Neural Discrimination of Nonprototypical Chords in Music Experts and Laymen: An MEG Study

Elvira Brattico[1,2], Karen Johanne Pallesen[3], Olga Varyagina[4], Christopher Bailey[3], Irina Anourova[1], Miika Järvenpää[1], Tuomas Eerola[2], and Mari Tervaniemi[1]

Abstract

■ At the level of the auditory cortex, musicians discriminate pitch changes more accurately than nonmusicians. However, it is not agreed upon how sound familiarity and musical expertise interact in the formation of pitch-change discrimination skills, that is, whether musicians possess musical pitch discrimination abilities that are generally more accurate than in nonmusicians or, alternatively, whether they may be distinguished from nonmusicians particularly with respect to the discrimination of nonprototypical sounds that do not play a reference role in Western tonal music. To resolve this, we used magnetoencephalography (MEG) to measure the change-related magnetic mismatch response (MMNm) in musicians and nonmusicians to two nonprototypical chords, a ''dissonant'' chord containing a highly unpleasant interval and a ''mistuned'' chord including a mistuned pitch, and a minor chord, all inserted in a context of major chords. Major and minor are the most frequently used chords in Western tonal music which both musicians and nonmusicians are most familiar with, whereas the other chords are more rarely encountered in tonal music. The MMNm was stronger in musicians than in nonmusicians in response to the dissonant and mistuned chords, whereas no group difference was found in the MMNm strength to minor chords. Correspondingly, the length of musical training correlated with the MMNm strength for the dissonant and mistuned chords only. Our findings provide evidence for superior automatic discrimination of nonprototypical chords in musicians. Most likely, this results from a highly sophisticated auditory system in musicians allowing a more efficient discrimination of chords deviating from the conventional categories of tonal music. ■

INTRODUCTION

Almost every individual is a music listener or music lover, provided with the cognitive and affective tools for understanding and appreciating music. Some individuals become expert musicians after several years of continuous practical and theoretical training. The diversification of musical competence renders music a unique tool for the objective investigation of the neural mechanisms underlying expert perception and discrimination (Hannon & Trainor, 2007; Münte, Altenmüller, & Jäncke, 2002).

In psychology, it is well accepted that discrimination of two stimuli is affected by the belongingness of those stimuli to a particular category. A category can be defined as a set of stimuli sharing common features and similarity to an ideal exemplar or prototype (e.g., Stenberg, 1999). Individuals internalize a prototype in a culture-specific manner, that is, after repeated presentations of a stimulus or due to innate perceptual constraints (Schellenberg, 2001). Western tonal music, that is, the majority of music we are exposed to, is constructed from a small set of sound elements, the 12-note equal-tempered chromatic scale (Krumhansl, 1990). Most genres of Western tonal music are characterized by the predominant use of chords (simultaneous sound combinations) including pitches related by approximate whole integer ratios. These chords are termed consonant and can be considered as prototypical in most genres of Western music (North & Hargreaves, 2000; Martindale & Moore, 1989). In particular, the major and minor triads (chords containing 3 different pitches and including the major third and the minor third interval, respectively) represent the prototypes or anchor points on which the induction of tonality (the weighting of pitches on the basis of fixed relationships that exist between them) is based (Krumhansl, 1990). In contrast, chords containing mistuned pitches deviating from the chromatic scale (Schellenberg, 2001; Burns, 1999) or pitches related by highly unpleasant (dissonant) intervals such as the minor and major second are rare and do not act as chord prototypes in most Western musical genres. Rather, some dissonant or even intentionally mistuned chords are less rare in those musical genres

[1]University of Helsinki, Finland, [2]University of Jyväskylä, Finland, [3]Aarhus University, Denmark, [4]I.P. Pavlov Institute of Physiology, St. Petersburg, Russia

to which professional musicians are likely exposed, such as jazz (particularly the modern avant-garde, modal, and freejazz styles) and classical music (particularly the romantic and modern styles; e.g., Sadie & Tyrrell, 2001). In sum, musical genres are characterized by conventions dictating the prototypical usage of certain sounds and sound combinations. It has been proposed that only the attentive, continuous exposure to music and active practicing during explicit musical training leads to automatic learning and internalization of prototypical interval and chord categories (Burns, 1999). On the other hand, some researchers claim that music expertise (intended as implicit knowledge of culture-specific musical conventions) is present to some extent in any individual passively exposed to a musical culture (e.g., Brattico, Tervaniemi, Näätänen, & Peretz, 2006; Bigand, 2003; Tillmann, Bharucha, & Bigand, 2000). The nature and extent of this implicit musicality is not yet clear.

In general, perceptual training increases the similarity between exemplars within the same category as well as the distinctiveness and discrimination of exemplars that lie in different categories (Goldstone, 1998). In the visual domain, perceptual expertise leads to a shift in recognition from the basic-level large categories (e.g., ''dog'') up to very specific subordinate categories (e.g., ''German shepherd''; Quinn & Tanaka, 2007; Bukach, Gauthier, & Tarr, 2006). For instance, the greater expertise to process faces compared with any other visual object leads to automatic face processing at the individual level, contrasted with the processing of other objects such as birds or trees at the category level (Tarr & Gauthier, 2000). Similarly, expert categorization in music may be identified by discrimination between more detailed and restricted categories, for instance, chords uncommon in Western tonal music. Perceptual learning is further characterized by sensitivization of the physical features that are category-relevant (Goldstone, 1998). In the auditory modality, this sensitivization seems to be based on more accurate neural encoding of familiar sound features at the level of the brainstem (Wong, Skoe, Russo, Dees, & Kraus, 2007) up to the auditory cortex (Pantev, Roberts, Schultz, Engelien, & Ross, 2001; Pantev et al., 1998). On the basis of these premises, we hypothesized that musical expertise would result in a ''fine-tuning'' of the chord perceptual space, reflected in musicians' higher automatic discriminatory skills even for chords atypical for Western tonal music.

In the auditory domain, the mismatch negativity (MMN) brain response (Picton, Alain, Otten, Ritter, & Achim, 2000; Näätänen, Gaillard, & Mäntysalo, 1978) reflects the accuracy of automatic neural discrimination between two classes of stimuli or the degree of similarity and separability between them. For instance, in a study of musical timbre, the MMN correlated linearly with the subjects' ratings of similarity between the stimuli (Toiviainen et al., 1998). Preexisting memory representations of sounds or sound patterns also affect the neural discriminatory abilities indexed by the MMN. MMN studies provided evidence that a pitch change is better discriminated by musicians than by nonmusicians particularly when the stimuli resemble a musical context. For instance, Brattico, Näätänen, and Tervaniemi (2001) showed that musicians did not differ from nonmusicians in processing a pitch change of isolated sinusoidal tones, but they were faster than nonmusicians in discriminating, nonattentively, a pitch change embedded in patterns consisting of five tones, as indexed by the MMN latency. Similarly, musicians had stronger magnetic MMN (or MMNm) to abstract changes in the relative pitch of short melodies than nonmusicians but their MMNm did not differ from that of nonmusicians in response to pitch changes of pure tones (Fujioka, Trainor, Ross, Kakigi, & Pantev, 2004). Furthermore, slight mistuning of chords was detected automatically and in a highly sensitive manner by musicians such as violinists, typically adept in choosing the right locations on their instrument for engendering in-tune chords (Koelsch, Schröger, & Tervaniemi, 1999). These results show superior neural mechanisms in musicians for discrimination of sounds characterizing their musical culture and performance practice.

However, electrophysiological evidence suggests that musical expertise may be associated with generally improved auditory discriminatory abilities. These superior discriminatory abilities of musicians are particularly evident for small rather than large pitch deviations and seem to be independent from the informational context in which they occur (Marques, Moreno, Luis Castro, & Besson, 2007). For instance, electrical brain responses to weak incongruities in the pitch intonation of final words in sentences or final notes in music were elicited in children with musical training and not in musically uneducated children (Magne, Schön, & Besson, 2006).

Hence, musical expertise may lead either to generally enhanced discriminatory skills for any kind of (musical or linguistic) sound, or to a superior differentiation of culture-specific musical categories, such as atypical chords, as determined by exposure. Neuloh and Curio (2004) indeed compared the discrimination by musically trained subjects of nonprototypical dissonant chords inserted in a dissonant context with their discrimination of stereotypical consonant chords inserted in a consonant context. They found that the MMN did not differ between the two experimental conditions showing the sophistication of the musicians' auditory system in automatically discriminating stereotypical chords as well as chord categories less often encountered in Western tonal music (Neuloh & Curio, 2004). The study did not, however, directly contrast brain responses of subjects with different levels of musical expertise, leaving open the issue of whether and how formal musical training modulates chord category discrimination.

By comparing musicians' and nonmusicians' discrimination of musical sounds that are more or less prototypical within the Western tonal music tradition, we wished to address the question of whether musicians' superiority in pitch discrimination is the result of the particular contents of their training or whether it is independent of the culture-specific categorical status of the sounds. If musicians' ability to discriminate any kind of sound or sound combination—being it common or atypical in Western music—were to be found superior, the hypothesis of a generalized predisposition for pitch discrimination would be confirmed. In contrast, if the brain responses are modulated by the prototypical status of the chords, then a more fine-grained effect of musical enculturation would emerge. Adhering to the cultural-exposure view, we hypothesized that a musician's auditory system would efficiently react even to not-prototypical chords.

