Psychophysiology, 46 (2009), 179–190. Wiley Periodicals, Inc. Printed in the USA.

DOI: 10.1111/j.1469-8986.2008.00752.x

Music-syntactic processing and auditory memory: Similarities and differences between ERAN and MMN

STEFAN KOELSCH[a,b]

[a]Department of Psychology, University of Sussex, Brighton, UK
[b]Max-Planck-Institute for Human Cognitive and Brain Sciences, Leipzig, Germany

Abstract

The early right anterior negativity (ERAN) is an event-related potential (ERP) reflecting processing of music-syntactic information, that is, of acoustic information structured according to abstract and complex regularities. The ERAN is usually maximal between 150 and 250 ms, has anterior scalp distribution (and often right-hemispheric weighting), can be modified by short- and long-term musical experience, can be elicited under ignore conditions, and emerges in early childhood. Main generators of the ERAN appear to be located in inferior fronto-lateral cortex. The ERAN resembles both the physical MMN and the abstract feature MMN in a number of properties, but the cognitive mechanisms underlying ERAN and MMN partly differ: Whereas the generation of the MMN is based on representations of regularities of intersound relationships that are extracted online from the acoustic environment, the generation of the ERAN relies on representations of music-syntactic regularities that already exist in a long-term memory format. Other processes, such as predicting subsequent acoustic events and comparing new acoustic information with the predicted sound, presumably overlap strongly for MMN and ERAN.

Descriptors: ERAN, MMN, Brain, Music, ERP

In 1992, a study from Saarinen, Paavilainen, Schöger, Tervaniemi, and Näätänen (1992) changed the concept of the mismatch negativity (MMN) dramatically. Whereas previous studies had investigated the MMN only with physical deviants (such as frequency, intensity, or timbre deviants), Saarinen et al. showed that a brain response reminiscent of the MMN can be elicited by changes of abstract auditory features (in that study, standard stimuli were tone pairs with frequency levels that varied across a wide range, but were always rising in pitch, whereas deviants were tone pairs falling in pitch). By introducing the concept of an "abstract feature MMN" (henceforth referred to as *afMMN*), Saarinen et al. implicitly changed the previous concept of the MMN as a response to a physical deviance within a repetitive auditory environment (henceforth referred to as *phMMN*) to a concept of the MMN as a negative ERP response to mismatches in general, that is, to mismatches that do not necessarily have to be physical in nature (for other studies reporting abstract feature MMNs see, e.g., Korzyukov, Winkler, Gumenyuk, & Alho, 2003; Paavilainen, Arajärvi, & Takegata, 2007; Paavilainen, Degerman, Takegata, & Winkler, 2003; Paavilainen, Jaramillo, & Näätänen, 1998; Paavilainen, Simola, Jaramillo, Näätänen, & Winkler, 2001; Schröger, Bendixen, Trujillo-Barreto, & Roeber, 2007).

Hence, when a few years after the study from Saarinen et al. (1992) a study on neurophysiological correlates of music processing reported a mismatch response for music-syntactic regularities (Koelsch, Gunter, Friederici, & Schröger, 2000), it was difficult to decide whether or not this mismatch response should be referred to as MMN: In that study (Koelsch et al., 2000), stimuli were chord sequences, each sequence consisting of five chords. There were three sequence types of interest: (1) sequences consisting of music-syntactically regular chords, (2) sequences with a music-syntactically irregular chord at the third position (i.e., in the middle) of the sequence, and (3) sequences with a music-syntactically irregular chord at the fifth (i.e., final) position of the sequence (Figure 1a; for studies using similar experimental stimuli see Leino, Brattico, Tervaniemi, & Vuust, 2007; Loui, Grent-'t Jong, Torpey, & Woldorff, 2005). Irregular chords were so-called Neapolitan sixth chords, which are normal, consonant chords when played in isolation, but which are harmonically only distantly related to the preceding harmonic context and, hence, sound highly unexpected when presented at the end of a chord sequence (right panel of Figure 1a). The same chords presented in the middle of these chord sequences (middle panel of Figure 1a), however, sound much less unexpected, but relatively acceptable (presumably because Neapolitan sixth chords are similar to subdominants, which are music-syntactically regular at that position of the sequence). In the experiments of Koelsch et al. (2000), chord sequences were presented in direct succession

I thank Erich Schröger, Matthew Woolhouse, Aniruddh Patel, Barbara Tillmann, Istvan Winkler, Elyse Sussman, Daniela Sammler, Niko Steinbeis, and Sebastian Jentschke for helpful discussion.

Address reprint requests to: Stefan Koelsch, Department of Psychology, Pevensey Building, University of Sussex, Brighton, BN1 9QH, UK. E-mail: S.Koelsch@sussex.ac.uk

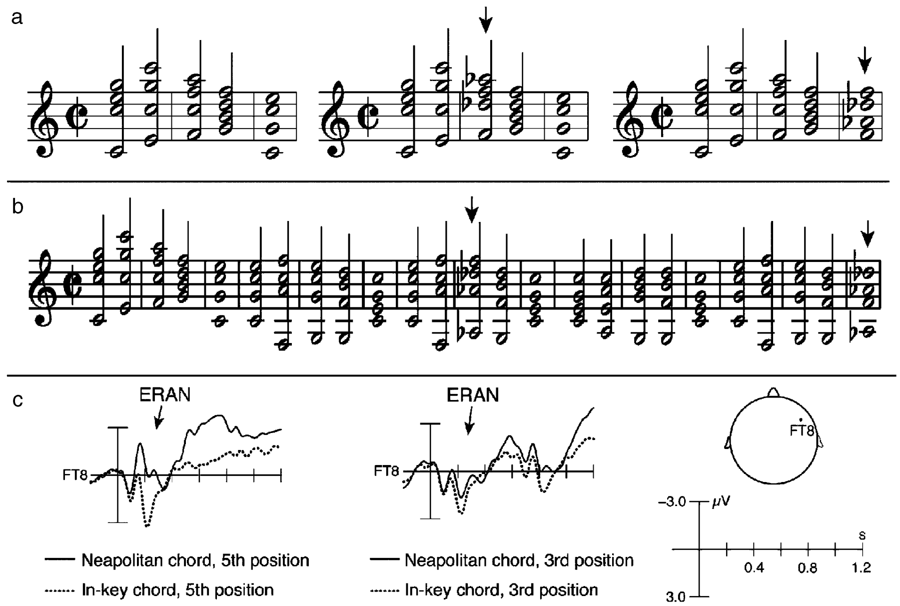

Figure 1. a: Examples of chord sequences containing in-key chords only (left) and a Neapolitan sixth chord at the third (middle) and at the fifth positions (right). In the experiment, sequences were presented in direct succession (b). Compared to regular in-key chords, the music-syntactically irregular Neapolitan chords elicited an ERAN (c). Note that when Neapolitans are presented at the fifth position of a chord sequence (where they are music-syntactically highly irregular), the ERAN has a larger amplitude compared to when Neapolitan chords are presented at the third position of the sequences (where they are music-syntactically less irregular than at the fifth position).

(reminiscent of a musical piece; Figure 1b), with 50% of the stimuli being regular sequences, 25% containing an irregular chord at the third, and 25% an irregular chord at the final position of the sequence.

The irregular chords elicited an ERP effect that had a strong resemblance to the MMN: It had negative polarity, maximal amplitude values over frontal leads (with right-hemispheric predominance), and a peak latency of about 150–180 ms (Figure 1c). This "music-syntactic MMN" was, however, not denoted as MMN, but as *early right anterior negativity* (ERAN; Koelsch et al., 2000). One reason for this terminology was that the ERAN was also strongly reminiscent of an ERP effect elicited by syntactic irregularities during language perception: the *early left anterior negativity* (ELAN; Friederici, 2002; see also below). Denoting the ERP response to harmonic irregularities as ERAN, thus, emphasized the notion that this ERP was specifically related to the processing of musical structure.

Nevertheless, some subsequent studies have also referred to this effect as music-syntactic MMN (Koelsch, Grossmann, et al., 2003; Koelsch, Gunter, Schröger, & Friederici, 2003; Koelsch, Maess, Grossmann, & Friederici, 2003; Koelsch, Schmidt, & Kansok, 2002), not only due to the resemblance with the MMN, but also because the term early *right* anterior negativity falls short when the effect elicited by irregular chords is not significantly lateralized. Lack of lateralization also led authors to label effects elicited by music-syntactically irregular events as *early anterior negativity* (Loui et al., 2005) or *early negativity* (Steinbeis, Koelsch, & Sloboda, 2006). However, other studies used the term ERAN even when the effect was not significantly right-lateralized, because this term had been established for the functional significance of this ERP component, rather than for its scalp distribution (Koelsch, Jentschke, Sammler, & Mietchen, 2007; Maess, Koelsch, Gunter, & Friederici, 2001; Miranda & Ullman, 2007). Note that similar conflicts exist for most (if not all) endogenous ERP components: For example, the P300 is often not maximal around 300 ms (e.g., McCarthy & Donchin, 1981), the N400 elicited by violations in high cloze probability sentences typically starts around the P2 latency range (Gunter, Friederici, & Schriefers, 2000; van den Brink, Brown, & Hagoort, 2001), and the MMN has sometimes positive polarity in infants (e.g., Friederici, Friedrich, & Weber, 2002; Winkler et al., 2003).

