DOI: 10.1111/nyas.14899

ORIGINAL ARTICLE

ANNALS OF THE NEW YORK ACADEMY OF SCIENCES

Short-term plasticity of neuro-auditory processing induced by musical active listening training

Peter Schneider[1,2,3,4] | Christine Groß[1,3] | Valdis Bernhofs[3] | Markus Christiner[3,4] | Jan Benner[1,2] | Sabrina Turker[5] | Bettina M. Zeidler[4] | Annemarie Seither-Preisler[4,6]

[1]Division of Neuroradiology, University of Heidelberg Medical School, Heidelberg, Germany

[2]Department of Neurology, Section of Biomagnetism, University of Heidelberg Medical School, Heidelberg, Germany

[3]Jazeps Vitols Latvian Academy of Music, Riga, Latvia

[4]Centre for Systematic Musicology, University of Graz, Graz, Austria

[5]Lise Meitner Research Group "Cognition and Plasticity", Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany

[6]BioTechMed, Graz, Austria

Correspondence
Peter Schneider and Annmarie Seither-Preisler, Centre for Systematic Musicology, University of Graz, Glaciesstraße 27, A-8010 Graz, Austria.
Email: schneider@musicandbrain.de and annemarie.seither-preisler@uni-graz.at

Funding information
Deutsche Forschungsgemeinschaft, Grant/Award Number: Heisenberg fellowship program SCHN 965/7-1

Abstract

Although there is strong evidence for the positive effects of musical training on auditory perception, processing, and training-induced neuroplasticity, there is still little knowledge on the auditory and neurophysiological short-term plasticity through listening training. In a sample of 37 adolescents (20 musicians and 17 nonmusicians) that was compared to a control group matched for age, gender, and musical experience, we conducted a 2-week active listening training (AULOS: Active IndividUalized Listening OptimizationS). Using magnetoencephalography and psychoacoustic tests, the short-term plasticity of auditory evoked fields and auditory skills were examined in a pre-post design, adapted to the individual neuro-auditory profiles. We found bilateral, but more pronounced plastic changes in the right auditory cortex. Moreover, we observed synchronization of the auditory evoked P1, N1, and P2 responses and threefold larger amplitudes of the late P2 response, similar to the reported effects of musical long-term training. Auditory skills and thresholds benefited largely from the AULOS training. Remarkably, after training, the mean thresholds improved by 12 dB for bone conduction and by 3–4 dB for air conduction. Thus, our findings indicate a strong positive influence of active listening training on neural auditory processing and perception in adolescence, when the auditory system is still developing.

KEYWORDS
active listening training, auditory evoked fields, AULOS, magnetoencephalography, musical practice, short-term plasticity, synchronization, Tomatis

INTRODUCTION

There is converging evidence that musically experienced listeners show numerous advantages in neural processing. Thus, the musical brain is an excellent model for neuroplasticity.[1–3] Active music making involves numerous neural processes that have a great long-term impact on perception, cognition, behavior, and brain activity from childhood[4–10] and adolescence[11] to adulthood.[12–16] Furthermore, valuable insights have been provided on how neural processing is related to musical expertise and auditory skills, such as the perception and discrimination of pitch, timbre, or timing.[17–21] Short-term studies of musical training have demonstrated that a remarkable neurofunctional cortical and subcortical plasticity can already be elicited in a time range of several weeks to months.[22–24] Moreover, studies

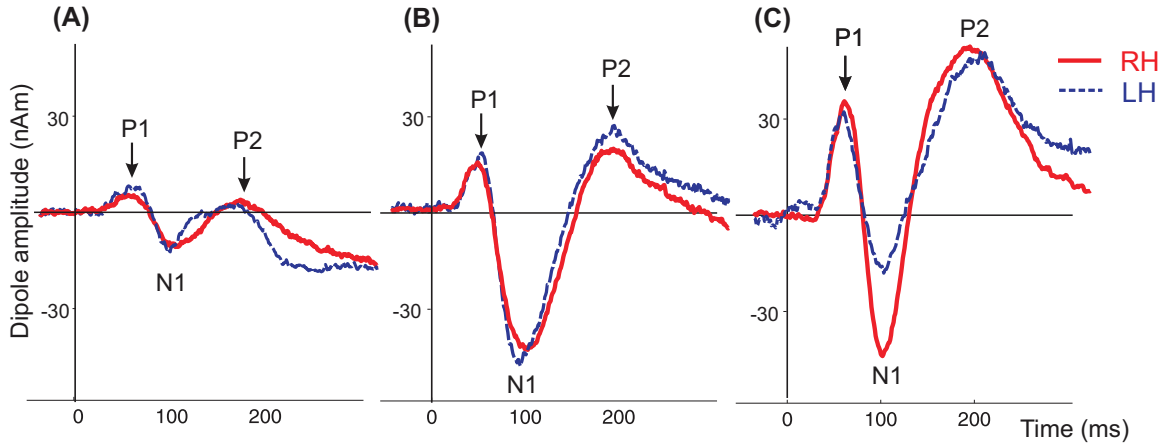

FIGURE 1 Individual auditory evoked responses of the P1–N1–P2 complex in three subjects while listening to the same musical sounds. The source waveform of each subject shows a different time course, thus representing a "personal fingerprint." (A) Response from an adolescent nonmusician with recognizable peak components, (B) response from a young amateur singer with pronounced peak components and a predominance of the secondary N1, (C) response from a musically highly experienced adult with a substantially enlarged P1–N1–P2 complex and a dominance of the secondary P2. Abbreviations: LH, left hemisphere; RH, right hemisphere.

associated with active auditory training and listening have revealed transfer effects to motor functions, musical performance qualities, and somatosensory integration.[25–29]

Auditory evoked responses are commonly used to study the development, neuroplasticity, and functional lateralization of the central auditory system. They are usually recorded during 15–30 min of passive or attentive listening to different types of sounds. The (late) auditory evoked responses originate from the primary and secondary auditory cortex. They typically form the P1–N1–P2 complex (e.g., Figure 1), followed by several task-related components like the N2a, the mismatch negativity, and the P3a.[30] Depending on the age and other factors, the P1 occurs between 30 and 80 ms, the N1 between 90 and 150 ms, and the P2 between 170 and 280 ms after stimulus onset in adolescents[31] and adults.[32] While the P1 emerges in early childhood,[33] the N1 develops during primary school age,[34–36] and the P2 later in adolescence.[34]

The primary P1, generated in the anterolateral part of Heschl's gyrus, is basically a representation of elementary sound features and is, therefore, relevant for the coding and analysis of spectral and temporal acoustic cues and auditory discrimination skills.[32,37] The N1, generated in the posteriorly situated planum temporale, is a more complex response that is sensitive to feature detection[38] and auditory attention.[39,40] The P2 response, partially hosted in Heschl's gyrus and adjacent regions of the superior temporal gyrus, is even more complex and can be considered a precognitive and learning-sensitive component that is preparing sensory integration.[34,41–43] There is converging evidence for a functional specialization of auditory processing in the two hemispheres. While the left auditory cortex is more strongly involved in the temporally precise analysis of short signal segments (<50 ms), being characteristic of many speech sounds, the right auditory cortex is specialized in the analysis of longer-lasting segments (>200 ms) and melodic information, as well as the parallel processing of sound spectra giving rise to timbral sensations.[44–46]

The different time windows of the two hemispheres should be precisely aligned to trigger a time-locked analysis and thus guarantee an efficient integration of fast and slow aspects of information.[47] Moreover, we have shown that on the individual level, there is a certain variability in neuroanatomical and functional lateralization patterns that correlate with sound perception preference.[32] As yet, it remains to be studied in detail how such hemispheric processing characteristics are related to elementary auditory skills (e.g., the discrimination of tone frequencies, intensities, durations, or timbral attributes) and more complex auditory pattern recognition (e.g., the subjective pitch of complex tones and rhythm perception) and whether these might also be reflected in right- and left-ear thresholds for air and bone conduction at the peripheral level. Noteworthy, the right auditory cortex was found to mature slightly earlier from infancy to adolescence than its left-hemispheric counterpart.[36,48–50]

Many studies have shown that the primary P1 response,[11,36,51,52] the secondary N1/P2 responses,[14,21,53] as well as the mismatch negativity evoked by unexpected stimuli[26,54] are related to musical expertise. In our previous studies,[32,51] we found that the primary auditory evoked response predominantly reflected the dispositional aspect of musicality, as measured in E. Gordon's music aptitude tests,[55] whereas the secondary responses tended to reflect training-related aspects. In the course of development, the N1 response complex typically becomes the major component in adult nonmusicians and musical amateurs (Figure 1A,B), whereas, in professional musicians, the P2 shows the highest magnitudes[4,14,53,56,57] (Figure 1C). Our previous studies with children and adolescents revealed that the degree of synchronization between the hemispheres was positively correlated to the amount of musical practice.[31,36] Also, in musically experienced adults, usually more balanced, synchronous P1–N1–P2 response patterns were observed as a consequence of musical long-term training.[32]

Recent short- and long-term studies have investigated changes in auditory processing during music listening with regard to elementary

discrimination abilities and complex pattern recognition skills, as well as brain connectivity.[54,58–60] Furthermore, there is evidence for rapid changes in event-related potentials due to auditory exposure.[61–63] However, there is still a lack of empirical studies on the dynamics of learning-induced plasticity and potential benefits for brain and behavior for the active listening programs introduced by the French ear, nose, and throat physician Alfred Tomatis.[64–66]

In our international longitudinal study AMseL[31,36,67] (Audio and Neuroplasticity of Musical Learning), which was conducted from 2009 to 2021 and included five follow-up measurement time points, we used magnetoencephalography (MEG) to investigate the neuroplasticity of musical learning in children and adolescents ($n = 220$). Short-term plasticity was studied during the fifth measurement timepoint in response to a 2-week active listening training (AULOS: Active IndividUalized Listening OptimizationS) in a subsample of 37 typically developing subjects. This in-house training program promotes the discrimination of acoustic features, the recognition of auditory patterns, the maintenance of auditory vigilance and attention, as well as sensorimotor and auditory–motor integration. The concept of "active listening," which is central to this approach, is based on the original ideas of Tomatis.[64–66] The auditory system is exposed to musical pieces and natural sounds both through the air and bone conduction.[66] The specific use of bone conduction[68,69] has been inspired by early descriptions of resonance phenomena in the inner ear.[70] The stimulation material is filtered and systematically fluctuates between a higher and lower frequency region, using a so-called electronic "sound rocker."[66] The parameters used for the preparation of the stimulation material are adapted according to the individual neuro-auditory profiles. The latter is measured by the in-house psychoacoustic testing battery "KLAWA" ("Klangwahrnehmung") also used in our recent studies,[71,72] the "Pitch Perception Preference Test" [32] to quantify subjective pitch perception and auditory thresholds tests.[73]

Previous work has demonstrated that in therapeutic applications, a combination of bone and air conduction combined with specific filtering techniques, as used in the original approach of Tomatis, has the capacity to considerably improve learning outcomes in conjunction with transfer effects to cognitive, linguistic, and sensorimotor domains.[74–77] Particularly, the efficacy of this method has been shown for children with learning and communication disorders[74] and attention deficits,[76] as well as for adults with psychomotoric and neurological dysfunctions[78] and chronic tinnitus.[79] The present study aimed to investigate the short-term effects of active listening on (1) the neuroplasticity of auditory evoked responses and its synchronization between the two hemispheres; (2) the functional lateralization between hemispheres that might be reflected in ear advantages; (3) the relative contributions of air and bone conduction; (4) the potential effects of musical expertise on elementary auditory skills (discrimination of frequency, intensity, onset ramp, and tone duration thresholds), more complex auditory pattern recognition (subjective pitch and rhythm perception), and related training-induced plasticity; and (5) bilateral and conduction-based balancing processes.

