

Absolute Pitch: Evidence for Early Cognitive Facilitation during Passive Listening as Revealed by Reduced P3a Amplitudes

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Abstract

■ Absolute pitch (AP) is the rare ability to identify or produce different pitches without using reference tones. At least two sequential processing stages are assumed to contribute to this phenomenon. The first recruits a pitch memory mechanism at an early stage of auditory processing, whereas the second is driven by a later cognitive mechanism (pitch labeling). Several investigations have used active tasks, but it is unclear how these two mechanisms contribute to AP during passive listening. The present work investigated the temporal dynamics of tone processing in AP and non-AP (NAP) participants by using EEG. We applied a passive oddball paradigm with between- and within-tone category manipulations and analyzed the MMN reflecting the early stage of auditory processing and the P3a response reflecting the later cognitive mechanism during the second

processing stage. Results did not reveal between-group differences in MMN waveforms. By contrast, the P3a response was specifically associated with AP and sensitive to the processing of different pitch types. Specifically, AP participants exhibited smaller P3a amplitudes, especially in between-tone category conditions, and P3a responses correlated significantly with the age of commencement of musical training, suggesting an influence of early musical exposure on AP. Our results reinforce the current opinion that the representation of pitches at the processing level of the auditory-related cortex is comparable among AP and NAP participants, whereas the later processing stage is critical for AP. Results are interpreted as reflecting cognitive facilitation in AP participants, possibly driven by the availability of multiple codes for tones. ■

INTRODUCTION

Music perception relies principally on understanding tone relations. Therefore, music tuition primarily aims at promoting a well-developed relative pitch (RP), meaning the ability to identify or produce tone intervals (Takeuchi & Hulse, 1993). Most interestingly, there are only a few humans who are able to categorize pitches effortlessly. Such individuals possess the rare ability called absolute (or perfect) pitch (AP), which is defined as the ability to identify the chroma (pitch class) of a tone or to produce a specific pitch without the aid of any reference tones (Levitin & Rogers, 2005; Zatorre, 2003; Takeuchi & Hulse, 1993; Baggaley, 1974). This rare ability occurs in less than 1% of the general population (Takeuchi & Hulse, 1993), whereby Asian people speaking tonal languages have a higher incidence rate of AP (Deutsch, Li, & Shen, 2013; Deutsch, Dooley, Henthorn, & Head, 2009; Deutsch, Henthorn, Marvin, & Xu, 2006; Deutsch, Henthorn, & Dolson, 2004a; Gregersen, Kowalsky, Kohn, & Marvin, 1999). Interestingly, whereas most of the AP possessors are musicians (Deutsch et al., 2009), a handful of them possess AP in terms of a savant skill in the context of

autism (Brenton, Devries, Barton, Minnich, & Sokol, 2008; Heaton, Davis, & Happé, 2008) or Williams syndrome (Lenhoff, Perales, & Hickok, 2001). Although hearing absolutely appears to be a rare phenomenon, it is the more fundamental and rudimentary cognitive feature than relational hearing (Levitin & Rogers, 2005). This view is supported by findings on infants preferring absolute over relative cues in auditory-based tasks (Saffran & Griepentrog, 2001) and by evolutionary research suggesting that RP is the more recent ability that emerged only after the divergence between birds and mammals (Hauser & McDermott, 2003).

Meanwhile, there is evidence showing that both genetic and environmental factors contribute to the acquisition of AP (Theusch, Basu, & Gitschier, 2009; Athos et al., 2007; Baharloo, Service, Risch, Gitschier, & Freimer, 2000; Gregersen et al., 1999; Baharloo, Johnston, Service, Gitschier, & Freimer, 1998). The latter includes learning factors such as early language exposure (Deutsch et al., 2004a, 2006; Deutsch, Henthorn, & Dolson, 2004b) and the nature of musical training and exposure to music during childhood (Gregersen, Kowalsky, Kohn, & Marvin, 2001). In a similar manner as for language acquisition, there is likewise evidence for a sensitive period during which these environmental inputs determine the emergence of AP (Gervain et al., 2013; Russo, Windell, & Cuddy, 2003; Miyazaki, 1988).

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This evidence shows that the earlier one begins with musical training, the more likely it is to develop AP (Meyer et al., 2011; Deutsch et al., 2006; Gregersen et al., 2001).

According to current knowledge, at least two separable processing stages have been proposed to contribute to the ability of AP (Schulze, Mueller, & Koelsch, 2013; Levitin & Rogers, 2005; Zatorre, 2003; Levitin, 1994; Deutsch, 1987). The first one reflects the early phase of pitch encoding at the processing level of the auditory-related cortex (“pitch memory”) and refers to pitch memory within fixed categories. The second processing stage (“pitch labeling”) is assumed to rely on a conditional associative memory mechanism and to be driven by the association of categorized pitches with verbal labels or other abstract codes (Zatorre & Beckett, 1989). Normally, these memory associations are acquired as a function of musical training and music exposure during the sensitive period (Russo et al., 2003; Zatorre, 2003; Miyazaki, 1988).

Some evidence supporting the hypothesis that the first processing stage operates differently in AP musicians has been provided by previous studies indicating that AP participants perceive tones more categorically (Schulze et al., 2013; Siegel, 1974), meaning that they encode tones within narrower pitch categories (Zatorre, 2003). In this context, AP participants were shown to exhibit altered neurophysiological responses during early stages of auditory processing (Matsuda et al., 2013; Schulze, Gaab, & Schlaug, 2009; Wu, Kirk, Hamm, & Lim, 2008; Itoh, Suwazono, Arao, Miyazaki, & Nakada, 2005; Ohnishi et al., 2001; Hirata, Kuriki, & Pantev, 1999). In addition, there is some evidence pointing to a differential structural architecture in the brain networks of AP participants involved in the early stage of auditory processing (Wengenroth et al., 2013; Jäncke, Langer, & Hänggi, 2012; Loui, Zamm, & Schlaug, 2012; Loui, Li, Hohmann, & Schlaug, 2011; Oechslin, Imfeld, Loenneker, Meyer, & Jäncke, 2010; Bermudez, Lerch, Evans, & Zatorre, 2009; Wilson, Lusher, Wan, Dudgeon, & Reutens, 2009; Luders, Gaser, Jancke, & Schlaug, 2004; Keenan, Thangaraj, Halpern, & Schlaug, 2001; Schlaug, 2001; Schlaug, Jancke, Huang, & Steinmetz, 1995). Nevertheless, to date it is still a matter of debate whether the specificity of the first processing stage is restricted to AP participants only. In fact, individuals without AP also possess the rudimentary ability to memorize pitches. This has been observed, for example, when nonmusicians have to produce songs from memory (Jakubowski & Müllensiefen, 2013; Levitin, 1994) or to judge the correctness of familiar soundtracks (Schellenberg & Trehub, 2003) or even telephone dial tones (Smith & Schmuckler, 2008). In the same vein, recent evidence indicates that mental representations of tone categories in AP participants are not fixed but rather changeable (Hedger, Heald, & Nusbaum, 2013; McLachlan, Marco, & Wilson, 2013), implying a certain extent of instability. Taken together, these findings suggest that pitch memory per se does not seem to be specific for AP.

Meanwhile, there is growing evidence supporting the view that the second processing stage is the crucial psychological process where AP musicians differ from non-AP (NAP) musicians (Elmer, Sollberger, Meyer, & Jäncke, 2013; Zatorre, Perry, Beckett, Westbury, & Evans, 1998; Crummer, Walton, Wayman, Hantz, & Frisina, 1994; Hantz, Crummer, Wayman, Walton, & Frisina, 1992; Wayman, Frisina, Walton, Hantz, & Crummer, 1992; Klein, Coles, & Donchin, 1984). Evidence pointing into this direction arises, for example, from Zatorre et al. (1998), who could show that the left posterior dorsolateral pFC, a brain region involved in conditional associative learning (Petrides, Alivisatos, Evans, & Meyer, 1993; Petrides, 1990), is selectively recruited during tone listening in AP participants. In addition, previous anatomical studies pointed to a differential architecture in the posterior dorsal frontal region of AP participants compared with participants without AP (Bermudez et al., 2009; Bermudez & Zatorre, 2005). Further evidence indicating a cognitive mechanism underlying AP has been collected by using EEG, which constitutes a particularly advantageous technique for capturing temporal dynamics. In this context, previous EEG studies using active oddball paradigms revealed that AP is associated with a reduction or absence of the P300 component, probably reflecting more parsimonious memory processes (Crummer et al., 1994; Hantz et al., 1992; Wayman et al., 1992; Klein et al., 1984). Moreover, by using a conceptual association task, Elmer, Sollberger, et al. (2013) identified later-occurring cognitively related brain responses (N400 and LPC; Kutas & Federmeier, 2011; Friedman & Johnson, 2000) as reliable and specific markers for AP.

Most of the published oddball studies (Crummer et al., 1994; Hantz et al., 1992; Wayman et al., 1992; Klein et al., 1984) used active tasks for evaluating AP. By contrast, to date only few oddball studies focused on passive listening paradigms (Matsuda et al., 2013; Meyer et al., 2011; Tervaniemi, Alho, Paavilainen, Sams, & Näätänen, 1993). Passive oddball paradigms are particularly fruitful in that they permit to determine the contribution of both mechanisms without potential contaminations of explicit top-down functions (Näätänen, Paavilainen, Rinne, & Alhod, 2007; Pulvermüller & Shtyrov, 2006). Until now, all passive oddball studies focused on MMN, which is a negative-going brain response elicited at about 100–250 msec after stimulus onset in response to a detectable change (deviation) within a repetitive stream of auditory stimuli (standard; Näätänen, 2000; Näätänen, Gaillard, & Mäntysalo, 1978). The MMN is assumed to reflect preattentive auditory memory at the processing level of the auditory-related cortex (Garrido, Kilner, Stephan, & Friston, 2009; Picton, Alain, Otten, Ritter, & Achim, 2000). By using a passive paradigm, Tervaniemi et al. (1993) did not find different MMN waveforms between participants with and without AP while processing tones. By contrast, Matsuda et al. (2013) reported larger MMN amplitudes in AP participants in response to mistuned tones. The same perspective is provided by Meyer

et al. (2011), who demonstrated different MMN responses in Suzuki children with weak to moderate AP abilities.

