Belin, and Penhune (2002) have proposed that the left and right auditory cortices serve complementary functions, resulting from the need to simultaneously optimize resolution in the temporal and frequency domains. High resolution is not possible in both domains at once, and they propose that the left auditory cortex has been optimized for temporal resolution and the right for spectral resolution. These constraints may underlie the role of the right auditory cortex in pitch perception.

If the mechanisms for pitch perception were damaged via a brain lesion or developmental disorder, music perception would be expected to be impaired. Congenital amusia, colloquially known as tone-deafness, appears to be an example of this. There are numerous anecdotal reports of tone-deaf individuals (Theodore Roosevelt and Che Guevera are alleged to have been examples), but a series of studies by Peretz and colleagues are the first rigorous investigation of the phenomenon. Subjects were recruited with newspaper ads seeking "musically impaired" individuals and then subjected to a battery of tests (Peretz et al., 2002; Ayotte, Peretz, & Hyde, 2002). They were found to have normal IQ, working memory capacity, and peripheral hearing abilities, but marked impairments in tasks of music perception. The most common deficit in such subjects is an inability to discriminate or recognize melodies, and this seems to be due to severe deficits in detecting pitch changes. Thresholds for detecting pitch changes are on the order of several semitones, at least an order of magnitude higher than those for normal subjects, and comparable to the deficits seen in patients with right hemisphere excisions (Johnsrude et al., 2000). Most of the pitch steps in typical melodies are thus below threshold for tone-deaf individuals, and it is no surprise that they are unable to recognize melodies. Recognition of environmental sounds is unimpaired, however, as is recognition of song lyrics. Rhythm perception is impaired in some but not all cases; pitch impairment is what most commonly characterizes "tone-deafness." Similar results have recently been reported by a separate group of investigators as well (Foxton, Dean, Gee, Peretz, & Griffiths, 2004).

Can congenital amusia and the results of the lesion studies discussed earlier be used to infer the presence of music-dedicated architecture? Clearly, most amusic individuals have basic perceptual deficits that are not necessarily specific to music. Indeed, in one experiment Peretz and colleagues showed that if linguistic information is removed from spoken sentences, amusic patients are impaired at detecting intonation changes in speech just as they are at detecting pitch changes in melodies (Ayotte et al., 2002; see also Patel, Peretz, Tramo, & Labrecque, 1998). However, the possibility remains that the early cortical mechanisms that seem to be abnormal in those with congenital amusia, and damaged in certain lesion patients, evolved as part of an adaptation for music and speech perception. Both music and speech perception necessitate or at least benefit from the fine-grained perception of pitch changes—music via melodies and speech via intonation patterns (Pierrehumbert, 1979). Pitch variations in speech are admittedly often much larger (on the order of seven semitones for pitch accents; Fitzsimons, Sheahan, & Staunton, 2001) than those in music (which are typically one or two semitones), but many unaccented pitch changes in speech are closer to the musical norms.

The hypothesis that the fine-grained perception of pitch changes might be the product of a uniquely human mechanism receives some intriguing support from the comparative literature reviewed earlier in this article. Nearly all studies of nonhuman animals have found that they have great difficulty extracting pitch changes and as a result cannot generally recognize transpositions of melodies; the Wright et al. (2000) study is the one exception. In contrast, even young human infants seem to extract the melodic contour from melodies without training (Trehub et al., 1984). It is thus possible that humans have mechanisms for perceiving pitch changes that are unique among the primates and that might have evolved to assist in speech or music perception. One wrinkle in the story is that the right hemisphere specialization in humans may have an analogue in nonhuman animals, as mentioned earlier. Right hemisphere lesions in gerbils greatly impair the discrimination of upward and downward FM sweeps, whereas left hemisphere lesions have no such effect (Wetzel et al., 1998). The FM sweeps used in these studies were an octave in extent, much larger than the intervals used in music and those that have been used in experiments in humans, but the presence of a similar asymmetry in gerbils is striking. At present it is unclear whether this pattern of results would be found generally in most mammals, but it is possible that right hemisphere mechanisms present in our nonhuman ancestors were adapted in humans to enable the perception of fine-grained pitch changes. Additional research in primates and other animals could help to clarify these issues.

