

The sound of music: Differentiating musicians using a fast, musical multi-feature mismatch negativity paradigm

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ABSTRACT

Musicians' skills in auditory processing depend highly on instrument, performance practice, and on level of expertise. Yet, it is not known though whether the style/genre of music might shape auditory processing in the brains of musicians. Here, we aimed at tackling the role of musical style/genre on modulating neural and behavioral responses to changes in musical features. Using a novel, fast and musical sounding multi-feature paradigm, we measured the mismatch negativity (MMN), a pre-attentive brain response, to six types of musical feature change in musicians playing three distinct styles of music (classical, jazz, rock/pop) and in non-musicians. Jazz and classical musicians scored higher in the musical aptitude test than band musicians and non-musicians, especially with regards to tonal abilities. These results were extended by the MMN findings: jazz musicians had larger MMN-amplitude than all other experimental groups across the six different sound features, indicating a greater overall sensitivity to auditory outliers. In particular, we found enhanced processing of pitch and sliding up to pitches in jazz musicians only. Furthermore, we observed a more frontal MMN to pitch and location compared to the other deviants in jazz musicians and left lateralization of the MMN to timbre in classical musicians. These findings indicate that the characteristics of the style/genre of music played by musicians influence their perceptual skills and the brain processing of sound features embedded in a musical context. Musicians' brain is hence shaped by the type of training, musical style/genre, and listening experiences.

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1. Introduction

Playing music is one of the most specialized skills that the human organism is capable of acquiring, placing immense demands on the underlying neural substrates as well as the brain's plastic potential. The study of how musicians' brains evolve through daily training and influence has emerged as an effective way of gaining insight into changes of the human brain during development and training. However, neuroscientific investigations during the last decade have mainly been treating musicians as a unified group, even though the demands set by their different musical activities differentiate them to a high degree (Tervaniemi, 2009). Here, we wished to test whether the style/genre of music played by different

kinds of musicians might influence their auditory discrimination skills, as measured by behavioral and brain responses.

The differences in musical cognitive skills between musicians and non-musicians can be traced to differences in both brain structure and function. Structurally, musicianship has been related to morphological differences in Corpus Callosum (Schlaug, Jancke, Huang, Staiger, & Steinmetz, 1995), areas related to motor activity, such as increases of cerebellar volume (Hutchinson, Lee, Gaab, & Schlaug, 2003), gray matter volume increases in primary motor and somatosensory areas in the left precentral gyrus, premotor areas, and left cerebellum (Gaser & Schlaug, 2003) and specific effects of musical training on white matter development (Bengtsson et al., 2005). Furthermore, the brains of musicians exhibit gray matter increases in areas involved in temporal structuring of language and music (Sluming et al., 2002) and in particular in areas involved in auditory perception (Gaser & Schlaug, 2003; Schneider et al., 2002).

Functional differences between musicians and non-musicians have consistently been found with regards to auditory processing. Using magnetoencephalography (MEG), Pantev et al. (1998)

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was first to show that, when compared with sinusoidal tones, the N1m brain response to sounds with a more complex timbre, is stronger in classical musicians than in non-musicians. Also, musicians' amplitude of the magnetic equivalent of the mismatch negativity (MMNm) is enhanced particularly in relation to the timbre of the instrument they play (Pantev, Roberts, Schulz, Engelien, & Ross, 2001). Recently, musical expertise has been related to increased amplitude and/or faster latency of several components of the auditory event-related potentials (ERPs) and magnetic fields (ERFs), such as the N19m-P30m (Schneider et al., 2002), the electric and magnetic N1 (Pantev et al., 1998, 2001; Shahin, Bosnyak, Trainor, & Roberts, 2003), the electric and magnetic MMN (Koelsch, Schröger, & Tervaniemi, 1999; Marie, Kujala, & Besson, 2012; Rüsseler, Altenmüller, Nager, Kohlmetz, & Münte, 2001; Van Zuijen, Sussman, Winkler, Näätänen, & Tervaniemi, 2004; Vuust et al., 2005), the early right anterior negativity (ERAN) (Koelsch, Schmidt, & Kansok, 2002), the N2b (Koelsch et al., 1999; Tervaniemi, Just, Koelsch, Widmann, & Schröger, 2005; Tervaniemi et al., 2009), the P3a (Jongsma, Desain, & Honing, 2004; Nikjeh, Lister, & Frisch, 2009), the P3b (Koelsch et al., 1999; Paller, McCarthy, & Wood, 1992), and the P600 (Besson & Faita, 1995).

As a tool to investigate differences between musicians and non-musicians in musical processing the mismatch negativity paradigm has proven particularly effective, mainly because it is elicited pre-attentively requiring neither subject's behavioral response nor attention towards the sounds (Alho, 1992; Näätänen, Gaillard, & Mantysalo, 1978; Paavilainen, Tiitinen, Alho, & Näätänen, 1993). Thereby, it is possible to avoid confounding factors such as differences between musicians and non-musicians in familiarity with and motivation in relation to performing musical tasks. The MMN is a component of the auditory event-related potential (ERP) recorded with electroencephalography (EEG) related to change in different sound features such as e.g., pitch, timbre, location of sound source, intensity, rhythm or in any abstract rule (Näätänen, 1992; Näätänen, Tervaniemi, Sussman, Paavilainen, & Winkler, 2001). It peaks around 100–200 ms after change onset and the amplitude and latency of the MMN depends on deviation magnitude and related perceptual discriminability, such that larger deviations yield larger and faster MMNs (Näätänen, Paavilainen, Alho, Reinikainen, & Sams, 1987). The amplitude and latency of the MMN indeed is closely linked with auditory behavioral measures (Lang et al., 1990; Sams, Paavilainen, Alho, & Näätänen, 1985), with a correlation between these two measures of neurocognition (Novitski, Tervaniemi, Huotilainen, & Näätänen, 2004; Tiitinen, May, Reinikainen, & Näätänen, 1994). Importantly, the MMN is sensitive to discrimination learning (Näätänen, Schröger, Karakas, Tervaniemi, & Paavilainen, 1993) and hereby also to musical expertise (Tervaniemi, 2009).

Musicians' neural skills depend highly on instrument, practice strategies as well as on the level of expertise. Musicians who need to intone while playing their instrument such as violinists display a greater sensitivity to small differences in pitch compared to non-musicians (Koelsch et al., 1999) and to other instrumental groups, singers respond with a stronger MMN than instrumentalists to small pitch changes (Nikjeh, Lister, & Frisch, 2008), conductors process spatial sound information more accurately than professional pianists and non-musicians (Münter et al., 2001) and rhythmically skilled jazz musicians respond to rhythmic deviations with a stronger, more left-lateralized and faster MMN than non-musicians (Vuust et al., 2005). Recently, it was shown that musicians who perform music primarily without a score learn more easily to detect contour changes in melodic patterns compared to musicians who mainly read music and that this is reflected pre-attentively by an enhanced MMN (Seppänen, Brattico, & Tervaniemi, 2007; Tervaniemi, Rytönen, Schröger, Ilmoniemi, & Näätänen, 2001). Taken together, these studies

indicate that musicians' brains process auditory information differently depending on their practice strategies and that the MMN is sensitive to acoustic features specific of a musical practice.

Some of the afore-mentioned studies indicate that the stimuli need to consist of realistic, complex musical material in order to disclose fine-grained processing differences between participants. When presented with simple sinusoidal tones with greater mistuning instead of fine-grained differences, the violinists were not superior to non-musicians in discriminating pitch changes (Koelsch et al., 1999). A similar lack of MMN differences was obtained when comparing processing of isolated infrequent sinusoidal tones or of infrequent minor chords within a sequence of major chords in different kinds of musicians against nonmusicians (Brattico et al., 2001, 2009; Fujioka et al., 2006). Seppänen et al. (2007) compared musicians who mainly employ auditory rehearsal and playing strategies to a non-aural group as determined by a questionnaire and found that practice strategies modulate the speed of neural discrimination of interval and contour changes within melody-like patterns but found no differences in the MMN to simple sound features.

