Human musicality and gene-culture coevolution:

Ten concepts to guide productive exploration

Aniruddh D. Patel

Dept. of Psychology, Tufts University

Program in Brain, Mind, and Consciousness, Canadian Institute for Advanced Research (CIFAR)

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Abstract

A growing number of researchers across the sciences and humanities theorize that human musicality arose via an interplay of cultural invention and biological evolution, or “gene-culture coevolution.” This chapter offers ten concepts to help guide productive cross-disciplinary discussions on this topic. Such interactions across traditional disciplinary boundaries are needed to propel deep explorations of human musicality. These explorations are important for the study of human origins because musicality may prove to be a model system for exploring cognitive gene-culture coevolution, a process increasingly thought to be central to the evolution of the human mind.

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 pre-human ancestors as a display to attract mates, laying the foundations for our strong emotional response to music and scaffolding the later evolution of articulate language. In contrast, William James, who generally favored Darwin’s view that our minds were replete with evolved instincts, held a non-adaptationist view of music’s origins. James touched lightly on music in *The Principles of Psychology* (1890), but what he wrote made it clear that he saw human musicality as a fortuitous byproduct of how our minds work, a “mere incidental peculiarity of the nervous system... of no teleological significance.” (Vol 2, p. 419). In short, Darwin claimed that we are an inherently musical species, while James claimed we are not.

Darwin’s and James never debated their positions. Darwin died eight years before *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 since their time. In the modern era, 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 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’ “byproduct” view has morphed into a number of detailed theories proposing that musical behavior is a purely cultural invention which builds 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 we 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 back to around 3,000 BCE. Humans invented literacy by drawing on our evolved capacities for language, fine motor control, detailed visual pattern perception, imitation, etc., to forge a purely cultural invention which 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 brain pathways and can be influenced by changes to those substrates. For example, certain genetic variants influence reading abilities and the risk of dyslexia (Centanni, 2020; Verhoef et al. 2021). This is not because humans have “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 to specifically facilitate the acquisition of this ability. This is unlike speech, where there is strong, converging evidence from multiple disciplines (including cognitive science, neuroscience, and cross-species research) that the human brain has been modified over evolutionary time to support a child’s ability to acquire spoken language (for one review, see Patel, 2008, Ch. 7). Of course, speaking also interfaces with neural circuitry which long predates the evolution of speech and which 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 with language after a stroke, can often recite overlearned prayers or count fluently.) The key point, however, is that there is broad consensus among researchers that *some* human cognitive and neural mechanisms have been specialized over evolutionary time for spoken language processing.

Relating this back to music, the modern version of the Darwin-James debate offers the conceptual alternatives of human brains evolving neural specializations for music processing vs. music relying entirely on brain circuits that evolved to serve other functions. In the latter view, such circuits get “neurally recycled” during brain development to serve music processing (Dehaene & Cohen, 2007). A few years ago I did an informal survey about this debate with the Auditory List, an international mailing list of thousands of researchers who specialize in the study of human auditory cognitive neuroscience. I asked list members to indicate which of these two positions they favored. The ~ 200 responses I received were almost perfectly split between the two positions. This was striking because there has been an explosion of research on music and the brain since around 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 which 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 their ventral occipito-temporal cortex comes to respond more strongly to orthography in their language than to other visual stimuli (Hervais-Adelman et al., 2019). This “visual word form area” or VWFA is involved in interpreting visual patterns as written characters, and connects to language regions which processes these characters phonologically, semantically and grammatically (Dehaene, 2010). The existence of the VWFA implies that finding brain regions which respond selectively to music vs. other sounds (i.e., regions “neurally selective for music”) would not help resolve the Darwin-James debate. Indeed, there is now robust evidence for such regions, which 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 music-selective brain regions, like the VWFA, could result from experience-dependent neural plasticity since music is a complex, meaningful sound pattern heard throughout life. Indeed, infants 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 rapidly developing (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 our brains have 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). While I emphasized music's ability to psychologically transform individual human lives and to shape the brain through mechanisms of neural plasticity, I felt there was insufficient evidence to argue that humans have evolved neural specializations for music processing. In the ensuing years, however, new empirical findings in music cognition and growing interest among evolutionary biologists in theories of gene-culture coevolution have led me to reconsider this view. In terms of empirical work, there have been surprising discoveries which indicate that seemingly basic aspects of human musical rhythmic and melodic cognition (i.e., aspects which develop without explicit training and which are culturally widespread) are not widely shared by other species and require surprisingly complex neural processing (see Patel 2019 for a review, and cf. Duengen, Sarfati, and Ravignani, this volume). This hints at possible evolved neural specializations underlying these abilities. Furthermore, recent large-scale genomic research on musicality (Niarchou et al., 2021) is ushering in a new era of neurogenetic research which can help test evolutionary hypotheses about the origins of musicality in our species.

