Musical activities and the development of neural sound discrimination

Vesa Putkinen

Cognitive Brain Research Unit, Cognitive Science, Institute of Behavioural Sciences
University of Helsinki, Finland

Finnish Centre of Excellence in Interdisciplinary Music Research
University of Jyväskylä
Finland

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Supervisors: Research Professor Minna Huotilainen, PhD
Cognitive Brain Research Unit
Cognitive Science, Institute of Behavioural Sciences
University of Helsinki, Finland *and*
Finnish Centre of Excellence in Interdisciplinary Music Research
University of Jyväskylä, Finland *and*
Finnish Institute of Occupational Health
Helsinki, Finland

Professor Mari Tervaniemi, PhD
Cognitive Brain Research Unit
Cognitive Science, Institute of Behavioural Sciences
University of Helsinki, Finland *and*
Finnish Centre of Excellence in Interdisciplinary Music Research
University of Jyväskylä, Finland

Reviewers: Assistant Professor Takako Fujioka, PhD
CCRMA, Department of Music, Stanford University
Stanford, USA

Professor Steven M. Demorest, PhD
Laboratory for Music Cognition, Culture and Learning
Department of Music Education, University of Washington
Seattle, USA

Opponent: Professor Viginia Penhune, PhD
Penhune Laboratory for Motor Learning and Neural Plasticity
Department of Psychology, Concordia University
Montreal, Canada

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Contents

Abstract

Musical experience may have the potential to influence functional brain development. The present thesis investigated how the maturation of neural auditory discrimination in childhood varies according to the amount of informal musical activities (e.g., singing and musical play) and formal musical training. Neural auditory discrimination was examined by recording auditory event-related potentials (ERP) to different types of sound changes with electroencephalography (EEG) in children of various ages. The relation of these responses to the amount of informal musical activities was examined in 2–3-year-old children. Furthermore, the development of the responses from early school-age until preadolescence was compared between children receiving formal musical training and musically nontrained children. With regard to typical maturation, the results suggest that neural auditory discrimination is still immature at the age of 2–3 years and continues to develop at least until pre-adolescence. Both informal musical experience and formal musical training were found to modulate various stages of neural auditory discrimination. Specifically, in the 2–3-year-old children, a high amount of informal musical activities was associated with response profiles consistent with enhanced processing of auditory changes and lowered distractibility. Furthermore, during school-age, musically trained children showed more rapid development of neural auditory discrimination than nontrained children especially for music-like sounds. Importantly, no differences were seen between the musically trained and nontrained children at the early stages of the training. Therefore, the group differences that emerged at later ages were most likely due to training and did not reflect pre-existing functional differences between the groups. Thus, the results (i) highlight the usefulness of change-related auditory ERPs as biomarkers for the maturation of auditory processing, (ii) provide novel evidence for the role of informal musical activities in shaping auditory skills in early childhood, and (iii) demonstrate that formal musical training shapes the development of neural auditory discrimination.

Tiivistelmä

Musiikillinen toiminta saattaa muokata aivojen kehitystä. Tässä väitöskirjassa tutkittiin, miten arkipäiväiset musiikilliset toiminnot (esim. laulaminen ja tanssiminen) ja ohjattu soittoharrastus heijastuvat äänien hermostollisen erottelun kehitykseen. Erottelukykyjä tarkasteltiin mittaamalla erilaisten äänissä tapahtuvien muutosten synnyttämiä kuuloherätevasteita aivosähkökäyrällä (EEG). Vasteiden yhteyttä arkipäiväisten musiikillisten toimintojen määrään tutkittiin 2-3-vuotiailla lapsilla. Lisäksi vasteiden kehitystä varhaisesta kouluiästä esimurrosikään verrattiin soittamista ja muita asioita harrastavien lasten välillä. Aivojen tyypillisen kehityksen osalta tulokset viittasivat siihen, että äänien hermostollinen erottelu on 2-3-vuoden iässä kypsymätöntä ja kehittyi ainakin esimurrosikään asti. Sekä arkipäiväisten musiikillisten toimintojen että ohjatun soittoharrastuksen havaittiin olevan yhteydessä äänien hermostolliseen erotteluun. Musiikillisesti aktiivisten 2-3-vuotiaiden lasten aivovasteprofiilit viittasivat tehostuneeseen äänissä tapahtuvien muutosten käsittelyyn ja alhaisempaan häiriintyvyyteen. Kouluiässä äänien hermostollinen erottelu kehittyy nopeammin musiikkia harrastavilla lapsilla muihin lapsiin verrattuna. Ryhmien välillä ei havaittu eroja musiikinharjoittelun alkuvaiheessa, mikä viittaa siihen, että myöhemmin esiin tulleet ryhmäerot heijastivat harjoittelun vaikutusta eikä ennen harjoittelua olemassa olleita eroja. Tulokset korostavat herätevasteiden hyödyllisyyttä aivojen kuulokykyjen kehityksen tutkimisessa, tarjoavat uutta tietoa arkipäiväisten musiikillisten toimintojen yhteydestä kuulokykyihin varhaisessa lapsuudessa sekä osoittavat soittoharrastuksen tehostavan äänien hermostollista erottelua.

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Sincerely,

Vesa Putkinen

List of original publications

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

I. Putkinen, V., Niinikuru, R., Lipsanen, J., Tervaniemi, M., & Huotilainen, M. (2012). Fast measurement of auditory event-related potential profiles in 2–3-year-olds. *Developmental Neuropsychology*, *37*, 51–75.

II. Putkinen, V., Tervaniemi, M., & Huotilainen, M. (2013). Informal musical activities are linked to auditory discrimination and attention in 2–3-year-old children: An event-related potential study. *European Journal of Neuroscience, 37,* 654–661.

III. Putkinen V., Tervaniemi, M., Ojala, P., Saarikivi, K., & Huotilainen, M. (2013). Enhanced development of auditory change detection in musically trained school-aged children: A longitudinal event-related potential study. *Developmental Science,* in press

IV. Putkinen V., Tervaniemi, M., Saarikivi, K., de Vent, N., & Huotilainen, M. (2014). Investigating the effects of musical training on functional brain development with a novel melodic mmn paradigm. *Neurobiology of Learning and Memory,* in press

Abbreviations

EEG	Electroencephalography
EOG	Electro-oculogram
ERP	Event-related potential
LDN	Late discriminative negativity
MEG	Magnetoencephalography
MMN	Mismatch negativity
MRI	Magnetic resonance imaging
RON	Reorienting negativity
SES	Socioeconomic status

1. Introduction

Mapping how brain maturation is modulated by experience remains a central goal in neuroscience. Since mastering a musical instrument requires years of exposure to complex, multimodal sensory input and training in highly precise motor coordination, musical training is a potential source of wide-ranging neuroplastic effects. Furthermore, musical training is often begun at an early age when the brain's capability for experience-dependent reorganization is believed to be the greatest (Knudsen, 2004; Penhune, 2011; Trainor, 2005). Indeed, the brains of adult musicians and non-musicians show differences in function and structure that are generally attributed to the perceptual, motor, and cognitive demands of long-term musical training (Herholz & Zatorre, 2012; Jäncke, 2009; Münte, Altenmüller, & Jäncke, 2002; Pantev & Herholz, 2011). With regard to auditory processing, event-related potential (ERP) studies have shown that adult musicians display enhanced encoding of sound characteristics at various cortical and subcortical levels of the auditory system (Kraus & Chandrasekaran, 2010; Tervaniemi, 2009).

An obvious short-coming of cross-sectional studies comparing adult musicians and non-musicians is that they cannot tease apart the effects of experience and pre-existing neural differences between individuals who seek out musical training and those who do not. In order to disambiguate the contribution of these factors, studies need to compare brain development in musically trained and non-trained individuals from the onset of the training preferably longitudinally in the same subjects. While a few pioneering studies have examined longitudinally the effects of short-term musical training on brain function and structure in children (see section 1.2), no large-scale longitudinal studies to date have investigated the long-term effects of musical training on functional brain maturation across several years.

While considerable attention has been paid to the effects of formal musical training on auditory processing, the putative effects of more informal musical activities remain largely uninvestigated in neuroscience. However, practicing a musical instrument obviously constitutes only a fraction of human musical behavior. For most young children, typical musical experiences consist of everyday musical activities such as singing, dancing, listening to recorded music, and musical play. Since everyday auditory experience can clearly have profound effects on the development of sound processing (cf. native language learning), there is an evident need for studies that examine if and how such informal musical activities affect brain maturation in childhood.

Change-related auditory ERPs such as the mismatch negativity (MMN), the P3a, and Late Discriminative Negativity (LDN) provide a relatively easy, completely non-invasive and safe method for investigating how musical activities are related to the development of important auditory skills such as auditory discrimination, memory, and attention in young children. Importantly for studies in children, the introduction of the so called Multi-feature paradigm (see section 1.1.4) has made it possible to collect responses to changes in a number of different sound features in a considerably more time-efficient manner than before. The studies included in the current thesis employ the change-related auditory ERPs to achieve three main goals: First, to test the feasibility of novel multi-feature paradigms for collecting MMN, P3a, and LDN responses in children, and second, to examine whether these responses are related to the amount of informal, everyday musical activities in early childhood, and third, to investigate the maturation of neural sound discrimination in musically-trained and nontrained children across school-age.

1.1. Development of auditory skills and the underlying neural systems

Behavioral and neuroscientific evidence converge in showing that the structural and functional state of the human auditory system remains immature at least until the second decade of life. A highly selective review of behavioral studies on the development of auditory skills is given in section 1.1.1. with emphasis on musical abilities while structural maturation of the auditory system is examined in section 1.1.2. Finally, section 1.1.3. gives an overview of the development of various auditory even-related potential components.

1.1.1. Behavioral studies on the maturation of auditory skills

While the auditory system is already functional by the last trimester of pregnancy enabling considerable capacity for auditory processing in fetuses and neonates (Lecanuet & Schaal, 1996; Moon & Fifer, 2000), behavioral studies indicate that many basic auditory capabilities are still highly immature in infancy. For instance, thresholds for detecting sounds in silence or in the presence of a masking stimulus (Maxon & Hochberg, 1982; Olsho, Koch, Carter, Halpin, & Spetner, 1988; Schneider, Trehub, Morrongiello, & Thorpe, 1989; Trehub, Schneider, Morrongiello, & Thorpe, 1988) and the discrimination differences in basic sound properties like frequency (Fischer & Hartnegg, 2004; Jensen & Neff, 1993; Maxon & Hochberg, 1982), intensity (Berg & Boswell, 2000; Buss, Hall, & Grose, 2009; Jensen & Neff, 1993; Maxon & Hochberg, 1982), duration (Elfenbein, Small, & Davis, 1993; Jensen & Neff, 1993; Morrongiello & Trehub, 1987), and the temporal structure of sound (as indexed by gap detection) (Irwin, Ball, Kay, Stillman, & Rosser, 1985; Wightman, Allen, Dolan, Kistler, & Jamieson, 1989) do not consistently reach adult levels until preschool or even early school-age. Thus, by conservative estimate, even some low-level auditory discrimination skills appear to undergo approximately a 10-year-long maturation. Psychophysical performance in more challenging tasks such as speech sound perception in noise shows improvements even later than this (Elliott, 1979; Johnson, 2000; Wilson, Farmer, Gandhi, Shelburne, & Weaver, 2010).

Nevertheless, infant auditory discrimination is accurate enough for detecting, for example, the smallest frequency and duration differences that are in practice relevant for Western music In fact, infants less than one year old are already able to process many fairly complex aspects of musical sounds: They can encode melodies and rhythms in terms of relative pitch (Trehub, Bull, & Thorpe, 1984; Trehub, Thorpe, & Morrongiello, 1987) and duration (Trehub & Thorpe, 1989), are sensitive to the tempo (Baruch & Drake, 1997; Pickens & Bahrick, 1997) and meter (Hannon & Johnson, 2005), are able to group individual tones by pitch (Thorpe, Trehub, Morrongiello, & Bull, 1988) and show long-term memory for musical pieces (Plantinga & Trainor, 2005).

Behavioral studies on later music-perceptual development have mostly centered on the acquisition of culture-specific, implicit musical knowledge. Such studies indicate that between infancy and preschool-age, children start to show tuning to “native” metric and scale structures (Corrigall & Trainor, 2009; Hannon & Trehub, 2005a, 2005b; Krumhansl, Toivanen, Eerola, Toiviainen, Järvinen, & Louhivuori, 2000; Lynch, Eilers, Oller, & Urbano, 1990; Trehub, Cohen, Thorpe, & Morrongiello, 1986; Trainor & Trehub, 1992). The sensitivity to harmony appears show more protracted development emerging in preschool age and reaching adult-level in adolescence (Corrigall & Trainor, 2009; Costa-Giomi, 2003; Trainor & Trehub, 1994).

In sum, on one hand, behavioral evidence suggests that many basic auditory skills are maturing still in school-age. On the other hand, a number of studies highlight that young children possess abilities for processing complex musically relevant auditory information. Coupled with their interest towards and apparent enjoyment of music (Nakata & Trehub, 2004; Zentner & Eerola, 2010) these skills enable children to eventually internalize culture-specific musical conventions.

As reviewed above, behavioral studies have contributed significantly to the understanding of auditory development. However, by measuring changes in overt behavior across age it is often impossible to disentangle the influence of neural changes in the auditory system *per se* and the development of attention, motivation, and motor abilities. Studies on the maturation of auditory system anatomy can help interpret the age-related changes seen in auditory skills. Importantly, recording the electrical activity of the brain during passive exposure to sounds can gauge auditory processing without the need for active attending and motor responses and thereby can potentially mitigate the above mentioned shortcomings of behavioral methods.

1.1.2. Structural maturation of the auditory brain

Auditory information is conveyed from the cochlea to the auditory cortex via brainstem, midbrain, and thalamic input (Malmierca & Hackett, 2010). The human auditory cortex is located in the supratemporal plane and comprises the primary auditory cortex in Heschl’s gyrus and several functionally heterogeneous non-primary auditory areas (Kaas, Hackett, & Tramo, 1999; Liégeois-Chauvel, Musolino, & Chauvel, 1990; Morosan et al., 2001; for reviews, see Griffiths & Warren, 2002; Rauschecker & Scott, 2009; Zatorre, Belin, & Penhune, 2002). The auditory cortex is believed to be responsible for integrating the features extracted from auditory input in the ascending pathway into a unitary auditory percept (Griffiths & Warren, 2004; Nelken, 2004) and for modifying the processing in the lower levels of the pathway via descending projections (Schofield, 2010).

Longitudinal structural neuroimaging studies indicate regionally heterogeneous developmental trajectories of gray and white matter (Brown et al., 2012; Gogtay et al., 2004; Lebel, Walker, Leemans, Phillips, & Beaulieu, 2008; Shaw et al., 2008). The typical conclusion drawn from these studies is that the structural development of the cerebral cortex proceeds from the early maturing primary sensory and motor regions towards late maturing higher order association areas (Gogtay & Thompson, 2010; Lenroot & Giedd, 2006). Unfortunately for the current purposes, the majority of these studies have not specifically examined the maturation of the auditory system. However, a very recent longitudinal study investigating the structural development of the Heschl's gyrus in autistic and typically developing control children and adolescents found that in the control group the gray matter volume increased during adolescence while white matter volume peaked in preadolescence and showed a reduction with age thereafter (Prigge et al., 2013). Furthermore, a cross-sectional study examining the covariance of gray matter between different cortical areas suggests that the Heschl's gyrus first connects most strongly to contralateral auditory cortex in preschool-age and then expands it connections to parietal and frontal areas by early adolescence (Zielinski, Gentas, Zhou, & Seeley, 2010).

Histological studies indicate that the structure of the fetal cochlea reaches relative maturity around the time of term birth (Moore & Linthicum, 2007). From the second trimester of pregnancy onwards, the auditory brainstem pathway shows rapid maturation (Moore, Guan, & Shi, 1996, 1998; Moore, Perazzo, & Braun, 1995). In infancy, the main input to the marginal layer I of the auditory cortex comes through projections from the reticular formation of the brainstem which are subsequently reduced during the first year of life (Moore & Guan, 2001). The thalamo-cortical connections, in turn, continue to mature until the age of five. Immunostaining of axonal neurofilaments indicates that the auditory cortex goes through over a decade long process of axonal and neuronal maturation starting from the superficial layer I and then proceeding from the deeper layers IV-VI at the ages 1 to 5 years towards layers II-III at the ages of 5 to 12 years (Eggermont & Moore, 2012; Moore & Guan, 2001; Moore &

Linthicum, 2007). Development of synaptic density in auditory cortex is characterized by initial overproduction of synapses during the first postnatal months followed by a period of stable synaptic density and a gradual reduction until early adolescence, all of which occur earlier in the auditory than in the prefrontal cortex (Huttenlocher & Dabholkar, 1997).

In sum, the fairly scarce literature on the structural maturation of the human auditory system suggests a peripheral–to–central developmental gradient that culminates in the maturation of the auditory cortical areas and their connections to other cortical regions in adolescence.

1.1.3. Maturation of auditory processing as measured by event-related potentials

The electroencephalography (EEG) measures the dynamics of the electrical field potentials generated by neuronal activity in the brain. Specifically, the EEG is believed to reflect the excitatory and inhibitory post-synaptic potentials of parallelly oriented and synchronously active neurons (Nunez & Srinivasan, 2006). By averaging EEG segments time-locked to auditory stimuli, the EEG activity that is not temporally synchronous with the stimuli is attenuated while the activity that remains sufficiently constant in latency and polarity across stimulus presentations is preserved (Luck, 2005; Picton, 2010)[1]. The latencies and amplitudes of resulting auditory event-related potential (ERP) can provide temporally fine-grained information about sound-evoked neuronal activity. With appropriate experimental manipulations, this information can be linked to the various stages of sound processing ranging from the early encoding of sound properties in the auditory brainstem to later, higher-order processes such as attention, memory, and language at the cortical level. Because ERPs are completely non-invasive and fairly easy to obtain even from neonates, they are the most widely used method in studying the functional maturation of auditory system (Trainor, 2008).

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[1] For a discussion on the contribution of phase resetting of ongoing oscillatory phenomena to the ERP signal, see Sauseng et al.(2007).

1.1.3.1. Maturation of ERP responses elicited by repeating sounds

Despite the apparent neuronal and axonal immaturity of the auditory cortex at birth, ERP responses with probable cortical origin can be obtained already from newborns (e.g., Kushnerenko et al., 2002). In agreement with this finding, neuroimaging studies have found robust hemodynamic changes in neonates and young infants in response to auditory stimulation (Dehaene-Lambertz, Dehaene, & Hertz-Pannier, 2002; Mahmoudzadeh et al., 2013; Perani et al., 2010). However, whereas in adults repeating sounds evoke a cascade of fast positive and negative peaks (see below), the neonate responses typically consist of a positivity between circa 100 and 400 ms followed by a negativity lasting approximately until 700 ms (Kushnerenko et al., 2002). After infancy, the different components of the sound-evoked ERP show heterogeneous maturation that continues at least until adolescence.

Specifically, the auditory brainstem response originating from the auditory nerve and brainstem within the first 10 ms from sound onset is estimated to mature approximately by the age of 2.5 years (Ponton, Eggermont, Coupland, & Winkelaar, 1992; Ponton, Moore, & Eggermont, 1996). By contrast, the following midlatency responses arising from the auditory cortex appear to take at least 10 years to reach adult morphology (McGee & Kraus, 1996). The vertex P1-N1-P2-N2-continuum (see Figure 1) and the temporal T-complex that characterize the late-latency responses in adults show even more prolonged maturation.

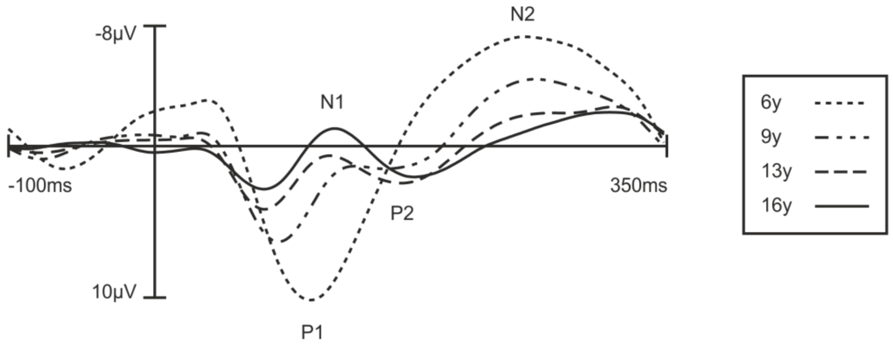

Figure 1. Responses to a major triad chord recorded from children aged 6,9,13, and 16 years (Putkinen, unpublished data) at a frontal electrode cite. Note the reduction in P1 and N2 amplitude and the emergence of the N1 and P2 with age.

