

Enhancement of Auditory-evoked Potentials in Musicians Reflects an Influence of Expertise but not Selective Attention

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Abstract

■ Instrumental tones and, in some instances, simple sine-wave tones were shown to evoke stronger auditory-evoked responses in musicians compared to nonmusicians. This effect was taken as an example for plasticity in the auditory cortex elicited by training. To date, however, it is unknown whether an enlarged cortical representation for (instrumental) tones or increased neuronal activity provoked by focused attention in musicians accounts for the reported difference. In an attempt to systematically investigate the influence of attention on the processing of simple sine wave and instrumental tones, we compared auditory-evoked potentials recorded from musicians and nonmusicians. During the electroencephalogram recording, the participants were involved in tasks requiring selective attention to specific sound features such as pitch or timbre. Our results

demonstrate that the effect of selective attention on the auditory event-related potential (AEP) has a different time course and shows a different topography than the reproduced effect of music expertise at the N1 component or the previously demonstrated effect at the P2 component. N1 peak potentials were unaffected by attention modulation. These results indicate that the effect of music expertise, which was traced by current density mapping to the auditory cortex, is not primarily caused by selective attention, and it supports the view that increased AEPs on tones in musicians reflect an enlarged neuronal representation for specific sound features of these tones. However, independent from the N1–P2 complex, attention evoked an Nd-like negative component in musicians but not in nonmusicians, which suggests that plasticity also affects top-down processes. ■

INTRODUCTION

Increasing evidence demonstrates that the auditory cortex is susceptible to plastic alterations. Animal studies showed reorganization in the primary auditory cortex (AI) of adult cats after cochlea damage (Rajan, Irvine, Wise, & Heil, 1993) and frequency training in monkeys resulted in an increased neuronal representation of the trained frequency bands (Recanzone, Schreiner, & Merzenich, 1993). A seminal study that reported plasticity effects in the human auditory cortex (Pantev et al., 1998) observed increased magnetoencephalography (MEG) responses to piano tones compared to sine-wave tones for pianists but not for nonmusicians. This observation was interpreted as an effect of long-term piano training. Meanwhile, some of the original findings have been slightly revised. Several studies employing electroencephalography (EEG) or MEG have provided evidence that instrumental tones elicit increased responses compared to sine-wave tones in nonmusicians, too (Lutkenhoner, Seither-Preisler, & Seither, 2006; Meyer, Baumann, & Jancke, 2006; Shahin, Roberts, Pantev, Trainor, & Ross, 2005). Nevertheless, the direct contrast of musicians to nonmusicians has been shown to reveal increased amplitudes in several auditory-evoked po-

tential (AEP) components or components of its magnetic equivalent, the auditory-evoked field (AEF) (Kuriki, Kanda, & Hirata, 2006; Shahin et al., 2005; Shahin, Bosnyak, Trainor, & Roberts, 2003, but see Lutkenhoner et al., 2006 for counterevidence). These effects mainly pertain to the AEP/AEF¹ negativity N1 and the positivity P2. Enhancement of these components is also found after training to discriminate specific sound features (Tremblay, Kraus, Mcgee, Ponton, & Otis, 2001; Menning, Roberts, & Pantev, 2000).

Referring to the studies by Recanzone et al. (1993) with trained monkeys, higher N1 and P2 amplitudes in music experts are usually interpreted as evidence for an increased neuronal representation of (instrumental) tones caused by intensive music training. However, not only a higher number of stimuli-sensitive neurons but also a top-down shift of attention may result in increased auditory activation and, finally, in increased auditory component amplitudes in musicians. In order to understand how plasticity affects the functional organization of the human brain, it is imperative to distinguish between transient top-down attention effects caused by a different relationship of musicians toward musical stimuli and permanent alteration of the functionality of the cortex caused by intensive training, which is independent of the current mental state.

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most plausible one to explain the data (“smoothness assumption”). In brief, the “smoothness assumption” is based on electrophysiological observations that functional neuronal activity does not occur completely randomly distributed in the cortex. The activity in neighboring columns is not independent from each other. If the activity in a local circuit is high, the chance is increased that neighboring circuits show higher activity, too. The assumption of this phenomenon leads to a considerable constraint on the likely spatial distribution of neuronal activity, and thus, a reduction of possible solutions of the inverse problem (details are described in Pascual-Marqui et al., 1994).

Here, we determined the current density distribution for epochs of electrical brain activity on a dense grid of 2394 voxels at 7-mm spatial resolution. LORETA refers to a three-shell spherical model registered to the Talairach human brain atlas (Talairach & Tournoux, 1988). The source locations were therefore provided as (x, y, z) coordinates in the stereotactic Talairach space. Registration between spherical and realistic head geometry used EEG electrode coordinates reported by Towle et al. (1993). The solution space was restricted to the cortical gray matter and the hippocampus, as determined by the corresponding digitized Probability Atlas also available from the Brain Imaging Centre, Montreal Neurologic Institute. Combined EEG and functional magnetic resonance imaging (fMRI) studies have demonstrated good correspondence between the location of current density maxima derived from AEPs and fMRI activation maxima (Mulert et al., 2001).

In order to verify the localization of the N1 and the P2 component, we calculated the LORETA current density maximum ($\sim\mu\text{A}/\text{mm}^2$) from the grand mean over all subjects of each group at the time windows (latency 100 ± 20 msec) for the N1 and (latency 200 ± 20 msec) for the P2 components, respectively. The same procedure was applied for the localization estimation of the processes underlying the observed components at the post hoc defined time periods between 150–200 msec and 300–350 msec respectively. We estimated the spatial localization for cortical areas showing enhanced activity in musicians versus controls for sine-wave tones and instrumental tones at the N1 time window (latency 100) by performing voxelwise t tests on the individual current density maps. Multiple comparison correction was performed by applying a nonparametric randomization test (Nichols & Holmes, 2002). Effects of the musician versus nonmusician comparison over the primary and secondary auditory cortices were evaluated by conducting a region-of-interest (ROI) analysis on the basis of individual mean current density values at ROIs defined by Brodmann’s areas 41/42 (exact location and size of the ROIs is described in Meyer et al., 2006). Current density values were extracted applying the LORETA ROI extractor tool and were then subjected to t tests checking for group differences.

