

CORTICAL ACTIVITY DURING PERCEPTION OF MUSICAL PITCH: COMPARING MUSICIANS AND NONMUSICIANS

ASSAL HABIBI, VINTHIA WIRANTANA, &
ARNOLD STARR
University of California, Irvine

THIS STUDY INVESTIGATES THE EFFECTS OF MUSIC training on brain activity to violations of melodic expectancies. We recorded behavioral and event-related brain potential (ERP) responses of musicians and nonmusicians to discrepancies of pitch between pairs of unfamiliar melodies based on Western classical rules. Musicians detected pitch deviations significantly better than nonmusicians. In musicians compared to nonmusicians, auditory cortical potentials to notes but not unrelated warning tones exhibited enhanced P200 amplitude generally, and in response to pitch deviations enhanced amplitude for N150 and P300 (P3a) but not N100 was observed. P3a latency was shorter in musicians compared to nonmusicians. Both the behavioral and cortical activity differences observed between musicians and nonmusicians in response to deviant notes were significant with stimulation of the right but not the left ear, suggesting that left-sided brain activity differentiated musicians from nonmusicians. The enhanced amplitude of N150 among musicians with right ear stimulation was positively correlated with earlier age onset of music training. Our data support the notion that long-term music training in musicians leads to functional reorganization of auditory brain systems, and that these effects are potentiated by early age onset of training.

Received: October 25, 2011, accepted September 29, 2012.

Key words: auditory event-related potentials, electroencephalography, pitch perception, music training, pitch deviations

RESearch on the effects of music training has provided growing evidence that the brains of musicians and nonmusicians respond differently to music. Many studies of neurophysiology have found such effects, and in particular electroencephalography (EEG) has been used to examine the steps in

neural processing associated with music perception using cortical event-related potentials (ERPs). In the current study we utilized ERPs in a paradigm involving the presentation of paired musical phrases that were presented either identical or with a pitch deviation. We assess the behavioral and neural effects of music training on the processing of these musical phrases generally, as well as the processing of the pitch deviations specifically.

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, mismatch negativity (MMN), early right anterior negativity (ERAN), and the P300.

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 generates the scalp recorded voltage field of this potential, which is typically distributed maximally over the frontal-central regions of the scalp (Picton, 1990; Richer, Alain, Achim, Bouvier, & Saint-Hilaire, 1989). The N100 has not been shown to be different between musicians and nonmusicians; however its magnetic counterpart N1m has been reported to be larger in musicians compared with nonmusicians when evoked by piano tones (Pantev, Oostenveld, Engelien, Ross, Roberts, & Hoke, 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 nontemporal sources such as frontal areas (Ferreira-Santos et al., 2011; McCarley, Faux, Shenton, Nestor, & Adams, 1991). 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. Specifically, the P200 amplitude accompanying

the processing of music has been reported larger in musicians compared to nonmusicians (Pantev, Engelien, Candia, & Elbert, 2001; Shahin, Bosnyak, Trainor, & Roberts, 2003).

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). A similar component to the MMN is the early right anterior negativity (ERAN), which is known to reflect the processing of music-related syntactic violations. The ERAN resembles the MMN with regard to the polarity, scalp distribution, and latency. The generation of the MMN is known to be related to the processing of auditory “mismatches” between expected and presented stimuli extracted online from the acoustic environment, whereas the ERAN has been shown to be generated based on deviation from music-syntactic information in long-term memory (Koelsch, 2009). The P300 is a positive potential also shown to be present in response to rare/deviant stimulus presented amongst frequent stimuli and to reflect the orienting of attention. It has peak latency between 250–700 ms, and is maximally distributed at fronto-central or parietal areas of the scalp depending on the type of stimulus eliciting the component (Donchin & Coles, 1988; Picton, 1992). Specifically, the P300 is comprised of two contributing subcomponents: the P3a and the P3b. The P3a has a peak latency often within ~300 ms, is generated primarily by anterior cingulate cortex, and thus displays a fronto-central distribution on the scalp. The P3a is related to automated orienting of attention seen in paradigms wherein distracting stimuli engage attention without relation to required behavioral response. The P3b usually peaks later than 300 ms, often from 300-500 ms or later and is generated primarily by medial temporal areas and the temporo-parietal junction, thus displaying a parietal distribution on the scalp. The P3b is elicited by stimuli that require behavioral response and/or clearly match with a target stimulus template held in working memory (Polich, 2007).

Musicians have been shown to have enhancements in both the early and largely preattentive processes indexed by the MMN and the related music-specific early right anterior negativity (ERAN) as well as the

later cognitive component P300 to the processing of deviations in music. The early component findings include increased amplitude in musicians of an early right anterior negativity (ERAN; latency ~150-200 ms) to harmonically inappropriate terminal chords (Koelsch, Schmidt, & Kansok, 2002), and a mismatch negativity (MMN latency ~150-250 ms) to pitch deviances (Tervaniemi, 2001). The later component findings include larger amplitude N2b-P3 potentials in response to pitch changes (latency ~350-700 ms) (Nikjeh, Lister, & Frisch, 2008; Tervaniemi, Just, Koelsch, Widmann, & Schroger, 2005; Trainor, Desjardins, & Rockel, 1999). In addition, a larger amplitude sustained late positive component (“LPC,” latency ~350-400 ms) has been reported in musicians in response to changes of pitch, which in this case the authors as well as other commentators have noted likely reflects the same processing usually referred to as P300/P3 (Granot & Donchin, 2002; Besson & Faïta, 1995).

In these studies, behavioral and cortical responses were measured to deviations of single notes or chords at fixed-locations, e.g., “terminal” within the melodies. This procedure allows assessment of brain responses to tonal progressions signaled by the terminal note or “tonic” that defines tonal structure in a melody or a chord sequence. There are only a few studies that have assessed brain activities to musical irregularities occurring at unpredictable locations within a melody (e.g., Brattico, Tervaniemi, Näätänen, & Peretz, 2006; Miranda & Ullman, 2007). Moreover, the majority of previous studies assessing EEG/ERP correlates of musical processing have not explored differences between musicians’ and nonmusicians’ behavioral and brain responses in an integrated paradigm involving both pitch and rhythmic irregularities. The present study addresses these issues by using unfamiliar melodies containing either rhythmic or melodic deviations, occurring at varying and unpredictable locations across melodies. It has been shown previously that there are differences between melodic and rhythmic processing (Bengtsson & Ullén, 2006) and studying pitch and rhythm irregularities in an integrated paradigm allows for comparative assessment of brain processes devoted to pitch versus rhythm deviation. The incorporation of rhythmic and tonal deviations distributed throughout experimental melodies results in more ecologically valid stimuli wherein deviations of different types occur throughout the musical phrases, increasing the tendency for listener’s attention to be more equally spread throughout the stimuli as occurs in normal music listening.

We focused on pitch violations within the framework of the common practice period (i.e., from 1600 to 1900)

TABLE 1. Musicians' Musical Background.

Primary instrument	Secondary instruments	Practice years	Onset age of training	Still playing any instrument	Weekly hours of practice
Piano	Flute, Tenor Sax, Bassoon, Piccolo	13	6.5	Yes	20
Piano	Voice, Guitar	12	5	Yes	3
Flute	Piano, Piccolo	11	3	Yes	1
Piano	Voice, Violin	10	5	No	-
Piano	Voice, Flute	16	3	Yes	21
Piano	Clarinet	14	4.5	Yes	10
Piano	Trumpet	15	6	Yes	1
Violin	No secondary instrument	14	3.5	Yes	1
Piano	No secondary instrument	16	4	Yes	10
Voice	Piano	12	5	Yes	5
Piano	Violin	11	5	Yes	7
Piano	Voice, Violin	14	5	Yes	2
Piano	Viola, Tenor Sax, Flute, Choir	15	3	No	-
Piano	Guitar, Bass, Drums	13	7	Yes	15
Piano	No secondary instrument	7	5	No	-
Piano	Guitar, Bass, Drums, Tuba	7	7.5	Yes	2
Piano	Viola	11	5	Yes	6
Violin	Piano, Guitar, Voice	15	7	Yes	5
Upright Bass	Bass Guitar, Piano, Voice	11	12	Yes	10
French Horn	Clarinet, Trumpet, Piano	10	7	Yes	10

of Western tonal music. Moreover, we used monaural presentation of musical phrases, a decision based on our plans to use the same paradigm with neurological patients, many of whom have hearing preserved preferentially in one ear. We compared musicians versus nonmusicians both on measures of accuracy of detection and brain activity (amplitude and latency of event-related potentials) to pairs of unfamiliar melodies containing deviations in pitch (the current paper) or rhythm (a subsequent paper) compared to pairs of melodies that were congruent.

