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The fate of sounds in conductors' brains: an ERP study

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Abstract

Professional music conductors are required to home in on a particular musician but at the same time have to monitor the entire orchestra. It was hypothesized that this unique experience should be reflected by superior auditory spatial processing. Event-related brain potentials were obtained, while conductors, professional pianists, and non-musicians listened to sequences of bandpass-filtered noise-bursts presented in random order from six speakers, three located in front and three to the right of the subjects. In different runs, subjects either attended the centermost or the most peripheral speaker in order to detect slightly deviant noise-bursts. For centrally located speakers, the ERPs showed a typical Nd attention effect for the relevant location with a steep decline for the neighboring speakers in all subject groups. For peripheral speakers, only the conductors showed attentional selectivity, while the Nd effect was of similar size for all three peripheral speakers in the other two groups. These ERP effects were paralleled by an enhanced behavioral selectivity in peripheral auditory space in conductors. Moreover, the pre-attentive monitoring of the entire auditory scene indexed by the mismatch negativity was superior in musicians compared to non-musicians. In conductors, the MMN was followed by a positivity suggesting an attention shift towards the deviant stimuli in this group only.

Theme: Neural basis of behavior

Topic: Cognition, Neural plasticity

Keywords: Event-related potentials; Conductors; Pianists; Attention; Music perception; MMN

1. Introduction

Conducting a large orchestra or choir requires more than artistry and musical taste. Especially during practice sessions, a conductor at the same time has to monitor the performance of the *entire* orchestra as well as that of *single* musicians. These are two apparently contradictory tasks: to home in on a single section or player the conductor has to use selective attention mechanisms, while the monitoring of the whole auditory scene likely requires different cognitive mechanisms such as the comparison with incoming information with some kind of internal model.

Previous neurophysiological studies in trained musicians have shown that event-related potentials or event-related magnetic fields can be quite useful to assess training-induced changes in brain functions. For example, in the motor domain it has been shown that increased use of hands in string players leads to an enlargement of the cortical representation of the fingers [5]. In the perceptual domain, it has been demonstrated that professional musicians are superior in pre-attentive processing of sounds: Koelsch et al. tested musicians and non-musicians in a passive task that entailed the presentation of pure (standard) and impure chords (infrequent deviant stimuli). Only the musicians showed a mismatch negativity (MMN) for impure chords indicating that sensory memory mechanisms

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can be modulated by training [11]. More recently, it has been shown that musicians also have a longer temporal window of sound integration [26] and appear to be able to use musical context to speed up preattentive detection of pitch anomalies [2]. Musicians who primarily perform without using a score also show a better ability to establish memory traces of invariant features of transposed musical melodies [35]. Moreover, a specificity of neurophysiological responses with regard to the instrument played by the musician (string/wind) has been reported [20] and musical subjects have been shown to be better than non-musical subjects at preattentively discriminating sounds on the basis of their timbre. In addition to training-induced changes in the pre-attentive processing of sounds, auditory selective attention capabilities in musicians are also improved. For example, we could recently show that musicians required to selectively attend to a series of sounds defined by a specific pitch while ignoring a concurrent series of sounds of different pitch showed an enhanced attention effect in the auditory ERP [12].

In addition to their importance for the elucidation of the perceptual and motor processes involved in making music, these studies in a more general sense illustrate the range and strength of experience-induced adaptivity of the cognitive processing system.

In the current study, we therefore asked the question, to what extent prolonged professional experience as a conductor alters processing of auditory stimuli in the spatial domain. With the aim to distinguish changes in ERPs specific to the conducting experience from general changes related to prolonged professional musicianship we included a group of pianists as controls in addition to non-musicians. To partially transfer the requirements of conducting to an experimental task we used an array of six speakers, three located in front of the subjects and three located to the right. Rapid sequences of standard and deviant sounds were presented from all of the speakers with one speaker being relevant at any given time. This experimental set-up is very similar to previous studies using ERPs to investigate spatial attention mechanisms in normal listeners [33,34] and congenitally blind subjects [25]. Here it was found that the ability to focus on a specific location is much reduced for normal listeners in peripheral compared to central auditory space reflected by a greatly increased false alarm rate to deviant sounds from irrelevant, neighboring locations. Congenitally blind subjects showed an improved auditory localization in peripheral space compared to seeing control subjects. Electrophysiologically, this was paralleled by modulations of the Nd (=negative displacement) effect. The Nd effect is defined as the difference between the ERP to a sound when it is attended and the ERP to the same sound when it is not attended [8]. For the central auditory space, the Nd effect was large for the attended speaker and showed a steep decline for the neighboring speakers in blind as well as sighted subjects. This indicated a good spatial selectivity for the central auditory space. In the periphery, normal sighted subjects showed an Nd effect also for sounds coming from the speakers next to the attended location, thus pointing to a worse spatial selectivity in peripheral space. By contrast, blind subjects' Nd was more pronounced for the attended location than for the neighboring locations even in peripheral auditory space [25].

As conductors and congenitally blind subjects share the need for exquisite auditory spatial resolution, we asked whether or not the modulation of the Nd effect would be similar in these two groups especially in peripheral auditory space. In addition to the spatial *attentional* selectivity, we were also interested in the ability of the three subject groups to *pre-attentively* monitor the unattended parts of the auditory space. An improved ability to do so might relate to the second task of the conductor, i.e., the simultaneous evaluation of a whole auditory scene. In much simpler experimental set-ups involving only two locations, it has been demonstrated long ago that infrequent sound changes in the unattended channel lead to a mismatch negativity [1,42].

