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Short-term effects of processing musical syntax: An ERP study

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ABSTRACT

We investigated influences of short-term experience on music-syntactic processing, using a chord-sequence paradigm in which sequences ended on a harmony that was syntactically either regular or irregular. In contrast to previous studies (in which block durations were rather short), chord sequences were presented to participants for around 2 h while they were watching a silent movie with subtitles. Results showed that the music-syntactically irregular chord functions elicited an early right anterior negativity (ERAN), and that the ERAN amplitude significantly declined over the course of the experiment. The ERAN has previously been suggested to reflect the processing of music-syntactic irregularities, and the present data show that the cognitive representations of musical regularities are influenced by the repeated presentation of unexpected, irregular harmonies. Because harmonies were task-irrelevant, the data suggest that cognitive representations of musical regularities can change implicitly, i.e., even when listeners do not attend to the harmonies, and when they are presumably oblivious of the changes of such representations. Although the ERAN amplitude was significantly reduced, it was still present towards the end of the experiment at the right anterior electrodes, indicating that cognitive representations of basic music-syntactic regularities cannot easily be erased.

1. Introduction

Humans familiar with major–minor ('Western') tonal music have a sophisticated knowledge about the syntactic regularities underlying this type of music. Some syntactic regularities of tonal music are grounded on acoustic principles (such as acoustic similarity of chords belonging to the same key, Leman, 2000; Bharucha and Krumhansl, 1983) and, thus, presumably do not need extensive, if any, musical experience to be recognized. However, other syntactic regularities are culture-specific (such as harmonic progressions typical for certain musical epochs, or styles) and, hence, depend on representations of music-syntactic regularities that are shaped by listening experience. How the neural mechanisms underlying music-syntactic processing are modified by listening experience is largely unknown.

Previous studies indicated effects of long-term experience on the processing of music-syntactic information by demonstrating that musicians show stronger neural reactions, or more accurate behavioural responses to music-structural irregularities than non-musicians. For example, Bigand et al. (1999) showed that musicians respond faster, and more accurately to harmonically slightly irregular chords (a tonic-subdominant ending of a harmonic sequence, see Fig. 1 for explanation of these terms). Using ERPs, Besson and Faita (1995) showed that incongruities in melodies (whether familiar or unfamiliar) elicit a larger late positive component (LPC) in musicians than in non-musicians. Similar results were

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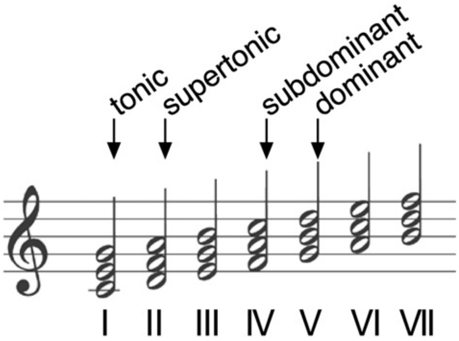

Fig. 1 – Illustration of chord functions (in *C*-major). In tonal music, the harmonies built on the steps of a scale are denoted as chord functions. For example, the chord built on the first scale tone is denoted as the tonic, the chord on the second scale tone as the supertonic, the chord on the fourth scale tone as the subdominant, and the chord on the fifth scale tone as the dominant. The combination of chord functions into harmonic progressions is guided by certain regularities (see also next figure).

reported by a study from Regnault et al. (2001) in which musicians showed larger P300 potentials to music-syntactically slightly irregular chords (also a tonic-subdominant ending of a harmonic sequence, similar to Bigand et al., 1999). Another study using chords as stimuli (Koelsch et al., 2002a) reported that early negative brain responses to music-syntactically irregular chord functions are larger in musicians than in non-musicians, and fMRI data showed that particularly inferior frontolateral cortical areas (including Broca's area) are activated more strongly in musicians than in non-musicians in response to such chords (for an overview see Koelsch and Siebel, 2005). Similar training effects on music-syntactic processing as in the study from Koelsch et al. (2002a) have also been shown for amateur musicians (in whom training effects were less pronounced than in musicians, Koelsch et al., 2007).

These studies indicate clear effects of long-term musical experience on music-syntactic processing. In the present study we investigated effects of short-term experience on the neural correlates of music-syntactic processing. We used the early right anterior negativity (ERAN) as a neurophysiological marker of such processing. The ERAN can be elicited in chord-sequence paradigms by music-syntactically irregular chord functions, and is taken to reflect the processing of a musical (and not simply acoustical) sound expectancy violation (Koelsch et al., 2000; Loui et al., 2005; Leino et al., 2005; Patel, 2003; Brattico, 2006; Fujioka et al., 2004; the term chord function is explained in Fig. 1). In previous studies investigating the ERAN, block durations were fairly short (usually around 10 min) to avoid a possible habituation of subjects to the irregular chords. In the present study, we investigated if the neural mechanisms of music-syntactic processing (as reflected in the ERAN) are influenced by the repeated presentation of irregular