We hypothesized 1) that musicians would detect changes in pitch more accurately than nonmusicians, and 2) that their correlated auditory cortical potentials in response to pitch irregularities would be enhanced in amplitude and have shorter latencies relative to nonmusicians, reflecting greater processing speed and strength to such musical deviations. Confirmation of both of these hypotheses in response to this unique paradigm, wherein both pitch and rhythm deviations are distributed throughout unfamiliar melodies, supports the notion that music training enhances central auditory processes accompanying detection of pitch irregularities even in a more varied and natural music listening condition than has been typically used in past experimentation. Lastly, we did not hypothesize any differences based on the laterality of stimulated ear, although as will be shown, significant differences between left and right ear stimulation were obtained across musician versus

nonmusician groups, confirming the understanding that enhanced left-lateralized neurophysiological processing in response to music is one of the hallmarks of long-term music training.

Method

SUBJECTS

Twenty-one musicians and twenty-one nonmusicians took part in the experiment, but data from two subjects (one from the musician group and one from the nonmusician 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 nonmusicians (20 right handed, 15 females) were thus included in the final experimental data. The musicians and nonmusicians did not differ in age, musicians = 20.1 ± 1.4 ; nonmusicians = 21.7 ± 4.6 , $t(38) = 1.53$, $p = .13$. Musicians had significantly more years of music training than the nonmusicians, musicians range = 7-16 years, 12.3 ± 2.75 ; nonmusicians range = 0-1 years, 0.05 ± 0.22 , $t(38) = 20.75$, $p < .0001$. The musical background of the musicians is listed in Table 1. Participants were all native English speakers and they received monetary compensation or extra credit points for 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 participants with abnormally deficient skills in processing music, 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 for the evaluation of musical perceptual abilities and musical memory skills of healthy adult listeners with a particular focus on discriminating individuals with amusia (Peretz, Champod, & Hyde, 2003). The original battery consists of six sections. However, in the interest of time, we chose the two sections—Scale (Pitch) and Rhythm—that were most relevant to our experimental questions. As this test is known to be abnormal in subjects with amusia, it was included so as to allow for the exclusion of any participants who may have shown evidence of amusia. In addition, measurements of pure-tone threshold as a function of frequency (audiogram) were obtained from all participants to ensure normal hearing.

EXPERIMENTAL PROTOCOL

During the experiment, subjects were presented with 10 unfamiliar melodies varying in duration from 5-11 s. The melodies were composed for these experiments (by David Reeder) based on Western classical rules and differed from one another in pitch and rhythmic content. Each trial was preceded by a warning tone (1,500 Hz pure tone, 250 ms duration, 70 dB SPL) 500 ms prior to the onset of the melody. This warning tone was included so as to alert the participants that the trial was about to begin. A pure tone was selected instead of a musical note so as to provide an alerting stimulus to reorient attention in the experimental participants to the auditory domain. 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-violated note compared to the target melody (pitch deviant case) or a rhythm-violated note compared to the target melody (rhythm deviant case). Of note, as previously shown (Brattico et al., 2006), in order to assess ERPs to deviations of pitch only, single melodies instead of pairs could be used. However, the paradigm used in the current study involved deviations of both pitch and rhythm. Thus, such a design was essential for eliciting rhythm deviations especially for nonmusicians who cannot easily form rhythmic expectations based on previous events of a single melody. There were a total of 300 trials presented in 10 blocks. Each block was comprised of a pseudorandom presentation of 30 melodies wherein

each of the ten melodies were presented once as a standard, once in the pitch deviant version, and once in the rhythm deviant version.

Pitch violation was created by modifying the note’s pitch to be out of the diatonic scale of the melody. In brief, the pitch organization of Western tonal musical system is based on the division of the octave into 12 equal semitones (i.e., chromatic scale). A selection of 7 tones from the 12 tones of the chromatic scale forms the diatonic scale. These 7 tones of the diatonic scale are known as in-key, whereas the remaining 5 tones are out-of-key; thus, each pitch violation involved changing one of the notes of the melody to one of the 5 out of key tones for the scale of the melody in question. Of note, in two of the ten melodies the pitch deviations also included a change in contour. In order to ensure that the presence of two melodies with both pitch and contour deviation did not introduce any significant alterations of the neurophysiologic processing as compared with pitch deviation alone, a subsequent subanalysis of the 8 melodies with pitch deviation and no contour change was executed. This subanalysis of the 8 melodies with pitch deviation alone yielded the same set of significant findings as the analysis below, characterizing the neurophysiological response to all 10 melodies.

The rhythm melody violations were created by changing the duration values 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 long) to a dotted eighth note (750 ms long) and a sixteenth note (250 ms long) in six of the ten melodies and similar variations in the other four melodies.

All melodies were computer-generated, created in MIDI format, using Finale Version 3.5.1 (Coda Music), and were then converted to WAV files with a “Grand Piano” sound font, using MidiSyn Version 1.9 (Future Algorithms). They were all played in the C major key. The melodies were written in binary tempi and the metronome was set at 60 bpm. Melodies varied in length, consisted of a different number of notes (12.4 ± 2.4) and rhythmic content. The location of the pitch changes varied across the 10 melodies but always occurred within 3-7 s after melody onset so as to avoid placing the deviance very close to the onset or ending of the melodies. (A complete list of all ten melodies in standard and with manipulations is available in the supplemental material section online.) In order 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, the standard and deviant notes, and the notes before and after the standard or 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 breaks between each block, as needed, and the entire experimental period lasted approximately 2 hr, including 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 nonmusicians 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. Order of ear stimulation was counterbalanced across subjects. Ongoing EEG was continuously monitored for evidence of sleep or drowsiness and if either occurred, the recording and stimulus train were paused and the subject was awakened and given opportunity for a break before continuing (this occurred only two times across all 40 participants).

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 a "SAME" or "DIFFERENT" tab on the monitor screen using an on-screen pointer controlled by a mouse. The participants were encouraged to make accurate responses and reaction time was 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; in the subsequent experimental session 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 two bipolar electrodes on the left and right outer canthi and two bipolar electrodes above and below the

right eye for defining the electro-oculogram (EOG). Signals were digitized at 1,000 Hz, amplified by a factor of 2,010, 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).

Results reported below are presented with respect to the behavioral accuracy and auditory evoked potential latency, amplitude, and scalp topography to pitch deviations in musicians compared to nonmusicians. The results regarding the effects found in response to the rhythm deviant trials will be reported in a separate publication.

DATA ANALYSIS

Continuous EEG data were divided into epochs starting 200 ms before and ending 1,000 ms after the onset of the standard and deviant notes and 1,500 ms after the onset of the warning tones. Epochs were baseline corrected (-200 to 0 ms prior to each note) and offline digitally filtered (bandpass 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 trials for standards in musicians was 94.9 ± 5.5 and in nonmusicians, 96.0 ± 3.8 whereas for pitch deviants in musicians, 94.1 ± 6.0 , and in nonmusicians 94.2 ± 6.5 , and *t*-tests comparing number of trials between groups was non-significant (standard: $p = .47$; pitch deviant: $p = .95$). ERP averaging was performed without regard to whether the subject made correct or incorrect responses. Behavioral data from each subject were recorded and analyzed in terms of correct detection of standard and deviant trials.

ERPs from each electrode were quantified for each subject in response to the warning tone, the first note, and the standard versus deviant notes of each melody. The deviant note refers to the pitch deviant note in the comparison melody and standard note refers to the same note in the trials wherein the target and comparison melodies were the same. In order to test any differences in the cortical response of musicians and nonmusicians to musical stimuli in general and to the pitch deviations in particular, we made two amplitude measurements. One dependent measurement, mean amplitude, was the mean voltage over the time interval of the averaged waveforms. We quantified the mean voltage of the ERPs for each stimulus category from 15 electrodes (F3, Fz, F4, FC3, FCz, FC4, CP3, CPz,

TABLE 2. Time Windows for ERP Quantification Per Stimulus Condition.

