

117. Yi, C. X. *et al.* Ventromedial arcuate nucleus communicates peripheral metabolic information to the suprachiasmatic nucleus. *Endocrinology* **147**, 283–294 (2006).
118. Malek, Z. S., Sage, D., Pevet, P. & Raison, S. Daily rhythm of tryptophan hydroxylase-2 messenger ribonucleic acid within raphe neurons is induced by corticoid daily surge and modulated by enhanced locomotor activity. *Endocrinology* **148**, 5165–5172 (2007).
119. He, Y. *et al.* The transcriptional repressor DEC2 regulates sleep length in mammals. *Science* **325**, 866–870 (2009).
120. Maywood, E. S., O'Neill, J. S., Chesham, J. E. & Hastings, M. H. Minireview: the circadian clockwork of the suprachiasmatic nuclei — analysis of a cellular oscillator that drives endocrine rhythms. *Endocrinology* **148**, 5624–5634 (2007).
121. Godinho, S. I. *et al.* The after-hours mutant reveals a role for *Fbxl3* in determining mammalian circadian period. *Science* **316**, 897–900 (2007).
122. Dijk, D. J. & Archer, S. N. *PERIOD3*, circadian phenotypes, and sleep homeostasis. *Sleep Med. Rev.* **14**, 151–160 (2010).
123. Reghunandanan, V. & Reghunandanan, R. Neurotransmitters of the suprachiasmatic nuclei. *J. Circadian Rhythms* **4**, 2 (2006).

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Competing interests statement

The authors declare no competing financial interests.

DATABASES

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SCIENCE AND SOCIETY

Music training for the development of auditory skills

Nina Kraus and Bharath Chandrasekaran

Abstract | The effects of music training in relation to brain plasticity have caused excitement, evident from the popularity of books on this topic among scientists and the general public. Neuroscience research has shown that music training leads to changes throughout the auditory system that prime musicians for listening challenges beyond music processing. This effect of music training suggests that, akin to physical exercise and its impact on body fitness, music is a resource that tones the brain for auditory fitness. Therefore, the role of music in shaping individual development deserves consideration.

Through years of sensory-motor training, often beginning in early childhood, musicians develop an expertise in their instrument or mastery over their voice¹. In the course of training, musicians increasingly learn to attend to the fine-grained acoustics of musical sounds. These include pitch, timing and timbre, the three basic components into which any sound that reaches the human ear — including music or speech — can be broken down². Pitch refers to the organization of sound on an ordered scale (low versus high pitch) and is a subjective percept of the frequency of the sound. Timing refers to specific landmarks in the sound (for example, the onset and offset of the sound) and timbre refers to the quality of the sound — a multidimensional attribute that results from the spectral and

temporal features in the acoustic signal. Attention to these components is emphasized during music training. For example, a violinist is trained to pay particular attention to pitch cues to effectively tune the violin, an instrumentalist playing in an orchestra has to have a keen sense of timing cues and a conductor needs to rely on timbre cues to differentiate the contribution of various instruments.

There is now evidence that music training induces changes in the brain. Indeed, the musician's brain has been used as a model of neuroplasticity^{3,4}. Early studies investigated how music training primes the brain for processing musical sounds and examined the extent to which such plasticity is specific to processing musical sounds^{1,4,5}. These studies revealed that music training induces

functional and structural changes in the auditory system⁶. For example, compared to non-musicians, pianists show increased neural activity (measured by magnetic source imaging) in the auditory cortex in response to hearing piano notes⁷. The strength of neuronal activation to piano notes was found to correlate with the age at which piano training began and with the number of years of music training. This suggests that enhanced functional plasticity reflects experience and is not merely a reflection of innate differences between musicians and non-musicians.

Musicians also show structural differences in the brain relative to non-musicians^{8,9}, with larger grey matter volume in areas that are important for playing an instrument. These areas include motor, auditory and visuo-spatial regions⁸. In addition, musical aptitude correlates with the volume of the primary auditory cortex and with neurophysiological responses to sinusoidal tones in this area⁹. Moreover, musicians show enhanced electrophysiological responses in the auditory cortex to contour and interval information in melodies¹⁰, and in the auditory brainstem¹¹ when listening to musical intervals.

Notably, many of these studies used correlational data to infer that functional and structural differences between the brains of musicians and non-musicians are a consequence of years of experience with music. However, causality cannot be derived from correlational analysis — the differences could reflect pre-existing genetic differences between the two groups. To address this issue, longitudinal studies have been conducted in which children were randomly assigned to music training and then periodically assessed over time^{12,13}. Compared with children who were assigned to art training, children who underwent music training showed enhanced brain responses to subtle pitch changes in musical stimuli¹³. Fifteen months of intense music training has also been shown to induce structural changes in the primary auditory and primary motor areas¹². These structural changes were associated with improved auditory and motor skills, respectively. Taken together, these data suggest that music training can cause functional and structural changes in the brain throughout our lifetimes, and that these changes may improve music processing.

Transfer effects

The impact of music training on the neural processing of music has now been well documented¹⁴. However, are the changes in a musician's brain specific to music processing

or do they transfer to other domains that involve the processing of pitch, timing and timbre cues? Below, we describe data that support the view that the fine-grained auditory skills of musicians, which are acquired through years of training, percolate to other domains, such as speech, language, emotion and auditory processing⁶. Thus, music training improves auditory skills that are not exclusively related to music^{15–18,22,60,62,64}.

