The neural basis of Western music chord categorisations – effects of development and music expertise

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Academic dissertation to be publicly discussed,
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at the University of Helsinki in Auditorium 13, in the University Main building,
Fabianinkatu 33, on the 14th of January, 2015, at 12 o'clock

University of Helsinki
Institute of Behavioural Sciences
Studies in Psychology 107: 2015

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ISSN-L 1798-842X
ISSN 1798-842X
ISBN 978-951-51-0531-8 (pbk.)
ISBN 978-951-51-0532-5 (PDF)
http://www.ethesis.helsinki.fi
Unigrafia
Helsinki 2015

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Abstract

Infants already demonstrate readiness for music processing. Although culture-specific music-processing skills are acquired through exposure to music, even in the absence of formal training, the processing of music sounds is known to be facilitated by music training from early on. Major *vs.* minor and consonance *vs.* dissonance categorisations have a central role in Western tonal music and are highly meaningful for Western listeners. However, their neural basis and its development have not been extensively studied. The present thesis examined the preattentive processing of Western music chord categorisations from infancy to adulthood by measuring event-related potentials (ERPs) of the electroencephalogram (EEG), using a mismatch negativity (MMN) paradigm. The effect of music expertise on their processing was studied in school-aged children and adults. In the MMN paradigm, minor chords, inverted major chords, and highly dissonant chords were presented infrequently as deviant sounds in the context of root form major chords. Since all chords were transposed to several frequency levels, the deviant chords introduced no new frequencies to the paradigm, and thus an MMN caused by simple physical deviance was prevented. The results demonstrate the facilitating effects of music expertise on Western music chord discrimination neurally in adults and school-aged children, and behaviourally in adults. Sensitivity to Western music chord categorisations, particularly consonance *vs.* dissonance, was evident already at birth. While there was no evidence of major *vs.* minor discrimination as indicated by MMN elicitation in school-aged children without music training, there was tentative evidence of it in newborn infants and non-musician adults. Only musician adults demonstrated sensitivity to root *vs.* inverted chords, indicating that the facilitating effect of music expertise on the neural processing of the chords grows with age and years of practice. The present thesis suggests that, building on early auditory skills, some implicit knowledge of Western music chord categorisations is acquired via exposure to music during development, without formal training. However, consistent neural representations of complex chord categories may require extensive amounts of formal music training.

Tiivistelmä

Jo vauvaikäisellä on valmiuksia musiikin käsittelyyn. Oman kulttuurin musiikin prosessointitaitoja omaksutaan musiikille altistumisen myötä myös ilman muodollista musiikkikoulutusta. Musiikin harrastaminen kuitenkin tehostaa musiikkiäänten käsittelyä jo lapsuudessa. Duuri vs. molli ja tasasointisuus vs. riitasointisuus ovat länsimaisessa musiikissa keskeisiä elementtejä, ja niillä on vahvoja merkityksiä länsimaiselle kuulijalle. Silti niiden hermostollista perustaa ja sen kehitystä ei ole kattavasti tutkittu. Tässä väitöskirjatyössä selvitettiin länsimaisen musiikin sointujen esitietoista käsittelyä vauvaiästä aikuisuuteen aivosähkökäyrän tapahtumasidonnaisia jännitevasteita mittaamalla, käyttäen nk. MMN-koeasetelmaa (*engl. mismatch negativity paradigm*). Musiikkikoulutuksen vaikutuksia sointujen käsittelyyn tutkittiin kouluikäisillä ja aikuisilla. MMN-koeasetelmassa mollisointuja, duurisointukäännöksiä ja voimakkaita riitasointuja esiintyi harvakseltaan poikkeavina ääninä perusmuotoisten duurisointujen joukossa. Koska kaikki soinnut oli transponoitu usealle äänenkorkeudelle, poikkeavat soinnut eivät tuoneet koeasetelmaan uusia äänenkorkeuksia, ja siten vältettiin MMN-vasteen syntyminen reaktiona yksinkertaisiin, fysikaalisiin poikkeamiin. Tulosten perusteella musiikkiharrastus on yhteydessä länsimaisen musiikin sointujen tehostuneeseen erotteluun sekä hermostollisesti kouluikäisillä ja aikuisilla että tehtäväsuoriutumisen tasolla aikuisilla. Jo vastasyntyneillä ilmeni valmiutta erotella länsimaisen musiikin sointuja, etenkin tasasointisia vs. riitasointisia sointuja. Kouluikäisillä, joilla ei ollut musiikkiharrastusta, ei ilmennyt näyttöä molli- vs. duurisointujen hermostollisesta, esitietoisesta erottelusta. Siitä oli jonkinasteista näyttöä vastasyntyneillä sekä aikuisilla, joilla ei ollut runsaasti musiikkikoulutusta. Vain aikuiset muusikot erottelivat esitietoisesti perusmuotoisia sointuja vs. sointukäännöksiä, minkä perusteella musiikkikoulutuksen yhteys sointujen tehostuneeseen hermostolliseen prosessointiin näyttää kasvavan iän ja harrastusvuosien myötä. Tämän väitöskirjatyön perusteella myös altistuminen länsimaiselle musiikille ilman muodollista musiikkikoulutusta voi tukea kykyä erotella länsimaisen musiikin sointutyyppejä, mutta jo varhaiset kuulovalmiudet luovat pohjaa sointujen käsittelylle. Vakaiden hermostollisten edustusten syntyminen monimutkaisille sointuluokitteluille voi kuitenkin vaatia pitkäkestoista musiikkikoulutusta.

Acknowledgements

I am so grateful to my supervisors, Professor Mari Tervaniemi and Research Professor Minna Huotilainen. Mari, I would like to thank you for your caring and supporting supervision, for always having time for me and helping me to understand what is important and what is not. Also, I want to express my gratitude for doing such excellent work as head of the Brain and Music Team in the Cognitive Brain Research Unit. Minna, I owe you my thanks for welcoming me in your project when I was just a 3rd year psychology student, for teaching me about the importance of self-confidence and the value of always saying “yes”, and sending me all around the world to learn about international collaboration. I want to thank both of you for being such excellent role models as highly proficient female scientists. Among many important things, you have taught me that science is about team work and collegial trust, and that combining family with academia is possible.

I am extremely grateful to my co-authors Dr. Eino Partanen, Docent Petri Paavilainen, Professor Vineta Fellman, Dr. Vesa Putkinen, and laboratory engineer Tommi Makkonen, for their valuable contributions to the articles of this thesis. I would like to especially thank Docent Petri Paavilainen for giving me a thorough introduction to the world of ERPs, Dr. Vesa Putkinen for teaching me almost everything about EEG analysis, and Dr. Eino Partanen for introducing me to the world of baby EEG together with Docent Anke Sambeth, for selflessly helping me in different phases of my work, and for showing me an example on how to move from being a PhD student to being a post-doctoral researcher. I thank laboratory engineer Tommi Makkonen for his excellent technical and psychological support during these years. Also Jari Lipsanen, Kalevi Reinikainen, and Miika Leminen deserve my gratitude for your generous help with the methodological and technical issues. To the list of co-authors I add my fellow psychology students on an experimental cognitive neuroscience course, supervised by Docent Petri Paavilainen, where the paradigm that grew to be this thesis was originally designed by the author together with Venla Berg, Maari Kivioja, Juha Purhonen and Dr. Marko Salmenkivi. I want to thank you for the enthusiasm and innovativeness that made me think about being a researcher. The Cognitive Brain Research Unit and the Brain and Music Team, have created a free, equal and friendly place for me to “grow up” as a researcher, learn about my strengths and limits and gain faith in myself and the power of science. Your collegial support and help has been amazing. In addition to those already mentioned, I want to thank my office roommate Tanja Linnavalli for sharing the ups and downs of PhD years with me, Katri Saarikivi for her friendship when we recorded EEG from a hundred children together, and Dr. Satu Pakarinen for being like a big sister to me during my first years in science. I am extremely thankful to all the children and adults who have participated in our experiments during these years.

I thank the highly skilled research nurse Tarja Ilkka for conducting the baby EEG measurements for this thesis, and Katharina Schäfer for her valuable assistance in the adult EEG recordings for this thesis. I owe my gratitude also to Professor Juha Ojala and Dr. Esa Lilja, for showing me the importance of enthusiasm, curiosity and courage in interdisciplinary research. I also want to thank my master students for teaching me so much and making my work easy. Thank you, Dr. Christian Hakulinen, Venla Berg, and Jaakko Airaksinen for sharing with me these interesting years of PhD studies.

Thank you, Piiu Lehmus, Riitta Salminen, and Marja Junnonaho for your help and patience with the administrative challenges I have had during these years.

I am utterly grateful to the expert reviewers of my thesis, Assistant Professor Sylvain Moreno and Professor Paavo Leppänen, as well as all the expert reviewers of the articles of this thesis. I want to thank Professor István Winkler for agreeing to act as the opponent of my thesis. It is truly a great honour for me. Also, I want to thank Professor Teija Kujala for hiring me as a post-doctoral researcher in her ambitious project and giving me her support and understanding during the final steps of my thesis.

I express my gratitude to Helsinki University Science Foundation and Emil Aaltonen Foundation for funding my PhD work, as well as the Finnish Konkordia Foundation and the grants of the University of Helsinki for supporting my international activities. The Finnish Centre of Excellence on Interdisciplinary Music Research by the Academy of Finland, led by Professor Petri Toiviainen, has provided the resources for our research team so that we have had the peace to work on years 2008–2013.

Finally, my love and gratitude go to my nearest and dearest people: my family, Anita, Esa and Janne Virtala, my dear, amazing boyfriend Pauli Perälä and my best, best friends Milka Pajukallio, Tiina-Maaria Laihi, Aino Korrensalo, and Arttu Haglund. So many other friends and relatives could be mentioned here, you know who you are. You all remind me of the priorities of life, value me regardless of my earthly accomplishments, and make my life worth living. I am so thankful to you all for helping me through bad times and enjoying the good times by my side. What can I say? I'll be there for you, 'cause you're there for me, too.

In Helsinki, 8.12.2014

Paula Virtala

List of original publications

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

I Virtala, P., Berg, V., Kivioja, M., Purhonen, J., Salmenkivi, M., Paavilainen, P., & Tervaniemi, M. (2011). The preattentive processing of major *vs.* minor chords in the human brain: An event-related potential study. *Neuroscience Letters, 487*, 406–410. doi: 10.1016/j.neulet.2010.10.066

II Virtala, P., Huotilainen, M., Putkinen, V., Makkonen, T., & Tervaniemi, M. (2012). Musical training facilitates the neural discrimination of major versus minor chords in 13-year-old children. *Psychophysiology, 49*, 1125–1132. doi:10.1111/ j.1469-8986.2012.01386.x

III Virtala, P., Huotilainen, M., Partanen, E., Fellman, V., & Tervaniemi, M. (2013). Newborn infants' auditory system is sensitive to Western music chord categories. *Frontiers in Psychology, 4*, 492, 1–10. doi: 10.3389/fpsyg.2013.00492

IV Virtala, P., Huotilainen, M., Partanen, E., & Tervaniemi, M. (2014). Musicianship facilitates the processing of Western music chords – An ERP and behavioral study. *Neuropsychologia, 61*, 247–258. doi: 10.1016/j.neuropsychologia.2014.06.028

Abbreviations

ANOVA-R	Repeated measures analysis of variance
ANOVA	Analysis of variance
EEG	Electroencephalography
EOAE	Evoked otoacoustic emission
EOG	Electro-oculogram
ERAN	Early right anterior negativity
ERP	Event-related potential
fMRI	Functional magnetic resonance imaging
LPC	Late positive component
LSD	Least-significant difference test
MEG	Magnetoencephalography
MMN	Mismatch negativity
PET	Positron emission tomography

1 Introduction

A growing body of evidence links music training to plastic changes in the brain structure and function (for reviews, see Habib & Besson, 2009; Herholz & Zatorre, 2012; Moreno & Bidelman, 2014; Münte, Altenmüller, & Jäncke, 2002; Pantev & Herholz, 2011; Peretz & Zatorre, 2005; Schlaug, 2001; Tervaniemi, 2009). The facilitating effect of music training is seen particularly in processing of sounds (review: Pantev & Herholz, 2011), and it seems to be pronounced when the sounds are complex or music-related (Fujioka, Trainor, Ross, Kakigi, & Pantev, 2004; Pantev et al., 1998; Pantev, Roberts, Schulz, Engelien, & Ross, 2001b), i.e., when the stimulation is highly familiar to musically trained individuals. Participation in music activities can shape the brain responses to sounds from early on (Trainor, Marie, Gerry, Whiskin, & Unrau, 2012). The auditory processing is shaped also by brain maturation for nearly two decades after birth (Ponton, Eggermont, Kwong, & Don, 2000). It has been proposed that the developing brain is especially sensitive to effects of music training due to the on-going maturation process, and that starting music training early may lead to greater and more long-lasting effects than starting later in life (Penhune, 2011; Trainor, 2005).

Still, readiness for processing music is present early in human development, already before significant exposure to music, as evidenced by studies on infants (for reviews, see Hannon & Trainor, 2007; Trainor & Corrigall, 2010; Trehub, 2003a, 2003b, 2004, 2010; Trehub & Hannon, 2006). The early-emerging sensitivities to musical sound properties build on general auditory skills, and serve as candidates for musical universals and biological predispositions for music processing (Hannon & Trainor, 2007). Through the process of musical enculturation, that is, the implicit adoption of rules and structures of one's own music culture during every day exposure to music, the processing of music from one's own culture is facilitated compared to unfamiliar music cultures also in the absence of formal music training (Hannon & Trainor, 2007; Trainor et al., 2012).

In Western tonal music, chords comprised of three or more simultaneously played notes can be categorised according to their interval structures as, e.g., *major* or *minor*. Interval structure defines the mutual pitch relationships between the notes of the chord. For Western listeners, major and minor modes carry different emotional connotations, which make the modes discriminable even in the absence of music training (Crowder, 1985a; Hunter, Schellenberg, & Schimmack, 2010; Pinchot Kastner & Crowder, 1990; Khalfa, Schön, Anton, & Liegeois-Chauvel, 2005). Another central factor in Western music chords is their perceived *consonance vs. dissonance*. Dissonance is attributable to certain tone combinations leading to an unpleasant perception of roughness (reviewed in Rossing, Moore, & Wheeler, 2002), and it elicits different activation patterns than consonance already in the subcortical levels of the auditory nervous system (reviewed in Bidelman, 2013). Despite their central role in Western music, neither the neural basis of Western music chord categorisations, nor the effects of maturation, musical enculturation, and music training on their processing, have been extensively studied in neuroscience of music (for some earlier studies see Brattico et al., 2009; Koelsch, Schröger, & Tervaniemi, 1999; McDermott, Lehr, & Oxenham, 2010; Putkinen, Tervaniemi, Saarikivi, Ojala, & Huotilainen, 2014b; Schön, Regnault, Ystad, & Besson, 2005; Tervaniemi, Sannemann, Nöyränen, Salonen, & Pihko, 2011).

The change-related preattentive auditory event-related potential (ERP) of the electroencephalogram (EEG) termed mismatch negativity (MMN) has proven an especially attractive tool for studies on music sound processing (for recent reviews, see Kujala, Tervaniemi, & Schröger, 2007; Näätänen, Kujala, & Winkler, 2011; Näätänen, Paavilainen, Rinne, & Alho, 2007; Paavilainen, 2013; section 1.1.1.1). Elicited early in brain development, even in sleeping newborn infants (Alho, Sainio, Sajaniemi, Reinikainen, & Näätänen, 1990), relatively independent of attention (for a review, see Sussman, 2007), but still associated with behavioural discrimination accuracy (Amenedo & Escera, 2000; Näätänen, Schröger, Karakas, Tervaniemi, & Paavilainen, 1993; Novitski, Tervaniemi, Huotilainen, & Näätänen, 2004), MMN is well-suited for studies on auditory processing and discrimination capabilities of infants and small children with limited capacities for attending to given tasks or giving behavioural responses. Furthermore, it is possible to compare processing differences that are related to long-term experience, for example differences between musicians and non-musicians (Näätänen et al., 2007).

In order to obtain maximal experimental control, the stimulation paradigms in brain research on music sound processing have been rather artificial. While a musical context is always complex and varying, the experimental paradigms are often repetitive and homogenous. For example the previous studies on major *vs.* minor chord processing have introduced single examples of major and minor chord types as experimental stimuli, leading to obvious frequency differences between the stimuli and thus compromising the interpretation of the obtained results (Brattico et al., 2009; Koelsch et al., 1999; Putkinen et al., 2014b; Tervaniemi et al., 2000b, 2011). Furthermore, as pointed out by Koelsch and Mulder (2002), the "music sounds" of ERP studies are often composed of sinusoidal tones instead of harmonically rich music sounds. Since there is evidence that the presence of harmonics may facilitate sound processing compared to sinusoidal tones (Novitski et al., 2004; Shahin, Roberts, Pantev, Trainor, & Ross, 2005; Shahin, Roberts, Pantev, Aziz, & Picton, 2007; Tervaniemi, Alho, Paavilainen, Sams, & Näätänen, 1993; Tervaniemi et al., 2000a; Kuriki, Kanda, & Hirata, 2006), attributable to information increase and higher stimulus familiarity of spectrally rich sounds compared to sinusoidal sounds (Tervaniemi et al., 2000a), the results of many studies may give misleading information on the neural basis of authentic music sound categorisations and lead to general underestimation of auditory processing capabilities. Studies of ERPs elicited by music sounds in a complex, variable context and direct comparisons of the ERPs elicited by harmonically rich music sounds and sinusoidal tones as well as their behavioural discrimination accuracy are thus called for, in order to obtain ecologically valid information on the neural basis of music sound processing in different participant groups.

The present thesis examines the neural basis of Western music chord categorisations in Western listeners as reflected by ERPs generated in a complex, variable sound context in three different age groups: newborn infants, school-aged children, and adults. In the latter two age groups, participants with and without formal music training are compared, in order to study the effects of musical enculturation *vs.* active instrument practice on the development of the chord categorisations. In adults, processing of sinusoidal *vs.* harmonically rich sounds as well as the relationship between preattentive ERPs and behavioural discrimination accuracy are compared. The study on newborn infants addresses the question of early sensitivity to chord categorisations that are highly relevant in Western music.

Below, the auditory ERPs as means to study music sound processing in the brain of adults, infants, and children are reviewed in section 1.1, with a focus on MMN as an index of preattentive sound discrimination, as it is the main method in the present study. Following this, the effect of music training and expertise on auditory brain plasticity in different age groups, mainly studied with ERPs, is reviewed in section 1.2. In section 1.3, a selective review on the development of auditory skills related to music sound processing is presented, with emphasis on early sensitivities to music processing and the process of musical enculturation. Finally, in section 1.4, the central Western music categorisations major-minor and consonance-dissonance are reviewed, focusing on their neural basis and development in the presence and absence of music training.

1.1 Auditory ERPs as means to study music sound processing in the brain

Due to high temporal resolution, non-invasiveness, and cost-effectiveness of the technique, EEG has deemed a central method in studies of auditory processing in the human brain from infancy to adulthood (Luck, 2005; Picton, 2010). The ERPs in response to sounds are calculated by averaging together tens or hundreds of epochs of the EEG time-locked to presentation of a certain sound. In this way, the activity unrelated to the sound is attenuated, and the ERP waveform that is left is understood to reflect the summation of postsynaptic potentials after simultaneous firing of a large group of neurons with parallel orientation, in response to the presented sound (Luck, 2005; Picton, 2010). In addition to EEG, magnetoencephalography (MEG) can be used to record the magnetic fields corresponding to ERPs measured with EEG. The magnetic counterparts of the ERP components are labelled with letter ‘m’ (e.g., the magnetic counterpart of MMN is labelled MMNm).

1.1.1 Auditory ERPs in adults

The waveform of the adult auditory ERP in response to a sound stimulus consists of a series of peaks labelled according to their polarity (P for positive, N for negative) and temporal order as P1 (around 50 ms from stimulus onset), N1 (100 ms), P2 (180 ms), and N2 (250 ms, for an overview see, e.g., Luck, 2005; Picton, 2010). These ERPs reflect basic auditory processing in the auditory cortex (for a review on N1, see Näätänen & Picton, 1987; on P2, see Crowley & Colrain, 2004; on N2, see Näätänen & Picton, 1986). Each peak in the ERP waveform reflects a contribution from several neural processes and functions, called subcomponents (Näätänen & Picton, 1987). As reviewed in section 1.1.2, these ERP peaks have different maturational tracts, with some of them appearing early in development and others only in late adolescence (Kushnerenko, 2003; Ponton, Eggermont, Khosla, Kwong, & Don, 2002; Ponton et al., 2000). Furthermore, the morphology and topography of the ERPs changes during maturation (Kushnerenko, 2003; Ponton et al., 2000, 2002). The N1 and P2 are modified by physical stimulus features as well as attention (Crowley & Colrain, 2004; Näätänen & Picton, 1987). The so-called basic N2 is elicited by repetitive identical sound stimuli (Näätänen & Picton, 1986). When an occasional deviant sound appears in the repetitive sound stream, an enhancement in the N2 latency is observed. This enhancement, termed MMN, is reviewed in the following section.

1.1.1.1 MMN as an index of preattentive auditory change detection

MMN is a negative-polarity deflection of the ERP waveform seen around 150–250 ms post-deviance by subtracting the ERP to frequently occurring standard sounds from the ERP to occasionally occurring deviant sounds in a so-called oddball paradigm (introduced by Näätänen, Gaillard, & Mäntysalo, 1978; for reviews, see Kujala et al., 2007; Näätänen, 1992; Näätänen et al., 2007, 2011). According to present understanding, MMN arises when the sensory information of the deviant stimulus violates the expectations that have been formed on the basis of the preceding standard stimuli (Näätänen et al., 2007, 2011). An alternative explanation for MMN elicitation suggests that rather than a distinct neural process, MMN is merely an enhancement of the N1 component caused by neuronal adaptation of the N1 response to standard stimuli, leading to larger N1 responses to deviant stimuli (May & Tiitinen, 2010). Various explanations have been given, however, for why this is unlikely (for reviews, see Kujala et al., 2007; Näätänen, Jacobsen, & Winkler, 2005; Näätänen et al., 2007, 2011; see also Garrido, Kilner, Stephan, & Friston, 2009).

For example, MMN is elicited not only by simple acoustic deviants, but also in the absence of acoustic deviance, by more complex deviancies based on violations of abstract rules defining, for example, sound order (Saarinen, Paavilainen, Schröger, Tervaniemi, & Näätänen, 1992; for reviews, see Näätänen, Tervaniemi, Sussman, Paavilainen, & Winkler, 2001; Paavilainen, 2013). Paavilainen, Jaramillo, Näätänen, and Winkler (1999) demonstrated that MMN can be elicited by deviances in frequency ratio (interval width) between sequential or parallel tones in a sound context that varies in absolute frequency. The capability of the brain to extract regularities between sounds is essential for understanding complex stimuli varying in physical parameters, like melodies transposed to different frequencies (Paavilainen et al., 1999) or phonemes pronounced by different speakers (Shestakova et al., 2002).

MMN is elicited preattentively, i.e., in passive listening and ignore conditions, and it is relatively unaffected by attention (Näätänen et al., 2011; Sussman, 2007). Still, MMN is associated with behavioural discrimination accuracy, i.e., a difference between sounds that is detectable in a listening task usually elicits an MMN response and vice versa, and the MMN amplitude size seems to correlate with detection accuracy (Amenedo & Escera, 2000; Lang et al., 1990; Näätänen et al., 1993; Novitski et al., 2004; Tervaniemi, Ilvonen, Karma, Alho, & Näätänen, 1997; see also Horváth, Winkler, & Bendixen, 2008; Tiitinen, May, Reinikainen, & Näätänen, 1994). MMN amplitude is related to deviance magnitude: larger deviance in the sound stream tends to elicit larger MMN responses (Jaramillo, Paavilainen, & Näätänen, 2000). On the other hand, MMN may be elicited even when the subject reports no explicit knowledge of the rules defining the deviants and cannot behaviourally detect them, suggesting that extracting the deviants remains implicit and preattentive (Paavilainen, Arajärvi, & Takegata, 2007; van Zuijen, Sussman, Winkler, Näätänen, & Tervaniemi, 2005; for a review see Paavilainen, 2013). Furthermore, appearance of MMN in a learning task may temporally precede behavioural discrimination ability, and thus predict learning outcomes (Atienza, Cantero, & Dominguez-Marin, 2002; Tremblay, Kraus, & McGee, 1998). The results thus demonstrate a relationship between behavioural discrimination accuracy and MMN elicitation, but suggest that the relationship is not straightforward. It is noteworthy that MMN can also reflect differences related to long-term experience and learning, as demonstrated by MMNs to native *vs.* foreign language phonemes (e.g,, Näätänen et al., 1997, Winkler et al., 1999) and differences between musicians and non-musicians (e.g., Koelsch et al., 1999).