RESULTS

Behavioral Data

The performance of the musicians in the tasks was close to perfect. The rate of correct button presses was 99.5 ± 0.2 (control), 99.2 ± 0.4 (pitch discrimination), 99.3 ± 0.5 (sine-wave discrimination), and 99.3 ± 0.3 (instrumental tone discrimination). Nonmusicians performed, particularly in the pitch discrimination task, worse: 99.2 ± 1.0 (control), 89.8 ± 9.2 (pitch discrimination), 96.4 ± 5.6 (sine-wave discrimination), and 98.1 ± 1.15 (instrumental tone discrimination). An ANOVA with the factors Group \times Task shows significant main effects for group [$F(1, 24) = 28.1, p < .001$], task [$F(3, 72) = 7.3, p = .006$], and for the interaction Group \times Task [$F(3, 72) = 6.71, p = .008$]. Thus, as expected, musicians perform significantly better in the tasks than nonmusicians. A more detailed analysis of the tasks with t tests reveals significant group differences for pitch discrimination [$t(24) = 3.68, p = .003$] and for instrumental tone discrimination [$t(24) = 3.743, p = .002$]. The differences for the control task [$t(24) = 1.26, p = .220$] and also for sine-wave tone discrimination were not significant [$t(24) = 1.85, p = .089$].

AEP Amplitudes

Figure 2 shows separate AEP curves (A, C)⁵ and RMS curves (B, D) for musicians and nonmusicians, for sine-wave tones and instrumental tones. All four tasks are collapsed in one curve for each condition and group. Clear peaks of N1 and P2 amplitudes were observed in all conditions at about 100 and 200 msec after sound onset, respectively. In musicians compared to nonmusicians, we observed higher mean AEP amplitudes of the N1 component, which were significant between 44 and 150 msec for sine-wave tones and 72 and 118 msec for instrumental tones and higher mean RMS potentials for the N1, which were significant in point-to-point comparisons between 76 and 130 msec for sine-wave tones and 72 and 104 msec for instrumental tones. Mean RMS values were higher in musicians in the time range of the P2 component, too, but they did not reach significance. A main effect for group was observed for N1 [$F(1, 24) = 11.9, p = .002$], but not for P2 peaks, indicating that increased potentials for musicians versus nonmusicians were only significant for the N1 component. Further main effects were observed for tone for N1 [$F(1, 24) = 44.2, p < .001$] and P2 peaks [$F(1, 24) = 70.7, p < .001$], reflecting general occurrence of higher amplitudes for instrumental tones, and for task only for the P2 peaks [$F(3, 72) = 4.8, p = .01$; lower P2 during selective attention tasks]. Of all possible interactions, only the one for Task \times Group for the P2 peaks was significant [$F(3, 72) = 3.4, p = .037$], indicating stronger reduction of P2 peaks during selective attention tasks in musicians.

Figure 2. AEP and RMS curves. AEP curves recorded at the Cz electrode site are shown for instrumental tones (A) and sine-wave tones (C), respectively. Curves are displayed in light gray for musicians and in black for nonmusicians. (B, D) The corresponding root mean square (or global field power) values are displayed in the panels on the right of the AEPs. Sound onset is set to time point zero. (E) The amplitudes of the N1 peaks.