With regard to the dual task posed by conducting—selective attention to a single musician on the one hand, change detection in a complex auditory scene on the other hand—we hypothesized that

(1) changes in spatial attention mechanisms should be present in conductors. In particular we predicted that they should be better in focusing stimuli and therefore should display a steeper attentional gradient, especially for peripheral auditory space both behaviorally and electrophysiologically.
(2) Conductors and possibly also professional pianists should display a larger mismatch negativity response to deviant stimuli outside the attentional focus as a sign of better pre-attentive discrimination.

2. Method

2.1. Subjects

Seven classical music conductors (mean age 45 S.D. 10, mean conducting experience 19 years, minimum 6 years), seven pianists (mean age 43 S.D. 13, professional playing mean 16 years, minimum 7 years) and seven non-musician controls (mean age 43, S.D. 11) were recruited. Non-musician controls never had any formal training in music and reported to listen to music occasionally for recreation. The numbers given for both musician groups pertain to the *professional* conducting and piano-playing experience only. Thus, the total period of musical experience in these subject groups was considerably longer. For the non-musician control group only subjects without any experience with musical instruments were included. All subjects were healthy and had normal hearing.

2.2. Stimuli

The experimental set-up comprised an aluminum semi-circle that was hung from the ceiling such that it was approximately at the eye-level of the subjects. The semi-circle had a radius of 130 cm with the subjects seated in the center. To this aluminum semi-circle six speakers were affixed with Velcro-tape. A central group of three speakers were placed immediately in front of the subjects (C1), and 6° (C2), and 12° (C3) to the right. A second, peripheral group of three speakers was placed 90° (P1), 84° (P2) and 78° (P3) to the right of C1 (see Fig. 1 for illustration). To limit the duration of the experiment and in adherence to the design of previous studies [25,34] no speakers were positioned to the left of the subjects. Moreover, a study employing left, center, and right attention conditions and using seven speakers spaced apart by 9° of angle did not reveal any differences for left and right auditory space with respect to behavior and ERPs [33].

Brief bursts of pink noise were delivered via these speakers in random order with interstimulus intervals ranging randomly between 90 and 270 ms (rectangular distribution). The majority of stimuli (84%) were so-called standard stimuli. For these, pink noise with frequencies between 500 and 5000 Hz (75 dB, 80-ms duration) was used. The remaining 16% of the stimuli had an increased bandwidth (500–15000 Hz, 75 dB, 80-ms duration) and will henceforth be called deviants. Of the six speakers only the centermost (C1) and rightmost (P1) speakers were relevant during the experiment. The subjects' task was to selectively attend—in different runs—to C1 or P1 and to press a button to the 'deviant' stimuli occurring at the designated location (=targets). All other stimuli were to be ignored. A total of 12 runs (six attend C1, six attend P1) lasting 6 min each were administered to each subject during a session of about 2.5 h length (including the application of electrodes).

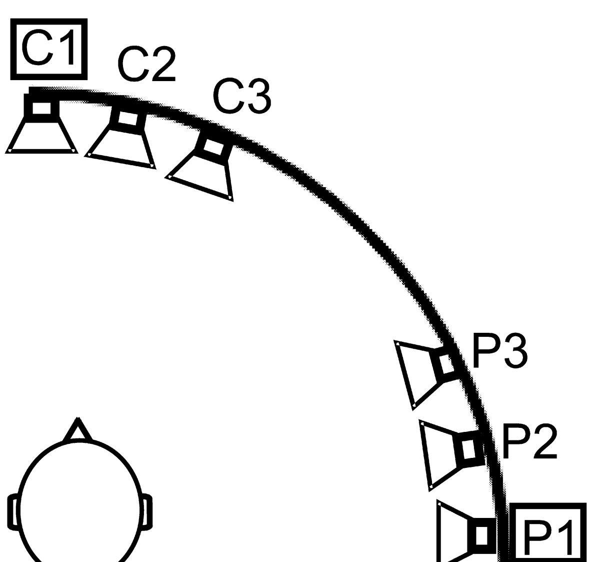

Fig. 1. Schematic drawing of experimental set-up.

2.3. Recording

The electroencephalogram was recorded using tin electrodes mounted in an electrode cap (Electro-Cap International) from Fp1, Fp2, F3, F4, F7, F8, C3, C4, P3, P4, FZ, CZ, PZ, F7, F8, T3, T4, T5, T6, FC1, FC2, CP5, CP6, P3, P4, PO1, PO2, O1, O2 of the international 10–20 system. The time-constant was 10 s and the low pass filter 100 Hz. Ocular fixation was verified by recordings of the horizontal electrooculogram (EOG). Eye blinks were detected with the vertical electroencephalogram. All scalp electrodes were referenced to an electrode located on the right mastoid and re-referenced off-line to the algebraic mean of the activity at the two mastoid processes. Behavioral performance was analyzed in terms of reaction time, hit rates and false alarm rates. Because of the high stimulation rate, the assignment of a given response to a preceding deviant was somewhat ambiguous. Responses were classified as hits or false alarms in the following way: if in a given run the C1 speaker was to be attended to, the time-window from 200 to 500 ms after target stimuli from that speaker was searched for responses. If a button-press code was found in this time-window, it was assumed that it occurred in response to the target stimulus and was classified as a 'hit'. Such responses were 'tagged' in the log-file containing information about the timing of stimuli and responses. In a subsequent search, log-files were examined again, this time for responses occurring in the time-window 200–500 ms after a deviant stimulus in the neighboring speaker C2. If an unassigned ('untagged') response was found in this time-window, it was assigned to C2, classified as a false alarm and tagged as well. Finally, the procedure was repeated searching for responses occurring after deviants presented in speaker C3.

