

Untangling syntactic and sensory processing: An ERP study of music perception

STEFAN KOELSCH,^{a,b} SEBASTIAN JENTSCHKE,^a DANIELA SAMMLER,^a AND DANIEL MIETCHEN^a

^aIndependent Junior Research Group Neurocognition of Music, Max-Planck-Institute for Human Cognitive and Brain Sciences, Leipzig, Germany

^bDepartment of Psychology, University of Sussex, Brighton, United Kingdom

Abstract

The present study investigated music-syntactic processing with chord sequences that ended on either regular or irregular chord functions. Sequences were composed such that perceived differences in the cognitive processing between syntactically regular and irregular chords could not be due to the sensory processing of acoustic factors like pitch repetition, pitch commonality (the major component of “sensory dissonance”), or roughness. Three experiments with independent groups of subjects were conducted: a behavioral experiment and two experiments using electroencephalography. Irregular chords elicited an early right anterior negativity (ERAN) in the event-related brain potentials (ERPs) under both task-relevant and task-irrelevant conditions. Behaviorally, participants detected around 75% of the irregular chords, indicating that these chords were only moderately salient. Nevertheless, the irregular chords reliably elicited clear ERP effects. Amateur musicians were slightly more sensitive to musical irregularities than nonmusicians, supporting previous studies demonstrating effects of musical training on music-syntactic processing. The findings indicate that the ERAN is an index of music-syntactic processing and that the ERAN can be elicited even when irregular chords are not detectable based on acoustical factors such as pitch repetition, sensory dissonance, or roughness.

Descriptors: Auditory processing, Music, EEG, MMN, ERAN, EAN, N5

All types of music show an organization of perceptually discrete elements (such as tones, intervals, and chords) into sequences that are structured according to syntactic regularities (Koelsch, 2005; Patel, 2003; Riemann, 1877/1971; Tillmann, Bharucha, & Bigand, 2000). The human brain has the capability to effortlessly acquire knowledge about music-syntactic regularities and to process musical information fast and accurately according to this knowledge. Such processing is a prerequisite for the understanding of music, and the neural mechanisms underlying music-syntactic processing appear also to be important for language-syntactic processing, as well as for other cognitive operations such as sequencing of auditory information (e.g., Janata & Grafton, 2003; Janata, Tillmann, & Bharucha, 2002; Koelsch, 2005; Koelsch & Siebel, 2005; Patel, 2003; see also General Discussion).

The present study investigates neural correlates of music-syntactic processing using music-theoretically described regular-

ities of major–minor (“Western”) tonal music. In major–minor tonal music, the temporal, or horizontal, aspect of harmonic structure is based on the progression of chord functions. Chord functions are, for example, chords built on the scale tones (Figure 1). The chord built on the first scale tone is denoted as the tonic, the chord built on the fifth scale tone is the dominant, and the chord built on the fourth scale tone is the subdominant. The arrangement of chord functions within a musical sequence follows regularities. For example, a dominant is often directly preceded by a subdominant, but rarely vice versa. Another instance of a musical regularity is the end of a harmonic progression being frequently marked by a dominant-tonic progression. In contrast, a tonic-dominant progression is not acceptable as a marker of the end of a harmonic progression.

Although nonmusicians usually do not have explicit knowledge about music theory, or of terms like “tonic” and “dominant,” they nevertheless have a sophisticated (implicit) knowledge of chord functions, harmonic relations between chord functions, and the complex regularities of their arrangement (nonmusicians acquire this implicit knowledge presumably during listening experiences of everyday life; Bigand, Tillmann, Poulin, D’Adamo, & Madurell, 2001; Koelsch, Gunter, Friederici, & Schröger, 2000; Tillmann et al., 2000).

We thank Richard Parncutt, Chris Darwin, and Marc Leman for helpful comments on an earlier version of this article. We thank Regine Asseburg, Clemens Maidhof, and Tobias Teichert for assistance in conducting and evaluating the experiments. Examples of the stimuli are available at <http://www.stefan-koelsch.de/ERAN-ST-DD>.

Address reprint requests to: Stefan Koelsch, Max-Planck-Institute for Human Cognitive and Brain Sciences, Stephanstr. 1a, 04103 Leipzig, Germany. E-mail: mail@stefan-koelsch.de

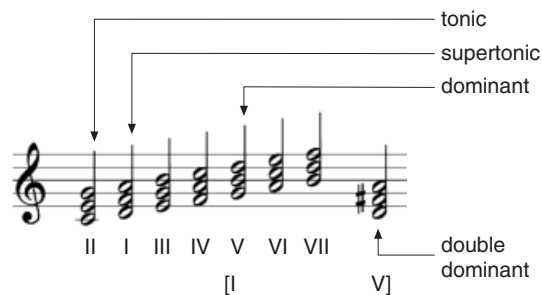


Figure 1. Examples of chord functions. The chord built on the first scale tone is denoted as the tonic, the chord on the second scale tone as the supertonic, and the chord on the fifth scale tone as the dominant. The major chord on the second tone of a scale can be interpreted as the dominant to the dominant (double dominant, see square brackets).

The regularities of the arrangement of chord functions within a harmonic sequence have been denoted as part of a musical syntax (Koelsch, 2005; Riemann, 1877/1971), and particularly the dominant-tonic succession is considered as a basic syntactic structure of major–minor tonal music (see also Tillmann et al., 2000). Previous studies examining neural mechanisms of processing musical syntax using event-related brain potentials (ERPs) indicated that processing of musical information is reflected in a variety of ERP components such as the P300 (Janata, 1995), late positive component (LPC; Besson & Faita, 1995; Regnault, Bigand, & Besson, 2001), right anterior temporal negativity (Patel, Gibson, Ratner, Besson, & Holcomb, 1998), and closure positive shift (Knoesche et al., 2005; Neuhaus, Knösche, & Friederici, 2006); the functional significance of these components has been reviewed elsewhere (Besson & Schön, 2001; Koelsch & Siebel, 2005).

Investigations on the processing of musical structure, however, are confronted with the problem that, for the most part, music-syntactic regularities co-occur with acoustic similarity. For example, in a harmonic sequence in C major, a C# major chord (that does not belong to C major) is music-syntactically irregular, but the C# major chord is also acoustically less similar to the C major context than any other chord belonging to C major (because the C# major chord consists of tones that do not belong to the C major scale). Thus, any experimental effects evoked by such a C# major chord cannot simply be attributed to music-syntactic processing. In fact, tonal hierarchies and music-syntactic regularities of major–minor tonal music are largely grounded on acoustic similarities (e.g., Leman, 2000). The aim to disentangle the “cognitive” mechanisms (related to music-syntactic processing) from the “sensory” mechanisms (related to the processing of acoustic information) has a certain tradition in music-psychological research (for overviews, see, e.g., the special issue of *Music Perception*, 17[4], 2001), and several experimental paradigms have been suggested to avoid the confound of music-syntactic and acoustic regularity (Bharucha & Stoeckig, 1987; Bigand, Poulin, Tillmann, Madurell, & D’Adamo, 2003; Tekman & Bharucha, 1998).

The present study is a continuation of studies that investigated processing of musical structure using *Neapolitan sixth chords* as music-structural irregularities (Koelsch et al., 2000, 2001; Koelsch, Schmidt, & Kansok, 2002; Loui, Grent-’t Jong, Torpey, & Woldorff, 2005; Maess, Koelsch, Gunter, & Friederici, 2001). The Neapolitan chords elicited an early right anterior negativity (ERAN, maximal around 200 ms) in the ERPs of

listeners familiar with the harmonic regularities of major–minor tonal music. Psychoacoustically, however, the use of Neapolitan chords was problematic in at least two respects. First, the Neapolitan chords had fewer pitches in common with the directly preceding chord than final tonic chords had. That is, the presentation of Neapolitans led to a higher degree of “sensory dissonance” than the presentation of tonic chords¹ (the term “sensory dissonance” is used here in the broader sense referring to the relations between successive sounds, as in Parncutt, 1989). The co-occurrence of music-syntactic irregularity and low pitch commonality with the preceding chord made it difficult to determine to what extent the ERAN was possibly overlapped by potentials related to the processing of sensory dissonance.

Second, Neapolitan chords also represented frequency deviants, because directly succeeding sequences were presented in the same tonal key, and the Neapolitan chords introduced pitches that occurred with a lower probability across sequences than the pitches of the control chords. That is, because chord sequences were usually presented in the same key, the auditory sensory memory could have established a sensory memory trace for the in-key scale tones. The Neapolitan chords introduced out-of-key notes (in C major: d flat and a flat) that did not match with the representation of tones stored in auditory sensory memory. Thus, it was difficult to determine to what extent the ERAN was possibly overlapped by a frequency mismatch negativity (MMN, e.g., Schröger, 1998; the MMN is an ERP component that can be evoked by acoustic changes in a repetitive auditory environment), or whether an ERAN could be elicited at all in the absence of a frequency deviance.

In the present study, we minimized acoustic differences between music-syntactically irregular and regular chords by taking into account three acoustical factors: pitch repetition, pitch commonality (the major component of sensory dissonance), and roughness. The data show that music-syntactically irregular chords still elicit an ERAN, arguing for syntactic rather than merely sensory processing underlying the generation of this ERP component.

EXPERIMENT 1

In the first experiment, two sequence types were composed, each comprising five chords (Figure 2A, B). According to the theory of harmony, the first four chords of the sequences were arranged in such a fashion that a tonic at the fifth position was the most regular chord function (e.g., Piston, 1948/1987; Schönberg, 1969). The regular sequences (Figure 2A) ended on a dominant-tonic progression. The final chord of the irregular sequences (Figure 2B) was a *double dominant* (DD; the DD is the major chord built on the second scale tone; see also Figure 1).²

With respect to the first four chords, both DDs and final tonics contained new pitches, that is, pitches that were not contained in any of the previous chords: Tonic chords contained two new pitches (in both the top voice and the base voice; see the f# and the d indicated by the arrows in Figure 2A), and DDs

¹This was mainly due to two dissonant semi-tone intervals between a Neapolitan (in C major f–a flat–d flat) and the dominant-seventh chord (in C major g–h–d–f) preceding the Neapolitan: the two semi-tone intervals between these chords are (in C major) g–a flat, and d–d flat.

