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Evaluating predisposition and training in shaping the musician's brain: the need for a developmental perspective

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Abstract

The study of music training as a model for structural plasticity has evolved significantly over the past 15 years. Neuroimaging studies have identified characteristic structural brain alterations in musicians compared to nonmusicians in school-age children and adults, using primarily cross-sectional designs. Despite this emerging evidence and advances in pediatric neuroimaging techniques, hardly any studies have examined brain development in early childhood (before age 8) in association with musical training, and longitudinal studies starting in infancy or preschool are particularly scarce. Consequently, it remains unclear whether the characteristic "musician brain" is solely the result of musical training, or whether certain predispositions may have an impact on its development. Moving toward a developmental perspective, the present review considers various factors that may contribute to early brain structure prior to the onset of formal musical training. This review introduces a model for potential neurobiological pathways leading to the characteristic "musician brain," which involves a developmental interaction between predisposition and its temporal dynamics, environmental experience, and training-induced plasticity. This perspective illuminates the importance of studying the brain structure associated with musical training through a developmental lens, and the need for longitudinal studies in early childhood to advance our understanding of music training-induced structural plasticity.

Keywords

music training; neuroplasticity; neuroimaging; development; early childhood

Music training as a model for structural plasticity

Decades of research has focused on uncovering the impact of musical training on perception, cognition, and brain plasticity. Musical training has been viewed as an optimal model to study training-induced or experience-dependent brain plasticity due to a musician's intensive

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long-term dedication to training in auditory, somatosensory, and motor domains.[1–5] While the influence of musical training on perception, cognition, and brain plasticity was studied primarily with behavioral and electrophysiological methods in the 1980s and 1990s,[6–11] advances in magnetic resonance imaging (MRI) have made it possible to study brain structure with improved spatial resolution. Employing these techniques, numerous studies have reported structural brain characteristics associated with musical training predominantly in adults,[12] with some isolated evidence in children ages 5–11.[13–16] While several of these studies report correlations between onset of musical training or intensity of musical training and certain aspects of brain structure,[17–19] only a few studies to date have longitudinally examined training-induced structural plasticity in childhood, with one study examining 7–9 year-old children[16] and a few others ranging from 5 to 6 years of age.[13,15,16] Although the field has gained valuable insight from these isolated findings, more studies are needed and there have yet to be longitudinal investigations of children from younger than age 5 utilizing MRI methods to investigate the developmental trajectories of brain structure in (subsequent) musicians compared to nonmusicians. This is currently a major limitation of the field, since observations are primarily made based on one specific period of time in brain development, without an understanding of the genetic and environmental factors *in utero*, infancy, and early childhood that may give rise to some underlying components of the brain characteristics identified as the “musician brain” in middle childhood/adolescence or adulthood.

In this perspective, we will summarize the structural alterations associated with musical training, examine potential predispositions and their temporal dynamics, and propose a working model that postulates a developmental interaction between predisposition, environment, and training-induced plasticity, which shapes the development of musical aptitude/skills and their underlying brain characteristics. While various behavioral and functional neuroimaging studies have been examining the development of musical skills in infants and young children,[20–28] the present review primarily focuses on the need for studies to characterize the developmental trajectories of the often-reported structural alterations in musicians from infancy to middle childhood. Since brain structure has been shown to precede function developmentally in infancy and early childhood[29,30] during the time when functional networks are first initiated, working to disentangle the impact of potential predispositions from training-induced plasticity on brain structure seems to be an important starting point. Ultimately, this review will make an argument for the significance of utilizing a developmental perspective and longitudinal designs to advance our understanding of the impact of musical training on brain structure. Discerning the relative contributions of potential factors in early childhood in shaping subsequent brain development has the potential to not only inform our understanding of the impact of musical training on brain plasticity, but also to provide implications for educational and clinical approaches to facilitating brain development in early childhood.

Structural brain alterations in musicians

Cross-sectional neuroimaging studies in adults have revealed differences in brain structure when comparing musicians to nonmusicians.[12] Gray matter differences, including structural asymmetry, have been identified in several brain regions engaged during musical training, particularly in auditory,[31–36] sensorimotor,[5,9,37–40] premotor/motor,[5,17,41] and visual-spatial areas.[32,35] In addition, these differences have been observed in regions facilitating auditory–motor integration.[42] Diffusion-weighted imaging has also revealed white matter differences between musicians and nonmusicians in terms of tract volume and fractional anisotropy (FA),[43] an indicator of tract diffusivity based on how restricted water diffusion is perpendicular to the dominant orientation of the tract.[44] Significant group differences have been repeatedly identified in the corpus callosum, a major fiber tract connecting left and right hemispheres. These findings suggest that musical training may be associated with greater interhemispheric connectivity.[13,15,18,39,45–48] Musical training has also been linked with auditory and motor-related white matter pathways, which in the auditory domain include the arcuate fasciculus[49] and superior longitudinal fasciculus.[50,51] Motor-related tracts include the corticospinal tract[39,51–53] and internal capsule;[39,40,47] however, mixed findings have been observed within these tracts.

