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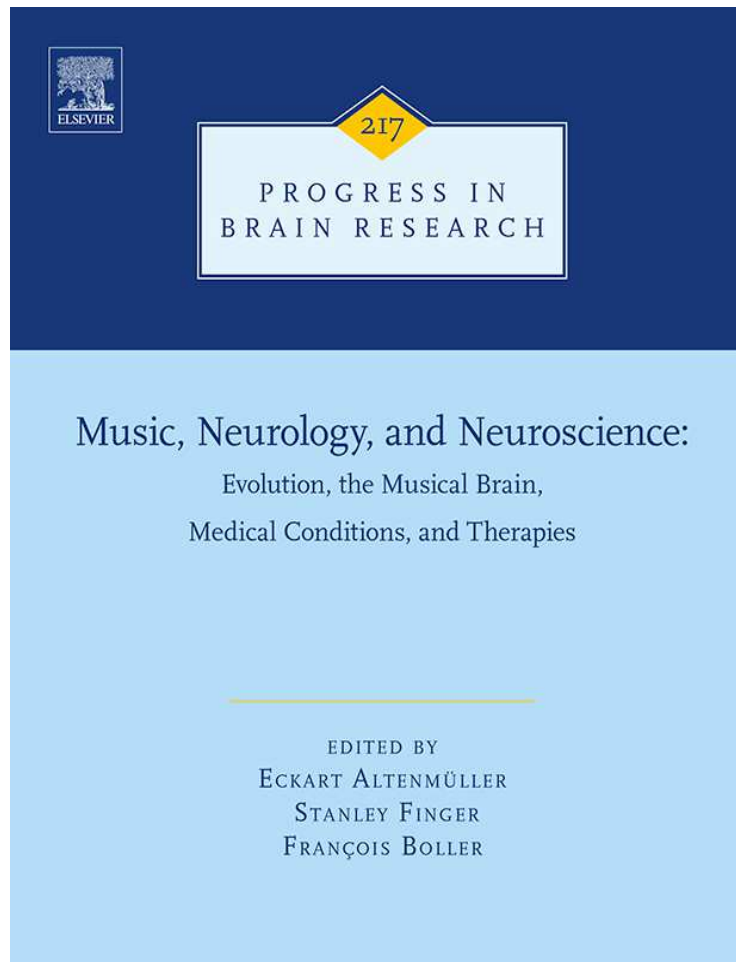
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# Music evolution and neuroscience<sup>☆</sup>

# 2

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## Abstract

There have been many attempts to discuss the evolutionary origins of music. We review theories of music origins and take the perspective that music is originally derived from emotional signals. We show that music has adaptive value through emotional contagion, social cohesion, and improved well-being. We trace the roots of music through the emotional signals of other species suggesting that the emotional aspects of music have a long evolutionary history. We show how music and speech are closely interlinked with the musical aspects of speech conveying emotional information. We describe acoustic structures that communicate emotion in music and present evidence that these emotional features are widespread among humans and also function to induce emotions in animals. Similar acoustic structures are present in the emotional signals of nonhuman animals. We conclude with a discussion of music designed specifically to induce emotional states in animals.

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## Keywords

adaptive value, cross-species parallels, emotional signals, emotions in music, evolution of music, music and speech interactions

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## 1 INTRODUCTION

What are the origins of music? Is music unique to humans or does it have an evolutionary history? Does music have an adaptive function and, if so, would this function have been of use to other species? What is the relationship between music and

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<sup>☆</sup>This chapter is dedicated to the memory of Michael J. Owren (1955–2014) whose influential work on emotional signals in human and nonhuman species has provided an empirical and theoretical basis for our writing.

language? Can music be related to emotional signaling in nonhuman animals? Are there emotional universals in music and in animal signals? If music can induce emotional states in listeners, can animal signals do the same? This chapter attempts to provide some answers to these questions. We take the perspective that music was derived from the emotional signals of other species and had as its initial primary function to induce emotional states in listeners. We will briefly review various theories of music origins and then provide data suggesting that music is adaptive in promoting social cohesion and has beneficial physiological effects in humans and other species. We then provide evidence that the emotional content of language is mediated by music-like structures involved both in vowel harmonics and in prosody. Prosody in human speech also influences the behavior of preverbal infants, as well as the behavior of other species, suggesting an evolutionary continuum. Next, we will consider the possibility of universals in the ways music induces emotions across cultures and look for similar universals in animal emotional signals. We will provide evidence on some experimental tests of playing music to animals and conclude with some suggestions for future directions.