On the theoretical front, evolutionary biologists are increasingly arguing that interactions between cultural invention and biological evolution have 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, the control of fire, and cooking have influenced the course of human biological evolution (Itan et al. 2009; Wrangham, 2009, 2017). While this theory of "gene culture coevolution" has been present in biology for some time (Lumsden and Wilson, 1981; Feldman & Laland, 1996), recent years have seen an uptick in applying this framework 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 begun to be explored in detail (e.g., Tomlinson, 2015; Podlipniak, 2017; Patel, 2018, Savage et al. 2021). Notably, the idea provides an alternative to the "adaptation vs. pure cultural invention" polarities that have dominated debates over music and evolution for over a century. That is, perhaps musical behavior started as a purely cultural invention in human ancestors, which 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 recent suggestions, see Savage et al. 2021, and Patel, 2021)

In formulating and testing gene-culture coevolutionary theories of musicality, it is essential to attend to the diversity of ways in which 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. The territories are very different, with distinct vocabularies, customs, and concerns (Shelemay, 2011; Feld, 2012; Margulis, 2014; Mundy, 2018 and this volume; Albouy et al. 2020). The goal of this chapter is to equip the explorer with some concepts that will help 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 readings and conversations with specialists in anthropology and ethnomusicology, and from accompanying ethnomusicologists into the field (Roberts, 2014). Thus the concepts inevitably reflect my own background. I hope this chapter

will lead to conversations with colleagues in other fields, who can help refine and augment this set of concepts to make them useful to scholars across a range of disciplines.

Music, musicality, and choosing musical abilities to study

The ten concepts listed in this chapter are premised on a fundamental conceptual 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, a point that is evident even within the boundaries of Western European music, where avant-garde composers have been challenging and expanding what counts as “music” for over a century. Ethnomusicologists note that while music occurs in every culture (Nettl, 2015), beyond the boundaries of Western Europe (or of WEIRD societies more generally, Henrich, 2020), many languages often have no single word for “music” which aligns with the commonplace meaning of this word in English. For example, Becker and colleagues note that the word “nkwa” among the Igbo of Nigeria encompass music and dance, and that the Basongwe of Zaire have names for individual genres of music but do not have a cover term for all of their genres (Trehub et al., 2015). 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 (Sykes, 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 ~7,000 extant human languages (Eberhard et al. 2021). Just as it is the *capacity for language* which is the explanatory target for scientists interested in the biological evolution of language, it is the capacity for music that is the explanatory target for evolutionary biologists interested in 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 special interest or talent in music. For example, one component of “musicality” in the cognitive sense is the ability to recognize a melody when it transposed up or down in pitch (e.g., recognizing the Happy Birthday tune whether played on a piccolo vs. 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). While this ability may seem so simple as to be neurologically trivial, numerous studies show that songbirds (who rely on complex, learned acoustic sequences for communication, and who 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 (see Patel, 2019 for a review)¹. Furthermore, neuroimaging work with humans reveals that the ability relies on an extended network of brain regions reaching far outside traditional auditory regions (Foster & Zatorre, 2010a,b). Another component of musicality in the cognitive sense is the ability to perceive a beat in rhythmic music and move in synchrony with this in a predictive 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, this ability is not experienced as effortful by humans, yet current research suggests that the ability is rare in other

¹ Indeed, at this point is unclear if any non-human primates have this ability, as there are only a few studies with contradictory results.

species, including nonhuman primates, and is neurally complex, engaging a distributed network of cortical and subcortical regions (for reviews, see Patel, 2014; Cannon and Patel 2021).

An important question about musicality concerns the avant-garde composers mentioned above. Such composers have been expanding Western notions of “music,” but have they also expanded what counts as musicality? For example, Leslie (this volume) describes her compositions integrating sonification of physiological signals into music. She has used her own brainwaves “passed through a sonification algorithm that imprints their spectral quality onto a bank of stored flute and voice sounds that I mix with my own live performance sound.” Leslie has also created an “algorithmically generated musical composition that breathed 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 the musical avant-garde can create new and valuable aesthetic experiences. Yet I doubt avant-garde music has changed human musicality in the cognitive sense, because musicality in that sense is based on musical practices which are *widespread* within a culture. Thus even icons of the avant-garde like 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.” (Schoenberg, 1930).

