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Expectancy effects on omission evoked potentials in musicians and non-musicians

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Abstract

An expanded omitted stimulus paradigm was investigated to determine whether expectancy would modulate the amplitude of the omission evoked potentials (OEPs). In addition, we examined the effects of musical expertise on OEPs. Trials started with 3–7 beats randomly and contained 5 omitted beats. Three types of trials ($n = 90$) were presented with 1, 2, or 3 beats occurring between omissions. A tap response at the end of each trial was used to determine timing accuracy. Clear OEPs were observed over midline sites. We found main omission effects with respect to an N150 and a P400 OEPs component, such that peak amplitudes diminished whenever the occurrence of an omitted stimulus could be expected. In addition, an N600 OEPs component emerged in response to expectedly omitted stimuli toward the end of each trial within the group of musicians. Thus, musical training seems to lead to more efficient and more refined processing of auditory temporal patterns.

Descriptors: Event-related potentials, Omitted stimuli, P300, Expectancy, Time estimation, Rhythm

The general aim of this study was to investigate how the brain processes temporal information and how a mental representation of a regular temporal sequence (or rhythm) leads to expectancies about events in the near future. This was investigated by means of evoked potentials.

Temporal information processing has been shown to involve a number of cognitive processes, such as attention, memory, anticipation, and expectancy (Desain, 1992; Karakas, 1997; Large & Jones, 1999), all being topics of interest in cognitive psychology. However, most studies concerned with temporal information processing so far have predominantly utilized motor response time experiments and judgmental rating experiments (Palmer & Krumhansl, 1990). Electroencephalography (EEG) and event-related potential (ERP) measurements, however, could have a number of advantages when studying temporal information processing and temporally driven expectancies. For example, in response time studies, response times can depend in part on the motor skill of the responder. One of the major advances of employing ERP measurements is that expectancy can be directly measured, without, for example, the interference of motor skill performance (Gaillard, 1988).

ERPs are small voltage fluctuations in the EEG resulting from sensory, cognitive, or motor-evoked neural activity and are commonly obtained by averaging EEG epochs time-locked to repetitious stimuli or events (Rugg & Coles, 1995). ERP components are typically divided into two types based on their latency (Coenen, 1995; Näätänen, 1990; Rugg & Coles, 1995). Components with latencies of up to 100 ms after stimulus onset are assumed to be primarily determined by the physical characteristics of the presented stimulus, and are therefore referred to as exogenous components (Blackwood & Muir, 1990; Shaw, 1988). The later occurring endogenous components (> 100 ms after a stimulus or event onset) are assumed to be determined by cognitive aspects of information processing (Blackwood & Muir, 1990; Gaillard, 1988; Shaw, 1988). Endogenous ERP components have long been used to explore constructs like "expectancy" and "surprise" (Donchin & Coles, 1988; Polich & Kok, 1995). ERPs to unexpected stimuli typically show a large positive wave approximately 300 ms after the onset of the unexpected stimulus, the so-called P300 (for review, see Polich & Kok, 1995). However, studying information processing by comparing endogenous ERP components like the P300 from different experimental designs is difficult because the interaction between exogenous and endogenous components results in complex waveforms (Gaillard, 1988).

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A P300-like positive wave can also be measured if a stimulus is omitted from a regular auditory temporal pattern (Bullock, Karamürsel, Achimowicz, McClune, & Basar-Eroglu, 1994; Ruchkin, Sutton, Munson, Silver, & Macar, 1981). Because these elicited omission evoked potentials, or OEPs, are elicited by the absence of a stimulus they consist entirely of endogenous components. Therefore, these OEPs can be wholly attributed to aspects of information processing involved with the (internal) event of stimulus omission (Blackwood & Muir, 1990; Takasaka, 1985). The omitted stimulus paradigm therefore provides an elegant and straightforward tool to selectively elicit endogenous ERP components. In addition, automatic mismatch responses (MMN) have been elicited by partial and total stimulus omissions (Hughes et al., 2001; Mustovic et al., 2003; Nordby, Hammerborg, Roth, & Hugdahl, 1994; Nordby, Roth, & Pfefferbaum 1988; Rüsseler, Altenmuller, Nager, Kohlmetz, & Munte, 2001; Yabe et al., 1998).

OEPs have been measured in human subjects by several researchers (Alain, Richer, Achim, & Saint Hilaire, 1989; Besson, Faïta, Czternasty, & Kutas, 1997; Bullock et al., 1994; Chao, Nielsen-Bohlman, & Knight, 1995; Janata, 2001; Jocoy, Arruda, Estes, Yagi, & Coburn, 1998; Kreitschmann-Andermahr et al., 1999; Nittono, Bito, Hayashi, Sakata, & Hori, 2000; Ruchkin et al., 1981; Simson, Vaughan, & Ritter, 1976; Takasaka, 1985; Tarkka & Stokic, 1998; Tervaniemi, Saarinen, Paavilainen, Damilova, & Näätänen, 1994; Yabe, Tervaniemi, Reinikainen, & Näätäten, 1997), and have been elicited using auditory (Ruchkin et al., 1981; Rüsseler et al., 2001) and visual stimuli (Bullock et al., 1994). OEPs are understood to reflect expectancy and are strongly influenced by attention (Besson et al., 1997; Blackwood & Muir, 1990; Bullock et al., 1994; Takasaka, 1985). Expectancy depends to a large degree upon memory and sense of time (Ruchkin et al., 1981; Ruchkin, McCalley, & Galser, 1977; Takasaka, 1985; Yabe et al., 1997).

Though several studies have found that high expectancy of a target event decreases the ERP P300 component (Kotchoubey, Grözinger, Kornhuber, & Hornhuber, 1997; Munson, Ruchkin, Ritter, Sutton, & Squires, 1984) our study is, to our knowledge, the first to explore these effects on the OEPs P300. Thus, when the event of stimulus omission occurs unexpectedly, high amplitude OEPs should be elicited. However, when the event of stimulus omission can be expected, low amplitude OEPs P300 or no OEPs P300 should occur.