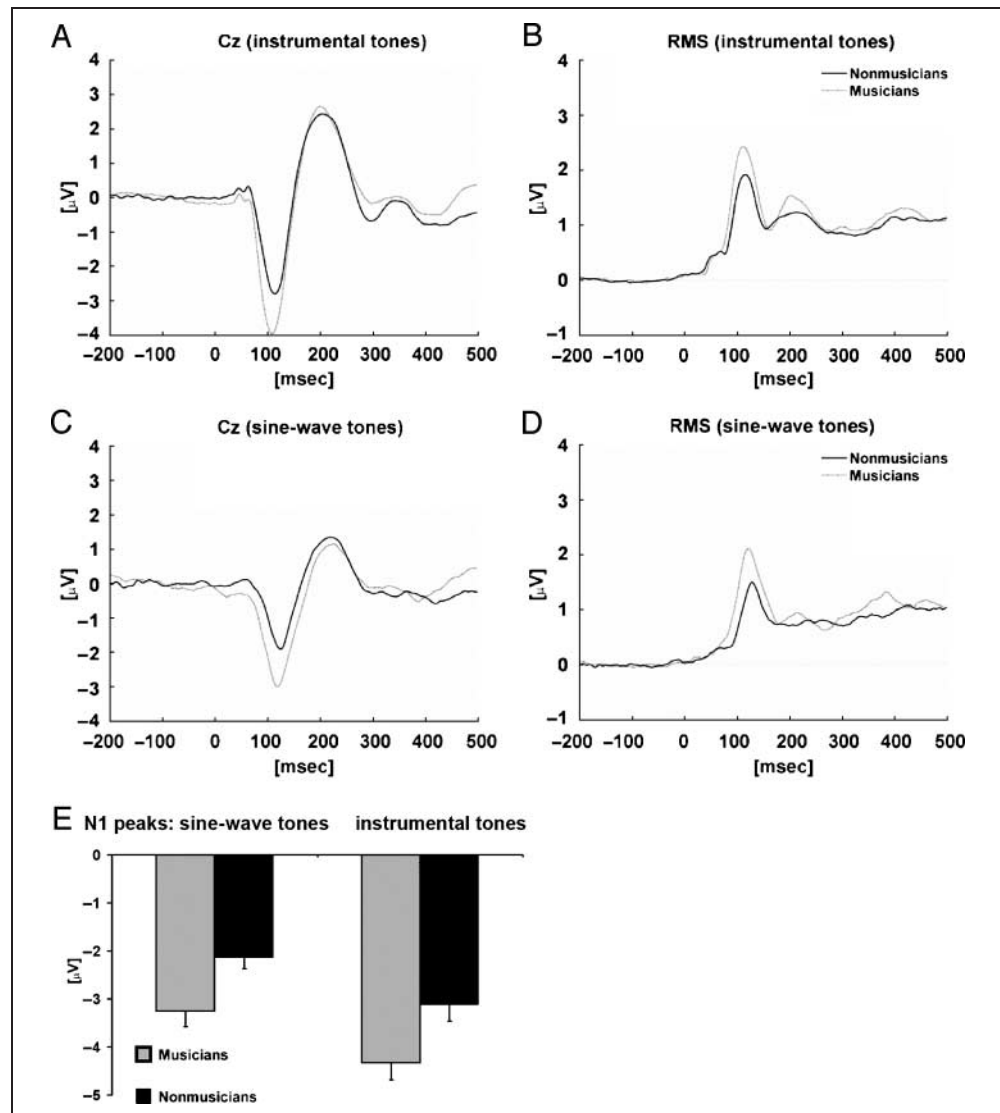


Figure 2E shows the results for *t* tests comparing the AEP amplitude peaks of the N1 component for sine-wave tones and instrumental tones between the two groups (pooling over all tasks). We found increased N1 potentials for musicians independent of the tone class [sine-wave tones: $t(24) = 2.75, p = .012$; instrumental tones: $t(24) = 2.43, p = .023$], but no significantly different P2 potentials. The difference between sine-wave tones and the corresponding instrumental tones was significant in all cases ($p < .001$).

Effects of Sound Feature Attention

In order to investigate the influence of attention to specific sound features such as pitch and timbre, we calculated the difference potentials between the auditory feature detection tasks versus the control task, which did not require attention to sound content. Because we found no Task \times Tone interactions in the previous peak analysis, we collapsed the two tone classes into one

difference potential for the three task comparisons. The difference potentials are shown in Figure 3 with separate panels for musicians (A) and nonmusicians (B). The strongest task effects emerged 200 msec after sound onset, peaking in positivities between 300 and 350 msec latency. These effects were observed in all “detection task versus control task difference curves” and in the two subject groups. The positivities were not only distinct from the classical AEPs N1 and P2 in their temporal occurrence but also in their spatial pattern. The maximal difference potentials were found consistently at the FCz electrode site slightly anterior to Cz. In musicians, we observed an additional negativity of the described difference potentials between 100 and 250 msec after sound onset with maxima between 150 and 200 msec, which was not present in nonmusicians. A *t* test between the detection tasks and the control task at the time window of 150–200 msec (Figure 3C) and 300–350 msec, respectively, revealed that the later effect was clearly significant for the nonmusicians [pitch detection: $t(12) = 4.81$,

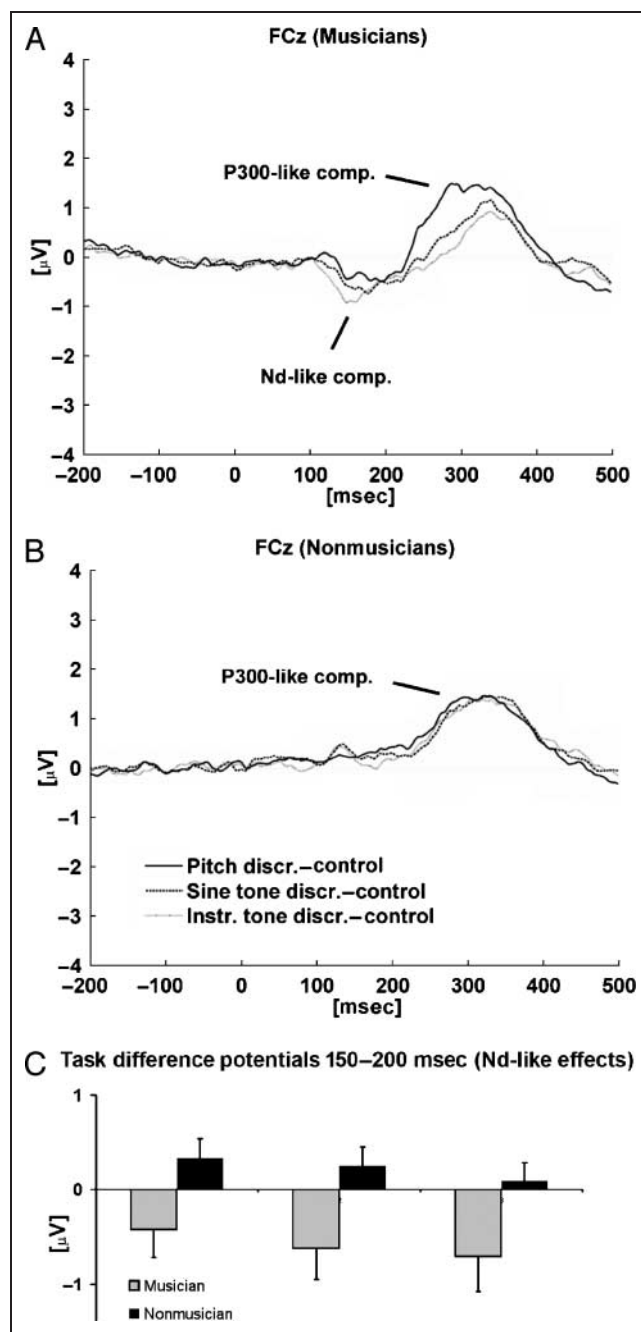


Figure 3. Difference potential curves for specific versus unspecific attention. Difference curves of subtracted potentials at FCz for specific attention versus unspecific attention (control) are displayed in the top panels for musicians (A) and nonmusicians (B). Pitch discrimination versus control is drawn in black, instrumental tone discrimination versus control is drawn in gray, and the sine-wave tone discrimination curve is represented by a dotted line. (C) Mean potential values for all difference curves are shown for the time window 150–200 msec (Nd-like component in musicians). The following conditions are depicted as bar graphs from left to right: pitch discrimination–control, sine tone discrimination–control, and instrumental tone discrimination–control.