Above I offered recognition of transposed melodies and the ability to synchronize to an auditory beat as examples of human musicality, but human musicality involves many more capacities than these. Developing a list of such abilities is an important (and thorny) issue which 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 are likely to be contested among scholars from different disciplines. However, the two abilities chosen above are sufficient to illustrate a key point for evolutionary research on musicality. One of these abilities (recognition of transposed melodies) could plausibly be regarded as a consequence of neural specializations for spoken language. Speech uses salient rises and falls in pitch to distinguish linguistically important categories (such as word meanings in tone languages, and pragmatic categories such as statement vs. question in many languages), and listeners need to recognize these “speech melodies” independent of absolute pitch since men, women, and children differ substantially in their spoken pitch registers (Ladd, 2008). Thus neural specializations for recognizing transposed melodies may have evolved to serve speech perception, and 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 periodic 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 interested in studying whether humans have evolved neural specializations for music processing, choosing aspects of musicality which are not easily explained as secondary uses of other, more obviously adaptive brain functions (such as speech) is an important consideration.

The broader conceptual point 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, our subcortical sound localization mechanisms are used when we process music, but these

mechanisms evolved in mammals to serve important ecological functions, such as localizing predators, long before humans came on the scene. It is highly unlikely that these mechanisms have been modified in humans to specifically 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 processes of gene-culture coevolution are responsible for this specialization.** With this question in mind, I now turn to ten concepts which can help guide researchers interested in pursuing this question through the borderlands between the sciences and humanities, and into the territories that meet at this border.

Concept 1: The value of music in human life does not depend on its evolutionary status

Many who are drawn to research on music respond strongly to it. When studying evolutionary questions this can create an implicit bias toward adaptationist theories. Implicit biases are dangerous because they can lead one to unwittingly focus on data that support one's 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 the value of an ability to human life is a completely different question from whether we have evolved neural specializations for that ability. Literacy provides a clear example of this distinction. Literacy has transformed human cultures and mental experience in positive ways, yet we have not evolved neural specializations for reading and writing (Wolf, 2007). Another example of this distinction comes from 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 predisposition or specializations for this activity (Lieberman, 2021). Similarly, the growing evidence for the beneficial neurological effects of musical activity in individuals with a variety of disorders (Loui et al., 2018) is not in the least diminished if it turns out we 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 "failure", but a perfectly acceptable outcome. This is because doing this research leads to valuable discoveries in cognitive and brain science, a point to which I return in the final section of this chapter "Why this research matters."

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 (like literacy) via experience-dependent neural plasticity. However, it is not the case that neural plasticity is the opposite of innateness. Neural plasticity also occurs in circuits that have been specialized over evolutionary time to serve particular functions. This is best documented via research on "critical periods" or "sensitive periods." These are 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 (1987) used "experience-expectant plasticity" to refer to the experience-driven molding of specialized circuits which occurs in critical periods and which has a significant influence on subsequent abilities. He noted that as a rule, such experiences (such as seeing with two eyes that can 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, the circuits can achieve greater levels of performance on complex tasks than can "hardwired" circuits with less flexibility. Greenough contrasted experience-expectant plasticity with "experience-dependent plasticity," with the latter referring to changes in the brain which can happen throughout life and which are based on experiences which are not common to all members of a species. (Literacy illustrates experience-dependent plasticity: even though it is over 5,000 years old it is still far from universal.²) For the current purposes, the key point is that if a human ability rests 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 requires learning specific words and grammatical structures which are not universal, and thus depends on experience-dependent plasticity. Thus a key question for gene-culture coevolutionary research on music is whether the development of any musical abilities involves experience-expectant plasticity, or only experience-dependent plasticity.

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" (Tomlinson, this volume), biological systems have gene-environment interactions even at rapid timescales. For example, when adult zebra finches hear rhythmic vs. arrhythmic versions of their conspecific songs, they show greater levels of immediate early gene expression in auditory forebrain areas in response to the former. 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 song learning vs. in evaluation of song structure once learning has occurred (Lampen et al. 2019, cf. Rouse et al. 2021). The larger point is that biological systems represent a constant interplay of genes and environment, even in brain circuits specialized by evolution to facilitate specific abilities.