Between infancy and early school-age the ERP response to repeating sounds is dominated by the P1-N2-complex (Čeponienė, Cheour, & Näätänen, 1998; Čeponienė, Rinne, & Näätänen, 2002; Kushnerenko et al., 2002). The P1 decreases in latency and amplitude past age 15 (Ponton, Eggermont, Kwong, & Don, 2000; Sharma, Kraus, McGee, & Nicol, 1997). Similarly, the N2 decreases drastically in amplitude between early childhood and adolescence (Cunningham, Nicol, Zecker, & Kraus, 2000; Enoki, Sanada, Yoshinaga, Oka, & Ohtahara, 1993; Ponton et al., 2000; Sussman, Steinschneider, Gumenyuk, Grushko, & Lawson, 2008). The P2 emerges as a distinct peak at frontal cites in early school-age and decreases in amplitude thereafter throughout adolescence (Ponton et al., 2000; Sharma et al., 1997; Sussman et al., 2008).

The vertex N1 (or N1b) generated in the superior temporal gyrus (Woods, 1995) around 100 ms is the most prominent peak of the adult response to repeating sounds. The N1 amplitude is strongly attenuated at fast stimulation rates in children (Sussman et al., 2008) and is typically not seen even in early school-aged children unless a fairly long inter-stimulus interval is used (Čeponienė et al., 1998; Sussman et al., 2008). During adolescence, the N1 increases in amplitude and decreases in latency (Cunningham et al., 2000; Mahajan & McArthur, 2012; Pang & Taylor, 2000; Ponton et al., 2000; Sussman et al., 2008).

The temporally dominant N1a (or Na) and N1c (or Tb), which are a part of the so called T-complex along with the positive Ta and T200 responses, are thought to originate from secondary auditory areas. In contrast to the vertex N1, the N1a and N1c, appear to be present already at preschool-age (Tonnquist-Uhlen, Ponton, Eggermont, Kwong, & Don, 2003). Although the evidence is rather mixed with regard the development N1a and N1c, studies mostly report reduction in the amplitude of the T-complex components during school-age and adolescence (Albrecht, Suchodoletz, & Uwer, 2000; Pang & Taylor, 2000; Ponton, Eggermont, Khosla, Kwong, & Don, 2002; Poulsen, Picton, & Paus, 2009; Tonnquist-Uhlen et al., 2003).

In sum, ERPs evoked by repeating sounds appear to follow a developmental progression in which the subcortically elicited responses mature in early childhood and the cortically elicited ones reach adult-like morphology at various times between preschool-age and adolescence.

1.1.3.2. The mismatch negativity

The mismatch negativity (MMN) is elicited by infrequent sounds that violate some invariant aspect(s) of preceding sounds (Näätänen, Paavilainen, Rinne, & Alho, 2007). The MMN has traditionally been recorded using the oddball paradigm where a change in a sequence of repetitive standard sounds is occasionally introduced by a presentation of a different stimulus, the deviant. In adults, the MMN is seen as a fronto-central negative response to the deviants between 100–250 ms. The MMN is interpreted to reflect the detection of a discrepancy between the deviant auditory input and predictions based on a perceptual model of the regularities in recently encountered sounds (Näätänen & Winkler, 1999; Winkler, Denham, & Nelken, 2009; Baldeweg, 2007; Garrido, Kilner, Stephan, & Friston, 2009). In other words, this theory holds that the MMN rests on a comparison between the features of incoming sounds and those predicted from a memory model of the invariant aspects of auditory environment. Simple stimulus specific adaptation of auditory cortical neurons to repeated stimuli has been suggested as a neuronal correlate of the memory trace for the standards (Nelken & Ulanovsky, 2007; May & Tiitinen, 2010) but this suggestion remains controversial (Näätänen, Jacobsen, & Winkler, 2005; Näätänen, Kujala, & Winkler, 2011). Recent computational work suggests that both adaptation as well as more complex prediction and comparison processes are needed to explain the MMN (Garrido et al., 2009).

Converging evidence from intracortical recordings and lesion studies (Kropotov et al., 1995; Kropotov et al., 2000), MMN source modeling (Alho et al., 1996; Levänen, Ahonen, Hari, McEvoy, & Sams, 1996; Rinne, Alho, Ilmoniemi, Virtanen, & Näätänen, 2000; Scherg, Vajsar, & Picton, 1989) as well as positron emission tomography (PET) (Tervaniemi et al., 2000) and functional magnetic resonance imaging (fMRI) studies (Opitz, Rinne, Mecklinger, von Cramon, & Schröger, 2002) indicate that the main cortical generators of the adult MMN are located in the temporal auditory cortical areas. There is also evidence for additional contribution from the frontal cortex (Alho, Woods, Algazi, Knight, & Näätänen, 1994; Doeller et al., 2003; Giard, Perrin, Pernier, & Bouchet, 1990; Marco-Pallares, Grau, & Ruffini, 2005; Rinne et al., 2000; Schönwiesner et al., 2007). It is typically presumed that the auditory cortex generators reflects the memory trace formation and comparison stages of the deviance detection process while the frontal source is involved in triggering involuntary attention allocation towards the sound changes (Näätänen et al., 2007; for a critical discussion regarding the existence and functional role of frontal MMN sub-component, see Deouell, 2007).

The MMN is an attractive tool for music-related studies in children for several reasons. Firstly, the MMN can be obtained to changes in complex regularities in acoustically varying sounds that are commonplace in music (Näätänen, Tervaniemi, Sussman, Paavilainen, & Winkler, 2001; Paavilainen, 2013). For instance, the MMN has been used to investigate the encoding of melodic contour and specific intervals (Trainor, McDonald, & Alain, 2002), rhythms and meter (Winkler & Schröger, 1995; Ladinig, Honing, Háden, & Winkler, 2009; Vuust, Ostergaard, Pallesen, Bailey, & Roepstorff, 2009), the structure of musical scales and chords (Brattico, Tervaniemi, Näätänen, & Peretz, 2006; Brattico et al., 2009; Virtala et al., 2011), different aspects of musical timbre (Caclin et al., 2006; Toiviainen et al., 1998), and auditory stream segregation (Yabe et al., 2001). In other words, the MMN appears to reflect brain mechanism for predicting how complex sound patterns unfold in time and evaluating the outcomes of such predictions which have long been recognized as key components of music processing (Meyer, 1956; Huron, 2006; cf. Trainor & Zatorre, 2009).

Moreover, the amplitude and latency of the MMN are closely associated with the accuracy and speed of the overt discrimination of the eliciting sounds (Amenedo & Escera, 2000; Kujala, Kallio, Tervaniemi, & Näätänen, 2001; Novitski, Tervaniemi, Huotilainen, & Näätänen, 2004; Näätänen, Schröger, Karakas, Tervaniemi, & Paavilainen, 1993; Tiitinen, May, Reinikainen, & Näätänen, 1994). Namely, the more accurate the behavioral discrimination, the larger the amplitude and/or shorter the latency of the MMN is. Therefore, the parameters of the MMN may provide an index of the accuracy of the sound representations underlying conscious perception (Näätänen & Winkler, 1999).

The MMN can also be employed as a measure of experience-dependent plasticity in the auditory cortex that accompanies auditory learning (Kujala & Näätänen, 2010). For instance, both short-term training (Kraus et al., 1995; Lappe, Herholz, Trainor, & Pantev, 2008; Menning, Roberts, & Pantev, 2000; Näätänen et al., 1993) and long-term auditory experience including such as language exposure (Näätänen, 2001) or musical training (see below), have been shown to influence the MMN.

Furthermore, the MMN is an automatic response in the sense that it is elicited irrespective of the direction of subjects' attention (e.g., Paavilainen, Tiitinen, Alho, & Näätänen, 1993; for a discussion, see Sussman, 2007). Consequently, the MMN can be obtained in a passive condition in which no overt responses are required which is of obvious importance for studies in young children. Furthermore, the automaticity of the MMN enables the comparison of musically trained and non-trained subjects that is not confounded by possible group differences in motivation, attention or explicit musical knowledge.

Mismatch responses to violations of complex auditory regularities can be obtained already from newborns and infants (Carral et al., 2005; He, Hotson, & Trainor, 2009; Stefanics et al., 2007, 2009; Winkler, Háden, Ladinig, Sziller, & Honing, 2009; Winkler et al., 2003) indicating that such change detection is an essential aspect of the auditory processing that emerges very early in ontogeny. However, compared to the adult MMN, the mismatch responses obtained in infants are often later in latency and display different scalp topographies (Cheour, Leppänen, & Kraus, 2000) and, notably, may be positive in polarity (Dehaene-Lambertz, 2000; Leppänen, Eklund, & Lyytinen, 1997; Novitski, Huotilainen, Tervaniemi, Näätänen, & Fellman, 2007). A number of studies have found immature positive mismatch responses still in preschool-age children (Lee et al., 2012; Maurer, Bucher, Brem, & Brandeis, 2003a, 2003b; Shafer, Yan, & Datta, 2010). In older children, by contrast, adult-like negative MMNs with little developmental change across school-age have been reported (Kraus et al., 1993; Kraus, Koch, McGee, Nicol, & Cunningham, 1999; Molholm, Gomes, Lobosco, Deacon, & Ritter, 2004; Molholm, Gomes, & Ritter, 2001; Ponton et al., 2000; Shafer, Morr, Kreuzer, & Kurtzberg, 2000). Consequently, in contrast to some of the responses introduced above (section 1.1.4.1), the MMN has been proposed to reflect an early maturing cortical mechanism that operates essentially in an adult-like manner already by school-age (Cheour, Korpilahti, Martynova, & Lang, 2001; Ponton et al., 2000; Kurtzberg, Vaughan, Kreuzer, & Fliegler, 1995). Other studies, in turn, suggest that the MMN might be less robust in school-aged children than in adults especially with more challenging paradigms (Gomes et al., 1999, 2000; Mahajan & McArthur, 2011; Sussman & Steinschneider, 2011; Sussman & Steinschneider, 2009) and that the MMN might, in fact, increase in amplitude with age in early adolescence (Bishop, Hardiman,

& Barry, 2011). Thus, the literature is mixed as to whether the MMN is still maturing in preadolescence. Importantly in the current context, no study to date has tracked the development of the MMN across several narrow age ranges using complex music-like sounds. Consequently, little is known about how the processing of such changes, as reflected by the MMN, develops in childhood and how this development might be affected by auditory experience.

1.1.3.3 The P3a as an index of auditory attention in childhood

In addition to the MMN, sound changes may also elicit a fronto-centrally maximal positive P3a response between 200–400 ms from stimulus onset (Squires, Squires, & Hillyard, 1975). In a typical experiment, the P3a is recorded to *novel sounds* (e.g., highly distinct environmental sounds) presented infrequently in a sequence of repeated standard tones (e.g., Escera, Alho, Winkler, & Näätänen, 1998). P3a-like responses can also be elicited by more subtle, non-novel but still distinct deviant tones (e.g., large pitch changes) (Yago, Corral, & Escera, 2001). In both adults and children, the P3a elicited by task-irrelevant sound changes is typically associated with deteriorated performance in a concurrent visual or auditory behavioral task (Escera et al., 1998; Gumenyuk, Korzyukov, Alho, Escera, & Näätänen, 2004; Wetzel, Widmann, Berti, & Schröger, 2006; however, see Wetzel, Schröger, & Widmann, 2013). Consequently, a common interpretation is that the P3a reflects involuntary attention switch towards task-irrelevant auditory changes (for reviews, see Escera, Alho, Schröger, & Winkler, 2000; Escera & Corral, 2007; Friedman, Cycowicz, & Gaeta, 2001; Linden, 2005; Polich, 2007)[2].

Several brain areas underlie the generation of the P3a to unattended sounds in adults: Frontal sources are implicated by intracortical recordings (Baudena, Halgren, Heit, & Clarke, 1995), lesion studies (Knight, 1984; Løvstad et al., 2012), ERP source modeling (Mecklinger & Ullsperger, 1995; Volpe et al., 2007; Takahashi et al., 2013)

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[2] In adults and school-aged children, the P3a to novel sounds often displays biphasic morphology at frontal cites suggesting two subcomponents for this response. According to a widely adopted framework, the early portion of the response is more closely related to the acoustic analysis of the eliciting sounds while the late portion reflects the actual attention allocation (Escera et al., 2000).

and scalp current density analysis (Schröger, Giard, & Wolff, 2000)**.** Evidence for auditory cortical contribution comes from MEG source analysis (Alho et al., 1998) and fMRI (Opitz, Mecklinger, von Cramon, & Kruggel, 1999). Finally, lesion of the temporo-parietal junction (Knight & Scabini, 1998) and direct recordings from the hippocampus (Knight, 1996) indicate that these areas are also involved in auditory P3a generation.

The neural mechanism underlying the P3a are affected by short and longer-term experience since its amplitude and latency are modulated, for example, by discrimination training (Atienza, Cantero, & Stickgold, 2004; Draganova, Wollbrink, Schulz, Okamoto, & Pantev, 2009), familiarity with the eliciting stimuli (Beauchemin et al., 2006; Kirmse, Jacobsen, & Schröger, 2009; Roye, Jacobsen, & Schröger, 2007), language learning (Jakoby, Goldstein, & Faust, 2011; Shestakova, Huotilainen, Čeponienė, & Cheour, 2003) and musical training (see below). Therefore, the P3a offers an index of experience dependent plasticity of frontally mediated auditory attention.

Novel sounds elicit P3a-like responses in children at all ages studied so far ranging from infancy to school-age (Čeponiené, Lepistö, Soininen, Aronen, Alku, & Näätänen, 2004; Birkas et al., 2006; Kushnerenko et al., 2007; Räikkönen, Birkás, Horváth, Gervai, & Winkler, 2006). P3a-like responses to more fine-grained deviant sounds have also been reported in infants and children (Kurtzberg, Vaughan, Kreutzer, & Flieger, 1995; Shestakova et al, 2003; Trainor et al., 2001). With regard to the development of the novel sound elicited P3a, the most consistent finding appears to be that the this response decreases in amplitude between preschool-age and adulthood at frontal cites (Gumenyuk, Korzyukov, Alho, Escera, & Näätänen, 2004; Määttä, Saavalainen, Könönen, Pääkkönen, & Muraja-Murro, 2005; Wetzel & Schröger, 2007b; Wetzel, Widmann, & Schröger, 2011; however, see Ruhnau, Wetzel, Widmann, & Schröger, 2010) and decreases in latency until adolescence (Fuchigami et al., 1995). The reduction in P3a amplitude suggests more efficient control over involuntary attention capture that might be related to the maturation of the prefrontal cortex. In contrast, the admittedly few studies that have examined the development of the P3a elicited by deviant tones report no change with age from early school-age to adolescence (Wetzel & Schröger, 2007a; 2007b). By visual inspection of the response figures, some studies even seem to suggest an age-related increase in the amplitude of the deviant-elicited P3a in school-age (Gomot, Giard, Roux, Barthélémy, & Bruneau, 2000; Horváth, Czigler, Birkás, Winkler, & Gervai, 2009; Shafer et al., 2000). The distinct developmental trajectories for the P3a-resposes to novel sounds and deviant tones argue for the position that sound changes that are well above discrimination threshold *vs.* more subtle auditory incongruities may trigger attention capture through distinct neural mechanisms (cf. Escera et al., 1998). Therefore, recording the P3a to novel sounds and deviant tones in children can shed light on how musical experience affects different aspects of auditory change detection and attention in the maturing brain.

1.1.3.4. The Late Discriminative Negativity (LDN)

In infants and children, deviant sounds often elicit a slow frontally maximal negative response commencing approximately at 400 ms after stimulus onset (Bishop et al., 2011; Čeponienė et al., 1998; Draganova, Eswaran, Murphy, Huotilainen, Lowery, & Preissl, 2005; Kushnerenko, Čeponienė, Balan, Fellman, & Näätänen, 2002). Although evidently related to sound discrimination, the exact functional role of the component, termed here as the Late Discriminative Negativity (LDN), is unclear. The LDN has been linked to phonemic or lexical mismatch detection based on a finding that in preschool-aged children words elicited a larger LDN than pseudowords or complex tones (Korpilahti, Krause, Holopainen, & Lang, 2001). However, this interpretation cannot account for the prominent LDNs elicited by non-linguistic tonal stimuli (Čeponienė et al., 1998). More relevant in the current context is the suggestion that, akin to the adult Reorienting negativity (RON) (Schröger & Wolff, 1998), the LDN reflects redirecting of attention to the primary task after distracting task-irrelevant auditory stimuli (Gumenyuk et al., 2001; Ortiz-Mantilla, Alvarez, & Benasich, 2010; Shestakova et al., 2003; Wetzel et al., 2006). LDN-like responses can indeed be obtained from children in similar active paradigms used to record the RON in adults (e.g., Gumenyuk et al., 2001). Furthermore, the correlation between the P3a and LDN (but not between MMN and LDN) found by Shestakova et al. (2003) and the negative correlation between the LDN amplitude and behavioural distraction found by Gumenyuk et al (2001) are in line with this distraction-reorientation interpretation of the LDN. However, LDN-like responses have been recorded to subtle sound changes that do not elicit the attention-related P3a response (Čeponienė et al., 1998) and are therefore probably not distracting. To account for such findings, another view holds that the LDN responses might reflect further, higher-order processing of the deviant sounds that follows the initial change detection reflected by the MMN (Čeponienė et al., 1998; Čeponienė, Lepistö, Soininen, Aronen, Alku, & Näätänen, 2004). The contrasting findings of the studies reviewed above suggest that instead of being a unitary response, the LDN reflects the contribution of functionally distinct components within the same latency range that are activated differentially depending on the age of the subjects and the stimuli and task employed in a given study.

Although sometimes termed as “late MMN”, the LDN differs from the MMN in a number of ways. With regard to the neural origins of these responses, scalp topography (Čeponienė et al., 2004) and current source density analyses (Hommet et al., 2009) of MMN and LDN suggest distinct neural generators for these responses. Furthermore, these components appear to be accompanied by different oscillatory phenomena: Bishop, Hardiman, and Barry (2010) found increased phase synchrony in the theta band in the MMN time range whereas the LDN was related to decrease in power in the delta, theta, and (low) alpha bands. The LDN and MMN also appear to respond differently to deviant magnitude. Generally, the MMN amplitude increases with increasing deviant-standard difference (Sams, Paavilainen, Alho, & Näätänen, 1985; Pakarinen, Takegata, Rinne, Huotilainen & Näätänen, 2007). The LDN, in contrast, may even display the opposite pattern to that of the MMN, namely, larger amplitude for smaller deviant (Bishop et al., 2010) and is otherwise differently affected by the acoustic properties of the eliciting stimuli than the MMN (Čeponienė, Yaguchi, Shestakova, Alku, Suominen, & Näätänen, 2002).

Although LDN-like responses have been also reported in adults (Alho et al., 1994; Horváth, Roeber, & Schröger, 2009; Näätänen, Simpson, & Loveless, 1982; Peter, Mcarthur, & Thompson, 2012), it is unknown whether these responses are in fact an adult analogue of the child LDN. In any case, longitudinal and cross-sectional studies indicate that the LDN amplitude is dramatically reduced between childhood and adulthood (Bishop, Hardiman, & Barry, 2011; Hommet et al., 2009; Müller, Brehmer, von Oertzen, & Lindenberger, 2008). Therefore, the LDN can be useful in inferring the maturational state of auditory processing (i.e., presence of a large LDN may indicate immature processing of auditory changes). Finally, the LDN is sensitive to language experience (Shestakova et al., 2003) raising the question whether it might provide a more general measure of auditory learning in childhood.