²A double dominant (in major) is often also referred to as *chromatic supertonic*.

Figure 2 consists of six musical staves, each showing a sequence of chords in 2/4 time.
 A: Tonic: A sequence of four chords in D major: D4, G4, F#4, and D5. An arrow points to the G#4 in the top voice of the final chord.
 B: DD: A sequence of four chords in D major: D4, G4, F#4, and D5. An arrow points to the G#4 in the top voice of the final chord.
 C: ST: A sequence of four chords in D major: D4, G4, F#4, and D5. An arrow points to the G#4 in the top voice of the final chord.
 D: Experiment 1: A sequence of four chords in D major: D4, G4, F#4, and D5.
 E: Experiments 2 & 3, DD-block: A sequence of four chords in D major: D4, G4, F#4, and D5.
 F: Experiments 2 & 3, ST-block: A sequence of four chords in D major: D4, G4, F#4, and D5.

Figure 2. Examples of musical stimuli. Top row: chord sequences in (D major), ending either on a tonic chord (regular, A), on a double dominant (irregular, B), or on a supertonic (irregular, C). Arrows indicate pitches that were not contained in the preceding chords. In Experiment 1, only sequence types A and B were presented (D). In Experiments 2 and 3, two blocks were presented, one block consisting of sequence types A and B (E) and the other block consisting of sequence types A and C (F). In all experiments, sequences from all 12 major keys were presented in pseudorandom order. Each sequence was presented in a tonal key that differed from the key of the preceding sequence, regular and irregular sequence endings occurred equiprobably ($p = 0.5$). In Experiment 1, sequences were presented in direct succession (D); in Experiments 2 and 3, sequences were separated by a pause of 1200 ms (E, F).

contained one new pitch (in the top voice; see arrow in Figure 2B). In contrast to DDs, the new pitches of tonic chords had been presented either one octave lower or one octave higher in the first chord. Thus, the new pitches of final tonics were perceptually more similar to pitches of the first chord than the new pitch of the DD was. However, because the octaves of the two new pitches of final tonics were only contained once in the very first chord of the sequence, these tones were masked by the second, third, and fourth chords. Therefore, we assumed that the new pitch of the DD would not represent a greater frequency deviant for the auditory sensory memory than the two new pitches of tonic chords.

To test this assumption, we modeled the acoustic congruency of the final chords with auditory sensory memory traces established by the first four chords using the IPeM toolbox (Leman, 2000; Leman, Lesaffre, & Tanghe, 2005). This auditory modeling estimates pitch images of the echoic memory: Acoustic information decays, but is kept in the echoic memory for a certain time. The aim of the modeling was to determine the correlation of the pitch image of a final chord with the pitch image of the first four chords stored in the echoic memory. The results of the modeling are shown in Figure 3A (echo of local images: 0.1 s, echo of global image: 1.5 s; see Leman, 2000; note that these values indicate half decay values and that—particularly due to the use of the 1.5-s gliding window—information of all preceding four chords affects the correlations between the last chord and the preceding chords). The pitch images of the final DDs correlated even higher than those of final tonic chords with the pitch images established by the first four chords.

Moreover, chord sequences were constructed such that the pitch commonality (calculated according to Parncutt, 1989) between the last two chords had even higher values for the music-syntactically irregular ending (dominant-DD) than for the regular ending (dominant-tonic; see Figure 3B).

Thus, with respect to both (a) the pitch commonality between final and penultimate chord and (b) the acoustic congruency between the final chord and the information of the first four chords stored in the echoic memory, music-syntactically irregular endings were acoustically even more similar to the previous chord(s) than music-syntactically regular endings. This excludes the possibility that ERP effects elicited by music-syntactically irregular final chords could be due to a higher degree of sensory dissonance or a higher incongruency with the memory traces stored in auditory sensory memory.

Note that the new pitch introduced by DDs was an out-of-key note (the G# in the top voice of Figure 2B), that is, a note that did not belong to the tonal key established by the preceding harmonic context. Moreover, DDs represented a new chord function within the sequence (unlike final tonic chords, which repeated the chord function of the first chord). Experiment 2 will investigate ERP effects elicited by music-syntactically irregular chords that do not introduce an out-of-key note and that do not introduce a new chord function.

The tonal key changed from sequence to sequence (i.e., each chord sequence was presented in a tonal key different from the key of the preceding sequence; see Figure 2D), and both sequence types occurred randomly with equal probability ($p = 0.5$). Because the superposition of intervals was identical for both final

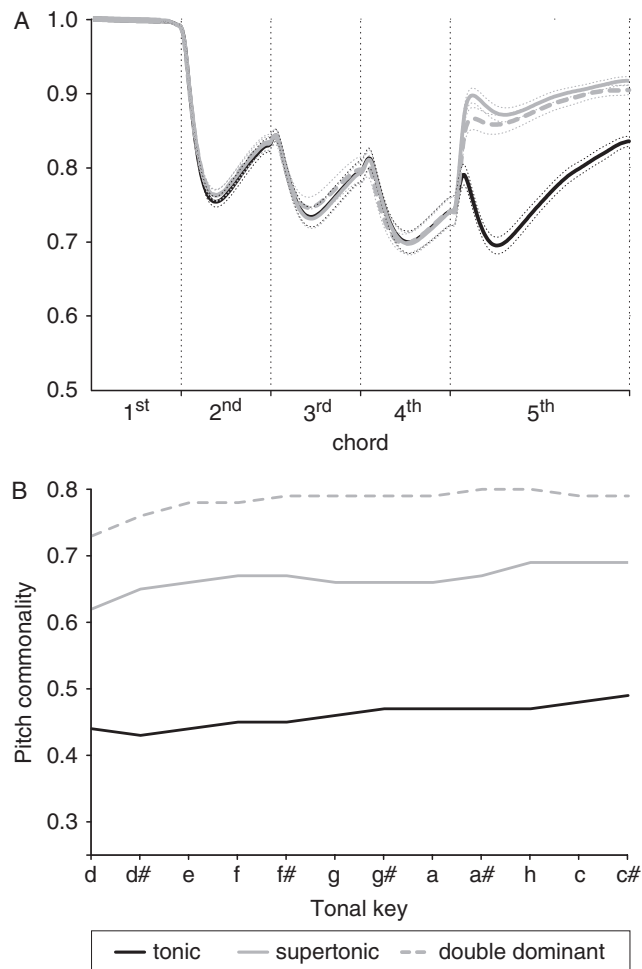


Figure 3. A: Correlation of local context (pitch image of the the current chord) with global context (echoic memory representation as established by previously heard chords). The data show that music-syntactically irregular chord sequence endings (STs: solid gray line, DDs: dashed gray line) were more congruent with the preceding harmonic context than music-syntactically regular endings (tonic chords: black line). For each sequence type, correlations were calculated for all 12 major keys (the line for each sequence type represents the mean correlation; the thin dotted lines indicate standard error of the mean). Auditory modeling was performed using the Contextuality Module of the IPeM Toolbox (Leman et al., 2005); length of local context integration window was 0.1 s; global context integration window was 1.5 s (as suggested by Leman, 2000). The abscissa represents the time line (each of the first four chords had a duration of 600 ms; the fifth chord was presented for 1200 ms); the ordinate depicts correlation values. B: Pitch commonality calculated for the different chord sequence endings (tonic chord, double dominant, supertonic) and the penultimate (dominant) chord. Values were computed separately for all 12 major keys according to Parncutt (1989) and connected with lines for better visualization. The graphs show that DDs and STs have an even higher pitch commonality with the directly preceding dominant than tonic chords have. Pitch commonality values were calculated for the 12 keys to illustrate the effect of transposition on pitch commonality and to show that the pitch commonality ranges for the three chord types tested do not overlap.

tonics and DDs, physically identical chords were music-syntactically regular in one sequence, but irregular in another (e.g., the final tonic chord of Figure 2A was a DD of sequences starting in C major, and the final DD of Figure 2B was a tonic in sequences

starting in E major). Therefore, any effect elicited by a DD could not be due to the properties of the chord itself.

Participants of Experiment 1 were nonmusicians (thus oblivious of concepts such as “double dominant,” or “tonic”), who listened to the sequences under the instruction to press one button for the regular chord sequence endings and another button for the irregular ones. It was hypothesized that the irregular endings (DDs) elicit an ERAN in comparison to the regular endings (tonic chords). Because the present study focuses on the ERAN, other ERP effects (such as N2b, P3, and N5) will be reported, but only briefly discussed in the General Discussion.

Methods

Participants

Twenty people participated in the experiment (age range 18–30 years, mean 23.0 years, 10 women). Participants were nonmusicians who had never participated in extracurricular music lessons or performances. All participants were right-handed (lateralization quotient at least 90% according to the Edinburgh Handedness Inventory; Oldfield, 1971) and reported having normal hearing.

Stimuli

There were two sequences, A and B (Figure 2A, B) that were transposed to the 12 major keys, resulting in 24 different sequences. Each sequence consisted of five chords, of which the first four chord functions were identical: tonic, subdominant, supertonic, dominant. The final chord function of type A was a tonic and that of type B a double dominant. Using only two sequences transposed to different keys gave us the maximum acoustic control of the musical stimulus (for studies investigating the ERAN with more naturalistic stimuli, see, e.g., Koelsch & Mulder, 2002; Steinbeis, Koelsch, & Sloboda, 2006).

Sequences were presented in direct succession (Figure 2D); there was no silent period between chords or sequences. Each sequence type occurred with a probability of .5, and both sequence types were randomly intermixed. Moreover, each sequence was presented pseudorandomly in a tonal key different from the key of the preceding sequence. Across the experiment, each sequence type was presented six times in each of the 12 major keys, resulting in 120 sequences for the entire experiment. The timing was identical to previous studies (e.g., Koelsch et al., 2000): Presentation time of chords 1 to 4 was 600 ms, chord 5 was presented for 1200 ms. Block duration was approximately 7 min. All chords had the same decay of loudness and were played with a piano-sound (General Midi sound #2) under computerized control on a synthesizer (ROLAND JV 8010; Roland Corporation, Hamamatsu, Japan).