For experimental blocks, in which the peripheral speaker P1 was attended, an analogous procedure was used. Thus, it was assumed that false alarms would occur only to deviants coming from neighboring speakers.

ERPs were averaged off-line for 1024-ms epochs beginning 100 ms before stimulus onset. Artifact rejection was performed off-line before averaging and excluded trials contaminated with ocular and other artifacts using individualized amplitude criteria. Waveforms were quantified in terms of mean amplitudes. Repeated-measures analyses of variance (ANOVA) were performed on behavioral and ERP data.

Brain electric source analysis (BESA, [28]) was performed for (deviant minus standard) difference waves obtained separately for central and peripheral stimuli (collapsed over positions 1–3) from the unattended direction. For this analysis, following previous descriptions of the source structure of the MMN [27,37], two symmetrical dipoles were first fitted for location and orientation near the supratemporal plane. Subsequently, a third source was introduced in order to improve the fit of the solution and to model the P3a component. A middle frontal dipole was introduced [7,24,39] and fitted for location and orientation.

3. Results

3.1. Behavior

The correctly detected target stimuli from C1 and P1 and the false alarms to deviant sounds from neighboring speakers are given in Table 1 in percent. Clearly, all three group showed a good selectivity for stimuli from the central speakers. For the peripheral speakers, however, the false alarm rates for neighboring speakers was much lower in the conductors indicating a better selectivity. Inspection of the means suggests that the pianists had a different response strategy than the other two groups as their overall response rate was lower. Thus, while they have slightly lower false alarm rates than the conductors for speakers C2 and C3, their hit-rate for speaker C1 was approximately 10% below that of the conductors as well. Likewise, for the peripheral speakers overall response rates of the pianists were lower than that of the other groups, while their selectivity was worse than that of the conductors.

When these data were entered into a repeated measures ANOVA with group as between subjects factor and direction (central versus peripheral) and speaker (attended, neighbor, next neighbor) as within subject factors, a highly significant group by direction by speaker interaction emerged ($F(4,36)=6.28$, $P(\mathrm{HF})=0.005$).

Reaction times were compared for the target-hit events, only. No significant group differences were found ($F(2,24)=1.77$, n.s.) but responses were significantly faster for the targets emanating from the centermost speaker ($F(1,18)=5.37$, $P<0.04$; C1/P1: conductors 395/404 ms, pianists 389/410 ms, non-musicians 412/424 ms).

3.2. Attention effects on standard stimuli

ERPs to standard stimuli from the different speakers are shown in Fig. 2. Only data from the Fz electrode are presented, which shows the attention effect most clearly. For the waveforms of the relevant speakers C1 and P1 all three subject groups show a typical electrophysiological attention effect of about equal size: ERPs to attended tones are more negative than the ERPs to the same tones when the other speaker is attended. For the center group of speakers, a smaller attention-related effect is seen for speaker C2. For speaker C3 there is virtually no attention-related effect in any of the subject groups.

By contrast, only the conductors show a steady decline of the attention-related ERP effect when the peripheral speaker was attended. The pianists as well as the non-musicians show attention-related effects of similar size for all three peripheral speakers. The attention effect was quantified by mean amplitude measures taken on the (attended direction) minus (unattended direction) difference waves in the 180–200-ms time-window. These measures were first entered into an omnibus ANOVA with group (conductor/pianist/non-musician) as between groups factor and direction (central/peripheral) and speaker (attended/nearest neighbor/second neighbor) as within subject factors. A complex three-way interaction was obtained in this ANOVA reflecting the fact that only conductors showed an attentional gradient in peripheral auditory space ($F(4,36)=3.15$, $P<0.03$). Also, a main effect of speaker was obtained ($F(1,18)=9.81$, $P<0.006$) reflecting the attentional gradient present from the attended to the neighboring speakers. To pinpoint this difference, a series of ANOVAs was performed separately for each pair of groups and central and peripheral sets of speakers.

Pairwise comparisons were conducted to compare the different subject groups for stimuli coming from central and peripheral space separately. While for central auditory space none of the comparisons yielded a significant group by speaker interaction, such an interaction was found for peripheral space (conductors/non-musicians $F(2,24)=5.15$, $P<0.015$; conductors/pianists: $F(2,24)=3.57$, $P<0.045$; pianists/non-musicians: $F(2,24)=0.06$, n.s.).

3.3. Attention effects on target stimuli

The ERPs to the target stimuli are shown in Fig. 3 for the midline parietal recording site (Pz). A clear difference emerges for central and peripheral stimuli. Attended targets at the centermost speaker were associated with a large P3 component that was more pronounced in the two groups of musicians. P3 amplitude in the periphery was considerably smaller in all three groups but again seemed to be most robust in the conductors.