Functional Significance

The ERAN reflects music-syntactic processing, that is, processing of abstract regularity-based auditory information. In major–minor tonal music (often simply referred to as "Western" music), musical syntax processing comprises several aspects, which are in the following described for the processing of chord functions (although musical syntax also comprises other structural aspects, such as melodic, rhythmic, metric, and timbral structure): (1) Music-syntactic processing of harmonic information starts with the extraction of a tonal center (e.g., *C* in the case of a passage in *C* major). Previous studies have shown that listeners tend to interpret the first chord of a sequence as the tonic (i.e., as the tonal center; Krumhansl & Kessler, 1982; see Figure 2a for explanation of the term "tonic"), and in case the first chord is not the tonic, listeners have to modify their initial interpretation of the tonal center during the perception of successive chords (Krumhansl & Kessler, 1982; for a conception of key identification within the tonal idiom, see the intervallic rivalry model from Brown, Butler, & Jones, 1994). (2) Subsequent chord functions are related to the tonal center in terms of harmonic distance from the tonal center (see Figure 2a for explanation of chord functions). For example, in *C* major, a *G* major chord is more closely related to *C* major than a *G#* major chord. (3) With the succession of chords, a tonal hierarchy (Bharucha & Krumhansl, 1983) is established, according to which the configuration of previously heard chord functions forms a tonal structure (or a structural context). For example, within the tonal hierarchy the tonic chord is the most "stable" (Bharucha & Krumhansl, 1983) chord, followed by the dominant and the subdominant, whereas chords such as the submediant and the supertonic represent less stable chords. Once such a hierarchy is established, moving away from a tonal center may be experienced as tensioning and moving back as releasing (see also Lerdahl, 2001; Patel, 2003). Notably, this also opens the possibility for recursion, because while moving away from a tonal center (e.g., to the dominant, i.e., in *C* major, a *G* major chord), a change of key might take place (e.g., from *C* major to *G* major), and within the new key (now *G* major)—which now has a new tonal center—the music might again move away from the tonal center (e.g., to the dominant of *G* major), until it returns to the tonal center of *G*, and then to the tonal center of *C* major (for EEG and fMRI studies investigating neural correlates of the processing of changes in tonal key see Janata et al., 2002; Koelsch, Fritz, Schulze, Alsop, & Schlaug, 2005; Koelsch, Gunter, et al., 2002; Koelsch, Gunter, et al., 2003). (4) The succession of chord functions follows statistical regularities, that is, probabilities of chord transitions (Riemann, 1877; Rohrmeier, 2005). For example, in the statistical study by Rohrmeier on the frequencies of diatonic chord progressions in Bach chorales, the supertonic was five times more likely to follow the subdominant than to precede it. These statistical regularities are the main characteristic of musical syntax with regard to the harmonic aspects of major–minor tonal music (other characteristics regard, e.g., the principles of voice leading). The representations of such regularities are stored in long-term memory, and by its very nature it needs experience (usually implicit learning) to extract the statistical properties of the probabilities for the transitions of chord functions (see also Tillmann, Bharucha, & Bigand, 2000). While listeners familiar with (Western) tonal music perceive a sequence of chords, they automatically make

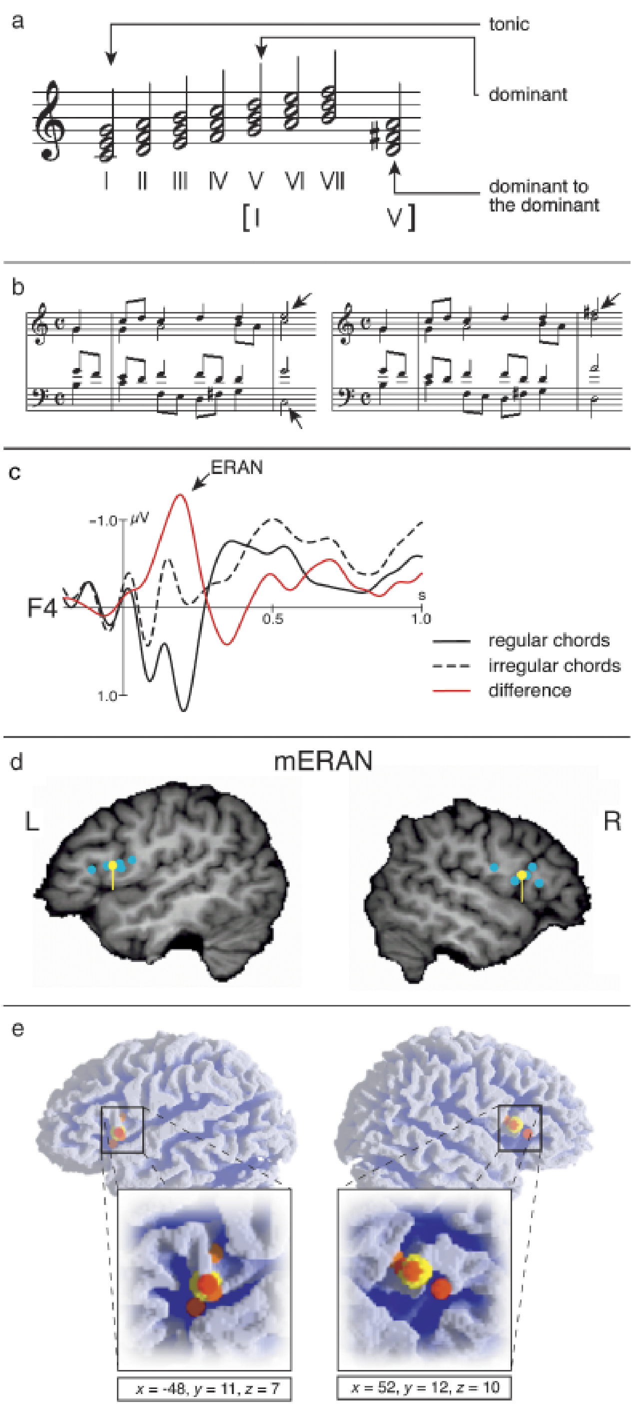

Figure 2. Chord functions are the chords built on the tones of a scale (a). The chord on the first scale tone, for example, is denoted as the tonic, the chord on the second scale tone (in major) as supertonic, on the third scale tone as mediant, on the fourth scale tone as subdominant, and the chord on the fifth scale tone as the dominant. The major chord on the second tone of a major scale can be interpreted as the dominant to the dominant (square brackets). In major–minor tonal music, chord functions are arranged within harmonic sequences according to certain regularities. One example for a regularity-based arrangement of chord functions is that the dominant-tonic progression is a prominent marker for the end of a harmonic sequence, whereas a tonic-dominant progression is unacceptable as a marker of the end of a harmonic sequence (see text for further examples). A sequence ending on a regular dominant-tonic progression is shown in the left panel of b. The final chord of the right panel of b is a dominant to the dominant. This chord function is irregular, especially at the end of a harmonic progression (sound examples are available at www.stefan-koelsch.de/TC_DD). In contrast to the sequences shown in Figure 1, the irregular chords are acoustically even more similar to the preceding context than regular chords (see text for details; modified from Koelsch, 2005). c: The ERPs elicited by the final chords of these two sequence types (recorded from a right-frontal electrode site [F4] from 12 subjects; from Koelsch, 2005). Both sequence types were presented in pseudorandom order equiprobably in all 12 major keys. Although music-syntactically irregular chords were acoustically more similar to the preceding harmonic context than regular chords, the irregular chords still elicit an ERAN (best to be seen in the red difference wave, which represents regular subtracted from irregular chords). With MEG, the magnetic equivalent of the ERAN was localized in the inferior frontolateral cortex (d; adapted from Maess et al., 2001; single-subject dipole solutions are indicated by blue disks, yellow dipoles indicate the grand-average of these source reconstructions). e: Activation foci (small spheres) reported by functional imaging studies on music-syntactic processing using chord sequence paradigms (Koelsch, Gunter, et al., 2002, 2005; Maess et al., 2001; Tillmann, Janata, & Bharucha, 2003) and melodies (Janata et al., 2002). Large yellow spheres show the mean coordinates of foci (averaged for each hemisphere across studies; coordinates refer to standard stereotaxic space). Modified from Koelsch and Siebel (2005).

predictions of likely chord functions to follow. That is, listeners extrapolate expectancies for sounds of regular chords to follow based on representations of music-syntactic regularities, and chords (or tones) that mismatch with the music-syntactic sound expectancy of a listener elicit an ERAN (Koelsch et al., 2000). The mathematical principles from which the probabilities for chord transitions within a tonal key might have emerged are under current investigation (see, e.g., Woolhouse & Cross, 2006, for the interval cycle-based model of pitch attraction), and it appears that many of these principles represent abstract, rather than physical (or acoustical) features (Woolhouse & Cross, 2006; note that, in addition to transition probabilities of chord functions, frequencies of co-occurrences, as well as frequencies of occurrences of chord functions and tones, also represent statistical regularities; see Tillmann et al., 2008).

