

What Does It Mean to Be Musical?

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Music can be seen as a model system for understanding gene × environment interactions and how these can influence neurocognitive development. The concept of musicality, however, is underspecified and not well understood. Here, I propose a framework for defining musicality to provide a foundation for studying the contributions of biological and environmental factors.

Musical ability is popularly regarded to be innate: one either is or is not born with musical talent. Increasingly, neuroscientists are collaborating with geneticists to understand the links between genes, brain development, cognition, and behavior (Ebstein et al., 2010; Posner et al., 2011). Music can be seen as a model system for understanding what genes can accomplish and how they relate to experience. On the practical side, identifying genetic components that underlie musical ability can also help us to predict who will succeed or, more interestingly, what types of instruction will be most successful for individuals according to their geneticcognitive profiles. In all domains, successful genotyping requires an accurately described phenotype. Unfortunately, the latter has not yet been accomplished for music, creating a significant hurdle to further progress. Part of the difficulty in describing the musical phenotype is its heterogeneity, the wide variety of ways in which musicality presents itself (Sloboda, 2008). My goal in this article is to review those factors that might be associated with the phenotype and to discuss definitions, measurement, and accuracy, three common obstacles in understanding the genetics of complex behavioral phenomena (Ebstein et al., 2010), with the hope that this may stimulate discussion and future work on the topic.

The Functional Neuroanatomy of Music

We now know that music activates regions throughout the brain, not just a single "music center." As with vision, music is processed component by component, with specific neural circuits handling pitch, duration, loudness, and timbre. Higher

brain centers bring this information together, binding it into representations of contour, melody, rhythm, tempo, meter, and, ultimately, phrases and whole compositions. The idea that music processing can be broken down into component operations was first proposed as a conceptual tool by cognitive theorists and has been confirmed by neuroimaging studies (Levitin and Tirovolas, 2009).

The early distinction that music processing is right hemisphere lateralized and that language is left hemisphere lateralized has been modified by a more nuanced understanding. Pitch is represented by tonotopic maps, virtual piano keyboards stretched across the cortex that represent pitches in a low-to-high spatial arrangement. The sounds of different musical instruments (timbres) are processed in well-defined regions of posterior Heschl's gyrus and superior temporal sulcus (extending into the circular insular sulcus). Tempo and rhythm are believed to invoke hierarchical oscillators in the cerebellum and basal ganglia. Loudness is processed in a network of neural circuits beginning at the brain stem and inferior colliculus and extending to the temporal lobes. The localization of sounds and the perception of distance cues are handled by a network that attends to (among other cues) differences in interaural time of arrival, changes in frequency spectrum, and changes in the temporal spectrum, such as are caused by reverberation. One can attain worldclass expertise in one of these component operations without necessarily attaining world-class expertise in others.

Higher cognitive functions in music, such as musical attention, musical memory, and the tracking of temporal

and harmonic structure, have been linked to particular neural processing networks. Listening to music activates reward and pleasure circuits in the nucleus accumbens, ventral tegmental area, and amygdala, modulating production of dopamine (Menon and Levitin, 2005). The generation of musical expectations is a largely automatic process in adults, developing in childhood, and is believed to be critical to the enjoyment of music (Huron, 2006). Tasks that require the tracking of tonal, harmonic, and rhythmic expectations activate prefrontal regions, in particular Brodmann areas 44, 45, and 47, and anterior and posterior cinqulate gyrus as part of a cortical network that also involves limbic structures and the cerebellum.

Musical training is associated with changes in gray matter volume and cortical representation. Musicians exhibit changes in the white matter structure of the corticospinal tract, as indicated by reduced fractional anisotropy, which suggests increased radial diffusivity. Cerebellar volumes in keyboard players increase as a function of practice. Learning to name notes and intervals is accompanied by a leftward shift in processing as musical concepts become lexicalized. Writing music involves circuits distinct from other kinds of writing, and there are clinical reports of individuals who have musical agraphia without textual agraphia. Double dissociations have also been reported between musical agraphia and musical alexia. Indeed, the patient literature is rich with accounts of individuals who have lost one specific aspect of musical processing while others remain intact, bolstering claims of distinct, componential processing of music (Marin and Perry, 1999).