The P3 component was quantified by a mean-amplitude measure (400–600 ms) for the target stimuli for electrode sites Pz/P3/P4. An overall ANOVA revealed a main effect of group ($F(2,18)=5.1$, $P<0.02$) reflecting the greater amplitude of the P3 in the musicians, as well as a main effect of direction ($F(1,18)=7.9$, $P<0.012$) indicating the

Table 1
Hit-rate for C1/P1 speakers, false alarm rates for C2/C3/P2/P3 speakers (percentage, S.D. in brackets)

	Conductors		Pianists		Controls	
C1	93.1	(17.9)	83.5	(14.6)	90.8	(20.1)
C2	18.1	(10.4)	14.9	(10.2)	22.3	(17.3)
C3	8.1	(7.6)	5.4	(6.1)	7.1	(6.5)
P1	83.0	(19.0)	63.5	(21.5)	82.4	(21.3)
P2	33.5	(19.7)	47.5	(27.0)	66.6	(28.2)
P3	19.5	(17.7)	38.0	(29.9)	61.2	(32.0)

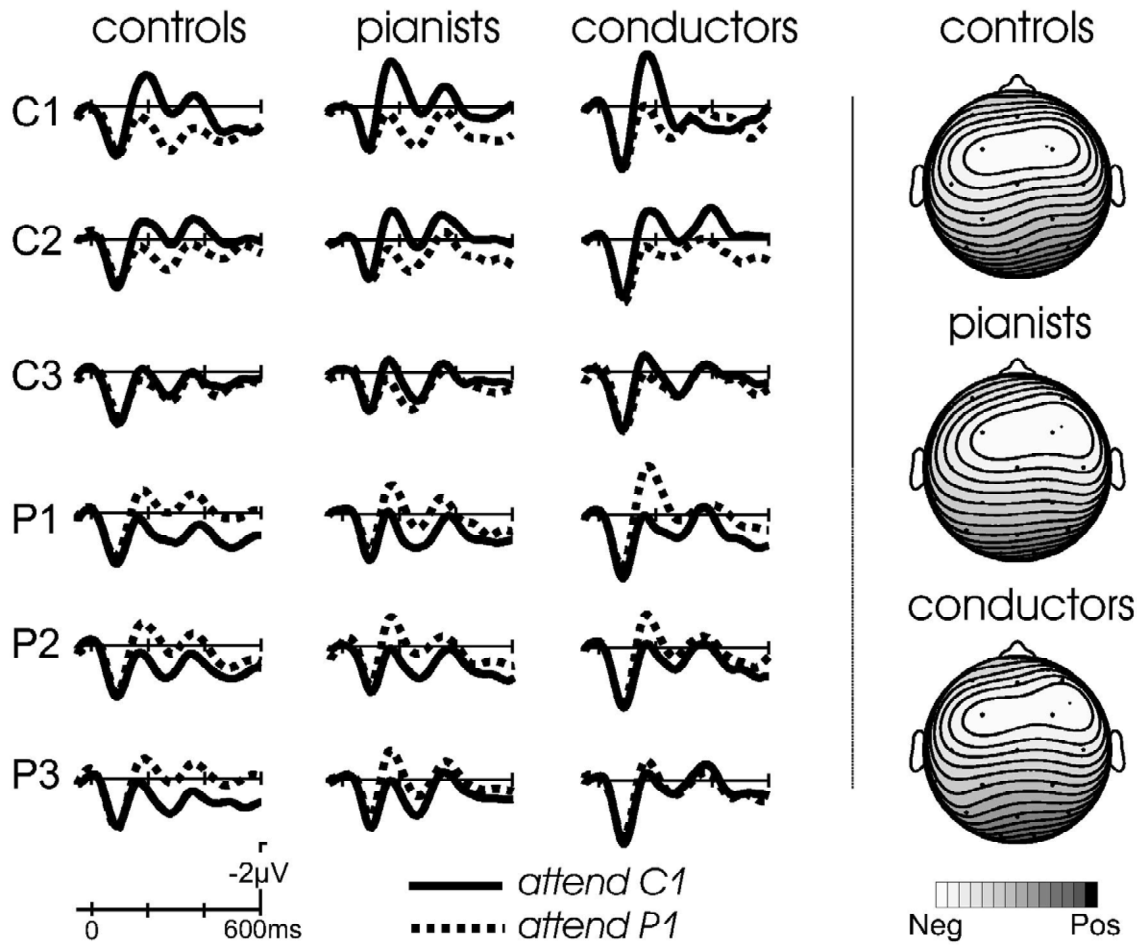

Fig. 2. Grand average potentials (Fz-site) for the different subject groups. Shown are ERPs to standard tones for each of the six loudspeakers, when either the center-most speaker (C1) was attended (solid line) or when the most peripheral speaker (P1) was attended (dotted line). Clearly, all three subject groups show a gradual decline of the attention effect for the three central speakers. By contrast, in the periphery only the conductors show an attentional gradient (see also Ref. [13]).