Surprisingly, none of the previous EEG studies took advantage of the P3a response for measuring the contribution of cognitive functions to AP. This specific brain response is elicited in the context of oddball paradigms, occurs subsequently to the MMN, and is characterized by a positive-going deflection peaking at about 300 msec poststimulus onset, with a maximal current distribution over frontocentral scalp sites (Kujala, Tervaniemi, & Schröger, 2007; Escera, Alho, Schröger, & Winkler, 2000). On the basis of the observation that P3a manifestations appear at a relatively late stage of cortical processing, this component has been linked to a range of cognitive processes underlying an attentional resource allocation. In fact, the P3a response originates from stimulus-driven frontal (phasic) attentional mechanisms (Polich, 2007; Squires, Squires, & Hillyard, 1975), indexes involuntary orienting of attention (Escera et al., 2000), and reflects attentional distraction (Comerchero & Polich, 1999) and novelty processing (Friedman, Cycowicz, & Gaeta, 2001; Knight, 1996). Interestingly, the P3a response stems from a distributed limbic-cortical circuit (Knight & Nakada, 1998; Knight, 1984, 1996; Knight, Grabowecy, & Scabini, 1995), also including a multimodal brain region, namely the temporal-parietal junction (Knight, Scabini, Woods, & Clayworth, 1989). Thus, this component has been shown to constitute a marker for assessing early multimodal processing (Jancke, Rogenmoser, Meyer, & Elmer, 2012; Boll & Berti, 2009). The latter point is of relevance, in that it permits to characterize the second processing stage of AP. This appears promising considering that AP participants are assumed to process tones multidimensionally by relying on multiple mental codes for tones (Hantz et al., 1992; Zatorre & Beckett, 1989; Klein et al., 1984). This specific view is supported by an older study of Zatorre et al. (1998) showing activation in brain areas involved in multimodal processing (bilateral middle and inferior temporal cortex). Although the specific cognitive processes reflected by the P3a, as well as its independence from the posterior P300 (P3b) component, are still a matter of debate (Polich, 2007), there is at least agreement that the P3a is linked to early cognitive processing during passive and attentive-free listening (Kujala et al., 2007; Escera et al., 2000).

In the present EEG study, we applied a passive oddball paradigm with between- and within-tone category manipulations and made use of the MMN and P3a components for reevaluating the two processing stages assumed to contribute to the ability of AP. In the case that AP is principally driven by a pitch memory mechanism occurring at the processing stage of the auditory-related cortex, one would expect between-group differences in the MMN responses, especially in response to between-tone category manipulations. Alternatively, if this ability is due to a cognitive mechanism, effects are more likely to be associated with P3a responses.

METHODS

Participants

Sixteen AP (four men, mean age = 25.4 years, $SD = 9.6$ years) and 10 NAP participants (two men, mean age = 24.4, $SD = 3.0$ years, all native German speakers) participated in this study. All AP (eight string players, eight pianists) and NAP participants (five string players, four pianists, and one flutist/pianist) were professional musicians and consistently right-handed (with the exception of two in the AP group and one in the NAP group who were left-handed), as revealed by the Edinburgh Handedness Inventory (Oldfield, 1971). None of them reported any history of present or past neurological, psychiatric, or audiological disorders, and all participants had an unremarkable audiological status, as revealed by pure tone audiometry (Home Audiometer software, www.esseraudio.com/de/home-audiometer-hoertest.html). All participants denied consumption of illegal drugs or regular medication. The participants were paid for participation, the local ethics committee approved the study, and written informed consent was obtained from all participants.

History of Musical Training

History of musical training was assessed by an in-house questionnaire previously used by our research group (Elmer, Hänggi, Meyer, & Jäncke, 2013; Elmer, Sollberger, et al., 2013; Elmer, Meyer, & Jäncke, 2012). This questionnaire was adopted to evaluate the age of onset of musical practice, the primary instruments played by the musicians, the number of years of musical training, and the self-estimated number of training hours per week during every 3-year period of life. On the basis of the subjective data reported by the participants, the total number of training hours across lifespan was extrapolated for each participant.

Musical Aptitude

To control for differences in musical aptitude between the two groups, all participants performed the Advanced Measures of Music Audition test (Gordon, 1989). This test consists of 30 successive trials in which the participants have to compare pairs of piano melodies and to decide whether these are equivalent, rhythmically different, or tonally different. On the basis of biographical information (history of musical training) and the Advanced Measures of Music Audition test, we estimated musical aptitude.

AP Ability

To verify and quantify AP ability, the participants performed a pitch-labeling test previously used by our research group (Jancke et al., 2012; Oechslin, Imfeld, et al., 2010; Oechslin, Meyer, & Jäncke, 2010). During this test, participants listened to 108 pure sine wave tones presented in a pseudorandomized order and were instructed to

Table 1. Study Design

	<i>Standard Tones (420 × p = .6)</i>		<i>Deviant Tones (Each 70 × p = .1)</i>		
Block A	440 Hz	438 Hz	422 Hz	416 Hz	264 Hz
Block C	264 Hz	416 Hz	422 Hz	438 Hz	440 Hz

Deviant tones are listed from left to right according to deviation level. In block A, the first two deviant tones differed within the category of the standard tone A, whereas the last two differed in terms of novel tone categories. In block C, all deviant tones differed more than one category from standard tone C.

write down the tonal label immediately after they heard the accordant tone. The tones ranged from A3 (tuning: A4 = 440 Hz) to A5 and were presented three times each, whereby same tones were never presented successively. Each tone presented during the test had a duration of 1 sec. The ISI had a duration of 4 sec and was filled with Brownian noise. The accuracy was evaluated by counting the total number of correct responses. Semitone errors were counted as incorrect responses to increase discriminatory power. However, participants were not asked to identify the adjacent octaves of the presented tones.

Cognitive Capability

Between-group differences in intelligence were controlled by applying a short German intelligence test (Mehrfachwahl-Wortschatz Intelligenz Test [MWT-B]), which is frequently used in German-speaking countries as a standard test to measure psychometric intelligence (Lehrl, Triebig, & Fischer, 1995). This test permits to estimate crystalline intelligence in a short time and was previously shown to correlate fairly well ($r = .72$) with the global intelligence quotient in healthy adults (Lehrl et al., 1995). The MWT-B consists of 37 items, which are ordered as a function of difficulty level. For each item, the participants had to choose the unique word with a meaning out of five pseudowords.

Stimuli and Procedure

The auditory stimuli presented during EEG recording were five piano tones taken from the study of Jancke et al. (2012), namely, an A tone (fundamental frequency $f_0 = 440$ Hz), a C tone ($f_0 = 264$ Hz), an A-flat tone ($f_0 = 416$ Hz), and two mistuned tones deviating from the A tone with different degrees. One of the mistuned tones had a frequency of 438 Hz (1/10-semitone deviation), whereas the other one had a frequency of 422 Hz (3/4-semitone deviation). All piano tones lasted 200 msec, were registered as 16-bit stereo files, matched for intensity by normalizing the amplitudes, and smoothed with a rise and fall time of 5 msec to avoid an abrupt decay. All these processing steps were performed by using Praat (www.fon.hum.uva.nl/praat/) and Adobe Audition 1.5 (tv.adobe.com/de/product/audition/). During EEG recording, all auditory stimuli were delivered binaurally

with a sound pressure level of about 70 dB (Digital Sound Level Meter 329, Voltcraft) by using HiFi headphones (Sennheiser, HD 25-1, 70 Ω , Ireland).

During EEG measurements, participants were instructed to focus their attention on a silent film while ignoring the five piano tones, which were simultaneously presented. The experiment consisted of five different blocks randomly presented across all participants and the two groups. In each block, one of the five tones was presented frequently (standard tone), whereas the remaining four tones were presented occasionally (deviant tones). Each block consisted of 420 standard tones and 4×70 deviant tones. The standard tone had an occurrence probability of .6 and each deviant of .1. For EEG analyses, we focused only on the blocks in which tone A (block A) and tone C (block C) were presented as standard tones, because in these two conditions deviation levels increased or decreased unambiguously and EEG components could be studied as particular functions of deviation magnitude. Block A provides information concerning tone processing in response to within- and between-tone categories, whereas block C reflects extreme conditions in the context of between-tone categories only. The term “tone category” refers to the smallest musical tone interval used in Western music. Table 1 gives an overview of the study design.

Each block started with a sequence of 15 successive standard tones, so that a stable memory trace could be established (Horváth, Czigler, Sussman, & Winkler, 2001; Näätänen & Winkler, 1999). After that, all tones were presented in a pseudorandomized order, whereby each deviant tone was followed by at least one standard tone, the same deviant tone was never presented successively, and at least two different tones were inserted before presenting again a specific deviant tone. The ISI was of 550 msec.

EEG Recording

During EEG recording, the participants were placed in a chair at a distance of about 100 cm from a monitor. The EEG (32 channels, subset of the 10/10 system) was recorded with a sampling rate of 1000 Hz and a band pass filter from 0.1 to 100 Hz using an EEG amplifier (Brain Products, Munich, Germany). We applied sintered silver/silver-chloride electrodes (Ag/AgCl) and used the nose position as online reference. Electrode impedance was reduced to <10 k Ω by using ElectroGel conductant.

Data Analyses

Preprocessing

For all steps of digital EEG raw data processing, we used Brain Vision Analyser software (Version 2.02, Brain Products, Munich, Germany). The data were high- and low-pass filtered offline at 1–20 Hz, and artifacts were removed by using an independent component analysis (Jung et al., 2000) in association with a semiautomatic raw data inspection. For the eight deviant tones and the two standard tones (see Table 1), segments of 500-msec duration were created, including a 100-msec prestimulus period. Furthermore, a baseline correction relative to the –100 to 0 msec prestimulus time period was applied. All segments were averaged to compute ERPs. In a next processing step, the ERPs in response to the standard tones were subtracted from the ERPs elicited by the deviant tones (physically identical stimuli presented in different blocks). Furthermore, we computed multi-subject grand averages for each group and difference waves.

MMN and P3a Calculation

In the present work, we specifically evaluated MMN and P3a responses (difference waves). On the basis of the voltage distribution over the scalp (see Figure 4) and to avoid multiple comparisons between neighboring electrodes as well as to increase the signal-to-noise ratio, nine frontal electrodes were pooled into one ROI (F3, Fz, F4, FC3, FCz, FC4, C3, Cz, and C4; Jancke et al., 2012; Eichele, Nordby, Rimol, & Hugdahl, 2005). The time windows (TWs) used for analyzing the MMN and the P3a responses were defined separately for each group and deviant condition, according to two consecutive global field power minima of the corresponding grand averages. MMN and P3a amplitudes were selected for each single participant and condition by using a semi-automatic peak detection algorithm. The labeled peaks

were additionally confirmed by visual inspection. Furthermore, the finding of a genuine MMN was validated by an inversion of polarity that became manifest at the lateral mastoid electrodes (TP9 and TP10). To verify the presence of MMN and P3a, the maximal amplitudes were statistically tested against zero by using one-sample *t* tests.