Despite advances in pediatric neuroimaging methods,[54] only a handful of studies have conducted structural neuroimaging in childhood. Structural differences have been shown among 7–11 year-old children with musical training compared to those without, in which musically trained children have shown greater gray matter volume in predominantly right-hemispheric auditory and premotor regions, as well as bilateral sensorimotor regions.[13,14] In addition to these cross-sectional comparisons, a few key longitudinal investigations of training-induced structural plasticity have been conducted with children from 5 to 11 years of age.[13–16]

Training-induced structural plasticity in musicians

The few longitudinal neuroimaging studies in school-age children and adults have demonstrated changes in brain structure following musical training. Specifically, training-induced structural changes have been shown among young school-age children following 1–2 years of instrumental musical training.[13,15] Relative to 5–7 year-old children who received only music education classes provided in the general school curriculum, age-matched children engaged in instrumental training over the course of 1 year demonstrated structural brain changes in several brain regions, particularly right-hemispheric primary auditory and premotor cortices, and the corpus callosum.[13] Another longitudinal study in 6-year-olds characterized brain structure following 2 years of musical training and also observed changes in auditory regions in terms of cortical thickness, and enhanced FA in the corpus callosum.[15] A different study focused solely on the auditory cortex did not observe significant structural changes over 1 year of musical training in 7–9 year-old children; however, significantly greater functional responses to auditory stimuli were shown to emerge over the training period.[16] In addition, white matter plasticity has been observed following short-term, targeted training, as adults engaged in left-handed, music-cued motor training showed FA increases in the right arcuate fasciculus after just 4 weeks.[55]

Considering the evidence for training-induced structural plasticity, recent research has examined whether there may be a developmental timeframe in which musical training may have the greatest impact on brain structure; that is, whether there may be a sensitive period for musical training.[56] Indeed, a “critical” age of 7 has been suggested,[45] but the underlying developmental framework for suggesting this specific age as being critical remains under-developed in these studies. Various aspects of brain structure have been associated with the age of onset of musical training among adult musicians.[17–19] Specifically, greater gray matter volume in the right prefrontal cortex has been shown to relate to the age of onset of musical training.[19] In terms of white matter, enhanced FA in the corpus callosum has been shown in musicians who started training before the age of 7 compared to those who started after,[18,45] and this has shown a significant relationship with the age of onset of musical training.[18] These findings bring forth implications that musical training in early childhood, during a time of rapid brain development and heightened brain plasticity, may play a significant role in shaping brain structure. However, it also illustrates the need for further research, as these retrospective studies have only inquired about the age of onset of musical training among adults, after several years of musical training. This study design precludes investigation of factors that may influence whether a child has an early start to musical training. Longitudinal studies are needed that track children developmentally from younger than age 7 so that the proposed notion of a sensitive period can be critically examined, the length of the period quantified, and developmental trajectories characterized. Yet, it remains unclear how these brain characteristics develop in early childhood and whether certain predispositions or temporal dynamics of gene expression may shape the observed alterations or facilitate the observed plasticity in response to musical training over time.

Overall, longitudinal studies have demonstrated structural changes following musical training, and one question of great interest to the field has been whether these changes may transfer to nonmusical skill development as well. Neuroimaging findings support the notion that musical training induces neuroplasticity in several brain regions and networks known to be involved in cognitive/perceptual processing, in domains such as speech,[57–59] language,[60–62] reading,[16] and higher order cognitive processing.[63–65] Numerous longitudinal studies investigating behavior and corresponding brain function have suggested that musical training may support certain aspects of academic achievement.[25,26,28,64,65] However, among the training studies investigating structural plasticity, those that included behavioral measures did not observe any changes in cognitive, language, or literacy skills corresponding to the structural changes observed.[13,16] At this time, the specificity of the findings has yet to be established and it remains questionable whether these effects reflect improvements that may transfer to nonmusical domains, particularly given the fact that far transfer effects are very rare in the cognitive domain.[66,99] Investigation of links between brain and behavior carries potential implications for musical training as a tool to consider in approaches to early intervention and rehabilitation. However, more studies with rigorous longitudinal designs in the behavioral domain are needed in order to determine if, and if so, the extent to which musical training leads to long-lasting, impactful far-transfer effects. A developmental approach offers the potential to spark more research on the functional implications of training-induced plasticity, and how this changes over the developmental trajectory, considering the period of heightened plasticity during early childhood.

Are the brain alterations observed in musicians solely explainable by training-induced plasticity?

A critical question that remains is to what extent the brain alterations observed in musicians compared to nonmusicians are exclusively the result of musical training, or whether these alterations may be influenced by additional contributing factors. Cross-sectional evidence hinges on the notion that the structural differences between musicians and nonmusicians observed are a reflection of the (formal) musical training participants have undertaken. Therefore, it is presumed that prior to musical training, the subsequent musicians and nonmusicians started with similar structural characteristics; that is, a "clean slate." A few training studies investigating brain structure confirmed that there were no structural differences between participants who subsequently commenced musical training and those in the other groups.[15,55,67] However, the notion of a "clean slate" continues to be challenged. For instance, these studies have only examined aspects of brain structure relevant to the specific study design employed. Meanwhile, emerging evidence suggests that neural predispositions may predict subsequent rates of learning music. A neuroimaging study in adults examined whether white matter structure prior to the onset of music training may predict subsequent learning speed in adults without previous musical experience.[51] A positive relationship was observed between the bilateral corticospinal tract and right superior longitudinal fasciculus with the speed of learning to play short piano melodies over the course of 3 training days.[51] Thus, white matter variability prior to training related to subsequent piano learning speed. In line with this finding, one functional MRI study observed that the neural correlates of melody perception and imagery within the right auditory cortex and subcortical regions predicted the speed of learning following a short piano training in adults.[68] These studies point toward the significance of possible predispositions for a "musician brain."