METHODS

Subjects

The training group participating in active listening was recruited on an optional basis from our longitudinal AMseL study. In particular, the training was offered to the subgroup of typically developing individuals with no signs of dyslexia or attentional problems. Thirty-seven young individuals (22 females; 20 musicians, $M_{age} = 17.5 \pm 0.6$ years; range: 13–20 years) were tested in a pre- and a post-condition that were 2.2 ± 0.4 weeks apart. Since our subjects were already experienced with the experimental procedure and had undergone the same neurological and psychoacoustic tests five times in the major long-term study, a short-term increase in familiarity from the pre- to post-condition would be highly unlikely. Nevertheless, we also included a control group from the AMseL study that was matched for age, gender, and musical experience. The control group stems from the same sample of typically developing children and comprises those individuals who were not able to participate in the listening training. As our AMseL participants had been selected according to standardized criteria in advance (including age, gender, and social variables), the two groups are perfectly matched. The controls ($n = 20$, 10 females, 11 musicians, $M_{age} = 17.9 \pm 0.5$ years, range 14–20 years) underwent the same neurological measurements and behavioral tests twice with a comparable time interval in between (2.7 ± 0.3 weeks).

An index of cumulative musical practice (I_{MP}) was calculated to assess musical competence. The I_{MP} was defined as the product of the number of years of formal music education and the number of hours per week spent practicing a musical instrument, as reported in our previous studies.[31,36,67] The age-adapted separation value for the $I_{MP} = \Sigma(\text{h/week} \times \text{years})$ was 12. According to the I_{MP}, in total (training and control group) 26 participants were classified as "nonmusicians" ($I_{MP} < 12$) and 31 as "musicians." For nonmusicians, the mean I_{MP} was 3.4 ± 0.7, and for musicians, it was 37.3 ± 5.8.

The AULOS listening training

The short-term plasticity of auditory processing was explored by active listening based on the principles of the electronic ear ("apparatus for conditioning hearing"; https://patents.google.com/patent/US4327252), as originally formulated by A. Tomatis.[64,65] Based on our own neurocognitive research, we have further developed this original approach and implemented it as the "AULOS listening training." This refined training takes into account individual neuro-auditory profiles, which are assessed by auditory thresholds and discrimination abilities that may be complemented with MEG recordings (www.musicandbrain.de). The AULOS training was developed as part of the Heisenberg Research Program by P. Schneider at the University of Heidelberg in collaboration with ear training professors and listening therapists (see Acknowledgments). In this study, directly before starting the listening training program, psychoacoustic discrimination

abilities (KLAWA), auditory thresholds for air and bone conduction, and auditory evoked fields (AEFs) were measured to define the subjects' individual neuro-auditory profiles ("pre condition"). Subsequently, subjects were exposed to preprocessed musical pieces and natural sounds for 20 h (2–3 h per day over a period of 2 weeks with 7–10 training days) and instructed to listen in a relaxed mood. Nevertheless, the training can be classified as a highly active program, which is based on Tomatis' "active listening principles" (see below). As a central component, the electronic "sound rocker" permanently directs the listener's attention to ongoing alterations between a lower and higher frequency region, as defined by a preselected cutoff frequency. This not only leads to continuous training of the involved ear muscles, especially the stapedius muscle, but also keeps up vigilance and stimulates higher attentional functions.

The used natural sounds (e.g., flowing water and bird songs) and music (usually classical pieces of W.A. Mozart and J.S. Bach, choral music, and Gregorian chants) are presented softly with high quality (24-bit resolution, sampling rate 48 kHz, volume range 50–70 dB SPL) via air and bone conduction. Air conduction was mediated via high-quality headphones (AKG 812). Bone conduction was applied separately via a small box with optimized loudspeakers,[79] which were placed directly behind the petrous bone (alternately on the left and right mastoid and in the midline at the position of the medulla oblongata) with a comfortable fabric headband. The sounds and music used in the AULOS training are systematically adapted to the initially assessed individual neuro-auditory profiles for air and bone conduction and modified according to further principles, which are explained below. Immediately after the listening training, the KLAWA, the Pitch Perception Preference Test, auditory threshold tests, and MEG recordings were performed for a second time ("post condition").

The core idea of the AULOS training encompasses four principles, which have been outlined previously by Tomatis.[64–66] First, the auditory stimuli are gradually high-pass filtered with cutoff frequencies that increase during the training. Filtering usually starts with 0 Hz (unfiltered) and increases stepwise up to 3 kHz and in some cases up to 8 kHz to progressively challenge the auditory system to complement missing information. Second, different auditory stimulation delays in a range of 0–2500 ms are used to control the timing of the two frequency channels of the sound rocker, which produces permanent fluctuations to keep up the listener's vigilance and continuous attention. Third, the training uses an interlocked stimulation of air and bone conduction. In each cycle of the sound rocker, stimuli are initially presented only via bone conduction, which plays the leading role in active listening. Then, air conduction is added with a delay of about 150–300 ms (up to 2 s) corresponding to typical subcortical and cortical neurophysiological delay times.[30] While air conduction is mediated via the outer ear canal, bone conduction is mediated by resonance vibrations that may directly stimulate the outer hair cells on the basilar membrane. Fourth, the "sound rocker" integrates the advantages of these three principles.[66] Triggered by the dynamics of the musical flow, segments of prepared music and sounds permanently switch in a controlled way between the low- and high-pass filtered channel relative to the selected cutoff frequency.

Magnetoencephalography

AEFs were measured by 122 planar gradiometers (Neuromag-122 whole-head MEG system[80]) in response to seven different sampled instrumental sounds (piano, guitar, flute, bass clarinet, trumpet, violin, and percussion) and five artificial simple harmonic complex tones, as used in previous studies.[14,21,31,32,36,67,71] All stimuli had the same length and superimposed onset and offset ramps (duration: 10 ms) to avoid clicks. AEFs were calculated post hoc from the ongoing changes of field distributions recorded over the head surface with a low-pass filter of 0.00 (DC)—330 Hz and a sampling rate of 1 kHz. Each of the stimuli was presented 100 times in pseudorandomized order (tone length 500 ms, interstimulus interval 300–400 ms). This guaranteed a high signal-to-noise ratio for robust source modeling as a basis for the analysis of the time course of AEFs and corresponding peak latencies and amplitudes. The presentation volume was set to 70 dB SPL, which was controlled by a Brüel and Kjaer artificial ear (type 4152). The stimuli were presented binaurally via 90 cm plastic tubes through foam ear pieces placed in the ear canal and connected to small shielded transducers that were fixed in boxes next to the subject's chair.

To avoid an overlaying influence of task-specific changes in the auditory evoked responses, subjects were measured in the MEG without a task. To control their vigilance, they were instructed to listen to the tones in a relaxed state and to watch a silent movie. The duration of the measurement session was 16 min. Data analysis was performed using BESA Research 6.0 software (MEGIS Software GmbH, Gräfelfing, Germany). Prior to averaging, data were inspected with the BESA Research Event-Related Field Module to automatically exclude 3–7 noisy (bad) channels, about 10% of all epochs exceeding a gradient of 600 fT/cm×s, and amplitudes either exceeding 3000 fT/cm or falling below 100 fT/cm. Signal strength was calculated relative to a 100 ms prestimulus baseline. The responses of each subject were collapsed into a grand average (1100 artifact-free epochs) in a 100 ms prestimulus to 400 ms poststimulus time window. Averaged channel waveforms were calculated at the sensor level for a representative selection covering temporal and frontocentral regions, including the rectangular (R) and circular (C) derivatives. Furthermore, based on a spherical head model,[81–83] spatiotemporal source modeling was performed to separate the primary response complex from the later secondary responses, using a two-dipole model with an equivalent dipole in each hemisphere.[31,32,36,71,83] Source modeling was done on an individual basis prior to group-averaging of the source waveforms. Since the head position of the subjects under the dewar of the MEG was not the same in the pre- and post-condition, source localizations and orientations were fitted separately with exactly the same fitting parameters. The fitting intervals were individually adjusted in four steps: (1) the dipoles were converted to a regional source in each hemisphere and the center of the P1–N1–P2 response complex was localized using an individually adjusted fitting interval between the P1 and P2 peaks, (2) the regional sources were converted back to single dipoles, (3) the orientation of the primary P1 response was fitted around its lower and upper half-sidelobes and directed toward the vertex before analyzing

P1 latencies and amplitudes, (4) the orientation of the N1 and P2 responses was fitted toward their lower and upper half-sidelobes while maintaining the direction of the P1 toward the vertex. Subsequently, the N1 and P2 latencies and amplitudes were taken from the source waveforms, with the N1 amplitude usually having negative values. The described procedure is well-established and has been used similarly in our earlier studies.[14,21,31,32,36,67,71] In addition, absolute asynchronies |peak latency {right – left}| and absolute amplitude asymmetries |peak amplitude {right – left}| were calculated in order to assess how well the latencies and amplitudes match between hemispheres.

Auditory discrimination tests

For the audiometric and psychoacoustic tests, the stimuli were presented binaurally using an RME Hammerfall DSP Multiface system and closed dynamic headphones (Sennheiser HAD 200) designed for high-quality hearing tests. These headphones provide about 30 dB of passive attenuation in the frequency region of the stimuli used. The intensity was controlled not to exceed 75 dB SPL. The auditory testing battery included the assessment of auditory discrimination abilities (KLAWA test)[71,72] and of subjective pitch perception.[32,84]

KLAWA is an in-house computer-based threshold test for children, adolescents, and adults based on an "alternative-forced-choice" procedure.[85] In this procedure, which automatically adapts to the subjects' performance, thresholds are calculated and then compared to an age-referenced norm group. The KLAWA measures the sensitivity for discriminating different acoustic parameters, namely intensity (dB; soft vs. loud), frequency (semitones/ST; low vs. high), onset ramp (ms; sharp vs. mellow), and tone duration (ms; short vs. long). The discrimination thresholds for these parameters may vary largely from subject to subject (> factor 100). In the frequency subtest, the standard is a 500 Hz pure tone and the difference between tones varies randomly by up to two STs. In the intensity subtest, the standard is fixed at 65 dB SPL, while the test tones vary between 45 and 65 dB SPL. In the onset ramp subtest, the standard has a linear rise time of 15 ms, a continuous segment of 735 ms, and a linear fall time of 50 ms, while the rise times of the test tones vary logarithmically up to 300 ms. In the duration subtest, the standard has a duration of 400 ms and the comparison tones are varied logarithmically from 400 to 600 ms. The KLAWA measures individual perceptual thresholds more accurately than conventional procedures with fixed preset thresholds.[86] Furthermore, rhythmic abilities are assessed by 24 pairs of rhythmic sequences that have to be classified as being the same or different.