Music and speech are perceptually distinct but share many commonalities at both an acoustic and cognitive level. At the acoustic level, music and speech use pitch, timing and timbre cues to convey information². At a cognitive level, music and speech processing require similar memory and attention skills, as well as an ability to integrate discrete acoustic events into a coherent perceptual stream according to specific syntactic rules¹⁹. Musicians show an advantage in processing pitch, timing and timbre of music compared with non-musicians²⁰. Music training also involves a high working-memory load, grooming of selective attention skills and implicit learning of the acoustic and

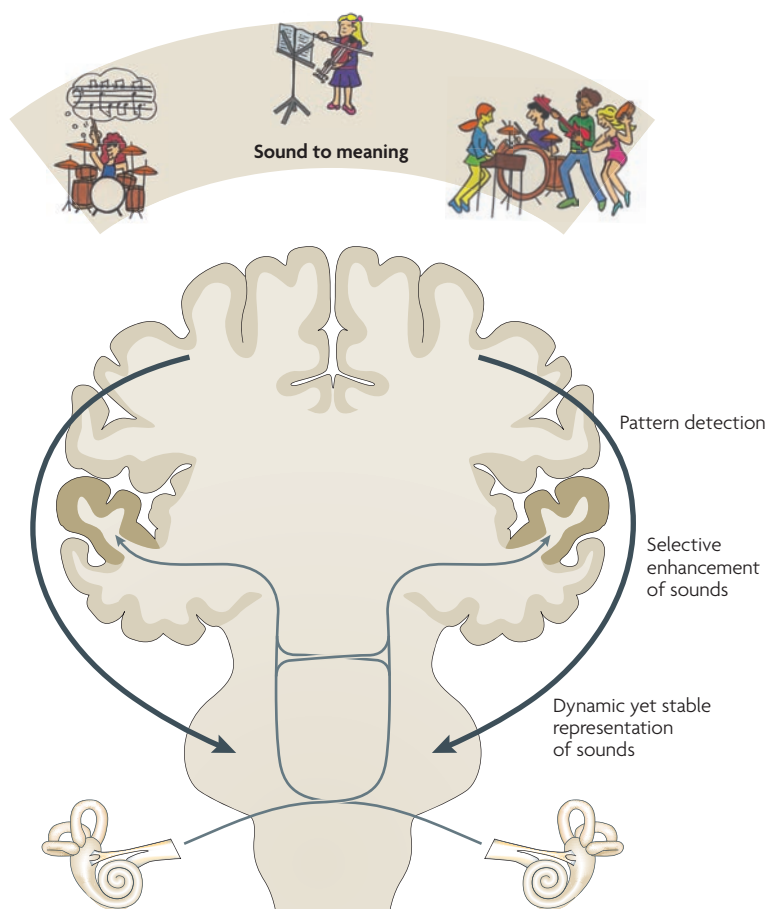
syntactic rules that bind musical sounds together. These cognitive skills are also crucial for speech processing. Thus, years of active engagement with the fine-grained acoustics of music and the concomitant development of ‘sound to meaning’ connections may result in enhanced processing in the speech and language domains.

Indeed, musicians show enhanced evoked potentials in the cortex and brainstem in response to pitch changes during speech processing compared with non-musicians^{16,21,22}. During speech processing, pitch has extra-linguistic functions (for example, it can help the listener to judge the emotion or intention of a speaker and determine the speaker’s identity²³) as well as a linguistic function (for example, in tone languages, a change in pitch within a syllable changes the meaning of a word). Musicians are also better able to detect small deviations in pitch contours that can determine whether a speaker is producing a statement or a question (demonstrated behaviourally as well as in terms of event-related potentials recorded over the cortex)¹⁶. Furthermore, compared

with non-musicians, musicians show a more faithful brainstem representation (measured using the frequency-following response (FFR)) of linguistic pitch contours in an unfamiliar language^{18,24}. These results suggest that long-term training with musical pitch patterns can benefit the processing of pitch patterns of foreign languages^{21,25}.

Do such transfer effects occur at automatic, pre-attentive (that is, before conscious perception) levels of auditory processing, that is, in the brainstem? Studies in humans and animals show that brainstem auditory processing (BOX1) is shaped by both long-term and short-term experience^{2,20,22,26,27,30,31}. Processing at the level of the brainstem can be non-invasively examined by measuring the onset response and the FFR^{28,29}. Such measurements have shown that the auditory brainstem response to speech reflects the physical properties of sound with such fidelity that when the electrical response recorded from the brainstem is played as a sound file, the response sounds a lot like the stimulus that evoked it^{28,29}. Thus, the onset response and the FFR can be used to

Box 1 | Cognitive–sensory interplay in musicians



Music training is a demanding task that involves active engagement with musical sounds and the connection of ‘sound’ to ‘meaning’, a process that is essential for effective communication through music, language and vocal emotion. Formation of efficient sound-to-meaning relationships involves attending to sensory details that include fine-grained properties of sound (pitch, timing and timbre) as well as cognitive skills that are related to working memory: multi-sensory integration (for example, following and performing a score), stream-segregation (the ability to perceptually group or separate competing sounds), interaction with other musicians and executive function (see the figure, top part). The cognitive–sensory aspects of music training promote neural plasticity and this improves auditory processing of music as well as of other sounds, such as speech (see the figure, lower part). Sound travels from the cochlea to the auditory cortex (shown by light, ascending arrows) via a series of brainstem nuclei that extract and process sound information. In addition, there are feedback pathways (known as the corticofugal network) that connect the cortex to the brainstem and the cochlea in a top-down manner (shown by dark, descending arrows). In musicians, neuroplastic changes have been observed in the auditory cortex as well as in lower-level sensory regions such as the auditory brainstem. The enhanced subcortical encoding of sounds in the brains of musicians compared to non-musicians is probably a result of the strengthened top-down feedback pathways. Active engagement with music improves the ability to rapidly detect, sequence and encode sound patterns. Improved pattern detection enables the cortex to selectively enhance predictable features of the auditory signal at the level of the auditory brainstem, which imparts an automatic, stable representation of the incoming stimulus.

understand how the brain represents pitch, timing and timbre (FIG. 1). These responses originate in the brainstem, but they are influenced by cortical structures via corticofugal feedback pathways³⁰. This feedback ensures top-down cortical influences even at the earliest stages of auditory processing^{20,30,31}.