In addition, we examined the effects of rhythmic training on the generation of OEP components. Musicians are generally found to be both more accurate and consistent in their responses compared to non-musicians (Aschersleben, 2002; Jongsma, Quian Quiroga, & Van Rijn, 2004). Possibly, musical training makes it easier to predict an upcoming stimulus. Therefore, we hypothesize OEPs will be different within musicians than in non-musicians.

OEPs P300 are conventionally obtained by averaging over a large number of trials. Although a component of interest may occur in individual trials, these components could become smeared in the average OEPs due to latency jitter. Musicians are generally found to be both more accurate and consistent in their responses compared to non-musicians (Aschersleben, 2002; Jongsma, Quian Quiroga, et al., 2004). In line, Rüsseler et al. (2001) also reported larger MMN to omitted sounds in musicians then in non-musicians. Therefore, in this study, we measured OEPs in both musicians and non-musicians. We hypothesize that musicians will respond with higher amplitude OEPs than non-musicians.

Thus, the general aim of this study was to investigate how the brain processes temporal information and how a mental representation of a regular temporal sequence (or rhythm) leads to expectancies about events in the near future. This was investigated by means of measuring evoked potentials in both musicians and non-musicians.

Methods

Participants

Fifteen musicians and 15 non-musicians took part in the experiment. Only healthy adults, not using medication and without a neurological history, were accepted. All participants signed a written statement of informed consent. They were not allowed to drink coffee or smoke cigarettes prior to the experiment. From each group, 3 participants were excluded due to loss of data (due to motoric artifacts in more then 50% of the trials, loss of behavioral data, or incomplete recording session). The data of the 12 remaining participants from each group were further analyzed.

The 12 musicians consisted of six drummers and six bass guitarists. They had on average 15.6 ± 11.2 (mean ± *SD*) years of musical experience and a mean age of 32.7 ± 12.7 (mean ± *SD*) years. The 12 non-musicians had no formal music or dance education, and had a mean age of 23.1 ± 4.08 (mean ± *SD*) years.

The participants sat comfortably in a chair during the experiment and were instructed to keep their eyes closed, to blink as seldom as possible, and to sit as still as possible. Participants were tested in an electrically shielded, sound-attenuated, dimly lit cubicle (inside dimensions: 2 × 2.2 × 2 m). A speaker was placed on a table in front of the participant that was used for the presentation of auditory stimuli. A tap pad, used to register the motor response, was situated on the table in comfortable reach of the participants' dominant hand. The stimuli were presented via a loudspeaker at a distance of 1 m in front of the participant. The sound consisted of a short "high woodblock" (General MIDI) percussion sound (1 ms attack, 10 ms decay to 6 dB below peak level) presented at a sound pressure level of 81 dB at the participants' position. The sound level of the last three stimuli of each trial was gradually decreased, indicating the end of a trial.

Experimental Design

A visual image of the paradigm is presented in Figure 1. A total of 90 trials were presented in random order. Each trial consisted of a regular pattern of beats in which five beats were omitted, with a fixed interstimulus interval (ISI) between beats and omitted beats of 800 ms. The first omitted beat of each trial was preceded randomly by between three and seven beats. Three trial types were used: omitted beats were interspersed, per trial, either by one, two, or three beats. A variable intertrial interval of 2.5–3.5 s was used. As a control measure, the EEG following each trial was marked as a sixth omitted beat (omission onset at 1 s preceding the first beat of the following trial). This sixth control omitted beat was taken into account because the stimulus characteristics were the same as for the other omitted beats (namely, just silence), the number of control omitted beats ($n = 90$) was the same as the experimentally omitted beats, and, finally, they were obtained during the same recording session, thus controlling for, for example, changes in level of vigilance. These control OEPs allowed us to test whether or not the applied method of wavelet denoising would result in artifact ERP components due to its settings. The task of the participants was to silently count the five

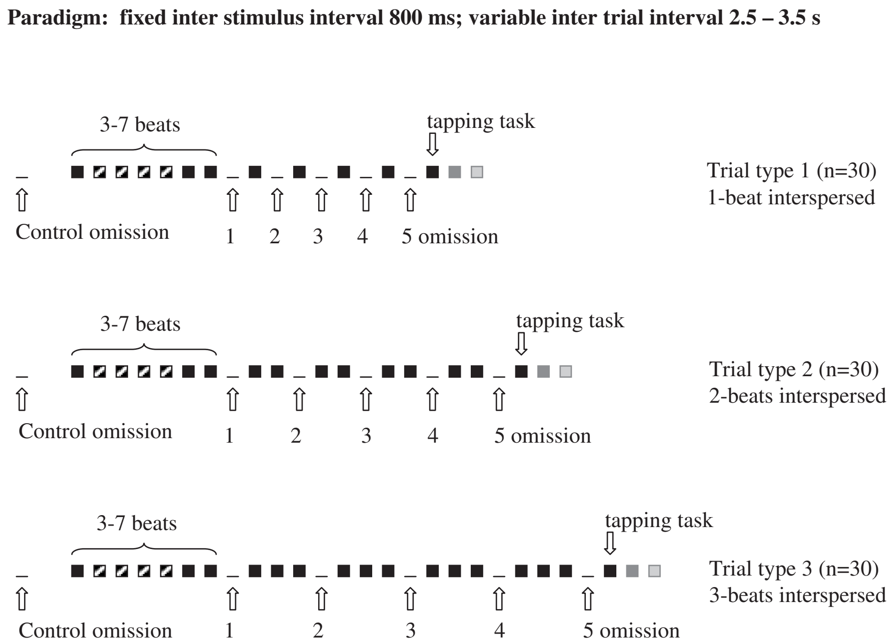

Figure 1. Diagram of the presented stimulus material. The first omitted beat of each trial was preceded randomly by three to seven beats. Omitted beats were interspersed, per trial, either by one, two, or three beats with a fixed 800 ms ISI and a variable 2.5–3.5 s intertrial interval. EEG following each trial was treated as a control omitted beat (number 6 of each trial, omission onset at 1 s preceding the first beat of the following trial). Participants had to silently count the five omitted beats and to tap along with the first beat after the fifth omission.

omitted beats and to tap along with the first beat after the fifth omission, thus making it possible to measure timing consistency. The fifth omission was followed by three more beats, with a decay in sound level, thus indicating the end of each trial.

