

Auditory perceptual learning in musicians and non-musicians

Event-related potential studies on rapid plasticity

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Academic dissertation to be presented,
with the permission of the Faculty of Behavioural Sciences
of the University of Helsinki, for public examination in
Auditorium XII, University main building
on 17 June 2013, at 12 noon.

University of Helsinki
Institute of Behavioural Sciences
Studies in Psychology 90: 2013

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ISSN-L 1798-842X
ISSN 1798-842X
ISBN 978-952-10-8921-3 (pbk.)
ISBN 978-952-10-8922-0 (PDF)
<http://www.thesis.helsinki.fi>
Unigrafia
Helsinki 2013

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Abstract

Music training shapes functional and structural constructs in the brain particularly in the areas related to sound processing. The enhanced brain responses to sounds in musicians when compared to non-musicians might be explained by the intensive auditory perceptual learning that occurs during music training. Yet the relationship between musical expertise and rapid plastic changes in brain potentials during auditory perceptual learning has not been systematically studied. This was the topic of the current thesis, in conditions where participants either actively attended to the sounds or did not. The electroencephalography (EEG) and behavioral sound discrimination task results showed that the perceptual learning of complex sound patterns required active attention to the sounds even from musicians, and that the different practice styles of musicians modulated the perceptual learning of sound features. When using simple sounds, musical expertise was found to enhance the rapid plastic changes (i.e., neural learning) even when attention was directed away from listening. The rapid plasticity in musicians was found particularly in temporal lobe areas which have specialized in processing sounds. However, right frontal lobe activation, which is related to involuntary attention shifts to sound changes, did not differ between musicians and non-musicians. Behavioral discrimination accuracy for sounds was found to be at maximum level initially in musicians, while non-musicians improved their accuracy in discerning behavioral discrimination between active conditions. Yet, the performances in standardized attention and memory tests did not differ between musicians and non-musicians. Taken together, musical expertise seems to enhance the preattentive brain responses during auditory perceptual learning.

Tiivistelmä

Muusikkous muovaa aivojen toiminnallisia ja rakenteellisia piirteitä erityisesti äänten käsittelyyn keskittyvillä aivoalueilla. Intensiivinen kuulohavainto-oppiminen musiikin harjoittelun aikana saattaa selittää sen, miksi muusikoilla nähdään usein voimakkaampia aivovasteita äänille verrattuna ei-muusikoihin. Aiemmissä tutkimuksissa ei tätä aihetta ole systemaattisesti tarkasteltu. Tässä väitöskirjassa tutkittiin muusikkouden yhteyttä aivovasteiden nopeisiin muutoksiin äänten havainto-oppimisen aikana osallistujien tarkkaillessa ääniä sekä tarkkaavaisuuden ollessa suunnattuna pois äänistä. Aivosähkökäyrämittausten (EEG:n) ja kuuntelutehtävien tulokset osoittivat, että monimutkaisten äänisarjojen havainto-oppiminen vaati äänten tarkkailua jopa muusikoilta ja että muusikoiden harjoittelutottumukset vaikuttivat millaisiin ääniin nopeita aivovasteiden muutoksia (ts. neuraalista oppimista) syntyi. Yksinkertaisemmilla ääniärsykkeillä tutkittuna muusikkouden havaittiin tehostavan nopeita aivovasteiden muutoksia myös tilanteessa, jossa ääniä ei tarkkailtu. Havainto-oppimiseen liittyviä muutoksia muusikoilla löydettiin erityisesti äänten käsittelyyn erikoistuneilla ohimolohkon alueilla. Sen sijaan oikean otsalohkon aktivaatio, joka liittyy tahattomaan tarkkaavaisuuden suuntaamiseen äänten poikkeavuuksille, ilmeni samankaltaisena muusikoilla ja ei-muusikoilla. Behavioraalinen äänten erottelu aktiivisissa tilanteissa oli alun alkaen parempi muusikoilla ja vain ei-muusikot paransivat erottelusuoritusta tehtävien välillä. Sen sijaan normitetuissa muisti- ja tarkkaavaisuustesteissä suoriutuminen ei eronnut muusikoiden ja ei-muusikoiden välillä. Löydökset viittaavat siihen, että muusikkous muovaa kuulohavainto-oppimisen hermostollisia mekanismeja erityisesti esitietoisten aivovasteiden osalta.

Acknowledgments

“Why would it be important to know what happens in the brain?” This question stated by one of my lecturers started to haunt me from the very first year of studying psychology. I was part of a workshop where students could practice and discuss classical experiments in cognitive psychology. I had studied the “black box” models of cognition in old textbooks. Often the experimental question was: when we put something into the box (the stimuli), what is the output (behavioral observations and results)? But what was in the black box? I probably could not answer back then, but now I have an urge to do so: I want to know what happens in the black box! Why are box models not common in neurocognitive science? Is it because there are no boxes in the brain? I entered the doctoral training with huge plans in mind. Years passed and I started to realize that the brain is a divergent and distributed system: instead of putting “all the eggs in one basket” the brain actively recycles its own mechanisms between different tasks, and is prepared to lose some connections and create new ones whatever the current demand is. How to apply these findings in practice is a whole new challenge. Not to mention that I would truly appreciate a technique that would apply to all brain activity and be fast, easy, and accurate to record, analyze and interpret. I believe, however, that a dream technique that would reveal all the brain’s secrets is evolving as we speak.

First, I want to give my warmest thanks to my principal supervisor, Professor Mari Tervaniemi, who has provided scholarly guidance all the way from the idea phase to the thesis in its final form. Our discussions have been crucial in the development of my scientific thinking and in learning to be an independent researcher. I am also deeply grateful to my second supervisor, Docent Anu-Katriina Pesonen, who has given me another perspective on the “self-evident,” namely that details are not unimportant. You have both been a great support to me. I would like to thank Dr. Jarmo Hämäläinen and Docent Elvira Brattico, who were exceptional co-authors and thus essential in promoting my doctoral studies. Both of you have given me valuable hands-on guidance in the most complex neurocognitive methodologies.

I am grateful to the current and former leaders of the Department of Psychology, Institute of Behavioural Science, University of Helsinki, and especially to Professor Risto Näätänen and Professor Teija Kujala, Heads of the Cognitive Brain Research Unit of the Institute of Behavioural Sciences (CBRU), for providing facilities for my scientific work. I am also very grateful for personal discussions with several professors and docents in the Institute of Behavioural Sciences (formerly Department of Psychology), University of Helsinki. Professor Veijo Virsu gave me both practical advice and encouragement when I made my first grant applications. I also had a useful discussion with Professor Istvan Winkler concerning the methodology I might adopt. I am thankful to many technical experts in CBRU, who played an important part in my working environment. In addition, Dr. Tuomas Teinonen kindly gave me help when setting up my EEG paradigm. I am deeply grateful to Eeva Pihlaja and Pentti Henttonen for their help in gathering data, and wish them the very best in their future careers. My special thanks for personal support go to the colleagues in the CBRU, the Brain Music Team and the Interdisciplinary Research of Music Centre of Excellence. I thank Dr.

Veerle Simoens for kindly commenting on one of the manuscripts included in this thesis. I also thank many of the collaboration project leaders and members for giving me new challenges and learning experiences during the doctoral training. I have been blessed by stimulating and supportive discussions, as well as sharing knowledge with colleagues in the department and CBRU. My special thanks go to Doc. Dee Nikjeh, who kindly hosted my visit in the University of South Florida (Tampa). Thank you Riikka Lindström for sharing with me your hilarious interpretations of the world. Also, thanks Timo S, for believing in me and the encouragement, before I even understood what a Ph.D. means.

I feel fortunate to have received reviews of my thesis from highly distinguished professionals in the field of neuroscience, Professors Lutz Jäncke and Jyrki Ahveninen. I also want to thank my opponent, Professor Nadine Gaab, for promising to share her expertise, time and effort to my doctoral dissertation.

I am also very grateful for the financial support of the Research Foundation of the University of Helsinki, the Finnish National Graduate School of Psychology, the Chancellor's travel grant award fund, as well as the Finnish Center of Excellence in Interdisciplinary Music Research (University of Jyväskylä, funded by the Academy of Finland) with Prof. Petri Toiviainen as its head. Moreover, this thesis would have not been completed without voluntary participants who were courageous enough to take part.

I want to give special thanks to my family who as a child gave me a musically encouraging atmosphere and the freedom to have as many hobbies as I wanted. I carry with me the *love* I experienced in my youth in Northern Carelia to this very day. My remodelling project called "Old School" gives me another reason to go more often back to my childhood neighbourhoods. Last but not least my thanks go to Olli: I have been fortuitous to share with you the example of your exceptional inner strength and determination. Finally, the greatest blessing in my life is our son Eliel, who brings the deepest joy into our hearts.

Marblehead, Massachusetts, May 2013

A handwritten signature in black ink, appearing to read "Aue Seppänen". The signature is written in a cursive, flowing style with some loops and flourishes.

List of original publications

This thesis is based on the following original publications, referred to in the text by their roman numerals (I-IV).

- I** Seppänen, M., Brattico, E., & Tervaniemi, M. (2007). Practice strategies of musicians modulate neural processing and the learning of sound-patterns. *Neurobiology of Learning and Memory*, 87, 236–247.
- II** Seppänen, M., Hämäläinen, J., Pesonen, A-K., & Tervaniemi, M. (2012). Music training enhances rapid neural plasticity of N1 and P2 source activation for unattended sounds. *Frontiers in Human Neuroscience*, 6. Doi: 10.3389/fnhum.2012.00043.
- III** Seppänen, M., Hämäläinen, J., Pesonen, A-K., & Tervaniemi, M. (in revision). Passive sound exposure induces rapid perceptual learning in musicians: Event-related potential evidence.
- IV** Seppänen, M., Pesonen, A-K., & Tervaniemi, M. (2012). Music training enhances the rapid plasticity of P3a/P3b event-related brain potentials for unattended and attended target sounds. *Attention, Perception, & Psychophysics*, 74, 600–612.

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Abbreviations

A1	Primary auditory cortex
ANOVA	Analysis of variance
EEG	Electroencephalography
EOG	Electrooculogram
ERP	Event-related potential
MEG	Magnetoencephalography
ISI	Interstimulus interval
MMN	Mismatch negativity
RP	Repetition positivity
rm-ANOVA	Repeated measures ANOVA
SEM	Standard error of the mean
SOA	Stimulus onset asynchrony
SSA	Stimulus-specific adaptation
WMS-R	Wechsler Memory Scale – Revised

1 Introduction

Brain functionality and structures for auditory processing have remarkable neural plasticity throughout the lifespan. Neural plasticity refers to the capacity of the brain to change its functional properties and/or structure either through maturation or learning (Pascual-Leone, Amedi, Fregni, & Merabet, 2005). The purpose of effective neural plasticity is to optimize the responsiveness for processing demands in various environments. At the cortical level, the learning-induced functional neural changes are reflected as increasingly synchronized neural populations and reorganized representation (neuronal ‘tuning’) for the learned sound feature. Functional neural changes may occur very rapidly after short-term exposure or learning, occurring within seconds to minutes (Weinberger & Diamond, 1987). These rapid neural changes may be a necessary precondition for longer-term plastic changes (Pascual-Leone et al., 2005). The high capacity of reorganization in the cortical functions after goal-oriented active training or through passive exposure enables the perceptual learning of new auditory stimuli, such as music or a foreign language (François & Schön, 2010; Marie, Kujala, & Besson, 2012), and the rehabilitation of auditory functions.

The improved ability of the senses to discriminate differences in the attributes of sounds is often called auditory perceptual learning (Gilbert, Sigman, & Crist, 2001; Goldstone, 1998). Perceptual learning is a type of procedural learning in which improved discrimination of stimuli at the sensory level can be evaluated by examining changes in neural processing and behavioral discrimination. In neural terms, auditory perceptual learning can be observed as rapid plastic changes in the responses to the specific learned stimuli. Figure 1 illustrates how perceptual learning and rapid plasticity (as well as musical expertise) could be seen as a continuum depending on the duration of plastic effects and the required amount of training. As a third dimension, these concepts may vary according to how stimulus-specific or generalizable the learning can be. Since perceptual learning incorporates rapid neuronal changes, and perceptual learning is studied by observing neural changes, these terms are used interchangeably here.

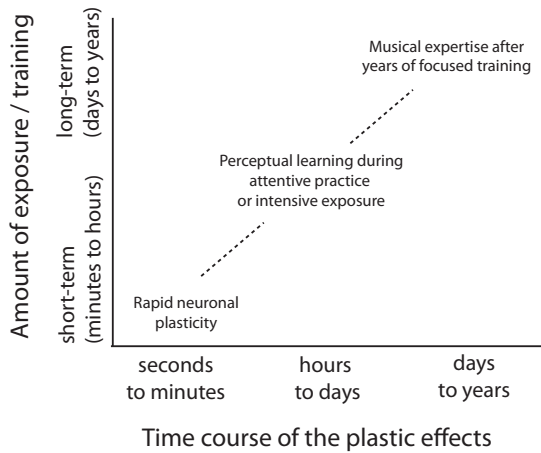


Figure 1. The time course and required amount of training for rapid plasticity, perceptual learning and musical expertise

Neural changes can be studied objectively with auditory event-related potentials (ERP) that are obtained recording electroencephalography (EEG). Typical learning-related plastic changes could consist of enhanced ERP responses (i.e., facilitation) or diminished responses with or without the capacity to recover for the auditory stimuli (i.e., habituation and adaptation, respectively). For example, neurocognitive studies on long-term learning effects have demonstrated that in adults, neural responses are enhanced for the phonemes that are part of their native language when compared to foreign language phonemes that they do not typically hear in daily life (Näätänen, Lehtokoski, Lennes, Cheour, Huotilainen et al., 1997). This finding illustrates the “use it or lose it” principle of the brain’s emergent reorganization and plasticity: the sounds that are not present or repeatedly heard (and are not relevant) in our environment do not have as large a representation in our cortical processing as familiar sounds like phonemes in the mother tongue. It also shows that the brain is capable of learning the sound structures in the native language without effortful training by passively extracting the statistical regularities in the auditory stream. Together with active goal-oriented training, learning by “passively” extracting the sound structures are likely neural mechanisms for auditory perceptual learning that are also present in active music training (Pascual-Leone et al., 2005).

Several neurocognitive studies have demonstrated that professional musicians generally have stronger and faster neural processing for sounds when compared to non-musicians (for reviews, see Jäncke, 2009; Pantev & Herholz, 2011; Tervaniemi, 2009). This is illustrated by the finding that musicians have enhanced processing for sounds played with the timbre of their own main instrument (Pantev, Roberts, Schulz, Engelien, & Ross, 2001). Also, the type of musicianship can modulate the auditory processing. For example, conductors who need to locate musical instruments from many spatial locations in the orchestra pit, show enhanced attention to spatially-located sounds when compared to other musicians and non-musicians (Nager, Kohlmetz, Altenmüller, Rodriguez-Fornells, & Münte, 2003).

These above-mentioned studies do not, however, directly address the question whether long-term auditory training could enhance rapid plastic changes during auditory perceptual learning. Thus, my thesis is aimed at comparing the rapid plastic changes in ERP responses to sounds between musicians and non-musicians. Since ERPs can be measured even when participants are not attending to listening sound stimuli (in passive conditions), it allows one to compare sound processing between groups having differences in motivation, attentional or behavioral discrimination skills. Most importantly, it is an ideal method for studying sound processing because the time resolution is very accurate.

1.1 Effects of short-term auditory training on rapid neural plasticity

Rapid plasticity after short-term auditory exposure or training can be seen functionally as enhanced neural processing for relevant events in the short (within seconds to minutes) time span (for reviews, see Pantev, Engelien, Candia, & Elbert, 2003; Schlaug, 2003). Although the exact neural mechanisms are not well understood, neurocognitive studies have consistently confirmed that the auditory system is capable of extracting the sound environment and its rules in a probabilistic manner without focused attention (Fiser, Berkes, Orban, & Lengyel, 2010). In other words, regularly repeated and familiar sounds are processed differently from irregular, deviating sounds. In practice, encoding statistical rules inherent in speech and music may enable auditory perceptual learning of these functions even without attention. In addition to encoding stimulus features, the

auditory system develops a prediction model for the sound environment that is used to process sound events in an optimized manner: repeated, familiar events typically habituate, while unexpected, deviating sounds initially produce stronger responses (Grill-Spector, Henson, & Martin, 2006; Todorovic, van Ede, Maris, & de Lange, 2011). Passive exposure type of perceptual learning could also lead to learning that can be generalized to untrained features (Zhang & Kourtzi, 2010). For example, learning to discriminate pitch contours in melodies could be generalized to the discrimination of linguistic pitch contours (i.e., prosody; see Marques, Moreno, Castro, & Besson, 2007). Feedback-guided attentional learning, on the other hand, could then lead to feature-dependent learning (Zhang & Kourtzi, 2010). Both forms of auditory perceptual learning, the short-term passive exposure to sounds and active auditory training, can be studied with scalp-recorded ERPs.

A large number of auditory ERP studies on rapid plasticity have been conducted within a stimulus paradigm where the neural responses (the magnitude and the speed of processing) to frequently repeated sounds (called as standard sounds) are examined. This enables us to see how the brain responds to increasingly familiar sounds. Auditory ERP components, such as P1, N1, and P2 (see detailed description below), are ideal for studying rapid plasticity for standard sounds because although they occur automatically after the presentation of any sound, these components are also sensitive to training and various top-down effects, such as active attention and reinforcement (Purdy, Kelly, & Thorne, 2001; Seitz & Watanabe, 2005). For example, the auditory evoked P1 response, which occurs 50–80 ms after the sound onset and reflects thalamo-cortical processing and a nonspecific gating (inhibiting the overstimulation of higher cortical processing) mechanism, is modulated by the level of attention (Boop, Garcia-Rill, Dykman, & Skinner, 1994). Although no rapid plasticity has been reported for P1, long-term musical training modulates P1 (see next section). The N1 response, peaking at 80–110 ms after sound onset, may reflect acoustic sound feature detection (Näätänen & Picton, 1987). For sounds, N1 is enhanced during selective attention tasks (e.g., Hillyard, Hink, Schwent, & Picton, 1973; Woldorff & Hillyard, 1991) and demonstrates rapid plasticity after 15–40 minutes of intensive training (Brattico, Tervaniemi, & Picton, 2003, Ross & Tremblay, 2009). The P2 response, which is elicited at 160–200 ms after sound onset, reflects further stimulus evaluation and classification and is typically enhanced after

prolonged training (Bosnyak, Eaton, & Roberts, 2004; Reinke, He, Wang, & Alain, 2003; Tremblay, Inoue, McClannahan, & Ross, 2010). Rapid plasticity in these ERPs can occur without behavioral improvements in discrimination accuracy or can even precede them (see e.g., Ross & Tremblay, 2009). P1, N1, and P2 studies implicate the automaticity of the neural system in extracting auditory events even without active attention to sounds.

In the so-called oddball paradigm, deviating sounds are presented randomly among standard sounds. These surprising changes produce a different neural response than with familiar sounds because of the mismatch in the sensory memory template. The mismatch negativity (MMN), a change-related ERP component, is considered an accurate marker of learning-induced neural plasticity for deviant sounds both after long- and short-term training (Kujala & Näätänen, 2010; Näätänen, Gaillard, & Mäntysalo, 1978). The MMN is a negative ERP that peaks at approximately 100–250 ms after an unexpected change in a physical feature of the stimulus, or an abstract pattern rule, or an omission of sound in a pattern (Kujala, Tervaniemi, & Schröger, 2007; Näätänen, Tervaniemi, Sussman, Paavilainen, & Winkler, 2001). Previous MMN studies on rapid plasticity with non-musician participants have shown that active attention and training is needed to elicit rapid (within one recording session) enhancement of the MMN response. For example, the MMN amplitude recorded during passive exposure to complex sound patterns was increased for deviating target sounds after an active discrimination task (Gottselig, Brandeis, Hofer-Tinguely, Borbély, & Achermann, 2004; Näätänen, Schröger, Karakas, Tervaniemi, & Paavilainen, 1993). Moreover, the rapid plasticity of the MMN was modulated by the difficulty of the target stimuli (Gottselig et al., 2004) and the initial MMN strength of the individual (Näätänen et al., 1993). Learning-related neural changes in MMN can, however, either precede or parallel behavioral improvement (Atienza, Cantero, & Dominguez-Marin, 2002; Tremblay, Kraus, & McGee, 1998; van Zuijen, Simoens, Paavilainen, Näätänen, & Tervaniemi, 2006). Since these studies do not report the effects of musical training, it is also unclear whether musical experts require focused attention for rapid plastic effects of MMN to emerge.

Another question is whether frontal and temporal generators of MMN have different plastic effects because these generators seem to have different functional roles (see e.g.,

Giard, Perrin, Pernier, & Bouchet, 1990; Rinne, Alho, Ilmoniemi, Virtanen & Näätänen, 2000). Brain imaging studies have consistently found bilateral superior temporal gyrus generators of the MMN in the auditory cortices (Deouell, 2007). MMN activation in the temporal lobes reflects feature-specific comparison of deviant (i.e., unexpected irregular sound) and standard (regularly presented sound) stimuli (Shalgi & Deouell, 2007). Temporal activation is typically followed with activation in the right frontal source at the inferior frontal gyrus (Giard et al., 1990, Rinne et al., 2000). Some studies suggest that the frontal component of the MMN shows right hemisphere dominance for pitch deviants and left hemisphere dominance for duration deviants (e.g., Molholm, Martinez, Ritter, Javitt, & Foxe, 2005). Frontal activation might reflect an involuntary switch of attention or inhibition of the response to the deviant (Deouell, 2007; Giard et al., 1990; Rinne et al., 2005). The existence of a frontal source of the MMN has been controversial in imaging and intracranial studies, while lesion studies have shown strong evidence for a frontal MMN source (Deouell, 2007).