Procedure

Participants were informed about the irregular chords and were asked to press a response button for the last chord of each sequence. There were two response buttons: one button for the regular chords and the other one for the irregular ones. Participants were asked to respond as fast as possible. Half of the subjects were instructed to press the left button for the regular endings; the other half pressed the right button for these endings. As examples, three sequences of type A and three sequences of type B were presented. During the experimental session, participants were instructed to look at a fixation cross.

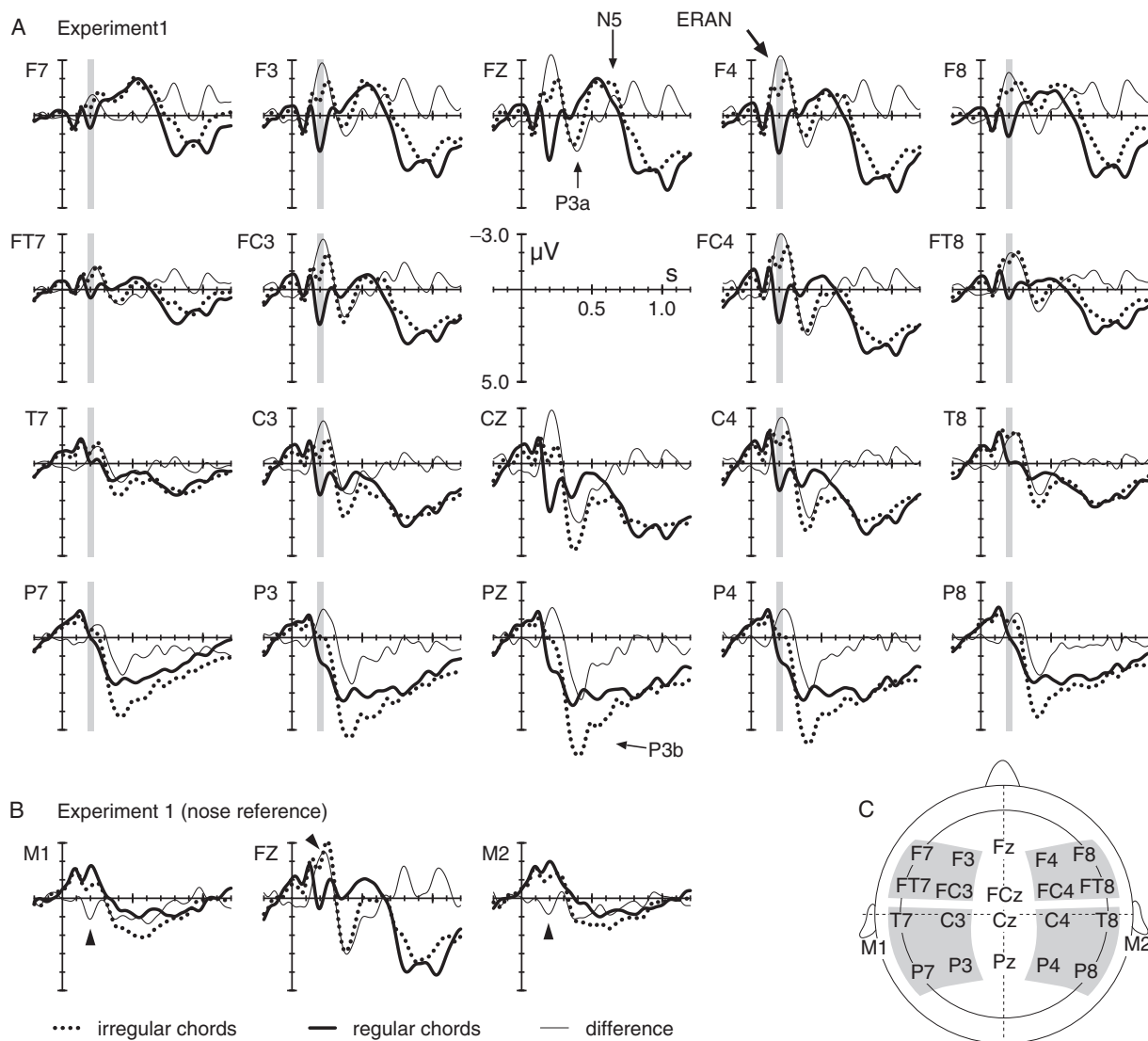


Figure 4. Grand-average ERP waveforms of Experiment 1. **A:** ERPs elicited by the final chords (referenced to the algebraic mean of both mastoid electrodes). The thick solid line indicates potentials elicited by regular (tonic) chords and the dotted line responses to irregular chords (double dominants). The thin solid line represents the difference wave (regular subtracted from irregular chords). Time interval used for the statistical analysis of the ERAN is indicated by the gray-shaded areas. **B:** When referenced to the nose electrode, the ERAN inverted polarity at mastoid leads (M1, M2; the polarity inversion is indicated by the small arrows). **C:** Head positions of electrodes depicted in A and B; regions of interest used for statistical analyses are shaded in gray.

Data Recording and Analysis

The EEG was recorded from 27 electrodes of the 10–20 system (FP1, FP2, F7, F3, FZ, F4, F8, FT7, FC3, FC4, FT8, T7, C3, CZ, C4, T8, CP5, CP6, P7, P3, PZ, P4, P8, O1, O2, nose-tip, and right mastoid), using an electrode placed on the left mastoid as reference. Sampling rate was 250 Hz. After the measurement, EEG data were re-referenced to the algebraic mean of the left and right mastoid electrodes (to obtain a symmetric reference), and filtered using a 0.25–25-Hz band-pass filter (1001 points, finite impulse response) to reduce artifacts. Horizontal and vertical electrooculograms (EOGs) were recorded bipolarly. For artifact rejection, each sampling point was centered in a gliding window and rejected if the standard deviation within the window exceeded a threshold value: Artifacts caused by drifts or body movements were eliminated by rejecting sampling points whenever the standard deviation of a 200-ms or 800-ms gliding win-

dow exceeded 25 μ V at any EEG electrode. Eye artifacts were rejected whenever the standard deviation of a 200-ms gliding window exceeded 25 μ V at the vertical or the horizontal EOG (rejections were controlled by the authors). ERPs were calculated using a 200-ms prestimulus baseline.

For statistical analysis, mean amplitude values were computed for four regions of interest (ROIs; see also Figure 4C): left anterior (F3, F7, FC3, FT7), right anterior (F4, F8, FC4, FT8), left posterior (C3, T7, P3, P7), and right posterior (C4, T8, P4, P8). To test if ERPs to regular and irregular chords differ from each other and whether such differences are lateralized or differ between anterior and posterior scalp regions, amplitude values of ERPs were analyzed statistically by repeated measures ANOVAs. ANOVAs were conducted with factors chord function (regular [tonic], irregular [DD]), hemisphere (left, right ROIs), and anterior–posterior distribution (anterior, posterior

ROIs). Although some ERPs will also be presented with nose reference (to examine polarity inversion of potentials at mastoid electrodes), all statistical analyses of ERPs were computed on the data referenced to the algebraic mean of M1 and M2. The time window for statistical analysis of the ERAN was 180–220 ms (this time window was centered around the peak amplitude of the ERAN). To facilitate legibility of ERPs, ERPs were low-pass filtered after statistical evaluation (10 Hz, 41 points, finite impulse response). Split analyses for correctly and incorrectly classified trials will not be presented, because some subjects had hit rates between 90% and 100% (leading to a poor signal-to-noise ratio of ERPs of incorrectly classified trials).

Results

On average, participants had 81% correct responses ($SD = 12\%$, range: 58–100%, 3% missed responses). A t test on the percentages of correct responses indicated that participants performed well above chance level ($p < .0001$). Participants responded correctly to 85% of the regular chords and to 77% of the irregular ones (a t test on the percentages of correct responses indicated that the difference between regular and irregular chords was marginally significant, $p < .06$).

Figure 4 shows the electric brain responses to all harmonically regular and irregular sequence endings. In comparison to regular endings, irregular endings elicited an ERAN that was maximal over fronto-midline electrodes and that had slightly larger amplitude values over right- than over left-hemisphere electrode sites. With nose reference, the ERAN inverted polarity at mastoid leads at around 200 ms (Figure 4B), indicating that this ERP effect is not an N2b (the N2b has a central maximum, is not lateralized, and does not invert polarity at mastoid sites; Näätänen, 1992; Schröger, 1998).

An ANOVA with factors chord function (regular, irregular ending), hemisphere, and anterior-posterior distribution for a time interval from 180 to 220 ms revealed an effect of chord function, $F(1,19) = 20.49$, $p < .0002$, an interaction between factors chord function and anterior-posterior distribution, $F(1,19) = 8.48$, $p < .01$, and an interaction between factors chord function and hemisphere, $F(1,19) = 6.13$, $p < .05$. When ERPs were compared for each ROI separately, the highest F value was indicated for the right anterior ROI, $F(1,19) = 36.5$, whereas no significant difference was indicated for the left posterior ROI.

The ERAN was followed (and partly overlapped) by an N2b-P3 complex reflecting the detection of the harmonically irregular chords and the decision to press the response button (e.g., Schröger, 1998). The N2b was maximal around 240 ms; the P3 peaked around 410 ms.

Previous studies had shown that, when the harmonically irregular chords are task irrelevant, the ERAN is followed by a negativity that is frontally predominant and maximal around 500 ms after the onset of an irregular chord (the N5; Koelsch et al., 2000; Koelsch, Schmidt, et al., 2002; Koelsch & Siebel, 2005; see also General Discussion). However, when participants are asked to respond to irregular chords (as in the present experiment), the N5 potentials are usually mainly overlapped by a P3 (Koelsch et al., 2000; Koelsch, Schröger, & Gunter, 2002). In the present study, a small negative peak at frontal and fronto-central electrodes was present around 650 ms that points to the presence of

an N5. The difference between the waveforms was statistically not significant.³

Discussion

Behaviorally, participants correctly classified about 80% of the sequence endings. Although these hit rates were clearly above chance level, participants still judged more than 20% of the DDs incorrectly as regular. This indicates that the DDs were perceived as rather subtle irregularities, and that the participants, therefore, had difficulties in reliably detecting them.