It is likely that Steps 1 and 2 can—at least approximately—be performed even by humans without prior experience of Western music (e.g., by newborns or by adult listeners naive to Western music). However, several studies suggest that the fine-grained cognitive processes required for tonic identification that are typically observed in Western listeners (even when they have not received formal musical training) are based on extensive musical experience (e.g., Lamont & Cross, 1994). Likewise, calculating subtle distances between chord functions and a tonal center appears to rely on extensive learning (see also Tekman & Bharucha, 1998).

Whether Step 3 can be performed without prior experience of Western music is unknown, but previous studies strongly suggest that the detailed nature of the tonal hierarchy schema is learned through early childhood (Lamont & Cross, 1994). That is, although it is conceivable that humans naive to Western music find the probabilities for chord transitions plausible (because they follow abstract mathematical principles that become apparent in specific transitions of chords; Woolhouse & Cross, 2006), repeated experience of Western music is necessary to acquire the knowledge about the probabilities of the transitions of chord functions as well as knowledge about frequencies of co-occurrences of chord functions and frequencies of occurrences of chord functions and tones (see above). Because this knowledge is essential for the prediction of subsequent chord functions (and, thus, for building up a harmonic sound expectancy), it is highly likely that the ERAN would not be elicited without such knowledge.

It is important to note that the ERAN can be elicited even when a music-syntactically irregular chord does not represent a physical deviance (as will be described below). In earlier studies, the Neapolitan chords (such as those shown in Figure 1a) did not only represent music-syntactic oddballs, but also physical (frequency) oddballs: The regular chords belonged to one tonal key; thus most notes played in an experimental block belonged to this key (e.g., in *C* major all white keys on a keyboard), whereas the Neapolitan chords introduced pitches that had not been presented in the previous harmonic context (see the flat notes of the Neapolitan chords in Figure 1b). Thus, the ERAN elicited by those chords was perhaps overlapped by a phMMN. Nevertheless, it is also important to note that the ERAN elicited by chords at the final position of chord sequences was considerably larger than the ERAN elicited by chords at the third position of the sequences (Figure 1c). This showed that the effects elicited by the Neapolitan chords at the final position of the chord sequences could not simply be an MMN, because an MMN would not have shown different amplitudes at different positions within the stimulus sequence (Koelsch et al., 2001; in that study the ERAN, but neither the phMMN nor the afMMN, differed between positions in the chord sequences).

Corroborating these findings, the study from Leino et al. (2007) showed that the amplitude of the ERAN, but not the amplitude of an MMN elicited by mistuned chords, differed between different positions within chord sequences. A very nice feature of that study was that chord sequences were comprised of seven chords and that they were composed in a way that Neapolitan chords occurring at the fifth position were music-syntactically *less* irregular than Neapolitans at the third position (contrary to the sequences presented in Figure 1a). Consequently, the ERAN elicited at the fifth position was smaller than the ERAN elicited at the third position (and the ERAN was largest when elicited by Neapolitan chords at the seventh position, where they were most irregular).

However, the fact that the ERAN elicited by music-syntactically irregular events is often partly overlapped by a phMMN results from the fact 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 can not simply be attributed to music-syntactic processing. Because such a *C#* major chord is (in the first inversion) the enharmonic equivalent of a Neapolitan sixth chord, it is likely that effects elicited by such chords in previous studies (e.g., Koelsch et al., 2000; Leino et al., 2007; Loui et al., 2005) are not entirely due to music-syntactic processing, but also partly due to acoustic deviances that occurred with the presentation of the Neapolitan chords (for further details, see also Koelsch et al., 2007).

In fact, tonal hierarchies, and music-syntactic regularities of major–minor tonal music are partly grounded on acoustic similarities (e.g., Leman, 2000), posing considerable difficulty on the investigation of music-syntactic processing. However, a number of ERP studies has been published so far that aimed at disentangling the ‘‘cognitive’’ mechanisms (related to music-syntactic processing) from the ‘‘sensory’’ mechanisms (related to the processing of acoustic information; Koelsch, 2005; Koelsch & Jentschke, 2008; Koelsch et al., 2007; Poulin-Charronnat, Bigand, & Koelsch, 2006; Regnault, Bigand, & Besson, 2001), and some of them showed that the ERAN can be elicited even when the syntactically irregular chords are acoustically more similar to a preceding harmonic context than syntactically regular chords (Koelsch, 2005; Koelsch & Jentschke, 2008; Koelsch et al., 2007). For example, in the sequences shown in Figure 2b, the music-syntactically regular chords (i.e., the final tonic chord of the sequence shown in the left panel) introduced two new pitches, whereas the irregular chords at the sequence ending (so-called double dominants, shown in the right panel) introduced only one new pitch (the new pitches introduced by the final chords are indicated by the arrows). Moreover, the syntactically irregular chords had more pitches in common with the penultimate chord than regular chords; thus the ‘‘sensory dissonance’’ (of which pitch commonality is the major component) between final and penultimate chord was not greater for the irregular than for the regular sequence endings. Nevertheless, the irregular chord functions (occurring with a probability of 50%) elicited a clear

ERAN, suggesting that this ERP can be elicited without the presence of a physical irregularity (Figure 2c).

In the sequences of Figure 2b, the irregular chords (i.e., the double dominants) did not belong to the tonal key established by the preceding chords (similar to the Neapolitan chords of previous studies). However, experiments using in-key chords as music-syntactically irregular chords have shown that an ERAN can also be elicited by such chords, indicating that the elicitation of the ERAN does not require out-of-key notes (Koelsch & Jentschke, 2008; Koelsch et al., 2007).

The peak latency of the ERAN is often between 170 and 220 ms, with the exception of three studies: Koelsch and Mulder (2002) reported an ERAN with a latency of around 250 ms, Steinbeis et al. (2006) reported an ERAN with a latency of 230 ms (in the group of nonmusicians), and Patel, Gibson, Ratner, Besson, and Holcomb (1998) reported an ERAN-like response (the *right anterior temporal negativity*, RATN) with a peak latency of around 350 ms. The commonality of these three studies was the usage of nonrepetitive sequences, in which the position at which irregular chords could occur was unpredictable. It is also conceivable that the greater rhythmic complexity of the stimuli used in those studies had effects on the generation of the ERAN (leading to longer ERAN latencies), but possible effects of rhythmic structure on the processing of harmonic structure remain to be investigated.

The ERAN can not only be elicited by chords. Two previous ERP studies with melodies showed that the ERAN can also be elicited by single tones (Brattico, Tervaniemi, Näätänen, & Peretz, 2006; Miranda & Ullmann, 2007). Moreover, a study from Schön and Besson (2005) showed that the ERAN can even be elicited by visually induced musical expectancy violations (that study also used melodies).

Comparison of ERAN and MMN

A crucial difference between the neural mechanisms underlying phMMN and afMMN on the one side and ERAN on the other is that the generation of both phMMN and afMMN is based on an online establishment of regularities—that is, based on representations of regularities that are extracted online from the acoustic environment. By contrast, music-syntactic processing (as reflected in the ERAN) relies on representations of music-syntactic regularities that already exist in a long-term memory format (although music-syntactic processing can modify such representations). That is, the statistical probabilities that make up music-syntactic regularities are not learned within a few moments, and the representations of such regularities are stored in a long-term memory format (as described above).