The traditional MMN paradigms used so far, however, are both time-consuming and far away from sounding musical. Näätänen, Pakarinen, Rinne, Takegata (2004) introduced a novel multi-feature MMN-paradigm in which several types of acoustic changes are presented in the same sound sequence. This allows for several MMNs to be independently elicited for different auditory attributes making the duration of the experiment significantly reduced to less than 20 min. Importantly, no difference was observed between the MMNs recorded using the new paradigm and the ones obtained in the traditional oddball-paradigm (with only one type of deviant). This shows that reliable MMNs can be elicited to deviants in complex auditory patterns. An additional experimental benefit of using a multi-feature paradigm is that it allows for direct comparison of more multiple sound aspects in a specific group of subjects in a specific experimental setting instead of having to compare across studies. Using this multi-feature paradigm on simple auditory features, it has been shown that amateur rock musicians do not differ from non-musicians in their sensitivity to pitch or duration cues but instead, they have facilitated discrimination on intensity and location cues which carry essential information in their electronic music (Tervaniemi, Castaneda, Knoll, & Uther, 2006).

The previous studies mentioned above have concentrated on either gross differences between musicians and non-musicians treating the category of musicians as a unified whole or on special skills of a certain instrument group. Here, we for the first time compare pre-attentive brain processing (MMN) in the three main types of musicians in Western music (and non-musicians) on a range of acoustic features. We employ a novel fast multi-feature MMN paradigm (Vuust et al., 2011) which is both short and musical sounding, to investigate pre-attentive processing of auditory features in musicians playing three distinct styles of music (classical, jazz, rock/pop) and in non-musicians. As feature-deviants we chose six types of acoustic changes relevant for musical processing in different musical genres and presented them in the same sound sequence. Specifically, five of the six musical features were aspects of musical sound that previously have been shown to elicit larger MMNs according to musical expertise: pitch mistuning, timbre, sound-source location, intensity, and rhythm. As a special addition we included a pitch slide typical for improvisational music as opposed to classical music.

We hypothesized that we would find the greatest auditory expertise in jazz musicians especially as compared with rock musicians and non-musicians. Jazz is characterized by complex harmonies, elaborate melodic and harmonic material that presents a challenge to many listeners. Moreover, since it is mostly improvised and variations of the harmonic progressions and rhythmic

feel are communicated between musicians during performance (Berliner, 1994; Monson, 1997; Vuust & Roepstorff, 2008) it places strong demands on ear-training skills. We therefore expected to find behavioral and brain indices of enhanced processing in these musicians as compared to classical-, rock- and non-musicians.

2. Materials and methods

2.1. Participants

11 non-musicians (4 women, 7 men), 7 classical musicians (5 women, 2 men), 10 jazz musicians (1 woman, 9 men), and 14 rock musicians (4 women, 10 men) gave informed consent and participated in the experiment (Table 1). All participants had normal hearing, reported no cognitive deficits or neurological diseases. The experiment protocols were done in accordance with the Declaration of Helsinki and approved by the Ethical committee of the Department of Psychology, University of Helsinki. Subjects were paid for their voluntary participation.

Non-musicians were university students with minimal musical background (not more than two years of formal lessons) and with occasional or no playing. They had no formal music training apart from music lessons at the primary and secondary school, and were never taught to play an instrument except for one subject who had played the piano for less than a year when he was 8 years old and another one that had started to play guitar and drums at the age of 13, playing approximately one hour per week.

Participants with musical background were recruited from music academies. Jazz and classical musicians were defined as having formal education in music academies or conservatories mainly concentrated on the jazz or the classical genre, or else as earning their living by teaching or performing classical or jazz music. In turn, the main criteria for classifying musicians as rock musicians was their active playing and regular performing in a rock or pop band; formal education in a pop/jazz conservatory, was not considered as crucial, since many rock musicians learn to play in informal situations (e.g., by imitating friends, listening to and playing along with records and jamming with other musicians) or are even autodidact.

Mean age was 32 ± 9 years for classical musicians, 34 ± 9 years for jazz musicians, 28 ± 7 years for rock musicians, and 26 ± 1 years for non-musicians. Onset age

Table 1
Demographic data.

Participant	Age	Gender	Main instrument	Onset of playing	Years of playing main instrument
Non-musicians (NM)					
NM1	27	Male			
NM2	26	Male			
NM3	26	Female			
NM4	25	Male			
NM5	25	Male			
NM6	27	Male			
NM7	24	Female			
NM8	26	Female			
NM9	26	Female			
NM10	28	Male			
NM11	27	Male			
Mean	26				
Classical musicians (CM)					
CM1	39	Female	Piano	9	30
CM2	26	Female	Piano	9	17
CM3	24	Female	Piano	6	18
CM4	25	Female	Piano	6	19
CM5	45	Female	Double bass	15	30
CM6	23	Male	Alto violin	5	18
CM7	41	Male	Singer/composer	9	32
Mean	32			8	23
Jazz musicians (JM)					
JM1	41	Male	Trumpet	13	28
JM2	24	Male	Drums	10	14
JM3	45	Male	Piano	5	40
JM4	43	Male	Guitar	10	32
JM5	28	Male	Double bass	16	12
JM6	23	Female	Alto saxophone	9	14
JM7	40	Male	Clarinet	10	30
JM8	26	Male	Drums	9	17
JM9	25	Male	Electric bass	10	15
JM10	42	Male	Guitar	16	26
Mean	34			11	23
Rock musicians (RM)					
RM1	26	Male	Bass guitar	15	9
RM2	28	Male	Guitar	13	15
RM3	26	Male	Keyboards	5	7
RM4	25	Male	Guitar	12	13
RM5	27	Male	Singing, guitar	12	15
RM6	28	Male	Drums	18	10
RM7	19	Female	Violin	6	13
RM8	26	Male	Guitar	15	11
RM9	26	Female	Piano	7	19
RM10	26	Male	Singing	8	18
RM11	20	Female	Steelpan	13	8
RM12	29	Male	Piano/keyboards	7	10
RM13	49	Male	Accordion	11	3
RM14	22	Female	Singing	4.5	12
Mean	26			10	9

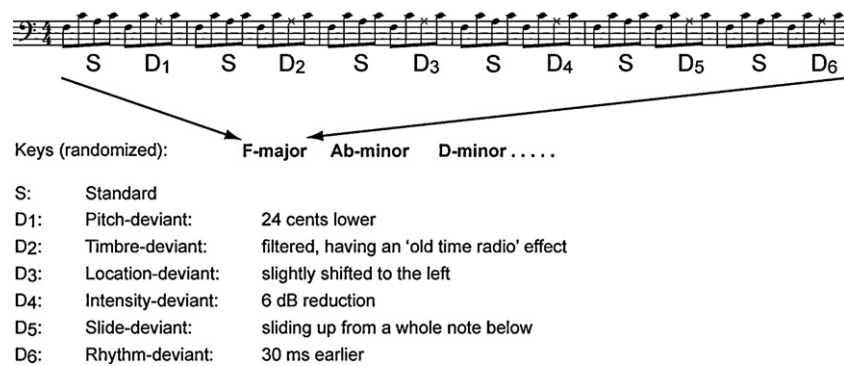
Stimulus (Alberti Bass)

Fig. 1. Stimulus. "Alberti bass" played with piano sounds. Patterns alternated between standard sequence and a deviant sequence, periodically transposed to different keys and or modality with an interval of 6 bars. Each tone was 200 ms in duration, having an SOA of 5 ms, yielding a tempo of around 146 beats/min. Comparisons were made between the third note of the standard sequence and the third note of the deviant sequence.

of playing did not differ between musician groups ($M = 8 \pm 3$ SD for classical musicians; $M = 11 \pm 3$ SD for jazz musicians; $M = 11 \pm 5$ SD for rock musicians). Years of playing their main instrument, however, differed significantly between groups (one-way ANOVA with Years as dependent variable and Group as independent variable: $F_{3,40} = 34.5$, $p < .001$): classical and jazz musicians had approximately ten more years of playing experience with their main instrument compared with rock musicians ($M = 23 \pm 7$ SD for classical musicians; $M = 23 \pm 10$ SD for jazz musicians; $M = 12 \pm 4$ SD for rock musicians). This difference indicates that some of the rock musicians shifted to a different main instrument than the one they started out with. It should also be noted that since the most common main instruments vary between musical styles, we chose to have a variety of instruments present in the different musical styles (for the list of instrument played by each subject, see Table 1).