EEG Recordings

EEG was registered with tin electrodes mounted in an elastic electrode cap (Electrocap International). EEG was derived from Fz, Cz, Pz, FP1, FP2, F3, F4, F7, F8, C3, C4, T7, T8, P3, P4, P7, P8, O1 and O2, according to the 10–20 electrode system (Jasper, 1958). Electrodes were off-line re-referenced to estimated mastoids (F7-P7 for LM; F8-P8 for RM). A ground electrode was placed on the forehead. Horizontal EOG recordings were made from the outer canthus of the left and right eyes; vertical EOG recordings were done from electrodes placed infra and supra orbital to the left eye. Electrode impedance of all cortical electrodes was less than 3 kΩ and impedance was less than 5 kΩ for EOG electrodes. EEG and EOG were filtered between 0.016 and 100 Hz, sampled at 500 Hz and off-line filtered with a low pass of 45 Hz. EEG was recorded continuously and off-line segmented around the markers.

Statistical Analyses

The EEG was visually checked off-line for EOG activity and other artifacts. Segments containing artifacts were excluded from further analysis. The EEG fragments time-locked to omission onsets were averaged for each trial type ($n = 3$) and omission position ($n = 6$) within a trial, thus resulting in 18 separate averages for each individual. Averaged OEPs elicited by the first omitted beat of all trials ($n = 90$) contained an N150 (maximum at Cz), a P400 (maximum at Pz), and an N600 (maximum at Fz). Scalp topographies were constructed using the average values in three 100-ms-wide time windows (100–200 ms for N150, 350–450 ms for P400, and 550–650 ms for N600). For the sake of data reduction, only data from midline sites (Fz, Cz, and Pz) were further analyzed. All individually averaged omissions were denoised by means of a recently proposed algorithm based on the wavelet transform (Quian Quiroga & Garcia, 2003). The accuracy of this method to smooth ERPs has been demonstrated with both simulated data as well as visual and auditory ERP data (Jongsma, Quian Quiroga, et al., 2004; Quian Quiroga & Garcia, 2003; Sambeth, Maes, Quian Quiroga, Van Rijn, & Coenen, 2004). Denoising parameters were the same for all participants. Because OEP peaks diminished rapidly within a trial, individual peak amplitudes and latencies were determined on OEPs elicited by all first beat omissions of all trials ($n = 90$). Individual peak latencies were kept constant hereafter. *T* tests were performed on peak latencies to test group differences. For all following OEPs, amplitudes at thus determined latencies were further analyzed. A repeated-measures ANOVA was performed for each component, with group (musicians vs. non-musicians) as a between-participant factor and with electrode site (Fz, Cz, Pz), interspersed beats (one-beat, two-beat, three-beat), and omitted beat position within a trial (first, second, third, fourth, fifth, and control omitted stimulus) as within-participant factors. Post hoc ANOVAs were performed to determine omission and beat effects for each group at each electrode site separately when appropriate.

In addition, grand average auditory evoked potentials were constructed of all AEPs preceding and following omissions (pooled over trial type), for both groups. AEPs contained a clear N_1 (latency ca. 100 ms, max at Fz), a P_2 (latency ca. 150 ms, max at Cz) component and an N_2 (latency ca. 270 ms, max at Cz) component. For each AEP component, component latencies were analysed using a repeated-measures ANOVA with group (musicians vs. non-musicians) as a between-participant factor and with order (preceding, following) and omitted beat position within a trial (first, second, third, and fourth omitted stimulus) as within-participant factors. For each AEP component, component amplitudes were analysed using a repeated-measures ANOVA with group (musicians vs. non-musicians) as a between-participant factor and with electrode site (Fz, Cz, Pz), order (preceding, following), and omitted beat position within a trial (first, second, third, and fourth omitted stimulus) as within-participant factors. AEPs preceding and following fifth omissions were not taken into account because AEPs in response to beats following fifth omissions contained motoric contamination due to response initiation. AEPs preceding and following control omissions were not taken into account because no AEPs preceding control omissions could be obtained. Post hoc ANOVAs were performed when appropriate. *SD*s of behavioral response times were also analysed (Jongsma, Quian Quiroga, et al., 2004).

Results

OEPs

Figure 2 shows the grand average AEPs (pooled over trial types) and OEPs (per trial type) at midline sites of both non-musicians (dotted lines) and musicians (solid lines). Figure 3 shows scalp distributions (pooled over trial types) of the OEP N150, P400, and N600 for both non-musicians (Figure 3, left panel) and musicians (Figure 3b, right panel). Table 1 summarizes all significant F and p values ($p < .05$) of OEPs component amplitudes (in bold). In addition, trends toward significant values ($p < .1$) are also listed in the table. Table 2 summarizes all significant F and p values of AEPs component latencies and amplitudes. Figure 4 the OEP N150, P400, and N600 component amplitudes for both non-musicians and musicians and post hoc results (all $p < .05$).

No group effects with respect to OEP peak latencies were observed. No main group effects with respect to OEP peak amplitudes were observed. However, main omission effects were observed for the OEPs N150 and P400 components (see Figure 4). In addition a trend toward an omission effect was observed with respect to the OEPs N600 component. Also a main lead effect was observed with respect to all three components, though this effect was only minorly significant ($p < .1$) with respect to the N150 and P400. Finally, a trend toward a beat effect was observed with respect to the P400.

