The Science-Music Borderlands

Reckoning with the Past and Imagining the Future

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1 Human Musicality and Gene-Culture Coevolution: Ten Concepts to Guide Productive Exploration

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Introduction

Debates over the evolution of human musicality have a long history and are far from resolved. Impressed by music's psychological power and cultural ubiquity, Charles Darwin (1871) theorized an adaptive origin for music in *The Descent of Man*. He proposed that wordless songs and rhythms arose in our prehuman ancestors as a display to attract mates, laying the foundation for our strong emotional response to music and scaffolding the later evolution of articulate language. In contrast, William James, who generally accepted Darwin's view that our minds are replete with evolved instincts, held a nonadaptationist view of music's origins. James touched lightly on music in *The Principles of Psychology* and saw human musicality as a fortuitous by-product of how our minds work, a "mere incidental peculiarity of the nervous system . . . of no teleological significance" (1890, vol. 2, p. 419). In short, Darwin claimed that we are an inherently musical species, while James claimed we are not.

Darwin and James never debated their positions. Darwin died eight years before James's *Principles* was published, and no correspondence between the two scholars has ever been found. Yet their conceptual alternatives have persisted in evolutionary debates over music. In the modern era, support for Darwin's theory that human music originated in sexual selection has waned, but several other adaptive theories of music's origins (e.g., rooted in social bonding, parent-infant communication, or signaling of coalition strength) have been proposed by biologists and psychologists and continue to attract attention (e.g., Dunbar, 2012; Mehr et al., 2021). Many scholars remain unconvinced, however, and James's by-product view has morphed into a number of detailed theories positing that musical behavior is a purely cultural invention building on brain functions that evolved for other reasons (e.g., Sperber, 1996; Pinker, 1997; Marcus, 2012).

It is certainly true that cultural invention can give rise to psychologically and socially powerful cognitive capacities that are not specifically predisposed by evolution.

Literacy proves this point. Psychologists, neuroscientists, and evolutionary biologists agree that human beings did not evolve to read and write (e.g., Wolf, 2007; Dehaene, 2010; Henrich, 2020). We are no more an "inherently literate" species than we are an "inherently bicycling" species. Literacy is a relatively recent human invention whose historical roots are known and date to around 3000 BCE. Humans invented literacy by drawing on evolved capacities for language, fine motor control, detailed visual pattern perception, imitation, and so forth to forge a purely cultural invention that has transformed human life. Note that "purely cultural" in this context does not mean immune from biological influences. Literacy, like any cognitive capacity, draws on specific brain regions and brain pathways and can be influenced by changes in those substrates. For example, certain genetic variants influence reading ability and the risk of dyslexia (Centanni, 2020; Doust et al., in press). This is not because humans have specific genes for reading but because those variants influence the development of brain areas or pathways that happen to be important for reading. Literacy is a purely cultural invention in the sense that no brain areas, pathways, or mechanisms have evolved specifically to facilitate the acquisition of this ability. This is unlike speech, for which there is strong, converging evidence from multiple disciplines (including cognitive science, neuroscience, and cross-species research) that the human brain has been modified over time to support a child's ability to acquire spoken language (Patel, 2008, ch. 7; Hagoort, 2017). Of course, speaking also interfaces with neural circuitry that long predates the evolution of speech and is unlikely to be specialized for language, such as brain circuits for motor habit formation. (Thus, individuals with nonfluent aphasia, who cannot generate novel sentences due to cognitive problems after a stroke, can often recite previously memorized prayers or count fluently.) The key point is that there is broad consensus among researchers that *some* human cognitive and neural mechanisms have been specialized over evolutionary time for the processing of spoken language.

Relating back to music, the modern version of the Darwin-James debate offers two conceptual alternatives: either human brains evolved neural specializations for music processing, or music relies entirely on brain circuits that evolved to serve other functions. In the latter view, such circuits are neurally "recycled" during brain development to serve music processing functions (Dehaene & Cohen, 2007). A few years ago I conducted an informal survey using an international mailing list of thousands of researchers who specialize in human auditory cognitive neuroscience. I asked the researchers to indicate which of the two positions they favored. I received about 200 responses, and they were almost perfectly split between the two alternatives. This was striking, given that there has been an explosion of research on music and the brain since 2000. Darwin and James cannot both be right, and it seems that modern neuroscientific findings have not moved the needle strongly toward one position or the other.