From the groups of classical and jazz musicians, AMMA data of two participants were missing in each, and of one participant from rock musicians.

2.2. Stimuli and procedure

The auditory stimuli were identical to the musical multi-feature MMN-paradigm (Vuust et al., 2011). This paradigm is based on the 'Optimal' paradigm presented in Näätänen et al. (2004), but the stimuli are more complex and musically enriched. In the 'Optimal' paradigm, a 'standard' simple tone is presented once after each 'deviant' tone. In this way, it is possible to record ERP responses for many auditory feature deviations in a considerably shorter time and with an equally good signal-to-noise ratio as with the traditional oddball paradigms. Similarly, in the present study, standards and deviants alternated, but each of them consisted of musical 4-tone patterns rather than single tones (Fig. 1).

The standard pattern consisted of either major or minor mode tones arranged in an 'Alberti bass' configuration, an accompaniment commonly used in the Western musical culture in both classical and improvisational music genres. To make the stimuli more musically interesting, we changed the key every 6th measure, allowing for 6 different types of deviants to appear exactly once in each key in a randomized order. The order of the 24 possible keys (12 major and 12 minor) was pseudo-randomized, so that each key appeared once for every 24 transpositions. The keys were kept in the middle register of the piano with the bass note between F3 and E4. Sound stimuli were generated using the Wizoo Acoustic Piano sample sounds from the software sampler Halion in Cubase (Steinberg Media Technologies GmbH). Deviant patterns were similar to standards, except that the third tone of the pattern was modified with Adobe Audition (Adobe Systems Incorporated) as illustrated in Fig. 1. The pitch deviant was created mistuning the third tone by 24 cents, tuned downwards in the major mode, upwards in the minor mode. For all analyses, major and minor pitch deviations were pooled. The rhythm deviant was created by anticipating the third note by 30 ms compared with when it was expected. The timbre used the 'old-time radio' effect provided with Adobe Audition using a 4 channel parametric equalizer (low shelf cutoff by -4.6 dB at 21.7 Hz; high shelf cutoff by -6.8 dB at 3354.9 Hz; 18.8 reduction at 83.7 Hz; 11 dB increase at 192.5 Hz; 11.6 dB increase at 623.1 Hz; 17.7 dB increase at 1663.7 Hz with a constant width of $1/4$ of each of the frequencies; 3 dB overall amplitude reduction) The location deviant was generated by decreasing the amplitude of the right channel up to 10 dB, perceptually resulting in a sound coming slightly from a location left centers ($\sim 70^\circ$). The loudness deviant was made by reducing the original intensity by 6 dB and the pitch-slide deviant by sliding up to the standard from two semitones below. Sounds (the individual tones) were amplitude normalized. Each tone was in stereo, 44,100 in sample frequency, and 200 ms in duration, having an ISI of 5 ms.

A pilot ERP study was conducted to optimize the deviants by their saliency, resulting in the parameter values used. Randomization was performed in Matlab and stimuli were presented with the Presentation software (Neurobehavioral Systems).

Auditory stimuli consisted of a 20-min block. Participants passively heard auditory sequences through headphones (Sony MDR-7506, sound pressure level 50 dB above individual threshold.). Their main task was to concentrate on a silenced document film while sitting on a comfortable chair in a shielded chamber. Before EEG recording, participants answered a background questionnaire consisting of questions about their musical knowledge. After the EEG recording, the Advanced Measure of Musical Audiation (AMMA) musicality test was conducted to obtain an additional behavioral measure of the musical skills of subjects (Gordon, 1989). The AMMA test has been standardized with more than 5000 American students, with and without musical background. It lasts about 15 min and includes 30 pairs of short melodies, 10 with a change in pitch (AMMA total score), 10 with a change in rhythm and 10 unchanged. After hearing two melodies played by a piano synthesizer, subjects were requested to decide if they were same or different during a 4-s silent period. Our subjects obtained, on average, a total raw AMMA score of 53.4 (SD = 6.4; range 43–68), a mean raw score for the tonal AMMA of 26.4 (SD = 4.5; range 19–34), and a mean raw score for the rhythm AMMA of 27.1 (SD = 2.8, range 24–34). These scores are comparable with the ones obtained by non-musicians and amateur musicians in previous studies (Schneider et al., 2002; Seppänen et al., 2007). Hence our subject sample did not differ from normal levels of tonal and rhythmic skills.

To test group differences in musical discrimination accuracy as resulting from the AMMA, we conducted repeated-measures ANCOVA with AMMA (Tonal, Rhythm, Total) as dependent variable, Group (classical musicians, jazz musicians, rock musicians, non-musicians) as independent variable. We used Age and Gender as covariates (regarding the rational of the choice of these covariates see below).

2.3. EEG recording and data analysis

The EEG was recorded with a BioSemi ActiveTwo system. A SignaGel electrolyte was injected into the electrode positions of the head-cap with a syringe. A 64-channel cap based on 10/5 system were used with active electrodes sampling rate during recordings at a maximum of 2048, down-sampled into 512 Hz with BDFDecimator. Double-sided adhesive electrode rings were used to attach the electrodes to the mastoids behind auricles EOG (below the lower eyelid of the right eye), and the reference electrode to the nose.

The EEG was offline filtered (bandpass 1–30 Hz). Further, epochs of 100 ms pre-stimulus and 400 ms post-stimulus periods were separately averaged for the 6 types of deviant stimuli in each condition and for the standard stimuli, divided into 6 groups preceding each deviant type. The mean voltage of the 100 ms pre-stimulus period served as a baseline for amplitude measurements. The epochs including an EEG or EOG change exceeding ± 100 μ V for more than 4 isolated channels were omitted from the averaging. Isolated channels with exceeding range were interpolated. Few contaminated channels were discarded in some subjects.

First, the MMN peak latencies were measured from the most negative peak at the frontal electrode approximating the Fz in the 10–20 system and the most positive peaks at the mastoid electrodes (LM and RM) occurring at the 100–200 ms post-stimulus period. These electrodes were chosen on the basis of visual inspection and the previous MMN literature, according to which that the largest negative MMN peak is typically obtained at Fz and the largest reversed potential at the mastoid electrodes. The mean MMN amplitudes were calculated as the average voltage at the 40 ms period centered at the individual peak latencies measured from Fz. Subsequently, to delineate the MMN and to include also the values from the mastoids, the standard stimulus (the third note of the standard Alberti pattern) ERPs were subtracted from the corresponding deviant-stimulus ERPs of the same sequence and hence re-referenced to the average values measured from both mastoid channels. This procedure resulted in 6 difference waveforms per each subject. For further statistical analysis testing the effects of feature deviation on MMN amplitudes, latencies

and scalp distribution, the individual mean MMN amplitudes and peak latencies were calculated as before. Particularly, we started by testing the significance of the MMN response against the zero baseline by paired-sample *t*-tests for the mean MMN amplitudes measured at Fz per each deviant condition and each subject.

