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Universality, domain-specificity, and development of psychological responses to music

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Abstract

Humans can find music happy, sad, fearful, or spiritual. They can be soothed by it or urged to dance. Whether these psychological responses reflect cognitive adaptations that evolved expressly for responding to music is an ongoing topic of study. In this Review, we examine three features of music-related psychological responses that help to elucidate whether the underlying cognitive systems are specialized adaptations: universality, domain-specificity, and early expression. Focusing on emotional and behavioural responses, we find evidence that the relevant psychological mechanisms are universal and arise early in development. However, the existing evidence cannot establish that these mechanisms are domain-specific. To the contrary, many findings suggest that universal psychological responses to music reflect more general properties of emotion, auditory perception, and other human cognitive capacities that evolved for non-musical purposes. Cultural evolution, driven by the tinkering of musical performers, evidently crafts music to compellingly appeal to shared psychological mechanisms, resulting in both universal patterns (such as form-function associations) and culturally idiosyncratic styles.

[H1] Introduction

Music, studied here as 'human-produced sound organized by melodies, rhythms, or both', is found in every society where researchers have looked^{1–4}. It suffuses social life, appearing in contexts as diverse as healing, dancing, and infant care^{1,5,6}, and occurs across the lifespan, through infancy⁷, childhood⁸, adolescence⁹, adulthood¹⁰, and old age¹¹. Music's importance

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We dedicate this article to Sandra Trehub (1938–2023), whose pioneering and inspiring work touched every corner of the psychology of music.

in the social lives of humans stems from its potent and diverse psychological effects, which range from pacifying infants^{12–15} to fomenting the collective, chaotic thrashing of rock concert mosh pits¹⁶.

A central question in the study of music is whether humans have evolved specialized cognitive adaptations to produce and respond to music. The psychology of music either comprises music-specific adaptations shaped by natural selection^{17–19}, or arises as a by-product of cognitive abilities serving non-musical functions. According to this by-product account, also known as the auditory cheesecake hypothesis, music is a package of cognitively compelling stimuli moulded via cultural evolution to trigger features of human psychology that evolved for non-musical ends^{20,21}. At least three features of music-related psychological processes can help determine whether the underlying cognitive systems are specialized adaptations: domain- specific if it has evolved to operate on a particular class of information. It is expressed early if infants exhibit the response. Universality, which can refer either to a behaviour or to an underlying feature of human psychology, is a feature that deserves further elaboration.

A behaviour is universal when it is expressed in all human populations, excepting mitigating factors. For instance, music production was expressed by 100% of populations in a sample of 315 mostly non-industrial human societies, including geographically diverse hunter-gatherers, pastoralists, and intensive agriculturalists¹. This universality naturally coexists with variability: not every individual in every culture is an expert producer of music (as only some individuals have extensive music training); some cultures use music less frequently than others (as with the Tsimane, who generally do not produce music in groups²²); and not every individual in every culture is equally motivated to produce music (as in individuals with musical anhedonia²³, for whom music production might be less rewarding than is typical). The production of music is nonetheless considered universal, as even in these cases, there is evidence for the behaviour in every population studied. A behaviour can be a near-universal (sometimes called a 'statistical universal') if it appears above a predefined threshold but not in 100% of cultures sampled².

Unlike a behaviour, a universal psychological mechanism or predisposition can manifest variably, not necessarily appearing in every individual in all populations²⁴. Jealousy exhibits considerable global variation, with individuals in some cultures reporting less severe jealousy²⁵. Yet this variation is structured: Cross-culturally, the severity of jealousy covaries with the frequency of extramarital sex and expectations of parental investment²⁵, suggesting that jealousy is a universal emotional response that functions to ensure either parental investment (for females) or paternity certainty (for males). Like jealousy, psychological responses to music can exhibit reliable cross-cultural differences while still reflecting universal predispositions that are variably expressed depending on one's environment.

To organize our discussion, we heuristically distinguish among three psychological processes at work in human musicality: music production, music perception, and musical response. 'Music production' refers to the auditory, motor, and vocal processes associated with singing or playing an instrument. 'Music perception' refers to processing that translates

In this Review, we synthesize the literature on universality, domain-specificity, and development of psychological responses to music. We first briefly discuss the mechanics of music production and music perception, before focusing on emotional and then behavioural responses to music — two rapidly advancing areas of research. By surveying cross-cultural, developmental, and neuroscientific approaches, we will demonstrate clear evidence for the universality and early development of emotional and behavioural responses to music. However, the evidence for domain-specificity is more mixed, suggesting that universal responses to music might draw on more general features of human psychology. We conclude by considering how cultural evolution interacts with universal aspects of human psychology to produce both cross- cultural similarities and cultural idiosyncrasies in the world's music.

[H1] Music production, perception, and response

Universality, development, and domain-specificity have been key research areas for each of the music-related psychological processes (production, perception, and response). For instance, music production is universal and the associated behaviours vary substantially less across cultures than within cultures¹. Humans have manufactured musical instruments for at least 35,000 years²⁷ and have likely produced vocal music for longer^{18,28,29}. The universality and deep history of music production suggest that it is underlain by psychological mechanisms shared across *Homo sapiens*.