With regards to the MMN, it is important to not confuse the online establishment of regularities with long-term experience or long-term representations that might influence the generation of the MMN: For example, pitch information can be decoded with higher resolution by some musical experts (leading to a phMMN to frequency deviants that are not discriminable for most non-experts; Koelsch, Schröger, & Tervaniemi, 1999) or the detection of a phoneme is facilitated when that phoneme is a prototype of one's language (leading to a phMMN that has a larger amplitude in individuals with a long-term representation of a certain phoneme compared to individuals who do not have such a representation; Näätänen et al., 1997; Winkler et al., 1999; Ylinen, Shestakova, Huotilainen, Alku, & Näätänen, 2006). However, in all of these studies (Koelsch et al., 1999; Näätänen et al., 1997; Winkler et al., 1999; Ylinen et al., 2006), the generation of the MMN was still dependent on representations of regularities that were extracted online from the acoustic environment: For example, in the classical study from Näätänen et al., the standard stimulus was the phoneme/e/, and one of the deviant stimuli was the phoneme/õ/, which is a prototype in Estonian (but not in Finnish). This deviant elicited a larger phMMN in Estonians than in Finnish subjects, reflecting that Estonians have a long-term representation of the phoneme/õ/(and that Estonians were, thus, more sensitive to detect this phoneme). However, the regularity for this experimental condition ("/e/is the standard and/õ/is a deviant") was independent of the long-term representation of the phonemes, and this regularity was established online by the Estonian subjects during the experiment (and could have been changed easily into "/õ/is the standard and/e/is the deviant"). That is, the statistical probabilities that make up the regularities in such an experimental condition are learned within a few moments, and the representations of such regularities are not stored in a long-term memory format.

With regards to the phMMN and the afMMN, Schröger (2007) describes four processes that are required for the elicitation of an MMN (perhaps with the exception of Process 3; see Schröger, 2007, p. 139), which are here related to the processes underlying the generation of the ERAN (see also Figure 3): (1) Incoming acoustic input is analyzed in multiple ways, resulting in the separation of sound sources, the extraction of sound features, and the establishment of representations of auditory objects. Basically the same processes are required for the elicitation of the ERAN (see also top left of Figure 3; for exceptions see Schön & Besson, 2005; Widmann, Kujala, Tervaniemi, Kujala, & Schröger, 2004). (2) Regularities inherent in the sequential presentation of discrete events are detected and integrated into a model of the acoustic environment. Similarly, Winkler (2007) states that MMN can only be elicited when sounds violate some previously detected intersound relationship. These statements nicely illustrate a crucial difference between the cognitive processes underlying the generation of MMN and ERAN: As mentioned above, during (music-) syntactic processing, representations of regularities already exist in a long-term memory format (similarly to the processing of syntactic aspects of language). That is, the regularities themselves do not have to be detected, and it is not the regularity that is integrated into a model of the acoustic environment, but it is the actual sound (or chord) that is integrated into a cognitive (structural) model according to long-term representations of regularities. That is, the representations of (music-) syntactic regularities are usually not established online, and they are, moreover, not necessarily based on the intersound relationships of the acoustic input (see top right of Figure 3). Note that, due to its relation to representations that are stored in a long-term format, music-syntactic processing is intrinsically connected to learning and memory. (3) Predictions about forthcoming auditory events are derived from the model (see also Winkler, 2007). This process is very similar (presumably at least partly identical) for the ERAN: A sound expectancy (Koelsch et al., 2000) for following musical events (e.g., a chord) is established based on the previous structural context and the knowledge about the most likely tone, or chord, to follow. As mentioned in Process 2, however, in the case of the MMN the predictions are based on regularities that are established online based on the intersound relationships of the acoustic input, whereas in the case of the ERAN the predictions are based on

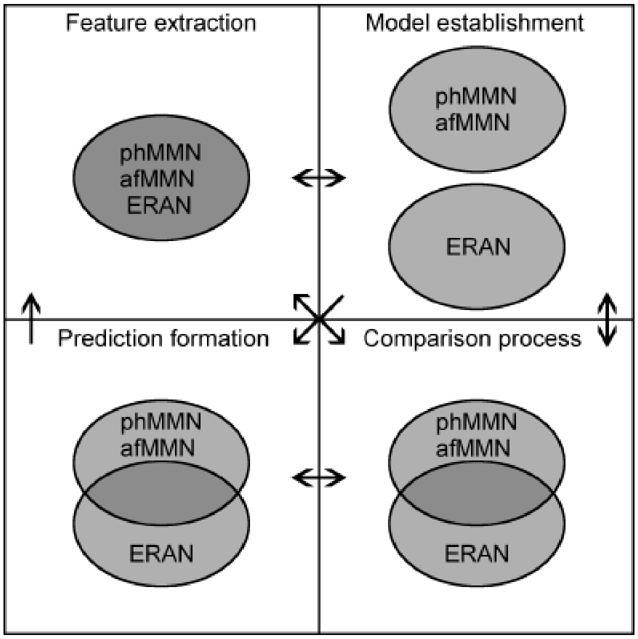

Figure 3. Systematic overview of processes required to elicit MMN and ERAN (see text for details). Whereas the extraction of acoustic features is identical for both MMN and ERAN (top left quadrant), MMN and ERAN differ with regard to the establishment of a model of intersound relationships (top right quadrant): In the case of the MMN, a model of regularities is based on intersound relationships that are extracted online from the acoustic environment. These processes are linked to the establishment and maintenance of representations of the acoustic environment and thus to the processes of auditory scene analysis. In the case of the ERAN, a model of intersound relationships is built based on representations of music-syntactic regularities that already exist in a long-term memory format. The bottom quadrants illustrate that the neural resources for the prediction of subsequent acoustic events, and the comparison of new acoustic information with the predicted sound, presumably overlap strongly for MMN and ERAN.

representations (of music-syntactic regularities) that already exist in a long-term memory format. To date it is not known to what degree the predictions underlying the generation of the MMN and the ERAN are established in the same areas or whether the predictions for the MMN are generated predominantly in sensory-related areas (i.e., in the auditory cortex) and the predictions for the ERAN (perhaps also for the afMMN) predominantly in hetero-modal areas such as premotor cortex (BA 6) and Broca's area (BA 44/45; see bottom left of Figure 3; for neural generators of the ERAN see the next section). (4) Representations of the incoming sound and the sound predicted by the model are compared. For the ERAN, this process is, again, presumably at least partly the same as for the MMN (see bottom right of Figure 3). However, similarly to Process 3 it is unknown whether such processing comprises more auditory areas for the MMN (where the sound representation might be more concrete, or "sensory," due to directly preceding stimuli that established the regularities) and more frontal areas for the ERAN (see also the next section for further details).

In addition, Winkler (2007) states that the primary function of the MMN-generating process is to maintain neuronal models underlying the detection and separation of auditory objects. This also differentiates the processes underlying the MMN from those underlying music-syntactic processing, because syntactic processing serves the computation of a string of auditory structural elements that—in their whole—represent a form that conveys meaning that can be understood by a listener familiar with the syntactic regularities (Koelsch & Siebel, 2005; Steinbeis & Koelsch, 2008).

The assumption that the ERAN reflects syntactic processing (rather than detection and integration of intersound relationships inherent in the sequential presentation of discrete events into a model of the acoustic environment) has been strongly supported by two previous studies (Koelsch, Gunter, Wittfoth, & Sammler, 2005; Steinbeis & Koelsch, 2008). In these studies, chord sequences were presented simultaneously with visually presented sentences to investigate possible interactions between music-syntactic and language-syntactic processing. Both studies found interactions between the ERAN elicited by irregular chords and the left anterior negativity (LAN) elicited by linguistic (morpho-syntactic) violations: The LAN elicited by words was reduced when the irregular word was presented simultaneously with an irregular chord (compared to when the irregular word was presented with a regular chord). Very similar findings have been reported by studies using behavioral methods (Slevc, Rosenberg, & Patel, 2007). In the study from Koelsch, Gunter, et al. (2005) a control experiment was conducted in which the same sentences were presented simultaneously with sequences of single tones. The tone sequences ended either on a standard tone or on a frequency deviant. The phMMN elicited by the frequency deviants did not interact with the LAN (in contrast to the ERAN), suggesting that the ERAN relies on neural resources related to syntactic processing (as evidenced by the interaction with the LAN), whereas the phMMN does not appear to consume such resources. Whether the afMMN consumes such resources remains to be investigated.

Neural Generators

A number of studies suggest that the ERAN receives its main contributions from neural sources located in the pars opercularis of the inferior fronto-lateral cortex (corresponding to inferior Brodmann's area [BA] 44), presumably with additional contributions from the ventrolateral premotor cortex and the anterior superior temporal gyrus (planum polare; Koelsch, 2006): An MEG study (Koelsch, 2000) using a chord sequence paradigm with the stimuli depicted in Figure 1a,b reported a dipole solution of the ERAN with a two-dipole model, the dipoles being located bilaterally in inferior BA 44 (see also Maess et al., 2001, and Figure 2d; the dipole strength was nominally stronger in the right hemisphere, but this hemispheric difference was statistically not significant). The main frontal contribution to the ERAN reported in that study stays in contrast to the phMMN, which receives its main contributions from neural sources located within and in the vicinity of the primary auditory cortex, with additional (but smaller) contributions from frontal cortical areas (Alain, Woods, & Knight, 1998; Alho et al., 1996; Giard, Perrin, Pernier, & Bouchet, 1990; Liebenthal et al., 2003; Molholm, Martinez, Ritter, Javitt, & Foxe, 2005; Opitz, Rinne, Mecklinger, von Cramon, & Schröger, 2002; Rinne, Degerman, & Alho, 2005; Schönwiesner et al., 2007; for a review, see Deouell 2007). Likewise, the main generators of the afMMN have also been reported to be located in the temporal lobe (Korzyukov et al., 2003). That is, whereas the phMMN (and the afMMN) receives main contributions from temporal areas, the ERAN appears to receive its main contributions from frontal areas.