For this purpose, musicians and nonmusicians were measured with magnetoencephalography (MEG) while they were presented with chords of varying prototypical status in Western tonal music: a mistuned chord deviating from the major chord as it contained an atypical note not even included in the conventional Western chromatic scale, an unpleasantly sounding (dissonant) chord nonprototypical due to its rarity (testified by its not having a standard name in Western music theory), and a minor chord. Minor chords are frequently used in most of the genres of Western tonal music, hence all listeners, including those without a formal musical training, are exposed to them. All chords were infrequently inserted into a major chord context. This context served to create a conventional musical reference from which the other chords would be discerned. The belongingness of the chords to a prototypical chord category was further contrasted with the acoustic distance between the deviant and standard chords: The mistuned chord which was the most distant in the perceptual chord space containing a pitch outside the Western musical scale included the smallest acoustic deviation from the major chord used as context (see Figure 1). Because the magnitude of the MMN increases according to the physical difference

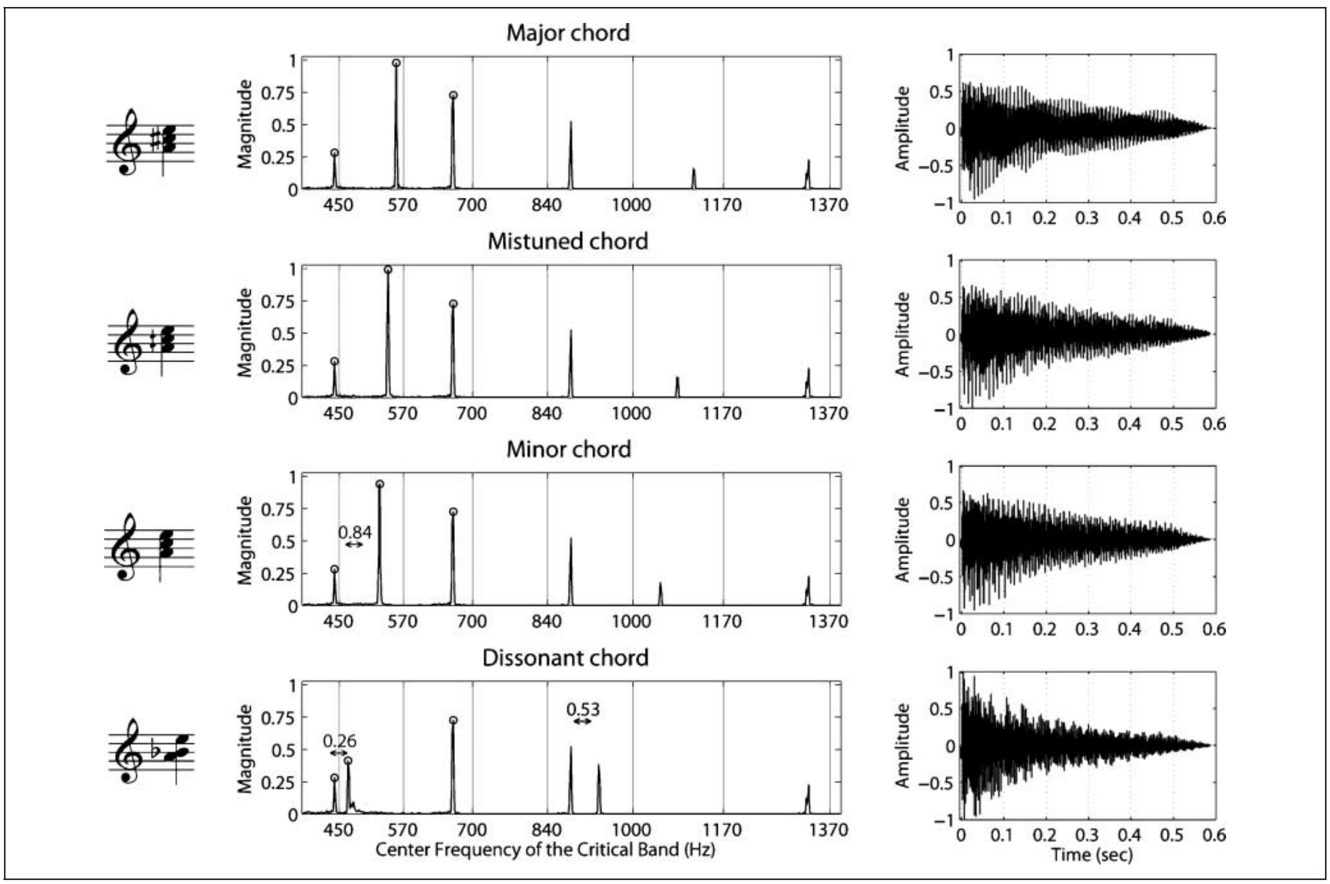


Figure 1. Acoustic description of the four stimuli used in the experiment. Left: Musical score representation. Middle: The fundamental frequencies (marked with a circle) and the first partials within the critical bandwidth. Each critical band is represented by a horizontal line. The *x*-axis is labeled according to Critical Band Center Frequencies (Hz), which demonstrates the way dissonance is generated according to psychoacoustic models: The maximum dissonance, relating to the interaction between excitation patterns in the basilar membrane, is obtained when two partials are 0.25 of critical bandwidth apart. To facilitate the interpretation of the dissonance, the fundamentals or partials that are within a critical band are labeled with the proportion of their critical bandwidth difference (the proportion between the first two fundamentals of the dissonant chord is 0.26, corresponding to very high sensory dissonance). The normalized magnitude of the partials is represented in the *y*-axis with arbitrary values from 0 to 1. Right: The amplitude envelopes of the four experimental stimuli.

between standard and deviant stimuli (e.g., Jaramillo, Paavilainen, & Näätänen, 2000), we predicted the smallest MMNm to be evoked by mistuned chords if they were neurally discriminated on the basis of acoustic distance rather than prototypical status.

Furthermore, we were interested in the relationship between automatic discrimination, musical expertise, and emotional connotations of musical chords. In a previous behavioral study, listeners without formal musical education were found to be equally able to denote minor, major, and dissonant chords according to sad, happy, and unpleasant emotional connotations, respectively (Crowder, 1985). Affective judgments may tap different mental and neural processes than auditory discrimination. In order to test the effects of musical expertise on the recognition of emotional connotations of isolated chords and how this would correlate with perceptual discrimination, we asked the subjects to rate the chords' emotional connotations of pleasantness and happiness.

METHODS

Subjects

We measured 26 subjects with normal audiological status and no history of neurological disease. The data of six subjects were rejected due to excessive amount of artifacts. The rest of the subjects were divided into two experimental groups. The "musicians" consisted of 10 subjects with a formal education at a music conservatory or academy and continuous regular practice with their main instrument (3 men; mean age = 26.2 ± 3.7 years; 1 left-handed; main instrument: 4 piano, 2 voice, 1 clarinet, 1 cello, 1 organ, 1 violin; 18.2 ± 4.5 years of practice; 2 ± 1 hours of daily practice), 4 of them were professional musicians and 6 of them were still studying at a music academy while at the same time already performing at a professional level. The other 10 subjects who did not have music as profession were classified as "nonmusicians" (3 men; mean age = 26.6 ± 4.6 years; 1 left-handed). Most of these subjects reported, however, to have received private music lessons for a short period or discontinuously (2.1 ± 3.2 years of practice; 3 subjects without any music experience). All nonmusicians described themselves as such, although they declared to like listening to music during their spare time (2 subjects listened also to classical and jazz music). The groups were comparable in terms of intelligence and socioeconomic status (all subjects had a Master's degree; 6 nonmusicians and 5 musicians were postgraduate students; 4 nonmusicians and 3 musicians were Russians and the majority of the other subjects were Finns). Informed consent to participate in the experiment was obtained from each subject. The experimental procedures were approved by the Ethics Commission of the University of Helsinki and the Helsinki University Hospital.

Stimuli

The stimuli (Figure 1) were four types of musical chords recorded with a MIDI keyboard Roland A-33 connected to AKAI S-2000 sampler, and played with a piano-like timbre (AKAI sample library). The chords were then edited using SoundForge and CoolEdit software to have the same intensity and duration (588 msec).

In all the chords, A3 was always the lowest and E4 the highest note. To construct the four chords of the experiment ("major," "minor," "dissonant," and "mistuned"), the middle note was manipulated. The "dissonant" chord contained a majority of dissonant intervals, such as the minor second and the augmented fourth. This chord does not have a standard name in traditional music theory due to its infrequent usage. On the other hand, this chord corresponds to 3–5B according to pitch-class set theory, which was originally developed to provide a theoretical framework for describing pitch organization of post-tonal contemporary music and that names every pitch combination existing in the 12-tone equally tempered system (not only familiar ones) (Forte, 1973).

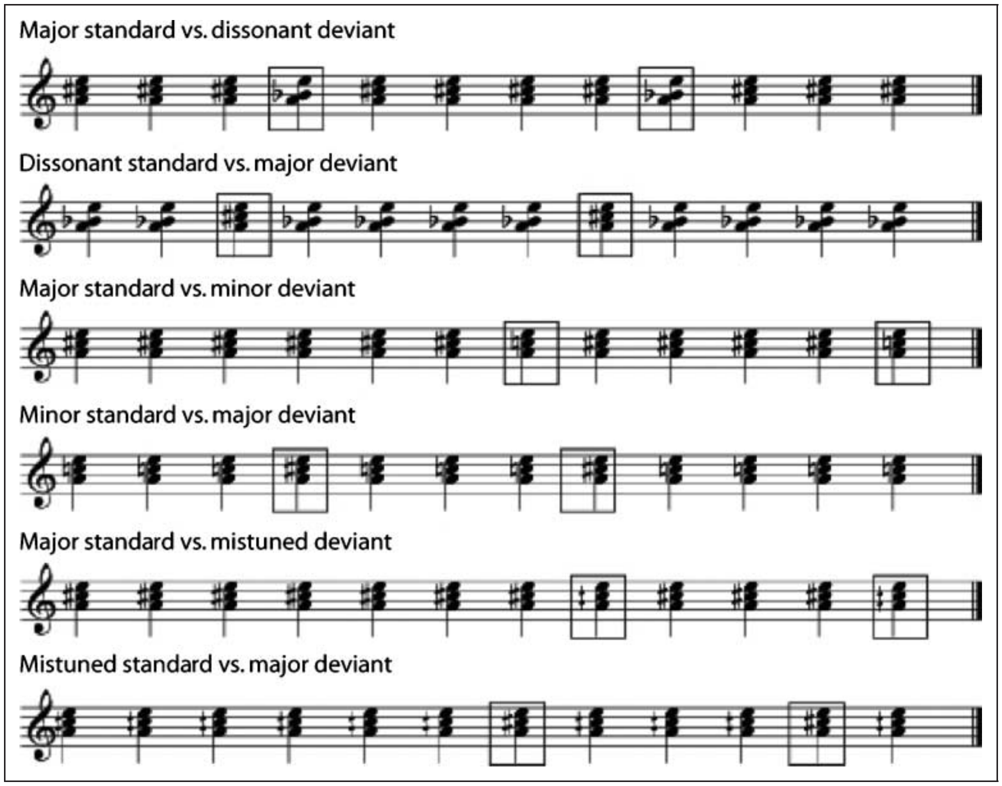
The "mistuned" chord had the middle note with a pitch between C and C sharp (C sharp decreased by 40 cents), thus sounding like a mistuned major chord. The frequency distance between the major chord and the mistuned chord was very small, having the middle pitch of the major chord, C sharp, a fundamental frequency of 277.183 Hz and the middle pitch of the mistuned chord, C sharp mistuned, a fundamental frequency of 270.96 Hz. In sum, the two pitches were separated by about 6 Hz and were related by a frequency ratio of approximately 2.55%. Note that 2 Hz has been consistently indicated as the difference limen (DL), or the smallest detectable change in frequency between two tones, one corresponding to 1 kHz (Moore, 2004).