1.1.4. Multi-feature paradigms for recording profiles of change-related auditory ERPs

To obtain the MMN (as well as the P3a and LDN) in the conventional oddball paradigm, it is necessary to have a low probability of the deviants relative to the standards (usually 10–20% of the trials) (Sinkkonen & Tervaniemi, 2000). Consequently, recording the MMN with an acceptable signal-to-noise ratio to changes in multiple auditory features in the oddball paradigm is highly time-consuming (e.g., Tervaniemi, Lehtokoski, Sinkkonen, Virtanen, Ilmoniemi, & Näätänen, 1999) and therefore not an optimal approach for studies in children. To combat this problem, Näätänen, Pakarinen, Rinne, and Takegata (2004) developed the so called the Multi-feature paradigm in which standard tones and five types of deviant tones with the probability of 10% per deviant types are presented in an alternating manner (see Figure 2) (see also Pakarinen et al., 2007; Sambeth et al., 2009; Fisher, Labelle, & Knott, 2008). In the original study of Näätänen et al. (2004), the deviant tones differed from the standard tones either in frequency, duration, intensity, perceived spatial origin, or by having a silent gap in the middle of the sound. Since earlier studies had shown that, at least in adults, the neural system underlying the MMN can process the different auditory features independently of one another (e.g., Gomes, Ritter, & Vaughan, 1995), it could be expected that the deviants would still elicit MMNs despite the overall probability of the deviants was 50%. Indeed, deviant tones elicited MMNs that were found to be comparable in amplitude and latency to those elicited by the same deviant tones presented in a separate oddball paradigms. Therefore, compared to the oddball paradigm, the time taken to collect MMNs to five types of deviants was reduced to one-fifth.

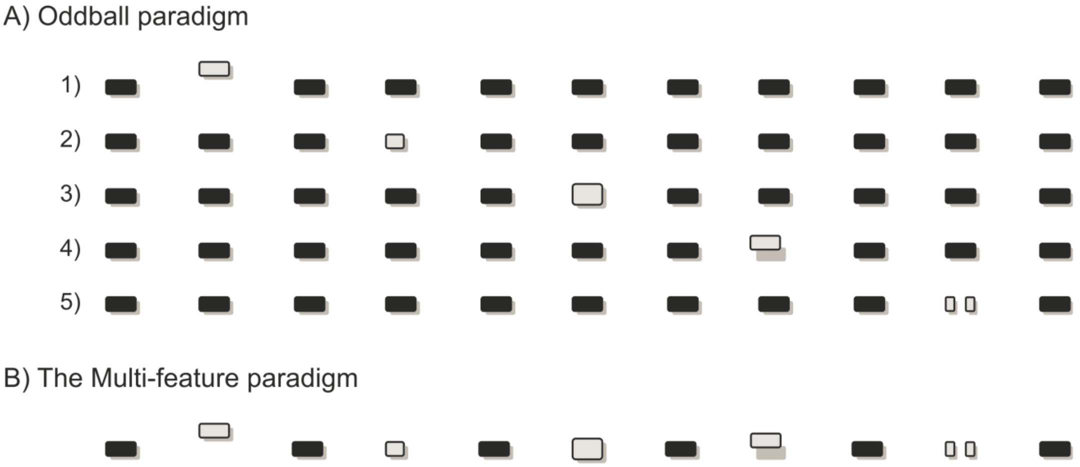

Figure 2. A) Oddball paradigms with frequency, duration, intensity, location, and gap deviants (A 1–5, respectively). B) Multi-feature paradigm with the same deviant stimuli.

As is clear from the description above, the original Multi-feature paradigm was designed to probe fairly basic, low-level auditory discrimination skills. Since the introduction of the paradigm, multi-feature paradigms for investigating the processing of more complex auditory information such as linguistic (Pakarinen, Lovio, Huotilainen, Alku, Näätänen, & Kujala, 2009; Partanen, Vainio, Kujala, & Huotilainen, 2011) and musical sounds (Huotilainen, Putkinen, & Tervaniemi, 2009; Vuust et al., 2011) have been developed. With regard to music, the so called *Melodic multi-feature paradigm* (Huotilainen et al., 2009) was designed for probing the detection of changes in various musically central auditory dimensions (see Figure 3). Unlike the original Multi-feature paradigm, the Melodic multi-feature paradigm is composed of short melodies and includes changes in melodic and rhythmic regularities as well as musical key, timbre, tuning, and timing. Furthermore, the stimuli are presented in a so called roving standard fashion (Cowan, Winkler, Teder, & Näätänen, 1993) so that frequent updating of the memory representation for melody, rhythm, and key is needed in order for the changes in these dimensions to be discriminated. The Melodic multi-feature paradigm has been used successfully to obtain mismatch responses from 2–3-year-old children (Huotilainen et al., 2009) and in revealing neural differences between adult folk musicians and non-musicians (Tervaniemi et al., submitted). Therefore, the paradigm shows promise as a method for studying how musical experience influences the maturation of musical sound feature processing.

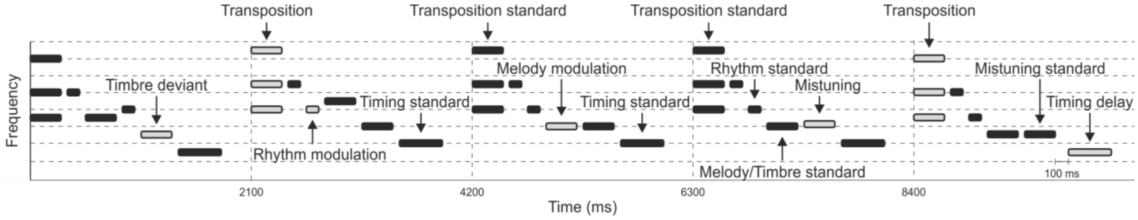

Figure 3. Illustration of the Melodic multi-feature paradigm with changes in melody, rhythm, key, timbre, tuning, and timing.

1.2. Musical training and brain development

Long-term experience in a given task is accompanied by specific neuroplastic changes in the underlying neural systems (e.g., Cheour et al., 1998; Gauthier, Skudlarski, Gore, & Anderson, 2000; Lazar et al., 2005; Maguire et al., 2000). Listening to music activates a wide network of subcortical and cortical areas supporting perception, cognition, and emotion (Chanda & Levitin, 2013; Koelsch & Siebel, 2005; Koelsch, 2010; Peretz & Zatorre 2005; Zatorre & Salimpoor, 2013). Although the neural correlates of musical performance are arguably less well understood than those of listening, playing a musical instrument, not to mention long-term musical training, obviously involves various additional sensory, motor, and cognitive demands (Zatorre, Chen, & Penhune, 2007). Therefore, musical training may have extensive neuroplastic effects on the brain.

In line with this notion, the brains of adult musicians and non-musicians differ in many respects both in terms of function and anatomy (Jäncke, 2009; Herholz & Zatorre, 2012; Pantev & Herholz, 2011). For instance, in adult musicians several sensory, motor, and higher-order cortical areas as well as regions in the hippocampus, cerebellum, and corpus callosum are enlarged (Bermudez, Lerch, Evans, & Zatorre, 2009; Elbert, Pantev, Wienbruch, Rockstroh, & Taub, 1995; Gaser & Schlaug, 2003; Groussard et al., 2010; Hutchinson, Lee, Gaab, & Schlaug, 2003; Schlaug, Jäncke, Huang, Staiger, & Steinmetz, 1995; Schneider, Scherg, Dosch, Specht, Gutschalk, & Rupp, 2002; Sluming, Brooks, Howard, Downes, & Roberts, 2007) and the architecture of various white matter tracts is altered (Bailey, Zatorre, & Penhune, 2013; Bengtsson, Nagy, Skare, Forsman, Forssberg, & Ullén, 2005; Imfeld, Oechslin, Meyer, Loenneker, & Jäncke, 2009; Schmithorst & Wilke, 2002; Steele, Bailey, Zatorre, & Penhune, 2013). Importantly, a longitudinal MRI study (Hyde et al., 2009) provided compelling evidence for the critical role of musical training (vs. pre-existing differences between musically trained and non-trained individuals) in shaping brain anatomy: While no group differences were seen before training, after 15 months of weekly keyboard lessons 6-year-old children showed enlargement of the corpus callosum, as well as auditory and motor cortices relative to control children (who received no musical training outside a weekly 40-min music class at school).

With regard to auditory processing, musicians display enhanced encoding of sounds at various levels of the auditory system. Several recent studies have found that the auditory brainstem response is enhanced in adult musicians and musically trained children either in terms of shorter latency, larger in amplitude, or more accurate representation of the frequency spectrum of the stimulus compared to those of non-musicians (Lee, Skoe, Kraus, & Ashley, 2009; Musacchia, Sams, Skoe, & Kraus, 2007; Strait, Kraus, Skoe, & Ashley, 2009; Strait, O'Connell, Parbery-Clark, & Kraus, 2013; Wong, Skoe, Russo, Dees, & Kraus, 2007). At the cortical level, repeated instrument and sinusoidal sounds elicit stronger ERP and electromagnetic field responses within the first 200 ms after sound onset in musicians than in non-musicians (Pantev, Oostenveld, Engelien, Ross, Roberts, & Hoke, 1998; Pantev, Roberts, Schulz, Engelien & Ross, 2000; Schneider et al., 2002; Shahin, Bosnyak, Trainor & Roberts, 2003). A longitudinal study by Fujioka et al. (2006) found that, when compared to musically nontrained peers, a magnetic N250 response with cortical origin elicited by violin tones peaked earlier and was larger in amplitude in the left hemisphere in preschool-age children who had taken Suzuki violin lessons for one year (Fujioka, Ross, Kakigi, Pantev, & Trainor, 2006; see also Shahin, Roberts, & Trainor, 2004).

Arguing for heightened susceptibility for training-induced neuroplasticity in early age, a number of studies have found that structural and functional changes are especially pronounced in musicians who have begun their training at an early age than in late-trained ones (Bailey et al., 2013; Bengtsson et al., 2005; Elbert et al., 1995; Schlaug et al., 1995; Steele et al., 2013; Wong et al., 2007).

A vast literature indicates that various ERP responses evoked by different types of auditory incongruities are also enhanced in adult musicians and musically trained children (Besson & Faïta, 1995; Besson, Faïta, Requin, 1994; Brattico, Tupala, Glerean, & Tervaniemi, 2013; James et al., 2008; Jentschke & Koelsch, 2009; Magne, Schön, &

Besson, 2006; Marie, Magne, & Besson, 2011; Marques, Moreno, & Besson, 2007; Moreno, Marques, Santos, Santos, & Besson, 2009; Schön, Magne, Besson, 2004). Out of such change-related responses, the MMN is probably the most extensively used in investigating auditory skills in adult musicians and non-musicians (for a review, see Tervaniemi, 2009). When compared to non-musicians, musicians display larger and/or earlier MMNs to violations of different types of spectral, temporal, and spatial regularities (Brattico et al., 2009; Brattico, Näätänen, & Tervaniemi, 2002; Fujioka, Ross, Trainor, Kakigi, & Pantev, 2004; 2005; Herholz, Boh, & Pantev, 2011; Koelsch, Schröger, & Tervaniemi, 1999; Nager, Kohlmetz, Altenmüller, Rodriguez-Fornells, & Münte, 2003; Nikjeh, Lister, & Frisch, 2008; 2009; Tervaniemi, Castaneda, Knoll, & Uther, 2006; Tervaniemi, Rytkönen, Schröger, Ilmoniemi & Näätänen, 2001; van Zuijen, Sussman, Winkler, Näätänen, & Tervaniemi, 2005; Vuust et al., 2005). Compared to MMNs to simple tonal stimuli, those elicited by musical sounds such as melodies or chords appear to differentiate musicians and non-musicians more consistently (Fujioka et al., 2004; Koelsch et al., 1999).

With regard to the development of the MMN enhancement in musicians, cross-sectional studies have reported enhanced MMNs in musically trained school-aged children for frequency changes in violin tones (Meyer, Elmer, Ringli, Oechslin, Baumann, & Jäncke, 2011), for changes from major chords to minor chords (Virtala, Huotilainen, Putkinen, Makkonen, & Tervaniemi, 2012), and for pitch and voice onset time (VOT) changes in speech sounds (Chobert, Marie, François, Schön, & Besson, 2011). Finally, a recent longitudinal study (Chobert, François, Velay, & Besson, 2013) found larger amplitude increase for the MMN to syllable duration and voice onset time deviants within a 12-month follow-up in 8–10-year old children who were randomly assigned to group music classes compared to children assigned to painting classes.

Augmented P3a responses have also been reported in adult musicians (Brattico et al., 2013; Trainor, Desjardins, & Rockel, 1999, Vuust et al., 2009) indicating that attention switch towards sound changes may be more readily triggered in musically trained than non-trained adults. Although musical training has been suggested to affect attention-related functions in childhood (e.g., Trainor, Shahin, & Roberts, 2009) altered P3as in musically trained children have not thus far been reported.

In sum, there is ample evidence of structural and functional differences between adult musicians and non-musicians brains and recent studies in children have begun to map the emergence of these differences at initial stages of training. More extensive longitudinal studies are needed to examine the long-term effects of musical training on functional brain maturation.

1.3. Informal musical activities and auditory skill development

As reviewed above, the neuroplastic effects of formal musical training have received considerable attention during recent decades. For most children, however, more informal musical activities such as singing, dancing, and musical play are much more characteristic of daily musical experience than formal training on a musical instrument. Whether such everyday musical activities can shape auditory development has not been investigated thoroughly so far.

Animal studies show that enriched ambient auditory stimulation can foster cortical reorganization that facilitates auditory functions such as response strength of auditory cortical neurons and auditory spatial and duration discrimination (Cai, Guo, Zhang, Xu, Cui, & Sun, 2009; Engineer et al., 2004; Percaccio et al., 2005). In humans, exposure to one’s native language in early childhood is an obvious example of informal auditory experience that results in profound, long-term changes in auditory abilities that not only shape speech sound processing but generalizes to non-linguistic sounds as well. For example, native speakers of Finnish—a quantity language—have repeatedly been shown to display enhanced sound duration processing as indexed by the MMN to duration changes in non-speech and speech sounds when compared to native speakers of French (Marie, Kujala, & Besson, 2012), German (Tervaniemi et al., 2006) or Russian (Nenonen, Shestakova, Huotilainen, & Näätänen, 2003). In the musical domain, several lines of evidence suggest that long-term incidental exposure to music affects auditory processing abilities. Firstly, even musically non-trained adults show (implicit) competence in processing some fairly nuanced aspects of music including tonality and harmony (Bigand & Pineau, 1997; Brattico et al., 2006; Cuddy & Badertscher, 1987; Honing & Ladinig, 2009; Koelsch, Grossmann, Gunter, Hahne, Schröger, & Friederici, 2003; Koelsch, Gunter, Friederici, & Schröger, 2000; Krohn, Brattico, Välimäki, &

Tervaniemi, 2007; Smith, Nelson, Grohskopf, & Appleton, 1994; Vuvan, Prince, & Schmuckler, 2011). Presumably, these idiosyncrasies of Western tonal music are internalized through everyday musical experiences. In infants, a development reminiscent of the tuning to native speech sounds (Kuhl, Williams, Lacerda, Stevens, & Lindblom, 1992; Cheour et al., 1998) appears to take place with regard to the processing of culturally typical *vs.* untypical metric (Hannon & Trehub, 2005a; 2005b) and scale structures (Trehub, Schellenberg, & Kamenetsky, 1999) in music. Consequently, adults show an advantage in processing music that follows the conventions of their culture (Demorest & Osterhout, 2012; Drake & El Heni, 2006; Kessler, Hansen, & Shepard, 1984; Krumhansl et al., 2000). Studies suggest that with regard to tonality and meter such musical enculturation can be accelerated in infants by interactive musical experience in playschool settings (Gerry, Faux, & Trainor, 2010; Gerry, Unrau, & Trainor, 2012). At the very least, these studies demonstrate that exposure to music and musical interaction without specific training is sufficient for learning culture-specific implicit musical knowledge. More generally, these effects raise the question whether informal exposure to music might also influence the development of auditory processing outside the musical domain.

An ERP study by Trainor, Lee, and Bosnyak (2011) found that exposure to recorded music can shape timbre processing in infants. Namely, 4-month-old infants who were randomly assigned either to a group that was exposed to recordings of melodies in a guitar timbre or to a group that heard the same melodies in marimba timbre showed enhanced ERP responses to tones in the timbre to which they were exposed. Furthermore, occasional pitch changes in the guitar tones elicited a mismatch response only in the guitar-exposed infants whereas pitch changes in the marimba tones did not elicit a significant mismatch response in either group. These results suggest that in infancy, even a relatively short exposure can strengthen the neural representations of a given timbre which is further reflected in enhanced processing of pitch in that timbre.

Thus, the evidence reviewed above suggests that even without formal training, auditory experience, including musical exposure, may shape auditory development in infants and young children. However, no study to date has explicitly looked at how variation in the amount of musical exposure in the home environment is related to auditory skills in early childhood.

2. Aims

The present thesis examines the effects of formal musical training on the maturation of neural auditory discrimination in school-aged children and the association between informal musical activities and auditory discrimination and attention in early childhood.

In *Study I* profiles of MMN, P3a and LDN responses were recorded in the Multi-feature paradigm from 2–3-year-old children in order to examine their ability to neurally discriminate changes in frequency, duration, intensity, sound-source-location and temporal structure of sound and detect salient novel sounds. In addition to the traditional group level analysis, the responses of each individual child were also examined.

Study II explored the relation between informal musical activities at home (e.g., singing and musical play) and the aforementioned ERP indices of auditory discrimination and attention. It was hypothesized that musically enriched home environment would be associated with heightened sensitivity to auditory changes reflected by augmented MMN and P3a responses to deviant tones, more mature processing of auditory changes reflected by diminished LDN, and lower distractibility by salient, surprising auditory events reflected by reduced P3a and LDN/RON to novel sounds.

Studies III and IV investigated the maturation of auditory change detection as indexed by the MMN in a (semi) longitudinal setting (i.e., the majority of the children participated in at least two measurements) in children who play a musical instrument and children who take no music lessons. Study III employed an oddball paradigm where occasional deviant minor chords are presented among repeating standard major chords and the Multi-feature paradigm frequency, duration, location, intensity, and gap deviants. Study IV, in turn, employed a novel Melodic multi-feature paradigm with changes in melody, rhythm, musical key, timbre, tuning, and timing. With regard to maturational effects, the MMN was hypothesized to increase in amplitude with age. With regard to the effects of training, the musically trained children were expected to display larger increase in MMN amplitude in comparison to the nontrained children especially for the more music-like stimuli. Furthermore, group differences were expected to be absent in the early stages of training and only gradually appear as the children taking music lessons accumulated musical expertise.

3. Methods

3.1. Subjects

In Studies I and II, the participants were 2–3-year-old children, and in Studies III and IV, school-aged musically trained and non-trained children. In all four studies, the participants had Finnish as their native language, were mainly from middle-class and upper-middle-class families from the Helsinki area, and had no illnesses and no reported hearing or other medical problems. A more detailed description of the subject characteristics is given below.

3.1.1. Studies I and II

Seventeen children participated in Study I. The data recorded from 3 subjects were discarded from the analysis because of an insufficient number of artefact-free trials. The mean age of the remaining 14 subjects (7 girls) was 2.76 years (range 2.17–3.25 years).

Thirty one children participated in Study II. The data from 6 subjects were discarded from the analysis either because of an insufficient number of artefact-free trials (n=4) or because of incomplete questionnaire data (n=2). The mean age of the remaining 25 subjects (13 girls) was 2.79 years (range 2.38–3.29 years). The data from 13 of the children were also included in Study I.

All children in Studies I and II had attended once a week the same playschool providing the children and their parents with guided musical group activities (e.g., singing in group, rhyming, moving along the music etc.).

3.1.2. Studies III and IV

In Studies III and IV, the Music group consisted of children who had started playing a musical instrument approximately at the age of seven. The most common instruments played were violin, viola, cello, double bass, guitar, and flute. The children in the Music group attended a public elementary school which has solo instrument lessons, choir and orchestra practice, and music theory studies integrated as part of the daily curriculum. The control group consisted of children who had neither formal musical training nor hobbies involving music and attended a standard public elementary school. According to a questionnaire filled by the parents, a great majority of the control children participated in some adult-guided, mostly sport-related extracurricular activity.