$p < .001$; sine-wave tone detection: $t(12) = 5.09$, $p < .001$; instrumental tone detection: $t(12) = 3.77$, $p = .003$] and for all but one detection tasks in the musicians [pitch detection: $t(12) = 4.68$, $p = .001$; sine-wave tone detection: $t(12) = 2.56$, $p = .025$]. The comparison of the instrumental tone detection task with the control task did not yield a significant result [$t(12) = 1.73$, $p = .11$]. Likewise, the comparisons at the 150–200 msec latency time window did not reach significance in both groups, although the effect was close to significance in the musicians. However, an ANOVA for the task effects in the same time windows using the variables group and task (pitch detection, sine-wave tone detection, instrumental tone detection) revealed a group effect for the time window 150–200 msec [$F(1, 24) = 4.6$, $p = .042$; stronger negative deflection in musicians during detection tasks] but not for the later time window 300–350 msec after sound onset. Neither of the two time windows showed significant task effects between the detection tasks. In summary, we find common attention effects in the two groups around 300 msec after sound onset, but the AEP of musicians show an additional attention effect, which is reflected by a negative deflection peaking between 150 and 200 msec after sound onset.

Source Estimation

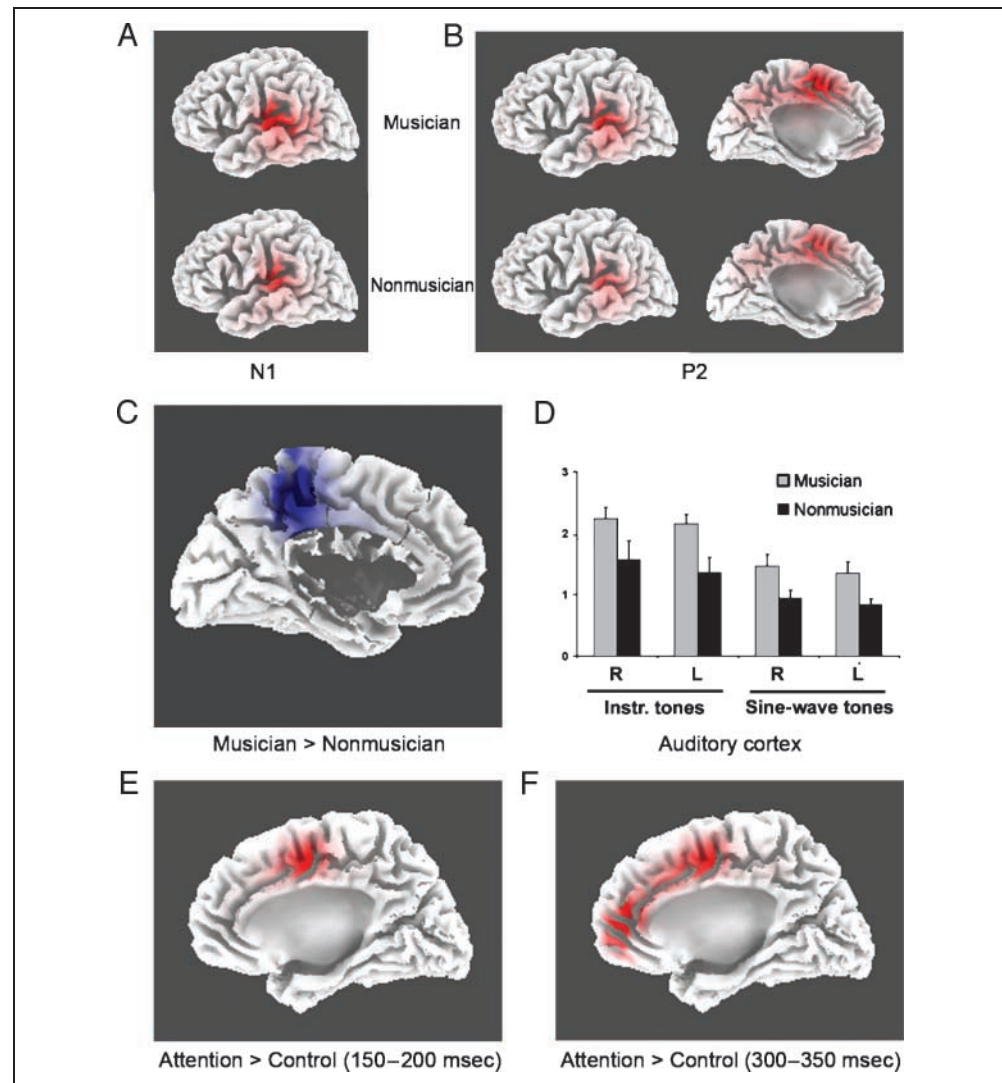
Applying the LORETA source estimation, we found bilateral maxima over the primary and secondary auditory cortices for the sine-wave tones and the instrumental tones for both the N1 and the P2 time windows (Figure 4A, B). In addition, we found a prominent secondary maximum in the anterior cingulum (ACC) in the P2 window. Talairach coordinates and current density values of all reported maxima are listed in Table 1.

The comparison between the estimated current density values for musicians and nonmusician controls processing instrumental tones revealed significant higher current density (corrected for multiple comparisons) in the right superior parietal lobe (BA 5/7) for musicians (Figure 4C).

We observed a maximum over the same area for the sine-wave tones, but this was not significant on a corrected level (Table 1). A closer investigation of the current density distribution in the auditory cortex by measures of an ROI analysis showed significantly higher current densities for the musicians against nonmusicians for instrumental tones [left: $t(24) = 2.14$, $p = .045$; right: $t(24) = 2.70$, $p = .014$] and sine-wave tones [left: $t(24) = 2.23$, $p = .037$; right: $t(24) = 2.48$, $p = .023$] in both the left and the right hemispheres (Figure 4D).