The "minor" chord was the traditional minor triad containing the minor third interval between A3 and C4. The "major" chord was also the traditional major triad, containing the major third interval between A3 and C#4.

Experimental Procedure

The chord stimuli were presented in six conditions with an interstimulus interval of 600 msec (Figure 2). Each condition included a chord presented frequently, the standard ($p = .8$), and an infrequent chord, the deviant ($p = .2$). The chords were contrasted so that each chord was standard in one condition and deviant in another condition: (1) major as standard and minor as deviant; (2) minor as standard and major as deviant; (3) major as standard and dissonant as deviant; (4) dissonant as standard and major as deviant; (5) major as standard and mistuned as deviant; (6) mistuned as standard and major as deviant.

Figure 2. Examples of the six experimental conditions used in the experiment written in musical notation.



In all experimental conditions, stimuli were presented at 60 dB SPL by the Presentation software (Neurobehavioral Systems) through plastic tubes and silicon earpieces to subjects' ears. The plastic tubes and earpieces were especially developed by the Helsinki University of Technology for optimal transmission of complex sounds, reducing the attenuation of high frequencies. The signal reaching the subject was estimated by convolving the original waveforms with the impulse response of the system (Palomäki, 2004).

During the recordings, subjects were placed in supine position on a bed and were instructed to concentrate on watching a silent movie with subtitles projected on the ceiling while ignoring the sounds. The presentation order of the different blocks was pseudorandomized across subjects, keeping always a distance between the blocks in which standards and deviants were the same. The experiment lasted approximately 3 hr including preparation, breaks, and refreshment.

The MEG was recorded (band-pass filter: 0.03–100 Hz; sampling rate: 600 Hz) in a magnetically shielded room (Euroshield) in the BioMag Laboratory of the Helsinki University Central Hospital with a Vectorview helmet-shaped, 306-channel whole-head magnetometer (Elekta Neuromag, Finland). Before the experiment, the positions of four marker coils placed on the scalp were determined in relation to the nasion and both preauricular anatomical points with an Isotrak 3-D digitizer (Polhemus, USA). The position of the magnetometer with respect to the head was determined for each experimental condition. Eye movements were monitored with vertical and horizontal bipolar electrooculograms (EOGs). In order to obtain the event-related fields (ERFs) to the stimulus categories, the MEG epochs, starting 100 msec before and ending 500 msec after stimulus onset, were averaged on-line separately for the standard and deviant stimuli. MEG epochs contaminated by artifacts larger than 150 μV or 1500 fT/cm in any of the EOG or MEG channels, respectively, were on-line rejected from averaging. At least 90 trials of deviants were included after rejections.

MEG Data Analysis

The responses were digitally band-pass filtered at 1–20 Hz off-line. For each subject and condition, we modeled the sources of the magnetic responses by means of a fitting procedure estimating the parameters of equivalent current dipoles (ECDs) within predetermined latency windows. The ECD models were evaluated on the basis of a selection of about 70 channels (containing triplets of two gradiometers and one magnetometer) above each temporal area separately for each subject's right and left hemispheres. In the ECD modeling, we used a spherical head model. The origin of the spherical model was determined individually for each subject from their anatomical magnetic resonance image (MRI; obtained with Siemens Sonata 1.5-T system) by fitting a sphere to the curvature of the outer surface of the brain in the temporal and centro-parietal cortical areas. The *x*-axis of the sphere coordinate system passed through the two preauricular points with the positive direction to the right; the *y*-axis passed through the nasion and was perpendicular to the x-axis with the positive direction to the front; the z-axis was perpendicular to the xy-plane with the positive direction to the top.

In order to obtain the MMNm responses, the magnetic responses to the dissonant, mistuned, and minor chords when they were presented as standards were subtracted from the responses to the same chords when they were presented as deviants. This subtraction aimed at highlighting the neural mechanisms specifically involved in discrimination processes isolated from those related to mere acoustic analysis. Particularly, the contribution of the N1m, the largest magnetic response to sound onset supposedly reflecting acoustic feature analysis, was minimized by subtracting the neural responses to the same sound stimulus however presented in contexts with different probability of stimulus occurrence (Näätänen, Jacobsen, & Winkler, 2005). MMNm sources were estimated using ECD fitting in the 110–290 msec window. Similarly, ECDs were determined in the 60–160 msec window for the P1m, which was the most prominent response to the dissonant, mistuned, and minor chords when presented as standards (due to fast stimulation rate, N1m was less visible; see Figure 3; cf. also Tervaniemi et al., 1999).

We selected the dipole models according to the following criteria: (1) the dipole location (in the auditory areas); (2) the strength of the response (the largest); (3) the goodness of fit (not lower than 60%, corresponding to the percentage of the magnetic field variance accounted for by the dipole solution); (4) the dipole orientation (P1m ECD corresponding to inflow of the magnetic field and MMNm ECD corresponding to outflow of the magnetic field at the fronto-central scalp regions). In three musicians and five nonmusicians for the MMNm, and in one nonmusician for the P1m, the dipole sources in either the right or left hemispheres could not be modeled in relation to some of the experimental conditions because responses were weak and, consequently, the goodness of fit was low. In such cases, the missing values were individually imputed, as recommended in the statistical literature especially in those cases, like the present one, when the missingness is not completely at random (Tabachnick & Fidell, 2001; Schafer, 1997). Particularly, the dipole strength was imputed with random small values (on a uniform distribution from 0 to 6), on the basis of prior knowledge, as small values would closely approximate the ones resulting from fitting dipoles with low goodness of fit (Hämäläinen, Hari, Ilmoniemi, Knuutila, & Lounasmaa, 1993). The latency and location parameters for the low goodness-of-fit dipoles were instead individually imputed by the expectation maximization (EM) algorithm (Tabachnick & Fidell, 2001; Schafer, 1997).

The strengths and latencies of the ECDs were compared in three-way repeated measures ANOVAs with group as a between-subject factor (levels: nonmusicians, musicians), and chord category (levels: dissonant, minor, mistuned) and hemisphere (levels: left, right) as within-subject factors. The differences in coordinate locations between the MMNm and P1m dipoles were studied separately for each hemisphere and axis with three-way repeated measures ANOVAs having group as a between-subject factor (levels: nonmusicians, musicians), and ERF response (levels: P1m, MMNm) and chord category (levels: dissonant, minor, mistuned) as within-subject factors.

To obtain an additional measure of the magnitude of the brain responses to chords, we computed areal mean

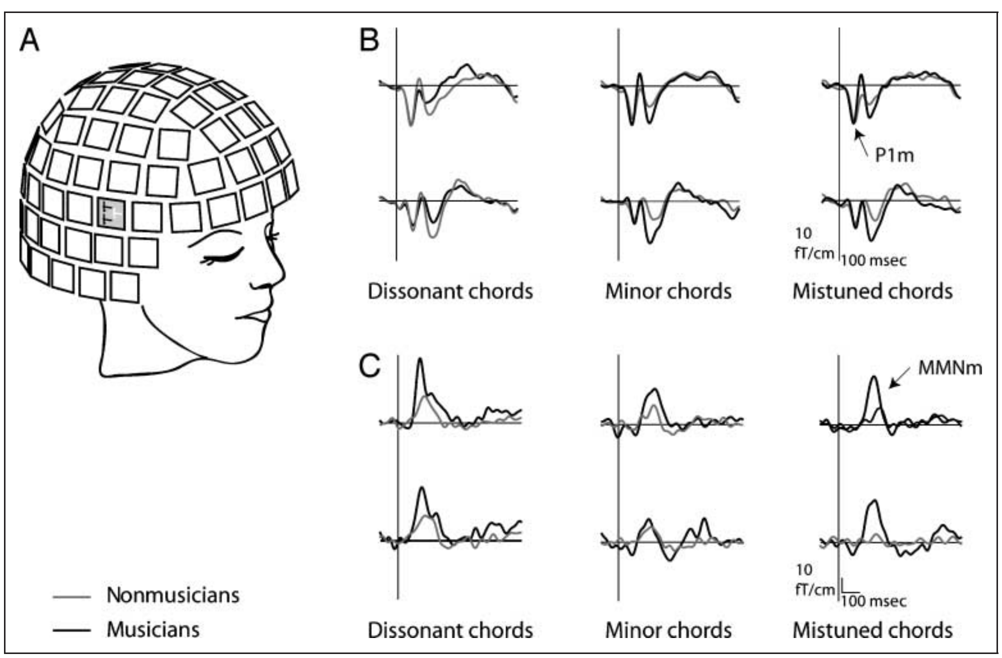


Figure 3. (A) Schematic illustration of the MEG sensors covering the head, with a single pair of planar gradiometers highlighted. (B) Grand-average (10 musicians and 10 nonmusicians) ERF waveforms to dissonant, minor, and mistuned chords when presented as standards, measured at two temporal planar gradiometer sensors over the right hemisphere. (C) Grand-average (10 musicians and 10 nonmusicians) difference waveforms measured at two temporal planar gradiometer sensors over the right hemisphere. The evoked responses to the dissonant, minor, and mistuned standard chords were subtracted from the responses to the same chords when presented as deviants.

curves over left and right frontal, temporal, and occipital areas. We first calculated vector sums of each sensor triplet by squaring the MEG signals, summing them together, and calculating the square root of this sum. The individual areal mean curves were obtained by averaging these vector sums for each ROI for each area, subject, and condition. The grand-average areal mean curves for musicians and nonmusicians were quantified by averaging the data across subjects, and by rejecting channels with deviations larger than 60 fT. Due to the way areal mean curves are calculated, they always have a positive value. The amplitudes averaged across 40 msec around the largest peaks of interest in the areal mean curves were compared in four-way repeated measures ANOVAs with group as a between-subject factor (levels: nonmusicians, musicians), and channel (levels: magnetometers, gradiometers), chord (levels: dissonant, minor, mistuned), frontality (frontal, temporal, occipital), and hemisphere (levels: left, right) as within-subject factors.