In order to disentangle the impact of potential predispositions from training-induced plasticity, developmental neuroimaging studies with longitudinal designs are needed that start prior to the onset of formal musical training. There is currently a lack of evidence characterizing early structural development, though numerous longitudinal studies have employed electrophysiological methods to characterize changes in brain function over the course of musical training in early childhood and revealed enhanced auditory-evoked potentials in preschool[20,21] and school-age children.[22,24–26,69] One of the studies in preschool-age children revealed pretraining differences in brain function, such that children in the musical training group demonstrated larger auditory-evoked potentials both before and after training relative to the control group.[20] Moreover, functional changes in response to musical engagement have even been observed within the first year of life, as 6-month-old infants have demonstrated enhanced neural responses to musical tones following 6 months in active music classes relative to infants passively exposed to music while playing with toys.[23] Thus, the importance of measuring brain development well before the start of formal musical training in early childhood is evident. This evidence suggests that there may be structural predispositions that may affect subsequent musical experience, yet the corresponding brain structure in early childhood remains unspecified. Experimental designs employed in the majority of the structural literature preclude determination of whether the differences observed between musicians and nonmusicians are exclusively the direct result of musical training, or whether additional factors, including temporal dynamics of gene expression, may play a role in shaping the neuroarchitecture observed. Therefore, the remainder of this perspective will consider the potential factors that could give rise to neural predispositions in early childhood.

Developmental interactions between predisposition and training: potential factors that shape the brain characteristics associated with musical training

Converging evidence brings forth a working hypothesis that the structural brain differences observed between musicians and nonmusicians are not solely explainable by training-induced plasticity; rather, a developmental interaction between predisposition and experience may shape musical development and its accompanying brain characteristics in all, or at least some, children. This suggests that brain structure in early childhood sets a foundation upon which ongoing experience and training further modifies. Therefore, this developmental working hypothesis warrants careful consideration of genetic, environmental, and neural factors and their respective interactions that may contribute to early brain structure prior to the onset of formal musical training.

A propensity for musical training has been indicated by measures of musical potential and linked with aspects of early cognitive and brain development. "*Musicality*," as defined by Gingras and colleagues, is the capacity for music perception and production regardless of formal training experience.[70] This construct has long been characterized in early childhood by measures of music aptitude,[71] which have been positively linked with cognitive-linguistic skills prior to the onset of formal musical training in school-age children.[67,72] Music aptitude has also shown associations with gray matter volume in primary auditory cortex, particularly in the right hemisphere, prior to the onset of musical training in school-age children.[16] These findings suggest that musicality may be related to neural characteristics associated with musical training before formal training has even commenced. Thus, evidence points toward the significance of examining potential factors in early childhood that may shape the observed characteristics associated with musical training.

Curiosity pertaining to the biological basis of musical potential has led to investigation of the potential role of genetics. Genetic variation has been put forth as a factor that may significantly impact musical potential and drive to commit to musical training,[73] as links between genetic variation and measures of music aptitude have been observed.[74,75] However, the field of genetics has uncovered the complexity of genetic interactions such that singular genes do not specify one particular behavior.[70] Rather, gene expression is an intricate and critical molecular process that regulates the development and functioning of cells and tissues in the human brain.[76] It is hypothesized that certain susceptibility genes and the pathways they regulate or interact with may shape neurobiological factors that make an individual more receptive to intensive training in music. This is reflected in work by Schlaug and colleagues, who hypothesized that the structural alterations associated with absolute pitch musicians, specifically hemispheric asymmetries, may be established *in utero* and further develop with early exposure to music.[77] Recent advances in genetic methods have identified that a "genetic blueprint" plays a critical role in early brain development, such as shaping the microstructure of the brain or establishing neural connections.[78] Therefore, genetic investigation has the potential to uncover whether there may be variant function/temporal dynamics in a combination of genes that lead to differences in gray matter microstructure or white matter myelination in regions that may be especially receptive to experience, for example, in the form of musical training. Pursuit of this work with a developmental focus is critical, as gene expression in the developing brain has revealed that temporal dynamics of the transcriptome are most rich and complex *in utero* compared to subsequent postnatal development.[76] We urge the field to take a multidimensional, multimodal view to the study of structural brain plasticity following musical training.

One other important dimension to consider is the role of the environment in shaping early brain development, which may consequently impact predispositions for success with musical training. For instance, socioeconomic status plays a significant role in the quality of education and access to resources, which may influence the pursuit of musical training. Families with a higher socioeconomic status, as determined by higher family income and education levels, are more often able to provide the resources and financial supports that are necessary to pursue musical training.[79] Moreover, socioeconomic status has been shown to have a critical impact on early brain development,[80] in bilateral networks that overlap with regions associated with musical training, particularly auditory regions. This may also be due to genetic–environmental covariation, as genetic polymorphisms have been shown to modulate the environmental impact on genetic expression. For instance, varying socioeconomic environmental conditions have shown differential alterations in gene expression.[81] These findings call for further investigation of the role that environmental aspects such as socioeconomic status may play in shaping early neural predispositions and providing access to subsequent musical training.