Statistical Analyses

The amplitudes as well as the latencies of the MMN and P3a amplitudes were evaluated by using the SPSS software (SPSS 19 for Windows; www.spss.com). In particular, we computed 2×4 ANOVAs with a two-way grouping factor (Group: AP vs. NAP) and a four-way repeated measurement factor (Deviation: four deviation levels as reflected by difference waves). Statistical analyses were adjusted for nonsphericity using Greenhouse–Geisser Epsilon when equal variances could not be assumed. Significant interaction effects were further inspected by using post hoc *t* tests. All post hoc *t* tests were corrected for multiple comparisons by using the Bonferroni procedure (corrected $\alpha' < .05/4 = .0125$). Because it is important to report the strength of an effect independent of the sample size, we also calculated the effect size (η_p^2) by dividing the sums of squares for the effects by the sums of squares for these effects plus its associated error variance within the ANOVA study. Correlation analyses (Pearson product–moment correlation coefficient) were used for investigating potential relationships between electrophysiological and biographical data.

RESULTS

Behavioral Data

Biographical Data, Cognitive Capability, and Musical Aptitude

The statistical evaluation of age, general cognitive capability, musical aptitude, age of onset of musical practice,

Table 2. Biographical Data

	AP	NAP	<i>p</i>
Age (years)	25.4 (9.6)	24.4 (3.0)	.76
General cognitive capability ^a	29.4 (3.8)	30.0 (3.6)	.68
Musical aptitude ^a	67.6 (6.5)	66.0 (6.6)	.55
Age onset of musical practice (years)	4.6 (1.6)	5.8 (2.1)	.11
Total number of years of music training	21.1 (8.5)	18.7 (4.1)	.41
Mean training hours per year	670.5 (331.7)	493.5 (169.0)	.13
Total number of training hours across lifespan ^b	1.7 (1.1)	1.2 (.5)	.19

Listed are the means of the variables of both groups and the *p* values (*t* tests). *SDs* are reported in brackets.

^aRaw scores were used.

^bUnits are given in 1×10^4 .

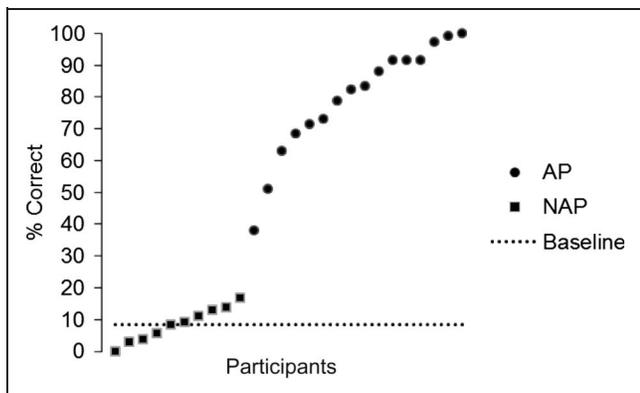


Figure 1. AP performance for each participant and the two groups.

total number of years of musical training, mean number of musical training hours per year, and the total number of musical training hours across lifespan did not reveal significant group differences. The results are listed in Table 2.

Pitch-labeling Test

Participants who claimed to have AP scored considerably better on the pitch-labeling test (mean score = 79.6%, $SD = 18.0\%$) than participants who claimed to not have

AP (mean score = 8.4%, $SD = 5.4\%$; $t(19) = 14.8$, $p < .001$). The distributions of the scores are depicted in Figure 1. Apparent are two nonoverlapping distributions, whereby the range within the AP group was wider. NAP participants did not score better than chance level (8.3%, $t(9) = 14.8$, $p = .943$).

Electrophysiological Data

MMN and P3a

In both groups, MMN and P3a responses were elicited in all deviation conditions. For each MMN waveform, saliently inversed polarity was observed at the mastoid electrodes within the expected TW of about 100–250 msec. The P3a responses showed positive-going amplitudes at the expected TW of about 200–350 msec. Furthermore, the positive voltage distributions over the scalps were in accordance with the typical P3a scalp topography. However, spatiotemporal pattern was less pronounced in the small deviation conditions. One-sample t tests revealed that all MMN and P3a amplitudes differed highly significantly from 0, which statistically justified their presences. Figures 2 and 3 illustrate the grand-averaged difference curves of all deviation conditions and both groups. The related scalp maps of the MMN and P3a responses are shown in Figure 4.

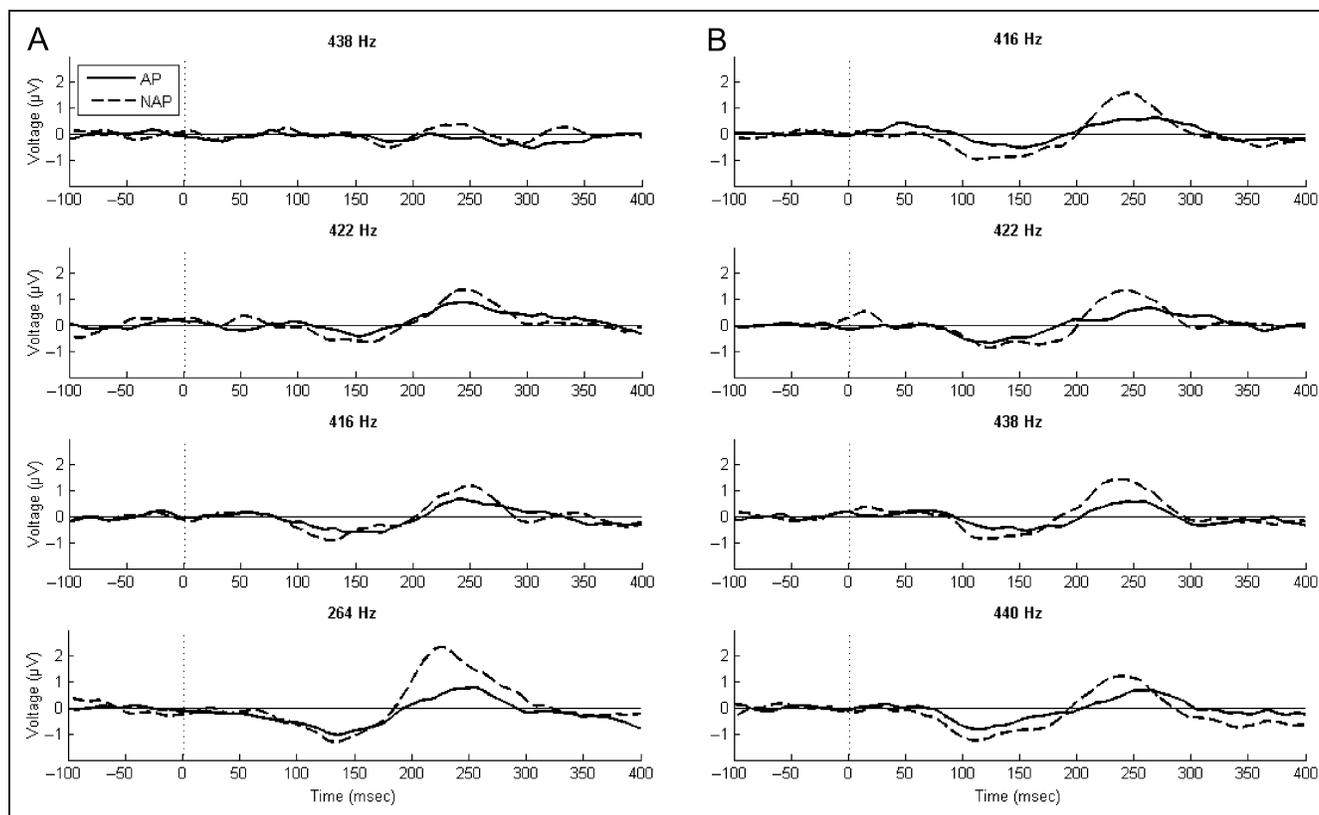


Figure 2. Grand averages of the difference waves at the frontal pool of electrodes depicted individually for each group and deviation condition (A = block A, B = block C).

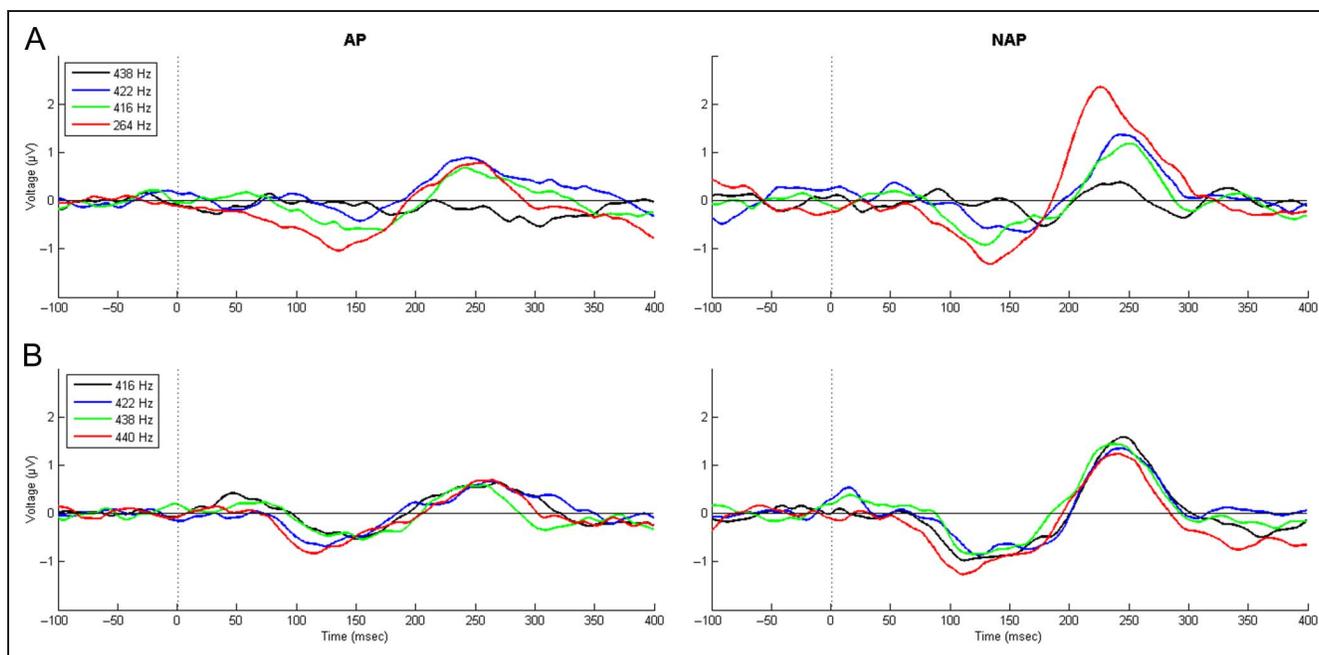


Figure 3. Grand averages of the difference waves at the frontal pool of electrodes depicted individually within each group (A = block A, B = block C).