In addition to perceiving the pitch change directions that contribute to the melodic contour, humans also encode the precise pitch intervals between notes. Being able to hear that a particular interval is five semitones rather than six, for instance, is probably critical to the perception of key and to the elaboration of the tonal hierarchy. Less is known about the mechanisms for extracting intervals, but evidence from neuropsychology suggests that they are distinct from the mechanisms for processing the melodic contour, perhaps relying on left hemisphere mechanisms (Peretz, 1990). It remains to be seen whether the ability to individuate different intervals is uniquely human.

Higher-Level Musical Structure

Once basic descriptions of pitch and rhythm have been extracted from musical stimuli, musical structure can be analyzed. The mechanisms that perform this structural analysis have been the subject of both neuropsychological and neuroimaging studies. Numerous examples exist of patients with brain damage, often from strokes, who experience deficits in recognizing music, which could conceivably be due to damage to music-specific mechanisms. However, most of these patients have also had other deficits as well, particularly in language (Basso, 1993), which precludes such an explanation. Over the last decade, a number of studies have demonstrated patients with brain damage–induced music deficits who seem markedly free of linguistic or other deficits. Some such cases can be explained in terms of basic perceptual deficits in detecting pitch direction or pitch intervals (Peretz, 1990; Liégeois-Chauvel et al., 1998) rather than higher-level music-specific impairments. However, several patients have been studied who have music deficits despite having pitch perception that is mostly normal.

One of the most interesting cases is that of G.L., who appears to have a selective deficit in knowledge of tonal organization (Peretz, 1993). As we have discussed, normal human listeners of conventional Western music encode pitches relative to a structure known as the tonal hierarchy. Different pitches within a key serve different functions, with the tonic being the most important. The mechanism that stores this structural information and links it to the pitches in a given piece of music appears to be disrupted in G.L., who has lesions in the left temporal and right frontal lobes. For most of his life, G.L. was an avid music listener, but in the aftermath of the lesions complained of being unable to recognize or enjoy music. When tested in the laboratory, G.L. was found to exhibit normal pitch and melodic contour discrimination. Interval information was disrupted but still partially available as measured by melody discrimination tasks. However, his knowledge of tonality seems to have been completely destroyed by his brain lesions. G.L. was found to be insensitive to scale violations ("sour" notes, to which untrained Western listeners are acutely sensitive), gave abnormal key profiles using the probe tone paradigm introduced by Krumhansl and colleagues, did not exhibit any preferences for melodies ending on the tonic (unlike normal control subjects), and lacked the normal preference for tonal over atonal music. There thus appears to be neural circuitry that represents tonal knowledge in normal Western listeners, which has unfortunately been damaged in G.L. This circuitry is apparently distinct from that which extracts and represents the more elementary representations of melodies in terms of pitch changes and intervals.

Janata and colleagues (2002) reported neuroimaging evidence for what may be related neural representations of tonal knowledge. Their results suggest the presence of a map of the perceptual space of key laid out in the prefrontal cortex of musically trained adult listeners. A small patch of cortex is active when subjects listen to music in the key of C; a different patch is active for the key of G; and so forth. Adjacent keys on the circle of fifths seem to be represented by adjacent bits of cortex, providing additional support for the hypothesis that the neural map actually represents the psychological relations between keys. The map is not fixed but rather reorganizes itself from scan to scan and is instantiated in regions of cortex that appear to serve other functions depending on the task. Nonetheless their results provide the first suggestion from functional imaging of where our representations of high-level musical structure might be represented in the brain, and the prefrontal regions they describe may correspond to the brain regions damaged in patient G.L.