The pitch perception preference test measuring subjective pitch perception includes 144 different pairs of harmonic complex tones. Each pair consists of two consecutive tones (duration: 500 ms, 10 ms rise-fall time, interstimulus interval 250 ms). Each test tone includes two, three, or four adjacent harmonics, omitting the fundamental frequency.[32] Audiometric pure tone thresholds (below referred to as "auditory thresholds") were measured in a frequency region of 125 Hz–12 kHz in dB SPL for both ears separately for air and bone conduction using standard protocols.[73]

Data analyses

With regard to the neurofunctional MEG data, four-way ANOVAs were calculated for the independent variables (first two: within-subjects repeated measurement factors, last two: between subjects grouping factors) "measurement timepoint" (MT_1: pre, MT_2: post), "hemisphere" (R, L), "treatment group" (training, control), and "musical expertise" (mus, non). Separate analyses were performed for the dependent variables P1/N1/P2 latencies and amplitudes. Moreover, like in previous studies,[31,36] the absolute differences of P1/N1/P2 latencies and amplitudes measured in the right and left hemispheres were considered as measures of functional lateralization in corresponding three-way ANOVAs. Likewise, performance in each of the psychoacoustic tests (KLAWA and Pitch Perception Preference Test) was analyzed in three-way ANOVAs with the following dependent variables: discrimination thresholds for "frequency," "intensity," "onset ramp," "tone duration," and scores for "rhythm perception" and "subjective pitch perception." With regard to auditory thresholds, as well for air conduction as for bone conduction, five-way ANOVAs were performed for the independent variables "measurement timepoint" (MT_1: pre, MT_2: post), "ear" (R, L), "frequency region" (low, mid, high), "treatment group" (training, control), and "musical expertise" (mus, non). Moreover, corresponding ANOVAs were calculated for absolute threshold differences with the dependent variables "absolute difference between left and right ear" (five-way ANOVA including the independent variable "threshold type," but not "ear"), "absolute difference pre-post for air and bone conduction" (five-way ANOVA including the independent variable "threshold type," but not "measurement timepoint"), and "absolute difference between air and bone conduction" (five-way ANOVA including all independent variables apart from "threshold type"). For all ANOVAs, post hoc tests were adjusted for multiple comparisons by Bonferroni correction.

RESULTS

The detailed findings of all performed ANOVAs can be found in Tables S1–S3 (MEG parameters for P1, N1, and P2) and Tables S4 and S5 (psychoacoustic parameters). Please note that in these tables, interactions are only indicated in case of significance.

Short-term plasticity of cortical auditory processing induced by AULOS listening training

The compact AULOS listening training resulted in remarkable changes in AEFs (Figure 2 and Table 1). With regard to P1 latency, none of the studied variables had a significant effect. However, for absolute P1 asynchrony, there was a significant interaction "MT × treatment group" ($F_{(1,53)} = 12.0$, $p = 0.001$, part. $\eta^2 = 0.19$). The listening training induced an impressive temporal synchronization of the left and right hemispheric responses in the training group (pre: 7.0 ms vs. post: 2.6 ms; $p = 2.9E\text{-}9$), but not in the control group (pre: 6.1 ms vs. post: 5.4 ms; n.s.). A corresponding interaction was also observed for P1

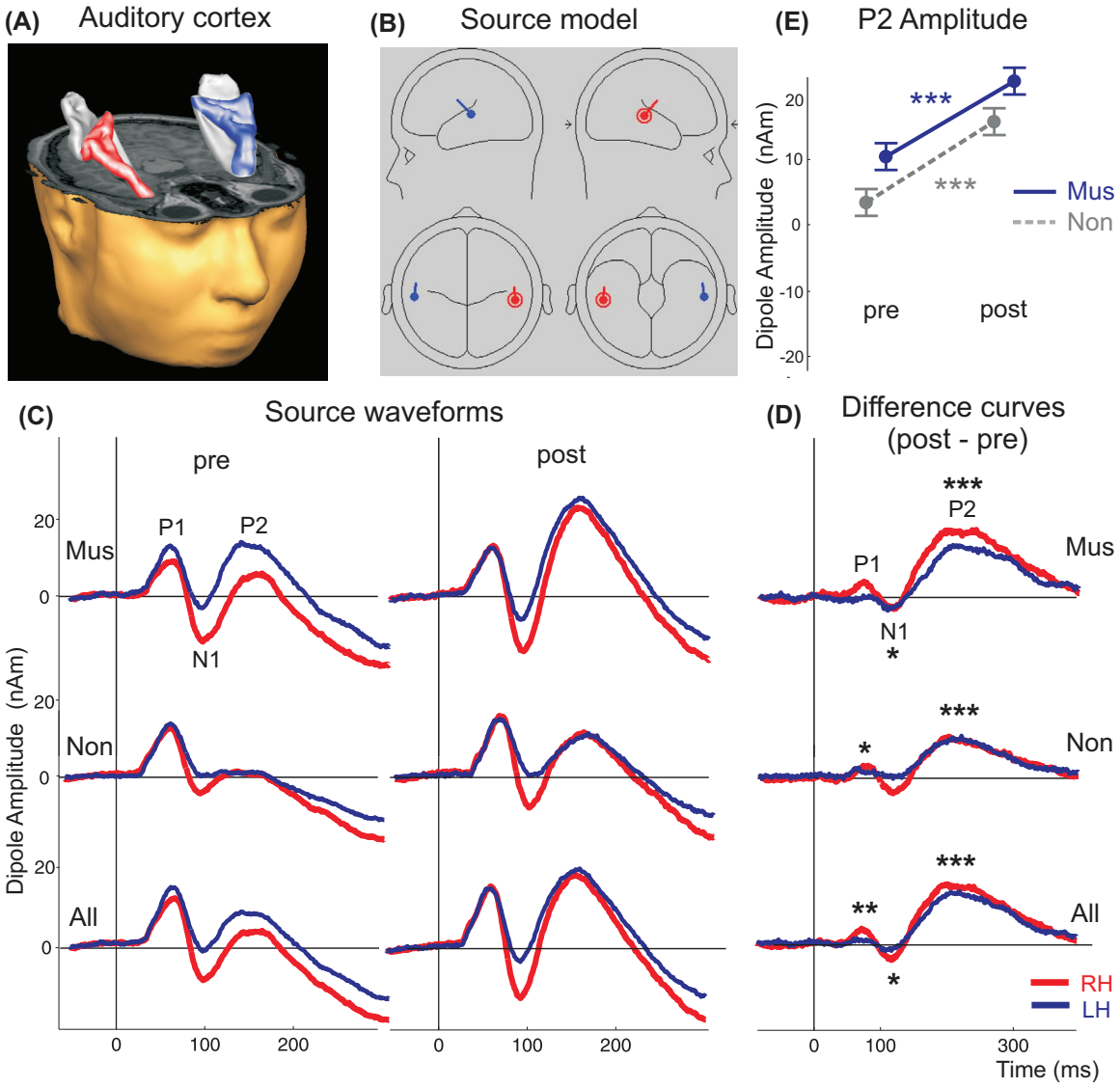

FIGURE 2 (A) Three-dimensional reconstructions of the right and left auditory cortex of an adolescent. (B) Two-dipole model to extract the individual source waveforms (activation over time) in the regions of the left (blue) and right (red) auditory cortex. (C) Averaged source waveforms of musicians (top), nonmusicians (middle), and all subjects (bottom) before (pre) and after (post) the 2-week listening training. (D) Difference curves for pre- and post-measurements. (E) Increase of the P2 amplitude after training. *$p < 0.05$; ** $p < 0.01$; ***$p < 0.001$.

amplitude ($F_{(1,53)} = 4.8$, $p = 0.033$, part. $\eta^2 = 0.08$), which increased in the training group (pre: 15.8 nAm vs. post: 18.2 nAm; $p = 0.009$), but not in the controls (16.2 vs. 15.3 ms; n.s.). Effects of musical expertise were not observed for P1 latency, absolute asynchrony, or amplitude.

Different from the P1, the latency of the N1 decreased in the training group (pre: 128.7 ms vs. post: 118.6 ms; $p = 0.004$), but remained stable in the controls (pre: 123.4 ms vs. post: 122.7 ms; n.s.). Also, the absolute N1 asynchrony was reduced almost by half only in the training group (pre: 11.2 ms vs. post: 6.4 ms; $p = 0.01$), but not in controls (pre: 9.1 ms vs. post: 9.3 ms; n.s.). With regard to N1 amplitude, a significant "MT × treatment group" interaction ($F_{(1,53)} = 4.5$, $p = 0.04$, part. $\eta^2 = 0.08$) showed that the magnitude of the N1 increased in the training group (pre: −7.3 nAm vs. post: −11.7 nAm; $p = 0.02$), but not in controls (pre: −11.0 nAm vs. post: −8.5 nAm; n.s.). In general, N1 responses were substantially larger in the right (−12.7 nAm) than in the left hemisphere (−6.5 nAm); $F_{(1,53)} = 18.8$, $p = 6.5E\text{-}5$, part. $\eta^2 = 0.26$. The increase of N1 amplitude due to training was only significant for the right ($\Delta = 7.7$ nAm; $p = 0.001$), but not for the left ($\Delta = 1.1$ nAm; n.s.) auditory cortex. This was also reflected in a training-induced increase of the absolute asymmetry of N1 amplitude (pre: 8.0 nAm vs. post: 13.0 nAm; $p = 0.002$) in comparison to the control group (pre: 7.0 nAm vs. post: 9.4 nAm; n.s.).