Stimulus Category	N100 (ms)	N150 (ms)	P200 (ms)	P3a (ms)
Warning Tone	100-150	–	180-260	–
First Note	115-155	–	180-260	–
Standard Note	100-150	–	150-280	–
Deviant Note	100-150	150-200	–	200-400

CP4, C3, Cz, C4, P3, Pz, P4) in time-windows centered on the peak of the respective component in the grand average waveform. The parameters of the time-windows are listed in Table 2 for each stimulus category. They were chosen for analysis based on previous findings of latencies in which the ERPs to spectrally complex deviant and standard stimuli diverged (Brattico et al., 2006; Brattico, Winkler, Näätänen, Paavilainen, & Tervaniemi, 2002; Tervaniemi, 2001) as well as the observed peak amplitude and latency of the grand average waveforms in this dataset. A second measurement, peak amplitude, was based on the maximum (or minimum in the case of negative N100 and N150 components) voltages in these particular time frames at the FCz electrode. Peak latency for each component was measured at the FCz electrode for the same time ranges. FCz was chosen for peak amplitude and latency measurement because the largest amplitude of each component was observed at this electrode.

STATISTICAL ANALYSIS

For peak amplitudes and latencies, separate F-tests for each latency range 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, nonmusicians) as the between-group factor and Pitch (standard, deviant), Frontality (F-line: F3, Fz, F4, FC-line: FC3, FCz, FC4, C line: C3, Cz, C4, CP line: CP3, CPz, CP4, P-line: P3, Pz, P4), and Laterality (Left: F3, FC3, C3, CP3, P3, Middle: Fz, FCz, Cz, CPz, Pz, Right: F4, FC4, C4, CP4, P4) as within-group factors. In order 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 reposted throughout the paper). Post-hoc tests were conducted using Tukey post-hoc statistical comparisons. For the sake of simplicity, and

because results always showed the same significant effects for peak amplitude and mean amplitude measurements during the specified time, we only report significance values for mean amplitude here. Mean latency results for each component are reported at FCz. The findings are first described without including stimulated ear as a comparison factor and then as a function of the stimulated ear.

Results

MONTREAL BATTERY OF EVALUATION OF AMUSIA (MBEA) AND PURE TONE THRESHOLDS

Both musicians (Scale: $86.7 \pm 9.4\%$; Rhythm: $87.1 \pm 9.1\%$) and nonmusicians (Scale: $84.2 \pm 10.4\%$; Rhythm: $84.2 \pm 9.0\%$) 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. 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, $F(1, 38) = 1.60, p = .11$. All participants, regardless of their music training, showed normal pure tone thresholds, below 25 dB HL, for frequencies (500–6,000 Hz).

BEHAVIORAL RESPONSE TO PITCH DEVIANT NOTES

Musicians were significantly more accurate in detecting the pitch deviances in melodies compared to nonmusicians, $F(1, 38) = 3.17, p < .05$. In response to the standard notes, however, there was no significant difference between the performance of musicians and nonmusicians, $F(1, 38) = 1.03, p = .30$. Figure 1 illustrates the performance in response to the standard and the pitch deviant notes for both groups.

EVENT RELATED POTENTIALS (ERPS) BRAIN ACTIVITY TO THE WARNING TONE AND TO THE FIRST NOTE

Cortical P200 but not N100 components differed between musicians and nonmusicians to the first note but not to the warning tone. The amplitude of the P200 component to the first note of the melodies was larger in musicians compared to nonmusicians, $F(1, 38) = 14.59, p < .05$; no differences were observed for the latency of

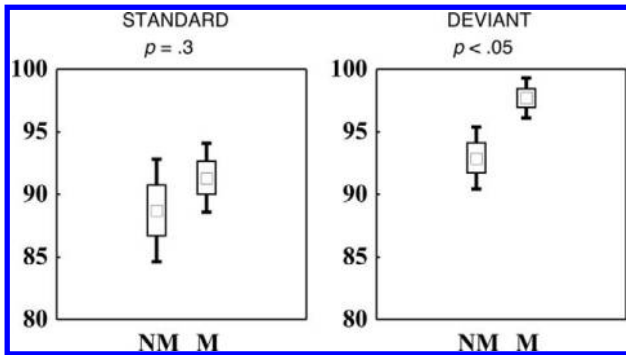


FIGURE 1. Behavioral performance of musicians (M) & nonmusicians (NM) in pitch standard & deviant conditions out of 100 trials (Mean \pm SE).

the P200, $F(1, 38) = 2.07$, $p = .16$. There were no significant differences detected for the amplitude of the N100, $F(1, 38) = 1.42$, $p = .24$, or the latency of the N100, $F(1, 38) = 0.04$, $p = .85$, to the first note. Figure 2 illustrates N100 and P200 responses of musicians and nonmusicians to the warning tone and the first note.

The difference between musicians and nonmusicians in the amplitude of the P200 component to the first note was largest at midline and frontal electrodes (FCz and Cz) as evidenced by main effects of Frontality, $F(4, 152) = 62.50$, $p < .05$, and Laterality, $F(2, 76) = 12.39$, $p < .05$, and three significant interactions: 1) Group \times Frontality, $F(4, 152) = 6.75$, $p < .05$, 2) Frontality \times Laterality, $F(4, 152) = 8.17$, $p < .05$, 3) Group \times Frontality \times Laterality, $F(8, 152) = 3.96$, $p < .05$. Table 3 includes the statistical analyses of the main effects and interactions in response to the warning tone and the first note.

BRAIN ACTIVITY TO THE DEVIANT NOTE

The activity to the pitch deviant note was comprised of two distinct negative peaks (N100 and N150) and a late positivity (P300/P3a), all three of which demonstrated greatest amplitude in fronto-central locations (FCz). The N100 and P300/P3a were identified in all subjects. In contrast, visual inspection of individual subject data revealed that the N150 component was identifiable in 17 of 20 musicians and only 6 of 20 nonmusicians. The inclusion criterion for the presence of N150 using visual inspection was based on the clear presence of a second negative component following the N100 between 150-200 ms from the onset of the stimulus. This difference in incidence of N150 was statistically significant across musician/nonmusician groups (Fisher's exact test, $p < .01$). The amplitude differences of N100 between musicians and nonmusicians was not

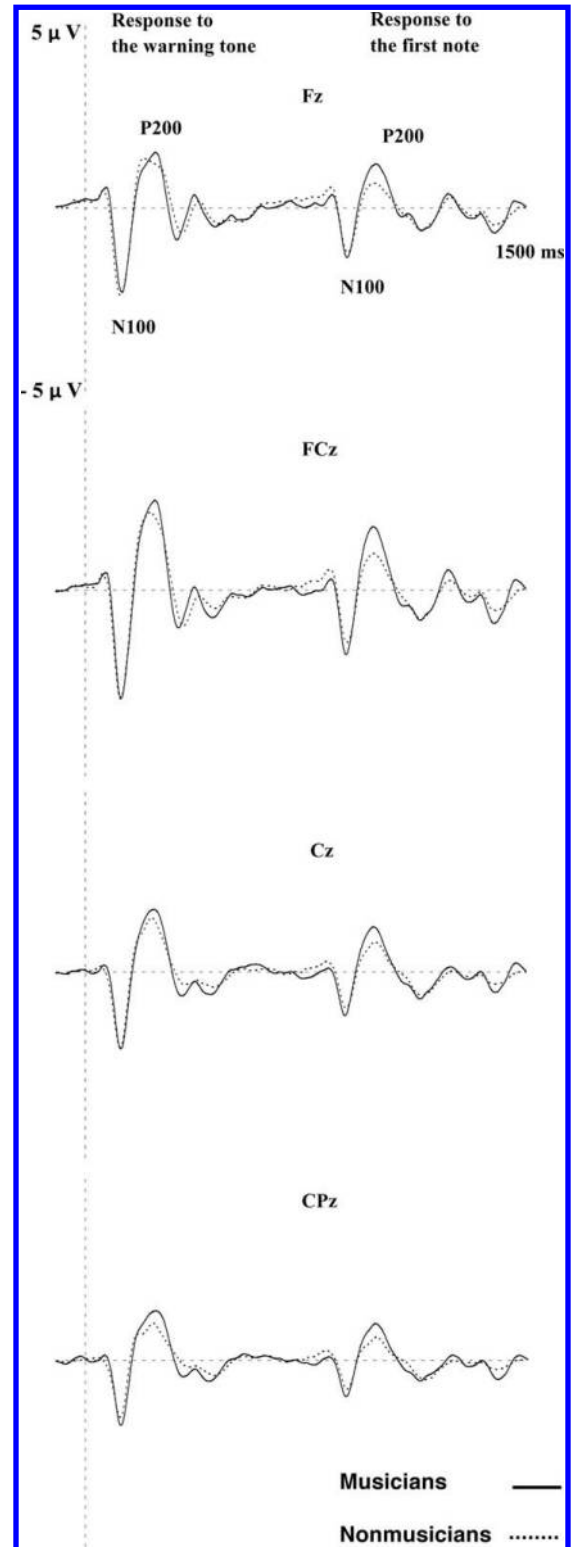


FIGURE 2. Grand average ERPs from musicians (solid line) and nonmusicians (dotted line) to the warning tone and the first note at midline electrodes, Fz, FCz, Cz, and CPz.