Given that there are brain regions representing the detailed knowledge of music that is acquired by nearly all members of a culture, it is of obvious interest to establish whether the neural circuits involved are programmed into the brain from birth and whether they serve other functions as well. In particular, many have suggested that music might rely on linguistic computational mechanisms. Perhaps surprisingly given the widespread interest in their potential relationship, relatively few studies have directly compared speech and music perception. Patel (2003) has proposed that music and language may rely on shared computational resources tapped by syntax in language and tonality in music. Consistent with this idea, a few imaging and electrophysiology studies report activations for music-related tasks in auditory association cortex that appear to overlap with regions thought to play a role in language, such as Broca's area (Patel, Gibson, Ratner, Besson, & Holcombe, 1998; Maess, Koelsch, Gunter, & Friederici, 2001; Koelsch et al., 2002; Levitin & Menon, 2003). Unfortunately there are few studies that have directly compared music and language with matched tasks in the same subjects. Using such studies to rigorously test the specificity of the brain circuitry involved in music will clearly be an important direction for future research.

Memory

Another example of deficits from brain damage that appear to be specific to music can be found in C.N., a patient with bilateral temporal lobe damage, now deceased, who appears to have had music agnosia—a memory deficit specific to music. Initially this patient had pronounced perceptual deficits in music as well (Peretz, Kolinsky, Tramo, & Labrecque, 1994), but over time these abilities mostly recovered while the memory deficits remained (Peretz, 1996). Patient C.N. was unable to recognize even highly familiar melodies, despite knowing the titles and lyrics. Nor could she hum back a familiar tune when prompted with a title. Many of the song titles evoked specific memories, but the musical information that had once accompanied them appeared mostly lost or inaccessible. Only when played a melody and forced to choose between two titles could C.N. successfully identify the name of the song. C.N. was also impaired at memorizing novel melodies, even with multiple repeated exposures, and did not even show implicit effects of repeated exposure to melodies (such as preferences for previously heard tunes). In all other respects her memory appears to be normal. The pattern of results suggests that there is a particular region of memory that is dedicated to music, which happens to have been damaged in C.N.

The case of C.N. is noteworthy for our purposes because it is difficult to explain the music-specific memory deficit by appealing to deficits of a more general capacity. But does this bolster the case for innate mechanisms for processing or storing music? It is certainly intriguing that memory for music may be segregated from other types of memories, even other types of sounds. It remains possible, however, that such a segregated organization arises naturally from the demands of storing different types of stimuli, with similar stimuli being stored nearby for reasons of retrieval efficiency. In general it is difficult to ascertain what effect C.N.'s lifetime of musical experience might have had on the organization of her memory prior to the brain damage.

In sum, studies of the brain have begun to characterize the various stages involved in the complex perceptual and cognitive processes that occur when we listen to music. It appears that there are distinct mechanisms for extracting the perceptual representations of melodies, for representing knowledge of musical structure, and for encoding music in memory. At this point it remains unclear whether any music-specific mechanisms might be hard-wired into the brain and thus candidates for the product of natural selection. Together with the comparative work on relative pitch perception, the characteristics of congenital amusia patients are consistent with a uniquely human mechanism for fine-grained relative pitch perception, but without more empirical support this possibility remains highly speculative. The mechanisms that encode tonal knowledge and possibly other aspects of musical structure are also candidates for uniquely human adaptations, but it remains unclear to what extent these mechanisms function exclusively for music perception. They could simply be co-opted from mechanisms that evolved for other functions. Future research will hopefully clarify this issue.

Discussion

This review was intended to sketch out a framework for studying the evolutionary origins and adaptive significance of music and to review the available evidence from a variety of relevant fields of inquiry. We contend that evolutionary theories of music will be facilitated if we can identify what, if any, innate constraints on music are present in the brain at birth and then determine which of these are unique to humans and specific to music. Evidence from many areas can converge to suggest innateness, and then comparative studies of other animals can establish the uniquely human, and possibly domain-specific, aspects of music.