Given the universality of music production, it is not surprising that many basic aspects of music perception are widespread and early-developing, such as mechanisms involved in hearing and understanding musical pitch (the psychological correlate of frequency, allowing it to be ordered on a frequency-related scale; in English, pitch is typically described as the highness or lowness of a tone)^{30–33}. Perception starts with feature extraction, during which low-level acoustic features like timbre [G], intensity, location, pitch height, and periodicity are decoded from the auditory stream³⁴. This acoustic information is analyzed to process melodic, rhythmic, timbral, and spatial groupings, eventually resulting in higher-level musical representations, such as tonal and metrical information (two foundational aspects of musical information³⁵) and harmonic structure [G]³⁴. Human auditory cortex is specialized for music perception³⁶, separately from speech perception^{37,38}, with special selectivity for vocal as opposed to instrumental music³⁹ and with connections to reward systems found in the midbrain^{40,41}. Whether the psychological mechanisms underlying music production and perception are best explained by domain-general processes, such as auditory scene analysis $[G]^{42}$, or domain- specific ones is up for debate, but the current overall picture is that many aspects of music production and perception form a basic part of human psychology which supports higher-level musical responses.

Musical response refers to the semantic, emotional, aesthetic, and other behavioural responses and inferences that follow music production and perception (Fig. 1). Musical responses occur in both producers and listeners of music and include many apparently higher- level responses to music, such as inferring musical meaning ('this song is about birds'), inferring expressed emotions in music ('this song sounds happy'), directly experiencing emotions evoked from music (a song makes a listener feel happy), and moving in response to music.

Whereas musical response is generally downstream of perception, the relationship is not completely linear or serial. Musical responses do not require the analysis of rhythmic or spatial groups; for instance, tones played in isolation (without other rhythmic or melodic structure) can convey meaning, such as by sounding 'brigh , 'feminine', or 'summery'^{43,44}. Moreover, there are indications that motor regions of the brain not only respond to structural features like rhythm and meter but also are involved in extracting beat, raising the possibility of feedback loops between music perception and response^{45–48}. Such feedback loops undoubtedly operate differently in the brain of a performer (who has more immediate access to motor information in music) than for a listener (who has less)⁴⁹. Nevertheless, our heuristic distinction between music production, perception, and response is justified by how humans process music psychologically^{26,50} and parallels distinctions used in language sciences⁵¹.

Here in this Review, we will largely leave aside the mechanics of music production and perception to concentrate on the domain-specificity, development, and universality of musical responses. For instance, we do not discuss cultural variation in the perception of dissonance⁵², the effects of musical experience on auditory processing⁵³, or the effects of antenatal exposure on auditory perception and neural development^{54,55}. Our coverage will focus on two sets of musical responses that have received considerable research attention and which are among the most important of music's psychological effects. We will start by discussing emotional inferences and responses, especially recognizing expressed emotions in music. We will then address behavioural inferences and responses, particularly being soothed and dancing.

[H1] Emotional responses to music

Individuals overwhelmingly consume and deploy music for emotional regulation^{9,10,56–60}. As such, much of the research on musical response has focused on emotional responses. This research often adopts a basic-emotions perspective, according to which there are basic or discrete emotions, such as happiness and fear, as well as complex or non-basic emotions, such as jealousy and solemnity⁶¹. Basic emotions are said to be innately expressed and identified, whereas non-basic emotions are seen to be less biologically fundamental and more culturally variable⁶¹. As in the broader emotion literature, the main alternatives to basic-emotion perspectives are dimensional perspectives, according to which emotions are organized around a few dimensions, most commonly valence (pleasantness) and arousal (activation)^{62–64}.

Regardless of the model of emotions that researchers adopt, the studies of emotional musical responses reviewed here suggest that such responses are not specialized adaptations. Whereas the psychological mechanisms underlying emotional responses seem to be largely conserved across populations, they reflect domain-general responses to emotion rather than music-specific psychological processes.

[H2] Cross-cultural similarities

Studies in which individuals were asked to rate emotions in foreign music have demonstrated that emotional expression is, to a modest degree, mutually intelligible across cultures^{65,66}. For example, Mafa individuals in northern Cameroon accurately recognized emotions in Western music designed to sound happy, sad, and fearful⁶⁷. Similarly, German, Norwegian, Korean, and Indonesian individuals identified happy and sad instrumental performances by German musicians⁶⁸. In another example, Indian, Japanese, and Swedish listeners identified expressed emotions in each other's traditions, as well as in Western music^{66,69}. Finally, U.S. and rural Cambodian individuals tasked with creating music that expressed emotions like 'sad' or 'happy' created similar melodies⁷⁰. The findings of these studies suggest broadly shared psychological mechanisms underlying the recognition of expressed emotions in music⁷¹.

Despite these similarities, culture still shapes how individuals recognize emotional expression in music. Participants might, on average, successfully recognize emotions in music from foreign cultures while nevertheless showing much lower accuracy than native participants. For example, although Mafa listeners successfully identified happiness, sadness, and fear in Western songs at a rate higher than chance, Canadian listeners accurately inferred the expressed emotion nearly twice as often⁶⁷ (Fig. 2). Experimenters found similar results in several additional experiments^{66,68,69}. In one, Canadian adults correctly identified joy, sadness, and anger but not 'peace' in North Indian classical music⁶⁵. In another, Swedish, Indian, and Japanese participants identified anger, fear, happiness, and sadness more successfully than supposedly 'non-basic emotions' like spirituality, solemnity, and longing in Western excerpts and each other's music⁶⁹. In a third study, Koreans and Indonesians identified happiness and sadness in German music with relative ease but had difficulty recognizing surprise and disgust⁶⁸. In fact, surprise and disgust were also hardest for Norwegians and Germans to recognize in German music (surprise tended to be confused with happiness and disgust was confused with fear and anger).