MMN is often followed by another change-related ERP component, P3a in passive exposure and P3b in attentive condition. The P3a response is a positive deflection that occurs 200–400 ms following either a low-probability novel (infrequent nontarget) or salient (infrequent target) change in a stream of predictable (frequent) auditory stimulations (Polich, 2007). Originally, the P3a was associated with novel auditory (or visual: Courchesne, Hillyard, & Galambos, 1975) processing; however, it can be elicited by the infrequent but non-novel changes in an oddball paradigm. For easily discriminated deviant sounds, P3a responses can occur even when a listener is instructed to ignore the auditory stimuli and to concentrate on other tasks (Schwent, Hillyard, & Galambos, 1976). Frontocentrally maximal P3a responses might reflect involuntary attention switching toward irregular deviant sounds that follow passive comparisons between regularly presented standard and irregularly presented deviant sounds (Polich, 2007). In contrast, slower and temporoparietally maximal P3b responses reflect controlled attention for task-relevant stimulus characteristics (Pritchard, 1981). In general, P3a and P3b responses are suitable for studying both bottom- and top-down influences; they are modulated by attention, subjective probability (familiarity), difficulty levels, and stimulus features, such as the relative salience when compared to frequent sounds. P3a and P3b responses show both short- and long-term plasticity

changes following auditory training (Atienza, Cantero, & Stickgold, 2004; Uther, Kujala, Huotilainen, Shtyrov, & Näätänen, 2006). Within a single session, P3a and P3b amplitudes have shown repetition-dependent reductions for target sounds in the frontal areas and a shift from frontal to parietal cortical activation during both active and passive listening conditions (Friedman, Kazmerski, & Cycowicz, 1998). Accordingly, repetition-dependent reduction may relate to auditory perceptual learning. In a recent study where late positivity (P3b/P600) amplitude was reduced in left-hemisphere electrodes during speech tasks (but not during tone-learning tasks), the results were interpreted as learning because the amplitude decrease was also paralleled by improved behavioral discrimination (Ben-David, Campeanu, Tremblay, & Alain, 2011). Reduced activation in the frontal areas may also reflect a lower demand for attentional processing of target sounds when the auditory memory template for sounds develops in temporoparietal areas in conjunction with auditory perceptual learning.

Taken together with the previous findings of rapid plasticity of various auditory ERP components, it is not clear in what conditions focused attention is required to elicit auditory perceptual learning. It is possible that complex sound patterns require attentive discrimination while more simple sounds would already elicit learning-related changes after passive exposure. In the present thesis, the effects of passive exposure and active attention to sounds were evaluated with both complex sound patterns (Study I) and relatively more simple sounds (Studies II, III and IV). Secondly, the differential roles of frontal and temporal ERP generators in rapid plasticity have not been systematically studied. Studies II and III addressed this question by examining the source estimates for both standard and deviant sound ERP activation. Thirdly, different ERP components seem to elicit either decrease or enhancement after auditory perceptual learning which precedes or parallels the behavioral improvement in discrimination accuracy. This suggests multiple neural mechanisms in auditory perceptual learning depending on the condition. The various patterns of rapid neural plasticity were examined for pre-attentive and attentive ERP components in conditions where participants were attending and not attending to the sounds. Finally, my thesis studies have investigated the effects of musical expertise on rapid plastic changes during auditory perceptual learning, a topic that has been largely ignored in previous ERP studies.

1.2 Effects of long-term music training on neural auditory processing

Long, intensive playing and training of a musical instrument leads to neuroplastic changes that can be observed often both as functional and structural changes in brain architecture. In addition to demonstrating the mechanisms of long-term experience-dependent neural plasticity, neurocognitive studies of musicians have revealed how expertise develops over the years (Münste, Altenmüller, & Jäncke, 2002). Structural changes related to music training can be seen in the specific brain regions which are involved in musical processing and skills (e.g., Gaser & Schlaug, 2003; Pantev, Ross, Fujioka, Trainor, Schulte et al., 2003; Schlaug, Jäncke, Huan, & Steinmetz, 1995). For example, gray matter volume in music-related brain areas was found to correlate positively with professional status in music: while professional musicians had the highest gray matter volume, amateur musicians had intermediate, and non-musicians the lowest gray matter volume in motor, auditory, and visuo-spatial brain regions (Gaser & Schlaug, 2003). In another study, musicians had 102% higher amplitudes and 130% larger gray matter volume of the primary auditory cortex in comparison to non-musicians (Schneider, Scherg, Dosch, Specht, Gutschalk et al., 2002).

Functional changes in professional musicians have been extensively studied with ERPs. When compared with non-musicians, enhanced auditory processing in musicians is demonstrated by increased amplitude and/or faster latency of several components of the auditory ERPs and magnetic fields (Pantev & Herholtz, 2011; Tervaniemi, 2009). The findings related to the impact of musical training in automatic processing of sounds, as indicated by the P1, N1, and P2 ERP components (based on traditional ERP analysis and ERP source estimates), are not entirely clear. For instance, P1 has been reported to show larger (P50m: Schneider, Sluming, Roberts, Scherg, Goebel et al., 2005) and smaller amplitudes (Nikjeh, Lister, & Frisch, 2009) as well as different lateralization (P1m: Kuriki, Kanda, & Hirata, 2006) in musicians compared to non-musicians. In addition, the findings about N1 plasticity have been discrepant. In some studies, the N1 response was larger or faster in musicians (Baumann, Meyer, & Jäncke, 2008; N1m: Kuriki et al., 2006; Pantev, Oostenveld, Engelien, Ross, Roberts et al., 1998; omission-related N1: Jongsma, Eichele, Quian Quiroga, Jenks, Desain et al., 2005) but not in

others (N1m: Lütkenhöner, Seither-Preisler, & Seither, 2006; Schneider et al., 2002). Further, the P2 response was larger in musicians than in non-musicians during passive listening (Shahin, Bosnyak, Trainor, & Roberts, 2003; Shahin, Roberts, Pantev, Trainor, & Ross, 2005) and active discrimination (Jongsma et al., 2005; P2m: Kuriki et al., 2006, see Baumann et al., 2008).

Neurocognitive studies have consistently shown enhanced preattentive sound (or sound pattern) processing for irregularly deviating sounds that are temporally and spectrally complex (and thus music-related) sounds in musicians when compared to non-musicians (e.g., enhanced MMN responses: Brattico et al., 2003; Fujioka, Trainor, Ross, Kakigi, & Pantev, 2004; Koelsch, Schröger, & Tervaniemi, 1999; Rüsseler, Altenmüller, Nager, Kohlmetz, & Münte, 2001; van Zuijen, Sussman, Winkler, Näätänen, & Tervaniemi, 2004; Vuust, Pallesen, Bailey, van Zuijen, Gjedde et al., 2005). For example, an MMN for slightly impure ('mistuned') chords was elicited only in professional violinists but not in non-musicians (Koelsch et al., 1999). During attentive discrimination, violinists discriminated better the slight mistunings and had enhanced N2b (shows typically in active condition instead of MMN and has differential generators) and P3b to the mistuned chords compared with non-musicians. In another study, complex sound patterns did not significantly elicit stronger MMN in musicians but still musicians were behaviorally more accurate in detecting more complex sound pattern deviants than non-musicians (Boh, Herholz, Lappe, & Pantev, 2011).

Apart from these findings of enhanced behavioral and/or neural processing in musicians, P3b responses were enhanced in musicians compared to non-musicians when listening attentively for pitch deviants (Tervaniemi, Just, Koelsch, Widmann, & Schröger, 2005; for late positivity, see Besson & Faïta, 1995), rhythmic irregularities (Vuust, Østergaard, Pallesen, Bailey, & Roepstorff, 2009), and sound location deviants (Nager et al., 2003). In rhythmically trained musicians, P3b latencies were shorter for irregular sound omissions in rhythmic contexts (Jongsma, Desain, & Honing, 2004). Similarly, P3a latencies for pitch deviant sounds were shorter when musically trained participants were asked to ignore sounds (Nikjeh et al., 2009). These findings indicate stronger and faster involuntary attention switching (P3a) and enhanced matching of the working memory trace (P3b) to relevant target sounds in musicians.

Commonly, enhanced sound processing in musicians is interpreted as resulting from several years of experience in actively playing and listening to music. This interpretation is supported by the findings where the duration and amount of music training correlate positively to the strength of the neural activation as well as structural changes in the auditory processing areas in musicians (e.g., Bengtsson, Nagy, Skare, Forsman, Forssberg et al., 2005; Ellis, Norton, Overy, Winner, Alsop et al., 2012; Pantev et al., 1998). Secondly, there seem to be sensitive periods in the development of sensory and motor skills when learning occurs exceptionally quickly with less effort than would be the case in adulthood. Such development can also be accompanied by large changes in the brain. For example, several correlational findings in musician studies have shown that when musical training has been started before the onset age of 9, the plastic changes are shown to be particularly strong in auditory processing areas and in fine motor skill areas (Elbert, Pantev, Wienbruch, Rockstroh et al., 1995; Hutchinson, Lee, Gaab, & Schlaug, 2003; Rosenkranz, Williamon, & Rothwell, 2007; but see Schwenkreis, El Tom, Ragert, Pleger, Tegenthoff et al., 2007; for a review, see Penhune, 2011). The third argument for experience-dependent plasticity in musicians is that, as discussed in the previous paragraph, the neural changes in musicians are particularly strong for musically relevant and complex stimuli when compared to non-musicians, and that there seem to be differences even between musicians using different instruments and practice styles (Vuust, Brattico, Seppänen, Näätänen, & Tervaniemi, 2012). Yet, there is no direct evidence of the genetic influence on the enhanced auditory processing in musicians (see Discussion, 5.1.3 *Auditory perceptual learning of deviant sounds*).

Although neurocognitive studies of musicians have provided ample evidence for the existence of various experience-dependent plasticity changes in the brain (Jäncke, 2009), the effects of musical expertise on rapid neural plasticity during short-term auditory perceptual learning have not been systematically studied. One previous study demonstrated that although musicians had stronger rapid plasticity for melodic sound patterns, both musicians and non-musicians required attentive discrimination training to elicit an MMN enhancement (Tervaniemi, Rytönen, Schröger, Ilmoniemi, & Näätänen, 2001). It was also tentatively shown that the learning of sound patterns is affected by the type of musical expertise. Musicians who did not use scores when practicing and

playing (for example, jazz musicians, improvisers, and musicians who often played by ear) seemed to be more accurate in detecting contour changes (i.e., the patterns of ups and downs in the pitches of a melody) within randomly transposed melodic patterns after the attentive discrimination task when compared with a group including both musicians who often did use scores and with non-musicians. These findings suggest that the characteristics of rapid plasticity during auditory perceptual learning can differ between different types of musicians and that plastic changes require active attention at least when more complex sound patterns are used. In Study I, the effects of different types of musicians were explicitly studied by using similar sound patterns than in Tervaniemi et al. (2001). Although the active attention is likely to be needed to learn complex sound patterns, it is not clear, however, whether active attention is needed for learning the statistical structures in simpler sound stimuli. This was systematically tested in Studies II-IV. In those studies, the difference in auditory perceptual learning between musicians and non-musicians was compared for standard and deviant sound ERP responses (Studies II-IV) and generators (Studies II and III) with simpler sounds also during passive exposure without interleaving active attention conditions.

2 The aims of the study

The overarching aim in this thesis was to study the neural basis of auditory perceptual learning. Four studies examined the effects of long-term auditory training (i.e., musical expertise) and focused attention on rapid plasticity during auditory perceptual learning after short-term passive exposure to sounds (in an unattended condition) and active auditory discrimination training for ERPs. The specific research questions were the following:

1. What effect does the type of one's musical expertise have on rapid plasticity during auditory perceptual learning? This question was studied by comparing the MMN response between musicians preferring aural practice strategies (i.e., improvising, training aurally without musical scores and by listening recordings) and musicians preferring non-aural practice strategies (Study I).

2. How does musical expertise modulate the rapid plasticity of regularly and irregularly presented sounds? This question was studied by comparing the P1, N1, and P2 responses for regularly presented standard sounds among oddball stimuli (Study II) as well as deviant ERP within a MMN time frame, and P3a and P3b ERP responses (Study III and Study IV) for irregularly presented deviant sounds with musicians and non-musicians.
3. Is auditory perceptual learning modulated differently by musical expertise in passive exposure to sounds versus active discrimination of sounds? This question was studied by comparing the ERP responses and source activation between passive experimental blocks which were not intervened by active listening (Studies II, III, and IV), and between passive blocks that were interleaved with the active deviant sound discrimination task (all studies).
4. Are there differences in rapid plasticity between temporal and frontal ERP source activation? This question was studied by examining the source activation for the ERPs (Studies II-III).

Based on the earlier findings of enhanced ERP responses in musicians, we hypothesized that rapid plasticity would differ between musicians and non-musicians (Studies II-IV). For question 4, we hypothesized that rapid plasticity would differ between temporal and frontal generators since these sources seem to have different functionality. Temporal cortices reflect the basic auditory processing while the frontal cortex is assumed to reflect the change detection (and the orientation reflex).

3 Methods

3.1 Participants

In all studies, the criteria for identifying musicians were that the individual was either studying to be a professional musician, had graduated from Finnish universities or polytechnics (Universities of applied sciences) providing professional musical education or was employed full-time as a musician. All participants filled in a questionnaire to assess their musical background and musicians also completed a questionnaire about

their practicing strategies. The non-musicians were mostly from the University of Helsinki, Finland. None of the non-musicians had received professional musical training. The participants were recruited by announcements in the student email lists and information boards. All participants had normal hearing, and normal or corrected vision. None of the participants reported a history of neurological or psychiatric disorder.

In **Study I**, all the participants were musicians (for a summary, see Table 1). On the basis of the practicing strategy questionnaire, musicians were divided into aural and non-aural groups. Aural strategy was defined by theoretically chosen variables such as improvising, playing by ear, and rehearsing by listening to recordings. Accordingly, criteria for the aural group were the following: improvised at least once a day, played by ear often or quite often, and practiced by listening to the music being studied from recordings (either of one's own playing or of another musician's playing) at least 10% of the total practice time or more. Those who reported improvising, playing by ear or practicing by listening to recordings were seldom or never categorized into the non-aural group. Finally, 13 participants (9 men and 4 women, $M_{\text{age}}=23$ years) were included in the aural group and 11 participants (3 men and 8 women, $M_{\text{age}}=22$ years) in the non-aural group. The age range for the analyzed participants was 18–29 years ($M_{\text{age}}=23\pm 3$ *SD*).

In **Studies II and III**, participants were musicians ($n=14$, 9 women, 5 men, age range = 21–39, $M_{\text{age}}=25\pm 5$ *SD*, for a summary, see Table 2) and non-musicians ($n=16$, 9 women, 7 men, age range = 19–31, $M_{\text{age}}=24\pm 3$ *SD*). Age did not differ significantly between groups. Musicians had played for a total of 18 years on average.

In **Study IV**, the participants from Studies II and III were included together with 11 additional participants (Table 2). The participants were musicians ($n=20$, 15 women, age range = 21–39 years) and non-musicians ($n=21$, 11 women, age range = 19–31 years). Musicians had an average of 18 years of playing and training experience, and reported practicing an average of 13 h/week. None of the non-musicians had received professional musical training; however, most had played an instrument during their first school years. Five of the non-musician participants reported currently practicing for 0.5–1 h/week.

Table 1. Musical background of participants in Study I

ID	Age	Sex	Main instrument	Second instruments	Playing experience in years ^a	Graduated musicians (grad) / Working in music / Studying music	Onset age of playing ^b	Overall practice hours for main and second instruments per week ^c
Aural musicians								
1	19	m	piano	vocals, drums	13	studying	6	12.5*+1
2	25	m	electric guitar	piano	13	studying	12	5+2
3	20	m	trombone	-	9	studying	11	10
4	28	m	piano	vocals	21	studying/grad	7	14
5	21	m	electric bass	afro drums	8	studying	13	4
6	29	f	piano	vocals	21	grad/working	8	14+7
7	19	f	vocalist	-	3	studying	16	12
8	29	m	cello	piano, vocals	23	studying/grad	6	13.5*+4
9	22	f	electric guitar	piano, vocals	13	studying/grad	9	15+4
10	21	f	violin	saxophone	15	studying	6	7+5
11	25	m	vocalist	guitar, drums, bass, keyboard, clarinet	3	studying	22	0+10
12	23	m	vocalist	trumpet	6	working	17	7+7
13	22	m	piano	percussions	16	grad/working	6	13.5*+10
<i>M</i> =23 <i>SD</i> =4					<i>M</i> =13 <i>SD</i> =7		<i>M</i> =11 <i>SD</i> =5	<i>M</i> =14 <i>SD</i> =6
Non-aural musicians								
1	23	f	piano	violin, vocalist, oboe	18	studying	5	7+8
2	24	f	clarinet	piano	17	studying/grad	7	15+1.5*
3	23	f	cello	piano	17	studying/grad	6	12+3
4	25	f	trombone	piano	18	studying	7	2
5	25	f	piano	vocals, harp, organs	19	grad/working	6	12+6*
6	21	m	cello	-	14	studying	7	24
7	22	f	piano	drums	16	studying	6	10+3
8	19	m	piano	cello	12	studying	7	25+1
9	23	f	piano	vocals	18	studying	5	3.5*+1.5*
10	21	f	harp	-	9	studying	12	21
11	18	m	piano	alto saxophone	13	working	5	35
<i>M</i> =22 <i>SD</i> =2					<i>M</i> =16 <i>SD</i> =3		<i>M</i> =7 <i>SD</i> =2	<i>M</i> =17 <i>SD</i> =9

Note. F = female, m= male. One participant in the non-aural group self-reported as dyslexic. All reported being right-handed except for two participants in the non-aural group who reported being left-handed.

- Playing experience in years have been computed based on the earliest onset age of playing and the age of the participant.
- For onset age, the earliest onset age of playing is presented in cases where a participant started playing with other music instruments before choosing the current main instrument.
- * denotes that the average hours have been computed based on the number of hours the participant reported. The second value represents the overall practice hours for the secondary instruments. For the total mean and standard deviation, the combined value of practice hours for main and secondary instruments has been used.

Table 2. Musical background of participants in Studies II, III, and IV

Musicians	Age	Sex	Main instrument ^a	Second instruments ^b	Playing experience in years	Graduated musicians (grad) / Working in music / Studying music	Onset age of playing	Overall practice hours for main and second instruments per week ^c
1**	21	f	piano	-	15	grad/work/studying	6	2
2**	24	f	piano	electric bass, cembalo, violin, vocals	18	grad/studying	6	13
3**	21	f	vocalist	piano	11	studying	10	14
4**	23	m	vocalist	N/A	14	grad/studying	9	5.5
5**	23	f	piano	vocals	17	studying	6	5.5
6**	25	f	violin	piano	19	grad	6	3.5
7**	29	f	piano	vocals, trumpet	21	grad/work	8	11
8**	21	f	violin	piano	17	studying	4	5
9**	22	m	electric bass	piano, vocals, guitar, drums	12	studying	10	1
10**	22	f	cello	piano	16	grad/work/studying	6	5
11**	23	m	violin	piano	18	grad/work/studying	5	28
12**	28	f	contrabass	piano	21	grad/work/studying	7	20
13**	39	m	vocalist	piano	31	grad/work	8	8
14**	26	m	guitar	piano	16	work/studying	10	24
15*	28	f	folk harp	piano	18	grad/work	12	6.5
16*	26	f	vocalist	drums	21	studying	5	11.25
17*	30	f	vocalist	piano, harpsichord	20	studying	10	15
18*	26	f	double bass	piano, guitar	16	grad/studying	10	28
19*	28	f	flute	piccolo	20	work/studying	8	27.5
20*	30	f	clarinet	piano, recorder	20	grad/work/studying	10	25
	<i>M</i> =26 <i>SD</i> =4				<i>M</i> =18 <i>SD</i> =4		<i>M</i> =8 <i>SD</i> =2	<i>M</i> =13 <i>SD</i> =9
Non-musicians	Age	Sex	Instruments played over 1 year		Had music theory lessons		Onset age of playing	Currently playing hours
1**	25	f			-			
2**	23	f	violin, piano		-		6	0.5
3**	25	m	-		-		-	-
4**	22	f	alto violin, piano, guitar		yes		7	0
5**	25	f	violin, flute		-		7	0
6**	23	f	-		-		-	-
7**	26	f	piano		-		7	0
8**	31	f	piano		-		8	0
9**	23	f	piano		-		6	0
10**	29	f	piano		-		7	0
11**	24	m	piano		yes		10	0.5
12**	24	m	guitar		yes		12	0.75
13**	22	m	guitar		-		8	0
14**	19	m	piano		-		5	-
15**	22	m	guitar		-		15	0.5
16**	25	m	-		-		-	-
17*	24	f	piano		-		10	0
18*	28	m	-		-		-	-
19*	25	f	violin		yes		7	0
20*	24	m	accordion		yes		7	0
21*	22	m	violin, piano, drums		-		5	0.5
	<i>M</i> =24 <i>SD</i> =3						<i>M</i> =8 <i>SD</i> =3	<i>M</i> =0.2 <i>SD</i> =0.3

Note. F = female, m = male. * These participants were analyzed in Study IV and ** in Studies II and III.