The main sources of MMN activation are in the auditory cortex (the temporal component) and, following it, in the frontal cortex, especially in the right hemisphere (the frontal component, for reviews, see Alho, 1995; Deouell, 2007; Näätänen et al., 2007). This is evidenced by studies using scalp current density mapping (Giard, Perrin, Pernier, & Bouchet, 1990), source modelling (Alho et al., 1998; Rinne, Alho, Ilmoniemi, Virtanen, & Näätänen, 2000; Scherg, Vajsar, & Picton, 1989), positron emission tomography (PET, in Tervaniemi et al., 2000b), functional magnetic resonance imaging (fMRI, in Opitz, Rinne, Mecklinger, von Cramon, & Schröger, 2002; Schall, Johnston, Todd, Ward, & Michie, 2003), optical imaging (Tse, Tien, & Penney, 2006), and intracranial recordings directly from the brain tissue in humans (Kropotov et al., 1995; Rosburg et al., 2005). According to present understanding, the earlier temporal component is mainly associated with preattentive change detection, while the later frontal component is more related to attention-switching towards the change (Näätänen et al., 2007). The function and exact location of the frontal component remain less well known than those of the temporal component (e.g., Tse & Penney, 2008; Deouell, 2007). The sources of MMN activation also tend to demonstrate the lateralisation of speech-sound processing to the left and music-sound processing to the right hemisphere in right-handed subjects (Tervaniemi et al., 2000b).

During the recent decades, the experimental paradigms for recording MMN have become increasingly complex, with less repetition and more natural stimulation (see, e.g., Näätänen, Pakarinen, Rinne, & Alho, 2004; Putkinen, Tervaniemi, Saarikivi, de Vent, & Huotilainen, 2014a; Tervaniemi, Huotilainen, & Brattico, 2014). This has shortened the recording times and also increased the ecological validity of the obtained results, since the surrounding auditory world is extremely complex and rich.

1.1.2 The development of auditory ERPs from infancy to adulthood

The infant auditory ERPs and their development have been studied already for decades (see, e.g., Kurtzberg et al., 1984a,b). According to present knowledge, the P1-N1-P2-N2-complex of auditory ERPs reaches an adult-like shape only in late adolescence, with different components decreasing in latency, increasing in amplitude, and finally decreasing in amplitude at different tempos during the childhood years (Ponton et al., 2000; Shahin, Roberts, & Trainor, 2004; Trainor, 2008a; Trainor & Unrau, 2012). These maturational tracts of the ERP components may even be different for different types of stimuli (Wunderlich et al., 2006), as well as between individuals, with the large inter-individual variance of infant ERPs gradually decreasing with age and resulting in more consistent ERP morphologies (Thomas et al., 1997; Trainor, 2008a).

The large differences between infant, child, and adult ERP waveforms make it challenging to interpret whether the responses in different age groups are analogous in terms of their neural basis and function. At birth, the auditory ERP waveform is typically dominated by a large positive deflection that peaks around 300 ms, followed by a low-amplitude negative deflection (Barnet, Ohlrich, Weiss, & Shanks, 1975; Kushnerenko et al., 2002a; Kushnerenko, Čeponiene, Balan, Fellman, & Näätänen, 2002; Trainor, 2008a; Wunderlich, Cone-Wesson, & Shepherd, 2006). A longitudinal study demonstrated that during the first postnatal months, an additional positive response followed by a negative response start to emerge around 100–300 ms after stimulus onset while the large positive deflection attenuates, and the auditory ERP waveform gradually achieves morphology of an early positive peak followed by two negative peaks (Kushnerenko et al., 2002a).

The first of those negative peaks, visible around 250ms after stimulus onset, is demonstrated quite consistently in the auditory ERP waveform in early childhood (Čeponiene, Rinne, & Näätänen, 2002; Ponton et al., 2002). The response, termed N2 or N250, decreases in amplitude during childhood (Enoki, Sanada, Yoshinaga, Oka, & Ohtahara, 1993; Fujioka, Ross, Kakigi, Pantev, & Trainor, 2006; Johnstone, Barry, Anderson, & Coyle, 1996; Ponton et al., 2002; Ponton et al., 2000; Sussman, Steinschneider, Gumenyuk, Grushko, & Lawson, 2008). N1, which dominates the auditory ERP waveform in adults, is often absent in children, especially with fast stimulus presentation rates (Albrecht, Suchodoletz, & Uwer, 2000; Kushnerenko, 2003; Ponton et al., 2000).

However, also consistent N1s have been reported already before school-age (Tonnquist-Uhlén, Borg, & Spens, 1995; see also Tonnquist-Uhlén et al., 2003, for the maturation of the so-called T-complex). Furthermore, there is uncertainty whether the N2 in children is comparable to adult N2 or, for example a subcomponent of the N1, termed N1b (Sharma, Kraus, McGee, & Nicol, 1997). In conclusion, while in adults the N1 is a robust response to any audible stimulus with sufficiently long stimulation intervals, in children, the N2 seems to demonstrate nearly comparable robustness and may thus serve as an index of auditory processing in childhood.

1.1.2.1 The infant-MMR and its development to adult-MMN

Unlike other ERPs, an adult-like MMN has been reported in studies of newborn infants (e.g., Alho et al., 1990) and even during the foetal period (Huotilainen et al., 2005) and in preterm infants (Cheour-Luhtanen et al., 1996). Also unlike the other ERPs, MMN responses demonstrate similar amplitudes throughout childhood (Morr, Shafer, Kreuzer, & Kurtzberg, 2002; Shafer, Morr, Kreuzer, & Kurtzberg, 2000). These resemblances between infant, child, and adult MMNs make MMN an attractive tool for research on the maturation of preattentive auditory discrimination (for reviews, see Cheour, Leppänen, & Kraus, 2000; Kushnerenko, Van den Bergh, & Winkler, 2013).

The change-related responses reported in infants have been MMN-like negativities in several studies (Alho et al., 1990; Čeponiene et al., 2002a; Cheour et al., 1998; He, Hotson, & Trainor, 2007; Kushnerenko, Čeponiene, Fellman, Huotilainen, & Winkler, 2001; Pang et al., 1998; Trainor, Sonnadara, Samuel, & Hallam, 2001). Many other studies, however, report positive mismatch responses (Cheour-Luhtanen et al., 1995; Cheour et al., 2000; Dehaene-Lambertz, 2000; Dehaene-Lambertz & Baillet, 1998; Dehaene-Lambertz & Dehaene, 1994; Friederici, Friedrich, & Weber, 2002; Leppänen, Eklund, & Lyytinen, 1997; Leppänen, Pihko, Eklund, & Lyytinen, 1999; Leppänen et al., 2004; Morr et al., 2002; Trainor et al., 2003a) or both positive and negative mismatch responses (Friederici et al., 2002; He, Hotson, & Trainor, 2009). For the sake of clarity, the term mismatch response (MMR) is used in this thesis for mismatch-like responses of both positive and negative polarity in infants.

Several explanations for these different polarities have been suggested (He et al., 2007, 2009; Trainor, 2012; for a review on possible explanations see Partanen, 2013). The polarities of the change-related responses in infants have been shown to correlate with the gestational age and cardiac measures, both related to maturation (Leppänen et al., 1997; Leppänen et al., 2004; Porges, Doussard-Roosevelt, Stifter, McClenny, & Riniolo, 1999). In a longitudinal study, young infants consistently demonstrated positive MMRs in response to sounds containing a silent gap in a context of sounds without a gap, while the prevalence of negative MMRs increased with age during the first months of life (Trainor et al., 2003a). These results associate the polarity differences of infant MMRs to maturational factors. Indeed, Trainor (2012) suggests that due to the layer-specific pattern of cortical maturation during infancy, more positive ERP components are generally expected than later on (for the neurobiology underlying infant ERPs, see also Moore & Guan, 2001; Moore & Linthicum, 2007).

Positive and negative mismatch responses have also been reported to occur in the same recording (Friederici et al., 2002; He et al., 2007), suggesting that different-polarity mismatch responses might have different underlying neural mechanisms (He et al., 2007, 2009; Trainor, 2012), and/or that MMRs may mature differently for different sound features (He et al., 2007). For example, positive MMRs have been obtained mostly when infants are asleep and negative MMRs only when the same infants are awake (Friederici et al., 2002), indicating a difference in the cognitive basis of the different-polarity MMRs. Also, negative MMRs have been obtained in small infants in response to large deviances, while small deviances only elicited positive MMRs (Morr et al., 2002; Leppänen et al., 1997).

The scalp distribution of MMN in children is generally wider and more central than in adults, and MMN is elicited during sleep in infants but not adults, suggesting differences in the neural basis of auditory sound discrimination in different age groups (Cheour et al., 2000). Trainor and colleagues (2003b) hypothesise that in infants, activity in cortical layers different from adult-MMN leads to MMR generation. Furthermore, the positive ERP enhancements to deviant stimuli in infants have been associated with the attention-related P3a response in adults, particularly when the deviant stimuli differ largely from the standards (as in the case of so-called “novel” sounds, Kushnerenko et al., 2013). Thus, even though the MMR in newborn infants and MMN in children and adults are generally interpreted as the same phenomenon, their neural basis suggests also differences.

1.2 Effect of music expertise on auditory processing

Musical expertise facilitates especially auditory processing in cortical (Gaser & Schlaug, 2003; Pantev et al., 1998; Schneider et al., 2002; Shahin, Bosnyak, Trainor, & Roberts, 2003; Sluming et al., 2002) and subcortical levels, as evidenced by differences in brainstem activity (Lee, Skoe, Kraus, & Ashley, 2009; Musacchia, Sams, Skoe, & Kraus, 2007; Wong, Skoe, Russo, Dees, & Kraus, 2007). Differences in brain structures between musicians and non-musicians are seen in morphology and grey matter density of the auditory cortical areas of Heschl’s gyrus (Gaser & Schlaug, 2003; Schneider et al., 2002) as well as Broca’s area (Sluming et al., 2002) and planum temporale (especially in possessors of absolute pitch, Bermudez, Lerch, Evans, & Zatorre, 2009; Elmer, Meyer, & Jäncke, 2012; Meyer, Elmer, & Jäncke, 2012; Ohnishi et al., 2001). Functional differences related to auditory processing in musicians have been widely studied with ERPs and their magnetic counterparts, demonstrating enhanced amplitudes and/or shorter latencies in musicians compared to non-musicians (reviewed in Näätänen et al., 2007; Pantev & Herholz, 2011). As Pantev and Herholz (2011) point out, the differences between musicians and non-musicians in auditory ERPs indicate functional brain plasticity, resulting possibly from newly formed synapses or increased synchronization of neuronal activity in the auditory brain areas of musicians. In this thesis, enhanced or facilitated auditory processing is used as a general description of all these possible neural mechanisms, associated with more accurate, faster, and/or more efficient processing of auditory information in the brain.

Professional musicians have typically started playing already in childhood. Studies on adult musicians demonstrate correlations between the starting age of music training and the magnitude of brain changes, showing that starting earlier is associated with more pronounced enhancements (e.g., Pantev et al., 1998; Bengtsson et al., 2005). It has been suggested that music training in childhood would have particularly large effects, because the training takes place during a sensitive or critical period in development (Penhune, 2011; Trainor, 2005). A growing body of evidence demonstrates changes in brain structure and function in children with music training compared to children without music training, and the effects are visible in young children after short periods of training (Fujioka et al., 2006; Hyde et al., 2009; Jentschke, Koelsch & Friederici, 2005; Jentschke & Koelsch, 2009; Magne, Schön, & Besson, 2006; Meyer et al., 2011; Moreno et al., 2009; Putkinen et al., 2014b; Shahin et al., 2004; Trainor, Shahin, & Roberts, 2003b). Below, studies demonstrating enhanced auditory processing in the brain of musician adults and musically trained children are reviewed in more detail.

1.2.1 Auditory processing in adult musicians as reflected by ERPs

In the 1990's, the pioneering work of Besson and colleagues (Besson & Faïta, 1995; Besson, Faïta, & Requin, 1994) demonstrated differences between musicians and non-musicians in processing incongruities in melodies, as evidenced by a larger and earlier late positive component (LPC) of the auditory ERPs in musicians than non-musicians. At the same time, Crummer and colleagues (Crummer, Walton, Wayman, Hantz, & Frisina, 1994) demonstrated enhanced processing of timbre information in musicians compared to non-musicians, and, later, Trainor, Desjardins and Rockel (1999) demonstrated enhanced processing of interval changes in melodies in musicians compared to non-musicians, reflected in both studies as enhanced amplitude and shorter latency of the attention-related P3 component (see also Nikjeh, Lister, & Frisch, 2008).

Since the early findings of enhanced music processing in musicians, also enhanced basic auditory processing as reflected by ERPs has been demonstrated in musicians in several studies. For example, larger N1 responses in musicians compared to non-musicians have been reported in response to music sounds (Pantev et al., 1998, 2001b; Shahin et al., 2003), pure tones (Shahin et al., 2003), and vocal sounds (Kaganovich et al., 2013). Similar results have been demonstrated for P2 responses to music sounds (Kuriki et al., 2006; Shahin et al., 2003, 2005; Trainor et al., 2003b). MMN studies have shown facilitated preattentive auditory discrimination in musicians compared to non-musicians, for example in processing of small frequency changes related to mistuning in chords (Koelsch et al., 1999), processing of temporal information as reflected by MMNs to sound omissions (Rüsseler, Altenmüller, Nager, Kohlmetz, & Münte, 2001), grouping of sequential sounds (van Zuijen et al., 2005), and processing of musical metre (Geiser, Sandmann, Jäncke, & Meyer, 2010), as evidenced by larger and/or earlier MMNs in musicians than non-musicians, or MMN elicitation only in musicians.

There is increasing evidence that the auditory processing reflected by ERPs may be enhanced in musicians mainly or only when the sounds are complex (Kaganovich et al., 2013; but for contrasting results see Nikjeh, Lister, & Frisch, 2009) or music-related (Fujioka et al., 2004; Fujioka, Trainor, Ross, Kakigi, & Pantev, 2005; Koelsch et al., 1999; Pantev, Engelien, Candia, & Elbert, 2001a; Pantev et al., 1998, 2001b, 2003). For example, in studies by Pantev and colleagues, musicians showed increased auditory cortical representations of music sounds but not sinusoidal tones, as evidenced by larger N1 amplitudes to music sounds in musicians compared to non-musicians (Pantev et al., 1998; but for contrasting evidence see Baumann, Meyer, & Jäncke, 2008). Fujioka and colleagues (2004) showed that MMN magnitude was greater in musicians compared to non-musicians in response to melodic contour and interval changes but not to simple frequency changes. Contrasting evidence is however provided by Lütkenhöner, Seither-Preisler and Seither (2006) who demonstrated that N1m amplitudes did not differ between musicians and non-musicians in response to sinusoidal tones or piano sounds.

Hemispheric lateralisation of auditory processes might also be altered in musicians when compared with non-musicians. Music sound (and pitch) processing in general is more lateralised to the right and speech (temporal) processing to the left hemisphere (Tervaniemi & Hugdahl, 2003; Zatorre, Belin, & Penhune, 2002). In a major-minor chord discrimination study by Tervaniemi and colleagues, however, a larger MMNm in musicians compared to non-musicians was only seen in the left hemisphere (Tervaniemi et al., 2011). Rhythmic incongruities have also been found to elicit left-lateralised MMNm responses in musicians and right-lateralised responses in non-musicians (Vuust et al., 2005). The results are in line with early dichotic listening studies on processing of musical sounds, demonstrating a left-ear advantage, indicating right-hemisphere dominance, in non-musicians, but the reverse pattern in musicians (Bever & Chiarello, 1974; Johnson, 1977; Kallman & Corballis, 1975; Messerli, Pegna, & Sordet, 1995; Peretz & Morais, 1979). Tervaniemi and colleagues (2011) hypothesised that the right hemisphere is maybe not sufficient for music processing in musicians, who are likely to process music in a more analytical way than non-musicians. Thus, while pronounced activation in the right hemisphere is generally expected in response to music sounds, music expertise may affect this pattern of lateralisation and even turn it around.

1.2.2 Effects of early music exposure and training on auditory processing

Music exposure and music training are associated with facilitated sound processing from early on. Exposure to music in infancy (Trainor, Lee, & Bosnyak, 2011; Trainor et al., 2012) and already during the foetal period (Partanen, Kujala, Tervaniemi, & Huotilainen, 2013) is associated with enhanced brain responses to sounds. For example, when 4-month-olds were exposed to music played with a certain timbre, brain responses to that timbre were selectively enhanced after only one week of exposure (Trainor et al., 2011). Moreover, a group of 6-month-old infants who participated in an active music class for 6 months demonstrated enhanced brain responses to piano sounds compared to a class where infants heard music in the background while they were playing (Trainor et al., 2012). The result suggests that already in infancy, active participation is more effective than passive exposure to music in shaping auditory processing.

Importantly, in the study by Trainor and colleagues (2012), the infants were randomly assigned to the two classes, without group differences at baseline when the classes began. Longitudinal studies with baseline measurements can provide causal evidence that the obtained results are attributable to music exposure and/or training, rather than pre-existing differences between individuals who begin music training and individuals who engage in other types of activities. In another longitudinal study of 6-year-olds during 15 months, motor and auditory brain areas were enlarged and motor and auditory skills enhanced in children who received individual keyboard lessons compared to children who participated in a group music class with no instrument training, without differences between the groups at baseline (Hyde et al., 2009). Functional results corresponding to the structural findings by Hyde and colleagues (2009) are demonstrated in a 6-year-longitudinal study by Putkinen and colleagues (2014b), where enhanced MMN and attention-related P3a responses were measured in school-aged children with music training compared to an age-matched group without music training, and the groups did not differ at baseline when most participants in the music group started their music training.

In the study by Putkinen and colleagues (2014b), the group differences were evident only in ERPs to musically relevant sounds and not to basic sound features. In a cross-sectional study, larger MMNs were seen in children who had attended Suzuki-training for several years compared to children without any music training in response to violations of basic sound features in violin sounds, while the reverse group difference was evident for sinusoidal tones (Meyer et al., 2011). In line with these findings, 4–6-year-old children in Suzuki-training demonstrated enhanced P1 and P2 amplitudes in response to music sounds, compared to a group of children without music training (Shahin et al., 2004). The enhancement in P2 amplitude was evident selectively to the instrument of training (violin or piano tone). However, differences between the groups at baseline and lack of a significant change in ERPs during the one-year follow-up period compromise the interpretation of the results as training effects. An additional study with 4–6-year old children demonstrated enhanced N250 responses to violin tones but not white noise bursts in children attending Suzuki-training during a follow-up of one year, however again with some differences between groups at baseline (Fujioka et al., 2006).

Together with adult studies reviewed in section 1.2.1, these ERP studies of children suggest that the effects of music training on sound processing may be mostly related to processing of music-related sounds. Additionally, Kraus and Chandrasekaran (2010) list evidence of transfer effects of music training to complex auditory tasks like speech sound processing and processing speech in noise (Besson, Schön, Moreno, Santos, & Magne, 2007; Parbery-Clark, Skoe, & Kraus, 2009; Wong et al., 2007). Indeed, enhanced processing of speech stimuli has been associated with music expertise in adults (Marques, Moreno, Castro, & Besson, 2007; Schön, Magne, & Besson, 2004) as well as in children (Chobert, François, Velay, & Besson, 2014; Jentschke & Koelsch, 2009; Magne et al., 2006; Moreno et al., 2009). For instance, in two studies children were pseudo-randomly assigned to music or painting training (Moreno et al., 2009; Chobert et al., 2014). Enhanced ERP responses to pitch changes in musical as well as linguistic stimuli were found in the music group only (Moreno et al., 2009), and enhanced MMN responses to (and thus preattentive discrimination of) syllabic duration and voice onset time in the music group only (Chobert et al., 2014).

In sum, while well-controlled studies of children engaged in music training are still needed, there is increasing evidence of music training shaping the auditory processing of children from early on, particularly with regard to musical sounds. In the following section, the development of music processing skills in the absence of formal music training is reviewed. While culturally important concepts and principles of music are acquired also implicitly, through musical enculturation (Hannon & Trainor, 2007; Trainor et al., 2012), there is evidence that active music training enhances the musical enculturation process compared to passive exposure to music (Corrigall & Trainor, 2009; Gerry, Unrau, & Trainor, 2012; Trainor et al., 2012). Gerry and colleagues (2012) have demonstrated that music classes already in infancy can enhance the acquisition of the principles of one's own music culture. Similarly, superior processing of mistuning in a familiar compared to unfamiliar music scale, seen in adults, is more pronounced in children with music training compared to children without music training (Lynch & Eilers, 1991). It is thus plausible that children who engage in formal music training may demonstrate music processing skills that in the absence of music training are seen only later in development.

1.3 The development of music processing in the brain

At birth, human infants have an immature auditory system (Moore & Guan, 2001; Moore & Linthicum, 2007). Still, from the last trimester of pregnancy, the foetus has been exposed to sounds from the environment, including speech and music. Recent evidence suggests that newborns already demonstrate the right-hemisphere dominance in processing of musical material, seen in adults, as well as show emotion-related brain activity to music (Perani et al., 2010), attributable to early experiences and/or innate auditory predispositions for music processing. The human infants' various auditory skills related to music processing are reviewed below in section 1.3.1.

After birth, throughout their life, almost all humans are passively exposed to as well as actively engaged with music. Western adults with near to no formal music training have had a lot of experience with the music of our culture. At the same time, their auditory system has undergone a long maturational process (Ponton et al., 2000, 2002), and various skills to process complex auditory material (including speech) have been acquired. The music processing skills in non-musician adults are thus a combination of biological predispositions, acquired complex auditory skills as well as experience with the familiar music culture. Below, the development of music processing skills in Western individuals in the absence of formal music training is reviewed in section 1.3.2.

1.3.1 Infants' readiness for music processing

In the first steps of life, humans already possess auditory skills that are necessary for music processing (Hannon & Trainor, 2007; Trehub, 2003a; 2003b; 2010; Trehub & Hannon, 2006). Infants demonstrate sensitivity to smallest pitch changes present in Western music (Trehub, Cohen, Thorpe, & Morrongiello, 1986), as well as changes in temporal grouping (Chang & Trehub, 1977b), meter (Hannon & Trehub, 2005a; 2005b), tempo (Baruch & Drake, 1997), duration (Thorpe & Trehub, 1989) and timbre (Trehub, Endman, & Thorpe, 1990). Moreover, as reviewed in section 1.4.2, infants discriminate between consonant and dissonant intervals (Schellenberg & Trainor, 1996) and melodies (Trainor & Heinmiller, 1998). Infants also remember melodies that they have heard (Plantinga & Trainor, 2009; Trainor, Wu, & Tsang, 2004), even when they are transposed to different frequency levels, indicating that infants have readiness for relative processing of pitch (Plantinga & Trainor, 2005; demonstrated already by Chang & Trehub, 1977a).

Infants tend to process music in a different manner than adults. For example, while Western 6-month-olds discriminate occasional mistunings in Western scale melodies as accurately as in melodies with an unfamiliar (Javanese) scale, Western adults are more accurate in the familiar Western scale context (Lynch, Eilers, Oller, & Urbano, 1990). Western adults are also better at discriminating changes that violate the Western scale structure than changes that do not violate it, while infants perform as accurately in both cases – in some occasions, even better than adults (Trainor & Trehub, 1992). These findings suggest that infants are not yet sensitive to Western music scale structure, and that they have readiness to learn any scale structure (a similar effect is seen in language learning, reviewed in Werker & Tees, 2005). In a similar fashion, alterations in the metrical structure of Balkan music are discriminable for 6-month-old North Americans and Balkan adults, but not for North American adults (Hannon & Trehub, 2005a).