The results of the MEG study (Koelsch, 2000) were supported by functional neuroimaging studies using chord sequence paradigms (Koelsch, Gunter, et al., 2002, 2005; Tillmann et al., 2006) and melodies (Janata et al., 2002), which showed activations of inferior fronto-lateral cortex at coordinates highly similar to those reported in the MEG study (Figure 2e). Particularly the fMRI study from Koelsch, Gunter, et al. (2005) supported the assumption of neural generators of the ERAN in inferior BA 44: As will be reported in more detail below, the ERAN has been shown to be larger in musicians than in nonmusicians (Koelsch, Schmidt, et al., 2002), and in the fMRI study from Koelsch, Gunter, et al. (2005) effects of musical training were correlated with activations of inferior BA 44 in both adults and children. Further support stems from EEG studies investigating the ERAN and the phMMN under propofol sedation: Whereas the phMMN is strongly reduced, but still significantly present under deep propofol sedation (Modified Observer's Assessement of Alertness and Sedation Scale level 2–3, mean Bispectral Index = 68), the ERAN is abolished during this level of sedation (Koelsch, Heinke, Sammler, & Olthoff, 2006). This highlights the importance of the frontal cortex for the generation of the ERAN, because propofol sedation appears to affect heteromodal frontal cortices earlier and more strongly than unimodal sensory cortices (Heinke & Koelsch, 2005; Heinke et al., 2004).

Finally, it is important to note that inferior BA 44 (which is in the left hemisphere, often referred to as Broca's area) plays a crucial role for the processing of syntactic information during language perception (e.g., Friederici, 2002). Thus, the neural resources for the processing of musical and linguistic syntax appear to be strongly overlapping, and this notion is particularly supported by the mentioned studies showing interactions between music-syntactic and language-syntactic processing (Koelsch, Gunter, et al., 2005; Slevc et al., 2007; Steinbeis & Koelsch, 2008).

Moreover, 5-year-old children with specific language impairment (characterized by marked difficulties in language-syntactic processing) do not show an ERAN (whereas children with normal language development do; Jentschke, Koelsch, Sallat, & Friederici, in press), and 11-year-old children with musical training do not only show an increase of the ERAN amplitude, but also an increase of the amplitude of the ELAN (reflecting language-syntactic processing; Jentschke, Koelsch, & Friederici, 2005; see also section on development below). The latter finding was interpreted as the result of training effects in the musical domain on processes of fast and automatic syntactic sequencing during the perception of language.

Automaticity

So far, several ERP studies have investigated the automaticity of music-syntactic processing. The ERAN has been observed while participants play a video game (Koelsch et al., 2001), read a self-selected book (Koelsch, Schröger, & Gunter, 2002), or perform a highly attention-demanding reading comprehension task (Loui et al., 2005). In the latter study, participants performed the reading task while ignoring all chord sequences, or they attended to the chord sequences and detected chords that deviated in their sound intensity from standard chords. These conditions enabled the researchers to compare the processing of task-irrelevant irregular chords under an attend condition (intensity detection task) and an ignore condition (reading comprehension task). Results showed that an ERAN was elicited in both conditions and that the amplitude of the ERAN was reduced (but still significant) when the musical stimulus was ignored (Figure 4a; because the ERAN was not significantly lateralized, it was denoted as *early anterior negativity* by the authors).

Another recent study (Maidhof & Koelsch, 2008) showed that the neural mechanisms underlying the processing of music-syntactic information (as reflected in the ERAN) are active even when participants selectively attend to a speech stimulus. In that study, speech and music stimuli were presented simultaneously from different locations (20° and 340° in the azimuthal plane). The ERAN was elicited even when participants selectively attended to the speech stimulus, but its amplitude was significantly decreased compared to the condition in which participants listened to music only. The findings of the latter two studies (Loui et al., 2005; Maidhof & Koelsch, 2008) show that the neural mechanisms underlying the processing of harmonic structure operate in the absence of attention, but that they can be clearly modulated by different attentional demands. Notably, the ERAN was not significantly lateralized in either of the two studies, perhaps because attentional factors modulate the lateralization of the ERAN.

With regard to the MMN, several studies have shown that the MMN amplitude can be reduced in some cases by attentional factors (for a review, see Sussman, 2007). However, it has been argued that such modulations could be attributed to effects of attention on the formation of representations for standard stimuli, rather than to the deviant detection process (Sussman, 2007), and that MMN is largely unaffected by attentional modulations (Grimm & Schröger, 2005; Sussman et al., 2004; Gomes et al., 2000). That is, the MMN seems to be considerably more resistant against attentional modulations than the ERAN.

This view is corroborated by the mentioned previous study investigating the ERAN and the phMMN under propofol

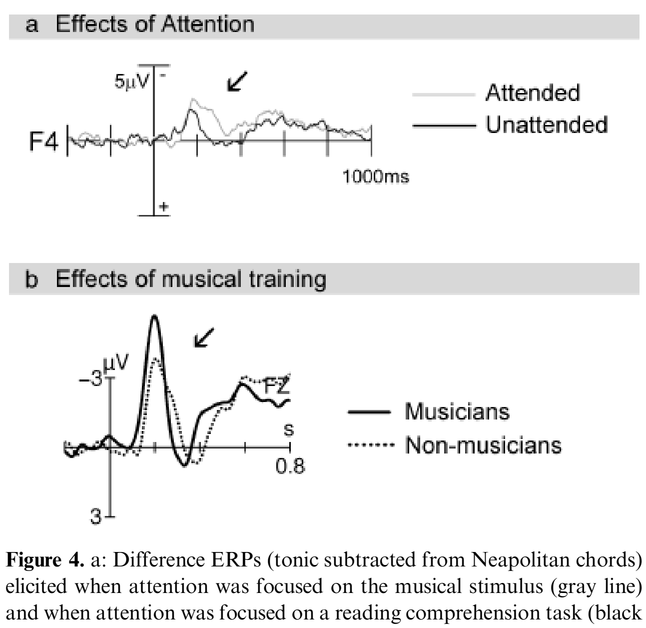

Figure 4. a: Difference ERPs (tonic subtracted from Neapolitan chords) elicited when attention was focused on the musical stimulus (gray line) and when attention was focused on a reading comprehension task (black line). The E(R)AN (indicated by the arrow) clearly differed between conditions, being smaller in the unattend condition (figure adapted from Loui et al., 2005). b: Difference ERPs (tonic subtracted from Neapolitan chords) elicited in musicians (solid line) and nonmusicians (dotted line). The ERAN (arrow) clearly differed between groups, being smaller in the group of nonmusicians.

sedation (Koelsch et al., 2006): This study reported that the ERAN was abolished under deep propofol sedation (where participants were in a state similar to natural sleep), in contrast to the phMMN, which was strongly reduced but still significantly present during this level of sedation. This suggests that the elicitation of the ERAN requires a different state of consciousness on the part of the listeners than the phMMN (see also Heinke & Koelsch, 2005; Heinke et al., 2004).

Effects of Musical Training

Like the MMN, the ERAN can be modulated by both long-term and short-term training. Effects of musical training have been reported for the MMN with regard to the processing of temporal structure (Rüsseler, Altenmüller, Nager, Kohlmetz, & Münte, 2001), the processing of abstract features such as interval and contour changes (Fujioka, Trainor, Ross, Kakigi, & Pantev, 2004; Tervaniemi, Rytkönen, Schröger, Ilmoniemi, & Näätänen, 2001), as well as for the processing of pitch (Koelsch et al., 1999). In all these studies, the MMN was larger in individuals with formal musical training ("musicians") than in individuals without such training ("nonmusicians"). With regard to the ERAN, studies investigating effects of musical long-term training showed that the ERAN is larger in musicians (Figure 4b; Koelsch, Schmidt, et al., 2002) and in amateur musicians (Koelsch et al., 2007) compared to nonmusicians. In the latter study, the difference between groups was just above the threshold of statistical significance, and two recent studies reported nominally larger ERAN amplitude values for musicians (compared to nonmusicians; Koelsch & Sammler, 2007) and amateur musicians (compared to nonmusicians; Koelsch & Jentschke, 2008), although the group differences did not reach statistical significance in these studies. However, using fMRI, significant effects of musical training on the processing of music-syntactic irregularities have also been shown for both adults and 11-year-old children (Koelsch, Fritz, et al., 2005).

