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Representation of harmony rules in the human brain: Further evidence from event-related potentials

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ABSTRACT

In Western tonal music, the rules of harmony determine the order and music-structural importance of events in a musical piece: for instance, the tonic chord, built on the first note of the diatonic scale, is usually placed at the end of chord sequences. A brain response termed the early right anterior negativity (ERAN) is elicited when a harmonically incongruous chord is inserted within or at the end of a musical sequence. The present study was conducted to test whether the ERAN reflects the processing of harmony rather than the building of a tonal context and whether the ERAN is also elicited by violations of the tuning of the sounds upon which harmony is based. To this aim, ten subjects listened to musical sequences containing either expected chords only, a harmonically incongruous chord in one of three positions within the cadence, or a harmonically congruous but mistuned chord in one of the three positions. Simultaneously, the electroencephalograph (EEG) was recorded. Incongruous chords violating the rules of harmony elicited a bilateral early anterior negativity, the amplitude of which depended on the degree of the harmony violation. On the contrary, mistuned chords, violating the rule of relations between all the sounds in the sequences, elicited a bilateral fronto-central negativity (the mismatch negativity, or MMN). The MMN was not modulated by the position of the violation within the musical sequence and had a longer peak latency than the anterior negativity elicited by the harmony rule violations. In conclusion, violations of the harmony and tuning rules of Western tonal music were found to generate specific and distinct electric responses in the human brain.

1. Introduction

When listening to music, a sequence of chords generates expectancies for notes or chords to follow. Such expectancy is vital to musical experience (e.g., Meyer, 1956). In particular, the harmonic context of a chord sequence primes the processing of chords related to the context and induces expectations by activating tonal representations existing in the mind of the listener (Bharucha and Stoeckig, 1987). Expectancies generated by a harmonic context reflect the innate or learned mental representation of tonal relationships, or tonality. Tonality (also termed musical key) refers to the organization

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of pitches in such a way that one central pitch dominates and attracts the others and gives name to the key (see e.g., Bharucha, 1984; Bharucha and Krumhansl, 1983; Krumhansl, 2000). The core of a functional harmonic context is often composed of tonic (T), dominant (D), and subdominant (S) chords. Compared to other chord functions, these three chord functions are perceived as more closely related to each other (Bharucha and Krumhansl, 1983). The dominant is perceived as tension-creating, demanding resolution to the stable position of the tonic, whereas the subdominant reflects an intermediate position between these two oppositions. Chords incorporating notes outside the prevailing harmonic context usually demand resolution to more stable harmonies of the system (Bharucha and Krumhansl, 1983). The mental representation of tonality may be established by very few notes or chords (Berent and Perfetti, 1993; Krumhansl and Kessler, 1982). Chords breaking these harmonic expectations may be perceived as erroneous, and a reinterpretation of the current tonality may occur (Berent and Perfetti, 1993).

Recently, several event-related potential (ERP) studies investigating the violation of harmonic expectations based on the rules of Western tonal music have been conducted (e.g., Koelsch et al., 2000, 2005; Loui et al., 2005; Maess et al., 2001). In these studies, inappropriate chords within or at the end of harmonic cadences (chord sequences) elicited an event-related potential (ERP) component called the early right anterior negativity (ERAN). The ERAN occurs at an early latency (150–250 ms after stimulus onset) and is maximal over anterior regions of the scalp with a tendency to be lateralized to the right. The ERAN has been most commonly recorded in a semi-attended paradigm, where the subjects' attention is directed towards the music by asking them to respond to infrequent chords played on a deviant instrument. It can also be elicited preattentively (Koelsch et al., 2002b), however its amplitude is modulated by the attentional load (Loui et al., 2005). The ERAN has been shown to be larger in musical experts than in novices (Koelsch et al., 2002c). Utilizing magnetoencephalography (MEG), Maess et al. (2001) localized the sources of the magnetic ERAN response in the Broca's area (BA44) and its right-hemispheric homologue with a non-significant tendency towards right-hemispheric superiority. The left-hemispheric Broca's area is involved in the processing of linguistic syntax (see e.g., Friederici et al., 2000). This result has been interpreted to demonstrate an analogy of the rules of harmony in music with the rules of linguistic syntax since both comprise of ordered succession of meaningful sound events in time (e.g., Koelsch and Siebel, 2005; Patel, 2003).