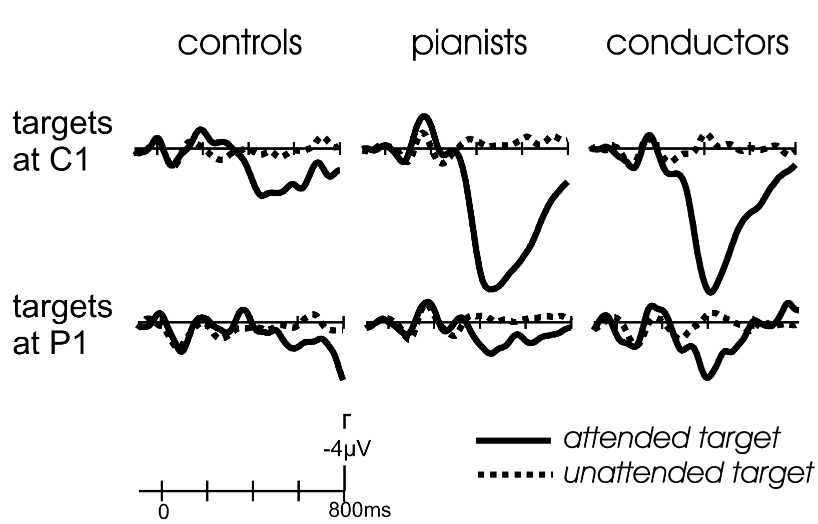

Fig. 3. Grand average potentials (Pz-site) for the different subject groups. Shown are ERPs to target tones for the two relevant speakers (C1 and P1).

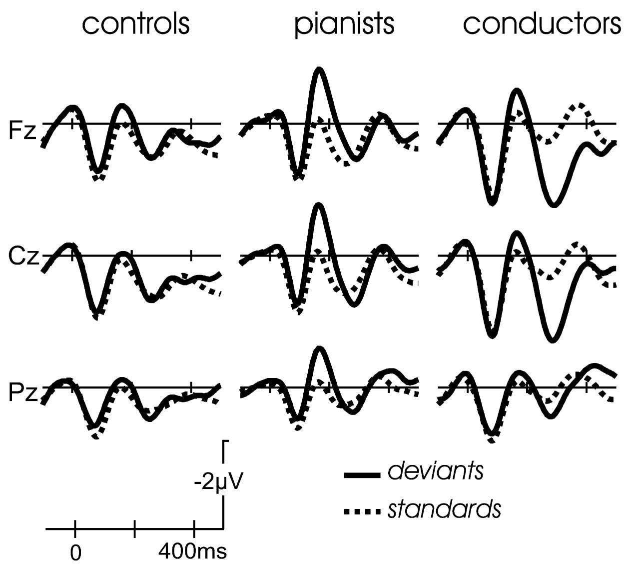

Fig. 4. Grand average potentials to deviant and standard stimuli coming from the periphery (averaged across speakers P1/2/3) when the centermost speaker was attended. Very different responses to deviant stimuli are found for the three subject groups: non-musicians show only a very rudimentary difference between deviants and standards (frontal MMN), the pianists display a very large mismatch MMN, while for the conductors a negativity immediately followed by a prominent frontocentral positive is found for the deviants.

larger amplitude of the P3 component for stimuli coming from the centermost speaker. Pairwise comparisons were conducted which revealed significant differences between the conductors and non-musicians for the central ($F(1,12)=6.3$, $P<0.03$) and peripheral speakers ($F(1,12)=4.91$, $P<0.05$). Likewise, a difference was found between pianists and non-musicians for the central ($F(1,12)=6.5$, $P<0.03$) but not for the peripheral speakers ($F(1,12)=1.12$, n.s.).

3.4. Deviant stimuli at unattended locations

To assess possible differences in ERPs for deviant sounds that are not attended, averages were computed across all deviant stimuli from central speakers when the rightmost speaker was attended and all deviants from peripheral speakers when the centermost speaker was attended. In addition, similar averages were obtained for standard stimuli.

Fig. 4 compares standard and deviant ERPs to peripheral sounds. A dramatic difference emerges between the three subject groups. While non-musician controls show at best a rudimentary difference between deviant and standard stimuli, a sizeable mismatch negativity is seen in the pianists. By contrast the conductors show a smaller negativity for the deviants followed immediately by a positivity with a fronto-central distribution.

Comparable effects were obtained for stimuli from central speakers. This is illustrated by the deviant minus standard difference waves for central and peripheral stimuli which in fact are very similar (see Fig. 5). The distribution of these effects is illustrated in Fig. 6 that depicts spline-interpolated isovoltage maps.

These difference waveforms were quantified by mean amplitude measures in time-windows designed to pick up