TABLE 3. Main Effects and Interactions in Response to the Warning Tone and First Note.

Warning Tone	ANOVA	F values	p values adjusted
N100			
Main Effects	Groups	$F(1, 38) = 0.01$.93
	Frontality	$F(4, 152) = 74.83$	< .0001
	Laterality	$F(2, 76) = 7.35$.003
Interactions	Frontality * Group	$F(4, 152) = 1.63$.21
	Laterality * Group	$F(2, 76) = 0.14$.81
	Frontality * Laterality	$F(8, 304) = 7.15$	< .0001
	Frontality * Laterality * Group	$F(8, 304) = 0.48$.75
P200			
Main Effects	Groups	$F(1, 38) = 0.54$.74
	Frontality	$F(4, 152) = 78.01$	< .0001
	Laterality	$F(2, 76) = 43.79$	< .0001
Interactions	Frontality * Group	$F(4, 152) = 0.82$.41
	Laterality * Group	$F(2, 76) = 0.49$.60
	Frontality * Laterality	$F(8, 304) = 17.58$	< .0001
	Frontality * Laterality * Group	$F(8, 304) = 1.02$.41
1st Note			
ANOVA			
F values			
p values adjusted			
N100			
Main Effects	Groups	$F(1, 38) = 1.42$.24
	Frontality	$F(4, 152) = 46.54$	< .0001
	Laterality	$F(2, 76) = 6.15$.01
Interactions	Frontality * Group	$F(4, 152) = 0.21$.72
	Laterality * Group	$F(2, 76) = 0.10$.83
	Frontality * Laterality	$F(8, 304) = 7.29$	< .0001
	Frontality * Laterality * Group	$F(8, 304) = 0.29$.90
P200			
Main Effects	Groups	$F(1, 38) = 14.59$	< .0001
	Frontality	$F(4, 152) = 62.50$	< .0001
	Laterality	$F(2, 76) = 12.39$	< .0001
Interactions	Frontality * Group	$F(4, 152) = 6.75$.01
	Laterality * Group	$F(2, 76) = 0.46$.59
	Frontality * Laterality	$F(8, 304) = 8.17$	< .0001
	Frontality * Laterality * Group	$F(8, 304) = 3.96$.001

significant for N100, $F(1, 38) = 2.03$, $p = .16$, and approached significance for N150, $F(1, 38) = 3.42$, $p = .07$. The latencies of the N100 and N150 elicited by the deviant note were not significantly different between the two groups: N100, $F(1, 38) = 1.48$, $p = .23$; N150, $F(1, 38) = 0.33$, $p = .57$. The amplitude of P3a was significantly larger in musicians than nonmusicians, $F(1, 38) = 9.27$, $p < .05$, and its latency was significantly earlier in musicians compared to nonmusicians, $F(1, 38) = 6.65$, $p < .05$. Figure 3 (see color plate section) illustrates the response of musicians and nonmusicians to the standard and deviant notes.

A significant interaction with respect to the P3a scalp distribution between the two groups was observed: Group x Frontality x Laterality, $F(8, 304) = 3.63$, $p < .05$, suggesting that the difference between musicians and nonmusicians was largest in frontal-central and frontal-right sided electrodes. Table 4 includes all

the main effects and the interactions in response to the deviant note.

BRAIN ACTIVITY TO THE STANDARD NOTE

In the trials where the target and the comparison melodies were identical, the N100 elicited by the standard note did not differ in amplitude, $F(1, 38) = 0.74$, $p = .39$, or latency, $F(1, 38) = 0.98$, $p = .33$, between musicians and nonmusicians. However, musicians showed a significantly larger amplitude P200 to the standard note compared to nonmusicians, $F(1, 38) = 6.52$, $p < .05$. There was no difference between the two groups with respect to the latency of P200 to the standard note, $F(1, 38) = 0.13$, $p = .72$.

The observed P200 component to the standard note was largest at frontal and central electrodes: Frontality at 150-280 ms: $F(4, 152) = 43.39$, $p < .05$; and Laterality at 150-280 ms: $F(2, 76) = 6.58$, $p < .05$. In addition, two

TABLE 4. Main Effects and Interactions in Response to Deviant Notes.

Deviant Note	ANOVA	F values	p values adjusted
N100			
Main Effects	Groups	$F(1, 38) = 2.03$.16
	Frontality	$F(4, 152) = 3.18$.06
	Laterality	$F(2, 76) = 8.32$.002
Interactions	Frontality * Group	$F(4, 152) = 1.05$.34
	Laterality * Group	$F(2, 76) = 2.69$.10
	Frontality * Laterality	$F(8, 304) = 1.65$.16
	Frontality * Laterality * Group	$F(8, 304) = 0.82$.52
N150			
Main Effects	Groups	$F(1, 38) = 3.24$.07
	Frontality	$F(4, 152) = 9.32$.001
	Laterality	$F(2, 76) = 3.52$.06
Interactions	Frontality * Group	$F(4, 152) = 0.43$.59
	Laterality * Group	$F(2, 76) = 0.88$.37
	Frontality * Laterality	$F(8, 304) = 2.10$.03
	Frontality * Laterality * Group	$F(8, 304) = 0.71$.60
P3a			
Main Effects	Groups	$F(1, 38) = 9.27$.004
	Frontality	$F(4, 152) = 121.12$	< .0001
	Laterality	$F(2, 76) = 6.97$.005
Interactions	Frontality * Group	$F(4, 152) = 2.88$.08
	Laterality * Group	$F(2, 76) = 1.11$.32
	Frontality * Laterality	$F(8, 304) = 12.39$	< .0001
	Frontality * Laterality * Group	$F(8, 304) = 3.63$.006

TABLE 5. Main Effects and Interactions in Response to Standard Notes.

Standard Note	ANOVA	F values	p values adjusted
N100			
Main Effects	Groups	$F(1, 38) = 0.74$.39
	Frontality	$F(4, 152) = 0.32$.86
	Laterality	$F(2, 76) = 1.00$.37
Interactions	Frontality * Group	$F(4, 152) = 1.97$.10
	Laterality * Group	$F(2, 76) = 1.30$.28
	Frontality * Laterality	$F(8, 304) = 0.82$.58
	Frontality * Laterality * Group	$F(8, 304) = 0.99$.44
P200			
Main Effects	Groups	$F(1, 38) = 6.52$.01
	Frontality	$F(4, 152) = 43.38$	< .0001
	Laterality	$F(2, 76) = 6.58$.005
Interactions	Frontality * Group	$F(4, 152) = 4.26$.03
	Laterality * Group	$F(2, 76) = 0.70$.46
	Frontality * Laterality	$F(8, 304) = 6.12$	< .0001
	Frontality * Laterality * Group	$F(8, 304) = 0.69$.62

significant interactions were observed with respect to the P200 component elicited by the standard note 1) Group x Frontality at 150-280 ms, $F(4, 152) = 4.42$, $p < .05$, indicating that the difference between the two groups was largest at frontal sites and 2) Frontality x Laterality at 150-280 ms, $F(8, 152) = 6.05$, $p < .05$ revealing amplitude of P200 was largest at frontal-midline electrode (FCz). Table 5 includes all the main

effects and the interactions in response to the standard note.

CORRELATIONS BETWEEN BRAIN ACTIVITY MEASURES AND BEHAVIOR

For both musicians and nonmusicians, the amplitude of the P3a component (but not the N100 or N150 components) correlated significantly with accuracy of

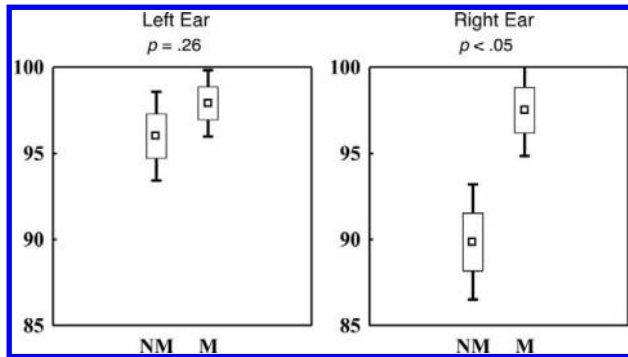


FIGURE 4. Behavioral performance to pitch deviant note for musicians (M) & nonmusicians (NM) out of 100 trials separated by stimulated ear.

responses; musicians: $r(8) = .51, p < .05$ and nonmusicians: $r(8) = .46, p < .05$. No significant correlations were observed between the amplitude or latency of N100, N150, P200 and P3a components and music training measures including onset age of training, years of practice, or hours of weekly practice.