In previous studies, the violation of the rules of harmony was realized by placing an inappropriate chord, the Neapolitan subdominant (Sn), into the authentic cadence (see Table 1). The Neapolitan subdominant is the first inversion of the major triad built on the flattened second degree of the scale (in C major or minor: F-Ab-Db). The Neapolitan chord includes notes outside of the prevailing tonality (or key) and is used in Western classical music as a variation of the subdominant, most often preceding a V-I cadence. In the previous experiments, the Neapolitan chord was presented either at position 3 or at the ending position 5 of the cadence. It is noteworthy that each trial in the previous ERAN studies was performed in a different key. Therefore the previous findings, showing a prominent ERAN mainly in position 5 (T) compared to position 3 (S), might be a consequence of a less well established key in position 3 rather than a violation of expectancies based on harmony rules of chord succession. Also note that at position 5 the Neapolitan chord always followed a dominant chord, which created a strong expectation for a tonic chord. In contrast, at position 3 the Neapolitan chord always followed a chord that created an expectation for a subdominant chord. According to Western musical theory, when used to replace a subdominant chord, the Neapolitan generates a chord progression more accepted in the theory of functional harmony than when placed after a dominant chord (Drabkin, 2002). The most appropriate resolution of the dominant is a tonic chord. When placed after a dominant chord, i.e. replacing the strongly expected tonic chord, the Neapolitan therefore creates an inappropriate chord succession. This is especially true when the chord that is to be replaced is the final chord of the cadence. The comparison used in the previous studies between Neapolitan chords at position 3 and at position 5 of a five-chord cadence is therefore unbalanced as it contrasts expectations which are formed by either the building of tonality or by the harmony rules of ordering of musical events. Consequently, also the elicitation of a larger ERAN by a Neapolitan in position 5 than in position 3 of the cadence (e.g., Koelsch et al., 2000) may be the result of a confound between the effects of the building of a tonal context and the processing of the harmony violation.

Table 1 – Examples of the chord sequences employed in Koelsch et al. (2000)

	Position 1	Position 2	Position 3	Position 4	Position 5
Standard	T	T3	S	D	T
Neapolitan at 3rd	T	T3	Sn	D	T
Neapolitan at 5th	T	T3	S	D	Sn

T = tonic, T3 = inverted tonic, S = subdominant, D = dominant, Sn = Neapolitan subdominant.

In our study we wished to separate the effects of tonality establishment within a musical context and the effects of a violation of harmony rules, which determine the succession and music-structural importance of chords within a cadence. To accomplish this, the present study was based on a chord sequence containing seven chords instead of five chords as in previous ERAN studies (see Table 2 and Fig. 1). Our standard chord sequence formed an authentic cadence (T-D-T-T3-S-D-T) following the rules of Western functional harmony. Three types of chord sequences containing Neapolitan chords addressed the abovementioned problems by reversing the order of expectation. At positions 3 and 7, the Neapolitan chord always followed a dominant chord, hence replacing a tonic chord. In this way, according to harmony rules, a very inappropriate succession was created. In one case, at position 3, the tonality was not yet established and in the other case, at position 7, the tonality was well established and a strong expectation for the final tonic chord was created (for the prominent role of the last chord of a cadence for evoking a feeling of closure, see Boltz, 1989; Palmer and Krumhansl,

Table 2 – Chord sequences for standard and Neapolitan conditions in the present study

	Position 1	Position 2	Position 3	Position 4	Position 5	Position 6	Position 7
Standard	T	D	T	T3	S	D	T
Neapolitan at 3rd	T	D	Sn	T3	S	D	T
Neapolitan at 5th	T	D	T	T3	Sn	D	T
Neapolitan at 7th	T	D	T	T3	S	D	Sn

T = tonic, T3 = inverted tonic, S = subdominant, D = dominant, Sn = Neapolitan subdominant.

1987). The effects of a harmony violation can therefore be assessed for both final and non-final cadence positions.

Moreover, the Neapolitan chord at position 5 always followed a tonic chord in the first inversion, hence replacing a subdominant chord and producing a more appropriate harmonic succession than at positions 3 and 7. On the other hand, the Neapolitan chord replacing a subdominant chord at position 5 contrasted in turn with the better established tonality expectations for the chord at position 5 than for the chord at the earlier position 3 (the chord at position 3 contrasting more with the expectations based on the rules of functional harmony). Thus, assuming that the ERAN response mainly reflects the processing of violations of harmony rules, as suggested previously, and not the establishment of tonality, the ERAN elicited by a Neapolitan chord in position 3 should be larger in amplitude than the ERAN elicited by a Neapolitan chord in position 5.