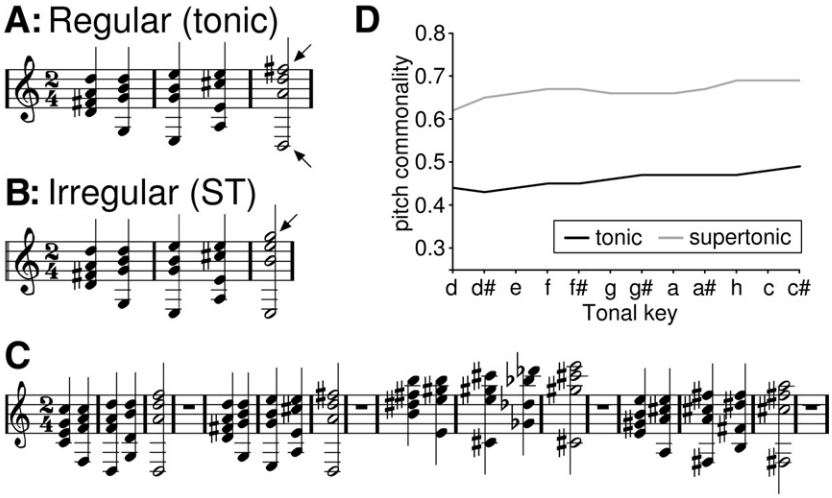

Fig. 2 – Examples of chord sequences. A and B illustrate the two chord sequence types (in *D*-major), the first four chords are identical for both sequences (tonic, subdominant, supertonic, dominant), sequence A ends on a tonic chord (regular), sequence B on a supertonic (irregular). Arrows indicate pitches that were not contained in the preceding chords. Note that supertonics introduced only one new pitch, whereas final tonic chords introduced two new pitches (making STs with respect to pitch repetition acoustically more similar to the previous chords than tonics). For the experiment, sequences were transposed to all twelve major keys, and presented in pseudo-random order (C). Each sequence was presented in a tonal key that differed from the key of the preceding sequence, regular and irregular sequence endings occurred with equal probability ($p = 0.5$). D: Pitch commonality calculated for the two chord-sequence endings (tonic and supertonic) and the penultimate (dominant) chord (adapted from Koelsch et al., 2007). Values were computed separately for all twelve major keys according to Parncutt (1989), and connected with lines for better visualization (pitch commonality values were calculated for the twelve keys to illustrate the effect of transposition on pitch commonality, and to show that the pitch commonality ranges for the two chord types tested do not overlap). The graphs show that STs have a higher pitch commonality with the directly preceding dominant chord than tonic chords have. Thus, with respect to *sensory dissonance* (of which pitch commonality is the major component), STs were even more similar to the preceding chord than final tonic chords were.

chords during the course of an experimental session which lasted around 120 min. The repeated presentation of an irregular chord function might lead to an alteration of the representation of musical regularity, and thus to a decrease of sound expectancy violation. We expected that such a decrease would be reflected in an amplitude decrease of the ERAN.

Another ERP of interest was the N5, an anterior negativity with a latency of around 550 ms which usually co-occurs with the ERAN (Koelsch et al., 2000; Loui et al., 2005; Koelsch and Siebel, 2005). The N5 is taken to reflect the harmonic integration of an unexpected chord into the preceding context (reminiscent of processes of semantic integration during the perception of language, Koelsch et al., 2000; Koelsch and Siebel, 2005). We expected that the harmonic integration of music-syntactically irregular chords would become easier with repeated exposure to such chords, and that, similar to the amplitude of the ERAN, the amplitude of the N5 would decrease over the course of the experiment.

The design of the present experiment was identical to that of previous experiments (Koelsch et al., 2007) with the exception that the current experiment lasted approximately 2 h, during which the subjects were watching a silent movie with subtitles. Chord sequences ended with equal probability on either a regular, or on a music-syntactically irregular chord function (Figs. 2A and B, in previous experiments, these chords have been shown to elicit both ERAN and N5 potentials). Our data show that music-syntactically irregular chords elicit both an ERAN as well as an N5, and that the amplitude of the ERAN decreased over the course of the experimental session. The results reveal how neural mechanisms underlying the processing of highly complex auditory (music-syntactic) information are modified by short-term musical experience.

2. Results

Behaviourally, participants detected 96.12% of the deviant instruments, indicating that the task to detect these events was not difficult, and that participants responded to deviances