Environmental aspects related to parent support, home environment, and enculturation also encompass potentially significant contributing factors. After all, the pursuit of musical training in early childhood may often be initiated and/or encouraged by the children's parents.[82] Numerous behavioral studies have investigated how parental factors may relate to children's musical experience, such as the musical background of parents[20] and parental personality traits.[82] In addition, the musical environment and exposure to music in early childhood have been suggested to play a role in children's subsequent musical pursuits.[20] Another relevant factor to consider is the culture-specific representations of music that are acquired through every day musical exposure, known as the process of enculturation.[83] Infants have shown a preference for music of their own culture,[84] and early exposure to culture-specific musical structure among Western infants has been shown to lead to specialized neural responses to Western musical tones within the first year of life.[23] Future studies are needed to link these music-related environmental factors to brain structure in early childhood, as this has yet to be investigated.

Introducing a model for potential neurobiological pathways leading to the “musician brain”

Taking into consideration the developmental factors that may play a role in shaping musicality and brain structure, here, we introduce a working model of the potential neurobiological pathways leading to the characteristic “musician brain” (Fig. 1), which is intended to stimulate future neurodevelopmental research in the field. Evidence suggests that musical training leads to either broad alterations in brain organization (e.g., corpus callosum), reorganization of specific brain regions that are engaged during musical engagement (e.g., motor, auditory, etc.), or an interaction of both over the course of training. Subsequently, musical training induces neuroplasticity in various functional and structural brain networks impacting other cognitive/perceptual skills such as speech, language, reading, and executive functioning abilities.[57,85,86] While a growing body of evidence supports these aspects of the model, the role of genetic and environmental factors in early development remains understudied (framed in yellow in the figure). Variation in specific genes and their temporal dynamics that play critical roles in early brain development may possibly establish certain structural predispositions that make the brain more receptive to music. These variations in genes critical to brain development may also support the development of perceptual/cognitive skills, which could explain some of the correlational effects observed between music and various perceptual/cognitive skills. In addition, it is possible that the neurodevelopmental changes observed over the course of musical training may not occur (solely) due to training-induced plasticity, but may be shaped by training-independent genetic effects that emerge over time. Advances in the research of the transcriptome in the human brain have shown variability of gene expression across different brain structures and systematic changes throughout development, particularly in childhood.[76] This is often overseen in studies that examine brain plasticity following musical training. This critique of the current methodology is independent of whether groups do not show differences in behavioral or neural measures at the onset of training.

Various environmental factors in early childhood are known to shape brain development within regions implicated in musical training, such as the impact of someone’s socioeconomic status on bilateral auditory regions.[80] This illuminates the importance of including nonmusical environmental experiences in our view of the pathways leading to the “musician brain.” Another likely possibility that should be considered in this context is genetic–environmental interactions, where the efficacy of training is moderated by genetic factors. Developmental studies are needed to determine how these early aspects may play a role in shaping the trajectory of brain development, and how these brain regions are then specifically altered through musical exposure, engagement, and formal training. To fill the missing links in the literature to date, see Table 1 for a starting point of recommendations to consider when designing future studies, employing a developmental perspective.

Approaching this work from a developmental perspective also has the potential to further our understanding of clinical applications of the brain plasticity induced by musical training. This could be particularly beneficial for clinical populations in facilitating traditional neural pathways, or establishing alternative neural networks. Rehabilitative potential has already been demonstrated, for instance, in case studies of stroke patients with speech areas impacted who have been shown to develop greater volume in the right-hemispheric arcuate fasciculus following Melodic Intonation Therapy (a singing-based speech therapy).[87,88] Through a developmental lens, emerging evidence has examined relationships between music and developmental disorders such as autism spectrum disorder and developmental dyslexia.[89,90] Broad reorganization of brain structure putatively shaped by musical training may enable protective or compensatory neural mechanisms that underlie the positive effects of music observed; yet, this remains understudied.

Overall, our field has the potential to address remaining gaps in our understanding by investigating the impact of musical training on the brain through a developmental lens in future studies. In the present perspective, we have put forth a model of the potential neurobiological pathways associated with musical training. Consideration of the ways in which early childhood experiences and predispositions may shape subsequent outcomes will lead us to a better understanding of the ways in which music plays a role in brain development and clinical applications of training-induced plasticity through a musical lens.

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References

1. Jäncke L. The plastic human brain. Restor Neurol Neurosci. 2009; 27:521–538. [PubMed: 19847074]
2. Munte TF, Altenmuller E, Jancke L. The musician's brain as a model of neuroplasticity. Nat Rev Neurosci. 2002; 3:473–478. [PubMed: 12042882]
3. Wan CY, Schlaug G. Music making as a tool for promoting brain plasticity across the life span. Neuroscientist. 2010; 16:566–577. [PubMed: 20889966]
4. Zatorre R, McGill J. Music, the food of neuroscience? Nature. 2005; 434:312–315. [PubMed: 15772648]
5. Schlaug G. The brain of musicians. A model for functional and structural adaptation. Ann NY Acad Sci. 2001; 930:281–299. [PubMed: 11458836]
6. Steele KM, et al. Prelude or requiem for the 'Mozart effect'? Nature. 1999; 400:827–828. [PubMed: 10476959]
7. Samson S, Zatorre RJ. Contribution of the right temporal lobe to musical timbre discrimination. Neuropsychologia. 1994; 32:231–240. [PubMed: 8190246]
8. Koelsch S, Schroger E, Tervaniemi M. Superior pre-attentive auditory processing in musicians. Neuroreport. 1999; 10:4.
9. Elbert T, Pantev C, Wienbruch C, et al. Increased cortical representation of the fingers of the left hand in string players. Am Assoc Adv Sci. 1995; 270:3.
10. Tervaniemi M, et al. Functional specialization of the human auditory cortex in processing phonetic and musical sounds: a magnetoencephalographic (MEG) study. Neuroimage. 1999; 9:330–336. [PubMed: 10075902]
11. Zatorre RJ, Beckett C. Multiple coding strategies in the retention of musical tones by possessors of absolute pitch. Mem Cognit. 1989; 17:582–589.
12. Herholz SC, Zatorre RJ. Musical training as a framework for brain plasticity: behavior, function, and structure. Neuron. 2012; 76:486–502. [PubMed: 23141061]
13. Hyde KL, et al. Musical training shapes structural brain development. J Neurosci. 2009; 29:3019–3025. [PubMed: 19279238]