There was an additional manipulation of the experimental paradigm introduced into our standard sequence mistuned chords, where the fifth of the chord was raised in pitch from its standard position in the musical scale. Similarly as the Neapolitan chords, the mistuned chords were included at positions 3, 5, and 7 of the chord cadence. This manipulation aimed at further studying the cognitive nature of electrical brain responses elicited by violations of chord progression. We hypothesized that the violation of the tuning of a chord would represent a musical-scale violation. This kind of a violation would not be regulated by the rules of chord progressions or by their music-structural importance within the cadence, but would be based on the comparison with the scale steps used in the previous chords of the cadence. In other words, this manipulation violated the tuning properties of all the sounds upon which harmony is based.

Violations of simple rules governing the properties of auditory information are known to elicit an ERP component called the mismatch negativity (MMN: see e.g., Näätänen and Winkler, 1999; Picton et al., 2000). The MMN has been shown to reflect the automatic formation of a short-term neural model of the physical or abstract regularities in the auditory environment (Winkler et al., 1996). The MMN is a fronto-central negative potential with sources in the primary and non-primary auditory cortex and a latency of 150–250 ms. In our paradigm, if the MMN reflected a tuning rule violation, it should be similar in amplitude and latency for all the three different cadence positions. In contrast, the ERAN, if truly an index of harmony violations, should be modulated by the development of a cognitive representation of tonality in the course of cadence presentation. The ERAN is also expected to have a different latency, amplitude, and scalp distribution than the MMN.
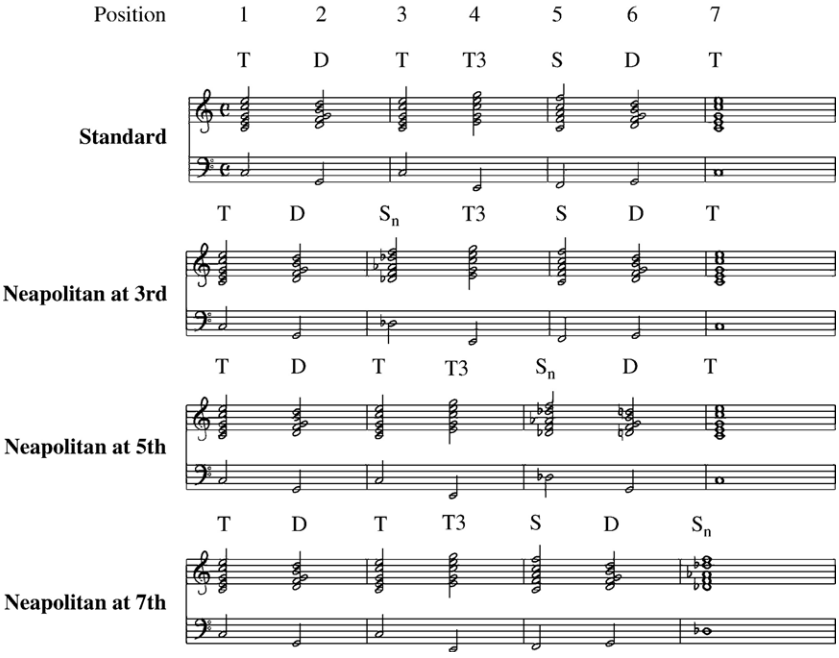
Fig. 1 – Example chord sequences for standard and Neapolitan conditions in the present study. T = tonic, T3 = inverted tonic, S = subdominant, D = dominant, Sn = Neapolitan subdominant.

2. Results

When presented within chord cadences following the rules of Western functional harmony, statistically significant ERP responses were elicited by both Neapolitan chords ($p < 0.05$) and mistuned chords ($p < 0.01$). Neapolitan chords, violating the rules of harmony, elicited a negative ERP response peaking on average 236 ms post-stimulus (see Fig. 2). Mistuned chords, violating the rules of musical-scale tuning, elicited a negative ERP response peaking on average 270 ms post-stimulus (see Fig. 3).