Most of the aforementioned studies are based on observations of infants' behavioural reactions to familiarised *vs.* new sound material, with assumptions that the infant demonstrates sufficient volitional control of movements and that the infant expresses preferences, for example to listen to novel stimulation. In general, the demands for behavioural responses make it challenging to study infants, particularly newborns. Therefore the electrophysiological methods, especially EEG and MEG, have become important tools for studies on early auditory skills (Trainor, 2012).

The ERP studies verify and extend many of the findings of behavioural studies, showing that newborn infants already demonstrate sensitivity to basic sound features like pitch (Alho et al., 1990) and duration (Kushnerenko et al., 2001; Leppänen et al., 1999), but also complex regularities in the auditory input, as indicated by MMR responses to violations in the auditory stream. For example, neonates neurally differentiate sounds based on deviant combinations of several sound features, indicating that the newborn brain binds together information from different sound features (Ruusuvirta, Huotilainen, Fellman, & Näätänen, 2003, 2004). Furthermore, newborn infants extract the direction of frequency change in ascending and descending tone pairs (Carral et al., 2005). Newborns are sensitive to changes in interval width between tone pairs in a sound context where the tone pairs vary in absolute frequency, offering further evidence of relative pitch processing at birth (Stefanics et al., 2009; see also Tew, Fujioka, He, & Trainor, 2009). Similarly, neonates show neural detection of pitch deviances even when the timbre of the sounds varies (Háden et al., 2009). Newborns show evidence of temporal grouping of sounds (Stefanics et al., 2007) and segregation of sound streams (Winkler et al., 2003). Moreover, newborn infants show sensitivity to beat of rhythmic patterns (Winkler, Háden, Ladinig, Sziller, & Honing, 2009).

The newborn infants demonstrate sensitivity for music sound processing in many respects, as evidenced by the aforementioned studies. Still, the auditory processes underlying music sound encoding are far from mature at birth. For example, the auditory processing of newborn infants can be compromised when the inter-stimulus interval between the presented stimuli is too long (Cheour et al., 2002) or too short (Leppänen et al., 1999), or when the differences between the sounds are small (Novitski, Huotilainen, Tervaniemi, Näätänen, & Fellman, 2007). Also, a central auditory skill in music, the processing of pitch in harmonically rich stimuli as evidenced by readiness to extract the missing fundamental frequency, seems to emerge only during the first postnatal months (He & Trainor, 2009).

1.3.2 The development of music processing through musical enculturation

Even in the absence of extensive formal music training, basically all humans obtain various music processing skills and implicit knowledge of the music of their culture (for reviews, see Bigand & Poulin-Charronnat, 2006; Ettlinger, Margulis, & Wong, 2011; Krumhansl, 1990b; Krumhansl & Cuddy, 2010). It has even been questioned whether the facilitating effects of formal music training on music processing are comparable in magnitude to the huge amount of practicing that musicians have engaged in (Bigand & Poulin-Charronnat, 2006).

For example, the implicit musical enculturation is seen in adults as enhanced recognition memory for the music of one’s own culture or a familiar music culture compared to an unfamiliar music culture (Demorest, Morrison, Beken, & Jungbluth, 2008; Morrison, Demorest, & Stambaugh, 2008). Also studies comparing culture-specific knowledge of Western infants and adults, introduced in the previous section, demonstrate sensitivity to the structures of familiar music culture in non-musician adults (Hannon & Trehub, 2005a, 2005b; Lynch et al., 1990; Trainor & Trehub, 1992). In a similar fashion, violations of Western music syntax elicit change-related ERP responses termed early right anterior negativities (ERAN) in Western non-musicians, suggesting implicit knowledge of music-syntactic rules (Koelsch, Gunter, Friederici, & Schröger, 2000), evident already at the age of five (Koelsch et al., 2003). The brain research methods have also demonstrated that for example violations of musical contour and interval size elicit change-related responses in participants without music training (Trainor et al., 1999; Trainor, McDonald, & Alain, 2002a), and for the contour violations the responses are of similar magnitude in musicians and non-musicians (Trainor et al., 1999).

A large proportion of Western adults have participated in formal or informal music activities during their life, and even more people listen to music on a daily basis. Thus, also a non-musician can have vast amounts of both explicit and implicit music exposure. Even informal music activities at home are known to shape brain development in childhood (Putkinen, Tervaniemi, & Huotilainen, 2013b), and everyday music listening of certain cultures' music enhances the perception of that music culture (Wong, Roy, & Margulis, 2009). Also, even though there seem to be sensitive periods for music acquisition (Penhune, 2011; Trainor, 2005), the capacity to learn remains through life, and plastic brain changes can take place at any age, even fairly quickly (for short-term training effects in adults see, e.g., Bosnyak, Eaton, & Roberts, 2004). In a culture filled with music and music-related activities, a true "non-musician" may be rarely encountered.

Trainor and Corrigall (2010) review the current literature on music acquisition and early musical skills, and suggest that in early infancy, readiness for music processing is based on pitch perception in harmonically rich sounds, sensitivity to consonance *vs.* dissonance as well as the ability to process relative sound properties in, for example, transpositions. On the other hand, the knowledge of culture-specific scale and harmony rules and structures may take several years to mature (Corrigall & Trainor, 2009, 2014; Trainor & Trehub, 1992, 1994). It is however notable that in studies of young children, brain methods can demonstrate implicit music processing skills that are absent in explicit behavioural tasks (Corrigall & Trainor, 2014). This discrepancy between behavioural and brain data is attributable to several factors, for example to the difficulty to design behavioural experiments for children and, on the other hand, to the differences in what processing stages the brain *vs.* behavioural methods reflect.

To conclude, while many rules and structures of music are culture-specific, they build on basic properties and restrictions of the auditory system (discussed by Trainor, 2008b). In the following section, the neural basis of Western music chord categorisations, namely, major-minor and consonance-dissonance, is reviewed. Due to their central role and emotional connotations in Western tonal music, major-minor and consonance-dissonance are highly familiar to all Western listeners.

1.4 Western music chord categorisations and their neural basis

Western tonal music is based on the differentiation between major and minor mode. In a major triad chord, comprised of three simultaneously played notes, the first two notes are separated by a major third interval, while in a minor triad chord, they are separated by a minor third interval (see, e.g., Helmholtz, 1885/1954; Rossing et al., 2002). The small acoustical difference in their notes makes major and minor chords sound very different: for Western listeners, major and minor carry contrasting emotional connotations (Crowder, 1985a; Hunter et al., 2010; Pinchot Kastner & Crowder, 1990; Khalfa et al., 2005).

Chords can be played in different forms that vary their interval structure while retaining their mode. In root form, the ground note of the chord (e.g., C in C-major) has the lowest pitch, while in inverted forms, one of the other notes of the triad has the lowest pitch, i.e., it is shifted to adjacent octave. As said, these chord inversions retain the chords mode, but in a harmonic context, inversions are considered more “in need of resolution” than root form chords.

Intervals of different widths have different positions in the consonance-dissonance continuum (Rossing et al., 2002). As a perceptual phenomenon, dissonance is defined as rough, unpleasant and unstable, whereas consonance is defined as smooth, harmonious, and stable (Rossing et al., 2002). While dissonance creates perceptual tension in music, consonance releases it (e.g., Smith & Cuddy, 2003). There is evidence that consonance-dissonance discrimination originates already in the peripheral auditory nervous system (e.g., Tramo, Cariani, Delgutte, & Braida, 2001; Bidelman, 2013), and that also other species differentiate between consonance and dissonance (e.g., Fishman et al., 2001; Izumi, 2000). The biological origin of consonance-dissonance discrimination has lead researchers to suggest that consonance-dissonance discrimination might serve as a universal building block for music processing (Hannon & Trainor, 2007).

Examples of major and minor chords as well as an inverted major chord and a chord introducing a highly dissonant interval structure are illustrated as triad chords in Figure 1. While the major chord, minor chord, and 2nd inversion of major chord are considered consonant in Western music, the fourth chord type introduces a minor second interval between the first two notes, followed by a tritone, both considered highly dissonant intervals (Helmholtz, 1885/1954; Rossing et al., 2002).

Below, the developmental and neural basis of the central Western music categorisations major *vs.* minor and consonance *vs.* dissonance are reviewed.

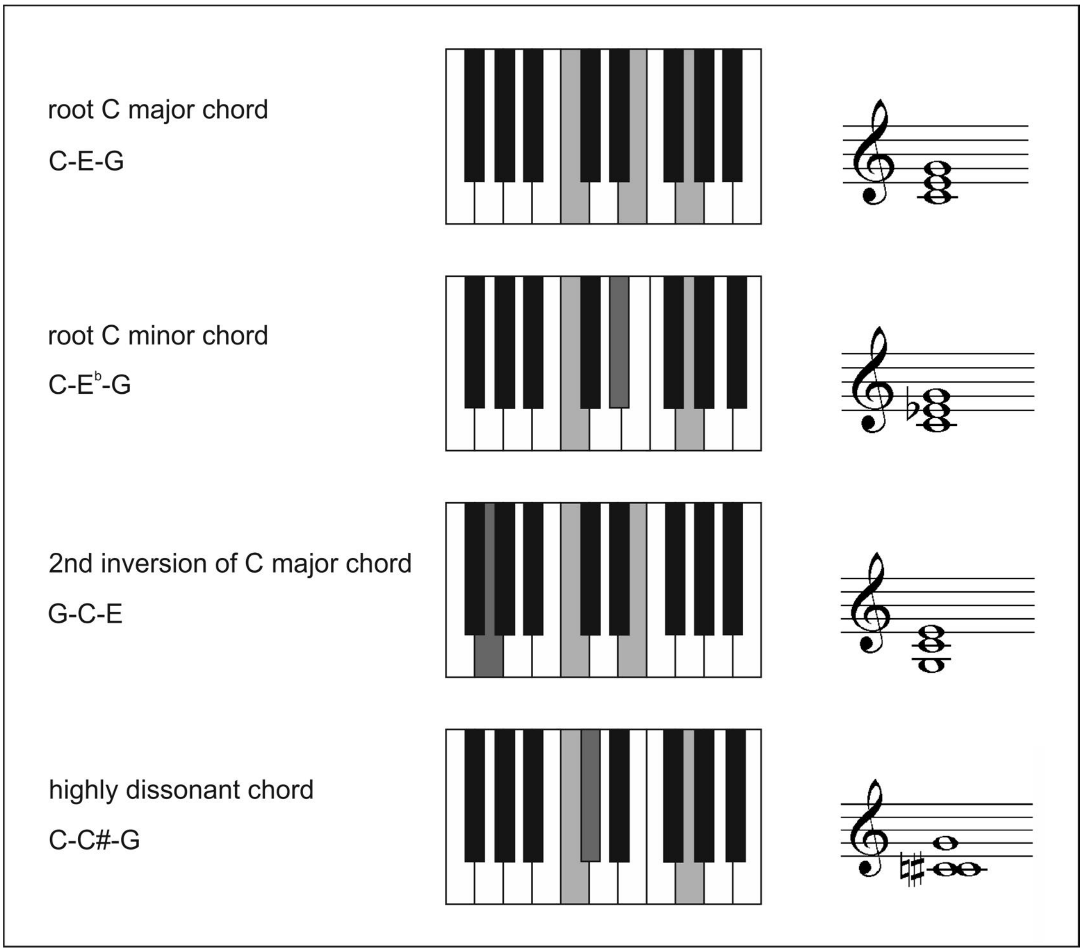

Figure 1. Interval structures of C major chord, C minor chord, 2nd inversion of C major chord, and a highly dissonant chord type illustrated as triad chords on a piano keyboard (in grey) and in musical notation. The dark grey keys illustrate how the chord differs from root major chord.

1.4.1 Major and minor modes

For Western listeners, major mode carries emotional connotations of brightness and joy, and minor mode is associated with sadness or calmness (Crowder, 1984, 1985a; Hunter et al., 2010; Pinchot Kastner & Crowder, 1990; Khalfa et al., 2005). Brain research has demonstrated that major and minor music activate partly different brain areas related to emotional processing (Khalfa et al., 2005; Mitterschiffthaler, Fu, Dalton, Andrew, & Williams, 2007), even when single chords are presented without a melody context (Pallesen et al., 2005).

In Western children, accurate categorisation of major and minor melodies based on their emotional connotations has been demonstrated after age five (6–7-year-olds in Gregory, Worrall, & Sarge, 1996; 8-year-olds in Gerardi & Gerken, 1995) or even as young as three (Pinchot Kastner & Crowder, 1990; but for contrasting evidence see Gerardi & Gerken, 1995; Gregory et al., 1996). Nieminen, Istok, Brattico, and Tervaniemi (2012) demonstrated that 6–9-year-old Western children preferred major over minor melodies. 8–9-year-olds also rated major melodies happier than minor melodies and minor melodies sadder than major melodies. Instead, no preference between major *vs.* minor chords has been demonstrated in infants, as indicated by their looking times towards sound sources (Crowder, Reznick, & Rosenkrantz, 1991). These results suggest that the emotional connotations of major and minor largely emerge during the process of musical enculturation, rather than reflect biological predispositions.

Discriminating major and minor melodies without the instruction to focus on the emotional connotations has been deemed difficult even for Western adults (Halpern, Bartlett, & Dowling, 1998; Halpern, Martin, & Reed, 2008; Leaver & Halpern, 2004). For example, while non-musicians performed at chance level in discriminating major from minor melodies, their performance increased markedly when they were instructed to use affective labelling happy *vs.* sad (Leaver & Halpern, 2004). On the contrary, another study demonstrated that when children were taught to describe melodies with terms “major” and “minor”, 5-year-olds already performed quite well in identifying mode changes (Costa-Giomi, 1996).

The maturation and neural basis of major-minor discrimination may be partly intertwined with their emotional connotations, and it is challenging to study mode discrimination independently of emotion processing and its development. While mode dominates the perceived emotions in music (Dalla Bella, Peretz, Rousseau, & Gosselin, 2001; Gagnon & Peretz, 2003), also many other musical properties are important. For example tempo may play an even greater role in emotional judgements of music than mode (Gagnon & Peretz, 2003; Khalfa et al., 2005), particularly in children (Dalla Bella et al., 2001). In music, the various emotional cues co-occur, making the emotional contents of the piece rich and pronounced. The present studies addressing major *vs.* minor chord processing and categorisation should not be treated as studies of their emotional connotations, let alone the general processing of emotions in music (reviewed elsewhere, see, e.g., Eerola & Vuoskoski, 2011; Hunter et al., 2010; Juslin & Sloboda, 2011). Rather, the present thesis aims to study the processing of complex interval structures underlying the emotional connotations of major and minor modes. By employing the electrophysiological measures, it is possible to study preattentive processing of major and minor interval structures in the absence or presence of a melody context.

Indeed, EEG and MEG have been used to study discrimination of single major and minor chords in adults (Brattico et al., 2009; Tervaniemi et al., 2011) and children (Putkinen et al., 2014b) with a simple oddball paradigm, where a minor chord is presented occasionally in the context of a repeating major chord. Both non-musician and musician adults demonstrated MMN responses to the minor chord in the major chord context, but while one study showed no differences in MMN amplitude between musicians and non-musicians (Brattico et al., 2009), the other study demonstrated larger MMNs in musicians and musically competent participants compared to non-musicians particularly in the left hemisphere (Tervaniemi et al., 2011). In a longitudinal study of school-aged children with and without music training, both groups elicited MMNs to the minor chord, and while the MMN amplitude increased with age in both groups, the increase was steeper among the children with music training (Putkinen et al., 2014b). The result demonstrates that music training in childhood seems to facilitate and/or speed up the adoption of musically relevant categorisations. In the oddball paradigm presented in all these studies, however, only one example chord of each mode is introduced, e.g. A major triad and A minor triad. Because the notes in the two chords differ, the deviant minor chord introduces a novel frequency to the paradigm along with the deviant mode. This compromises the interpretation of the elicited MMN as an index of major-minor discrimination, since the MMN could be a response to the deviant frequency alone, with no contribution of the deviant interval structure.

Furthermore, in an ERP study where musicians were presented with major and minor melodies, change-related P3-responses were elicited by minor melodies and not major melodies, indicating that major was processed as “the default mode” (Halpern et al., 2008). The non-musicians demonstrated no change-related ERPs. Individual data showed that a part of them performed above chance in the discrimination task, thus indicating a discrepancy between behavioural detection and the ERPs. Major/minor discrimination accuracy of chords is also enhanced with increasing levels of music training (Crowder, 1985b). These results, demonstrating effects of music expertise on mode processing, further support the view that the differential connotations of major and minor are mainly learned, and that they require several years of musical enculturation (as well as maturation of emotion processing capabilities in general).

On the other hand, minor chords are also considered more dissonant than major chords by Western listeners (Roberts, 1986). This is attributable to the note structure of major and minor chords: while the notes of the major chord occur naturally in the beginning of the harmonic series as partials of the fundamental, the notes of the minor chord do not (reviewed in Crowder, 1984; Helmholtz, 1885/1954). The dissonance of the minor chord has been proposed to be the cause of its emotional connotation (Helmholtz, 1885/1954). This hypothesis was examined in an fMRI study, where minor, major, and highly dissonant melodies were presented to Western non-musicians (Green et al., 2008). The participants rated the minor mode melodies as sadder than major mode melodies. The emotion-related limbic activation elicited by the minor mode melodies was only partly explained by the activity elicited by dissonant melodies. The researchers concluded that the major *vs.* minor difference is not merely attributable to the dissonance of the minor. The following section reviews the psychoacoustic theories and neural basis of dissonance in more detail.

1.4.2 The consonance-dissonance continuum

Sensations of consonance and dissonance are rooted in frequency combinations of simultaneously played tones and, in the case of harmonically rich sounds, the frequency combinations of their overtones (reviewed in Bidelman, 2013; Helmholtz, 1885/1954; Krumhansl, 1990a; Plomp & Levelt, 1965; Rossing et al., 2002). The early conceptions of consonance *vs.* dissonance trace back to Pythagoras, who proposed that the ratio of the fundamental frequencies of simultaneously played tones defines how harmonious the interval sounds (Helmholtz, 1885/1954; Rossing et al., 2002). According to this principle, the intervals with simplest frequency ratios, e.g., 1:1 (unison), 1:2 (octave) or 2:3 (perfect fifth), are considered most consonant. Complex frequency ratios, e.g., 15:16 (minor second), lead to a sensation of roughness and are considered dissonant. This is related to *beating*, slow periodic fluctuation in the amplitude of the sound wave: When fundamental frequencies or overtones of the simultaneously played sounds have small frequency differences, beating occurs. When these frequency differences are large enough to cause 30–40 beats per second, a sensation of roughness appears (Helmholtz, 1885/1954). Plomp and Levelt (1965) further discussed the role of critical bands of hearing in the perception of consonance *vs.* dissonance: if either the fundamental frequencies or overtones of the simultaneously played sounds lie sufficiently far apart but within a critical band on the basilar membrane of the inner ear, their amplitude envelopes overlap in the membrane, leading to a stronger sensation of roughness and dissonance. Thus, they proposed that frequency difference rather than frequency ratio of the simultaneously played sounds is essential in the sensation of consonance *vs.* dissonance.

McDermott and colleagues (2010), on the other hand, demonstrated that consonance perception was related to harmonicity, namely, how closely the fundamental frequencies and overtones of the simultaneously played sounds match simple harmonic proportions (of the fundamental frequencies), i.e., belong to one harmonic series. They found no association between consonance-dissonance perception and beating/roughness. In line with this finding, a sensation of dissonance has emerged also in dichotic listening settings, where the dissonant interval is created by one tone presented to one ear and another tone presented to the other ear, compromising the Plomp and Levelts' (1965) interpretation of critical bands in the inner ear leading to perceptual dissonance (e.g., Bidelman & Krishnan, 2009).

Brain research has demonstrated that consonant and dissonant intervals are differentiated in low levels of the auditory nervous system (for a recent review, see Bidelman, 2013). This is seen in the firing patterns of the auditory nerve (Tramo et al., 2001), brainstem activity (Bidelman & Krishnan, 2009), as well as cortical oscillatory activity in both humans and monkeys (Fishman et al., 2001). In line with this biological basis of dissonance perception, consonance-dissonance categorisation has been observed in birds (Watanabe, Uozumi, & Tanaka, 2005), monkeys (Izumi, 2000), and human infants with minimal exposure to music (Perani et al., 2010; Schellenberg & Trainor, 1996; Trainor, 1997; Trainor & Trehub, 1993). For example, Schellenberg and Trainor (1996) demonstrated that, similarly in Western adults and 7-month-old infants, consonance is more important than interval width when judging the similarity of two intervals. Also 6- and 9-month-old infants more accurately processed intervals with simple frequency ratios than complex frequency ratios, suggesting an early sensitivity to consonance (Schellenberg & Trehub, 1996).

Furthermore, in a PET study, Western non-musician participants heard excerpts of music with varying levels of dissonance (Blood, Zatorre, Bermudez, & Evans, 1999). The participants' pleasantness ratings of the excerpts correlated negatively with the degree of dissonance in the excerpts, which, in turn, correlated with activity in emotion-related paralimbic brain areas. Infants already demonstrate this preference of consonant over dissonant intervals and melodies (Crowder et al., 1991; Trainor & Heinmiller, 1998; Trainor, Tsang, & Cheung, 2002b; Zentner & Kagan, 1998), possibly independent of whether they have heard music in utero (Masataka, 2006). However, recent evidence suggests no consonance preference in infants (Plantinga & Trehub, 2014).

Thus, like major-minor categorisation, also the consonance-dissonance continuum carries emotional connotations in music, and the connotations may have a more biological basis than in the case of major-minor distinction. Even though consonance-dissonance categorisation is possible for infants and other species, the biological basis of the preference of consonance over dissonance remains a controversial issue, since there is contrasting evidence of whether other species prefer consonance (Chiandetti & Vallortigara, 2011; McDermott & Hauser, 2004), and whether it even is a human universal (Butler & Daston, 1968; Fritz et al., 2009; Koelsch, Fritz, Von Cramon, Müller, & Friederici, 2006; Maher, 1976). A native African population naïve to Western music seemed to prefer consonance over dissonance in Western music (Fritz et al., 2009), but Indian listeners judged the dissonant sounds to be less “in need of resolution” than Canadian listeners, suggesting that culture had influenced their conceptions of consonance (Maher, 1976).

Also, the preference of consonance over dissonance in Western listeners is modified by the amount of formal music training (McDermott et al., 2010). Similarly, in one study, the ERPs were different in response to consonant compared to dissonant intervals in both musicians and non-musicians, but the ERPs differed earlier for musicians than non-musicians (Schön et al., 2005). Furthermore, dissonant melodies are associated with more unpleasant emotions (Pallesen et al., 2005; Schön et al., 2005) and stronger physiological reactions in musicians compared to non-musicians (Dellacherie, Roy, Hugueville, Peretz, & Samson, 2011). These results suggest that while consonance-dissonance processing is present in absence of music training and maybe even in the absence of exposure to Western music, it is not independent of experience.

Moreover, in music, consonance-dissonance is a complex continuum that varies with time and culture (Rossing et al., 2002), and rather than pleasant, pure consonance can be considered uninteresting. Terhardt (1984) acknowledges this discrepancy in consonance-dissonance definitions between psychoacoustics and music. He differentiates between *sensory consonance*, “the graded absence of annoying factors”, a psychoacoustic phenomenon not specific to music, and *harmony*, the music-specific component of consonance. In conclusion, while a notion of universal or species-independent preference for consonant intervals and melodies remains highly controversial and while music culture has a notable contribution to the human perception of consonance *vs.* dissonance, there is increasing evidence of sensitivity to sensory consonance *vs.* dissonance early in development and in nonhuman species.

2 Aims

A large body of evidence shows associations between music expertise and facilitated processing of music sounds, as well as sensitivity for music processing already in infancy and in the absence of music training. Yet, no comprehensive overview of the neural basis of central Western music chord categorizations and the effects of development, musical enculturation, and music expertise on it has been conducted. To this end, the present thesis examines and compares the neural basis of Western music chord categorizations major *vs.* minor, consonance *vs.* dissonance, and root *vs.* inversion and the effects of development and music expertise on it by recording the ERPs elicited in a newly developed MMN paradigm in non-musician adults, school-aged children with *vs.* without music training, newborn infants, as well as musician *vs.* non-musician adults. In the paradigm, deviant chord types minor, dissonant, and inverted major were presented occasionally in a context of standard root form major chords. The chords varied in absolute frequency, so that no novel frequencies were present in the deviant chords and no harmonic context was established in the paradigm. In this way, the only property that varied between the chord types was the interval structure, which differentiates them by definition.