Some features of music are interpreted more variably across cultures than others, which further complicates the recognition of expressed emotion in music⁷². For instance, UK participants and participants from north-western Pakistani tribes made similar emotional inferences from features such as tempo, loudness, and pitch. However, UK participants associated the major mode [G] with happiness and the minor mode [G] with sadness, whereas Pakistani participants apparently did not pay attention to mode in in one study⁷³ and exhibited the opposite set of responses in another⁷⁴. In a similar vein, the extent to which both Chinese and Papua New Guinean participants associated the major and minor modes with positive and negative emotions respectively was predicted by their familiarity with Western music^{75,76}.

Although more precise evidence is needed concerning the exact effects of cross-cultural musical experience, together the results above suggest that the recognition of expressed emotion in music involves a combination of culturally learned emotion cues and more universal psychological mechanisms.

[H2] Developmental trajectory

Children can identify some emotions in music by 3 or 4 years of age, although findings have been variable (Fig. 3a). For example, British 3-year-olds were presented with novel children's music and asked to indicate whether performances sounded 'happy' or 'sad'. The children successfully identified happiness and sadness in both vocal and instrumental music⁷⁷, with markedly better performance on 'happy' music. Likewise, Finnish and Hungarian 3 and 4-year- olds identified happiness and sadness in diverse musical performances (a folk song, stimuli produced by musicians) but not anger or fearfulness⁷⁸. In another study, Canadian 5- to 8-year- olds identified high-arousal emotions (happiness and scariness) more successfully than low- arousal emotions (peacefulness and sadness) in musical stimuli designed for emotion recognition experiments; however, they were not as successful as 11-year-olds, who exhibited adult-like levels of accuracy⁷⁹. Contrasting with evidence of early emotion recognition abilities, several studies have found that 3 and 4-year-olds failed to distinguish happy from sad songs^{80,81}, although this might reflect experimenters using Western classical music, complicating their interpretation.

Although developmental changes to emotional recognition in music parallel changes to emotional recognition in non-musical speech⁸², it remains unclear to what extent developmental differences are due to culture-specific learning. On the one hand, inferring emotional expression from mode seems both to develop after 5 years of age and to be cross- culturally variable in adulthood, suggesting a role for cultural learning^{73,80}. On the other hand, children and even adolescents have difficulty identifying anger and fear in music^{78,81,83}, yet these are among the emotions that adults recognize in music most reliably across cultures^{65,67–69}, suggesting that some developmental trajectories play out similarly the world over.

Whether infants and toddlers can recognize emotion in music remains an open question. Several studies conducted in North America show that 9-month-olds can discriminate happy music from sad music^{84–86}. However, discrimination does not imply recognition, and, with few exceptions⁸⁷, very little research has investigated emotional recognition in music in toddlers and infants younger than 3 years of age. This gap is somewhat surprising, given that many developmental paradigms, such as measuring looking time toward cross-modally matched faces and musical examples, could be straightforwardly adapted for such investigations. Indeed, several findings have raised the possibility that infants and toddlers can infer emotional content in music. For example, infants are both surrounded by music and fascinated by it^{7,88}; they are attentive to the emotions of individuals with whom they interacted^{89,90}; and infants showed a distinct set of psychophysiological responses to unfamiliar foreign lullabies relative to non-lullabies¹⁴. Thus, studies on emotional recognition in young infants are feasible and will help resolve to what extent infants are predisposed to associate emotions with acoustic phenomena.

[H2] Mechanisms for emotional recognition

The evidence that emotional recognition in music involves universal psychological mechanisms does not imply that those mechanisms are domain-specific. Rather, at least three lines of research suggest that emotional recognition in music draws on the same domain-general mechanisms involved in judging expressed emotion from non-musical stimuli, such as non- musical vocalizations and facial expressions.

First, vocalizations produced in both musical and non-musical contexts use similar cues to communicate emotion. For example, in both music and speech, variations in tempo, volume, and pitch often (although not always) communicate similar emotional states^{91–93}. Like happy- sounding speech in English and Tamil, happy-sounding music in Western music and South Indian music uses larger pitch intervals⁹⁴. Angry speech and angry music are both characterized by faster and louder vocalizations, contrasting with the slower and softer sounds of music not typically found in angry contexts, such as lullabies¹. Non-musicians incorporate cues such as tempo and volume when producing emotional music⁹⁵. When asked to make music sound happier, sadder, or angrier, Finnish 3- to 5-year-olds adjusted tempo, pitch, and volume in ways that mimic emotion cues in speech⁹⁶. Chinese adults even attributed arousal and valence to environmental sounds, such as clapping, thunder, or a car engine, when those sounds displayed tempo, volume, and pitch cues that signal emotion in music and speech⁹⁷.

Second, activity in brain regions during emotional recognition in music seems to correlate with brain activity involved in processing emotions in non-musical stimuli^{98,99}. For instance, damage to the amygdala impairs the recognition of both scary music and fearful faces, and patients' performance on both tasks was correlated^{100,101}. In other research, participants exhibited activity in the medial prefrontal cortex not only when asked to track the emotional content of musical and non-musical linguistic vocalizations¹⁰², but also when processing the emotional content of body movements, facial expressions, and non-linguistic interjections (such as "aah")¹⁰³. Finally, watching movements and hearing sounds associated with emotions evoked similar neural representations in visual and auditory areas of the brain, respectively, which suggested that emotional stimuli presented in diverse modes can elicit common representational structures¹⁰⁴.