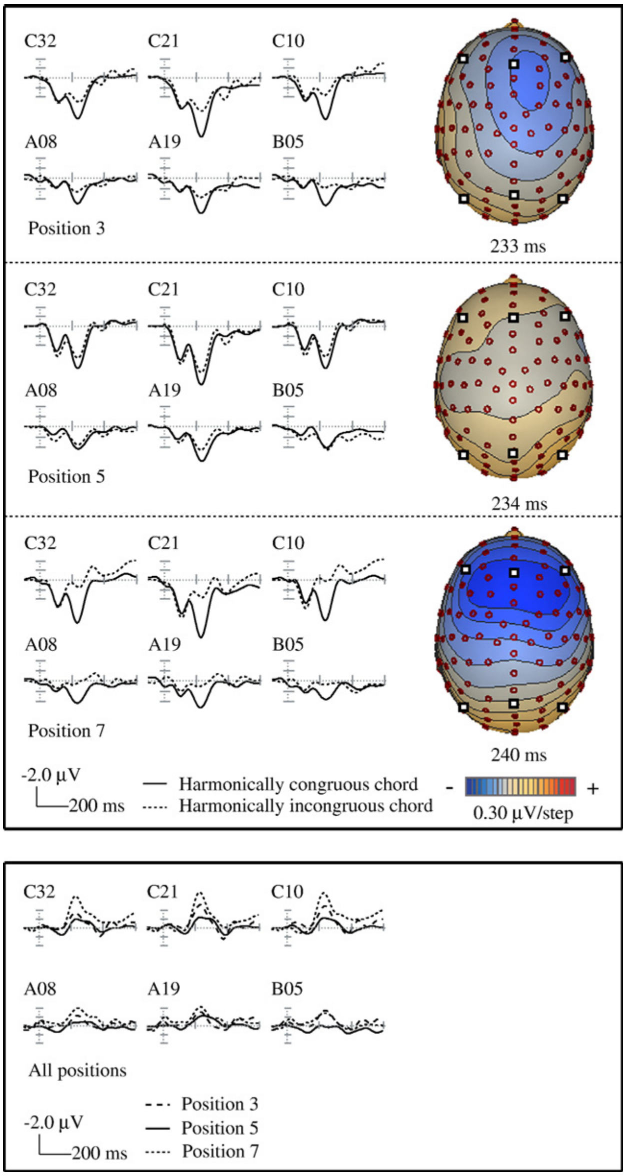

Fig. 2 – Panels 1–3 from top, left: grand-averaged ERPs to harmonically congruous chords and harmonically incongruous Neapolitan chords in different cadence positions. Panels 1–3 from top, right: EEG voltage isopotential maps of the difference between responses to harmonically congruous and incongruous chords in different cadence positions at average peak latency. Channels used in ERP waveform illustrations are marked in white. Bottom panel: difference waves between responses to harmonically congruous and incongruous chords in different cadence positions.

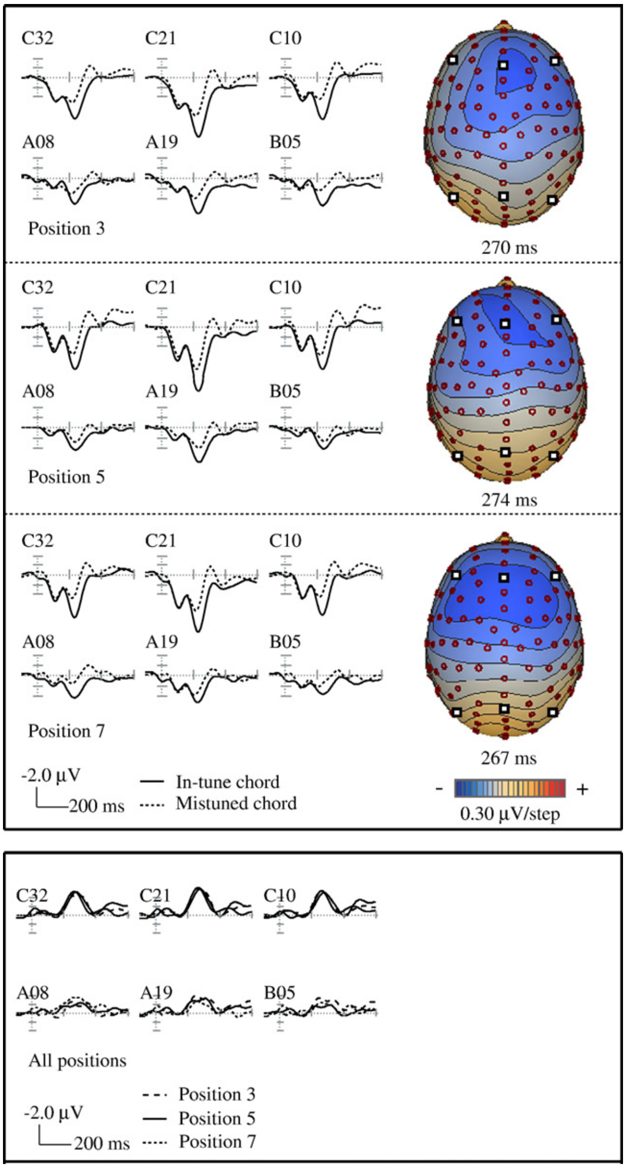

Fig. 3 – Panels 1–3 from top, left: grand-averaged ERPs to in-tune and mistuned chords in different cadence positions. Panels 1–3 from top, right: EEG voltage isopotential maps of the difference between responses to in-tune and mistuned chords in different cadence positions at average peak latency. Channels used in ERP waveform illustrations are marked in white. Bottom panel: difference waves between responses to in-tune and mistuned chords in different cadence positions.