Defining Musicality

Each of the components mentioned above-for example, reading or remembering music, listening to various attributes of a musical performance, playing an instrument-seem intuitively to be involved in constructing a profile of musical abilities. The fact that they are distinguishable neuroanatomically lends credence to them as real, not merely theoretical, concepts and suggests the possibility of genetic correlates influencing neural development and differentiation. Rather than there being a single "music gene," the most likely scenario is that we will discover genes that support component brain structures and thereby, by extension, component musical behaviors. Genetic polymorphisms, such as the catechol-O-methyl transferase (COMT) gene, have been shown to modulate dopamine in the prefrontal cortex, and thereby working memory function (Posner et al., 2011; Robbins and Kousta, 2011). Other polymorphisms no doubt influence the development of eve-hand coordination in rhythmic sequences or the structure and function of auditory long-term memory.

The crux of the phenotype problem is that musicality presents itself in a number of different ways that may be uncorrelated with each other. How might one go about characterizing, and ultimately quantifying, the musical phenotype? I suggest that if an individual presented any one of the following behaviors at a high level of competence (say, two standard deviations above the population mean) we would regard that individual as having musical abilities: playing an instrument, composing, orchestrating, or conducting.

It is necessary, however, to further fractionate these skills into subskills (e.g., McPherson, 1995). For example, some instrumentalists excel as soloists, and others as ensemble players or accompanists; some excel at sight reading, and others (in fact most musicians in the world) play only by ear. Within the domain of music reading, some musicians are good sight readers, and others are better at reading slowly and deliberately in the service of preparing pieces; some read single lines, and others can read many lines simultaneously, as conductors must do when scanning an orchestral score. Some musicians improvise, and

many others do not. Many outstanding musicians are better known for a sense of rhythm than pitch (Buddy Rich, Charlie Watts). Composers tend to excel at a particular style or genre-popular, jazz, classical, film music, hip-hop, countryand a test of classical music ability, for example, would exclude not only many of the best-known composers of our era, but also most of the world's musicians who neither read nor write music. It is also worth noting the manifest lack of a correlation among these abilities. Players (e.g., Arthur Rubinstein) do not typically compose or arrange, and composers do not even necessarily play instruments: the composer Irving Berlin ("White Christmas," "God Bless America") famously was unable to play his own songs.

An adequate theory of musicality must account for all these different ways that musicality presents itself. So far, my list shows a production bias; it does not account for the many individuals who show an intense receptive sensitivity to music. In our studies of individuals with the neurogenetic disorder Williams Syndrome, for example (Levitin et al., 2004), we have seen people who are powerfully moved by music. After listening to sad music, parents report that they stay in a sad mood much longer than typically developing individuals, and, similarly, happy music "lifts them up" and allows them to maintain a positive mood state significantly longer than others. Other examples of people with receptive musicality include disc jockeys, music critics, recording engineers, film music supervisors, and record company talent scouts. Lacking formal musical training or the ability to play an instrument does not necessarily put them at a disadvantage, and yet their professions require various sorts of receptive (perceptual) musical skills. Choreographers and dancers, who set bodily movements to music, may constitute a separate category of crossmodal musical artists with distinct skill sets and neurocognitive processes to support their work.

There also exist individuals with the auditory equivalent of eidetic imagery or photographic memory, what we might call phonographic memory. Some DJs can listen to the briefest excerpt of a musical piece, often 1 s or less, and identify the title, composer, and performers and distinguish several different performances of the same piece by the same group. DJs can introduce new connections between music we might not otherwise notice and introduce us to new music we might not otherwise discover. The connection, for example, between the Baroque composer Foscarini and the classic rock band Led Zeppelin only becomes apparent when Foscarini's "Toccata in E" is played back to back with Led Zeppelin's "Gallows Pole" (the rhythms, articulation, and chords are hauntingly close, despite being separated by 350 years). To discover these connections, a person requires a detailed musical memory coupled with the ability to extract certain elements of the music. While hearing one song, the listener must be consciously or unconsciously searching a vast mental repertoire of music to find a template match for chords, melodies, rhythms, timbres, or other component features, while performing mental transpositions to place them into equivalent keys and tempi (Levitin, 2006). Recognizing these sorts of musical connections is not something that all musicians and not even all great musicians can do.