Third, children exhibit similar developmental trajectories for recognizing emotion in speech and in music. Children start to recognize some emotions in speech and in music by the age of four; they are better at identifying happiness and sadness than fear or anger in speech and in music; and they are capable of identifying emotions in other languages, although they are most accurate when listening to their native language^{82,105–107}. When asked to rate clips of speech, music, and affect bursts (such as laughter), the performance of Australian children in three age groups (7–11 years, 12–14 years, and 15–17 years) and adults (18–20 years) was not distinguishable when labelling speech and music, although they were more accurate when labelling affect bursts⁸². Thus, the same developmental changes that allow children to recognize emotion in speech appear to be involved in recognizing emotion in music.

Despite many indications that recognition of musical and non-musical emotion expression draws on the same cognitive mechanisms, how emotion is communicated in music

remains unresolved¹⁰⁸⁻¹¹⁰. Consistent with basic-emotions theories, basic emotions (such as happiness and fear) appear to be recognized in music both earlier in development and, in some studies, more reliably within and across cultures relative to non-basic emotions (such as jealousy and solemnity)^{65,67,69,79,91}. However, researchers do not agree on which emotions are basic; there is conflicting evidence on whether there are distinct physiological correlates distinguishing basic emotions; and many canonical findings on emotional expression in speech come from studies in which actors portrayed emotional states (such as by acting happy), which might not accurately reflect naturalistic emotional displays⁶³. These criticisms have inspired dimensional perspectives on communication of emotion in music, especially those centring on valence and arousal $^{62-64}$. In support of such theories, an analysis of 53 studies published since 2003 found that a dimensional structure based on valence and arousal explains more variance in participants' recognition of emotions in music than does a structure based on 5 basic emotions (anger, fear, happiness, love-tenderness, and sadness)⁶³. In addition, English-speakers from 60 countries rating unfamiliar, foreign songs from 86 societies largely agreed with one another in their ratings of songs' valence and arousal⁵. Thus, valence and arousal are reliably detectable dimensions of musical expression by listeners.

Resolving how emotion is communicated in music is complicated by studies of emotions felt while listening to music, which are difficult to reconcile with either the basic-emotions or the dimensional perspective. A series of experiments with French-speaking listeners resulted in a 9-factor solution for recognized emotions in music (with factors such as amazement, tranquillity, and power) and a related although distinct 9-factor solution for emotions felt from music (with factors such as transcendence, peacefulness, and tension)¹¹¹. Neither 9-factor solution was accounted for by basic-emotions or dimensional theories. In another study, experimenters presented thousands of music samples to participants from the U.S.A. and China and asked them to label how the music made them feel, either by choosing from a list of 28 emotional categories or by rating each sample on 11 distinct Likert scales¹¹². Thirteen dimensions of subjective experience were shared across both cultures, including basic emotions such as fear, joy, and sadness as well as non-basic emotions like annoyance, triumph, and dreaminess. Contrary to basic-emotions accounts, non-basic emotions exhibited higher correlations across cultures than presumably basic emotions. Meanwhile, valence and arousal exhibited lower cross-cultural convergence than many other subjective experiences, challenging the theory that emotions, whether in music or more broadly, are constructed from these basic building blocks.

Although the structure of emotional communication in music remains unresolved, a general conclusion is clear: there is little reason to suspect that humans have specialized cognitive mechanisms for expressing and recognizing emotion in music. Rather, existing evidence suggests that individuals employ domain-general mechanisms for emotional communication in both music and speech. In this light, some basic aspects of musical understanding accord with the view that music is embedded in biology as one of several types of vocal signals¹⁸. As with much of human behaviour, emotional expression in music involves 'variations on a theme', where universal predispositions are modified by cultural exposure²⁴. Individuals from distinct cultures can recognize emotions in each other's music, yet they more successfully recognize some emotions relative to others and can fail to accurately

interpret some acoustic cues. Similarly, young children can recognize expressed emotions in music although with limited and variable success. Thus, the role of domain-general mechanisms for the expression of emotion in music demonstrates how the diversity of the world's music is structured by pan-human psychological predispositions.

[H1] Behavioural responses to music

In addition to processing purely auditory information (like pitch or timbre) and inferring emotional content (like expressed emotion described in the previous section), listeners also make inferences about the behavioural functions of music. By behavioural functions, we mean the social and behavioural ends for which people apparently produce music, including soothing an infant, accompanying dance, and healing illness. Although these functions can leave sonic signatures on a recording, such as the sound of thumping feet in a group dance, this is not necessarily the case, as the behavioural function is foremost determined by the performers' goals.

Although behavioural functions are related to the emotional content of music, they are a separable concept of interest for at least two reasons. First, individuals worldwide produce music for specific behavioural functions, such as dance or infant care, and comparative research suggests that many of these specific behavioural functions themselves appear reliably across societies^{1,5}. Second, genetic evolutionary theories often explain the evolution of music in the context of specific behavioural functions, such as enabling dancing^{18,29}, soothing infants^{18,28}, signalling mate quality¹¹³, and promoting social bonding¹⁹. Insofar as the music faculty involves domain-specific cognitive adaptations, we should expect those adaptations to be specialized for these behavioural functions.