Study III reports data from 250 recordings from 125 children for the Chord paradigm and data from 261 recordings from 121 children for the Multi-feature paradigm. The number of subjects in the Music and Control groups in the final sample and their age are given separately in Table 1 for the two paradigms used in the study. The overall percentage of boys was approximately 40% for the Music and 54% for the Control group. However, at age 13 (i.e., when the group difference in response amplitude was expected to be the most pronounced) there was no statistically significant difference between the groups in gender ratio (Multi-feature paradigm: 41% and 46% of boys in the Control and Music groups, respectively, $\chi 2(1, N = 50) = .152$, $p = .696$; Chord: 39% and 46% of boys in the Control and Music groups, respectively; $\chi 2(1, N = 51) = .274$, $p = .601$) or socioeconomic status (SES) (Multi-feature paradigm: $t(48)=1.08$, $p = .288$; Chord: $t(46)=1.22$, $p = .227$) as measured by parental income and education (Income scale: 1 = under a 1 000 Euros/month, 2 = 1 000–2 000 Euros/month, 3 = 2 000–3 000/month, 4 = 3 000–4 000/month, 5 = 4 000–5 000 Euros/month, 6 = over 5 000/month; Education scale: 1 = comprehensive school, 2 = upper secondary school or vocational school, 3 = a higher degree than upper secondary school or vocational school which is not a bachelor’s, master’s, licenciate, or doctoral degree, 4 = Bachelor's degree or equivalent, 5 = Master’s degree or equivalent, 6 = licenciate or doctoral level degree).

Table 1. The number of subjects (N), their age for the Music and Control groups in the Chord and Multi-feature paradigms at ages 7–13 (Y) in Study III.

	Multi-feature paradigm				Chord paradigm			
	N		Mean age		N		Mean age	
Y	Music	Control	Music	Control	Music	Control	Music	Control
7	39	27	7.19	7.51	44	28	7.2	7.5
9	38	28	9.27	9.24	41	30	9.23	9.26
11	37	31	11.53	11.51	37	30	11.53	11.5
13	22	28	13.08	13.25	23	28	13.07	13.24

Data from 185 recordings from 117 children are reported in Study IV. The number of subjects in the Music and Control groups in the final sample and their age are given in Table 2. At age 13 there was no statistically significant difference between the groups SES (t(48)=1.08). Because of the considerable difference in the percentage of boys and girls between the groups in Study IV gender was included as a factor of no interest in the statistical analysis (see below).

Table 2. The number of subjects (N), their mean age, age range and gender distribution for the Music and Control groups in Study IV.

	Mean age (range)		N (N of girls)	
Y	Music	Control	Music	Control
9	9.28 (8.75–9.94)	9.28 (8.79–9.72)	27 (20)	24 (10)
11	11.55 (10.60–12.75)	11.41 (10.43–12.60)	38 (24)	34 (12)
13	13.17 (12.55–13.91	13.16 (12.61–13.85	26 (18)	36 (16)

Studies III and IV are a part of a larger ongoing longitudinal study in which the same children are invited to participate in several EEG experiments and a new group of children is recruited every two years. Therefore, the children who were recruited earlier had already participated in several measurements while those recruited last had been measured only once. There were also 16 recordings with the Multi-feature paradigm and 14 recordings with the Chord paradigm in Study III and 12 recordings in Study IV from which the data were discarded because of too few accepted trials. Some subject attrition also occurred due to scheduling issues or because some children were not reached at the time when the recordings were conducted. The number of children who participated in a given number of recordings are listed in Table 3. Note that in Study III and IV, the follow-up consisted of four and three measurements, respectively.

Table 3. The number of children in the Music and Control group who participated in one, two, three, or four successful EEG recordings in Studies III and IV.

	Study III				Study IV	
	Number of subjects					
Number of Recordings	Chord		Multi-feature paradigm		Melodic multi-feature paradigm	
	Music	Control	Music	Control	Music	Control
1	15	30	9	25	24	36
2	26	26	24	28	26	20
3	7	4	12	5	5	6
4	12	5	13	5	-	-

3.2. Procedure

During the experiments, the children sat in a recliner chair in an acoustically attenuated and electrically shielded room. In Studies I and II, the children were accompanied by a parent. The children and their parents were instructed to move as little as possible and to silently concentrate on a self-selected book and/or children's DVD (with the volume turned off) during the experiment. In Studies I and II the stimuli were presented through two loudspeakers in front of the participant at a distance of 1.5 m and at an angle of 45° to the right and to the left. In Studies III and IV, the stimuli were presented via headphones.

A signed informed consent was obtained from the parents for their child's participation in the experiment. The child's consent was obtained verbally. The experiment protocol was approved by the Ethical Committee of the former Department of Psychology, University of Helsinki, Finland. A great deal of effort was made to ensure that measurements were as comfortable as possible for the children. Child-appropriate ways to explain the experiments and to enquire their consent for participation were developed. The youngest children were always accompanied by a parent throughout the experiment. A psychologist or student of psychology was always present in measurements to monitor the emotional state of the children and ensure that all possible ethical considerations were met

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3.3. Stimuli

3.3.1. Study I and II

Studies I and II employed a modified version of the Multi-feature paradigm in which standard tones (p ~ .50, N= 1 875) were presented in an alternating manner with deviant tones (p ~ .42, N = 1 590) from five categories and novel sounds (p ~ .08, N=280) from two categories. The order of the non-standard sounds was random with the restriction being that two successive deviant tones or novel sounds were not from the same category. The stimuli were presented with a stimulus-onset-asynchrony (SOA) of 800 ms making the duration of the whole sequence approximately 50 minutes.

The standard and deviant tones were complex tones that included the first two harmonics (-3 and -6 dB in intensity compared to the fundamental). The standard tones had a fundamental frequency of 500 Hz and a duration of 200 ms (including 10 ms rise and 20 ms fall times) and were presented at an intensity of 60 dB (SPL) The deviant tones differed from the standard tones in either in frequency, intensity, duration, sound-source location, or by having a silent gap in the middle. Otherwise the deviant and standard tones were identical. The magnitude of the frequency and the duration deviants was manipulated on three levels and for the frequency deviants both up and down. There frequency deviants had the fundamental frequencies of 333.3, 750 (large), 400, 625 (medium), 454.5, and 550 Hz (small frequency decrements and increments, respectively). The durations of the three levels of the duration deviants were 100, 150, and 175 ms (large, medium, and small, respectively). The intensity deviants were −6 dB and +6 dB compared to the standard. The sound-source location deviants were delivered through either only the left or only the right speaker. Finally, the gap deviant had a silent gap (5-ms gap with 5-ms fall and rise times) in the middle of the sound.

The six frequency deviants were presented 70 times each (i.e., 140 repetitions/level) and the three duration deviants were presented 140 times each. The intensity, sound-source location, and gap deviants, in turn, were presented 250 times each.

In addition, there were two types of novel sounds. Similarly to the standard tones, the duration of the novel sounds was 200 ms. The repeating novel sound, the word /nenä/ (meaning ‘nose’ in Finnish) spoken in a neutral female voice, was presented 72 times. The varying novel sounds, in turn, were either machine-like sounds, animal calls, or noises and these were presented 216 times. To retain the novelty value of the varying novel sounds throughout the recording session, each individual novel sound was presented up to a maximum of four times during the whole experiment. Furthermore, one-third of the varying novel sounds were presented through the left, one-third through the right, and one-third through both loudspeakers.

3.3.2. Study III

Basic auditory processing was investigated in the Multi-feature paradigm that included frequency, duration, intensity, location, and gap deviants while the detection of musically more relevant sound changes was examined in an oddball paradigm with major chords as standards and minor chords as deviants.

In the Multi-feature paradigm, the standard tones (p = .50, N = 1200) again alternated with deviants (p = .10, N = 120/deviant type) that were presented in a pseudo-random order so that two successive deviant tones were never from the same category.

The standard and deviant tones were complex tones that included the first two harmonics (−3 and −6 dB in intensity compared to the fundamental). They had a fundamental frequency of 500 Hz and were 100 ms in duration (including 5-ms rise and fall times). The frequency deviants had the fundamental frequency of 450 or 550 Hz. The duration deviants were 65 ms in duration. The intensity deviants were -5 dB compared to the standard. The location deviants were presented only from the left or right head phone. Finally, the gap deviants had a 4-ms silent gap in the middle of the tone. The stimuli were presented with a SOA of 500 ms making the duration of the sequence 10 minutes.

In the Chord paradigm, deviant C minor triad chords (p = ~.16, N = 75) were presented among standard C major triad chords (p = ~.84, N = 455) in a pseudo random order with the restriction that at least two standards always followed a deviant. The fundamental frequencies of the sinusoidal tones composing the chords were 262, 330, and 392 Hz for the standard chords and 262, 311, and 392 Hz for the deviant chords. The duration of the chords was 125 ms (including 5-ms rise and fall times) and they were presented with the SOA of 725 ms making the duration of the sequence approximately 6.5 minutes.

3.3.3. Study IV

The Melodic multi-feature paradigm consisted of melodies played in a digital piano timbre. The melodies were composed of a major triad chord followed by five tones that belonged to the same major key as the chord in accordance of Western music tradition (see Figure 3). The frequencies of the tones used to construct the stimuli ranged from 233.1 to 466.2 Hz

The duration of the chord at the beginning of each melody was 300 ms. The duration of two out of the four following tones was 125 ms (short inter-tones), and the duration of the other two was 300 ms (long inter-tones). The final tone of each melody was always the tonic and was 575 ms in duration. The chord and the tones within a melody were separated by 50-ms silent intervals and the last tone of the melody was followed by a 125-ms silent period lasting until the beginning of the next melody. Therefore, the interval from the beginning of each melody to the beginning of the next one was 2.1 sec in total. The duration of the whole stimulus sequence was approximately 13 minutes.

Occasionally one of six changes took place in the melodies. In 80 melodies, one of the long inter-tones at the fourth or fifth position of the melody was replaced with another in-key tone (Melody modulation, see Figure 3). In 72 melodies, the duration of two successive tones were switched, i.e., the rhythmical pattern was changed (Rhythm modulation). Ninety-six of the melodies were transposed by a semitone up or down (Transposition). In 96 melodies, one of the long inter-tones or the final tones was played with a flute timbre instead of the piano timbre (Timbre deviant). In 72 melodies, one of the long inter-tones was mistuned by a ½ semitone, i.e., less than 3% (Mistuning). Finally, in 100 melodies, one of the short or long inter-tones or the final tones was presented 100 ms too late (Timing delay).

After a melody or rhythm modulation or a transposition, the melody was repeated with the new rhythmic or pitch pattern or in the new key until the next corresponding change at least once and on average 3–4 times in the so called roving standard manner (cf. Cowan et al., 1993).

3.4. EEG recordings

3.4.1. Studies I & II

The EEG was recorded (NeuroScan 4.3, NeuroScan Co., El Paso, TX, USA) from the electrodes F3, F4, C3, C4, Pz, and the left and right mastoids (LM and RM, respectively) by using Ag/AgCl electrodes with a common reference electrode placed at Fpz (band pass filter during recording 0.10–70 Hz, 24 dB per octave roll off, sampling rate 500 Hz). To monitor eye movements and blinks, the electro-oculogram (EOG) was recorded using electrodes placed above and at the outer canthus of the right eye.

3.4.2. Studies III & IV

The EEG recordings were conducted either using a Neuroscan or a BioSemi Active-Two system. In the recordings conducted with the Neuroscan system, the EEG was registered the channels F3, Fz, F4, C3, Cz, C4, P3, Pz, P4, and the left and right mastoids using Ag/AgCl electrodes with a common reference electrode placed at the nose (band pass filter during recording 0.10–70 Hz, 24 dB per octave roll off, sampling rate 500 Hz). The EOG was recorded with electrodes placed above and at the outer canthus of the right eye. In the recordings conducted with the BioSemi system (BioSemi, Amsterdam, the Netherlands), the EEG was registered with a sampling rate of 512 Hz from 64 active electrodes mounted in a Biosemi head cap according to the International 10-20 system. The EOG was recorded with active electrodes situated below and at the outer canthus of the right eye. Additional active electrodes were placed at the nose and to the right and left mastoid.

3.5. Data analysis

3.5.1. Study I

The data were filtered offline between 0.5–30 Hz. EEG epochs from 100 ms before to 800 ms after tone onset were baseline corrected against the 100-ms pre-stimulus interval. Epochs with voltage exceeding ±125 μV at any channel were discarded and the remaining epochs were re-referenced to the average of the two mastoids.

The data of each subject were spatially filtered to reduce noise. For each response (MMN, P3a, LDN) for each deviant tone and novel sound type, spatial templates were defined by measuring the amplitudes from the grand average deviant/novel sound-minus-standard difference signals at channels F3, F4, C3, C4, and Pz at the latencies of the MMN and LDN defined at F4 and the P3a defined at C3. Thereafter, single-trial difference signals for each deviant and novel sound (i.e., the unaveraged EEG epochs time-locked to each non-standard sound minus subject's average response to the standard sound) were spatially filtered (using NeuroScan EDIT, version 4.4) and the signals of interest were retained according to the spatial templates.

The single-trial difference signals of the frequency decrement deviants, frequency increment deviants, and duration deviants were filtered according to the spatial template defined from the grand average difference signal of the largest frequency decrement (333.3 Hz), frequency increment (750 Hz) or duration deviant (100 ms), respectively. For all other non-standard responses, each type of single-trial difference signal was filtered according to the spatial templates that were defined from the grand average difference signal of the corresponding type.

At the individual level of the analysis, MMN, P3a, and LDN mean amplitudes were calculated over a 40-ms time windows from the spatially-filtered single-trial difference signals. To determine whether the responses significantly differed from zero for individual subjects, a hierarchical linear model analysis (e.g., Bryk, 1992) was conducted separately for each response using the Mixed module in a SAS (version 9.2) statistical package.

For the group level analysis, the spatially filtered single-trial data for each deviant and novel sound were averaged separately for each subject. Mean amplitudes were calculated over a 40-ms time window from these signals and the grand mean of these values for each deviant and novel sound was compared to zero using two-tailed one-sample t-tests. For the duration deviant, frequency increment and frequency decrements, a one-way repeated measures analysis of variance (ANOVA) was conducted to test the effect of the deviant size (3 levels: small, medium, and large). Greenhouse-Geisser corrections were made when appropriate. For the t-tests and the hierarchical linear model analysis, the False Discovery Rate (FDR) correction ($p < .05$) was used to control for multiple comparisons (Benjamini & Hochberg, 1995).

3.5.2. Study II

The data were filtered offline between 0.5–20 Hz. EEG epochs from 100 ms before to 800 ms after tone onset were baseline corrected against the 100-ms pre-stimulus interval. Epochs with voltage exceeding ±100 μV at any channel were discarded. The remaining epochs were averaged separately for each stimulus and subject and re-referenced to the average of the two mastoids.

For the frequency and duration deviants, only the responses to the largest deviants were included in the analysis because of their better signal-to-noise ratio compared to the responses to the smaller deviants. For the novel sounds, in turn, only the responses to the varying novel sounds were included in the analysis since they were thought to be more likely to trigger cognitive processes related to novelty detection and distraction than the repeating novel sounds.

For the analysis of the MMN and P3a, mean amplitudes of the responses were calculated from channels F3, F4, C3 and C4 over 50-ms time windows centered on the peak latencies of these responses at F3 which was deemed as a representative of the response for all the four channels included in the analysis. These values were then averaged together separately for each response and the average value was used for testing the significance of the response and for the correlation analyses (see below). An identical procedure was used for the LDN and novelty P3a except that a 100-ms time window was used in the analyses as these responses spanned a longer time period than the MMN and the P3a elicited by the deviant tones.

The parents of the children filled out a detailed questionnaire concerning the musical behaviour of their children and their own musical activities at home. With regard to singing, both parents were asked to report (i) how often they sang to their children, and more specifically (ii) how often this involved singing familiar songs (e.g., well-known children’s songs) or (iii) songs they had invented themselves. With regard to the musical behaviours of the children at home, the parents rated (i) how often their children sang familiar melodies, (ii) sang self-invented melodies, (iii) drummed rhythms, or (iv) danced at home. For all the aforementioned questions, the answers were given using a five point scale (1 = almost never; 2 = once a month at most; 3 = several times a month; 4 = approximately once a week; 5 = almost daily).

The scores for the questions related to singing were added together to form a composite singing score separately for both parents. Similarly, the scores for the questions regarding the musical behaviour of the children were summed to form a composite musical behaviour score for each child. Finally, these composite scores were normalized by subtracting the mean of the variable from each score and dividing this difference by the standard deviation of the variable. The normalized musical behaviour scores and father's singing scores were added together to form an overall composite score for musical activities at home. The overwhelming majority of the mothers responded with the highest possible value to all the questions related to child-directed singing. In contrast, there was considerable variation in the amount of singing reported by the fathers. Therefore, for the questions regarding child-directed singing, only the fathers' scores were included in the analysis.

To test the statistical significance of the MMN, P3a and the LDN for a given deviant, the mean amplitudes were compared to zero with two-tailed one-sample t-test. Pearson's correlation coefficients between the overall musical behavior score and the MMN, P3a, and LDN amplitudes were calculated. Partial correlations between the response amplitudes and the overall musical activities at home score were also calculated to control for the child's age, gender, and SES (measured as in Study II).

3.5.3. Study III

For the 64-channel Biosemi data, noisy channels were interpolated or excluded from further analysis, and an automatic artifact correction system implemented in BESA 5.1 software was used. These data were down-sampled to 500 Hz to match the data recorded with the Neuroscan system. Both sets of data were filtered offline between 1–20 Hz. EEG epochs from 100 ms before to 400 ms after tone onset were baseline corrected against the 100-ms pre-stimulus interval and those with voltage changes exceeding ±100 μV were excluded from further analyses. The epochs of each participant were averaged separately for each deviant and standard sound and re-referenced to the average of the two mastoid channels.

From these signals, the MMN and P3a mean amplitudes were calculated over 50-ms time windows from the average of deviant-minus-standard difference signals at F3, Fz, and F4. These windows were chosen so that they were all within the expected latency range of the MMN or P3a and covered the responses of both Music and Control groups at all ages (see the original publication for details).

Linear mixed model analyses were performed using SPSS to estimate the rate of change in the amplitudes of the MMN and P3a as function of the repeated variable Age (7, 9, 11, and 13) and the Group factor (Music *vs.* Control). On the basis of Schwarz's Bayesian Criterion (BIC) compound symmetry was chosen as the covariance structure. When the Linear mixed model analysis revealed a significant interaction between age and group, a pairwise comparison of the response amplitudes between the Music and Control groups at age 7 was performed using independent samples t-tests to test for group differences at baseline.

3.5.4. Study IV

The offline filtering, channel exclusion and interpolation, artifact correction and rejection were conducted as in Study III (see above). Epoch from 50 ms before to 350 ms after sound onset were baseline corrected against the 50-ms pre-stimulus period, averaged separately for each sound type and subject, and re-referenced to the average of the two mastoid channels.

The responses to the changes were compared to responses elicited by standard tones that were matched in duration and (approximate) position within the melody for each change type (see Figure 3). The responses to the melody modulation and mistuning were compared to the responses elicited by the long inter-tones. For the transpositions, the standards were the chords at the beginning of non-transposed melodies. For the rhythm modulations and timing delays, in turn, both the long inter-tones and short inter-tones served as the standards. Finally, for the timbre deviants, the standards included the long inter-tones and the final tones at the end of the melodies. Furthermore, since our preliminary analyses of the data indicated that the early part of the response to the changes and the long latency responses evoked by the preceding sounds overlapped, the standards were also matched separately for each change type by the duration and type of the preceding sound (i.e., inter-tone *vs.* chord; change *vs.* repeated tone) to avoid differences in the responses to the standards and changes arising from the differential responses to the preceding sounds.

The MMN mean amplitudes were calculated from Fz for each deviant over a 50-ms time windows centered on the latency of the most negative peak between 100–200 ms in the average of channels F3, Fz and F4.