Effects of Group, Deviation, and Interaction

Concerning the MMN amplitudes, the ANOVA calculations revealed an effect of Deviation, however, only in block A ($F(1, 24) = 10.9, p = .003, \eta_p^2 = .314$; block C: $F(1, 24) = 0.92, p = .348; \eta_p^2 = .037$). Otherwise,

no Group differences (block A: $F(1, 24) = 1.77, p = .195, \eta_p^2 = .069$; block C: $F(1, 24) = 3.5, p = .073, \eta_p^2 = .128$) nor interaction effects (block A: $F(1, 24) = 0.42, p = .524, \eta_p^2 = .017$; block C: $F(1, 24) = 0.014, p = .908, \eta_p^2 = .001$) were found. Similarly, the MMN latencies showed an effect of Deviation, however, only in block A

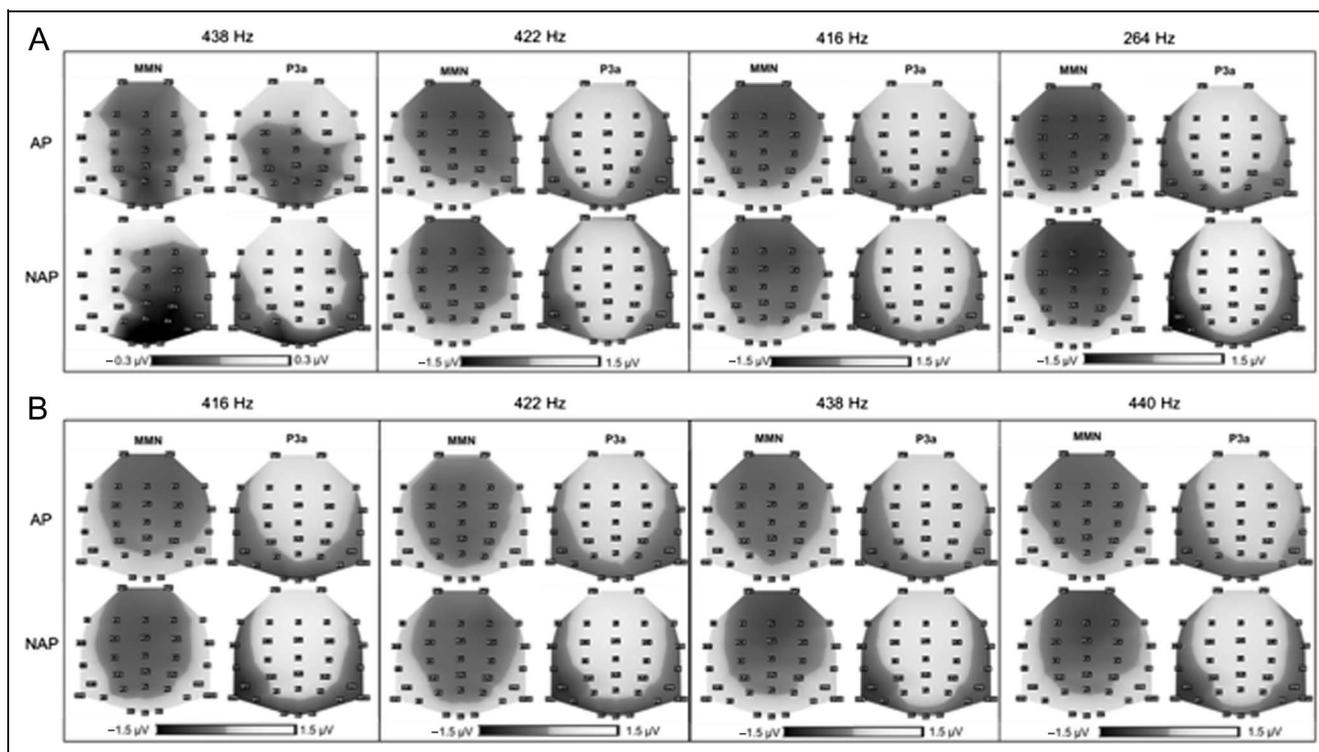


Figure 4. Scalp maps of the voltage distributions reflecting the MMN and P3a components for each group and deviation condition (A = block A, B = block C).

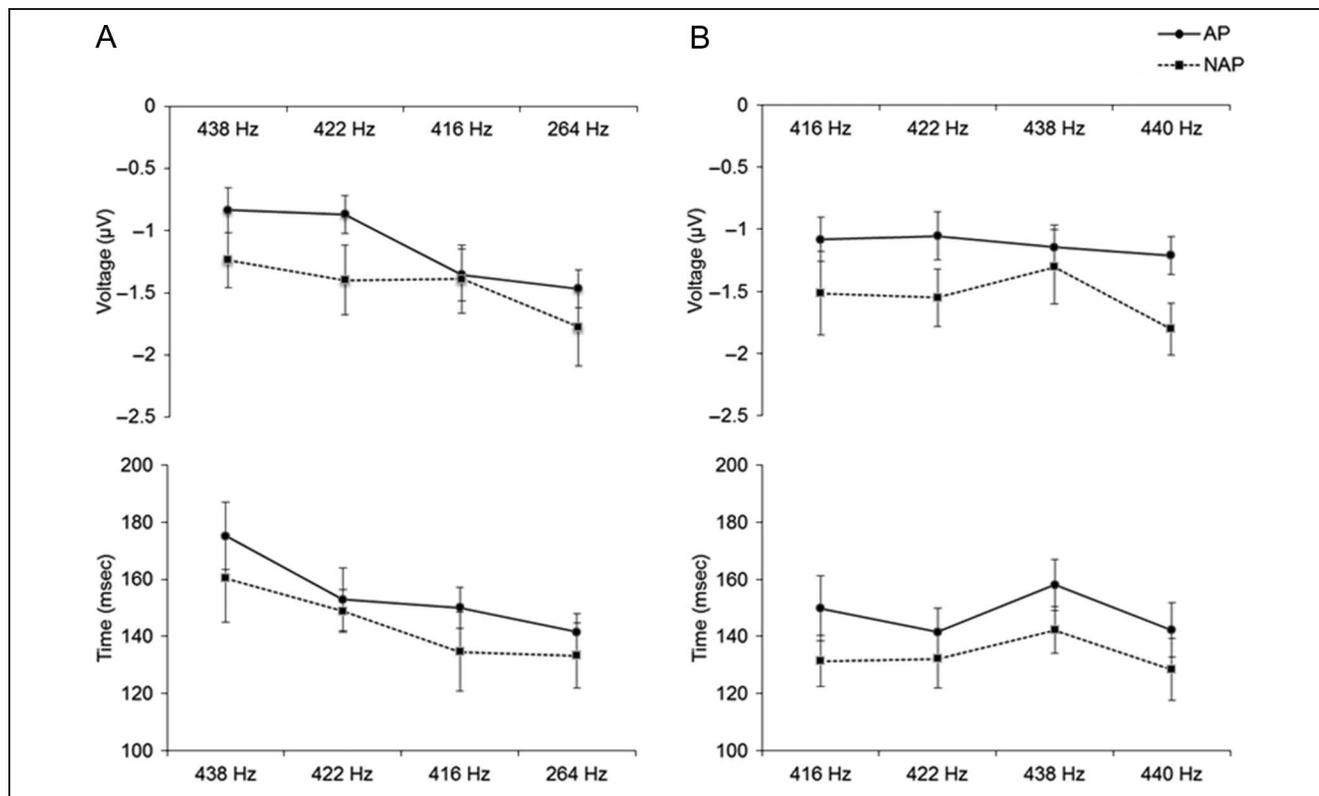


Figure 5. Amplitudes (top) and latencies (bottom) of the MMN components broken down for both groups and all deviation conditions (A = block A, B = block C). The bars depict SEMs.

($F(1, 24) = 5.87, p = .023, \eta_p^2 = .196$; block C: $F(1, 24) = 0.018, p = .895, \eta_p^2 = .001$). The MMN latencies showed no Group differences (Block A: $F(1, 24) = 1.78, p = .195, \eta_p^2 = .069$; block C: $F(1, 24) = 2.05, p = .165, \eta_p^2 = .079$) nor interaction effects (block A: $F(1, 24) = 0.010, p = .920, \eta_p^2 < .001$; block C: $F(1, 24) = 0.031, p = .863, \eta_p^2 = .001$). MMN amplitudes and latencies are depicted in Figure 5.

Concerning the P3a responses in block C, the AP participants exhibited overall significantly smaller amplitudes than the ones exhibited by NAP participants ($F(1, 24) = 6.87, p = .015, \eta_p^2 = .223$). No further Deviation ($F(1, 24) = 0.305, p = .586, \eta_p^2 = .013$) nor interaction effect ($F(1, 24) = 0.312, p = .582, \eta_p^2 = .013$) was found in this block. In block A, however, a Group difference ($F(1, 24) = 10.0, p = .004, \eta_p^2 = .294$), an effect of Deviation ($F(1, 24) = 33.8, p < .001, \eta_p^2 = .585$), and an interaction between Group and Deviation ($F(1, 24) = 9.02, p = .006, \eta_p^2 = .273$) were revealed. To further explore the interaction effect in block A, we compared the P3a amplitudes of the two groups across the four deviation conditions by performing *t* tests for independent samples. These post hoc *t* tests revealed a significant between-group difference in the 264 Hz condition ($t(24) = -4.62, p < .001$, Bonferroni-corrected $\alpha' < .05/4 = .0125$). In summary, NAP participants exhibited larger P3a amplitudes, particularly in response to between-tone category deviations (see Figure 6).