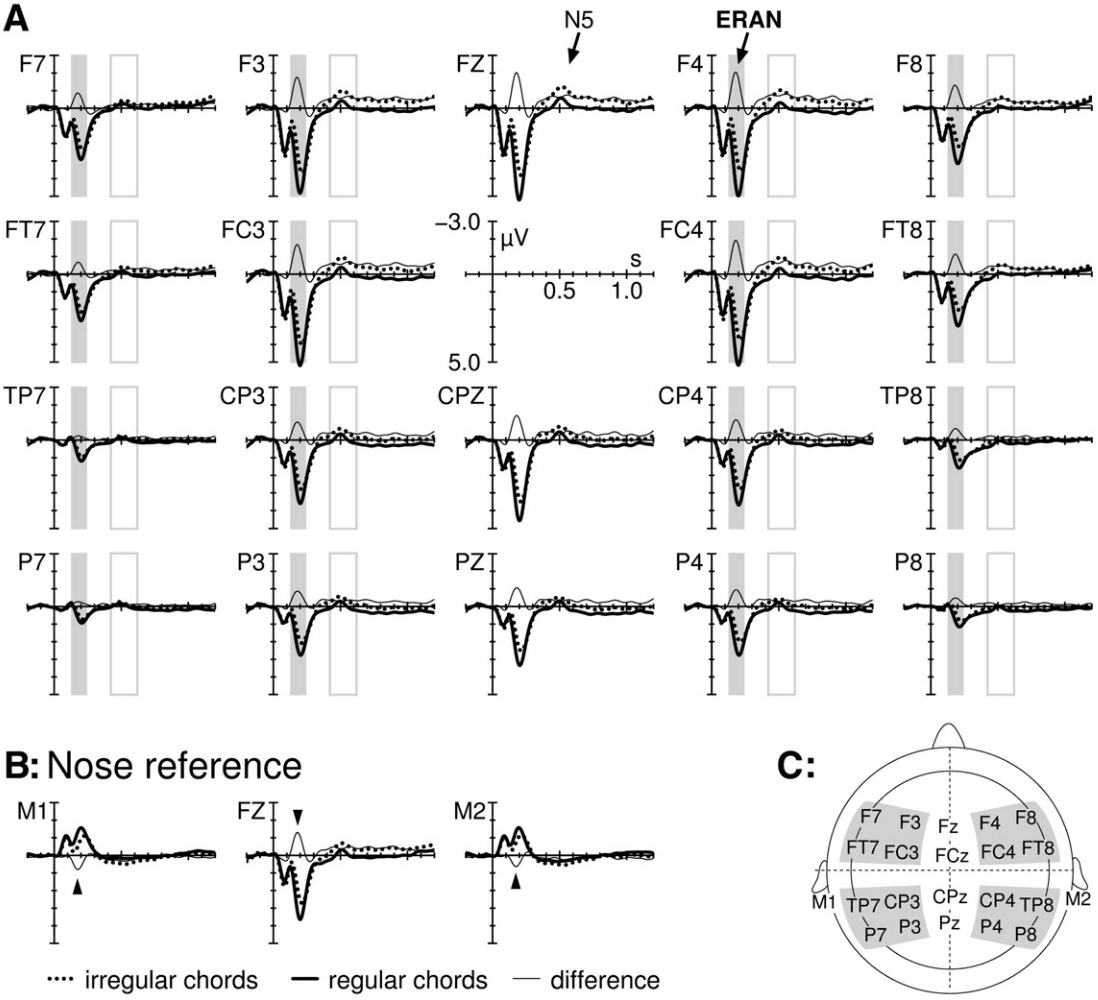

Fig. 3 – Grand-average of ERPs elicited by the fifth chord (A, thick solid line: tonic chords, dotted line: supertonics), referenced to the algebraic mean of both mastoids electrodes. Time intervals used for the statistical analysis are indicated by grey shaded areas (ERAN), and grey rectangles (N5). B: When referenced to the nose electrode, the ERAN inverted polarity at mastoid electrodes (M1, M2, see arrows). A similar polarity inversion is visible for the N5. C shows the head positions of the electrodes presented in A and B.

within the physical dimension of the musical stimulus despite watching the silent movie.

The ERP data show that (task-irrelevant) STs elicited a clear ERAN compared to tonic chords (Fig. 3A). The ERAN peaked at around 180 ms, and was maximal at right anterior scalp sites (although the ERAN was also clearly present over left anterior sites). At mastoid electrodes, the ERAN inverted polarity when potentials were referenced to the nose electrode (as in previous studies, see Koelsch et al., 2002b, 2007, see also Fig. 3B).

To investigate whether the ERAN amplitude changed over the course of the experiment, data were split into five segments (see Methods). As can be seen in Fig. 4, the ERAN amplitude decreased with increasing duration of the experimental session (while the ERAN latency was similar across segments, latencies for segments 1 to 5 were: 180, 176, 180, 176, and 172 ms).

A MANOVA for the time-window from 120–240 ms with factors chord function (regular, irregular), segment (1–5), hemisphere, and anterior–posterior distribution revealed an effect of chord function ($F(1,19) = 29.15$; $p < 0.001$), an interaction between factors chord function and anterior–posterior distribution ($F(1,19) = 27.87$; $p < 0.001$), and an interaction between factors chord function and hemisphere ($F(1,19) = 5.51$; $p = 0.03$). These interactions reflect that the ERAN had maximal amplitude values at right anterior electrodes. Moreover, the MANOVA yielded an interaction between factors chord function, segment, and anterior–posterior distribution ($F(4,16) = 7.57$; $p < 0.001$), indicating that the ERPs elicited by the two chord functions differed between segments at anterior electrodes. Within the same MANOVA, a test for linear trends (using polynomial contrasts) revealed a significant linear trend for the interaction between chord function, segment and anterior–posterior distribution ($F(1,19) = 16.10$; $p < .001$), reflecting that the ERAN amplitude decreased over the course of the experiment (particularly at frontal leads).