To determine whether transfer effects occur at subcortical stages of auditory processing, researchers have measured the brainstem responses as musicians and non-musicians hear speech sounds. These studies have revealed that musicians show brainstem plasticity not only for music stimuli but also for speech stimuli²². Specifically, compared with non-musicians, musicians showed superior representation (greater correspondence between stimulus and neural response) of voice pitch cues — including fundamental frequency as well as harmonic components in speech and time-varying components in speech — at the level of the brainstem^{17,22,32}, and superior encoding of linguistic pitch contours^{18,33} (FIG. 1). This suggests that music training causes changes in auditory processing in the subcortical sensory circuitry.

In all of these studies, the neural encoding of sound was positively correlated with the number of years of music training. This, together with longitudinal data^{12,13}, suggests that experience promotes neuroplasticity.

Musicians are also more accurate at judging timbre differences between different instruments, as well as during voice processing³⁴, and auditory brainstem responses from musicians show faster neural responses to the onset of, and to other acoustic landmarks in, the speech sounds that reflect the dynamic transition from a consonant to a vowel^{17,22}.

There has been considerable interest and controversy in relation to the effects of musical experience on general cognitive abilities. Although there are indications that music training can enhance cognitive ability³⁵, the extent and specificity — whether the changes are due to music training per se or to the cognitive effort involved in music training — of such improvements are still unclear^{36–38} and warrant further research. Issues such as these make the use of pre-attentive neural indices²⁸ (FIG. 1) particularly enticing, as these neural measures do not require active participation or cognitive engagement from participants. Indeed, the auditory brainstem response to sound can be collected even when an individual is sleeping or engaged in another task (for example, watching a subtitled movie). Thus, the auditory brainstem response reflects the current state of the nervous system

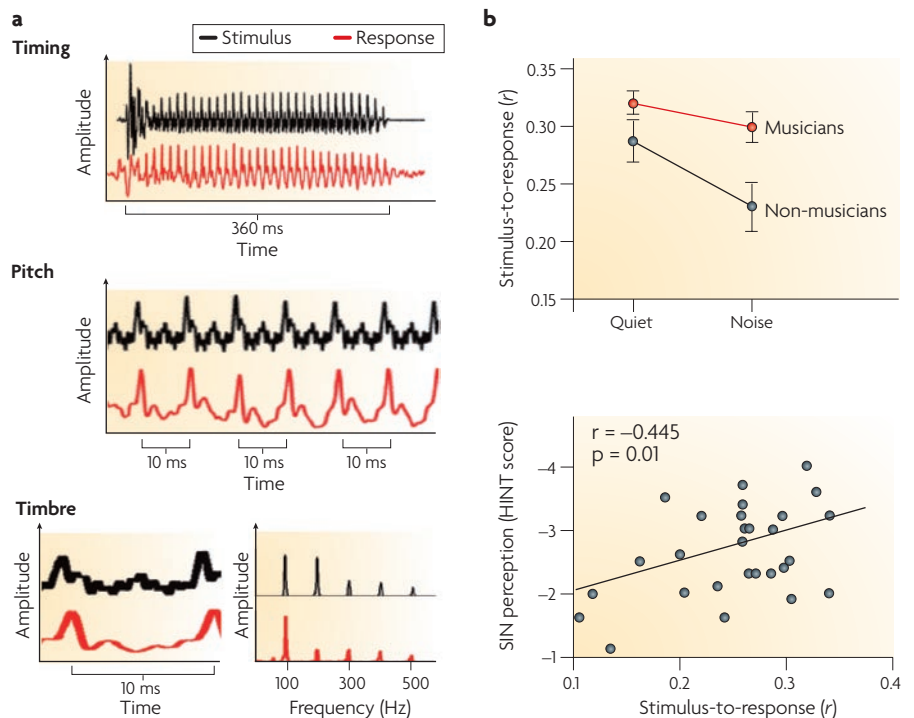


Figure 1 | Neural representation of pitch, timing and timbre in the human auditory brainstem.

Timing, pitch and timbre are the basic information-bearing elements in music and speech. The auditory brainstem response represents a faithful reconstruction of these features and can be recorded in a non-invasive manner in human participants. **a** | The auditory brainstem response to a speech sound can be studied in the time domain as changes in amplitude across time (top, middle and bottom-left panels) and in the spectral domain as spectral amplitudes across frequency (bottom-right panel). The auditory brainstem response reflects acoustic landmarks in the speech signal with submillisecond precision in timing and phase-locking that corresponds to (and physically resembles) pitch and timbre information in the stimulus. Here, a speech stimulus (/da/) and the brainstem response to this stimulus are shown by black and red traces, respectively. **b** | A comparison of stimulus-to-response correlations in musicians and non-musicians. In musicians and non-musicians the brainstem response is positively correlated with the entire speech stimulus. However, when the stimulus is presented in the presence of background noise, musicians represent the sound features more faithfully than non-musicians (top panel). More faithful stimulus-to-response correlations in musicians are functionally relevant; individuals who had higher correlations between the stimulus and the brainstem response to the stimulus in the presence of background noise exhibited better speech-in-noise (SIN) perception in standardized tests (for example, the Hearing in Noise Test (HINT)) (bottom panel). Part **b**, top panel is reproduced, with permission, from REF. 17 © (2009) Society for Neuroscience. Part **b**, bottom panel, data from REF. 17.

— the state at that time, formed by an individual's life experience with sound. Through examination of this neural index in musicians (in comparison with a control group of non-musicians), we can examine auditory processing in the absence of attention or working-memory confounds.