It has been suggested that the primary purpose of music is to convey emotion, and this must also be considered in evaluating musicality. Some musicians are extraordinarily adept at communicating emotions through music, and this becomes especially clear when those musicians lack some of the other attributes we would normally associate with high levels of musical ability. Consider, for example, Bob Dylan and Bruce Springsteen, whose voices convey great emotional depth and nuance to millions of listeners. Both of them lack the beautiful voice and vocal clarity one traditionally associates with singers. Yet, even if they were not great songwriters, Dylan and Springsteen would be known for their ability to convey emotion with their voices.

Another important notion concerns a cluster of attributes surrounding distinctiveness, novelty, and innovativeness. Not all great musicians possess these qualities, but those who do are highly prized in our society and by other musicians. Mozart, Louis Armstrong, and The Beatles are appreciated for these qualities, quite

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apart from the other musical skills they possessed. That is, they were able to bring uncommon amounts of creativity to their music (in spite of the technical limitations that the latter two had as instrumentalists).

Nonmusical Genetic Factors

A number of general cognitive and physical factors are necessary for musical success, such as single mindedness, seriousness, conscientiousness, and goal directedness, qualities that are no doubt required to achieve mastery or expertise in any field (Ericsson and Smith, 1991; Kalbfleisch, 2004). There may well be genetic correlates to these traits. In particular, neural structures mediating these traits and propensities probably have genetic underpinnings, and yet the genetic basis needs to be triggered environmentally by exposure to music, access to musical instruments, and some combination of internal and external positive reinforcement. The data favor gene × environment (G x E) interactions (e.g. Hyde et al., 2011) and the changing role of genes in childhood. In this regard, genes may predict who will benefit from which kinds of training, and what kinds of interventions will modulate gene expression. The interaction between parenting interventions and the DRD4 gene-associated with novelty seeking, effortful control, and dopaminergic function-may be a good starting point (Posner et al., 2011).

Part of the difficulty in distinguishing "nature" from "nurture" with music is that the child raised in a musical household-regardless of her genotype-is almost certainly apt to receive more musical input, feedback, and encouragement than the child raised in a nonmusical household. Although young children clearly start out with widely different musical abilities and interests, their actual achievements correlate most significantly with practice, hard work, and time on task, not with observed early potential. Self-reports of world-class musicians, as well as experimental studies, point strongly to the view that practice accounts for a significant proportion of the variance in who becomes an expert musician and who does not (Howe et al., 1998).

What factors cause some children to practice more than others? Some are no doubt genetic, such as goal directedness, self-confidence, reflexes, finger speed, motor coordination, auditory memory, and auditory structuring abilities. Others are environmental, including having a teacher or family member who encourages or motivates the child and having access to musical stimulation and musical instruments. There may also exist individual differences in the capacity for forging neural connections and building up mental schemas (what Donald Hebb termed "Intelligence A") that could serve to increase the chances that an individual will become a successful musician. General intelligence, an ability to practice. and exposure to music may account for a good deal of the variance in who becomes a professional musician and who does not.

Amusia

An adequate, overarching theory of musicality should account for the entire range of abilities observed in the population, including those at the low end of the spectrum. A small percentage of the population appears to lack musical ability or sensitivity, and this condition of amusia has been known for over a century. In the popular press, the terms tone deafness and tin-ear syndrome have also been used. However, the amusias comprise a heterogeneous set of disabilities with distinct etiologies, sometimes present from birth and sometimes acquired following injury, disease, or other organic trauma. Some individuals simply cannot identify songs; a self-reported sufferer, Ulysses S. Grant, quipped, "I only know two tunes: one of them is 'Yankee Doodle' and the other one isn't." Others retain identification ability but cannot sing in tune, producing abnormal variability in the tones they generate. Some individuals have an inability to detect a single aberrant note falling outside of a musical key. This is believed to be associated with abnormal gray and white matter in the auditory cortex and inferior frontal cortex. Based on one small aggregation study, such "wrong note" detection appears to have a hereditary component (Peretz et al., 2007). Specific deficits in rhythm, pitch, and timbre have also been observed, as a result of either brain injury or congenital defect. The characterization of amusia remains an active area of research.