The mean amplitudes and peak latencies of the ERP responses elicited by Neapolitan and mistuned chords in each cadence position are listed in Table 3. The mean amplitudes of the ERP responses elicited by Neapolitan and mistuned chords did not significantly differ (main effect of Violation type, $F(1,9) = 0.56$, $p = 0.47$). The mean amplitudes of both responses were most prominent over anterior regions

Table 3 – Average mean amplitudes (in μV) and peak latencies (in ms) of the ten subjects' ERP responses to harmonically incongruous and mistuned chords placed in different cadence positions

	Mean amplitude [μV]			Peak latency [ms]		
	Position 3	Position 5	Position 7	Position 3	Position 5	Position 7
Neapolitan chord	−1.99	−0.81	−2.98	233	234	240
Mistuned chord	−2.15	−2.07	−2.36	270	274	267

(significant main effect of Distribution, $F(1,9)=26.16$, $p<0.001$; non-significant interaction of Violation type and Distribution, $F(1,9)=0.20$, $p=0.67$). No significant differences in mean response amplitude between the left and right hemispheres were observed with either response (main effect of Hemisphere, $F(1,9)=1.46$, $p=0.26$; interaction of Violation type and Hemisphere, $F(1,9)=0.30$, $p=0.60$).

However, while the ERAN and MMN amplitudes did not differ overall, they did differ in how they were modulated by the position of the violation within the chord cadence. In particular, the early negativity to the Neapolitan chord varied according to the position of the chord within the cadence, whereas the amplitude of the negativity elicited by tuning rule violations did not vary depending on the position of the mistuned chord in the cadence (significant interaction of Violation type and Position, $F(2,18)=5.97$, $p<0.05$). Mean amplitudes of the responses to Neapolitan and mistuned chords in different positions are illustrated in Fig. 4. Post hoc tests revealed that the amplitude was larger for harmonically incongruous Neapolitan chords both in position 3 ($p<0.05$) and 7 ($p<0.01$) than in position 5, and also tended to be larger for a Neapolitan chord in position 7 than in position 3 ($p=0.09$).

The peak latency of the ERP response elicited by Neapolitan chords was on average 34 ms shorter than the peak latency of the response elicited by mistuned chords (significant main effect of Violation type, $F(1,9)=16.79$, $p<0.01$). The position of the inappropriate chord in the cadence, however, had no significant effect on the peak latency of the responses to either Neapolitan or mistuned chords (main effect of Position, $F(2,18)=0.62$, $p=0.55$; interaction of Violation type and Position, $F(2,18)=2.42$, $p=0.12$).

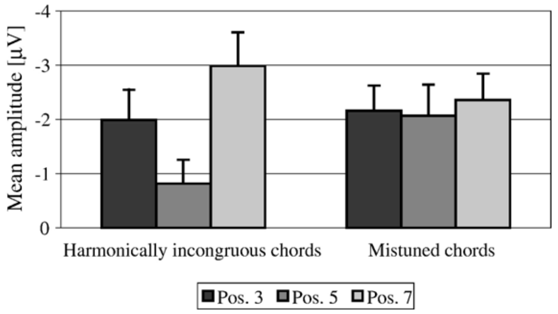

Fig. 4 – Average mean amplitudes (in μV) of the ERP responses to harmonically incongruous and mistuned chords placed in different cadence positions. Error bars indicate SEM. Mean amplitudes were obtained from regions of interest using 40-ms time windows determined on the basis of peak amplitude latencies of the grand-averaged ERP waveforms.

3. Discussion

The present study was conducted to elucidate the relationship between the neural processing of harmony rules, tuning rules, and the establishment of tonality. Harmonically inappropriate chords (Neapolitan subdominants) were found to elicit a brain response which was modulated by the degree of the violation of harmony rules. The results allow us to discern the effects of tonality establishment within a chord cadence from those of the violation of the rules of Western functional harmony on a change-related brain response. Chords violating tuning rules were found to elicit a functionally and temporally separable brain response which was not modulated according to the order of the chords within the cadence.