With regard to P2 latency, no training-related effects or hemispheric differences were found. P2 latencies were slightly longer in musicians (202.6 ms) than in nonmusicians (183.8 ms); $F_{(1,53)} = 6.4$, $p = 0.02$, part. $\eta^2 = 0.11$. Like for the P1 and N1, the listening training caused a prominent reduction of absolute asynchrony in the P2 component

TABLE 1 Paired pre-post comparisons for all measured MEG parameters separately listed for the training group (middle column) and control group (right column)

		Training group			Control group		
MEG parameters	**Mus. Exp. /Hemi.**	**Pre**	**Post**	**Sign.**	**Pre**	**Post**	**Sign.**
P1 latency (ms)	Mus R	72.8 ± 2.2	72.9 ± 2.1	n.s.	73.4 ± 2.8	72.6 ± 2.8	n.s.
	Mus L	73.7 ± 2.3	72.7 ± 2.1	n.s.	74.4 ± 3.0	74.1 ± 2.8	n.s.
	Non R	68.5 ± 2.3	68.2 ± 2.3	n.s.	70.9 ± 3.1	71.7 ± 3.1	n.s.
	Non L	68.5 ± 2.5	68.0 ± 2.3	n.s.	71.7 ± 3.3	71.0 ± 3.1	n.s.
Absolute P1 asynchrony |R−L| (ms)	Mus	6.4 ± 1.1	2.7 ± 0.8	$p = 4.7E\text{-}5$	4.8 ± 1.6	5.8 ± 1.5	n.s.
	Non	7.6 ± 1.2	2.5 ± 0.8	$p = 8.0E\text{-}7$	7.9 ± 1.8	6.9 ± 1.6	n.s.
P1 amplitude (nAm)	Mus R	15.7 ± 1.8	18.1 ± 2.0	n.s.	15.6 ± 2.4	16.6 ± 2.4	n.s.
	Mus L	17.4 ± 2.1	18.7 ± 2.2	n.s.	18.9 ± 2.8	18.9 ± 3.0	n.s.
	Non R	13.4 ± 1.8	17.2 ± 2.2	$p = 0.021$	13.8 ± 2.7	10.7 ± 2.7	n.s.
	Non L	16.7 ± 2.4	18.7 ± 2.4	n.s.	16.4 ± 3.1	15.1 ± 3.3	n.s.
Absolute asymmetry of P1 amplitude |(R−L)/(R+L)|	Mus	5.1 ± 1.1	4.7 ± 0.9	n.s.	4.8 ± 1.6	5.8 ± 1.5	n.s.
	Non	4.6 ± 1.2	5.0 ± 1.0	n.s.	7.9 ± 1.8	6.9 ± 1.6	n.s.
N1 latency (ms)	Mus R	134.7 ± 6.5	119.3 ± 2.4	$p = 0.004$	128.6 ± 7.6	128.2 ± 3.7	n.s.
	Mus L	134.6 ± 6.2	121.3 ± 4.3	$p = 0.003$	131.0 ± 7.2	128.1 ± 5.6	n.s.
	Non R	122.2 ± 7.0	114.9 ± 2.6	n.s.	118.6 ± 8.4	114.8 ± 4.1	n.s.
	Non L	123.2 ± 6.7	119.1 ± 4.7	n.s.	115.2 ± 8.0	120.0 ± 6.1	n.s.
Absolute N1 asynchrony |R−L| (ms)	Mus	15.1 ± 2.7	7.0 ± 2.2	$p = 0.004$	9.3 ± 3.4	10.6 ± 2.9	n.s.
	Non	7.2 ± 2.9	5.8 ± 2.4	n.s.	8.9 ± 3.8	7.9 ± 3.2	n.s.
N1 amplitude (nAm)	Mus R	−10.9 ± 2.9	−19.5 ± 5.0	$p = 0.004$	−11.6 ± 5.1	−15.5 ± 6.6	n.s.
	Mus L	−4.7 ± 3.1	−6.3 ± 4.5	n.s.	−10.0 ± 5.1	−7.4 ± 6.0	n.s.
	Non R	−7.8 ± 3.2	−14.6 ± 5.4	$p = 0.030$	−11.9 ± 5.6	−9.7 ± 7.3	n.s.
	Non L	−5.9 ± 3.4	−6.5 ± 4.9	n.s.	−9.6 ± 5.6	−1.3 ± 6.6	n.s.
Absolute asymmetry of N1 amplitude |(R−L)| (nAm)	Mus	11.8 ± 1.4	17.4 ± 2.6	$p = 0.007$	7.8 ± 1.9	9.9 ± 3.2	n.s.
	Non	4.3 ± 1.5	8.5 ± 2.8	$p = 0.05$	6.2 ± 2.1	8.9 ± 3.5	n.s.
P2 latency (ms)	Mus R	209.7 ± 7.8	201.9 ± 6.2	n.s.	201.5 ± 8.7	202.6 ± 6.3	n.s.
	Mus L	207.2 ± 8.5	203.6 ± 6.3	n.s.	196.2 ± 10.6	198.5 ± 8.7	n.s.
	Non R	191.1 ± 8.5	186.3 ± 6.7	n.s.	180.4 ± 10.8	179.7 ± 9.1	n.s.
	Non L	183.4 ± 9.3	187.7 ± 6.9	n.s.	180.4 ± 11.7	181.8 ± 9.6	n.s.
Absolute P2 asynchrony |R−L| (ms)	Mus	16.4 ± 3.9	6.5 ± 1.9	$p = 0.022$	7.4 ± 4.8	9.5 ± 2.4	n.s.
	Non	14.8 ± 4.2	8.2 ± 2.1	n.s.	15.6 ± 5.3	7.9 ± 2.7	n.s.
P2 amplitude (nAm)	Mus R	6.9 ± 2.8	26.6 ± 4.3	$p = 8.6E\text{-}11$	6.8 ± 4.1	7.8 ± 5.6	n.s.
	Mus L	12.9 ± 2.5	25.6 ± 3.4	$p = 9.9E\text{-}8$	8.9 ± 4.0	10.7 ± 5.0	n.s.
	Non R	5.8 ± 3.0	19.0 ± 4.7	$p = 7.0E\text{-}6$	−4.3 ± 4.5	−5.7 ± 6.2	n.s.
	Non L	5.8 ± 2.7	15.9 ± 3.7	$p = 3.4E\text{-}5$	0.2 ± 4.4	−0.7 ± 5.5	n.s.
Absolute asymmetry of P2 amplitude |(R−L)| (nAm)	Mus	8.3 ± 1.6	8.0 ± 1.5	n.s.	5.8 ± 2.1	5.7 ± 1.9	n.s.
	Non	6.0 ± 1.8	8.3 ± 1.6	n.s.	7.7 ± 2.4	5.5 ± 2.1	n.s.

Note: Values are shown in different rows according to musical expertise.
Abbreviations: Hemi, hemisphere; L, left; Mus, musicians; Non, nonmusicians; R, right; Sign, significance.

in the training group (pre: 15.6 ms vs. post: 7.4 ms; $p = 0.01$), but not in controls (pre: 11.5 ms vs. post: 8.7 ms; n.s.). Remarkably, in response to training, the P2 amplitude showed an almost threefold increase (pre: 7.9 nAm vs. post: 21.8 nAm; $p = 3.3E\text{-}12$), while no changes were observed in the control group (pre: 2.9 nAm vs. post: 3.0 nAm; n.s.); $F_{(1,53)} = 27.6$, $p = 2.7E\text{-}6$, part. $\eta^2 = 0.34$. The "MT × hemisphere × treatment group" interaction revealed that this training-induced amplitude increase, although strong in both hemispheres, was more pronounced on the right ($\Delta = 16.4$ nAm, $p = 1.8E\text{-}12$) than on the left side ($\Delta = 11.4$ nAm, $p = 6.8E\text{-}10$; $F_{(1,53)} = 7.7$, $p = 0.008$, part.

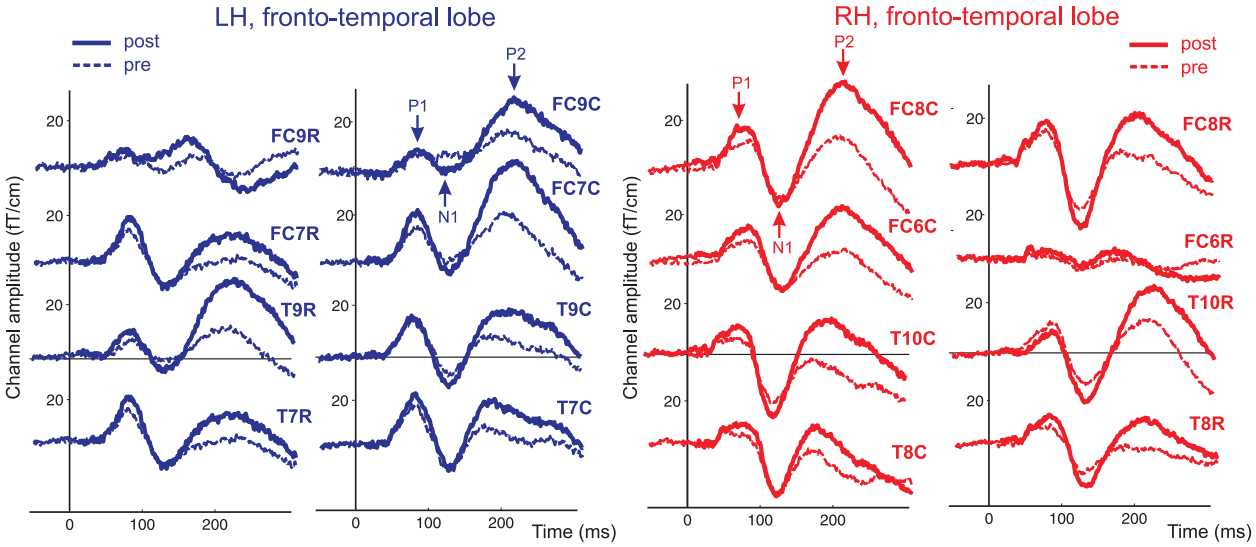

FIGURE 3 Sensor waveforms from a representative selection of channels, covering temporal (T7–T10) and frontocentral regions (FC6–FC9) over the right and left hemispheres, averaged over all subjects of the training group. Abbreviations: LH, left hemisphere; RH, right hemisphere.

$\eta^2 = 0.13$). Moreover, the P2 response was significantly larger in musicians (13.3 nAm) than in nonmusicians (4.5 nAm); $F_{(1,53)} = 5.0$, $p = 0.03$, part. $\eta^2 = 0.09$.

Furthermore, the averaged channel waveforms at the sensor level were calculated for a representative selection covering temporal and frontocentral regions, including the rectangular (R) and circular (C) derivatives at the positions T10, T8, FC8, FC6, T9, T7, FC9, and FC7. Like for the source waveform analyses, an enhancement of the late P2 response was clearly visible, thus corroborating the above-reported findings (Figure 3).

Short-term plasticity of auditory skills

Almost all of the tested psychoacoustic parameters demonstrated substantial improvements due to the listening training. In the training group, the discrimination of frequency was refined from 0.27 to 0.18 STs ($p = 0.01$), of intensity from 0.89 to 0.56 dB ($p = 0.002$), of onset ramp from 19 to 8 ms ($p = 0.001$), and of rhythm from 82% to 89% ($p = 3.8E\text{-}8$). No significant training-induced changes were observed for tone duration and subjective pitch. There were no significant changes in the control group for any of the tested psychoacoustic parameters. Also, there were no significant differences between musicians and nonmusicians, except for frequency (non: 0.35 ST, mus: 0.16 ST; $F_{(1,53)} = 14.7$, $p = 3.3E\text{-}4$, part. $\eta^2 = 0.22$; see Figure 4A–F and Table 2.

Short-term plasticity of auditory thresholds through active listening training

Figure 4G presents the hearing thresholds separately for air and bone conduction. With regard to air conduction, there were no training-induced effects reflected in a corresponding "MT × treatment group" interaction, nor was there a difference related to musical expertise.

For bone conduction, musicians undergoing the listening training showed a significant improvement in threshold from 5.7 to 1.2 dB SPL ($p = 0.049$), which was not observed in nonmusicians and untrained controls. Moreover, there were no differences in the mean sensitivities of the left and right ear for both types of transmission. However, when comparing the absolute differences between the two ears, bone conduction showed a larger left-right difference (5.1 dB) than air conduction (3.5 dB); $F_{(1,53)} = 18.0$, $p = 8.8E\text{-}5$, part. $\eta^2 = 0.25$. The absolute ear difference furthermore depended on frequency region ($F_{(1,53)} = 7.1$, $p = 0.002$, part. $\eta^2 = 0.12$), with high frequencies being more strongly lateralized (5.1 dB) than middle frequencies (4.1 dB; $p = 0.009$), and low frequencies (3.7 dB; $p = 0.007$).