- Vocalists and instrumental musicians were analyzed as one group.
- In professional musician education, it is typical to have at least one secondary instrument. Most often it is the piano, which is a basic requirement for passing some of the music theory studies.

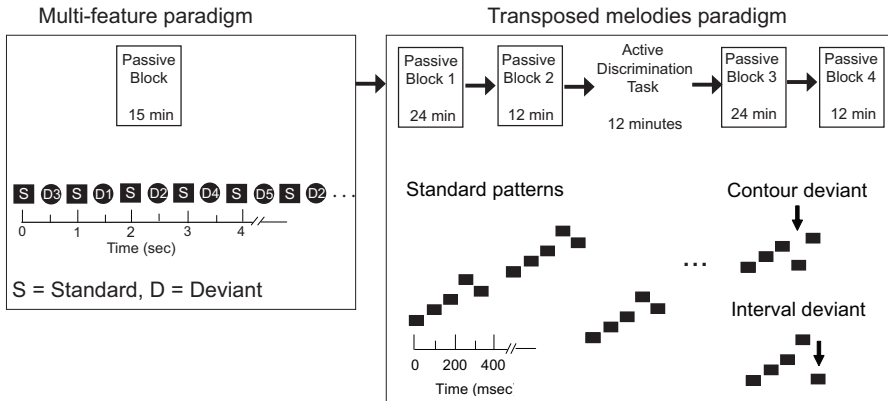
- c) The reported hours of practice may not tell how much a musician played in general since the education requires intensive participation in orchestras and performing, which may not have been reported as solo “practice.” Questions on the frequency of solo chamber music or orchestra performances revealed that 11 musicians had at least one solo performance per month (one reporting a couple of performances in one week), 8 musicians had at least one small music group performance in a month and four musicians had a group performance once a week (the same musician was allowed to report several different activities). Five musicians had at least one orchestra performance per month and five reported having 1-2 orchestra performances per week. It should also be noted that musicians participating in the current study had already passed the highly competitive entrance selection for studying to be professional musicians.

3.2 Procedure

All experiments were done in the EEG laboratory of the former Department of Psychology, Cognitive Brain Research Unit (CBRU), University of Helsinki. During the EEG recordings, participants sat on a comfortable chair in an electrically-shielded chamber. During all passive blocks, participants were asked to ignore the sounds and concentrate on a muted and subtitled self-chosen movie with subtitles while hearing the stimuli (described in detail in the next section). During the active tasks, participants were instructed to press a button whenever they noticed a deviant sound among the standard sounds. The summary of EEG designs and stimuli in studies I-IV can be found in Figure 2. In all studies, participants gave written informed consent before the experiment. They also read the instructions before the experiment as well as received oral instructions. The participants were compensated for their voluntary participation with hourly- based monetary reward (Study I) or movie tickets (Studies II-IV). The experimental protocol was conducted in accordance with the Declaration of Helsinki and approved by the ethics committee of the former Department of Psychology at the University of Helsinki.

In **Study I**, EEG recordings started with the multi-feature oddball paradigm (15 min) followed by a transposed-melody paradigm. The transposed-melody paradigm included two ignore conditions interrupted by an attentive condition when participants were instructed to look at a fixation point, listen to the sounds, and push a button immediately after hearing any deviant stimulus. Participants were not told that there were two different kinds of deviants in the sequences. This instruction was intentionally kept non-directive. During the ignore conditions, participants watched a self-selected silent and subtitled movie while being presented with the stimuli via headphones at a 65 dB sound pressure level. The behavioral tasks (the Advanced Measures of Music Audiation test,

1 EEG Design in Study I



2 EEG Design in Studies II-IV

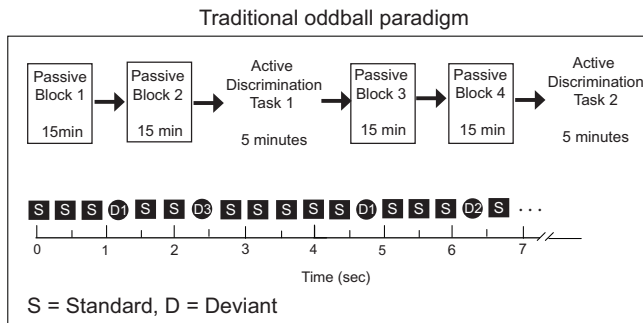


Figure 2. Summary of EEG designs and stimuli in the thesis studies. In Study I, two different oddball paradigms were presented. First, a multi-feature paradigm, which consisted of standard sounds alternating with one of the deviant sounds (frequency, duration, sound source location, intensity or gap) was presented. Secondly, a series of blocks (interleaved with one active discrimination task) were presented. In all these blocks, a transposed-melodies paradigm, consisting of melody-like sound patterns, was presented. In this paradigm, two deviating patterns, contour and interval, occurred infrequently among frequent standard patterns. In Studies II, III, and IV (2), the design included a traditional oddball stimuli where single deviating sound (either frequency, duration, or sound source location) occurred infrequently among standard sounds.

Gordon, 1989, and a questionnaire about musical background) were presented on another day.

In **Studies II–IV**, the first day consisted of the EEG recording together with psychophysiological measures of the peripheral nervous system (to be reported elsewhere). Before the EEG recording, participants answered the Edinburgh Handedness Questionnaire (Oldfield, 1971) and a questionnaire on their musical

training history. The stimuli were presented at 50 dB above the individual threshold (measured before the recordings). The stimuli were presented in Passive Blocks 1 and 2, Active Task 1, Passive Blocks 3 and 4, and Active Task 2 (see the illustration in Figure 2). Passive blocks lasted 15 minutes each, and the active tasks lasted 5 minutes each. This design allowed us to examine the effects of passive exposure to sounds (i.e., neural changes between blocks 1 and 2 before the active task), as well as the effects of active attention on ERP responses to unattended sounds (i.e., neural changes between blocks presented before and after active task). Before the first active task, all participants had a self-paced short practice. After this, half of the participants in the musician and the non-musician groups were allocated into feedback and no-feedback groups. The feedback group received visual feedback after each correct answer. There was no visual feedback for incorrect or missed answers. The remaining participants were told to look at the fixation cross on the screen, while the sound stimuli and the task were the same as with the feedback group. The purpose of the feedback was to offer guidance, especially to non-musicians, who had not been trained in auditory discrimination tasks like the musicians. We could not study the effects of feedback on the neural measures reliably, due to the small group sizes, which resulted in problems with the signal-to-noise ratio. Therefore, the ERP results are reported as pooled across the feedback and no-feedback groups. However, preliminary analyses of behavioral effects of feedback showed that only non-musicians who had visual feedback during the active task improved the discrimination of difficult deviants between Active Tasks 1 and 2 ($\chi^2=6.88$, $p=.03$), while non-musicians without feedback did not show this effect. Since arousal can influence the neural responses, participants gave a self-evaluation of how aroused they felt before and after each task. Self-reported arousal level before and after each active task did not differ between musicians and non-musicians.

During the second testing day (approx. one week after the first session), participants did a follow-up of the behavioral discrimination task (Active Task 3) without any visual feedback. Participants also did a series of personality questionnaires (not reported here) and cognitive tests, which consisted of the Finnish versions of Immediate and Delayed Auditory Verbal Memory scales as well as the Digit span scale of the Wechsler Memory Scale–Revised (WMS-R; Wechsler, 1996) and the Stroop Color-Word Interference Test (original formulation, see Stroop, 1935). The Stroop test score is the difference between

the number of correct items in color-word naming and color-naming tasks. In the color-word naming task, participants are asked to name as quickly as possible the name of the color for the printed words “yellow,” “red,” “blue,” and “green” (in Finnish). The color contrasted with the printed word (e.g., “yellow” was printed in blue). In the color-naming task, participants are asked to name aloud the color of the letters “xxxx” printed either in blue, red, yellow, or green. In WMS-R auditory verbal tests, the participant’s task is to recall the word pairings. In the Digit Span Test, the experimenter reads a series of digits, increasing in length, that the participant has to repeat either forward (3 to 8 digits) or backward (3 to 7 digits).

3.3 Stimuli in EEG recordings

The summary of stimuli and paradigms in all studies is presented in Figure 2. In Study I, the auditory perceptual learning of interval and contour changes within musical patterns was studied with the transposed melodies paradigm, which was adapted from the study by Tervaniemi et al. (2001): the Contour deviant was the same as in their original study, whereas the Interval deviant was added in order to compare the differences between the neural processing of those two music-relevant features and to increase the difficulty of the paradigm. Each melody-like pattern consisted of five different 50-ms sinusoidal tones separated by the 50-ms silent interval. The stimulus onset asynchrony (SOA) between the patterns was 1200 ms. Patterns were transposed randomly on 15¹ frequency levels (tones varying between 330 and 1100 Hz). All the standard patterns ($p=.86$) followed an ABCED structure in terms of musical “form” (see Figure 2). In the Contour deviant the 4th tone of the melody pattern was different (ABCAD in formal terms) and in the Interval deviant the last, (5th), tone was different (e.g., ABCEA) ($p=.07$ for both). A rule was adopted in the presenting of stimuli according to which two identical high sound patterns would not appear consecutively. Altogether, 1800 melody patterns were presented during each ignore condition and 600 patterns in the attentive condition. Before the transposed melodies paradigm, a multi-feature experiment (Näätänen, Pakarinen, Rinne, & Takegata, 2004) was presented.

¹ Erratum to Seppänen et al., 2007: In 2.4.2 the transposed-melody experiment description says that there were 12 frequency levels although 15 is the correct number.

This paradigm consisted of five deviant sounds that were presented ($p=.10$ each) so that every other tone was a standard sound ($p=.50$). Deviating sounds were the following: frequency (10% higher or lower than the standard repeated tone), duration (25 ms longer or shorter than the standard tone), sound source location (90° degree to the left or right from the binaurally perceived standard tone), intensity (10 dB louder or softer than the standard tone), and gap (cutting out 7 ms from the middle of the tone). SOA was 500 ms and all tones lasted 75 ms (except the duration deviants). Stimuli were presented using the BrainStim program (developed at the CBRU) .

In Studies II–IV, during both passive and active conditions, oddball stimuli consisting of infrequent deviant sounds and frequent standard sounds (70% of all stimuli) were presented. Standard sounds consisted of harmonically rich tones of 466.16, 493.88 or 523.25 Hz that varied randomly between blocks (and active tasks). The fundamental frequency was 150 ms in duration, with 10-ms rise and fall times (added with two harmonic partials in proportions of 60%, 30%, and 15%). The fundamental frequency was varied between blocks to avoid frequency-specific neuronal fatigue (which could also be considered short-term plasticity) caused by repetition of the same physical stimulus (Grill-Spector, Henson, & Martin, 2006). Among the standard sounds, pitch, duration, and location deviances of three difficulty levels (easy, medium, and difficult) were presented (10% equally distributed throughout the three difficulty levels). The pitch deviants were 5%, 2.5%, and 1% higher than the standard tones at the easy, medium, and hard difficulties, respectively. Duration deviants were from easy to difficult, as follows: 75 ms (50% shorter than standard), 112.5 ms (25% shorter), and 131.25 ms (12.5% shorter), respectively. The Location deviant was generated by creating interaural time and decibel level differences between the left and right ear. On the stereo channels representing the left ear, the sound started either 1200 μ s (easy), 700 μ s (medium), or 300 μ s (difficult) later in time, so that deviants were perceived as coming from the right ear. SOA was 400 ms in both passive and attentive conditions. At least one standard tone was presented after each deviant. Stimuli were presented using Presentation (Neurobehavioral Systems, Inc., USA) software.

In each passive block, each deviant sound (three deviant types with three difficulty levels, nine altogether) was presented 75 times among 1575 standard sounds. In active tasks, the stimuli and SOA were the same as in passive blocks but the number of trials

for each deviant was dependent on the number of correct answers that the participant gave; after five successive correct responses, the difficulty level was raised. Although we intentionally used simple tones rather than long, melodic stimuli that would have given an advantage to the musicians, the adaptive task also allowed for an assessment of improved discrimination for demanding (difficult) deviances. The average numbers of correct trials in Active Tasks 1 and 2 were not significantly different between musicians and non-musicians (Study IV).

3.4 EEG acquisition and signal processing

3.4.1 Study I

EEG was recorded using a 32-electrode cap (Lectron, Finland) with a nose-reference and additional electrodes placed on the left and right mastoids. The horizontal electrooculogram (EOG) was recorded using electrodes placed at the outer canthi of the left and right eyes and the vertical EOG was monitored from the Fpz location. The EEG was amplified, digitized (sampling rate of 500 Hz; online filter 0.1 and 100 Hz) and the offline band pass filtered (1-20 Hz) using the Acquire and Edit programs (Compumedics NeuroScan, El Paso, Texas). Epochs (-100-1200 ms, with 100 ms prestimulus interval) were averaged separately for each of the deviant and standard stimuli for each subject with an EEG or EOG change exceeding 100 μ V excluded from the averaging. The resulting ERPs were then baseline corrected from 100ms before the sound onset to the beginning of the sound.

Difference waveforms were computed individually for each deviant by subtracting the ERP to the standard stimulus from the ERP to the deviant stimulus. The difference waveforms were then re-referenced to the averaged value of both mastoids. A grand average for each experimental group was computed from all the individual ERP averaged difference waveforms. From the grand average difference wave, the most negative peak at the latency between 100 and 200 ms after the deviant sound onset was quantified. The individual MMN amplitudes were then computed at 9 electrodes (F3, Fz, F4, FC3, FCz, FC4, C3, Cz, and C4) as the mean value of ± 20 ms window centered at the grand average MMN peak latency measured from the frontocentral electrode FCz.

The MMN latency was detected in each individual subject for each deviant as the most negative peak between 100 and 200 ms at the FCz electrode.

3.4.2 Studies II-IV

EEGs were recorded with the BioSemi ActiveTwo measurement system (BioSemi, The Netherlands) with a 64-channel cap with active electrodes and nose reference. Additional electrodes were used to record EOG, below the lower eyelid of the right eye and mastoids. EEG data were down-sampled to 512 Hz offline from online 2048 Hz before further processing and filtering in BESA v5.2 software (MEGIS Software GmbH, Germany). Large muscular artifacts were first visually checked and removed manually, and channels having relatively large high-frequency noise compared with the neighboring channels were interpolated. Automatic adaptive artifact correction was conducted for the continuous data using 150 μ V criteria for horizontal EOG and 250 μ V for vertical EOG (Berg & Scherg, 1994; Ille, Berg, & Scherg, 2002). Further artifacts (such as blinks) that were not corrected were excluded based on each subject's individual amplitude thresholds (determined by the interactive BESA Artifact scanning tool) after epoching. Thereafter EEG was 0.5 Hz high pass filtered and 35 Hz low pass filtered. The data were divided into 500-ms epochs beginning 100 ms before sound onset (prestimulus baseline) and ended 400 ms after the sound onset. Epochs were baseline-corrected (from -100 to 0 ms prestimulus). Thereafter, deviant and standard ERPs were averaged separately for each participant, condition, and stimuli. Grand-average waveforms were computed for each stimulus, condition, and group. The sound location deviant was omitted from all statistics after failing to show reliable deviant sound ERP responses. Nose-referenced averaged files were converted into ASCII multiplexed format for further analysis in Matlab R2008a (MathWorks, Inc., Natick, MA, USA).

In **Study II**, the peak latencies for each standard stimulus in each block were determined from grand average waves for each group by visual inspection from Fz (P1) and Cz (N1, P2). Peak latencies were determined between 40 and 90 ms for P1 (maximum) from Fz, 80-140 ms for N1 (minimum) from Cz, and 120-200 ms for P2 (maximum) from Cz. Mean amplitudes for standard were computed \pm 20 milliseconds

around the peak latency of the grand average for each participant, block, and stimulus. P1, N1, and P2 were not analyzed from the active tasks but only from passive blocks.

In **Study III**, peak latencies for each deviant stimulus in each passive block were determined from grand average waves for each group by visual inspection from Fz within MMN time frame, and from left and right mastoid electrodes. After this, mean amplitudes of the twelve channels (F3, Fz, F4, FC3, FCz, FC4, C3, Cz, C4, P3, Pz, P4) for each participant, deviant stimulus (deviant type and difficulty level) and block were computed ± 20 milliseconds around the groups' peak latency of the grand average. After this, individual peak latencies were determined between 100-250 ms for all participants for each deviant stimulus in each block. Deviant ERPs in Study III were analyzed only from passive blocks when attention was directed to another task (i.e., watching a movie). This procedure prevents the by-products of attentional processes such as the N2b response, which overlaps with the deviant ERP (including MMN) within this time period during focused attention (Sinkkonen & Tervaniemi, 2000). Unlike here, MMN is often analyzed from difference waves (subtracting the standard response from the deviant sound response) (Duncan, Barry, Connolly, Fischer, Michie et al., 2009). Since there were significant differences even in the standard sound ERPs between musicians and non-musicians (see Results for Study II), the average waveforms were used in deviant ERP quantification in Study III instead of difference waveforms (yet these are shown in Seppänen, Hämäläinen, Pesonen, & Tervaniemi, in revision). By this choice we ensured that the differences in ERP results cannot be attributed to, or are not caused by, differences in standard responses. Also, the difference waveforms reflect a computational outcome between standard and deviant responses, unavoidably consisting of both endogenous (MMN) and exogenous (N1, P2) processes that originate from different neural mechanisms. Taken these considerations into account, the analyzed response in Study III is thus called a *deviant ERP within a MMN time frame* instead of MMN.

In **Study IV**, grand-average waveforms were used to determine peak latencies for each group, by visual inspection from Fz for P3a responses (passive blocks), and Pz for P3b responses (active tasks). Peak latencies were used to calculate mean amplitudes ± 20 ms around the peak latency for each participant, deviant type, difficulty level, and block. Peak latencies for the maximum values were calculated between 200 and 400ms

for the P3a and P3b responses. It is possible to have longer onset latencies for P3b; however, due to the short stimulus onset asynchrony (400 ms), the selected time window avoided overlapping responses. Due to technical difficulties, the data from one non-musician participant were missing from Passive Block 4, and the medium and difficult deviants were missing from Passive Block 3. To keep the signal-to-noise ratio consistent, only participants completing a minimum of 14 trials per deviant were analyzed in the active tasks (Cohen & Polich, 1997). On average, the number of completed trials was higher (as reported in Study IV).

3.5 ERP Source analysis (Studies II and III)

BESA Research v5.3 was used for source analysis with preprocessed grand average data without further filtering. ERP source activation was only analyzed from passive blocks. The BESA realistic head model for adults was used. Regional sources with three orientations were used to model a single source. Compared with dipole modeling, regional sources are more realistic for source modeling because these assume multiple active sites in the cortex instead of one (dipole). However, computationally they may give redundant information in cases of basic sensory activation, which typically require only one orientation for accurate estimation of the generator. Exact localization of the brain activity (or comparing the location of the sources between blocks) were not the main goals here and thus regional sources were used to capture the brain activity originating from a relatively wide area in the range of centimeters. The four passive experimental blocks (1, 2, 3, and 4) were combined to make robust seed models for standard and deviant stimuli (separately). Separate seed models were obtained for musicians and non-musicians, and for each deviant stimulus. Seed models were calculated for the 40 ms interval, ± 20 ms around the local maximum in the global field power. After calculating the seed models, individual source waveforms (with peak latency and mean amplitude) and orientations (with first orientation set at maximum) were computed with the Simplex algorithm provided by BESA, for each ERP and each passive block separately by using the fixed source locations of the corresponding seed model, and by adjusting the latency window to the maximum individually when the maximum was at a different time interval.

Seed models for P1, N1, P2 (standard sounds) and deviant ERP within a MMN time frame (deviant sounds) consisted of four sources (see the source locations in Figure 3, and a complete illustration of deviant ERP sources in Seppänen et al., in revision). Based on the previous literature, one source was placed and fitted near the auditory cortex in each hemisphere with symmetry constraint (e.g. Huotilainen, Winkler, Alho, Escera, Virtanen et al., 1998; Picton, Alain, Woods, John, Scherg et al., 1999; Weisser, Weisbrod, Roehrig, Rupp, Schroeder et al., 2001). Even though two temporal sources are often enough to approximate the source model for auditory events, frontal activation may also involve the processing of sound change (e.g. Deouell, 2007). Thus sources in the left and right frontal areas were also assumed. Although sources for P1, N1, and P2 were relatively similar (cf. Yvert, Fischer, Bertrand, & Pernier, 2005), separate models can be justified by the previous studies that have shown different localizations and functionality for these components (Godey, Schwartz, de Graaf, Chauvel, & Liégeois-Chauvel, 2001; Hari, Pelizzone, Mäkelä, Hällström, Leinonen et al., 1987; Ross & Tremblay, 2009). After comparing different models for the deviant ERP source for the Easy Duration deviant, six regional sources were used instead of four. The different source structure for this condition could be due to either different cognitive process engaged for processing easy duration changes or to the overlap of obligatory responses to the offset of the tone. However, additional parietal sources did not show significant effects and were not evaluated further.