The evidence from the mentioned studies indicates that the effects of musical long-term training on the ERAN are small but reliable and consistent across studies. This is in line with behavioral studies showing that musicians respond faster and more accurately to music-structural irregularities than nonmusicians (e.g., Bigand, Madurell, Tillmann, & Pineau, 1999) and with ERP studies on the processing of musical structure showing effects of musical training on the generation of the P3 using chords (Regnault et al., 2001) or the elicitation of a late positive component (LPC) using melodies (Besson & Faita, 1995; see also Magne, Schön, & Besson, 2006; Moreno & Besson, 2006; Schön, Magne, & Besson, 2004). The ERAN is presumably larger in musicians because musicians have (as an effect of the musical training) more specific representations of music-syntactic regularities and are, therefore, more sensitive to the violation of these regularities.

With regards to short-term effects, a recent experiment presented two sequence types (one ending on a regular tonic chord, the other one ending on an irregular supertonic) for approximately 2 h (Koelsch & Jentschke, 2008; subjects were watching a silent movie with subtitles). The data showed that music-syntactically irregular chords elicited an ERAN and that the amplitude of the ERAN decreased over the course of the experimental session. These results revealed that neural mechanisms underlying the processing of music-syntactic information are modified by short-term musical experience. Although the ERAN amplitude was significantly reduced, it was still present at the end of the experiment, indicating that cognitive representations of basic music-syntactic regularities are remarkably stable and cannot easily be modified (for effects of musical training in children, see the next section).

Development

The youngest individuals in whom music-syntactic processing has been investigated so far with ERPs were, to my knowledge, 4-month-old babies. These babies did not to show an ERAN (unpublished data from our group; irregular chords were Neapolitan chords). However, some of the babies were asleep during the experiment, which could have prevented possible ERAN effects (adults who are sleeping due to propofol sedation do not show an ERAN; Koelsch et al., 2006). In 2.5-year-old children (30 months) we observed an ERAN to supertonics and Neapolitans (unpublished data from our group). In this age group, the ERAN was quite small, suggesting that the development of the neural mechanisms underlying the generation of the ERAN commence around or not long before this age.

By contrast, MMN-like responses can be recorded even in the fetus (Draganova et al., 2005; Huotilainen et al., 2005), and a number of studies have shown MMN-like discriminative responses in newborns (although sometimes with positive polarity; Ruusuvirta, Huotilainen, Fellman, & Näätänen, 2003, 2004; Winkler et al., 2003; Maurer, Bucher, Brem, & Brandeis, 2003; Stefanics et al., 2007) to both physical deviants (e.g., Alho, Kainio, Sajaniemi, Reinikainen, & Näätänen, 1990; Cheour, Ceponiene, et al., 2002; Cheour, Kushnerenko, Ceponiene, Fellman, & Näätänen, 2002; Kushnerenko et al., 2007; Winkler et al., 2003; Stefanics et al., 2007) and abstract feature deviants (Ruusuvirta et al., 2003, 2004; Carral et al., 2005). Cheour Leppänen, and Kraus (2000) reported that, in some experiments, the amplitudes of such ERP responses are only slightly smaller in infants than the MMN usually reported in school-age children (but see also, e.g., Friederici, 2005; Kushnerenko et al., 2007; Maurer et al., 2003; for differences). The findings that MMN-like responses can be recorded in the fetus and in newborn infants support the notion that the generation of such discriminative responses is based on the (innate) capability to establish representations of intersound regularities that are extracted online from the acoustic environment (and the innate capability to perform auditory scene analysis), whereas the generation of the ERAN requires representations of musical regularities that first have to be learned through listening experience, involving the detection of regularities (i.e., statistical probabilities) underlying, for example, the succession of harmonic functions.

Children at the age of 5 years show a clear ERAN, but with longer latency than adults (around 230–240 ms; Jentschke et al., in press; in that study the ERAN was elicited by supertonics). Similar results were obtained in another study using Neapolitans as irregular chords (Koelsch, Grossmann, et al., 2003). It is not known whether the longer latency in 5-year-olds (compared to adults) is due to neuro-anatomical differences (such as fewer myelinated axons) or due to less specific representations of music-syntactic regularities (or both).

At the age of 9, the ERAN appears to be very similar to the ERAN of adults. In a recent study, 9-year-olds with musical training showed a larger ERAN than children without musical training (unpublished data from our group), and the latency of the ERAN was around 200 ms in children both with and without musical training (thus still being longer than in older children and adults). With fMRI, it was observed that children at the age of 10 show an activation pattern in the right hemisphere that is strongly reminiscent of that of adults (with clear activations of inferior frontolateral cortex elicited by Neapolitan chords; Koelsch, Fritz, et al., 2005). In this study, children also showed an effect of musical training, notably a stronger activation of the right pars opercularis in musically trained children (as in adults, see above).

In 11-year-olds, the ERAN has a latency of around 180 ms (regardless of musical training) and is practically indistinguishable from the ERAN observed in adults (Jentschke et al., 2005). As in 9-year-olds, 11-year-old children with musical training show a larger ERAN than children without musical training (Jentschke et al., 2005).

With regard to its scalp distribution, we previously reported that 5-year-old girls showed a bilateral ERAN, whereas the ERAN was rather left-lateralized in boys (Koelsch, Grossmann, et al., 2003; irregular chords were Neapolitans). However, in another study with 5-year-olds (Jentschke et al., in press; irregular chords were supertonics) no significant gender difference was observed, and nominally the ERAN was even more right-lateralized in boys and more left-lateralized in girls. Thus, when interpreting data obtained from children, gender differences in scalp distribution should be treated with caution.

Interestingly, it is likely that, particularly during early childhood, the MMN system is of fundamental importance for music-syntactic processing: MMN is inextricably linked to the establishment and maintenance of representations of the acoustic environment and thus to the processes of auditory scene analysis. The main determinants of MMN comprise the standard formation process (because deviance detection is reliant on the standard representations held in sensory memory), detection and separation of auditory objects, and the organization of sequential sounds in memory. These processes are indispensable for the establishment of music-syntactic processing, for example, when harmonies are perceived within chord progressions and when the repeated exposure to chord progressions leads to the extraction and memorization of statistical probabilities for chord or sound transitions. In addition, because music-syntactic irregularity and harmonic distance is often related to acoustic deviance (see the section about functional significance of the ERAN), the acoustic deviance detection mechanism proliferates sometimes information about the irregularity (i.e., unexpectedness) of chord functions and perhaps even the harmonic distance between some chords. Such information aids the detection of music-syntactic regularities and the buildup of a structural model. Importantly, when processing an acoustically deviant music-syntactic irregularity, MMN-related processes also draw attention to music.

Conclusions

In summary, the ERAN reflects processing of music-syntactic information, that is, of acoustic information structured according to abstract and complex regularities that are usually represented in a long-term memory format. The ERAN resembles the MMN with regard to a number of properties, particularly polarity, scalp distribution, time course, and sensitivity to acoustic events that mismatch with a preceding sequence of acoustic events and sensitivity to musical training. Therefore, the ERAN has previously also been referred to as music-syntactic MMN. In cognitive terms, the similarities between both MMN and ERAN comprise the extraction of acoustic features required to elicit both ERPs (which is identical for both ERPs), the prediction of subsequent acoustic events, and the comparison of new acoustic information with a predicted sound, processes which presumably overlap strongly for MMN and ERAN.

However, there are also differences between ERAN and MMN, the most critical being that the generation of both phMMN and afMMN is based on a model of regularities that is establishment based on intersound relationships that are extracted online from the acoustic environment. By contrast, music-syntactic processing (as reflected in the ERAN) is based on a structural model that is established with reference to representations of syntactic regularities already existing in a long-term memory format. That is, the representations of regularities building the structural model of the acoustic environment are, in the case of the MMN, more sensory and, in the case of the ERAN, more cognitive in nature. It is perhaps this difference between ERAN and MMN that leads to the different topographies of neural resources underlying the generation of both components, with the ERAN usually showing more frontal and less temporal lobe involvement than the MMN.

Notably, MMN is inextricably linked to the establishment and maintenance of representations of the acoustic environment and thus to the processes of auditory scene analysis. These processes are indispensable for the acquisition of representations of music-syntactic regularities during early childhood, for example, when the repeated exposure to chord progressions leads to the extraction and memorization of statistical probabilities for chord or sound transitions. Thus, the mechanisms required for the MNN also represent the foundation for music-syntactic processing.

REFERENCES

Alain, C., Woods, D. L., & Knight, R. T. (1998). A distributed cortical network for auditory sensory memory in humans. *Brain Research*, *812*, 23–37.

Alho, K., Sainio, K., Sajaniemi, N., Reinikainen, K., & Näätänen, R. (1990). Event-related brain potential of human newborns to pitch change of an acoustic stimulus. *Electroencephalography and Clinical Neurophysiology*, *77*, 151–155.