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## 2 THEORIES OF MUSIC ORIGINS

There is a variety of ideas about the evolution of music that focus on whether music is adaptive or not, ranging from the “music as cheesecake” hypothesis of [Pinker \(1997\)](#) that music is nice but has no adaptive function to the idea that music is sexually selected and is important in mate choice ([Charlton, 2014](#); [Darwin, 1871](#); Kleinman, in the first volume; [Miller, 2000](#)), to the Mixed Origins of Music hypothesis ([Altenmüller et al., 2013](#)) which maintains that the early roots of music may lie in an ancient affective signaling system that is common to many socially living mammals. However, later on music also induced aesthetic emotions and facilitated a safe practice environment for auditory learning, promotion of social cohesion, and for psychological and physiological well-being.

The origins of music have been hypothesized to be uniquely human following after the evolution of language, since music requires many of the cognitive skills associated with language ([Patel, 2008](#)) or has evolved simultaneously with language (the music language hypothesis; [Brown, 2000](#)). As an alternative to music being unique to humans, [Juslin and Västfjäll \(2008\)](#) and [Levitin \(2008\)](#) have proposed that music has evolved from emotional communication and that the musical components of speech provide honest communication about emotions. This is the view that we will support in this chapter. We agree with [Altenmüller et al. \(2013\)](#) that there is more to music than simply affective or emotional communication, but from a phylogenetic perspective we can focus only on observable behaviors.

In studying the evolution of a phenomenon, there are two separate questions that need to be answered. The first question has to do with adaptation or function. Can we discern obvious benefits to music that cannot be found with other types of auditory inputs such as speech or other sounds? If there is no clear adaptive function that can be detected then what we study might simply be an artifact of another evolved

function. Thus, music might simply have been an incidental component to the evolution of a complex auditory system that is needed to process speech sounds. The second question has to do with time course or phylogeny. A trait might be adaptive solely for modern humans and could have evolved after branching off, or a trait may have appeared even in nonhuman mammals and may thus be ancestral and shared by other species as well.

There are two models of phylogeny—divergent and convergent evolution. Most people are familiar with divergent evolution: that traits studied in one species might be shared with a common ancestor. Thus, for humans, apes and monkeys are our closest relatives and traits shared among several species suggest a common ancestor dating back to when the lines diverged. Less well known is the concept of converging evolution: that species with similar problems to solve may have developed similar adaptations regardless of phylogenetic closeness. Thus, many have argued that songbirds are good models for human speech and music, since vocal signals appear to play a much more important role for humans and songbirds than for our closest relatives. We need to evaluate both adaptation and phylogeny to understand the origins of music.

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### 3 MUSIC IS ADAPTIVE

We first need to demonstrate how music can be adaptive. One of the best known putative adaptive advantages has been music as a sexually selected trait that allows males to compete for females. This idea was initially suggested by Darwin (1871) and subsequently advocated by Miller (2000). Haselton and Miller (2006) found increased attractiveness of men expressing creative intelligence as short-term sexual partners at the time of ovulation in women. Charlton (2014) has reported that peri-ovulatory women show significant short-term mating preferences for men who are attributed as composers of complex music. The “complex” music used by Charlton (2014) is still relatively simple compared with most composed music, which may make these short-term mate preferences even stronger with most music.

As articulated by Owren and Rendall (2001) for animal signals, emotional signals can induce emotional states in others that can lead to social cohesion with shared emotions and increased cooperation within a group. Mithen (2005) has suggested this social cohesion function of music for our prehistoric ancestors. Emotional signals can also influence cognition and have effects on the physiology and neuroendocrine systems of listeners.

One contemporary study provides evidence for the social cohesion function of music. Kirschner and Tomasello (2010) studied two groups of 4-year-old children. In one condition, pairs of children marched around an artificial pond containing toy frogs, while singing a song to musical accompaniment and picking up the frogs in time to the song to wake them up. In the other group, pairs of children engaged in the same actions but without singing. The children were then tested on a task that involved cooperation with the other child and on a task where one child could choose to help the other child. In the joint singing condition, children were significantly more likely to cooperate with and to help one another than in the condition without music.

Several cognitive and physiological effects of music have been demonstrated in human and in nonhuman animals. When neuroanatomical terms are presented in the form of a song, college students learned the terms more rapidly and retained more of the terms when tested up to 10 days later (Panksepp and Bernatzky, 2002). Adding speech to music (as in a song) may lead to greater memory. Weiss et al. (2012) measured recognition memory for old versus new melodies using piano, banjo, marimba, and voice, with greater recognition occurring for sung melodies. Emotional mood induction by music (happy or sad) can influence whether happy or sad memories can be recalled (Parrott and Sabini, 1990).