In order to directly compare the auditory plasticity of air and bone conduction, we calculated the absolute pre-post difference values. In the training group, there was a very strong effect of threshold type, showing a more than threefold higher plasticity for bone (11.7 dB) than for air conduction (3.3 dB); $F_{(1,53)} = 20.3$, $p = 3.7E\text{-}5$, part. $\eta^2 = 0.28$; see Figure 4H.

To account for possible balancing effects between air and bone conduction, the absolute air–bone difference values were also considered (Figure 4I). There was a clear "MT × treatment group" interaction ($F_{(1,53)} = 23.1$, $p = 1.3E\text{-}5$, part. $\eta^2 = 0.30$). Remarkably, in the training group, mean absolute differences were almost halved from 12.0 dB (pre) to 6.5 dB (post); $p = 3.1E\text{-}10$, while no changes were observed in the control group (pre: 8.1 dB vs. post: 8.3 dB; n.s.). Moreover, the balancing effect observed in the training group depended on frequency region ($F_{(1,53)} = 6.6$, $p = 0.002$, part. $\eta^2 = 0.11$). While balancing was substantial in the mid- (pre: 13.3 vs. 5.2 dB; $p = 5.9E\text{-}13$) and high- (pre: 13.0 vs. 6.2 dB; $p = 1.4E.6$) frequency regions, no significant change

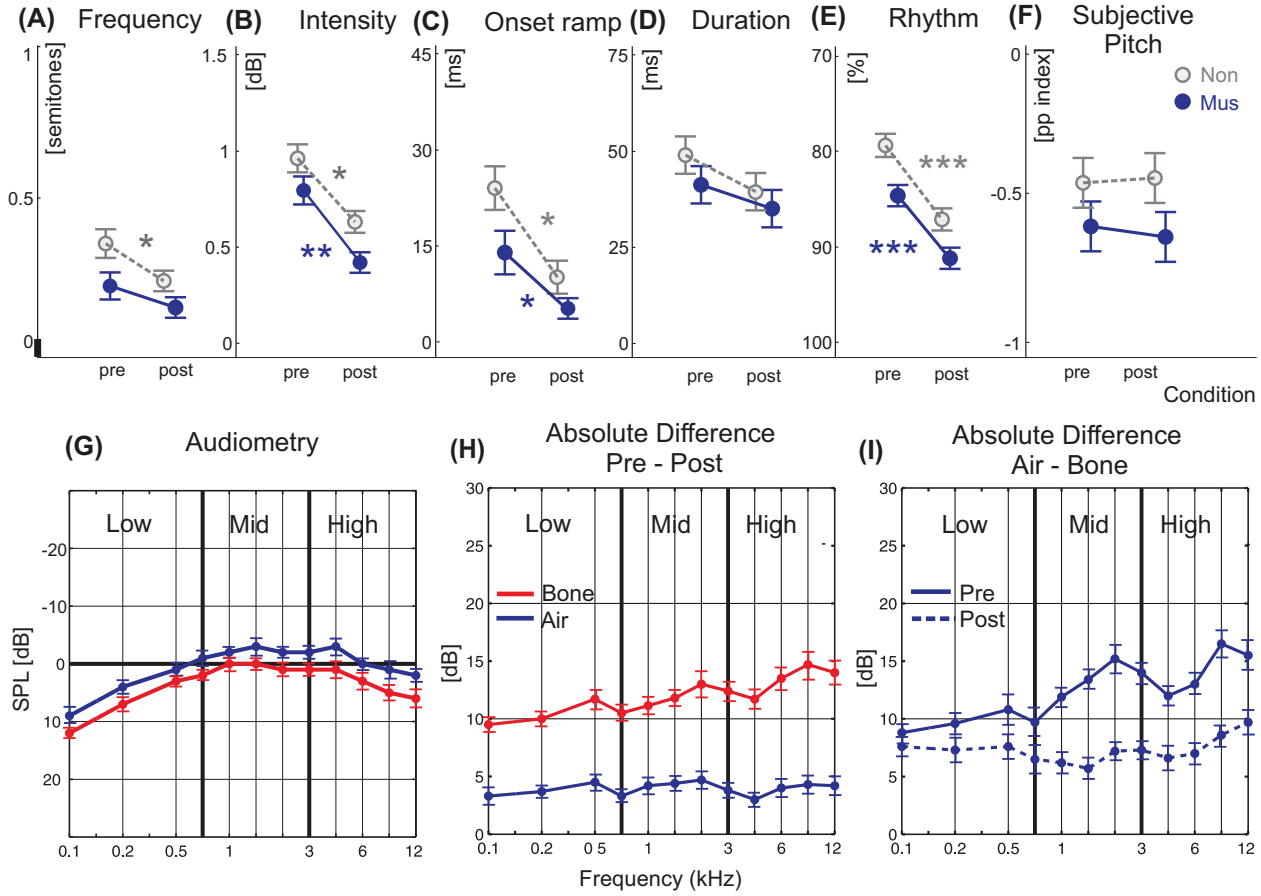

FIGURE 4 Short-term plasticity of auditory skills. Apart from the perception of tone duration (D) and subjective pitch (F), all auditory domains (A, B, C, E) substantially benefited from the short-term listening training (musicians: filled circles, nonmusicians: open circles). (G) Averaged hearing thresholds (measured in dB SPL) for all subjects. (H) The absolute difference between pre- and post-measurement for bone (red) and air (blue) conduction. (I) The absolute difference between air and bone conduction for pre- (solid) and post- (dashed) measurement. $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$.

was observed for the low-frequency region (pre: 9.7 dB vs. post: 8.0 dB; n.s.).

Interestingly, the initial high variability among subjects was lower after the training, signifying a homogenization of response patterns toward average values. There were no effects of musical expertise on auditory thresholds.

DISCUSSION

In this study, we first report neurophysiological and psychometric indicators of high efficiency for short-term active listening. Specifically, we found a strong bilateral synchronization between left and right hemispheric activation, which was most pronounced for the primary P1 response. Second, we observed a substantial increase in the magnitude of the late auditory evoked P2 response. Third, the most relevant auditory discrimination skills showed consistent improvements. In the following, we will first outline the basic effect mechanisms of this training and then relate them to our specific neurological and behavioral findings.

Principles of active listening and potential neuro-auditory mechanisms

Human perception relies on the segregation of relevant information from meaningless background events.[87] In audition, this means the recognition of objects like a sprinkling fountain, a laughing friend, or a melody from the radio based on spectral and temporal cues. Acoustic signals are converted into spectral and temporal excitation patterns in the auditory periphery, including the cochlea and auditory nerve.[88–90] At the cortical level, the two hemispheres are specialized for complementary aspects of auditory processing, such that temporal resolution is better in the left hemisphere and spectral resolution is better in the right hemisphere.[32,44,91,92] This enables a precise spectro-temporal representation of auditory features, which is essential to comprehend the acoustic environment and adequately respond to it.

Remarkably, auditory pattern recognition skills show large interindividual differences[21,32,93] and are sensitive to long-term musical training.[11,18,20,24,31,36,94] The latter is reflected in an enhanced speed and synchrony of auditory evoked responses, indicating an increased neural efficiency in the brains of musicians.[21,93] While there

TABLE 2 Paired pre-post comparisons for all measured psychoacoustic parameters separately listed for the training group (middle column) and control group (right column)

		Training group			Control group		
Psychoacoustic parameters	**Mus. Exp.**	**Pre**	**Post**	**Sign.**	**Pre**	**Post**	**Sign.**
Frequency (semitones)	Mus	0.21 ± 0.06	0.14 ± 0.04	n.s.	0.14 ± 0.07	0.15 ± 0.05	n.s.
	Non	0.34 ± 0.06	0.23 ± 0.04	$p = 0.034$	0.41 ± 0.08	0.42 ± 0.06	n.s.
Intensity (dB)	Mus	0.83 ± 0.16	0.47 ± 0.10	$p = 0.009$	0.49 ± 0.21	0.45 ± 0.14	n.s.
	Non	0.95 ± 0.17	0.65 ± 0.11	$p = 0.043$	0.76 ± 0.23	0.82 ± 0.16	n.s.
Onset ramp (ms)	Mus	14.5 ± 4.9	5.3 ± 1.9	$p = 0.038$	5.9 ± 6.6	5.3 ± 2.6	n.s.
	Non	24.1 ± 5.9	10.4 ± 2.3	$p = 0.011$	19.0 ± 7.3	17.3 ± 2.9	n.s.
Tone duration (ms)	Mus	44.6 ± 5.5	38.5 ± 5.4	n.s.	41.1 ± 7.5	40.3 ± 7.2	n.s.
	Non	49.6 ± 6.0	41.8 ± 5.8	n.s.	50.6 ± 8.2	56.2 ± 8.0	n.s.
Rhythm (% correct responses)	Mus	84.4 ± 1.8	90.2 ± 1.6	$p = 2.7E-4$	84.5 ± 2.4	86.4 ± 2.2	n.s.
	Non	79.2 ± 1.9	87.5 ± 1.7	$p = 4.0E-6$	78.2 ± 2.6	77.8 ± 2.4	n.s.
Subjective pitch (−1: fundamental / +1: spectral pitch)	Mus	−0.59 ± 0.11	−0.66 ± 0.12	n.s.	−0.66 ± 0.15	−0.64 ± 0.16	n.s.
	Non	−0.45 ± 0.12	−0.38 ± 0.13	n.s.	−0.52 ± 0.16	−0.53 ± 0.18	n.s.
Auditory threshold for air conduction (dB SPL)	Mus	−1.5 ± 0.9	−1.7 ± 1.1	n.s.	0.2 ± 1.2	0.6 ± 1.5	n.s.
	Non	−0.8 ± 1.0	−0.7 ± 1.2	n.s.	−1.1 ± 1.4	−1.8 ± 1.6	n.s.
Auditory threshold for bone conduction (dB SPL)	Mus	5.7 ± 2.4	1.2 ± 1.3	$p = 0.049$	−1.5 ± 3.2	−1.2 ± 1.8	n.s.
	Non	0.1 ± 2.6	3.5 ± 1.5	n.s.	−3.8 ± 3.6	−6.4 ± 2.0	n.s.
Absolute threshold difference between left and right ear (dB)	Mus	4.4 ± 0.4	4.1 ± 0.4	n.s.	3.6 ± 0.6	4.4 ± 0.6	n.s.
	Non	5.6 ± 0.5	4.0 ± 0.4	$p = 0.010$	3.5 ± 0.5	4.7 ± 0.5	n.s.
Absolute threshold difference pre-post for air conduction (dB)	Mus	3.0 ± 0.5			3.4 ± 0.7		
	Non	3.6 ± 0.6			4.0 ± 0.8		
Absolute threshold difference pre-post for bone conduction (dB)	Mus	12.0 ± 1.1			4.7 ± 1.5		
	Non	11.4 ± 1.2			6.6 ± 1.7		
Absolute threshold difference between air and bone conduction (dB)	Mus	13.2 ± 1.0	6.4 ± 0.6	$p = 4.2E-9$	7.6 ± 1.3	8.6 ± 0.8	n.s.
	Non	10.8 ± 1.1	6.6 ± 0.6	$p = 1.6E-4$	8.5 ± 1.5	8.1 ± 0.9	n.s.