Because interaction effects or trends toward interaction effects ($p < .1$) with both lead and group were observed for all three components (for summary see Table 1), post hoc two-within ANOVAs (interspersed beats: three levels; omitted beat position within a trial; six levels) were performed per group, per electrode site.

Post hoc analyses (see Figure 4) revealed that with respect to the N150 component amplitude an omission effect occurred within the group of musicians at Fz and Cz such that the N150 was larger (more negative) in response to the first stimulus omission than to later occurring stimulus omissions within a trial (see Figure 4, left column). Within the group of non-musicians both an omission effect and a beat effect occurred with respect to the N150 at Cz such that the N150 was larger (more negative) in response to the first stimulus omission than to later occurring stimulus omissions within a trial and N150 was slightly more negative with two beat trials than with one or three beat trials.

With respect to the OEP P400 component amplitudes, significant omission effects were observed within the group of non-musicians at Fz, Cz, and Pz such that P400 was larger in response to the first two omissions than to later occurring stimulus omissions within a trial. Within the group of musicians this effect was observed at Fz and was minorly significant ($p < .1$) at Cz. Interestingly, at Pz, the group of musicians showed both a significant omission effect and a beat effect, such that amplitudes were maximal within one beat trials, medium in two beat trials, and minimal in three beat trials. A closer look at the data revealed that this effect was most visible in response to the second omission in a trial where P400 was highest within one-beat-interspersed trials, lower within two-beat-interspersed trials, and had disappeared within three-beat-interspersed trials (see also Figure 4, middle panel in the bottom row).

With respect to the N600 only within the group of musicians at Fz was an omission effect and a beat effect observed within the group of musicians such that N600 was larger (i.e., more negative) in response to both the first and the last stimulus omission than to the in-between stimulus omissions within a trial at Fz (see Figure 4, last column, third panel from the bottom). In line with the P400, amplitudes were maximal within one beat trials, medium in two beat trials, and minimal in three beat trials at Fz. Instead of an N600 component, we observed a positive peak in this time window within the group of non-musicians over Cz and Pz (see Figure 4, last comlun, second and third panels from the top). However, this late positive component had only a minor significant omission effect ($p < .1$), such that, like the P400, amplitudes were larger in response to the first two omissions than to later occurring stimulus omissions within a trial.

AEPs

With respect to the N1 latency, an Order $\times$ Group interaction was observed. Post hoc repeated-measures ANOVAs were performed per group with omitted beat position within a trial (first, second, third, fourth) and order (preceding, following) as within-participant factors. These analyses revealed an order effect only for musicians ($p < .05$), such that N1 latencies of AEPs following omissions were shorter in comparison to N1 latencies of AEPs preceding omissions.

With respect to the N1 amplitude a main order effect, and an Order $\times$ Omission interaction were observed. Post hoc repeated-measures ANOVAs were done per omission with electrode site (Fz, Cz, Pz) and order (preceding, following) being the within-participant factors. An order effect was revealed only for the first omission ($p < .05$), such that N1 amplitudes of AEPs following the first omissions were increased in comparison to N1 amplitudes of AEPs preceding first omissions.

With respect to the AEP P2 component, main effects of omission, order, and lead were observed. In addition, interaction effects of Lead $\times$ Group and Lead $\times$ Order were observed.

Post hoc repeated-measures ANOVAs, per lead and per group separately,with omission (first, second, third, fourth) and order (preceding, following) as within-participant factors revealed no effects whatsoever within the group of non-musicians. However, within the group of musicians, order effects were observed at Fz and Cz leads, such that P2 amplitudes of AEPs following omissions were increased compared to P2 amplitudes of AEPs preceding omissions.

Discussion

In this study, an expanded omitted stimulus paradigm was used in order to determine whether varying the expectancy of the omitted stimuli could modulate the amplitude of the OEP components. In addition, we examined the effects of rhythmic training on the generation of OEPs.