A bilateral, anteriorly maximal negative ERP component with an early peak latency of approximately 235 ms post-stimulus was elicited by harmonically inappropriate Neapolitan chords inserted into a harmonic context. The early anterior negative component presently observed is analogous with the ERAN component reported previously. In the present study, the early negative component was bilaterally distributed over the two hemispheres. This is in contrast with the majority of the previous studies, reporting a right-lateralized ERAN instead (Koelsch et al., 2000, 2001, 2005; Koelsch et al., 2002b,c). However, some earlier studies have also reported a non-lateralized response to harmony violations (Loui et al., 2005; Maess et al., 2001). The early negativity found in the present study might therefore be best termed simply an early anterior negativity (EAN) rather than the early right anterior negativity (ERAN). A similar nomenclature has recently been adopted by Loui et al. (2005), who describe a similarly non-lateralized EAN.

The amplitude of the EAN was found to depend on the position of the Neapolitan chord in the chord sequence (see Fig. 4): the EAN responses elicited by a Neapolitan chord in both position 3 and in position 7 were larger in amplitude than the EAN response elicited by a Neapolitan chord in position 5. The Neapolitan chord is a subdominant minor chord with a raised fifth and has a strong tendency to resolve to the dominant using partly chromatic voice leading. For that reason it has historically been used as a substitution for the subdominant chord whereas the resolution of the dominant to a Neapolitan is very unusual in Western tonal music. Hence, according to the rules of functional harmony in Western music, a Neapolitan chord following the tonic chord in the authentic cadence, replacing a subdominant chord (position 5), is more appropriate and more expected than when used instead of a tonic chord and following a dominant chord (positions 3 and 7). The smaller EAN amplitude for a Neapolitan chord in position 5 thus directly reflected the chord being used in a way more appropriate in terms of the rules of functional harmony. This suggests that the early negativity can indeed be interpreted as an index of a violation of the musical harmony rules and the degree of the violation. On the other hand, in position 3 the tonality of the cadence was less well established than in position 5. The larger amplitude of the EAN response elicited in position 3 than in position 5 thus suggests that the response does not mainly reflect the establishment of tonality. Interestingly, the EAN elicited by a Neapolitan chord in the final position 7 had a tendency to be larger in amplitude than the EAN elicited by a Neapolitan chord in position 3. This could index either the better established tonality in the final position or effects of closure of the chord progression. All in all, the present results can be taken as further evidence that the early anterior negativity reflects the violation of the rules of functional harmony and, furthermore, that specific neural mechanisms exist for the processing of these musical rules.

In the present study, mistuned chords inserted into a chord sequence, violating the interval properties of all the sounds upon which harmony is based, elicited a bilateral, anteriorly distributed mismatch negativity (MMN) with a peak latency of approximately 270 ms post-stimulus. This result is in line with previous findings of Brattico et al. (2006), who obtained an MMN-like response to mistuned pitches replacing in-key pitches within unaccompanied unfamiliar melodies. The relationship between MMN and E(R)AN has previously been electrophysiologically investigated by Koelsch et al. (2001) and Koelsch et al. (2005). In the previous studies, the E(R)AN was found to have a larger amplitude than the MMN. In contrast with previous results, in the present study, no significant difference between E(R)AN and MMN amplitudes was found. However, in the experiments by Koelsch et al. the MMN was elicited by single tones not inserted in a full harmonic context, in contrast to the E(R)AN, which was elicited by harmonically inappropriate Neapolitan chords within a harmonic context. In the present study, instead, the same musical context was used to elicit both the MMN and the EAN responses. In other words, the chords violating the harmony and tuning rules were matched in both spectral and temporal complexity, whereas previously they were either not matched (Koelsch et al., 2001) or only matched in spectral complexity (Koelsch et al., 2005). Koelsch et al. (2001, 2005) also found the E(R)AN to have a longer latency than the MMN, while in the present study the EAN was elicited earlier than the MMN. One possible explanation for the latency difference is that the longer MMN latency would be associated to the neural analysis of the acoustic features of mistuned chords, possibly more time-consuming than that of in-tune chords or single tones such as those used in previous studies. It has been observed that the detection of slightly mistuned sounds requires a fine-grained system of pitch discrimination that is especially sensitive in musically experienced subjects (Koelsch et al., 1999; see however Tervaniemi et al., 2005).

In contrast to the EAN elicited by harmonically inappropriate chords, the MMN component observed in this study did not differ in amplitude depending on the position of the mistuned chord in the sequence (see Fig. 4). By using a more balanced stimulation, we thus replicated the results described by Koelsch et al. (2001, 2005). While the early negative component appears to reflect harmony rule processing, a separable ERP component that here we identify with the MMN rather indexes more basic processes of change detection where sound events are not ordered according to their music-structural importance or by rules of succession. This repeated pattern strongly suggests that the E(R)AN reflects the processing of rule deviations much more complex than those known to elicit an MMN. Previous studies have found that also musical rules, such as the intervals of the diatonic equal-tempered scale, can elicit and affect the MMN (e.g., Brattico et al., 2001, 2006). However, no complex musical rule, determining the music-structural importance of sounds, has been associated with the MMN, only with the E(R)AN. The present evidence can be seen to further support the view that the E(R)AN may be considered of a more cognitive nature than the MMN response, as suggested by Koelsch et al. (2001), the E(R)AN being dependent on the music-structural, temporal organization of the harmonic structure within a piece of music.