One reason that neuroscience has had little impact on this debate (so far) is that during ontogeny the brain can acquire neural specializations for activities we did not specifically evolve to do, via experience-dependent neural plasticity. For example, when a person learns to read and write, a region in the ventral occipitotemporal cortex begins to respond more strongly to orthography in that person's language than to other visual stimuli (Hervais-Adelman et al., 2019). This visual word form area (VWFA) is involved in interpreting visual patterns as written characters and connects to language regions that process these characters phonologically, semantically, and grammatically (Dehaene, 2010). The existence of the VWFA implies that identifying brain regions that respond selectively to music rather than to other sounds (i.e., regions neurally selective for music) would not help resolve the Darwin-James debate. Indeed, there is now robust evidence for the existence of such regions. This is interesting because, to date, the only sounds for which category-selective neural regions have been found are speech and music (Norman-Haignere et al., 2015; Boebinger et al., 2021). Yet, like the VWFA, music-selective brain regions could result from experience-dependent neural plasticity because music is a complex, meaningful sound pattern heard throughout life. Indeed, humans begin hearing and learning about music before birth (Hepper, 1991; Partanen et al., 2013) and are regularly exposed to music throughout infancy and early childhood, when the brain is developing rapidly (Lewis, 2016; Trehub & Cirelli, 2018; de Almeida et al., 2020; Mendoza & Fausey, 2021). Thus, the existence of music-selective brain regions in adults is not conclusive evidence that the brain has evolved neural specializations for music processing.

About a decade ago, based on evidence from cognitive neuroscience and other disciplines, I argued for a purely cultural view of music's origins (Patel, 2008, 2010). Although I emphasized music's ability to have a psychologically transformative effect on individual human lives and to shape the brain through mechanisms of neural plasticity, I believed there was insufficient evidence to argue that humans had evolved neural specializations for music processing. In the ensuing years, however, new empirical findings about music cognition and evolutionary biologists' growing interest in theories of gene-culture coevolution have led me to reconsider my position. In terms of empirical work, surprising discoveries indicate that seemingly basic aspects of human musical rhythmic and melodic cognition (i.e., aspects that develop without explicit training and are culturally widespread) are not widely shared by other species and require surprisingly complex neural processing (for a review, see Patel, 2019; cf. chapter 3 in this volume). This hints that evolved neural specializations may underlie these abilities. Furthermore, recent large-scale genomic studies of musicality (Niarchou et al., 2022) are ushering in a new era of neurogenetic research that can help test evolutionary hypotheses about the origins of musicality in our species.

On the theoretical front, a number of evolutionary biologists are arguing that interactions between cultural invention and biological evolution played a key role in shaping the human mind (e.g., Henrich, 2016; Laland, 2017). This work is rooted in growing evidence that cultural inventions such as agriculture, fire control, and cooking have influenced the course of human biological evolution (Itan et al., 2009; Wrangham, 2009, 2017). Although this theory of gene-culture coevolution has been present in biology for some time (Lumsden & Wilson, 1981; Feldman & Laland, 1996), recent years have seen an uptick in its application to the evolution of human cognition (e.g., Fisher & Ridley, 2013; Dennett, 2017). The idea that gene-culture coevolution played a role in the emergence of human musicality was articulated 20 years ago (Cross, 2003), yet only recently has this idea been explored in detail (e.g., Tomlinson, 2015; Podlipniak, 2017; Patel, 2018, 2021; Savage et al., 2021; Shilton, 2022). Notably, this theory provides an alternative to the adaptation versus cultural invention polarities that have dominated debates over music and evolution for more than a century. For instance, perhaps musical behavior started as a purely cultural invention in our human ancestors and then later triggered processes of gene-culture coevolution due to its impact on survival. The question, of course, is how to test such a view (for suggestions, see Savage et al., 2021; Patel, 2021).

In formulating and testing gene-culture coevolutionary theories of musicality, it is essential to consider the diverse ways music is made, used, and perceived. In other words, research from ethnomusicology, anthropology, and musicology is crucial to this enterprise. However, crossing back and forth between the natural sciences, social sciences, and humanities is far from trivial. These territories are very different, with distinct vocabularies, customs, and concerns (Shelemay, 2011; Feld, 2012; Margulis, 2014; Mundy, 2018, chapter 4 in this volume; Albouy et al., 2020). The goal of this chapter is to equip the explorer with some concepts that will make these journeys productive. These concepts are based on my own experience and training in cognitive neuroscience and evolutionary biology and on my limited knowledge of how music varies across cultures, gleaned from my readings, conversations with specialists in anthropology and ethnomusicology, and field trips with ethnomusicologists (Roberts, 2014). I hope this chapter will lead to conversations with colleagues in other fields who can refine and augment these concepts to make them useful to scholars across a range of disciplines.