Selective enhancement in the brain

The effect of music training on brain plasticity is not just a 'volume-knob effect' — not every feature of the auditory signal improves to the same extent — but leads to the fine-tuning of auditory signals that are salient (with 'sound to meaning' significance) (FIG. 2). Musicians, compared with non-musicians, more effectively represent the most meaningful, information-bearing

elements in sounds — for example, the segment of a baby's cry that signals emotional meaning³⁹, the upper note of a musical chord^{11,40} or the portion of the Mandarin Chinese pitch contour that corresponds to a note along the diatonic musical scale³³. Furthermore, musicians show improvements in auditory verbal memory and auditory attention, but not in visual memory or visual attention^{41,38}. Thus, music training induces an enhancement of the processing of auditory signals, the characteristics of which depend on the nature of the training (for example, conductors show superior peripheral spatial auditory processing relative to pianists⁴²), on the practice strategies (for example, musicians who learn 'by ear' show superior auditory encoding of musical

sounds relative to those who rely on non-aural strategies⁴³) and on behavioural relevance (for example, the upper note, which often carries the melody in Western music and evokes a stronger neural response in musicians, or the emotion-bearing segment of a baby's cry) (FIG. 2).

A brain wired to regularities

An adaptive auditory system is primed to extract sound regularities in a predictive manner⁴⁴. The ability to extract statistical regularities in soundscapes probably underlies the well-described statistical learning processes that the brain uses to segment linguistic and non-linguistic inputs^{44,45,56}. For example, we are able to track a friend's voice (a predictable regularity) in a noisy restaurant that has plenty of competing voices. Adaptive sensory processing is especially beneficial in challenging listening conditions, when the incoming auditory information is noisy or unreliable⁴⁶. The typical auditory

system is capable of extracting regularities in the signal implicitly, even without the need for conscious attention⁴⁴. Subcortical enhancement of stimulus regularities accompanies success with linguistic tasks, such as reading and hearing speech in noise⁵⁶.

Through training, musicians learn to pick out sound objects from a complex soundscape, and this improves their ability to track regularities in the environment⁴⁴. Selective enhancement of the sound stimulus in the musician's brain (FIG. 2) may result from a superior ability to encode predictable, relevant events in the incoming sensory stream^{14,17,44,47}. Higher-level cognitive areas assess the relevance and predictability of information-bearing elements in an auditory signal, and these elements are subsequently represented with greater fidelity (greater stimulus-to-response correspondence) in the auditory system via feedback loops^{46,48} that are provided by corticofugal pathways (BOX 1). In this way, aspects of the signal

that are deemed to be important may be enhanced, whereas irrelevant information is suppressed⁴⁶.

Differences between musicians and non-musicians in the ability to extract relevant information from the incoming signal have been studied using the mismatch negativity (MMN) as an index. An MMN occurs when the brain detects a change (or violation) in a predictable auditory stream (for example, a rarely presented 'oddball' in the context of a frequently occurring and predictable sound event). Detection of a change in pattern requires a strong neural representation of the predictable stimulus. The magnitude of the MMN response has been shown to closely reflect a person's auditory perceptual ability, that is, a larger MMN reflects a greater perceived distance between two sounds⁴⁴. Musicians show stronger MMN to musical stimuli⁴⁹, to linguistic pitch contours²⁴ (a transfer effect) and to abstract sound features⁵⁰ compared with non-musicians. This indicates that music training may promote an efficient top-down feedback system that is continuously (and automatically) engaged to extract and robustly represent regularities in the auditory system. Consistent with this idea, induced oto-acoustic emissions^{51,52} have revealed evidence that there are stronger efferent (top-down) effects on cochlear biomechanics in musicians than in non-musicians.

There is considerable debate regarding the biological utility of music and the part that music has played in human evolution⁵³⁻⁵⁵. A recent proposal posits that music has an important role in shaping the brain within an individual person's lifespan⁵⁴. According to this proposal, engagement with music induces alterations in the brain and thereby provides a direct biological benefit. Consistent with this proposal, we argue that active engagement with music promotes an adaptive auditory system that is crucial for the development of listening skills. An adaptive auditory system that continuously regulates its activity based on contextual demands is crucial for processing information during everyday listening tasks^{56,62}.

Practical implications

Does a selective enhancement in auditory processing and an improved ability to extract regularities in sounds place musicians at an advantage during everyday listening conditions? Few studies have examined this question, but their results have important practical implications. Musicians are more successful than non-musicians in learning to incorporate sound