Concept 3: Musical behavior could 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 vis-à-vis the control of fire in human evolution). This idea is put 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

² For a fascinating discussion of how literacy spread in Europe between ~1500-1900, see Henrich (2020), p. 3-17.

habit.” Gene-culture coevolutionary theories of musicality are thus concordant with views that posit that early musical behavior was not spurred by some genetic change in human ancestors, but arose when non-musical behaviors in human ancestors (such as coordinated group rhythmic vocalizations, as occur in chimpanzees and bonobos) were culturally repurposed in ways that began to resemble musical behavior. The crucial issue is whether this resulted in some consistent advantage in survival or reproduction, which 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 the section on “Human beat perception and synchronization and gene-culture coevolution” in 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 (1871) 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.” (p. 333). Darwin’s assertion that basic human music perception capacities are widely shared among animal species has been challenged by modern research, as discussed above with respect to recognition of transposed melodies. However, his conceptual distinction between musical capacities and the motivation to engage in musical behaviors (his “enjoyment”) remains crucially important for research on the evolutionary foundations of musicality. It is conceivable, for example, that evolution has enhanced our motivation to engage in musical behaviors without any evolved neural specializations for processing specific rhythmic or melodic aspects of music (Trehub, 2003). In this case, the relevant neural changes would only be in pathways that support intrinsic reward in response to certain activities, including deep brain structures such as the ventral striatum and the connections of these areas to relevant cortical structures involved in music processing (Belfi & Loui, 2020; Mas-Herrero et al. 2021). On the other hand, selection may have acted on both motivational mechanisms (proclivity) and on brain regions and pathways supporting the capacity for musical processing (Patel, 2021, Savage et al., 2021). In either case, a gene-culture coevolution view of musicality is premised on the idea that there has been some evolutionary neural specialization for brain mechanisms involved in musical behavior.

Concept 5: Abilities based on evolved neural specializations can vary widely

A commonly heard 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, i.e., special interest or talent in 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, however, is that such variance provides no evidence *against* such abilities being supported by evolved neural specializations because abilities based on evolved neural specializations can vary widely in a population. Face recognition illustrates this point. There is compelling evidence that face recognition relies on brain circuits specialized over evolutionary time for this function, which are shaped by experience-expectant plasticity in early development (Moulson et al. 2009; Todorov, 2017, Ch. 12,13; Cabral et al., 2020; Kosakowski et al., 2021). Yet face recognition abilities vary widely in neurologically intact individuals, who range from those with very poor abilities to “super-recognizers” (Sacks, 2011). Notably, even though twin studies indicate a substantial genetic contribution to severe face recognition deficits (developmental prosopagnosia, Wilmer, 2010), and despite the important role of face recognition to 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 abilities that human brains are specialized for.

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, which is likely much younger than the origins of musical behavior in humans, since singing leaves no trace in the fossil record (Morley, 2013; Nettl, 2015; Savage et al., 2015, Mehr et al., 2019; Higham et al. 2012). While the age and ubiquity of music are certainly consistent with theories which posit evolved neural specializations for musicality, these facts provide no evidence for such specializations. This is because humans likely have some ancient, universal, and culturally prominent cognitive traits which are byproducts of evolved aspects of cognition, as William James suggested in *Principles of Psychology*. Belief in ghosts or other spirits is one example of this. Such beliefs are universal in human culture (Norenzayan et al., 2016), but not because our brains have been specifically evolved to have supernatural beliefs because of their survival value³. 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 our reliance on cultural learning (to an extent that will even override direct experience or intuition), our 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 our species, and thus far older than the oldest known musical instruments. Such beliefs should remind us that not every ancient and culturally-universal human mental trait is a result of our brain having evolved neural specializations for that trait.

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

Concept 7: Evolutionary specialization and adaptive function are conceptually distinct issues

Research on musicality and evolution has often focused on questions of music's adaptive value. Yet as pointed out by Tinbergen (1963), the question of 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? Relating this to musicality, one can study the evolutionary history of the components of musicality independently of questions of adaptation. Research on the human ability to synchronize movements to a musical beat provides an example of this. 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 yields testable predictions and has led to numerous empirical studies. More recently, Patel (2021) updated this hypothesis to suggest that vocal learning acted as a preadaptation for beat perception and synchronization (BPS), and that subsequent evolutionary neural specialization for BPS then 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 the hypothesis makes no commitment to precisely what that value was. 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 argued that it signaled coalition strength to other groups (e.g., Mehr et al., 2021). The relevant point is that scientists can look for evidence of evolved neural specializations for BPS without waiting for such adaptationist debates to be resolved. To take an analogy from physical anthropology, researchers in that discipline have provided convincing evidence that human bodies are specialized for bipedal locomotion compared to other primates, even though debates over *why* bipedalism was advantageous to 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 integration of research across numerous disciplines, including neuroscience, genetics, cross-species research, 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 of musicality 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. Such deterministic views were held by some early music psychologists, such as Carl Seashore, who developed auditory pattern perception tests with the aim of identifying children who