LATERALITY OF THE EAR STIMULATED

The laterality of the ear stimulated was counterbalanced across both musicians and nonmusicians so that within each group there were ten subjects with right ear stimulation and ten with left ear stimulation. As delineated below, findings indicated significant interactions between laterality of ear stimulated and both behavior and brain responses to pitch deviant notes.

LATERALITY OF EAR STIMULATED AND BEHAVIOR

Musicians, compared to nonmusicians, were more accurate in detecting pitch deviations generally, $F(1, 38) = 3.17, p < .05$. For the musician group there were no observed differences in performance accuracy with left versus right ear stimulation, $F(1, 18) = 0.24, p = .81$. In contrast, the nonmusician group performed significantly better with left ear stimulation than with right ear stimulation, $F(1, 18) = 2.85, p < .05$, (illustrated in Figure 4). Furthermore, musicians did not differ from nonmusicians with left ear stimulation, $F(1, 18) = -1.15, p = .26$, but the performance between the two groups significantly differed with right ear stimulation, $F(1, 18) = -3.51, p < .05$.

LATERALITY OF THE EAR STIMULATED AND BRAIN ACTIVITY TO PITCH DEVIANT NOTES

The amplitude and latency of all of the components of the cortical evoked potentials for both musicians and nonmusicians in response to the warning tone, the first note, and the standard note were not significantly

different as a function of the test ear. However, in response to the deviant note the laterality of the tested ear did interact with the measures of brain activity. Specifically, for the N100 the Group x Ear interaction was significant, $F(2, 72) = 1.36, p = .05$. Post-hoc analysis revealed that when the left compared to right ear was stimulated, nonmusicians tended to show larger N100 amplitudes at 100-150 ms ($p = .19$), while musicians showed no trend toward difference in the amplitude of the N100 with left versus right ear stimulation ($p = .86$). Further analysis of the interaction revealed that when the right ear was stimulated, musicians exhibited a larger N100 response compared to nonmusicians at a strong trend-level ($p = .08$). However, when the left ear was stimulated, amplitudes of N100 did not significantly differ between the groups ($p = .98$). In addition, musicians showed larger N150 amplitudes at 150-200 ms with right versus left ear stimulation, whereas in nonmusicians the amplitude of the N150 did not differ between ears, Group x Ear interaction, $F(2, 72) = 4.35, p < .05$. Further post-hoc analysis of this interaction revealed that when the right ear was stimulated musicians exhibited a larger N150 response ($p < .05$) compared to nonmusicians. However, when the left ear was stimulated, there was no difference in the amplitude of N150 between the groups ($p = 0.99$). Figure 5 (see color plate section) illustrates the N150 response for musicians and nonmusicians separated by stimulated ear. No difference of P3a amplitude was observed between musicians and nonmusicians with respect to the stimulated ear. Table 6 includes all the main effects of the stimulated ear and the Group x Ear interactions in response to the pitch deviant note.

As described above, we tested each participant monaurally and counterbalanced the order of ear stimulation across subjects. To assess the stability of the N150 and behavioral effects found for right ear but not left ear stimulation, we asked our participants to return for a second session to test their other ear. We were only able to recruit seven participants from the musician group (three left ear and four right ear previously tested) and eight from the nonmusicians group (five left ear and three right ear previously tested) to return for repeat testing of the ear that was previously unstimulated. The results failed to replicate that there was a significant difference between the amplitude of N150 between musicians and nonmusicians specific to right ear stimulation ($p = .70$). However, a power analysis of the original finding showed that we needed 17 out of 20 from each group to return to replicate these findings, thus our repeat study was underpowered due to inability to recruit enough returning participants.

TABLE 6. Main Effects and Interactions in Response to Deviant Note Separated by Ear.

	ANOVA	F values	p values adjusted
N100			
Main Effects	Group	$F(1, 36) = 2.18$.15
	Ear	$F(1, 36) = 0.77$.38
Interactions	Group* Ear	$F(1, 36) = 3.96$.05
	Frontality * Ear	$F(4, 144) = 0.38$.62
	Laterality * Ear	$F(2, 72) = 0.04$.89
	Frontality * Group* Ear	$F(4, 144) = 1.44$.24
	Laterality * Group* Ear	$F(2, 72) = 0.53$.52
	Frontality * Laterality * Ear	$F(8, 288) = 0.38$.84
	Frontality * Laterality* Ear * Group	$F(8, 288) = 2.53$.04
N150			
Main Effects	Group	$F(1, 36) = 2.18$.07
	Ear	$F(1, 36) = 0.77$.25
Interactions	Group* Ear	$F(1, 36) = 3.96$.04
	Frontality * Ear	$F(4, 144) = 0.38$.18
	Laterality * Ear	$F(2, 72) = 0.04$.70
	Frontality * Group* Ear	$F(4, 144) = 1.44$.34
	Laterality * Group* Ear	$F(2, 72) = 0.53$.50
	Frontality * Laterality * Ear	$F(8, 288) = 0.38$.34
	Frontality * Laterality* Ear * Group	$F(8, 288) = 2.53$.60
P3a			
Main Effects	Group	$F(1, 36) = 2.18$.004
	Ear	$F(1, 36) = 0.77$.37
Interactions	Group* Ear	$F(1, 36) = 3.96$.25
	Frontality * Ear	$F(4, 144) = 0.38$.55
	Laterality * Ear	$F(2, 72) = 0.04$.47
	Frontality * Group* Ear	$F(4, 144) = 1.44$.41
	Laterality * Group* Ear	$F(2, 72) = 0.53$.63
	Frontality * Laterality * Ear	$F(8, 288) = 0.38$.45
	Frontality * Laterality* Ear * Group	$F(8, 288) = 2.53$.34

CORRELATIONS WITH THE STIMULATED EAR

Within the musician group, correlations of the amplitude and latency of the N100, N150, and P3a components elicited by the deviant note with the music training factors were analyzed. These factors included onset age of music training, number of years of practice, and hours of weekly practice. Amplitude of the N150 elicited by the deviant pitch note correlated significantly with the onset age of music training only with the right ear stimulation, $r(8) = .68$, $p < .05$, but not with left ear stimulation, $r(8) = .41$, $p = .22$. No other correlations were observed.

Discussion

We defined three key findings in this study of the effects of music training on auditory cortical activity: 1) Musicians had enhanced amplitude P200 component compared to nonmusicians to both the initial and standard musical notes but not to the 1.5 kHz warning tone that signaled the onset of the melodies. 2) Compared to nonmusicians, musicians detected deviant notes more

accurately and showed larger N150 and P3a components in response to deviant notes with the latter having shorter peak latency. 3) Both the behavioral and early cortical activity (N100, N150) differences found between musicians and nonmusicians were present with stimulation of the right but not the left ear.

EFFECTS OF MUSIC TRAINING ON PROCESSING MUSICAL NOTES VERSUS PURE TONES

Our findings confirmed earlier studies that music training increased the amplitude of the P200 but not N100 to musical notes (Shahin et al., 2003; Shahin, Roberts, Pantev, Trainor, & Ross, 2005). Similar results have been found in relation to P200 amplitude and acoustic training. Tremblay, Kraus, McGee, Ponton, and Otis (2001) observed enhancement of the P200 when nonmusicians were trained to discriminate temporal features of speech signals. Similarly, Atienza, Cantero, and Dominguez-Marín (2002) reported an enhancement of the P200 when subjects were trained to detect pitch deviants in a short stream of pitch stimuli. Finally, Bosnyak, Eaton, and Roberts (2004) trained nonmusician subjects to

discriminate small changes in the carrier frequency of 40 Hz amplitude modulated pure tones and found discrimination improvement was accompanied by enhancement of the P200. In all of these studies P200 amplitude was increased with training but the N100 did not change in any study. These results suggest that the neural mechanisms underlying the P200 potential can change by experience, and support that enhancement of P200 amplitude to the musical stimuli found in musicians, compared to nonmusicians, reflects changes in auditory processing specifically associated with experience of long-term training.