The MMN amplitude was analyzed using linear mixed model (SPSS) with Age (9, 11, and 13) and the Group (Music *vs.* Control) as factors. The main effect of Gender was also entered in the model as a factor of no interest to control for the unequal distribution of boys and girls in the Music and Control groups. Compound symmetry was chosen as the covariance structure on the basis of Schwarz's Bayesian Criterion (BIC). Bonferroni corrected pair-wise post-hoc comparisons were performed when a significant main effect of Group or the Group × Age interaction was found.

4. Results

4.1. Measuring auditory event-related potential profiles in 2–3-year-old children.

The aim of Study I was to test the feasibility of using the Multi-feature paradigm to record individual profiles of MMN, P3a and LDN responses from 2–3-year-old children to changes in frequency, duration, intensity, perceived sound-source-location and to gap deviants as well as to surprising novel sounds.

The difference signals for the deviant tones are illustrated in Figure 4 A. A significant negative response in the expected MMN time range was elicited by the gap deviant, all the duration deviants, the large frequency increment deviant, the sound-source location deviants, and the intensity deviants ($t(13) = 2.59–6.14$, $p < .05$). The large duration deviant, the gap deviant, the large frequency decrement, the large and medium frequency increments and the sound-source location deviants elicited significant positive P3a-like responses ($t(13) = 1.94–4.57$, $p < .05$). Finally, all deviants elicited significant LDN responses ($t(13) = 2.93–9.60$, $p < .05$).

The difference signals for the novel sounds are illustrated in Figure 4 B. Both novel sounds elicited a prominent P3a-like response (varying novel sounds: $t(13) = 9.00$, $p < .001$; repeated novel sounds: $t(13) = 8.50$, $p < .001$) followed by an LDN/RON (varying novel sounds: $t(13) = 9.70$, $p < .001$; repeated novel sounds: $t(13) = 7.15$, $p < .001$).

Thus, at the group level, the results demonstrate that the Multi-feature paradigm is well suited for recording comprehensive multicomponental profiles of change-related auditory ERPs from 2–3-year-old children.

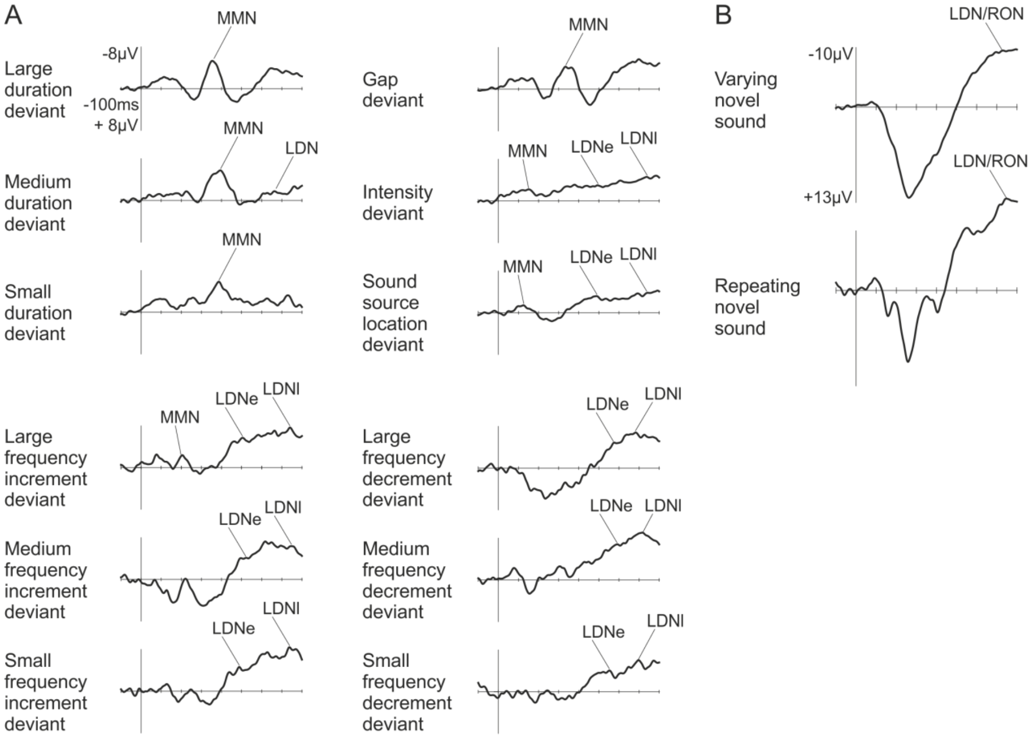

Figure 4. The difference signals for the deviant tones (A) and novel sounds (B) at F4 obtained in the Multi-feature paradigm in Study I. LDNe and LDNl refer to the early and late part of the LDN, respectively.

The FDR threshold for the individual responses was approximately .015. The statistically significant responses of the individual subjects to the deviant tones and novel sounds are listed in Table 4 along with the corresponding effect sizes (Cohen’s d). Note that, to reduce the number of statistical tests, not all responses evident at the group level were analysed in individual subjects. The responses of individual subjects are illustrated in Figure 5.

For the deviant tones, the number of significant responses after the FDR correction remained fairly low with the gap deviant producing significant responses most consistently. In contrast, the majority of the subjects had P3a and LDN/RON responses to the novel sounds that were statistically highly significant. The responses to the novel sounds were characterized by relatively high amplitudes and fairly consistent morphology across subjects as is illustrated in Figure 5.

Table 4. The *p*-values (*p*) and Cohen’s d (*d*) for the individual spatially-filtered difference signals obtained in Study I. Significant *p*-values (after the FDR correction at *p*<,05; adjusted critical value = .015) are marked in bold. LDNl refer to the early and late part of the LDN.

			Subject													
			1	2	3	4	5	6	7	8	9	10	11	12	13	14
Large frequency increment (750 Hz)	MMN	*p*	0.18	0.51	0.40	0.33	0.48	0.40	0.35	0.56	0.35	0.47	0.44	**0.01**	0.42	0.72
		d	.21	.15	.16	.17	.11	.22	.22	.14	.15	.16	.12	.53	.28	.07
	P3a	*p*	0.19	0.17	0.07	0.20	**0.01**	0.21	0.94	0.86	0.91	0.02	0.04	0.15	0.58	0.89
		d	.22	.27	.29	.18	.42	.23	.02	.03	.02	.47	.26	.30	.12	.03
	LDNl	*p*	0.71	0.41	0.05	0.76	0.23	0.57	0.05	0.14	0.02	0.13	0.30	**0.00**	0.48	0.36
		d	.07	.15	.23	.05	.16	.13	.45	.27	.33	.35	.15	.49	.20	.20
Large frequency decrement (333.3 Hz)	P3a	*p*	0.19	0.29	**0.00**	0.80	**0.01**	0.35	0.28	0.70	**0.00**	**0.01**	**0.00**	0.31	**0.00**	0.04
		d	.24	.15	.34	.03	.38	.13	.20	.06	.52	.54	.56	.17	.61	.34
	LDNl	*p*	0.05	0.10	0.04	0.18	0.15	0.84	0.29	**0.00**	0.85	0.42	0.57	**0.01**	0.20	0.07
		d	.40	.29	.29	.17	.22	.03	.22	.58	.03	.13	.09	.47	.25	.32
Large duration change (100 ms)	MMN	*p*	0.12	0.12	0.91	0.12	**0.00**	0.68	0.04	0.37	**0.00**	0.64	**0.00**	0.11	0.41	0.02
		d	.16	.17	.01	.16	.35	.04	.24	.09	.43	.07	.37	.17	.12	.27
	P3a	*p*	0.38	0.62	0.39	0.42	0.10	0.07	0.87	0.67	0.53	0.17	0.99	0.68	0.91	0.77
		d	.14	.07	.10	.13	.22	.22	.03	.06	.08	.25	.00	.06	.03	.05
	LDN	*p*	0.66	0.04	0.89	0.27	0.25	0.97	**0.01**	0.24	0.02	0.77	0.66	**0.01**	0.21	0.13
		d	.06	.24	.01	.13	.13	.00	.32	.15	.26	.04	.05	.33	.22	.18
Intensity deviant	MMN	*p*	0.90	0.56	0.52	0.02	0.09	0.73	0.08	0.43	0.13	0.86	0.70	0.20	0.93	0.30
		d	.01	.06	.06	.25	.13	.03	.19	.10	.12	.02	.04	.12	.01	.11
	LDNl	*p*	0.39	0.02	0.15	0.05	0.08	0.49	0.05	0.04	**0.00**	0.40	0.23	**0.00**	0.07	0.03
		d	.08	.21	.09	.17	.12	.06	.17	.19	.30	.08	.10	.27	.24	.21
Sound-source location deviant	MMN	*p*	0.83	0.23	0.53	0.82	0.82	0.94	0.84	0.84	0.82	0.95	0.97	0.82	0.87	0.87
		d	.05	.22	.12	.05	.04	.01	.05	.05	.04	.02	.01	.04	.05	.03
	P3a	*p*	0.50	0.73	0.95	0.84	0.07	0.81	0.33	0.26	0.36	0.27	0.51	0.63	0.28	0.02
		d	.07	.04	.01	.03	.17	.02	.11	.12	.08	.17	.07	.04	.15	.28
	LDNl	*p*	0.26	**0.00**	0.02	**0.01**	0.08	0.98	0.16	0.77	0.11	0.95	0.13	**0.00**	0.03	0.04
		d	.09	.28	.15	.22	.13	.00	.15	.03	.12	.01	.13	.34	.22	.20
Gap deviant	MMN	*p*	0.98	**0.00**	0.33	0.07	**0.00**	**0.00**	0.43	0.03	**0.01**	0.49	0.04	0.53	0.58	**0.00**
		d	.00	.32	.07	.14	.43	.27	.07	.16	.18	.07	.16	.05	.06	.30
	P3a	*p*	**0.01**	0.73	0.27	0.11	**0.00**	0.03	0.56	0.59	0.43	0.06	**0.00**	0.31	0.23	0.86
		d	.20	.03	.09	.13	.36	.18	.05	.04	.05	.19	.27	.08	.15	.02
	LDN	*p*	0.07	**0.00**	**0.01**	0.29	**0.00**	**0.01**	0.05	**0.01**	**0.00**	0.04	0.08	**0.00**	0.06	0.02
		d	.13	.34	.17	.07	.33	.20	.18	.21	.24	.20	.14	.34	.21	.23
Varying novel sounds	P3a	*p*	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	0.07	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
		d	.59	.80	.45	.59	.74	.37	.66	.17	.62	.77	.54	.55	.74	.76
	LDN	*p*	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	0.02	**0.00**	**0.00**	**0.00**	**0.00**	**0.01**	**0.00**	**0.00**	**0.00**
		d	.27	.61	.23	.30	.50	.20	.35	.55	.36	.32	.23	.85	.67	.62
Repeating novel sounds	P3a	*p*	0.41	**0.00**	0.02	0.83	**0.01**	**0.00**	**0.00**	0.27	**0.00**	0.04	**0.00**	**0.00**	**0.00**	**0.00**
		d	.12	.45	.30	.03	.35	.86	.80	.22	.72	.34	.45	.90	.92	.64
	LDN	*p*	0.09	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	0.24	**0.00**	**0.01**	**0.00**	**0.00**	0.11	**0.00**
		d	.30	.59	.62	.46	.56	.46	.74	.20	.51	.56	.56	.80	.31	.50

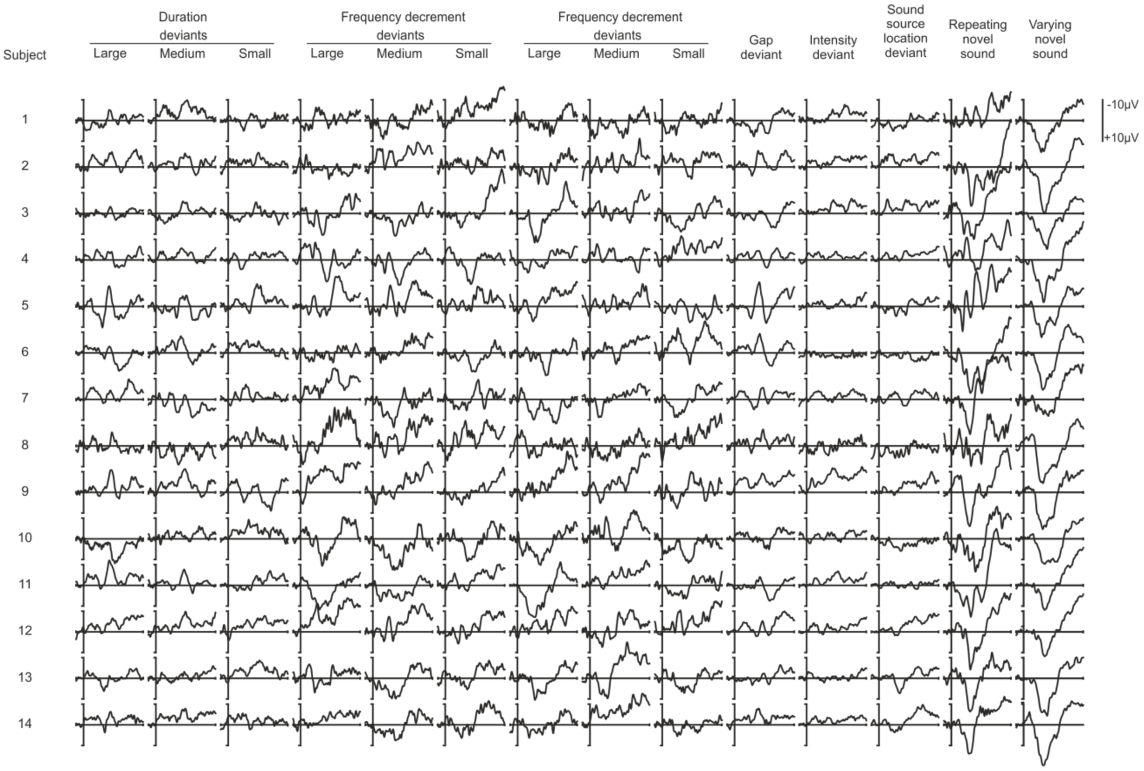

Figure 5. Individual difference signals (not spatially-filtered) at F4 obtained in Study I.

4.2. Informal musical activities and auditory discrimination in early childhood

The aim of Study II was to examine the relation between informal musical activities at home and neural sound discrimination skills reflected by the MMN, P3a, LDN, and RON responses recorded in the Multi-feature paradigm from 2–3-year-old children.

The responses to the deviant tones and novel sounds obtained in Study II and scatterplots illustrating the correlation of the response amplitudes with the amount of informal musical activities are shown in Figure 6. Higher amount of informal musical activities at home was associated with larger P3as elicited by the gap and duration deviants, smaller LDNs elicited by all deviant types, and smaller P3a elicited by the novel sounds. Paternal singing was associated with smaller RON responses to the novel sounds. More detailed description of the statistical results is given in Table 5.

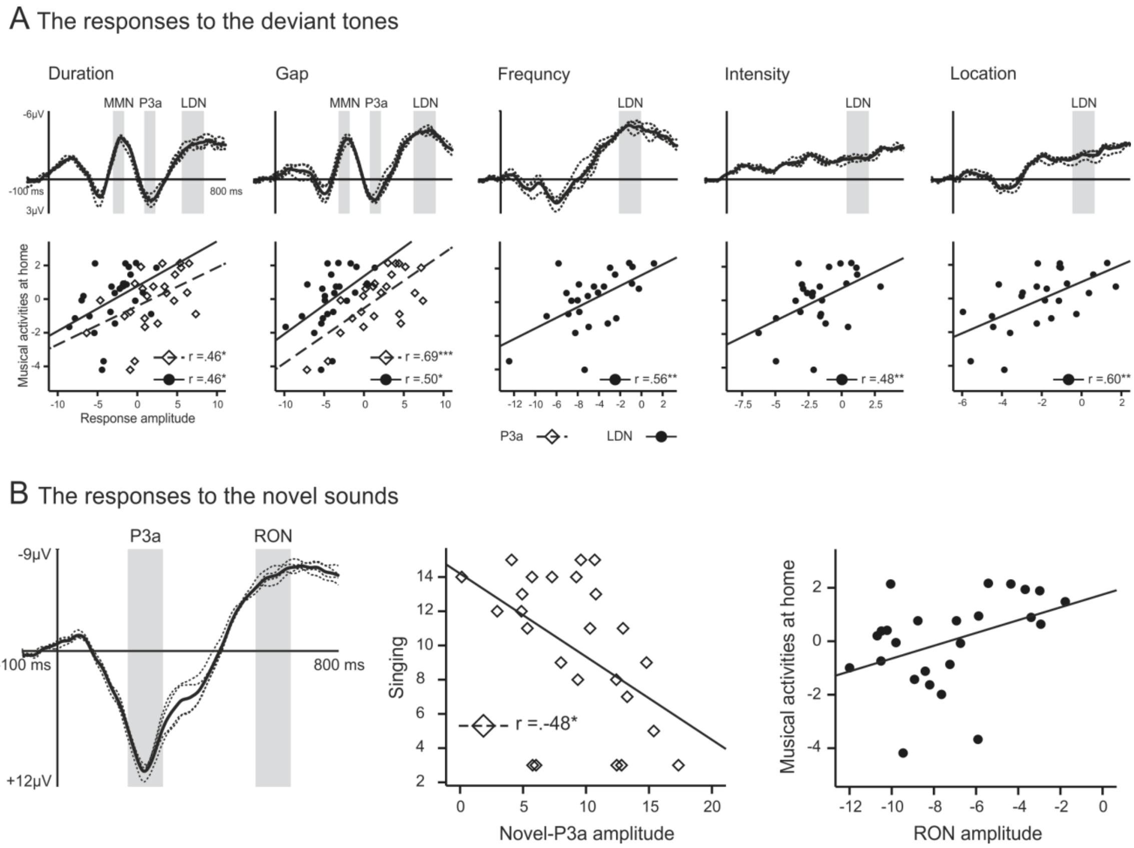

Figure 6. The difference signals for the deviant tones (A) and novel sounds (B) and the scatter plots illustrating the correlations between the P3a (diamonds) and LDN (dots) amplitudes and the amount of musical activities at home. In the ERP figures, the thin dashed lines are the responses at the channels F3, F4, C3, and C4 and the thick solid line is the average of the signals at these channels. The grey bars indicate the latency windows from which the response mean amplitudes were calculated. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Table 5. The mean amplitudes and peak latencies of the responses to the deviant tones and the t-values for the mean amplitudes for Study II. Pearson's correlation coefficients between the response mean amplitudes and the musical activities score and the corresponding r-squared values are listed in columns r and r^2, respectively. The rightmost column lists the partial correlations controlling for the child's age, gender, SES, the number of hours the parents listened to recorded music with their children, and the duration of the children's attendance at the playschool.

Deviant	Response	Amplitude	Latency	t(24)	Cohen's d	R	r2	partial r
Duration	MMN	-3.2	326	-7.12***	2.91	ns		ns
	P3a	1.71	464	2.49*	1.02	.46*	.21	.48*
	LDN	-2.96	652	-5.06***	2.07	.46*	.21	.66**
Gap	MMN	-3.31	326	-6.07***	2.48	ns		ns
	P3a	1.5	450	2.20*	0.90	.69***	.48	.69**
	LDN	-4.03	652	-8.10***	3.31	.50*	.25	.69**
Frequency	LDN	-4.60	588	-7.50***	3.06	.56**	.31	.59**
Intensity	LDN	-1.71	598	-4.00**	1.63	.48*	.23	.47*
Location	LDN	-2.05	536	-5.13***	2.09	.60**	.38	.72**

Note. * $p < .05$. ** $p < .01$.*** $p < .001$.

4.3. Musical training and the development of auditory discrimination during school-age

The aim of Studies III and IV was to investigate the effects of formal musical training on the development of neural auditory discrimination. In both studies, the musically trained children showed enhanced discrimination of several auditory change types when compared to the non-trained children. Specifically, in Study III, the MMN and P3a elicited by the chord deviants (Figure 7) increased in amplitude more in the Music group between the ages of 7 and 13 (Age × Group interaction, p < .05).