Music, Musicality, and Choosing Which Musical Abilities to Study

The ten concepts listed in this chapter are premised on a fundamental distinction central to modern evolutionary work on music—namely, the distinction between *music* and *musicality* (Honing et al., 2015). *Music* is a socially constructed category; this is evident even within the boundaries of western European music, where avant-garde composers have been challenging and expanding what counts as music for more than a century. Ethnomusicologists note that although music occurs in every culture (Nettl, 2015), beyond the boundaries of western Europe or WEIRD (Western, educated, industrialized, rich, and democratic) societies more generally (Henrich, 2020), many languages have no single word for *music* that aligns with the common meaning of this word in English. For example, Trehub, Becker, and Morley (2015) note that the word *nkwa* among the Igbo of Nigeria encompasses music and dance and that the Basonge of Zaire have names for individual genres of music but have no term that encompasses all their genres. Furthermore, any human musical tradition is the product of a rich historical process and is embedded in a complex web of social and political meanings (see chapter 9 in this volume). Thus, it makes no more sense to discuss the biological evolution of music than it does to discuss the biological evolution of French or any of the other approximately 7,000 extant human languages (Eberhard et al., 2021). Just as the capacity for language is the target for scientists interested in explaining the biological evolution of language, the capacity for music is the target for evolutionary biologists interested in explaining music. The human capacity for music, or human *musicality*, can be defined as the spontaneously developing cognitive, sensorimotor, and affective capacities supporting human musical behavior. (Here, "spontaneously developing" means emerging without explicit instruction.)

This cognitive sense of musicality is quite different from the colloquial meaning of the term, which connotes a special interest in or talent for music. For example, one component of musicality in the cognitive sense is the ability to recognize a melody when it is transposed up or down in pitch (e.g., being able to recognize the song "Happy Birthday" whether it is played on a piccolo or a tuba). This is subjectively effortless for human listeners, develops early in life without any special training (Plantinga & Trainor, 2005), and appears to be a universal feature of human music cognition (Nettl, 2015). This ability may seem so simple as to be neurologically trivial, yet numerous studies have shown that songbirds (which rely on complex, learned acoustic sequences for communication and can learn to recognize human melodies) do not have this ability, indicating that it is not an automatic consequence of having a complex auditory system (for a review, see Patel, 2019).[1] Furthermore, neuroimaging reveals that this human ability relies on a network of brain regions extending far outside traditional auditory regions (Foster & Zatorre, 2010a, 2010b). Another component of musicality in the cognitive sense is the ability to perceive a beat in rhythmic music and move in synchrony with that beat in a predictable and tempo-flexible fashion (e.g., via clapping, bobbing, or dancing). This ability emerges without special training in early childhood and is culturally widespread (Savage et al., 2015). Again, although humans can do this effortlessly, current research suggests that this ability is rare in other species, including nonhuman primates, and is neurally complex, engaging a distributed network of cortical and subcortical regions (for reviews, see Patel, 2014; Cannon & Patel, 2021).

An important question about musicality concerns avant-garde composers' expansion of Western notions of music. Have they also expanded the concept of musicality? For example, Leslie (in chapter 13 of this volume) describes her compositions that integrate physiological signals into music. By passing her own brain waves "through a sonification algorithm that imprints their spectral quality onto a bank of stored flute and voice sounds," she mixes her own live performance sound. Leslie has also created an "algorithmically generated musical composition that breathes softly along with its listener, either according to a predetermined ideal breathing rate or in response to data streamed online from a respiration sensor worn by the listener." This innovative work illustrates how musical avant-gardists can create new and valuable aesthetic experiences. Yet I doubt that avant-garde music has changed human musicality in the cognitive sense, because such musicality is based on musical practices that are *widespread* within a culture. Thus, even icons of the avant-garde like Arnold Schoenberg, who have appreciative and responsive listeners (Auner, 1999; Mencke et al., 2019), have a limited public reach. "Called upon to say something about my public," Schoenberg wrote in a 1930 essay, "I have to confess: I do not believe I have one" (Stein, 1975, pp. 96–99).