Note: Values are shown in different rows according to musical expertise.
Abbreviations: Mus, musicians; Non, nonmusicians; Sign., significance.

is convincing evidence for the effectiveness of long- and short-term musical training on brain and behavior,[3–16,18–29] systematic studies on the short-term plasticity of the auditory system in response to the active listening concept of Tomatis have been scarce. Until today, his therapeutic approach has only partially been scientifically recognized and accepted even though he was very successful, and the effectiveness of his approach had been proven in various studies.[74–79] With our present study, we demonstrate for the first time the high efficacy of his active listening principles as implemented in the "electronic ear."[66]

As already outlined, the AULOS training integrates four original principles of Tomatis.[64–66] The first principle is that auditory stimuli are progressively filtered during the course of the 2-week listening training, which increasingly challenges the auditory system to complete missing information. It has been emphasized by Tomatis[64] and later by Alos[66] that it is particularly the high-frequency stimulation that is most efficient. Our present findings largely confirm this assumption by showing that the plasticity induced by the listening training was largest in the mid- and high-frequency regions (Figure 4H). In the following, we will try to give a physiological explanation for the great importance of high-frequency stimulation: Harmonic sounds, which are widely used in the AULOS training, are characteristic of voiced sounds of speech, like vowels, and of most musical instruments. Due to the quasi-logarithmic frequency representation along the cochlea, low harmonics stimulate spatially well-separated frequency channels, that is, their maxima are clearly distinguished ("spectrally resolved"). With increasing harmonic numbers, spectral resolution progressively decreases due to an overlap of stimulated frequency channels. As a consequence, in the high-frequency region, cochlear excitation patterns are sharply synchronized to the superposition of unresolved harmonics, which has a periodicity corresponding to the harmonic tone's fundamental frequency. In hair cells, the mechanical excitation patterns induce synchronous voltage fluctuations of their membrane potentials, which in turn elicit neural activity patterns in the auditory nerve.[68] The latter is encoded by neural phase-locking, which is largely preserved in subsequent nuclei along the auditory pathway. Thus, the temporal neural encoding of musical and speech sounds as well as melodies highly relies upon temporal synchronization processes along the auditory

pathway up to the auditory cortex, with a particular involvement of the left hemisphere showing a finer temporal resolution. We have previously shown that a high synchronization in the auditory periphery is mirrored by enhanced amplitudes of AEFs at the cortical level.[93–96] The temporal encoding of auditory features through phase-locking becomes increasingly important in the spectrally, partly resolved mid- and unresolved high-frequency regions.[89,90] It is thus not surprising that the efficiency of AULOS, which heavily relies on high-pass filtered musical stimulation, was strongest in the mid- and high-frequency regions.

As a second principle, the AULOS training uses varying delays in auditory stimulation in a time range of 0–2500 ms to ensure auditory attention. Such temporal fluctuations counteract fatigue effects (physiological adaptation in the auditory periphery and higher-order cognitive habituation), thereby enhancing the amplitudes of cortical auditory evoked responses.[95–98]

As a third principle, the training uses an interlocked stimulation of air and bone conduction. While air conduction is mediated by the direct stimulation via the outer ear canal, the ossicles in the middle ear, and the traveling wave patterns on the basilar membrane,[99] bone conduction is mediated by vibrations of the petrous bone, which are transduced by the outer hair cells into electrical potentials. Previous work has demonstrated that a combination of both transmission types has the capacity to enhance auditory and cognitive learning, initiate multisensory integration processes, and induce transfer effects into other domains in therapeutic applications.[74–79]

According to the Australian neuroscientist and acoustician Andrew Bell, the specific effects of bone conduction may be explained by biomechanical resonance principles,[100,101] as already suggested in the 19th century by Hermann von Helmholtz.[70] The latter invented metallic spherical resonators (so-called "Helmholtz resonators") to identify the various frequencies or musical pitches present in music and everyday noises. On a more general level, biological resonators have been described as "enclosed volumes of air or water that communicate with the outside world through a small opening,"[102] which also seems to be the case in nerve cells[103] and hair cells in the cochlea.[100] Bell demonstrated that on the basilar membrane, the cilium tufts of the outer hair cells are arranged in the form of resonators of different lengths corresponding to the musical chromatic scale.[101] He postulated that the arrival of an external sound activates a pre-established internal tuning similar to the pipes of an organ.[66,100]

As a fourth principle, a so-called "sound rocker" integrates the advantages of the former principles. It combines preset filter settings with predefined delays. Relative to a selected cutoff frequency, segments of prepared music and natural sounds are low- and high-pass filtered and switch between the lower and higher channel, respectively, according to the dynamics of the musical flow.

Neural efficiency and synchronization of AEFs

We found a clear bilateral synchronization of the P1–N1–P2 complex after the listening training, which was strongest for the primary P1 response (Table 1). Moreover, changes were more pronounced for bone than for air conduction as a function of the listening training (Figure 4H). Bone conduction manifests as a multisensory resonance phenomenon, sensorily encoded by the outer hair cells,[66,100] which should further be encoded along the auditory pathway. We suggest that the observed strong P1 synchronization may be based on synchronizing principles that are already effective in the auditory periphery and propagate up to the primary cortical level.

Furthermore, the listening training elicited an increase in the magnitudes of the entire P1–N1–P2 complex. In principle, such an increase may be due to enlarged cell assemblies sensitive to the processing of a certain aspect of information. Alternatively, as the amplitudes of auditory evoked responses measured over the head surface reflect the strengths of underlying dipoles, which are generated by the synchronous activity of neural assemblies, the amplitudes of these AEFs can also be interpreted as a measure of local neural synchrony. Therefore, while the above-mentioned findings of bilateral synchronization reflect a widespread interhemispheric temporal alignment, the growth of the P1–N1–P2 complex may be a sign of local temporal alignment. The amplitude increase was by far strongest for the P2 component, signifying the greatest influence of the listening training on this late AEF component. The latter has precognitive and learning-sensitive characteristics, which are relevant for preparing sensory integration.[14,25,57] However, there was also a significant influence on the P1 amplitude, supporting elementary sound processing and auditory discrimination skills.[42] Moreover, there was an influence on the N1 amplitude generated in the planum temporale, which subserves auditory feature detection,[38] attentional functions,[39,40,104] and spatial sound localization.[105] This suggests that the listening training predominantly affects higher integrative auditory functions, thereby catalyzing a multitude of transfer effects into related domains.[74–79] In this regard, it is noteworthy that a high degree of cortical synchronization can be considered as a sign of neural efficiency.[106] Thus, it seems justified to postulate that active listening promotes neural efficiency in different subregions of the auditory cortex, thereby facilitating elementary sound discrimination, auditory attention, and multisensory integration. Additionally, we found a higher training-induced, short-term plasticity of N1 and P2 amplitudes in the right hemisphere.

AEF latencies were largely preserved after the training for the entire P1–N1–P2 complex. This is not surprising, as response latencies are mostly a function of long-term biological maturational processes,[4,33,35] like the myelination of nerve fibers.[36] Musical expertise was related to a broadened shape of the P2, resulting in a prolonged latency of this component. This may be due to an evocation of different P2 subcomponents as a result of long-term musical training.

Effects of listening training on auditory discrimination abilities

Auditory discrimination abilities and thresholds substantially benefited from the AULOS training. The most prominent improvement was observed for rhythmic abilities, but there were also significant

benefits for the discrimination of onset ramps, intensities, and frequencies, reflected by decreased threshold values (Figure 4A–D). No significant effects were found for tone duration or subjective pitch.

Significant absolute changes (pre – post) were observed for both types of hearing thresholds (air and bone conduction) in response to the listening training. The plasticity of these absolute changes turned out to be about three to four times larger for bone conduction (12 dB, on average) than for air conduction (3 dB on average, Figure 4H), independent of musical expertise. Such differences were practically invisible in the averaged curves (mean changes <1 dB) because the thresholds for air and bone conduction changed in opposite directions in different subjects. In some participants, bone conduction was initially hypersensitive (subthreshold), whereas, in others, it was hyposensitive (suprathreshold). Thus, the mechanism of action has to be considered to be more important for bone conduction than for air conduction and should, therefore, receive more attention in future research and training procedures.

Furthermore, our study revealed that the listening training systematically equalized bone and air conduction, that is, the absolute difference between the two types of conduction was approximately halved (Figure 4I). The equalization effect was highly significant in the mid- and high-frequency regions, but not detectable in the low-frequency region. This may be due to the fact that in the listening training, high-pass filtering above 1 kHz was used to emphasize the middle and higher frequency regions, which are most important for language processing. While the middle frequency region predominantly conveys information about speech vowels (<3 kHz), including the first two formants and the third "singer formant," the high-frequency region is particularly relevant for the transmission of consonants which comprise components of up to 10 kHz[68]—especially while whispering when only high sibilant sounds are conveyed.

In conclusion, our findings indicate a strong positive influence of active listening training on neural auditory processing and perception in adolescence, when the auditory system is still developing.

ACKNOWLEDGMENTS

Supported by the German Research Foundation (DFG; Heisenberg fellowship program "Sound perception between outstanding musical abilities and auditory dysfunction: The neural basis of individual predisposition, maturation, and learning-induced plasticity in a lifespan perspective"). The authors further acknowledge the financial support by the University of Graz.

The AULOS listening training has been developed in cooperation with ear training professors Elke Hofmann, Musikhochschule, Basel, Switzerland; Doris Geller, Musikhochschule, Mannheim-Heidelberg, Germany; Valdis Bernhofs, Jāzeps Vītols, Music Academy, Riga, Latvia), and the listening therapists Kirsten Klopsch, Staufen, Germany; Friedrich Huchting, Eutin-Gothendorf, Germany; Pierre Romain, Charleroi, Belgium; Marianne Eichenberger, Bern, Switzerland; Patricia Anklin, Biel, Switzerland; Anna Meazza, Mailand, Italy; and Liliana Sacarin, Seattle, Washington, USA.

AUTHOR CONTRIBUTIONS

P.S., C.G. and M.C. were involved in the admistration of the listening training and the acquisition of data. P.S., C.G. and J.B. did the analysis of the MEG raw data and psychoacoustic tests. P.S. and A.S.-P. wrote the manuscript and finalized the work. A.S.-P. performed the statistical analysis. All authors contributed to the article and approved the submitted version.

COMPETING INTERESTS

The authors declare no competing interests

PEER REVIEW

The peer review history for this article is available at: https://publons.com/publon/10.1111/nyas.14899.