Within an analogous MANOVA computed for anterior ROIs only, a significant linear trend was yielded (again using polynomial contrasts) for the interaction between chord function and segment ($F(1,19) = 6.72$; $p < .02$, confirming that the ERAN amplitude decreased with increasing duration of the experiment). User-defined contrasts investigating the ERAN separately for each segment revealed a significant ERAN for each of the first four segments ($p < .006$ for each contrast), but not for the fifth segment ($p < .09$). When analyzing the data of the fifth segment for the right anterior ROI only, the ERAN was statistically significant ($F(1,19) = 10.17$; $p < .005$). The latter results indicate that the ERAN was not completely abolished, and that a small ERAN was still present at right anterior electrodes at the end of the experiment (i.e., after around 100–120 min).

The ERAN amplitude (regular subtracted from irregular chords) was nominally slightly larger in amateur musicians (−0.91 μV, anterior ROIs) than in non-musicians (−0.81 μV), but this difference between groups was statistically not significant ($p > .7$). When comparing the mean ERAN amplitude between groups for the first segment only (more closely corresponding in duration to previous experiments, Koelsch et al., 2007), the difference between groups was slightly larger (amateur musicians −1.41 μV, non-musicians: −0.87 μV), but again statistically not significant ($p > .2$).

The ERAN was followed by a bilateral N5 that had an anterior preponderance and was maximal around 520ms. As can be seen in Fig. 3B, the N5 inverted polarity at mastoid electrodes (similar to the ERAN) when potentials were referenced to the nose electrode (as in previous studies, see Koelsch et al., 2002b, 2007). Compared to the ERAN, the amplitude of the N5 was relatively small and did not clearly change across the experiment. A MANOVA for the time-window from 420–620ms with factors chord function, hemisphere, anterior–posterior distribution, and segment (1–5), revealed an effect of chord function ($F(1,19) = 28.84$; $p < 0.001$), an interaction between factors chord function and anterior–posterior distribution ($F(1,19) = 7.26$; $p = 0.014$), and no interaction between factors chord function and hemisphere. Within a MANOVA for anterior ROIs (analogous to the MANOVA conducted for the ERAN), no linear trend was revealed for a tested interaction between factors chord function and segment ($p > .7$), indicating that the amplitude of the N5 did not significantly decrease over the course of the experimental session.

The N5 amplitude (regular subtracted from irregular chords) was larger in amateur musicians (−0.70 μV, anterior ROIs) than in non-musicians (−0.34 μV): an ANOVA with factors chord function, group, and hemisphere conducted for anterior ROIs indicated an effect of chord function ($F(1,18) = 49.37$; $p < 0.001$), and an interaction between factors chord function and group ($F(1,18) = 6.01$; $p = 0.025$).

As mentioned in the Methods, STs were minor chords (in contrast to tonic chords, which were major chords). The number of major (tonics) and minor (STs) chords at the final position of the sequences was equal, but minor chords had a lower probability with respect to all chords of the sequences (30%) than major chords (70%), because STs also occurred in each chord sequence at the third position. Note that STs did not represent deviants with respect to their superposition of intervals, because this superposition was different for all chords. Moreover, chords were composed such that the

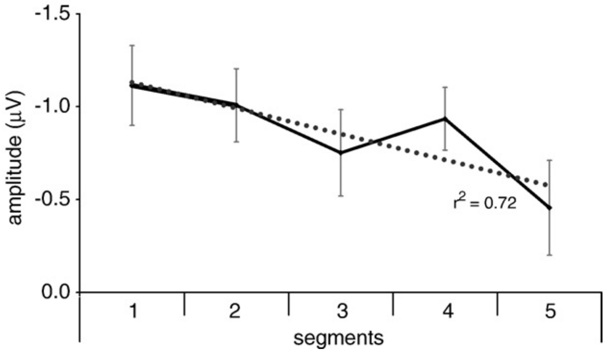

Fig. 4 – Decline of the ERAN amplitude. Data were split into five segments, and the ERAN amplitude was calculated for each segment (difference potentials, regular subtracted from irregular chords). The solid line runs through the mean ERAN amplitude values of the five segments (grand-average of single-subject amplitude values, calculated for the anterior regions of interest and the 120–240 ms time interval used for statistical analyses, vertical lines indicate SEM). The dashed line indicates the linear regression ($y = 0.14x - 1.27$).

roughness values (calculated according to Bigand et al., 1996) were even more similar between final STs and the preceding chords than between final tonics and the preceding chords (see Methods), rendering it highly unlikely that STs were detected as deviant because of differences in roughness. However, it is possible that the algorithm from Bigand et al. (1996) does not provide entirely accurate values, or that even the high probability of 30% elicited a residual mismatch negativity (although a probability of around 20% has been reported to be necessary to elicit the MMN; Näätänen et al., 2005). Thus, we also analyzed ERPs elicited by the STs presented at the third position of the chord sequences (which were always minor chords, see Figs. 2A, B). If the generation of the ERAN would have been due to any acoustic deviance of minor chords, STs at the third position should have elicited negative effects similar to those elicited by the STs at the fifth position.