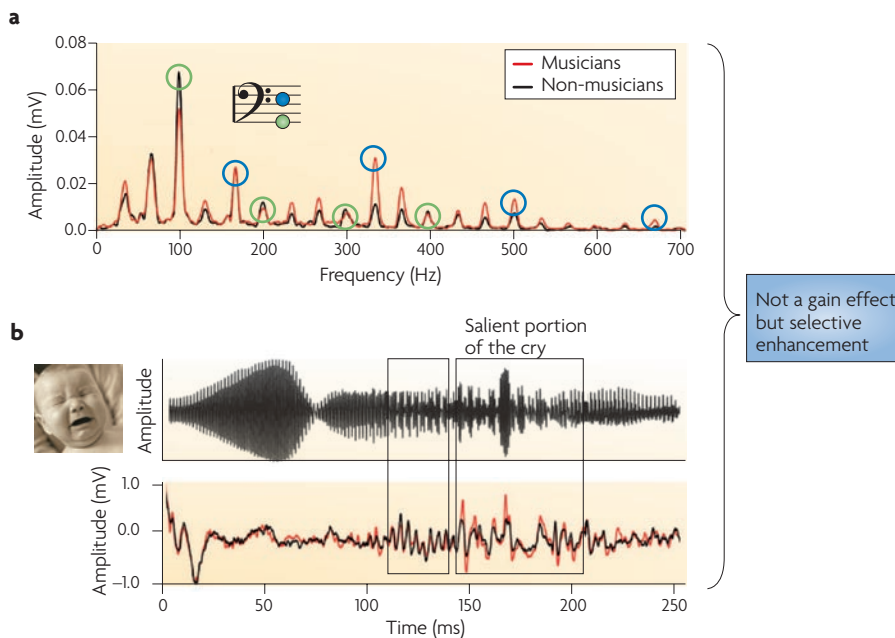


Figure 2 | **Transfer effect and selective enhancement in musicians.** **a** | Ensemble neural responses that are recorded from the auditory brainstem show that compared with non-musicians, musicians show enhanced subcortical representations of music (shown by black and red traces, respectively). The figure shows the response in musicians and non-musicians to hearing a chord. The blue circles depict regions in the spectral domain in which musicians show a stronger response than non-musicians. Importantly, spectral enhancement for musicians is only seen for the upper note, which in Western music often carries the melody. No enhancement is observed for lower notes. The green circles depict lower notes to which musicians show no enhanced response. **b** | Musicians also show an enhanced subcortical representation of non-musical sounds. The response of musicians and non-musicians to hearing a baby cry is shown by red and black traces, respectively. Crucially, the neural enhancement is highly specific and selective. Musicians represent the most complex, salient portion of a child's cry (shown by the box, right) more strongly than the earlier-occurring portion (shown by the box, left). Thus, music training does not confer an overall gain effect but rather selective enhancement of key stimulus features that have sound-to-meaning relationships. Part **a** is reproduced, with permission, from REF. 11 © (2009) Society for Neuroscience. Part **b** is reproduced, with permission, from REF. 32 © (2009) Wiley InterScience.

patterns of a new language into words²⁵. This is likely to be a result of functional and structural brain changes in musicians^{22,57,58}. Furthermore, children who are musically trained show stronger neural activation to pitch patterns of their native language²¹, have a better vocabulary¹⁵ and a greater reading ability^{59,60} compared with children who did not receive music training. This suggests that musicians have an advantage in everyday speech and language tasks. The link between reading ability and auditory skills (for example, in terms of processing time-varying signals, speed of processing and statistical learning) is well-acknowledged^{60,61}. Deficiencies in the neural representation of essential sound elements are associated with poor reading ability^{56,62,63}, whereas this neural representation is enhanced in musicians.

Whether music training provides a benefit in listening to speech during challenging listening environments has also been examined. Speech perception in noise is a challenging task for all individuals, particularly for older adults and young children⁶². For successful perception of speech in noise, individuals must extract relevant signals from other sounds, a task that requires selective attention, sensory representation of sound and various cognitive skills that include auditory stream segregation and voice tagging. Musicians have shown superior performance in each of these skills compared with non-musicians⁶². For example, musicians show better speech-in-noise perception than non-musicians during experiments in which participants had to repeat sentences word-for-word as background noise parametrically increased until the participant was unable to repeat the sentences successfully^{17,64}.

Musicians also show superior working-memory performance, which positively correlates with performance in the speech-in-noise task⁶⁴. In addition, the neural representation of timing and harmonic features of the speech signal in the presence of background noise is stronger in musicians than non-musicians¹⁷ (FIG. 1). Thus, musicians exhibit enhanced cognitive and sensory abilities that give them a distinct advantage for processing speech in challenging listening environments compared with non-musicians. This advantage develops over the lifetime through consistent practice routines⁶⁴ and is enhanced by music training that starts early in life^{7,37,59}. Future research needs to focus on the time frame of the experience-dependent plasticity. Understanding the temporal trajectory of

plastic changes that are induced by music training will allow us to explore the extent and limits of plasticity in the brain.

Implications for education

Studies that compare musicians and non-musicians have identified four determinants of music-training related plasticity: age of training onset⁷, number of years of continuous training^{18,22}, amount of practice⁶⁵ and aptitude⁹. Plasticity is influenced by the extent to which a person actively engages in music training relatively early in their life⁶⁶. The importance of the age of onset of music training can be gleaned from a study that controlled for the number of years of music training and practice⁶⁷. In this study, musicians who began training before the age of 7 showed superior sensory-motor integration (reflected in a motor sequencing task) compared with those who began music training later in life. Neuroplasticity is also determined by the amount of practice, so benefits of music training should occur even in individuals who begin training later in life^{17,22,32}. Aptitude also plays a part, but is not the sole determinant of neuroplasticity. The results of these studies suggest that the benefits of music training may be accessible to everyone and not just to those who show an aptitude towards music. However, in today's society, musicians are often the product of years of private instruction, a luxury that is possible only for a select few. Taking into consideration what we know about the positive effects of music training, it seems imperative that we afford all children an equal opportunity to improve their listening skills through music training.

A large-scale effort to provide music training early in life can only be achieved through the school system. However, there is growing concern in the United States that the quality and extent of music training that is provided at schools is on the decline owing to other curricular demands⁶⁸. It is possible that this trend may impair academic achievement in the long term. However, instruction in music and the time that is spent participating in music events do not hamper academic achievement⁶⁹, and we argue that in fact music training may benefit academic achievement by improving learning skills and listening ability, especially in challenging listening environments. Classrooms, for a variety of reasons, are inherently noisy. There is a strong negative relationship between noise levels in classrooms and academic achievement, even after socio-economic factors have been controlled for⁷⁰. An effective music training

program in schools could reduce the negative influences of external noise⁶² and better prepare a child for everyday listening challenges beyond the challenges that directly relate to music.

Children with learning disorders are particularly vulnerable to the deleterious effects of background noise^{56,62,71–73}. Music training seems to strengthen the same neural processes that are often impaired in individuals with developmental dyslexia or who have

Glossary

Auditory stream segregation

The ability to piece together discrete perceptual events into streams.

Contour and interval information

Aspects of melodic information in music that are related to contour (upward or downward patterns of pitch changes) and interval (pitch distances between successive notes).

Frequency-following response

A neuronal ensemble response that phase-locks to the incoming stimulus.

Fundamental frequency

The lowest frequency of a voice, determined by the rate of vibration of the vocal folds. It generally corresponds to the voice's pitch.

Harmonic components in speech

Aspects of speech that depend on the rate of vibration of the vocal cords. A voice is composed of a fundamental tone and a series of higher frequencies that are called harmonics.

Magnetic source imaging

The detection of the changing magnetic fields that are associated with brain activity, and their subsequent overlaying onto magnetic resonance images to identify the precise source of the signal.