14. Schlaug G, Norton A, Overy K, Winner E. Effects of music training on the child's brain and cognitive development. Ann NY Acad Sci. 2005; 1060:219–230. [PubMed: 16597769]
15. Habibi A, , et al. Childhood music training induces change in micro and macroscopic brain structure: results from a longitudinal study. Cereb Cortex. 2017. https://doi.org/10.1093/cercor/bhx286
16. Seither-Preisler A, Parncutt R, Schneider P. Size and synchronization of auditory cortex promotes musical, literacy, and attentional skills in children. J Neurosci. 2014; 34:10937–10949. [PubMed: 25122894]
17. Amunts K, et al. Motor cortex and hand motor skills: structural compliance in the human brain. Hum Brain Mapp. 1997; 5:206–215. [PubMed: 20408216]
18. Steele CJ, Bailey JA, Zatorre RJ, Penhune VB. Early musical training and white-matter plasticity in the corpus callosum: evidence for a sensitive period. J Neurosci. 2013; 33:1282–1290. [PubMed: 23325263]
19. Bailey JA, Zatorre RJ, Penhune VB. Early musical training is linked to gray matter structure in the ventral pre-motor cortex and auditory–motor rhythm synchronization performance. J Cogn Neurosci. 2014; 26:755–767. [PubMed: 24236696]
20. Shahin A, Roberts LE, Trainor LJ. Enhancement of auditory cortical development by musical development in children. Neuroreport. 2004; 15:1917–1921. [PubMed: 15305137]
21. Fujioka T. One year of musical training affects development of auditory cortical-evoked fields in young children. Brain. 2006; 129:2593–2608. [PubMed: 16959812]
22. Kraus N, et al. Music enrichment programs improve the neural encoding of speech in at-risk children. J Neurosci. 2014; 34:11913–11918. [PubMed: 25186739]
23. Trainor LJ, Marie C, Gerry D, et al. Becoming musically enculturated: effects of music classes for infants on brain and behavior. Ann NY Acad Sci. 2012; 1252:129–138. [PubMed: 22524350]
24. Habibi A, Cahn BR, Damasio A, Damasio H. Neural correlates of accelerated auditory processing in children engaged in music training. Dev Cogn Neurosci. 2016; 21:1–14. [PubMed: 27490304]
25. Chobert J, Francois C, Velay JL, Besson M. Twelve months of active musical training in 8- to 10-year-old children enhances the preattentive processing of syllabic duration and voice onset time. Cereb Cortex. 2014; 24:956–967. [PubMed: 23236208]
26. Moreno S, et al. Musical training influences linguistic abilities in 8-year-old children: more evidence for brain plasticity. Cereb Cortex. 2009; 19:712–723. [PubMed: 18832336]
27. Trehub SE, Hannon EE. Conventional rhythms enhance infants' and adults' perception of musical patterns. Cortex. 2009; 45:110–118. [PubMed: 19058799]
28. Francois C, Chobert J, Besson M, Schon D. Music training for the development of speech segmentation. Cereb Cortex. 2012; 23:2038–2043. [PubMed: 22784606]
29. Saygin ZM, et al. Connectivity precedes function in the development of the visual word form area. Nat Neurosci. 2016; 19:1250–1255. [PubMed: 27500407]
30. Dehaene-Lambertz G, Spelke ES. The infancy of the human brain. Neuron. 2015; 88:93–109. [PubMed: 26447575]
31. Schneider P, et al. Morphology of Heschl's gyrus reflects enhanced activation in the auditory cortex of musicians. Nat Neurosci. 2002; 5:688–694. [PubMed: 12068300]
32. Gaser C, Schlaug G. Gray matter differences between musicians and nonmusicians. Ann NY Acad Sci. 2003; 999:514–517. [PubMed: 14681175]
33. Gaser C, Schlaug G. Brain structures differ between musicians and non-musicians. J Neurosci. 2003; 23:9240–9245. [PubMed: 14534258]
34. Bermudez P, Lerch JP, Evans AC, Zatorre RJ. Neuroanatomical correlates of musicianship as revealed by cortical thickness and voxel-based morphometry. Cereb Cortex. 2009; 19:1583–1596. [PubMed: 19073623]
35. Foster NE, Zatorre RJ. Cortical structure predicts success in performing musical transformation judgments. Neuroimage. 2010; 53:26–36. [PubMed: 20600982]
36. Jancke L, Schlaug G, Huang Y, Steinmetz H. Asymmetry of the planum parietale. Neuroreport. 1994; 5:1161–1163. [PubMed: 8080979]