The current density maxima for the observed components of the task difference waves at the time windows between 150 and 200 msec latency and between 300 and 350 msec latency are listed also in Table 1 (see also Figure 4E, F for examples). The maxima at the 150–200 time window in the musicians were observed in the ACC for all tasks. This was also the case for the maxima at the

Figure 4. Current density distributions. The maxima of the current density distributions for instrumental tones at the time windows for N1 (80–120 msec) (A) and P2 (180–220 msec) (B) are displayed for musicians (top) and nonmusicians (bottom). Panel C shows the significant voxels ($p < .05$, corrected for multiple comparisons) derived from voxelwise comparison between musicians and nonmusicians for instrumental tones. The data from an ROI analysis of the same contrast in the auditory cortex is shown in the panel on the right (D). In the bottom panels, the current density maxima of the difference waves derived from the specific versus unspecific attention tasks are displayed at the time windows 150–200 msec (E) and 300–350 msec (F), covering the components that were most sensitive to attention. The maps derived from the instrumental discrimination versus control conditions in musicians form representative examples for the data listed in more detail in Table 1.



300–350 time window for the two groups. However, in the musicians prominent further maxima were observed in the posterior cingulum and in the medial frontal gyrus.

DISCUSSION

First, we will briefly consider to what extent our data are in line with previous investigations showing an enhanced AER to instrumental and sine-wave tones in musicians compared to nonmusicians. Furthermore, we will discuss the results with respect to previous interpretations of these group differences. Second, we will point out how the AER in the two groups is affected by selective attention to specific sound features and we will show evidence that increased selective attention is not responsible for stronger AER in musicians.

AEP Differences between Musicians and Controls

Our data clearly support previous studies that showed an enhanced N1 component of the AER in musicians

compared to nonmusicians. The significance of this difference is particularly remarkable because, in accordance with numerous previous studies, our data show a considerable intersubject variability (see also Lutkenhoner et al., 2006). This variability might be a reason why we do not find a significantly increased P2 component in musicians versus nonmusicians, although we find mean RMS potential increases of comparable magnitude as for N1. Attentional top-down processes, another source of variance that affects specifically the P2 time range, will be discussed further below. Due to the high intersubject variability of the N1–P2 ratio and because several studies showed an enhanced AER P2 component (Kuriki et al., 2006; Shahin et al., 2003, 2005), we abstain from speculating about a particular role of one of the two main AER components (N1 and P2) for musical expertise but discuss the AER mainly in respect to the N1–P2 complex as an entity.

In contrast to earlier reports (Pantev & Lutkenhoner, 2000; Pantev et al., 1998), we find enhanced N1 amplitudes for sine-wave tones, in addition to timbre tones, in

Table 1. List of Current Density Maxima

<i>Time Window</i>	<i>Condition</i>	<i>Current Density</i>	<i>Coordinates</i>			<i>Hemisphere</i>	<i>Cortical Area BA</i>
			<i>x</i>	<i>y</i>	<i>z</i>		
N1 (80–120 msec)	Sine tone musician	1.72	−59	−32	8	L	42
		1.77	60	−39	−15	R	22
	Instrumental tone musician	2.01	−59	−32	8	L	42
		2.13	60	−39	8	R	22
	Sine tone nonmusician	1.4	−59	−32	8	L	42
		1.44	60	−32	−15	R	42
	Instrumental tone nonmusician	1.61	−59	−32	8	L	42
		1.58	60	−39	15	R	42
P2 (180–220 msec)	Sine tone musician	1.38	−59	−39	8	L	22
		1.41	60	−39	15	R	42
	Instrumental tone musician	1.23	4	3	43	R	24
		1.56	−59	−39	8	L	22
		1.5	60	−39	15	R	22
		1.32	−4	−4	50	L	24
	Sine tone nonmusician	1.27	−59	32	8	L	42
		1.18	60	−39	22	R	22
	Instrumental tone nonmusician	1.28	4	3	43	R	24
		1.41	−59	−39	8	L	22
		1.42	60	−39	15	R	42
		1.3	4	3	43	R	24
150–200 msec	Musicians						
	Instrumental discrimination–Control	0.81	4	−4	50	R	24
	Sine discrimination–Control	0.7	4	−4	50	R	24
	Pitch discrimination–Control	0.56	−3	11	50	L	24
300–350 msec	Nonmusicians						
	Instrumental discrimination–Control	1.07	4	10	43	R	32
	Sine discrimination–Control	1.02	4	3	43	R	24
	Pitch discrimination–Control	1.05	4	3	43	R	24
	Musicians						
	Instrumental discrimination–Control	0.9	4	−4	43	R	24
		0.67	−3	45	−6	L	10
	Sine discrimination–Control	0.84	4	−4	43	R	24
		0.78	4	45	1	R	32
	Pitch discrimination–Control	1.1	4	−4	50	R	24
<i>Voxelwise Comparison</i>	<i>Musicians vs. Nonmusicians</i>	<i>t Value</i>	<i>Coordinates</i>			<i>Hemisphere</i>	<i>Cortical Area BA</i>
			<i>x</i>	<i>y</i>	<i>z</i>		
N1 (80–120 msec)	Instrumental tone	3.34	−10	−53	57	L	7
	Sine tone	3.11	−10	−46	57	L	7

Current density maxima are listed by calculated time window including current density value [$\mu\text{A}/\text{mm}^2$] $\times 10^{-3}$, Talairach coordinates, hemisphere, and cortical area defined by Brodmann's area (BA). For voxelwise comparisons, the *t* value is reported. The threshold for significant voxels corrected for multiple comparisons is at a *t* value of 3.21 ($p < .05$).

comparisons of musicians versus nonmusicians. Similar enhancement for both tone classes is confirmed by the absence of a Group \times Tone interaction. Differences between musicians and nonmusicians in components of the N1–P2 complex evoked by pure tones are, however, well in line with the data presented by Shahin et al. (2003, 2005), who reported magnified P2 and N1c components of the AER to sine-wave tones in musicians. These results suggest that musical training could also affect the processing of not specifically trained tones, indicating potential transfer effects. This means that plasticity effects that are observed following the presentation of untrained stimuli, such as sine tones, suggest that the training does not necessarily lead to an exclusive increase of the representation of the trained stimuli as earlier suggested by Pantev et al. (1998). A training-mediated increase of neuronal resources in the auditory cortex that provides a higher resolution for basic auditory features such as pitch or timbre, and so forth, would better explain an increase of the AER, which is not restricted to trained stimuli. Such an increase of auditory neuronal resources that enhances the discrimination of basic auditory sound features would predict an improvement in the performance of auditory tasks. It is widely accepted that musicians perform better in auditory tasks such as pitch or timbre detection in a musical context (see also Behavioral Data of this study). In addition, an increasing number of studies show evidence that cognitive processes beyond music, such as vocal timbre processing (Chartrand & Belin, 2006) or pitch detection in language (Magne, Schon, & Besson, 2006), profit from musical training as well.