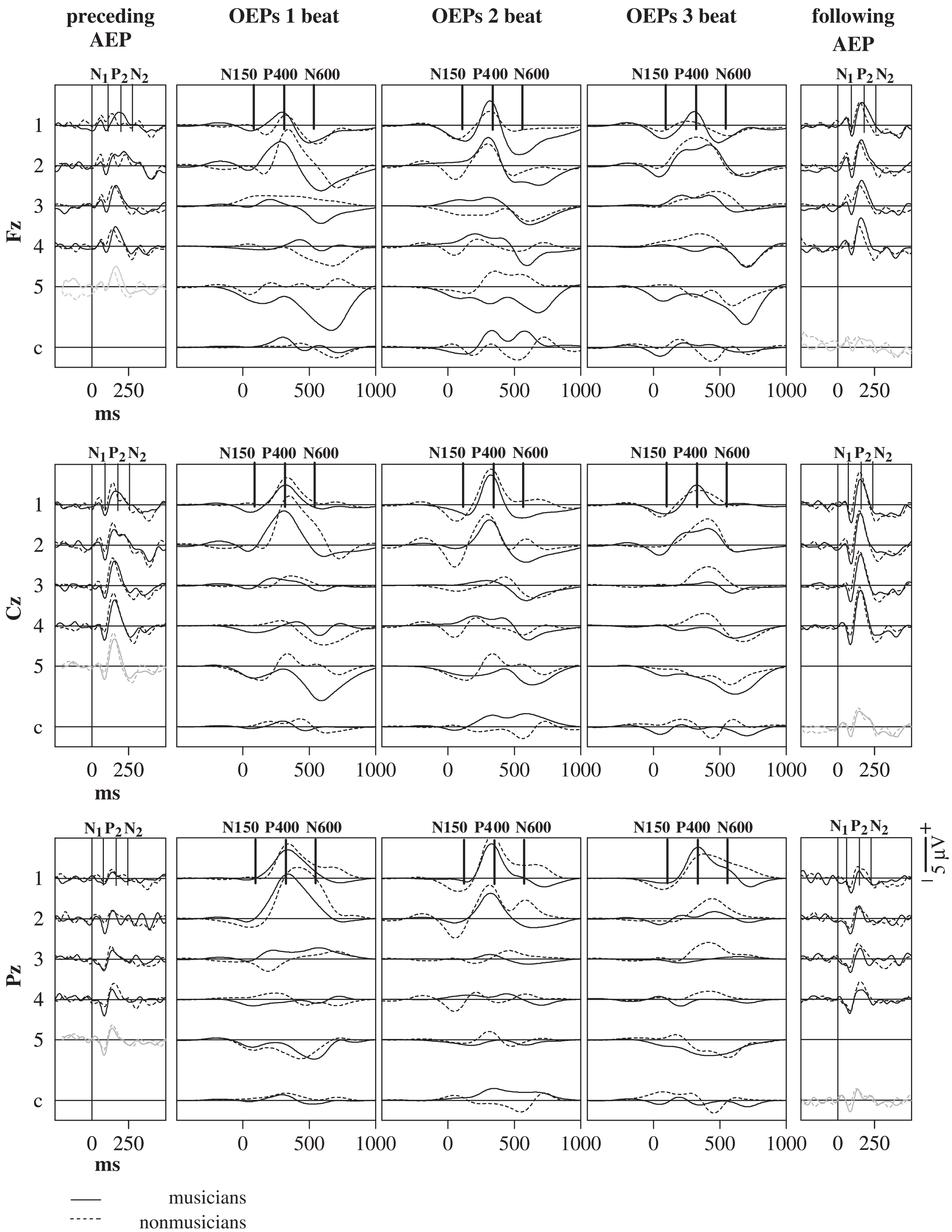

Figure 2. Grand averages. From left to right: grand average AEPs to beats preceding omitted stimuli (pooled over trial type) followed by grand average OEPs elicited by omitted stimuli within one-, two-, and three-beat-interspersed trials, respectively, and at the right grand average AEPs to beats following omitted stimuli (pooled over trial type). Grand average AEPs and OEPs are depicted for Fz, Cz, and Pz (from top to bottom of both non-musicians ($n = 12$; dotted lines) and musicians ($n = 12$; solid lines). The x-axis shows time (in milliseconds) in relation to omission or beat onset (at 0). The y-axes shows the position of the omitted stimulus within a trial (1–5) and the control OEPs (c).

The OEPs N150

In this study, an N150 in response to the first omitted stimulus of a trial was observed but diminished rapidly on following omitted stimuli. Earlier studies on omitted stimuli focused on the P300-like component to an omission (see also Donchin, 1981; Ruchkin & Sutton, 1978; Ruchkin, Sutton, & Tueting, 1975; Simson et al.,