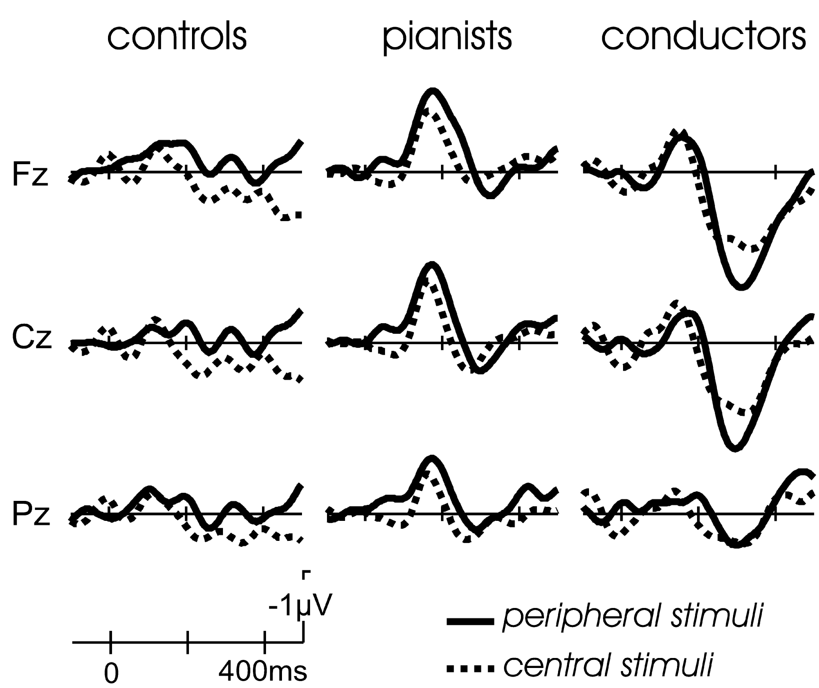

Fig. 5. Deviant minus standard difference waves for the peripheral stimuli (when the centermost-speaker was attended) and the central stimuli (when the most peripheral speaker was attended). A very different morphology of the difference waves is found for the three subject groups (see text).

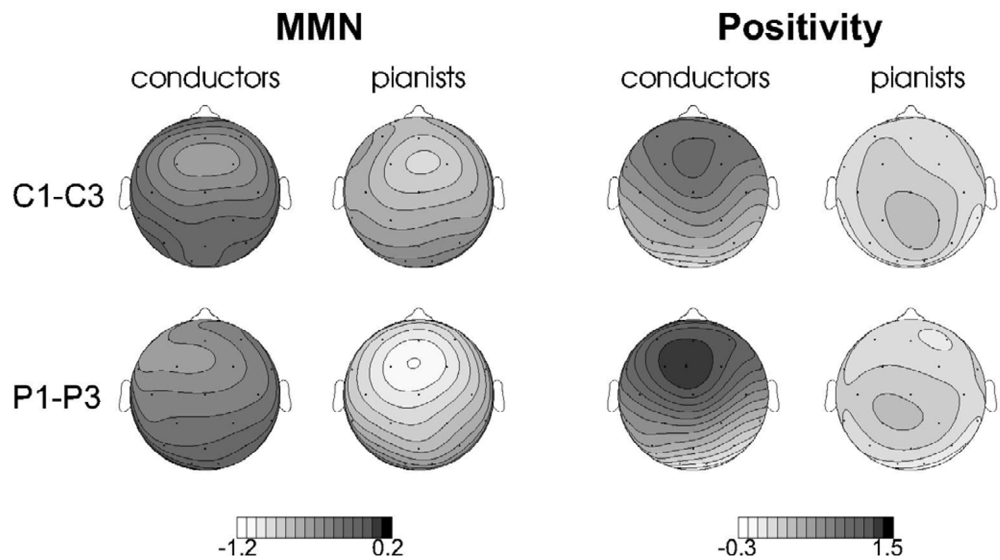

Fig. 6. Spline-interpolated isopotential maps derived from the deviant-minus-standard difference waves for the MMN (time-window 140–190 ms) and the following positivity (time-window 240–340 ms). Both sets of maps are scaled to encompass the minimal and maximal voltages for these conditions across groups. No maps were computed for non-musician controls, as no sufficient differential response for deviants versus standards was present in this group.

the mismatch negativity (140–190 ms, electrodes Fz/Cz) and subsequent positivity (250–350 ms, electrodes Fz/Cz). For the early time-window encompassing the MMN a main effect of group was found ($F(2,18)=4.35$, $P<0.03$). No main effect of stimulus location (central versus periphery) was found ($F(1,12)=0.07$, n.s.). The main group effect was followed up by pairwise comparisons, which revealed a significant difference between pianists and non-musicians ($F(1,12)=5.54$, $P<0.04$). The amplitude difference of the MMN between conductors and pianists did not reach significance ($F(1,12)=3.03$, $P<0.11$).

For the later time-window (250–350 ms), the positivity that was present in the conductor group was statistically reflected in a main effect of group ($F(2,18)=6.1$, $P<0.01$). When followed up by pairwise comparisons, a significant difference emerged for conductors versus non-musicians ($F(1,12)=13.55$, $P<0.004$) and conductors versus pianists ($F(1,12)=6.16$, $P<0.03$).

To get an estimate of the neural generators underlying the mismatch effects in the present study, a brain-electric source analysis (BESA) was performed on the grand average (deviant minus standard) difference waves of the conductors and pianists. As the mismatch effect was too small in the non-musicians, no source analysis was performed in this group. While the obtained fits are far from perfect, mismatch effects can be explained by a three source model with two sources located in the superior temporal lobe and an additional medial source located frontally (residual variance: conductors, peripheral/central, MMN (125–175 ms) 10.4/13.4%, positivity (250–350 ms) 12.2/9.4%; pianists, peripheral/central, MMN 14.6/18.4%, positivity 15.8/32.8%). Interestingly, it appears that the medial frontal source is much more active in the conductors compared to the pianists especially in the later time-window, which explains the fact that less of the variance is accounted for in pianists in this time-window.