For all statistical analyses, type I errors were controlled for by Mauchly's test and the Greenhouse–Geisser epsilon when appropriate. Post hoc comparisons were performed using the least significant difference (LSD) test. Finally, the presence of correlations between years of musical training or behavioral ratings and the strength of the ECDs were tested with the Pearson's r.

Behavioral Test

At the end of the experiment, subjects were asked to fill in a questionnaire in order to judge the emotional connotations of the experimental chords (each presented three times in random order). Subjects evaluated the chords according to two 11-point scales, from -5 to $+5$. On the first scale, -5 meant "extremely unpleasant" and $+5$ meant "extremely pleasant." On the second scale, -5 meant "extremely sad" and $+5$ "extremely happy." 0 values corresponded in both scales to "neutral" judgments. Two-way repeated measures ANOVAs, with group (levels: musicians, nonmusicians) and chord (levels: major, dissonant, minor, mistuned) as factors, and LSD post hoc tests were used to statistically analyze the pleasantness and happiness judgments.

RESULTS

Part B of Figure 3 shows the grand-average ERF waveforms in response to dissonant, minor, and mistuned chords when presented as standards (in chord sequences in which major deviant chords intervened randomly), whereas Part C illustrates the grand-average difference waveforms for the MMNm to dissonant, minor, and mistuned chords when presented as deviants. The dissonant, minor, and mistuned chords were inserted in a context of major chords and for extracting the MMNm response the ERF to those chords when presented as deviants was subtracted from the ERF to the same chords when presented as standards. The ERF and difference waveforms of Figure 3 illustrate the good signal-to-noise (S/N) ratio of the data and the succession of the neurophysiological components elicited by the chords in both groups of subjects. Part A of Figure 4 represents the areal mean curves in response to dissonant, minor, and mistuned deviant chords occurring in a context of major standard chords (subtracted from the responses to same chords when used as standards). These figures suggest that musicians yielded larger MMNm responses than nonmusicians to dissonant and mistuned chords, whereas the difference in responses to minor chords was negligible. The MMNm response to the mistuned chords appeared relatively late in both musicians and nonmusicians.

P1m Strength and Latency

Bilateral ECDs were determined for the P1m component with the mean value of goodness of fit varying from 73% to 97% (M = 90% for the dipoles successfully fitted) in nonmusicians and from 76% to 98% (M = 92% for the dipoles successfully fitted) in musicians. Neither the dipole strength nor the latency of the P1m response differed significantly between the two experimental groups, the two hemispheres, or the three chord types.

MMNm Strength and Latency

The goodness of fit of the successfully fitted ECDs for the MMNm responses ranged from 60% to 98% (M = 78%) in nonmusicians and from 60% to 97% (M = 84%) in musicians. As illustrated in Figure 4, the ANOVA revealed a significant main effect of group [$F(1, 18) = 9.6, p < .01$]. The MMNm strength also differed significantly according to the chord factor [$F(2, 36) = 9.5$, $p < .001$, $\varepsilon = 0.9$]. Furthermore, the factor group significantly interacted with the factor chord [$F(2, 36) = 3.4$, $p < .05$; see Figure 4]. The most prominent difference in MMNm strength between groups was obtained for the dissonant and mistuned chords, their MMNm being significantly stronger in musicians than nonmusicians for these two chord types, as indicated by the significant main effects of group in separate ANOVAs [$F(1, 18) = 10.2$, $p < .01$ for dissonant chords and $F(1, 18) = 11.7$, $p < .01$ for the mistuned chords]. In contrast, no significant group effect was observed for the minor chords. Furthermore, nonmusicians had a smaller MMNm to the mistuned chords as compared with the dissonant and minor chords, as indicated by the significant main effect of chord [$F(2, 18) = 4.4, p < .05$] and the post hoc tests ($p < .05$) for both. In musicians, the MMNm dipole moments also differed according to the chord type, as indicated by the significant main effect of chord [$F(2, 18) = 7.4, p < .01$], although in a different way than in nonmusicians: The MMNm strength to dissonant chords was larger than to the minor chords

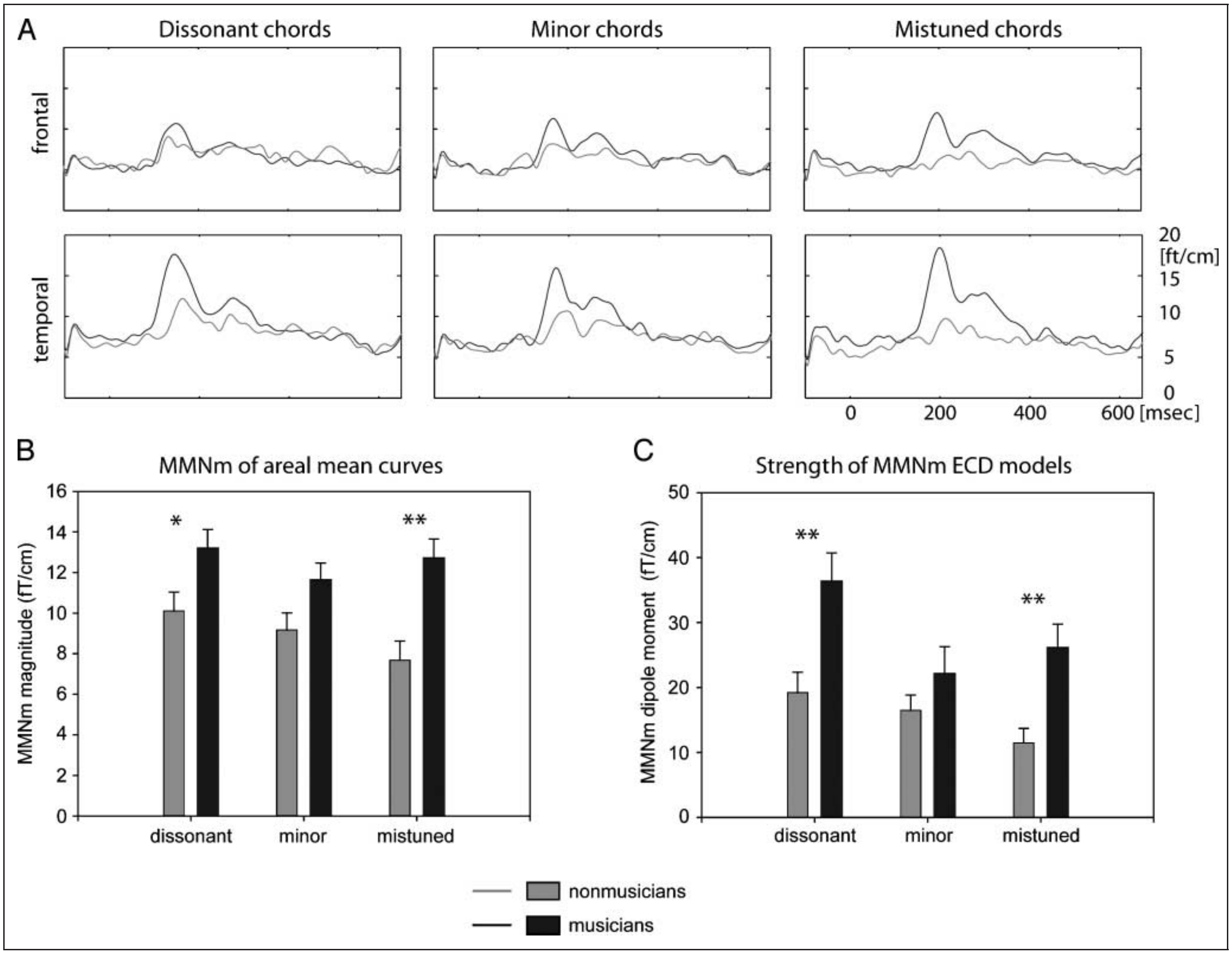


Figure 4. (A) Areal mean curves of the grand-average (10 musicians and 10 nonmusicians) difference waveforms to dissonant, minor, and mistuned chords at frontal and temporal regions of interest. (Bottom, left) The mean ECD strengths in musicians (black bars) and nonmusicians (gray bars) of the MMNm elicited by dissonant, minor, and mistuned deviant chords occurring in a context of major standard chords. To obtain the MMNm dipoles, the ERF responses to the dissonant, minor, and mistuned chords were subtracted from the ERF responses to the same chords when used as standards in sequences in which major chords served as deviants. (B) The mean amplitudes of the areal mean curves averaged over frontal and temporal regions of interest in musicians and nonmusicians of the MMNm elicited by the dissonant, minor, and mistuned deviant chords. (C) The mean strengths of the MMNm ECD models elicited by the dissonant, minor, and mistuned deviant chords. In B and C, the vertical lines indicate the standard errors of the mean; *$p < .05$, **$p < .01$.

($p < .01$) and marginally to the mistuned chords ($p = .07$), whereas the MMNm strength to mistuned chords did not differ from that to the minor chords (cf. Figure 4). Finally, the MMNm dipole moment did not differ between the left and right hemispheres, as indicated by the not-significant effect of hemisphere or interactions containing hemisphere as a factor.