In the ERPs, the music-syntactically irregular DDs elicited an ERAN that was maximal around 200 ms. The ERAN inverted polarity at mastoid electrodes with nose reference (in accordance with previous studies; Heinke et al., 2004; Koelsch, Heinke, Sammler, & Olthoff, 2006) and had a slight right-hemispheric weighting.

As described in the Introduction, the final DDs did not have a lower pitch commonality with the preceding dominant chord than the final tonic chords had. Thus, the elicitation of the ERAN by the DDs cannot be due to a lower degree of pitch commonality, indicating that the neural mechanisms underlying the generation of the ERAN are capable of operating in the absence of sensory dissonance.

Moreover, with respect to the first four chords, DDs introduced one new pitch, whereas tonic chords introduced two new pitches. Although those two pitches were perceptually more similar to the first chord than the new pitch of a DD was, the auditory modeling showed that DDs matched even better than final tonic chords with the sensory memory traces established by the first four chords. This rules out the possibility that the ERAN effect observed was simply a frequency MMN. This interpretation is corroborated by previous data showing that an ERAN can be elicited by DDs even if the out-of-key note of DDs occurs (one octave lower) in the musical context directly preceding DDs (Koelsch, 2005). However, it should be noted that DDs introduced an out-of-key note and that DDs introduced a new chord function. These issues will be addressed in Experiment 2.

It is interesting to note that participants were nonmusicians who did not know concepts such as “tonic” or “double dominant.” Nevertheless, they distinguished regular and irregular chords clearly above chance level, and the music-syntactically irregular chords elicited clear ERP effects. This supports previous findings that even nonmusicians have an (implicit) knowledge of musical regularities and that nonmusicians have the ability to process musical information according to this knowledge (Koelsch et al., 2000; Koelsch & Siebel, 2005). Differences between MMN and ERAN as well as between ERAN and language-related brain functions will be considered in the General Discussion.

³We also performed a spatial principal component analysis (PCA) of the channel covariance matrix. This PCA clearly disentangled P3b and N5, corroborating the assumption that the DDs also elicited an N5. The PCA indicated that the P3 had a maximal amplitude at 410 ms and the N5 at 640 ms (onset of the N5 was at around 400 ms). The PCA also showed that the ERAN was maximal at 200 ms and the N2b maximal at 240 ms. For the sake of brevity, the details of the PCA are not presented in this article.

EXPERIMENT 2

In Experiment 1, chords were task relevant (participants had to differentiate between regular and irregular chords). One aim of Experiment 2 was to investigate if the ERAN can be elicited even when DDs are task irrelevant and participants are not informed about the irregular chords. This question is relevant for three reasons. First, ERPs reflecting processing of musical information can be investigated without being overlapped by potentials that emerge when irregular chords have to be detected (such as N2b and P3). Second, task-irrelevant processing provides information about the amount of attentional resources needed to activate the neural processes underlying the generation of the ERAN: The behavioral data of Experiment 1 indicated that DDs represented only a subtle irregularity, and it was of interest if these subtle irregularities elicit specific ERP effects even if participants do not have a task regarding these chords. Third, because participants did not have a task related to the regularity of chords (subjects were not informed about the regularity of chords), Experiment 2 allowed us to test if an ERAN can also be elicited when no task-related strategic processes are at work (that might emerge when trying to detect the harmonic irregularities).

To investigate these issues, a block with sequences ending on either DDs or tonic chords (as in Experiment 1) was presented under the instruction to listen carefully to the timbre of the chords, and to detect chords that were infrequently played with an instrumental timbre other than the standard piano timbre (e.g., marimba, guitar).

Another aim of Experiment 2 was to investigate if the ERAN can also be elicited by an in-key chord function (i.e., by a chord that belongs to the tonal key established by the previous harmonic context). In Experiment 1, DDs did not belong to the tonal key established by the preceding four chords (DDs introduced one out-of-key note that was not contained in the four chords preceding a DD), leaving open the possibility that an ERAN can only be elicited by out-of-key chords. To investigate this, Experiment 2 comprised another block in which DDs were replaced by *supertonic*s (STs; see Figures 1 and 2C).⁴ In major keys, the ST is the (in-key) chord built on the second scale tone. In the sequences used in the present experiments, this chord function is regular when played, for example, at the third position of the sequence (as in all sequences presented in Figure 2). In contrast, STs are structurally irregular when presented at the fifth position of the sequence after a dominant chord. Importantly, STs are in-key chord functions, and can, thus, not be detected as irregular by the occurrence of out-of-key notes.

As in the sequences ending on DDs, the modeling of the acoustic congruency of the final STs with auditory sensory memory traces established by the first four chords (again using the IPEM toolbox from Leman et al., 2005) showed that the pitch images of the final STs correlated more highly than those of final tonic chords with the pitch images established by the first four chords (Figure 3A). That is, similarly to DDs, STs matched even better than tonic chords with the information of the first four chords stored in auditory sensory memory traces. Note that—unlike DDs—the new pitch introduced by final STs was presented in its lower octave in the third chord of the sequence. That is, with respect to pitch repetition, final STs were more similar to the preceding chords than both final tonics and DDs.

Moreover, chord sequences ending on STs were constructed in a way that the pitch commonality between penultimate and final chord was even higher for STs than for final tonic chords (see Figure 3B; values were computed according to Parncutt, 1989).

To control for the roughness of final chords (as calculated according to Bigand, Parncutt, & Lerdahl, 1996), chord sequences were composed such that the roughness of the (minor) ST was comparable to the roughness of the directly preceding dominant chord. For example, in the sequences presented in Figure 2, roughness values for chords one to four were 0.51 (tonic), 0.37 (subdominant), 0.44 (supertonic), and 0.37 (dominant). The value of the final ST (last chord of Figure 2C) was 0.39, and the value of the final tonic (last chord of Figure 2A) was 0.29 (value of the DD of Figure 2B was 0.26).⁵ That is, with respect to (a) pitch commonality, (b) congruency with auditory sensory memory traces, and (c) roughness, the irregular STs were acoustically more similar to the preceding chords than (regular) tonic chords were. In contrast to tonic chords, STs were minor chords, but it is important to note that final STs were not the only minor chords of the sequences: All chords at the third position were also minor chords, leading to a probability of 30% for the occurrence of such chords across sequences.

Methods

Participants

Twenty-four people participated in the experiment (age range 20–28 years, mean 24.0 years, 12 women). None of them had participated in Experiment 1. Participants had no or moderate musical training: 16 participants were nonmusicians who had never participated in extracurricular music lessons or performances, 8 were amateur musicians (7 had learned an instrument for 2–4 years, 1 had infrequently received instrumental lessons for 11 years, mean: 3.88 years). All participants were right-handed (lateralization quotient at least 90% according to the Edinburgh Handedness Inventory; Oldfield, 1971), and reported having normal hearing.

Stimuli

There were three types of sequences: A, B, and C (Figure 2A–C). Sequence types A and B were identical to Experiment 1; sequence type C was identical to sequence types A and B, except that the final chord was a supertonic (instead of tonic or DD). In one experimental block (DD block), only types A and B were presented (Figure 2E). In the other block (ST block), only types A and C were used (Figure 2F). The order of the two blocks was counterbalanced across subjects (half of the subjects was presented first with the block consisting of sequence types A and B; the other half was presented first with types A and C). Randomization and probability of final chords was identical to Experiment 1.

Experiment 2 differed from Experiment 1 in three aspects: (a) in 20% of the sequences, one chord of a sequence was played with an instrumental timbre other than piano (e.g., trumpet, organ, violin; see also below), (b) in each block, 100 sequences were presented, and (c) there was a 1200-ms silent period between sequences (in Experiment 1, ERP effects lasted longer than the

⁴A supertonic (in major) is often also referred to as *diatonic supertonic*.

⁵The roughness value of the initial tonic is different from the roughness value of the final tonic due to the different superposition of intervals.

presentation time of the last chord; thus a pause was inserted to prevent the potentials elicited by the final chords being overlapped by those elicited by the following chord). Block duration was approximately 8 min.

Procedure

Participants were not informed about the harmonically irregular chords. The tasks were to detect the infrequently occurring chords played with a deviant instrumental timbre and to indicate the detection by pressing a response button. As examples, two sequences were presented, one without and one with a chord played on a deviant instrument. The deviant instruments were only employed to control whether participants attended the timbre of the stimulus (this method has already been used in previous studies; e.g., Koelsch et al., 2000). As in Experiment 1, participants were instructed to look at a fixation cross during the experimental session.

Data Recording and Analysis

Recording and analysis were identical to those in Experiment 1, except that (a) the EEG was recorded with 40 electrodes (FP1, FPZ, FP2, AF7, AF3, AFZ, AF4, AF8, F7, F5, F3, FZ, F4, F6, F8, FT7, FC5, FC3, FCZ, FC4, FC6, FT8, T7, C3, CZ, C4, T8, CP5, CP6, P7, P3, PZ, P4, P8, POZ, O1, O2, M1, M2, nose), (b) an additional factor block (DD block \times ST block) was computed within the ANOVAs, (c) parietal ROIs comprised the electrodes P3, P7, CP3, TP7 (left posterior), and P4, P8, CP4, TP8 (right posterior), and (d) a longer time interval was used for the statistical evaluation of the ERAN (this was possible because the ERAN was not overlapped by N2b potentials), leading to a higher reliability of the statistical analysis. Sequences with deviant instruments were excluded from further data analysis (their ERPs will not be shown because only a few trials were used to control for the participants' behavior).

Results

Participants detected on average 96.0% of the deviant instruments, indicating that participants attended to the timbre of the musical stimulus, and that they did not have difficulties in reliably detecting the timbre deviants.