3.6 Statistical analyses

ERP responses were analyzed for the passive conditions in all studies and for the active conditions in Study IV. In Studies I, II and III, repeated measures ANOVAs were used to analyze the ERP changes between blocks. In Study IV, a mixed-effects model of the ANOVA was used because it allowed a flexible dependency structure for the model and did not exclude the participant when a missing value was encountered (Gueorguieva & Krystal, 2004). In Study I, the statistical significance of the MMN component (i.e., existence of the response when compared to the standard response) was determined with one-tailed t-tests against zero at the FCz electrode. In Studies III and IV, pairwise t-test comparisons were used to determine whether the mean amplitudes for deviant sounds

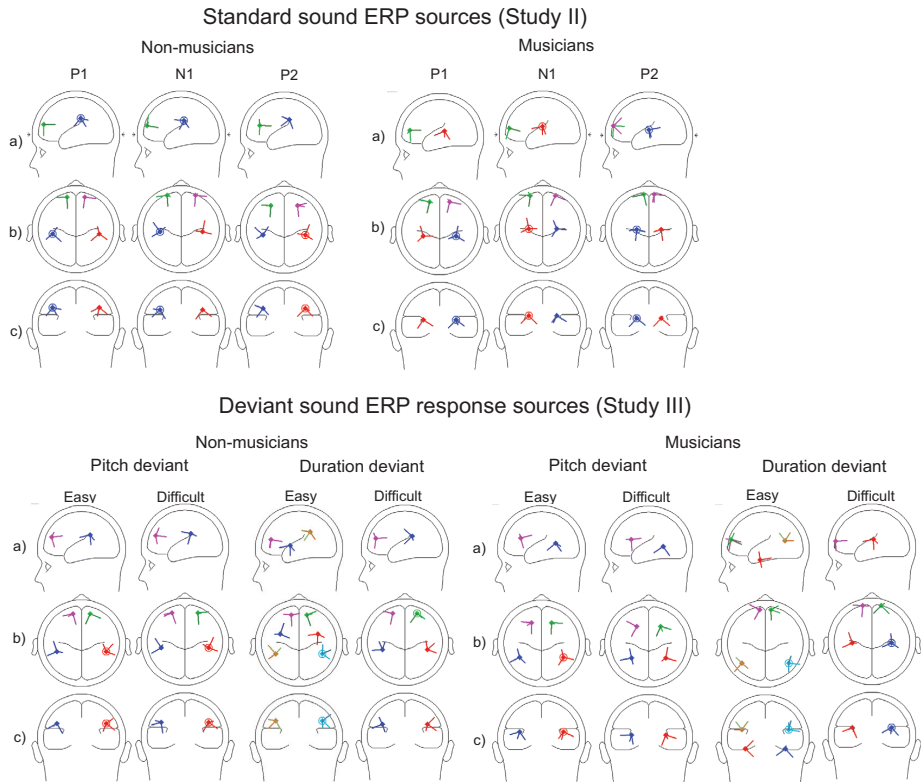


Figure 3. ERP source locations of the seed models in Studies II and III. Musicians' and non-musicians' sources for the standard and deviant ERPs are presented from the a) sagittal, b) vertical, and c) coronal viewpoints. The complete figure including source locations for the medium deviant in Study III are shown in Seppänen et al., in revision.

differed significantly from the mean amplitudes for standard sounds in Fz for the deviant ERP within a MMN time frame and P3a and in left and right mastoid electrodes for the temporal (mastoid) component of the deviant ERP (in a MMN time frame) as well as Cz for P3b within each group. All statistical tests are reported with the alpha level of .05 as the significance criterion. All *p*-values for ANOVAs are reported with Greenhouse-Geisser corrected values with uncorrected *F*-values. Post hoc tests are reported with Bonferroni adjusted *p*-values for multiple comparisons unless otherwise stated (Studies II-IV) and with a priori planned comparisons in Study I (without corrections). Statistics were computed with SPSS v11 (SPSS Inc., USA) in Study I, and with SPSS v16 (SPSS Inc., USA) and SPSS v18 (SPSS Inc., an IBM company, USA) statistical softwares in Studies II, III, and IV.

3.6.1 Study I

MMN amplitudes and latencies of transposed-melody experiments were analyzed with repeated measures analysis of variance (rm-ANOVAs) using Deviant type (Contour and Interval), Sagittal (anterior vs. posterior electrodes) and Coronal (left, central vs. right electrodes) divisions as within-subject factors, Condition (before vs. after active task) and Group (aural and non-aural) as a between-subject factor. The Sagittal division factor included frontal (F3, Fz, and F4), frontocentral (FC3, FCz, and FC4), and centroparietal (C3, Cz, and C4) electrodes (see Figure 4). The Coronal division factor included left (F3, FC3, and C3), central (Fz, FCz, and Cz), and right (F4, FC4, and C4) electrodes. The MMN latencies to the Interval and Contour deviants of the transposed-melody experiment were equalized by subtracting 100 ms from the Interval MMN latency because the tone deviations occurred at different positions between the Interval and Contour melody patterns. The multi-feature paradigm was analyzed in the same way excluding the Condition factor. The Deviant type levels also consisted of frequency, intensity, sound location, duration and gap.

The behavioral data of the attentive condition for the transposed-melody experiment were analyzed as follows: button presses occurring 100–1200 ms after the deviant melody onsets were classified as hits. The remaining button presses were classified as false alarms.

3.6.2 Studies II-III

In **Study II**, for standard sounds, amplitudes and latencies were analyzed separately for each component (P1, N1, and P2) using blocks (Passive Blocks 1, 2, 3, and 4), frontality (frontal: F3, Fz, F4, frontocentral: FC3, FCz, FC4, central: C3, Cz, C4, parietal: P3, Pz, P4), and laterality (left hemisphere: F3, FC3, C3, P3, middle row: Fz, FCz, Cz, Pz, right hemisphere: F4, FC4, C4, P4) as within-subject factors and musical training (musician, non-musician) as the between-subjects factor. To determine whether rapid plasticity between blocks was related to length of musical training or onset age of playing in musicians, Pearson correlations were computed between these variables and P1, N1, and P2 changes between blocks.

In **Study III**, mean amplitudes and latencies were separately analyzed for the frontally maximal subcomponent and the auditory–cortex generated (mastoid leads) component of deviant ERP within a MMN time frame using blocks (Passive blocks 1, 2, 3, and 4), deviant type (pitch, duration), difficulty (easy, medium, difficult level), and frontality (F3, Fz, F4 for frontal, FC3, FCz, FC4 for frontocentral, C3, Cz, C4 for central, P3, Pz, P4 for the parietal region), as repeated measures, and musical expertise (musicians, non-musicians) as the between-subjects factor. In a separate rm-ANOVA, only main effects and interactions concerning laterality (F3, FC3, C3, P3 for the left hemisphere, Fz, FCz, Cz, Pz for middle line, F4, FC4, C4, P4 for the right hemisphere) were tested, with otherwise the same variables. The same factors were used for temporal (mastoidal) ERP analysis except for replacing frontality and laterality with only one factor, the electrode (left hemisphere mastoid, right hemisphere mastoid).

Statistical analysis for ERP source activation mean amplitudes and peak latencies was conducted with the same parameters as with traditional ERPs except that frontality and laterality were replaced by the Source (left frontal, right frontal, left temporal, right temporal). We used only maximum orientation for the statistical analysis of all sources.

3.6.3 Study IV

Separate mixed-model ANOVAs were calculated for the P3a and P3b responses. For the passive conditions, blocks (Passive Blocks 1, 2, 3, or 4) were used as a repeated measure, participant as a random effect, deviant type (pitch and duration), difficulty level (easy, medium, and difficult), and frontality (F3, Fz, and F4 for the frontal region; FC3, FCz, and FC4 for the frontocentral region; C3, Cz, and C4 for the central region; P3, Pz, and P4 for the parietal region) as within-subjects effects, and music training (musicians and non-musicians) as the between-subjects effect. Laterality was tested with similar parameters, with the exception of frontality, for which a within-subjects effect of laterality (F3, FC3, C3, and P3 for the left hemisphere; Fz, FCz, Cz, and Pz for midline; F4, FC4, C4, and P4 for the right hemisphere) was substituted.

For the active conditions, separate mixed-model ANOVAs were calculated for pitch and duration deviants; only duration deviants had a sufficient number of trials at both medium and difficult levels, whereas pitch deviants had enough trials only at the difficult level. The small number of trials for easy deviants in the active task was due to

the fact that task difficulty was adapted on the basis of individual learning profiles and most participants discriminated easy deviants well enough to quickly move to the medium (and eventually into the hard-difficult) difficulty level. For both the duration and pitch analyses, the task (Active Tasks 1 and 2) was used as a repeated measure, with frontality or laterality as a within-subjects effect. For duration deviants only, the difficulty level was also used as a within-subjects effect.

Behavioral performance in Active Tasks 1, 2, and 3 (the follow-up) was evaluated with a χ^2 test separately for musicians and non-musicians. Due to small group sizes (and low signal-to-noise ratio after movement corrections), the effects of feedback on the neural measures were not studied except for the behavioral performance. For P3a and P3b, the relationships between the improvements in behavioral discrimination accuracy and the active task, age, WMS-R memory scales, Stroop score, and neural changes were analyzed using Spearman's nonparametric correlations and reported with adjusted significance criterion (dividing the level of significance by the number of tests).

4 Results

4.1 The effects of different types of musical expertise on auditory perceptual learning

In Study I, the main aim was to examine the effects of different types of musical expertise on auditory perceptual learning of complex sound patterns. Musicians preferring aural practice strategies (i.e., improvising, training aurally without musical scores and by listening to recordings) were compared to musicians preferring non-aural practice strategies. In the transposed melodies paradigm probing auditory perceptual learning, participants heard oddball stimuli consisting of regularly presented standard melody patterns and irregularly presented Contour and Interval (each 7% of the time) melody patterns. Irregular melody patterns had one of their tone components misplaced as compared to the standard pattern so that the Contour pattern had a deviating sound as the penultimate tone and the Interval pattern had a deviating sound as the last tone. All the patterns were randomly transposed to different frequency levels. The EEG was recorded from two ignore conditions that were interleaved with an attentive condition which included behavioral discrimination of the deviant patterns. In the beginning of the experiment, the EEG was also recorded from a multi-feature paradigm where every other tone was a standard sound followed by a deviant sound (deviating either for frequency, intensity, duration, gap or sound location from standard sound) (adopted from Näätänen et al., 2004). In both paradigms, MMN responses were analyzed for difference waveforms which were computed by subtracting the standard responses from the deviating sound response.

In the transposed melody paradigm, MMN latency was significantly shorter in the aural group to the Interval deviant (the last note changing in a sound pattern) before and after the attentive condition than the non-aural group [Deviant type \times Group: $F_{1,22}=86.08$, $p<.001$; Deviant type \times Block \times Group: $F_{1,22}=24.84$, $p<.001$, see Figure 4]. On the other hand, the non-aural group had significantly shorter MMN latency to the Contour deviant (the second last note changed in a sound pattern) after the attentive condition than the aural group. MMN amplitude of Interval or Contour deviants,

however, did not show group-specific learning effects, although visual inspection of the difference waves (see Figure 4) suggested that the MMN amplitude decreased after the attentive condition in the aural group for both types of deviants.

These findings suggest that musicians preferring aural practice strategies (such as improvising) process essentially the continuation of the melody more efficiently because in improvisation the endings of the melodies are important clues as to how to continue the improvisation. Yet, the musicians preferring other strategies, had actually more music theory lessons ($U=20$, $p<.01$, with 8.2 vs. 15.5 points) and had higher scores in the Musicality test (Total scores: $F_{1,22}=4.82$, $p<.04$) and in the Tonal subtest ($F_{1,22}=4.71$, $p<.05$) but not the Rhythm tests. They might be more experienced in perceiving the violations in the middle of melody structures. The aural and non-aural groups did not differ, however, in the onset age of playing, practice hours per week, the number of musical activities or years of music training. Moreover, the groups did not differ in the basic sound processing for various isolated sound features that were measured by the multi-feature paradigm (Figure 4).

Behaviorally, the musician groups did not differ in their accuracy to detect the deviants: based on Grier's A non-parametric detection scores (indexing the response sensitivity; Grier, 1971), the percentage of hit rates and false alarms (wrong button presses), or the reaction times for either of the Interval and Contour pattern deviants did not differ significantly between groups. Both deviants were detected well above chance by both groups (the mean false rate for the Contour deviant was 15% and for the Interval deviant 14%). Furthermore, the behavioral accuracy for both deviants correlated significantly with the MMN amplitude before the attentive condition (Interval-MMN: $r(22)=.55$, $p<.01$, Contour-MMN: $r(22)=.47$, $p<.05$), which suggests that although MMN amplitude did not differ between groups, there was systematic individual variation in both the behavioral and neural discrimination of deviants in the transposed-melody paradigm.

To sum up the findings in the first study, the auditory perceptual learning of melodic contour and interval deviants was different between musicians preferring aural practice strategies than in musicians preferring non-aural practice strategies. More specifically, the aural group had faster auditory processing for contour sound patterns in general, and the non-aural group had faster processing for interval sound patterns than the aural

group, but this was seen only after the active discrimination task of the sound patterns. There were no differences between groups in simple sound processing or behavioral discrimination accuracy, however. Yet, behavioral accuracy correlated to the initial MMN amplitude (as recorded before the active task) in all participants.

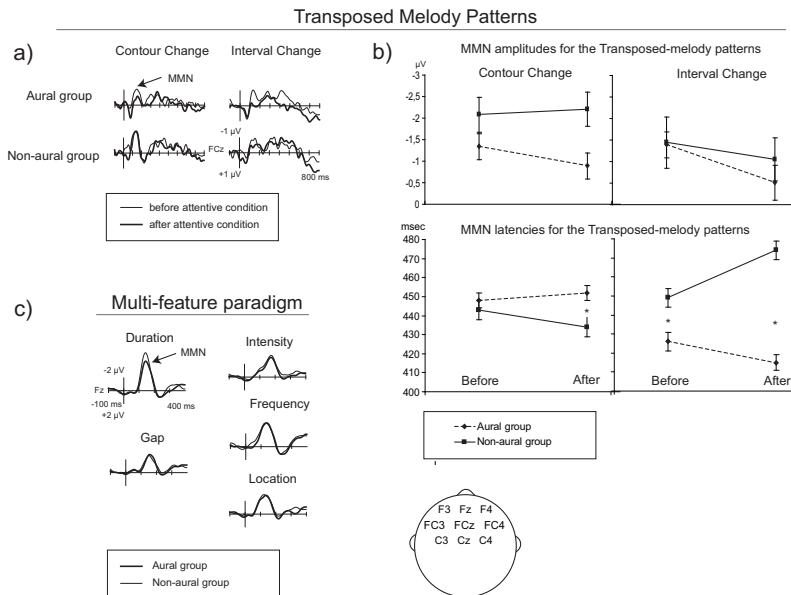


Figure 4. The summary of ERP results in Study I. The difference waveforms (standard ERP response subtracted from the deviant ERP response) for aural and non-aural groups are presented in section a). The mean amplitude and peak latency changes in FCz between the passive blocks before and after the attentive condition are presented in panel b). Notice that the latencies for the Interval deviant are for comparison purposes transformed by subtracting 100 ms from the absolute peak latency value. The significant differences between the aural and non-aural groups are marked by an asterisk. Error bars represent standard error measures (SEMs). The MMN difference waveforms for the multi-feature deviants are presented in panel c).

4.2 Effects of musical expertise on rapid plasticity of regularly presented sounds

The aim in Study II was to compare the rapid plasticity of P1, N1, and P2 ERP responses and source activation of musicians and non-musicians. Specifically, we examined the neural modulation for regularly presented standard sounds among oddball stimuli during one hour of passive exposure to sounds. Most learning studies using oddball stimulation in non-musicians have only investigated deviating sounds, and not

the standard sounds. Also, the learning effects for deviant sounds have often been quantified using difference waveforms in which the standard ERP is subtracted from the deviant ERP. In such a procedure, it is possible that the effects attributed to musical expertise in encoding the deviance could be explained partly by the ERP for frequent standard sounds. For these reasons, it is important to resolve whether music training actually also enhances auditory perceptual learning (observed as rapid plastic changes in ERPs) for unattended standard sounds, and not only for deviant sounds, as the larger amount of literature on MMN suggests. Here, P1, N1, and P2 ERPs and generators for the standard sounds between the four passive blocks were tested in repeated measures ANOVAs. Of specific interest was the interaction between Block and Musical training, which indicate enhanced rapid plasticity between experimental blocks as a function of long-term musical training.

In the ERP analysis, no plastic effects were observed for P1. N1 was enhanced (i.e., became more negative) in musicians from Passive Block 1 to 3 but only in the parietal left and right hemisphere electrodes (Block \times Frontality \times Laterality \times Music training $F_{18,504}=2.28$, $p=.022$, $\eta_p^2=.08$, Figure 5). The P2 amplitude was enhanced in both groups from Block 1 to 2 in most frontal electrodes (Block \times Frontality, $F_{9,252}=3.11$, $p=.016$, $\eta_p^2=.10$, post hoc tests *ns*). The P2 amplitude changes also showed a quadratic pattern (enhancement between successive passive blocks and decrease after the active task) in both groups in a lateral comparison (Block \times Laterality $F_{6,168}=2.87$, $p=.024$, $\eta_p^2=.09$; post hoc tests *ns*). Unlike the P1, N1, and P2 source estimates, there were no main effects of music training for either ERP component. Also, there were no significant rapid plastic effects of ERP latencies.

In source analysis of P1, N1 and P2 for regularly presented standard sounds in oddball paradigm, rapid plasticity in source activation was observed in musicians for N1 and P2 components but not for P1 (Figure 6). Only with the musicians did the N1 and P2 source activation decrease from Block 1 to 2 [Block \times Music training, $F_{3,84}=4.41$, $p=.012$, $\eta_p^2=.14$]. P2 source activation, however, increased after the attentive condition, from Block 2 to 4 (Block \times Music training, $F_{3,84}=3.93$, $p=.027$, $\eta_p^2=.12$). Thus, passive exposure to sounds produced rapid plasticity of the N1 and P2 sources for standard sounds even before the active task, but the P2 source activation recovered after the active auditory discrimination task in musicians. No plastic effects were observed for

P1, N1 and P2 Event-Related Potentials for Standard Sounds

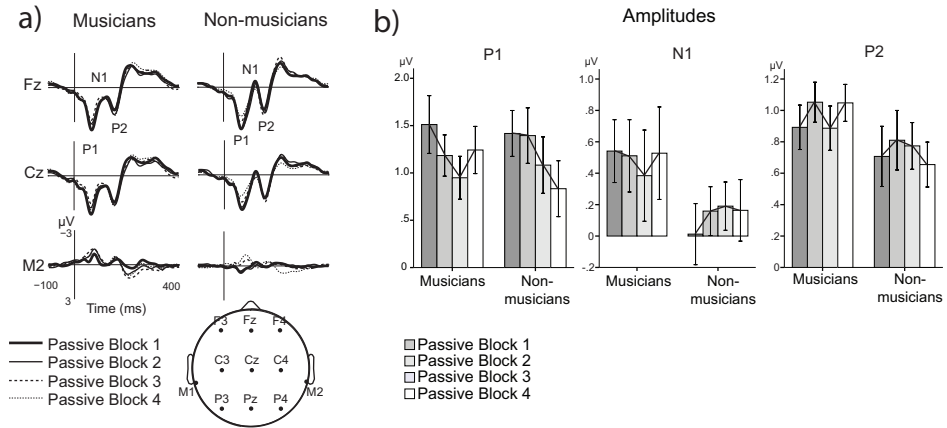


Figure 5. The summary of results for P1, N1, and P2 ERPs for standard sounds (Study II). In panel a) the grand average waveforms are presented for the passive blocks 1-4. The amplitude changes between passive blocks are shown in panel b) with the standard errors of the means (SEM) error bars. Notice that scales in panel b) vary between components.

source latencies. Also, no differences in frontal or temporal generators were found for rapid plasticity.

Additionally, we determined whether the length of musical training or onset age of playing would influence the neural changes between the blocks that showed significant effects. Correlation analysis showed that the younger the musicians had started to play their main instrument, the more P2 ERP amplitude enhanced between the Passive Blocks 1 and 2 ($r=.648, p=.012$) at frontal electrodes. However, the more years the musicians had received supervised instrument training, the less P2 ERP amplitude changed between the two first blocks ($r=-.602, p=.029$). In other words, the length of training induced less short-term plasticity but the early childhood musical experience enhanced short-term plasticity for P2 responses on regular standard sounds. No significant correlation was found between current intensity of practice and neural changes.