Mismatch negativity

A cortical event-related potential, measured using electroencephalography, that is elicited when a sequence of repeated stimuli (standards) is interrupted by an infrequent stimulus that deviates in sensory characteristics, such as intensity, frequency or duration.

Onset response

A neuronal ensemble response to the onset of sound.

Oto-acoustic emissions

Sounds that are generated in the inner ear, which can be recorded non-invasively. They serve as acoustic signatures of the cochlear biomechanical activity.

Pitch contours

Pitch changes that minimally contrast words in a tone language, such as Mandarin Chinese.

Time-varying components in speech

Dynamically changing acoustic events (for example, formant transitions) that correspond to articulatory changes during speech production.

Voice tagging

The ability to use voice pitch as a cue to 'tag' a familiar talker amid fluctuating background noise.

difficulty hearing speech in noise^{56,62,63,74}. To put this in perspective, music training cannot and should not replace traditional intervention methods for children with learning problems (for example, children with reading difficulties who undergo phonological and/or auditory training). We suggest that, together with traditional remediation approaches, active engagement with music provides a value-added proposition — an enjoyable social experience that improves listening skills. It should be noted that we learn best about things that we care about; therefore, the engagement of the neural circuitry that underlies emotion during music-making is likely to be helpful in this regard^{175,76}.

The data discussed in this article suggest that the role of music training in schools should be reassessed. Research into the effect of music training in schools would also benefit our understanding of brain plasticity. Most of the studies that have been carried out so far have examined musicians who have had years of private instruction. This has provided useful insights, but much remains to be learned. What are the effects of the musical education that is delivered in schools on the nervous system and on learning outcomes? Are musicians predisposed to learning and processing music and other auditory stimuli in a different way to non-musicians? To what extent are the brain changes that are seen in musicians a result of experience-dependent plasticity¹³?

There are some additional issues regarding the effects of music training on the brain that deserve consideration. The considerable diversity in the training and performance profiles of musicians⁷⁷ yields a relatively heterogeneous population of individuals who are often lumped together as a single group of ‘musicians’ in neuroscience studies. This makes it hard to examine the effects of specific forms of music training. In addition, there is a potential selection bias in studies that have compared musicians with non-musicians. It is possible that non-musicians did not continue with music training because they did not experience any training-related benefits, perhaps owing to genetic factors or poor auditory processing abilities. A longitudinal study of children who begin music training as a part of the school curriculum may be an effective way of addressing the issues of innateness and heterogeneity. Further studies should also address the effectiveness of different music training approaches (for example, the Suzuki method, which emphasizes aural learning over sight reading) as well as performance profiles (for example, improvisational versus classical,

instrumental versus vocal learning and solo versus group learning) in determining the effects of music training on brain plasticity.

In conclusion, music training results in structural and functional biological changes throughout our lifetime. Such neuroplasticity not only benefits music processing but also percolates to other domains, such as speech processing. The musician’s brain selectively enhances information-bearing elements of auditory signals — a process that reflects efficient sound-to-meaning relationships — as well as enhancing the extraction of regularities in the signal. Neural changes such as these have practical implications, as they help to prepare people who actively engage with music for the challenges of language learning and everyday listening tasks. The beneficial effects of music training on sensory processing confer advantages beyond music processing itself. This argues for an improvement in the quality and quantity of music training in schools.

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1. Zatorre, R. J., Chen, J. L. & Penhune, V. B. When the brain plays music: auditory–motor interactions in music perception and production. *Nature Rev. Neurosci.* **8**, 547–558 (2007).
2. Kraus, N., Skoe, E., Parbery-Clark, A. & Ashley, R. Experience-induced malleability in neural encoding of pitch, timbre, and timing. *Ann. NY Acad. Sci.* **1169**, 543–557 (2009).
3. Habib, M. & Besson, M. What do music training and musical experience teach us about brain plasticity? *Music Percept.* **26**, 279–285 (2009).
4. Zatorre, R. & McGill, J. Music, the food of neuroscience? *Nature* **434**, 312–315 (2005).
5. Peretz, I. & Zatorre, R. J. Brain organization for music processing. *Annu. Rev. Psychol.* **56**, 89–114 (2005).
6. Hannon, E. E. & Trainor, L. J. Music acquisition: effects of enculturation and formal training on development. *Trends Cogn. Sci.* **11**, 466–472 (2007).
7. Pantev, C. *et al.* Increased auditory cortical representation in musicians. *Nature* **392**, 811–814 (1998).
8. Gaser, C. & Schlaug, G. Brain structures differ between musicians and non-musicians. *J. Neurosci.* **23**, 9240–9245 (2003).
9. Schneider, P. *et al.* Morphology of Heschl’s gyrus reflects enhanced activation in the auditory cortex of musicians. *Nature Neurosci.* **5**, 688–694 (2002).
10. Fujioka, T., Trainor, L. J., Ross, B., Kakigi, R. & Pantev, C. Musical training enhances automatic encoding of melodic contour and interval structure. *J. Cogn. Neurosci.* **16**, 1010–1021 (2004).
11. Lee, K. M., Skoe, E., Kraus, N. & Ashley, R. Selective subcortical enhancement of musical intervals in musicians. *J. Neurosci.* **29**, 5832–5840 (2009).