ORCID

Annemarie Seither-Preisler https://orcid.org/0000-0003-3084-1911

REFERENCES

1. Muente, T. F., Altenmueller, E., & Jaencke, L. (2002). The musician's brain as a model of neuroplasticity. *Nature Neuroscience*, *3*, 473–3478.
2. Zatorre, R. (2005). Music, the food of neuroscience? *Nature*, *434*, 312–315.
3. Wan, C. Y., & Schlaug, G. (2010). Music making as a tool for promoting brain plasticity across the life span. *Neuroscientist*, *16*, 566–577.
4. Fujioka, T. (2006). One year of musical training affects development of auditory cortical-evoked fields in young children. *Brain*, *129*, 2593–2608.
5. Hyde, K. L., Lerch, J., Norton, A., Forgeard, M., Winner, E., Evans, A. C., & Schlaug, G. (2009). Musical training shapes structural brain development. *Journal of Neuroscience*, *29*, 3019–3025.
6. Moreno, S., Marques, C., Santos, A., Santos, M., Castro, S., & Besson, M. (2009). Musical training influences linguistic abilities in 8-year-old children: More evidence for brain plasticity. *Cerebral Cortex*, *19*, 712–723.
7. Ellis, R. J., Bruijn, B., Norton, A. C., Winner, E., & Schlaug, G. (2013). Training-mediated leftward asymmetries during music processing: A cross-sectional and longitudinal fMRI analysis. *Neuroimage*, *75*, 97–107.
8. Chobert, J., Francois, C., Velay, J.-L., & Besson, M. (2014). Twelve months of active musical training in 8- to 10-year-old children enhances the preattentive processing of syllabic duration and voice onset time. *Cerebral Cortex*, *24*, 956–967.
9. Slater, J., Skoe, E., Strait, D. L., O'Connell, S., Thompson, E., & Kraus, N. (2015). Music training improves speech-in-noise perception: Longitudinal evidence from a community-based music program. *Behavioural Brain Research*, *291*, 244–252.
10. Habibi, A., Damasio, A., Ilari, B., Elliott Sachs, M., & Damasio, H. (2018). Music training and child development: A review of recent findings from a longitudinal study. *Annals of the New York Academy of Sciences*, *1423*, 73–81.
11. Tierney, A. T., Krizman, J., & Kraus, N. (2015). Music training alters the course of adolescent auditory development. *Proceedings of the National Academy of Sciences*, *112*, 10062–10067.
12. Pantev, C., Oostenveld, R., Engelien, A., Ross, B., Roberts, L. E., & Hoke, M. (1998). Increased auditory cortical representation in musicians. *Nature*, *392*, 811–814.

13. Herdener, M., Esposito, F., Di Salle, F., Boller, C., Hilti, C. C., Habermeyer, B., Scheffler, K., Wetzel, S., Seifritz, E., & Cattapan-Ludewig, K. (2010). Musical training induces functional plasticity in human hippocampus. *Journal of Neuroscience*, *30*, 1377–1384.
14. Benner, J., Wengenroth, M., Reinhardt, J., Stippich, C., Schneider, P., & Blatow, M. (2017). Prevalence and function of Heschl's gyrus morphotypes in musicians. *Brain Structure & Function*, *222*, 3587–3603.
15. James, C. E., Altenmüller, E., Kliegel, M., Krüger, T. H. C., Van De Ville, D., Worschech, F., Abdili, L., Scholz, D. S., Jünemann, K., Hering, A., Grouiller, F., Sinke, C., & Marie, D. (2020). Train the brain with music (TBM): Brain plasticity and cognitive benefits induced by musical training in elderly people in Germany and Switzerland, a study protocol for an RCT comparing musical instrumental practice to sensitization to music. *BMC Geriatrics*, *20*, 1–19.
16. Olszewska, A. M., Gaca, M., Herman, A. M., Jednoróg, K., & Marchewka, A. (2021). How musical training shapes the adult brain: Predispositions and neuroplasticity. *Frontiers in Neuroscience*, *15*, 204.
17. Zatorre, R. J., Chen, J. L., & Penhune, V. B. (2007). When the brain plays music: Auditory–motor interactions in music perception and production. *Nature Reviews Neuroscience*, *8*, 547–558.
18. Kraus, N., & Chandrasekaran, B. (2010). Music training for the development of auditory skills. *Nature Reviews Neuroscience*, *11*, 599–605.
19. Zatorre, R. J., & Salimpoor, V. N. (2013). From perception to pleasure: Music and its neural substrates. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(Suppl. 2), 10430–10437.
20. Strait, D. L., & Kraus, N. (2014). Biological impact of auditory expertise across the life span: Musicians as a model of auditory learning. *Hearing Research*, *308*, 109–121.
21. Wengenroth, M., Blatow, M., Heinecke, A., Reinhardt, J., Stippich, C., Hofmann, E., & Schneider, P. (2014). Increased volume and function of right auditory cortex as a marker for absolute pitch. *Cerebral Cortex*, *24*, 1127–1137.
22. Besson, M., Chobert, J., & François, C. (2015). Influence of musical expertise on the perception of pitch, duration and intensity variations in speech and harmonic sounds. In C. Astesano & M. Jucla, (Eds.), *Neuropsycholinguistic perspectives on language cognition* (pp. 106–120). Psychology Press.
23. Herholz, S. C., Coffey, E. B. J., Pantev, C., & Zatorre, R. J. (2016). Dissociation of neural networks for predisposition and for training-related plasticity in auditory-motor learning. *Cerebral Cortex*, *26*, 3125–3134.
24. Kraus, N., & White-Schwoch, T. (2017). Neurobiology of everyday communication: What have we learned from music? *Neuroscientist*, *23*, 287–298.
25. Pantev, C., Lappe, C., Herholz, S. C., & Trainor, L. (2009). Auditory-somatosensory integration and cortical plasticity in musical training. *Annals of the New York Academy of Sciences*, *1169*, 143–150.
26. Virtala, P., Huotilainen, M., Putkinen, V., Makkonen, T., & Tervaniemi, M. (2012). Musical training facilitates the neural discrimination of major versus minor chords in 13-year-old children. *Psychophysiology*, *49*, 1125–1132.
27. Lappe, C., Lappe, M., & Keller, P. E. (2018). The influence of pitch feedback on learning of motor-timing and sequencing: A piano study with novices. *PLoS One*, *13*, e0207462.
28. Lappe, C., Bodeck, S., Lappe, M., & Pantev, C. (2017). Shared neural mechanisms for the prediction of own and partner musical sequences after short-term piano duet training. *Frontiers in Neuroscience*, *11*, 165.
29. Lappe, C., Lappe, M., & Pantev, C. (2016). Differential processing of melodic, rhythmic and simple tone deviations in musicians—An MEG study. *Neuroimage*, *124*, 898–905.
30. Sur, S., & Sinha, V. K. (2009). Event-related potential: An overview. *Industrial Psychiatry Journal*, *18*, 70.
31. Serrallach, B., Groß, C., Bernhofs, V., Engelmann, D., Benner, J., Gündert, N., Blatow, M., Wengenroth, M., Seitz, A., Brunner, M., Seither, S., Parncutt, R., Schneider, P., & Seither-Preisler, A. (2016). Neural biomarkers for dyslexia, ADHD, and ADD in the auditory cortex of children. *Frontiers in Neuroscience*, *10*, 324.
32. Schneider, P., Sluming, V., Roberts, N., Scherg, M., Goebel, R., Specht, H. J., Dosch, H. G., Bleeck, S., Stippich, C., & Rupp, A. (2005). Structural and functional asymmetry of lateral Heschl's gyrus reflects pitch perception preference. *Nature Neuroscience*, *8*, 1241–1247.
33. Sharma, A., Martin, K., Roland, P., Bauer, P., Sweeney, M. H., Gilley, P., & Dorman, M. (2005). P1 latency as a biomarker for central auditory development in children with hearing impairment. *Journal of the American Academy of Audiology*, *16*, 564–573.
34. Habibi, A., Cahn, B. R., Damasio, A., & Damasio, H. (2016). Neural correlates of accelerated auditory processing in children engaged in music training. *Developmental Cognitive Neuroscience*, *21*, 1–14.
35. Sharma, A., Kraus, N., Mcgee, T. J., & Nicol, T. G. (1997). Developmental changes in P1 and N1 central auditory responses elicited by consonant-vowel syllables. *Electroencephalography and Clinical Neurophysiology*, *104*, 540–545.
36. Seither-Preisler, A., Parncutt, R., & Schneider, P. (2014). Size and synchronization of auditory cortex promotes musical, literacy, and attentional skills in children. *Journal of Neuroscience*, *34*, 10937–10949.
37. Herdener, M., Esposito, F., Scheffler, K., Schneider, P., Logothetis, N. K., Uludag, K., & Kayser, C. (2013). Spatial representations of temporal and spectral sound cues in human auditory cortex. *Cortex*, *49*, 2822–2833.
38. Horváth, J., Winkler, I. N., & Bendixen, A. (2008). Do N1/MMN, P3a, and RON form a strongly coupled chain reflecting the three stages of auditory distraction? *Biological Psychology*, *79*, 139–147.
39. Näätänen, R. (1990). The role of attention in auditory information processing as revealed by event-related potentials and other brain measures of cognitive function. *Behavioral and Brain Sciences*, *13*, 201–233.
40. Woldorff, M. G., & Hillyard, S. A. (1991). Modulation of early auditory processing during selective listening to rapidly presented tones. *Electroencephalography and Clinical Neurophysiology*, *79*, 170–191.
41. Posner, M. I. (2005). Timing the brain: Mental chronometry as a tool in neuroscience. *PLoS Biology*, *3*, e51.
42. Brattico, E., Bogert, B., & Jacobsen, T. (2013). Toward a neural chronometry for the aesthetic experience of music. *Frontiers in Psychology*, *4*, 206.
43. Lappe, C., Trainor, L. J., Herholz, S. C., & Pantev, C. (2011). Cortical plasticity induced by short-term multimodal musical rhythm training. *PLoS One*, *6*, e21493.
44. Zatorre, R. J. (2001). Spectral and temporal processing in human auditory cortex. *Cerebral Cortex*, *11*, 946–953.
45. Poeppel, D. (2003). The analysis of speech in different temporal integration windows: Cerebral lateralization as 'asymmetric sampling in time.' *Speech Communication*, *41*, 245–255.
46. Boemio, A., Fromm, S., Braun, A., & Poeppel, D. (2005). Hierarchical and asymmetric temporal sensitivity in human auditory cortices. *Nature Neuroscience*, *8*, 389–395.
47. Giraud, A.-L., & Poeppel, D. (2012). Cortical oscillations and speech processing: Emerging computational principles and operations. *Nature Neuroscience*, *15*, 511–517.
48. Chiron, C. (1997). The right brain hemisphere is dominant in human infants. *Brain*, *120*, 1057–1065.
49. Homae, F., Watanabe, H., Nakano, T., & Taga, G. (2007). Prosodic processing in the developing brain. *Neuroscience Research*, *59*, 29–39.
50. Perani, D., Saccuman, M. C., Scifo, P., Anwander, A., Spada, D., Baldoli, C., Poloniato, A., Lohmann, G., & Friederici, A. D. (2011). Neural