What have we learned? In our view there is suggestive evidence that, at least to some extent, the structure of music is constrained by innate features of the brain. Most obviously, music is defined in part by pitch changes. These have perceptual prominence even in young infants, suggesting that the auditory system is set up to represent stimuli in terms of such pitch changes. Perhaps unsurprisingly, a case can also be made for the biological basis of the octave, which seems predisposed to have a central role in music; it is both prevalent in musical systems worldwide and perceptually privileged, at least in some cases, in nonhuman primates. There is also some evidence that simple ratios are predisposed to have important roles in music. They are common in the music of many cultures, modern and ancient, and have a unique perceptual status in both human infants and adults. Evidence from infant, animal, and cross-cultural studies also suggests that "tonal" melodies (composed with notes from the diatonic scale) are processed differently by the brain than atonal ones (composed with notes from equal interval scales), again at least in part independent of experience. Certain elementary musical preferences also appear to be potentially innate, as they are found in very young infants. Lullabies provide another example of innate constraints on an aspect of music, as they are apparently universal, engineered with consistent acoustic features across cultures, and unique to humans. Finally, there is some preliminary evidence that there are culturally invariant cues to emotion in music. Evidence from developmental psychology, however, is consistent with a prominent role for learning and could indicate that the major/minor mapping is the arbitrary product of cultural exposure.

One central question is whether the prevalence and special perceptual status of these aspects of music are the result of a uniquely human adaptation or are rather a byproduct of auditory mechanisms that evolved for other purposes. It is generally accepted, for instance, that the importance of the octave derives at least in part from mechanisms for estimating the pitch of complex tones (Terhardt, 1974), which we most likely inherited from nonhuman ancestors or at least evolved independently (Heffner & Whitfield, 1976; Chung & Colavita, 1976; Cynx & Shapiro, 1986; Tomlinson & Schwarz, 1988; Bendor & Wang, 2005). With regard to relative pitch, "natural" intervals, "tonality," and preferences, evidence for uniqueness is less clear, due in part to the relatively thin comparative database. The available data are consistent with the idea that the primacy and fine-grained resolution of relative pitch in humans might be unique among other animals and as such would be a candidate for a relatively recent adaptation. Preferences for consonance over dissonance and perhaps in general may also be unique to humans. Little is known about the status of different kinds of musical intervals or the various features of tonal music in animals. At this point, therefore, additional studies are needed before we can speculate about the evolutionary and developmental origins of such characteristics of music.

Any innate biases for music must somehow be instantiated in the brain, but at present there is little evidence for neural circuitry dedicated to music. It might well be the case that any music-specific adaptation is not anatomically punctate, in which case it might be hard to detect with functional imaging or neuropsychology. In our view, the two best candidates at this point are the mechanisms for detecting pitch changes and for representing the tonal hierarchy. Many of the other perceptual biases we have reviewed may result from general-purpose features of the auditory system. For instance, as we have discussed, it might be the case that the special perceptual status of simple intervals also derives from mechanisms for inferring pitch. Pitch perception involves analyzing the relationships between the harmonics of a complex sound signal, the frequencies of which are often related by simple ratios. Due to the demands of such analysis, the neural representations of such frequencies could perhaps develop connectivity that causes simple intervals to be processed differently than complex ones. Such connectivity could also conceivably emerge from mere exposure to harmonic sounds. Given that connections between neurons that fire at the same time tend to be strengthened over time (Sejnowski, 1999), harmonic sounds might tend to strengthen the connections between neurons coding frequencies related by simple ratios. Computational modeling could help to test these ideas.