In **Study I**, the MMN paradigm was presented to non-musician adults, in order to examine whether non-musicians show evidence of implicit preattentive discrimination of Western music chord types in the newly designed paradigm. The results of the study, demonstrating moderate sensitivity to Western music chord types in adult non-musicians and the effectiveness of the paradigm, left open the questions whether these sensitivities are present earlier in development and how they are shaped by music expertise.

To address these questions, in **Study II** MMN elicitation in response to minor and inverted major chords as well as N2-like responses to standard root major chords were studied in musically trained and non-trained 13-year-old children. This made it possible to examine group differences in the ERPs, the level of maturation of Western music chord processing in school-age, and the role of formal music training in shaping this maturation.

The school-aged children do, however, already have a lot of experience of the music of their culture. In order to further study the early sensitivity to Western music chord types, and to better understand their biological basis and the auditory skills of newborns, **Study III** was designed, where MMR elicitation in response to minor chords, highly dissonant chords, and inverted major chords as well as ERPs to standard root major chords were studied in sleeping newborn infants.

While an overview of the preattentive discrimination of Western music chords in different age groups had now been obtained, the group of highly proficient music experts, namely, musicians, was missing. Also, there was no information on how the obtained ERP results would correlate to behavioural discrimination accuracy of the chord types, and whether the original paradigm, comprised of sinusoidal tones, was ecologically valid for studies on the processing of musical sounds. These questions were addressed in **Study IV** by examining MMN elicitation in response to minor and inverted major chords as well as N1 responses to major, minor and inverted major chords in musician and non-musician adults, with chords composed of sinusoidal tones as well as harmonically rich piano sounds. The relationship between preattentive ERPs and behavioural discrimination accuracy of the chord types was additionally addressed. Finally, the study aimed to replicate Study I with higher experimental control of the participants' music backgrounds and ecological validity of the stimuli.

The main hypotheses of the present thesis were as follows:

1. Music expertise facilitates the processing of Western music chord categorisations as evidenced by larger ERP amplitudes and superior behavioural discrimination of chord types in children and adults with music training compared to age-matched groups without music training.
2. The processing of Western music chords is enhanced with age also in the absence of music expertise, as evidenced by more pronounced MMNs to chord deviants in adult non-musicians than in school-aged children without music training or in newborn infants. Consonance-dissonance categorisation is evident already in infancy as evidenced by MMRs in response to the highly dissonant chords, while major-minor categorisation may depend more on musical enculturation and thus a MMR to minor chords may be absent in the infants while evident in older participant groups.
3. The processing of Western music chords is lateralised to the right hemisphere as evidenced by larger ERP amplitudes and/or more pronounced response source strengths in the right compared to the left electrode sites, but music expertise may affect the lateralisation.
4. The processing of Western music chords is facilitated with harmonically rich music sounds compared to sinusoidal tones, as indicated by larger ERP amplitudes to harmonically rich music sounds, particularly in individuals with music expertise.

3 Methods

3.1 Participants

The participants were adult non-musicians in Study I, 13-year-old children with music training (Music group) or without music training (Control group) in Study II, healthy newborn infants in Study III, and adult musicians (Musician group) and non-musicians (Non-musician group) in Study IV. The details of the participants whose data were included in the final analyses are listed in Table 1 and Table 2.

Table 1. Participant details (Studies I-IV).

		Subjects (males)	**Mean age (range)**
Study I		16(6)	28 (21–47) years
Study II	Music group	10(4)	12.9 (11.0–13.5) years
	Control group	14(7)	13.1 (12.5–13.5) years
Study III		19(11)	1.7 (1–4) days
Study IV	Musician group	16(7)	23 (19–32) years
	Non-musician group	14(6)	25 (19–34) years

In Study I, the participants were students recruited from the University of Helsinki and the study was conducted there in a teaching laboratory in the former Department of Psychology. The study was approved by the ethical committee of the department. None of the participants were professional musicians, but eight of 16 had participated in extracurricular music lessons.

In Study II, all the children were participants of a longitudinal study on musical training and its neurocognitive determinants and the study was conducted as a part of the follow-up measurements in the 7th grade of the Finnish elementary school. The children were recruited from elementary schools in the Helsinki area.

In Study III, the participants were newborn infants born, recruited, and measured by a trained nurse, in Women's Hospital, Helsinki University Central Hospital. The study was approved by the Ethics Committee for Paediatrics, Adolescent Medicine and Psychiatry, Hospital District of Helsinki and Uusimaa.

In Study IV, the participants were recruited from local music academies and universities. One-way ANOVA of education level with three steps (upper secondary school, bachelor's degree, master's degree) demonstrated no difference between the Musician and Non-musician groups, $F(1,31) = 1.40$, $p > .10$.

Studies II and IV were conducted in the Cognitive Brain Research Unit at the Institute of Behavioural Sciences of the University of Helsinki, and were approved by the Ethical Committee of the Institute of Behavioural Sciences at University of Helsinki (Study II) and by the University of Helsinki Review Board in Humanities and Social and Behavioral Sciences (Study IV).

The participants in Studies I and IV and the parent(s) of the participants in Studies II and III gave written informed consent to participate in the study prior to the experiment. The parents in Study II were told that the child was allowed to stop the experiment at any time without stating the reason. The procedure was also carefully explained to the children before and during the experiment, and they gave their consent orally. All participants and their parents were informed about their rights, and their safety, well-being, and comfort was taken care of during the experimental sessions. Participants in Studies I, II, and IV received a participation fee (movie ticket vouchers, vouchers for cultural or exercise activities) after completing the study.

In all studies, the participants had normal hearing and no neurological problems according to their own report (Studies I and IV) or the parents' report (Study II). The newborn infants in Study III were healthy and had normal hearing according to the routine screening of the hospital (otoacoustic emission test EOAE, ILO88, Dpi, Otodynamics Ltd., Hatfield, UK). The adult participants in Studies I and IV were all right-handed.

Table 2. Health information of newborn infant participants (Study III).

	Duration of pregnancy (weeks+days)	**Weight (g)**	**Height (cm)**	**5-min Apgar score**
Mean	39 + 6	3644	50	9.2
Range	37 + 6 – 42 + 3	2774–4260	45–54	9–10

3.1.1 Music background of the participants (Studies II and IV)

3.1.1.1 Study II

The Music group children were enrolled in a public elementary school with instrument lessons, music theory, and orchestral practice as part of the daily curriculum. All the children had begun their instrument practice no later than at age 7, resulting in a minimum of 6 years of formal instrument practice. While the typical instrument choices in the Music group included violin, cello, and oboe, the typical hobbies in the Control group ranged from football, swimming, and horse riding to scouts and arts and crafts, including no extracurricular music-related hobbies.

3.1.1.2 Study IV

Participants in the Musician group were either currently full-time students in a music academy or professional musicians with a music academy degree. Participants in the Non-musician group had a maximum of 2 years of formal instrument practice. The music-related activities of the participants are listed in Table 3.

In the Musician group, the mean starting age of first instrument was 6 years (standard deviation 2.5; range 3–12), the mean duration of formal instrument practice was 16 years (2.7; 12–21), and the mean amount of current daily practice was 3.3 hours (1.2, 0.5–5). The current main instruments were, in order of frequency, piano and singing, violin, cello, contrabass, flute, oboe, bassoon, and saxophone. The prior main instruments or current secondary instruments were, in order of frequency, piano, singing, acoustic and electric guitar, acoustic and electric bass, violin, drums, and harmonium. No one reported having absolute pitch. 13 of 16 reported playing mostly classical music as opposed to other music genres, and 13 of 16 reported playing mostly by using musical notation (as opposed to improvising or playing by ear).

When asked about the personal importance of their music activities, all participants in the Musician group rated the importance of their formal as well as informal music activities (listening to music, going dancing, going to concerts etc.) as quite or very important. Among the participants of the Non-musician group, 4 of 14 rated their formal music activities and 8 of 14 their informal music activities as quite or very important.

Table 3. Amounts of participants who reported music-related activities (Study IV).

	Musician group (n = 16)	Non-musician group (n = 14)
Instrument practice	16	2 (1–2 yrs)
Music play school	10	5
Choir / Singing group	14	3
Band	15	4
Dance classes	7	6
Regular music listening*	15	9

*The average amounts of reported music listening per week among the musicians *vs.* non-musicians were 6.3h *vs.* 4.9h active listening and 9.7h *vs.* 7.6h passive listening.

3.1.2 Group differences in general cognitive abilities (Study IV)

In order to rule out differences in general cognitive abilities between the two groups, suggested in prior studies (George & Coch, 2011; Ho, Cheung, & Chan, 2003; Moreno et al., 2011; Schellenberg, 2006), the musician and non-musician participants were presented with parts of the Wechsler Intelligence Scale (WAIS-III, subtests: Similarities, Symbol search, Digit span, and Block design, Wechsler, 1997a) and Wechsler Memory Scale (WMS-III, subtests: Logical memory I–II, Paired associates I–II, and Faces I–II, Wechsler, 1997b) as well as the Trail-Making Test A and B. These tests measure cognitive abilities related to linguistic and visual reasoning as well as visuo-motor skills, working memory, linguistic and visual memory, executive functions, and processing speed.

Two-tailed independent samples t-tests demonstrated lower standardised scores in Musician *vs.* Non-musician group in Logical memory I, 11.8 *vs.* 13.5, t(26) = -2.06, p < .05, and Similarities, 11.5 *vs.* 13.5, t(27) = -4.66, p < .001. These subtests are related to linguistic skills (Wechsler, 1997a, 1997b), and it was hypothesised that the group differences may be attributable to the more literary study fields of the participants in the Non-musician group compared to the Musician group. Thus, among the participants of Study IV, there was no evidence of enhanced general cognitive skills or superior skills related to auditory working memory in musicians compared to non-musicians.

3.2 Experimental procedure

In Studies I, II, and IV, EEG experiments were conducted in a chamber, where the participant sat on a comfortable chair while the EEG was recorded, and sound sequences were presented with a comfortable loudness binaurally via headphones. The participant watched a self-chosen DVD movie with subtitles and without sounds, and was instructed to focus on the movie, not to move or blink a lot, and not pay attention to the sounds (i.e., the experiment was conducted in "ignore condition"). The participants were not informed about the nature of the stimulus types. In Study I a "detection condition" followed, where the EEG recording continued but the movie was turned off and the participant was instructed to detect target sounds (with softer intensity) in the sequences by pressing a response button during or immediately after the target sound. The EEG experiment as a whole lasted 2–2.5 hours (including the electrode attachment and removal) in Studies I, II, and IV. In Study IV, a second session 2 h in duration followed 8–54 days (mean 24 days) after the EEG recording. During the second visit, the participant completed behavioural tests, namely, a deviant chord detection task based on the sound sequences presented in the EEG experiment, and the cognitive tests.

During the EEG experiment in Study III, the infant was lying in a crib in a hospital room, with the head facing randomly either to the left or to the right, so that the other ear was partly obscured. While the EEG was recorded, sound sequences were presented from two loudspeakers placed outside the crib near the left and right corner close to the infant's feet. The sound level was about 60 dB SPL at the approximate location of the infant's head. The background noise level in the hospital room was approximately 46 dB SPL. The EEG recording was performed by a trained nurse who observed the infant throughout the measurement, documenting the apparent sleep stages and activity of the infant. Only data from sleeping infants were included in this study. Data recorded in different sleep stages (active *vs.* quiet sleep) were analysed together, and thus the possible differences in ERPs between different sleep stages were not taken into account in the present study.

3.3 Experimental stimuli and paradigms

In all the studies, the sound sequences presented to the participants introduced a complex auditory oddball paradigm with Western music chords transposed to several frequency levels. In all the paradigms, the frequently repeating standard stimuli were root major chords transposed to 12 frequency levels, while the occasionally presented deviant stimuli varied somewhat between the studies. The deviant chord types were root minor chords, inverted major chords (2^{nd} inversion), and highly dissonant chords, each transposed to 3 frequency levels. Inverted major chords were included in the paradigm in order to add a deviant type that would introduce a deviant interval structure but not a deviant mode. In the paradigms the stimuli were presented in random order, with the exception of at least one standard stimulus preceding every deviant stimulus. The time from the beginning of the stimulus until the beginning of the next stimulus was 1000 ms in each paradigm presented in the EEG experiments, and 2000 ms in the behavioural experiment of Study IV. An example of each chord type is illustrated in Figure 1. The details of the experimental paradigms are presented in Table 4 and Figure 2 and the stimuli are listed in Table 5.

Additionally, in Study I, part of the root major chords were presented with about 10 dB softer intensity. Soft major chords were included in the paradigm as deviant stimuli in order to ensure that a classical physical-feature MMN would be elicited in the complex setting of the paradigm. Additionally, the soft major chords served as targets in the detection condition, in order to ensure that the participants' attention was directed to the sounds, while still avoiding motor artefacts from the button presses or ERPs related to target stimuli obscuring the MMNs in response to the other deviant types, which were of main interest in the present study. In Table 5 and Figure 2, the soft major chords are not mentioned (they are included in the standard root major chords).

As illustrated in Figure 2C, in all the paradigms, all the tones in the deviants were already present in the standards. Among the standard chords, some of the notes from C' to F#" occurred in two different octaves (' indicating the lower octave and " the higher octave). Because of this, the frequencies in the middle of the range occurred more often than the frequencies at the high and low ends. Only these most common pitches of the standard chords were used in the deviant chords. In this way, the MMN elicited by the deviant chords could not be simply a response to a rare, deviant frequency as only the tone combinations, i.e., interval structures, varied between standards and deviants.

In all the studies, the stimuli in the paradigms were triad chords comprised of three components (tones) with equal temperament frequencies ranging from C4 (262 Hz) to F#5 (740 Hz). While the stimuli were comprised of sinusoidal tones and had a stimulus length of 250 ms with 25 ms rise and fall time in all the studies, Study IV additionally included a paradigm with chords comprised of piano sounds (650 ms with 10 ms rise and fall times and an additional 100 ms shaped from the end), and a paradigm with longer chords comprised of sinusoidal tones (650 ms with 10 ms rise and fall times).

The stimuli in the piano chord paradigm were constructed of Steinway Grand soft piano sounds from the McGill University Master Samples DVD collection (Opolko & Wapnick, 2006). While the aim was to replicate the findings of Studies I-III with harmonically rich piano chords, identical in duration with sinusoidal chords, the stimulus duration of 250 ms used in prior studies appeared too short in order for the harmonically rich piano sounds to sound natural. In this regard, a longer duration of 650 ms was considered optimal for the piano stimuli. A paradigm with 650-ms-long sinusoidal chords was then added to the study, in order to make sure that possible differences between the results of sinusoidal and piano paradigms would not be due to duration differences between the stimuli. Thus, in Study IV, three versions of the paradigm were presented in the EEG experiment in random order: a paradigm with short sinusoidal chords (stimulus length 250 ms), a paradigm with long sinusoidal chords (650 ms), and a paradigm with piano chords (650 ms).

In Study I, the paradigm was presented in eight sequences (duration of each 6 minutes 45 seconds). The first four sequences were presented in the ignore condition and the second four in the detection condition. Each deviant type was presented 108 times in each condition. The stimuli in Study I were presented with the STIM audio system and STIM2 4.0 software. In Study II, the paradigm (duration 8 min 20 s) was presented once in the end of a 1-hour-long measurement session of the longitudinal study. Each deviant type was presented 75 times. In Study III, the stimuli were presented in three sequences (duration of each 9 min 11 s). Deviants were presented a total of 108 times for the dissonant and minor chords, and 216 times for the inverted major chords. In study IV, in the EEG experiment, each of the three paradigms was presented once (duration of each 15 min). Each deviant type was presented 134 or 135 times per paradigm. The stimuli (Studies II-IV) were presented and the behavioural responses in the deviant chord detection task (Study IV) recorded with the Presentation software v 16.0.

3.3.1 Behavioural chord detection task (Study IV)

In addition to the EEG experiment, a deviant chord detection task based on the oddball paradigm presented in the EEG experiment was introduced in Study IV. The task consisted of four parts: minor chord detection with 650-ms-long sinusoidal chords and 650-ms-long piano chords and inverted major chord detection with 650-ms-long sinusoidal chords and 650-ms-long piano chords. Sinusoidal and piano parts were introduced in counter-balanced order, but the minor chord detection task always preceded the inverted major chord detection task. (This fixed order was used so that the presumably easier task would precede the presumably more difficult task.)

The deviant chord detection task is illustrated in Figure 2B. All parts of the task consisted of a teaching session with 60 stimuli (duration 2 minutes), followed by a test session with 150 stimuli (duration 5 minutes). In the teaching session, the participants were asked to listen to the sounds and look at the computer screen in front of them. A red circle appeared on the screen immediately after a target sound (a deviant), and the participants were asked to try and learn to detect the target sounds. The identity of the sounds was left unknown to the participants, with only a description that the target sounds “have a different name in music” compared to the other sounds. In the test session, the participants were instructed to press a button during or immediately after each (target) sound that was followed by a red circle in the teaching session.

Table 4. The experimental oddball paradigms (Studies I-IV). Root form major chords were presented as standards in all the paradigms. Different deviant types were presented in the same oddball paradigm.

	Stimulus types	**Condition**	**Deviant types**
Study I, EEG	Sinusoidal, 250 ms	Ignore	Minor chords Inverted major chords Dissonant chords Soft major chords
		Detection	Minor chords Inverted major chords Dissonant chords Soft major chords
Study II, EEG	Sinusoidal, 250 ms	Ignore	Minor chords Inverted major chords
Study III, EEG	Sinusoidal, 250 ms	Ignore	Minor chords Inverted major chords Dissonant chords
Study IV, EEG	Sinusoidal, 250 ms	Ignore	Minor chords Inverted major chords
	Sinusoidal, 650 ms	Ignore	Minor chords Inverted major chords
	Piano, 650 ms	Ignore	Minor chords Inverted major chords
Study IV, Behavioural	Sinusoidal, 650 ms	Detection	Minor chords
		Detection	Inverted major chords
	Piano, 650 ms	Detection	Minor chords
		Detection	Inverted major chords

Table 5. Experimental stimuli and their probabilities in the oddball paradigms (Studies I-IV). The notes in the octave starting from C4 are labelled with ' and the notes in the higher adjacent octave starting from C5 are labelled with ".

		Study I	**Study II**	**Study III**	**Study IV**	
		EEG	EEG	EEG	EEG	Behavioural
Standards: Root major triad chords		79.9	70	73.9	70	79.9
C major	C'-E'-G'	6.7	5.8	6.2	5.8	6.7
C# major	C#'-F'-G#'	6.7	5.8	6.2	5.8	6.7
D major	D'-F#'-A'	6.7	5.8	6.2	5.8	6.7
D# major	D#'-G'-A#'	6.7	5.8	6.2	5.8	6.7
E major	E'-G#'-B'	6.7	5.8	6.2	5.8	6.7
F major	F'-A'-C"	6.7	5.8	6.2	5.8	6.7
F# major	F#'-A#'-C#"	6.7	5.8	6.2	5.8	6.7
G major	G'-B'-D"	6.7	5.8	6.2	5.8	6.7
G# major	G#'-C"-D#'	6.7	5.8	6.2	5.8	6.7
A major	A'-C#"-E"	6.7	5.8	6.2	5.8	6.7
A# major	A#'-D"-F"	6.7	5.8	6.2	5.8	6.7
B major	B'-D#"-F#"	6.7	5.8	6.2	5.8	6.7
Deviants		20.1	30	26.1	30	20.1
Minor triad chords		6.7	15	6.5	15	20.1 or 0
F minor	F'-G#'-C"	2.8	5	2.2	5	6.7 or 0
F# minor	F#'-A'-C#"	2.8	5	2.2	5	6.7 or 0
G minor	G'-A#'-D"	2.8	5	2.2	5	6.7 or 0
Inverted major triad chords		6.7	15	13.1	15	20.1 or 0
A major (inv.)	E'-A'-C#"	2.8	5	4.4	5	6.7 or 0
A# major (inv.)	F'-A#'-D"	2.8	5	4.4	5	6.7 or 0
B major (inv.)	F#'-B'-D#"	2.8	5	4.4	5	6.7 or 0
Highly dissonant triad chords		6.7	.	6.5	.	.
disson1	E'-F'-B'	2.8	.	2.2	.	.
disson2	F#'-G'-C#"	2.8	.	2.2	.	.
disson3	G#'-A'-D#"	2.8	.	2.2	.	.

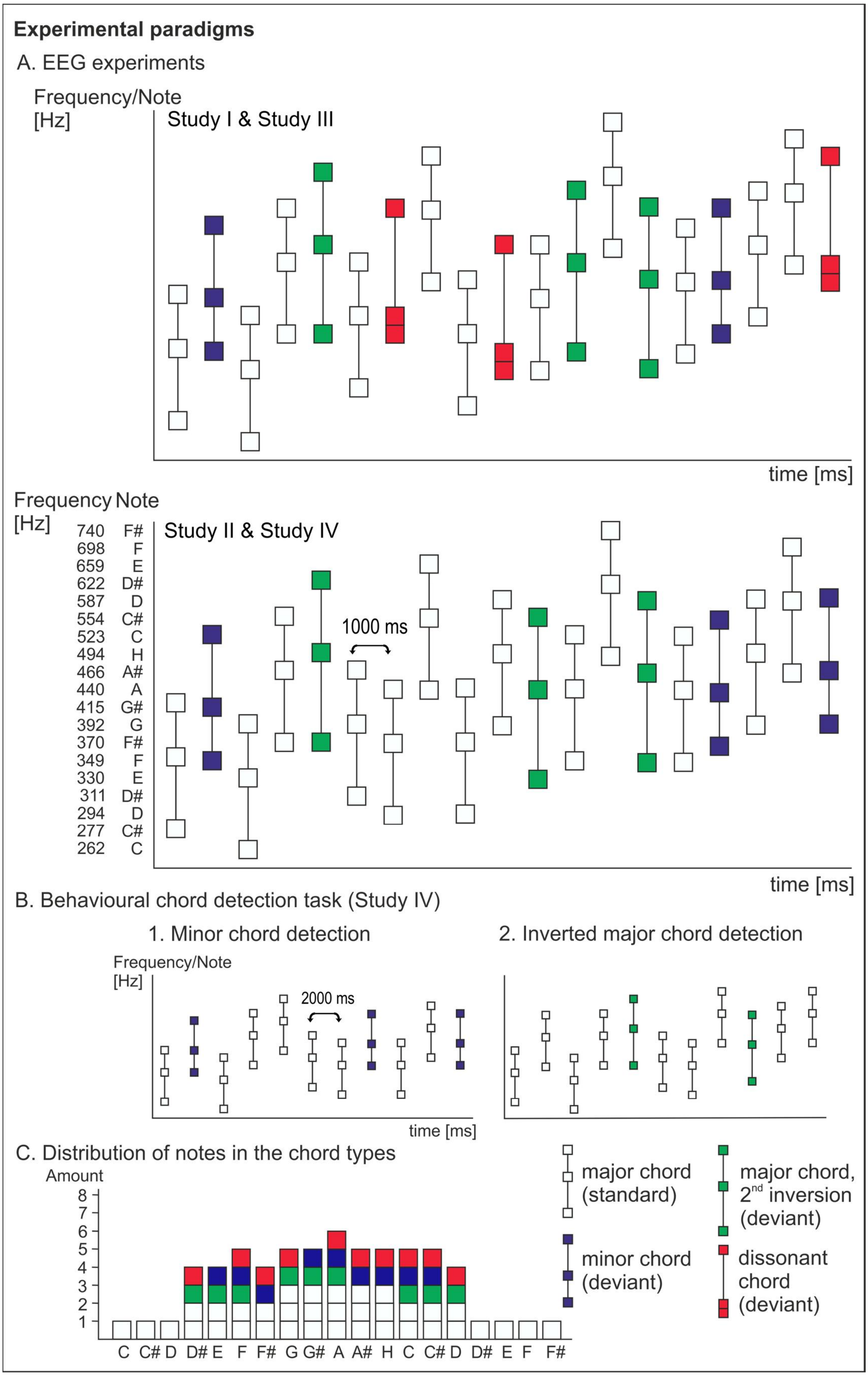

Figure 2. A. The experimental paradigms in the EEG experiments (Studies I-IV). B. The experimental paradigm in the behavioural chord detection task in Study IV. C. Distribution of individual notes in the triad chords, labelled with colours according to chord type.