language networks at birth. *Proceedings of the National Academy of Sciences of the United States of America*, *108*, 16056–16061.
51. Schneider, P., Scherg, M., Dosch, H. G., Specht, H. J., Gutschalk, A., & Rupp, A. (2002). Morphology of Heschl's gyrus reflects enhanced activation in the auditory cortex of musicians. *Nature Neuroscience*, *5*, 688–694.
52. Bosnyak, D. J. (2004). Distributed auditory cortical representations are modified when non-musicians are trained at pitch discrimination with 40 Hz amplitude modulated tones. *Cerebral Cortex*, *14*, 1088–1099.
53. Shahin, A., Bosnyak, D. J., Trainor, L. J., & Roberts, L. E. (2003). Enhancement of neuroplastic P2 and N1c auditory evoked potentials in musicians. *Journal of Neuroscience*, *23*, 5545–5552.
54. Putkinen, V., Tervaniemi, M., Saarikivi, K., Ojala, P., & Huotilainen, M. (2014). Enhanced development of auditory change detection in musically trained school-aged children: A longitudinal event-related potential study. *Developmental Science*, *17*, 282–297.
55. Gordon, E. E. (1999). All about audiation and music aptitudes: Edwin E. Gordon discusses using audiation and music aptitudes as teaching tools to allow students to reach their full music potential. *Music Educators Journal*, *86*, 41–44.
56. Shahin, A., Roberts, L. E., & Trainor, L. J. (2004). Enhancement of auditory cortical development by musical experience in children. *Neuroreport*, *15*, 1917–1921.
57. Shahin, A., Roberts, L. E., Pantev, C., Trainor, L. J., & Ross, B. (2005). Modulation of P2 auditory-evoked responses by the spectral complexity of musical sounds. *Neuroreport*, *16*, 1781–1785.
58. Reybrouck, M., & Brattico, E. (2015). Neuroplasticity beyond sounds: Neural adaptations following long-term musical aesthetic experiences. *Brain Sciences*, *5*, *69*.
59. Reybrouck, M., Vuust, P., & Brattico, E. (2018). Music and brain plasticity: How sounds trigger neurogenerative adaptations. In V. Chaban (Ed.), *Neuroplasticity: Insights of neural reorganization* (pp. 85–103). Rijeka: InTech.
60. Reybrouck, M., Vuust, P., & Brattico, E. (2018). Brain connectivity networks and the aesthetic experience of music. *Brain Sciences*, *8*, 107.
61. Shtyrov, Y., Nikulin, V. V., & Pulvermuller, F. (2010). Rapid cortical plasticity underlying novel word learning. *Journal of Neuroscience*, *30*, 16864–16867.
62. Macgregor, L. J., Pulvermüller, F., Van Casteren, M., & Shtyrov, Y. (2012). Ultra-rapid access to words in the brain. *Nature Communications*, *3*, 1–7.
63. Kimppa, L., Kujala, T., Leminen, A., Vainio, M., & Shtyrov, Y. (2015). Rapid and automatic speech-specific learning mechanism in human neocortex. *Neuroimage*, *118*, 282–291.
64. Tomatis, A. (1991). *The conscious ear: My life of transformation through listening*. Station Hill Press.
65. Tomatis, A., & Keeping, F. (2005). *The ear and the voice*. Scarecrow Press.
66. Alos, C. (2020). *Bridging audiology and psychology: The secrets of the auditory system*. Independent Publisher.
67. Groß, C., Serrallach, B. L., Möhler, E., Pousson, J. E., Schneider, P., Christiner, M., & Bernhofs, V. (2022). Musical performance in adolescents with ADHD, ADD and dyslexia—Behavioral and neurophysiological aspects. *Brain Sciences*, *12*, 127.
68. Pickles, J. (2008). *An introduction to the physiology of hearing*. Brill.
69. Stenfelt, S. (2015). Inner ear contribution to bone conduction hearing in the human. *Hearing Research*, *329*, 41–51.
70. Helmholtz von, H. (1863). *Die Lehre von den Tonempfindungen als physiologische Grundlage für die Theorie der Musik*. J. Vieweg.
71. Christiner, M., Serrallach, B. L., Benner, J., Bernhofs, V., Schneider, P., Renner, J., Sommer-Lolei, S., & Groß, C. (2022). Examining individual differences in singing, musical and tone language ability in adolescents and young adults with dyslexia. *Brain Sciences*, *12*, 744.
72. Christiner, M., Renner, J., Groß, C., Seither-Preisler, A., Benner, J., & Schneider, P. (2022). Singing Mandarin? What elementary short-term memory capacity, basic auditory skills, musical and singing abilities reveal about learning Mandarin. *Frontiers in Psychology*, *13*, 1–14.
73. Schneider, P., Andermann, M., Wengenroth, M., Goebel, R., Flor, H., Rupp, A., & Diesch, E. (2009). Reduced volume of Heschl's gyrus in tinnitus. *Neuroimage*, *45*, 927–939.
74. Gilmor, T. (1999). The efficacy of the Tomatis method for children with learning and communication disorders: A meta-analysis. *International Journal of Listening*, *13*, 12–23.
75. Thompson, B. M., & Andrews, S. R. (2000). An historical commentary on the physiological effects of music: Tomatis, Mozart and neuropsychology. *Integrative Physiological and Behavioral Science*, *35*, 174–188.
76. Sacarin, L. (2013). *Early effects of the Tomatis listening method in children with attention deficit*. Antioch University Seattle.
77. Picciolini, O., Porro, M., Meazza, A., Giannì, M. L., Rivoli, C., Lucco, G., Barretta, F., Bonzini, M., & Mosca, F. (2014). Early exposure to maternal voice: Effects on preterm infants development. *Early Human Development*, *90*, 287–292.
78. Vervoort, J., de Voigt, M. J. A., & van den Bergh, W. (2007). The improvement of severe psychomotoric and neurological dysfunctions treated with the Tomatis audio-psycho-phonology method measured with EEG brain map and auditory evoked potentials. *Journal of Neurotherapy*, *11*, 37–49.
79. Piccinini, C. (2018). Audiopsychophonology for tinnitus treatment. *Confinia Cephalalgica et Neurologica*, *28*, 135–147.
80. Hämäläinen, M., Hari, R., Ilmoniemi, R. J., Knuutila, J., & Lounasmaa, O. V. (1993). Magnetoencephalography—Theory, instrumentation, and applications to noninvasive studies of the working human brain. *Reviews of Modern Physics*, *65*, 413.
81. Hamalainen, M. S., & Sarvas, J. (1987). Feasibility of the homogeneous head model in the interpretation of neuromagnetic fields. *Physics in Medicine and Biology*, *32*, 91.
82. Sarvas, J. (1987). Basic mathematical and electromagnetic concepts of the biomagnetic inverse problem. *Physics in Medicine and Biology*, *32*, 11.
83. Scherg, M. (1990). Fundamentals of dipole source potential analysis. *Auditory evoked magnetic fields and electric potentials. Advances in Audiology*, *6*, 25.
84. Schneider, P., & Wengenroth, M. (2009). The neural basis of individual holistic and spectral sound perception. *Contemporary Music Review*, *28*, 315–328.
85. Jepsen, M. L., Ewert, S. D., & Dau, T. (2008). A computational model of human auditory signal processing and perception. *Journal of the Acoustical Society of America*, *124*, 422–438.
86. Sutcliffe, P., & Bishop, D. (2005). Psychophysical design influences frequency discrimination performance in young children. *Journal of Experimental Child Psychology*, *91*, 249–270.
87. Bregman, A. S. (1994). *Auditory scene analysis: The perceptual organization of sound*. MIT Press.
88. Shamma, S. (2001). On the role of space and time in auditory processing. *Trends in Cognitive Sciences*, *5*, 340–348.
89. Seither-Preisler, A., Krumbholz, K., & Lütkenhöner, B. (2003). Sensitivity of the neuromagnetic N100m deflection to spectral bandwidth: A function of the auditory periphery? *Audiology and Neurotology*, *8*, 322–337.
90. Seither-Preisler, A., Patterson, R., Krumbholz, K., Seither, S., & Lütkenhöner, B. (2006). Evidence of pitch processing in the N100m component of the auditory evoked field. *Hearing Research*, *213*, 88–98.
91. Zatorre, R. J., Belin, P., & Penhune, V. B. (2002). Structure and function of auditory cortex: Music and speech. *Trends in Cognitive Sciences*, *6*, 37–46.

92. Schönwiesner, M., Rübsamen, R., & Von Cramon, D. Y. (2005). Hemispheric asymmetry for spectral and temporal processing in the human antero-lateral auditory belt cortex. *European Journal of Neuroscience*, *22*, 1521–1528.
93. Seither-Preisler, A., Johnson, L., Krumbholz, K., Nobbe, A., Patterson, R., Seither, S., & Lütkenhöner, B. (2007). Tone sequences with conflicting fundamental pitch and timbre changes are heard differently by musicians and nonmusicians. *Journal of Experimental Child Psychology*, *33*, 743.
94. Herholz, S. C., & Zatorre, R. J. (2012). Musical training as a framework for brain plasticity: Behavior, function, and structure. *Neuron*, *76*, 486–502.
95. Krumbholz, K. (2003). Neuromagnetic evidence for a pitch processing center in Heschl's gyrus. *Cerebral Cortex*, *13*, 765–772.
96. Seither-Preisler, A., Krumbholz, K., Patterson, R., Seither, S., & Lütkenhöner, B. (2004). Interaction between the neuromagnetic responses to sound energy onset and pitch onset suggests common generators. *European Journal of Neuroscience*, *19*, 3073–3080.
97. Seither-Preisler, A., Patterson, R. D., Krumbholz, K., Seither, S., & Lütkenhöner, B. (2006). From noise to pitch: Transient and sustained responses of the auditory evoked field. *Hearing Research*, *218*, 50–63.
98. Lütkenhöner, B., Seither-Preisler, A., Krumbholz, K., & Patterson, R. D. (2011). Auditory cortex tracks the temporal regularity of sustained noisy sounds. *Hearing Research*, *272*, 85–94.
99. Békésy, von G., & Wever, E. G. (1960). *Experiments in hearing* (Vol. 195). McGraw-Hill.
100. Bell, A. (2012). A resonance approach to cochlear mechanics. *PLoS One*, *7*, e47918.
101. Bell, A. (2019). A natural theory of music based on micromechanical resonances between cochlear sensing cells. *Journal of Hearing Science*, *9*(3), 39–49.
102. Encyclopædia Britannica. (1993). Encyclopædia Britannica.
103. Helmholtz, H. (1842). De fabrica systematis nervosi evertebratorum (Doctoral dissertation).
104. Jäncke, L., Mirzazade, S., & Joni Shah, N. (1999). Attention modulates activity in the primary and the secondary auditory cortex: A functional magnetic resonance imaging study in human subjects. *Neuroscience Letters*, *266*, 125–128.
105. Krumbholz, K., Schönwiesner, M., Von Cramon, D. Y., Rübsamen, R., Shah, N. J., Zilles, K., & Fink, G. R. (2005). Representation of interaural temporal information from left and right auditory space in the human planum temporale and inferior parietal lobe. *Cerebral Cortex*, *15*, 317–324.
106. Engel, A. K., & Singer, W. (2001). Temporal binding and the neural correlates of sensory awareness. *Trends in Cognitive Sciences*, *5*, 16–25.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Schneider, P., Groß, C., Bernhofs, V., Christiner, M., Benner, J., Turker, S., Zeidler, B. M., & Seither-Preisler, A. (2022). Short-term plasticity of neuro-auditory processing induced by musical active listening training. *Ann NY Acad Sci*., 1–15.
https://doi.org/10.1111/nyas.14899