In studying the origins of music we would ultimately like to explain the prevalence of certain features of music as well as the aesthetic and emotional responses that are arguably its most important and salient feature. However, much of the work we have reviewed describes something quite different—perceptual sensitivity differences in human infants, adults, and nonhumans for certain musical and nonmusical structures. Sensitivity differences are no doubt a popular target of research in part because sensitivity is often easier to measure than aesthetic or emotional responses. One might nonetheless wonder as to their significance, given that they are not obviously an important part of musical experience. Sensitivity differences are important because they presumably are due to neural circuits tuned to musical structures and as such indicate how the brain might be shaped for music. Notably, the documented sensitivity differences occur for musical structures that are prevalent in music and that adults prefer to hear in the context of music (e.g., simple ratios, tonal melodies). Although it seems unlikely that this is merely a coincidence, it is not obvious how differences in sensitivity might be causally related to preferences for some structures over others or to the prevalence of these structures in popular music. It is possible that the observed sensitivity differences could somehow result from innate generative rules for music (Lerdahl & Jackendoff, 1983). This kind of explanation would also account for the prevalence of the structures we are sensitive to, because the same rules that give rise to the sensitivity would also in part determine what people would be capable of producing. Another possibility is that sensitivity differences derive from certain signals being better encoded and remembered. In this case the prevalence of certain features of music could result from these features being transmitted with greater likelihood from person to person. At this point, these suggestions are speculative, with little supporting evidence one way or the other. We think, however, that they represent an important avenue for future research.

In addition to suggesting that certain features of music are the result of innate biases, the available evidence suggests that other aspects are learned through cultural exposure. The sensitivity that adults have to key structure (Krumhansl, 1990; Trainor & Trehub, 1992) and culturally specific scale structure is not present in infants (Lynch et al., 1990), suggesting that it is acquired through experience, perhaps subject to certain constraints. It is unclear whether there are music-specific learning mechanisms involved in this process, and experiments on the effects of musical exposure on nonhuman primates might help to clarify both the evolution and development of this capacity.

There is some evidence from young infants that certain basic musical preferences are innate, namely the preference for consonance over dissonance. The absence of such preferences in nonhumans, if confirmed in species other than those that we have tested, might indicate that musical preferences are unique to humans and perhaps part of a music-specific adaptation. Such patterns could also mean that the preferences in infants are the product of their exposure. It would be useful to test infants and adults from non-Western cultures to see if they have similar preferences, at least with respect to the consonant/dissonant distinction.

One point is clear: Much remains to be studied. A number of topics have scarcely been touched at all, and we have therefore shied away from them in this review. The enjoyment of rhythm and dancing is also apparently universal—people everywhere like to move to music, and dancing is as ubiquitous as is the performance and enjoyment of music itself. At present, very little is known about these most mysterious features of music. Human adults are often spontaneously entrained to musical rhythms, moving in time with the beat. As with other aspects of music perception, we would like to determine whether this response to music is learned or innate and whether it is uniquely human. The entrainment that occurs during dancing could simply be learned from examples, but entrainment also occurs outside the realm of dance, as evidenced by head nodding and foot tapping, which apparently are often executed unconsciously. Studies in young infants could help to address how and to what extent experience shapes this capacity. However, Trehub (personal communication) reports that very young infants, although clearly engaged by music, do not move much at all in response to it. Indeed, this may be the main reason that parents sing to their infants. Although infants start to move to rhythmic music toward the end of their first year, and often move somewhat more to music with fast tempos, their movements are not synchronized to the music. Synchronized movement to music does not emerge until at least several years later. The capacity to become entrained by rhythms is likely limited to some extent by the development of motor coordination, but in any case behavioral studies in human infants seem unlikely to resolve the role of learning in this behavior. Comparative studies of these issues would clearly also be of interest, as the role of learning and musical exposure could be controlled. While there are a few examples of animals maintaining a musical rhythm after having been trained to do so (e.g., the Thai elephant orchestra), we know of no demonstrations of animals spontaneously becoming entrained to rhythms as people do. There are numerous well-known examples of elaborate dances in animal courtship rituals, but as with animal song, these have a very specific and narrow function. We think animal dances are unlikely to be related to dance in humans, but it might nonetheless be profitable to examine whether movements in such dances are synchronized to song.