4. Discussion

The present results not only show a clear difference between musician and non-musician subjects, they also demonstrate that among professional musicians of comparable experience it matters what 'role' or specialization a particular musician has. Below we will argue that behavioral and ERP-data suggest that conductors are much better than pianists and non-musicians in attentively focusing in on relevant auditory information in space. Moreover, they also appear superior in the pre-attentive registration of deviant stimuli outside the attentional focus.

4.1. Spatial attention effects

When subjects were required to attend to the centermost speaker of the array (C1), all three groups showed a similar and rather precise behavioral selectivity, indicated by the relatively low false alarm rates for the neighboring speakers C2 and C3. The ERPs to the standard stimuli showed a typical attention effect, i.e., sounds from the C1 speaker were associated with an enhanced negativity (Nd), when they were attended to compared to when attention was directed to the peripheral speaker. There was a sharp decline in the amplitude of the Nd effect, i.e., the difference between ERPs from the attention central and attention peripheral condition, for neighboring speakers C2 and C3, indicating that the spatial selectivity probably acts at the stage of perceptual selection. The effects for the central speakers are very similar to previous studies using normal [33,34] and blind subjects [25].

By contrast, the spatial selectivity in peripheral space was much reduced both in terms of behavioral and electrophysiological effects in professional pianists and non-musicians. The conductors, however, still showed a rather good behavioral and electrophysiological selectivity for sounds in peripheral space. Their findings are thus reminiscent to previous findings obtained in a similar experiment with blind subjects [25]. In this earlier study the distribution of the Nd effect was found to be different in blind subjects and sighted controls, suggesting that the electrophysiological attention effect in these two subject groups is supported by partially different neuronal populations. This was taken as a clue for functional/anatomical reorganization in the brain of blind subjects. In the present study, however, the scalp distribution of the Nd attention effect (Fig. 2, right side) was virtually identical for the three subject groups. Thus, while conductors appear to use spatial attention much more effectively than pianists or non-musicians, they apparently use the same cortical brain mechanisms to achieve the superior behavioral results.

The Nd-wave can be taken as an index for the initial selection of stimuli according to certain stimulus features, in this case location. Within an attended channel, the subject has to then achieve the standard-target discrimination. A plethora of studies has demonstrated that detected target tones (hits) are associated with a late positive component, the P3 [23]. The amplitude of the P3 varies as a function of a number of factors that have been formalized in a model suggested by Johnson [10] some time ago. Crucially, the subjective decision confidence has been shown to correlate with P3 amplitude. In the present study, the P3 amplitude for targets from C1 speaker was much larger in the two groups of musicians compared to the non-musicians. P3 amplitude for peripheral targets was greatly reduced in all three subject groups but was best preserved in the conductors. This suggests that, while the hit rate for the central targets was rather similar for all three subject groups, the responses in the musicians were much more confident than those of the non-musicians. Also, peripheral targets in general appear to have been responded to with a greatly decreased confidence.

4.2. Pre-attentive processing

Behavioral data point to a superior role of spatial cues in auditory scene analysis [15]. Moreover, it has been shown that a pre-attentive system that monitors the auditory input for deviance, indexed by the mismatch negativity (MMN), provides the basis for attentive auditory perception [18,38]. Faster automatic encoding of spatial than spectral information into neural representations has been reported by Schröger and Wolff [32]. Moreover, the MMN has been successfully employed to probe the perceived extent of a sound source [40] and crossmodal audio-visual spatial integration in the ventriloquism illusion [3].

In the current paradigm, many of the sounds occurred outside the attentional focus of the subjects. It was therefore of interest to what extent the three subject groups would show electrophysiological signs of change detection for stimuli coming from the unattended direction. Interestingly, all three groups showed different patterns of electrophysiological responses for deviant stimuli: while non-musician controls showed at best a very rudimentary MMN-response, suggesting that they only had a very limited pre-attentive registration of deviant sounds coming from the unattended direction, both musician groups showed sizeable mismatch effects. Professional pianists showed a typical MMN for deviants from the unattended direction, regardless of whether the sounds came from the central or peripheral speakers. In conductors, a smaller MMN was followed by a positivity, which showed a similar frontocentral distribution as the preceding MMN.

How can this pattern be interpreted in light of current evidence regarding the electrophysiological correlates of change detection? While the MMN, usually recorded in so-called passive listening situation, can occur automatically, i.e., regardless of whether or not the stimulus is attended or not, it has been demonstrated, especially for more subtle deviants, that the amplitude of the MMN is sensitive to attention [1,41,42]. One possibility for the increased MMN amplitude in musicians could therefore be that these subjects devote part of their attention to the to be ignored part of the auditory scene. A second possibility is that the pre-attentive mismatch detection process, as indexed by the MMN, is more powerful in the musicians as a result of their experience. This would be compatible with other reports showing a more prominent MMN in musicians [11,26,35,36]. In the conductors the MMN is followed immediately by a positivity. We propose that this positivity might be an instance of the P3a component, which is found to deviant/novel auditory items [4,6]. This P3a-effect maps nicely onto a model proposed by Schröger [31], in which he envisions the mismatch detection process as comprising several stages: the features of an incoming stimulus are initially compared with the established representation of the standard stimulus. The feature-specific mismatch signals are then integrated, giving rise to the MMN. If the integrated mismatch signal exceeds a (variable) threshold, conscious detection of the deviant takes place and initiates an involuntary attention shift which ultimately leads to the identification of the stimulus. The initiation of the involuntary attention shift has been associated with the P3a effect [6]. This line of reasoning thus suggests that the threshold for conscious detection of the mismatch signal is exceeded only in conductors.