3.4 EEG recording and quantification

3.4.1 Study I

EEG was recorded (amplification factor 500, sampling rate 250 Hz, on-line filter 0.05–40 Hz) with NeuroScan Acquire 4.1.1 software with Ag/AgCl-electrodes placed on seven scalp locations according to the international 10/20-system: Fpz, Fz, F3, F4, Cz, Pz, and Oz. Additional 5 external electrodes were placed below the participant's left eye and the left canthus (vertical and horizontal EOG) in order to record eye movements, the tip of the nose (common reference) and the left and right mastoids behind the ears.

ERPs were averaged separately for each participant, electrode, and stimulus type in each condition. The epoch duration was 450 ms post-stimulus, with a 100-ms pre-stimulus baseline. All epochs including voltage changes exceeding ±100 µV on the EOG electrodes remaining after filtering and baseline correction were omitted in order to exclude eye movement artefacts. The ERPs were digitally band-pass filtered (1–30 Hz). A baseline correction for -100–0 ms was applied to all epochs prior to statistical testing.

3.4.2 Studies II and IV

EEG was recorded (sampling rate 512 Hz) continuously from 64 electrodes (headcap and amplifier: Biosemi ActiveTwo, mk1, BioSemi B. V., Amsterdam, The Netherlands) placed according to the international 10-20-system, with additional 5 external Ag/AgCl-electrodes placed below the participant's left eye and the left canthus (vertical and horizontal EOG) in order to record eye movements, the tip of the nose (common reference), and the left and right mastoids behind the ears.

The recorded EEG was imported to the BESA (BESA GmbH, Gräfelfing, Germany) analysis program, where it was filtered (in Study II low-pass 0.5 Hz, high-pass 30 Hz, slope 12 dB/oct, zero phase; in Study IV low-pass 1 Hz, high-pass 30 Hz, slope 12 dB/oct, zero phase) and re-referenced to the mean of the mastoid electrodes in order to display the maximal MMN response at the frontal electrode sites (as recommended by Kujala et al., 2007). Automatic eye-artefact-removal was conducted (BESA, Berg & Scherg, 1994).

ERPs were averaged separately for each participant, electrode, and chord type. In Study II, the epoch duration was 450 ms post-stimulus, with a 100-ms pre-stimulus baseline. In Study IV, it was 450 ms post-stimulus in the paradigm with short sinusoidal chords and 650 ms post-stimulus in the paradigms with long sinusoidal and piano chords, with a 100-ms pre-stimulus baseline. In both studies, all epochs with voltage changes exceeding ±120 µV remaining after filtering and baseline correction were omitted from further analysis in order to exclude movement-related artefacts. A baseline correction for -100–0 ms was applied to all epochs prior to statistical testing.

3.4.2.1 Source modelling (Study IV)

In order to examine hemispheric differences in the ERPs, source modelling was conducted with BESA 6.0 analysis program. For source modelling, the raw EEG was filtered (high-pass 1 Hz, notch filter 50 Hz with a width of 2 Hz), and an epoch duration ranging from 200 ms pre-stimulus to 800 ms post-stimulus was used for averaging. Prior to the source analysis, a low-pass filter of 30 Hz and the automatic eye artefact correction were added. The averaged files with less than 70% accepted epochs were excluded from source analysis.

For the remaining files, two mirrored dipoles were calculated in order to explain the data during the time windows used in MMN and N1 analyses (described in section 3.5.1.4). The fitting of the location, orientation, and strength parameters was conducted separately for each participant, stimulus type and paradigm, respectively. When the goodness of fit value of the solution was below 70 % for two dipoles or fitting of the locations was poor by visual inspection (dipoles next to each other in the middle of the head, or outside the brain), the model was excluded from further analysis.

Principal component analysis for the grand-average waveforms conducted separately for each paradigm and stimulus type showed that one mono- or bipolar component could explain on average 99.0% (range 97.5–99.7%) of the data on N1 latency window, and 95.7% (range 93.8–97.8%) on MMN latency window (only Musician group analysed). In the source analysis, only 38% of the MMN fittings met the goodness of fit or location criteria, and thus the MMN dipole strengths were not analysed. Instead, 78% of the N1 fittings were successful, and the dipole strengths were further analysed with statistical tests. Data from 11 musicians and 12 musicians in the sinusoidal-250 paradigm, 9 musicians and 9 non-musicians in the sinusoidal-650 paradigm, and 8 musicians and 7 non-musicians in the piano-650 paradigm were included in the final analyses of the dipole source strengths.

3.4.3 Study III

EEG was recorded (sampling rate 500 Hz) using NeuroScan Synamps 2 amplifier with Ag/AgCl-electrodes placed on 11 scalp locations according to the international 10/20-system: F3, F4, C3, Cz, C4, P3, P4, T7, and T8. Additional two electrodes were placed next to the infant's right eye in order to monitor and record eye movements (EOG) and the right mastoid behind the right ear (reference).

The recorded EEG was imported to the BESA (BESA GmbH, Gräfelfing, Germany) analysis program and was filtered (high-pass 0.5 Hz, low-pass 30 Hz). ERPs were averaged separately for each participant, electrode, and stimulus type. The epoch duration was 600 ms post-stimulus, with a 100-ms pre-stimulus baseline. All epochs including voltage changes exceeding ±150 µV remaining after filtering and baseline correction were omitted in order to exclude movement-related artefacts. A baseline correction for -100–0 ms was applied to all epochs prior to statistical testing.

3.5 Data analysis

3.5.1 EEG

In order to conduct statistical analyses on MMN/MMR amplitudes, subtraction waveforms were calculated by subtracting the ERP to the standard stimuli from the ERP to the deviant stimuli, separately for each deviant type. All statistical analyses of mean amplitudes were conducted with latest versions of the SPSS Statistics (IBM).

3.5.1.1 Study I

MMN mean amplitude was calculated from 150–250 ms post-stimulus on Fz electrode, where MMN typically shows maximal amplitude (Kujala et al., 2007). MMN amplitudes on Fz electrode in response to each deviant type in each condition were compared to zero with one-sample t-tests. A two-way repeated-measures analysis of variance (ANOVA-R) was employed to compare differences between deviant types (minor, inverted major, dissonant, soft) and conditions (ignore, detection) as well as their interactions. Statistically significant effects with more than two levels were further analysed with least-significant difference (LSD) t-tests.

3.5.1.2 Study II

MMN mean amplitudes were calculated by centring 30-ms time windows around the most negative peaks of the grand-average waveforms for each deviant type and group on Fz occurring at 230–270 ms post-stimulus onset, where MMN-like negativities were visible, consistent with previous studies of child-MMN latencies (Shafer et al., 2000). These time windows were employed to calculate MMN mean amplitudes on electrodes F3, F1, Fz, F2, F4, FC3, FC1, FCz, FC2, FC4, C3, C1, Cz, C2, and C4.

Statistical analyses of MMN were carried out for the mean of Fz and Cz electrodes, where the response was of maximal amplitude, in order to improve the signal-to-noise ratio. MMN amplitudes in response to each deviant type were compared to zero with one-sample t-tests with groups pooled together and separately for each group. ANOVA-R was employed to compare differences between deviant types (minor, inverted major) and groups (Music group, Control group) as well as their interactions. Another ANOVA-R with electrodes F3, F1, Fz, F2, F4, FC3, FC1, FCz, FC2, FC4, C3, C1, Cz, C2, and C4 with additional factors left-right (5 levels) and front-back (3 levels) was employed to analyse the spatial distribution of the MMN responses. Statistically significant effects with more than two levels were further analysed with Bonferroni-corrected pairwise-t-tests. In ANOVA-Rs, when sphericity could not be assumed as indicated by a statistically significant p-value ($p < .05$) in Mauchly's test of sphericity, a Greenhouse-Geisser correction was used.

The same time window, window length, and electrodes (mean of Fz and Cz) as in the MMN analyses were used to quantify the mean amplitudes of the N2-like responses to standard stimuli. N2 amplitudes were compared to zero with one-sample t-tests with groups pooled together and independently in each group, and then the groups were compared with independent samples t-tests.

3.5.1.3 Study III

In order to explore the optimal latency window for MMR mean amplitude calculation, running-t-tests (compared to zero) with 50 ms and 100 ms time windows were conducted for the subtraction waveforms on electrodes F3, F4, C3, C4, P3, and P4. The latency window chosen for the analyses was such that around it, latency windows starting from more than 10 consecutive time points gave a statistically significant t-test result on at least one electrode. This was done in order to minimise the risk of a false positive result in the t-tests for the responses. As a result, a 50-ms window 240–290 ms was used to calculate the MMR mean amplitudes on all the aforementioned electrodes. Based on the running-t-test protocol described above, 100-ms windows 20–120 ms and 250–350 ms were used to calculate the mean amplitudes of the two peaks of the ERP to standard root major chords.

MMR amplitudes on each electrode site in response to each deviant as well as amplitudes of the two standard responses on each electrode site were compared to zero with one-sample t-tests. Effect size of the t-tests was calculated using Cohen's d. Separate ANOVA-Rs were employed to analyse the spatial distribution of the MMRs to each deviant and the two responses to standards, with factors left-right (2 levels) and front-back (3 levels) as well as their interactions, including measures of observed statistical power. Statistically significant effects with more than two levels were further analysed with Bonferroni-corrected pairwise-t-tests. In ANOVA-R, when sphericity could not be assumed, a Greenhouse-Geisser correction was used.

3.5.1.4 Study IV

In order to evaluate the MMN, a t-test of the group-average ERP in response to standard root major chord *vs.* group-average ERP in response to each deviant chord type was conducted independently for each data point in the MMN latency range 150–250 ms post-stimulus on Fz electrode. However, large numbers of conducted t-tests increase the risk of obtaining false positive results, and, furthermore, there is correlation of consecutive data points (autocorrelation) in the EEG signal. The autocorrelation of the signal was calculated with MatLab autocorrelation function, and, based on the criteria suggested by Guthrie & Buchwald (1991), sufficient criteria for MMN was defined as 9 consecutive data points (a time interval of ~18ms, autocorrelation 0.9 on average) reaching statistical significance ($p < .05$) in the MMN latency range. The MMN has been assessed by analyzing consecutive data points in several previous studies (see Bauer et al., 2009; McGee, Kraus, & Nicol, 1997; Petermann et al., 2009). Cohen's d was calculated as a measure of effect size in the t-tests.

For further statistical testing, MMN amplitudes were calculated as mean amplitudes of 50-ms time windows for each participant, paradigm, deviant type, and electrode location, respectively. The time windows were centred around the midpoints of the statistically significant time intervals described above, separately for each paradigm. These time windows were employed to calculate mean amplitudes on 35 electrodes F5, F3, F1, Fz, F2, F4, F6, Fc5, Fc3, Fc1, Fcz, Fc2, Fc4, Fc6, C5, C3, C1, Cz, C2, C4, C6, Cp5, Cp3, Cp1, Cpz, Cp2, Cp4, Cp6, P5, P3, P1, Pz, P2, P4, and P6. ANOVA-R was employed for all the 35 electrodes to compare paradigms (short sinusoidal, long sinusoidal, piano), chord types (major, minor, inverted major), groups (Musician group, Non-musician group), and scalp distribution (left-right with 7 levels, front-back with 5 levels, only left-right analysed), as well as their interactions. Statistically significant effects with more than two levels were further analysed with Bonferroni-corrected pairwise-t-tests.

N1 mean amplitudes were calculated from 30-ms windows centred around the first clear negative peak on grand-average waveforms on Fz electrode, separately for each paradigm (short sinusoidal, long sinusoidal, piano). These time windows were employed to calculate mean amplitudes on the 35 electrodes listed above. ANOVA-R was employed for all the 35 electrodes to compare chord types (major, minor, inverted major), groups (Musician group, Non-musician group), and scalp distribution (left-right with 7 levels, front-back with 5 levels, only left-right analysed), as well as their interactions. The analysis was conducted separately for each paradigm, due to obvious acoustic differences between the stimuli that are likely to cause differences in the N1 due to their different spectral composition and rise times (Näätänen & Picton, 1987). Statistically significant effects with more than two levels were further analysed with Bonferroni-corrected pairwise-t-tests.

In N1 analyses, when statistically significant left-right effects were found, the hemispheric differences were further analysed with source modelling as described in section 3.4.2.1. The means of absolute values of the dipole strengths in the hemispheres were compared with ANOVA-Rs, with factors hemisphere (left, right), chord type (major, minor, inverted major), and group (Musician group, Non-musician group) as well as their interactions. In ANOVA-Rs, when sphericity could not be assumed, a Greenhouse-Geisser correction was used.

3.5.2 Behavioural data (Study IV)

The performance in the chord detection task was quantified as hits-per-button-presses ratios for each participant in each part of the task. Since the proportion of deviant chords in each task was 20%, a hit-ratio (hits-per-button-presses) above 20% indicated above-chance performance. Performance in both groups in each task was compared to chance level with one-sample t-tests. Differences in performance between stimulus types (sinusoidal and piano chords), deviant types (minor and inverted major), and groups as well as their interactions were analysed with ANOVA-R. When sphericity could not be assumed, a Greenhouse-Geisser correction was used.

The relationship between deviant chord detection performance and N1 and MMN amplitudes was analysed with 2-tailed Pearson correlations with groups pooled together. In order to take into account the effect of group, a step-wise linear regression analysis was conducted where chord detection performance was predicted with N1 and MMN amplitudes (step 1), and group and its interaction with N1 and MMN amplitudes (step 2) as dependent variables. In the interaction analyses, in order to reduce possible multicollinearity, continuous variables were mean-centred. Homogeneity of variances was analysed with Levene's tests, which indicated no differences in variance between the two groups.

4 Results

The aim of the present studies was to examine Western music chord categorisations in different age groups as evidenced by MMN elicitation (Studies I-IV) and performance in a deviant chord detection task (Study IV), as well as the effects of music training on them (Studies II and IV). In order to study basic auditory processing of the chords, ERP responses to standard stimuli (Studies II-IV) and differences between chords in the N1 response (Study IV) were additionally studied. Furthermore, in order to examine the hemispheric lateralisation of the underlying neural processes, the scalp distribution of the brain activity was analysed (Studies II-IV) and source modelling was conducted (Study IV).

The ERP and behavioural results are described in the following sections 4.1–4.4. ERP waveforms of Studies I-IV, illustrating responses to standard root major chords and deviant minor chords, inverted major chords, dissonant chords (Studies I and III), and soft root major chords (Study I) as well as the deviant-minus-standard subtraction waves are illustrated in Figure 3. MMN/MMR amplitudes in Studies I-IV are presented in Table 6. The results of the ANOVA-Rs comparing MMN/MMR amplitude differences between deviant types, groups (Studies II and IV), conditions (Study I), and/or paradigms (Study IV) as well as the scalp distributions (Studies II-IV) are shown in Table 7.

4.1 Major-minor and consonance-dissonance processing in non-musicians (Study I)

In the adult non-musicians, MMN was elicited by minor chords, $t(15) = -2.40$, $p < .05$, dissonant chords, $t(15) = -3.07$, $p < .01$, and soft root major chords, $t(15) = -4.03$, $p < .01$, in the context of root major chords in the ignore condition. In the detection condition, MMN was elicited by dissonant chords, $t(15) = -2.86$, $p < .05$, and soft root major chords that served as targets, $t(15) = -4.10$, $p < .001$, while MMN to minor chords did not reach statistical significance, $t(15) = -0.78$, $p > .05$. No MMN was elicited by inverted major chords in ignore condition, $t(15) = 0.26$, $p > .05$, or detection condition, $t(15) = 1.28$, $p > .05$.

In ANOVA-R, MMN amplitude was larger (more negative) in response to soft major chords compared to dissonant chords, larger to dissonant chords and soft major chords compared to minor chords and larger to soft major chords, dissonant chords and minor chords compared to inverted major chords. There were no statistically significant differences in MMN amplitude between ignore and detection conditions.

Table 6. MMN/MMR amplitudes in µV with standard deviations in parentheses, statistically significant ($p < .05$) responses in bold (Studies I-IV).

		Minor	**Inverted**	**Dissonant**	**Soft**
Non-musicians (Study I)	Ignore condition	**-0.35(-0.6)**	0.04(-.6)	**-0.58(-0.8)**	**-0.82(0.8)**
	Detection condition	-0.13(-0.7)	0.19(-.6)	**-0.40(-0.6)**	**-1.02(-1.0)**
13-year-olds (Study II)	Music group	**-2.28(1.3)**	-0.74(2.0)	.	.
	Control group	-0.49(1.5)	0.45(2.2)	.	.
Newborn infants (Study III)	F3	0.44(2.9)	no*	**1.29(2.6)**	.
	F4	-0.17(2.8)	no*	**1.46(2.5)**	.
	C3	0.02(2.3)	no*	0.61(1.8)	.
	C4	-0.76(3.0)	no*	0.68(3.0)	.
	P3	-1.02(2.3)	no*	0.34(1.8)	.
	P4	**-1.40(2.7)**	no*	-0.32(2.2)	.
Musicians and non-musicians (Study IV)	Musician group				
	Sinusoidal-250	**-0.48(0.7)**	**-0.76(0.7)**	.	.
	Sinusoidal-650	**-0.58(0.7)**	**-0.64(0.6)**	.	.
	Piano-650	**-0.38(0.8)**	**-0.62(0.5)**	.	.
	Non-musician group				
	Sinusoidal-250	0.06(.6)	-0.30(.6)	.	.
	Sinusoidal-650	-0.10(.7)	-0.09(.5)	.	.
	Piano-650	0.11(.7)	0.12(.6)	.	.

* In Study III, the running-t-tests did not demonstrate a sufficient number (10) of consecutive statistically significant ($p < .05$) data points in the subtraction curves. Therefore, no mean amplitudes were calculated.

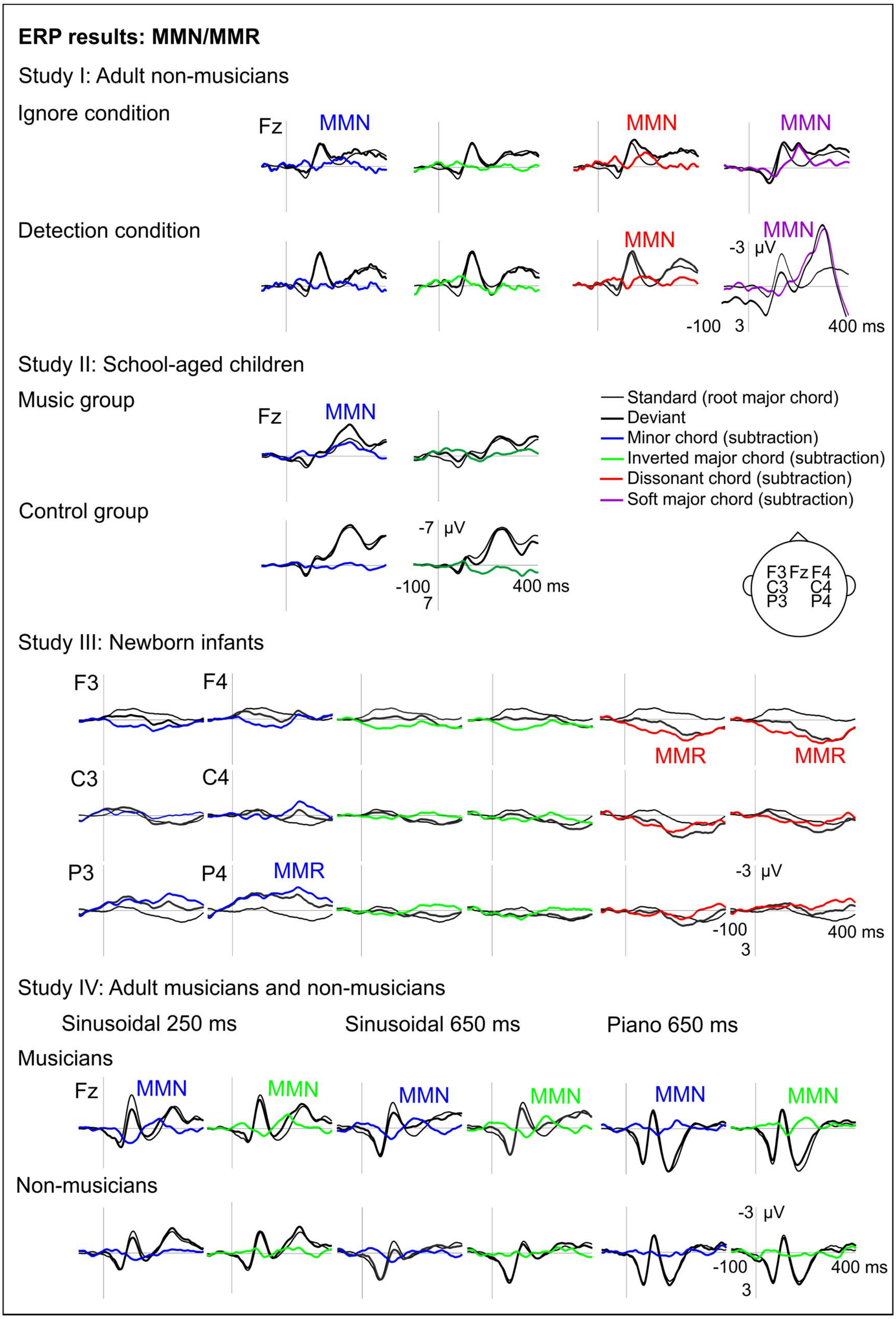

Figure 3. MMN results in Studies I-IV. Group-averaged ERP waveforms elicited by standard root major chords and each deviant chord type, and deviant-minus-standard subtraction waveforms illustrating the MMNs/MMRs. Statistically significant MMN/MMR responses are marked in the figure.

Table 7. Results of ANOVA-Rs of MMN amplitude with pair-wise comparisons for significant effects. Statistically significant interactions are shown. Effect sizes (η_p^2) of statistically significant effects are listed.

	Effect	F(df)	p	η_p^2	Pair-wise comparisons*
Study I					
	Chord type	12.31(3,45)	**< .001**		soft < dissonant, minor, inverted dissonant < minor, inverted minor < inverted
	Condition	0.37(1,15)	> .10		
Study II					
	Chord type	6.14(1,22)	**< .05**	0.22	minor < inverted
	Group	7.04(1,22)	**< .05**	0.24	music group < control group
Scalp distribution	Front-back	2.87(1,30)	.09		
	Left-right	2.48(2,49)	.09		
	Chord type	4.05(1,22)	.06		
	Group	6.11(1,22)	**< .05**	0.22	music < control
	Left-right x Group	3.73(2,49)	**< .05**	0.15	middle, middle-right, right: music < control music: middle-left, middle-right < left
Study III					
minor-MMR	Front-back	3.23(1,24)	.07		
	Left-right	2.72(1,18)	> .10		
dissonant-MMR	Front-back	3.77(2,36)	**< .05**	0.17	
	Left-right	0.23(1,18)	> .10		
Study IV					
	Paradigm	1.85(2, 54)	> .10		
	Chord type	1.20(1, 27)	> .10		
	Group	15.31(1, 27)	**< .01**	0.36	musician < non-musician
	Left-right	5.39(2, 65)	**< .01**	0.17	no
	Left-right x Deviant	4.07(3, 71)	**< .05**	0.13	inverted: far left > middle-left far-right > middle-left, middle, middle-right, right
Musician group	Left-right	5.36(2, 32)	**< .01**	0.29	far left > left, middle-left, middle
	Paradigm	1.05(2, 28)	> .10		
	Chord type	0.14(1, 14)	> .10		
Non-musician group	Left-right	1.27(2,28)	> .10		
	Paradigm	2.03(2,26)	> .10		
	Chord type	1.21(1,13)	> .10		

* In Study I, the pairwise comparisons were conducted with least-significant difference tests. In Studies II–IV, Bonferroni-corrected results are reported. Because MMN has a negative polarity, smaller numerical values indicate larger MMN responses.