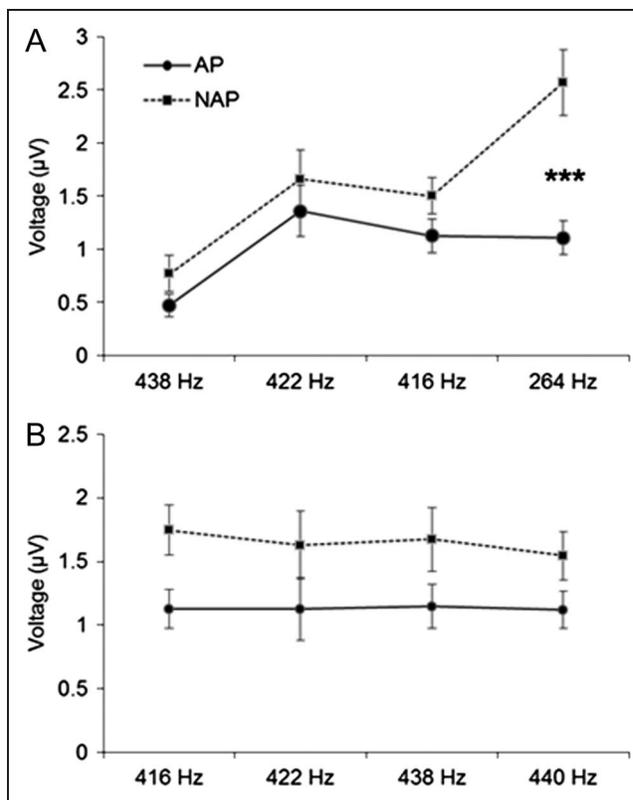


Figure 6. Amplitudes of the P3a component for both groups and all deviation conditions (A = block A, B = block C). The bars depict SEs. The asterisks indicate significant effects ($***p < .001$).

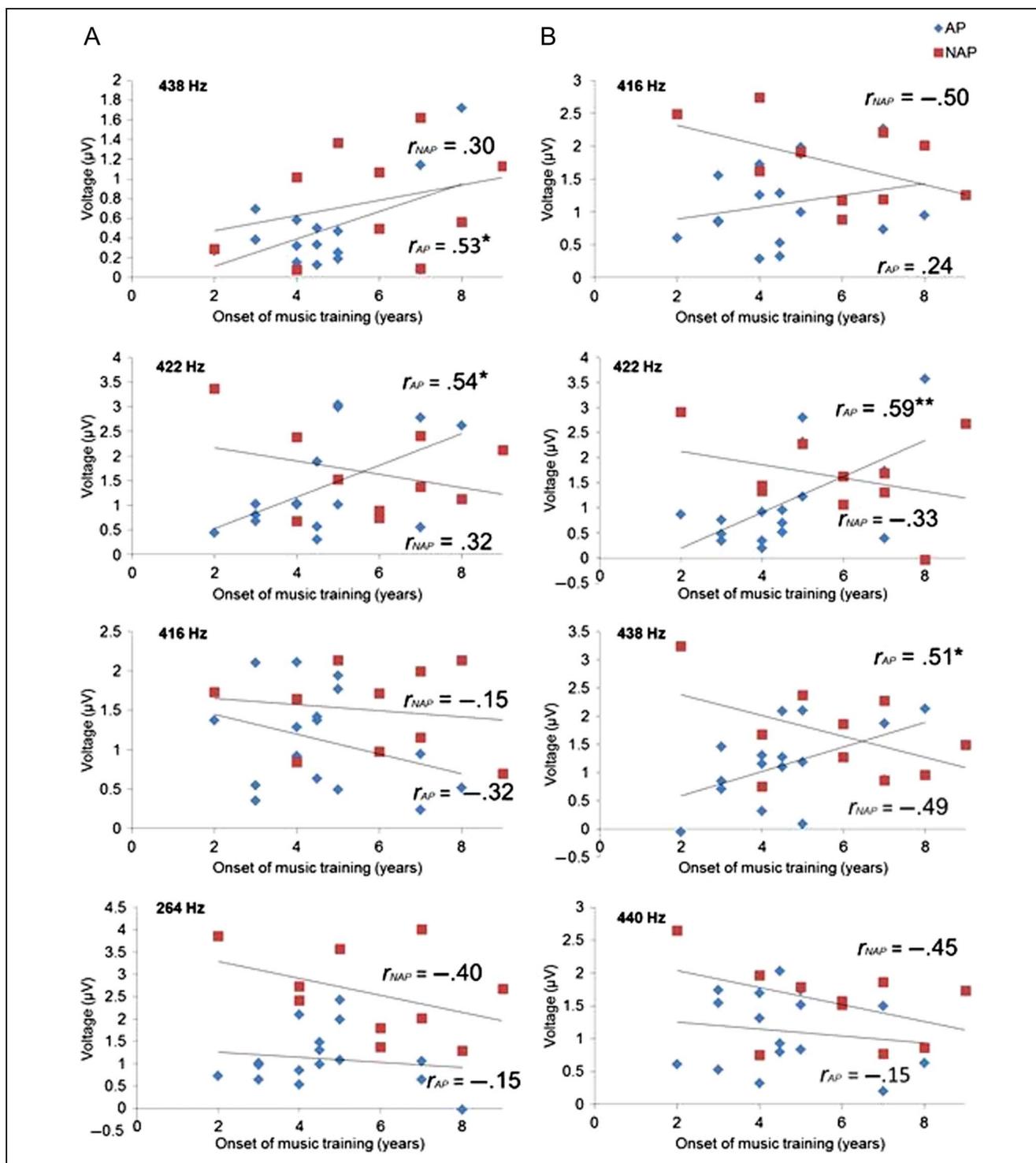


Figure 7. Correlations between age of onset of music training and the P3a amplitudes among both groups and for each deviation condition (A = block A, B = block C). The asterisks indicate the level of significant threshold ($*p < .05$, $**p < .01$).

Correlation Analyses

Correlation analyses revealed systematic relationships between the age of onset of musical training and the P3a amplitudes, however, only within the AP group. Significant positive correlations were only found in conditions

with mistuned deviant tones in block A (438 Hz: $r = .53$, $p = .017$; 422 Hz: $r = .54$, $p = .016$; 416 Hz: $r = -.32$, $p = .115$; 264 Hz: $r = -.15$, $p = .295$) and in block C (416 Hz: $r = .24$, $p = .184$; 422 Hz: $r = .59$, $p = .008$; 438 Hz: $r = .51$, $p = .021$; 440 Hz: $r = -.15$, $p = .291$). Within the NAP sample no significant correlations were found

between the age of onset of musical training and the P3a amplitudes neither in block A (438 Hz: $r = .30, p = .201$; 422 Hz: $r = .32, p = .181$; 416 Hz: $r = -.15, p = .340$; 264 Hz: $r = -.4, p = .124$) nor in block C (416 Hz: $r = -.50, p = .069$; 422 Hz: $r = -.33, p = .178$; 438 Hz: $r = -.49, p = .074$; 440 Hz: $r = -.45, p = .094$). All correlations are depicted in Figure 7.

DISCUSSION

General Discussion

In the present work, we used a passive oddball paradigm for assessing the contribution of the two different processing stages to AP during passive listening. In particular, we measured the two subsequent processing stages of tone processing (i.e., early stage of auditory processing and later cognitive processing as indicated by the MMN and P3a responses, respectively) in AP and NAP participants by exploiting the excellent time resolution of the EEG technique. A first innovative aspect of our work is that we used a multiple-deviant paradigm that enables to investigate tone processing under multiple conditions (i.e., within- and between-tone categories) and degrees of deviation. A further novelty of this study is that we minimized the potential influence of top-down mechanisms, leading to the opportunity to capture the genuine and automatic features of AP (Näätänen et al., 2007; Pulvermüller & Shtyrov, 2006). Finally, in contrast to previous oddball studies (Matsuda et al., 2013; Meyer et al., 2011; Tervaniemi et al., 1993), here we controlled for the influence of physical stimulus attributes, so that both the deviant and the standard tones elicited equal frequency-specific brain responses. We consider this an important point, because it has been shown that AP participants do not process pitch types equally, especially when tones are out of tune (Levitin & Rogers, 2005; Miyazaki, 1988).

In line with our hypotheses, we did not find evidence from MMN responses supporting the view that AP is related to an early pitch memory mechanism at the processing level of the auditory-related cortex. By contrast, our results confirm the specificity of the second processing stage for AP, namely, an underlying cognitive mechanism, as reflected by reduced P3a responses in AP participants. Notably, P3a responses also significantly correlated with the age of commencement of musical training, confirming the influence of early musical exposure on the ability of AP. A further innovative aspect of our work is that we are, to the best of our knowledge, the first to study the P3a component in the context of AP processing. This specific measurement is particularly fruitful in that it permits to give access to the purest and initial allocative and cognitive mechanism that is less contaminated by the influence of hierarchically higher cognitive processes, which are, for instance, likewise engaged in RP performance (see Hirose et al., 2002). In turn, we will place the results of this study in a broader

context by integrating biographical and electrophysiological data.

MMN Responses

The MMN component reflects auditory preattentive processing, operates at the sensory memory level (Garrido et al., 2009; Picton et al., 2000), but is also influenced by long-term memory (Pulvermüller & Shtyrov, 2006). Thus, this specific ERP reflects the ability to perform automatic, preattentive comparisons between successive stimuli and is considered to be an index for sound discrimination accuracy (Novak, Ritter, Vaughan, & Wiznitzer, 1990). According to a great body of studies, MMN amplitudes are known to get larger (and latencies shorter) with increased deviation level (Novitski, Tervaniemi, Huotilainen, & Näätänen, 2004; Amenedo & Escera, 2000; Sams, Paavilainen, Alho, & Näätänen, 1985).