12. Hyde, K. L. *et al.* Musical training shapes structural brain development. *J. Neurosci.* **29**, 3019–3025 (2009).
13. Moreno, S. *et al.* Musical training influences linguistic abilities in 8-year-old children: more evidence for brain plasticity. *Cereb. Cortex* **19**, 712–723 (2009).
14. Münte, T. F., Altenmüller, E. & Jäncke, L. The musician’s brain as a model of neuroplasticity. *Nature Rev. Neurosci.* **3**, 473–478 (2002).
15. Forgeard, M., Winner, E., Norton, A. & Schlaug, G. Practicing a musical instrument in childhood is associated with enhanced verbal ability and nonverbal reasoning. *PLoS ONE* **3**, e3566 (2008).
16. 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.* **18**, 199–211 (2006).
17. Parbery-Clark, A., Skoe, E. & Kraus, N. Musical experience limits the degradative effects of background noise on the neural processing of sound. *J. Neurosci.* **29**, 14100–14107 (2009).
18. Wong, P. C., Skoe, E., Russo, N. M., Dees, T. & Kraus, N. Musical experience shapes human brainstem encoding of linguistic pitch patterns. *Nature Neurosci.* **10**, 420–422 (2007).
19. Patel, A. D. Language, music, syntax and the brain. *Nature Neurosci.* **6**, 674–681 (2003).
20. Tzounopoulos, T. & Kraus, N. Learning to encode timing: mechanisms of plasticity in the auditory brainstem. *Neuron* **62**, 463–469 (2009).
21. Besson, M., Schon, D., Moreno, S., Santos, A. & Magne, C. Influence of musical expertise and musical training on pitch processing in music and language. *Restor. Neurol. Neurosci.* **25**, 399–410 (2007).
22. Musacchia, G., Sams, M., Skoe, E. & Kraus, N. Musicians have enhanced subcortical auditory and audiovisual processing of speech and music. *Proc. Natl Acad. Sci. USA* **104**, 15894–15898 (2007).
23. Belin, P. Voice processing in human and non-human primates. *Phil. Trans. R. Soc. Lond. B* **361**, 2091–2107 (2006).
24. Chandrasekaran, B. & Kraus, N. The scalp-recorded brainstem response to speech: neural origins and plasticity. *Psychophysiology* **47**, 236–246 (2010).
25. Wong, P. C. M. & Perrachione, T. K. Learning pitch patterns in lexical identification by native English-speaking adults. *Appl. Psycholinguist.* **28**, 565–585 (2007).
26. Song, J. H., Skoe, E., Wong, P. C. & Kraus, N. Plasticity in the adult human auditory brainstem following short-term linguistic training. *J. Cogn. Neurosci.* **20**, 1892–1902 (2008).
27. Krishnan, A., Xu, Y. S., Gandour, J. & Cariani, P. Encoding of pitch in the human brainstem is sensitive to language experience. *Cogn. Brain Res.* **25**, 161–168 (2005).
28. Skoe, E. & Kraus, N. Auditory brain stem response to complex sounds: a tutorial. *Ear Hear.* **31**, 302–324.
29. Galbraith, G. C., Arbage, P. W., Branski, R., Comerci, N. & Rector, P. M. Intelligible speech encoded in the human brain stem frequency-following response. *Neuroreport* **6**, 2363–2367 (1995).
30. Suga, N. Role of corticofugal feedback in hearing. *J. Comp. Physiol. A, Neuroethol. Sens. Neural. Behav. Physiol.* **194**, 169–183 (2008).
31. Suga, N. & Ma, X. Multiparametric corticofugal modulation and plasticity in the auditory system. *Nature Rev. Neurosci.* **4**, 783–794 (2003).
32. Strait, D. L., Kraus, N., Skoe, E. & Ashley, R. Musical experience and neural efficiency: effects of training on subcortical processing of vocal expressions of emotion. *Eur. J. Neurosci.* **29**, 661–668 (2009).
33. Bidelman, G. M., Gandour, J. T. & Krishnan, A. Cross-domain effects of music and language experience on the representation of pitch in the human auditory brainstem. *J. Cogn. Neurosci.* 19 Nov 2009 (doi:10.1162/jocn.2009.21362).
34. Chartrand, J. P. & Belin, P. Superior voice timbre processing in musicians. *Neurosci. Lett.* **405**, 164–167 (2006).
35. Schellenberg, E. G. Music lessons enhance IQ. *Psychol. Sci.* **15**, 511–514 (2004).
36. Schellenberg, E. G. in *The Child as Musician: A Handbook of Musical Development* (ed. McPherson, G. E. E.) 111–134 (Oxford Univ. Press, Oxford, UK, 2006).
37. Schellenberg, E. G. & Peretz, I. Music, language and cognition: unresolved issues. *Trends Cogn. Sci.* **12**, 45–46 (2008).