Here, we review evidence that universal characteristics of human psychology guide individuals to respond to particular acoustical forms in similar ways. For example, humans around the world find slow, melodic music soothing and dance in response to louder, rhythmically dominated songs. In many experiments and a variety of populations, naïve listeners intuit these associations: Not only do they expect associations between song form and function, but they reliably identify the behavioural functions of unfamiliar songs. Research demonstrates that behavioural responses to music, particularly to dance songs and lullabies, develop early and reliably across societies, although existing studies cannot determine whether those responses reflect domain-specific mechanisms.

[H2] Universal behavioural functions

A general tendency across animals is for communicative behaviours to be shaped by their intended function, manifesting as form-function associations in vocalizations¹¹⁴. For instance, low-frequency, harsh vocalizations tend to signal hostility because they are reliable indicators of body size^{115,116}. Similar form-function associations characterize many human vocalizations, including spontaneous laugher¹¹⁷ and infant-directed speech¹⁵.

A series of experiments has investigated form-function associations in music using three related approaches: asking naïve participants whether they can infer relationships between the form and function of foreign music; computationally identifying the acoustic

features associated with particular behavioural functions in music; and analyzing how those acoustic features explain listeners' inferences^{1,5,15,118–120}. These approaches are informative for two reasons. First, they test whether songs that share behavioural functions exhibit common acoustical designs across societies, helping uncover whether universals in human psychology guide both musical production and response. Second, they test whether individuals have shared conceptions of what songs should sound like^{5,120}. Although it can be difficult to determine whether these conceptions result from cultural learning or intuitions that predate cultural encounters with music, studying them in young children or infants helps elucidate to what extent form-function intuitions are shaped by cultural experience¹¹⁸. Methodologically, form-function experiments share a basic structure^{1,5,15,118–120}. Naïve listeners are presented with random excerpts of foreign songs, typically field recordings from small-scale societies. They are then asked to evaluate the songs' functions, such as by rating them on scales or selecting behavioural functions in forced-choice tasks. Finally, researchers identify acoustic features that predict listeners' inferences to deduce listeners' intuitions about song functions.

Across a variety of populations — among young children¹¹⁸, in small-scale societies¹²⁰, in massive online experiments conducted with English speakers 1,15 , and in multilingual online experiments with participants in 59 countries 120 — naïve listeners infer the behavioural function of foreign songs above chance⁵ (Fig. 4). At least three lines of evidence suggest that this performance reflects reliably developing intuitions grounded in a universal human psychology more so than encounters with similar music. First, listeners' familiarity with globalized musical culture does not explain their ability to identify song functions. Individuals in small-scale societies with limited access to Western music successfully identified form-function relationships, and listeners whose experiences more closely matched the culture of the singer (whether measured in linguistic or geographic distance) were only modestly more successful at identifying them¹²⁰. Second, children performed roughly equivalently to adults (with significant but very small effects of age), suggesting that abilities to infer form-function relationships required little experience¹¹⁸. Third, individuals unfamiliar with particular song domains — namely. Westerners unfamiliar with healing songs — nevertheless identified form-function relationships^{1,5}, suggesting that intuitions develop even without exposure to the relevant domain.

Analyses of acoustic properties of songs have provided strong evidence of form-function associations in the world's music. For one, low-level acoustic properties of songs extracted using automated techniques, such as roughness or inharmonicity, reliably co-occurred with behavioural functions across diverse, distantly related human societies¹. Moreover, a machine learning model successfully classified songs' behavioural functions on the basis of acoustic features, even when it was trained on data from songs from some societies (such as from 29 of 30 world regions or from all Old World societies) and evaluated using song data from other societies (such as from the 30th world region or all New World Societies)¹. Acoustic features predicted not only the actual song behavioural functions but also listeners' inferences of the behavioural functions^{1,118}. Together, these analyses suggest that universal features of human psychology predispose individuals in any society to associate particular sounds with certain behavioural functions.

[H2] Development and domain specificity

The universality of form-function associations suggests that different psychological mechanisms are involved in responses to songs of distinct behavioural functions. Turning to development and domain specificity, we focus here on responses to lullabies and dance songs, for several reasons. Lullabies and dance songs are the most stereotyped song domains across cultures and are identified by naïve participants with the highest accuracy^{1,5,118,120}. They have also been hypothesized to be central to the evolution of music^{19,121}, such as in the context of credible signaling^{18,28,29}. Among the different behavioural responses to music, responses to lullabies and dance songs are most likely to reflect evolved specialized adaptations, making them prime candidates for studying early development and domain-specificity.

As we review here, the psychological responses underlying both lullabies and dance songs appear early in development in human populations around the world. However, whether these responses reflect domain-specific cognitive processes remains unresolved.

[H3] Lullabies—Infants seem predisposed to respond to infant-directed songs and, in particular, to songs that are intended to soothe them or put them to sleep (lullabies) (Fig 3b). Canadian infants preferred infant-directed songs over noninfant-directed songs¹²² and preferred maternal infant- directed song over maternal infant-directed speech¹²³. Infants were soothed by familiar songs more than unfamiliar ones¹² and, in at least one experimental paradigm, by lullabies more than play songs (vocal music directed towards children, often characterized by excitatory, amusing characteristics)¹³. Such behavioural responses are a likely reason why, across demographics, most parents in the U.S. sing to their infants daily⁷.

