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Cortical Activity during Perception of Musical Rhythm; Comparing Musicians and Non-musicians

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Abstract

This study investigates the effects of musical training on brain activity to violations of rhythmic expectancies. We recorded behavioral and event-related brain potential (ERP) responses of musicians and non-musicians to discrepancies of rhythm between pairs of unfamiliar melodies based on Western classical rules. Rhythm deviations in the second melody involved prolongation of a note, thus creating a delay in the subsequent note; the duration of the second note was consequently shorter because the offset time was unchanged. In the first melody, on the other hand, the two notes were of equal duration. Musicians detected rhythm deviations significantly better than non-musicians. A negative auditory cortical potential in response to the omitted stimulus was observed at a latency of 150–250 ms from where the note should have been. There were no significant differences of amplitude or latency between musicians and non-musicians. In contrast, the N100 and P200 to the delayed note after the omission were significantly greater in amplitude in musicians compared to non-musicians especially in frontal and frontal-central areas. These findings indicate that long term musical training enhances brain cortical activities involved in processing temporal irregularities of unfamiliar melodies.

Keywords

Auditory Event-Related Potentials; Electroencephalography; Rhythm Perception; Musical training; Rhythm Deviations

Musicians are able to detect deviations of pitch more rapidly and accurately than non-musicians (Besson & Fäita, 1995; Brattico, Tervaniemi, Näätänen, & Peretz, 2006; Fujioka, Trainor, Ross, Kakigi, & Pantev, 2005; Gaser & Schlaug, 2003; Granot & Donchin, 2002; Habibi, Wirantana, & Starr, 2013; Koelsch, Schröger, & Tervaniemi, 1999; Pantev, Engelen, Candia, & Elbert, 2001). The aim of the present report was to investigate the effects of musical training on the neurophysiologic and behavioral capacities in detecting deviations of rhythm in unfamiliar melodies using cortical event-related potentials (ERPs).

ERPs are averages of the EEG signal time-locked to repeated stimuli that allow for the identification of sensory, motor and cognitive processing steps of the brain response to such stimuli. ERPs are typically named with regards to the electrical sign of the EEG deviation (N for negative, P for positive) observed in combination with the approximate latency in milliseconds of the peak. In the auditory domain some of the well characterized ERP components include the N100, P200 and the Mismatch Negativity (MMN).

The N100 is a large negative potential that is elicited to an auditory stimulus independent of the task demand. It peaks between 80–120 ms after the onset of a stimulus. Source analysis of the auditory N100 suggests that a generator in the superior aspect of the temporal lobe in each hemisphere generate the scalp recorded voltage field of this potential which is typically distributed maximally over the frontal-central regions of the scalp (Picton & Scherg, 1991; Richer, Alain, Achim, Bouvier, & Saint-Hilaire, 1989). The N100 has not been shown to be different between musicians and non-musicians; however its magnetic counterpart N1m has been reported to be larger in musicians compared with non-musicians when evoked by piano tones (Pantev et al., 1998). The P200 peaks at about 200 ms (varying between about 150 and 275 ms) after the onset of a stimulus and is shown to be generated in associative auditory temporal regions with additional contributions from non-temporal sources such as frontal areas (Ferreira-Santos et al., 2012). P200 was traditionally considered to be an automatic response, modulated only by stimulus; but it has been shown that its latency and amplitude are sensitive to learning and attention processes. Enhancement of P200 was observed when participants were trained to discriminate temporal features of speech signals (Tremblay, Kraus, McGee, Ponton, & Otis, 2001) or when non-musician subjects learned to detect pitch deviants in a short stream of pitch stimuli (Atienza, Cantero, & Dominguez-Marin, 2002). Similarly, Ross and colleagues (Ross & Tremblay, 2009), reported enhancement of the P200 between two experimental sessions of passive listening in a MEG study, underlining the sensitivity of the P200 response to perceptual learning, memory and training. Finally, comparing musicians and non-musicians, the P200 amplitude in processing of musical timbre, has been reported larger in musicians (Pantev, Roberts, Schulz, Engelien, & Ross, 2001; Shahin, Bosnyak, Trainor, & Roberts, 2003) reflecting possible changes in auditory processing specifically associated with experience of long-term training.

The Mismatch Negativity (MMN) is a negative cortical evoked potential with peak latency between 150–200 ms. The MMN is typically recorded in an oddball paradigm wherein a series of tones are presented with infrequent deviant tones embedded amongst frequent standard tones, and is calculated by subtracting the ERP to frequent auditory stimuli from the ERP of infrequent auditory stimuli (Näätänen, 1992). The main generator for the MMN is within the vicinity of the primary auditory cortex with additional smaller contributions from frontal cortical areas (Alain, Woods, & Knight, 1998).

Deviations of rhythm are typically created by omitting and/or delaying an auditory stimulus (e.g. a tone or a beat) from a previously established temporal sequence. These temporal deviations have been shown to elicit a negative potential beginning between 150–200 ms followed by a positivity peaking between 300–1000 ms (P300) (Jongsma et al., 2005; Nittono, Bito, Hayashi, Sakata, & Hori, 2000; Rüsseler, Altenmüller, Nager, Kohlmetz, & Münte, 2001). While some studies have shown that musicians, compared to non-musicians,

have larger amplitude negative potentials in response to the omission of a tone in a sequence of tones presented during EEG recording sessions (Jongsma et al., 2005; Jongsma, Desain, & Honing, 2004; Rüsseler et al., 2001), others have shown that the amplitude and latency of omission-related potentials did not differ between musicians and non-musicians (Besson & Faita, 1995). This apparent contradiction in the previous literature may be a consequence of different experimental design and stimuli. For instance, while the studies finding differences in omission-related activity investigated non-musical stimuli such as tones or beats (Jongsma et al., 2005, 2004; Rüsseler et al., 2001) the study finding no such difference to rhythmic incongruities used musical melodies (Besson & Faita, 1995). Further, in the one previous study utilizing musical stimuli (melodies), temporal deviations were inserted at the final position of the melody possibly focusing the listener's attention to the location of the deviance (Besson & Faita, 1995). This temporal cue (provided by fixating the location of deviant note) may have contributed to the nearly perfect detection of deviation for both musicians and non-musicians and the lack of a differential brain response.