The ERP waveforms elicited by task-irrelevant DDs and STs show an ERAN that was maximal at around 200 ms over anterior electrode sites. Amplitude values were slightly larger over right- than over left-hemisphere leads (best seen in the difference waves of Figure 5A, B). As in Experiment 1, the ERAN inverted polarity at mastoid leads when potentials were referenced to the nose electrode (Figure 5C, D). The amplitude of the ERAN did not differ between blocks.

An ANOVA for the time interval of 180–260 ms with factors chord function (regular, irregular), block (DD block, ST block), hemisphere, and anterior–posterior distribution revealed an effect of chord function, $F(1,23) = 17.13$, $p < .0005$, an interaction between factors chord function and anterior–posterior distribution, $F(1,23) = 8.44$, $p < .01$, and an interaction between factors chord function and hemisphere, $F(1,23) = 5.77$, $p < .05$. The reported interactions reflect that the ERAN had an anterior maximum with a slight right-hemispheric weighting. When ERPs were compared for each ROI separately, the highest F value was indicated for the right anterior ROI, $F(1,23) = 34.5$, whereas no significant difference was indicated for the left posterior ROI (as in Experiment 1). The ANOVA did not indicate

an interaction between factors chord function and block ($p > .6$), reflecting that the amplitude of the ERAN did not differ between blocks.

In both blocks, the ERAN was followed by an N5 that had a bilateral scalp distribution and was maximal around 500–550 ms. At parietal sites, a bilateral late positive component (LPC) was maximal around 900 ms. ANOVAs with factors chord function, block, hemisphere, and anterior–posterior distribution, conducted separately for time intervals from 450 to 650 ms (N5) and from 500 to 1200 ms (LPC) revealed interactions between factors chord function and anterior–posterior distribution for both time windows (N5: $F[1,23] = 13.54$, $p < .002$; LPC: $F[1,23] = 18.49$, $p < .0005$), reflecting that the N5 had a frontal, and the LPC a parietal maximum (no interactions between factors chord function and hemisphere were indicated, as expected). A separate ANOVA for frontal ROIs with factors chord function and block for the N5 time window indicated an effect of chord function, $F(1,23) = 5.35$, $p < .05$. Likewise, an analogous ANOVA for parietal ROIs for the LPC time window indicated an effect of chord function, $F(1,23) = 7.87$, $p < .01$. No interaction between factors chord function and block were indicated in any of the ANOVAs, reflecting that the amplitudes of N5 and LPC did not differ between blocks (N5: $p > .3$, LPC: $p > .7$).

Because a previous study (Koelsch, Schmidt, et al., 2002) reported that the ERAN is larger in musicians than in nonmusicians, a similar effect might be expected for a comparison between amateur musicians and nonmusicians. Mean amplitude values of the ERAN (regular subtracted from irregular chords) were calculated separately for nonmusicians and amateur musicians for the frontal regions of interest within the ERAN time window used for statistical analyses (180–260 ms).

The mean ERAN amplitude value was significantly larger for amateur musicians (mean: $-1.67 \mu\text{V}$, $SEM = 0.35$) than for nonmusicians (mean: $-0.92 \mu\text{V}$, $SEM = 0.28$): An ANOVA with factors chord function and group (amateur musicians, nonmusicians, time interval 180–260 ms) indicated an effect of chord function, $F(1,22) = 22.03$, $p < .0001$, and a two-way interaction, $F(1,22) = 6.44$, $p < .05$. The analogous ANOVA, conducted for the data of nonmusicians only, indicated an effect of chord function ($p < .005$), demonstrating that the presence of the ERAN in the grand-average data was not simply due to the subgroup of amateur musicians.

A comparison of the ERP data from the DD block and from Experiment 1 (where DDs were to be detected) indicates that the ERAN virtually did not differ between experiments. This holds especially for potentials elicited at mastoid sites (where the N2b only marginally overlaps with the ERAN; Figure 6A, B). An ANOVA for frontal ROIs (180–220 ms time interval) with factors chord function and experiment (Experiment 1, DD block of Experiment 2) indicated an effect of chord function, $F(1,42) = 45.56$, $p < .0001$, and no two-way interaction ($p > .2$). Additionally, the analogous ANOVA conducted for mastoid electrodes (referenced to the nose electrode) did not reveal an interaction ($p > .9$).

Discussion

Both DDs and STs elicited an ERAN. No N2b-P3 complex was elicited, reflecting that participants did not respond behaviorally to the irregular chords. The presence of the ERAN indicates that the neural processes underlying the generation of the ERAN

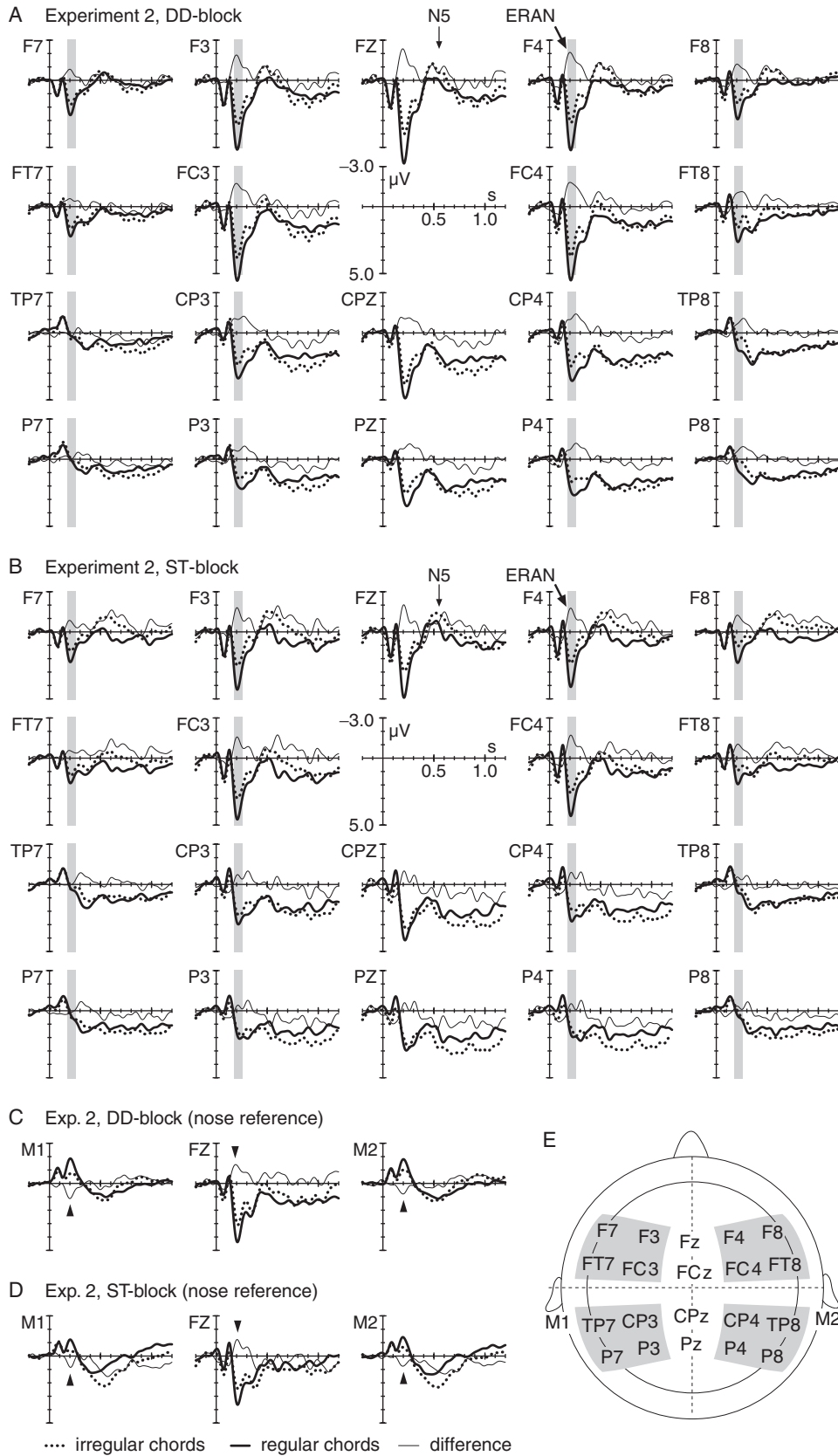


Figure 5. Grand-average ERP waveforms of Experiment 2. **A:** ERPs elicited by the fifth chord in the DD block (thick solid line: tonic chords; dotted line: double dominants), referenced to the algebraic mean of the two mastoid electrodes. Time interval used for the statistical analysis of the ERAN is indicated by the gray-shaded areas. **B:** ERPs elicited by the fifth chord in the ST block (thick solid line: tonic chords; dotted line: supertonics), reference as in **A**. When referenced to the nose electrode, the ERAN inverted polarity at mastoid sites (M1, M2) in both the DD block (**C**) and the ST block (**D**). **E:** Head positions of electrodes depicted in **A–D**; regions of interest used for statistical analyses are shaded in gray.

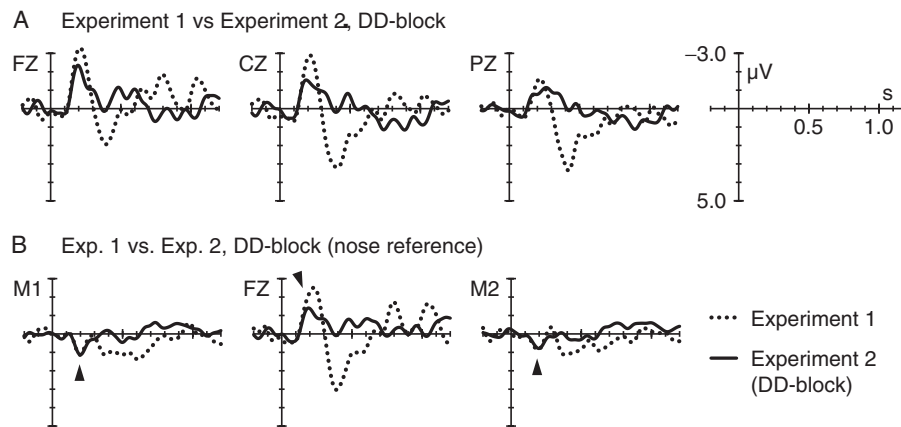


Figure 6. Comparison of ERPs between Experiment 1 and DD block of Experiment 2 (referenced to mastoid leads, A). The dotted line represents the ERP effects elicited in Experiment 1 (difference wave; regular subtracted from irregular chords); the thick solid line represents the difference wave of the DD block of Experiment 2. The difference between the two waveforms around 240 ms appears to be mainly due to an N2b elicited in Experiment 1 (the N2b effect was maximal at the CZ electrode). The N2b was followed by a P3. With nose reference (B), the potentials measured at mastoid sites (where the ERAN virtually does not overlap with the N2b) do not indicate a difference between experiments, whereas at Fz (where the ERAN overlaps with the N2b) the two waveforms differ from each other (see arrows).

operate even when chords are not task relevant, consistent with other studies in which an ERAN was elicited while participants were reading a book (Koelsch, Schröger, et al., 2002), playing a video game (Koelsch et al., 2001), or performing a reading comprehension task (Loui et al., 2005).