Music has also been used in therapeutic situations with reports suggesting music reduces anxiety and improves mood for medical and surgical patients (Kemper and Danhauer, 2005), with specific effects on pain reduction and pain distress in the early postoperative days in patients undergoing abdominal surgery (Vaajoki et al., 2011), and with soothing music increasing oxytocin levels after open heart surgery (Nilsson, 2009). Music also reduces anxiety and depression, and blood volume pulse amplitude in caregivers of cancer patients (Lai et al., 2011). Although music could not have evolved initially to alleviate stress in patients, the more general conclusions are that soothing music can influence physiological process that bring about enhanced physical and mental well-being, and these could have had important adaptive functions.

Listening to music has been shown to modulate activity in a network of structures associated with reward and pleasure in the brain. Using functional magnetic resonance imaging (fMRI) and functional and effective connectivity analyses in human participants, Menon and Levitin (2005) demonstrated activation of the nucleus accumbens and ventral tegmental area with subsequent connections to the hypothalamus, insula, and orbitofrontal cortex. Salimpoor et al. (2013) used similar methods with people listening to a piece of music for the first time and found that the aesthetic rewards of music correlated with the interaction of the nucleus accumbens with the auditory cortex, amygdala, and ventromedial prefrontal cortex. These results help explain why listening to music is highly pleasurable.

Studies in nonhuman animals provide similar findings to those in humans, suggesting some sort of continuity across species. Thus, music reduces the distress vocalizations produced by newborn chicks in isolation (Panksepp, 1998) similar to the effects of injecting the social hormones, prolactin, or oxytocin into the brain (Panksepp, 1996). Music also increases levels of dopamine and norepinephrine in the brain, both of which are involved in processes of arousal and attention and lead to rewarding effects (Panksepp and Bernatzky, 2002). Music has been shown to have several other effects. For example, dogs in shelters were calmer after listening to classical music and barked more after listening to heavy metal (Wells et al., 2002). However, music by Mozart (*Symphony #40*) decreased heart rate in hypertensive rats, whereas music by Ligetti (*String Quartet #2*) increased blood pressure in hypertensive rats (Lemmer, 2008), suggesting that classical music should not be treated as a unitary genre. Playing of Mozart's Adagio (from *Divertimento #7, K. 205*) reduced blood pressure and stimulated dopamine synthesis in hypertensive rats

(Akiyama and Sutoo, 2011), but only music in the range of rat vocalizations (4–16 kHz) was effective, illustrating that the type of music played should be related to the auditory system of the species being studied (see below). Prenatal exposure to Mozart's *Piano Sonata (K. 443)* led rats when adults to learn maze tasks more quickly (Chikahisa et al., 2006). Ames and Arehart (1972) exposed lambs to music of Montovani or to white noise and found decreased heart rate and decreased heart rate variability in music-exposed lambs.

One would not normally expect fish to be responsive to music, but several studies in fish have reported effects on growth rate and physiology. Gilthead seabream showed increased growth rate and weight gain, but decreased dopamine levels when exposed to Mozart's *Eine Kleine Nachtmusik (K. 525)* (Papoutsoglou et al., 2008), similar to results in common carp (Papoutsoglou et al., 2007).

In summary, taken together these human and animal studies suggest a role for music in emotional induction and coordination of behavior, increased cognitive skills, in beneficial physiological effects, and positive neurochemical changes. However, it is not clear what aspects of music have positive physiological and cognitive effects in humans and animals. In many cases, the precise music being used is not specified, and in other cases music by Mozart is used ostensibly to mimic the now discredited “Mozart effect” on human cognition (Steele et al., 1999). It is likely that different aspects of music—tempo, harmony versus dissonance, major versus minor keys, note duration, and familiarity—may all have an influence on these processes. Future work should examine with greater precision which aspects of music have specific effects on both humans and animals. With nonhuman animals, researchers should consider the range of auditory sensitivity in the tested species, as well as typical tempos in animal vocalizations when testing with music, since the literature also reports many studies where music has no effect on animal development, physiology, or behavior.

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## 4 MUSIC AND PHYLOGENY

The second evolutionary issue concerns whether music or music-like phenomena are seen in other species. If we do see aspects of music in other species, then the origins of music may predate our own species. There already have been several reviews on this by Altenmüller et al. (2013), Fitch (2006), Hauser and McDermott (2003), and Patel (2008, 2010), each reaching different conclusions. Hauser and McDermott (2003) assert that any features of music perception found in nonhuman animals must be related to similar perceptual systems and not to music, since they assume that music is not to be found in animals. Fitch (2006) is more open-minded and considers that learned song in birds, whales, and other species might represent convergence to music in humans whereas drumming by apes might represent a potential homology. Patel (2010) argues in partial agreement with Hauser and McDermott that any aspects of music cognition that are based on brain functions were developed for other purposes and cannot be part of the natural selective processes for music. However,

like Fitch he thinks that species with vocal learning might be able to display with humans the ability to synchronize behavior to the changing of tempi in music, and that this may represent a phylogenetic origin of the ability to keep time with a beat. Indeed, [Patel et al. \(2009\)](#) have shown that a cockatoo is able to synchronize to a changing beat. Here, we adapt the view of [Altenmüller et al. \(2013\)](#) of two emotional systems, with “strong” emotions having close parallels with emotional communication in other species and “aesthetic” emotions being derived in humans.