In addition to the ability to recognize transposed melodies and synchronize to an auditory beat, human musicality involves many more capacities. Developing a list of such abilities is an important (and thorny) issue that would benefit from multidisciplinary discussions. While some items on this list are likely to be uncontroversial, such as the ability to remember a melodic phrase and sing it back or the capacity to be emotionally moved by music, others would probably be contested among scholars from different disciplines. However, the two abilities cited are sufficient to illustrate a key point for evolutionary research on musicality. One of these abilities (recognition of transposed melodies) can plausibly be regarded as a consequence of neural specializations for spoken language. In speech, salient rises and falls in pitch are used to distinguish linguistically important categories (e.g., word meanings in tone languages and pragmatic categories, such as statement versus question, in many languages). Listeners need to be able to recognize these "speech melodies" independent of absolute pitch because the pitch registers of men, women, and children differ substantially (Ladd, 2008). Thus, neural specializations that allow the recognition of transposed melodies may have evolved to serve speech perception, and they may be employed *by* music cognition without any additional neural specialization *for* music cognition. In the parlance of evolutionary biology, our ability to recognize transposed musical melodies might be an exaptation of the neural infrastructure for speech, without any subsequent evolutionary specialization for music (Gould & Vrba, 1982). In contrast, our ability to synchronize movements to a rhythmic beat is not so easily explained as a secondary use of speech-related brain processes. Ordinary speech does not have a periodic beat; nor do we bob, tap, or dance to ordinary speech (Patel, 2008). For biologists studying whether humans have evolved neural specializations for music processing, choosing aspects of musicality that are not easily explained as secondary uses of other, more obviously adaptive brain functions (such as speech) is an important consideration.

The broader concept is that music cognition draws on a diverse set of brain mechanisms, many of which are unlikely to be specialized over evolutionary time for music cognition (Trainor, 2015). For example, subcortical sound localization mechanisms are used when we process music, but these mechanisms evolved in animals to serve important ecological functions, such as locating predators, long before humans came on the scene. It is highly unlikely that these mechanisms were modified in humans specifically to facilitate musical processing, even though listening to music (or to any sound, for that matter) engages these mechanisms. Thus, the question at the heart of this chapter is whether music engages *any* brain mechanisms that have been specialized over evolutionary time for music cognition, and if so, whether gene-culture coevolution is responsible for this specialization. With this question in mind, I now turn to ten concepts that can guide researchers through the borderlands between the sciences and the humanities and into the territories that meet at this border.

Concept 1: Music's Value Does Not Depend on Its Evolutionary Status

Many who are drawn to music research respond strongly to music themselves. When studying evolutionary questions, this can create an implicit bias toward adaptationist theories. Implicit biases are dangerous because they can lead a researcher to unwittingly focus on data that support a favored theory and ignore contradictory data or to examine supportive data with a less critical eye than unsupportive data. To minimize such biases, it is important to remember that a particular ability's value to human life is unrelated to whether neural specializations for that ability have evolved in humans. Literacy provides a clear example. Literacy has transformed human cultures and mental experiences in positive ways, yet humans have not evolved any neural specializations for reading and writing (Wolf, 2007). Another example is exercise. Exercise is enormously valuable for physical and mental health (Ratey, 2008), yet recent research in human evolutionary biology suggests that we have no evolutionary predispositions or specializations for this activity (Lieberman, 2021). Similarly, there is growing evidence that musical activity has beneficial neurological effects in individuals with a variety of disorders (Loui et al., 2018), yet these benefits will not be diminished if it turns out that human beings are not an inherently musical species. More generally, if research on music and gene-culture coevolution ends up supporting the conclusion that humans have not evolved any neural specializations for music, this would not be a failure; it would be a perfectly acceptable outcome. This is because doing this research will lead to valuable discoveries in cognitive and brain science, a point to which I return in the final section of this chapter.

Concept 2: There Are Two Types of Neural Plasticity: Experience-Expectant and Experience-Dependent

As noted in the introduction, during ontogeny human brains can acquire neural specializations for purely cultural inventions (e.g., literacy) via experience-dependent neural plasticity. However, neural plasticity is not the opposite of innateness. Neural plasticity also occurs in circuits that have become specialized over evolutionary time to serve particular functions. This is best documented by research on critical or sensitive periods—that is, times in early development when experience is known to be essential for the correct wiring and tuning of the brain's specialized systems, including those for vision, language, and social cognition (Reh et al., 2020). Greenough, Black, and Wallace (1987) used the term "experience-expectant plasticity" to refer to the experience-driven molding of specialized circuits that occurs during critical periods and has a significant influence on subsequent abilities. As a rule, such experiences (e.g., seeing with two eyes that focus on the same point in space or receiving regular social input from a caregiver) are common to all members of a species. By allowing experience to sculpt rapidly developing specialized circuits, these circuits can perform complex tasks better than hard-wired circuits with less flexibility. Greenough's group contrasted experience-expectant plasticity with experience-dependent plasticity, defined as changes in the brain that can happen throughout life and are based on experiences that are not common to all members of a species. (Literacy is an example of experience-dependent plasticity: even though it is more than 5,000 years old, it is still far from universal.[2]) The key point is that if a human ability is based on evolved neural specializations *and* is strongly influenced by culture, it will engage both types of plasticity. Spoken language is a good example: learning to speak requires the development of phonological and lexical processing mechanisms that are shaped by experience-expectant plasticity (Kuhl, 2010; Reh et al., 2020), but mastering a particular language involves learning specific words and grammatical structures that are not universal, requiring experience-dependent plasticity. Thus, a key question for gene-culture coevolutionary research on music is whether the development of any musical ability involves experience-expectant plasticity or only experience-dependent plasticity (Penhune, 2020).