We have also avoided discussion of the literature on perfect or absolute pitch (Zatorre, 2003), mainly because it is a rare phenomenon that is of questionable relevance to music perception in the vast majority of listeners. It has been suggested, however, that all humans are born with absolute pitch, and that most people learn to hear relative pitch as the result of exposure to speech and music in which the absolute pitch varies and what matters is the relative pitch of the different syllables or tones. Consistent with this notion, some evidence suggests that infants rely more on absolute pitch than do adults (Saffran & Griepentrog, 2001; Saffran, 2003), although infants seem to readily hear the relative pitch sequences that define a melody's contour (Trehub et al., 1984). It is important to note, though, that any hypothetical enhanced absolute pitch perception in infants would be quite different from that in adults with perfect pitch, in which verbal category labels are key. Normal humans, though lacking the large number of fixed pitch categories found in those possessing perfect pitch, nonetheless have the usual ability to make limited absolute judgments along a perceptual dimension (Miller, 1956), and it is unclear that infants can do any better. They may simply place more emphasis on crude absolute pitch information than they do on relative pitch. Complicating matters are recent suggestions that normal humans may have much better memory for absolute pitch than has been traditionally thought, at least for familiar melodies (Levitin, 1994; Schellenberg & Trehub, 2003). As noted earlier, the capacity for fine-grained relative pitch perception is key to music perception and might be unique to humans; further experiments clarifying the relationship between and development of absolute and relative pitch would be most useful.

One of the most interesting aspects of music, particularly from the standpoint of cognitive science, is the modulation of tension that occurs within a piece (Lerdahl & Jackendoff, 1983; Narmour, 1990; Lerdahl, 2001). This is in part a function of cognitive representations of tonality (Krumhansl, 1990, 1996; Smith & Cuddy, 2003), which appear to be learned, perhaps subject to innate constraints. But the very fact that tension and resolution are associated with music is itself interesting and, we think, worthy of investigation. We suspect that certain acoustic cues to tension (increases in volume or tempo, for instance) may well be innate and could be present in animals. The origins of the association between tension and various other cues, such as those that involve tonality, are less clear. Given the importance of introducing and resolving tension in music, this will certainly be a worthwhile focus of future research, but we have largely avoided its discussion due to the paucity of work on the topic.

In general, our coverage of music perception in this review has been highly Western-centric. This is mainly a reflection of the state of music perception research, most of which occurs in the West and is conducted by researchers who are most familiar with Western music, using subjects who have generally had extensive exposure to Western music. It is important to note, though, that many features of Western music are not as central in other cultures (harmony being perhaps the most notable), and that many features of music in other cultures are not as central in Western music (complex rhythms, for instance). Rhythm is arguably more important than melody and harmony in many cultures' music, and we have almost entirely avoided its discussion. This is again mainly because there is less empirical work addressing whether any aspects of rhythm perception are innate (though see Trehub, Hill, & Kamenetsky, 1997a; Hannon & Trehub 2005). It is also worth noting that the function of music in Western culture is not entirely representative of how music is used in other cultures. In many indigenous cultures music is often more closely tied to particular rituals, and indeed one of the most obvious universal properties of music is its association with religion (Nettl, 1983), which occurs in every culture so far as we know. Although we consider one of the most interesting features of music to be the fact that it is often made purely for enjoyment's sake, it is unclear how often this is actually the case in less developed cultures. The differences between Western music and those of the many other cultures around the globe should thus not be overlooked.

Our interest in the innate components of music is motivated by the desire to understand its evolutionary origins and adaptive significance. At present we have some intriguing clues about innate perceptual biases related to music, but probably not enough to seriously constrain evolutionary hypotheses. It seems that humans have an innate drive to make and enjoy music and that they are predisposed to make music with certain features (the octave, simple ratios, unequal intervals). These features seem to be related to perceptual sensitivities to musical structure found in human infants and perhaps also nonhuman animals in the absence of extensive experience. There is also some evidence for innate musical preferences in human infants, preferences that do not seem to be shared by our primate relatives. These observations are consistent with most of the proposed evolutionary theories. To constrain evolutionary accounts, further work must clarify which other features are innate and of these which are unique to humans, because these innate, unique features are the candidates for music-specific adaptations. We are hopeful that the framework established by the research reviewed here will help guide future studies of these fascinating issues.

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