We will detail support for this view in later sections but first address some other data from animals. Patel and others have argued that vocal learning is a prerequisite for beat synchronization and a study of rhesus macaques (which do not learn vocalizations) found that the macaques could detect rhythmic groupings but not the beat ([Honing et al., 2012](#)). However, a recent study on one sea lion ([Cook et al., 2013](#)) demonstrated the ability to entrain movement to rhythmic auditory stimuli. Thus, vocal learning may not be a prerequisite for keeping the beat.

Many studies have demonstrated absolute pitch in nonhuman animals ([Hulse and Page, 1988](#)), but only one study (in rhesus macaques) has demonstrated octave generalization, the ability to recognize melodies when transposed one octave higher or lower ([Wright et al., 2000](#)). Interestingly, the macaques could generalize only when melodies were taken from the diatonic scale; when they were tested with atonal melodies, octave generalization disappeared. Most studies have used atonal melodies and the success of generalization with the diatonic scale suggests that the diatonic scale may have some fundamental perceptual features that can be found even in distantly related animals. It is interesting to note that research on bird songs (most commonly suggested as analogous to human music) has failed to find evidence of harmonic intervals that match the chromatic, major diatonic, or major pentatonic scales ([Arala-Salas, 2012](#); [Dobson and Lemon, 1977](#)). Thus bird song is not really musical. This suggests that, even if one used a diatonic scale, one would not find octave generalizations or relative pitch in songbirds.

Several researchers have examined whether animals can discriminate between different types of music and whether they show preferences. [Porter and Neuringer \(1984\)](#) found that pigeons slowly learned to discriminate between music by Bach and Stravinsky, but the pigeons showed rapid generalization to novel pieces by Buxtehude and Scarlatti with Bach, and to pieces by Carter and Piston with Stravinsky. Human subjects showed similar generalization ability. [Watanabe and Nemoto \(1998\)](#) found half of Java sparrows tested preferred Bach to Schönberg and subsequently generalized to Vivaldi versus Carter. [Watanabe and Sato \(1999\)](#) reported that five of seven Java sparrows discriminated between Bach and Schönberg and generalized to novel examples from the same composers, as well as to music by Vivaldi (for Bach) and Carter (for Schönberg). [Otsuko et al. \(2009\)](#) trained rats to discriminate between music by Bach and by Stravinsky and found that rats could generalize to novel examples, but they also found that, although rats could discriminate between composers, they did not exhibit any preferences. Since the auditory range of rat vocalizations (unlike pigeons and sparrows) is much higher than that of human music, and because rats have subsequently been found to react only to the high-frequency



components of music (Akiyama and Sutoo, 2011), it is difficult to interpret the lack of preference for human music by rats. We address this general issue in greater detail later in this chapter.

There have been contradictory findings with respect to whether animals have a preference for consonant over dissonant music. Sugimoto et al. (2010) found that one infant chimpanzee showed a preference for consonant over dissonant music, whereas Koda et al. (2013) reported that Campbell's monkeys did not show any preference for consonance. However, Chiandetto and Vallortigara (2011) found that chickens did prefer consonant music. It is hard to make sense of this pattern of results in terms of phylogeny.

In summary, there is considerable controversy about the degree to which music-like phenomena are found in nonhuman animals, and results from different species do not suggest consistent phylogenetic homologies or a consistent pattern of convergent analogies. We think that the data are much clearer with respect to emotional signals. In the next section, we shall consider musico-emotional effects in human language and emotional communication and then shall seek parallels in animal signals.

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## 5 MUSIC AND EMOTION IN HUMAN SPEECH AND PARALLELS IN OTHER SPECIES