Unexpected omission of an auditory stimulus from a regular series of stimuli has also been shown to affect the brain response to the stimulus following the omission (e.g. delayed tone). The N100 response to a note following an inserted pause was shown to be larger in amplitude and shorter in latency when compared to notes preceding the pause (Nittono et al., 2000). Similarly, Raij and colleagues (Raij, McEvoy, Mäkelä, & Hari, 1997) showed that the amplitude of the N100 and P200 responses to the tone after the omission are larger than responses to tones preceded by other tones. Specifically, the enhancement of the N100-P200 response to a stimulus (percussion sound) following the omission of a beat has been shown to be more pronounced in musically trained participants when compared to non-musicians (Jongsma et al., 2005). These N100 and P200 enhancement can be explained by increased levels of attention in musicians as it is reasonable to expect that within musicians, more attention is directed to the stimulus following the omission, due to their enhanced ability to closely attend to a rhythmic pattern. This difference in brain response of musicians relative to non-musicians to a delayed stimulus following an omission has yet to be demonstrated within paradigms using musical stimuli with unexpected rhythmic deviations.

The present study aimed to address the issues regarding the differences between findings in behavior and brain processing of musicians versus non-musicians to temporal deviance by using unfamiliar musical melodies that contain rhythmic deviations, occurring at varying and unpredictable locations across the melodies. Specifically, the incorporation of rhythmic deviations distributed throughout musical phrases allows for more ecologically valid stimuli and increases the tendency for listener's attention to be more equally spread throughout the stimuli as occurs in normal music-listening condition. The rhythmic deviation consisted of changing the durations of two consecutive notes- the first note was prolonged and the onset of the second note was thus delayed-allowing for the examination of brain responses not only to the onset of the omission of the note but also to the response to the actual deviant delayed note.

We hypothesized that 1) musicians would detect changes in rhythm more accurately than would non-musicians; 2) an omission-related potential would be elicited at the temporal position when the note should have occurred and its amplitude would be larger and latency

shorter in musicians compared to non-musicians. 3) Both sensory and cognitive (N100 and P200) cortical potentials to the delayed note would be enhanced in amplitude and have shorter latencies in musicians relative to non-musicians given that musicians can allocate greater attentional resources to the musical stimuli. Confirmation of these predictions would support the hypothesis that musical training enhances auditory cortical processing related to detecting not only spectral but also fine temporal irregularities.

Experimental Procedures

Subjects

Twenty-one musicians and twenty-one non-musicians took part in this experiment. Data from two subjects (one from the musician group and one from the non-musician group) were not included because of excessive movement artifact in their electroencephalogram (EEG), rendering the definition of evoked potentials components unreliable. Twenty musicians (19 right handed, 16 females) and twenty non-musicians (20 right handed, 15 females) were thus included in the final experimental data. The musicians and non-musicians did not differ in age (musicians: 20.1 ± 1.4 ; non-musicians: 21.7 ± 4.6 , $t(38) = 1.53$, $p = 0.13$). Musicians had significantly more years of musical training than the non-musicians (musicians: range=7–16 years, 12.3 ± 2.75 ; non-musicians: range=0–1 years, 0.05 ± 0.22 , $t(38) = 20.75$, $p < 0.0001$). The musical background of the musicians is listed in Table 1. Participants were all native English speakers. They received monetary compensation or extra credit points for undergraduate psychology courses for their participation. The Institutional Review Board of the University of California, Irvine, approved the study.

Behavioral Assessment of Musical Abilities

In order to exclude any non-musician with abnormally deficient skills in musical processing, prior to participating in the experiment each participant completed the Scale and Rhythm sections of the Montreal Battery of Evaluation of Amusia (MBEA). The MBEA is a battery of musical tests developed and adjusted by Peretz (Peretz, Champod, & Hyde, 2003) for the evaluation of musical perceptual and memory deficits of healthy adult listeners with a particular focus on discriminating individuals with amusia. The original battery consists of six sections. However, in the interest of time, we chose the two sections, Scale (Pitch) and Rhythm, which were most relevant to our experimental questions. In addition, measurements of pure-tone threshold as a function of frequency (audiograms) were obtained from all participants to ensure normal hearing.

Experimental Protocol

Subjects were presented with 10 unfamiliar pairs of melodies varying in duration from 5–12 seconds played at a sound level of 70 dB SPL. The melodies were composed for these experiments (by David Reeder) based on Western classical rules (within the framework of common practice period, i.e., from 1600 to 1900) and differed from one another in pitch and rhythmic content. Each trial was preceded by a warning tone (1500 Hz pure tone, 250 ms duration, 70dB SPL) 500 ms prior to the onset of the melody. Each trial consisted of an initial “target melody” and a subsequent “comparison melody” separated by a 1500 ms silent interval. The comparison melody was either the same as the target melody (standard case),

or contained a pitch violation note compared to the target melody in the pitch deviant case, or a rhythm-violated note compared to the target melody in the rhythm deviant case. Results reported below are presented with respect to the rhythm deviant stimuli. The results regarding the effects found in response to the pitch deviant trials were reported in a separate publication (Habibi et al., 2013).

There were a total of 300 trials presented in 10 blocks. Each block consisted of a pseudorandom presentation of 30 melodies in which each of the ten experimental melodies was presented once as a standard, once in the pitch deviant version, and once in the rhythm deviant version. In six of the ten melodies, rhythm deviation was created by changing the duration of two adjacent notes to alter the rhythmic grouping by temporal proximity while retaining the same meter and total number of notes. This was done by changing two eighth notes, each 500 ms in length, to a dotted eighth note and a sixteenth note, 750 and 250 ms in length, respectively. In the remaining four melodies, rhythm deviation was created differently (e.g. by changing two eighth notes to a sixteenth note followed by a dotted eighth note). Analysis was done only on the six melodies with the same pattern of rhythmic deviation and the results reported here reflect findings from the six melodies wherein two eighth notes were replaced by a dotted eighth note and a sixteenth note. Throughout this article, the “standard note” refers to the second note of the two equal length notes in the standard case; the “delayed note” or “delayed deviant note” refers to the shortened 250 ms note in the deviant case; and the “the omitted stimulus” refers to the absence of a note at 500 ms in the deviant case (Figure 1).