Alho, K., Tervaniemi, M., Huotilainen, M., Lavikainen, J., Tiitinen, H., Ilmoniemi, R. J., et al. (1996). Processing of complex sounds in the human auditory cortex as revealed by magnetic brain responses. *Psychophysiology*, *33*, 369–375.

Besson, M., & Faita, F. (1995). An event-related potential (ERP) study of musical expectancy: Comparison of musicians with non-musicians. *Journal of Experimental Psychology. Human Perception and Performance*, *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. *Journal of Experimental Psychology: Human Perception and Performance*, *25*, 184–197.

Brattico, E., Tervaniemi, M., Näätänen, R., & Peretz, I. (2006). Musical scale properties are automatically processed in the human auditory cortex. *Brain Research*, *1117*, 162–174.
Brown, H., Butler, D., & Jones, M. R. (1994). Musical and temporal influences on key discovery. *Music Perception*, *11*, 371–391.
Carral, V., Huotilainen, M., Ruusuvirta, T., Fellman, V., Näätänen, R., & Escera, C. (2005). A kind of auditory 'primitive intelligence' already present at birth. *European Journal of Neuroscience*, *21*, 3201–3204.
Cheour, M., Ceponiene, R., Leppänen, P., Alho, K., Kujala, T., Renlund, M., et al. (2002). The auditory sensory memory trace decays rapidly in newborns. *Scandinavian Journal of Psychology*, *43*, 33–39.
Cheour, M., Kushnerenko, E., Ceponiene, R., Fellman, V., & Näätänen, R. (2002). Electric brain responses obtained from newborn infants to changes in duration in complex harmonic tones. *Developmental Neurophysiology*, *22*, 471–479.
Cheour, M., Leppänen, P. H., & Kraus, N. (2000). Mismatch negativity (MMN) as a tool for investigating auditory discrimination and sensory memory in infants and children. *Clinical Neurophysiology*, *111*, 4–16.
Deouell, L. Y. (2007). The frontal generator of the mismatch negativity revisited. *Journal of Psychophysiology*, *21*, 188–203.
Draganova, R., Eswaran, H., Murphy, P., Huotilainen, M., Lowerey, C., & Preissl, H. (2005). Sound frequency change detection in fetuses and newborns, a magnetoencephalographic study. *NeuroImage*, *28*, 354–361.
Friederici, A. D. (2002). Towards a neural basis of auditory sentence processing. *Trends in Cognitive Science*, *6*, 78–84.
Friederici, A. D. (2005). Neurophysiological markers of early language acquisition: From syllables to sentences. *Trends in Cognitive Science*, *9*, 481–488.
Friederici, A. D., Friedrich, M., & Weber, C. (2002). Neural manifestation of cognitive and precognitive mismatch detection in early infancy. *NeuroReport*, *13*, 1251–1254.
Fujioka, T., Trainor, L. J., Ross, B., Kakigi, R., & Pantev, C. (2004). Musical training enhances automatic encoding of melodic contour and interval structure. *Journal of Cognitive Neuroscience*, *16*, 1010–1021.
Giard, M. H., Perrin, F., Pernier, J., & Bouchet, P. (1990). Brain generators implicated in the processing of auditory stimulus deviance: A topographic event-related potential study. *Psychophysiology*, *27*, 627–640.
Gomes, H., Molholm, S., Ritter, W., Kurtzberg, D., Cowan, N., & Vaughan, H. G., Jr. (2000). Mismatch negativity in children and adults, and effects of an attended task. *Psychophysiology*, *37*, 807–816.
Grimm, S., & Schröger, E. (2005). Preattentive and attentive processing of temporal and frequency characteristics within long sounds. *Cognitive Brain Research*, *25*, 711–721.
Gunter, T. C., Friederici, A. D., & Schriefers, H. (2000). Syntactic gender and semantic expectancy: ERPs reveal early autonomy and late interaction. *Journal of Cognitive Neuroscience*, *12*, 556–568.
Heinke, W., Kenntner, 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.
Heinke, W., & Koelsch, S. (2005). The effects of anesthetics on brain activity and cognitive function. *Current Opinion in Anaesthesiology*, *18*, 625–631.
Huotilainen, M., Kujala, A., Hotakainen, M., Parkkonen, L., Taulu, S., Simola, J., et al. (2005). Short-term memory functions of the human fetus recorded with magnetoencephalography. *NeuroReport*, *16*, 81–84.
Janata, P., Birk, J., Van Horn, J. D., Leman, M., Tillmann, B., & Bharucha, J. J. (2002). The cortical topography of tonal structures underlying Western music. *Science*, *298*, 2167–2170.
Jentschke, S., Koelsch, S., & Friederici, A. D. (2005). Investigating the relationship of music and language in children: Influences of musical training and language impairment. *Annals of the New York Academy of Science*, *1060*, 231–242.
Jentschke, S., Koelsch, S., Sallat, S., & Friederici, A. D. (in press). Children with specific language impairment also show impairment of music-syntactic processing. *Journal of Cognitive Neuroscience*.
Koelsch, S. (2000). *Brain and Music—A contribution to the investigation of central auditory processing with a new electrophysiological approach*. Ph.D. thesis, University of Leipzig, Leipzig, Germany.
Koelsch, S. (2005). Neural substrates of processing syntax and semantics in music. *Current Opinion in Neurobiology*, *15*, 1–6.
Koelsch, S. (2006). Significance of Broca's area and ventral premotor cortex for music-syntactic processing. *Cortex*, *42*, 518–520.
Koelsch, S., Fritz, T., Schulze, K., Alsop, D., & Schlaug, G. (2005). Adults and children processing music: An fMRI study. *NeuroImage*, *25*, 1068–1076.
Koelsch, S., Grossmann, T., Gunter, T. C., Hahne, A., Schröger, E., & Friederici, A. D. (2003). Children processing music: Electric brain responses reveal musical competence and gender differences. *Journal of Cognitive Neuroscience*, *15*, 683–693.
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., Schröger, E., & Friederici, A. D. (2003). Processing tonal modulations: An ERP study. *Journal of Cognitive Neuroscience*, *15*, 1149–1159.
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., von Cramon, D. Y., Zysset, S., Lohmann, G., & Friederici, A. D. (2002). Bach speaks: A cortical 'language-network' serves the processing of music. *NeuroImage*, *17*, 956–966.
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. (2008). Short-term effects of processing musical syntax: An ERP study. *Brain Research*, *1212*, 55–62.
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., 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., & Sammler, D. (2007). *Cognitive components of processing auditory regularities*. Manuscript submitted for publication.
Koelsch, S., Schmidt, B. H., & Kansok, J. (2002). Inuences 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., Schröger, E., & Tervaniemi, M. (1999). Superior pre-attentive auditory processing in musicians. *NeuroReport*, *10*, 1309–1313.
Koelsch, S., & Siebel, W. (2005). Towards a neural basis of music perception. *Trends in Cognitive Science*, *9*, 578–584.
Korzyukov, O. A., Winkler, I., Gumenyuk, V. I., & Alho, K. (2003). Processing abstract auditory features in the human auditory cortex. *NeuroImage*, *20*, 2245–2258.
Krumhansl, C., & Kessler, E. (1982). Tracing the dynamic changes in perceived tonal organization in a spatial representation of musical keys. *Psychological Review*, *89*, 334–368.
Kushnerenko, E., Winkler, I., Horváth, J., Näätänen, R., Pavlov, I., Fellman, V., et al. (2007). Processing acoustic change and novelty in newborn infants. *European Journal of Neuroscience*, *26*, 265–274.
Lamont, A., & Cross, I. (1994). Children's cognitive representations of musical pitch. *Music Perception*, *12*, 27–55.
Leino, S., Brattico, E., Tervaniemi, M., & Vuust, P. (2007). Representation of harmony rules in the human brain: Further evidence from event-related potentials. *Brain Research*, *1142*, 169–177.
Leman, M. (2000). An auditory model of the role of short-term memory in probe-tone ratings. *Music Perception*, *17*, 481–509.
Lerdahl, F. (2001). *Tonal pitch space*. Oxford: Oxford University Press.
Liebenthal, E., Ellingson, M. L., Spanaki, M. V., Prieto, T. E., Ropella, K. M., & Binder, J. R. (2003). Simultaneous ERP and fMRI of the auditory cortex in a passive oddball paradigm. *NeuroImage*, *19*, 1395–1404.

Loui, P., Grent-'t Jong, T., Torpey, D., & Woldorff, M. (2005). Effects of attention on the neural processing of harmonic syntax in Western music. *Brain Research Cognitive Brain Research*, *25*, 678–687.

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.

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

Maidhof, C., & Koelsch, S. (2008). *Effects of selective attention on neurophysiological correlates of syntax processing in music and speech*. Manuscript submitted for publication.