In a previous study, Shahin et al. (2003) reported that in musicians the amplitude of the P200 component was enhanced in response to pure tones as well as musical notes, whereas we did not find such a difference to the pure tone warning stimulus in our data. There are two explanations that may account for this discrepancy. First, in Shahin's study, the "non-musical stimuli" were pure tones matched in fundamental frequency to the musical notes providing pitches resembling those of notes. In the current study, the non-musical stimuli were 1,500 Hz pure tones that were not matched in frequency with the musical notes and served as a "warning" that the melody would begin. We suggest that the tones in these two studies were likely processed differently: as a warning signal in the present study and as "music" in Shahin's study. Additionally, in that study, pure-tones were presented intermixed in an unpredictable sequence with musical notes whereas in the current study, the pure-tone stimulus was presented 500 ms before the onset of each melody. Therefore, it is likely that in Shahin's study, the musical and non-musical stimuli received equal attention while in the present study the pure-tones required less purposeful attention compared to the musical notes. Thus, the enhancement of the P200 in musicians found in the current study to be specifically associated with musical notes and not the pure-tones could be the result of music training affecting processing of music or of increased level of attention to the musical notes compared to the pure tones in the current design. To eliminate the difference in the levels of attention to the musical versus pure tone stimuli in the future, a randomized order of presentation of tones and musical notes would equate attention to the two different stimuli.

EFFECTS OF MUSIC TRAINING ON PROCESSING PITCH DEVIANT NOTES

We used the pitch and rhythm subsections of the MBEA (Montreal Battery of Evaluation of Amusia) to assess the ability of our subjects to detect pitch and rhythm

deviations so as to rule out participants with amusia from participating. Given that this is a test designed to be easy for normal participants without brain damage or amusia (Peretz et al., 2003), our finding that musicians and nonmusicians both scored very well and were not differentiated from each other is due to a ceiling effect of this particular test, but was an important internal control so as to disallow any amusic nonmusicians from skewing our data. In contrast to the results of the MBEA, musicians were significantly more accurate in their detection of pitch deviant notes to the experimental stimuli of our auditory ERP paradigm. The effect of music training was also accompanied by an increase in the occurrence and amplitude of the N150 potential as well as an increase in the amplitude and shortening of latency for the later P3a potential.

In regards to the N150 component described here, a family of negative potentials occurring with peak latency around 150 ms (N150) have been previously defined in relation to acoustic stimuli other than music. For instance, N150 is found in response to silent gaps in continuous noise, and omission of a stimulus in a train (Jongsma et al., 2005; Michalewski, Starr, Nguyen, Kong, & Zeng, 2005). Michalewski et al. reported that when gap durations in noise were longer than 20 ms, the N100 potential to gap onset (offset of the noise) consisted of two separate components: an early component peaking at 90 ms, and a later component peaking at approximately 150 ms. They proposed two possible explanation for the N150 peak, suggesting it could be related either to a separate perceptual distinction made by the subjects to longer gap durations (Phillips, 1999) similar to a type of MMN representing stimulus change (Näätänen, 1992), or to a combination of offset/onset responses to noise and gap (Michalewski et al., 2005). In a companion study (Pratt, Bleich, & Mittelman, 2005), the N150 component in response to gap onsets was suggested to reflect the transition to silence. The N150 component in our study is not evoked by silent gaps or absence of a repetitive stimulus but rather by a pitch deviant musical stimulus. Its frontal scalp distribution and latency (approximately 150 ms) and the fact that it reverses polarity at mastoid electrodes mark this activity as similar to that found with MMN to stimulus change that typically reflects a "pre-attentive" processing of auditory sensory memory (Näätänen, 1992). The N150 reported in the present study was, however, evident without resorting to subtracting cortical activity to deviant notes, from the standard notes as has been typically required for identifying MMN. The N150 is similar to another described potential, the early right

anterior negativity (ERAN), which is thought to be specific for processing musical syntactic deviations in melody or chord sequences and has been shown to have larger amplitudes in musicians than in nonmusicians in response to musical irregularities (Koelsch et al., 2002; Miranda & Ullman, 2007; Paller, McCarthy, & Wood, 1992; Patel, Gibson, Ratner, Besson, & Holcomb, 1998). In our study, the incidence of N150 in individual subjects was significantly higher in musicians and its amplitude was larger (approaching significance).

The ERAN is shown to be generated as a result of deviations from musical information that already exists in a long-term memory format (Koelsch, 2009). In contrast, our template-matching paradigm required comparison of unfamiliar paired melodies and detection of irregularities that were extracted in reference to recent memory traces, which is more similar to the processes involved in generation of MMN. We are therefore of the opinion that the N150 found here is related to the MMN. Its increased incidence/amplitude in musicians accompanying the presentation of a deviant note likely reflects enhanced pre-attentive processing and template-matching of musical melodies in this group as a result of music training.

Musicians compared to nonmusicians also showed larger amplitude and shorter latencies of a late positive component (P300) to pitch deviant notes. The fronto-central scalp distribution of this component and its shorter latency are consistent with the subcomponent of P300 known as the P3a. The P3a subcomponent is considered to index automatic attention to novel or deviant stimuli (Goldstein, Spencer, & Donchin, 2002; Polich, 2007; Snyder & Hillyard, 1976) and is generated primarily by anterior cingulate activation (Ebmeier et al., 1995; Kirino, Belger, Goldman-Rakic, & McCarthy, 2000).

Previous studies have examined the effect of music training on P300 (Nikjeh et al., 2008; Nikjeh, Lister, & Frisch, 2009; Tervaniemi et al., 2005; Trainor et al., 1999), reporting both amplitude increases and decreases in latency associated with long-term music training. Our results replicated these findings and also found that the magnitude of the P3a amplitude in musicians and nonmusicians was linearly correlated with their enhanced accuracy of detecting deviant notes. This association between enhanced P300/P3a amplitude and improved performance measures has been frequently reported in the literature (Polich, 2007). In musicians and nonmusicians, the P3a component was maximal over frontal regions, similar to the results of Trainor et al. (1999) with no significant group \times location effects

on amplitude, indicating that brain regions generating the P3a to deviant notes are similar in musicians and nonmusicians. The shorter latency of P3a peak is known to reflect stimulus processing speed (Kutas, McCarthy, & Donchin, 1977; Polich, 2007). Although we did not include measurements of reaction time that could provide a behavioral measure of cognitive processing speed, the observed shorter latency P3a observed in musicians likely reflects faster categorization processes underlying the detection of deviant notes in musicians.

We consider that the N150 and P3a component differences between musicians and nonmusicians to deviant notes reflect activity in two distinct but overlapping central neural processes occurring during the processing of our musical stimuli: 1) matching the second or “comparison” melody to the first or “target” melody maintained in working memory; and 2) making musical congruity judgment of just the second melody based on its compatibility of its diatonic scale to Western tonal music tradition. We suggest that the N150 differences between musicians and nonmusicians may relate to a better template-matching process in musicians resulting in increased accuracy in detecting deviant notes. The differences of P3a amplitude and latency in musicians compared to nonmusicians may be related to musician’s better knowledge of the rules of tonality, and therefore enhanced and faster ability to detect deviations from it.

Two important notes in interpretation of the findings are to be considered: 1) two musician participants in our study were not actively playing their instrument at the time of the study as described in Table 1. We found, however, that the results from the 18 musicians who actively practiced showed the same significant results as the results from all 20 musicians averaged together. 2) In two of the 10 melodies, the pitch deviations also included a change in contour. It is important to note that tonal deviations with and without contour violations have been shown to be processed differently (Schiavetto, Cortese, & Alain, 1999; Trainor, McDonald, & Alain, 2002). Specifically, musicians have been shown to have larger MMNm response to deviations of pitch compared to of contour (Fujioka, Trainor, Ross, Kakigi, & Pantev, 2004). We found that the results from the eight melodies wherein there was no violation of contour showed the same significant results as the results from all ten melodies averaged together. Nonetheless, to eliminate the possibility of interactions of these two processes, selecting pitch deviations with the same contour in future designs would better isolate the brain processing to changes in pitch specifically.

MUSIC TRAINING AND EAR DOMINANCE

Post-hoc testing of the significant interaction between ear stimulated and both behavioral performance and N150 amplitude indicated that with stimulation of the left ear, no difference in behavioral performance or amplitude of N150 was observed between musicians and nonmusicians. In contrast, with right ear stimulation musicians relative to nonmusicians demonstrated more accurate detection of pitch deviations and displayed larger amplitude N150 (as well as trend larger amplitude N100) in response to pitch deviant notes.