The latency of MMNm dipoles differed only according to the Chord factor [$F(2, 36) = 16.6$, $p < .0001$]: Mistuned chords elicited later MMNm responses than both dissonant and minor chords (post hoc tests: $p < .0001$ and $p < .05$, respectively), and dissonant chords elicited faster MMNm responses than minor chords (post hoc test: $p < .01$; $M = 159$ msec for MMNm to dissonant chords, $M = 175$ msec for MMNm to minor chords, and $M = 197$ msec for MMNm to mistuned chords).

MMNm Magnitude

The magnitude of the MMNm responses were computed as 40-msec mean amplitudes around the peaks in the 110–290 msec time window of the areal mean curves. The MMNm response was overall larger in musicians than nonmusicians, as demonstrated by the significant main effect of group [$F(1, 18) = 9.2$, $p < .01$; Figure 4]. The ANOVA also revealed a significant Chord × Group interaction [$F(2, 36) = 3.7$, $p < .05$]. The interaction was derived from the larger MMNm responses to dissonant and mistuned but not minor chords in musicians as compared to nonmusicians, as shown by the significant main effects of group in separate ANOVAs [$F(1, 18) = 5.5$, $p < .05$ for dissonant chords and $F(1, 18) = 14.1$, $p < .01$ for mistuned chords]. The interaction Chord ×

Hemisphere × Group was also significant [$F(2, 36) = 7.3$, $p < .01$], deriving from the lack of group difference particularly in the right hemisphere for the minor chords.

Separate ANOVAs revealed a distinct modulation of chord type in musicians and nonmusicians, with a significant main effect of chord in nonmusicians [$F(2, 18) = 7.2$, $p < .01$], and a significant interaction Chord × Frontality in musicians [$F(2, 18) = 11.7$, $p < .001$]. In nonmusicians, the mistuned MMNm was smaller than both the dissonant and minor MMNm ($p < .01$ and $p < .05$ in post hoc tests, respectively), whereas the dissonant MMNm did not differ from the minor one (Figure 4). In contrast, in musicians, the only significant difference was obtained for the temporal area in the comparison between the dissonant MMNm and the minor one ($p < .05$ in post hoc test), with the minor MMNm having the smallest mean magnitude of all.

MMNm and P1m Generator Loci

Figure 5 illustrates the ECD loci of the P1m and MMNm responses, showing that overall the loci of the P1m dipoles were distinct from those of the MMNm dipoles: For instance, P1m dipoles seem to be located more lateral than MMNm dipoles in the left hemisphere. Statistical comparisons for the ECD loci of P1m and MMNm showed a significant difference at the right and left hemispheres in the medio-lateral direction (x-axis), with

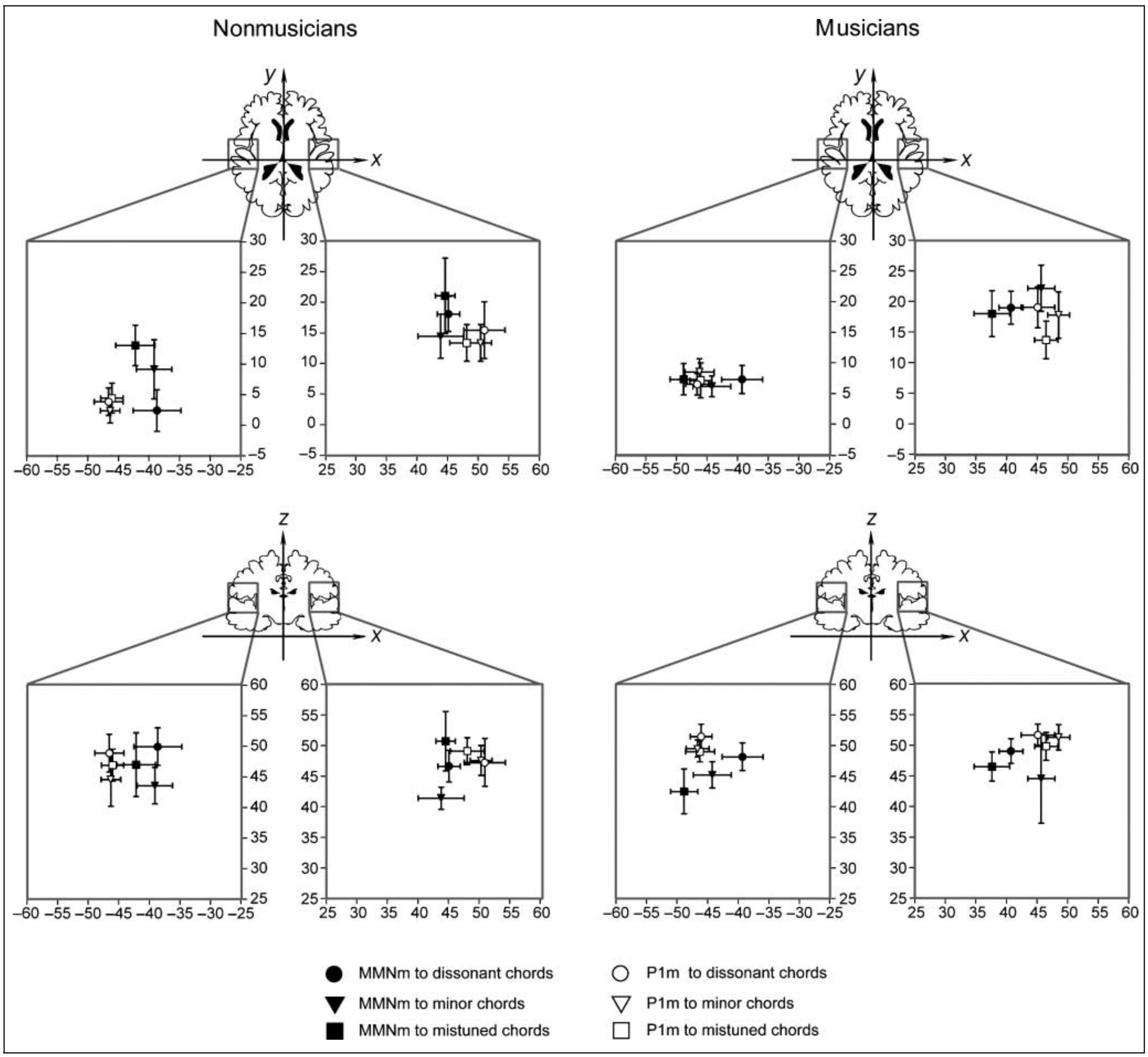


Figure 5. Mean ECD loci for the MMNm, P1m, and P2m responses in the x, y, and z Cartesian axes. The x-axis of the head coordinate system passed through the two preauricular points with positive to the right. The y-axis passed through the nasion and was perpendicular to the x-axis. The z-axis pointed up and was perpendicular to the xy-plane.

the MMNm more medial than the P1m, as indicated by the significant main effects of ERF response [$F(1, 18) = 8.4$, $p < .01$ for the left hemisphere and $F(1, 18) = 16$, $p < .001$ for the right hemisphere], and at the left hemisphere in the anterior–posterior direction, with the MMNm more frontal than the P1m, as indicated by the significant main effect of ERF response [$F(1, 18) = 5.1$, $p < .05$]. This effect was more prevalent in nonmusicians, as shown by the significant interaction Group × ERF response [$F(1, 18) = 7.7$, $p < .05$]. The ECD loci did not differ according to the group in any other coordinate direction.

Correlation between ERFs and Years of Training

As is visible from Figure 6, years of musical training in all subjects correlated significantly with the MMNm strength for dissonant chords [$r(20) = .53$, $p < .02$, two-tailed] and for mistuned chords [$r(20) = .51$, $p < .03$, two-tailed]. The correlation coefficient was not statistically reliable for minor chords [$r(20) = .18$]. No significant correlation between years of musical training and P1m strength was yielded (Figure 6).

MMNm and P1m to Major Chords in Different Contexts

We further analyzed the MMNm dipoles to major chords when presented as deviants (subtracted from the responses to the same chords when presented as standards) in the three chord contexts. The ECDs for the MMNm responses were successfully modeled with goodness of fit ranging from 61% to 92% ($M = 66\%$) for nonmusicians and from 60% to 97% ($M = 75\%$) for musicians. The MMNm strength to major chords did not differ according to the different context, as indicated by the nonsignificant main effects or interactions containing context as factor, nor according to the subject groups, as indicated by the nonsignificant main effect of group [$F(1, 18) = 2.3$, $p = .1$]. The latency of the MMNm ECD models differed between musicians and nonmusicians, as shown by the significant main effect of group [$F(1, 18) = 7.3$, $p < .05$], with nonmusicians having slower MMNm responses to major chords inserted within dissonant, mistuned, or minor contexts than musicians ($M = 201$ msec for nonmusicians and $M = 174$ msec for musicians). No other main effects or interactions were significant.

P1m dipoles were successfully modeled for all subjects (expect for one chord condition in one subject) with a goodness of fit ranging from 71% to 96% ($M = 88\%$) for nonmusicians and from 73% to 97% ($M = 92\%$) for musicians. The P1m strength to major chords did not differ according to the chord contexts, between cerebral hemispheres or subject groups, as demonstrated by the nonsignificant main effects or interactions containing context, hemisphere, or group as factors. Similarly, the P1m latency did not yield any significant effect or interaction.