Before studying the differences between groups in MMN parameters and AMMA scores, we studied whether the groups were matched in the demographic variables, i.e., gender and age. A one-way ANOVA with gender as dependent variable and group as independent variable showed a marginally significant effect ($F_{3,41} = 2.5$, $p = .06$). A one-way ANOVA with age as dependent variable and group as independent variable showed also a significant effect ($F_{3,41} = 2.8$, $p = .05$). Hence, we opted to perform repeated-measures ANCOVAs for studying MMN parameters and AMMA scores, which always included Gender and Age as covariates to account for the group differences unrelated to the variables of interest (namely, the content of musical training). An ANCOVA testing differences in MMN latencies between groups utilized as dependent variable the MMN peak latency values calculated at Fz per each subject and condition. We performed ANCOVAs for studying differences in MMN amplitudes were calculated on data recorded from a subset of electrodes (F3, F4, C3, C4, P3, P4) with Feature (pitch, timbre, intensity, slide, sound location, rhythm), Frontality (frontal, central, parietal) and Laterality (left, right) as within-subjects factors and Group (jazz musicians, rock musicians, classical musicians, non-musicians) as between-subjects factor. MMN latencies were tested similarly but only from values obtained at Fz electrode, thus omitting the Frontality and Laterality variables. Results are reported with Greenhouse–Geisser corrected test values with the uncorrected degrees of freedom. LSD post hoc tests were used to test the direction of the effects obtained in the repeated-measures ANCOVA. For all the significant findings we report effect sizes as indexed by partial the eta-squared, η_p^2 .

The relationship between discrimination accuracy during the AMMA test and MMN parameters was analyzed with Pearson's *r* or Spearman's ρ correlation tests for all subjects. Pearson's *r* or Spearman's ρ were reported for all correlations. The alpha level for these correlations was adjusted to $p < .01$ according to Bonferroni's method (α/n). The number of variables used as dividend was equal to six since we obtained six components with eigenvalue > 1 from principal component analysis with varimax rotation.

3. Results

3.1. Group differences in musical practice and skills

In repeated-measures ANCOVA, as expected, AMMA differed based on its subtypes ($F_{2,62} = 47.1$, $p < .001$, $\eta_p^2 = .492$), and, more importantly, overall AMMA performances varied significantly according to experimental groups (main effect of Group: $F_{3,31} = 6$, $p = .003$, $\eta_p^2 = .341$): jazz musicians performed better than rock musicians and non-musicians ($p < .02$ in LSD post hoc tests), without differing significantly from classical musicians ($p = .1$ in LSD post hoc test), whereas rock musicians scored higher than non-musicians ($p = .04$ in LSD post hoc test). Furthermore, the AMMA subscores testing different types of musical skills (Tonal and Rhythm) were differently modulated by musicianship, as revealed by the significant interaction Group $\times$ AMMA ($F_{6,62} = 3.9$, $p = .002$, $\eta_p^2 = .123$). In particular, according to a separate one-way ANCOVA evidencing a significant main effect of Group ($F_{3,31} = 3.5$, $p = .03$, $\eta_p^2 = .244$), jazz musicians scored higher in the Tonal AMMA subtest as compared with non-musicians and rock musicians ($p = .006$ and $p = .04$, respectively, according to LSD post hoc tests). Also Rhythm AMMA subscores varied according to musicianship (main effect of Group: $F_{3,31} = 9.2$, $p < .0001$, $\eta_p^2 = .459$): non-musicians obtained the worst performance of all groups ($p < .05$), and jazz musicians slightly outperformed rock musicians ($p = .04$), while only tending to differ from classical musicians ($p = .09$).

3.2. Group differences in MMN amplitude and latency

As illustrated in Fig. 2, the fast multi-feature paradigm produced MMNs for all six feature deviations in all musician groups, as demonstrated by the significant differences between the mean amplitudes to deviant versus standard stimuli recorded at Fz (Table 2).

We found a significant main effect of Group on the MMN amplitudes ($F_{3,36} = 5.3$, $p = .004$, $\eta_p^2 = .301$; Fig. 3), deriving from the largest MMN across deviants in jazz musicians compared with

all other groups ($p < .01$ in post hoc LSD tests). The interaction Group $\times$ Feature was not significant ($F < 1$), although in separate ANCOVAs for the Feature factor (conducted to study the significant 4-way interaction, as reported below), the slide MMN showed a significant main effect of Group ($F_{3,36} = 3.3$, $p = .03$, $\eta_p^2 = .210$), with jazz musicians having the largest MMN amplitudes ($p < .05$). Also, the pitch MMN was marginally significant for the Group factor ($F_{3,36} = 2.8$, $p = .05$, $\eta_p^2 = .171$), similarly deriving from the larger MMN amplitudes of jazz musicians compared with non-musicians and rock musicians ($p < .02$; pitch MMN of jazz musicians differed only marginally to that of classical musicians: $p = .07$). Hence, the enhanced slide and pitch MMN amplitudes in jazz musicians play a main role in driving the significance of the Group main effect in the omnibus ANCOVA.

Across groups, MMN amplitudes also differed according to the feature (main effect of Feature: $F_{5,180} = 2.6$, $p = .03$, $\eta_p^2 = .06$). This was due to the largest MMN elicited by the location deviant compared with all the others ($p < .0001$ in LSD post hoc tests) and the smallest MMNs to the intensity and rhythm deviants compared with all the others ($p < .0001$ in LSD post hoc tests; rhythm and intensity MMNs, in turn, did not differ from each other: $p = .5$).

The MMN latencies (see Table 2) tended to vary according to the feature type (main effect of Feature: $F_{5,180} = 2.1$, $p = .06$), with pitch eliciting the longest MMN latency of all features ($p < .0001$ in LSD post hoc tests), and location and rhythm the shortest of all ($p < .03$ in LSD post hoc tests; location and rhythm MMN latencies did not differ between each other: $p = .5$). More importantly, there was a marginal difference between groups ($F_{3,36} = 2.4$, $p = .09$), caused by jazz musicians having slightly shorter MMN latencies than rock musicians.

3.3. Group differences in scalp distribution of the MMN

The distribution of the MMN over the scalp was also modulated by musicianship (Fig. 4), as testified by the significant interactions Group $\times$ Frontality ($F_{6,72} = 3.9$, $p = .002$, $\eta_p^2 = .0212$; but Feature $\times$ Frontality $\times$ Group: $F < 1$). Overall, the MMN amplitudes did not differ in their scalp distribution between cerebral hemispheres, as evidenced by a non-significant main effect of Laterality ($F < 1$), and by the non-significant interactions including Group and Laterality as factors (Group $\times$ Laterality, Feature $\times$ Laterality $\times$ Group: $F < 1$; Frontality $\times$ Laterality $\times$ Group: $F_{6,360} = 1.2$, $p = .3$). However, as mentioned above, while the overall interaction Feature $\times$ Group was not significant, the four-way interaction Feature $\times$ Frontality $\times$ Laterality $\times$ Group showed a modulation of MMN amplitudes to the different features over the scalp ($F_{30,360} = 1.6$, $p = .02$, $\eta_p^2 = .11$).

For studying scalp distributions of MMN across groups, we conducted separate ANCOVAs for the Feature factor. The pitch MMN was significantly modulated in the front–back distribution over the scalp between groups (interaction Frontality $\times$ Group: $F_{6,72} = 4.1$, $\eta_p^2 = .214$, $p < .05$), due to the larger MMN amplitudes of jazz musicians as compared with that of rock musicians and nonmusicians only at frontal electrodes (main effect of Group in a separate ANCOVA for frontal electrodes: $F_{3,36} = 4.8$, $p = .007$, $\eta_p^2 = .244$; $p < .02$ in LSD post hoc tests and only marginally significant difference between frontal pitch MMN of jazz musicians and that of classical musicians: $p = .07$). The other two ANCOVAs for pitch MMN amplitudes measured at central and parietal electrodes did not yield any significance for main effects or interactions containing the Group factor (all $F \leq 1$ except for main effect of Group at central electrodes: $F_{3,36} = 2.6$, $p = .07$). Similarly, the Laterality factor for pitch MMN did not yield any significant interaction with Group ($F < 1$).