In interpreting this ear effect, it is important to note that the auditory cortices are excited most strongly by acoustic stimulation of the contralateral ear (Andreassi, Okamura, & Stern, 1975; Connolly, Manchanda, Gruzelie, & Hirsch, 1985; Langers, van Dijk, & Backes, 2005; Woldorff et al., 1999). We have been able to find no previous studies using monoaural assessments of music perception such as the one we used here. Nonetheless, a number of studies have generated relevant useful information regarding the laterality of binaural musical processing in musicians and nonmusicians. In general, nonmusicians have shown greater activity in right auditory areas, including superior temporal gyrus and Heschel's gyrus, during processing of pitch information (Tervaniemi et al., 2000; Zatorre, 1998, 2001). In contrast, long-term music training has been shown to correlate with greater relative activity in the left hemisphere during processing of musical stimuli (Bever & Chiarello, 1974; Johnson, 1977; Ohnishi et al., 2001; Ono et al., 2011; Tervaniemi, Sannemann, Noyranen, Salonen, & Pihko, 2011). In a study using a dichotic listening task to compare musicians with nonmusicians, Johnson (1977) reported that musicians and nonmusicians showed similar performance when the discriminatory task was processed by the left ear but that musicians showed a significantly better performance than nonmusicians when the discriminatory stimulus was presented to the right ear. The finding was interpreted as reflecting that musicians preferentially engage the left hemisphere in musical processing while nonmusicians preferentially engage the right hemisphere.

Our findings of enhanced behavioral and early cortical activity (N150) in response to pitch deviations with stimulation of the right compared to the left ear supports the suggestion that the left hemisphere of musicians is particularly engaged in the processing of musical information as a result of long-term music training. In addition, for musicians, increased activity of left auditory areas, including planum temporale, have been shown to correlate with the age at which musicians

began their music training (Ohnishi et al., 2001; Pantev et al., 2001). Our results also indicate that the degree of enhancement of the N150 amplitude in musicians with right ear stimulation significantly correlated with earlier onset age of music training consistent with the notion that enhanced recruitment of left cortical auditory areas by musical stimuli may be favored by early music training. In interpreting this ear effect in relation to the amplitude of N150, it is important to note that, as described previously, our findings are limited to testing one ear in each participant as we were unable to recruit back enough participants to replicate the findings in the other ear.

The asymmetry of hemispheric activation in musicians favoring left auditory cortical areas during music related tasks may reflect both structural and functional reorganization of auditory cortex during long-term music training (Gaser & Schlaug, 2003; Pantev et al., 2001). For instance, the volume of gray matter in left Heschl's gyrus is greater in musicians than in nonmusicians (Gaser & Schlaug, 2003), thus facilitating musicians' capacity to process music differently than nonmusicians (Bever & Chiarello, 1974; Johnson, 1977). Musicians do retain right hemisphere capabilities of pitch processing but they may analyze music as a "language," preferentially engaging the left hemisphere's semantic capabilities.

In summary, we have shown that musicians compared to nonmusicians have a greater ability to detect pitch deviant notes accompanied by enhanced amplitudes of N150 and P3a potentials and decreased latency P3a to pitch deviations. Additionally, based on the enhanced right ear performance and N150 amplitude to pitch deviant notes, musicians compared to nonmusicians showed evidence of enhanced left hemisphere involvement in such detections. Lastly, we showed that the N150 amplitude to right ear stimulation correlated with onset of music training. These findings provide further evidence that music training is associated with reorganization of neural processes involved in music perception and the degree of this reorganization appears related to the age at which music training began.

Author Note

We thank David Reeder for composing the melodies for this study. We also thank Drs. Amy Bauer and Andrew Dimitrijevic for their assistance in creating the stimuli. The authors appreciate helpful comments of Drs. B. Rael Cahn, Hillel Pratt, Lenny Kitzes, and three

anonymous reviewers on early versions of the manuscript. This research was supported by a grant from Center of Hearing Research at University of California, Irvine and partially supported by grant DC 02618 from the National Institutes of Health.

Correspondence concerning this article should be addressed to Assal Habibi, University of Southern California, University Park Campus, B29b Hedco Neurosciences, HNB B29b, M/C 2520, Los Angeles, CA 90089-2520. E-mail: assal.habibi@usc.edu

References

- ALAIN, C., WOODS, D., & KNIGHT. (1998). A distributed cortical network for auditory sensory memory in humans. *Brain Research*, *812*, 23-37.
- ANDREASSI, J. L., OKAMURA, H., & STERN, M. (1975). Hemispheric asymmetries in the visual cortical evoked potential as a function of stimulus location. *Psychophysiology*, *12*, 541-546.
- ATIENZA, M., CANTERO, J. L., & DOMINGUEZ-MARIN, E. (2002). The time course of neural changes underlying auditory perceptual learning. *Learning and Memory*, *9*, 138-150.
- BENGTSOON, S., & ULLÉN, F. (2006). Dissociation between melodic and rhythmic processing during piano performance from musical scores. *Neuroimage*, *30*, 272-284.
- BESSON, M., & FAÏTA, F. (1995). An event-related potential (ERP) study of musical expectancy: Comparison of musicians with nonmusicians. *Journal of Experimental Psychology: Human Perception and Performance*, *21*, 1278-1296.
- BEVER, T. G., & CHIARELLO, R. J. (1974). Cerebral dominance in musicians and nonmusicians. *Science*, *185*, 537-539.
- BOSNYAK, D. J., EATON, R. A., & ROBERTS, L. E. (2004). Distributed auditory cortical representations are modified when nonmusicians are trained at pitch discrimination with 40 Hz amplitude modulated tones. *Cerebral Cortex*, *14*, 1088-1099.
- BRATTICO, E., TERVANIEMI, M., NÄÄTÄNEN, R., & PERETZ, I. (2006). Musical scale properties are automatically processed in the human auditory cortex. *Brain Research*, *1117*, 162-174.
- BRATTICO, E., WINKLER, I., NÄÄTÄNEN, R., PAAVILAINEN, P., & TERVANIEMI, M. (2002). Simultaneous storage of two complex temporal sound patterns in auditory sensory memory. *Neuroreport*, *13*, 1747-1751.
- CONNOLLY, J. F., MANCHANDA, R., GRUZELIER, J. H., & HIRSCH, S. R. (1985). Pathway and hemispheric differences in the event-related potential (ERP) to monaural stimulation: A comparison of schizophrenic patients with normal controls. *Biological Psychiatry*, *20*, 293-303.
- DONCHIN, E., & COLES, M. G. (1988). Is the P300 component a manifestation of context updating? *Behavioral and Brain Sciences*, *11*, 357-427.
- EBMEIER, K. P., STEELE, J. D., MACKENZIE, D. M., O'CARROLL, R. E., KYDD, R. R., GLABUS, M. F., ET AL. (1995). Cognitive brain potentials and regional cerebral blood flow equivalents during two- and three-sound auditory "oddball tasks." *Electroencephalography Clinical Neurophysiology*, *95*, 434-443.
- FERREIRA-SANTOS, F., SILVEIRA, C., ALMEIDA, P. R., PALHA, A., BARBOSA, F., & MARQUES-TEIXEIRA, J. (2011). The auditory P200 is both increased and reduced in schizophrenia? A meta-analytic dissociation of the effect for standard and target stimuli in the oddball task. *Clinical Neurophysiology*, *123*, 1300-1308.
- FUJIOKA, T., TRAINOR, L., ROSS, B., KAKIGI, R., & PANTEV, C. (2004). Musical training enhances automatic encoding of melodic contour and interval structure. *Journal of Cognitive Neuroscience*, *16*, 1010-1021.
- GASER, C., & SCHLAUG, G. (2003). Brain structures differ between musicians and nonmusicians. *Journal of Neuroscience*, *23*, 9240-9245.
- GOLDSTEIN, A., SPENCER, K. M., & DONCHIN, E. (2002). The influence of stimulus deviance and novelty on the P300 and novelty P3. *Psychophysiology*, *39*, 781-790.
- GRANOT, R., & DONCHIN, E. (2002). Do re mi sol la ti-Constrains, congruity and musical training: An event-related brain potentials study of musical expectancies. *Music Perception*, *19*, 487-528.
- ILLE, N., BERG, P., & SCHERG, M. (2002). Artifact correction of the ongoing EEG using spatial filters based on artifact and brain signal topographies. *Journal of Clinical Neurophysiology*, *19*, 113-124.
- JOHNSON, P. R. (1977). Dichotically-stimulated ear differences in musicians and nonmusicians. *Cortex*, *13*, 385-389.
- JONGSMA, M. L., EICHELE, T., QUIAN QUIROGA, R., JENKS, K. M., DESAIN, P., HONING, H., ET AL. (2005). Expectancy effects on omission evoked potentials in musicians and nonmusicians. *Psychophysiology*, *42*, 191-201.
- KIRINO, E., BELGER, A., GOLDMAN-RAKIC, P., & MCCARTHY, G. (2000). Prefrontal activation evoked by infrequent target and novel stimuli in a visual target detection task: An event-related functional magnetic resonance imaging study. *Journal of Neuroscience*, *20*, 6612-6618.
- KOELSCH, S. (2009). Music-syntactic processing and auditory memory: Similarities and differences between ERAN and MMN. *Psychophysiology*, *46*, 179-190.
- KOELSCH, S., SCHMIDT, B. H., & KANSOK, J. (2002). Effects of musical expertise on the early right anterior negativity: An event-related brain potential study. *Psychophysiology*, *39*, 657-663.
- KUTAS, M., MCCARTHY, G., & DONCHIN, E. (1977). Augmenting mental chronometry: The P300 as a measure of stimulus evaluation time. *Science*, *197*, 792-795.