As a main finding in Study II, we found that professionally-trained musicians had enhanced rapid plasticity of N1 and P2 generators and N1 ERPs for unattended standard sounds that were presented regularly among irregularly presented deviant sounds. Source analysis for event-related potentials showed that N1 and P2 source activation

Source waveforms for Standard Sounds

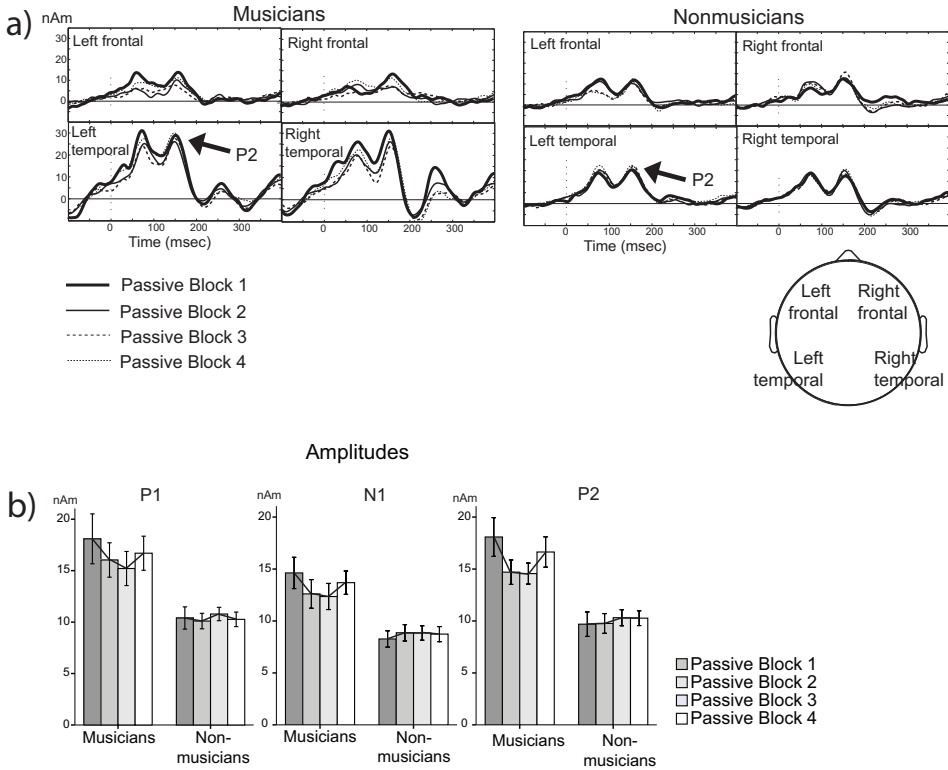


Figure 6. An example of BESA source waveforms is presented in panel a). This source waveform was elicited when evaluating the P2 ERP sources in passive blocks 1-4. In panel b), the source waveform amplitude changes (with standard errors of the means) between passive blocks are illustrated².

was selectively decreased in musicians after fifteen minutes of passive exposure to sounds and that P2 source activation was found to be re-enhanced after the active task in musicians. Additionally, ERP analysis revealed that in both musicians and non-musicians, P2 ERP amplitude was enhanced after fifteen minutes of passive exposure but only at the frontal electrodes. Furthermore, in musicians, the N1 ERP was enhanced after the active discrimination task but only at the parietal electrodes. Furthermore, we found that the rapid neural plasticity of N1 and P2 in the auditory system did not require active attention or reinforcement but had already occurred during unattended, passive exposure to sounds. The present findings suggest that N1 and P2 could be used as

² Erratum to Seppänen et al., 2012: In the article, in Figure 5 the P1 bar chart showed a zero at the origin although it was scaled so that it started with 8. Here, the scale has been corrected.

indicators for rapid neural plasticity, auditory perceptual learning and long-term auditory training.

4.3 Effects of musical expertise on the rapid plasticity of irregularly presented sounds

Two of our studies aimed at exploring whether rapid plasticity in response to deviating sounds is differentially reflected in the deviant-related ERP within a MMN time frame (Study III) and P3a/P3b (Study IV) between musicians and non-musicians. In Study III, rapid plasticity was studied by analyzing changes in the frontal and temporal (mastoidal) ERPs and sources in response to infrequently deviating single sounds among frequently presented sounds between four passive blocks that were interleaved with an active discrimination task. This design allowed us to investigate changes in the deviant ERPs in blocks before the attentive condition (i.e., whether focused attention is needed for short-term learning) as well as compare changes between blocks before and after the active task (i.e., whether focused attention enhances rapid plasticity). Study IV employed a similar approach but only ERPs (and not source activation) were analyzed. In addition, P3b in Active tasks was analyzed and the relationship between behavioral discrimination accuracy in active tasks as well as cognitive tasks, and neural measures was examined.

In **Study III**, the ERP analysis of the frontally maximal component of the deviant ERP showed in all participants a decrease of mean amplitude from Block 1 to 3 at the parietal electrodes only. Although deviant ERP mean amplitudes did not differ between musicians and non-musicians, the mastoid responses showed that musicians had a mastoidal positivity that was over three times stronger than that of non-musicians (Musical expertise, $F_{1,28}=5.98$, $p=.021$, $\eta_p^2=.176$, musicians $M=1.01$ μV , non-musicians $M=0.30$ μV , see Figure 7). No learning effects were observed in the mastoidal response mean amplitudes. The frontal component's peak latencies became shorter between each block at all but the most frontal electrodes (Block \times Frontality, $F_{9,252}=2.63$, $p=.03$, $\eta_p^2=.086$; post hoc tests *ns*). Mastoid latency increased only in non-musicians from Blocks 3 to 4 for the pitch deviants (Block \times Deviant type \times Musical expertise, $F_{3,84}=3.13$, $p=.038$, $\eta_p^2=.101$).

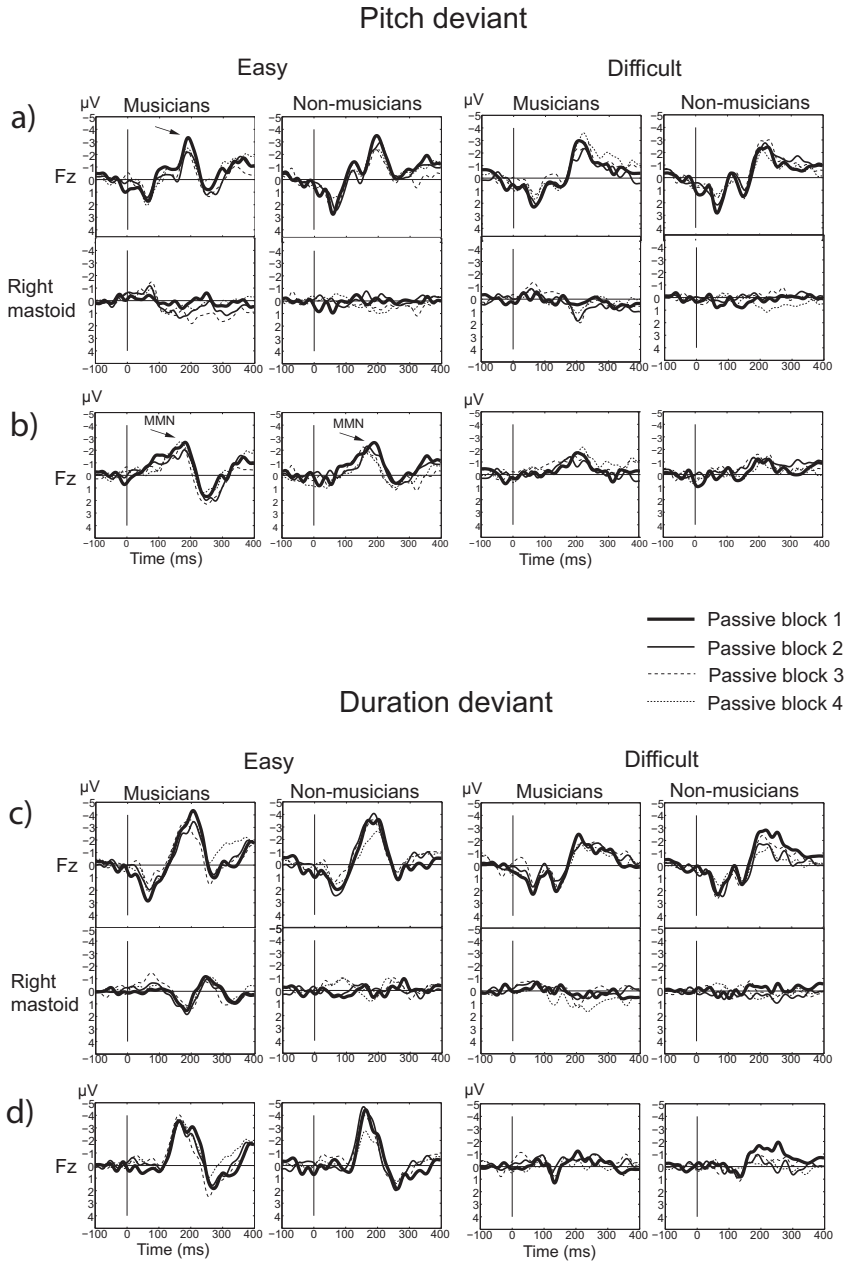


Figure 7. Study III: Grand-average waveforms at the Fz electrode and right mastoid for pitch and duration deviants for easy and difficult levels are presented in panels a) and c) in passive blocks 1-4. In panels b) and d), the same data are shown as difference waveforms where the standard ERP response is subtracted from the deviant ERP response at the Fz electrode. The difference waves are shown here only for illustration purposes and were not statistically analyzed.

The source analysis showed that mean amplitude of the source activation for deviant ERP responses showed rapid plastic changes between the blocks only in musicians (Block, $F_{3,84}=4.95$, $p=.01$, $\eta_p^2=.150$; Musical expertise, $F_{1,28}=14.32$, $p=.001$, $\eta_p^2=.338$; Block \times Difficulty level \times Source, $F_{18,504}=2.17$, $p=.02$, $\eta_p^2=.072$; Block \times Difficulty level \times Source \times Musical expertise, $F_{18,504}=1.94$, $p=.04$, $\eta_p^2=.065$, Figure 8). According to post hoc tests, musicians had a decrease in right temporal source activation for easy deviants (from Block 1 to 3, and from Blocks 2 to 3, left temporal activation (from Block 1 to 2, 3 and 4) and left frontal activation (from Block 1 to 2 and 3). For medium deviants, musicians had a decrease in right temporal activation from Block 1 to 2 and 4. For difficult deviants the left frontal activation reduced from Block 1 to 2. No significant plastic changes in source strength were observed in non-musicians. Because the active task was after Block 2, our findings indicate that rapid plastic changes in source strength in musicians did not require focused attention. For source peak latencies, there were no significant plastic changes during the experimental session.

In general, musicians had significantly stronger activation than non-musicians for all sources for pitch deviants but only in temporal sources for duration deviants (Deviant type \times Source \times Musical expertise $F_{3,84}=21.51$, $p<.001$, $\eta_p^2=.434$). Musicians also had shorter latencies for source activation for easy and medium pitch deviants and for the difficult duration deviant compared to non-musicians (Musical expertise, $F_{1,28}=31.98$, $p<.001$, $\eta_p^2=.533$; Deviant type \times Difficulty level \times Musical expertise, $F_{2,56}=22.82$, $p<.001$, $\eta_p^2=.449$). Moreover, source mean amplitudes were stronger from both temporal sources for duration than pitch deviants at the easy and medium levels. For difficult level, pitch deviants had stronger activation than duration deviants at both frontal sources (Deviant type \times Difficulty level \times Source, $F_{6,168}=31.11$, $p<.001$, $\eta_p^2=.526$).

The main result of **Study III** was the finding that rapid plasticity of the deviant ERP response (measured from the MMN time period) during non-attended sound exposure was enhanced in musicians. This finding was supported by the habituation (decrease) of the source activation between successive passive blocks before focused attention. Rapid plastic effects in musicians were observed at the left and right temporal generators and the left frontal source but not the right frontal source. In other words, these rapid plastic changes may indicate the auditory perceptual learning that occurred only in musicians in response to deviations in an otherwise constant auditory stream. This finding suggests

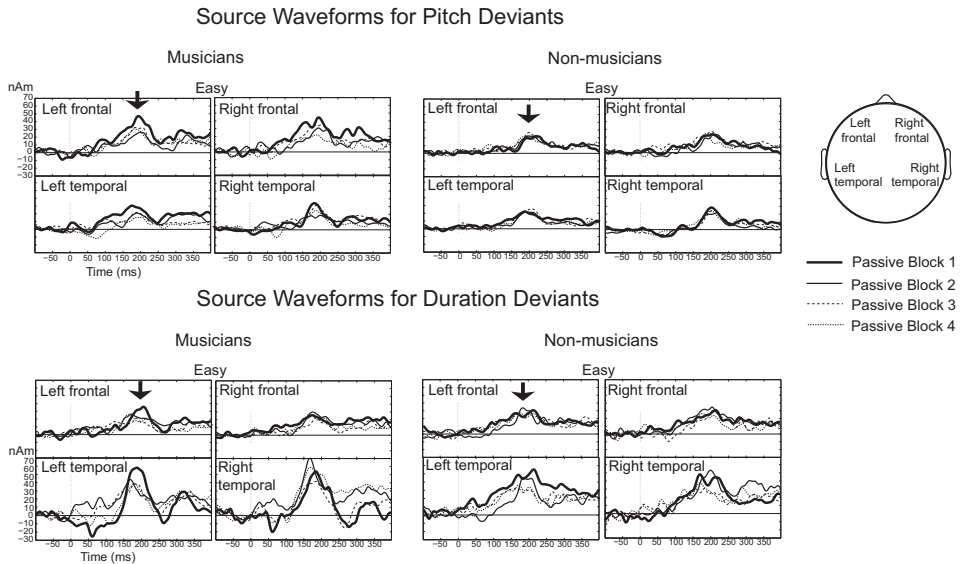


Figure 8. Study III: Examples of the BESA source waveforms for deviant ERP within a MMN time frame. These deviant tones are presented for the easy level in passive blocks 1-4 based on grand-average waveforms for ERPs.

that despite musical expertise, the right frontal cortical source has a special role in sound change-related ERP response generation and may not show rapid plasticity. Finally, both musicians and non-musicians exhibited habituation at the scalp-recorded parietal sites but only after focused attention. Thus, the current data indicate that rapid plastic effects in sound change discrimination and perceptual learning differ between musicians and non-musicians.

In **Study IV**, during passive exposure to sounds, musicians initially showed an enhancement of P3a but habituation after the active task, while non-musicians showed enhancement of P3a only after the active task [Block \times Music training: $F_{3,8146}=21.05$, $p<.001$; see upper left panel of Figure 9]. In musicians, P3a amplitude enhanced from Blocks 1 to 2 but reduced from Blocks 1, 2, and 3 to Block 4. In non-musicians, however, P3a amplitude enhanced from Blocks 1 and 2 to Blocks 3 and 4. Also, the deviant type (pitch and duration) as well as difficulty level interacted with the P3a amplitude changes between blocks for the different groups [Block \times Deviant Type \times Difficulty Level \times Music Training: $F_{6, 8139}=17.12$, $p<.001$]. To sum up the most important post hoc findings, for musicians, P3a amplitudes for easy and difficult pitch

deviants were rapidly enhanced between the first two blocks but were diminished (habituated) after the active task. For medium-difficulty pitch deviants, however, P3a amplitude diminished rapidly in musicians but was enhanced in non-musicians, which was a pattern that continued after the active task. P3a responses habituated for easy duration deviants in both groups but were enhanced for difficult duration deviants after the first active task in musicians. Medium-difficulty duration deviants showed habituation in non-musicians, with temporary enhancement observed after the active task.

Although there was no main effect of musical training in the grand-average waveforms, pitch deviant P3a was visible and significant only for musicians. For duration deviants, non-musicians also exhibited a P3a response for the easy and medium difficulty levels (Figure 9). For difficult-level pitch and duration deviants, there is no clear P3a for either musicians or non-musicians. One of the musicians displayed highly variable amplitude values for some of the deviants that may have eliminated the main effect of the musical training.

During passive exposure, P3a latencies were shortened in both musicians and non-musicians from Block 1 to 2, and forward but increased from Block 2 to 3 in non-musicians only [Block \times Music training: $F_{3,8110}=12.00, p<.001$]. As with P3a amplitude, deviant type and difficulty level also modulated the rapid plasticity of P3a latencies [Block \times Deviant Type \times Difficulty Level \times Music Training: $F_{6,8105}=5.36, p<.001$]. To summarize the significant post hoc findings, in musicians, the P3a latency for easy pitch deviants shortened rapidly, while in non-musicians, the P3a latency was shortened only after the active task. P3a latencies for the medium difficulty pitch and duration deviants were shortened only in non-musicians from Block 1 to Block 2, with an additional latency shortening for medium-difficulty duration deviants from Blocks 3 to 4. In both groups, the latencies shortened for hard-difficulty pitch deviants only after the active task. Musicians also showed increased latencies from Blocks 3 to 4. Moreover, in both groups, the P3a latency for difficult duration deviants shortened from Blocks 1 to 2, while the P3a latency increased after the active task in musicians only. No changes of P3a latency were found for the easy duration deviant.

In the active tasks (Figure 10), P3bs were analyzed separately for duration and pitch deviants. The hard-difficulty-level deviants that had not yielded significant responses

P3a in Passive Exposure to Sounds

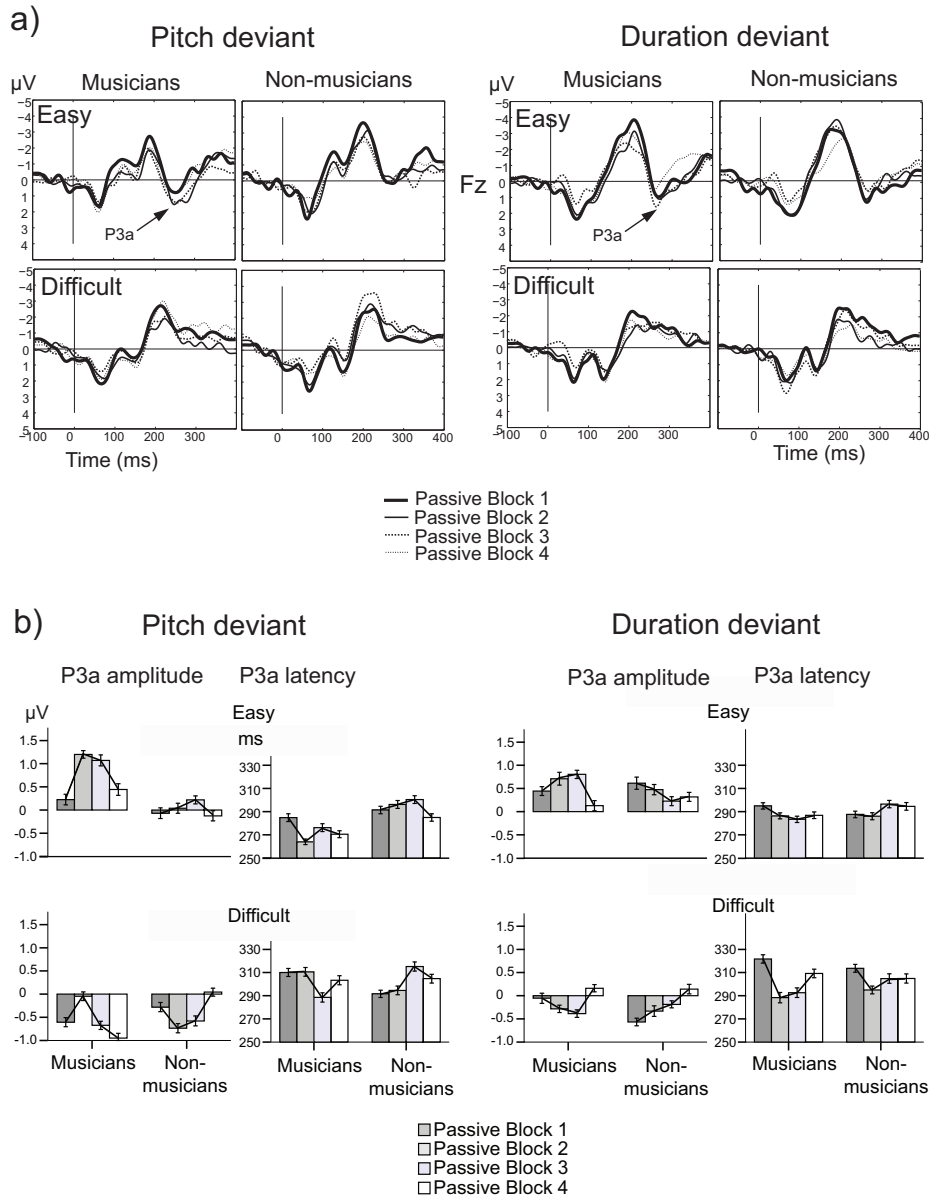


Figure 9. Study IV: The grand-averaged waveforms illustrate the pitch and duration deviant P3a ERPs in passive blocks 1-4. Only the easy and difficult levels are presented here (panel a). The amplitude and latency changes between passive blocks (with standard errors of the means) are illustrated in the lower panel b).

during the passive condition produced significant responses in the active tasks. For duration deviants in the active tasks (medium- and hard-difficulty levels analyzed), the P3b amplitude was diminished between Active Tasks 1 and 2 for medium- and hard-difficulty levels only in musicians [Block \times Difficulty Level \times Music Training: $F_{1,351}=4.38$, $p=.04$, Figure 10]. In addition, P3b amplitudes for duration deviants were significantly diminished in all but the most frontal electrodes in musicians. In non-musicians, however, P3b responses were diminished significantly only in the most frontal electrodes [Block \times Frontality \times Music Training: $F_{3,400}=4.74$, $p=.01$]. P3b latencies were shortened between Active Tasks 1 and 2 in musicians for medium duration deviants and for the difficult duration deviants in both groups [Block \times Difficulty Level \times Music Training: $F_{1,682}=8.85$, $p=.01$].