In asking this question, it is important to remember that both types of plasticity build circuits that have ongoing gene-environment interactions throughout an individual's life. As entailed in Tomlinson's idea of "radical niche construction" (see chapter 2 in this volume), biological systems have gene-environment interactions even at rapid timescales. For example, when adult zebra finches hear rhythmic versus arrhythmic versions of their conspecific songs, they exhibit greater levels of immediate early gene expression in auditory forebrain areas in response to the latter. In contrast, juvenile zebra finches show exactly the opposite pattern. This developmental reversal in rapid gene-environment interactions may reflect differences in how rhythm is used in learning songs versus evaluating song structure once learning has occurred (Lampen et al., 2019; cf. Rouse et al., 2021). The important point is that biological systems represent a constant interplay of genes and environment, even in brain circuits specialized by evolution to facilitate certain abilities.

Concept 3: Musical Behavior Might Have Originated as a Purely Cultural Invention

The concept of gene-culture coevolution entails the idea that purely cultural inventions can lead to heritable genetic changes (as discussed earlier regarding fire control in human evolution). This idea is stated succinctly by Fisher and Ridely (2013): "The smallest, most trivial new habit adopted by a hominid species could—if advantageous—have led to the selection of genomic variations that sharpened that habit." Gene-culture coevolutionary theories of musicality are thus concordant with the view that early musical behavior was not spurred by some genetic change in human ancestors but arose when nonmusical behaviors in those ancestors (e.g., coordinated group rhythmic vocalizations, as occur among chimpanzees and bonobos) were culturally repurposed in ways that began to resemble musical behavior. The crucial issue is whether this resulted in a consistent advantage in survival or reproduction that ultimately led to selection for genomic variations favoring the proclivity and capacity for these new behaviors. (For a proposal on how this could have taken place, see Patel, 2021.)

Concept 4: Capacity and Proclivity Are Conceptually and Neurally Distinct Targets for Natural Selection

In the first edition of *The Descent of Man*, Darwin wrote, "the perception, if not the enjoyment, of musical cadences and of rhythm is probably common to all animals and no doubt depends on the common physiological nature of their nervous systems" (1871, vol. 2, p. 333). Darwin's assertion that the basic human capacity to perceive music is widely shared among animal species has been challenged by modern research. However, his conceptual distinction between musical capacity and the motivation to engage in musical behavior (i.e., "enjoyment") remains crucial for research on the evolutionary foundations of musicality. It is conceivable, for example, that evolution has enhanced our motivation to engage in musical behavior without any evolved neural specialization for processing specific rhythmic or melodic aspects of music (Trehub, 2003). In this case, the relevant neural changes would occur only in pathways that support intrinsic reward in response to certain activities, including deep brain structures such as the ventral striatum and the connections between these areas and the relevant cortical structures involved in music processing (Belfi & Loui, 2020; Mas-Herrero et al., 2021). Conversely, selection may have acted on both motivational mechanisms (proclivity) and brain regions and pathways supporting the capacity for musical processing (Patel, 2021; Savage et al., 2021). In either case, a gene-culture coevolutionary view of musicality is premised on the existence of some evolutionary neural specialization for brain mechanisms involved in musical behavior.

Concept 5: Abilities Based on Evolved Neural Specializations Can Vary Widely

A common objection to the idea that humans are inherently musical is the observation that musical abilities vary widely among people. Such claims often implicitly focus on musicality in the informal sense—that is, having a special interest in or talent for music. When one focuses on components of musicality in the cognitive sense, such as implicit knowledge of the norms of one's native musical system or the ability to move in time with a musical beat, variance is likely to be lower (Rohrmeier & Rebuschat, 2012; Tranchant et al., 2016). Yet even these sorts of abilities can show substantial variation (Tranchant et al., 2021). The key point is that such variance provides no evidence *against* such abilities being supported by evolved neural specializations. Facial recognition illustrates this point. There is compelling evidence that facial recognition relies on brain circuits specialized over evolutionary time and shaped by experience-expectant plasticity in early development (Moulson et al., 2009; Todorov, 2017, chs. 12, 13; Cabral et al., 2020; Kosakowski et al., 2022). Yet the capacity for facial recognition varies widely in neurologically intact individuals, ranging from those with very poor abilities to "super-recognizers" (Sacks, 2011). Notably, even though twin studies indicate a substantial genetic contribution to severe facial recognition deficits (developmental prosopagnosia; Wilmer et al., 2010), and despite the important role of facial recognition in human social interaction, individuals with developmental prosopagnosia have not been "weeded out" by natural selection. This shows that there will always be humans who struggle with certain abilities for which the human brain is specialized.