- LANGERS, D. R., VAN DIJK, P., & BACKES, W. H. (2005). Lateralization, connectivity and plasticity in the human central auditory system. *Neuroimage*, 28, 490-499.
- MCCARLEY, R. W., FAUX, S. F., SHENTON, M. E., NESTOR, P. G., & ADAMS, J. (1991). Event-related potentials in schizophrenia: Their biological and clinical correlates and a new model of schizophrenic pathophysiology. *Schizophrenia Research*, 4, 209-231.
- MICHALEWSKI, H. J., STARR, A., NGUYEN, T. T., KONG, Y. Y., & ZENG, F. G. (2005). Auditory temporal processes in normal-hearing individuals and in patients with auditory neuropathy. *Clinical Neurophysiology*, 116, 669-680.
- MIRANDA, R. A., & ULLMAN, M. T. (2007). Double dissociation between rules and memory in music: An event-related potential study. *Neuroimage*, 38, 331-345.
- NÄÄTÄNEN, R. (1992). *Attention and brain function*. Hillside, NJ: Lawrence, Erlbaum Associations.
- NIKJEH, D. A., LISTER, J. J., & FRISCH, S. A. (2008). Hearing of note: An electrophysiologic and psychoacoustic comparison of pitch discrimination between vocal and instrumental musicians. *Psychophysiology*, 45, 994-1007.
- NIKJEH, D. A., LISTER, J. J., & FRISCH, S. A. (2009). The relationship between pitch discrimination and vocal production: Comparison of vocal and instrumental musicians. *Journal of the Acoustical Society of America*, 125, 328-338.
- OHNISHI, T., MATSUDA, H., ASADA, T., ARUGA, M., HIRAKATA, M., NISHIKAWA, M., ET AL. (2001). Functional anatomy of musical perception in musicians. *Cerebral Cortex*, 11, 754-760.
- ONO, K., NAKAMURA, A., YOSHIYAMA, K., KINKORI, T., BUNDO, M., KATO, T., ET AL. (2011). The effect of musical experience on hemispheric lateralization in musical feature processing. *Neuroscience Letters*, 496, 141-145.
- PALLER, K. A., MCCARTHY, G., & WOOD, C. C. (1992). Event-related potentials elicited by deviant endings to melodies. *Psychophysiology*, 29, 202-206.
- PANTEV, C., ENGELIEN, A., CANDIA, V., & ELBERT, T. (2001). Representational cortex in musicians. Plastic alterations in response to musical practice. *Annals of the New York Academy of Sciences*, 930, 300-314.
- PANTEV, C., OOSTENVELD, R., ENGELIEN, A., ROSS, B., ROBERTS, L., & HOKE, M. (1998). Increased auditory cortical representation in musicians. *Nature*, 392, 811-814.
- PATEL, A. D., GIBSON, E., RATNER, J., BESSON, M., & HOLCOMB, P. J. (1998). Processing syntactic relations in language and music: An event-related potential study. *Journal of Cognitive Neuroscience*, 10, 717-733.
- PERETZ, I., CHAMPOD, A. S., & HYDE, K. (2003). Varieties of musical disorders. The Montreal Battery of Evaluation of Amusia. *Annals of the New York Academy of Sciences*, 999, 58-75.
- PHILLIPS, D. P. (1999). Auditory gap detection, perceptual channels, and temporal resolution in speech perception. *Journal of the American Academy of Audiology*, 10, 343-354.
- PICTON, T. W. (1990). Auditory evoked potentials. *Current practice of clinical electroencephalography* (2nd ed., pp. 625-678). New York: Raven Press.
- PICTON, T. W. (1992). The P300 wave of the human event-related potential. *Journal of Clinical Neurophysiology*, 9, 456-479.
- POLICH, J. (2007). Updating P300: An integrative theory of P3a and P3b. *Clinical Neurophysiology*, 118, 2128-2148.
- PRATT, H., BLEICH, N., & MITTELMAN, N. (2005). The composite N1 component to gaps in noise. *Clinical Neurophysiology*, 116, 2648-2663.
- RICHER, F., ALAIN, C., ACHIM, A., BOUVIER, G., & SAINT-HILAIRE, J. (1989). Intracerebral amplitude distributions of the auditory evoked potential. *Electroencephalography Clinical Neurophysiology*, 74, 202-208.
- SCHIAVETTO, A., CORTESE, F., & ALAIN, C. (1999). Global and local processing of musical sequences: An event-related brain potential study. *Neuroreport*, 10, 2467-2472.
- SHAHIN, A., BOSNYAK, D. J., TRAINOR, L. J., & ROBERTS, L. E. (2003). Enhancement of neuroplastic P2 and N1c auditory evoked potentials in musicians. *Journal of Neuroscience*, 23, 5545-5552.
- SHAHIN, A., ROBERTS, L. E., PANTEV, C., TRAINOR, L. J., & ROSS, B. (2005). Modulation of P2 auditory-evoked responses by the spectral complexity of musical sounds. *Neuroreport*, 16, 1781-1785.
- SNYDER, E., & HILLYARD, S. A. (1976). Long-latency evoked potentials to irrelevant, deviant stimuli. *Behavioral Biology*, 16, 319-331.
- TERVANIEMI, M. (2001). Musical sound processing in the human brain. Evidence from electric and magnetic recordings. *Annals of the New York Academy of Sciences*, 930, 259-272.
- TERVANIEMI, M., ILVONEN, T., SINKKONEN, J., KUJALA, A., ALHO, K., HUOTILAINEN, M., ET AL. (2000). Harmonic partials facilitate pitch discrimination in humans: Electrophysiological and behavioral evidence. *Neuroscience Letters*, 279, 29-32.
- TERVANIEMI, M., JUST, V., KOELSCH, S., WIDMANN, A., & SCHROGER, E. (2005). Pitch discrimination accuracy in musicians vs nonmusicians: An event-related potential and behavioral study. *Experimental Brain Research*, 161, 1-10.
- TERVANIEMI, M., SANNEMANN, C., NOYRANEN, M., SALONEN, J., & PIHKO, E. (2011). Importance of the left auditory areas in chord discrimination in music experts as demonstrated by MEG. *European Journal of Neuroscience*, 34, 517-523.
- TRAINOR, L. J., DESJARDINS, R., & ROCKEL, C. (1999). A comparison of contour and interval processing in musicians and nonmusicians using event-related potentials. *Australian Journal of Psychology*, 51, 147-153.
- TRAINOR, L. J., McDONALD, K. L., & ALAIN, C. (2002). Automatic and controlled processing of melodic contour and

- interval information measured by electrical brain activity. *Journal of Cognitive Neuroscience*, 14, 430-442.
- TREMBLAY, K., KRAUS, N., MCGEE, T., PONTON, C., & OTIS, B. (2001). Central auditory plasticity: Changes in the N1-P2 complex after speech-sound training. *Ear and Hearing*, 22, 79-90.
- WOLDORFF, M. G., TEMPELMANN, C., FELL, J., TEGELER, C., GASCHLER-MARKEFSKI, B., HINRICHS, H., ET AL. (1999). Lateralized auditory spatial perception and the contralaterality of cortical processing as studied with functional magnetic resonance imaging and magnetoencephalography. *Human Brain Mapping*, 7, 49-66.
- ZATORRE, R. J. (1998). Functional specialization of human auditory cortex for musical processing. *Brain*, 121, 1817-1818.
- ZATORRE, R. J. (2001). Neural specializations for tonal processing. *Annals of the New York Academy of Sciences*, 930, 193-210.