All melodies were computer-generated, created in MIDI format, using Finale Version 3.5.1 (Coda Music), and were then converted to audio wave files with a “Grand Piano” sound font, using MidiSyn Version 1.9 (Future Algorithms). They were all played in the key of C major. The melodies were written in binary time signature, and the metronome was set at 60 beats per minute. Melodies varied in length, consisting of a different number of notes (12.4 ± 2.4) and rhythmic content. The location of the rhythmic changes varied across the melodies. An example of the melodies in standard and deviant format is illustrated in Figure 1. To ensure precise time-locking for the analysis of the data relative to the presentation of each individual note, a marker was sent by the stimulus presentation software (Matlab, Mathworks, 2009) to the EEG amplifier over the trigger channel at the onset of the warning tones as well as at the onset of the first notes of each melody and the standard and deviant notes.

Procedure

EEG was recorded while participants listened to the experimental paradigm involving 300 trials comprised of 10 blocks of 30 trials each. The subjects were given time for a break between each block as needed and the entire experimental period lasted approximately two hours, including the breaks. Subjects were seated in a comfortable reclining chair 70 cm from a 16-inch LCD monitor in a dark, quiet (acoustically and electrically shielded) testing room. In anticipation of comparing our findings from musicians and non-musicians with patients with hearing impairments – who typically have better hearing in one ear than the other – the melodies were presented monaurally via ER-4 insert earphones (Etymotic

Research) at an intensity level of 70 dB SPL. Some subjects were stimulated with left ear and some with right ear and the laterality of ear stimulation was counter balanced across subjects.

Participants were instructed to perform a “same-different” classification after the presentation of the second of each pair of melodies. Prior to the warning tone at the beginning of each pair of melodies, a fixation mark appeared in the center of the screen. The mark remained until the end of the trial, when it was replaced by the words “same” and “different.” The words remained until the subject responded by pressing the “same” or “different” tab on the screen using an on-screen pointer controlled by a mouse. The participants were encouraged to respond accurately and reaction times were not recorded. Prior to the experimental session, each subject participated in a practice session containing five melodies with feedback (“Correct” or “Incorrect”) provided after each same/different categorization response. If the response was incorrect, in addition to providing feedback, the trial was repeated until the participant was able to identify the correct response for all the five trials. In the case where the two melodies were different, feedback was provided to the location of deviation in the second melody so as to further assist participants to recognize the difference between the pair of melodies; in the subsequent experimental sessions, no such feedback was given.

EEG recording

A 64-channel Neuroscan Synamps2 recording system was used to collect electrophysiological data. Electrode placements included the standard 10–20 locations and intermediate sites. Impedances were kept below 10 k Ω . Lateral and vertical eye movements were monitored using bipolar electrodes on the left and right outer canthi and above and below the right eye for defining the electro-oculogram (EOG). Signals were digitized at 1,000 Hz, amplified by a factor of 2010, and band-pass filtered (cutoffs at 0.05 and 200 Hz). Offline analysis included re-referencing the recordings to an average reference (excluding EOG channels). Eye movement effects on scalp potentials were removed offline in the continuous recording from each subject using a singular value decomposition-based spatial filter utilizing principal component analysis of averaged eye blinks for each subject (Ille, Berg, & Scherg, 2002).

Data Analysis

The analysis was done on the six out of the ten melodies which had the same pattern of temporal deviation (going from two eighth notes, each 500 ms in length, in the standard case to a dotted eighth note and a sixteenth note, 750 and 250 ms in length in the deviant case). The other four melodies contained different temporal deviations and given that there were not enough trials to reliably elicit ERP components from these trials they were not analyzed. Continuous EEG records for both standard and deviant cases were divided into epochs starting 200 ms before and ending 1,000 ms after the onset of the first note. Epochs were baseline corrected (subtracting the activity from 0 ms 200 ms prior to the first note) and digitally filtered offline (band-pass 0.05–20 Hz). Epochs with a signal change exceeding +/- 150 microvolt at any EEG electrode were not included in the averages. The total number of included standard trials in musicians, 57.4 ± 3.2 and in non-musicians, 57.6 ± 2.4 whereas

for rhythm deviants in musicians, 56.4 ± 3.7 and in non-musicians 57.1 ± 3.4 . T-tests comparing number of trials between groups was non-significant (standard: $p = .52$; rhythm deviant: $p = .78$). Behavioral data from each subject were recorded and analyzed in terms of correct detection of standard and deviant trials. ERP averaging was performed only on the trials wherein the subject made a correct response.

ERPs from each electrode were quantified for each subject in response to the 1) standard note, 2) omitted stimulus, and 3) delayed deviant. In order to test any differences in the cortical response of musicians and non-musicians to rhythm deviations, we measured *mean amplitude*, the mean voltage over the time interval of the averaged waveforms. We quantified the mean voltage of the ERPs for each stimulus category from 9 out of 12 following electrodes (F3, Fz, F4, FC3, FCz, FC4, C3, Cz, C4, CP3, CPz, CP4) in time-windows centered on the peak of the respective component in the grand average waveform. The selection of the appropriate 9 electrodes and parameters of the time-windows are listed in Table 2 for each stimulus category and were chosen for analysis based on peak amplitude and latency of the grand average waveforms. A second measurement, *peak latency*, for each component was measured at the FCz electrode for the same time ranges. FCz was chosen for the peak latency measurement because the largest amplitude of each component was observed at this electrode.

Statistical Analysis

For peak latencies, separate *F*-tests for each peak latency were used to determine whether there was a difference between musicians and non-musicians. For mean voltage, the mean amplitudes of the ERP components of interest were compared with repeated-measures ANOVA analysis using Group (musicians, non-musicians) as between-group factors, and Rhythm (standard, deviant), Frontality (F-line: F3, Fz, F4; FC-line: FC3, FCz, FC4; C line: C3, Cz, C4; CP line: CP3, CPz, CP4), and Laterality (Left: F3, FC3, C3, CP3; Middle: Fz, FCz, Cz, CPz; Right: F4, FC4, C4, CP4) as within-group factors. To delineate the effects of which ear was stimulated, a second set of analyses were performed with the inclusion of ear stimulated (left, right) as an additional between-group factor in addition to all of the above factors. In all statistical analyses, type I errors were reduced by decreasing the degrees of freedom with the Greenhouse–Geisser epsilon (the original degrees of freedom for all analyses are reported throughout the paper). *Post-hoc* tests were conducted using Tukey post-hoc statistical comparisons. The findings are first described without including the stimulated ear as a comparison factor and then as a function of the stimulated ear.