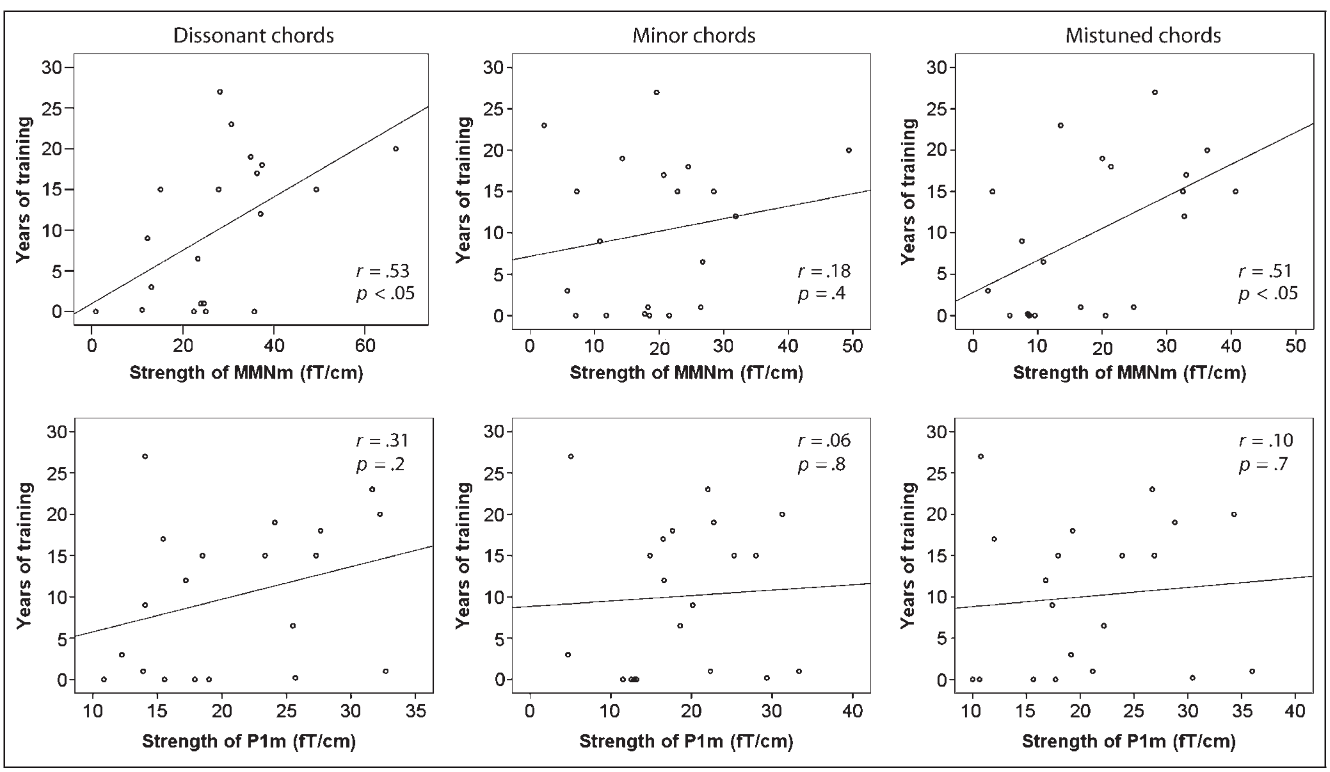


Figure 6. Top: Graphs plotting the correlation between years of musical training and the MMNm strength values in all subjects ($n = 20$). Bottom: Graphs plotting the correlation between years of musical training and the P1m strength in all subjects ($n = 20$).

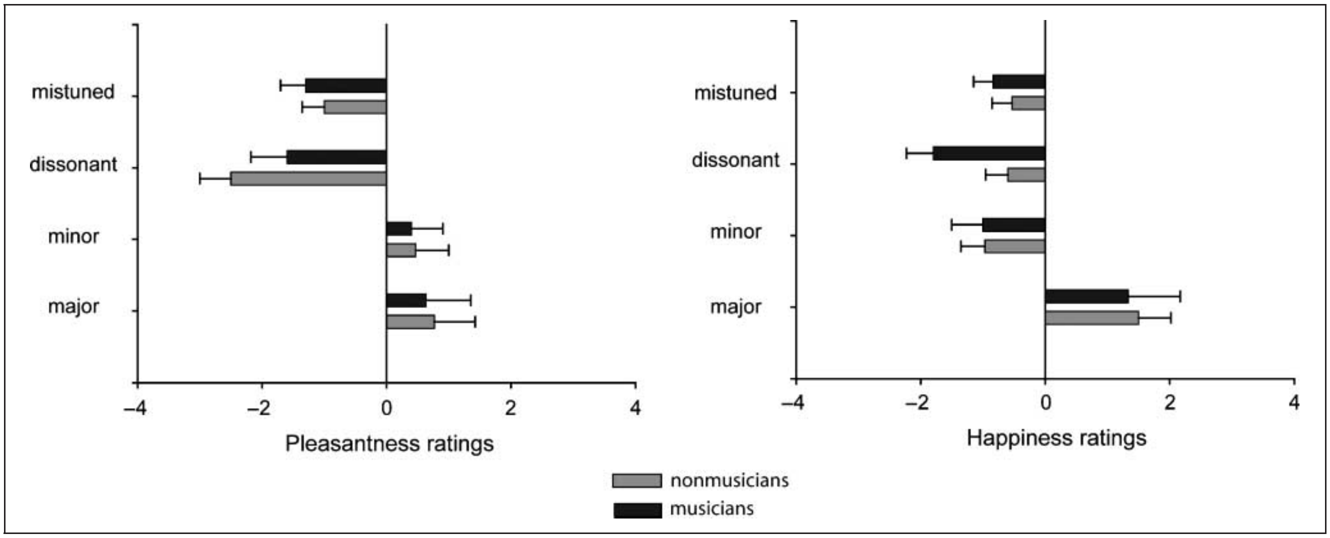


Figure 7. Graphs plotting the behavioral ratings of pleasantness and happiness for major, minor, dissonant, and mistuned chords by musicians and nonmusicians.

Behavioral Test

The paper-and-pencil test showed that the major and minor chords sounded more pleasant to both subject groups than the dissonant and mistuned chords [$F(3, 54) = 15.2$, $p < .0001$, $\varepsilon = 0.8$; post hoc tests: $p < .05$–$.0001$; Figure 7]. The dissonant chord obtained the lowest ratings and those marginally differed also from the pleasantness ratings of the mistuned chord ($p = .07$). In contrast, the ratings of major chords did not differ from those of minor chords. No group differences were obtained in the pleasantness ratings. In the happiness ratings, both musicians and nonmusicians gave more positive judgments to the major chord than to all the other chords, whose ratings did not differ between each other [$F(3, 54) = 10.1$, $p < .001$, $\varepsilon = 0.5$; post hoc tests: $p < .001$–$.005$]. A tendency toward more negative judgments of all the chords by musicians was also observed, as indicated by the main effect of group [$F(1, 18) = 4.4$, $p = .051$].

Correlations between ERF Responses and Behavioral Results

The behavioral ratings of pleasantness correlated negatively with the strength of the MMNm elicited by the minor chords only [$r(20) = -.5$, $p < .03$, two-tailed]. No other significant correlation between behavioral ratings of pleasantness or happiness and the MMNm or P1m strength to the three chord types was yielded.

DISCUSSION

In our MEG investigation, we found that the discrimination of nonprototypical mistuned and dissonant chords was facilitated in musicians compared to nonmusicians as indexed by MMNm strength. In contrast, the MMNm responses to minor chords inserted in a context of major chords were less affected by the level of musical training. Additionally, the strength of the MMNm to the nonprototypical chords was correlated with the length of musical education, whereas the MMNm to the minor chord was not. Taken together, these findings suggest that cortical discrimination of chords not typical of Western tonal music is dependent on the amount of musical training, whereas conventional sounds are discriminated equally well by musicians and nonmusicians.

The dissonant chords, similarly to the mistuned chords, were rated by both experimental groups as more unpleasant than major and minor chords. However, the subjective unpleasantness of the dissonant and mistuned chords observed in the behavioral ratings is accounted for by different processes (as also testified by the tendency for a difference between the ratings for the two chords). Highly dissonant chords are rare in Western tonal music. The preference for consonant chords, which is associated with their frequent choice by music makers, originates from the physiological constraints of our auditory system. In other words, the unpleasantness associated with the dissonant chord used in this experiment corresponded to the sensory roughness originating from beats in the spectral waveform (Leman, 2000). The mistuned major chord, on the other hand, contained no strong beats (see Figure 1) and its unpleasantness was mainly related to the violated expectations for the prototypical pitch templates. Behavioral literature documents that infants are not biased for the specific tuning of musical scales: They detect equally well violations of a common tune when played in an unfamiliar unequal step scale or in the familiar major musical scale, whereas adults detect the violations only when inserted in the major scale (Trehub, Schellenberg, & Kamenetsky, 1999).

Our electrophysiological results showing an enhanced MMNm to impure chords containing a mistuned pitch in musicians compared with the almost absent MMNm in nonmusicians partially confirms previous results obtained with EEG recordings. Koelsch et al. (1999) showed that violinists were more sensitive to slight pitch mistunings in sinusoidal chords than nonmusicians, with no corresponding group difference to pitch changes in isolated sinusoidal tones. It is of note that discrimination of mistunings is particularly crucial for the performance practice of violinists who have to adjust their hands' positions in order to obtain tuned sounds from their instrument, as compared, for instance, to pianists who play an instrument with fixed tuning. In our study, we used an acoustically more obvious mistuning, thus obtaining MMNm responses in any kind of musician. In sum, the present results may imply musicians' enhanced accuracy during a complex process including the accurate neural representation of the in-tune chord template, the neural analysis of the spectral components of the mistuned chord, and the automatic discernment of the subtle discrepancy between the two stimuli. The complexity of this process is further indexed in our data by the delayed latency of the MMNm to mistuned chords in both experimental groups. Previously, prolonged MMN latencies have been associated with highly demanding sound discrimination in adults or deteriorated discrimination in clinical groups (e.g., Jansson-Verkasalo et al., 2003; Winsberg et al., 1993).

The dissonant chord was also discriminated more accurately from major chords by musicians than nonmusicians, as indicated by the MMNm dipole moment data. Musicians seem to respond to dissonance more efficiently than nonmusicians. In line with this, previous behavioral results showed that musicians respond faster to dissonant chords than do nonmusicians (Bigand, Madurell, Tillmann, & Pineau, 1999). Moreover, the N1 differed between dissonant and consonant chords in musicians but not in nonmusicians, possibly indicating greater difficulty of the nonmusician's brain to process the beating present in the dissonant chord (Regnault, Bigand, & Besson, 2001).