Human vowel sounds are based on the chromatic scale. In a series of studies, Purves and collaborators have shown that the statistical structure of human speech shows a probability distribution with peaks at frequency ratios that match the chromatic scale. This appears to be a direct result of the resonances of the human vocal tract, and suggests that music and speech are closely linked. Peaks in the distribution were especially prominent at the octave, the fifth, the fourth, the major third, and the major sixth forming the intervals of the pentatonic scale and most of the intervals on a diatonic scale (Schwartz et al., 2003). The authors sampled not only English speakers but speakers of Tamil, Farsi, and Mandarin and found similar relationships within each language. Han et al. (2011) examined music and speech from three tonal languages and three nontonal languages and found that changes in pitch direction occurred more frequently and had larger changes in pitch direction in tonal languages, and that the music typical of the cultures with tonal language also showed similar frequent and large changes in pitch direction, suggesting a coevolution of music and language. Gill and Purves (2009) showed that the most widely used scales across time and across cultures are those that are similar to harmonic series. The authors suggest that humans prefer tone combinations that reflect the spectral relationships of human vocalizations. Bowling et al. (2010) sampled speech spectra from excited versus subdued speech and found that the spectral distribution of excited speech showed similarities to the distribution of major intervals, whereas the spectral distribution of subdued speech matched the spectral pattern of minor intervals. This was particularly noteworthy with respect to major and minor thirds. Thus, the

harmonic structure of speech closely parallels that of music across cultures, and affective changes in emotion are evident in different harmonic structures of speech just as they are in music.

A second source of music in language is prosody—the intonation contours of speech. It seems quite likely that we detect emotional signals more clearly through pitch and intonation contours than we do through actual words. A clear test of this is in studies of communication between human parents and preverbal infants, where specific prosodic (musical) features have been identified that can influence the behavioral state of the infant (Fernald, 1992). Several short, upwardly rising staccato calls lead to increased arousal. Long descending intonation contours have a calming effect, and behavior can be stopped with a single short plosive note. These patterns were observed across speakers of several different languages. Interestingly, similar features appear in the calls and whistles used by humans to control the behavior of working animals (dogs and horses) (McConnell, 1990, 1991). The convergence of signal structure that humans use to communicate with both preverbal infants and nonhuman animals suggests that these signals are effective across species. The communication of affect through voice is not unique to humans, and the acoustic structures involved must have similar effects on the nervous system of both human infant and animal recipients.

Prosody can be used to induce behavioral changes in others. In the case of humans who are attempting to manage the behavior of infants and animals, the speakers need not be directly experiencing the emotion they are trying to induce. Rather, they are using specific signal types to induce a form of emotional contagion in their listeners. We know very little about the effects of natural animal signals on inducing emotions in other animals, a point we will try to address below.

Juslin and Laukka (2003) examined a large number of studies that evaluated how emotions were conveyed in spoken language and in music performance, and they found notable similarities between the two modes in the accuracy with which listeners could identify discrete emotions and the specific types of acoustical cues used to convey discrete emotions in both music and speech. There is indeed a very close relationship between emotional communication in speech and language.

Given that nonhuman animals respond behaviorally to the same affective signals that human infants do, we must next ask whether humans have the ability to distinguish affective states in the calls of other species. Belin et al. (2008) presented humans with positive and negative affective vocalizations from humans, cats, and monkeys, and they found that humans were adept at discriminating human affective calls, but were at chance level with the cat and monkey vocalizations. However, when the same participants were presented with the same stimuli while undergoing fMRI of their brains, they found that the animal vocalizations activated the same areas that human vocalizations with similar valence activated. Specifically bilateral regions of the auditory cortex were activated more by negative vocalizations from all three species; bilateral regions of the lateral inferior prefrontal cortex were activated more by positive vocalizations of all three species; and the right orbital frontal cortex responded more to negative vocalizations of all species.

Thus, although the human participants did not display conscious recognition of different animal calls of different emotional valences, their nervous systems distinguished between these calls.

In another study of cat calls, [Nicastro and Owren \(2003\)](#) found a modest ability of humans to discriminate between positive and negative calls, and also found that participants who owned cats or interacted frequently with cats were more adept at discrimination. Similarly, [Scheumann et al. \(2014\)](#) tested human ability to discriminate between agonistic and affiliative calls of humans, dogs, chimpanzees, and tree shrews and found that whereas discrimination of human calls was easy for everyone, there was a clear effect of familiarity with a species and with the contexts of agonism or affiliation, leading to more accurate discrimination. Thus, although human brains appear responsive to affiliation and agonistic calls of other species, conscious discrimination of these calls appears to require significant familiarity with the species.

In summary, music and speech appear to be closely linked, and the linkage is clearest at the level of emotional expression. Both the prosody of speech and the spectral distribution of speech sounds can convey emotional meaning. These same characteristics are effective in altering the behavior of nonverbal human infants and of working animals (e.g., horses, herding dogs), suggesting that these emotional signals are effective across species. The brain areas in humans involved in distinguishing between positive and negative emotions in human and animal calls appear to be the same and can be activated even if the human is unable to make a conscious discrimination between the affective calls of another species. However, with experience, humans can make accurate discriminations. Let us now turn to the question of whether there exist emotional universals in human music, and then consider whether similar universals are present in animal calls.