Results

Montreal Battery of Evaluation of Amusia (MBEA)

Both musicians (Scale: $86.7 \pm 9.4\%$; Rhythm: $87.1 \pm 9.1\%$) and non-musicians (Scale: $84.2 \pm 10.4\%$; Rhythm: $84.2 \pm 9\%$) performed within the normal range of scores reported by Peretz et al. (2003) indicating intact ability to perceive pitch and temporal changes while listening to music. Specifically, no participants were excluded from further analysis as all participants in both groups scored in the normal range and no participants scored in the range indicative of amusia. Further, there was no significant difference between the two

groups in their performance on the scale [$F(1, 38) = 0.92, p = .36$] or rhythm tasks [$F(1, 38) = 1.6, p = .11$].

Behavioral Response to Rhythm Deviant Notes

Musicians were significantly more accurate in detecting the rhythm deviances compared to non-musicians ($F(1, 38) = 3.60, p < .05$). In response to the standard notes, there was no significant difference between the performance of musicians and non-musicians [$F(1, 38) = 0.44, p = .6$]. Figure 2 illustrates the performance in response to the standard and the rhythm deviant notes for both groups.

Event Related Potentials (ERPs)

Brain activity in response to the standard note

In the trials in which the target and the comparison melodies were identical, the N100 and P200 elicited by the standard note did not differ in amplitude between musicians and non-musicians [N100: ($F(1, 38) = 2.32, p = .14$); P200: ($F(1, 38) = 1.63, p = .21$)]. However, in these trials musicians compared to non-musicians did exhibit a significantly earlier latency of the N100 ($F(1, 38) = .25, p < .05$) but not P200 ($F(1, 38) = .35, p = .70$) component. The peak latency of the N100 potential, at FCZ, for musicians was on average 115 ms whereas for non-musicians was 122 ms.

Brain activity in response to the omitted onset

A negative component was elicited by the omission of the onset of the note in the deviant case (where the first note was prolonged and second note was delayed) between 150–250 ms from where the note should have occurred (Figure 3a). Neither the amplitude ($F(1, 38) = .002, p = .90$) nor the latency ($F(1, 38) = .69, p = .4$) of this omission related negativity differed between musicians and non-musicians. The negativity was largest at right side electrodes as evidenced in Figure 3b and by the main effect of laterality at 150–250 ms ($F(2, 76) = 4.16, p < .05$). Table 3 includes all of the main effects and interactions in response to the omitted note.

Brain activity in response to the deviant notes

As demonstrated in Figures 3a and 3b, in the deviant trials the amplitude of the N100 to the delayed note was greater in musicians than non-musicians ($F(1, 38) = 3.72, p = .06$), and a Group x Frontality interaction was significant ($F(2, 76) = 7.73, p < .05$) for the N100 indicating that this observed N100 difference between musicians and non-musicians was more pronounced at frontal and frontal-central electrodes. The amplitude of P200 elicited by the delayed note ($F(1, 38) = 4.63, p < .05$) was also larger in musicians compared to non-musicians. No differences were observed between groups with respect to latency of either the N100 or P200 elicited by the delayed note in the deviant trials. Table 4 includes all of the main effects and the interactions in response to the deviant delayed note.

The laterality of stimulated ear

The laterality of the ear stimulated was counterbalanced across both musicians and non-musicians so that within each group there were ten subjects with right ear stimulation and ten with left ear stimulation.

Laterality of stimulated ear and behavior

Compared to non-musicians, musicians performed better in detecting rhythm deviations regardless of left ($F(1, 18) = 3.49, p < .05$) or right ($F(1, 18) = 1.85, p = .08$) ear stimulation. For musicians, there were no observed differences in performance accuracy with left versus right ear stimulation ($F(1, 18) = .22, p = .82$). Non-musicians performed somewhat better with left ear stimulation than they did with right ear stimulation, however this difference was not significant ($F(1, 18) = 1.22, p = .23$).

Laterality of stimulated ear and brain activity to rhythmically deviant notes

The amplitude of the P200 to the delayed note was significantly larger with left compared to right ear stimulation ($F(1, 36) = 5.04, p < .05$) for both musicians and non-musicians. A relationship between stimulated ear and amplitude was not observed with respect to the N100 or the omission related potential in the standard or the deviant case.

To further assess the dissociation of the P200 and behavioral effect in relation to left ear stimulation, we asked our participants to return for a second session of testing of their other ear. We were only able to recruit 7 from the musician group (3 left ear and 4 right ear previously tested) and 8 from the non-musicians group (5 left ear and 3 right ear previously tested) to return for repeat testing of the ear that was previously unstimulated; therefore our repeat study was underpowered to evaluate the original findings due to inability to recruit enough returning participants.

Discussion

We defined three main findings of the effects of musical training on monaural detection of rhythmic deviations in musical phrases: First, musicians compared to non-musicians were more accurate in detecting rhythm-deviant notes. Second, at the time of the omission, both musicians and non-musicians showed an early right lateralized negative component in response to the omitted stimuli, the amplitude and latency of which did not differ between the two groups; Third, cortical potentials (N100, P200) to the delayed note following the omission were significantly larger in musicians than non-musicians.

Effects of musical training on detecting rhythmic deviations

Our results are in line with and extend the findings of an earlier study, showing that musical training enhances the detection of rhythmic deviations (Jongsma et al., 2004), not only in paradigm using non-musical beat sequences but within musical melodies containing unexpected rhythmic deviations. We presented pairs of short melodies with rhythmic or tonal irregularities introduced into the second of the two melodies. Musicians showed an increased rate of detecting rhythmic deviations in the second melody similar to their increased detection of tonal deviations, as previously reported with this same cohort (Habibi

et al., 2013). However, the improved performance of musicians was significantly greater for detecting rhythm than pitch deviant notes resulting in a larger difference between groups in the rhythm task. These findings suggest that processing temporal deviations may be more enhanced compared than pitch deviations by musical training, although an alternate explanation is that the rhythm task was simply more difficult than the pitch task (Habibi et al., 2013). In contrast, Besson and Faita (1995) found that musicians did not identify rhythmic incongruities better than non-musicians. We suggest that the different results may reflect differences in the manner in which temporal deviations were presented. In Besson and Faita's study, temporal deviations were created by delaying the last note of melodies, which provides a clear temporal location cue. Also, the delay time was 600 ms, resulting in less difficulty in detecting deviations and thereby possibly masking any differences between musicians' and non-musicians' performances due to ceiling effects. Shorter delays and unpredictable locations result in more subtle deviations that are more difficult to detect and therefore likely better demonstrate the differences between musicians' and non-musicians' abilities to detect rhythmic deviations.