were worthy of further 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." (Cary, 1922). In contrast to this view, modern research posits that genetic influences on specific components of musicality are subtle, with genetic variants acting probabilistically and dynamically to influence, 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 (GWAS) of beat perception and synchronization (BPS) 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., 2021). That is, BPS is a complex or "polygenic" trait, in which many common genetic variants weakly influence the trait, 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 that show that the genetics of rhythm are not solely attributable to generally cognitive effects. Importantly, in this new study genetic variance explained only about 13-16% of phenotypic variance in the ability to clap in time to a musical beat, indicating that variance in BPS ability is genetically influenced but far from genetically determined. This means that interactions between genes, experience, and culture will be 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 which 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 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 musical recordings from 304 small-scale cultures from around the world (taken from the *Garland Encyclopedia of World Music*), while Mehr et al. (2019) examined ethnographic descriptions from 60 traditional societies from around the world, chosen to represent 60 cultural clusters from among the 315 cultures in the Human Relations Area Files. Mehr et al. (2019) also analyzed audio recordings from 86 traditional societies around the world, taken mainly from the Archive for World music in the Harvard music library. While these studies examined many more cultures than previous comparative work on music and applied modern analysis methods to generate quantitative comparative data, it is worth remembering that many cultures are 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 will 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) both recently proposed evolutionary theories of music which emphasize collective music making. Yet there are traditional societies, not included in their earlier cross-cultural studies, in which music-making is a primarily a solo endeavor (Patel & von Rueden, 2021). Without developing a list of such cultures and understanding why they opt for solo vs. collective musicality, theories of music and evolution based on collective music making remain incomplete. For the current purposes, the relevant point is that researchers interested in musical diversity should not solely rely 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, it was such writings and conversations that led Patel & von Rueden (2021) to learn about the predominance of solo musical behavior in multiple small-scale cultures (including several hunter-gatherer societies), none of whom appeared in the cross-cultural studies of Savage et al (2015) or Mehr et al. (2019). Fortunately for those who want to study musical diversity and develop hypotheses to help explain it, anthropology and ethnomusicology are thriving disciplines, so that one can readily seek out primary sources and scholars for consultation.

Concept 10: Variance in musicality is an asset for gene-culture coevolution research

As noted in near the start of this chapter, “musicality” in the cognitive sense refers to the widespread and spontaneously developing mental and physical abilities which underlie the human capacity for music. Measurement of such abilities typically reveals substantial individual variability. For example, Tranchant et al (2021, Fig. 6) recently provided data from nonmusicians on the 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 the ability of musically untrained individuals to accurately sing back a simple pitch interval when the model interval is presented within or outside of their vocal range. Both studies revealed considerable individual variation. Significant variation in musicality is not limited to perception and production skills, it is also present in responsiveness to music. Recent research has revealed that a few percent of individuals in Western European cultures do not derive pleasure from music, even though they do not suffer from depression or other neuropsychological disorders, are not musically tone deaf, and can get 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 to be and how strongly connected auditory and reward regions are (Loui et al., 2017; Martínez-Molina et al., 2019; Belfi and Loui, 2020). In other words, whether measuring perceptual, motor, or affective aspects of musicality, it is evident that there is considerable variability across individuals. From the standpoint of theories of music and gene-culture coevolution, this variance is good, because it is precisely this variance which can be leveraged to study mechanistic links between

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

genes, experience, brains, culture, and musicality. This will require combining research in music neuroscience with high-quality measures of basic musical abilities and responsiveness, focusing on measures that can be adapted to different cultures, ages, and degrees of musical training. (For some currently available 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 in turn will need to link to emerging methods for studying relations between human genetics, brain structure, and natural selection (Tilot et al., 2021).

Conclusion: Why this research matters

What is the broader relevance of research on musicality to the study of human evolution?

Understanding the evolution of the human mind is a central issue in human origins. Among biologists interested in 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, in a recent book on this topic, Laland (2017) argues that compared to other species humans have experienced an unusually strong interaction between cultural and genetic processes in our evolution:

“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.” (p. 29-30).

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

However, what if decades hence, after many studies motivated by gene-culture coevolutionary theories of music, we conclude that music is a purely cultural invention based on brain function 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 the surprising discoveries of the past dozen years, 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 between human genes, brains, experience, and culture, whether or not we prove to be an inherently musical species.

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