The MMN amplitudes to intensity deviants varied over the scalp depending on musicianship, as evidenced by the significant Frontality $\times$ Laterality $\times$ Group interaction ($F_{6,72} = 4.2$, $p = .001$,

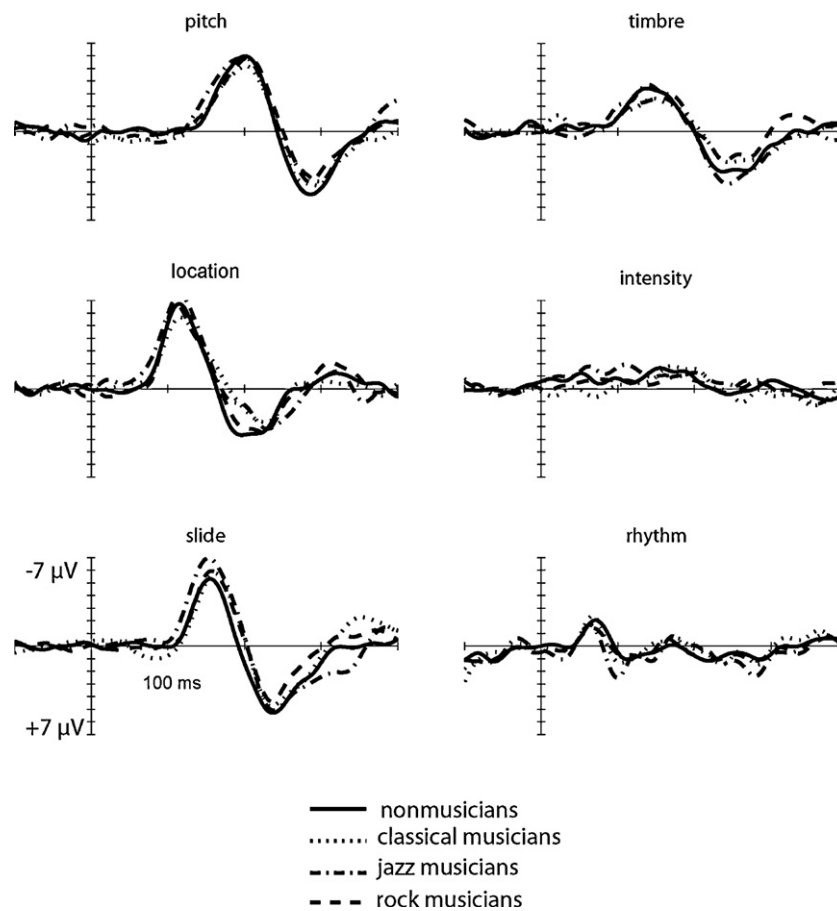


Fig. 2. Grand average ERPs in non-musicians, jazz musicians, classical musicians and rock musicians for the 6 types of deviations recorded at a frontocentral (approximately Fz) site. Note that the onset of the rhythm deviant was –30 ms corresponding to the intersection of the y-axis.

Table 2
MMN-amplitudes and latencies.

	Mean Amplitude	SD	t-Value	df	p-Value (2tailed t-test vs 0)	Mean Latency	SD
Non-musicians (NM)							
Pitch	–5.68	1.54	–12.22	10	0	201	14
Timbre	–3.40	1.63	–6.91	10	0	146	20
Location	–5.89	2.37	–8.23	10	0	119	7
Intensity	–2.06	1.33	5.15	10	0	148	39
Slide	–4.86	2.12	–7.60	10	0	155	12
Rhythm	–1.99	1.13	–5.82	10	0	119	55
Classical musicians (CM)							
Pitch	–4.84	1.84	–6.94	6	0	193	25
Timbre	–3.01	1.58	–5.04	6	0.002	142	36
Location	–4.83	1.32	–9.70	6	0	120	15
Intensity	–1.72	1.21	–3.79	6	0.009	165	33
Slide	–4.34	2.71	–4.24	6	0.005	157	11
Rhythm	–1.78	0.78	–6.00	6	0.001	137	35
Jazz musicians (JM)							
Pitch	–6.44	1.86	–10.92	9	0	197	21
Timbre	–4.02	1.72	–7.37	9	0	148	26
Location	–7.31	1.24	–18.63	9	0	123	26
Intensity	–2.57	1.66	–4.89	9	0.001	122	24
Slide	–7.25	3.52	–6.51	9	0	156	20
Rhythm	–1.91	2.13	–2.83	9	0.02	105	47
Rock musicians (RM)							
Pitch	–5.26	2.00	–9.84	13	0	207	25
Timbre	–2.60	1.48	–6.56	13	0	155	30
Location	–5.63	1.20	–17.61	13	0	118	9
Intensity	–1.51	1.30	–4.34	13	0.001	158	47
Slide	–5.53	2.44	–8.47	13	0	163	15
Rhythm	–1.56	1.92	–3.03	13	0.01	143	48