38. Strait, D., Kraus, N., Parbery-Clark, A. & Ashley, R. Musical experience shapes top-down auditory mechanisms: evidence from masking and auditory attention performance. *Hear. Res.* **261**, 22–29 (2010).
39. Strait, D. L., Kraus, N., Skoe, E. & Ashley, R. Musical experience promotes subcortical efficiency in processing emotional vocal sounds. *Ann. NY Acad. Sci.* **1169**, 209–213 (2009).
40. Fujioka, T., Trainor, L. J., Ross, B., Kakigi, R. & Pantev, C. Automatic encoding of polyphonic melodies in musicians and nonmusicians. *J. Cogn. Neurosci.* **17**, 1578–1592 (2005).
41. Chan, A. S., Ho, Y. C. & Cheung, M. C. Music training improves verbal memory. *Nature* **396**, 128 (1998).
42. Nager, W., Kohlmetz, C., Altenmüller, E., Rodriguez-Fornells, A. & Münte, T. F. The fate of sounds in conductors' brains: an ERP study. *Brain Res. Cogn. Brain Res.* **17**, 83–93 (2003).
43. Seppänen, M., Brattico, E. & Tervaniemi, M. Practice strategies of musicians modulate neural processing and the learning of sound-patterns. *Neurobiol. Learn. Mem.* **87**, 236–247 (2007).
44. Winkler, I., Denham, S. L. & Nelken, I. Modeling the auditory scene: predictive regularity representations and perceptual objects. *Trends Cogn. Sci.* **13**, 532–540 (2009).
45. Saffran, J. R., Aslin, R. N. & Newport, E. L. Statistical learning by 8-month-old infants. *Science* **274**, 1926–1928 (1996).
46. Luo, F., Wang, Q., Kashani, A. & Yan, J. Corticofugal modulation of initial sound processing in the brain. *J. Neurosci.* **28**, 11615–11621 (2008).
47. Trainor, L. J. & Zatorre, R. in *Oxford Handbook of Music Psychology* (eds Hallen, S., Cross, I. & Thaut, M.) 171–182 (Oxford Univ. Press, Oxford, UK, 2009).
48. Suga, N., Xiao, Z., Ma, X. & Ji, W. Plasticity and corticofugal modulation for hearing in adult animals. *Neuron* **36**, 9–18 (2002).
49. Koelsch, S., Schroger, E. & Tervaniemi, M. Superior pre-attentive auditory processing in musicians. *Neuroreport* **10**, 1309–1313 (1999).
50. van Zuijen, T. L., Sussman, E., Winkler, I., Naatanen, R. & Tervaniemi, M. Auditory organization of sound sequences by a temporal or numerical regularity — a mismatch negativity study comparing musicians and non-musicians. *Brain Res. Cogn. Brain Res.* **23**, 270–276 (2005).
51. Brashears, S. M., Morlet, T. G., Berlin, C. I. & Hood, L. J. Olivocochlear efferent suppression in classical musicians. *J. Am. Acad. Audiol.* **14**, 314–324 (2003).
52. Perrot, X., Micheyl, C. & Khalfa, S. Stronger bilateral efferent influences on cochlear biomechanical activity in musicians than in non-musicians. *Neurosci. Lett.* **262**, 167–170 (1999).
53. Fitch, W. T. The biology and evolution of music: a comparative perspective. *Cognition* **100**, 173–215 (2006).
54. Patel, A. D. in *Emerging Disciplines* (ed. Bailar, M.) 91–144 (Rice Univ. Press, Houston, 2010).
55. Pinker, S. *How the Mind Works* (Allen Lane, London, 1997).
56. Chandrasekaran, B., Hornickel, J. M., Skoe, E., Nicol, T. & Kraus, N. Context-dependent encoding in the human auditory brainstem relates to hearing speech in noise: implications for developmental dyslexia. *Neuron* **64**, 311–319 (2009).
57. Wong, P. C., Perrachione, T. K. & Parrish, T. B. Neural characteristics of successful and less successful speech and word learning in adults. *Hum. Brain Mapp.* **28**, 995–1006 (2007).
58. Wong, P. C. et al. Volume of left Heschl's Gyrus and linguistic pitch learning. *Cereb. Cortex* **18**, 828–836 (2008).
59. Overy, K. From timing deficits to musical intervention. *Ann. NY Acad. Sci.* **999**, 497–505 (2003).
60. Tallal, P. & Gaab, N. Dynamic auditory processing, musical experience and language development. *Trends Cogn. Sci.* **29**, 382–390 (2006).
61. Tallal, P. Auditory temporal perception, phonics, and reading disabilities in children. *Brain Lang.* **9**, 182–198 (1980).
62. Chandrasekaran, B. & Kraus, N. Music, noise-exclusion, and learning. *Music Percept.* **27**, 297–306 (2010).
63. Hornickel, J., Skoe, E., Nicol, T., Zecker, S. & Kraus, N. Subcortical differentiation of stop consonants relates to reading and speech-in-noise perception. *Proc. Natl Acad. Sci. USA* **106**, 13022–13027 (2009).
64. Parbery-Clark, A., Skoe, E., Lam, C. & Kraus, N. Musician enhancement for speech-in-noise. *Ear Hear.* **30**, 653–661 (2009).
65. Musacchia, G., Strait, D. & Kraus, N. Relationships between behavior, brainstem and cortical encoding of seen and heard speech in musicians and non-musicians. *Hear. Res.* **241**, 34–42 (2008).
66. Trainor, L. J. Are there critical periods for musical development? *Dev. Psychobiol.* **46**, 262–278 (2005).
67. Watanabe, D., Savion-Lemieux, T. & Penhune, V. The effect of early musical training on adult motor performance: evidence for a sensitive period in motor learning. *Exp. Brain Res.* **176**, 332–340 (2007).
68. Kratus, J. Music education at the tipping point. *Music Educ. J.* **94**, 42 (2007).
69. Kinney, D. W. Selected demographic variables, school music participation, and achievement test scores of urban middle school students. *J. Res. Music Educ.* **56**, 145–161 (2008).
70. Shield, B. M. & Dockrell, J. E. The effects of environmental and classroom noise on the academic attainments of primary school children. *J. Acoust. Soc. Am.* **123**, 133–144 (2008).
71. Sperling, A. J., Lu, Z. L., Manis, F. R. & Seidenberg, M. S. Deficits in perceptual noise exclusion in developmental dyslexia. *Nature Neurosci.* **8**, 862–863 (2005).
72. Ziegler, J. C., Pech-Georgel, C., George, F., Alario, F. X. & Lorenzi, A. J., Lu, Z. L., Manis, F. R. & Seidenberg, M. S. Deficits in speech perception predict language learning impairment. *Proc. Natl Acad. Sci. USA* **102**, 14110–14115 (2005).
73. Ziegler, J. C., Pech-Georgel, C., George, F. & Lorenzi, C. Speech-perception-in-noise deficits in dyslexia. *Dev. Sci.* **12**, 732–745 (2009).
74. Banai, K. et al. Reading and subcortical auditory function. *Cereb. Cortex* **19**, 2699–2707 (2009).
75. Meltzoff, A. N., Kuhl, P. K., Movellan, J. & Sejnowski, T. J. Foundations for a new science of learning. *Science* **325**, 284–288 (2009).
76. Shahin, A. J., Roberts, L. E., Chau, W., Trainor, L. J. & Miller, L. M. Music training leads to the development of timbre-specific gamma band activity. *Neuroimage* **41**, 113–122 (2008).
77. Tervaniemi, M. Musicians — same or different? *Ann. NY Acad. Sci.* **1169**, 151–156 (2009).

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Competing interests statement

The authors declare no competing financial interests.

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