Our MMN results, at least in block A, are fully in line with the expectation of increased amplitudes and shorter latencies as functions of increased deviation levels. In block C, however, we did not reveal such an effect of deviation. This lack of amplitude and latency modulation can easily be explained by the fact that all deviation levels reflected extreme conditions, in which the least pronounced deviation level (264 Hz vs. 416 Hz) was of eight semitones, probably leading to a salient detection effect. In line with the work of Tervaniemi et al. (1993), we did not reveal between-group differences in terms of MMN amplitudes and latencies in block A nor in block C. On the basis of these findings, we infer that AP is not necessarily driven by a differential pitch encoding ability at the processing level of the auditory-related cortex. By contrast, we propose that AP ability is more likely dependent on the second processing stage, namely the later cognitive process related to pitch labeling. Our results are further supported by a previous EEG study by Elmer et al. (Elmer, Hänggi, et al., 2013; Elmer, Sollberger, et al., 2013), which also did not reveal any differences with respect to neurophysiological processes indicating early sensory processing between AP and NAP musicians during passive listening. Certainly, we are fully aware that other authors (Matsuda et al., 2013; Schulze et al., 2013; Wu et al., 2008; Itoh et al., 2005; Ohnishi et al., 2001; Hirata et al., 1999) found evidence for auditory processing differences as a function of AP ability. However, Ohnishi et al. (2001) as well as Schulze et al. (2013) used the fMRI technique, a procedure that is very loud and might contaminate brain responses in the auditory cortex, making it nearly impossible to disentangle whether the BOLD responses are due to scanner noise or experimental stimuli. In addition, the hemodynamic response to the auditory stimulus is too slow to disentangle the different processes on a millisecond basis, which are involved in processing the auditory information. Furthermore, in the EEG study of Hirata et al. (1999), the authors compared AP musicians with nonmusicians, without controlling for

musicianship. Therefore, results are possibly more likely driven by musical practice than by AP per se. In addition, the study of Itoh et al. (2005) is not directly in contrast with our work. In fact, the authors identified an early left posterior temporal negativity, which was only present in AP participants at about 150 msec after tone presentation during tone listening and pitch-naming tasks. However, this specific deflection has been identified using scalp electrodes, which does not necessarily lead to the interpretation that the neural sources are located underneath the surface electrodes. Wu et al. (2008) were able to identify N1 effects, however, only in an active labeling task. Finally, Matsuda et al. (2013) reported larger MMN amplitudes in AP participants in response to mistuned tones but did not control for the physical attributes of the stimuli.

P3a Responses

Notably, in line with our predictions, the P3a component turned out to be a specific marker for AP. Likewise the MMN, the P3a response is driven by the magnitude of deviation (Berti, Roeber, & Schröger, 2004). However, pertaining to our data, this was only the case in block A. The lack of P3a amplitude modulation in block C was probably driven by the saliency of the deviant stimuli (see the previous section concerning the MMN). Besides this aspect, of noticeable relevance is that participants with AP exhibited overall smaller P3a amplitudes than participants without AP. This specific result suggests that tone processing in AP participants may rely on a different allocation of cognitive processes. This perspective is consistent with a large number of previous AP studies that adopted overt paradigms and reported reduced or even absent P300 amplitudes in AP participants (Crummer et al., 1994; Hantz et al., 1992; Wayman et al., 1992; Klein et al., 1984). Further evidence for the involvement of cognitive mechanisms in AP participants arises from labeling tasks, as manifested by a reduction in the P3b component, a reduction in the posterior positive and anterior negative slow waves (Itoh et al., 2005), or by increased N400 and LPC responses (Elmer, Sollberger, et al., 2013). Overall, the reduced P3a amplitudes in our study can be explained as decreased susceptibility among AP participants responding to tones, suggesting more efficient and parsimonious cognitive processing (Bendixen et al., 2010; Wetzel & Schröger, 2007; Wetzel, Widmann, Berti, & Schröger, 2006; Berti et al., 2004; Roeber, Berti, & Schröger, 2003; Gumenyuk et al., 2001; Escera, Alho, Winkler, & Näätänen, 1998; Schröger & Wolff, 1998).

Interestingly, we also revealed a Group \times Deviation level interaction effect. In block A AP participants exhibited reduced P3a responses, which were modulated as a function of deviation level. In other words, AP participants additionally differed from NAP participants, depending on whether the heard deviant tones appertained to the same tone category as the standard tone (within-tone category conditions) or corresponded to

novel tone categories (between-tone category conditions). Thus, AP participants responded with even less susceptibility to such tones, gaining inefficiency. This perspective is supported by a previous behavioral study showing that AP participants react faster and more accurately when identifying musical intervals in conditions with whole tone categories (Miyazaki, 1992).

Indeed, the post hoc comparisons within block A only revealed a significant difference at the 264-Hz level (not at the 416-Hz level corresponding to A-flat). However, we still consider our line of argumentation as convincing because of the unambiguous group difference we revealed in block C comprising only between-tone category conditions. The lack of significant group difference at the 416-Hz level in block A is possibly due to a context effect. In fact, recent findings have shown that the context (e.g., chords) strongly influences tone processing (McLachlan et al., 2013). In block A, the majority of the deviant tones were narrowly spread around the standard tone, which might have had an interfering effect on processing categorical borderlines.

Taken together, our findings suggest that AP participants engage less cognitive resources while processing whole tone categories. These tones refer to the semitones used in Western music, to which one is frequently exposed to. Therefore, our interpretation is compatible with a notion established in cognitive psychology, namely that exposure frequency increases perceptual fluency and thus facilitates information processing (Bornstein & D'Agostino, 1994).

The Influence of Early Musical Training on AP

AP is assumed to develop within a sensitive period during childhood in which pitch label associations are formed (Gervain et al., 2013; Russo et al., 2003; Miyazaki, 1988). Given that during this early maturational stage the brain exhibits a high degree of plasticity (Schlaug, 2001), optimal conditions for developmental potentials are given. In connection with the impact of the sensitive period on AP acquisition, a large number of studies also reported benefits in starting earlier with musical training (Deutsch et al., 2006; Gregersen et al., 2001), as reflected by neurophysiological and neuroanatomical correlates (Meyer et al., 2011; Imfeld, Oechslin, Meyer, Loenneker, & Jancke, 2009; Ohnishi et al., 2001). In line with this perspective, we revealed positive correlations between the age of commencement of musical training and P3a amplitudes, meaning that AP participants who started earlier with musical training were characterized by reduced P3a amplitudes. However, this relationship was only found in conditions in which the deviant tones were mistuned, indicating that the later the AP participants started with music training, the larger the P3a amplitudes peaked in response to tones that are not considered as being part of the Western musical system. Therefore, we may speculate whether early training commencement

may facilitate more demanding pitch processing. Finally, the question arises here whether transfer effects between the processing of tones from the Western musical system and the processing of tones from not acquired tonal systems are modulated by the exposure to musical training during early childhood.

Multiple Codes and Pitch-labeling Performance

AP ability has been suggested to be dependent on mental codes, which are supposed to facilitate labeling performance (Zatorre et al., 1998; Zatorre & Beckett, 1989). Evidence in this direction arises from previous work, indicating decreased working memory loads (reduced P300 responses) in AP participants while counting auditory oddballs (Hantz et al., 1992; Klein et al., 1984). Furthermore, there is evidence showing that blocking verbal rehearsal in AP participants does not seem to affect tone label retention (Zatorre & Beckett, 1989), this suggesting that multiple codes (verbal, auditory imagery, sensorimotor cues) are involved in AP (Zatorre, 2003; Zatorre et al., 1998; Zatorre & Beckett, 1989). Taken together, these previous results suggest that AP underlies multimodal processes that are dependent on associative brain areas (Zatorre et al., 1998).

On the basis of a vast body of evidence suggesting that multimodal processing has facilitatory effects on task performance (Shams & Seitz, 2008; Fort, Delpuech, Pernier, & Giard, 2002; Giard & Peronnet, 1999), we argue that the reduced P3a amplitudes we revealed in AP participants are possibly related to the availability of multiple codes, enabling a more efficient allocation of attentional functions. In fact, it appears plausible to assume that the pitch types, which have explicitly been acquired in the coding process during the sensitive period, are more efficiently processed. Possibly, the reduction of the P3a responses in this context reflects the establishment of cognitive resources on which pitch labeling relies, because reduced P3a responses have repeatedly been associated with more efficient cognitive and behavioral performance (Bendixen et al., 2010; Wetzel & Schröger, 2007; Wetzel et al., 2006; Berti et al., 2004; Roeber et al., 2003; Gumenyuk et al., 2001; Escera et al., 1998; Schröger & Wolff, 1998).

Conclusion

By means of a passive oddball paradigm, we provide first evidence showing that even in a passive listening condition rather a cognitive than a sensory mechanism contributes to the phenomenon of AP. The reduction in the P3a responses we revealed in AP participants reflects a more efficient and parsimonious allocation of cognitive demands because of a multidimensional tone processing. Efficiency appears to depend on the extent of experience in processing pitches during the sensitive period. Our findings are in line with the growing consensus (Elmer, Hänggi, et al., 2013; Elmer, Sollberger, et al., 2013; Levitin

& Rogers, 2005; Zatorre et al., 1998; Levitin, 1994) considering the later-occurring and cognitively based processing stage as the crucial operation for AP.

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REFERENCES

- Amenedo, E., & Escera, C. (2000). The accuracy of sound duration representation in the human brain determines the accuracy of behavioural perception. *European Journal of Neuroscience*, *12*, 2570–2574.
- Athos, E. A., Levinson, B., Kistler, A., Zemansky, J., Bostrom, A., Freimer, N., et al. (2007). Dichotomy and perceptual distortions in absolute pitch ability. *Proceedings of the National Academy of Sciences*, *104*, 14795–14800.
- Baggaley, J. (1974). Measurement of absolute pitch. *Psychology of Music*, *2*, 11–17.
- Baharloo, S., Johnston, P. A., Service, S. K., Gitschier, J., & Freimer, N. B. (1998). Absolute pitch: An approach for identification of genetic and nongenetic components. *The American Journal of Human Genetics*, *62*, 224–231.
- Baharloo, S., Service, S. K., Risch, N., Gitschier, J., & Freimer, N. B. (2000). Familial aggregation of absolute pitch. *The American Journal of Human Genetics*, *67*, 755–758.
- Bendixen, A., Grimm, S., Deouell, L. Y., Wetzel, N., Mädebach, A., & Schröger, E. (2010). The time-course of auditory and visual distraction effects in a new crossmodal paradigm. *Neuropsychologia*, *48*, 2130–2139.
- Bermudez, P., Lerch, J. P., Evans, A. C., & Zatorre, R. J. (2009). Neuroanatomical correlates of musicianship as revealed by cortical thickness and voxel-based morphometry. *Cerebral Cortex*, *19*, 1583–1596.
- Bermudez, P., & Zatorre, R. J. (2005). Conditional associative memory for musical stimuli in nonmusicians: Implications for absolute pitch. *The Journal of Neuroscience*, *25*, 7718–7723.
- Berti, S., Roeber, U., & Schröger, E. (2004). Bottom-up influences on working memory: Behavioral and electrophysiological distraction varies with distractor strength. *Experimental Psychology*, *51*, 249–257.
- Boll, S., & Berti, S. (2009). Distraction of task-relevant information processing by irrelevant changes in auditory, visual, and bimodal stimulus features: A behavioral and event-related potential study. *Psychophysiology*, *46*, 645–654.
- Bornstein, R. F., & D'Agostino, P. R. (1994). The attribution and discounting of perceptual fluency: Preliminary tests of a perceptual fluency/attributional model of the mere exposure effect. *Social Cognition*, *12*, 103–128.
- Brenton, J. N., Devries, S. P., Barton, C., Minnich, H., & Sokol, D. K. (2008). Absolute pitch in a four-year-old boy with autism. *Pediatric Neurology*, *39*, 137–138.
- Comerchero, M., & Polich, J. (1999). P3a and P3b from typical auditory and visual stimuli. *Clinical Neurophysiology*, *110*, 24–30.
- Crummer, G. C., Walton, J. P., Wayman, J. W., Hantz, E. C., & Frisina, R. D. (1994). Neural processing of musical timbre by