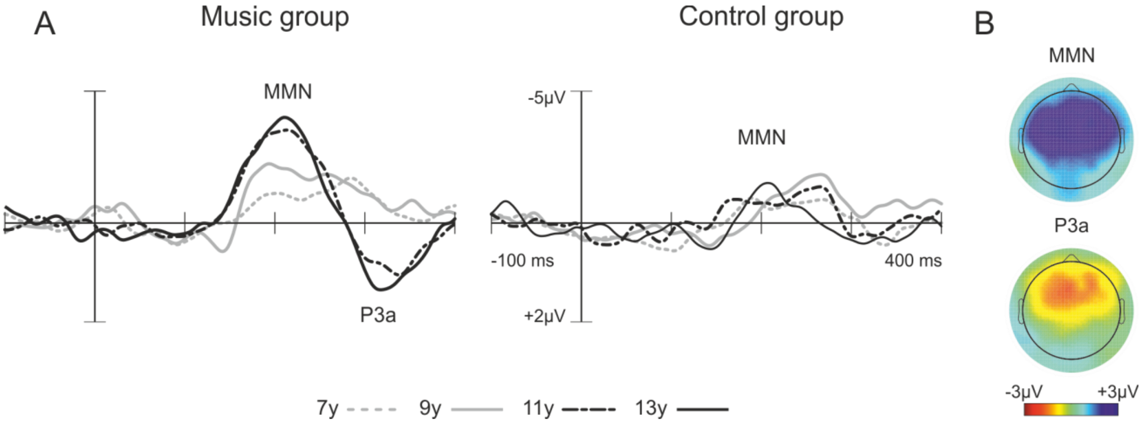

Figure 7. A) The difference signal for the Music and Control group for the Chord paradigm in Study III. B) The scalp distribution of the MMN and P3a in the Music group at age 13.

A similar trend was found for MMN to the location deviant in the Multi-feature paradigm (*p* = .054, see Figure 8). No group differences were found for the other change types in Multi-feature paradigm. The MMN elicited by the frequency, gap, intensity deviants increased with age regardless of musical training whereas the duration deviant elicited a prominent MMN already at age 7 without further age-related amplitude increase (see Table 6 for detailed statistical results).

Table 6. The results of the linear mixed model analysis for the responses MMN and P3a responses obtained in Study III.

	Main effect of Group			Main effect of Age			Group × Age interaction		
Response	Df	F	*p*	Df	F	*p*	Df	F	*p*
Chord MMN	1,243.14	0.013	.908	1,237.15	8.699	.004	1,237.15	4.813	**.029**
Chord P3a	1,243.96	2.073	.151	1,220.86	14.482	**.000**	1,220.86	4.585	**.033**
Location MMN	1,252.11	2.075	.151	1,249.92	43.526	**.000**	1,249.92	3.740	**.054**
Frequency MMN	1,115.58	2.669	.105	1,249.88	27.759	**.000**	1,249.88	0.125	.724
Duration MMN	1,117.50	2.243	.137	1,251.76	1.145	.286	1,251.76	0.018	.892
Gap MMN	1,117.76	0.043	.837	1,246.48	18.869	**.000**	1,246.48	2.820	.094
Intensity MMN	1,116.01	0.108	.743	1,253.53	3.932	**.048**	1,253.53	1.166	.281

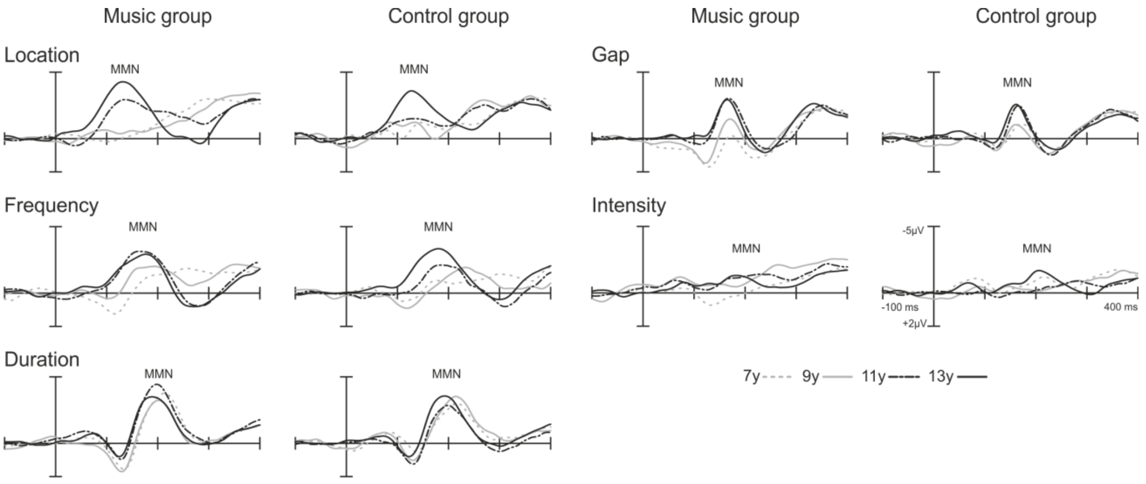

Figure 8. The difference signals for the Music and Control group for the Multi-feature paradigm in Study III.

In Study IV, in turn, the MMN-like responses elicited in the Melodic multi-feature paradigm by the melody modulations were larger in the Music group than in the Control group at age 13 whereas for the Rhythm modulation, Timbre deviant and Mistuning similar group difference was found already at age 11 (see Figure 9). Also, a positive mismatch response elicited by delayed tones was larger in amplitude in the musically trained than in the non-trained children at age 13 (see Table 7 for detailed statistical results). In both studies no significant differences were found at the baseline measurement (i.e., age 7 in Study III and age 9 in Study IV).

Table 7. The results of the linear mixed model analysis for the responses MMN and P3a responses obtained in Study IV.

	Main effect of Group			Main effect of Age			Group × Age interaction		
Response	Df	F	*p*	Df	F	*p*	Df	F	*p*
Melody MMN	1,113.21	1.673	.199	2,133.61	1.381	.255	2,133.61	3.790	**.025**
Rhythm MMN	1,113.31	3.210	.076	2,142.60	2.407	.094	2,142.60	3.676	**.028**
Mistuning MMN	1,105.91	17.294	**.000**	2,122.04	7.737	**.001**	2,122.04	6.792	**.000**
Timbre MMN	1,133.44	4.923	**.028**	2,120.93	38.780	**.000**	2,120.93	3.033	.052
Time MMN	1,116.84	0.142	.707	2,134.07	3.227	**.043**	2,134.07	0.742	.478
Time P3a	1,105.61	7.126	**.009**	2,150.72	0.391	.677	2,150.72	0.810	.447
Transposition MMN	1,101.87	0.664	.417	2,134.66	1.163	**.316**	2,134.66	1.877	.157

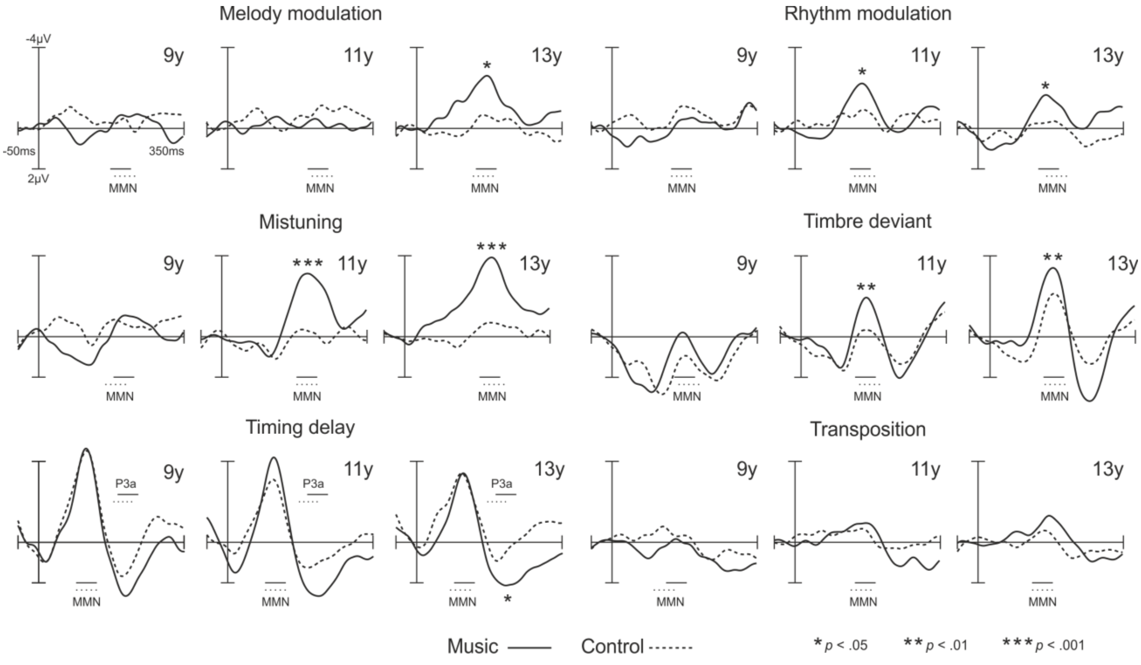

Figure 9. The difference signals for the Music and Control group for the Melodic multi-feature paradigm in Study IV. The asterisks indicate significance level of the pairwise post-hoc comparisons. The horizontal lines below or above the response peaks indicate the latency windows used in calculating the mean response amplitudes (solid line = Music group, dashed line = Control group).

In sum, together Studies III and IV showed that musical training is associated with enhanced MMNs especially to changes in musically relevant sound dimensions in childhood. As no group differences were found at the baseline, these studies suggest that the later enhancement of the responses in the Music group was due to the training received by these children and not pre-existing differences between the groups.

5. Discussion

The studies included in this thesis investigated how the maturation of neural auditory discrimination in childhood varies according to the amount of informal musical activities and formal musical training. To this end, auditory ERPs elicited by different types of sound changes were recorded from 2–3-year-old children in Studies I and II and from school-aged children in Studies III and IV. In Study II, the relation of these responses to the amount of informal musical activities reported by the parents was examined. Studies III and IV, in turn, compared the development of the responses obtained from musically trained and non-trained school-aged children in a semi-longitudinal setting. The results showed, firstly, that the novel, fast paradigms employed in the studies for collecting auditory ERPs to a number of sounds changes are applicable in toddlers and school-aged children. Furthermore, both informal musical experience and formal musical training modulated the various stages of neural auditory discrimination indexed by the MMN, P3a and LDN/RON. Specifically, in Study II, high amount of informal musical activities was associated with response profiles consistent with enhanced attention, more mature processing of auditory changes and lowered distractibility. In Studies III and IV, in turn, the musically trained school-aged children showed enlarged MMNs and for several sound change types and enhanced P3a responses to deviant minor chords presented among standard major chords. No differences were seen between the musically trained and non-trained children at the early stages of the training. Therefore, the group differences that emerged at later ages were most likely due to training and did not reflect pre-existing functional differences between the groups. With regard to maturational effects, Study I and II suggest that neural auditory discrimination is still immature at the age of 2–3 years and Studies III and IV indicate that this auditory skill continues to develop at least until pre-adolescence.

The implications of the results on the development of auditory change detection are discussed in more detail in section 4.1. while the effects of formal musical training and informal musical activities on the functions reflected by the different change-related auditory ERPs are discussed in sections 4.2. and 4.3., respectively.

5.1. Maturation of neural auditory discrimination

Studies I-IV examined auditory development across a wide age range: While in Studies I and II response profiles were recorded from 2–3-year-old children—an understudied age group in auditory ERP literature—Studies III and IV are, notably, the first to report MMN maturation (semi) longitudinally across school-age for a number of different sound change types. While the main aim of the present thesis was to examine the putative effects of formal musical training and informal musical activities on auditory development, together Studies I-IV also allow some conclusions to be drawn about typical development of neural auditory discrimination.

5.1.1. The maturation of the neural auditory discrimination reflected by the Mismatch negativity

In contrast to some of the responses elicited by repeating tones such as the N1 that show a highly prolonged maturation (see section 1.1.4.1), the MMN has often been described as an early maturing, developmentally stable response (Ponton et al., 2000; Cheour et al., 2000; Trainor, 2008). In keeping with this view, a number of studies have obtained infant mismatch responses that appear in many respects similar to those reported in adults (Alho, Sainio, Sajaniemi, Reinikainen, & Näätänen, 1990; Čeponienė Kushnerenko, Fellman, Renlund, Suominen, & Näätänen, 2002). Furthermore, some studies have failed to find clear differences in MMN amplitude between preschool-aged children and adults (Kraus et al., 1999; Shafer et al., 2000) suggesting that the MMN system operates at an adult level by school-age. Studies I and II, in turn, indicate that the MMN is quite inconsistently elicited in 2–3-year-old children and remains small in amplitude for many change types. Furthermore, Studies III and IV found that, in contrast to the results of some previous studies, the MMN increased in amplitude from early school-age to pre-adolescence.

5.1.1.1. Mismatch negativity in early childhood

In Studies I and II, only the duration and gap deviants elicited clear negative MMN-like responses resembling the adult responses obtained in previous studies in the Multi-feature paradigm (e.g., Näätänen et al., 2004). In contrast, although negative in polarity and statistically significant, the MMN-like responses to the sound-source location and intensity deviants and the largest frequency increment were fairly small in amplitude and had poorly defined morphology (i.e., these responses did not display very clear MMN-P3a-complex typical in adults, see Figure 4). No significant MMNs were obtained to the medium and small frequency increments. The frequency decrements, in turn, elicited positive mismatch responses. Although the design of Studies I and II precludes direct observations of age-related differences in response amplitudes, adult studies conducted using highly similar multi-feature paradigms with comparable deviant magnitudes suggest considerably larger MMNs in adults than in those obtained in Studies I and II. For instance Pakarinen et al. (2007) obtained MMNs to 5dB intensity deviants and 10% frequency changes that were -3.4 and -4.0 μV in amplitude respectively, while in Study I the MMN elicited by the 6dB intensity deviant was -1.71 μV in amplitude and the 12.5% frequency change failed to elicit a significant MMN (see also Näätänen et al., 2004). Furthermore, Study III, which is discussed in more detail in the next section, revealed for example that the MMN elicited by frequency deviants approximately equal in magnitude to smallest frequency deviants in Studies I and II increased in amplitude from age 7 onwards and ultimately reached an amplitude of roughly 3 μV at age 13. Although such comparisons between studies should be made with caution, these striking differences in MMN amplitudes between age groups suggest that the MMNs measured in the Multi-feature paradigm show substantial increase in amplitude between the age of 3 years and adulthood. This conclusion is in agreement with previous studies indicating immature mismatch responses in preschool-aged children (Ahmmed, Clarke, & Adams, 2008; Lee et al., 2012; Maurer et al., 2003a; 2003b; Morr, Shafer, Kreuzer, & Kurtzberg, 2002; Partanen et al., 2013; Shafer, Yan, & Datta, 2010). For instance, Morr et al. (2002) found no evidence of a mismatch response to 1200-Hz deviants among 1000-Hz standards in 2–47-month-old infants and children except for a very small negativity around 300 ms after stimulus onset in the oldest children (aged 31–47 months). Only with 2000-Hz deviants was a negative MMN-like response elicited in another sample of children aged 3–44 months. This finding suggests that the elicitation of mismatch response reminiscent of the adult MMN requires relatively large deviants in preschool-aged children. Furthermore, a number of studies have reported positive mismatch responses in preschool-aged children (Maurer et al., 2003a; 2003b; Shafer et al., 2010; Lee et al., 2013) akin to those often seen in infants (Dehaene-Lambertz, 2000; Novitski, Huotilainen, Tervaniemi, Näätänen, & Fellman, 2007; Leppänen et al., 1997). Together these studies indicate that the MMN is still maturing during preschool-age.

As already mentioned, the duration deviants elicited highly prominent MMNs in Studies I and II. Also in Study III, large duration MMNs were obtained already at the age of seven with no further age-related amplitude increase. This might reflect the children's exposure their native language Finnish—a so called quantity language—in which sound duration is important for distinguishing the meaning of words. In line with this notion, disproportionately large duration MMNs are a typical finding in native Finnish speaking adults when compared to speakers of non-quantity languages (Marie et al., 2010; Tervaniemi et al., 2006; Nenonen et al., 2003)[3].

5.1.1.2. The maturation of the Mismatch negativity during school-age

A number of studies suggest that by school-age the MMN has become robust and relatively stable in amplitude (Gomot et al., 2000; Kraus et al., 1993; Kraus et al., 1993; Kraus et al., 1999; Kurtzberg et al., 1995; Shafer et al., 2000). For instance, Shafer et al. (2000) found no difference in amplitude of the amplitude of an MMN elicited by 1200-Hz deviant tones among 1000-Hz standard tones between adults and 4, 5–6, 7–8, and 9–10-year-old children (see also Csépe et al. [1995] and Ponton et al., [2000] for more informal descriptions of results in line with mature MMNs in school-aged children).

In Study III, in contrast, the MMN increased in amplitude with age for the frequency, gap, location, and intensity deviants and started to acquire an adult-like morphology generally at the age of 11 irrespective of musical training. Similarly, in Study IV, the MMNs elicited by the salient timbre deviants showed age-related increase in amplitude in both the musically trained and the nontrained children. In agreement with these results, Bishop et al. (2011) found smaller MMN amplitudes in 7–12-year-old children than in adults for frequency and speech sound deviants. Furthermore,

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[3] It bears mention, that all three studies employed duration decrements as deviants making temporally misaligned "obligatory" responses an unlikely explanation for the large duration MMNs: In infants and adults subtracting the responses to short tones from those elicited by longer tones should not produce negative MMN-like artifacts in the difference signal (Kushnerenko, Čeponienė, Fellman, Huotilainen, & Winkler, 2001) while in adults duration decrement deviants might even underestimate the MMN amplitude (Jacobsen & Schröger, 2003).

Gomes et al. (2000) reported that a 5% frequency change failed to elicit an MMN in 8–12-year-old children in a passive oddball condition whereas in adults this stimulus contrast did so. Sussman and Steinschneider (2011) reported a corresponding difference between 6–9-year-old children and adults for 15dB intensity deviants. In Study IV, in turn, the MMNs in the Control group for the Melody and Rhythm modulations and Mistunings did not show age-related changes and remained fairly small in amplitude throughout the follow-up period. In contrast, Tervaniemi et al. (submitted) found clear MMNs for these change types in the Melodic multi-feature paradigm in non-musician adults suggesting that the MMNs to these changes also increase in amplitude with age but only after pre-adolescence.

In light of these results, some of the earlier studies appear to have overestimated the similarity of the MMN in school-age and adulthood. Perhaps the most obvious explanation for these conflicting findings is that the adult-like MMNs in the earlier studies were due to the use the oddball sequences with relatively easy-to-discriminate deviants such as large pitch changes (Kurtzberg et al., 2000; Shafer et al., 2000) or changes in highly familiar, native language speech sound (Kraus et al., 1993; however, see Bishop et al., 2011). Therefore, it is plausible that no age effects for the MMN amplitude were detected in the aforementioned studies because of a ceiling effect. Arguably, the multi-feature paradigms used in the Studies I-IV might be more demanding for the developing auditory system since they require simultaneous monitoring of variation in several auditory features and highly frequent detection of (subtle) deviants and include less repetition of the standard than the oddball paradigm. Although in healthy adults these factors appear not to influence the amplitude of MMN (Näätänen et al., 2004) in children the neural sound discrimination reflected by the MMN might be more readily disrupted by such complex stimulation.

The more protracted maturation of the MMN than previously thought is arguably better in line with the finding that the axonal, neuronal, and synaptic maturation of the auditory cortex is still ongoing in preadolescence (Huttenlocher & Dabholkar, 1997; Moore & Guan, 2001). Also, behavioral evidence indicates that even basic low-level auditory skills such frequency and intensity discrimination may undergo age-related improvement even past the age thirteen (Fischer & Hartnegg, 2004).