The ERAN elicited by DDs virtually did not differ between experiments. The small difference at frontal sites appears to be due to the overlap of ERAN and N2b in Experiment 1: When using a nose reference, the ERAN potentials were identical for both experiments at mastoid leads (where the N2b is only marginally observable). This result indicates that the amplitude of the ERAN is not substantially influenced by the task relevancy of chords (but see also General Discussion).

In contrast to DDs, all pitches of the STs, or their lower octaves, had been presented by the chords preceding the STs. Thus, the pitches of the final STs matched with the sensory memory trace at least as well as the pitches of the final tonic chords, and it is therefore not possible that STs were detected simply based on a frequency-MMN mechanism. Note that, unlike DDs, STs did not introduce a new chord function (chords at the third position of the sequences were also STs). These results additionally indicate that the ERAN can also be elicited by chord functions that repeat a previous chord function of a harmonic sequence (in other words, the ERAN can not only be elicited by new chord functions). Moreover, STs were in-key chord functions (i.e., all notes of the STs belonged to the tonal key established by the chords preceding the STs). Results thus also show that an ERAN can be elicited by in-key chords, that is, without the presence of an out-of-key note, and in the absence of a tonal irregularity.

As mentioned earlier, STs were minor chords (in contrast to tonic chords, which were major chords). However, because final STs were not the only minor chords of the sequences (chords at the third position were also minor chords), the global probability for the occurrence of a minor chord was 30%, which is too high to elicit an MMN response (in auditory oddball paradigms, deviants occurring with a probability of more than 20–25% hardly elicit any deviance-related negativity; e.g., Schröger,

1998). Recent data from our laboratory (Koelsch, Jentschke, & Sammler, 2007) moreover indicate that, in contrast to final STs, the STs presented at the third position of the sequences (which also occurred with a probability of 30%) do not elicit an ERAN. The elicitation of the ERAN by final STs can thus not be due to the probability of 30% for minor chords. Note that, with respect to their roughness, STs were even more similar to the preceding chords than tonic chords were, despite the fact that they were minor chords (see Introduction). Hence, the generation of the ERAN could not simply be due to any systematic difference in roughness values between STs and the chords preceding the STs.

The ERAN was followed by an N5 and by a late positive component (LPC); these effects, as well as differences between nonmusicians and amateur musicians, will be discussed in the General Discussion.

EXPERIMENT 3

In Experiment 2, the musical syntax was task irrelevant (participants detected the infrequently occurring deviant instrumental timbres). Thus, no behavioral data were obtained that indexed how well nonmusicians and amateur musicians are able to detect the STs. To investigate this issue, a behavioral study was conducted in which the musical stimulus used in Experiment 2 was presented to nonmusicians and amateur musicians under the instruction to press one button for the regular sequence endings and another button for the irregular ones. Because the ERAN amplitude did not differ between STs and DDs in Experiment 2, it was expected that the behavioral results would also not differ between these two chord types.

Methods

Participants

Twenty-two people participated in the experiment (age range 21–26 years, mean 23.0 years, 10 women). None of the

individuals had participated in Experiment 1 or 2. Sixteen participants were nonmusicians (10 of them had never participated in any extracurricular music lessons or performances, 6 of them had less than 1 year of instrumental lessons), and 6 participants were amateur musicians who had received instrumental lessons for 1.5–8 years (mean 2.8 years). All participants were right-handed (lateralization quotient at least 90% according to the Edinburgh Handedness Inventory; Oldfield, 1971), and reported having normal hearing.

Stimuli and Procedure

Stimulus material was identical to that of Experiment 2. As in Experiment 2, the order of blocks (DD block and ST block) was counterbalanced across subjects. In contrast to Experiment 2, participants were informed about the harmonically irregular sequence endings. Before each of the two blocks, six sequences were presented as examples, three ending on the (regular) tonic and three ending on the (irregular) DD or ST. The task for both experimental blocks was to press as fast as possible one button for the regular sequence endings, and one for the irregular ones (left–right buttons for regular and irregular endings were counterbalanced across subjects). The instruction regarding which button to press for the (ir)regular sequence endings remained on a computer screen during the entire experimental session. If participants did not press a button during the presentation of the last chord, they were instructed via the computer monitor to respond faster. Participants were asked to ignore the chords played with deviant instrumental timbres. Sequences containing chords with deviant instrumental timbres were excluded from further data evaluation.

Results

Across both blocks, participants had on average 81% correct responses ($SD = 14$, range: 58%–100%; there were less than 1% missed responses in each block). Percentages of correct responses virtually did not differ between blocks (DD block: 80%, ST block: 81%). Participants detected the regular endings better than the irregular endings (correct responses for tonic chords in DD block: 91%, tonic chords in ST block: 90%, DDs: 71%, STs: 72%).

Hit rates differed between nonmusicians and amateur musicians: While nonmusicians achieved 76% correct responses ($SD = 14$, range: 58%–99%), amateur musicians achieved 92% ($SD = 9$, range: 77%–100%; see Figure 7). An ANOVA for the percentages of correct responses with factors chord function (regular, irregular), group (nonmusicians, amateur musicians), and block (DD, ST) revealed an effect of chord function, $F(1,20) = 7.43$, $p < .02$, indicating that regular endings were better detected than irregular endings, and an effect of group, $F(1,20) = 6.57$, $p < .02$. No two- or three-way interactions were indicated. t tests on the percentages of correct responses revealed that each group performed well above chance level in each block ($p < .0005$ in each test).

Across both groups, reaction times (RTs) of correct responses for regular endings were 670 ms ($SD = 193$ ms) in the DD block and 728 ms ($SD = 258$ ms) in the ST block. RTs for DDs were 724 ms ($SD = 210$ ms) and for STs they were 771 ms ($SD = 246$ ms). Although in both blocks RTs were nominally faster for regular endings, RTs did not significantly differ between regular and irregular endings, $F(1,20) = 0.93$, n.s. Amateur musicians responded nominally slightly faster (RT: 616 ms, $SD = 151$ ms)

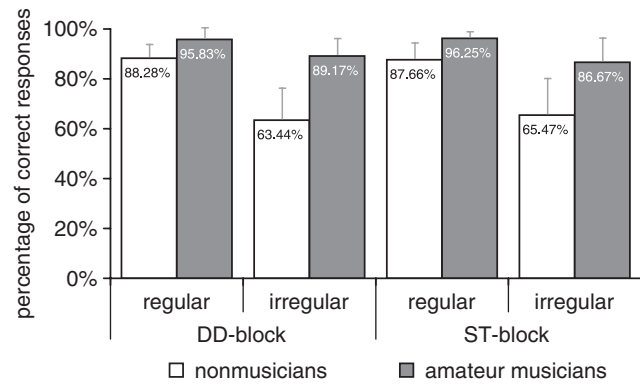


Figure 7. Hit rates of Experiment 3, separately for DD block and ST block. Data of nonmusicians are represented by white columns and data of amateur musicians by gray columns. Error bars indicate SD .

than nonmusicians (RT: 763 ms, $SD = 184$ ms), but this group difference was not significant, $F(1,20) = 1.30$, n.s. A comparison between the hit percentages of Experiment 1 and the DD block of Experiment 3 did not indicate differences between experiments, as expected.

Discussion

Both nonmusicians and amateur musicians were able to differentiate between regular and irregular sequence endings. The percentages of correct responses in the DD block replicate the behavioral data of Experiment 1 and support the statement that the irregular chords used in the present study represented quite subtle music-syntactic irregularities. No differences of correct responses were found between the DD and the ST blocks, in line with results of Experiment 2, where ERP effects elicited by irregular chord functions did not differ between blocks. This indicates that the irregular chord functions used in the present study had a comparable salience, irrespective of whether they were in-key (STs) or out-of-key chord functions (DDs; see also Discussion of Experiment 2). Responses of nonmusicians differed from those of amateur musicians, which will be discussed in the following section.

General Discussion

Early ERP effects

Both DDs and STs clearly elicited an ERAN. Previous studies that used Neapolitan sixth chords as music-syntactically irregular chords raised the question of whether the ERAN may merely represent a frequency MMN or simply a reaction of the auditory cortex to sensory dissonance (which was not balanced between Neapolitan chords and control chords).

In the present study, the music-syntactically irregular chords (STs and DDs) had an even higher pitch commonality (and, correspondingly, a lower degree of sensory dissonance) with the preceding chord than the music-syntactically regular (tonic) chords had. Moreover, the pitches of both STs and DDs matched better with the information stored in auditory sensory memory traces than pitches of the (regular) final tonic chords. STs repeated even more pitches of the preceding chords than final tonic chords: STs introduced only one new pitch (see arrow in Figure

2C), whereas final tonics introduced two new pitches (indicated by the two arrows in Figure 2A). Thus, it is not possible that STs were detected as deviants simply based on a frequency-MMN mechanism. DDs introduced only one new pitch (see arrow in Figure 2B), but because this pitch was an out-of-key note that was not contained in any of the previous chords, this new pitch was perceptually less similar to pitches of the first chord than the new pitches of final tonics (that were contained either one octave lower or one octave higher in the first chord). However, this octave relation of the two new pitches of final tonics was masked by the second, third, and fourth chord, and a previous study using an auditory oddball paradigm showed that frequency deviants separated from standard tones by one octave elicit even larger MMN potentials than frequency deviants separated from standards by a mistuned fourth (although the latter deviant is perceptually less similar to standards than the former one; Opitz, Rinne, Mecklinger, von Cramon, & Schröger, 2002, p. 170). Our assumption that not only STs but also DDs represented even smaller frequency deviants than final tonic chords was clearly supported by the auditory modeling, which showed that pitch images of both STs and DDs had a higher congruency with the pitch images of auditory sensory memory traces established by the preceding chords than pitch images of final tonic chords.