In the face of the relatively low number of subjects in each of the groups, the dipole solutions obtained for the mismatch effects (c.f. Fig. 7) have to be interpreted with caution. The finding that the medial frontal source is more

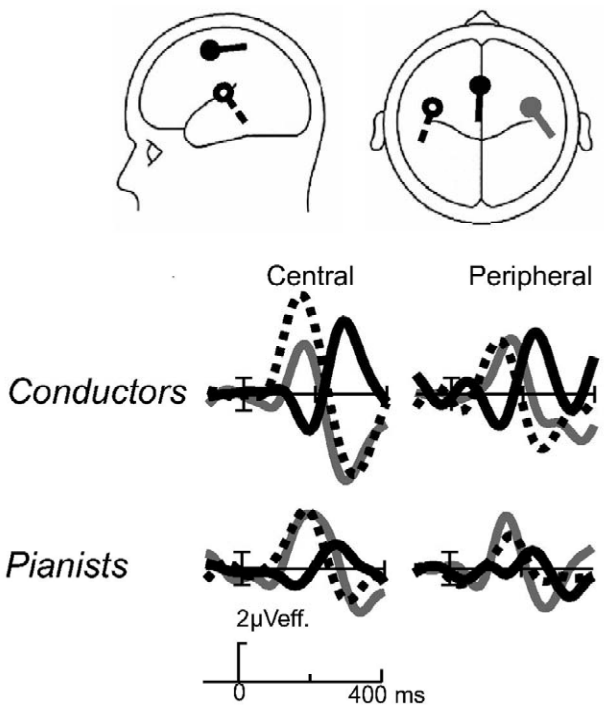

Fig. 7. Dipole solutions for the (deviant-minus-standard) difference waves.

active in the conductors, however, is certainly compatible with the view that the detection of a deviant triggers a further processing stage in the conductors. This frontal source has been first suggested by Giard et al. [7]. Picton et al. [21] speculate that this source represents a response to information processed in the temporal lobes and might represent 'stimulus independent' processing. A recent multi-channel ERP study also proposed a frontal source component nearby the anterior cingulate cortex with a delayed temporal onset relative to the superior temporal sources [39]. Also, in a combined MEG/EEG study Rinne et al. [24] found the expected delay for the frontal source, although only the temporal sources appeared in the MEG data. The authors suggested that different frontal areas including the inferior and superior frontal gyrus the anterior cingulate cortex might contribute to this frontal source, which is further corroborated by a combined fMRI/ERP study [17].

4.3. Neuroplasticity?

The present experiment demonstrates profound changes of the brain responses related to attentive and pre-attentive processing of sounds differing in spatial location in musicians in general and professional conductors in particular. The question therefore arises, whether these changes signal neuroplasticity. Obviously, there is not one single definition of the term. Neuroplasticity in its broadest sense would include all those processes which permit the adaptation of the brain to environmental factors that cannot be anticipated by genetic programming. The neural and behavioral changes attributed to plasticity have been observed on different time scales, ranging from several minutes to the whole life-time of the individual. Different processes underlie plastic changes at the extremes of this time-line. Long-term plasticity can be explained by the de novo growth of new dendrites, synapses, and neurons [22], while changes on a shorter time-scale rely on the disinhibition or inhibition of preexisting lateral connections between neurons by sensory input [9]. The former mechanism entails structural changes at the microscopic and macroscopic level and indeed anatomical changes have been observed in professional musicians who began their training early in life [14,29,30]. Changes in neural processing occurring on a shorter time-scale have been attributed to changes in synaptic connections in the sense of Hebbian learning.

Previously, increased amplitudes (or dipole moments) of event-related potentials/fields in musicians have been interpreted as a sign of functional anatomical reorganization of the cortex of musicians indicating the recruitment of more neurons [19]. Note, that such a statement does not differentiate between a situation, in which more neurons are available because of de novo growth as a result of extensive training, or the case in which more neurons are firing because of enhanced synaptic connectivity. With regard to the Nd attention effect in the present study, no difference in the absolute, maximal amplitude was observed between the three subject groups. Moreover, unlike a similar study in blind subjects [25], no differences in the topography were observed. Thus, neither the underlying neuronal population (topography) nor the number of recruited neurons (amplitude) differed between the groups. While the more peaked appearance of the Nd in the conductors especially for the attended speakers (Fig. 2) might reflect an enhanced synchronization, we are reluctant to speculate about this. Thus, the only obvious difference in the spatial attention effect was the more precise tuning of the Nd-effect in the conductor group. This might well reflect experience related functional of even anatomical changes at an earlier (subcortical) stage of the auditory processing cascade. The present data do not allow such a conclusion, however.

With regard to the pre-attentive detection of deviants, the pattern of ERP responses suggest a profound experience-related change of quality in the processing of deviant sounds in pianists and conductors. Previous studies employing the MMN have demonstrated that it can reflect apparently experience-related hard-wired interindividual differences in phoneme representation [16]. Thus, the observed amplitude differences between musicians and non-musicians with regard to the MMN might well reflect similar functional and anatomical changes in the mismatch detectors of the auditory cortex.

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