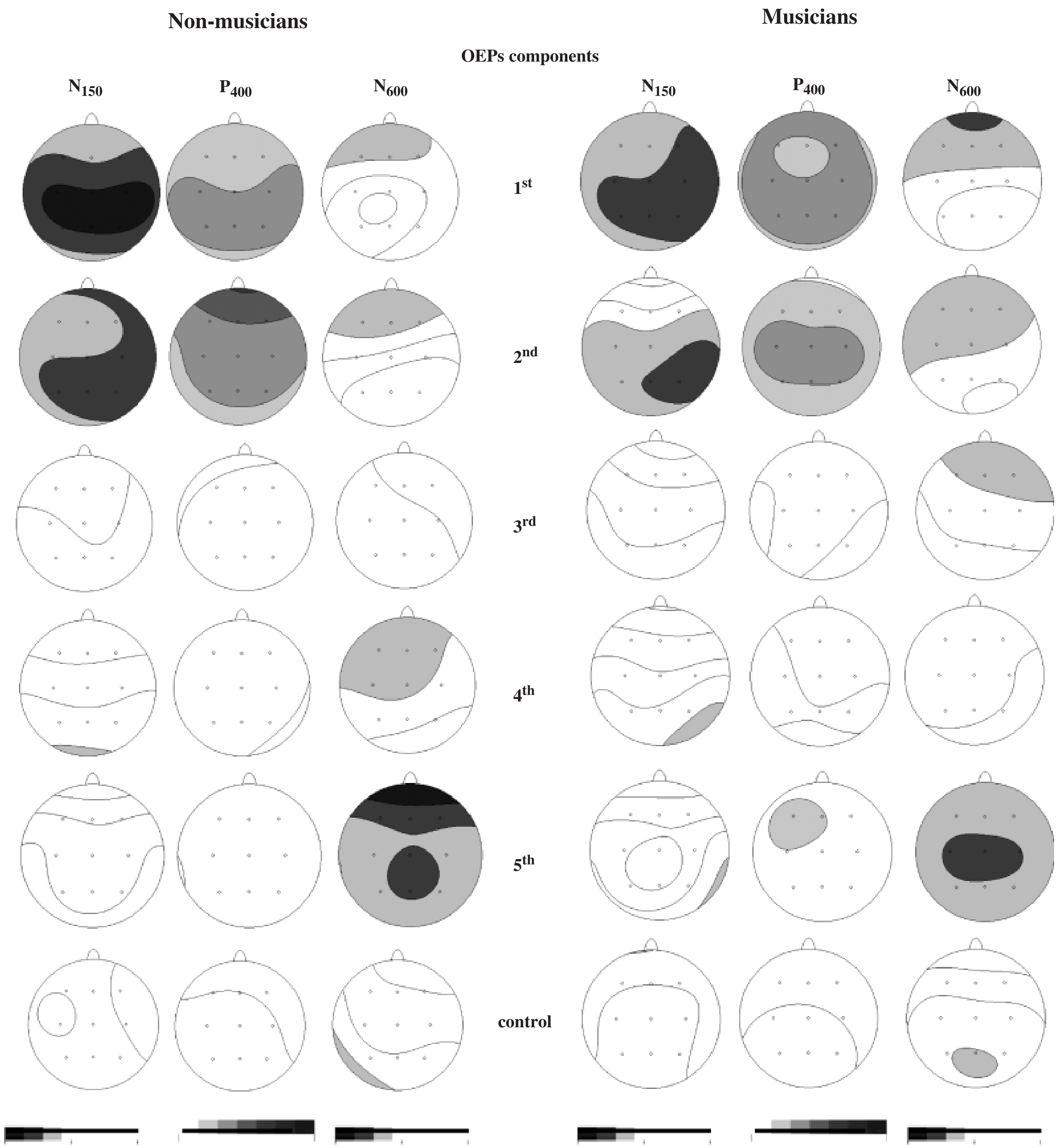

Figure 3. Scalp distributions of the OEPs for both non-musicians (left panel) and musicians (right panel). Scalp distributions are given for all six OEPs pooled over trial type. Scalp topographies were constructed using the average values in three 100-ms-wide time windows (100–200 ms for N150, 350–450 ms for P400, and 550–650 ms for N600). Coloring was kept constant. From dark to light: $-2\ \mu$V to $0\ \mu$V for the N150, $4\ \mu$V to $0\ \mu$V for the P400, and $-2\ \mu$V to $0\ \mu$V for the N600. The rapid disappearance of components over consecutive omitted stimuli is thus clearly visualized.

1976; Sutton, Tueting, Zubin, & John, 1967). Though others have also reported the elicitation of an earlier negative wave, peaking between 120 and 200 ms (Besson & Faïta, 1995; Nittono et al., 2000), this component has until now not been discussed in much detail.

Though automatic mismatch responses (MMN) have been elicited by partial and total stimulus omissions (Hughes et al., 2001; Mustovic et al., 2003; Nordby et al., 1988, 1994; Yabe et al., 1998), the upper limit to the ISI to elicit such responses seems to be around 200 ms. Therefore, it is unlikely that the N150 elicited in the current experiment, applying an 800-ms ISI, can be related to automatic mismatch responses (Nordby et al., 1988).

An alternative explanation is to view the OEPs N150 component as an early N2b-like potential reflecting general

Table 1. *Summary ANOVA Results OEPs*

	ANOVA results	*F* values	*p* values
OEPs N150			
Main effects	Omission	$F(5,18) = 6.08$	= **.002**
	Lead	$F(2,21) = 3.34$	= .055
Interaction effects	Beat × Group	$F(2,21) = 11.46$	= **.015**
	Lead × Omission	$F(10,13) = 2.32$	= **.012**
OEPs P400			
Main effects	Omission	$F(5,18) = 2.56$	< **.001**
	Beat	$F(2,21) = 2.80$	= .084
	Lead	$F(2,21) = 3.06$	= .068
Interaction effects	Lead × omission	$F(10,13) = 2.39$	= .072
	Lead × beat × group	$F(4,19) = 2.52$	= .075
OEPs N600			
Main effects	Omission	$F(5,18) = 2.20$	= .099
	Lead	$F(2,21) = 17.63$	< **.001**
Interaction effects	Omission × Lead	$F(10,13) = 8.52$	< **.001**
	Beat × Lead × Omission	$F(20,3) = 21.31$	= **.014**
	Beat × Lead × Omission × Group	$F(20,3) = 5.80$	= .086

The table summarizes significant *F* and *p* values (bold) of ANOVA results for the OEPs component amplitudes. In addition, trends toward significant values are also listed in the table.

orienting reactions (Raij, McEvoy, Mäkelä, & Hari, 1997). Such a view appears to be in line with the current literature concerning the N2 component, first, because of the strong association of N2b and P3 components elicited by oddball deviants (Loveless, 1986; Näätänen, 1992), which appears to apply also to OEPs (Raij et al., 1997; Simson et al., 1976). Second, the fact that the N150 observed here was maximal over central leads is in favor of an N2b-like component. The significant interaction effect showing that musicians had a larger N150 amplitude elicited by the first omitted stimulus within a trial might thus be explained by larger orienting reactions in this group (Raij et al., 1997).

The OEPs P400

The most salient component of the OEPs appeared to be a large P400. The classical P3 component (occurring between 200 and 600 ms after onset of a target stimulus) has long been used to explore constructs like "expectancy" and "surprise" (Donchin & Coles, 1988; Polich & Kok, 1995). Indeed, P400 disappeared rapidly in response to expectedly omitted beats.

Table 2. *Summary ANOVA Results OEPs*

	ANOVA results	*F* values	*p* values
AEP N1 latencies			
Interaction effects	Order × Group	$F(1,22) = 5.09$	= **.034**
AEP N1 amplitudes			
Main effects	Order	$F(1,22) = 10.98$	= **.003**
Interaction effects	Order × Omission	$F(3,20) = 3.45$	= **.036**
AEP P2 amplitudes			
Main effects	Omission	$F(3,20) = 3.62$	= **.031**
	Order	$F(1,20) = 21.97$	< **.001**
	Lead	$F(2,21) = 71.64$	< **.001**
Interaction effects	Lead × Group	$F(2,21) = 3.53$	= **.048**
	Lead × Order	$F(2,21) = 11.75$	< **.001**
AEP N2 amplitudes	—	—	—

The table summarizes *F* and *p* values of ANOVA results for the AEPs component latencies and amplitudes.

Within the current literature a distinction between a P3a and P3b component has been made. That is, the P3a, or novelty P3, exhibits an anterior/frontal scalp distribution and precedes the P3b with a maximum amplitude over the central/parietal areas (Comerchero & Polich, 1999). Conventionally, the P3a is elicited by unattended or attended yet ignored salient stimuli (Escera, Alho, Winkler, & Näätänen, 1998) whereas the P3b is thought to be related to the capture of attention by salient events and of great interest to an investigation of automatic as opposed to controlled processes. In this study, a P3b-like component (namely, maximal over Pz with a latency of 400 ms) emerged in reaction to unexpectedly omitted beats. This is in line with previous experiments using ERPs to study music processing reporting that unexpected or "wrong" notes at the end of a melody elicit a late positive component comparable to a P3b (Besson & Faïta, 1995). Therefore, this component has been proposed to be a good electrophysiological marker of (e.g., musical) expectancy.