Effects of musical training on cortical potentials to the omitted stimulus

The omission of a note in the melody elicited a negative potential beginning approximately 150 ms after the time the note would have occurred. This negative potential, with larger amplitude over the right than the left hemisphere was elicited by the absence of an expected stimulus and has features resembling the mismatch negativity (Raij et al., 1997). Stimulus omission in an auditory task is known to elicit a negative response at 150–200 ms followed by a P300 like positive deflection at 300–1000 ms (Besson & Faita, 1995; Jongsma et al., 2005; Nittono et al., 2000; Raij et al., 1997; Rüsseler et al., 2001; Yabe et al., 1998). Some refer to the negative potential as an “early N2” component reflecting attention to an unexpected change in the environment (Jongsma et al., 2005; Raij et al., 1997). We suggest instead that the omission-related negative potential is likely a mismatch negativity (MMN) similar to previously shown MMN elicited by partial and total stimulus omissions (Hughes et al., 2001; Nordby, Roth, & Pfefferbaum, 1988; Yabe et al., 1998). The negative potential we observed to the omitted musical note reversed polarity at the mastoid, which is a feature of MMN further supporting that this is as a mismatch response reflecting neural processing of the automatic detection of a change in the acoustic environment (Brattico et al., 2006; Rüsseler et al., 2001; Yabe et al., 1998). However, given that a robust MMN response typically requires a large number of trials, it is also possible that the observed negative potential is related to the auditory contingent negative variation (CNV) in anticipation of the upcoming delayed note (Gómez et al., 2004). However, the right frontal topography of the negative component seen here weakens this possibility as the CNV has been shown to have a bilateral frontal distribution that is related to the orientation induced by the warning stimulus (Weerts & Lang, 1973). Source analysis of this omission related negativity would be helpful to verify the generator of the component and to differentiate whether it is indeed related to an anticipation or detection of a delay response.

Previous studies on omitted stimuli also have focused on a positive (P300-like) component in response to an omission (Donchin, 1981; Ruchkin & Sutton, 1978). We did not observe such a P300 response to the omitted stimulus. This is likely related to the fact that in the

current task, the rhythm-deviant note was delayed only for 250 ms. Therefore, any possible P300 response to the omission overlapped with the early processing (P50, N100-P200) related to the delayed note.

In contrast to other reports (Jongsma et al., 2005; Rüsseler et al., 2001) we did not find significant differences in the MMN amplitude or latency between musicians and non-musicians. Jongsma et al. (2005) showed that, musicians compared to non-musicians have a larger amplitude potential to an unexpected omitted stimulus. Likewise, Rüsseler et al. (2001) reported larger MMN in musicians (compared to non-musicians) to an omitted stimulus in an otherwise regular tone-series at inter-stimulus intervals of 180 and 220 ms.

This apparent contradiction with previous findings of the effect of musical training on the omission related response may be related to either a smaller and less regular (across different metric positions, see below) number of omitted stimuli in our design or the template matching nature of our task. Unlike previous studies, our rhythmic deviation was not created by a complete absence of a repetitive stimulus but rather by delaying an expected note which eventually occurred. Therefore, while maintaining a representation of the target melody in memory, participants may have devoted less attentional resources to the omitted note per se and may have detected the rhythmic deviation after the occurrence of the note following the omission. In support of this view, although there were no differences observed in the potentials accompanying the omitted stimuli between musicians and non-musicians, we did observe differences in the potentials the delayed deviant tones and the musician group did demonstrate superior detection of rhythmic deviations as indicated by behavioral performance. Furthermore, in interpreting the apparent lack of difference between musicians and non-musicians to the omission-related response, it is important to note that, within our paradigm, the metrical position of the rhythmic deviation varied in location across the different melodies. Given the small number of trials for each metric position, we could not reliably assess differences of the ERP response to rhythm deviations in different metrical positions. However, in light of previous findings on differences in brain response to different metrical positions (Fujioka, Zendel, & Ross, 2010; Ladinig, Honing, Haden, & Winkler, 2009), it is possible that the lack of group difference in the omitted related response is due to this variation in metric position. To eliminate this variance, selecting temporal deviations within the same metrical position in future designs would better isolate the brain processing to changes in rhythm specifically.

Effects of musical training on processing the delayed note following omission

The amplitude of both N100 and P200 components were enhanced to the note after the omission in musicians compared to non-musicians and the N100 difference was most pronounced at frontal sites.

The amplitude of the auditory N100 component has been considered to represent sensory processes reflecting physical attributes of the auditory stimulus such as intensity (Davis, Mast, Yoshie, & Zerlin, 1966) and presentation rate. However, the N100 amplitude has also been shown to be affected by cognitive processes such as attention (Näätänen & Picton, 1987; Picton & Hillyard, 1974), expectancy (Starr, Aguinaldo, Roe, & Michalewski, 1997), rhythm processing (Geiser, Ziegler, Jancke, & Meyer, 2009; Schaefer, Vlek, & Desain,

2011), and memory (Conley, Michalewski, & Starr, 1999; Kaufman, Curtis, Wang, & Williamson, 1992). The increase of N100 amplitude to rhythm-deviant stimuli in musicians compared to non-musicians observed in the present study may reflect enhanced neural synchrony and/or of neural elements responsive to temporal deviations in musicians. We suggest that musicians, due to their training, may maintain a stronger mental representation of rhythmic pattern of the target melody in their auditory memory and thus subsequently better detect the delayed stimuli that define rhythmic deviation in the comparison melody. The N100 amplitude difference between musicians and non-musicians was most pronounced at frontal electrodes, suggesting engagement of auditory attention and memory mechanisms, possibly originating from auditory association areas, to underlie the enhanced processing of the rhythm-deviant stimuli in musicians; although source analysis of this effect would be required to substantiate this interpretation.