37. Chen JL V, Penhune B, Zatorre RJ. Listening to musical rhythms recruits motor regions of the brain. Cereb Cortex. 2008; 18:2844–2854. [PubMed: 18388350]
38. Chen JL V, Penhune B, Zatorre RJ. Moving on time: brain network for auditory–motor synchronization is modulated by rhythm complexity and musical training. J Cogn Neurosci. 2008; 20:226–239. [PubMed: 18275331]
39. Bengtsson SL, et al. Extensive piano practicing has regionally specific effects on white matter development. Nat Neurosci. 2005; 8:1148–1150. [PubMed: 16116456]
40. Han Y, et al. Gray matter density and white matter integrity in pianists' brain: a combined structural and diffusion tensor MRI study. Neurosci Lett. 2009; 459:3–6. [PubMed: 18672026]
41. Bangert M, Schlaug G. Specialization of the specialized in features of external human brain morphology. Eur J Neurosci. 2006; 24:1832–1834. [PubMed: 17004946]
42. Zatorre RJ, Chen JL, Penhune VB. When the brain plays music: auditory–motor interactions in music perception and production. Nat Rev Neurosci. 2007; 8:547–558. [PubMed: 17585307]
43. Moore E, Schaefer RS, Bastin ME, et al. Can musical training influence brain connectivity? Evidence from diffusion tensor MRI. Brain Sci. 2014; 4:405–427. [PubMed: 24961769]
44. Pierpaoli C, Jezzard P, Basser PJ, et al. Diffusion tensor MR imaging of the human brain. Radiology. 1996; 201:637–648. [PubMed: 8939209]
45. Schlaug G, Jancke L, Huang Y, et al. Increased corpus callosum size in musicians. Neurospsychologia. 1995; 33:1047–1055.
46. Schlaug G, Forgeard M, Zhu L, et al. Training-induced neuroplasticity in young children. Ann NY Acad Sci. 2009; 1169:205–208. [PubMed: 19673782]
47. Schmithorst VJ, Wilke M. Differences in white matter architecture between musicians and non-musicians: a diffusion tensor imaging study. Neurosci Lett. 2002; 321:57–60. [PubMed: 11872256]
48. Elmer S, Hanggi J, Jancke L. Interhemispheric transcallosal connectivity between the left and right planum temporale predicts musicianship, performance in temporal speech processing, and functional specialization. Brain Struct Funct. 2016; 221:331–344. [PubMed: 25413573]
49. Halwani GF, Loui P, Ruber T, Schlaug G. Effects of practice and experience on the arcuate fasciculus: comparing singers, instrumentalists, and non-musicians. Front Psychol. 2011; 2:156. [PubMed: 21779271]
50. Oechslin MS, Imfeld A, Loenneker T, et al. The plasticity of the superior longitudinal fasciculus as a function of musical expertise: a diffusion tensor imaging study. Front Hum Neurosci. 2009; 3:76. [PubMed: 20161812]
51. Engel A, et al. Inter-individual differences in audio–motor learning of piano melodies and white matter fiber tract architecture. Hum Brain Mapp. 2014; 35:2483–2497. [PubMed: 23904213]
52. Imfeld A, Oechslin MS, Meyer M, et al. White matter plasticity in the corticospinal tract of musicians: a diffusion tensor imaging study. Neuroimage. 2009; 46:600–607. [PubMed: 19264144]
53. Ruber T, Lindenberg R, Schlaug G. Differential adaptation of descending motor tracts in musicians. Cereb Cortex. 2015; 25:1490–1498. [PubMed: 24363265]
54. Raschle N, Zuk J, Ortiz-Mantilla S, et al. Pediatric neuroimaging in early childhood and infancy: challenges and practical guidelines. Ann NY Acad Sci. 2012; 1252:43–50. [PubMed: 22524338]
55. Moore E, Schaefer RS, Bastin ME, et al. Diffusion tensor MRI tractography reveals increased fractional anisotropy (FA) in arcuate fasciculus following music-cued motor training. Brain Cogn. 2017; 116:40–46. [PubMed: 28618361]
56. Penhune VB. Sensitive periods in human development: evidence from musical training. Cortex. 2011; 47:1126–1137. [PubMed: 21665201]
57. Patel AD. Why would musical training benefit the neural encoding of speech? The OPERA hypothesis. Front Psychol. 2011; 2:142. [PubMed: 21747773]
58. Patel AD. Can nonlinguistic musical training change the way the brain processes speech? The expanded OPERA hypothesis. Hear Res. 2014; 308:98–108. [PubMed: 24055761]
59. Weiss MW, Bidelman GM. Listening to the brainstem: musicianship enhances intelligibility of subcortical representations for speech. J Neurosci. 2015; 35:1687–1691. [PubMed: 25632143]