Fig. 5 shows that this was not the case: the ERP waveform elicited by the ST at the third position (where the ST was music-syntactically regular) was virtually identical to the waveforms of the regular major chords (subdominant at the second position, dominant at the fourth position, and tonic at the fifth position, see Fig. 5A). By contrast, the amplitude of the ST presented at the fifth position (where the ST was music-syntactically irregular) clearly differed from the amplitude values of both the regular major chords, and the ST presented at the third position (see also Fig. 5B).[1]

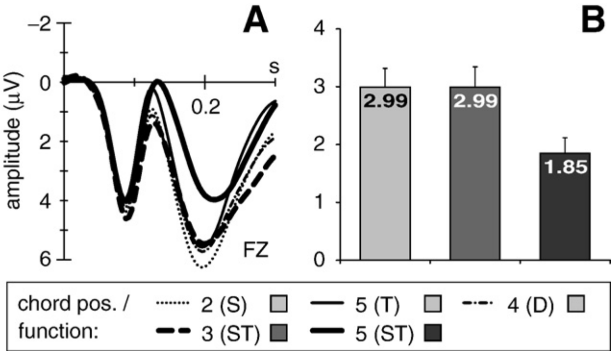

Fig. 5 – A: ERP waveforms (elicited at Fz) of the supertonics presented at the third (3 (ST)) and at the fifth positions (5 (ST)), as well as of the non-ST chord functions (2 (S): subdominant presented at the second position, 4 (D): dominant at the fourth position, 5 (T): tonic at the fifth position of the chord sequences). Note that supertonics were music-syntactically irregular at the fifth, but regular at the third position of the chord sequences. Consequently, ERPs elicited by STs at the third position were similar to those of the other regular chord functions, whereas STs of the fifth position elicited an ERAN. This indicates that the ERAN was elicited due to music-syntactic irregularity, and not due to the physical properties of the chord itself. B shows mean amplitude values measured at the anterior ROIs, computed for the ERAN time interval (120–240 ms) for regular non-ST chord functions (average of 2 (S), 5 (T), and 4 (D), left column), for supertonics at the third position (3 (ST), middle column), and for supertonics at the fifth position (5 (ST), right column). When presented at the third position of the chord sequences supertonics elicited the same ERP amplitude as the other regular in-key chords, whereas ERP amplitude elicited by (music-syntactically irregular) supertonics of the fifth position clearly differed from the potentials elicited by the other chords.

For statistical evaluation, mean amplitude values of chords were computed for the ERAN time-window and anterior ROIs. A two-tailed *t*-test comparing the amplitude of the ST at the third position with the averaged values of regular major chords did not indicate a difference ($p > .98$, mean amplitude difference was less than 0.003 μV). By contrast, the analogous *t*-test comparing the amplitude of the ST at the fifth position with the averaged values of regular major chords indicated a significant difference ($t(19) = 6.93$; $p < .0001$). This indicates that an ERAN was elicited only by final STs (which were syntactically irregular), but not by STs at the third position of the chord sequences (which were syntactically regular).

3. Discussion

Music-syntactically irregular STs elicited a clear ERAN, replicating findings from a previous experiment using the same chord sequences (Koelsch et al., 2007), as well as of other studies using similar chord-sequence paradigms (Loui et al., 2005; Leino et al., 2005). Notably, final STs represent quite subtle music-syntactic irregularities: In our mentioned previous study (Koelsch et al., 2007), participants (non-musicians and amateur musicians, as in the present study) detected on average only 72% of the final STs. That is, even though subjects are often not aware of the music-syntactically irregular chords, these chords nevertheless elicited an ERAN. The ERAN was evoked under a condition in which subjects were watching a silent movie with subtitles (while the regularity of chords was task-irrelevant), results thus also support previous findings showing that the neural mechanisms underlying the generation of the ERAN operate even when subjects do not focus their attention on the musical stimulus (Koelsch et al., 2001, 2002b, 2007; Loui et al., 2005).

Importantly, the ERAN amplitude decreased moderately (but significantly) across the experimental session, indicating that the processing of musical irregularities was influenced by short-term experience: It appears most likely that, due to the repeated presentation of irregular chord functions, the participants' initial representation of an ST at the end of a chord sequence being irregular was modified, and that, thus, final STs were perceived as less unexpected during the course of the experiment. Because the harmonies were task-irrelevant, results suggest that cognitive representations of musical regularities change implicitly, i.e., even when listeners do not attend to the harmonies, and even when they are presumably not consciously aware that these representations actually change. Moreover, we find it noticeable that after approximately 2 h experimental session (and several hundred presentations of the irregular chord), a small ERAN can still be

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[1] Potentials of the first chord were excluded from comparisons because P1, N1, and P2 potentials of the first chord considerably differ from those of the following chords due to the pause preceding each sequence.

elicited (significant at right anterior electrodes). This shows that cognitive representations of basic music-syntactic regularities cannot easily be erased.

It is important to note that, with respect to (a) pitch repetition, (b) pitch commonality with the preceding chord, and (c) roughness of chords, final STs were even more similar to the preceding harmonic context than final tonic chords. That is, music-syntactic regularity did not confound with acoustic similarity. Particularly the comparison of the ERPs elicited by final STs (syntactically irregular) with those elicited by STs at the third position of the sequences (syntactically regular) indicates that the ERAN was not elicited because of the properties of the chord itself, but because the STs had an irregular music-syntactic function at the end of the chord sequences: If the ERAN was merely due to a physical deviance of STs, then an ERAN should also have been elicited by the STs presented at the third position of the sequences (which was not the case; see also Koelsch et al., 2001). The present data, thus, strongly suggest that the ERAN elicited by final STs is a neurophysiological correlate of music-syntactic processing and not simply a reflection of the processing of an acoustic deviance (see also Koelsch et al., 2007, for further discussion).