Concept 6: Ancient, Universal Cognitive Traits Are Not Necessarily Based on Evolved Neural Specializations for Those Traits

Proponents of adaptationist theories of music's origins often point out that music is far older and more widespread than purely cultural inventions such as literacy. Music occurs in every culture, and the earliest known instruments are around 40,000 years old. This is likely much younger than the origins of musical behavior in humans, as singing leaves no trace in the fossil record (Higham et al., 2012; Morley, 2013; Nettl, 2015; Savage et al., 2015, Mehr et al., 2019). While the age and ubiquity of music are certainly consistent with theories that posit evolved neural specializations for musicality, they provide no evidence of such specializations. This is because humans likely have some ancient, universal, and culturally prominent cognitive traits that are byproducts of evolved aspects of cognition, as William James suggested in *Principles of Psychology*. Belief in ghosts or other spirits is one example. Such beliefs are universal in human culture (Norenzayan et al., 2016), but not because our brains evolved to encourage supernatural beliefs due to their survival value.[3] Rather, several authors have argued that certain features of our evolved psychology make us *susceptible* to belief in supernatural agents (e.g., Dennett, 2006). For example, Boyd (2018) and Henrich (2020) argue that such features include a reliance on cultural learning (to such an extent that it overrides even direct experience or intuition), tendencies to infer what others are thinking (theory of mind), and a bias for causal explanations based on the actions of agents. Supernatural beliefs may well be as old as articulate language in the human species and thus far older than the oldest known musical instruments. Such beliefs remind us that not every ancient and culturally universal human mental trait is a result of the brain evolving neural specializations for that trait.

Concept 7: Evolutionary Specialization and Adaptive Function Are Conceptually Distinct Issues

Research on musicality and evolution has often focused on music's adaptive value. Yet as pointed out by Tinbergen (1963), adaptation (what is it for?) is only one question about the evolution of a behavior. A second, equally important question concerns evolutionary history or phylogeny: how did it evolve? With respect to musicality, the evolutionary history of its components can be studied independently of questions about adaptation. Research on the human ability to synchronize movements to a musical beat provides an example. Patel (2006) hypothesized that this ability has its origins in the neural capacity for complex vocal learning, since both abilities involve sophisticated forebrain auditory-motor processing and engage some of the same neural circuits. This hypothesis yielded testable predictions and led to numerous empirical studies. More recently, Patel (2021) updated this hypothesis to suggest that vocal learning acted as a preadaptation for spontaneous beat perception and synchronization (BPS) and that subsequent evolutionary neural specialization for BPS took place via processes of gene-culture coevolution. This hypothesis assumes that synchronized movement to a beat in social contexts had adaptive value in early human groups, but it does not commit to just one specific adaptive function. Some theorists argue that synchrony to a beat in social contexts enhanced social bonding outside of those contexts (e.g., Savage et al., 2021), while others argue that it signaled coalition strength to other groups (e.g., Mehr et al., 2021): these theories are not mutually exclusive. The relevant point is that scientists can look for evidence of evolved neural specializations for BPS without waiting for these adaptationist debates to be resolved. To take an analogy from physical anthropology, researchers have provided convincing evidence that, compared with other primates, humans' bodies are specialized for bipedal locomotion, even though debates over *why* bipedalism was advantageous to our human ancestors are far from resolved (reviewed in Lieberman, 2013). In the case of bipedalism, evidence for specialization comes from research on comparative anatomy, biomechanics, development, and other disciplines (e.g., Richard et al., 2020). Similarly, determining whether BPS or other aspects of musicality are based on evolved neural specializations will require the integration of research across numerous disciplines, including neuroscience, genetics, cross-species studies, ethnomusicology, and developmental psychology. It is possible that we may one day have strong evidence of evolved neural specializations for musicality, even while debates over the original adaptive value of musical behavior remain unresolved.