In order to gain more information on the nature of the additional activity (increased N1–P2 complex) found in musicians, we estimated the location of the underlying cortical generators by mapping the LORETA-derived current density distribution. We observed bilateral current density maxima in the auditory cortex for all classes of tones for both the N1 and P2 components. This location is in agreement with our expectation and previous dipole source estimations (Pantev, Roberts, Elbert, Ross, & Wienbruch, 1996; Hari et al., 1987) as well as LORETA-based source estimations (Meyer et al., 2006). We would expect that an intensified recruitment of neuronal resources in the auditory cortex of musicians listening to tones would lead to increased current density in auditory areas. Thus, the current density distribution derived from the AEPs of the two groups was analyzed in a voxelwise comparison. In fact, the current density-based ROI analysis revealed significantly increased activity in the primary and secondary auditory cortices of musicians compared to nonmusicians, which support an increased recruitment of neuronal resources in these areas.

Interestingly, we found the maxima of the current source density differences in superior parietal areas (Figure 4). Although several fMRI studies demonstrated a privileged role of this brain area when comparing musi-

cians to nonmusicians (Baumann et al., 2007; Haslinger et al., 2005; Hasegawa et al., 2004), when investigating musical training (Stewart, 2005; Stewart et al., 2003) and imagery of music performance (Meister et al., 2004), assigning a specific role for this area in the context of the present task would be speculative. However, this maximum, in combination with further extra-auditory maxima in the cingulum detected in the attention contrast, is a reminder that neuronal activation during auditory tasks is not necessarily confined to the auditory cortex, but may also originate from areas that have not yet been attributed to auditory perception.

Influence of Attention on the AEP

The ANOVA for the N1 peak potentials for which the clearest group differences were observed in this study did not reveal task effects. This finding indicates that selective attention is not a plausible explanation for the observed group differences of the N1 component. However, the analysis of P2 potentials showed influences of selective attention in the same ANOVA. In addition of the main effect of task, we also observed a Group \times Task interaction, which indicates that the attention effect differed between musicians and nonmusicians. This observation was confirmed by inspection of the potential difference curves between the sound feature detection tasks and the control task, which did not require selectivity auditory attention. In order to decide whether attention effects could potentially explain the previously demonstrated increase of the P2 component in musicians, we need to understand the underlying processes of the task difference curves.

The difference curves show an influence on the AEP by top-down selective attention to pitch and timbre of the tones. In our case, the difference curves at central electrodes showed a positive component with peaks between 300 and 350 msec after sound onset and a negative component with peaks at a latency of 150–200 msec, which was mainly observed in musicians (Figure 3). We think that both of these components could be explained by previously described processes in the context of attention, even though our procedures are somewhat different from the original paradigms. The later positivity shows similar features (time range, polarity, and topography) to the P300 component (reviewed in Donchin & Coles, 1988; Hillyard & Picton, 1987; and more recently, Polich, 2007). The P300 is usually obtained by an “oddball” paradigm or more rarely by infrequent targets that are attended. The attended tones are typically contrasted to the not-attended tones of the same block. In our case, we compared the AEPs of tones whose features were selectively attended in one block to tones of another block which were not selectively attended. Because of this slight difference in the paradigm compared to standard procedures, we called the later selective attention evoked positivity as the “P300-like”

effect. Similarly, we referred to the earlier selective attention negativity between 150 and 200 msec as the “Nd-like” effect. The negative difference (Nd) (Hansen & Hillyard, 1980) is usually calculated by contrasting selectively attended tones with ignored tones. Interpretations of the P300 and the Nd effects are well in line with the task contrast of the current study. Polich (1987) has previously shown that active tasks produce larger P300 amplitude than passive tasks, and the Nd was explained by channel selection for attended features (Näätänen, 1982).

Although the ANOVA showed task effects in the time range of the P2 component, a careful analysis of the AEP displacements evoked by attention modulation clearly suggests that the “P300-like” positivity and the “Nd-like” negativity (Figure 3) are independent from the observed increase of the P2 potentials of musicians in previous studies and hinted in the present study (Figure 2). The P300-like positivity occurs clearly too late to influence the P2 component which peaks later than 200 msec after sound onset. The Nd-like negativity overlaps with the P2 potential (which is obviously the reason for the P2 task effects in the ANOVA), but its peaks are considerably earlier than the peaks of the effect of expertise at the P2 component (halfway between the N1 and the P2) and the topography of the negativity shows a more anterior maximum. This is also reflected in the different current density maxima for the P2 increase and the Nd-like effect. All these observations indicate that the Nd-like effect evoked by selective attention in musicians is independent from the effect of musical expertise at the P2. Most importantly, however, the two phenomena show different polarities. Selective attention leads to a reduction of the P2 component while musical expertise increases the P2. Thus, an increase of selective attention is not a plausible explanation for the effects of musical expertise at the N1 or at the P2 component. However, the reduction at the P2 component caused by overlapping attention effects might be one reason why the observed group differences of the P2 peaks were not significant in our study. More generally spoken, interference of top-down attention may contribute to the considerable variance in the P2 time range and the N1–P2 of AERs as shown in previous studies (see discussion above).