Attempts have been made to find parallels in physiological changes in the auditory cortex revealed by *post-mortem* studies and for instance the development of the P1 (Ponton et al., 2000), N1 (Eggermont & Ponton, 2003) and infant mismatch responses (Trainor et al., 2003). As suggested by Trainor et al. (2003) the seemingly adult-like mismatch responses might not in fact be analogous to the adult MMN in terms of neural origin. The results of Study III, in turn, follow the time course of the axonal and synaptic maturation of layers II and III of the auditory cortex where the generators of the adult MMN have been proposed to reside (see section 1.1.4.1., cf. Trainor et al., 2003). At this point, however, linking structural maturation of the auditory cortex and the development of neural auditory discrimination reflected by the MMN remains highly speculative. There is an evident need for multi-methodological studies examining the maturation of auditory system with structural and functional neuroimaging methods in tandem with electrophysiological as well as behavioral measures of auditory processing.

In sum, in light of the results of Studies I-IV, the notion that the MMN is adult-like by school-age might need to be revised. At the very least, whether children display adult-like MMNs appears to be highly dependent on the type of stimuli used. Together Studies I-IV suggest that, in healthy children without musical training, the MMN is still quite immature at the age of 2–3 years and increases in amplitude at least until pre-adolescence for changes in basic physical features of tonal stimuli but remains small for more complex music-like sounds. The current results do not refute the findings that with certain stimulus configurations highly robust MMNs can be obtained from young children. This is crucial for the MMN to be applicable for studying central auditory dysfunctions in early childhood. On the other hand, if the MMN would not show age-related changes it would obviously be unsuitable for examining auditory development. Therefore, the current results highlight the usefulness of the MMN as a marker of maturation of neural auditory discrimination.

5.1.1.3. The attention-related functions reflected by P3a in early childhood

The Multi-feature paradigm used in Studies I and II also proved suitable for probing auditory attention allocation triggered by novel sounds and more fine-grained changes in sounds. Specifically, as expected on the basis of previous studies in infants (Kushnerenko et al., 2002), school-aged children (Gumenyuk et al., 2004) and adults (Escera et al., 1998), the novel sounds elicited a prominent P3a-like positivity. Furthermore, the duration and gap deviants also elicited a P3a-like response, indicating that not only salient novel sounds but also more subtle deviants can cause involuntary shift of attention in early childhood. Consistent with the studies in adults (Escera et al., 1998), preschool-aged and school-aged children (Wetzel & Schröger, 2007b) the P3a to the novel sounds was clearly larger in amplitude than the P3a elicited by the deviant tones. Furthermore, as in adults, the P3a-like response elicited by the deviants was modulated by the deviance magnitude (cf. Yago et al., 2001), i.e., the response amplitude increased with increasing deviant-standard difference. Therefore, Studies I and II suggest that in some respects the involuntary attention allocation reflected by the P3a functions similarly in toddlers and adults (cf. Kushnerenko et al., 2002; Niemitalo-Haapola et al., 2013).

Despite these similarities, however, there are good reasons to assume that the functions reflected by the P3a show developmental changes long after early childhood. With regard to function, neuropsychological studies have established that various aspects of attentional control continue to mature throughout childhood (Garon, Bryson, & Smith, 2008; Best, Miller, & Jones, 2009). With regard to the neural origin, the adult P3a is regarded as an index of frontal functions and indeed receives significant contribution from prefrontal cortical areas (Baudena et al., 1995, Knight 1984; Opitz et al., 1999) which are immature at the age of 2–3 years (Huttenlocher & Dabholkar, 1997). Thus, it seems plausible that the component structure of the P3a in toddlers differs from that of adults perhaps by receiving relatively more contribution from auditory areas that mature earlier than the frontal ones (see section 1.1.3.3). Furthermore, as reviewed in the Introduction, both the amplitude of the P3a to novel sounds and the disruption in behavioural performance caused by such sounds decrease with age consistent with increasing control over involuntary attention (Gumenyuk et al., 2004;

Määttä et al., 2005; Wetzel & Schröger, 2007b; Wetzel et al., 2011). The results of Studies I and II provide a starting point for future studies mapping the age-related changes in the neural generators of the P3as elicited by novel sounds and more subtle deviants from early childhood onwards.

5.1.1.4. The late negativities in preschool aged children

In Studies I and II, prominent LDN responses were elicited by all deviant tones including even the smallest frequency and duration changes. Therefore, even though no clear MMN was elicited by some of the changes, all of them were nonetheless discriminated from the standards by the children.

With regard to the functional role of the late negativities in Studies I and II, it seems unlikely that the smallest deviants were very distracting. Therefore, the LDN responses elicited by these deviants were probably not analogous to the adult Reorientation negativity response (RON) (cf. Čeponienė et al., 2004). Furthermore, arguing against the distraction-reorientation interpretation, the LDN elicited by the small deviants were not preceded by a P3a. Furthermore, unlike the adult RON, the LDNs to duration and frequency deviants were not modulated by deviance magnitude (cf. Yago et al., 2001). Studies I and II corroborate previous findings that prominent LDNs can be elicited by tonal stimuli (Čeponienė et al., 1998). Therefore the functions reflected by these responses could not be closely linked to the processing of speech sounds as has been proposed for some LDN-like responses (Goswami, 2009; Korpilahti et al., 2001). Other suggestions for the functional significance of the LDN include sensitization for the detection of subsequent changes (Alho et al., 1994) or non-specific, higher-order processing of auditory changes (Čeponienė et al., 2004) but the current data do not allow further evaluation of these hypotheses.

Study I suggests that in toddlers the LDN might in some cases prove to be a better index of neural auditory discrimination than the MMN as the LDN was elicited even by minor acoustic deviances, was large in amplitude and appeared to be fairly constant morphologically across individual subjects (see Figure 5). The LDN should be considered an important measure of auditory learning and development alongside the MMN as it displays experience-dependent plasticity (Shestakova et al., 2003) and reduces substantially in amplitude with age providing an index of the maturational state of the auditory system (Bishop et al., 2011; Hommet et al., 2009; Kraus et al., 1993; Müller et al., 2008). The LDN also shows promise as an marker of auditory processing deficits in childhood language disorders (for results pertaining to dyslexia, see Czamara et al., 2011; Neuhoff et al., 2012; Schulte-Körne et al., 1998). However, studies aiming at a better understanding of the functional role(s) of the LDN-like responses are needed. These would entail recording the LDN to a number of different stimulus contrasts (both acoustically complex and simple, linguistic and non-linguistic), systematic exploration of both normal and abnormal development of this responses, mapping its neural generators, investigating its relation to overt stimulus discrimination, and exploring how it is influenced by short and long-term experience and by attentional and other task demands. The various versions of the Multi-feature paradigm might prove useful in this undertaking.

In Studies I and II the novel sounds also elicited a large negativity in the LDN time range. As acoustically salient novel sounds are likely to cause distraction (Escera et al., 1998), the attention interpretation seems more plausible here than for the LDNs elicited by the relatively subtle deviants. Thereby this response was termed as RON according to the adult response (Schröger & Wolff, 1998). Presumably, the children's attention was first involuntarily shifted towards the novel sounds after which the children reoriented their attention back to the primary task (i.e., watching a movie) eliciting the RON. It should be noted, however, that the relation of the RON-like component reported here and the adult RON response is uncertain especially as the young age of the subjects precluded the use of behavioral measures of distraction. Still, based on previous studies it seems likely that processes related to attention allocation contributed to this component. For example, Gumenyuk et al. (2004) found that in school-aged children the reaction time in a visual task and the amplitude of a late negativity elicited by concurrently presented task irrelevant novel sounds correlated positively (i.e., the longer the reaction times, the larger the RON responses) indicating that the late negativities elicited by novel sounds are related to the amount of behavioral distraction caused by the unexpected sound also in children.

To summarize, Studies I and II indicate that—consistent with immature neural auditory discrimination in early childhood—the profile of change-related auditory ERPs recorded in the Multi-feature paradigm in 2–3-year-old children is characterized by (i) small MMNs to changes in frequency, intensity, and sound-source-location, (ii) larger MMNs and fairly adult-like P3as to changes in duration and temporal structure of sounds, and (iii) highly prominent LDN responses even for relatively small deviants. At this age, novel sounds elicit highly prominent P3as and LDN/RON responses that are robust even in individual children. Finally, Studies III and IV suggest that in school-age the MMN shows age-related increase in amplitude for changes in physical features of tonal stimuli and may do so for more complex, music-like sounds even after pre-adolescence.

The following sections will discuss how the maturation of the MMN in school-age is affected by formal musical training (Section 4.2.) and how the early response profiles might be modulated by informal musical experience (Section 4.3.).

5.2. Musical training enhances the maturation of neural auditory discrimination

In Studies III and IV, the musically trained children displayed heightened sensitivity to various sound changes as indexed by the enhanced development of their MMN and P3a responses. Specifically, in Study III, the MMN and P3a elicited by the deviant minor chord amongst standard major chords increased in amplitude more steeply in the Music than in the Control group between the ages 7 to 13 years. In the Multi-feature paradigm, in contrast, only the MMN to the location deviant showed a trend towards a similar group difference. In Study IV, the MMNs elicited by changes in melody, rhythm, timbre, and tuning in the Melodic multi-feature paradigm were enhanced in the musically trained children by age 13 at the latest. No group differences were found in the early stages of training in either Study III (i.e., at age 7) or Study IV (i.e., at age 9).

5.2.1. Training effects on MMN amplitude

The findings of Studies III and IV extend those of previous studies that have found augmented MMNs in musically trained children. Namely, Meyer et al. (2011) obtained an MMN with larger area to frequency changes in violin tones in 8–12-year-old children taking Suzuki violin lessons than in control children with no musical training. Virtala et al. (2011), in turn, found evidence for enhanced discrimination of physically varying major and minor chords in musically trained 13-year-old children. Finally, Chobert and co-workers have reported larger amplitudes of MMNs to voice onset time and duration changes in syllables in children with musical training (Chobert et al., 2011; Chobert et al., 2013). Thus, by school-age the MMN is enhanced in musically trained children for wide range of complex sounds.

5.2.1.1. Musical training enhances the encoding of complex auditory information

The musical Chord paradigm in Study III and the Melodic multi-feature paradigm in Study IV were found to be highly effective in differentiating musically trained and nontrained children. In contrast, Study III found no evidence for MMN enhancement in the musically trained children for changes in the frequency, duration, intensity, and temporal structure in the simpler, non-musical Multi-feature paradigm. The contrasting findings suggest that facilitating effects of musical training on neural auditory discrimination are fairly specific to sound changes that are especially relevant for music processing. Also in adult musicians, enhanced MMNs have been found most consistently for changes in musical rather than simple non-musical sounds. For instance, Koelsch et al. (1999) found that a slight pitch change embedded in a major chord elicited a larger MMN in musicians than in non-musicians. In contrast, an equal change in the frequency of a simple repeating tone did not differentiate the two groups. Similarly, Fujioka et al. (2004) found that while musicians displayed larger MMNs than non-musicians for pitch changes in one note of melodic tone patterns, no difference was found in MMN amplitudes for a pitch change of the same magnitude in an oddball paradigm. Furthermore, Meyer et al. (2011) obtained an augmented MMN to frequency changes in violin sounds but not in sine tones in musically trained children. Together these results suggest that musically trained individuals do not merely display more fine-grained sensory resolution since in the studies reviewed above the musical context and not the deviance magnitude determined whether the musicians displayed a larger MMN than the controls. In other words, musically trained individuals are not just more accurate at detecting small acoustic differences (although this might also be true; Nikjeh et al., 2008) but more advanced at processing complex, abstract auditory information than non-musicians. It appears unlikely that the enhancement of MMN in musical contexts reflects the existence of specific memory templates for musical sounds as has been argued with regard to enhanced MMNs elicited by native speech sound (Näätänen, 2001). Rather it signals a more general ability in processing complex auditory information although familiarity with the musical context such as scale structure or timbre does appear to enhance various auditory ERPs (Brattico et al., 2006; Neuloh & Curio, 2004; Pantev et al. 2001). In any event, the results of Studies III and IV converge with previous findings in adults and children by suggesting that, as has been argued by Kraus and others (Kraus & Chandrasekaran, 2010; Kraus, Skoe, Parbery-Clark, & Ashley, 2009), musical training does not lead to an overall gain in auditory encoding ability but most strongly enhances auditory skills that are most relevant for music processing.

This is not to say that the effects of musical training on auditory skills are specific to the music: The enhanced discrimination of fine-grained sound changes can obviously be useful in other, non-musical domains. Indeed, as already mentioned, transfer effects have been demonstrated for example between musical training and the processing of speech sounds (Chobert et al., 2011; Moreno et al., 2009; Musacchia et al., 2007). As argued by Patel (2011), the encoding of speech sounds in musicians might be enhanced because musical training requires highly precise processing from neural networks that appear to encode spectral and temporal features in both music and speech.

Finally, in Study III, the MMN elicited by the location deviant in the Multi-feature paradigm also showed a strong trend towards increasing more steeply in the Music than in the Control group. This result is in agreement with those of Tervaniemi et al. (2006) who found enhanced MMNs in adult amateur rock musicians only for location deviants in the Multi-feature paradigm. As was suggested by the Tervaniemi et al. (2006), the importance of attending to sounds from spatially distinct sources while playing in an ensemble with other musicians might explain the enhancement of auditory localization in adult musicians. This explanation seems plausible for Study III also as the training of children in the Music group involved playing in orchestra and singing in a choir.

5.2.1.2. Musial training enhances the development of neural auditory discrimination

Importantly, owing to the (semi) longitudinal design of Studies III and IV, the developmental dynamics of the MMN enhancement in musically trained children could be revealed. The absence of significant group differences at baseline in MMN amplitude in both Study III and IV indicates that accumulation of training was crucial for the enhancement of the MMN that emerged at later age(s) in the Music group. Along the same lines, previous longitudinal studies have revealed differences between musically trained and nontrained children in other aspects of brain function (Chobert et al., 2012; Fujioka et al., 2006; Moreno et al., 2009) and in the structure of auditory and motor cortical areas and the corpus callosum (Hyde et al., 2009). These latter group differences can also be attributed with high confidence to experience-dependent plasticity either because random assignment of subjects to the music and control groups was employed (Chobert et al., 2012; Moreno et al., 2009) or because no group differences were found at the beginning of the training (Fujioka et al., 2006; Hyde et al., 2009). Thus, the current results converge with the previous literature highlighting the role of musical experience in shaping brain development.

Interestingly, group differences in MMN amplitude in Studies III and IV emerged relatively slowly, i.e., they were not seen before the children in the Music group had received at least 3 years of training. Some previous studies, by contrast, have found neuroplastic changes in children already after considerably shorter training periods. For instance, Fujioka et al. (2006) found that after only six months of Suzuki violin lessons 6-year-old children showed enhancement of an early MEG response elicited by violin sounds. A study by Chobert et al. (2012) suggests that also the MMN can be enhanced by musical training already within a year in children in school-aged children. Although Chobert et al. (2012) used a fairly complex multi-feature paradigm with speech sounds, the Melodic multi-feature paradigm is arguably even more challenging not only because of the complex regularities and subtle deviants the paradigm contains but also because of the memory demands set by the roving standard manner in which the melody and rhythm modulations and transposition were presented. Thus the difficulty of the paradigm might at least in part explain the slow emergence of the MMN enhancement in the Music group in Study IV.

Comparison between Studies III and IV and those conducted in adults suggest that the differences between musically trained and nontrained individuals in neural auditory discrimination might diminish with age or even disappear for certain sounds. In Study IV, with the exception of the responses to the timing delays, the MMNs to in the control group were fairly small. However, as already mentioned, the Tervaniemi et al. (submitted) found prominent MMNs in the same paradigm not only in a musician group but also in non-musicians. In contrast to Study IV, only the mistuning elicited clearly larger MMNs in musicians than in the non-musicians while more subtle group differences in scalp distribution were revealed for the other change types. Furthermore, in contrast to Study III, Brattico et al. (2009) found no difference between adult musicians and non-musicians in the strength of the magnetic counterpart of the MMN recorded to minor chord deviants amongst major chord standards indicating that by adulthood non-musicians may acquire the same level of proficiency in neutrally discriminating these sounds as musicians. Moreover, a study by Virtala et al. (2012) found an MMN-like response to minor chord deviants in musically trained 13-year-old children but no evidence for an MMN in musically nontrained children. In another study employing the highly similar stimuli, by contrast, Virtala and co-workers (2011) did obtain a significant MMN in adult non-musicians. Thus, even though at age 13 only musically trained children showed evidence of neurally discriminating the sounds, by adulthood non-musicians had also developed this skill. Musical training is clearly not a prerequisite for the ability to encode basic building blocks of music such as rhythm or melody or for detecting the difference between major and minor chords in adulthood (cf. Bigand & Poulin- Charronnat, 2006). However, converging evidence from Studies III and IV together with the literature reviewed above indicate that without musical training the ability to automatically discriminate subtle changes in some musical features is not consistently achieved until sometime between pre-adolescence and adulthood.

5.2.2. Training effects on attentional orienting reflected by the P3a

In the Chord paradigm of Study III, a P3a-like response emerged with age only in the Music group indicating that over time the changes from major to minor chords became gradually more attention catching for the musically trained children than for the control children. Studies in adults have found that, compared to non-musicians, musicians show larger P3as to changes in intervals (Trainor et al., 1999) and rhythms (Vuust et al., 2009), unexpected Neapolitan chords (Brattico et al., 2013; Steinbeis, Koelsch, & Sloboda, 2006) as well as earlier P3a for changes in pitch of tonal stimuli (Nikjeh et al., 2008). Similarly to the MMN effects discussed above, no group difference in P3a amplitude was found at age 7 indicating enhanced development of this response in the Music group resulted from training.

No group differences in P3as were found for the Multi-feature paradigm in Study III and thereby the P3a the response enhancement was specific to the musically more relevant chord change. Several studies using a wide variety of stimuli have shown that familiarity with the eliciting sounds is associated with enlarged P3as (Beauchemin et al., 2006; Kirmse et al., 2009; Roye et al., 2007). With regard to musical sounds, Neuloh and Curio (2004) obtained a significantly larger P3a from musicians in a familiar context of deviant minor chords and standard major chords than in an unfamiliar, atonal context of dissonant deviant and standard chords. In light of these results, it could be speculated that the augmented P3a in the musically trained children in Study III could reflect the familiarity or significance of the major-minor contrast for the musically trained children.

The timing delays in Study IV also elicited a positive P3a-like component that was larger in amplitude in the musically trained children at age 13 than in the nontrained children. It should be noted, however, that even though this response was approximately in the expected latency range of the P3a with regard to the onset of the delay (i.e., the zero time point in Figure 9), relative to the onset of the delayed tone (i.e., 100 ms in Figure 9) it fell in the time range of the P1 response. In school-aged children, the P1 is enlarged with prolonged inter-stimulus intervals (Sussman et al., 2008). Therefore, it cannot be ruled out that a less refractory P1 elicited by the delayed tone contributed to the positivity seen in the difference signal for the Timing delays. The P1 has also been previously reported to be enlarged in musically trained children (Shahin et al., 2004) further suggesting that the enhanced positivity in the Music group for the Timing delays might in fact be the P1.

In sum, Study III (and arguably also Study IV) indicates that attention-related functions reflected by the P3a can be enhanced by formal musical training. Indeed, attention and, more generally, executive functions are malleable by training programs specifically designed for this purpose (e.g., Rueda, Rothbart, McCandliss, Saccomanno, & Posner, 2005). Musical training certainly requires great deal of concentration and thereby it seems plausible that it too might enhance not only auditory processing but attention-related functions as well. In line with this notion, emerging evidence suggests that musical training may enhance various aspects of executive functions such as selective attention and inhibitory control (Bialystok & DePape, 2009; Degé, Kubicek, & Schwarzer, 2011; Moreno et al., 2011).

Whether the attentional orienting reflected by the P3a is linked to more generally to executive functions is unclear. Furthermore, the enhanced P3as in musicians have thus far been incidental findings in studies designed to measure the MMN (Nikjeh et al., 2008; Trainor et al., 1999; Vuust et al., 2009) or the early right anterior negativity (ERAN) (Brattico et al., 2013; Steinbeis et al., 2006). Therefore, interplay between the P3a and different facets of executive functions should be examined more thoroughly and studies specifically designed to measure the P3a in musically trained and nontrained subjects should be carried out. Transfer effects of musical training to executive functions clearly have important implications since enhancement of these functions may positively affect cognitive performance in a number of different domains (cf. Trainor et al., 2009, however, see Schellenberg, 2011).