Concept 8: A Trait Can Be Genetically Influenced without Being Genetically Determined

Gene-culture coevolution theories posit that certain components of musicality are genetically influenced. Crucially, modern views of how musical (or other cognitive) abilities are genetically influenced differ in important ways from deterministic views of the relation between genes and cognition. One of the early music psychologists who held such deterministic views was Carl Seashore, who developed auditory pattern perception tests with the aim of identifying children who were worthy of music education. “The gift of music is inborn,” remarked Seashore, “and inborn in specific types which can be detected early in life, before time for beginning serious musical education” (quoted in Cary, 1922). In contrast, modern research posits that genetic influences on specific components of musicality are subtle, with genetic variants acting probabilistically and dynamically to influence but not determine such capacities. This is in line with modern research on the behavioral genetics of cognitive traits, which emphasizes feedback loops created by gene-environment interactions during child development (Harden, 2021).

For example, a recent large-scale genome-wide association study of musical beat synchronization revealed that variation in this ability is associated with particular genetic variants occurring at numerous positions along the genome, with 67 loci reaching genome-wide significance (Niarchou et al., 2022). That is, the ability to synchronize movement to a musical beat is a complex or polygenic trait that can be weakly influenced by many common genetic variants, rather than a Mendelian trait strongly influenced by variation at a single gene. The results of the study were virtually unchanged by controlling for general cognition, consistent with results from the twin literature showing that the genetics of rhythm are not solely attributable to generally cognitive effects. Importantly, in this new study, genetic variance explained only about 13 to 16 percent of phenotypic variance in the ability to clap in time to a musical beat, indicating that variance in this ability is genetically influenced but far from genetically determined. This means that interactions among genes, experience, and culture are essential in understanding how this trait develops in individuals.

Concept 9: Studying Cultural Variation in Music Requires Reading Primary Sources and Talking with Specialists

Recent years have seen a growth in “big data” studies of music that draw on ethnographic databases or collections of audio recordings to study cross-cultural patterns in musical structure or behavior using quantitative analyses. Such studies have provided valuable information and are well worth conducting, and when they are published in high-profile journals (e.g., Savage et al., 2015; Mehr et al., 2019), they are frequently cited by cognitive scientists seeking to understand musical diversity. Yet such studies are far from the final word on musical diversity because they draw on a limited sample of the world’s cultures. For example, Savage et al. (2015) examined 304 diverse recordings of traditional music from around the world (taken from the *Garland Encyclopedia of World Music*), while Mehr et al. (2019) examined ethnographic descriptions from

60 traditional societies chosen to represent 60 cultural clusters from among the 315 cultures in the Human Relations Area Files. Mehr's group also analyzed audio recordings from 86 traditional societies around the world, taken mainly from the Archive for World Music in Harvard's music library. Although these studies examined more cultures than previous comparative work on music and applied modern methods of analysis to generate quantitative comparative data, many cultures were not represented in these samples (recall that there are around 7,000 extant languages on earth today; Eberhard et al., 2021). Theories built on limited samples inevitably reflect the biases of those samples.

For example, building on their previous cross-cultural work, Savage et al. (2021) and Mehr et al. (2021) proposed evolutionary theories of music that emphasize collective music making. Yet there are some traditional societies, not included in their earlier cross-cultural studies, where music making is primarily a solo endeavor (Patel & von Rueden, 2021). Without developing a list of such cultures and understanding why they opt for solo rather than collective musical behavior, theories of music and evolution remain incomplete. The relevant point is that researchers interested in musical diversity should not rely solely on existing cross-cultural "big data" studies. There is no substitute for reading primary research and talking with researchers who have spent years in the field with small-scale traditional societies. For example, such readings and conversations led Patel and von Rueden (2021) to learn about the predominance of solo musical behavior in multiple small-scale cultures (including several hunter-gatherer societies), none of which appeared in Savage's and Mehr's earlier cross-cultural studies. Fortunately for those who want to study musical diversity and develop hypotheses to help explain it, anthropology and ethnomusicology are thriving disciplines with primary sources and scholars available for consultation.

Concept 10: Variance in Musicality Is an Asset for Gene-Culture Coevolution Research

As noted earlier, musicality in the cognitive sense refers to the widespread and spontaneously developing mental and physical abilities that underlie the human capacity for music. Measurement of such abilities typically reveals substantial individual differences. For example, Tranchant et al. (2021, fig. 6) provided data on nonmusicians' ability to synchronize movements to a beat and to perceive beat in the absence of movement, and Jacoby et al. (2019, fig. 2) provided cross-cultural data on musically untrained individuals' ability to accurately sing back a simple pitch interval when the model is presented either within or outside their vocal range. Both studies revealed considerable individual variation. Significant variation in musicality is not limited to perception and production skills but is also apparent in responsiveness to music.