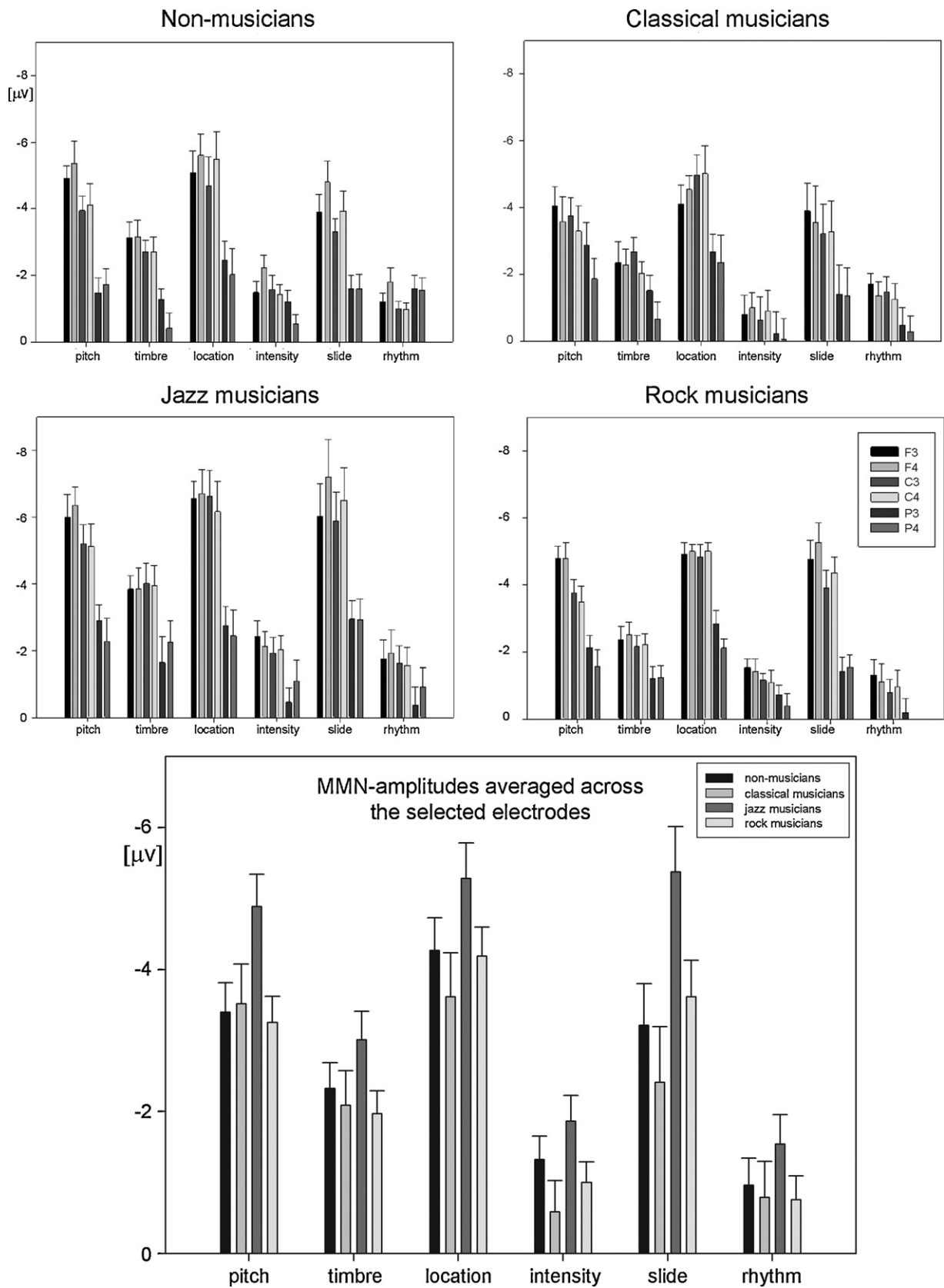


Fig. 3. Top four panels: MMM amplitude according to musical group for each of the sound features and electrodes. Bottom panel: MMN amplitude to the different sound features, averaged across the selected electrodes.

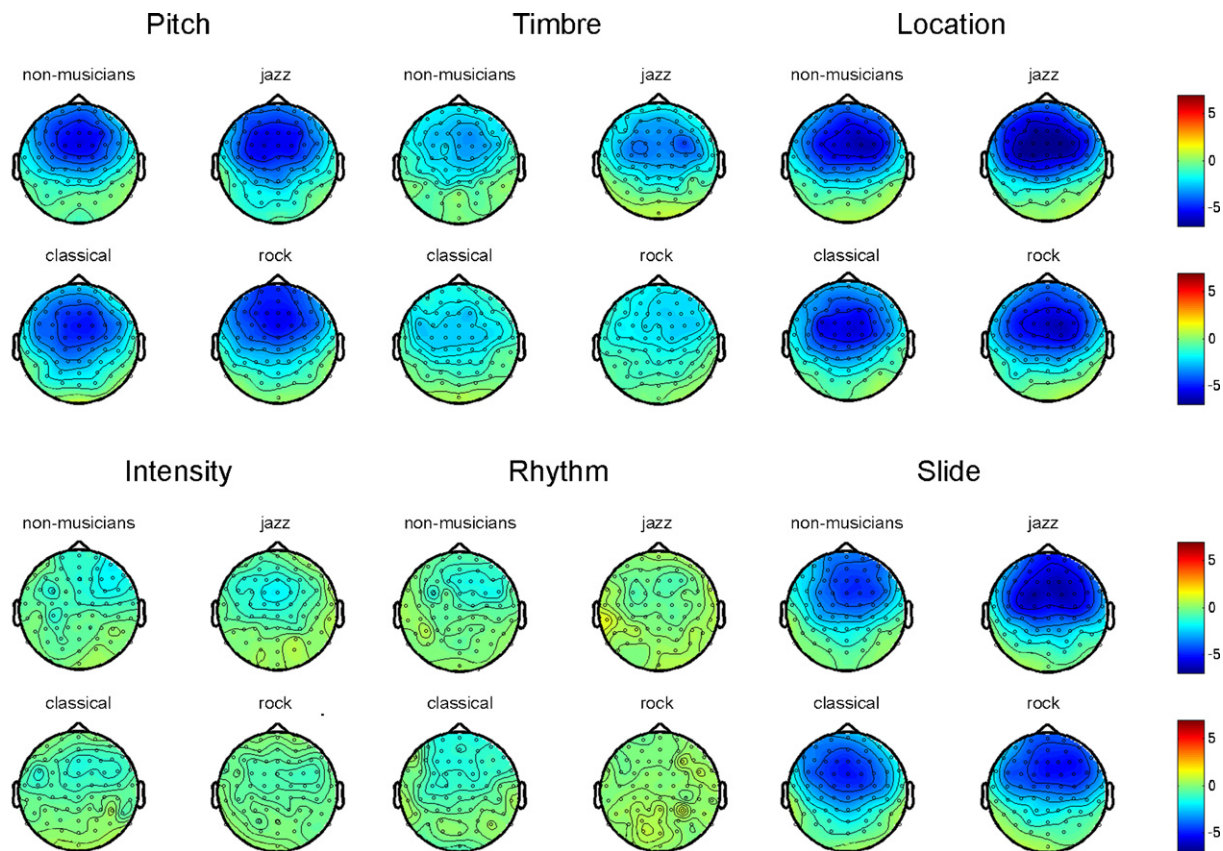


Fig. 4. EEG voltage isopotential maps of the difference between the responses to deviants and standards averaged in an interval of ± 20 ms around maximal peak amplitudes.

$\eta_p^2 = .224$; the interaction Frontality $\times$ Group was only marginally significant: $F_{6,72} = 2$, $p = .08$). Separate ANCOVAs testified that the intensity deviant elicited an MMN which differentiated the groups only at frontal electrodes (main effect of Group: $F_{3,36} = 3.2$, $p = .04$, $\eta_p^2 = .192$; also at central electrodes there was a marginally significant main effect of Group: $F_{3,36} = 2.8$, $p = .05$), derived from larger intensity MMN of jazz musicians compared with that of classical and rock musicians ($p < .02$; no significant difference in MMN amplitudes of jazz musicians and non-musicians: $p = .1$). Additionally, at frontal electrodes only, the intensity MMN was modulated in amplitude between the hemispheres (interaction Laterality $\times$ Group: $F_{3,36} = 3.8$, $p = .02$, $\eta_p^2 = .192$) with larger MMN at the right frontal site (F4) compared to the left frontal site (F3) in non-musicians ($p = .03$ in a paired t -test). We also found a slightly significant interaction Laterality $\times$ Group for intensity MMN at parietal electrodes ($F_{3,36} = 2.9$, $p < .05$, $\eta_p^2 = .131$) but it was so negligible (as also reflected by the effect size measure η_p^2) that post hoc LSD and paired t -tests did not evidence any significance ($p > .1$).

MMNs to *timbre*, *location*, *slide*, and *rhythm* deviants did not clearly differentiate the groups for MMN topography ($F \leq 1$ except for the interaction Frontality $\times$ Laterality $\times$ Group of the timbre MMN, $F_{6,72} = 1.7$, $p = .1$, the interaction Frontality $\times$ Group of the location MMN, $F_{6,72} = 1.8$, $p = .1$, and the interaction Frontality $\times$ Laterality $\times$ Group of the rhythm MMN, $F_{6,72} = 1.7$, $p = .1$).