5.2.3. Possible caveats in Studies III and IV

Random assignment was not feasible in Studies III and IV as the goal of these studies was to investigate the effects of long-term musical training in an ecologically valid sample of motivated children. Furthermore, the musically nontrained children were not given training in a non-musical activity (e.g., sports, visual arts) which would have controlled for the possible effects of participating in *any* adult-guided activity.

Therefore, it could be argued that self-selection and differences in the overall amount activities might have contributed to the group differences.

However, the finding that there was no significant difference between the Music and Control groups in the responses at baseline indicates that there was no sample bias with regard to the MMN amplitude—the main outcome variable of Studies III and IV. Furthermore, it seems unlikely, that the overall level of activities would explain MMN and P3a enhancement that was fairly specific to musical stimuli. The developmental changes seen in the MMN for the Multi-feature paradigm in the Control group indicate that the auditory system of the control children was developing normally. Therefore the results cannot be attributed to group differences in general brain maturation. Finally, the majority of the children in the control group also participated in some extracurricular activity and did not differ from the control children with regard socioeconomic status.

As is to be expected for longitudinal studies spanning several years, not all subjects participated in every measurement. Most of the children who were contacted and refused to participate in the follow-up measurements in studies III and IV reported that they were either too busy (e.g., with school work) or that they simply did not want to participate in another experiment again having already done so one to three times. For others, the data quality was unsatisfactory or they were not were not reached at the time when the recordings were conducted. These factors are most likely unrelated to MMN amplitude and therefore there seems to be no reason to suspect that the subject attrition introduced a bias towards finding group differences in MMN amplitude. Importantly, the attrition in the Music group appeared not to be related to the continuation or discontinuation of playing. Thus, the results of Studies III and IV were most likely not confounded by increasingly selective sampling of musically trained children

5.2.4. Future studies

The training-induced physiological changes that underlie the enhanced MMN in musically trained individuals are not well understood. Animal studies indicate that the kind of online perceptual learning that is thought give rise to the MMN involves mechanisms such as rapid synaptic plasticity that modifies receptive fields in the auditory cortex (e.g., Eytan, Brenner, & Marom, 2003; Farley, Quirk, Doherty, & Christian, 2010; Ulanovsky, Las, Farkas, & Nelken, 2004; Ulanovsky, Las, & Nelken, 2003; for a review see May & Tiitinen, 2010). In principle, changes in such mechanism could contribute the enhancement of the MMN in musically trained individuals. Unfortunately, current *in vivo* imaging methods do not allow direct observation of the possible effects of long-term auditory experience on such micro-level mechanisms in humans. Future studies in animal models may shed light on this issue.

In humans, various methods are available that could be combined with ERPs to investigate the underlying mechanisms of MMN enhancement. Interestingly, recent neuroimaging studies have revealed connections between individual differences in white and gray matter and those in brain function and behavior (for a review see Kanai & Rees, 2011). Future studies could examine the relationship between the functional differences between musically trained and non-trained individuals, such as the ones found in Studies III and IV, and those seen in overt discrimination and in brain anatomy. The study by Schneider et al. (2002) serves as an example of such an multi-methodological approach: In this study the dipole strength of an early cortical MEG response to sounds, performance in the Advanced Measures of Music Audiation (AMMA) tonal test, and volume of the Heschl's gyrus were found to correlate strongly (for other music-related studies demonstrating correlations between brain function and structure, see Foster & Zatorre, 2010; Hyde et al., 2009). It stands to reason then that the enhanced MMN profiles measured with the Melodic multi-feature paradigm in musically trained individuals might also be reflected both in the structure of the brain and in behavioral measures of auditory discrimination. As the mechanisms underlying the system-level changes in gray and white matter become better understood, such studies may yield insight on changes at the cellular and molecular level, manifested as enhanced behavioral performance and brain function (for a review of such candidate mechanisms, see Zatorre, Fields, & Johansen-Berg, 2012).

With regard to more present day goals, open questions for EEG studies that would contribute to current discussions in neuroscience of music include whether the positive effects of musical training on neural auditory discrimination are retained after active training has been discontinued (cf. Skoe & Kraus, 2012), whether musicians trained at an early age display stronger functional enhancement than late-trained musicians (cf. Penhune, 2011), and whether the auditory change detection at cortical level is related to auditory encoding at the brain stem level (cf. Kraus & Chandrasekaran, 2010).

5.3. Informal musical activities and auditory discrimination in early childhood

Study II suggests that—in addition to formal musical training examined in Studies III and IV—informal musical activities such as musical play and singing at home may shape auditory skills in early childhood. Specifically, high amount of such musical activities was associated with enlarged P3a-like responses to duration and gap deviants but reduced P3a responses to the novel sounds. Furthermore, children who engaged in high amount of informal musical activities showed diminished LDN responses across all five deviant types and LDN/RON responses to the novel sounds.

Contrary to the hypotheses, the amplitude of the MMN did not correlate with the amount of informal musical activities. Although null results are difficult to interpret, Study II indicates tentatively that, in early childhood the MMN might not be sensitive to differences in the kinds of informal musical experience examined in Study II.

5.3.1. Informal musical activities and the P3a and LDN/RON

Interestingly, the P3a-like responses to the deviant tones and those to the novel sounds displayed opposing relationships with the amount of musical activities. The enlarged P3a to duration and gap deviants in the children with more musical activities suggest that their attention was more readily drawn towards these sounds and therefore implies more accurate detection of fine-grained changes in the temporal aspects of sounds. In line with this conclusion, short-term auditory training can enhance the P3a elicited by different types of subtle auditory changes in adults (Atienza et al., 2004; Uther, Kujala, Huotilainen, Shtyrov, & Näätänen, 2006) as well as in children (Lovio, Halttunen, Lyytinen, Näätänen, & Kujala, 2012). Furthermore, as reviewed above, augmented P3as to difficult-to-detect deviants are seen in subjects with highly accurate auditory abilities such as musicians and in musically trained children as was shown in Study III. In contrast, the reduced P3a to the novel sounds that were most likely well above discrimination threshold for all the children might result from enhanced control over the involuntary attention in the children from musically more active homes. As reviewed in the Introduction (section 1.1.4.3), the P3a to novel sounds is considered a marker of distraction since the amplitude of this response is inversely associated with performance in concurrent behavioral tasks (Gumenyuk et al., 2005; Gumenyuk et al., 2004; however see Wetzel et al., 2013). Furthermore, the novel-sound-P3a has been found to be enlarged in highly distractible children such as those with attention deficit hyperactivity disorder (Van Mourik, Oosterlaan, Heslenfeld, Konig, & Sergeant, 2007) and major depression (Lepistö, Soininen, Čeponienė, Almqvist, Näätänen, & Aronen, 2004). The P3a to novel sound also diminishes with age in parallel with age-related increase in attentional control (Gumenyuk et al., 2004; Määttä et al., 2005; Wetzel & Schröger, 2007b; Wetzel et al., 2011). Thus, the P3a effects found in Study II suggest that everyday musical activities might influence attention-related functions and more specifically that such activities might enhance the detection of fine-grained sound changes but reduce distractibility by highly salient ones.

With regard to the novel-sound-P3a, the correlation was specific to parental singing suggesting that especially *listening* to informal musical performances (as opposed to more active musical play) may reduce distractibility. Parental singing is indeed effective in maintaining the attention of young infants (Trehub, 2003) and singing by the father might be especially engaging for infants as indicated by behavioral measures of visual attention during listening to paternal *vs.* maternal singing (O'Neill, Trainor, & Trehub, 2001).

At first glance it might seem surprising that the children with more musical activities showed smaller LDN responses to the deviant tones than the less musically active children. However, as reviewed in section 1.1.4.4., large LDN amplitude is in fact typical for immature auditory discrimination and the LDN decreases in amplitude with age as the brain matures (Bishop et al., 2011; Hommet et al., 2009; Kraus et al., 1993; Müller et al., 2008) to the extent that it is usually not seen in adults. Therefore the reduced amplitude of the LDN in children with more musical activities at home could be interpreted to reflect more mature auditory processing in these children.

Finally, the late negativity elicited by the novel sounds was also significantly correlated with the overall score for musical activities at home. For reason outlined above (see section 4.1.1.4), this response was interpreted as the Reorienting negativity (RON) (Schröger & Wolff, 1998) and thereby assumed to be related to distraction. The reduction in amplitude of this response alongside the P3a to the novel sounds in the children with high amount of informal musical activities further suggest that these children were less easily distracted by these sounds than children from less musically active home environments.

These results suggest that informal musical activities could perhaps be harnessed to tune highly important auditory discrimination and attention skills in early childhood. The implication of the results pertaining to auditory discrimination seem especially important with regard to typical and atypical language development, since several studies indicate that early auditory discrimination abilities predict later language skills (Benasich & Tallal, 2002; Guttorm, Leppänen, Poikkeus, Eklund, Lyytinen, & Lyytinen, 2005; Molfese, 2000; Molfese, Molfese, & Modgline, 2001) and that basic auditory dysfunction might be a key feature of dyslexia (e.g., Tallal & Gaab, 2006). The attention-related effects found in Study II have corresponding implications for the normal and disturbed development of attentional control which is of obvious importance for later school performance. Thus, the findings of Study II suggest that musical activities may improve several neurocognitive functions and thereby encourage the incorporation of such activities into various educational settings (daycare, schools) for typically developing children and those with special needs (see e.g., Uibel, 2012).

5.3.2. Do informal musical activities shape auditory skills in childhood?

The correlational data in Study II cannot reveal whether the link between musical activities and the P3a and LDN/RON responses was causal. Some musical skills and behaviors seem to be partially hereditary (see section 4.5) and therefore it is conceivable that children from “musical” families would display enhanced auditory skills as well as engage in high amount of informal musical activities without there being a causal relation between these factors. Animal studies, however, indicate that exposure to an acoustically enriched environment (and conversely auditory deprivation) shapes the development of cortical auditory processing (Engineer et al., 2004; Percaccio et al., 2005; Xu, Yu, Cai, Zhang, & Sun, 2009; Zhang, Cai, Zhang, Pan, & Sun, 2009). For instance, Engineer et al. (2004) found that exposure to different types of tones and other more complex sounds including music altered various response properties of auditory cortical neurons in rats. For obvious reasons animal studies cannot model human musical interaction very accurately. They do however indicate that fundamental aspects of cortical auditory processing may be shaped even by ambient exposure to complex auditory stimulation. In humans, it is well established that native speech sound learning and musical enculturation which results from incidental exposure and everyday experience without specific training *per se* lead to long-lasting changes in auditory discrimination abilities (Hannon & Trainor, 2007; Näätänen, 2001). Recent controlled experimental studies have provided compelling evidence that informal musical activities can enhance the acquisition of music perceptual skills (Gerry et al., 2012; Gerry et al., 2010; Hannon, der Nederlanden, Christi, & Tichko, 2009) and that exposure to recorded music can shape neural auditory change detection in infants (Trainor et al., 2011). Finally, a randomized clinical study showed that music listening can support cognitive recovery after stroke suggesting that mere listening to pleasant music may have wide-ranging neuroplastic effects (Särkämö et al., 2008). Therefore, it seems at least plausible that also the types of everyday musical activities examined in Study II might affect the maturation of the neural auditory discrimination skills. However, without further controlled experimental studies this cannot be conclusively determined.

5.3.3. Possible caveats in Study II

Possible caveats related to the influence external variables and the generalizability of the results of Study II deserve consideration. With regard to the influence of external, confounding factors on the observed correlations, a number of such variables were controlled for. In short, as can be seen from Table 5 in the Results section, the socio-economic factors of parents' education and income which are known to be associated with brain development (Hackmann & Farah, 2009), the age and gender of the children, or the amount of exposure to recorded music appeared not be sufficient to explain the associations between the musical activities and the response amplitudes. Furthermore, there was negligible variation between the children in the overall number of hobbies or musical activities outside the home excluding these factors as possible confounds. Finally, the responses of children with musician parents did not differ from those of the rest of the children.

Since all the children in Study II (and Study I) had regularly attended a musical playschool, it could be argued that the results might not be fully generalizable to children who have no musical activities outside the home. However, the musical activities in the playschool were of low intensity and concentrated on enjoyment of musical group activities rather than on specific music-educational goals. Furthermore, the finding that the duration of the playschool attendance was not associated with any of the neurophysiological or questionnaire measures, speaks against the suggestion that the associations between the response amplitudes and musical activities were modulated by the playschool attendance.

5.4. Multi-feature paradigms as measures of auditory skill development

The studies included in this thesis demonstrate the feasibility of using complex multi-feature paradigms for recording comprehensive multicomponental profiles of change-related auditory ERPs even in toddlers. Furthermore, these studies attest to their usefulness in studying the maturation of auditory change detection, auditory memory, and attention in children with varying amount of formal and informal musical experience. Since the elicitation change-related responses in the multi-feature paradigms requires that the features in which the changes take place are processed independently of one another (see section 1.1.4.5), these results indicate that children as young as 2–3 years are (at least to some degree) capable of parallel processing of different sound features.

Multi-feature paradigms have been employed in studying auditory skills in both typically developing children and infants (Lovio et al., 2009; Niemitalo-Haapola et al., 2013; Partanen, Pakarinen, Kujala, & Huotilainen, 2013; Partanen, Torppa, Pykäläinen, Kujala, & Huotilainen, 2013; Sambeth, Pakarinen, Ruohio, Fellman, van Zuijen, & Huotilainen, 2009), those with Aspergers syndrome (Kujala, Kuuluvainen, Saalasti, Jansson-Verkasalo, Wendt, & Lepistö, 2010), or at heightened risk for dyslexia (Lovio, Näätänen, & Kujala, 2010), and children fitted with cochlear implants (Torppa et al., 2012) and recurrent acute otitis media (Haapala et al., 2013). The most obvious advantage of the multi-feature paradigms is the reduction in measurement time relative to the traditional oddball paradigm which is clearly important for studies in children as well as in clinical subject groups. The overall profile of the MMNs measured in the multi-feature paradigm also shows better test-re-test reliability than the MMNs to any of the individual deviants in recorded an oddball paradigm (Paukkunen, Leminen & Sepponen, 2011). Furthermore, since natural auditory environments are composed of varying sounds, multi-feature paradigms are arguably more ecologically valid measures for auditory discrimination than simplistic oddball paradigms. This argument seems especially relevant with regard to the Melodic multi-feature paradigm vis-à-vis actual music. As argued above this might explain why these paradigms were so sensitive to maturational change in MMN amplitude. Along the same lines, at least in dyslexic subjects, the multi-feature paradigm appears more effective in revealing sensory processing difficulties in than the responses recorded in separate oddball blocks (Kujala, Lovio, Lepistö, Laasonen, & Näätänen, 2006).

Due to these advantages, multi-feature paradigms have become an increasingly popular method for recording comprehensive profiles of MMNs and other change-related auditory ERPs in both healthy subjects and clinical groups. The paradigm has proven a flexible platform for developing new stimulus configurations for investigating for example the processing of various changes in speech sounds (Pakarinen et al., 2009), words (Shtyrov, Kimppa, Pulvermüller, & Kujala, 2011) and pseudowords (Partanen et al., 2011), piano tones (Torppa et al., 2012) and musical sounds patterns (arpeggiated chords) (Vuust et al., 2011). In Study IV, the feasibility of a novel Melodic multi-feature paradigm for probing musical sound feature processing in school-aged children was established (see also Huotilainen et al., 2009). In future studies, even more fine-grained picture of pre-attentive processing of musically central sound features could be obtained by introducing deviants of various difficulty levels to the Melodic multi-feature paradigm. By doing so, the paradigm could also be tailored to specific subjects of different ages (infants, toddlers) and for example for musicians representing different musical genres (cf. Vuust, Brattico, Seppänen, Näätänen, & Tervaniemi, 2012).

5.5. The role of heritable differences in musical abilities

It should be noted that while Studies III and IV support the causal role of experience-dependent plasticity in the functional differences between musically trained and nontrained individuals, they do not refute possible contribution to genetic factors to such group differences. Behavioural genetics provide evidence for ubiquitous influence of hereditary factors to human behaviour. Several indices of brain function ranging from elementary reaction time tasks (Luciano, Wright, Smith, Geffen, Geffen, & Martin, 2001) to EEG oscillations and various ERP components (van Beijsterveldt & van Baal, 2002) and hemodynamic effects during working memory tasks (Koten et al., 2009) show substantial heritability (i.e., the proportion of the phenotypic variation accounted by genetic factors). Furthermore, twin studies have revealed genetic contribution to individual difference in the anatomy of various cortical areas (for reviews, see Peper, Brouwer, Boomsma, Kahn, & Hulshoff Pol, 2007; Toga & Thompson, 2005) including high heritability for grey matter density in Heschl’s gyrus (Hushoff Pol et al., 2006).

Therefore, it would not seem highly surprising if inter-individual variation in some musically relevant perceptual skills would also be related to genotypic differences (cf. Levitin, 2012, for a critical discussion, see Howe, Davidson, & Sloboda, 1998). Indeed, significant heritability has been reported for performance in the so called distorted tunes test (Drayna, Manichaikul, Lange, Snieder, & Spector 2001) that requires the detection of wrong notes within well-known melodies as well as for self-reports of musical engagement (Vinkhuyzen, Van der Sluis, Posthuma, & Boomsma, 2009). Recent studies have also begun to link performance in musicality tests as well as musical interest and creativity to specific genes (Park et al., 2012; Pulli, Karma, Norio, Sistonen, Göring, & Järvelä, 2008; Theusch, Basu, & Gitschier, 2009; Ukkola, Onkamo, Raijas, Karma, & Järvelä, 2009; Ukkola-Vuoti, Oikkonen, Onkamo, Karma, Raijas, & Järvelä, 2011). Furthermore, familial contribution to absolute pitch and congenital amusia—a severe and apparently fairly music specific perceptual impairment—has been demonstrated (Baharloo, Johnston, Service, Gitschier, & Freimer, 1998; Peretz, Cummings, & Dube, 1998). Thus, there is evidence that genetic factors contribute to music perceptual abilities.

It is a wholly different question, however, whether early individual differences in such perceptual skills can predict musical abilities in musically trained individuals in any meaningful sense. The amount of practice is certainly a key determinant of musical ability (Ericsson, & Charness, 1994) although other factors related to music perceptual skills and general cognitive performance alongside the amount of practice have been found to explain unique variance in musical achievement (Ruthsatz, Detterman, Griscom, & Cirullo, 2008). Obviously, less music specific individual factors with strong genetic basis such as personality and ability to focus attention most likely play a role in whether an individual is willing to invest the time and effort to master a musical instrument (cf. Corrigall, Schellenberg, & Misura, 2013). In conclusion, even though experience-related re-organization contributes to the neural differences in the musicians and non-musicians—as was shown in Studies II and III—genetic factors may still also explain inter-individual variation in these measures. Efforts to disentangle the contribution of training-related and genetic factors or predispositions in musical skill development will undoubtedly continue to drive future research (for discussions, see Levitin, 2012; Zatorre, 2013).

5.6. Conclusions

Musical experience is a potential source of neuroplastic changes in the developing auditory system. The studies included in the current thesis attest to the feasibility of using fast multi-feature paradigms to investigate the effects of musical experience on the development of the various stages of neural auditory discrimination throughout childhood. With regard to typical development, the present thesis suggests that these functions are immature in early childhood and continue to develop at least until pre-adolescence. With regard to the effects of musical experience, the main findings of the present thesis are that the maturation of neural auditory discrimination is enhanced by formal musical training in school-age and may be influenced by informal musical activities in early childhood. Specifically, the results showed that with age and accumulation of musical experience musically trained children become more sensitive to various musically relevant sounds changes than nontrained children. Importantly, this enhancement appeared to result from training and not to reflect pre-existing group differences. Thereby, these results relate to the long-standing question of whether the neural differences between adult musicians and non-musicians reflect experience-dependent plasticity or genetic factors. Furthermore, the present thesis provides novel evidence for the role of informal musical activities such as singing and dancing in shaping auditory skills in early childhood. Namely, children who engage in high amount of such activities showed evidence of more accurate and mature discrimination of sound changes and less distractibility by surprising sounds than less musically active children. In sum, the results indicate that various types of musical activities have the power to shape the development of neural auditory discrimination and attention which are also highly important outside the musical domain.

6. References

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