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## 6 ARE THERE EMOTIONAL UNIVERSALS IN HUMAN MUSIC?

Emotions can be expressed in music and there have been several attempts to describe the structures that convey emotions. [Scherer \(1995\)](#) suggested that sadness is conveyed by slow tempos, a narrow frequency range, decreases in pitch, and a slow rate of articulation. (This is similar to the intonation contours that lead to calming in preverbal infants and nonhuman animals.) Joy is conveyed by fast tempos, increasing pitches that are highly variable, and by increased rates of articulation. (This is similar to the intonation contours that lead to increased activity and arousal in preverbal infants and nonhuman animals.) Anger is conveyed by an increase in fundamental frequency and by higher intensity (amplitude), and fear is shown with an increase in fundamental frequency, many high-frequency components, and a faster rate of articulation.

[Snowdon and Teie \(2013\)](#) hypothesized that harmonic structures and pure tones would be associated with positive states, whereas dissonant (or noisy) structures would be associated with aggression, fear, and defense. Staccato calls would be

arousing, whereas legato notes would be calming. Regular rhythms should be associated with positive states or events, whereas irregular rhythms would be associated with negative states or events.

In a review of several studies on how emotions were expressed in both speech and in music, [Juslin and Laukka \(2003\)](#) reported that the structural patterns matched very closely the predictions made by [Scherer \(1995\)](#). [Bresin and Friberg \(2011\)](#) experimentally tested the validity of Scherer's classification by having 20 trained musical performers manipulate seven different variables (i.e., tempo, sound level, articulation, phrasing, register, timbre, and attack speed) to communicate five emotions (i.e., neutral, happy, sad, fear, and calm). Happiness was communicated by a fast tempo, staccato articulation, high register, high intensity, and fast attack. Fear was communicated by a fast tempo, staccato articulation, moderate intensity, low register, and slow attack rate. Sadness was communicated by a slow tempo, very low intensity, legato articulation, mid-range register, and slow attack speeds. Calmness was communicated by a slow tempo, low intensity, legato articulation, high register, and slow attack rate. Thus, when musicians were asked to express different emotions in the same piece of music, they explicitly used the same acoustic variables that Scherer hypothesized to be involved in emotional expression.

[Gomez and Danuser \(2007\)](#) studied the relationship between the emotional aspects of music and psychophysiological response to music. Participants evaluated the degree of pleasantness and arousal of different types of music, while simultaneous measurements were made of skin conductance, heart rate, and respiration. There was a close connection between self-reported emotional evaluation and the physiological responses with mode, harmonic complexity and rhythmic articulation differentiating between negative and positive valences and tempo, acceleration and rhythmic articulation discriminating between high and low arousal. Thus, participants not only evaluated the music appropriately, but the music actually induced emotional responses.

However, all of these studies have been done using Western listeners and musicians as well as with Western music. Does emotional communication generalize to music of different cultures, and are listeners who are unfamiliar with music from another culture still able to distinguish emotions? [Balkwell and Thompson \(1999\)](#) presented Western listeners with no prior experience with Indian ragas with excerpts from ragas recorded in the field in northern India. Each excerpt was intended to convey one of four emotions (i.e., joy, sadness, anger, and peace), and Western participants were able to identify the ragas associated with joy, sadness, and anger, although peace was confused with sadness. Among the key features for discrimination were rising notes and a fast tempo for joy, and falling notes and a slow tempo for sadness—again reflecting the prosodic features used by humans with preverbal children and with animals to arouse or calm them, respectively. Despite the great differences between Indian and Western music, the same structural features appear to encode the strong emotions of joy, fear, and anger.

In summary, one can find acoustic structures in music that reliably communicate different emotions. Experienced musicians can manipulate these structures when

asked to communicate a specific emotion, and naive listeners can identify emotions even within musical genres that are unfamiliar to them. There appear to be some emotional universals in music.

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## 7 ARE THERE EMOTIONAL UNIVERSALS IN ANIMAL CALLS?

Based on the results on how music communicates and induces emotions in humans, we can now ask if similar structures are found in the calls of other species. If we can find similar acoustic variables influencing emotional calls in nonhuman species, then it seems likely that the “strong” emotions (see [Altenmüller et al., 2013](#)) could have served as precursors for human music. The best known model of affective signals in animals is the motivational-structural model of [Morton \(1977\)](#). Morton evaluated call structures in fear and aggressive contexts in a variety of bird and mammal species and suggested that high-pitched, narrow-band, legato calls were used in fear contexts and that low-pitched, broad band (or noisy) calls signaled aggression.