Several lines of research indicate that early developing responses to lullabies are universal. Parents worldwide sing to their infants,¹ and infant-directed songs exhibit acoustic regularities^{14,15}. U.S. infants relaxed in response to foreign lullabies, more so than to non-lullabies, and relaxed the most to lullabies that exemplify infant-directedness¹⁴, suggesting that lullabies use common features to evoke similar psychological responses¹⁵. Although this idea might seem intuitive, consider that most lullabies infants hear come from their caregivers. Infants are highly sensitive to the identities of the individuals who interact with them, forming inferences about individuals on the basis of the language or dialect they speak¹²⁴, the foods they eat¹²⁵, and the music they produce^{126,127}. Given this, infants might well be calmed by anything a trusted caregiver does for them. However, infants relax in response to lullabies produced by unfamiliar individuals in unfamiliar cultures and in unfamiliar languages that the infant cannot understand, showing that lullabies produced worldwide are well-designed to calm infants, even in the absence of rich social cues of caregiver identity.

Evidence is mixed for whether behavioural responses to lullabies reflect domain-specific adaptations. On the one hand, humans seem to respond most to lullabies during infancy, consistent with specialized cognitive mechanisms being expressed in the developmental stages when they are most useful. On the other hand, according to a preprint that has not yet undergone peer review, many English-speakers use lullaby-like music (such as pop

music including a 'lullaby' genre label on Spotify) to fall asleep¹²⁸, and many features of lullabies (such as lower tempo, loudness, and energy) are reliably present in many other forms of music¹²⁸. Furthermore, infants are soothed by many sounds other than lullabies, most notably shushing^{129,130}. Sounds with minimal formant structure, including shushing or white noise, were effective at masking other sounds such as tones or speech¹³¹, facilitating sleep in both infants¹³⁰ and adults¹³² (as they were less likely to hear random sounds and be awoken by them). It therefore remains unclear whether lullabies soothe infants because of cognitive mechanisms specialized to respond to them or because the songs appeal to cognitive mechanisms that evolved for non-musical functions.

[H3] Dance songs—The perception and processing of rhythmic information, essential for the behaviours associated with dance, begin early (Fig 3b). Newborns discriminated between languages with differing rhythmic profiles¹³³, and Hungarian neonates' patterns of neural activity indicated sensitivity to onsets and offsets of musical rhythm, as well as the rate at which sounds are presented^{134,135}. Indeed, infants' music perception abilities are tuned in to rhythms. European 2-month-olds perceived differences in rhythm and tempo in tone sequences^{136–138} whereas Canadian 7- month-olds showed EEG responses frequencylocked to rhythms¹³⁹. Moreover, the developmental trajectory of rhythm perception is suggestive of perceptual narrowing: North American infants reacted similarly to disruptions of Western and Balkan rhythms at 6 months yet did not react to disruptions of Balkan rhythms at 12 months^{140,141}. Infants also move in response to rhythms. In two experiments, Swiss and Finnish infants aged 5 to 24 months listened to clips of music, rhythm, and speech¹⁴². Although no infant demonstrated entrainment — the synchronization of actions, such as body movements, to a recurring rhythmic event — the infants moved more to music and rhythms than to speech. In addition, although the youngest infants moved more inconsistently, the experimenters found no changes in infants' responses between the ages of 7 and 24 months. Humans appear to come into the world ready to respond to rhythm.

Despite their early music perception abilities, individuals nevertheless must learn to entrain to a beat¹⁴³. 8-month-old U.S. infants discriminated between synchronous and asynchronous dancing that they observed¹⁴⁴, yet studies with Japanese infants and German preschoolers suggested that reliable beat entrainment does not appear to develop until toddlerhood^{145,146}. Even so, the ability to synchronize to a beat is modest at such young ages, as any parent can tell you. Studies with U.S. participants suggest that the accuracy of synchronized movements does not approach adult levels until 10 to 12 years of age^{147,148}.

Whether dance and other rhythmic behavioural responses to music reflect domain- specific specializations remains an open question. The only animals aside from humans who spontaneously perceive a beat and synchronize to it are parrots^{46,149,150}. This observation has been taken as evidence that a capacity for rhythm is not a derived adaptation but rather a by- product of advanced vocal learning abilities, which both parrots and humans exhibit¹⁴⁹. Vocal learning involves intrinsic rewards for predicting the temporal structure of auditory sequences and establishes tight reciprocal communication between motor planning regions and forebrain auditory structures⁴⁶. As a result, individuals are motivated to produce synchronized action, such as dancing or singing to music, which is intrinsically rewarding. This explanation of beat entrainment is similar to that developed within a predictive coding

of music model, which also posits that synchronized action is a way of reducing reward prediction error (although without invoking humans' advanced ability for vocal learning)¹⁵¹. Regardless, these explanations suggest that the rhythmic aspects of spontaneous dancing might derive their pleasurable outcomes^{152–155} via cognitive mechanisms that are not specific to music.

Some observations still raise the possibility that the cognitive mechanisms involved in beat perception and entrainment are domain-specific adaptations⁴⁶. First, the capacity for beat perception and synchronization is not shared with the closest living relatives of humans, chimpanzees¹⁵⁶. Second, a complex neural architecture underpins rhythmic entrainment in humans⁴⁵. Third, humans can and do entrain to rhythms for long periods of time, unlike parrots, who only entrain for shorter durations¹⁵⁰. Fourth, beat entrainment is typically a social activity in humans^{2,157}, whereas in parrots it is not. Last, two genetic loci associated with the self- reported ability to synchronize (by clapping) to a beat are in 'human accelerated regions'¹⁵⁸— that is, in regions of the human genome that have substantially diverged from chimpanzees. Together, these observations have been taken as evidence for the hypothesis that humans evolved specialized adaptations for music, potentially through gene–culture coevolution — the interaction of genetic and cultural evolutionary processes — which could have contributed to the evolution of human musicality if the cultural invention of music subsequently selected for domain-specific (music) adaptations^{19,46}.