P3b in Active Discrimination Tasks

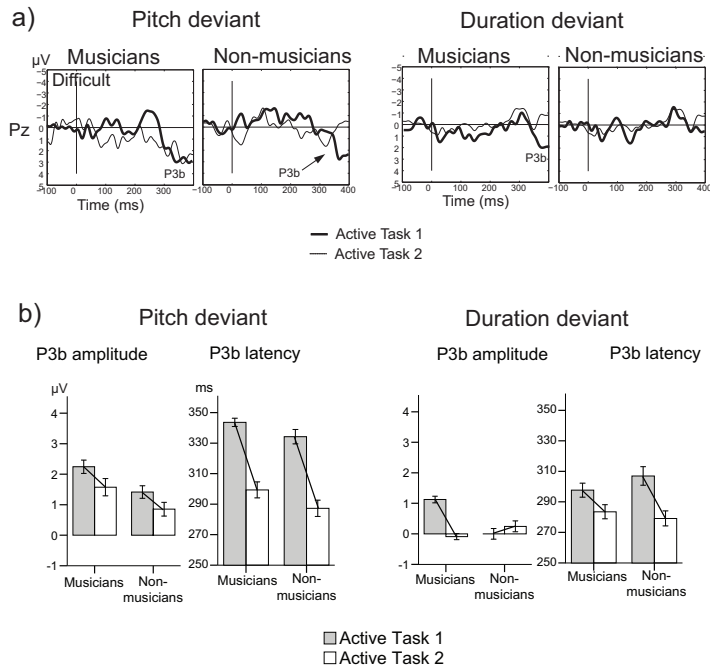


Figure 10. Study IV: The grand-averaged waveforms illustrate the pitch and duration deviant P3b ERPs in Active Tasks 1 and 2. Only the hard-difficult level is presented here (panel a). The amplitude and latency changes between active tasks (with standard errors of the means) are presented in panel b).

Separate analyses for pitch (only hard-difficult level analyzed) showed a significant reduction in P3b amplitudes between active tasks only in musicians [Block \times Music Training: $F_{1,344}=5.73$, $p=.02$]. In all participants, P3b latencies were shortened between active tasks [Block: $F_{1,335}=69.84$, $p<.001$]. Of note, the optimal paradigm to evoke and analyze P3b responses during active conditions would require a longer stimulus onset asynchrony than was used here (400 ms).

Behavioral discrimination accuracy improved significantly only in non-musicians and only for hard-difficulty deviant sounds (sum score comprising both pitch and duration deviants) between Active Tasks 1 and 2 ($\chi^2=15.59$, $p=.01$) and between Active Tasks 1 and 3 (the follow-up after ~ 1 week) ($\chi^2=7.37$, $p=.03$). In musicians, accuracy started at ceiling level and remained there throughout testing (see Figure 11). No significant improvement in behavioral discrimination accuracy was found between Active Tasks 2 and 3 in either group. It should be noticed that there was no significant difference in the number of standard or deviant trials in Active Task 1, which was used as a probe for active attention. Thus, there was no more frequent exposure (i.e., having more trials) to the difficult deviant sounds in musicians although they discriminated these sounds better than non-musicians.

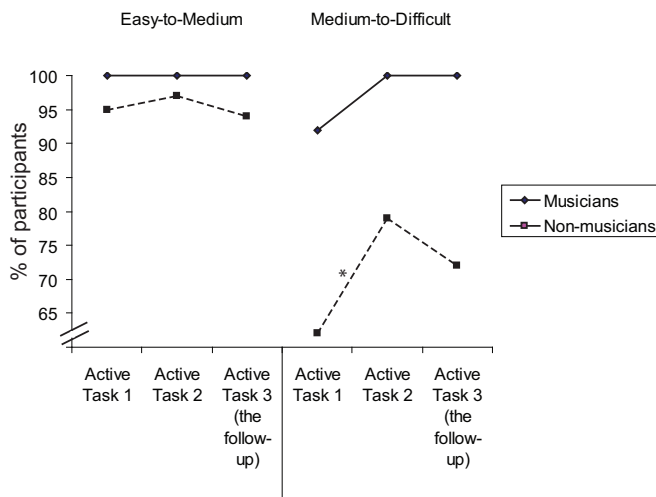


Figure 11. Study IV: Behavioral discrimination accuracy in Active Tasks 1, 2, and 3 (the follow-up approximately after one week from the EEG recording). Significantly more non-musicians showed improvement for discriminating the more difficult deviants (marked with an asterisk). In other words, the elevation of discrimination accuracy from easy level to medium level was high in both groups while elevation from medium level to difficult deviant level improved significantly only in non-musicians. The discrimination accuracy is a sum score comprising both duration and pitch deviants.

Correlation analyses between the P3a and P3b changes between blocks and the behavioral measures showed that participants who exhibited better discrimination performance during the active tasks tended to have a higher working memory capacity, as evaluated by the WMS-R Digit Span Test (see Table 3). Improved discrimination during the active tasks was also related to decreased changes in P3a responses between passive blocks. No significant correlations were found between changes in P3a/P3b responses between blocks and either the cognitive tests (the WMS-R Immediate and Delayed Auditory Verbal Memory scales and the Stroop Color-Word Interference Test) or age. While cognitive test scores did not differ between musicians and non-musicians, musicians showed larger variances in cognitive tests, especially the Stroop test (Levene’s test, $p=.05$; Figure 12). It is possible that with a larger sample, musical training might have been found to influence auditory attention measures in a statistically significant manner.

Table 3. Significant correlations between behavioral discrimination accuracy in active tasks, WMS-R Digit Span, and P3a/P3b changes

	Deviant	Difference	Behavioral accuracy in Active Task 1	Behavioral accuracy in Active Task 2	Behavioral accuracy in the follow-up task
WMS digit span			$r=.410, p=.009^a$	$r=.429, p=.008^b$	$r=.522, p=.002^c$
P3a amplitude	Medium pitch	Δ Passive blocks 2 and 3	$r=-.475, p=.002^a$		
	Difficult pitch	Δ Passive blocks 2 and 3		$r=-.431, p=.008^b$	
	Easy Duration	Δ Passive blocks 1 and 4		$r=-.485, p=.002^b$	
	Difficult Duration	Δ Passive blocks 1 and 2			$r=-.449, p=.008^c$
P3a latency	Easy pitch	Δ Passive blocks 1 and 2	$r=-.479, p=.002^d$		
	Medium pitch	Δ Passive blocks 1 and 4	$r=.501, p=.001^a$		

Note. Difference values (Δ) have been computed by subtracting the difference in the amplitude or latency between blocks. For P3a response, the values were extracted from Fz, and for P3b response, the values were extracted from Pz. Correlations reaching the adjusted p -value of .009 are reported. The number of participants varied: ^a $n=39$, ^b $n=37$, ^c $n=33$, ^d $n=40$, ^e $n=34$. The discrimination accuracy is a sum score comprising both duration and pitch deviants.

To summarize, the results from Study IV suggest that auditory perceptual learning, as measured by rapid neural changes in P3a and P3b responses and behavioral discrimination accuracy, differs between musicians and non-musicians. During passive exposure to sounds, musicians showed P3a habituation for pitch deviant sounds, while non-musicians showed mostly P3a enhancement between blocks. Between active tasks of discrimination of deviant sounds, musicians showed greater habituation for duration deviants than did non-musicians and showed more posterior scalp topography for

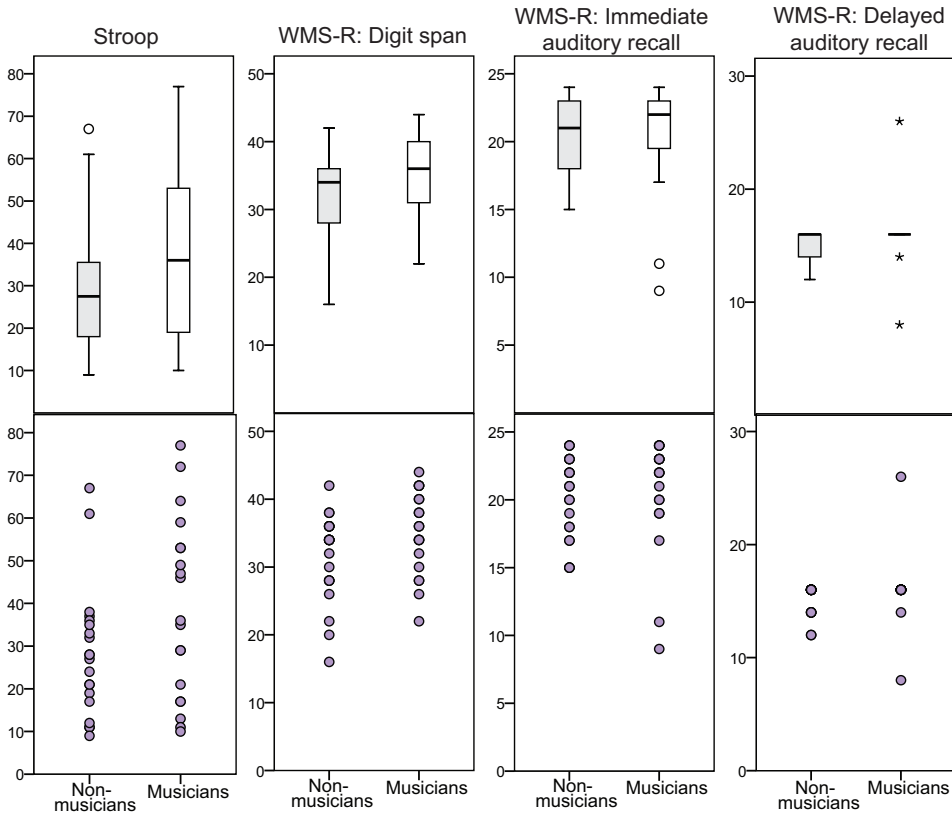


Figure 12. Boxplots and scatterplots for cognitive tests. WMS-R tests showed normal attentional and auditory memory skills in all participants. Data from one non-musician is missing from the Stroop analysis.

habituation when compared to the P3bs of non-musicians. In both groups, the P3a and P3b latencies were shortened for deviating sounds. In addition, musicians were better than non-musicians at discriminating target deviants. Regardless of musical training, better discrimination was associated with higher working memory capacity. Rapid plastic effects of P3a and P3b may indicate that music training modifies the exposure type of perceptual learning for pitch deviants and the attention-gated perceptual learning for duration deviant sounds. Yet another explanation for the differences in rapid plasticity between musicians and non-musicians is that musical training may improve attentional skills and the encoding of features and rules in the auditory environment.

5 Discussion

This thesis investigated the effects of different types of musical expertise and long-term musical training in general on rapid plasticity during auditory perceptual learning after passive exposure to sound and active sound discrimination tasks. As indicators of auditory perceptual learning, rapid plastic (electrophysiological) changes as well as behavioral discrimination accuracy for sounds were compared between musicians and non-musicians (Studies II-IV), as well as between musician groups having different practice strategies (Study I). The main findings were that musical expertise modulates the rapid plasticity of sounds: neural changes were faster or stronger in musicians when compared to non-musicians. Another finding was that rapid plastic changes during auditory perceptual learning for relatively simple sounds did not require focused attention but the neural changes occurred quickly (within fifteen to thirty minutes) during passive exposure for repeated sounds. Moreover, rapid plastic effects were more likely to be found in the temporal cortical areas and left frontal source but not in the right frontal source, which suggests that frontal areas processing the concomitants of the changed events are not as plastic as the sound processing areas in the temporal cortex. These findings are discussed in more detail below under the following topics: 1) How does musical expertise modulate the neural processing during auditory perceptual learning? 2) What are the roles of focused attention and preattentive processing during auditory perceptual learning? 3) What is the neural basis of auditory perceptual learning? and 4) What are the theoretical and practical implications of these four studies?

5.1 The effects of musical expertise on neural processing during auditory perceptual learning

The neural basis of musical expertise has been extensively studied over the last twenty years or so. Besides various structural changes, professional musicians, after years of extensive training, show typically enhanced functional auditory processing when compared to non-musicians (Jäncke, 2009; Pantev & Herholz, 2011; Tervaniemi, 2009). Yet, the question whether musicians also have enhanced rapid plasticity during short-term auditory training (as opposed to long-term effects of musical training) has

been largely ignored. It is highly probable that musicians apply the mechanisms of rapid plasticity during auditory perceptual learning in their daily practice. These rapid plastic changes may be a necessary precondition for longer-term plastic changes (Pascual-Leone et al., 2005). In my thesis, this topic was studied by comparing musicians with different practice strategies as well as by comparing musicians with non-musicians. The main findings in Studies II, III, and IV were that musical training significantly modulates rapid plasticity during both passive exposure and active discrimination of relatively simple isolated sounds. Also, the type of musical expertise (and practice strategies) may modulate the perceptual learning of complex sound patterns (Study I).

5.1.1 Auditory perceptual learning of complex sounds in musicians preferring different practice strategies

Neurocognitive studies of different kinds of musicians have demonstrated how the selection of a musical instrument, musical genre or even practice styles can change the way sounds are processed in the brain (Nikjeh, Lister, & Frisch, 2008; Vuust et al., 2012, for a review, see Tervaniemi, 2009). It is then possible that the type of musical expertise also has an influence on auditory perceptual learning. Tentative evidence of enhanced perceptual learning of complex sound patterns was found in musicians playing mainly without a score when contrasted with a composite of non-homogenous groups of musicians and non-musicians (Tervaniemi et al., 2001). In Study I, we tested explicitly the possibility that the type of musical expertise influences the rapid neural changes during auditory perceptual learning of complex sound patterns by comparing musicians preferring aural practice strategies (improvising, playing by ear and rehearsing by listening to a recorded piece of music) to musicians preferring other practice strategies (using scores and having had more formal music theory and ear training than the aural group). Firstly, preattentive auditory processing of relatively simple sound features (as indicated by MMN to changes in the frequency, intensity, gap inclusion, duration, and spatial location of isolated tones) did not differ between the aural and the non-aural group. Such processing might hence be a prerequisite for music perception in any professional musician, regardless of the particular kind of expertise involved. Second, in contrast with previous studies, the MMN *amplitude* for complex

sound patterns did not differ after attentive discrimination of those patterns (i.e., the short-term training) between groups (as in Tervaniemi et al., 2001 where only one deviating sound pattern was tested, however). Instead, we found that the MMN *latency* was shorter after training for the Interval deviant in the aural group and longer in the non-aural group. On the other hand, the non-aural musicians had shorter MMN latency for Contour deviants after the attentive condition when compared with the aural musicians.

Our findings for the aural group (for Interval deviant) are similar to the findings in Näätänen et al. (1993) for the ‘good non-improvers’ group, which already showed initially a sizeable MMN to deviant sound patterns, and no enhancement in MMN amplitude was seen after attentive training. However, the MMN latency became shorter after short-term training as was also the case with the Interval deviant in the aural group. Other subjects (‘improvers’) showed MMN enhancement after the attentive discrimination task (Näätänen et al., 1993). Moreover, Interval deviants, which required extracting the relational intervals according to the musical scale, may have been easier to process in an aural group who improvise and play by ear. Supporting this idea, MMN amplitude does not seem to increase further after participants have learned to discriminate the deviants well (as in Tervaniemi et al. 2001 after the second attentive task). Correspondingly, in Study I, amplitudes for both interval and contour MMNs were seemingly reduced after attentive condition in the aural group, but not to a statistically significant degree. The relationship between rapid neural changes after the attentive training condition and behavioral discrimination accuracy was not found in Study I (unlike in Gottselig et al., 2004; Näätänen et al., 1993). This finding might be explained by the different time course of the learning: in Tremblay et al. (1998) some participants had preattentive neural changes during learning and even before any improvement in behavioral performance was observed.

We also tested the behavioral discrimination skills of complex melody-like patterns by comparing the performance in musicality test (Advanced Measures of Musical Audiation). We found that the non-aural group had higher scores for the Tonal (pitch change) subtest and for the whole test in comparison to the aural group. This result cannot be accounted for by the age of commencement of playing, the main musical instruments, practice hours per week, musical working experience, or study year in the

current school because these did not differ between groups. Based on their greater experience of music theory studies, it could be speculated that the higher AMMA performance of the non-aural group benefited from formally learned analytical skills. The rhythm subtest scores, on the other hand, did not differ significantly between groups but it was affected by the age of commencement in band or orchestra playing. Most importantly here, we found that musicians who had higher AMMA scores (especially the Rhythm subtest) had enhanced MMN to Contour deviants (a pitch shift modifying the contour of the melody pattern; see Figure 4) after the attentive condition. Despite the fact that rapid plastic changes in MMN to deviant sounds did not relate to behavioral discrimination of those sounds, the enhanced MMN in general related to behavioral discrimination in the musicality test. This result generalizes the previous findings showing that high performance in a musicality test is correlated with an enhanced MMN elicited by the same melody patterns employed in the test (Lang, Nyrke, Ek, Aaltonen, Raimo et al., 1990; Tervaniemi, Ilvonen, Karma, Alho, & Näätänen, 1997). Nevertheless, these musicality tests or MMN paradigms did not separate rhythmical or tonal processing.

There are other studies that have also shown differences in auditory processing between different types of musicians (Vuust et al., 2012, for a review, see Tervaniemi, 2009) but this study was the first one to investigate explicitly the effects of practice styles on auditory perceptual learning. Our findings suggest that not only practice strategies but also individual skills (e.g., music theory skills) can influence auditory perceptual learning in professional musicians. It is, however, possible that the rapid plasticity seen with MMN might be caused by the rapid plastic changes in standard sound responses, which were extracted from the deviant-sound responses (and thus produced the analyzed MMN). Also, musicians may have a considerable practice benefit when processing complex sound patterns when compared to non-musicians. Since we compared the auditory perceptual learning between musicians and non-musicians in Studies II, III and IV, in order to avoid the practice effect and mixing the standard and deviant responses, we investigated separately the standard and deviant responses for simpler, isolated, tones. Likewise, the attentional skills during attentive behavioral tasks can significantly influence the discrimination accuracy. To control this, the individual level of attentional skills was evaluated by the standardized cognitive

tests. Finally, in Study I, the genders were unequally represented in the resulting subject groups; however, this should not affect the MMN data obtained. For instance Nagy, Potts, and Loveland (2003) compared several ERP components (including MMN) but found gender difference only in P2 and N2 components. In Studies II, III, and IV gender-balanced groups were used.

5.1.2 Auditory perceptual learning of standard sounds

Several studies of non-musicians have shown rapid plastic changes for repeated sounds without any changing deviant sounds (also called the ‘standards only’ condition, e.g., Kuriki et al., 2006; Pantev et al., 1998; Schneider et al., 2005; Shahin et al., 2005). In Study II, the neural responses for frequently presented (standard) sounds among frequent deviant sounds (called oddball stimuli) were compared between musicians and non-musicians. Instead of subtracting the standard sound responses from deviant sound responses (as in Study I), here only the standard sound response was analyzed with both traditional ERP averaging as well as examining the ERP generators with source activation analysis for right and left hemisphere frontal and temporal generators. We found that while in general musicians had stronger temporal source activation for all components (P1, N1, and P2) than non-musicians, musical training only enhanced the rapid plasticity of N1 and P2 responses but not P1 responses for standard sounds: N1 and P2 source activation decreased in the early phase of passive auditory stimulation (i.e., between the first two fifteen-minute blocks before the active task) only in the musicians group. Scalp-recorded P2 response (collapsing the temporal and frontal sources statistically), however, showed amplitude enhancement at the frontal electrodes between the first two blocks in both musicians and non-musicians.

The habituation of N1 and P2 source activation in musicians may indicate a fast learning capacity in the auditory system to extract both sound features and the rules for differentiating the standard sounds from deviant sounds. Enhanced extraction of relations between different sounds may facilitate the predicting of simple auditory events even without active attention. Previously, decreased N1m (electromagnetic equivalent of N1 ERP) and increased P2m for repeated speech stimuli was found in non-musicians (Ross & Tremblay, 2009). In our study, non-musicians did not show this

pattern probably because instead of listening to the same repeated sound stimuli, they were presented with oddball stimuli which contain repeated standard sounds among the irregularly deviating sounds. The oddball paradigm may require more processing resources from the auditory system because oddball stimuli require the passive extraction of simple rules (e.g., probability, deviancy) between standard and deviating sounds (Korzyukov, Winkler, Gumenyuk, & Alho, 2003; Winkler, Teder-Sälejärvi, Horvath, Näätänen, & Sussman, 2003). Even when not attending to standard sounds, they serve as comparison templates against deviating sounds (e.g., Bendixen, Roeber, & Schröger, 2007). The habituation for standard sounds may well indicate prediction coding also for deviating sounds (Friston, 2005) as well as perceptual learning (e.g., Baldeweg, 2007; Bendixen et al., 2007; Haenschel, Vernon, Dwivedi, Gruzelier, & Baldeweg, 2005). Our findings suggest that in musicians, the extraction process between standard sounds and deviant sounds (and probably the auditory perceptual learning as defined earlier) is pronounced when compared to non-musicians.

In Study II, N2 could have been analyzed from standard sound responses since visually the waveforms showed some group differences in N2. The meaning of N2 is not totally clear for standard sounds but it may reflect the mix-up with the succeeding stimulus in a short interstimulus interval as was used here (400 ms). Despite this possibility, this was not controlled here. Multi-feature paradigms (Näätänen et al., 2004), however, where a standard sound alternates with deviant sounds (e.g., Standard-Deviant1-Standard-Deviant3-Standard-Deviant2-Standard...), produce equally good ERP responses for standards and deviants than a traditional oddball paradigm where at least two or more standard sounds are presented between two deviant sounds (Näätänen et al., 2004). In other words, multi-feature paradigms have shown that there is a neural capacity to establish a separate trace even between two successive sounds if they have some different feature, such as frequency or duration. So-called roving ERP paradigms are also based on these assumptions. Saturation from deviant sound to the following standard is, however, a danger for very short ISIs/SOAs, and this cannot be totally ruled out.