4.2 Major-minor processing in 13-year-olds with and without music training (Study II)

4.2.1 MMNs to minor chords

In 13-year-olds, MMN was elicited by minor chords in the context of root major chords when the groups were analysed together, $t(23) = -3.67$, $p < .01$. When the groups were analysed separately, the MMN to minor chords was statistically significant in the Music group, $t(9) = -5.43$, $p < .001$, but not in the Control group, $t(13) = -1.25$, $p > .10$. No MMN was elicited by inverted major chords when the groups were analysed together, $t(23) = -0.10$, $p > .10$, or separately in Music group, $t(9) = -1.14$, $p > .10$, or Control group, $t(13) = 0.76$, $p > .10$.

In ANOVA-R, MMN amplitudes were larger to minor chords than to inverted major chords, and larger in the Music group compared to the Control group. In ANOVA-R of scalp distribution, MMN amplitudes were larger in the Music group compared to the Control group. An interaction between the left-right electrode location dimension and group demonstrated larger MMN amplitudes in the Music group compared to the Control group in the right and middle but not in the left electrode sites. In the Music group, middle-left electrode sites demonstrated larger MMNs than left electrode sites, and middle-right electrode sites demonstrated larger MMNs than left electrode sites. Overall, the MMN amplitudes in the Music group demonstrated a U-shaped curve in the left-right dimension, with largest amplitudes in the middle electrode sites. The scalp distribution of the MMN amplitudes in the Music group is illustrated in the upper panel of Figure 4.

4.2.2 The N2-like response to standard major chords

In 13-year-olds, an N2-like response was elicited by the standard root major chords when the groups were analysed together, $t(23) = -8.17$, $p < .001$, as well as independently in the Music group, $t(9) = -4.74$, $p < .01$, and the Control group, $t(13) = -9.14$, $p < .001$. The response was larger (more negative) in the Control group (mean amplitude -5.54 µV; standard deviation 2.3) than in the Music group (-2.38; 1.6), $t(22) = -3.78$, $p < .01$.

4.3 Major-minor and consonance-dissonance processing in newborn infants (Study III)

4.3.1 MMRs to minor and dissonant chords

In the newborn infants, in the context of root major chords, a negative MMR was elicited by minor chords on parietal electrode P4, $t(18) = -2.26$, $p < .05$, $d = 0.80$, and a positive MMR was elicited by dissonant chords in the frontal electrodes F3, $t(18) = 2.13$, $p < .05$, $d = 0.65$, and F4, $t(18) = 2.51$, $p < .05$, $d = 0.77$. No MMR was elicited by inverted major chords, as indicated by the running-t-tests not demonstrating enough statistically significant consecutive data points.

In ANOVA-Rs of scalp distribution, there were differences in dissonant chords' MMR amplitude between electrode locations in the front-back dimension, demonstrating a nearly significant tendency for larger MMRs in the frontal than parietal electrode sites. However, the observed power of the effect was low (0.65). The minor chords demonstrated no scalp distribution effects on MMR amplitude.

4.3.2 A negative-positive response complex to standard major chords

In the newborn infants, an early negative response around 20–120 ms, followed by a later positive response around 250–350 ms, were elicited by the standard root major chords. The early negative response was statistically significant on fronto-central electrode sites F3, $t(18) = -4.63$, $p < .001$, $d = 1.49$, F4, $t(18) = -4.24$, $p < .001$, $d = 1.37$, and C3, $t(18) = -2.39$, $p < .05$, $d = 0.76$, and the late positive response on centro-parietal electrode sites C3, $t(18) = 2.73$, $p < .05$, $d = 0.95$, C4, $t(18) = 3.15$, $p < .01$, $d = 1.04$, P3, $t(18) = 4.79$, $p < .001$, $d = 1.61$, and P4, $t(18) = 2.33$, $p < .05$, $d = 0.78$. The amplitudes of the responses to standard root major chords are listed in Table 9.

In ANOVA-Rs, there were differences in response amplitude between electrode locations in the front-back dimension both in the early negative response, $F(1,23) = 12.99$, $p < .001$, $\eta_p^2 = 0.42$, and late positive response, $F(1,23) = 5.70$, $p < .05$, $\eta_p^2 = 0.24$, demonstrating larger early negative responses on the frontal than central or parietal electrode sites and larger late positive responses on central than frontal electrode sites (in all $p < .01$). However, the observed power was above 0.80 only for the early negative response.

Table 8. The mean amplitudes (μV) of the standard responses on each electrode with standard deviations in parentheses (Study III).

	F3	**F4**	**C3**	**C4**	**P3**	**P4**
Early negative (20–120 ms)	-0.61(0.57)	-0.61(0.63)	-0.29(0.54)	-0.26(0.64)	-0.17(0.42)	-0.08(0.64)
Late positive (250–350 ms)	-0.15(1.06)	-0.10(1.11)	0.54(0.86)	0.58(0.80)	0.65(0.59)	0.58(1.08)

4.4 Major-minor and inversion-root form processing in musicians and non-musicians (Study IV)

4.4.1 EEG results

4.4.1.1 MMNs to minor and inverted major chords

In the adult Musician group, MMN was elicited by minor chords and inverted major chords in the context of root major chords in all the three paradigms with short sinusoidal chords, long sinusoidal chords and piano chords, as demonstrated by 9 or more consecutive data points differing statistically significantly ($p < .05$) from baseline in the MMN latency range. No MMNs were elicited by minor chords or inverted major chords in the Non-musician group.

In ANOVA-Rs, MMN amplitudes were larger in the Musician group compared to the Non-musician group. There were no statistically significant differences in MMN amplitude between paradigms or chord types, neither when the groups were analysed together nor when they were analysed separately. There were differences in MMN amplitude between electrode locations in the left-right dimension both when the groups were analysed together and separately in the Musician group. When the groups were analysed together, there was an interaction of left-right dimension with chord type.

While the source analysis of MMN responses was not successful, left-right lateralisation was further analysed with pairwise comparisons. There were no statistically significant differences between left-right electrode locations when the groups were analysed together. Further investigation of the interaction between left-right dimension and chord type demonstrated statistically significant differences ($p < .05$) in the left-right dimension in the MMNs in response to inverted major chords, so that the MMNs were larger (more negative) in the middle-left than far-left and in the middle-left, middle, middle-right, and right than far-right. When the Musician group was analysed separately, pairwise comparisons revealed statistically significant differences between the electrode sites in the left right dimension, so that the MMNs were larger (more negative) in the left, middle-left, and middle than far-left. Overall, both when the groups were analysed together and separately in the Musician group, the pairwise comparisons between the levels of left-right dimension suggested a U-shaped curve of the MMN amplitudes, with largest (most negative) responses in the middle electrode sites and no statistically significant differences between the left and right electrode sites. The scalp distribution of the MMN amplitudes in the Musician group in the paradigm with short sinusoidal chords is illustrated in the bottom panel of Figure 4.

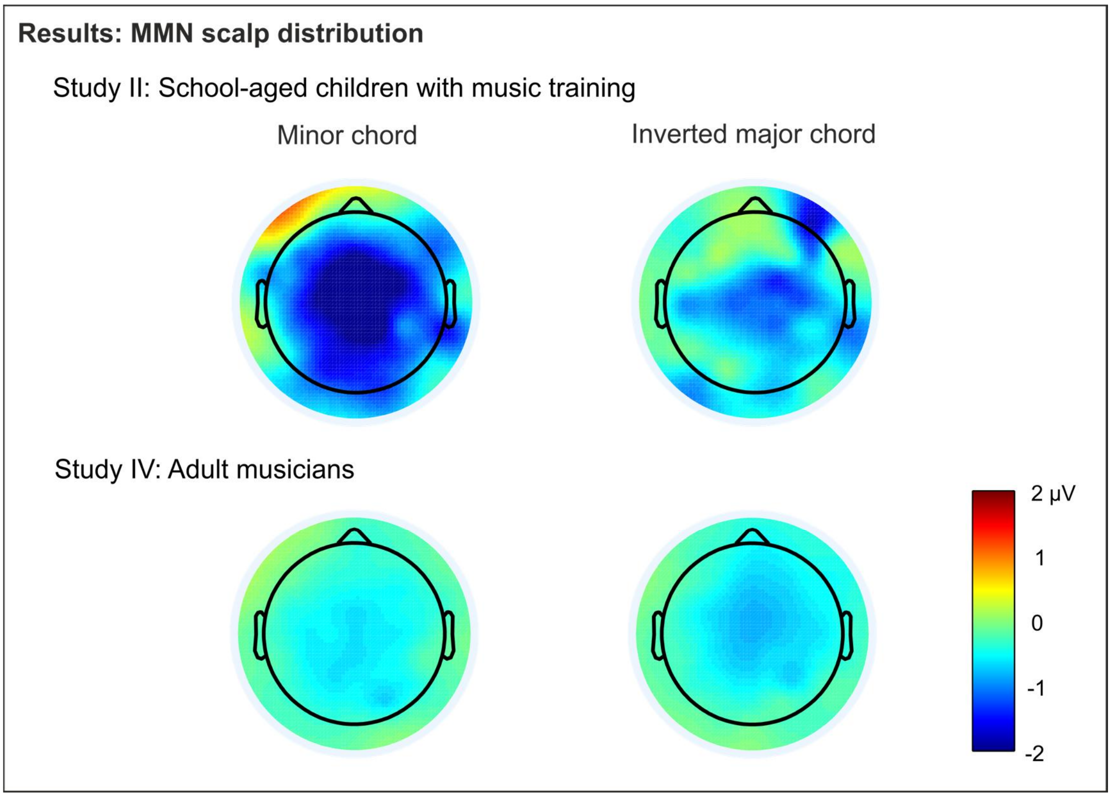

Figure 4. Scalp distributions of MMN mean amplitudes in school-aged children with music training (Study II) and adult musicians (Study IV) in the paradigm with short sinusoidal chords.

4.4.1.2 N1 responses to major, minor, and inverted major chords

In adult musicians and non-musicians, N1 responses were visible to all stimuli in all paradigms in both groups, and their statistical significance was not analysed. The N1 amplitudes are listed in Table 9. In the paradigm with short sinusoidal chords, N1 amplitude demonstrated a stimulus effect, $F(2, 56) = 8.66$, $p < .01$, $\eta_p^2 = 0.24$, so that N1 amplitude was smaller (less negative) in response to minor chords than to standard root major chords ($p < .01$) or inverted major chords ($p < .05$). In the paradigm with long sinusoidal chords, N1 amplitude demonstrated a stimulus effect, $F(2, 54) = 6.69$, $p < .01$, $\eta_p^2 = 0.20$, so that it was smaller to minor chords than to standard root major chords (p

< .05), and a group effect, $F(1, 27) = 4.43$, $p < .05$, $\eta_p^2 = 0.14$, so that it was larger in the Musician group compared to the Non-musician group. The paradigm with piano chords demonstrated no stimulus type or group differences in N1 amplitude.

In ANOVA-Rs of scalp distribution, there were differences in N1 amplitude between electrode locations in the left-right dimension in all the three paradigms with short sinusoidal chords, $F(2, 63) = 17.40$, $p < .001$, $\eta_p^2 = 0.38$, long sinusoidal chords, $F(2, 66) = 3.63$, $p < .05$, $\eta_p^2 = 0.12$, and piano chords, $F(2, 68) = 15.58$, $p < .001$, $\eta_p^2 = 0.36$. Left-right lateralisation was further analysed by comparing dipole strengths of N1 responses between the two hemispheres.

In ANOVA-Rs of N1 dipole strengths, there were statistically nearly significant differences in N1 dipole strength between left and right hemisphere in the paradigms with short sinusoidal chords, $F(1,21) = 3.13$, $p = .09$, $\eta_p^2 = 0.13$ long sinusoidal chords, $F(1,16) = 3.55$, $p = .08$, $\eta_p^2 = 0.18$, and piano chords, $F(1,13) = 3.95$, $p = .07$, $\eta_p^2 = 0.23$, indicating a stronger source on the right than on the left hemisphere. In the paradigm with long sinusoidal chords, there was a nearly significant stimulus effect, $F(2,32) = 3.10$, $p = .06$, $\eta_p^2 = 0.16$, indicating a tendency of weaker sources to minor chords compared to inverted major chords ($p = .07$). Figure 5 illustrates the N1 results in ERP waveforms, head figures as well as bars representing dipole source strengths in the two hemispheres.

Table 9. The mean amplitudes (μV) of the N1 responses to major, minor, and inverted major chords in the three paradigms and two groups, with standard deviations in parentheses (Study IV).

	Major	**Minor**	**Inverted major**
Short sinusoidal			
Musician group	-1.99(1.4)	-1.08(1.0)	-1.63(1.3)
Non-musician group	-1.25(1.0)	-.87(1.3)	-1.29(1.3)
Long sinusoidal			
Musician group	-1.50(1.2)	-.87(1.0)	-1.08(1.3)
Non-musician group	-.62(.7)	-.08(.8)	-.45(1.1)
Piano			
Musician group	-.90(1.1)	-.74(1.3)	-.90(1.1)
Non-musician group	-.81(.9)	-.77(1.2)	-.81(.9)

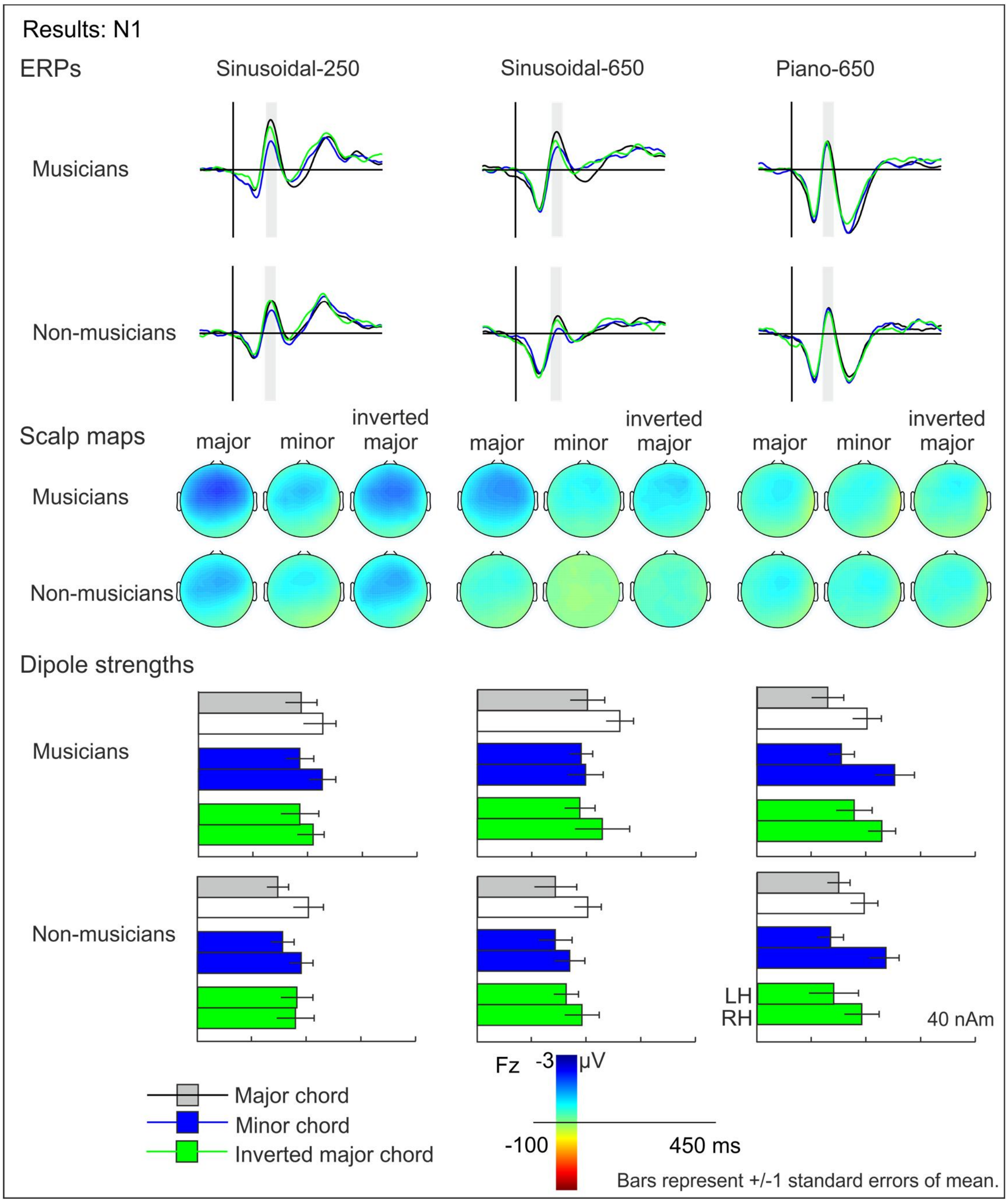

Figure 5. N1 results in Study IV. A. Group-averaged ERP waveforms elicited by standard and deviant stimuli in the three experimental paradigms on Fz electrode, with latency windows where the N1 mean amplitudes were calculated for statistical analyses marked with the grey-shaded bars. B. Scalp maps illustrating voltage distributions of N1 mean amplitudes. C. N1 dipole source strengths in the left and right hemispheres, with error bars indicating ±1 standard errors of mean.

4.4.2 Behavioural results

The Musician group detected minor chords and inverted major chords in the context of root major chords above chance both when the chords were comprised of sinusoidal tones and piano sounds. This was indicated as hit-rates differing statistically significantly from the chance level (in all $p < .01$). The Non-musician group detected minor chords in the context of root major chords above chance both when the chords were comprised of sinusoidal tones and piano sounds (in both $p < .01$), but inverted major chords were detected above chance only when the chords were comprised of sinusoidal tones ($p < .01$) and not when they were comprised of piano sounds ($p > .10$).

In ANOVA-R, performance was more accurate over groups when the chords were sinusoidal compared to piano chords, $F(1, 23) = 10.78$, $p < .01$, $\eta_p^2 = 0.32$, and in the minor chord detection task compared to the inverted major chord detection task, $F(1, 23) = 19.89$, $p < .001$, $\eta_p^2 = 0.46$, and the Musician group performed more accurately than the Non-musician group, $F(1, 23) = 46.88$, $p < .001$, $\eta_p^2 = 0.67$. Interaction of stimulus type (sinusoidal *vs.* piano) with chord type (minor *vs.* inverted major), $F(1, 23) = 5.42$, $p < .05$, $\eta_p^2 = 0.19$, and group, $F(1, 23) = 5.99$, $p < .05$, $\eta_p^2 = 0.21$, demonstrated that performance was more accurate with sinusoidal than piano chords only in the Non-musician group ($p < .001$) and only in the inverted major chord detection task ($p < .01$). Figure 6A illustrates the hit-ratios in the deviant chord detection task.

4.4.2.1 Relationship between ERPs and behavioural performance

Since performance in all parts of the deviant chord detection task strongly correlated with other parts, a combined performance score was calculated for overall behavioural performance by averaging the hit-ratios in the four parts of the task together, in order to study the relationships between behavioural performance and ERP amplitudes. Similarly, as both N1 and MMN amplitudes to minor chords and inverted major chords correlated with each other within the paradigms (Sinusoidal-650 and Piano-650), combined variables N1-Sinusoidal, N1-Piano, MMN-Sinusoidal, and MMN-Piano were calculated by averaging the N1s and MMNs to minor chords and inverted major chords on Fz electrode together. ERPs elicited in the Sinusoidal-250 paradigm were not compared to behavioural performance.

As described in Figure 6B, there was a correlation between overall behavioural performance and MMN amplitude to piano chords, as well as overall behavioural performance and N1 amplitude to sinusoidal chords, demonstrating increasingly negative (larger) MMN and N1 amplitudes with higher hit-ratio over groups, while MMN to sinusoidal chords or N1 to piano chords did not demonstrate statistically significant correlations with behavioural performance.

In the regression analysis with MMN and N1 amplitudes, a larger (increasingly negative) MMN amplitude to piano chords was associated with more accurate behavioural performance, b = -.15, t = -2.22, p < .05. When musicianship and its interactions with MMN and N1 amplitudes were added to the model, the association between MMN amplitude to piano chords and behavioural performance remained statistically significant, b = -.16, t = -2.23, p < . 05, and, additionally, musicianship was associated with better behavioural performance, b = 0.36, t = 4.76, p < .001. Musicianship moderated the association between MMN amplitude to piano chords and behavioural performance, b = 0.23, t = 2.21, p < .05, with group-wise correlations demonstrating that larger (increasingly negative) MMN amplitude to piano chords was associated with more accurate behavioural performance in the Non-musician group only, r = -.60, p < .05. N1 amplitudes to piano and sinusoidal chords and MMN amplitudes to sinusoidal chords were not statistically significantly associated with behavioural performance in either of the models (in all p > .05).

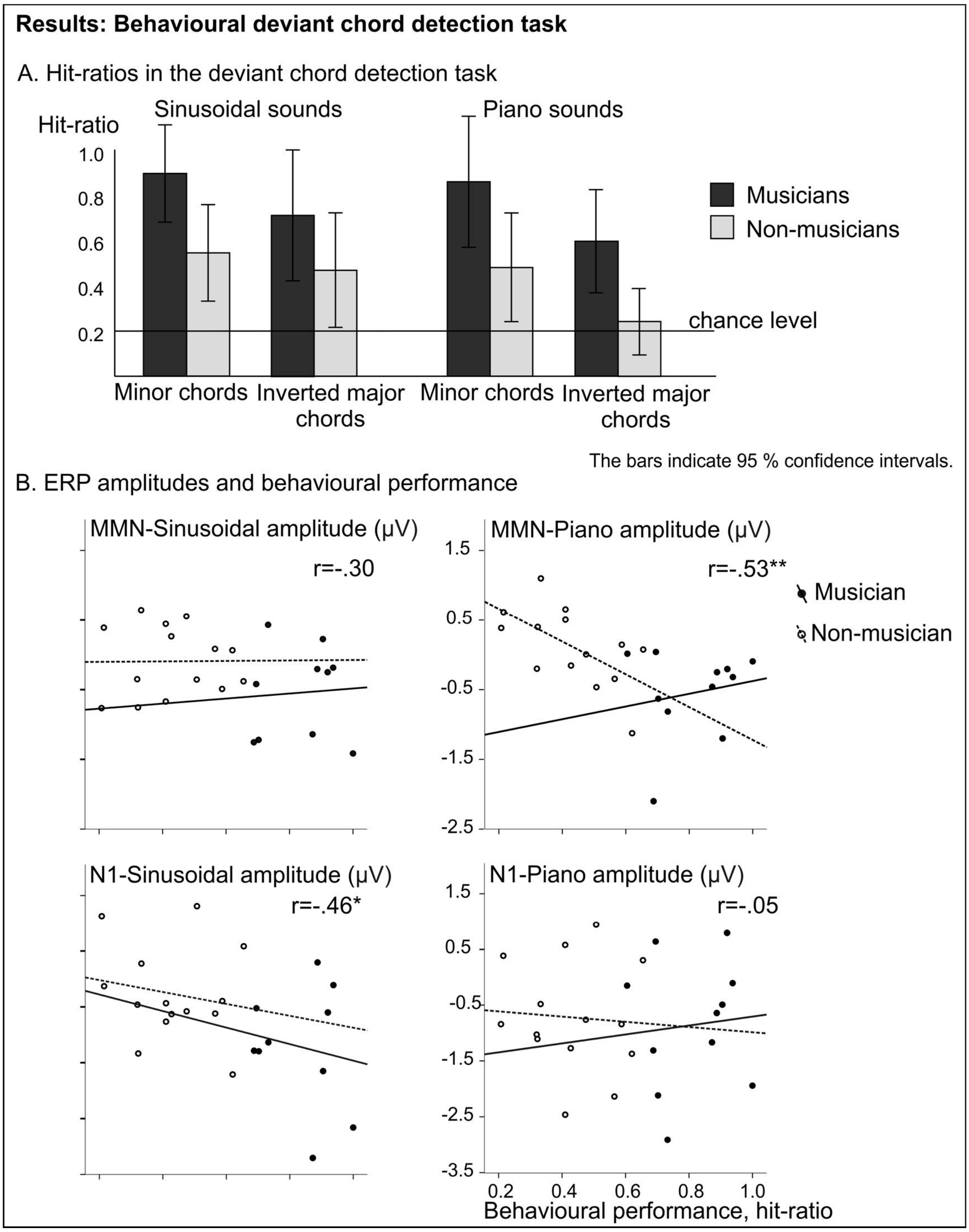

Figure 6. A. Results of the behavioural chord detection task in Study IV. Hit-ratios demonstrate hits-per-button-presses separately for each part of the task in musicians and non-musicians. B. Scatterplots demonstrating associations between ERPs and performance in the behavioural chord detection task. Correlations are calculated with groups pooled together.