- musicians, nonmusicians, and musicians possessing absolute pitch. *The Journal of the Acoustical Society of America*, *95*, 2720–2727.
- Deutsch, D. (1987). The tritone paradox: Effects of spectral variables. *Perception & Psychophysics*, *41*, 563–575.
- Deutsch, D., Dooley, K., Henthorn, T., & Head, B. (2009). Absolute pitch among students in an American music conservatory: Association with tone language fluency. *The Journal of the Acoustical Society of America*, *125*, 2398–2403.
- Deutsch, D., Henthorn, T., & Dolson, M. (2004a). Speech patterns heard early in life influence later perception of the tritone paradox. *Music Perception: An Interdisciplinary Journal*, *21*, 357–372.
- Deutsch, D., Henthorn, T., & Dolson, M. (2004b). Absolute pitch, speech, and tone language: Some experiments and a proposed framework. *Music Perception: An Interdisciplinary Journal*, *21*, 339–356.
- Deutsch, D., Henthorn, T., Marvin, E., & Xu, H. (2006). Absolute pitch among American and Chinese conservatory students: Prevalence differences, and evidence for a speech-related critical period. *The Journal of the Acoustical Society of America*, *119*, 719–722.
- Deutsch, D., Li, X., & Shen, J. (2013). Absolute pitch among students at the Shanghai Conservatory of Music: A large-scale direct-test study. *The Journal of the Acoustical Society of America*, *134*, 3853–3859.
- Eichele, T., Nordby, H., Rimol, L. M., & Hugdahl, K. (2005). Asymmetry of evoked potential latency to speech sounds predicts the ear advantage in dichotic listening. *Cognitive Brain Research*, *24*, 405–412.
- Elmer, S., Hänggi, J., Meyer, M., & Jäncke, L. (2013). Increased cortical surface area of the left planum temporale in musicians facilitates the categorization of phonetic and temporal speech sounds. *Cortex*, *49*, 2812–2821.
- Elmer, S., Meyer, M., & Jäncke, L. (2012). Neurofunctional and behavioral correlates of phonetic and temporal categorization in musically trained and untrained subjects. *Cerebral Cortex*, *22*, 650–658.
- Elmer, S., Sollberger, S., Meyer, M., & Jäncke, L. (2013). An empirical reevaluation of absolute pitch: Behavioral and electrophysiological measurements. *Journal of Cognitive Neuroscience*, *25*, 1736–1753.
- Escera, C., Alho, K., Schröger, E., & Winkler, I. (2000). Involuntary attention and distractibility as evaluated with event-related brain potentials. *Audiology and Neuro-otology*, *5*, 151–166.
- Escera, C., Alho, K., Winkler, I., & Näätänen, R. (1998). Neural mechanisms of involuntary attention to acoustic novelty and change. *Journal of Cognitive Neuroscience*, *10*, 590–604.
- Fort, A., Delpuech, C., Pernier, J., & Giard, M.-H. (2002). Dynamics of cortico-subcortical cross-modal operations involved in audio-visual object detection in humans. *Cerebral Cortex*, *12*, 1031–1039.
- Friedman, D., Cycowicz, Y. M., & Gaeta, H. (2001). The novelty P3: An event-related brain potential (ERP) sign of the brain's evaluation of novelty. *Neuroscience & Biobehavioral Reviews*, *25*, 355–373.
- Friedman, D., & Johnson, R. (2000). Event-related potential (ERP) studies of memory encoding and retrieval: A selective review. *Microscopy Research and Technique*, *51*, 6–28.
- Garrido, M. I., Kilner, J. M., Stephan, K. E., & Friston, K. J. (2009). The mismatch negativity: A review of underlying mechanisms. *Clinical Neurophysiology*, *120*, 453–463.
- Gervain, J., Vines, B. W., Chen, L. M., Seo, R. J., Hensch, T. K., Werker, J. F., et al. (2013). Valproate reopens critical-period learning of absolute pitch. *Frontiers in Systems Neuroscience*, *7*, 1–11.
- Giard, M. H., & Peronnet, F. (1999). Auditory-visual integration during multimodal object recognition in humans: A behavioral and electrophysiological study. *Journal of Cognitive Neuroscience*, *11*, 473–490.
- Gordon, E. (1989). *Manual for the advanced measures of music education*. Chicago: G.I.A. Publications, Inc.
- Gregersen, P. K., Kowalsky, E., Kohn, N., & Marvin, E. W. (1999). Absolute pitch: Prevalence, ethnic variation, and estimation of the genetic component. *The American Journal of Human Genetics*, *65*, 911–913.
- Gregersen, P. K., Kowalsky, E., Kohn, N., & Marvin, E. W. (2001). Early childhood music education and predisposition to absolute pitch: Teasing apart genes and environment. *American Journal of Medical Genetics*, *98*, 280–282.
- Gumenyuk, V., Korzyukov, O., Alho, K., Escera, C., Schröger, E., Ilmoniemi, R. J., et al. (2001). Brain activity index of distractibility in normal school-age children. *Neuroscience Letters*, *314*, 147–150.
- Hantz, E. C., Crummer, G. C., Wayman, J. W., Walton, J. P., & Frisina, R. D. (1992). Effects of musical training and absolute pitch on the neural processing of melodic intervals: A P3 event-related potential study. *Music Perception: An Interdisciplinary Journal*, *10*, 25–42.
- Hauser, M., & McDermott, J. (2003). The evolution of the music faculty: A comparative perspective. *Nature Neuroscience*, *6*, 663–668.
- Heaton, P., Davis, R. E., & Happé, F. G. E. (2008). Research note: Exceptional absolute pitch perception for spoken words in an able adult with autism. *Part Special Issue: What is the Parietal Lobe Contribution to Human Memory?*, *46*, 2095–2098.
- Hedger, S. C., Heald, S. L. M., & Nusbaum, H. C. (2013). Absolute pitch may not be so absolute. *Psychological Science*, *24*, 1496–1502.
- Hirata, Y., Kuriki, S., & Pantev, C. (1999). Musicians with absolute pitch show distinct neural activities in the auditory cortex. *NeuroReport*, *10*, 999–1002.
- Hirose, H., Kubota, M., Kimura, I., Ohsawa, M., Yumoto, M., & Sakakihara, Y. (2002). People with absolute pitch process tones with producing P300. *Neuroscience Letters*, *330*, 247–250.
- Horváth, J., Czigler, I., Sussman, E., & Winkler, I. (2001). Simultaneously active pre-attentive representations of local and global rules for sound sequences in the human brain. *Cognitive Brain Research*, *12*, 131–144.
- Imfeld, A., Oechslin, M., Meyer, M., Loenneker, T., & Jäncke, L. (2009). White matter plasticity in the corticospinal tract of musicians: A diffusion tensor imaging study. *Neuroimage*, *46*, 600–607.
- Itoh, K., Suwazono, S., Arao, H., Miyazaki, K., & Nakada, T. (2005). Electrophysiological correlates of absolute pitch and relative pitch. *Cerebral Cortex*, *15*, 760–769.
- Jakubowski, K., & Müllensiefen, D. (2013). The influence of music-elicited emotions and relative pitch on absolute pitch memory for familiar melodies. *The Quarterly Journal of Experimental Psychology*, *66*, 1259–1267.
- Jäncke, L., Langer, N., & Hänggi, J. (2012). Diminished whole-brain but enhanced peri-sylvian connectivity in absolute pitch musicians. *Journal of Cognitive Neuroscience*, *24*, 1447–1461.
- Jäncke, L., Rogenmoser, L., Meyer, M., & Elmer, S. (2012). Pre-attentive modulation of brain responses to tones in coloured-hearing synesthetes. *BMC Neuroscience*, *13*, 151.
- 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.
- Keenan, J. P., Thangaraj, V., Halpern, A. R., & Schlaug, G. (2001). Absolute pitch and planum temporale. *Neuroimage*, *14*, 1402–1408.