Based on the regularity of the isochronous series of beats at the beginning of each trial, a beat was expected at the moment that the first omission occurred. In accordance, a large N150 and P400 component emerged in response to these first, unexpectedly omitted beats. Because the number of beats between the first and second omission defined the pattern for a given trial, it was possible to predict the occurrence of the third through fifth omitted stimulus in all *three* trial types. Indeed, no visible OEPs emerged in response to these expectedly omitted beats. The exact moment of the occurrence of the second omission in a trial was also unpredictable (either one, two, or three beats could be interspersed between two consecutive omitted beats) However, because the occurrence of the first omission was an indication that the chain of omissions had begun, an expectancy for a second omission could be formed although the exact moment in time could not be predicted. Large OEPs P400 emerged in response to these second, unpredictable omissions. As one would expect, P400 in response to the second stimulus omission appeared to be maximal for the one-interspersed-beat trials and medium within the two-interspersed-beat trials. Within three-interspersed-beat trials, OEPs P400 seems to have disappeared. This effect reached significance at Pz within the group of musicians, but not within the group of non-musicians.

This is interesting because it suggests that musicians, because of their experience with auditory patterns, may be more aware of the fact that an omission must necessarily follow after three interspersed beats, and thus seem to be more able to take into account higher order characteristics of the presented stimulus material.

Others have also reported differences in ERPs between musicians and non-musicians with regard to, for example, superior detection of temporal deviations in musicians (Jongsma, Desain, & Honing, 2004; Rüsseler et al., 2001), detection of pitch and harmony (Koelsch, Schroger, & Tervaniemi, 1999) and temporal and harmonic incongruities (Besson & Faïta, 1995). Others, however, failed to find differences in detection of harmonic incongruities (Regnault, Bigand, & Besson, 2001).

The OEPs N600

Although a main group effect was absent, post hoc analyses to unravel the four-way interaction between all factors showed that musicians had more negative N600 amplitudes than non-musicians at fronto-central sides following the first two and the last omitted stimulus within a trial.

With respect to the first omitted stimuli, this component might correspond to the "frontal slow wave" (McCallum, Curry,

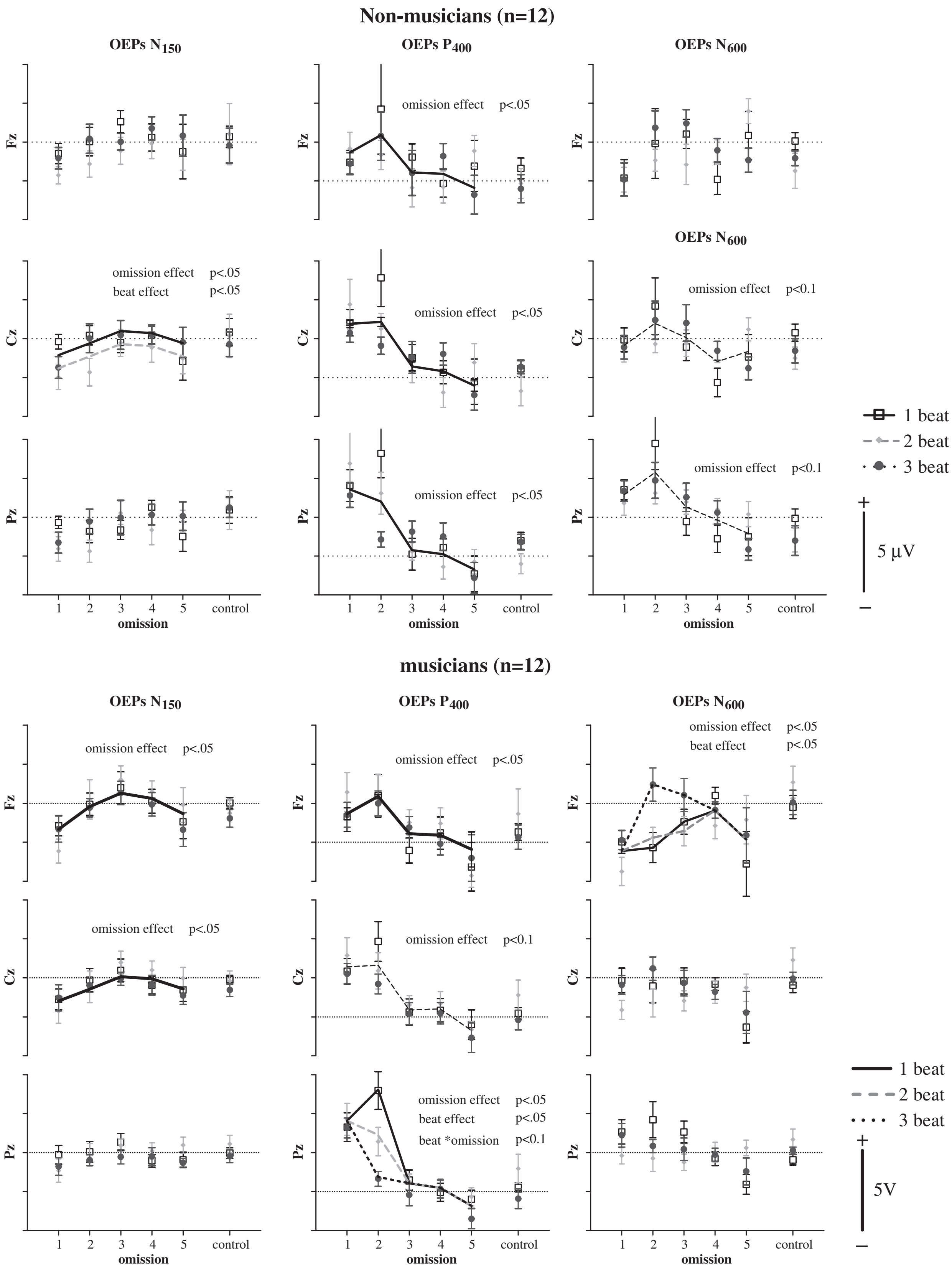

Figure 4. The OEPs component amplitudes of both non-musicians (top) and musicians (bottom) at Fz, Cz, and Pz, for the OEPs N150, P400, and N600. Significant effects of omission position and interspersed beats are added where appropriate. Amplitudes collected from one-beat-interspersed trials are depicted by open squares, two-beat-interspersed trials by gray diamonds, and three-beat-interspersed trials by dark gray circles. Whenever post hoc tests showed significant omission or beat effects, connecting lines were added to the concurrent panel.