5 Discussion

The aim of this thesis was to examine the processing of Western music chord categorisations major-minor, root-inversion, and consonant-dissonant in different age groups preattentively, as reflected by ERPs (Studies I-IV), and behaviourally in a deviant chord detection task (Study IV). Furthermore, the effect of music expertise on chord processing was examined (Studies II and IV). By studying the ERPs, especially the preattentive MMN evoked by the chord types, it was possible to employ the same method for studying adults, children as well as newborn infants with limited resources in terms of attention and control for behavioural responses. Moreover, the method allowed group comparisons between children and adults with *vs.* without music training, who may demonstrate differences in, e.g., attentional resources. To this end, a new MMN paradigm was developed, where the chord types were presented from various frequency levels, so that all individual frequencies in the deviants were also present in the standards, and an MMN in response to simple physical deviance was avoided. Additionally, the paradigm introduced the chords in random order, so that no harmonic context was elicited. This omits the possibility that ERPs related to violations of Western music harmony would be elicited (ERAN; see Koelsch et al., 2000).

Study I showed that major-minor and consonance-dissonance chord categorisations were evident in the brains of non-musician adults as evidenced by MMN elicitation, suggesting that these categorisations have been learned implicitly, without extensive amounts of formal music training. Study I demonstrated that the new chord paradigm was suitable for studying preattentive chord discrimination: MMNs were elicited by deviant chord types in the absence of new frequencies in the deviants, and this was interpreted as processing of the deviant *vs.* standard chord types as different stimulus categories.

Study II showed that while musically trained 13-year-olds elicited MMNs to minor chords in the context of root major chords, an age-matched group of children without music training did not. The group difference was evident in the right but not in the left electrode sites. Together with the results of Study I, the result indicates that music training can enhance and/or speed up the adoption of Western music chord categorisations. Unexpectedly, N2-like responses to standard major chords were smaller in the Music group compared to the Control group.

Study III introduced a tentative finding, that along with consonance-dissonance, major-minor chord categorisations can be evident in the brain of newborn infants as evidenced by MMRs, even though the auditory system of newborn infants is immature in many respects and the infants have minimal prior exposure to Western music. The polarities of the MMRs to dissonant and minor chords differed, indicating that they are differentially processed in the newborn brain. The result demonstrating early sensitivity to major-minor categorisation seems to contrast with Study II, where minor-MMN was not elicited in 13-year-olds without music training.

Study IV demonstrated MMNs to both minor and inverted major chords in the context of root major chords in musician adults, but no MMNs in non-musician adults. While the obtained group difference is similar to Study II with school-aged children, the results contrast with Study I where non-musician adults elicited minor-MMNs. A behavioural chord detection task also demonstrated superior performance in musicians, although it showed that even non-musicians could learn to discriminate the chord types from each other. While the chords were composed of sinusoidal tones in Studies I-III, Study IV introduced the chords with both sinusoidal tones and harmonically rich music sounds, demonstrating no differences in MMNs or behavioural detection accuracy between them. In one of the three paradigms, musicians demonstrated larger N1 amplitudes than non-musicians. A decrement of the N1 amplitude in response to minor compared to major chords was evident in both groups, suggesting possibly an early mode discrimination process. In the studies of the present thesis, adult musicians were the only group showing MMNs in response to inverted major chords in the context of root major chords, indicating that this categorisation may require extensive explicit training in order to appear in the preattentive level of auditory processing. Notably, results of the cognitive tests in Study IV demonstrated that the group differences were not attributable to superior general cognitive skills among the musicians.

Taken together, the present thesis adds to our understanding of processing complex, music-related auditory information in the developing brain and the effects of music expertise on it. It gives a thorough image of the preattentive processing of Western music chord types in different age groups with and without formal music training. The implications of the results are reviewed in detail below, where the results are discussed in relation to the hypotheses of the thesis. In section 5.1, the effects of music expertise on Western music chord processing are discussed, in light of the obtained evidence from adults and school-aged children. Section 5.2 focuses on Western music chord processing in the absence of formal music training, discussing the process of musical enculturation as well as early readiness for music processing. In section 5.3, the neural basis of Western music chords is re-visited based on the present results, with the aim to discuss the contributions of biology and culture in their processing. Finally, in sections 5.4 and 5.5, possible caveats and future considerations in the study design as well as interpretation of the results are discussed.

5.1 The effect of music expertise on Western music chord processing in adults and school-aged children

MMN was elicited in response to minor chords in the context of major chords in musician adults but not non-musician adults (Study IV) and musically trained children but not children without music training (Study II). While also the non-musicians of Study I demonstrated MMNs to minor chords, the musicians of Study IV were still the only group to demonstrate preattentive discrimination of inverted vs. root form chords. In line with the MMN results, behavioural discrimination of the chord types was more accurate in musician than non-musician adults (Study IV). Adult musicians demonstrated larger N1 amplitudes in response to chords compared to non-musicians in one of the paradigms of Study IV. The results confirm hypothesis 1 of the present thesis, suggesting facilitated neural and behavioural processing of Western music chord categorisations in musically trained individuals. On the contrary, two of the three paradigms of Study IV did not demonstrate group differences in N1 amplitudes. Furthermore, in Study II, the N2-like response to standard major chords was *smaller* in musically trained than non-trained children.

5.1.1 Musician adults

The present results of Study IV are in line with prior studies demonstrating enhanced sound discrimination in musicians both neurally and behaviourally (e.g., Fujioka et al., 2004; Koelsch et al., 1999). Regarding chord processing, larger MMNs have been demonstrated in musicians than non-musicians in response to mistuning in chords (Koelsch et al., 1999), as well as to minor chords in context of major chords (Tervaniemi et al., 2011). Still, in contrast to the present findings, an MMNm to minor chords was present in earlier studies also in the absence of music training (Tervaniemi et al., 2011), and even demonstrated a similar magnitude in musicians and non-musicians, indicating no effect of music expertise in such a central music sound discrimination (Brattico et al., 2009). Since only one example of major and minor chords is presented in the paradigm used in the aforementioned studies, deviant frequencies co-occur with deviant mode (minor) and compromise the interpretation of the obtained MMN as an index of mode discrimination (discussed in section 1.4.1). The results of Study IV suggest that in the absence of deviant frequencies in the deviant chord types, consistent preattentive discrimination of major *vs.* minor chords may require music expertise.

While both MMN and behavioural evidence demonstrated superior chord processing in musicians than non-musicians in Study IV, the results failed to demonstrate a correlation between MMN amplitudes and behavioural detection accuracy among the musicians, in contrast with previous findings (e.g., Amenedo & Escera, 2000). The lack of correlation may be attributable to a ceiling effect in the behavioural task, since almost all of the musicians demonstrated highly accurate chord detection.

The paradigm in the present thesis introduced chords comprised of sinusoidal tones in Studies I-IV. In addition, chords comprised of harmonically rich piano sounds were introduced in Study IV. Based on previous work, it was hypothesised that the superior processing in musicians compared to non-musicians would be pronounced with the harmonically rich piano sounds, since enhancement of sound processing in musicians has been seen especially when the sounds are familiar due to music training (e.g., from the musician's own instrument, Pantev et al., 2001b), music-related (Fujioka et al., 2004, 2005; Koelsch et al., 1999; Pantev et al., 1998, 2001a, b, 2003) or complex (Kaganovich et al., 2013; van Zuijen et al., 2005). In contrast, brain responses to simple sounds or categorisations do not always show differences as a function of music training (Fujioka et al., 2004; Pantev et al., 1998). The present study, however, demonstrated similar group differences, and, in general, similar results, in neural and behavioural discrimination of chord types with sinusoidal tones versus harmonically rich piano sounds. Possible explanations for the result are further discussed in section 5.3.3.

In Study IV, N1 amplitude was larger in musicians than non-musicians in one of the three paradigms, the one with long sinusoidal chords, while two of the three paradigms, the one with short sinusoidal chords and the one with piano chords, demonstrated no group differences in N1 amplitude. Larger N1 amplitudes in response to sounds have been demonstrated in musicians compared to non-musicians (N1m in Kuriki et al., 2006, Pantev et al., 1998, 2001b; sub-component N1c in Shahin et al., 2003; N1 in Baumann et al., 2008, Kaganovich et al., 2013). There are also contrasting results, demonstrating no differences in N1m responses between musicians and non-musicians (Lütkenhöner et al., 2006). While it seems that the obtained group differences largely depend on the type of stimulation (for example on their music-relatedness or complexity, reviewed in section 1.2), it remains unclear why the long sinusoidal chords did and the short sinusoidal chords or the most musical piano chords did not demonstrate enlarged N1 amplitudes in musicians compared to non-musicians in the present study. Physical differences between the stimuli in the different paradigms could explain the different results. Still, since the results between the paradigms are inconsistent, the group difference or absence of it should be interpreted with caution. A more systematic comparison between musicians and non-musicians in several ERP components in terms of both amplitude and latency should be conducted in the future, in order to put in context the various prior results and to examine the differences between them. For example, also the P2 response has been suggested to be modified by music training (Kuriki et al., 2006; Seppänen, Hämäläinen, Pesonen, & Tervaniemi, 2012; Shahin et al., 2003, 2005), already in childhood (Shahin et al., 2004; Trainor et al., 2003b).

5.1.2 School-aged children

The results of Study II are in line with prior studies, demonstrating larger change-related ERPs in musically trained compared to non-trained children in response to deviations in complex and/or music-related sound stimuli (e.g., Magne et al., 2006; Meyer et al., 2011; Moreno et al., 2009; Putkinen et al., 2014b). Particularly, a recent study showed larger MMNs in children with music training compared to children without music training in response to minor chords in the context of major chords (Putkinen et al., 2014b). However, the oddball paradigm in the study was simpler than in the present study, and also demonstrated MMNs to minor chords in children without music training.

In Study II, the group difference in MMN amplitudes was present in the right but not in the left electrode sites, while there was no evidence of hemispheric differences in MMN amplitudes over groups or separately in the Music group. The adult brain generally demonstrates lateralisation of music sound processing to the right hemisphere (Tervaniemi & Hugdahl, 2003; Zatorre et al., 2002). On the other hand, in adult musicians, left auditory areas seem to have a pronounced role in music processing (Tervaniemi et al., 2011; Vuust et al., 2005). In the future, the differences in lateralisation of music sound processing between musically trained and untrained children should be studied with methods better suited for spatial analysis (for example MEG or fMRI instead of EEG; Luck, 2005). The lateralisation of chord processing is further discussed in section 5.3.2.

Furthermore, the decreased N2-like response to standard major chords in the Music group compared to the Control group is in contrast with prior work that has demonstrated larger early ERPs in children with music training compared to children without music training (Fujioka et al., 2006; Shahin et al., 2004; Trainor et al., 2003b). Particularly, Fujioka and colleagues (2006) showed that in 4–6-year-old children, N250m in response to violin sounds, comparable in latency to the N2-like response in Study II, had a greater amplitude and earlier latency in those children who participated in Suzuki music training compared to children without any music training. The authors proposed that the result could be attributable to involuntary attention switch in the musically trained children towards the musically relevant stimuli, and/or to a general enhancement of auditory skills due to music training (since prior studies have shown that N2 in children correlates with behavioural measures of auditory skills, see, e.g., Cunningham, Nicol, Zecker, & Kraus, 2000).

The children in the study by Fujioka and colleagues (2006) were, however, only 4–6 years old, while Study II introduced results of 13-year-olds. A growing body of evidence shows that N2 amplitude generally decreases with age (Cunningham et al., 2000; Enoki et al., 1993; Fujioka et al., 2006; Johnstone et al., 1996; Ponton et al., 2002; Ponton et al., 2000; Sussman et al., 2008). A possible explanation for smaller N2 amplitude in the Music group than the Control group in the present study may thus be attributable to more mature ERP morphology in children with music training compared to children without music training. In a study of 2–3-year old children, a smaller LDN response to deviances in basic sound features was associated with more frequent engagement in informal music activities, and it was interpreted as more mature processing in these children, since LDN typically vanishes with maturation (Putkinen et al., 2013b; see also Shahin et al., 2004). However, this hypothesis of faster ERP maturation in children due to music training awaits further research.

The unexpected group difference in Study II may also be attributable to superior attention skills of the musically trained children, enabling them to more intensely concentrate on the given task (watch the movie, ignore the sounds), since music training has been associated with increases in cognitive functions (Schellenberg, 2004). Since the N2 response may be related to attention switching (as hypothesised by Fujioka et al., 2006), the larger N2-like response in the Control group than the Music group children may be related to greater distractibility in the Control group children. Karhu and colleagues (1997), on the other hand, demonstrated that the N2 amplitude was enhanced in school-aged children when an identical stimulus was repeated. The authors hypothesized that this sensitisation to repeating stimulus may reflect the build-up of a neuronal representation. In the present Study II, the larger N2 amplitude in the Control group children could thus be interpreted as a developing neuronal representation of the standard root major chord. While the root major chord was already highly familiar to the Music group children, no such enhancement of the N2 response was seen in the Music group.

It is also noteworthy that in the present Study II, the N2-like response was calculated from the standard waveform from the same latency window as the MMN response. It is thus possible that the apparent group difference in MMN elicitation is attributable to a smaller N2 response to standard chords in the Music group compared to the Control group, but a similar-amplitude N2 response to minor chords in the two groups.

Rather problematically, both enlarged responses and smaller responses can thus be interpreted as enhanced processing in musically trained compared to non-trained children, and reasons for differential results between studies are poorly understood. To conclude, while differences in early auditory processing between children with and without music training are often found, understanding the neurocognitive basis of these differences requires further research.

5.2 Music processing and its development in the absence of formal music training

In the complex stimulation paradigm of the present studies, participant groups with minimal amounts of formal music training demonstrated only weak evidence of preattentive or attentive discrimination of Western music chord types. School-aged children with no music training in Study II and the carefully-screened non-musician adults in Study IV demonstrated no MMN responses to minor or inverted major chords in the context of root form major chords. In contrast, non-musician adults in Study I did demonstrate MMNs to minor chords as well as highly dissonant chords. The discrepancy of the results may be attributable to the larger amounts of formal music training in the non-musicians of Study I than Study IV. Even though the non-musician adults in Study IV showed no evidence of MMN elicitation, they did demonstrate above-chance performance in the deviant chord detection task, suggesting that they could learn to detect minor and, to some extent, inverted major chords from the context of root form major chords. The newborn infants in Study III demonstrated MMRs to dissonant chords and tentatively to minor chords, suggesting an early readiness to discriminate between Western music chord types. The results partly confirmhypothesis 2 of the present thesis: They demonstrate moderate readiness for Western music chord processing in non-musician adults, attributable to maturation and/or musical enculturation. Furthermore, the results show evidence of consonance-dissonance categorisation and, tentatively, also major-minor categorisation, already at birth.

5.2.1 On the "musical infant"

The newborn infants of Study III demonstrated preattentive sensitivity to both consonant-dissonant and major-minor chord categorisations, as evidenced by MMR elicitation on one or more of the analysed electrode sites. While the MMR in response to minor chords was negative in polarity, the MMR in response to the highly dissonant chords had a positive polarity. The MMR in response to highly dissonant chords was statistically significant in two frontal electrode sites, in line with the spatial distribution found in previous MMN/MMR studies (Cheour et al., 2000; Kujala et al., 2007). In contrast, the MMR in response to minor chords was only statistically significant in one parietal electrode site. Furthermore, while sensitivity to dissonance has been demonstrated previously in infants (Perani et al., 2010; Schellenberg & Trainor, 1996; Zentner & Kagan, 1998), sensitivity to mode is a more novel finding. Thus, the MMR in response to the minor chords introduces pioneering, tentative evidence of sensitivity to major *vs.* minor chord structures in the newborn auditory system. Before similar results are obtained in other studies, the implications of this finding should be discussed with caution.

It is noteworthy that in the present paradigm, in order to extract the deviant stimuli from standard stimuli, the auditory system of the infant has to categorise the stimuli based on their interval structures, i.e., the relative relationships between simultaneously played notes. This requires processing of transpositions, since the chords vary in absolute frequency. The present results are in line with prior work, demonstrating newborn infants' sensitivity to both simple physical deviations (Alho et al., 1990; Kushnerenko et al., 2001) and violations of abstract rules (Carral et al., 2005; Ruusuvirta et al., 2003, 2004; Stefanics et al., 2007; Winkler et al., 2003) in the sound stream. More specifically, the results support the hypothesis that newborn infants are capable of processing relative sound properties (Stefanics et al., 2009; Tew et al., 2009). All of these early auditory skills are important for perception of both music and language. While the chord stimuli of the present paradigm are central in Western music, the question remains whether the categorisation of chord types requires music-specific skills or, rather, more general complex auditory skills.

Furthermore, the mechanism of this early readiness is left unknown. There is evidence of foetal auditory learning, reflected as enhanced ERPs after birth to sounds heard in utero (Partanen et al., 2013). This suggests that prenatal exposure to Western music may have contributed to the elicitation of the MMRs in Study III. On the other hand, newborn infants demonstrate statistical learning in speech segmentation, i.e., they are able to group syllables into words based on their tendency to appear together in a syllable stream after only 15 minutes of exposure to the words (Teinonen, Fellman, Näätänen, Alku, & Huotilainen, 2009). Thus, comparing ERPs in the first and last part of the 30-minute-long EEG experiment of Study III may have revealed appearance of MMRs during the experiment – indicative of rapid acquisition of the rules and regularities of the chords' interval structures, rather than a predisposition to discriminate between them. Finally, these early sensitivities to Western music chord categorisations can also be attributable to biological predispositions to music (as proposed by Hannon & Trainor, 2007). Particularly the sensitivity to dissonance has been suggested to serve as a predisposition for music processing (Hannon & Trainor, 2007). The possible biological underpinnings of Western music chord categorisations are discussed in detail in section 5.3.1.

5.2.1.2 Interpreting the newborn ERPs to Western music chords

In Study III, the repetitive standard major chords presented to newborn infants elicited a response pattern with a negative peak around 20–120 ms post-stimulus followed by a broader positive peak around 300 ms post-stimulus. While the negativity was more pronounced in the fronto-central electrode sites, the positivity had a more parietal distribution. The positivity around 300 ms is typically seen in newborn infants, however on fronto-central rather than parietal electrode sites (Barnet et al., 1975; Kushnerenko et al., 2002a; Trainor, 2008a; Wunderlich & Cone-Wesson, 2006; Wunderlich et al., 2006). In contrast, the early negativity has been reported in very few earlier studies (e.g., in response to clicks but not tones at 5 weeks: Little, Thomas, & Letteman, 1999). The infant ERP waveform varies a lot between studies, and the functional role of its components is not well understood.

Furthermore, the MMR elicited by minor chords had a negative polarity, while the MMR in response to dissonant chords was broad and positive. Prior studies have demonstrated that MMRs at birth may vary in polarity for several possible reasons (e.g., He et al., 2007, 2009; Trainor, 2012). For example, it has been suggested that maturational differences (Leppänen et al., 2004) or differences in the state of alertness (awake or asleep, Friederici et al., 2002) may account for inter-individual variability in MMR polarity. In the present study, however, positive and negative MMRs were elicited in the same infant group in the same measurement. The different-polarity MMRs in the present study may still be attributable to stimulus-specific maturational differences in ERPs (proposed by Trainor, 2008a), and/or different cortical origins of the MMRs to different deviant types (as suggested by He et al., 2007; Trainor, 2012).

The MMR elicitation in response to minor chords in newborn infants seems to contrast with the absence of MMNs to minor chords in school-aged children without music training in Study II and non-musician adults in Study IV. If the underlying neural processes and function of the infant-MMR are similar to those of child- and adult-MMNs, the results could be interpreted as a disappearance of the sensitivity to these chord categorisations with maturation. This interpretation is, however, in contrast with previous studies demonstrating that exposure to Western music during development facilitates its processing (e.g., Demorest et al., 2008; Morrison et al., 2008). Although Western infants may demonstrate equal or even more accurate processing of music than Western adults in some occasions, this has only been shown when the changes in music do not violate the structures of Western music, or the structure of the music is unfamiliar to Western listeners (Hannon & Trehub, 2005a, 2005b; Lynch et al., 1990; Trainor & Trehub, 1992). In these occasions, Western adults tend to be biased by their experience with Western music, while infants tend to process the music in a more universal manner and demonstrate readiness to learn any music system.

A possible explanation for the discrepancy between the results may be that the infant-MMR reflects a different neural process than the mature MMN (as suggested by Trainor et al., 2003a). More research is needed in order to better understand what the infant-MMR reflects and how it relates to the adult MMN. For now, the interpretation of MMR elicitation in Study III is restricted to an index of implicit, preattentive capacity to differentiate between the chord categories, since they elicit different patterns of brain activity. Finally, while in adults the MMN responses are at least moderately associated with behavioural discrimination accuracy (Amenedo & Escera, 2000; Horváth et al., 2008; Näätänen et al., 1993; Novitski et al., 2004; Tiitinen et al., 1994), as demonstrated also in the Non-musician group of the present Study IV, the question of how electrophysiological reactions translate into cognitive processes – the mind-body problem – is especially difficult to answer in the case of newborn infants, who are largely unable to give behavioural responses.

5.2.2 On the “musical non-musician”

MMNs were elicited by minor chords and highly dissonant chords in non-musicians of Study I, in line with several previous findings demonstrating implicit music knowledge in non-musicians (Koelsch et al., 2000; Trainor et al., 1999; 2002a). For example, change-related ERPs were elicited in non-musicians in response to violations in musical contour and interval size (Trainor et al., 1999; 2002a), and Western music syntax in a chord cadence (Koelsch et al., 2000).

In contrast with these findings, no MMNs were demonstrated in the non-musicians of Study IV. Even though neither the participants of Study I, nor the non-musicians of Study IV included professional musicians, half of the participants in Study I reported having formal music training, while in Study IV no participant had more than 2 years of formal music training and only two of 14 one year or more. Rapid plasticity in the brain as well as learning effects are known to take place after short training periods both in children (Hyde et al., 2009) and adults (Lappe, Herholz, Trainor, & Pantev, 2008; Seppänen et al., 2012). Furthermore, not only musicians but also amateur musicians demonstrate facilitated processing of music when compared to non-musicians (Tervaniemi, Castaneda, Knoll, & Uther, 2006). These results suggest that even informal music activities or only a few months or years of formal music training, possibly especially during the sensitive period in childhood, can have effects on auditory processing. Thus, the preattentive major-minor chord categorisation demonstrated in the non-musicians of Study I could be attributable to the most presumably higher average amount of formal music training compared to the non-musicians of Study IV, rather than merely implicit adoption of Western music structures. Unfortunately, however, there is no detailed data available on the years of music practice of the participants in Study I.

Despite the absence of MMN responses, the non-musicians in Study IV showed above-chance performance in behavioural detection of the chord types, suggesting that also non-musicians with near to no formal music training in the past are able to learn complex music-related categorisations. In the behavioural chord detection task, a non-verbal teaching part preceded the test part, and the task description did not include musical terms. In this way, non-musicians were able to become familiar with the sound material prior to testing, and the instructions did not postulate understanding of music theory.

Furthermore, a decrement of the N1 response to minor compared to major chords in both musicians and non-musicians in Study IV, consistently in both paradigms with sinusoidal chords, suggests similarities in chord processing between the groups. The results indicate differences in the neural activity elicited by minor vs. major chords, which could be interpreted as a low-level, preattentive auditory discrimination process. In contrast with the present results, smaller N1 amplitudes to standard compared to deviant stimuli are generally expected due to neural refractoriness effects, when the response to the repeating standard stimulus attenuates more than the response to the occasional deviant (Näätänen & Picton, 1987). Neural refractoriness effects are, however, unlikely to appear in the present paradigm, since all the frequencies in the deviants are already present in the standards and thus no simple physical deviance is introduced in the deviant chord types. To conclude, the decrement of the N1 amplitude in response to minor chords in Study IV is an unexpected finding, awaiting further research.