Thus, whereas STs and DDs were music-syntactically irregular, they did not represent greater frequency deviants than (music-syntactically regular) tonics, and they did not have a lower pitch commonality with the preceding chord than final tonics. Consequently, neither frequency deviance nor sensory dissonance can account for the ERAN observed in Experiments 1 and 2. Although DDs introduced an out-of-key note and a new chord function within the sequence (unlike final tonics), STs were matched with tonic chords in these respects (because STs were also presented at the third position of each sequence). Thus, the data of Experiment 2 also show that the ERAN can be elicited by a chord function that had already been presented within the preceding chord sequence.

Taken together, the present data allow us to exclude the possibility that the ERAN elicited by DDs and STs is simply an enhanced N1 related to the processing of sensory dissonance or a frequency MMN elicited by the processing of frequency deviants. The present results thus indicate that the neural operations reflected in the ERAN are related to music-syntactic processing. It remains to be determined, though, whether the stimuli used in the present experiments contain further acoustic cues (other than pitch commonality, pitch repetition, and roughness) that could also elicit deviance-related negative potentials.

Previous studies using behavioral measures showed harmonic priming effects that were not based on previously activated sensory memory traces but on higher order knowledge about musical structure (see Bharucha & Stoeckig, 1987; Bigand et al., 2003; Tekman & Bharucha, 1998). It is likely that the very first chords of each sequence activated representations of a tonal schema that entails representations of the in-key tones of a scale and a "hierarchy of stability" of chord functions (Bharucha & Krumhansl, 1983). Such representations may exert top-down influences on the processing of pitches on the level of auditory sensory memory, but this possibility remains to be specified (notably, recent data from our laboratory also showed an ERAN response in sequences that did not begin with a tonic chord; Koelsch, 2005).

In a previous study investigating ERP effects of harmonically related chords (tonic chords) and harmonically less related chords (subdominants), no ERAN was observed in response to harmonically less related chords (Regnault et al., 2001). This difference between studies is presumably due to differences in the degree of irregularity: The DDs and STs used in the present study had a higher degree of music-syntactic irregularity than the subdominant chords used in the study from Regnault et al. Although the subdominants used in the latter study were less regular than tonic chords, the low degree of irregularity represented by those subdominants was presumably too small to elicit a clear ERAN (unpublished data from our laboratory suggest that experimental paradigms using considerably more trials, leading to a higher SNR, reveal a small ERAN even to such subdominant chords when subjects attend the stimuli).

Processing of Syntactic Information

Brain mechanisms that process sequential (auditory) information according to complex, syntactic regularities are obviously not only relevant for the processing of music, but also important for the processing of language. A variety of studies showed that processing of (syntactic) phrase-structure violations in language may be reflected in an early left anterior negativity (ELAN; Friederici, 2002). Interestingly, the ERAN strongly resembles the ELAN: Both components have a similar time course, invert polarity at mastoid leads with nose reference, rely on at least partly the same generators, and are sensitive to the violation of an expected structure (for overviews, see Koelsch, 2005; Koelsch & Siebel, 2005). It appears that the mechanisms underlying the generation of syntax-related mismatch negativities (such as ERAN and ELAN) are not specific for auditorily presented information: Previous studies suggest that visually induced musical expectancy violations may also elicit an ERAN (Gunter, Schmidt, & Besson, 2003; Schön & Besson, 2005) and that the ELAN can also be elicited with visually presented stimuli (Gunter, Friederici, & Hahne, 1999).

Interactions between music-syntactic and language-syntactic processing have also been shown in a recent study (Koelsch, Gunter, Wittfoth, & Sammler, 2005) in which the ERAN, but not the (frequency) MMN, interacted with the left anterior negativity (LAN; the LAN was elicited by morpho-syntactic violations). This finding suggests that the ERAN consumes neural resources related to syntactic processing (as evidenced by the interaction with the LAN), whereas the frequency MMN does not appear to consume such resources.

Automaticity of the ERAN

The comparison of Experiments 1 and 2 suggests that the ERAN can be elicited under both task-relevant and task-irrelevant conditions, even when music-syntactic irregularities are only subtle. This finding is consistent with previous studies showing that the ERAN can be evoked when subjects read a book (Koelsch, Schröger, et al., 2002), play a video game (Koelsch et al., 2001), or perform a reading comprehension task (Loui et al., 2005). However, the recent study from Loui et al. showed that the mechanisms underlying the generation of the ERAN can be influenced by attention, especially when attention is strongly captured by competing tasks.

Lateralization of the ERAN

The lateralization of the ERAN was only weak in the present study and even absent in some previous studies investigating

music-syntactic processing with the ERAN (Loui et al., 2005; Steinbeis et al., 2006). Likewise, some recent data from our own laboratory do not show a pronounced lateralization of the ERAN, and a previous study suggested differences in lateralization between males and females (Koelsch, Maess, Grossmann, & Friederici, 2003). Our current notion is that the lateralization of the ERAN becomes weaker when musical irregularities become less salient, but this issue needs further investigation. Because the term ERAN falls short as a descriptor for an effect that is not lateralized, Loui et al. simply termed the effect EAN instead of ERAN. However, for the time being, we prefer the term ERAN, because some previous literature has established this term as a label for its functional significance, rather than for its scalp topography.

Late ERP Effects

In Experiment 2, the ERAN was followed by an N5 that showed a bilateral scalp distribution and was maximal around 500–550 ms. It appears that an N5 was also elicited in Experiment 1, but overlapped by a P3. As mentioned in the Introduction, the N5 is taken to reflect processes of harmonic integration: The first four chords of the sequences built up a harmonic context toward the end of the sequence. The harmonic context buildup has been shown to correlate with an amplitude decrease of the N5 elicited by in-key chords (Koelsch et al., 2000). Regular final chords can easily be integrated into the established musical context, whereas irregular chords require a larger amount of harmonic integration (because they do not easily fit into the harmonic fabric established by the first four chords), presumably leading to a larger amplitude of the N5. The processes of harmonic integration appear to resemble processes of semantic integration during the perception of language (reflected in the N400; e.g., Kutas & Federmeier, 2000) and might at least partly reflect processing of musical meaning (irregular chord functions and deceptive cadences are prominent elements of major–minor tonal music that are used by composers as a means of expression; Koelsch et al., 2004; Koelsch & Siebel, 2005). The exact relation between N5 and processing of musical meaning, however, remains to be specified.

In Experiment 2, irregular chords also elicited a late positive component (LPC; e.g., Besson & Faïta, 1995; Patel et al., 1998). This finding was unexpected, because the harmonies were task irrelevant, and other studies with an experimental design similar to that of Experiment 2 did not show an LPC (Koelsch et al., 2000, 2001; Koelsch, Schröger, et al., 2002). Previous studies of musical perception using the LPC suggest that the LPC reflects processes of structural integration and possibly processes of structural repair (Besson & Schön, 2001; Koelsch & Siebel, 2005; Patel et al., 1998). These processes usually follow the detection of a structural irregularity, and they seem to be most pronounced when participants have a task connected to the irregular chords (similarly to the P600; Patel et al., 1998). That is, whereas the N5 is probably related to the processing of meaning information, the LPC might reflect processes related to structural integration and repair (Koelsch & Siebel, 2005).

Effects of Musical Training

In Experiment 2, the ERAN amplitude elicited in amateur musicians was slightly larger than the ERAN of nonmusicians (no amateur musicians were investigated in Experiment 1). In Experiment 3, amateur musicians classified the sequence endings with significantly higher accuracy than nonmusicians, corroborating

results of Experiment 2. These results are in line with a previous ERP study showing that musical training influences processes of music-syntactic analysis (Koelsch, Schmidt, et al., 2002). In that study, the ERAN was larger in musicians than in nonmusicians. The present results show that small differences can already be observed between nonmusicians and amateur musicians. It is likely that musical training leads to more specific representations of musical regularities and, thus, to a better differentiation between regular and irregular musical events. Importantly, the ERAN elicited in Experiment 2 was significant when analyzing the data of nonmusicians only, ruling out the possibility that effects were simply due to the subgroup of amateur musicians.

It is interesting to note that effects were elicited in nonmusicians by quite subtle musical irregularities, supporting the notion that even nonmusicians have a sophisticated representation of musical regularities (e.g., Bigand, Madurell, Tillmann, & Pineau, 1999; Bigand & Pineau, 1997; Koelsch et al., 2000) and that they process musical information fast and quite automatic according to these representations. Nonmusicians most presumably acquire implicit knowledge about musical regularities by listening to music in everyday life (Koelsch & Siebel, 2005; Tillmann et al., 2000).

Conclusions

The present results show that the ERAN is not simply an ERP effect elicited by the processing of acoustical features such as pitch commonality and roughness and that the generation of the ERAN does not result from differences in pitch repetition between regular and irregular chords.

This is of particular importance because in major–minor tonal music, syntactic regularities on the one hand and acoustic factors on the other are closely intertwined (music-syntactically irregular chords usually also being acoustically deviant). For an adequate understanding of the neural correlates of music perception, it is, thus, relevant to determine which neural processes are due to acoustic factors and which are due to music-syntactic processing. Previous studies have shown that acoustic factors (such as pitch, timbre, intensity, and roughness) modulate earlier ERP components (especially P1 and N1) and that automatic change detection of acoustic factors is reflected in the MMN (for references, see Koelsch & Siebel, 2005). Our data show that music-syntactic irregularities elicit an ERAN, even in the absence of acoustic factors that would otherwise lead to modulation of P1 and N1 potentials, or to the elicitation of a “classical” MMN. Because acoustical factors were more thoroughly controlled than in some previous ERP studies, the present study represents a step toward untangling music-syntactic and sensory processing of harmonies.