[Snowdon and Teie \(2013\)](#) applied their framework of emotional structures in music to the calls of cotton-top tamarins. Recordings of spontaneous calls were presented to musicians, who evaluated the timbre, tempo, rate of articulation, and pitch of calls without knowing the context in which the calls were given. Five different clusters of calls were found and subsequently associated with the actual contexts in which they were given: calls used for affiliation had harmonic structure, legato articulation with ascending pitch, and narrow bandwidth; calls used for high arousal and threat were characterized by broadband staccato calls with clear harmonic intervals; calls used in fear contexts were characterized by noisy, dissonant, staccato sounds; and calls signifying confident threats were characterized by legato, harmonic sounds with rising pitches; the approach context was characterized by calls in triple meter with moderately long notes displaying harmonic structure but with both rising and falling intonations. The acoustic properties hypothesized for human emotional expression and music also appear to have parallels in the vocal repertoire of tamarins.

Research on several other species provides supporting evidence for some of these acoustic structures being involved in emotional communication. [Yang et al. \(2013\)](#) removed estrus females from male mice and found an increase in ascending components of ultrasonic vocalizations (indicating arousal) and a return to flat frequency calls (indicating calm) when reunited with females. In contrast, [Brudzynski \(2013\)](#) found alarm and threat calls (initiated by release of acetylcholine) in both rats and cats were characterized by low frequency, constant pitch, and long notes, whereas positive appetitive vocalizations (initiated by release of dopamine) were higher in pitch with frequency modulation and short notes (equivalent to the prosodic features that lead to arousal in preverbal infants and working animals). [Soltis \(2013\)](#) reported that dominance interactions in African elephants were associated with increased amplitude and duration of calls, whereas social agitation was associated with increased and more variable fundamental frequency and shorter duration notes. Aggression and mating were also characterized by high-frequency vocalizations.

In nonhuman primates, [Zimmermann \(2009\)](#) showed that gray mouse lemur calls increased in pitch and in duration during conditions of high arousal. A startled lemur produces loud, noisy, and plosive grunts, and females rejecting male mating approaches also produce short, frequency-modulated calls. Males courting females, however, use long, frequency-modulated or broadband calls. Infant mouse lemurs gave short frequency-modulated calls in threats, longer and less modulated calls when isolated, and low-pitched purrs while being groomed. [Lemasson et al. \(2012\)](#) studied three species of arboreal Old World primates under two conditions of affect intensity. As seen with mouse lemurs, each of these species produced higher pitched calls of longer duration when in the high-intensity condition. Thus, it appears that increased arousal in these species is communicated with longer calls, rather than the short, frequency-modulated prosodic variables that humans use to induce arousal. However, in cats [Scheumann et al. \(2012\)](#) reported intensity was coded by longer duration calls with shorter intercall intervals but decreased fundamental frequency.

In a comprehensive review of 39 studies across the mammalian order, [Zimmermann et al. \(2013\)](#) found increases in call rate were associated with alarm/disturbance and agonistic contexts and to some extent with affiliation as well. Call duration was longer with both affiliative and agonistic contexts, and increased fundamental frequency was seen with both alarm and agonistic contexts. However, there was also much variation between species, with call rate showing the most consistent correlation with arousal.

All socially living animals have to discriminate between individuals as well as context, and several studies have looked at whether different acoustic parameters are used for individual recognition or contextual information. In general, the results suggest that source and filter-related variables (e.g., fundamnet frequency, peak frequency, bandwidth) code for individual recognition whereas temporal (e.g., call duration, intercall interval), source-related, and tonal (e.g., voicing, harmonic to noise ratio) parameters code arousal (for cats, see [Scheumann et al., 2012](#); for baboons, see [Rendall, 2003](#)). In addition, different types of affective calls differ in the likelihood of coding individual features. Thus, mother baboons could easily discriminate the contact calls of their own infants, but not their distress screams ([Rendall et al., 2009](#)). There may be adaptive value in structuring a distress scream for an immediate response without taking additional time and resources to encode individuality.

Emotional contagion is frequently seen when animals vocalize. Singing birds, duetting titi monkeys and gibbons, pant-hooting chimpanzees, howling wolves, and many other species show emotional contagion. When one animal or pair begins to call, others of the same species join in, until many members of one group or pair are calling to members of other groups and pairs. The contagious calling serves to reinforce social relationships within a pair or group, and serves to keep others away from the pair or group, just as music was hypothesized to promote social cohesion in our human ancestors.

In summary, there are many parallels between the structures of signals used to communicate specific emotional states across animal species, just as there are among humans. This is especially clear with respect to arousal and less clear with respect to

states such as fear, aggression, or affiliation. Emotional contagion is common in many animal species and serves to promote social cohesion among group members and to keep others away.

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## 8 HOW DO ANIMALS RESPOND TO SPECIES-RELEVANT MUSIC?