In sum, even though MMNs were not elicited in adults (Study IV) and children (Study II) with no music training in the complex context of the present paradigm, the above-chance behavioural detection of the chord types, and, possibly, the N1-decrement to minor chords, indicate moderate readiness to process the chord categorisations at least in adults. In order for the chord categories to be consistently neurally encoded as discriminate sound objects, explicit training may still be required.

5.3 The neural basis of Western music chord processing

"Music is built on general, universal features of human sound processing that have deep evolutionary roots." – Laurel Trainor, 2008, Nature

The results of the present thesis demonstrate, on one hand, an early sensitivity to central Western music chord categorisations in the newborn brain, and, on the other hand, facilitated Western music chord processing in children and adults who have extensive amounts of formal music training. In the non-musicians of Study I, dissonant chords elicited larger MMNs than minor chords, suggesting that the dissonant chords introduced larger deviance than minor chords in the chord context (Jaramillo et al., 2000). In the newborn infants of Study III, dissonant chords elicited broad positive MMRs, while the MMRs to minor chords were of negative polarity, suggesting that the consonance-dissonance and major-minor categorisations were differentially encoded in the auditory system of infants. Finally, extensive training may even be a necessity in preattentive discrimination of root and inverted forms of chords, as evidenced by MMNs to chord inversions in musicians only.

As discussed in the previous section, the present results of sensitivity to high levels of dissonance already at birth (Study III) and in non-musicians (Study I) are in line with hypothesis 2 of the present thesis, while the inconclusive evidence of major-minor chord categorisation in children and adults without formal music training partly contrasts with it. These results are reviewed below in relation to previous research on Western music chord categorisations. Regarding the neural basis of Western music chords, partly in contrast with hypothesis 3, the results demonstrate only weak evidence of pronounced chord processing in the right hemisphere, and no evidence of music expertise changing the right-dominant pattern of lateralisation. Furthermore, in contrast with hypothesis 4, no evidence of facilitated processing of chords composed of harmonically rich music sounds compared to sinusoidal tones was obtained. Possible explanations for these results are discussed in the following sections.

5.3.1 Western music chord categorisations – contributions of biology and culture

In line with the present results, prior findings have demonstrated sensitivity to dissonant versus consonant interval structures even in non-human species (Fishman et al., 2001; Izumi, 2000; Watanabe et al., 2005), as well as in human newborn infants (Perani et al., 2010; Schellenberg & Trainor, 1996; 2002b; Zentner & Kagan, 1998). The present results verify and extend the findings of previous behavioural and brain studies in infants, providing evidence of neonatal sensitivity to consonant *vs.* dissonant interval structures in a varying sound context, in the absence of other acoustic cues like novel frequencies that could contribute to the MMR elicitation.

As described in section 1.4.2, sensory dissonance is rooted in the low levels of the auditory nervous system (Bidelman & Krishnan, 2009; Tramo et al., 2001). In music, dissonance is a complex and relative concept that has changed in the course of music history (Rossing et al., 2002). Conceptual distinction between sensory and musical dissonance is central in interpreting the present results, which apply only for high levels of sensory dissonance (Terhardt, 1984). Also, while there is evidence of discrimination of dissonance from consonance, preference of consonance across species or cultures is a more controversial topic, outside the scope of this thesis (for infant results, see Crowder et al., 1991, Masataka, 2006, Plantinga & Trehub, 2014, Trainor & Heinmiller, 1998, Trainor et al., 2002b, Zentner & Kagan, 1998; for animal results, see Chiandetti & Vallortigara, 2011, McDermott & Hauser, 2004; for cultural comparisons, see Butler & Daston, 1968, Fritz et al., 2009, Koelsch et al., 2006, Maher, 1976).

While the minor-MMR elicitation in newborn infants should be interpreted with caution, MMNs to minor chords were consistently seen only in children and adults with formal music training in the present thesis. Indeed, even though it seems that discrimination between major versus minor mode should be familiar to all people in Western culture, previous studies have shown that without other emotional cues, even discrimination of major from minor melodies may be difficult for non-musicians (Halpern et al., 1998; 2008; Leaver & Halpern, 2004).

A large body of evidence however demonstrates that Western music modes have contrasting emotional connotations to Western non-musicians (Crowder, 1985a; Hunter et al., 2010; Pinchot Kastner & Crowder, 1990; Khalfa et al., 2005), and that major and minor mode music activate different emotion-related brain areas in Western individuals (Green et al., 2008; Khalfa et al., 2005; Mitterschiffthaler et al., 2007; Pallesen et al., 2005). MMN studies have demonstrated mode discrimination in non-musicians, although in simpler experimental paradigms than in the present thesis (Brattico et al., 2009; Putkinen et al., 2014b; Tervaniemi et al., 2011). In line with these findings, sensitivity to mode was seen also in the present studies in newborn infants' minor-MMRs, non-musician adults' minor-MMNs in Study I, as well as in the behavioural detection and N1-decrements in non-musicians of Study IV.

While the musician adults in Study IV demonstrated MMNs of similar amplitude in response to minor and inverted major chords, the behavioural detection of minor chords was more accurate than the detection of inverted major chords in both musicians and non-musicians. Moreover, above-chance detection of inverted major chords was consistently seen only in musicians. Furthermore, while minor chords elicited MMNs/MMRs in infants, children, and adults, inverted major chords elicited MMNs in adult musicians only. The results seem to support the central role of mode in Western tonal music for Western listeners. While inversions are typical in Western music, they still retain the chords' mode, employing more subtle changes in the chord than mode change. Furthermore, these results suggest that while many skills to process music develop even in the absence of formal music training, the acquisition of consistent neural representations of complex categorisations like inverted versus root forms of chords may require extensive amounts of training and, possibly, explicit knowledge of the categorisations.

5.3.2 Chord processing in the hemispheres: weak evidence of lateralisation to the right

The spatial distribution and, particularly, hemispheric lateralisation, of ERPs was analysed in Studies II-IV of the present thesis in order to examine whether the brain responses to chord stimuli demonstrate lateralisation to the right hemisphere, typically seen in music processing (Tervaniemi & Hugdahl, 2003; Zatorre et al., 2002), and to study possible differences between musically trained and non-trained groups, suggested in prior studies (Tervaniemi et al., 2011; Vuust et al., 2005).

In school-aged children of Study II, the difference between the Music and Control group in MMN amplitude was only evident in the right and middle electrode sites, and not in the left. The MMNs were, however, not statistically significant (or visible) in the Control group, and there were no differences between right and left electrode sites in the Music group in the post hoc comparisons. The presence of the group difference in the right hemisphere alone may be attributable to several factors, for example a non-significant tendency for more negative amplitudes in the Control group in the left hemisphere compared to the right hemisphere, or larger inter-individual variability in the amplitudes in the left hemisphere compared to the right hemisphere. Without additional evidence, these results and their relationship to lateralisation of music sound processing in the brain of musically trained and non-trained children is left unclear.

In Study IV, source analysis of N1 responses demonstrated a non-significant tendency for stronger dipole strengths in the right than in the left hemisphere in all the three experimental paradigms in adult musicians and non-musicians. The present results are in line with prior studies demonstrating a right-hemispheric dominance in processing music sounds (Tervaniemi & Hugdahl, 2003; Zatorre et al., 2002), while they contrast with findings emphasizing the role of the left hemisphere in music processing of musically trained individuals (Bever & Chiarello, 1974; Johnson, 1977; Peretz & Morais, 1979; Tervaniemi et al., 2011; Vuust et al., 2005).

To conclude, while the results offer weak evidence of lateralisation of chord processing to the right hemisphere, no differences in lateralisation based on music expertise are demonstrated. The MMN analyses in Studies II and IV failed to demonstrate differences between left and right electrode sites, while, for example, MMN to a mistuned chord was right-lateralised in a previous study (Garza Villarreal, Brattico, Leino, Ostergaard, & Vuust, 2011). In the future, methods with higher spatial resolution should be employed to study the spatial distribution of the brain activity elicited by Western music chord types in different age groups, in order to further analyse the hemispheric lateralisation and how development and music expertise may affect it.

5.3.3 No evidence of facilitated processing of harmonically rich music sounds?

In the present Study IV, no difference in MMN amplitude was seen between harmonically rich music sounds and sinusoidal tones, nor was there a statistically significant interaction effect between stimulus type and group. The behavioural discrimination accuracy was facilitated when the chords were comprised of sinusoidal tones instead of harmonically rich piano tones, however only in non-musician adults and only in the inverted major chord detection task. These results are in contrast with several previous studies, demonstrating facilitated processing of harmonically rich sounds versus sinusoidal tones independent of music training neurally (Novitski et al., 2004; Shahin et al., 2005, 2007; Tervaniemi et al., 1993, 2000a) and behaviourally (Tervaniemi et al., 2000a). Also, they contrast with evidence showing that musical training particularly facilitates processing of musically relevant material, familiar to musicians (Fujioka et al., 2004, 2005; Koelsch et al., 1999; Pantev et al., 1998, 2001a, b, 2003).

The results may be attributable to the fact that chords composed of both sinusoidal tones and harmonically rich sounds are rather complex and musical in the present paradigm, as is the nature of the categorisation (deviant chord structure, rather than deviance in a basic auditory feature like frequency). This is different from previous studies, where frequency discrimination has been studied with single sinusoidal tones versus sinusoidal tones with added harmonic partials (Tervaniemi et al., 1993, 2000a).

Only in non-musicians and only with chords composed of harmonically rich music sounds, a larger MMN amplitude was associated with superior general performance in the behavioural chord detection task, in line with prior studies (Amenedo & Escera, 2000; Novitski et al., 2004). Since statistically significant MMNs were not elicited in the Non-musician group, the obtained association may suggest that a subgroup of the non-musicians elicited MMNs and performed above group average in the behavioural task. Alternatively or at the same time, this result indicates possibly greater consistency between behavioural performance and neural representations when the sounds are harmonically rich music sounds than when they are sinusoidal tones, attributable to higher salience or relevance of harmonically rich music sounds compared to sinusoidal tones.

5.4 Possible caveats in the studies

While the strengths of the present thesis lies in the carefully controlled experimental paradigm and wide age range of the participants, some possible caveats remain in the methodology of the studies. Particularly in Study II, the sample sizes are relatively small (less than 15 participants in each group), and additionally it was only possible to design a 10-minute-long paradigm due to the other paradigms that were presented as part of the EEG recording of the longitudinal study, leading to rather small amounts of data. Also, although the Control group children also had some adult-guided extracurricular hobbies, these activities were less frequent and less time-consuming than the instrument practice in the Music group, included in the curriculum of their elementary school. Some additional caveats related to the music background of the participants and the cross-sectional setting of the present thesis are further discussed below. The properties of the experimental paradigm are discussed in the following section.

5.4.1 Music background of the participants

A limitation in how much is known about the music background of the participants and how it should be taken into account remains a restriction in all of the present studies. First, the non-musicians in Study I are not optimally recruited, since the only criterion for them was that they are not professional musicians. In Finland, instrument training is a rather typical activity in childhood, and in this sample, half of the participants had had formal music training during their childhood or adulthood. There is no detailed information available on the amount or intensity of this training in the participants of Study I. Thus, it is left open whether the obtained minor-MMNs are due to implicit exposure or explicit training.

Second, in Study IV, the non-musicians were carefully screened, and only 2 of 14 had even a small amount of formal music training several years ago. Still, they reported varying levels of informal music activities (section 3.1.1, Table 3). Furthermore, in Study II, there is no information available on the informal music activities of the Control group children. Not only extensive formal music training but varying amounts and types of music-related activities can have effects on the brain level (Putkinen, Saarikivi & Tervaniemi, 2013a; Putkinen et al., 2013b; Tervaniemi et al., 2006). Even short periods of music training during the sensitive period in childhood may lead to long-lasting effects in the brain, visible in adults who consider themselves non-musicians (Skoe & Kraus, 2009). For most Western adults, music listening is the most important contact to music, but not much is currently known about how music listening affects the brain responses to music. In the present Study IV, participants both in the Musician group and in the Non-musician group reported listening to music on a regular basis. Choosing the participant inclusion and exclusion criteria in studies comparing (professional) musicians and non-musicians is complicated, and may significantly affect the obtained results (for a related review, see Margulis, 2008).

Third, importantly and unfortunately, there is no information available on the music background of newborn infants in Study III. Recent work has shown that foetal exposure to music has effects on post-natal auditory processing (Partanen et al., 2013). In the participant group of Study III, inter-individual differences in the amount of prenatal exposure to music may be evident, and the results might even be solely explained by a sub-group of infants with extensive prenatal music exposure and, due to that, large MMRs to the chord deviants. The future challenge for neuroscience of music is acknowledgement of music background in all its forms and the examination of its correlations to musical abilities and auditory skills as well as brain structure and function.

5.4.2 Effects of music training or pre-existing differences?

In the present thesis, the effects of formal music training are studied with cross-sectional evidence from two different age groups. This compromises any interpretations of causal effects of music training, since pre-existing differences between individuals who begin instrument training and individuals who engage in different types of activities may explain the obtained group differences. For example, it has been recently demonstrated that cognitive abilities and personality traits (Corrigal, Schellenberg, & Misura, 2013), together with inherited properties (Mosing, Madison, Pedersen, Kuja-Halkola, & Ullén, 2014), would to a large extent explain individual differences in musical abilities, who will engage in music training, and how long the training continues. Importantly, in Study IV of the present thesis, psychological tests did not demonstrate facilitated cognitive abilities in musicians compared to non-musicians. However, psychological tests were not included in the large longitudinal study of school-aged children that the present Study II was part of, and thus there is no information available on the cognitive abilities of children with *vs.* without music training.

Many longitudinal and intervention studies demonstrate facilitated auditory processing in children beginning music training (Hyde et al., 2009; Putkinen et al., 2014b), even when the children are randomly assigned to music practice or some other activity (Chobert et al., 2014; Moreno et al., 2009), as well as training effects in adults (Lappe, Herholz, Trainor, & Pantev, 2008; Lappe, Trainor, Herholz, & Pantev, 2011). In fact, the present Study II presents cross-sectional data of the children in the longitudinal study by Putkinen and colleagues (2014b). Thus, based on the analyses of Putkinen and colleagues (2014b), it is known that the 13-year-old children with *vs.* without music training in Study II did not differ in their ERPs to several auditory stimuli at baseline (age 7). Also, the brain changes in musicians are shaped according to the special requirements of their instrument (Bangert & Schlaug, 2006; Elbert, Pantev, Wienbruch, Rockstroh, & Taub, 1995; Geiser, Sandmann, Jäncke, & Meyer, 2010; Nager, Kohlmetz, Altenmüller, Rodriguez-Fornells, & Münte, 2003; Pantev, Roberts, et al., 2001), choice of music genre (Tervaniemi, Rytkönen, Schröger, Ilmoniemi, & Näätänen, 2001; Tervaniemi et al., 2006, 2014; Vuust, Brattico, Seppänen, Näätänen, & Tervaniemi, 2012), and practice styles (Seppänen, Brattico, & Tervaniemi, 2007). The magnitude of these effects is related to the amount of instrument training (Amunts et al., 1997; Bangert & Schlaug, 2006; Bengtsson et al., 2005; Nikjeh, Lister, & Frisch, 2008; Schneider et al., 2002), as well as onset of music practice (Elbert et al., 1995; Imfeld, Oechslin, Meyer, Lönneker, & Jäncke, 2009; Pantev et al., 1998; Schlaug, Jäncke, Huang, Staiger, & Steinmetz, 1995).

Taken together, these studies strongly suggest that the differences in brain function and auditory processing associated with music training are largely due to the training. This is particularly likely in the present thesis, where the presented auditory stimulation was highly relevant in Western music and thus belongs to the core area of musicians' training and expertise. Still, a longitudinal study would have made it possible to study maturational effects on the ERPs in the present thesis.

5.5 Paradigm development: novelty value and future considerations

The aim of this thesis was to test the newly developed, carefully controlled oddball paradigm. In the paradigm, three main issues were considered. First, no new frequencies were present in the deviants compared to the standards, so that only the interval structure would vary between chords, and an MMN response to a simple physical deviance would be avoided. Because each chord type was transposed to several frequency levels, the interval structures in general and not the certain specific transpositions were studied. Second, all possible transpositions within an octave were introduced as standard major chords, and several transpositions were introduced as deviant chords, presented in pseudo-random order with at least one standard after a deviant chord. This omits the possibility that a harmonic context emerges, and thus the elicitation of ERPs related to processing of music harmony (ERAN, see Koelsch et al., 2000). Third, single chord transpositions, whether standard or deviant, had approximately the same, small presentation probability in the oddball paradigm (see Table 5, p. 45). Taken together, these properties of the paradigm minimise the contribution of neural refractoriness effects in the obtained MMN responses (May & Tiitinen, 2010). Notably, while the probabilities of standard and deviant chord types vary somewhat between the four studies of the present thesis (approximate standard probabilities between 70 and 80% and deviant probabilities per deviant type between 7 and 15%), all of them should be sufficient for obtaining reliable MMN responses (Sinkkonen & Tervaniemi, 2000). A few future considerations for further developing the paradigm are reviewed below.

5.5.1 Choosing the chord types

The original idea of the new paradigm developed in the first study of this thesis was to introduce inverted major chords in the paradigm as a deviant interval structure without a deviant mode. It was considered that the inverted major chord, where one of the notes of the root major chord is transposed to an adjacent octave, introduces an even larger interval structure difference when compared to root form major chords as does the minor chord, where one note differs from the root major chord only by one semitone, the smallest possible frequency difference in Western tonal music. Later on, it was acknowledged that due to the upper harmonics and complex relationships between them, minor chords are actually considered more dissonant than root or inverted major chords by a Western listener (Helmholtz, 1885/1954; Roberts, 1986; Rossing et al., 2002) and, in this sense, minor chords introduce a larger deviance in the context of root major chords than inverted major chords.

A similar interpretational problem appears when the interval widths are compared between the chord types of the present paradigm. Namely, the lower interval is narrower than the higher interval in minor chords and the highly dissonant chord types but not in the root or inverted major chords. Thus, the obtained results could be attributable to lower interval size processing only. Disentangling the major-minor difference from the interval structures (major third versus minor third) is not possible, since the interval structures and their acoustic properties define the chords' mode. In the future, more than one example of a dissonant chord structure could still be added to the paradigm, in order to study the neural underpinnings of different degrees of sensory dissonance, and to make sure that the obtained result is generalisable to other highly dissonant interval structures.

Furthermore, in the present experimental paradigm, a root form major chord was always presented as the frequently occurring standard stimulus. In a prior ERP study, minor melodies elicited change-related responses, while major melodies did not, suggesting that major was processed as "the default mode" (Halpern et al., 2008). Indeed, major chords are much more common in Western music than minor chords, and when asked to imagine a chord, Western people tend to imagine a major chord (Huron, 2006). Therefore, using the minor chord as the standard in the paradigm of the present thesis could have yielded different results.

5.5.2 In search for the MMN

In the experimental paradigm of the present thesis, while no new frequencies appear in the deviants of the paradigm, the frequency range is wider in the standards than in the deviants, i.e., the standards introduce frequencies that are not included in the deviants (see Figure 2). This is because each deviant chord type is transposed to only three frequency levels. This was done in order to keep the probabilities of individual chord transpositions, whether standard or deviant, as similar as possible, and in order to avoid any new frequencies from occurring in the deviants: while, for example C, C#, D, and D# root major chords are introduced among standards, second inversions of them would have introduced novel frequencies from the lower adjacent octave, namely, G3, G#3, A3, and A#3.

The fact that deviant stimuli are less probable in the oddball paradigm always leaves the issue of possible refractoriness effects open (as pointed out by May & Tiitinen, 2010). However, in the present paradigm, a significant contribution of refractoriness effects to MMN responses is unlikely due to several factors listed above. It is still possible that particularly the highly dissonant chords, introducing a noticeable acoustic deviance to the sound sequence, would have elicited a different

ERP response than the standard root major chords even when presented alone. In the future, it would be valuable to replicate the obtained results with an additional "control condition", where highly dissonant chords are presented with the same probability as in the oddball paradigm but in a context where they are not considered deviant (discussed by Kujala et al., 2007). If the ERP to the highly dissonant chords would elicit an MMN even when compared to the ERP elicited by the same chords in the control condition, the interpretation of the MMN as a "true MMN" would be more reliable. Because the mechanisms of the infant-MMRs are less well known than those of adults, particularly the newborn infant Study III would have benefited from a control condition.

5.5.3 The behavioural chord detection task

Related to properties of the paradigm, some restrictions appear in the deviant chord detection task of Study IV. Since the paradigm was kept as similar as possible to the passive listening task of the EEG experiment, the behavioural task introduced an oddball paradigm, where the participants were only instructed to react to targets (i.e., deviants). This excludes the possibility to quantify responses using d' (d prime, Kaplan, Macmillan, & Creelman, 1978), designed for same/different tasks. Instead, hits-per-button-presses-ratio was chosen as the measure of performance accuracy, and the amounts of button presses were compared between groups in order to ensure that the Musician and Non-musician groups made an equal effort to perform in the task. Also, as in the EEG paradigm, the deviant chords were composed of notes from the middle of the standards' frequency range. Thus, if the participant learned to ignore the stimuli with highest or lowest frequencies and only consider the middle frequency stimuli as possible targets, the task became easier independent of knowledge of interval structure. This restriction does not compromise the interpretations regarding the relative differences in performance between groups or parts of the task.

Finally, in Study IV, the behavioural chord detection task was conducted after the EEG recording, in a separate session, and the EEG was recorded in a passive listening situation. A similar procedure has been chosen in prior studies, as well (Amenedo & Escera, 2000; Novitski et al., 2004), in order to avoid motor artefacts and attention-related ERPs in response to target stimuli overlapping with MMNs. The procedure compromises straightforward comparisons of MMNs and behavioural performance, and may explain the partial absence of correlations between ERP amplitudes and behavioural detection performance in the study. For example, stimulus familiarity from the EEG experiment as well as the short teaching session prior to the behavioural task are likely to improve the participants' detection accuracy (for short-term training effects on chord discrimination in adults, see Oechslin, Läge, & Vitouch, 2012). Thus, an additional EEG recording during or after the behavioural task would possibly have demonstrated different results than the first recording, and may, for example, have resulted in MMN elicitation in non-musicians, as well (see, e.g., Seppänen, Hämäläinen, Pesonen, & Tervaniemi, 2013).

5.6 General conclusions

While the effects of music expertise on auditory processing in children and adults attract increasing attention in the field of neuroscience of music, the central Western music chord categorisations major versus minor and consonance versus dissonance have received only little prior attention in the neuroscience of music. Also, the complex, music-related auditory skills of newborn infants are not yet well understood.

The present thesis demonstrates sensitivity to central Western music chord categorisations already at birth, indicating readiness for complex, rule-based auditory discriminations. The sensitivity to major *vs.* minor chord categorisations seems to be facilitated by formal music training in school-age, as evidenced by MMN elicitation only in children with music training, and in adulthood, as evidenced by MMN elicitation only in musicians and superior behavioural discrimination of the chord types in musicians compared to non-musicians. Furthermore, the difference between individuals with and without formal music training seems to grow with age and practice years, since the preattentive discrimination of root form chords from inverted form chords was only evident in adult musicians. This indicates that while some properties of music culture can be learned implicitly, others may require extensive levels of formal training in order to happen in the preattentive processing stages.

Even so, the present results show evidence of some music processing skills also in the absence of formal music training or professional levels of musicianship. In addition to the infant results, this is evidenced by MMNs in response to minor chords in non-musician adults with some formal music training, and behavioural detection of minor chords (and, to some extent, inverted major chords) in non-musicians with no formal music training.

To conclude, the neural basis of Western music chord categorisations is rooted in the biological properties of the auditory system. The early auditory skills seem to include at least sensitivity to high levels of dissonance and readiness to process relative sound properties. During development, the processing of Western music chords is facilitated by music expertise, resulting in the case of musicians to highly precise neural representations of musically relevant categorisations.

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