Experiments 1 and 3 showed that even nonmusicians can detect the irregular chords used in the present study well above chance level. These chords were not very salient for nonmusicians, as indicated by a hit rate of only around 75% for the irregular chords. Nevertheless, these chords elicited reliable effects in the ERPs. The difference in behavioral discrimination performance, as well as in the ERAN amplitude between amateur musicians and nonmusicians, supports the notion that the ERAN is sensitive to long-term (musical) training. These results also show that even moderate musical training can lead to changes in the neural mechanisms underlying music-syntactic

processing. Because effects were also elicited in subjects without formal musical training, the present findings underscore the notion that the ability to acquire knowledge about complex musical

regularities and the ability to process musical information quickly and automatically according to this knowledge are general abilities of the human brain.

REFERENCES

- Besson, M., & Faita, F. (1995). An event-related potential (ERP) study of musical expectancy: Comparison of musicians with nonmusicians. *Journal of Experimental Psychology. Human Perception and Performance*, *21*, 1278–1296.
- Besson, M., & Schön, D. (2001). Comparison between Language and Music. In R. J. Zatorre & I. Peretz (Eds.), *The biological foundations of music* (Annals of the New York Academy of Sciences, Vol. 930, pp. 232–258). New York: The New York Academy of Sciences.
- Bharucha, J., & Krumhansl, C. (1983). The representation of harmonic structure in music: Hierarchies of stability as a function of context. *Cognition*, *13*, 63–102.
- Bharucha, J., & Stoeckig, K. (1987). Priming of chords: Spreading activation or overlapping frequency spectra? *Perception and Psychophysics*, *41*, 519–524.
- 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.
- Bigand, E., Parncutt, R., & Lerdahl, J. (1996). Perception of musical tension in short chord sequences: The influence of harmonic function, sensory dissonance, horizontal motion, and musical training. *Perception and Psychophysics*, *58*, 125–141.
- Bigand, E., & Pineau, M. (1997). Global context effects on musical expectancy. *Perception and Psychophysics*, *59*, 1098–1107.
- Bigand, E., Poulin, B., Tillmann, B., Madurell, F., & D'Adamo, D. A. (2003). Sensory versus cognitive components in harmonic priming. *Journal of Experimental Psychology. Human Perception and Performance*, *29*, 159–171.
- Bigand, E., Tillmann, B., Poulin, B., D'Adamo, D. A., & Madurell, F. (2001). The effect of harmonic context on phoneme monitoring in vocal music. *Cognition*, *81*, B11–B20.
- Friederici, A. D. (2002). Towards a neural basis of auditory sentence processing. *Trends in Cognitive Science*, *6*, 78–84.
- Gunter, T. C., Friederici, A. D., & Hahne, A. (1999). Brain responses during sentence reading: Visual input affects central processes. *NeuroReport*, *10*, 3175–3178.
- Gunter, T. C., Schmidt, B. H., & Besson, M. (2003). Let's face the music: A behavioral and electrophysiological exploration of score reading. *Psychophysiology*, *40*, 742–751.
- Heinke, W., Kennner, R., Gunter, T. C., Sammler, D., Olthoff, D., & Koelsch, S. (2004). Differential effects of increasing propofol sedation on frontal and temporal cortices: An ERP study. *Anesthesiology*, *100*, 617–625.
- Janata, P. (1995). ERP measures assay the degree of expectancy violation of harmonic contexts in music. *Journal of Cognitive Neuroscience*, *7*, 153–164.
- Janata, P., & Grafton, S. T. (2003). Swinging in the brain: Shared neural substrates for behaviors related to sequencing and music. *Nature Neuroscience*, *6*, 682–687.
- Janata, P., Tillmann, B., & Bharucha, J. (2002). Listening to polyphonic music recruits domain-general attention and working memory circuits. *Cognitive, Affective and Behavioral Neuroscience*, *2*, 121–140.
- Knoesche, T., Neuhaus, C., Haueisen, J., Alter, K., Maess, B., & Witte, O. W. (2005). Perception of phrase structure in music. *Human Brain Mapping*, *24*, 259–273.
- Koelsch, S. (2005). Neural substrates of processing syntax and semantics in music. *Current Opinion in Neurobiology*, *15*, 1–6.
- Koelsch, S., Gunter, T. C., Friederici, A. D., & Schröger, E. (2000). Brain indices of music processing: “Non-musicians” are musical. *Journal of Cognitive Neuroscience*, *12*, 520–541.
- Koelsch, S., Gunter, T. C., Schröger, E., Tervaniemi, M., Sammler, D., & Friederici, A. D. (2001). Differentiating ERAN and MMN: An ERP-study. *NeuroReport*, *12*, 1385–1389.
- Koelsch, S., Gunter, T. C., Wittfoth, M., & Sammler, D. (2005). Interaction between syntax processing in language and in music: An ERP Study. *Journal of Cognitive Neuroscience*, *17*, 1565–1579.
- Koelsch, S., Heinke, W., Sammler, D., & Olthoff, D. (2006). Auditory processing during deep propofol sedation and recovery from unconsciousness. *Clinical Neurophysiology*, *117*, 1746–1759.
- Koelsch, S., Jentschke, S., & Sammler, D. (2007). Short-term effects of processing musical syntax. Manuscript submitted for publication.
- Koelsch, S., Kasper, E., Sammler, D., Schulze, K., Gunter, T. C., & Friederici, A. D. (2004). Music, language, and meaning: Brain signatures of semantic processing. *Nature Neuroscience*, *7*, 302–307.
- Koelsch, S., Maess, B., Grossmann, T., & Friederici, A. D. (2003). Electric brain responses reveal gender differences in music processing. *NeuroReport*, *14*, 709–713.
- Koelsch, S., & Mulder, J. (2002). Electric brain responses to inappropriate harmonies during listening to expressive music. *Clinical Neurophysiology*, *113*, 862–869.
- Koelsch, S., Schmidt, B. H., & Kansok, J. (2002). Influences of musical expertise on the ERAN: An ERP-study. *Psychophysiology*, *39*, 657–663.
- Koelsch, S., Schröger, E., & Gunter, T. C. (2002). Music matters: Preattentive musicality of the human brain. *Psychophysiology*, *39*, 1–11.
- Koelsch, S., & Siebel, W. (2005). Towards a neural basis of music perception. *Trends in Cognitive Science*, *9*, 578–584.
- Kutas, M., & Federmeier, K. (2000). Electrophysiology reveals semantic memory use in language comprehension. *Trends in Cognitive Science*, *4*, 463–470.
- Leman, M. (2000). An auditory model of the role of short-term memory in probe-tone ratings. *Music Perception*, *17*, 481–509.
- Leman, M., Lesaffre, M., & Tanghe, K. (2005). IPEM toolbox for perception-based music analysis (version 1.02). Available at: <http://www.ipem.ugent.be/Toolbox/index.html>.
- Loui, P., Grent-’t Jong, T., Torpey, D., & Woldorff, M. (2005). Effects of attention on the neural processing of harmonic syntax in Western music. *Cognitive Brain Research*, *25*, 589–598.
- Maess, B., Koelsch, S., Gunter, T. C., & Friederici, A. D. (2001). “Musical syntax” is processed in the area of Broca: An MEG study. *Nature Neuroscience*, *4*, 540–545.
- Näätänen, R. (1992). *Attention and brain function*. Hillsdale, NJ: Erlbaum.
- Neuhaus, C., Knösche, T., & Friederici, A. (2006). Effects of musical expertise and boundary markers on phrase perception in music. *Journal of Cognitive Neuroscience*, *18*, 472–493.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh Inventory. *Neuropsychology*, *9*, 97–113.
- Opitz, B., Rinne, T., Mecklinger, A., von Cramon, D. Y., & Schröger, E. (2002). Differential contribution of frontal and temporal cortices to auditory change detection: fMRI and ERP results. *NeuroImage*, *15*, 167–174.
- Parncutt, R. (1989). *Harmony: A psychoacoustical approach*. Berlin: Springer.
- Patel, A. D. (2003). Language, music, syntax and the brain. *Nature Neuroscience*, *6*, 674–681.
- Patel, A. D., Gibson, E., Ratner, J., Besson, M., & Holcomb, P. (1998). Processing syntactic relations in language and music: An event-related potential study. *Journal of Cognitive Neuroscience*, *10*, 717–733.
- Piston, W. (1948/1987). *Harmony*. New York: Norton.
- 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.
- Riemann, H. (1877/1971). *Musikalische Syntaxis: Grundriss einer harmonischen Satzbildungslehre*. Niederwalluf: Sändig.
- Schön, D., & Besson, M. (2005). Visually induced auditory expectancy in music reading: A behavioural and electrophysiological study. *Journal of Cognitive Neuroscience*, *17*, 694–705.

- Schönberg, A. (1969). *Structural functions of harmony* (rev. ed). New York: Norton.
- Schröger, E. (1998). Measurement and interpretation of the mismatch negativity (MMN). *Behavior Research Methods, Instruments, and Computers*, *30*, 131–145.
- Steinbeis, N., Koelsch, S., & Sloboda, J. (2006). The role of harmonic expectancy violations in musical emotions: Evidence from subjective, physiological, and neural responses. *Journal of Cognitive Neuroscience*, *18*, 1380–1393.
- Tekman, H. G., & Bharucha, J. J. (1998). Implicit knowledge versus psychoacoustic similarity in priming of chords. *Journal of Experimental Psychology. Human Perception and Performance*, *24*, 252–260.
- Tillmann, B., Bharucha, J., & Bigand, E. (2000). Implicit learning of Tonality: A Self-Organized Approach. *Psychological Review*, *107*, 885–913.

(RECEIVED August 11, 2006; ACCEPTED January 2, 2007)