Maurer, U., Bucher, K., Brem, S., & Brandeis, D. (2003). Development of the automatic mismatch response: From frontal positivity in kindergarten children to the mismatch negativity. *Clinical Neurophysiology*, *114*, 808–817.

McCarthy, G., & Donchin, E. (1981). A metric for thought: A comparison of P300 latency and reaction time. *Science*, *211*, 77–80.

Miranda, R. A., & Ullman, M. T. (2007). Double dissociation between rules and memory in music: An event-related potential study. *NeuroImage*, *38*, 331–345.

Molholm, S., Martinez, A., Ritter, W., Javitt, D. C., & Foxe, J. J. (2005). The neural circuitry of pre-attentive auditory change-detection: An fMRI study of pitch and duration mismatch negativity generators. *Cerebral Cortex*, *15*, 545–551.

Moreno, S., & Besson, M. (2006). Musical training and language-related brain electrical activity in children. *Psychophysiology*, *43*, 287–291.

Näätänen, R., Lehtokoski, A., Lennes, M., Cheour, M., Huotilainen, M., Iivonen, A., et al. (1997). Language-specific phoneme representations revealed by electric and magnetic brain responses. *Nature*, *385*, 432–434.

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.

Paavilainen, P., Arajärvi, P., & Takegata, R. (2007). Preattentive detection of nonsalient contingencies between auditory features. *NeuroReport*, *18*, 159–163.

Paavilainen, P., Degerman, A., Takegata, R., & Winkler, I. (2003). Spectral and temporal stimulus characteristics in the processing of abstract auditory features. *NeuroReport*, *14*, 715–718.

Paavilainen, P., Jaramillo, M., & Näätänen, R. (1998). Binaural information can converge in abstract memory traces. *Psychophysiology*, *35*, 483–487.

Paavilainen, P., Simola, J., Jaramillo, M., Näätänen, R., & Winkler, I. (2001). Preattentive extraction of abstract feature conjunctions from auditory stimulation as reflected by the mismatch negativity (MMN). *Psychophysiology*, *38*, 359–365.

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.

Poulin-Charronnat, B., Bigand, E., & Koelsch, S. (2006). Processing of musical syntax tonic versus subdominant: An event-related potential study. *Journal of Cognitive Neuroscience*, *18*, 1545–1554.

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). *Musikalische Syntaxis: Grundriss einer harmonischen Satzbildungslehre* [*Musical syntax: Foundations of a theory of harmony*]. Niederwalluf: Sändig.

Rinne, T., Degerman, A., & Alho, K. (2005). Superior temporal and inferior frontal cortices are activated by infrequent sound duration decrements: An fMRI study. *NeuroImage*, *26*, 66–72.

Rohrmeier, M. (2005). Towards modelling movement in music: Analysing properties and dynamic aspects of pc set sequences in Bach's chorales. MPhil thesis. University of Cambridge. Published as *Darwin College Research Reports 04*, available from http://www.dar.cam.ac.uk/dcrr/dcrr004.pdf.

Rüsseler, J., Altenmüller, E., Nager, W., Kohlmetz, C., & Münte, T. F. (2001). Event-related brain potentials to sound omissions differ in musicians and non-musicians. *Neuroscience Letters*, *308*, 33–36.

Ruusuvirta, T., Huotilainen, M., Fellman, V., & Näätänen, R. (2003). The newborn human brain binds sound features together. *NeuroReport*, *14*, 2117–21119.

Ruusuvirta, T., Huotilainen, M., Fellman, V., & Näätänen, R. (2004). Newborn human brain identifies repeated auditory feature conjunctions of low sequential probability. *European Journal of Neuroscience*, *20*, 2819–2821.

Saarinen, J., Paavilainen, P., Schöger, E., Tervaniemi, M., & Näätänen, R. (1992). Representation of abstract attributes of auditory stimuli in the human brain. *NeuroReport*, *3*, 1149–1151.

Schön, D., & Besson, M. (2005). Visually induced auditory expectancy in music reading: A behavioural and electrophysiological study. *Journal of Cognitive Neuroscience*, *17*, 694–705.

Schön, D., Magne, C., & Besson, M. (2004). The music of speech: Music training facilitates pitch processing in both music and language. *Psychophysiology*, *41*, 341–349.

Schönwiesner, M., Novitski, N., Pakarinen, S., Carlson, S., Tervaniemi, M., & Naatanen, R. (2007). Heschl's Gyrus, posterior superior temporal gyrus, and mid-ventrolateral prefrontal cortex have different roles in the detection of acoustic changes. *Journal of Neurophysiology*, *97*, 2075–2082.

Schröger, E. (2007). Mismatch negativity—A microphone into auditory memory. *Journal of Psychophysiology*, *21*, 138–145.

Schröger, E., Bendixen, A., Trujillo-Barreto, N. J., & Roeber, U. (2007). Processing of abstract rule violations in audition. *PLoS ONE*, *2*, e1131.

Slevc, L. R., Rosenberg, J. C., & Patel, A. D. (2007). *Making psycholinguistics musical: Evidence for shared processing of linguistic and musical syntax*. Paper presented at the Language and Music as Cognitive Systems Conference, May 11–13, 2007, Cambridge, UK.

Stefanics, G., Háden, G., Huotilainen, M., Balázs, L., Sziller, I., Beke, A., et al. (2007). Auditory temporal grouping in newborn infants. *Psychophysiology*, *44*, 697–702.

Steinbeis, N., & Koelsch, S. (2008). Shared neural resources between music and language indicate semantic processing of musical tension-resolution patterns. *Cerebral Cortex*, *18*, 1169–1178.

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.

Sussman, E., Kujala, T., Halmetoja, J., Lyytinen, H., Alku, P., & Näätänen, R. (2004). Automatic and controlled processing of acoustic and phonetic contrasts. *Hearing Research*, *190*, 128–140.

Sussman, E. S. (2007). A new view on the MMN and attention debate: The role of context in processing auditory events. *Journal of Psychophysiology*, *21*, 164–170.

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.

Tervaniemi, M., Rytkönen, M., Schröger, E., Ilmoniemi, R. J., & Näätänen, R. (2001). Superior formation of cortical memory traces for melodic patterns in musicians. *Learning and Memory*, *8*, 295–300.

Tillmann, B., Bharucha, J. J., & Bigand, E. (2000). Implicit learning of tonality: A self-organized approach. *Psychological Review*, *107*, 885–913.

Tillmann, B., Janata, P., & Bharucha, J. J. (2003). Activation of the inferior frontal cortex in musical priming. *Brain Research*. *Cognitive Brain Research*, *16*, 145–161.

Tillmann, B., Janata, P., Birk, J., & Bharucha, J. J. (2008). Tonal centers and expectancy: Facilitation or inhibition of chords at the top of the harmonic hierarchy? *Journal of Experimental Psychology*. *Human Perception and Performance*, *34*, 1031–1043.

Tillmann, B., Koelsch, S., Escoffier, N., Bigand, E., Lalitte, P., Friederici, A. D., & von Cramon, D. Y. (2006). Cognitive priming in sung and instrumental music: Activation of inferior frontal cortex. *NeuroImage*, *31*, 1771–1782.

van den Brink, D., Brown, C. M., & Hagoort, P. (2001). Electrophysiological evidence for early contextual influences during spoken-word recognition: N200 versus N400 effects. *Journal of Cognitive Neuroscience*, *13*, 967–985.

Widmann, A., Kujala, T., Tervaniemi, M., Kujala, A., & Schröger, E. (2004). From symbols to sounds: Visual symbolic information activates sound representations. *Psychophysiology*, *41*, 709–715.

Winkler, I. (2007). Interpreting the mismatch negativity. *Journal of Psychophysiology*, *21*, 147–160.

Winkler, I., Kujala, T., Tiitinen, H., Sivonen, P., Alku, P., Lehtokoski, A., et al. (1999). Brain responses reveal the learning of foreign language phonemes. *Psychophysiology*, *36*, 638–642.

Winkler, I., Kushnerenko, E., Horváth, J., Ceponiene, R., Fellman, V., Huotilainen, M., et al. (2003). Newborn infants can organize the auditory *world. Proceedings of the National Academy of Sciences, USA*, *100*, 11812–11815.

Woolhouse, M. H., & Cross, I. (2006). An interval cycle-based model of pitch attraction. In: *Proceedings of the 9th International Conference on Music Perception & Cognition* (pp. 763–771). [Compact disk].

Ylinen, S., Shestakova, A., Huotilainen, M., Alku, P., & Näätänen, R. (2006). Mismatch negativity (MMN) elicited by changes in phoneme length: A cross-linguistic study. *Brain Research*, *1072*, 175–185.

(Received December 7, 2007; Accepted April 29, 2008)