When analyzing the scalp distribution within groups, hence, taking out the Group factor, additional differences also for the location, intensity and timbre MMNs were obtained. Specifically, for jazz musicians we found a significant interaction Feature $\times$ Frontality ($F_{10,70} = 3.5$, $p = .02$; $\eta_p^2 = .193$), due to marginally significant effects of Frontality for pitch ($F_{2,14} = 3.3$, $p = .06$) and intensity ($F_{2,14} = 2.9$, $p = .08$). In turn, main effects or interactions containing Laterality as factor did not yield any significance

($F < 1$ for all except for main effect of Laterality: $F_{1,7} = 4.8$, $p = .06$), hence indicating a bilateral MMN topography in jazz musicians. In classical musicians, we obtained a significant interaction Feature $\times$ Laterality ($F_{5,20} = 3.9$, $p = .01$, $\eta_p^2 = .274$), deriving from the left-lateralized MMN to timbre deviants (main effect of Laterality for timbre MMN in a separate ANCOVA for the Feature factor: $F_{1,4} = 16.5$, $p = .02$, $\eta_p^2 = .492$), and from the right-lateralized MMN to location deviants (main effect of Laterality for location MMN: $F_{1,4} = 11.5$, $p = .03$, $\eta_p^2 = .402$), with the MMN amplitudes to other feature deviants being bilaterally distributed (in separate ANCOVAs main effects of Laterality: $F \leq 1$ except for rhythm MMN: $F_{1,4} = 2.3$, $p = .2$). In classical musicians, no other interaction with Feature was significant (Feature $\times$ Frontality: $F < 1$ for all except for Feature $\times$ Frontality $\times$ Laterality: $F_{10,40} = 1.8$, $p = .09$). In turn, the MMN amplitudes of rock musicians and non-musicians did not vary in their distribution over the scalp depending on the eliciting deviant feature ($F < 1$).

3.4. Correlations between MMN and musical skills

Across the whole sample of participants, the scores in AMMA Tonal test negatively correlated with the amplitude of the MMN response to timbre deviation recorded at Fz ($r = -0.4$, $p = .008$), meaning that larger MMN amplitudes to timbre corresponded to better performance in the AMMA Tonal test (Fig. 5). Similarly, the total scores in the two AMMA tests negatively correlated with the MMN amplitude to pitch ($r = -0.4$, $p = .01$) demonstrating the relation between the negative amplitude of the MMN to pitch deviation and the musical discriminatory skills as assessed with AMMA test.

We additionally explored the likely relations between MMN amplitudes, latencies and type of musical expertise by non-parametric Spearman's correlation tests. In non-musicians, the

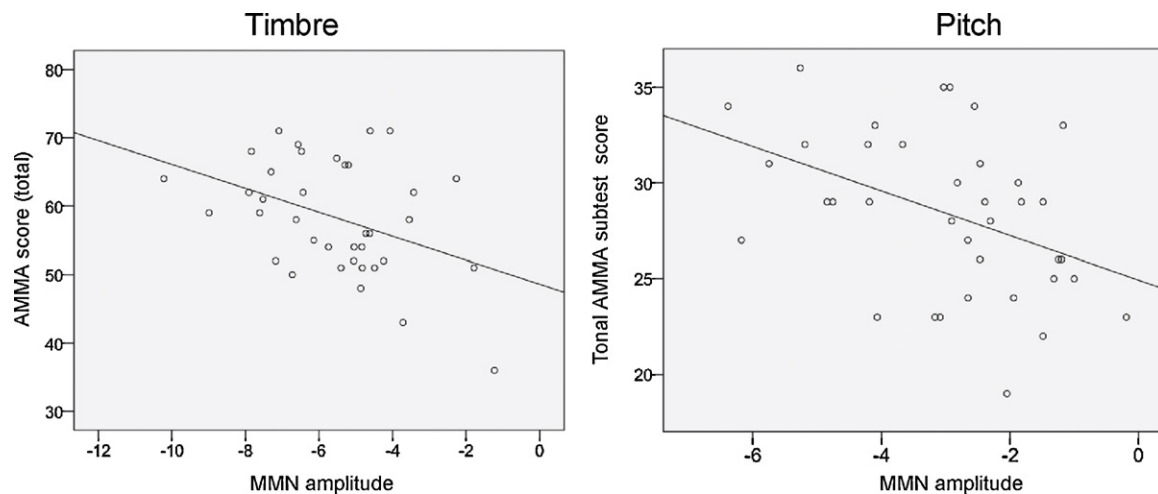


Fig. 5. Significant correlations between the AMMA test and MMN-amplitudes recorded at the Fz electrode in all subjects. The left panel shows the correlation between the total AMMA test scores and the amplitude of the timbre deviant ($r = -0.4$, $p = .008$), the right panel the correlation between the total AMMA subtest and amplitude of the pitch deviant ($r = -0.4$, $p = .01$).

rhythmic discrimination skills as measured by the Rhythm AMMA subscore were negatively correlated with the MMN amplitude to pitch deviant ($\rho = -0.8$; $p = .008$), i.e., better rhythmic discrimination abilities were associated with an enhanced (more negative) MMN to pitch. In jazz musicians, the MMN amplitude to intensity deviant was positively correlated with the scores obtained in the Rhythm AMMA test ($\rho = 0.9$; $p = .006$), indicating hence that the larger the MMN to intensity deviant the worse were the subjects discriminating the rhythmic changes in the AMMA test. Conversely, the MMN latency to the rhythm deviant was positively correlated with the scores in the Rhythm AMMA test ($\rho = 0.9$; $p = .005$), showing that the speed of neural auditory discrimination as indexed by MMN to rhythm deviant was associated with the success in performance in the Rhythm AMMA test.

4. Discussion

Studying differences between jazz, classical, rock musicians and non-musicians, using a novel musical multi-feature MMN-paradigm and behavioral measures, we here show that the style/genre of music, that professional musicians are engaged with, influences early auditory skills. In particular, we obtained larger overall MMN amplitude in jazz musicians as compared with classical musicians, rock musicians and non-musicians across six different sound features. This indicates a greater overall sensitivity to sound changes in jazz musicians as compared to other types of musicians. Notably, we found evidence of enhanced processing particularly of the pitch deviant and pitch slide deviant in jazz musicians, only. The present paradigm is the first MMN-paradigm to include the pitch slide deviant. Sliding to tones is a typical feature in improvisational music such as jazz music as opposed to classical music, where it most often is considered to be inappropriate. This may explain the enhanced MMN to this feature in jazz musicians. We also observed a tendency for a shorter MMN latency in jazz musicians compared to rock musicians and a significant modulation of the scalp topography for pitch and location features in jazz musicians. These results were paired with the fact that jazz musicians score higher in musical aptitude tests than rock musicians and non-musicians, especially with regards to tonal abilities.

In addition, the MMN to timbre was left lateralized in classical musicians only. Taken together our findings indicate that the characteristics of the style/genre of music played by musicians influence

their overall early auditory skills, also targeting specific sound features embedded in a musical context. Brain plasticity seems hence to be at least partially sensible to the specificity of training and listening experiences even within one modality.

Our data hence indicates differences in both behavioral and brain processes between the musical groups. All musical groups outperformed the non-musicians with respect to the total AMMA score and to the tonal AMMA sub-score. The jazz musicians in turn outperformed rock musicians but not classical musicians in the total AMMA score. Jazz musicians also surpassed the rock musicians in the tonal and rhythmic subscores of the AMMA test with a tendency to score better on rhythm than the classical musicians.

These results may primarily be explained by two factors: (1) the musical learning strategies of a particular style/genre of music and (2) enhanced brain processing of acoustic and musical information most essential to the musical style/genre that performers spend their time on. Jazz musicians learn and perform music to a great extent by using the ear (Berliner, 1994; Monson, 1997) and separate ear training classes are taught at all the primary jazz schools around the world. Furthermore, jazz music in its modern form is characterized by complex chord changes, rich harmonies and challenging rhythmic structures such as polyrhythms that place great demands on listeners and performers' theoretical and ear training skills. In comparison, even though rock musicians, playing primarily pop and rock, learn music primarily by ear, they are typically exposed to less complex musical material. At the other end of the spectrum the teaching tradition within classical music focuses less on ear training taking sheet music as a starting point, even though some schools such as the Suzuki method (Galvao, 1999) teaches music by ear in the early years of childhood. Hence, the combination of typical learning strategies with a strong focus on ear training skills taught in separate classes and included in the instrumental training, and the acoustic and the music theoretical complexity inherent to the style/genre may account for the fact that jazz musicians had greater overall strength of the pre-attentive ERP-amplitude to music-related auditory deviants, and excelled in the behavioral AMMA test of tonal and rhythmic discrimination.