With regards to ERPs that are more strongly dependent on the acoustic properties of sounds, previous studies have shown that the N1-P2 amplitude decreases rapidly (seconds to minutes), and then remains relatively stable (e.g., Ritter et al., 1968; Roeser and Price, 1969). Short-term (across several seconds) and long-term (across several minutes) decrements of the N1-P2 amplitude may be independent, and reflect different mechanisms (such as refractoriness and habituation, Woods and Elmasian, 1986; Roth et al., 1976; Näätänen and Picton, 1987; Budd et al., 1998). McGee et al. (2001) reported an amplitude decrease of the MMN (elicited by consonant–vowel syllables) over the course of several minutes (for a similar finding regarding the frequency-MMN see de Tommaso et al., 2004), suggesting that the neural mechanisms underlying the generation of the MMN are influenced by short-term experience (for effects of short-term training on the MMN see Tervaniemi et al., 2001). Habituation of ERPs reflecting language-syntactic processing (such as early left anterior negativity, left anterior negativity, and P600), have to our knowledge not been reported (presumably because this has not been investigated so far).

The music-syntactically irregular STs also elicited a significant N5 (although the amplitude values of the N5 were considerably smaller than those of the ERAN). The N5 has been suggested to reflect processes of harmonic integration, reminiscent of processes of semantic integration during language perception (Koelsch and Siebel, 2005). The N5 has been reported to be elicited in experiments in which participants ignored the musical stimulus while reading a self-selected book (Koelsch et al., 2002b), while playing a video game (Koelsch et al., 2001), or while performing a reading comprehension task (Loui et al., 2005). In the study from Loui et al. (2005), the N5 amplitude was reduced under the ignore condition compared to an attend condition, and other previous data showed that the N5 is abolished when subjects are forced to focus their attention on synchronously presented words (whereas an ERAN was still clearly observable, Koelsch et al., 2005). Particularly the latter finding suggests that the neural operations underlying the N5 are considerably less automatic than those underlying the ERAN.

In contrast to the ERAN, the amplitude of the N5 did not decrease over the course of the experiment. Given that the N5 amplitude was fairly small in the present experiment (due to the participants ignoring the harmonies), it is likely that the signal was too low to yield a statistically significant amplitude reduction. Future studies involving more attention on the part of the subjects might lead to a higher signal-to-noise ratio than in the present experiment, and might, thus, provide more information about effects of short-term experience on the N5 amplitude.

4. Conclusions

Our results show how cognitive representations of musical regularity are influenced by short-term experience: The ERAN amplitude (reflecting the processing of a music-syntactic sound expectancy violation) linearly declined during the repeated presentation of irregular chords over the course of about 2 h, but the ERAN was not abolished at the end of the experiment. This shows on the one hand that the representations of music-syntactic regularity can be altered by short-term experience, and that (because the ERAN could still be elicited at right anterior electrode sites after several hundred presentations of irregular chords) the cognitive representations of basic music-syntactic regularities cannot easily be erased. Because harmonies were task-irrelevant, the data also show that cognitive representations of musical regularities change implicitly (i.e., even when listeners are presumably oblivious of a change of these representations), and even when listeners do not focus their attention to the harmonies. Due to the strong overlap of neural mechanisms underlying the processing of syntactic information in both language and music (e.g., Patel et al., 1998; Koelsch et al., 2005, Fedorenko et al., 2007; Slevc et al., 2007), similar findings could be expected for short-term experience on syntactic language processing.

5. Experimental procedures

5.1. Participants

20 individuals participated in the experiment (age range 20 to 30 years, mean = 24.5 years, 11 females). 11 subjects were non-musicians who never participated in extracurricular music lessons or performances, 9 subjects were amateur musicians who had learned an instrument or sung in a choir for 2–10 years (mean = 5.4 years). All subjects were right-handed (laterality quotient was >90% according to the Edinburgh Handedness Inventory, Oldfield, 1971), and reported to have normal hearing.

5.2. Stimuli

There were two sequences, A and B (Figs. 2A and B) that were transposed to the twelve 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, and dominant. That is, 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 final chord function of type A was a tonic, of type B a supertonic (ST; in major, the ST is the in-key chord built on the second scale tone, and is often also referred to as *diatonic supertonic*). 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., Steinbeis et al., 2006). Note that, in the sequences used in the present experiment, STs are regular chord functions when played, e.g., at the third position of the sequence (as in all sequences presented in Fig. 2). By contrast, STs are structurally irregular when presented at the fifth position of the sequence after a dominant chord.