Although the data support the notion that musical training increases the amplitude of N1–P2 independently from top-down attention modulation, the significant group differences in the attention contrasts suggest that the highlighted selective attention processes are subject to plasticity themselves. The top-down evoked Nd-like component is only visible in musicians and is virtually absent in nonmusicians. A previous study by Nager, Kohlmetz, Altenmüller, Rodríguez-Fornells, and Munte (2003) and Munte, Kohlmetz, Nager, and Altenmüller (2001) already demonstrated modulation of the Nd by attention and musical expertise. Specific attention to

sounds from spatially different sources evoked stronger Nd components in conductors compared to pianists and nonmusicians. This finding has been explained by the acquired skill of conductors to locate specific instruments in a concert hall. The Nd component was understood as an index for the initial selection of stimuli according to certain stimulus features and therefore its enhancement in conductors was taken as an example for neuroplasticity due to training. In our study we can similarly explain the Nd-like component by an intensive long-term training for the attended stimuli features, namely pitch and musical timbre, resulting in an increased expertise in the discrimination of these features (see also Behavioral Data).

The demonstrated Nd-like effect represents a novel finding indicating that, in addition to increased N1–P2 components generated in the auditory cortex, plasticity also affects top-down processes in skilled musicians. A role of attention for the Nd-like and P300-like components is further supported by the estimated location of their current density maxima in the ACC. The ACC has repeatedly been proposed to play an important part in the network for attention control (Hopfinger, Buonocore, & Mangun, 2000; Turken & Swick, 1999; Posner & Dehaene, 1994).

Conclusion

The present study reveals clear evidence for enhanced activity in the auditory cortex of musicians compared to nonmusician controls during perception of sine-wave and instrumental tones, with the first supporting plasticity transfer beyond musical context. A detailed investigation on the influence of sound feature specific attention demonstrates that the observed top-down attention effects do not explain the reported differences between the two groups. Our results support the view that the observed group effects are the result of sustained neural alterations in the auditory cortex, which lead to increased AERs independent from transient, top-down controlled attention effects. In addition, we revealed novel group differences between musicians and nonmusicians who selectively attended auditory features of tones. These differences suggest that plasticity as a consequence of long-term musical training is not restricted to low-level sensory processes but also affect top-down controlled processes alike.

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Notes

1. For the readers' convenience, AEP/AEF is simplified to "auditory-evoked response" (AER) when both meanings are included in the present document.
2. Voltcraft 329, Conrad Electronics, Wernberg, Germany.
3. Group was treated as a "between-subject" factor.
4. www.unizh.ch/keyinst/NewLORETA/LORETA01.htm.
5. Supplementary figures showing AEP curves of additional electrode sites are available on www.neurowissenschaft.ch/mmeyer/JCN07/.

REFERENCES

- Alho, K. (1992). Selective attention in auditory processing as reflected by event-related brain potentials. *Psychophysiology*, *29*, 247–263.
- Annett, M. (1970). A classification of hand preference by association analysis. *British Journal of Psychology*, *61*, 303–321.
- Baumann, S., Koeneke, S., Schmidt, C. F., Meyer, M., Lutz, K., & Jancke, L. (2007). A network for audio-motor coordination in skilled pianists and non-musicians. *Brain Research*, *1161*, 65–78.
- Chartrand, J. P., & Belin, P. (2006). Superior voice timbre processing in musicians. *Neuroscience Letters*, *405*, 164–167.
- Donchin, E., & Coles, M. G. H. (1988). Is the P300 component a manifestation of context updating. *Behavioral and Brain Sciences*, *11*, 357–374.
- Hansen, J. C., & Hillyard, S. A. (1980). Endogenous brain potentials associated with selective auditory attention. *Electroencephalography and Clinical Neurophysiology*, *49*, 277–290.
- Hari, R., Pelizzone, M., Makela, J. P., Hallstrom, J., Leinonen, L., & Lounasmaa, O. V. (1987). Neuromagnetic responses of the human auditory-cortex to onsets and offsets of noise bursts. *Audiology*, *26*, 31–43.
- Hasegawa, T., Matsuki, K. I., Ueno, T., Maeda, Y., Matsue, Y., Konishi, Y., et al. (2004). Learned audio-visual cross-modal associations in observed piano playing activate the left planum temporale. An fMRI study. *Cognitive Brain Research*, *20*, 510–518.
- Haslinger, B., Erhard, P., Altenmuller, E., Schroeder, U., Boecker, H., & Ceballos-Baumann, A. O. (2005). Transmodal sensorimotor networks during action observation in professional pianists. *Journal of Cognitive Neuroscience*, *17*, 282–293.
- Hillyard, S. A., Hink, R. F., Schwent, V. L., & Picton, T. W. (1973). Electrical signs of selective attention in human brain. *Science*, *182*, 171–180.
- Hillyard, S. A., & Picton, T. (1987). Electrophysiology of cognition. In F. Plum (Ed.), *Handbook of physiology, Section 1: Neurophysiology, Volume V: Higher functions of the brain* (pp. 519–584). Washington, DC: American Physiological Society.
- Hopfinger, J. B., Buonocore, M. H., & Mangun, G. R. (2000). The neural mechanisms of top-down attentional control. *Nature Neuroscience*, *3*, 284–291.
- Huynh, H., & Feldt, L. S. (1970). Conditions under which the mean square ratios in repeated measurements designs have exact F distributions. *Journal of Neuroscience*, *26*, 4046–4053.
- Jancke, L. (1996). The hand performance test with a modified time limit instruction enables the examination of hand performance asymmetries in adults. *Perceptual and Motor Skills*, *82*, 735–738.
- Jung, T. P., Makeig, S., Humphries, C., Lee, T. W., McKeown, M. J., Iragui, V., et al. (2000). Removing electroencephalographic artifacts by blind source separation. *Psychophysiology*, *37*, 163–178.
- Kuriki, S., Kanda, S., & Hirata, Y. (2006). Effects of musical experience on different components of MEG responses elicited by sequential piano-tones and chords. *Journal of Neuroscience*, *26*, 4046–4053.
- Lutkenhoner, B., Seither-Preisler, A., & Seither, S. (2006). Piano tones evoke stronger magnetic fields than pure tones or noise, both in musicians and non-musicians. *Neuroimage*, *30*, 927–937.
- Magne, C., Schon, D., & Besson, M. (2006). Musician children detect pitch violations in both music and language better than nonmusician children: Behavioral and electrophysiological approaches. *Journal of Cognitive Neuroscience*, *18*, 199–211.
- Mangun, G. R. (1995). Neural mechanisms of visual selective attention. *Psychophysiology*, *32*, 4–18.
- Meister, I. G., Krings, T., Foltys, H., Boroojerdi, B., Muller, M., Topper, R., et al. (2004). Playing piano in the mind—An fMRI study on music imagery and performance in pianists. *Cognitive Brain Research*, *19*, 219–228.
- Menning, H., Roberts, L. E., & Pantev, C. (2000). Plastic changes in the auditory cortex induced by intensive frequency discrimination training. *NeuroReport*, *11*, 817–822.
- Meyer, M., Baumann, S., & Jancke, L. (2006). Electrical brain imaging reveals spatio-temporal dynamics of timbre perception in humans. *Neuroimage*, *32*, 1510–1523.
- Mulert, C., Jager, L., Schmitt, R., Bussfeld, P., Pogarell, O., Moller, H. J., et al. (2001). Integration of fMRI and simultaneous EEG: Towards a comprehensive understanding of localization and time-course of brain activity in target detection. *Neuroimage*, *22*, 83–94.
- Munte, T. F., Kohlmetz, C., Nager, W., & Altenmuller, E. (2001). Neuroperception—Superior auditory spatial tuning in conductors. *Nature*, *409*, 580.
- Näätänen, R. (1982). Processing negativity—An evoked-potential reflection of selective attention. *Psychological Bulletin*, *92*, 605–640.
- Näätänen, R. (1990). The role of attention in auditory information-processing as revealed by event-related potentials and other brain measures of cognitive function. *Behavioral and Brain Sciences*, *13*, 201–232.
- Näätänen, R., Gaillard, A. W. K., & Mantysalo, S. (1978). Early selective-attention effect on evoked-potential reinterpreted. *Acta Psychologica*, *42*, 313–329.
- Nager, W., Kohlmetz, C., Altenmuller, E., Rodriguez-Fornells, A., & Munte, T. F. (2003). The fate of sounds in conductors' brains: An ERP study. *Cognitive Brain Research*, *17*, 83–93.
- Nichols, T. E., & Holmes, A. P. (2002). Nonparametric permutation tests for functional neuroimaging: A primer with examples. *Human Brain Mapping*, *15*, 1–25.
- Pantev, C., & Lutkenhoner, B. (2000). Magnetoencephalographic studies of functional organization and plasticity of the human auditory cortex. *Journal of Clinical Neurophysiology*, *17*, 130–142.
- Pantev, C., Oostenveld, R., Engelien, A., Ross, B., Roberts, L. E., & Hoke, M. (1998). Increased auditory cortical representation in musicians. *Nature*, *392*, 811–814.
- Pantev, C., Roberts, L. E., Elbert, T., Ross, B., & Wienbruch, C. (1996). Tonotopic organization of the sources of human auditory steady-state responses. *Hearing Research*, *101*, 62–74.
- Pascual-Marqui, R. D. (1999). Reviews of methods for solving the EEG inverse problem. *International Journal of Bioelectromagnetism*, *1*, 75–86.