Although each of the five observations above represents a promising area to test the domainspecificity of rhythmic abilities, each is still consistent with rhythmic entrainment being a by-product of vocal learning. The social aspects of dance could simply reflect humans' profound sociality, as opposed to any specialization for rhythm. The complex neural architecture, increased motivation for rhythmic engagement, and absence of beat perception and synchronization in non-human primates could all reflect selection for sophisticated vocal learning in the human lineage ^{159–161}. By studying the overlap of mechanisms involved in beat perception and synchronization with those of vocal learning, future research will better pinpoint whether human psychology is specialized for rhythm.

In summary, humans appear universally predisposed to find lullabies soothing and to move rhythmically in response to dance songs, and these predispositions appear early in the populations where they have been studied. However, current research cannot establish whether lullabies and dance songs stem from domain-specific, evolved specializations or are instead by-products of mechanisms that evolved for non-musical functions. More generally, work on behavioural responses to music advances the understanding of musical diversity and function. It demonstrates that music is not a fixed biological response, adapted for a single end like mating or group bonding. Rather, it is deployed for many social goals, some of which — particularly, soothing infants and dancing — appear to be universal. This universality reflects shared features of human psychology, which predispose humans to respond in particular ways to certain sounds and which, in turn, produce form-function relationships in the world's music.

[H1] Cultural transmission of music

The world's music exhibits both profound similarities and striking idiosyncrasies. These patterns of universality and diversity can emerge and persist through cultural evolution, which both crafts ubiquitous musical traditions adapted to shared features of human psychology and canalizes idiosyncratic cultural differences in musicality.

As an example, consider the universal tendency of vocal music to be composed of predominantly small melodic intervals and rhythmic patterns defined by integer ratios [G]¹. These characteristics could reflect biological specializations to produce music^{18,19,121}. Alternatively, they could also emerge as individuals preferentially adopt and perform music that is easier to learn and transmit^{162,163}, paralleling how language-like systems evolve to become more transmissible across generations^{164–166}. For instance, Scottish participants were asked to imitate random drum sequences; their attempts became the model stimuli for the next group of participants, who in turn produced sequences for a subsequent group. Over the course of the study, as participants transmitted their attempts, random sequences evolved into rhythmically structured patterns¹⁶². The patterns exhibited near-universal rhythmic features, such as hierarchical structure and isochronous beats [G], arguably because they were easier to learn and transmit. Similarly, participants who produced and transmitted sets of whistled signals eventually developed whistled patterns that exhibited some, but not all, melodic near- universals¹⁶⁷. Ubiquitous musical features might emerge simply as performances adapt to the constraints of memory and learning; biological adaptation need not be the primary explanation for such effects.

Cultural evolution can produce widespread patterns in music through mechanisms beyond making performances easier to learn and reproduce. Researchers increasingly focus on how individuals produce and selectively retain cultural products evaluated as best satisfying an individuals' goals, a process labelled 'subjective selection'¹⁶⁸. Subjective selection seems to underlie the evolution not only of useful technology 168,169, but also of many domains of so- called 'symbolic' culture, including social norms^{170,171}, fictional narratives^{172,173}, and religious practices and beliefs^{174–176}. Subjective selection is a promising explanation for some musical universals. As long as individuals consistently perceive certain musical features to be useful for producing particular ends, then cross-cultural convergence should be expected¹⁶⁸. If individuals everywhere tend to dance to certain sounds, or to be soothed by certain sounds, or to regard certain sounds as communicating particular emotions, then cultural evolution should lead to similarities as individuals craft and retain music that seems to best satisfy those ends. As we have shown, shared features of human psychology indeed predispose humans to respond to music in similar ways. Such predispositions might result from human-specific adaptations, such as the physical limits of human auditory perception, or they might result from constraints that are shared across species¹¹⁵. Cultural evolution likely exploits these shared psychological predispositions to produce compelling performances, yielding reliable cross-cultural associations between musical form and emotional content^{66–68} or musical form and behavioural function^{1,5,119,120}.

Cultural transmission also sustains and drives musical diversity. Differences in music can emerge for many reasons, such as social structure^{6,177}, motor constraints¹⁷⁸, or

stochasticity¹⁶². These differences can in turn stabilize as individuals' cultural exposure canalizes how they produce or respond to music¹⁷⁹. For instance, Australian undergraduates show memory advantages for melodies in familiar compared to unfamiliar tuning systems^{180,181}. Similarly, North American and Western European adults have difficulty remembering or producing rhythmic patterns that do not exhibit a familiar metrical structure (isochrony)^{182–185}. These types of biases seem to develop early, as infants become accustomed to the music they are exposed to^{140,141}. Such musical enculturation, a topic of longstanding interest in music research¹⁸⁶, has been corroborated by cross-cultural studies, which reveal patterns consistent with a core set of musical universals underlying broad cross-cultural diversity. For example, according to a preprint that has not yet undergone peer review, in 39 participant groups across 15 countries, differences were documented in the distributions of preferred rhythmic integer ratios in a tapping task, often reflecting local musical traditions¹⁸⁷. Nevertheless, all participant groups favoured small integer ratios, indicating that discrete representations of rhythm were universal. As cultural traditions diverge and differences become canalized, music diversifies^{188–191}, but it apparently always retains some universal properties.