5.1.3 Auditory perceptual learning of deviant sounds

While the standard responses showed rapid plasticity, the ERPs to deviating sounds (Studies III and IV) also showed significant effects of musical expertise on rapid plasticity during auditory perceptual learning. In Study III, musicians had a significant decrease (habituation) in source activation strength in response to deviant sounds within a MMN time frame even before focused attention. In general, musicians had stronger responses in mastoid sites (ERP analysis) and source activation when compared to non-musicians. Previous studies showing enhanced MMN during perceptual learning (and in general an enhanced MMN in musicians) have typically used difference waves, subtracting the standard sound response from a deviant sound response (e.g., Atienza et al., 2004; Näätänen et al., 1993; Tervaniemi et al., 2001; van Zuijen et al., 2006), while average waves (no subtracting) were used here. Thus, it is uncertain whether those results could be explained by changes in the standard sound responses. Also, the sound stimuli used here were simpler (isolated harmonic tones) compared to those of previous studies that used complex melodic sound patterns (e.g., Gottselig et al., 2004; Näätänen et al., 1993). Relatively simple stimuli might help avoid the practice effect that musicians have demonstrated in the active discrimination tasks for musically relevant, melodic and complex auditory stimuli (Tervaniemi, 2009). On account of simpler auditory stimuli, even non-musicians, who were not as familiar with auditory discrimination tasks as musicians, discriminated the deviating sounds relatively well in the current design (Study IV). Moreover, in the case of more complex sounds there may be associative learning and facilitation (increases of the ERP response amplitude) instead of habituation (decreases of ERP response amplitude).

One probable explanation for the differences between Study III and previous studies is the use of average waveforms with a nose-reference instead of difference waveforms with a mastoid re-reference. Difference waves are justified when controlling the differences in baselines between groups or conditions, as well as when comparing the neural processing between standard and deviant stimuli (for a critical discussion of the difference wave procedure, see May & Tiitinen, 2009). However, in our study we have demonstrated rapid plastic effects also on the N1 and P2 ERP responses to standard sounds (Study II) which overlap temporally with the MMN. It may thus follow that functionally different components (such as N1 and P2 here) might have biased the

interpretation of the difference wave components (such as MMN) when temporally overlapping. In future studies of MMN using difference waves, these components could be analyzed for standard sounds. After all, in the oddball context, standard sounds serve as comparison templates for rule violations (see also Baldeweg, Williams, & Gruzelier, 1999; Winkler, Karmos, & Näätänen, 1996) (for further discussion of the averaging concerns, see *Methods* section 3.4.2 *Studies II-IV*).

Another factor influencing the results is the location of the reference electrode. Here, we used a nose-reference while in many MMN studies a mastoid reference is used to maximize the measured response in frontal sites. Mastoidal positivity occurs together with MMN with a slight time difference and may reflect more directly the auditory cortical response. Importantly, in the present study the mastoidal response was enhanced along with the source activation in the auditory cortical (temporal) areas. These findings indicate that musical training modulates especially sound processing and change detection (governed by the temporal lobe mechanisms) while the change-detection related involuntary attention shift (probably reflected by the right frontal generator of the MMN) might be a more general mechanism and thus not subject to top-down influences such as training (see also the discussion in section 5.3 *Neural mechanisms of auditory perceptual learning*).

In Study IV, the P3a, which often follows the MMN during passive exposure to sounds, demonstrated a differential plasticity between musicians and non-musicians especially for the pitch deviants: when asked to ignore the sounds, musicians showed greater P3a habituation to pitch changes than non-musicians, who showed enhancement of P3a amplitudes. In fact, P3a responses were nearly absent for all pitch deviants in non-musicians, although they had significant P3b responses for the difficult pitch deviants during active tasks. These findings suggest that music training might be required for eliciting P3a responses for unattended pitch changes. Stronger P3a habituation in musicians for unattended deviating pitch sounds might also indicate enhanced change detection and involuntary attention switching to familiar pitch sounds. This interpretation is consistent with a previous study that found that classically trained musicians process pitch in a facilitated manner (e.g., Koelsch et al., 1999). P3a responses for duration deviants (at least for the easy level), however, were processed similarly in musicians and non-musicians while in active task, only musicians showed

discernible P3b responses (for the hard-difficulty duration deviants). After the first active task, P3a responses were reduced for easy deviants and enhanced for difficult duration deviants between passive blocks in both groups. In addition, P3a latencies were shortened in both groups for selective deviants. In non-musicians, the P3a response decreased at a faster rate than in musicians for the easy- and medium-difficulty duration deviants. In general, the relatively strong P3a responses for duration deviants may reflect the fact that Finnish participants are familiar with duration variations which are essential for semantic differentiation in Finnish (Marie et al., 2012; Tervaniemi, Jacobsen, Röttger, Kujala, Widmann et al., 2006). When attending to deviating sounds, the comparison between active tasks showed that musicians had P3b amplitude habituation for both medium-level duration deviants and hard-difficulty pitch and duration deviants while non-musicians showed habituation generally in the frontal electrodes and only for pitch deviants (as did the participants in Romero & Polich, 1996).

We also found that while musicians were better able to discriminate deviating target sounds, only non-musicians exhibited improvement in their behavioral discrimination accuracy between Active Tasks 1 and 2. There was no significant improvement in behavioral discrimination accuracy between Active Task 2 and the follow-up of this task (approx. after one week) suggesting that the essential portion of auditory perceptual learning occurred during the first experimental (EEG) session. For all participants, better behavioral discrimination of deviant sounds in active tasks was related to higher auditory working memory capacity, as evaluated by the digit span test. Although this finding may be biased by the maximal discrimination level in musicians (i.e., ceiling effect), it is possible that regardless of musical training, auditory working memory capacity may independently influence the behavioral discrimination of sounds in non-musicians (see more about the auditory working memory discussion in section 5.3.3 *Relationship between auditory working memory and rapid plastic changes during active attention*).

Taken together the main findings in Studies I-IV are that musical expertise significantly facilitates rapid plasticity and enhances sound processing during auditory perceptual learning, either due to familiarity of the stimuli (especially complex sound patterns), the ceiling level of processing (for simpler sounds), or enhanced prediction

coding for sound events (see the next section for further discussion). Secondly, the type of musical expertise may also modulate auditory perceptual learning at least for complex sound patterns. Thirdly, with musical experts the passive exposure to sounds may lead to rapid plastic changes (in this case habituation) even without focused attention (see next sections). Enhanced perceptual learning during passive exposure in musicians suggests that music training modulates the exposure type of perceptual learning (Zhang & Kourtzi, 2010) particularly for the pitch of the sound. This skill could explain why musicians may be able to generalize their auditory skills (i.e., pitch processing) beyond musically relevant tasks, such as discriminating pitch violations in foreign language prosody (Marques et al., 2007).

In addition to music training, it is possible that other factors, such as musically enriched home environments in the childhood, cognitive skills, and genetic predispositions influence sound processing. However, in a previous study, no evidence of preexisting cognitive, music, motor, or structural brain differences were found between children starting instrumental training and the control groups at the pretraining phase (Norton, Winner, Cronin, Overy, Lee et al. 2005). In fact, in their study the performance in musicality test correlated to cognitive skills (such as tests of non-verbal test of visuo-spatial reasoning, and phonemic awareness) in all children despite the music training. Furthermore, the length of music training and the strength of neural processing for sounds have correlated positively in several neurocognitive studies on musicians (Jäncke, 2009). This kind of individual variation even among musicians was also found in Study I, where behavioral performance in the musicality test correlated to MMN response to deviating sounds. Although the selection effect caused by potential preexisting differences between musicians and non-musicians cannot be totally ruled out, here we tried to control some part of the variance in cognitive capacity by using standardized attention tasks (Studies II-IV). We did not find significant differences between musicians and non-musicians with standardized attention capacity tests, although musicians had more variability in their attention task performance (Study IV).

Since there is a genetic component in the development of neuroanatomical structures (most importantly here, the temporal lobes) in the brain (Deary, Penke, & Johnson, 2010), this may cause significantly different individual variation in neural functionality. Notwithstanding, this functionality may explain other cognitive processes than simple

sensory processing, such as attentional skills. After all, there is a fairly long developmental maturation in secondary auditory cortices which makes it highly plastic to experiences in childhood. Thus musically enriched environment could be another explanation for enhanced auditory processing. Moreover, most of the sensory modalities have sensitive periods during childhood, most notably motor functions. In general, it is not evident whether learning capacity in the adulthood is explained by genetics or childhood experiences.

5.2 Focused attention and preattentive processing during auditory perceptual learning

The role of active and focused attention during auditory perceptual learning has often been studied by comparing the rapid plastic changes in ERP responses for sounds between successive blocks of either passive exposure or active discrimination of sounds. Neurocognitive studies have demonstrated that even early automatic ERPs can be modulated by the attention and top-down effects, such as musical expertise (see Introduction). On the other hand, the auditory system adapts rapidly even when attention is not focused on sounds. For example, the findings in Studies II, III and IV showed that focused attention may not be needed for rapid plasticity when learning simple (isolated harmonic) sounds, but there was significant habituation between passive blocks before the attentive condition. Even in the absence of focused attention and behavioral discrimination improvement, habituation could be considered to be auditory perceptual learning since rapid plastic effects can even precede improvements in behavioral discrimination (see also Tremblay et al., 1998). Rapid plastic changes in Studies I-IV are thus considered neural correlates for auditory perceptual learning.

As discussed in the previous section, however, during passive conditions, rapid plastic changes in deviant source waveforms within the MMN time frame were only evident in musicians and for selective sources, while scalp-recorded ERPs showed a decrease at parietal electrodes in both musicians and non-musicians but only after the active task (Study III). Scalp-recorded ERPs cannot show the generators reliably so it is to the task of future studies to examine whether our findings reflect the parietal sources which have been found for the MMN (Levänen, Ahonen, Hari, McEvoy, & Sams, 1996;

Kasai, Nakagome, Itoh, Koshida, Hata et al., 1999; Molholm et al., 2005). In the case of parietal activation for the MMN, it may reflect the attention switching and P3a responses that often follow the MMN during passive oddball paradigms, global (and not sound feature-related) auditory change detection (Levänen et al., 1996), or automatization of processing due to active attention (Pugh, Shaywitz, Shaywitz, Fulbright, Byrd et al., 1996).

It should be noted that in previous MMN studies on auditory perceptual learning of melodic patterns, using a difference waveforms analysis for scalp-recorded ERPs has shown an increase in MMN amplitude only *after* the attentive condition (when comparing two passive conditions interleaved with an active discrimination task) (for non-musicians: Gottselig et al., 2004; Näätänen et al., 1993; for both non-musicians and musicians: Tervaniemi et al., 2001). In Study I, we used a difference waveforms analysis to study the perceptual learning of complex sound patterns with different kinds of musicians (preferring aural or non-aural practice strategies) but instead of amplitude enhancement we found a latency shortening.

Taken together, current findings of the deviant-related ERPs within MMN time frame in passive conditions suggest three conclusions: 1) preattentive processing of simpler deviating sounds produce rapid ERP habituation (i.e., ERP decrease and not increase as more complex sound patterns may do), 2) the habituation in ERP responses and source activation during auditory perceptual learning does not require focused attention to the sounds, at least in musical experts, and 3) when deviant-related ERP response reaches a certain amplitude level for complex sound patterns in musical experts, the auditory perceptual learning after active task is shown as latency shortening and not a further amplitude enhancement. Depending on the stimuli, the habituation or the requirement for focused attention may not be met during perceptual learning. For example, deviant-related ERPs within the MMN time frame in Study III showed mostly habituation, while in Study IV we found that P3a, which reflects the involuntary attention switching to perceived sound (Polich, 2007), was mostly habituated for pitch deviants and enhanced for difficult duration deviants after the active task with musicians but was enhanced for medium-level pitch deviants with non-musicians. In both musicians and non-musicians, P3a latencies shortened for selective deviants. Thus,

different ERPs for the same auditory stimuli may not show a similar kind of rapid plastic effects during auditory perceptual learning.

Focused attention to deviating sounds induced greater habituation between Active Tasks 1 and 2 in musicians' P3b for duration deviants when compared to non-musicians. For pitch deviants, however, P3b amplitude and latency reduced between tasks in both groups. Generally, habituation was stronger for easier deviants, while responses were enhanced for more difficult deviants. The latency shortening might reflect faster stimulus evaluation times for the deviating target sounds as processing becomes easier during focused attention. Previous findings had shown that for easier deviants, P3b latency is faster and larger during focused attention (Fitzgerald & Picton, 1983; Mazaheri & Picton, 2005). Also, a shortened P3a latency typically indicates faster stimulus evaluation and plasticity changes (i.e., habituation) for repeatedly presented nontarget (i.e., not asked to attentively discriminate) novel stimuli (Debener, Makeig, Delorme, & Engel, 2005; Friedman et al., 1998). Our findings suggest that stimulus evaluation for more difficult deviating sounds can be enhanced within one session for participants without musical training but that in general it requires focused attention on the deviating sounds. This interpretation is in line with the idea that when the processing has not reached the ceiling level yet and there is still space for learning, the ERP response increases along with improved perceptual learning (see discussion for Näätänen et al., 1993 in previous section). Alternatively, the reduced P3b latencies and the habituation of P3b amplitudes may indicate that the prediction error for task-relevant deviating sounds was diminished (Vuust et al., 2009, see also section 5.4 *Theoretical and practical implications* for further discussion).

In Studies I, III and IV, the rapid plastic effects during auditory perceptual learning were analyzed for deviating sounds that were infrequently presented among frequently presented repeated 'standard' sounds (the so-called oddball paradigm). It is likely that standard sounds play a crucial role when developing the memory template for comparison with deviating 'oddball' stimuli during auditory perceptual learning. To investigate this possibility, the rapid plasticity for standard sounds was evaluated in Study II. We found that musicians had enhanced rapid (between the first two blocks within 15-30 minutes) plasticity of N1 and P2 source activation to standard sounds during passive exposure. Although active attention was not necessary for these plastic

effects, after the initial habituation, P2 source activation enhanced (showing similar pattern of changes as the scalp-recorded N1 ERP response at parietal electrodes) after the active task (from blocks before the active task to blocks after the active task). P1 did not show rapid plastic changes. Our N1 findings corroborate partially with previous findings where N1 ERP has decreased with unattended, repeated sounds (Alain & Snyder, 2008; Brattico et al., 2003; Ross & Tremblay, 2009), but not with other studies showing no change or increase of N1 within one session (Atienza et al., 2002; Clapp, Kirk, Hamm, Shepherd, & Teyler, 2005). Lateralized parietal (scalp-recorded) N1 enhancement (instead of typical maximum of N1 at vertex) may indicate the automatization of processing due to active attention (Pugh et al., 1996). P2 findings are also only partially consistent with previous studies (using only non-musician groups) where scalp-recorded P2 was enhanced (Alain & Snyder, 2008; both in speech sound training and untrained groups: Sheehan, McArthur, & Bishop, 2005) or remained unchanged (Clapp et al., 2005). The dissociation between the behavioral performance and P2 plasticity was seen in Sheehan et al. (2005) study, where both the training and the control group had P2 enhancement but behavioral discrimination improved only with training. They suggested that P2 enhancement would not reflect perceptual learning, but, instead, reinforced inhibitory processes for repeated standard sounds.

It is, however, possible that an increased inhibition for standard sounds (i.e., the recovery of P2) could indeed represent a mechanism for auditory perceptual learning during the oddball paradigm and not just repetition effects. The inhibition for unattended standard sounds could be one of the mechanisms (along with enhancement or habituation of ERP responses) in the auditory system trying to optimize and predict the processing demands for incoming auditory events. Consequently, the processing demands are different whether succeeding auditory events are different or familiar to each other and relevant or irrelevant for the current task. Moreover, simple repetition effects cannot explain the fact that neural changes often precede or coincide with behavioral improvement in the discrimination of sounds (e.g., Tremblay et al. 1998; Ross & Tremblay, 2009). In the present studies (II-IV), behavioral improvement of deviating sounds between active tasks was significant only in non-musicians while musicians exhibited neural plasticity before and after the active task but behavioral discrimination remained at the ceiling level already in the first active task. There was no

further improvement in the behavioral discrimination in the follow-up, which was approximately one week after the EEG recordings. This finding suggests that the neural changes and behavioral discrimination in the first session indicated auditory perceptual learning that occurred mostly within one session and that while behavioral discrimination cannot improve further (as in musicians), there can be rapid plastic effects independently of active focused attention.

5.3 The neural mechanisms of auditory perceptual learning

Auditory perceptual learning has been studied for various stages of auditory processing with EEG and behavioral methods. The common goal in these studies has been to find the essential neural mechanisms for learning language and music, as well as rehabilitating auditory functions. In the previous sections, the focus of discussion has been on how passive exposure and the active, attentive sound discrimination task modulate rapid neural plasticity for regularly and irregularly presented sounds. Some of the rapid changes apparent in musicians only, were selective to particular ERP components or neural generators (based on ERP source analysis), and did not require focused attention. Correlations also revealed the relationship between the working memory and neural detection of deviating sounds. Next, the neural basis of auditory perceptual learning is discussed in the light of the source analysis findings.

5.3.1 Rapid plastic changes for deviant sounds in temporal vs. frontal sources

One of the research questions in Studies II and III was whether the auditory cortical (temporal) and frontal cortical sources have differential roles in rapid plasticity in musicians and non-musicians. These subcomponents have shown functionally different roles in sound change perception (Shalgi & Deouell, 2007) and differential rapid plasticity for deviating sounds (Baldegweg et al., 1999). Frontal activation is typically associated with an orienting response to new stimuli, or the involuntary switching of attention during change-detection for the attended stimuli. Temporal sources, on the other hand, reflect the basic processing of sounds and sound features in the primary and

secondary auditory cortices. Most importantly, previous evidence has shown enlarged grey matter volume in professional musicians, particularly in the temporal cortex (Schneider et al., 2002). Structural changes in sound processing areas most likely reflect long intensive exposure to music training (and the intensive auditory processing as part of their profession) since these changes were gradually larger the longer the period of musical expertise. In Study III, we found that musicians had enhanced rapid plasticity (i.e., habituation) in deviant ERP sources in both the auditory cortices and the left frontal cortex in response to easy deviants. With difficult deviants, only left frontal source activation habituated. Non-musicians did not show any of these rapid plastic changes in source activation. Although previous ERP findings show that musicians have especially accurate processing of small pitch deviants when compared with non-musicians (from MMN difference waves: Koelsch et al., 1999; Tervaniemi et al., 2005), according to current findings (in Study III) there was no difference in the *rapid plasticity* between pitch and duration deviants in musicians. Still, in general, musicians did have a stronger overall deviant ERP source strength within the MMN time frame at both auditory cortical (temporal) and frontal sources for pitch deviants than non-musicians; however, for duration deviants, musicians had stronger source strength than non-musicians only at the auditory cortex sources.

One possible explanation for the lack of significant rapid plastic changes in the right frontal source in musicians might be related to automatic change-detection processes such as the involuntary switching of attention or the inhibition of the response (Deouell, 2007; Rinne et al., 2005) to pitch deviants. In a previous imaging study comparing MMN generator activation for pitch and duration deviants, the right frontal source was pronounced for pitch changes in non-musicians (Molholm et al., 2005). In all participants (i.e., both musicians and non-musicians) in our study, duration had stronger temporal source activation, while pitch had stronger activation in both left and right hemisphere frontal sources. The rapid plastic changes, however seen only in musicians, as discussed in the previous paragraph, were not differential between the pitch and duration deviants but varied based on the level of difficulty. Further studies are needed to confirm whether the right frontal mechanism is pronounced for pitch deviants (taking into consideration that both frontal generators showed stronger responses for pitch deviants in musicians when compared to non-musicians here) and whether it is not as

responsive to the effects of musical expertise or rapid plastic effects (such as habituation) as the temporal generators.

In Study IV, rather than a source analysis, the neural mechanisms of auditory perceptual learning were studied using the statistical comparison of ERP data from anterior versus posterior and left versus right hemisphere electrodes. When comparing Active Tasks 1 and 2 for duration deviants, P3b habituated between tasks in the frontal electrodes in non-musicians, but in posterior electrodes in musicians. The frontal habituation in non-musicians may indicate a developing memory template for new auditory stimuli. In line with this idea, the P3 for attended novel sounds decreased at frontal electrodes in a previous study (Friedman et al., 1998). The plastic effects in parietal responses in musicians may reflect more automated task performance among the musicians during active conditions. Temporoparietal activation is also associated with auditory selective attention (Pugh et al., 1996) and use of the auditory working memory (Baddeley, 2003). Previous studies have also suggested that reduced activation at parietal and prefrontal brain regions is associated with higher performance in behavioral working memory tasks, probably reflecting practice effects (Jansma, Ramsey, Slagter, & Kahn, 2001). Indeed, in Study IV we found that musicians had superior (ceiling-level) behavioral discrimination accuracy in active tasks, but only non-musicians exhibited improved accuracy between the tasks (see section 5.1). In future studies, the potential differences in frontal and temporoparietal networks between musicians and non-musicians should be examined using imaging methods.