Furthermore, although musicians had larger change-related neural responses to less common chords in Western tonal music compared to nonmusicians, the two groups did not differ in their brain responses to widely used chords such as the minor ones. Musical expertise derived from formal musical training, hence, seems to be specifically reflected in the cortical automatic discrimination of nonprototypical chords. In the visual processing literature, categories are more differentiated when they are familiar and recognition reaches the subordinate level according to the level of expertise with a particular category of objects (e.g., Quinn & Tanaka, 2007). In this sense, the higher automatic discrimination in musicians between prototypical and nonprototypical chords may result from their internalization of common as well as uncommon nonprototypical chords. For instance, chords including mistuned notes or dissonant chords not even having a name in Western harmony theory are classified automatically and efficiently distinguished from the prototypical major chords by musicians. Nonmusicians show comparable discriminatory abilities with chords that are very common in Western tonal music. We could hence propose that they have not reached the type of perceptual expertise that musicians possess, characterized by distinctiveness between fine chord categories, even when represented by nonprototypical exemplars.

An opposite interpretation of the results would suggest that musicians have overall more sophisticated auditory abilities than nonmusicians. Those abilities would lead them to be more sensitive to the deviance of dissonant and mistuned events, particularly consisting of the beats in the dissonant chord and the small physical distance between mistuned and major chords. This account is in line with findings of higher neural processing skills in musicians for both language and musical sounds (Magne et al., 2006). On the other hand, we did not find any difference in the P1m responses to the four chords between groups, indicating that chord sensory processing was unaffected by formal musical training, as further discussed below. Although in music, sensory and cognitive aspects are often intersected, additional studies should attempt at unambiguously ruling out the effects of auditory skills on expert culture-specific categorical perception.

A complementary view would suggest that musicians possess accurate templates also for the standard prototypical chords to which the nonprototypical ones are compared. In support of this, the MMNm strength depended on the categorical distance between standard and deviant chord stimuli. Particularly, the smallest MMNm was obtained to the minor chord in musicians and to the mistuned chord in nonmusicians. Consequently, in less expert subjects, chords are ordered according to their acoustic distance, the mistuned chord being the closest to the major chord used as repetitive context. In contrasts, in music experts, the chords are the least similar when belonging to a different categorical status, the mistuned chord being the least prototypical and the major chord being the most typical one in the most diffuse musical genre (i.e., Western tonal music). Hence, these results are based on the precise encoding of the major chords according to their prototypical status and on a more defined categorical space in musicians as compared with nonmusicians (for similar conclusions based on behavioral findings, see Burns, 1999).

Our results may derive from the musicians' being more familiar with chords that are atypical for Western tonal music as a result of their performing of and listening to some musical genres such as, in particular, classical music. Classical music of the Western tradition (and especially some styles or subgenres of it such as Romantic and Modern) is a musical genre characterized by higher perceptual and grammatical complexity than other musical genres (Lévy, 1995). In classical music and even in some modern styles of jazz music, it is likely to be exposed to nonprototypical chords such as intentionally mistuned or highly dissonant ones. Nonmusicians mainly listen on a daily basis to the popular and rock music genres, characterized by a more generalized usage of standard chords (except for some less widespread subgenres where sensory dissonance is more common due to extensive use of distorted guitar, such as in gothic metal or alternative rock). In our study, we obtained a significant interaction between group and chord type, and a correlation between years of training and MMNm strength was absent only for the minor chords. Minor chords are relatively common in all Western tonal music, and even nonmusicians are presumably equally exposed to them. The amount of active exposure to classical music may hence lead to a flexible and highly sophisticated auditory system able to respond to any kind of musical event, even alien to the principles of Western tonal music. In support of this interpretation, behavioral data indicate that whereas less musically trained subjects perform better in detecting the mistunings from Western musical scales than from non-Western (Javanese) musical scales, musicians perform the task equally well with both scales (Lynch, Eilers, Oller, Urbano, & Wilson, 1991).

Change-related responses of the brain are influenced not only by the amount of music exposure but also by the quality of the mechanisms involved. The continuous attention demanding training of musicians, as well as rehearsal and consolidation of the acquired conceptual and procedural skills, is the most apt way to develop perceptual expertise for music categories. According to general theories of perceptual expertise, attentive and long-term continuous training with multiple stimuli leads to increased differentiation of the important stimulus features at the cost of the irrelevant ones (Goldstone, 1998). Moreover, there is a growing body of evidence showing that attention during sound exposure is needed to acquire neural abilities, which can lead to automatic encoding of sounds in sensory memory (Atienza, Cantero, & Dominguez-Marin, 2002; Tervaniemi, Rytkönen, Schröger, Ilmoniemi, & Näätänen, 2001; Menning, Roberts, & Pantev, 2000; Näätänen, Schröger, Karakas, Tervaniemi, & Paavilainen, 1993). Musicians' attentive exposure to chord categories would have enabled them to fine-tune their chord representations, as evidenced by automatic superior discrimination of chords differing in their prototypical status.

Alternatively, the role of training and exposure in the acquisition of these specific auditory skills is possibly accompanied by innate predispositions for refined sound discrimination in certain individuals. Tervaniemi, Ilvonen, Karma, Alho, and Näätänen (1997) found differences in the automatic neural change-processing of temporally complex tone patterns but not of isolated major versus minor chords in musically untrained subjects grouped as musical or unmusical according to a musicality test. Moreover, the presence of congenital disorders of music perception and cognition (e.g., Peretz, Brattico, & Tervaniemi, 2005) and of genetic differences in pitch recognition (Drayna, Manichaikul, de Lange, Snieder, & Spector, 2001) indicates that enhancement in chord discrimination is at least partly affected by innate predispositions in those subjects that have chosen music as their profession.

In contrast with the current electrophysiological findings, the behavioral ratings on the perceptual quality and emotional connotations of sounds obtained after the MEG experiment did not show any difference between musicians and nonmusicians. In particular, both groups rated the dissonant and mistuned chords as more unpleasant than the major and minor ones. A negative correlation with years of training for the minor chord, indicating more frequent unpleasantness ratings in musicians, provides a mild tendency for experience-dependent affective responses to chords. However, in general, these findings are in line with previous literature showing negative judgments of dissonant chords by adult listeners even lacking a formal musical education (e.g., Pallesen, Brattico, & Carlson, 2003; Blood, Zatorre, Bermudez, & Evans, 1999; Kameoka & Kuriyagawa, 1969). Moreover, they suggest that neural measures are a more appropriate tool for studying cortical plasticity than behavioral tests (Münte et al., 2002).

Interestingly, the main difference in the magnetic brain responses was obtained in the MMNm to deviant chords inserted in a major context, whereas the obligatory sensory P1m to the chords when presented as standards differentiated neither between chord types nor subject groups. This shows that the initial feature analysis of sounds in the primary and nonprimary auditory cortex (Näätänen & Winkler, 1999; Liegeois-Chauvel, Musolino, Badier, Marquis, & Chauvel, 1994), reflected by the P1m elicitation, does not differ between the experimental conditions and groups, possibly thanks to the optimal balance between the basic acoustic parameters of the chords (shape of the sound wave, intensity, frequency range). Furthermore, the MMNm to the major chords when presented as deviants inserted in contexts of minor, dissonant, or mistuned chords also did not differentiate musicians from nonmusicians, defining the effect of musical expertise on the neural change-related responses to nonprototypical chords.

In sum, the differences in the MMNm response to chords unconventional in Western tonal music index effects of musical sophistication and enculturation on sensory memory and discrimination processes. Moreover, the present results suggest limitations in the implicit musicality possessed by any individual exposed passively to a musical culture; this musicality seems to be confined to the neural processing of sounds commonly used in Western music but not to more unconventional ones. Correspondingly, musical education may be accompanied with the neural tools necessary to process, understand, and appreciate musical structures that are less attractive to majority of the listeners.

Acknowledgments

We thank Dr. Antti Korvenoja and Dr. Synnöve Carlson, Dr. Tuire Kuusi, Prof. Peter Vuust, Samu Taulu (Neuromag, Elekta), and Prof. Petri Toiviainen for help in various stages of the experiment. The study was funded by the Academy of Finland (projects 77322 and 73038), the Pythagoras Graduate School in Sound and Music Research (Ministry of Education, Finland), the Consiglio Nazionale delle Ricerche (CNR, Italy), the Jenny and Antti Wihuri Foundation (Finland), and the Center for International Mobility (CIMO, Finland).

Reprint requests should be sent to Elvira Brattico, Cognitive Brain Research Unit, Department of Psychology, University of Helsinki, P.O. Box 9, 00014 Finland, or via e-mail: elvira.brattico@helsinki.fi.

REFERENCES

Atienza, M., Cantero, J. L., & Dominguez-Marin, E. (2002). The time course of neural changes underlying auditory perceptual learning. *Learning and Memory, 9,* 138–150.

Bigand, E. (2003). More about the musical expertise of musically untrained listeners. *Annals of the New York Academy of Sciences, 999,* 304–312.

Bigand, E., Madurell, F., Tillmann, B., & Pineau, M. (1999). Effect of global structure and temporal organization on chord processing. *Journal of Experimental Psychology: Human Perception and Performance, 25,* 184–197.

Blood, A. J., Zatorre, R. J., Bermudez, P., & Evans, A. C. (1999). Emotional responses to pleasant and unpleasant music correlate with activity in paralimbic brain regions. *Nature Neuroscience, 2,* 382–387.

Brattico, E., Näätänen, R., & Tervaniemi, M. (2001). Context effects on pitch perception in musicians and nonmusicians: Evidence from ERP recordings. *Music Perception, 19,* 1–24.

Brattico, E., Tervaniemi, M., Näätänen, R., & Peretz, I. (2006). Musical scale properties are automatically processed in the human auditory cortex. *Brain Research, 1117,* 162–174.

Bukach, C. M., Gauthier, I., & Tarr, M. J. (2006). Beyond faces and modularity: The power of an expertise framework. *Trends in Cognitive Sciences, 10,* 159–166.