Although there are some similarities in emotional signaling, there are also species differences that must be considered. This becomes most obvious in the case of playing human music to nonhuman animals. [Akiyama and Sutoo \(2011\)](#), in an effort to see if playing Mozart would have any effect on blood pressure in hypertensive rats, found that, if they filtered the music, the components above 4 kHz were as effective as playing the unfiltered music. Given that rats use frequencies into the human ultrasound range for communication and are sensitive to a higher frequency range than humans, this makes sense. However, many other studies have failed to consider the ecological relevance of human music to other species.

[McDermott and Hauser \(2007\)](#) tested common marmosets and cotton-top tamarins for preferences for Mozart versus heavy metal and found a preference for Mozart. But when they tested Mozart against silence, they found the monkeys preferred silence, and they concluded that monkeys are indifferent to music. However, the monkeys they tested have small bodies and communicate in a frequency range three octaves above human speech and at a tempo at least twice as fast. It seems premature to conclude that monkeys are indifferent to music.

Playbacks of animal sounds are often used as the gold standard for evaluating the functional significance of animal signals, but [Owren and Rendall \(1997\)](#) have proposed an affect-conditioning model of primate affective signals. If affective responses are conditioned to calls, then it becomes difficult to find naive subjects to evaluate emotional responses. One solution to this problem is to create species-relevant music in the frequency range and with the tempos appropriate to the species being tested, and then to build features into the compositions that are hypothesized to be of affective significance. Using this strategy, [Snowdon and Teie \(2010\)](#) presented cotton-top tamarins with music composed in their frequency range and tempos, and compared their responses with music composed for humans having similar features. Tamarins responded to “tamarin music” with arousing features with increased activity and increased signs of anxiety, and sought increased social interactions with group mates. In contrast, they responded to “tamarin music” with calming features by reducing activity, increasing foraging, and decreasing social contact. Thus, different emotional states could be induced in monkeys with appropriate species-specific music. However, music composed to induce similar affective responses in humans had no effect on the tamarins (similar to results of [McDermott and Hauser, 2007](#)).

Recently, [Snowdon et al. \(in review\)](#) have used music designed to be relevant to cats (higher pitched than human music with tempos similar to purring or sucking) and



found that cats preferred this music to calming music composed for humans. Furthermore, cat music led to a significant increase in calm behavior in the cats. The use of species-relevant music may have many practical effects on behavior of animals in laboratories, zoos, and shelters, but to date most facilities use human music—generally the genres preferred by the caretakers—and the results evaluating the effects of music have been inconsistent.

In summary, there is much contradictory literature about the effects of human-based music on nonhuman species with some authors claiming other species have no appreciation for music. However, there has been little effort to consider the effects of specific types of music and even less effort to make music ecologically relevant to other species. When music is composed that takes into account the ecological differences between humans and another species, music has been shown to be effective in inducing emotional responses.

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## 9 SUMMARY AND CONCLUSIONS

In this chapter, we have argued that music has adaptive functions for humans including increasing cooperation and helping, and modulating physiological responses. It may also have value in mate selection, but in our view, this would be a more recently evolved effect. Musical structures are found in the distribution of harmonics in speech and in the prosodic features of speech that communicate emotions. Prosodic features are also used by humans to manipulate the activities and emotional states of preverbal infants and working animals. Although humans find it difficult to consciously identify the emotional valence in the calls of other species without direct exposure and experience with those species, there is some evidence of unconscious discrimination of affective state in animal calls using brain imaging.

Emotions in music can be differentiated by both musicians and nonmusicians, and Western listeners unfamiliar with Hindu ragas can nonetheless discriminate the emotional intent of the composers of the ragas. Many of the acoustic features seen in how emotions are presented in music are also seen in similar emotional signals in many mammalian species ranging from rodents to primates. This consistency in the acoustic structures underlying different affective states supports our notion that music has emerged in humans based on strong emotional signals and consequently has early phylogenetic origins.

However, there is still critical research to be done. Are the differences in affective signals in some species real or due to different paradigms and different definitions of behavioral contexts? Can researchers manipulate the affective states of animals through music that is species relevant? Music is frequently used as psychological enrichment in shelters, laboratories, and zoos, but rarely does the selection of music relate to the specific goals of enrichment (does one want more active or calmer animals?), nor are species-relevant aspects considered. More work needs to be done on the intriguing possibility that human brains might be capable of analyzing animal sounds at a subconscious level. Finally, the music we enjoy listening to is not just



about strong emotions. Our species has developed a complexly structured corpus of music that affects us emotionally but also affects us aesthetically (Altenmüller et al., 2013). How and why this development occurred is the central question in the evolution of music, and we are still some distance away from understanding this occurrence.

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