Research has revealed that a small percentage of individuals from western European cultures do not derive pleasure from music, even though they do not suffer from depression or other neuropsychological disorders, are not tone deaf, and can derive pleasure from other arts (Mas-Herrero et al., 2012, 2018). Brain imaging suggests that these "musically anhedonic" individuals have a low degree of neural coupling between auditory processing and reward regions of the brain (Martínez-Molina et al., 2016; Loui et al., 2017).[4] Importantly, it appears that such individuals are at the low end of a continuum in terms of how rewarding people find music and how strongly connected their auditory and reward regions are (Loui et al., 2017; Martínez-Molina et al., 2019; Belfi & Loui, 2020). In other words, whether measuring perceptual, motor, or affective aspects of musicality, there is considerable variability across individuals. From the standpoint of theories of music and gene-culture coevolution, this variance is good because it can be leveraged to study mechanistic links among genes, experience, brains, culture, and musicality. This will require research using measures of musical ability and responsiveness that can be adapted to different cultures, ages, and degrees of musical training. (For some current measures of musicality, see Mas-Herrero et al., 2012; Sandstrom & Russo, 2013; Harrison & Müllensiefen, 2018; Jacoby et al., 2019; Zentner & Gingras, 2019.) Ultimately, this work will need to connect with emerging methods for studying the relations among human genetics, brain structure, and natural selection (Tilot et al., 2021).

Conclusion: Why This Research Matters

How is research on musicality relevant to the broader study of human evolution? Understanding the evolution of the human mind is a central issue in determining human origins. Among biologists studying the evolution of the mind, there is growing interest in the idea that gene-culture coevolution played a key role in this process. For example, Laland argues that compared to other species, humans experienced an unusually strong interaction between cultural and genetic processes:

> Human culture is not just a magnificent end product of the evolutionary process, an entity that, like the peacock's tail or the orchid's bloom, is a spectacular outcome of Darwinian laws. For humans, culture is a big part of the explanatory process too. The evolution of the truly extraordinary characteristic of our species—our intelligence, language, cooperation, and technology—have proven difficult to comprehend, because, unlike most other evolved characters, they are not adaptive responses to extrinsic conditions. Rather, humans are creatures of their own making. The learned and socially transmitted activities of our ancestors, far more than climate, predators, or disease, created the conditions under which our intelligence evolved. Human minds are not just built *for* culture; they are built *by* culture. (2017, pp. 29–30)

Yet despite interest in the idea that gene-culture coevolutionary dynamics shaped the human mind, evidence supporting this view remains scarce. Convincing examples of gene-culture coevolution in human biology come from studies of genetic and physiological nonneural adaptations related to diet, climate, and disease (Laland et al., 2010; Richerson et al., 2010). Musicality may prove to be a more tractable domain for developing and testing theories of cognitive gene-culture coevolution than others mentioned by Laland, such as language and cooperation. This is because there are well-developed disciplines that study cultural variation in music and individual variation in musicality and because several core cognitive components of musicality (e.g., beat processing) are likely to be easier to understand in terms of neural mechanisms than are core cognitive components of language (e.g., lexical processing) or cooperation (e.g., theory of mind) (cf. Cannon & Patel, 2021; Cannon, 2021). Also, core components of musicality are likely to be more amenable to exploration in animal models, aiding in the elucidation of links among genes, brains, and cognition. In other words, there are several reasons why musicality may be a promising model for studying cognitive gene-culture coevolution in human beings. The methods and findings emerging from such research may prove valuable for gene-culture coevolutionary research on other key human mental faculties, such as language.

However, what happens if, decades from now, after many studies motivated by gene-culture coevolutionary theories of music, we conclude that music is a purely cultural invention based on brain functions that evolved for other reasons, like literacy? Even if this should transpire, research on the evolution of musicality will have been fruitful. As shown by a growing body of surprising discoveries, cross-species research on musicality (motivated by evolutionary hypotheses) is a powerful way to illuminate distinctive features of human nonlinguistic cognition. Furthermore, I suspect that evolutionary research on musicality will lead to breakthroughs in our understanding of the mechanistic links among human genes, brains, experience, and culture, regardless of whether we prove to be an inherently musical species.

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Notes

1. At this point, it is unclear whether any nonhuman primates have this ability, as there are only a few studies with contradictory results.

2. For a fascinating discussion of how literacy spread in Europe between 1500 and 1900, see Henrich (2020, pp. 3–17).

3. Belief in ghosts or spirits is distinct from organized religion, and the latter is not present in all human cultures. In today's world there are many people who do not believe in the supernatural, but this is likely a relatively recent historical phenomenon associated with the rise of modern, scientifically based education. However, even in cultures where such education is prominent, there are many who still believe in the supernatural.

4. The extent to which these neurological patterns are a cause or a consequence of the lack of engagement with music remains unclear, and it has yet to be determined whether genetics plays a role in musical anhedonia.

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