Quantifying Musicality and the Future of Music Phenotyping

The most commonly used musical assessment tests over the last century have been based on Seashore's standardized tests (Seashore, 1919). These are narrowly focused on perception, although there is no firm evidence that perception and production are correlated. Moreover, the tests allow no opportunity for the test taker to demonstrate individuality, emotion, or creativity. In one module of the test, for example, individuals listen to a sequence of tones that play a simple melody. A second sequence is played, and students simply have to answer whether the two sequences are "same" or "different." As the test progresses, the sequences become increasingly difficult. A parallel version is administered in which musical rhythms are presented.

The chief psychometric problem is that many individuals who would be considered musical (e.g., those making a living as professional orchestral musicians) only score in the middle range of the Seashore tests, while many without musical training or externally observable ability do very well on them. On three of six Seashore items, professional symphony players scored below the 50th percentile, making their performance indistinguishable from that of nonmusicians. Correlations between standardized musical aptitude tests and real-world musical achievement are consistently low. I believe that in an effort to control stimuli and reduce music to its atomic elements, the makers of standardized tests have removed its essence, its dynamic and emotional nature. In short, they have removed the muse from music.

I argue for a new approach that is both broader based and more naturalistic. Because such research is still in its infancy, I advocate casting a wide net: an inclusive approach to capture as many musical behaviors as possible in initial studies of understanding what it means to be musical.

To begin with, we need to be more sensitive to the variety of ways that assessing musicality can present itself, such as in production and perception, and technically and emotionally. Assessments need to allow for spontaneity and creativity. Consider the ways that musicians evaluate one another: it is not



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through objective yes/no testing, but through auditions and a process of subjective evaluation. After a century of cognitive psychology and psychophysics embracing objective methods as the gold standard, I believe the time is right to reintroduce the opinions and ratings of qualified observers. As Justice Potter Stewart might have said, we may not be able to define musicality, but we know it when we hear it. Subjective evaluations, properly done with blind coding and tests of interrater reliability, can yield repeatable and rigorous results and have greater real-world validity.

Musicality can also be evaluated for individuals who are not players. Disc jockeys already compile demonstration tapes to exhibit their ability to create meaningful playlists and segues. Potential music critics are given assignments, and their work output is evaluated by more experienced critics and editors. The future of music phenotyping should allow for inclusive definitions of musicality, with subjective ratings made by experienced professionals according to replicable scoring guidelines.

Designing a suitable test would ideally recruit the involvement of experts from music perception and cognition, education, performance, statistics, and psychometrics. It would involve several steps:

- (1) Cataloguing those behaviors that we regard as musical. A partial list might include: (a) Playing a musical instrument or singing; (b) Composing; (c) Arranging and orchestrating music; (d) Conducting; (e) Programming music for aesthetic purposes or for finding connections between songs (disc jockeys, film supervisors); (f) Great receptive sensitivity to music and its emotional content; (g) Ability to detect out-of-tune or out-of-key notes; (h) Crossmodal practices, such as writing about or choreographing music.
- (2) Creating test items and batteries that tap into these behaviors.
- (3) Creating a set of guidelines by which performance can be assessed by qualified, independent judges.
- (4) Performing standard psychometric test construction operations, such

- as test-retest reliability, interrater reliability, face validity, and construct validity.
- (5) Cataloguing objective measures of success that one might use to correlate the items of (1) above. Examples include being a member of a world-class symphony orchestra, winning awards (such as the Polar Prize, Grammy Awards, or the Gershwin Prize), or having the respect of peers. The validity of the measures of (1) would be supported with such real-world achievements. The point is not that everyone who performs well on the tests will have achieved real-world recognition, but that we would expect that those who have achieved such recognition should do well on the tests (modus ponens).
- (6) Norming the test against a suitable number of participants drawn from a range of musical backgrounds and abilities.
- (7) Conducting factor analysis (or similar data reduction techniques) to uncover latent mathematical relations among variables. Factor analysis will allow the researcher to bind together variables that are intercorrelated, that is, groups of two or more test items that are tapping in to some common, underlying neurocognitive process.
- (8) Association studies should then be conducted on the reduced set of supervariables or orthogonal factors obtained from the previous sten

A comprehensive investigation of the genetic correlates of musicality should also include data from personality and various psychosocial instruments. Of particular interest would be measures of the Big Five Factor Structure, the Tellegen Absorption Scale, the Creativity Achievement Questionnaire, and measures of self-discipline and interpersonal communication, alongside measures of musical engagement and background, such as The Salk and McGill Musical Inventory and the Queens University Musical Experience Questionnaire. Ideally, these should be correlated with scores on the music battery, as well as with genes and neural structures.