Burns, E. M. (1999). Intervals, scales, and tuning. In D. Deutsch (Ed.), *The psychology of music* (pp. 215–264). San Diego: Academic Press.

Crowder, R. G. (1985). Perception of the major/minor distinction: II Experimental investigations. *Psychomusicology, 5,* 3–23.

Drayna, D., Manichaikul, A., de Lange, M., Snieder, H., & Spector, T. (2001). Genetic correlates of musical pitch recognition in humans. *Science, 291,* 1969–1972.

Forte, A. (1973). *The structure of atonal music*. New Haven, CT: Yale University Press.

Fujioka, T., Trainor, L. J., Ross, B., Kakigi, R., & Pantev, C. (2004). Musical training enhances automatic encoding of melodic contour and interval structure. *Journal of Cognitive Neuroscience, 16,* 1010–1021.

Goldstone, R. L. (1998). Perceptual learning. *Annual Review of Psychology, 49,* 585–612.

Hämäläinen, M., Hari, R., Ilmoniemi, R. J., Knuutila, J., & Lounasmaa, O. V. (1993). Magnetoencephalography—Theory, instrumentation, and applications to noninvasive studies of the working brain. *Reviews of Modern Physics, 65,* 413–497.

Hannon, E. E., & Trainor, L. J. (2007). Music acquisition: Effects of enculturation and formal training on development. *Trends in Cognitive Sciences, 11,* 466–472.

Jansson-Verkasalo, E., Ceponiene, R., Kielinen, M., Suominen, K., Jäntti, V., Linna, S.-L., et al. (2003). Deficient auditory processing in children with Asperger syndrome, as indexed by event-related potentials. *Neuroscience Letters, 338,* 197–200.

Jaramillo, M., Paavilainen, P., & Näätänen, R. (2000). Mismatch negativity and behavioural discrimination in humans as a function of the magnitude of change in sound duration. *Neuroscience Letters, 290,* 101–104.

Kameoka, A., & Kuriyagawa, M. (1969). Consonance theory Part II: Consonance of complex tones and its calculation method. *Journal of the Acoustical Society of America, 45,* 1460–1469.

Koelsch, S., Schröger, E., & Tervaniemi, M. (1999). Superior pre-attentive auditory processing in musicians. *NeuroReport, 10,* 1309–1313.

Krumhansl, C. L. (1990). *Cognitive foundations of musical pitch*. New York: Oxford University Press.

Leman, M. (2000, December 7–9). *Visualization and calculation of the roughness of acoustical musical signals using the synchronization index model (SIM)*. Paper presented at the COST G-6 Conference on Digital Audio Effects (DAFX-00), Verona, Italy.

Lévy, F. (1995). *Complexite Grammatologique et complexite apercetive en musique*. Retrieved from http://recherche.ircam.fr/equipes/repmus/Rapports/TheseFabLevy.pdf. Accessed on 24 August 2004.

Liegeois-Chauvel, C., Musolino, A., Badier, J. M., Marquis, P., & Chauvel, P. (1994). Evoked potentials recorded from the auditory cortex in man: Evaluation and topography of the middle latency components. *Electroencephalography and Clinical Neurophysiology, 92,* 204–214.

Lynch, M. P., Eilers, R. E., Oller, K. D., Urbano, R. C., & Wilson, P. (1991). Influences of acculturation and musical sophistication on perception of musical interval patterns. *Journal of Experimental Psychology: Human Perception and Performance, 17,* 967–975.

Magne, C., Schön, D., & Besson, M. (2006). Musician children detect pitch violations in both music and language better than nonmusician children: Behavioral and electrophysiological approaches. *Journal of Cognitive Neuroscience, 18,* 199–211.

Marques, C., Moreno, S., Luis Castro, S., & Besson, M. (2007). Musicians detect pitch violation in a foreign language better than nonmusicians: Behavioral and electrophysiological evidence. *Journal of Cognitive Neuroscience, 19,* 1453–1463.

Martindale, C., & Moore, K. (1989). Relationship of musical preference to collative, ecological, and psychophysical variables. *Music Perception, 6,* 431–446.

Menning, H., Roberts, L. E., & Pantev, C. (2000). Plastic changes in the auditory cortex induced by intensive frequency discrimination training. *NeuroReport, 11,* 817–822.

Moore, B. J. C. (2004). *Introduction to the psychology of hearing*. San Diego, CA: Academic Press.

Münte, T. F., Altenmüller, E., & Jäncke, L. (2002). The musicians' brain as a model of neuroplasticity. *Nature Reviews Neuroscience, 3,* 473–478.

Näätänen, R., Gaillard, A. W., & Mäntysalo, S. (1978). Early selective-attention effect on evoked potential reinterpreted. *Acta Psychologica, 42,* 313–329.

Näätänen, R., Jacobsen, T., & Winkler, I. (2005). Memory-based or afferent processes in mismatch negativity (MMN): A review of the evidence. *Psychophysiology, 42,* 25–32.
Näätänen, R., Schröger, E., Karakas, S., Tervaniemi, M., & Paavilainen, P. (1993). Development of a memory trace for a complex sound in the human brain. *NeuroReport, 4,* 503–506.
Näätänen, R., & Winkler, I. (1999). The concept of auditory stimulus representation in cognitive neuroscience. *Psychological Bulletin, 125,* 826–859.
Neuloh, G., & Curio, G. (2004). Does familiarity facilitate the cortical processing of music sounds? *NeuroReport, 15,* 2471–2475.
North, A. C., & Hargreaves, D. J. (2000). Collative variables versus prototypicality. *Empirical Studies of the Arts, 18,* 13–17.
Pallesen, K. J., Brattico, E., & Carlson, S. (2003). Emotional connotations of major and minor musical chords in musically untrained listeners. *Brain and Cognition, 51,* 188–190.
Palomäki, K. (2004). *An evaluation of audio systems of the Biomag laboratory*. Retrieved from www.cis.hut.fi/kpalomak/pubs/biomagaudio.pdf#search=%22palom%C3%A4ki%20biomag%22. Accessed on 10 February 2005.
Pantev, C., Oostenveld, R., Engelien, A., Ross, B., Roberts, L. E., & Hoke, M. (1998). Increased auditory cortical representation in musicians. *Nature, 392,* 811–814.
Pantev, C., Roberts, L. E., Schultz, M., Engelien, A., & Ross, B. (2001). Timbre-specific enhancement of auditory cortical representations in musicians. *NeuroReport, 12,* 169–174.
Peretz, I., Brattico, E., & Tervaniemi, M. (2005). Abnormal electrical brain responses to pitch in congenital amusia. *Annals of Neurology, 58,* 478–482.
Picton, T. W., Alain, C., Otten, L., Ritter, W., & Achim, A. (2000). Mismatch negativity: Different water in the same river. *Audiology & Neuro-Otology, 5,* 111–139.
Quinn, P. C., & Tanaka, J. W. (2007). Early development of perceptual expertise: Within-basic-level categorization experience facilitates the formation of subordinate-level category representations in 6- to 7-month-old infants. *Memory & Cognition, 35,* 1422–1431.
Regnault, P., Bigand, E., & Besson, M. (2001). Different brain mechanisms mediate sensitivity to sensory consonance and harmonic context: Evidence from auditory event-related brain potentials. *Journal of Cognitive Neuroscience, 13,* 241–255.
Sadie, S., & Tyrrell, J. (Eds.) (2001). *The new grove dictionary of music and musicians*. London: Oxford University Press.
Schafer, J. L. (1997). *Analysis of incomplete multivariate data* (Vol. 72). London: Chapman & Hall.
Schellenberg, E. G. (2001). Asymmetries in the discrimination of musical intervals: Going out-of-tune is more noticeable than going-in-tune. *Music Perception, 19,* 223–248.
Stenberg, R. J. (1999). *Cognitive psychology* (2nd ed.). Fort Wox, TX: Harcourt Brace College.
Tabachnick, B. G., & Fidell, L. S. (2001). *Using multivariate statistics*. Needham Height, MA: Allyn and Bacon.
Tarr, M. J., & Gauthier, I. (2000). FFA: A flexible fusiform area for subordinate-level visual processing automatized by expertise. *Nature Neuroscience, 3,* 764–769.
Tervaniemi, M., Ilvonen, T., Karma, K., Alho, K., & Näätänen, R. (1997). The musical brain: Brain waves reveal the neurophysiological basis of musicality in human subjects. *Neuroscience Letters, 226,* 1–4.
Tervaniemi, M., Kujala, A., Alho, K., Virtanen, J., Ilmoniemi, R. J., & Näätänen, R. (1999). Functional specialization of the human auditory cortex in processing phonetic and musical sounds: A magnetoencephalographic (MEG) study. *Neuroimage, 9,* 330–336.
Tervaniemi, M., Rytkönen, M., Schröger, E., Ilmoniemi, R. J., & Näätänen, R. (2001). Superior formation of cortical memory traces of melodic patterns in musicians. *Learning and Memory, 8,* 295–300.
Tillmann, B., Bharucha, J. J., & Bigand, E. (2000). Implicit learning of tonality: A self-organizing approach. *Psychological Review, 107,* 885–913.
Toiviainen, P., Tervaniemi, M., Louhivuori, J., Huotilainen, M., Saher, M., & Näätänen, R. (1998). Musical timbre: Convergence of neural, behavioral, and computational approaches. *Music Perception, 16,* 223–241.
Trehub, S. E., Schellenberg, E. G., & Kamenetsky, S. B. (1999). Infants' and adults' perception of scale structure. *Journal of Experimental Psychology: Human Perception and Performance, 25,* 965–975.
Winsberg, M. G., Javitt, D. C., Silipo, G. S., & Doneshka, P. (1993). Mismatch negativity in hyperactive children: Effects of methylphenidate. *Psychopharmacological Bulletin, 29,* 229–233.
Wong, P. C. M., Skoe, E., Russo, N. M., Dees, T., & Kraus, N. (2007). Musical experience shapes human brainstem encoding of linguistic pitch patterns. *Nature Neuroscience, 10,* 420–422.