- Pascual-Marqui, R. D., Esslen, M., Kochi, K., & Lehmann, D. (2002). Functional imaging with low-resolution brain electromagnetic tomography (LORETA): A review. *Methods and Findings in Experimental and Clinical Pharmacology*, *24*(Suppl. C), 91–95.
- Pascual-Marqui, R. D., Michel, C. M., & Lehmann, D. (1994). Low resolution electromagnetic tomography: A new method for localizing electrical activity in the brain. *International Journal of Psychophysiology*, *18*, 49–65.
- Polich, J. (1987). Comparison of P300 from a passive tone sequence paradigm and an active discrimination task. *Psychophysiology*, *24*, 41–46.
- Polich, J. (2007). Updating P300: An integrative theory of P3a and P3b. *Clinical Neurophysiology*, *118*, 2128–2148.
- Posner, M. I., & Dehaene, S. (1994). Attentional networks. *Trends in Neurosciences*, *17*, 75–79.
- Rajan, R., Irvine, D. R. F., Wise, L. Z., & Heil, P. (1993). Effect of unilateral partial cochlear lesions in adult cats on the representation of lesioned and unlesioned cochleas in primary auditory-cortex. *Journal of Comparative Neurology*, *338*, 17–49.
- Recanzone, G. H., Schreiner, C. E., & Merzenich, M. M. (1993). Plasticity in the frequency representation of primary auditory-cortex following discrimination-training in adult owl monkeys. *Journal of Neuroscience*, *13*, 87–103.
- 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.
- Steingruber, H. J. (1971). Measuring of laterality. *Zeitschrift für Experimentelle und Angewandte Psychologie*, *18*, 337–357.
- Stewart, L. (2005). A neurocognitive approach to music reading. *Annals of the New York Academy of Sciences*, *1060*, 377–386.
- Stewart, L., Henson, R., Kampe, K., Walsh, V., Turner, R., & Frith, U. (2003). Brain changes after learning to read and play music. *Neuroimage*, *20*, 71–83.
- Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain*. Stuttgart, Germany: Georg Thieme Verlag.
- Towle, V. L., Bolanos, J., Suarez, D., Tan, K., Grzeszczuk, R., Levin, D. N., et al. (1993). The spatial location of EEG electrodes: Locating the best-fitting sphere relative to cortical anatomy. *Electroencephalography and Clinical Neurophysiology*, *86*, 1–6.
- 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.
- Turken, A. U., & Swick, D. (1999). Response selection in the human anterior cingulate cortex. *Nature Neuroscience*, *2*, 920–924.
- Woldorff, M. G., & Hillyard, S. A. (1991). Modulation of early auditory processing during selective listening to rapidly presented tones. *Electroencephalography and Clinical Neurophysiology*, *79*, 170–191.