Musical learning strategies have been hypothesized to influence behavior and neural responses (Altenmüller, 2001; Tervaniemi, 2009; Tervaniemi et al., 2001). Our findings are in line with Seppänen and colleagues (2007) who found differences in behavior between an aural and a non-aural group of musicians, indicating that AMMA performance benefits from formally learned analytical

skills. This is consistent with the fact that the jazz musicians in the present study had received an intensive education in formal music theory and ear training, and that they scored higher than rock musicians in the AMMA test. In contrast to our data and indicative data from earlier studies (Tervaniemi et al., 2001), Seppänen and colleagues found only MMN latency differences in neural processing of patterns between the aural and non-aural group, but no differences in MMN-amplitude. However, they did not divide the participants according to style/genre of music but instead according to learning strategies. Hence, it is likely that the long-term learning strategies that are typical for a specific musical genre, are a prerequisite for acquiring auditory skills resulting in measurable changes in pre-attentive brain processes. This is supported by Tervaniemi and colleagues (2006), who showed that amateur rock musicians had selectively enhanced MMN for location changes compared to non-musicians, suggesting that brain processing of music is enhanced by learning strategies especially in relation to the acoustic information most essential to musical genre.

The analyses of the scalp distributions in the present study corroborated the hypothesis that engagement with music of a specific genre enhances brain processing of acoustic information most essential to musical genre. First, the timbre feature was left lateralized in classical musicians only. Enhancing the instrumental sound or timbre is given much attention in the training of classical musicians. Also N1m-amplitude to instrumental sounds is selectively enhanced in violinists and trumpet players when listening to their own instruments (Pantev et al., 2001). The present result extends this finding suggesting qualitatively different neural processing of timbre in classical musicians. Second, in jazz musicians, MMN to location and pitch deviants was frontally more dominant than to other deviants. Locating sound sources is especially important to jazz musicians using auditory cues when communicating with other musicians while they play (Vuust, Ostergaard, & Roepstorff, 2006). Third, the jazz musicians had enhanced MMN to the slide deviant, a typical feature in their musical style. Furthermore, the ability to extract pitch information is essential in order to excel in the tonal part of the AMMA test in which the jazz musicians performed significantly better than rock musicians and non-musicians but not better than classical musicians. In extension, the strong rhythmic element in jazz music (Pressing, 2002) may account for the fact that jazz musicians score better in the rhythm subtest of the AMMA than all other groups.

That stylistic features of the music material influences the auditory processing of musicians may also explain the fact that rock musicians performed no better (actually worse) than the classical musicians on the AMMA test, even though the learning strategy in this style/genre of music is clearly more based on the ear. Another factor that may account for this result is that the rock musicians had played their main instrument for a much shorter time than the classical musicians even though they had been involved in music performance for the same number of years. Instrumental skills and specific challenges in playing a certain instrument often generalizes to enhanced abilities in specific domains (Gaser & Schlaug, 2003; Pantev et al., 1998), and enhancement in behavior, brain anatomy and function, are typically positively correlated with the early commencement of the instrumental training (Costa-Giomi, Gilmour, Siddell, & Lefebvre, 2001; Hutchinson et al., 2003; Keenan, Thangaraj, Halpern, & Schlaug, 2001). Taken together our results add to the growing body of evidence suggesting that differentiated musical abilities results in quantitatively and qualitatively different neuronal processing of sound features.

It may seem puzzling that the observed difference in MMN-amplitude between jazz musicians and classical musicians showed up only as a non-significant tendency in the AMMA tests. It is however important to note that in contrast to the AMMA test the ERPs investigated here are pre-attentive, elicited in the absence of

subjects' attention towards the stimuli (Alho, 1992; Fujioka, Trainor, Ross, Kakigi, & Pantev, 2004) and that the musical multi-feature paradigm is acoustically a much more comprehensive test than the AMMA test in that it tests discrimination of 6 different features of sound. The AMMA, on the other hand, is a forced-choice test requiring full attention from the participants. Hence, the musical multi-feature paradigm discloses aspects of sound discrimination abilities that are not tested by the AMMA test.

Interestingly, we found a correlation between the total score of the AMMA test and amplitude of the MMN to the pitch deviant across all subjects. Our results hence suggest that enhanced pre-attentive neural response to pitch deviations in an ecologic musical context may be a general indication of ear training skills. We also observed a correlation between the tonal subtest score of the AMMA and the amplitude of the MMN to timbre across all subjects. Many studies have found a relationship between musical training and enhanced neural response to the specific timbre of one's own instrument (Pantev et al., 2001; Shahin, Roberts, Chau, Trainor, & Miller, 2008). Our results indicate that pre-attentive processing of timbre in complex pitch patterns is an important component of melodic discrimination abilities. The inverse relationship between the rhythm subscore of the AMMA test and the MMN-amplitude of the pitch deviant in non-musicians indicates that a high competence in one of these two fundamental aspects of music (Krumhansl, 1990; Palmer & Krumhansl, 1990) may come at the expense of the other in these relatively unskilled subjects. The positive correlation between the AMMA rhythm score and rhythm latency and intensity amplitude in jazz musicians is difficult to interpret and may be caused by the fact that these two features were also the features with significantly lower MMN-amplitude than the other features. Future studies should aim at testing whether these correlations are still present with rhythm and intensity deviants of various magnitudes.

The observed differences between musician groups are striking in that we for the first time have been able to measure pre-attentive ERPs in different musician groups to a range of deviants embedded in continuous streams of music-like material. Previous studies indicate that the stimuli need to consist of realistic, complex musical material in order to disclose fine-grained processing differences between participants (Brattico et al., 2001; Koelsch et al., 1999; Seppänen et al., 2007). The present results suggest not only that there are competence-related auditory differences between musicians from different styles of music, but also that these differences are measurable pre-attentively while musicians listen to ongoing music-like material.

The fact that the musical multi-feature paradigm differentiates musicians could potentially be of particular interest to music education. For instance, in the case that future developments of the ERP-method will reach sensitivity and reliability even at the individual level, whereas currently ERPs are sensitive and reliable only at the group level, it will be possible to draw individual multi-attribute "profiles" of sound discrimination abilities. On the other hand, caution should be taken to advocate "objective" auditory measures as the sole basis for recruiting and evaluating musical students. Musical abilities depend on a number of different factors difficult to measure objectively (Woody & Mcpherson, 2010), such as having a characteristic individual style, rehearsal stamina, creativity, and motivation.

The array of tasks and the diversity of neural structures and functions involved in musical performance make musicians an ideal population for investigating learning-dependent brain plasticity. The specificity of task demands and learning methods of different musical styles presents opportunities for brain scientist for acquiring detailed knowledge about the development of particular brain processes. The present data indicate a relationship between stylistic features of a style/genre of music influences auditory brain

processing it is not possible to rule out the possibility of innate differences between musician groups. In fact, a recent study indicates personality differences between classical musicians and jazz/rock musicians suggesting that musicians partly choose musical careers on the basis of personality traits (Vuust et al., 2009). Future studies should try to vary personality traits and musical affiliation systematically in order to tease out the contribution of nature and nurture.

5. Conclusion

In the present study, we for the first time have disclosed fine-grained auditory processing differences between participants from various musical backgrounds using only one short, musical multi-feature MMN paradigm. Taking both behavioral and brain measures into account, we found that jazz musicians outperformed other types of musicians in terms of general auditory abilities. This indicates that the musical learning strategies, the stylistic features and possibly also music complexity of this style of music influence musical skills and brain processing of auditory features embedded in a musical context. This suggests that brain development is sensible to the specificity of training and listening experiences.

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