Cooper, Pocock, & Papkostopoulos, 1983; Näätänen, 1992) associated with maintaining a task set in memory. This process seems to follow the findings of the P400 component such that N600 in response to the second omitted beat appeared to be maximal for the one-interspersed-beat trials, medium within the two-interspersed-beat trials, and had disappeared within three-interspersed-beat trials.

With respect to the last omitted stimulus, the N600 component preceded the motor response to "tap along with the first beat after the fifth omitted stimulus." This component can therefore be considered to be a motor-locked readiness potentials' negative slope (NS′; Brunia & van Boxtel, 2000). Ordinarily, this component is observed whenever the ERP wave is time-locked to the motor response, occurring some 800 ms after the omitted stimulus, making this a negative wave preceding the motor response by ca. 200 ms. However, within our group of non-musicians, no such component was observed. We propose that this difference can be ascribed to the reduced latency variability of motor responses within the group of musicians (Jongsma, Quian Quiroga, et al., 2004). This way, more response-locked activity remains visible in the OEPs that is time-locked to the preceding event of an omitted stimulus.

Instead of an N600 component, we observed a positive peak in this time window within the group of non-musicians at Cz and Pz. In addition, though only marginally significant, this "P600" showed the same pattern as the P400 component at Cz within this group (e.g., such that *it was* maximal after the first two "unexpectedly" omitted stimuli and decreased from the third to the fifth omitted stimulus. In addition, inspection of the grand average *ERP*s at Pz shows a broader (and occasionally double) peak ranging between 400 and 600 ms for the group of non-musicians. Because latencies up to 600 ms are not uncommon for the P3b component (e.g., Alain, Arnott, & Picton, 2001) we argue that this peak can be seen as an extended P3b component within the group of non-musicians, possibly meaning that the task at hand is perceived as being more complex for this group (Coulson, King, & Kutas, 1998).

AEP Effects

Although the scope of the current article concerns OEPs, AEPs on beats preceding and following omitted beats were also obtained and will be briefly discussed. Again, no main group effects with respect to AEP components were observed. However, we did observe order effects with respect to the N1 such that N1 amplitudes were increased and latencies decreased after an omission. This is in line with findings of Nittono et al. (2000). In addition, P2 amplitudes were also increased after an omitted beat. Order effects on N1 and P2 peak amplitudes were more pronounced within the group of musicians.

When stimuli are presented in a close (0.5–5 s) temporal relationship, commonly, an AEP amplitude decrement of the later AEP responses relative to the first AEP response is found. This response suppression has been referred to as gating (Freedman, Adler, Waldo, Pachtman, & Franks, 1983; Noldy, Neiman, El-Nesr, & Carlen, 1990) and has been most often described with respect to an early P50 component amplitude (Light & Braff, 1998) though similar effects on later AEP components have also been reported (Besson & Faïta, 1995; Jongsma et al., 2000; Jongsma, Van Rijn, Dirksen, & Coenen, 1998) and have been proposed to reflect recovering phenomena or the physiological refractory period (Nittono et al., 2000). Therefore, when a train of stimuli is discontinued, one would expect a recovery in AEP amplitude to the first stimulus after an omission has occurred (Jongsma et al., 1998; Jongsma, Coenen, & Van Rijn, 2002).

This is in line with our observed effects of the AEP component amplitudes. We found an order effect for the N1 amplitude within our group of musicians. The AEP N1 component is known to reflect an aspect of attention (Näätänen, 1990). One could therefore argue that within the group of musicians more attention is directed toward beats following omissions, possibly due to the task—of counting the omitted beats—at hand.

In line, the order effects on P2 amplitude were also more pronounced within our group of musicians. Interestingly, Shahin, Bosnyak, Trainor, and Roberts (2003) reported an enhancement of the AEP P2 in musicians elicited by tones. In addition, the P2 has been found to be sensitive to neuroplastic remodeling reflecting improved perception (Tremblay, Kraus, McGee, Ponton, & Otis, 2001). Possibly, this might explain why P2 order effects were more pronounced within our group of musicians

In this study OEPs were elicited within a new oddball paradigm, studying modulating effects of expectancy on the generation of OEPs. In reaction to unexpectedly omitted stimuli, clear OEPs were elicited consisting of three clearly discernable peaks: an N150, a P400, and an N600 component. Though a P3-like component has long been known to appear in reaction to unexpectedly omitted stimuli, the N150 and N600 OEPs components have been less extensively described. We found that OEPs components rapidly diminished when the event of an omitted stimulus could be expected. In addition, the N600 increased on an expectedly omitted stimulus at the end of the trials related to response initiation.

In addition, we recorded OEPs within a group of musicians and a group of non-musicians. Due to their rhythmical expertise musicians showed a more pronounced N150 in response to the first omitted stimulus, suggesting a stronger orienting reaction within this group. In addition, the P400 showed more refined modulations of the paradigm, showing higher order pattern recognition capabilities within this group. Finally the N600 in response to the last omitted stimuli was associated with a decrease in response variability within this group. Thus, musical training seems to lead to more efficient and more refined processing of auditory temporal patterns.

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