By crafting products that are memorable, transmissible, and (most importantly) compelling for achieving specific ends, such as dancing or communicating emotion, cultural evolution creates auditory cheesecake. In other words, generations of cultural transmission and ingenious tinkering interact to produce compelling auditory stimuli that appeal to psychological mechanisms which exist for non-musical functions.

[H1] Summary and future directions

In this Review, we provided evidence of the universality and early development of many psychological responses to music yet uncovered few indications of innate domain-specificity. Although the systems underlying these responses could become specialized for or adapted to music over the course of development¹⁹², the current evidence is consistent with music communicating emotions, soothing infants, urging individuals to dance, and inducing other emotional and behavioural responses by appealing to features of human psychology which have evolved for non-musical functions. Moving forward, it will become important to further investigate how genetic and cultural evolution give rise to musical behaviour while expanding the musical responses under consideration. In that vein, our Review highlights four key topics for future work to address.

First, research in neuroscience and genetics provides powerful new tools for studying the neural and genetic mechanisms underlying musical responses. These tools, in turn, will allow researchers to better assess whether humans have evolved specialized adaptations for responding to music. For instance, research has shown that the neural and genetic mechanisms involved in beat perception and synchronization are also involved in vocal learning, consistent with the by-product account reviewed above^{46,159,193}. Similar approaches applied to other emotional and behavioural responses can help map out the proximate and ultimate reasons humans find music so compelling.

Second, future research will help clarify how universal psychological responses give rise to the profound musical diversity observed in human societies. Although explaining and studying musical diversity is a focus in ethnomusicology^{6,194,195}, cognitive and behavioural research on music has, with few exceptions^{178,196}, overlooked the question of why musical traditions vary in the ways they do. As researchers gain a better grasp of how and why psychology and culture vary across populations^{25,197,198}, the ability to explain the drivers of musical diversity will also improve.

Third, research on psychological responses beyond emotion will help elucidate music's diverse social roles. Most research on psychological responses to music has focused on emotional communication, yet music has many other effects, including many beyond the emotional and behavioural responses covered here. Across cultures, individuals use music to heal illness, mourn death, tell stories, greet visitors, and demonstrate virtuosity¹. Music can influence the content, vividness, and sentiment of directed imagination¹⁹⁹ and help induce mystical experiences for individuals taking psychedelic drugs²⁰⁰. Songs can evoke animals, as in the Sámi yoik tradition²⁰¹, as well as communicate a staggering richness of information²⁰². Depending on the culture, people can interpret differences in pitch to mean that particular sounds are hot, far, smooth, old, full, active, happy, sleepy, wintry, masculine, and either like a crocodile or like individuals who follow crocodiles⁴⁴. Strikingly, even these inferences are, to some degree, interpretable across cultures, suggesting cross-domain, crossculturally consistent mappings that connect concepts, acoustic features and other sensory information^{44,70,203}. Research on responses beyond emotion can advance our understanding not only of music's diverse effects but also of the more general processes involved in deriving meaning from sensory stimuli.

Last, musical aesthetics represents a uniquely controversial and difficult topic for future research. The most obvious aspect of music perception is that music sounds good. But aesthetic value in music is poorly understood²⁰⁴. This gap is demonstrated by the ongoing difficulty of accurately predicting individual music preferences²⁰⁵, even by corporations that benefit hugely from doing so, such as music streaming and recommendation services like Spotify or Apple Music. Research investigating why music is pleasant will expand the understanding of why individuals produce and listen to music.

Research connecting the psychology of music to its cultural and biological evolutionary roots has exploded in the last two decades, uncovering new insights about the origins of this pervasive yet puzzling behaviour. We expect that successful research in these four topics will accelerate scientific insights, helping uncover not just why humans produce and respond to music but also how cultural and biological evolution interact more generally to shape human behaviour.

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Glossary terms

Timbre

Perceived quality of a sound that makes notes produced by different sources, such as the human voice and a piano, sound different from each other, even when produced at the same pitch, duration, and intensity.

Harmonic structure

The grouping of harmonies in a musical example, where harmonies are combinations of tones (such as chords) that are functionally related to one another; when listeners hear a melody, they automatically build representations of its potential harmonic structure.

Auditory scene analysis

The auditory system process involved in gathering information about which sounding objects are present in the environment and determining where they are located

Major mode

In Western classical and popular music, a collection of notes (which can be played at the same time, as in a chord, or not, as in a melody) whose third note is four semitones from the tonal centre

Minor mode

In Western classical and popular music, a collection of notes (which can be played at the same time, as in a chord, or not, as in a melody) whose third note is three semitones from the tonal centre

Isochronous beat

Periodic rhythm in which beats have the same duration; most music is structured around the isochronous beat, and it is typically perceived as the basic rhythmic foundation of the music (for example, when one taps one's foot to music, one typically taps to the isochronous beat).

Integer ratio

In music, the organization of pitch or duration information in a melody or rhythm via a simple ratio of integers, such as a duration pattern of 2:1, where the first musical event is twice as long as the second

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Fig. 1. Musical response and music perception comprise distinct psychological processes, both of which are at work in human musicality.

Fig. 2. Emotional communication in music.

Fig. 3. Ontogeny of emotional and behavioural responses.

Fig. 4. Evidence of universal form-function inferences in song.