Interestingly, the E(R)AN component, elicited by violations of harmony rule structure in music, has remarkably similar temporal and spatial properties as another early anterior negative ERP component, described in the neurolinguistic literature. This component, showing a tendency towards left-hemispheric superiority, has been named the early left anterior negativity, or ELAN (e.g., Friederici et al., 1996; Hahne and Friederici, 2002; Neville et al., 1991). The ELAN component reflects the detection of phrase structure violations in online auditory sentence processing. Mirroring the ERAN, sources of the ELAN component have been localized in Broca's area, with left-hemispheric dominance (Friederici et al., 2000). ERP results obtained from singular studies of the processing of musical and linguistic rule violations, along with fMRI studies revealing considerable overlap between musical and linguistic processing (e.g., Koelsch et al., 2002a; Schmithorst, 2005; Vuust et al., 2005, 2006), have led to numerous comparisons and analogies between the processing of harmony rules and the processing of linguistic syntax (see e.g., Koelsch, 2005; for a contrasting viewpoint, see e.g., Bigand et al., 2006; Peretz and Zatorre, 2005).

Prompted by previous electrophysiological findings, Koelsch and Siebel (2005) have recently formulated a detailed neurocognitive model of music perception containing, among other individual modules, a module for syntactic structure building. It has been uncertain, however, whether previous E(R)AN studies actually were evidence of the establishment of key instead of the processing of musical rules. The present results, giving additional support to the view that the E(R)AN component reflects the processing of harmony rules, can thus be interpreted as further evidence for the existence of a neural module for processing of the musical rules of harmony. The contribution of a modality-independent module for syntactic processing in music perception, however, remains a matter of debate (see e.g., Bigand et al., 2006), and assuming rules of functional harmony to be musical syntax may be somewhat simplistic. Little direct evidence for shared neural mechanisms between musical and linguistic rule processing exists (see, however, Koelsch et al. (2005) for an interaction between brain responses reflecting musical and linguistic rule violations). Further studies directly comparing the processing of musical rules and linguistic syntax are therefore needed to clarify the issue. Additionally, while linguistic syntax exists in all languages, many of the world's music cultures are not based on functional harmony. Both music and language are indeed rule-based, temporally organized structures attributing structural importance to isolated sound events. However, the hierarchical ordering of language phrases within a sentence has not been observed in a musical context (Addessi and Caterina, 2000; cf. also Deliège, 2000). The term syntax should therefore be used with care when discussing a musical context (for similar conclusions, see Jackendoff and Lerdahl, 2006), even in the light of findings that the processing of rules of functional harmony and violations of linguistic syntax have similar neural bases, and any direct equation between linguistic and musical syntax would not presently be fully justified. Nevertheless, our results provide support for the presence of specific neural mechanisms processing the rules of harmony that can be separated from the processing of other musical rules by a brain response with a distinct latency and morphology.

4. Experimental procedures

4.1. *Participants and stimuli*

Ten right-handed subjects (5 male, 5 female; age range 22–30 years, mean age 26 years) participated in the experiment. All participants had normal hearing and no musical expertise or explicit knowledge of music theory. Written informed consent was received from all participants. Participants received monetary compensation for taking part in the experiment.

The stimuli used in the experiment were digitally generated piano and organ chords organized into cadences. The stimulus chords were prepared in accord with rules of voice leading of Western functional harmony and further edited to have equal duration and intensity. Each stimulus cadence consisted of six 600 ms long chords followed by one 1200 ms long chord. The last 50 ms of each chord was gradually faded out, and each chord in the cadence was separated by a 5 ms silent period.

Cadences consisting of chords played with a piano timbre were created for seven different experimental conditions and in twelve different keys. In the standard condition, each of the seven chords in the cadence belonged to the same key and together they composed a simple chord sequence following the rules of Western functional harmony. In the three Neapolitan conditions, one of the chords of the standard cadence was replaced with a Neapolitan subdominant. The Neapolitan subdominant replaced the third tonic chord of the cadence (position 3), the fifth subdominant chord of the cadence (position 5), or the seventh tonic chord of the cadence (position 7). In the three mistuned conditions, one of the chords of the standard cadence was replaced by a mistuned major triad, in which the fifth of the chord (at pitch distance of a fifth, or seven semitones, from the lowest note of the chord; see Fig. 1) was increased by 50 cents. Mirroring the Neapolitan conditions, the mistuned chord replaced either the third tonic chord of the cadence (position 3), the fifth subdominant chord of the cadence (position 5), or the seventh tonic chord of the cadence (position 7).