The selection and choice of variables for heritability studies should be data driven. Searching for heritability of one supervariable called "music" is too coarse a level of analysis and will miss the many nuances of musicality described above. On the other hand, attempting to correlate genes with every possible behavioral variant is too fine a level of analysis and will obscure any latent unifying or underlying factors that bind together different variables. Association studies should include those nonmusical genetic factors and personality trait variables discussed above.

Furthermore, it is important to use large samples in order to avoid false positives that may arise from the enormous number of genes involved compared to the sample size of individuals (Robbins and Kousta, 2011). Also important are independent replications and family-based association methods in which genetic differences both within and between families are used (Ebstein et al., 2010). The subsequent narrowing of criteria should be data driven, and the distinctions or correlations between musical potential and musical achievement will ideally be revealed in the data. Such an approach should allow researchers to remain alert to the presence of endophenotypes that may arise from psychological, neurochemical, or biological bases. As with any other complex trait, music is likely to be the result of thousands of small-effect loci, which together can produce significant heritability quotients.

Targeting Genes

A study of the genetics of dance (Bachner-Melman et al., 2005) found evidence for involvement of the AVPR1a (vasopressin) gene, which had been previously shown to mediate affiliative, social, and courtship behaviors, learning and memory, and, interestingly, pain sensitivity. In addition, significant differences were found between dancers and nondancers in the serotonin transporter SLC6A4, which had previously been shown to play a role in spiritual experiences. Moreover, SLC6A4 enhances the release of vasopressin in the brain, creating a link between the two genes and their expression in professional dancers and suggesting epistasis, or gene-gene interactions.

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The vasopressin gene has also been implicated in musical activities (Ukkola-Vuoti et al., 2011). AVPR1a was shown to be associated with listening behavior and audio structuring ability. Highly significant epistatic interactions have also been observed between promoter region polymorphisms in the AVPR1a and SLC6A4 genes and musical memory (Ebstein et al., 2010). Future studies would be well advised to study genes that encode for oxytocin (OXTR), a neuropeptide with a pervasive role in mammalian social behaviors, including empathy, and with a known association with the AVPR1a gene.

AVPR1a has been linked to anxiety and depression, and the connection between musical creativity and these traits is well known. Taken together, this suggests a role for AVPR1a as part of a putative genetic basis for both creativity and the artistic temperament.

Linking genetic polymorphisms to personality variables is an area of active research. Data from these investigations should be brought to bear on the question of identifying candidate genes for musicality to the extent that those personality variables are discovered to be linked to the musical phenotype.

Conclusions

In summary, musicality is polymorphic. It is a complex interaction of physical, emotional, cognitive, and psychosocial traits, including some that are overtly "musical" and others that are not but that contribute to musicality in a variety of supporting ways. Musicality presents as both productive and receptive ability, and skill can manifest itself as primarily technical, cognitive, intuitive, or emotional, or in various combinations. If research is to provide an adequate account of how music, genes, environment, and neural development interact, it must embrace the full variety of musical experiences and contexts (Sloboda, 2008).

Studies of the genetics of music promise both practical and theoretical benefits. They can help in music education through identifying those students with high potential in specific areas of musical endeavor and can ultimately help teachers to select the most efficient instructional methods based on a student's background and aptitudes. The important theoretical promise is in identifying and learning to measure component musical abilities more accurately so that musical behaviors can be correctly linked to genetics, to brain structures, and to other, nonmusical behaviors. In this latter case, there has been great interest in the question of cognitive transfer, that is, whether "music makes you smarter" (e.g., Kraus and Chandrasekaran, 2010). Questions such as these would benefit by a fractionating of musical ability, so that we can know which aspects of music correlate specifically with which other cognitive abilities. Finally, more accurately quantifying the musical phenotype is a necessary precursor to performing rigorous genetic studies.

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