Importantly, final STs introduced only one new pitch, in contrast to final tonics, which introduced two new pitches (see arrows in Figs. 2A, B). Thus, pitches of final STs matched better with the information stored in the auditory sensory memory than pitches of final tonics (i.e., STs did not represent greater frequency deviants than final tonics; see also Koelsch et al., 2007). It is, hence, not possible that STs could simply be detected as irregular based on the operation of neural processes that are sensitive to the occurrence of deviant pitches (such as a frequency-MMN mechanism). Moreover, chord sequences ending on STs were constructed in a way that the pitch commonality between penultimate and final chords was even higher for STs than for final tonic chords (see Fig. 2D, values were computed according to Parncutt, 1989). Thus, final STs did not have a greater sensory dissonance (of which pitch commonality is the major component) than tonic chords. Finally, STs were minor chords (in contrast to final tonics), and depending on the superposition of intervals, minor chords may have a greater roughness than major chords. Therefore, chord sequences were composed such that the roughness values of the (minor) ST (as calculated according to Bigand et al., 1996) was comparable to the roughness values of the preceding chords. For example, in the sequences presented in Fig. 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 was 0.39, and the value of the final tonic was 0.29 (the roughness value of the initial tonic is different from the roughness value of the final tonic due to the different superposition of intervals; see also Koelsch et al., 2007). 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.

That is, with respect to (a) congruency with auditory sensory memory traces, (b) pitch commonality, and (c) roughness, the irregular STs were acoustically even more similar to the preceding chords than (regular) tonic chords were. On the other hand, STs were music-syntactically less regular at the end of the chord sequences than tonic chords. Thus, deviance-related negativities elicited by the final STs would reflect processing of syntactic, rather than of acoustic irregularity.

The timing for the presentation of chords was similar to previous experiments (Koelsch et al., 2007): presentation time of chords 1 to 4 was 600 ms, chord 5 was presented for 1200 ms. Sequences were presented in direct succession (Fig. 2C), with a silence period of 1200 ms between sequences. Each sequence type occurred with a probability of 0.5, and both sequence types were randomly intermixed. Moreover, each sequence was presented pseudo-randomly in a tonal key different from the key of the preceding sequence. In about 9% 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). 675 sequences ending on a tonic, 675 sequences ending on a supertonic, and 120 sequences with a deviant instrument were presented, resulting in a length of the experimental stimulus of approximately 2 h. 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).

5.3. *Methods*

While playing the musical stimulus, a silent movie (with subtitles) was presented. Participants were not informed about the harmonically irregular chords. The task was to watch the silent movie. To control that participants did not fall asleep during the experimental session, participants were instructed to monitor the timbre of the acoustic stimulus and to detect the infrequently occurring chords played with a deviant instrumental timbre (participants were asked to indicate the detection by pressing a response button; this method has already been used in previous studies, e.g. Koelsch et al., 2000, 2007). As examples, two sequences were presented, one without and one with a chord played on a deviant instrument.

5.4. *Data recording and analysis*

The EEG was recorded using 43 electrodes (FP1, FP2, AF7, AFZ, AF8, F9, F7, F3, FZ, F4, F8, F10, FT7, FC3, FC4, FT8, T7, C3, CZ, C4, T8, TP7, CP5, CP3, CPZ, CP4, CP6, TP8, P9, P7, P3, PZ, P4, P8, P10, PO7, POZ, PO8, O1, O2, M1, M2, nose-tip), the electrode placed on the left mastoid was used as reference. Sampling rate was 250Hz. 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 artefacts. Horizontal and vertical electro-oculograms (EOGs) were recorded bipolarly. For artefact rejection, each sampling point was centred in a gliding window, and rejected if the standard deviation within the window exceeded a threshold value: Artefacts caused by drifts or body movements were eliminated by rejecting sampling points whenever the standard deviation of a 200 ms or 800 ms gliding window exceeded 25 μV at any EEG-electrode. Eye-artefacts were rejected whenever the standard deviation of a 200 ms gliding window exceeded 25 μV at the vertical, or the horizontal EOG (rejections were controlled by the authors). ERPs were calculated using a 200 ms pre-stimulus baseline.

For statistical analysis, mean amplitude values were computed for four regions of interest (ROIs, see also Fig. 3C): left anterior (F3, F7, FC3, FT7), right anterior (F4, F8, FC4, FT8), left posterior (P3, P7, CP3, TP7), and right posterior (P4, P8, CP4, TP8). To investigate possible alterations of ERAN and N5 amplitudes across the experiment, data of the entire experiment were divided into five segments (each segment comprising around 300 chord sequences; comparable results were obtained when dividing the data into nine, twelve, or fifteen segments).

Amplitude values of ERPs were analyzed statistically by repeated measures MANOVAs. MANOVAs were conducted with factors chord function (regular, irregular), hemisphere (left, right ROIs), anterior–posterior distribution (anterior, posterior ROIs), and segment (5 levels). Although some ERPs will additionally be presented with nose reference, 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 was 120–240 ms for the ERAN, and 420–620 ms for the N5 (time-windows were centred at the peak amplitudes of ERAN, and N5, respectively). To facilitate legibility of ERPs, ERPs were low-pass filtered after statistical evaluation (10 Hz, 41 points, finite impulse response). Sequences with deviant instruments were excluded from further data analysis (their ERPs will not be shown because they were only used to control for the participants' behaviour).

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REFERENCES

Besson, M., Faita, F., 1995. An event-related potential (ERP) study of musical expectancy: comparison of musicians with non-musicians. J. Exp. Psychol. Hum. Percept. Perform. 21, 1278–1296.

Bharucha, J., Krumhansl, C., 1983. The representation of harmonic structure in music: Hierarchies of stability as a function of context. Cognition 13, 63–102.