P200 amplitude was also increased in musicians compared to non-musicians in our data, confirming prior findings of the enhancing effects of training on P200 amplitude. Tremblay et al., (Tremblay, Kraus, McGee, Ponton, & Otis, 2001) observed enhancement of the P200 amplitude when non-musicians were trained to discriminate temporal features of speech signals. Similarly, Atienza and colleagues (Atienza, Cantero, & Dominguez-Marin, 2002) reported an enhancement of the P200 when subjects were trained to detect pitch deviants in a short stream of pitch stimuli. Enhancement of the P200 was also observed between two experimental sessions of passive listening task in an MEG study (Ross & Tremblay, 2009) highlighting the sensitivity of the P200 response to perceptual learning, memory and training. Finally, Bosnyak and colleagues (Bosnyak, Eaton, & Roberts, 2004) also found enhanced P200 amplitude to be increase in trained non-musician subjects while discriminating changes of pure tones.

Musical training and ear dominance

We have previously reported (Habibi et al., 2013) that musicians, compared to non-musicians showed an enhanced performance in detecting pitch deviations presented to the right versus left ear. This suggested that the left hemisphere of musicians as a result of long-term musical training may be engaged more fully in the processing of spectral information which is known to generally be preferentially processed in the right hemisphere (Zatorre & Belin, 2001). In contrast, in regards to detecting rhythm deviations, our present findings show that regardless of the ear stimulated, musicians compared to non-musicians demonstrated more accurate detection of rhythm deviations and there was no effect of stimulated ear on performance measures. In concert with this, we also found no difference in ERP component measures between groups.

For the rhythm-deviant stimuli both groups did demonstrate larger amplitude of the P200 potential to the delayed note with left ear stimulation compared to the right. In interpreting this ear effect, it is relevant that the auditory cortices are excited most strongly by acoustic stimulation of the contralateral ear (Andreassi, Okamura, & Stern, 1975; Connolly, Manchanda, Gruzelier, & Hirsch, 1985; Langers, van Dijk, P., & Backes, 2005). The results from our behavioral performance suggest that for both musicians and non-musicians, input preferentially to each of the two hemispheres was equally effective in supporting the

detection of rhythm deviations. However, this was not supported by the P200 amplitude which suggested possibly increased right hemisphere activity in response to the delayed note. Although the P200 potential indexes a step in the auditory processing of the delayed note, it is apparently not associated with the behavioral response. In fact we did not find any correlation between either the amplitude or latency of the P200 and the accuracy of detecting temporal deviations. As shown in other studies (Ross & Tremblay, 2009), changes in physiological response and behavioral performance are not always in line with each other, complicating conclusions about the relation between the two measures. In this case, the accuracy in detecting rhythm deviation may be related to not only the P200 response to the delayed note but the response to both the omission and delayed stimuli.

Traditionally, processing of temporal information has been shown to recruit areas in both hemispheres, but with greater response from the left (Zatorre & Belin, 2001). Temporal processing in our task, however, was not isolated from melodic processing. Rhythm changes were embedded within melodies, which generally have greater response from right auditory areas. This combined presentation of rhythm changes within melodies may have contributed to the lack of lateralization pattern for processing task-related temporal deviations in our study. To eliminate the effects of melody from rhythm in the future, temporal patterns without pitch information might be useful. This might easily be accomplished by using trains of beat stimuli wherein the only deviation between comparison musical phrases is rhythmic. In support of this view, Vuust and colleagues (Vuust et al., 2005) have suggested an expert-related pattern of lateralized brain activation in response to rhythmic and metric violations. Using broadband drum sounds without any pitch information, they showed that while musicians' response to rhythmic incongruities is left lateralized, non-musicians' response to violation of rhythm is stronger in the right hemisphere.

In summary, by using more ecological valid musical stimuli, our findings show that musicians compared to non-musicians, are significantly better at detecting subtle and unexpected rhythmically deviant notes. Musicians showed enhanced amplitudes of N100 and P200 potentials to the delayed note following omissions but did not demonstrate a difference of auditory evoked potentials to the omitted stimuli. These findings suggest that musical training is accompanied by enhanced brain processing of both spectral and temporal aspects of music and imply specifically that enhanced N100/P200 amplitudes to delayed deviant stimuli may play a role in the enhanced perceptual capacities that musicians demonstrate in detecting rhythmic deviations.

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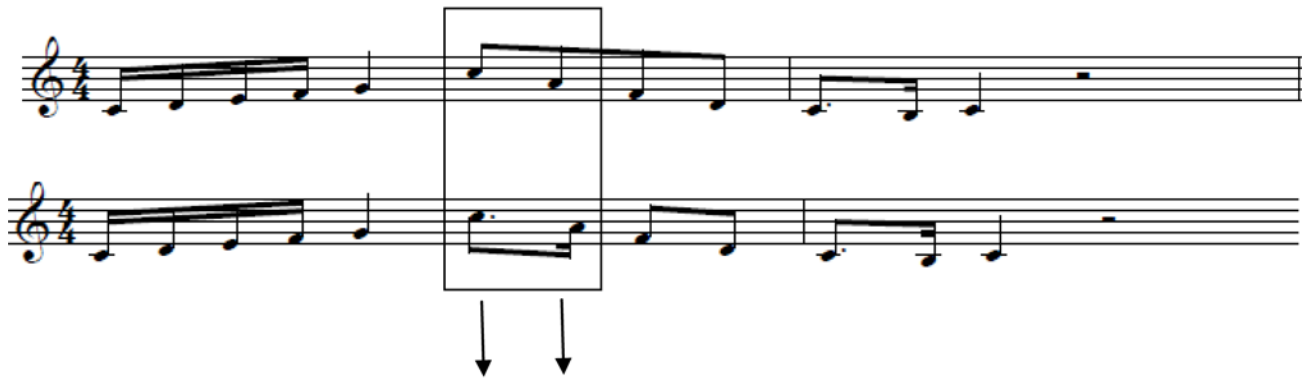
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a.



b.

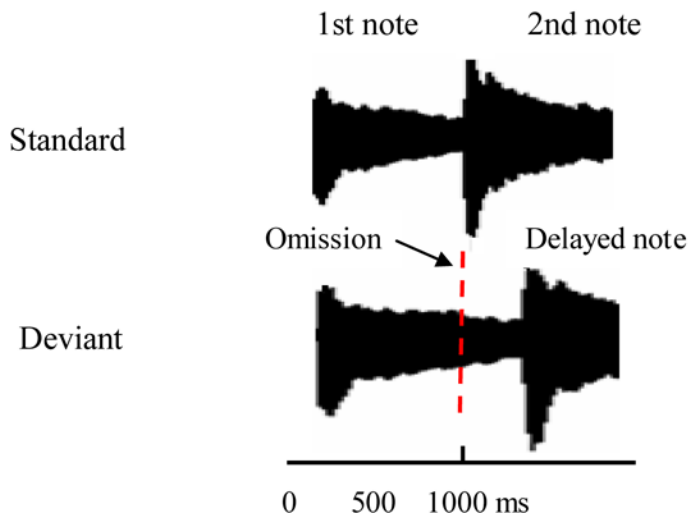


Figure 1.
 a- A sample melody in standard (top) and rhythmic deviant (bottom) version. b. A visual illustration of the standard and rhythmic deviant notes.