60. Magne C, Schon D, Besson M. Musician children detect pitch violations in both music and language better than nonmusician children: behavioral and electrophysiological approaches. J Cogn Neurosci. 2006; 18:199–211. [PubMed: 16494681]
61. Moreno S, Besson M. Musical training and language-related brain electrical activity in children. Psychophysiology. 2006; 43:287–291. [PubMed: 16805867]
62. Wong PCM, Skoe E, Russo NM, et al. Musical experience shapes human brainstem encoding of linguistic pitch patterns. Nat Neurosci. 2007; 10:420–422. [PubMed: 17351633]
63. Zuk J, Benjamin C, Kenyon A, Gaab N. Behavioral and neural correlates of executive functioning in musicians and non-musicians. PLoS One. 2014; 9:e99868. [PubMed: 24937544]
64. Sachs M, Kaplan J, Der Sarkissian A, Habibi A. Increased engagement of the cognitive control network associated with music training in children during an fMRI Stroop task. PLoS One. 2017; 12:e0187254. [PubMed: 29084283]
65. Moreno S, et al. Short-term music training enhances verbal intelligence and executive function. Psychol Sci. 2011; 22:1425–1433. [PubMed: 21969312]
66. Noack H, Lovden M, Schmiedek F. On the validity and generality of transfer effects in cognitive training research. Psychol Res. 2014; 78:773–789. [PubMed: 24691586]
67. Norton A, et al. Are there pre-existing neural, cognitive, or motoric markers for musical ability? Brain Cogn. 2005; 59:124–134. [PubMed: 16054741]
68. Herholz SC, Coffey EB, Pantev C, Zatorre RJ. Dissociation of neural networks for predisposition and for training-related plasticity in auditory–motor learning. Cereb Cortex. 2016; 26:3125–3134. [PubMed: 26139842]
69. Kraus N, Hornickel J, Strait DL, et al. Engagement in community music classes sparks neuroplasticity and language development in children from disadvantaged backgrounds. Front Psychol. 2014; 5:1403. [PubMed: 25566109]
70. Gingras B, Honing H, Peretz I, et al. Defining the biological bases of individual differences in musicality. Philos Trans R Soc B Biol Sci. 2015; 370:20140092.
71. Gordon EE. All about audition and music aptitudes. Music Educ J. 1999; 86:41–44.
72. Schellenberg EG. Music lessons enhance IQ. Psychol Sci. 2004; 15:511–514. [PubMed: 15270994]
73. Mosing MA, Madison G, Pedersen NL, et al. Practice does not make perfect: no causal effect of music practice on music ability. Psychol Sci. 2014; 25:1795–1803. [PubMed: 25079217]
74. Drayna D, Manichaikul A, de Lange M, et al. Genetic correlates of musical pitch recognition in humans. Science. 2001; 291:1969–1972. [PubMed: 11239158]
75. Ullen F, Mosing MA, Holm L, et al. Psychometric properties and heritability of a new online test for musicality, the Swedish Musical Discrimination Test. Personal Individ Differ. 2014; 63:87–93.
76. Naumova OY, Lee M, Rychkov SY, et al. Gene expression in the human brain: the current state of the study of specificity and spatiotemporal dynamics. Child Dev. 2013; 84:76–88. [PubMed: 23145569]
77. Keenan JP, Thangaraj V, Halpern AR, Schlaug G. Absolute pitch and planum temporale. Neuroimage. 2001; 14:1402–1408. [PubMed: 11707095]
78. Bae BI, Jayaraman D, Walsh CA. Genetic changes shaping the human brain. Dev Cell. 2015; 32:423–434. [PubMed: 25710529]
79. Schellenberg EG. Long-term positive associations between music lessons and IQ. J Educ Psychol. 2006; 98:457–468.
80. Noble KG, et al. Family income, parental education and brain structure in children and adolescents. Nat Neurosci. 2015; 18:773–778. [PubMed: 25821911]
81. Cole SW. Social regulation of human gene expression. Curr Dir Psychol Sci. 2009; 18:132–137. [PubMed: 21243077]
82. Corrigall KA, Schellenberg EG. Predicting who takes music lessons: parent and child characteristics. Front Psychol. 2015; 6:282. [PubMed: 25852601]
83. Hannon EE, Trainor LJ. Music acquisition: effects of enculturation and formal training on development. Trends Cogn Sci. 2007; 11:466–472. [PubMed: 17981074]