Bigand, E., Madurell, F., Tillmann, B., Pineau, M., 1999. Effect of global structure and temporal organization on chord processing. J. Exp. Psychol. Hum. Percept. Perform. 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. Percept. Psychophys. 58, 125–141.

Brattico, E., 2006. Cortical processing of musical pitch as reflected by behavioural and electrophysiological evidence. Doctoral Thesis, Cog Brain Res Unit, Univ. of Helsinki, Finland.

Budd, T.W., Barry, R.J., Gordon, E., Rennie, C., Michie, P.T., 1998. Decrement of the N1 auditory event-related potential with stimulus repetition: habituation vs. refractoriness. Int. J. Psychophysiol. 31 (1), 51–68.

Fedorenko, E., Patel, A.D., Casasanto, D., Winawer, J., Gibson, E., 2007. Structural integration in language and music: a shared system. Paper Presented at the 20th CUNY Sentence Processing Conference, March 29–31, 2007, San Diego.

Fujioka, T., Trainor, L.J., Ross, B., Kakigi, R., Pantev, C., 2004. Musical training enhances automatic encoding of melodic contour and interval structure. J. Cogn. Neurosci. 16, 1010–1021.

Koelsch, S., Gunter, T.C., Friederici, A.D., Schröger, E., 2000. Brain indices of music processing: 'non-musicians' are musical'. J. Cogn. Neurosci. 12, 520–541.

Koelsch, S., Gunter, T.C., Schröger, E., Tervaniemi, M., Sammler, D., et al., 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. J. Cogn. Neurosci. 17, 1565–1579.

Koelsch, S., Jentschke, S., Sammler, D., Mietchen, D., 2007. Untangling syntactic and sensory processing: an ERP study of music perception. Psychophysiology 44, 476–490.

Koelsch, S., Schmidt, B.H., Kansok, J., 2002a. Influences of musical expertise on the ERAN: an ERP-study. Psychophysiology 39, 657–663.

Koelsch, S., Schröger, E., Gunter, T.C., 2002b. 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 Cogn. Sci. 9, 578–584.

Leino, S., Brattico, E., Tervaniemi, M., Vuust, P., 2005. Representation of harmony rules in the human brain: further evidence from event-related potentials. Brain Res. 1142, 169–177.

Leman, M., 2000. An auditory model of the role of short-term memory in probe-tone ratings. Music Percept. 17, 481–509.

Loui, P., Grent-'t Jong, T., Torpey, D., Woldorff, M., 2005. Effects of attention on the neural processing of harmonic syntax in Western music. Cogn. Brain Res. 25, 589–998.

McGee, T.J., King, C., Tremblay, K., Nicol, T.G., Cunningham, J., Kraus, N., 2001. Long-term habituation of the speech-elicited mismatch negativity. Psychophysiology 38, 653–658.

Näätänen, R., Picton, T., 1987. The N1 wave of the human electric and magnetic response to sound: a review and an analysis of the component structure. Psychophysiology 24 (4), 375–425.

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.

Oldfield, R.C., 1971. The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychiatrie 9, 97–113.

Parncutt, R., 1989. Harmony: a Psychoacoustical Approach. Springer, Berlin.

Patel, A., 2003. Language, music, syntax, and the brain. Nat. Neurosci. 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. J Cogn. Neurosci. 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. J Cogn. Neurosci. 13, 241–255.

Ritter, W., Vaughan Jr, H.G., Costa, L.D., 1968. Orienting and habituation to auditory stimuli: a study of short term changes in average evoked responses. Electroencephalogr. Clin. Neurophysiol. 25 (6), 550–556.

Roeser, R.J., Price, L.L., 1969. Effects of habituation on the auditory evoked response. J. Aud. Res. 9, 306–313.

Roth, W.T., Krainz, S.K., Ford, J.M., Tinkelberg, J.R., Rothbart, R.M., Kopell, B.S., 1976. Parameters of temporal recovery of the human auditory evoked potential. Electroencephalogr. Clin. Neurophysiol. 40, 623–632.

Schönberg, A., 1969. Structural functions of harmony. Norton, New York. rev. ed.

Slevc, L.R., Rosenberg, J.C., Patel, A.D., 2007. Language, music, and modularity: self-paced reading time evidence for shared processing of linguistic and musical syntax. Paper Presented at the 20th CUNY Sentence Processing Conference, March 29–31, San Diego.

Steinbeis, N., Koelsch, S., Sloboda, J., 2006. The role of harmonic expectancy violations in musical emotions: evidence from subjective, physiological, and neural responses. J Cogn. Neurosci. 18, 1380–1393.

Tervaniemi, M., Rytkönen, M., Schröger, E., Ilmoniemi, R.J., Näätänen, R., 2001. Superior formation of cortical memory traces for melodic patterns in musicians. Learn. Mem. 8 (5), 295–300.

Tommaso, M., Guido, M., Libro, G., Losito, L., Difruscolo, O., Sardaro, M., Puca, F.M., 2004. Interictal lack of habituation of mismatch negativity in migraine. Cephalalgia 24 (8), 663–668.

Woods, D.L., Elmasian, R., 1986. The habituation of event-related potentials to speech sounds and tones. Electroencephalogr. Clin. Neurophysiol. 65, 447–459.