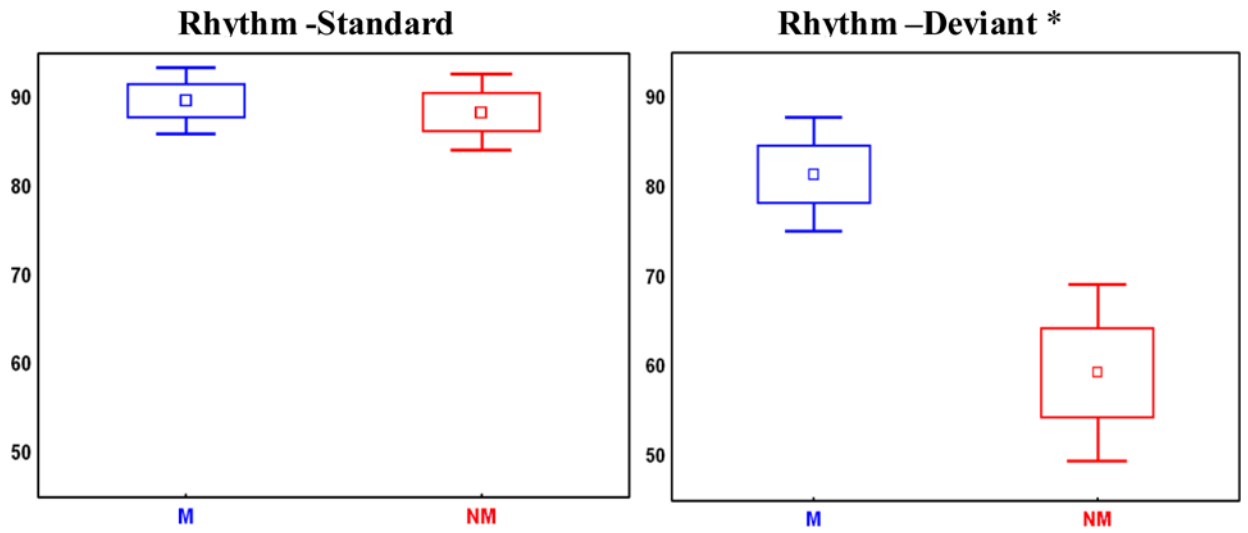


Figure 2. Musicians' and non-musicians' performance (percentage correct) to rhythm standard and deviant (Mean \pm SE)

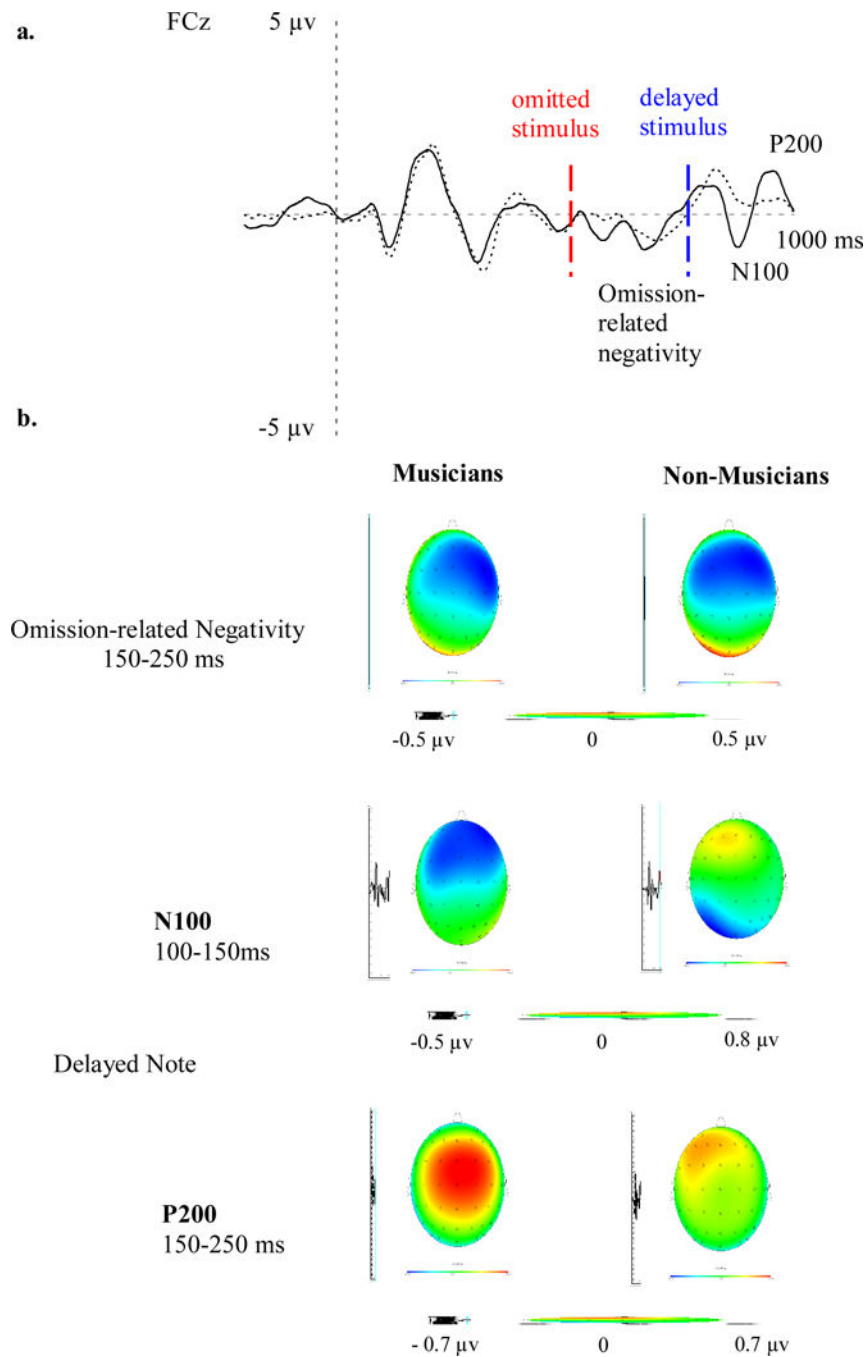


Figure 3.
 a. Grand average ERPs for musicians (solid) and non-musicians (dotted) to rhythm deviant notes (omitted and delayed). b. Voltage maps of the omission related negativity, N100 and P200 to the delayed note in musicians and non-musicians