84. Soley G, Hannon EE. Infants prefer the musical meter of their own culture: a cross-cultural comparison. Dev Psychol. 2010; 46:286–292. [PubMed: 20053025]
85. Kraus N, Chandrasekaran B. Music training for the development of auditory skills. Nat Rev Neurosci. 2010; 11:599–605. [PubMed: 20648064]
86. Diamond A, Lee K. Interventions shown to aid executive function development in children 4 to 12 years old. Science. 2011; 333:959–964. [PubMed: 21852486]
87. Schlaug G, Marchina S, Norton A. Evidence for plasticity in white-matter tracts of patients with chronic Broca's aphasia undergoing intense intonation-based speech therapy. Ann NY Acad Sci. 2009; 1169:385–394. [PubMed: 19673813]
88. Zipse L, Norton A, Marchina S, Schlaug G. When right is all that is left: plasticity of right-hemisphere tracts in a young aphasic patient. Ann NY Acad Sci. 2012; 1252:237–245. [PubMed: 22524365]
89. Rolka EJ, Silverman MJ. A systematic review of music and dyslexia. Arts Psychother. 2015; 46:24–32.
90. Simpson K, Keen D. Music interventions for children with autism: narrative review of the literature. J Autism Dev Disord. 2011; 41:1507–1514. [PubMed: 21203898]
91. Dreyer BP, Mendelsohn AL, Tamis-LeMonda CS. [Accessed on March 21, 2018] StimQ Cognitive Home Environment. 2001. https://med.nyu.edu/pediatrics/developmental/research/belle-project/stimq-cognitive-home-environment
92. Barratt W. [Accessed on March 21, 2018] The Barratt simplified measure of social status (BSMSS): measuring SES. 2006. http://socialclassoncampus.blogspot.com/2012/06/barratt-simplified-measure-of-social.html
93. Mehr S. Music in the home: new evidence for an intergenerational link. J Res Music Educ. 2014; 62:78–88.
94. Gordon E. A factor analysis of the musical aptitude profile, the primary measures of music audiation, and the intermediate measures of music audiation. Bull Counc Res Music Educ. 1986; 87:17–25.
95. Peretz I, et al. A novel tool for evaluating children's musical abilities across age and culture. Front Syst Neurosci. 2013; 7:30. [PubMed: 23847479]
96. Law LN, Zentner M. Assessing musical abilities objectively: construction and validation of the profile of music perception skills. PLoS One. 2012; 7:e52508. [PubMed: 23285071]
97. Zentner M, Strauss H. Assessing musical ability quickly and objectively: development and validation of the Short-PROMS and the Mini-PROMS. Ann NY Acad Sci. 2017; 1400:33–45. [PubMed: 28704888]
98. Bailey JA, Penhune VB. Rhythm synchronization performance and auditory working memory in early- and late-trained musicians. Exp Brain Res. 2010; 204:91–101. [PubMed: 20508918]
99. Sala G, Gobet F. When the music's over. Does music skill transfer to children's and young adolescents' cognitive and academic skills? A meta-analysis. Educ Res Rev. 2017; 20:55–67.

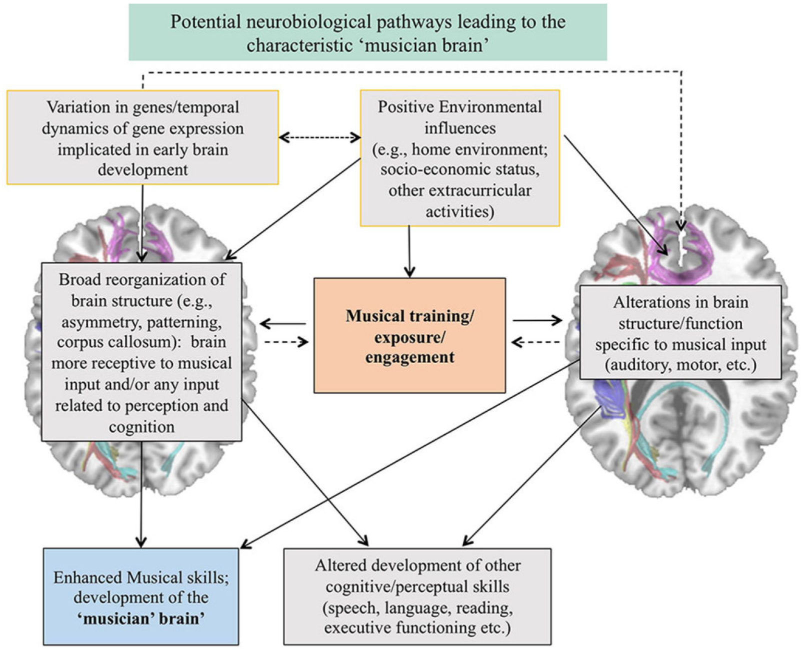

Figure 1.

A working model outlining potential neurobiological pathways that can lead to the characteristic "musician brain." Boxes outlined in yellow remain especially understudied. Solid lines represent pathways supported by empirical evidence; dashed lines represent possible pathways that warrant further investigation.

Table 1

Recommendations for study design, methods, and group classification for future investigations employing a developmental perspective

Recommendations for investigations with a developmental focus	
Study design	• Longitudinal designs that track brain and behavioral development starting in infancy/early childhood • Employ multimodal experimental techniques to further uncover structural–functional relationships and examine functional implications of this work • Examine gene expression of typical and atypical development through studies of the transcriptome in the brain, particularly in childhood • Seek to disentangle genetic and environmental contributions to musical skill, aptitude, and brain plasticity (which will have important implications beyond the music cognition field) • Examine intergenerational transmission of brain structure
Methods	• Whole-genome expression analyses in the developing brain (e.g., DNA microarrays, sequencing techniques for gene expression profiling, for more, see a review by Naumova and colleagues[76]) • Questionnaires that document: – The home environment (e.g., StimQ to measure a family's cognitive home environment[91]) – Socioeconomic status (e.g., Barratt Simplified Measure of Social Status[92]) – Informal music exposure and experiences (e.g., surveys employed in recent publications[20,93]) – Family musical background[20] • Establish and validate measures that characterize: – The music environment of infants, toddlers, and preschoolers – Motivation to train in music/growth mindset/attitudes toward musical training – Intergenerational musicality • Measure musical aptitude in children at a young age and in their family members (e.g., Gordon's Measures of Music Audiation,[94] The Montreal Battery of Evaluation of Musical Abilities,[95] and The Profile of Music Perception Skills[96,97])
Group classification	• Acquire details of musical training (e.g., length of training, age of onset of training, frequency of practice, instruments studied, etc.) • Consider utilizing established questionnaires for detailed documentation, such as the Musical Experience Questionnaire[98]

NOTE: These recommendations are offered as a starting point of examples to consider in future study design.