5.3.2 Rapid plastic changes for standard sounds in temporal vs. frontal sources

Based on source waveform analysis for ERPs, there were no differences in rapid plasticity between P1, N1, or P2 frontal and temporal generators for standard sounds (Study II). N1 and P2 source activation habituated only in musicians and in ERP analysis, P2 showed enhancement in both musicians and non-musicians at the frontal electrodes. N1 may reflect the automatic feature detection of the sound and has shown rapid plastic effects in previous studies (see *1. Introduction*). While the exact function of P2 is not well known, P2 is considered to reflect a secondary stage of relaying

information of the stimulus to the larger cortical areas. Based on both our own and on previous P2 findings, P2 seems to be prone to the effects of long-term auditory (musical) training as well as rapid plasticity. This is further supported by findings in which P2 generators were located in the secondary auditory cortices where plasticity is considered high (Crowley & Colrain, 2004; Jääskeläinen, Ahveninen, Belliveau, Raij, & Sams, 2007). P2 enhancement in the ERP analysis (and habituation for source waveforms) may be caused by the different effects of musical expertise on temporal and frontal sources or the summated scalp response from various other P2 sources that were not modeled here separately but were reflected as combined activity in analyzed source activation (see Godey et al., 2001). Thus, P2 plasticity seems to be evident (see also section 5.2) but the underlying mechanisms remain a subject of further research.

In general, source analysis results based on ERPs (and not on more accurate localization techniques, such as MEG or imaging methods) should be viewed with caution. Even though the EEG technique (and ERPs) can provide an objective and temporally highly accurate evaluation of the effectiveness of learning and rehabilitation on auditory neurocognition, the EEG method cannot, however, show accurately the activation loci for the generators or functional connectivity between different neural generators. EEG does not reach all the relevant activation especially from the deeper sources but it can summate the activation from simultaneous processes and from multiple sites in the cortex because of low spatial accuracy. Additional studies using functional and structural imaging (e.g., functional magnetic resonance imaging, diffusion tensor imaging) are needed to resolve learning-related changes in deeper ERP generators and in the functional connectivity between different neural structures. It is possible that musical training enhances particularly the functional connectivity from the sound processing areas to the other relevant areas, such as motor or vocal areas (for singers, see Halwani, Loui, Rüber, & Schlaug, 2011). Furthermore, the restrictions introduced by the averaging method (as used here) limit the reliability which could be in principle alleviated using other than traditional averaging (e.g., single trial approach).

Theoretically, the P2 findings could relate to so-called repetition positivity (RP, a positive wave after 50–250 ms after sound onset) that is often elicited for the repeated standard sounds before the following deviant sound (and the MMN response). RP may correlate for the stimulus-specific adaptation (SSA) in the auditory cortex (for a review,

see Baldeweg, 2007). There are, however, several differences between previous RP studies and our Study III. First, RP is typically found in a roving paradigm instead of in oddball paradigms (as here) so that standards are analyzed by averaging the responses to sounds that are presented in a particular position in the series of standard sounds (e.g., first position, last position before the deviant) (Haenschel et al., 2005). In the oddball paradigm, responses for the standard sounds are averaged over the block regardless of the position of the sound stimulus. The required timescale for the plastic effects may then be longer in the oddball context than is typically discussed in RP studies. Having said this, it is possible that memory formation for standard sounds shares the same neural processes during repetition positivity as it does in our case (see also Bendixen, Schröger, & Winkler, 2009 for the P1 (or earlier) response of omitted sounds in a non-roving paradigm; Garrido, Kilner, Kiebel, Stephan, Baldeweg et al., 2009 for the connectivity analysis for the repetition effect in the roving paradigm). The second issue is that RP has been evidenced only for sound frequency, not so far for sound duration. For example, when participants attended to the duration of the sounds, there was no significant RP effect (other methodological differences were also present, see Bendixen et al., 2007). Repetition of standard sounds (even when unattended) might still have a crucial role for perceptual learning and predicting auditory events since standard sounds also help the auditory system to build rules for irregular events (e.g., Baldeweg et al., 2007; Bendixen et al., 2007; Haenschel et al., 2005).

One possible model for the neural mechanisms of auditory perceptual learning comes from the single-neuron studies using the oddball paradigm. Using oddball stimuli in anesthetized animals, Ulanovsky, Las, & Nelken (2003) found that standard sounds elicited stronger neuronal adaptation (decrease in responses) than deviants in primary auditory cortex (A1) neurons. The adaptation was stronger the larger the frequency difference, and the smaller the deviant probability difference there was between the standard and deviant sounds. In other words, when using easier deviants (large difference to standards) with small probability (rare compared to standards), the neurons in the A1 show largest adaptation to standard sounds. Although it is highly overgeneralized to make hypotheses concerning human studies, one might speculate that if same neuronal processes also apply to humans, musical expertise would then modulate the neuronal adaptation so that the adaptation is stronger for standard sounds

(resembling the habituation seen in the present thesis) because even the smaller deviants become “easier” to process with musical training.

Further, in Ulanovsky et al. (2003), neuronal adaptation was mostly found at the cortical level of A1, and not in the auditory thalamic neurons which showed very small reflection of these processes (such as longer-term, i.e., seconds or longer, adaptation based on probability between deviant and standard sounds). They proposed that the rapid SSA in A1 could be equivalent to the MMN relating to auditory novelty detection and auditory sensory memory processes. In other words, the MMN could be a sum of many SSA processes occurring in the auditory cortex. This opens up new questions for MMN studies in general, as well as studies on the neural mechanisms of auditory perceptual learning: what neural areas are related to the adaptation process, and in what time scale. Investigating these aspects, at least two forms of SSA-related neuronal adaptation were found, the subcortical and not stimulus-specific, and the cortical SSA having longer memory for the presented sounds (Ulanovsky, Las, Farkas, & Nelken, 2004). Ulanovsky et al. (2004) proposed a two-stage mechanism for the adaptation starting with the elicitation of the response to the sound (which failed more often to standard sounds than to infrequently deviating sounds, explaining some portion of the adaptation in oddball conditions), and secondly, when the response to the sound was elicited, its firing rate was decreased (i.e., the response was diminished). It was proposed that the neuronal adaptation is influenced by both short (~1.5 sec) memory processes comparing the immediate stimuli difference as well as long (~tens of seconds) probability encoding processes. These observations require more studies among human subjects before further conclusions can be made, but they do provide some relevant possibilities for explaining the neural mechanisms of auditory perceptual learning. Our findings of stronger habituation in musicians may be related to the functional changes in how neurons in A1 are encoding the acoustic features of sounds as well as auditory sensory memory processes, which are the probable mechanisms for rapid plastic changes that we saw during auditory perceptual learning.

5.3.3 Relationship between auditory working memory and rapid plastic changes during active attention

In addition to enhanced rapid plasticity for automatic and preattentive ERPs in musicians, Study IV demonstrated that musical expertise also modulated the later, attention-sensitive processing such as P3b responses which also have a positive relationship to auditory discrimination and working memory capacity (Polich, Howard, & Starr, 1983). Indeed, a recent study showed that music training enhanced performance in working memory tasks (George & Coch, 2011). More efficient auditory working memory in musicians could explain why musicians had enhanced activation in the left auditory cortex and frontal cortices in response to melodic pattern deviances when compared to non-musicians (Habermeyer, Herdener, Esposito, Hilti, Klarhöfer et al., 2009). In their study, neural activation correlated with behavioral musical aptitude scores. Here, we observed a positive relationship between behavioral discrimination accuracy of the deviating sounds in active tasks and working memory skills in the digit span test but unlike earlier studies, we did not find differences between musicians and non-musicians for the standardized tests of attentional inhibition and auditory working memory skills, nor did these results relate to P3a or P3b plasticity (Study IV). It may be that the simple and artificial sine tones used in our studies were unsuitable for studying the effects of auditory working memory functions, which are thought to help to maintain larger chunks of stimulus material. Also, further generalization into more complex learning in natural settings is limited also because the stimuli in Study IV (as in many ERP studies) were repeated several hundred times in a short time window. Moreover, it is possible that large individual variation in both behavioral performances in attention tests as well as in ERPs hindered the group comparisons in the present thesis. Again, background variables such as different forms of attention that have not been tested here may have an effect on ERPs. In future ERP studies, individual attentional skills and working memory capacity should be taken more carefully into account and also be controlled for between groups. The communication between the sensory memory and the working memory may be crucial in learning new auditory material, allowing more flexible sound feature processing and rule extraction for various auditory events. Future studies should investigate the neural connections between different memory systems

and clarify whether musical training enhances these mechanisms when learning other than musically relevant stimuli such as spoken foreign languages (François & Schön, 2010) or multimodal stimuli (Lappe, Herholz, Trainor, & Pantev, 2008). Yet, it should be taken into consideration that although short-term and long-term memory are typically measured differently *behaviorally*, from a *neural* point of view these skills may share the same neural substrates and reflect more like a continuum of processes rather than totally separate structures (Jääskeläinen, Ahveninen, Andermann, Belliveau, Raji et al., 2011, for further discussion, see the following section).

5.4 Theoretical and practical implications

One of the first theories of how musical expertise develops was introduced by Ericsson, Krampe, and Tesch-Römer (1993). They suggested that at least ten years are needed to achieve the expertise-level cognitive processing which was enabled by chunking mechanisms (i.e., the capacity to process larger units in the working memory) and the so-called long-term working memory (Ericsson & Kintsch, 1995). Enhanced processing of larger amounts of sound information may well describe the neural process of facilitated auditory perceptual learning, or statistical learning, in musicians (Paraskevopoulos, Kuchenbuch, Herholz, & Pantev, 2012). Consistent with this idea, musicians seem to develop more efficient auditory working memory skills that may support the chunking process for more complex sound stimuli (George & Coch, 2011; Habermeyer et al., 2009). In the present studies, however, we did not find a significant difference in working memory tests between musicians and non-musicians probably because of large variance within musician group. Supporting evidence for chunking (or, in neurocognitive terms processing spectrally and temporally more complex sound structures) comes from various neurocognitive studies of musicians (e.g., Koelsch et al., 1999; Rüsseler et al., 2001; van Zuijen et al., 2004; Vuust et al., 2005). Since musicians are better at discriminating musically relevant and complex stimuli in learning tasks, we decided in our studies to use relatively simple sound stimuli when examining auditory perceptual learning. The downside of this decision is certainly a decrease in ecological validity and generalization into a more natural sound environment. For example, musicians and musically advanced school-children may learn more efficiently foreign

phonemes that are rare in their own language. Some indication of this has already been found (Marques et al., 2007; Milovanov & Tervaniemi, 2011). In future studies, the connections between basic sound processing (sensory memory), the working memory and the long-term working memory should be investigated by using more elaborate paradigms and stimuli than have been used here. Rapid neural changes, with or without improvements in behavioral discrimination accuracy for to-be-learned stimuli, may be a necessary precondition to longer-term learning-related plastic effects and perceptual learning (Pascual-Leone et al., 2005).

Although behavioral tasks, such as standardized cognitive tests, can provide useful information, such as screening how participants perform against the *normative* performance (as we measured here in participants in Studies II, III and IV), behavioral measures cannot determine to what degree the memory and attentional capacity and skills (as well as motivational and arousal levels) influence the task performance and learning. Dissociation between behavioral and neural measures was also evident in our studies where behavioral evidence for auditory perceptual learning (i.e., improved discrimination accuracy of deviating sounds during active tasks) was found only in non-musicians, while musicians had maximal accuracy in discrimination in the active tasks (Study IV). In addition, musicians demonstrated a greater degree of rapid plasticity (mostly habituation), which could also reflect the neural mechanisms of auditory perceptual learning of sounds.

In the studies presented here, we replicated previous neurocognitive studies in which musical training enhances neural sound processing. To extend this literature, we also demonstrated that musical training facilitates very efficiently rapid plasticity during the auditory perceptual learning of sounds. One practical implication from the current thesis findings could be that while musical training enhances basic sound processing and learning, musical training may also enhance the neural processing of other auditory information such as foreign language phonemes. Whether this is the case or not, it sends out an important message to educational institutions: music education as part of the regular school curriculum can play an important role in supporting spoken and written language learning. Studies in future could further investigate the relationship between sound perception and production, such as whether the auditory perceptual learning of

music and speech sounds transfers to the production of speech in that language (for the existing evidence, see Milovanov & Tervaniemi, 2011).

Another practical implication from our studies is that musical training seems to facilitate basic sound processing and learning even in conditions when attention is not focused on sounds. Music training could also be particularly rewarding for young children and students who do not yet have attentional skills which allow them to focus their attention for longer periods of time. Listening to and playing music gives instant feedback and does not require effortful attention at all times. Moreover, music training may also influence other memory forms, such as rhythmic and motor memory skills. For example, a recent study has demonstrated that musical activities have a positive influence on rehabilitation with middle cerebral artery stroke patients (Särkämö, Tervaniemi, Laitinen, Forsblom, Soynila et al., 2008). Further neurocognitive studies should examine closer the effects of musical training on learning and rehabilitation of motor and fine-motor maintenance. Neurocognitive studies of development of expertise would also benefit from evaluating the different stages of musical training in longer-term follow-ups. One possibility is to use a cross-sectional approach for many age groups. Illustrating this kind of approach, a recent study demonstrated that brain areas relating to attentive auditory rhythm processing, and motor and auditory working memory areas develop during normal maturation while for example the development of auditory-motor coordination relates to musical training (Ellis et al., 2012).

Apart from the practical implications, one of the theoretical implications from our studies was that auditory perceptual learning does not necessarily require selective and focused attention to the to-be-learned material, at least when relatively simple sounds are used. This was evidenced particularly in musicians who had enhanced habituation in automatic and preattentive sound processing during passive exposure, even before focused attention. Habituation to deviating sounds was also observed in non-musicians but only after the attentive task. Of importance here is to notice that the attentive task was only five minutes long, which could mean that even non-musicians are able to have relatively rapid plasticity during auditory perceptual learning. Furthermore, rapid plasticity was observed at various stages of sound processing including automatic and preattentive ERP components (N1, P2 and deviant ERP within a MMN time frame) as well as for ERP components reflecting attentive processing (P3b). Our findings for N1

and P2 for standard sounds and P3 findings for deviating sounds corroborated in some aspects the previous findings while deviant ERP findings in Study III somewhat contradicted previous findings of both perceptual learning (previous studies showing mostly enhancement to the learned stimuli) and musician studies (previous studies showing a main effect of musical training for the frontally maximal MMN ERP). These latter contradictions may well be explained by the fact that previous studies used a difference wave approach instead of the average-wave approach used here (Studies II-IV).

In Studies II, III and IV, we found that auditory perceptual learning of simple sounds elicited habituation (a decrease in ERP amplitude) in various stages of sound processing. While P1 did not show rapid plasticity, N1 and P2 showed rapid plasticity in musicians for regular sounds (Study II). For deviating sounds, deviant-related ERP within a MMN time frame showed habituation in musicians in auditory processing areas (temporal cortex) and the left frontal generator (Study III). Additionally, the rapid plasticity of P3a and P3b was modulated by musical expertise and was related to working memory capacity. For more difficult sound discrimination, P3b enhanced (Study IV). It may be that complex associations and rules produce enhancement in ERPs while auditory perceptual learning of simpler sounds produce habituation. In common terms, when a stimulus becomes easily predictable and familiar after repetition, the processing demands (encoding the sound features and extracting the rules) decrease and processing becomes more automatized (i.e., without the need for attentive processing). Neurally, this may be evidenced as a habituating response.

Habituation is a primitive form of learning of repeated stimuli that have become familiar and do not elicit an orienting response. Thus, habituation could be an essential mechanism of the hearing system and of auditory perceptual learning. Habituation reflects the filtering of relevant, new stimuli from the auditory stream and decreases processing resources committed to non-surprising events. Unlike neuronal adaptation, habituation is an active process and dishabituation can be caused by experimental manipulation (Picton, Hillyard, & Galambos, 1976). For example, the oddball paradigm introduces both repetition of regular sounds (which could elicit adaptation) but also irregular deviating sounds. With this in mind, the stimulation in Studies II, III and IV may have been easier to process for musicians and may have led to greater habituation

when compared to non-musicians. In general, auditory tasks could have been easier for musicians than for non-musicians, requiring fewer neural resources in musical experts (Jäncke, Shah, & Peters, 2000).

When trying to model the current rapid plastic findings at the system level, habituating responses for learned stimuli can be explained by prediction coding (Friston, 2005). This framework resembles the model of the perceptual cycle introduced by Neisser (1976). Applied to neural processing, when new material is assimilated to the existing internal “template” (i.e., memory content), it does not require that much effortful processing other than processing totally new information that requires accommodation and causing probably a prediction error for the perception. The habituation may not, however, change the way in which very familiar but highly irregular sounds or sound patterns are processed. An example of a relevant but irregular sound pattern could be a personal mobile phone tune, which catches the attention even when it is heard a thousand times.

The prediction coding framework has been used to explain the decrease of MMN during auditory perceptual learning (Garrido et al., 2009). According to this model, MMN amplitude decreases when a person learns to predict the deviating auditory event and the prediction error is reduced (i.e., when deviants become too predictable). Thus, the auditory system actively creates a set of rules between varying sound events. Researchers have presented a model of perceptual learning where rapid plastic effects first evolve nonlinearly from the rapid adaptation phase to perceptual learning. As auditory perceptual learning proceeds and predictability increases (along with the repetition of a stimulus), the connections between auditory and frontal areas decrease (Garrido et al., 2009). Although we did not examine neural connectivity (like Garrido et al. did), applied to our findings, temporal and left frontal source habituation in musicians (Study III) could indicate the suppression of the prediction error for deviating sounds.

Another model for explaining frontal habituation for difficult deviants (Study III) could be the attention-gated reinforcement learning model (Roelfsema, van Ooyen, & Watanabe, 2010). Applying this model to auditory perceptual learning, sounds that have been processed in the primary auditory areas, are feedforwarded into higher-level cortical areas. Based on neuronal competition, the frontal cortex sends the feedback to

lower-level cortices that determine which behavioral response is relevant and whether to attend to particular stimuli. The winning neurons receive the most feedback (i.e., attention) from frontal areas (Roelfsema et al., 2010). Based on this model, frontal habituation (in the left hemisphere) might then be explained by a decreased need for neuronal competition (and thus a decreased allocation of attention) to deviating target sounds. In line with this hypothesis, a single-cell study in animals showed that the neurons in the frontal cortex could shape the rapid plasticity in the primary auditory cortex by directing the selective attention to sounds (Fritz, David, Radtke-Schuller, Yin, & Shamma, 2010). In their study, frontal processing attenuated selectively to standard sounds and was enhanced for deviating target sounds. The authors propose that their findings would likely reflect target (deviant sound) recognition and not just arousal, pure sensory or motor effects, or motor planning.

In neurocognitive studies, one goal is to reveal the neural mechanisms underlying cognitive processes. Theoretically it is important to notice that from the neural point of view cognitive and sensory processes are not isolated as was previously thought. This increases the complexity of studying and especially modeling the basic mechanisms of cognitive or even low-level sensory processes. Emotions, expectations and experiences (commonly termed top-level processes) can significantly modulate lower-level processing, such as basic sensory processing. Consequently, neurocognitive studies may not always support ‘modular’ structures of the memory or learning functions. For example, in the case of perceptual learning, short-term plasticity (referred to here as rapid plasticity) may be a supporting mechanism for both the sensory and the short-term memory, selective and involuntary attention, and perceptual learning (Jääskeläinen et al., 2011). Although these cognitive functions are often separated behaviorally, they may share neural processes: depending on the input stimulus type (bottom-up vs. top-down) and the abstraction level, either memory or attention processes are activated (for a review, see Jääskeläinen et al., 2011). On the other hand, in the present thesis, only the system- (high-) level approach to neural functions was investigated. Molecular neuroscience has provided important insights into the neural mechanisms of learning (e.g., long-term potentiation and depression) but that approach is still not easily used in human subjects, and to apply generalizations from molecular studies to human cognition is a complex albeit desirable undertaking.

5.5 Concluding remarks

Neurocognitive evidence has consistently shown remarkable long-term effects of musical expertise on the brain structure and its functions, as well as how musical expertise develops in the long run (Jäncke, 2009; Münte et al., 2002; Pantev & Herholz, 2011; Tervaniemi, 2009). Studies on the neural basis of musical expertise can also benefit the study of learning and the rehabilitation of auditory functions. One of the main findings in this thesis suggests that the auditory system is capable of fine-tuning based on particular needs, such as practice strategies. In Study I, we found that while different types of musical experts share some basic sound processing, practice strategies (ear-based playing vs. other strategies) may influence the way musicians process and learn complex sound patterns. Also, a consistent finding was that musical expertise enhanced rapid cortical plasticity for regularly and irregularly presented sounds that occurred within 15-30 minutes for simpler sounds (Studies II, III and IV). These changes were observable even without focused attention to sounds, during passive exposure to sounds. Furthermore, in musicians this exposure type of auditory perceptual learning was pronounced for pitch deviants while attention-gated perceptual learning was also observed for duration deviant sounds. Auditory perceptual learning of more complex sound patterns (like measured rapid plastic effects), however, required focused attention even in musicians (Study I). On the other hand, Studies II-IV demonstrated that musical experts did not only have enhanced sensory encoding of sound features and rules between varying auditory stimuli, they also had improved attentional processing of sounds. The current findings encourage further study on whether musical training could be used more widely to enhance auditory attentional skills and learning in auditory tasks beyond music, such as learning a new language or rehabilitating auditory functions.

6 References

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