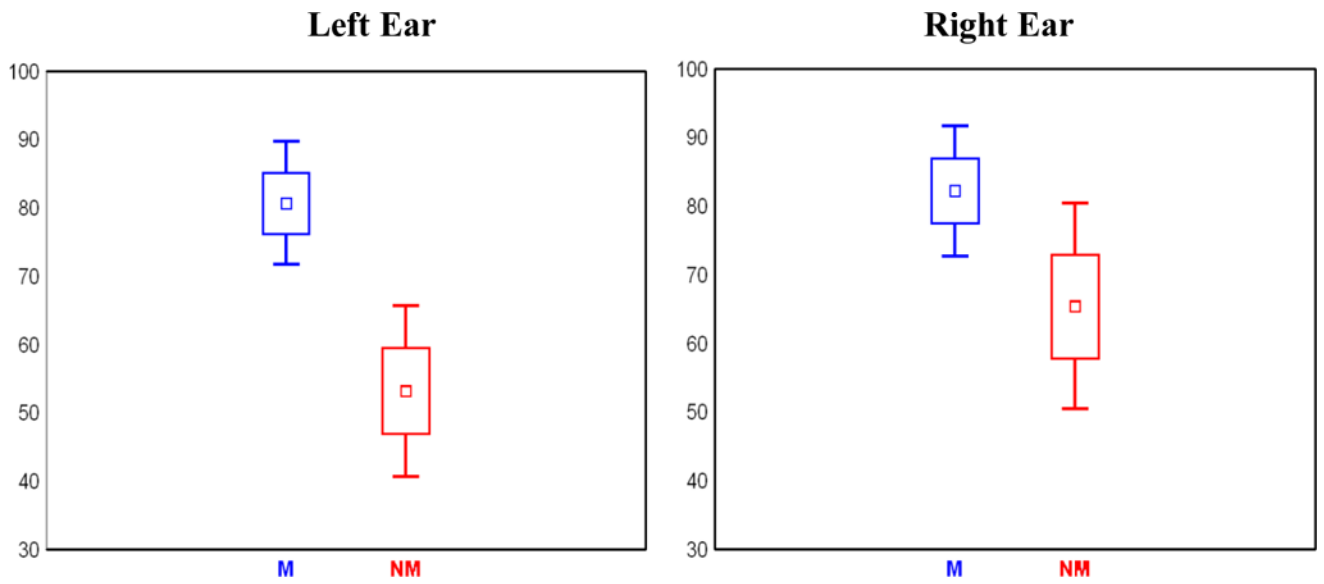


Figure 4.
Performance (percentage correct) to the deviant rhythm for musicians and non-musicians separated by ear

Table 1

Musicians' musical background

Primary instrument	Secondary instruments	Practice years	Onset age of training
Piano	Flute, Tenor Sax, Bassoon, Piccolo	13	6.5
Piano	Voice, Guitar	12	5
Flute	Piano, Piccolo	11	3
Piano	Voice, Violin	10	5
Piano	Voice, Flute	16	3
Piano	Clarinet	14	4.5
Piano	Trumpet	15	6
Violin	No secondary instrument	14	3.5
Piano	No secondary instrument	16	4
Voice	Piano	12	5
Piano	Violin	11	5
Piano	Voice, Violin	14	5
Piano	Viola, Tenor Sax, Flute, Choir	15	3
Piano	Guitar, Bass, Drums	13	7
Piano	No secondary instrument	7	5
Piano	Guitar, Bass, Drums, Tuba	7	7.5
Piano	Viola	11	5
Violin	Piano, Guitar, Voice	15	7
Upright Bass	Bass Guitar, Piano, Voice	11	12
French Horn	Clarinet, Trumpet, Piano	10	7

Table 2

Time windows and electrodes for ERP quantification separately for each stimulus condition

Stimulus Category	N100 (ms)	Electrodes	P200 (ms)	Electrodes
Standard 1 st and 2 nd note	100–150	F, FC & C lines	150–250	FC, C & CP lines
Omitted Note	150–250	F, FC & C lines	–	–
Delayed Note	100–150	F, FC & C lines	150–250	FC, C & CP lines

Table 3

Main effects and interactions in response to the omitted note

Omitted Note	ANOVA	<i>F</i> values	<i>p</i> values adjusted
MMN			
Main Effects	Groups	$F(1,38) = 0.002$.96
	Frontality	$F(2,72) = 2.86$.09
	Laterality	$F(2,72) = 4.16$.02
Interactions	Frontality * Group	$F(2,72) = 0.54$.52
	Laterality * Group	$F(2,76) = 0.66$.49
	Frontality * Laterality	$F(4,152) = 0.22$.80
	Frontality * Laterality * Group	$F(4,152) = 0.96$.39

Table 4

Main effects and interactions in response to first deviant and delayed notes

Delayed Note	ANOVA	<i>F</i> values	<i>p</i> values adjusted
N100			
Main Effects	Group	$F(1,38) = 3.72$.06
	Frontality	$F(2,72) = 4.77$.03
	Laterality	$F(2,72) = 2.03$.14
Interactions	Frontality * Group	$F(2,72) = 7.73$.00
	Laterality * Group	$F(2,76) = 0.17$.83
	Frontality * Laterality	$F(8,304) = 0.34$.78
	Frontality * Laterality * Group	$F(8,304) = 3.37$.02
P200			
Main Effects	Group	$F(1,38) = 4.63$.04
	Frontality	$F(2,72) = 9.92$.00
	Laterality	$F(2,72) = 2.71$.57
Interactions	Frontality * Group	$F(2,72) = 0.39$.31
	Laterality * Group	$F(2,76) = 1.17$.59
	Frontality * Laterality * Group	$F(8,304) = 0.73$.53