Tonic chords played with an organ timbre were used as target stimuli for the behavioral task to be performed during EEG recordings. The deviant organ chords were uniformly distributed among conditions and matched with the piano chords in all aspects except timbre. An organ chord was presented twelve times in each condition, each time in a different key (approximately 8% of all cadences). The organ chord always replaced a tonic chord of the cadence.

4.2. *Methods*

Each experimental condition was presented in twelve different keys and 144 times in total. Each cadence was presented 5 ms after the preceding cadence, preserving the musical meter, in order to give an impression of real, flowing music. Stimulus cadences in different keys and with different experimental manipulations were presented in random order, while the subject was sitting in a comfortable chair in a soundproof room and wearing headphones. The stimuli were presented with Presentation 9.30 at a volume of 50 dB above the individual hearing threshold of the subject, determined at the beginning of the experiment. A semi-attended experimental paradigm was used, in which the subject was instructed to attend to the musical sequences and press the response button as soon as he or she heard a chord played on an organ. The purpose of the task was to ensure that the subject was attending to the stimuli without asking him or her to attend to the Neapolitan or mistuned chords (see also e.g., Koelsch et al., 2002c). The stimuli were presented in eight separate stimulus blocks of approximately 10 min each in duration. While the subject was attending to the stimuli, EEG was measured. The duration of the entire experiment was approximately 3 h, including preparation.

EEG was measured using the BioSemi measuring system (BioSemi, Inc., Netherlands; http://www.biosemi.com). Scalp EEG was recorded with 128 active scalp electrodes fitted into a stretching cap and following the BioSemi ABC position system. Additionally, three active electrodes were placed on the subject's nose and mastoid areas and four more around the eyes to monitor eye muscle activity. 24-bit EEG data were recorded with BioSemi ActiView 5.32 using no reference, a sampling rate of 2048 Hz, and a recording bandwidth of up to 417 Hz.

4.3. *Data analysis*

The EEG data for each subject were resampled offline for event-related potential analysis using a sampling rate of 256 Hz. ERPs were averaged for each condition and cadence. The analysis period was 600 ms starting from the onset of the target chord (third, fifth, or seventh chord of the cadence). The 100 ms period preceding the onset of the target chord was used as a pre-stimulus baseline. Channels with excessively noisy data and trials containing eye movement or other data artefacts were individually rejected for each subject. Before averaging, the EEG data were filtered with a 0.5-Hz high-pass filter. After averaging, the ERP data were filtered with a low-pass filter of 40 Hz and re-referenced to the average of the mastoids. Difference waveforms were calculated by subtracting the responses to the standard chords from the responses to the Neapolitan or mistuned chords. The ERP data were then statistically evaluated using repeated measures analyses of variance (ANOVAs) with either mean ERP amplitude or peak amplitude latency as the dependent variable. When necessary, degrees of freedom of the ANOVA were corrected using the Greenhouse–Geisser epsilon. Newman–Keuls post hoc tests were used when appropriate. After statistical evaluation, grand-averaged ERPs were filtered with a 10-Hz low-pass filter for illustration purposes only.

Mean ERP amplitudes were calculated for each subject and each of the seven conditions from within 40-ms time windows surrounding grand-averaged ERP peak amplitude latencies on channel C21 (corresponding to Fz in the 10–20 system). Mean amplitude values were computed for four regions of interest (ROIs): left anterior (C25, C26, C32, D3, D4), right anterior (C3, C4, C10, C12, C13), left posterior (A5, A6, A7, A8, A18), and right posterior (A31, A32, B3, B4, B5). The statistical significance of the responses to Neapolitan and mistuned chords was determined with *t* tests. The mean amplitude data were then analyzed using a four-way repeated measures ANOVA with within-subjects factors of Violation type, Position (anterior–posterior), Distribution, and Hemisphere. Average mean amplitudes were calculated across all regions of interest to be displayed in the figures and tables. To investigate differences in the peak latency of responses to different violations, average peak amplitude latencies of the responses to the Neapolitan and mistuned chords were determined individually for each subject and each violation condition from channel C21. Individual peak amplitude latency data were then entered into a two-way repeated measures ANOVA using within-subjects factors of Violation type and Position.

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