- Klein, M., Coles, M. G. H., & Donchin, E. (1984). People with absolute pitch process tones without producing a P300. *Science*, *223*, 1306–1309.
- Knight, R. (1984). Decreased response to novel stimuli after prefrontal lesions in man. *Electroencephalography and Clinical Neurophysiology Evoked Potentials*, *59*, 9–20.
- Knight, R. (1996). Contribution of human hippocampal region to novelty detection. *Nature*, *383*, 256–259.
- Knight, R. T., Grabowecky, M. F., & Scabini, D. (1995). Role of human prefrontal cortex in attention control. *Advances in Neurology*, *66*, 21–36.
- Knight, R. T., & Nakada, T. (1998). A review of EEG and blood flow data. *Reviews in the Neurosciences*, *9*, 57–70.
- Knight, R. T., Scabini, D., Woods, D. L., & Clayworth, C. C. (1989). Contributions of temporal–parietal junction to the human auditory P3. *Brain Research*, *502*, 109–116.
- Kujala, T., Tervaniemi, M., & Schröger, E. (2007). The mismatch negativity in cognitive and clinical neuroscience: Theoretical and methodological considerations. *Biological Psychology*, *74*, 1–19.
- Kutas, M., & Federmeier, K. D. (2011). Thirty years and counting: Finding meaning in the N400 component of the event-related brain potential (ERP). *Annual Review of Psychology*, *62*, 621–647.
- Lehrl, S., Triebig, G., & Fischer, B. (1995). Multiple choice vocabulary test MWT as a valid and short test to estimate premorbid intelligence. *Acta Neurologica Scandinavica*, *91*, 335–345.
- Lenhoff, H. M., Perales, O., & Hickok, G. (2001). Absolute pitch in Williams syndrome. *Music Perception: An Interdisciplinary Journal*, *18*, 491–503.
- Levitin, D. (1994). Absolute memory for musical pitch: Evidence from the production of learned melodies. *Perception & Psychophysics*, *56*, 414–423.
- Levitin, D. J., & Rogers, S. E. (2005). Absolute pitch: Perception, coding, and controversies. *Trends in Cognitive Sciences*, *9*, 26–33.
- Loui, P., Li, H. C., Hohmann, A., & Schlaug, G. (2011). Enhanced cortical connectivity in absolute pitch musicians: A model for local hyperconnectivity. *Journal of Cognitive Neuroscience*, *23*, 1015–1026.
- Loui, P., Zamm, A., & Schlaug, G. (2012). Enhanced functional networks in absolute pitch. *Neuroimage*, *63*, 632–640.
- Luders, E., Gaser, C., Jancke, L., & Schlaug, G. (2004). A voxel-based approach to gray matter asymmetries. *Neuroimage*, *22*, 656–664.
- Matsuda, A., Hara, K., Watanabe, S., Matsuura, M., Ohta, K., & Matsushima, E. (2013). Pre-attentive auditory processing of non-scale pitch in absolute pitch possessors. *Neuroscience Letters*, *548*, 155–158.
- McLachlan, N., Marco, D., & Wilson, S. (2013). Pitch and plasticity: Insights from the pitch matching of chords by musicians with absolute and relative pitch. *Brain Sciences*, *3*, 1615–1634.
- Meyer, M., Elmer, S., Ringli, M., Oechslin, M., Baumann, S., & Jancke, L. (2011). Long-term exposure to music enhances the sensitivity of the auditory system in children. *European Journal of Neuroscience*, *34*, 755–765.
- Miyazaki, K. (1988). Musical pitch identification by absolute pitch possessors. *Perception & Psychophysics*, *44*, 501–512.
- Miyazaki, K. (1992). Perception of musical intervals by absolute pitch possessors. *Music Perception: An Interdisciplinary Journal*, *9*, 413–426.
- Näätänen, R. (2000). Mismatch negativity (MMN): Perspectives for application. *International Journal of Psychophysiology*, *37*, 3–10.
- Näätänen, R., Gaillard, A. W. K., & Mäntysalo, S. (1978). Early selective-attention effect on evoked potential reinterpreted. *Acta Psychologica*, *42*, 313–329.
- Näätänen, R., Paavilainen, P., Rinned, T., & Alhod, K. (2007). The mismatch negativity (MMN) in basic research of central auditory processing: A review. *Clinical Neurophysiology*, *118*, 2544–2590.
- Näätänen, R., & Winkler, I. (1999). The concept of auditory stimulus representation in cognitive neuroscience. *Psychological Bulletin*, *125*, 826–859.
- Novak, G. P., Ritter, W., Vaughan, H. G., Jr., & Wiznitzer, M. L. (1990). Differentiation of negative event-related potentials in an auditory discrimination task. *Electroencephalography and Clinical Neurophysiology*, *75*, 255–275.
- Novitski, N., Tervaniemi, M., Huotilainen, M., & Näätänen, R. (2004). Frequency discrimination at different frequency levels as indexed by electrophysiological and behavioral measures. *Cognitive Brain Research*, *20*, 26–36.
- Oechslin, M. S., Imfeld, A., Loenneker, T., Meyer, M., & Jäncke, L. (2010). The plasticity of the superior longitudinal fasciculus as a function of musical expertise: A diffusion tensor imaging study. *Frontiers in Human Neuroscience*, *3*, 1–11.
- Oechslin, M. S., Meyer, M., & Jäncke, L. (2010). Absolute pitch—Functional evidence of speech-relevant auditory acuity. *Cerebral Cortex*, *20*, 447–455.
- Ohnishi, T., Matsuda, H., Asada, T., Aruga, M., Hirakata, M., Nishikawa, M., et al. (2001). Functional anatomy of musical perception in musicians. *Cerebral Cortex*, *11*, 754–760.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, *9*, 97–113.
- Petrides, M. (1990). Nonspatial conditional learning impaired in patients with unilateral frontal but not unilateral temporal lobe excisions. *Neuropsychologia*, *28*, 137–149.
- Petrides, M., Alivisatos, B., Evans, A. C., & Meyer, E. (1993). Dissociation of human mid-dorsolateral from posterior dorsolateral frontal cortex in memory processing. *Proceedings of the National Academy of Sciences*, *90*, 873–877.
- Picton, T. W., Alain, C., Otten, L., Ritter, W., & Achim, A. (2000). Mismatch negativity: Different water in the same river. *Audiology and Neurotology*, *5*, 111–139.
- Polich, J. (2007). Updating P300: An integrative theory of P3a and P3b. *Clinical Neurophysiology*, *118*, 2128–2148.
- Pulvermüller, F., & Shtyrov, Y. (2006). Language outside the focus of attention: The mismatch negativity as a tool for studying higher cognitive processes. *Progress in Neurobiology*, *79*, 49–71.
- Roeber, U., Berti, S., & Schröger, E. (2003). Auditory distraction with different presentation rates: An event-related potential and behavioral study. *Clinical Neurophysiology*, *114*, 341–349.
- Russo, F. A., Windell, D. L., & Cuddy, L. L. (2003). Learning the “special note”: Evidence for a critical period for absolute pitch acquisition. *Music Perception: An Interdisciplinary Journal*, *21*, 119–127.
- Saffran, J. R., & Griepentrog, G. J. (2001). Absolute pitch in infant auditory learning: Evidence for developmental reorganization. *Developmental Psychology*, *37*, 74–85.
- Sams, M., Paavilainen, P., Alho, K., & Näätänen, R. (1985). Auditory frequency discrimination and event-related potentials. *Electroencephalography and Clinical Neurophysiology Evoked Potentials*, *62*, 437–448.
- Schellenberg, E. G., & Trehub, S. E. (2003). Good pitch memory is widespread. *Psychological Science*, *14*, 262–266.
- Schlaug, G. (2001). The brain of musicians. *Annals of the New York Academy of Sciences*, *930*, 281–299.
- Schlaug, G., Jancke, L., Huang, Y., & Steinmetz, H. (1995). In vivo evidence of structural brain asymmetry in musicians. *Science*, *267*, 699–701.

- Schröger, E., & Wolff, C. (1998). Behavioral and electrophysiological effects of task-irrelevant sound change: A new distraction paradigm. *Cognitive Brain Research*, 7, 71–87.
- Schulze, K., Gaab, N., & Schlaug, G. (2009). Perceiving pitch absolutely: Comparing absolute and relative pitch possessors in a pitch memory task. *BMC Neuroscience*, 10, 106.
- Schulze, K., Mueller, K., & Koelsch, S. (2013). Auditory Stroop and absolute pitch: An fMRI study. *Human Brain Mapping*, 34, 1579–1590.
- Shams, L., & Seitz, A. (2008). Benefits of multisensory learning. *Trends in Cognitive Sciences*, 12, 411–417.
- Siegel, J. A. (1974). Sensory and verbal coding strategies in subjects with absolute pitch. *Journal of Experimental Psychology*, 103, 37–44.
- Smith, N. A., & Schmuckler, M. A. (2008). Dial A440 for absolute pitch: Absolute pitch memory by non-absolute pitch possessors. *The Journal of the Acoustical Society of America*, 123, EL77–EL84.
- Squires, K. C., Squires, N. K., & Hillyard, S. A. (1975). Decision-related cortical potentials during an auditory signal detection task with cued observation intervals. *Journal of Experimental Psychology: Human Perception and Performance*, 1, 268–279.
- Takeuchi, A. H., & Hulse, S. H. (1993). Absolute pitch. *Psychological Bulletin*, 113, 345–361.
- Tervaniemi, M., Alho, K., Paavilainen, P., Sams, M., & Näätänen, R. (1993). Absolute pitch and event-related brain potentials. *Music Perception*, 10, 305–316.
- Theusch, E., Basu, A., & Gitschier, J. (2009). Genome-wide study of families with absolute pitch reveals linkage to 8q24.21 and locus heterogeneity. *The American Journal of Human Genetics*, 85, 112–119.
- Wayman, J. W., Frisina, R. D., Walton, J. P., Hantz, E. C., & Crummer, G. C. (1992). Effects of musical training and absolute pitch ability on event-related activity in response to sine tones. *The Journal of the Acoustical Society of America*, 91, 3527–3531.
- Wengenroth, M., Blatow, M., Heinecke, A., Reinhardt, J., Stippich, C., Hofmann, E., et al. (2013). Increased volume and function of right auditory cortex as a marker for absolute pitch. *Cerebral Cortex*, 24, 1127–1137.
- Wetzel, N., & Schröger, E. (2007). Cognitive control of involuntary attention and distraction in children and adolescents. *Brain Research*, 1155, 134–146.
- Wetzel, N., Widmann, A., Berti, S., & Schröger, E. (2006). The development of involuntary and voluntary attention from childhood to adulthood: A combined behavioral and event-related potential study. *Clinical Neurophysiology*, 117, 2191–2203.
- Wilson, S. J., Lusher, D., Wan, C. Y., Dudgeon, P., & Reutens, D. C. (2009). The neurocognitive components of pitch processing: Insights from absolute pitch. *Cerebral Cortex*, 19, 724–732.
- Wu, C., Kirk, I., Hamm, J., & Lim, V. (2008). The neural networks involved in pitch labeling of absolute pitch musicians. *NeuroReport*, 19, 851–854.
- Zatorre, R., & Beckett, C. (1989). Multiple coding strategies in the retention of musical tones by possessors of absolute pitch. *Memory & Cognition*, 17, 582–589.
- Zatorre, R. J. (2003). Absolute pitch: A model for understanding the influence of genes and development on neural and cognitive function. *Nature Neuroscience*, 6, 692–695.
- Zatorre, R. J., Perry, D. W., Beckett, C. A., Westbury, C. F., & Evans, A. C. (1998). Functional anatomy of musical processing in listeners with absolute pitch and relative pitch. *Proceedings of the National Academy of Sciences*, 95, 3172–3177.